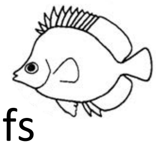
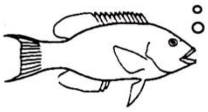
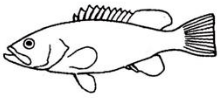
Galbraith, Gemma Frances (2021) *The ecology of fishes on submerged pinnacle coral reefs*. PhD Thesis, James Cook University.

The Ecology of Fishes on Submerged Pinnacle Coral Reefs







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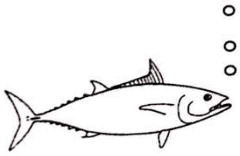

A thesis submitted to James Cook University for the degree of
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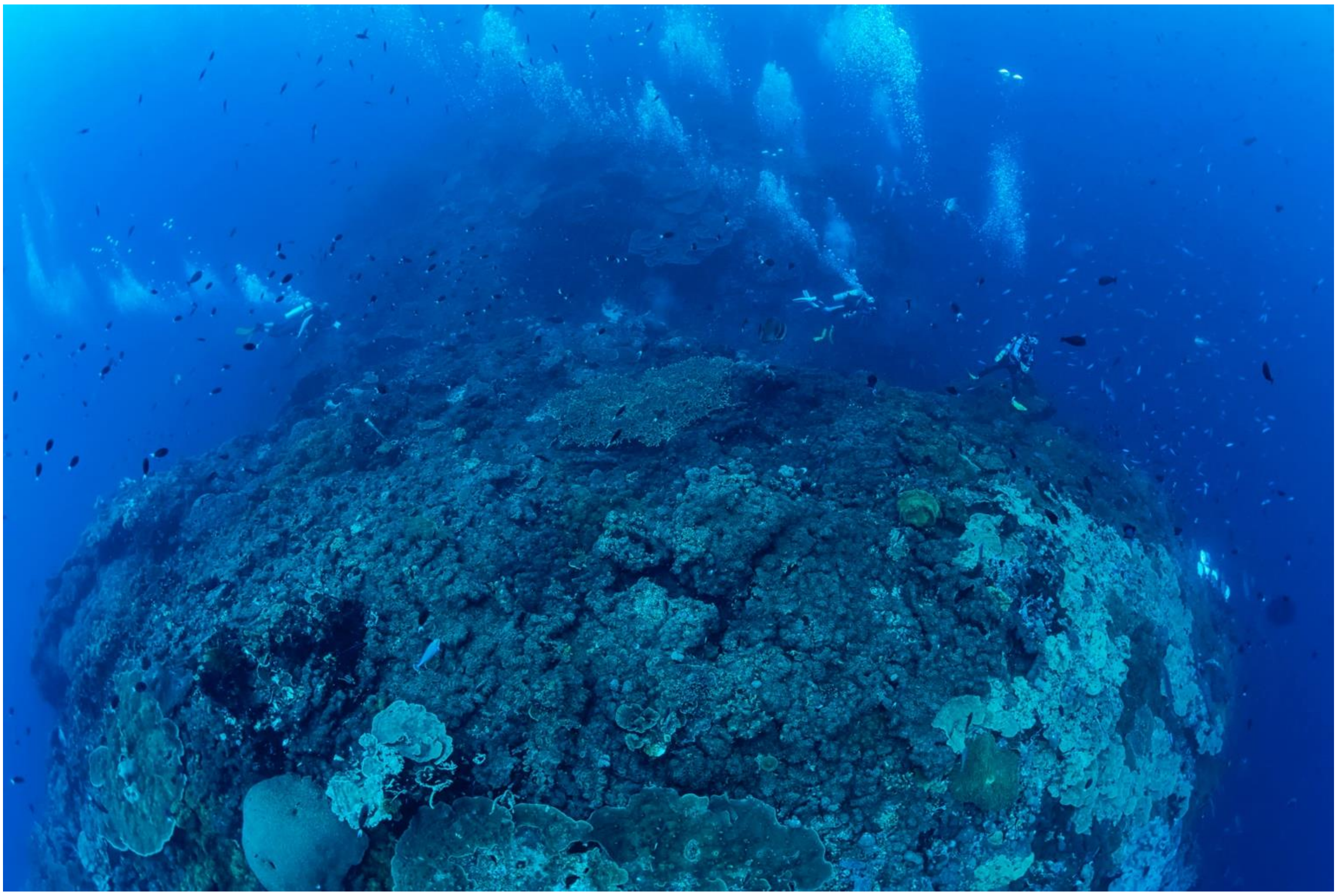

Frontispiece

Bradford Shoals, Kimbe Bay, Papua New Guinea.
A submerged pinnacle coral reef, the top of which sits at 25m depth.

Photo credit Don Silcock
Indopacific Images

Declaration and Data Availability

This thesis is the result of my own work and has not been previously submitted, in part or whole, to any university or tertiary education institution for any degree, diploma, or other qualification. All information derived from the published or unpublished work of others has been appropriately referenced and full acknowledgement given to the owners of any reproduced material.

All data collected and used in this thesis has been uploaded onto the Research Data JCU platform.

Signed :

Date : 20/04/2021

Statement of the Contribution of Others

This thesis was supervised by Prof. Geoffrey Jones, Prof Mark McCormick and Dr Tom Bridge. I developed the project and research questions, collected and analysed all the data and wrote all the chapters. My advisory team contributed to the development of my ideas, study design, financial support and editorial assistance for all chapters in this thesis, as well as the associated publications and manuscripts. Ben Cresswell contributed significantly to all fieldwork and data collection. These contributions and others are listed below:

Intellectual Support	
Supervision	**Professor Geoffrey Jones** College of Science and Engineering, JCU & ARC Centre of Excellence for Coral Reef Studies
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	Dr Tom Bridge ARC Centre of Excellence for Coral Reef Studies & Museum of Tropical Queensland
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Data Collection	Benjamin Cresswell

Declaration of Ethics and Permits

The research and data collection presented in this thesis was conducted within the guidelines for research ethics outlined in *the James Cook University Code for the Responsible Conduct of Research (2019)* and the *James Cook University Animal Welfare and Ethics Statement (2018)*. Specifically, video survey methods and the collection of fish undertaken in this project were implemented in accordance with James Cook University Animal Ethics and a Scientific Research Visa granted by the National Research Institute of Papua New Guinea.

James Cook University Animal Ethics:

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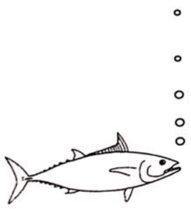

Thesis Abstract

Global patterns in biological diversity are shaped by numerous complex interactions between organisms and the physical environment. On coral reefs, these connections generate predictable, well-described patterns. Most coral reef ecology, however, is based on studies conducted in the upper 10m of the sea surface on shallow, emergent coral reefs. Although coral reef research is now expanding below the well-studied shallows to incorporate mesophotic coral ecosystems (MCEs, 30-150m) typically, the majority of studies are still conducted on reef morphologies which have emergent habitat that reaches the upper 0-10m. Submerged reefs, which do not breach the sea surface (crests >10m) are however ubiquitous across coral reef seascapes and remain understudied. These reefs exist in a variety of forms that differ in size, shape and geological origin, but all possess a significant water column above the coral reef habitat. Steep-sided, conical features like seamounts and smaller (but physically similar) pinnacles are one type of distinct submerged feature, known to possess strong hydrodynamics as a product of interactions between the structure and surrounding currents. This introduces a further suite of environmental gradients both above and around the entire reef that are not present on emergent reefs. Consequently, patterns and processes shaping coral reef communities on submerged pinnacle and seamount reefs are likely to differ from emergent reef habitats.

Seamounts remain one of the most understudied marine habitats, but existing studies have shown that these sites are often characterised by high abundance and biomass of fishes, as well as diverse benthic communities. Scientific studies of pinnacle coral reefs are even scarcer in the literature. Given the physical similarities between seamounts and pinnacles, parallels in biodiversity and mechanisms shaping coral reef communities are plausible, but have not been quantified. Indeed, the global extent of submerged reef habitats has not been fully established, let alone the potential differences in the ecology of reef fishes in these habitats. Further, as shallow emergent reefs continue to degrade as a result anthropogenic stressors, understanding the role of submerged coral reef habitats in providing refuge through connectivity with the shallows and resilience through distinct

environmental conditions is increasingly important for understanding the future of all coral reefs.

In this thesis I conducted the first quantified surveys of coral reef communities on a series of submerged pinnacle coral reefs in Kimbe Bay, Papua New Guinea. The complex bathymetry and diverse seascape of Kimbe Bay presents an excellent opportunity to compare multiple reef morphologies, including emergent fringing, atoll and submerged reefs. The overarching aim of this study was to establish ecological baselines for submerged pinnacle reefs in the bay and investigate how ecological patterns and processes found on these distinct reef habitats may differ to those on emergent reefs. In the four data chapters comprising this thesis I compare multiple aspects of reef fish ecology between submerged offshore pinnacles and emergent reefs, including assemblage diversity and structure, productivity, and characterise key differences in environmental drivers. Throughout the thesis, all data were collected from the same twelve reefs representing three reef types; offshore submerged pinnacle reefs, offshore emergent reefs and nearshore emergent reefs.

In **chapter two** I investigated variation in fish and benthic communities between submerged pinnacles and emergent reefs using broad diversity metrics and assemblage structure. I found that pinnacle reefs supported nearly four times the abundance and almost twice the species richness of fish as emergent reefs. Fish community structure was distinct across reef types, with pinnacles most similar to offshore reefs. Benthic complexity (based on morphological and taxonomic richness, diversity and hard coral cover) did not vary across reef types and fish assemblages were only weakly related to some benthic habitat variables. Reef type, however, was the most consistent predictor of fish community metrics. The results of my study demonstrate that the pinnacle reefs in Kimbe Bay support high coral reef fish biodiversity despite their small habitat area and relative isolation by depth and offshore setting. Given the lack of clear fish-benthic relationships at the depths surveyed, mechanisms as to how such amplified biodiversity is sustained are likely to involve other habitat-specific environmental drivers generated by the distinct geomorphology of pinnacles.

Hydrodynamics are one such suite of environmental drivers of coral reef biodiversity. The movement of water and associated physico-chemical gradients connects coral reef communities with nutrients and energy from the pelagic environment. Hydrodynamic regimes, however, may vary depending upon the geomorphology of reefs, their depth profiles and distance offshore. The submerged steep sided structure of seamounts is thought to generate distinct hydrodynamics that drive high biological productivity in these habitats. Given the similarities in physical structure between seamounts and pinnacles, in **chapter three** I investigated aspects of hydrodynamics and compared annual regimes between reef morphologies. In-situ current meters were installed at each study reef for 12 months and recorded current speed, direction and water temperature. Pinnacles experienced stronger, more variable current speeds and lower temperatures compared to emergent reefs. I also found different patterns in current speeds and temperature at all three reef types throughout the year. These results may reflect an energetic mechanism that supports high biodiversity on small submerged coral reefs, similar to biophysical coupling processes thought to occur on seamounts. My study therefore highlights important nuances in environmental processes on morphologically distinct coral reef habitats that should be considered for a holistic approach to understanding biodiversity and productivity on coral reefs and also for spatial planning, conservation and management.

Using the hydrodynamic data obtained in chapter three, in **chapter four** I then investigated the relative importance of hydrodynamics compared to other well-known drivers of reef fish biodiversity. I used random forest regression trees to establish whether hydrodynamic, spatial or habitat-related variables explained the most variation in fish richness, abundance, diversity and biomass across all three reef morphologies. Hydrodynamics consistently outranked spatial and habitat variables in model importance and I found evidence of distinct hydrodynamic regimes on pinnacle reefs compared to emergent coral reefs. Relationships between fish biodiversity metrics and hydrodynamic variables were examined using generalized mixed effect models. Whilst this analysis did not yield conclusive results, it did further highlight the association of the pinnacle hydrodynamic regime with high fish richness, abundance and biomass. This chapter continues to demonstrate the ecological value of small, submerged coral reefs, which are globally numerous yet remain understudied in coral reef ecology.

The human value attached to reef fish communities, together with ecological functions are often delineated by trophic structure. In **chapter five** I therefore compare how communities on submerged pinnacles, nearshore and offshore emergent reefs are structured in terms of four broad trophic groups using modern quantitative approaches. I found pinnacles to clearly support highest total abundance, biomass and annual productivity (fish mass gained per year). Trophic structure for abundance was broadly similar between reef types, but pinnacles were top-heavy in terms of biomass and productivity with the highest proportion accounted for by piscivores and planktivores. Distance-based linear modelling revealed that temperature variability, maximum current speeds and total hard coral cover explained most variability in biomass and productivity of fish assemblages. Trophic groups exhibited different trends with these environmental variables, highlighting varied responses across reef fish biomass and productivity structure to environmental gradients. Although there is natural variability in reef fish trophic structure, few studies account for differences arising from reef morphology. Understanding variation in fish assemblage structure and productivity across all forms of coral reef is, however, a critical consideration in the light of a changing global climate. The results of my study found pinnacles to be highly productive coral reef habitats with potential as effective management units. This emphasises the importance of incorporating distinct submerged reef morphologies into on-going resource management and the conservation of ecological functions on coral reefs.

This thesis demonstrates that coral reefs outside of well-studied emergent morphologies support diverse, abundant and productive fish communities. Small, submerged patch coral reefs like pinnacles are ubiquitous across coral seascapes but still constitute a largely unquantified aspect of coral reef ecology. Differences in energetic mechanisms defining patterns in biodiversity on emergent and submerged reefs highlight a need to expand coral reef ecology, mapping and conservation actions beyond typically studied shallow reef morphologies. More broadly, my findings emphasise that quantifying variable patterns in biodiversity is essential for understanding how ecological communities on all forms of coral reef will respond to the changing global environment.

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Chapter 1: General Introduction

1.1 Biodiversity: from global scales to local habitats

Patterns of biological diversity and the mechanisms through which species and individuals are organised in space and time are central to all ecology (Odum 1953; Krebs 1972). Our understanding of this organisation is founded on relationships between living organisms and the physical environment. Although early ecological studies were often descriptive (typically quantifying species richness and/or abundance of a few key species), the importance of "...the total relations of the animal both to its inorganic and its organic environment" was known and recognised (Haeckel 1870). Modern ecology now approaches these interactions as systems, where combinations of biotic and abiotic gradients shape whole communities, their structure and function (Odum 1964). Predictable patterns are evident at multiple scales, from global biodiversity gradients to patterns of coexistence within local habitats (Gaston 2000; Whittaker et al. 2001; Willig et al. 2003; Jenkins and Ricklefs 2011). However, as ecologists, we can no longer immerse ourselves in the pure wonder of biodiversity, but must understand these patterns within the context of maintaining, conserving and managing ecosystem services and resources. In an era of global environmental change, the need to understand patterns in global biodiversity and the ecological processes maintaining them continues to be of (de)pressing concern.

Conservation ecology has emerged as a new discipline to combine ecological understanding with the management of natural systems and their now over-exploited resources (Diamond et al. 1976; Soulé 1985; Simberloff 1988). Global biodiversity is vast and accurate assessments of biodiversity are still critical for effective conservation and management of natural systems (Cardinale et al. 2012). Needless to say, our knowledge of true species numbers and their full geographical distribution are still inadequate (e.g. the Linnean and Wallacean shortfalls (Whittaker et al. 2005; Bini et al. 2006; Cardoso et al. 2011).

Classical approaches to conservation sought to navigate these knowledge-gaps by drawing upon theories of island biogeography (Diamond et al. 1976), metapopulation ecology (Soule 1987; Hanski and Gilpin 1991) and geometric principles to inform reserve design (Diamond 1975). Debate about trade-offs within this reserve-based approach were prevalent and since the 1990s conservation actions have moved toward landscape-scale processes (Hobbs 1994; Farina 1998; Opdam and Wascher 2004). Whilst the landscape approach does afford greater holistic consideration of ecological processes, conservation ecology is now surrounded by new challenges stemming from global environmental, social and economic change (Vitousek 1994; Donaldson et al. 2017). A significant portion of these challenges arises from the now prevalent and increasing level of habitat degradation and fragmentation (Sala et al. 2000; Fahrig 2003). As such, conservation ecology is increasingly concerned with returning to understanding fundamental relations between organisms and their habitats (Pimm et al. 1995; Wallington et al. 2005; Hodgson et al. 2011).

At the community level, the *habitat*, defined here as “the features of the immediate surroundings which determine where a species can occur” (Bamford and Calver 2014), is the primary interface between individuals and the environment. Within a given habitat, species occupy ecological niches (Grinnell 1917; Hutchinson 1957), range limits are set (Haldane 1948; Kirkpatrick and Barton 1997) and connections between populations and individuals established (Elton 1927; Whittaker et al. 1973). Habitats often display strong patterns in zonation, where local-scale environmental gradients shape distinct biological assemblages. Notable examples include canopy stratification in forests (Adams 1941; Smith 1973), vertical zonation of rocky shores (Stephenson and Stephenson 1949; Connell 1972), altitudinal zonation in mountainous regions (Whittaker 1960; Beals 1969; Huey 1978) and also the distinct and highly diverse habitat zones exhibited by coral reefs (Goreau 1959; Bak 1977).

1.2 Coral reefs: biodiversity and habitat zonation

Early studies on coral reef ecosystems identified their immense diversity and productive capacity (Odum et al. 1955; Kinsey 1983; Hatcher 1988). The numerous and intricate relationships between reef organisms and the coral reef habitat makes coral reefs one of the most ecologically fascinating and economically valuable natural systems on the planet (Moberg and Folke 1999; Cesar 2000). However, early estimates of this intrinsic and economic value (Spurgeon 1992; Costanza et al. 1997) are now paled by the growing and precarious dependency of the human population on coral reef resources (Cinner et al. 2012; de Groot et al. 2012; 2015; McClanahan et al. 2015). Current and projected future climate change is also now rapidly altering coral reefs around the globe, changing ecological community structures and disrupting vital connections between and within them (Crossland et al. 1991; Kinsey and Hopley 1991; Munday et al. 2008; Hoegh-Guldberg 2014; Hughes et al. 2017; Williams et al. 2019). Because these organism-habitat connections define ecological function and the provision of resources (Morrison et al. 2012), understanding these relationships is the basis for unravelling shifting ecosystem functions (Dobson et al. 2006), predicting species and community response to change (Graham et al. 2020) and the capacity of natural systems for resilience (Nyström et al. 2008; Cumming 2011). A better understanding of organism-habitat relationships on coral reefs will therefore not only enable ecological impacts to be better assessed, but will also increase the capacity for sustainable management and effective conservation actions (Rogers et al. 2018).

On individual coral reefs, ecological communities are strongly associated with particular physical, structural and biotic features of recognisable reef zones; the reef slope, reef crest, reef flat lagoon and back reef slope (Fig. 1.1) (Williams 1991; Gratwicke and Speight 2005). Assemblages of corals, fishes and other reef organisms are characteristic of each zone on a “typical” coral reef. Light, temperature and carbon input from the pelagic realm are the three primary abiotic drivers of reef habitat zonation and community structure within these zones (Muscatine et al. 1981; Sheppard 1982; Kleypas et al. 1999; Monismith 2007). Gradients in these energetic sources exist vertically, with depth, and also horizontally, with distance from the windward crest of a reef.

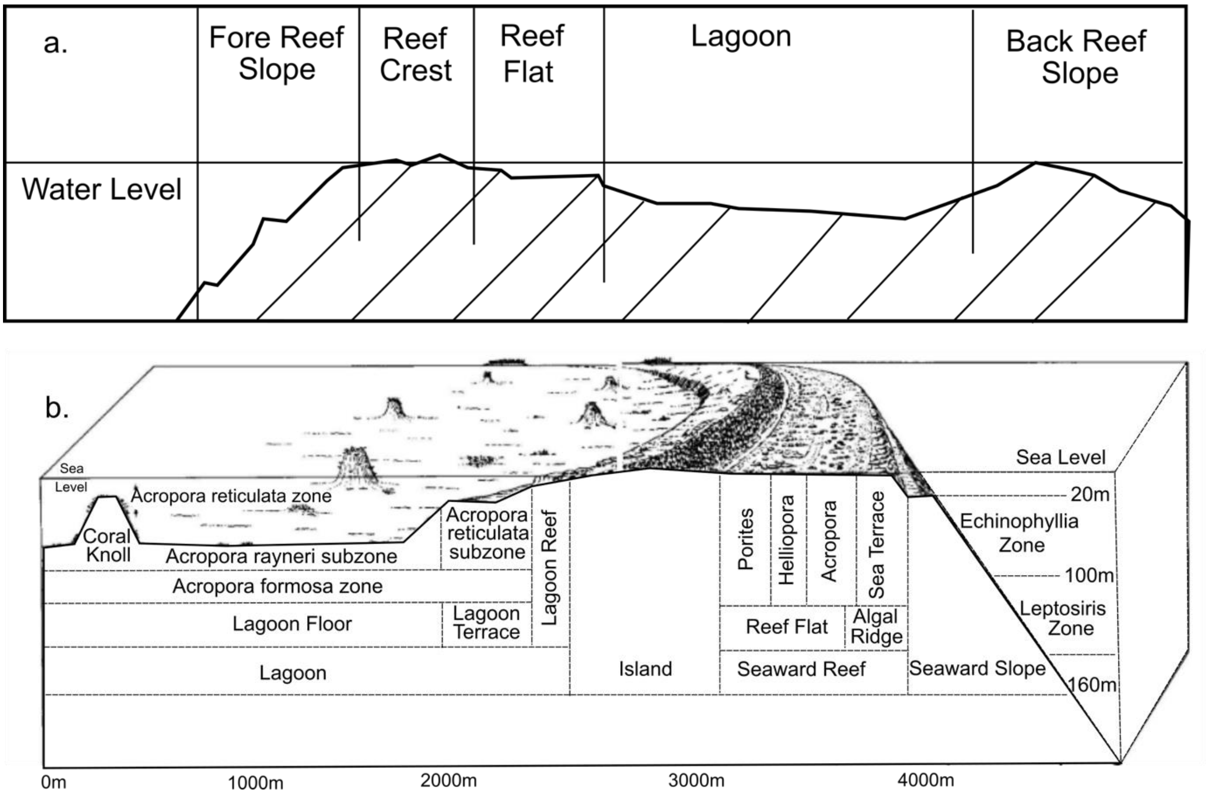


Figure 1.1 (a) Schematic of "typical" reef zonation taken from Sale (1991) **(b)** More detailed zonation redrawn from Done (1983) based on Bikini Atoll. The classification of these zones, their physical nature and characteristic fish communities is a core foundation of reef fish ecology. However, this zonation typically always includes a shallow emergent portion of habitat reaching the sea surface (0-10m).

On a larger seascape scale, three main reef habitat types have been the subject of nearly all coral reef ecological studies (Darwin 1842; Maxwell 1968; Hopley 1982): 1) Nearshore fringing reefs associated with the coastline of continental mainland and islands; 2) Barrier reefs that border coastlines with wide lagoons separating land from reef, and; 3) Coral atolls with a deep central lagoon found in offshore settings (Ladd 1977; Steers and Stoddart 1977; Hopley et al. 2007). These three reef morphologies share common patterns in zonation (e.g. all possess a reef crest, rising from the seaward edge typically to within 0-10m of the surface), but also have distinct habitat features which generate ecological variability (e.g. the lagoon of atoll reefs or close proximity to terrestrial influences for fringing reefs (Fig. 2).

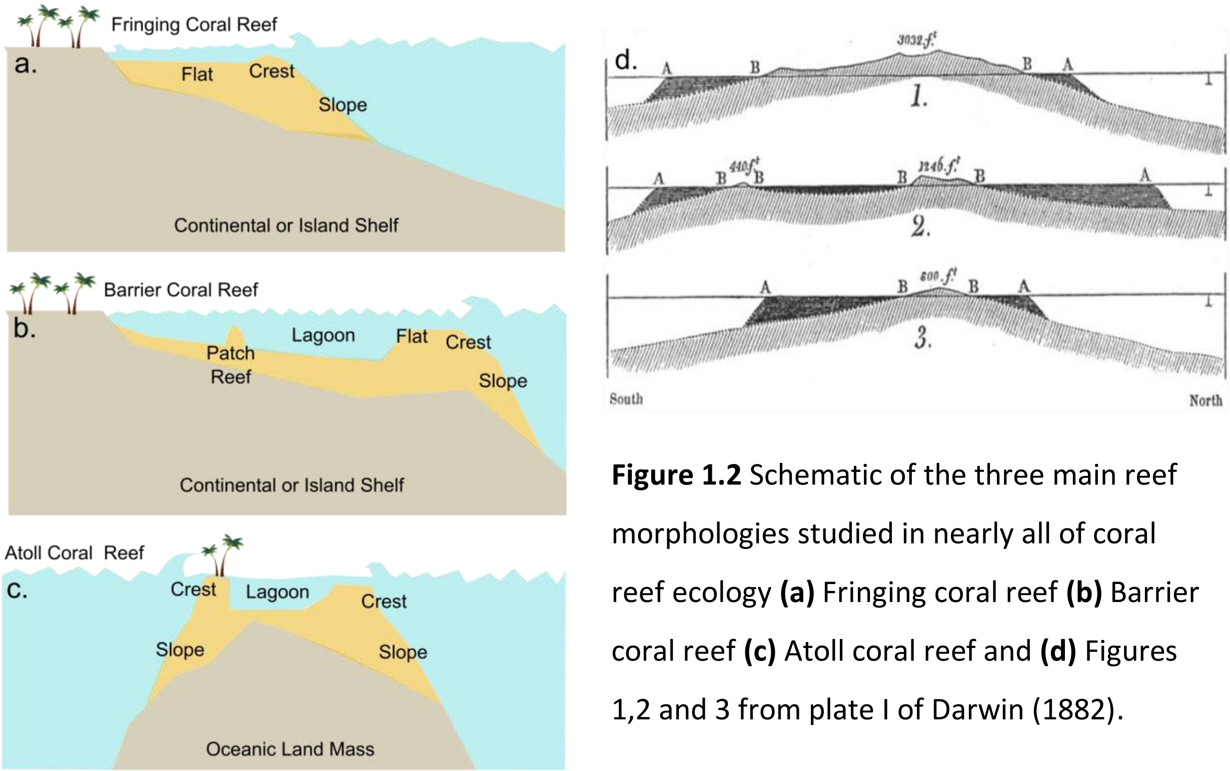


Figure 1.2 Schematic of the three main reef morphologies studied in nearly all of coral reef ecology **(a)** Fringing coral reef **(b)** Barrier coral reef **(c)** Atoll coral reef and **(d)** Figures 1,2 and 3 from plate I of Darwin (1882).

Ecological assemblage variability as a product of reef morphology is therefore well known and widely recognised. However, most studies on all coral reefs are conducted in the upper 0-30m of the habitat and often research efforts are more realistically focused within even narrower depth bands (e.g. between 0-10m). Additionally, shallow, emergent portions of reefs are easily mapped by remote sensing techniques including aerial photography, Light Detection And Ranging (LiDAR) and satellite imagery (e.g. LANDSAT Geological Survey Series). Readily available open-source spatial data derived from these remote sensing methods has now made spatial analysis of coral reefs highly accessible through Geographic Information System (GIS) software and web-based platforms (Great Barrier Reef Marine Park Authority 2004; Purkis et al. 2019; Allen Coral Atlas 2020), even for those in remote, offshore locations (Lyons et al. 2020). However, given the physical complexity and inherent variability in the marine environment, remote sensing is typically limited to around 30m penetration of the water column (Pittman et al. 2013). Further, these data still require ground surveys to verify habitat maps, community structure and ecosystem heath, all of which often fails to keep up with the rate of remote sensing data acquisition (Hopley et al. 2007).

Technological advances over the last decade have however, greatly enhanced the ability to survey fish communities below 30m. Advanced closed-circuit diving, remotely operated vehicles (ROVs), remote video (e.g. baited and un-baited remote underwater video, B/RUVs) and submersible technologies have all driven a rapid expansion in the study of depth gradients and deeper coral reef communities (Andradi-Brown et al. 2016; Asher et al. 2017; Turner et al. 2017; Pyle and Copus 2019). This has led to the classification of discrete depth zones well below those investigated in foundational coral reef research (Hinderstein et al. 2010). The study of fish ecology in mesophotic coral ecosystems (MCEs) which occupy the depths ranging from 30-150m (Fig. 3), is a rapidly emerging field (Mesophotic Coral Ecosystems 2019).

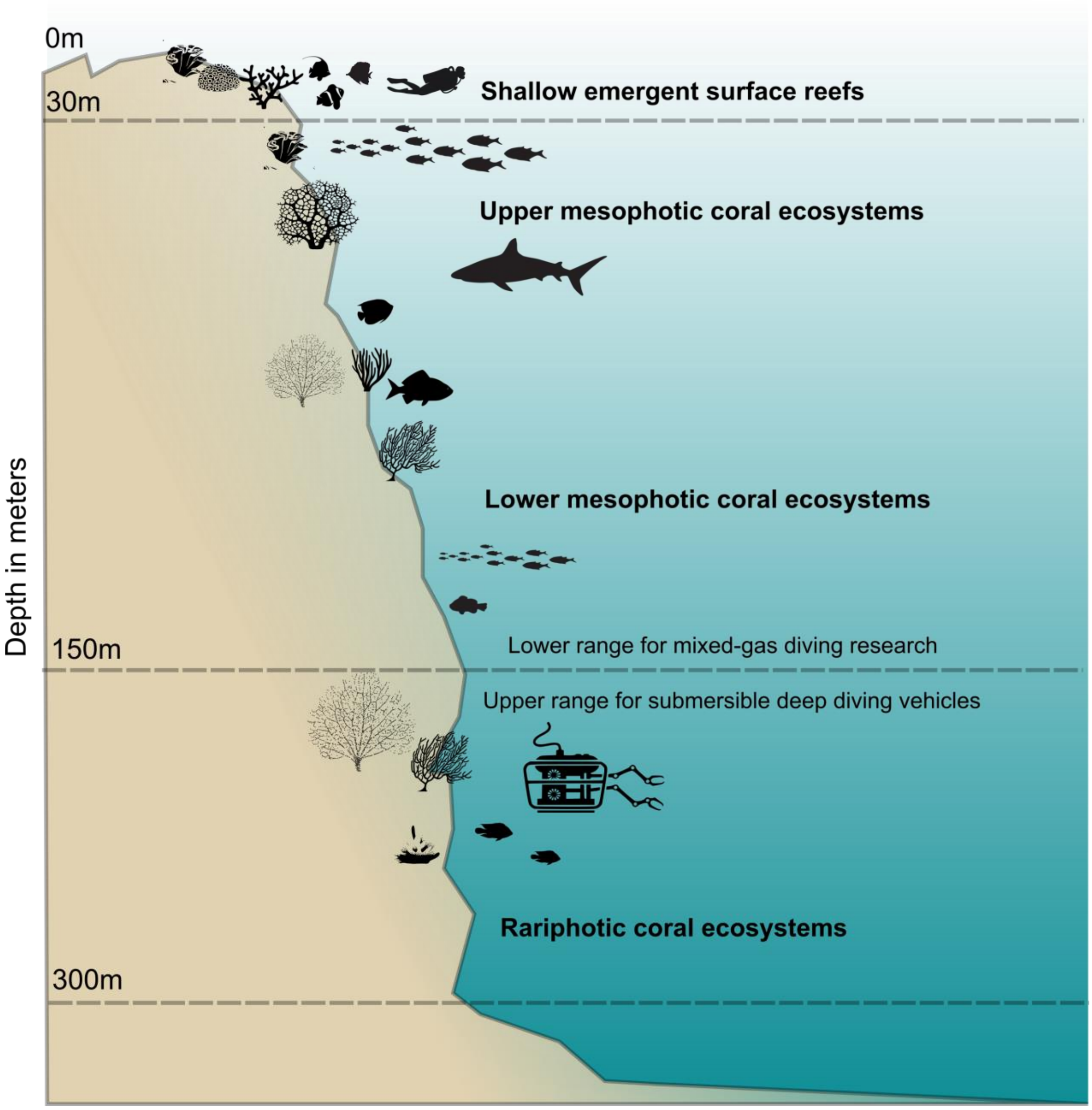


Figure 1.3 Depth zonation of coral reef fish habitats Shallow reef fish communities are considered to occupy the upper altiphotic zone between 0-30m and beyond theses depths, communities transition into the mesophotic from 30-150m (Tamir et al. 2019). The mesophotic zone itself is divided into upper, middle and lower zones, where further community breaks and assemblage shifts occur (Pinheiro et al. 2016; Lesser et al. 2019). Below this the rariphotic zone represents the final part of the depth continuum for tropical reef fishes and is the last discrete faunal zone before the deep sea (Baldwin et al. 2018).

1.3 The ecology of fishes on coral reefs

Zonation on coral reefs was one of the earliest and most fundamental patterns described in coral reef fish ecology (Goreau 1959; Done 1983) and numerous early studies documenting fish-habitat interactions emphasise the clear role of the habitat in shaping diversity and ecological structure (Gosline 1965; Sale 1977; Roberts and Ormond 1987). The intrinsically patchy nature of coral reefs through zonation has led to the evolution of one of the planet's most diverse ecosystems (Choat and Bellwood 1991). For the emerging field of reef-fish ecology in the 1950s, this diversity was mirrored by the wealth of opportunities presented to biologists and ecologists, ranging from population and community ecology to behavioural, physiological and evolutionary studies.

The publication of The Ecology of Fishes on Coral Reefs (1991) was a landmark review of the current understanding and research of reef fish ecology at the time. Since then, further volumes (Sale 2002, 2006; Mora 2015) have collated progress in the field, much of which has contributed significantly to major general ecological concepts (Sale 1977, 1978; Chesson and Warner 1981; Doherty 1982; Victor 1983; Hixon 1991; Hixon and Carr 1997; Munday 2004; Jones et al. 2005; Hixon 2015; Jones 2015). Studies have also been extended to large spatial biogeographical and evolutionary time scales (Almany et al. 2017; Bellwood et al. 2018; Siqueira et al. 2021), while new paradigms are emerging and debate continues over the mechanisms driving coral reef biodiversity (Mora 2015; Morais and Bellwood 2018; Roberts et al. 2019).

Understanding fish-habitat interactions has taken a number of different directions. The functional roles of fish species have been keenly investigated, linking morphology, behaviour and physiology to ecological performance and roles on the reef (Ogden and Lobel 1978; Hay 1981; Lewis 1986; Choat 1991; Kingsford 1992; Hixon and Beets 1993; Done et al. 1996; Beukers and Jones 1998; Bellwood et al. 2019b). Interactions between individuals and with the surrounding habitat have been quantified and ecological mechanisms on coral reefs unravelled (Jones 1987; Syms and Jones 2000; Jones and McCormick 2002; Almany 2004; Hixon and Jones 2005).

There is an increasing appreciation of the high level of habitat specialisation in reef fishes, particularly in light of current and rapid habitat degradation of coral reefs (Munday 2004; Bonin 2012; Pratchett et al. 2012; Holbrook et al. 2015). Prominent examples include the obligate dependency on a single coral species for shelter in some goby species (Munday et al. 1997) and the requirement of some butterflyfishes for live coral as food (Pratchett 2005). The morphological and physiological attributes together with behavioural traits that determine habitat specialisation also mediate key processes of predation (Munday and Jones 1998; Brooker et al. 2013) , competition (Munday 2001), foraging (Brandl et al. 2015) and recruitment patterns (Feary et al. 2007; McCormick et al. 2010). Specialisation is therefore a key factor affecting local abundances and geographic distributions (Williams 1991; Munday 2002) and eventually scales to drive overall community structure (Messmer et al. 2011; Komyakova et al. 2018), speciation (Schluter 2000; Munday 2002; Rocha et al. 2005), ecosystem functioning and stability (Clavel et al. 2011; Bellwood et al. 2019b)**.** Although coral reefs are disturbance driven systems, the increasing frequency and intensity of anthropogenic disturbance renders highly specialised species of reef fish vulnerable to population declines and extinction when habitat is degraded or lost (Jones et al. 2004; Wilson et al. 2007; Pratchett et al. 2011; Coker et al. 2014). These changes to community structure disrupt the natural provision of multiple resources and ecological functions (Pratchett et al. 2008; Cinner et al. 2012; Rogers et al. 2014). Further, because many facets of habitat specialisation are still unknown, the effects of global loss of live coral cover and physical structural complexity on coral reefs likely has much further reaching consequences than we currently understand (Munday et al. 2008; Graham et al. 2011).

Much of current coral reef fish ecology now focuses on how community structure translates into ecological function and subsequently, resource provision for the human population (Bellwood et al. 2019a; Williams and Graham 2019; Woodhead et al. 2019). Although the conservation of reef fish has maintained the importance of holistic ecosystem-based approaches, this framework is increasingly shifting towards functional trait-based triage and the acceptance of novel, irreversibly altered assemblages (Graham et al. 2014, 2017; Bellwood et al. 2019b; Williams and Graham 2019).

1.4 The incomplete picture of coral reef fishes

To date, most studies on coral reef fishes have been conducted on nearshore, shallow and therefore easily accessible reefs. Although remote offshore reefs are sometimes utilised to reduce the confounding effects of human influence, these sites are still shallow near-sea-surface reef habitats (Dulvy et al. 2004; Knowlton and Jackson 2008). Although this shortfall is understandable based on logistic feasibility, a sampling bias persists in coral reef fish ecology towards emergent reefs representing certain depths and morphologies.

Ecological processes affecting coral reef fishes are still not well known in deep reef habitats, but progress has been made to understand drivers of fish assemblage structure and connections with shallow reef communities (Kahng et al. 2014; Turner et al. 2017; Lesser and Slattery 2018; Eyal and Pinheiro 2020). Although increasing depth generally leads to declines in fish diversity, the results of many studies remain variable, especially at different locations, across different spatial scales and reef morphologies (Thresher and Colin 1986; Edmunds and Leichter 2016; Pinheiro et al. 2016; Gress et al. 2018). Many of these changes are attributed to decreasing complex coral cover as a product of decreasing photosynthetic productivity with lower light (Brokovich et al. 2008). However, it now appears that there are likely additional energetic inputs to ecological processes, which may determine the structure of deep reef fish communities (Cerrano et al. 2019; Kahng et al. 2019). These include: modified trophic pathways, especially increased prevalence of heterotrophy in corals (Mass et al. 2007; Lesser et al. 2010) and the greater importance of deep currents and internal waves over surface driven hydrodynamics to deliver nutrients and regulate temperatures (Leichter et al. 2003; Wolanski et al. 2004; Kahng et al. 2012). Many of these habitat characteristics are suggested to confer resilience to environmental stressors which has generated considerable interest in MCEs as refuge habitats for shallow coral reef species (Glynn 1996; Bongaerts and Smith 2019). Although this “Deep Reef Refuge Hypothesis” (DRRH) is still the subject of debate, it serves to highlight the persistent gaps in basic knowledge of coral reefs below 30m (Turner et al. 2019).

In addition to our poor understanding of coral reef fishes in deep water, there are also morphologically distinct coral reef habitats that remain poorly described and underexplored. Submerged reefs do not breach the sea surface and whilst some forms do have shallow habitat extensions, others exist on detached, isolated and abrupt bathymetric features. These coral reefs do not conform to typical reef morphologies or patterns of habitat zonation. They are logistically challenging to explore and due to their depth are not readily detected by many remote sensing methods. As such, ecological communities and processes on submerged reefs are largely unquantified and their contribution to coral reef biodiversity unknown.

1.5 Submerged reefs as fish habitat

1.5.1 Definition, geomorphology and extent

The International Hydrographic Organisation defines a submerged reef as “an isolated elevation of the seafloor, over which the depth of water is relatively shallow but sufficient for navigation” (IHO 2008). In terms of habitat suitable for coral reef formation and persistence of coral reef communities, these “relatively shallow depths” are most commonly taken to range between 20-150m (Abbey and Webster 2011; Bridge et al. 2012; Thomas et al. 2015). By contrast, emergent reefs, also referred to as shallow or near sea surface (NSS) reefs, reach the upper 0-10m and often breach the sea surface.

Modern day submerged reefs originated as emergent reefs during periods of lower sea level (Abbey and Webster 2011). Dramatic sea level rise (~120m) since the last glacial maximum (19-20kya) led to many emergent reefs being “drowned” below the zone of photosynthetic growth (Montaggioni 2005). Whilst these drowned, now “relic”, reefs cannot support modern coral reef communities and are primarily studied for records of paleo-environmental change, there are also submerged reefs that remain within suitable depths for the growth reef-forming corals (Bridge et al. 2012). Unlike the more dynamic balance between coral growth and erosion on emergent reefs, submerged reefs have slower growth rates of coral reef habitat, with sometimes little or no upward accretion (Harris et al. 2004). Although submerged reefs were of interest to historic mariners and geologists (Jukes-

Browne and Harrison 1891; Montaggioni and Macintyre 1991), due to greater depths and offshore settings, their biological communities have been historically overlooked by coral reef ecologists.

However, recent work using in bathymetric mapping has shown that the extent of suitable habitat for the formation of coral reefs is greatly increased when accounting for submerged reefs (Harris et al. 2013). This includes coral reef communities that span the transition zone between shallow emergent coral reefs (~20-30m) and mesophotic coral reef communities (30-150m). On the Great Barrier Reef alone, the area of available coral reef habitat is increased by 160% when reefs deeper than 20m are included in estimates (Harris et al. 2013; Bridge et al. 2019). In addition to the growing scientific study of submerged reefs, increased survey efforts by international mapping collaborations and non-profit foundations are providing the most high-resolution bathymetry maps to date. For example, the Seabed 2030 project is a collaboration between The General Bathymetric Chart of The Oceans (GEBCO) and the Nekton Foundation and aims to facilitate the mapping of the complete ocean floor by 2030 (Jakobsson et al. 2017). The Schmitt Ocean Institute and their research vessel R/V Falkor have also recently provided a platform for enhanced bathymetry mapping and deep-sea exploration in numerous global locations. These efforts in further exploring the mesophotic zone are revealing multiple forms of submerged reef that are ubiquitous across global oceans (Beaman et al. 2008; Raineault 2019).

1.5.2 Morphology of submerged bathymetric features

Just as emergent reefs may be categorised into distinct morphologies (i.e. barrier, fringing and atoll coral reefs), seascape setting and geological origin define various submerged reef morphologies. Flat-topped forms are found on geologically stable continental shelves as platforms and terraces cut into the slope or banks and shoals on top of the shelf (Abbey and Webster 2011). These typically form deep contiguous systems that parallel the coastline. Platform and terrace submerged reefs often have shallow emergent habitat extensions where the continuum of the shelf slope eventually reaches current shallow water coral reef habitats. Submerged patch reefs also exist, either detached from the shelf or as smaller features associated with a larger submerged morphology. In zones of active tectonism these are usually seamounts, which rise from oceanic plates (Wessel et al. 2010; Staudigel et al. 2015). Although the seamount biome is regarded as a deep-sea habitat, shallow seamounts that reach the photic zone in low latitudes provide hard substrate for the formation of coral reefs (Rogers 1994; Ceccarelli et al. 2013). It should be noted that the classification of “shallow” habitats in seamount geology and ecology is still much deeper than emergent NSS reefs (>20m). Seamounts can also breach the sea surface, either forming islands (e.g. the Hawaiian Island chain) or as flat topped guyots (Hess 1946; Gischler 2016), both of which can support shallow (0-20m) coral reef communities.

Typically, true seamounts are at least 1000m in height from the seafloor, are volcanic in origin and are situated on deep oceanic plates (Wessel 2001). The global seamount biome is extensive, but understudied and to date only relatively few seamounts have been scientifically surveyed (Etnoyer et al. 2010; Stocks et al. 2012). There are numerous other submerged features found across continental shelves and surrounding subsiding oceanic islands. These include smaller steep-sided submerged pinnacles, knolls, hills and bommies, which vary by height, geological formation, shape and setting (Table 1.1, Fig. 1.4). Pinnacles are physically very similar structures to seamounts, but are not usually formed by volcanic activity, and are mostly associated with continental and island shelves rather than oceanic plates (Stoddart 1969; Harris et al. 2003; Heap and Harris 2008). The extent of coral reef habitat specifically on pinnacles has not been quantified, but these submerged patch reefs are abundant on nautical charts and have been shown to support highly diverse and productive fish communities (Fitzpatrick et al. 2012; Richert et al. 2017; Samoilys et al. 2018; Linklater et al. 2019).

Table 1.1 Some definitions of submerged geomorphologies. Distinctions are made based on depth, size, geological origin and tectonic setting. Some of these features will rise to emergent depths and support shallow water coral reef communities but in many cases may be completely submerged with no emergent portion of habitat. Definitions follow (Kuchler 1987; Heap and Harris 2008; IHO 2008).

Submerged Feature	**Description**
Slope	The slope seaward from the shelf edge to the upper edge of a continental rise or the point where there is a general reduction in slope.
Bank	An elevation over which the depth of water is relatively shallow but normally sufficient for safe surface navigation.
Shoal	An offshore hazard to surface navigation that is composed of unconsolidated material
Knoll	A relatively small isolated elevation of a rounded shape.
Hill	A small isolated elevation
Ridge	(i) A long, narrow elevation with steep sides. (ii) A long, narrow elevation often separating ocean basins. (iii) The linked major mid-oceanic mountain systems of global extent.
Seamount	A large isolated elevation, 41000 m in relief above the seafloor, characteristically of conical form and volcanic in origin.
Guyot	A seamount having a comparatively smooth flat top
Pinnacle	Any high tower or spire-shaped pillar or rock or coral, alone or cresting a summit. It may extend above the surface of the water. It may or may not be a hazard to surface navigation.
Terrace	A relatively flat horizontal or gently inclined surface, sometimes long and narrow, which is bounded by a steeper ascending slope on one side and by a steeper descending slope on the opposite side.
Plateau	A flat or nearly flat area of considerable extent, dropping off abruptly on one or more sides
Bommie	An isolated patch reef that rises to the surface typically in lagoon settings. Often used to describe a single species formation e.g. a P*orties* sp. bommie

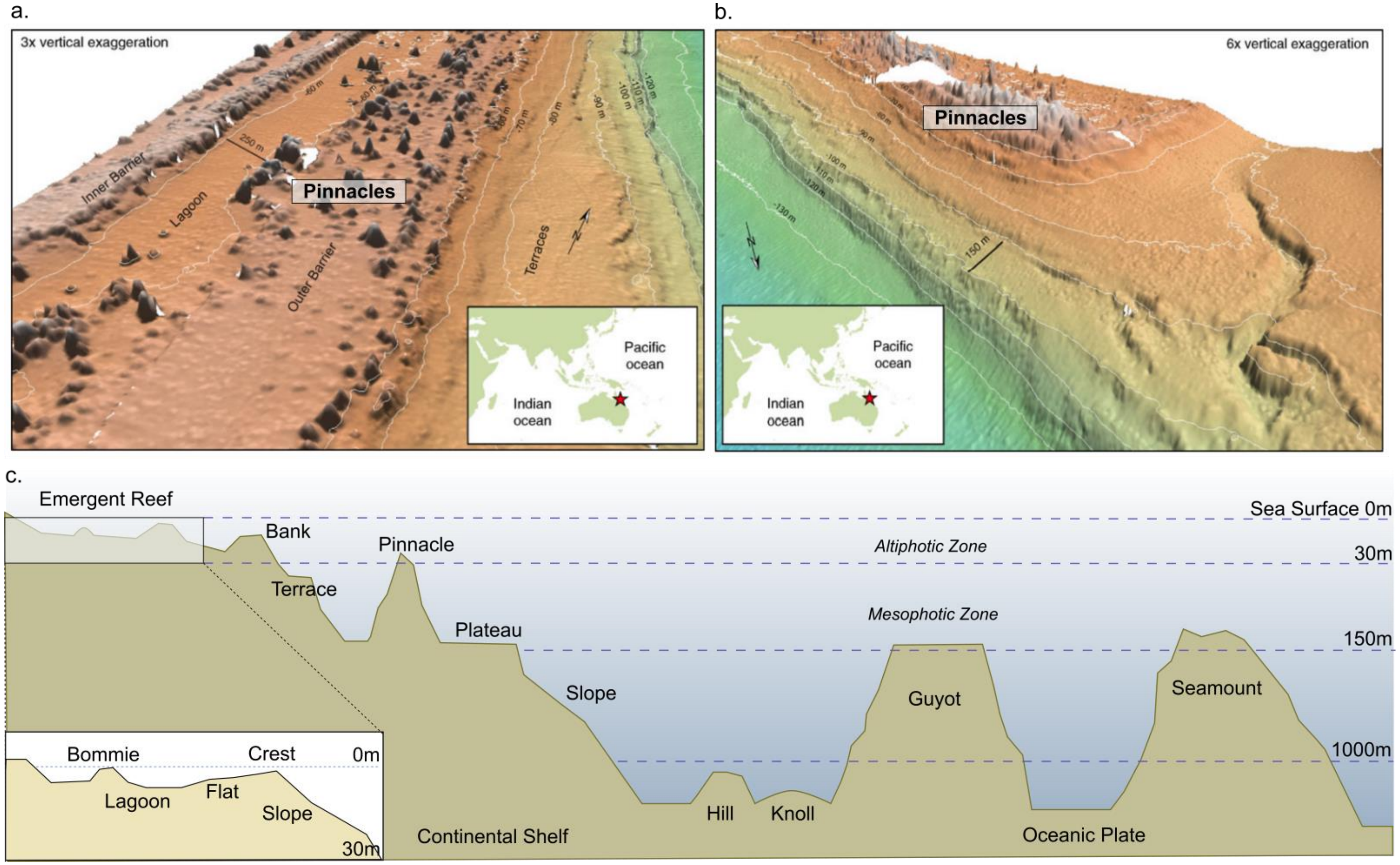


Figure 1.4 (a) and **(b)** from Abbey and Webster 2011 high-resolution bathymetry mapping of the Great Barrier Reef shelf reveals extensive areas of submerged reefs and pinnacles **(c)** Schematic of some submerged geomorphological features. Depth is not to scale but is presented to illustrate the capacity of these features to support coral reef ecosystems within suitable depth zones. The emergent reef inset highlights the typical patterns of zonation on shallow coral reef habitats relative to submerged reef geomorphologies.

1.5.3 Seamounts and pinnacles – physical similarities and ecological parallels?

Seamounts are also known to support diverse and highly productive ecological communities (Hubbs 1959; Brainard 1986; Rogers 2004). These deep submerged patch habitats have been identified as hotspots of pelagic diversity in the open ocean (Morato et al. 2010) and often support high abundance and biomass of fishes (Uda and Ishino 1958; Boehlert and Seki 1984). Although one of the planet's least known and inaccessible habitats, multiple hypotheses have been proposed to explain how ecological communities are supported on these isolated habitats surrounded by relatively homogenous deep-sea environments (Rogers 2004; Rowden et al. 2010b; Clark et al. 2012). Primary mechanisms are mostly related to the physical characteristics of the seamount habitat and interactions with oceanographic processes (Boehlert 1988; Mullineaux and Mills 1997; White et al. 2007). These interactions generate local dynamic responses that provide enhanced energetic subsidies to ecological communities at great depths and in spatially isolated seascape settings (Doty and Oguri 1956; Schlacher et al. 2010; Woolley et al. 2016).

Seamounts dramatically alter the flow of surrounding currents (Bohlert and Genin 1987; Lavelle and Mohn 2010). They can increase current speeds and turbidity around the structure, which in turn increases the rate of particulate food delivery to suspension feeders (Genin et al. 1986; Eriksen 1991). This mechanism results in diverse benthic communities on seamounts including octocorals, scleractinian corals and sponges (McClain et al. 2010; Schlacher et al. 2014). The water column above seamount summits is also a key habitat feature thought to contribute to the retention of plankton and nutrients. This occurs via physical trapping (Genin 2004), density-driven stratification (Roden 1991) and the formation of vertical vortices known as Taylor columns (Chapman and Haidvogel 1992; Beckmann and Mohn 2002). Euphotic seamount summits, slopes and flanks rise from considerable depth (>1000m) and nutrient supplements are delivered to biological communities by upwelling and internal waves propagating from deep, cold, nutrient dense currents (Dower et al. 1992; Mohn et al. 2013). Although evidence for the existence of Taylor columns is inconclusive (Genin and Dower 2007), hydrodynamic regimes have been shown to drive strong biophysical coupling between physical processes on seamounts, productivity and their ecological communities.

Anecdotally, the ecology of fishes on pinnacle coral reefs appears distinct from many patterns on shallow emergent coral reefs and instead may share more similarities with seamounts. For example, pinnacles are highly sought-after recreational dive sites, known for high diversity and dense aggregations of reef and pelagic fishes. Recreational and commercial fishers also often target the abundant fish communities found at these habitats (Clark et al. 2010; Richert et al. 2017). As on seamounts, pinnacle fish communities are also often comprised of higher trophic levels and aggregations of top predators (Morato et al. 2010; Vassallo et al. 2018; Letessier et al. 2019). Both pinnacles and seamounts are essentially deep patch reef habitats and in shallow coral reef ecology, the dynamics of patch reefs have long been recognised as distinct from other reef morphologies (Sale 1980; Sale and Douglas 1984; Sale et al. 1994). Seamount ecology also has numerous empirical models and theories explaining patterns in fish biodiversity (Pitcher et al. 2007; Rowden et al. 2010a; Rogers 2018). Given the physical similarities between seamounts and submerged pinnacles, it therefore seems reasonable to explore the ecology of fishes on pinnacle coral reefs within the context of ecological paradigms derived from both shallow coral reefs and seamounts.

Differences in scale, geological origin and seascape setting mean these processes likely do not operate at the same magnitudes on pinnacles as on seamounts. Nevertheless, the clear difference in physical habitat structure between pinnacles and emergent reefs suggests that distinct habitat-specific environmental conditions may arise in these submerged coral reef habitats. Physical differences include a significant water column above the entire reef, no direct terrestrial gradients and relatively isolated positions in offshore or outer shelf positions. Key gradients in light, temperature and hydrodynamics will still govern the biodiversity of reef fish communities on pinnacles, but probably not in the linear patterns typical of emergent reefs. This also means ecological responses to environmental change are likely to differ. Habitat-generated environmental conditions, like increased nutrients or cooler water delivered by currents, may confer some elements of resilience to ecological communities on submerged pinnacles (Rogers et al. 2016; Bongaerts and Smith 2019). When combined with greater depth, which also buffers the effects of sea-surface level disturbance, pinnacle coral reefs potentially represent naturally resilient coral reef habitats.

Pinnacle coral reefs are also likely widespread in all coral reef seascapes, making them potentially important stepping-stones for the dispersal and movement marine organisms (Randall 1998; O'Hara and Tittensor 2010). Organism movement contributes to multiple large-scale population dynamics (e.g. range expansion), but also has implications for local energetic processes. For example, mobile consumers exhibit numerous foraging patterns which range on both spatial and temporal scales (e.g. diurnal hunting, seasonal or ontogenetic migration). Consumers are therefore key mediators of the flow of energetic subsides between habitats, which in turn will affect community composition and trophic dynamics (Polis et al. 1997). Highly mobile pelagic and reef-associated predators are frequently observed on seamounts and pinnacles (Holland and Grubbs 2007; Litvinov 2007; Clark et al. 2010). When combined with physical processes that enhance productivity or trap and retain nutrients, pinnacles and seamounts may provide important energetic subsidies to other marine habitats and different reef types. Spatial heterogeneity is an essential consideration for understanding ecological patterns processes in all habitats, even those which appear discrete and isolated.

Many of the physical habitat characteristics that make pinnacle coral reefs intriguing systems to study also, however, present significant difficulties. Although progress has been made to quantify the extent of submerged reef habitats in general, pinnacles are small and isolated units that still present logistical challenges to survey. Additionally, scientific interest in submerged reefs is still mostly focused on geological studies with only 14 peer-reviewed papers including the terms "pinnacle, coral reef "(Web of Science search, March 2021). Of these, only 7 are published in biological journals and only 1 has a specific focus on pinnacle coral reefs (Galbraith et al. 2021 - Chapter 2 of this thesis).

1.6 Knowledge Gaps

Although global environmental decline has shifted the focus of many ecological studies to documenting disaster or quantifying overexploitation, there is still a crucial requirement to understand fundamental aspects of ecology. Coral reefs are an almost unfathomably complex system so, as anthropogenic stressors alter known patterns and processes, we must develop a new ecological understanding of the changes to these systems. This should not only include novel communities that have shifted from their natural state, but also communities found in currently unexplored and understudied habitats. For reef fish communities such habitats may be found in the deeper mesophotic and morphologically distinct submerged coral reef ecosystems introduced here in this first chapter.

Identifying the capacity for resilience, refuge and the scope for fisheries use are key challenges facing coral reef science in the Anthropocene (Friedlander 2015; McClanahan et al. 2015; Mcleod et al. 2019). Yet, we have little information about how submerged coral reefs contribute to the overall function of the coral reef biome, connectivity with shallow reefs or how these systems may respond differently to environmental change. A number of key research questions therefore exist coupled with opportunities for studies ranging from population ecology to behavioural and physiological research:

- How do ecological communities differ from shallow water reefs and how are these communities connected?
- What is the extent of submerged coral reef habitat, particularly morphologically distinct submerged features like pinnacles?
- How do ecological processes on submerged reefs differ from shallow reefs and what are the primary drivers of patterns in biodiversity in these habitats?
- Are there habitat effects on the fitness of individuals? Do conspecifics differ in condition or growth patterns on submerged reefs? Are acclimatisation capabilities required to live deeper?
- How do energetic pathways differ from emergent reefs and what is the role of submerged reef communities in nutrient cycles and trophic relay across seascapes?
- What is the role of submerged patch reefs in dispersal and seascape connectivity? Are these habitats sources, sinks or both for larval dispersal? Do pinnacles facilitate movement for pelagic species?
- How can submerged reefs be more effectively incorporated into conservation spatial planning and marine reserve networks? How do we adapt the capacity of current conservation and management measures to include submerged reef ecosystems?
- To what extent will submerged reefs be affected by climate change and how will these impacts differ from shallow emergent coral reefs?

1.7 Thesis aims, geographic setting and chapter outlines

The overarching aim of this thesis was to investigate aspects of the ecology of fishes on submerged pinnacle coral reefs to begin to answer these questions. Within the context of this distinct, but relatively unknown reef habitat type, my four data chapters comprise: fundamental patterns in reef fish diversity (**Chapter 1**), physical processes (**Chapter 2**) and environmental conditions that define fish communities (**Chapter 3**) and finally, their functional and resource-derived role in reef fish productivity (**Chapter 4**) (Fig. 1.5). I draw upon multiple paradigms from seamount ecology, based on the similar physical structure between these deep-sea patch habitats and pinnacle coral reefs. Although clearly distinct ecological systems, there are potentially parallel mechanisms contributing to the support of ecological communities on each of these abrupt bathymetric features. I apply many of these ideas and concepts to the context of the study and discussion of results in each chapter.

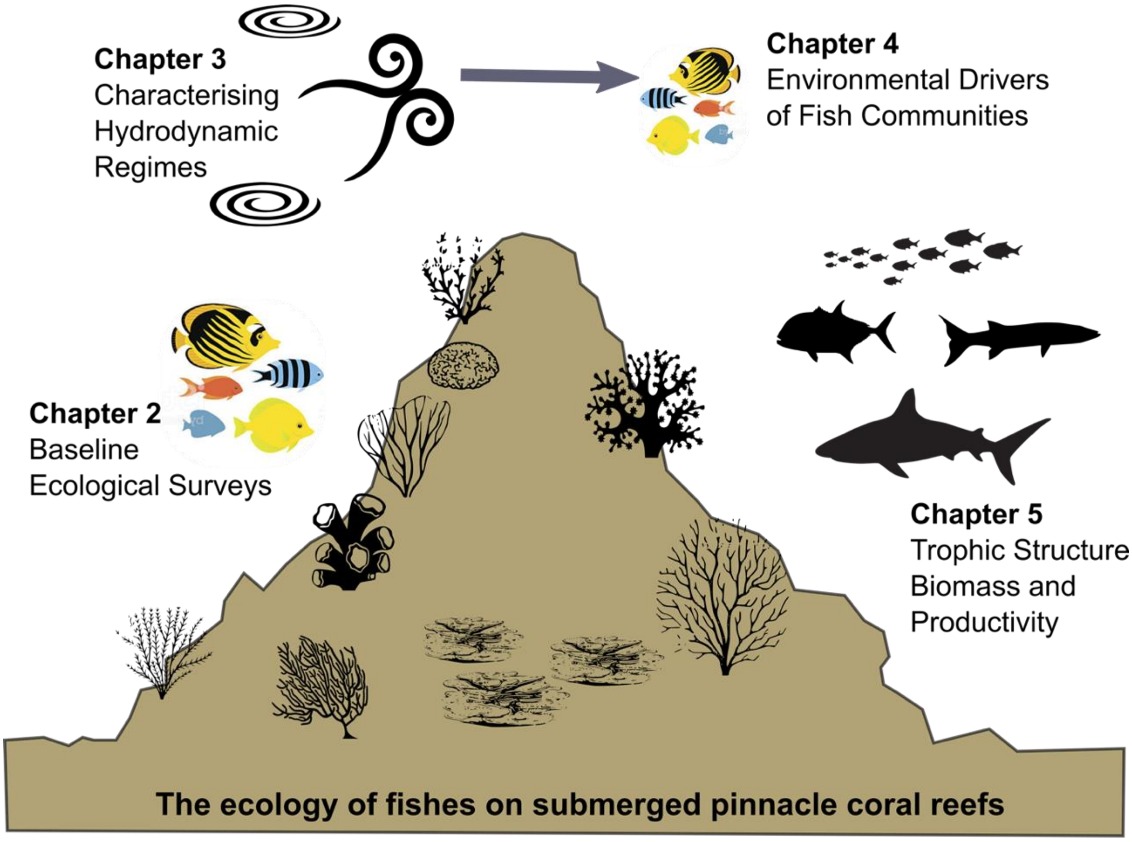


Figure 1.5 Conceptualisation of thesis.

This study took place in Kimbe Bay, West New Britain Province, Papua New Guinea (5°30’S, 150°05’E). A long-standing partnership between G. Jones and colleagues, and Mahonia Na Dari Conservation and Research Centre has led to the publication of over 150 peer-reviewed publications of marine ecological studies conducted at this location. Many of these have been high-impact international collaborations which have considerably advanced the study of reef fishes, particularly in the fields of recruitment, larval dispersal and marine reserves (Jones et al. 2005; Almany et al. 2007, 2017; Planes et al. 2009). The bathymetry of Kimbe Bay is however incredibly complex, and as such the bay possesses a rich and diverse seascape. Fringing reefs, emergent offshore guyots and steep sided pinnacles are found in relatively close proximity in both near- and offshore positions. New Britain Island is highly volcanic and a submerged caldera (sunken volcano now drowned by historic sea level rise) central to the bay creates this varied seascape (Fig. 1.6).

Although much research has been conducted on the nearshore fringing reefs and emergent shallow reefs around islands in the bay, fish communities on the pinnacle reefs had not been quantified. Kimbe Bay therefore presented an ideal opportunity for baseline ecological studies of the offshore pinnacles and to draw comparisons with the ecology of emergent reefs. Cross shelf and seascape position gradients determine patterns in reef fish ecology, including in Kimbe Bay (MacDonald et al. 2016). I therefore selected emergent reefs in close proximity to land and also in similar offshore positions to the pinnacles. Nearshore reefs were selected from a Locally Managed Marine Area network (Kimbe Bay LMMA, Green et al. 2007) to reduce the confounding effect of fishing at reefs closest to human populations. Throughout this thesis the same set of twelve reefs is used in each chapter, representing three reef habitat types: submerged pinnacle reefs, nearshore emergent reefs and offshore emergent reefs (n = 4 of each, Fig. 1.5 and Table 1.2). All surveys and environmental data were collected within a 20-30m depth band on all reef types.

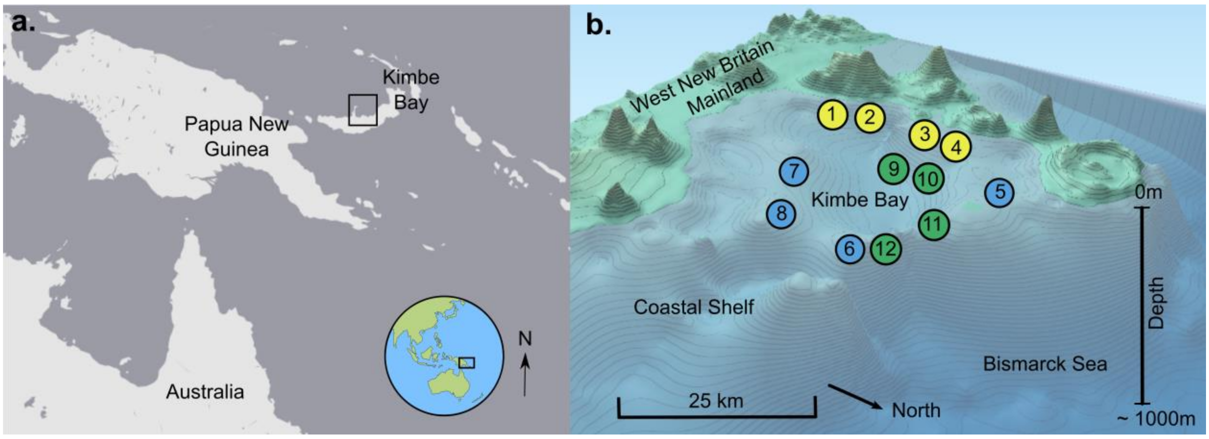


Figure 1.6 Study location and reef sites in Kimbe Bay **(a)** Global location of Kimbe Bay on New Britain Island, West New Britain Province, Papua New Guinea **(b)** Bathymetric map of Kimbe Bay showing individual study reefs as coloured circles; nearshore emergent reefs (1-4, yellow), offshore emergent reefs (5-7, blue) and offshore submerged pinnacles (9-12, green).

Table 1.2 Characteristics of individual study reefs and categorisation as emergent nearshore, emergent offshore and submerged pinnacle reef types. Numbers in brackets and colour correspond to numbered coloured circles in Figure 1.6b.

Reef Site	Reef Habitat Type	Crest Depth	Distance from Land
Lady Di (1)	Emergent Nearshore	1m	0.7
Madaro (2)		<1m	0.8
Donnas (3)		1m	3.7
Susans (4)		2m	4.2
Ema (5)	Emergent Offshore	1m	8.8
Kimbe Island (6)		4m	25.0
Ottos (7)		2m	17.7
Hogu (8)		7m	11.3
Inglis Shoals (9)	Submerged Offshore Pinnacle	18m	10.2
Joelles (10)		21m	11.6
Bradford Shoals (11)		25m	15.2
Kimbe Bommie (12)		30m	25.0

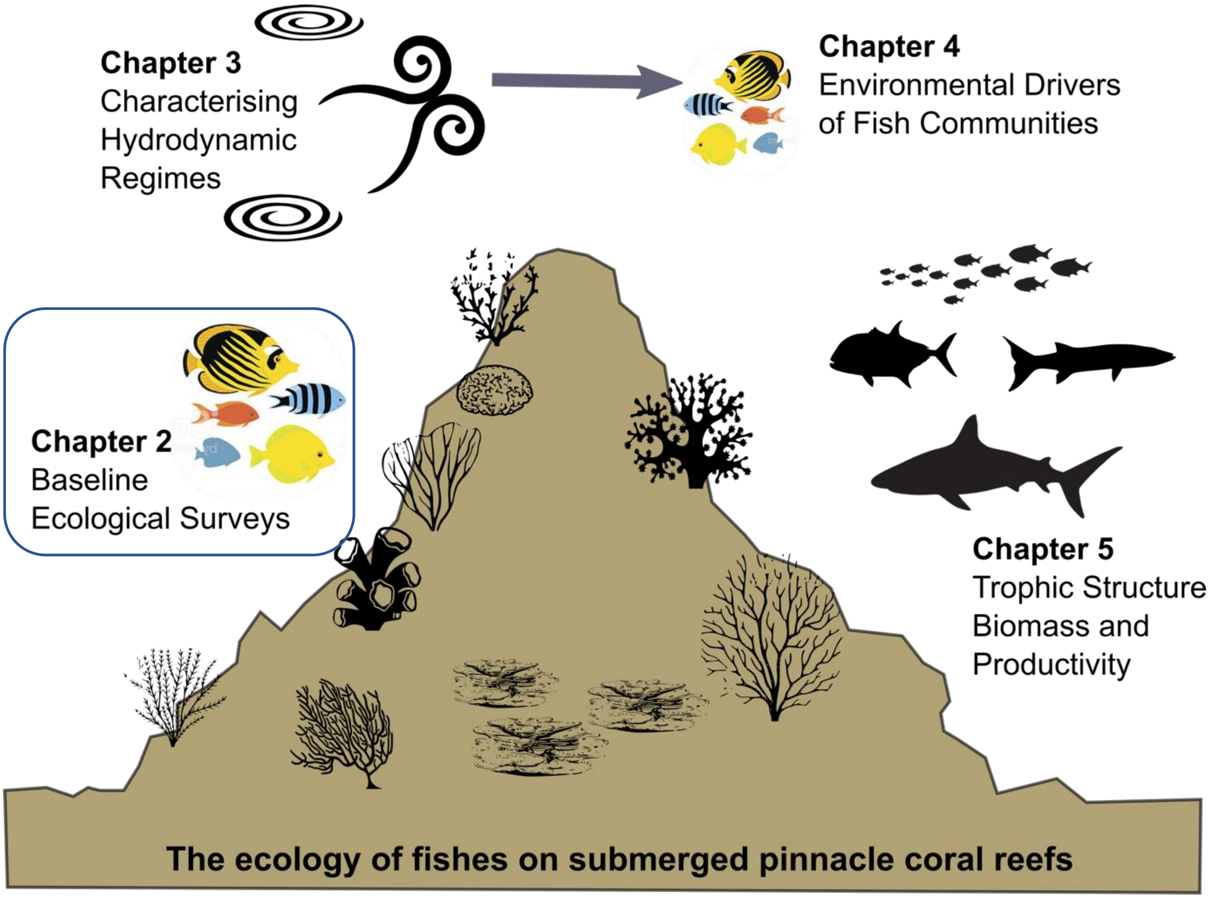
In **Chapter 2** I conducted baseline ecological surveys to test whether reef fish diversity, abundance and species richness differed between submerged pinnacles, nearshore emergent and offshore emergent reefs. I also conducted benthic surveys at the same reefs and used broad taxonomic groups and morphologies to assess elements of benthic habitat complexity; benthic richness, diversity and total hard coral cover. I then used these benthic metrics to explore basic relationships between fish diversity and habitat drivers that are well known to influence fish community structure.

In **Chapter 3** I tested the hypothesis that currents are important environmental features on submerged pinnacles and are distinct from those on emergent reefs. To characterise hydrodynamic regimes at each study reef I installed in-situ current meters to record current speed, direction and water temperature for a twelve-month period. I compared current and temperature profiles between the three reef habitat types and derived summary statistics including annual and monthly means, maxima and variability. Chapter 3 provided fine-scale environmental data from each reef site for use in subsequent chapters.

Chapter 4 combines hydrodynamic data from Chapter 3 with spatial and habitat-related variables known to strongly influence fish community structure. Using these data, I collated a set of 19 environmental variables and used Random Forest Regression Analysis to establish their relative importance as drivers of variability in reef fish biodiversity. Specifically I asked: do hydrodynamic variables override other well-known drivers of reef fish biodiversity at submerged depths of 20-30m? This chapter uses two sets of fish community surveys conducted within the 12-month period. The first surveys were the same as for Chapter 1 and the second set were conducted 6-months later. Both surveys were conducted using a stereo-video system to obtain length estimates and to calculate biomass. Biomass was then used together with fish abundance, species richness and diversity in the Random Forest analysis.

In **Chapter 5** I investigate whether the trophic structure of submerged pinnacles differs from emergent reefs at the same depth. This follows the hypothesis that, like seamounts, pinnacles will support top-heavy fish communities with high biomass and abundance at higher trophic levels. I also utilise two measures of reef fish productivity (standing biomass and fish biomass gained over time) to test the hypothesis that submerged pinnacles are highly productive reef habitats compared to emergent reefs at the same depth. Finally, I use environmental variables from Chapter 4 to examine drivers of biomass and productivity between reef habitat types and trophic groups. I investigate how environmental conditions shape reef fish trophic structure and what the implications for fisheries management on submerged pinnacles are in a changing global environment.

Chapter 2



Chapter 3
Characterising Hydrodynamic Regimes
Chapter 4
Environmental Drivers of Fish Communities
Chapter 2
Baseline Ecological Surveys
Chapter 5
Trophic Structure Biomass and Productivity
The ecology of fishes on submerged pinnacle coral reefs

Chapter 2: High diversity, abundance and distinct fish assemblages on submerged coral reef pinnacles compared to shallow emergent reefs

The content of this chapter has been published as:

Galbraith GF, Cresswell BJ, McCormick MI, Bridge TC and Jones GP (2021) High diversity, abundance and distinct fish assemblages on submerged coral reef pinnacles compared to shallow emergent reefs, *Coral Reefs,* 40 (2), 335-354

2.1 Abstract

Coral reefs exhibit consistent patterns in biodiversity across multiple spatial scales, from local to global clines in species richness, abundance and community structure. Knowledge of fundamental processes driving these patterns is largely derived from studies of shallow, emergent and nearshore reefs. Although research efforts are expanding to deeper mesophotic coral reef ecology, distinct and isolated reef morphologies like submerged pinnacles or seamounts have received scant attention. Despite being potentially important for connectivity and as refugia, the extent to which established patterns and processes in coral reef ecology apply to these systems is unknown. Here I examine the fish and benthic communities associated with coral reefs found on submerged pinnacles in Kimbe Bay, Papua New Guinea. Community structure and diversity metrics are compared with emergent reefs at the same depth in both near and offshore settings. I then explicitly test whether benthic complexity variables known to influence reef fish communities exhibit similar patterns at each reef type. Pinnacles were characterised by 3.70 times the mean fish abundance and 1.98 times the species richness recorded at the same depths on emergent reefs. Fish community structure showed distinct separation across reef morphologies, with pinnacles most similar to offshore reefs. Benthic habitat complexity did not vary across reef types while fish assemblages were weakly related to benthic habitat variables, with reef morphology the most consistent predictor of fish community metrics. The pinnacles in this study support high coral reef fish biodiversity despite their small habitat area and relative isolation by depth and offshore setting. My results suggest that habitat-specific environmental conditions are generated by the distinct geomorphology of pinnacles. As

coastal reefs become more increasingly disturbed, understanding ecological patterns on deep patch reef habitats like pinnacles will be useful to provide a more holistic understanding of coral reef seascapes and their resilience.

2.2 Introduction

Coral reefs encompass a range of diverse and complex habitat structures, including fringing reefs, barrier reefs, atolls and isolated patch reefs (Stoddart 1969; Hopley 2011). These recognisable reef types form under different environmental conditions of depth, distance offshore and exposure, and ecological patterns and processes vary in predictable ways along these environmental gradients (Hopley et al. 2007; Malcolm et al. 2010; Williams et al. 2015; Samoilys et al. 2019). The stability of different reef structures also varies, and predicting how these patterns and processes may respond to environmental change is now central to much coral reef science (Harvey et al. 2018; Williams et al. 2019). However, most research has been restricted to near-sea-surface, nearshore continuous reef systems, where accessibility has facilitated extensive global studies (Spalding and Grenfell 1997; Bellwood and Hughes 2001; Connolly et al. 2003; Hinderstein et al. 2010). There are significant areas of submerged habitat available for coral reef formation which have historically been overlooked, unexplored and remain understudied (Venn et al. 2009; Harris et al. 2013; Moura et al. 2016; Moore et al. 2017). Interest in these kinds of habitats has accelerated because of the potential for deep reefs to function as a refuge for species being adversely affected by reef degradation in shallow coastal waters (Bridge et al. 2013; Laverick et al. 2016; Macdonald et al. 2018).

Both the deep-sea and continental shelves possess a variety of distinct bathymetric features that can support rich and diverse coral reef ecosystems where the summits reach the euphotic zone (~0-150m) (Bridge et al. 2011b; Du Preez et al. 2016; Linklater et al. 2019). Global bathymetric mapping reveals large areas of deep habitat available for coral reef formation (Vora and Almeida 1990; Bridge et al. 2012; Harris et al. 2013). Submerged reefs can be defined as “isolated elevations of the seafloor, over which the depth of water is relatively shallow but sufficient for navigation (IHO 2008) and have their shallowest points below 10-20m (Thomas et al. 2015). They can support extensive, diverse coral and fish communities, which span both altiphotic (<30m) and mesophotic zones (30-150m) (Bridge et al. 2011a; Roberts et al. 2015; Moore et al. 2017; Cooper et al. 2019). Many deep reefs are likely to be more isolated from physical disturbances (e.g. storms, wave action), fishing pressure and thermally induced bleaching events than emergent near-sea-surface counterparts (Slattery et al. 2011; Lindfield et al. 2016; Baird et al. 2018; Crosbie et al. 2019).

Although most of the studies investigating the ecology and distribution of submerged coral reef ecosystems have occurred on Australia's Great Barrier Reef, submerged reefs constitute extensive areas of coral reef habitat across most low-latitude continental shelves of the globe (Locker et al. 2010; Abbey and Webster 2011; Pinheiro et al. 2015; Heyward et al. 2019). Pinnacle coral reefs are perhaps the most distinct submerged form and I define these as *abrupt, conical structures, either isolated or at the summit of a larger bathymetric feature such as ridges or banks that reach the euphotic zone, but do not breach the sea surface*. I make a distinction from seamounts, where pinnacles are more closely associated with continental shelves and slopes as opposed to deep oceanic sea-floor settings. Pinnacles tend to be comparatively smaller structures and unlike seamounts, are usually not formed directly by volcanic hotspots on the sea floor. They are often a part of larger geological features which have been submerged during periods of sea level rise and subsequent erosional processes. In ecological terms pinnacles and seamounts both however, provide a hard substratum for coral recruitment, forming isolated patch reefs in otherwise open pelagic systems (Veron and Done 1979; Rogers 2004; Koslow et al. 2016).

The geomorphological structure of coral reefs on small seamounts and pinnacles diverges from classical zonation models derived from emergent reefs. Summits are usually small in area with steep slopes and walls descending to considerable depths (>500m). They are comprised of only exposed crests surrounded by open waters, with no sheltered reef-flat or lagoon. Currents are often complex and strong as water passes around abrupt topographies (Genin et al. 1986; Boehlert 1988; Lavelle and Mohn 2010). On seamounts, resulting interactions between topography and hydrodynamics have been suggested to contribute to enhanced productivity within these habitats (Genin and Dower 2007; Richert et al. 2017). Studies from seamounts have shown that upwellings in particular are an important component of bio-physical coupling which supports high diversity and abundance of fishes, often from higher trophic levels (White et al. 2007; Letessier et al. 2019). Given the similarities in structure between seamounts and pinnacles, it seems likely that pinnacles are also highly influenced by upwellings and strong, deep-water currents. The extent of these effects and the potential for enahnced biophysical-coupling on pinnacles probably depends on their size and location within the seascape. Studies reporting high-productivity on seamounts connected with upwellings have mostly come from deep mid-ocean settings where these sites are exposed to large scale oceanographic processess.

Studies specifically focussed on coral reef pinnacles however, are scarce. In their absence and given the similarities in physical structure, paradigms from seamount ecology provide useful parallels to inform our ecological understanding of submerged pinnacles. Both shallow seamounts and pinnacles frequently host large aggregations of pelagic fish alongside demersal and reef-associated species (Genin 2004; Morato and Clark 2007; Jorgensen et al. 2016) generating hotspots of diversity in open ocean settings (Morato et al. 2010). Schooling mesopredators, highly-mobile apex predators and migrating megafauna also use seamounts as navigational way-points, and they are significant habitats for feeding, breeding and rest (Holland and Grubbs 2007; Litvinov 2007; Garrigue et al. 2015; Gargan et al. 2017; Letessier et al. 2019). For corals, clear, oligotrophic oceanic waters surrounding offshore reefs can enable complex coral habitat to extend to mesophotic depths (Baker et al. 2016; Roberts et al. 2019) concurrently expanding the range of suitable habitat for fishes (Thresher and Colin 1986; Kane and Tissot 2017).

Explanations of observed spatial variation in patterns of abundance, diversity and richness of reef fish communities often involve habitat variables, including substrate diversity, rugosity, vertical relief and live coral cover (Roberts and Ormond 1987; Hixon and Beets 1993; Munday 2000; Almany 2004; Gratwicke and Speight 2005). Although the nature of these fish-habitat relationships vary spatially, temporally and differ between trophic groups, live coral and habitat complexity remain fundamental drivers of reef fish abundance, richness and diversity (Caley and John 1996; Jones et al. 2004; Pratchett et al. 2008; Coker et al. 2014; Kerry and Bellwood 2015). However, depth associated physical gradients can lead to altered patterns in benthic community composition and habitat complexity (e.g., light, temperature) (Brokovich et al. 2006; Lesser et al. 2009; Roberts et al. 2015). For example, spatial heterogeneity is reduced at depth where coral morphologies tend be simpler in comparison to shallower depths (Kahng et al. 2012). Other benthic taxa, like sponges, macroalgae and octocorals can be more prominent (García-Hernández et al. 2018; Lesser and Slattery 2018) and complex morphologies may provide additional or alternative habitat for fishes at depth (Knudby et al. 2013; Kahng et al. 2017; Spalding et al. 2019). These differences in benthic community composition have been shown to strongly influence patterns of fish abundance and functional composition on submerged reefs (Brokovich et al. 2008; Pereira-Filho et al. 2011; Kane and Tissot 2017; Cooper et al. 2019).

The high diversity and productivity of pinnacles and shallow seamounts may enhance their potential to act as refuges from disturbance for some reef species (Bak et al. 2005; Bongaerts et al. 2017). In addition, the unique physical structures of pinnacles may generate further habitat-specific environmental conditions that confer resilience, however this is speculative because the ecological connections between deep and shallow reefs are largely unstudied (Slattery et al. 2011; Bongaerts and Smith 2019). Coral reefs on offshore pinnacles therefore represent physically and potentially ecologically distinct tropical habitats that are relatively accessible. Although research is now expanding significantly into submerged and mesophotic coral ecosystems, few studies aim to resolve fine-scale ecological patterns on these distinct bathymetric features. Characterising ecological communities on unexplored, deeper forms of coral reef will be critical to understanding their contribution to the maintenance of biodiversity within the wider seascape. Most coral reef systems are composed of mosaics of varied reef morphologies, but baseline knowledge is still required to understand ecological similarities and connectivity between varied forms of emergent and submerged reefs, as well as to inform effective spatial conservation planning.

Here I provide the first detailed assessment of fish and benthic communities on a series of submerged coral pinnacles in Kimbe Bay, Papua New Guinea, an area renowned in the diving industry for pinnacle diving. To determine whether pinnacles are hotspots for biodiversity I compare fish and benthic communities on pinnacles to emergent reefs in both nearshore and offshore locations. I then examine whether typical drivers of fish diversity, abundance, species richness and community structure apply to pinnacles. Kimbe Bay lies in the Coral Triangle, one of the world's most diverse coral reef regions, but the distribution and abundance of species inhabiting coral reef pinnacles in this area are currently unquantified. Specifically, the aims of this study were to: 1. Describe benthic communities and quantify habitat complexity based on total hard coral cover, benthic cover type richness and benthic diversity across reef morphologies. I predicted that pinnacles and offshore reefs would have highest percentage cover of hard coral at the depths surveyed (20-30m), due to clearer offshore waters and lower terrestrial influence. These factors may also enhance benthic richness and diversity at offshore sites. 2. Characterise fish communities found on offshore submerged pinnacle reefs and compare them to emergent reef morphologies. I expected that abundance would be high given the aggregating properties of physical structures for fishes, but that diversity and species richness may be lower given the relative isolation of pinnacles as small patch habitats. 3. Examine how fish-benthic relationships differ between reef morphologies, specifically the effect of total hard coral cover and benthic diversity on fish diversity, abundance, richness and species evenness. I hypothesised that established relationships between benthic habitats would be evident at all reef habitats, especially where coral cover is highest at offshore locations.

2.3 Methods

2.3.1 Study site and survey design

This study took place during October 2018 in Kimbe Bay (5°30'S, 150°05'E, Fig. 2.1), Papua New Guinea, an area with a diverse bathymetry including emergent reefs and submerged pinnacles. The study incorporated a total of 12 reefs: 4 nearshore emergent reefs, 4 offshore emergent reefs and 4 offshore submerged pinnacle reefs. Nearshore reefs were defined as those <5km from nearest main landmass and offshore reefs were all between 9-25km from nearest main landmass. The distinction between emergent and submerged morphology was made based on crest depth, where crests above 10m were considered emergent and those below 10m submerged since pinnacles deeper than 10 m are unlikely to ever experience breaking waves (Harris et al. 2013; Thomas et al. 2015). The pinnacles in my study rise to within 15-30m of the sea surface from a deep (c.300m, GEBCO 2019) submerged ring central to the bay. The centre of this ring descends to around 600m in the middle of the bay but on the seaward side drops to >1000m on the shelf of the South Bismarck Plate (Fig. 2.1a and b). Offshore emergent reefs in Kimbe Bay are also extensions of this submerged central ridge system but reach the upper 0-10m. Many take the form of shallow flat-topped guyots, which also have steep sides and ridges descending to considerable depths. Nearshore emergent sites are gently sloping with hard coral cover down to around 70m (author pers. obs; Longenecker et al. 2019). All surveys were carried out within a 20-30m depth band. For emergent reefs, sites with substantial deep horizontal ridges or low gradient slopes were selected for the study to account for aspect. Surveys on walls or steep slopes were avoided. Although I control for aspect as much as feasibly possible, ecological assemblages vary considerably between reef zones. How these changes manifest between zones on different reef morphologies at different depths is the subject of another manuscript currently in preparation.

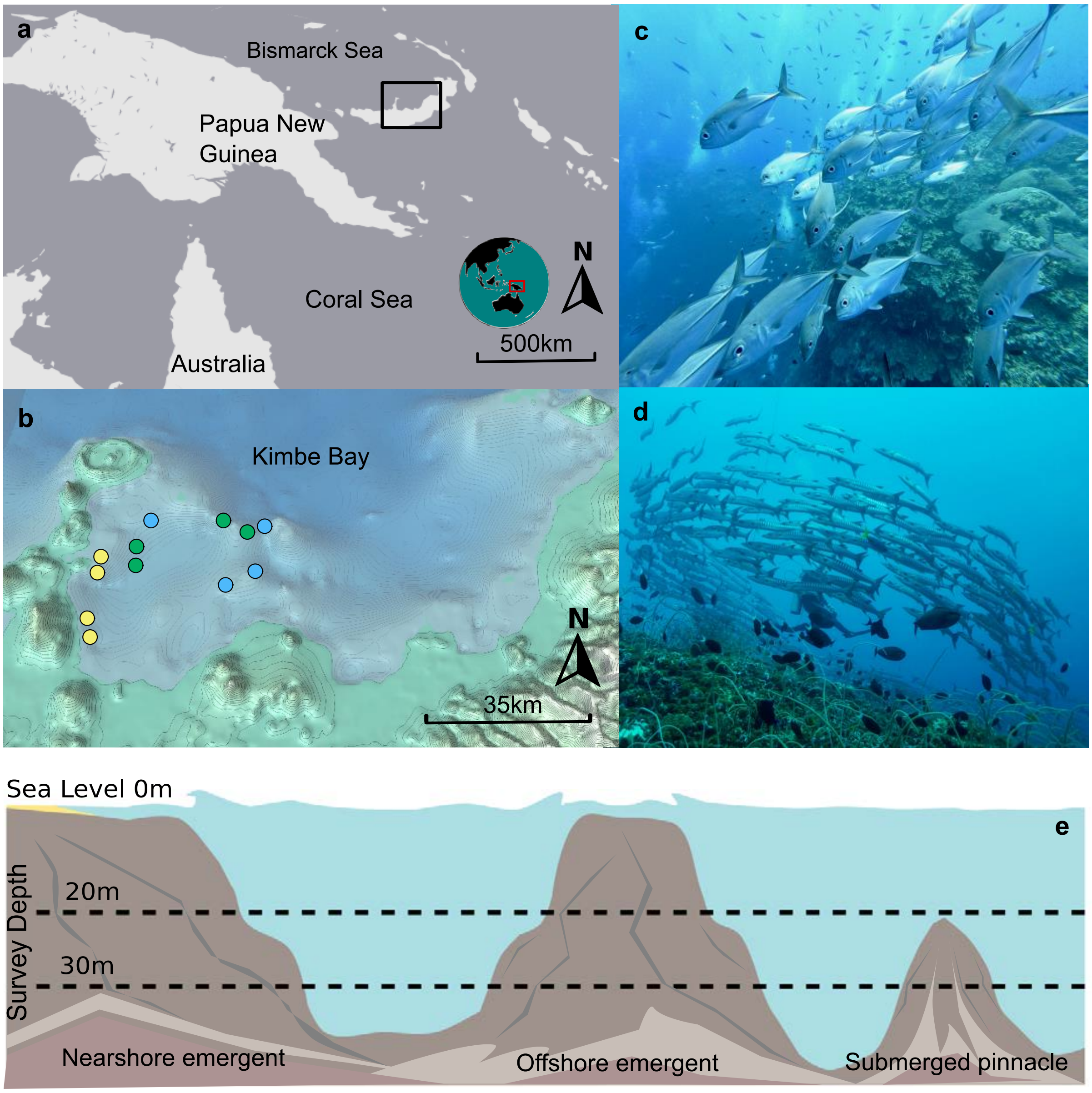


Figure 2.1 Study area locations, Kimbe Bay, Papua New Guinea **(a)** Papua New Guinea and Kimbe Bay **(b)** Kimbe Bay bathymetry with location of pinnacle (green), offshore (blue) and nearshore (yellow) reefs **(c)** Schools of *Caranx sexfasciatus* at Joelles Reef (pinnacle) **(d)** *Sphyraena qenie* at Bradford Shoals (pinnacle) **(e)** Schematic of reef morphologies surveyed.

2.3.2 Data collection

Fish and benthic video surveys

Fish and benthic surveys were conducted along 30m x 5m high-definition (HD) stereo-video transects within a depth band of 20-30m. 5 transects were conducted at each site which was primarily dictated by the small size of the pinnacles. Broadly, stereo-video methods followed standard operating procedures outlined in Goetez et al. 2019. Briefly, a diver-operated stereo-video system (SeaGIS) housing two GoPro Hero-4 cameras was held horizontally to the benthos, facing forwards as the diver swam the transect maintaining a depth of 0.5m above the reef. A second diver followed with a tape reel and indicated to the first diver when 30m was reached, who ended the transect. Both divers returned along the reel conducting a video point-intercept transect using another GoPro Hero-4 held at 0.5m above the reef pointing directly downward.

Benthic video PIT analysis

The HD-video footage was replayed at a low frame rate and the benthos immediately underneath each point along the transect (60 points/30m) identified and placed into one of 47 groups (Appendix A Table S2.11). These 47 groups were used to calculate benthic diversity (H'), benthic richness and total hard coral cover. Benthic habitat diversity, habitat heterogeneity and amount of hard coral cover are established factors determining community composition and organisation of coral reef fishes (Bell and Galzin 1984; Messmer et al. 2011; Komyakova et al. 2013).

From these 47 fine-scale categories I derived 14 broader categories of benthic cover type, which have been shown to influence fish (Appendix A Table S2.11). These 14 groups were; massive and sub-massive coral, encrusting coral, laminar coral, complex coral, algae, coralline crustose algae (CCA), soft corals and octocorals, encrusting Porifera, complex Porifera, other hexacorals, coral rubble, sand and silt, rock and reef matrix. I chose these groups based on similar submerged reef studies on the GBR (Macdonald et al. 2016; Cooper et al. 2019), but as reefs in Kimbe Bay possess a conspicuous abundance of morphologically distinct sponges and other forms of hexacorallia and octocorallia (Horowitz et al. 2020) I also included complex porifera, encrusting porifera and other hexacorals.

Fish video transect analysis

Fish transect videos were analysed in the software EventMeasure Stereo (SeaGIS, https://www.seagis.com.au/bundle.html) which, together with the calibration of the cameras provides a known field-of-view (2.5m either side of the transect). Every individual fish that entered the lower two thirds of the screen was counted and identified to species based on Allen et al. (2003). Only individuals that were readily observable within these parameters were recorded i.e. not obscured by the benthos or within crevices.

2.3.3 Statistical analysis

All analysis was performed in R (R Core Development Team 2021) and all plots produced using the packages ggplot2 (Wickham 2016) and ggvegan (Simpson 2019).

Fish and benthic assemblages

Differences in the composition of reef fish assemblages among reef morphologies were explored visually using non-metric multidimensional scaling (nMDS) to examine broad patterns in community structure. For both fish and benthic community data, species abundances were transformed using the Hellinger method to reduce the influence of highly abundant taxa (Legendre and Gallagher 2001) and used in a Bray-Curtis dissimilarity matrix which does not increase similarity between two samples when a common species absence occurs (Clarke 1993; Anderson 2001). To explore species driving the nMDS, species scores were extracted and plotted as vectors for both fish and benthic data using the function ‘envfit’ in the vegan package (Oksanen et al. 2019). Species or benthic groups with the strongest correlation were plotted, where the direction and strength of the gradient is indicated by arrows.

To test for differences in fish and benthic assemblages between reef morphologies, a one-way permutation-based multivariate ANOVA (PERMANOVA) was performed with the same data using the function “adonis” in vegan. Post-hoc tests were then conducted to identify significant between-group differences identified by the PERMANOVA using “emmeans” (Lenth 2019). For each analysis 9999 permutations were performed to calculate p values. Although generally considered robust to heterogeneity in data sets, PERMANOVA tests between-group variation where a significant result can either suggest differences in location of centroids between groups or, that average within-group dispersion is not equal (Anderson and Walsh 2013). PERMDISP is a resemblance-based permutation test focused strictly on the null hypothesis of homogeneity of multivariate dispersions (Anderson 2006) and was used to test the hypothesis of equal within group dispersion. This test can additionally provide insights into within group variation. The function “betadisp” in vegan was used to perform the PERMDISP test for all PERMANOVAs. The SIMPER routine (Clarke and Warwick 2001) was then used to identify species and benthic variables contributing the most dissimilarity among reef types using the “simper” function in vegan.

Fish biodiversity and benthic complexity

Differences in mean fish species richness, total fish abundance (individuals/150m^2), fish diversity (Simpson diversity), evenness (Pielou’s J’), benthic richness and benthic diversity (H’) were identified using Generalised Linear Models (GLMs) with reef morphology as the categorical explanatory factor. Standard exploratory techniques were used to assess appropriate error structures to apply to each GLM. Benthic diversity, total hard coral, fish evenness and fish diversity were analysed with Gaussian error distribution and identity link. Fish richness, abundance and benthic richness were all analysed using GLMs with negative binomial error distributions and log link (Tables S1,S2). Differences between reef morphologies of mean percentage cover of the 14 benthic cover categories were also tested using GLMs. GLMs were mainly fitted using negative-binomial error distributions with a log link but where certain categories were found to be zero-inflated, a zero-inflated negative-binomial (ZINB) error distribution was used (Appendix A Table S2.6). For all GLMs, model fits were evaluated using residual plots and performed using the packages lme4 and MASS (Venables and Ripley 2002; Bates et al. 2015). Differences between means at each reef habitat type were tested using Wald Chi square or F tests and Tukey’s HSD post-hoc pair-wise tests conducted using the package “emmeans” (Lenth 2019).

Fish-benthic relationships

To explicitly examine the nature and strength of relationships between fish and two metrics of benthic habitat complexity (benthic diversity and total hard coral) I used mixed-effects models using the R package lme4. I only examined the effects of these two habitat complexity metrics because benthic richness was highly correlated with benthic diversity and several other benthic cover categories. The effect of total percentage hard coral and benthic diversity on fish richness, diversity, evenness and abundance were tested in 8 separate models with either Negative Binomial (abundance and richness GLMMs) or Gaussian (diversity and evenness LMMs) error distribution. For all models the main effect was either total hard coral percentage or benthic diversity, with “reef type” as a fixed effect. An interaction term between the main effect and “reef type” was included in each model to test whether the nature of any relationship varied between reef morphologies. Site was included as a random factor nested within reef type. Likelihood ratio tests with a null model were used to determine model fits and overall goodness-of-fit of all models was assessed via the standard techniques of Q-Q plots (normality), residuals plotted against predicted values against all explanatory variables (homogeneity of variance) and calculations of dispersion. Pseudo-R-Square estimates were obtained for all mixed-effects models using r.squaredGLMM from the MuMIn package (Bartoń 2019) based on Nakagawa and Schielzeth (2013) and Nakagawa et al. (2017). This produces a marginal $R^2_{GLMM(m)}$ (an approximation variance explained by fixed effects) and a conditional $R^2_{GLMM(c)}$ (an approximation of variance explained by the entire model including fixed and random effects). Estimates and 95% confidence intervals for each models’ effects were calculated where the evidence does not support a significant effect at the 0.05 level if the confidence interval contains zero. Tests of fixed factor effects were conducted using likelihood-ratio tests for GLMMs and conditional F-tests with Kenward-Roger correction for LMMs using the “Anova” function in “car” (Fox and Weisberg 2019) and “anova’ from R (R Core Development Team, 2020). Correlation analysis and simple slopes tests using “emmeans” were performed to explore the nature and strength of relationships.

Finally, distance based multiple linear modeling was used to examine the multivariate relationship between differences in fish communities and benthic habitat to find the combination of benthic variables that best explained the greatest variation in fish community structure. Benthic variables included all 14 benthic categories, benthic diversity and benthic richness. Multicollinearity was explored between all benthic variables using Spearman's rank correlation. Benthic diversity and benthic richness were highly corelated (Spearman's rho, ρ = 0.78, $p < 0.001$). As benthic richness was also correlated with complex hexacorals (ρ = 0.48, p = 0.001) it was removed prior to model fitting.

The function "ordiR2step" in vegan was then used to conduct stepwise forward selection based on the Aikaike Information Criterion (AIC) (Akaike et al. 1973) of variables from all 14 benthic categories as well as benthic diversity. The stepwise routine was run using 9999 permutations and adjusted R^2 as the selection criterion (Blanchet, Legendre and Borcard 2008). Each model proposed by ordiR2step was tested for significance using vegan's permutational ANOVA function (Monte Carlo permutation test) and only constraints with $p < 0.05$ after adjustment for multiple testing selected for the final model. The most suitable model to explain the relationship between benthic cover types and variation in fish assemblages between reef habitat types was then visualized by constrained ordination using distance-based redundancy analysis (db-RDA) (Anderson et al. 2008). db-RDA can be used when the response data are available as a dissimilarity matrix and provides an opportunity to use ecological distances in constrained ordination analysis (Paliy and Shankar 2016). Benthic variables from the final model were overlaid as a vector, together with fish species that were most correlated with assemblage variation.

2.4 Results

2.4.1 Benthic communities show similar complexity between reef types

I found no significant difference in any of the benthic complexity metrics between reef morphologies; benthic diversity (GLM, F = 1.13, p = 0.33), benthic richness (GLM NB, $\boxed{\text{c}}2$ = 1.58, p = 0.45) or total hard coral (GLM, F = 0.96, p = 0.39) (Fig. 2.2, Appendix A Table S2.2). Pinnacle reefs however, showed the greatest range in both benthic diversity (1.94 – 2.52) and benthic richness (12.20-17.41) compared to offshore (benthic diversity = 2.12-2.23, benthic richness = 12.40-13.80) and nearshore emergent reefs (benthic diversity = 2.03-2.31, benthic richness = 12.60-14.00) suggesting high variability between individual pinnacle sites (Appendix A Table S2.5).

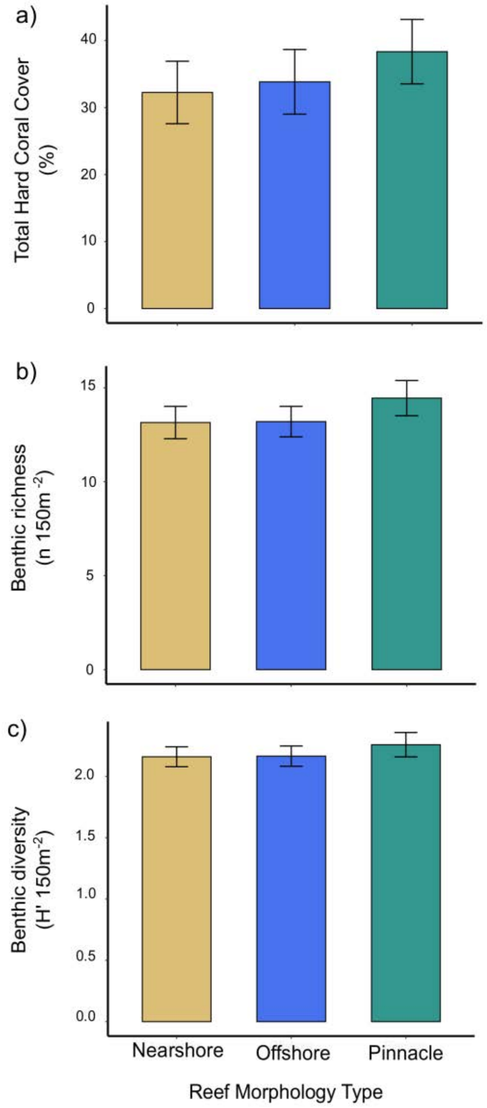


Figure 2.2 Mean ± SE of three benthic complexity metrics for each reef morphologies **(a)** total hard coral cover % **(b)** richness of benthic cover types **(c)** diversity of benthic cover types.

Of the 14 benthic cover types, 8 showed significant differences in mean percentage cover between reef morphologies (Fig. 2.3, Appendix A Table S2.6).

Pinnacle reefs were characterised by highest mean percent cover of complex hard corals, massive and sub-massive hard corals, encrusting hexacorals and octocorals. Offshore reefs had the lowest mean percent cover of complex hard corals, but high proportions of laminar hard corals and encrusting porifera. Nearshore reefs were notably high in algae. Benthic communities were similar to each other ranging between 34-40% dissimilarity (Table 2.1). The highest overall dissimilarity was between pinnacle and nearshore reefs (40%). Benthic cover types contributing the most to overall dissimilarity were algae, complex hard coral, encrusting hexacoral, rubble and massive hard coral (Table 2.1).

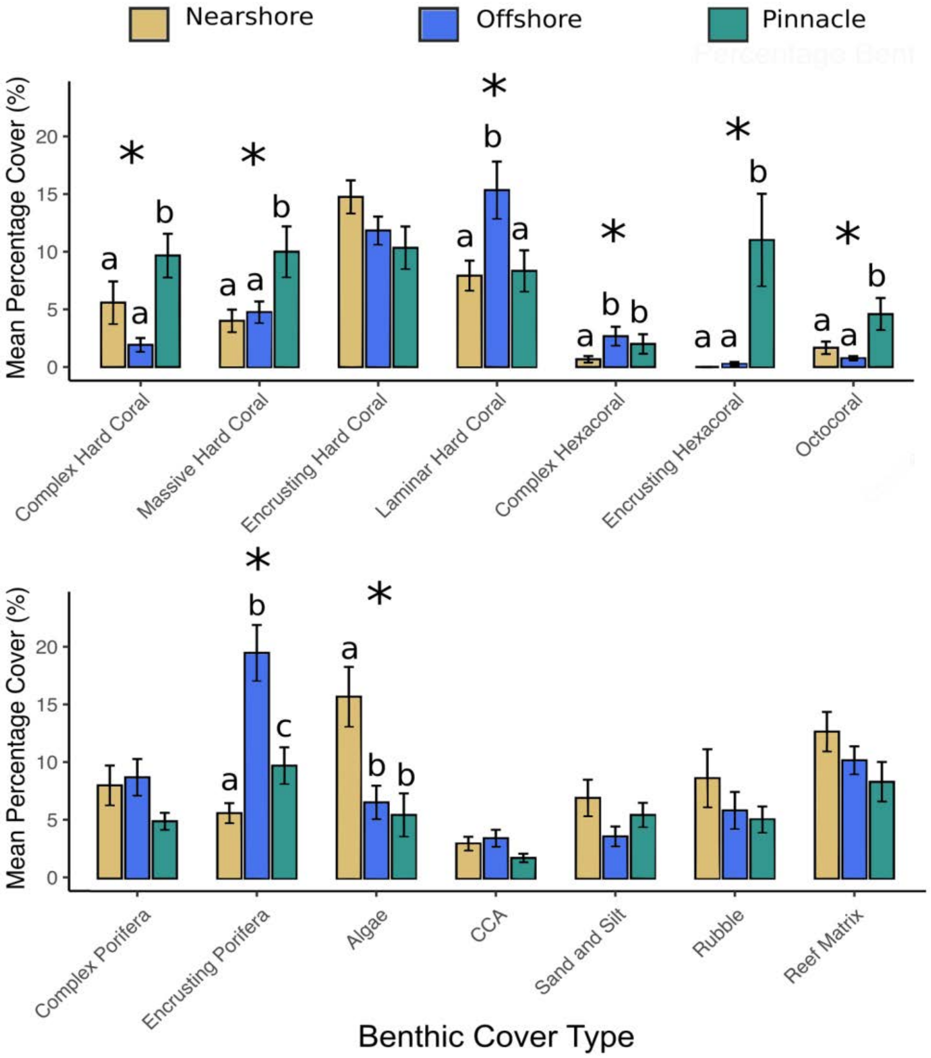


Figure 2.3 Differences in mean percent cover per transect ± SE of 14 benthic cover types across the three reef habitat types (n=20 per reef morphology). Significant differences are represented by * ($p < 0.05$, GLM); Letters indicate statistically similar pairwise means ($p < 0.05$, Tukey HSD). Full GLMs results Appendix A Table S2.6.

Table 2.1 Summary of SIMPER results showing top five fish species and benthic cover categories that contributed most to overall dissimilarity between assemblages for pair-wise comparisons between reef type.

Species **Reef Type Contrast**	**% Contribution**	**Mean Abundance/150m^2**		**Benthic Habitat** **Reef Type Contrast**	**% Contribution**	**Mean percentage cover**	
Pinnacle - Offshore Overall Dissimilarity 74.5%		Pinnacle	Offshore	**Pinnacle - Offshore** Overall Dissimilarity 38%		Pinnacle	Offshore
Pseudanthias tuka	6.84	32.40	51.85	Complex Hard Coral	9.54	9.67	1.92
Caesio cuning	6.08	8.70	28.95	Encrusting Hexacoral	9.32	11.0	0.25
Acanthurus thompsoni	5.63	72.60	11.45	Laminar Hard Coral	9.15	8.33	15.33
Pterocaesio tile	2.95	11.60	14.85	Algae	8.94	5.92	7.08
Chromis amboinensis	2.77	8.40	4.90	Encrusting Porifera	7.77	10.5	21.0
Pinnacle - Nearshore Overall Dissimilarity 87.8%		Pinnacle	Nearshore	**Pinnacle - Nearshore** Overall Dissimilarity 40%		Pinnacle	Nearshore
Acanthurus thompsoni	5.70	72.60	4.75	Algae	12.15	5.92	16.92
Pomacentrus nigromanus	5.48	0.00	7.60	Complex Hard Coral	9.16	9.67	5.58
Pseudanthias tuka	4.08	32.40	4.95	Encrusting Hexacoral	9.04	11.0	0
Caesio cuning	3.35	8.70	9.00	Rubble	8.44	5.5	9.33
Ctenochaetus tominiensis	3.09	0.45	3.00	Massive Hard Coral	8.33	10.0	4.00
Offshore - Nearshore Overall Dissimilarity 79.5%		Offshore	Nearshore	**Offshore - Nearshore** Overall Dissimilarity 34%		Offshore	Nearshore
Pseudanthias tuka	9.05	51.85	4.95	Algae	11.99	7.08	16.92
Caesio cuning	6.86	28.95	9.00	Encrusting Porifera	11.01	21.0	6.08
Pomacentrus nigromanus	6.53	3.00	2.60	Rubble	9.64	6.33	9.33
Acanthurus thompsoni	3.86	11.45	4.75	Sand & Silt	8.69	3.91	7.50
Chrysiptera anarzae	3.09	1.05	2.30	Laminar Hard Coral	8.41	15.33	7.90

PERMANOVA indicated significant differences in benthic community assemblages among reef types (Pseudo-F = 4.74, 9999 permutations, p(perm) = 0.001), but the PERMDISP test also yielded a significant result (F = 4.16, p = 0.02). As with the fish communities this suggests unequal within-group dispersion. Benthic communities showed less clear separation between reef morphologies as fish but, there were still distinct groupings (Fig. 2.4a). Notably, five centroids attributable to the same pinnacle site (Kimbe Bommie) were clearly separated from other pinnacle centroids. Massive hard coral, encrusting hexacoral and laminar hard coral were more associated with pinnacle reefs whereas complex hexacorals, complex porifera and encrusting porifera were more associated with nearshore and offshore sites (Fig. 2.4b).

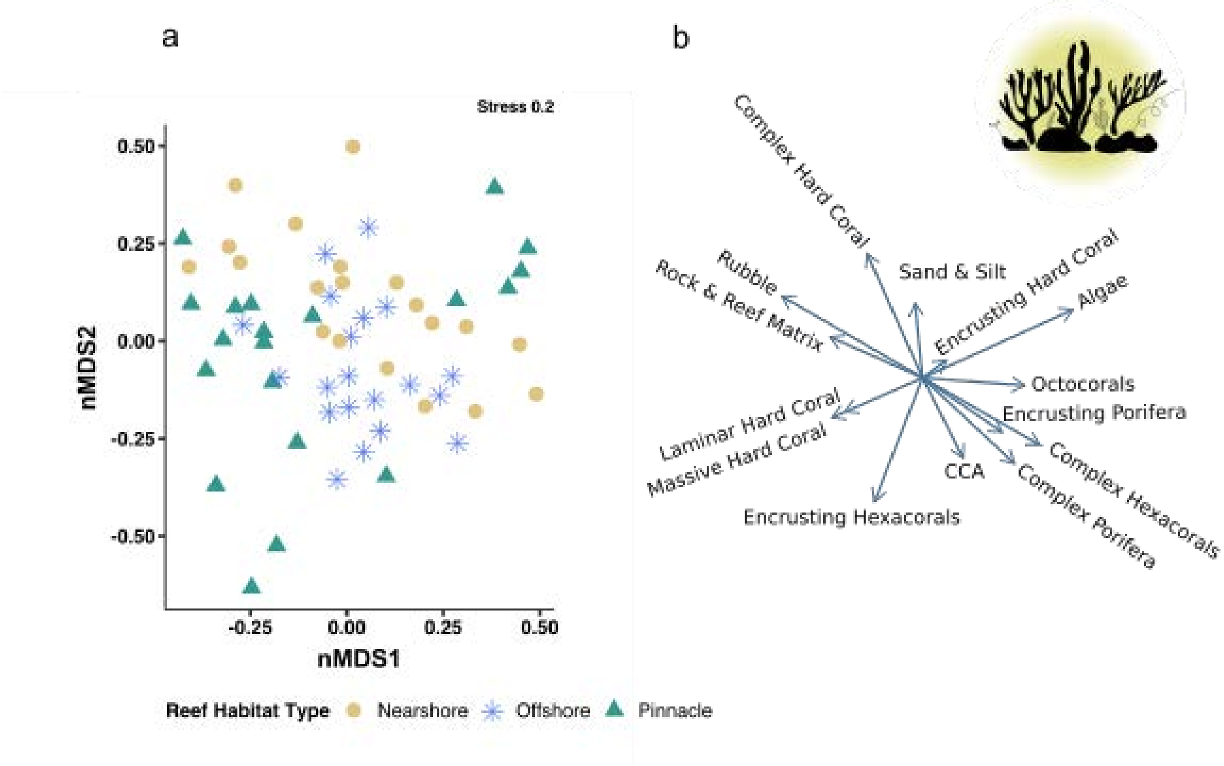


Figure 2.4 (a) nMDS of benthic communities aggregated by reef morphology **(b)** Vector plot showing strength and direction of relationship between benthic category and nMDS axes.

2.4.2 Reef fish biodiversity and assemblages differ between reef types

A total of 11,460 individual fishes representing 230 species and 87 genera were recorded across all transects from the 12 reefs. Pinnacles had the highest number of species recorded (172) across all transects and also the highest number of unique species (75). The numerous unique species included many larger predatory species including *Pinjalo lewisi*, *Caranx melampygus*, *Caranx sexfasicatus*, *Carcharhinus amblyrhynchos* and *Carcharinus melanopterus* that were not observed on emergent reefs (Appendix A Table S2.3). Offshore emergent reefs had the lowest total number of species recorded (87) and also only 3 unique species. Of the total 230 species observed across all reef types, only 47 (20.5%) were shared by all three (Fig. 2.5).

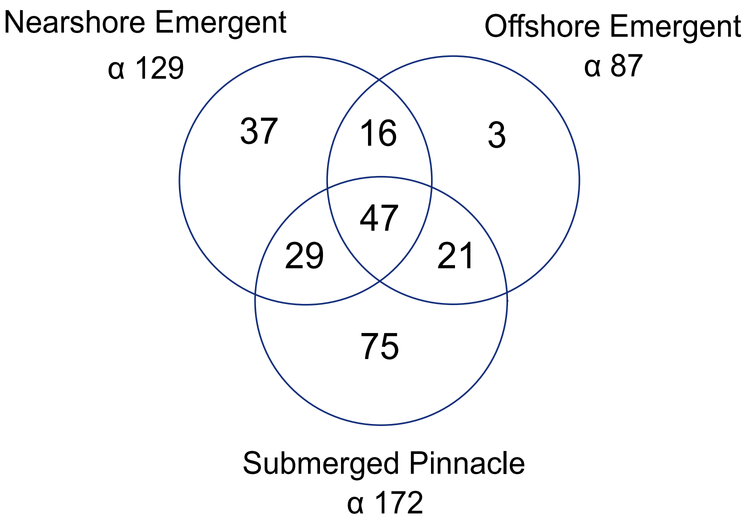


Figure 2.5 Alpha and beta diversity for each reef morphology. Number of unique species at each reef type are located in sectors of circles with no overlap.

The pinnacles in my study supported almost twice the mean number of fish species per unit area (32.45) as near (16.35) and offshore reefs (16.50) (Fig. 2.6; GLM, χ2 = 67.23, p < 0.001). I also found a clear increasing trend in fish abundance from nearshore to offshore reefs, culminating in three times observed total abundance on the pinnacles (GLM, χ2 = 67.67, p < 0.001). High variation in abundance on pinnacles was due to large schools of *Sphraena qeini* and *Acanthurus thompsoni* recorded in several transects at multiple sites, similarly, large schools of *Caesio* sp. drove higher abundance on offshore sites compared to nearshore reefs. Consequently, species evenness showed significant differences across reef morphologies (GLM, χ2 = 14.97, p < 0.001). Simpson's diversity was highest on nearshore reefs (0.81) and lowest on offshore reefs (0.72), but differences were not significant between the reef morphologies (GLM, χ2 = 5.10, p = 0.07) (Fig. 2.6, Appendix A Table S2.1).

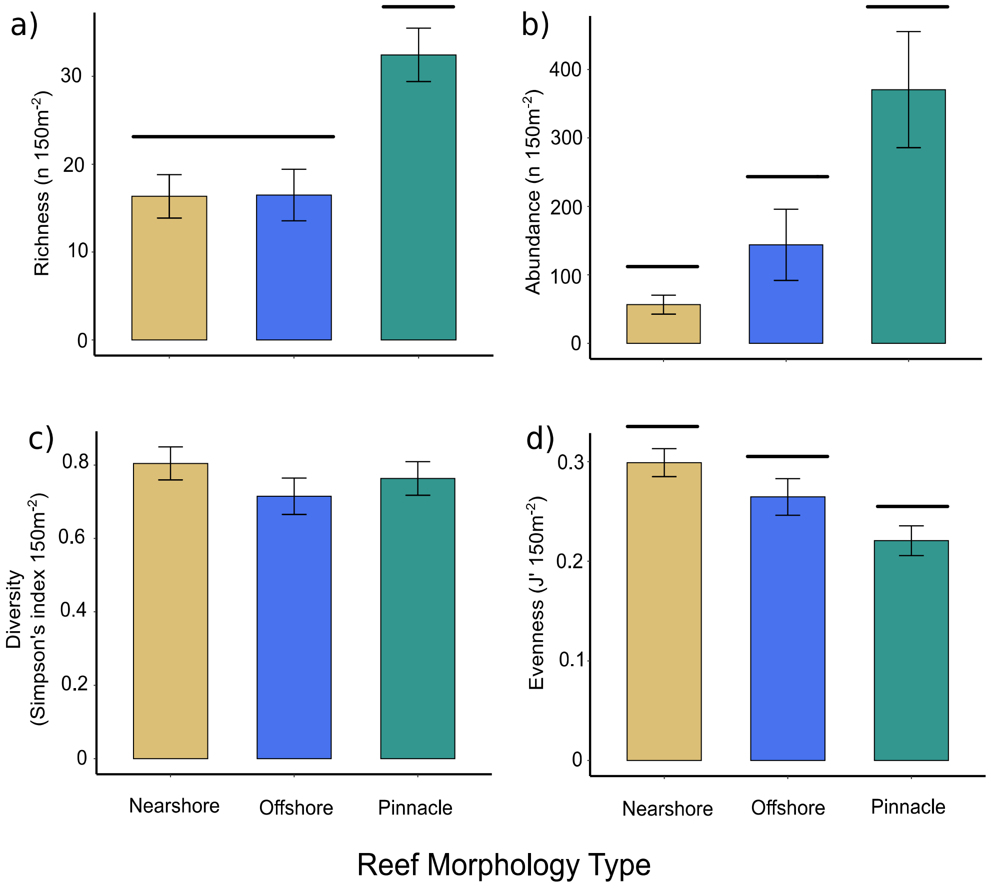


Figure 2.6 Differences in fish community metrics between reef morphologies. Mean per 150m2 transect ± SE bars **(a)** fish species richness **(b)** Total abundance of individuals **(c)** Simpson's diversity **(d)** Community evenness Pielou's J'. Significant differences for GLMs (p < 0.05) and pair-wise differences (p < 0.05, Tukey HSD) are indicated by grouping lines above. Further information Appendix A Tables S2.1 and S2.5.

The local structure of fish assemblages was clearly distinct between reef types (PERMANOVA; pseudo-F = 8.67, 9999 permutations, p (perm) = 0.001). Pinnacle reef sites showed distinct clustering with little to no overlap with offshore and nearshore emergent reefs (Fig. 2.7a). The species composition of pinnacles was most similar to offshore emergent reefs and most distinct from Inshore emergent reefs. The species most strongly aligned with pinnacle reefs included two mesopredators (*Macolor macularis* and *Caranx melampygus*) as well as several species of schooling planktivores (*Hemitaurichthys polylepis, Acanthurus thompsoni, Dascyllus trimaculatus* and *Acanthurus nubilis*) (Fig. 2.7b). Species most correlated with nearshore sites included several small pomacentrids (*Chrysiptera rollandi, Pomacentrus nigromanus, Chrysiptera arnazae, Neoglyphidodon nigrorus)* and two labrid species (*Halichoeres cholopterus* and *Oxycheilinus celebicus*). Offshore reefs showed some distinct clustering of centroids but showed a more variable ordination pattern than pinnacle sites and also had more overlap with nearshore sites (Fig. 2.7a).

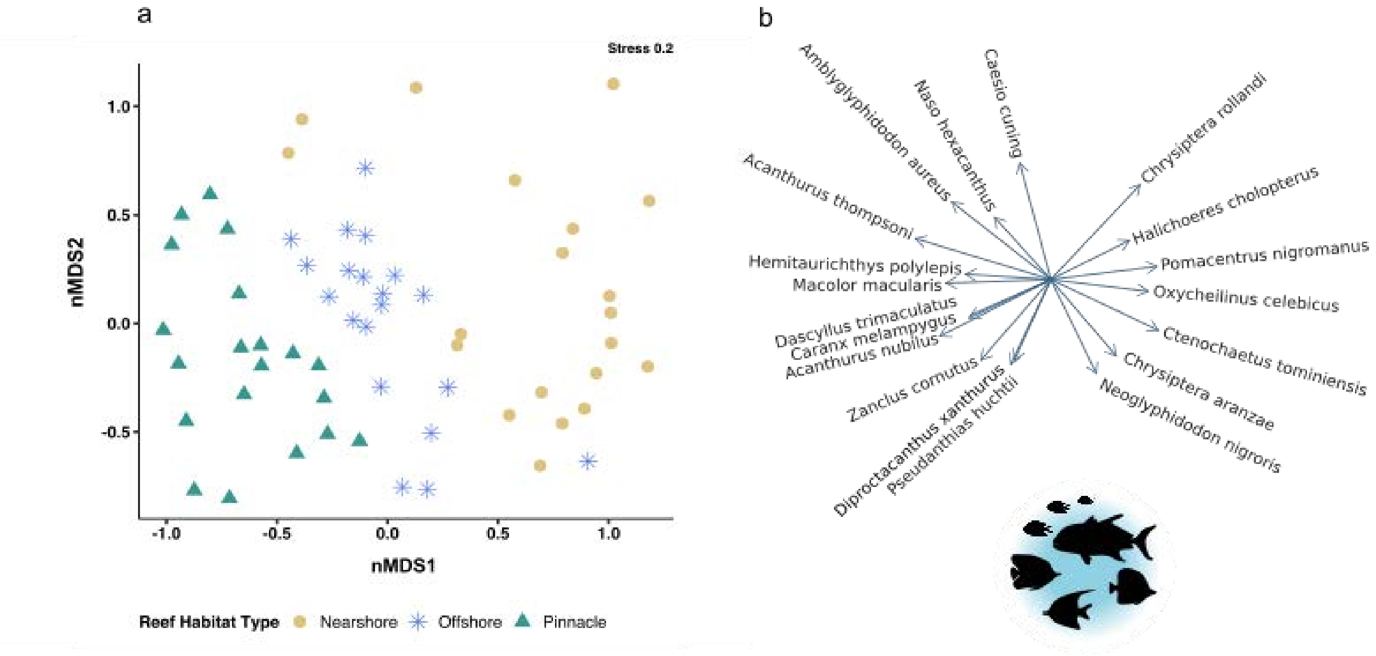


Figure 2.7 (a) nMDS of fish communities aggregated by reef morphology **(b)** Vector plot showing the strength and direction of relationship between fish species and nMDS axes.

Although the result of the PERMANOVA indicated distinct fish assemblages on the different reef types, the result of the PERMDISP test (F = 3.97, p = 0.02, Appendix A Table S2.2a) suggests that there is also unequal within-group dispersion. Notably, nearshore reefs showed more variable assemblage structure than offshore or pinnacle reefs (Fig. 2.7a). Unlike benthic communities, fish communities showed high dissimilarity between all reef types ranging between 74.5-87.8% (Table 2.1). The combination of species contributing most to these differences consistently included *Pseudanthias tuka, Caesio cuning, Acanthurus thompsoni, Pomacentrus nigromanus* and *Ctenochaetus tominiensis.* These were the important contributors to dissimilarity between pinnacle and nearshore reefs. The only different species to appear in the top five overall contributors to community dissimilarity between nearshore and offshore reefs was *Chrysiptera anarzae* (Table 2.1).

2.4.3 Fish-habitat relationships – weak associations at all reef types

"Reef type" had a significant effect on fish abundance and richness in models for total hard coral cover (LRT abundance; p = 0.002, richness; p = 0.002) and benthic diversity (abundance p = 0.003, richness; p = <0.001) but had no effect on fish diversity or evenness in any of the models (Table 2.2). Neither benthic diversity nor total hard coral cover had a significant effect on any fish metric across all 8 models, nor was there any significant interaction between independent variables (Fig. 2.8, Table 2.2, Appendix A Table S2.9 for estimate coefficients and confidence intervals). Offshore reefs did however show some moderate positive correlation between benthic diversity and fish diversity (ρ = 0.30, p =0.20), whereas pinnacle and nearshore reefs showed weak negative relationships (pinnacles; ρ = -0.07, p =0.76; nearshore (ρ = -0.13, p =0.57). None of the relationships however, were significant ($p<0.05$).

Table 2.2 Analysis of deviance or variance tables for main effects in all fish-benthic mixed effects models. For GLMMs (total fish abundance and species richness), Likelihood-ratio tests were used to test main effects. For LMMs (diversity and evenness) Wald-F tests with Kenward-Rogers df were used. All main effects and interactions (“:”) are shown. Significant results ($p < 0.05$) in bold.

		Total Abundance/150m^2		**Simpson Diversity**		**Species richness**		**Species evenness**	
Variable	Df	**LRT**	***p*-value**	***F***	***p*-value**	**LRT**	***p*-value**	***F***	***p*-value**
Total Hard Coral %	2	0.81	0.37	1.94	0.17	2.35	0.13	0.42	0.52
Reef Type	**1**	**49.58**	**<0.001**	1.69	0.20	**65.50**	**<0.001**	1.11	0.34
Total Hard Coral: Reef Type	1	2.35	0.31	1.42	0.25	2.19	0.33	1.11	0.34
Benthic Diversity (H’)	2	1.25	0.26	0.11	0.74	0.03	0.85	0.19	0.67
Reef Type	**1**	**28.87**	**<0.001**	0.95	0.40	**65.54**	**<0.001**	0.17	0.84
Benthic Diversity: Reef Type	*1*	*5.03*	*0.08*	1.21	0.31	1.03	0.60	0.19	0.83

Other contrasting patterns included a negative relationship between abundance and hard coral cover on pinnacle reefs (ρ = -0.42, p = 0.07), whereas nearshore reefs showed a weak positive trend (ρ = 0.32, p = 0.16) and there was no correlation between fish abundance and hard coral cover on offshore reefs (ρ = -0.03, p = 0.89). Benthic diversity and fish diversity showed a moderate negative association at offshore reefs (ρ = -0.29, p = 0.22), but was moderately positive on pinnacles (ρ = 0.07, p = 0.78 and nearshore reefs (ρ = 0.29, p = 0.22). Again, however, none of these contrasting relationships were significant. Benthic diversity and hard coral cover had reasonable explanatory power in respective models for fish richness and abundance with $R^2_{(m)}$ ranging between 52-54%. Fish diversity and evenness however, were poorly predicted by either benthic diversity or hard coral cover in combination with reef type with $R^2_{(m)}$ ranging between 7-13%. See Appendix A, tables S2.8 and S2.9 for model summaries and Spearman's rank correlation coefficients.

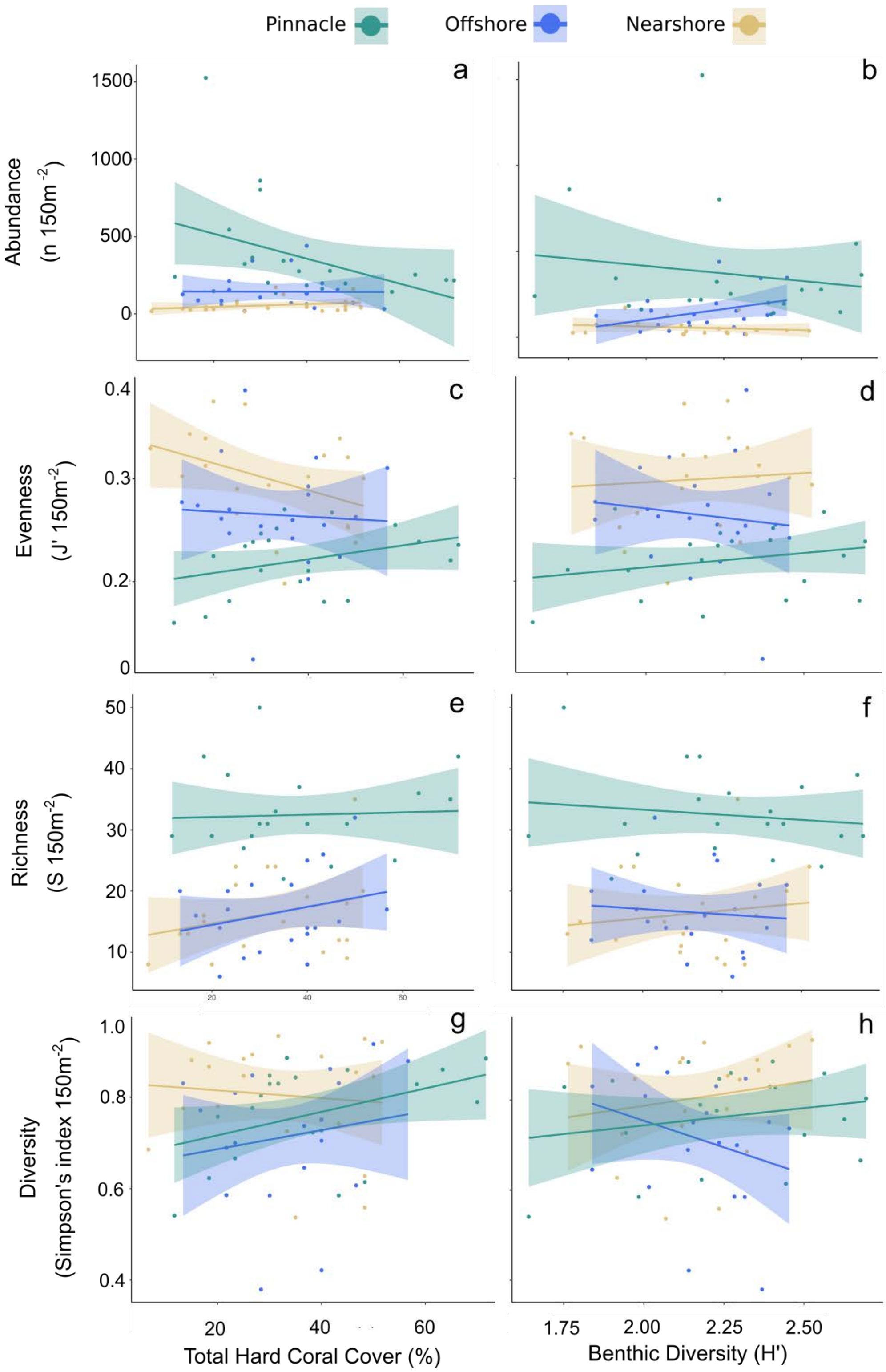


Figure 2.8 Relationships between fish community metrics and benthic complexity variables for each reef type. Shaded areas depict 95 % confidence intervals from mixed effects models. Full summary of coefficients in models **a-h** in Appendix A Table S2.9.

The full distance based linear model containing all 14 benthic habitat variables (Appendix A Table S2.11) together with benthic diversity explained 21.98% of variation in fish communities. After adjusting for multiple testing, the final model indicated 3 variables were significant in explaining variability in fish communities (cumulative $_{Adj.}R^2 = 0.129$; Algae (5.84%), encrusting octocorals (3.90%) and encrusting porifera (3.25%) (Appendix A Table S2.7). When visualized in the db-RDA plot, the first two axes represented together 74.06% of fitted variation and 15.32% of total variation (Fig. 2.9a). Species most correlated with increasing algal cover included *C. tominiensis, P. nigromanus* and *C. rollandi. P. tuka* showed strongest correlation with octocorals, whereas *Naso vlamingii* and *A. thompsoni* were more associated with higher cover of encrusting Porifera more prevalent on offshore and pinnacle reefs (Fig. 2.9b).

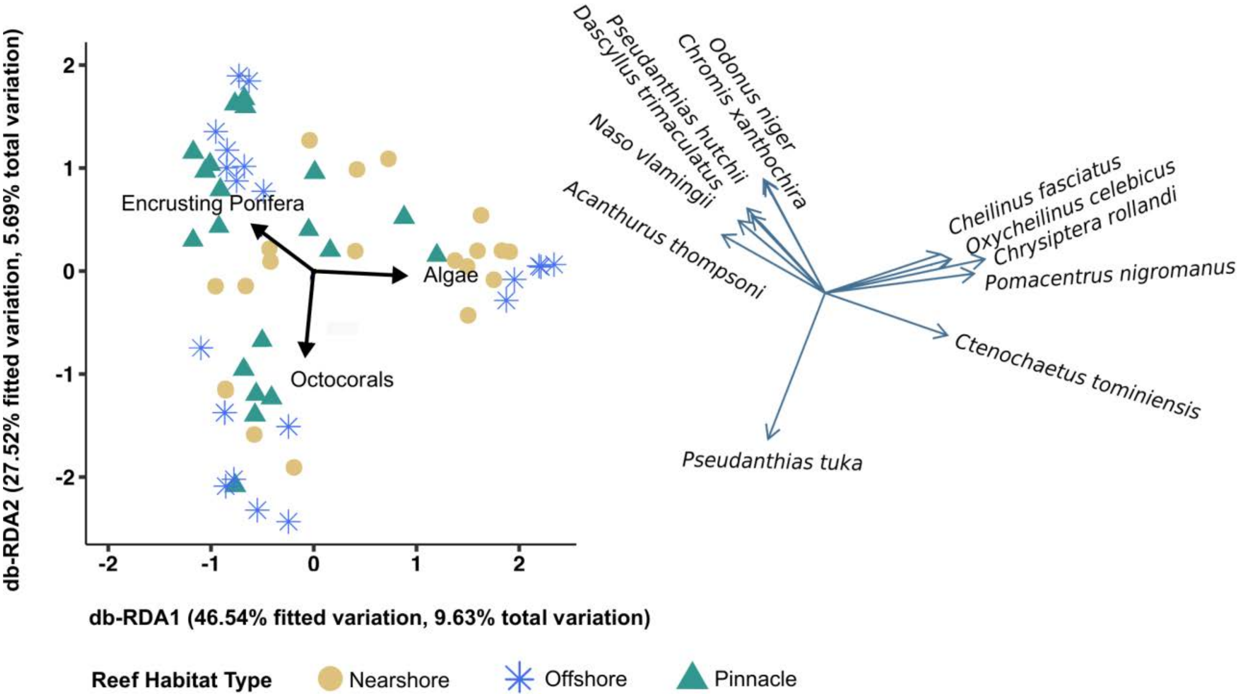


Figure 2.9 (a) Distance-based redundancy analysis (db-RDA) plot of the ordiR2step model based on benthic variables that better explained variability among fish communities across reef habitat types (n=20 for each reef type). Significant benthic variables are overlaid as a vector and fish species most correlated with each axis are presented to the right of the main plot **(b)** Vector length and direction of the arrow represents the size and direction of the relationships.

2.5 Discussion

2.5.1 Benthic assemblages – similar complexity but varied composition

My study presents the first baseline assessment of fish and benthic communities on submerged pinnacles in the Coral Triangle. The benthic habitat structure on pinnacles did not differ markedly from emergent reefs, although there were differences in coral growth forms and proportional cover. Although I accounted for the effect of aspect through site selection across morphologies, the flat tops of pinnacle summits in clear, offshore locations experience greater irradiance at the same depth than emergent reefs (Lesser et al. 2009). This perhaps explains higher complex and massive coral morphologies on pinnacles at these depths, which strongly influence the abundance and distribution of many coral-associated fishes (Jones et al. 2004; Coker et al. 2014; Pratchett 2014). Cooper et al. (2019) suggest that reefs on the Great Barrier Reef support higher numbers of individual fishes than inshore sites, as a result of clearer waters allowing greater light penetration for photosynthetic processes, resulting in increased feeding opportunities across a range of functional groups. In my study, of the four species of obligate-coral feeding butterflyfish recorded, all were recorded on pinnacles, where complex coral cover was highest, but not on nearshore or offshore reefs. This follows established patterns for coral obligates and suggests that fine-scale differences in benthic communities are more important for some fish species than broader, simple measures of overall complexity.

Although situated in similarly remote positions in the bay, benthic communities on offshore emergent reefs had the lowest proportion of complex hard coral and were dominated by laminar coral and encrusting porifera. Corals adapting to lower light at greater depths also often display flatter, low relief morphologies. Shading by steep walls and emergent shallow crests reduces light irradiance on the lower reef slopes of emergent reefs (Lesser et al. 2009). Flatter coral morphologies have been shown to influence fish-habitat associations, constraining the depth distribution of some species (Brokovich et al. 2008; Lesser et al. 2009; Smallhorn-West et al. 2017) which may partly explain low fish diversity on offshore reefs despite their offshore position.

The high algal cover on nearshore reefs is likely due to close proximity to large-scale terrestrial agricultural activity, including high levels of deforestation and associated high inputs of allochthonous run-off (Munday 2004; Green et al. 2009). High algal cover tends to be a characteristic of degraded coastal reefs (Hughes 1994; Graham et al. 2006; Roth et al. 2018) and altered fish communities (Jones et al. 2004; Chong-Seng et al. 2012; Ainsworth and Mumby 2015). This may be driving lower fish diversity and abundance at nearshore sites than would naturally be found without chronic land-based disturbances.

2.5.2 Fish assemblages - unique fish communities found on pinnacles

I found that submerged pinnacles support highly diverse, abundant and distinct fish assemblages, with many unique species not found at the equivalent depth on emergent reefs in either nearshore or offshore locations. My findings confirm my expectation that distinct submerged physical structures possess high abundance of fishes, in this case driven by large schools of *S. qeni, Caranx* sp. and *A. thompsoni*. Associative behaviour between fish and physical structures is well known (Fréon and Dagorn 2000) and explanations for this behaviour are thought to include resting, spawning, seeking shelter from predators and access to cleaning stations and feeding opportunities (Paterson 1998; Barreiros et al. 2002) however these paradigms are untested for the pinnacles in my study.

Contrary to my expectations, there was no difference in diversity across the three reef morphologies. Pinnacles however, did have the highest species richness and number of unique species. Although I did not directly measure habitat area or isolation by distance, Kimbe Bay's nearshore reefs are larger reefs, closely situated to each other and also to coastal nursery habitats (Green et al. 2009). Nearshore reefs may therefore be expected to receive higher numbers of juveniles and recruits (sources of immigration) and support higher absolute numbers of individuals and species, over a larger overall area of available habitat (MacArthur and Wilson 1967). Although these patterns are less established than in terrestrial ecology, biogeographic factors are known to influence marine habitats and reef fish communities (Mora et al. 2003; Kulbicki et al. 2013; Bennett et al. 2018; Quimbayo et al. 2018), albeit with contrasting results. Sandin et al. (2008) found classical relationships between reef fish abundance and isolation (negative) and habitat area (positive), but others have shown that increasing isolation from land-based disturbance and associated geographical environmental gradients leads to increased biomass and abundance, (DeMartini et al. 2008; Stallings 2009; Williams et al. 2011; Brewer et al. 2012; Kattan et al. 2017).

Given the relatively small area of Kimbe Bay (15x25km) and the strong dispersal capabilities of many fishes (Mora et al. 2003; Almany et al. 2017; Bode et al. 2019) it is unlikely that horizontal dispersal ability limits offshore recruitment and may explain the weak biogeographic patterns in diversity observed (Hobbs et al. 2012). Nevertheless, the offshore emergent reefs and pinnacles are similarly isolated from nearshore habitats, yet there is still an anomaly between abundance and richness on these two morphologies. This may be attributable to high temporal variability in species abundances as some evidence suggests that small isolated reefs are subject to greater demographic and environmental stochasticity (Mellin et al. 2010). The persistence of the patterns observed in this study should therefore be assessed by replicated surveys to identify longer-term trends in biodiversity metrics.

The pinnacles in Kimbe Bay appear to provide sufficient habitat to support high fish diversity, abundance and richness, despite their small size and relative isolation from other reefs by both depth and distance. As small, island-like habitats in offshore, reefs on submerged pinnacles represent patchy habitats with high perimeter-to-area ratios. The interface of the coral reef and pelagic environment represents the edges of both these distinct marine habitats. The term "edge effect" is used to describe the influence of the mixed environment created at the boundaries of conjoining habitats on ecological community structure and processes (Fahrig 2003; Fonseca, 2008). Here, species associated with adjacent habitats are brought into contact which may lead to novel interactions, the formation of dispersal barriers or the creation of spatial subsidies (Fagan et al. 1999). Edge effects, however, are generally not well known in marine environments as the theoretical base is rooted in terrestrial ecology (but see Smith et al. 2007; Sambrook et al. 2016). Yet, given their small size and typical isolated position within seascapes, it seems plausible that coral reefs on submerged pinnacles experience some of form of edge effect. The combination of coral reef and pelagic habitat theoretically increases habitat heterogeneity; not necessarily in terms of structural complexity but by increasing the breadth of resources available to a wider range of species and individuals. This could explain the presence of both highly reef-associated and mobile pelagic species observed at pinnacle sites, leading to high species richness, distinct community structures and the highest number of unique species.

2.5.3 Weak fish-habitat relationships

Species richness, abundance and composition on pinnacles was only weakly related to habitat structure and is most likely driven by other aspects of the unique morphology of pinnacle habitats. Empirical studies examining linear correlations between reef fish and simple habitat variables have similarly shown contrasting and, or surprisingly weak relationships (reviewed in Jones and Syms 1998), but most have been conducted at shallow depths (<20m). My surveys were conducted at 20-30m and it is known that some fish-habitat links can decline with increasing depth on emergent reefs, usually attributable to declining complex and branching coral cover and the changing influence of other abiotic factors (Brokovich et al. 2008). This may explain the lack of strong fish-benthic relationships at all reef morphologies.

Although live coral cover is consistently the most important habitat variable affecting the distribution of many coral-associated fishes (Coker et al. 2014), the generalisation of simple linear patterns in fish-habitat relationships is further complicated by the huge variety of ways different species utilise coral reefs (Jones and Syms 1998). For example, some species will alter habitat associations during ontogeny (Bonin et al. 2011; Komyakova et al. 2018) and positive effects of habitat complexity on fish abundance can depend on numerous predator-prey and conspecific interactions (Beukers and Jones 1998; Almany 2004). The different proportions of certain benthic cover types and morphologies may also reflect the distinct fish communities, where certain morphologies or benthic organisms provide more or less favourable habitat for certain fishes. A detailed investigation of trophic assemblage composition and potential differences in condition (e.g. body size, growth rates) would help to further understand how different types of reef habitat could confer benefits to particular functional groups and individuals.

Many fish species have less direct relationships with biogenic micro-habitats in general, instead, being attracted to physical structure and associated abiotic conditions (Auster 2007). In my study, the negative relationship between fish abundance and hard coral cover on the pinnacles (Fig. 2.6g) was largely a result of the high percentage cover of encrusting corallimorph colonies (Hexacorallia) combined with the presence of large schools of *S. qeni* and *A. thompsoni*. Mobile mesopredators tend to use coral reefs less directly than highly site-attached fishes, hunting and foraging in other adjacent connected habitats during different diurnal periods (Papastamatiou et al. 2015) while high abundances of planktivores like *A. thompsoni* at reef edges and greater depths is likely driven by proximity to higher plankton availability brought by strong currents (Thresher and Colin 1986; Hobson 1991; Quimpo et al. 2018). Stronger currents on reefs can be a product of both offshore positions receiving higher exposure to wind-generated water motion and waves, but also interactions between reef topography and oceanographic processes (Hearn 2011). Fish species on abrupt physical structures may therefore have less direct relationships with biogenic habitat, but instead rely on favourable feeding and abiotic conditions generated at dynamic all-surrounding boundaries between reef and pelagic habitats.

2.5.4 Hydrodynamics and pelagic influence as drivers of fish communities on pinnacles

I propose that both habitat-specific physical processes and high pelagic influences are plausible mechanisms which explain distinct and highly abundant fish communities on small offshore submerged pinnacle reefs. On shallow emergent reefs, the crest is the most diverse and productive zone (Done 1983; Russ 1984, 2003) where reef fish communities benefit significantly from oceanic production (Wyatt et al. 2012; Fisher et al. 2018; Le Bourg et al. 2018). Pinnacle reefs diverge from classical models of spatial reef zonation where, as the summits are small in area, lacking any significant area of back-reef or flat; they are composed almost entirely of reef crest. Furthermore, the pelagic environment surrounds not only the circumference of reef but also constitutes a significant water column of pelagic habitat above the benthos. Thus, on a pinnacle the majority of the reef may experience high pelagic energetic inputs via multidirectional currents, not just at the seaward edge as on emergent reefs. For example, high abundances of planktivores found at reef edges fix important allochthonous inputs (Wyatt et al. 2012) and exposed zones on emergent reefs have been shown to receive significant pelagic energetic subsidies through this mechanism, explaining exceptional levels of productivity even on low coral-cover reefs (Morais and Bellwood 2019).

Hydrology on coral reefs can therefore shape reef-fish assemblages (Fulton and Bellwood 2005; Eggertsen et al. 2016) and submerged topographies can generate distinct hydrodynamic environments, upwellings and currents which are important mechanisms for nutrient and plankton retention (Genin et al. 1986; Lueck and Mudge 1997; Fulton et al. 2005; Morato et al. 2009; Lavelle and Mohn 2010; Mosquera Giménez et al. 2019). This extension of the species-energy hypothesis (Wright 1983) has been proposed as a mechanism which allows these habitats to support abundant communities, often composed of species from high trophic levels (Pitcher and Bulman 2007; Jorgensen et al. 2016; Richert et al. 2017). The presence of diverse and abundant fish communities on pinnacles rich with large populations of planktivores and piscivores perhaps reflects strong bio-physical coupling in the same way it is thought to on seamounts (Genin 2004; Morato et al. 2010). Although the small scale of this study does not fully capture the abundance and distribution of large mobile predators, sharks were only observed in transects at pinnacle reefs. This could suggest that these habitats support higher trophic levels and more complex food-webs than nearshore reefs at the same depth, which may be lower-energy environments. Greater sampling effort and additional studies, however, are needed to ascertain an accurate reflection of habitat use on pinnacle reefs by large predatory fishes.

The hydrological-energy mechanisms I suggest as drivers of high diversity on pinnacles do occur on emergent reefs, but are largely focused on the shallow crests by surface waves and upwellings travelling up the slope. As such, productivity, nutrient concentrations and larval supply are again focused in this zone rather than the lower slopes (Wolanski and Delesalle 1995; Sponaugle et al. 2002; Leichter et al. 2005; James et al. 2020). Interactions between hydrodynamics and reef topography clearly differ between reef zones but there have been few comparisons between emergent reefs and submerged reefs. Despite the difference in absolute crest depth between emergent and submerged reefs, the culmination of hydrodynamics on the crest may lead to greater assemblage similarities in this zone between reef morphologies, regardless of depth. Additionally, in terms of habitat, emergent reefs typically have large areas of high coral cover on the crest, which is likely to concentrate the majority of reef-associated individuals and species. It was notable in my study how many species usually associated with shallow crests on emergent reefs were also observed on the crests of submerged pinnacles, most likely a result of aspect and clear offshore waters.

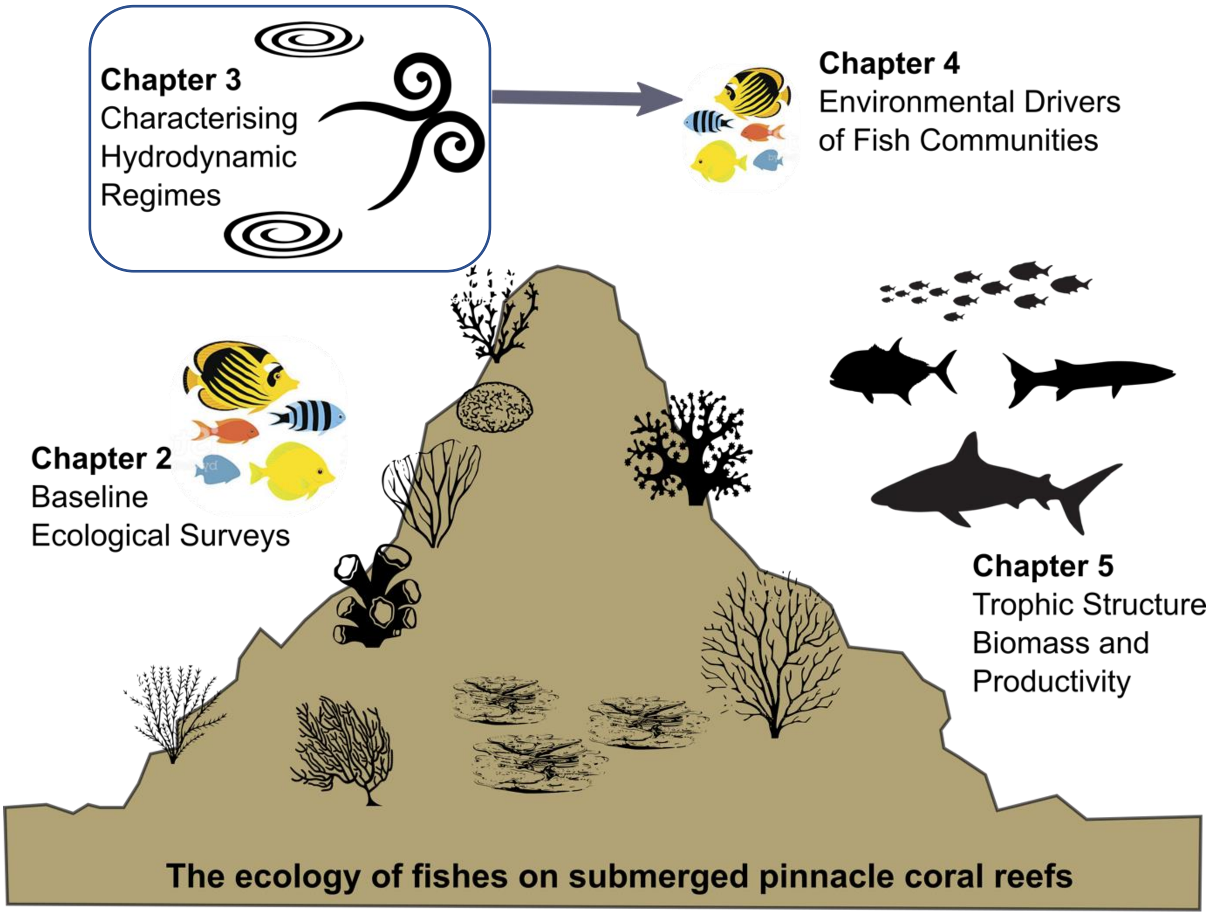
Comparative investigations of patterns in reef zonation along depth gradients will help further explain how communities change across the full range of available habitat on both emergent and submerged reefs. Disentangling the relative effects of reef zone, depth and hydrodynamics on submerged pinnacles will require fine-scale in-situ measurements of currents and associated abiotic factors to reveal new information about these unusual habitats rather than relying on generalised trends from shallow and mesophotic coral reef literature (Pearson and Stevens 2015).

As isolated, but ubiquitous patch habitats, submerged pinnacles also present significant opportunities to assess connectivity between emergent and deep reefs as well as the wider pelagic environment. Just as seamounts are thought to act as steppingstones for dispersal in the deep sea, pinnacles may play a significant role in connectivity across large scale coral reef systems. Multiple forms of submerged reef supporting diverse marine ecosystems are widely distributed across the continental shelf of both north-east and north-west Australia (Bridge et al. 2012, 2019; Roberts et al. 2015; Moore et al. 2017; Heyward and Radford 2019), but have largely been excluded from management and monitoring efforts. Results from this study and others demonstrate the requirement for further study of submerged coral reef habitats and inclusion into management plans.

2.5.5 Conclusions

This baseline assessment indicates that pinnacles represent a distinct form of submerged coral reef that supports highly species rich and abundant fish communities. Assemblages here are likely shaped by complex interactions of hydrology, physical structure and high levels of pelagic influence, resulting from greater crest depth and offshore locations. These processes are present on emergent, nearshore reefs, but largely only at shallow seaward edges, and their effects may attenuate with depth as the reef structure changes. Further studies are required to assess how the combination of pelagic and reef habitats on small submerged pinnacles generate distinct abiotic and physical conditions and how they might enhance productivity and the variety of available resources. Isolation by depth and offshore setting may also confer aspects of natural resilience in addition to beneficial hydrodynamics. In a rapidly changing marine environment, it is important to establish how distinct reef morphologies may respond to climate change and the extent to which they may provide refuge to degrading shallow reef organisms. As ubiquitous features across all low-latitude coastal shelves, deep and distinct coral habitats are becoming increasingly important components of the future global coral reef biome. Further work is warranted to quantify the spatial extent of these unique coral reef habitats, characterise their ecological communities and understand their role in coral reef ecosystems.

Chapter 3


Chapter 3
Characterising
Hydrodynamic
Regimes
Chapter 4
Environmental Drivers
of Fish Communities
Chapter 2
Baseline
Ecological Surveys
Chapter 5
Trophic Structure
Biomass and
Productivity
The ecology of fishes on submerged pinnacle coral reefs

Chapter 3: Contrasting hydrodynamic and temperature regimes of submerged pinnacle and emergent coral reefs

3.1 Abstract

Coral reefs are subject to strong and variable hydrodynamic conditions. However, hydrodynamic regimes vary depending upon the geomorphology of reefs, their depth profiles and distance offshore. Submerged coral reefs on steep-sided, conical bathymetric features like seamounts and pinnacles are thought to experience enhanced water circulation as a result of interactions between the abrupt physical structure and impinging currents. Such mechanisms are known to support high biological productivity through enhanced biophysical-coupling. There may also be a strong interaction between submerged pinnacles and regional water currents in offshore conditions, while shallow reefs may be more subject to surface currents driven by wind, waves and tide. Here I tested whether submerged coral pinnacles experienced stronger and more variable currents compared to emergent reefs in both nearshore and offshore positions. Current speeds and temperature were monitored for 12 months at 11 reefs, representing the three different reef categories. I found different patterns in the two variables examined among reef types throughout the year and between seasons. Submerged pinnacles exhibited stronger, more variable current speeds and lower temperatures compared to emergent reefs. A cross-shore gradient was apparent for current speeds which were lowest on sheltered nearshore reefs. Temperature regimes exhibited considerable variability between and within reef categories. This was particularly true for some offshore reefs which despite greater exposure to wider regional circulations, experienced the highest temperatures recorded during the study. Additionally, periods of highest or lowest temperatures and current speeds were temporally mismatched between reef types. Distinct hydrodynamic processes have been documented on large seamounts and my results suggest that these are also likely to occur to some extent on smaller but physically similar submerged structures. Most of our understanding of the structure and function of coral reef ecosystems comes from shallow water emergent coral

reefs, but my findings highlight important nuances in environmental processes that occur on morphologically distinct coral reef habitats. This is an essential consideration for a holistic approach to understanding bio-physical processes on all coral reefs and also incorporating small but potentially highly productive submerged patch reefs into conservation spatial planning.

3.2 Introduction

Hydrodynamics are important drivers of ecological communities in all marine habitats (Jokiel 1978; Barry and Dayton 1991; Wolanski et al. 1992). Tides, waves and currents define the movement of water and generate gradients in physical and biochemical processes that in turn affect ecological processes (Legendre 1981; Wolanski and Hamner 1988; Van Wesenbeeck et al. 2007; Green et al. 2018). On shallow emergent coral reefs, surface-driven wave action is a key hydrodynamic influence (Geister 1977; Graus and Macintyr 1989). Emergent reef crests rise to the upper 10m of water where most wave-driven hydrodynamic energy is focused (Young 1989). Resulting gradients in wave energy, nutrients and temperature regimes drive well-documented patterns in habitat zonation and ecological community structure on coral reefs (Bradbury and Young 1981; Done 1983; Symonds et al. 1995). Submerged reefs however, are less affected by surface driven waves as the crests are found below 10-20m, where the effects of wave energy dissipates (Roberts et al. 2015; Thomas et al. 2015). Typically found as isolated elevations of the seafloor in mid-shelf or offshore positions, submerged reefs are ubiquitous across global oceans and coastal shelves and constitute significant areas of habitat available for the formation of coral reefs (IHO 2008; Bridge et al. 2012; Harris et al. 2013). Many aspects of hydrodynamic regimes on shallow emergent coral reefs are relatively well understood (Monismith 2007; Hearn 2011; Lowe and Falter 2015), but we have a limited understanding of the role of hydrodynamics on morphologically distinct submerged coral ecosystems.

Comparative studies between shallow emergent coral reefs and submerged coral reefs have shown considerable variability in ecological communities (Cooper et al. 2019). Fundamental differences in depth and reef morphology generate distinct biotic and abiotic habitat characteristics at each of these reef types that are important in shaping fish and coral assemblages (Lara and González 1998; Roberts et al. 2015). Unlike the established pattern of habitat zonation on emergent coral reefs, many submerged coral reefs are found on top of steep sided bathymetric features including banks, shoals and abrupt structures like seamounts, pinnacles, bommies and knolls (Abbey et al. 2010; Whiteway et al. 2013). Seamounts are large (>1000m elevation) conical structures typically formed by volcanic activity on oceanic plates (Clark et al. 2011; Staudigel et al. 2015) and can possess diverse and abundant ecological communities (Roberts et al. 2006; Koslow et al. 2016; Rogers 2018). In mid to low latitudes where these structures reach the photic zone (<300m) they also provide hard substrate for the formation of tropical coral reefs (Veron and Done 1979; Longenecker et al. 2019; Stefanoudis et al. 2019). Pinnacles are superficially similar features, generally smaller than seamounts and usually associated with coastal shelves or as part of other larger submerged topographies (Birkeland 1971; Abbey and Webster 2011; Bridge et al. 2011; Sherman et al. 2019). In ecological terms, seamounts and pinnacles are physically similar submerged structures that can support diverse and highly abundant ecological communities (Thresher et al. 2011; Richert et al. 2017; Rogers 2018; Leitner et al. 2021).

Interactions between currents and abrupt physical bathymetric features can generate distinct hydrodynamic regimes (Genin et al. 1986; Bohlert and Genin 1987; Lavelle and Mohn 2010). On seamounts these interactions manifest in localised secondary circulations including fast, turbulent currents, reticulating eddies, wakes, internal waves and upwelling (Capella 1983; Roden 1986; Eriksen 1991; Chapman and Haidvogel 1992; Baines 2007; Perfect et al. 2018). Such processes are thought to drive strong biophysical coupling through enhanced mixing and retention of nutrients, leading to high productivity and diverse ecological assemblages (Boehlert 1988; Genin 2004; White et al. 2007; Morato and Clark 2008). In a recent study, I found high abundance, biomass and similar diversity of fishes on a series of small, submerged pinnacles compared to larger emergent reefs in Kimbe Bay, Papua Guinea (Galbraith et al 2021, Chapter 2). I hypothesise that these patterns may also be driven by strong hydrodynamic regimes. Despite differences in scale and seascape setting, the morphological similarities between pinnacles and seamounts provides a suitable framework for investigating hydrodynamic regimes on pinnacle coral reefs.

As on seamounts, it seems plausible that currents will be stronger and more variable, in terms of strength and direction, on pinnacles due to interactions between prevailing oceanic flow and the distinct abrupt topography. Figure 3.1 illustrates a conceptualisation of how similar hydrodynamic processes may occur on pinnacles and seamounts. These processes may operate at a smaller scale on submerged pinnacles which unlike seamounts, are unlikely to disrupt large scale oceanographic flows. However, I hypothesize that the similar abrupt physical structure can generate localised hydrodynamic responses which subsequently drive variability in ecological patterns and processes on pinnacles. Numerous hydrodynamic processes occur on emergent reefs, but can dissipate around the reef or propagate up the slope to the crest. Shallow crests are therefore dominated more by surface driven waves and other shallow water hydrodynamics like tidal flushing. Hydrodynamics on submerged pinnacles are therefore likely enhanced compared to those on emergent reef slopes at the same depth. Additionally, offshore locations are more exposed to regional currents and so the strength and prevailing direction of currents will also reflect the seascape setting. This may manifest in currents reaching the reef from all directions and could also include exposure to deep circulations and upwellings which tend to be cooler, nutrient rich waters.

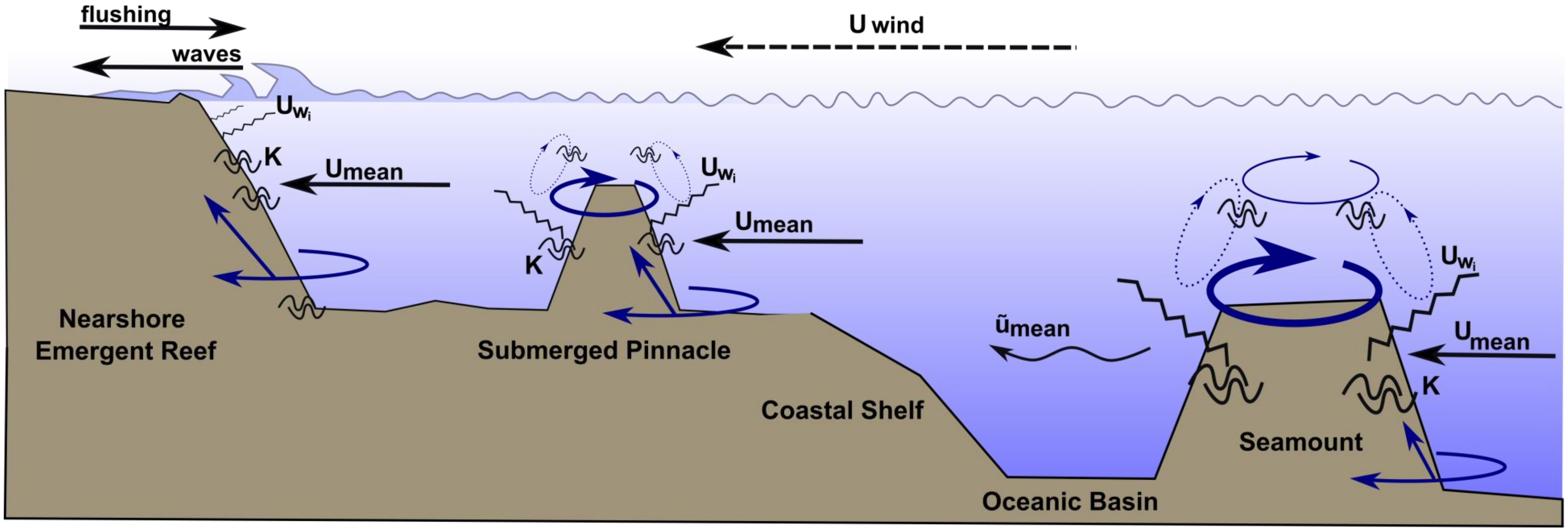


Figure 3.1 Conceptual diagram of processes occurring on emergent reefs, submerged pinnacles and seamounts. Adapted from Lavelle and Mohn (2010). Interactions between abrupt submerged physical structure, incidental mean current (Umean), eddies (ũmean) and turbulence (Uwi), internal waves (K), oscillating flows and the water column above can lead to doming, upwelling and vertical circulating cells near or above a seamount summit. Similar processes seem plausible on submerged pinnacles but may not generate larger scale disruptions to current flow like island wakes (ûmean) or trapped cells above the summit (e.g. Taylor Cones). On emergent reefs, most hydrodynamic energy is focused on the crest. In nearshore positions in particular these processes are dominated by tides and surface waves which generate an exchange between incoming oceanic water and water flushed from lagoons.

The global degradation of many shallow coral reefs caused by climate change has highlighted the need to understand how future changes in physical environmental conditions will affect ecological processes (Hughes et al. 2017). This is particularly true for deeper mesophotic coral ecosystems where environmental conditions differ from shallow emergent reefs, generally down a continuous gradient from 0 - 300m (Lesser et al. 2009, 2018; Bridge et al. 2013; Kahng et al. 2019; Tamir et al. 2019). Submerged reefs, however, represent a distinct form of deeper reef, with no continuum of habitat extending into shallow water. Many of the proposed localised hydrodynamic responses at seamounts are facilitated by the depth of summit and the extent of the water column above the physical structure (Chapman and Haidvogel, 1991). Unlike emergent reefs, submerged coral reefs with deep crests may therefore be subject to additional hydrodynamic processes that may benefit other biophysical dynamics. The lack of comparative studies between emergent and submerged reefs represents a significant knowledge gap in both fundamental ecological processes and also our understanding of how patterns in biodiversity on coral reefs may change.

The aim of this study was to characterise hydrodynamic regimes on a series of submerged pinnacle coral reefs in Kimbe Bay, Papua New Guinea and to compare them with shallow emergent coral reefs in nearshore and offshore seascape positions. I examined current speeds and temperatures for a full year at 11 reefs and assessed how patterns vary between reef morphologies at the same depth. Specifically, I tested hypotheses based on the potential for hydrodynamic similarities between seamounts and pinnacles illustrated in Figure 3.1:

1) Currents will be stronger and more variable in strength on pinnacle reefs than on emergent reefs at the same depth. Hydrodynamic studies on seamounts attribute the formation of accelerated currents and localised eddies to strong interactions between surrounding flows and abrupt conical submerged physical structures (Genin et al. 1986; Boehlert 1988).

2) Additionally, I predicted currents would be stronger on all offshore reefs (including pinnacles) and nearshore reefs will experience lowest current velocities due to bay position, away from oceanic influences and exposure to prevailing weather.

3) Lastly, I predicted that temperature regimes will vary between all reef types as a result of both differences in morphology and seascape position. Regional currents can drive smaller circulations which may result in either a greater degree of cooler water flushing or enclosed warm water cells. Reef location is therefore an important determinant of temperature, especially at the scale of a small seascape.

3.3 Methods

3.3.1 Study site and survey design

Kimbe Bay is a relatively large (140 x 70km) tropical bay on the island of New Britain in the Bismarck Sea (5°30'S, 150°05'E, Fig. 3.2). The bay possesses a diverse seascape including nearshore emergent fringing coral reefs, offshore emergent atolls and guyots as well as numerous submerged coral pinnacles (Green et al. 2007). This makes it an ideal site for a comparative study of differing reef morphologies. The pinnacle summits are small (130 – 827 m^2) relatively flat and, being situated in the photic zone with their reef tops between 40-20m, are capped by coral reef building benthic communities. The sides of both pinnacles and offshore reefs are steep and drop off to 600m in the bay itself and to over 1000m on the northern edge of the coastal shelf. Tides in Kimbe Bay are relatively small (1m range at spring tides) and are mostly diurnal (Steinberg et al. 2006), making it feasible to disentangle the effects of localised currents from tidal flows. Prevailing seasonal currents and circulation in Kimbe Bay are driven by larger eddies in the eastern Bismarck Sea, which in turn are driven by the southern Equatorial Current (Steinberg et al. 2006). To account for differences in exposure to these regional currents I initially selected 12 reef sites in both sheltered nearshore and offshore seascape positions of different morphologies; 4 nearshore emergent reefs, 4 offshore emergent reefs and 4 offshore submerged pinnacles. All emergent reefs had crests at depths above 8m and submerged pinnacle crests were all deeper than 18m. Nearshore reefs were less than 5km from mainland and offshore reefs between 9-25km.

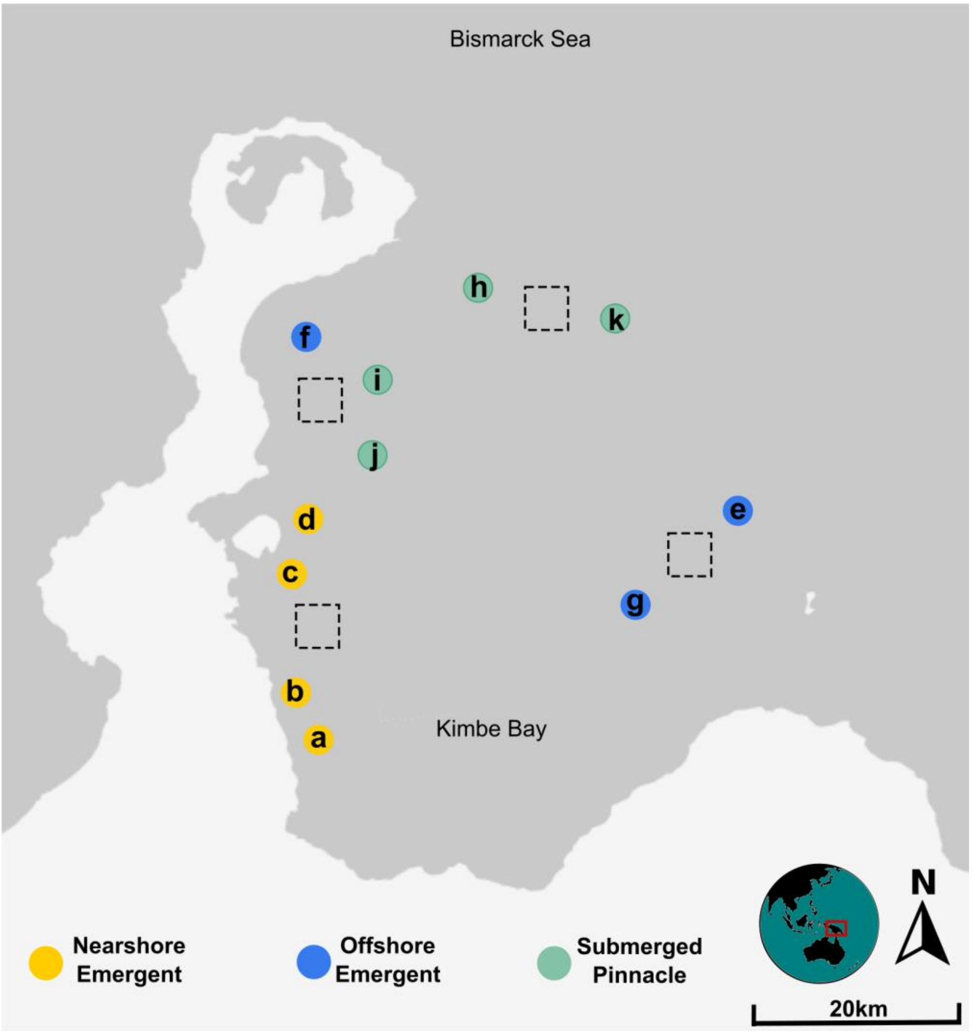


Figure 3.2 Map of Kimbe Bay with location of each site. Reef type for each site is indicated by the colour of marker circle, nearshore (yellow), offshore (blue) and pinnacle (green). Four dashed boxes represent the 4x4km grids used to collect average Sea Surface Temperatures (SST) over the same annual period.

3.3.2 Data collection – current speed and temperature

To characterise current flow and thermal regimes at each site, Marotte HS Drag Tilt Current Meters (Marine Geophysics Laboratory, Australia) were installed at 25-30m depth during May-July 2018. Current meters were placed on horizontal north-orientated areas of each reef where there were no surrounding obstacles to prevent free movement of the instrument. The current meters recorded temperature (°C), current direction (degree from north) and current speed (m s^{-1}) every 10 seconds during deployments. Current meters were recovered in September-October 2019 and data downloaded and processed using the software MarotteHSConfig (http://www.marinegeophysics.com.au/software/). One current meter deployed at an offshore emergent site (Kimbe Island) was not successfully recovered during the study, reducing the total number of reefs in this study to 11.

3.3.3 Data analysis: Characterising differences in hydrodynamic regimes between reef morphologies

All data were analysed in R 4.0.1 (R Core Development Team 2021). Data from all current meters were collated and standardised to span the time period between September 2018 to September 2019. To assess spatial patterns in current speeds and direction at each site, wind rose plots were used to visualise the frequency, strength and direction of currents at each survey reef. To visually compare temperatures associated with current speeds recorded at each site, polar plots were also created for each reef. Wind rose and polar plots used hourly means for each reef site during the full 1-year period and were created using the package “openair” (Carslaw and Ropkins 2012).

Kimbe Bay does not exhibit typical seasonal trends in weather and climate (Srinivasan and Jones 2006). Instead, the area possesses a distinct wet season between December and February and a windy season between June to August. The months in between these “seasons” represent generally stable transitional periods (Srinivasan and Jones 2006). For the purpose of this study however, I do use typical seasons based on the defined annual periods for the southern hemisphere, i.e spring occurs in September-November, summer in December-February, autumn in March-May and winter in June-August. I used Generalized

Linear Models (GLMs) to compare measures of temperature and current speed between reef types and also between seasons using the package “MASS” (Venables and Ripley 2002). Daily average values (mean, maximum, minimum) for temperature and current speed were calculated for each reef type, as annual metrics and for each season. I also calculated mean daily standard deviation as a measure of variability in current speeds and temperatures.

In order to assess differences in water temperature from the surface to my study depth, I also compared in-situ temperatures (25-30m) with sea surface temperatures (SST) recorded by remote sensing over the same time period. SSTs were obtained from the 8d MODIS-Aqua satellite time-series, area-averaged 4µm (night) data product using four 4x4km grids (locations in Fig. 2) covering the approximate location of the study reefs via the NASA portal Giovanni v4.34 (Acker and Leptoukh 2007; NASA 2020). Appropriate error distributions were chosen based on standard exploratory techniques and model goodness-of-fit assessed using Q-Q plots (normality), residual plots (homogeneity of variance) in the “DHARMa” package (Hartig 2020). Generally temperature models were fitted with a gaussian error structure and some current speed GLMs fitted with a gamma error structure and inverse link. For each GLM adjusted Tukey’s tests were used to identify pairwise differences between reef types and seasons using “emmeans” (Lenth 2020). Estimates and 95% confidence intervals are presented on the response scale, where a confidence interval that does not contain zero is evidence for a significant difference. Full results from all GLMs are presented in Appendix B Tables S3.1 -3.16.

3.4 Results

3.4.1 Annual and seasonal temperature regimes

During the year-long study period, the highest mean daily temperatures were recorded on offshore emergent reefs (31.33°C ; 95% CI = 31.27 – 31.39) and lowest on pinnacle reefs (30.53°C ; 95% CI = 30.47 – 30.58). Pairwise contrasts in annual mean daily temperatures between all reef types were significantly different, with pinnacles on average recording significantly lower temperatures than both offshore and nearshore reefs. All reef types on average recorded significantly higher temperatures compared to SSTs (Table 3.1, Fig. 3.3). Within each reef type category, average annual temperatures were generally quite consistent, as reflected by narrow 95% confidence intervals.

Table 3.1 Annual daily mean temperature (°C) at each reef type (constituent sites indicated as letters relating to Fig. 3) and for SST. Pairwise contrast estimate and 95% confidence intervals. Means are estimated marginal means and contrast estimates represent the difference between each pairwise contrast. 95% confidence intervals (CI) for pairwise contrasts are interpreted as significant if the interval does not contain zero.

Reef Type	*Mean Daily Temperature* (°C)	*SE*	*95% CI*	*Contrast*	*Contrast Estimate* (°C)	*SE*	*95% CI*
Pinnacle (sites h-k)	30.53	0.03	30.47 - 30.58	Pinnacle - Offshore	-0.81	0.04	-0.91 - -0.70
Offshore (sites e-g)	31.33	0.03	31.27 - 31.39	Pinnacle - Nearshore	-0.48	0.04	-0.58 - -0.37
Nearshore (sites a-d)	31.00	0.03	30.95 - 31.05	Pinnacle - SST	1.63	0.08	1.41 - 1.84
SST	28.90	0.08	28.75 - 29.05	Offshore - Nearshore	0.33	0.04	0.23 - 0.43
				Offshore - SST	2.43	0.08	2.22 - 2.65
				Nearshore - SST	2.10	0.08	1.89 - 2.31

Differences in temperature throughout the year are also reflected by the polar plots (Fig. 3.3). These plots additionally illustrate variation among reefs within each of the three reef categories. For example, one nearshore site (Fig. 3.3b; Madaro) was particularly cool and recorded a minimum temperature of 28.75°C during the survey period. The offshore reef "Ottos" recorded the highest hourly average temperature of 35.24°C (Fig. 3.3g) whereas other offshore sites "Ema" and "Hogu" were cooler (Fig. 3.3e-f). All pinnacle sites generally displayed cooler temperatures (Fig. 3.3h-k) which did not exceed 30.72 °C as an average annual maximum (Appendix B Table 3.1).

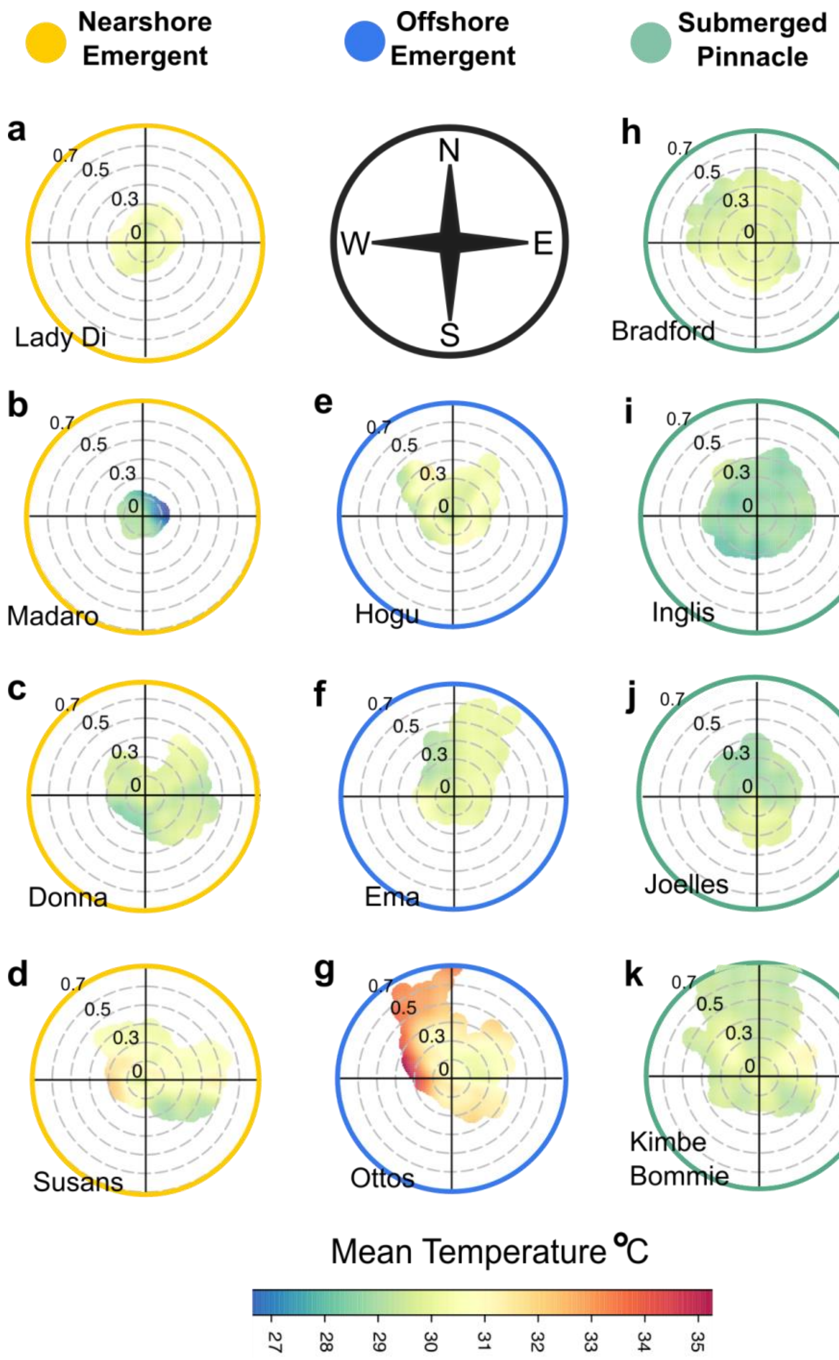


Figure 3.3 Polar plots showing the direction (degrees from north), strength (m s $^{-1}$) and temperature (^{o}C) of currents at each reef site. Letters a-k correspond to site locations in Figure 2. Plots were constructed using hourly means from each site for the 1-year study period, represented by each coloured pixel.

In terms of seasons, the warmest daily mean water temperatures at pinnacle sites were recorded in autumn (31.08 °C ; 95% CI = 31.00 – 31.17), which was also when temperature was most variable at these sites (mean SD = 0.12 °C ; 95% CI = 0.11 -0 .12). Temperatures at offshore reefs however, were warmest in winter (32.29 °C; 95% CI = 32.18 – 32.40) and coolest in spring (30.65°C; 95% CI = 30.56 – 30.74). This was the same for nearshore reefs which were also warmest in winter (31.32°C; 95% CI = 31.22 – 31.43) and coolest in the spring months (30.34°C; 95% CI= 30.23 – 30.44). See table 3.4 for all seasonal temperature means and Appendix B Tables S3.3-6 for full GLM results. Sea surface temperature (SST) was consistently lower than temperatures at all other reef types during all seasons. The annual trend broadly followed temperature patterns on the study reefs but with some inverse peaks and was on average lower by 2.05°C during the year (Fig. 3.5). Full GLM outputs and pairwise estimates for temperature comparisons between reef types and seasons are reported in Appendix B Tables S3.3-16.

3.4.2 Annual and seasonal current regimes; speed, direction and variability

Current speeds were strongest on the pinnacles (0.082 m s^{-1} ; 95% CI = 0.081-0.085) and lowest on nearshore (0.052 m s -1; 95% CI = 0.051 -0.054) and offshore (0.053 m s -1; 95% CI = 0.052-0.055) sites. Pairwise contrasts show evidence for a significant difference between average daily current speeds between pinnacles and both nearshore and offshore reefs respectively, but not between nearshore and offshore reefs which had very similar mean daily current speeds (Table 3.2). Mean daily standard deviation in current speed was highest at pinnacle sites (SD = 0.035 m s -1) and I found evidence to suggest a significant difference between nearshore (contrast estimate = 0.008 m s -1; 95% CI = 0.006-0.009) and offshore reefs (contrast estimate = 0.009 m s -1; 95% CI = 0.007 -0.010). There was no difference in daily current variability between nearshore and offshore reefs (contrast estimate = 0.002 m s -1; 95% CI = -0.001 – 0.004). Full results of GLMs comparing annual mean current speed measures are presented in Appendix B Table S3.2.

Table 3.2 Annual daily mean current speed (m s $^{-1}$) at each reef type and pairwise contrast estimate with 95% confidence intervals. Means are estimated marginal means and contrast estimates represent the difference between each pairwise contrast. 95% confidence intervals for these pairwise contrasts are interpreted as significant if the interval does not contain zero.

Reef Type	*Mean Daily Current Speed* (m s $^{-1}$)	*SE*	*95% Confidence Interval*	*contrast*	*Estimate* (m s $^{-1}$)	*SE*	*95% Confidence Interval*
Pinnacle	0.082	0.001	0.081 - 0.085	Pinnacle - Offshore	0.029	0.001	0.026 - 0.032
Offshore	0.053	0.0007	0.052 - 0.055	Pinnacle - Nearshore	0.031	0.001	0.027 - 0.034
Nearshore	0.052	0.0006	0.051 - 0.054	Offshore - Nearshore	0.002	0.001	-0.0008 - 0.004

Spatial patterns of the direction frequency of currents and speed are visualised in Figure 3.4. Wind rose plots for pinnacle sites (Fig. 3.4h-k) show the highest current speeds recorded during the study period. Current speeds of up to 0.60 m s^{-1} were recorded at the pinnacle site at “Kimbe Bommie, which was the maximum value observed in this study (Table 3.3; Appendix BI Table S3.17). Although some offshore sites recorded similarly high maximum current speeds (e.g “Otto’s Reef “= 0.59 m s-1 and “Ema Reef” = 0.50 m s-1, Fig. 3.4g and f, SI Table 17) they did not occur as frequently as on pinnacle sites.

Table 3.3 Absolute minimum, maximum and range of temperature and current speeds recorded at each reef type during the study period. Site-specific values are listed in Appendix B Table S2.14

	Temperature (°C)			**Current Speed (m s $^{-1}$)**		
Reef Type	Min	Max	Range	Min	Max	Range
Pinnacle	28.14	32.84	4.70	0.00	0.6030	0.6030
Offshore	28.75	35.24	6.50	0.0004	0.5976	0.5975
Nearshore	25.49	35.25	9.76	0.0004	0.4132	0.4131

Dominant currents on pinnacles came primarily from the north – northwest and were mainly between 0.1 – 0.3 m s-1 (Fig. 3.4h-k). On offshore reefs currents were more frequently recorded at less than 0.1 m s-1 (Fig. 3.4e-g) and varied more in direction, with no clear prevailing source of current. The majority of currents on nearshore reefs did not frequently rise above 0 - 0.1 m s^{-1} (Fig. 3.4a-d) but the sites “Donna’s” and “Susan’s” did experience some stronger velocities of up to 0.2 m s-1 from the east and south-east. Notably 50% of currents on the nearshore site “Madaro” did not exceed 0.1m s^{-1}. Whilst both pinnacles and offshore reefs experienced currents from all directions throughout the course of the study, this did not occur on some nearshore sites. Notably, “Madaro” (Fig. 3.4b) did not receive any currents from the south-east, “Donna” (Fig. 3.4c) none from the north and “Susans” (Fig. 3.4d) no currents from the south-west.

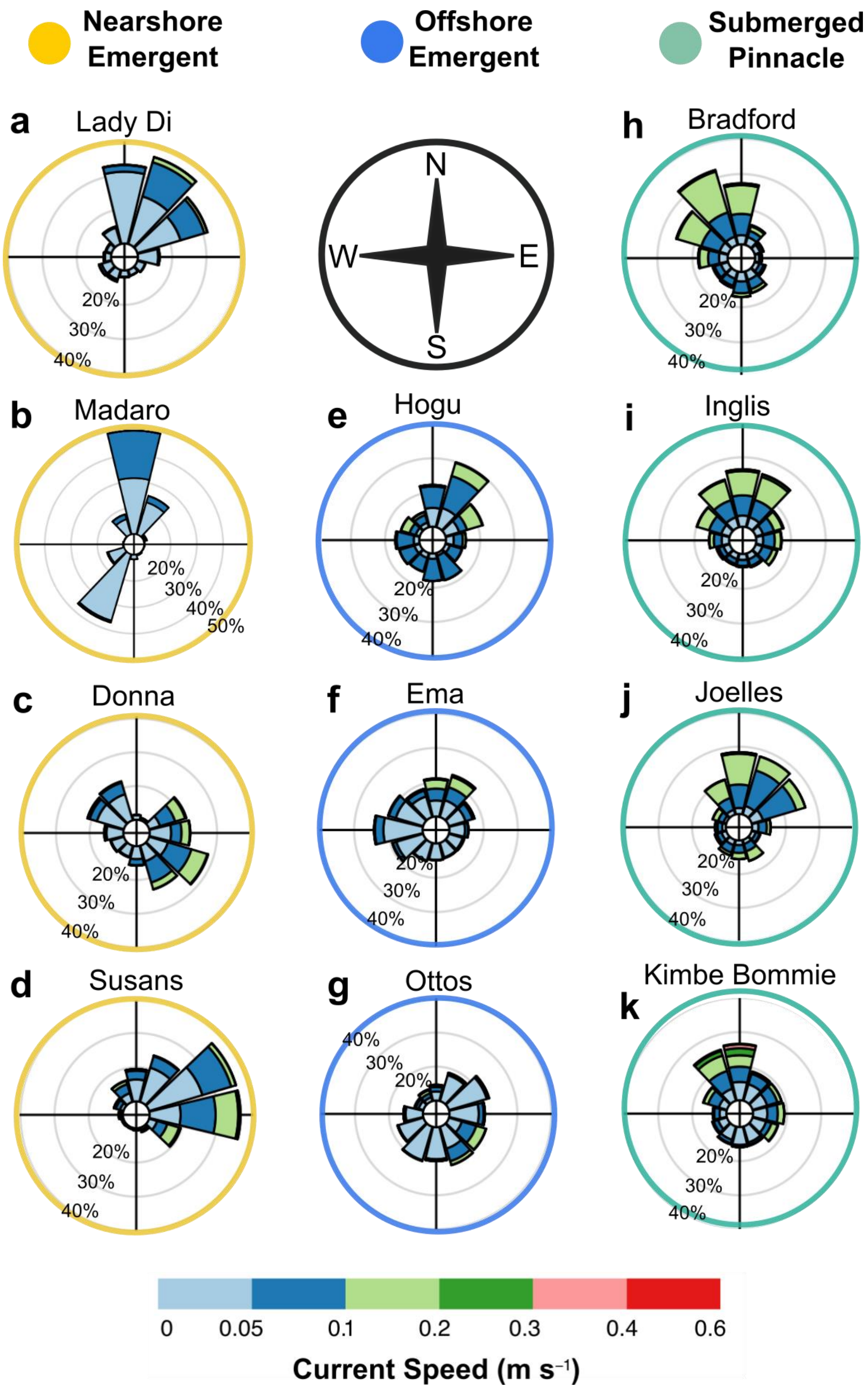


Figure 3.4 Wind rose plots showing the strength (m s^{-1}) and frequency of direction (percentage) of currents at each site. Letters a-k correspond to site locations in Figure 2. Plots were constructed using hourly means from each site for the 1-year study period.

Mean daily current speeds differed between all seasons on pinnacles and were strongest during summer (0.09 m s^{-1}; 95% CI = 0.088 – 0.097) and winter (0.11 m s^{-1}; 95% CI= 0.102 – 0.113) (Table 3.4, Fig. 3.5). Currents on pinnacles exhibited a highly variable trend throughout the year with repetitive sharp peaks in current speeds in all seasons (Fig. 3.5). In each season, daily mean current speed variability (standard deviation) on pinnacles was higher than on offshore sites and on nearshore sites except in winter.

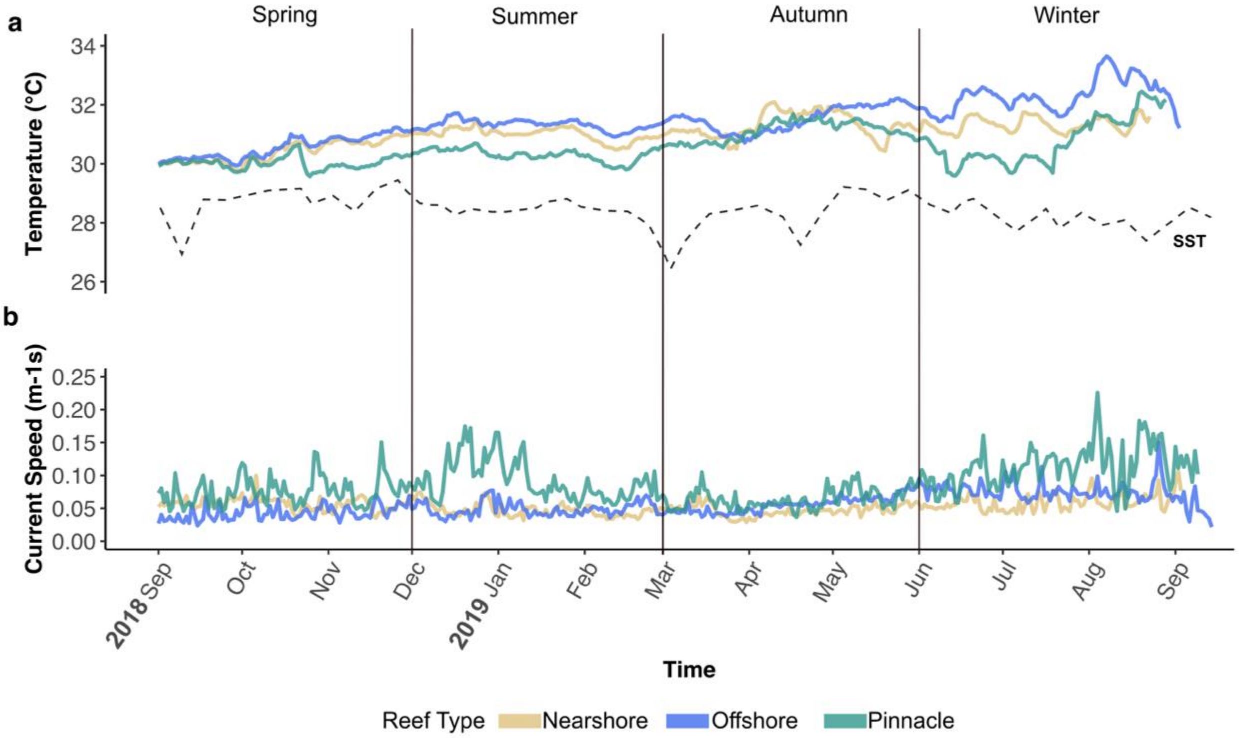


Figure 3.5 Time series for a) daily mean temperature (°C) and b) daily mean current speed (m s^{-1}) at nearshore (yellow, n = 4 sites, 1440 observations), offshore (blue, n = 3 sites, 1080 observations) and pinnacle (green, n = 4 sites, 1440 observations) reefs in Kimbe Bay between Sept 2018 – Sept 2019. The dashed line in the temperature panel represents daily mean sea surface temperature (SST) obtained from remote sensing data and averaged over 4x4km grid squares corresponding with the locations of study reefs in Kimbe Bay (200 daily observations).

At offshore reefs, current speeds during spring, summer and autumn were similar, ranging between 0.044 – 0.054 m s^{-1}. Although pairwise comparisons suggested some evidence for differences between spring and autumn it was quite weak (contrast estimate = -0.010; 95% CI = -0.015 - -0.005). I found strongest evidence for seasonal differences between the highest current speeds in winter (0.077 m s -1; 95% CI = 0.072-0.082) and all other seasons. Similarly, current speed variability was generally low at offshore sites (Range of mean SD = 0.020 – 0.029 m s^{-1}) during all seasons, particularly in autumn.

Current speeds on nearshore reefs exhibited less seasonal variation (range; 0.046-0.058 m s^{-1}) but were strongest during winter (0.058 m s -1) and the spring (0.058 m s -1). The winter months at nearshore reefs also produced the highest mean daily maximum current speed (0.153 m s-1 ; 95% CI = 0.146 – 0.161) and mean daily minimum current speed (0.009 m s-1; 95% CI = 0.008 – 0.010), also reflecting this variability. Appendix B supplementary tables 3.7-14 and 3.17 detail all GLM outputs and pairwise comparisons for annual and seasonal current speeds.

Table 3.4 – Mean daily values of temperature and current speeds at nearshore (n = 4 sites), offshore (n = 3 sites) and pinnacle (n = 4 sites) reefs in Kimbe Bay. Daily mean, mean variability as standard deviation, mean daily minimum and mean daily maximum are shown for each season. Numbers in brackets represent the standard error of each mean. Pairwise tests of all values between reef type and season are listed in Appendix B SI Tables 3.3-17.

Season	**Spring**				**Summer**				**Autumn**				**Winter**			
								Mean Daily Temperature (^{o}C)								
Reef Type	**Temp**	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**
Pinnacle	30.02	0.089	29.75	30.18	30.29	0.093	30.02	30.47	31.08	0.123	30.77	31.34	30.54	0.092	30.30	30.73
	(0.04)	(0.002)	(0.04)	(0.04)	(0.03)	(0.002)	(0.03)	(0.03)	(0.07)	(0.003)	(0.07)	(0.07)	(0.07)	(0.003)	(0.07)	(0.07)
Offshore	30.73	0.083	30.47	30.89	31.32	0.081	31.08	31.49	31.64	0.116	31.34	31.88	32.29	0.102	32.00	32.48
	(0.04)	(0.002)	(0.04)	(0.04)	(0.03)	(0.002)	(0.03)	(0.03)	(0.09)	(0.004)	(0.09)	(0.09)	(0.06)	(0.003)	(0.06)	(0.07)
Nearshore	30.53	0.074	30.29	30.67	31.01	0.083	30.77	31.17	31.39	0.106	31.11	31.61	31.32	0.076	31.10	31.47
	(0.04)	(0.002)	(0.04)	(0.04)	(0.03)	(0.002))	(0.03)	(0.03)	(0.07)	(0.003)	(0.07)	(0.07)	(0.05)	(0.002)	(0.05)	(0.05)
SST	29.38				29.08				29.14				28.80			
	(0.10)				(0.10)				(0.21)				(0.14)			
								Mean Daily Current Speed ($m\ s^{-1}$)								
	Speed	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**	**Speed**	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**
Pinnacle	0.079	0.037	0.012	0.177	0.093	0.038	0.019	0.183	0.073	0.036	0.013	0.167	0.108	0.036	0.192	0.038
	(0.002)	(0.001)	(0.001)	(0.005)	(0.002)	(0.001)	(0.001)	(0.005)	(0.002)	(0.001)	(0.001)	(0.003)	(0.002)	(0.001)	(0.003)	(0.005)
Offshore	0.047	0.030	0.006	0.147	0.049	0.028	0.009	0.146	0.066	0.022	0.028	0.146	0.077	0.028	0.176	0.035
	(0.002)	(0.001)	(0.001)	(0.005)	(0.001)	(0.001)	(0.001)	(0.004)	(0.002)	(0.001)	(0.002)	(0.004)	(0.002)	(0.001)	(0.002)	(0.005)
Nearshore	0.056	0.030	0.017	0.152	0.047	0.029	0.013	0.142	0.049	0.025	0.015	0.127	0.058	0.034	0.153	0.009
	(0.002)	(0.001)	(0.001)	(0.005)	(0.001)	(0.001)	(0.001)	(0.004)	(0.001)	(0.001)	(0.001)	(0.003)	(0.002)	(0.001)	(0.003)	(0.003)

3.5 Discussion

This study presented year-long monitoring of in situ hydrodynamic data acquired from coral reefs in Kimbe Bay, Papua New Guinea. The reefs represented three distinct geomorphologies that differed in shelf position, crest depth and overall physical structure. I found that both current speeds and temperature exhibited distinct patterns at these reefs throughout the year.

3.5.1 Distinct hydrodynamics on submerged coral pinnacles are defined by strong and variable current speeds

My results were consistent with the expectation that pinnacles and offshore reefs would experience the strongest currents as a result of greater exposure to prevailing regional currents and weather. Cross-shelf gradients in exposure and environmental stressors are well documented on coral reefs that span continental and coastal shelves (Williams 1982; Lentz and Fewings 2012; Lowe and Falter 2015). Reefs in nearshore, mid-shelf and offshore positions experience distinct environmental regimes which lead to variation in habitat structure and ecological assemblages (Emslie et al. 2010; Malcolm et al. 2010; Macdonald et al. 2016; McClure et al. 2019). Although the offshore reefs in Kimbe Bay experienced a similar absolute range of current velocities as pinnacles (Table 3.3), these high current speeds were not sustained, as reflected by lower average maximum and mean values. As such, I found no evidence to suggest that most annual attributes of current speed (mean, variability, min) were different between nearshore and offshore reefs (Appendix B Table S3.2). This suggests that despite seascape position, hydrodynamics at the depths surveyed were more similar on all emergent reefs and that pinnacles consistently experienced stronger and more variable current velocities.

I propose that these differences are a product of distinct interactions between submerged physical structures, deeper crests and impinging oceanic flows. I do not suggest that these phenomena are of the scale associated with seamounts, such as Taylor cones (Huppert 1975) or enclosed circulation cells (Beckmann and Mohn 2002). However, my results suggest that there may be some localised interactions generating accelerated currents on submerged coral pinnacles. Some primary factors that determine the character of flow at seamounts include seamount height, local ocean density stratification (dependent on salinity, temperature and pressure), seamount morphology (base width and slope) and impinging steady and oscillatory currents (Lavelle and Mohn, 2010). The pinnacles in my study reach to 20-30m, rising steeply from depths of 600m in the middle of the bay. The bay also possesses several distinct internal circulations which are also influenced by stronger regional gyres (Steinberg et al. 2006) and the coastal shelf of West New Britain descends steeply to depths of over 1000m in the north of the bay. I therefore find it reasonable that currents reaching pinnacles will be modified by the same factors that determine dynamic currents on seamounts, albeit on a smaller scale. Although currents clearly reach the deep slopes of emergent reefs, refraction and the propagation of internal waves can distribute energy horizontally around the structure or vertically up the slope (Wolanski and Delesalle 1995; Wolanski et al. 2004; Davis et al. 2020). In this way, much hydrodynamic energy continues to be focused on the crest or is dissipated around the structure. In contrast, on submerged features, the water column above the summit or crest facilitates localized hydrodynamic responses which may then be retained and focused on the summit (Fig. 3.1). Flow enhancement is often more pronounced on elevated features of a seamount (Ramirez-Llodra et al. 2010; Watling and Auster 2017) and my study supports others which show that these effects also occur on isolated pinnacles and other bathymetric highs (Leitner et al. 2021).

These processes have important biological implications as stronger currents tend to enhance feeding opportunities for some organisms and can therefore shape ecological assemblages (Hamner et al. 1988; Lenihan et al. 2015; Watling and Auster 2017). Additionally, increased turbulence can re-suspend sediment and detritus that has been trapped on the summit, generating further benefits to sessile suspension feeders like sponges and corals (Genin et al. 1986). Temporary eddies and small vortexes can also enhance the availability of dissolved particulate matter and nutrients in multiple directions by downflux, upwelling flux and retention over a summit (Mullineaux and Mills 1997; Lavelle and Mohn 2010). In offshore settings with clearer waters, this enhanced nutrient availability may increase complex coral cover at greater depths. Similarly for fish, although peaks in diversity can vary with depth on emergent reefs (Brokovich et al. 2008; Bejarano et al. 2014; Pyle et al. 2019) enhanced hydrodynamic environments coupled with complex habitat could explain observations of high species richness and abundance of fishes at small, isolated submerged coral reefs, despite greater absolute depth.

3.5.2 Reef type variability in temperature regimes

Rising sea temperature is a key factor contributing to the global loss of significant areas of shallow water coral reef communities (Heron et al. 2016; Hoey et al. 2016; Dietzel et al. 2020). Localized hydrodynamics like upwelling and internal waves can moderate the ecological impacts of thermal stress and on some reefs may offer temporary or seasonal refuge (Randall et al. 2019; Storlazzi et al. 2020; Wyatt et al. 2020). Therefore, understanding processes that confer resilience by thermal buffering is critical to identify the distribution of future coral reef habitats. Although hydrodynamics have a strong influence on thermodynamics on all reefs (Leichter et al. 2005; Rogers et al. 2016; Green et al. 2019; Reid et al. 2019), differences in current regimes between emergent and submerged morphologies may lead to divergent responses to thermal stress. Temperatures are generally lower on deeper reefs (Slattery et al. 2011), but the extent to which site-specific currents influence thermal regimes is not well known. Depth does not represent a panacea for shallow reef communities (Bridge et al. 2013; Frade et al. 2018; Rocha et al. 2018; Bongaerts and Smith 2019), but thermal refuges may be more pronounced on submerged bathymetries with strong hydrodynamic environments. Pinnacles had the smallest range in temperature throughout the year (4.7 ^{o}C) suggesting more stable thermal environments with restricted maximum temperatures. One of the most pronounced differences I found was during the winter when the average temperature on pinnacle reefs was 1.75 ^{o}C cooler than on offshore sites. If these differences are generated by unique submerged structure-flow interactions, it highlights the importance of reef morphology rather than depth alone for the future distribution of coral reef communities under climate change.

Whilst this study did not directly assess the relationship between current speed and temperature there were some moderate negative correlations at two pinnacle reefs, Joelles (r = -0.25, p < 0.01) and Inglis Shoals (r = -0.20, p<0.001). In contrast, positive correlations were found at two offshore reefs, Ottos (r = 0.29, p<0.001) and Hogu (r=0.67, p <0.001). Nearshore reefs had variable trends including a strong negative correlation at Donna's (r = -0.58, p <0.001), but positive correlations at other nearshore sites (Appendix B Table S3.19). Whilst this does suggest some thermoregulatory effect of strong currents at some sites it also highlights site-specific variability in hydrodynamics.

Although I classified my study sites by grouping reefs with broadly similar morphological structure, there is still considerable variation in overall reef size, slopes, surrounding bathymetry and seascape position. The large range between absolute maximum and minimum temperatures (9.76 ^{o}C) observed on nearshore reefs probably reflects the proximity of these sites to higher inputs of cooler fresh water from run-off and river plumes (Neves et al. 2016). Stronger, but warmer currents at some offshore sites could be due to the location of these sites within pockets of enclosed circulations which have less exchange with cooler seasonal gyres in the wider Bismarck Sea. Certainly the lack of currents reaching some nearshore sites from particular directions indicates that different circulating currents operate across the bay.

3.5.3 Mismatched in-situ temperatures and SST

During the 2018-2019 study period, coral reefs in Kimbe Bay experienced average annual temperatures (30.53 – 31.33 ^{o}C) that exceed coral reef global average maxima (29.5 ^{o}C) (Kleypas et al. 1999). Kimbe Bay is located in the Western Pacific Warm Pool (WPWP), one of the warmest parts of the ocean and so temperatures tend to be relatively warm and stable throughout the year (Ayliffe et al. 2004). The WPWP is also strongly connected to El Niño Southern Oscillation (ENSO) events (Lindstrom et al. 1987) and the onset of an ENSO event in December 2018 which extended until August 2019 may reflect high and slight upward trend in temperatures at all reef types throughout the year. My in-situ temperature data was between 1.63 – 2.43 ^{o}C warmer than the average annual temperature obtained from SST data (28.90 ^{o}C) (Table 3.1). This contrast supports the wide recognition of mismatches between global models of sea surface temperature and field results (Sully et al.

2019). The inverse stratification evident in my results is consistent with my experience of diving in Kimbe Bay. Cooler surface waters could be explained by the semi-enclosed nature of the bay together with its large river catchments and high annual rainfall (3,180 mm per annum, Steinberg et al. 2006). This has important consequences for the mixing of water layers and therefore differences in energy and nutrient cycles between depths (Tilstra et al. 2018). Lower temperatures on pinnacles could also represent some degree of isothermal doming of cooler deeper water over the summit, which is another prominent hydrodynamic process on seamounts (Read and Pollard 2017; Hosegood et al. 2019). A more detailed investigation of water column properties including salinity, dissolved oxygen, turbidity, chlorophyll concentrations and temperature to greater depths would be required to comprehensively describe stratification patterns in Kimbe Bay.

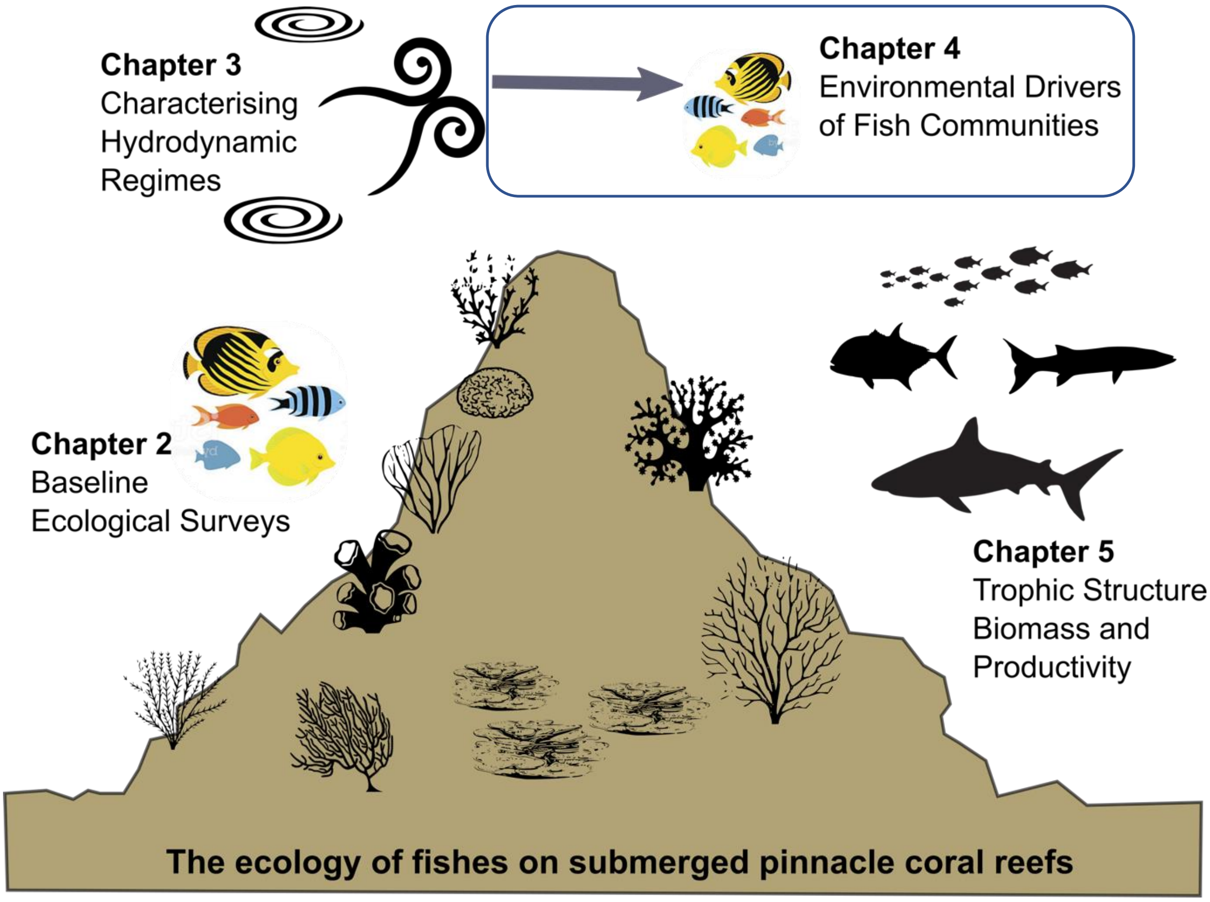
3.5.4 Potential influence of broader regional seasonality driving mismatches in thermal maxima

Kimbe Bay does not experience typical seasonality but instead two distinct seasons associated with the Southeast Asian/Australian monsoon system (Srinivasan and Jones 2006; Steinberg et al. 2006). Between November to March (Summer) the Northwest monsoon system brings higher rainfall and prevailing easterly currents. In May to October (Winter) a drier season prevails with strong south-easterly trade winds which can reverse the direction of local currents and gyres in the Bismarck Sea (S.Choukroun, pers.com). These changes clearly influence temperature regimes in Kimbe Bay throughout the year. However, the seasonal differences I observed were not consistent between reef types. The warmest season on pinnacles was Autumn, but was Winter for nearshore and offshore reefs. The higher autumn temperatures on pinnacles corresponded with the lowest and least variable current speeds at these sites. Temperatures then dropped in Winter which corresponded with increased frequency of strong spikes in current velocities. Although currents were also highest in Winter for nearshore and offshore reefs, this did not correspond with lower temperatures. The high frequency of spikes in stronger currents corresponding with lower temperatures could indicate upwelling signatures on pinnacle reefs. Nearshore and offshore reefs did experience some spikes in current speed throughout the year, but these patterns were not of the same magnitude. Upwelling can occur along the coast of New Britain and Kimbe Bay during the southeast trades when the wind is oriented offshore (Cresswell, 2000). These currents may be amplified on steep-sided pinnacles in the bay resulting from the flow-structure interactions already suggested (Fig. 3.3).

3.5.5 *Conclusions*

While hydrodynamic forcing and thermodynamics on fringing, barrier and atoll reef systems have been well investigated (Lowe and Falter 2015; Rogers et al. 2016), few studies have examined variation in these processes between submerged and emergent reefs in one geographic region. My results highlight that differing reef morphologies can experience distinct spatio-temporal variation in hydrodynamics at the same depth over the same annual period. Hydrodynamics on coral reefs are important ecological drivers and my results provide a good foundation for further studies examining patterns of biodiversity on submerged reefs. Future work should also include the collection high-resolution physical data (e.g. salinity, chlorophyll, dissolved oxygen) to enhance our understanding of biophysical coupling on submerged coral reefs and significantly expand on the preliminary results presented in this study. My results likely extend to other submerged pinnacle coral reefs, but studies in additional locations are required to determine the generality of these patterns. Hydrodynamics that enhance productivity and drive thermoregulatory mechanisms are especially important in light of future warming from climate change and global degradation of shallow reefs (Rogers et al. 2016; Randall et al. 2020; Storlazzi et al. 2020). Although depth and isolation are often held to afford some degree of refuge, distinct environmental conditions generated by abrupt submerged morphologies highlights the importance of submerged coral reefs in future coral seascapes.

Chapter 4


Chapter 3
Characterising Hydrodynamic Regimes
Chapter 4
Environmental Drivers of Fish Communities
Chapter 2
Baseline Ecological Surveys
Chapter 5
Trophic Structure Biomass and Productivity
The ecology of fishes on submerged pinnacle coral reefs

Chapter 4: Strong hydrodynamic drivers of coral reef fish biodiversity on submerged pinnacles

4.1 Abstract

Hydrodynamic processes are important features in all marine environments and on coral reefs are important determinants of habitat zonation, community structure and biodiversity. However, differences in reef attributes including size, depth and location can affect the nature of these processes. Submerged reefs are less affected by surface wave energy and often possess distinct localised currents as a result of interactions between the physical structure, the water column above and impinging flows. These mechanisms are thought to drive enhanced biophysical coupling helping to explain patterns of high abundance and biomass of fishes at these habitats. I characterised and compared fish biodiversity on emergent and submerged pinnacle coral reefs in Papua New Guinea. Submerged pinnacles possessed higher fish biomass, abundance and species richness than emergent reefs. Differences in diversity were not large between reef types, but pinnacles supported similar levels of diversity despite their much smaller habitat area. I collected in-situ current speed and temperature data over a full year at each reef to define hydrodynamic regimes and used random forest analysis to investigate the relative influence of hydrodynamics compared to other well-established drivers of reef fish biodiversity. Nineteen environmental variables explained 73% and 55% of variability in models for fish species richness and abundance respectively. This was lower for models of biomass, 35% of variability explained and diversity, 16% of variability explained. In all models reef area, maximum current speeds, measures of current speed variability, maximum temperature and variability of temperature were consistently amongst the most influential variables. Hydrodynamics were also constantly ranked as highly important and I found evidence of distinct hydrodynamic regimes on pinnacle reefs compared to emergent coral reefs. Pinnacles experienced stronger and more variable current speeds, which may reflect an energetic mechanism that supports high biodiversity on small patch habitats, similar to

biophysical coupling processes thought to occur on seamounts. Relationships between fish biodiversity metrics and hydrodynamic variables were examined using generalized mixed effect models. This particular analysis did not yield conclusive results, but did highlight the association of the pinnacle hydrodynamic regime with high fish richness, abundance and biomass. My study demonstrates the ecological value of small, submerged coral reefs, which are globally numerous yet remain understudied in coral reef ecology.

4.2 Introduction

Patterns in biodiversity are driven by numerous biotic and abiotic factors operating across multiple spatial and temporal scales (Gaston 2000; Violle et al. 2014; Worm and Tittensor 2018). A central tenet of ecology is to understand the relative influence of these drivers in structuring ecological communities (Pianka 1966; Dunning et al. 1992; Gilbert and Lechowicz 2004). In marine environments, hydrodynamic processes are a fundamental group of physico-chemical factors that define environmental conditions through the movement of water. At global scales, oceanographic processes such as surface-driven waves, deeper density-driven circulations and tidal cycles connect oceans physically and biologically (Carr and Kearns 2003; Treml et al. 2008; White et al. 2010). At smaller spatial scales, within individual habitats, local hydrodynamic conditions create important physico-chemical gradients that can determine the structure of ecological communities (Depczynski and Bellwood 2003; Burgess et al. 2007; Wolanski and Kingsford 2014; Eggertsen et al. 2016). These site-specific hydrodynamic mechanisms include wave energy gradients, upwelling, internal waves, flushing and thermoregulatory currents (Possingham and Roughgarden 1990; Wolanski and King 1990; Green et al. 2018; Randall et al. 2019). Hydrodynamics therefore closely connect physical and biological processes in all marine systems (Werner et al. 2007; Ramesh et al. 2019).

Coral reefs are a notable example of how hydrodynamic processes are closely linked to distinct patterns and processes in marine biodiversity. The paradox of these thriving and diverse ecosystems is that they are surrounded by otherwise clear, oligotrophic tropical waters (Hatcher 1990; de Goeji et al. 2013). This was recognised by Darwin (1842) who also noted “that the strongest and most massive corals flourish, where most exposed” - at the seaward edges. Numerous studies have now demonstrated how ocean currents bring allochthonous nutrients to coral reef communities and the wealth of hydrodynamic mechanisms that shape coral reef communities (Hamner et al. 1988; Wolanski and Hamner 1988; Leichter et al. 2003; Gove et al. 2016). For example, the distinct pattern of habitat zonation on shallow coral reefs is initially driven by waves at the seaward edge where mechanical action and turbidity are high (Goreau 1959; Bradbury and Young 1981; Symonds et al. 1995). Distinct ecological communities are found in each zone following a gradient of hydrodynamic energy as waves dissipate from the crest into the lagoon (Done 1983; Lowe et al. 2009).

Currents and tidal flows also play a fundamental role in connecting marine populations and defining distributions (Schill et al. 2015; Teske et al. 2016; Fisher et al. 2018; Bode et al. 2019; Nalesso et al. 2019). At the evolutionary scale, spatial patterns in marine diversity have been shaped by long-term oceanographic processes, facilitating range expansions, randomising recruitment events and also forming barriers to dispersal (Barber et al. 2000; Cowen et al. 2006; Gaines et al. 2007). At the scale of the individual the fluid-mechanics of water enhance diversity on coral reefs by creating energetic costs and opportunities that drive behavioural and physiological adaptations to the dynamic environment (Sebens 1997; Koehl et al. 2001; Liao 2007). In fishes, multiple swimming modes, body forms and fin morphologies have evolved to deal with strong and variable current flows in order to gain better access to resources (Fulton 2007; Binning and Roche 2015; Bridge et al. 2016). A practical knowledge of hydrodynamic processes also informs effective conservation measures, such as incorporating currents into protected area network design (Roberts 1997; Munguia-Vega et al. 2018; O’Leary and Roberts 2018) and understanding how ecological responses to disturbances are potentially mediated by water flow (McClanahan et al. 2005; Comeau et al. 2014; Rogers et al. 2016; Storlazzi et al. 2020).

There is now a substantial body of literature detailing the biological and environmental factors driving tropical coral reef communities (Forrester 2015; Mora 2015; Jouffray et al. 2019; Samoilys et al. 2019) and our understanding of hydrodynamics and biophysical-coupling on coral reefs has also advanced considerably in recent decades (Wolanski 2000; Monismith 2007; Lowe and Falter 2015). Most research however, has focused on shallow emergent coral reefs. Emergent reefs rise to within the upper 10m of water and so hydrodynamics here are dominated by surface driven waves and tides (Munk and Sargent 1948; Gourlay 1996; Hearn 2011; Lugo-Fernández and Roberts 2011). Shelf-position (exposure), geomorphology and habitat zonation also determine multiple gradients in wave and tidal energy which determine subsequent ecological effects (Hutchings et al. 2002; Kench and Brander 2006; Williams et al. 2013; Gove et al. 2015; Bellwood et al. 2018; Samoilys et al. 2019). Few studies however, have examined aspects of coral reef hydrodynamics at depths below 20m (but see Vaz et al. 2016; De Clippele et al. 2018; Williams et al. 2018; Valle-Levinson et al. 2020).

This represents a substantial knowledge gap, as globally there are significant areas of coral reef habitat on submerged bathymetric features, which I define as reefs with crests occurring below 10-20m (Bridge et al. 2012; Harris et al. 2013; Thomas et al. 2015). These include large contiguous banks and ridges descending from continental shelves and also distinct detached patch habitats like seamounts and smaller similar structures: pinnacles, bommies and knolls (Abbey and Webster 2011). Not only are these reef morphologies less well studied than emergent coral reefs, many are still being discovered by increased global bathymetry mapping efforts (Schmitt Ocean Institute 2020). Where seamounts are large (>1000m elevation) conical structures typically formed by volcanic activity on oceanic plates (Wessel 2001; Clark et al. 2011) pinnacles are smaller conical features usually associated with coastal shelves, or are part of other larger submerged topographies (Birkeland 1971; Abbey et al. 2010). In ecological terms, seamounts and pinnacles are physically similar structures which can support diverse and highly abundant ecological communities (Thresher et al. 2011; Koslow et al. 2016; Richert et al. 2017). Submerged coral reefs are ubiquitous across tropical seascapes, but few studies have compared patterns of biodiversity or environmental drivers with shallow emergent coral reefs.

Although hydrodynamic processes clearly shape ecological patterns on all coral reefs, submerged pinnacle reefs do not fit the typical model of coral reef habitat zonation or morphological structure. On shallow emergent reefs the most influential hydrodynamic processes occur in the upper 10m of water (Done 1983; Massel and Gourlay 2000; Gourlay and Colleter 2005). Currents and upwellings travel up the slope, waves break over the crest and hydrodynamic energy dissipates over the reef flat, forming a linear gradient from the seaward edge into the lagoon (Goreau 1959; Symonds et al. 1995; Lowe et al. 2009; Davis and Monismith 2011). Due to greater crest depths (>10m), submerged reefs are generally less affected by surface driven hydrodynamics like waves (Roberts et al. 2015). Additionally, the summits of features like pinnacles and small seamounts are typically small in area and have no reef flat or lagoon. Instead, they are surrounded by the pelagic environment and currents potentially flow over the entire reef from multiple directions. Hydrodynamic activity on submerged reefs will therefore be distinct from emergent, wave-driven coral reef habitats. It follows that biological interactions with differing environmental gradients will also result in different patterns in key metrics of biodiversity including species richness, the abundance of individuals and ecological productivity.

The differing expectations for pinnacles and emergent reefs is evident from ecological studies describing patterns in biodiversity on seamounts. These submerged habitats are often characterised by high abundance and biomass of fishes, largely attributed to strong biophysical-coupling generated by distinct hydrodynamic regimes (Boehlert and Genin 1987; Lavelle and Mohn 2010; Mohn 2010). Strong, multi-directional currents impinge on the abrupt physical structure at depth, resulting in upwelling, localised eddies, enhanced vertical mixing, creating a dome of density-stratified nutrient-rich waters above the seamount (White et al. 2007). These physical processes focus and retain vertical and horizontal fluxes of trophic subsidies, promoting productivity that in turn supports higher trophic levels (Genin 2004; Genin and Dower 2007). As on seamounts, pinnacle coral reefs are known to aggregate diverse and abundant fish communities consisting of both pelagic and reef-associated species (Reed et al. 2005; Farmer et al. 2017; Richert et al. 2017). Given the physical similarities between seamounts and pinnacles, pinnacles likely share some aspects of these biophysical-coupling mechanisms, albeit on a smaller scale. Although there has been substantial investigation of hydrodynamics on shallow coral reefs and also on large mid-ocean seamounts, submerged pinnacles have received little scientific attention. The extent to which hydrodynamics influence fish community richness, diversity, abundance and productivity at these habitats therefore is relatively unknown.

The aim of this study was to establish the relative importance of hydrodynamics in shaping fish communities on morphologically distinct coral reefs in Kimbe Bay, Papua New Guinea (5°30’S, 150°05’E, Fig. 4.1). Reef types include nearshore and offshore emergent reefs and a series of offshore submerged pinnacle coral reefs. In Chapter 2 I found that these pinnacles support distinct communities of fishes, with a significantly greater abundance and species richness compared to emergent reefs in both nearshore and offshore locations (Galbraith et al. 2021). The pinnacle crests sit between 18-30m of water, are relatively small and spatially isolated, located 9-25km offshore from other large contiguous reef habitats in the bay (Green et al. 2009). In that study, both emergent and submerged reef morphologies were surveyed at the same depth (20-30m) and I found that established habitat-based drivers of reef fish diversity did not explain variation in fish communities well. This suggests that at the depths surveyed, other environmental factors are more influential in driving fish community structure. The present study therefore combines ecological community data from Chapter 1 with the in-situ temperature and current data from Chapter 3 to investigate aspects of hydrodynamics as key drivers of fish biodiversity on emergent and submerged reefs below 20m. Given the similarities in physical structure between seamounts and pinnacles, I hypothesise that distinct hydrodynamics on submerged pinnacle coral reefs support higher biodiversity than would be expected at small, isolated patch reefs. I specifically asked the following questions:

1) Do hydrodynamic variables override the relative importance of other well-established drivers of reef fish diversity? Numerous habitat and spatial variables are important determinants of reef fish community composition, especially when investigating ecological drivers on different reef morphologies (Bennett et al. 2018; Samoilys et al. 2019). For example, aspects of biogeography theory are particularly pertinent to community structure on small, isolated patch habitats like pinnacles (MacArthur and Wilson 1967; Hobbs et al. 2012; Hachich et al. 2015). However, on coral reefs where currents are both strong and variable, the relative influence of

hydrodynamics may be higher compared to other key environmental drivers of fish community structure, especially at greater depths. I therefore aimed to establish the relative influence of a combination of habitat, hydrodynamic and biogeographical variables on reef fish communities below 20m.

2) Does the nature of the relationship between fish diversity and hydrodynamic variables differ between reef morphologies? If current speeds and associated temperature regimes differ between reef with emergent and submerged morphologies in Kimbe Bay, I expect that changes in magnitude of important hydrodynamic variables may result in different associations with fish diversity metrics.

4. 3 Methods

4.3.1 Study area and sampling design

Kimbe Bay is a large tropical bay on the island of New Britain in the Bismarck Sea (5°30’S, 150°05’E, Fig. 4.1). The bay possesses a rich seascape including nearshore emergent fringing coral reefs, offshore emergent atolls and guyots as well as numerous submerged coral pinnacles (Green et al. 2007). A total of 12 reef sites were chosen for this study; 4 nearshore emergent reefs, 4 offshore emergent reefs and 4 offshore submerged pinnacles. All emergent reefs had crests at depths above 10m whereas submerged pinnacle crests were all deeper than 18m. All nearshore reefs were within 5km from mainland coastline and all offshore reefs between 9-25km from the nearest main landmass (Appendix C Table S4.1).

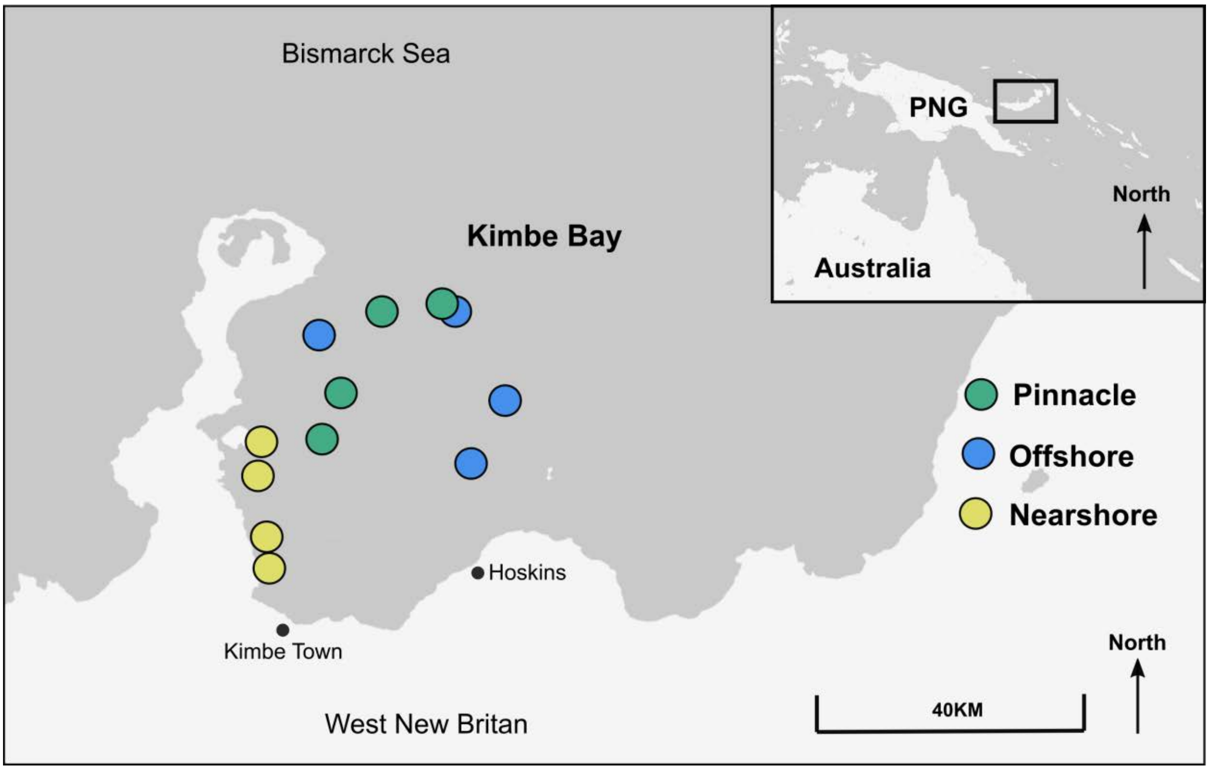


Figure 4.1 Study site location and survey reefs; Offshore submerged pinnacles (green), offshore emergent reefs (blue) and nearshore emergent reefs (yellow). Black dots show the locations of the main population centre of Kimbe Town and the airport at Hoskins.

4.3.2 Data Collection

Fish and benthic surveys

To establish measures of fish and benthic community diversity at each reef, surveys were conducted on SCUBA in October-November 2018 (survey 1) and April-May 2019 (survey 2). At each site, five replicate 30x5m transects were conducted within a depth band of 20-30m. Fish communities were surveyed using diver-operated stereo-video transects following protocols described in Goetze et al. 2019. Briefly, a stereo-video system (SeaGIS Pty Ltd, Australia) housing two GoPro Hero 4 cameras was swum pointing forwards at 0.5m above the reef by a diver swimming at a steady speed (approx. 20m/min). A second diver followed behind with a tape and signalled to the first diver when to end the transect. Both divers then returned along the transect, using another GoPro Hero 4 camera to conduct a video benthic point-intercept transect. The tape was marked with two random points every meter and the benthos directly under the tape filmed. Surveys were not conducted on steep slopes or walls. Near-horizontal ridges and low gradient slopes were selected at each reef to account for the effects of reef slope aspect which is a known driver of coral reef community differences (Jankowski et al. 2015; Oakley-Cogan et al. 2020).

Video Analysis – Fish

Fish survey videos were analysed in the specialist stereo-video software EventMeasure Stereo (SeaGIS, Pty Ltd, Australia). Cameras used to conduct stereo-video surveys were calibrated before and after the surveys using a 3D calibration cube and CAL software (SeaGis Pty Ltd, Australia). This allows for lengths of fish to be estimated within a known field-of-view (2.5m either side of transect). For each transect every individual that entered the lower two-thirds of the screen was identified to species based on Allen et al. 2003. Length estimates were made in EventMeasure Stereo using fork-length. Visual surveys tend to underestimate counts of small, benthic-dwelling or cryptic fish (Galland et al. 2017), therefore these groups are not well represented in this present study.

Video Analysis – Benthic

Benthic video point intercept transects were played back at a slow frame rate and the benthic substrate directly beneath each point identified. The substrate was classified as one of 47 types based on taxonomic group and morphology (Appendix C Table S4.2). From this data, I then calculated benthic diversity (Simpson's D), total hard coral cover (percentage), complex hard coral cover (percentage) and richness (number of substrate types) for each transect.

Hydrodynamic data - Current and temperature

To characterise current flow and thermal regimes at each site, Marotte HS Drag Tilt Current Meters (Marine Geophysics Laboratory, Australia) were installed at 20-30m depth during

May-July 2018. Current meters were installed on northerly sides of each reef at horizontal areas of reef where there were no surrounding obstacles to prevent free movement of the instrument. The current meters recorded temperature (°C), current direction (degree from north) and current speed (m s^{-1}) every 10 seconds during deployments. Current meters were recovered in September-October 2019, data downloaded and processed using the software MarotteHSConfig (http://www.marinegeophysics.com.au/software/). One current meter deployed at an offshore emergent site (Kimbe Island) was not successfully recovered during the study and so this site was removed from all further analysis. Using the data collected from current meters for the full study period (one year), an annual daily mean and standard deviation were calculated for both temperature and current speed at each site. Daily means using the same data were also calculated for each survey period at each site (Appendix C Table S4.3).

Selection of environmental variables

To compare the relative influence of hydrodynamic variables with other important environmental drivers of reef fish assemblage structure, I chose 12 measures of water temperature and current speed during different seasons and sampling periods using current meter data (hydrodynamics). I also derived 7 other environmental variables relevant to reef fish ecology and the scale of my study; two biogeographical and five habitat-related. Distance to nearest neighbouring reef (km) and distance to nearest mainland (km) were selected as biogeographical variables. Benthic diversity, benthic richness, total hard coral cover (%), complex hard coral cover (%) and reef area (km^2), from in-situ surveys and GIS spatial analysis were used as habitat-related variables (Table 4.1). Rationale and supporting literature for these variables are presented in an extended table in Appendix C Table S4.12.

Variable	Description	Source	Range	Unit
Biogeographical				
Nearest Mainland	Distance to closest mainland coast	GIS	0.73 – 24.59	Km
Nearest Neighbouring Reef	Distance to closest area of coral reef	GIS	0.11 – 12.01	Km
Hydrodynamic				
Annual Mean Temperature	Daily mean 12-month period	Current Meter	29.7 - 32.03	°C
Annual Mean Current	Daily mean 12-month period	Current Meter	0.04 - 0.09	m s^{-1}
Annual Temperature Variability (SD)	Standard deviation 12-month period	Current Meter	0.47 – 1.16	°C
Annual Current Variability (SD)	Standard deviation 12-month period	Current Meter	0.007 - 0.047	m s^{-1}
Annual Temperature Maximum	Average daily maximum 12-month period	Current Meter	31.2 – 35.2	°C
Annual Current Maximum	Average daily maximum 12-month period	Current Meter	0.09 – 0.60	m s^{-1}
Sampling Season Temperature Mean	Daily mean during sampling season	Current Meter	29.03 – 33.34	°C
Sampling Season Current Mean	Daily mean during sampling season	Current Meter	0.02 - 0.09	m s^{-1}
Sampling Season Temperature Variability (SD)	Standard deviation during sampling season	Current Meter	0.16 – 1.29	°C
Sampling Season Current Variability (SD)	Standard deviation during sampling season	Current Meter	0.004 – 0.06	m s^{-1}
Sampling Season Temperature Max	Average daily maximum during sampling season	Current Meter	29.7 – 35.0	°C
Sampling Season Current Max	Average daily maximum during sampling season	Current Meter	0.02 – 0.32	m s^{-1}
Habitat				
Hard Coral Cover	Percent cover of hard coral	Benthic point-intercept video transects	6.67 – 71.67	% cover
Complex Hard Coral Cover	Percent cover of complex hard coral		0 - 30	% cover
Benthic Diversity	Simpson's D		0.52 – 0.91	D
Benthic Richness	Variety of different benthic groups		8 - 15	n
Reef Area	Total area of reef habitat above 30m depth contour	GIS emergent reefs In-water surveys on submerged pinnacles	0.00013 – 0.62	km^2

Table 4.1 19 Environmental variables used in random forest analysis, data source, range and units. Hydrodynamic variables include averages, standard deviations and maxima for the annual period (Sept 2018 – Sept 2019) and for each sampling period during which fish surveys were conducted. Rationale and supporting literature for these variables are presented in an extended table in Appendix C Table S4.12.

4.3.3 Data analysis

All data analysis was conducted in R Studio (R Core Development Team 2021).

Fish diversity metrics

Using counts and length measurements obtained from stereo-video analysis I calculated four metrics of fish community diversity for each transect: fish species richness (S $150m^{-2}$), diversity (Simpson's index $150m^{-2}$), abundance (total individuals $150m^{-2}$) and biomass (kg $150m^{-2}$). Biomass was calculated using the length-weight equation:

$$W = aL^b$$

L represents fish fork length (cm), W is weight in grams and a and b are species specific constants obtained from FishBase (Froese et al. 2013) using the R package "rfishbase" (Boettiger et al. 2012).

I compared mean fish diversity metrics between reef types with Generalized Linear Models (GLMs) using the package "MASS" (Venables and Ripley 2002) with data pooled from both survey years. Models for fish species richness and abundance were fitted with a negative binomial error distribution and log link and models for fish diversity and (log10) biomass were fitted with Gaussian error distribution and identity link. Standard model diagnostics were performed for normality, homogeneity of variance and linearity using the "DHARMa" package (Hartig 2020). For each model, coefficient estimates and 95% confidence intervals were extracted and plotted including pairwise comparisons between estimates made using "emmeans" (Lenth 2020). For standardized partial effects the evidence suggests a significant effect if the confidence interval does not contain zero and for estimates on the odds ratio scale if the confidence interval does not contain one.

Relative influence of environmental variables on fish communities

Random forest models were used to assess the relative influence of 19 environmental variables on univariate fish diversity metrics: Simpson's diversity, species richness, abundance and biomass. Random forest (RF) is a machine learning technique well suited to inherent issues of non-linearity and multi-correlation characteristic of ecological data (Breiman 2001). Additionally, RF is an effective approach when the numbers of observations are comparatively low compared to the number of predictors (Svetnik et al. 2003). Briefly, RF constructs an ensemble of multiple decision trees using bootstrapped random samples of the original data. The results are aggregated and the relative importance of each predictor on the response is scored based on its effect on mean squared error (MSE) i.e. factors with the greatest effect on MSE have the largest influence on the response (Breiman 2001). RF models were implemented in R using "randomForest" with the default setting of 2/3 available data used to grow each tree and 1/3 data used for internal model validation (Liaw and Wiener 2002). RF model parameters ntree (the number of trees to grow) and mtry (the number of variables to consider at a given split) and node size were optimized for each model using the package "caret" (Kuhn 2020) and an overall R^2 value for each model generated. Variable importance plots were generated based on percentage increased MSE and partial dependency plots for the effect on the response when all other variables are held constant were produced for the top 4 environmental predictors in each model.

Relationships between fish diversity and important environmental variables

Although partial plots from RF models are excellent visualisations of the general trends assessed in the model, they do not allow for detailed exploration of these relationships, particularly when trying to examine differences in a response between different groups. I therefore used Generalised Linear Mixed Effects Models (GLMMs) to examine the relationships between the most important environmental variables identified by the Random Forest analysis and fish diversity. For each diversity fish metric (richness, Simpson's index, abundance and biomass) I constructed models with different combinations of the top three environmental predictors using the package glmmTMB (Brooks et al. 2017). Each model contained an interaction effect between continuous fixed effects and the categorical fixed effect ‘reef type’ (3 levels: “nearshore”, “offshore” and “pinnacle”. ‘Site’ nested within ‘reef type’ and ‘year’ was included in all models to account for potential differences between individual reef sites and the year they were surveyed. Where the ranges of the continuous co-variate in a model differed substantially between the three reef types, values for each reef type were scaled individually to fit the model and then back transformed for final interpretation.

Model construction began with the top three environmental variables from RF analysis and final model structure was determined using AIC scores and overall model convergence. Model fit was assessed using standard diagnostic techniques for normality, homogeneity of variance and linearity using the “performance” (Lüdecke et al. 2020) and “DHARMa” (Hartig, 2020) packages. For each model, coefficient estimates and 95% confidence intervals were extracted and plotted including pairwise comparisons between estimates made using the functions emmeans and emtrends from the package “emmeans” (Lenth 2020). For standardized partial effects the evidence suggests a significant effect if the confidence interval does not contain zero and for estimates on the odds ratio scale if the confidence interval does not contain one. r.squaredGLMM from the “MuMin” package (Bartoń 2019) was used to calculate a pseudo-R-Square estimate (Nakagawa and Schielzeth 2013; Nakagawa et al. 2017) which produces a marginal R^2(m) (an approximation variance explained by fixed effects) and a conditional R^2 (c) (an approximation of variance explained by the entire model including fixed and random effects). All plots for GLMMs were created using “ggplot2” (Wickham 2016).

4.4 Results

4.4.1 Fish biodiversity

A total of 13,122 individuals representing 191 fish species were identified from the combined survey data. Pinnacle reefs had highest mean species richness (S= 36.50, 95% CI = 33.30 - 40.01), which was 2.28 times that of offshore reefs (95% CI = 1.89 - 2.75) and 2.74 times the mean richness of nearshore reefs (95% CI = 2.30 - 3.27) (Fig. 4.2a).

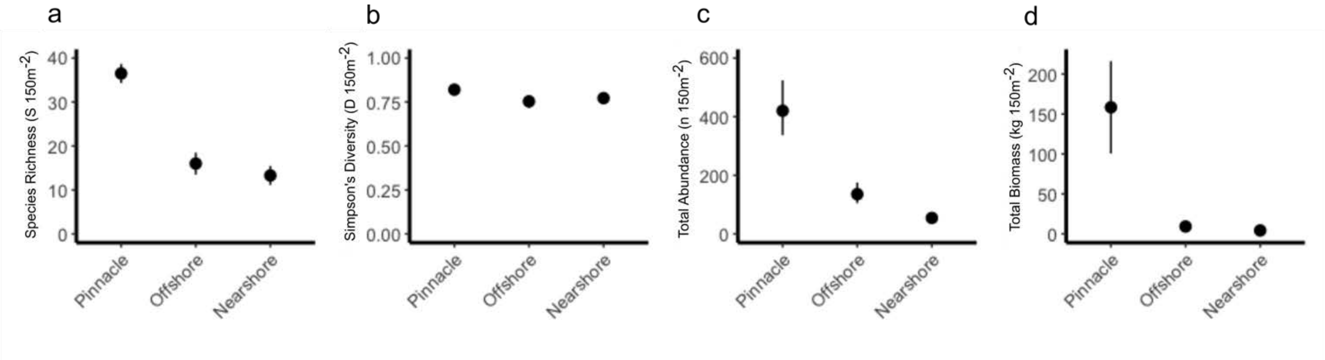


Figure 4.2 Estimated mean diversity metrics observed at each reef type **(a)** Species richness (S 150m^{-2}); **(b)** Diversity (Simpson's D 150m^{-2}); **(c)** Total abundance (individuals 150m^{-2}) and; **(d)** Total biomass (kg 150m^{-2}). Point ranges represent 95% confidence intervals (CI).

Pinnacles also had highest diversity (Simpson's: 0.82; 0.79 - 0.85), but the magnitude of the difference between nearshore (0.05; 0.01- 0.10) and offshore reefs (0.07; 0.01 - 0.12) respectively although significant, was not large (Fig. 4.2b, Appendix C Table S4.5). The pinnacles had highest total fish abundance (individuals = 420.23; 95% CI = 336.86 - 524.22) (Fig. 4.2c) and highest total biomass (kg = 501.3; 95% CI = 339.45 - 740.33) (Fig. 4.2d). These results are consistent with a previous study conducted at the same reef sites (Galbraith et al. 2021).

4.4.2 Relative influence of hydrodynamics and other environmental variables

Environmental variables differed considerably among reef types. Pinnacles are all smaller than other reef sites and were characterized by higher average current speeds, variability in current speed and lower temperatures (Appendix C Table S4.4). Offshore reefs experienced highest mean temperatures annually and during both survey periods and are larger in area than other reef types. Nearshore reefs were closest to other neighbouring reefs, mainland, and had the lowest range in current speed, but the highest range in temperature. The other habitat-related variables did not differ substantially between reef sites or morphologies, but complex coral cover was generally higher at pinnacle reefs (3.17-14.83%) compared to offshore (0.33-5.00%) and nearshore (0.67 – 7.67%) sites (Appendix C Table S4.6).

The random forest model for fish species richness ranked annual current variability, annual mean current, reef area and survey season temperature variability as the most influential factors. These were followed by 5 other hydrodynamic variables (Fig. 4.3a R^2=0.73). Most habitat-related variables were among the least influential. Partial plots of the four most influential variables show a generally increasing trend in fish richness with annual current variability (Fig. 4.3a.i) and mean annual current speeds (Fig. 4.3a.ii) that asymptote after 0.25 m s^{-1} and 0.075 m s^{-1} respectively. Richness was lowest on reefs with larger areas (Fig. 4.3a.iii) and higher on reefs with greater variability in temperature during the survey period (Fig. 4.3a.iv).

The RF model for fish diversity ranked reef area, maximum current observed during the survey, annual maximum temperature and variability of survey water temperature as the top four most influential variables (Fig. 4.3b; R^2=0.16). Larger reefs had lower fish diversity (Fig. 4.3b.i) as did reefs with higher annual maximum temperatures (Fig. 4.3b.ii). Increasing maximum current speeds during the survey period to around 0.23 m s^{-1} corresponded with a sharp increase in fish diversity (Fig. 4.3b.iii). Survey temperature variability showed a minor and major peak in diversity at around 0.3 m s^{-1} and 0.5 m s^{-1} respectively (Fig. 4.3b.iv). Habitat and other biogeographic variables were ranked as relatively low importance in the model.

Biogeographic and habitat variables were most important in the random forest model for fish biomass (Fig. 4.3c; $R^2=0.55$). Distance to nearest neighbouring reef was the most influential variable which showed a peak response in biomass at around 4km which remained generally high with increasing distance (Fig. 4.3c.i). Area was the second most influential variable, showing the same trend as richness and diversity (Fig. 4.3c.ii). Annual current variability was the third most influential variable for biomass which showed a similar response to species richness; increasing annual current variability led to increased biomass (Fig. 4.3c.iii). Mean annual current speed was the fourth most important variable and showed a sudden increase in biomass at current speeds over 0.08 m s^{-1} (Fig. 4.3c.iv).

The final random forest model for fish abundance ranked annual mean current speed, annual current variability, reef area and distance to nearest mainland as the top four most important variables (Fig. 4.3d, $R^2=0.35$). Increasing mean annual current speed (Fig. 4.3d.i) and mean annual current variability (Fig.4.3d.ii) resulted in increasing fish abundance whereas reef area demonstrated the same relationship as the other three models; smaller reefs had more fish (Fig. 4.3d.iii). Between 5-10km from nearest mainland, abundance of fish increased sharply and peaked at around 15km (Fig. 4.3d.iv). Results from all random forest models are presented in Appendix C Table S4.7.

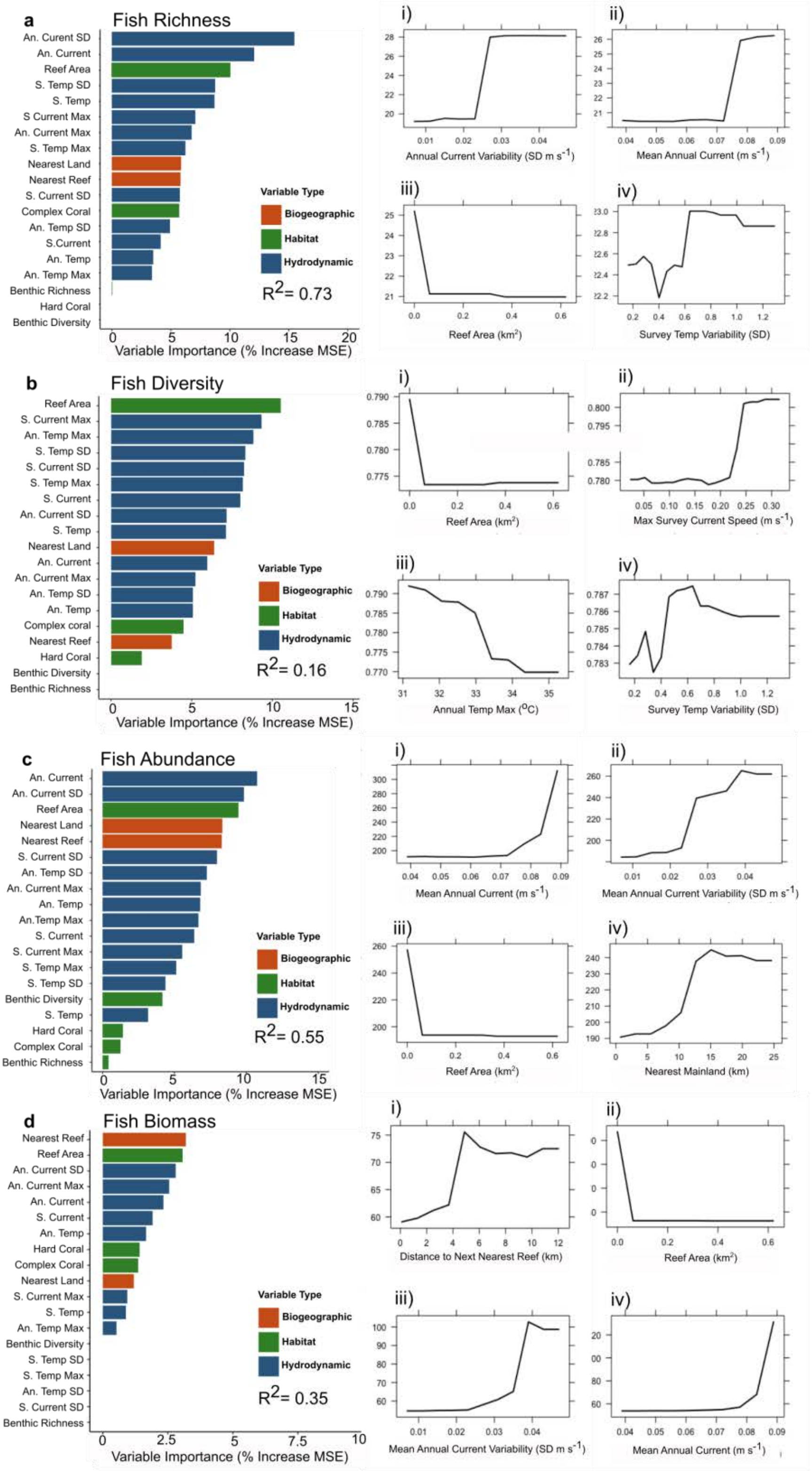


Figure 4.3 Relative importance of biogeographic, habitat and hydrodynamic variables in **(a)** fish richness **(b)** fish diversity **(c)** total fish abundance and **(d)** total fish biomass random forest models for fish communities in Kimbe Bay. Factors with highest values of percent increase in mean square error indicate more important variables in the Random Forest model. Partial plots for the top four most influential variables are denoted by numerals i-iv for each model.

4.4.3 Effect of environmental variables on fish diversity

The final GLMM for fish species richness used annual current speed variability with reef type as an interaction term (R^2m =0.74 , R^2c = 0.87) (Fig. 4.4a, Appendix C Table S4.8). There was no evidence of a significant effect of increasing current speed variability on fish richness for pinnacle reefs (slope estimate = 0.03, 95% CI = -0.08 – 0.14), but nearshore reefs showed a small positive trend (slope estimate = 0.4, 95% CI = 0.20 - 0.61) and offshore conversely a negative trend (slope estimate= -0.55, CI = -0.91 - 0.20). Pairwise tests of slopes confirmed that only nearshore and offshore reefs differed in the nature of response in fish richness to increasing current speed variability (offshore-nearshore contrast estimate = -5.90, 95% CI = -8.86 - -2.95) (Fig. 4.5a).

The final model for fish diversity contained maximum survey current speed and an interaction term with reef type (R^2m = 0.09, R^2c = 0.39) (Fig. 4.4b). Although results from the random forest analysis showed reef area to be the most influential environmental variable, these models account for a certain amount of interaction between variables, unlike univariate analyses. Given that area was highly correlated with both maximum survey current speed (the second most important variable) and annual maximum temperature (the third most important variable) and my study aimed to understand the relationship between fish diversity and hydrodynamics I chose maximum survey current speed as the main fixed factor in this model, but also included area in the model selection process (Appendix C Table S4.8). Although I found evidence that mean fish diversity is greatest on pinnacles at average maximum survey current speed (Simpsons's D estimate = 0.82, 95% CI = 0.75-0.89) pairwise comparisons with nearshore (estimate difference = 0.05, 95% CI = -0.12-0.22) or offshore reefs (estimate difference = 0.07, 95% CI = -0.11 – 0.24) were not significant (Appendix C Table S4.10). There was also no evidence to suggest that the nature of the relationship between fish diversity and maximum survey current speed differed between reef types (Fig. 4.5b, Appendix C Table S4.11).

Mean annual current speed, together with its interaction term with reef type, was selected as the final model for fish abundance (R^2m = 0.88 , R^2c = 0.92, Fig. 4.4c, Appendix C Table S4.8). At mean annual current speed at each reef type, pinnacles had 2.82 times the number of fish compared to offshore reefs (95% CI = 1.48 – 5.83) and 8.62 times the number of fish compared to nearshore reefs (95% C = 4.72 – 15.74). However, I only found evidence to suggest that increasing mean annual current speed increased fish abundance on nearshore reefs (slope estimate = 21.55, 95% CI = 4.24 - 38.87). No pairwise slope contrasts were significant due to large confidence intervals (Fig. 4.5c).

The final model for fish biomass included annual current variability and an interaction term with reef type ($R^2m = 0.67$, $R^2c = 0.71$, Fig. 4.4d, Appendix C Table S4.8). At an average level of annual current speed variability, pinnacle reefs had 28.94 times the estimated biomass of fish compared to nearshore reefs (95% CI = 14.14 – 59.25) and 8.14 time that on offshore reefs (95% CI = 3.75-17.65). Offshore reefs also had 3.56 times estimated biomass than nearshore reefs (95% CI = 1.64 – 7.71). I found no evidence for contrasting slopes (Fig. 4.5d). Full results of all GLMMs and pairwise comparisons are reported in Appendix C Tables S4.8 – 11.

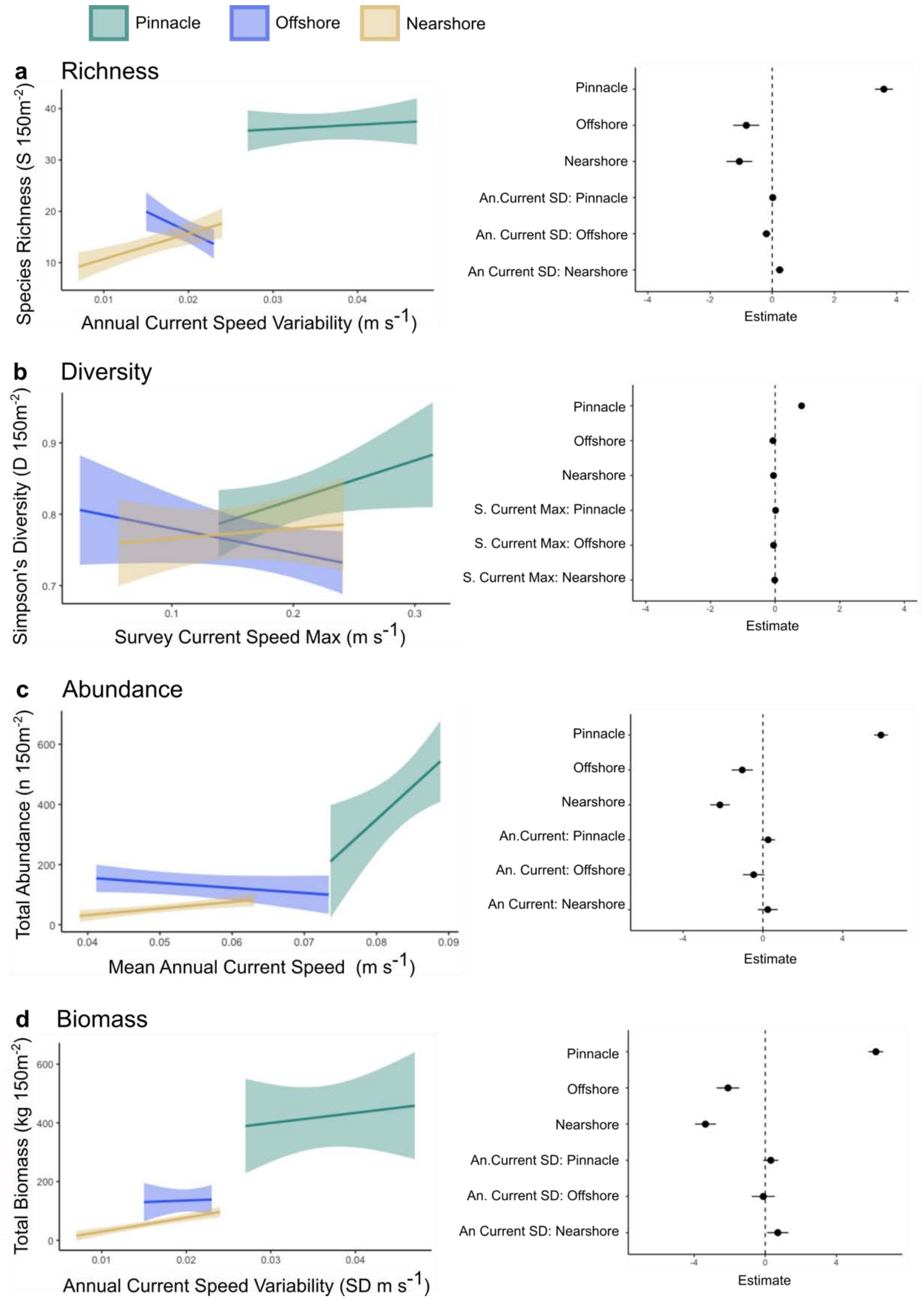


Figure 4.4 Generalized Linear Mixed Effects models for **(a)** species richness **(b)** Simpson's diversity **(c)** total abundance and (**d)** biomass for fish communities on three different reef types in Kimbe Bay. Each model used the most important environmental variable identified by random forest analysis together with an interaction term with 'reef type' as fixed factors. Site and year were included as random factors nested within reef type.

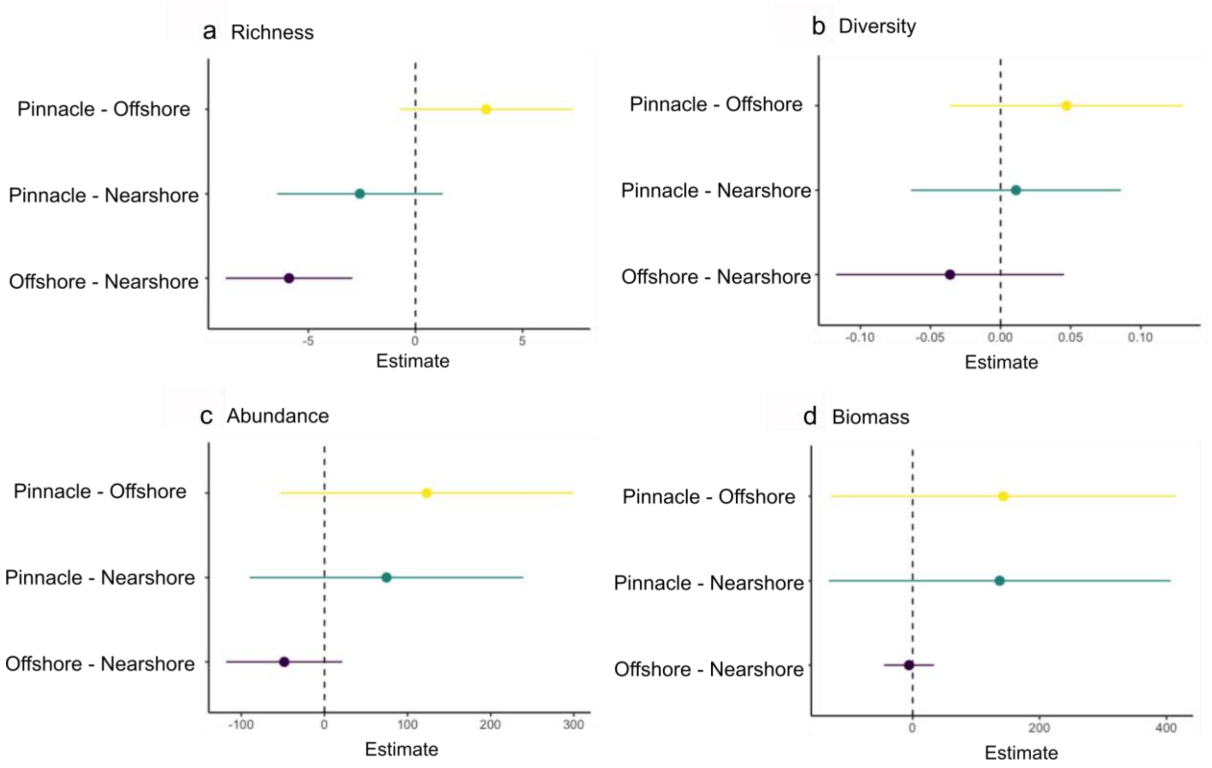


Figure 4.5 Estimated pairwise slopes contrasts for **(a)** Species richness **(b)** Simpson's Diversity **(c)** Total abundance and **(d)** Biomass. Contrast estimates plotted with 95% confidence intervals represent the difference between pairwise reef type groups. There is evidence to suggest a significant difference if the confidence interval does not contain zero.

4.5 Discussion

My study strongly suggests that the higher richness, diversity, abundance and biomass of fishes on submerged pinnacles is primarily driven by hydrodynamic processes. I found that average, maximum and variability in current speeds explained most variation in fish metrics between the three different reef habitat types. Maximum temperature and variability in average temperature was also important for fish abundance, diversity and species richness. Reef area was the only habitat variable to consistently rank highly in random forest models and the nature of the relationship with fish metrics was always negative (i.e the smallest reefs supported greatest fish biodiversity). This suggests that habitat-specific environmental conditions are generated by different reef morphologies at the depths studied.

This contributes to growing evidence that deep patch coral reef habitats can support high species richness, abundance, biomass and possess similar diversity of fishes, even when smaller in size compared to larger, shallow coral reef habitats. These results are also consistent with studies of seamount ecological communities that have shown reefs on these features to support abundant and diverse ecological communities (Boehlert 1988; Morato et al. 2010; Thresher et al. 2011; Rogers 2018). Habitat-specific environmental variables like higher current speeds, high variability in currents (which suggests sudden pulses or upwellings) and lower maximum temperatures may confer elements of resilience to degradation of the direct reef habitat due to environmental change (Rogers et al. 2016; Reid et al. 2019; Storlazzi et al. 2020). However, fish communities will still be sensitive to changes in water temperature and altered regional or global circulations, both of which likely to occur as climate change continues (Munday et al. 2012; Winton et al. 2013; Poloczanska et al. 2016; Shedrawi et al. 2017; Illing et al. 2020) .

Reefs in Kimbe Bay span a wide range of biogeographic, ecological and hydrodynamic gradients for the environmental variables examined. Hydrodynamic variables were consistently in the top four most highly influential environmental variables affecting fish biodiversity (Fig. 4.3a and b). The hydrodynamic variables used in GLMMs for richness, abundance and biomass explained 74%, 88% and 67% of variance in the data respectively. Although all biodiversity metrics were highest on pinnacles I found no evidence of significant relationships with the magnitude of the hydrodynamic covariate for pinnacle reefs in any GLMM. There is however, a notable difference in the ranges of all hydrodynamic covariates in each model. For example, no pinnacle site experienced average annual current speeds lower than 0.07 m s $^{-1}$ whereas nearshore and offshore reefs did not exceed this value during the study period (Fig. 4.4c). Similarly, survey season maximum current speeds on pinnacles ranged between 0.14 – 0.32 m s $^{-1}$ while nearshore and offshore reefs collectively ranged between 0.02 - 0.24 m s $^{-1}$ (Fig. 4.4b). Near and offshore reefs broadly overlap in range of current speeds and variability, but pinnacles exhibited higher ranges with little to no overlap with the other reef types. My results align with the idea that abrupt submerged topographies generate distinct hydrodynamic conditions as a result of interactions between the physical structure, crest depth and impinging flow and that these conditions in turn may result in distinct biotic communities (Lueck and Mudge 1997; White et al. 2007; Lavelle and Mohn 2010; Leitner et al. 2021).

Whilst it is unlikely that pinnacles generate large-scale hydrodynamic features like Taylor-Columns, disruption to surrounding currents will generate some localized response. The water column above submerged structures can facilitate the formation of secondary circulations like increased turbulence, small vortexes and amplified flow (Eriksen 1991; Brink 1995). These mechanisms on seamounts are proposed to enhance vertical mixing and food availability, supporting high species richness and biomass often from higher trophic levels (Bohelert and Gennin 1987; Morato et al. 2010). The consistently high current speeds and fluxes on pinnacles could represent a consistently enhanced supply of resources to these small patch reefs, sustaining higher levels of productivity and explaining the greater richness, abundance and biomass I observed.

For species richness, abundance and biomass, longer-term annual measurements were generally ranked higher than those recorded for the survey season only, suggesting the importance of prevailing hydrodynamic conditions. Although random forest models ranked survey season maximum current speed as the most important hydrodynamic variable, the GLMM for diversity and maximum survey current only explained 9% of variability in the data. There was also no strong evidence for large differences in Simpson's diversity between reef types (Fig. 4.2, Appendix C Table S4.5). Many larger reef fish are known to aggregate in strong currents where they benefit from enhanced plankton supply (Hamner et al. 1988) and predatory species are known to exploit fast currents to enhance prey capture success (Hill and Grossman 1993; Porter and Motta 2004). Large-bodied schooling planktivores (*Naso hexacanthus, Naso vlamingii, Acanthurus thompsoni, Acanthurus nubilis*) and barracuda (*Sphyraeana qenie*) were highly abundant at the pinnacle sites during my surveys. The diversity index I used (Simpson's D) relies on the dominance of common species and is relatively insensitive to changes in absolute species richness. The hyper-abundance of these species (largest school of *S. qenie* ~ 800 individuals) common in high-current environments such as pinnacles is probably driving the lack of large differences in diversity between reef types and highlighting the importance of maximum current speed in these systems.

Biogeographic variables were ranked highly in random forest models for fish abundance and biomass (Fig. 4.3c and d). Fish abundance increased with distance from land, consistent with studies that demonstrate how this gradient is typically driven by anthropogenic influence and land-based disturbances (Demartini et al. 2008; Williams et al. 2011, 2015; Neves et al. 2016; Smallhorn-West et al. 2020). Although fishing pressure is relatively low in Kimbe Bay (Green et al. 2009), nearshore reefs are most accessible to coastal villages and few people have access to outboard engines to fish offshore which may explain this trend. Distance to the nearest other reef was the single most important factor for fish biomass which was higher at more isolated reefs. The effect of isolation on community structure is however highly complex and hard to disentangle at large scales from other important habitat characteristics like area and landscape arrangement (Haddad et al. 2015; De Camargo et al. 2018; Fahrig 2020; Jones et al. 2020).

The classic model of Island Biogeography Theory (IBT) predicts that smaller, more isolated islands have less species than larger ones closer to mainland (MacArthur and Wilson 1967). A recent functional and trophic extension to IBT on coral reefs found that small isolated reefs have a higher proportion of large-sized species compared to more connected reefs of larger area (Jacquet et al. 2017). This was true of the pinnacles in my study where schools of large-bodied planktivores and predatory fishes drove high abundance and biomass at these sites. Reef area was an important habitat factor in predicting fish richness and diversity, but contrary to IBT I found highest richness and diversity on the smallest reef sites, the pinnacles. Based on the dominance of hydrodynamic variables in my study, one explanation for this is that site-specific environmental conditions may increase resource availability within a small habitat area, in turn increasing species richness and abundance through the provision of energetic subsidies (Wright 1983; Srivastava and Lawton 1998; Carrara and Vázquez 2010).

High variability in currents on the pinnacles in my study could result in fluxes of oceanic-derived nutrients from internal waves or current-driven upwelling (Mullineaux and Mills 1997; Lavelle and Mohn 2010) which would benefit fish communities by increasing feeding opportunities (Rowden et al. 2005; Genin and Dower 2007; Morais and Bellwood 2019). Additionally, some species of fish use areas of high currents to rest, hunt and thermoregulate (Matern et al. 2000; Barreiros et al. 2002; Porter and Motta 2004; O ’toole et al. 2010). Currents flowing over submerged reefs therefore extend available habitat both above and around the reef, providing resources for semi-pelagic species as well as site-attached residents. On nearshore reefs, fish species richness and biomass exhibited a small positive trend in this relationship. Average current speeds at nearshore sites were generally low and so pulses of higher currents may deliver these benefits to fish biodiversity on sheltered, low-energy nearshore reefs, albeit in a reduced form.

The ability of currents to boost biodiversity should be considered in conjunction with habitat complexity. I observed weak negative trends in species richness and abundance at offshore sites with increasing annual current speed and variability in contrast to nearshore sites. Although high current flow can provide enhanced feeding opportunities on coral reefs it also presents increased energetic costs to individual organisms (Fulton et al. 2013; Johansen 2014; Nadler et al. 2018; Marcoux and Korsmeyer 2019). Currents may therefore increase niche space and resources for some species while restricting the distribution of others. To take advantage of these conditions, morphological adaptations have developed in some species to enhance swimming performance and reduce energetic costs (Fulton and Bellwood 2005; Liao 2007; Heatwole and Fulton 2013). For reef fishes with lower critical-flow limits (i.e the water velocity at which they can no longer swim against the current), behavioural adaptations have also evolved that allow these individuals to occupy highly turbulent and wave swept habitats (Johansen et al. 2008). These behaviours depend on the availability of sufficient complex habitat which not only provides important refuge from predation, but is also used to shelter from strong currents (Kerry and Bellwood 2015, 2017). Even small, low-relief benthic structures have been shown to reduce flow velocity on coral reefs and other marine habitats and may be important habitat features as flow refuges (Gerstner 1998; Johansen et al. 2008; Eggertsen et al. 2016). The feed-rest hypothesis proposed by Genin (2004) suggests that small-bodied fishes can access high food availability provided by strong currents on abrupt topographies by intermittently emerging from complex benthic habitat and resting between feeding. The presence of structurally complex habitat is therefore important for many reef fishes to access ecological benefits of high flow environments, even if they do not possess morphological adaptations for living in high currents.

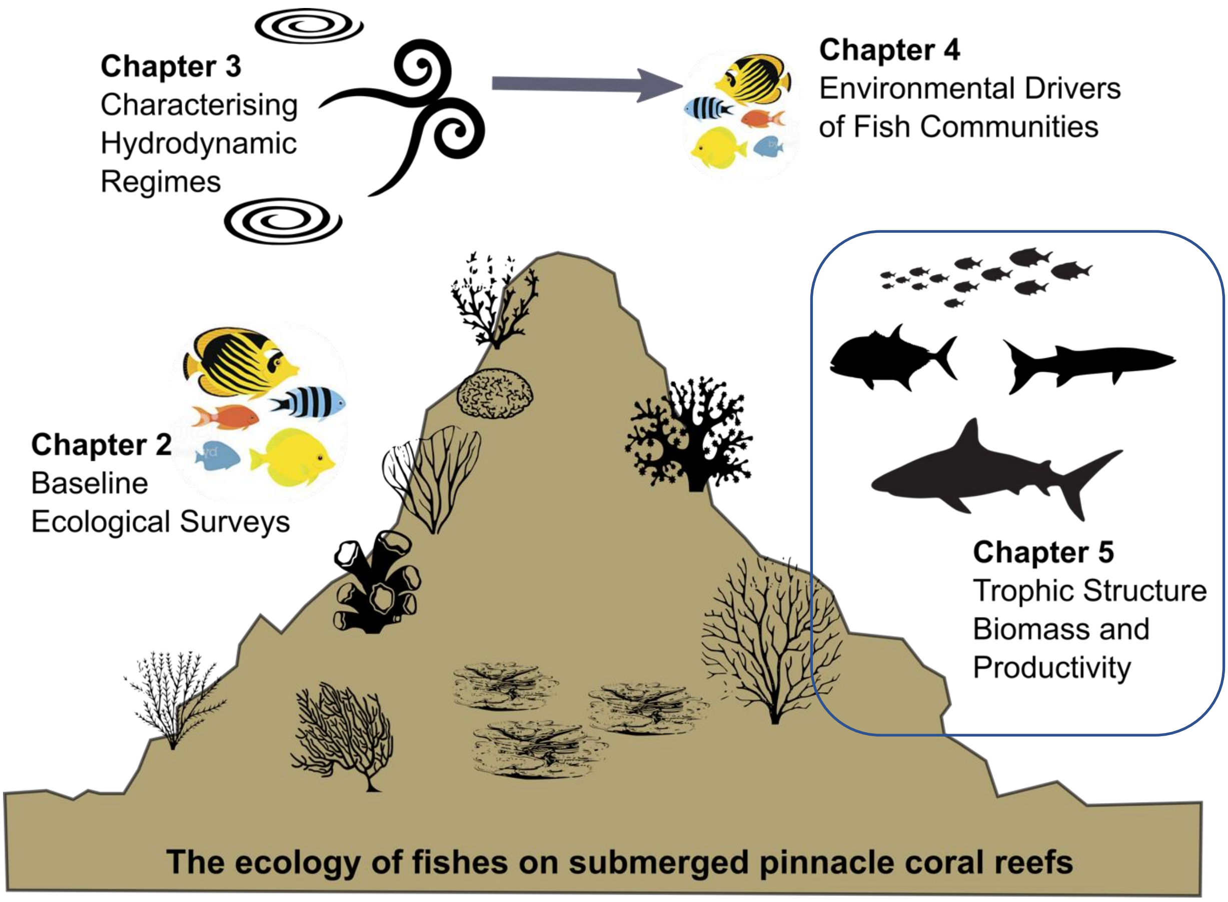
Pinnacle sites did have the highest percentage cover of complex coral morphologies (Appendix C Table S4.6). Although broad patterns show complex hard coral cover to decline with depth, submerged reefs in clear offshore waters receive greater light, and less shading from emergent reef structure above the crest and lower impact of surface waves. On pinnacles, this may allow a greater abundance of small, site-attached species to occupy these strong hydrodynamic habitats regardless of swimming capabilities and benefit from enhanced current-derived resources (Johansen et al. 2008). The small negative trend on offshore reefs may reflect the lower amount of complex coral cover at these sites and therefore the absence of shelter for species with poor swimming ability in high current speeds. Offshore reefs experienced higher annual maximum and mean current speeds than nearshore reefs. Although offshore reefs therefore receive higher energetic and current derived resources than nearshore reefs, without sufficient complex habitat for refuge many species may be limited in distribution and abundance at these sites.

Benthic diversity, benthic richness and total hard coral cover were similar between reef types which may explain why these variables had relatively little influence on reef fish biodiversity. This may also reflect both the depth and the scale of my study as fish-habitat relationships are known to be weaker at greater depths and can be highly scale-dependent (Chittaro 2004; Jankowski et al. 2015; Hale et al. 2019) . In terms of fish communities however, the pinnacles are dominated by large semi-pelagic piscivores and numerous small planktivorous species (Galbraith et al. 2021). Many species of larger reef fish are not as closely associated with small-scale benthic habitat (Walsh 1985; Bohnsack 1989; Graham et al. 2011; McClanahan et al. 2011; Friedman et al. 2020) and so habitat-related variables would be expected to be less important for such communities. Further, even amongst smaller-bodied species, habitat-related resources may be less important if the community is predominantly composed of planktivorous or detritivorous generalist species rather than those which rely closely up on live coral cover or physical structure. These species are presumably abundant as their food supply is concentrated on pinnacles by both the offshore setting of these patch habitats and some of the hydrodynamic mechanisms discussed already. Certainly, there is a conspicuous absence of many small coral-associated species which presents interesting avenues for further study on both fish-habitat relationships on pinnacles and recruitment dynamics.

Lastly, although temperature-related hydrodynamic variables did not feature prominently in my results, survey temperature variability was the fourth most important variable for fish richness and diversity random forest models. Offshore sites had highest mean temperatures throughout the study period (annual average 31.33 ^{o}C; Appendix C Tables S4.3 and S4.4) with maximum temperatures as high as 35.24 ^{o}C recorded at some sites. Conversely, on pinnacles, temperatures were cooler throughout the year (annual average 30.53 ^{o}C). If these cooler temperatures are associated with distinct hydrodynamic processes like upwelling or stratified doming of cooler waters over submerged reefs, this could reduce the potential for thermal stress on communities at these sites (Hamburg et al.; Randall et al. 2019; Leitner et al. 2020). A growing body of work is emerging within the climate change literature, seeking to understand the effects of thermal variability on marine organisms, including coral reef fishes. This work is important to determine both the negative effects of thermal stress itself and also to identify resilient communities living in naturally warmer and more variable thermal environments (Palumbi et al. 2014). My results hint at thermoregulatory processes on submerged pinnacles, but investigation of vertical water column profiles and fine-scale currents are needed to establish a connection between temperatures and currents at my sites.

Submerged reefs, such as the pinnacles in this study, are ubiquitous across coastal shelves supporting productive ecological communities, yet remain understudied compared to emergent reefs. Established ecological paradigms for seamounts suggest that biophysical-coupling by strong and distinct hydrodynamics are drivers of biodiversity on these structures, but these mechanisms have been poorly investigated on physically similar submerged pinnacle reefs. My results provide some evidence that strong and variable currents generated on submerged reefs may operate in a similar way, which could explain how these patch habitats can support higher numbers of species and individuals than might be expected for the small area. Fish communities with properties of high biomass and abundance are crucial components of conservation spatial planning. Additionally, some aspects of hydrodynamics on submerged structures could confer elements of thermal buffering for ecological communities. The global coral reef seascape is changing but morphologically distinct, deeper and diverse submerged reefs represent highly productive and potentially resilient coral habitats. These hotspots of diversity warrant further investigation in other seascapes and their ecological value should be considered in marine management and conservation.

Chapter 5


Chapter 3
Characterising
Hydrodynamic
Regimes
Chapter 4
Environmental Drivers
of Fish Communities
Chapter 2
Baseline
Ecological Surveys
Chapter 5
Trophic Structure
Biomass and
Productivity
The ecology of fishes on submerged pinnacle coral reefs

Chapter 5: Enhanced biomass, productivity and unique trophic structure of fish assemblages on submerged coral reef pinnacles

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5.1 Abstract

The trophic structure of coral reef fish communities exhibits substantial spatial variation across environmental gradients and among habitat types. This variation is important as it determines patterns in energy transfer and rates of coral reef fish biomass production – two essential components of ecosystem function. While these processes provide food for millions of people dependant on reef resources, shallow coastal reef ecosystems have been adversely affected by over-exploitation and habitat degradation. Submerged reefs are a globally extensive coral reef habitat type and offshore pinnacles are often characterised by high fish abundance and biomass. However, patterns in trophic structure and productivity of fish communities in these habitats are largely unknown. To address this, I quantified and compared trophic structure, total fish abundance, biomass and productivity between submerged pinnacles and two types of emergent reef habitat in a tropical seascape. I also modelled the distribution of biomass and productivity along several key environmental gradients. Pinnacles supported highest total abundance, biomass and annual productivity compared to emergent reef types by several orders of magnitude. All reef types were numerically dominated by planktivores, comprising 66-85% of total abundance. However, there were substantial differences in biomass and productivity in different trophic groups. Pinnacles were top-heavy communities with piscivores accounting for ~50% of the biomass and 67% of the productivity, while planktivores accounted for most productivity on emergent reefs. Distance-based linear modelling revealed that temperature variability, maximum current speeds and total hard coral cover explained most variability in multivariate analyses of biomass and productivity in fish assemblages. These three environmental variables exhibited positive and negative trends depending on the trophic group. The top-heavy trophic structure and high productivity on pinnacles may be explained by complex hydrodynamics around and over the reefs, which may increase pelagic energetic subsidies. Condensed ecological interactions on small patch habitats like pinnacles may also

enhance efficiency in energy transfer across multiple trophic pathways. Accounting for these differences in response to habitat-specific conditions and a changing global climate is a critical consideration for future reef fish assemblage structure, biomass and productivity.

5.2 Introduction

Ecological communities have complex food webs that can be simply and effectively described in terms of their trophic structure (Polis and Strong 1996). The relative abundances of organisms feeding on different resources govern how energy is captured, transferred and stored as biomass at different trophic levels (Odum and Barret 1971). Quantifying this energy transfer in natural systems is important for understanding both ecological structure and function and also how ecosystem services are used, managed and sustained (Heath et al. 2014; Bierwagen et al. 2018; Hayden et al. 2019). Coral reefs are characterised by efficient energy transfer and high ecological productivity which are the essential goods and services that provide resources for millions of people in tropical countries (Burke et al. 2011; de Groot et al. 2012; Cruz-Trinidad et al. 2014). However, changes in trophic structure to coral reef fish communities are now widely documented, particularly on shallow, accessible coastal reefs (Jones et al. 2004; Graham et al. 2006; Richardson et al. 2017; Robinson et al. 2019). Multiple human impacts including overfishing, climate change and habitat damage are impairing critical ecosystem processes that support natural communities and food resources (Nyström et al. 2000; Hoegh-Guldberg et al. 2007; Graham et al. 2017). These changes ultimately lead to shifts in ecological regimes, community structure and energy flux on degraded coastal reefs (Roberts 1995; Pratchett et al. 2011; Hempson et al. 2017). As shallow emergent reefs continue to degrade, human use of marine resources is extending to deeper and more isolated habitats (Roberts 2002; Richert et al. 2017).

Fish abundance, standing biomass and productivity in terms of fish mass are three complementary measures of assessing coral reef health and the level of exploitation reefs can support (Nash and Graham 2016; Morais and Bellwood 2020). Where abundance and biomass can provide direct insights into the impacts of fishing (Pauly et al. 1998; Robinson et al. 2017; Palomares et al. 2020) and the effects of protected area establishment (Russ and Alcala 2003; Williamson et al. 2004; McClure et al. 2020), measures of productivity consider relationships between community structure, biomass growth and energy transfer (Depczynski and Bellwood 2003; Lamb and Johnson 2010). The need to consider these elements of fish community structure jointly has been highlighted by studies that show mismatches between standing biomass and productivity (Odum et al. 1955; Morais et al. 2020) and models that account for species-specific growth and mortality (Morais and Bellwood 2020). The ability to differentiate between standing biomass capacity and on-going productivity is therefore essential for informing future sustainable resource management and is also closely linked to ecosystem recovery potential. Additionally, because responses to changes in abiotic conditions vary between species and individuals (Syms and Jones 2000; McCormick et al. 2013; Poloczanska et al. 2016; Munday et al. 2019) accounting for differences in assemblage structure is essential for understanding how trophic dynamics and fish productivity will be affected by climate change (Williams et al. 2015; Hayden et al. 2019; Audzijonyte et al. 2020).

Like all ecological communities, reef fish assemblages vary spatially across geographic locations, along natural environmental gradients and among distinct habitat types (Vellend 2016; Bennett et al. 2018; Jouffray et al. 2019; Samoilys et al. 2019; Heenan et al. 2020). These differences and subsequent biotic interactions govern relative species abundance, resulting in various forms of trophic structure. Examples include bottom-heavy trophic pyramids where the majority of the community is comprised of low trophic level consumers (e.g. detritivores and herbivores) (Graham et al. 2017; Hempson et al. 2018) and inverted pyramids where high trophic levels and top predators dominate (Friedlander and DeMartini 2002; DeMartini et al. 2008; Sandin et al. 2008; Sandin and Zgliczynski 2015). On coral reefs, principal mechanisms that drive variation in trophic structure are light availability and oceanic primary production (Williams et al. 2015; Samoilys et al. 2019; Heenan et al. 2020). Light drives benthic primary production and subsequent bottom-up synthesis of biomass in lower-level consumers (Russ 2003; Gattuso et al. 2006; Nemeth and Appeldoorn 2009). For mid- to high-level consumers, enhanced inputs of pelagic energy from oceanic production drive increased biomass of planktivores and piscivores (Williams et al. 2015; Mccauley et al. 2018; Morais and Bellwood 2019). Because species-specific demographic traits dictate rates of growth, mortality and energy allocation (e.g. reproduction and feeding rates), how an assemblage is structured also impacts the overall productivity of a system (Duffy et al. 2016; Morais et al. 2020).

Most research on reef fish trophic structure has been conducted on shallow, emergent coral reefs that conform to classically defined habitat zones (e.g. reef crest, slope, flat etc.) and ecological processes (Goreau 1959; Done 1983). Predictable environmental gradients across these zones support characteristic fish assemblages (Choat and Bellwood 1991; Brokovich et al. 2010; Darling et al. 2017). These differences manifest in reef-scale variability in fish abundance, biomass and productivity (Gust et al. 2001; Cheal et al. 2012; Bellwood et al. 2018). Gradients in resource provision to coral reefs typically focus on the crest which is the most biologically diverse and energetic zone (Bradbury and Young 1981; Huston 1985). Here, energy is captured by two key mechanisms: 1) from the pelagic environment by planktivorous fish and benthic filter feeders (Hamner et al. 1988), and 2) the shallow crest depths (0-10m) allow maximum light penetration for benthic primary production (Wiebe et al. 1975; Barnes and Devereux 1984). Productivity therefore declines with both depth (due to light attenuation) and distance from the seaward crest (due to decreasing allochthonous inputs) (Campbell and Aarup 1989; Fox and Bellwood 2007; Andradi-Brown et al. 2016; Kahng et al. 2019). However, little work on assessing these patterns has been conducted outside the classic shallow emergent reef paradigm.

As reef fish communities continue to change under climate-driven disturbances, it is important to determine both how new species configurations have the capacity to support future coral reef functions and resources (Harborne and Mumby 2011; Graham et al. 2014; Audzijonyte et al. 2020). This will also include quantifying novel communities found in understudied coral reef habitats like mesophotic coral ecosystems and distinct submerged reef morphologies (Holstein et al. 2019; Eyal et al. 2021). Submerged reefs constitute significant areas of habitat available for the formation of coral reefs but, are globally under-studied and under-protected (Bridge et al. 2012, 2013). On the Great Barrier Reef alone, the area of available coral reef habitat is increased by 160% when reefs at depths greater than 20m are included in estimates (Harris et al. 2013; Bridge et al. 2019). Therefore, accounting for natural variation in trophic structure and productivity must consider both shallow emergent and submerged reef morphologies.

Submerged reefs, which do not breach the sea surface (crest depth >10-20m) do not exhibit the same patterns in zonation as emergent reefs (IHO 2008; Bridge et al. 2013; Thomas et al. 2015). Small, isolated conical pinnacle reefs are a distinct form of submerged reef that share physical and ecological similarities with deep-sea seamounts. Seamounts, pinnacles and other bathymetric highs are known to support high fish abundance, diversity and biomass despite greater depths and isolation in offshore positions (Morato et al. 2010; Richert et al. 2017; Leitner et al. 2021). Mechanisms supporting communities on abrupt bathymetric features involve distinct hydrodynamics that enhance energetic inputs and productivity at depth (Genin 2004; White et al. 2007; Lavelle and Mohn 2010). Fish assemblages have also been shown to be distinct on submerged reef morphologies compared to those at the same depth on emergent reefs, supporting both reef-associated and pelagic species (Galbraith et al. 2021). In particular, many semi-pelagic and pelagic species of higher trophic levels aggregate around physical structures in open water (Holland and Dean Grubbs 2007; Morato et al. 2010; Letessier et al. 2019). How trophic structure is related to environmental drivers on these hyper-abundant coral reefs is unknown and they currently have received limited attention in coral reef research or conservation planning.

The aim of this study was to quantify differences in the trophic structure and measures of productivity of fish assemblages found on submerged pinnacles and emergent reefs in Kimbe Bay, Papua New Guinea. To do this I compare abundance, biomass and productivity between fish assemblages found at the same depths on emergent and submerged pinnacle reef types. Specifically, I test the hypotheses that:

1) Pinnacles will support higher abundance, biomass and productivity than emergent reefs at the same depth.

2) Reef types will have differences in the relative proportions of four broad trophic groups for these measures. I predict that fish communities on offshore reefs and pinnacles will have greater proportions of planktivores due to higher pelagic influence and that pinnacles will possess a top-heavy trophic structure.

3) Currents and other aspects of hydrodynamics will be a strong driver of biomass and productivity, which are pronounced on pinnacle reefs.

5.3 Methods

5.3.1 Study site

This study was undertaken in Kimbe Bay, Papua New Guinea (5°30’S, 150°05’E) during April-May of 2018 and March 2019. Kimbe Bay has a complex bathymetry and diverse seascape consisting of shallow emergent fringing reefs, offshore emergent reefs and a submerged caldera central to the bay that possesses numerous pinnacle coral reefs. Twelve reefs were selected as survey sites representing three reef morphologies: submerged pinnacle reefs, offshore emergent reefs and nearshore emergent reefs (n = 4 sites per reef type; Figure 5.1). Emergent reef crests were all above 10m depth and submerged reef crests below 15-20m. Offshore reefs were greater than 9km from nearest mainland coast and nearshore reefs were less than 5km. I controlled for fishing pressure at sites closest to local villages by selecting reefs that are part of a locally managed marine area and offshore reefs in Kimbe Bay are not heavily fished (Green et al. 2007).

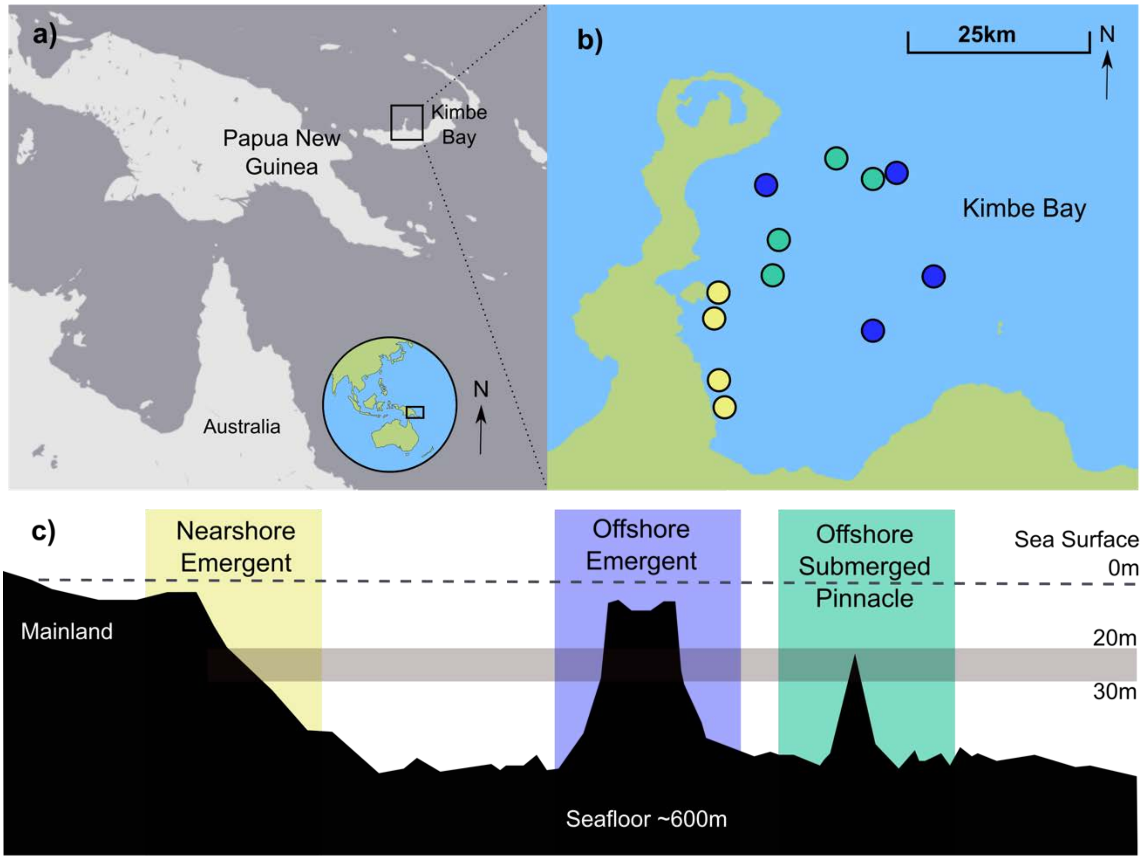


Figure 5.1 (a) Study site location: Kimbe Bay, Papua New Guinea **(b)** Survey reef locations in Kimbe Bay. Yellow circles represent nearshore emergent reefs, blue circles are offshore emergent reefs and green circles are offshore submerged pinnacle reefs **(c)** Schematic of Kimbe Bay bathymetry to illustrate morphological differences between emergent reefs and submerged pinnacles. Coloured boxes correspond to reef type as per **(b)** dashed line is sea surface level and the grey band represents survey depth.

5.3.2 Data collection

Fish and benthic surveys were conducted at each reef within a depth band of 20-30m. This incorporated the summits of the pinnacles and near-horizontal areas on emergent reef slopes to account for aspect as much as possible. Surveys were conducted in daylight hours between 0800 – 1500. At each reef, divers recorded five replicate high-definition video transects (30x5m = 150m^{-2} per transect) using a stereo-video system (SeaGis, Australia). The system uses two GoPro Hero 5 cameras that were calibrated before and after surveys using the software CAL (SeaGis, Australia). This allowed for the measurement of fish lengths and also provided a known field of view. The video operator swam approximately 0.5m above the reef at a constant steady speed (~20m/minute) with the cameras facing directly forward. Detailed methods broadly followed Goetze et al. (2019). Benthic point intercept video transects were then conducted on return along the same transect. The transect tape was marked by two random points every 1m. A separate GoPro Hero 5 camera in waterproof housing was used to film the transect tape and underlaying benthos continuously pointing directly down at the reef.

Video analysis – fish and benthic

Fish survey videos were analysed in the stereo-video software EventMeasure Stereo (SeaGis, Australia). Each individual entering a known field-of-view (5m width calculated by 3D co-ordinates in Eventemeasure Stereo) was measured (fork length mm), identified to species level and assigned to a trophic group based on trophic level estimates (TL), diet and feeding behaviour obtained from the FishBase database (Froese and Pauly 2020). For the purpose of this study four broad trophic level bins were used: 1. primary consumers (browsers, detritivores, grazers); 2. secondary consumers (corallivores, scrapers, invertivores, omnivores); 3. planktivores, and 4. piscivores. Playback of videos at slow speeds and frame rates helped identification and ensured no individual was counted twice. Where length estimates were not possible for some individuals (partial screen capture or physically obscured), the average length for that species from the same reef was applied. For schooling species, as many individuals as possible were measured and an average length calculated (sensu Andradi-Brown et al. 2016). The maximum number of individuals present on the screen at one time was estimated and the average length applied. Benthic videos were watched back using a standard media player (VLC, 2020). For each point along the transect the benthic substrate directly underneath the point was categorised by type, taxa and morphology. This included both biogenic groups (e.g. hard coral, porifera, soft coral) and also rock, sand and reef matrix. A full list of benthic groupings is provided in Appendix D Table S5.1.

Environmental data

Twelve environmental variables representing spatial, hydrodynamic and habitat-related drivers that are known to influence reef fish communities were collected for each reef. Reef area (km^2), distance to nearest mainland (km) and distance to nearest neighbouring reef (km) were estimated using GIS software GRASS (GRASS Development Team, 2017). For submerged pinnacles, which are small and cannot be seen in satellite images, reef area was measured in situ by divers around a 30m contour. Total hard coral cover (%), benthic substratum diversity (D), richness (no. of substrata) and complex coral cover (%) were derived from benthic video surveys. Given the prominence of hydrodynamics in supporting high biomass and trophic levels on seamounts (Genin 2004), as well as recent studies suggesting their importance on pinnacle coral reefs (Galbraith et al 2021), data for current speeds and temperature were collected using current meters (Marotte HS, Marine Geophysics Laboratory, Australia) deployed at each reef for a full year (Sep 2018- Sept 2019). Variables derived from these data included annual averages, maxima and variability (SD). See Appendix D Table S5.2 for environmental variable summaries.

5.2.3 Statistical analysis

All statistical analysis was conducted in R version 4.2 (R Core Development Team 2021). Fish abundance was calculated as total number of individuals (n m^{-2}). Fish standing biomass (g m^{-2}) was calculated using the length-weight relationship (Equation 1).

$$W = aL^b$$

Equation 1 Fish length-weight relationship. L represents fish fork length (cm), W is weight in grams and a and b are species specific constants obtained from Fish Base (Froese et al. 2013) using the R package “rfishbase” (Boettiger et al. 2012).

A recent framework that accounts for somatic growth as well as mortality over time was applied to estimate total annual productivity (g m^{-2} $year^{-1}$) (Morais and Bellwood 2020). The R package “fishProdr” which implements this framework was used to apply species-specific length-weight relationships to estimate somatic growth and mortality as per-capita mass loss over the time period of one year (Morais and Bellwood 2020). Like all models, this approach is somewhat limited. However, as a relative measure it does allow comparison across the three reef types. Additionally, using multiple measures of productivity contributes to a more balanced consideration of the system, as opposed to a single metric approach.

Total abundance, biomass and productivity

Generalized linear mixed effects models (GLMMs) were used to test for differences in total fish abundance, biomass and productivity between reef type using the package “glmmTMB” (Brooks et al. 2017). Model fit was assessed and tests for homogeneity of variance, overdispersion and normality and an appropriate error family and link function selected using the package “DHARMa” (Hartig 2020). Model formula included “reef type” as a fixed factor and “survey year” and “site” as random factors. Estimated marginal means and 95% confidence intervals were calculated using the package “emmeans” (Lenth 2020).

Trophic structure: relative abundance, biomass, productivity

GLMMs were also used to tests for differences in abundance, biomass and productivity for each trophic level. Model structure included “reef type” and “trophic group” as fixed factors with an interaction and “survey year” and “site” as random factors. Selection of error family, model fit and estimated marginal means were assessed in the same way as GLMMs above for fish totals. The relative abundance, biomass and productivity of each trophic level at each reef type was calculated as a percentage and used to constructed trophic pyramids.

Environmental influence on the trophic structure of biomass and productivity

Distance-based redundancy analysis (dbRDA) was used to identify explanatory environmental variables that may be important in structuring trophic biomass and productivity in the fish assemblages. dbRDA is a multivariate analysis that conducts constrained ordination on data using non-Euclidean distance measures (Lengendre and Anderson 1999). Two separate dbRDAs for biomass (kg) and productivity (kg year^{-1}) for each transect (150m^{-2}) were implemented on Bray-Curtis dissimilarity matrices of Hellinger-transformed data using the package “vegan” and the functions “vegdist” and “capscale” (Oksanen et al. 2019). A full global model of the 12 environmental variables was initially fitted. To find the most parsimonious model, forward variable selection using the “ordiR2step” function was used based on pseudo-Akaike Information Criterion (AIC) and the proportion of variation in the global model (all variables) explained by each variable (R^2_{adj}). The final model was then visualized on two primary axes (canonical analysis of principal components) which represent the distance on direction of higher biomass or productivity for site and species scores. Biomass or productivity were scaled as bubbles for each reef type and a biplot of correlated ($r > 0.05$) trophic groups and environmental variables plotted as vectors. A pseudo-F value as a measure of the significance of the overall analysis ($p < 0.05$, 9999 permutations), the proportion of total variation (%) accounted for by each axis and an adjusted R^2 value are presented for each dbRDA.

5.4 Results

5.4.1 Reef type variation in total abundance, biomass and productivity

Estimates from GLMMs show clearly that the pinnacles in this study support higher total abundance, biomass and productivity of fishes compared to offshore and nearshore emergent reefs in Kimbe Bay (Fig. 5.2). There were nearly three times the density of fish on pinnacles (~2.8 fish per m^2) compared to offshore reefs (~0.9 per m^2) and over seven times the density compared to nearshore reefs (~0.4 fish per m^2) (Table 5.1).

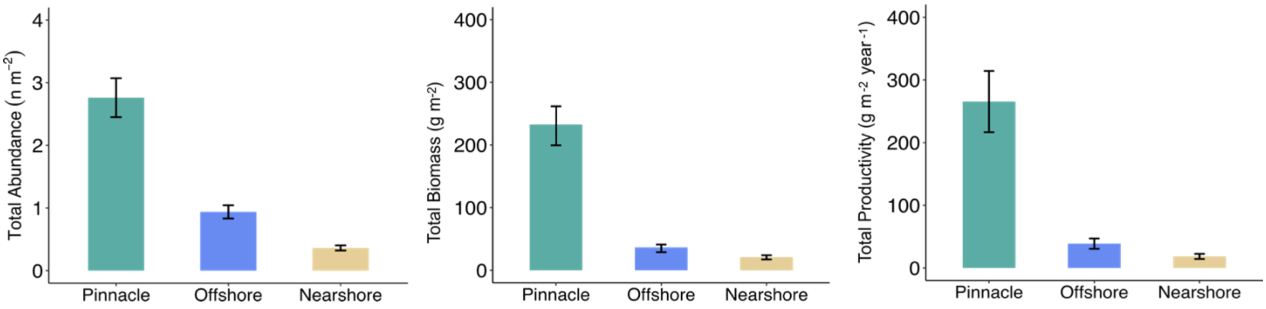


Figure 5.2 Comparison of mean **(a)** total abundance (individuals m^{-2}) **(b)** total biomass (g m^{-2}) and **(c)** total annual productivity (g m^{-2}) at pinnacle, nearshore emergent and offshore emergent reef types. Error Bars represent standard errors.

Table 5.1 Estimated marginal means, pairwise contrasts and 95% confidence intervals for total Abundance (n m^{-2}) total biomass (g m^{-2}) and total annual productivity (g m^{-2} year^{-1}) from generalized linear mixed effect models.

Reef type	Mean (SE)	df	95% CI		Contrast	Contrasts estimate (SE)	95% CI	
Abundance (individuals m^{-2})								
Pinnacle	2.76 (0.31)	116	2.15	3.38	Pinnacle - Offshore	1.82 (0.33)	1.04	2.60
Offshore	0.94 (0.11)	116	0.73	1.15	Pinnacle - Nearshore	2.40 (0.31)	1.65	3.14
Nearshore	0.36 (0.04)	116	0.28	0.44	Offshore - Nearshore	0.58 (0.11)	0.31	0.84
Biomass (g m^{-2})								
Pinnacle	223.63 (31.11)	116	162.01	285.26	Pinnacle - Offshore	191.57 (31.45)	116.91	266.23
Offshore	32.06 (4.57)	116	23.00	41.12	Pinnacle - Nearshore	206.18 (31.21)	132.08	280.28
Nearshore	17.45 (2.49)	116	12.52	22.39	Offshore - Nearshore	14.61 (5.21)	2.24	26.98
Productivity (g m$^{-2\ year-1}$)								
Pinnacle	265.46 (48.88)	115	168.64	362.28	Pinnacle - Offshore	226.70 (49.56)	109.02	344.39
Offshore	38.75 (8.22)	115	22.48	55.03	Pinnacle - Nearshore	247.04 (49.05)	130.56	363.51
Nearshore	18.42 (4.13)	115	10.25	26.59	Offshore - Nearshore	20.33 (9.19)	-1.50	42.17

This pattern was consistent for biomass with pinnacles supporting 223.6g m^{-2} compared to 32.1 g m^{-2} on offshore reefs (contrast estimate = 191.6, 95% CI = 116.9 – 266.2) and only 17.5 g m^{-2} on nearshore reefs (contrast estimate = 206.2, 95% CI = 132.1 - 280.3). Differences between pinnacles and emergent reefs were greatest in terms of productivity, with pinnacles producing 226.7g m^{-2} $year^{-1}$ more than offshore reefs (95% CI = 109.0 – 344.4) and 247.0g m^{-2} $year^{-1}$ more than nearshore reefs (95% CI = 130.57 – 363.5). Productivity was the only pairwise comparison that did not provide evidence to suggest a difference between offshore and nearshore emergent reefs (contrast estimate = 20.3, 95% CI = -1.5 – 42.2). See Table 5.1 for all pairwise contrast estimates and 95% confidence intervals.

5.4.2 Trophic structure: relative abundance, biomass, productivity

Pinnacles had the highest abundance of individuals from each trophic level (Table 5.2). The only pairwise comparison of abundance that found no difference between reef types based on 95% confidence intervals was between nearshore and offshore reefs for piscivores and primary consumers. Abundance of all other trophic levels between all reef types were highest on pinnacles, followed by offshore reefs and lowest on nearshore reefs. This is consistent with the pattern found in total overall abundance (Fig. 5.2a). Despite differences in absolute total number of fishes, the trophic structure in terms of abundance was similar for each reef type (Fig. 5.3). Planktivores contributed the greatest proportion of total fish abundance at all three reef types (66-81%) followed by secondary consumers as the next most abundant group (16-21%). Piscivores made up 11.22% of abundance on pinnacle reefs, but only 0.92% on offshore reefs and 2.94% on nearshore reefs. Only small proportions of abundance at each reef type were comprised of primary consumers (1.9 – 5.1%).

Table 5.2 Estimated marginal means, pairwise contrasts and 95% confidence intervals for Abundance (n m^{-2}) of each trophic level at each reef type from generalized linear mixed effect mode

Reef type and Trophic Group	Abundance n m^{-2} (SE)	df	95% CI		Contrast	Contrast Estimate (SE)	95% CI	
Primary Consumers								
Pinnacle	0.13 (0.03)	116	0.07	0.19	Pinnacle - Offshore	5.69	0.05	0.18
Offshore	0.02 (0.00)	116	0.01	0.03	Pinnacle - Nearshore	4.55	0.04	0.18
Nearshore	0.02 (0.00)	116	0.01	0.03	Offshore - Nearshore	-4.42	-0.01	0.01
Secondary Consumers								
Pinnacle	0.50 (0.06)	116	0.38	0.62	Pinnacle - Offshore	7.26	0.20	0.50
Offshore	0.15 (0.02)	116	0.12	0.19	Pinnacle - Nearshore	5.25	0.28	0.57
Nearshore	0.07 (0.01)	116	0.06	0.09	Offshore - Nearshore	-5.08	0.03	0.12
Planktivores								
Pinnacle	1.81 (0.23)	116	1.36	2.26	Pinnacle - Offshore	26.62	0.46	1.63
Offshore	0.76 (0.10)	116	0.57	0.95	Pinnacle - Nearshore	41.49	1.00	2.09
Nearshore	0.26 (0.03)	116	0.20	0.33	Offshore - Nearshore	7.62	0.26	0.74
Piscivores								
Pinnacle	0.32 (0.08)	116	0.16	0.48	Pinnacle - Offshore	13.25	0.12	0.51
Offshore	0.01 (0.00)	116	0.00	0.01	Pinnacle - Nearshore	16.66	0.12	0.51
Nearshore	0.01 (0.00)	116	0.00	0.01	Offshore - Nearshore	0.00 (0.00)	-0.01	0.01

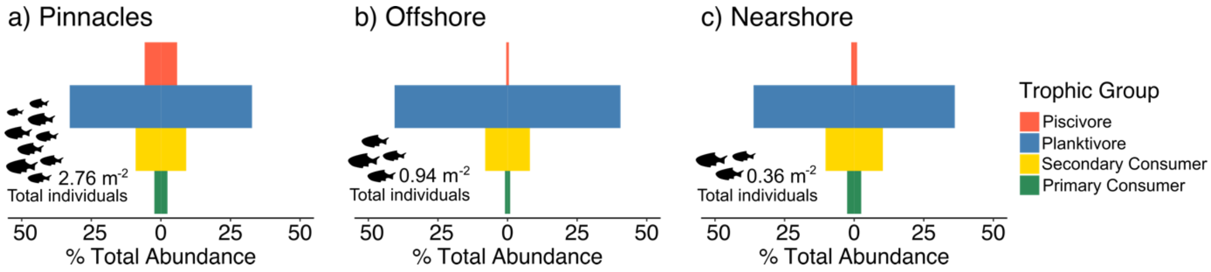


Figure 5.3 Relative abundance as a percentage of total fish m^{-2} for each trophic group at: **(a)** submerged pinnacles **(b)** offshore emergent reefs and **(c)** nearshore emergent reefs.

The GLMM for biomass found evidence for highest mean biomass at each trophic level on the pinnacle reefs (Table 5.3). Offshore and nearshore reefs had similar biomass at each trophic level except planktivores, which had greater biomass on offshore reefs (contrast estimate = 14.2g m^{-2} year^{-1}, 95% CI = 7.6 – 20.7). Trophic pyramids showed reef type variability in biomass structure (Fig. 5.4). Pinnacle reefs assumed a clear top-heavy structure with the majority of biomass accounted for by piscivores (50.7%). This structure tapered sequentially to 31.9% biomass represented by planktivores, 8.8% secondary consumers and 8.5% from primary consumers. Offshore reef biomass was dominated by planktivores (50.5%) followed by piscivores (19.7%) and relatively even proportions of secondary (15.4%) and primary (14.50%) consumers. Nearshore reefs took the most bottom-heavy biomass structure with lower trophic levels of primary (32.5%) and secondary (38.7%) contribution the majority of biomass and planktivores (11.7%) and piscivores contributing the least (17.2%).

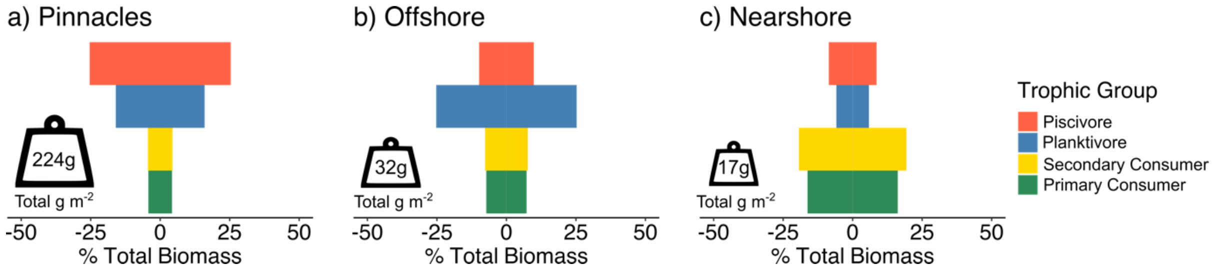


Figure 5.4 Relative biomass as a percentage of total g m^{-2} for each trophic group at **(a)** submerged pinnacles **(b)** offshore emergent reefs and **(c)** nearshore emergent reefs.

Table 5.3 Estimated marginal means, pairwise contrasts and 95% confidence intervals for biomass (g m^{-2}) of each trophic level at each reef type from generalized linear mixed effect models.

Reef type and Trophic Group	**Biomass g m^{-2} (SE)**	**df**	**95% CI**		**Contrast**	**Contrast estimate (SE)**	**95% CI**	
Primary Consumers								
Pinnacle	19.03 (3.54)	116	12.01	26.04	Pinnacle - Offshore	14.38 (3.66)	5.69	23.07
Offshore	4.65 (0.91)	116	2.83	6.46	Pinnacle - Nearshore	13.36 (3.71)	4.55	22.17
Nearshore	5.67 (1.10)	116	3.49	7.85	Offshore - Nearshore	-1.02 (1.43)	-4.42	2.38
Secondary Consumers								
Pinnacle	19.73 (3.07)	116	13.66	25.81	Pinnacle - Offshore	14.81 (3.18)	7.26	22.35
Offshore	4.93 (0.82)	116	3.30	6.56	Pinnacle - Nearshore	12.99 (3.26)	5.25	20.73
Nearshore	6.75 (1.10)	116	4.57	8.93	Offshore - Nearshore	-1.82 (1.38)	-5.08	1.45
Planktivores								
Pinnacle	71.42 (11.74)	116	48.17	94.67	Pinnacle - Offshore	55.23 (12.05)	26.62	83.83
Offshore	16.19 (2.72)	116	10.81	21.58	Pinnacle - Nearshore	69.38 (11.74)	41.49	97.26
Nearshore	2.04 (0.40)	116	1.24	2.84	Offshore - Nearshore	14.15 (2.75)	7.62	20.68
Piscivores								
Pinnacle	113.45 (39.49)	116	35.23	191.67	Pinnacle - Offshore	107.16 (39.55)	13.25	201.07
Offshore	6.30 (2.21)	116	1.93	10.67	Pinnacle - Nearshore	110.46 (39.51)	16.66	204.25
Nearshore	3.00 (1.05)	116	0.92	5.08	Offshore - Nearshore	3.30 (2.44)	-2.50	9.10

Productivity was highest on pinnacles for all trophic levels except for planktivores, which were equally productive on pinnacles (64.6 g m^{-2} year^{-1}) and offshore (31.3 g m^{-2} year^{-1}) reefs (contrast estimate = 33.3, 95% CI = -1.8 – 68.5). There was no difference in productivity between offshore and nearshore emergent reefs for any trophic level based on 95% confidence intervals and pairwise contrast estimates from the GLMM (Table 5.4). Productivity structure also displayed variation in trophic structure between reef types (Fig. 5.5). Pinnacle reefs retained a top-heavy structure with productivity again dominated by piscivores (67.3%) and planktivores (23.0%). Offshore reef productivity reflected trophic abundance structure more so than biomass, with planktivores accounting for a much higher proportion (80.4%) than the standing biomass (50.5%). Remaining offshore productivity was relatively evenly distributed amongst piscivore (6.6%), secondary (5.6%) and primary (7.45%) consumer levels. Nearshore reef trophic productivity was also mostly comprised of planktivores (75.8%) and overall structure reflected that of trophic abundance (72.3%) rather than standing biomass (32.5%). Total and relative proportions of abundance, biomass and productivity are presented in Table 5.5.

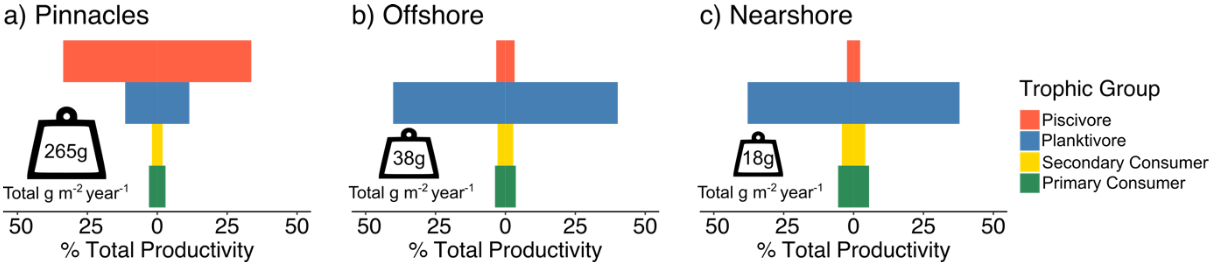


Figure 5.5 Relative productivity as a percentage of total g m^{-2} year^{-1} for each trophic group at **(a)** submerged pinnacles **(b)** offshore emergent reefs and **(c)** nearshore emergent reefs.

Table 5.4 Estimated marginal means, pairwise contrasts and 95% confidence intervals for annual productivity (g m^{-2} year^{-1}) of each trophic level at each reef type from generalized linear mixed effect models.

Reeftype and Trophic Group	Productivity m^{-2} year^{-1}(SE)	df	95% CI		Contrast	Contrasts estimate (SE)	95% CI	
Primary Consumers								
Pinnacle	15.80 (2.98)	115	9.89	21.70	Pinnacle - Offshore	12.92 (3.07)	5.64	20.20
Offshore	2.88 (0.72)	115	1.45	4.31	Pinnacle - Nearshore	13.75 (3.03)	6.55	20.94
Nearshore	2.05 (0.54)	115	0.97	3.13	Offshore - Nearshore	0.83 (0.90)	-1.32	2.98
Secondary Consumers								
Pinnacle	11.45 (1.75)	115	7.98	14.91	Pinnacle - Offshore	9.21 (1.80)	4.93	13.49
Offshore	2.24 (0.44)	115	1.37	3.11	Pinnacle - Nearshore	9.79 (1.78)	5.56	14.03
Nearshore	1.65 (0.34)	115	0.98	2.33	Offshore - Nearshore	0.58 (0.55)	-0.73	1.90
Planktivores								
Pinnacle	64.62 (13.13)	115	38.60	90.63	Pinnacle - Offshore	33.33 (14.79)	-1.79	68.45
Offshore	31.29 (6.81)	115	17.80	44.78	Pinnacle - Nearshore	50.72 (13.53)	18.59	82.85
Nearshore	13.90 (3.27)	115	7.43	20.37	Offshore - Nearshore	17.39 (7.55)	-0.54	35.32
Piscivores								
Pinnacle	178.48 (46.94)	115	85.50	271.46	Pinnacle - Offshore	175.83 (46.95)	64.34	287.31
Offshore	2.65 (1.06)	115	0.55	4.75	Pinnacle - Nearshore	177.43 (46.94)	65.97	288.89
Nearshore	1.05 (0.46)	115	0.14	1.97	Offshore - Nearshore	1.60 (1.16)	-1.14	4.34

Table 5.5 Relative abundance (n m^{-2}), biomass (kg m^{-2}) and annual productivity (kg m^{-2} $year^{-1}$) as a percentage of mean totals for each trophic level at each reef type.

Reeftype	**Trophic Group**	**Abundance n m^{-2} (SE)**	**Total abundance**	**Relative Abundance (%)**	**Biomass g m^{-2} (SE)**	**Total Biomass**	**Relative Biomass (%)**	**Annual Productivity g m^{-2} $year^{-1}$ (SE)**	**Total Productivity**	**Relative Productivity (%)**
Pinnacle	Primary Consumer	0.13 (0.04)	2.76	4.71	19.03 (2.70)	223.63	8.51	15.67 (6.70)	264.80	5.92
Pinnacle	Secondary Consumer	0.50 (0.08)		18.16	19.73 (2.97)		8.82	10.18 (2.82)		3.84
Pinnacle	Planktivore	1.81 (0.19)		65.48	71.42 (8.85)		31.94	60.76 (13.40)		22.95
Pinnacle	Piscivore	0.32 (0.16)		11.66	113.45 (31.14)		50.73	178.18 (113.73)		67.29
Offshore	Primary Consumer	0.02 (0.00)	0.94	1.86	4.65 (0.81)	32.06	14.49	2.86 (0.47)	38.42	7.45
Offshore	Secondary Consumer	0.15 (0.02)		16.07	4.93 (0.73)		15.37	2.17 (0.42)		5.64
Offshore	Planktivore	0.76 (0.09)		81.14	16.19 (3.26)		50.50	30.87 (6.52)		80.35
Offshore	Piscivore	0.01 (0.00)		0.92	6.30 (1.92)		19.64	2.52 (0.89)		6.56
Nearshore	Primary Consumer	0.02 (0.00)	0.36	5.06	5.67 (1.40)	17.45	32.47	2.03 (0.59)	18.33	11.08
Nearshore	Secondary Consumer	0.07 (0.01)		20.59	6.75 (2.04)		38.67	1.54 (0.32)		8.41
Nearshore	Planktivore	0.26 (0.04)		72.29	2.04 (0.52)		11.69	13.90 (4.38)		75.82
Nearshore	Piscivore	0.01 (0.00)		2.07	3.00 (1.45)		17.17	0.86 (0.36)		4.69

5.4.3 Environmental influence on the trophic structure of biomass and productivity

The final distance-based model of the contributions of environmental variables and trophic groups on the multivariate distribution of biomass per transect (kg 150m^{-2}) explained 18.30% (**R$^2_{adj}$**) of variability in fish assemblages (Table 5.6). Maximum current speed, temperature variability and total hard coral cover were selected as the best model and explained 7.15 %, 6.62% and 4.53% of this variability respectively (Table 5.6). Visualisation of the final model in the dbRDA plot showed a decreasing biomass trend in the direction of increasing temperature variability (Fig. 5.6). Secondary consumers were most closely correlated with this trend, whereas primary consumers were more aligned with the direction of increasing hard coral cover and moderate biomass. Planktivores and piscivores were both correlated with the maximum current speed. Piscivores also appeared to be associated with transects of highest total biomass.

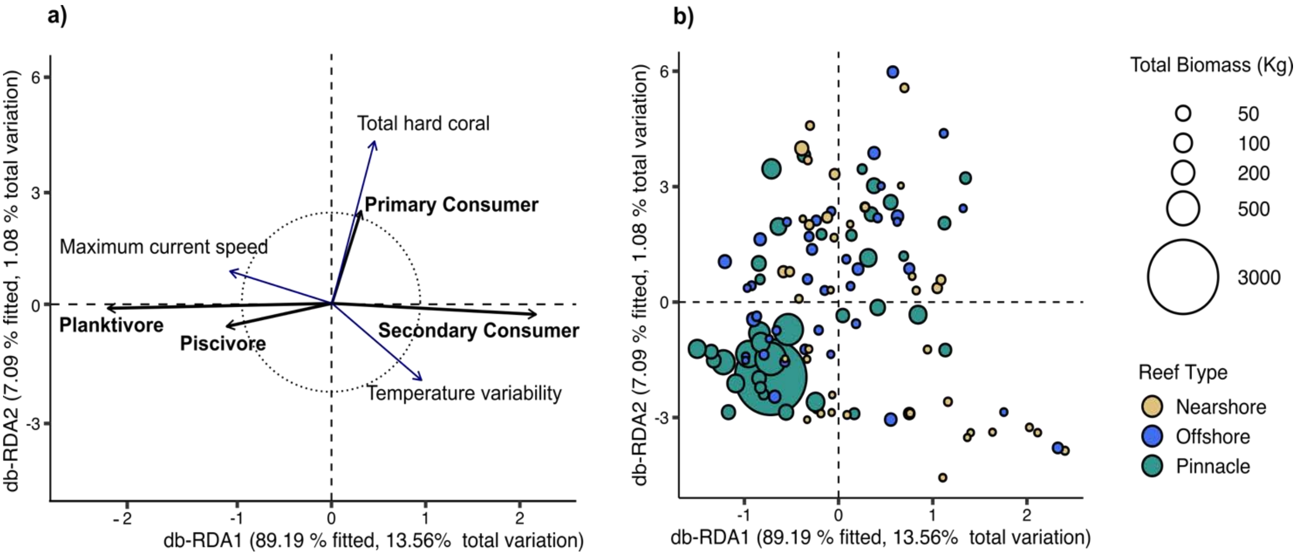


Figure 5.6 Distance-based redundancy analysis (db-RDA) on the fish assemblage biomass at each reef type **(a)** Vector plot along the first and second fitted axes showing the strength and direction of relationships between trophic groups and environmental variables to fish biomass **(b)** bubbles are scaled to represent the total biomass at each transect from each reef type (kg 150m^{-2}).

Table 5.6 Variables included in full and final distance-based modelling of total fish biomass per transect used in the ordistep variable selection process. F and p values are based on a permutational test of significance for each overall model (ANOVA, 9999 permutations) and subsequent tests for each model term (ANOVA, 200 permutations).

Variable	**R^2_{adj}**	**F**	**p**	**Variable**	**R^2_{adj}**	**F**	**p**
Maximum current speed	7.15	7.02	0.001	Maximum current speed	7.15	7.43	0.001
Temperature variability	5.61	7.43	0.60	Temperature variability	6.62	7.19	0.001
Current speed variability	4.62	3.06	0.01	Hard coral cover	4.53	5.25	0.002
Hard coral cover	1.81	2.14	0.07	**Final model**	**18.30**	**6.94**	**0.001**
Average current speed	1.95	9.39	0.001				
Maximum temperature	1.54	3.41	0.01				
Complex coral cover	0.80	1.85	0.106				
Nearest neighbouring reef	0.72	2.13	0.05				
Nearest mainland	0.59	0.65	0.64				
Average temperature	-0.20	0.71	0.60				
Reef area	-0.30	0.64	0.64				
Global full model	**28.51**	**3.49**	**0.001**				

The distance-based linear model for total productivity per transect (kg $150m^{-2}$ $year^{-1}$) showed that 15.5% (R^2_{adj}) of variation was attributed to two of the 11 environmental variables: temperature variability (9.3%) and maximum current speed (6.3%) (Table 5.7). Highest productivity in the dbRDA plot was broadly aligned with planktivores and piscivores (Fig. 5.7). Interestingly, regions of productivity driven by planktivores in the plot were aligned with an increasing trend in maximum current speeds, but bubbles aligned with piscivores were negatively associated with this trend. Low productivity bubbles were associated with the increasing trend in temperature variability and secondary consumers. The distribution of productivity associated with primary consumers was negatively associated with the trend in temperature variability.

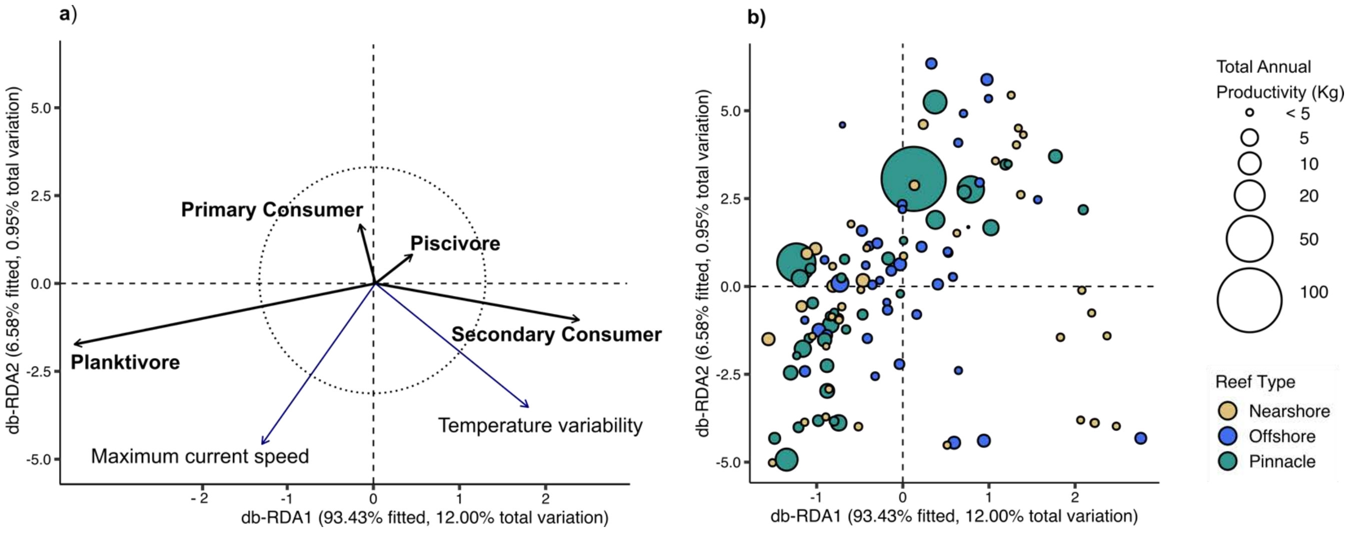


Figure 5.7 Distance-based redundancy analysis (db-RDA) on the assemblage productivity **(a)** Vector plot along the first and second fitted axes showing the strength and direction of relationships between trophic groups and environmental variables to fish productivity **(b)** bubbles are scaled to represent the total productivity at each transect from each reef type (kg 150m^{-2} year^{-1}).

Table 5.7 Variables included in full and final distance-based linear modelling of total fish productivity per transect used in the ordistep variable selection process. F and p values are based on a permutational test of significance for each overall model (ANOVA, 9999 permutations) and subsequent tests for each model term (ANOVA, 200 permutations).

Variable	R^2_{adj}	F	p	Variable	R^2_{adj}	f	p
Temperature variability	9.25	1.18	0.288	Temperature variability	9.25	9.77	0.001
Maximum current speed	5.22	3.79	0.006	Maximum current speed	6.29	7.13	0.001
Current speed variability	2.61	0.94	0.43	**Final model**	**15.54**	8.70	0.001
Maximum temperature	2.42	1.78	0.12				
Reef area	1.53	2.45	0.06				
Complex coral cover	1.24	1.25	0.27				
Hard coral cover	0.17	0.67	0.61				
Average current speed	0.04	3.13	0.03				
Average temperature	0.007	1.18	0.29				
Nearest neighbouring reef	0.00	1.33	0.24				
Nearest mainland	0.00	0.37	0.84				
Global full model	**19.65**	**2.58**	**0.001**				

5.5 Discussion

The predictions that pinnacles would support higher abundance, biomass and productivity were supported by this study. The pinnacles supported highest total abundance, biomass and annual productivity compared to emergent reef types by several orders of magnitude. In terms of trophic groups, all reef types were numerically dominated by planktivores, comprising 66-85% of total abundance. However, patterns in biomass and productivity differed among reefs. Pinnacles were top-heavy communities where piscivores accounted for ~50% of the biomass and 67% of the productivity. Nearshore emergent reefs were bottom heavy for biomass, but productivity was driven by planktivores, which despite representing only 11.7% of biomass contributed 75.9% of total productivity. Offshore emergent reefs were dominated by planktivores in abundance, biomass and productivity, exhibiting a consistently middle driven trophic structure. Distance-based linear modelling showed that temperature variability, maximum current speeds and total hard coral cover explained most variability in multivariate analyses of biomass and productivity in fish assemblages. Overall, I show that offshore submerged pinnacles are a productive type of coral reef with distinct trophic structure.

5.5.1 Highest total abundance, biomass and productivity on pinnacles:

The pinnacles supported greatest total abundance, biomass and productivity at every trophic level. Compared to nearshore emergent reefs, this equated to 7 times the abundance, 12 times the biomass and 14 times the productivity. Differences with offshore reefs were 3 times the abundance, 7 times the biomass and 7 times the productivity. Large numbers of reef-associated primary and secondary consumers, schooling planktivores and semi-pelagic predatory fishes are all sustained on these small patch habitats, generating overall highest biomass and productivity. This pattern must be driven by enhanced energetic inputs to all trophic levels at these depths. Models predicting patterns in biodiversity, energy transfer and productivity on coral reefs are often based on variants of this species-energy (SE) hypothesis. Theoretically as energy declines in a system, less species and individuals are able to co-exist (Brown 1981; Wright 1983). On emergent coral reefs, these energy gradients are predominantly represented by light, temperature and pelagic influence, which drive benthic and pelagic productivity (Done 1983; Hatcher 1990; Fraser and Currie 1996). Typically, these decline monotonically with depth and distance from the crest (Huston 1985). Submerged reefs however, lack this continuum of shallow habitat within the upper ranges of these key energetic gradients. Inconsistencies between theory and realised patterns in ecological communities have been found on coral reefs and underscore the need to consider alternative explanations. I hypothesise several alternative or modified energetic mechanisms in submerged reef fish communities that account for the highest levels of biomass and productivity found here. These are decoupled from depth *per se* and instead arise as a result of the submerged nature of these reefs, which enhances energy to the system at depth.

5.5.2 Variation in trophic structure; mismatches in patterns of abundance, biomass and productivity

I also found clear differences in reef fish trophic structure among three different reef habitat types in my study seascape. Fish abundance for all reef types was dominated by planktivores. Although traditionally viewed as secondary to benthic primary production (Hatcher 1988), pelagic energetic subsidies captured by planktivores are a major trophic pathway on coral reefs (Hobson 1991; Morais and Bellwood 2019). The prevalence of planktivory forms an essential connection between benthic and pelagic food webs (Emery 1968; Hamner et al. 1988) and has also recently been shown as a key trophic driver of global patterns in coral reef fish diversity (Siqueira et al. 2021). Pelagic subsidies appear to be particularly important on deeper reefs. Recent studies from mesophotic coral ecosystems (MCEs, 30-150m) have highlighted the prevalence of planktivory in fish and coral communities as a key energetic input when light limits photosynthetic productivity (Lesser et al. 2010; Kahng et al. 2019). The high relative abundance of planktivores at each reef type reflects the prevalence of planktonic energetic pathways to fish communities at the depths surveyed in this study.

The broadly similar trophic structure for abundance across reef types was not however, consistent for biomass or productivity. Differences in habitat type can influence species composition and diversity (Sale and Dybdahl 1978; Andrefouet and Guzman 2005; Bennett et al. 2018). This variation in community composition generates differences in rates of biomass productivity and turnover, as a result of species-specific growth patterns and other life-history traits (Depczynski et al. 2007; Stearns and Stearns 2000; Thillainath et al. 2016). On the pinnacles, planktivore communities included large-bodied *Acanthurus* sp. and *Naso* sp*.,* whereas at the same depth on nearshore reefs, planktivores were mostly small-bodied *Chromis* sp*., Pesudanthias* sp*. and Chrysiptera* sp*.* Standing biomass of planktivores on nearshore reefs was therefore lower than relative abundance, but equated to the highest contribution to productivity, likely a result of fast growth and high turnover in abundant, small planktivorous species (Barneche et al. 2016). I also found mismatches amongst primary and secondary consumers on all reefs, where the proportion of biomass translated to a lower proportion of relative productivity. Larger bodied species that attain large adult final sizes may exhibit slow growth rates (Calder 1984; Roff 1992). This translates as high standing biomass, but lower rates of fish mass gained over time. Many of these larger-bodied, long-lived species, like parrotfishes, represent functionally important trophic pathways in on coral reefs, however these life-history traits also make them vulnerable to overexploitation (Juan-Jordá et al. 2015; Taylor et al. 2018). The mismatches described here demonstrate how variable assemblage structure arising from habitat-type differences determines overall productivity. Previous work conducted on the same reefs as this study found pinnacle fish assemblages to be distinct from emergent reef habitats (Galbraith et al. 2021). These findings, together with my current study, highlight how quantifying trophic structure in understudied reef habitats is required to understand the full extent of coral reef fish productivity. Different habitats, different communities and different life-histories are therefore an essential consideration for predicting future fisheries productivity (Pinsky and Byler 2015; Stawitz and Essington 2018).

The pinnacles displayed a top-heavy structure for biomass and productivity. These inverted pyramids are consistent with my expectations of studies on seamount fish assemblages (Morato and Clark 2007; Letessier et al. 2019), the prevalence of predators at remote reefs and seamounts (Friedlander and DeMartini 2002; Barnett et al. 2012; Letessier et al. 2016) and the aggregating effect of isolated physical structures (Koslow 1997; Pitcher et al. 2007; Morato and Clark 2008). Mechanisms promoting and maintaining inverted trophic pyramids include multiple endogenous and exogenous pathways (Mccauley et al. 2018) many of which are plausible explanations for the structure of fish communities found on the pinnacles in this study.

Firstly, the small area of the pinnacles may lead to increased foraging efficiency of consumers, therefore increasing the efficiency of energy transfer in these habitats (Stephens and Krebs 1986; Mccauley et al. 2018). These small submerged patch reefs exhibit an ecological “lens” effect, focusing individuals, energy and interactions on the relatively small amount of available habitat. Populations of reef-associated and semi-pelagic species are found in close proximity which can facilitate close coupling of trophic levels through multiple pathways. For example, piscivore biomass on the pinnacles was dominated by large schools (800+ individuals) of *Sphyraena qenie* and *Caranx* sp. These groups are mostly observed in slow swimming aggregations, presumably resting during daylight hours. This in itself is a physiological and behavioural mechanism that retains energy in habitats (Papastamatiou et al. 2018), and interactions between these predators and other consumers also enhance rates of endogenous energy transfer. Large Acanthurids and *Naso* species are frequently seen consuming the faeces of these reef predators (Robertson 1982, Author pers. obv). This broadens the dietary breadth in lower-level consumers and the high-quality food source of predator faeces could be routing energy and biomass more effectively up the food-web (DeBruyn et al. 2007; Cebrian et al. 2009; Utne-Palm et al. 2010). A similar relationship appears to exist between the schools of *Acanthurus thompsoni* and *Macolour* sp. on the pinnacles though in this case the source of energy for predators is fish eggs. These “egg boons” produced by spawning fish have been identified as a major trophic pathway for essential amino acids (Fuiman et al. 2015) and can influence the fitness of consumers (Fraser and McCormick 2014). Although neither of these relationships were measured directly in this study, these readily observed behaviours demonstrate how species interactions can enhance the efficiency and directionality of energy transfer in submerged pinnacle reefs especially in condensed small patch habitats.

Secondly, although movement patterns in mesopredators are not known for Kimbe Bay, other studies have shown numerous piscivorous species to exhibit high site-fidelity combined with off-reef foraging movements (Papastamatiou et al. 2015; Shantz et al. 2015).

Diurnal and seasonal movement of predators has been suggested as an important contribution to nutrient transfer between offshore waters and nearshore coral reefs (McCauley et al. 2012; Williams et al. 2018). In this way external nutrients are delivered to reef-attached species at these sites, enhancing feeding opportunities for a range of species (Skinner et al. 2021). This represents another pathway for enhanced energy input to pinnacle reefs from beyond the immediate habitat boundaries. Again, the small habitat area concentrates these subsidies, which would be much more dispersed on larger reef habitats. The use of submerged coral habitats by predators therefore represents both increased energetic input to these reefs and energetic feedback within the habitat that may sustain productivity in other trophic levels

Further, in a previous study conducted on the same reefs and at the same depths, I also found higher levels of complex coral cover on the pinnacles compared to emergent reefs (Galbraith et al. 2021). Sufficient levels of habitat complexity promotes resources for prey, thereby facilitating predator access to a wider range of prey (Crowder and Cooper 1982; Wang et al. 2009). Benthic and cryptobenthic fishes are a key source of energy supporting reef productivity and particularly rely on benthic complexity (Frisch et al. 2014; Brandl et al. 2019; Morais and Bellwood 2019). Reef-associated mesopredators (e.g. *Cephalopolis* sp. and *Ephinephelus* sp.) also contributed to the top-heavy trophic structure found in pinnacle fish communities. These site-attached predators derive their food source from benthic and epibenthic prey species, rather than large social fishes occupying the water column (Mihalitsis et al. 2021). They also make use of complex habitat themselves for shelter and ambush sites (Beukers and Jones 1998). Habitat complexity in combination with a diversity of species life histories may therefore support multiple modes of predator-prey relationships, enhance fish piscivory and support high trophic level biomass.

5.5.3 Environmental drivers of ecosystem processes on pinnacles: the potential for alternative energetic processes

I found that temperature variability, maximum current speeds and total hard coral cover were the strongest environmental drivers of the trophic distribution of biomass and productivity. These three variables represent key habitat features and physical and gradients in coral reef systems. Coral cover is particularly important for primary consumers, including many species of highly-specialist obligate corallivores (Pratchett 2014). The availability of primary resources like live coral and also algae is tightly linked to gradients in light energy which decline with depth (Huston 1985; Anthony and Connolly 2004; Brokovich et al. 2010). Differences in reef morphology and seascape setting could affect light levels at the depth of my study and could therefore account for differences in primary consumer biomass. On the pinnacles, primary productivity at depth could be greater due to lack of shading by emergent habitat and clear offshore waters where terrestrial inputs are lower. This would enhance food availability directly for primary consumers, but will also contribute to elevated total abundance, biomass and productivity at all trophic levels through bottom up processes (Alvarez-Filip et al. 2011; Russ et al. 2020). This gradient in light energy strongly influences photosynthetic productivity on all reefs, but on submerged morphologies is likely deep-shifted as there is no available habitat in the shallows (Thresher and Colin 1986; Kahng et al. 2010; Laverick et al. 2020). Alternatively, on emergent reefs consumers reliant on primary productivity are typically concentrated in the shallows where light availability, and therefore primary productivity and hard coral cover is higher (Brokovich et al. 2010; Bejarano et al. 2014). I did not survey fish communities found in shallow habitat on emergent reefs, but further investigation of how fish communities change down depth gradients on both submerged and emergent morphologies is warranted. The shallowest point of each reef type, regardless of depth, represents the region of greatest light energy but are changes in benthic and fish communities concurrent and how do community breaks compare down this gradient?

Temperature gradients also strongly determine coral reef productivity, but rising global temperature is altering coral reef fish population structures and productivity (Munday et al. 2008, 2012; Williams et al. 2019). Although my results did not identify average or maximum temperature as significant drivers explaining variation in biomass and productivity, temperature variability (standard deviation) was chosen in both final dbRDA models. Primary and secondary consumers were most aligned with temperature variability, although they exhibited opposite trends. In both cases, secondary consumer biomass and productivity increased with temperature variability whereas primary consumers declined. This supports the concept of variable responses amongst trophic groups to habitat-scale differences in environmental drivers (Heenan et al. 2016; Free et al. 2019) and also suggests that multiple properties of temperature gradients are important determinants of reef fish trophic structure.

Differences in temperature regimes among reef types in Kimbe Bay were found in Chapter 3. The pinnacles were characterised by lower temperatures over a 12-month period compared to both emergent reef types. Across broad latitudinal gradients lower temperature is linked to lower rates of primary production (Longhurst 2007) however, water temperatures in Kimbe Bay are relatively high year-round (28-31°C) and there is limited defined seasonality (Srinivasan and Jones 2006). Instead, temperature fluctuations and thermal stability may be more important than absolute highs or lows. Temperatures on emergent reefs in Kimbe Bay have however been recorded up to 36°C. When coupled with high variability, this could represent periodically extreme thermal environments, which are known to compromise the production and transfer of biomass by fishes (Brandl et al. 2020).

Although hotly debated, deeper reefs are suggested to function as thermal refuges when surface waters warm under predicted climate change models (Bongaerts and Smith 2019). Additionally, bathymetric features like seamounts frequently experience an upwelling of cooler water from depth (Genin and Boehlert 2009; Oliveira et al. 2016; Rogers 2018) and these currents may moderate the effects of near-surface warming (Randall et al. 2019; Sawall et al. 2020). The management of reef fisheries under climate change should therefore strongly consider not only variability in local or regional thermal-process, but also those generated by specific habitat types, which may confer resilience to heat-stress.

Of the three main potential drivers, the differences in hydrodynamic processes among reef types are likely to be the major determinant of differences in energetic pathways and trophic structures. On emergent reefs, most pelagic inputs are captured by planktivorous species concentrated on windward crests and slope (Hamner et al. 1988; Morais and Bellwood 2019). This pelagic-benthic interface is greatly increased on submerged reefs by the water column above the reef structure. This directly exposes the full extent of the reef to pelagic resources, closely linking benthic and pelagic energetic pathways over a greater proportion of the habitat. This also generates differences in hydrodynamic properties of the habitat. Interactions between the physical structure and surrounding oceanic process above and around submerged reefs result in stronger current speeds that appear particularly influential (Eriksen 1991). In my models, maximum current speed explained most variation in the distribution of biomass and the second most variation in productivity. In both models planktivores and piscivores both aligned with gradients in maximum current speeds.

Over evolutionary time planktivores have been highly successful in partitioning resources on coral reefs. However, high abundance and productivity within this trophic group is dependant on the regular supply of abundant planktonic resources (Hobson 1991; Siqueira et al. 2021). On submerged reefs these conditions are likely to be met by localised bathymetrically-modified hydrodynamics, where amplified currents enhance energetic input to the system, despite greater depth (Leitner et al. 2021; Chapter 3 and 4). This occurs via faster rates of plankton delivery to the reef from all directions (Genin 2004; Genin and Dower 2007), retention of plankton in the habitat by eddies, or physical trapping (Mullineaux and Mills 1997; Beckmann and Mohn 2002), greater mixing and resuspension of detritus (Lavelle et al. 2004; van Haren et al. 2017). These mechanisms are also important for the enhanced input and retention of nutrients for lower trophic level detritivores.

High abundance of piscivores was associated, not just with higher maximum current speed, but also the sites of highest overall biomass. Some of the energetic mechanisms linking piscivores with high pelagic productivity have already been discussed, but just as stronger currents provide benefits for planktivores through enhanced feeding opportunities, strong current flow generates energetic benefits for predators. High-current habitats afford enhanced hunting conditions, the opportunity for resting and sites for the formation of spawning aggregations (Sancho et al. 2000; Barreiros et al. 2002; Potts 2009; Eggertsen et al. 2016). Conversely, for productivity high piscivore abundance were negatively associated with increasing maximum current speed. Swimming in high current speeds represents a significant energetic cost to fishes (Liao 2007) and so although high current habitats provide energetic opportunities for piscivores, extremes in flow speeds also represent a source of energy loss through elevated movement costs (Di Santo et al. 2017; Roff et al. 2019). Highly exposed reefs have been shown to be detrimental to smaller grazer-detritivores, probably as a consequence of poor swimming ability in strong currents (Bejarano et al. 2017).

Currents therefore may also explain highest total primary producer biomass on pinnacles, as these individuals are likely to be larger species or individuals with greater swimming capabilities. Some recent studies have investigated fitness consequences of habitat variability and energy allocation across the depth gradients in coral reef fishes (Goldstein et al. 2016b, 2016a, 2017) and similar investigation of fish populations inhabiting deeper submerged reefs would be beneficial.

5.3.4 Future challenges and opportunities for submerged reef fishes and fisheries

The maintenance of ecological functions and resource provision by coral reefs is a major challenge for ecologists, conservationists and managers in the Anthropocene (Brandl et al. 2019; Williams et al. 2019). The high biomass and productivity found on submerged pinnacle reefs in this study presents both challenges and opportunities for future conservation planning and coral reef fisheries management. Productive offshore pinnacle reefs are valuable sources of larval recruits, but are also desirable fisheries targets (Harrison et al. 2012; Lavin et al. 2021). Additionally, distance to nearest land (a proxy for anthropogenic disturbance like fishing) was not a significant driver of biomass or productivity distribution in either of the dbRDA models. Human influences clearly shape reef fish trophic structure, but I found that variability in biomass and productivity was mostly driven by the surrounding energetic environment (maximum current speeds and temperature variability). Until recently, coral reef mapping efforts had not revealed the full extent of submerged coral reefs (Harris et al.2013; Bridge et al 2013) and as such these habitats are under-represented in protected area networks and management plans (Clark et al. 2012; Wagner et al. 2020). As small, discrete and productive patch habitats, coral reefs on seamounts and pinnacles have the potential to be highly effective “bang-for-buck” management units that are numerous in all coral reef seascapes (McCook et al. 2009; Clark et al. 2010; O’Leary and Roberts 2018). There is therefore great opportunity to include submerged reefs in marine reserves, but further studies are needed to quantify fundamental ecological processes and connectivity with shallow emergent reefs.

Overall, my study builds upon growing evidence that submerged bathymetric features like pinnacles are important coral reef habitats that support diverse, distinct and highly productive fish assemblages. Evidence presented here also supports the understanding of local environmental conditions that drive variability in natural structure and energy flow in reef fish communities. However, comparisons between submerged and emergent reef types are lacking - even studies of mesophotic coral reefs are typically focused on reefs with physical habitat linking the surface to ecological communities at depth. Of the few published studies to date, variation in local environmental conditions and biological communities on submerged reefs appears considerable (Moore et al. 2017; Cooper et al. 2019; Galbraith et al. 2021; Leitner et al. 2021). This study on the contrasting patterns in trophic structure between emergent reefs and submerged pinnacles signals further important habitat differences in the processes structuring fish assemblages, transferring energy up trophic levels and determining overall reef productivity. The unique hydrodynamic processes generated by the physical structure are likely the key mechanisms enhancing energetic input at depth on these small and isolated reefs. These unfamiliar coral reef structures present intriguing opportunities to test models explaining patterns in biodiversity and are an important consideration for future-proofing reef fish productivity.

Chapter 6: General Discussion

6.1 Overview

The ecology of fishes on coral reefs has advanced significantly over the past 70 years. However, gaps remain in our knowledge of habitats that lay beyond the well-studied habitat zones on shallow emergent reefs. Conservation science depends upon accurate information of fundamental patterns in biodiversity, and submerged seascapes represent a significant, yet unexplored habitat that offers great potential as a refuge. In this thesis, I examined several important aspects of the ecology of reef fishes on iconic coral reef pinnacles. My overarching aim was to compare patterns of biodiversity and ecological processes on distinct submerged pinnacle habitats with shallow emergent coral reefs with a more typical reef morphology.

To set the scene, I first conducted a baseline assessment of fish communities associated with submerged pinnacles (**Chapter 2**). This demonstrated that the pinnacles support diverse and distinct assemblages compared to emergent reef habitat types. However, some well-established relationships between fish and the coral reef habitat did not explain this variability well. In order to establish other key environmental drivers, I therefore characterised fine-scale hydrodynamic regimes (**Chapter 3**). I addressed the hypothesis that pinnacles, like seamounts, possess stronger and more dynamic currents and found evidence to support this. Together with other spatial and habitat variables, I then used this hydrodynamic data to assess the relative influence of hydrodynamics in shaping patterns of fish community structure across all three reef types (**Chapter 4**). Variables associated with water current were consistently the most important in explaining fish community structure. Finally, I examined the functional implications of differences in community structure and habitat-specific environmental conditions by addressing differences in trophic structure, biomass and productivity (**Chapter 5**). Overall, my thesis demonstrates that submerged pinnacle coral reefs are distinct and highly productive coral reef habitat types that warrant further investigation, both for their unique ecology and as potential sites of conservation significance. In this concluding section, I briefly highlight several key findings arising from my thesis, some limitations to my work and suggest further directions for the study of reef fish ecology on submerged coral reefs.

6.2 Ecological value of pinnacles: function, management and future directions

The key finding from my research, that submerged pinnacle coral reefs support diverse and highly abundant reef fish communities, is ecologically significant given the small size and relative isolation of these deeper patch habitats. Both the species-area relationship and island biogeography theory would predict the opposite; that diversity and the numbers of species and individuals would be lower than those on larger, contiguous emergent reefs (Preston 1960; MacArthur and Wilson 1967; Connor and McCoy 1979; Coleman 1981). The mechanisms driving these patterns are more consistent with the species-energy hypothesis (Wright 1983). I propose that the diverse assemblages on pinnacles are supported by enhanced energetic inputs delivered by distinct local hydrodynamics which arise as a result of interactions between the physical structure and surrounding oceanographic processes. Although hydrodynamic processes are important on all coral reefs, my research highlights how submerged morphologies exhibit strong current regimes at depth and these are associated with abundant and diverse fish communities. Although these mechanisms are known from seamount ecological studies, the study of hydrodynamics on coral reefs is mostly focused on surface driven waves, currents and tidal flows (Monismith 2007). Variability in environmental conditions is especially important within the context of global environmental change as some hydrodynamic conditions, specific to certain reef morphologies, may confer elements of resilience to coral reef communities (Rogers et al. 2016; Green et al. 2018; Reid et al. 2019) . There is a clear need for further investigation of physical processes on pinnacles. This would not only broaden our understanding of coral reef ecology, but would be useful for testing theories of seamount ecology. Seamounts remain understudied as a result of their deep-sea setting and remote locations, consequently, it has been suggested that proxy habitats should be used to investigate their ecological paradigms (Clark et al. 2012; Stocks et al. 2012). Pinnacles would be an ideal model system to take this approach.

Another central result of my research is that submerged pinnacle fish communities also exhibit distinct trophic structure and support highly productive communities. Identifying productivity for fisheries is central to conservation spatial planning and fisheries management. However, the productive nature of submerged pinnacles also makes them vulnerable to overexploitation as extractive pressures are currently extending into deeper, more isolated fish stocks (Roberts 2002). Further, the fish assemblages on the pinnacles represent a combination of reef-associated and semi-pelagic environments to a much greater extent than on shallow emergent coral reefs. Due to the combination of species, it follows that these habitats will feature in multiple productivity pathways, particularly in terms of trophodynamics and larval source dynamics. My results highlight that submerged reefs should be incorporated into conservation planning and fisheries management, not only for direct protection as biodiversity hotspots, but also their likely important role in larval source dynamics. When combined with their ubiquitous seascape distribution, this makes submerged pinnacle reefs ecologically valuable habitats that have important roles in connecting seascapes and sustaining future coral reef fisheries.

One key tool for conserving and managing fisheries, marine reserves, requires on-going studies of connectivity between populations (Jones et al. 2007; Harrison et al. 2012; Green et al. 2014). Unfortunately, it is uncertain how effective current management strategies will be for protecting fish populations as community structures shift with anthropogenic stressors and climate change (Bruno et al. 2018; Graham et al. 2020). This emphasises the continual need to approach coral reef ecology as a holistic science and strive to include logistically challenging reef habitat types in global assessments. However, estimates of ecosystem value, functions, numbers of species and habitat availability for coral reefs are typically based on readily observable, shallow, emergent coral reef habitats. My research emphasises that not all reef types are equal in terms of their biodiversity and productivity, or their importance as fishery resources (Messmer et al. 2014; Cinner et al. 2018; Morais et al. 2020). Because patchworks of habitats scale-up to generate large scale biogeographic patterns, by excluding coral reef habitats beneath the upper 20m of the sea surface we risk missing vital ecological connections and processes. This has particularly important implications for the transfer of energy and individuals across seascapes. Coral reefs on seamounts and pinnacles therefore seem to be important marine habitats both in terms of generating enhanced subsidies and potentially facilitating complex trophic linkages to distribute these recourses to other reef types.

An obvious limitation of my research is the spatial restriction to one study site. Kimbe Bay is situated in the species-rich coral triangle and so the magnitude of differences, particularly in species richness, found between pinnacles and emergent reefs may be somewhat amplified. Even so, submerged features are ubiquitous across all continental shelves and oceanic island slopes. A natural progression to this body of work would therefore be the expansion of similar studies to other regional and global locations. Another limitation was that my assessments of fish communities using diver-operated stereo-video systems, were biased towards easily visible species and did not include cryptic components of the assemblage. Cryptobenthic fishes are known to contribute significantly to the structure, function and productivity of coral reefs (Brandl et al. 2019). Specifically, with reference to the ability of submerged pinnacles to support such high abundance and biomass of fishes, the cryptobenthic pathway is likely another key energetic mechanism that was not investigated within the scope of my research. Additional studies to address this would provide further valuable insights to the mechanisms supporting submerged pinnacle reef fish communities, particularly in terms of energy acquisition, turnover and fisheries productivity.

Although the importance of depth has been consistently acknowledged and discussed throughout this thesis, my research did not investigate the potential for differential shifts in diversity patterns between submerged and emergent reefs, their different reef zones and with depth. For example, the 20-30m depth band surveyed on all reefs incorporated the summits of the pinnacles which are essentially entirely composed of horizontal reef crest habitat. Whilst site selection of near-horizontal gradients on emergent reef sites mitigates the potential effects of aspect, the studies presented are essentially comparing pinnacle crests/summits with emergent slopes. It is highly likely that although at the depths surveyed pinnacles exhibited higher numbers of species and individuals, with increasing depth on pinnacles, this biodiversity will also decline. A study assessing depth gradient patterns on submerged reefs would determine how communities shift with depth and could also contribute to resolving the well-held idea that diversity is directly coupled to depth. This could be achieved by utilising Remotely Operated Vehicles (ROVs) or technical diving technologies to survey ecological communities below SCUBA diving depths. Reef aspect and some of the alternative energetic mechanisms discussed in the chapters of this thesis are clearly crucial determinants of fish communities at depth, not only depth *per se*.

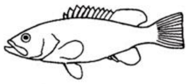
Future directions for the ecology of submerged pinnacle coral reefs must involve investigation of patterns of connectivity, along depth gradients with shallow coral reefs and the wider seascape. Advancing bathymetric mapping capabilities will continue to assist us in pushing past these logistical barriers to sampling. This must, however, be followed by ecological exploration of deeper morphologically distinct coral reef habitats to further our understanding of these truly complex systems. Movement studies, genetic techniques and the use of stable isotopes are clear opportunities to assess how these habitats are connected to the shallows, the mesophotic and the wider seascape. These methods would provide greater insight to habitat use by individuals, population connectivity and also the transfer of energetic subsidies to and from pinnacle coral reefs. Like most coral reef fish ecology, my research utilised daylight surveys only, but it is well-known that many fishes, particularly predators, exhibit diurnal foraging patterns (Papastamatiou et al. 2015; Williams et al. 2018). This is a particularly fascinating avenue for future research to extend our insight to the functional roles of mobile predators on coral reefs and also examine the mechanisms by which nutrients are potentially concentrated on pinnacle coral reefs.

My research involved the use of in-situ loggers to characterise physical environmental conditions but, there are numerous other oceanographic methods and technologies which could validate many of the further questions arising from my work. The distinct environmental conditions on pinnacles and their relationships with fish communities must be teased out and brought into the wider literature. Pinnacles also present great opportunities for conservation spatial planning and the design of marine reserve networks. They are discrete habitat units that can be effective components of conservation strategies (Almany et al. 2009; McCook et al. 2009). Again, if these habitats are not accounted for by habitat mapping and ecological assessments, benefits to conservation, fisheries and the adaptive capacity of marine resource management are lost. Overall, my research suggests that the ecology of coral reef fishes is a substantially broader field when coral reef habitats outside of well-studied, shallow, nearshore systems are considered.

6.3 Concluding remarks

The formative collection of ecological studies presented in the “Ecology of Fishes on Coral Reefs” (Sale 1991) undoubtedly advanced the understanding of key ecological theories and initiated the concerted organisation of the study of coral reef fishes. Ecological processes which were previously thought impossible to capture have been discovered and are now routine elements of reef fish ecology (Jones 2015). In the most recent book, “Ecology of Fishes on Coral Reefs” (Mora 2015), knowledge of the basic ecology of reef fishes is now complemented by a greater understanding of human impacts, emerging challenges to conservation and shifting ecological paradigms. While anthropogenic threats were acknowledged by all contributors to Sale (1991), the current volume reflects the rapid global shift in ecological questions addressed for coral reef fishes over the past 30 years. Coral reef ecology now comprises a necessary multi-disciplinary science which encompasses social-sciences, marine policy and law, biogeography, economics and the documentation of decline.

The need for societal change in the use and management of global ecological systems is clear, albeit perpetually slow to progress. The shifting research focus in coral reef ecology is now often geared towards documenting decline or offering quick-fix restorative solutions. However, the future of coral reef conservation and management will always depend on developing our understanding of fundamental ecological patterns and processes. This includes the ecology, not just of novel communities formed as a result of ecological shifts and anthropogenic stressors, but also communities found in understudied habitats. The findings presented in this thesis demonstrate that remarkably, understudied coral reef habitats still exist for ecologists, and there is much to do to unravel their patterns and processes. Knowledge of submerged coral reef habitats can only assist us in navigating the ecology of coral reef fishes through the uncertain future of the Anthropocene.



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Appendix A – Supplementary Material for Chapter 2

Table S2.1 Analysis of deviance/variance table of GLMs for fish Diversity (Simpson's Index), Species Richness, Species Evenness (Pielou's J') and Total Abundance. To test for differences between mean values at each reef type, F tests were used for linear models and Wald chi squared tests were used for generalized linear models.

Fish community metric	Mean (se)						GLM Family-link	χ2 / F	p	df	Tukey HSD p <0.05
	Pinnacles (P)		Offshore (OS)		Nearshore (NS)						
Diversity Simpsons	0.76	(0.05)	0.72	(0.05)	0.81	(0.04)	LM	5.10	0.07	2	-
Richness	**32.45**	**(3.03)**	**16.50**	**(2.93)**	**16.35**	**(2.47)**	**NB - log**	**67.23**	**<0.001**	**2**	**P-OS** **P-NS**
Evenness	**0.22**	**(0.02)**	**0.27**	**(0.02)**	**0.30**	**(0.01)**	**LM**	**14.97**	**<0.001**	**2**	**OS-NS** **P- NS** **OS-P**
Total Abundance	**370.50**	**(84.80)**	**143.80**	**(52.07)**	**56.40**	**(13.75)**	**NB - log**	**67.67**	**<0.001**	**2**	**OS-NS** **P- NS** **OS-P**

Table S2.2. Analysis of deviance table of GLMs for benthic diversity (Shannon H') and richness. To test for differences between mean values at each reef type, F tests were used for linear models and Wald chi squared tests were used for generalized linear models.

Benthic Metric	Mean (se)						Model error-link	χ2 / F	p	df	Tukey HSD p <0.05
	Pinnacles (P)		Offshore (OS)		Nearshore (NS)						
Diversity	2.26	(0.10)	2.16	(0.08)	2.16	(0.0)	LM	1.13	0.33	2	-
Richness	14.45	(0.93)	13.20	(0.81)	13.15	(0.86)	NB - log	1.58	0.45	2	-
Total Hard Coral %	38.33	(4.81)	33.83	(4.82)	32.25	(4.66)	LM	0.96	0.39	2	-

Table S2.3 Species list and relative abundance**.** Relative abundance was calculated as a percentage of the total number of individuals observed at each reef type.

Reef Type	**Nearshore**	**Offshore**	**Pinnacle**
Total Species Richness	**129**	**87**	**172**
Species	**Relative Abundance (%)**		
Acanthurus thompsoni	8.36	7.95	19.51
Acanthochromis polyacanthus	1.14	2.85	0.99
Acanthurus albipectoralis	-	-	0.03
Acanthurus auranticavus	0.53	-	0.03
Acanthurus blochii	-	-	-
Acanthurus fowleri	0.26	0.10	0.12
Acanthurus grammoptilus	0.09	0.03	-
Acanthurus guttatus	-	-	-
Acanthurus maculiceps	0.09	-	0.01
Acanthurus mata	-	-	0.21
Acanthurus nigricauda	0.09	0.07	0.07
Acanthurus nigrofuscus	0.09	-	-
Acanthurus nubilis	-	0.66	0.82
Acanthurus nubilus	-	-	0.08
Acanthurus pyroferus	0.44	0.10	0.38
Amblyglyphidodon aureus	1.67	2.01	1.69
Amblyglyphidodon curacao	0.09	-	-
Amblyglyphidodon leucogaster	1.67	0.94	1.16
Amphiprion clarkii	-	0.07	0.05
Amphiprion perideraion	-	-	0.15
Anampses melanurus	-	-	0.01
Anampses neoguinaicus	0.09	-	-
Anyperodon leucogrammicus	0.09	-	0.01
Apogon angustatus	0.09	-	-
Apogon chrysotaenia	0.09	-	-
Arothron nigropunctatus	-	0.03	0.03
Aspidontus taeniatus	0.09	-	-
Balistapus undulatus	0.18	0.10	0.05
Balistoides conspicillum	-	-	0.03
Balistoides viridescens	0.35	0.03	-
Bodianus anthioides	-	-	0.01
Bodianus diana	-	-	0.01
Bodianus dictynna	0.09	-	0.03
Bodianus mesothorax	0.26	-	0.04
Caesio cuning	15.85	20.10	2.34

Caesio lunaris	-	1.42	5.29
Caesio teres	-	-	2.97
Cantherhines dumerilii	0.44	-	0.19
Canthidermis maculatus	-	-	0.17
Canthigaster solandri	0.09	-	-
Carangoides bajad	-	-	0.08
Caranx ignobilis	-	-	0.01
Caranx melampygus	-	-	0.39
Caranx sexfasciatus	-	-	1.50
Carcharhinus amblyrhynchos	-	-	0.07
Carcharhinus melanopterus	-	-	0.01
Centropyge bicolor	-	0.03	0.07
Centropyge vroliki	0.18	-	0.01
Cephalopholis argus	0.09	-	0.03
Cephalopholis cyanostigma	-	0.21	0.07
Cephalopholis leopardus	0.18	-	-
Cephalopholis microprion	0.26	0.03	0.01
Cephalopholis miniata	-	-	0.01
Cetoscarus bicolor	0.09	-	-
Cetoscarus ocellatus	-	-	0.03
Chaetodon auriga	-	-	0.03
*Chaetodon baronessa**	0.26	0.03	0.05
Chaetodon kleinii	0.35	0.17	0.30
Chaetodon lineolatus	-	-	0.15
Chaetodon lunula	0.09	-	0.03
*Chaetodon lunulatus**	-	0.10	0.07
*Chaetodon ocellicaudus**	-	-	0.01
*Chaetodon octofasciatus**	0.26	0.03	0.01
Chaetodon oxycephalus	-	-	0.01
Chaetodon vagabundus	0.35	0.10	0.05
Cheilinus fasciatus	0.88	-	0.04
Cheilinus undulatus	-	-	0.04
Chlorurus bleekeri	0.44	0.07	0.01
Chlorurus microrhinos	0.09	0.10	-
Chlorurus sordidus	0.09	0.07	0.09
Chromis alpha	0.09	0.03	0.16
Chromis amboinensis	2.64	3.40	2.26
Chromis analis	-	-	0.42
Chromis atripes	0.09	-	0.11
Chromis delta	-	-	0.04
Chromis elerae	0.18	-	0.32
Chromis margaritifer	0.18	0.07	3.99
Chromis nigroris	-	-	0.01

Chromis parasema	1.06	-	-
Chromis retrofasciata	3.26	1.01	0.20
Chromis ternatensis	0.09	0.17	1.63
Chromis viridis	0.18	-	-
Chromis weberi	0.09	-	0.03
Chromis xanthochira	-	-	0.38
Chromis xanthura	1.32	0.59	0.85
Chrysiptera cyanea	0.26	-	-
Chrysiptera anarzae	4.05	0.73	-
Chrysiptera rollandi	2.90	-	-
Chrysiptera talboti	0.18	0.17	-
Cirrhilabrus solorensis	0.09	-	-
Cirrhilabrus walindii	-	-	0.01
Ctenochaetus binotatus	0.09	-	0.05
Ctenochaetus striatus	0.62	0.03	0.27
Ctenochaetus tominiensis	4.58	2.08	0.12
Dascyllus melanurus	0.09	-	-
Dascyllus reticulatus	0.09	-	0.15
Dascyllus trimaculatus	0.18	0.03	0.99
Diproctacanthus xanthurus	-	-	0.04
Elagatis bipinnulata	-	0.03	0.04
Epinephelus areolatus	-	-	0.01
Epinephelus coeruleopunctatus	0.09	-	0.01
Epinephelus fasciatus	-	-	0.03
Epinephelus polyphekadion	-	-	0.01
Forcipiger flavissimus	0.35	0.63	0.23
Genicanthus melanospilos	-	-	0.01
Gomphosus varius	-	-	0.03
Gracila albomarginata	-	-	0.01
Grammatorcynus bilineatus	-	-	0.03
Gymnosarda unicolor	-	0.03	0.05
Halichoeres chlorocephalus	-	-	0.01
Halichoeres chloropterus	0.26	-	-
Halichoeres chrysus	-	-	0.03
Halichoeres hortulanus	0.18	-	0.04
Halichoeres marginatus	0.09	-	-
Halichoeres prosopeion	0.53	0.24	0.04
Halichoeres richmondi	0.09	-	-
Halichoeres trimaculatus	-	-	0.07
Halichores trimaculatu	-	-	0.01
Hemigymnus fasciatus	0.09	0.03	-
Hemitaurichthys polylepis	-	0.45	1.68
Heniochus acuminatus	-	0.14	0.50

Heniochus chrysostomus	-	0.07	0.07
Heniochus diphreutes	-	-	0.12
Heniochus singularius	0.09	0.07	-
Heniochus varius	0.09	0.07	-
Hipposcarus longiceps	-	-	0.01
Hologymnosus doliatus	-	-	0.01
Labroides bicolor	0.09	0.07	-
Labroides dimidiatus	1.41	0.35	0.38
Labroides pectoralis	-	-	0.01
Lepidozygus tapeinosoma	-	-	1.60
Lethrinus erythracanthus	-	-	0.01
Lutjanus biguttatus	0.35	0.24	0.11
Lutjanus bohar	0.09	-	0.07
Lutjanus carponotatus	0.09	-	0.03
Lutjanus ehrenbergii	0.09	-	0.03
Lutjanus gibbus	0.35	0.28	0.17
Lutjanus kasmira	-	-	0.07
Lutjanus monostigma	0.09	0.21	-
Lutjanus semicinctus	0.35	-	-
Macolor macularis	0.09	1.01	0.70
Macolor niger	-	0.07	0.09
Meiacanthus crinitus	0.09	-	-
Meiacanthus grammistes	0.09	-	-
Meiacanthus vittatus	-	-	0.04
Melichthys vidua	0.44	0.31	0.73
Monotaxis grandoculis	0.09	-	0.03
Monotaxis heterodon	-	0.03	-
Myripristis berndti	0.09	-	0.04
Myripristis kuntee	0.09	0.10	-
Myripristis murdjan	-	-	0.04
Myripristis vittata	-	-	0.05
Naso brevirostris	-	-	0.01
Naso caeruleacauda	-	-	0.07
Naso caesius	-	0.03	0.01
Naso hexacanthus	-	0.52	1.02
Naso lituratus	0.62	0.17	0.08
Naso unicornis	-	-	0.03
Naso vlamingii	-	0.10	0.71
Neoglyphidodon melas	0.09	-	-
Neoglyphidodon mitratus	0.18	-	-
Neoglyphidodon nigroris	0.88	0.17	-
Neopomacentrus bankieri	0.44	-	-
Odonus niger	3.79	0.03	1.37

Oxycheilinus celebicus	0.97	0.07	-
Oxycheilinus digrammus	0.18	0.03	-
Oxycheilinus orientalis	0.09	-	-
Paracirrhites forsteri	-	-	0.05
Parupeneus multifasciatus	0.09	-	-
Pholidichthys leucotaenia	0.09	-	-
Pictichromis paccagnellae	0.09	0.03	0.01
Pinjalo lewisi	-	-	0.62
Platax batavianus	0.09	-	-
Platax teira	-	0.07	0.59
Plectorhinchus picus	-	-	0.01
Plectroglyphidodon dickii	0.09	-	-
Plectropomus leopardus	-	-	0.05
Plectropomus maculatus	0.09	-	0.03
Plectropomus oligacanthus	0.18	0.21	0.03
Pomacanthus navarchus	0.26	0.07	0.01
Pomacanthus sexstriatus	0.09	0.03	-
Pomacentrus amboinensis	-	0.14	-
Pomacentrus lepidogenys	-	-	0.01
Pomacentrus nigromanus	13.38	0.38	-
Pomacentrus nigromarginatus	-	-	0.01
Pomacentrus philippinus	0.09	-	-
Pomacentrus reidi	0.18	-	-
Priacanthus hamrur	-	-	0.01
Pseudanthias bartlettorum	-	-	0.62
Pseudanthias bicolor	-	-	0.47
Pseudanthias dispar	-	-	1.88
Pseudanthias huchtii	-	-	4.18
Pseudanthias smithvanizi	-	-	1.17
Pseudanthias squamipinnis	-	-	0.01
Pseudanthias tuka	8.71	36.01	8.70
Pseudochromis paccagnellae	0.35	-	0.01
Pseudocoris yamashiroi	0.35	-	-
Pterocaesio chrysozona	-	-	1.68
Pterocaesio tile	-	10.31	3.12
Pygoplites diacanthus	0.18	0.21	0.16
Sargocentron caudimaculatum	-	-	0.03
Scarus chameleon	0.09	-	0.01
Scarus dimidiatus	0.26	-	0.01
Scarus flavipectoralis	0.44	0.03	0.08
Scarus frenatus	0.09	-	-
Scarus ghobban	0.09	-	-
Scarus niger	0.79	0.28	0.04

Scarus oviceps	0.26	-	0.01
Scarus prasiognathos	0.35	0.03	0.01
Scarus psittacus	-	0.03	-
Scarus rubroviolaceus	0.09	-	0.09
Scarus spinus	0.09	0.03	0.09
Scarus tricolor	0.09	0.07	0.08
Scolopsis affinis	-	-	0.09
Siganus vulpinus	0.26	0.07	0.03
Sphyraena qenie	-	-	12.60
Sufflamen bursa	0.70	0.03	0.11
Sufflamen chrysopterum	-	-	0.03
Sufflamen fraenatum	0.18	0.03	0.01
Thalassoma amblycephalum	-	-	0.01
Thalassoma hardwicke	-	-	0.01
Thalassoma jansenii	0.09	-	-
Thalassoma lunare	0.09	-	0.04
Thalassoma lutescens	-	-	0.01
Thalassoma quinquevittatum	0.09	-	-
Variola albimarginata	-	0.03	0.11
Zanclus cornutus	0.62	0.14	0.46
Zebrasoma scopas	-	0.35	0.17
Zebrasoma veliferum	-	-	0.12

Table S2.4 Results of PERMANOVA, SIMPER and betadisp tests for both fish (a) and (b) benthic assemblages.

a. Fish Assemblages

	df	SS	MS	Pseudo-F	P(perm)	permutations	R2
Reef Type	2	4.1473	2.07366	8.6657	0.001	9999	0.23316
Residual	57	13.6398	0.23929				
Total	59	17.7871					

Pairs	Average overall dissimilarity	F	R2	P
Pinnacles - Offshore	74.5%	6.3964	0.14	0.001
Pinnacles - Nearshore	87.8%	9.9972	0.21	0.001
Offshore - Nearshore	79.5%	7.5907	0.17	0.001

Analysis of variance (betadisp) ANOVA $F_{2,57} = 3.97$, $p = 0.02$

b. Benthic Assemblages

	df	SS	MS	Pseudo-F	P(perm)	permutations	R2
Reef Type	2	0.5904	0.295222	4.7412	0.001	9999	0.14263
Residual	57	3.593	0.062268				
Total	59	4.1397					

Pairs	Average overall dissimilarity	F	R2	P
Pinnacles - Offshore	38%	5.3015	0.12	0.001
Pinnacles - Nearshore	40%	4.8515	0.11	0.001
Offshore - Nearshore	34%	5.9432	0.14	0.001

Analysis of variance (betadisp) ANOVA $F_{2,57} = 4.1628$, $p = 0.02$

Table S2.5. Summary of mean fish and benthic community metrics per transect (150m^2) for all three reef types and individual sites. Reef type n = 20, each individual site n = 5. Numbers in brackets are SE.

Reef Type (Individual Sites)	**Benthic Diversity (H')**	**Benthic Richness**	**Hard Coral % Cover**	**Fish Diversity (Simpsons)**	**Fish Abundance**	**Fish Richness**	**Fish Evenness (J')**
Pinnacle	2.26 (0.15)	14.45 (1.42)	23.00 (5.01)	0.76 (0.05)	370.5 (169.51)	32.45 (3.49)	0.76 (0.05)
Bradford	1.94 (0.13)	13.20 (0.65)	9.60 (2.19)	0.74 (0.06)	754.2 (255.11)	34.80 (5.56)	0.74 (0.07)
Joelles	2.35 (0.10)	15.01 (1.25)	21.40 (2.95)	0.82 (0.03)	238.0 (18.13)	33.80 (3.38)	0.82 (0.03)
Inglis	2.21 (0.07)	12.20 (0.96)	20.60 (2.48)	0.72 (0.06)	187.4 2(1.06)	29.80 (2.22)	0.72 (0.06)
Kimbe Bomie	2.52 (0.10)	17.41 (1.35)	15.00 (2.91)	0.78 (0.04)	302.4 (84.95)	31.40 (2.39)	0.78 (0.04)
Offshore	2.16 (0.09)	13.20 (0.90)	20.30 (3.51)	0.72 (0.05)	143.8 (57.21)	16.50 (3.25)	0.72 (0.07)
Ema	2.15 (0.09)	13.20 (0.96)	24.40 (3.49)	0.83 (0.03)	115.2 (65.80)	20.00 (3.59)	0.83 (0.04)
Ottos	2.23 (0.07)	13.80 (0.74)	30.40 (2.97)	0.67 (0.05)	183.6 (72.89)	15.60 (2.80)	0.67 (0.03)
Hogu	2.12 (0.10)	13.40 (0.67)	24.60 (3.37)	0.76 (0.09)	110.0 (37.06)	13.60 (3.17)	0.76 (0.05)
Kimbe Island	2.17 (0.10)	12.40 (1.24)	24.20 (4.59)	0.60 (0.03)	166.4 (57.15)	16.80 (3.56)	0.60 (0.10)
Nearshore	2.16 (0.10)	13.15 (0.90)	19.35 (4.27)	0.80 (0.04)	56.4 (23.09)	16.35 (3.43)	0.80 (0.06)
Lady Di	2.23 (0.07)	13.01 (1.12)	15.00 (2.89)	0.76 (0.06)	52.6 (21.18)	13.60 (2.25)	0.76 (0.07)
Madaro	2.03 (0.12)	13.01 (1.12)	30.80 (5.53)	0.83 (0.04)	24.8 (3.88)	12.00 (1.32)	0.83 (0.05)
Susans	2.31 (0.09)	14.00 (0.71)	15.80 (1.52)	0.90 (0.02)	40.0 (9.12)	19.00 (2.24)	0.90 (0.02)
Donnas	2.07 (0.09)	12.60(0.91)	18.80 (3.45)	0.72 (0.06)	108.2 (27.33)	20.80 (5.24)	0.72 (0.06)

Table S2.6 Analysis of deviance for each GLM comparing means of benthic cover categories across all three reef habitat types. Significant differences are in bold and accompanied by significant post-hoc pairing. P = Pinnacle, NS = Nearshore, OS = Offshore.

Benthic cover category	**Mean % Cover (se)**						**GLM Family-link**	**χ2**	**p**	**df**	**Tukey HSD p <0.05**
	Pinnacles (P)		Offshore (OS)		Nearshore (NS)						
Complex Hard Coral	**9.67**	**(4.21)**	**1.92**	**(1.33)**	**5.58**	**(1.09)**	**ZINB - logit**	**14.95**	**<0.001**	**2**	**P-O and NS-P**
Massive/Sub-massive Hard Coral	**10.00**	**(4.90)**	**4.80**	**(2.08)**	**4.00**	**(2.19)**	**NB - log**	**7.87**	**0.02**	**2**	**NS-P**
Encrusting Hard Coral	10.33	(4.14)	11.83	(2.70)	14.75	(3.21)	NB - log	4.43	0.11	2	-
Laminar Hard Coral	**8.30**	**(3.99)**	**15.00**	**(5.55)**	**7.90**	**(2.92)**	**NB - log**	**7.28**	**0.03**	**2**	**OS-NS and OS-P**
Complex Hexacoral	**2.00**	**(0.84)**	**2.67**	**(0.82)**	**0.67**	**(0.28)**	**ZINB - logit**	**6.52**	**0.04**	**2**	**NS-OS and NS-P**
Encrusting Hexacoral	**11.00**	**(4.02)**	**0.25**	**(0.18)**	**0.00**	**(0.00)**	**ZINB - logit**	**22.87**	**<0.001**	**2**	**OS-P and NS-P**
Octocorals	**4.58**	**(1.40)**	**0.75**	**(0.19)**	**1.67**	**(0.54)**	**ZINB - logit**	**28.4**	**<0.001**	**2**	**NS-P and OS-P**
Encrusting Porifera	**10.50**	**(1.71)**	**21.00**	**(2.59)**	**6.08**	**(0.93)**	**NB - log**	**39.59**	**<0.001**	**2**	**NS-P , OS-P and NS-OS**
Complex Porifera	5.33	(0.78)	9.42	(1.70)	8.67	(1.82)	NB - log	4.402	0.11	2	-
Algae	**5.92**	**(2.00)**	**7.08**	**(1.55)**	**16.92**	**(1.77)**	**ZINB - logit**	**8.35**	**0.015**	**2**	**NS-OS**
CCA	1.92	(0.39)	3.75	(0.78)	3.25	(0.63)	NB - log	5.51	0.06	2	-
Sand and Silt	5.92	(1.12)	3.92	(0.92)	7.50	(1.69)	NB - log	3.49	0.17	2	-
Rubble	5.50	(1.20)	6.33	(1.72)	9.33	(2.70)	ZINB - logit	2.41	0.3	2	-
Rock/Reef Matrix	9.00	(1.85)	11.00	(1.30)	13.67	(1.84)	NB - log	3.27	0.2	2	-

Table S2.7 Sequential tests of benthic habitat variables during forward selection of variables by OrdiR2step in the distance-based linear model to find the most parsimonious solution. Variables and associated p values in bold indicate those selected for the final model used to construct the db-RDA (Fig.2.9).

Habitat Variable	**AIC**	**p**	**% Variation Explained ($_{adj}R^2$)**	**F**
Algae	**174.09**	**0.015**	**5.84**	**4.28**
Octocorals	**175.24**	**0.015**	**3.90**	**3.68**
Encrusting porifera	**175.63**	**0.015**	**3.25**	**3.37**
Encrusting hexacorals	175.81	0.080	3.00	2.09
Complex hexacorals	176.04	0.178	2.56	2.43
Massive and sub-massive hard corals	176.24	0.400	2.23	2.23
Sand and Silt	176.21	>0.05	2.22	2.26
Complex hard corals	176.41	>0.05	1.92	2.06
Complex porifera	176.78	>0.05	1.29	1.67
Laminar hard coral	176.95	>0.05	1.00	1.52
CCA	176.97	>0.05	0.0096	1.50
Encrusting hard coral	177.06	>0.05	0.0081	1.41
Benthic habitat diversity (H’)	177.20	>0.05	0.00557	1.27
Rock and reef matrix	177.25	>0.05	0.0048	1.23
Rubble	177.30	>0.05	0.0039	1.17
			$_{adj}R^2$ = 21.98	

Table S2.8 Spearman's rank correlation between fish community metrics and two benthic habitat variables, Total percentage hard coral and benthic Shannon diversity. Significant correlations are indicated in bold.

Response	Predictor	Spearman's Rho (ρ)	p
Pinnacles			
Fish Richness	Total % hard Coral	0.00	0.99
Fish Richness	Benthic Diversity (H')	-0.08	0.76
Fish Diversity	Total % hard Coral	0.39	0.09
Fish Diversity	Benthic Diversity (H')	0.07	0.78
Fish Abundance	Total % hard Coral	-0.42	0.07
Fish Abundance	Benthic Diversity (H')	-0.07	0.76
Fish Evenness	Total % hard Coral	0.34	0.15
Fish Evenness	Benthic Diversity (H')	0.21	0.37
Offshore			
Fish Richness	Total % hard Coral	0.22	0.35
Fish Richness	Benthic Diversity (H')	-0.04	0.51
Fish Diversity	Total % hard Coral	0.28	0.23
Fish Diversity	Benthic Diversity (H')	-0.29	0.22
Fish Abundance	Total % hard Coral	-0.03	0.89
Fish Abundance	Benthic Diversity (H')	0.30	0.20
Fish Evenness	Total % hard Coral	-0.11	0.63
Fish Evenness	Benthic Diversity (H')	-0.17	0.49
Nearshore			
Fish Richness	Total % hard Coral	0.23	0.33
Fish Richness	Benthic Diversity (H')	0.08	0.73
Fish Diversity	Total % hard Coral	0.01	0.98
Fish Diversity	Benthic Diversity (H')	0.29	0.22
Fish Abundance	Total % hard Coral	0.32	0.16
Fish Abundance	Benthic Diversity (H')	-0.13	0.57
Fish Evenness	**Total % hard Coral**	**-0.46**	**0.04**
Fish Evenness	Benthic Diversity (H')	0.05	0.83

Reef fish species richness - Negative binomial-log link GLMM

R^2m: 0.54
R^2c: 0.54

	Estimate	St Error	Lower CI	Upper CI	z value	p-value
(Intercept)	2.5036	0.1938	2.124	2.883	12.920	<0.001
Total % Hard coral	0.0088	0.0054	-0.002	0.019	1.626	0.1039
Reef Type: Offshore	0.0025	0.3003	-0.586	0.591	0.008	0.9933
Reef Type: Pinnacle	**0.9544**	**0.2476**	**0.469**	**1.440**	**3.854**	**0.0001**
Total % HC: Offshore	-0.0002	0.0083	-0.016	0.016	-0.019	0.9852
Total % HC: Pinnacle	-0.0082	0.0065	-0.021	0.005	-0.258	0.2085

R^2m: 0.52
R^2c: 0.52

	Estimate	St Error	Lower CI	Upper CI	z value	p-value
(Intercept)	2.1721	0.7944	0.6152	3.7291	2.734	0.00625
Benthic Diversity	0.2873	0.3651	-0.4283	1.0028	0.787	0.43139
Reef Type: Offshore	1.0767	1.2344	-1.3427	3.4961	0.872	0.38306
Reef Type: Pinnacle	1.5360	0.9362	-0.2991	3.3710	1.641	0.10089
Benthic Diversity: Offshore	-0.4933	0.5685	-1.6075	0.6208	-0.868	0.38548
Benthic Diversity: Pinnacle	-0.3886	0.4252	-1.2219	0.4447	-0.914	0.36073

Reef fish diversity (Simpsons Index) – LMM

R^2m: 0.13
R^2c: 0.49

	Estimate	St Error	Lower CI	Upper CI	t value	p-value
(Intercept)	0.8353	0.0983	0.6426	1.0280	8.496	<0.001
Total % Hard coral	-0.0010	0.0022	-0.0053	0.003	-0.434	0.6659
Reef Type: Offshore	-0.1950	0.1431	-0.4755	0.0856	-1.362	0.1795
Reef Type: Pinnacle	-0.0032	0.1403	-0.4979	0.0519	-1.590	0.1193
Total % HC: Offshore	0.0032	0.0032	-0.0031	0.0094	0.988	0.3274
Total % HC: Pinnacle	0.0049	0.0030	-0.0008	0.0106	1.682	0.0991

R^2m: 0.10
R^2c: 0.31

	Estimate	St Error	Lower CI	Upper CI	t value	p-value
(Intercept)	0.6669	0.3050	0.0692	1.2646	2.187	0.0331
Benthic Diversity	0.0637	0.1387	-0.2101	0.3375	0.456	0.6502
Reef Type: Offshore	0.4905	0.4497	-0.3909	1.3719	1.091	0.2803
Reef Type: Pinnacle	-0.0487	0.3878	-0.8087	0.7113	-0.126	0.9005
Benthic Diversity: Offshore	-0.2680	0.2059	-0.6716	0.1355	-1.302	0.1987
Benthic Diversity: Pinnacle	0.0007	0.1743	-0.3409	0.3423	0.004	0.9969

Reef fish abundance Negative binomial log link GLMM

R^2m: 0.54
R^2c: 0.60

	Estimate	St Error	Lower CI	Upper CI	z value	p-value
(Intercept)	3.5680	0.4612	2.6641	4.4719	7.737	<0.001
Total % Hard coral	0.0113	0.0137	-0.0155	0.0381	0.827	0.4081
Reef Type: Offshore	1.5130	0.6937	0.1534	2.8726	2.181	0.0292
Reef Type: Pinnacle	**2.8681**	**0.6835**	**1.5284**	**4.2078**	**4.196**	**<0.001**
Total % HC: Offshore	-0.0152	0.0197	-0.0537	0.0234	-0.772	0.4398
Total % HC: Pinnacle	-0.0281	0.0183	-0.0641	0.0078	-1.533	0.1252

R^2m: 0.54
R^2c: 0.68

	Estimate	St Error	Lower CI	Upper CI	z value	p-value
(Intercept)	5.2780	1.5772	2.1867	8.3692	3.346	<0.001
Benthic Diversity	-0.6409	0.7228	-2.0575	0.7757	-0.887	0.3752
Reef Type: Offshore	-4.0514	2.2856	-8.5310	0.4282	-1.773	0.0763
Reef Type: Pinnacle	0.4153	2.0842	-4.5002	3.6696	-0.199	0.8421
Benthic Diversity: Offshore	**2.3405**	**1.0456**	**0.2913**	**4.3898**	**2.239**	**0.0252**
Benthic Diversity: Pinnacle	1.0392	0.9333	-0.7899	2.8681	1.114	0.2655

Reef fish evenness **- LMM**

R^2m: 0.07							R^2m: 0.09						
R^2c: 0.91							R^2c: 0.88						
	Estimate	**St Error**	**Lower CI**	**Upper CI**	**t value**	**p-value**		**Estimate**	**St Error**	**Lower CI**	**Upper CI**	**t value**	**p-value**
(Intercept)	0.3191	0.1208	0.0823	0.5559	2.641	0.011	(Intercept)	0.2634	0.143	-0.0182	0.5450	1.833	0.0725
Total % Hard coral	-0.0006	0.0008	-0.0027	0.0009	-0.792	0.4321	Benthic Diversity	0.0165	0.0495	-0.0805	0.1135	0.333	0.7403
Reef Type: Offshore	-0.0636	0.1712	-0.3992	0.2720	-0.371	0.7120	Reef Type: Offshore	0.0346	0.2066	-0.3703	0.4395	0.167	0.8678
Reef Type: Pinnacle	-0.1374	0.1710	-0.4725	0.1977	-0.803	0.4257	Reef Type: Pinnacle	-0.0975	0.1929	-0.4759	0.2805	-0.506	0.6152
Total % HC: Offshore	0.0009	0.0011	-0.0013	0.0031	0.786	0.4355	Benthic Diversity: Offshore	-0.0318	0.0720	-0.1729	0.1092	-0.442	0.6600
Total % HC: Pinnacle	0.0016	0.0010	-0.0040	0.0037	1.573	0.1220	Benthic Diversity: Pinnacle	0.0078	0.0623	-0.1144	0.1300	0.125	0.9006

Table S2.9 Full model summaries for fish-benthic relationship GLMMs and LMMs. Model error family, estimates and 95% confidence intervals are presented.

Table S2.10 Mean percentage cover per transect (150m^2) for each reef habitat type (n = 20) and within reef type individual sites (n = 5 per site). SE in brackets.

Reef-Type/Site	**Complex Hard Coral**	**Massive Hard Coral**	**Laminar Hard Coral**	**Complex Hexocoral**	**Encrusting Hexacoral**	**Octocoral**	**Encrusting Porifera**	**Algae**	**Rubble**	**Rock & Reef Matrix**	**CCA**	**Sand & Silt**	**Encrusting Hard Coral**	**Complex Porifera**
Pinnacle	9.67 (1.89)	10.00 (2.19)	8.33 (1.79)	2.00 (0.84)	11.00 (4.02)	4.58 (1.40)	10.50 (1.71)	5.92 (2.00)	5.50 (1.20)	9.00 (1.85)	1.92 (0.39)	5.92 (1.12)	10.33 (1.85)	5.33 (0.78)
Bradford	1.33 (1.09)	8.67 (4.66)	9.99 (5.62)	1.33 (1.09)	37.67 (8.22)	4.00 (1.62)	12.33 (5.48)	2.67 (1.26)	2.34 (0.95)	7.00 (1.81)	2.33 (0.74)	1.33 (0.70)	5.00 (1.56)	4.00 (1.12)
Joelles	13.67 (4.46)	18.34 (5.83)	8.00 (0.37)	0.33 (0.37)	4.67 (3.97)	1.00 (0.75)	6.33 (1.60)	1.00 (0.75)	11.00 (2.40)	7.00 (2.31)	1.33 (0.70)	9.33 (3.36)	11.33 (5.73)	6.67 (1.18)
Inglis	11.00 (5.73)	10.00 (4.49)	14.67 (3.46)	0 (0)	0.66 (0.75)	0.00	7.88 (1.99)	0.00	8.67 (1.60)	20.00 (3.95)	3.00 (1.24)	6.00 (2.61)	15.00 (5.24)	3.00 (1.09)
Kimbe Bommie	12.67 (0.75)	3.00 (1.08)	0.67 (0.47)	6.33 (2.73)	1.00 (0.75)	13.33 (2.95)	15.33 (4.14)	20.00 (3.06)	0.00	2.00 (1.08)	1.00 (0.46)	7.00 (0.91)	10.00 (1.67)	7.67 (2.47)
Offshore	1.92 (0.60)	4.75 (0.90)	15.33 (2.48)	2.67 (0.82)	0.25 (0.18)	0.75 (0.19)	2.00 (2.59)	7.08 (1.55)	6.33 (1.72)	11.00 (1.30)	3.75 (0.78)	3.92 (0.92)	11.83 (1.21)	9.42 (1.70)
Ema	0.33 (0.37)	4.00 (1.26)	23.00 (6.89)	1.67 (1.02)	0.00	1.00 (0.46)	10.67 (2.25)	2.00 (1.49)	11.67 (6.51)	9.00 (2.40)	2.00 (1.09)	7.67 (2.67)	13.00 (2.97)	14.00 (4.19)
Ottos	0.33 (0.37)	3.67 (1.80)	19.33 (5.36)	4.00 (2.17)	1.00 (0.75)	1.00 (0.46)	15.66 (3.10)	1.67 (1.18)	3.67 (1.10)	16.33 (2.73)	7.33 (2.09)	2.33 (1.39)	12.33 (2.47)	11.33 (4.84)
Hogu	4.67 (1.8)	4.67 (3.02)	6.00 (1.92)	4.67 (2.53)	0.00	0.67 (0.46)	35.00 (5.43)	8.67 (1.98)	1.33 (1.09)	8.67 (2.53)	4.00 (1.40)	1.67 (1.44)	9.67 (2.79)	10.33 (1.50)
Kimbe Island	2.33 (0.95)	6.67 (2.20)	13.00 (3.79)	0.33 (0.37)	0.00	0.33 (0.37)	22.66 (3.36)	16.00 (2.61)	8.67 (2.24)	10.00 (2.89)	1.67 (083)	4.00 (1.51)	12.33 (3.15)	2.00 (0.70)
Nearshore	5.58 (1.88)	4.00 (0.98)	7.92 (1.30)	0.66 (0.28)	0.00	1.67 (0.54)	6.08 (0.93)	16.92 (2.77)	9.33 (2.70)	13.67 (1.84)	3.25 (0.63)	7.50 (1.69)	14.75 (1.44)	8.67 (1.85)
Lady Di	2.00 (1.08)	4.33 (2.67)	7.67 (1.26)	0.33 (0.32)	0.00	1.66 (0.83)	7.00 (1.70)	21.33 (2.46)	3.33 (2.36)	13.00 (2.31)	4.00 (1.51)	6.67 (2.57)	17.33 (3.15)	11.33 (4.39)
Madaro	0.67 (0.74)	0.67 (0.74)	3.33 (1.95)	1.67 (1.02)	0.00	3.00 (1.71)	4.67 (1.60)	31.33 (5.12)	2.67 (1.40)	11.67 (6.30)	2.67 (0.95)	14.00 (4.51)	11.33 (1.90)	12.33 (4.95)
Susans	6.33 (5.32)	5.33 (1.24)	12.33 (4.02)	0.67 (0.46)	0.00	0.67 (0.46)	9.33 (2.54)	13.33 (0.83)	9.00 (5.58)	9.67 (1.90)	4.00 (1.62)	4.00 (4.02)	16.67 (4.29)	8.67 (4.22)
Donnas	13.33 (4.45)	5.66 (2.92)	8.33 (2.50)	0.00 (0.00)	0.00	1.33 (0.59)	3.33 (1.44)	1.67 (1.44)	22.33 (7.50)	20.33 (3.30)	2.33 (1.72)	5.33 (2.53)	13.67 (3.14)	2.33 (0.75)

Table S2.11 – 47 benthic cover categories used to analyse benthic video transect

Benthic Cover Type	Morphology – 47 types used to calculate benthic diversity, richness and total hard coral		Broad Scale Grouping (14 benthic categories)
Algae	Turf Brown Red EAM	Calcareous Cyanobacteria Filamentous	Algae
Hard Coral	Branching Tabulate	Foliaceous Columnar	Complex Hard Coral
	Massive	Sub-massive	Massive and Sub-Massive Hard Coral
	Encrusting		Encrusting Hard Coral
	Laminar		Laminar Hard Coral
Hexacoral	Whip Fan Digitate	Tree Bottlebrush Pinnulate	Complex Hexacoral
	Solitary Spreading Encrusting		Encrusting Hexacoral
Octocoral	Whip Fan Bottlebrush Spreading	Tree Pinnulate Encrusting Mushroom	Octocoral
Porifera	Barrel Vase Irregular	Rope Globose	Complex Porifera
	Encrusting		Encrusting Porifera
Ascidian	Encrusting Solitary		Rock and Reef Matrix
Rock	-		
Reef Matrix	-		
Unknown	-		
Rubble	-		Rubble
Sand	-		Sand and Silt
Silt	-		
CCA	-		CCA

Appendix B - Supplementary Material Chapter 3

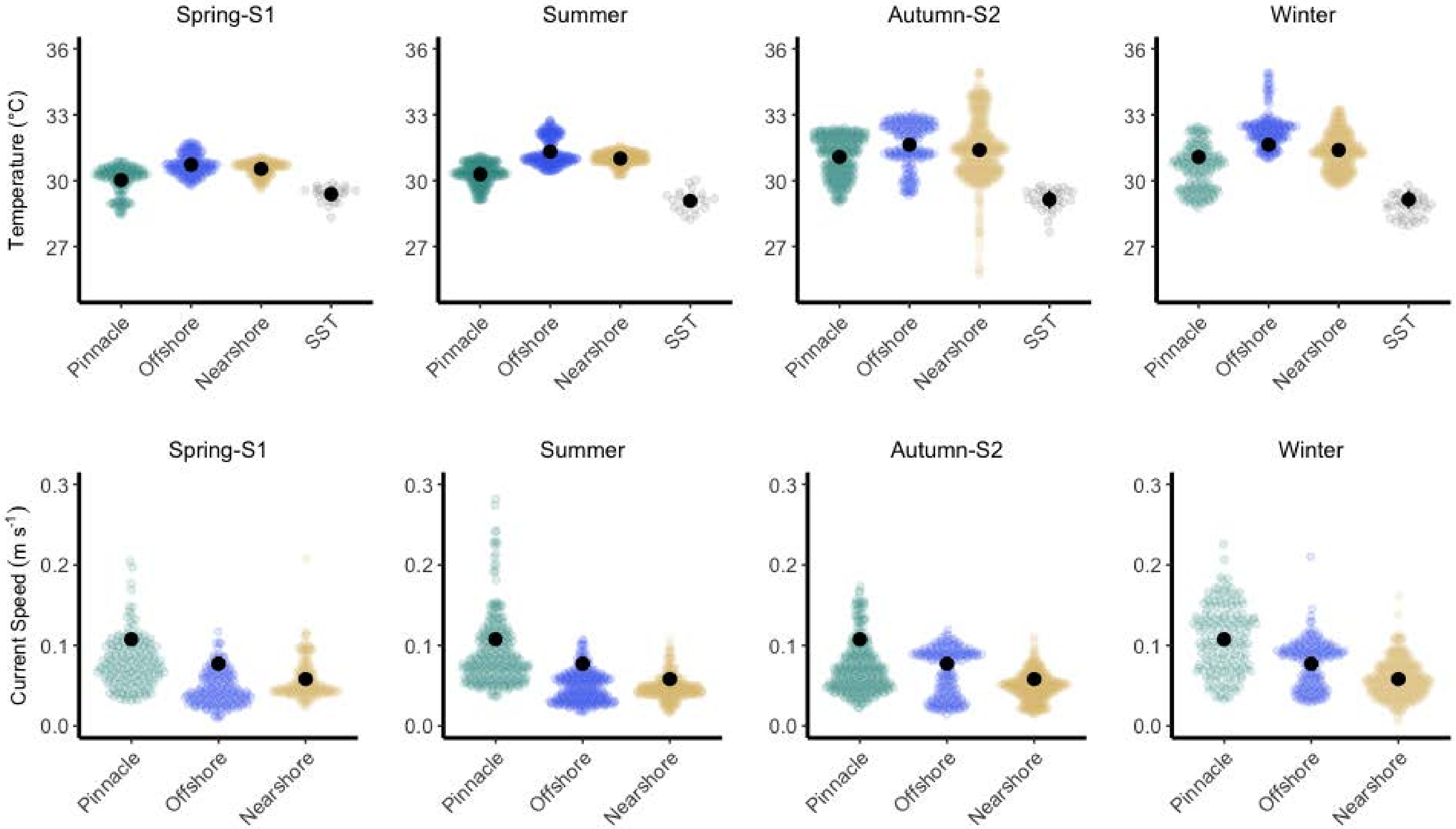

Figure S3.1 Mean Temperature (°C) and current speeds (m s $^{-1}$) at each reef type during each season for the survey period September 2018 to September 2019. Black points represent estimated marginal means and jittered coloured dots represent daily mean values. 95% confidence intervals are too small to be visible

Table S3.1 GLM (Gaussian -Identity Link) results comparing annual mean daily temperature (^{o}C) between reef types and SST for the deployment period Sept 18 – Sept 19. Pairwise contrasts and 95% confidence intervals are presented based on adjusted Tukeys method. Pinnacles n = 1440 daily mean values, Offshore n = 1080, Nearshore n = 1440 and SST values n = 200.

Reef Type	*estimate*	*SE*	*lower.CL*	*upper.CL*	*contrast*	*estimate*	*SE*	*lower.CL*	*upper.CL*
Annual Mean Temperature									
Pinnacle	30.53	0.03	30.47	30.58	Pinnacle – Offshore	-0.81	0.04	-0.91	-0.70
Offshore	31.33	0.03	31.27	31.39	Pinnacle – Nearshore	-0.48	0.04	-0.58	-0.37
Nearshore	31.00	0.03	30.95	31.05	Pinnacle – SST	1.63	0.08	1.41	1.84
SST	28.90	0.08	28.75	29.05	Offshore – Nearshore	0.33	0.04	0.23	0.43
					Offshore – SST	2.43	0.08	2.22	2.65
					Nearshore – SST	2.10	0.08	1.89	2.31
Annual Mean Temperature Variability SD									
Pinnacle	0.10	0.00	0.10	0.10	Pinnacle – Offshore	0.01	0.00	0.01	0.02
Offshore	0.09	0.00	0.09	0.09	Pinnacle – Nearshore	0.02	0.00	0.01	0.02
Nearshore	0.08	0.00	0.08	0.09	Offshore – Nearshore	0.00	0.00	-0.00	0.01
Average Annual Max Temperature									
Pinnacle	30.72	0.03	30.66	30.78	Pinnacle – Offshore	-0.79	0.04	-0.90	-0.69
Offshore	31.51	0.03	31.45	31.57	Pinnacle – Nearshore	-0.45	0.04	-0.54	-0.35
Nearshore	31.17	0.03	31.11	31.22	Offshore – Nearshore	0.35	0.04	0.25	0.45
Average Annual Min Temperature									
Pinnacle	30.25	0.03	30.19	30.31	Pinnacle – Offshore	-0.83	0.04	-0.93	-0.74
Offshore	31.08	0.03	31.02	31.14	Pinnacle – Nearshore	-0.51	0.04	-0.61	-0.42
Nearshore	30.76	0.03	30.71	30.81	Offshore – Nearshore	0.32	0.04	0.23	0.41

Table S3.2 GLM (Gaussian -Identity Link) results comparing annual mean daily current speed (m s^{-1}) between reef types for the deployment period Sept 18 – Sept 19. Pairwise contrasts and 95% confidence intervals are presented based on adjusted Tukeys method. Pinnacles n = 1440 daily mean values, Offshore n = 1080, Nearshore n = 1440 and SST values n = 200.

Reef Type	*estimate*	*SE*	*lower.CL*	*upper.CL*	*contrast*	*estimate*	*SE*	*lower.CL*	*upper.CL*
Annual Mean Current									
Pinnacle	0.0830	0.0012	0.0806	0.0853	Pinnacle - Offshore	0.029	0.001	0.026	0.032
Offshore	0.0539	0.0008	0.0524	0.0554	Pinnacle - Nearshore	0.031	0.001	0.028	0.034
Nearshore	0.0521	0.0007	0.0508	0.0535	Offshore - Nearshore	0.002	0.001	-0.001	0.004
Annual Mean Current Variability SD									
Pinnacle	0.035	0.001	0.034	0.036	Pinnacle - Offshore	0.009	0.001	0.007	0.010
Offshore	0.027	0.001	0.026	0.028	Pinnacle - Nearshore	0.008	0.001	0.006	0.009
Nearshore	0.028	0.000	0.027	0.029	Offshore - Nearshore	-0.001	0.001	-0.003	0.000
Average Annual Max Current									
Pinnacle	0.1727	0.0021	0.1686	0.1767	Pinnacle - Offshore	0.0264	0.0029	0.0195	0.0333
Offshore	0.1463	0.0021	0.1422	0.1504	Pinnacle - Nearshore	0.0350	0.0028	0.0285	0.0416
Nearshore	0.1377	0.0019	0.1340	0.1413	Offshore - Nearshore	0.0086	0.0028	0.0021	0.0152
Average Annual Min Current									
Pinnacle	0.0185	0.0007	0.0172	0.0198	Pinnacle - Offshore	0.0031	0.0009	0.0009	0.0053
Offshore	0.0154	0.0007	0.0141	0.0167	Pinnacle - Nearshore	0.0031	0.0009	0.0010	0.0052
Nearshore	0.0154	0.0006	0.0142	0.0166	Offshore - Nearshore	0.0000	0.0009	-0.0021	0.0021

Table S3.3 GLM (Gaussian -Identity Link) results comparing mean daily temperature (°C) between reef types in spring (Sep- Nov 2018). Pairwise contrasts and 95% confidence intervals are presented based on adjusted Tukeys method. Pinnacles n = 360 daily mean values, Offshore n = 276, Nearshore n = 360.

Reef Type	*estimate*	*SE*	*lower.CL*	*upper.CL*	*contrast*	*estimate*	*SE*	*lower.CL*	*upper.CL*
Spring Mean Temperature									
Pinnacle	30.02	0.04	29.95	30.10	Pinnacle - Offshore	-0.71	0.05	-0.84	-0.57
Offshore	30.73	0.04	30.66	30.80	Pinnacle - Nearshore	-0.51	0.05	-0.65	-0.38
Nearshore	30.53	0.04	30.46	30.61	Pinnacle - SST	0.64	0.10	0.37	0.91
SST	29.38	0.10	29.19	29.57	Offshore - Nearshore	0.20	0.05	0.06	0.33
					Offshore - SST	1.35	0.10	1.08	1.61
					Nearshore - SST	1.15	0.10	0.88	1.42
Spring Mean Temperature Variability SD									
Pinnacle	0.089	0.002	0.085	0.093	Pinnacle - Offshore	0.006	0.003	-0.001	0.013
Offshore	0.083	0.002	0.079	0.087	Pinnacle - Nearshore	0.015	0.003	0.008	0.022
Nearshore	0.074	0.002	0.070	0.078	Offshore - Nearshore	0.009	0.003	0.002	0.016
Average Spring Max Temp									
Pinnacle	30.18	0.04	30.11	30.26	Pinnacle - Offshore	-0.71	0.05	-0.83	-0.58
Offshore	30.89	0.04	30.82	30.96	Pinnacle - Nearshore	-0.49	0.05	-0.62	-0.36
Nearshore	30.67	0.04	30.60	30.75	Offshore - Nearshore	0.22	0.05	0.09	0.34
Average Annual Min Temp									
Pinnacle	29.75	0.04	29.68	29.83	Pinnacle - Offshore	-0.72	0.05	-0.85	-0.60
Offshore	30.47	0.04	30.40	30.54	Pinnacle - Nearshore	-0.54	0.05	-0.67	-0.42
Nearshore	30.29	0.04	30.22	30.37	Offshore - Nearshore	0.18	0.05	0.06	0.30

Table S3.4 GLM (Gaussian -Identity Link) results comparing mean daily current speed (m s^{-1}) between reef types in summer (Dec 2018 – Feb 2019). Pairwise contrasts and 95% confidence intervals are presented based on adjusted Tukeys method. Pinnacles n = 360 daily mean values, Offshore n = 276, Nearshore n = 360.

Reef Type	*estimate*	*SE*	*lower.CL*	*upper.CL*	*contrast*	*estimate*	*SE*	*lower.CL*	*upper.CL*
Summer Mean Temperature									
Pinnacle	30.29	0.03	30.24	30.35	Pinnacle - Offshore	-1.03	0.04	-1.13	-0.92
Offshore	31.32	0.03	31.26	31.38	Pinnacle - Nearshore	-0.71	0.04	-0.82	-0.61
Nearshore	31.01	0.03	30.95	31.06	Pinnacle - SST	1.22	0.10	0.95	1.48
SST	29.08	0.10	28.88	29.27	Offshore - Nearshore	0.31	0.04	0.21	0.42
					Offshore - SST	2.24	0.10	1.97	2.51
					Nearshore - SST	1.93	0.10	1.66	2.20
Summer Mean Temperature Variability SD									
Pinnacle	0.093	0.002	0.089	0.098	Pinnacle - Offshore	0.012	0.003	0.005	0.019
Offshore	0.081	0.002	0.077	0.085	Pinnacle - Nearshore	0.010	0.003	0.003	0.018
Nearshore	0.083	0.002	0.079	0.087	Offshore - Nearshore	-0.002	0.003	-0.009	0.005
Average Summer Max Temp									
Pinnacle	30.47	0.03	30.41	30.53	Pinnacle - Offshore	-1.02	0.04	-1.12	-0.92
Offshore	31.49	0.03	31.43	31.55	Pinnacle - Nearshore	-0.70	0.04	-0.80	-0.60
Nearshore	31.17	0.03	31.11	31.23	Offshore - Nearshore	0.32	0.04	0.22	0.42
Average Summer Min Temp									
Pinnacle	30.02	0.03	29.96	30.08	Pinnacle - Offshore	-1.06	0.04	-1.16	-0.96
Offshore	31.08	0.03	31.03	31.14	Pinnacle - Nearshore	-0.75	0.04	-0.85	-0.65
Nearshore	30.77	0.03	30.71	30.83	Offshore - Nearshore	0.31	0.04	0.21	0.41

Table S3.5 GLM (Gaussian -Identity Link) results mean daily temperature (°C) between reef types in autumn (Mar – May 2019). Pairwise contrasts and 95% confidence intervals are presented based on adjusted Tukeys method. Pinnacles n = 368 daily mean values, Offshore n = 276, Nearshore n = 368.

Reef Type	*estimate*	*SE*	*lower.CL*	*upper.CL*	*contrast*	*estimate*	*SE*	*lower.CL*	*upper.CL*
Autumn Mean Temperature									
Pinnacle	31.08	0.07	30.94	31.22	Pinnacle - Offshore	-0.56	0.11	-0.86	-0.27
Offshore	31.64	0.09	31.47	31.82	Pinnacle - Nearshore	-0.31	0.10	-0.56	-0.06
Nearshore	31.39	0.07	31.26	31.52	Pinnacle - SST	1.94	0.23	1.36	2.52
SST	29.14	0.21	28.72	29.56	Offshore - Nearshore	0.25	0.11	-0.03	0.53
					Offshore - SST	2.50	0.23	1.91	3.09
					Nearshore - SST	2.25	0.22	1.68	2.82
Autumn Mean Temperature Variability SD									
Pinnacle	0.123	0.003	0.116	0.129	Pinnacle - Offshore	0.007	0.005	-0.006	0.019
Offshore	0.116	0.004	0.108	0.124	Pinnacle - Nearshore	0.016	0.005	0.006	0.027
Nearshore	0.106	0.003	0.100	0.112	Offshore - Nearshore	0.010	0.005	-0.002	0.022
Average Autumn Max Temp									
Pinnacle	31.34	0.07	31.19	31.48	Pinnacle - Offshore	-0.55	0.12	-0.82	-0.27
Offshore	31.88	0.09	31.71	32.06	Pinnacle - Nearshore	-0.27	0.10	-0.51	-0.04
Nearshore	31.61	0.07	31.48	31.74	Offshore - Nearshore	0.27	0.11	0.01	0.54
Average Autumn Min Temp									
Pinnacle	30.77	0.07	30.62	30.91	Pinnacle - Offshore	-0.57	0.12	-0.85	-0.30
Offshore	31.34	0.09	31.16	31.52	Pinnacle - Nearshore	-0.34	0.10	-0.58	-0.11
Nearshore	31.11	0.07	30.98	31.24	Offshore - Nearshore	0.23	0.11	-0.03	0.49

Table S3.6 GLM (Gaussian -Identity Link) results comparing mean daily temperature (°C) between reef types in winter (June – Aug 2019). Pairwise contrasts and 95% confidence intervals are presented based on adjusted Tukeys method. Pinnacles n = 368 daily mean values, Offshore n = 276, Nearshore n = 368.

Reef Type	*estimate*	*SE*	*lower.CL*	*upper.CL*	*contrast*	*estimate*	*SE*	*lower.CL*	*upper.CL*
Winter Mean Temperature									
Pinnacle	30.54	0.07	30.42	30.67	Pinnacle – Offshore	-1.75	0.09	-1.98	-1.51
Offshore	32.29	0.06	32.17	32.41	Pinnacle – Nearshore	-0.77	0.08	-0.98	-0.56
Nearshore	31.32	0.05	31.22	31.41	Pinnacle – SST	1.75	0.15	1.36	2.14
SST	28.80	0.14	28.53	29.07	Offshore – Nearshore	0.98	0.08	0.77	1.18
					Offshore – SST	3.49	0.15	3.10	3.88
					Nearshore – SST	2.52	0.15	2.14	2.90
Winter Mean Temperature Variability SD									
Pinnacle	0.092	0.003	0.086	0.098	Pinnacle – Offshore	-0.010	0.004	-0.020	-0.000
Offshore	0.102	0.003	0.096	0.108	Pinnacle – Nearshore	0.016	0.004	0.007	0.025
Nearshore	0.076	0.002	0.072	0.081	Offshore – Nearshore	0.026	0.004	0.017	0.035
Average Winter Max Temp									
Pinnacle	30.73	0.07	30.60	30.86	Pinnacle – Offshore	-1.75	0.09	-1.98	-1.53
Offshore	32.48	0.07	32.36	32.61	Pinnacle – Nearshore	-0.74	0.09	-0.94	-0.54
Nearshore	31.47	0.05	31.36	31.57	Offshore – Nearshore	1.02	0.08	0.82	1.21
Average Winter Min Temp									
Pinnacle	30.30	0.07	30.17	30.43	Pinnacle – Offshore	-1.70	0.09	-1.91	-1.49
Offshore	32.00	0.06	31.88	32.12	Pinnacle – Nearshore	-0.80	0.08	-0.99	-0.60
Nearshore	31.10	0.05	31.00	31.20	Offshore – Nearshore	0.90	0.08	0.71	1.09

Table S3.7 GLM results comparing mean daily current speed (m s $^{-1}$) between reef types in Spring (Sept – Nov 2018). Pairwise contrasts and 95% confidence intervals are presented based on adjusted Tukeys method. Pinnacles n = 360 daily mean values, Offshore n = 276, Nearshore n = 360.

Reef Type	*estimate*	*SE*	*lower.CL*	*upper.CL*	*contrast*	*estimate*	*SE*	*lower.CL*	*upper.CL*
Spring Mean Current Speed – Gamma-Inverse link									
Pinnacle	0.079	0.002	0.076	0.083	Pinnacle - Offshore	0.033	0.003	0.027	0.039
Offshore	0.047	0.002	0.043	0.050	Pinnacle - Nearshore	0.023	0.003	0.017	0.029
Nearshore	0.056	0.002	0.052	0.060	Offshore - Nearshore	-0.010	0.003	-0.016	-0.003
Spring Mean Current Speed Variability SD – Gaussian-identity link									
Pinnacle	0.037	0.001	0.035	0.040	Pinnacle - Offshore	0.007	0.002	0.003	0.012
Offshore	0.030	0.001	0.028	0.033	Pinnacle - Nearshore	0.007	0.002	0.003	0.012
Nearshore	0.030	0.001	0.027	0.033	Offshore - Nearshore	0.000	0.002	-0.004	0.005
Average Spring Max Current Speed – Gamma-Inverse link									
Pinnacle	0.177	0.005	0.167	0.187	Pinnacle - Offshore	0.030	0.007	0.013	0.046
Offshore	0.147	0.005	0.138	0.157	Pinnacle - Nearshore	0.025	0.007	0.008	0.042
Nearshore	0.152	0.005	0.142	0.162	Offshore - Nearshore	-0.004	0.007	-0.021	0.012
Average Spring Min Current Speed – Gamma-Inverse link									
Pinnacle	0.012	0.001	0.010	0.015	Pinnacle - Offshore	0.007	0.002	0.003	0.011
Offshore	0.006	0.001	0.003	0.008	Pinnacle - Nearshore	-0.005	0.002	-0.009	-0.000
Nearshore	0.017	0.001	0.015	0.019	Offshore - Nearshore	-0.011	0.002	-0.015	-0.007

Table S3.8 GLM results comparing mean daily current speed (m s $^{-1}$) between reef types in summer (Dec 18 – Feb 19). Pairwise contrasts and 95% confidence intervals are presented based on adjusted Tukeys method. Pinnacles n = 360 daily mean values, Offshore n = 276, Nearshore n = 360.

Ref Type	*estimate*	*SE*	*lower.CL*	*upper.CL*	*contrast*	*estimate*	*SE*	*lower.CL*	*upper.CL*
Summer Mean Current Speed – Gamma – Inverse link									
Pinnacle	0.093	0.002	0.088	0.097	Pinnacle - Offshore	0.044	0.003	0.038	0.050
Offshore	0.049	0.001	0.046	0.051	Pinnacle - Nearshore	0.045	0.003	0.039	0.051
Nearshore	0.047	0.001	0.045	0.049	Offshore - Nearshore	0.002	0.002	-0.002	0.005
Summer Mean Current Speed Variability SD – Gaussian - Identity Link									
Pinnacle	0.038	0.001	0.035	0.040	Pinnacle - Offshore	0.009	0.002	0.006	0.013
Offshore	0.028	0.001	0.026	0.030	Pinnacle - Nearshore	0.008	0.002	0.004	0.012
Nearshore	0.029	0.001	0.027	0.031	Offshore - Nearshore	-0.001	0.001	-0.004	0.002
Average Summer Max Current Speed – Gamma Inverse Link									
Pinnacle	0.183	0.005	0.172	0.193	Pinnacle - Offshore	0.037	0.007	0.021	0.053
Offshore	0.146	0.004	0.137	0.154	Pinnacle - Nearshore	0.041	0.007	0.025	0.057
Nearshore	0.142	0.004	0.134	0.150	Offshore - Nearshore	0.004	0.006	-0.010	0.018
Average Summer Min Current Speed – Gamma Inverse Link									
Pinnacle	0.019	0.001	0.017	0.021	Pinnacle - Offshore	0.010	0.001	0.007	0.013
Offshore	0.009	0.001	0.008	0.010	Pinnacle - Nearshore	0.006	0.001	0.003	0.010
Nearshore	0.013	0.001	0.011	0.014	Offshore - Nearshore	-0.004	0.001	-0.006	-0.002

Table S3.9 GLM (Gamma -Inverse Link) results comparing mean daily current speed (m s $^{-1}$) between reef types in autumn (March – May 2019). Pairwise contrasts and 95% confidence intervals are presented based on adjusted Tukeys method. Pinnacles n = 368 daily mean values, Offshore n = 276, Nearshore n = 368.

Reef Type	*estimate*	*SE*	*lower.CL*	*upper.CL*	*contrast*	*estimate*	*SE*	*lower.CL*	*upper.CL*
Autumn Mean Current Speed									
Pinnacle	0.073	0.002	0.070	0.076	Pinnacle - Offshore	0.007	0.002	0.001	0.012
Offshore	0.066	0.002	0.063	0.070	Pinnacle - Nearshore	0.024	0.002	0.019	0.029
Nearshore	0.049	0.001	0.046	0.052	Offshore - Nearshore	0.017	0.002	0.012	0.023
Autumn Mean Current Speed Variability SD – Gaussian Identity Link									
Pinnacle	0.036	0.001	0.034	0.037	Pinnacle - Offshore	0.014	0.001	0.011	0.017
Offshore	0.022	0.001	0.020	0.024	Pinnacle - Nearshore	0.010	0.001	0.008	0.013
Nearshore	0.025	0.001	0.024	0.027	Offshore - Nearshore	-0.003	0.001	-0.006	-0.000
Autumn Max Current Speed									
Pinnacle	0.167	0.003	0.161	0.174	Pinnacle - Offshore	0.021	0.005	0.009	0.033
Offshore	0.146	0.004	0.139	0.154	Pinnacle - Nearshore	0.040	0.004	0.030	0.051
Nearshore	0.127	0.003	0.121	0.133	Offshore - Nearshore	0.019	0.005	0.008	0.031
Autumn Min Current Speed									
Pinnacle	0.013	0.001	0.011	0.015	Pinnacle - Offshore	-0.015	0.003	-0.021	-0.009
Offshore	0.028	0.002	0.023	0.033	Pinnacle - Nearshore	-0.002	0.001	-0.005	0.001
Nearshore	0.015	0.001	0.013	0.017	Offshore - Nearshore	0.013	0.003	0.007	0.019

Table S3.10 GLM (Gamma -Inverse Link) results comparing mean daily current speed (m s^{-1}) between reef types in winter (June-Aug 2019). Pairwise contrasts and 95% confidence intervals are presented based on adjusted Tukeys method. Pinnacles n = 368 daily mean values, Offshore n = 276, Nearshore n = 368.

Reef Type	*estimate*	*SE*	*lower.CL*	*upper.CL*	*contrast*	*estimate*	*SE*	*lower.CL*	*upper.CL*
Winter Mean Current Speed									
Pinnacle	0.108	0.002	0.103	0.112	Pinnacle - Offshore	0.030	0.003	0.023	0.038
Offshore	0.077	0.002	0.073	0.082	Pinnacle - Nearshore	0.049	0.003	0.043	0.056
Nearshore	0.058	0.002	0.055	0.062	Offshore - Nearshore	0.019	0.003	0.012	0.026
Winter Mean Current Speed Variability SD – Gaussain Identity Link									
Pinnacle	0.036	0.001	0.033	0.038	Pinnacle - Offshore	0.008	0.002	0.004	0.011
Offshore	0.028	0.001	0.026	0.030	Pinnacle - Nearshore	0.002	0.002	-0.002	0.005
Nearshore	0.034	0.001	0.032	0.036	Offshore - Nearshore	-0.006	0.001	-0.009	-0.003
Average Winter Max Current Speed									
Pinnacle	0.192	0.005	0.182	0.203	Pinnacle - Offshore	0.017	0.007	-0.000	0.033
Offshore	0.176	0.005	0.166	0.185	Pinnacle - Nearshore	0.039	0.006	0.024	0.054
Nearshore	0.153	0.003	0.147	0.160	Offshore - Nearshore	0.022	0.006	0.009	0.036
Average Winter Min Current Speed									
Pinnacle	0.038	0.003	0.033	0.043	Pinnacle - Offshore	0.003	0.004	-0.005	0.012
Offshore	0.035	0.002	0.030	0.039	Pinnacle - Nearshore	0.029	0.003	0.023	0.036
Nearshore	0.009	0.000	0.008	0.010	Offshore - Nearshore	0.026	0.002	0.020	0.031

Table S3.11 GLM (Gamma -Inverse Link) results comparing mean daily current speed ($m\ s^{-1}$) between seasons on four pinnacle reefs in Kimbe Bay. Pairwise contrasts and 95% confidence intervals are presented based on adjusted Tukeys method. Spring n = 360, summer n = 360, autumn n = 368, winter n = 368.

Season	*estimate*	*SE*	*lower.CL*	*upper.CL*	*contrast*	*estimate*	*SE*	*lower.CL*	*upper.CL*
Mean Current Speed									
Spring	0.078	0.002	0.073	0.083	Spring - Summer	-0.015	0.003	-0.023	-0.006
Summer	0.093	0.002	0.088	0.097	Spring - Autumn	0.014	0.003	0.006	0.023
Autumn	0.063	0.002	0.059	0.068	Spring - Winter	-0.030	0.004	-0.039	-0.020
Winter	0.108	0.003	0.102	0.113	Summer - Autumn	0.029	0.003	0.021	0.037
					Summer - Winter	-0.015	0.004	-0.024	-0.006
					Autumn - Winter	-0.044	0.004	-0.053	-0.035
Mean Current Speed Variability SD – Gaussian Identity link									
Spring	0.036	0.001	0.034	0.038	Spring - Summer	-0.001	0.001	-0.005	0.002
Summer	0.038	0.001	0.036	0.039	Spring - Autumn	0.004	0.001	0.001	0.008
Autumn	0.032	0.001	0.030	0.034	Spring - Winter	0.001	0.002	-0.003	0.005
Winter	0.036	0.001	0.033	0.038	Summer - Autumn	0.005	0.001	0.002	0.009
					Summer - Winter	0.002	0.002	-0.002	0.006
					Autumn - Winter	-0.003	0.002	-0.007	0.001
Average Max Current Speed									
Spring	0.174	0.004	0.166	0.182	Spring - Summer	-0.009	0.006	-0.024	0.006
Summer	0.183	0.004	0.175	0.191	Spring - Autumn	0.024	0.006	0.009	0.039
Autumn	0.150	0.004	0.143	0.158	Spring - Winter	-0.018	0.007	-0.035	-0.001
Winter	0.192	0.005	0.182	0.202	Summer - Autumn	0.033	0.006	0.018	0.047
					Summer - Winter	-0.009	0.006	-0.026	0.007
					Autumn - Winter	-0.042	0.006	-0.058	-0.025
Average Min Current Speed									
Spring	0.014	0.002	0.011	0.017	Spring - Summer	-0.005	0.002	-0.010	0.000
Summer	0.019	0.001	0.016	0.022	Spring - Autumn	0.004	0.002	-0.001	0.009
Autumn	0.010	0.001	0.007	0.013	Spring - Winter	-0.024	0.002	-0.030	-0.018
Winter	0.038	0.002	0.034	0.041	Summer - Autumn	0.009	0.002	0.004	0.014
					Summer - Winter	-0.019	0.002	-0.025	-0.013
					Autumn - Winter	-0.028	0.002	-0.034	-0.022

Table S3.12 GLM (Gamma -Inverse Link) results comparing mean daily current speed (m s $^{-1}$) between seasons on three offshore reefs in Kimbe Bay. Pairwise contrasts and 95% confidence intervals are presented based on adjusted Tukeys method. Spring n = 276, summer n = 276, autumn n = 276, winter n = 276.

Season	*estimate*	*SE*	*lower.CL*	*upper.CL*	*contrast*	*estimate*	*SE*	*lower.CL*	*upper.CL*
Mean Current Speed									
Spring	0.044	0.001	0.042	0.046	Spring - Summer	-0.005	0.002	-0.009	0.000
Summer	0.049	0.001	0.046	0.051	Spring - Autumn	-0.010	0.002	-0.015	-0.005
Autumn	0.054	0.002	0.051	0.057	Spring - Winter	-0.033	0.003	-0.040	-0.026
Winter	0.077	0.003	0.072	0.082	Summer - Autumn	-0.005	0.002	-0.010	0.000
					Summer - Winter	-0.029	0.003	-0.036	-0.021
					Autumn - Winter	-0.024	0.003	-0.031	-0.016
Mean Current Speed Variability SD – Gaussian Identity Link									
Spring	0.029	0.001	0.027	0.031	Spring - Summer	0.001	0.001	-0.003	0.004
Summer	0.028	0.001	0.026	0.030	Spring - Autumn	0.009	0.001	0.005	0.012
Autumn	0.020	0.001	0.019	0.022	Spring - Winter	0.001	0.002	-0.003	0.005
Winter	0.028	0.001	0.025	0.030	Summer - Autumn	0.008	0.001	0.005	0.011
					Summer - Winter	0.000	0.002	-0.003	0.004
					Autumn - Winter	-0.007	0.001	-0.011	-0.004
Average Max Current Speed									
Spring	0.142	0.004	0.135	0.149	Spring - Summer	-0.003	0.005	-0.017	0.010
Summer	0.146	0.004	0.138	0.153	Spring - Autumn	0.015	0.005	0.001	0.028
Autumn	0.127	0.004	0.120	0.135	Spring - Winter	-0.033	0.007	-0.050	-0.016
Winter	0.176	0.006	0.165	0.187	Summer - Autumn	0.018	0.005	0.005	0.032
					Summer - Winter	-0.030	0.007	-0.047	-0.013
					Autumn - Winter	-0.048	0.007	-0.065	-0.031
Average Min Current Speed									
Spring	0.006	0.000	0.005	0.006	Spring - Summer	-0.003	0.001	-0.005	-0.001
Summer	0.009	0.001	0.008	0.010	Spring - Autumn	-0.014	0.002	-0.018	-0.010
Autumn	0.020	0.001	0.017	0.023	Spring - Winter	-0.029	0.003	-0.036	-0.022
Winter	0.035	0.003	0.029	0.040	Summer - Autumn	-0.011	0.002	-0.015	-0.007
					Summer - Winter	-0.026	0.003	-0.033	-0.018
					Autumn - Winter	-0.015	0.003	-0.023	-0.007

Table S3.13 GLM results comparing mean daily current speed (m s $^{-1}$) between seasons on four nearshore reefs in Kimbe Bay. Pairwise contrasts and 95% confidence intervals are presented based on adjusted Tukeys method. Spring n = 360 , summer n = 360, autumn n = 368, winter n = 368.

Season	*estimate*	*SE*	*lower.CL*	*upper.CL*	*contrast*	*estimate*	*SE*	*lower.CL*	*upper.CL*
Mean Current Speed – Gamma Inverse link									
Spring	0.058	0.001	0.055	0.060	Spring - Summer	0.010	0.002	0.006	0.015
Summer	0.047	0.001	0.045	0.049	Spring - Autumn	0.011	0.002	0.007	0.015
Autumn	0.046	0.001	0.045	0.048	Spring - Winter	-0.001	0.002	-0.005	0.004
Winter	0.058	0.001	0.056	0.061	Summer - Autumn	0.001	0.001	-0.003	0.004
					Summer - Winter	-0.011	0.002	-0.015	-0.007
					Autumn - Winter	-0.012	0.002	-0.016	-0.008
Mean Current Speed Variability SD – Gaussian Identity link									
Spring	0.026	0.001	0.024	0.028	Spring - Summer	-0.004	0.001	-0.007	-0.000
Summer	0.029	0.001	0.028	0.031	Spring - Autumn	0.003	0.001	-0.001	0.006
Autumn	0.023	0.001	0.021	0.025	Spring - Winter	-0.008	0.001	-0.012	-0.005
Winter	0.034	0.001	0.032	0.036	Summer - Autumn	0.006	0.001	0.003	0.010
					Summer - Winter	-0.005	0.001	-0.008	-0.001
					Autumn - Winter	-0.011	0.001	-0.014	-0.008
Average Max Current Speed - Gamma Inverse link									
Spring	0.140	0.004	0.133	0.147	Spring - Summer	-0.002	0.005	-0.015	0.011
Summer	0.142	0.004	0.135	0.149	Spring - Autumn	0.020	0.004	0.009	0.032
Autumn	0.120	0.003	0.114	0.125	Spring - Winter	-0.013	0.005	-0.027	0.000
Winter	0.153	0.004	0.146	0.161	Summer - Autumn	0.022	0.005	0.011	0.034
					Summer - Winter	-0.011	0.005	-0.025	0.003
					Autumn - Winter	-0.034	0.005	-0.046	-0.021
Average Min Current Speed - Gamma Inverse link									
Spring	0.022	0.001	0.020	0.025	Spring - Summer	0.010	0.001	0.006	0.013
Summer	0.013	0.001	0.011	0.014	Spring - Autumn	0.005	0.002	0.001	0.009
Autumn	0.017	0.001	0.015	0.019	Spring - Winter	0.014	0.001	0.010	0.017
Winter	0.009	0.001	0.008	0.010	Summer - Autumn	-0.004	0.001	-0.007	-0.001
					Summer - Winter	0.004	0.001	0.002	0.006
					Autumn - Winter	0.008	0.001	0.006	0.011

Table S3.14 – GLM (Gaussian Identity Link) results comparing mean daily temperatures (^{o}C) between seasons on four pinnacle reefs in Kimbe Bay. Pairwise contrasts and 95% confidence intervals are presented based on adjusted Tukeys method. Spring n = 360 , summer n = 360, autumn n = 368, winter n = 368.

Season	*estimate*	*SE*	*lower.CL*	*upper.CL*	*contrast*	*estimate*	*SE*	*lower.CL*	*upper.CL*
Mean Temperature									
Spring	30.09	0.05	30.00	30.19	Spring - Summer	-0.20	0.07	-0.37	-0.03
Summer	30.29	0.04	30.21	30.38	Spring - Autumn	-0.99	0.06	-1.16	-0.83
Autumn	31.08	0.04	31.00	31.17	Spring - Winter	-0.46	0.07	-0.65	-0.27
Winter	30.55	0.06	30.44	30.66	Summer - Autumn	-0.79	0.06	-0.95	-0.63
					Summer - Winter	-0.26	0.07	-0.44	-0.07
					Autumn - Winter	0.54	0.07	0.35	0.72
Mean Temperature Variability SD									
Spring	0.09	0.00	0.08	0.09	Spring - Summer	-0.01	0.00	-0.02	0.00
Summer	0.09	0.00	0.09	0.10	Spring - Autumn	-0.03	0.00	-0.04	-0.02
Autumn	0.12	0.00	0.11	0.12	Spring - Winter	-0.01	0.00	-0.02	0.00
Winter	0.09	0.00	0.09	0.10	Summer - Autumn	-0.03	0.00	-0.04	-0.02
					Summer - Winter	0.00	0.00	-0.01	0.01
					Autumn - Winter	0.03	0.00	0.02	0.04
Average Max Temperature									
Spring	30.25	0.05	30.16	30.35	Spring - Summer	-0.22	0.07	-0.39	-0.05
Summer	30.47	0.05	30.38	30.56	Spring - Autumn	-1.08	0.07	-1.25	-0.91
Autumn	31.33	0.04	31.24	31.42	Spring - Winter	-0.48	0.08	-0.67	-0.28
Winter	30.73	0.06	30.62	30.84	Summer - Autumn	-0.86	0.06	-1.02	-0.70
					Summer - Winter	-0.26	0.07	-0.45	-0.07
					Autumn - Winter	0.60	0.07	0.41	0.79
Average Min Temperature									
Spring	29.83	0.05	29.73	29.92	Spring - Summer	-0.20	0.06	-0.36	-0.03
Summer	30.02	0.04	29.94	30.11	Spring - Autumn	-0.95	0.06	-1.11	-0.78
Autumn	30.77	0.04	30.69	30.86	Spring - Winter	-0.47	0.07	-0.66	-0.28
Winter	30.30	0.06	30.19	30.41	Summer - Autumn	-0.75	0.06	-0.91	-0.59
					Summer - Winter	-0.28	0.07	-0.46	-0.09
					Autumn - Winter	0.47	0.07	0.29	0.66

Table S3.15 GLM (Gaussian Identity Link) results comparing mean daily temperatures (°C) between seasons on three offshore reefs in Kimbe Bay. Pairwise contrasts and 95% confidence intervals are presented based on adjusted Tukeys method. Spring n = 276, summer n = 276, autumn n = 276, winter n = 276.

Season	*estimate*	*SE*	*lower.CL*	*upper.CL*	*contrast*	*estimate*	*SE*	*lower.CL*	*upper.CL*
Mean Temperature									
Spring	30.65	0.05	30.56	30.74	Spring - Summer	-0.67	0.07	-0.84	-0.50
Summer	31.32	0.05	31.22	31.41	Spring - Autumn	-0.80	0.07	-0.98	-0.62
Autumn	31.44	0.05	31.34	31.55	Spring - Winter	-1.64	0.07	-1.83	-1.45
Winter	32.29	0.06	32.18	32.40	Summer - Autumn	-0.13	0.07	-0.31	0.06
					Summer - Winter	-0.97	0.07	-1.17	-0.78
					Autumn - Winter	-0.85	0.08	-1.05	-0.65
Mean Temperature Variability SD									
Spring	0.08	0.00	0.07	0.08	Spring - Summer	-0.00	0.00	-0.01	0.00
Summer	0.08	0.00	0.08	0.09	Spring - Autumn	-0.02	0.00	-0.03	-0.01
Autumn	0.10	0.00	0.09	0.10	Spring - Winter	-0.03	0.00	-0.03	-0.02
Winter	0.10	0.00	0.10	0.11	Summer - Autumn	-0.02	0.00	-0.03	-0.01
					Summer - Winter	-0.02	0.00	-0.03	-0.01
					Autumn - Winter	-0.00	0.00	-0.01	0.00
Average Max Temperature									
Spring	30.80	0.05	30.71	30.89	Spring - Summer	-0.69	0.07	-0.87	-0.51
Summer	31.49	0.05	31.39	31.59	Spring - Autumn	-0.86	0.07	-1.04	-0.67
Autumn	31.66	0.05	31.55	31.76	Spring - Winter	-1.68	0.08	-1.88	-1.49
Winter	32.48	0.06	32.37	32.60	Summer - Autumn	-0.17	0.07	-0.36	0.02
					Summer - Winter	-0.99	0.08	-1.19	-0.80
					Autumn - Winter	-0.83	0.08	-1.03	-0.62
Average Min Temperature									
Spring	30.41	0.05	30.32	30.50	Spring - Summer	-0.68	0.07	-0.85	-0.51
Summer	31.08	0.05	30.99	31.18	Spring - Autumn	-0.77	0.07	-0.96	-0.59
Autumn	31.18	0.05	31.08	31.29	Spring - Winter	-1.59	0.07	-1.78	-1.40
Winter	32.00	0.06	31.89	32.11	Summer - Autumn	-0.10	0.07	-0.28	0.08
					Summer - Winter	-0.92	0.07	-1.11	-0.73
					Autumn - Winter	-0.82	0.08	-1.02	-0.62

Table S3.16 GLM (Gaussian Identity Link) results comparing mean daily temperatures (°C) between seasons on four nearshore reefs in Kimbe Bay. Pairwise contrasts and 95% confidence intervals are presented based on adjusted Tukeys method. Spring n = 360 , summer n = 360, autumn n = 368, winter n = 368

Season	*estimate*	*SE*	*lower.CL*	*upper.CL*	*contrast*	*estimate*	*SE*	*lower.CL*	*upper.CL*
Mean Temperature									
Spring	30.34	0.05	30.23	30.44	Spring - Summer	-0.67	0.08	-0.87	-0.47
Summer	31.01	0.05	30.90	31.11	Spring - Autumn	-0.97	0.07	-1.16	-0.79
Autumn	31.31	0.05	31.21	31.40	Spring - Winter	-0.98	0.08	-1.18	-0.79
Winter	31.32	0.05	31.22	31.43	Summer - Autumn	-0.30	0.07	-0.49	-0.11
					Summer - Winter	-0.31	0.08	-0.51	-0.12
					Autumn - Winter	-0.01	0.07	-0.20	0.17
Mean Temperature Variability SD									
Spring	0.07	0.00	0.06	0.07	Spring - Summer	-0.01	0.00	-0.02	0.00
Summer	0.08	0.00	0.08	0.09	Spring - Autumn	-0.03	0.00	-0.04	-0.02
Autumn	0.10	0.00	0.10	0.11	Spring - Winter	-0.01	0.00	-0.02	0.00
Winter	0.08	0.00	0.07	0.08	Summer - Autumn	-0.02	0.00	-0.03	-0.01
					Summer - Winter	0.01	0.00	0.00	0.02
					Autumn - Winter	0.03	0.00	0.02	0.03
Average Max Temperature									
Spring	30.46	0.05	30.36	30.57	Spring - Summer	-0.71	0.08	-0.90	-0.51
Summer	31.17	0.06	31.06	31.28	Spring - Autumn	-1.05	0.07	-1.24	-0.87
Autumn	31.52	0.05	31.42	31.61	Spring - Winter	-1.00	0.08	-1.20	-0.81
Winter	31.47	0.05	31.36	31.57	Summer - Autumn	-0.35	0.07	-0.54	-0.16
					Summer - Winter	-0.30	0.08	-0.50	-0.10
					Autumn - Winter	0.05	0.07	-0.14	0.24
Average Min Temperature									
Spring	30.11	0.05	30.01	30.21	Spring - Summer	-0.66	0.08	-0.86	-0.47
Summer	30.77	0.05	30.67	30.88	Spring - Autumn	-0.92	0.07	-1.11	-0.74
Autumn	31.03	0.05	30.94	31.13	Spring - Winter	-0.99	0.07	-1.18	-0.80
Winter	31.10	0.05	30.99	31.20	Summer - Autumn	-0.26	0.07	-0.45	-0.07
					Summer - Winter	-0.33	0.08	-0.52	-0.13
					Autumn - Winter	-0.07	0.07	-0.25	0.12

Table S3.17 Mean temperature (°C) and current speed (m s $^{-1}$) summaries at each reef type during full duration of deployment September 2018-19. Pinnacles n = (4 reefs), offshore n = (3 reefs) and nearshore n = (4 reefs). N = 6427 logs taken in 10 second intervals at each reef.

Site	**Reef Type**	**Temperature**	**SD**	**SE**	**Min**	**Max**	**Range**	**Variance**	**Current speed**	**SD**	**SE**	**Min**	**Max**	**Range**	**Variance**
Bradford	Pinnacle	30.69	0.75	0.003	28.75	32.84	4.09	0.556	0.0875	0.05	0.00018	0.00	0.3453	0.3453	0.00234
Inglis	Pinnacle	29.70	0.50	0.002	28.14	31.35	3.21	0.246	0.0854	0.05	0.00018	0.0001	0.3092	0.3091	0.00240
Joelles	Pinnacle	29.88	0.53	0.002	28.66	32.01	3.35	0.276	0.0891	0.04	0.00016	0.0004	0.2715	0.2711	0.00183
Kimbe Bommie	Pinnacle	30.68	0.79	0.003	29.02	32.73	3.71	0.622	0.0701	0.06	0.00024	0.0004	0.6030	0.6026	0.00410
Ottos	Offshore	31.70	1.14	0.004	28.93	35.24	6.31	1.300	0.0408	0.037	0.0001	0.0001	0.5976	0.5975	0.00014
Hogu	Offshore	30.73	0.91	0.003	28.75	33.17	4.43	0.827	0.0685	0.037	0.0001	0.0002	0.3318	0.3316	0.00014
Ema	Offshore	30.52	0.67	0.003	28.84	31.92	3.08	0.452	0.0425	0.04	0.0002	0.0001	0.5086	0.5085	0.00016
Donna	Nearshore	30.47	0.60	0.002	28.75	35.25	6.50	1.704	0.0646	0.045	0.0002	0.0001	0.3233	0.3232	0.00205
Susans	Nearshore	31.35	1.31	0.005	25.49	31.16	5.67	0.638	0.0622	0.046	0.0002	0.0001	0.4132	0.4131	0.00215
Madaro	Nearshore	29.78	0.80	0.003	28.75	32.29	3.54	0.516	0.0423	0.008	0.00003	0.002	0.0913	0.0893	0.00007
Lady Di	Nearshore	30.85	0.72	0.003	28.66	32.12	3.36	0.367	0.0389	0.025	0.00009	0.0001	0.1765	0.1764	0.00061

Table S3.18 Seasonal ranges of temperature (^{o}C) and current speed (m s^{-1}) at pinnacle, nearshore and offshore reefs in Kimbe Bay between September 2018 – September 2019.

	Spring			**Summer**			**Autumn**			**Winter**		
						Temperature (^{o}C)						
Reef Type	**Maximum**	**Minimum**	**Range**	**Maximum**	**Minimum**	**Range**	**Maximum**	**Minimum**	**Range**	**Maximum**	**Minimum**	**Range**
Pinnacle	30.96	28.42	2.54	31.24	29.07	2.17	32.46	29.02	3.44	32.55	28.84	3.71
Offshore	31.78	29.76	2.02	32.81	30.22	2.59	33.06	29.30	3.76	34.95	30.98	3.97
Nearshore	31.09	29.58	1.51	31.13	30.13	1.52	34.96	25.49	9.47	33.36	29.73	2.63
						Current Speed (m s^{-1})						
	Maximum	**Minimum**	**Range**	**Maximum**	**Minimum**	**Range**	**Maximum**	**Minimum**	**Range**	**Maximum**	**Minimum**	**Range**
Pinnacle	0.2249	0.005	0.2194	0.3951	0.0057	0.3951	0.3148	0.0058	0.3090	0.3148	0.0058	0.3090
Offshore	0.2405	0.0020	0.2385	0.1840	0.0013	0.1840	0.2126	0.0059	0.2067	0.3913	0.0182	0.3731
Nearshore	0.2414	0.0012	0.2402	0.2257	0.0050	0.2257	0.1851	0.0009	0.1842	0.3461	0.0029	0.342

Table S3.19 Spearman's correlation coefficients between mean daily temperature (°C) and mean daily current speed (m s $^{-1}$) for the annual period Sept 2018 – Sept 2019 **a)** collective correlation coefficients for each reef type **b)** correlation coefficients for each site.

a.

Reef type	r	P value
Pinnacle	-0.18	<0.001
Offshore	0.10	<0.001
Nearshore	0.003	0.27

b.

Reef Type	Site	r	P value
Pinnacle	Bradford	-0.043	0.33
	Joelles	-0.25	<0.01
	Kimbe Bommie	0.043	0.02
	Inglis	-0.20	<0.001
Offshore	Ottos	0.29	<0.001
	Hogu	0.67	<0.001
	Ema	-0.17	<0.01
Nearshore	Donnas	-0.58	<0.001
	Susans	0.24	<0.01
	Lady Di	0.14	<0.01
	Madaro	0.10	0.34

Appendix C - Supplementary Material Chapter 4

Table S4.1 Spatial characteristics of each Individual reef site

Site	Reef Type	Reef Area m^2/km^2	Nearest Reef (km)	Nearest Land (km)
Bradford	Pinnacle	$390m^2$	5.12	15.22
Inglis	Pinnacle	$416m^2$	4.24	10.18
Joelles	Pinnacle	$827m^2$	3.88	11.60
Kimbe Bommie	Pinnacle	$130m^2$	12.01	24.59
Ottos	Offshore	$0.067km^2$	8.40	17.70
Hogu	Offshore	$0.620km^2$	4.50	11.30
Ema	Offshore	$0.030km^2$	5.75	8.80
Donna	Nearshore	$0.035km^2$	0.55	3.70
Susans	Nearshore	$0.026km^2$	0.24	4.20
Madaro	Nearshore	$0.017km^2$	0.11	0.86
Lady Di	Nearshore	$0.007km^2$	0.15	0.734

Table S4.2 Benthic groups used in benthic point intercept video transect analysis.

Benthic Cover Type	Morphology – 47 types used to calculate benthic diversity, richness and total hard coral		Broad Scale Grouping (14 benthic categories)
Algae	Turf Brown Red EAM	Calcareous Cyanobacteria Filamentous	Algae
Hard Coral	Branching Tabulate	Foliaceous Columnar	Complex Hard Coral
	Massive	Sub-massive	Massive and Sub-Massive Hard Coral
	Encrusting		Encrusting Hard Coral
	Laminar		Laminar Hard Coral
Hexacoral	Whip Fan Digitate	Tree Bottlebrush Pinnulate	Complex Hexacoral
	Solitary Spreading Encrusting		Encrusting Hexacoral
Octocoral	Whip Fan Bottlebrush Spreading	Tree Pinnulate Encrusting Mushroom	Octocoral
Porifera	Barrel Vase Irregular	Rope Globose	Complex Porifera
	Encrusting		Encrusting Porifera
Ascidian	Encrusting Solitary		Rock and Reef Matrix
Rock	-		
Reef Matrix	-		
Unknown	-		
Rubble	-		Rubble
Sand	-		Sand and Silt
Silt	-		
CCA	-		CCA

Table S4.3a Summary Statistics for annual and survey period current speeds at each individual reef site. The annual period was between September 2018 – September 2019, Survey 1 October 2018-November and Survey 2 April-May 2019.

Site	**Reef Type**	**Annual Mean Current**	**Annual Max Current**	**Annual Current SD**	**Survey 1 Mean Current**	**Survey 1 Current SD**	**Survey 1 Max Current**	**Survey 2 Mean Current**	**Survey 2 Current SD**	**Survey 2 Mean Max Current**
Bradford	Pinnacle	0.809	0.35	0.039	0.071	0.048	0.225	0.071	0.044	0.225
Inglis	Pinnacle	0.085	0.31	0.031	0.064	0.044	0.155	0.084	0.041	0.204
Joelles	Pinnacle	0.085	0.27	0.027	0.079	0.029	0.146	0.079	0.045	0.139
Kimbe Bommie	Pinnacle	0.074	0.63	0.047	0.056	0.043	0.189	0.057	0.060	0.315
Ottos	Offshore	0.042	0.59	0.023	0.044	0.043	0.240	0.049	0.041	0.213
Hogu	Offshore	0.073	0.33	0.022	0.056	0.053	0.241	0.094	0.023	0.189
Ema	Offshore	0.041	0.51	0.015	0.050	0.043	0.158	0.016	0.009	0.024
Donna	Nearshore	0.057	0.32	0.024	0.073	0.053	0.203	0.064	0.044	0.185
Susans	Nearshore	0.063	0.41	0.019	0.071	0.057	0.241	0.066	0.033	0.183
Madaro	Nearshore	0.042	0.09	0.007	0.044	0.004	0.056	0.048	0.006	0.062
Lady Di	Nearshore	0.039	0.18	0.011	0.046	0.023	0.116	0.030	0.028	0.106

Table S4.3b Summary Statistics for annual and survey period temperatures at each individual reef site. The annual period was between September 2018 – September 2019, Survey 1 October 2018-November and Survey 2 April-May 2019.

Site	**Reef Type**	**Annual Mean Temp**	**Annual Max Temp**	**Annual Temp SD**	**Survey 1 Mean Temp**	**Survey 1 Temp SD**	**Survey 1 Max Temp**	**Survey 2 Mean Temp**	**Survey 2 Temp SD**	**Survey 2 Mean Max Temp**
Bradford	Pinnacle	31.00	32.84	0.55	30.55	0.224	30.96	31.40	0.639	32.46
Inglis	Pinnacle	29.70	31.35	0.50	29.02	0.326	30.59	30.03	0.520	31.26
Joelles	Pinnacle	30.20	32.01	0.57	30.03	0.295	29.73	31.28	0.275	31.64
Kimbe Bommie	Pinnacle	30.86	32.73	0.75	30.31	0.229	30.88	31.91	0.396	32.45
Ottos	Offshore	32.03	33.17	0.85	31.22	0.361	31.78	32.50	0.320	33.06
Hogu	Offshore	30.92	33.17	0.84	30.42	0.272	30.96	30.83	0.164	31.45
Ema	Offshore	30.82	31.92	0.47	30.55	0.349	31.16	31.31	0.164	31.45
Donna	Nearshore	30.65	35.25	0.48	30.47	0.385	31.06	30.85	0.385	31.92
Susans	Nearshore	31.69	31.16	1.16	30.64	0.252	31.00	33.34	0.697	34.96
Madaro	Nearshore	29.83	32.29	0.97	30.15	0.250	30.60	29.59	1.289	30.88
Lady Di	Nearshore	31.09	32.12	0.49	30.65	0.294	31.09	31.48	0.397	32.20

Table S4.4 Estimated marginal means of hydrodynamic variables derived from daily averaged current meter data at each reef type.

Reef type	*estimate*	*SE*	*lower.CL*	*upper.CL*	*contrast*	*estimate*	*SE*	*asymp.LCL*	*asymp.UCL*
Survey 1 Temperature ^{O}C									
Pinnacle	30.02	0.04	29.95	30.10	Pinnacle - Offshore	-0.71	0.05	-0.84	-0.57
Offshore	30.73	0.04	30.66	30.80	Pinnacle - Nearshore	-0.51	0.05	-0.65	-0.38
Nearshore	30.53	0.04	30.46	30.61	Offshore - Nearshore	0.20	0.05	0.06	0.33
Survey 1 Temperature Variability ^{O}C (SD)									
Pinnacle	0.27	0.04	0.20	0.35	Pinnacle - Offshore	0.09	0.05	-0.02	0.21
Offshore	0.18	0.04	0.10	0.26	Pinnacle - Nearshore	-0.13	0.05	-0.24	-0.02
Nearshore	0.40	0.04	0.33	0.48	Offshore - Nearshore	-0.22	0.05	-0.34	-0.11
Survey 1 Temperature Maximum ^{O}C									
Pinnacle	30.18	0.04	30.11	30.26	Pinnacle - Offshore	-0.71	0.05	-0.83	-0.58
Offshore	30.89	0.04	30.82	30.96	Pinnacle - Nearshore	-0.49	0.05	-0.62	-0.36
Nearshore	30.67	0.04	30.60	30.75	Offshore - Nearshore	0.22	0.05	0.09	0.34
Annual Temperature ^{O}C									
Pinnacle	30.53	0.03	30.47	30.58	Pinnacle - Offshore	-0.81	0.04	-0.91	-0.71
Offshore	31.33	0.03	31.27	31.39	Pinnacle - Nearshore	-0.48	0.04	-0.57	-0.38
Nearshore	31.00	0.03	30.95	31.05	Offshore - Nearshore	0.33	0.04	0.24	0.43
Annual Temperature Variability ^{O}C (SD)									
Pinnacle	0.59	0.03	0.53	0.66	Pinnacle - Offshore	-0.13	0.05	-0.25	-0.01
Offshore	0.72	0.04	0.64	0.80	Pinnacle - Nearshore	-0.18	0.05	-0.29	-0.07
Nearshore	0.77	0.03	0.71	0.84	Offshore - Nearshore	-0.06	0.05	-0.18	0.07
Annual Temperature Maximum ^{O}C									
Pinnacle	30.72	0.03	30.66	30.78	Pinnacle – Offshore	-0.79	0.04	-0.90	-0.69
Offshore	31.51	0.03	31.45	31.57	Pinnacle – Nearshore	-0.45	0.04	-0.54	-0.35
Nearshore	31.17	0.03	31.11	31.22	Offshore – Nearshore	0.35	0.04	0.25	0.45

Continued on next page

Table 4.4 continued

Reef type	*estimate*	*SE*	*lower.CL*	*upper.CL*	*contrast*	*estimate*	*SE*	*asymp.LCL*	*asymp.UCL*
Pinnacle	31.08	0.07	30.94	31.22	Pinnacle - Offshore	-0.56	0.11	-0.86	-0.27
Offshore	31.64	0.09	31.47	31.82	Pinnacle - Nearshore	-0.31	0.10	-0.56	-0.06
Nearshore	31.39	0.07	31.26	31.52	Offshore - Nearshore	0.25	0.11	-0.03	0.53
Survey 2 Temperature Variability ^{O}C (SD)									
Pinnacle	0.45	0.04	0.38	0.53	Pinnacle - Offshore	0.09	0.05	-0.02	0.21
Offshore	0.36	0.04	0.28	0.44	Pinnacle - Nearshore	-0.13	0.05	-0.24	-0.02
Nearshore	0.58	0.04	0.51	0.66	Offshore - Nearshore	-0.22	0.05	-0.34	-0.11
Survey 2 Temperature Maximum ^{O}C									
Pinnacle	31.34	0.07	31.19	31.48	Pinnacle - Offshore	-0.55	0.12	-0.82	-0.27
Offshore	31.88	0.09	31.71	32.06	Pinnacle - Nearshore	-0.27	0.10	-0.51	-0.04
Nearshore	31.61	0.07	31.48	31.74	Offshore - Nearshore	0.27	0.11	0.01	0.54
Annual Current Speed m s^{-1}									
Pinnacle	0.08	0.00	0.08	0.09	Pinnacle - Offshore	0.03	0.00	0.03	0.03
Offshore	0.05	0.00	0.05	0.06	Pinnacle - Nearshore	0.03	0.00	0.03	0.03
Nearshore	0.05	0.00	0.05	0.05	Offshore - Nearshore	0.00	0.00	-0.00	0.00
Annual Current Speed Variability m s^{-1} (SD)									
Pinnacle	0.04	0.00	0.03	0.04	Pinnacle - Offshore	0.02	0.00	0.01	0.02
Offshore	0.02	0.00	0.02	0.02	Pinnacle - Nearshore	0.02	0.00	0.02	0.02
Nearshore	0.02	0.00	0.01	0.02	Offshore - Nearshore	0.00	0.00	0.00	0.01
Annual Current Speed Maximum m s^{-1}									
Pinnacle	0.1727	0.0021	0.1686	0.1767	Pinnacle - Offshore	0.0264	0.0029	0.0195	0.0333
Offshore	0.1463	0.0021	0.1422	0.1504	Pinnacle - Nearshore	0.0350	0.0028	0.0285	0.0416
Nearshore	0.1377	0.0019	0.1340	0.1413	Offshore - Nearshore	0.0086	0.0028	0.0021	0.0152
Survey 1 Current Speed m s^{-1}									
Pinnacle	0.08	0.00	0.07	0.08	Pinnacle - Offshore	0.03	0.00	0.03	0.04
Offshore	0.05	0.00	0.04	0.05	Pinnacle - Nearshore	0.02	0.00	0.02	0.03
Nearshore	0.06	0.00	0.05	0.06	Offshore - Nearshore	-0.01	0.00	-0.01	-0.00

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Table 4.4 continued

Reef type	*estimate*	*SE*	*lower.CL*	*upper.CL*	*contrast*	*estimate*	*SE*	*asymp.LCL*	*asymp.UCL*
Survey 1 Current Speed Variability m s^{-1} (SD)									
Pinnacle	0.05	0.00	0.04	0.05	Pinnacle - Offshore	0.01	0.00	0.00	0.02
Offshore	0.04	0.00	0.03	0.04	Pinnacle - Nearshore	0.01	0.00	0.01	0.02
Nearshore	0.03	0.00	0.03	0.04	Offshore - Nearshore	0.00	0.00	-0.01	0.01
Survey 1 Current Speed Maximum m s^{-1}									
Pinnacle	0.177	0.005	0.167	0.187	Pinnacle - Offshore	0.030	0.007	0.013	0.046
Offshore	0.147	0.005	0.138	0.157	Pinnacle - Nearshore	0.025	0.007	0.008	0.042
Nearshore	0.152	0.005	0.142	0.162	Offshore - Nearshore	-0.004	0.007	-0.021	0.012
Survey 2 Current Speed m s^{-1}									
Pinnacle	0.07	0.00	0.07	0.08	Pinnacle - Offshore	0.01	0.00	0.00	0.01
Offshore	0.07	0.00	0.06	0.07	Pinnacle - Nearshore	0.02	0.00	0.02	0.03
Nearshore	0.05	0.00	0.05	0.05	Offshore - Nearshore	0.02	0.00	0.01	0.02
Survey 2 Current Speed Variability m s^{-1} (SD)									
Pinnacle	0.04	0.00	0.04	0.05	Pinnacle - Offshore	0.01	0.00	0.00	0.02
Offshore	0.03	0.00	0.03	0.04	Pinnacle - Nearshore	0.01	0.00	0.01	0.02
Nearshore	0.03	0.00	0.02	0.03	Offshore - Nearshore	0.00	0.00	-0.01	0.01
Survey 2 Current Speed Maximum m s^{-1}									
Pinnacle	0.167	0.003	0.161	0.174	Pinnacle - Offshore	0.021	0.005	0.009	0.033
Offshore	0.146	0.004	0.139	0.154	Pinnacle - Nearshore	0.040	0.004	0.030	0.051
Nearshore	0.127	0.003	0.121	0.133	Offshore - Nearshore	0.019	0.005	0.008	0.031

Table S4.5 GLM results for fish diversity metrics **a)** fish species richness; negative binomial model with log link **b)** fish Simpson's diversity; Gaussian model with identity link **c)** Fish abundance; negative binomial model with log link and d) log fish biomass; Gaussian model with identity link. For each model estimated marginal means with 95% confidence intervals are presented with pairwise comparisons using adjusted Tukey post hoc tests. Estimates are presented on the response scale.

a.

Reef type	***Mean Richness***	***SE***	***asymp.LCL***	***asymp.UCL***	***contrasts.***	***Contrast ratio***	***SE***	***asymp.LCL***	***asymp.UCL***
Pinnacle	36.50	1.71	33.30	40.01	Pinnacle / Offshore	2.28	0.18	1.89	2.75
Offshore	16.00	1.02	14.11	18.14	Pinnacle / Nearshore	2.74	0.20	2.30	3.27
Nearshore	13.30	0.77	11.87	14.91	Offshore / Nearshore	1.20	0.10	0.98	1.47
b.	***Mean Diversity***					***Contrast estimate***			
Pinnacle	0.82	0.02	0.79	0.85	Pinnacle - Offshore	0.07	0.02	0.01	0.12
Offshore	0.75	0.02	0.72	0.79	Pinnacle - Nearshore	0.05	0.02	0.01	0.10
Nearshore	0.77	0.02	0.74	0.80	Offshore - Nearshore	-0.02	0.02	0.08	0.04
c.	***Mean Abundance***					***Contrast ratio***			
Pinnacle	420.23	47.41	336.86	524.22	Pinnacle / Offshore	3.10	0.54	2.07	4.65
Offshore	135.60	17.75	104.91	175.26	Pinnacle / Nearshore	7.71	1.24	5.29	11.23
Nearshore	54.53	6.25	43.56	68.25	Offshore / Nearshore	2.49	0.43	1.65	3.74
d.	***Mean Biomass***					***contrast. ratio***			
Pinnacle	501.31	99.72	339.45	740.33	Pinnacle / Offshore	8.14	2.47	3.99	16.59
Offshore	61.60	14.15	39.27	96.62	Pinnacle / Nearshore	28.94	8.14	14.97	55.96
Nearshore	17.32	3.45	11.73	25.58	Offshore / Nearshore	3.56	1.08	1.74	7.25

Table S4.6 GLM results for benthic complexity metrics **a)** benthic richness Gaussian model with identity link **b)** benthic Simpson's diversity; Gaussian model with identity link **c)** total hard coral percent cover; Gaussian model with identity link and d) total complex hard coral percentage cover; negative binomial with log link. For each model estimated marginal means with 95% confidence intervals are presented with pairwise comparisons using adjusted Tukey post hoc tests. Estimates are presented on the response scale where there is evidence for a significant effect if the confidence interval does not contain zero.

a.

Reef type	*Mean Richness*	*SE*	*asymp.LCL*	*asymp.UCL*	*contrasts.*	*Contrast estimate*	*SE*	*asymp.LCL*	*asymp.UCL*
Pinnacle	11.15	0.22	10.72	11.58	Pinnacle / Offshore	0.58	0.34	-0.21	1.37
Offshore	10.57	0.25	10.07	11.07	Pinnacle / Nearshore	1.25	0.31	0.52	1.98
Nearshore	9.90	0.22	9.47	10.33	Offshore / Nearshore	0.67	0.34	-0.12	1.46
b.	*Mean Diversity*					*Contrast estimate*			
Pinnacle	0.82	0.01	0.81	0.84	Pinnacle - Offshore	-0.01	0.01	-0.04	0.02
Offshore	0.83	0.01	0.81	0.85	Pinnacle - Nearshore	-0.01	0.01	-0.04	0.02
Nearshore	0.83	0.01	0.81	0.85	Offshore - Nearshore	0.00	0.01	-0.03	0.04
c.	*Mean Hard Coral*					*Contrast estimate*			
Pinnacle	40.29	2.18	36.02	44.56	Pinnacle / Offshore	5.23	3.33	-2.57	13.04
Offshore	35.06	2.52	30.12	39.99	Pinnacle / Nearshore	8.38	3.08	1.15	15.60
Nearshore	31.92	2.18	27.64	36.19	Offshore / Nearshore	3.14	3.33	-4.66	10.94
d.	*Mean Complex Coral*					*contrast. estimate*			
Pinnacle	10.21	1.97	6.36	14.06	Pinnacle / Offshore	7.82	2.05	3.01	12.63
Offshore	2.39	0.59	1.24	3.54	Pinnacle / Nearshore	6.29	2.12	1.32	11.26
Nearshore	3.92	0.79	2.36	5.47	Offshore / Nearshore	-1.53	0.99	-3.84	0.78

Table S4.7 Results and optimized parameters for four random forest models used to determine relative influence of 19 environmental variables in determining fish species richness, fish diversity (Simpson's index), fish total abundance and fish biomass (kg). Variables are ranked based on the percentage reduction of mean standard error, where a greater percentage indicates greater importance of the variable in model.

Optimized Random Forest Output				
Response	**Fish Richness**	**Fish Diversity**	**Fish Abundance**	**Fish Biomass**
# trees	400	500	500	500
Mtry	6	4	4	4
MAE	5.22	0.079	106.95	73.34
RMSE	6.73	0.098	183.96	295.11
% Variance Explained	73.29	15.62	55.31	34.76

Environmental Variables	**% Reduction in Mean Standard Error**			
Biogeographical				
Reef Area	9.99	10.46	9.43	3.01
Nearest Reef	5.83	3.76	8.29	3.19
Nearest Mainland	5.87	6.38	8.31	1.20
Hydrodynamic				
Annual Mean Temperature	3.53	5.06	6.77	1.66
Annual Temperature Variability	4.94	5.09	7.25	-1.20
Annual Mean Current	12.09	5.97	10.75	2.33
Annual Current Variability	15.45	7.16	9.85	2.81
Annual Max Temperature	3.38	8.82	6.67	0.51
Annual Max Current	6.77	5.24	6.82	2.56
Survey Mean Current	4.12	8.01	6.36	1.90
Survey Max Current	7.09	9.35	5.55	0.94
Survey Current Variability	5.77	8.23	7.94	-1.23
Survey Mean Temperature	8.71	7.14	3.18	0.89
Survey Max Temperature	6.24	8.16	5.12	-0.49
Survey Temperature Variability	8.74	8.32	4.37	-0.28
Habitat				
Hard Coral Cover	-0.33	1.91	1.42	1.42
Benthic Diversity	-0.88	-2.43	4.18	-0.15
Benthic Richness	0.03	-6.15	0.40	-2.26
Complex Hard Coral Cover	5.69	4.51	1.25	1.35

Table S4.8 Model selection based on lowest AIC Scores. Where AIC was equal or within 2 units the model using the fewest degrees of freedom was chosen. Bolded text indicates the final chosen model structure for each response.

Response and Model	Model Formula – Fixed Factors	Random Factors	Df	AIC
Fish Species Richness	Annual current variation * Reeftype + Area	1|Year/Reeftype/Site	10	715.4072
Poisson model	**Annual current variation * Reeftype**	**1|Year/Reeftype/Site**	**9**	**717.9291**
Log link	Annual current variation + Area	1|Year/Reeftype/Site	7	733.0560
	Annual current variation + Reeftype + Area	1|Year/Reeftype/Site	8	732.2288
Fish Diversity (Simpsons Index)	**Survey Max Current * Reeftype**	**1|Year/Reeftype/Site**	**10**	**-185.24**
Gaussian model	Survey Max Current * Reeftype+Area	1|Year/Reeftype/Site	11	-184.07
Identity link	Survey Max Current + Area	1|Year/Reeftype/Site	7	-184.51
	Annual Max Temperature + Reeftype + Area	1|Year/Reeftype/Site	8	-189.20
Fish Abundance (Total Individuals)	**Mean Annual Current * Reeftype**	**1|Year/Reeftype/Site**	**10**	**1305.98**
Negative Binomial model	Mean Annual Current * Reeftype+Area	1|Year/Reeftype/Site	11	1306.44
	Mean Annual Current + Area	1|Year/Reeftype/Site	10	n/a
	Annual Current Mean Annual Current *	1|Year/Reeftype/Site	10	n/a
	Reeftype Variability + Reeftype	1|Year/Reeftype/Site	8	1310.03
Log-Fish Biomass (kg per 150m^2)	**Annual Current Variability * Reeftype**	**1|Year/Reeftype/Site**	**10**	**347.69**
Gaussian model	Annual Current Maximum * Reeftype	1|Year/Reeftype/Site	10	358.86
Identity link	Annual Current Variability + Area	1|Year/Reeftype/Site	8	363.08
	Annual Current Variability + Nearest Reef	1|Year/Reeftype/Site	10	352.33

Table S4.9 Estimates and 95% confidence intervals for GLMMs

term	*estimate*	*std.error*	*statistic*	*p.value*	*conf.low*	*conf.high*
Fish Richness – Poisson – Log link – R^2m = 0.73 R^2c = 0.87						
(Intercept)	3.56	0.16	22.36	0.00	3.25	3.88
Reef Type - Offshore	-1.00	0.23	-4.31	0.00	-1.45	-0.54
Reef Type -Nearshore	-0.69	0.23	-3.03	0.00	-1.14	-0.25
Annual Current Variability (SD)	0.03	0.06	0.46	0.65	-0.08	0.14
Reef type -Offshore: Annual Current Variability (SD)	-0.55	0.18	-3.06	0.00	-0.91	-0.20
Reef Type: Nearshore: Annual Current Variability	0.40	0.11	3.83	0.00	0.20	0.61
Fish Diversity – Gaussian – Identity link – R^2m = 0.09 R^2c = 0.39						
(Intercept)	0.82	0.04	22.29	0.00	0.75	0.89
Reef Type - Offshore	-0.07	0.05	-1.25	0.21	-0.17	0.04
Reef Type -Nearshore	-0.05	0.05	-0.93	0.35	-0.15	0.05
Survey Max Current Speed	0.02	0.02	0.71	0.48	-0.03	0.06
Reef type -Offshore: Survey Max Current Speed	-0.05	0.04	-1.34	0.18	-0.12	0.02
Reef Type: Nearshore: Survey Max Current Speed	-0.01	0.03	-0.35	0.73	-0.07	0.05

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Table S4.9 continued

Fish Abundance – Poisson – Log link – R^2m = 0.88 R^2c = 0.92						
Pinnacle	5.92	0.18	33.22	0.00	5.57	6.26
Reef type: Offshore	-1.04	0.27	-3.81	0.00	-1.57	-0.50
Reef type: Nearshore	-2.15	0.25	-8.51	0.00	-2.65	-1.66
Mean Annual Current Speed	0.26	0.18	1.45	0.15	-0.09	0.61
Offshore: Mean Annual Current Speed	-0.46	0.28	-1.68	0.09	-1.00	0.08
Nearshore: Mean Annual Current Speed	0.24	0.26	0.94	0.35	-0.26	0.74
Fish Biomass(log10) – Gaussian – Identity link – R^2m = 0.67 R^2c = 0.71						
(Intercept)	6.22	0.21	29.17	0.00	5.80	6.63
Reef Type - Offshore	-2.10	0.33	-6.44	0.00	-2.73	-1.46
Reef Type -Nearshore	-3.37	0.30	-11.17	0.00	-3.96	-2.77
Annual Current Variability (SD)	0.31	0.22	1.43	0.15	-0.11	0.73
Reef type -Offshore: Annual Current Variability (SD)	-0.11	0.33	-0.35	0.73	-0.76	0.53
Reef Type: Nearshore: Annual Current Variability	0.70	0.31	2.31	0.02	0.11	1.30

Table S4.10 Estimated Means and Pairwise Contrasts for fish richness, diversity, abundance and biomass at and between each reef type.

REEFTYPE	*estimate*	*SE*	*df*	*lower.CL*	*upper.CL*	*contrast*	*ratio*	*SE*	*df*	*lower.CL*	*upper.CL*
Richness											
Pinnacle	36.24	5.35	107	27.04	48.57	Pinnacle / Offshore	2.30	0.49	107	1.39	3.82
Offshore	15.76	2.42	107	11.63	21.36	Pinnacle / Nearshore	2.88	0.61	107	1.74	4.77
Nearshore	12.59	1.92	107	9.31	17.03	Offshore / Nearshore	1.25	0.27	107	0.75	2.09
Diversity											
Pinnacle	0.82	0.04	106	0.75	0.89	Pinnacle/ Offshore	0.07	0.05	106	-0.11	0.24
Offshore	0.75	0.04	106	0.68	0.83	Pinnacle/ Nearshore	0.05	0.05	106	-0.12	0.22
Nearshore	0.77	0.04	106	0.70	0.85	Offshore/ Nearshore	-0.02	0.05	106	-0.19	0.15
Abundance											
Pinnacle	370.79	66.03	106	260.49	527.79	Pinnacle / Offshore	2.82	0.77	106	1.48	5.38
Offshore	131.53	27.06	106	87.47	197.78	Pinnacle / Nearshore	8.62	2.18	106	4.72	15.74
Nearshore	43.01	7.75	106	30.09	61.48	Offshore / Nearshore	3.06	0.84	106	1.60	5.86
Biomass											
Pinnacle	501.31	106.84	106	328.55	764.90	Pinnacle / Offshore	8.14	2.65	106	3.75	17.65
Offshore	61.60	15.16	106	37.81	100.33	Pinnacle / Nearshore	28.94	8.72	106	14.14	59.25
Nearshore	17.32	3.69	106	11.35	26.43	Offshore / Nearshore	3.56	1.16	106	1.64	7.71

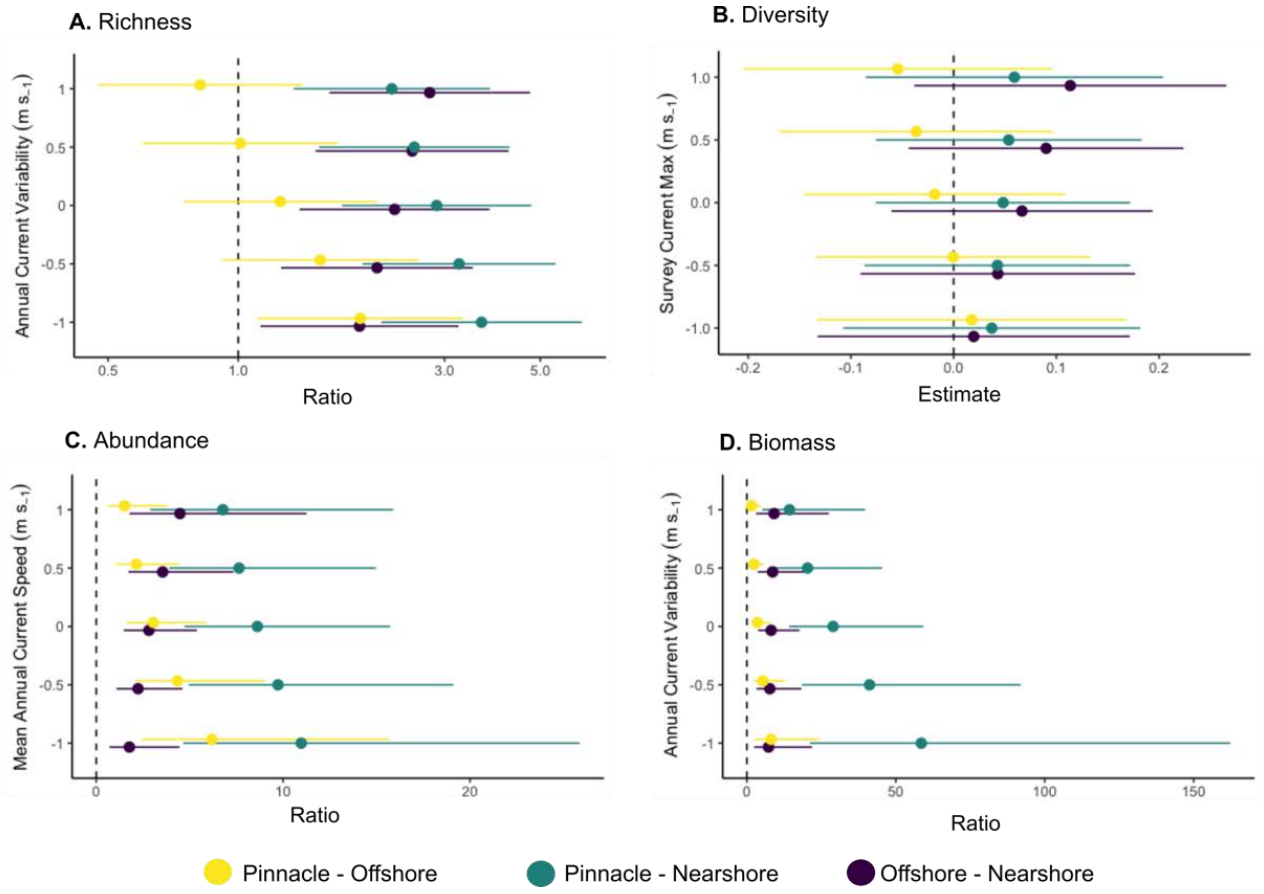

Figure S4.1 Pairwise estimates of estimated mean a. Fish richness b. Simpson's Diversity c. Total abundance and d. Biomass at different levels of hydrodynamic co-variants. For each model, mean level of each co-variate is centered on 0 and estimates plotted at 0.5 and 1 standard deviations greater and lower than the mean.

Table S4.11 Estimated slopes and pairwise contrasts for fish richness, diversity, abundance and biomass at and between each reef type.

REEFTYPE	*estimate*	*SE*	*df*	*lower.CL*	*upper.CL*	*contrast*	*Estimate*	*SE*	*df*	*lower.CL*	*upper.CL*
Richness	**Annual Current Speed Variability (SD) Trend**										
Pinnacle	0.64	1.41	107	-2.16	3.44	Pinnacle - Offshore	3.31	1.70	107	-0.73	7.34
Offshore	-2.67	0.94	107	-4.54	-0.79	Pinnacle - Nearshore	-2.59	1.63	107	-6.46	1.27
Nearshore	3.23	0.81	107	1.63	4.84	Offshore - Nearshore	-5.90	1.24	107	-8.86	-2.95
Diversity	**Survey Current Speed Max Trend**										
Pinnacle	0.02	0.02	106	-0.03	0.06	Pinnacle - Offshore	0.05	0.04	106	-0.04	0.13
Offshore	-0.03	0.03	106	-0.08	0.02	Pinnacle - Nearshore	0.01	0.03	106	-0.06	0.09
Nearshore	0.01	0.02	106	-0.04	0.05	Offshore - Nearshore	-0.04	0.03	106	-0.12	0.05
Abundance	**Annual Current Speed Trend**										
Pinnacle	96.24	68.66	106	-39.89	232.37	Pinnacle - Offshore	123.00	74.18	106	-53.32	299.32
Offshore	-26.76	28.06	106	-82.40	28.88	Pinnacle - Nearshore	74.69	69.21	106	-89.83	239.22
Nearshore	21.55	8.73	106	4.24	38.87	Offshore - Nearshore	-48.31	29.39	106	-118.18	21.56
Biomass	**Annual Current Speed Variability (SD) Trend**										
Pinnacle	154.70	113.20	106	-69.73	379.13	Pinnacle / Offshore	142.76	114.28	106	-128.90	414.42
Offshore	11.94	15.70	106	-19.20	43.07	Pinnacle / Nearshore	137.13	113.32	106	-132.25	406.51
Nearshore	17.57	5.30	106	7.06	28.07	Offshore / Nearshore	-5.63	16.57	106	-45.03	33.76

Table S4.12 Expanded table 4.1 detailing rationale behind selected variables for random forest analysis and supporting references.

Variable	Description	Source	Range	Unit	Rationale	References
Biogeographical						
Nearest Mainland	Distance to closest mainland coast	GIS	0.73 – 24.59	Km	Isolation – patterns of habitat fragmentation strongly influence reef fish communities both positively and negatively e.g increased distance from terrestrial/anthropogenic impacts but also other important marine habitats.	(MacArthur and Wilson 1967; Hubbell 2001; Fahrig 2013; Luiz et al. 2015; Quimbayo et al. 2019; Jones et al. 2020)
Nearest Neighbouring Reef	Distance to closest area of coral reef	GIS	0.11 – 12.01	Km	Connectivity and biogeography – habitats closer to other sources of immigration and recruitment.	
Hydrodynamic						
Annual Mean Temperature	Daily mean 12 month period	Current Meter	29.7-32.03	°C	Longer-term temperature trends critically determine species distributions to sites with values within tolerable thermal ranges. Potential metabolic effects on growth and biomass.	(Wright 1983; Brown et al. 2004; Fulton et al. 2005; Brierley and Kingsford 2009; Munday et al. 2009; Carrara and Vázquez 2010; Binning and Roche 2015; Mellin et al. 2016; Duffy et al. 2016; Eggertsen et al. 2016; Kerry and Bellwood 2017; Harborne et al. 2017; Day et al. 2018; Fisher et al. 2018)
Annual Mean Current	Daily mean 12 month period	Current Meter	0.04-0.09	$m\ s^{-1}$	Longer-term current speed trends may determine species distributions to sites with values within tolerable ranges. Species with physiological or behavioural adaptations to living in high currents.	
Annual Temperature Variability (SD)	Standard deviation 12 month period	Current Meter	0.47 – 1.16	°C	Energetic variability can influence population dynamics. Variability in sea temperature affects a number of important ecological processes that may affect fish community structure.	
Annual Current Variability (SD)	Standard deviation 12 month period	Current Meter	0.007-0.047	$m\ s^{-1}$	Energetic variability can influence population dynamics. High variability in current speed and a stochastic hydrodynamic environment may determine species distributions and enhance biophysical coupling.	
Annual Temperature Maximum	Average daily maximum 12 month period	Current Meter	31.2 – 35.2	°C	Thermal maxima are known to limit species distributions, metabolic processes and reef energetics. Annual average maximum define habitat suitability for some fishes.	
Annual Current Maximum	Average daily maximum 12 month period	Current Meter	0.09 – 0.60	$m\ s^{-1}$	Strong currents provide energetic costs and opportunities. Longer-term maximum current speeds define habitat suitability for some fishes.	
Sampling Season Temperature Mean	Daily mean during sampling season	Current Meter	29.03 – 33.34	°C	Temperature seasonality may affect fish observations during survey months. These temperatures may not reflect longer-term conditions that have shaped fish communities.	

Table S4.12 continued Expanded table 1 detailing rationale behind selected variables for random forest analysis and supporting references.

Variable	Description	Sorce	Range	Unit	Rationale	References
Sampling Season Current Mean	Daily mean during sampling season	Current Meter	0.02-0.09	$m\ s^{-1}$	Current speed seasonality may affect fish observations during survey months. These currents may not reflect longer-term conditions that have shaped fish communities.	
Sampling Season Temperature Variability (SD)	Standard deviation during sampling season	Current Meter	0.16 – 1.29	°C	Energetic variability can influence population dynamics. Stochasticity in temperature during the survey period may affect fish observations. Variability in sea temperature affects a number of important ecological processes and fish biodiversity patterns.	
Sampling Season Current Variability (SD)	Standard deviation during sampling season	Current Meter	0.004 – 0.06	$m\ s^{-1}$	Energetic variability can influence population dynamics. Stochasticity in current speeds during the survey period may affect fish observations. E.g. Fluxes in pelagic subsidies, seasonal aggregations behavioural adaptations.	
Sampling Season Temperature Max	Average daily maximum during sampling season	Current Meter	29.7 – 35.0	°C	Thermal maxima are known to limit species distributions, metabolic processes and reef energetics. This may therefore affect fish distributions during the survey season and therefore visual observations.	
Sampling Season Current Max	Average daily maximum during sampling season	Current Meter	0.02 – 0.32	$m\ s^{-1}$	Strong currents can both attract and cause fish to shelter. This may therefore affect fish distributions during the survey season and therefore visual observations.	
Habitat						
Hard Coral Cover	Percent cover of hard coral	Benthic point-intercept video transects	6.67 – 71.67	% cover	Hard coral cover affects abundance of coral-associated species and increases habitat complexity.	(Arrhenius 1921; Bell and Galzin 1984; Chittaro 2002; Friedlander et al. 2003; Jones et al. 2004; Messmer et al. 2011; Komyakova et al. 2013; Darling et al. 2017)t
Complex Hard Coral Cover	Percent cover of complex hard coral	Benthic point-intercept video transects	0 - 30	% cover	Higher complex coral cover increases habitat complexity and subsequently reef fish diversity.	
Benthic Diversity	Simpson's D	Benthic point-intercept video transects	0.52 – 0.91	D	Increased diversity of benthic habitat increases habitat complexity and subsequently reef fish diversity.	
Benthic Richness	Variety of different benthic groups	Benthic point-intercept video transects	8 - 15	n	Increased variety of benthic habitat increases habitat complexity and subsequently reef fish diversity	
Reef Area	Total area of reef habitat above 30m depth contour	GIS emergent reefs In-water surveys pinnacles	0.00013 – 0.62	Km^2	Species-area and biogeography – larger areas of habitat support higher numbers of species and individuals.	

Appendix D – Supplementary Material Chapter 5

Table S5.1 47 benthic cover categories used to analyse benthic video transect

Benthic Cover Type	Morphology – 47 types used to calculate benthic diversity, richness and total hard coral		Broad Scale Grouping (14 benthic categories)
Algae	Turf	Calcareous	Algae
	Brown	Cyanobacteria	
	Red	Filamentous	
	EAM		
Hard Coral	Branching	Foliaceous	Complex Hard Coral
	Tabulate	Columnar	
	Massive	Sub-massive	Massive and Sub-Massive Hard Coral
	Encrusting		Encrusting Hard Coral
	Laminar		Laminar Hard Coral
Hexacoral	Whip	Tree	Complex Hexacoral
	Fan	Bottlebrush	
	Digitate	Pinnulate	
	Solitary		Encrusting Hexacoral
	Spreading		
	Encrusting		
Octocoral	Whip	Tree	Octocoral
	Fan	Pinnulate	
	Bottlebrush	Encrusting	
	Spreading	Mushroom	
Porifera	Barrel	Rope	Complex Porifera
	Vase	Globose	
	Irregular		
	Encrusting		Encrusting Porifera
Ascidian	Encrusting		Rock and Reef Matrix
	Solitary		
Rock	-		
Reef Matrix	-		
Unknown	-		
Rubble	-		Rubble
Sand	-		Sand and Silt
Silt	-		
CCA	-		CCA

Table S5.2 Summary of environmental variables used in dbRDA for biomass and productivity of fish communities. Variable ranges represent all reef types, submerged pinnacles, offshore emergent and nearshore emergent. Annual values are from a 12-month period between September 2018 and September 2019. Survey periods were October-November 2018 (survey 1) and April-May 2019 (survey 2)

Variable	Description	Source	Range	Unit
Nearest Mainland	Distance to closest mainland coast	GIS	0.73 – 24.59	Km
Nearest Neighbouring Reef	Distance to closest area of coral reef	GIS	0.11 – 12.01	Km
Annual Mean Temperature	Daily mean 12 month period	Current Meter	29.7-32.03	ºC
Annual Mean Current	Daily mean 12 month period	Current Meter	0.04-0.09	m s $^{-1}$
Annual Temperature Variability (SD)	Standard deviation 12 month period	Current Meter	0.47 – 1.16	ºC
Annual Current Variability (SD)	Standard deviation 12 month period	Current Meter	0.007-0.047	m s $^{-1}$
Annual Temperature Maximum	Average daily maximum 12 month period	Current Meter	31.2 – 35.2	ºC
Annual Current Maximum	Average daily maximum 12 month period	Current Meter	0.09 – 0.60	m s $^{-1}$
Sampling Season Temperature Mean	Daily mean during sampling season	Current Meter	29.03 – 33.34	ºC
Sampling Season Current Mean	Daily mean during sampling season	Current Meter	0.02-0.09	m s $^{-1}$
Sampling Season Temperature Variability (SD)	Standard deviation during sampling season	Current Meter	0.16 – 1.29	ºC
Sampling Season Current Variability (SD)	Standard deviation during sampling season	Current Meter	0.004 – 0.06	m s $^{-1}$
Sampling Season Temperature Max	Average daily maximum during sampling season	Current Meter	29.7 – 35.0	ºC
Sampling Season Current Max	Average daily maximum during sampling season	Current Meter	0.02 – 0.32	m s $^{-1}$
Hard Coral Cover	Percent cover of hard coral	Benthic point-intercept video transects	6.67 – 71.67	% cover
Complex Hard Coral Cover	Percent cover of complex hard coral	Benthic point-intercept video transects	0 - 30	% cover
Benthic Diversity	Simpson's D	Benthic point-intercept video transects	0.52 – 0.91	D
Benthic Richness	Variety of different benthic groups	Benthic point-intercept video transects	8 - 15	n
Reef Area	Total area of reef habitat above 30m depth contour	GIS emergent reefs In-water surveys pinnacles	0.00013 – 0.62	Km ^{2}