Fine-Scale Foraging and Movement Behaviour of *Chaetodon* Butterflyfish Along a Turbidity Gradient on a Coral Reef in the Solomon Islands

Emily Grace Jupp Steele

A research component submitted to Auckland University of Technology in partial fulfilment of the requirements for the degree of Master of Science (MSc)

2024

School of Science
Department of Environmental Science

Abstract

Coral reefs stand as the pinnacle of ecological biodiversity, playing a vital role in supporting a diverse array of organisms. But they are under threat. Anthropogenic influence impacts how coral reefs, and the animals and people they support, function. Conventional methods of assessing coral reef health typically rely on species abundance and biomass estimates, potentially overlooking subtle changes occurring early in the degradation process. This study explores the concept that fine-scale alterations in the movement patterns and foraging behaviour of coral reef fish can serve as indicators of coral reef degradation. Employing stereo-video methodology, footage of coral reef fish behaviour was captured along a turbidity gradient at Vavanga Reef on Kolombangara Island, Solomon Islands. Vavanga Reef receives sedimentation from Vavanga River, creating a turbidity gradient that is exacerbated by historic logging practices. Analysis of foraging substrates, bite rates, bite distances, and three-dimensional tracking data of three species of *Chaetodon* butterflyfish species revealed insights into their foraging and movement behaviour. The hard-coral specialist foragers, *C. baronessa* and *C. lunulatus*, showed significant trends across the turbidity gradient, whereas *C. vagabundus*, the generalist omnivore, did not. *C. baronessa* displayed a clear preference for *Acropora*, with high total bite percentages and preference ratios that depended on substrate availability and turbidity. *C. lunulatus* consistently preferred *Porites* across the turbidity gradient; however, this was not seemingly impacted by substrate availability or turbidity, and their foraging substrate choice appeared random. The body mass and length of *C. baronessa* and *C. lunulatus* decreased with increasing turbidity, suggesting that turbidity and coral availability influence fish physiology and growth or that these species are distributed along the turbidity gradient according to age. Further investigation of the physiological condition of the species would provide a more definitive answer. The velocity of *C. baronessa* and *C. lunulatus* increased with turbidity, indicating adjustments in swimming behaviour to compensate for reduced visibility or prey availability. Furthermore, increased overall dynamic body acceleration values in *C. baronessa* at sites with lower live coral cover suggest elevated energy expenditure associated with foraging efforts in less favourable conditions. These results may indicate an adaptive response of *C. baronessa* to changing reef conditions. The discoveries resulting from this research emphasise the importance of identifying nuanced changes in coral reef fish behaviour to understand and address the ongoing degradation of coral reef ecosystems. This research is crucial in the face of escalating pressures that threaten coral reefs and the communities they support.

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“I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person (except where explicitly defined in the acknowledgements), nor material which to a substantial extent has been submitted for the award of any other degree or diploma of a university or other institution of higher learning.”

Signature:

Date: 03/04/2024

Acknowledgements

First and foremost, I would like to thank the tāngata, whenua, and moana of Vavanga, Kolombangara. Your hospitality, generosity, and openness to me and my research are the highlight of my project. I thank you for your willingness to allow me to conduct my science on your reef and your dedication to keeping me fed and sheltered while I did so. I acknowledge that the science I undertake is nascent in comparison to the indigenous knowledge that your community holds, and I give special recognition and appreciation to Woody Laufanua and Chite Silas for sharing this with me daily. Thank you, Koimata Nixon Silaspio, for allowing us to conduct our research in your village and Mareta for humbly cooking and cleaning for us. Thank you, Jillian, for sharing your personal story and for being the reason for this connection between Vavanga and Aotearoa. Leanhola, Vavanga Village, for graciously welcoming and caring for me. I will always think of you fondly, and I dedicate this thesis to you.

To my supervisor, Associate Professor Armagan Sabetian, thank you for giving me this opportunity of a lifetime. Thank you for keeping me on track and keeping me grounded and stress-free. You truly are a one-of-a-kind supervisor, and I appreciate all the time and effort you have put into me as your student over the years. I also wish to thank my additional supervisor, Julian Lilkendey, for hatching this research idea and your guidance throughout this project. Thank you for encouraging my independence; you have taught me how to be a better scientist, and I am truly grateful for that.

To Lance, Nat, and Kelly at LS Electrical, my sincerest thanks for providing a space for me to work and focus on this thesis.

Special thanks go to my colleague and friend, Sanaa Nair. Thank you for your knowledge contribution in the statistical analysis stage and for the moral support throughout. You have made the process of writing this thesis smoother and more bearable.

Thank you to my family, Mum, Dad, Kirsten, Jodie, Luke, Maisie, and Layne. You have always supported me in every endeavour and knowing that you’re right behind me has kept me going when it got tough. Thank you and I love you from the bottom of my heart.

To my husband, Ned Steele, you have made this entire thesis possible. You consistently encourage me, hold me accountable, and provide a place for me to decompress. You have selflessly put this research before your needs, which truly deserves the highest commendation. Thank you for being by my side in the field and for keeping me fed and hydrated throughout the analysis and writing stage, too. You truly are the best research assistant I could ask for and I’m so blessed to be able to drag you on all my expeditions in the future!

Preface

Jillian was born and raised in Vavanga Village in Kolombangara, Western Province, Solomon Islands. The following is a personal account of Jillian's connection with the ocean (personal communication, February 12, 2024). In this passage, she reflects on the deep-rooted cultural bonds her village maintains with the ocean and how these traditions were imparted to her over time.

> My childhood was very similar to the experience of kids on the Island of Kolombangara today. I had a deeply enriching and interconnected relationship with the marine ecosystem during my childhood, adolescent, and formative years on this tropical rainforest. The sea, coral reefs, and marine life not only provided sustenance, but also served as a playground and source of curiosity and education while growing up. We observed and studied every creature and their environment. But we were also passed on traditional ecological information from our parents and elders about a wide array of topics, ranging from seasonal events, ecological and biological information, fishing methods, poisonous and dangerous things in the sea, and even what sort of fish not to eat during different life stages. For example, elders often advocate for the avoidance of consuming large migratory pelagic fish, such as tuna and swordfish, particularly among pregnant women and young children due to their tendency to accumulate high levels of heavy metals from their diet. The importance of the sea for food security and subsistence to our community cannot be overstated. Coral reefs often support diverse ecosystems that sustain fisheries, providing protein and livelihoods for many people. We were acutely aware of this, and cognisant of conserving this vital resource. For example, I distinctly remember my grandfather impressing on us the importance of not harassing marine life, killing things unnecessarily, and keeping a clean existence so that our activities on land didn't impact the reef and its organisms. Because of this importance, there are also spiritual and cultural belief attached to the sea. For

example, the fishing god Kesoko is a deity that has the body of a man and the head of a frigatebird. In the old days, fishers used to call out to Kesoko and ask him to make their journey a bountiful one. Such spiritual and cultural connections have deep roots in our community's history and traditions, shaping practices related to fishing, storytelling, and celebrations. Preserving both the ecological and cultural integrity of the marine environment is essential for ensuring the continued well-being of our community and future generations. It's a beautiful testament to the intricate relationship between humans and nature, particularly in coastal regions where reliance on the sea is paramount.

Chapter 1: Introduction

1.1 Coral reef ecosystems

Coral reefs are intricate marine ecosystems formed through the collective effort of small, soft-bodied organisms called coral polyps (Class Anthozoa). These polyps secrete calcium carbonate to form skeletons around their soft bodies. Many Anthozoan coral species live in colonies, and the secretion of calcium carbonate from numerous individual polyps will form large structures. Eventually, the large structures formed by multiple coral species will create entire coral reefs. These coral reefs are typically found in tropical and subtropical waters between latitudes of 30° North and 30° South (National Oceanic and Atmospheric Association, n.d.), as colder sea temperatures (<16 °C) negatively impact coral respiration and photosynthetic output of the symbiotic zooxanthellae that live in the cells of the coral (Kemp et al., 2011; Saxby et al., 2003). Many shallow-water corals contain these unicellular zooxanthellae (Genus *Symbiodinium*); the coral provides protection and nutrients for the zooxanthellae, which they use for photosynthesis, and the zooxanthellae return some of their photosynthetic nutrients to the coral in a mutually beneficial relationship (Muscatine & Porter, 1977).

Coral reefs are often marine biodiversity hotspots, creating habitats and niches for many species of marine organisms and supporting their survival by facilitating essential ecological processes such as recruitment, predation, and competition (Hixon & Beets, 1993; Syms & Jones, 2000). Some coral reefs have thousands of reef fish species relying on them (Allen, 2008), and when considering all other species of teleosts, elasmobranchs, mammals, and invertebrates, the species richness of a single coral reef surpasses many other ecosystems around the world.

Coral reefs are important areas for many coastal communities, providing risk reduction, hazard mitigation, food, income, employment, economic revenue, and cultural significance to these communities (Burke et al., 2011; Ferrario et al., 2014; Hatcher & Hatcher, 2004; Hoegh-Guldberg et al., 2019; Moberg & Folke, 1999; Salvat, 1992; Turner et al., 2007; Wilkinson, 1996). There are an estimated one billion people whose livelihood benefits either directly or indirectly from the ecosystem services provided by coral reefs (NOAA Office for Coastal Management, 2023), and, additionally, many people who are dependent on coral reefs for their livelihood live in poverty (Burke et al., 2011; Whittingham et al., 2003).

1.1.1 Coral reefs as biodiversity hotspots

One way that coral reef ecosystems support such great biodiversity and life is due to their structural complexity. Natural processes, including coral skeletal growth, mechanical erosion (for example, weather events and water movement), and biological erosion (for example, parrotfish), play key roles in influencing the rate of expansion and reduction of the reef substrate. The extent of this reef substrate complexity is commonly quantified using a fundamental surface roughness index known as reef rugosity (Luckhurst & Luckhurst, 1978; McCormick, 1994). The rugosity, in turn, determines the diversity of the available habitat (C. G. Jones et al., 1994; Nash et al., 2014; Richardson et al., 2017), and typically, extensive cover of live coral enhances the rugosity and overall architectural complexity of a reef (Graham & Nash, 2013).

This habitat complexity, observed across different environments, supports high taxonomic diversity and abundance by providing areas for shelter, mediating competition, and serving as a nursery ground (Chong-Seng et al., 2012; Coker et al., 2014; Graham & Nash, 2013; Guinan et al., 2009; Huston, 1979; Shmuel et al., 2022; Stella et al., 2011). Research on global coral reefs has associated the loss of live coral with reductions in habitat complexity, resulting in a decline in reef fish and invertebrate abundance and diversity (Alvarez-Filip et al., 2009; Crowder & Cooper, 1982; Graham et al., 2006; Graham & Nash, 2013; Stachowicz, 2001; Walker et al., 2009). Findings from Messmer et al.'s (2011) study reflect the narrative that high coral species richness positively affects fish species richness. However, they also identify certain coral species that disproportionately support fish diversity, with monotypic areas of specific coral species supporting levels of fish diversity and abundance similar to areas with many coral species. Additionally, certain areas of coral reef structural complexity create microhabitats that support distinct fish communities (Messmer et al., 2011). Altogether, this demonstrates that the overall structural complexity of coral reefs has a profound impact on the abundance and diversity of organisms at both an ecosystem and species level. Coral reefs characterised by high structural complexity create environments that support high biodiversity.

Another crucial component of coral reef biodiversity is their ability to support many species through the habitat and food they supply, creating a dense area of organisms that form symbiotic relationships with one another (Castro, 1988). In one form of symbiosis, coral reefs serve as a meeting area for interactions, such as the cleaning services provided by smaller fish and invertebrates to larger ‘clients’, including reef fish, grouper, moray eel, barracuda, turtles, and elasmobranch species (Corso et al., 2023; Quimbayo et al., 2017; Sazima et al., 2010). Other examples of symbiosis, both mutualistic and parasitic, exist between species living on coral reefs. These examples include the relationships between alpheid shrimps and gobiid fishes (Karplus & Thompson, 2011), anemonefishes and sea anemones (Astakhov et al., 2016; Dunn, 1981), Trapezia crabs and live corals (Galil, 1987; Knudsen, 1967; Rinkevich et al., 1991), and various species of parasitic invertebrates (including trematodes, cestodes, nematodes, annelids, crustaceans, and hydroids) living on and within macrofauna species (Castro, 1988; Justine, 2010; Rigby et al., 1999). These symbiotic interactions occur due to the high biodiversity initiated and maintained by coral reefs. Consequently, these symbiotic relationships play a crucial role in supporting coral reef biodiversity by increasing the fitness and/or survival of at least one species involved in each symbiotic partnership.

Other general inter- and intra-species interactions, including mating, predation, and harassment, help to drive coral reef diversity and productivity. Nutrient cycling is one of the more nuanced ways that these interactions contribute to biodiversity. This nutrient cycling can be on microscopic scales, where the health of a coral microbiome (including bacteria, archaea, fungi, and viruses) directly correlates with coral bleaching and disease (Rädecker et al., 2015). Nutrient cycling can also be on larger scales, where entire communities of coral reef fish consume and release nutrients through excretion and egestion into the environment where it can be recycled (Schiettekatte et al., 2023).

The drivers of coral reef biodiversity are long-term ecological and evolutionary processes, such as niche partitioning and speciation, that foster genetic diversity that results in the intricate community structures found in today's coral reefs. The importance of genetic diversity for the vitality of entire coral reef ecosystems is explained by Selkoe et al. (2016), who found that large reefs with high coral cover exhibit the highest average overall genetic diversity across a spectrum of sampled species. Habitat area, coral cover, rugosity, and structural complexity create a network of combined influence on the genetic diversity of a coral reef site (Selkoe et al., 2016). Furthermore, species interactions also contribute to the aggregate genetic diversity of a site, as these interactions dictate what species are found where (Whitham et al., 2006). Some examples include the growth of coral influencing the diversity of associated fauna and the availability of prey species influencing the diversity of predator species.

Selkoe et al.'s (2016) study also showed that the genetic resilience of whole coral reef communities is threatened by factors that reduce coral cover or habitat availability. Their study showed that thermal stress on coral negatively correlated with genetic diversity. Even though this is only a correlation, it reflects previous research, which shows that thermal stress impacts coral by leading to increased Heat Shock Protein expression, elevated antioxidant production, disrupted calcium ion balance, restructured extracellular matrix, rearrangement of the actin cytoskeleton, decreased ribosomal protein expression, and activation of pro-apoptotic responses (Abrego et al., 2008; Barshis et al., 2013; Cziesielski et al., 2019; DeSalvo et al., 2010; Kenkel et al., 2013; Maor-Landaw & Levy, 2016). If these responses occurred in coral from Selkoe et al.'s (2016) study, this could explain the loss of overall genetic diversity. Furthermore, it highlights how other factors known to impact coral cover and availability, including acidification (Hill & Hoogenboom, 2022; Mollica et al., 2018), sedimentation (Erftemeijer et al., 2012), pollution (Edinger et al., 1998; Pastorok & Bilyard, 1985), cyclonic weather events (Guillemot et al., 2010; Madin et al., 2018), and destructive fishing practices (McManus et al., 1997; S. K. Wilson et al., 2010), may have knock-on effects for entire reef communities.

While Selkoe et al. (2016) shed light on broader coral reef community genetic diversity, insights from Underwood et al. (2018) offer a more fine-scale perspective on the genetic diversity of coral species. Their decade-long study across tropical Australia shows that, despite cyclones and severe bleaching events, high levels of genetic diversity persist in the sampled corals. However, this resilience is not uniform across all species. These results, when considered alongside the aforementioned responses in coral when subjected to stress events, demonstrate the importance of in-built mechanisms in some coral species that enhance their evolutionary resilience to environmental factors. Furthermore, Underwood et al.’s (2018) study challenges the results of Selkoe et al. (2016) in that stressful events to coral may not have widespread negative impacts on genetic diversity. However, a limitation of Underwood et al.’s (2018) study is that they only focused on one species of coral, with differences in results at different spatial scales. These limitations demonstrate that some coral in certain areas may have some resilience, but it is crucial not to assume that this is ubiquitous across all coral species worldwide (Voolstra et al., 2023). It should, therefore, be a priority to support natural resilience in coral reefs and protect other species by mitigating and minimising man-made pressures that impact reef structural complexity, coral cover, and species interactions, and, subsequently, the overall health of coral reef ecosystems.

Structural complexity, coral cover, species interactions, and genetic diversity are important traits of coral reefs that act in unison, one influencing the other, to create coral reef ecosystems of high biodiversity. However, it is important to acknowledge the existence of other potential factors that may influence biodiversity. Future research spanning various temporal, spatial, and taxonomic scales on environmental and anthropogenic factors impacting coral reefs is essential. This research will help reveal the interconnectedness of these factors with coral reef traits and further uncover how changes to these coral reef traits will impact entire reef communities.

1.1.2 Coral reefs and coastal communities

Coastal communities benefit from an array of ecosystem services from coral reefs, many of which are integral to their livelihood and survival. These services include providing food, employment, income, economic revenue, and damage and risk mitigation. Furthermore, coral and the reefs they form are culturally significant to many indigenous people and local communities.

Gregg et al. (2015) gathered Native Hawaiian oral, material, and other indigenous ecological knowledge to describe some of the most significant cultural symbolisms and uses given to corals in Hawai'i. Through local perspectives and narratives, the cultural, ecological, and social relevance and importance of coral to the Native Hawaiian people can be accurately told; this methodology of collecting traditional knowledge directly from indigenous people and local communities is the best way to correctly convey the relationships that coastal communities have with coral reefs (Benner et al., 2021; Goulding et al., 2016; Todd et al., 2023). Gregg et al. (2015) discuss how, in the Hawaiian worldview, everything existing in the natural world, including ko'a (coral), possesses mana (spiritual energy) and is considered akua (a deity). The mele ko'ihonua (genealogical chant) entitled 'Kumulipo' tells of how Hawaiians recognised tiny coral larvae giving birth to the coral head; this chant is an example of Hawaiians observing the biological process of coral reef formation before western scientists (Dobbs, 2005). Mele (chants) and mo'olelo (stories) provide examples of coral playing significant roles associated with rebirth, healing, and the provision of food. Hawaiian proverbs ('ōlelo no‘eau) refer to coral as symbols of resilience and strength in the face of adversity due to their steadfast nature under adverse weather and sea conditions; these proverbs may be even more pertinent today as we try to understand the extent of their resilience to modern-day impacts.

Throughout the tropical Pacific, where coral reefs are a prominent feature of the coastal seascapes, many communities from different nations have their own unique cultural significance for coral. Around New Georgia Island in the Western Province of the Solomon Islands, coral reefs serve as navigational features, areas for resource extraction, signs that define property rights, and certain reefs embody tribal ideologies and identities (Aswani, 2014). In north-eastern Australia, the Great Barrier Reef has been under the guardianship of Aboriginal and Torres Strait Islander traditional owners for millennia (Australian Government, n.d.). These traditional owners of the Great Barrier Reef cared for the reef by weaving their spirituality, culture, and traditional ecological knowledge with sustainable utilisation, resulting in Aboriginal and Torres Strait Islander descendants today holding a strong cultural affiliation with the reef (Australian Government, n.d.). Over in Raja Ampat, West Papua Province, Indonesia, one person talks of how, even though they did not attend school, they learnt the importance of coral through knowledge passed down from their elders (Prasetyo et al., 2020). They understood that all living things of the ocean have souls like humans and there are parallels between humans living in houses and fish living in coral; if the coral is damaged, the biota that depends on it will not be able to find shelter and food and lay their eggs (Prasetyo et al., 2020). Globally, where coral is found, indigenous people and local communities have not only historically depended on the coral reefs for their livelihood but have developed a significant cultural and spiritual relationship with the reefs and the coral itself.

An estimated 6 million people in 99 countries directly depend on coral reef fisheries for their livelihood (Teh et al., 2013). An overwhelming number of these countries are developing, and one study estimates that, in these developing countries, reef fisheries contribute to one-quarter of the total fish catch (Jameson et al., 1995). Coral reef fish are an important source of protein and nutrients, making up more than half of the essential protein and mineral intake for over 400 million people living in some of the highest poverty countries in Africa and South Asia. Furthermore, coral reef fish account for 50-90% of protein in some rural communities of the Pacific (Bell et al., 2009; Cinner, 2014; Dulvy & Allison, 2009; Kawarazuka & Béné, 2010).

Coral reefs provide not only sustenance but also employment through the fisheries or tourism sectors. This employment provides income and, subsequently, means coral reefs are of national economic value. Giving coral reefs a monetary value is a helpful way to underscore their economic importance, incentivise conservation efforts, and raise awareness about the benefits they provide to communities (Lachs & Oñate-Casado, 2020). Methods to evaluate coral reef ecosystems produce different results (Brander et al., 2007; Cesar et al., 2003; Craig, 2008; Laurans et al., 2013), but Lachs and Oñate-Casado (2020) found that the standardised method of Cesar et al. (2003) best provided insight into the estimated worth of coral reefs. Incorporating four major ecosystem services (fisheries, coastal protection, tourism, and biodiversity maintenance), coral reefs provide an estimated US$ 30 billion in net beneficial goods and services to the global economy every year (Cesar et al., 2003). Notably, the value of reef fisheries ranked the lowest among these ecosystem services, accounting for US$ 5 billion. Reef biodiversity, through conservation, research, and medical value, was estimated at US$ 5.5 billion, and the value of coastal protection was estimated at US$ 9 billion. Tourism emerged as the highest-ranking service, with an annual global value of US$ 9.6 billion (Cesar et al., 2003). These values are significant when considering that around 60% of coral reefs are located in developing countries (Ban et al., 2011; Donner & Potere, 2007), and the employment, income, and revenue generated (either directly or through mitigating property damage) from these services can directly impact coastal communities.

Damage and risk mitigation represent a crucial aspect of the significance of coral reefs to coastal communities. Essentially, coral reefs provide coastal protection through the dissipation of wave energy through the friction of the reef structures (Gourlay, 1996; Hearn, 1999; Lugo-Fernández et al., 1998; Monismith et al., 2015; Reguero et al., 2018; Sheppard et al., 2005). The high structural complexity of a coral reef results in the frictional dissipation of wave energy over a relatively short distance (Lowe et al., 2005; Nelson, 1994; J. S. Rogers et al., 2016), allowing human populations to settle on tropical coasts (Ferrario et al., 2014). The degradation of benthic structural complexity could lead to a significant increase in wave height, leading to coastal erosion and property damage to coastal communities (Ferrario et al., 2014; Harris et al., 2018). However, it is important to consider that coastal communities are subject to additional threats that cannot be extinguished by coral reefs, including high-energy weather events such as cyclones, storm surges, and tsunamis.

One notable area of high coral reef cover and high dependency of communities on coral reefs is the Coral Triangle (Burke et al., 2011). The Coral Triangle encompasses tropical water in the South Pacific from Malaysia to the Solomon Islands, only covering a mere 1.6% (~6 million km^2) of the world's total ocean surface area. Comparative to its small size, it is estimated to contain 37% of all reef fishes (Allen, 2008), over 76% of all shallow-water reef-building coral species (Veron et al., 2009), and the world’s largest mangrove forest (Polidoro et al., 2010). The Coral Triangle is thought to support the livelihood of over 120 million people, many of whom are from countries with low socio-economic status (Burke et al., 2011).

The Solomon Islands is one country within the Coral Triangle with high coral reef-associated biodiversity and a heavy dependence on coral reefs (Veron et al., 2009). Burke et al. (2011) found that the Solomon Islands scored high or very high for all six indicators of coral reef dependency (reef-associated population, fisheries employment, reef-derived nutrition, reef-derived exports, reef tourism, and shoreline protection). In the same study, the Solomon Islands was also one of the lowest-scoring countries for adaptive capacity to reef degradation and loss, meaning the country may face significant challenges in addressing and mitigating the impacts of reef degradation on their livelihoods. Furthermore, the Solomon Islands are classified as a United Nations Least Developed Country; they exhibit the lowest indicators of socioeconomic development, including low income, weak human assets (such as low education and health levels), and economic vulnerability (United Nations Conference on Trade and Development, n.d.). The Solomon Islands and other similar tropical countries depend greatly on the ecosystem services provided by coral reefs, and their livelihood directly depends on the health and diversity of their local coral reef ecosystems.

1.1.3 Threats to coral reefs

Coral reefs are delicate ecosystems that are susceptible to minute stressors, natural or anthropogenic. Hermatypic corals thrive in a specific range of environmental conditions, requiring warm, light-intense, low-nutrient waters with a specific range of salinity and other inorganic compounds (Guan et al., 2015). Disruptions to these conditions can cause changes in coral reef fitness, health, and survival, consequently impacting both the reef biota and the people who depend on it (Anthony et al., 2007; Coles & Jokiel, 1992; Diaz-Pulido et al., 2009; Lesser, 2004). Disruptions operate on local and global scales, and only 6% of the world's coral reefs are estimated not to be affected by stressors (Guan et al., 2020). Furthermore, some of these stressors are naturally occurring, and some are caused or exacerbated by anthropogenic influence. Finally, some threats are direct and specific, such as damaging fishing practices (H. E. Fox & Caldwell, 2006), whereas others are indirect and broad and often a result of accumulative factors over time, such as the effects of the changing climate on disease, distribution or viability of certain coral species (Howells et al., 2020; C. J. Randall & Van Woesik, 2015).

Pollution also threatens coral reefs; it can occur further inland and be washed toward the sea or deposited directly onto the reef. Coral reef pollutants can originate from agricultural, urban, industrial, shipping, landfill, and accidental sources (Negri et al., 2011). For example, an large quantity of coral deaths on the Great Barrier Reef are attributed to nutrient pollution, namely from the agricultural sector (Brodie et al., 2013; Robinson et al., 2016). In Indonesia, line-intercept transect surveys of 15 reefs showed that reefs subject to land-based pollution (including sewage and industrial pollution) showed up to a 60% reduction in diversity (Edinger et al., 1998). Globally, other sources of pollution include the thousands of commercial and recreational vessels that pass near coral reefs daily. Pollutants include contaminated bilge water, fuel, sewage, solid waste, and invasive species.

Destructive practices, including blast fishing, anchor damage, and ship groundings, cause acute damage to coral reefs. Edinger et al.'s (1998) study found that bombed or anchor-damaged reefs are up to 50% less diverse than undamaged reefs in the same region. In the Philippines, reefs have lost coral to blasting, sodium cyanide, and coral-grabbing anchors, decreasing the potential coral recovery rate by about one-third (McManus et al., 1997). Recurrent destructive practices can impact the ability of coral to recover, reducing their resilience to natural perturbations and leading to the formation of coral assemblages characterised by small, sparse corals (H. E. Fox & Caldwell, 2006; McManus et al., 1997).

Global warming and ocean acidification are compounding the already present threats impacting coral reefs, and historical coral reef biodiversity crises seemingly coincide with episodes of warming temperatures and ocean acidification (Kiessling & Simpson, 2011). As atmospheric carbon dioxide (CO_2) increases, carbonate ions (CO_3^{2-}) in seawater decrease, resulting in lower calcium carbonate ($CaCO_3$) production by corals; this may lead to reef erosion exceeding reef accretion across much of the tropic and sub-tropical region (Hoegh-Guldberg et al., 2007; Kiessling & Simpson, 2011; Silverman et al., 2009). In this scenario, the resulting reefs will be less structurally complex, supporting less diverse reef communities. Furthermore, ocean acidification is predicted to reduce the skeletal density of some coral species, leaving them more susceptible to bioerosion, dissolution, and anthropogenic and natural damage (Madin et al., 2012; Mollica et al., 2018; Sammarco & Risk, 1990; van Woesik et al., 2013).

Ocean warming takes coral beyond its upper thermal limit, with the resulting thermal stress disturbing the coral-algae symbiosis, leading to coral bleaching. Bleaching is a phenomenon where coral will expel their symbiotic zooxanthellae, causing the coral to turn white. The coral is not immediately dead upon zooxanthellae expulsion and can survive short-term bleaching events. However, given that zooxanthellae are the primary source of endogenous nutrients for the coral, they are under more stress in a bleached state, meaning they are more susceptible to stressors, resulting in higher mortality rates amongst bleached coral (Bruno et al., 2007; Lough et al., 2018; Matsuda et al., 2020). However, some corals have a level of adaptive capacity and differing levels of sensitivity to different factors. For example, reefs that have experienced past thermal stress are more likely to recover from another thermal stress event versus reefs that have experienced historically stable temperatures (Guest et al., 2012; Matsuda et al., 2020).

Finally, land-use change, specifically sedimentation, threatens the health and fitness of coral reefs (R. Jones et al., 2016; McCook et al., 2015). The effects of sedimentation on corals include decreased growth by shading and abrasion (Dodge & Vaisnys, 1977; Humanes et al., 2017; Miller & Cruise, 1995; Riegl & Branch, 1995; C. S. Rogers, 1990; Rushmore, 2016), changes in zooxanthellae-inducing photosynthetic activity (Philipp & Fabricius, 2003), increases in respiration and mucous production (Abdel-Salam & Porter, 1988; Bessell-Browne et al., 2017; Ricardo et al., 2016; Telesnicki & Goldberg, 1995), reductions in reproduction, larval settlement, and larval survival (Gilmour, 1999; Richmond et al., 2018; Te, 1992), and, ultimately, death by smothering (Fabricius & Wolanski, 2000; Marszalek, 1981; Nugues & Roberts, 2003). These effects vary depending on the location of the coral, as deep-sea or outer reef corals may not experience the same land-based sediment exportation that in-shore and mid-shore corals experience. Coral adaptations to survive temporary increases in sedimentation, such as zooxanthellae expulsion and mucous excretion, prove successful in combatting short-lasting sedimentation events; however, prolonged periods of high sediment input from anthropogenic activities, including dredging and logging, prove detrimental to coral reefs (Erftemeijer et al., 2012; Hamilton et al., 2017; Wenger et al., 2020).

Corals and the reef habitats they comprise are crucial for coastal communities, indigenous people, and the biota that they support. Escalating instances of coral bleaching, diseases, destructive practices like blast fishing, and the insidious impacts of pollution and sedimentation contribute to the alarming decline in live coral cover and habitat complexity worldwide. The subsequent loss of the architectural complexity of the reef is intricately linked to a reduction in the abundance and diversity of associated reef organisms (Alvarez-Filip et al., 2009; Graham et al., 2006; Graham & Nash, 2013;

Walker et al., 2009). Disturbance events, intensified by climate change, further exacerbate this decline, fostering homogenised coral assemblages dominated by stress-tolerant species and resulting in significant declines in 3D structural complexity (Burns et al., 2019; Darling et al., 2013; Pratchett, Trapon, et al., 2011; Richardson et al., 2017). These threats not only harm the delicate balance of coral reef ecosystems but may have repercussions across coastal communities and economies globally, emphasising the need for research into the consequences of anthropogenic impacts on coral reefs.

1.1.4 Indicators of ecosystem health

Numerous intricate processes play pivotal roles in managing the vitality and functionality of coral reefs, encompassing trophic interactions, nutrient cycling, productivity, bioerosion, predation, and herbivory. (Brandl et al., 2019). Studying these processes can help identify indicators of ecosystem health, which can then be used as proxies to understand stressors on coral reefs from intrinsic and extrinsic drivers (Brandl et al., 2019; Graham et al., 2015; Graham & Nash, 2013).

Substantial research has been focused on herbivory, one of the intrinsically driven coral reef processes between the coral reef matrix and associated fauna (Brandl et al., 2019). Herbivorous organisms in a coral reef ecosystem place top-down control on macroalgal communities by consuming the fleshly macroalgae and controlling their populations beneath a certain threshold (Burkepile & Hay, 2006; Cernohorsky et al., 2015; Mumby et al., 2007; Poore et al., 2012; Roff & Mumby, 2012; Williams et al., 2001). Without this control, macroalgal density and abundance increase; in high enough numbers, macroalgae have the ability to outcompete corals and hinder their re-colonisation (Bruno et al., 2009; Cernohorsky et al., 2015; Jessen & Wild, 2013; Mumby et al., 2016; Rasher et al., 2012; Smith et al., 2010). An experiment by Suchley and Alvarez-Filip (2017) found that coral that were completely excluded from herbivorous fish had macroalgae covering almost half of their structures, whereas coral exposed to herbivorous fish had almost absent macroalgae growth. Furthermore, calcification (growth) of coral was suppressed by almost half in herbivory-excluded coral, showing coral growth as negatively correlated to macroalgae growth (Suchley & Alvarez-Filip, 2017). The findings of this study build on previous research demonstrating a negative relationship between fish grazing and macroalgae distribution, supporting the idea that herbivory influences algae community structure (Adam et al., 2011; R. J. Fox & Bellwood, 2007; Mumby, 2009). This body of research provides meaningful data on the importance of herbivorous reef fish for the ecosystem functioning of coral reefs and highlights areas for future research to investigate the relationship between other animal foraging strategies and coral reefs.

The main driver of herbivory, and indeed, most coral reef processes, is the behaviour of biota within the coral reef matrix; therefore, analysis of assemblage dynamics, such as species abundance, distribution, and physiology, can be used as indicators to measure coral reef ecosystem functioning and health (Chong-Seng et al., 2012; Grottoli et al., 2018; Illing & Rummer, 2017; Khalil et al., 2013).

However, a study by Díaz-Pérez et al. (2016) found fewer correlations than would be expected between indicators of coral reef health and metrics of biology, ecology, and diversity of fish populations. These results contrast with other studies that show healthy corals supporting higher abundances of fish (Noonan et al., 2012) and species abundance and functional groups changing as corals degrade and die (Huang et al., 2023). Díaz-Pérez et al. (2016) used two coral reef health indices to validate their results, whereas other studies only used measurements of coral structure and observations of coral health. The findings of Díaz-Pérez et al. (2016) shed light on a previously overlooked aspect, suggesting that the conventional methods of using fish population dynamics to assess coral reef health may need revaluation. This study highlights the need to complement basic coral reef fish biology, ecology, and population metrics with other, more fine-scale metrics to improve accuracy. For example, evidence suggests that predatory shark growth rates are slower in 'pristine' ecosystems when compared to sites exposed to anthropogenic impacts (Bradley et al., 2017; Papastamatiou et al., 2009; Stevens & McLoughlin, 1991). Future research should investigate the validity of using animal life history traits and potentially other variables, such as animal behaviour, to complement current assessment methods or even as a proxy for ecosystem health and functioning, especially in coral reef ecosystems.

Goatley et al. (2016) argue that we should move beyond visible and obvious environmental changes and explore other fine-scale factors to identify at-risk ecosystems. Their study of an inshore coral reef on the Great Barrier Reef following severe climatic disturbances demonstrates that the herbivorous reef fish community biomass or present functional groups did not change. However, intrinsic, fished-related ecosystem processes showed significant changes, including a decline in herbivorous grazing by over 90%. While declines in coral cover and/or macroalgae are commonly used to assess reef health, Goatley et al. (2016) argue that these more obvious signs are often visible too late in the degradation process. There is an urgent need for future studies to investigate and validate sensitive, fine-scale metrics, such as grazing and bite rates, as effective ecological tools in detecting subtle degradation signs on coral reefs. This way, at-risk coral reefs can be identified for future conservation strategies, and intervention can occur earlier than it would otherwise (Abelson et al., 2016; Lirman & Schopmeyer, 2016).

1.2 Insights from animal behaviour studies

One possible metric to investigate indicators of ecosystem health and function is animal behaviour. The term ‘animal behaviour’ is very broad and encompasses perhaps everything an animal does throughout its lifetime. In a more general and intuitive sense, the term ‘animal behaviour’ is best summed up by Manning and Dawkins (1998):

> It is about the chase of the hunter and the flight of the hunted. It is about the spinning of webs, the digging of burrows, and the building of nests. It is about incubating eggs and suckling young. It is about the migration of a hundred thousand animals and the flick of a tail of one. It is about remaining motionless and concealed as well as about leaping and flying. (p. 1)

Indeed, animal behaviour includes a plethora of behaviours, including the non-random spacing in a gannet colony, the similarities in sequences of feline play and predation, bees foraging for pollen, the sexual advertisement of frogs at a breeding pond, the parental investment of a mother spider monkey, the percussive communications of a bottlenose dolphin, the group living of a flock of grazing pink-footed geese, the list goes on (Huntingford, 1984; Lusseau, 2006). Arguably, all these behaviours stem from a primitive drive to survive. At its core, survival includes consuming nutrients, avoiding injury, resting, thermoregulation, and successful reproduction through the survival of genes beyond inevitable death.

Environmental change can induce a behavioural response in individuals of a population either directly or indirectly through manifested physiological changes (Rahman & Candolin, 2022). For example, receding ice sheets due to climate change have caused polar bears (*Ursus maritimus*) to shift their foraging locations and prey habits from hunting seals on the ice to foraging ashore on land-based prey that includes caribou (*Rangifer tarandus*), snow geese (*Chen caerulescens caerulescens*), and waterfowl eggs. In a lab-based study, warming water and air had different effects on the predation rate of the intertidal northern striped dogwinkle (*Nucella ostrina*) (Yamane & Gilman, 2009). Increased predation behaviour was observed in higher water temperatures, but decreased predation behaviour was observed in higher air temperatures, demonstrating different behavioural responses depending on the environmental variable that has changed (Yamane & Gilman, 2009).

Anthropogenic disturbances also invoke behavioural responses in animals. Rapid human population growth and urbanisation in the Florida Keys over the past 30 years has led to a change in habitat choice for the Key deer (*Odocoileus virginianus clavium*) (Harveson et al., 2007). Furthermore, Harveson et al. (2007) found a significant negative relationship between flight distance and deer utilisation of urban areas, highlighting the potential for domestication measures to be used as a proxy for the impact of urbanisation on wildlife. A different study by Bonte and Van Dyck (2009) investigates the effect that the logging and deforestation of tropical cloud forests has on a species of forest butterfly (*Salamis parhassus*). In fragmented and deteriorated forests, the butterfly changed to a patrolling strategy over the typical perching strategy when locating a mate (Bonte & Van Dyck, 2009). This behavioural change results in higher mobility of the butterfly as they try to occupy light gaps faster. This is another example where fine-scale study of animals that rely on a specific variable (in this example, light) can elucidate changes in their environment. Another study by Frid et al. (2008) explores the theoretical idea that the removal of the Pacific sleeper shark (*Somniosus pacificus*) from an ecosystem due to fishing-related mortality can indirectly influence predation pressure on certain fish species. The model predicts the behavioural responses of harbour seal (*Phoca vitulina richardsi*) predation on Pacific herring (*Clupea pallasii*) and walleye pollock (*Theragra chalcogramma*). The seals feed on the herring that inhabit the surface waters (Thomas & Thorne, 2003) because the more predictable food source (pollock) is located in deeper strata, which is a preferred habitat of the sharks (Frid et al., 2007; Hulbert et al., 2006; Trumble et al., 2003). Seals exhibit risk-management behaviour in scenarios where shark populations are prevalent; however, shark removal scenarios lead to a behavioural change in seal movement and foraging as they shift from a herring-based diet to a pollock-based diet that requires them to hunt at deeper strata (Frid et al., 2008). These results show that mesopredator diet can indicate anthropogenic impacts, such as fishing, that reduce predator populations and highlights the need for in-field and diet analysis studies to verify model-based predictions.

These specific examples underscore the broader concept of using animal behaviour as an indicator of ecosystem health. The observed shifts in behaviours, whether prompted by climate change, anthropogenic disturbances, or habitat alterations, collectively emphasise the intricate relationship between environmental shifts and the responses of individual species. This reveals a novel approach for evaluating ecosystem health and anticipating degradation by adopting a reverse perspective on studying animal behaviour. Gathering data on animal behaviours and their responses to environmental changes lays the groundwork for understanding how environmental and anthropogenic influences impact animal interactions within an ecosystem. Carefully scrutinising these subtle behavioural nuances at a more detailed level has the potential to identify shifts in behaviour that precede a notable decline in ecosystem health. This, in turn, enables us to model and anticipate forthcoming changes. Consequently, studying animal behaviour emerges as a dual-purpose endeavour, offering insights into the assessment of current ecosystem health and predicting future degradation. Through this lens, the study of animal behaviour becomes not just an observation of the natural world but a pivotal tool for informed decision-making, particularly concerning the future management and conservation of important and vulnerable ecosystems.

For this novel approach, one must consider the reasons behind behavioural responses. Sih (2013) proposes a conceptual framework for behavioural responses. First, Sih (2013) proposes animals have evolved a set of rules that they use to make quick decisions when faced with something different in their system. We can use this as an advantage if we want to use behaviour as a proxy for ecosystem health; if we know they will rely on a behavioural change under a specific circumstance, we can anticipate that behaviour, which can direct future research. Next, Sih (2013) suggests that the degree of behavioural flexibility in an organism, whether it is a generalist (adaptable to various conditions) or a specialist (specialised for specific conditions), influences its response to novel situations. Generalists might be more adaptable to changes, while specialists may struggle with new environmental conditions, highlighting the importance of choosing species from different functional groups within a taxa. This is reflected in a study on the feeding ecology of rabbitfish (Genus *Siganus*) by Ebrahim et al. (2020), whose results demonstrate the difference in bite rates between generalist and specialist species. Finally, Sih (2013) introduces the idea that evolutionary processes have selected behaviours advantageous in historical environments, including predation or temperature changes. This highlights the importance of looking at animal behavioural responses to both naturally and anthropogenically (modern) influenced changes within ecosystems.

Fish behaviours tend to be simpler than those of socially dynamic and cognitively advanced taxa (Goldenberg & Wittemyer, 2020; Kuczaj & Eskelinen, 2014; Wiper &

Semple, 2007); typically, fish behaviours involve locomotion, foraging, feeding, anti-predator behaviour, spawning and breeding behaviours, parental behaviours, and social organisation (for example, pairing or schooling) (Keenleyside, 1979). Stimulants for these behaviours may be intrinsic to the animal (for example, hunger (Morgan, 1988)) or extrinsic, such as courting from a conspecific (Endler, 1987), a roaming predator (Domenici, 2002; Lönnstedt et al., 2012), or environmental changes (Sandlund et al., 2017).

As previously mentioned, these behaviours can be examined to provide information about the environment that the fish is in. A review by Whitfield and Elliott (2002) discusses how anthropogenic factors can directly impact various aspects of estuarine habitats, including salinity, temperature, turbidity, river flow, and tidal exchange. In response, these environmental changes can directly or indirectly change fish distribution, diet, growth, recruitment, predation, competition, abundance, and biomass. Whitfield and Elliott (2002) examine the rationale for using fish as bio-indicators as they respond to human-induced changes in estuaries and potentially other aquatic environments. For example, Sabetian et al. (2021) use the elemental chemistry profiles of snapper (*Chrysophrys auratus*) otoliths to examine movement patterns as ecological indicators of nearshore nursery quality.

A study by Persson and Nilsson (2007) looked at how the feeding behaviour of benthic fish can be used to understand the condition of shallow lakes. Benthivorous fish contribute to the turbidity of shallow lakes through the resuspension of sediment by foraging on benthic invertebrates. Persson and Nilsson (2007) suggest ongoing monitoring of the foraging behaviour of benthivores because a high giving-up density and larger maximum benthivore size indicate high habitat quality (Blindow et al., 2006). Therefore, changes in the foraging behaviour of benthivorous fish, specifically correlated with maximum size, may serve as an early detection tool for ecosystem change in shallow lakes.

Indeed, there is growing evidence for the theory that fish behaviour may be used as a proxy for ecosystem health, with the strongest contender for a behavioural variable being foraging. In coral reef ecosystems, the reef matrix closely influences how fish move and forage in their environment (Eggertsen et al., 2019). Studying the interactions of coral reef-associated fish and the reefs they inhabit provides insights into the ecosystem's health, as species that rely on the reef for survival are most affected by changes influencing the reef. Studies focusing on fish foraging on coral reefs are important in unlocking the relationship between coral reefs and the fish that inhabit them (Ebrahim et al., 2020; Francini-Filho et al., 2010).

1.3 Target species: Genus *Chaetodon*

The best way to study fine-scale foraging patterns of reef fish is to study fish that are closely associated with the reef itself. Among herbivorous fish, families including Labridae, Acanthuridae, and Chaetodontidae contribute substantially to coral reefs through their foraging behaviour. The Labrid subfamily Scarinae (parrotfish) mainly consumes cyanobacteria and other autotrophic microorganisms (Clements et al., 2016). After scraping the substrate during foraging, they digest the edible components and excrete the substrate as sand, simultaneously preventing algal overgrowth and contributing to sand distribution in the reef biome. Acanthuridae (surgeonfish) typically consume turf algae, such as algae growing on coralline crustose algae (CCA), likely facilitating the growth of reef-cementing CCA and maintaining macroalgal growth (Duran et al., 2019). Chaetodontidae (butterflyfish) have a broad range of foraging behaviours, from specialist corallivores to generalists consuming algae and a wide variety of marine invertebrates (Berumen & Pratchett, 2008; Chandler et al., 2016; Liedke et al., 2016). The name Chaetodon translates from Greek, chaite meaning hair and odus meaning teeth, referencing their bristle-like teeth.

For this study, we decided to focus on butterflyfish as our target genus due to the diversity of their foraging behaviours amongst species, their prevalence at our research site, and their ease of identification. Furthermore, Lawton et al. (2012) theorise that the degradation of coral reefs is likely to affect the population structure of different species of butterflyfish depending on their feeding strategy (generalist versus specialist), and the study stresses the need for future research to assess butterflyfishes' sensitivity to environmental change.

Butterflyfish are a group of ray-finned fish and, generally speaking, grow rapidly, reaching asymptotic size within one to two years post-settlement (Berumen, 2005). Their maximum size and longevity are intermediate amongst other reef fish (Berumen et al., 2012; Munday & Jones, 1998). Butterflyfish fertilise externally, are gonochoric, and have a distinct planktonic larval phase (Choat & Bellwood, 1991). Some butterflyfish species employ a haremic mating system, but characteristically butterflyfish exhibit pair bonding, and pairs can often be seen patrolling a reef together (Whiteman & Côté, 2004).

Butterflyfish have strong associations with benthic, coral-dominated habitats (Halford et al., 2004; Harmelin-Vivien & Bouchon-Navaro, 1983; Pratchett et al., 2006). Research shows that >60% of coral reef fish species experience significant abundance declines following coral depletion (G. P. Jones et al., 2004; Pratchett, Hoey, et al., 2011; Sano et al., 1987). Butterflyfish responses to coral loss vary depending on space, time, and taxonomy (Pratchett et al., 2006); highly specialised obligate coral-feeding butterflyfish are among the first and worst affected, demonstrating their ability to be used as an indicator species for coral reef health (Pratchett et al., 2009; Pratchett, Hoey, et al., 2011; Pratchett, Munday, et al., 2008; S. K. Wilson et al., 2006).

To accurately represent a broad range of feeding modes within the scope of this study, we chose three abundant species of butterflyfish from different feeding guilds: *Chaetodon baronesssa*, *C. lunulatus*, and *C. vagabundus*.

1.3.1 *Chaetodon baronessa*

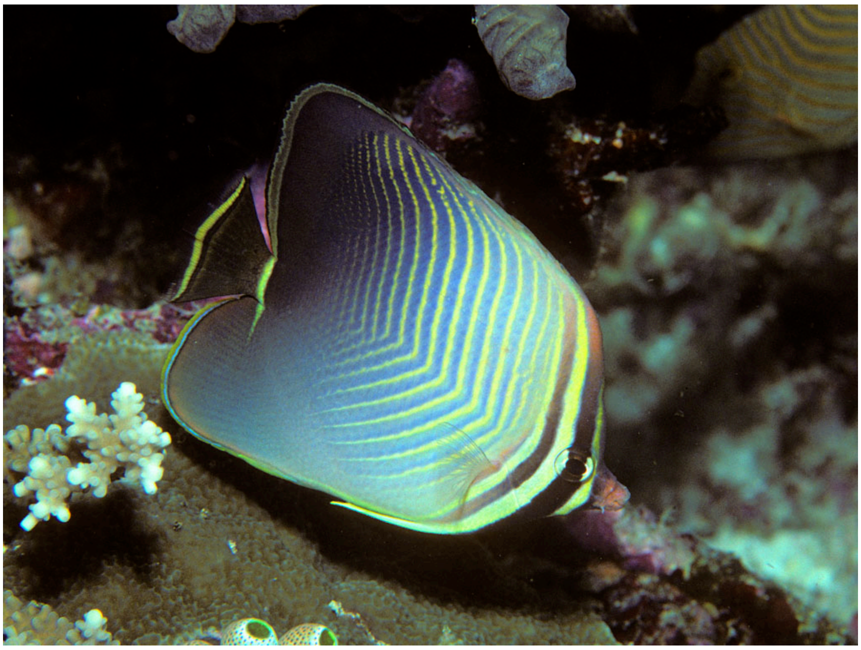
C. baronessa (Cuvier, 1836), or the eastern triangle butterflyfish, are predominantly yellow with a repeating, darker chevron-shaped pattern on their body, dark bars on the head, and a distinctive red beak (Figure 1.3.1.1). They grow to a maximum total length (TL) of 16 cm (Kuiter & Tonozuka, 2001) and can reach up to 12 years of age (Berumen, 2005). *C. baronessa* are distributed around the western Pacific and found in clear waters of fringing reefs (Rocha, Pyle, Myers, et al., 2010). Typically, adults of this species occur in pairs, actively driving away other butterflyfish that approach their food source (Nowicki et al., 2018; Steene, 1980).

C. baronessa are highly specialised obligate corallivores, feeding predominantly on the polyps of the tubular *Acropora* corals (Pratchett, 2005). When prey is abundant, they feed preferentially and almost exclusively on *Acropora* coral; however, when this coral species is scarce, they are less selective and consume a wider range of coral prey (Berumen et al., 2005). Interestingly, Berumen et al. (2005) found that their physiological condition worsens in areas where the quantity and/or quality of prey is not preferable, further demonstrating their highly specialised nature and dependence on *Acropora* coral.

Specific information on how *C baronessa*. forage and feed is not readily available. Gregson et al. (2008) determined the species' bite rate to be approximately 12 bites per minute.

Figure 1.3.1.1

*The Eastern Triangle Butterflyfish (*Chaetodon baronessa*)*



Note. By Bernard E. Picton, 1997, Wikipedia. (https://commons.wikimedia.org/w/index.php?curid=3288949). CC BY-SA 4.0.

1.3.2 *Chaetodon lunulatus*

C. lunulatus (Quoy & Gaimard, 1825), or the oval butterflyfish, are predominantly yellow with a repeating, darker horizontal striped pattern on their body, dark bars on the head, and red dorsal and anal fins (Figure 1.3.2.1). They have been reported to grow up to 26.7 cm TL (Akiona et al., 2022) and can reach 12 years of age (Berumen, 2005). *C. lunulatus* is found around the western Pacific in coral lagoons and reefs and is often seen as a pair (Nowicki et al., 2018; Rocha, Pyle, Craig, et al., 2010).

C. lunulatus is a generalist corallivore, feeding on many corals (Pratchett et al., 2004). Pratchett (2005) found that unlike *C. baronessa*, *C. lunulatus* also consume soft coral and macroinvertebrates; however, similarly to *C. baronessa*, physiological condition of *C. lunulatus* is worse in areas where the quantity and/or quality of prey is not preferable (Berumen et al., 2005).

Gregson et al. (2008) found the bite rate of *C. lunulatus* to be approximately 10 bites per minute. Their average bite rates were higher at midday and throughout the afternoon than in the morning (Gregson et al., 2008).

Figure 1.3.2.1

*The Oval Butterflyfish (*Chaetodon lunulatus*)*

Note. By Das Stealthwater, 2012, Wikipedia. (https://commons.wikimedia.org/w/index.php?curid=19784964). CC BY-SA 3.0.

1.3.3 *Chaetodon vagabundus*

C. vagabundus (Linnaeus, 1758), or the vagabond butterflyfish, are grey/white with two series of diagonal lines on their body, one dark, vertical band on their head, and a yellow posterior (Figure 1.3.3.1). Typically reaching 15 cm TL (Bouhlel, 1988), they can reach a maximum TL of 23 cm (Lieske & Myers, 1996). *C. vagabundus* is widespread, found in coastal coral reef habitats from the eastern Indian Ocean across the Pacific as far as French Polynesia (Myers & Pratchett, 2010). Adults of this species are often found in pairs around reef flats, lagoons, and even turbid waters subject to freshwater runoff (Froese & Pauly, 2023; Nowicki et al., 2018).

C. vagabundus are generalist omnivores, consuming hard and soft coral, algae, and invertebrates, including nematodes, nudibranchs, amphipods, sponges, hydroids, ascidians, and molluscan eggs (Narayani et al., 2015; Pratchett, 2005). Narayani et al. (2015) consider *C. vagabundus* foraging behaviour highly random, although Pratchett et al. (2013) recorded the species consuming coral genera approximately per its availability and seemingly not consuming specific coral genera. Their bite rate averages around six bites per minute but can reach 10 bites per minute (Berumen & Almany, 2009; Gregson et al., 2008).

Figure 1.3.3.1

*The Vagabond Butterflyfish (*Chaetodon vagabundus*)*

Note. By Dr. Dwayne Meadows, 2006, NOAA/NMFS/OPR, Wikipedia. (http://www.photolib.noaa.gov/htmls/reef0520.htm, Public Domain, https://commons.wikimedia.org/w/index.php?curid=2116071). Public Domain.

1.4 Study techniques: fish movement and foraging

Ecological studies focusing on the behaviour, movement, and life history of a marine specimen can be conducted through a range of techniques. Large-scale movement-based studies typically deploy tags onto individuals, including pop-up satellite archival, radio, acoustic, archival, and standard individual tags (Block et al., 2005; Francis et al., 2019; Koehn et al., 2009; Mitamura et al., 2008; Pursche et al., 2014; Skomal et al., 2017; Thorstad et al., 2014). These tags can provide specific information on horizontal and vertical movement and temperature fluctuations. Typically, tags are applied through surgical implantation, external attachment, or oral gastric insertion, all of which pose restrictions on the type of animal that can be tagged (Pursche et al., 2014). Larger, easier-to-catch or approach animals are great candidates for this methodology, which is not the case for chaetodontid fishes, who are quick, small, and wary of predators. Additionally, chaetodontids are closely associated with the reef matrix, so these tags are not fine-scale enough for a fish with relatively smaller movement patterns.

There is the potential for negative side effects when using more invasive methodologies. For example, a study by Lower et al. (2005) found increased cortisol release from carp (*Cyprinus carpio*) and roach (*Rutilus rutilus*) fish that had been surgically implanted with tags. This increased cortisol response has also been noted in marine mammals after various tagging methods (Harcourt et al., 2010). A study by

Hoolihan et al. (2011) found over half of all externally tagged pelagic fish species exhibited potentially irregular behaviour post-release, likely due to capture and handling stress. These behavioural changes have also been noted in penguins (*Pygoscelis* sp.) and green turtles (*Chelonia mydas*) fitted with external tags; external tags increase resistance in the water, resulting in decreased swimming speeds and increased energy expenditure (Bannasch et al., 1994; K. P. Watson & Granger, 1998). Together, not only do these impacts negatively affect the animals, but they may also skew the collected data due to the changes in stress and behaviour.

For a study that requires data collected on fish movement and foraging, it is necessary to both track the individuals and watch them forage, the latter of which cannot be done through tags alone. This data is typically collected by divers conducting transects, following fish and recording behaviours, or using BRUVs (Choat & Bellwood, 1985; Ebrahim et al., 2020; Nash et al., 2012). However, video recording is the best methodology for this as it enhances data accuracy by capturing information that can be analysed remotely. Video data can be collected through diver-operated cameras or stationary video camera set-ups. Branconi et al. (2019) highlighted that, when deciding between these methodologies, it is important to consider the specific behavioural data required for the study. Their research of the humbug damselfish (*Dascyllus aruanus*) found that fish behaviours occurring near coral were recorded more effectively by the scuba diver observer, while rapid or repetitive fish behaviour was captured more accurately from the stationary video camera set-up (Branconi et al., 2019). They also observed that scuba diver presence had minimal effects on fish behaviour when compared to fish behavioural data collected without a diver present (Branconi et al., 2019); however, some behavioural changes, including decreased feeding and increased flexion, yawning, and reproductive behaviours, could indicate that the fish perceives the diver as a threat (Gauff et al., 2018; Rasa, 1971). These results are similar to those of other studies that found invasive methodologies (BRUVs and diver-operated cameras) lead to varying results (Andradi-Brown et al., 2016; Cheal et al., 2021; D. L. Watson et al., 2010). Furthermore, Lester et al. (2020), found that mesopredatory reef fishes adjust their feeding behaviours in response to predators. This evidence emphasises the importance of limiting the exposure of the fish to potential perceived threats, such as humans, and invasions, like BRUVs, to reduce the chance of biased data.

Therefore, a stationary camera set-up is ideal to collect non-invasive fine-scale movement and foraging data of chaetodontids (Zamora, 2022). Video recordings from camera set-ups minimise human time in the field and allow for broader spatial coverage (Goetze et al., 2019). Furthermore, adding a stereo-video component increases the useability of the data. Stereo-video footage is recorded by two synchronised cameras from slightly different perspectives, enabling measurements to be taken of objects in the footage. This process, called videogrammetry, is more accurate than even experienced diver estimates of fish length (Harvey et al., 2001) and, furthermore, allows for three-dimensional tracking of fish movement.

López-Macías et al. (2023) compared measurement accuracy of two videogrammetric analysis software, VidSync (Neuswanger, 2008) and EventMeasure by SeaGIS (Jim Seager, 2006). Both software provided high measurement accuracy of a known length (López-Macías et al., 2023), and, furthermore, both software have been used effectively in studies to identify and measure fish species (Donofrio et al., 2018; Elliott et al., 2016; Neuswanger et al., 2016; Salinas-de-León et al., 2015; Unsworth et al., 2014; Zamora, 2022). The main difference between the two software is price; VidSync is free, open-source software whereas SeaGIS software and hardware costs are in the thousands (SeaGIS, 2024).

Reef fish foraging studies often attempt to sample multiple locations that cover a gradient in resource availability and habitat dynamic (Ebrahim et al., 2020; Francini-Filho et al., 2010); for example, sampling two different reefs, one that has been exposed to disturbance and one that is relatively "pristine" (Nash et al., 2012). One limitation of this methodology is that, by using data from independent locations, other influencing variables are introduced. One way to combat this is by finding a location that offers a gradient of resource availability and habitat dynamics in one location, for example, on one reef. Cooper et al. (2008) found that long-term turbidity levels exceeding certain thresholds lead to sublethal or severe stress effects on corals at shallow depths, showing that turbidity may be one contributing factor to declines in coral health. These findings are supported by Fabricius et al. (2012) who found that turbidity was the best predictor of changes in benthic community species composition and coral diversity and biomass. Turbidity refers to the amount of suspended particulate matter and organic compounds in the water column and their effect on light attenuation (Te, 1997; Fabricius, 2005), and, based on available evidence, turbidity appears to be a reliable and measurable variable that can be used as an indicator of coral reef health (Bejarano & Appeldoorn, 2013). Furthermore, despite occupying 12% of reefs globally (Sully & van Woesik, 2020), turbid coral reefs remain understudied. This data deficit is likely due to the logistical issue of working in conditions with such low visibility, leading to an inferior understanding of how these reefs function in comparison to their less turbid counterparts (Zweifler et al., 2021).

A methodology that utilises stereo-video camera set-ups on one reef subject to a gradient of turbidity would provide a comprehensive approach to unlocking fine-scale movement and foraging behaviours of target species amidst varying environmental conditions. By conducting observations within a single reef environment that exhibits a range of turbidity levels, we can more closely isolate the influence of turbidity on fish behaviour while minimising the confounding effects of other variables associated with different reef locations. This focused approach allows for a more thorough understanding of how fish respond to changes in turbidity within their natural habitat, providing valuable insights into their movement and foraging behaviours. Ultimately, such research contributes to the development of informed conservation and management strategies aimed at preserving the health and resilience of coral reef ecosystems.

1.5 Aim and objectives

Goatley et al. (2016) discuss how subtle, measurable changes in ecosystem metrics, such as fish movement and foraging, may be effective in detecting early ecosystem degradation. This is because such discrete changes may occur before more noticeable shifts, such as alterations to species abundance, occur. If coral reefs can be monitored for these small changes, at-risk ecosystems can be identified, and effective management decisions can be initiated sooner.

Thus, this research aims to explore the idea that fine-scale changes in movement patterns and foraging behaviour of coral reef fish can be studied to investigate coral reef ecosystems undergoing habitat change. Selecting two chaetodontids of varying intensity of specialisation and one chaetodontid that is a generalist omnivore allows this study to compare the effects of gradual changes in environmental variables on fish foraging and movement on one stretch of reef and how these changes impact fish differently depending on their adaptations.

The specific objectives of this research are to:

- Use stereo-video footage of butterflyfish (*C. baronessa, C. lunulatus*, and *C. vagabundus*) collected on a coral reef subjected to a turbidity gradient to obtain the species' foraging substrate preferences, bite rates, bite distances, and 3D tracking data.

- Compare movement and foraging behaviour between the species across sampling sites representing various turbidities.
- Provide insights into the methodology of stereo-video data collection to inform future research in this space.

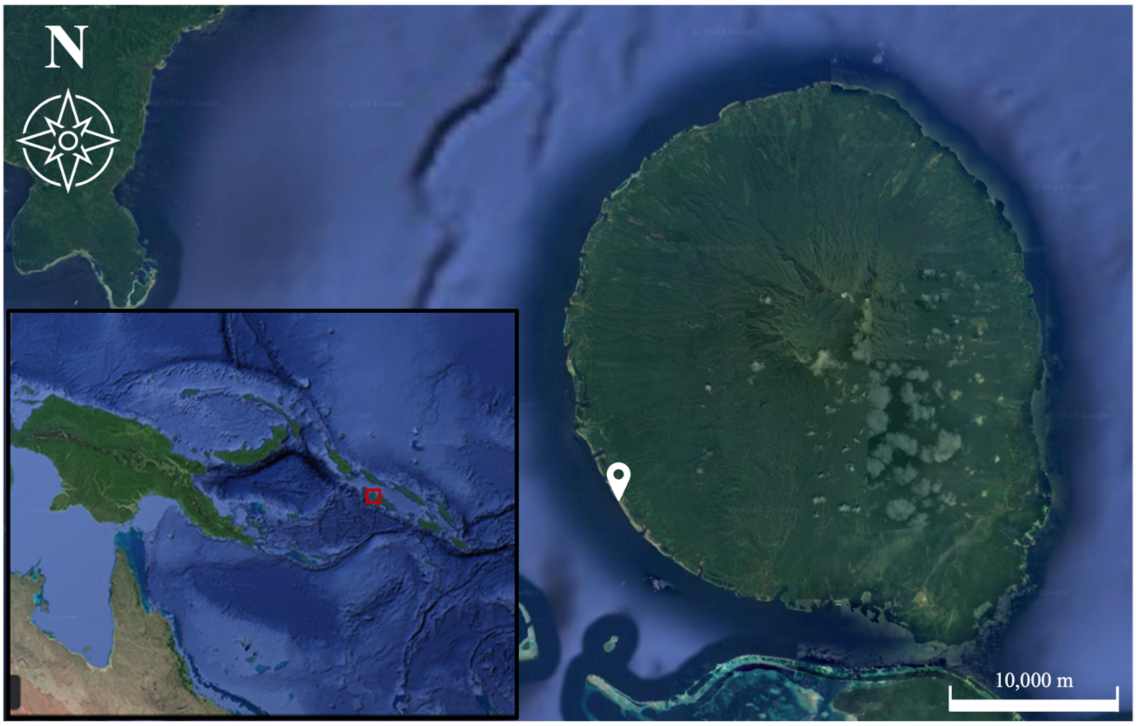
Chapter 2: Methodology

2.1 Location

This study was conducted on the reefs of Vavanga Village, located on the southwest coast of Kolombangara Island, Western Province, Solomon Islands (8°03’41” S, 156°58’05” E) (Figure 2.1.1). Kolombangara Island is a 30-kilometre-wide stratovolcano covered in montane rainforest, reaching an altitude of 1,770 metres above sea level. From its peaks run approximately 80 rivers and streams that feed into the surrounding ocean, reflecting its customary name in the local Nduke language: kolo (water) and bangara (chief/god). The island is encircled by fringing reefs that are regularly intersected by discharge from freshwater rivers.

Figure 2.1.1

Location of Vavanga, Kolombangara Island, Western Province, Solomon Islands



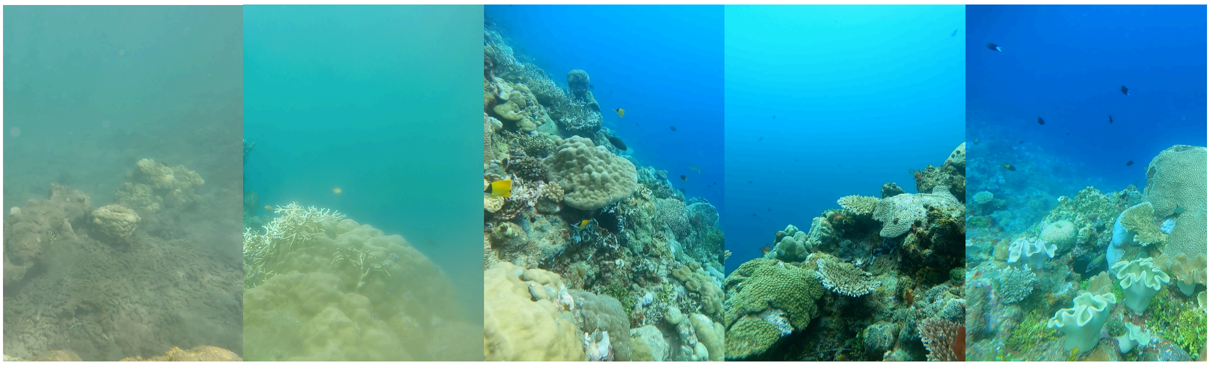
Note. Kolombangara Island is located within the red box (inserted image). Papua New Guinea and north-eastern Australia are located west and southwest of the Solomon Islands. The area of data collection for this research (Vavanga) is denoted by the white pin. From Google Earth. n.d. (https://earth.google.com).

Vavanga’s reefs are divided into a northern reef and a southern reef by the Vavanga River, its borders at both ends dictated by customary boundaries. The South Vavanga Reef is where we focussed our data collection. South Vavanga Reef (hereby referred to as “Vavanga Reef”) is characterised by a reef flat extending approximately 200 metres from the shoreline and averaging 0.8–2 metres in depth depending on the tide. This area is typical of reef flat substrate distribution, extending from a sandy beach covered with seagrass meadows to a more coral-dominated habitat seaward, culminating at the reef crest. The fringing reefs then begin with a gentle sloping fore-reef down to 10-15 metres, after which a near vertical reef wall zone begins and extends down to 50 meters, at which point hermatypic corals give way to sand and rubble, which extend down the seafloor. Hard coral cover is near 100% along the reef, but diversity and density do noticeably change in close proximity to the river mouth (Figure 2.1.2).

This location provided a suitable study site for multiple reasons. First, my supervisor, Associate Professor Armagan Sabetian, has longstanding ties with Vavanga Village and has spent over two decades fostering a reciprocal relationship with the community. Second, Solomon Islands reefs, particularly those found in the Western Province, are in relatively healthy condition, especially considering the stressors coral reefs encounter globally, including wave action and tsunami, crown-of-thorns starfish invasion, fishing pressure, and other anthropogenic factors (Cinner et al., 2016; Denley et al., 2020; White et al., 2014). Third, the Vavanga River feeds directly onto the adjacent reefs, bridging with it fluvial influence dominated by heavy terrestrial sediment input. This freshwater discharge creates a naturally occurring turbidity gradient that decreases with distance from the river mouth and increases again with proximity to the next river mouth (Figure 2.1.2). However, the coral reefs of Kolombangara Island have also been subject to historical and ongoing anthropogenic activity due to logging. Since the early 1900s, most of the island has been regularly logged up to 400 metres above sea level (Katovai et al., 2012). This anthropogenic activity has accentuated the naturally occurring turbid reef areas, especially at the river mouths. However, turbidity declines quickly away from the river mouths and leads onto long stretches of relatively thriving coral reefs. Kolombangara Island's diverse features, including Vavanga Reef, offer an ideal study site for examining species movement and foraging dynamics across a turbidity gradient on one continuous stretch of reef.

Figure 2.1.2

Photographs Taken Along Vavanga Reef



Note. Vavanga Reef, Kolombangara, Western Province, Solomon Islands. The reef is subject to both fluvial and anthropogenic sediment input as a result of logging activity resulting in a turbidity gradient along the reef. Photographs are ordered in increasing distance from the river mouth (left to right).

We obtained permission from the community leaders of Vavanga to utilise the reef for our non-invasive data collection activities. Throughout our fieldwork, we actively accommodated the local cultural customs, sometimes resulting in days when we refrained from data collection to show respect for these traditions. We maintained open and consistent communication with the village, engaging in various forms of knowledge sharing. This involved regular dialogues with indigenous guides to learn about fish identification and gain insights into the local environment. We actively participated in a community-wide meeting where we discussed our research objectives, answered questions, and sought their input. This collaborative approach not only ensured the suitability of the location for our study from both a data collection and cultural perspective but also fostered a harmonious relationship with the community.

2.1.1 Social and cultural background

Much of the Solomon Island’s population lives in rural areas (Solomon Islands Government, 2012), where access to natural terrestrial and marine resources is vital to their subsistence and artisanal existence. A report by Andersen et al. (2013) discusses how both terrestrial and marine resources in the Western Province of the Solomon Islands are abundant and provide a stable income and food source for local communities. However, resource availability is expected to diminish as fish supply decreases and global anthropogenic pressures increase (Cheung et al., 2010; Cinner et al., 2012). As food security is threatened, a rise in consumption of imported foods high in fat, salt, and carbohydrates and low in fibre will increase the prevalence of disease risk factors, including high blood pressure, high cholesterol, and high blood glucose (Alwan, 2011; Andersen et al., 2013). In the Solomon Islands, like many countries in the developing world, there is a disconnect between having enough nutritious food, reducing poverty, and protecting the environment (Adams, 2004; Hardy et al., 2013; Rice, 2011; Sanderson, 2005). Understanding the balance between external influences on natural systems and the need to use and safeguard those systems is crucial, especially in countries like the Solomon Islands, where challenges threatening food security and individual livelihoods persist (Hardy et al., 2013).

Customary Marine Tenure (CMT) constitutes a framework that facilitates, structures, and oversees the intricate interplay between coastal communities and the ocean (Hviding, 1996). CMT embodies a system of ancestral privileges, responsibilities, and rights, empowering individuals to effectively utilise marine areas and assert authority over specific territories and resource access (Lam, 1998). CMT plays a central role in Vavanga's relationship with the stewardship of their reef as it gives them the capacity to determine environmental outcomes and protect their livelihood (Aswani, 2002). However, Vavanga's reefs face local and global challenges that are beyond the community's control, such as the effects of nearby logging activities and climate change. These external influences undermine local tenure and threaten food security by changing the reef habitat and, consequently, have the power to alter animal movement patterns and behaviour. After using indigenous knowledge for generations to manage resources sustainably, abrupt ecological changes could make it difficult for indigenous people and local communities (IPLC) to anticipate and adapt. Historically, IPLC have used complex and highly localised knowledge systems about their natural world in response to environmental change (Hosen et al., 2020; Schlingmann et al., 2021). However, with emerging modern and global pressures, the integration of other knowledge sources aims to enhance the well-being and support communities like Vavanga (Makondo & Thomas, 2018).

2.2 Equipment and sampling

Our objective was to gather stereo-video data, requiring us to have equipment tailored for the software (VidSync) that we would use to analyse the footage (Neuswanger, n.d.). An 80x40 centimetre camera calibration frame was constructed in accordance with the software developer. Three racks (rack width: 1 metre; rack height: 0.5 metres) were constructed from steel bars, and camera mounts were clamped on either end (Figure

2.2.1). These three racks were named Rack 1, Rack 2, and Rack 3. Due to camera availability in the field, Rack 1 was allocated two GoPro Hero 5s in its mounts, and Rack 2 and Rack 3 were allocated two GoPro Hero 9s in each of their mounts. Each Go Pro camera had a 32 gigabyte SD card, capturing approximately 1.5 hours of video footage.

Figure 2.2.1

Steel Rack Used to Mount Stereo-Video Cameras

To estimate substrate cover, we fashioned a one-by-one-metre quadrat from plastic piping (Figure 2.2.5). We also used a GoPro Hero 9 to take overhead photographs of the underwater quadrat.

No sonde was available in the field, so other ways of quantifying marine parameters were developed using the available equipment. A 20-centimetre diameter Secchi disk was attached to a 100-metre measuring tape for underwater clarity observations; the Secchi disk provides a clear visual target underwater (Figure 2.2.2). One diver holds the Secchi disk and swims away from a second diver, who watches until the disk disappears from view and takes a measurement reading. Secchi disks are typically used to measure turbidity; however, we were unable to use this method because often we could see the bottom of the reef in the less turbid sites. So, an iPhone 12 Pro Max was used to access the EyeOnWater - Colour application to make observations on water colour in reference to the Forel-Ule Index (Figure 2.2.3) (Citclops, n.d.).

Figure 2.2.2

Secchi Disk and Measuring Tape Being Used to Ascertain Underwater Visibility

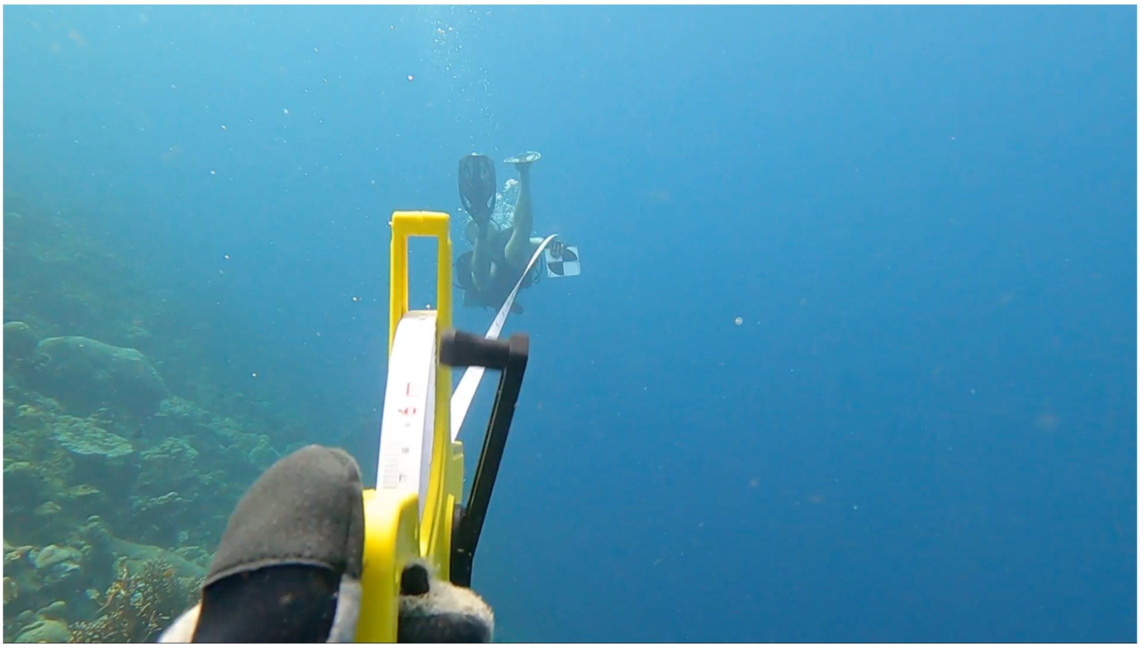


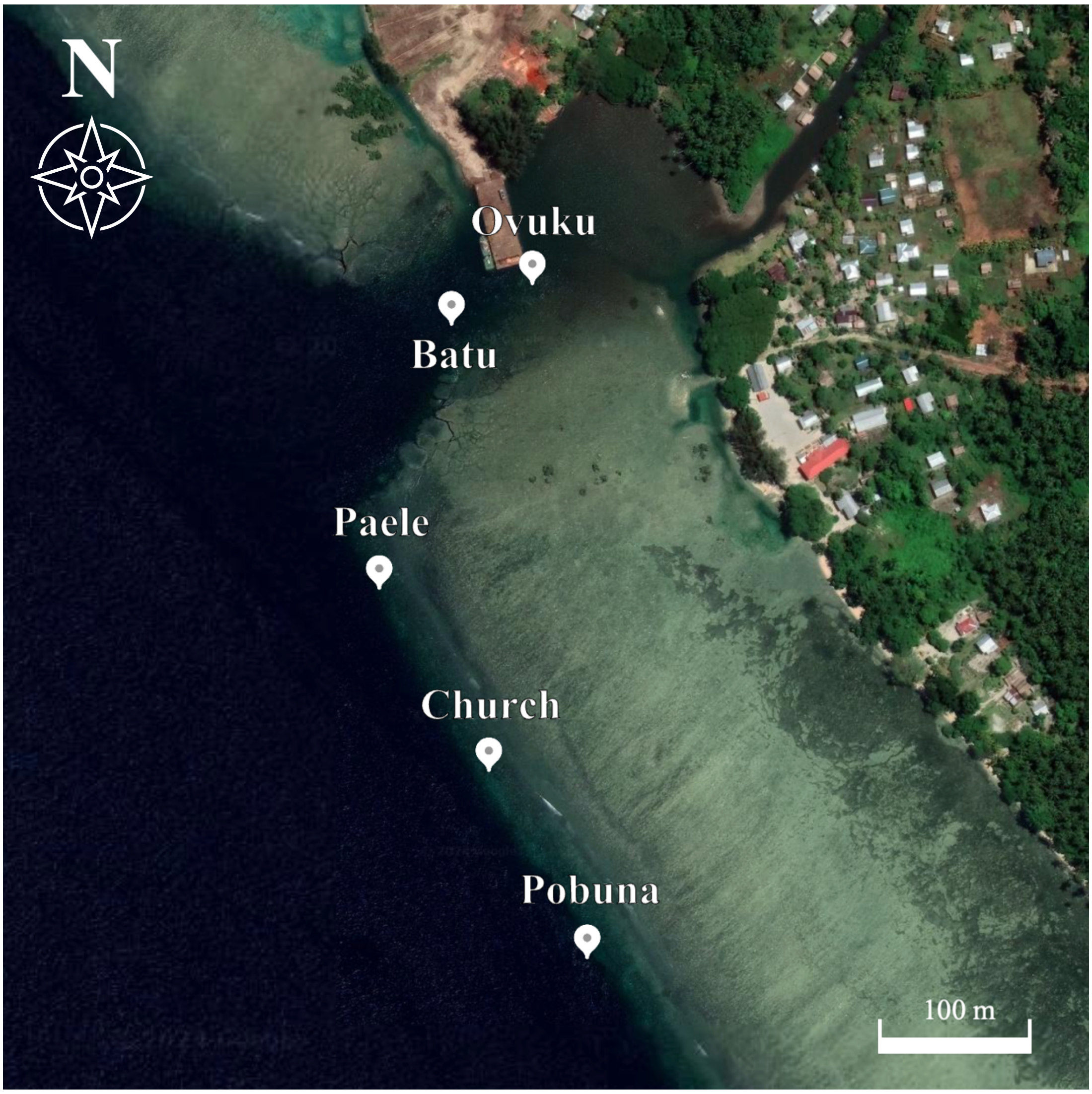
Figure 2.2.3

Forel-Ule Index of Water Colour

Sampling sites were selected by choosing five approximately equally distanced areas along the reef, starting in the river mouth, and then moving south away from the river (see Table A5 in the Appendix). This way, we could sample evenly along Vavanga Reef's turbidity gradient and the gentle sloping fore-reef allowed us to sample different depths at each site. Local guidance recommended locations based on identifiable landmarks that were relatively evenly spaced from one another (W. Laufanua, personal communications, January 2023). The sites were thus named based on these landmarks using local dialect. The site closest to the river mouth was named Ovuku (river mouth), then following was Batu (rock), Paele (meeting house), Church, and Pobuna (named after a detonated explosive that caused a dip in the reef) (Figure 2.2.4).

Figure 2.2.4

Location of Sampling Sites on Vavanga Reef, Kolombangara, Western Province, Solomon Islands



Note. The sites are named using Nduke dialect: Ovuku (river mouth); Batu (rock); Paele (meeting house); Pobuna (named after a detonated explosive that caused a dip in the reef).

We began sampling on the 5th of January 2023 and aimed to sample each site at least twice (three racks × two trips = six samples per site) until the 17th of January 2023. Our indigenous guides, Woody Laufanua and Chite Silas, took us by boat to each sampling site, where we would deploy an anchored buoy and collect metadata, including GPS coordinate and Forel Ule Index.

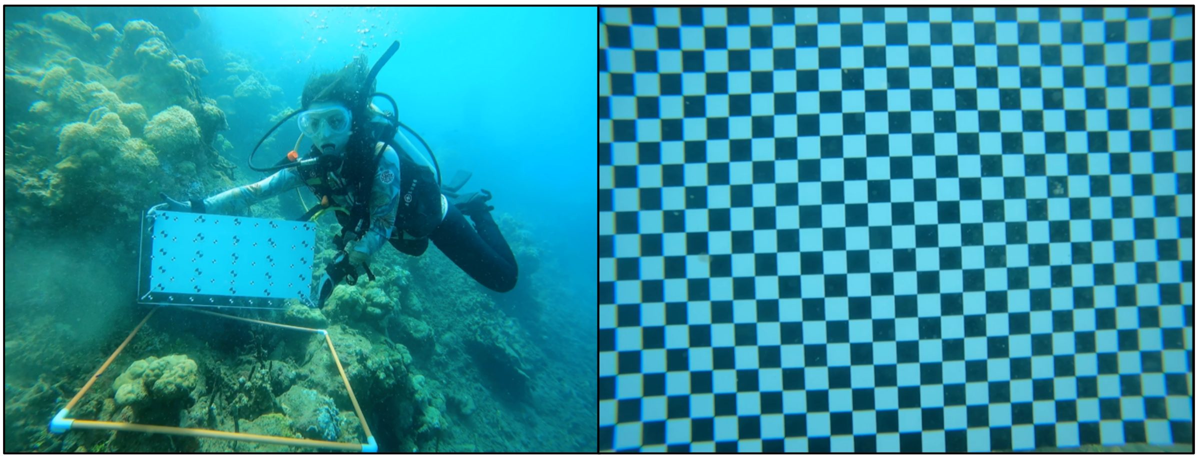
Upon entering the water on SCUBA, the Secchi device was used by one diver holding the handle of the measuring tape and staying stationary and another diver holding the disc and swimming in the opposite direction. The diver holding the measuring tape handle waited until the sight of the disc was lost and recorded the measurement displayed on the tape. This gave us a measurement of water clarity.

Next, a suitable location for the rack placement was selected. The primary considerations in this decision were the rack's proximity to the buoy to ensure easy retrieval and the substrate it was placed on to ensure stability and prevent any potential tipping caused by water current movements. In cases where these criteria were met, rack placement followed a random pattern. The quadrat was then placed in front of the cameras to estimate substrate availability and to maximise the applications of the video footage in the future.

Once the quadrat and the rack were placed in a suitable location, both GoPro cameras were turned on to begin recording, a dive watch was flashed in front of one of the cameras to capture the depth of the rack and SST, and the calibration took place. The calibration process, as described by Neuswanger (n.d.), involved first holding the calibration frame in front of both cameras, then holding the "chessboard-like pattern" toward each camera independently (Figure 2.2.5). The calibration process was restarted if the rack was accidentally knocked.

Figure 2.2.5

Examples of Stereo-Video Calibration



Note. Diver holding the stereo-video calibration frame above an orange quadrat (left image) and the chessboard-like pattern of the calibration frame (right image).

After calibration, an overhead photograph was taken of the quadrat to be later used to estimate substrate cover in that area. The quadrat was collected, and the process was repeated for any subsequent racks. The accuracy of the calibration process and the speed of the entire process were essential, as data was being collected once those first cameras were turned on. However, this initial footage was unusable due to the likely disturbance our presence caused to the ecosystem. We aimed to get out of the water as soon as possible to cause minimal disturbance, and for any disturbance our presence did cause, we wanted enough time for things to return to normal while the cameras were recording. The accuracy and speed improved with time, and we found that both were greatly increased after a week in the field.

2.2.1 Indigenous people and local community involvement

I would like to recognise the involvement of the Vavanga people in the formulation of the research goals and data collection process of this study. From guidance in choosing the sampling sites, discussions about fish abundance and identification, and the contribution of time, resources, and knowledge that got us on and into the water safely, their involvement was paramount to the success of this methodology. Additionally, we had local assistance throughout the placement of our racks and in locating and retrieving them after footage capture. This collaboration was essential in creating a research project that asked novel questions with relevance to the community involved. I am by no means an indigenous community engagement expert, so included as a part of this methodology is recognition of my positionality as a developed-world scientist who brought western science to Vavanga Village. Full engagement with community leaders and incorporation of IPLC knowledge is a crucial part of this methodology and must be incorporated if this study will encourage more western science to travel to coral reefs of indigenous communities to conduct similar research (Asase et al., 2022).

2.3 Data analysis

2.3.1 Video analysis

2.3.1.1 Video synchronisation

Video footage captured in the field was catalogued and stored in “chapters”. This chaptering, a characteristic of GoPro camera files, involves breaking down one continuous video recording into multiple discreet segments, typically around four gigabytes. The chaptering had an implication for our analysis because the stereo-video analysis software, VidSync (Neuswanger, 2008), requires the dual footage (the footage recorded by the two cameras on one rack) to be synchronised. It would be possible to import the dual footage into VidSync one chaptered segment at a time; however, it is difficult to synchronise the footage accurately, so doing this multiple times for one video would add unnecessary time and effort. A solution was to use Adobe Premiere Pro (2023) to join the chaptered segments into one long recording.

Once all chaptered segments were joined, the files could be imported into VidSync. Footage from both left and right cameras was imported, and the two videos were synchronised. Synchronisation could be achieved by using obvious visual cues such as the movement of a fish fin, the movement of a diver's hand, or, commonly, the release of bubbles from a SCUBA regulator.

2.3.1.2 Lens distortion correction

Once synchronised, the distortion of the footage was corrected. The GoPro cameras used to record footage in the field had noticeable non-linear radial distortion and correcting this ensured accurate 3D reconstruction. This distortion correction was done in VidSync using the ‘Lens Distortion’ tool. After locating where the chessboard-like pattern came into the frame on each camera, plumblines were autodetected using the downhill simplex method (Nelder & Mead, 1965); plumblines were manually altered to fit the chessboard pattern as needed. The distortion parameters were calculated using the Brown-Conrady model (Brown, 1966) expanded to 13 parameters, encompassing radial and decentring distortion effects. The 13 parameters include the centre of distortion (u_0, v_0), seven coefficients for radial (k_1 through k_7) distortion, and four for decentring (p_1 through p_4). This entire process was done separately for each camera. For detailed information on the calculations for distortion, please see the methodology of Neuswanger et al. (2016).

2.3.1.3 Three-dimensional calibration

The 3D calibration was calculated after the lens distortion was corrected. First, each node's real-world coordinates (x, z) were measured on the calibration frame and imported into VidSync. Then, in VidSync, the centre of each node on the front and back pane of the calibration frame was clicked on to give corresponding in-software coordinates in pixels (u_d, v_d). VidSync corrects these points for non-linear distortion to obtain undistorted screen coordinates (u_u, v_u). For detailed information on the calculations for 3D coordinates, please see the methodology of Neuswanger et al. (2016).

2.3.1.4 Fish tracking

Because VidSync is a software designed for 3D measurements, it has a hierarchal organisation system to record and store these measurements (Neuswanger, n.d.-a). At the top is an Object, which in the case of this analysis was always “Fish”. One Object can have multiple Events, including movement tracks, length measurements, and bite records. Each Event was customised for this analysis (see Table A1 in the Appendix). Each Event may have one or more Points containing the measurements, and each Point belongs to one Event.

Now, the target species needed to be located in the footage. This involved systematically watching all of the footage and creating a Point within an Event labelled "Sighting" to denote the appearance of the three target butterflyfish species: *C. baronessa, C. lunulatus*, and *C. vagabundus*. Then, another Point was created to mark their disappearance from view. The appearance of the target species was recorded at any location in the footage and was not solely confined to within the quadrat. The compiled data, organised by site and species, was used to calculate the total time each fish remained visible on camera. Each individual was sorted by descending time on camera. Only the top ten longest tracks for each species at each site were chosen for analysis to ensure the analysis was kept within the time restraints of a master's research project while still providing enough data for reliable results. Each of the individual top ten longest tracks was analysed to ensure they were of acceptable quality, which meant the footage was not heavily obscured (by light, turbidity, or an organism) and the fish was visible for a significant quantity of the footage. If the quality of a track was deemed unacceptable, it was ignored for analysis, and the next longest track was included instead. Once all tracks were deemed acceptable for use in analysis, each track was allocated a code corresponding to its species (species_xx, e.g., baronessa_01).

The systematic tracking of each individual fish (target) commenced by creating a Point on its snout every six frames for the duration of its visible time on screen. In instances where the snout was momentarily obscured (for example, another fish swam in front of the target, or the target swam behind some substrate), the location of its snout was estimated, and a Point was still recorded. The snout location was estimated by using other visible body parts of the target or following the approximate trajectory of the snout before it was obscured. If the estimation of snout location proved too difficult, the footage was skipped forward in six-frame increments until a Point could be accurately recorded. A bite Point was recorded when the target took a bite. A bite was indicated when the target exhibited rapid acceleration and reversal of the snout into a substrate or when the mouth was observed attaching and detaching from a substrate. If the target was harassed by another fish (only recorded harassments were by damselfish (*Neoglyphidodon melas*), the beginning of the harassment episode was recorded with a Point. A harassment episode began once a fish suddenly advanced toward the target, and the target visibly changed its speed and course to escape. This entire tracking process was methodically repeated for every target.

In total, there were 39 *C. baronessa*, 45 *C. lunulatus*, and 49 *C. vagabundus* targets that were tracked. The variation stems from the fact that less than ten targets were available for tracking at some sites. Furthermore, due to the meticulous process of tracking each fish and time restraints, some of the longer tracks were shortened to only the first ten seconds of footage. All footage was analysed to identify potential targets and of the total footage collected, 2014.27 seconds were selected for further analysis as they contained the longest fish tracks across all sites.

Additional information on sampling site parameters and fish tracking can be found in Table A2 in the Appendix.

2.3.2 Estimating fish mass

First, TL for each fish was converted from millimetres to centimetres. Species-specific length-weight relationships were taken from FishBase (Froese et al., 2014; Froese & Pauly, 2024) , and the body mass (g) for each individual was calculated using Equation 1, where a and b are species-specific coefficients, and Total Length is the total length (cm) of each individual fish. The coefficients for each species are as follows: *C. baronessa*: $a = 0.04480$, $b = 2.828$; *C. lunulatus*: $a = 0.24099$, $b = 2.099$; *C. vagabundus*: $a = 0.02776$, $b = 2.973$.

$$\text{Body Mass} = a \times \text{Total Length}^{b} \tag{1}$$

2.3.3 Extracting information from 3D trajectories

2.3.3.1 Data cleaning

To ensure data quality, outliers were identified in the spatial coordinates and removed using the Interquartile Range (IQR) method in R (R Core Team, 2021). IQR is a statistical measure representing the range within which the middle 50% of data values lie, making it useful for assessing data variability and identifying outliers. Data points that fell below the lower bound (Q1 - 1.5 * IQR) and above the upper bound (Q3 + 1.5 * IQR) were removed using a threshold of 1.5 times the IQR (Lilkendey et al., 2024). Two butterflyfish individuals were excluded as they only had a limited number of observed XYZ coordinates (lunulatus_06 with 10 and lunulatus_41 with 33 XYZ coordinates).

2.3.3.2 Velocity and ODBA

Changes in velocity derived from the 3D trajectories of butterflyfishes were analysed to quantify energy expenditure. The velocity in three dimensions (X, Y, Z), measured in centimetres per second (cm s^{-1}), was computed by calculating the spatial differences between consecutive points along each axis. This was achieved by employing the `lead` function in R to determine the displacement (diff_X, diff_Y, diff_Z) by subtracting the current position from the subsequent position for each coordinate. Similarly, velocity in body lengths per second was calculated by dividing the fish's velocity in centimetres per second by its total length in centimetres, expressing the speed relative to the fish's body size. Acceleration (cm s^{-2}) was calculated using the differences in velocity between observations.

ODBA was computed as a measure of energy expenditure, incorporating the magnitudes of acceleration in all three axes (X, Y, Z) (R. P. Wilson et al., 2006). This was achieved by dividing each axis's acceleration by the acceleration due to gravity (981 cm s^{-2}) to convert it into g-units and then summing their absolute values (Equation 2).

$$\mathrm{ODBA} = \frac{|\,\mathrm{Acceleration\ X}\,| + |\,\mathrm{Acceleration\ Y}\,| + |\,\mathrm{Acceleration\ Z}\,|}{\mathrm{g}} \tag{2}$$

2.3.3.3 Bite distance and bite rate

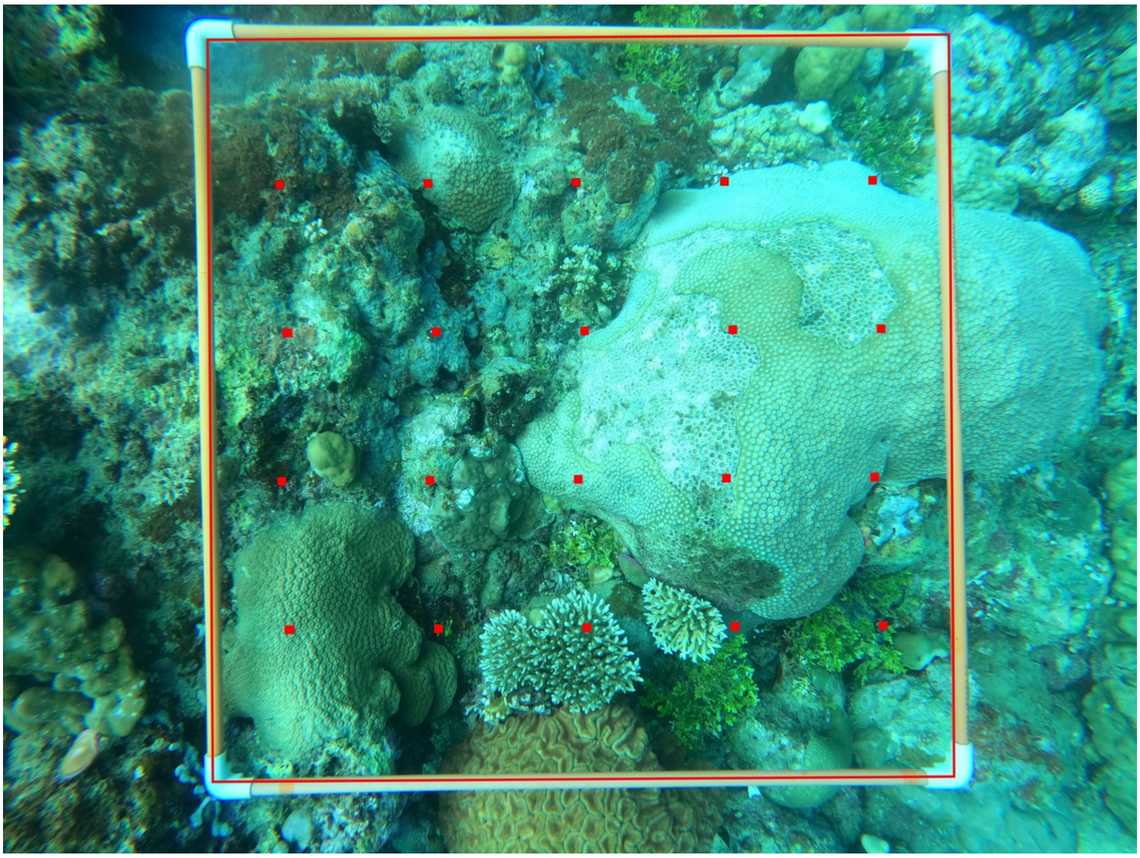
The bite rates of each fish were calculated considering the total time of observation and the total number of recorded bites. Bite rate is expressed as the number of bites taken from substrates per minute. Distances between bites were computed by considering the spatial coordinates of consecutive bites. The mean bite distances for each fish trajectory were calculated.

2.3.4 Substrate percentage cover

The overhead quadrat photographs were superimposed with a 20-point grid (Figure 2.3.4.1), and the substrate underneath each point was recorded. Coral was identified to genus level if possible. All substrate records at each site were averaged to give an average total percentage estimate for substrate at each sampling site.

Figure 2.3.4.1

Substrate Estimation Quadrat Grid



2.3.5 Statistical analysis

2.3.5.1 Environmental variables

To investigate the relationship between the Forel-Ule Index and visibility at each sampling site, a scatterplot was generated using the ggplot2 package in R. A correlation analysis was performed using Pearson's product-moment correlation coefficient to quantify the strength and direction of the relationship between the Forel-Ule Index and visibility.

2.3.5.2 Foraging preferences

Manly's preference ratio (Manly et al., 2002) (Equation 3) was calculated to assess the foraging substrate preference of *C. baronessa*, *C. lunulatus*, and *C. vagabundus* across substrates and sampling sites. The preference ratio represents the ratio between a specific substrate's observed use and expected use based on substrate availability. A ratio of 1 means the substrate is used in proportion to its availability, greater than 1 indicates substrate preference, and less than 1 indicates avoidance; the further from 1 the ratio is, the stronger the preference or avoidance.

$$\text{Preference Ratio} = \frac{\text{Expected Use}}{\text{Observed Use}} \tag{3}$$

Where species had foraged on one substrate at three or more sites, linear correlation analysis was conducted between the percentage cover of that substrate and the preference ratio of that species for that substrate. *Acropora* was not present in our sampling quadrats at Ovuku; however, fish were still foraging on that substrate at that site. This is likely because there is such a small percentage cover of *Acropora* at Ovuku that it was not picked up in the quadrats. Therefore, for this specific linear correlation analysis, a small value of 1% was allocated for *Acropora*.

2.3.5.3 Bite distance, bite rate, mass, ODBA, and velocity

To investigate the relationship between the measured variables bite distance, bite rate, mass, ODBA, and velocity, and also between the Forel-Ule Index and the measured variables, scatterplots were generated using the ggplot2 packing in R. A correlation analysis was performed using Pearson's product-moment correlation coefficient to quantify the strength and direction of the relationship between variables.

Analyses of variance for *C. baronessa*, *C. lunulatus*, and *C. vagabundus* were carried out separately for bite distance, bite rate, ODBA, and velocity (dependent variables) across all five sampling sites (independent variable). Then, Tukey's HSD post-hoc tests were carried out to reveal the specific significant differences. Where the ANOVA assumption of normality was violated, the Kruskal-Wallis rank sum test and corresponding Dunn Kruskal-Wallis Multiple Comparison test with Bonferroni method adjusted p-values were conducted instead.

Chapter 3: Results

3.1 Environment

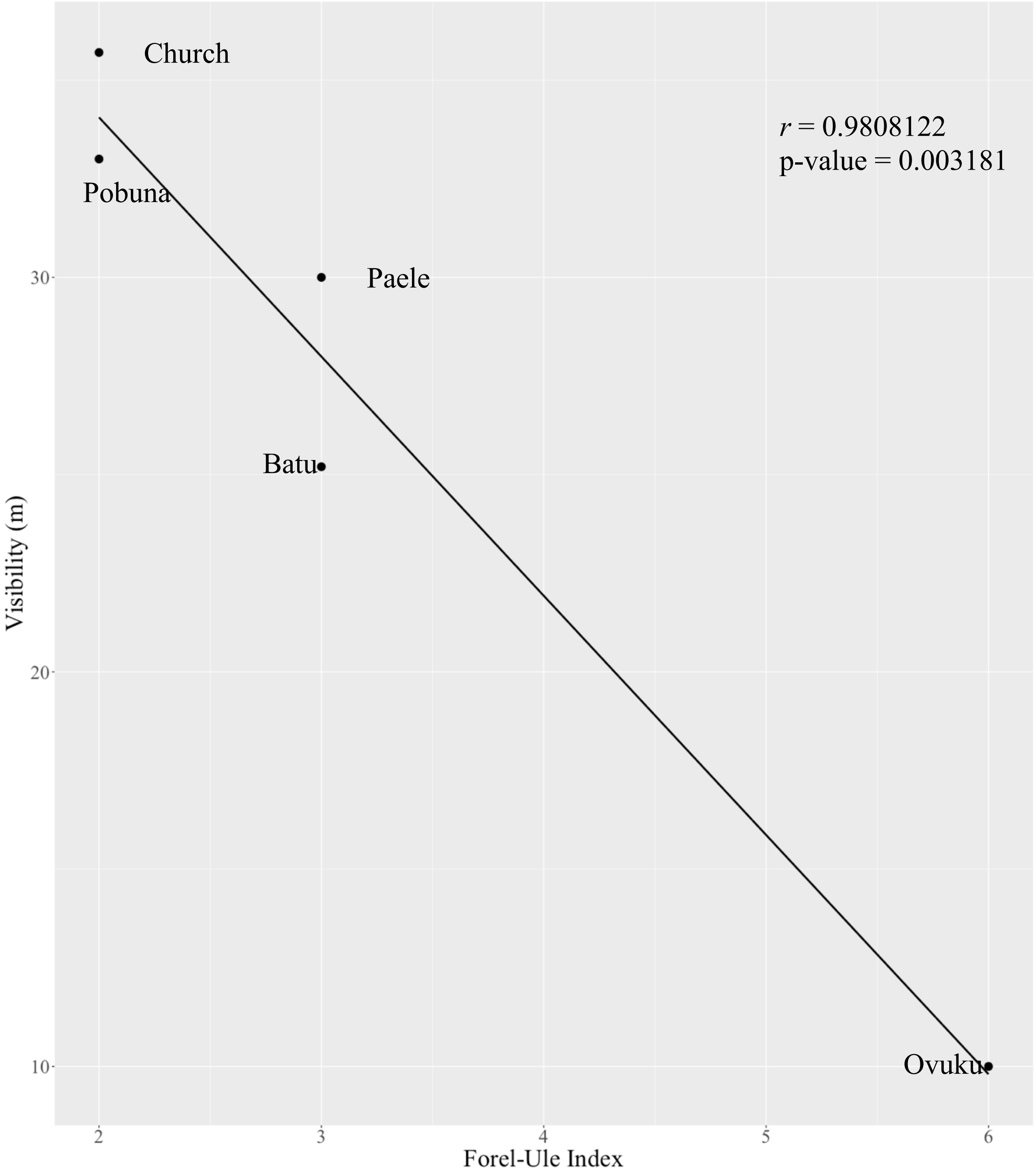
Mean Forel-Ule Index is highest at Ovuku with a value of 6, then drops to 3 at Batu, where it remains through to Paele. It drops to 2 at Church and remains here through to Pobuna. Mean visibility is lowest at Ovuku at 10 metres and increases to 25.2 metres at Batu, 30 metres at Paele, 35.7 metres at Church, and drops to 33 metres at Pobuna. Forel-Ule Index and visibility showed a strong negative correlation (Pearson's product-moment correlation: $p = 0.003$, cor = 0.981) (Figure 3.1.1). Consequently, they are likely good proxies for turbidity as visibility increases and Forel Ule decreases in distance from the river mouth. Pobuna may experience sediment input from the next river mouth, indicating that Church might be the site that is centred between fluvial input from Ovuku and the next river.

Total available substrate was highest at Paele and Church, which both had 14, followed by Pobuna with 13, Batu with nine, and Ovuku with seven. Total available substrate was strongly, negatively correlated with the Forel-Ule Index (Pearson's product-moment correlation: $p = < 0.001$, cor = -0.797), showing that as turbidity increased, the variation in substrate decreased (Figure 3.1.2). For the total percentage cover of all substrates, see Table A3 in the Appendix. Total available substrate was lowest at Ovuku and increased at Batu and Paele, where it plateaued to Church, then dipped slightly at Pobuna (Figure 3.1.3). Of all available substrates, only eight were foraged by the target species. The percentage cover of each of the eight substrates was plotted against the sampling sites, revealing high variations in substrate coverage among sites (Figure 3.1.4). Ovuku exhibited the highest coverage of dead coral of all the sites and was the only site that did not have *Acropora* coral, while Batu showed the highest coverage of both *Acropora* and *Porites* coral of all the sites. Furthermore, as the sites progressed further from Ovuku, EAM increased in cover.

Analysis of foraged substrates showed significant differences in *Acropora* (ANOVA: $F(4, 26) = 3.435$, $p = 0.0221$) and dead coral (ANOVA: $F(4,26) = 3.602$, $p = 0.0183$) between sites. Tukey's HSD post-hoc test revealed that the percentage cover of *Acropora* is significantly different between Ovuku and Paele ($p = 0.0495705$) (Figure 3.1.5) and revealed that the percentage cover of dead coral is significantly different between Ovuku and Church ($p = 0.0153397$) and between Ovuku and Paele ($p = 0.0439948$) (Figure 3.1.6).

Figure 3.1.1

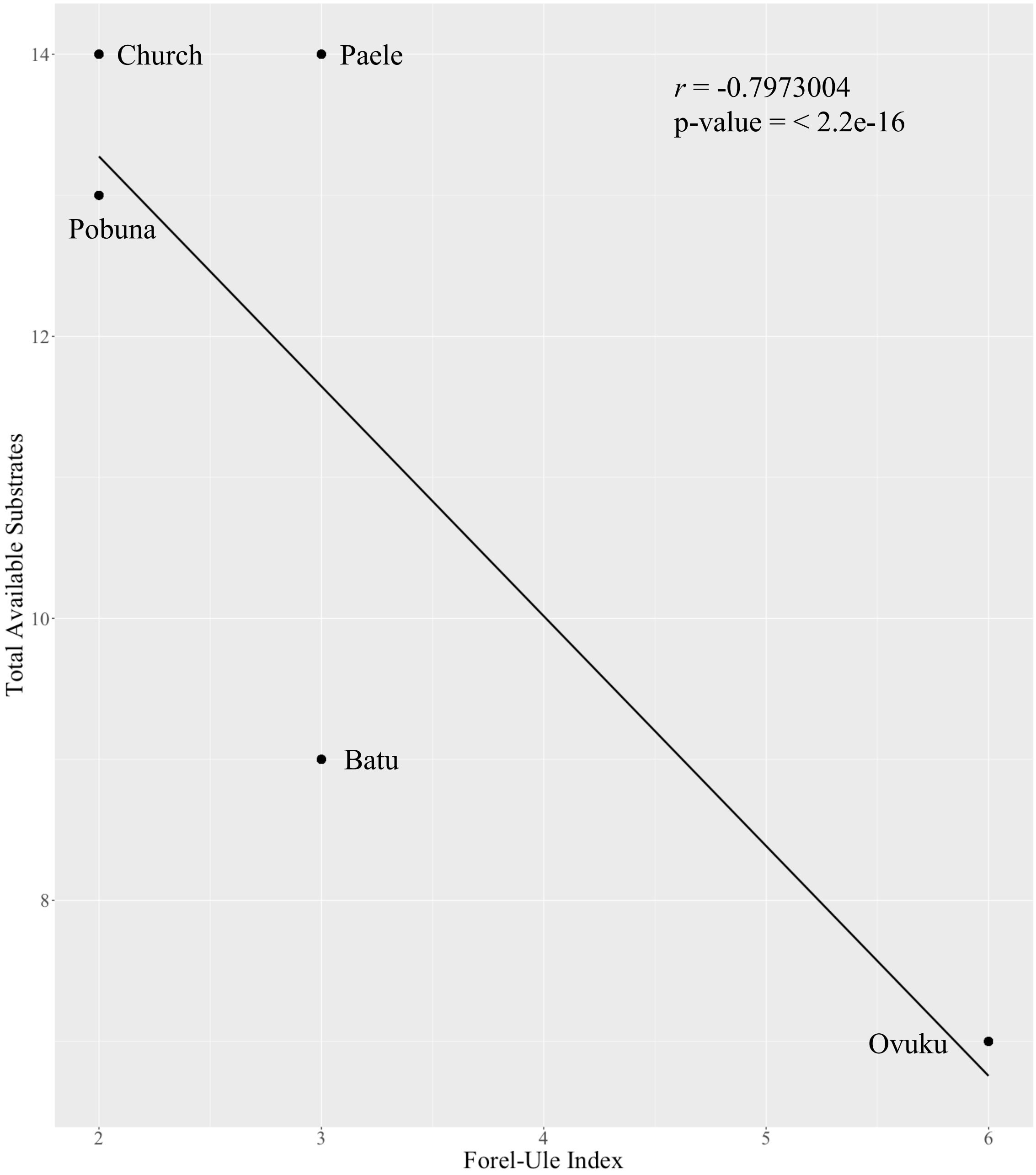
Relationship Between Forel-Ule Index and Visibility at Sampling Sites Along a Turbidity Gradient: Pearson's Product-Moment Correlation



Note. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Listed in increasing distance from the mouth of Vavanga River, the sampling sites are Ovuku, Batu, Paele, Church, and Pobuna.

Figure 3.1.2

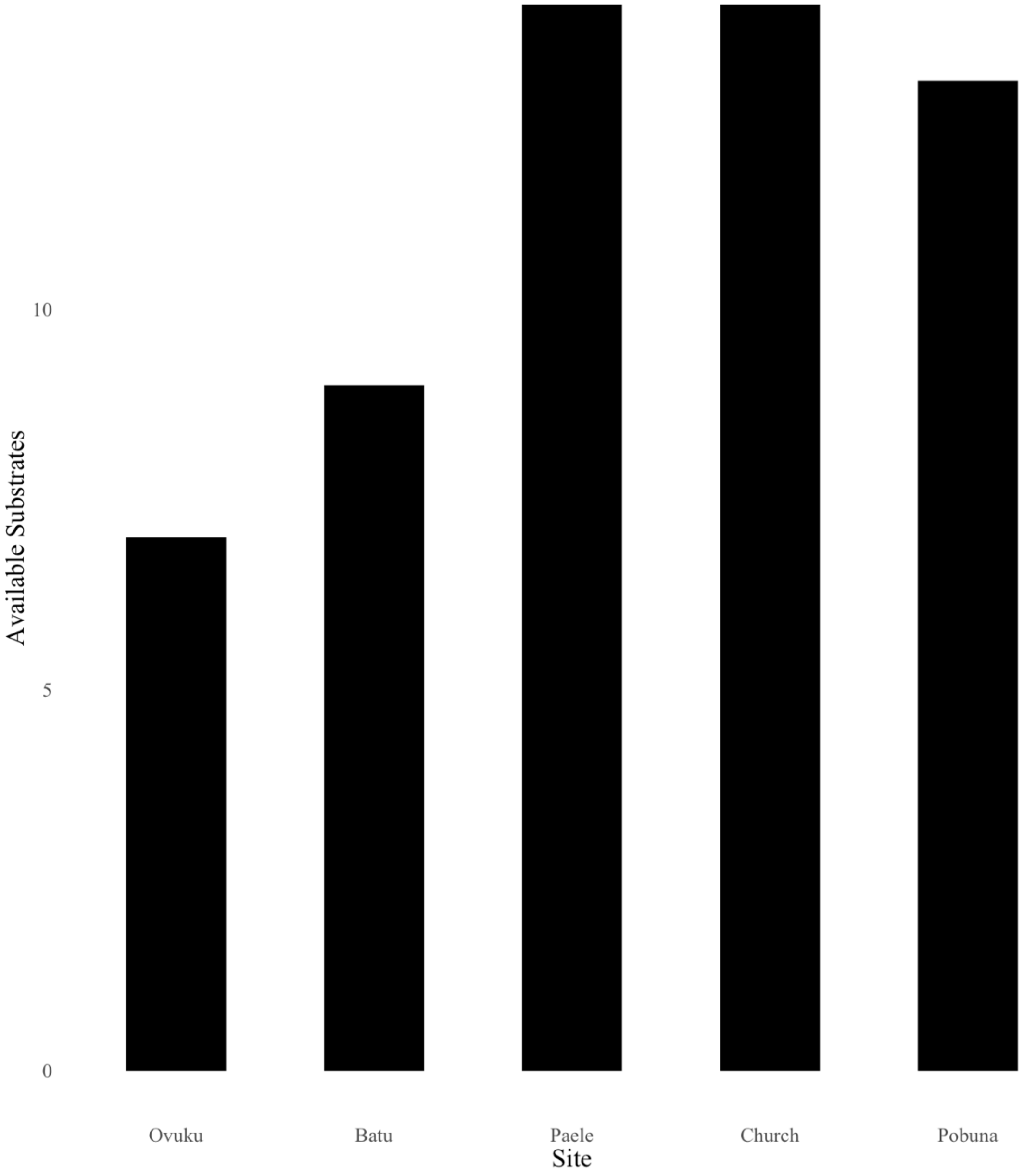
Relationship Between Forel-Ule Index and Total Available Substrate at Sampling Sites Along a Turbidity Gradient: Pearson's Product-Moment Correlation



Note. Available substrates include *Acropora* spp., dead coral, *Diploastrea* spp., EAM, *Echinopora* spp., Faviidae spp., Favities spp., *Fungia* spp., Goniastrea spp., *Lobophyllia* spp., *Millepora* spp., *Montipora* spp., *Pavona* spp., *Platygyra* spp., *Pocillopora* spp., *Porites* spp., sand, *Sarcophyton* spp., *Sinularia* spp., *Porifera* spp., *Stylaster* spp., Zooanthid. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Listed in increasing distance from the mouth of Vavanga River, the sampling sites are Ovuku, Batu, Paele, Church, and Pobuna.

Figure 3.1.3

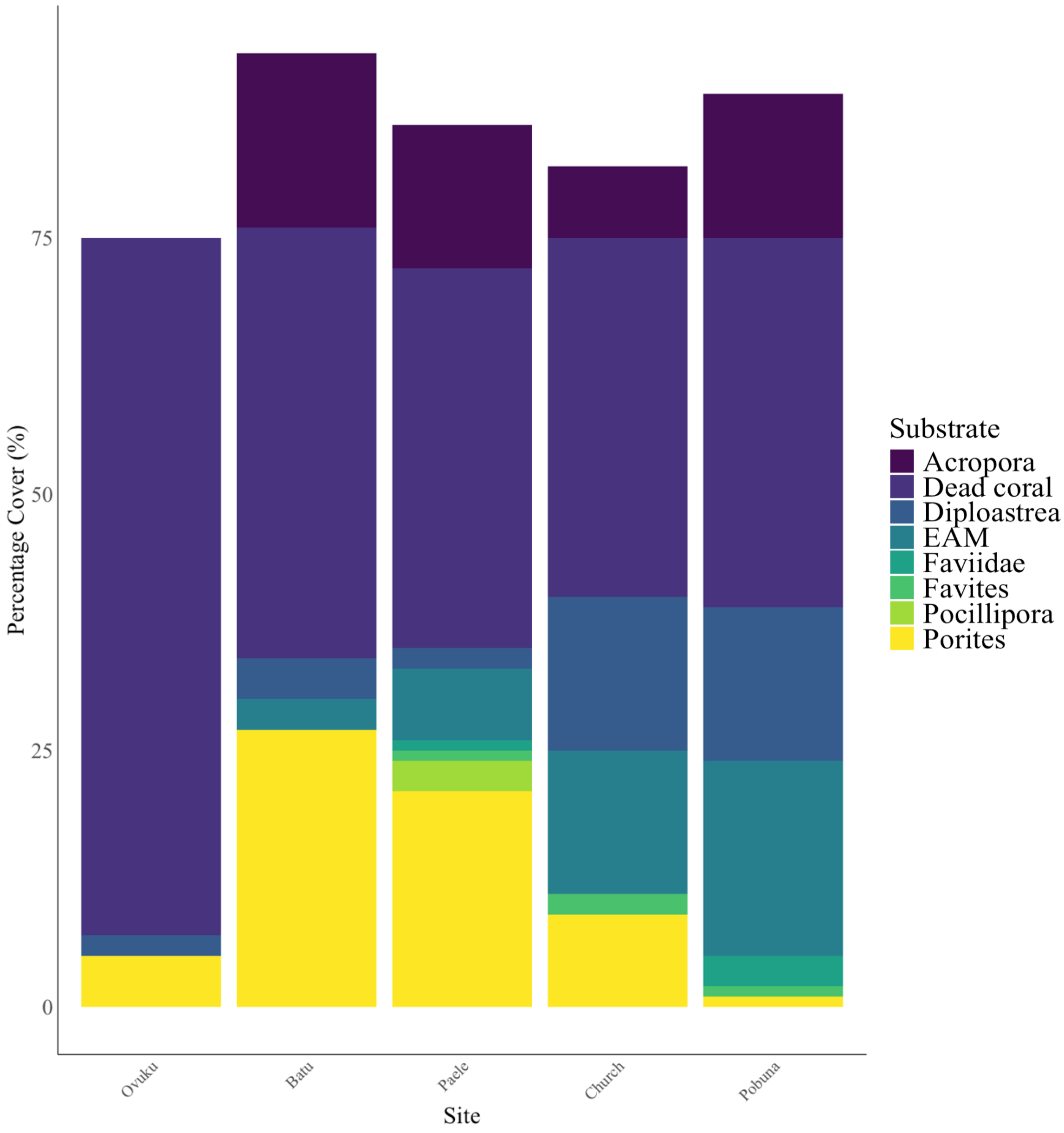
Total Available Substrates at Sampling Sites Along a Turbidity Gradient



Note. Available substrates include *Acropora* spp., dead coral, *Diploastrea* spp., EAM, *Echinopora* spp., Faviidae spp., Favities spp., *Fungia* spp., Goniastrea spp., *Lobophyllia* spp., *Millepora* spp., *Montipora* spp., *Pavona* spp., *Platygyra* spp., *Pocillopora* spp., *Porites* spp., sand, *Sarcophyton* spp., *Sinularia* spp., *Porifera* spp., *Stylaster* spp., Zooanthid. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Sites are listed in increasing distance from the mouth of Vavanga River.

Figure 3.1.4

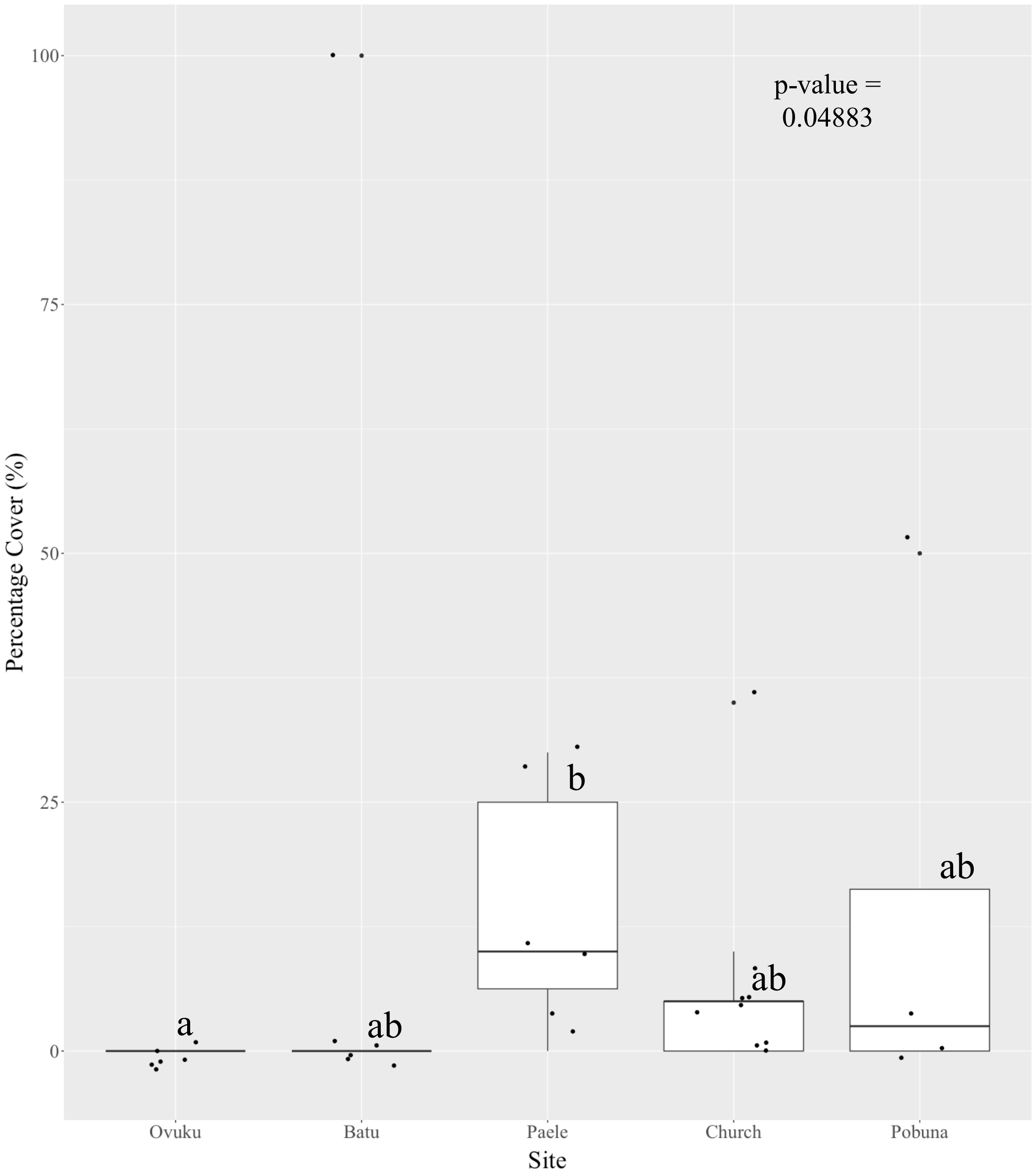
Percentage Substrate Cover at Sampling Sites Along a Turbidity Gradient



Note. Only substrates used in further analyses were plotted for clarity's sake. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Sites are listed in increasing distance from the mouth of Vavanga River.

Figure 3.1.5

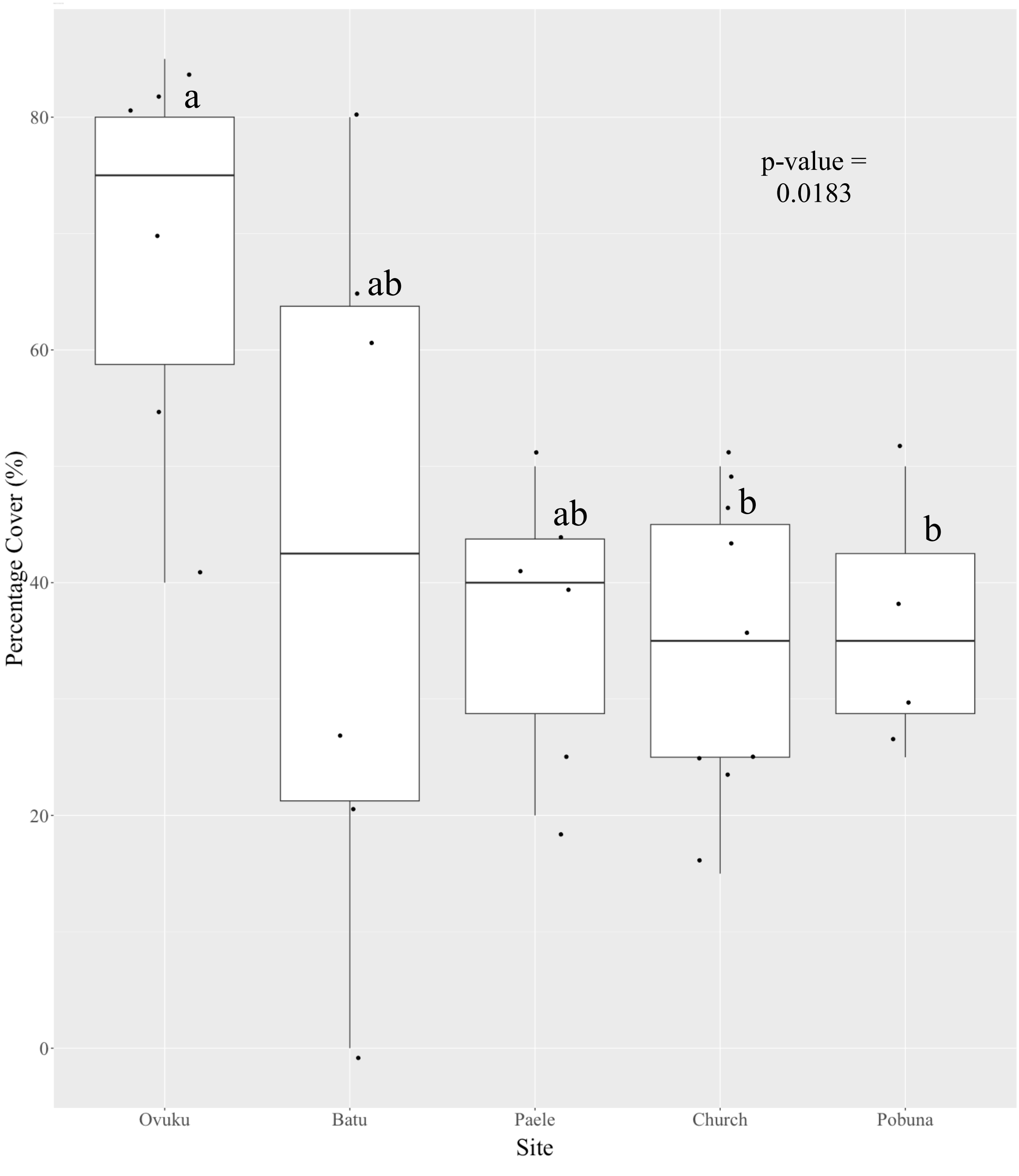
Comparison of Acropora *Percentage Cover at Sampling Sites Along a Turbidity Gradient*



Note. Different letters above the box plots represent statistically significant differences between groups according to Tukey's HSD post-hoc test. Groups sharing the same letter are not significantly different from each other, while groups with different letters are significantly different. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Sites are listed in increasing distance from the mouth of Vavanga River.

Figure 3.1.6

Comparison of Dead Coral Percentage Cover at Sampling Sites Along a Turbidity Gradient



Note. Different letters above the box plots represent statistically significant differences between groups according to Tukey's HSD post-hoc test. Groups sharing the same letter are not significantly different from each other, while groups with different letters are significantly different. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Sites are listed in increasing distance from the mouth of Vavanga River.

3.2 Foraging substrate preferences

Foraging substrates varied between species; *C. baronessa* foraged on four substrates, *C. lunulatus* foraged on six substrates, and *C. vagabundus* foraged on five substrates (Table 3.2.1). *C. baronessa* foraged mostly on *Acropora* at every sampling site except Batu, where it foraged mainly on *Porites* (Figure 3.2.1). *C. lunulatus* was not recorded foraging at Pobuna; at all other sites, *C. lunulatus* foraged mainly on *Porites* and EAM with varying preference (Figure 3.2.2). Dead coral was preferred by *C. vagabundus* at both Church and Pobuna, with a more generalist approach to foraging substrate at other sites (Figure 3.2.3).

Analysis of Manly's preference ratio revealed varying feeding preferences among species (for a list of all preference ratios, see Table A4 in the Appendix). *C. baronessa* preferred *Acropora*, *Montastraea*, *Porites*, and Faviidae at different sampling sites but avoided *Porites* at Pobuna (Figure 3.2.4). Their specialist prey species, *Acropora*, was not preferred as high as Faviidae at Church. Their strongest preferred substrate was *Acropora* at Ovuku, and they also had an exclusive preference for this species at Paele. *C. lunulatus* showed a preference for EAM, *Porites*, Favites, *Pocillopora*, and *Acropora* at different sampling sites and avoided dead coral at Batu (Figure 3.2.5). *C. lunulatus* showed a strong preference for EAM at Ovuku. *C. vagabundus* preferred EAM, *Porites*, *Acropora*, and dead coral at different sampling sites (Figure 3.2.6). They avoided *Diploastrea* at Church and dead coral at Paele.

Linear correlations between Manly's preference ratio and percentage substrate cover were able to be performed for *C. baronessa* and *Acropora*, *C. lunulatus* and *Porites*, and *C. vagabundus* and dead coral (based on the criterion in section 2.3.4.2). For *C. baronessa* and *Acropora*, Manly's preference ratio and percentage cover showed a strong negative relationship (Pearson's product-moment correlation: $p = 0.138$, $cor = -0.862$) showing that as *Acropora* coverage increased, *C. baronessa*'s preference for it decreased; however, this is not significant (Figure 3.2.7). For *C. lunulatus* and *Porites*, Manly's preference ratio and percentage cover showed a weak negative relationship; however, it was not significant. (Pearson's product-moment correlation: $p = 0.632$, $cor = 0.368$) (Figure 3.2.8). For *C. vagabundus* and dead coral, Manly's preference ratio and percentage cover showed a weak negative relationship; however, it was not significant (Pearson's product-moment correlation: $p = 0.445$, $cor = -0.766$) (Figure 3.2.9).

Table 3.2.1

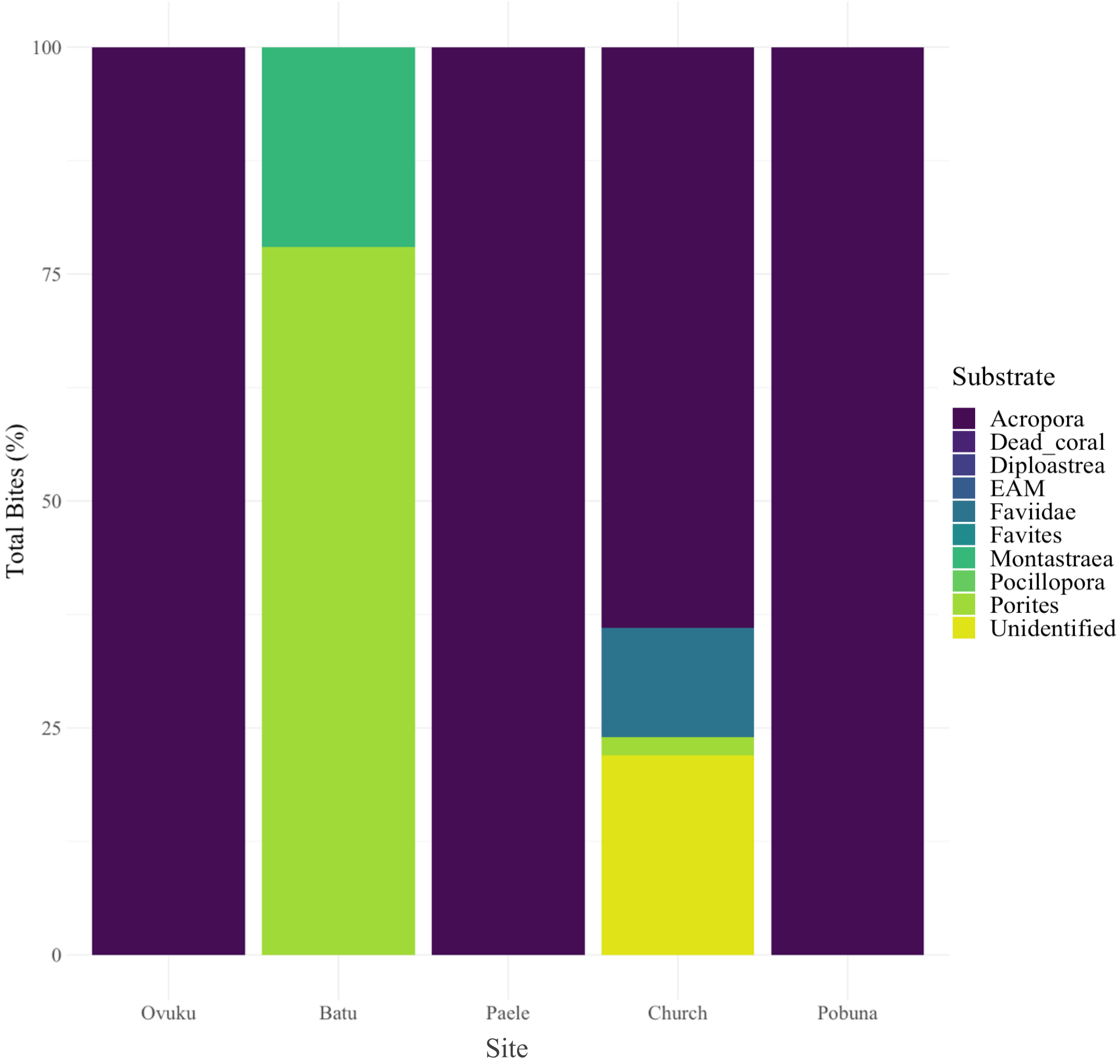
Percentage of Total Bites Taken on Substrate by Chaetodon *Butterflyfish Across Sampling Sites*

Species	Site name	Acropora	Dead coral	Diploastrea	EAM	Faviidae	Favites	Montastraea	Pocillopora	Porites	Unidentified
C. baronessa	Ovuku	**100%**	0%	0%	0%	0%	0%	0%	0%	0%	0%
C. baronessa	Batu	0%	0%	0%	0%	0%	0%	**22%**	0%	**78%**	0%
C. baronessa	Paele	**100%**	0%	0%	0%	0%	0%	0%	0%	0%	0%
C. baronessa	Church	**66%**	0%	0%	0%	**14%**	0%	0%	0%	**4%**	**16%**
C. baronessa	Pobuna	**100%**	0%	0%	0%	0%	0%	0%	0%	0%	0%
C. lunulatus	Ovuku	0%	0%	0%	**88%**	0%	0%	0%	0%	**12%**	0%
C. lunulatus	Batu	0%	**2%**	0%	0%	0%	**10%**	0%	0%	**88%**	0%
C. lunulatus	Paele	0%	0%	0%	**62%**	0%	0%	0%	**15%**	**23%**	0%
C. lunulatus	Church	**25%**	0%	0%	0%	0%	0%	0%	0%	**75%**	0%
C. vagabundus	Ovuku	0%	0%	0%	**84%**	0%	0%	0%	0%	**11%**	**5%**
C. vagabundus	Batu	**50%**	0%	0%	0%	0%	0%	0%	0%	**37%**	**13%**
C. vagabundus	Paele	0%	**20%**	0%	0%	0%	0%	0%	0%	0%	**80%**
C. vagabundus	Church	0%	**96%**	**4%**	0%	0%	0%	0%	0%	0%	0%
C. vagabundus	Pobuna	0%	**100%**	0%	0%	0%	0%	0%	0%	0%	0%

Note. Percentages > 0 are bolded. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Listed in increasing distance from the mouth of Vavanga River, the sampling sites are Ovuku, Batu, Paele, Church, and Pobuna.

Figure 3.2.1

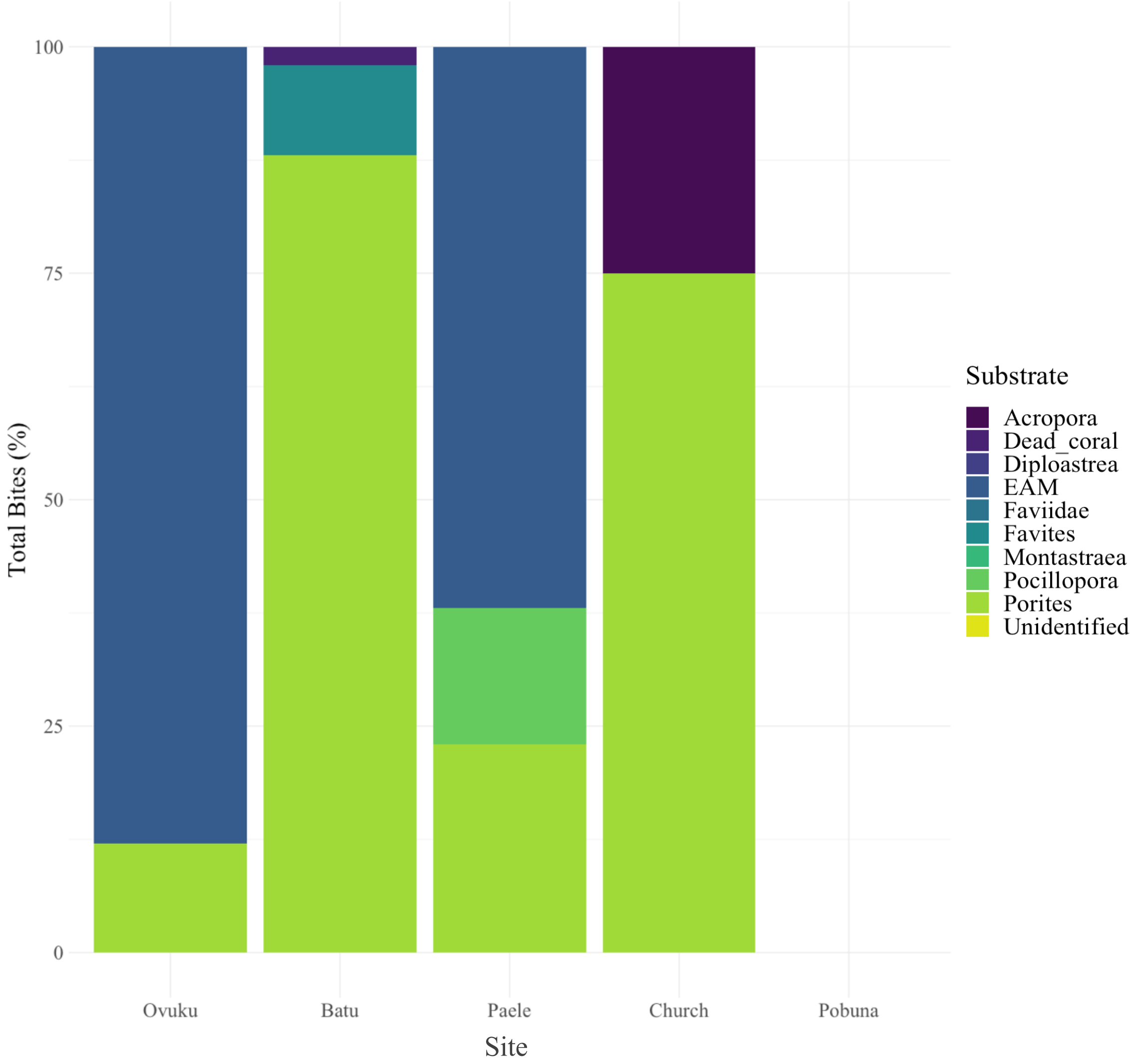
Foraging Substrates of Chaetodon baronessa *at Sampling Sites Along a Turbidity Gradient*



Note. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Sites are listed in increasing distance from the mouth of Vavanga River.

Figure 3.2.2

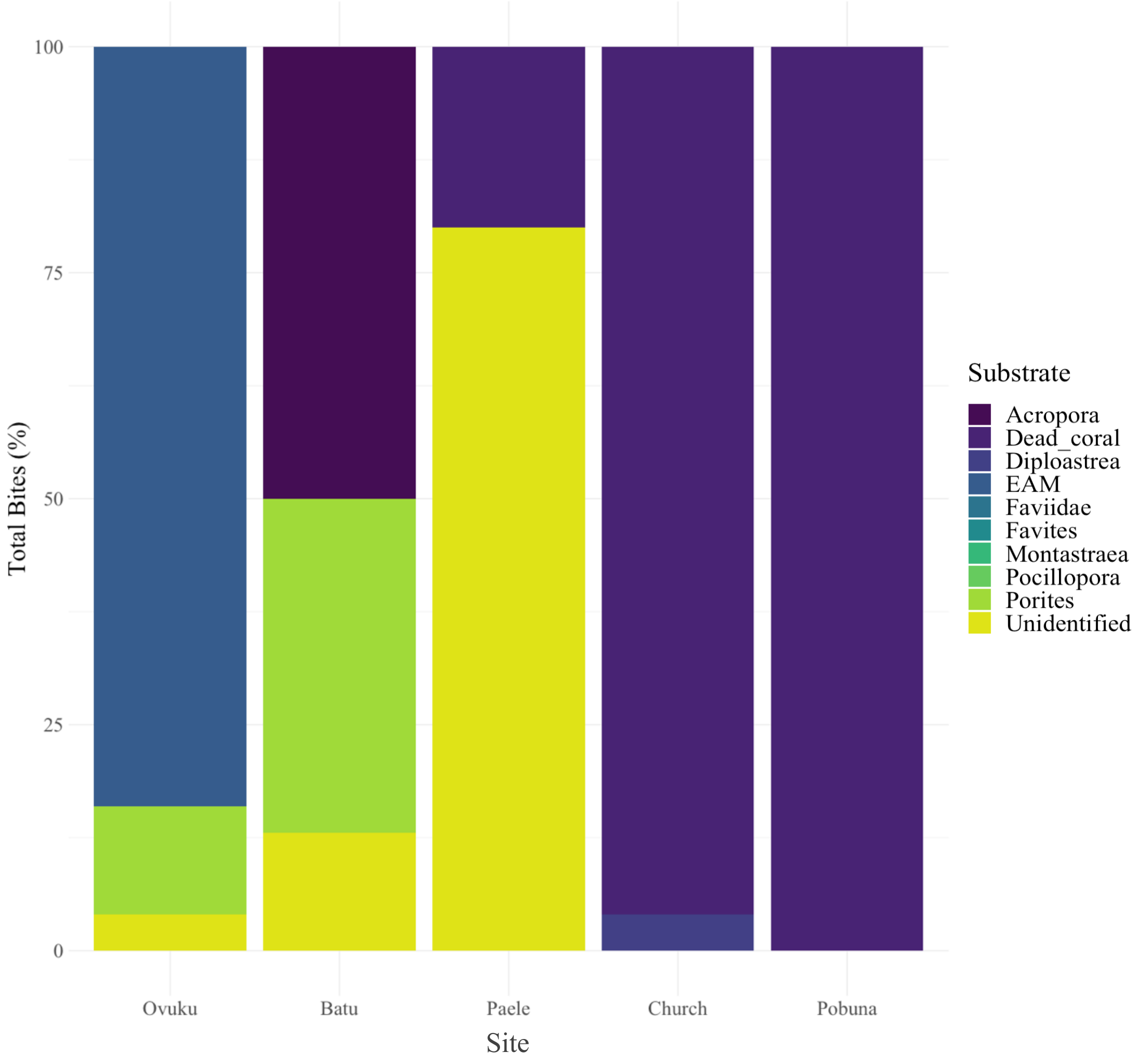
Foraging Substrates of Chaetodon lunulatus *at Sampling Sites Along a Turbidity Gradient*



Note. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Sites are listed in increasing distance from the mouth of Vavanga River.

Figure 3.2.3

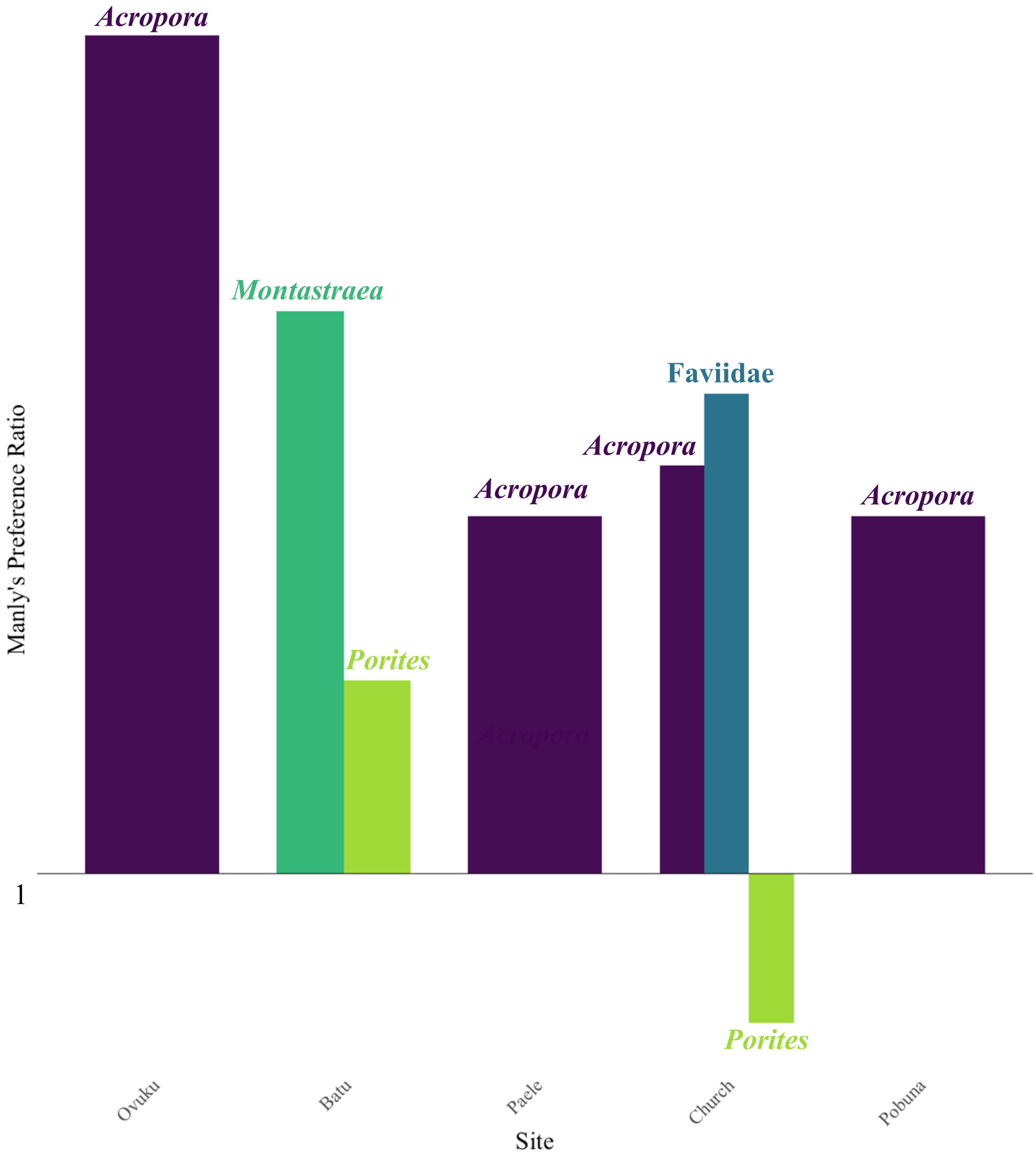
Foraging Substrates of Chaetodon vagabundus *at Sampling Sites Along a Turbidity Gradient*



Note. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Sites are listed in increasing distance from the mouth of Vavanga River.

Figure 3.2.4

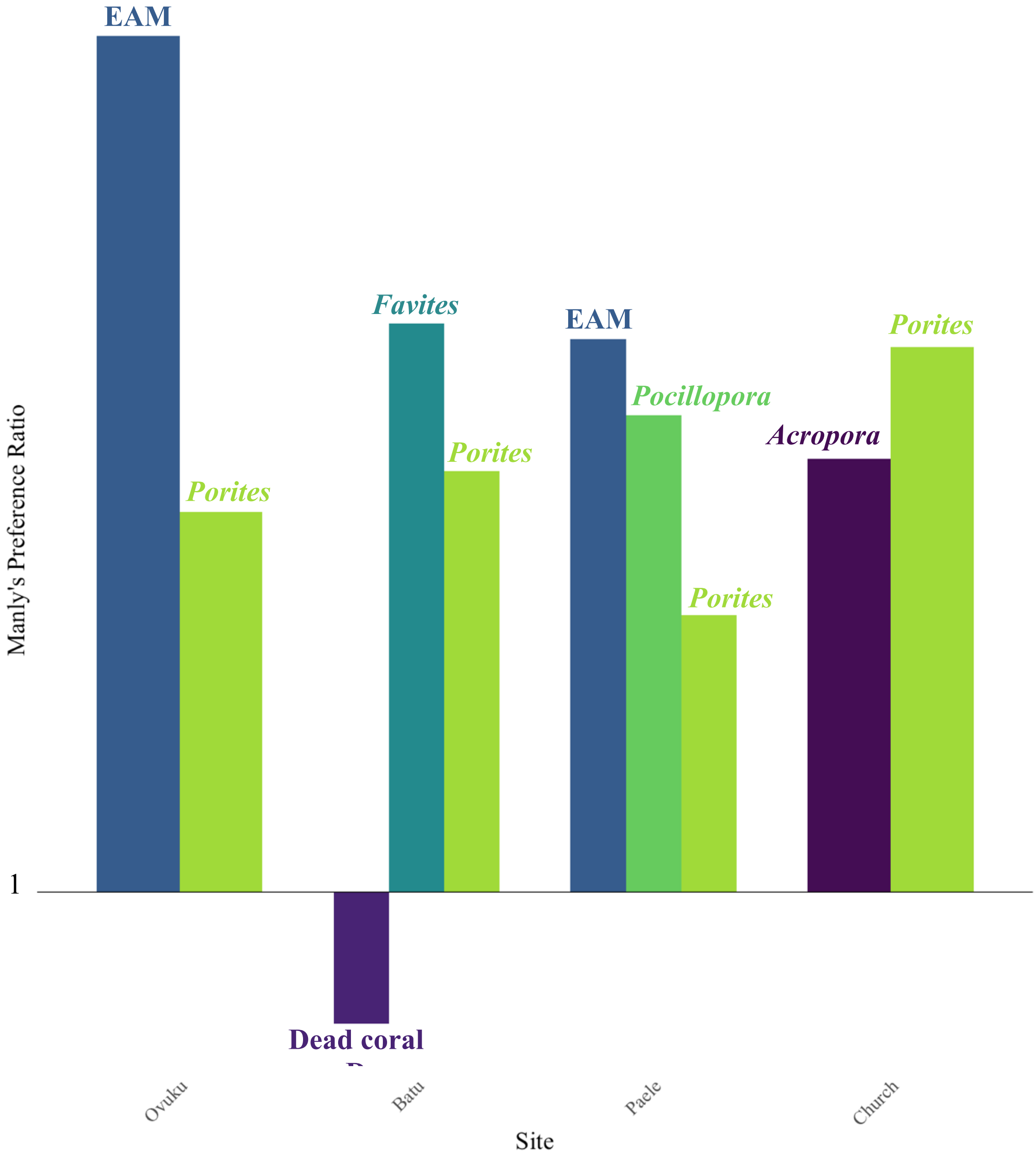
Manly's Preference Ratio of Substrates for Chaetodon baronessa *at Sampling Sites Along a Turbidity Gradient*



Note. Preference ratio > 1 indicates substrate preference; preference ratio < 1 indicates avoidance. Manly's preference ratio values are log-transformed to better visualise the data, which includes extreme values. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Sites are listed in increasing distance from the mouth of Vavanga River.

Figure 3.2.5

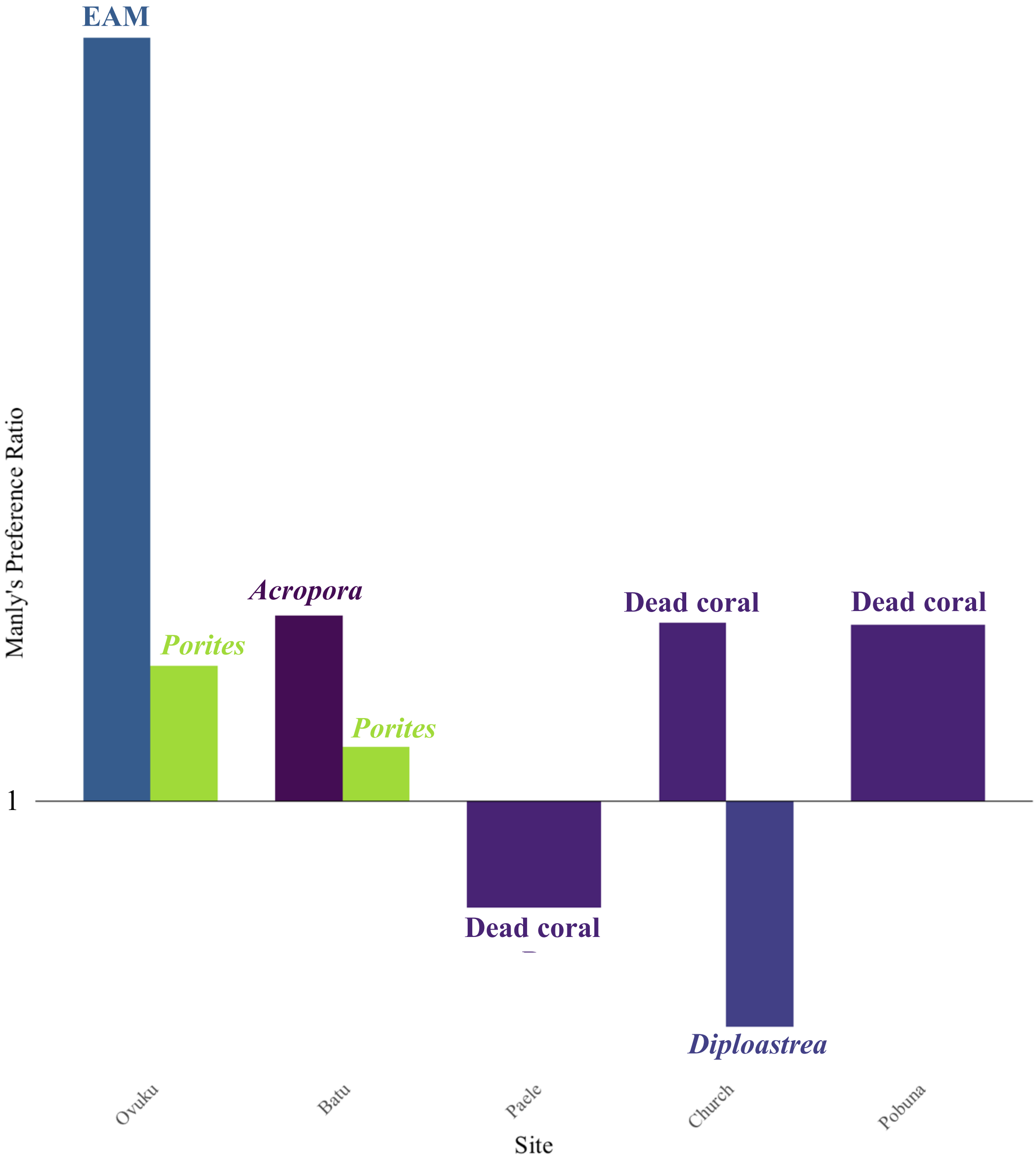
Manly's Preference Ratio of Substrates for Chaetodon lunulatus *at Sampling Sites Along a Turbidity Gradient*



Note. Preference ratio > 1 indicates substrate preference; preference ratio < 1 indicates avoidance. Manly's preference ratio values are log-transformed to better visualise the data, which includes extreme values. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Sites are listed in increasing distance from the mouth of Vavanga River.

Figure 3.2.6

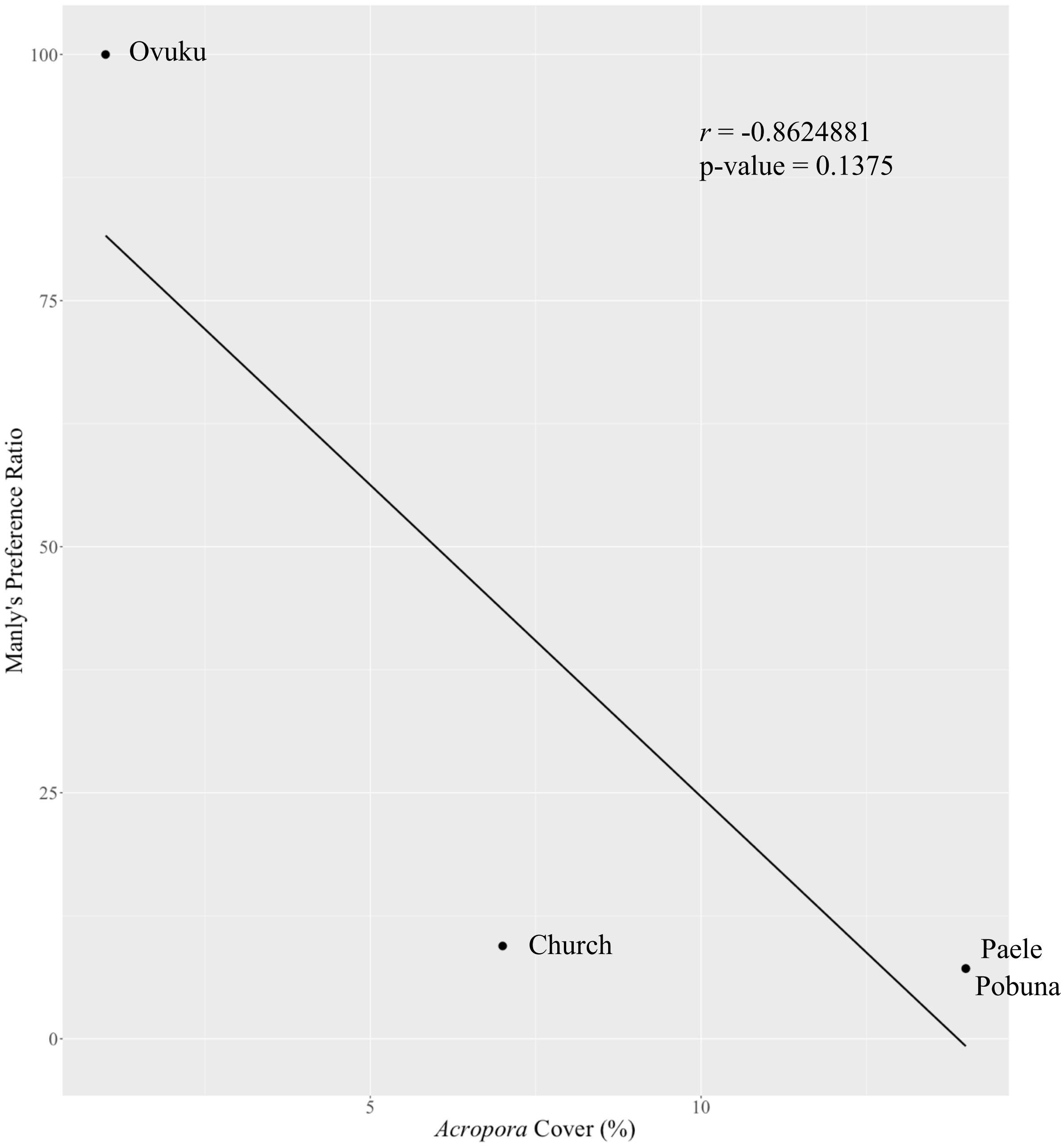
Manly's Preference Ratio of Substrates for Chaetodon vagabundus *at Sampling Sites Along a Turbidity Gradient*



Note. Preference ratio > 1 indicates substrate preference; preference ratio < 1 indicates avoidance. Manly's preference ratio values are log-transformed to better visualise the data, which includes extreme values. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Sites are listed in increasing distance from the mouth of Vavanga River.

Figure 3.2.7

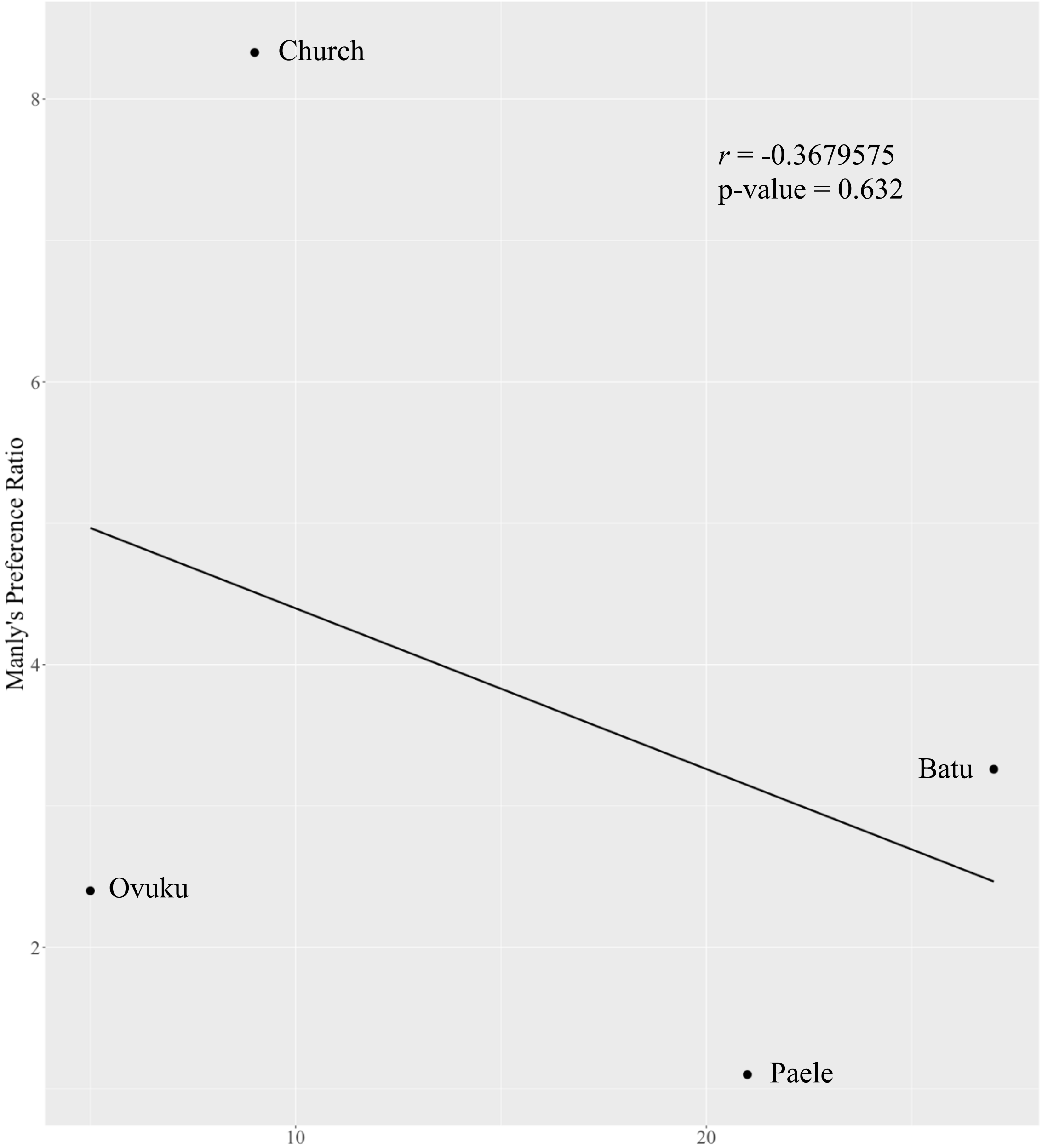
Relationship Between Acropora *Percentage Cover and Manly's Preference Ratio of* C. baronessa *for* Acropora*: Pearson's Product-Moment Correlation*



Note. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Listed in increasing distance from the mouth of Vavanga River, the sampling sites are Ovuku, Paele, Church, and Pobuna.

Figure 3.2.8

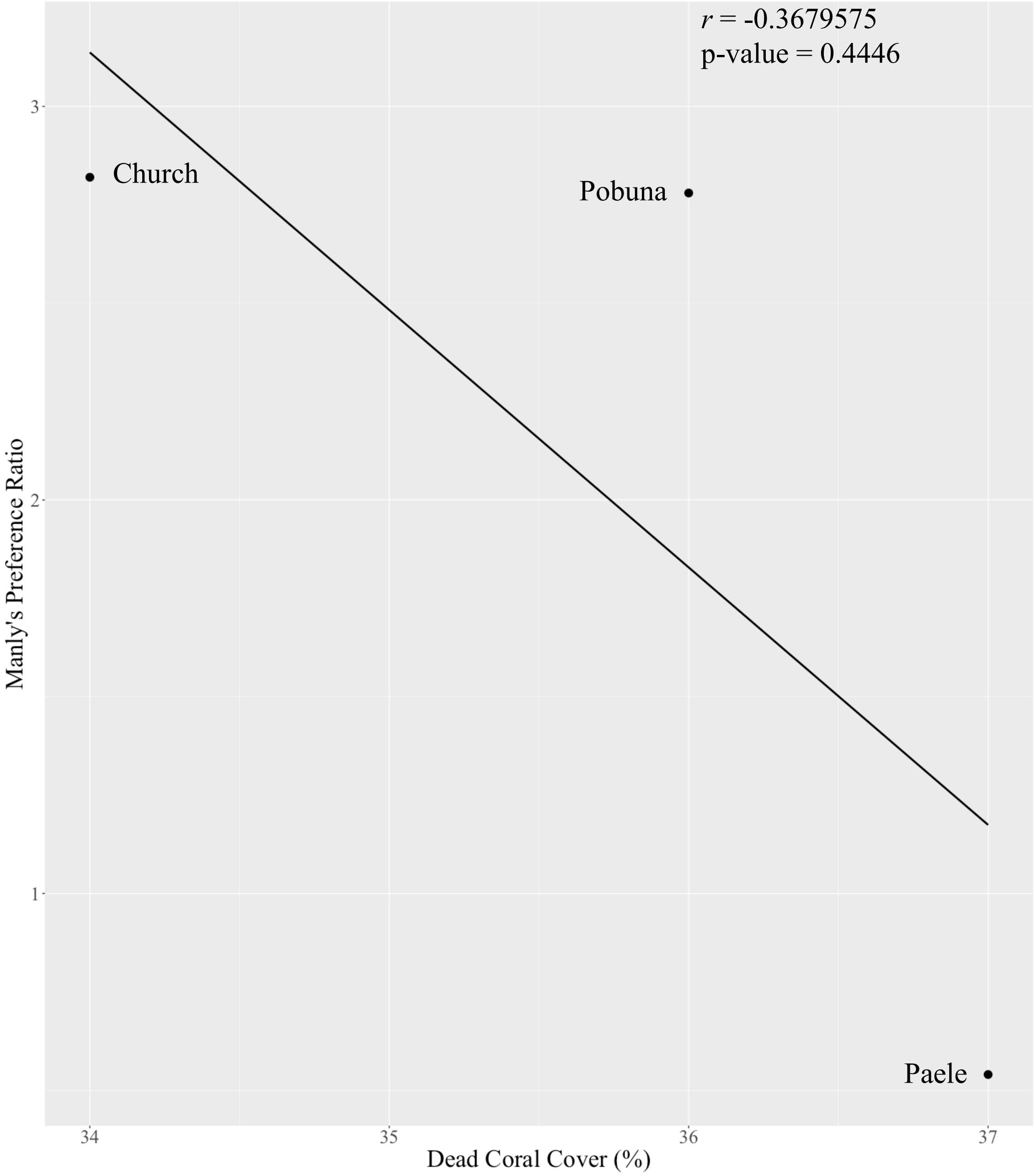
Relationship Between Porites *Percentage Cover and Manly's Preference Ratio of* C. lunulatus *for* Porites*: Pearson's Product-Moment Correlation*



Note. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Listed in increasing increasing distance from the mouth of Vavanga River, the sampling sites are Ovuku, Batu, Paele, and Church.

Figure 3.2.9

Relationship Between Dead Coral Percentage Cover and Manly's Preference Ratio of C. vagabundus *for Dead Coral: Pearson's Product-Moment Correlation*



Note. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Listed in increasing increasing distance from the mouth of Vavanga River, the sampling sites are Paele, Church, and Pobuna.

3.3 Analysis of measured variables

Scatterplots were created to explore the relationship between the measured variables bite distance, bite rate, mass, ODBA, and velocity for *C. baronessa* (Figure 3.3.1), *C. lunulatus* (Figure 3.3.2), and *C. vagabundus* (Figure 3.3.3). The scatterplots depict the distribution of data points with a fitted line obtained from linear regression. Pearson's product-moment correlation analysis revealed a correlation coefficient for each pair, indicating the strength and direction of the correlation along with a p-value to determine statistical significance (Table 3.3.1). *C. baronessa* and *C. lunulatus* showed a significant, positive correlation between velocity and ODBA (Pearson's product-moment correlation: *C. baronessa* p = < 0.003, cor = 0.465; *C. lunulatus* p = 0.004, cor = 0.433. *C. lunulatus* showed a significant, negative correlation between mass and bite rate (Pearson's product-moment correlation: p = 0.004, cor = -0.643). *C. vagabundus* did not show correlations between any of the measured variables.

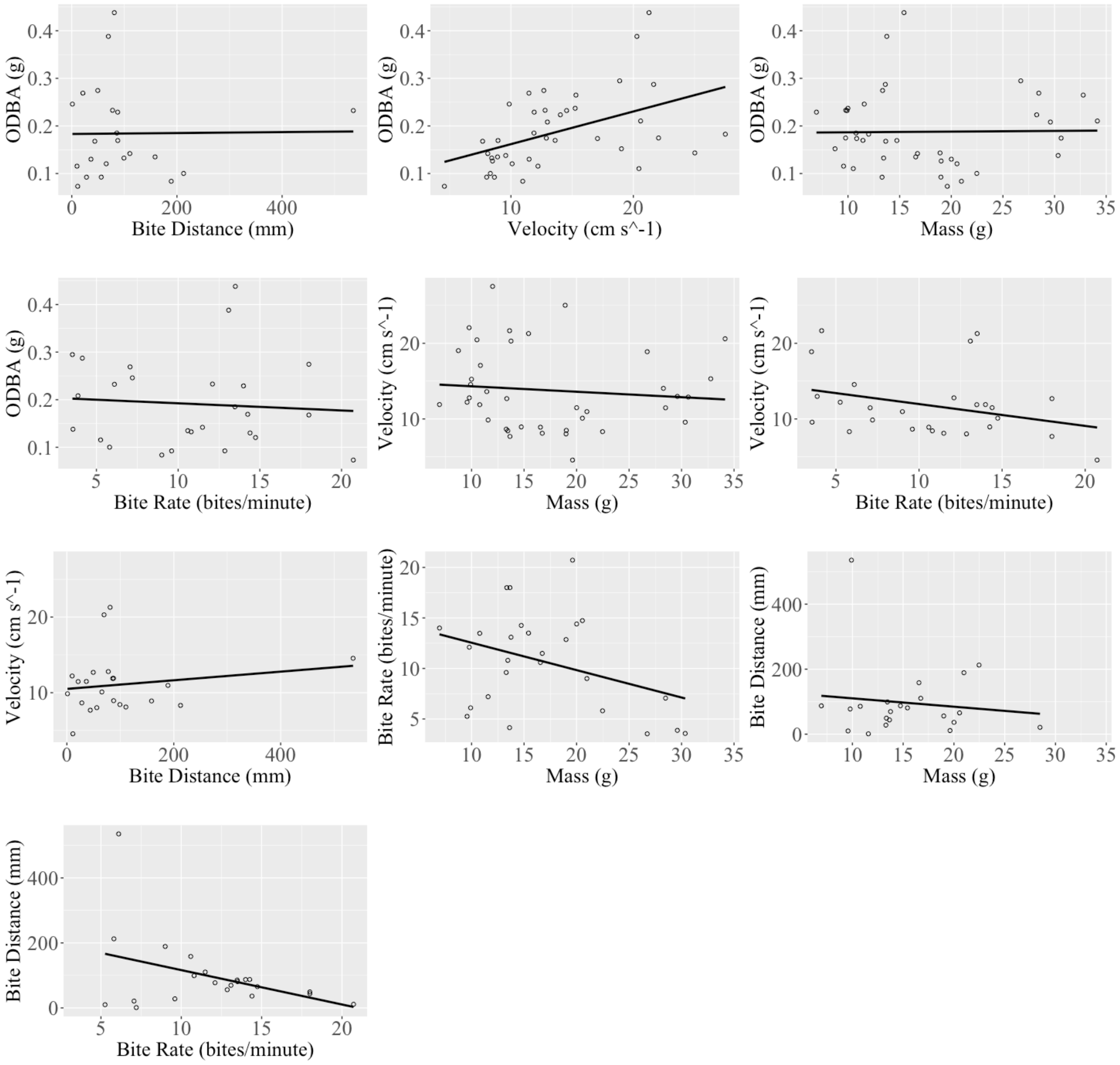
Scatterplots were also created to explore the relationship between Forel-Ule Index and bite distance, bite rate, mass, ODBA, total length, and velocity for *C. baronessa* (Figure 3.3.4), *C. lunulatus* (Figure 3.3.5), and *C. vagabundus* (Figure 3.3.6). The scatterplots depict the distribution of data points with a fitted line obtained from linear regression. Pearson's product-moment correlation analysis revealed a correlation coefficient for each pair, indicating the strength and direction of the correlation along with a p-value to determine statistical significance (Table 3.3.2). *C. baronessa* and *C. lunulatus* showed a significant, positive correlation between the Forel-Ule Index and velocity (Pearson's product-moment correlation: *C. baronessa* p = < 0.001, cor = 0.598; *C. lunulatus* p = 0.022, cor = 0.347). *C. baronessa* and *C. lunulatus* showed a significant, negative correlation between the Forel-Ule Index and mass (Pearson's product-moment correlation: *C. baronessa* p = 0.029, cor = -0.350; *C. lunulatus* p = 0.002, cor = -0.462) and between the Forel-Ule Index and total length (Pearson's product-moment correlation: *C. baronessa* p = 0.040, cor = -0.330; *C. lunulatus* p = 0.004, cor = -0.428). *C. baronessa* showed a significant, positive correlation between the Forel-Ule Index and ODBA (Pearson's product-moment correlation: *C. baronessa* p = < 0.001, cor = 0.540). *C. vagabundus* did not show correlations between the Forel-Ule Index and any of the measured variables.

There was a significant difference in the bite rate of *C. baronessa* and *C. vagabundus* across all sites (ANOVA: F(2, 65) = 4.486, p = 0.015; Tukey's HSD post-hoc test: p adj = 0.01) (Figure 3.3.7); specifically the bite rate of *C. vagabundus* was significantly lower than that of *C. baronessa*. However, there was no significant difference in the bite rate between *C. lunulatus* and either *C. baronessa* or *C. vagabundus* (Tukey's HSD post-hoc test: adjusted p-values > 0.05).

For a table of all measured variables, see Table A6 in the Appendix.

Figure 3.3.1

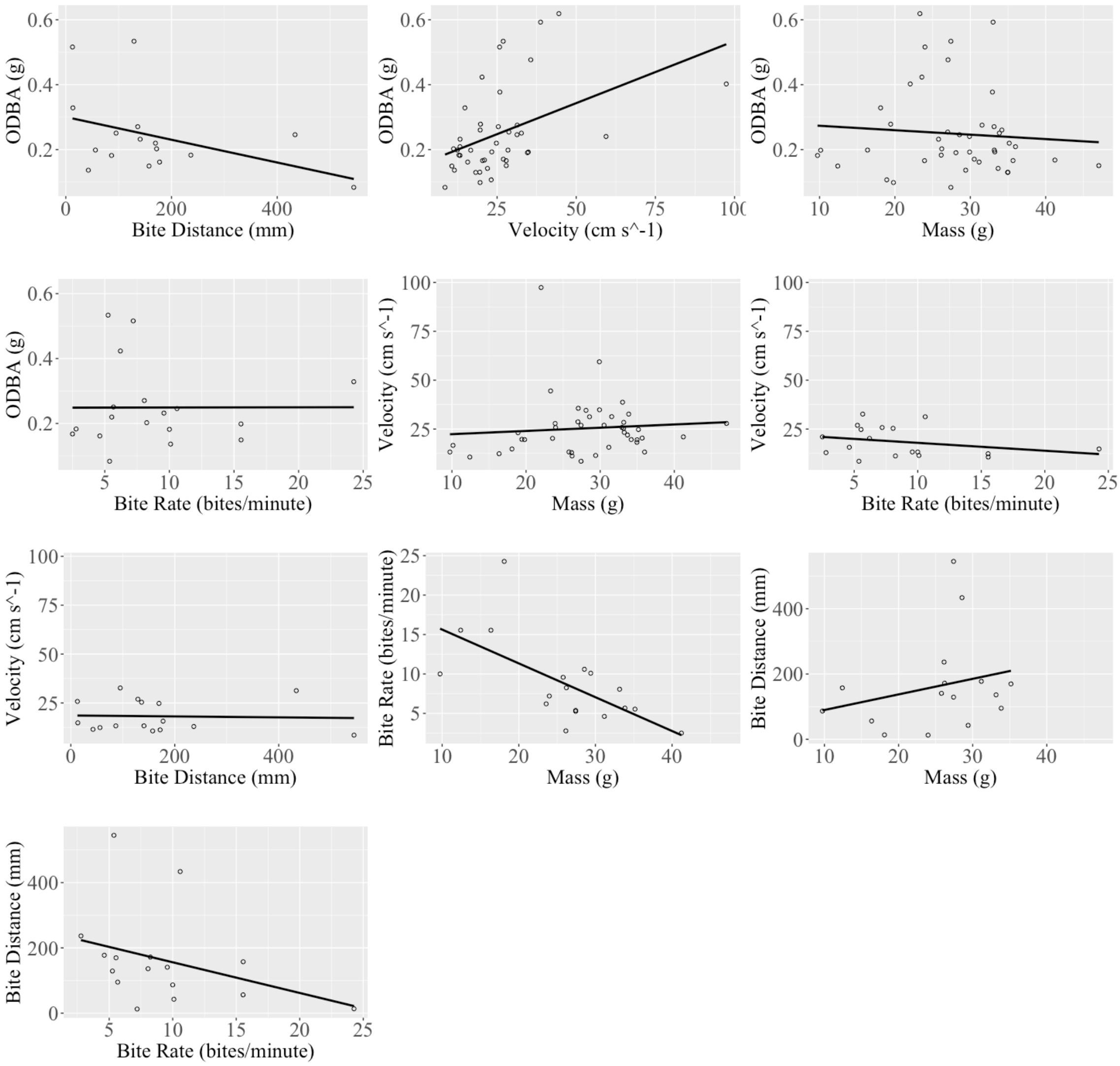
Relationships between Bite Distance, Bite Rate, Mass, ODBA, and Velocity for Chaetodon baronessa



Note. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands.

Figure 3.3.2

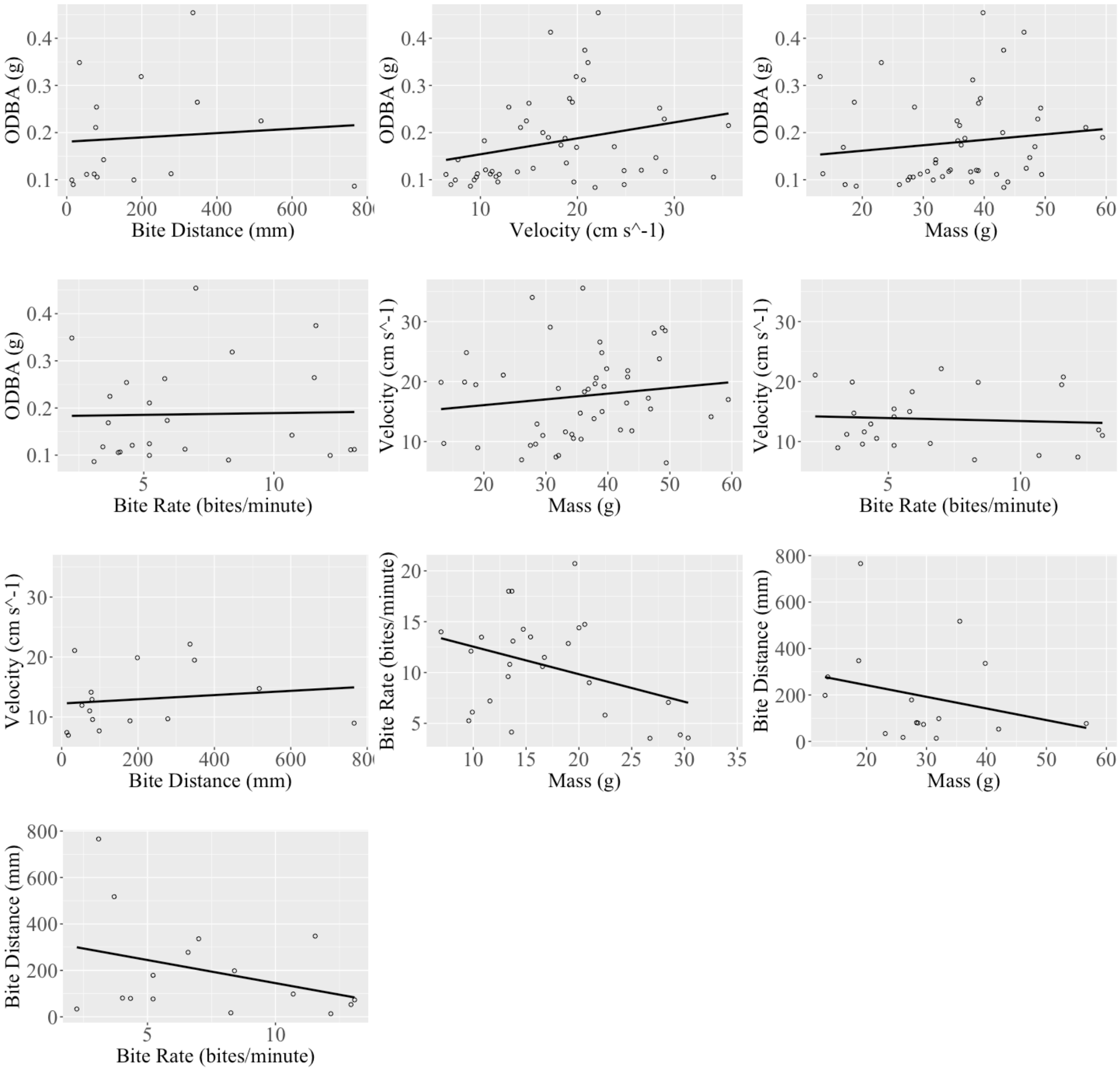
Relationships between Bite Distance, Bite Rate, Mass, ODBA, and Velocity for Chaetodon lunulatus



Note. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands.

Figure 3.3.3

Relationships between Bite Distance, Bite Rate, Mass, ODBA, and Velocity for Chaetodon vagabundus



Note. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands.

Table 3.3.1

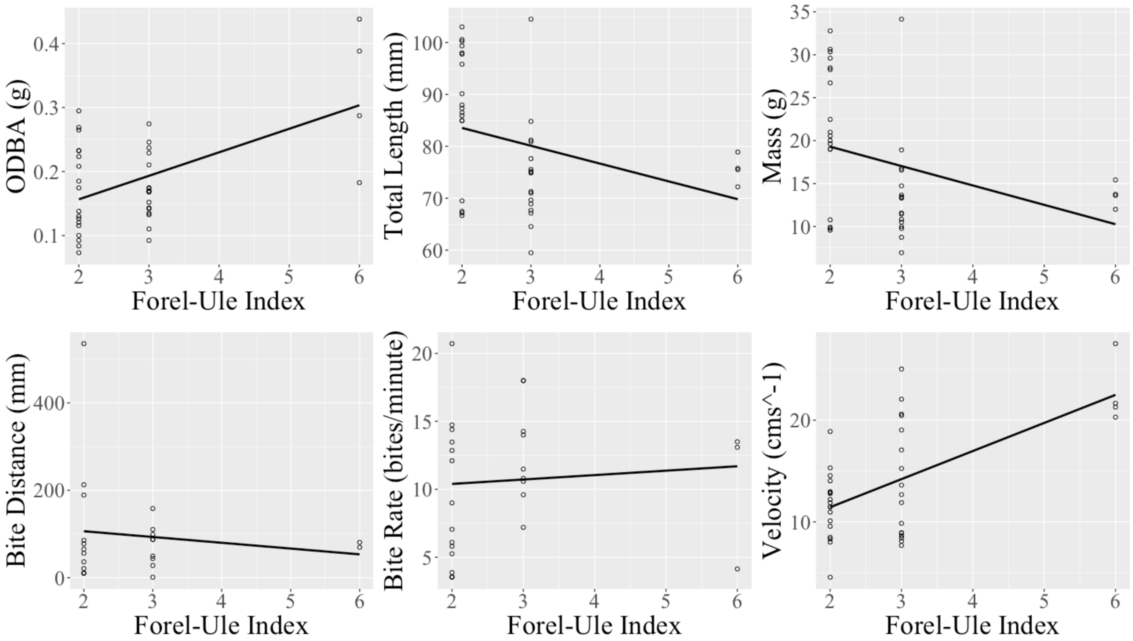
Correlations between Measured Variables in Chaetodon *Butterflyfish Species: Pearson's Product-Moment Correlation*

Species	Independent variable	Dependent variable	Pearson's correlation coefficient	p-value
C. baronessa	Bite distance	ODBA	0.01135525	0.96
C. baronessa	**Velocity**	**ODBA**	**0.4653343**	**0.002835**
C. baronessa	Mass	ODBA	0.01379178	0.9336
C. baronessa	Bite rate	ODBA	-0.07742239	0.707
C. baronessa	Mass	Velocity	-0.100657	0.5421
C. baronessa	Bite rate	Velocity	-0.3191469	0.112
C. baronessa	Bite distance	Velocity	0.1659031	0.4606
C. baronessa	Mass	Bite rate	-0.3630863	0.06829
C. baronessa	Mass	Bite distance	-0.1175183	0.6025
C. baronessa	Bite rate	Bite distance	-0.3900146	0.07275
C. lunulatus	Bite distance	ODBA	-0.4051483	0.1195
C. lunulatus	**Velocity**	**ODBA**	**0.4325885**	**0.003766**
C. lunulatus	Mass	ODBA	-0.08008695	0.6097
C. lunulatus	Bite rate	ODBA	0.00236976	0.9926
C. lunulatus	Mass	Velocity	0.08566369	0.5849
C. lunulatus	Bite rate	Velocity	-0.2821916	0.2566
C. lunulatus	Bite distance	Velocity	0.04239579	0.8761
C. lunulatus	**Mass**	**Bite rate**	**-0.6429698**	**0.003999**
C. lunulatus	Mass	Bite distance	0.2498697	0.3507
C. lunulatus	Bite rate	Bite distance	-0.3532588	0.1795
C. vagabundus	Bite distance	ODBA	0.08528514	0.7535
C. vagabundus	Velocity	ODBA	0.2657178	0.07104
C. vagabundus	Mass	ODBA	0.1335242	0.3709
C. vagabundus	Bite rate	ODBA	0.02494542	0.9079
C. vagabundus	Mass	Velocity	0.4105953	0.3459
C. vagabundus	Bite rate	Velocity	-0.07103798	0.7415
C. vagabundus	Bite distance	Velocity	0.143101	0.597
C. vagabundus	Mass	Bite rate	-0.07103798	0.7415
C. vagabundus	Mass	Bite distance	-0.2670356	0.3174
C. vagabundus	Bite rate	Bite distance	-0.3524881	0.1806

Note. Correlation coefficients significant at p-value < 0.05 are indicated in bold. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands.

Figure 3.3.4

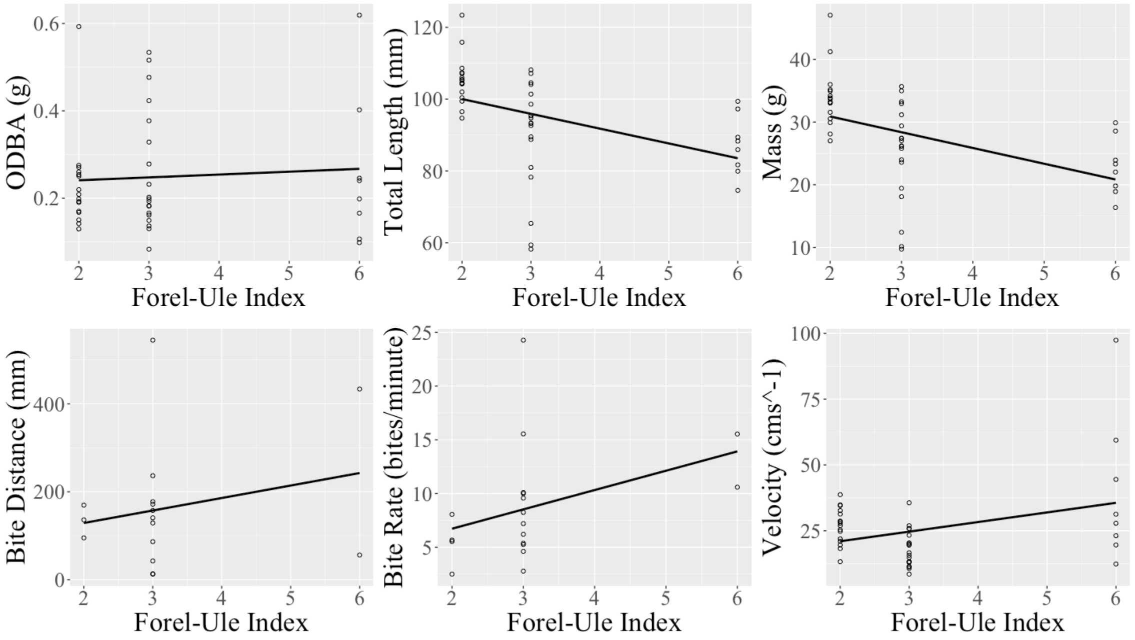
Relationships between Forel-Ule Index and Bite Distance, Bite Rate, Mass, ODBA, and Velocity for Chaetodon baronessa



Note. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands.

Figure 3.3.5

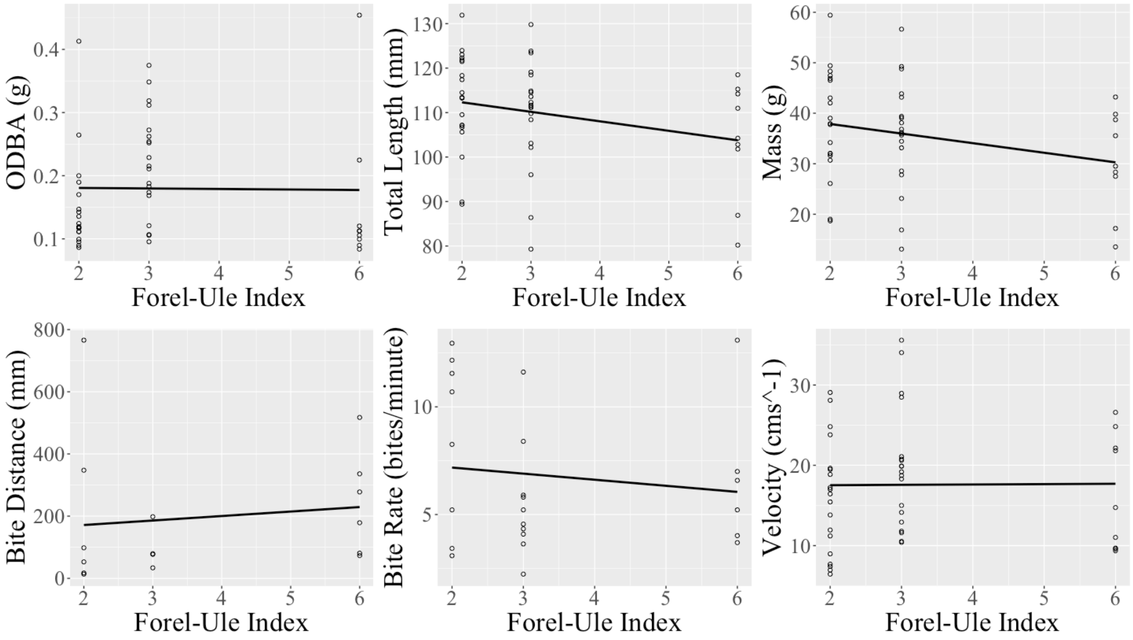
Relationships between Forel-Ule Index and Bite Distance, Bite Rate, Mass, ODBA, and Velocity for Chaetodon lunulatus



Note. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands.

Figure 3.3.6

Relationships between Forel-Ule Index and Bite Distance, Bite Rate, Mass, ODBA, and Velocity for Chaetodon vagabundus



Note. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands.

Table 3.3.2

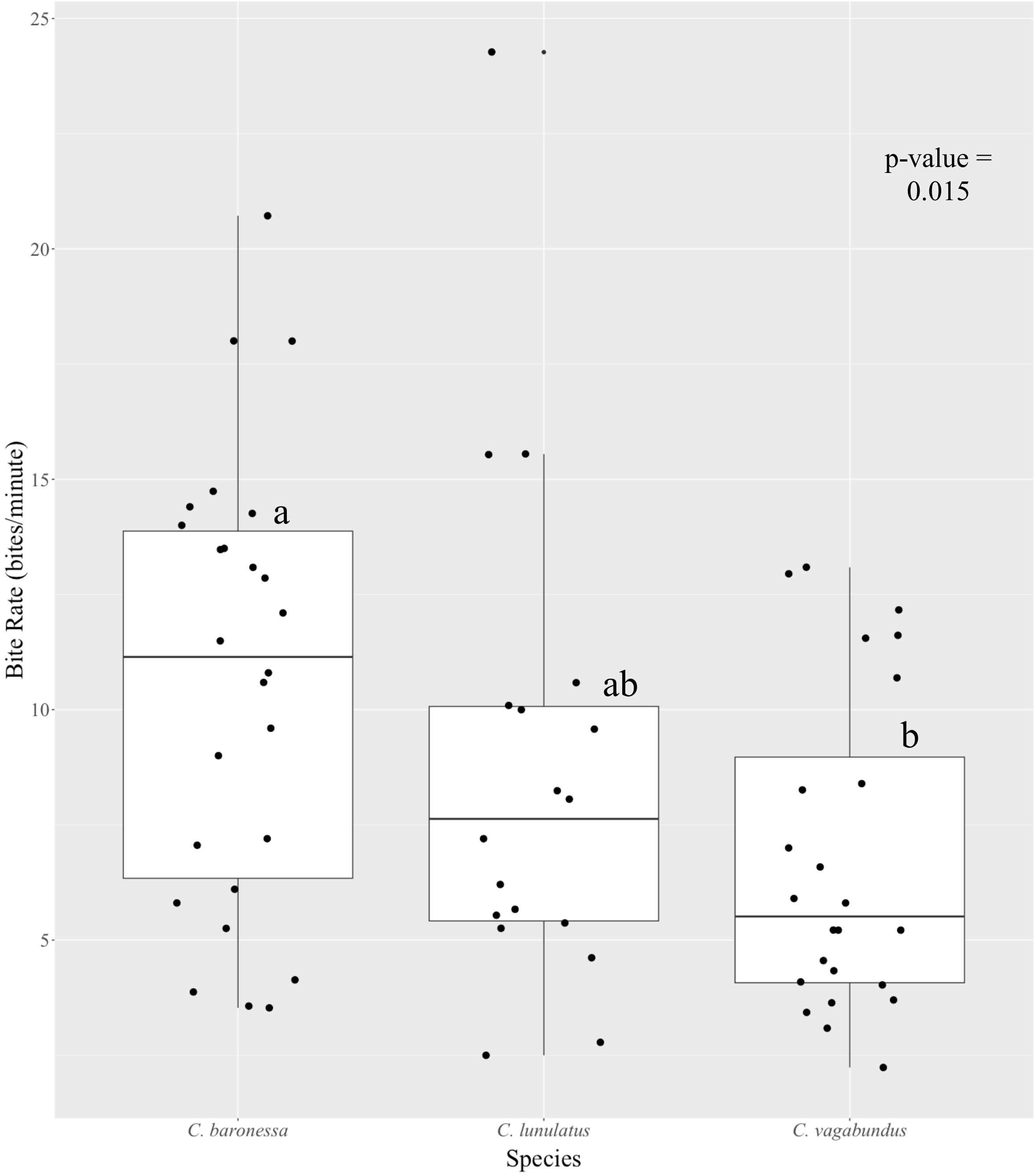
Correlations between Forel-Ule Index and Measured Variables in Chaetodon *Butterflyfish Species: Pearson's Product-Moment Correlation*

Species	Independent variable	Dependant variable	Pearson's correlation coeeficient	p-value
C. baronessa	Forel-Ule index	Bite distance	-0.1353321	0.5482
C. baronessa	Forel-Ule index	Bite rate	0.08495336	0.6799
C. baronessa	**Forel-Ule index**	**Mass**	**-0.3496557**	**0.02911**
C. baronessa	**Forel-Ule index**	**ODBA**	**0.5396648**	**0.0003918**
C. baronessa	**Forel-Ule index**	**Velocity**	**0.5977138**	**5.87E-05**
C. baronessa	**Forel-Ule index**	**Total length**	**-0.3298465**	**0.0403**
C. lunulatus	Forel-Ule index	Bite distance	0.2311391	0.3891
C. lunulatus	Forel-Ule index	Bite rate	0.3809256	0.1189
C. lunulatus	**Forel-Ule index**	**Mass**	**-0.4621313**	**0.00181**
C. lunulatus	Forel-Ule index	ODBA	0.07047172	0.6534
C. lunulatus	**Forel-Ule index**	**Velocity**	**0.3474144**	**0.02245**
C. lunulatus	**Forel-Ule index**	**Total length**	**-0.4279713**	**0.004198**
C. vagabundus	Forel-Ule index	Bite distance	0.1273049	0.6358
C. vagabundus	Forel-Ule index	Bite rate	-0.1299195	0.5451
C. vagabundus	Forel-Ule index	Mass	-0.2589844	0.07878
C. vagabundus	Forel-Ule index	ODBA	-0.01289278	0.9315
C. vagabundus	Forel-Ule index	Velocity	0.00895096	0.9524
C. vagabundus	Forel-Ule index	Total length	-0.2554625	0.08308

Note. Correlation coefficients significant at p-value < 0.05 are indicated in bold. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands.

Figure 3.3.7

Comparison of Average Bite Rates for Three Species of Chaetodon *Butterflyfish*



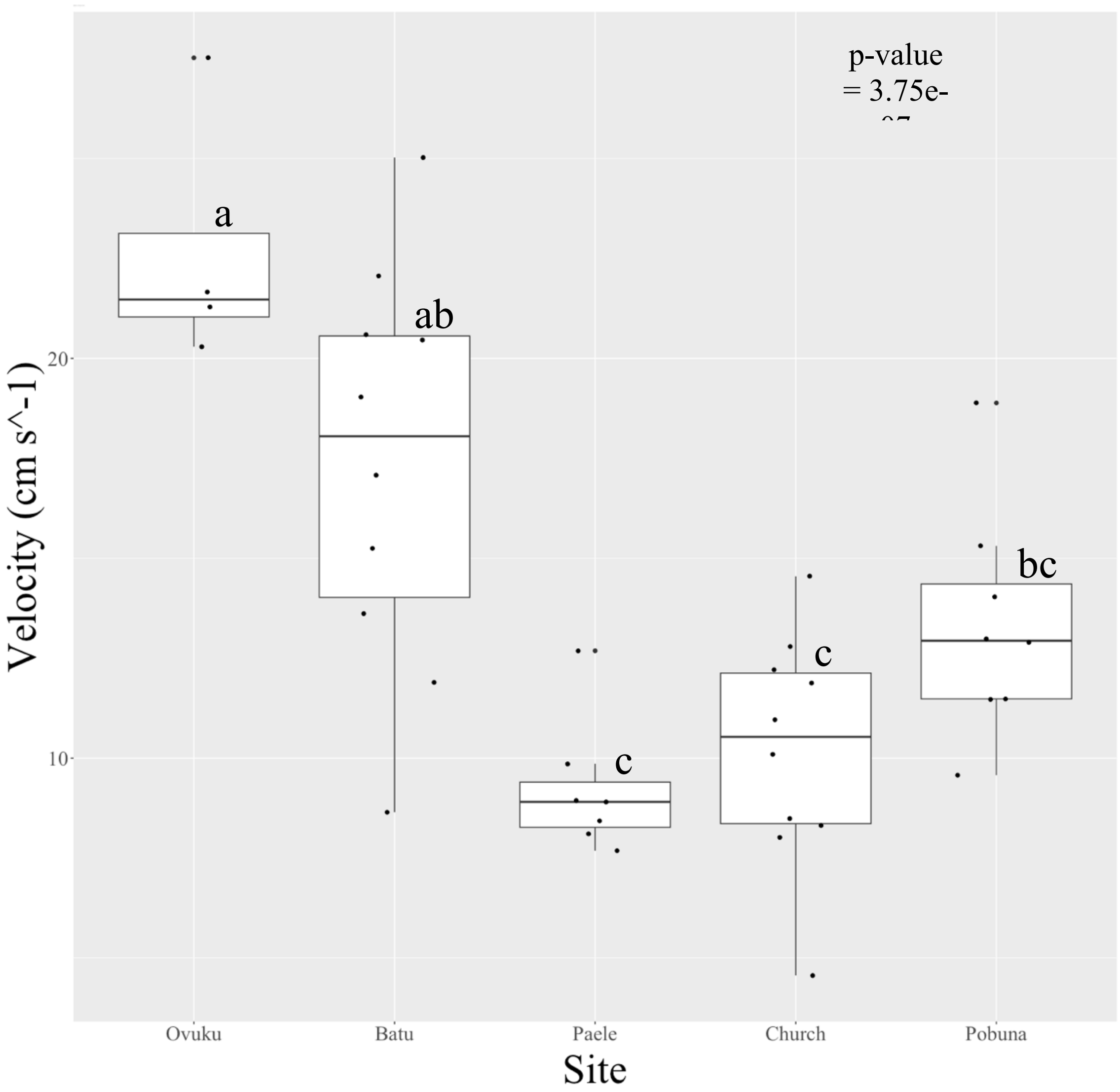
Note. Different letters above the box plots represent statistically significant differences between groups according to Tukey’s HSD post-hoc test. Groups sharing the same letter are not significantly different from each other, while groups with different letters are significantly different. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands.

3.3.1 *Chaetodon baronessa*

Significant differences in velocity (ANOVA: F(4, 34) = 14.97, $p = < 0.001$) and ODBA (ANOVA: F(4, 34) = 6.836, $p = < 0.001$) existed between sites. Tukey's HSD post-hoc test revealed velocity to be significantly different between fish at half of the sampling sites (Figure 3.3.1.1, Table 3.3.1.1) and ODBA to be significantly different between fish at Ovuku and all other sampling sites except Pobuna (Figure 3.3.1.2, Table 3.3.1.2). There was also a significant difference in mass (Kruskal-Wallis rank sum test: $\chi^2(4) = 17.671$, $p = 0.001431$) between Batu and Pobuna (Figure 3.3.1.3, Table 3.3.1.3). Analysis did not yield a significant effect of the sampling sites on bite distance or bite rate.

Figure 3.3.1.1

Comparison of Velocity for Chaetodon baronessa *at Sampling Sites Along a Turbidity Gradient*



Note. Different letters above the box plots represent statistically significant differences between groups according to Tukey's HSD post-hoc test. Groups sharing the same letter are not significantly different from each other, while groups with different letters are significantly different. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Sites are listed in increasing distance from the mouth of Vavanga River.

Table 3.3.1.1

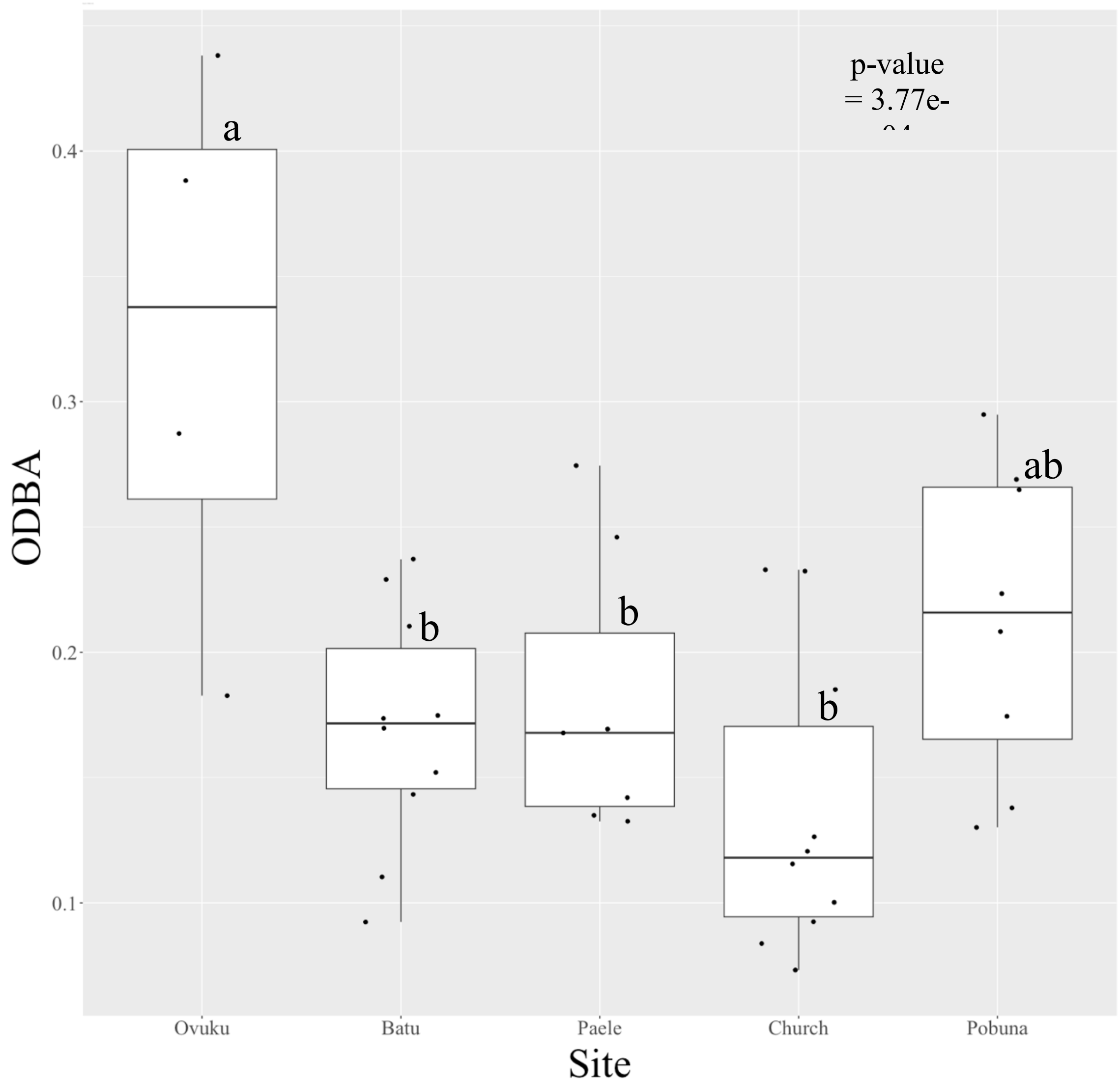
Tukey's HSD Post-Hoc Test for Velocity of Chaetodon baronessa *Between Sampling Sites*

Comparison Groups	Diff	Lower Bound	Upper Bound	p Adjusted
Church-Batu	**-7.1761232**	**-11.6452716**	**-2.7069749**	**0.0004767**
Ovuku-Batu	5.3234137	-0.5887139	11.2355413	0.0943066
Paele-Batu	**-8.1334477**	**-13.0582093**	**-3.208686**	**0.0003248**
Pobuna-Batu	-4.0356459	-8.7758935	0.7046018	0.1262538
Ovuku-Church	**12.4995369**	**6.5874094**	**18.4116645**	**0.0000063**
Paele-Church	-0.9573244	-5.8820861	3.9674372	0.9799426
Pobuna-Church	3.1404774	-1.5997703	7.8807251	0.3327662
Paele-Ovuku	**-13.4568614**	**-19.7205059**	**-7.1932168**	**0.0000047**
Pobuna-Ovuku	**-9.3590596**	**-15.478693**	**-3.2394261**	**0.0008984**
Pobuna-Paele	4.0978018	-1.0742324	9.269836	0.1757389

Note. Sampling sites significant at $p < 0.05$ are indicated in bold. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Listed in increasing increasing distance from the mouth of Vavanga River, the sampling sites are Ovuku, Batu, Paele, Church, and Pobuna.

Figure 3.3.1.2

Comparison of ODBA for Chaetodon baronessa *at Sampling Sites Along a Turbidity Gradient*



Note. Different letters above the box plots represent statistically significant differences between groups according to Tukey's HSD post-hoc test. Groups sharing the same letter are not significantly different from each other, while groups with different letters are significantly different. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Sites are listed in increasing distance from the mouth of Vavanga River.

Table 3.3.1.2

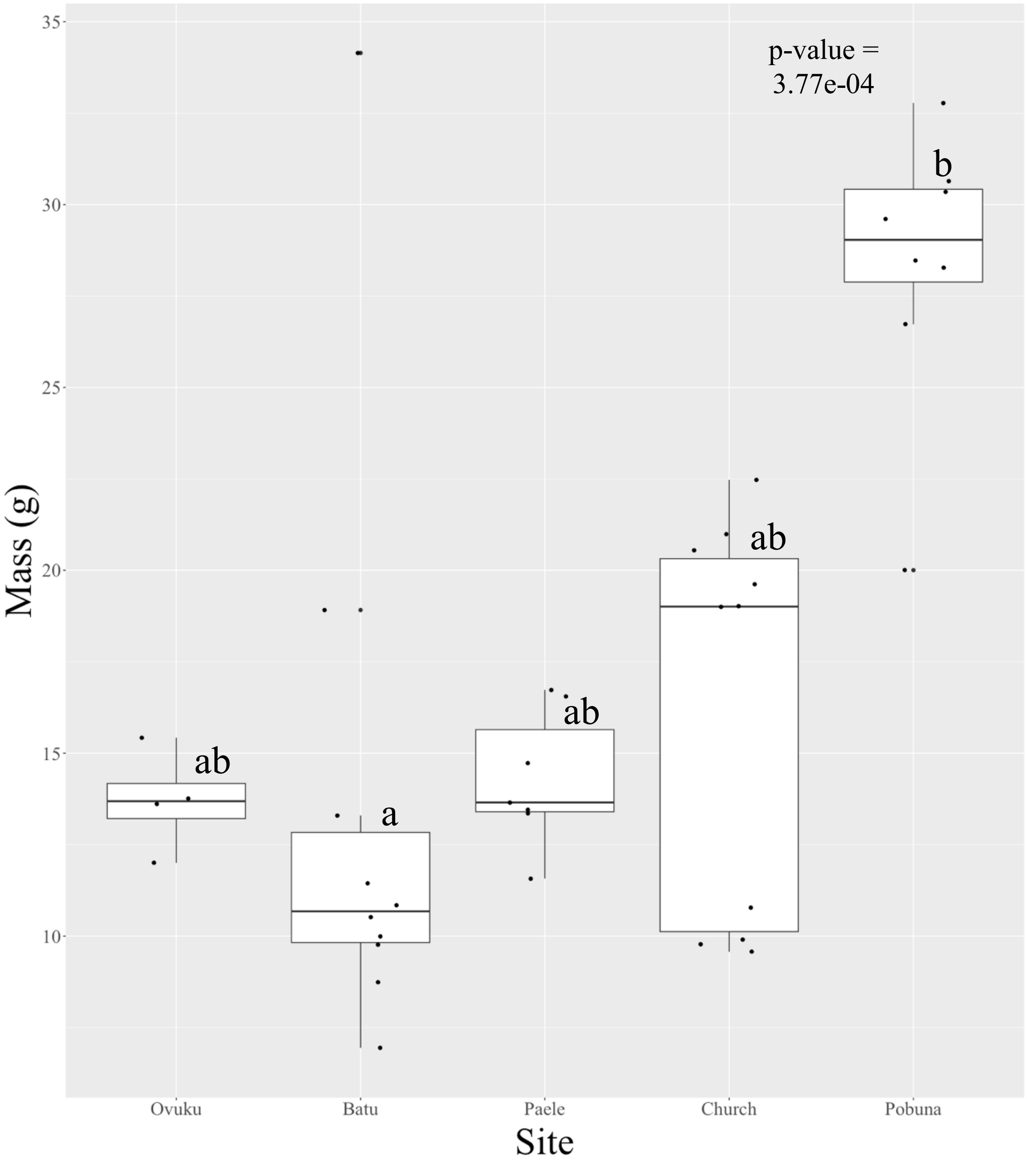
Tukey's HSD Post-Hoc Test for ODBA of Chaetodon baronessa *Between Sampling Sites*

Comparison Groups	Diff	Lower Bound	Upper Bound	p Adjusted
Church-Batu	-0.03302791	-0.114567465	0.048511651	0.770033
Ovuku-Batu	**0.15478625**	**0.046919553**	**0.262652945**	**0.001942**
Paele-Batu	0.01174328	-0.078108933	0.1015955	0.9955278
Pobuna-Batu	0.04358187	-0.042903888	0.130067635	0.6000741
Ovuku-Church	**0.18781416**	**0.07994746**	**0.295680852**	**0.0001525**
Paele-Church	0.04477119	-0.045081026	0.134623407	0.6102062
Pobuna-Church	0.07660978	-0.009875981	0.163095542	0.1030264
Paele-Ovuku	**-0.14304297**	**-0.257323084**	**-0.028762847**	**0.0082211**
Pobuna-Ovuku	-0.11120438	-0.222857013	0.000448263	0.0513477
Pobuna-Paele	0.03183859	-0.062525112	0.126202292	0.8660036

Note. Sampling sites significant at $p < 0.05$ are indicated in bold. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Listed in increasing increasing distance from the mouth of Vavanga River, the sampling sites are Ovuku, Batu, Paele, Church, and Pobuna.

Figure 3.3.1.3

Comparison of Mass for Chaetodon baronessa *at Sampling Sites Along a Turbidity Gradient*



Note. Different letters above the box plots represent statistically significant differences between groups according to Dunn Kruskal-Wallis Multiple Comparison Test. Groups sharing the same letter are not significantly different from each other, while groups with different letters are significantly different. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Sites are listed in increasing distance from the mouth of Vavanga River.

Table 3.3.1.3

Dunn Kruskal-Wallis Multiple Comparison Test for Mass of Chaetodon baronessa *Between Sampling Sites (P-Values Adjusted with the Bonferroni Method)*

Comparison Groups	Z	p Unadjusted	p Adjusted
Batu - Church	-1.39242456	1.64E-01	1
Batu - Ovuku	-0.81537425	4.15E-01	1
Church - Ovuku	0.23719978	8.13E-01	1
Batu - Paele	-1.06783496	2.86E-01	1
Church - Paele	0.19576974	8.45E-01	1
Ovuku - Paele	-0.06996503	9.44E-01	1
Batu - Pobuna	**-4.09091395**	**4.30E-05**	**0.000429677**
Church - Pobuna	-2.77812348	5.47E-03	0.054673836
Ovuku - Pobuna	-2.38108196	1.73E-02	0.17261871
Paele - Pobuna	-2.73260231	6.28E-03	0.062836153

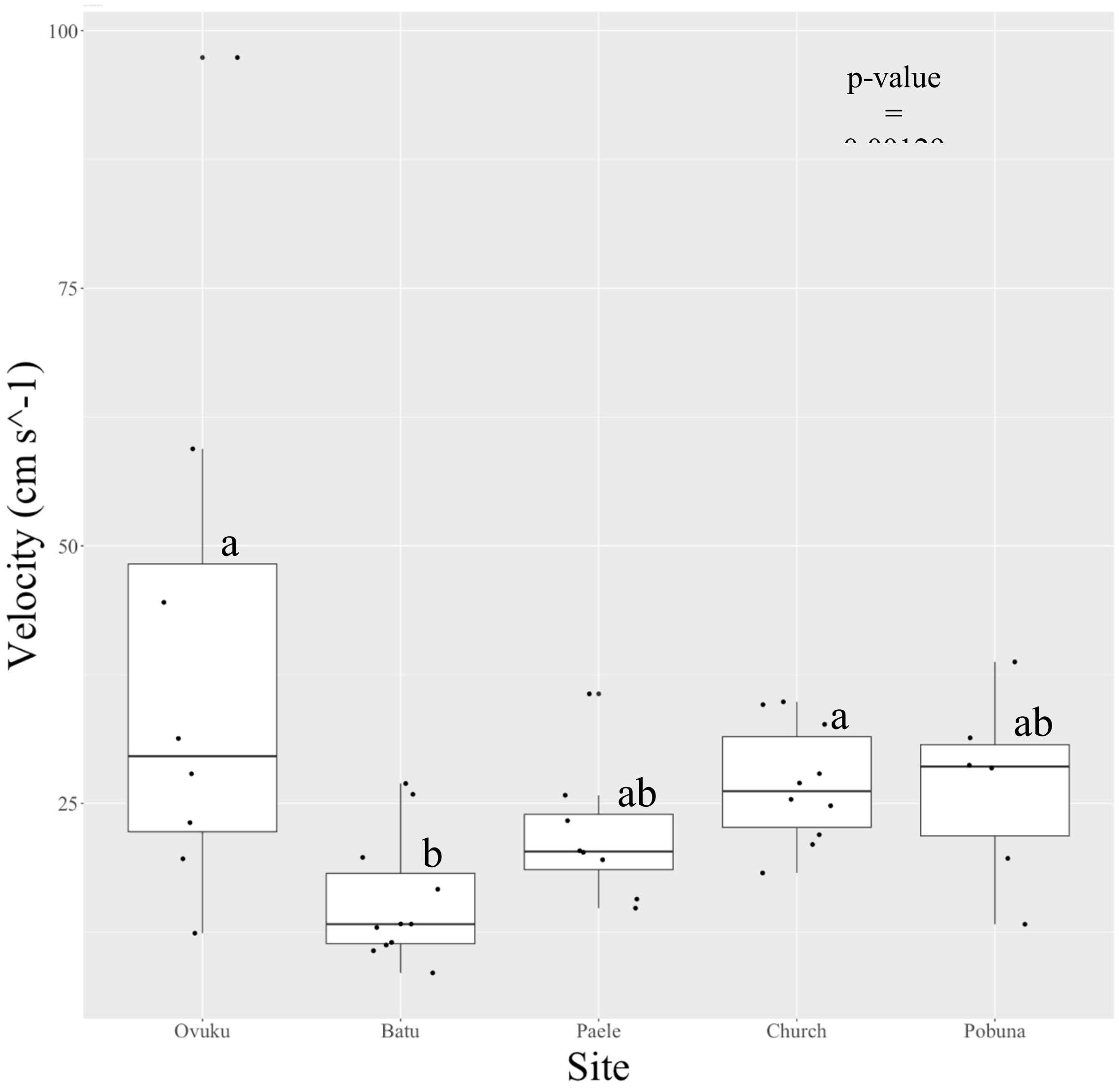
Note. Sampling sites significant at $p < 0.05$ are indicated in bold. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Listed in increasing increasing distance from the mouth of Vavanga River, the sampling sites are Ovuku, Batu, Paele, Church, and Pobuna.

3.3.2 *Chaetodon lunulatus*

There was a significant difference in velocity (ANOVA: F(4, 38) = 3.908, p = 0.00938) between Batu and Ovuku and between Batu and Church (Figure 3.3.2.1, Table 3.3.2.1). Analysis did not yield a significant effect of the sampling sites on bite distance, bite rate, mass, or ODBA.

Figure 3.3.2.1

Comparison of Velocity for Chaetodon lunulatus *at Sampling Sites Along a Turbidity Gradient*



Note. Different letters above the box plots represent statistically significant differences between groups according to Tukey’s HSD post-hoc test. Groups sharing the same letter are not significantly different from each other, while groups with different letters are significantly different. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Sites are listed in increasing distance from the mouth of Vavanga River.

Table 3.3.2.1

Tukey's HSD Post-Hoc Test for Velocity of Chaetodon lunulatus *Between Sampling Sites*

Comparison Groups	Diff	Lower Bound	Upper Bound	p Adjusted
Church-Batu	**0.59058651**	**0.09144262**	**1.0897304**	**0.0134729**
Ovuku-Batu	**0.80521117**	**0.27439039**	**1.336032**	**0.0009084**
Paele-Batu	0.37436571	-0.15645508	0.9051865	0.2766168
Pobuna-Batu	0.55035204	-0.02943026	1.1301343	0.0698241
Ovuku-Church	0.21462467	-0.32725608	0.7565054	0.7876265
Paele-Church	-0.2162208	-0.75810155	0.3256599	0.7831117
Pobuna-Church	-0.04023447	-0.6301595	0.5496906	0.99966
Paele-Ovuku	-0.43084547	-1.00203792	0.140347	0.217029
Pobuna-Ovuku	-0.25485913	-0.8718175	0.3620992	0.7610414
Pobuna-Paele	0.17598634	-0.44097203	0.7929447	0.9238655

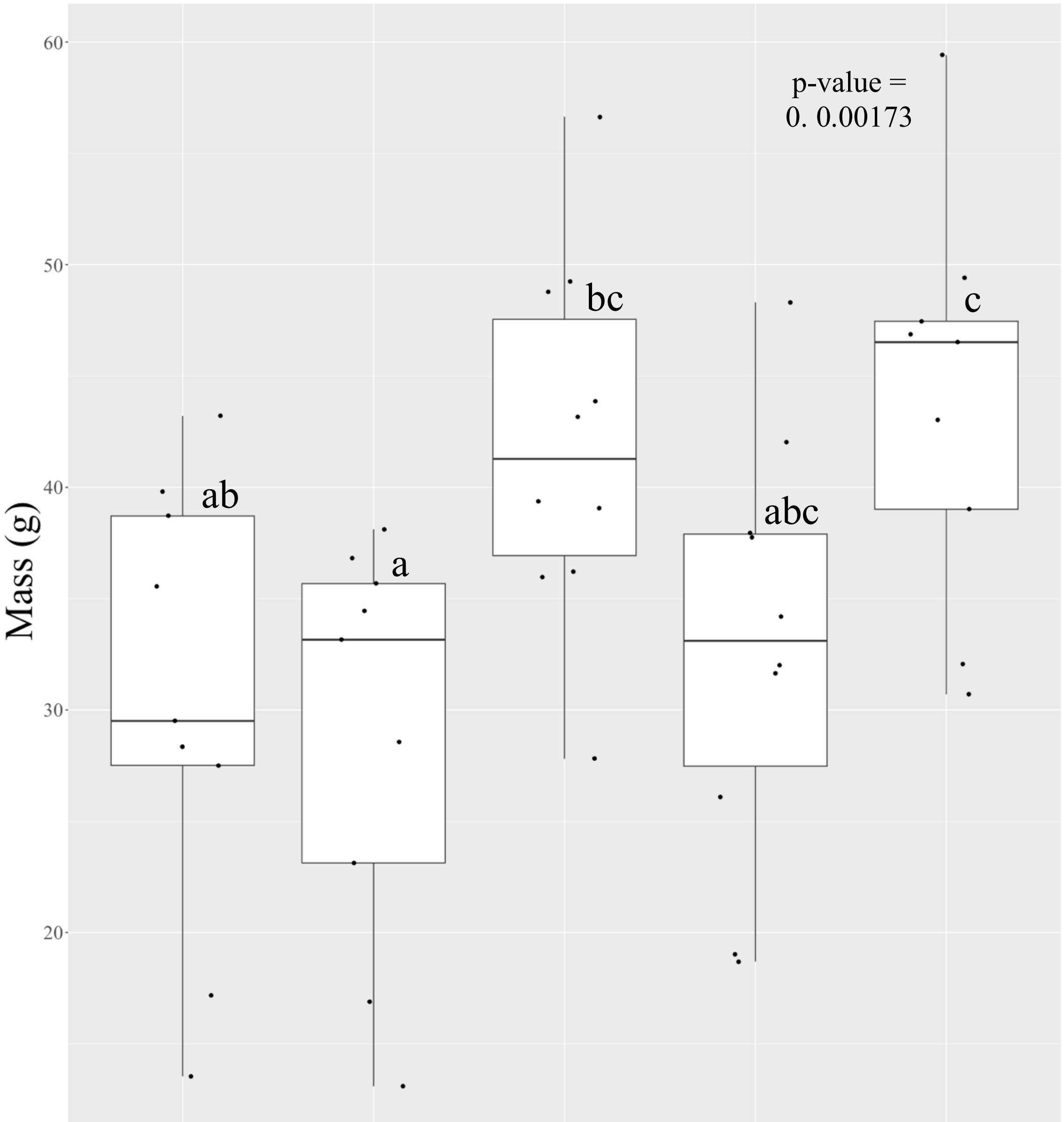
Note. Sampling sites significant at $p < 0.05$ are indicated in bold. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Listed in increasing increasing distance from the mouth of Vavanga River, the sampling sites are Ovuku, Batu, Paele, Church, and Pobuna.

3.3.3 *Chaetodon vagabundus*

There was a significant difference in mass (ANOVA: $F(4, 42) = 5.19$, $p = 0.002$) between Ovuku and Pobuna, Batu and Paele, and Batu and Pobuna. (Figure 3.3.3.1, Table 3.3.3.1). Analysis did not yield a significant effect of the sampling sites on bite distance, bite rate, ODBA, or velocity.

Figure 3.3.3.1

Comparison of Mass for Chaetodon vagabundus *at Sampling Sites Along a Turbidity Gradient*



Note. Different letters above the box plots represent statistically significant differences between groups according to Tukey’s HSD post-hoc test. Groups sharing the same letter are not significantly different from each other, while groups with different letters are significantly different. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Sites are listed in increasing distance from the mouth of Vavanga River.

Table 3.3.3.1

Tukey's HSD Post-Hoc Test for Mass of Chaetodon vagabundus *Between Sampling Sites*

Comparison Groups	Diff	Lower Bound	Upper Bound	p Adjusted
Church-Batu	3.891072	-8.1454898	15.927633	0.8870881
Ovuku-Batu	1.495826	-10.8534256	13.845078	0.996828
Paele-Batu	**13.137185**	**1.100623**	**25.173746**	**0.0262895**
Pobuna-Batu	**14.95588**	**2.6066285**	**27.305132**	**0.0106704**
Ovuku-Church	-2.395246	-14.4318075	9.641316	0.9791141
Paele-Church	9.246113	-2.469416	20.961642	0.1820924
Pobuna-Church	11.064808	-0.9717533	23.10137	0.0848498
Paele-Ovuku	11.641359	-0.395203	23.67792	0.0622874
Pobuna-Ovuku	**13.460054**	**1.1108025**	**25.809306**	**0.0265756**
Pobuna-Paele	1.818696	-10.2178661	13.855257	0.9925711

Note. Sampling sites significant at $p < 0.05$ are indicated in bold. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Listed in increasing increasing distance from the mouth of Vavanga River, the sampling sites are Ovuku, Batu, Paele, Church, and Pobuna.

Chapter 4: Discussion

This study aimed to investigate whether fine-scale movement patterns and foraging behaviours of coral reef fish can serve as indicators for infering habitat changes within coral reef ecosystems. Focusing on chaetodontids as our coral reef-associated species of interest, this research sought to expand upon existing knowledge of this family's role as indicators of ecosystem health. Stereo-video data was collected on Vavanga Reef in the Solomon Islands; this reef presented a unique opportunity for our study because the influence of riverine discharge and historical logging resulted in a coral reef with a gradient of turbidity that was qualified with the Forel-Ule Index and visibility measurements. Data collection was focussed along this gradient, capturing footage of fish movement and foraging behaviours at different sites representing different levels of turbidity. From this footage, VidSync stereo-video analysis software was used to measure and track, in 3D space, three species of butterflyfish. *C. baronessa* is a highly specialised obligate corallivore, feeding mainly on the polyps of *Acropora* corals. *C. lunulatus* is a generalist corallivore; however, it is also known to consume macroinvertebrates occasionally. *C. vagabundus* is a generalist omnivore consuming a wide variety of corals, algae, and invertebrates. From the length and tracking data, bite distance and rate, mass, ODBA, and velocity were calculated for each fish.

4.1 Environmental factors influencing substrates

Results showed that the Forel-Ule Index and visibility were good proxies for turbidity. Furthermore, turbidity and substrate diversity have a significantly strong, negative relationship along our sampling sites. At Vavanga Reef, it is likely that turbidity is influencing substrate availability. Lab experiments on the effects of light availability, turbidity, and sediment settling show that chronic sedimentation has a greater negative effect on coral than a reduction in light levels, highlighting the effect that turbidity has on coral survival (Junjie et al., 2014). Furthermore, the severity of turbidity impacts on coral varies amongst species, likely due to differences in their morphology and physiology (R. Jones et al., 2020; Junjie et al., 2014). At our most turbid site, Ovuku, dead coral was distinctly higher than at any other site, and this was the only site where sand was recorded. Although there is evidence for the strong impact of turbidity on coral, this study lacked data on other potentially confounding factors, such as salinity and temperature. Due to the freshwater that Vavanga River deposits directly onto the reef, it is likely that salinity is a variable impacting living substrate availability. Studies have shown that *Acropora*, *Montipora*, *Pocillopora*, and *Porites* (all found at Vavanga) cannot survive in hyposaline conditions (26 parts per thousand salinity and 26 Practical Salinity Units) (Berkelmans et al., 2012; Coles, 1992; Edmondson, 1928). Therefore, it is likely that decreased salinity, alongside increased turbidity, is contributing to the low abundance or absence of certain coral species at Ovuku and Batu.

The decline in Forel-Ule Index, visibility, and total available substrate from Church to Pobuna suggests that Pobuna may be influenced by riverine input from a nearby estuary. However, substantial seagrass meadows cover large parts of the reef flat adjacent to Pobuna, potentially tempering excess sediment input (de Boer, 2007; Martin, 2024). Confounding variables may also have contributed to this, and since our sampling of Pobuna only happened over a period of two days (15 January – 16 January 2023), the tide may have impacted the sediment at this site. We could have continued to sample further past Pobuna, but we were restricted by customary boundaries.

There are visible differences in substrate diversity, both from photographs taken in the field (Figure 2.1.2) and stacked bar charts depicting the average percentage cover of substrates at each site (Figure 3.1.4). Of the substrates relevant to this study (id est, the substrates that were foraged on by the target species), only two of them showed significant differences in percentage cover across sites: *Acropora* and dead coral. Non-surprisingly, the average percentage cover of dead coral decreased with distance from Ovuku, but the only significant difference in dead coral found at Ovuku was with Church and Pobuna. This is even though there is a 27% decrease in dead coral cover from Ovuku to Batu. It is easy to become consumed by statistical significance; however, Batu is a mere ~58 metres away from Ovuku, which is an indication of how significant this dramatic change in substrate availability is.

Porites availability was not statistically significant across sites; however, there is a dramatic percentage cover increase from 5% to 27.5% from Ovuku to Batu. Then, *Porites* decreases to 21%, 9%, and 1% across the following sites. *Porites* were the most abundant live coral at Batu, and the reason for this may be two-fold. *Porites* have unique abilities, including the ability to increase their algal density under turbid conditions (R. Jones et al., 2020) and withstand lower salinities compared to other corals (Van Woesik et al., 1995). Furthermore, hyposaline-induced bleaching has been seen to reverse in *Porites* (Van Woesik et al., 1995). These unique abilities may enable *Porites* to outcompete other corals that cannot withstand unfavourable conditions. Ovuku may be too severe for them to withstand the constant influx of sediment and freshwater, but Batu may be "just right".

As distance from Batu increases, other corals can survive the more favourable conditions, leading to a decline in *Porites*.

Our substrate results differ from most research that typically associates high EAM cover with lower-quality habitats, such as those at Ovuku and Batu (Diaz-Pulido et al., 2009). However, in our results, EAM steadily increased along sampling sites. This may be due to inadequate sampling in the field, or it may have ecological significance, in that herbivores (not only the target species from this study) are consuming high quantities of EAM at Ovuku and Batu and, in more "pristine" areas of the reef such as Paele, Church, and Ovuku, species are focussing their foraging efforts on more preferable coral and macroinvertebrates. Species that prefer EAM can essentially dip in and out of what may be an unfavourable habitat at Ovuku and Batu, and rest, defecate, and reproduce in the more "pristine" sites and forage algae in the unfavourable sites. Moreover, herbivorous fish disperse algal fragments through defecation (Vermeij et al., 2013), so if this hypothesis is true, their defecation in more pristine zones may contribute to the increased presence of EAM. More research on other species occupying a range of trophic guilds is necessary to understand the unique distribution of EAM at Vavanga Reef.

4.2 Species-specific foraging substrate preferences

4.2.1 *Chaetodon baronessa*

C. baronessa took most of their total bites on *Acropora* at Ovuku, Paele, Church, and Pobuna, but did not take any bites at Batu. *C. baronessa* had a clear preference for *Acropora*, represented by their high total bite percentage, and this reflects what the literature says about their preference and exclusivity for consuming *Acropora* polyps (Pratchett, 2005). These results both do and do not reflect those of Berumen et al. (2005), who showed that, similar to our results, the relative use of *Acropora* corals by *C. baronessa* varies at fine scales, even within a single reef. However, Berumen et al. (2005) also state that, when *Acropora* is scarce, *C. baronessa* is less selective and consumes a wider range of coral prey. Our results reflect this at Batu, where *Acropora* cover is low, and *C. baronessa* are foraging on *Porites* and *Montastraea*; but, at Ovuku, where *Acropora* is available in low densities, they are exclusively foraging on it. Therefore, the high preference for *Acropora* at Ovuku may be due to low substrate sampling effort instead of preferential foraging.

Manly's preference ratio provided further insight into *C. baronessa*'s foraging behaviours. Counterintuitively, when the average *Acropora* percentage cover increased,

C. *baronessa*'s preference for it decreased; even though not statistically significant, there may be an emerging trend at Vavanga Reef where *C. baronessa* consumes *Acropora* disproportionately to its availability. Regardless, when considering the percentages of total bites taken on *Acropora* across the sampling sites, the results show that *Acropora* is an almost unanimously preferred foraging substrate for *C. baronessa*, similar to those of Nagelkerken et al. (2009) and Pratchett (2005).

It is interesting to note the anomaly of high *Porites* foraging and absent *Acropora* foraging at Batu. Data from Ovuku shows that *C. baronessa* will preferentially feed on *Acropora* even if it exists in low densities; *Acropora* and *Porites* percentage cover are highest at Batu, so it appears that, at this site, there is something influencing this species' foraging preferences, but this study does not have the scope to assess this influence accurately. Possible influences may include turbidity, salinity, age or physiological condition of individuals, inter- or intraspecific competition for a preferred resource, or too small of a sampling size. This highlights the need for more fine-scale studies building on this research to further reveal the foraging behaviour of this coral-feeding specialist.

There is a significant increase in total length across the sites as turbidity decreases. Thus, it could be possible that age, and not substrate availability, turbidity, salinity, or any other factors are impacting *C. baronessa*'s foraging behaviours. Berumen (2006) hypothesise that a decrease in *Acropora* availability can cause decreased growth rates in *C. baronessa*, so it does not make ecological sense that there would be individuals living at Ovuku and still foraging on what little *Acropora* was available. Our study does not provide information on *C. baronessa* abundance or the physiological condition of individuals, so it is difficult to ascertain why there is a negative correlation between total length and turbidity and why the smallest individuals are located at the site with the lowest *Acropora* coverage.

Only three individuals were recorded at Ovuku, meaning results from this site may not be reliable. Further sampling in this area, including transects to assess population size at Ovuku, must be conducted. Due to the low abundance of its preferred prey item (*Acropora*) at Ovuku, fish population estimates will help decipher the importance of this site to *C. baronessa*.

4.2.2 *Chaetodon lunulatus*

C. lunulatus was recorded foraging on two more substrates (n = 6) than *C. baronessa* (n = 4). There is no apparent trend for *C. lunulatus*'s foraging behaviour other than it consistently prefers *Porites* at all sites. *Porites* preference was not affected by *Porites* abundance across sites. The highest preferences were recorded for EAM, Favites, and *Porites*, although this varied between sites.

Pratchett et al. (2014) found that *C. lunulatus* at Lord Howe Island take most of their bites on *Acropora* (37%), *Pocillopora* (29%), and *Porites* (21%). Our study observed all these corals to be foraged on, with respective bite rates of 25%, 15%, and 12-88%. Our results are slightly lower; however, there is wide variation in foraging bites on *Porites*.

EAM was not recorded at Ovuku; however, *C. lunulatus* took 88% of its total bites on this substrate at this site. As before, we can assume that EAM was present in low (< 1%) abundance to have avoided our sampling efforts, resulting in a high preference for this substrate at Ovuku. *C. lunulatus*'s preference for EAM was not affected by EAM abundance across sites. It is interesting that both *C. baronessa* and *C. lunulatus* have extreme preferences for rarely available substrate at the river mouth; further research is imperative in deciphering the reason for this interesting behaviour.

4.2.3 *Chaetodon vagabundus*

Indicative of its generalist, omnivorous feeding behaviour, *C. vagabundus* foraged on a range of substrates (n = 5), including algae and live and dead corals. There is a faint, negative relationship between the abundance of dead coral and *C. vagabundus*'s preference for foraging on it, potentially indicating that as live coral cover becomes more readily available, they switch to it. However, this relationship is not statistically significant, so this is a good area for future research to focus on how live versus dead coral cover impacts a generalist omnivore. Furthermore, Narayani et al. (2015) consider *C. vagabundus* to forage randomly, perhaps what we see in our results. Conversely, Pratchett et al. (2013) provide evidence that *C. vagabundus* foraging behaviour is impacted by coral availability. Our study did not provide us with data to assess this accurately, as we only recorded *C. vagabundus* foraging on three live corals, and these instances were not prolific enough to correlate with substrate cover across sites. Moreover, these results potentially highlight *C. vagabundus*'s resilience to habitat change and degradation, as they can switch to more predominant substrates. This aligns with previous knowledge about generalist species' ability to dominate after disturbances that cause coral decline (S. K. Wilson et al., 2008) and the idea that visual predators foraging on mobile prey may switch to immobile prey in areas of high turbidity (Johansen & Jones, 2013).

Likewise, our results match that of Pratchett et al. (2006), who found that non-coral feeders, including *C. vagabundus*, seem to remain unaffected by reductions in coral cover, specifically *Acropora*, *Porites*, and *Montipora*. Their study recorded mean densities of butterflyfish species by conducting transects, whereas our study cannot comment on the species densities; still, our results indicate that, similarly, *C. vagabundus* remain unaffected by changes in coral cover due to no significant differences or correlations between our measured variables across the sampling sites. Contrary to the significant differences and correlations seen between the two specialist species from this study, it appears that *C. vagabundus* does not alter its foraging or movement behaviour in relation to turbidity or coral cover. This may be because of its diet. *C. vagabundus* are omnivorous generalists, rarely consuming corals and, consequently, may not depend as heavily on coral health for survival. This is reflected in the results, where *C. vagabundus* is the only species in this study to forage on dead coral substrate at Paele, Church, and Pobuna.

4.2.4 Concluding thoughts on species-specific foraging substrate preferences

There are emerging trends between turbidity, substrate availability, and generalist versus specialist foraging behaviours. Caution should be used when interpreting these results, as many correlations lack statistical significance and can be explained by confounding variables. Nevertheless, the fact that differences in foraging behaviour are occurring within mere metres of one another is significant, even if not statistically. This research has provided a starting point for future investigations to conduct extensive and directed sampling at Vavanga Reef to attempt to expose nuances in foraging behaviour that can be used to intercept global coral reefs that may otherwise be silently suffering.

4.3 Analysis of measured variables

4.3.1 Bite rates

No significant differences in bite rates between sites for any of the target species existed. However, considering the sites' proximity to one another, it is still worth discussing the differences. The average bite rate across all sites for *C. baronessa* was 10.66 (± 4.84) bites per minute, which is close to previous estimates of 12 bites per minute (Gregson et al., 2008). Median bite rates from Ovuku to Church were about 12.1 bites per minute while Pobuna's median was 3.87 bites per minute (see Figure A1 in the Appendix); however, there was no apparent effect of sampling site on bite rate, although increased sampling may reveal any underlying correlations (Table 3.3.1).

The average bite rate across all sites for *C. lunulatus* was 8.73 (± 5.34) bites per minute, which is lower than previous estimates of 10 and 16.69 bites per minute (Gregson et al., 2008; Pratchett et al., 2014). However, previous estimates also noted that bites tended to be higher at midday and through the afternoon, something that we did not account for in our data as we lumped all samplings from one site together, no matter what time of day they were collected. For example, at Pobuna, data was collected across a period of three days with start times of 9:05 am, 4:17 pm, and 1:45 pm. This small but significant discrepancy could affect the results, especially for species like *C. lunulatus*, which are known to have time-dependent foraging patterns. Future research should consider this during data collection and either conduct collection at similar times each day or conduct data collection across the day but include temporal distinctions in the analysis. See Figure A2 in the Appendix for a box plot of bite rates across sampling sites.

The average bite rate across all sites for *C. vagabundus* was 6.78 (± 3.44), which reflected previous estimates of 6-10 bites per minute (Berumen & Almany, 2009; Gregson et al., 2008). A study by Berumen and Almany (2009) suggests that *C. vagabundus* are impervious to external disturbances and that their foraging behaviour does not change. Our results are similar and suggest that *C. vagabundus* foraging and movement is unaffected by external perturbances, including turbidity, coral cover, or coral diversity. See Figure A3 in the Appendix for a box plot of bite rates across sampling sites.

Our data provides no evidence to support the idea that turbidity, coral cover, or coral diversity affects the bite rates of the target *Chaetodon* species at Vavanga Reef. Some slight differences in species bite rates between sites indicate potential underlying patterns. Additionally, a significant difference exists between the bite rates of *C. baronessa* and *C. vagabundus*, indicating that guild (id est, specialist or generalist) may influence a species' bite rate. Increased sampling across these sites would provide more data points to reveal the presence of underlying trends in butterflyfish bite rates across a gradient of turbidity or coral cover and would create baseline knowledge of how these factors affect bite rates of species from different feeding guilds.

4.3.2 Mass and length

Our results show that the body mass of specialist hard-coral grazers *C. baronessa* and *C. lunulatus* declines with increasing turbidity. However, our mass data was calculated by applying species-specific length-weight relationships to length measurements taken from our stereo-video footage. Furthermore, a significant negative relationship exists between turbidity and body length of *C. baronessa* and *C. lunulatus*, indicating that perhaps juvenile fish prefer more turbid areas while adults prefer less turbid areas. However, knowing that the mass data was calculated from length data shows that the correlation between mass and turbidity simply reflects the correlation between length and turbidity.

The physiological condition of *C. baronessa and C. lunulatus* is worse in areas where the quantity and/or quality of prey is not preferable (Berumen et al., 2005). Furthermore, two species of highly selective corallivorous butterflyfish (*C. plebeius* and *C.trifascialis*) experience little or no growth when feeding on strongly avoided coral species, and the highest growth rate was observed when feeding on highly preferred coral species (Berumen, 2006). Considering that juvenile *C. baronessa* settles alongside adults (Pratchett, Berumen, et al., 2008), it is possible that our results are indicative of decreased physiological conditions at sites with unfavourable environmental conditions. The smaller individuals measured at more turbid sites may indeed be adult butterflyfish who, with low availability of preferred prey and high energy expenditure (see section 4.1), have lower growth rates and decreased physiological conditions. This study lacks the evidence to support this theory; still, it reveals correlations between turbidity and fish mass and length that emphasise the need for future research to include age composition data and physiological condition measurements of fish at each site. Then, it can be determined if turbidity and live coral availability are impacting the population distribution and/or physiological fitness of specialist butterflyfish at Vavanga Reef. This has huge implications for the theory that fine-scale changes in chaetodontids provide evidence for coral reef ecosystem health.

As expected, *C. vagabundus* did not show any correlations between the measured variables. The lack of significant results is likely a reflection of this species as a generalist forager that is able to navigate and adapt to environmental changes and, therefore, has less variation in its foraging behaviour, movement, and body condition between sites with differing turbidities.

4.3.3 Velocity

The velocity of *C. baronessa* and *C. lunulatus* increased as turbidity increased. *C. baronessa* velocity was significantly higher at Ovuku than at Paele, Church, or Pobuna. Velocity was also significantly higher at Batu than at Paele or Church. Overall, these results were dissimilar to those of *C. lunulatus*, whose high-velocity measures at Ovuku were not significantly different from those at Paele, Church, or Pobuna. However, the overall positive correlation between velocity and turbidity is worth further investigation, as this contrasts with previous research on the role of turbidity on the behaviour of coral reef fish by Newport et al. (2021). Their study of the Picasso triggerfish (*Rhinecanthus aculeatus*), a generalist omnivore (J. E. Randall, 1985), found that the fish moved faster in less turbid conditions (Newport et al., 2021). However, their study was conducted in laboratory conditions where the fish were physically handled; they also used visual observations of fish travelling distance and foraging time. Our study was conducted in situ with stereo-video analysis to ascertain velocity measurements to quantify fish movement more accurately. Furthermore, our study incorporated two specialist corallivores and a generalist omnivore for comparison. Although our results differ, it is important to consider these methodological differences. Our study shows how in situ observations may differ from behavioural studies conducted in laboratory environments.

Increased velocity represents faster swimming speeds of *C. baronessa* and *C. lunulatus* in more turbid environments. This may be because the fish must swim faster to cover more ground in search of prey because of the decreased visibility or live coral cover at the more turbid sites. To the best of our knowledge, no other studies have quantified velocity for butterflyfish across a turbidity gradient, so these results serve as baseline data for future research to build on.

4.3.4 ODBA

Because other unmeasured factors, including water drag and buoyancy control, increase energy expenditure in fish, the specific measurement values of ODBA presented in this study should be referenced with caution (Gleiss et al., 2011). Here, it is the changes in ODBA that are relevant.

Only *C. baronessa* showed a significant difference in ODBA between sites. ODBA was significantly higher at Ovuku compared to Batu, Paele, and Church. Although not significantly higher at Ovuku than at Pobuna, visualisation of the data presents Ovuku as much higher than Pobuna. A p-value of 0.051 of this relationship suggests a higher sampling size could tease out any existing significant difference in ODBA between Ovuku and Pobuna. Regardless, the higher ODBA value at Ovuku may provide insight into the energy expenditure of *C. baronessa* foraging in less favourable environments. The decreased availability of *Acropora* combined with *C. baronessa*'s very strong preference for it may explain the high ODBA value. *C. baronessa* may have higher activity levels and elevated energy expenditure (reflected in the high ODBA) as they attempt to locate and forage on their preferred prey. No literature has attempted to quantify the energy expenditure of *C. baronessa* along a gradient of reef health, so it is hard to interpret this ODBA result; however, using previous knowledge of the positive relationship between *C. baronessa*'s preference for *Acropora* and *Acropora* availability (Berumen, 2005), it makes ecological sense that *C. baronessa* exerts more energy searching for coral prey at a site like Ovuku that has reduced live coral cover. This correlation may reflect an adaptive foraging strategy in response to unfavourable changes in environmental conditions.

4.3.5 Concluding thoughts on the analysis of measured variables

Our results for bite rates closely follow previous evidence for each species (Berumen & Almany, 2009; Gregson et al., 2008). However, Gregson et al. (2008) did not explicitly discuss specific environmental parameters, habitat complexity, or coral cover at their study site. Thus, it is unwise to make comparisons as we do not know what confounding variables affect bite rates in the above-cited studies, and we did not account for time of day in our study. Our study builds on such literature and essentially provides baseline data on bite rates of *C. baronessa*, *C. lunulatus*, and *C. vagabundus* when exposed to different environmental variables.

No statistically significant differences in bite rate between sites existed for any species; however, small, statistically insignificant patterns were evident, highlighting the need for more in-depth research. Emerging patterns between bite rates of *C. baronessa* between sites could be the result of turbidity and coral availability's effect on their foraging behaviour. If this hypothesis is accepted, this could provide evidence for fine-scale foraging behaviour of specialist hard-coral feeders to be used as a proxy for reef health early on in coral reef degradation scenarios.

Correlations between the length and mass of *C. baronessa* and *C. lunulatus* with turbidity have multiple possible explanations. Further study into population dynamics and the physiological condition of these species will help elucidate the reason for this correlation.

No literature provides baseline information on velocity or ODBA for *Chaetodon* species, thus making it difficult to assume our measurements are accurate by comparison. Regardless, our results are a starting place for this area of research and provide a baseline for future studies to measure against in terms of velocity or energy expenditure change along gradients of reef health.

4.4 Implications for coral reef health assessment

Chaetodontids are regarded as bioindicators in that their presence, or lack thereof, on coral reefs may give insight into the health of that reef, as the abundance of butterflyfish depends on the cover of live corals (Yusuf & Ali, 2004). However, more recent research indicates that herbivorous fish community biomass or the presence of herbivorous functional groups does not always change after visible shifts within coral reef environments (Goatley et al., 2016). Investigating the fine-scale physical and behavioural responses to environmental change of species closely associated with the coral reef by their dietary and habitat requirements may be a viable technique in assessing fragile ecosystems (Rahman & Candolin, 2022). Similar research has already shown that chemical pollutants disrupt olfactory communication in swordtail fish (*Xiphophorus* spp.) and affect shoaling behaviour in European perch (*Perca fluviatilis*) and banded killifish (*Fundulus diaphanous*) (Brodin et al., 2013; Ward et al., 2008). Temperature changes the agnostic behaviour of three species of crayfish: *Orconectes limosus* spent more time motionless, *Pacifastacus leniusculusi* became more subordinate, and *Procambarus clarkia* stayed the same as before the temperature increased (Gherardi et al., 2013). Trinidadian guppies (*Poecilia reticulata*) living at sites with high and low abundance of predators show differences in diet (Bassar et al., 2010). These examples provide evidence that changes in ecosystems, whether chemical pollutant discharge, temperature increases, or high or low predator populations, can impact the choices that a species makes in their environment. Our study builds on this knowledge and provides the first investigation into the foraging and movement behavioural changes of butterflyfish residing on one coral reef exposed to a gradient of turbidity and live coral cover.

A study by Moustaka et al. (2018) found overall species richness and the abundance of planktivorous omnivores and herbivorous scrapers declined at more turbid sites. In contrast, our study had all three of our target species at all our sampling sites, but it was their behaviour that told the story; a simple species richness and abundance study may not have yielded results that indicate ecosystem change. However, this does highlight the need for richness and abundance studies on coral reef fish at Vavanga Reef to identify if any correlations exist that can be aligned with the results from this study. Analysing this type of data and comparing it with results from this fine-scale research will reveal the extent to which broader studies may overlook valuable information. This can guide future research of other coral reef ecosystems to ensure the best methodologies are adopted for addressing the research question.

Interpreting our study's findings in the context of coral reef conservation and ecosystem management is a delicate tightrope. We must be aware of the limitations of these results and that, due to these limitations, they may not accurately represent what is happening in the ecosystem. However, keeping this in mind, this study has provided results that indicate that turbidity and live coral cover and diversity are impacting the foraging behaviours and energy expenditure of specialist corallivore butterflyfish while not impacting generalist omnivore butterflyfish. This discovery is profound and holds immense implications for future conservation efforts focused on identifying at-risk coral reefs. If specific and directed future research can further bolster the argument presented in this research, fine-scale stereo-video technology can be a valuable tool in assessing global coral reefs before degradation reaches a critical point, allowing conservation measures to be implemented earlier than they otherwise would be.

4.4.1 Implications for the Vavanga Village Community

It is important to acknowledge the impact of these results on the local community of Vavanga Village as the traditional owners of the reef whose livelihood depends on it. Furthermore, the following, and indeed this entire thesis, is written in recognition of the indigenous and local knowledge held by the people of Vavanga in hopes of contributing to it rather than overshadowing it. The history of logging at Vavanga has accentuated the naturally occurring fluvial turbidity at Ovuku (Wenger et al., 2020). Our results emphasise the potential severity of that accentuation in altering butterflyfish foraging and movement behaviours. Butterflyfish, however, are not a substantial part of Vavanga's diet (W. Laufanua, personal communications, January 2023), and hence, further research into the behavioural and physiological changes associated with reef degradation of more relevant fish species would be beneficial. Still, this research has provided the community with insight into the extent and implications of the degradation of their reef and justifies ongoing monitoring of ecosystem health. Eventually, effective conservation strategies can be developed alongside the community and implemented to ensure the preservation of their livelihood, which is inextricably intertwined with their reef. This strengthens the ongoing relationship between our research team and Vavanga Village, which is crucial in generating positive conservation outcomes (Ens et al., 2016; Fa et al., 2020; Ferraro & Hanauer, 2011; Reyes-García et al., 2022; Schuster et al., 2019).

4.5 Limitations and further considerations

4.5.1 Environmental data

Our study used the Forel-Ule Index and underwater visibility as a proxy for turbidity. This was due to the unavailability of a sonde device, and our remote field location meant we had to be ingenuitive and use what we had to hand. Upon reflection, a nephelometer, a device that emits light and measures scattered particles, would be beneficial to measure Nephelometric Turbidity Units (NTUs) and provide an accurate reading of turbidity. Our method of assessing turbidity through measured proxies qualifies the assessment rather than quantifies it in the conventional sense of directly measuring NTUs.

Furthermore, other variables should have been measured to ensure this study accounted for confounding variables. No literature appears to have investigated salinity's role in the foraging and movement behaviours of coral reef fish, or even marine teleosts in general. Due to freshwater input from Vavanga River onto Vavanga Reef, there is likely an existing salinity gradient, too. Controlled experiments into the role of salinity on coral reef fish behaviours will help to understand how important salinity is and if it is a worthy confounding variable to be considered in these results. Temperature is another variable to consider; however, SST was consistently 30°C at all sampling events. Underwater temperature measurements at each rack placement would yield more accurate temperature data.

Our footage collection methodology gave us a bias of sampled substrate in our video footage; this may have contributed to the unique foraging behaviours of *C. baronessa* on *Acropora* at Ovuku. Our criteria for choosing the placement of the stereo-video camera racks (see section 3.2) meant there was some limitation in rack placement; apart from these criteria, we randomly placed the racks on each dive. However, the bias occurs when the camera unintentionally points towards certain substrates, leading to an overrepresentation in the data. An updated methodology is proposed that aims to diversify the sampling approach whereby shorter videos are captured across more locations at each sampling site relative to how abundant each substrate is at each site.

This could be implemented by first conducting a line transect survey to assess substrate cover at each site more accurately (Perry et al., 2002). Alternatively, Martin's (2024) fine-scale habitat zonation geospatial analysis provides high-quality substrate data that could be used to assess the abundance and distribution across our sampling sites. After substrate cover has been estimated, the stereo-video cameras can be positioned relative to the abundance of different substrates, ensuring that each substrate type is adequately represented in the video footage.

Reflecting on our original methodology reveals that our quadrat analysis can be improved. Due to time restraints, we only used 20 points within each quadrat, which resulted in outliers at almost all the sites (Figure 3.1.5). Increasing the number of quadrats at each site and the number of classification points within each quadrat will result in a more accurate representation of the sampled environment. Alternatively, using AI to improve the accuracy and speed of identifying substrates is another methodology to consider (González-Rivero et al., 2020; Reef Support, 2023). AI can increase the speed of coral annotation by 90% whilst still preserving accuracy (Pavoni et al., 2022).

The time constraints of a master's thesis with a due date were also limitations of this research. The meticulous nature of the video preparation and analysis process took most of the available time, even after the data was whittled down to a practicable amount. This is a consideration for future research that is considering this methodology. Again, the use of AI is a useful tool to automatically track the fish; however, we opted for manual tracking to increase the accuracy of the tracks.

4.5.2 Foraging and movement data

The turbidity of the water limited the collection of foraging and movement data. At more turbid sites, decreased visibility meant that the quantity of fish tracked was likely less, as I could not see fish further from the camera. Also, the length of some tracks was shortened due to decreased visibility, as sometimes fish swam through areas where I could no longer see them. This limitation is unavoidable and inherent to working in high-turbidity environments.

Because our study employed minimally invasive methods, we estimated fish mass using length measurements of each fish. However, in this case, mass is not a reliable predictor of physiological condition because we do not know the age of the fish and cannot determine if each fish falls within the expected weight range for its age. To address this issue, it may be beneficial to first validate the relationship between length and mass within the populations at our sampling sites. This could involve collecting data on both length and mass from a subset of individuals across the sampling sites and comparing the measured values to ensure the relationship holds true. Then, examining the otolithic sagittae (Labonne et al., 2008) of these individuals would clarify the relationship between length and age (Berumen, 2005) while also providing an understanding of the distribution of age classes across the sampling sites, something that our study could not account for.

The method of obtaining mass measurements from length measurements could have introduced a confounding factor that affects the observed relationships. For example, the negative relationship between mass and turbidity may just be a reflection of the relationship between length and turbidity. Moreover, since there is evidence that adverse conditions halt the growth of some butterflyfish species and that juveniles and adults are found alongside one another, we cannot be sure that our results suggest that some of our target species are distributed by age class along the turbidity gradient. It may be that the level of turbidity and corresponding coral cover is affecting the physiological condition of the specialist foragers in this study. By returning to the sampling sites and collecting length, mass, and age data directly from the species, we can provide evidence for or against this theory.

Another possible limitation of our study was the process of condensing our collected data into sampling sites. By choosing this method, we were obliged to average the turbidity measurements to fit them into the five sampling sites, as the sampling sites were introduced to allow us to measure against a turbidity gradient based on location along the reef. However, by doing this, variability within our data was reduced, effectively limiting the granularity of the analysis. In doing so, information about the turbidity gradient within each sampling site was lost, which may have inadvertently limited the insights drawn from the data. However, by designating sampling sites, we were able to group the data into areas of percentage coral cover, which was another important aspect of this research. A suggestion for combatting this limitation is to retain the individual turbidity measurements and treat turbidity as a continuous variable instead of averaging it. The measured variables could then be analysed along this turbidity continuum instead of along the spatial gradient represented by our sites.

Also worth considering is the method of measuring turbidity. The Forel-Ule Index consists of only 21 units, whereas NTUs span a much larger spectrum. Measuring NTUs means more variability in the data. Furthermore, it allows the location to not be so important in the analysis; rather, NTU measurements could be grouped, and analysis could be conducted along these groupings instead of along sampling sites. However, this still does not account for other confounding variables such as salinity and substrate cover.

The best methodology would incorporate a spatially explicit fine-scale grid sampling system covering the entire area. This grid system would ensure systematic coverage of the entire area instead of our more patchily distributed sampling site system. Turbidity, salinity, and water temperature would be measured and averaged at each grid point. Transect surveys of the substrate at each grid point would be used to assess substrate composition and percentage coverage. Geographic information systems analysis could create spatial maps of the grids and corresponding environmental variables to visualise the environmental gradients along Vavanga Reef (Martin, 2024).

This study aimed to provide a novel method for assessing coral reef health through fine-scale analysis of butterflyfish. However, this approach must first be refined and then validated by assessing coral reef health through other methodologies, including the Coral Reef Health Index and Ecosystem Health Index (Adi et al., 2023).

4.6 Future research

Future research can employ our refined methodology to uncover the relationships between coral reef fish foraging and movement behaviours and their changing environment. It would be beneficial to build on this study by repeating the research at varying temporal scales, including different seasons, a range of times of day when fish are active, after periods of large rainfall that increase fluvial sediment input, and over the space of years.

The physiological condition of *C. baronessa*, *C. lunulatus*, and *C. vagabundus* must be investigated across the sampling sites. This can be done using the methodology of Berumen et al. (2005) who assessed body condition using estimates of hepatocyte vacuolation as an indirect measure of total liver lipid stores (Pratchett et al., 2004). This is essential for investigating the theory that less favourable conditions are responsible for physiological decline in butterflyfish.

Although the results of *C. baronessa* and *C. lunulatus* substrate feeding preferences were not significant, an interesting trend is apparent that deserves further attention. Utilising the refined grid sampling methodology will yield more accurate data points along a finer environmental health continuum.

Finally, future research must continue to investigate the use of fine-scale behavioural changes of coral reef fish to identify at-risk ecosystems (Goatley et al., 2016). In a world where anthropogenically induced changes are impacting ecosystems in ways they never have before, it is crucial to utilise all available tools to develop successful conservation strategies that aim to protect some of our most vulnerable and universally important ecosystems.

4.7 Conclusion

This study sought to explore the feasibility of utilising subtle variations in coral reef fish foraging and movement behaviours as indicators to identify coral reef ecosystem dynamics. The specific objectives included using stereo-video footage of *C. baronessa, C. lunulatus*, and *C. vagabundus* collected on the coral reef at Vavanga to obtain measurements of bite distances, bite rates, ODBA, and velocity. Subsequent to data collection on these parameters, information on substrates foraged by the species could be used to gain insight into their foraging preferences. These measured variables were then compared between species and along the gradient of turbidity apparent at Vavanga Reef.

Our results show a turbidity gradient at Vavanga Reef influenced by fluvial input from Vavanga River and accentuated by historical logging practices. Furthermore, this sedimentation has likely resulted in a gradient of coral cover and substrate diversity that increases with distance from the river mouth.

This gradient impacts the foraging and movement behaviours of two specialist corallivores, *C. baronessa* and *C. lunulatus*. Results present a trend of *C. baronessa* consuming its preferred prey, *Acropora*, disproportionately to its availability. This opposes previous research that states that when *Acropora* is scarce, *C. baronessa* is less selective, but our results show a high preference for *Acropora* even at scarce sites. Additionally, *C. baronessa* velocity, and correspondingly ODBA, is higher at Ovuku, meaning that their speed and potential energy expenditure are greater in areas with high turbidity. This may correspond with the low availability of preferred prey as *C. baronessa* attempts to locate it in poor visibility and unfavourable conditions.

C. lunulatus showed an increase in velocity with increasing turbidity, revealing a trend worthy of further investigation. Furthermore, *C. lunulatus* showed nuances in their foraging preferences. However, uncovering trends or interpreting these without further data collection is difficult. *C. vagabundus* did not respond to the turbidity or coral cover gradient, which may reflect their adaptation as a generalist omnivore. Overall, this study provided key baseline data on *C. baronessa*, *C. lunulatus*, and *C. vagabundus* foraging at Vavanga Reef.

Our research had limitations, including the methodology of data collection and the lack of collection of confounding variables. However, this research has still shown significant results that support further investigation into the use of specialist foragers as proxies for reef health. Future research is encouraged to build on this study in the hopes that we can unlock, through fine-scale analysis of stereo-video footage, the secrets of coral reef fish and what their foraging and movement patterns might tell us about their environment.

Finally, as the first of its kind, this study's methodology provides guidance to future studies about best practices for collecting and analysing this data. Footage collected from this study is already being used to analyse the foraging and movement behaviours of other coral reef fish present at Vavanga Reef. This study has highlighted key areas for future studies to improve upon, which gets the scientific community another step closer to effective coral reef ecosystem conservation.

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Glossary

3D: three-dimensional

AI: artificial intelligence

ANOVA: Analysis of variance

BRUV: baited remote underwater video

EAM: epithelial algal matrix

GPS: Global Positioning System

HSD: Honestly Significant Difference

ODBA: overall body dynamic acceleration

PCA: principal component analysis

SCUBA: self-contained underwater breathing apparatus

SST: surface sea temperature

Appendix

Table A1

VidSync Event Default Attributes

Attribute	Length	Track	Bite	Harrassment
Max # of points	2	No limit	No limit	No limit
All points in event must have same timecode?	Yes	No	No	No
Label length?	Yes	No	No	No
Label speed?	No	No	No	No
Connecting line label length units	mm	mm	mm	mm
Multiplier	1	1	1	1
Digits passed decimal	1	1	1	1
Event type description	Length measurement	Tracking fish movement	Records when the fish takes a bite of substrate	Individual begins to get harrassed by a damsel fish

Note. VidSync (Neuswanger, 2008) is stereo-video videogrammetric analysis software. https://www.vidsync.org/HomePage

Table A2

Environmental Attributes and Sampling Information from a Stereo-video Study Conducted at Vavanga Reef

Site name	Latitude	Longitude	Translation	Proximity to river mouth	Average Forel-Ule Index	Average visibility (m)
Ovuku	8.0611417° S	156.9669267° E	River mouth	1	6	10
Batu	8.0614733° S	156.9664733° E	Rock	2	3	25.2
Paele	8.062875° S	156.9660433° E	Meeting house	3	3	30
Church	8.064005° S	156.966660° E	Church	4	2	35.7
Pobuna	8.06498°S	156.96724°E	Explosion	5	2	33

Note. The proximity to the river mouth is indicated by numerical values, with 1 representing the closest distance to the Vavanga River mouth and 5 indicating the furthest distance. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands.

Table A2 continued from previous page

Site name	Average depth of rack placement (m)	Average SST (°C)	Number of times site sampled	Total available substrates	Total *C. baronessa* tracked	Total *C. lunulatus* tracked	Total *C. vagabundus* tracked
Ovuku	1.8	30	6	7	4	9	9
Batu	3	30	6	9	10	11	10
Paele	5.17	30	6	14	7	8	10
Church	6.14	30	8	14	10	10	10
Pobuna	4.15	30	6	13	8	7	10

Table A3

Percentage Cover (%) of Substrates at Sampling Sites Along a Turbidity Gradient

	Ovuku	Batu	Paele	Church	Pobuna
Acropora	0.00	**16.67**	**14.17**	**7.22**	**13.75**
Dead coral	**68.33**	**41.67**	**36.67**	**35.00**	**36.25**
Diploastrea	**2.50**	**4.17**	**2.50**	**15.00**	**15.00**
EAM	0.00	**3.33**	**7.50**	**13.89**	**18.75**
Echinopera	0.00	**0.83**	0.00	0.00	0.00
Faviidae	0.00	0.00	**0.83**	0.00	**2.50**
Favites	0.00	0.00	**0.83**	**1.67**	**1.25**
Fungia	0.00	0.00	**0.83**	0.00	0.00
Goniastrea	**1.67**	0.00	0.00	**1.11**	**1.25**
Lobophyllia	0.00	0.00	**0.83**	**2.78**	0.00
Millepora	0.00	**5.83**	0.00	**0.56**	0.00
Montipora	0.00	0.00	**3.33**	0.00	**3.75**
Pavona	0.00	0.00	0.00	**0.56**	0.00
Platygyra	0.00	0.00	0.00	**1.67**	0.00
Pocillopora	0.00	0.00	**3.33**	0.00	0.00
Porifera	0.00	0.00	**6.67**	**10.56**	**2.50**
Porites	**5.00**	**27.50**	**20.83**	**9.44**	**1.25**
Sand	**22.50**	0.00	0.00	0.00	0.00
Sarcophyton	0.00	0.00	**0.83**	0.00	**1.25**
Sinularia	0.00	0.00	0.00	0.00	**1.25**
Stylaster	0.00	0.00	0.00	0.00	**1.25**
Zooanthid	0.00	0.00	**0.83**	**0.56**	0.00

Note. Values > 0.00 are bolded. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Listed in increasing distance from the mouth of Vavanga River, the sampling sites are Ovuku, Batu, Paele, Church, and Pobuna.

Table A4

Manly's Substrate Preference Ratio Values of Chaetodon *Butterflyfish at Sampling Sites Along a Turbidity Gradient*

Species	Site name	Substrate	Total substrate cover (%)	Total bites	Total bites (%)	Manly's preference ratio
C. baronessa	**Ovuku**	***Acropora***	**<1**	**6**	**100%**	**100.00**
C. baronessa	**Batu**	***Montastraea***	**1**	**2**	**22%**	**22.00**
C. baronessa	**Batu**	***Porites***	**27**	**7**	**78%**	**2.89**
C. baronessa	**Paele**	***Acropora***	**14**	**28**	**100%**	**7.14**
C. baronessa	**Church**	***Acropora***	**7**	**33**	**66%**	**9.43**
C. baronessa	**Church**	**Faviidae**	**1**	**7**	**14%**	**14.00**
C. baronessa	Church	*Porites*	9	2	4%	0.44
C. baronessa	**Pobuna**	***Acropora***	**14**	**9**	**100%**	**7.14**
C. lunulatus	**Ovuku**	**EAM**	**1**	**7**	**88%**	**88.00**
C. lunulatus	**Ovuku**	***Porites***	**5**	**1**	**12%**	**2.40**
C. lunulatus	Batu	Dead coral	40	1	2%	0.05
C. lunulatus	**Batu**	***Favites***	**1**	**4**	**10%**	**10.00**
C. lunulatus	**Batu**	***Porites***	**27**	**36**	**88%**	**3.26**
C. lunulatus	**Paele**	**EAM**	**7**	**8**	**62%**	**8.86**
C. lunulatus	**Paele**	***Pocillopora***	**3**	**2**	**15%**	**5.00**
C. lunulatus	**Paele**	***Porites***	**21**	**3**	**23%**	**1.10**
C. lunulatus	**Church**	***Acropora***	**7**	**2**	**25%**	**3.58**
C. lunulatus	**Church**	***Porites***	**9**	**6**	**75%**	**8.33**
C. vagabundus	**Ovuku**	**EAM**	**1**	**16**	**84%**	**84.00**
C. vagabundus	**Ovuku**	***Porites***	**5**	**2**	**11%**	**2.20**
C. vagabundus	**Batu**	***Acropora***	**17**	**8**	**50%**	**2.94**
C. vagabundus	**Batu**	***Porites***	**27**	**6**	**37%**	**1.37**
C. vagabundus	Paele	Dead coral	37	1	20%	0.54
C. vagabundus	**Church**	**Dead coral**	**34**	**28**	**96%**	**2.82**
C. vagabundus	Church	*Diploastrea*	15	1	4%	0.27
C. vagabundus	**Pobuna**	**Dead coral**	**36**	**5**	**100%**	**2.78**

Note. Ratios > 0 are bolded. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Listed in increasing distance from the mouth of Vavanga River, the sampling sites are Ovuku, Batu, Paele, Church, and Pobuna.

Table A5

Sampling Site Distances (metres) From One Another

Site	Ovuku	Batu	Paele	Church	Pobuna
Ovuku	-	57.79	230.71	365.82	500.59
Batu	57.79	-	172.92	308.03	442.8
Paele	230.71	172.92	-	135.11	269.88
Church	365.82	308.03	135.11	-	134.77
Pobuna	500.59	442.8	269.88	134.77	-

Note. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Listed in increasing distance from the mouth of Vavanga River, the sampling sites are Ovuku, Batu, Paele, Church, and Pobuna.

Table A6

Total Length, Total Bites, Bite Rates, and Mean Mass, Velocity, ODBA, and Bite Distance for Three Species of Chaetodon *Butterflyfish at Sampling Sites on Vavanga Reef, Kolombangara, Western Province, Solomon Islands*

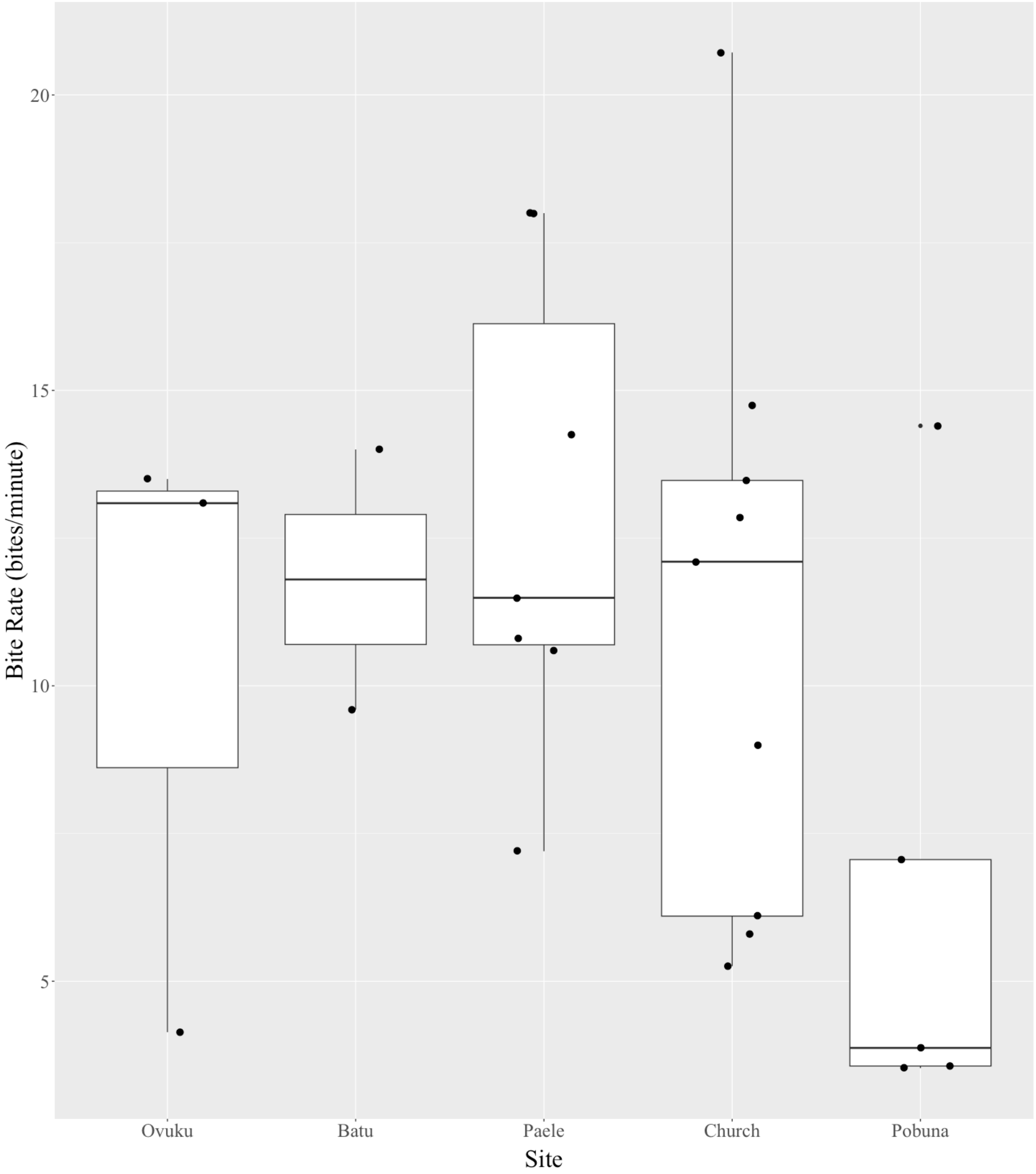
Site	Species	Individual ID	Total Length (mm)	Mean Mass (g)	Mean Velocity (cms-1)	Mean ODBA (g)	Total Bites	Bite Rate (bites/minute)	Mean Bite Distance (mm)
Ovuku	*C. baronessa*	baronessa_01	72.2	12.00110426	27.51673678	0.182681453	0	-	-
Ovuku	*C. baronessa*	baronessa_02	75.77	13.75613225	20.29086344	0.388186997	2	13.09090909	69.57754826
Ovuku	*C. baronessa*	baronessa_03	78.9	15.4245243	21.28204778	0.438099421	3	13.5	80.89484425
Ovuku	*C. baronessa*	baronessa_42	75.5	13.61795809	21.66115693	0.287288338	1	4.137931034	-
Ovuku	*C. lunulatus*	lunulatus_01	81.7	19.80400915	19.62304081	0.098453103	0	-	-
Ovuku	*C. lunulatus*	lunulatus_02	79.93	18.91415393	23.13526954	0.106847791	0	-	-
Ovuku	*C. lunulatus*	lunulatus_03	74.6	16.36356103	12.40426247	0.198546807	6	15.53956835	56.08277091
Ovuku	*C. lunulatus*	lunulatus_04	88.3	23.31151712	44.51101354	0.61895908	0	-	-
Ovuku	*C. lunulatus*	lunulatus_05	85.95	22.02830728	97.39155189	0.402314614	0	-	-
Ovuku	*C. lunulatus*	lunulatus_07	99.4	29.88911407	59.40874058	0.240381782	0	-	-
Ovuku	*C. lunulatus*	lunulatus_08	97.27	28.56056312	31.2977531	0.245884343	2	10.58823529	433.8013956
Ovuku	*C. lunulatus*	lunulatus_09	89.4	23.9252494	27.87006631	0.165886775	0	-	-
Ovuku	*C. vagabundus*	vagabundus_01	115.27	39.80173477	22.1457646	0.454146732	7	7	336.0468677
Ovuku	*C. vagabundus*	vagabundus_02	102.83	28.34338615	9.578076188	0.105558959	2	4.022346369	80.88246897
Ovuku	*C. vagabundus*	vagabundus_03	101.8	27.50765734	9.359659759	0.099529591	2	5.217391304	178.841897
Ovuku	*C. vagabundus*	vagabundus_04	104.23	29.50610416	11.01746494	0.112118633	2	13.09090909	73.22421897
Ovuku	*C. vagabundus*	vagabundus_05	110.97	35.54804073	14.74195354	0.224717818	3	3.698630137	517.3803973
Ovuku	*C. vagabundus*	vagabundus_06	86.9	17.1840393	24.8270107	0.08970909	0	-	-
Ovuku	*C. vagabundus*	vagabundus_07	80.2	13.53723159	9.691383893	0.112678191	3	6.585365854	277.8637819
Ovuku	*C. vagabundus*	vagabundus_08	118.5	43.20998518	21.82198919	0.083699975	0	-	-
Ovuku	*C. vagabundus*	vagabundus_09	114.2	38.7133531	26.59582906	0.120218022	0	-	-
Batu	*C. baronessa*	baronessa_12	59.5	6.94403647	11.89887914	0.229040611	7	14	87.27592388
Batu	*C. baronessa*	baronessa_13	67.13	9.767834492	22.05988705	0.174746298	0	-	-
Batu	*C. baronessa*	baronessa_14	64.55	8.743082962	19.02924139	0.152059149	0	-	-
Batu	*C. baronessa*	baronessa_15	74.87	13.29904838	8.6479875	0.092392879	2	9.6	27.9919637
Batu	*C. baronessa*	baronessa_16	68.9	10.51385477	20.45716841	0.110368188	0	-	-
Batu	*C. baronessa*	baronessa_17	69.65	10.84074037	17.07253473	0.173593817	0	-	-
Batu	*C. baronessa*	baronessa_18	71	11.44554887	13.61066859	0.16967632	0	-	-
Batu	*C. baronessa*	baronessa_19	104.5	34.1459251	20.59603501	0.210430447	0	-	-
Batu	*C. baronessa*	baronessa_20	84.8	18.91391723	25.02326492	0.143326754	0	-	-
Batu	*C. baronessa*	baronessa_21	67.67	9.991677343	15.2472086	0.237143571	0	-	-
Batu	*C. lunulatus*	lunulatus_18	93.25	26.1391787	12.95809832	0.182990211	2	2.77992278	236.5996317
Batu	*C. lunulatus*	lunulatus_19	95.4	27.42022791	8.545570129	0.083583239	3	5.373134328	544.8979137
Batu	*C. lunulatus*	lunulatus_20	65.4	12.41357051	10.69975349	0.149309123	13	15.54817276	157.484424
Batu	*C. lunulatus*	lunulatus_21	92.65	25.78740054	13.29907394	0.231987871	5	9.574468085	140.7026572
Batu	*C. lunulatus*	lunulatus_22	59.4	10.14324159	16.66431492	0.198020345	0	-	-
Batu	*C. lunulatus*	lunulatus_23	95.4	27.42022791	26.92941492	0.5338649	2	5.255474453	129.0468175
Batu	*C. lunulatus*	lunulatus_24	93.37	26.20983385	11.25231177	0.202419875	9	8.244274809	171.8038304
Batu	*C. lunulatus*	lunulatus_25	98.6	29.38641897	11.51113446	0.136495698	3	10.09345794	42.63913219
Batu	*C. lunulatus*	lunulatus_26	104.1	32.93275801	25.87510312	0.377289899	0	-	-
Batu	*C. lunulatus*	lunulatus_27	80.97	19.43441132	19.75866844	0.278346417	0	-	-
Batu	*C. lunulatus*	lunulatus_46	58.23	9.728416018	13.28043801	0.18194386	4	10	86.53771259
Batu	*C. vagabundus*	vagabundus_20	86.4	16.89175673	19.91647632	0.168647593	1	3.636363636	-
Batu	*C. vagabundus*	vagabundus_21	96.03	23.12678491	21.08788241	0.348390233	2	2.236024845	33.85731784
Batu	*C. vagabundus*	vagabundus_22	79.3	13.09057272	19.87950838	0.318653639	8	8.396501458	198.2447078
Batu	*C. vagabundus*	vagabundus_23	111.1	35.67199176	10.40298638	0.18262386	0	-	-
Batu	*C. vagabundus*	vagabundus_24	109.8	34.44531962	10.52847821	0.120865672	1	4.556962025	-
Batu	*C. vagabundus*	vagabundus_25	112.3	36.82972509	18.73245406	0.187844557	0	-	-
Batu	*C. vagabundus*	vagabundus_26	103.1	28.56521345	12.92566835	0.254081535	2	4.337349398	79.3342456
Batu	*C. vagabundus*	vagabundus_27	113.6	38.11178071	20.62509417	0.311644542	0	-	-
Batu	*C. vagabundus*	vagabundus_29	108.4	33.15595319	11.60771221	0.106693173	1	4.090909091	-

Table A6 (continued from previous page)

Site	Species	Individual ID	Total Length (mm)	Mean Mass (g)	Mean Velocity (cms-1)	Mean ODBA (g)	Total Bites	Bite Rate (bites/minute)	Mean Bite Distance (mm)
Paele	*C. baronessa*	baronessa_04	71.28	11.57365798	9.858746911	0.245963325	2	7.2	1.154781621
Paele	*C. baronessa*	baronessa_05	81.2	16.73025131	8.107553693	0.14200296	6	11.4893617	110.4068764
Paele	*C. baronessa*	baronessa_06	75.57	13.65369446	7.686499497	0.16785186	5	18	43.81516718
Paele	*C. baronessa*	baronessa_07	75.17	13.45030096	8.429276878	0.132517366	3	10.8	99.21527916
Paele	*C. baronessa*	baronessa_08	77.63	14.73267755	8.942740929	0.169365211	4	14.25742574	87.45226334
Paele	*C. baronessa*	baronessa_09	80.9	16.55603871	8.905396165	0.13495125	3	10.58823529	158.3999245
Paele	*C. baronessa*	baronessa_10	74.97	13.34934308	12.68566506	0.274495636	5	18	49.39601013
Paele	*C. lunulatus*	lunulatus_10	107.13	34.97698984	19.534174	0.130281607	0	-	-
Paele	*C. lunulatus*	lunulatus_11	108.13	35.66581083	20.40736375	0.16618834	0	-	-
Paele	*C. lunulatus*	lunulatus_12	104.57	33.24562803	23.3199063	0.192937243	0	-	-
Paele	*C. lunulatus*	lunulatus_13	101.4	31.16539884	15.70734812	0.161602424	4	4.615384615	177.4599514
Paele	*C. lunulatus*	lunulatus_14	89.5	23.98145742	25.78933607	0.51610537	2	7.2	12.65182671
Paele	*C. lunulatus*	lunulatus_15	94.77	27.04152626	35.63355203	0.476652913	0	-	-
Paele	*C. lunulatus*	lunulatus_16	78.27	18.09904365	14.83047922	0.328628949	6	24.26966292	13.40353299
Paele	*C. lunulatus*	lunulatus_17	88.77	23.57272649	20.24536109	0.423377439	1	6.206896552	-
Paele	*C. vagabundus*	vagabundus_10	119.1	43.86368647	11.79290187	0.095402802	0	-	-
Paele	*C. vagabundus*	vagabundus_11	118.47	43.17747095	20.76391073	0.374701998	1	11.61290323	-
Paele	*C. vagabundus*	vagabundus_12	114.55	39.06716303	15.00180686	0.262193351	1	5.806451613	-
Paele	*C. vagabundus*	vagabundus_13	114.85	39.37213118	19.18925525	0.272313965	0	-	-
Paele	*C. vagabundus*	vagabundus_14	123.83	49.24824764	28.48445566	0.251915732	0	-	-
Paele	*C. vagabundus*	vagabundus_15	102.17	27.80596106	34.03763451	0.105477025	0	-	-
Paele	*C. vagabundus*	vagabundus_16	111.4	35.95912655	35.58489106	0.215075802	0	-	-
Paele	*C. vagabundus*	vagabundus_17	123.43	48.77679821	28.9639141	0.228750013	0	-	-
Paele	*C. vagabundus*	vagabundus_18	111.67	36.21885563	18.30517253	0.17356055	1	5.901639344	-
Paele	*C. vagabundus*	vagabundus_19	129.8	56.64807058	14.1374635	0.210811237	2	5.217391304	77.14671399
Church	*C. baronessa*	baronessa_22	67.17	9.784303125	12.78960838	0.232923518	8	12.10084034	77.51999932
Church	*C. baronessa*	baronessa_23	67.47	9.908390228	14.5473345	0.232373487	2	6.101694915	535.4526765
Church	*C. baronessa*	baronessa_24	69.5	10.77484525	11.88254669	0.185101954	7	13.47593583	85.7391827
Church	*C. baronessa*	baronessa_25	66.65	9.571606783	12.20792087	0.115521167	2	5.255474453	9.917490626
Church	*C. baronessa*	baronessa_26	87.33	20.55361794	10.09748846	0.120536823	7	14.73684211	65.50064294
Church	*C. baronessa*	baronessa_27	84.93	18.99603114	8.017513217	0.092508617	7	12.85714286	56.0226212
Church	*C. baronessa*	baronessa_28	85.9	19.61601032	4.564534872	0.07319914	8	20.71942446	11.23405364
Church	*C. baronessa*	baronessa_29	90.13	22.47235544	8.317513853	0.100224606	5	5.806451613	212.6527014
Church	*C. baronessa*	baronessa_30	84.97	19.02134324	8.493056029	0.1263303	0	-	-
Church	*C. baronessa*	baronessa_31	87.97	20.98245209	10.96412599	0.083779352	4	9	189.1384855
Church	*C. lunulatus*	lunulatus_28	115.85	41.22083697	21.01231596	0.167720979	1	2.5	-
Church	*C. lunulatus*	lunulatus_29	99.43	29.908052	34.8552512	0.192497889	0	-	-
Church	*C. lunulatus*	lunulatus_30	107.4	35.16227841	24.77050202	0.219776127	2	5.538461538	169.6259479
Church	*C. lunulatus*	lunulatus_31	104.43	33.15227072	25.38632855	0.270610896	3	8.059701493	136.1059601
Church	*C. lunulatus*	lunulatus_32	107.1	34.95643386	18.24679717	0.129650351	0	-	-
Church	*C. lunulatus*	lunulatus_33	105.47	33.8490652	32.67154775	0.25076183	2	5.669291339	95.11976413
Church	*C. lunulatus*	lunulatus_34	123.38	47.04590046	27.88672355	0.150599997	0	-	-
Church	*C. lunulatus*	lunulatus_35	105.23	33.68759288	21.96130295	0.141954953	0	-	-
Church	*C. lunulatus*	lunulatus_36	96.5	28.088067	34.5815183	0.190473797	0	-	-
Church	*C. lunulatus*	lunulatus_37	100.4	30.52376385	26.97687834	0.17041763	0	-	-
Church	*C. vagabundus*	vagabundus_30	89.9	19.00846403	8.968511668	0.086351094	2	3.090128755	765.8129519
Church	*C. vagabundus*	vagabundus_31	113.25	37.7637455	13.81520482	0.116850675	0	-	-
Church	*C. vagabundus*	vagabundus_32	107.13	32.01438598	18.86309757	0.13550937	0	-	-
Church	*C. vagabundus*	vagabundus_33	113.43	37.94247039	19.63693334	0.095299929	0	-	-
Church	*C. vagabundus*	vagabundus_34	89.4	18.69587971	19.48204399	0.26440129	6	11.55080214	347.6740436
Church	*C. vagabundus*	vagabundus_35	123.03	48.30835356	23.8048777	0.170031997	0	-	-
Church	*C. vagabundus*	vagabundus_36	100	26.0867191	6.955863958	0.089696669	5	8.256880734	17.32341178
Church	*C. vagabundus*	vagabundus_37	106.7	31.63386674	7.410924159	0.099383555	10	12.16216216	13.5636151
Church	*C. vagabundus*	vagabundus_38	109.53	34.19411212	11.20290398	0.117645732	1	3.428571429	-
Church	*C. vagabundus*	vagabundus_39	117.4	42.02838616	11.94159361	0.111422811	5	12.94964029	52.96625791
Pobuna	*C. baronessa*	baronessa_33	98	28.47510643	11.46998054	0.268969904	2	7.058823529	21.0690995
Pobuna	*C. baronessa*	baronessa_35	100.23	30.34587017	9.57269268	0.137937564	1	3.564356436	-
Pobuna	*C. baronessa*	baronessa_36	86.5	20.00596782	11.48451693	0.130145271	4	14.4	36.46493812
Pobuna	*C. baronessa*	baronessa_37	100.57	30.63788565	12.89155397	0.174431406	0	-	-
Pobuna	*C. baronessa*	baronessa_38	97.75	28.27015752	14.03872784	0.223442944	0	-	-
Pobuna	*C. baronessa*	baronessa_39	95.83	26.72786213	18.88361511	0.294829365	1	3.529411765	-
Pobuna	*C. baronessa*	baronessa_40	99.35	29.5984354	12.97861557	0.208263226	1	3.870967742	-
Pobuna	*C. baronessa*	baronessa_41	103	32.77794223	15.30943076	0.264857736	0	-	-
Pobuna	*C. lunulatus*	lunulatus_38	94.7	26.99961849	28.71228727	0.254066061	0	-	-
Pobuna	*C. lunulatus*	lunulatus_39	102	31.55373561	31.35267548	0.275372048	0	-	-
Pobuna	*C. lunulatus*	lunulatus_40	104.47	33.17893021	28.43023313	0.198379257	0	-	-
Pobuna	*C. lunulatus*	lunulatus_42	108.6	35.99198713	13.27047699	0.208870644	0	-	-
Pobuna	*C. lunulatus*	lunulatus_43	105.97	34.18676454	19.65213731	0.260279211	0	-	-
Pobuna	*C. lunulatus*	lunulatus_44	104.23	33.01914157	38.73057451	0.592841885	0	-	-
Pobuna	*C. vagabundus*	vagabundus_40	107.17	32.04993674	7.683046048	0.142364749	3	10.69306931	98.21709215
Pobuna	*C. vagabundus*	vagabundus_41	121.48	46.52133644	17.23329424	0.412895337	0	-	-
Pobuna	*C. vagabundus*	vagabundus_42	121.8	46.88661177	15.43988246	0.12426002	1	5.217391304	-
Pobuna	*C. vagabundus*	vagabundus_43	118.33	43.02595256	16.43793314	0.199920154	0	-	-
Pobuna	*C. vagabundus*	vagabundus_44	123.97	49.41396658	6.447091693	0.111225571	0	-	-
Pobuna	*C. vagabundus*	vagabundus_46	131.9	59.41652372	17.00626019	0.189678094	0	-	-
Pobuna	*C. vagabundus*	vagabundus_47	114.5	39.01648792	24.81736103	0.11927386	0	-	-
Pobuna	*C. vagabundus*	vagabundus_48	122.3	47.46115671	28.0972302	0.146930513	0	-	-
Pobuna	*C. vagabundus*	vagabundus_49	105.63	30.7000473	29.07137756	0.11781496	0	-	-

Figure A1

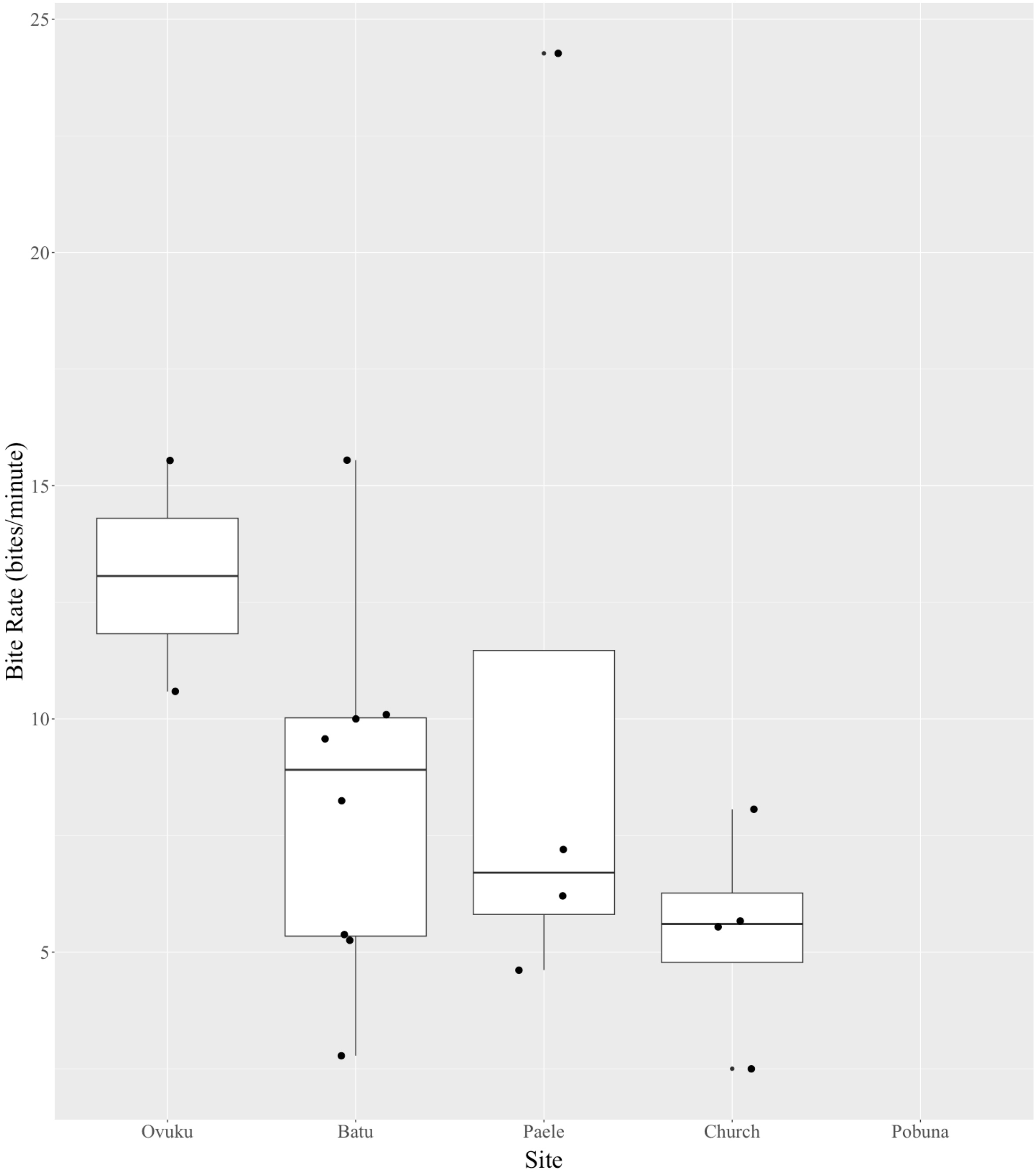
Comparison of Bite Rates for Chaetodon baronessa *at Sampling Sites Along a Turbidity Gradient*



Note. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Sites are listed in increasing distance from the mouth of Vavanga River.

Figure A2

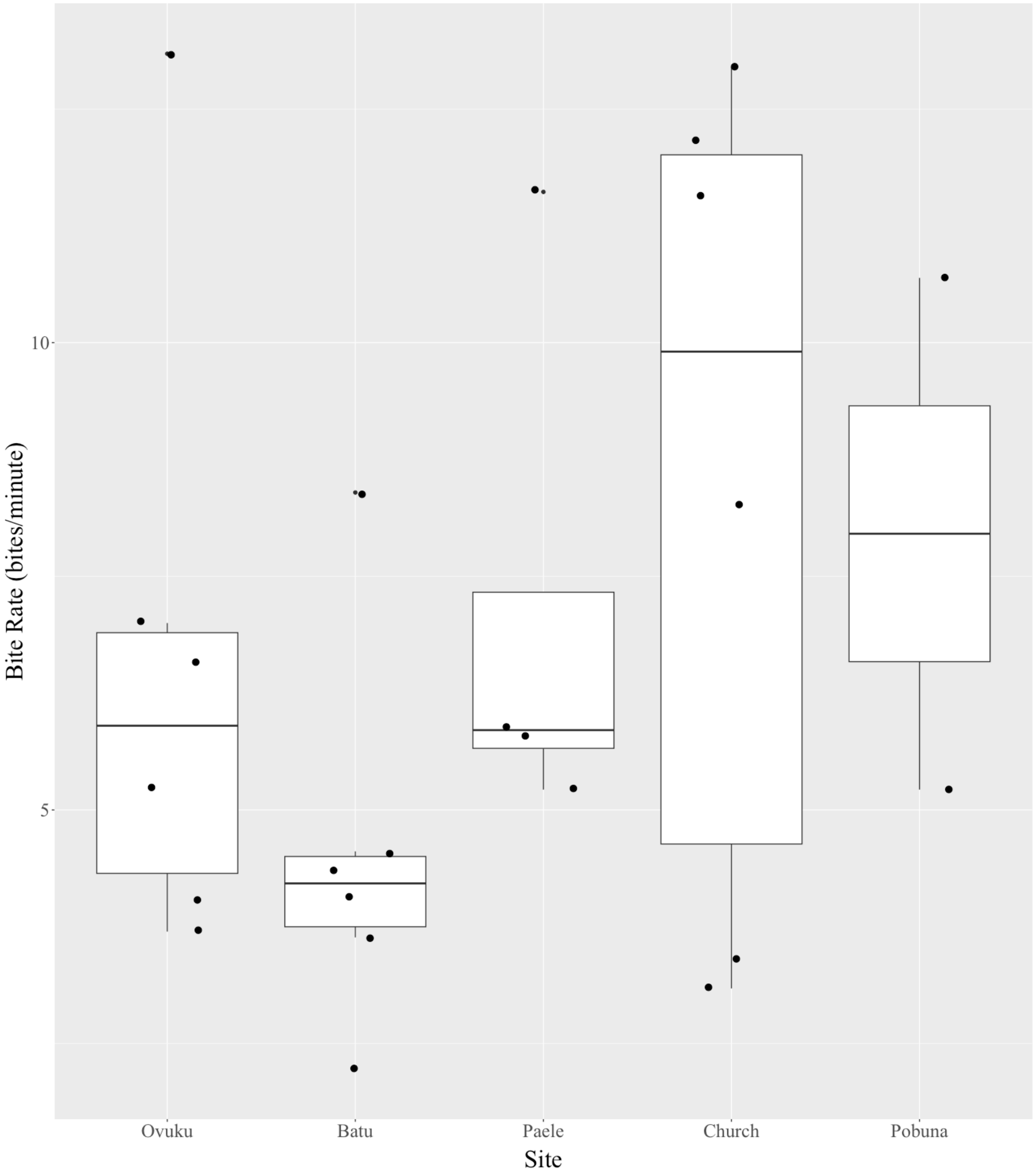
Comparison of Bite Rates for Chaetodon lunulatus *at Sampling Sites Along a Turbidity Gradient*



Note. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Sites are listed in increasing distance from the mouth of Vavanga River.

Figure A3

Comparison of Bite Rates for Chaetodon vagabundus *at Sampling Sites Along a Turbidity Gradient*



Note. Data collected on Vavanga Reef, Kolombangara, Western Province, Solomon Islands. Sites are listed in increasing distance from the mouth of Vavanga River.