Fine-Scale Foraging Behaviour and Energy Expenditure of Nominally Herbivorous Coral Reef Fishes; a Comparative Analysis Across a Turbidity Gradient on a Coral Reef in the Solomon Islands

Dominic Bravenboer

A thesis submitted to
Auckland University of Technology
in partial fulfilment of the requirements for the degree of
Master of Philosophy (MPhil)

2025

School of Science

Abstract

Coral reefs are some of the most biodiverse habitats on Earth and provide numerous ecosystem services to humans. However, coral reefs worldwide are under threat from increasing anthropogenic impacts such as climate change, overfishing, and sedimentation from land use. Phase shifts from coral dominated habitats to macroalgal dominated habitats are becoming increasingly frequent. While coral reefs have some natural resilience to disturbance, and the coral-macroalgal phase shift may be reversible, it is thought that the resilience and potential for reversal of phase shifts is largely dependent on the complementary effect of different feeding functional groups of fishes. Reefs in which certain functional groups are overfished have far less resilience and tend to shift to a permanent macroalgal dominated state. The study of different feeding functional groups of reef fish in the context of anthropogenic disturbance is now therefore, more important than ever. Here we examine the foraging behaviour and energy expenditure of two fish with contrasting feeding functional groups on the fringing reef at Vavanga off Kolombangara Island in the Solomon Islands. This naturally turbid reef receives fluvial inputs resulting in a natural turbidity gradient, making an ideal proxy for studying the effects of anthropogenic turbidity and habitat degradation from land-use changes. Five sites were selected along this turbidity gradient, ranging from a highly turbid river mouth, to offshore reef with relatively high coral cover and clear water. Remote stereo video analysis was used to analyse fish movements in 3D which allowed in-situ estimation of energy expenditure and fine-scale foraging behaviour. The aim was to identify how these traits are influenced by increasing turbidity and potentially elucidate early behavioural warning signs of reef degradation. We found that the generalist detritivore *Ctenochaetus striatus* was relatively resistant to turbidity, showing no significant trends with water clarity. Furthermore, it appeared to prefer moderate turbidity levels, feeding consistently on the epilithic algal matrix (EAM) with increasing bite rates in relation to site turbidity, possibly due to eutrophication increased productivity in the EAM. This trend continues until the most turbid site where feeding ceases and energy expenditure increases. This implies a high turbidity threshold for this species, and we conclude that it would likely not be an ideal candidate for revealing early signs of degradation. The excavating *Chlorurus bleekeri,* a specialist consumer of endolithic microbes, was recorded feeding so infrequently that no assumptions could be made about the effects of turbidity or habitat composition on its foraging behaviour. Furthermore, it showed no response in energy expenditure to visibility or site. Thus, we conclude that this species is also not an ideal candidate for modelling the effects of elevated turbidity and degradation. This study highlights that some coral reef fish are relatively resistant to turbidity and subsequent shifts in habitat composition, and perhaps such species will be crucial for maintaining reef resilience in the face of anthropogenic disturbances. This research could be furthered by AI automation of 3D video analysis, allowing for more data to be gathered on a greater number of species.

Table of Contents

Abstract 2
  Table of Contents 3
  List of Figures 5
  List of Tables 7
  Acknowledgements 9
1.0 Introduction 10
  1.2 Feeding strategies and trade-offs 11
  1.3 Coral reefs 14
    1.2.1 Anthropogenic impacts 15
    1.2.2 Ecosystem resilience and health indicators 18
  1.3 Herbivorous and nominally herbivorous fish 21
    1.3.1 Study species 24
    1.3.1.1 *Ctenochaetus striatus* 24
    1.3.1.2 *Chlorurus bleekeri* 25
  1.4 Aims and Objectives 27
2.0 Methodology 29
  2.1. Location 29
  2.2. Equipment and sampling 31
    2.2.1 Sampling site locations 33
  2.3 Data analysis 34
    2.3.1 Video analysis 34
      2.3.1.1 Video synchronisation 34
      2.3.1.2 Lens distortion correction 34
      2.3.1.3 Three-dimensional calibration 35
      2.3.1.4 Fish tracking 35
    2.3.2 Fish mass estimation 37
    2.3.3 Extracting information from 3D trajectories 37
      2.3.3.1 Removal of outliers 37
      2.3.3.2 Velocity, overall dynamic body acceleration, and metabolic rate calculations 37
      2.3.3.3 Bite distance and bite rate 38
    2.3.4 Statistical analysis 38
      2.3.4.1 Environmental and feeding preferences 38
      2.3.4.2 Feeding preferences 39
      2.3.4.3 Analysis of fish traits 39
      2.3.4.4 Environmental effects on behavioural traits and energy expenditure 39

2.3.4.5 Site level analysis 40
3.0 Results 42
3.1 Environmental analysis 42
3.2 Foraging prefegrences 50
3.2.1 *C. striatus* 51
3.2.3 *C. bleekeri* 51
3.3 Corelations between fish traits 55
3.3.1 *C. striatus* 55
3.3.2 *C. bleekeri* 56
3.4 Environmental relationships with behavioural traits and energy expenditure 60
3.4.1 *C. striatus* 60
3.4.2 *C. bleekeri* 60
3.5 Site level analysis 72
3.5.1 *C. striatus* 72
3.5.2 *C. bleekeri* 73
4.0 Discussion 78
4.1 Environment of the Vavanga Reef 78
4.2 Foraging preferences 80
4.2.1 *C. striatus* 80
4.2.2 *C. bleekeri* 81
4.3 Corelations between fish traits 85
4.3.1 *C. striatus* 86
4.3.2 *C. bleekeri* 86
4.4 Effects of visibility and Forel-Ule 86
4.4.1 *C. striatus* 86
4.4.2 *C. bleekeri* 89
4.5 Site level analysis 91
4.5.1 *C. striatus* 91
4.5.2 *C. bleekeri* 93
4.6 Conclusions and future directions 94
References 99
Glossary 127
Appendix 130

List of Figures

Figure 1.3.1.1 The striated surgeonfish (*Ctenochaetus striatus*) 25

Figure 1.3.1.2 Bleeker's parrotfish, terminal phase (*Chlorurus bleekeri*) 26

Figure 1.3.1.3 Bleeker's parrotfish, initial phase (*Chlorurus bleekeri*) 29

Figure 2.1.1 Location and map of Kolombangara Island 29

Figure 2.1.2 Images of turbidity gradient along Vavanga Reef 30

Figure 2.2.1 Camera rack setup and calibration frame 31

Figure 2.2.2 Forel-Ule index colour chart 32

Figure 2.2.3 Aerial photograph of Vavanga reef, showing each site along the turbidity gradient 33

Figure 2.2.4 Underwater stereo video calibration procedure and quadrat placement 34

Figure 3.1.1 Site comparisons of visibility 43

Figure 3.1.2 Site comparisons of Forel-Ule 44

Figure 3.1.3 Relationship between Forel-Ule index and visibility by site 45

Figure 3.1.4 Relationship between total available substrates and visibility by site 46

Figure 3.1.5 Percentage cover of each substrate at each site 47

Figure 3.1.6 Site comparisons of EAM cover 48

Figure 3.1.7 Relationship between visibility and EAM cover 49

Figure 3.1.8 Site comparisons of dead coral cover 50

Figure 3.2.1 Percentage of fish feeding at each site 52

Figure 3.2.2 Percentage of total bites taken on different substrate types at each site 53

Figure 3.2.3 Manly's preference ratios for key substrates at each site 54

Figure 3.2.4 Percentage of initial and terminal phase individuals at each site 55

Figure 3.3.1 Relationships between FMR, velocity, and bite distance in *C. striatus* 56

Figure 3.3.2 Relationships between bite rate, mass, FMR, bite distance, and velocity in *C. striatus* 57

Figure 3.3.3 Relationships between FMR, velocity, and bite distance in *Chlorurus bleekeri* 57

Figure 3.3.4 Relationships between bite rate, mass, FMR, bite distance, and velocity in *Chlorurus bleekeri* 58

Figure 3.4.1 Relationships between velocity and visibility 62

Figure 3.4.2 Relationships between FMR and visibility 63

Figure 3.4.3 Relationships between bite distance and visibility 64

Figure 3.4.4 Relationships between velocity and Forel-Ule index 65

Figure 3.4.5 Relationships between FMR and Forel-Ule index 66

Figure 3.4.6 Relationships between bite distance and Forel-Ule index 67

Figure 3.4.7 Relationship between bite distance and depth in *C. striatus* 68

Figure 3.4.8 Relationship between FMR and EAM cover in *C. striatus* 68

Figure 3.4.9 Relationship between bite distance and EAM cover in *C. bleekeri* 69

Figure 3.5.1 Site comparisons of mass 74

Figure 3.5.2 Site comparisons of bite rate, velocity, and FMR in *C. striatus* 75

Figure 3.5.3 site comparisons of bite rate, velocity, and FMR in *C. striatus* 76

Figure 3.5.4 Site comparisons of FMR for initial phase and terminal phase *C. bleekeri* 77

List of Tables

Table 3.3.1 Simple linear model results for relationships between bite distance, FMR, mass, and velocity in *C. striatus* ______ 58

Table 3.3.2 Simple linear model results for relationships between bite distance, FMR, mass, and velocity in *C. bleekeri* ______ 59

Table 3.3.3 Generalised additive model results for bite rate and predictor variables in *C. striatus* __ 59

Table 3.3.4 Generalised additive model results for bite rate and predictor variables in *C. bleekeri* __ 59

Table 3.4.1 Linear mixed model results showing effects of visibility, EAM cover, and depth on behavioural response variables (velocity, FMR, and bite distance) in *C. striatus* ______ 69

Table 3.4.2 Linear mixed model results showing effects of Forel-Ule, EAM cover, and depth on behavioural response variables (velocity, FMR, and bite distance) in *C. striatus* ______ 70

Table 3.4.3 Linear mixed model results showing effects of visibility, EAM cover, and phase on behavioural response variables (velocity, FMR, and bite distance) in *C. bleekeri* ______ 71

Table 3.4.4 Linear mixed model results showing effects of Forel-Ule, EAM cover, and phase on behavioural response variables (velocity, FMR, and bite distance) in *C. bleekeri* ______ 72

Table A1 Vidsync event settings ______ 130

Table A2 Environmental data and sampling information for sites at the Vavanga Reef______ 130-131

Table A3 Sampling site distances ______ 131

Table A4 Percentage cover of substrates at each sample site ______ 132

Table A5 Percentage of total bites on each substrate and Manly’s preference ratios ______ 133

Table A6 Raw data for each individual *C. striatus* recorded. Including mass, length, mean velocity, velocity, FMR, total bites, mean bite rate, and mean bite distance______ 134-135

Table A7 Raw data for each individual *C. bleekeri* recorded. Including mass, length, mean velocity, velocity, FMR, total bites, mean bite rate, and mean bite distance______ 136-137

“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 used artificial intelligence tools or generative artificial intelligence tools (unless it is clearly stated, and referenced, along with the purpose of use), 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.”

Signed: _______________

Date: 11/11/2025

Acknowledgements

Firstly, I would like to extend my sincere thanks to my supervisor, Armagan Sabetian, and acknowledge the dedication and hard work he put in to both bring this research to fruition and ensure that I succeeded in completing this thesis. Throughout the course of this project, I encountered many trials and tribulations, yet Armagan was always there to support me and assist me in whatever way he could. He went above and beyond to guide me through my research and writing and furthermore assisted me in achieving my scholarships which allowed me the freedom to focus on this research. I will always be extremely grateful for this.

I would also like to show my gratitude to my co-supervisor Julian Lilkendey for the work that he put into this research and for lending me his scientific and statistical expertise whenever I needed it. Julian's knowledge of marine ecology and data analysis cannot be understated. Without his generous assistance, I certainly would not have been able to complete this work to the standard that I have.

While I was unfortunately not involved in the field work of the wider project on which my research is based, I would like to thank all those involved in the field work for making this possible. This includes Armagan, Julain, Emily Steele, and of course the people of the Vavanga Village for providing their indispensable indigenous knowledge of the area and assisting in the deployment of research equipment on the reef. I would also like to thank Sam Van Iersel for assisting me with the stereo-video analysis part of this project. Stereo-video analysis can be an exhausting and time-consuming process and without Sam's help, I would not have had the quality nor the quantity of data that I had to work with.

Lastly, I want to thank my loving parents, Christine and Rueben, for their unwavering support leading up to and during this thesis. Both of my parents have always nurtured my love of marine life and have motivated me to pursue my passion in this field. Without their guidance and support, I may never have come this far.

I also acknowledge that ChatGPT was used to assist with R-coding for data organization, statistics, and graph generation. ChatGPT was also used as an editing tool to assist in refinement of writing such as grammar, paragraph structure, and conciseness after content was manually written by me.

1.0 Introduction

Primary productivity via photosynthesis forms the basis of almost every ecosystem on Earth (Lieth & Whittaker, 2012). The energy sequestered through primary production is taken up by consumers and is passed up through trophic levels. However, this flux of energy is not linear and is generally more akin to a complex web, with different species adapting to enter this web wherever they can (Dobson, 2009). This has led to an incredible array of different feeding strategies and adaptations, from herbivores that simply graze on plants or algae, to predators that specialise in feeding on these herbivores, to parasites which feed on both of the latter, and even to hyperparasites which feed on these parasites (Dobson, 2009; Gleason et al., 2014)

Every animal has a basal metabolic rate (BMR)—the core rate of energy consumption required simply to stay alive—thus requiring some minimum rate of calorie intake (Hulbert & Else, 2004). Beyond this, there are additional metabolic costs for every other process an organism must go through to stay alive and successfully reproduce. These processes include defence/evasion of predators, foraging, migrations, growth, and of course breeding and reproduction. Altogether these can be extremely energy consuming, making the field metabolic rates of animals measure much higher than their BMR (Brönmark et al., 2014; Karasov, 1992). Therefore, any excess energy that can be obtained beyond what is required for BMR will convey a massive benefit to the overall fitness and reproductive success of an animal. Unsurprisingly, there is heavy selective pressure for morphological and behavioural traits that enhance an animal's ability to forage and feed efficiently, as well as traits that allow the utilisation of new food resources (Galis & Metz, 1998; Rosenberger, 1992).

Although the focus of this research is on foraging behaviour and energy expenditure, it is important to understand how different foraging behaviours have come about from an evolutionary perspective as the need for energy is intrinsically linked to evolution and has resulted in the vast assortment of feeding strategies and complex ecological interplay between these strategies seen today (Polechová & Barton, 2005; Schoener, 1971). Behavioural and morphological adaptations to new resources co-occur with speciation, and where there are more resources there is more speciation (Sobel et al., 2010). Consequently, regions with high productivity tend to have higher biodiversity, and this is one of the leading hypotheses for why the most biodiverse regions on Earth are found in the tropics (Sherratt & Wilkinson, 2009). As net primary productivity (NPP) is dependent on temperature and water availability, the warm wet climates of tropical regions result in high NPP and thus more resources. Theoretically two species cannot coexist in direct competition, such that resource scarcity increases extinction rates. In the tropics however, higher resource availability dissipates competition and allows more room for niche partitioning while opening avenues for new niches to be exploited (Brown, 2014).

1.2 Feeding strategies and trade-offs

Of the myriad feeding and foraging strategies found in the natural world, each seems to have its own trade-off between the abundance of the targeted food resource, how difficult it is to digest, its nutrient and energy content, and the energy expended in obtaining it. Carnivores specialise in consuming animal matter, which is high in energy, protein, and fat, and is easily digestible. Such a diet alone would convey a great fitness benefit; however, carnivores generally must risk injuries pursuing prey and expend a greater amount of energy in the process of foraging and prey pursuit. Consequently, they require a higher field metabolic rate than herbivores (Karasov & Douglas, 2013; Mukherjee & Heithaus, 2013; Nagy et al., 1999). Conversely, herbivores rarely have difficulty obtaining their food and are often surrounded by it, thereby using relatively little energy in the foraging process. The trade-off here is that plant/algae matter tends to be a much lower quality food in terms of energy/nutrient content and digestibility (Linton & Greenaway, 2007). Even large herbivores such as American bison and domestic cattle must consume around 10% or more of their body weight per day in plant matter, while carnivores such as big cats (*Panthera*) need only consume 4-4.5% of their body weight in prey per day (Emmons, 1987; Huntington et al., 2019). Additionally, herbivores require large, complex, and energy consuming digestive tracts which have long food retention times to extract sufficient energy and nutrients from their fibrous, low quality diets (Chivers, 1989; Elsden & Phillipson, 1948). Cellulose is a major component of plant matter, and most herbivores and some omnivores employ some form of fermentation to metabolise cellulose into energy, as mammals are not capable of producing cellulase enzymes (Froidurot & Julliand, 2022). Ruminants use foregut fermentation and have a four chambered stomach consisting of a rumen, reticulum, omasum, and abomasum to accommodate this process, and altogether the stomach takes up 75% of the abdominal volume in domestic cattle (Luginbuhl, 1983). The larger quantities of poorly digestible matter ingested by herbivores also require a large quantity of enzymes to aid in digestion, with rabbits producing 100–150 mL of bile per kilogram of bodyweight daily, while dogs only produce around 20 mL per kilogram of bodyweight daily (Davies & Davies, 2003). These herbivorous digestive processes each have their own metabolic cost, altogether resulting in much lower utilization efficiency and overall digestive efficiency for herbivorous animals (Karasov & Douglas, 2013).

Omnivores appear to mitigate some of the trade-offs faced by both strict herbivores and carnivores. Where carnivores may struggle to locate and successfully capture enough prey in times of food scarcity, an omnivore is able to survive on plant matter until suitable animal prey is found (Coll & Guershon, 2002; Coogan et al., 2018). In comparison to herbivores, omnivores require a less complex and energy consuming digestive system, as on average their diet is of a higher energy content and digestibility than herbivores (Dimijian, 2000; O'Hara et al., 2012). Omnivory is also particularly well suited to high latitude habitats, where extreme seasonal variations in climate can result in highly variable resource availability, omnivores can alternate between animal based diets in winter when suitable plant matter is scarce, and plant based diets in summer when plants are fruiting and growing more readily (Ballard, 1992).

Despite this, omnivory still has its own unique trade-offs. Omnivores are less effective at digesting plant matter than herbivores, and shorter food retention times combined with lower fermentative capacities seem to prohibit many omnivores from thriving on extremely fibrous food such as grass (Mcanally & Phillipson, 1944). Thus, omnivores generally must be more selective in the plant matter they consume. The omnivorous wild boar (*Sus scrofa*), for example, tends to selectively feed on plant matter which is higher in nutritional quality and digestibility, such as fruits, seeds, bulbs, and roots (Ballari & Barrios-García, 2014). Furthermore, many omnivores are obligate omnivores and cannot survive on just carnivorous or herbivorous diets alone. It is thought that prior to the agricultural revolution, humans (*Homo sapiens*)—particularly in cold climates—were obligate omnivores, as humans were likely not proficient enough as hunters to survive only on animal meat, while vitamin B12 is essential to humans and can only be found in animal tissue (Kerna et al., 2021). Interestingly, many omnivorous animals appear to be equally effective hunters as predatory carnivores. Some omnivorous species, such as chimpanzees, have even been observed to have higher hunting success rates than lions (45% in chimpanzee hunts vs 15-43% in lion hunts); though this could be due to omnivorous species only engaging in hunting when it is convenient, while predatory carnivores must hunt frequently to survive (Lamprecht, 1981; Uehara, 1997).

Hutchinson (1957) described a species niche as an "n-dimensional hypervolume", where the axes of this volume are the multitude of environmental conditions and resources which allow this species to survive. Different species will utilise comparatively different breadths of each of these axes. Those species that tend to utilise a large breadth of an axis are often referred to as generalists with respect to that given axis, while those that utilise comparatively less are referred to as specialists. For example, on an axis of "prey species consumed" a species that consumes many prey species would be considered a generalist predator, while a species that consumes only a few or even a single prey species would be considered a specialist predator. Though this concept of specialists and generalists is often portrayed as a dichotomy in the literature, it is important to note that in reality it should be viewed as a continuum ranging from highly specialised to highly generalised. Thus, species are defined in this manner on a contrastive basis (Futuyma & Moreno, 1988).

Generalists are often referred to as "jacks of all trades, masters of none", as in many cases it is found that the benefit of being able to utilise a wide range of resources comes at the cost of not being particularly efficient in utilising any single one of them. Conversely, specialists are often much more efficient in utilising their chosen resources but are at the disadvantage of having fewer resource options available to them (Drummond, 1983). This trade-off could be the result of any number of adaptational differences between specialists and generalists and could be physiological, morphological, or behavioural in nature (Kotrschal & Thomson, 1986; Yamaoka, 1983; Zera & Harshman, 2001). A behavioural example of this trade-off can be seen in some North American garter snake species. *Thamnopsis elegans* and *Thamnopsis sirtalis* are considered generalists, hunting in a wide range of habitats from terrestrial to aquatic and preying on many terrestrial, aquatic, and even amphibious genera. In contrast, *Thamnopsis couchi* and *Thamnopsis melanogaster* are aquatic specialists, and hunt almost exclusively in aquatic environments. When the aquatic hunting abilities of these four species were compared under both experimental and in situ conditions, the two aquatic specialists were able to catch significantly more fish in a given time period, as they utilised a much more diverse array of specialised aquatic hunting behaviours (Drummond, 1983).

This ability of dietary specialists to utilise their preferred food with comparatively high efficiencies often puts them at an advantage over more generalist species when their preferred food is in abundance. Indeed, some specialist species have been found to forage with greater efficiencies than generalists which often translates into higher reproductive success (Bernays, 1999; Korpimäki et al., 2020). Additionally, within species, some individuals may specialise in certain diets more than others and those individuals have often been shown to have higher foraging efficiencies and reproductive success (Annett & Pierotti, 1999; Oppenheim & Gould, 2002). However, in theory generalists are expected to be much more resilient to scarcity of preferred food than specialists. This is because species which are willing or able to utilise a wider range of food sources can simply switch to another food source if one becomes scarce (Rutz & Bijlsma, 2006). While some specialists are also able to switch to an alternate food source in this case, they tend to be much less efficient than generalists at utilising alternate food sources (Terraube et al., 2011).

Animals which are adapted to habitats with constant or frequent food scarcity are also commonly generalists (Behn & Baxter, 2019; Trajano, 2001). For example, many cave fish species are generalist feeders; in such a food scarce environment, it is a fitness benefit to be able to consume any source of nutrition that presents itself. Thus, most cave fish species are generalist carnivores or omnivores, and will feed on a wide range of insects and crustaceans, many are also cannibalistic and some have even been observed feeding on bacteria and bat guano (Trajano, 2001). The ability of generalists to feed opportunistically and resist food scarcity is thought to make them less likely to face extinction in the event of environmental changes, while specialists are often at a greater risk of extinction (Shultz et al., 2005; Suhonen et al., 2014). Additionally, in many cases, this makes generalists more able to invade new habitats (Crowder & Snyder, 2010). Such traits have resulted in many extremely successful generalist species which have massive geographical distributions. A few examples of such species are humans (*H. sapiens*), brown bear (*Ursus arctos*), Mozambique tilapia (*Oreochromis mossambicus*), and the Asian house gecko (Curry-Lindahl, 1972; Hoskin, 2010; Russell et al., 2012).

1.3 Coral reefs

Coral reefs are typically defined as shallow marine areas which have been built up above the sea floor by photosynthetic "reef building" corals; they are generally confined to warm seas between 31°40'S and 32°50'N (Perry & Larcombe, 2003; Yamano et al., 2001). The reef building corals (order: Scleractinia), commonly known as hard or stony corals, continuously deposit a hard calcium carbonate skeleton around their soft tissue throughout their lifespan (Wang et al., 2021). This strong inorganic calcium carbonate skeleton remains after the death of the soft tissue, thus, over time these skeletons accrete on the sea floor and build a complex three-dimensional structure that creates an ideal habitat for a plethora of marine life (Goreau et al., 1979). As a result of this unique habitat structure, coral reefs are likely the most biodiverse marine habitats on Earth (Knowlton et al., 2010).

Unsurprisingly, coral reefs are also extremely productive habitats and provide numerous ecosystem services to humans (Hatcher, 1990; Moberg & Folke, 1999). Cesar et al, (Cesar et al., 2003) estimated that coral reefs provided goods and services to global economies worth around US $30 billion per year and this number has likely grown since then. Probably one of the most important and direct services coral reefs provide to humans is food. It is estimated that worldwide, over 6 million people fish within coral reefs and likely many more are supported directly by the catch of these fishers (Teh et al., 2013). Of these coral reef fisheries the vast majority are small scale and subsistence fisheries, meaning the communities serviced by these fisheries are highly dependent on their local coral reefs for food and thus highly vulnerable to fluctuations in reef productivity (Bell et al., 2011; Leenhardt et al., 2016). In addition to food harvesting, there is also a multi-billion dollar ornamental fish trade, wherein over 4000 species of coral reef fish are exported by around 50 countries (Biondo & Burki, 2020). Mining of coral—both dead and alive—for use as construction material is an unfortunate service that coral reefs provide as it is extremely damaging to reef health and has thus been banned in several countries; however, the practice is still prevalent in some areas (Brown, 2011). Coral reefs have also been shown to have high value to public health as the marine biotechnology industry has emerged. The unique biochemical adaptations found in coral reef life have now yielded many promising medicinal products, including antiviral, anticancer, and painkiller drugs, among others (Bruckner, 2002).

Coral reefs act as an important buffer zone between the land and the sea, providing a service known as "coastal protection" (Harris et al., 2018). The built-up structure of coral reefs provides a significant barrier to dissipate wave energy, with one study showing that reefs can reduce wave energy by up to 97% (Ferrario et al., 2014). An analysis done by a risk insurance agency found that restoring reefs was always a significantly more cost-effective approach to enhancing coastal protection when compared to artificial protection such as breakwaters (*CCRIF Annual Report 2009-2010 | CCRIF SPC*, n.d.). Without protection from coral reefs, many beaches would be much more susceptible to erosion processes; indeed, it has been shown that exposed beaches have significantly higher net sediment exchange than reef protected beaches (Martins et al., 2019).

1.2.1 Anthropogenic impacts

Reefs built by calcifying spongelike organisms appeared in the fossil record ~520 Ma (million years ago); the first modern reefs dominated by the scleractinian corals began appearing around 215 Ma (Stanley, 1981). During this vast geological history coral reefs have suffered and recovered from several mass extinction events and many more second order extinction events (Hallock, 1997). Thus, on a geological timescale, coral reefs are extremely resilient. Despite this, modern coral reefs are adapted to a relatively stable and specific set of environmental conditions and exist in somewhat of a delicate balance (Riegl et al., 2009). Unsurprisingly then, entering the environmentally volatile anthropogenic era, it seems that coral reefs may be facing their next extinction event. It has been estimated that roughly 20% of coral reefs have been effectively destroyed since the advent of this era, with a further 24% being under imminent risk of collapse and 26% being under long term risk of collapse (Côté & Reynolds, 2006). It is now widely accepted that anthropogenic activity has been degrading coral reefs at an increasing rate. Furthermore, the anthropogenic threat to coral reefs is multifaceted, with significant impacts recorded from overharvesting, increasing global temperatures, ocean acidification, and sedimentation/pollution (Riegl et al., 2009).

Much of the recent coral reef conservation literature is centred around examining and predicting the effects of climate change, and for good reason. The average global surface temperature has increased by approximately 1°C since 1900; additionally, the rate of temperature rise is also increasing, with temperatures rising by about 0.2°C per decade since 1975 (Hansen et al., 2006). The most notable and widespread symptom of this global temperature increase seen in reefs is coral bleaching. Corals are dependent on a symbiotic relationship with the dinoflagellates *Symbiodinium,* these photosynthetic symbionts give coral their yellow-brown colouration and more importantly, provide a source of carbohydrate (Goreau et al., 1979). The biochemical coordination required for the relationship between coral and *Symbiodinium* is sensitive and is thus susceptible to major stressors. Severe stressors such as temperature extremes, too much light, too little light, sedimentation, and pathogen infections can cause coral to expel the *Symbiodinium,* giving the coral a bleached appearance (Douglas, 2003). The coral may survive up to several months like this; however, if the stress is too severe or prolonged, death will occur (Douglas, 2003). In the case of high temperatures photosynthetic pathways can be overexcited, and damage can occur to photosystem II; it is thought that this causes the release of reactive oxygen species, which then triggers expulsion of *Symbiodinium* by the host coral (Oakley & Davy, 2018). This is an issue, as coral often naturally experience seasonal maximum temperatures within 1-1.5°C of their upper thermal tolerance (Riegl et al., 2009). As a result the number of significant coral bleaching events has increased steeply since 1980s; prior to this, bleaching events were generally rare and small scale

(Glynn, 1996). Interestingly, this coincides with the accelerated global warming seen post-1975 (Hansen et al., 2006). Globally, the risk of severe bleaching events is increasing rapidly at 4.3% per annum, with the current risk standing at around 17% per annum (Hughes et al., 2018). One major bleaching event in 2015-2016 affected 75% of 100 globally distributed reef locations examined by Hughes et al., (2018), with many of these locations experiencing bleaching over hundreds of kilometres of reef. With global temperatures still rising it is expected that bleaching rates will continue to increase. While coral reefs do have the ability to recover from these events given the time, the dramatically increasing rate of severe events has the potential to overwhelm this resilience in the future, especially when compounded by other stressors such as ocean acidification (Schoepf et al., 2015).

Unfortunately, increasing global temperatures are a symptom of increasing anthropogenic greenhouse gases, predominantly CO_2. This in itself is increasingly being recognised as a major potential issue for marine ecosystems worldwide (Riegl et al., 2009). When dissolved in water CO_2 can undergo a hydration reaction, becoming H_2CO_3, carbonic acid. (Reddy & Balasubramanian, 2013). In sea water the hydrogen ion which dissociates from carbonic acid then goes on to react with carbonate ions (CO_3^{2-}) to produce bicarbonate again. This reaction can become a problem for calcifying organisms such as corals, as it reduces the availability of free carbonate ions, which they sequester to construct their aragonite (calcium carbonate) skeletons (Gattuso et al., 1998). Anthropogenic activity has now increased atmospheric [CO_2] to 380ppm, at least 80ppm higher than pre industrial levels; this has driven ocean [CO_3^{2-}] down by 30 µmol kg^{-1}—a concerning figure considering that calcium carbonate accretion becomes negative at [CO_3^{2-}] below 200 µmol kg^{-1} (Hoegh-Guldberg et al., 2007). This increase in atmospheric [CO_2] has reduced sea surface pH from its pre-industrial level of 8.16 to 8.05 at present (Guinotte & Fabry, 2008). While corals have been shown to grow in laboratory conditions at pH values as low as 7.31 and carbonate concentrations as low as 40 µmol kg^{-1}, in nature no coral reefs are present where [CO_3^{2-}] is <200 µmol kg^{-1}, indicating that the seemingly modest reduction in growth rate seen at [CO_3^{2-}] 200 µmol kg^{-1} is likely enough to prevent coral reef formation when combined with other environmental variables and stressors (Inoue et al., 2011; Kleypas et al., 1999).

Currently, it is difficult to delineate the in-situ effects of ocean acidification on corals from other stressors such as increased temperature, thus any current damage caused by ocean acidification remains unquantified. However, under the current rate of atmospheric CO_2 accumulation it is expected that atmospheric [CO_2] will exceed 500ppm by the year 2100; this is enough to drive [CO_3^{2-}] below 200 µmol. Under this scenario, it is likely that most coral reefs worldwide would be pushed past a tipping point from which recovery is nearly impossible (Hoegh-Guldberg et al., 2007).

Coral reefs interact with the land through hydrologic channels such as rivers and groundwater discharge. The quality of this discharge is highly dependent on the state of the land surrounding these hydrologic channels. Thus, changes in land use can have strong impacts on downstream coral reef health, most notable are agriculture, deforestation, and urbanisation. These land use changes damage coral reef health predominantly through increasing sediment and nutrient loads as coral reefs are typically naturally low sediment and low nutrient environments (Carlson et al., 2019). The effects of nutrient enrichment on coral reefs has been a contentious issue, however, it is thought that nitrogen (N) enrichment could be particularly damaging, as many coral reefs are N-limited (D'Angelo & Wiedenmann, 2014; Furnas et al., 2005). Wiedenmann et al. (2013) showed that enriching N alone can result in the bleaching of corals exposed to heat and light stress, however, when both N and phosphorous were enriched, the corals remained healthy when exposed to the same stressors. Though this was a simple in vitro study, it highlights that nutrient imbalances may be more insidious than nutrient enrichment. Adam et al. (2020) used a time-series approach to show that reefs with consistently high N decreased in coral cover and increased in macroalgal cover over time, while reefs with low N retained healthy coral cover. While this study does not account for phosphorous or other potential co-occuring stressors like sedimentation, it supports evidence that macroalgae can outcompete coral in eutrophic environments.

It is well known that forest cover has a positive association with coral reef health and the implications of deforestation on coral reefs are becoming increasingly studied (Carlson et al., 2019). Deforestation impacts coral reefs largely through increasing sediment loads, as removal of forest can increase rates of soil erosion by several orders of magnitude (Walling & Fang, 2003). While Maina et al. (2013) predicted that a 25% decrease in forest cover could nearly double sediment loads in some areas of Madagascar. Excess sediment can damage or kill corals by attenuating light through the water column or by smothering; furthermore, smothering with organic rich sediment can increase bacterial respiration and production of free radicals on the corals surface, leading to higher mortality (Tuttle & Donahue, 2022; Weber et al., 2012). Corals are known to withstand high sediment loads for brief periods, as flooding is a natural occurrence, and corals can remove sediment with cilia and mucus; however, these mechanisms are easily overloaded with prolonged and excessive sediment exposure (Stafford-Smith, 1993; Stafford-Smith & Ormond, 1992). Concordantly, a large review of experimental studies on coral sediment exposure by Tuttle and Donahue (2022) suggests that adult coral are very resilient to high sediment loads for short periods (<2 weeks), while longer exposures (>4 weeks) often cause significant mortality and even full colony mortality. Unfortunately, the Tuttle and Donahue (2022) review also shows that larval and juvenile corals are much less resilient, experiencing mortality in a matter of days or even hours. This shows that while established coral may be resilient to sedimentation, coral reef ecosystems may be vulnerable even to low levels of sedimentation as a result of reduced coral recruitment. The impacts of deforestation and sedimentation on a coral reef can be seen in Merusu Lagoon in the Solomon Islands which sits downstream of a heavily logged catchment. This reef had only 5 g m^{-2} of herbivorous fish biomass and a coral cover of 9.3%, while a less degraded reef nearby had approximately 35 g m^{-2} and 41.6% respectively (Albert et al., 2014)

1.2.2 Ecosystem resilience and health indicators

Considering the multitude of threats potentially facing coral reefs, it is important that we have methods to determine the current impacts of these threats, as well as predict how they may affect coral reefs into the future. This requires an understanding of the natural (i.e. pre-anthropogenic) state of a coral reef and metrics which indicate how degraded a reef is in comparison to its natural state. This potentially presents an issue, as the majority of coral reefs have not been studied before being impacted by anthropogenic activities (Braverman, 2020). Thus, a reef which appears to be in a healthy state may actually have already experienced significant unquantified degradation; conversely, reefs which appear degraded may have naturally been in this state, and human intervention (with the intention of rehabilitation) could in fact be harmful (Bruno et al., 2014). Furthermore, processes typically referred to as degradation, such as loss of fish biodiversity, loss of coral cover, and increase in macroalgae cover, are processes that can happen independently of anthropogenic activity (Aronson et al., 2003; Roth et al., 2018). This highlights the importance of long-term monitoring projects which track indicators of ecosystem health over time; with this approach persistent degradation can be delineated more easily from normal ecosystem variations. Unsurprisingly, many such long-term studies do show persistent decline in indicators of coral reef health, particularly in coral cover (Gardner et al., 2003; Lin et al., 2021; Sweatman et al., 2011). However, many also show no degradation in some aspects of ecosystem health, or much less than might be expected; for example, one 26 year monitoring project on the Great Barrier Reef showed no trend in macroalgal cover over this period (Cheal et al., 2008; Fabricius et al., 2023; Galzin et al., 2015).

Coral cover makes an excellent indicator of coral reef ecosystem health as corals are the structural foundation of their own habitats and reductions in coral cover can be disastrous for their entire ecosystem. Unsurprisingly, coral cover is often strongly associated with biodiversity and biomass of other reef organisms such as fish, making it a good proxy for overall ecosystem health (Bell & Galzin, 1984; Jones et al., 2004; Pratchett et al., 2011). As such, coral cover is one of the oldest and most commonly used metrics for assessing coral reef ecosystem health (Bruno & Selig, 2007). As the literature is replete with examples of fish biodiversity and biomass declining with receding coral cover, these metrics have also become commonplace proxies for coral reef ecosystem health (Jones et al., 2004; Pratchett et al., 2011; Russ et al., 2021). However, in some cases these fish population dynamics may not be ideal indicators of reef health or recovery, as they can lag behind changes in coral cover and can take many years to recover even after coral populations have recovered from disturbance (Bellwood et al., 2012). A pitfall of these indicators of ecosystem health is that they can only describe a change of some kind without addressing the agents that effect these changes, making it difficult—even in many long term studies—to separate anthropogenically driven changes from natural changes. Downs et al. (2005) therefore call for a more mechanistic approach to assessing ecosystem health, measuring ecosystem health indicators in conjunction with Anthropogenic stressors such as turbidity, excess nutrients, and fishing pressure. With this approach, variation in stressors can be correlated with aspects of degradation, providing valuable information on the potential mechanisms of degradation, allowing for more targeted and effective management strategies (Downs et al., 2005).

Macroalgae are a natural component of coral reefs and these producers form a key entry point for nutrients into the ecosystem and are essential for the functioning of coral reefs (McCook, 1999). On healthy coral reefs macroalgae are cropped intensively by herbivorous fish to form dense, short mats which cover available substratum known as an epilithic algal matrix (EAM) (Gibson & Atkinson, 2003). However, under certain circumstances of environmental stress, macroalgae can rapidly grow upwards to outcompete coral and drastically change ecosystem functioning. As macroalgae are in direct competition with coral for space and light, increasing macroalgal growth and cover can create a negative feedback loop by further reducing coral growth and recruitment by shading and occupying recruitment substrates (Kuffner et al., 2006; Lirman, 2001; Tanner, 1995). For example, Thurber et al. (2012) experimentally grew five species of coral in close contact with macroalgae, and growth rates were reduced by an average of 36.8% when compared to control coral not exposed to macroalgae. Fleshy macroalgae are generally far superior to corals in their ability to respond to and recover from environmental stress; they are much faster growing, have a stronger growth response to increased nutrients, are more resistant to turbidity and sedimentation, and have higher recruitment rates than coral (D'Angelo & Wiedenmann, 2014; McManus & Polsenberg, 2004; Schaffelke & Klumpp, 1998; Sura et al., 2021; Tanner, 1995). Thus, macroalgae are much better adapted to the current era of anthropogenic impacts and environmental instability, and as a result many coral reefs worldwide are shifting towards macroalgal dominance (McManus & Polsenberg, 2004).

Without anthropogenic impacts the scientific consensus is that coral reefs exist in a relatively stable state of coral dominance and generally recover to this state after disturbances. However, ecosystems may have alternate stable states, and it is now well documented that many coral reefs are transitioning into an alternate stable state characterised by high macroalgal cover and low coral cover compared to their natural stable state. This transition, termed the "coral-algal phase shift", is associated with anthropogenic stressors and results in declining ecosystem functioning and services, and is thus considered a degradation process (Fung et al., 2011; Holbrook et al., 2016). While many coral reefs appear to have undergone a permanent shift to this state, some reefs have been shown to recover rapidly after disturbances which increase macroalgal abundance and decrease coral cover—particularly Indo-Pacific coral reefs—suggesting that some reefs have retained their natural resilience to return to a coral dominated stable state (Cheal et al., 2010). The same resilience, however, is notably lacking in Caribbean reefs, many of which have shifted—seemingly permanently—to a degraded state. A review by Bruno et al. (2009) found Caribbean reefs had a mean of 20% coral cover and 23.6% macroalgae cover, while Indo-Pacific coral reefs had mean covers of 33.2% and 11.7% respectively. Furthermore, a series of surveys on Caribbean reefs conducted in the 1970s and 1980s found that macroalgal cover averaged ~6%; the fourfold increase in macroalgal cover seen by 2009 indicates a long term region wide loss of resilience in Caribbean reefs, which is leading to widespread ecosystem phase-shifts (Bruno et al., 2009).

The disparity in resilience seen between Caribbean and Indo-Pacific reefs has now been well studied and has provided important insights into the processes which maintain ecosystem resilience. While a multitude of factors influence coral reef resilience, herbivory is now thought to play a central role in maintaining resilience and preventing permanent coral-macroalgal phase shifts (Holbrook et al., 2016). Herbivores place top-down control on macroalgae, and on healthy coral reefs, herbivory is generally sufficient to control macroalgae and retain coral dominance (Burkepile & Hay, 2006; Lirman, 2001). However, when herbivores are removed or heavily overfished, the top-down control is removed and macroalgae can flourish, particularly in the face of disturbances such as hurricanes and ocean heatwaves (Holbrook et al., 2016). In the Caribbean, coral cover began declining in the 1980s; prior to this, herbivorous fish stocks had already been heavily depleted by overfishing, although the herbivorous urchin *Diadema antillarum* was still highly abundant and appeared to provide sufficient levels of herbivory to control macroalgae (Jackson et al., 2001). However, in 1983 *D. antillarum* populations began experiencing mass mortality—likely due to disease—and by 1984 over 93% of the Caribbean *D. antillarum* population had perished (Lessios, 1988). Immediately following this event, a dramatic decrease in coral cover was observed, along with a corresponding dramatic increase in macroalgal cover; this trend then continued for decades, a trend which has largely not yet reversed (Adam et al., 2015; Hughes, 1994).

Such a dramatic phase shift did not go unnoticed, and subsequently many studies looked to identify relationships between herbivory, macroalgae, and coral in order to better understand the underpinnings of reef resilience (Adam et al., 2015). Williams and Polunin (2001) conducted a large-scale observational study on 19 reef areas in 7 locations throughout the Caribbean in order to find the relationship between herbivorous fish biomass and macroalgal cover using drift diving. They found a strong negative correlation between herbivorous fish biomass and macroalgal cover, with the lowest fish biomasses (<5 g/m^2) corresponding to macroalgae covers of over 60%, while the highest fish biomass (15 g/m^2) corresponded to a macroalgae cover of only ~5%. While convincing, correlation does not imply causation, and fortunately many experimental caged herbivore exclusion studies now exist, which provide strong evidence of the importance of herbivory in maintaining coral cover and preventing macroalgal growth (Adam et al., 2015). Lirman (2001) used cages to exclude herbivores from the corals *Porites asteroides* and *Siderastrea sideria,* along with uncaged, open sided cages, and open topped cages as control treatments. In the fully caged treatments macroalgal biomass increased significantly over the approximately 4-month duration of the experiment, particularly for *Dictyota* spp.

and *Halimeda* spp., which were noted to come into contact with and shade corals more frequently than other algae genera. Herbivore exclusion heavily affected *P. asteroides* growth, with approximately four-fold higher growth rates in control groups. *S. sideria* experienced modestly reduced but non-statistically significant growth rates with herbivore exclusion, indicating some coral species may have more resilience to macroalgal crowding. Unfortunately, this study combined the effects of all three control treatments in statistical analysis, making delineation of cage effects difficult (Lirman, 2001). Hughes et al. (2007) conducted a similar experiment in the Great Barrier Reef using full open topped fish exclusion cages, partial cages, which allowed fish entrance to control for cage effects, and open plots as controls. After 120 weeks in the fully caged treatments macroalgal cover increased from close to 0% to an average of 56%, while both partial and uncaged plots consistently remained below 10% macroalgal cover over the duration of the experiment. Caged treatments also reduced coral recruitment by approximately 50% compared to partial cages and open plots. Furthermore, caged treatments more than doubled mortality rates of existing mature corals, with 24.2% mortality and only around 10% mortality for caged and control treatments respectively after 120 weeks. The relative absence of cage structure effects and strong effects of full cages shown in this experiment, provides convincing evidence of the importance of herbivory in preventing macroalgal phase shifts and retaining reef resilience, highlighting the importance of further research into herbivory and its importance in marine conservation (Hughes et al., 2007).

1.3 Herbivorous and nominally herbivorous fish

While herbivorous fishes as a whole are extremely important in the functioning and resilience of healthy coral reefs, they are an extremely ecologically and morphologically variable group of fishes which play many different ecological roles and provide a variety of different ecosystem functions (Green & Bellwood, 2009). It is important to note that many of the fish typically classified as herbivorous are only nominally herbivorous and actually feed on a variety of non-algal matter such as detritus, sediments, and cyanobacteria (Choat et al., 2002). Fishes can be classified into different 'functional groups', originally this term was used to classify fish based on taxonomy and jaw morphology and hence the physical mechanisms by which they feed, assuming that this indicated exactly what the fish consumes (Bellwood & Choat, 1990). It is now known that this is not always the case, and many fish species which were once lumped into the same functional group are now known to have considerably different target resources and functioning in terms of how they affect their ecosystem; thus, here we will use the term 'functional group' to describe a fishes ecological functioning, which has been described by Bellwood et al. (2019) as "the movement or storage of energy or material within an ecosystem" (Bellwood et al., 2019; Clements, 2017). Herbivorous fish can broadly be separated into four main functional groups, excavators, scrapers, grazers/detritivores, and browsers. However, recent research suggests in many cases that these classifications are somewhat rudimentary and should be subdivided into even finer scale functional groups (Fox & Bellwood, 2013; Green & Bellwood, 2009; Semmler et al., 2021).

All excavators and scrapers are parrotfish (Scaridae); parrotfish have fused beak-like teeth which are capable of damaging the hard calcium carbonate substrate of coral reefs in order to feed (Bellwood & Choat, 1990). Excavators have large, powerful jaw muscles and feed by digging into the substratum of coral reefs in order to ingest the porous calcium carbonate matrix which contains endolithic microorganisms (Clements et al., 2017). Scrapers have much weaker jaw muscles but more articulated mandibular morphology and hence take much shallower bites or scrapes out of the substratum; these shallower scrapes are perhaps a form of niche partitioning in order to target different endolithic organisms such as sponges (Nicholson & Clements, 2024). Excavators are thought to be one of the most important agents of bioerosion on some reefs, and contribute greatly to sand/rubble production and subsequent formation of beaches and atolls (Bruggemann et al., 1996; Morgan & Kench, 2016). However, some large scrapers have been shown to produce equivalent rates of bioerosion to excavators when size effects are accounted for (Ong & Holland, 2010). Interestingly, it is a topic of controversy whether parrotfish in general are beneficial for maintaining reef resilience and coral health. While it has been noted that they can control macroalgae and open space for larval coral recruitment by creating bare substrate patches, some parrotfish species are partially corallivorous, and there is also evidence that parrotfish biomass is negatively correlated with juvenile coral density (Trapon et al., 2013). However, it is thought that the positive effects of parrotfish grazing and hence control of algal growth likely outweighs these negative effects (Mumby, 2009).

Grazers feed extensively on epilithic algal turf, these include many species of rabbitfish (Siganidae, *Siganus*), angelfish such as *Centropyge* spp., and many surgeonfish (*Acanthuridae*) species, with *Acanthurus* and *Ctenochaetus* being particularly prolific grazers on many reefs (Choat et al., 2002; Green & Bellwood, 2009). However, within the grazer functional group there is a great deal of niche partitioning, with some species specialising in cropping the tips of microalgae, others often concurrently or preferentially consuming detritus within the algal matrix, and some specialising in feeding in crevices (Choat et al., 2002). Algal croppers—such as many *Acanthurus* species—have specialised, fine, serrated teeth for excising thin algal filaments from algal turfs (Tebbett et al., 2017a). Species which specialise in the removal of detritus from algal turfs, such as the aptly named combtooth surgeonfishes (*Ctenochaetus* spp) have very fine and thin comb-like teeth which selectively sift sediments and detritus, while largely leaving algal filaments intact (Tebbett et al., 2022). Grazers and detritivores are thought to be particularly important in ecosystem functioning and maintaining resilience as they continuously maintain algae in a low turf-like state, preventing it from smothering or shading coral (Green & Bellwood, 2009). One study that observed biomass of various herbivorous fish functional groups along with macroalgal cover in 240 reef locations throughout American Samoa found that grazer and detritivore biomass had the strongest negative association with macroalgal cover, hinting at the strength of this functional group in maintaining ecosystem stability and resilience (Heenan & Williams, 2013).

Browsers feed predominantly on macroalgae and include some unicornfishes (Acanthuridae, *Naso*) and many *Kyphosus* species (Green & Bellwood, 2009). Browsers tend to have a mix of incisor like teeth and some more conically pointed canine like teeth in order to penetrate and shear thicker, fleshy macroalgae (Sakai & Nakabo, 2006; Tebbett et al., 2022). Browsers tend to be larger in size than other herbivorous functional groups, making them desirable fishing targets and considerably more vulnerable to overfishing (Edwards et al., 2014). This is unfortunate considering that the diet of these fishes likely makes them highly important contributors to reef resilience and potentially reversing macroalgal phase shifts (Green & Bellwood, 2009).

Given the huge diversity of feeding functional groups found in herbivorous marine fish, and the fact that many of these functional groups are highly specialised and may only target specific microhabitats or algal species, it is unsurprising that a diversity of these functional groups is critical to maintaining ecosystem functioning and resilience (Burkepile & Hay, 2008, 2011; Green & Bellwood, 2009). This concept—known as complementarity—generally refers to the combined effect that multiple functional groups have on their environment, in essence complementing each other's ecological functions and resulting in better overall ecosystem functioning (Petchey, 2003). Burkepile and Hay (2008) conducted in situ caging experiments to identify the effects of herbivore diversity on a variety of indicators of ecosystem health, they used the redband parrotfish (*Sparisoma aurofrenatumand*) a grazer which also consumes macroalgae, the ocean surgeonfish (*Acanthurus bahianus*) a grazer/detritivore, and the princess parrotfish (*Scarus taeniopterus*) a scraper (Dromard et al., 2015). It was found that the redband parrotfish had a disproportionately large effect on maintaining low cover and biomass of most macroalgal species when compared to ocean surgeonfish and princess parrotfish. However, it was not capable of controlling several of the measured macroalgal species, and there was a large effect when both princess parrotfish and ocean surgeonfish were combined, with this treatment having considerably less (6-29%) of the algal biomass of individual species treatments. When princess parrotfish were combined with redband parrotfish, it was found that crustose coralline algae cover was significantly higher (52-64%) than in individual species treatments, a promising figure given that crustose coralline algae are preferred settlement sites for larval coral (Burkepile & Hay, 2008). This evidence points to the importance of maintaining herbivore diversity on reefs and continuing research into the different modes of herbivory and how they underpin coral reef resilience (Green & Bellwood, 2009; Heenan & Williams, 2013).

1.3.1 Study species

1.3.1.1 *Ctenochaetus striatus*

Ctenochaetus striatus (Quoy & Gaimard, 1825)—commonly known as the lined bristletooth or striated surgeonfish—attain a total length of up to 28 cm, they are coral reef associated fish which are abundant throughout most of the Indo-Pacific region (Randall & Clements, 2001; Randall, 1997). *C. striatus* inhabit a variety of reef types including lagoons, reef flats, back reefs, and fore reefs down to 30 m, and they may be solitary or occur in large schools (Randall, 1997).

C. striatus was originally classed as a grazing herbivore, though more recent research suggests that it is more likely a detritivore (Tebbett et al., 2017a). However, evidence exists to support that *C. striatus* may engage in both detritivory, and to a small extent, herbivory (Marshell & Mumby, 2012). The thin comb-like teeth shared by all *Ctenochaetus* species are mechanically much more effective at sifting detritus from algal mats, and relatively ineffective at removing algal filaments (Tebbett et al., 2017a). Indeed, studies have shown that the gut contents of *C. striatus* consist almost exclusively of sediment and detritus (Tebbett et al., 2017a). Detailed analysis of *C. striatus* mandibular morphology and feeding behaviour has revealed that they have a 'retention palate' posterior to the upper teeth which is covered in soft papillae, it appears that they use their lower jaw in a sweeping motion to brush detritus from algal turf and retain it in the retention palate in what is described as a "dustpan and brush" feeding mechanism (Tebbett, Goatley, et al., 2018). Tebbett et al., (2017a) also analysed algal removal from bite marks of *C. striatus* in situ and found that there was practically no reduction in algal turf length, while the related *Acanthurus nigrofuscus* greatly reduced turf length in bite marks.

Figure 1.3.1.1

Striated surgeonfish (*Ctenochaetus striatus*).

Diego Delso, CC BY-SA 4.0, https://commons.wikimedia.org/w/index.php?curid=118872848

1.3.1.2 *Chlorurus bleekeri*

Chlorurus bleekeri (De Beufort, 1940), commonly known as Bleeker's parrotfish, can attain a total length of 49 cm. As with *C. striatus* they are coral reef associated and distributed widely throughout the Indo-Pacific region and are abundant in much of their range. They are most commonly found in inner reefs, lagoons, and channel reefs (Randall et al., 1990). As with most other parrotfish species, they are protogynous, beginning life as females (initial phase), later transitioning into males (terminal phase). Initial phase *C. bleekeri* are drab in colouration and often display schooling behaviour, while terminal phase individuals are much more strikingly coloured and are solitary (Bucol et al., 2021; Kuiter & Tonozuka, 2001). *C. bleekeri* is also of some commercial significance, and is intensively fished in some areas (Mansyur et al., 2021).

C. bleekeri, as with most other *Chlorurus* species, is an excavator (Bellwood & Choat, 1990). Seemingly no research has been done on the feeding morphology of *C. bleekeri* specifically; however, as with other excavating *Chlorurus* species it likely possesses powerful jaw muscles and robust mandibular bones, which are less able to articulate than scraping species, making them adept at gouging chunks of calcareous substratum in order to ingest endolithic autotrophs such as cyanobacteria (Bellwood & Choat, 1990; Clements et al., 2017). It also appears that *C. bleekeri* has a moderate preference for biting substrates covered in crustose coralline algae in comparison to other parrotfish species, perhaps as a form of niche partitioning (Nicholson & Clements, 2024).

Figure 1.3.1.2

Terminal phase Bleeker's parrotfish (*Chlorurus bleekeri*).

zsispeo / Flickr. License: CC by Attribution-NonCommercial-ShareAlike.

Figure 1.3.1.3

Initial phase Bleeker's parrotfish (*Chlorurus bleekeri*).

Rickard Zerpe, CC BY 2.0 <https://creativecommons.org/licenses/by/2.0>, via Wikimedia Commons

1.4 Aims and Objectives

Many studies aiming to reveal the health of coral reef ecosystems make use of the relatively simple and conveniently measured metrics, such as fish biomass, biodiversity, coral cover, and macroalgal cover. While such metrics can provide valuable information about how degraded an ecosystem might be in comparison to its natural state, they only reveal damage after it has been done, and often this damage is largely irreversible (Holbrook et al., 2016; Tkachenko et al., 2023). Thus, these metrics are of little use if we intend to take a more preventative approach to coral reef conservation. This highlights the need for more innovative and sensitive methods which can detect early signs of ecosystem decline and instability so that action can be taken to prevent further degradation.

With this study, we intend to identify behavioural signals in fish which may serve as early indicators of environmental degradation. Is the foraging behaviour of herbivorous coral reef fishes shaped by energetic trade-offs between reefs subjected to different turbidity pressures?

The aim of this study is to compare and contrast the foraging behaviour and energy expenditure of nominally herbivorous coral reef fishes across a reef ecosystem subjected to different turbidity pressures. Turbidity can serve as a valuable proxy for modelling reef degradation, as it impacts ecosystem variables similarly to how they are expected to change under future conditions of increasing environmental stress (climate change, ocean acidification, overfishing etc.). Specifically, turbidity can increase macroalgal cover and biomass, decrease coral cover, and decrease fish biodiversity and biomass (De'ath & Fabricius, 2010; Moustaka et al., 2018; Zweifler et al., 2021).

The specific objectives are to:

a) Use stereo-video recordings of fish foraging behaviour to ascertain bite rate and bite distance on different substrates.

b) Compare and contrast foraging behaviour between two nominally herbivorous fish with contrasting functional groups, the excavator *C. bleekeri* and the grazer/detritivore *C. striatus*, across the turbidity gradient.

c) Use stereo-video recordings of herbivorous fish swimming behaviour to ascertain how swimming velocity and energy expenditure are affected across the turbidity gradient.

2.0 Methodology

2.1. Location

This study was conducted on Vavanga reef, located adjacent to its namesake, Vavanga Village, which is situated 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 which is largely covered by native forest. Typical of stratovolcanoes, Kolombangara is conical in shape, has steep sides, and has many rivers that run from its peak of approximately 1770 meters above sea level. Kolombangara Island is sparsely populated and has around 6000 inhabitants, most of which live in small coastal communities around the perimeter of the island. The extensive native forest which covers most of Kolombangara Island is perhaps its most easily accessible economic resource and thus logging is now the main industry on the island.

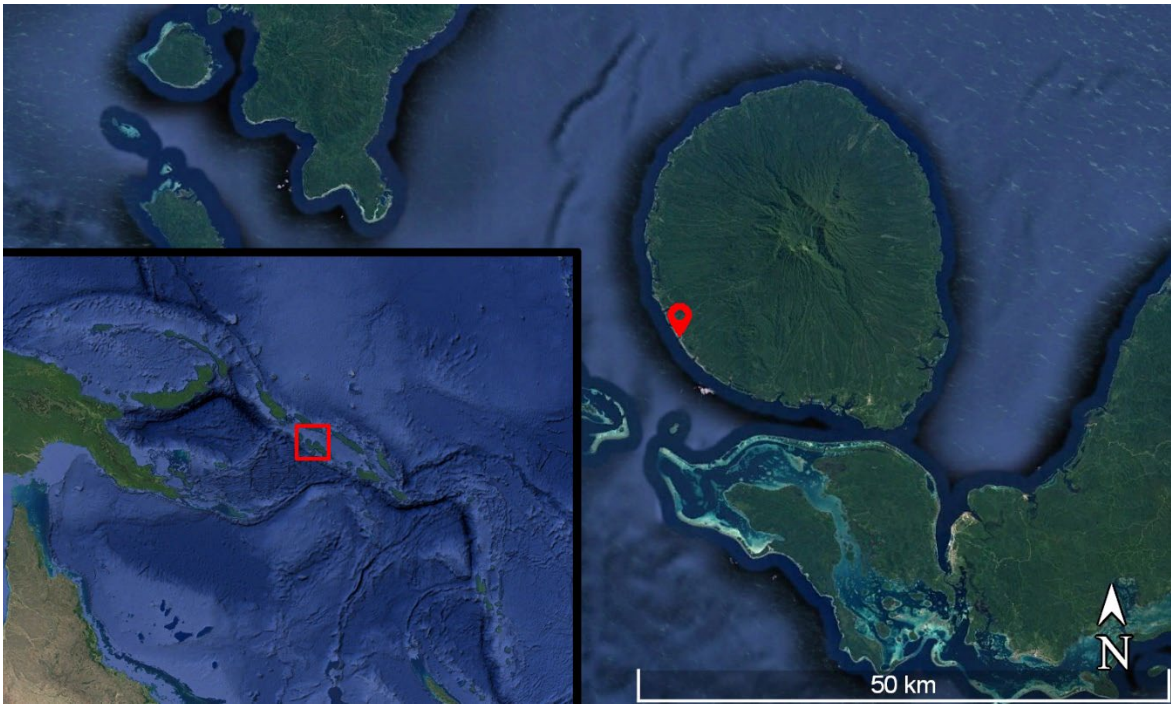

Figure 1.1.1

Location of Kolombangara Island and study location. *Note.* Insert denotes the location of Kolombangara Island (red box) within the wider Micronesian region. The location of Vavanga Village and reef on Kolombangara Island are denoted by the red place marker.

As with most of Kolombangara Island’s coastline, Vavanga Reef is a fringing reef. Vavanga Reef is split into South Vavanga Reef and North Vavanga Reef by the Vavanga River, which discharges next to Vavanga Village. Our study was conducted on the South Vavanga Reef. This reef consists of a shallow (average 0.8-2 m) reef flat which extends approximately 200 metres from shore. As with many fringing reefs, Vavanga Reef is dominated by seagrass beds in the sandy beaches nearest to shore, transitioning to stony coral dominance with proximity to the reef crest. A forereef zone then slopes down to 10-15 meters, after which the seafloor steeply drops to 50 metres.

The South Vavanga reef was selected as an ideal location for this study, as the discharge from Vavanga River is relatively turbid, and this turbidity dissipates out across the surrounding reefs, creating a natural turbidity gradient (Figure 2.1.2). While this river would have naturally discharged terrestrial sediments and thus created a turbidity gradient, this turbidity has been exacerbated by upstream land use changes, particularly the many previous logging operations. Major land clearing operations began on the island in 1903, and such operations are still ongoing to this day but are restricted to forest below 400m elevation (Katovai et al., 2012). This excessive anthropogenic turbidity is particularly damaging near the river mouth and allows us to examine areas of reef which are degraded beyond what we would expect to see in a naturally turbid reef. Furthermore, the reefs of the Solomon Islands are generally still in a pristine and healthy state, and have been shown to be very resilient to major stressors and events such as logging, overfishing, and tsunamis (Kopp et al., 2010; Van Der Ploeg et al., 2020). The same is true for Vavanga Reef, and non-turbid areas of the reef are in an extremely healthy condition with high stony coral cover and low macroalgal cover. The above factors provide an ideal turbidity gradient for the purpose of this study, with some areas being in a pristine state and some areas being extremely turbid and degraded (Figure 2.1.2). Importantly, the supervisor of this project, Associate Professor Armagan Sabetian, has developed an excellent reciprocal relationship with the Vavanga Village community over the last 20 years. Collaboration with the community was instrumental for the field work of this project, and the importance of the local knowledge provided by the Vavanga people cannot be overstated. The community provided us with important information on fish identification, where to choose our sampling sites, and contributed their time and numerous resources to assist us in our research, and this project may not have been possible without their generous assistance.

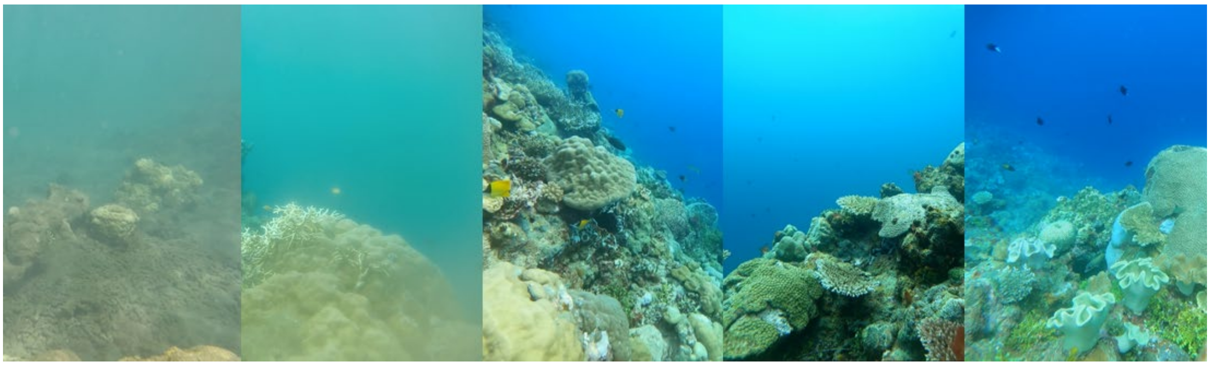

Figure 2.1.2

Images showing the turbidity gradient along Vavanga Reef

2.2. Equipment and sampling

Stereo-video analysis is a process which requires synced footage from two or more cameras with overlapping fields of view, using computer algorithms, the exact 3D coordinates of objects in this footage can be calculated—much like our ability to perceive the location of objects in space—making it highly useful for animal behavioural analysis. Furthermore, it can yield much more accurate dimensional measurements than singular video systems (Harvey et al., 2002). Stereo-video footage was to be used on the software VidSync, so all equipment used in the stereo-video recording process was constructed in accordance with the recommendations of the software developer (Neuswanger, n.d). This included three stereo-video racks, each rack was made from steel bars and had two GoPro cameras attached one meter apart at either side of the racks, racks were 0.5 meters high to lift the cameras above the substratum and obtain a clear view of the reef (Figure 2.1.3). Rack 1 used two GoPro Hero 5s, while racks 2 and 3 used GoPro Hero 9s. Each camera was equipped with a 32 gigabyte SD card, enabling us to capture 1.5 hours of footage at each camera drop. Stereo-video footage requires calibration; thus, we constructed an appropriate 80x40 centimetre calibration frame using printouts from the developer's website and fixing these to panels of acrylic glass which were held apart by aluminium spacers (Figure 2.1.3).

Figure 2.2.1

Camera rack set-up and calibration frame (background).

In order to measure turbidity, a Secchi disk and a 100-metre tape was initially used, however, this proved to ineffective at the low turbidity sites as the bottom of the reef could be seen from the surface, so this method was discarded. Instead, the EyeOnWater app was used to compare the water colour to the Forel-Ule index so that the Forel-Ule index could be inferred for each site (Citclops, n.d.). The Forel-Ule index is a simple colour comparator scale which allows for easy quantification of water colour in the field and can be used as a proxy for turbidity (Wernand & Woerd, 2010) (Figure 2.1.4).

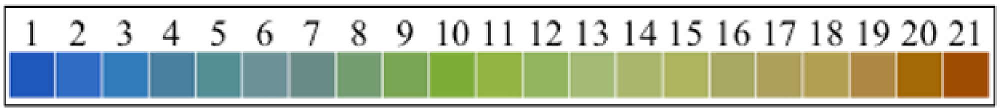

Figure 2.2.1

Forel-Ule Index.

Estimations of substrate cover were made by randomly placing a 1x1 metre quadrat on the reef surface at each sampling point and taking an image of the substrate and quadrat from above using a GoPro Hero 9. A 20-point grid was then overlaid on the photo within the 1x1 metre quadrat, then the substrate beneath each grid point was recorded with each point representing 5% cover. The different substrate types recorded were: Acropora spp., dead coral, Diploastrea spp., epilithic algal matrix (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., and zooanthids.

Sampling was conducted between the 5th of January 2023 and the 17th January 2023. We selected five sampling sites which started at the river mouth, with the following four sites being placed at equal distances in a southward direction from the river. The sites used in this study were positioned on the sloping fore-reef. At each site, two samples were taken (i.e. two different camera drops), and all three camera racks were dropped for each site, giving a total of six samples for each site. The sites were designated local names which correspond to nearby landmarks, these were Ovuku (river mouth), Batu (rock), Paele (meeting house), Church (local church), and Pobuna (a crater in the reef left when an explosive was detonated) (Figure 2.2.3).

Fig 2.2.3
Sampling site locations along the turbidity gradient on Vavanga Reef. Ovuku is closest to the Vavanga River mouth and the remaining sites are spead evenly along the turbidity gradient that originates from the Vavanga river.

2.2.1 Sampling site locations

Equipment was transported to each sampling site by boat, and buoys were anchored to the seafloor to mark positions of camera rack drops, then GPS coordinates and Forel Ule index was measured for each of these sites. SCUBA divers then entered the water and determined a suitable location for the camera rack within the vicinity of the anchored buoy. Care was taken to ensure that racks were placed on a stable area of substrate so that steady footage would be recorded for analysis. The quadrat was then placed directly in front of the rack for substrate cover analysis, and both cameras were set to record. Depth and SST were recorded by displaying a dive watch in front of one of the cameras.

The calibration process then commenced in accordance with procedures recommended by Neuswanger (n.d). The calibration frame contains an array of circular black and white nodes on both the front and back panes, which are used to 3D-calibrate the stereo-video set (Figure 2.2.4). This side of the calibration frame was gradually moved towards the rack. Then the calibration frame was flipped to display the checkerboard pattern to each camera at a range where the pattern filled the entire frame. The distortion in the checkerboard pattern seen in the cameras would later be used for lens distortion correction (Figure 2.2.4). Once this process was completed, an overhead image was taken of the quadrat was taken for analysis of substrate cover, and the quadrat was removed. Upon completion of these procedures, divers promptly left the water to ensure minimal disturbance to fish behaviour.

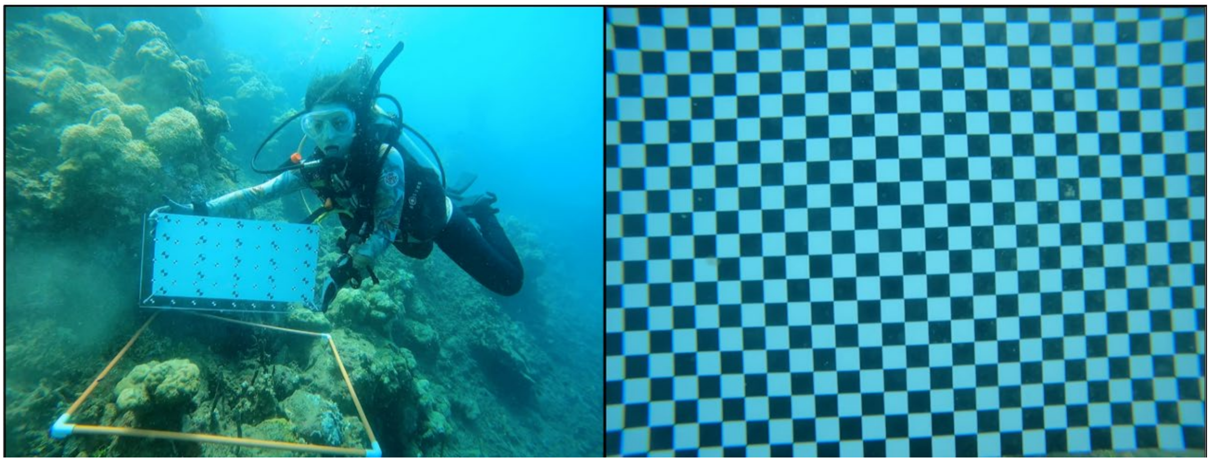

Figure 2.2.4

Stereo-video calibration procedure with quadrat placement.

2.3 Data analysis

2.3.1 Video analysis

2.3.1.1 Video synchronisation

GoPro cameras are only capable of recording approximately four gigabyte segments of video at a time, which was only a fraction of the 1.5-hour videos. To speed up the video analysis process, these video segments were stitched together in Adobe Premiere Pro (2023). The stitched video sets (two separate videos per rack) were then imported into VidSync (Neuswanger, 2008). For accurate 3D reconstruction of the footage, the videos had to be perfectly synchronised in time. This was a relatively simple process and was generally done by matching a visual event on both videos. The appearance of bubbles exiting a diver's SCUBA regulator was the most accurate way of achieving this, as the sudden appearance of the same set of bubbles was generally visually unmistakable on both cameras.

2.3.1.2 Lens distortion correction

GoPro cameras have relatively wide-angle lenses, meaning that they film a wide angle of view at the expense of radial distortion (or barrel distortion) of the field of view, which appears to make the image bulge outward from a point in the centre. This can be noted on the checkerboard in figure 2.2.4, which in reality has perfectly symmetrical squares. This distortion interferes with 3D reconstruction and must be corrected for. This radial distortion may also not be perfectly centred in the cameras field of view because of potential aberrations in the lenses, this is known as decentering distortion, which also must be corrected for. This was corrected for with the VidSync lens distortion feature, which autodetects ‘plumblines’ which follow the artificial vertical and horizontal curvatures on the checkerboard pattern created by the lens distortion. Plumblines are autodetected using the downhill simplex method (Nelder & Mead, 1965). However, this method as—well as the GoPro footage—was not perfect, and plumblines were manually added when required for better results. To correct for both radial and decentering distortion using the curvature of these plumblines, VidSync uses the Brown-Conrady model (Brown, 1996). These methods are mathematically complex and beyond the scope of this research; Neuswanger et al. (2016) should be referred to if an understanding of the mathematical underpinnings of these models is sought.

2.3.1.3 Three-dimensional calibration

In order for VidSync to estimate real-world 3D coordinates of objects, the real-world distances between the nodes on the front and back panes of the calibration frame were measured (x,z) (these nodes can be seen in figure 2.2.1) and uploaded to VidSync. Then in VidSync the centres of the corresponding nodes are clicked on in both the front and back panes. VidSync can then establish these corresponding real-world coordinates in pixels on-screen. These points are then corrected for non-linear distortion to obtain undistorted coordinates of objects on screen. As with the lens distortion correction, relatively complex mathematical methodology is used in this process, and Neuswanger et al. (2016) should be referred to for further understanding.

2.3.1.4 Fish tracking

VidSync employs a hierarchal system for recording of information from videos. ‘Objects’ are able to be created by the user (e.g. various fish species), and within the objects, the user is able to create multiple ‘event’ classes which can be applied to each object. In this project three objects were created for the target species, ‘C. striatus, ‘C. bleekeri’, and ‘C. bleekeri_IP’ (for initial phase *C. bleekeri*). The events created were ‘Track’ for fish tracks, ‘Length’ for fish length measurements, ‘Bite’ for each time a tracked target species took a bite, and ‘Aggression’ for events where a tracked target species was involved in an aggressive encounter with another fish.

The footage then had to be manually watched through to identify and note down the time of where the target species were in the video. The first 10 minutes of footage was always skipped, as the behaviour of our target species could potentially have been influenced by the activity of divers dropping the racks and returning to the boat. The footage was then simply watched through until one of the target species appeared on screen. The annotation feature on VidSync was then used to note the entrance of the fish into the field of view, the annotation feature overlays a timer on screen, which was used to time how long the fish was on screen for. Once the fish exited the screen, the annotation was given a name which contained the fish species and the time in seconds that it was on screen (e.g. C. striatus, 22.3). The annotation feature made it convenient to relocate each fish, as the annotation name could be clicked on, and the video would return to where this fish entered the screen. Target species which were only present in the field of view for a few seconds or less were generally ignored and not annotated, as these would not have provided quality data. The exception to this was in the highly turbid sites, where often very few of the target species could be located (Ovuku and Batu). Once all videos from a site were watched through and every potentially trackable target species in the site had been annotated, each fish was given a unique ID code containing species name and a number, e.g. bleekeri_01. Then each of the two target species was ranked by the time they were on screen. While there were two object classes for *C. bleekeri* (C. bleekeri and C. bleekeri_IP), these were lumped together for screen time rankings. It was decided that, due to the time-consuming nature of manually tracking fish, only ten of the longest and/or best quality tracks would be recorded for each species at each of the five sites.

Tracking began with the fish at the top of the screen time rankings and subsequently moved down the list. However, many tracks were found to be of poor or unusable quality—for example, the fish was too far in the background, remained obscured behind objects for long periods of time, or remained in the peripheries of the screen (resulting in much worse lens distortion). In such cases, the next longest viable track was used. Due to the extremely time-consuming nature of manually tracking fish in 3D, only the first 10 seconds the fish track was recorded. Where the fish was on screen for sufficient time, tracking commenced when the fish had moved past approximately the peripheral 15% of the frame and closer to the centre, this was due to the heavy lens distortion around the peripheral edges of the frame, which produced inaccurate 3D coordinates in VidSync.

To track the fish, a ‘Track’ event was created for the individual fish, and then the exact same spot on the fish’s mouth was clicked on in both videos in the stereo-video set. This allows VidSync to pinpoint the fish’s location in space and creates one data point containing XYZ coordinates and time. The video was then skipped ahead six frames, and this process was repeated until 100 data points had been collected, this represents a 10 second track, as the GoPro footage was filmed at 60 frames per second. Fish would often momentarily be occluded by rocks, coral, or other fish. In cases where the location of the mouth of the fish was easily predicted, i.e. most of the fish was still visible, the location of the mouth was estimated, and a data point was still taken. However, where the fish was too obscured to make a reliable estimate of the mouth location, the video was skipped ahead 6 frames at a time until the mouth was visible on both screens again. Once tracking of the fish was completed, at least three length measurements (total length) were made by clicking on the tip of the nose of the fish and then on the end of the tail, again on both screens so that XYZ coordinates could be used to calculate the distance between these two points. Bites were recorded by creating a ‘Bite’ event for the individual, and then clicking one screen at the exact moment the fishes mouth came into contact with the substratum. Clicking on both screens was not required for bites, as the timecode of the bite could be synced with the timecode from the track data to give the XYZ coordinates of the bite. Harassment events were seldom seen, although they were recorded when either the tracked fish made a swift movement towards another fish or chased it, or when another fish did this to the tracked fish. It was then noted which fish was the aggressor and the other species involved.

2.3.2 Fish mass estimation

As specific length-weight relationship studies have not been done on either *C. striatus* or *C. bleekeri,* length-weight data for these species were taken from FishBase. FishBase references Froese et al. (2014), who used a Bayesian approach to estimate length-weight relationships for data poor species using known length weight relationships of closely related species with similar body morphologies. The body mass in grams of each species was calculated using the equation (Body Mass = $a \times$ Total Length^{b}), where a and b are species specific coefficients. The coefficients for *C. striatus* are a = 0.02399 and b = 2.96. For *C. bleekeri* they are a = 0.02754 and b = 3.01.

2.3.3 Extracting information from 3D trajectories

2.3.3.1 Removal of outliers

As VidSync can only estimate the 3D coordinates of a fish based on mathematical assumptions, there were often noticeable outlying XYZ data points in the trajectories of the fish tracks which needed to be removed. Outliers were removed using the interquartile range (IQR) method as described in Lilkendey et al. (2024). IQR is a simple descriptive statistic which is the data contained between the lower 25th percentile and the upper 75th percentile of a data distribution, i.e. the middle 50% of the data. Data points were removed if they exceeded a threshold of 1.5 × IQR, thus datapoints below the lower bound ($Q1 - 1.5 \times IQR$) and above the upper bound ($Q1 + 1.5 \times IQR$) were removed.

2.3.3.2 Velocity, overall dynamic body acceleration, and metabolic rate calculations

Fish velocity was calculated by measuring the spatial distance between consecutive XYZ coordinates using the *lead()* function in R. This calculates the displacement between positions (diff_X, diff_Y, diff_Z) by subtracting each coordinate from its previous coordinate, returning the fishes velocity between each data point in centimetres per second (cm s^{-1}). Relative velocity (body lengths s^{-1}) was calculated by dividing velocity by the fish's body length, giving the velocity of the fish relative to its length. Relative velocity was used in statistical analysis to account for differences in fish length.

Acceleration (cm s^{-2}) was calculated using from the differences in velocity between data points. Overall dynamic body acceleration (ODBA) is a measure of energy expenditure, which is calculated by dividing the acceleration in each axis (XYZ) by the acceleration of gravity (981 cm^{-2}) to convert each XYZ acceleration value into g-units and taking the sum of these (Wilson et al., 2006). The equation is as follows:

$$ODBA = \frac{Acceleration\,X + Acceleration\,Y + Acceleration\,Z}{g}$$

Metabolic rate was calculated from a respirometry dataset which contained standard metabolic rate (SMR g O_2 d^{-1}) and mass (g) measurements from different individuals of *C. striatus* and *Odonus niger* (a surrogate for *C. bleekeri* as no direct respirometry data could be found for this species). A log-log regression was then run for each species, modelling the species specific allometric relationship between mass and SMR. The slope and exponential of the intercept of this model represent the *K* (normalisation constant) and *E* (mass scaling exponent) values of the allometric relationship between metabolic rate (*R*) and body mass (*M*) typically expressed as $R = K \,.\, M^E$. The *K* and *E* values can then be used to calculate the field metabolic rate (FMR) of individuals from ODBA and mass as follows:

FMR (mg O_2 g^{-1} d^{-1}) = K . (Mass^E) . ODBA . $Q_{10}^{(\mathrm{Tstudy} - \mathrm{Tref})/10}$. 1000

Where Q_{10} is the temperature coefficient (change in reaction rate over a 10°C temperature range), indicating how sensitive enzyme reaction rate is to temperature change. This is often between 1.5-2.5 for most fish and other ectotherms, so a Q_{10} of 2 was chosen in this instance (Bennett, 1985; Jutfelt, 2020; Morris, 1962). T_{study} is the temperature of our study (30°C) and T_{ref} is the temperature of the reference study in which the respirometry data was collected (28°C). Thus $Q_{10}^{(\mathrm{Tstudy} - \mathrm{Tref})/10}$ gives a temperature adjustment factor. 1000 converts g to mg.

2.3.3.3 Bite distance and bite rate

Bite rates for each fish were calculated by dividing the number of bites a fish took per track by the time of the track. Bite distance was calculated by measuring the distance between XYZ coordinates of consecutive bites and taking the average of this for each track.

2.3.4 Statistical analysis

2.3.4.1 Environmental and feeding preferences

Relationships between continuous environmental variables such as visibility and EAM cover were visually explored with scatterplots (R package *ggplot2*), and data was modelled with simple linear regression, given that model assumptions of normality and homoscedasticity were satisfied. Model assumptions of linearity, homoscedasticity, and normality were tested using residual vs fitted plots, QQ plots, and Shapiro-Wilk tests. The relationship between EAM cover and visibility was modelled with a zero inflated beta regression, as EAM cover was proportional data (0-100%) and zero inflated (containing many zero values). Comparisons between sites were visually assed with box plots or bar plots, and where necessary were statistically compared with ANOVA if model assumptions were satisfied. ANOVA and Tukey's HSD assumptions of normality were tested with QQ plots and the Shapiro-Wilk test, and homoscedasticity was tested with the Levene test. If ANOVA assumptions of normality and homoscedasticity failed, the Kruskal-Wallis rank sum test was used to identify if there was a site effect, and if so, the Dunn's multiple comparison tests with Benjamini-Hochberg adjusted p-values was used as a post-hoc test to identify significant differences between sites.

2.3.4.2 Feeding preferences

Feeding substrate preferences between sites and species were visually compared with bar plots. Manly's preference ratios were calculated by dividing the percentage bites taken on a substrate at a site over the average cover of that substrate at the site.

2.3.4.3 Analysis of fish traits

The relationships between fish traits (fish mass, bite distance, bite rate, relative velocity, and metabolic rate) were visually assessed with scatterplots (R package *ggplot2*). Simple linear regressions were then run to model relationships between these variables and test the significance of the correlations. After the models were created, diagnostic tests were run to ensure that the assumptions for simple linear regression were met. Residual vs fitted plots were generated to visually inspect the assumptions of linearity and homoscedasticity of residuals. Quantile-quantile plots (QQ plots) were generated to visually inspect normality of residuals. Shapiro-Wilk tests were also run to statistically test the probability that the data was normally distributed; where p was <0.05, the data was assumed to be non-normally distributed. In the case that any linear regression assumptions were violated, one of the variables was log transformed, and the linear model and assumption tests were re-run. If assumptions were still violated, then the other variable was log transformed, and the linear model and assumption tests were rerun. FMR required log transforming for both species. Bite rate data was zero-inflated as many fish did not take bites over the sampling duration. Zero-inflated data cannot be log-transformed to satisfy model assumptions, so in this case the data was modelled with more flexible generalised additive models with a Tweedie distribution (R package *mgcv*) which are able to effectively model nonlinear and zero-inflated data.

2.3.4.4 Environmental effects on behavioural traits and energy expenditure

Relationships between fish behavioural metrics (bite distance, velocity, and metabolic rate) and turbidity proxies (visibility and Forel-Ule index) were initially explored using scatterplots (R package *ggplot2*). To identify the best predictors of the behavioural response variables, linear mixed models (LMMs; R package *lme4*) were fitted, incorporating relevant covariates such as EAM cover, dead coral cover, depth; phase was also included for *Chlorurus bleekeri*. LMMs were chosen to account for the hierarchical structure of the study design (individual < unique identifier < site) and the non-independence of observations due to potential resampling of individual fish. The unique identifier (i.e., individual video) was included as a random effect, allowing for variation in intercepts across videos and controlling for repeated measures within the same sampling unit. After fitting, model assumptions of linearity, homoscedasticity, and normality were tested using residual vs fitted plots, QQ plots, and Shapiro-Wilk tests and variables were log transformed when assumptions were not met. Results from models with log transformed variables were back transformed for interpretability of results. The variables which required log transforming for both *C. striatus* and *C. bleekeri* were velocity (body lengths s^{-1}) and FMR (mg O_2 g d^{-1}). Bite rate was not modelled with LMMs due to the zero-inflated data. To identify the best covariates to include in the models and avoid overfitting, models with different covariates were compared using their Akaike information criterion (AIC) value. AIC calculates how well a model fits the data while penalising for the number of model parameters, lower AIC values indicate a better model. Thus, the models with the lowest AIC value were selected for each species. Variance inflation factors (VIFs) were also calculated for the covariates to identify multicollinearity. VIF values >5 indicate high multicollinearity, in such cases, the less important covariate was removed from the model.

The models which had the best fit for *C. striatus* were:
Behavioural response ~ Visibility + EAM + depth + (1|unique identifier)
Behavioural response ~ Forel-Ule + EAM + depth + (1|unique identifier)

The models which had the best fit for *C. bleekeri* were:
Behavioural response ~ Visibility + EAM + phase + (1|unique identifier)
Behavioural response ~ Forel-Ule + EAM + phase + (1|unique identifier)

2.3.4.5 Site level analysis

Site comparisons between the dependent variables (fish mass, bite distance, bite rate, velocity, and FMR) were analysed with analysis of variance (ANOVA) for both species. To identify significant site differences in these variables, Tukey's HSD post hoc tests were conducted if ANOVA revealed a significant site level effect ($p < 0.05$). ANOVA and Tukey's HSD assumptions of normality were tested with QQ plots and the Shapiro-Wilk test, and homoscedasticity was tested with the Levene test. Where assumptions were violated, the dependent variable was log-transformed, and the ANOVA and assumption tests were re-run. Where log transformation did not sufficiently improve normality or homoscedasticity, non-parametric tests were used. The Kruskal-Wallis rank sum test was used to identify if there was a site effect, and if so, the Dunn's multiple comparison tests with Benjamini-Hochberg adjusted p-values was used as a post-hoc test to identify significant differences between sites. Zero-inflated negative binomial generalized linear models (GLMs) with a log link and offset for observation time were used to assess site differences in bite rate (R package *glmmTMB*). These models were used as (1) there was some variation in observational time (some fish could only be tracked for as little as two seconds while most were tracked for ten seconds), and (2) many fish were not recorded feeding over the sampling duration, resulting in zero inflated data. Estimated marginal means for bite rates at each site were calculated from the model using the *emmeans* package, and pairwise comparisons were conducted with Tukey-adjusted p-values to identify significant differences between sites. Tukey’s HSD multiple comparison test was not appropriate for comparing site differences in bite rate, as the zero inflated distribution of this data violates the Tukey’s HSD test assumption that the data is normally distributed (Lane, 2010).

3.0 Results

3.1 Environmental analysis

Mean visibility generally increased with increasing distance from Vavanga river. Visibility was lowest at Ovuku at 9.5 metres, increasing to 25.2 metres at Batu, then to 30.7 metres at Paele, and reaching a maximum of 35.7 metres at Church, before dropping marginally to 33 metres at Pobuna (Figure 3.1.1). A Kruskal-Wallis test indicated significant site differences in visibility ($p < 0.001$). A Dunn's multiple comparison test showed that Ovuku had significantly lower visibility than Church (p. adj < 0.001), Pobuna (p. adj = 0.037), and Paele (p. adj = 0.043) (Figure 3.1.1). Forel-Ule followed an inverse pattern to visibility (lower Forel-Ule index indicates lower turbidity). Forel-Ule was highest at Ovuku at 6.43, dropping to 3 at Batu and Paele, and reaching its lowest point of 1.67 at Church before increasing slightly to 2.25 at Pobuna (Figure 3.1.2). A Kruskal-Wallis test indicated significant site differences in Forel-Ule ($p < 0.001$). A Dunn's multiple comparison test showed that Ovuku had significantly lower Forel-Ule than Church (p. adj = < 0.001), Pobuna (p. adj = 0.003), and Paele (p. adj = 0.03) (Figure 3.1.1). The drop in visibility and increase in Forel-Ule from Church to Pobuna indicates that Church may have been the point of minimum turbidity before it began increasing again with proximity to the next river. Mean Forel-Ule index had a strongly negative linear correlation with mean visibility ($R^2 = -0.98$, $p = 0.003$) (Figure 3.1.3). The increase in visibility and decrease in Forel-Ule with distance from the river mouth along with their strong correlation together indicates that both metrics are good proxies for turbidity.

The different substrate types recorded were: Acropora spp., dead coral, Diploastrea spp., epilithic algal matrix (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., and zooanthids. The total number of substrates increased with increasing distance from Vavanga river, with live coral species increasing in both number and percentage cover along the turbidity gradient. Ovuku had only 5 substrates, Batu had 7, Paele and Pobuna had the most at 14, and Church had 13. There was a strong positive correlation between mean visibility and the number of substrates, indicating that substrate diversity decreases with increasing turbidity ($R^2 = 0.89$, $p = 0.044$) (Figure 3.1.4). Mean EAM cover increased with distance from the Vavanga river. Mean EAM cover was lowest at Ovuku at 0%, increasing to 3.33% at Batu, 7.5% at Paele, 13.9% cover at Church, and 25.8% cover at Pobuna (Figure 3.1.6). An ANOVA revealed significant site differences in EAM cover ($p = 0.005$), and a Tukey's HSD revealed that Pobuna had significantly higher EAM cover than Ovuku ($p = 0.005$) and Batu ($p = 0.017$) (Figure 3.1.6). EAM cover tended to increase with visibility (Figure 3.1.7). A zero-inflated beta regression indicated that visibility did not significantly affect the percentage cover of

EAM when present (β = 0.034, SE = 0.024, p = 0.157). However, visibility significantly decreased the probability of EAM absence (β = −0.127, SE = 0.045, p = 0.004) (Figure 3.1.7). Mean dead coral cover increased with proximity to Vavanga River. Ovuku had the highest dead coral coverage at 68.3%, this decreased to 41.7% at Batu, 36.7% at Paele, 35% at Church, and was lowest at Pobuna at 30.8% (Figure 3.1.8). ANOVA revealed significant site differences in dead coral cover (p = 0.01), and Tukey's HSD revealed that dead coral was significantly higher at Ovuku than Pobuna (p = 0.012), Church (p = 0.015), and Paele (p = 0.044) (Figure 3.1.8).

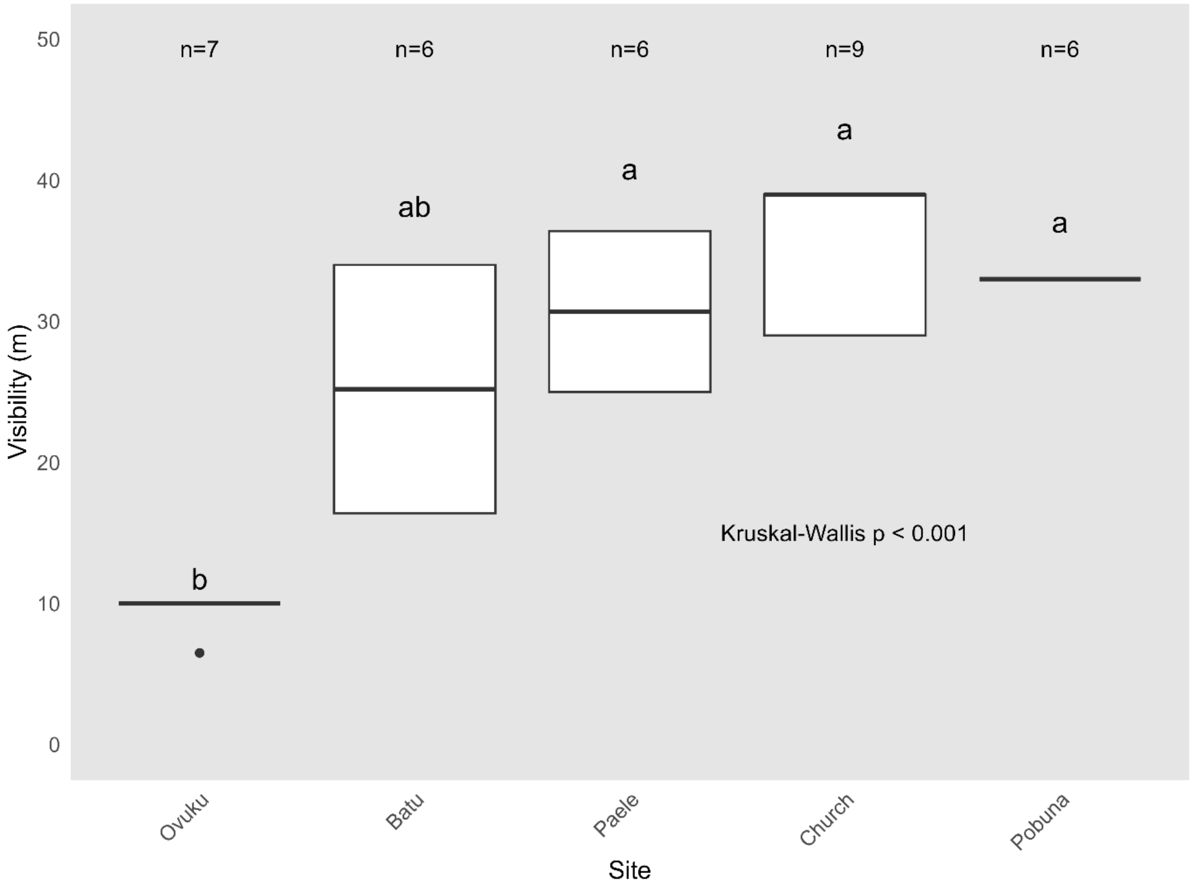

Figure 3.1.1

Site comparisons of visibility (m). Different letters above boxplots indicate statistically significant differences between sites ($p < 0.05$), based on Dunns post-hoc test following Kruskal-Wallis test. Kruskal-Wallis test p-value is displayed on the plot. Sample sizes (n) for each site are shown above the plots.

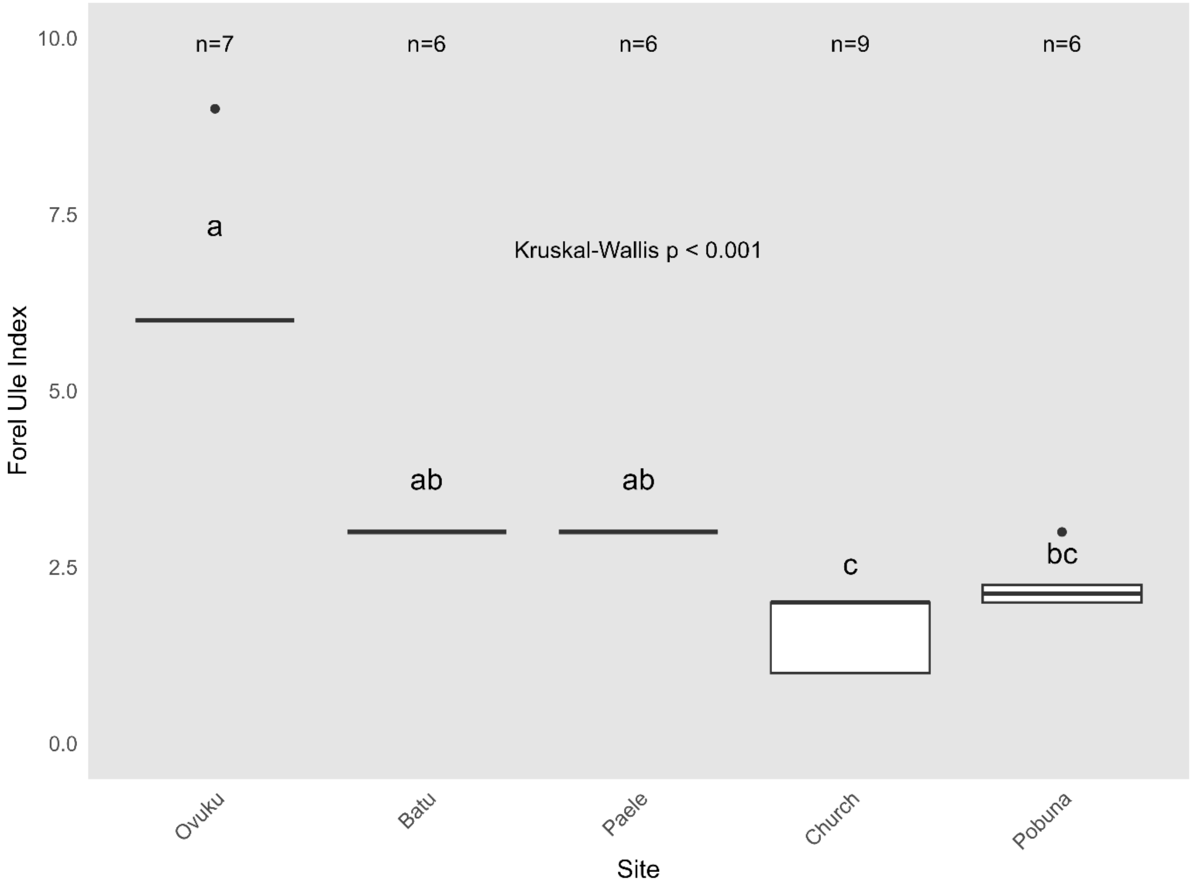

Figure 3.1.2

Site comparisons of Forel-Ule index. Different letters above boxplots indicate statistically significant differences between sites ($p < 0.05$), based on Dunns post-hoc test following Kruskal-Wallis test. Kruskal-Wallis test p-value is displayed on the plot. Sample sizes (n) for each site are shown above the plots.

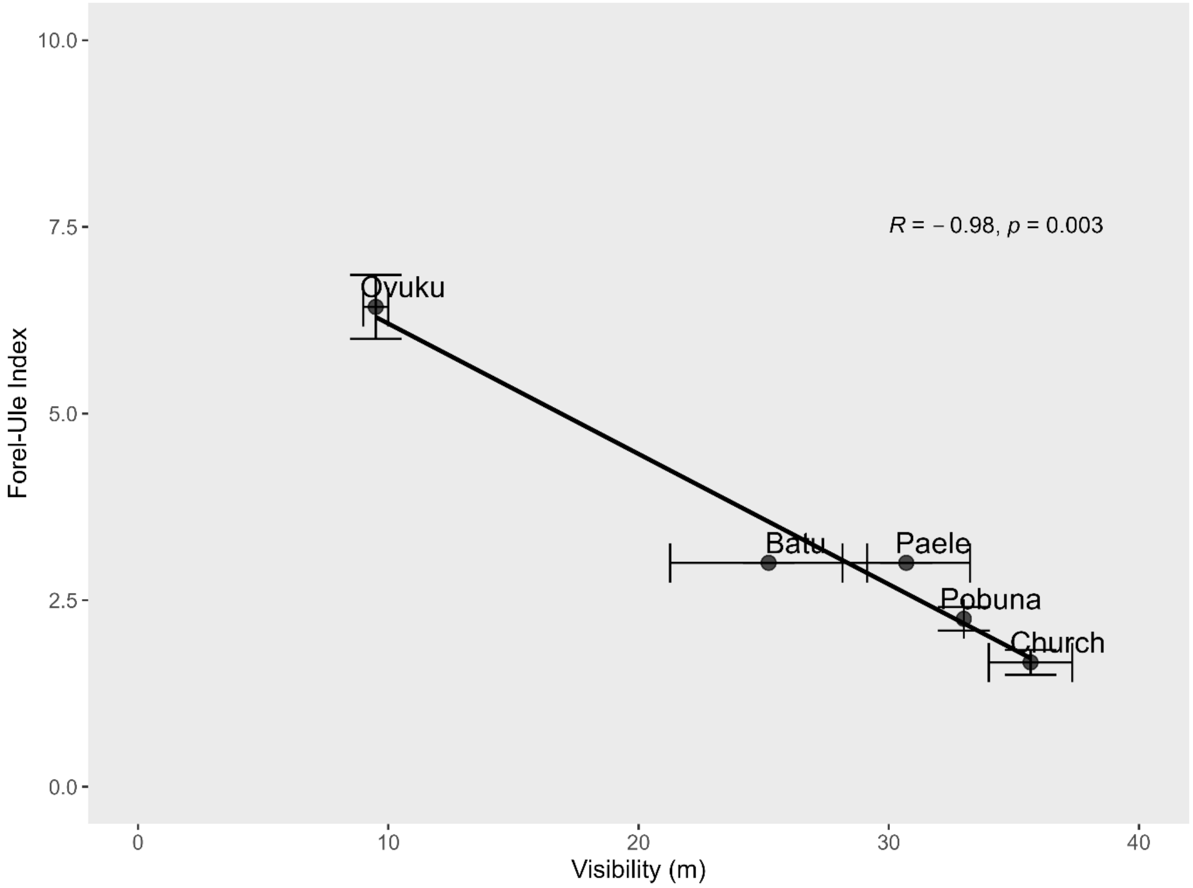

Figure 3.1.3

Relationship between mean Forel-Ule index and mean visibility at sampling sites. Standard error bars are displayed at each site point for both visibility and Forel-Ule index. Black line represents fitted regression line. R^2 and p value from linear regression are displayed on graph. Note: Sites in order of proximity to Vavanga River: Ovuku, Batu, Paele, Church, Pobuna.

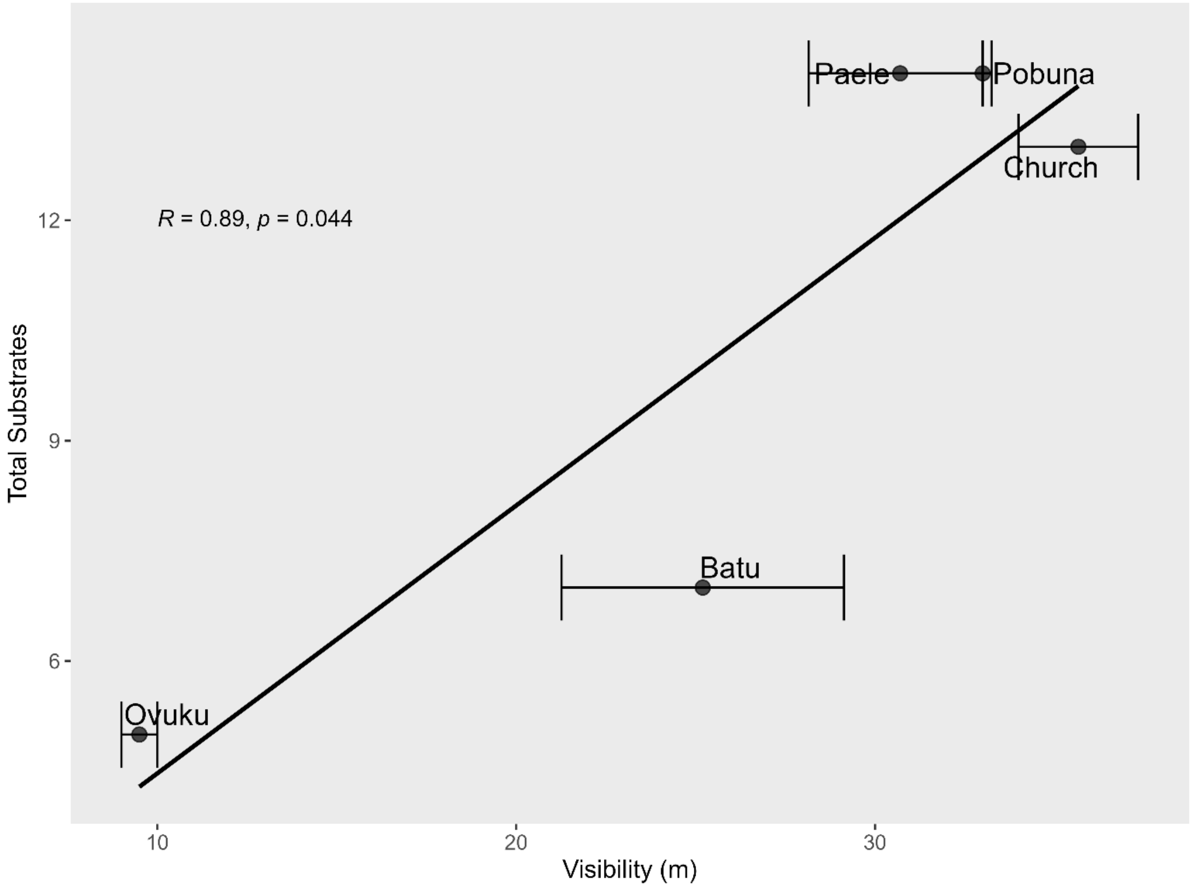

Figure 3.1.4

Relationship between mean visibility and total number of substrates at each sampling site. Standard error bars are displayed for visibility at each site point. Black line represents fitted regression line. R^2 and p value from linear regression are displayed on graph.

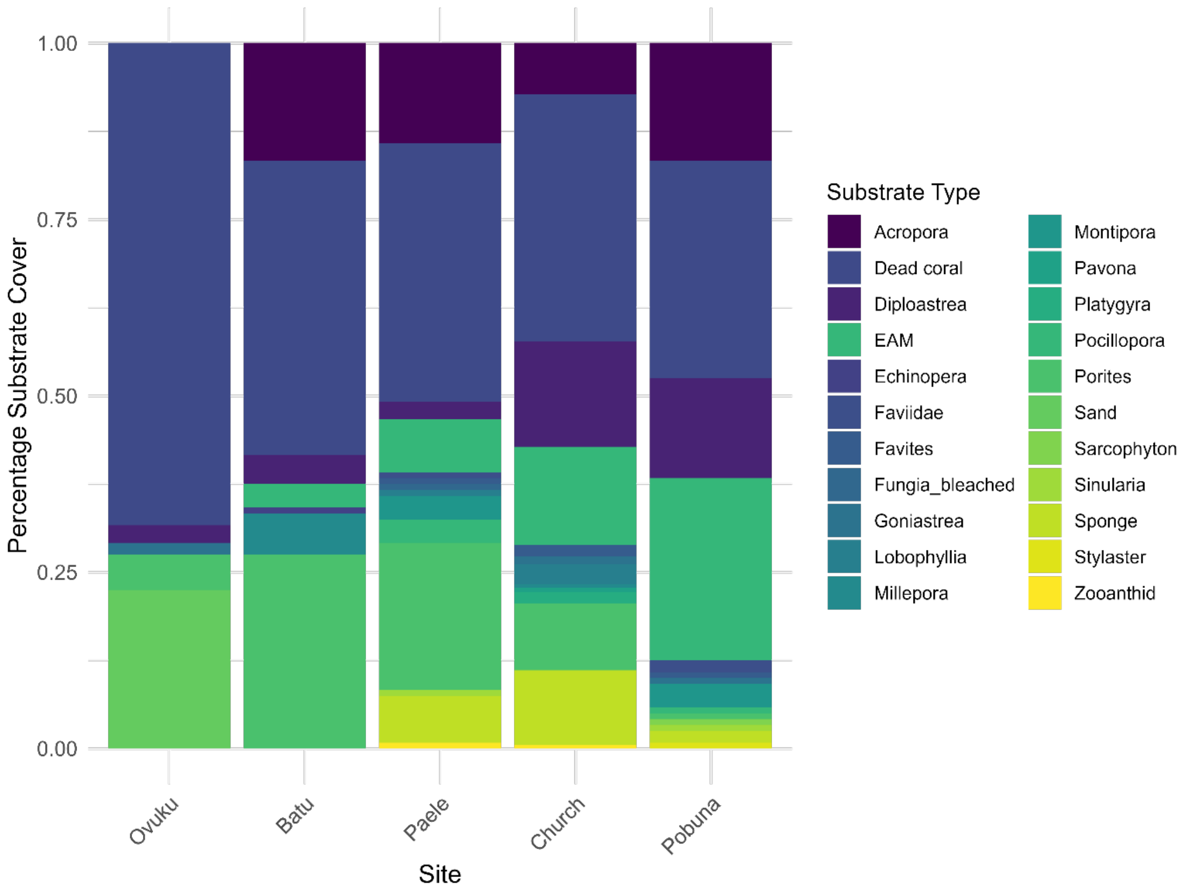

Figure 3.1.5

Percentage cover of substrates at each sampling site. Legend indicates colours corresponding to each substrate type.

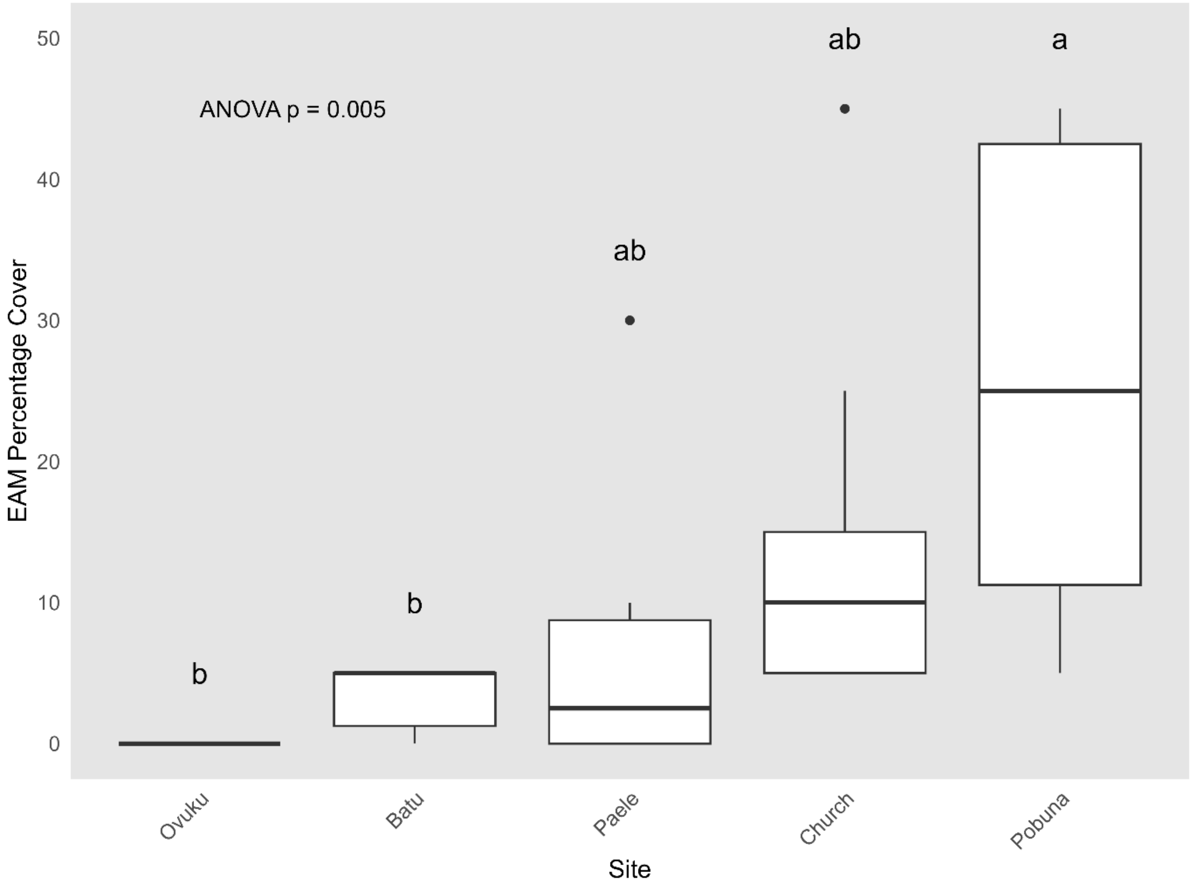

Figure 3.1.6

Site comparisons of EAM cover. Different letters above boxplots indicate statistically significant differences between sites ($p < 0.05$), based on Tukey's HSD post-hoc tests following ANOVA. ANOVA p-values are displayed on the plot. Sample sizes (n) for each site are shown above the plots.

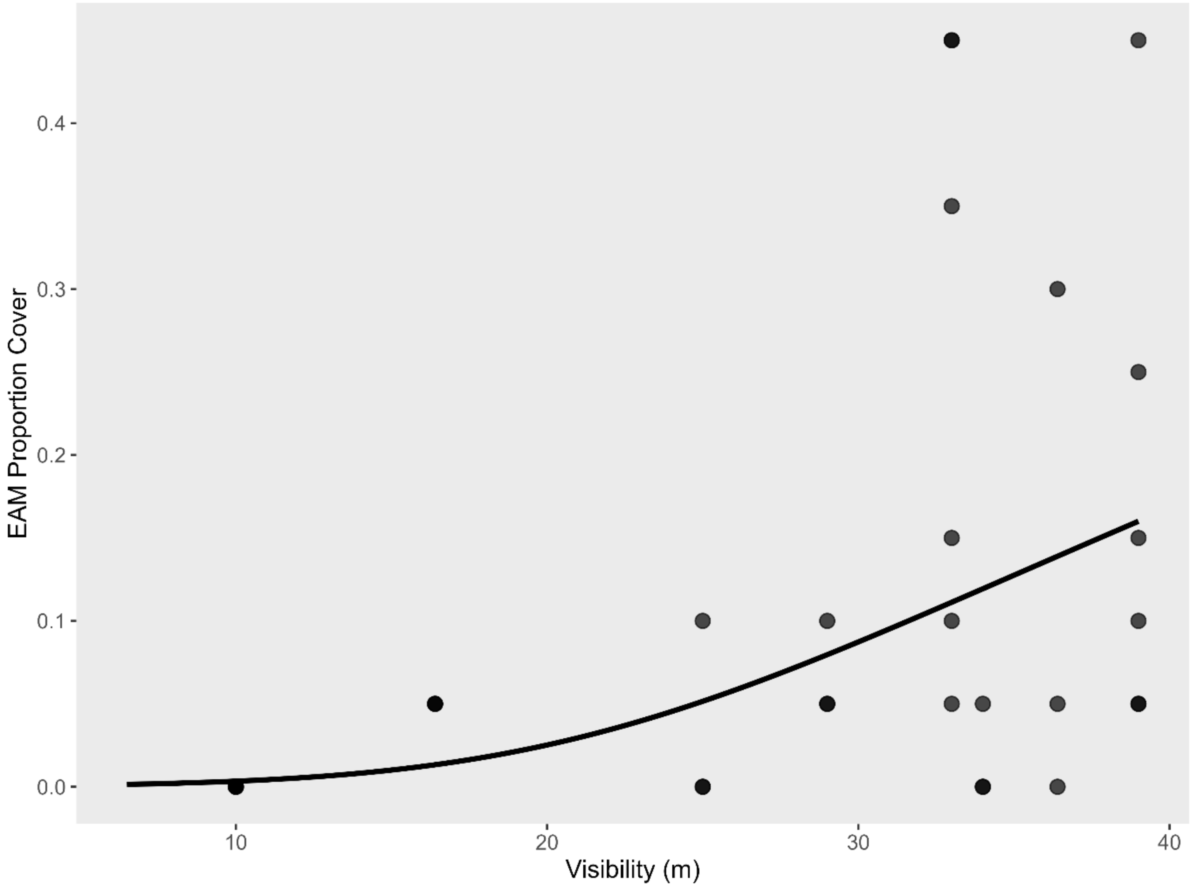

Figure 3.1.7

Relationship between visibility and EAM proportional cover, showing how EAM cover tends to increase with visibility. Black line represents predicted EAM cover from a zero-inflated beta regression.

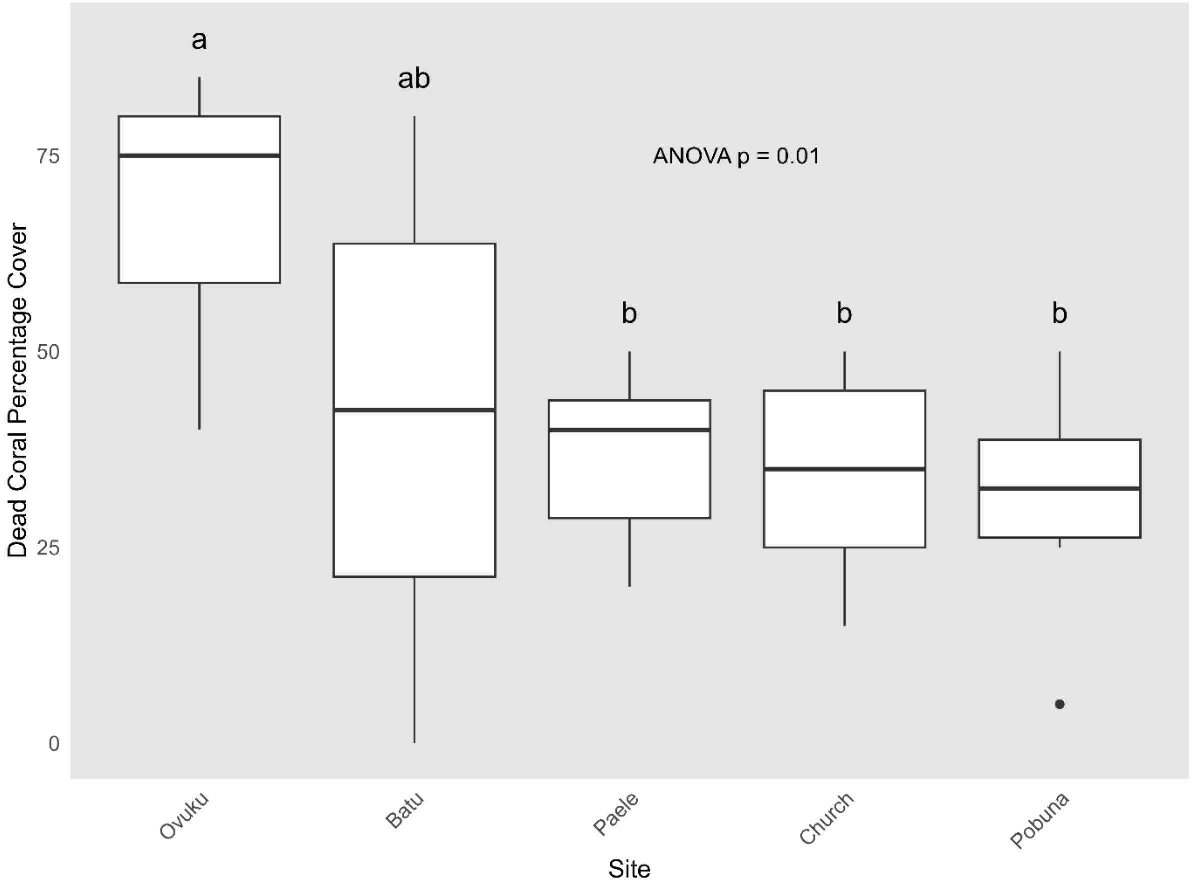

Figure 3.1.8

Site comparisons of dead coral cover. Different letters above boxplots indicate statistically significant differences between sites ($p < 0.05$), based on Tukey's HSD post-hoc tests following ANOVA. ANOVA p-values are displayed on the plot. Sample sizes (n) for each site are shown above the plots.

3.2 Foraging preferences

It is important to note that in this study an observation of a fish biting on a particular substrate does not necessarily indicate that the fish was selectively feeding on or consuming that substrate. This is because 1. due to the low colour accuracy and somewhat grainy nature of the underwater GoPro footage it was often difficult to differentiate between EAM, dead coral, bare accreted coral rock, or various other substrates. And 2. Some fish which appear to feed on visible surface biota like EAM are targeting alternate food sources, such as in the *Chlorurus* and *Scarus* species which often target endolithic microorganisms (Clements, 2017), and *C. striatus,* a detritivore which scrapes detritus from EAM (Marshell & Mumby, 2012). Only three substrates were observed to be bitten on in this study: EAM, dead coral, and coral rubble.

3.2.1 *C. striatus*

C. striatus fed much more frequently with 37 of the 70 recorded individuals (52.9%) feeding, though no bites were recorded at Ovuku (Figure 3.2.1 a). The percentage of fish feeding then increased markedly at Batu to 87.5%, before decreasing to 70% at Paele, then dropping to 30% at Church, before increasing to 65.38% at Pobuna; thus, the percentage of fish feeding increased with increasing turbidity with the exception of Ovuku and Pobuna (Figure 3.2.1 a). *C.* striatus bit almost exclusively on EAM apart from 26.37% and 11.76% of bites being on dead coral at Paele and Pobuna respectively (Figure 3.2.2 a). Manly's preference ratio for EAM was unusually high at batu (30.0), though this could reflect challenges in substrate classification on GoPro footage (Figure 3.2.3 a). This then decreased to 9.8 at Paele, 7.2 at Church, and 3.4 at Pobuna, indicating a strong preference (ratio >1) for EAM at each site which decreased with distance from the Vavanga River mouth with the exception of Ovuku (Figure 3.2.3 a). Manly's preference ratios for dead coral were <1 at both Paele and Pobuna, indicating avoidance.

3.2.3 *C. bleekeri*

Though 66 *C. bleekeri* were recorded, only 7 (10.6%) were recorded feeding. No feeding was recorded at Batu or Church and the percent of individuals feeding was consistently low at other sites; 12.5% at Pobuna, 40% at Paele, and 50% at Ovuku, though only two individuals were recorded at Ovuku (Figure 3.2.1 b). *C. bleekeri* was only observed biting on coral rubble at Ovuku (n = 2), at Paele 25% of bites were on EAM and 75% on dead coral, at Pobuna 100% of bites were on EAM (Figure 3.2.2 b). There was no visible site level trend in the Manly's preference ratios for *C. bleekeri.* However, it showed preference for both dead coral and EAM at both Paele and Pobuna as preference ratios were >1 (Figure 3.2.3 b).

Terminal phase individuals fed at a lower rate than initial phase individuals, with only 4 of the 52 terminal phase individuals feeding (7.7%) and 3 of the 14 initial phase individuals feeding (21.43%). The ratio of terminal phase to initial phase individuals varied considerably between sites, with Batu having almost exclusively terminal phase individuals and Church being entirely terminal phase (Figure 3.2.4). The two sites with the highest terminal phase ratios (Batu and Church) were also the sites where no feeding activity was recorded.

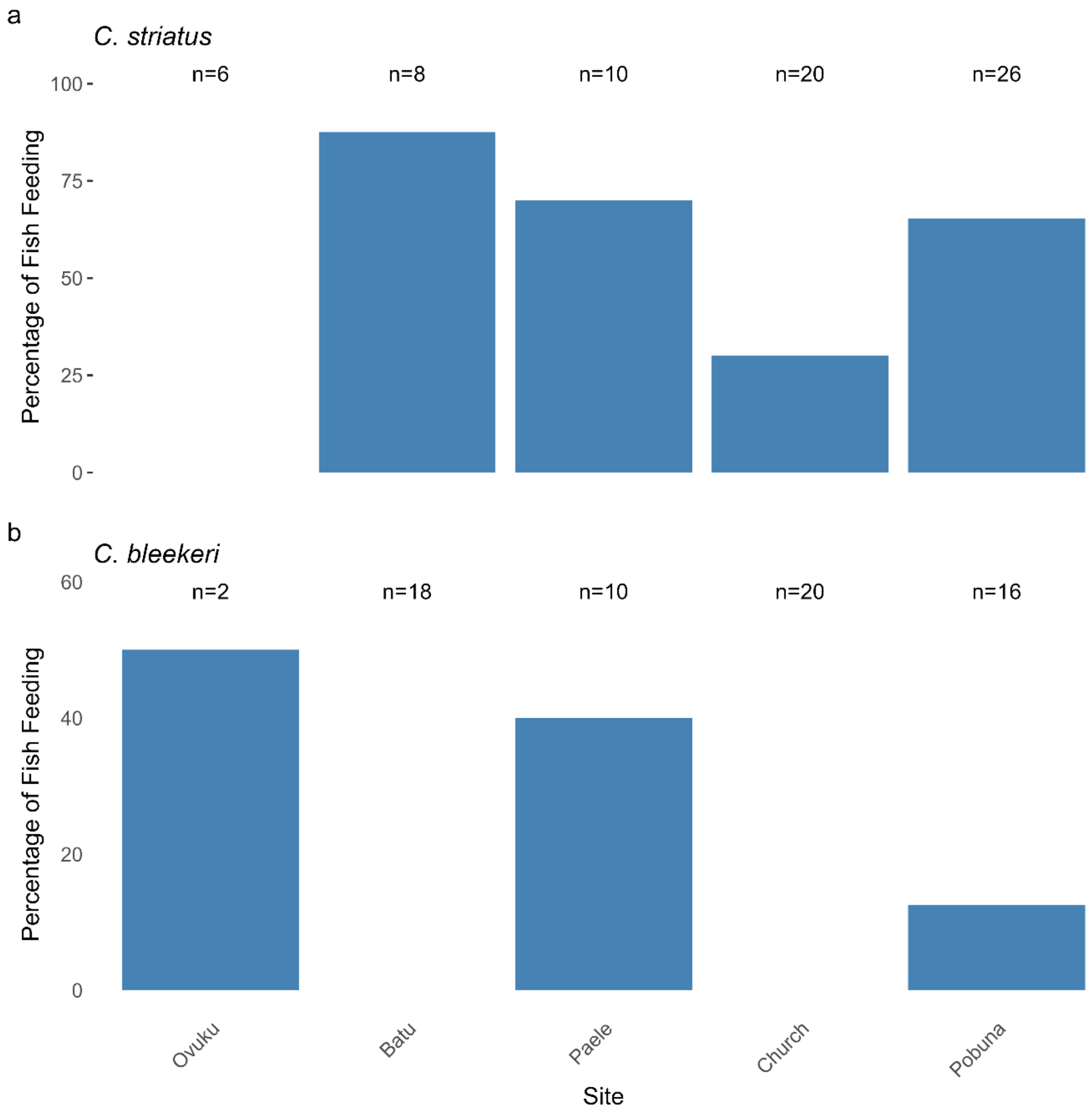

Figure 3.2.1

Percentage of fish feeding at each site for (a) *C. striatus* and (b) *C. bleekeri* with sample sizes above each bar.

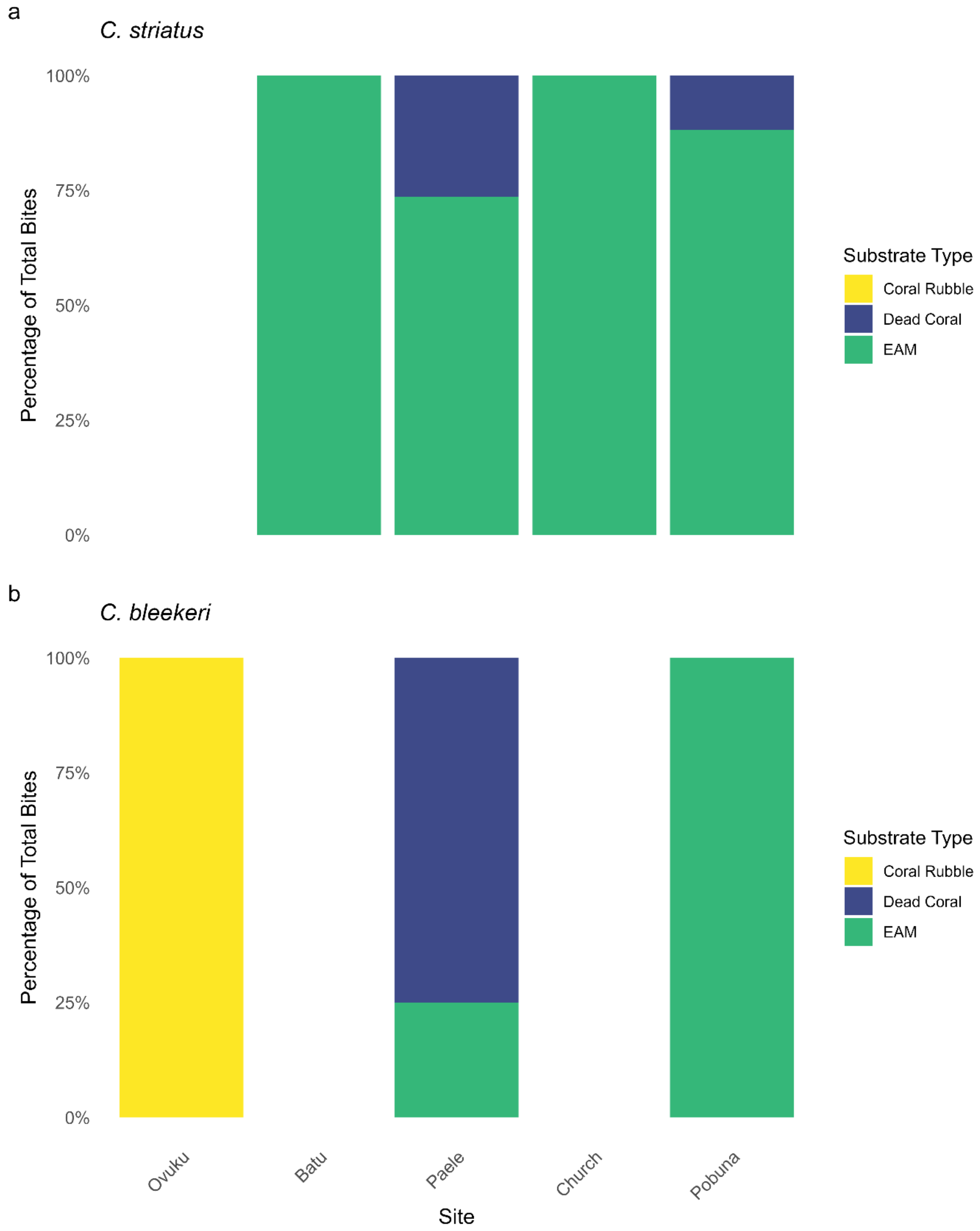

Figure 3.2.2

Percentage of total bites taken on different substrate types at each sampling site for: (a). *Chlorurus bleekeri,* and (b). *Ctenochaetus striatus.* Note. Sites are listed in order of proximity to Vavanga river.

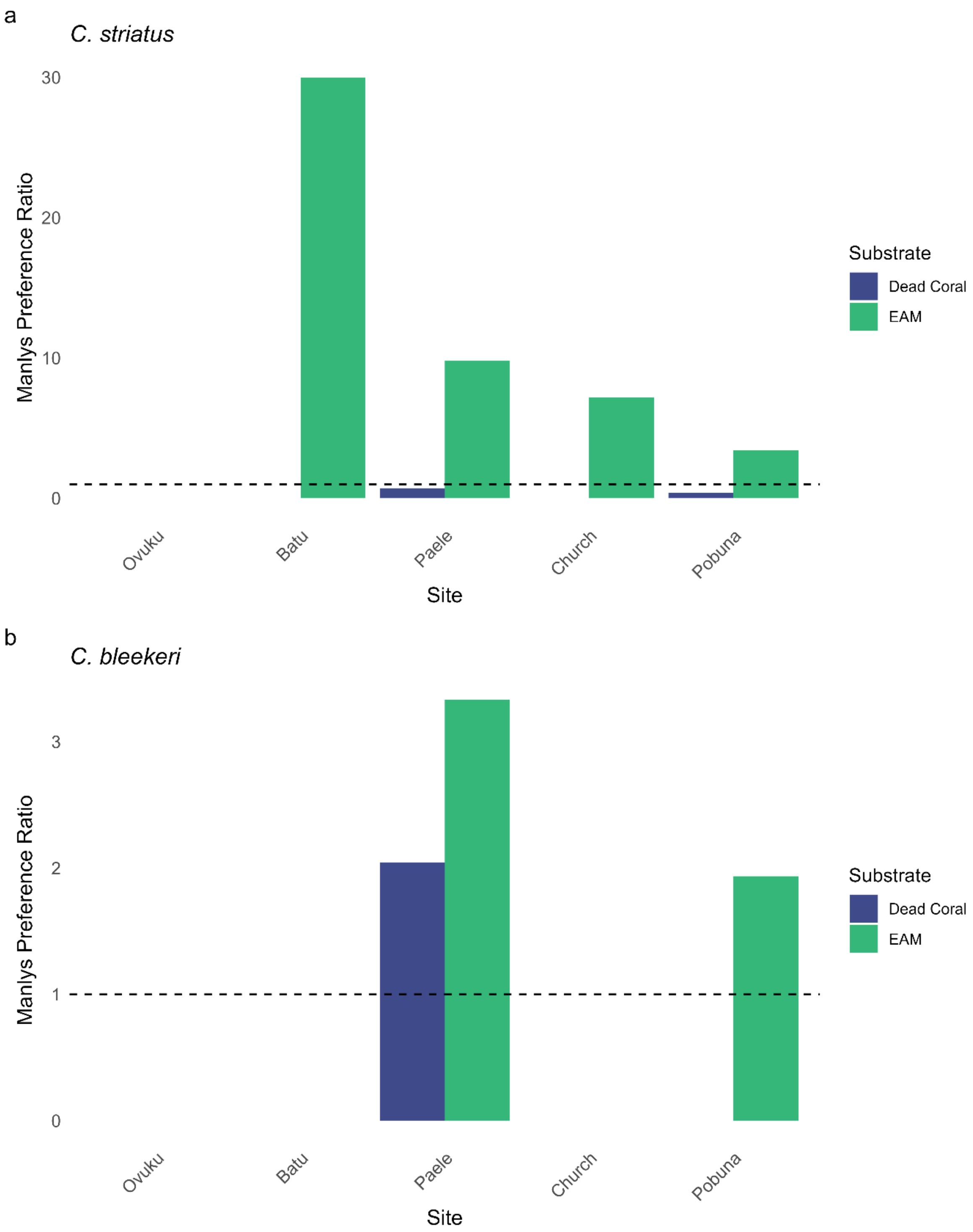

Figure 3.2.3

Manly's preference ratios of (a) *C. striatus* and (b) *C. bleekeri* for key substrates at each site. Note. A preference ratio of >1 indicates preference, while a preference ratio of <1 indicates avoidance. Sites are listed in order of proximity to Vavanga river.

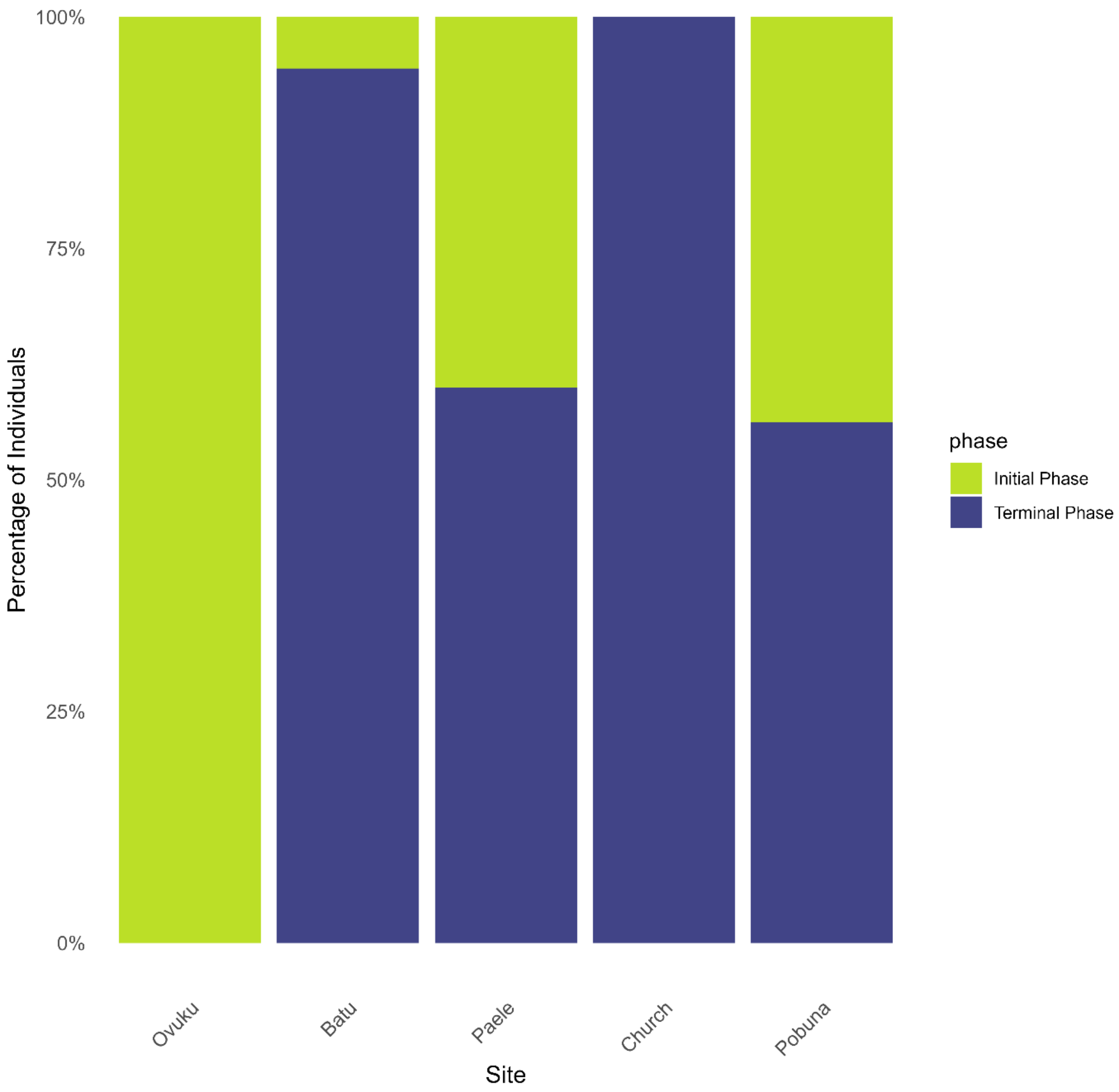

Figure 3.2.4

Percentage of initial phase and terminal phase *C. bleekeri* at each site.

3.3 Corelations between fish traits

3.3.1 *C. striatus*

Mean velocity had a moderately strong positive relationship with mass, with velocity increasing 0.16 cm s^{-1} with every additional gram of fish weight (95% CI [0.22, 0.098, $R^2 = 0.29$, $p < 0.001$) (Figure 3.2.1). Fish of lower weight appeared to bite more frequently than larger fish; mass explained 15.6% of the deviance in bite rate (Adj. $R^2 = 0.15$, $p = 0.002$) (Figure 3.2.2). All other relationships appeared relatively weak and were insignificant (Figure 3.2.2).

3.3.2 *C. bleekeri*

Mean velocity had a moderate positive relationship with mass, with velocity increasing by 0.039 cm s^{-1} with every additional gram of fish weight (95% CI [0.057, 0.020], $R^2 = 0.18$, $p < 0.001$) (Figure 3.2.3). Bite rate appeared to increase with bite distance and bite distance explained 63.6% of the deviance in bite rate (Adj. $R^2 = 0.491$, $p = 0.025$) (Figure 3.2.4). Bite rate appeared to increase with velocity in fish that were feeding, with velocity explaining 17.4% of the deviance in bite rate (Adj. $R^2 = 0.09$, $p = 0.005$) (Figure 3.2.4).

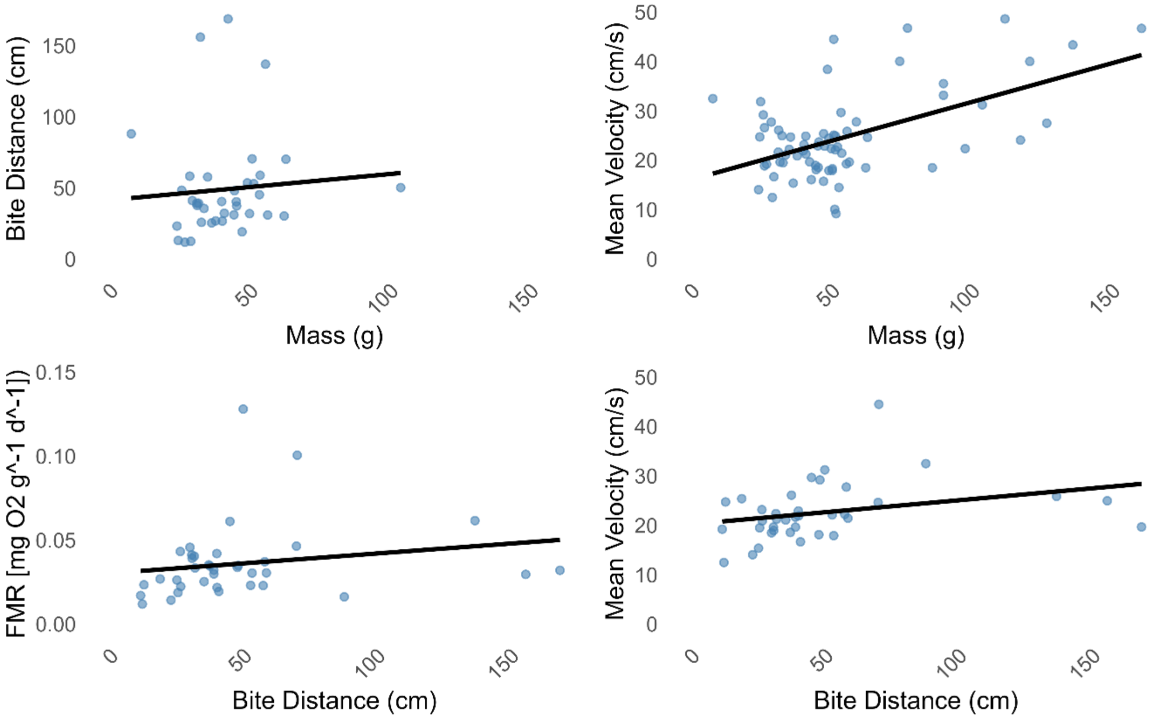

Figure 3.3.1

Relationships between FMR, velocity, and bite distance in *C. striatus.*

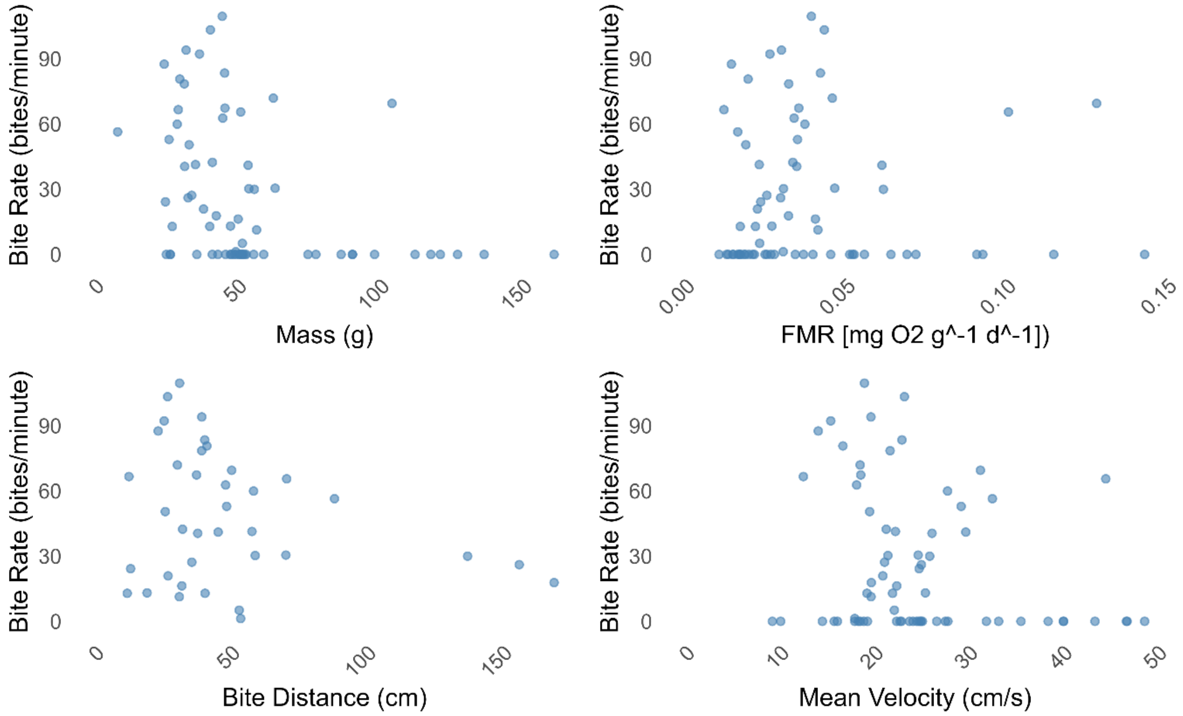

Figure 3.3.2

Relationships between bite rate, mass, FMR, bite distance, and velocity in *C. striatus*.

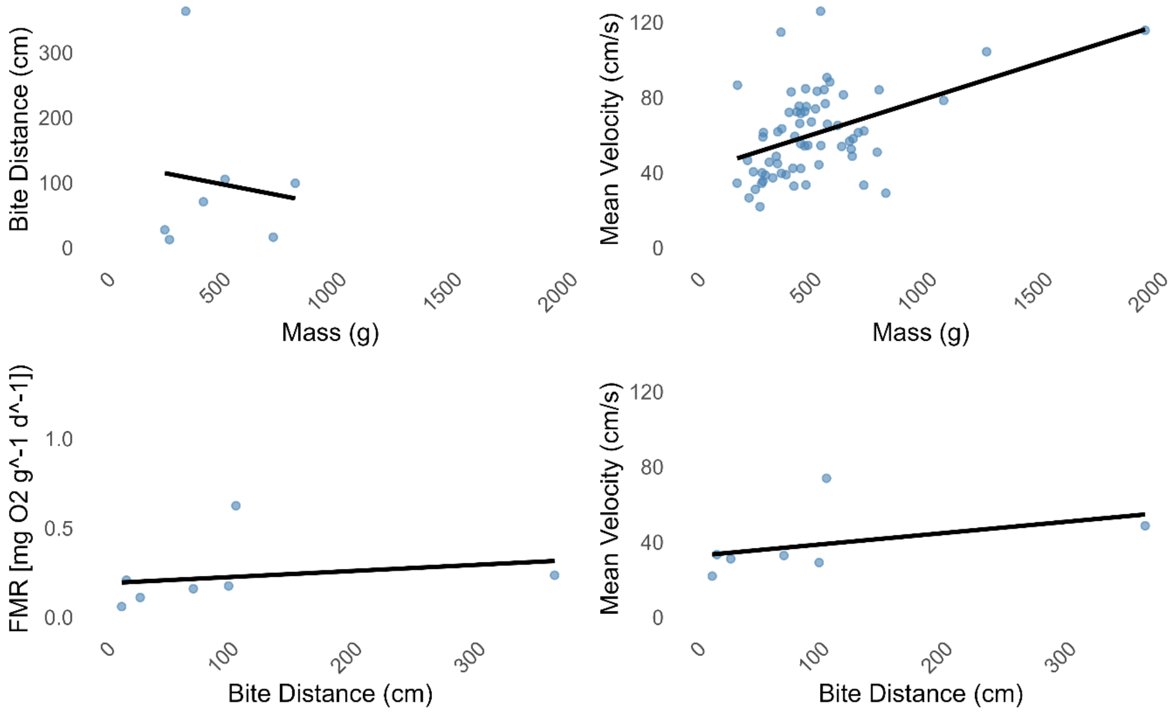

Figure 3.3.3

Relationships between FMR, velocity, and bite distance in *Chlorurus bleekeri*.

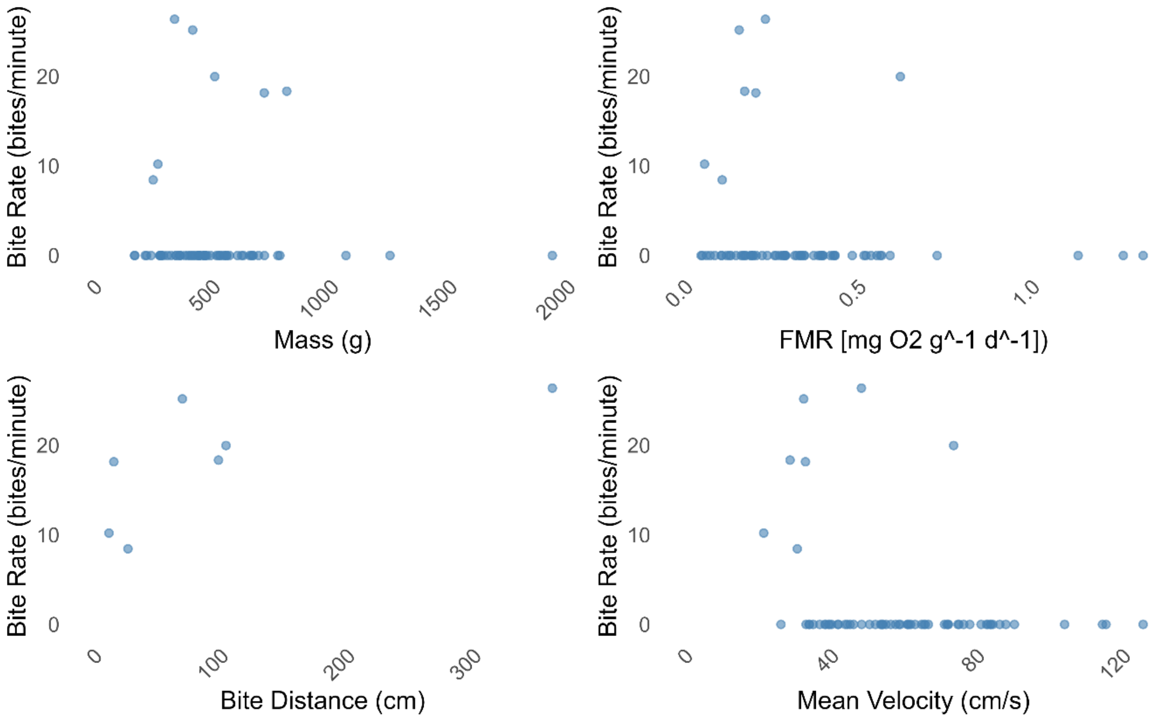

Figure 3.3.4

Relationships between bite rate, mass, FMR, bite distance, and velocity in *Chlorurus bleekeri.*

Table 3.3.1

Simple linear model results for relationships between bite distance, FMR, mass, and velocity in *C. striatus*.

model	Estimate	Std Error	T value	R^2	P value
Bite Distance ~ Mass	0.1833	0.3787	0.4840	0.0066	0.6314
Mean velocity ~ Mass	**0.1569**	**0.0298**	**5.2590**	0.2891	1.5860e-06
Log FMR ~ Bite Distance	0.0033	0.0022	1.4925	0.0598	0.1445
velocity ~ Bite Distance	0.0484	0.0262	1.8460	0.0887	0.0734

Table 3.3.2

Simple linear model results for relationships between bite distance, FMR, mass, and velocity in *C. bleekeri*.

model	Estimate	Std Error	T value	R^2	P value
Bite Distance ~ Mass	-0.0689	0.2473	-0.2788	0.0153	0.7916
Mean velocity ~ Mass	**0.0389**	**0.0094**	**3.7433**	**4.125**	0.0001
Log FMR ~ Bite Distance	0.0022	0.0024	0.9133	0.1430	0.4030
velocity ~ Bite Distance	0.0016	0.0012	1.3049	0.2541	0.2487

Table 3.3.3

Generalised additive model results for relationships between bite rate and predictor variables in *C. striatus.*

Model	F-statistic	Deviance explained	Adj. R^2	p-value
Bite rate ~ Mass (g)	**10.49**	**15.6%**	**0.15**	0.002
Bite rate ~ FMR	0.003	0.0048%	-0.0147	0.953
Bite rate ~ Bite distance	3.104	10.9%	0.0288	0.105
Bite rate ~ Velocity	3.964	5.21%	0.031	0.051

Table 3.3.4

Generalised additive model results for relationships between bite rate and predictor variables in *C. bleekeri*

Model	F-statistic	Deviance	Adj. R^2	p-value
Bite rate ~ Mass (g)	0.006	0.02%	-0.0156	0.94
Bite rate ~ FMR	2.521	7.78%	0.0007	0.137
Bite rate ~ Bite distance	**10.1**	**63.6%**	**0.491**	0.025
Bite rate ~ Velocity	**5.828**	**17.4%**	**0.09**	0.005

3.4 Environmental relationships with behavioural traits and energy expenditure

3.4.1 *C. striatus*

Visibility Models

Visibility had few significant relationships with the feeding and activity metrics in *C. striatus*. Velocity (body lengths s^{-1}) had a negative but non statistically significant relationship with visibility (Figures 3.3.1 a). FMR also had a negative but non statistically significant relationship with visibility (Figures 3.3.2 a). Bite distance had a non-statistically significant relationship with visibility (Figure 3.3.3 a) but decreased by 0.21 cm per metre of depth (95% CI [-0.016, -0.40], p = 0.041) (Figure 3.3.7). *C. striatus* was observed feeding across a visibility range of 16.4 metres to 39.0 metres (Figure 3.3.3 a).

Forel-Ule Models

In general, Forel-Ule had stronger relationships with feeding and activity metrics in *C. striatus*. Velocity (body lengths s^{-1}) had a positive relationship with Forel-Ule index, with Velocity increasing by 1.29 body lengths s^{-1} with each unit of Forel-Ule (95% CI [1.12, 1.48], p = 0.048) (Figure 3.3.4 a). FMR also had a positive relationship with Forel-Ule, increasing by 0.013 mg O2 g^{-1} d^{-1} per unit Forel-Ule (95% CI [0.011, 0.015], p = 0.048) (Figure 3.3.5 a). FMR also had a positive relationship with EAM cover, increasing by 0.014 mg O2 g^{-1} d^{-1} per percent increase in EAM cover (95% CI [0.013, 0.014], p = 0.033) (Figure 3.3.8). Bite distance and Forel-Ule had a non-statistically significant relationship (Figure 3.3.6 a). Feeding was only observed in a narrow band of Forel-Ule between 2.0 and 3.0 (Figure 3.3.6 a).

3.4.2 *C. bleekeri*

Visibility Models

Visibility had few significant relationships with feeding and activity metrics of *C. bleekeri.* There was a negative but non statistically significant relationship between velocity and visibility (Figure 3.3.1 b). There was no statistically significant relationship between FMR and visibility (Figure 3.3.2 b). Bite distance had a strong negative relationship with visibility, with bite distance decreasing by 15.6 cm per metre increase in visibility (95% CI [-7.0, -24.2], p = 0.013) (Figure 3.3.3 b). *C. bleekeri* was observed feeding across a visibility range of 10.0 metres to 34.0 metres (Figure 3.3.3 b).

Phase effects: phases showed differing FMR responses to visibility. Initial phase individuals showed a strong negative relationship between FMR and visibility (Figure 3.3.2 b), while terminal phase showed no trend here (Figure 3.3.2 c). Terminal phase had significantly higher FMR (0.412 mg O2 g^{-1} d^{-1}) compared to initial phase (0.147 mg O2 g^{-1} d^{-1}). On average terminal phase FMR was 280.6%

higher (CI [193%, 408.1%], $p < 0.001$). Terminal phase individuals had significantly higher velocity (85.5 cm s^{-1}) than initial phase individuals (60.7 cm s^{-1}). On average they swam 41% faster (95% CI [14.3%, 74%], $p = 0.002$). However, there was no significant difference in velocity in body lengths s^{-1} between the two phases.

Forel-Ule Models

Velocity had a weakly positive but non-statistically significant relationship with Forel-Ule (Figure 3.3.4 b). FMR also had a weakly positive but non-statistically significant relationship with Forel-Ule (Figure 3.3.5 b). Bite distance had a positive relationship with Forel-Ule index, with bite distance increasing by 126.2 cm per Forel-Ule unit (95% CI [147.8, 104.5], $p < 0.001$) (Figure 3.3.6). Bite distance also had a positive relationship with EAM cover, increasing by 3.6 cm per percent increase in EAM cover (95% CI [5.3, 2.0], $p = 0.004$), (Figure 3.3.9). Feeding was observed in a relatively large band of Forel-Ule between 2.25 and 6.0 (Figure 3.3.6 b).

Phase effects: phases showed differing FMR responses to Forel-Ule. Initial phase individuals showed a strong positive relationship between FMR and Forel-Ule (Figure 3.3.5 b), while terminal phase showed no trend here (Figure 3.3.5 c). The Forel-Ule models also indicated Terminal phase had both significantly higher FMR ($p < 0.001$) and velocity ($p = 0.003$) than initial phase.

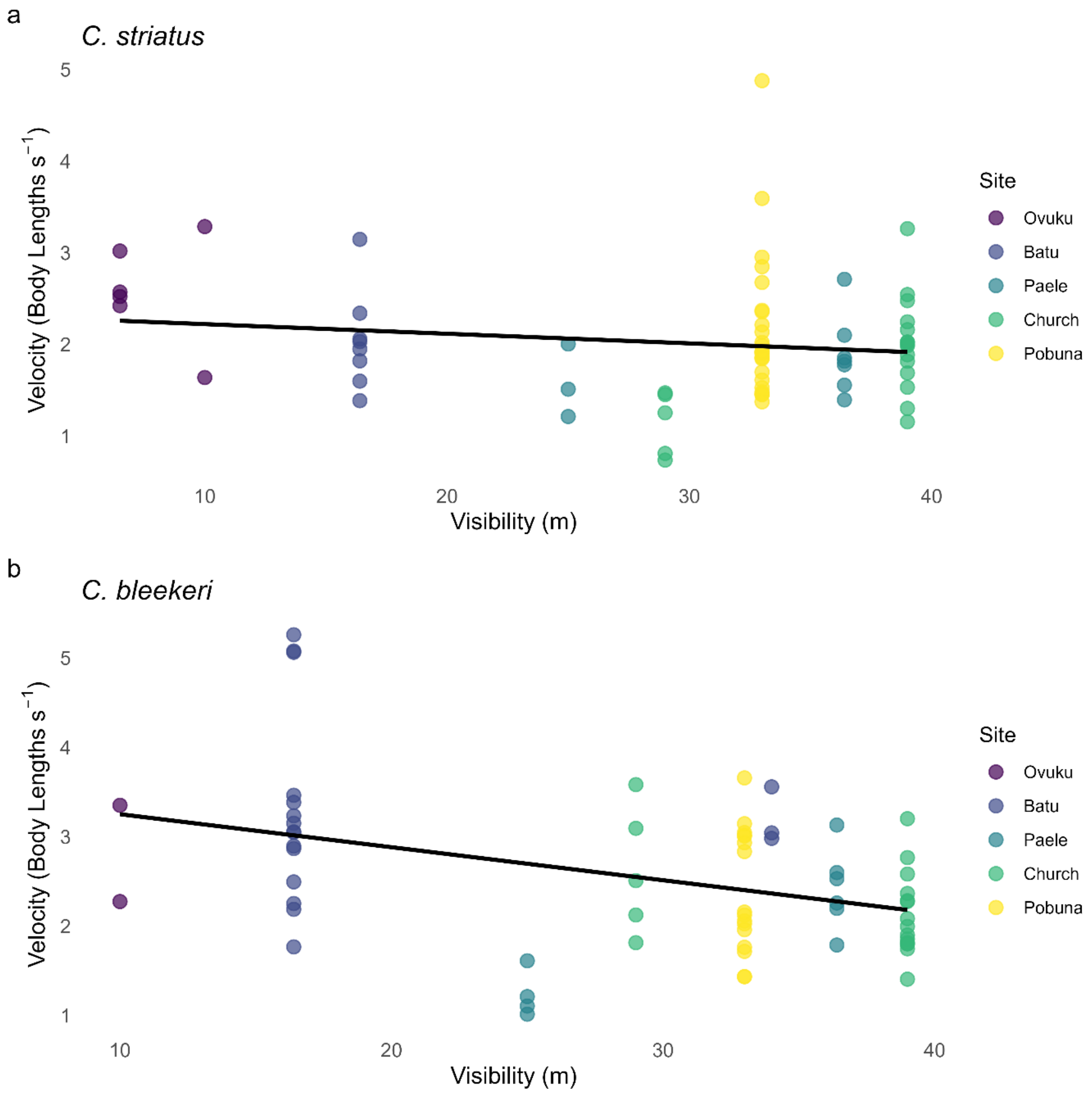

Figure 3.4.1

Relationships between velocity (body lengths s^{-1}) and visibility (m) for (a) *C. striatus* and (b) *C. bleekeri*. Black lines represent fitted regression lines. Data points are colour-coded by site, and legend sites are ordered by distance from the Vavanga River.

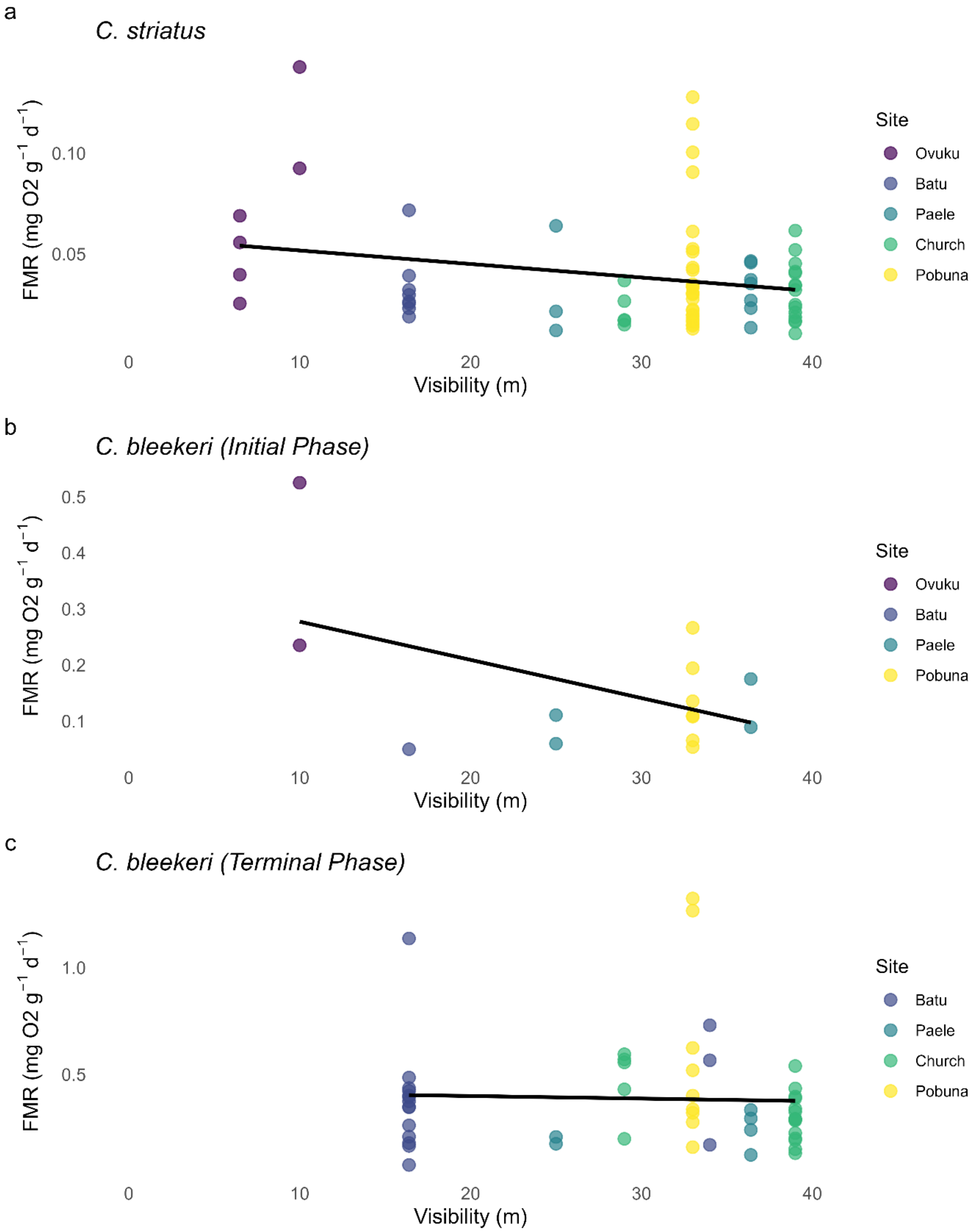

Figure 3.4.2

Relationships between FMR (mg O2 g^{-1} d^{-1}) and visibility (m) for (a) *C. striatus* and (b) *C. bleekeri* initial phase and (c) *C. bleekeri* terminal phase. Black lines represent fitted regression lines. Data points are colour-coded by site, and legend sites are ordered by distance from the Vavanga River.

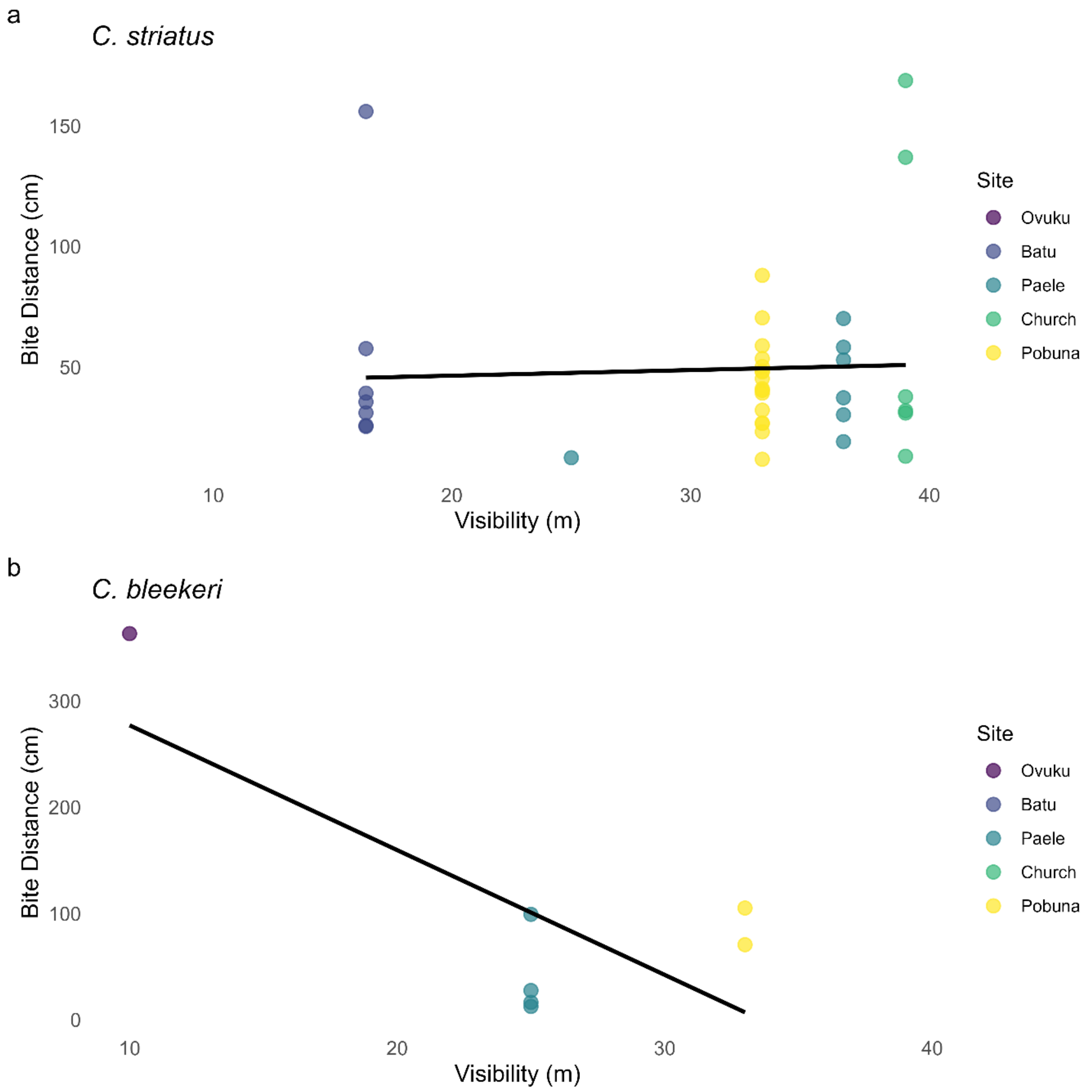

Figure 3.4.3

Relationships between bite distance (cm) and visibility (m) for (a) *C. striatus* and (b) *C. bleekeri*. Black lines represent fitted regression lines. Data points are colour-coded by site, and legend sites are ordered by distance from the Vavanga River.

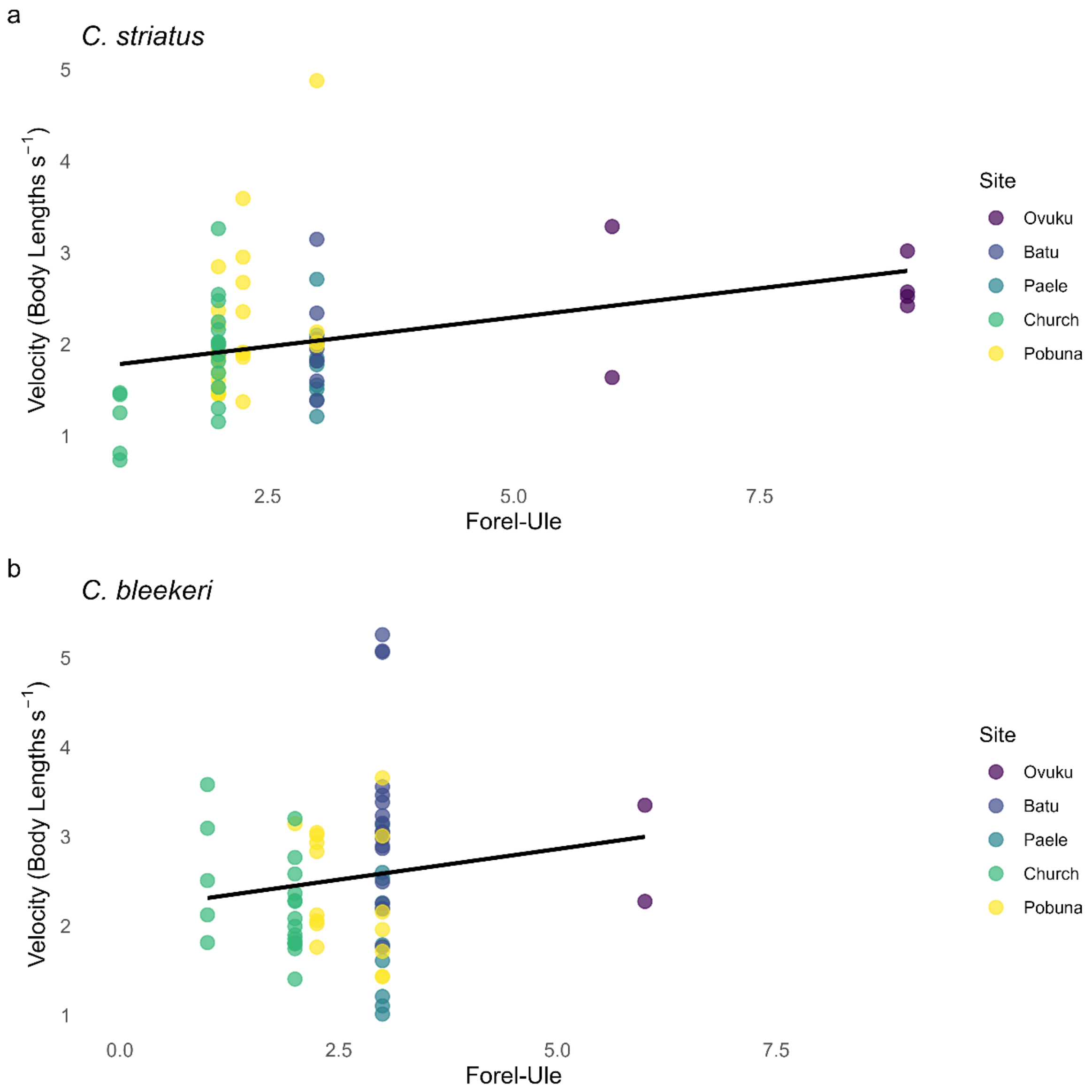

Figure 3.4.4

Relationships between velocity (body lengths s^{-1}) and Forel-Ule index for (a) *C. striatus* and (b) *C. bleekeri*. Black lines represent fitted regression lines. Data points are colour-coded by site, and legend sites are ordered by distance from the Vavanga River.

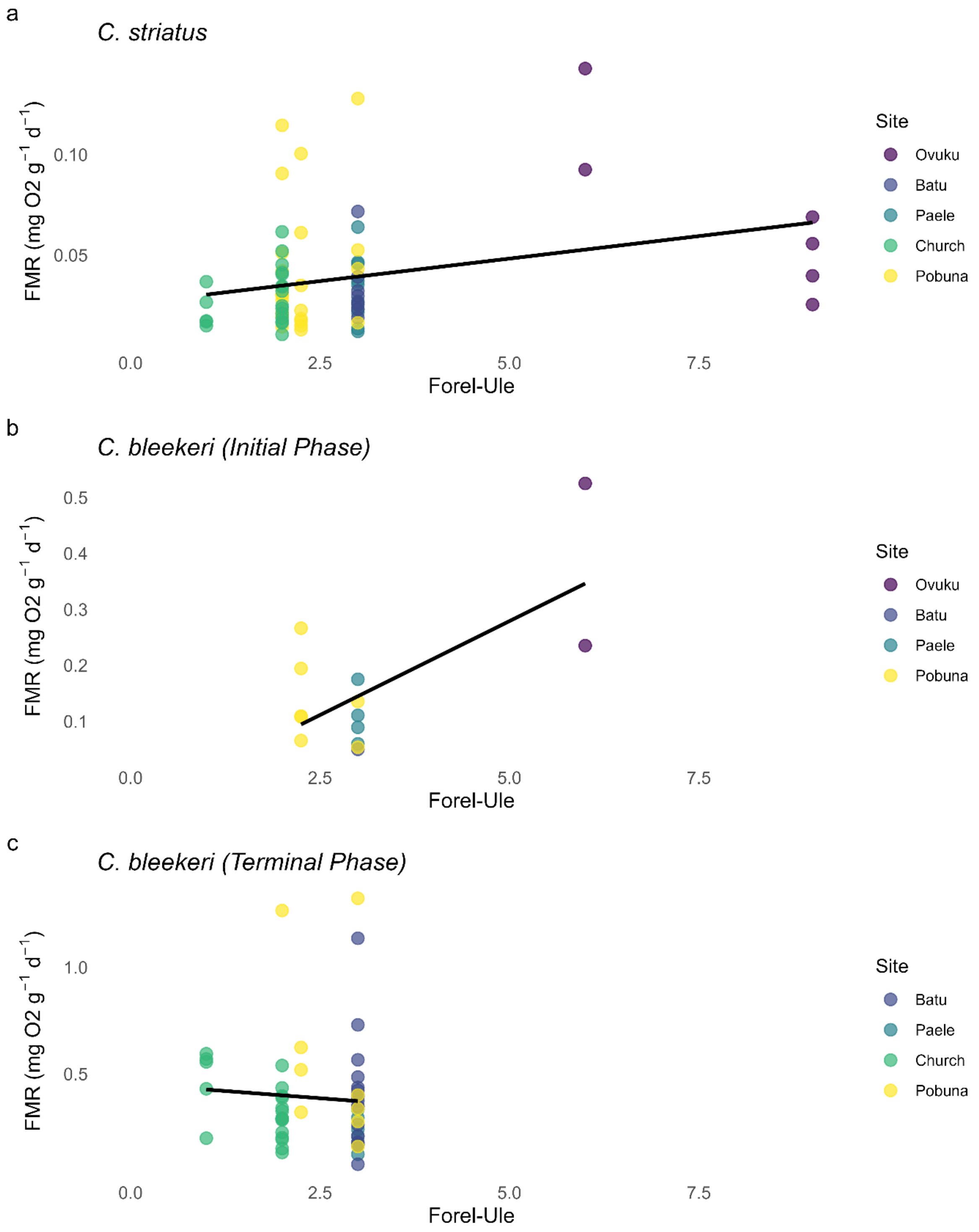

Figure 3.4.5

Relationships between FMR (mg O2 g^{-1} d^{-1}) and Forel-Ule index for (a) *C. striatus* and (b) *C. bleekeri* initial phase and (c) *C. bleekeri* terminal phase. Black lines represent fitted regression lines. Data points are colour-coded by site, and legend sites are ordered by distance from the Vavanga River.

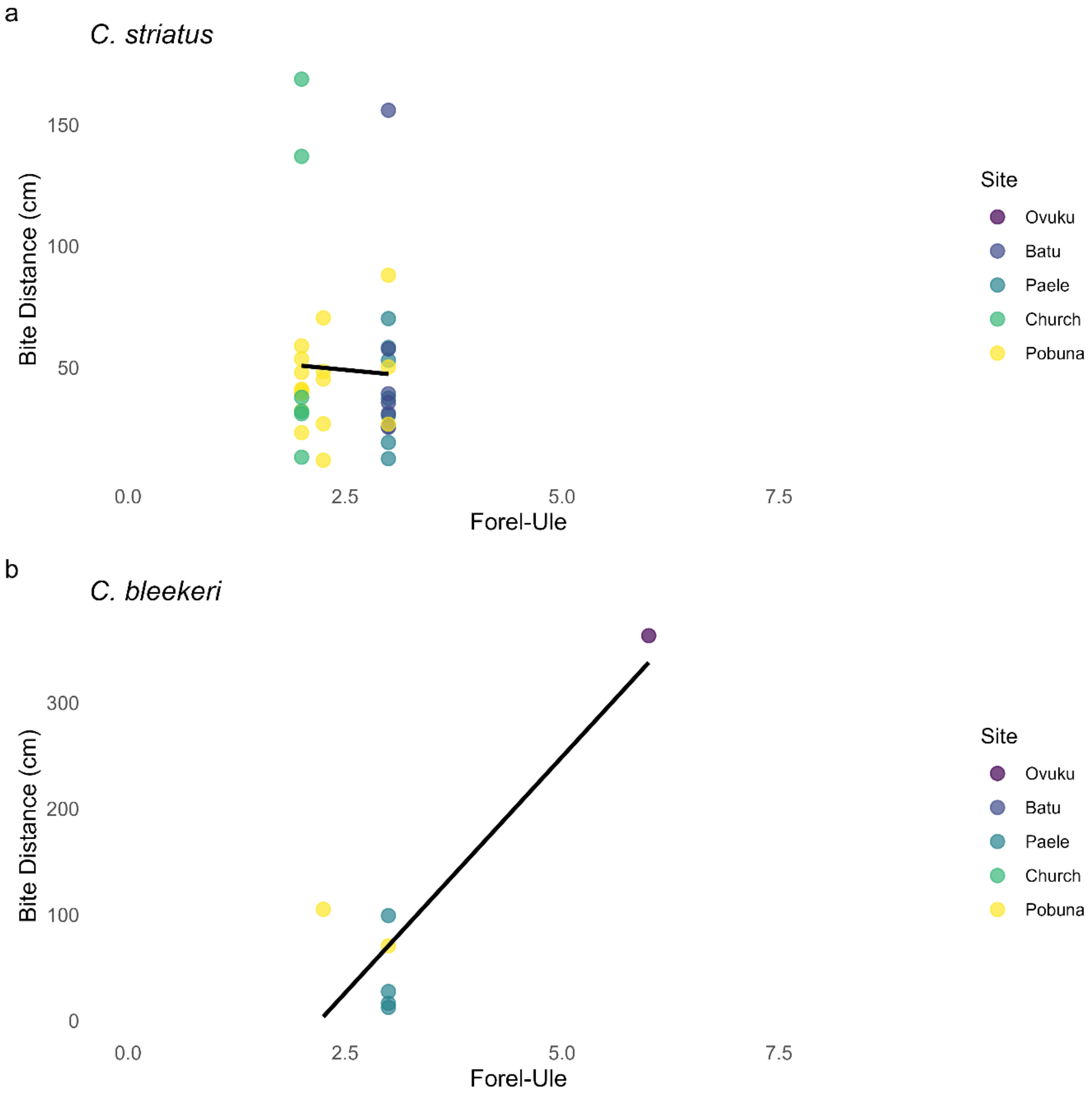

Figure 3.4.6

Relationships between bite distance and Forel-Ule index for (a) *C. striatus* and (b) *C. bleekeri*. Black lines represent fitted regression lines. Data points are colour-coded by site, and legend sites are ordered by distance from the Vavanga River.

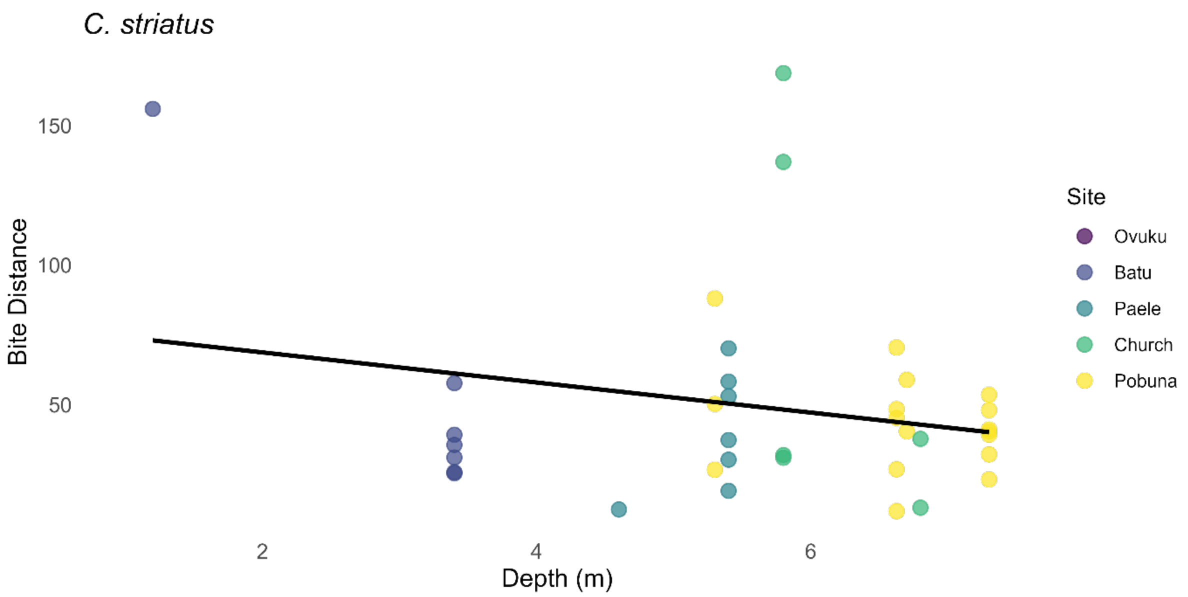

Figure 3.4.7

Relationship between bite distance and depth in *C. striatus*. Black lines represent fitted regression lines. Data points are colour-coded by site, and legend sites are ordered by distance from the Vavanga River.

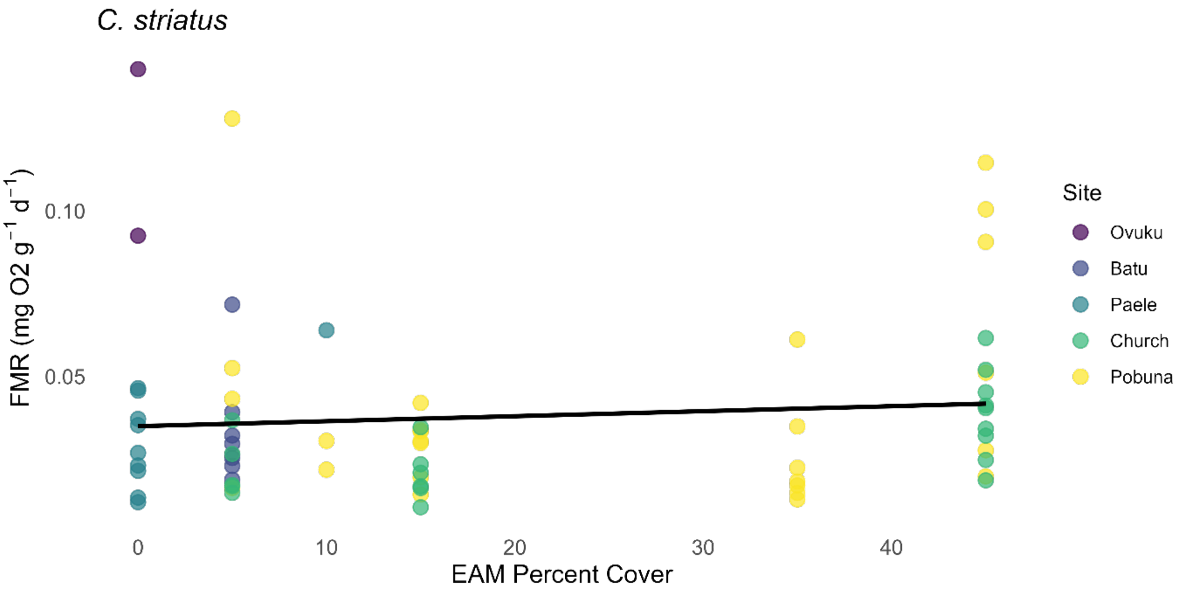

Figure 3.4.8

Relationship between FMR (mg O2 g^{-1} d^{-1}) and percent EAM cover in *C. striatus*. Black lines represent fitted regression lines. Data points are colour-coded by site, and legend sites are ordered by distance from the Vavanga River.

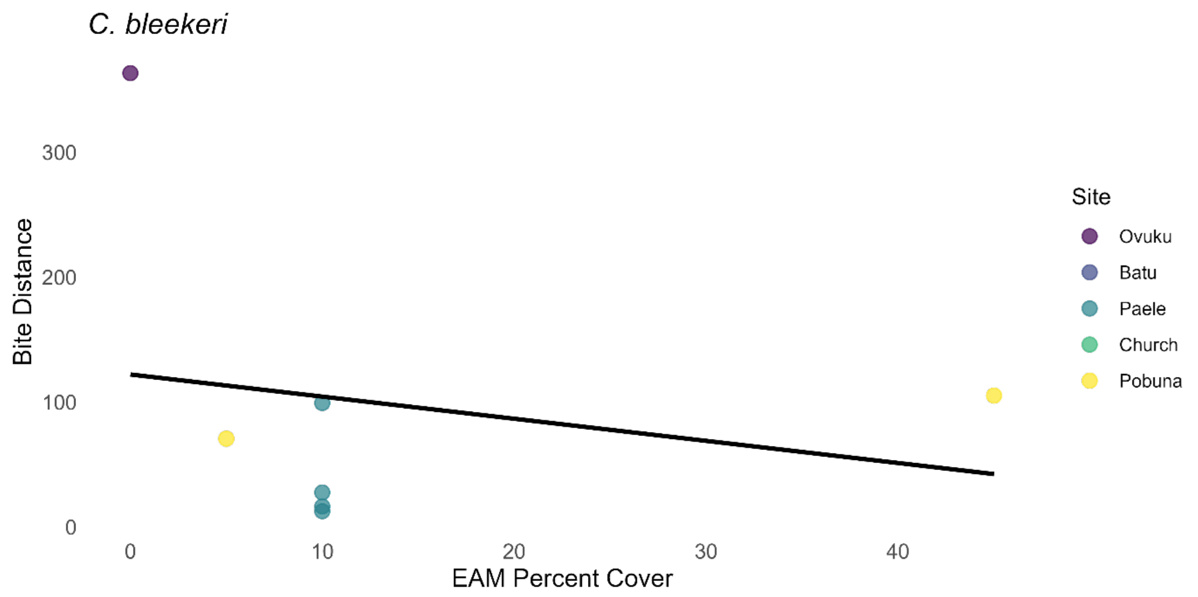

Figure 3.4.9

Relationship between bite distance (cm) and percent EAM cover in *C. bleekeri*. Black lines represent fitted regression lines. Data points are colour-coded by site, and legend sites are ordered by distance from the Vavanga River.

Table 3.4.1

Linear mixed model results showing effects of visibility, EAM cover, and depth on behavioural response variables (velocity, FMR, and bite distance) in ***C. striatus.*** With significant results highlighted in bold.

Response	Predictor	Estimate	SE	t-value	p	n
Log velocity (body lengths s^{-1})	Visibility	0.0031	0.0144	0.2144	0.8336	66
	EAM cover	0.0058	0.0046	1.2642	0.2280	66
	Depth	-0.0590	0.0728	-0.8114	0.4309	66
Velocity (cm s^{-1})	Visibility	-0.1352	0.3411	-0.3963	0.6993	66
	EAM cover	0.2000	0.1076	1.8583	0.0885	66
	Depth	-1.3548	1.7146	-0.7901	0.4447	66
Log FMR	Visibility	-0.0206	0.0232	-0.8882	0.3967	66
	EAM cover	0.0145	0.0074	1.9651	0.0787	66
	Depth	-0.0855	0.1182	-0.7236	0.4852	66
Bite distance	Visibility	0.0273	0.0188	1.4509	0.1552	37
	EAM cover	0.0096	0.0066	1.4433	0.1574	37
	Depth	**-0.2078**	**0.0979**	**-2.1232**	**0.0405**	**37**

Note: EAM = epilithic algal matrix, FMR = field metabolic rate, SE = standard error.

Table 3.4.2

Linear mixed model results showing effects of Forel-Ule, EAM cover, and depth on behavioural response variables (velocity, FMR, and bite distance) in ***C. striatus***. With significant results highlighted in bold.

Response	Predictor	Estimate	SE	t-value	p	n
Log velocity	**Forel-Ule**	**0.1537**	**0.0712**	**2.1602**	**0.0476**	**66**
(body lengths s^{-1})	EAM cover	0.0058	0.0038	1.5082	0.1618	66
	Depth	0.0134	0.0458	0.2924	0.7745	66
Velocity	**Forel-Ule**	**4.1241**	**1.5938**	**2.5876**	**0.0218**	**66**
(cm s^{-1})	EAM cover	0.1889	0.0858	2.2010	0.0537	66
	Depth	-0.2498	1.0267	-0.2433	0.8118	66
Log FMR	**Forel-Ule**	**0.3421**	**0.1105**	**3.0954**	**0.0065**	**66**
	EAM cover	**0.0141**	**0.0056**	**2.5318**	**0.0328**	**66**
	Depth	-0.0383	0.0695	-0.5509	0.5909	66
Bite distance	Forel-Ule	-0.2987	0.4531	-0.6593	0.5294	37
	EAM cover	0.0081	0.0095	0.8496	0.4221	37
	Depth	-0.1832	0.1151	-1.5921	0.1471	**37**

Note: EAM = epilithic algal matrix, FMR = field metabolic rate, SE = standard error.

Table 3.4.3

Linear mixed model results showing effects of visibility, EAM cover, and phase on behavioural response variables (velocity, FMR, and bite distance) in ***C. bleekeri***. With significant results highlighted in bold.

Response	Predictor	Estimate	SE	t-value	p	n
Log velocity	Visibility	-0.0084	0.0080	-1.0523	0.3130	66
(body lengths s^{-1})	EAM cover	0.0015	0.0058	0.2610	0.7979	66
	Terminal phase	0.0720	0.0994	0.7245	0.4713	66
Log velocity	Visibility	-0.0110	0.0075	-1.4689	0.1706	66
(cm s^{-1})	EAM cover	0.0017	0.0055	0.3020	0.7673	66
	Terminal phase	**0.3436**	**0.1073**	**3.2023**	**0.0021**	**66**
Log FMR	Visibility	-0.0091	0.0110	-0.8284	0.4425	66
	EAM cover	0.0077	0.0084	0.9115	0.3863	66
	Terminal phase	**1.0319**	**0.1910**	**5.4011**	**1.94e-06**	**66**
Bite distance	**Visibility**	**-15.5958**	**4.3928**	**-3.5503**	**0.0132**	**7**
	EAM cover	1.7439	2.2105	0.7889	0.4662	7
	Terminal phase	42.1486	32.4882	1.2974	0.2708	7

Note: EAM = epilithic algal matrix, FMR = field metabolic rate, SE = standard error.

Table 3.4.4

Linear mixed model results showing effects of Forel-Ule, EAM cover, and phase on behavioural response variables (velocity, FMR, and bite distance) in ***C. bleekeri.*** With significant results highlighted in bold.

Response	Predictor	Estimate	SE	t-value	p	n
Log velocity	Forel-Ule	0.0322	0.0779	0.4132	0.6843	66
(body lengths s^{-1})	EAM cover	0.0004	0.0062	0.0689	0.9459	66
	Terminal phase	0.0658	0.1036	0.6351	0.5277	66
Log velocity	Forel-Ule	0.0634	0.0771	0.8223	0.4211	66
(cm s^{-1})	EAM cover	0.0009	0.0060	0.1502	0.8825	66
	Terminal phase	**0.3487**	**0.1137**	**3.0676**	**0.0031**	**66**
Log FMR	Forel-Ule	0.1444	0.1148	1.2585	0.2268	66
	EAM cover	0.0098	0.0087	1.1246	0.2820	66
	Terminal phase	**1.1086**	**0.2040**	**5.4331**	**9.52e-07**	**66**
Bite distance	**Forel-Ule**	**126.1759**	**11.0509**	**11.4177**	**8.87e-06**	**7**
	EAM cover	**3.6453**	**0.8476**	**4.3008**	**0.0036**	**7**
	Terminal phase	48.7127	22.1219	2.2020	0.0635	7

Note: EAM = epilithic algal matrix, FMR = field metabolic rate, SE = standard error.

3.5 Site level analysis

3.5.1 *C. striatus*

There were several significant site differences in the feeding and energetic traits in *C. striatus,* notably between Ovuku and the remaining sites. The mean mass of *C. striatus* was 54.3 g. Mean mass was significantly higher at Ovuku (122.5 g) than any of the other sites (p. adj < 0.001) (Figure 3.4.1 a). None of the other sites had significant differences in mass (Figure 3.4.1 a). The overall mean bite rate was 25.68 bites min^{-1}. Mean bite rate was highest at Batu (53.17 bites min^{-1}), which was significantly higher than Church (7.00 bites min^{-1}, p. adj = 0.013) and Pobuna (35.3 bites min^{-1}, p. adj = 0.009) (Figure 3.4.2 a). The overall mean velocity was 2.01 body lengths s^{-1}. Ovuku had the highest mean velocity at 2.58 body lengths s^{-1} which was significantly higher than that of Church (1.79 body lengths s^{-1}, p. adj = 0.048), which had the lowest mean velocity (Figure 3.4.2 b). Other than Ovuku there was little difference in velocity between sites, and no other significant differences were found (Figure 3.4.2 b). Overall mean FMR was 0.038 mg O2 g^{-1} d^{-1}. The highest mean FMR was at Ovuku (0.071 mg O2 g^{-1} d^{-1}) which was significantly higher than Church (0.029 mg O2 g^{-1} d^{-1}, p. adj = 0.019)

(Figure 3.4.2 c). FMR levels were relatively homogenous between Batu and Pobuna and there were no other significant differences (Figure 3.4.2 c).

3.5.2 *C. bleekeri*

The overall mean mass of *C. bleekeri* was 505.4 g and there was little variation between sites, no significant differences were found (Figure 3.4.1 b). No fish were recorded feeding over the sampling duration at Batu or Church and the sample sizes of fish which were recorded feeding at the remaining three sites were too small to make meaningful statistical inference about site differences in bite rate (Ovuku n = 1, Pobuna n = 2, Paele n = 4) (Figure 3.4.3 a). Overall mean velocity was 2.53 body lengths s^{-1}. Mean velocity was highest at Batu (3.27 body lengths s^{-1}), and this was significantly higher than Church (2.25 body lengths s^{-1}, p. adj = 0.003), Paele (1.95 body lengths s^{-1}, p. adj < 0.001), and Pobuna (2.39 body lengths s^{-1}, p. adj = 0.024) (Figure 3.4.3 b). Overall mean FMR was 0.338 mg O2 g^{-1} d^{-1} and there was very little variation between sites and no significant differences (Figure 3.4.3 c). Overall mean FMR for initial phase *C. bleekeri* was 0.156 mg O2 g^{-1} d^{-1}. The mean initial phase FMR at Ovuku was over twice this at 0.380 mg O2 g^{-1} d^{-1}, though this was based on only 2 samples. A significant site effect was found for FMR in initial phase *C. bleekeri* (ANOVA; p = 0.048). However post-hoc tests revealed no significant pairwise comparisons (Figure 3.4.4 a). The mean FMR for terminal phase *C. bleekeri* was 0.387 mg O2 g^{-1} d^{-1}. There was no significant site effect for terminal phase *C. bleekeri* (Figure 3.4.4 b).

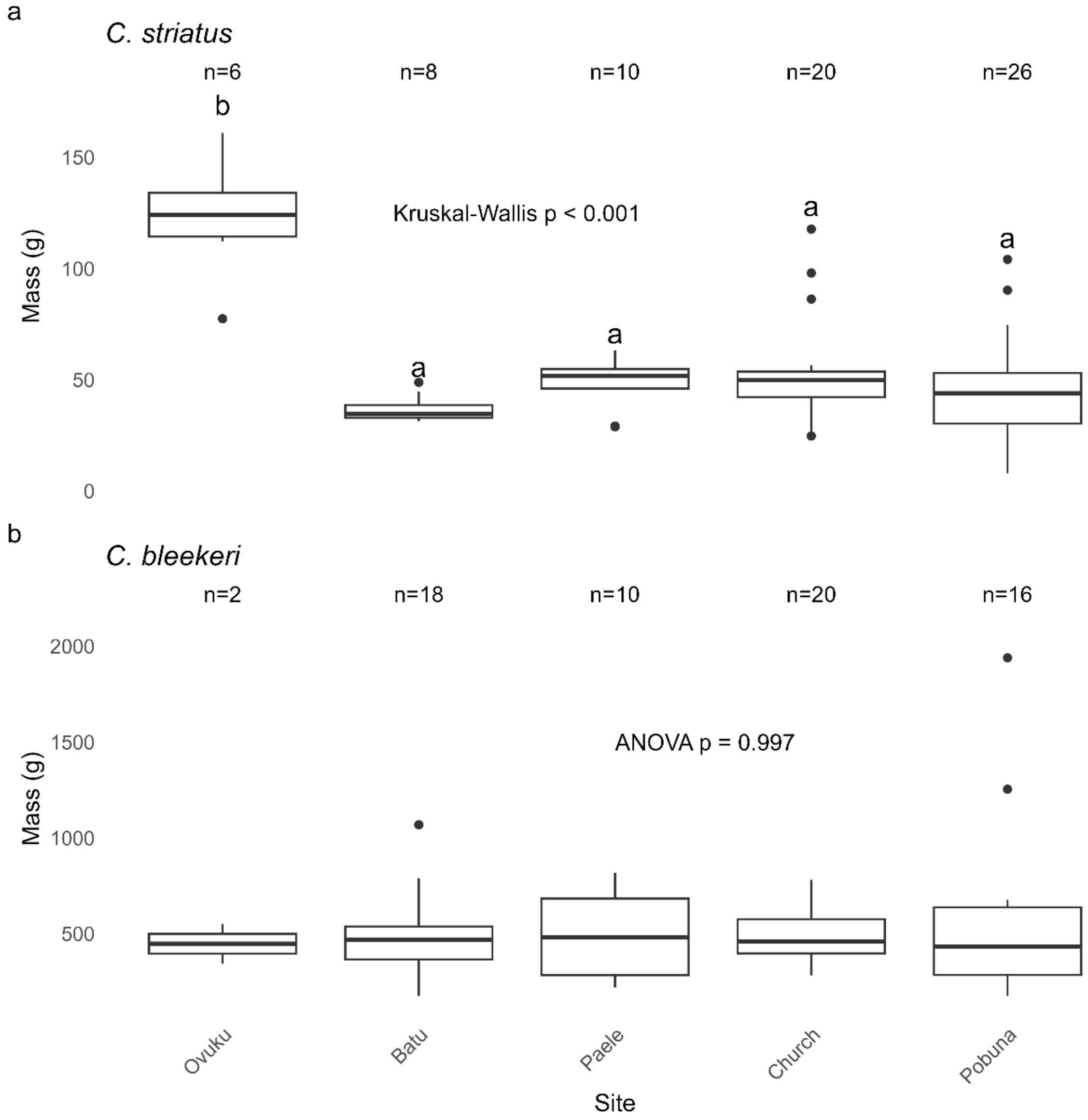

Figure 3.5.1

Site comparisons of mass in (a) *C. striatus* and (b) *C. bleekeri*. Different letters above boxplots in plot (a) indicate statistically significant differences between sites ($p < 0.05$), based on Dunns post-hoc tests following a Kruskal-Wallis test. Kruskal-Wallis p-value is displayed for panel (a). Sample sizes (n) for each site are shown above the plots.

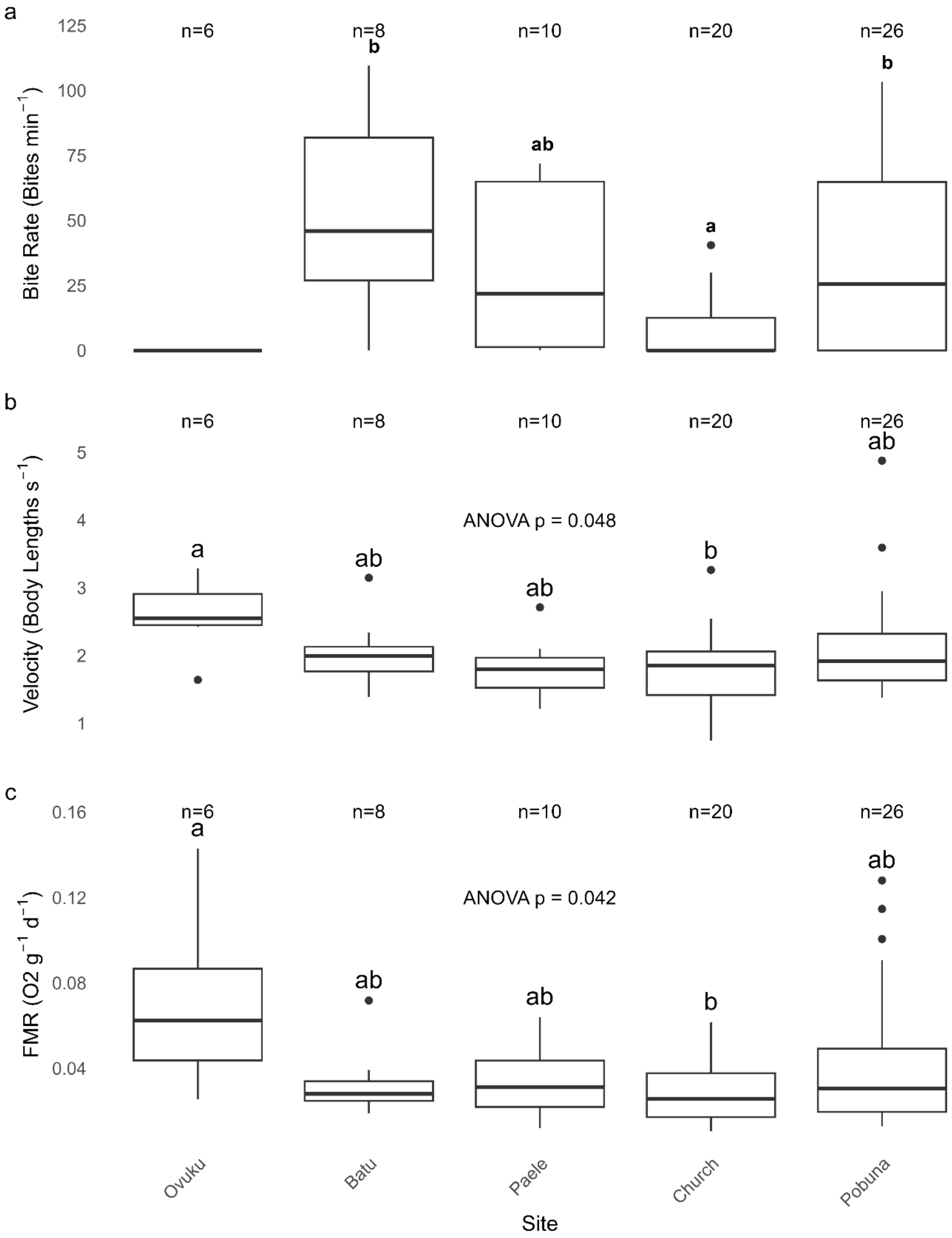

Figure 3.5.2

Site comparisons of (a) bite rate (bites min^{-1}), (b) swimming velocity (body lengths s^{-1}), and (c) field metabolic rate (FMR; O_2 g^{-1} d^{-1}) in *C. striatus*. Different letters above boxplots indicate statistically significant differences between sites ($p < 0.05$), based on a generalized linear model (GLM) for (a) and Tukey's HSD post-hoc tests following ANOVA for (b) and (c). ANOVA p-values are displayed for panels (b) and (c). Sample sizes (n) for each site are shown above the plots

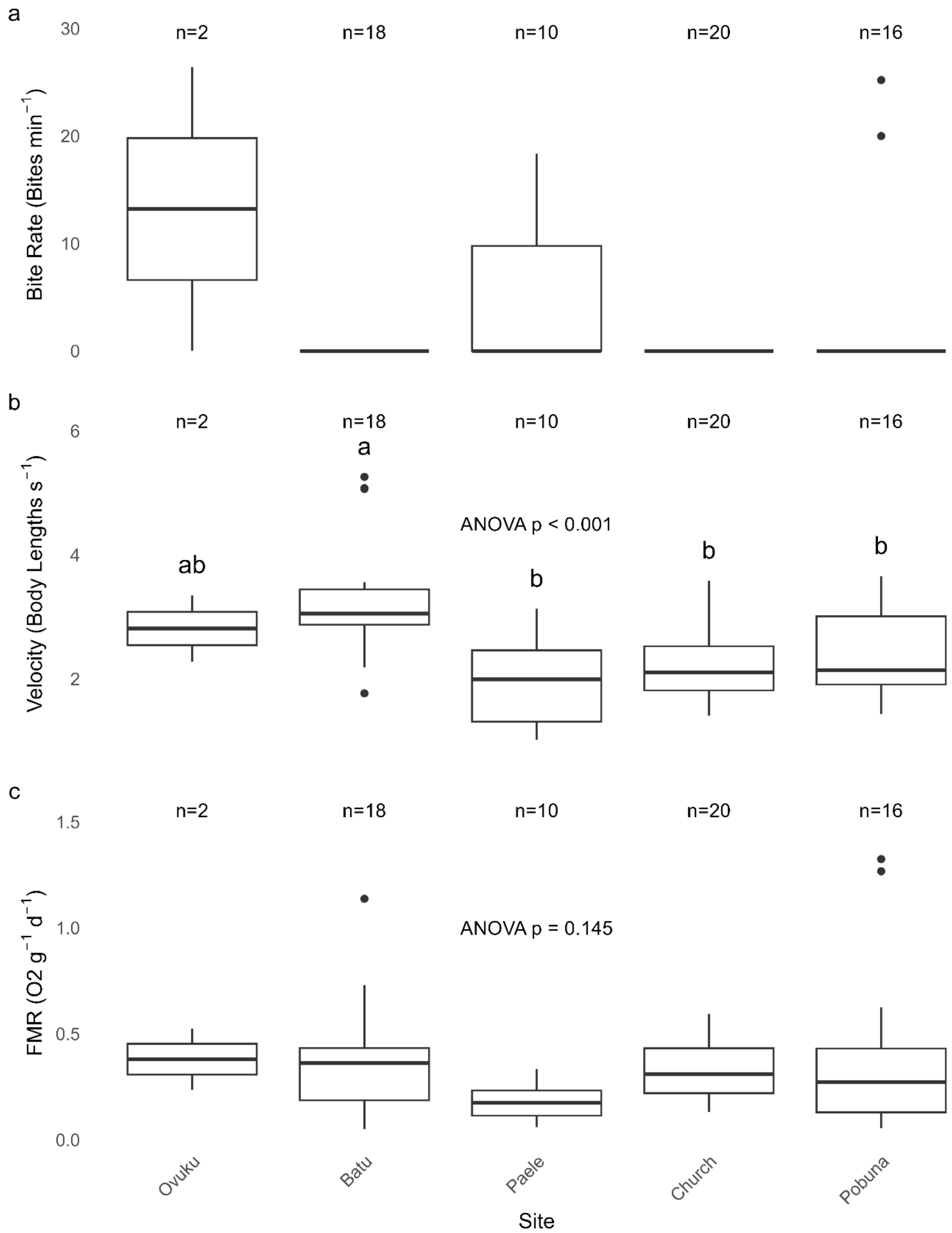

Figure 3.5.3

Site comparisons of (a) bite rate (bites min^{-1}), (b) swimming velocity (body lengths s^{-1}), and (c) field metabolic rate (FMR; O_2 g^{-1} d^{-1}) in *C. bleekeri*. Different letters above boxplots indicate statistically significant differences between sites ($p < 0.05$), based on Tukey's HSD post-hoc tests following ANOVA. ANOVA p-values are displayed for panels (b) and (c). Sample sizes (n) for each site are shown above the plots.

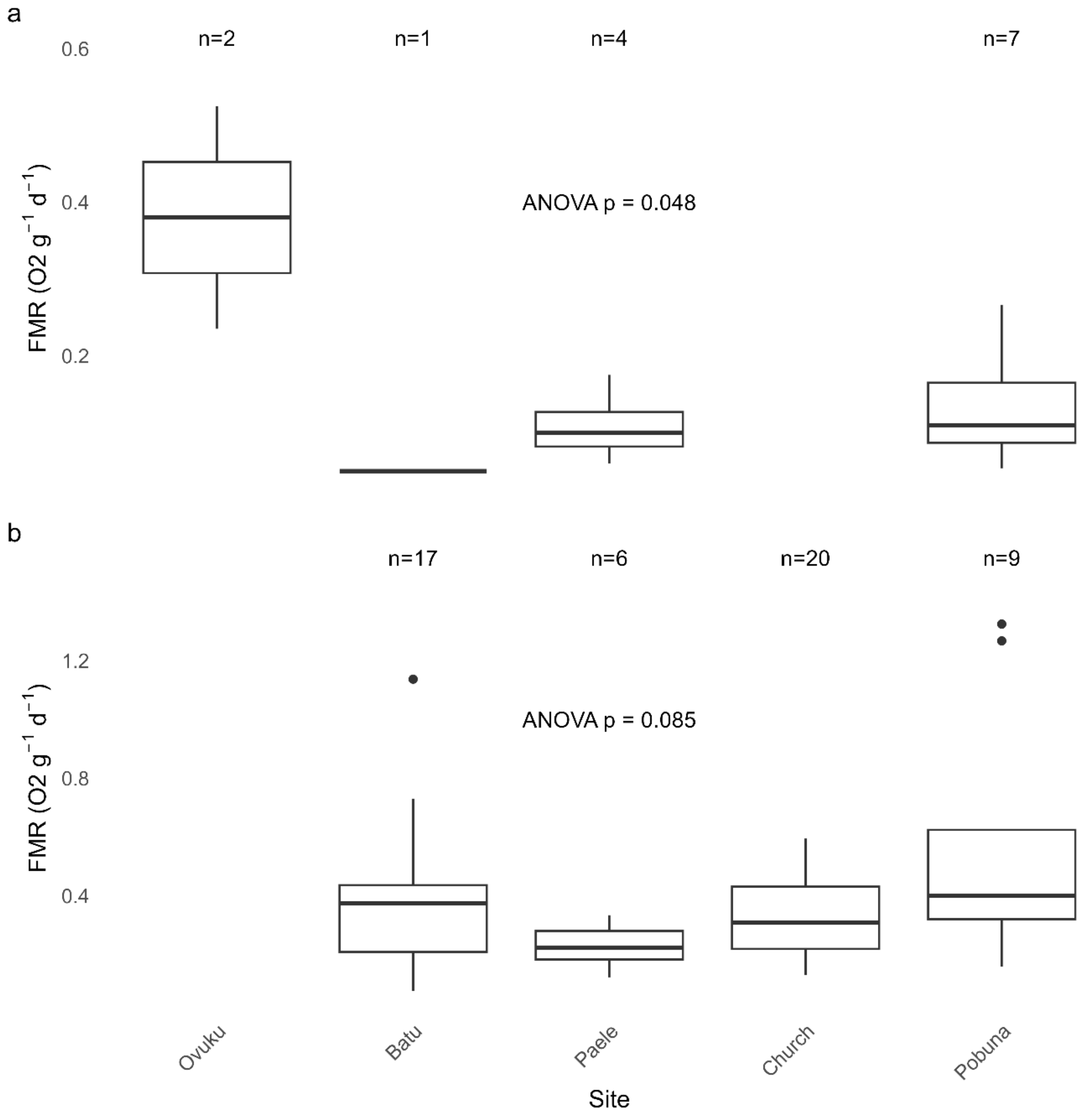

Figure 3.5.4

Site comparisons of FMR (O_2 g^{-1} d^{-1}) in *C. bleekeri* for (a) initial phase and (b) terminal phase. ANOVA p-values are displayed on plots. Sample sizes (n) for each site are shown above the plots.

4.0 Discussion

In this study, we aimed to analyse the in-situ effects of turbidity on the feeding behaviour and energy expenditure of two coral reef fish with contrasting feeding behaviours. This was made possible by the unique geography of Kolombangara Island, with nearly 80 rivers, the Island is host to naturally turbid reefs such as the Vavanga reef, which makes an ideal proxy for studying the effects of turbidity from anthropogenic land use changes. Sediment from the Vavanga River results in a natural turbidity gradient on this reef, allowing for the comparison of fish behaviour through stereo video along the turbidity gradient. The study species, *C. striatus* and *C. bleekeri*, display uniquely contrasting feeding mechanisms and behaviours. *C. striatus* is a generalist grazing detritivore which generally forms schools (Marshell & Mumby, 2012). Whereas *C. bleekeri* is a specialist excavator with distinct adult phases: initial-phase individuals are schooling, while terminal-phase individuals are exclusively solitary (Nicholson & Clements, 2023). The study of these strikingly ecologically distinct species allows us to determine how these different ecological strategies are individually impacted by turbidity and perhaps determine how species of different ecological niches could be used as early warning signals for environmental degradation.

4.1 Environment of the Vavanga Reef

Our measurements of turbidity proxies indicated that there was a steep and significant turbidity gradient sequentially along our study sites. With Ovuku (site closest to the Vavanga River) having the lowest visibility at 9.5 meters, and Church (second farthest from the Vavanga River) having the highest visibility at 25.2 meters (Figure 3.1.1). The same trend is seen in the Forel-Ule measurements, with Ovuku having the highest measurement at 6.43, while Church was lowest at 1.67 (Figure 3.1.2). Visibility increased sharply and Forel-ule decreased sharply after Ovuku, indicating that this site received by far the most intense sedimentation. While the turbidity gradient is still visually evident from Batu to Paele to Church, these sites are not statistically significantly different in visibility (Figure 3.1.1). Though, Church is significantly lower in Forel-Ule than Batu and Paele. This indicates a somewhat localised effect of turbidity which is by far the most intense at Ovuku and gradually dissipates across the rest of the reef. This is concordant with other research that the sediment loads from small rivers may be localised but very high where present (Minton et al., 2022). Pobuna (the furthest site from the Vavanga River) was an exception to this otherwise consistent turbidity gradient as it had slightly lower visibility and slightly higher Forel-Ule, though neither of these metrics were statistically different from Church. It is possible that Pobuna was in close enough proximity to the next river to be receiving some level of sedimentation. There was also a strong linear relationship between Forel-Ule (a qualitative measurement based on colour) and visibility, indicating that both metrics were likely good proxies for turbidity.

Substrate diversity (substrates classified in this study are: Acropora spp., dead coral, Diploastrea spp., epilithic algal matrix (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., and zooanthids.) increased along the turbidity gradient. With Ovuku – the most turbid site - having only 5 substrates, and Pobuna having the most at 14 (Figure 3.1.4). Dead coral cover showed the opposite trend to this, averaging 68.3% at Ovuku and only 30.8% at Pobuna (Figure 3.1.8). These trends are unsurprising considering the strong evidence of the deleterious effects of excess turbidity and thus sedimentation on sessile marine life. Varying levels of sedimentation affect coral at the settlement, larval, and adult phases (Zweifler et al., 2021). Settling coral can be particularly sensitive to turbidity and sedimentation as layering of sediments on solid substrates can prevent settlement (Ricardo et al., 2021). Adult coral, while less vulnerable to sedimentation, can still experience mortality when persistent or high levels of exposure occur (Jones et al., 2019). The light attenuating effects of turbidity also play a role in coral mortality and it has been found that the interaction between light reduction and suspended sediments results in increased coral mortality, as opposed to suspended sediments alone (Bessell-Browne et al., 2017). Importantly Jones et al. (2021) shows that high levels of suspended sediments decrease light in a biologically meaningful way, attenuating blue light and shifting the spectrum to the less photosynthetically active green-yellow waveband around 575 nm.

EAM cover increased steadily along the turbidity gradient with Ovuku having 0% EAM cover and this rose steadily to 25.8% cover at Pobuna (Figure 3.1.6). EAM cover also had a relatively strong but non-linear correlation with visibility; locations with higher visibility tended to have higher EAM cover. However, some sites with the very high visibility had no EAM cover (Figure 3.1.7). This could potentially be due to difficulties in EAM classification on GoPro footage, as EAM mats can appear cryptic against the mats of different benthic organisms. Alternatively, patches of EAM mats may have been completely removed by intense grazing in some of the less turbid areas. The trend seen here of EAM abundance decreasing with turbidity may seem contradictory as often higher algal abundances are associated with reef degradation (McManus & Polsenberg, 2004). However, while high abundances of fleshy macroalgae are indeed considered a symptom of reef degradation, EAM is an integral source of primary productivity in healthy coral reefs and is often the dominant substrate (Diaz-Pulido et al., 2009; Tebbett & Bellwood, 2021). Many large fleshy macroalgae are apparently extremely tolerant of sedimentation—in some cases even increasing in growth rate with excess sedimentation—and may grow to several meters high, negating the effects of turbidity and its light attenuating effects (Grier et al., 2025; Shepherd et al., 2009). Most species of turfing algae are very small (generally < 2 cm) and hold together the matrix of sediment and microfauna which compose the EAM (Airoldi, 1998; Connell et al., 2014). It is quite possible that chronically high sediment loads would simply smother these short algae and starve them of light, resulting in loss of EAM beds in the more turbid sites. It may also be a factor that detritivores such as *C. striatus* preferentially feed on EAM in more turbid areas, as there is more detritus for them to sift, damaging the algal mats, though this will be discussed further in the next chapter.

4.2 Foraging preferences

4.2.1 *C. striatus*

C. striatus was recorded feeding very frequently, with 52.9% of individuals being recorded taking at least one bite over the short ~10 second sampling durations. This is likely because *C. striatus* is functionally a grazing detritivore, with many studies confirming that the gut contents of *C. striatus* usually consist almost entirely of detritus (Marshell & Mumby, 2012; Tebbett et al., 2017a). This observation is in accordance with many studies showing that detritivores have high feeding rates and gut throughput times, with Polunin et al. (1995) finding that *C. striatus* had a gut turnover rate of 5.5 d^{-1} and a bite rate of 12633 d^{-1} (Goatley & Bellwood, 2010). The high rate of consumption seen in detritivores can be attributed to the relatively low nutritional content of detritus which is comparable to algae, requiring large volumes to be consumed frequently to meet nutritional and caloric requirements (Crossman et al., 2001).

C. striatus fed almost exclusively on EAM surfaces at each site, though a small number of bites were recorded on dead coral at Paele and Pobuna (Figure 3.2.2 a). This indicates that *C. striatus* rarely if ever deviates from its preferred feeding substrate of EAM and is likely an obligate detritivore specialising in sifting detritus from EAM as many other studies confirm (Marshell & Mumby, 2012; Tebbett et al., 2017a; Tebbett, Goatley, et al., 2018). Manly's preference ratio for EAM was consistently high at each site (other than Ovuku where no feeding was recorded) and increased consistently towards the Vavanga River mouth (Figure 3.2.3 a). This follows an inverse pattern to EAM abundance in our study, as it was found that EAM cover decreased consistently towards the Vavanga River mouth. This should not be misconstrued as an indication that *C. striatus* prefers EAM more the closer it gets to the river mouth, as Manly's preference ratio is a simple calculation which only indicates how much an animal is using a resource in relation to the abundance of the resource. As *C. striatus* fed almost exclusively on EAM at each site, it indicates that selectivity for EAM remains extremely high even when apparent EAM abundance is very low. Another indicator that *C. striatus* is likely an obligate EAM sifting detritivore.

In the most turbid site (Ovuku) no fish were observed feeding (Figure 3.2.1). This is likely due to the extremely high sediment load at this site causing an apparent absence of EAM here (the preferred feeding substrate of *C. striatus*). While it is possible that some EAM may exist here, any existing EAM is likely saturated with so much inorganic terrigenous sediment that it is no longer a viable feeding substrate, as *C. striatus* requires organic detritus rather than inorganic sediments as a food source (Polunin et al., 1995; Tebbett et al., 2017a). Indeed, it has been shown experimentally that *C. striatus* takes less bites and rejects bites more frequently in EAM which has been saturated by fine sediments and river sediments (Tebbett et al., 2017b). Interestingly, the percentage of fish feeding was highest at the second most turbid site (Batu), with 87.5% of fish feeding (Figure 3.2.1). The percentage of fish feeding then decreases with distance from the Vavanga River mouth, dropping to 30% at Church (the least turbid site) before increasing again to 65.38% at Pobuna which is somewhat more turbid (Figure 3.2.1). These observations suggest that feeding rates in *C. striatus* are positively related to turbidity and that it may in fact feed preferentially in somewhat turbid locations, up to a point where sediment loads become too high and feeding ceases completely. An explanation for this could be that the increased eutrophication in the moderately turbid sites caused increased primary productivity and thus more organic rich detritus for *C. striatus* to feed on. Iron is a photosynthetically limiting nutrient in clean sea water, however, it has been found that sediments on reef surfaces contain significantly higher iron concentrations than sea water (Entsch et al., 1983). Thus, it is possible that the amounts of sediment deposited at the moderately turbid sites enrich the EAM with iron (and probably other nutrients) sufficiently to cause higher growth rates of the microbes living within the EAM, resulting in higher protein concentrations in the detritus which *C. striatus* may prefer. Goatley and Bellwood (2010) analysed sediment removal and transport by *C. striatus* on Lizard Island in the Great Barrier Reef and found that *C. striatus* primarily feeds on the shallower upper reef crest and primarily defecates in the deeper lower reef crest. This is consistent with our results where the sites with the two highest ratios of fish feeding (Batu and Paele) were both relatively shallow on average at 3.2 metres and 5.2 metres respectively, while the site with the lowest ratio of fish feeding (Church) was relatively deep at 6.1 metres. An exception to this is Pobuna which averages 6.6 metres and 65.38% of the fish were feeding. Interestingly, several studies suggest that sediment within the EAM is lowest on reef crests compared to other areas of the reef (Harper et al., 2015; Purcell, 2000). This contrasts with our findings that *C. striatus* preferentially feeds in areas of higher turbidity, and thus likely areas of higher sediment. Though, as no direct sediment measurements were taken in our study it cannot be confirmed that the areas of high feeding rates had higher levels of sediment. It could also be that *C. striatus* simply feeds on shallow reef crests regardless of sediment levels.

4.2.2 *C. bleekeri*

C. bleekeri was recorded feeding very infrequently in comparison to *C. striatus*, with only 10.6% of fish being recorded feeding. Though 50% of fish were recorded feeding at Ovuku, this observation was based on only two initial phase individuals. The site where the most fish were recorded feeding was Paele, where 40% of individuals were feeding, Batu and Church had no feeding activity, and only 12.5 % of fish were recorded feeding at Pobuna (Figure 3.2.1 b). *C. bleekeri* was recorded feeding on a more varied range of substrates than *C. striatus*, feeding on coral rubble at Ovuku, predominantly on dead coral at Paele, and only on EAM at Pobuna (Figure 3.2.2 b). Manly's preference ratio for both

EAM and dead coral was > 1 at Paele, and > 1 for EAM at Pobuna, indicating that it fed somewhat selectively on these substrates at these sites, though all ratios were < 4, which indicates that it was not particularly selective for any substrate (Figure 3.2.3 b). This contrasts with *C. striatus* which had extremely high ratios (> 5) at several sites. The results stated above show that no real trends are obvious in the feeding behaviour of *C. bleekeri*, and very little can be inferred about its feeding responses to turbidity and site level differences in habitat composition. However, the fact that *C. bleekeri* was recorded feeding so little and seemingly at random potentially hints at the unique ecology and dietary specialisation of this species.

C. bleekeri—as with most other *Chlorurus* species—is functionally classed as an excavator. Excavators possess highly modified and robust jaw morphologies, including fused beak-like mandibles, robust pharyngeal jaws, and large adductor mandibulae muscles. They use these specialised jaws to gouge out chunks of the substratum in order to ingest both epilithic and endolithic organisms (Hoey, 2018). Interestingly, excavators are often found to have relatively high feeding rates, with bite rates comparable to—but often somewhat lower than—those of other feeding functional groups such as scrapers and grazers (Lange et al., 2020; Ong & Holland, 2010; Yarlett et al., 2018). In fact, Bellwood and Choat (1990) found that *C. bleekeri* had a bite rate of 15.6 bites min^{-1}, which is comparable to bite rates of *C. striatus* recorded by Goatley and Bellwood (2010), which were 15.4 and 21.2 bites min^{-1} at two different sites. Initially, these results appear contradictory to the findings in this study which suggest that *C. bleekeri* feeds much less than *C. striatus.* However, Bellwood and Choat (1990) observed that *C. bleekeri*, among other parrotfish species, engage in short feeding forays of ~5 bites which were “interspersed with relatively long periods of social interaction and movement”. Thus, they concluded that a 3-minute minimum observation time (with observations up to 16 minutes) was required to record sufficient feeding behaviour. Our study only recorded short ~10 second observations due to the time-consuming nature of manual 3D video analysis. These short recording times were likely not sufficient to capture the brief feeding forays of *C. bleekeri*, and as a result, fish were rarely recorded feeding. Additionally, many parrotfish (though not *C. bleekeri* specifically) have been shown to exhibit daily bimodal feeding patterns, with one peak in feeding activity around 11:00 h and one larger peak between 15:00 and 16:00 h (Yarlett et al., 2018). It is possible that many of the videos recorded for this study did not coincide with the daily feeding peaks of *C. bleekeri*. Interestingly, at Paele—the site where the most fish were recorded feeding (4/10)—all video samples were taken in the late afternoon (14:30 – 16:57 h). While at the sites where no feeding was recorded (Batu and Church), all video samples in which *C. bleekeri* was recorded were taken in the morning between 9:08 h and 12:06 h.

Our observation that *C. bleekeri* feeds seemingly at random on a variety of substrates including EAM, dead coral, and unconsolidated coral rubble suggests that *C. bleekeri* is a generalist feeder. This is consistent with many other observational studies indicating that excavating parrotfish are generalist herbivores which indiscriminately take bites out of the reef surface in order to ingest endolithic algae, EAM, and detritus (Bruggemann, 1995; Carlson et al., 2017; El Rahimi et al., 2021). Additionally, the gut contents of these species usually consist visually of calcareous particles and unidentifiable organic matter, making it difficult to identify any unique dietary components which might point towards specialisation (Choat et al., 2002). However, analysis of short chain fatty acid (SCFA) composition of gut contents, detailed morphometric trait analysis, and more recently microhistology and rRNA analysis of bite cores (substrate samples taken from directly around a parrotfish bite), all point to parrotfish being highly specialised microphages with a great degree of niche partitioning between species (Clements, 2017; Nicholson & Clements, 2021, 2023).

One of the first lines of evidence that *C. bleekeri,* along with many other parrotfish, are not simply generalist herbivores came from chemical analysis of gut contents (Choat et al., 2002). High levels of SCFA in the gut—particularly the hindgut—generally indicate fermentation of carbohydrate-rich plant or algal matter and are thus found in high levels in herbivorous animals (Mountfort et al., 2002; Stevens & Hume. ID, 1995). SCFA concentrations are generally found in comparatively low levels in the gut contents of animals with protein rich, low carbohydrate diets, instead relatively high concentrations of isovalerate—a catabolite of the highly abundant amino acid leucine—are found in the guts of these animals, indicating either carnivory or consumption of bacteria, which are both protein rich food sources (Choat & Clements, 1998). Choat et al. (2002) showed that, in addition to containing no notable algal material in the gut, the excavating *Chlorurus microrhinos* and *Chlorurus sordidus* (which have nearly identical feeding habits to *C. bleekeri*) had extremely low levels of SCFA in the gut but extremely high levels of isovalerate, indicating their diets are likely high in bacteria and perhaps even meiofauna (Nicholson & Clements, 2021). Furthermore, Clements and Choat (2018) also show that several parrotfish species contain high foregut content protein concentrations (16.8 – 44.9%) and low carbohydrate concentrations (4.0 – 4.6%) when compared to known herbivorous fish species, which had gut protein concentrations of (7.7 – 11.0%) and high carbohydrate concentrations of (28.8 – 42.1%).

The fact that excavating parrotfish remove parts of the substratum indicates that they must be obtaining important endolithic resources from the calcareous material that they ingest. As classical optimal foraging theory predicts, this energy consuming activity would be otherwise deleterious if no benefit was obtained from it (Pyke, 2019). The most recent research suggests that, rather than epilithic algae, parrotfish are specialist consumers of endolithic micro-autotrophs, particularly cyanobacteria (Clements, 2017). One of the first lines of evidence to support this was fatty acid analysis of fish tissue, as fatty acids generally represent the diet of an animal (Kelly & Scheibling, 2012). Piché et al., (2010) homogenised whole fish in a blender to analyse the general fatty acid composition of several different reef fish, the 15 fatty acids chosen for analysis were then analysed with discriminant function analysis. It was found that the analysis placed parrotfish in an entirely different grouping to all other feeding functional groups, even those which would consume considerable levels of micro-autotrophs living in EAM (Piché et al., 2010).

Stable isotope analysis also points towards parrotfish being consumers of cyanobacteria, as they generally show a depleted δ15N signature in comparison to other fish (Clements, 2017). Cyanobacteria are nitrogen fixing organisms and the δ15N isotope of nitrogen produced by them is low (-2% in comparison to normal atmosphere), while the δ15N content of various algae is generally 8-10% more than atmospheric (Dailer et al., 2010; Karlson et al., 2014; Viana & Bode, 2015).

Recent bite core analysis provides some of the most convincing evidence pointing towards parrotfish as specialist consumers of endolithic cyanobacteria and perhaps other endolithic organisms. Bite cores are pieces of the substratum which have been physically drilled out of the substratum with a hole-saw, allowing a chunk of substratum containing a parrotfish bite to be removed for later study (Nicholson & Clements, 2021). Nicholson and Clements (2023) analysed bite core samples from the excavators *C. bleekeri*, *Cetoscarus ocellatus,* and *Chlorurus microrhinos,* as well as the scrapers *Scarus altipinnis, Scarus globiceps*, and *Scarus oviceps.* They used a combination of techniques including visual inspection of the substratum benthos directly around the bite, scrapes from the bite to identify endolithic filamentous cyanobacteria density, and 16S and 18S rRNA sequencing of the scrape samples to identify endolithic taxa. It was found that there was a great deal of variation in all of these metrics between the bite cores of these species, indicating a high level of specialisation and fine-scale niche partitioning. Some species greatly preferred surfaces covered in cyanobacterial tufts, while others completely avoided these. Some species also were either highly preferential or highly avoidant of surfaces covered in crustose coralline algae (CCA). *C. bleekeri* almost completely avoided biting on surface cyanobacterial tufts, and almost always bit on surfaces covered in CCA on heavily bioeroded substrates. There was also a great deal of variation in preference for endolithic cyanobacterial filament, boring algae, and other taxa such as sponges. *C. bleekeri* tended to bite on surfaces with relatively low filamentous cyanobacterial densities and low sponge densities, though it bit on surfaces with the highest taxon richness of any of the other fish species. It also tended to bite on surfaces with much higher algal turf height compared to the other species and appeared to prefer substratum containing the boring microalgae *Ostreobium,* which often forms dense layers under CCA, perhaps also explaining the preference of *C. bleekeri* for CCA-covered substrates (Nicholson & Clements, 2023; Tribollet & Payri, 2001). All together this points to *C. bleekeri* being a highly specialised excavator of relatively mature substrates that have had time to develop sufficient CCA and a highly diverse endolithic biota. This also may explain why it was rarely observed feeding in this study, as it is on the search for very specific substrates on which to feed. Additionally, the apparent high protein content of their diet may allow for their long periods of non-feeding activity which were evident in our footage.

Terminal phase individuals fed at a much lower rate than initial phase individuals, with only 7.7% of fish being recorded feeding, compared to 21.43% of initial phase fish recorded feeding. Additionally, the sites where no feeding was recorded (Batu and Church) were dominated by terminal phase fish. One reason for this could simply be the allometric relationship between body size and metabolic rate, as terminal phase fish are older and almost always larger than initial phase fish. As an animals mass increases its mass specific metabolic rate decreases, thus requiring a lower ratio of food intake for its mass than a smaller animal (Clarke & Johnston, 1999). A larger fish is therefore more metabolically efficient; however, it still has a higher overall metabolic rate and requires more food than a smaller fish. For example in the walleye (*Stizostedion vitreum*), the rate of food intake increases from ~4 g d^{-1} at 2 years of age to ~13 g d^{-1} at 8 years of age (Nagy, 2005; Trudel et al., 2000). The same trend has been shown in multiple parrotfish species with rates of scraped area (cm^2 min^{-1}) increasing exponentially with body length (Lokrantz et al., 2008). However, this size dependent increase in dietary intake appears to be accompanied by an exponential increase in bite area in parrotfish; put simply, larger fish require more food but take substantially bigger bites, and this combined with their lower mass-specific metabolic rate perhaps results in the need to feed less frequently (Hoey, 2018). Hoey (2018) explicitly showed that bite area increases exponentially with length in several species of parrotfish, but bite rate (bites min^{-1}) decreases with length in all but one species. This trend of feeding frequency decreasing with body size has been documented in numerous other species (Choat & Clements, 1993; Nunes et al., 2021).

The other possible explanation for reduced feeding rates in terminal phase individuals is that they are spending more time on territory defence and potentially searching for breeding partners, as some parrotfish species are known to breed year round (Abu-Taweel et al., 2023; Clifton, 1995). Terminal phase *C. bleekeri* were recorded displaying aggression toward other conspecifics in our study, indicating that *C. bleekeri* is a territorial species, at least in its terminal phase. Numerous studies have documented the territorial behaviour of terminal phase parrotfish (though none specifically for *C. bleekeri*) (Buckman & Ogden, 1973; Manning & McCoy, 2023; Welsh & Bellwood, 2012). Tracking of GPS tagged terminal phase fish indicates that they have home ranges that do not overlap, indicating a high degree of territoriality (Manning & McCoy, 2023). Mumby and Wabnitz (2002) noted that aggression events were observed frequently in 5 Caribbean parrotfish species, and ~90% of aggression events were intraspecific and almost always involved the fish chasing the invading fish from its territory. The GPS tracking of the 5 parrotfish species by Manning and McCoy (2023) and acoustic telemetry tracking of *Chlorurus microrhinos* by Welsh and Bellwood (2012) showed that parrotfish tend to have territories that are in very close proximity and often border on each other. This would likely create an almost constant requirement for territorial defence, leaving little time for feeding. Thus, it is likely that feeding is done in very brief forays with long bouts of territorial patrol.

4.3 Corelations between fish traits

4.3.1 *C. striatus*

Velocity was positively correlated with mass, as would be expected (Figure 3.2.1). The low slope and low R^2 value of the regression show that the relationship is relatively weak and does not suggest that there is any meaningful ecological process driving this relationship; rather, the larger fins of larger fish simply allow for more propulsion and faster swimming speeds (Wainwright et al., 2002). Smaller fish of around 50 g appeared to feed more frequently, with many of the larger fish > 75 g not observed feeding at all (Figure 3.2.2). As stated in the above section, this could be due to the lower mass-specific metabolic rate of larger individuals, meaning they need to feed less frequently, and additionally allocate more of their time and energy to reproductive or territorial activities than to foraging (Clarke & Johnston, 1999; Wootton, 1985). *C. striatus* is known to be weakly territorial, and it is likely that larger breeding fish would be more territorial and therefore spend less time foraging (Marshell & Mumby, 2012)

4.3.2 *C. bleekeri*

Velocity also had a relatively weak positive relationship with mass, as in *C. striatus*, and very likely for the same reason, larger fish have more fin area for propulsion (Figure 3.2.3) (Wainwright et al., 2002). Bite rate appeared to increase with bite distance (Figure 3.2.4). This seems counterintuitive, as higher bite rates should produce shorter bite distances; however, the fact that *C. bleekeri* has been observed to have brief feeding forays followed by periods of non-foraging activity can likely explain this (Bellwood & Choat, 1990). An overall high bite rate could be observed if a fish was recorded making a foray and travelling some distance before making another foray, leading to a high mean bite distance. This could also potentially explain why bite rate appeared to increase with velocity; fish making multiple forays in one observation would increase the average recorded velocity while moving between feeding locations while also producing a high average bite rate (Figure 3.2.4). While these results were statistically significant, it is important to note that the bite rate data for *C. bleekeri* were based off only 7 observations and thus may not capture the true nature of the fish's feeding behaviour in these cases.

4.4 Effects of visibility and Forel-Ule

4.4.1 *C. striatus*

Different fish species show varied swimming responses to turbidity, and several mechanisms may explain why fish might adjust their swimming velocity under reduced visibility (Rodrigues et al., 2023). For instance, fish may decrease swimming speed when it becomes more difficult to visually locate prey or foraging sites, as observed in the Picasso triggerfish (*Rhinecanthus aculeatus*) (Newport et al., 2021). Conversely, lake sturgeon increase mobility in turbid conditions, which

Wishingrad et al (2015) hypothesised allows them to forage more rapidly while remaining visually obscured from predators.

Gray et al. (2014) experimentally examined the effects of turbidity on five fish species and found that some increased swimming speed in turbid conditions, while others decreased it. They suggested that suspended sediments lodged in the gills of species with reduced swimming speeds impaired aerobic performance, thereby limiting swimming ability. Fish may also increase swimming velocity to locate more suitable habitat or to reduce predation risk when predators are more difficult to detect visually. Alternatively, they may decrease velocity if turbidity itself provides concealment from predators. However, apparently no direct evidence currently exists in the literature to support these latter hypotheses.

A review by Rodrigues et al. (2023) also shows that many fish have either negligible or no response to increases in turbidity, which is concordant with our observation that visibility had no apparent effect on velocity or FMR in *C. striatus* (Figure 3.3.1a; 3.3.2a). This is likely due to the fact that *C. striatus* is a geographically wide-ranging generalist detritivore that inhabits a variety of reef types, and is often abundant on degraded and naturally turbid reefs (Nelson & Wilkins, 1988; Tebbett et al., 2017b, 2020). *C. striatus* appears to be particularly resilient to degraded habitats and habitat disturbances. For example, Putra et al. (2025) studied fish population densities in a reef in Nias Island, Indonesia both before and after a large earthquake which caused substantial ecological destruction on the reef. Before the earthquake, other reef fish such as *Scarus rivulatus* were much more abundant than *C. striatus,* however, directly after the earthquake *C. striatus* was approximately twice as abundant as any other species and its population was only reduced by ~20%, while most other species' population densities were reduced by at least 50% (Putra et al., 2025). Other studies have also shown that *C. striatus* biomass and population density are negatively associated with high hard coral cover and positively associated with habitats with reduced coral cover and high short algal turf coverage—indicators of degraded or turbid reefs (Lin et al., 2021; Russ et al., 2018; Zweifler et al., 2021). The apparent preference of *C. striatus* to moderately degraded or turbid conditions makes sense in light of its role as a detritivore that predominantly subsists on detritus sifted from EAM, a pristine reef with high coral cover and low algal biomass would offer it little of its preferred resource. The ability of *C. striatus* to thrive in relatively degraded and turbid habitats also likely explains why bite distance was not significantly affected by visibility (Figure 3.3.3 a).

Despite visibility having no significant effect on velocity or FMR, these metrics had a significant positive association with Forel-Ule index, indicating that fish swam at higher velocities and expended more energy at higher Forel-Ule values (Figure 3.3.4a; Figure 3.3.5a). Forel-Ule index is a qualitative colour scale with 21 discrete colour classes ranging from indigo blue (1) to green (~10) to brown (21); higher values likely indicate eutrophication and/or turbidity (Ye & Sun, 2022). Almost all Forel-Ule index measurements in this study were < 6, indicating relatively blue water; however, one video sample from Ovuku had a Forel-Ule of 9, indicating green water (Figure 3.1.2). A group of *C. striatus* in this video sample appeared to be swimming at a much higher average velocity than in all other video samples. This anomalously high Forel-Ule location may have contributed disproportionately to the significant effect observed on velocity and FMR.

As visibility is a continuous and quantitative variable, there was much more variation in visibility within sites and overlap between sites, while Forel-Ule is an ordinal index with discrete steps, which resulted in less within-site variation but greater categorical separation between sites. It is possible that these characteristics led to differences in velocity and FMR being more apparent when analysed as a function of Forel-Ule. Additionally, as Forel-Ule is colour-based it may capture aspects of habitat degradation that visibility does not. For example, low visibility only suggests suspended particulate matter in the water, while a moderately high Forel-Ule (green to yellow) is more suggestive of eutrophication (Liu et al., 2022). Eutrophication of reefs has long been known to cause excessive algal growth (Bell, 1992). Longer algal turfs trap sediments, which are less palatable to *C. striatus*, and it is known to avoid locations with longer algal turfs and macroalgae. Consequently, it is possible that they swim at higher velocities in eutrophic, high Forel-Ule waters in search of more favourable foraging grounds (Lin et al., 2021; Tebbett et al., 2017a; Tebbett & Bellwood, 2020).

Bite distance was found to decrease with depth, suggesting that *C. striatus* may feed more in deeper parts of the reef (Figure 3.3.7). This is inconsistent with the observational study by Goatley and Bellwood (2010) which analysed spatial feeding patterns and sediment transport in *C. striatus* and found that the fish primarily feed in the shallower upper reef crest. However, they also observed that *C. striatus* still feeds substantially on the lower reef crest (~ 6 metres), though to a lesser extent. Additionally, the association between depth and bite distance observed in this study was relatively weak and the effect was small, with bite distance decreasing by only 0.21 cm per metre of depth. The study by Goatley and Bellwood (2010) was also only conducted in two reef locations on Lizard Island in the Great Barrier Reef; it is possible that *C. striatus* has different spatial feeding patterns in different locations depending on levels of detritus, EAM, and sediments. In this case, it could be that the shallower areas of the reef accumulate fine inorganic sediments from the Vavanga River, creating less favourable feeding conditions (Tebbett et al., 2017b).

FMR had a positive relationship with EAM cover, indicating that fish expended more energy where EAM cover was higher (Figure 3.3.8). This may seem counterintuitive as EAM is the preferred foraging substrate of *C. striatus* (Figure 3.2.2 a) (Tebbett et al., 2017a). Thus, they might be expected to forage more in areas of high EAM cover, which would likely lead to slower average swimming velocities and reduced FMR. However, the fact that there was no statistically significant relationship between velocity and EAM cover indicates that the increase in FMR associated with EAM cover is not simply a function of velocity. FMR in this study is calculated from ODBA, a measure of activity that incorporates acceleration dynamically in the X, Y, and Z axes of a 3D space (Halsey et al., 2011). Therefore, ODBA estimates the energy expenditure of more complex movement patterns better than simple average velocity does. This could mean that fish may not have been swimming faster in areas of high EAM coverage, rather, they were expending more energy because of the erratic movement patterns involved in foraging. It was observed in this study that *C. striatus* would make quick back-and-forward lurches in order to take bites, likely an energy-consuming manoeuvre in comparison to normal swimming.

While foraging may be an energy consuming activity, increased foraging rates were not actually associated with EAM cover; in fact, the highest foraging rates were in sites with relatively low apparent EAM cover (Figure 3.1.6; Figure 3.2.1 a). It may be that areas of high EAM cover are not ideal foraging grounds for *C. striatus* on Vavanga Reef, possibly because the highest EAM covers were found in the most pristine (high visibility, low Forel-Ule index) areas of the reef which potentially have less detritus. Lin et al. (2021) observed that *C. striatus* displays a positive feeding response, increased biomass, and increased population density in moderately disturbed habitats. Furthermore, while the relationship was not statistically significant, *C. striatus* did show a positive association between velocity and EAM cover (Table 3.3.1; Table 3.3.2). Therefore, it could be that fish were swimming somewhat faster in these pristine, high EAM zones, as they were not foraging.

4.4.2 *C. bleekeri*

Visibility and Forel-Ule had no significant effect on velocity or FMR in *C. bleekeri* (Figure 3.3.1 b; Figure 3.3.2 b, c; Figure 3.3.4 b; Figure 3.3.5 b, c). One might expect *C. bleekeri* to show a stronger velocity/energy expenditure response to turbidity and habitat degradation than *C. striatus* given its apparent specialist feeding niche. However, while *C. bleekeri* may have a specialised diet, it is possible that it is more generalist in terms of its habitat use. *C. bleekeri* is highly abundant throughout the Indo-Pacific region and is found in a variety of habitats from shallow reef flats to deep reefs of ~30 metres, including relatively degraded low coral/high algal cover reefs (Mansyur et al., 2021; Tresnati et al., 2019). Furthermore, *C. bleekeri* is a roving species which potentially has very large home ranges (Plass-Johnson et al., 2018). The closely related *Chlorurus microrhinos* has been shown to have extremely large home ranges of up to 12,869 m^2 (Welsh & Bellwood, 2012). It may be that due to its wide habitat use and potentially large home range *C. bleekeri* is entirely accustomed to passing through low visibility and/or degraded habitats and does not accordingly adjust its velocity or energy expenditure. Furthermore, there is evidence to suggest that *C. bleekeri* populations are able to persist in degraded habitats and are possibly capable of dietary plasticity in response to such habitat changes (Plass-Johnson et al., 2018).

Plass-Johnson et al., (2018) analysed $\delta^{15}N$ and $\delta^{13}C$ stable isotope ratios in muscle tissue of *C. bleekeri* captured from a variety of reef habitats in the Spermonde Archipelago, ranging from degraded algal dominated habitats with ~8% live coral cover and ~36% coral rubble, to pristine reefs dominated by live coral (~36% cover). *C. bleekeri* was found to have a much wider range of $\delta^{15}N$ and $\delta^{13}C$ ratios between sites than the other species studied (*Dischistodus prosopotaenia*), indicating greater dietary plasticity and wider trophic range. The muscle tissue $\delta^{15}N$ and $\delta^{13}C$ ratios were found to be significantly correlated with coral rubble cover; the range of $\delta^{15}N$ values being much wider and the range of $\delta^{13}C$ much lower at high coral rubble locations. Plass-Johnson et al. (2018) hypothesise that this indicates food source diversity is lower in high coral rubble locations, and thus *C. bleekeri* begins to feed across a wider trophic range to compensate.

Despite the potential dietary plasticity of *C. bleekeri,* we observed that bite distance had a strong negative relationship with visibility and a strong positive relationship with Forel-Ule (Figure 3.3.3 b; Figure 3.3.6 b). These results were likely disproportionately affected by one initial phase individual that was observed taking two spatially distant bites on coral rubble in Ovuku, where visibility was ~10 metres. All other *C. bleekeri* bites were observed in locations with visibility >25 metres (Figure 3.3.3). These observations are consistent with the study by Plass-Johnson et al. (2018), indicating that *C. bleekeri* is capable of dietary plasticity and will feed on different substrates when its preferred resources are not available. However, bite distance was lowest, and more bites were taken in relatively non-turbid areas of the reef in our study, indicating that *C. bleekeri* has preferred resources which reside in these areas of the reef—possibly CCA and EAM covered substratum containing *Ostreobium*—and may engage in more specialist feeding where these resources are available (Nicholson & Clements, 2023; Tribollet & Payri, 2001).

The initial phase individual mentioned above is also likely the reason why a significant negative relationship was found between bite distance and EAM cover (Figure 3.3.9). As no EAM was found in the sample in which this fish was recorded. Though, this further highlights the potential dietary plasticity of *C. bleekeri*, given that Nicholson and Clements (2023) found that *C. bleekeri* preferred substrates with longer EAM.

Phases showed differing FMR responses to the turbidity proxies, with initial phase showing a strong negative relationship with visibility and a positive relationship with Forel-Ule, while terminal phase appeared to have no relationship (Figure 3.3.2 b, c; Figure 3.3.5 b, c). Again, this observation was likely disproportionately affected by the two initial phase individuals at Ovuku, one of which had an unusually high FMR. The sample in which these fish were recorded had a visibility of 10 metres, while no terminal phase individuals were recorded below a visibility of 16.4 metres. It may be that there is a turbidity threshold somewhere in this range which triggers a response to relocate—for example, to more suitable foraging grounds—thus increasing energy expenditure. Furthermore, terminal phase individuals may not enter the highly turbid areas as they have established home ranges in areas where more suitable foraging substrates are present.

Terminal phase had a significantly higher FMR than initial phase across all visibilities and levels of Forel-Ule (Figure 3.3.2 b, c; Figure 3.3.5 b, c). This was not due to terminal phase individuals simply swimming faster, as relative velocity (body lengths s^{-1}) was not significantly higher. This could be explained by the territorial nature of terminal phase individuals and may reflect the energetic cost of territory maintenance. Terminal phase parrotfish are known to be highly territorial and frequently chase off conspecifics (Manning & McCoy, 2023; Mumby & Wabnitz, 2002; Welsh & Bellwood, 2012). It may be that, while not necessarily swimming faster, terminal phase individuals move in a more erratic manner as a means of patrolling their territory or certain patches of favourable foraging substrate. Additionally, aggression events would be hugely energy consuming in comparison to normal swimming or foraging, and several aggression events were observed in this study between terminal phase individuals.

4.5 Site level analysis

4.5.1 *C. striatus*

The mean mass of *C. striatus* (54.3 g) was very similar between sites other than Ovuku, where mass was over twice the overall mean (122.5 g) (Figure 3.4.1 a). It is possible that this was the result of misidentification as the low visibility (~10 m) in Ovuku made visual identification of species more difficult. However, the other species which are present in the Solomon Islands and are potentially easily confused with *C. striatus* (*Acanthurus nigrofuscus, Ctenochaetus binotatus, Ctenochaetus cyanocheilus,* and *Ctenochaetus tominiensis*), all attain shorter maximum published lengths than *C. striatus,* making misidentification unlikely to be the cause of the disparity in mass between Ovuku and the other sites (Randall, 1956; Randall & Clements, 2001). It is more likely that this is a case of size segregated schooling, a phenomenon where fish tend to form schools of similar mass/length, which has been well documented in teleost fish in general (Hoare et al., 2000; Kasumyan & Pavlov, 2023; Ranta et al., 1992; Theodorakis, 1989). Though not specifically documented in *Ctenochaetus* species, size segregated schooling has been documented in relatively closely related *Acanthurus* species (Lawson et al., 1999). It is therefore possible that this was the result of a school of large individuals passing through Ovuku during the sampling period.

Bite rate decreased along the turbidity gradient from Batu to Church before increasing again at Pobuna, with Batu and Pobuna exhibiting significantly higher bite rates than Church (Figure 3.4.2a). This pattern is consistent with the proportion of fish recorded feeding, which was highest in Batu and lowest in Church (excluding Ovuku, where no feeding was observed) (Figure 3.2.1). However, these results appear somewhat contradictory to our finding that bite distance had no relationship with visibility or Forel–Ule index (Figure 3.3.3a; Figure 3.3.6a), although bite distance is only weakly correlated with bite rate (Figure 3.2.2).

It may be that feeding frequency is not directly influenced by visibility itself, but rather by changes in habitat composition associated with turbidity and sedimentation. Thus, trends in feeding rates may be better understood at the site level, as sites along the turbidity gradient differ markedly in benthic habitat composition. As discussed in the foraging preferences section, the decrease in bite rates along the turbidity gradient suggests that *C. striatus* may feed preferentially in areas of moderately high turbidity and/or eutrophication. This may reflect increased concentrations of photosynthetically limiting nutrients such as iron and nitrogen in these areas, which can elevate primary productivity, protein content, and consequently the palatability of the epilithic algal matrix (EAM) (Entsch et al., 1983).

Both velocity and FMR were significantly higher at Ovuku than at Church (Figure 3.4.2b; Figure 3.4.2c). However, neither velocity nor FMR increased steadily along the turbidity gradient. Instead, they remained relatively stable from Batu to Pobuna before increasing sharply at Ovuku, the most turbid site (Figure 3.4.2b; Figure 3.4.2c). This suggests that turbidity may exert a threshold effect on activity, where fish do not adjust their movement or metabolic expenditure until turbidity exceeds a certain level, at which point activity increases rapidly. This pattern aligns with the apparent threshold response observed in feeding behaviour of *C. striatus*. Fish fed relatively frequently across all sites except Ovuku, where no feeding was observed, possibly due to the apparent absence of EAM. The elevated velocity and FMR recorded at Ovuku may therefore reflect fish transiting through the area in search of more suitable foraging habitat rather than actively feeding.

Alternatively, this trend may be the result of increased turbidity reducing the reactive distance to visual signals. This has been shown to reduce foraging efficiency, as suitable food becomes more difficult to visually locate, though it has been shown to result in lower swimming speeds in the Picasso triggerfish while foraging (Newport et al., 2021). However, it is possible that where no suitable foraging sites are present, reduced reactive distance could trigger an increase in velocity and thus FMR as fish move to locate more suitable foraging areas, although there is currently no direct evidence of this mechanism in the literature. Another possibility is that fish increase velocity under turbid conditions as a predator-avoidance response, as their reactive distance to predators would also be reduced. However, there is also no direct evidence of this in the literature, and a meta-review found that across fish species there is no consistent effect of turbidity on activity levels (Rodrigues et al., 2023).

Interestingly, both velocity and FMR were slightly lower at Church than at the other feeding-active sites. Given that Church had the second-lowest bite rate and proportion of feeding individuals, one might expect increased movement associated with searching for food. However, as noted previously, Church may serve as a defecation site, as it is relatively deep, and C. striatus has been observed to defecate primarily in deeper reef crest areas (Goatley & Bellwood, 2010). Thus, fish may have been conserving energy here as they were not engaging in active searching and foraging, which are often relatively energy intensive activities (Killen et al., 2023). Though not a closely related species, the bonefish (*Albula vulpes*) has been shown in situ to have lower rates of energy expenditure in deeper areas, as they tend not to forage in deeper areas (Brownscombe et al., 2017)

4.5.2 *C. bleekeri*

Overall, site had little effect on *C. bleekeri*, and no clear trends were apparent. This provides further evidence for the theory that *C. bleekeri* is a habitat generalist, as their behaviour remains relatively homogeneous across sites. The only significant site effect found in *C. bleekeri* was in velocity (body lengths s^{-1}), which was significantly higher at Batu than at Church, Paele, or Pobuna (Figure 3.4.3 b). There appears to be no particular trend along the turbidity gradient, as Batu is the second most turbid site. Therefore, this effect is likely not driven by turbidity. A possible explanation for this is that Batu had one of the highest ratios of terminal phase individuals (~95%). Terminal phase individuals swim at a higher velocity than initial phase individuals, but not at a higher velocity in body lengths s^{-1}, though this analysis was conducted across sites and did not individually examine velocity at each site. Additionally, Church, which was 100% terminal phase, did not have a particularly high mean velocity (body lengths s^{-1}). Thus, terminal phase individuals do not always swim at higher velocities. However, it is possible that the fish at Batu were engaging in different types of behaviour compared to those at Church and the other sites. Perhaps at Batu, the terminal phase individuals were engaging in more territorial disputes and patrolling territories more frequently than at the other sites. Indeed, terminal phase parrotfish have territories that they frequently patrol for other conspecifics, which they then aggressively chase out of their home ranges (Buckman & Ogden, 1973; Manning & McCoy, 2023; Mumby & Wabnitz, 2002). This could not be a case of diurnal patterns in feeding or behaviour, as all terminal phase samples taken at both Batu and Church were recorded either in the morning or midday. This result is also likely not due to differences in feeding behaviour between the two sites, as no fish were recorded feeding at either site.

When phases are analysed individually, there is a significant site effect on FMR in initial phase individuals, but not terminal phase individuals (Figure 3.4.4). Ovuku had by far the highest FMR in initial phase individuals. This is likely due to the two initial phase individuals that were swimming at unusually high velocities at Ovuku. This again could have been caused by several aforementioned mechanisms. Firstly, the fish may simply have been passing through and thus swimming faster because their preferred resources were either not present or were smothered in sediment. Secondly, it could be a case of reduced reactive distances to visual stimuli, making foraging less efficient and potentially causing fish to swim faster as a predator avoidance mechanism (Newport et al., 2021;

Rodrigues et al., 2023). However, as mentioned above, there is not enough evidence in the literature to conclusively explain why the fish in this study were swimming faster in highly turbid locations.

While no terminal phase individuals were found at Ovuku, it is possible that had they been recorded there, they would also have exhibited heightened velocities and FMR. However, it is unlikely that terminal phase individuals would be recorded here, as they maintain spatial territories and would be unlikely to establish a territory in a highly turbid, unfavourable location such as Ovuku. As parrotfish are highly selective specialist foragers, they would likely establish territories in locations where their preferred substrates are abundant. This may explain why Batu and Church consisted almost exclusively of terminal phase fish; perhaps Batu and Church had more ideal foraging substrates than the other sites. Indeed, terminal phase parrotfish have been shown to establish territories in close proximity to one another, forming clusters of territories, presumably where preferred resources are available (Manning & McCoy, 2023).

One possible explanation for the phase disparity between sites is that initial phase individuals feed on different resources to terminal phase individuals, or perhaps they are more generalised in this respect. There is some evidence for this in our study, as two initial phase individuals at Ovuku were recorded feeding on unconsolidated coral rubble, which appeared to be covered by long, sediment saturated algae strands. One study by Bonaldo et al. (2006) analysed foraging preferences of initial phase and terminal phase *Sparisoma* parrotfish in situ. They found that both phases generally fed on the same items, though there was often a great difference in utilization for some resources. For example, terminal phase *Sparisoma altum* had a bite rate of 32 bites min^{-1} on algal turfs over the duration of observation, while initial phase individuals had a bite rate of 386 bites min^{-1}, a more than tenfold increase. Initial phase individuals also had a bite rate of 20 bites min^{-1} on green macroalgae, while terminal phase individuals almost completely avoided it. This suggests that in some parrotfish species there is a degree of resource partitioning between terminal phases and initial phases. Unfortunately, there is no evidence in the literature to support this phenomenon in *C. bleekeri* or other *Chlorurus* species.

4.6 Conclusions and future directions

In this study, we examined the varying environmental conditions on the naturally turbid Vavanga Reef and linked them to the feeding behaviour and energy expenditure of two nominally herbivorous fish with contrasting functional groups. Through environmental analysis of the turbidity proxies visibility and Forel-Ule, it was found that fluvial inputs from the Vavanga River indeed resulted in a turbidity gradient along the reef. Furthermore, through substrate quadrat analysis, it was found that there was a corresponding gradient of substrate taxon composition and diversity along the reef. With the most turbid sites having the lowest benthic biodiversity, high levels of dead coral, and low covers of live coral and EAM. These indicators of habitat degradation then begin gradually reversing as turbidity decreases site by site along the turbidity gradient, and the least turbid sites had high substrate diversity, low covers of dead coral, and high covers of live coral and EAM—typical signs of a pristine, low turbidity reef (Pratchett et al., 2014; Zweifler et al., 2021).

The importance of this research is that it potentially allows us to model how fish with different ecologies and functional modes of feeding may respond to future anthropogenic impacts. As the human population grows, coastal land use changes are resulting in progressively increasing sediment and nutrient loads on coral reefs world-wide and it is now estimated that over 60% of coral reefs have experienced damage from anthropogenic impacts (Carlson et al., 2019). If coral reefs are to survive in the anthropogenic era, it is now more important than ever to predict future impacts so that well informed conservation management strategies and preventative measures can be implemented before rather than after potentially irreversible ecosystem shifts occur (Riegl et al., 2009).

Our study species *C. striatus* and *C. bleekeri*, which have contrasting ecologies and feeding modes showed contrasting responses to turbidity at the site level. The FMR and bite rate of *C. striatus* showed a fairly clear trend along the turbidity gradient, while no trend was evident in the feeding behaviour or energy expenditure metrics of *C. bleekeri*.

Here we were able to elucidate how the foraging behavior and energy expenditure of *C. striatus* was influenced by varying levels of natural turbidity and subsequent habitat compositional changes. Overall, our results indicate that *C. striatus* is highly resilient to elevated levels of turbidity and altered habitat composition, such as reduced benthic diversity and apparent low abundances of its preferred resource—EAM. Furthermore, at least in terms of foraging, it appears that they in fact prefer moderately high levels of turbidity and what might be considered moderately ‘degraded’ reef habitats. They displayed the highest and bite rate and proportion of fish feeding in the second most turbid site, Batu. A turbidity tipping point is then seemingly reached at Ovuku, where feeding ceases and FMR is considerably elevated, possibly due to extreme changes in EAM quality or cover.

Though Batu may be naturally turbid, it has ecological characteristics which are typically defined in the literature as signs of habitat degradation, such as high levels of dead coral, low benthic species diversity, low coral cover, and low EAM cover (Hughes, 1994; Pratchett et al., 2014; Tebbett et al., 2018). This further points to *C. striatus* being a resilient generalist, a sentiment that is relatively well supported in the literature. With several studies documenting the ability of *C. striatus* to persist and even thrive in degraded reefs (Lin et al., 2021; Putra et al., 2025; Russ et al., 2018; Zweifler (Zvifler) et al., 2021).

Altogether, this could be considered evidence that *C. striatus* would make a poor indicator of reef health, and the study of its behaviour likely would not reveal signs of degradation until turbidity becomes extremely high. Indeed, many studies aiming to classify degradation states or identify ecosystem ‘warning signals’ operate on the basis that degradation is deleterious and thus focus on decreasing feeding rates, signs of stress, or population parameters such as decreased recruitment and increased mortality rates (Goatley et al., 2016; Kuffner et al., 2006). However, the feeding behaviour of *C. striatus* does show a consistent relationship with apparent habitat degradation, the ratio of fish feeding and bite rate both steadily increase as turbidity increases and benthic biodiversity decreases, before reaching a turbidity threshold where feeding appears to cease completely. Thus, fine-scale analysis of their feeding behaviour could be of some use as an indicator of the degradation state of coral reefs. Even the modest and non-statistically significant increase in turbidity from Church (the least turbid site) was associated with an increased bite rate and proportion of fish feeding. Therefore, monitoring of *C. striatus* bite rates over time could potentially serve as an early warning indicator of increases in turbidity and loss of benthic diversity before any tipping point is reached. However, further research would be required to confirm this, including identifying whether *C. striatus* shows the same feeding behaviour shifts in the context of anthropogenically driven turbidity increases and associated benthic habitat changes.

Unfortunately, from this research little can be inferred about the effects of turbidity on the feeding behaviour and energy expenditure of *C. bleekeri* other than that they appear overall to show no response in velocity or FMR to elevated turbidity levels. It is possible, however, that the different phases show differing responses to turbidity, with initial phase individuals potentially showing a large increase in FMR and velocity in the most turbid of conditions at Batu. Though, the small sample size of initial phase individuals makes a conclusive inference about this unreliable. It is unlikely that fine-scale analysis of energy expenditure in *C. bleekeri* would be a good indicator of coral reef health, nor would it reveal any early warning signs of degradation. As mentioned in the discussion, *C. bleekeri* may be a habitat generalist, and it has been shown in other studies to persist in relatively unhealthy, degraded reefs (Mansyur et al., 2021; Tresnati et al., 2019). However, as *C. bleekeri* is likely quite specialised in its foraging behaviour and resource selection, it is possible that more comprehensive research may reveal more sensitive foraging behaviour responses to habitat degradation that were not captured in this study.

A shortcoming of this study was that the extremely time-consuming nature of manual 3D video analysis only permitted short 10 second video samples per fish to obtain a sufficient sample size of individuals. These short sample durations were apparently sufficient to capture the fine-scale foraging behaviour of *C. striatus.* However, due to the unique foraging behaviour reported in *C. bleekeri* of making brief feeding forays of only a few bites which are interrupted with long periods of non-feeding activity, this study recorded only 7 individuals feeding. Future studies on fine-scale foraging behaviour in *C. bleekeri* should have a minimum 3 minute sample period as was determined necessary by Bellwood & Choat, (1990).

Substrate classification was another challenge of this study which could be improved upon. Substrate classifications were derived from GoPro photographs taken within quadrats. GoPro cameras are designed as portable 'action' cameras which have relatively good video quality for their compact form; however, their small image sensor makes for relatively poor-quality, grainy photos, particularly in the reduced light conditions found several meters underwater. Furthermore, red light is attenuated strongly by water and may only penetrate several meters in the clearest waters, and much less so under turbid conditions (Duntley, 1963; Wozniak & Dera, 2007). Thus, the substrate photos had relatively poor definition and colour legibility, making differentiation of visually similar benthic organisms quite difficult. It was often hard to tell EAM apart from other 'mat-like' organisms such as some sponges and other encrusting taxa. Therefore, EAM cover estimates may have been unreliable. It seemed questionable that the highest *C. striatus* bite rates were at Batu, where mean EAM cover was apparently only 3.33%. This problem could be solved by using a higher quality camera designed for still photography and using a flash. This would result in a more defined and contrasting photo which reveals the true colour of the substratum.

As the manual process of 3D video analysis was a limiting factor in this study, future research in this area could benefit greatly from artificial intelligence (AI) assisted fish identification and tracking. If this process could be automated in such a way, a greater number of samples could be taken in a shorter amount of time and tracks could be made longer. This would likely make tracking the fine-scale foraging behaviour of species which feed infrequently (such as *C. bleekeri*) more viable. Furthermore, more species could be tracked and analysed, potentially leading to the discovery of species which are more suitable as indicators of early environmental damage. Additionally, the analysis could be done on an even finer scale; tracking fish frame by frame would be possible, as opposed to every 6th frame as was the case in this study. While still in its infancy, AI has already been used with great success in tracking fish and analysing their energy expenditure in situ. Lilkendey et al. (2024) employed a convolutional neural network (CNN)—a deep learning algorithm primarily developed for object detection in images—to detect fish in stereo video recordings. The CNN was trained on over 30,000 images of 52 species including reef fish and corals and was able to successfully detect fish among other reef structures. Furthermore, they combined the CNN with the DeepSORT algorithm to differentiate and track multiple fish at the same time and record their velocities and trajectories. This allowed for accurate ODBA and thus energy expenditure estimations of multiple individuals simultaneously. As advancements in neural networks and other AI technologies are further progressing, it may not be long before the entire pipeline of this research, including fish identification, tracking, energy expenditure estimation, identification of bites, and on which substrate, can be entirely automated (Li et al., 2023).

Finally, the impact of this field of research could be further enhanced by employing it on anthropogenically turbid and eutrophic reefs to truly reveal how the foraging behaviours and energy expenditures of coral reef fish are impacted by human-driven land use changes. Ideally, remote stereo video analysis could be employed as a form of long-term monitoring on a healthy and undisturbed reef which is predicted to be affected by future planned land use changes nearby. This would reveal chronologically how behaviour and energy expenditure of fish are impacted, and detailed analysis of this data would likely reveal the most sensitive indicators of ecosystem health and ‘early warning’ signals of anthropogenically driven coral reef degradation.

References

Abu-Taweel, G. M., Al-Fifi, Z., Abada, E., Khemira, H., Almalki, G., Modafer, Y., Mohamed Khedher, K., & Mundher Yaseen, Z. (2023). Parrotfish: An overview of ecology, nutrition, and reproduction behaviour. *Journal of King Saud University - Science*, *35*(7), 102778. https://doi.org/10.1016/j.jksus.2023.102778

Adam, T., Burkepile, D., Holbrook, S., Carpenter, R., Claudet, J., Loiseau, C., Thiault, L., Brooks, A., Washburn, L., & Schmitt, R. (2020). Landscape-scale patterns of nutrient enrichment in a coral reef ecosystem: Implications for coral to algae phase shifts. *Ecological Applications*, *31*, e2227. https://doi.org/10.1002/eap.2227

Adam, T., Burkepile, D., Ruttenberg, B., & Paddack, M. (2015). Herbivory and the resilience of Caribbean coral reefs: Knowledge gaps and implications for management. *Marine Ecology Progress Series*, *520*, 1–20. https://doi.org/10.3354/meps11170

Airoldi, L. (1998). Roles of Disturbance, Sediment Stress, and Substratum Retention on Spatial Dominance in Algal Turf. *Ecology*, *79*(8), 2759–2770. https://doi.org/10.1890/0012-9658(1998)079%255B2759:RODSSA%255D2.0.CO;2

Albert, S., Grinham, A., Gibbes, B., Tibbetts, I., & Udy, J. (2014). Indicators of coral reef ecosystem recovery following reduction in logging and implementation of community-based management schemes in the Solomon Islands. *Pacific Conservation Biology*, *20*(1), 75–85. Scopus. https://doi.org/10.1071/pc140075

Annett, C. A., & Pierotti, R. (1999). Long-Term Reproductive Output in Western Gulls: Consequences of Alternate Tactics in Diet Choice. *Ecology*, *80*(1), 288–297. https://doi.org/10.1890/0012-9658(1999)080%255B0288:LTROIW%255D2.0.CO;2

Aronson, R. B., Bruno, J. F., Precht, W. F., Glynn, P. W., Harvell, C. D., Kaufman, L., Rogers, C. S., Shinn, E. A., & Valentine, J. F. (2003). Causes of Coral Reef Degradation. *Science*, *302*(5650), 1502–1504. https://doi.org/10.1126/science.302.5650.1502b

Ballard, W. B. (1992). BEAR PREDATION ON MOOSE: A REVIEW OF RECENT NORTH AMERICAN STUDIES AND THEIR MANAGEMENT IMPLICATIONS. *Alces: A Journal Devoted to the Biology and Management of Moose*, 162–176.

Ballari, S. A., & Barrios-García, M. N. (2014). A review of wild boar us scrofa diet and factors affecting food selection in native and introduced ranges. *Mammal Review*, *44*(2), 124–134. https://doi.org/10.1111/mam.12015

Behn, K. E., & Baxter, C. V. (2019). The trophic ecology of a desert river fish assemblage: Influence of season and hydrologic variability. *Ecosphere*, *10*(1), e02583. https://doi.org/10.1002/ecs2.2583

Bell, J., & Galzin, R. (1984). Influence of live coral cover on coral-reef fish communities. *Marine Ecology Progress Series*, *15*, 265–274. https://doi.org/10.3354/meps015265

Bell, J., Johnson, J., AS, G., Gehrke, P., Hobday, A., Hoegh-Guldberg, O., Borgne, R., Lehodey, P., Lough, J., Pickering, T., MS, P., & Waycott, M. (2011). *Vulnerability of Tropical Pacific Fisheries and Aquaculture to Climate Change. Summary for Pacific Island Countries and Territories*.

Bell, P. R. F. (1992). Eutrophication and coral reefs—Some examples in the Great Barrier Reef lagoon. *Water Research*, *26*(5), 553–568. https://doi.org/10.1016/0043-1354(92)90228-V

Bellwood, D. R., Baird, A. H., Depczynski, M., González-Cabello, A., Hoey, A. S., Lefèvre, C. D., & Tanner, J. K. (2012). Coral recovery may not herald the return of fishes on damaged coral reefs. *Oecologia*, *170*(2), 567–573. https://doi.org/10.1007/s00442-012-2306-z

Bellwood, D. R., & Choat, J. H. (1990). A functional analysis of grazing in parrotfishes (family Scaridae): The ecological implications. In M. N. Bruton (Ed.), *Alternative life-history styles of fishes* (pp. 189–214). Springer Netherlands. https://doi.org/10.1007/978-94-009-2065-1_11

Bellwood, D. R., Streit, R. P., Brandl, S. J., & Tebbett, S. B. (2019). The meaning of the term ‘function’ in ecology: A coral reef perspective. *Functional Ecology*, *33*(6), 948–961. https://doi.org/10.1111/1365-2435.13265

Bennett, A. F. (1985). Temperature and muscle. *Journal of Experimental Biology*, *115*(1), 333–344. https://doi.org/10.1242/jeb.115.1.333

Bernays, E. A. (1999). When host choice is a problem for a generalist herbivore: Experiments with the whitefly, Bemisia tabaci. *Ecological Entomology*, *24*(3), 260–267. https://doi.org/10.1046/j.1365-2311.1999.00193.x

Bessell-Browne, P., Negri, A. P., Fisher, R., Clode, P. L., Duckworth, A., & Jones, R. (2017). Impacts of turbidity on corals: The relative importance of light limitation and suspended sediments. *Marine Pollution Bulletin*, *117*(1), 161–170. https://doi.org/10.1016/j.marpolbul.2017.01.050

Biondo, M. V., & Burki, R. P. (2020). A Systematic Review of the Ornamental Fish Trade with Emphasis on Coral Reef Fishes-An Impossible Task. *Animals: An Open Access Journal from MDPI*, *10*(11), 2014. https://doi.org/10.3390/ani10112014

Bonaldo, R. M., Krajewski, J. P., Sazima, C., & Sazima, I. (2006). Foraging activity and resource use by three parrotfish species at Fernando de Noronha Archipelago, tropical West Atlantic. *Marine Biology*, *149*(3), 423–433. https://doi.org/10.1007/s00227-005-0233-9

Braverman, I. (2020). Shifting baselines in coral conservation. *Environment and Planning E: Nature and Space*, *3*(1), 20–39. https://doi.org/10.1177/2514848619882560

Brönmark, C., Hulthén, K., Nilsson, P. A., Skov, C., Hansson, L.-A., Brodersen, J., & Chapman, B. B. (2014). There and back again: Migration in freshwater fishes. *Canadian Journal of Zoology*, *92*(6), 467–479. https://doi.org/10.1139/cjz-2012-0277

Brown, B. E. (2011). Mining/Quarrying of Coral Reefs. In D. Hopley (Ed.), *Encyclopedia of Modern Coral Reefs: Structure, Form and Process* (pp. 707–711). Springer Netherlands. https://doi.org/10.1007/978-90-481-2639-2_115

Brown, D. (1996). Decentering distortion of lenses. *Photogrammetric Engineering*, *32*(3), 444–462.

Brown, J. H. (2014). Why are there so many species in the tropics? *Journal of Biogeography*, *41*(1), 8–22. https://doi.org/10.1111/jbi.12228

Brownscombe, J. W., Cooke, S. J., & Danylchuk, A. J. (2017). Spatiotemporal drivers of energy expenditure in a coastal marine fish. *Oecologia*, *183*(3), 689–699. https://doi.org/10.1007/s00442-016-3800-5

Bruckner, A. W. (2002). Life-Saving Products from Coral Reefs. *Issues in Science and Technology*, *18*(3), 39–44.

Bruggemann, J. H. (1994). Parrotfish grazing on coral reefs. *Wageningen, The Netherlands: Posen & Looijen bv*

Bruggemann, J. H., van Kessel, A. M., van Rooij, J. M., & Breeman, A. M. (1996). Bioerosion and sediment ingestion by the Caribbean parrotfish *Scarus vetula* and *Sparisoma viride*: Implications of fish size, feeding mode and habitat use. *Marine Ecology Progress Series*, *134*(1/3), 59–71.

Bruno, J. F., Precht, W. F., Vroom, P. S., & Aronson, R. B. (2014). Coral reef baselines: How much macroalgae is natural? *Marine Pollution Bulletin*, *80*(1), 24–29. https://doi.org/10.1016/j.marpolbul.2014.01.010

Bruno, J. F., & Selig, E. R. (2007). Regional Decline of Coral Cover in the Indo-Pacific: Timing, Extent, and Subregional Comparisons. *PLOS ONE*, *2*(8), e711. https://doi.org/10.1371/journal.pone.0000711

Bruno, J. F., Sweatman, H., Precht, W. F., Selig, E. R., & Schutte, V. G. W. (2009). Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology*, *90*(6), 1478–1484. https://doi.org/10.1890/08-1781.1

Buckman, N. S., & Ogden, J. C. (1973). Territorial Behavior of the Striped Parrotfish *Scarus Croicensis* Bloch (Scaridae). *Ecology*, *54*(6), 1377–1382. https://doi.org/10.2307/1934202

Bucol, A. A., Abesamis, R. A., Stockwell, B. L., Lowe, J. R., & Russ, G. R. (2021). Development of reproductive potential in protogynous coral reef fishes within Philippine no-take marine reserves. *Journal of Fish Biology*, *99*(5), 1561–1575. https://doi.org/10.1111/jfb.14861

Burkepile, D. E., & Hay, M. E. (2006). Herbivore Vs. Nutrient Control of Marine Primary Producers: Context-Dependent Effects. *Ecology*, *87*(12), 3128–3139. https://doi.org/10.1890/0012-9658(2006)87%255B3128:HVNCOM%255D2.0.CO;2

Burkepile, D. E., & Hay, M. E. (2008). Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences*, *105*(42), 16201–16206. https://doi.org/10.1073/pnas.0801946105

Burkepile, D. E., & Hay, M. E. (2011). Feeding complementarity versus redundancy among herbivorous fishes on a Caribbean reef. *Coral Reefs*, *30*(2), 351–362. https://doi.org/10.1007/s00338-011-0726-6

Carlson, P., Davis, K., Warner, R., & Caselle, J. (2017). Fine-scale spatial patterns of parrotfish herbivory are shaped by resource availability. *Marine Ecology Progress Series*, *577*, 165–176. https://doi.org/10.3354/meps12258

Carlson, R. R., Foo, S. A., & Asner, G. P. (2019). Land Use Impacts on Coral Reef Health: A Ridge-to-Reef Perspective. *Frontiers in Marine Science*, *6*. https://doi.org/10.3389/fmars.2019.00562

CCRIF Annual Report 2009-2010 | CCRIF SPC. (n.d.). Retrieved September 19, 2024, from https://www.ccrif.org/en/publications/annual-report/ccrif-annual-report-2009-2010?language_content_entity=en

Cesar, H., Burke, L., & Pet-Soede, L. (2003). *The economics of worldwide coral reef degradation*. https://agris.fao.org/search/en/providers/122412/records/6473698a08fd68d546062c52

Cheal, A. J., MacNeil, M. A., Cripps, E., Emslie, M. J., Jonker, M., Schaffelke, B., & Sweatman, H. (2010). Coral–macroalgal phase shifts or reef resilience: Links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. *Coral Reefs*, *29*(4), 1005–1015. https://doi.org/10.1007/s00338-010-0661-y

Cheal, A. J., Wilson, S. K., Emslie, M. J., Dolman, A. M., & Sweatman, H. (2008). Responses of reef fish communities to coral declines on the Great Barrier Reef. *Marine Ecology Progress Series*, *372*, 211–223. https://doi.org/10.3354/meps07708

Chivers, D. J. (1989). Adaptations of digestive systems in non-ruminant herbivores. *The Proceedings of the Nutrition Society*, *48*(1), 59–67. https://doi.org/10.1079/pns19890010

Choat, J., Clements, K., & Robbins, W. (2002). The trophic status of herbivorous fishes on coral reefs. *Marine Biology*, *140*(3), 613–623. https://doi.org/10.1007/s00227-001-0715-3

Choat, J. H., & Clements, K. D. (1993). Daily feeding rates in herbivorous labroid fishes. *Marine Biology*, *117*(2), 205–211. https://doi.org/10.1007/BF00345664

Choat, J. H., & Clements, K. D. (1998). VERTEBRATE HERBIVORES IN MARINE AND TERRESTRIAL ENVIRONMENTS: A Nutritional Ecology Perspective. *Annual Review of Ecology, Evolution, and Systematics*, *29*(Volume 29, 1998), 375–403. https://doi.org/10.1146/annurev.ecolsys.29.1.375

Clarke, A., & Johnston, N. M. (1999). Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of animal ecology*, *68*(5), 893-905.

Clements, K. D. (2017). Integrating ecological roles and trophic diversification on coral reefs: Multiple lines of evidence identify parrotfishes as microphages. *Biological Journal of the Linnean Society*, *120*(4), 729.

Clements, Kendall D., and J. Howard Choat. "Nutritional ecology of parrotfishes (Scarinae, Labridae)." *Biology of parrotfishes*. CRC Press, 2018. 42-68.

Clifton, K. (1995). Asynchronous food availability on neighboring Caribbean coral reefs determines seasonal patterns of growth and reproduction for the herbivorous parrotfish *Scarus iserti*. *Marine Ecology Progress Series*, *116*, 39–46. https://doi.org/10.3354/meps116039

Coll, M., & Guershon, M. (2002). Omnivory in Terrestrial Arthropods: Mixing Plant and Prey Diets. *Annual Review of Entomology*, *47*(Volume 47, 2002), 267–297. https://doi.org/10.1146/annurev.ento.47.091201.145209

Connell, S., Foster, M., & Airoldi, L. (2014). What are algal turfs? Towards a better description of turfs. *Marine Ecology Progress Series*, *495*, 299–307. https://doi.org/10.3354/meps10513

Coogan, S. C. P., Raubenheimer, D., Stenhouse, G. B., Coops, N. C., & Nielsen, S. E. (2018). Functional macronutritional generalism in a large omnivore, the brown bear. *Ecology and Evolution*, *8*(4), 2365–2376. https://doi.org/10.1002/ece3.3867

Côté, I. M., & Reynolds, J. D. (2006). *Coral Reef Conservation*. Cambridge University Press.

Crossman, D. J., Choat, H. J., Clements, K. D., Hardy, T., & McConochie, J. (2001). Detritus as food for grazing fishes on coral reefs. *Limnology and Oceanography*, *46*(7), 1596–1605. https://doi.org/10.4319/lo.2001.46.7.1596

Crowder, D. W., & Snyder, W. E. (2010). Eating their way to the top? Mechanisms underlying the success of invasive insect generalist predators. *Biological Invasions*, *12*(9), 2857–2876. https://doi.org/10.1007/s10530-010-9733-8

Curry-Lindahl, K. (1972). The Brown Bear (*Ursus arctos*) in Europe: Decline, Present Distribution, Biology and Ecology. *Bears: Their Biology and Management*, *2*, 74–80. https://doi.org/10.2307/3872571

Dailer, M. L., Knox, R. S., Smith, J. E., Napier, M., & Smith, C. M. (2010). Using δ15N values in algal tissue to map locations and potential sources of anthropogenic nutrient inputs on the island of Maui, Hawai‘i, USA. *Marine Pollution Bulletin*, *60*(5), 655–671. https://doi.org/10.1016/j.marpolbul.2009.12.021

D’Angelo, C., & Wiedenmann, J. (2014). Impacts of nutrient enrichment on coral reefs: New perspectives and implications for coastal management and reef survival. *Current Opinion in Environmental Sustainability*, *7*, 82–93. https://doi.org/10.1016/j.cosust.2013.11.029

Davies, R. R., & Davies, J. A. E. R. (2003). Rabbit gastrointestinal physiology. *The Veterinary Clinics of North America. Exotic Animal Practice*, *6*(1), 139–153. https://doi.org/10.1016/s1094-9194(02)00024-5

De’ath, G., & Fabricius, K. (2010). Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef. *Ecological Applications*, *20*(3), 840–850. https://doi.org/10.1890/08-2023.1

Diaz-Pulido, G., McCook, L. J., Dove, S., Berkelmans, R., Roff, G., Kline, D. I., Weeks, S., Evans, R. D., Williamson, D. H., & Hoegh-Guldberg, O. (2009). Doom and Boom on a Resilient Reef: Climate Change, Algal Overgrowth and Coral Recovery. *PLOS ONE*, *4*(4), e5239. https://doi.org/10.1371/journal.pone.0005239

Dimijian, G. G. (2000). Evolving Together: The Biology of Symbiosis, Part 1. *Baylor University Medical Center Proceedings*, *13*(3), 217a–2226. https://doi.org/10.1080/08998280.2000.11927678

Dobson, A. (2009). Food-web structure and ecosystem services: Insights from the Serengeti. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1524), 1665–1682. https://doi.org/10.1098/rstb.2008.0287

Douglas, A. E. (2003). Coral bleaching—how and why? *Marine Pollution Bulletin*, *46*(4), 385–392. https://doi.org/10.1016/S0025-326X(03)00037-7

Downs, C. A., Woodley, C. M., Richmond, R. H., Lanning, L. L., & Owen, R. (2005). Shifting the paradigm of coral-reef 'health' assessment. *Marine Pollution Bulletin*, *51*(5), 486–494. https://doi.org/10.1016/j.marpolbul.2005.06.028

Dromard, C. R., Bouchon-Navaro, Y., Harmelin-Vivien, M., & Bouchon, C. (2015). Diversity of trophic niches among herbivorous fishes on a Caribbean reef (Guadeloupe, Lesser Antilles), evidenced by stable isotope and gut content analyses. *Journal of Sea Research*, *95*, 124–131. https://doi.org/10.1016/j.seares.2014.07.014

Drummond, H. (1983). Quatic foraging in garter snakes: a comparison of specialists and generalists. *Behaviour*, *86*(1-2), 1-30.

Duntley, S. Q. (1963). Light in the Sea*. *JOSA, Vol. 53, Issue 2, Pp. 214-233*. https://doi.org/10.1364/JOSA.53.000214

Edwards, C. B., Friedlander, A. M., Green, A. G., Hardt, M. J., Sala, E., Sweatman, H. P., Williams, I. D., Zgliczynski, B., Sandin, S. A., & Smith, J. E. (2014). Global assessment of the status of coral reef herbivorous fishes: Evidence for fishing effects. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1774), 20131835. https://doi.org/10.1098/rspb.2013.1835

El Rahimi, S. A., Hendra, E., Isdianto, A., & Luthfi, O. M. (2021). Feeding preference of herbivorous fish: Family Scaridae. *IOP Conference Series: Earth and Environmental Science*, *869*(1), 012004. https://doi.org/10.1088/1755-1315/869/1/012004

Elsden, S. R., & Phillipson, A. T. (1948). Ruminant Digestion. *Annual Review of Biochemistry*, *17*(Volume 17, 1948), 705–726. https://doi.org/10.1146/annurev.bi.17.070148.003421

Emmons, L. H. (1987). Comparative feeding ecology of felids in a neotropical rainforest. *Behavioral Ecology and Sociobiology*, *20*(4), 271–283. https://doi.org/10.1007/BF00292180

Entsch, B., Sim, R. G., & Hatcher, B. G. (1983). Indications from photosynthetic components that iron is a limiting nutrient in primary producers on coral reefs. *Marine Biology*, *73*(1), 17–30. https://doi.org/10.1007/BF00396281

Fabricius, K. E., Crossman, K., Jonker, M., Mongin, M., & Thompson, A. (2023). Macroalgal cover on coral reefs: Spatial and environmental predictors, and decadal trends in the Great Barrier Reef. *PLOS ONE*, *18*(1), e0279699. https://doi.org/10.1371/journal.pone.0279699

Ferrario, F., Beck, M. W., Storlazzi, C. D., Micheli, F., Shepard, C. C., & Airoldi, L. (2014). The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. *Nature Communications*, *5*(1), Article 1. https://doi.org/10.1038/ncomms4794

Fox, R. J., & Bellwood, D. R. (2013). Niche partitioning of feeding microhabitats produces a unique function for herbivorous rabbitfishes (Perciformes, Siganidae) on coral reefs. *Coral Reefs*, *32*(1), 13–23. https://doi.org/10.1007/s00338-012-0945-5

Froese, R., Thorson, J. T., & Reyes Jr, R. B. (2014). A Bayesian approach for estimating length-weight relationships in fishes. *Journal of Applied Ichthyology*, *30*(1), 78–85. https://doi.org/10.1111/jai.12299

Froidurot, A., & Julliand, V. (2022). Cellulolytic bacteria in the large intestine of mammals. *Gut Microbes*, *14*(1), 2031694. https://doi.org/10.1080/19490976.2022.2031694

Fung, T., Seymour, R. M., & Johnson, C. R. (2011). Alternative stable states and phase shifts in coral reefs under anthropogenic stress. *Ecology*, *92*(4), 967–982. https://doi.org/10.1890/10-0378.1

Furnas, M., Mitchell, A., Skuza, M., & Brodie, J. (2005). In the other 90%: Phytoplankton responses to enhanced nutrient availability in the Great Barrier Reef Lagoon. *Marine Pollution Bulletin*, *51*(1–4), 253–265. https://doi.org/10.1016/j.marpolbul.2004.11.010

Futuyma, D. J., & Moreno, G. (1988). The Evolution of Ecological Specialization. *Annual Review of Ecology and Systematics*, *19*, 207–233.

Galis, F., & Metz, J. A. (1998). Why are there so many cichlid species? *Trends in Ecology & Evolution*, *13*(1), 1–2. https://doi.org/10.1016/s0169-5347(97)01239-1

Galzin, R., Lecchini, D., Lison de Loma, T., Moritz, C., Parravicini, V., & Siu, G. (2015). Long term monitoring of coral and fish assemblages (1983-2014) in Tiahura reefs, Moorea, French Polynesia. *Cybium*.

Gardner, T. A., Côté, I. M., Gill, J. A., Grant, A., & Watkinson, A. R. (2003). Long-Term Region-Wide Declines in Caribbean Corals. *Science*, *301*(5635), 958–960. https://doi.org/10.1126/science.1086050

Gattuso, J.-P., Frankignoulle, M., Bourge, I., Romaine, S., & Buddemeier, R. W. (1998). Effect of calcium carbonate saturation of seawater on coral calcification. *Global and Planetary Change*, *18*(1), 37–46. https://doi.org/10.1016/S0921-8181(98)00035-6

Gibson, R. N., & Atkinson, R. J. A. (2003). *Oceanography and Marine Biology, An Annual Review, Volume 41: An Annual Review: Volume 41*. CRC Press.

Gleason, F. H., Lilje, O., Marano, A. V., Sime-Ngando, T., Sullivan, B. K., Kirchmair, M., & Neuhauser, S. (2014). Ecological functions of zoosporic hyperparasites. *Frontiers in Microbiology*, *5*, 244. https://doi.org/10.3389/fmicb.2014.00244

Glynn, P. W. (1996). Coral reef bleaching: Facts, hypotheses and implications. *Global Change Biology*, *2*(6), 495–509. https://doi.org/10.1111/j.1365-2486.1996.tb00063.x

Goatley, C., & Bellwood, D. (2010). Biologically mediated sediment fluxes on coral reefs: Sediment removal and off-reef transportation by the surgeonfish *Ctenochaetus striatus*. *Marine Ecology Progress Series*, *415*, 237–245. https://doi.org/10.3354/meps08761

Goatley, C. H. R., Bonaldo, R. M., Fox, R. J., & Bellwood, D. R. (2016). Sediments and herbivory as sensitive indicators of coral reef degradation. *Ecology and Society*, *21*(1). https://www.jstor.org/stable/26270335

Goreau, T. F., Goreau, N. I., & Goreau, T. J. (1979). Corals and Coral Reefs. *Scientific American*, *241*(2), 124–137.

Green, A. L., & Bellwood, D. R. (2009). *Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience: A practical guide for coral reef managers in the Asia Pacific region*. IUCN.

Grier, S. R., Hà, B. A., Ryznar, E. R., Smith, L. L., & Fong, P. (2025). Sediment, light, and interspecific interactions have strong but independent species-specific effects on two dominant coral reef macroalgae. *Marine Biology*, *172*(2), 38. https://doi.org/10.1007/s00227-024-04590-4

Guinotte, J. M., & Fabry, V. J. (2008). Ocean Acidification and Its Potential Effects on Marine Ecosystems. *Annals of the New York Academy of Sciences*, *1134*(1), 320–342. https://doi.org/10.1196/annals.1439.013

Hallock, P. (1997). Reefs and Reef Limestones in Earth History. In C. Birkeland (Ed.), *Life and Death of Coral Reefs* (pp. 13–42). Springer US. https://doi.org/10.1007/978-1-4615-5995-5_2

Halsey, L. G., Shepard, E. L. C., & Wilson, R. P. (2011). Assessing the development and application of the accelerometry technique for estimating energy expenditure. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *158*(3), 305–314. https://doi.org/10.1016/j.cbpa.2010.09.002

Hansen, J., Sato, M., Ruedy, R., Lo, K., Lea, D. W., & Medina-Elizade, M. (2006). Global temperature change. *Proceedings of the National Academy of Sciences*, *103*(39), 14288–14293. https://doi.org/10.1073/pnas.0606291103

Harper, B. B., Puga-Bernabéu, Á., Droxler, A. W., Webster, J. M., Gischler, E., Tiwari, M., Lado-Insua, T., Thomas, A. L., Morgan, S., Jovane, L., & Röhl, U. (2015). Mixed Carbonate–Siliciclastic Sedimentation Along the Great Barrier Reef Upper Slope: A Challenge To the Reciprocal Sedimentation Model. *Journal of Sedimentary Research*, *85*(9), 1019–1036. https://doi.org/10.2110/jsr.2015.58.1

Harris, D. L., Rovere, A., Casella, E., Power, H., Canavesio, R., Collin, A., Pomeroy, A., Webster, J. M., & Parravicini, V. (2018). Coral reef structural complexity provides important coastal protection from waves under rising sea levels. *Science Advances*, *4*(2), eaao4350. https://doi.org/10.1126/sciadv.aao4350

Harvey, E., Shortis, M., Stadler, M., & Cappo, M. (2002). A Comparison of the Accuracy and Precision of Measurements from Single and Stereo-Video Systems. *Marine Technology Society Journal*, *36*(2), 38–49. https://doi.org/10.4031/002533202787914106

Hatcher, B. G. (1990). Coral reef primary productivity. A hierarchy of pattern and process. *Trends in Ecology & Evolution*, *5*(5), 149–155. https://doi.org/10.1016/0169-5347(90)90221-X

Heenan, A., & Williams, I. D. (2013). Monitoring Herbivorous Fishes as Indicators of Coral Reef Resilience in American Samoa. *PLOS ONE*, *8*(11), e79604. https://doi.org/10.1371/journal.pone.0079604

Hoare, D. J., Krause, J., Peuhkuri, N., & Godin, J.-G. J. (2000). Body size and shoaling in fish. *Journal of Fish Biology*, *57*(6), 1351–1366. https://doi.org/10.1111/j.1095-8649.2000.tb02217.x

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., Harvell, C. D., Sale, P. F., Edwards, A. J., Caldeira, K., Knowlton, N., Eakin, C. M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R. H., Dubi, A., & Hatziolos, M. E. (2007). Coral Reefs under Rapid Climate Change and Ocean Acidification. *Science*, *318*(5857), 1737–1742.

Hoey, A. S. (2018). Feeding in Parrotfishes: The Influence of Species, Body Size, and Temperature. In *Biology of Parrotfishes*. CRC Press.

Holbrook, S. J., Schmitt, R. J., Adam, T. C., & Brooks, A. J. (2016). Coral Reef Resilience, Tipping Points and the Strength of Herbivory. *Scientific Reports*, *6*(1), 35817. https://doi.org/10.1038/srep35817

Hoskin, C. (2010). The invasion and potential impact of the Asian House Gecko (*Hemidactylus frenatus*) in Australia. *Austral Ecology*, *36*, 240–251. https://doi.org/10.1111/j.1442-9993.2010.02143.x

Hughes, T. P. (1994). Catastrophes, Phase Shifts, and Large-Scale Degradation of a Caribbean Coral Reef. *Science*, *265*(5178), 1547–1551. https://doi.org/10.1126/science.265.5178.1547

Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., Baird, A. H., Baum, J. K., Berumen, M. L., Bridge, T. C., Claar, D. C., Eakin, C. M., Gilmour, J. P., Graham, N. A. J., Harrison, H., Hobbs, J.-P. A., Hoey, A. S., Hoogenboom, M., Lowe, R. J., … Wilson, S. K. (2018). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science*, *359*(6371), 80–83. https://doi.org/10.1126/science.aan8048

Hughes, T. P., Rodrigues, M. J., Bellwood, D. R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M. S., Steneck, R. S., & Willis, B. (2007). Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change. *Current Biology*, *17*(4), 360–365. https://doi.org/10.1016/j.cub.2006.12.049

Hulbert, A. J., & Else, P. L. (2004). Basal metabolic rate: History, composition, regulation, and usefulness. *Physiological and Biochemical Zoology: PBZ*, *77*(6), 869–876. https://doi.org/10.1086/422768

Huntington, G., Woodbury, M., & Anderson, V. (2019). Invited Review: Growth, voluntary intake, and digestion and metabolism of North American bison. *Applied Animal Science*, *35*(2), 146–160. https://doi.org/10.15232/aas.2018-01798

Hutchinson, G. E. (1957). Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, *22*, 415–427. https://doi.org/10.1101/SQB.1957.022.01.039

Inoue, M., Suwa, R., Suzuki, A., Sakai, K., & Kawahata, H. (2011). Effects of seawater pH on growth and skeletal U/Ca ratios of Acropora digitifera coral polyps. *Geophysical Research Letters*, *38*(12). https://doi.org/10.1029/2011GL047786

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J., & Warner, R. R. (2001). Historical Overfishing and the Recent Collapse of Coastal Ecosystems. *Science*, *293*(5530), 629–637. https://doi.org/10.1126/science.1059199

Jones, G. P., McCormick, M. I., Srinivasan, M., & Eagle, J. V. (2004). Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences*, *101*(21), 8251–8253. https://doi.org/10.1073/pnas.0401277101

Jones, R., Fisher, R., & Bessell-Browne, P. (2019). Sediment deposition and coral smothering. *PLOS ONE*, *14*(6), e0216248. https://doi.org/10.1371/journal.pone.0216248

Jones, R., Pineda, M.-C., Luter, H. M., Fisher, R., Francis, D., Klonowski, W., & Slivkoff, M. (2021). Underwater Light Characteristics of Turbid Coral Reefs of the Inner Central Great Barrier Reef. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.727206

Jutfelt, F. (2020). Metabolic adaptation to warm water in fish. *Functional Ecology*, *34*(6), 1138–1141. https://doi.org/10.1111/1365-2435.13558

Karasov, W. H. (1992). Daily Energy Expenditure and the Cost of Activity in Mammals1. *American Zoologist*, *32*(2), 238–248. https://doi.org/10.1093/icb/32.2.238

Karasov, W. H., & Douglas, A. E. (2013). Comparative Digestive Physiology. *Comprehensive Physiology*, *3*(2), 741–783. https://doi.org/10.1002/cphy.c110054

Karlson, A. M. L., Gorokhova, E., & Elmgren, R. (2014). Nitrogen Fixed By Cyanobacteria Is Utilized By Deposit-Feeders. *PLOS ONE*, *9*(8), e104460. https://doi.org/10.1371/journal.pone.0104460

Kasumyan, A. O., & Pavlov, D. S. (2023). Size, Shape, Numbers and Composition of Fish Schools. *Journal of Ichthyology*, *63*(7), 1234–1250. https://doi.org/10.1134/S0032945223070032

Katovai, E., Burley, A. L., & Mayfield, M. M. (2012). Understory plant species and functional diversity in the degraded wet tropical forests of Kolombangara Island, Solomon Islands. *Biological Conservation*, *145*(1), 214–224. https://doi.org/10.1016/j.biocon.2011.11.008

Kelly, J. R., & Scheibling, R. E. (2012). Fatty acids as dietary tracers in benthic food webs. *Marine Ecology Progress Series*, *446*, 1–22. https://doi.org/10.3354/meps09559

Kerna, N. A., Flores, J. V., Holets, H. M., Hafid, A., Pruitt, K. D., Carsrud, N. D. V., & Anderson, I. I. (2021). The Truth: Are Humans Vegetarian, Carnivore, or Omnivore? A Review Based on the Anatomy and Physiology of the Human Digestive Tract. *EC Nutrition*, *16*(8), 78-86..

Killen, S., Munson, A., & Cortese, D. (2023). Costs of foraging: Energetics of foraging decisions. *Reference Module in Life Sciences*.

Kleypas, J. A., McManus, J. W., & Meñez, L. A. (1999). Environmental limits to coral reef development: Where do we draw the line? *American Zoologist*, *39*(1), 146–159.

Knowlton, N., Brainard, R. E., Fisher, R., Moews, M., Plaisance, L., & Caley, M. J. (2010). Coral Reef Biodiversity. In *Life in the World's Oceans* (pp. 65–78). John Wiley & Sons, Ltd. https://doi.org/10.1002/9781444325508.ch4

Kopp, D., Bouchon-Navaro, Y., Louis, M., Mouillot, D., Bouchon, C., Louis, M., Mouillot, D., & Bouchon, C. (2010). Herbivorous fishes and the potential of Caribbean marine reserves to preserve coral reef ecosystems. *Aquatic Conservation-Marine And Freshwater Ecosystems*, *20*(5), 516–524. https://doi.org/10.1002/aqc.1118

Korpimäki, E., Hongisto, K., Masoero, G., & Laaksonen, T. (2020). The difference between generalist and specialist: The effects of wide fluctuations in main food abundance on numbers and reproduction of two co-existing predators. *Journal of Avian Biology*, *51*. https://doi.org/10.1111/jav.02508

Kotrschal, K., & Thomson, D. A. (1986). Feeding patterns in eastern tropical Pacific blennioid fishes (Teleostei: Tripterygiidae, Labrisomidae, Chaenopsidae, Blenniidae). *Oecologia*, *70*(3), 367–378. https://doi.org/10.1007/BF00379499

Kuffner, I. B., Walters, L. J., Becerro, M. A., Paul, V. J., Ritson-Williams, R., & Beach, K. S. (2006). Inhibition of coral recruitment by macroalgae and cyanobacteria. *Marine Ecology Progress Series*, *323*, 107–117. https://doi.org/10.3354/meps323107

Kuiter, R. H., & Tonozuka, T. (2001). *Pictorial guide to Indonesian reef fishes. Part 2. Fusiliers—Dragonets, Caesionidae—Callionymidae.* Zoonetics, Australia.

Lamprecht, J. (1981). The function of social hunting in larger terrestrial carnivores. *Mammal Review*, *11*(4), 169–179. https://doi.org/10.1111/j.1365-2907.1981.tb00004.x

Lane, D. M. (2010). Tukey's Honestly Significant Difference (HSD). In *Encyclopedia of Research Design* (pp. 1566–1570). SAGE Publications, Inc. https://doi.org/10.4135/9781412961288

Lange, I. D., Perry, C. T., Morgan, K. M., Roche, R., Benkwitt, C. E., & Graham, N. A. (2020). Site-Level Variation in Parrotfish Grazing and Bioerosion as a Function of Species-Specific Feeding Metrics. *Diversity*, *12*(10), 379. https://doi.org/10.3390/d12100379

Lawson, G. L., Kramer, D. L., & Hunte, W. (1999). Size-related habitat use and schooling behavior in two species of surgeonfish (*Acanthurus bahianus* and *A. coeruleus*) on a fringing reef in Barbados, West Indies. *Environmental Biology of Fishes*, *54*(1), 19–33. https://doi.org/10.1023/A:1007477527663

Leenhardt, P., Lauer, M., Madi Moussa, R., Holbrook, S., Rassweiler, A., Schmitt, R., & Claudet, J. (2016). Complexities and Uncertainties in Transitioning Small-Scale Coral Reef Fisheries. *Frontiers in Marine Science*, *3*. https://doi.org/10.3389/fmars.2016.00070

Lessios, H. A. (1988). Mass Mortality of Diadema Antillarum in the Caribbean: What Have We Learned? *Annual Review of Ecology and Systematics*, *19*, 371–393.

Li, C., Li, X., Chen, M., & Sun, X. (2023). Deep Learning and Image Recognition. *2023 IEEE 6th International Conference on Electronic Information and Communication Technology (ICEICT)*, 557–562. https://doi.org/10.1109/ICEICT57916.2023.10245041

Lieth, H., & Whittaker, R. H. (2012). *Primary Productivity of the Biosphere* (Vol. 14). Springer Science & Business Media.

Lilkendey, J., Barrelet, C., Zhang, J., Meares, M., Larbi, H., Subsol, G., Chaumont, M., & Sabetian, A. (2024). Herbivorous fish feeding dynamics and energy expenditure on a coral reef: Insights from stereo-video and AI -driven 3D tracking. *Ecology and Evolution*, *14*(3), e11070. https://doi.org/10.1002/ece3.11070

Lin, X., Hu, S., Liu, Y., Zhang, L., Huang, H., & Liu, S. (2021). Disturbance-Mediated Changes in Coral Reef Habitat Provoke a Positive Feeding Response in a Major Coral Reef Detritivore, Ctenochaetus striatus. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.682697

Lin, Y.-J., Rabaoui, L., Basali, A. U., Lopez, M., Lindo, R., Krishnakumar, P. K., Qurban, M. A., Prihartato, P. K., Cortes, D. L., Qasem, A., Al-Abdulkader, K., & Roa-Ureta, R. H. (2021). Long-term ecological changes in fishes and macro-invertebrates in the world's warmest coral reefs. *Science of The Total Environment*, *750*, 142254. https://doi.org/10.1016/j.scitotenv.2020.142254

Linton, S. M., & Greenaway, P. (2007). A review of feeding and nutrition of herbivorous land crabs: Adaptations to low quality plant diets. *Journal of Comparative Physiology B*, *177*(3), 269–286. https://doi.org/10.1007/s00360-006-0138-z

Lirman, D. (2001). Competition between macroalgae and corals: Effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. *Coral Reefs*, *19*(4), 392–399. https://doi.org/10.1007/s003380000125

Liu, Y., Wu, H., Wang, S., Chen, X., Kimball, J. S., Zhang, C., Gao, H., & Guo, P. (2022). Evaluation of trophic state for inland waters through combining Forel-Ule Index and inherent optical properties. *Science of The Total Environment*, *820*, 153316. https://doi.org/10.1016/j.scitotenv.2022.153316

Lokrantz, J., Nyström, M., Thyresson, M., & Johansson, C. (2008). The non-linear relationship between body size and function in parrotfishes. *Coral Reefs*, *27*(4), 967–974. https://doi.org/10.1007/s00338-008-0394-3

Luginbuhl, J. M. (1983). Comparative anatomy of the digestive tract in cattle, sheep and goats: A review.

Maina, J., de Moel, H., Zinke, J., Madin, J., McClanahan, T., & Vermaat, J. E. (2013). Human deforestation outweighs future climate change impacts of sedimentation on coral reefs. *Nature Communications*, *4*(1), 1986. https://doi.org/10.1038/ncomms2986

Manning, J. C., & McCoy, S. J. (2023). Territoriality drives patterns of fixed space use in Caribbean parrotfishes. *Ecology and Evolution*, *13*(2), e9833. https://doi.org/10.1002/ece3.9833

Mansyur, S. A. S., Umar, M. T., Irmawati, Yasir, I., Yanti, A., Rahmani, P. Y., Aprianto, R., Tuwo, A., & Tresnati, J. (2021). Intensive catched parrotfish *Chlorurus bleekeri* (de Beaufort, 1940) in Wallace Line, Makassar Strait, Indonesia. *IOP Conference Series: Earth and Environmental Science*, *860*(1), 012016. https://doi.org/10.1088/1755-1315/860/1/012016

Marshell, A., & Mumby, P. J. (2012). Revisiting the functional roles of the surgeonfish *Acanthurus nigrofuscus* and *Ctenochaetus striatus*. *Coral Reefs*, *31*(4), 1093–1101. https://doi.org/10.1007/s00338-012-0931-y

Martins, K. A., Pereira, P. de S., Esteves, L. S., & Williams, J. (2019). The Role of Coral Reefs in Coastal Protection: Analysis of Beach Morphology. *Journal of Coastal Research*, *92*(SI), 157–164. https://doi.org/10.2112/SI92-018.1

Mcanally, R. A., & Phillipson, A. T. (1944). Digestion in the Ruminant. *Biological Reviews*, *19*(2), 41–54. https://doi.org/10.1111/j.1469-185X.1944.tb00301.x

McCook, L. J. (1999). Macroalgae, nutrients and phase shifts on coral reefs: Scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs*, *18*(4), 357–367. https://doi.org/10.1007/s003380050213

McManus, J. W., & Polsenberg, J. F. (2004). Coral–algal phase shifts on coral reefs: Ecological and environmental aspects. *Progress in Oceanography*, *60*(2), 263–279. https://doi.org/10.1016/j.pocean.2004.02.014

Minton, D., Burdick, D., & Brown, V. (2022). Changes in coral reef community structure along a sediment gradient in Fouha Bay, Guam. *Marine Pollution Bulletin*, *181*, 113816. https://doi.org/10.1016/j.marpolbul.2022.113816

Moberg, F., & Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological Economics*, *29*(2), 215–233. https://doi.org/10.1016/S0921-8009(99)00009-9

Morgan, K. M., & Kench, P. S. (2016). Parrotfish erosion underpins reef growth, sand talus development and island building in the Maldives. *Sedimentary Geology*, *341*, 50–57. https://doi.org/10.1016/j.sedgeo.2016.05.011

Morris, R. W. (1962). Body Size and Temperature Sensitivity in the Cichlid Fish, *Aequidens portalegrensis* (Hensel). *The American Naturalist*, *96*(886), 35–50.

Mountfort, D. O., Campbell, J., & Clements, K. D. (2002). Hindgut Fermentation in Three Species of Marine Herbivorous Fish. *Applied and Environmental Microbiology*. https://doi.org/10.1128/AEM.68.3.1374-1380.2002

Moustaka, M., Langlois, T. J., McLean, D., Bond, T., Fisher, R., Fearns, P., Dorji, P., & Evans, R. D. (2018). The effects of suspended sediment on coral reef fish assemblages and feeding guilds of north-west Australia. *Coral Reefs*, *37*(3), 659–673. https://doi.org/10.1007/s00338-018-1690-1

Mukherjee, S., & Heithaus, M. R. (2013). Dangerous prey and daring predators: A review. *Biological Reviews of the Cambridge Philosophical Society*, *88*(3), 550–563. https://doi.org/10.1111/brv.12014

Mumby, P. J. (2009). Herbivory versus corallivory: Are parrotfish good or bad for Caribbean coral reefs? *Coral Reefs*, *28*(3), 683–690. https://doi.org/10.1007/s00338-009-0501-0

Mumby, P. J., & Wabnitz, C. C. C. (2002). Spatial Patterns of Aggression, Territory Size, and Harem Size in Five Sympatric Caribbean Parrotfish Species. *Environmental Biology of Fishes*, *63*(3), 265–279. https://doi.org/10.1023/A:1014359403167

Nagy, K. A. (2005). Field metabolic rate and body size. *Journal of Experimental Biology*, *208*(9), 1621–1625. https://doi.org/10.1242/jeb.01553

Nagy, K. A., Girard, I. A., & Brown, T. K. (1999). Energetics of free-ranging mammals, reptiles, and birds. *Annual Review of Nutrition*, *19*, 247–277. https://doi.org/10.1146/annurev.nutr.19.1.247

Nelder, J. A., & Mead, R. (1965). A Simplex Method for Function Minimization. *The Computer Journal*, *7*(4), 308–313. https://doi.org/10.1093/comjnl/7.4.308

Nelson, S. G., & Wilkins, S. DeC. (1988). Sediment processing by the surgeonfish *Ctenochaetus striatus* at Moorea, French Polynesia. *Journal of Fish Biology*, *32*(6), 817–824. https://doi.org/10.1111/j.1095-8649.1988.tb05425.x

Nicholson, G. M., & Clements, K. D. (2021). Ecomorphological divergence and trophic resource partitioning in 15 syntopic Indo-Pacific parrotfishes (Labridae: Scarini). *Biological Journal of the Linnean Society*, *132*(3), 590–611. https://doi.org/10.1093/biolinnean/blaa210

Nicholson, G. M., & Clements, K. D. (2023). Fine-scale analysis of substrata grazed by parrotfishes (Labridae:Scarini) on the outer-shelf of the Great Barrier Reef, Australia. *Marine Biology*, *170*(10), 121. https://doi.org/10.1007/s00227-023-04277-2

Nicholson, G. M., & Clements, K. D. (2024). A role for encrusting, endolithic sponges in the feeding of the parrotfish *Scarus rubroviolaceus*? Evidence of further trophic diversification in Indo-Pacific Scarini. *Coral Reefs*, *43*(3), 541–556. https://doi.org/10.1007/s00338-024-02482-z

Nunes, L. T., Barneche, D. R., Lastrucci, N. S., Fraga, A. A., Nunes, J. A. C. C., Ferreira, C. E. L., & Floeter, S. R. (2021). Predicting the effects of body size, temperature and diet on animal feeding rates. *Functional Ecology*, *35*(10), 2229–2240. https://doi.org/10.1111/1365-2435.13872

Oakley, C. A., & Davy, S. K. (2018). Cell Biology of Coral Bleaching. In M. J. H. van Oppen & J. M. Lough (Eds.), *Coral Bleaching: Patterns, Processes, Causes and Consequences* (pp. 189–211). Springer International Publishing. https://doi.org/10.1007/978-3-319-75393-5_8

O'Hara, P. J., Murray, P. J., & Klieve, A. V. (2012). A review of the nutrition of Australian peramelid marsupials. *Australian Mammalogy*, *34*(2), 133–144. https://doi.org/10.1071/AM11008

Ong, L., & Holland, K. N. (2010). Bioerosion of coral reefs by two Hawaiian parrotfishes: Species, size differences and fishery implications. *Marine Biology*, *157*(6), 1313–1323. https://doi.org/10.1007/s00227-010-1411-y

Oppenheim, S. J., & Gould, F. (2002). BEHAVIORAL ADAPTATIONS INCREASE THE VALUE OF ENEMY-FREE SPACE FOR HELIOTHIS SUBFLEXA, A SPECIALIST HERBIVORE. *Evolution*, *56*(4), 679–689. https://doi.org/10.1111/j.0014-3820.2002.tb01379.x

Neuswanger, J. R., Wipfli, M. S., Rosenberger, A. E., & Hughes, N. F. (2016). Measuring fish and their physical habitats: versatile 2D and 3D video techniques with user-friendly software. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(12), 1861-1873.

Perry, C. T., & Larcombe, P. (2003). Marginal and non-reef-building coral environments. *Coral Reefs*, *22*(4), 427–432. https://doi.org/10.1007/s00338-003-0330-5

Petchey, O. L. (2003). Integrating Methods That Investigate How Complementarity Influences Ecosystem Functioning. *Oikos*, *101*(2), 323–330.

Piché, J., Iverson, S., Parrish, F., & Dollar, R. (2010). Characterization of forage fish and invertebrates in the Northwestern Hawaiian Islands using fatty acid signatures: Species and ecological groups. *Marine Ecology Progress Series*, *418*, 1–15. https://doi.org/10.3354/meps08814

Plass-Johnson, J. G., Bednarz, V. N., Hill, J. M., Jompa, J., Ferse, S. C. A., & Teichberg, M. (2018). Contrasting Responses in the Niches of Two Coral Reef Herbivores Along a Gradient of Habitat Disturbance in the Spermonde Archipelago, Indonesia. *Frontiers in Marine Science*, *5*. https://doi.org/10.3389/fmars.2018.00032

Polechová, J., & Barton, N. H. (2005). Speciation Through Competition: A Critical Review. *Evolution*, *59*(6), 1194–1210. https://doi.org/10.1111/j.0014-3820.2005.tb01771.x

Polunin, N. V. C., Harmelin-Vivien, M., & Galzin, R. (1995). Contrasts in algal food processing among five herbivorous coral-reef fishes. *Journal of Fish Biology*, *47*(3), 455–465. https://doi.org/10.1111/j.1095-8649.1995.tb01914.x

Pratchett, M. S., Hoey, A. S., & Wilson, S. K. (2014). Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. *Current Opinion in Environmental Sustainability*, *7*, 37–43. https://doi.org/10.1016/j.cosust.2013.11.022

Pratchett, M. S., Hoey, A. S., Wilson, S. K., Messmer, V., & Graham, N. A. J. (2011). Changes in Biodiversity and Functioning of Reef Fish Assemblages following Coral Bleaching and Coral Loss. *Diversity*, *3*(3), Article 3. https://doi.org/10.3390/d3030424

Purcell, S. W. (2000). Association of epilithic algae with sediment distribution on a windward reef in the northern Great Barrier Reef, Australia. *Bulletin of Marine Science*, *66*(1), 199–214.

Putra, R. D., Siringoringo, R. M., Abrar, M., Puranamasari, N. W., Bengen, D. G., Zamani, N. P., Subhan, B., Aji, L. P., Giyanto, G., Almanar, I. P., & Dollu, E. A. (2025). Reef fish resilience following a significant earthquake disaster in the Nias Islands, Indonesia. *Biodiversitas Journal of Biological Diversity*, *26*(4). https://doi.org/10.13057/biodiv/d260433

Pyke, G. (2019). Optimal foraging theory: An introduction. In J. C. Choe (Ed.), *Encyclopedia of animal behavior* (Vol. 2, pp. 111–117). Elsevier Academic Press. https://doi.org/10.1016/B978-0-12-809633-8.01156-0

Randall, J. E. (1956). A Revision of the Surgeon Fish Genus Acanthurus. *Pac Sci, 10(2),* 159-235.

Randall, J. E., & Clements, K. D. (2001). Second Revision of the Surgeonfish Genus Ctenochaetus (Perciformes: Acanthuridae), with Descriptions of Two New Species. Bernice Pauahi Bishop Museum.

Randall, J. E. (1997). *Fishes of the Great Barrier Reef and Coral Sea*. Honolulu : University of Hawaii Press. http://archive.org/details/fishesofgreatbar0000rand

Ranta, E., Juvonen, S.-K., & Peuhkuri, N. (1992). Further evidence for size-assortative schooling in sticklebacks. *Journal of Fish Biology*, *41*(4), 627–630. https://doi.org/10.1111/j.1095-8649.1992.tb02689.x

Reddy, S. K., & Balasubramanian, S. (2013). Carbonic acid: Molecule, crystal and aqueous solution. *Chemical Communications*, *50*(5), 503–514. https://doi.org/10.1039/C3CC45174G

Ricardo, G. F., Harper, C. E., Negri, A. P., Luter, H. M., Abdul Wahab, M. A., & Jones, R. J. (2021). Impacts of water quality on *Acropora* coral settlement: The relative importance of substrate quality and light. *Science of The Total Environment*, *777*, 146079. https://doi.org/10.1016/j.scitotenv.2021.146079

Riegl, B., Bruckner, A., Coles, S. L., Renaud, P., & Dodge, R. E. (2009). Coral Reefs. *Annals of the New York Academy of Sciences*, *1162*(1), 136–186. https://doi.org/10.1111/j.1749-6632.2009.04493.x

Rodrigues, J. N., Ortega, J. C. G., Petsch, D. K., Padial, A. A., Moi, D. A., & Figueiredo, B. R. S. (2023). A meta-analytical review of turbidity effects on fish mobility. *Reviews in Fish Biology and Fisheries*, *33*(4), 1113–1127. https://doi.org/10.1007/s11160-023-09785-4

Rosenberger, A. L. (1992). Evolution of feeding niches in new world monkeys. *American Journal of Physical Anthropology*, *88*(4), 525–562. https://doi.org/10.1002/ajpa.1330880408

Roth, F., Saalmann, F., Thomson, T., Coker, D. J., Villalobos, R., Jones, B. H., Wild, C., & Carvalho, S. (2018). Coral reef degradation affects the potential for reef recovery after disturbance. *Marine Environmental Research*, *142*, 48–58. https://doi.org/10.1016/j.marenvres.2018.09.022

Russ, G. R., Payne, C. S., Bergseth, B. J., Rizzari, J. R., Abesamis, R. A., & Alcala, A. C. (2018). Decadal-scale response of detritivorous surgeonfishes (family Acanthuridae) to no-take marine reserve protection and changes in benthic habitat. *Journal of Fish Biology*, *93*(5), 887–900. https://doi.org/10.1111/jfb.13809

Russ, G. R., Rizzari, J. R., Abesamis, R. A., & Alcala, A. C. (2021). Coral cover a stronger driver of reef fish trophic biomass than fishing. *Ecological Applications*, *31*(1), e02224. https://doi.org/10.1002/eap.2224

Russell, D. J., Thuesen, P. A., & Thomson, F. E. (2012). A review of the biology, ecology, distribution and control of Mozambique tilapia, *Oreochromis mossambicus* (Peters 1852) (Pisces: Cichlidae) with particular emphasis on invasive Australian populations. *Reviews in Fish Biology and Fisheries*, *22*(3), 533–554. https://doi.org/10.1007/s11160-011-9249-z

Rutz, C., & Bijlsma, R. G. (2006). Food-limitation in a generalist predator. *Proceedings. Biological Sciences*, *273*(1597), 2069–2076. https://doi.org/10.1098/rspb.2006.3507

Sakai, K., & Nakabo, T. (2006). Taxonomic reviews of two Indo-Pacific sea chubs, *Kyphosus cinerascens* (Forsskål, 1775) and *Kyphosus sydneyanus* (Günther, 1886). *Ichthyological Research*, *53*(4), 337–356. https://doi.org/10.1007/s10228-006-0355-1

Schaffelke, B., & Klumpp, D. W. (1998). Nutrient-limited growth of the coral reef macroalga Sargassum baccularia and experimental growth enhancement by nutrient addition in continuous flow culture. *Marine Ecology Progress Series*, *164*, 199–211. https://doi.org/10.3354/meps164199

Schoener, T. W. (1971). Theory of Feeding Strategies. *Annual Review of Ecology and Systematics*, *2*, 369–404.

Schoepf, V., Grottoli, A. G., Levas, S. J., Aschaffenburg, M. D., Baumann, J. H., Matsui, Y., & Warner, M. E. (2015). Annual coral bleaching and the long-term recovery capacity of coral. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1819), 20151887. https://doi.org/10.1098/rspb.2015.1887

Semmler, R. F., Brandl, S. J., Keith, S. A., & Bellwood, D. R. (2021). Fine-scale foraging behavior reveals differences in the functional roles of herbivorous reef fishes. *Ecology and Evolution*, *11*(9), 4898–4908. https://doi.org/10.1002/ece3.7398

Shepherd, S. A., Watson, J. E., Womersley, H. B. S., & Carey, J. M. (2009). *Long-term changes in macroalgal assemblages after increased sedimentation and turbidity in Western Port, Victoria, Australia*. *52*(3), 195–206. https://doi.org/10.1515/BOT.2009.036

Sherratt, T. N., & Wilkinson, D. M. (2009). *Big Questions in Ecology and Evolution*. Oxford University Press, Incorporated. http://ebookcentral.proquest.com/lib/aut/detail.action?docID=430616

Shultz, S., B. Bradbury, R., L. Evans, K., D. Gregory, R., & M. Blackburn, T. (2005). Brain size and resource specialization predict long-term population trends in British birds. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1578), 2305–2311. https://doi.org/10.1098/rspb.2005.3250

Sobel, J. M., Chen, G. F., Watt, L. R., & Schemske, D. W. (2010). THE BIOLOGY OF SPECIATION. *Evolution*, *64*(2), 295–315. https://doi.org/10.1111/j.1558-5646.2009.00877.x

Stafford-Smith, M. G. (1993). Sediment-rejection efficiency of 22 species of Australian scleractinian corals. *Marine Biology*, *115*(2), 229–243. https://doi.org/10.1007/BF00346340

Stafford-Smith, M. G., & Ormond, R. F. G. (1992). Sediment-rejection mechanisms of 42 species of Australian scleractinian corals. *Marine and Freshwater Research*, *43*(4), 683–705. https://doi.org/10.1071/mf9920683

Stanley, G. D., Jr. (1981). Early history of scleractinian corals and its geological consequences. *Geology*, *9*(11), 507–511. https://doi.org/10.1130/0091-7613(1981)9%253C507:EHOSCA%253E2.0.CO;2

Stevens, C. E., & Hume. ID, H. I. (1995). *Comparative physiology of the vertebrate digestive system.* https://www.cabidigitallibrary.org/doi/full/10.5555/19961408239

Suhonen, J., Korkeamäki, E., Salmela, J., & Kuitunen, M. (2014). Risk of Local Extinction of Odonata Freshwater Habitat Generalists and Specialists. *Conservation Biology*, *28*(3), 783–789. https://doi.org/10.1111/cobi.12231

Sura, S. A., Bell, A., Kunes, K. L., Turba, R., Songer, R., & Fong, P. (2021). Responses of two common coral reef macroalgae to nutrient addition, sediment addition, and mechanical damage. *Journal of Experimental Marine Biology and Ecology*, *536*, 151512. https://doi.org/10.1016/j.jembe.2021.151512

Sweatman, H., Delean, S., & Syms, C. (2011). Assessing loss of coral cover on Australia's Great Barrier Reef over two decades, with implications for longer-term trends. *Coral Reefs*, *30*(2), 521–531. https://doi.org/10.1007/s00338-010-0715-1

Tanner, J. E. (1995). Competition between scleractinian corals and macroalgae: An experimental investigation of coral growth, survival and reproduction. *Journal of Experimental Marine Biology and Ecology*, *190*(2), 151–168. https://doi.org/10.1016/0022-0981(95)00027-O

Tebbett, S. B., & Bellwood, D. R. (2020). Sediments ratchet-down coral reef algal turf productivity. *Science of The Total Environment*, *713*, 136709. https://doi.org/10.1016/j.scitotenv.2020.136709

Tebbett, S. B., & Bellwood, D. R. (2021). Algal turf productivity on coral reefs: A meta-analysis. *Marine Environmental Research*, *168*, 105311. https://doi.org/10.1016/j.marenvres.2021.105311

Tebbett, S. B., Bellwood, D. R., & Purcell, S. W. (2018). Sediment addition drives declines in algal turf yield to herbivorous coral reef fishes: Implications for reefs and reef fisheries. *Coral Reefs*, *37*(3), 929–937. https://doi.org/10.1007/s00338-018-1718-6

Tebbett, S. B., Goatley, C. H. R., & Bellwood, D. R. (2017a). Clarifying functional roles: Algal removal by the surgeonfishes *Ctenochaetus striatus* and *Acanthurus nigrofuscus*. *Coral Reefs*, *36*(3), 803–813. https://doi.org/10.1007/s00338-017-1571-z

Tebbett, S. B., Goatley, C. H. R., & Bellwood, D. R. (2017b). Fine sediments suppress detritivory on coral reefs. *Marine Pollution Bulletin*, *114*(2), 934–940. https://doi.org/10.1016/j.marpolbul.2016.11.016

Tebbett, S. B., Goatley, C. H. R., Huertas, V., Mihalitsis, M., & Bellwood, D. R. (2018). A functional evaluation of feeding in the surgeonfish *Ctenochaetus striatus*: The role of soft tissues. *Royal Society Open Science*, *5*(1), 171111. https://doi.org/10.1098/rsos.171111

Tebbett, S. B., Goatley, C. H. R., Streit, R. P., & Bellwood, D. R. (2020). Algal turf sediments limit the spatial extent of function delivery on coral reefs. *Science of The Total Environment*, *734*, 139422. https://doi.org/10.1016/j.scitotenv.2020.139422

Tebbett, S. B., Siqueira, A. C., & Bellwood, D. R. (2022). The functional roles of surgeonfishes on coral reefs: Past, present and future. *Reviews in Fish Biology and Fisheries*, *32*(2), 387–439. https://doi.org/10.1007/s11160-021-09692-6

Teh, L. S. L., Teh, L. C. L., & Sumaila, U. R. (2013). A Global Estimate of the Number of Coral Reef Fishers. *PLOS ONE*, *8*(6), e65397. https://doi.org/10.1371/journal.pone.0065397

Terraube, J., Arroyo, B., Madders, M., & Mougeot, F. (2011). Diet specialisation and foraging efficiency under fluctuating vole abundance: A comparison between generalist and specialist avian predators. *Oikos*, *120*(2), 234–244. https://doi.org/10.1111/j.1600-0706.2010.18554.x

Theodorakis, C. W. (1989). Size segregation and the effects of oddity on predation risk in minnow schools. *Animal Behaviour*, *38*(3), 496–502. https://doi.org/10.1016/S0003-3472(89)80042-9

Thurber, R. V., Burkepile, D. E., Correa, A. M. S., Thurber, A. R., Shantz, A. A., Welsh, R., Pritchard, C., & Rosales, S. (2012). Macroalgae Decrease Growth and Alter Microbial Community

Structure of the Reef-Building Coral, *Porites astreoides*. *PLOS ONE*, *7*(9), e44246. https://doi.org/10.1371/journal.pone.0044246

Tkachenko, K. S., Dung, V. V., Ha, V. T., & Huan, N. H. (2023). Coral reef collapse in South-Central Vietnam: A consequence of multiple negative effects. *Aquatic Ecology*, *57*(1), 65–83. https://doi.org/10.1007/s10452-022-09994-2

Trajano, E. (2001). Ecology of Subterranean Fishes: An Overview. *Environmental Biology of Fishes*, *62*(1), 133–160. https://doi.org/10.1023/A:1011841913569

Trapon, M. L., Pratchett, M. S., & Hoey, A. S. (2013). Spatial Variation in Abundance, Size and Orientation of Juvenile Corals Related to the Biomass of Parrotfishes on the Great Barrier Reef, Australia. *PLOS ONE*, *8*(2), e57788. https://doi.org/10.1371/journal.pone.0057788

Tresnati, J., Yasir, I., Aprianto, R., Yanti, A., Rahmani, P. Y., & Tuwo, A. (2019). Long-Term Monitoring of Parrotfish Species Composition in the Catch of Fishermen from the Spermonde Islands, South Sulawesi, Indonesia. *IOP Conference Series: Earth and Environmental Science*, *370*(1), 012015. https://doi.org/10.1088/1755-1315/370/1/012015

Tribollet, A., & Payri, C. (2001). Bioerosion of the coralline alga *Hydrolithon onkodes* by microborers in the coral reefs of Moorea, French Polynesia. *Oceanologica Acta*, *24*(4), 329–342. https://doi.org/10.1016/S0399-1784(01)01150-1

Trudel, M., Tremblay, A., Schetagne, R., & Rasmussen, J. B. (2000). Estimating food consumption rates of fish using a mercury mass balance model. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*(2), 414–428. https://doi.org/10.1139/f99-262

Tuttle, L. J., & Donahue, M. J. (2022). Effects of sediment exposure on corals: A systematic review of experimental studies. *Environmental Evidence*, *11*(1), 4. https://doi.org/10.1186/s13750-022-00256-0

Uehara, S. (1997). Predation on mammals by the chimpanzee (*Pan troglodytes*). *Primates*, *38*(2), 193–214. https://doi.org/10.1007/BF02382009

Van Der Ploeg, J., Jupiter, S., Hughes, A., Eriksson, H., Notere Boso, D., & Govan, H. (2020). *Coral reef conservation in Solomon Islands: Overcoming the policy implementation gap.* https://hdl.handle.net/20.500.12348/4460

Viana, I. G., & Bode, A. (2015). Variability in δ15N of intertidal brown algae along a salinity gradient: Differential impact of nitrogen sources. *Science of The Total Environment*, *512–513*, 167–176. https://doi.org/10.1016/j.scitotenv.2015.01.019

Wainwright, P. C., Bellwood, D. R., & Westneat, M. W. (2002). Ecomorphology of Locomotion in Labrid Fishes. *Environmental Biology of Fishes*, *65*(1), 47–62. https://doi.org/10.1023/A:1019671131001

Walling, D. E., & Fang, D. (2003). Recent trends in the suspended sediment loads of the world's rivers. *Global and Planetary Change*, *39*(1–2), 111–126.

Wang, X., Zoccola, D., Liew, Y. J., Tambutté, E., Cui, G., Allemand, D., Tambutté, S., & Aranda Lastra, M. (2021). The Evolution of Calcification in Reef-Building Corals. *Molecular Biology and Evolution*, *38*. https://doi.org/10.1093/molbev/msab103

Weber, M., de Beer, D., Lott, C., Polerecky, L., Kohls, K., Abed, R. M. M., Ferdelman, T. G., & Fabricius, K. E. (2012). Mechanisms of damage to corals exposed to sedimentation. *Proceedings of the National Academy of Sciences*, *109*(24), E1558–E1567. https://doi.org/10.1073/pnas.1100715109

Welsh, J. Q., & Bellwood, D. R. (2012). Spatial ecology of the steephead parrotfish (*Chlorurus microrhinos*): An evaluation using acoustic telemetry. *Coral Reefs*, *31*(1), 55–65. https://doi.org/10.1007/s00338-011-0813-8

Wernand, M. R., & Woerd, H. J. van der. (2010). Spectral analysis of the Forel-Ule ocean colour comparator scale. *Journal of the European Optical Society-Rapid Publications*, *5*, 10014s. https://doi.org/10.2971/jeos.2010.10014s

Wiedenmann, J., D'Angelo, C., Smith, E. G., Hunt, A. N., Legiret, F.-E., Postle, A. D., & Achterberg, E. P. (2013). Nutrient enrichment can increase the susceptibility of reef corals to bleaching. *Nature Climate Change*, *3*(2), 160–164. https://doi.org/10.1038/nclimate1661

Williams, I., & Polunin, N. (2001). Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. *Coral Reefs*, *19*(4), 358–366. https://doi.org/10.1007/s003380000121

Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R., & Butler, P. J. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: The case of the cormorant. *Journal of Animal Ecology*, *75*(5), 1081–1090. https://doi.org/10.1111/j.1365-2656.2006.01127.x

Wootton, R. J. (1985). Energetics of Reproduction. In P. Tytler & P. Calow (Eds.), *Fish Energetics: New Perspectives* (pp. 231–254). Springer Netherlands. https://doi.org/10.1007/978-94-011-7918-8_9

Wozniak, B., & Dera, J. (Eds.). (2007). Light Absorption by Suspended Particulate Matter (SPM) in Sea Water. In *Light Absorption in Sea Water* (pp. 167–294). Springer. https://doi.org/10.1007/978-0-387-49560-6_5

Yamano, H., Hori, K., Yamauchi, M., Yamagawa, O., & Ohmura, A. (2001). Highest-latitude coral reef at Iki Island, Japan. *Coral Reefs - CORAL REEF*, *20*, 9–12. https://doi.org/10.1007/s003380100137

Yamaoka, K. (1983). *Feeding Behaviour and Dental Morphology of Algae Scraping Cichlids (Pisces: Teleostei) in Lake Tanganyika*. https://doi.org/10.14989/68000

Yarlett, R., Perry, C., Wilson, R., & Philpot, K. (2018). Constraining species-size class variability in rates of parrotfish bioerosion on Maldivian coral reefs: Implications for regional-scale bioerosion estimates. *Marine Ecology Progress Series*, *590*, 155–169. https://doi.org/10.3354/meps12480

Ye, M., & Sun, Y. (2022). Review of the Forel–Ule Index based on in situ and remote sensing methods and application in water quality assessment. *Environmental Science and Pollution Research*, *29*(9), 13024–13041. https://doi.org/10.1007/s11356-021-18083-0

Zera, A. J., & Harshman, L. G. (2001). The Physiology of Life History Trade-Offs in Animals. *Annual Review of Ecology, Evolution, and Systematics*, *32*(Volume 32, 2001), 95–126. https://doi.org/10.1146/annurev.ecolsys.32.081501.114006

Zweifler, A., O'Leary, M., Morgan, K., & Browne, N. K. (2021). Turbid Coral Reefs: Past, Present and Future—A Review. *Diversity*, *13*(6), Article 6. https://doi.org/10.3390/d13060251

Glossary

3D: three-dimensional

AI: artificial intelligence

AIC: Akaike information criterion

ANOVA: analysis of variance

Anthropogenic: related to or caused by humans

Bayesian: a statistical approach that combines prior knowledge or information (such as known length–weight relationships of related species) with observed data to estimate parameters for data-poor species.

Benthic: associated with or living on the bottom or substrate of a body of water

Benthos: benthic organisms or communities of organisms

BMR: basal metabolic rate

CO_2: carbon dioxide

CO_3^{2-}: carbonate ion

Crustose: an organism that forms a thin crust-like layer over surfaces

EAM: epilithic algal matrix

Endolithic: living within the substrate

Epilithic: living on the surface of the substrate

Eutrophication: the process by which a body of water becomes enriched with nutrients (particularly nitrogen and phosphorus)

FMR: field metabolic rate

GAM: generalised additive model

GLM: generalised linear model

GPS: global positioning system

H_2CO_3: carbonic acid.

Homoscedasticity: data that display a constant variance for all levels of the independent variable

IP: initial phase

IQR: interquartile range

LMM: linear mixed model

Macroalgae: large multicellular algae which are visible to the naked eye

Meiofauna: small benthic invertebrates

Micro-autotroph: a microbe that fixes its own nitrogen from atmospheric diatomic nitrogen

Microphage: an organinism that feeds on microbial organisms

Microalgae: microscopic algae which are generally not visible to the naked eye and may be unicellular or form small cell colonies

Morphological: Relating to the form and structure of an organism

N: Nitrogen

Non-parametric test: a statistical hypothesis test that does not make assumptions about the distribution of the data being analysed. e.g. does not assume that the data is normally distributed.

NPP: net primary productivity

ODBA: overall dynamic body acceleration

Post-hoc: a statistical test which is done after initial testing such as ANOVA to determine pairwise differences between groups

QQ plot: quantile-quantile plot - a diagnostic plot for checking if residuals of a model are normally distributed

rRNA: ribisomal ribonucleic acid

SCFA: shorth chain fatty acid

SCUBA: self-contained underwater breathing apparatus

Stereovideo: a video system using two or more cameras, allowing for triangulation of video subjects in a 3D space

SST: sea surface temperature

TP: terminal phase

VIF: variance inflation factor

Zero-inflated: data with many zero values

Appendix

Table A1.

Vidsync event default attributes

Attribute	Length	Track	Bite	Aggression
Max # Points	2	No limit	No limit	No limit
Points 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 a bite of substrate is taken	Aggression to or from another fish

Note. Vidsync (Neuswanger, 2008) https://www.vidsync.org/HomePage

Table A2.

Environmental attributes and sampling information for sites at the Vavanga Reef

Site	Latitude	Longitude	Translation	Proximity	Average	Average
Ovuku	8.0611417° S	156.9669267° E	River	1	6	10
Batu	8.0614733° S	156.9664733° E	Rock	2	3	25.2
Paele	8.062875° S	156.9660433° E	Meeting	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

Table A2 continued

Site name	Average depth of rack placement (m)	Average SST (°C)	Number of times site sampled	Total available substrates	Total C. striatus tracked	Total IP C.bleekeri tracked	Total TP C.bleekeri tracked
Ovuku	1.8	30	6	7	6	2	0
Batu	3	30	6	9	8	1	17
Paele	5.17	30	6	14	10	4	6
Church	6.14	30	8	14	20	0	20
Pobuna	4.15	30	6	13	26	7	9

Table A3.

Sampling site distances (metres)

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	-

Table A4.

Percentage cover of substrates at each sampling site

	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
Diplostrea	2.50	4.17	2.50	15.00	15.00
EAM	0.00	3.33	7.50	13.89	18.75
Echinopora	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	0.00
Zoanthid	0.00	0.00	0.83	0.56	0.00

Table A5.

Percentage of total bites on each substrate and Manly's preference ratios

Species	**Site name**	**Substrate**	**% Cover**	**Total bites**	**Total bites**	**Manly's**
C. bleekeri	Ovuku	Coral rubble	-	7	100.00	-
C. bleekeri	Paele	Dead coral	36.67	8	75.00	2.05
C. bleekeri	Paele	EAM	7.50	2	25.00	3.33
C. bleekeri	Pobuna	EAM	25.83	4	50.00	1.94
C. striatus	Batu	EAM	3.33	74	100.00	30.00
C. striatus	Paele	Dead coral	36.67	16	26.37	0.72
C. striatus	Paele	EAM	7.50	44	73.63	9.82
C. striatus	Church	Dead coral	35.00	0	0.00	0.00
C. striatus	Church	EAM	13.89	24	100.00	7.20
C. striatus	Pobuna	Dead coral	30.83	18	11.76	0.38
C. striatus	Pobuna	EAM	25.83	133	88.24	03.42

Table A6.

*Raw data for each individual C. striatus recorded. Including mass (g), length (cm), mean velocity (cm s^{-1}), velocity (body lengths s^{-1}), FMR (**O2 g^{-1} d^{-1}), total bites, mean bite rate (min^{-1}), and mean bite distance (cm)***

site name	**individual id**	**Mass (g)**	**Length (cm)**	**mean velocity (cm s^{-1})**	**Velocity (body lengths s^{-1})**	**mg O2 g^{-1} d^{-1}**	**Total bites**	**Mean bite rate (min^{-1})**	**Mean bite distance (cm)**
Ovuku	Striatus_3	121.06	16.51	40.01	2.42	0.0557	0	0.00	
Ovuku	striatus_1	160.92	18.15	46.69	2.57	0.0397	0	0.00	
Ovuku	striatus_2	112.20	16.10	48.61	3.02	0.0253	0	0.00	
Ovuku	striatus_4	136.40	17.18	43.35	2.52	0.0689	0	0.00	
Ovuku	striatus_5	127.09	16.78	27.51	1.64	0.0925	0	0.00	
Ovuku	striatus_6	77.43	14.23	46.75	3.29	0.1429	0	0.00	
Paele	striatus_23	55.62	12.74	19.27	1.51	0.0214	0	0.00	
Paele	striatus_24	29.20	10.28	12.48	1.21	0.0120	11	66.60	12.50
Paele	striatus_22	51.70	12.43	24.93	2.00	0.0639	0	0.00	
Paele	striatus_15	62.52	13.25	18.49	1.40	0.0457	18	71.93	30.31
Paele	striatus_16	45.56	11.92	18.55	1.56	0.0353	10	67.35	37.36
Paele	striatus_17	47.50	12.09	25.39	2.10	0.0269	4	13.08	19.17
Paele	striatus_18	51.66	12.43	22.11	1.78	0.0231	3	5.13	53.03
Paele	striatus_19	63.14	13.29	24.63	1.85	0.0464	5	30.48	70.20
Paele	striatus_20	28.82	10.23	27.75	2.71	0.0371	8	59.94	58.32
Paele	striatus_21	52.45	12.49	22.71	1.82	0.0133	0	0.00	
Batu	striatus_10	33.91	10.80	21.08	1.95	0.0253	6	27.21	35.61
Batu	striatus_11	31.32	10.52	21.66	2.06	0.0321	11	78.49	39.26
Batu	striatus_12	44.60	11.84	18.94	1.60	0.0392	17	109.57	31.12
Batu	striatus_13	35.22	10.94	22.23	2.03	0.0229	6	41.34	57.73
Batu	striatus_14	36.64	11.09	15.38	1.39	0.0263	12	92.21	25.44
Batu	striatus_9	33.00	10.71	19.49	1.82	0.0188	8	50.48	25.85
Batu	striatus_7	48.85	12.20	38.39	3.15	0.0717	0	0.00	
Batu	striatus_8	32.63	10.67	24.97	2.34	0.0296	13	26.06	156.01
Pobuna	striatus_70	53.94	12.61	21.43	1.70	0.0305	5	30.27	58.92
Pobuna	striatus_71	40.24	11.44	21.92	1.92	0.0218	2	12.89	40.47
Pobuna	striatus_63	29.74	10.34	16.66	1.61	0.0195	14	80.69	41.14
Pobuna	striatus_64	44.80	11.85	18.12	1.53	0.0338	9	62.73	48.04
Pobuna	striatus_65	49.36	12.24	17.92	1.46	0.0304	17	1.27	53.58
Pobuna	striatus_66	41.16	11.52	21.25	1.84	0.0334	7	42.38	32.22
Pobuna	striatus_67	31.95	10.59	19.63	1.85	0.0299	16	94.02	39.28
Pobuna	striatus_68	24.27	9.66	14.05	1.45	0.0143	13	87.55	23.23
Pobuna	striatus_69	45.45	11.91	22.91	1.92	0.0420	11	83.46	40.37
Pobuna	striatus_58	74.66	14.05	40.03	2.85	0.1146	0	0.00	
Pobuna	striatus_59	50.55	12.34	17.92	1.45	0.0197	0	0.00	
Pobuna	striatus_60	50.62	12.35	18.29	1.48	0.0276	0	0.00	
Pobuna	striatus_61	90.24	14.97	33.15	2.21	0.0511	0	0.00	
Pobuna	striatus_62	90.24	14.97	35.52	2.37	0.0907	0	0.00	

Table A6 continued.

site name	**individual id**	**Mass (g)**	**Length (cm)**	**mean velocity (cm s^{-1})**	**Velocity (body lengths s^{-1})**	**mg O2 g^{-1} d^{-1}**	**Total bites**	**Mean bite rate (min^{-1})**	**Mean bite distance (cm)**
Pobuna	striatus_57	51.08	12.38	44.50	3.59	0.1005	7	65.56	70.49
Pobuna	striatus_50	43.08	11.70	16.08	1.37	0.0148	0	0.00	
Pobuna	striatus_51	26.39	9.94	26.60	2.68	0.0182	0	0.00	
Pobuna	striatus_52	25.97	9.88	29.18	2.95	0.0349	6	52.89	48.42
Pobuna	striatus_53	53.68	12.59	29.67	2.36	0.0611	5	41.05	45.29
Pobuna	striatus_54	26.39	9.94	18.87	1.90	0.0128	0	0.00	
Pobuna	striatus_55	38.07	11.23	20.89	1.86	0.0224	3	20.91	26.87
Pobuna	striatus_56	27.10	10.03	19.21	1.92	0.0170	4	12.89	11.86
Church	striatus_37	47.81	12.11	22.86	1.89	0.0452	0	0.00	
Church	striatus_38	49.33	12.24	24.48	2.00	0.0520	0	0.00	
Church	striatus_39	52.96	12.53	14.49	1.16	0.0248	0	0.00	
Church	striatus_40	45.79	11.94	23.71	1.99	0.0342	0	0.00	
Church	striatus_41	47.45	12.08	15.74	1.30	0.0186	0	0.00	
Church	striatus_42	42.50	11.65	19.67	1.69	0.0321	3	17.80	168.82
Church	striatus_43	50.18	12.31	22.37	1.82	0.0404	4	16.31	31.95
Church	striatus_44	56.64	12.82	19.65	1.53	0.0412	3	11.31	31.02
Church	striatus_45	55.85	12.76	25.85	2.03	0.0616	5	29.97	137.01
Church	striatus_30	25.01	9.76	31.85	3.26	0.0104	0	0.00	
Church	striatus_31	35.71	10.99	24.70	2.25	0.0168	0	0.00	
Church	striatus_32	51.13	12.39	25.08	2.03	0.0162	0	0.00	
Church	striatus_34	31.43	10.53	26.10	2.48	0.0346	5	40.50	37.78
Church	striatus_35	41.13	11.52	24.89	2.16	0.0209	0	0.00	
Church	striatus_36	24.70	9.72	24.73	2.54	0.0234	4	24.22	13.11
Pobuna	striatus_46	40.45	11.46	23.17	2.02	0.0432	15	103.34	26.71
Pobuna	striatus_47	7.95	6.66	32.49	4.88	0.0163	8	56.42	88.08
Pobuna	striatus_48	104.10	15.70	31.23	1.99	0.1280	8	69.49	50.27
Pobuna	striatus_49	59.14	13.00	27.78	2.14	0.0525	0	0.00	
Church	striatus_25	86.27	14.75	18.50	1.25	0.0172	0	0.00	
Church	striatus_26	98.00	15.39	22.35	1.45	0.0265	0	0.00	
Church	striatus_27	117.72	16.36	24.08	1.47	0.0367	0	0.00	
Church	striatus_28	51.45	12.41	10.07	0.81	0.0168	0	0.00	
Church	striatus_29	51.91	12.45	9.19	0.74	0.0148	0	0.00	

Table A7.

*Raw data for each individual C. bleekeri recorded. Including phase, mass (g), length (cm), mean velocity (cm s^{-1}), velocity (body lengths s^{-1}), FMR (**O_2 g^{-1} d^{-1}), total bites, mean bite rate (min^{-1}), and mean bite distance (cm)***

site name	individual id	phase	Mass (g)	Length (cm)	mean velocity (cm s^{-1})	Velocity (body lengths s^{-1})	mg O2 g^{-1} d^{-1}	Total bites	Mean bite rate (min^{-1})	Mean bite distance (cm)
Ovuku	bleekeri(ip)_1	Initial Phase	344.56	21.40	48.66	2.27	0.2352	7	26.39	363.35
Ovuku	bleekeri(ip)_2	Initial Phase	551.43	25.10	84.11	3.35	0.5252	0	0.00	
Paele	bleekeri(ip)_6	Initial Phase	254.00	19.29	31.09	1.61	0.1107	2	8.44	27.64
Paele	bleekeri(ip)_7	Initial Phase	274.17	19.80	21.89	1.11	0.0597	2	10.20	12.63
Paele	bleekeri_22	Terminal Phase	723.19	27.52	33.33	1.21	0.2077	3	18.16	16.46
Paele	bleekeri_23	Terminal Phase	818.40	28.70	29.11	1.01	0.1754	3	18.35	99.26
Paele	bleekeri_21	Terminal Phase	433.03	23.12	72.38	3.13	0.3343	0	0.00	
Paele	bleekeri(ip)_4	Initial Phase	528.89	24.75	44.25	1.79	0.1751	0	0.00	
Paele	bleekeri(ip)_5	Initial Phase	220.55	18.39	46.52	2.53	0.0892	0	0.00	
Paele	bleekeri_18	Terminal Phase	314.00	20.73	45.57	2.20	0.1233	0	0.00	
Paele	bleekeri_19	Terminal Phase	565.59	25.32	65.80	2.60	0.2406	0	0.00	
Paele	bleekeri_20	Terminal Phase	723.96	27.53	62.17	2.26	0.2943	0	0.00	
Batu	bleekeri_15	Terminal Phase	789.18	28.19	84.02	2.98	0.7306	0	0.00	
Batu	bleekeri_16	Terminal Phase	471.28	23.80	84.65	3.56	0.5664	0	0.00	
Batu	bleekeri_17	Terminal Phase	289.12	20.16	61.33	3.04	0.1705	0	0.00	
Batu	bleekeri(ip)_3	Initial Phase	176.58	17.05	86.57	5.08	0.0499	0	0.00	
Batu	bleekeri_11	Terminal Phase	521.31	24.63	83.33	3.38	0.4363	0	0.00	
Batu	bleekeri_12	Terminal Phase	699.45	27.21	61.28	2.25	0.3745	0	0.00	
Batu	bleekeri_13	Terminal Phase	329.74	21.08	37.25	1.77	0.0763	0	0.00	
Batu	bleekeri_14	Terminal Phase	536.23	24.86	125.85	5.06	0.1789	0	0.00	
Batu	bleekeri_10	Terminal Phase	450.19	23.43	71.41	3.05	0.3482	0	0.00	
Batu	bleekeri_4	Terminal Phase	467.56	23.73	72.48	3.05	0.3466	0	0.00	
Batu	bleekeri_5	Terminal Phase	474.56	23.85	75.14	3.15	0.3938	0	0.00	
Batu	bleekeri_6	Terminal Phase	576.38	25.48	88.24	3.46	0.4857	0	0.00	
Batu	bleekeri_7	Terminal Phase	364.82	21.82	114.71	5.26	0.4013	0	0.00	
Batu	bleekeri_8	Terminal Phase	443.77	23.32	75.40	3.23	0.4227	0	0.00	
Batu	bleekeri_9	Terminal Phase	368.63	21.89	63.37	2.89	0.2617	0	0.00	
Batu	bleekeri_1	Terminal Phase	1068.61	31.42	78.36	2.49	1.1371	0	0.00	
Batu	bleekeri_2	Terminal Phase	350.91	21.53	61.73	2.87	0.2088	0	0.00	
Batu	bleekeri_3	Terminal Phase	537.63	24.89	54.43	2.19	0.1655	0	0.00	
Pobuna	bleekeri_54	Terminal Phase	1254.39	33.18	104.33	3.14	1.2674	0	0.00	
Pobuna	bleekeri_52	Terminal Phase	556.81	25.18	76.69	3.05	0.5197	0	0.00	
Pobuna	bleekeri_53	Terminal Phase	514.42	24.52	73.93	3.02	0.6245	4	19.98	105.21
Pobuna	bleekeri(ip)_10	Initial Phase	175.27	17.01	34.45	2.03	0.0656	0	0.00	
Pobuna	bleekeri(ip)_11	Initial Phase	245.34	19.07	40.49	2.12	0.1094	0	0.00	
Pobuna	bleekeri(ip)_12	Initial Phase	286.59	20.10	35.44	1.76	0.1080	0	0.00	
Pobuna	bleekeri(ip)_13	Initial Phase	286.59	20.10	58.95	2.93	0.1944	0	0.00	
Pobuna	bleekeri(ip)_14	Initial Phase	446.07	23.36	66.18	2.83	0.2664	0	0.00	

Table A7 continued.

site name	individual id	phase	Mass (g)	Length (cm)	mean velocity (cm s^{-1})	Velocity (body lengths s^{-1})	mg O2 g^{-1} d^{-1}	Total bites	Mean bite rate (min^{-1})	Mean bite distance (cm)
Pobuna	bleekeri_51	Terminal Phase	627.32	26.22	53.94	2.06	0.3205	0	0.00	
Church	bleekeri_29	Terminal Phase	387.13	22.26	38.87	1.75	0.1926	0	0.00	
Church	bleekeri_30	Terminal Phase	496.54	24.22	67.00	2.77	0.2920	0	0.00	
Church	bleekeri_31	Terminal Phase	473.04	23.83	33.50	1.41	0.2011	0	0.00	
Church	bleekeri_32	Terminal Phase	297.52	20.36	38.68	1.90	0.1503	0	0.00	
Church	bleekeri_33	Terminal Phase	283.12	20.02	39.95	2.00	0.1313	0	0.00	
Church	bleekeri_34	Terminal Phase	349.95	21.51	44.81	2.08	0.3398	0	0.00	
Church	bleekeri_35	Terminal Phase	467.56	23.73	54.20	2.28	0.3260	0	0.00	
Church	bleekeri_36	Terminal Phase	416.69	22.82	42.34	1.86	0.2844	0	0.00	
Church	bleekeri_37	Terminal Phase	366.65	21.85	39.65	1.81	0.2259	0	0.00	
Church	bleekeri_38	Terminal Phase	481.45	23.97	54.54	2.28	0.3879	0	0.00	
Church	bleekeri_39	Terminal Phase	450.47	23.44	42.20	1.80	0.2916	0	0.00	
Church	bleekeri_40	Terminal Phase	780.93	28.25	50.90	1.80	0.5398	0	0.00	
Church	bleekeri_41	Terminal Phase	450.19	23.43	55.41	2.36	0.2882	0	0.00	
Church	bleekeri_42	Terminal Phase	400.08	22.51	72.06	3.20	0.4348	0	0.00	
Church	bleekeri_43	Terminal Phase	424.81	22.97	59.31	2.58	0.3964	0	0.00	
Pobuna	bleekeri(ip)_8	Initial Phase	226.72	18.56	26.62	1.43	0.0537	0	0.00	
Pobuna	bleekeri(ip)_9	Initial Phase	281.50	19.98	34.29	1.72	0.1355	0	0.00	
Pobuna	bleekeri_46	Terminal Phase	676.98	26.91	58.03	2.16	0.4010	0	0.00	
Pobuna	bleekeri_47	Terminal Phase	668.64	26.80	52.50	1.96	0.3370	0	0.00	
Pobuna	bleekeri_48	Terminal Phase	409.05	22.68	82.95	3.66	0.2768	0	0.00	
Pobuna	bleekeri_49	Terminal Phase	421.01	22.90	32.85	1.43	0.1597	5	25.19	70.71
Pobuna	bleekeri_50	Terminal Phase	1940.07	38.47	115.69	3.01	1.3245	0	0.00	
Church	bleekeri_24	Terminal Phase	661.53	26.70	56.71	2.12	0.4304	0	0.00	
Church	bleekeri_25	Terminal Phase	673.28	26.86	48.73	1.81	0.1987	0	0.00	
Church	bleekeri_26	Terminal Phase	563.81	25.29	90.59	3.58	0.5950	0	0.00	
Church	bleekeri_27	Terminal Phase	634.89	26.33	81.45	3.09	0.5704	0	0.00	
Church	bleekeri_28	Terminal Phase	610.34	25.98	65.16	2.51	0.5568	0	0.00	