# Variation in corallite morphology and Symbiodiniaceae communities of corals at the Rangitāhua archipelago

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# General Abstract

Anthropogenic activity is causing climate change, exposing corals to intolerable conditions. The depletion of corals can severely degrade reef-associated species. Therefore, a greater understanding of corals' responsiveness to environmental conditions is needed, especially near their tolerance limits. Here, we examined the corallite morphology and Symbiodiniaceae community of corals at Rangitāhua (the Kermadec Islands), New Zealand. Due to the high latitude of Rangitāhua, corals and their symbionts experience light conditions near their lower tolerance limit, therefore we expected to find morphological signatures of adaptation to low-light conditions indicative of a trophic shift, Symbiodiniaceae depth zonation (5-30m), and a high abundance of the physiologically diverse coral symbiont *Cladocopium*. We also expected that environments might differ among islands, and therefore corallite morphology and symbiont communities would vary among locations. We found a high abundance of *Cladocopium*, and a much lower abundance of *Symbiodinium, Breviolum,* and *Fugacium.* At Napier Island, Symbiodiniaceae communities of *Astrea curta, Hydnophora pilosa,* and *Montipora spongodes* had the fewest unique Symbiodiniaceae types and were most compositionally dissimilar to the communities at the more sheltered Meyer Islands. Furthermore, corals at Napier Island had small, densely arranged corallites, with few, short septa, suggesting low water flow. Over depth, shallow corals (5m) had high tissue coverage (i.e., large, close corallites of *M. spongodes* and greater corallite coverage of *H. pilosa*) presumably to optimise autotrophic feeding in energy-rich waters. The greater corallite spacing seen over depth could be a mechanism to alleviate self-shading but could also be indicative of poor health. The Symbiodiniaceae communities at intermediate depths (10-20m) were taxonomically richer and compositionally dissimilar from communities at the edges of the depth gradient (5-10m and 20-25m). Although there were general trends, the corallite morphology and Symbiodiniaceae community of *Goniastrea favulus, Montipora capricornis,* and *Turbinaria frondens* were relatively consistent across the depth and locations sampled. Nearly half of the Symbiodiniaceae types identified (22/42) were undocumented, highlighting the significance of marginal populations to our understanding of how environmental conditions can influence corals. Our examination of the coral population at Rangitāhua

further supports the well-documented trends of a high abundance of *Cladocopium* symbionts at high latitudes, specialised corallite morphology to increase the light-gathering abilities of shallow corals, and increased corallite spacing over depth, as well as Symbiodiniaceae depth zonation and diversity among nearby locations. Overall, we provide insights into the morphological and symbiont diversity of marginal coral populations in low light conditions, helping us to understand how corals may persist, and perhaps refuge, in high latitudes.

# Contents

# Chapter 1: General introduction

## 1.1 Climate change impacts coral reefs

Anthropogenic climate change is exceeding the rate of natural environmental change seen on Earth in the past 400,000 years, thereby threatening numerous species (Hughes et al., 2003; Karl & Trenberth, 2003; Hoegh-Guldberg et al., 2007). As heat energy gradients shift poleward, species are forced to adapt, acclimate, or move to new locations to avoid population decline. In particular, corals, the foundational species of reef ecosystems, are highly sensitive to changing conditions (Hughes et al., 2003). The duration and magnitude of warming events are closely correlated with the severity of degradation of corals' symbionts (Symbiodiniaceae) (Miller et al., 2011; Arora et al., 2021; Jiang et al., 2021). Corals often expel degraded Symbiodiniaceae and are left without pigmentation, a phenomenon known as mass coral bleaching, leading to higher mortality rates (Douglas, 2003; McWilliams et al., 2005). Species may recover from heat stress if conditions return to tolerable levels for an extended period (Tomanek & Somero, 2000). However, climate change during the Anthropocene era has increased the frequency of warming events by three-fold (1985-2006) (Heron et al., 2016) and future predictions estimate corals will annually experience conditions near their upper heat threshold (Jiang et al., 2021).

Some species may be able to shift their range to avoid unfavourable conditions caused by one stressor (Perry et al., 2005), however, as heat energy gradients shift, light energy supply will likely remain stable, creating unfamiliar environmental conditions for some species (Spence & Tingley, 2020). Furthermore, during winter in high latitudes, light energy travels further through the atmosphere at a more acute angle, compared to equatorial conditions, thereby restricting the amount of light energy available (Muir et al., 2015). As a result of the lower light intensity at high latitudes, poleward shifts to avoid heat stress may pressure light-dependent species to increasingly shallower waters to receive a sufficient light supply to function (Muir et al., 2015; Spence & Tingley, 2020). During periods of reduced light energy, the weight and respiratory rate of *Pocillopora damicornis* reduced (Gaither & Rowan, 2010). Exposure to conditions below a species' light tolerance can degrade their functionality. Furthermore, corals' calcification rates can have diverse responses to variations in oceanic chemistry (Jury et al., 2010), which can fluctuate among relatively close locations (Qu et al., 2015). Local stressors (i.e anthropogenic fine sediment, land use, overfishing) can have synergistic effects with climate change accumulating greater risk for species' survival (Hoegh-Guldberg et al., 2007). For example, exposure to anthropogenic fine sediment reduces *Porites astreoides*' tolerance to increasing temperatures (Fourney & Figueiredo, 2017). In summary, the specific environmental conditions that populations experience can significantly impact their species' tolerance and survival.

Current climatic predictions estimate that by the end of this century 90% of coral reefs may suffer degradation of their long-term health (Grottoli et al., 2014). Coral reefs have experienced the most rapid increase of economic value per land coverage (4101.44% from 1997 to 2011) of all marine biomes yet have recorded the fastest global declines (-54.84%) (Costanza et al., 2014). The degrading of reef ecosystems threatens the livelihood and food security of more than 100 million people (Ferrario et al., 2014) in some of the poorest and most food-insecure populations (Teh et al., 2013; Cabral & Geronimo, 2018). For example, in the Philippines, declining reef ecosystems cause fishers to travel further from home, for longer durations, and have lower catch rates (Muallil et al., 2014; Anticamara & Go, 2016). On a commercial scale, reef ecosystems function as a habitat and nursery for marine life (Brander et al., 2012) which supports the socio-economic well-being of 6 million reef fishers. Moreover, within the global tourism industry, reef degradation threatens the annual US$35.8 billion reef tourism industry (Spalding et al., 2017). The income produced from reef tourism can fund better quality health care for the citizens of resource-limited tropical regions (Hatcher & Hatcher, 2004). Additionally, the physical presence of reef ecosystems can protect coastal communities from wave action by 97% (Ferrario et al., 2014; Hoegh-Guldberg et al., 2019). Therefore, the well-being of coral reefs is of high conservation importance.

As a foundational species, corals' survival defines the survival of the whole reef ecosystem. By providing structural habitat, foundational species (such as corals) can expand the distribution range of associated species (Crain & Bertness, 2006), as well as the abundance and functionality (Stella et al., 2011). However, foundational species must be in sufficient abundance and health to provide an ecosystem service (Layton et al., 2019). Although the physical presence of dead corals, before erosion, may provide structure, functioning corals are essential for most coral-associated species (Alvarez-Filip et al., 2009; Stella et al., 2011). Furthermore, reef-associated species can exhibit a preference for particular coral species (Stella et al., 2011). As a result, the loss of even a few corals could have far-reaching impacts on the reef ecosystem (Stella et al., 2011).

## 1.2 Mechanisms for surviving climate change impacts

Phenotypic variation, in response to the environment, can relieve the intensity of stress that species may experience during changing conditions (Snell-Rood et al., 2018) and expand their tolerance (Ho & Zhang, 2018). Phenotypic variation can occur through phenotypic plasticity (varying phenotypic expression of a single genotype, based on environmental conditions), as well as genetically (through the natural selection of particular phenotypes that are linked to genotypes) (R. J. Fox et al., 2019). Some phenotypic variability is likely due to a combination of both mechanisms, such as the larger limbs and shorter heads of green anole (*Anolis carolinensis*) near the Equator, compared to higher latitude populations (Jaffe et al., 2016). Alternatively, between two genetically distinct groups of pumpkinseed sunfish (*Lepomis gibbosus*) there was no difference in muscle mass, reflective of its prey-crushing ability, however, phenotypic plasticity was identified as the main factor of varying jaw morphology (Mittelbach et al., 1999). Phenotypic variation often occurs in feeding structures as feeding is essential for survival (Mcalister & Miner, 2018), and such variety within and among populations can expand a species' overall environmental tolerance and broaden the species' potential nutrient supply (Jaffe et al., 2016).

Corals are mixotrophs as they can feed through autotrophic and heterotrophic techniques (Lesser et al., 2010). Specifically, corals can obtain nutritional energy through symbiotic photosynthesis, from dinoflagellate algal endosymbionts ('zooxanthellae') of the family Symbiodiniaceae (LaJeunesse et al., 2018); or through heterotrophic activity, obtaining zooplankton which flow through the water column (Burmester et al., 2018; Mies et al., 2018). Environmental conditions such as light energy availability and water flow are the main drivers of corals' trophic shifts (Lesser et al., 2010; Williams et al., 2018). For instance, high summer temperatures can induce heat stress for Symbiodiniaceae of *Mussismilia hispida*, consequently causing coral bleaching (Mies et al., 2018). Corals can compensate through greater heterotrophic feeding (Mies et al., 2018). Such variation in corals' trophic behaviour can be reflected in their corallite morphology, including septa characteristics (Einbinder et al., 2009; Palazzo et al., 2021). For example, the distinct deep *Montastraea cavernosa* morphology (i.e., large inter-corallite spacing with short septa) reduces intra- and inter-corallite self-shading which can promote corals' light-gathering abilities and increase photosynthetic rates in low-energy conditions (Ow & Todd, 2010; Goodbody-Gringley & Waletich, 2018).

The identity and diversity of symbionts can also cause an expansion and variation of corals' tolerance (Gerz et al., 2018). Corals' heat tolerance can be influenced by their Symbiodiniaceae community (Berkelmans & van Oppen, 2006; Sampayo et al., 2008; LaJeunesse et al., 2010). For instance, *Acropora millepora* exhibits a 1-1.5°C increased heat tolerance when *Durusdinium* symbiont type (formally clade D) are highly abundant in their tissues (Berkelmans & van Oppen, 2006). As a result, as environmental conditions vary over geographic gradients, such as the reduction of heat energy over depth, *Seriatopora hystrix* displayed a shift of Symbiodiniaceae genera from *Durusdinium*- to *Cladocopium*-dominated colonies (Cooper et al., 2011). As environmental conditions change, corals can rapidly respond through a quantitative change in the relative abundance of existing symbiont (shuffling), as well as a qualitative change by recombination with additional Symbiodiniaceae acquired from the surrounding water column (switching), to re-establish their Symbiodiniaceae communities to better align with their new conditions (Baker, 2003; Boilard et al., 2020). However, restructuring Symbiodiniaceae communities can only provide finite aid, as frequent renewal of Symbiodiniaceae increases corals' exposure to disease and viruses (Lawrence et al., 2017; Boilard et al., 2020).

## 1.3 The Rangitāhua (Kermadec Islands) archipelago: a marginal coral community

The pristine Rangitāhua archipelago (the Kermadec Islands; 29° to 31°S; Figure 2.1 (a)) is located 900km north of the New Zealand mainland within the Tonga-Kermadec ridge (Karig, 1970). Rangitāhua harbours one of the most isolated and highest latitude shallow-water Scleractinian coral populations in the southern hemisphere (Wicks et al., 2010a). Since 1990, the volcanic archipelago (Nelson et al., 2018), and surrounding waters (12 nautical miles) have been protected within The Kermadec Islands Marine Reserve (Duffy & Ahyong, 2015). As a result of geographic isolation and government protection, there is an absence of local anthropogenic stressors, such as terrestrial runoff and overfishing (Wicks et al., 2010a; Edgar et al., 2014). The marine ecosystem surrounding Rangitāhua is exposed to high wave action and varying water flow conditions (Wicks et al., 2010a; Sutton et al., 2012), and has low connectivity between closely located sites (<1km) (Wood & Gardner, 2007). The relatively recent geographic history of the islands (<2.58 million years) (Brook, 1998) is likely an important factor in the composition of the ecosystem (Schiel et al., 1986).

Within the marine ecosystem at Rangitāhua, the greatest habitat and species diversity are identified surrounding Raoul Island (Francis et al., 1987; Brook, 1999; Duffy & Ahyong, 2015), where many taxa (filamentous/fleshy macroalgal and soft and hard corals) have exhibited the highest abundance identified at Meyer Island (Wicks et al., 2010a). The fish populations are constructed of a mixture of temperate and tropical species (Schiel et al., 1986). Surrounding Raoul Island, echinoids and coral colonies (hard and soft) have patchy distributions. The abundance of hard corals, like other local taxa (fish and soft coral), is highest in shallow waters (20-40%; 1-6m) (Duffy & Ahyong, 2015). Additionally, corals have a second peak abundance at 18-25m (15-25%) (Duffy & Ahyong, 2015). Although the coverage of corals at Rangitāhua is similar to other high latitude populations (5-8%; Julian Rocks and Cook Island, NSW AUS), there has been significantly less diversity identified in the corals at Rangitāhua (16 species) (Wicks et al., 2010a) (11 species) (Richards & Liggins, 2015).

Despite being one of the most marginal locations of Scleractinia corals in the world, knowledge about the coral population at Rangitāhua is still limited (Brook, 1999; Gardner et al., 2006; Wicks et al., 2010a). Assessments of Scleractinian coral morphology at Rangitāhua are limited to the mesophotic corals (>50m) which are heterotrophic (Cairns, 1995). *Anthemiphyllia dentata* at Rangitāhua displayed intrapopulation variation and were smaller, with a more concave corallum and fewer septa in comparison to counterparts around the globe (Cairns, 1995). Furthermore, a prior assessment of the shallow coral-Symbiodiniaceae at Rangitāhua (5-10m), via internal transcribed spacer region denaturing gradient gel electrophoresis fingerprints ITS2-DGGE, was limited to identifying only the most abundant Symbiodiniaceae type per host (Wicks et al., 2010b). Symbiodiniaceae from the genus *Cladocopium* (formally clade C) were commonly identified, along with a rarer presence of *Breviolum* (formally clade B) in soft corals (Wicks et al., 2010b). Advances in genomic research such as next-generation sequencing (NGS) technologies have enabled parallel sequencing of many DNA fragments simultaneously, and bioinformatic pipelines can now provide higher resolution genetic delineations and identify the whole community of Symbiodiniaceae present in corals (Hume et al., 2019).

## 1.4 Thesis overview

Our research objective is to contribute to the knowledge of coral morphology and symbionts at Rangitāhua; one of the highest latitude and most isolated shallow-water coral populations in the world. Through assessment of corallite morphology, as well as the assessment of Symbiodiniaceae taxonomic richness and community composition of corals, we aim to better understand the variation of corals over depth and space. Composed of four chapters; chapters two and three have been prepared as independent manuscripts for submission to peer-reviewed scientific journals. Consequently, there is some repetition of content throughout the chapters. These manuscripts will be submitted with co-authors, therefore I use a plural first-person in Chapters two and three. Nonetheless, the thesis research is my own, completed under the guidance of my academic supervisors.

**Chapter two** examines the morphological variation of corals at Rangitāhua by measuring corallites and their structural support to calculate principal component traits over geographic gradients. Corallite traits that increase light-gathering abilities are known to increase over depth (Ow & Todd, 2010; Goodbody-Gringley & Waletich, 2018). However, despite well-documented morphological variation in corals (Goodbody-Gringley & Waletich, 2018; Soto et al., 2018; Kahng et al., 2019), little is known about the morphology of corals at Rangitāhua. We examine the trend in corallite (and septa) morphology over depth and among locations. Next, we investigate trends between corallite morphology indicative of autotrophic and/or heterotrophic feeding behaviour. We predict corallites will have less structural support to alleviate self-shading over the depth gradient, along with morphological variation in response to environmental variation. Additionally, we expect to find indications of trophic zonation. Overall, we aim to understand how the morphology of the marginal coral population at Rangitāhua varies over small-scale geographic gradients so that we can better predict how corals may respond to decoupling light and heat energy gradients as climate change occurs.

**Chapter three** examines the variation in coral-symbionts relationships at Rangitāhua. Based on the ecological diversity of Symbiodiniaceae communities, coral hosts can display distinct environmental tolerances (Baker et al., 2004; Berkelmans & van Oppen, 2006; Yuyama et al., 2016; Ziegler et al., 2017), therefore, greater variation in Symbiodiniaceae communities can broaden a coral's tolerance range (Bongaerts et al., 2015). To expand our knowledge of coral- Symbiodiniaceae symbioses at Rangitāhua, we identify the genera and assess the taxonomic richness and composition of Symbiodiniaceae communities over depth and space. Following prior research of other high latitude populations, we expect to find an overall high abundance of *Cladocopium* (Wicks et al., 2010b; Cooper et al., 2011). Additionally, we predict variation in Symbiodiniaceae community composition and taxonomic richness across geographic gradients, associated with the varying environmental conditions. We aim to better understand the coral-Symbiodiniaceae relationships of a population near the edge of its tolerance range to predict the future responses of corals as light and heat energy gradients further decouple.

In **chapter four** I synthesise the findings of chapters two and three to provide a greater understanding of corals’ response to environmental variation at Rangitāhua. Furthermore, I connect the evident variation in corallite morphology and corals’ symbiosis, over depth and among locations, to indications of shifts in trophic behaviour and possible impact on their ecosystem. I discuss the limitations of my study regarding limited sampling and lack of in-depth environmental knowledge of the specific islands. Furthermore, I provide suggestions for further research to expand on our findings and better understand the variation in the coral population at Rangitāhua.

# Chapter 2: Variation in corallite morphology at the Rāngitahua archipelago

## 2.1 Abstract

Anthropogenic climate change may force corals to endure conditions beyond their tolerance. Coral morphology can be influenced by environmental conditions and can alter corals’ capacity to endure particular conditions. Additionally, variation in coral morphology, in response to environmental change, can reflect corals’ trophic feeding patterns. Here, we assessed the variation of corallite morphology across geographic gradients for one of the highest latitude, marginal, coral populations at Raoul Island, in the Rangitāhua archipelago (Kermadec Islands), New Zealand. We examined the corallite morphology (and structural support) of six coral taxa, over depth and among locations. We found distinct morphology across the observed depth gradient (5-30m) but patterns varied among taxa. For instance, presumably, to increase their light gathering abilities and optimise autotrophic feeding in energy-rich waters, the corallites of the shallowest *Montipora spongodes* were relatively large and close whilst *Hydnophora pilosa* had high corallite coverage with short septa. Additionally, the corallites of *M. spongodes* were further apart with shorter septa as depth increased (5-30m), perhaps to alleviate self-shading as energy reduced however, excessive spacing may also be indicative of poor health, and unexpectedly the structural support of *Montipora capricornis, Goniastrea favulus,* and *H. pilosa* increased over depth. Among locations, the corallites of *M. spongodes* were small and densely arranged, with few short septa at Napier Island suggesting low water flow. Although there were general trends of varying morphology, the morphology of *G. favulus, M. capricornis,* and *Turbinaria frondens* was relatively consistent over depth and space. Our findings at Rangitāhua support the well-document trends of specialised shallow corallite morphology presumably to increase the light-gathering ability in energy-rich waters, increased corallite spacing over depth, and variation in corallite morphology among locations. Overall, this study provides insight into the morphological variation of a marginal coral population, to better inform predictions of corals' response to Anthropogenic induced environmental changes.

## 2.2 Introduction

Many species rely on primary energy — heat and light. Low latitudes and shallower waters have a greater energy supply than high latitudes and deeper waters (Muir et al., 2015). Species experiencing conditions beyond their tolerance, especially suddenly and/or frequently, can threaten the health of organisms (Jansen et al., 1998; Djurichkovic et al., 2019; Magel et al., 2020). For example, during periods of insufficient light energy, marine and terrestrial plants' photosynthetic ability is restricted (Jansen et al., 1998; Ralph et al., 2007). However, intervals of excessive light energy can damage plant cells and inhibit their growth (Gieskes & Buma, 1997; Jansen et al., 1998). For fish, phases of insufficient heat energy can reduce respiratory function (Djurichkovic et al., 2019), whilst periods of excessive heat energy can cause physiological stress and, consequently, reduce biomass (Magel et al., 2020). Furthermore, the duration of the post-stress period can impact a species' likelihood of recovery. For instance, after heat stress, the brown turban snail (*Tegula brunnea*) requires stable conditions for a longer period to repair protein damage than the black turban snail (*Tegula funebralis*) (Tomanek & Somero, 2000). Moreover, plants were only able to expand their tolerance range in response to gradual energy changes, as opposed to sudden increases (Law & Crafts-Brandner, 1999). Therefore, some species may not be able to survive the increasingly rapid and/or frequent energy fluctuations of the Anthropocene era (Hovick et al., 2014).

Heat energy gradients are currently shifting poleward at unprecedented rates. Anthropogenic activity is suggested to have contributed to 94% of global warming over the last 20 years (Woolway et al., 2022), and consequently, regional die-off events are widely considered to increase by 5-fold (Adams et al., 2009). To avoid heat stress, species may follow shifting heat gradients to higher latitudes or deeper waters. For example, greater heat energy in the Mediterranean basin may have pressured the mediterranean parrotfish (*Parisoma cretense*) outside its typical distribution range in search of more tolerable conditions (Guidetti & Boero, 2002; Arvedlund, 2009). However, although heat energy gradients are shifting not all environmental gradients that impact species' survival are predicted to shift or shift at a similar rate. For example, as heat gradients shift poleward, light energy gradients will remain constant (Muir et al., 2015). Therefore, species may be able to shift their range to avoid unfavourable conditions caused by one stressor. However, the decoupling of energy gradients creates unfamiliar environmental conditions. The disentanglement of the previously parallel light and heat energy gradients may challenge species to survive in novel ways.

Foundational species provide habitat and modify environmental conditions for associated species (Angelini et al., 2011). For example, spiny kelp (*Ecklonia radiata*) inhabit over 8,000 km of the Australian coastline and can modify the water flow, sediment, and irradiance of its environment, as well as provide habitat for its community (Bennett et al., 2015; Layton et al., 2019; Morris et al., 2019). However, the kelps' capacity to modify its environment relies on its spatial arrangement and abundance (Layton et al., 2019). Therefore, the well-being of foundational species is of high conservation importance. For instance, tropical reef invertebrates depend on live coral, often with a specific preference (Stella et al., 2011). Therefore, the loss of even a couple of coral species could trigger a sequence of mortality events throughout a reef ecosystem (Stella et al., 2011). Furthermore, the loss of a broader range of coral, a critical component of habitat structure, has the greatest and most immediate impact on reef fishes' survival (Pratchett et al., 2008). Therefore, the resilience of foundational species influences the health of their ecosystem.

Greater phenotypic plasticity can expand a species' tolerance to environmental conditions. Phenotypic plasticity is an observable change in an organism (varying phenotypic expression of a single genotype), which enhances their function and fitness, in response to a change in the environment (Murren et al., 2015). Along with phenotypic plasticity, the natural selection of particular phenotypes can cause genetic variation and similarly display an observation change within species (R. J. Fox et al., 2019). Greater phenotypic variation can expand a species' tolerance to environmental conditions, thereby increasing their survival rate (Eriksson & Rafajlović, 2022). For instance, likely driven by a combination of phenotypic plasticity and adaptive genetic change, populations of green anole (A*nolis carolinensis*) closer to the Equator, have longer limbs and wider shorter heads compared to its higher latitude counterparts (Jaffe et al., 2016).

Greater phenotypic variation among populations can expand species' overall potential nutrient sources and consequently their tolerance to seasonal variation of energy supplies (Jaffe et al., 2016). As obtaining nutrients is essential for survival, phenotypic variation often occurs in feeding structures (Mcalister & Miner, 2018).

Corals are mixotrophic, as they can feed through autotrophic and heterotrophic mechanisms (Lesser et al., 2010; Williams et al., 2018). Photoautotrophic Symbiodiniaceae, harboured in coral tissue, require a specific amount of light energy to synthesise organic compounds (Wicks et al., 2010b; LaJeunesse et al., 2018). Whilst gathering zooplankton from the water column can fund heterotrophic feeding (Mies et al., 2018). Variation in trophic behaviour can occur over environmental gradients. *Montastraea cavernosa* in the Bahamas and *Pocillopora meandrina* at Palmyra Atoll are autotrophic-dominant in shallow depths; however, as light energy attenuates over depth, deeper corals rely more heavily on heterotrophic feeding (Lesser et al., 2010; Williams et al., 2018). The light conditions that corals experience can influence their trophic behaviour (Williams et al., 2018).

Consequently, as ocean acidity and temperatures increase, corals migrating to higher latitudes to avoid heat stress are likely to experience a notable decline in their light conditions (Muir et al., 2015; Burger et al., 2022). In response to varying environmental conditions (i.e., light energy and water movement), corals can display changes in corallite morphology (including septa characteristics). For example, large inter-corallite spacing with short septa of deeper *M. cavernosa* colonies is hypothesised to alleviate self-shading in response to the low light supply in deeper waters (Ow & Todd, 2010; Goodbody-Gringley & Waletich, 2018). In general, the shallowest corals experience energy-rich and physically stressful conditions, and as depth increases, light energy attenuates limiting the supply of autotrophic compounds. Furthermore, due to the Earth's curvature and orientation, sunlight reaches higher latitudes at an indirect angle which prevents light from penetrating the ocean as deeply as at lower latitudes (Muir et al., 2015). Therefore, marginal populations, at high latitudes, experience light conditions at the edge of their species' tolerance range.

One of the highest latitude Scleractinian coral communities inhabits the Rangitāhua archipelago (the Kermadec Islands; Figure 2.1 (a)) (Wicks et al., 2010a). Located in the Tonga-Kermadec ridge (Karig, 1970), the islands receive a low light energy supply and have limited shelter from the region's high-velocity hydrodynamic conditions (Wicks et al., 2010a). Of high latitude coral populations, the Rangitāhua coral population has the closest affinity with similarly low coverage (8%) to corals in southeastern Australia but is less diverse (Wicks et al., 2010a). This study aims to assess the corallite morphology of the most abundant shallow-water Scleractinian corals at Rangitāhua, over the depth gradient (5-30m) and among four locations. These data will contribute to a greater understanding of coral morphology at the edge of their tolerance range to help inform potential responses of corals colonising higher latitudes. Due to extreme conditions in shallow waters, we predict to see different morphology for the shallowest corals (5m) compared to all deeper corals, and as light energy attenuates over depth, we expect to find a reduction in structural support and greater corallite spacing to alleviate self-shading (Goodbody-Gringley & Waletich, 2018; Soto et al., 2018). Due to varying environmental conditions, we predict distinct morphology among locations (Sutton et al., 2012). Additionally, we predict to see morphological variation indicative of a trophic shift, as high latitude corals often experience insufficient light energy to supply to sustain autotrophic feeding in deeper waters (Lesser et al., 2010). A greater understanding of the morphological gradients of coral populations at Rangitāhua could assist in predicting how coral may respond to the decoupling energy gradients.

## 2.3 Methods

### 2.3.1 Study site

Rangitāhua archipelago harbours one of the world’s highest latitudinal Scleractinian coral populations, close to the lower limits of their distributional range (Figure 2.1 (a)) (Wicks et al., 2010a). Raoul Island is the largest and northernmost of the four islands that make up Rangitāhua and the focal region for our study (Figure 2.1 (b). Surrounding Raoul Island, we selected four locations — Napier Island, Dayrell Island, Dougall Rock, and North Meyer Island (Figure 2.1 (c)) — where the subtidal topography allowed us to sample the complete depth gradient of interest in a single SCUBA dive.

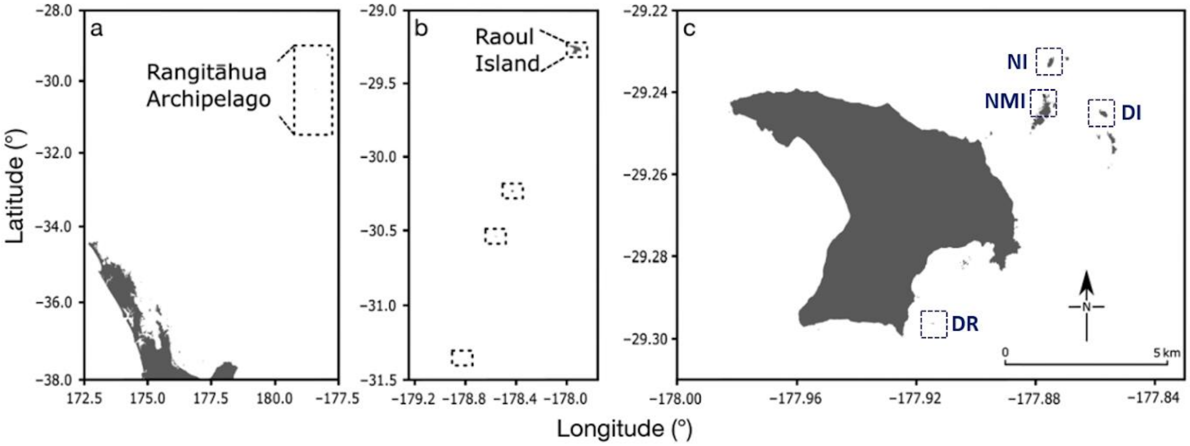

Figure 2.1 (a) Rangitāhua archipelago (inside the dashed box) relative to Te Ika a Māui, Aotearoa (New Zealand’s North Island). (b) Raoul Island, relative to the other islands in the Rangitāhua archipelago. (c) The sampling locations that are distributed around Raoul Island: Napier Island (NI), Dayrell Island (DI), and North Meyer Island (NMI) on the western side, as well as Dougall Rock (DR) on the eastern side of Raoul Island

### 2.3.2 Field methods

To assess morphological differences among Scleractinian corals at Rangitāhua fellow researchers collected fragments of coral during expeditions in 2015, 2016 and 2017 in the austral autumn (September-November). We used a depth stratified design with six focal depth strata; 5, 10, 15, 20, 25, and 30m at each of the four locations (Figure 2.1 (c)). Each location was further divided into three dive sites where collections were made at each depth strata, varying based on local abundance. Divers collected coral fragments (~5cm), using a hammer and chisel, which were placed in a Ziplock bag underwater. Upon return to the expedition vessel, the coral fragments were individually labelled and then placed in a weak chlorine solution (for ~72 hours) until all live tissue had detached. The remaining exoskeleton was left to air dry and then was stored in tissue paper and a zip lock bag for transport to the laboratory for examination.

Although divers collected fragments from all coral species present, only six species, representing almost half of the known coral species at Rangitāhua (16 species) (Wicks et al., 2010a) (11 species) (Richards & Liggins, 2015), were found in sufficient abundance for analysis of morphological variation across a sufficient range of depths and locations. Putative species were identified through morphological features from skeletons (Richards & Liggins, 2015) and separated into two groups, 'circular' and 'meandering'. Based on general corallite morphology; taxa with 'circular' corallites with distinct walls were *Astrea curta* (Dana, 1846)*, Montipora capricornis* Veron, 1985*, Montipora spongodes* Bernard, 1897*,* and *Turbinaria frondens* (Dana, 1846) (Table 1); whilst taxa with irregularly shaped corallites with meandering walls were *Hydnophora pilosa* (Veron, 1985) and *Goniastrea favulus* (Dana, 1846) (Table 1).

### 2.3.3 Morphological trait measurement

Here, we consider a suite of corallite and septa characteristics that are likely indicative of corals' feeding behaviour which is expected to differ over a geographic gradient. For instance, corallites too near each other can cause interference, however, when corallites are too far apart, corals may struggle to capture sufficient nutrients (Amaral, 1994). Similarly, support structures within each corallite provide substrate for tissue attachment (Foster, 1977; Brown et al., 1985), but also can create self-shading (Soto et al., 2018). For species with circular corallite morphology, we measured corallite density, and minimum inter-corallite distance (Table 1, Figure 2.2 (a)), as well as septa length, number of septa, fossa diameter, and corallite area (Table 1, Figure 2.2 (b)), using a combination of Scanning Electron Microscope (SEM) and dissecting microscope images (as described below). For species with meandering corallite morphology, we measured corallite coverage, and septa density (Table 1, Figure 2.3 (a)), as well as septa length, septa width, inter-septa distance, and valley width (Table 1, Figure 2.3 (b)), using dissecting microscope images (as described below). All measures of septa refer only to primary septa.

Table 2.21 Morphological traits for circular and meandering corals. All measures of septa refer only to primary septa.

| Traits | Abbreviation | Coral type | Description | Unit of measure | Max measures per specimen |
|---|---|---|---|---|---|
| Corallite area | C.area | Circular | Area of a corallite | cm | 3 |
| Minimum inter-corallite distance | IC.dis | Circular | Distance between a corallite and their closest neighbour | cm | 3 |
| Corallite density | C.den | Circular | Number of corallites | 1cm$^{-2}$ | 1 |
| Fossa diameter | F.dia | Circular | Avenge diameter of a fossa | cm | 3 |
| Number of septa | S.No. | Circular | Number of septa per corallite |  | 5 |
| Septa length | S.len | Circular | Length of septa (from corallite wall peak) | cm | 5 |
|  |  | Meandering |  | cm | 6 |
| Septa width | S.wid | Meandering | Width of septa crest | cm | 3 |
| Septa density | S.den | Meandering | Number of septa | 0.25cm$^{-2}$ | 1 |
| Inter-septa distance | IS.dis | Meandering | Distance between septa | cm | 3 |
| Corallite coverage | C.cov | Meandering | Area of corallite coverage | 1cm$^{-2}$ | 2 |
| Valley distance | V.dis | Meandering | Distance between corallite wall peaks | cm | 3 |

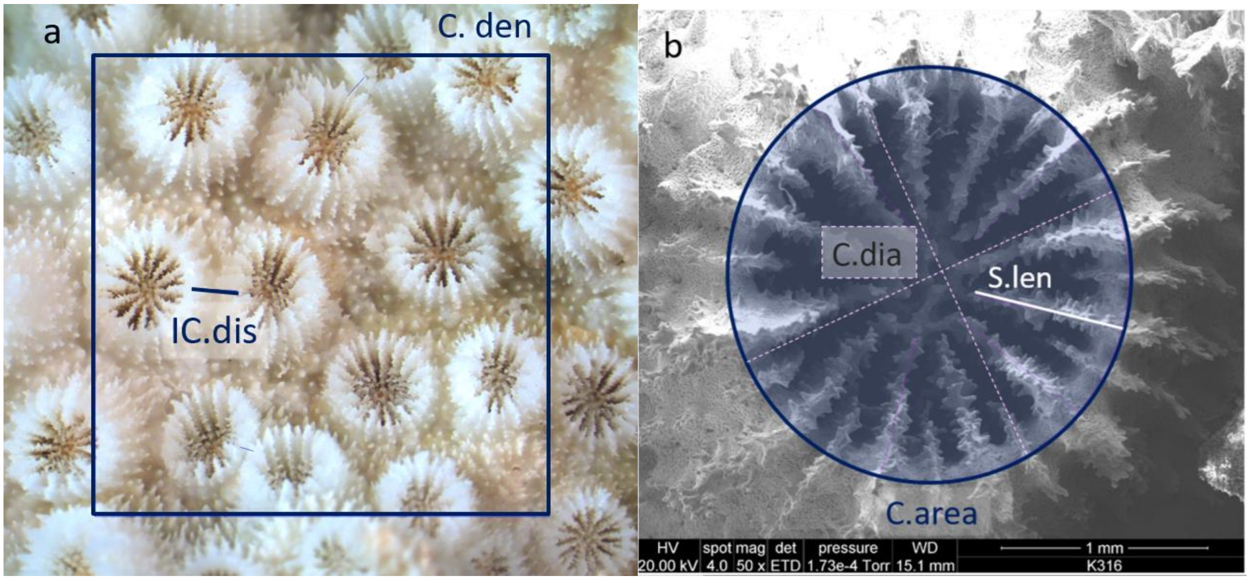

Figure 2.2 (a) Dissection microscope image of a coral skeleton with circular corallites. C.den: corallite density. IC.Dis: minimum inter-corallite density. (b) Scanning electron microscope image of corallite from circular coral. C.area: Corallite area. S.len: septa length. C.dia: corallite diameter.

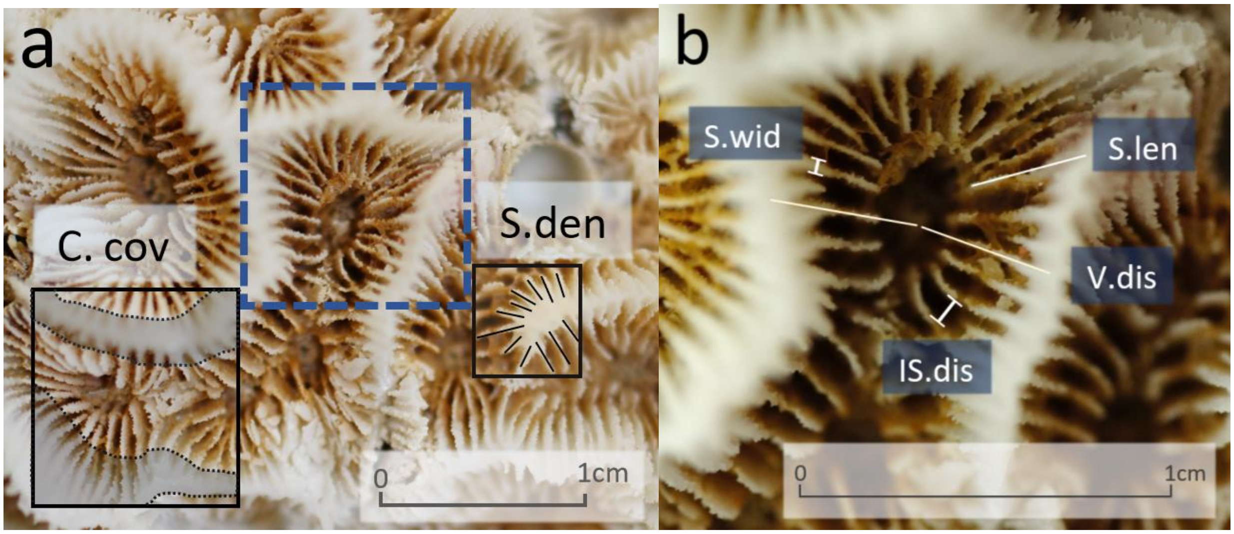

Figure 2.3 (a) Dissecting microscope image of a coral with meandering corallites. C.cov: corallite coverage. S.den: septa density. The Blue dashed box is (b) S.wid: septa width. IS.dis: inter-septa distance. S.len: septa length. V.dis: valley distance.

For corals with circular corallites, SEM (Figure 2.2 (b)) images were taken of three randomly selected corallites per specimen. All subsequent image manipulation and trait measurement was performed in ImageJ (Rasband, 1997–2012); calibrated using a scale marked within each image. First, an oval was drawn over the peak of the corallite wall, and the area inside was measured as the “corallite area”. Lines were added to mark the widest cross-section of the corallite, and then a line perpendicular to the widest cross-section was added sectioning the corallite into quarters. The lengths of these two lines were averaged to calculate a mean corallite diameter (used to calculate other trait measures). Five septa, at least one from each quarter, were measured along their crest from the peak of the corallite wall to the end of the septa. The mean of these lengths was used as “septa length”. To calculate “fossa diameter”, the mean septa length was doubled and deducted from the mean corallite diameter. Last from SEM images, all septa within each corallite were counted to calculate the “number of septa”.

For dissecting microscope images (Figure 2.2 (a)), we used a sandbag to support the samples such that the surface of the skeleton with the focal corallites was parallel to the micoscope. All subsequent image manipulation and trait measurement was performed in ImageJ (Rasband, 1997–2012); calibrated using a ruler in each image. For corals with circular corallites, the distance between the peak of the corallite wall of a haphazardly selected corallite to the peak of the corallite wall of the closest neighbouring corallite was measured as “minimum inter-corallite distance”. Last, a $1cm^2$ box was drawn over a randomly selected section of the coral surface and the count of corallites per box was the “corallite density”.

For corals with meandering corallites (Figure 2.3), separate septa were haphazardly selected for each septa trait. The length along the septa crest from the peak of the corallite wall to the septa terminus was measured as “septa length”. “Septa width” was measured as the width across the thickest section of the septa crest, whilst “inter-septa distance” was the distance between the septa crests of two neighbouring septa. Three $0.25cm^2$ boxes were drawn over a haphazardly selected section of the coral surface. “Septa density” was calculated by counting how many septa had approximately 80% of their length inside each box. Additionally, two $1cm^2$ boxes were drawn over a haphazardly selected section of the coral surface. Within each box, outlines were drawn around the peaks of the meandering corallite walls. The area that each corallite covered within the larger 1cm$^2$ boxes was then converted to a percentage for “corallite coverage”. Lastly, only for *G. favulus*, where corallite walls were parallel, separate measures were taken from each corallite wall to the centre of the corallite valley and summed together to give “valley distance”.

### 2.3.4 Statistical analysis

For each putative species, we performed one-way ANOVA and Tukey’s HSD tests to quantify differences in mean values of the morphological measurements (car and stats) (Weisberg, 2019; R. C. Team, 2021). Depth and location were considered fixed categorical factors, and all were analysed using *lm* function of the base package for R v4.1.0 (R. Team, 2020; R. C. Team, 2021). Due to natural variation in the abundance of corals surrounding Raoul Island, not all depths were sampled for all species at each site and as such we could not examine the depth-by-location interaction in our study. The significance of each factor, as well as pairwise differences among levels, were assessed using the *ANOVA* (car) (Weisberg, 2019) and *tukeyHSD* (stats) (R. C. Team, 2021) functions, respectively. Acknowledging that the raw morphological measurements we considered were likely to be correlated, we examined associations among the raw morphological measures by calculating the principal components of the correlation matrix for the scaled and centred morphological measurements.  We then examined variation in the composite traits described by the first three PCA scores using a linear model with depth and location as fixed categorical factors as described above for the raw morphological measurements.

## 2.4 Results

### 2.4.1 *Astrea curta*

**Principal components**

For *A. curta*, the first three principal components of the trait correlation matrix accounted for almost 80% of the variation in corallite morphology (Table 2.2). The first principal component (PC1) described a trait gradient of smaller corallites (C.area) with fewer septa (S.No.) at one extreme whilst the other extreme had larger corallites (C.area) with more septa (S.No.). The second principal component (PC2) described a trait gradient between corallites with longer septa (S.len) and smaller fossa (F.dia) at one extreme and corallites with shorter septa (S.len) and larger fossa (F.dia) at the other extreme. The third principal component (PC3) described a trait gradient between corallites that were more densely packed (C.den) and closer together (IC.dis) at one extreme and corallites that were sparser (C.den) and further apart (IC.dis) at the other extreme.

Table 2.2 Eigenvectors and values (λ) of raw morphological measurements considered for *Astrea curta.* Bold values indicate measurable traits that heavily contribute to the first three principal components. PC1: principal component one. PC2: principal component two. PC3: principal component three. PC4: principal component four. PC5: principal component five. PC6: principal component six. S.len: septa length. S.No.: number of septa. F.dia: fossa diameter. C.area: corallite area. C.den: corallite density. IC.dis: minimum inter-corallite distance.

| Traits | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 |
|---|---|---|---|---|---|---|
| S.len | -0.261 | **0.699** | 0.102 | 0.226 | -0.015 | 0.617 |
| S.No. | **-0.577** | -0.188 | -0.272 | 0.098 | -0.739 | -0.041 |
| F.dia | -0.382 | **-0.567** | -0.078 | 0.374 | 0.501 | 0.369 |
| C.area | **-0.578** | 0.349 | -0.064 | -0.032 | 0.415 | -0.606 |
| C.den | 0.343 | 0.162 | **-0.476** | 0.757 | -0.020 | -0.237 |
| IC.dis | -0.042 | -0.082 | **0.824** | 0.475 | -0.174 | -0.239 |
| *λ* | *0.348* | *0.252* | *0.195* | *0.128* | *0.048* | *0.029* |

## Depth

None of the 6 raw and 3 composite *A. curta* trait means varied significantly over its observed depth gradient (Table 2.3). There was a general trend of corallites of shallower *A. curta* (5-10m) were more densely arranged than deeper corallites, in which corallites were the least densely arranged at 15 metres (C.den; Figure 2.4).

## Location

The corallites of *A. curta* were closer and more densely arranged at Dougall Rock and Napier Island, whereas corallites were further apart and less densely arranged at North Meyer and Dayrell Islands, of which, the corallites arrangements at Dougall Rock and Dayrell Island were the most extreme (IC.dis, PC3; Table 2.2, 2.3, Figure 2.5).

Table 2.3 ANOVA of *Astrea curta* for depth and location. S.len: septa length. S.No.: number of septa. F.dia: fossa diameter. C.area: corallite area. C.den: corallite density. IC.dis: minimum inter-corallite distance. PC1: principal component one. PC2: principal component two. PC3: principal component three. Significant values are in bold.

| Traits | **Depth** | | | | **Location** | | | |
|---|---|---|---|---|---|---|---|---|
| | *DF* | *Sum Sq* | *F* | *P* | *DF* | *Sum Sq* | *F* | *P* |
| S.len | 4 | 0.003 | 0.447 | 0.774 | 3 | 0.001 | 0.240 | 0.868 |
| S.No. | 4 | 32.44 | 0.573 | 0.685 | 3 | 3.95 | 0.093 | 0.963 |
| F.dia | 4 | 0.026 | 0.541 | 0.707 | 3 | 0.017 | 0.473 | 0.704 |
| C.area | 4 | 0.006 | 0.212 | 0.929 | 3 | 0.005 | 0.253 | 0.859 |
| C.den | 4 | 2.419 | 2.240 | 0.096 . | 3 | 1.646 | 2.033 | 0.137 |
| IC.dis | 4 | 0.001 | 0.262 | 0.899 | 3 | 0.027 | 10.487 | **<0.001 ***** |
| PC1 | 4 | 3.971 | 0.397 | 0.809 | 3 | 1.135 | 0.151 | 0.928 |
| PC2 | 4 | 3.155 | 0.451 | 0.770 | 3 | 1.990 | 0.380 | 0.769 |
| PC3 | 4 | 3.605 | 1.371 | 0.275 | 3 | 16.402 | 8.316 | **<0.001***** |

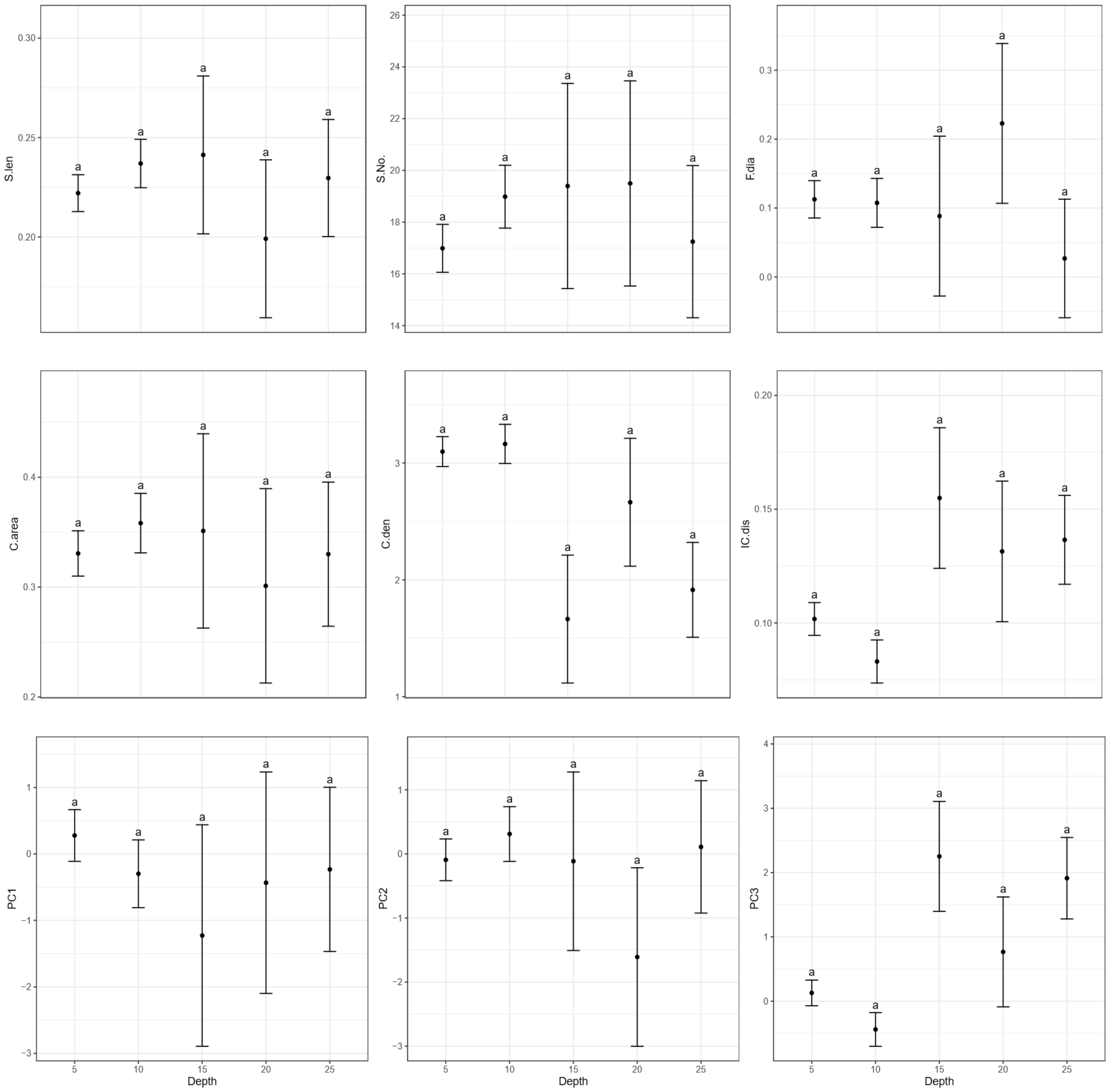

Figure 2.4 Mean (±SE) of traits for *Astrea curta* over depth gradient at locations surrounding Raoul Island. S.len: septa length. S.No.: number of septa. F.dia: fossa diameter. C.area: corallite area. C.den: corallite density. IC.dis: minimum inter-corallite distance. PC1: principal component one. PC2: principal component two. PC3: principal component three. Letters denote Tukey HSD post-hoc groupings.

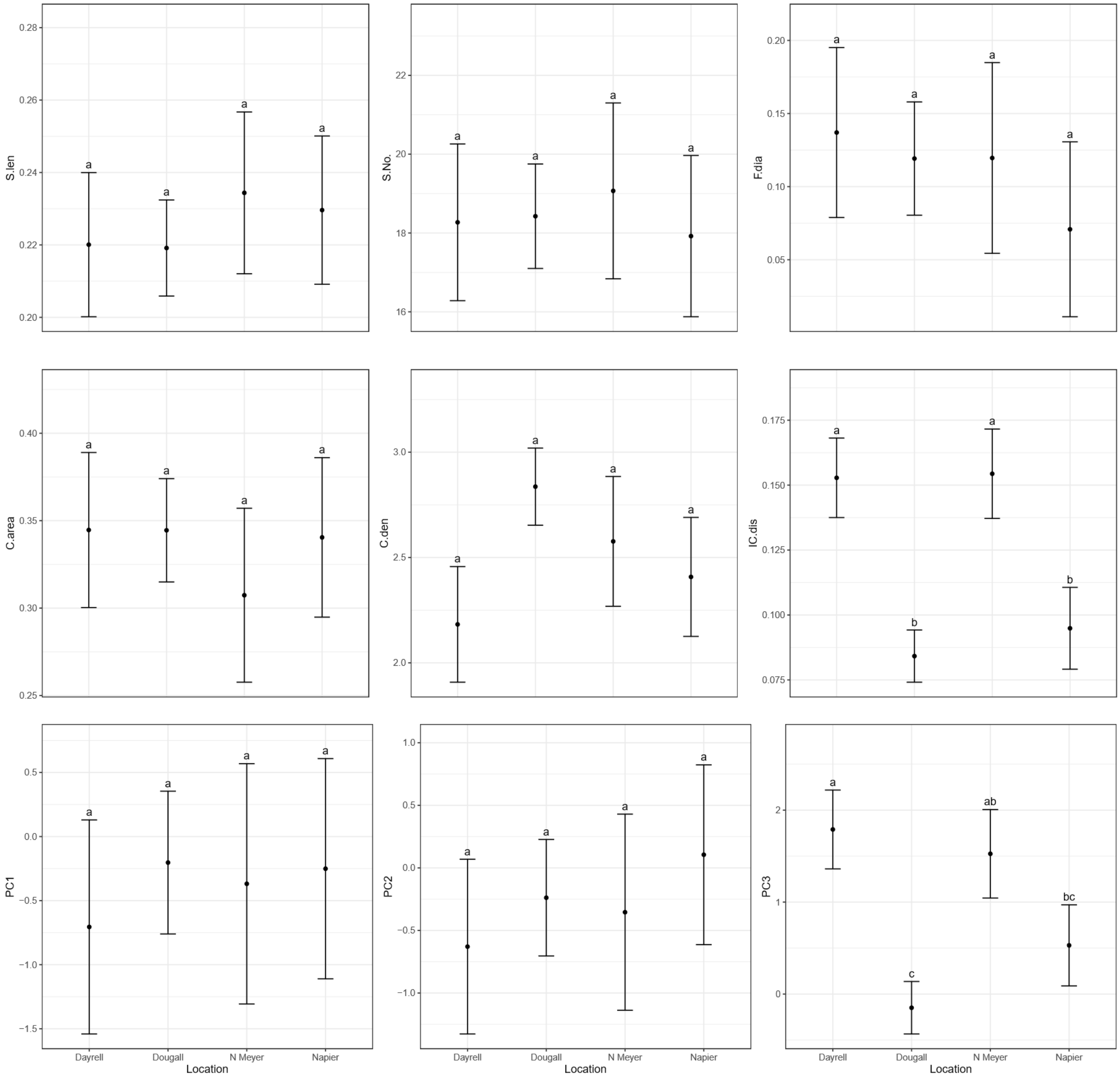

Figure 2.5 Mean (±SE) of traits for *Astrea curta* at four locations surrounding Raoul Island. S.len: septa length. S.No.: number of septa. F.dia: fossa diameter. C.area: corallite area. C.den: corallite density. IC.dis: minimum inter-corallite distance. PC1: principal component one. PC2: principal component two. PC3: principal component three. Letters denote Tukey HSD post-hoc groupings.

## 2.4.2 *Montipora capricornis*

**Principal components**

For *M. capricornis* the first three principal components of the trait correlation matrix explained over 80% of the variation in corallite morphology (Table 2.4). The first principal component (PC1) described a trait gradient between corallites with smaller fossa (F.dia) and longer septa (S.len) at one extreme and corallites with larger fossa diameter (F.dia) and shorter septa (S.len) at the other extreme. The second principal component (PC2) described a trait gradient between smaller corallites (C.area) with fewer septa (S.No.) at one extreme and larger corallites (C.area) with more septa (S.No.) at the other extreme. The third principal component (PC3) describes a trait gradient between large (C.area) densely arranged corallites (C.den) that are closer together (IC.dis) at one extreme and smaller (C.area) and sparser corallites (C.den) which are further apart (IC.dis) at the other extreme.

Table 2.4 Eigenvectors and values (λ) of the raw morphological measurements considered for *Montipora capricornis.* Bold values indicate measurable traits that heavily contribute to the first three principal components. PC1: principal component one. PC2: principal component two. PC3: principal component three. PC4: principal component four. PC5: principal component five. PC6: principal component six. S.len: septa length. S.No.: number of septa. F.dia: fossa diameter. C.area: corallite area. C.den: corallite density. IC.dis: minimum inter-corallite distance.

| Traits | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 |
|---|---|---|---|---|---|---|
| S.len | **-0.567** | 0.288 | -0.164 | -0.120 | -0.321 | 0.671 |
| S.No. | 0.121 | **0.631** | -0.019 | -0.527 | 0.556 | -0.001 |
| F.dia | **0.614** | 0.007 | -0.035 | 0.363 | 0.204 | 0.670 |
| C.area | 0.166 | **0.571** | **-0.531** | 0.410 | - 0.314 | -0.312 |
| C.den | -0.337 | -0.314 | **-0.646** | 0.182 | 0.581 | 0.002 |
| IC.dis | -0.382 | 0.307 | **0.521** | 0.612 | 0.333 | -0.059 |
| *λ* | *0.398* | *0.277* | *0.149* | *0.087* | *0.086* | *0.003* |

### Depth

None of the 6 raw and 3 composite *M. capricornis* trait means varied significantly over its observed depth gradient (Table 2.5). There was a general trend of corallites with the longest septa (S.len; Figure 2.6) and the smallest fossa diameters (F.dia) at 30 metres.

### Location

All 6 raw and 3 composite *M. capricornis* trait means were consistent among locations (Table 2.5).

Table 2.5 ANOVA of *Montipora capricornis* for depth and location. S.len: septa length. S.No.: number of septa. F.dia: fossa diameter. C.area: corallite area. C.den: corallite density. IC.dis: minimum inter-corallite distance. PC1: principal component one. PC2: principal component two. PC3: principal component three. Significant values are in bold.

| Trait | **Depth** | | | | **Location** | | | |
|---|---|---|---|---|---|---|---|---|
| | *DF* | *Sum Sq* | *F* | *P* | *DF* | *Sum Sq* | *F* | *P* |
| S.len | 5 | 0.002 | 2.156 | 0.087 . | 3 | <0.001 | 0.250 | 0.861 |
| S.No. | 5 | 6.398 | 0.900 | 0.495 | 3 | 0.374 | 0.088 | 0.966 |
| F.dia | 5 | 0.006 | 1.252 | 0.311 | 3 | <0.001 | 0.330 | 0.804 |
| C.area | 5 | <0.001 | 0.958 | 0.460 | 3 | <0.001 | 0.647 | 0.591 |
| C.den | 5 | 35.74 | 0.350 | 0.878 | 3 | 69.22 | 1.129 | 0.354 |
| IC.dis | 5 | 0.001 | 0.470 | 0.796 | 3 | <0.001 | 0.035 | 0.991 |
| PC1 | 5 | 11.025 | 0.832 | 0.537 | 3 | 0.595 | 0.075 | 0.973 |
| PC2 | 5 | 10.679 | 1.224 | 0.323 | 3 | 0.122 | 0.023 | 0.995 |
| PC3 | 5 | 4.6670 | 1.098 | 0.383 | 3 | 3.780 | 1.482 | 0.240 |

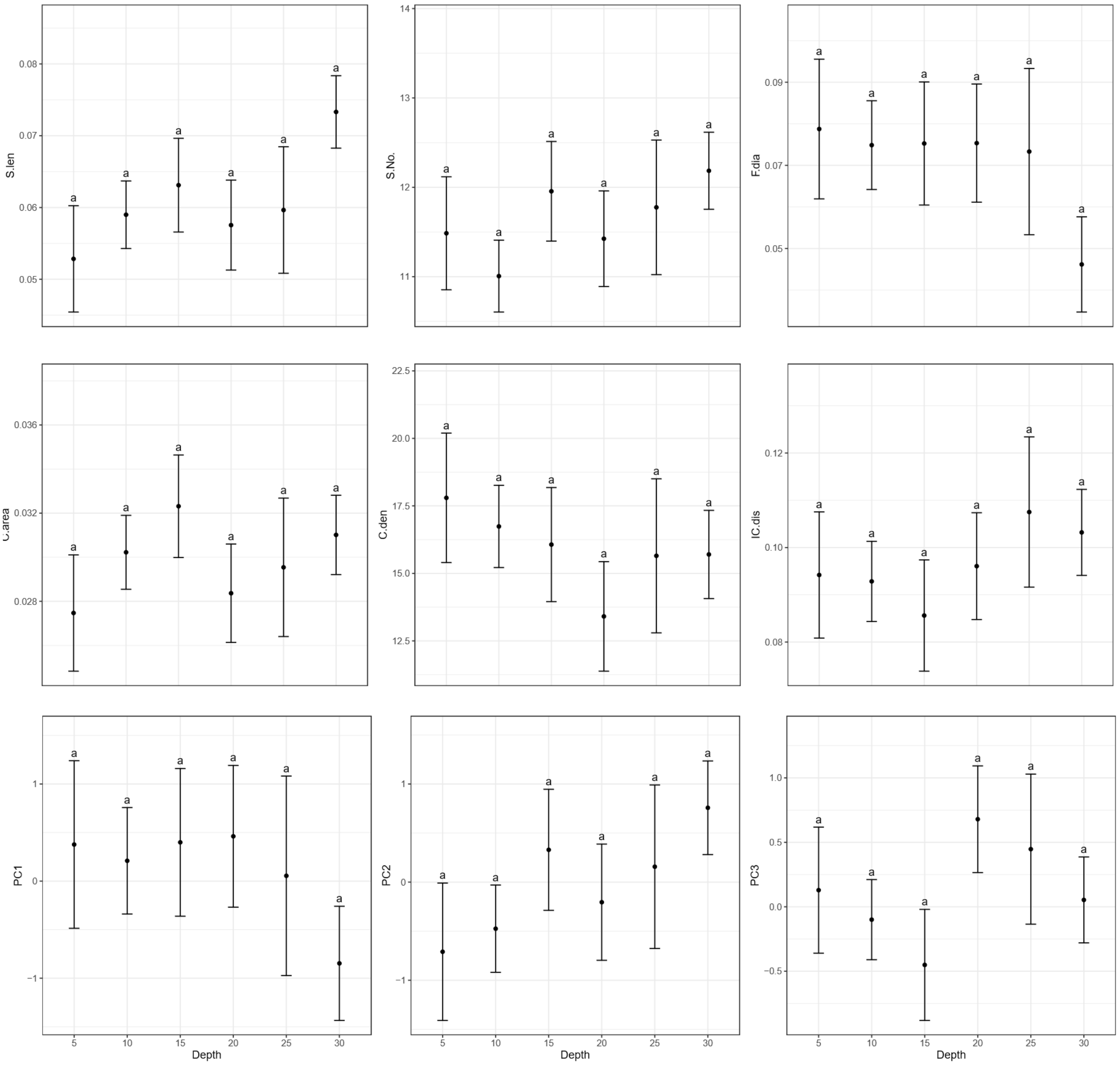

Figure 2.6 Mean (±SE) of traits for *Montipora capricornis* over depth gradient at locations surrounding Raoul Island. S.len: septa length. S.No.: number of septa. F.dia: fossa diameter. C.area: corallite area. C.den: corallite density. IC.dis: minimum inter-corallite distance. PC1: principal component one. PC2: principal component two. PC3: principal component three. Letters denote Tukey HSD post-hoc groupings.

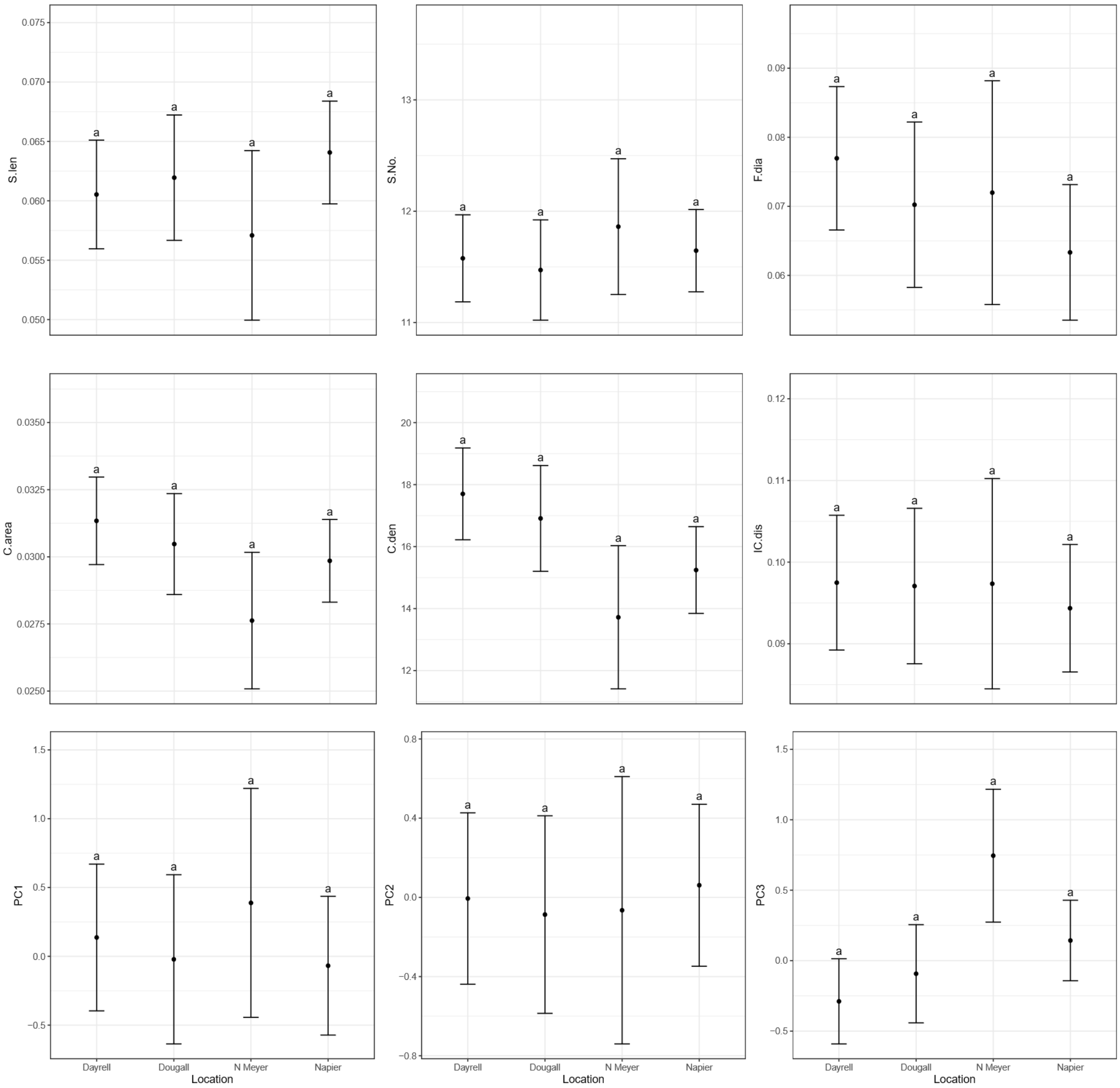

Figure 2.7 Mean (±SE) of traits for *Montipora capricornis* at four locations surrounding Raoul Island. S.len: septa length. S.No.: number of septa. F.dia: fossa diameter. C.area: corallite area. C.den: corallite density. IC.dis: minimum inter-corallite distance. PC1: principal component one. PC2: principal component two. PC3: principal component three. Letters denote Tukey HSD post-hoc groupings.

### 2.4.3 *Montipora spongodes*

**Principal components**

For *M. spongodes*, the first three principal components of the trait correlation matrix accounted for over 85% of the trait variation (Table 2.6). The first principal component (PC1) described a trait gradient between larger (C.area) more sparsely arranged corallites (C.den) with longer septa (S.len) at one extreme and smaller corallites (C.area) that were more densely arranged (C.den) with shorter septa (S.len) at the other extreme. The second principal component (PC2) described a trait gradient between corallites that were further apart (IC.dis) with fewer septa (S.No) and smaller fossa (F.dia) at one extreme and corallites that were closer together (IC.dis) with more septa (S.No) and larger fossa (F.dia) at the other extreme. The third principal component (PC3) describes a trait gradient between corallites with many septa (S.No.) at one extreme and corallites that were fewer septa (S.No.) at the other extreme.

Table 2.6 Eigenvectors and values (λ) of the raw morphological measurements considered for *Montipora spongodes.* Bold values indicate measurable traits that heavily contribute to the first three principal components. PC1: principal component one. PC2: principal component two. PC3: principal component three. PC4: principal component four. PC5: principal component five. PC6: principal component six. S.len: septa length. S.No.: number of septa. F.dia: fossa diameter. C.area: corallite area. C.den: corallite density. IC.dis: minimum inter-corallite distance.

| Traits | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 |
|---|---|---|---|---|---|---|
| S.len | **0.554** | 0.271 | -0.171 | 0.144 | -0.141 | 0.741 |
| S.No. | -0.018 | **-0.453** | **-0.888** | -0.071 | -0.036 | -0.019 |
| F.dia | -0.267 | **-0.548** | 0.251 | 0.567 | -0.413 | 0.269 |
| C.area | **0.594** | -0.050 | 0.047 | 0.028 | -0.598 | -0.534 |
| C.den | **-0.479** | 0.349 | -0.112 | -0.402 | -0.671 | 0.155 |
| IC.dis | -0.198 | **0.544** | -0.324 | 0.700 | -0.001 | -0.262 |
| *λ* | *0.432* | *0.312* | *0.130* | *0.088* | *0.030* | *0.009* |

**Depth**

The largest, closest, and least densely arranged corallites with the longest septa and smallest fossa were at 5 metres (C.area, C.den, IC.dis, S.len, F.dia, PC1; Table 2.6, 2.7, Figure 2.8). The size and density of corallites along with the length of its septa suddenly varied below 5 metres (C.area, C.den, S.len, PC1), whilst the fossa diameter gradually increased over depth (F.dia). Moreover, corallites at intermediate depths (15-20m) were most densely arranged and the closest to each other with the most septa (C.den, IC.dis, S.No, PC3).

### Location

The smallest and most densely arranged corallites, with a few very short septa, were found at Napier Island (C.area, C.den, S.No., S.len, PC1; Table 2.6, 2.7, Figure 2.9). The corallites at Dougall Rock were the closest together in the lowest density arrangement and had the most septa (IC.dis, C.den, S.No.). Corallites at North Meyer Island were large and sparsely arranged, with a few very long septa (S.len, C.area, S.No, PC1). The corallites at Dayrell lacked extreme measures, but were generally large and far apart (C.area, IC.dis).

Table 2.7 ANOVA of *Montipora spongodes* for depth and location. S.len: septa length. S.No.: number of septa. F.dia: fossa diameter. C.area: corallite area. C.den: corallite density. IC.dis: minimum inter-corallite distance. PC1: principal component one. PC2: principal component two. PC3: principal component three. Significant values are in bold.

| Trait | **Depth** | | | | **Location** | | | |
|---|---|---|---|---|---|---|---|---|
| | *DF* | *Sum Sq* | *F* | *P* | *DF* | *Sum Sq* | *F* | *P* |
| S.len | 5 | 0.036 | 6.032 | **0.001 ***** | 3 | 0.011 | 3.041 | **0.046 *** |
| S.No. | 5 | 77.231 | 3.888 | **0.009 **** | 3 | 48.959 | 4.108 | **0.015 *** |
| F.dia | 5 | 0.063 | 3.937 | **0.008 **** | 3 | 0.009 | 0.929 | 0.440 |
| C.area | 5 | 0.153 | 12.994 | **<0.001 ***** | 3 | 0.014 | 1.962 | 0.144 |
| C.den | 5 | 78.632 | 2.880 | **0.034 *** | 3 | 23.904 | 1.459 | 0.249 |
| IC.dis | 5 | 0.023 | 1.961 | 0.11975 | 3 | 0.0271 | 3.833 | **0.022 *** |
| PC1 | 5 | 49.516 | 8.894 | **<0.001 ***** | 3 | 8.271 | 2.476 | 0.085 . |
| PC2 | 5 | 6.943 | 0.840 | 0.534 | 3 | 13.424 | 2.707 | 0.067 . |
| PC3 | 5 | 10.007 | 3.669 | **0.013 *** | 3 | 2.018 | 1.233 | 0.319 |

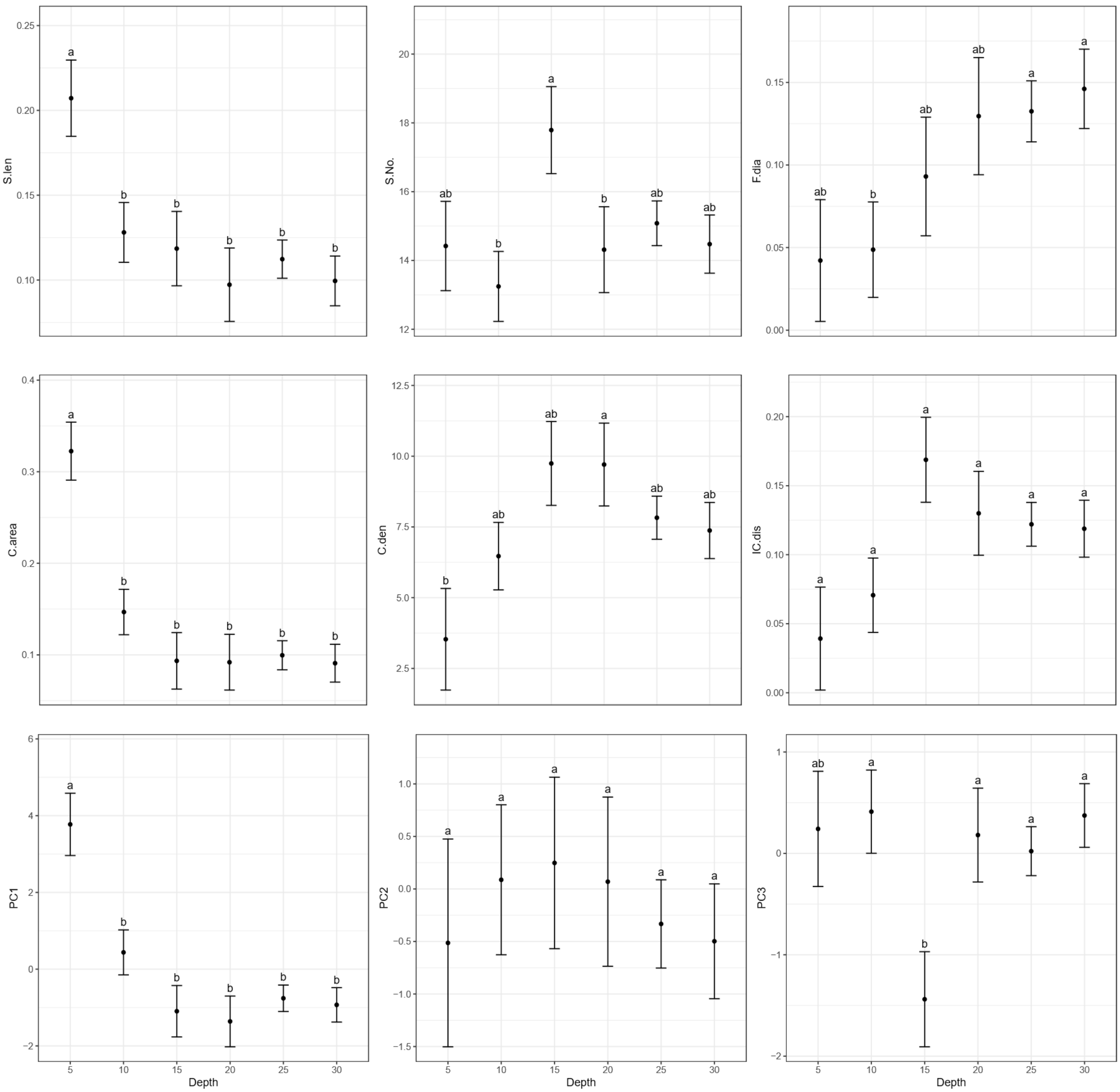

Figure 2.8 Mean (±SE) of traits for *Montipora spongodes* over depth gradient at locations surrounding Raoul Island. S.len: septa length. S.No.: number of septa. F.dia: fossa diameter. C.area: corallite area. C.den: corallite density. IC.dis: minimum inter-corallite distance. PC1: principal component one. PC2: principal component two. PC3: principal component three. Letters denote Tukey HSD post-hoc groupings.

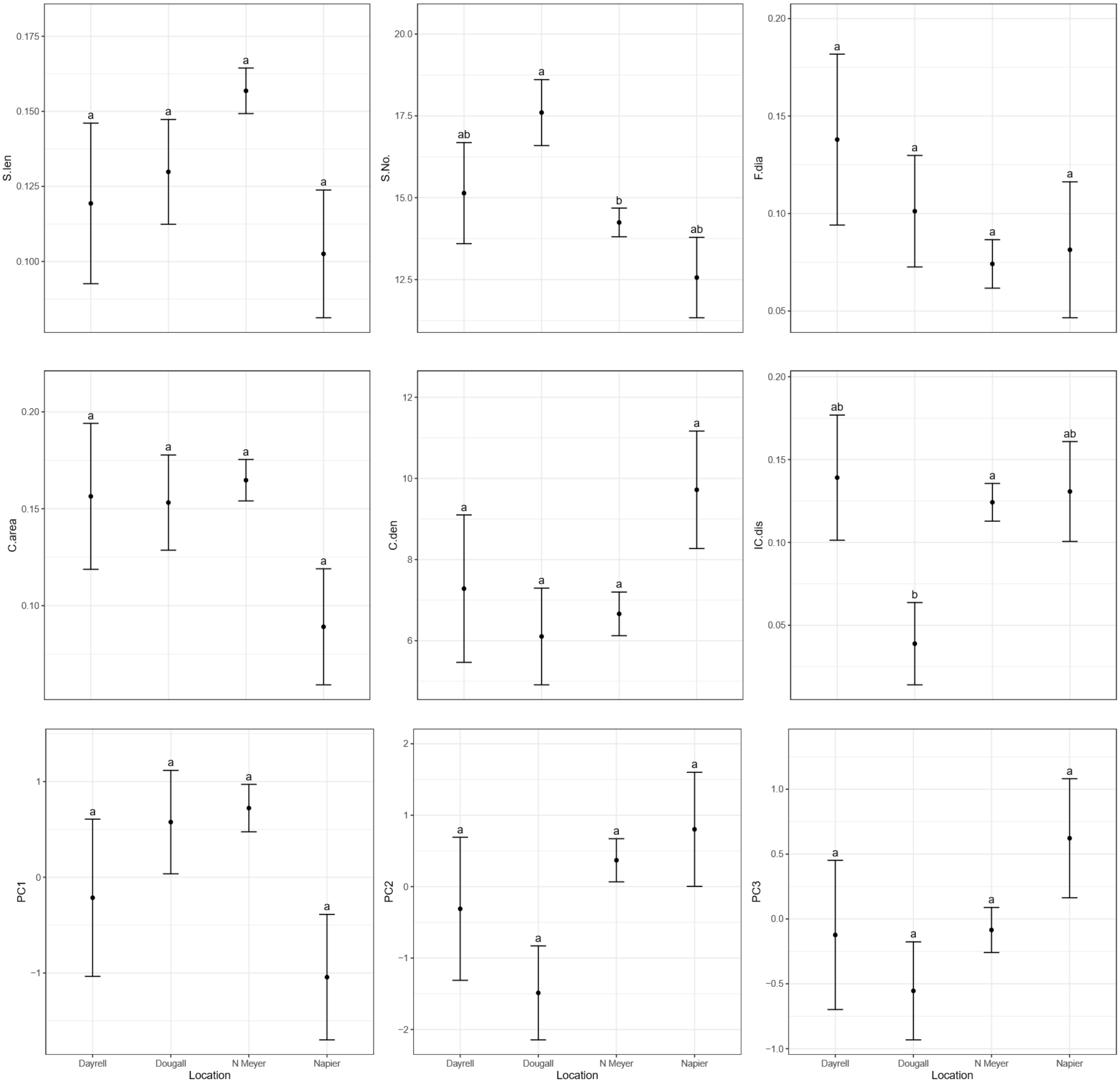

Figure 2.9 Mean (±SE) of traits for *Montipora spongodes* at four locations surrounding Raoul Island. S.len: septa length. S.No.: number of septa. F.dia: fossa diameter. C.area: corallite area. C.den: corallite density. IC.dis: minimum inter-corallite distance. PC1: principal component one. PC2: principal component two. PC3: principal component three. Letters denote Tukey HSD post-hoc groupings.

### 2.4.4 *Turbinaria frondens*

**Principal components**

For *T. frondens*, the first three principal components of the trait correlation matrix explained over 75% of the variation in corallite morphology (Table 2.8). The first principal component (PC1) described a trait gradient between corallites with longer septa (S.len) and smaller fossa (F.dia) at one extreme and corallites with shorter septa (S.len) and larger fossa (F.dia) at the other extreme. The second principal component (PC2) described a trait gradient between corallites that were more densely packed (C.den) and closer together (IC.dis) at one extreme and corallites that were sparser (C.den) and further apart (IC.dis) at the other extreme. The third principal component (PC3) describes a trait gradient between larger corallites (C.area) at one extreme and smaller corallites (C.area) at the other.

Table 2.8 Eigenvectors and values (λ) of raw morphological measurements considered for *Turbinaria frondens.* Bold values indicate measurable traits that heavily contribute to the first three principal components. PC1: principal component one. PC2: principal component two. PC3: principal component three. PC4: principal component four. PC5: principal component five. PC6: principal component six. S.len: septa length. S.No.: number of septa. F.dia: fossa diameter. C.area: corallite area. C.den: corallite density. IC.dis: minimum inter-corallite distance.

| Traits | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 |
|---|---|---|---|---|---|---|
| S.len | **0.609** | 0.177 | 0.236 | 0.215 | 0.127 | -0.692 |
| S.No. | -0.348 | -0.370 | 0.324 | 0.712 | 0.360 | -0.004 |
| F.dia | **-0.520** | -0.201 | 0.383 | -0.388 | -0.293 | -0.553 |
| C.area | 0.269 | 0.054 | **0.821** | - 0.157 | -0.107 | 0.462 |
| C.den | 0.314 | **-0.602** | -0.123 | 0.241 | -0.682 | 0.030 |
| IC.dis | -0.256 | **0.652** | 0.056 | 0.462 | -0.541 | 0.005 |
| *λ* | *0.380* | *0.208* | *0.199* | *0.116* | *0.094* | 0.002 |

### Depth

None of the 6 raw and 3 composite *T. frondens* trait means varied significantly over its observed depth gradient (Table 2.9). The shallowest (5m) corallites of *T. frondens* were close together and densely arranged, with many septa (IC.dis, S.No., PC2; Table 2.8, Figure 2.10). As the depth increased, the distance between neighbouring corallites increased (IC.dis). Corallites had the longest septa and smallest fossa at 20 metres (S.len, F.dia, PC1).

### Location

We found no evidence of *T. frondens* having any significant difference in the raw or composite morphological trait means among locations (Table 2.9).

Table 2.9 ANOVA of *Turbinaria frondens* for depth and location. S.len: septa length. S.No.: number of septa. F.dia: fossa diameter. C.area: corallite area. C.den: corallite density. IC.dis: minimum inter-corallite distance. PC1: principal component one. PC2: principal component two. PC3: principal component three. Significant values are in bold.

| Traits | **Depth** | | | | **Location** | | | |
|---|---|---|---|---|---|---|---|---|
| | *DF* | *Sum Sq* | *F* | *P* | *DF* | *Sum Sq* | *F* | *P* |
| S.len | 4 | 0.001 | 1.105 | 0.371 | 3 | <0.001 | 0.624 | 0.605 |
| S.No. | 4 | 23.102 | 1.312 | 0.286 | 3 | 7.016 | 0.531 | 0.664 |
| F.dia | 4 | 0.002 | 0.790 | 0.540 | 3 | 0.002 | 0.713 | 0.551 |
| C.area | 4 | <0.001 | 0.840 | 0.510 | 3 | <0.001 | 0.401 | 0.754 |
| C.den | 4 | 13.390 | 0.807 | 0.530 | 3 | 6.353 | 0.510 | 0.678 |
| IC.dis | 4 | 0.014 | 2.326 | 0.0776 . | 3 | 0.004 | 0.875 | 0.464 |
| PC1 | 4 | 9.084 | 0.947 | 0.450 | 3 | 3.071 | 0.427 | 0.7352 |
| PC2 | 4 | 9.994 | 2.203 | 0.091 . | 3 | 2.489 | 0.732 | 0.541 |
| PC3 | 4 | 3.117 | 0.584 | 0.677 | 3 | 0.715 | 0.179 | 0.910 |

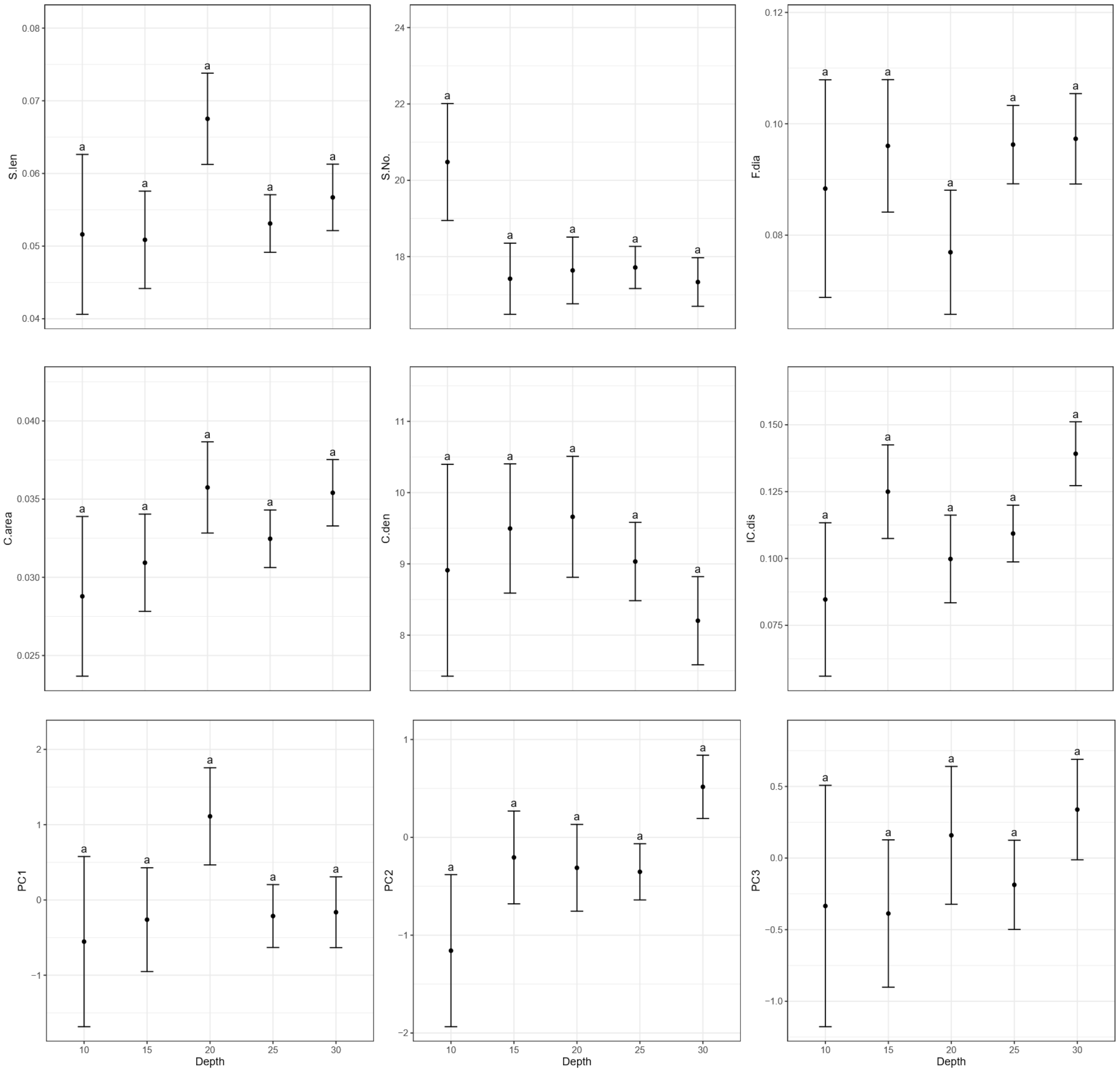

Figure 2.10 Mean (±SE) of traits for *Turbinaria frondens* over depth gradient at locations surrounding Raoul Island. S.len: septa length. S.No.: number of septa. F.dia: fossa diameter. C.area: corallite area. C.den: corallite density. IC.dis: minimum inter-corallite distance. PC1: principal component one. PC2: principal component two. PC3: principal component three. Letters denote Tukey HSD post-hoc groupings.

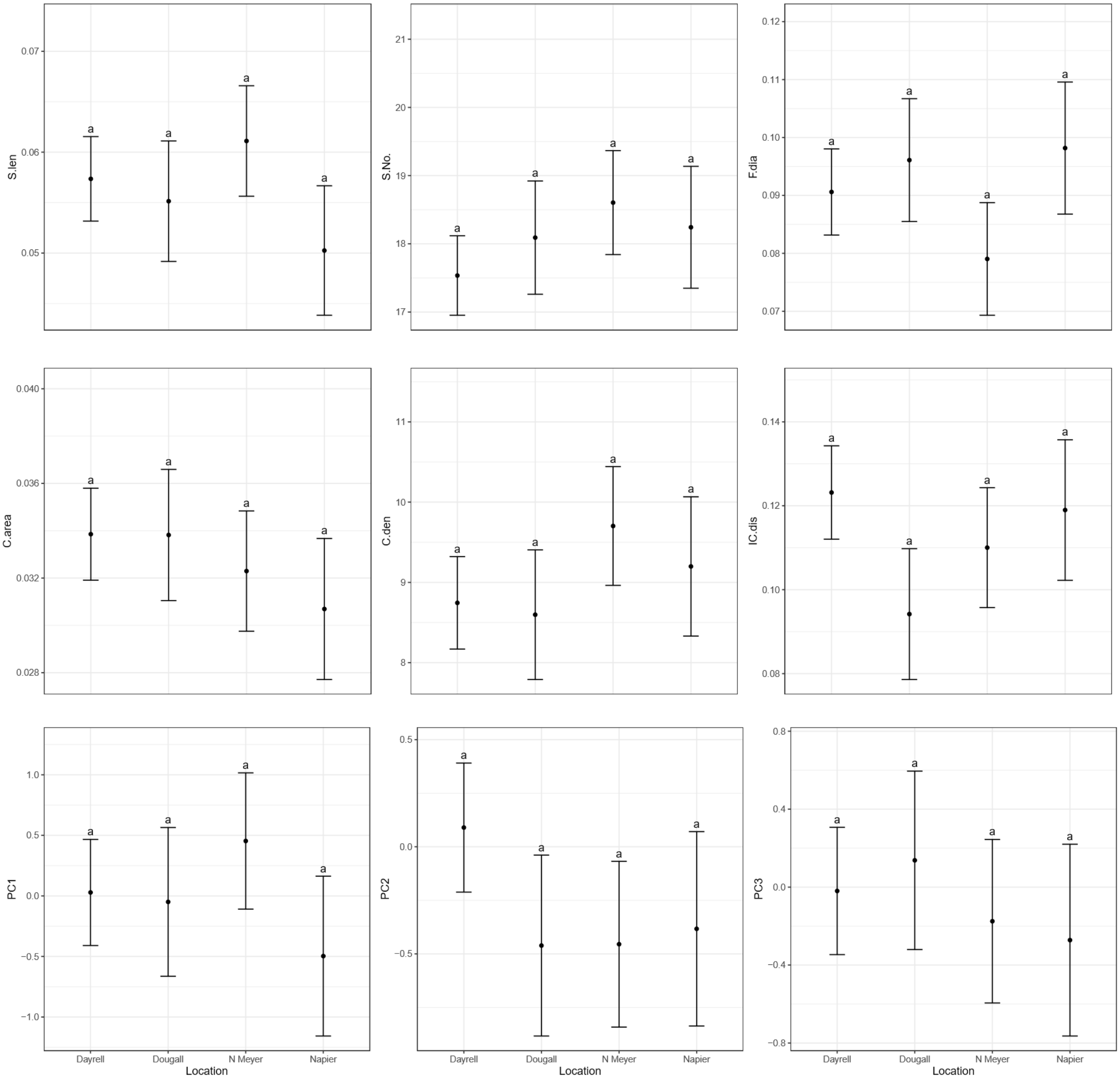

Figure 2.11 Mean (±SE) of traits for *Turbinaria frondens* at four locations surrounding Raoul Island. S.len: septa length. S.No.: number of septa. F.dia: fossa diameter. C.area: corallite area. C.den: corallite density. IC.dis: minimum inter-corallite distance. PC1: principal component one. PC2: principal component two. PC3: principal component three. Letters denote Tukey HSD post-hoc groupings.

## 2.4.5 *Goniastrea favulus*

**Principal components**

For *G. favulus*, the first three principal components of the trait correlation matrix explained 75% of the variation in corallite morphology (Table 2.10). The first principal component (PC1) described a trait gradient between corallites further apart (V.wid), with longer septa (S.len) which were more sparsely arranged (S.den) and further apart (IS.dis) at one extreme and corallites closer together (V.wid) with shorter septa (S.len), which were more densely arranged (S.den), and closer together (IS.dis) at the other extreme. The second principal component (PC2) described a trait gradient between coral colonies with a lower corallite coverage (C.cov) and septa which were further apart (IS.dis) at one extreme whilst the other extreme had coral colonies with a higher corallite coverage (C.cov) and septa which were closer together (IS.dis). The third principal component (PC3) describes a trait gradient with corallites with wider septa (S.wid) at one extreme and corallites with narrower septa (S.wid) at the other.

Table 2.10 Eigenvectors and values (λ) of raw morphological measurements considered for *Goniastrea favulus.* Bold values indicate measurable traits that heavily contribute to the first three principal components. PC1: principal component one. PC2: principal component two. PC3: principal component three. PC4: principal component four. PC5: principal component five. PC6: principal component six. S.len: septa length. S.wid: septa width. S.dis: inter-septa distance. S.den: septa density. C.cov: corallite coverage. V.dis: valley distance.

| Traits | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 |
|---|---|---|---|---|---|---|
| S.len | **0.486** | 0.347 | -0.194 | -0.427 | 0.067 | 0.647 |
| S.wid | 0.193 | -0.055 | **0.931** | -0.155 | -0.246 | 0.087 |
| IS.dis | **0.416** | **-0.496** | -0.257 | 0.260 | -0.659 | 0.116 |
| S.den | **-0.472** | 0.089 | -0.146 | -0.637 | -0.576 | -0.098 |
| C.cov | -0.240 | **-0.768** | 0.014 | -0.313 | 0.360 | 0.353 |
| V.dis | **0.523** | -0.181 | -0.085 | -0.471 | 0.198 | -0.653 |
| *λ* | *0.426* | *0.202* | *0.166* | *0.118* | *0.055* | *0.030* |

### Depth

We found no evidence of *G. favulus* having any significant difference in the raw or composite morphological trait means along the depth gradient (Table 2.11). However, there was a general trend of septa length increasing over the depth (Figure 2.12).

### Location

We found no evidence of *G. favulus* having any significant difference in the raw or composite morphological trait means among the locations (Table 2.11). However, there was a general trend that corallites at Dayrell Island had the widest septa, whilst the corallites with the narrowest septa were found at North Meyer Island (S.wid. PC3; Table 2.10, Figure 2.13).

Table 2.11 ANOVA of *Goniastrea favulus* for depth and location. S.len: septa length. S.wid: septa width. S.dis: inter-septa distance. S.den: septa density. C.cov: corallite coverage. V.dis: valley distance. PC1: principal component one. PC2: principal component two. PC3: principal component three. Significant values are in bold.

| Traits | **Depth** | | | | **Location** | | | |
|---|---|---|---|---|---|---|---|---|
| | *DF* | *Sum Sq* | *F* | *P* | *DF* | *Sum Sq* | *F* | *P* |
| S.len | 5 | 0.025 | 2.128 | 0.090 . | 3 | 0.008 | 1.179 | 0.335 |
| S.wid | 5 | <0.001 | 0.817 | 0.547 | 3 | <0.001 | 2.891 | 0.052 . |
| IS.dis | 5 | 0.001 | 0.604 | 0.697 | 3 | <0.001 | 0.564 | 0.643 |
| S.den | 5 | 60.109 | 1.187 | 0.340 | 3 | 88.891 | 2.924 | 0.051 . |
| C.cov | 5 | 0.069 | 1.390 | 0.258 | 3 | 0.027 | 0.899 | 0.454 |
| V.dis | 5 | 0.028 | 1.176 | 0.345 | 3 | 0.003 | 0.235 | 0.872 |
| PC1 | 5 | 7.468 | 0.682 | 0.641 | 3 | 14.750 | 2.246 | 0.105 |
| PC2 | 5 | 9.515 | 1.639 | 0.183 | 3 | 1.189 | 0.341 | 0.796 |
| PC3 | 5 | 4.778 | 1.103 | 0.381 | 3 | 7.603 | 2.925 | 0.051 . |

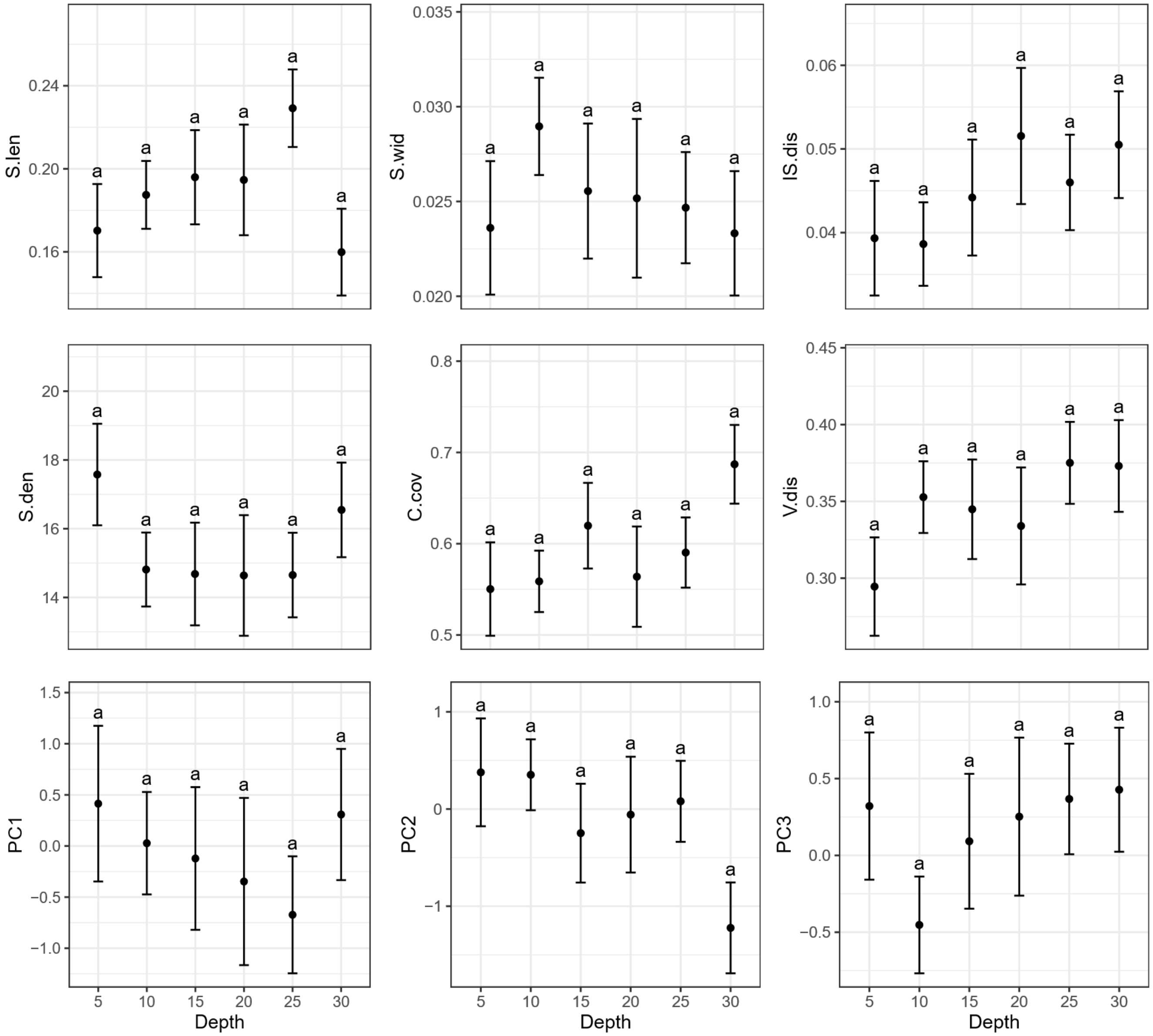

Figure 2.12 Mean (±SE) of traits for *Goniastrea favulus* over depth gradient at locations surrounding Raoul Island. S.len: septa length. S.wid: septa width. S.dis: inter-septa distance. S.den: septa density. C.cov: corallite coverage. V.dis: valley distance. PC1: principal component one. PC2: principal component two. PC3: principal component three. Letters denote Tukey HSD post-hoc groupings.

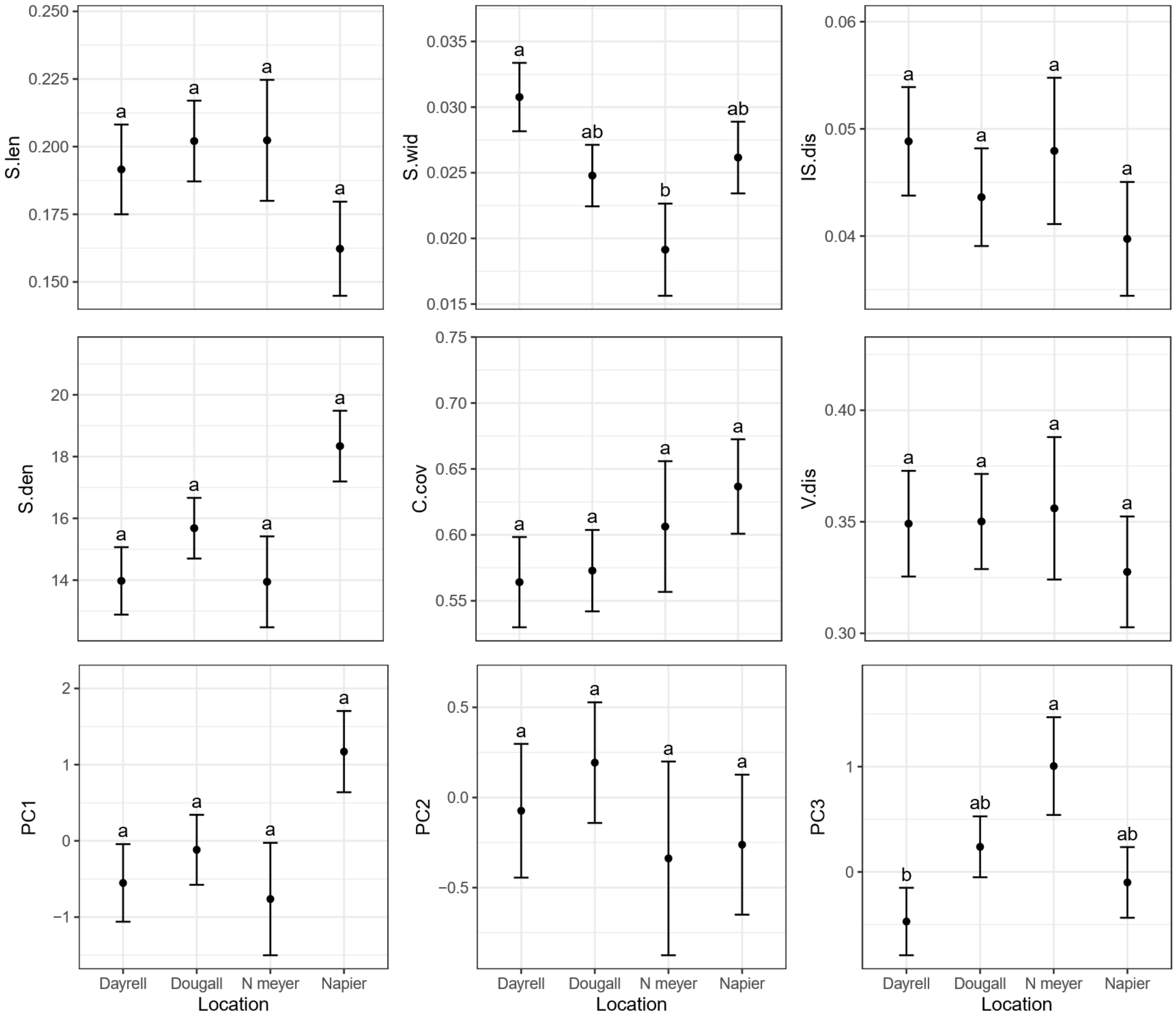

Figure 2.13 Mean (±SE) of traits for *Goniastrea favulus* at four locations surrounding Raoul Island. S.len: septa length. S.wid: septa width. S.dis: inter-septa distance. S.den: septa density. C.cov: corallite coverage. V.dis: valley distance. PC1: principal component one. PC2: principal component two. PC3: principal component three. Letters denote Tukey HSD post-hoc groupings.

## 2.4.6 *Hydnophora pilosa*

**Principal components**

For *H. pilosa*, the first three principal components of the trait correlation matrix accounted for 80% of the variation in corallite morphology (Table 2.11). The first principal component (PC1) described a trait gradient between corallites with longer and wider septa (S.len, S.wid), which were more sparsely arranged (S.den) and further apart (IS.dis) at one extreme and for the other extreme corallites had shorter and narrower septa (S.len, S.wid), which were more densely packed (S.den) and closer together (IS.dis). The second principal component (PC2) described a trait gradient between coral colonies with higher corallite coverage (C.cov) with wider septa (S.wid) at one extreme whilst the other extreme had coral colonies with a lower corallite coverage (C.cov) and narrower septa (S.wid). The third principal component (PC3) describes a trait gradient between coral colonies with a lower corallite coverage (C.cov) and wider septa (S.wid) that are close together (IS.dis) at one extreme and coral colonies with a higher corallite coverage (C.cov) with narrower septa (S.wid) that are further apart (IS.dis) at the other extreme.

Table 2.12 Eigenvectors and values (λ) of raw morphological measurements considered for *Hydnophora Pilosa.* Bold values indicate measurable traits that heavily contribute to the first three principal components. PC1: principal component one. PC2: principal component two. PC3: principal component three. PC4: principal component four. PC5: principal component five. S.len: septa length. S.wid: septa width. IS.dis: inter-septa distance. S.den: septa density. C.cov: corallite coverage.

| Traits | PC1 | PC2 | PC3 | PC4 | PC5 |
|---|---|---|---|---|---|
| S.len | **-0.555** | 0.064 | 0.343 | -0.622 | 0.429 |
| S.wid | **-0.402** | **0.566** | **0.406** | 0.279 | -0.525 |
| IS.dis | **-0.474** | -0.345 | **-0.517** | -0.281 | -0.557 |
| S.den | **0.543** | 0.311 | 0.074 | -0.676 | -0.382 |
| C.cov | -0.103 | **0.678** | **-0.667** | 0.007 | 0.290 |
| *λ* | *0.392* | *0.232* | *0.184* | *0.106* | *0.086* |

### Depth

Within the corallites of *H. pilosa* the length, width, and distance between septa increased over depth, whilst septa density decreased (PC1, S.len, S.wid, S.den; Table 2.12, 2.13, Figure 2.14). Septa were most sparsely arranged at 15m (S.den) and longest at 25m (S.len).

### Location

We found no evidence of *H. pilosa* having any significant difference in the raw or composite morphological trait means among locations (Table 2.13).

Table 2.13 ANOVA of *Hydnophora Pilosa* for depth and location. S.len: septa length. S.wid: septa width. S.dis: inter-septa distance. S.den: septa density. C.cov: corallite coverage. PC1: principal component one. PC2: principal component two. PC3: principal component three. Significant values are in bold.

| Traits | **Depth** | | | | **Location** | | | |
|---|---|---|---|---|---|---|---|---|
| | *DF* | *Sum Sq* | *F* | *P* | *DF* | *Sum Sq* | *F* | *P* |
| S.len | 5 | 0.023 | 2.417 | **0.041 *** | 3 | 0.002 | 0.397 | 0.755 |
| S.wid | 5 | 0.001 | 1.434 | 0.219 | 3 | 0.001 | 2.040 | 0.113 |
| IS.dis | 5 | 0.002 | 0.915 | 0.474 | 3 | 0.001 | 0.781 | 0.507 |
| S.den | 5 | 198.20 | 2.277 | 0.053 . | 3 | 28.53 | 0.546 | 0.652 |
| C.cov | 5 | 0.0572 | 1.459 | 0.210 | 3 | 0.032 | 1.369 | 0.257 |
| PC1 | 5 | 23.665 | 2.568 | **0.032 *** | 3 | 3.521 | 0.637 | 0.593 |
| PC2 | 5 | 10.408 | 1.916 | 0.099 . | 3 | 6.219 | 1.908 | 0.133 |
| PC3 | 5 | 2.455 | 0.532 | 0.751 | 3 | 4.444 | 1.606 | 0.193 |

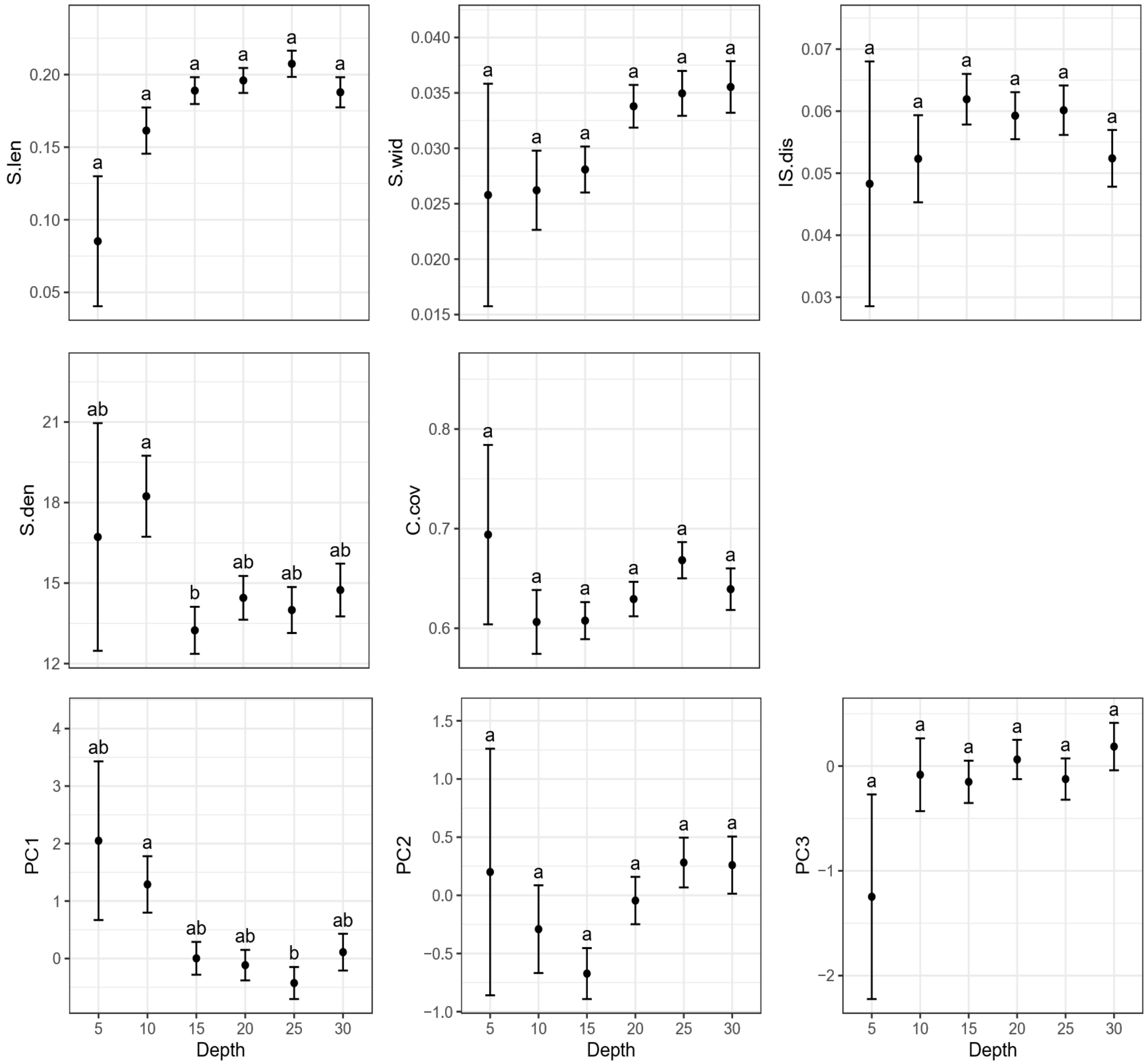

Figure 2.14 Mean (±SE) of traits for *Hydnophora Pilosa* over depth gradient at locations surrounding Raoul Island. S.len: septa length. S.wid: septa width. S.dis: inter-septa distance. S.den: septa density. C.cov: corallite coverage. PC1: principal component one. PC2: principal component two. PC3: principal component three. Letters denote Tukey HSD post-hoc groupings

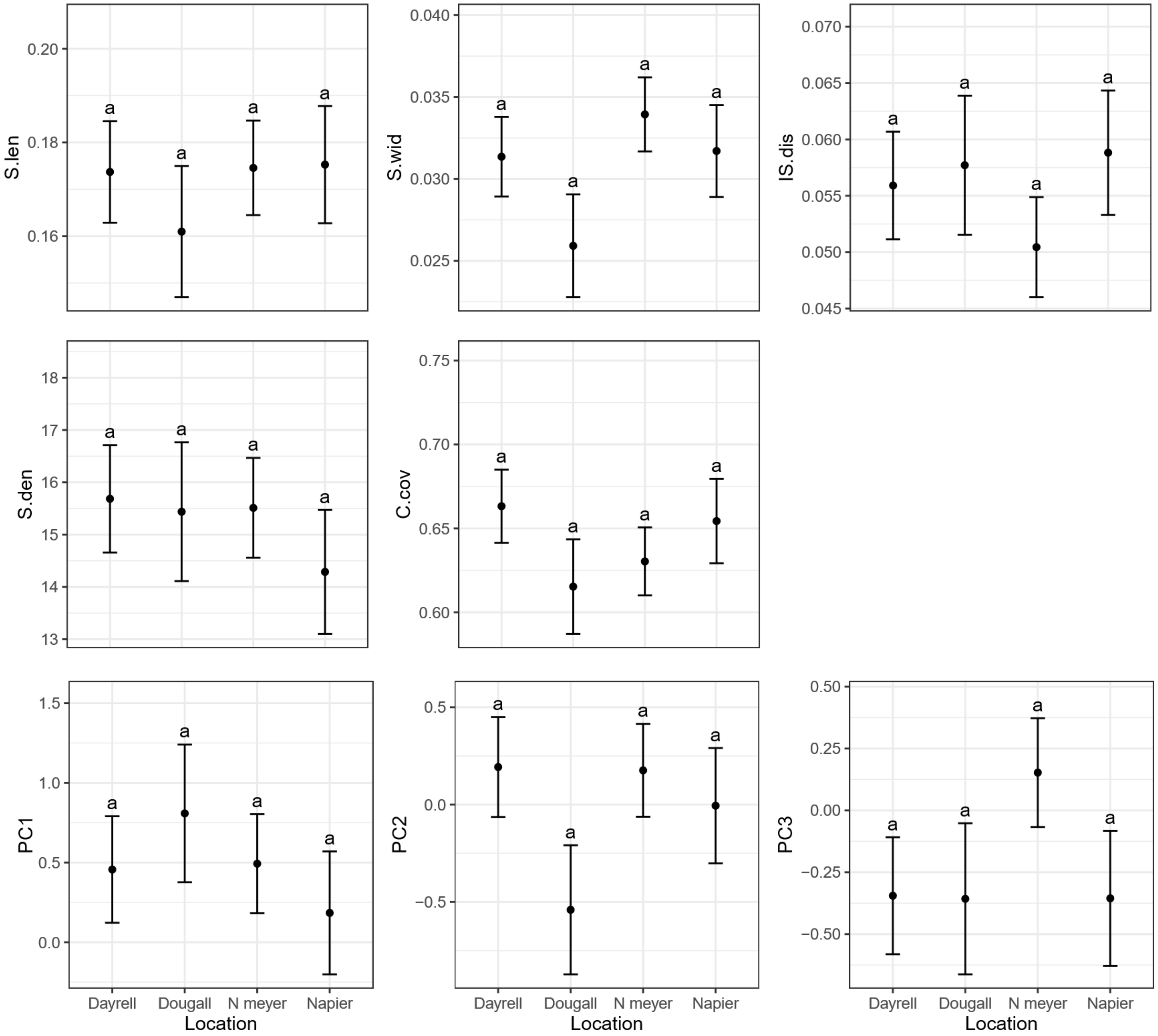

Figure 2.15 Mean (±SE) of traits for *Hydnophora Pilosa* at four locations surrounding Raoul Island. S.len: septa length. S.wid: septa width. S.dis: inter-septa distance. S.den: septa density. C.cov: corallite coverage. PC1: principal component one. PC2: principal component two. PC3: principal component three. Letters denote Tukey HSD post-hoc groupings.

## 2.5 Discussion

Our study provides an assessment of the morphological variation — across depth and spatial location — of the most abundant coral species at Rangitāhua. In response to extreme  and energy-rich conditions of shallow waters, we predicted extreme morphology in the shallowest corals, as found in *M. spongodes, T. frondens,* and *H. pilosa.* As light energy attenuate over depth, we predicted a negative relationship between depth and the length of structural support which was only observed in corallites of *M. spongodes,* along with larger fossa. Contrarily, corallites of *M. capricornis, H. pilosa,* and *G. favulus* had a positive relationship between depth and structural support (i.e., length, width, and the number of septa). Additionally, as depth increased, the corallites of *M. spongodes* and *T. frondens* were further spaced. Unexpectedly, most corals had distinct morphology at intermediate depths (15-20m), such as the corallites of *M. spongodes* were the smallest, the most densely arranged and the furthest apart with the highest number of septa, the corallites of *A. curta* were the least dense, and the septa of *H. pilosa* were longest and the least dense. The well-document dissimilarity of shallow Symbiodiniaceae communities is expected due to the more dramatic environmental conditions of shallow waters (Bongaerts et al., 2015). Symbiodiniaceae depth zonation is thought to be indicative of corals' responsiveness to varying environmental conditions as depth increases (Bongaerts et al., 2015).

Among locations, we predicted variation in environmental conditions to imprint on corallite morphology. Among locations, the corallite of *A. curta* and *M. spongodes* were closest at Dougall Rock, whilst the corallites of *M. spongodes* at Napier Island were small and densely arranged with few, short septa indicative of low water flow conditions. Although there were general trends of varying morphology, the morphology of *G. favulus, M. capricornis,* and *T. frondens* was relatively consistent throughout the population. The morphological variation found across depths and locations might indicate improved coral fitness through greater light-gathering abilities (Kahng et al., 2019), more secure tissue attachments (Tambutté et al., 2007), and variations of trophic mechanisms to expand a coral's potential feeding supply (Crabbe & Smith, 2006; Todd, 2008). A greater understanding of the morphological distinction within a marginal coral population could help inform predictions of corals' responses to changing environmental conditions.

## 2.5.1 Depth

Shallow corals can maximize light capture, through specialized morphology, to utilize high light energy conditions  (Kahng et al., 2019). The shallowest corallites of *M. spongodes* were the largest and closest and the shallowest *H. pilosa* had high corallite coverage and short septa which can increase tissue coverage (Kahng et al., 2019). Comparably, corallites of *M. cavernosa* in northeastern Brazil were the largest and most dense in the shallowest corals (Amaral, 1994). Large, close corallites with less structural support enable tissue to occupy a greater surface area (Crabbe & Smith, 2006; Kahng et al., 2019). Optimizing tissue coverage predominantly occurs to promote autotrophic feeding (Crabbe & Smith, 2006; Kahng et al., 2019) presumably in response to a high light supply of shallow waters (Todd, 2008).

Shallow water has unique environmental conditions (Helmuth & Sebens, 1993; Nir et al., 2011; Kahng et al., 2019). The shallowest *M. spongodes* and *T. frondens* had extremely high measures of structural support (i.e., number and length of septa) compared to their deeper counterparts. For *Acropora clathrata* from Mauritius, septa development appeared to be dependent on wave action and currents (Hodgson & Carpenter, 1995). Corallites with greater wave exposure had more well-developed septa (Hodgson & Carpenter, 1995), which can indicate more tissue-anchoring cells (desmocytes; (Bourne, 1899) to create more secure tissue attachments to the skeleton (Muscatine et al., 1997; Tambutté et al., 2007). Although surface swell and turbulence are most pronounced in shallow waters (Helmuth & Sebens, 1993), it is not possible to pinpoint the morphological distinction in shallow coral to a particular environmental factor (Nir et al., 2011).

As depth increases, the stress induced by extreme shallow conditions recedes and deeper water has more stable abiotic conditions (Kahng et al., 2019). We found distinct corallite morphology at intermediate depths (15-20m). For instance, the corallites of *M. spongodes, T. frondens,* and *H. pilosa* had increased structural support (i.e., number and length of septa). Additionally, the septa of *H. pilosa* and corallites of *A.*

*curta* were the least dense, whilst corallites of *M. spongodes* were the densest and the furthest apart. The association between corallite morphology and feeding behaviour can be more pronounced below intermediate depths, presumably due to the attenuation of light (Lasker, 1981). An assessment of ultraviolet radiation A, used by microscopic marine algae for photosynthesis (Helbling et al., 1992), showed the most intense measures at ~15m, and exponentially decreases as depth further increases (Kahng et al., 2019). Corals in the South Sea of China, have a higher abundance at 15m compared with their shallower (1-5m) and deeper (18-20m) counterparts (Titlyanov & Latypov, 1991). Therefore, the low-stress yet energy-rich conditions of intermediate depths may provide unique conditions for corals (Chow et al., 2019), resulting in distinct morphology.

An inadequate supply of light energy can constrain coral growth (Einbinder et al., 2009) and influence distinct morphological features. The deeper corallites of *M. spongodes* and *T. frondens* were further apart. Similarly, in other subtropical studies, the distance between corallites of *M. cavernosa, Stylophora pistillata*, *Favia speciosa*, and *Pocillopora verrucosa* increased over depth, possibly to reduce self-shading (Todd et al., 2004; Einbinder et al., 2009; Goodbody-Gringley & Waletich, 2018; Soto et al., 2018). However, excessive corallite spacing can indicate a poor use of the surface area to survive. Previous research on *M. cavernosa* found that increased inter-corallite spacing could be a result of inadequate light energy supply (Amaral, 1994). To survive an insufficient energy supply, corals may modify their morphology to require lower energy input (Battey & Porter, 1988). Higher latitudes and/or deeper waters generally experience lower light energy conditions (Muir et al., 2015), which can limit coral growth and calcification rate by 10-fold, compared to their equatorial and shallow counterparts (Mass et al., 2007). Future research accessing growth over time, or plate thickness could clarify if deeper corallite spacing at Rangitāhua is a response to an inadequate energy supply (Anthony & Hoegh-Guldberg, 2003; Luck et al., 2013; Kahng et al., 2019).

Reduced structural support over depth can increase a coral’s light-gathering ability in response to decreasing light energy (Ow & Todd, 2010; Goodbody-Gringley &

Waletich, 2018). As predicted *M. spongodes* displayed a reduction in septa length and had larger fossa as depth increased. Similarly, corallites of *M. cavernosa* throughout the western Atlantic and *P. verrucosa* off eastern Taiwan had less structural support (i.e., septa length and height) in deeper waters than their shallow counterparts (Goodbody-Gringley & Waletich, 2018; Soto et al., 2018). Structural support is opaque, blocking light energy and, consequently, restricting the rate of photosynthesis (Dustan, 1982). Therefore, corals commonly sacrifice structural support in deeper waters to reduce self-shading and to maximize the limited light supply (Goodbody-Gringley & Waletich, 2018; Soto et al., 2018; Kahng et al., 2019).

Some corals in low light conditions can utilize their structural support to increase their light-gathering ability (Wangpraseurt et al., 2014; Smith et al., 2017). Unexpectedly, half of the species examined (*M. capricornis, G. favulus,* and *H. pilosa*) displayed a positive relationship between depth and structural support (i.e., length, width, and the number of septa). Findings from the Great Barrier Reef have suggested that modulation of structural support is a strategy to enhance light capture when paired with certain proteins (Wangpraseurt et al., 2014; Smith et al., 2017). Photoconvertible red fluorescent proteins (pcRFPs) can transform photons of blue light into orange-red light (Smith et al., 2017), which deeper corals are deprived of as it attenuates shallower in the water column than blue light (Chiang & Chen, 2011). Orange-red light is beneficial to corals as it can penetrate deeper within Symbiodiniaceae-containing tissues, than blue light, and can reflect off coral skeletons, like a mirror, increasing the probability of light energy reaching Symbiodiniaceae (Wangpraseurt et al., 2014; Smith et al., 2017). Therefore, longer septa, when coupled with pcRFPs, may enable a more homogenous distribution of light energy throughout a corallite, consequently, enhancing photosynthesis (Smith et al., 2017). Furthermore, less densely arranged structural support can accommodate more tissue and, consequently, more Symbiodiniaceae, which may increase the probability of photosynthesis occurring (Wangpraseurt et al., 2014). The increase of structural support in deeper corallites of *H. pilosa* and *G. favulus* was accompanied by a greater distance between septa or less densely arranged septa, optimizing the amount of tissue exposed to the possibly redistributed light energy. Evaluating the optic characteristics of the support structures and assessing proteins within corals surrounding Rangitāhua, could clarify if greater structural support improves or diminishes corals' light-gathering abilities.

Utilizing multiple feeding strategies can improve corals' resilience to environmental fluctuations and nutrient-limited conditions (M. D. Fox et al., 2018). Deeper corallites of *M. spongodes* were smaller than their shallow counterparts, as seen in *S. pistillata* in the red sea and *M. cavernosa* from the Gulf of Mexico (Einbinder et al., 2009; Studivan et al., 2019). Corals with small polyps appear to have a higher rates of prey capture per unit coral biomass than larger polyps (Sebens, 1997), promoting a higher volume capture of heterotrophic food (Sebens, 1997; Lesser et al., 2000). However, other studies have found small corallites to be more commonly associated with autotrophic feeding (Crabbe & Smith, 2006; Raja et al., 2021). Primarily utilizing autotrophy in summer, *Cladocora caespitosa* of northwestern Italy seasonally shifts to heterotrophic feeding as compensation for the restricted photosynthetic rates during low-energy winter months (Ferrier-Pagès et al., 2011). The combination of autotrophic and heterotrophic feeding can increase corals' rates of calcification and build tissue reserves, which in turn, can accommodate more Symbiodiniaceae (Hoogenboom et al., 2010; Ferrier-Pagès et al., 2011). The combination of deeper corals with smaller corallites and a higher abundance of symbionts (and chlorophyll *a* and *c2*)*,* than their shallower counterparts, has been observed in *S. pistillata* and *M. cavernosa* (as mentioned above) (Einbinder et al., 2009; Studivan et al., 2019). A high abundance of symbionts in deep corals may help counteract the limitations of autotrophy in low light energy conditions (Hoogenboom et al., 2010; Lesser et al., 2010). Nonetheless, further assessment of tentacle behaviour and/or symbionts (and chlorophyll) abundance may clarify how indicative the depth variation in corallite size is of corals' environmental responsiveness and feeding behaviour shifts.

### 2.5.2 Location

Although Rangitāhua is a small archipelago, environmental variation among the surrounding islands is dramatic (Wicks et al., 2010a; Duffy & Ahyong, 2015) and presumably influences corals' trophic behaviour and, consequently, their morphology (Todd, 2008; Williams et al., 2018). The corallites of *M. spongodes* at Napier Island were the smallest and the densest, with the fewest and shortest septa. The corallites of *A. clathrata* had longer and more calcified septa in locations with greater water flow conditions (Hodgson & Carpenter, 1995) which may indicate that water flow conditions at Napier Island are weak. Corallites exposed to intense water movement may achieve more secure tissue attachments through greater structural support (Tambutté et al., 2007). *G. favulus* had the thinnest structural support at North Meyer Island and widest at Dayrell Island. Although dissimilar among species, the variation in septa morphology suggests fluctuating water flow conditions among locations at Rangitāhua.

Stronger water flow can be associated with greater heterotrophic feeding which can influence corallite morphology (Todd, 2008; Williams et al., 2018). The corallites of *M. spongodes* at Napier Island had the lowest number of septa, whereas corallites had the highest number of septa at Dougall Rock. In some species, the number of septa per corallite positively corresponds with the number of tentacles per polyp (Duerden, 1904), as observed in a 1:1 ratio of *Stylaraea punctata* (Kitano et al., 2014). The number of tentacles per polyp can positively correspond with the volume of Zooplankton that corals can capture through heterotrophic feeding (Crabbe & Smith, 2006; Einbinder et al., 2009). As sessile organisms, corals' heterotrophic feeding is dependent on water flow to transport Zooplankton throughout the water column (Wainwright & Koehl, 1976; Williams et al., 2018). Therefore corallites of *M. spongodes* at Dougall Rock seem more adjusted to heterotrophic feeding than their counterparts at Napier Island, presumably driven by varying exposure to water flow conditions (Williams et al., 2018).

Greater water flow can also transport higher volumes of sediment throughout the Kermadec Arc (Mcleod, 2010). For *M. spongodes,* 43.2% of corallite morphology was accounted for in PC1, heavily defined by a positive relationship between corallite area and septa length, which was highest at North Meyer Island and Dougall Rock and lowest at Napier Island. Larger corallites and/or corallites with more septa are more able to expel sediment than their counterparts that are smaller and/or have fewer septa (Marshall, 1931; Hodgson & Carpenter, 1995; Todd, 2008). Recent satellite recordings suggest increased sediment surrounding Rangitāhua (Sutton et al., 2012). Sediments around Raoul Island are coarse, containing crustose coralline algae (red algae), bryozoan fragments, and coral rubble, with free-living *Cycloseris vaughani*, and unidentified bivalve and gastropod molluscs (Brook, 1998). Sediment exposure can deplete corals' energy reserves through coping mechanisms such as tentacle movement and/or mucus production (Tuttle & Donahue, 2022). The variation of corallite morphology among locations may serve as a stable and long-term solution to increase corallites' abilities to remove sediment, relieving the possible fatigue and stress of sediment exposure (Tuttle & Donahue, 2022).

Corallite spacing is commonly considered to have a positive relationship with light conditions (Todd, 2008; Einbinder et al., 2009). The corallites of *A. curta* and *M. spongodes* were the closest to their neighbouring corallites at Dougall Rock, as well as at Napier Island for *A. curta.* Light available to the benthos can vary among locations based on the angle, orientation, and reflectance properties of the substrate (Brakel, 1979). However, greater knowledge of the specific environmental variation among the islands surrounding Raoul Island is needed to further presume the ecological reasoning for varying corallite spacing for corals at different locations.

### 2.5.3 Limitations

The taxonomy of corals at Rangitāhua is very poorly understood and has only been approached from a traditional morphological taxonomic perspective. Although traditionally accepted, when solely using morphological classification to identify coral species, the results can cause bias (Todd et al., 2004; Terraneo et al., 2019). For instance, within a family of coral, there can be blurred partitioning between subspecies (Amaral, 1994), species, ectomorphs, and morphotypes (Todd et al., 2004). As observed in this study and many others, coral morphology can vary based on the environmental conditions they experience (Todd et al., 2004; Goodbody-Gringley & Waletich, 2018; Soto et al., 2018). Moreover, more isolated reefs can have distinct morphology than the respective species in more interconnect regions (Ramírez-Portilla et al., 2021). However, for future research, the results found in this study (of six putative corals' morphological variation) can contribute to further defining the morphological classification. Moreover, to elucidate the role of cryptic diversity in mediating patterns of morphological variation, further studies should use molecular indication methods (Todd et al., 2004). Combining morphological identification with another line of evidence can ensure more accurate classifications (Terraneo et al., 2019), and may account for some of the morphological variations we found within the coral community at Rangitāhua.

Low species abundance can limit the number of replicate samples collected and thereby statistical precision. Previous assessments of corals at Rangitāhua have found the population to have low coverage (Wicks et al., 2010a). Similarly in our research, the number of replicate skeletal samples for each location and depth combination was incomplete. As a result, the interactions between geographic variables were not able to be analysed. However, we completed a preliminary assessment of the morphology of the most abundant coral species over depth and among locations at Rangitāhua.

### 2.5.4 Conclusion

Half of the most abundant coral species at Rangitāhua displayed significant variation in morphology. Greater phenotypic variation, representing feeding ability, can expand a species' ecological tolerance and resilience during periods of nutrient limitation (Jaffe et al., 2016; Ho & Zhang, 2018). Therefore, if anthropogenically induced climate change causes the environmental conditions at Rangitāhua to change, our findings indicate *A. curta, H. pilosa,* and *M. spongodes* may endure a wider range of environmental conditions compared to *G. favulus, M. capricornis,* and *T. frondens*. A more in-depth assessment of the corals at Rangitāhua may be able to clarify if phenotypic plasticity or genetic variation drives the morphological variability of *A. curta, H. pilosa,* and *M. spongodes.*

Our study provides the first in-depth assessment of corallite morphology of shallow-water Scleractinian corals at Rangitāhua. Evidence of morphological distinction across fine-scale geographic gradients highlights the importance of considering local environmental conditions when predicting corals' response to climate change. This assessment provides inferences on corals' trophic patterns and feeding abilities which future studies could build upon. Particularly, further understanding is needed to differentiate whether certain morphological characteristics reflect poor health rather than greater light-gathering ability.

# Chapter 3: Compositional variation in Symbiodiniaceae communities of corals at Rāngitahua

## 3.1 Abstract

Anthropogenic climate change may force corals to endure intolerable conditions. It is well recognised that the Symbiodiniaceae relationships of a corals can alter their tolerance range. Here, we examined the Symbiodiniaceae communities of corals from the high latitude and isolated population at the Rangitāhua archipelago (the Kermadec Islands), New Zealand. We analysed the composition and taxonomic richness of Symbiodiniaceae communities of corals over depth and among islands (<1km). We found a high abundance of the coral symbiont *Cladocopium*, followed by a much lower abundance, yet higher diversity of *Symbiodinium,* as well as a low abundance of *Breviolum*, and *Fugacium.* Of the ITS2 type profiles found in the coral population at Rangitāhua, nearly half (22/42) were new to the *Symportal* database – a repository for all known Symbiodiniaceae. Among locations, the Symbiodiniaceae communities of *Astrea curta, Hydnophora pilosa,* and *Montipora spongodes* at the Meyer Islands had the most unique types and the greatest compositional dissimilarity compared to communities at Napier Island. Furthermore, the Symbiodiniaceae communities of *A. curta* at Meyer Islands had the highest taxonomic richness. Over depth, Symbiodiniaceae communities of shallow *A. curta* were distinct from its deeper counterparts and, as expected, the communities of *H. pilosa* had greater compositional dissimilarity and more unique Symbiodiniaceae types among shallow communities than its deeper counterparts (25-30m) presumably due to the extreme environmental conditions in shallow waters. Furthermore, Symbiodiniaceae communities of *A. curta, Goniastrea favulus, H. pilosa, Montipora capricornis,* and *M. spongodes* were taxonomically richest at intermediate depths, presumably due to the unique energy-rich conditions. The reduction in taxonomic richness below intermediate depths may indicate the well-documented trend of a shift from autotrophy to heterotrophy as light attenuates. Although there were general trends of varying Symbiodiniaceae communities, the Symbiodiniaceae of *G. favulus, M. capricornis,* and *Turbinaria frondens* were relatively consistent throughout the population. Our assessment of Symbiodiniaceae communities

of corals at Rangitāhua supports the well-documented trends of a high abundance of *Cladocopium* in high latitude regions, Symbiodiniaceae depth zonation, and the potential for the distinctness of Symbiodiniaceae communities even among spatially close locations. Overall, this study provides insight into the variation of coral-Symbiodiniaceae for a marginal population, which may help the understanding of how corals may respond to Anthropogenic induced environmental changes.

## 3.2 Introduction

Primary energy — heat and light — is fundamental for life on Earth. Due to the curvature of the Earth and the density of water, lower latitudes and shallower waters receive a greater energy supply than higher latitudes and deeper waters (Muir et al., 2015; Chen et al., 2019). Experiencing conditions beyond a species' tolerance range, especially sudden and/or frequent exposure, can threaten the health of organisms (Jansen et al., 1998; Djurichkovic et al., 2019; Magel et al., 2020). For example, exposure to an excessive light energy supply can damage plant cells and inhibit growth; however, intervals of insufficient light energy can also restrict a plant's photosynthetic rate, leading to starvation (Jansen et al., 1998). Similarly, fluctuations of increased heat energy can cause fish physiological stress, reducing their biomass (Magel et al., 2020), whilst during periods of insufficient heat energy fish' respiratory function can degrade (Djurichkovic et al., 2019). Although the health of these populations can recover during periods of more tolerable conditions (e.g., killifish (*Austrofundulus limnaeus*) following ultraviolet radiation) (Wagner & Podrabsky, 2015), an expansion of a population of species' tolerance can require energy conditions to incrementally change (Law & Crafts-Brandner, 1999). Therefore, greater frequency, magnitude, and/or rates of changing energy conditions during the Anthropocene period may threaten the survival of many species.

Anthropogenic activity is causing rapid poleward shifts of global heat energy gradients. Human activity has caused marine heatwaves to increase by 20-fold (Laufkötter et al., 2020). Thus, the number of species exposed to excessive heat energy is increasing, causing fragmentation, and disrupting ecosystems (Fattorini, 2020; Moore et al., 2021). For instance, the theoretic elevation of temperatures beyond bees' heat tolerance could have implications on their ecosystem, such as the extinction of associated plant and bird species (González-Tokman et al., 2020). To avoid heat stress, species may move into regions that have more tolerable energy conditions as documented for many marine species which are shifting away from the increasing temperatures in low latitudes (Arvedlund, 2009). However, as isotherms are shifting poleward, the amount of light energy supplied to a particular latitude is unlikely to change (Muir et al., 2015). Although some species may be able to shift their range to avoid unfavourable conditions caused by one stressor, the decoupling of energy gradients creates unfamiliar environmental conditions challenging species to endure other conditions outside their tolerance range.

The resilience of foundational species can impact the health of their ecosystem. Foundational species support greater abundance, biodiversity, and functionality in their ecosystem by modifying conditions and providing structure (Pratchett et al., 2008; Angelini et al., 2011; Stella et al., 2011). For example, when comparing two regions within the Western Mediterranean Sea, with similar environmental conditions and substrate, regions with foundational sea sponge species have greater richness than those lacking the presence of sea sponges (de la Torriente et al., 2020). Depletion of foundational species, such as reef-building coral is causing a reduction in marine vertebrates' abundance and diversity (Wilson et al., 2006; Pratchett et al., 2008; Graham, 2014), along with reduced diversity of reef-associated invertebrates (Idjadi & Edmunds, 2006; Stella et al., 2011). Therefore, the loss of functioning corals is one of the greatest and most rapidly developing risks to reef ecosystems (Pratchett et al., 2008). As the degradation of foundational species threatens entire ecosystems (de la Torriente et al., 2020; Layton et al., 2020), a greater understanding of foundational species' resilience to fluctuating energy conditions is of high conservation importance.

Corals heavily rely on their symbiotic relationship with Symbiodiniaceae; a type of dinoflagellate endosymbiont ('zooxanthellae'), harboured in their tissue, which powers coral growth by photosynthesizing organic compounds (Wicks et al., 2010b; LaJeunesse et al., 2018). Symbiotic relationships can buffer the effects of changing environmental conditions by altering and/or expanding species' tolerance (Augé, 2001). For instance, *Symbiodinium linucheae* has been found predominantly in tidal and shallow *Favia gravida* (Teschima et al., 2019). The mycosporine-like amino acids (MAAs) found in *Symbiodinium* (formally clade A) can offer UV protection for its hosts (Banaszak et al., 2000), consequently, expanding corals' tolerance to acute thermal stress as experienced in tidal pools (Teschima et al., 2019). Therefore, the environmental conditions that corals experience are likely to influence the diversity of their Symbiodiniaceae communities, thereby impacting host corals' ability to withstand certain environments.

The decoupling of heat and light energy gradients may force corals to endure environmental conditions beyond their tolerance range. If corals follow shifting heat gradients to higher latitudes, to avoid heat stress, they may be forced to survive a lower light energy supply. The Symbiodiniaceae of corals inhabiting the South Sea of China display latitudinal zonation presumably due to the varying environmental conditions (Chen et al., 2019). Varition in environmental conditions can be followed by corals re-establishing their Symbiodiniaceae communities through quantitative change of the abundance of current symbionts (shuffling) or qualitative change through restricting their communities with additional symbionts acquired from the water column (switching) in order to better tolerate their new conditions (Baker, 2003). However, frequent restructuring of corals' Symbiodiniaceae communities can degrade corals' health (e.g., increased exposure to viruses which can cause disease for corals) (Lawrence et al., 2017; Boilard et al., 2020). Coral populations inhabiting high latitude archipelagos provide an opportunity to assess the fine-scale variation of corals' Symbiodiniaceae communities at the lower limit of corals' energy tolerance.

One of the highest latitudinal coral communities, found at Rangitāhua (29° 12' S, 177° 55' W; Figure 3.1 (a)), exhibits a close affinity with the communities inhabiting southeastern Australian, but not other high latitude communities, nor more tropical Australian communities (Wicks et al., 2010a). Although corals at Rangitāhua have low coverage like southeastern Australian populations (8%), there is a less diverse range of corals at Rangitāhua (11-16 spp.) (Wicks et al., 2010a; Richards & Liggins, 2015) perhaps due to the extreme wave action, narrow/low thermal range (Wicks et al., 2010a), and lack of a prior land bridge (Brothers & Searle, 1970). Previous studies of the Symbiodiniaceae community in corals of Rangitāhua have been restricted to identifying the single most abundant Symbiodiniaceae species per coral host (Wicks et al., 2010b). However, advances in genomic research such as next-generation sequencing technologies that enable parallel sequencing of many DNA fragments simultaneously, and bioinformatics pipelines, such as *Symportal,* can now provide higher resolution genetic delineations of Symbiodiniaceae and reveal the whole community of Symbiodiniaceae present (Hume et al., 2019). Updating the genomic research of Symbiodiniaceae of corals at Rangitāhua to identify Symbiodiniaceae communities could further clarify the limits of Symbiodiniaceae-corals' tolerance.

Here we study the taxonomic richness and composition of the Symbiodiniaceae communities of Scleractinian corals at Rangitāhua based on the internal transcribed spacer 2 (ITS2) of corals' symbionts over the depth gradient (5-30m) and among locations. As a marginal population, we aim to identify the coral-Symbiodiniaceae relationships at the edge of their tolerance range. We predict a high abundance of *Cladocopium* (formally clade C) as previously observed at Rangitāhua and other high latitude populations (Wicks et al., 2010b; Chen et al., 2019). Due to the dramatic variation in environmental conditions surrounding the islands (Wicks et al., 2010a), we expected to find variation in the taxonomic richness and the composition of the Symbiodiniaceae communities among the studied locations. We also predicted to see a common pattern of greater dissimilarity among the Symbiodiniaceae communities in shallow waters, compared to the variation among deeper depths, due to the higher energy supply in shallow waters (Bongaerts et al., 2015). A greater understanding of Rangitāhua's coral-Symbiodiniaceae relationships could help to better predict the potential of coral resilience to decoupling energy gradients.

## 3.3 Methods

### 3.3.1 Field sampling and study design

To characterize the diversity of Symbiodiniaceae communities inhabiting shallow-water Scleractinian corals at Rangitāhua, we collected small fragments of live colonies for the six of the most common species present, during October and November of 2015, 2016, and 2017. Due to the low abundance of colonies per coral species (Wicks et al., 2010a), the selection of species was based on which species were found in sufficient abundance. Putative species were identified through morphological features of skeletons; *Astrea curta* (Dana, 1846), *Goniastrea favulus* (Dana, 1846), *Hydnophora hermo* (Veron, 1985), *Montipora capricornis* Veron, 1985, *Montipora spongodes* Bernard, 1897, and *Turbinaria frondens* (Dana, 1846), which represent almost half of the known coral species at Rangitāhua (16 species) (Wicks et al., 2010a) (11 species) (Richards & Liggins, 2015).

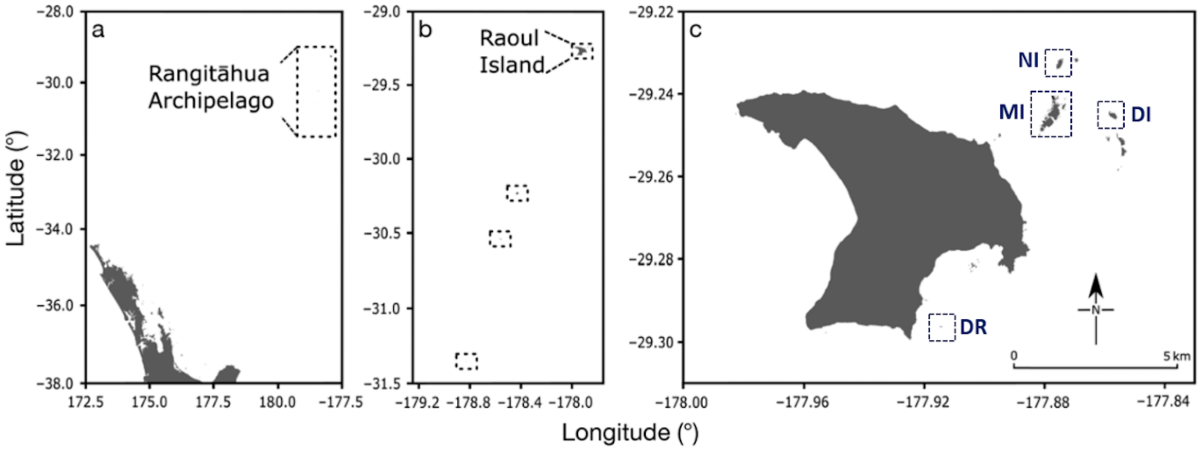

Figure 3.1 (a) The Rangitāhua archipelago (inside the dashed box) relative to Te Ika a Māui of Aotearoa (New Zealand's North Island). (b) Raoul Island, relative to the other islands in the Rangitāhua archipelago. (c) The sampling locations that are distributed around Raoul Island: Dayrell Island (DI), Meyer Islands (MI), and Napier Island (NI) on the northern side, as well as Dougall Rock (DR) on the eastern side of Raoul Island.

Depending on their local abundance, up to five replicate samples of each species at six depth strata (5, 10, 15, 20, 25, and 30m) were collected at the four locations; Dayrell Island, Dougall Rock, Meyer Islands, and Napier Island (Figure 3.1 I). Samples of approximately 150 grams of live coral (tissue and skeleton) were collected and immediately placed in 2ml tubes filled with 100% ethanol. The ethanol in each 2ml vial was changed daily for the first three days or until the ethanol solution was clear. Samples were stored at 4°C until the completion of each expedition and transferred to -80°C as soon as practicable.

### 3.3.2 Genetic laboratory work, library preparation, and sequencing

To assess the internal transcribed spacer 2 (ITS2) region of Symbiodiniaceae, their genomic DNA was extracted from coral fragments using the Power Plant® Pro DNA Isolation Kit (Qiagen) following the manufacturer protocol with minor modifications. For each coral fragment, 20-50g of a sample was placed in PowerPlant Bead tubes, with 450 µL of lysis solution (PD1), 50 µL of SL and 5 µL of proteinase K to incubate for 30 mins at 55°C. Next, 3 µL RNAse were added at room temperature and the samples were allowed to rest for 5 minutes. Coral fragments were then hermos zed using the TissueLyser (Qiagen) at maximum speed (30 RPM) for 10 minutes. The next steps were followed as specified in the manufacturer protocol. UltraPure Dnase/RNAase-Free Water (Thermo Fisher; hereafter water) was used in the final step rather than the elution buffer.

To assess the quality and quantity of the genomic DNA extracted, each DNA extraction was run on a 1% agarose gel, using a 1kb ladder and visualized using GelRed® Nucleic acid gel stain (Biotium, Inc.). DNA yield was estimated using gel electrophoresis and confirmed using Nanodrop (ACTGene ASP-3700) and Qubit fluorometer (Qubit™ dsDNA BR Assay Kit) for some of the samples. DNA concentration of all genomic DNA extractions was normalized to 10-20ng/µL by diluting samples in water.

To amplify a ~234–266bp fragment of the ITS2 region of Symbiodiniaceae, we used the primers SYM_VAR_5.8S (GAATTGCAGAACTCCGTGAACC) (Hume, 2013) and SYM_VAR_REV (CGGGTTCWCTTGTYTGACTTCATGC) (Hume, 2013) modified to include the Ilumina™ overhang adaptors. One PCR was carried out for each sample in a total volume of 20µL containing: 1 µL of genomic DNA (10-20ng/µL), 10 µL Kapa HiFi HotStart ReadyMix (KAPA), 0.6 µl (10 µmol/µL) of each forward and reverse primers, 0.8 µl of DMSO (99%) and 7 µL of water. The hermos-cycling regime followed Hume et al. (2018) briefly, initial denaturation at 98°C for 2 min, followed by 35 cycles of 10s at 98°C, 30s at 56°C, and 30s at 72°C, with a final extension for 5 min at 72°C before returning to room temperature, using a SureCycler 8800 Thermal Cycler (Agilent Technologies, USA). For each set of PCR amplification, a negative PCR control was also included using 1µL water instead of genomic DNA.

The success of the PCR was assessed using a 100bp ladder in the 1% agarose gel. For each successful amplification, 20 µl of the DNA amplicons (>10ng/ µl) were sent to the Australian Genome Research Facility (AGRF, Victoria, Australia) where indexing occurred using the Nextera™ DNA library Prep Kit (Illumina, California, USA). The libraries were loaded and sequenced on an Illumina NovaSeq™ System SP-500 using paired-end 250 bp reads.

### 3.3.3 Bioinformatic and statistical analyses

Raw sequences of demultiplexed paired fastq.gz files were submitted to the *Symportal* framework for analysis (Symportal.org) (Hume et al., 2019). As part of the submission, quality control was performed along with filtration of non- Symbiodiniaceae sequences and sequence artifacts. Briefly, quality control was accomplished using mothur (Schloss et al., 2009), Blast+ (Camacho et al., 2009) and minimum entropy decomposition (MED) (Eren et al., 2015). Whilst other approaches only identify the most abundant ITS2 sequences, *Symportal* additionally assesses all other ITS2 sequences within a community. ITS2 sequences that occur in sufficient abundance are considered defining intragenomic variants (DIVs). Based on the presence and abundance of DIVs, along with the genera they were assigned to, DIVs are then used to characterize the ITS2 type profiles which represent putative Symbiodiniaceae taxa. It is worth noting that, since the establishment of the *Symportal* framework, Symbiodiniaceae taxonomy has recently been revised, and former clades within the genus *Symbiodinium* (clade A-I), are now classified as distinct genera within the family Symbiodiniaceae to better reflect its evolutionary history (LaJeunesse et al., 2018; Nitschke et al., 2020; Pochon & LaJeunesse, 2021).

For all analyses, ITS2 sequences, DIVs, and ITS2 type profile data were used directly from *Symportal* output in R v4.1.0 (R. Team, 2020). Data for each of the six putative coral species were analysed separately. To investigate Symbiodiniaceae communities, based on the ITS2 type profiles, we examined differences in the Symbiodiniaceae taxonomic richness and community composition across locations and a depth gradient for each coral species. For data visualisation, a bar plot was constructed, using *ggplot* (ggplot2) (Wickham, 2016), to depict the abundance of present ITS2 type profiles per sample collected from each depth and location. To better display less abundant DIVs, ITS2 type profile abundance was transformed into the fourth root. Due to the unbalanced collection of samples across depth and location, for posterior analysis, some host species were separated into two datasets either containing two depth levels at all locations or a greater depth coverage at one location. Specifically, for *M. spongodes* the two datasets were '*M. spongodes* deep' for examining patterns at 25-30 metres depth at Dougall Rock, Meyer Islands, and Dayrell Island and '*M. spongodes* Meyer Islands' for examining patterns at 15-30 metres depth at Meyer Islands only. Whilst *Astrea curta* was separated into '*A. curta* shallow' for examining patterns at 5-10 metres at all four sites and '*A. curta* Dougall Rock' for examining patterns at 5-25 metres depth for Dougall Rock only.

Trends in Symbiodiniaceae richness of ITS2 type profiles were assessed using a linear model with depth and location as fixed categorical factors using the *lm* function in the R base statistics package (R. C. Team, 2021). The significance of each factor, as well as pairwise differences among levels, were assessed using the *ANOVA* (car) (Weisberg, 2019) and *tukeyHSD* (stats) (R. C. Team, 2021) functions, respectively. The estimated marginal means were displayed using *emmeans* (Lenth, 2022).

Next, to assess trends in ITS2 type profile composition, a distance-based redundancy analysis (dbRDA) was conducted using Bray-Curtis dissimilarity in ITS2 type profile abundance among samples by using *capscale* function in vegan (Oksanen et al., 2020). Due to the wide range of abundance in ITS2 type profiles, data were fourth root transformed (as described above). Collection depth and location were considered fixed categorical factors. To assess the marginal effect of each factor we performed a permutation test using the *ANOVA* function (car) (Weisberg, 2019). Additionally, the Symbiodiniaceae compositions of corals were further analysed to identify levels of significance using *scores* in vegan and visualized through *ggplot2* (Wickham, 2016).

## 3.4 Results

We examined the Symbiodiniaceae taxonomic richness and community composition of 213 coral host samples. Nine samples were removed due to their insufficient concentration of ITS2 sequences. The 204 samples returned a total of 207,649,376 sequence reads, which after quality control and removing non-Symbiodiniaceae ITS2 sequences (as explained in the methods), 145,497,372 sequence reads remained (70.1%). We obtained between $1.3\times10^7$ and $4.1\times10^7$ ITS2 sequences for each host coral species (Table 3.1). There was a total of 616 distinct IS2 sequences (ranging between 117-243 distinct ITS2 sequences per host species; Table 3.1). Only the ITS2 sequences that were found in sufficient abundance were considered DIVs. We obtained a total of $1.3\times10^8$ DIVs (range $1.1\times10^7$-$3.5\times10^7$ per host species). The DIVs were used to construct the 42 ITS2 type profiles (Hume et al., 2019) found within our samples (ranging between 12-26 distinct ITS2 type profiles per host species), 22 of which had not yet been identified within the *Symportal* database.

Through the assignment of DIVs to Symbiodiniaceae genera taxonomy, ITS2 type profiles are constructed. Although *Cladocopium* was found in the highest abundance, the genus *Symbiodinium* was found to have the greatest diversity in ITS2 type profiles. Of all six host species, most (97.19%) of the DIVs obtained were assigned to the genus *Cladocopium,* followed by 2.80% assigned to the genus *Symbiodinium* (Figure 3.2 and Table 3.1). *Symbiodinium* had 21 ITS2 type profiles assigned to the genus, compared to the 16 ITS2 type profile types assigned to *Cladocopium*. Except for six samples with their most abundant ITS2 type profiles assigned to *Symbiodinium* (Figure 3.2). The remaining 0.01% of DIVs were assigned to the genera *Fugacium* (formerly clade F; three ITS2 type profiles), and *Breviolum* (formerly clade B; two ITS2 type profiles).

Table 3.31 Summary of *Symportal* output for corals collected surrounding Raoul Island. Within each Symbiodiniaceae genus, N: Number of distinct ITS2 type profiles assigned to each genus per host species. %: percentage of DIVs assigned to each genus from all DIVs of the respective host species. The % of the most abundant ITS2 type profiles refers to the percentage of DIVs contributing to the most abundant ITS2 type profile from all DIVs obtained for the respective host species.

| | | | *Astrea curta* | *Turbinaria frondens* | *Goniastrea favulus* | *Hydnophora pilosa* | *Montipora capricornis* | *Montipora spongodes* |
|---|---|---|---|---|---|---|---|---|
| Number of samples | | | 38 | 38 | 33 | 55 | 20 | 20 |
| Number of distinct ITS2 sequences | | | 222 | 220 | 243 | 226 | 117 | 159 |
| Total ITS2 sequences ($\times10^{7}$) | | | 2.6 | 2.7 | 2.1 | 4.1 | 1.3 | 1.5 |
| Range of distinct ITS2 sequences per sample | | | 1-45 | 13-45 | 16-62 | 10-44 | 3-39 | 12-42 |
| Number of distinct ITS2 type profiles | | | 22 | 17 | 21 | 26 | 12 | 17 |
| Total DIVs ($\times10^{7}$) | | | 2.4 | 2.4 | 1.9 | 3.5 | 1.1 | 1.3 |
| Symbiodiniaceae assigned to each genus | *Cladocopium* | N | 9 | 10 | 7 | 7 | 5 | 5 |
| | | % | 99.53 | 98.71 | 99.47 | 94.07 | 95.35 | 96.74 |
| | *Breviolum* | N | | | | | | 2 |
| | | % | | | | | | 0.09 |
| | *Symbiodinium* | N | 12 | 7 | 12 | 19 | 7 | 10 |
| | | % | 0.47 | 1.29 | 0.52 | 5.92 | 4.64 | 3.17 |
| | *Fugacium* | N | 1 | | 2 | | | |
| | | % | $5.8\times10^{-4}$ | | $8.5\times10^{-3}$ | | | |
| Most abundant ITS2 type profiles | | | C50b/C3-C3bh-C3bm-C50f (68%) | C1-C42.2-C1b-C3ih-C1ea-C1h-C1ab-C1by (71%) | C3-C3bC3ey-C1-C1ia (52%) | C3-C3bC3ey-C1-C1ia (46%), C3-C3b-C3ey-C3ia (32%) | C1/C1z-C42.2-C1b-C3-C42au-C1ab (82%) | C1.C3.C42.2.C1by.C1cz.C3hz (57%) |

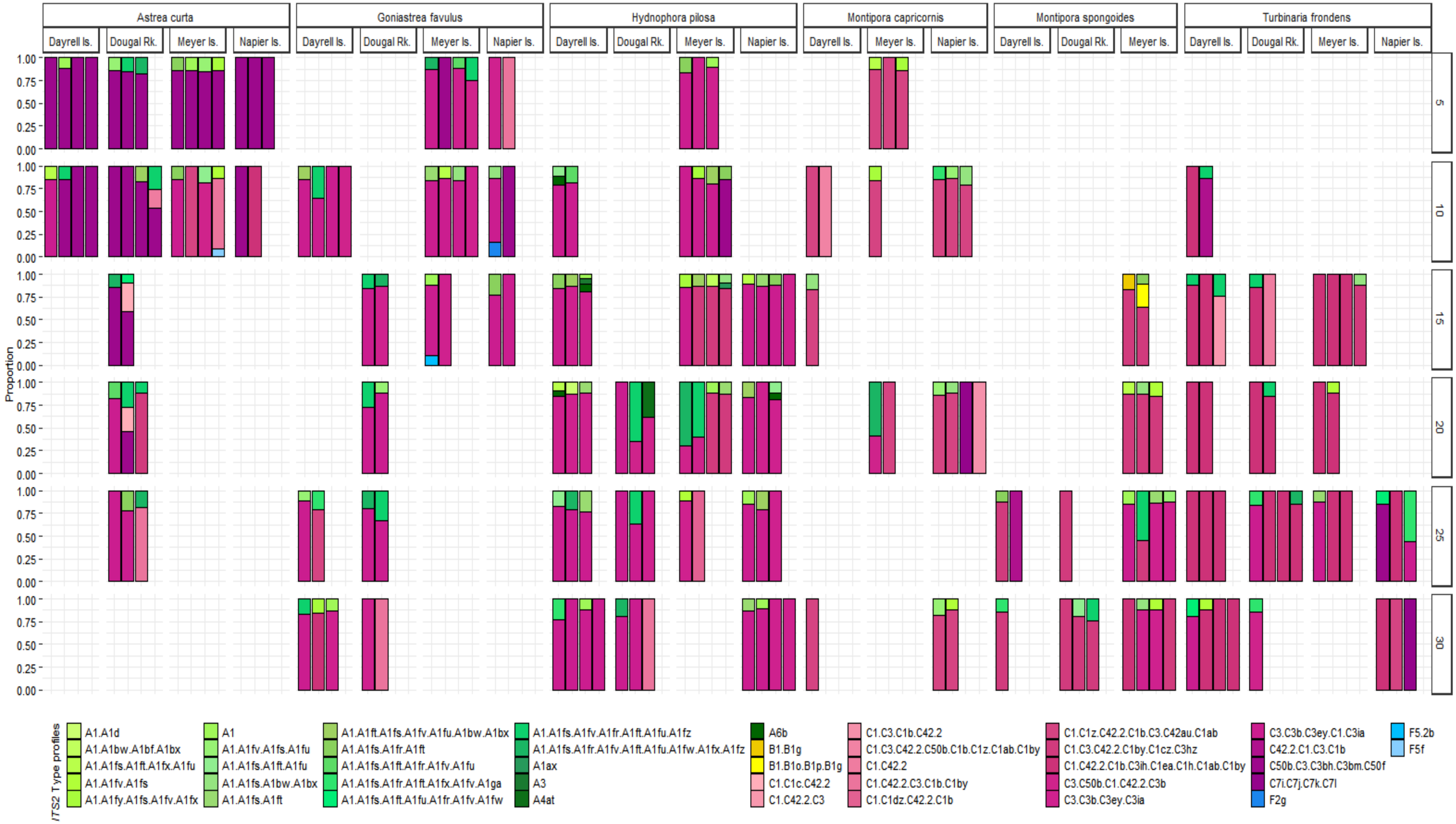

Figure 3.2 Proportion of ITS2 type profiles for each coral host species at each location and depth (m) collected surrounding Raoul Island. Results are displayed as the fourth root transformed.

Table 3.2 ANOVA of Symbiodiniaceae taxonomic richness(R) and community composition (CC) of coral species across the depth gradient and among locations surrounding Raoul Island. Significant results are bolded.

| **Geographic factor** | | | **Depth** | | | | **Location** | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | *DF* | *Sum Sq* | *F* | *P* | *DF* | *Sum Sq* | *F* | *P* |
| *A. curta* | Shallow | R | 1 | 0.001 | 0.003 | 0.960 | 3 | 3.946 | 4.495 | **0.013*** |
| | | CC | 1 | 0.811 | 4.664 | **0.001***** | 3 | 0.886 | 1.697 | 0.058. |
| | Dougall Rk. | R | 4 | 1.417 | 0.773 | 0.567 | | | | |
| | | CC | 4 | 2.171 | 2.949 | **0.001 ***** | | | | |
| *G. favulus* | | R | 5 | 1.188 | 0.636 | 0.675 | 3 | 0.390 | 0.348 | 0.791 |
| | | CC | 5 | 2.016 | 1.109 | 0.334 | 3 | 0.526 | 0.482 | 0.959 |
| *H. pilosa* | | R | 5 | 3.338 | 2.015 | 0.094. | 3 | 2.949 | 2.968 | **0.042 *** |
| | | CC | 5 | 3.172 | 2.021 | **0.017 *** | 3 | 2.066 | 2.192 | **0.017 *** |
| *M. capricornis* | | R | 1 | 0.083 | 0.351 | 0.562 | 2 | 0.782 | 1.650 | 0.225 |
| | | CC | 1 | 0.133 | 0.614 | 0.700 | 2 | 0.262 | 0.607 | 0.816 |
| *M. spongodes* | Deep | R | 1 | 0.008 | 0.028 | 0.869 | 2 | 0.167 | 0.290 | 0.754 |
| | | CC | 1 | 0.130 | 0.441 | 0.789 | 2 | 1.410 | 2.388 | **0.040 *** |
| | Meyer Is. | R | 3 | 1.423 | 2.846 | 0.098. | | | | |
| | | CC | 3 | 1.502 | 1.664 | 0.148 | | | | |
| *T. frondens* | | R | 4 | 0.121 | 0.105 | 0.980 | 3 | 0.309 | 0.357 | 0.784 |
| | | CC | 4 | 1.121 | 1.069 | 0.352 | 3 | 0.846 | 1.076 | 0.346 |

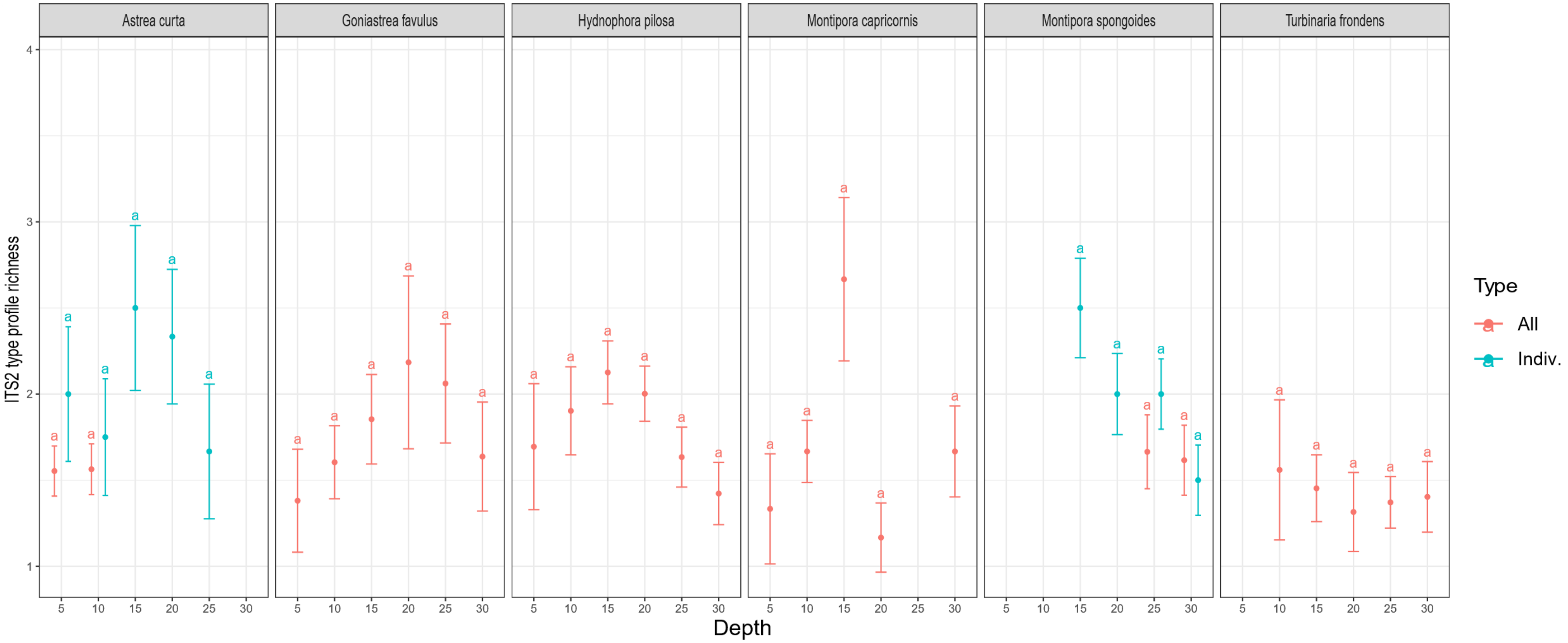

Figure 3.3 Symbiodiniaceae' taxonomic richness of each coral species across the depth (m) gradient for the sampled locations at Raoul Island. All: refers to all the locations each respective species was found at. Indiv: refers to the respective single location subset data of *A. curta* Dougall Rock and *M. spongodes* Meyer Islands. Letters denote Tukey HSD post-hoc groupings.

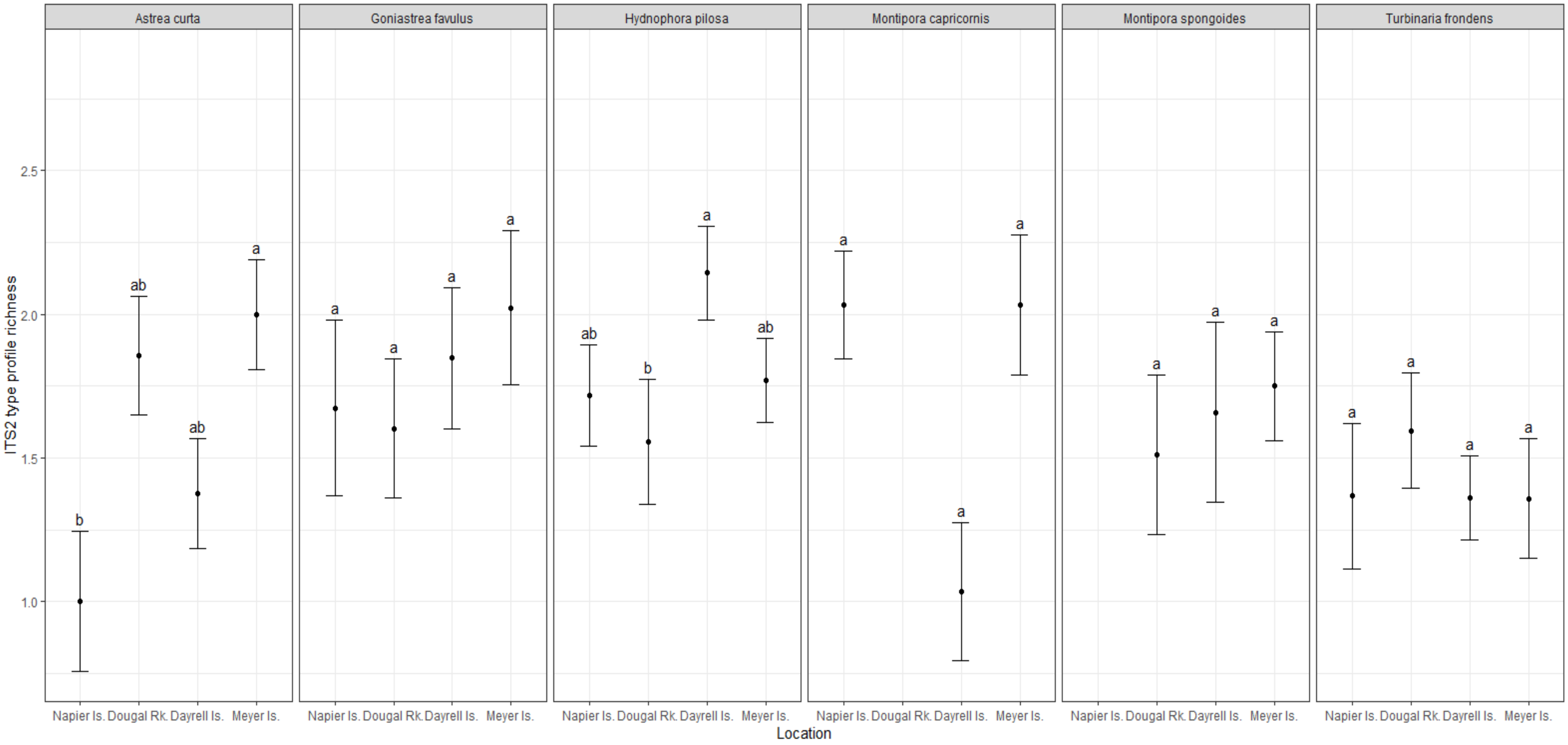

Figure 3.4 Symbiodiniaceae' taxonomic richness of coral species at locations surrounding Raoul Island. Letters denote Tukey HSD post-hoc groupings. *Astrea curta*: *A. curta* shallow. *Montipora spongodes*: *M. spongodes* deep.

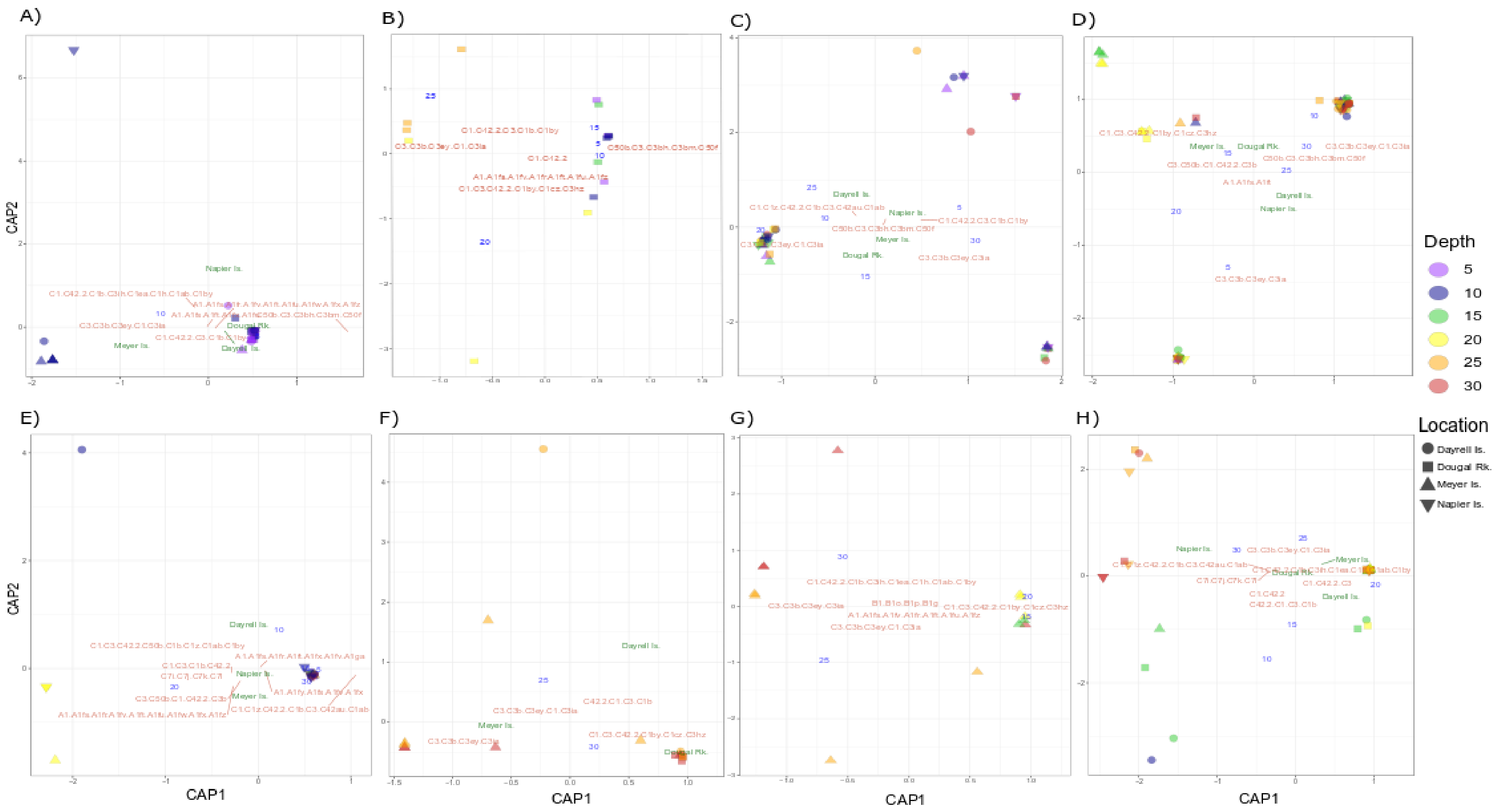

Figure 3.5 Symbiodiniaceae’ community composition (coordinates of the most common ITS2 type Symbiodiniaceae profiles indicated in the red text) of coral species across the depth gradient (centroids for levels of depth are indicated by the blue text) and among locations surrounding Raoul Island (centroids for levels of location are indicated by the green text). A) *Astrea curta* shallow B) *Astrea curta* Dougall Rk. C) *Goniastrea favulus* D) *Hydnophora Pilosa* E) *Montipora capricornis* F) *Montipora spongodes* deep G) *Montipora spongodes* Meyer Is. H) *Turbinaria frondens*

### 3.4.1 Depth

**Richness**

None of the coral species had a significant difference in their Symbiodiniaceae' taxonomic richness over depth (Table 3.2). However, we observed general trends within our results for some coral species. For *A. curta* Dougall Rock and *M. spongodes* Meyer Islands, as well as *G. favulus, H.pilosa*, and *M. capricornis* at all locations*,* the highest Symbiodiniaceae taxonomic richness was found at intermediate depths (15-20m) and the lowest taxonomic richness at the edges of the studied depth range (Figure 3.3). The shallowest Symbiodiniaceae communities of *M. spongodes* Meyer Islands were at intermediate depth, as a result, the communities of *M. spongodes* Meyer Islands had a negative relationship between their taxonomic richness and depth, with higher taxonomic richness in shallower communities than in deeper communities. Whereas, for the communities of *A. curta* shallow and *M. spongodes* deep there was consistent taxonomic richness over depths. Moreover, we found consistent taxonomic richness in *T. frondens* across the depth gradient.

**Community composition**

For *A. curta* shallow, the Symbiodiniaceae communities at 10m had ten unique ITS2 type profiles, whilst communities at 5m only had four unique ITS2 type profiles (Figure 3.2). Only considering ITS2 type profiles assigned to *Cladocopium*, communities at 5m had a single ITS2 type profile, whilst communities at 10m had an additional six, four of which were found in high abundance (>100,000 DIVs). Within the communities of *A. curta,* the genus *Fugacium* was only found in communities at 10m.

For *A. curta* Dougall Rock, Symbiodiniaceae communities at shallower depths (5 and 10m, $P_{(PERM)}$=0.13) were more similar to each other and more clustered together than the composition of deeper communities (Figure 3.5.B). Symbiodiniaceae communities at 15m were distinct from the shallower (10m; $P_{(PERM)}$=0.03) and deeper (20m; $P_{(PERM)}$=0.05) Symbiodiniaceae communities, whereas the deepest communities (20-25m) were more alike ($P_{(PERM)}$=0.09). Whilst most of the shallower communities (<15m) shared a common most abundant ITS2 type profile, there was a lack of similarity in the most abundant ITS type profiles of deeper (20m and 25m) communities (Figure 3.2).

We found a difference in the compositions of the Symbiodiniaceae community of *H. pilosa* along the studied depth gradient (Table 3.2). There was a compositional distinction among the Symbiodiniaceae communities at shallow depths (5 and 10m; $P_{(PERM)}$=0.009, 10 and 15m; $P_{(PERM)}$=0.01) and between some deeper Symbiodiniaceae communities (20 and 25m; $P_{(PERM)}$=0.04; Figure 3.5.D). However, the composition of the Symbiodiniaceae communities at intermediate depths (15-20m) was similar to each other ($P_{(PERM)}$=0.69), as were communities at deeper depths (25 and 30m; $P_{(PERM)}$=0.81). The number of unique ITS2 type profiles per depth, relative to the number of samples, gradually decreased over the depth gradient (excluding 5m due to low abundance (*n* = 3; Figure 3.2). At most depths (10, 15, 25, 30m), the ITS2 type profile with the highest abundance was the same (C3.C3b.C3ey.C1.C3ia). However, for communities 5m and 20m, the most abundant ITS2 type profile (C3.C3b.C3ey.C3ia) was the same, whereas, both the ITS2 type profiles were found in a high abundance in communities at 15 metres.

For *G. favulus* and *M. capricornis* we found no significant differences in the composition of Symbiodiniaceae communities over depth (Table 3.2). However, we found a distinction in the Symbiodiniaceae communities at intermediate depths in both coral species (10-20m). Symbiodiniaceae communities of *M. capricornis* at 20m were significantly different from the deepest Symbiodiniaceae communities (20 and 30; $P_{(PERM)}$=0.04), whilst the composition of Symbiodiniaceae communities of *M. capricornis* at all other depths was more similar to each other ($P_{(PERM)}$=0.62-1.00). Similarly, the composition of the Symbiodiniaceae communities of *G. favulus* at 10m was different to the communities at 30m ($P_{(PERM)}$=0.05), whilst the composition of the Symbiodiniaceae communities of *G. favulus* at other depths was more similar to each other ($P_{(PERM)}$=0.34-0.80).

We found no evidence of a difference in the Symbiodiniaceae community composition over the observed depth of *M. spongodes* deep, *M. spongodes* Meyer Islands, and *T. frondens* (Table 3.2).

## 3.4.2 Location

### Richness

For Symbiodiniaceae communities of *H. pilosa* and *A. curta,* we found a difference in the taxonomic richness among locations (Table 3.2). For Symbiodiniaceae communities of *H. pilosa,* taxonomic richness was the highest at Dayrell Island and the lowest at Dougall Rock, whilst Symbiodiniaceae communities of *A. curta* shallow had the highest richness at Meyer Islands and lowest at Napier Island (Figure 3.4) Although the taxonomic richness for Symbiodiniaceae communities of *G. favulus*, and *M. capricornis* did not significantly differ among locations, there was a general trend of the highest taxonomic richness of Symbiodiniaceae at Meyer Islands (Figure 3.4). The taxonomic richness of Symbiodiniaceae communities from *M. spongodes* deep and *T. frondens* were consistent among locations.

### Community composition

The Symbiodiniaceae communities of half the host coral species studied, *A. curta, H. pilosa,* and *M. spongodes,* differed among locations (Table 3.2). Symbiodiniaceae communities of *A. curta* shallow had a compositional distinction between Napier Island and Meyer Islands ($P_{(PERM)}$=0.03), whereas communities at Napier Island were like those at Dayrell Island and Dougall Rock ($P_{(PERM)}$=0.57-0.83; Figure 3.5.A). For Symbiodiniaceae communities of *A. curta,* we found more ITS2 type profiles unique to Meyer Islands than the other three locations. When considering only the ITS2 type profiles within the genus *Cladocopium,* five ITS2 type profiles were found unique at Meyer Islands, whilst we found two ITS2 type profiles unique to each Dayrell Island and Dougall Rock, and only a single unique ITS2 type profile found at Napier Island (Figure 3.2). Additionally, we found six ITS2 type profiles within the genus *Symbiodinium* unique to Meyer Islands, along with the presence of the genus *Fugacium*. For at least 80% of samples at Napier and Dayrell Islands as well as Dougall Rock, we found C50b.C3.C3bh.C3bm.C50f in high abundance, whereas the same ITS2 type profile was found in high abundance for only 50% of the samples at Meyer Islands.

The composition of the Symbiodiniaceae communities of *H. pilosa* at Dougall Rock was like those at Dayrell Island ($P_{(PERM)}$=0.30) and Napier Island ($P_{(PERM)}$=0.18;

Figure 3.5.D), whereas the composition of the Symbiodiniaceae communities at Napier Island was distinct from the communities at Meyer Islands ($P_{(PERM)}$=0.04). The most abundant ITS2 type profile (C3-C3bC3ey-C1-C1ia) was the same among the communities at Dougall Rock, Dayrell Island, and Napier Island, whereas, for the communities at Meyer Islands, the most abundant ITS2 type profile was unique to Meyer Islands (C1.C3.C42.2.C1by.C1cz.C3hz; Figure 3.2). Communities at Meyer Islands had 7 unique ITS2 type profiles, which was the most of any one location, followed by Dayrell Island and Dougall Rock with two, whereas there were no unique ITS2 type profiles found within the Symbiodiniaceae communities at Napier Island.

There was a compositional distinction between the Symbiodiniaceae communities of *M. spongodes* deep between Meyer Islands and Dougall Rock ($P_{(PERM)}$=0.01), whereas the Symbiodiniaceae communities of Dougall Rock and Dayrell Island were similar ($P_{(PERM)}$=0.32; Figure 3.2). For communities at Dougall Rock and Dayrell Island, the most abundant ITS2 type profile (C1/C3-C42.2-C1by-C1cz-C3hz) was the same, whereas a different ITS2 type profile (C3-C3b-C3ey-C3ia) was found in the highest abundance in the communities at Meyer Islands. Communities at Meyer Islands had 11 unique ITS2 type profiles, which is the most of any location, followed by Dayrell Island with two, and Dougall Rock with one unique ITS2 type profile. The genus *Breviolum,* was only found in shallow communities at Meyer Islands associated with the host *M. spongodes*; however, Meyer Islands was the only location where *M. spongodes* was found in shallow waters (<20m) and therefore excluded from the analysis of variation among locations.

We found no evidence of a difference in the Symbiodiniaceae community composition of *M. capricornis, G. favulus,* and *T. frondens* among locations (Table 3.2).

## 3.5 Discussion

Our study provides an assessment of the Symbiodiniaceae communities of the most abundant shallow-water Scleractinian corals at Rangitāhua. The Symbiodiniaceae genus *Cladocopium* was found in the highest abundance, as previously observed at Rangitāhua (Wicks et al., 2010b), followed by a lower abundance, yet higher diversity of *Symbiodinium.* Furthermore, a low abundance of *Breviolum* and *Fugacium* was identified, of which only *Breviolum* had been previously identified in Alcyoniidae corals at Rangitāhua (Wicks et al., 2010b). As expected for a high latitude, isolated, and rarely sampled coral community, nearly half of the ITS2 type profiles obtained (22/42) in our study were previously unrepresented in *Symportal*. A greater understanding of the distribution of coral-Symbiodiniaceae present in marginal regions could help predict the likelihood and rate of corals' responsiveness to changing environmental conditions.

The Symbiodiniaceae communities of *A. curta, H. pilosa,* and *M. spongodes* at the Meyer Islands had the most unique Symbiodiniaceae types and were compositionally distinct compared to communities at other locations, especially at Napier Island. Additionally, the Symbiodiniaceae communities of *A. curta* had the highest taxonomic richness at Meyer Islands and the poorest at Napier Island. Symbiodiniaceae diversity among locations may be due to dramatic variation in the environmental conditions at Rangitāhua (Wicks et al., 2010a; Duffy & Ahyong, 2015). Over depth, Symbiodiniaceae communities of shallow *A. curta* were distinct from their deeper counterparts and the communities of *H. pilosa* had greater compositional dissimilarity and more unique Symbiodiniaceae types among shallow communities than their deeper counterparts (25-30m) presumably due to the fluctuating environmental conditions in shallow waters. Moreover, for *A. curta, G. favulus*, *H. pilosa*, *M. capricornis,* and *M. spongodes*, communities at the edges of the depth gradient (5-10m and 20-25m) were compositionally more uniform, with lower taxonomic richness, compared to the taxonomically richer communities at intermediate depths (10-20m). The reduction in taxonomic richness below intermediate depths may indicate the well-documented trend of a transition from autotrophy to heterotrophy as light attenuates. Although there were general trends of varying Symbiodiniaceae communities, the

Symbiodiniaceae of *G. favulus, M. capricornis,* and *Turbinaria frondens* were relatively consistent throughout the population.

## 3.5.1 Presence and abundance of genera

In our study, *Cladocopium* was the most abundant genus of Symbiodiniaceae, across the six coral species we examined, representing between 94-99% of DIVs per species. A high abundance of *Cladocopium* has similarly been identified in previous assessments of coral-symbiont relations at Rangitāhua (Wicks et al., 2010b), and at various latitudes of the South China Sea (Chen et al., 2019)*Cladocopium* is the most globally abundant and physiologically diverse Symbiodiniaceae genus (LaJeunesse et al., 2018; Chen et al., 2019; Eckert et al., 2020; de Souza et al., 2021; Jain et al., 2021). Although the Symbiodiniaceae types C1 and C3 (which heavily contribute to the most common ITS2 type profiles in this study) can survive a wide range of conditions (Pettay & Lajeunesse, 2013), they are not considered resilient to rapid environmental fluctuations (Chen et al., 2019). In tropical corals, *Cladocopium* is more commonly found in deeper waters which generally have low light and heat energy supplies, similar to what we might expect in shallower waters of sub-tropical regions (Cooper et al., 2011; Sawall et al., 2014; Silverstein et al., 2017; Eckert et al., 2020). The coral population at Lord Howe Island (of similar latitude; 31 ° S) similarly C1 was found in a high abundance (Brian et al., 2019). Although *Cladocopium* was the most abundant genus, it was not the most diverse – a pattern also observed in coral communities of Singapore (Smith et al., 2020) – instead, we found the highest diversity in the genus *Symbiodinium*.

All other genus of symbionts were found in much lower abundance. The second most abundant genus was *Symbiodinium*, with ~0.5-6% of DIVs per coral species assigned to the genus. The high diversity found within the genus *Symbiodinium* may be due to its tolerance to fluctuating light conditions and its tolerance to high UV conditions (Rosic & Dove, 2011; LaJeunesse et al., 2018). A very low abundance of *Breviolum* was found, predominantly B1, which had previously been found at Rangitāhua but only in Alcyoniidae coral (Wicks et al., 2010b). *Breviolum* is commonly found in high-latitude coastal habitats (Rodriguez-Lanetty et al., 2001; LaJeunesse et al., 2003), as they are thought to be well adapted for low light and low-temperature conditions (Valentin, 2001; Knowlton & Rohwer, 2003; Garren et al., 2006; Varasteh et al., 2021). Furthermore, comparable to prior global research (Klein et al., 2019; Hume et al., 2020; Fujise et al., 2021; Mote et al., 2021), *Fugacium* was rarely found in our study. Previous research has found seasonal fluctuations in *Fugacium* abundance, and due to the limited research, greater knowledge of the ecological attributes of *Fugacium* remains largely unknown (LaJeunesse et al., 2018).

The coral-Symbthe singleeae relationships at Rangitāhua displayed a high proportion of a single most abundant ITS2 type profile per coral species. Our study found that 46-82% of DIVs per coral species were a single abundant ITS2 type profile. A study based in the South Sea of China covering ~10° of latitude, found high abundance coral-Symbiodiniaceae relationships were more common in higher latitudes (Chen et al., 2019). Coral hosts with a high abundance of a single ITS2 type profile may be more stable, than those with lower abundance and seemingly transient Symbiodiniaceae interactions (Lee et al., 2016; Chen et al., 2019). However, ITS2 type profiles found in low abundance may enhance the host's tolerance of varying environmental conditions (Bongaerts et al., 2015). Due to the isolation of Rangitāhua, and limited connectivity, Symbiodiniaceae selection by the coral host is likely limited to intra-populational selection (Wood & Gardner, 2007; Wicks et al., 2010a).

Nearly half of the ITS2 type profiles identified (22/42) lacked prior identification in *Symportal.* It is common for novel Symbiodiniaceae types to be found in studies of unsurveyed locations or when using more in-depth techniques (e.g. assessments at the Great Barrier Reef identified 8 novel types at Lizard Island; 5 types at Heron Island) (Sampayo et al., 2007; Tonk et al., 2014). Evidence of unrecorded Symbiodiniaceae types in unsurveyed locations, or locations not previously surveyed using new high-throughput genomic techniques, highlights the impact of local environmental conditions in determining Symbiodiniaceae diversity (Bongaerts et al., 2015). Furthermore, Symbiodiniaceae inhabiting high latitudes experience higher levels and greater fluctuations in atmospheric $CO_2$ than equatorial waters (LaJeunesse et al., 2022). Therefore, Symbiodiniaceae surrounding Rangitāhua may have enhanced photosynthesis mechanisms and be more resilient to future climatic conditions (LaJeunesse et al., 2022). The discovery of novel Symbiodiniaceae types at marginal distributions demonstrates the importance of assessing marginal and isolated coral populations.

### 3.5.2 Locations

Symbiodiniaceae communities are strongly structured by environmental variation, specifically temperature and water flow (LaJeunesse et al., 2010; Chen et al., 2019; Howells et al., 2020; de Souza et al., 2021; Jain et al., 2021). Half of the host species studied (*A. curta, H. pilosa*, and *M. spongodes*) displayed significant differences in community composition among the locations surrounding Raoul Island. From small-scale studies within Kāneʻohe Bay of Hawaii (<10km) (de Souza et al., 2021) to studies covering 10° of latitude in the South Sea of China (Chen et al., 2019), heat energy supply was found to be the main driver of variation in Symbiodiniaceae composition among locations (Pettay & Lajeunesse, 2013; Chen et al., 2019; Chen et al., 2020). Additionally, greater water flow may increase a host's opportunity to acquire more diverse Symbiodiniaceae promoting autotrophic feeding (Williams et al., 2018; Lim et al., 2019). Furthermore, variations in multiple environmental factors can compound the impact on coral-Symbiodiniaceae relationships. For instance, research on common corals from Mauritius observed a positive correlation between water flow and the degree of coral bleaching which can reduce corals' tolerance to extreme temperature variations (McClanahan et al., 2005). Greater knowledge of the abiotic conditions (temperature, water flow, etc.) of the islands surrounding Raoul Island could provide more in-depth ecological reasoning for the distinctness of Symbiodiniaceae among locations.

The Symbiodiniaceae communities of *A. curta, H. ppilosa,* and *M. spongodes* at the Meyer Islands had the most unique Symbiodiniaceae types and had dissimilar Symbiodiniaceae types found in a high abundance compared to communities at other locations, as well as a higher presence of rare genera (*Breviolum* and *Fugacium*) identified at Meyer Islands. Previous studies at Rangitāhua have found a higher density of macroalgae as well as soft and hard coral populations at Meyer Islands than in other locations at Rangitāhua (Wicks et al., 2010a). Despite being only a few 100m's from the

Meyer Islands, Symbiodiniaceae communities of *A. curta, H. ppilosa,* and *M. spongodes* were compositionally most dissimilar at Napier Island with the fewest unique ITS2 type profiles, and the communities of *A. curta* had the lowest taxonomic richness. Similarly, a lower abundance of filamentous/fleshy macroalgal and soft corals has been identified at Napier Island compared to other locations at Rangitāhua (Wicks et al., 2010a). The similarity between the coral-Symbiodiniaceae distribution trends and the distribution of other taxa may be indicative of a common environmental driver, or as corals are the foundation of coral reef ecosystems (Jones et al., 2004; Pratchett et al., 2008; Stella et al., 2011), the coral-Symbiodiniaceae distribution may influence other taxa.

## 3.5.3 Depth

Shifts in symbiont community composition with depth can increase a host's flexibility to survive in unfamiliar environmental conditions (Bongaerts et al., 2015). Symbiodiniaceae communities of *A. curta* were dissimilar between shallow depths (5m and 10m) due to a greater number of unique Symbiodiniaceae types at 10m. Corals with smaller depth distributions generally lack variation in Symbiodiniaceae communities over depth (Bongaerts et al., 2015). However, Symbiodiniaceae zonation of *Orbicella franski* in the Southern Caribbean was found over a small depth range (15m) (Bongaerts et al., 2015). Over a wider depth range, depth zonation of Symbiodiniaceae is typically partitioned as a break between 'deep' and 'shallow' communities (Eckert et al., 2020). When considering *A. curta* only at Dougall Rock in our study, with a larger depth range, shallow Symbiodiniaceae communities (5-10m) were compositionally similar to each other and dissimilar to the deeper communities. Given that *A. curta* is more abundant in shallow waters (J.D. Aguirre, *unpublished data*) (Brook, 1999; Duffy & Ahyong, 2015), the distinct composition of deeper communities could indicate corals' demand for different Symbiodiniaceae to survive atypical lower energy conditions (Bongaerts et al., 2015; Eckert et al., 2020).

Corals' stress tolerance, recovery threshold, and resilience are likely influenced by the distribution of Symbiodiniaceae (Teschima et al., 2019). In our study, Symbiodiniaceae communities of *H. ppilosa* were more dissimilar in the shallows (5-15m) than the more compositionally uniform deeper communities (25-30m), additionally, the amount of unique Symbiodiniaceae types identified reduced over depth. Similarly, for *Montastraea cavernosa* at the Belize Barrier Reef and *Madracis decactis* in the Southwest Atlantic Ocean, shallow Symbiodiniaceae communities were more dissimilar from each other compared to the more homogeneous deeper communities (Eckert et al., 2020; Varasteh et al., 2021). Moreover, in the Caribbean, greater diversity and more unique types were found in shallow Symbiodiniaceae communities compared with their deeper counterparts (Bongaerts et al., 2015). Symbiodiniaceae depth zonation is thought to represent corals' responsiveness to varying environmental conditions as depth increases (Bongaerts et al., 2015). Therefore, the well-documented dissimilarity of shallow Symbiodiniaceae communities is expected due to the more dramatic environmental conditions of shallow waters (Bongaerts et al., 2015), especially due to the lack of sheltered areas at Rangitāhua (Wicks et al., 2010a).

Extreme environmental conditions in shallow waters may be too extreme for certain Symbiodiniaceae to endure. The Symbiodiniaceae communities of *A. curta, G. favulus, H. pilosa, M. capricornis,* and *M. spongodes* were taxonomically richest at intermediate depths. Furthermore, Symbiodiniaceae communities of *A. curta, G. favulus*, and *M. capricornis* at the edges of the depth gradient (5-10m and 20-25m) were compositionally uniform and were dissimilar to the communities at intermediate depths (10-20m). Previous studies have found a higher variation in the types of genera in shallow (<6m) hosts, compared to their deeper counterparts (Baker, 2003; Lim et al., 2019). The depth-dependent symbiont zonation of *O. franski*, in the Southern Caribbean, over the 15m range was unsurprising due to the pronounced environmental conditions of shallow waters (Bongaerts et al., 2015). For instance, in Okinawa Reef (southern Japan) shallow corals (3m) had evidence of greater symbiont expulsion causing coral mortality than corals, with less UV exposure, at 10m (Van Woesik et al., 2004). The extreme environmental conditions (e.g. high UV levels, greater and more varying temperatures (Biton & Gildor, 2011), etc.) of shallow waters may limit and/or refine the Symbiodiniaceae of shallow corals.

Corals at intermediate depths may experience unique energy-rich conditions. Although *Cladocopium* was the most abundant genus for the majority of samples, some samples had a higher abundance of *Symbiodinium* and these were commonly found at intermediate depths. The genus *Symbiodinium* is known for having a tolerance to high UV conditions (Rosic & Dove, 2011; LaJeunesse et al., 2018). Some reefs experience peak light intensity at ~15m (Kahng et al., 2019). Therefore, the peak in *Symbiodinium* abundance and peak in taxonomic richness, at intermediate depths, might be in response to the light-rich conditions.

The exponential attenuation of light energy below 15 metres (Kahng et al., 2019) can restrict the photosynthetic rate of Symbiodiniaceae (Mass et al., 2007), especially at high latitudes (Muir et al., 2015). To compensate in low light conditions corals can rely more heavily on heterotrophic feeding, which can imprint on corallite morphology (Palazzo et al., 2021). For instance, the reduction of autotrophic morphology over depth has been observed in *Galaxea fascicularis* in Indonesia (Crabbe & Smith, 2006). In our previous chapter, shallow *H. pilosa* and *M. spongodes* had morphology associated with high tissue coverage (i.e., large, close corallites, high corallite coverage, and short septa) presumably to enhance the supply of light reaching Symbiodiniaceae within corals' tissue (Crabbe & Smith, 2006; Kahng et al., 2019). As that coral morphology can be correlated to Symbiodiniaceae abundance (Hoogenboom et al., 2010), the reduction of Symbiodiniaceae taxonomic richness below intermediate depth may be indicative of the well-documented reduction in corals' autotrophic feeding as light attenuates over depth (Lesser et al., 2010; Williams et al., 2018). As Rangitāhua is within the Tonga-Kermadec ridge, upwelling likely transports Zooplankton into the water column at times (Karig, 1970; Abed, 2013; Lim et al., 2019). Nutrient-rich waters can supply corals with a sufficient source of heterotrophic feeding supply (Radice et al., 2019). More in-depth assessment of corals' trophic behaviour such as Symbiodiniaceae abundance and/or tentacle behaviour may further explain the diversity in Symbiodiniaceae of corals at Rangitāhua.

### 3.5.4 Limitations

Although some host corals (*G. favulus, M. capricornis,* and *T. frondens*) displayed consistent Symbiodiniaceae richness and/or community composition across at least one geographic gradient in our study, intraspecific variation of Symbiodiniaceae types could influence their ecological function (Swain et al., 2017; Eckert et al., 2020). For example, Symbiodiniaceae of *Pocillopora verrucosa* had stable cell richness over depth; however, the amount of Chlorophyll *a* per Symbiodiniaceae increased over depth (Ziegler et al., 2014). Some deeper Symbiodiniaceae have developed unique light-gathering abilities to better survive low light conditions (Einbinder et al., 2016). Moreover, Symbiodiniaceae species are more likely to adapt when associated with a coral host rather than free-living (Díez-Vives et al., 2017; O'Brien et al., 2019). Moreover, symbiont acquisition may impact symbiont diversity in coral populations. Based on breeding mechanism, symbiont acquisition can occur as horizontal transmission; from the water column (regardless of past generations' communities common for broadcasters) or vertical transmission (maternal inheritance common for brooders) of Symbiodiniaceae (Wicks, 2009). Vertical transmission of coral symbionts has been linked to a higher proportion of unique symbiont types (Wicks, 2009). Therefore, the observed uniformity in Symbiodiniaceae in some host corals at Rangitāhua may reflect limited samples or symbiont acquisition (breeding mechanism) rather than the Symbiodiniaceae diversity. Further observations of corals' symbiont acquisition and Symbiodiniaceae functionality at Rangitāhua could help to better understand hosts' reliance on Symbiodiniaceae (Bongaerts et al., 2015; Chen et al., 2019; de Souza et al., 2021).

As a marginal, isolated population on a relatively young island (Brook, 1999), the coral population at Rangitāhua is small (Wicks et al., 2010a). Consequently, the number of replicate samples for each location and depth combination was limited resulting in an unbalanced design and preventing us from examining the interactions between geographic variables. Although our results should be interpreted with caution given the low representation in certain depths or locations, this research can provide baseline knowledge the Symbiodiniaceae communities of corals at Rangitāhua which could assist future assessments of changes in coral-Symbiodiniaceae relationships in future.

### 3.5.5 Conclusion

In summary, the Symbiodiniaceae communities of *A. curta, H. pilosa,* and *M. spongodes* had significant compositional dissimilarity and/or varied taxonomic richness across at least one geographic gradient. Coral species with more diverse Symbiodiniaceae communities are thought to have a greater tolerance range (Bongaerts et al., 2015). Therefore, if anthropogenically induced climate change causes the environmental conditions at Rangitāhua to change, coral species with greater Symbiodiniaceae variability may be better able to endure environmental changes than species with less diverse or more homogeneous Symbiodiniaceae communities. The functionality of corals, as a foundational species, can influence the health of their ecosystem (Pratchett et al., 2008; Stella et al., 2011). Therefore, if the relatively similar Symbiodiniaceae communities of *G. favulus, M. capricornis,* and *T. frondens* have limited ranges of tolerance to environmental conditions, hosts may be less able to endure varying environmental conditions, creating a conservation concern.

On a global scale, our findings further support that *Cladocopium* is found in a high abundance in high latitude populations (Cooper et al., 2011; Chen et al., 2019). However, anthropogenic climate change is causing heat energy gradients to shift poleward (Woolway et al., 2022), which may pressure species' distributions to shift (Arvedlund, 2009). Coral species pressured to migrate to higher latitudes, to avoid heat stress, may share environments with corals that have a high abundance of *Cladocopium* (Cooper et al., 2011). As a result, some migrating corals may acquire a higher abundance of Symbiodiniaceae from the genus *Cladocopium,* however due to host-symbiont specificity formed in during early develop stages, Symbiodiniaceae abundance may remain constraint through environmental changes and range shifts (Weis et al., 2001). Nonetheless, Symbiodiniaceae communities are responsive to local environmental variations (Bongaerts et al., 2015), as evident through the identification of 22 undocumented ITS type profiles and variability in Symbiodiniaceae community composition within this fine-scale study. As such, when predicting the response corals may have to climate change, it is essential to consider local environmental conditions.

We identified significant variability among Symbiodiniaceae communities of half of the most abundant coral species at Rangitāhua. The geographic variation in Symbiodiniaceae communities was parallel to previous assessments of taxa (e.g., filamentous/fleshy macroalgal and soft and hard corals) at Rangitāhua (Wicks et al., 2010a). As corals can rapidly expel Symbiodiniaceae and restructure their communities, our findings could be integrated into a local time series examination to further understand how responsive coral-Symbiodiniaceae associations can be to environmental fluctuations. Nonetheless, a greater understanding of the variation in the ecological functions of Symbiodiniaceae' types, particularly the novel Symbiodiniaceae first described in this study, is needed to further inform predictions of corals' response to climate change.

# Chapter 4: General discussion

This research described variation in corallite morphology, the composition of Symbiodiniaceae communities and Symbiodiniaceae taxonomic richness of shallow water Scleractinian corals over small-scale geographic gradients at Rangitāhua. Here I describe the major findings of the thesis, elaborate on the findings in the context of related research, and suggest some future research avenues building on the presented work.

## 4.1 Major findings of the thesis

Examining the morphology and Symbiodiniaceae communities of corals at Rangitāhua recovered some expected results and some novel inferences. For Symbiodiniaceae communities, expectedly, there was a high abundance of the coral symbiont, *Cladocopium* (formally clade C), followed by a lower abundance of *Symbiodinium* (formally clade A), *Breviolum* (formally clade B), and *Fugacium* (formally clade F). At the Meyer Islands, the Symbiodiniaceae communities of *Astrea curta* (Dana, 1846), *Hydnophora pilosa* (Veron, 1985), and *Montipora spongodes* Bernard, 1897 had the most unique types and were compositional dissimilar compared to communities at other locations, especially at Napier Island. Additionally, the Symbiodiniaceae communities of *A. curta* had the highest taxonomic richness at the Meyer Islands presumably due to high water flow exposure. I expand on these results below in 4.3 The influence of local environments on the morphology and Symbiodiniaceae communities of corals.

In terms of morphology, the corallites of *M. spongodes* at Napier Island had the smallest and the most densely arranged corallites, with few short septa, whilst, the corallites of *A. curta* were closer and more densely arranged at Dougall Rock and Napier Island. The shallowest corallites of *M. spongodes* were the largest and closest and the shallowest *H. pilosa* had high corallite coverage and short septa which can increase tissue coverage (Kahng et al., 2019). I further examine the significance of these morphological features, and changes across geographic gradients below, in 4.3 The influence of local environments on the morphology and Symbiodiniaceae communities of corals.

Overall, I expected to find the greatest changes in Symbiodiniaceae communities and the morphology of corals across the depth gradient examined at Rangitāhua. In chapter two I found the corallites of the shallowest *M. spongodes* were the largest and closest and the shallowest *H. pilosa* had high corallite coverage, and short septa, presumably to increase their light-gathering abilities and optimise autotrophic feeding in energy-rich waters. In chapter three, I found the Symbiodiniaceae communities of *A. curta* were compositionally clustered in the shallow waters (5-10m), whilst communities of *H. pilosa* had greater dissimilarity among shallow communities (5-15m) than their deeper counterparts. Unexpectedly, corals had distinct mechanisms at intermediate depths (15-20m). For instance, Symbiodiniaceae communities at the edges of the depth gradient (5-10m and 20-25m) were compositionally more uniform, with lower taxonomic richness than the communities at intermediate depths. Furthermore, at intermediate depths, the corallites of *M. spongodes* were denser and further spaced with more septa, the corallites of *A. curta* were the least dense, and the septa of *H. pilosa* were the longest and the least dense, perhaps in response to the extreme environmental conditions. Although there were general trends, the morphology and Symbiodiniaceae relationships of *Goniastrea favulus* (Dana, 1846), *Montipora capricornis* Veron, 1985, and *Turbinaria frondens* (Dana, 1846) were relatively consistent throughout the population. I further investigate the responsiveness of corals' mechanisms over depth below in 4.2 Linking patterns in morphology and Symbiodiniaceae communities of corals across geographic gradients.

## 4.2 Linking patterns in morphology and Symbiodiniaceae communities of corals across geographic gradients

Host morphology can influence the richness of Symbiodiniaceae communities (Lim et al., 2019), which may explain the coupling of results I found between morphological changes and changes in the Symbiodiniaceae communities of corals at Rangitāhua. Symbiodiniaceae communities of *M. spongodes* were taxonomically richest at intermediate depths, and their corallites were the densest with the most septa. Furthermore, among locations, the largest corallites of *M. spongodes* with the longest septa were found at Meyer Islands, along with the most unique Symbiodiniaceae types apart of communities that were compositionally dissimilar compared to communities at other locations. In giant clams (Tridacnidae), the richness of Symbiodiniaceae can be driven by host morphology (i.e., positive relationship with shell length; reflective of growth rate) (Beckvar, 1981; Lim et al., 2019). Longer clams have more diverse (Lim et al., 2019), more abundant (Griffiths & Klumpp, 1996), and compositionally distinct Symbiodiniaceae communities compared to their shorter counterparts (Ikeda et al., 2017). Smaller clams are associated with *Symbiodinium* (Ikeda et al., 2017), which can protect hosts from UV damage (Rosic & Dove, 2011; LaJeunesse et al., 2018), whilst larger clams are associated with more photosynthetically efficient *Cladocopium,* consequently promoting hosts' growth (Lim et al., 2019). Greater knowledge is needed to elucidate if hosts' morphology and their Symbiodiniaceae associations influence each other, perhaps in relation to trophic trends, or if the mechanisms respond similarly to environmental conditions.

At intermediate depths (15-20m), the corallite morphology of *A. curta, M. spongodes, T. frondens,* and *H. pilosa* differed from their shallower and deeper counterparts. Moreover, Symbiodiniaceae communities of *A. curta*, *G. favulus*, *H. pilosa*, *M. capricornis,* and *M. spongodes,* at intermediate depths had higher taxonomic richness and were compositionally dissimilar compared to the more compositionally uniform communities at the edges of the depth gradient (5-10m and 20-25m). Although *Cladocopium* was the most abundant genus for most samples, at intermediate depths, some samples had a higher abundance of *Symbiodinium*. Peak abundance of the genus *Symbiodinium* of *Favia gravida* was found in energy-rich tidal pools of the Atlantic Ocean, perhaps due to the presence of mycosporine-like amino acids (MAAs) in *Symbiodinium* which may offer their hosts UV protection (Teschima et al., 2019). An assessment of ultraviolet radiation A in reef environments found the most intense at ~15 metres and then exponentially decreases with depth (Kahng et al., 2019). The distinction in corallite morphology and Symbiodiniaceae communities at intermediate depths compared to their deeper counterparts may be due to the attenuation of light energy. Corals commonly vary from predominantly autotrophic feeding in energy-rich conditions to predominantly heterotrophic feeding in lower light energy conditions

(Lesser et al., 2010; Williams et al., 2018). Intermediate depths may provide corals with an optimum combination of low stress yet high light energy supply (Chow et al., 2019).

Trophic plasticity in response to environmental variation (Sturaro et al., 2021), can leave a signature in coral skeletal structure (Palazzo et al., 2021). As light attenuates over depth, corals often shift from autotrophic to heterotrophic feeding (Mass et al., 2007; Lesser et al., 2010). I found the shallowest *H. pilosa* (5m) had high corallite coverage, and short septa and the corallites of *M. spongodes* were large and close, presumably to maximise corallite coverage in energy-rich conditions (Kahng et al., 2019). Greater corallite coverage, consequently, increases a coral's light-gathering abilities which may be a response to optimising its photosynthetic rate in energy-rich conditions (Todd et al., 2004). For example, shallow *Stylophora pistillata* in the red sea had distinct morphology compared to deeper corals. Additionally, the net photosynthetic rate of deeper corals is less than half that of their shallow counterparts in summer, and less than a quarter in winter (Mass et al., 2007). For corals to persist through the restricted light energy conditions of deep waters during winter, corals may seasonally utilize heterotrophic feeding (Ferrier-Pagès et al., 2011). Smaller corallites in deeper *M. spongodes* suggest a combination of autotrophic and heterotrophic feeding. In addition, my findings in chapter three showed the taxonomic richness of Symbiodiniaceae communities of *A. curta*, *G. favulus*, *H. pilosa*, *M. capricornis,* and *M. spongodes* decreased below intermediate depths, presumably indicating a reduction in autotrophic feeding in lower light conditions. More direct and seasonal assessments (i.e., tentacle behaviour, optical, biochemical approaches, Symbiodiniaceae abundance) could provide greater clarity to the trophic zonation of coral populations at Rangitāhua.

The trends of variation for the morphology and the Symbiodiniaceae communities of *A. curta, H. pilosa,* and *M. spongodes* were similar across depth and locations (most dissimilar between Meyer Islands and Napier Island), presumably due to environmental drivers. Greater phenotypic variation and/or more diverse symbiont association can expand a species' tolerance (Cooper et al., 2011; Bongaerts et al., 2015; Jaffe et al., 2016; Ho & Zhang, 2018). Therefore, *A. curta, H. pilosa,* and *M. spongodes* may be more resilient to climate change compared to the more homogeneous trends of *G.*

*favulus, M. capricornis,* and *T. frondens* which may be a conservation concern for the ecosystem. As reef-associated species can have preferences for specific coral species, the loss of even a few coral species could have detrimental impacts on the marine ecosystem at Rangitāhua (Stella et al., 2011).

## 4.3 The influence of local environments on the morphology and Symbiodiniaceae communities of corals

Despite being separated by only 100 metres, the sampled locations surrounding Raoul Island have dramatic variations in environmental conditions (Wicks et al., 2010a; Duffy & Ahyong, 2015). Among locations, the Symbiodiniaceae communities were most dissimilar between Meyer Islands and Napier Island. The Symbiodiniaceae communities of half of the studied corals (*A. curta, H. pilosa,* and *M. spongodes*) at Meyer Islands had the most unique Symbiodiniaceae types and were most compositionally different from communities at Napier Island, perhaps due to variation in water flow conditions (Lim et al., 2019). Additionally, the Symbiodiniaceae communities of *A. curta* had the lowest taxonomic richness at Napier Island. Greater water flow can increase corals' opportunity to acquire a higher abundance and more diverse Symbiodiniaceae, as well as more water-borne particles, overall funding greater autotrophic (Williams et al., 2018; Lim et al., 2019) and heterotrophic feeding opportunities (Wainwright & Koehl, 1976). In alignment with Symbiodiniaceae communities, the variation in morphology (i.e., corallite size, length, and number of septa) of *M. spongodes* suggests a lower water flow rate, and less sediment, at Napier Island compared to at the other locations. In high water flow conditions, increased skeletal density may improve the efficiency of food capture and gas exchange (Todd, 2008), as seen in the more calcified and longer septa of *A. clathrata* in high water flow conditions (Hodgson & Carpenter, 1995). Although water flow can provide corals with a higher abundance of Symbiodiniaceae and food particles, greater water flow can also transport more sediment within the Kermadec Arc (Mcleod, 2010) which can induce stress in corals (Tuttle & Donahue, 2022). Based on morphological findings in chapter two, the large corallites, with many septa, of *M. spongodes* appear better able to remove harmful sediment at North Meyer Island and Dougall Rock than the corallites at Napier Island (Marshall, 1931; Hodgson &

Carpenter, 1995; Todd; Tuttle & Donahue, 2022). The bathymetry of a region can heavily impact the rate of water flow (Niwa & Hibiya, 2001). Within the broad region of the Kermadec Ridge, water flow is created by water movement flowing over underwater mountains (Walters et al., 2001; Mcleod, 2010), perhaps, on a smaller scale, the cluster of small islands surrounding Meyer Islands causes greater water flow conditions compared to the conditions of more peripheral islands such as Napier Island. The isolation of Rangitāhua restricts the ease and accessibility as a research site (Gardner et al., 2006) limiting the background knowledge of specific environmental conditions.

The angle, orientation, and substrate can also alter the light variability for benthic species (Brakel, 1979). High volumes of sediment in the water column can reduce light penetration and damage the surface of corals degrading their feeding ability (Duckworth et al., 2017). Sediments around Raoul Island are coarse, containing crustose coralline algae (red algae), bryozoan fragments, and coral rubble, along with free-living *Cycloseris vaughani*, and unidentified bivalve and gastropod molluscs (Brook, 1998), which may impact the inhabiting coral population. Light variation induced by sediment, substrate, or orientation may account for the variation in corallite spacing of *A. curta, M. spongodes,* and *T. frondens* among locations (i.e., closest at Dougall Rock), as corallite spacing is commonly considered to have a positive relationship with light (Todd, 2008; Einbinder et al., 2009). The lack of knowledge about abiotic conditions among specific locations surrounding Raoul Island limits the validity of assumptions. More in-depth ecological research (temperature, chlorophyll a, sediment, light, bathymetry, orientation, pH, water flow, etc.) among the islands of Rangitāhua may provide a greater understanding of the variation among corals across small-scale geographic gradients.

Shallow waters experience unique environmental conditions. Our results identified greater Symbiodiniaceae diversity (i.e., the highest abundance of Symbiodiniaceae assigned to rare genera, the highest taxonomic richness, and the most samples with a high abundance of *Symbiodinium*) of corals at intermediate depths than at shallow depths. In Okinawa Reef (southern Japan) shallow corals (3m) had evidence of greater symbiont expulsion causing coral mortality than corals, with less UV exposure, at 10m (Van Woesik et al., 2004). The extreme environmental conditions (e.g. high UV levels, greater and more varying temperatures (Biton & Gildor, 2011), etc.) of shallow waters may limit and/or refine the Symbiodiniaceae of shallow corals. Furthermore, the shallowest *M. spongodes* and *T. frondens* had high measures of structural support (i.e., number and length of septa), similarly, *Acropora clathrata* had more well-developed septa in response to wave action (Hodgson & Carpenter, 1995), which can indicate more tissue-anchoring cells (desmocytes) (Bourne, 1899) to create more secure tissue attachments to the skeleton (Muscatine et al., 1997; Tambutté et al., 2007). Although surface swell and turbulence are most pronounced in shallow waters (Helmuth & Sebens, 1993), it is not possible to pinpoint the morphological distinction in shallow coral to a particular environmental factor (Nir et al., 2011).

Spatial trends in Symbiodiniaceae biodiversity were similar to other taxa at Rangitāhua. Among locations the Symbiodiniaceae communities at the Meyer Islands were distinct and more diverse compared to communities at other locations, reflecting biodiversity patterns of macroalgae, and Alcyonacea and Scleractinian corals (Wicks et al., 2010a). Similarly, in a study from the Arabian Peninsula, Symbiodiniaceae diversity reflected patterns of diversity in corals, fishes, and other reef-associated fauna diversity (Sheppard et al., 1992; Burt et al., 2011; Bauman et al., 2013; Ziegler et al., 2017). Reef ecosystems could be similarly responding to common environmental drivers, for instance, a wide range of reef taxon at the Great Barrier Reef (such as plankton, coral, fishes, seabirds, marine reptiles, etc.) are all sensitive to environmental conditions (i.e., increasing temperatures) (Johnson & Marshall, 2007). However, the majority (75%) of coral reef fishes (Jones et al., 2004) and half of the coral-associated invertebrates (Stella et al., 2011) rely on coral, often with a specific preference (Stella et al., 2011). As foundational species, the climate change effects on corals can have cascading effects on the highly productive ecosystem they provide for.

## 4.4 Considerations and future research

As evident in the current research, along with many others, corals' corallite morphology and Symbiodiniaceae relationships are sensitive and responsive to abiotic variation (Todd, 2008; Bongaerts et al., 2015; Goodbody-Gringley & Waletich; Chen et al., 2019; Studivan et al., 2019; de Souza et al., 2021). However, the low, single, or frequent lack of sample replicates at certain depth/location combinations, may limit the accuracy of these results. Therefore, the plausibility of current findings and assumptions should be taken with caution. Nonetheless, an assessment of the morphological diversity and community composition of Symbiodiniaceae was completed for the coral population at Rangitāhua which provides a baseline for future research.

The reproductive mechanism of corals can also impact corallite morphology and Symbiodiniaceae relationships. Half of the coral population at Rangitāhua are broadcast spawners; gametes are released and fertilised in the water column, whereas the other half are brooding species; internal fertilization and then released as larva (Babcock, 1995; Wicks, 2009). The internal fertilisation of brooders results in vertical transmission (maternal inheritance) of Symbiodiniaceae, whilst broadcasters generally acquire Symbiodiniaceae through horizontal transmission; from the water column (regardless of past generations' communities) (Wicks, 2009). Sexual dimorphism appears to be dependent on the reproductive mechanism of the coral (i.e., density, diameter, and inter-corallite distance) (González-Espinosa et al., 2018; Pedraza-Pohlenz et al., 2022). For broadcasters, males have larger corallites perhaps enabling greater sperm release, consequently, increasing fertilization success, whilst, for brooders, females have larger internal space within each corallite to accommodate larger larva (González-Espinosa et al., 2018; Pedraza-Pohlenz et al., 2022). As reproductive mechanism (and sex) influences both the morphology and Symbiodiniaceae of corals, a greater understanding of the reproductive mechanism of Rangitāhua coral could further elucidate the trends found across small-scale geographic gradients.

Corals display distinct environmental tolerances depending on the ecological diversity of their Symbiodiniaceae communities (Baker et al., 2004; Yuyama et al., 2016; Ziegler et al., 2017). For instance, during the juvenile stage of corals, *Durusdinium*-dominance has been found to increase heat resilience, as compared to *Cladocopium*-dominance (Yuyama et al., 2016). I found no evidence of the Symbiodiniaceae genus *Durusdinium* in the coral at Rangitāhua. The abundance of *Durusdinium* increases nearer to the Equator (Terraneo et al., 2019), as they are thermo-tolerant (Berkelmans & van Oppen, 2006), and provide the greatest stress tolerance (Baker et al., 2004;

Yuyama et al., 2016). Our research further supports the lack of association between high latitude corals and *Durusdinium,* suggesting corals near the lower limits of their energy tolerance range can survive without thermo-tolerant Symbiodiniaceae.

As energy gradients further decouple, corals may experience lethal amounts or periods of heat stress. Findings in this current research, along with many others, have identified the sensitivity and responsive of corals' corallite morphology and Symbiodiniaceae relationships to varying environmental conditions (Todd, 2008; Bongaerts et al., 2015; Goodbody-Gringley & Waletich, 2018; Chen et al., 2019; Studivan et al., 2019; de Souza et al., 2021). As a result, environmental fluctuations due to anthropogenic climate change may drive corals to adjust morphologically and/or switch Symbiodiniaceae to better align with changing conditions. Although phenotypic variation can provide a stable and long-term expansion to corals' ecological tolerance (Ow & Todd, 2010), their calcification rate is relatively slow, delaying the benefits of morphological variation (Todd, 2008). Whereas, restructuring Symbiodiniaceae communities can rapidly alter a coral's ecological tolerance (Boilard et al., 2020). Therefore, anthropogenic warming could pressure corals at Rangitāhua to acquire thermo-tolerant Symbiodiniaceae (such as *Durusdinium*) (Berkelmans & van Oppen, 2006). Whereas corals at the higher end of their heat tolerance may migrate to higher latitudes to avoid heat stress (Arvedlund, 2009). The lower light conditions over increasing latitudes may pressure migrating corals to acquire a higher abundance of Symbiodiniaceae more tolerant to fluctuating light conditions (such as *Symbiodinium*) (Rosic & Dove, 2011; LaJeunesse et al., 2018), lower light conditions (such as *Breviolum*) (Valentin, 2001; Knowlton & Rohwer, 2003; Garren et al., 2006; Varasteh et al., 2021), or may drive seasonally shifts to heterotrophic feeding (Ferrier-Pagès et al., 2011) which, overtime could result in morphological variation such as an expansion corallite spacing to alleviate self-shading (Ow & Todd, 2010). Although anthropogenic climate change is impacting many global abiotic trends (pH, ocean circulation, global warming, atmospheric $CO_2$) (Brierley & Kingsford, 2009), local conditions are also being altered (anthropogenic fine sediment, land use, overfishing, regional weather patterns) (Hoegh-Guldberg et al., 2007). Half of the coral species we examined (3/6) responded to variation in local environmental conditions, therefore, knowledge of local environments is essential to make accurate predictions of how corals may respond to climate change.

## 4.5 Conclusion

A greater understanding of the variability of corallite morphology and Symbiodiniaceae communities of corals at Rangitāhua promotes the importance of considering local environmental conditions when predicting corals' response to climate change. Overall, we provided a baseline for future studies to expand upon geographically, or to integrate into local time series. Greater knowledge distinguishing high latitude coral populations from their more tropical counterparts may further help predict corals' response to Anthropocene change.

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