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Coral colony size and morphology as predictors of associated fish assemblage composition in branching *Acropora* and *Pocillopora*

Master thesis, MSc in Marine Biology

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List of abbreviations

AAR	Abundance–Area Relationship
AIC	Akaike Information Criterion
AR	Artificial Reef
edf	Estimated degrees of freedom
GAM	Generalised Additive Models
N	(Fish) Abundance
NMDS	Non-Metric Multidimensional Scaling
NR	Natural Reef
PERMANOVA	Permutational Analysis of Variance
RSE	Residual Standard Error
S	(Fish) Species richness
SAR	Species–Area Relationship
SD	Standard Deviation
SIMPER	Similarity Percentage
SVS	Stereo-Video System
Tukey's HSD test	Tukey's Honestly Significant Difference test
VIF	Variance Inflation Factor

Abstract

Coral reefs are among the most diverse ecosystems on Earth, largely due to the structurally complex habitats created by hermatypic coral colonies. These colonies serve as microhabitats that shape the broader reef fish community, often hosting their own distinct fish assemblages. Understanding how coral morphology influences associated fish assemblages is crucial for predicting reef fish recruitment — particularly in the context of coral propagation on artificial reefs. This study investigates the predictive power of volumetric size, structural complexity and contextual environment of *Acropora* and *Pocillopora* colonies on associated fish assemblage metrics – including species richness (*S*), abundance (*N*) and ontogenetic distribution. Fieldwork was conducted on three natural reefs and one artificial reef in Dauin, Philippines during October and November of 2024. Fish assemblage data were quantified from video analysis and colony morphology was measured using photogrammetric 3D models. A total of 59 fish species were identified from observations of 111 coral colonies, though only a few of these occurred frequently with the predominant being *Thalassoma lunare* and *Dascyllus reticulatus*. Colony volume emerged as a strong predictor of fish assemblage metrics, with both *S* and *N* scaling according to asymptotic power-law models. *Pocillopora* exhibited faster fish assemblage growth ($\approx S \times 2$ and $N \times 4$ per order-of-magnitude volume increase) than *Acropora* ($\approx S \times 1.5$ and $N \times 2$). However, saturation effect was less defined in *Pocillopora* possibly due to limited data on large colonies. An overall higher *S* and *N* were observed on *Acropora*. Colony complexity and environmental context further influenced fish metrics, though primarily in interaction with colony size. Higher-complexity colonies supported more juvenile fish and had elevated *S* and *N*. Similarly, isolated colonies showed increased *N*, suggesting aggregation effects. Ecological patterns appeared consistent on the AR, though a limited dataset decreased the strength of statistical comparisons. Field observations and model predictions suggest that both coral genera can reliably be expected to support fish communities from colony sizes as small as ~270 – 350 cm^3, potentially within the first year of growth. These findings highlight the predictive value of coral morphology for estimating the ecological contributions of propagated colonies, offering valuable insight for reef restoration planning.

1. Introduction

1.1 Aims and objectives

One of the most well-understood relationships in ecology is how species richness (*S*) increases with the spatial extend of an environment. This species-area relationship (SAR) has also been studied in coral reef habitats, though other factors are often found to be equally or more important in predicting community compositions (Chittaro, 2002; Belmaker *et al*. 2006; Huntington & Lirman, 2012). Scleractinian corals, commonly known as stony corals, are of vital ecological importance. Their structural complexity promotes huge biodiversity, and it is believed that upwards of a third of all marine life is dependent on coral reefs in some part of their life cycle, even though coral reefs take up less than 0.2 % of the ocean's surface area (Knowlton *et al*. 2010). Due to this disproportionate effect on global biodiversity coral reefs have been dubbed "the rainforest of the sea" (Jackson, 1991; Knowlton *et al*. 2010). Coral reefs also provide vital ecosystem services, and it is estimated that over 800 million people worldwide rely upon them for coastal protection, nutrition and income revenue as major tourist attractions (Higgins *et al*. 2022). Similarly to rainforests they are highly vulnerable to anthropogenic impacts and their reduction could have dire consequences for the health of the global marine ecosystem. Motivations to conserve these ecosystems have therefore existed for decades, traditionally with a focus on protection and preservation but gradually progressing into ideals of coral reef restoration. Several methods exist for restoring reefs many of which focuses on planting corals (Boström-Einarsson *et al*. 2020). A relatively new restoration strategy is the deployment of Artificial Reefs (ARs) which have historically been utilized primarily by the tourism, oil- & gas- and fishing industry without scientific insight. Research that examines the efficiency of ARs as coral reef restoration tools is therefore relatively sparse and there exists a need to compare population dynamics on such structures to that of natural coral reefs (Higgins *et al*. 2022). Understanding how size, morphology and quality of corals affect their ability as host habitats for fish biodiversity is one such vital research topic. This study therefore aims to investigate the effects of coral colony dimensions on fish assemblages on three natural coral reefs (NRs) in the Southern Philippines and to compare the findings to replicated observations from an AR in the same area. Data for this study is collected on a single colony scale with a focus on coral-dwelling fish. A positive relationship between coral colony size and *S* and *N* is expected whilst parameters such as surrounding coral cover, increased colony rugosity and fish community composition is expected to also have significant effect on these metrics.

1.2 The Coral reef ecosystem

1.2.1 Corals as ecosystem engineers

Scleractinia belong to the phylum *Cnidaria*, which they share with animals such as jellyfish and sea anemones (the latter of which belongs to the same class and subclass as stony corals. Respectively: *Anthozoa* and *Hexacorallia*) (Jackson 1991; NOAA, 2007). Stony corals are named such because of their ability to produce $CaCO_3$ in a crystallised form called aragonite which they use to produce a rigid skeleton (Ries *et al*. 2006). This trait is the foundation of their great ecological influence as these skeletons can grow in a variety of structural shapes creating large varied three-dimensional structures of high rugosity. Even as a coral dies its skeleton remains as an ideal stony substrate for new corals to grow upon thus enlarging the reef. Scleractinian corals that form reefs are categorised as hermatypic corals and these are typically modular consisting of magnitudes of identical, yet individual polyps created asexually through a process called "budding" (Harrison, 2010). Coral reefs therefore grow as a collection of ever larger colonies. A single colony, if undisturbed, may live for centuries or even millennia and grow bigger than any other species of animal (Jackson, 1991; Hobson, 2024). Hermatypic corals are mixotroph filter feeders and gain a substantial part of their nutritional requirements through intracellular symbiosis with photosynthetic dinoflagellates of the genus *Symbiodinium*. This enables the corals to thrive in oligotrophic conditions so long as they are exposed to sufficient illumination, which is why they are mostly associated with tropical coastal environments (Goldberg, 2018). They are also very diverse with at least 800 recognized species divided in more than 80 genera (COTW, 2016) which grow in a large variety of sizes and morphological growth forms. When growing in proximity, corals can thus create a myriad of various microhabitats that are well protected from environmental and predatorial threats. These make ideal refuges and roosting spots for an abundance of organisms. Additionally, the rugose seascape created by corals serve to dissipate wave energy creating both a more stable environment internally on the reef and protecting the coast from mechanical impacts. Higher structural complexity is shown to positively affect biodiversity in several ecosystems both terrestrial and aquatic (Graham & Nash, 2012). The actual abundance of species that rely on coral reefs worldwide is poorly understood and remains understudied, yet estimations fall anywhere in the range of 500,000 to 10 million species (Knowlton *et al*. 2010) with the hotspot of biodiversity being concentrated on the Indo-pacific region around the Indonesian/Philippine archipelago, also known as the coral triangle (Veron *et al.* 2010).

1.2.2 Coral reef fish biology

The most abundant vertebrates found on coral reefs are teleost, perciform fishes (Wen *et al*. 2013). More than 4000 species, equivalent of roughly 25% of all marine teleost fish, are associated with coral reefs and a large portion of these are reef obligates meaning they depend on the coral reefs for food or shelter for some, if not all, of their life stages (Munday *et al.* 2008; Wen *et al.* 2013). They are possibly the most well-researched animal group on coral reefs and have historically served as surrogates for overall assessments on coral reef biodiversity and health (Dwita *et al.* 2022), likely because many fishes are less cryptic than most invertebrates and because they provide a substantial ecosystem service as an important food source (Knowlton *et al.* 2010). Furthermore, with the increased advancements and accessibility of SCUBA equipment in the last half a century, reef fish became likewise accessible to observe and study. The warm clear water of their environment makes for ideal field work conditions (so long as one has a means of respiration) and the abundance of fish species, unmatched by any other ecosystem, has attracted much scientific interest (Sale, 1991). The advancements of eDNA surveys in recent time has even revealed that visually obvious fish species are a minority and that most of a coral reefs fish diversity is attributed to the vastly understudied group of cryptobenthic fishes that are often missed in visual monitoring (Brodnicke *et al*. 2024). This exemplifies how much ambiguity there still exist in the knowledge of coral reef fish ecology, especially since this diversity in species is reflected in equally diverse life histories, trophic levels, habitat use and coral association (Sale & Ehrlich, 1991; Mora, 2015). Predicting fish assemblages in coral habitats might therefore be as reliant on the quality of fishes as it is on the quality of corals.

Fish are probably the most noticeable life-forms in any coral reef habitat. Most fish found on coral reefs are relatively small and sedentary with smaller home-ranges than expected in vertebrates of their size (Sale 1991; Nash *et al.* 2014). An extreme example of this is seen in certain species of damselfish (*Pomacentridae*) that have home ranges concentrated around singular branching coral colonies and rarely swim further than a few meters outside of said colony (Cowlishaw, 2014; Chase *et al.* 2020). Generally home range is expected to be related to body size (Nash *et al.* 2014), but is also influenced by trophic levels (Cowlishaw, 2014) and sexual maturity (Welsh *et al.* 2013). Dispersal of coral reef fishes does not generally happen in the adult individuals, but instead in their pelagic larval stage. Most coral reef fishes have a dual life cycle with a pelagic non-reproductive stage that differs greatly in habitat, food and behaviour from their adult counterparts (Leis, 1991). Reproduction in coral reef fish can vary greatly with spawning strategies ranging from highly dependent on temporal cues such as lunar or seasonal changes, to spawning being near constant or random. Certain species simply release their gonads into the water column, whilst others disperse them on the substratum. Some even show nesting behaviour and parental care and there also exist viviparous coral fish (Robertson, 1991; Møller *et al*. 2016). Most species, however, hatch into pelagic planktonic organisms that are subject to transportation by ocean currents. Pelagic larval duration differs greatly between species (and is probably flexible within) but has been observed to last up to over 100 days in which time the larvae could potentially be moved across oceans (Leis, 1991; Jones, 2015). Conversely, the emerging view seems to be that there is a larger percentage of self-recruitment happening within fish populations than previously thought. The dispersal kernels of coral reef larvae have historically been poorly understood and despite major advancements through chemical tagging, biophysical modelling and population genomics there is still debate as to how "open" reef fish populations are (Jones, 2015, Torquato and Møller 2022). Similarly, the mechanisms of how fish transition from their pelagic state to settling on the reef habitat also remains challenging to properly ascertain. However, it is generally accepted that the shift is rapid, typically occurring overnight and patterns of settlement appear to peak during the dark half of the lunar cycle (Sponaugle, 2015). After settlement the fish is typically considered juvenile and have well developed sensory and locomotor systems (Goatley & Bellwood, 2016). They can therefore start navigating the environment and gradually grow into their adult size. The life span and growth rate of coral reef fish varies both between species and within making it hard to standardise (Booth & Beretta, 2021). Most reef fish are, however, subject to several ontogenetic shifts in their ecology. Habitat use, home range, mortality rate and trophic level are all related to body size, which means that a small juvenile fish might occupy a very different ecological niche compared to their larger adult conspecifics (Kulbicki *et al*. 2015). Parrotfish for instance shift from a carnivorous diet as juveniles to a corallivorous or herbivorous diet as they mature (Neves *et al.* 2015). Similarly, reef fish also might appear very different as juveniles. Drastic ontogenetic morphological change is common in their transition to adulthood. Typically, the smaller fish will be more transparent or dull to avoid predation and detection, whilst the larger fish will

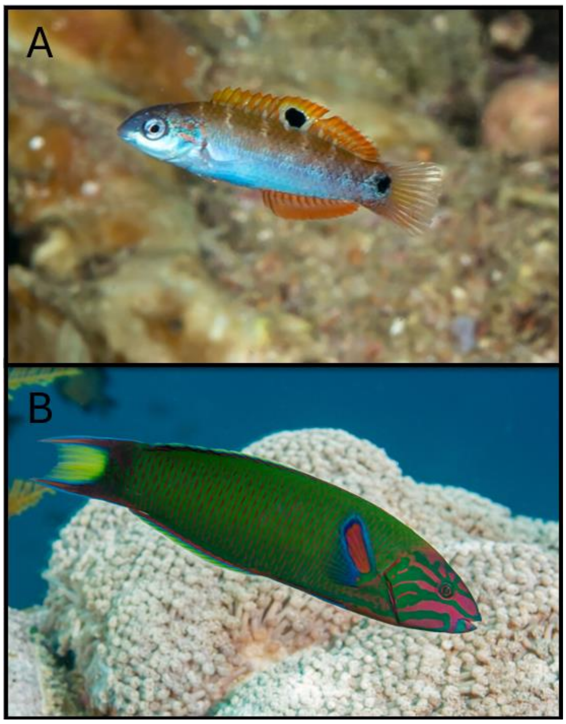

Figure 1: Example of ontogenetic morphology change in *Thalassoma lunare*. **(A)** juvenile **(B)** adult (Photos from Spanglers (n.d.))

develop bolder colourisations that may be involved in sexual or territorial display (See Figure 1) (Cortesi *et al*. 2016). Generally, these ontogenetic shifts help minimize intraspecific competition between juveniles and adults (Kimirei *et al*. 2013). Small fish, such as juveniles, are typically more abundant than large fish but also have a higher mortality rate (Kulbicki *et al*. 2015). This, along with the differences in ecosystem niches, reflects the importance of considering not just the species but also the ontogenetic status of observed fish when doing ecological assessments of reef fish assemblages.

1.2.3 The microhabitat of branching coral colonies

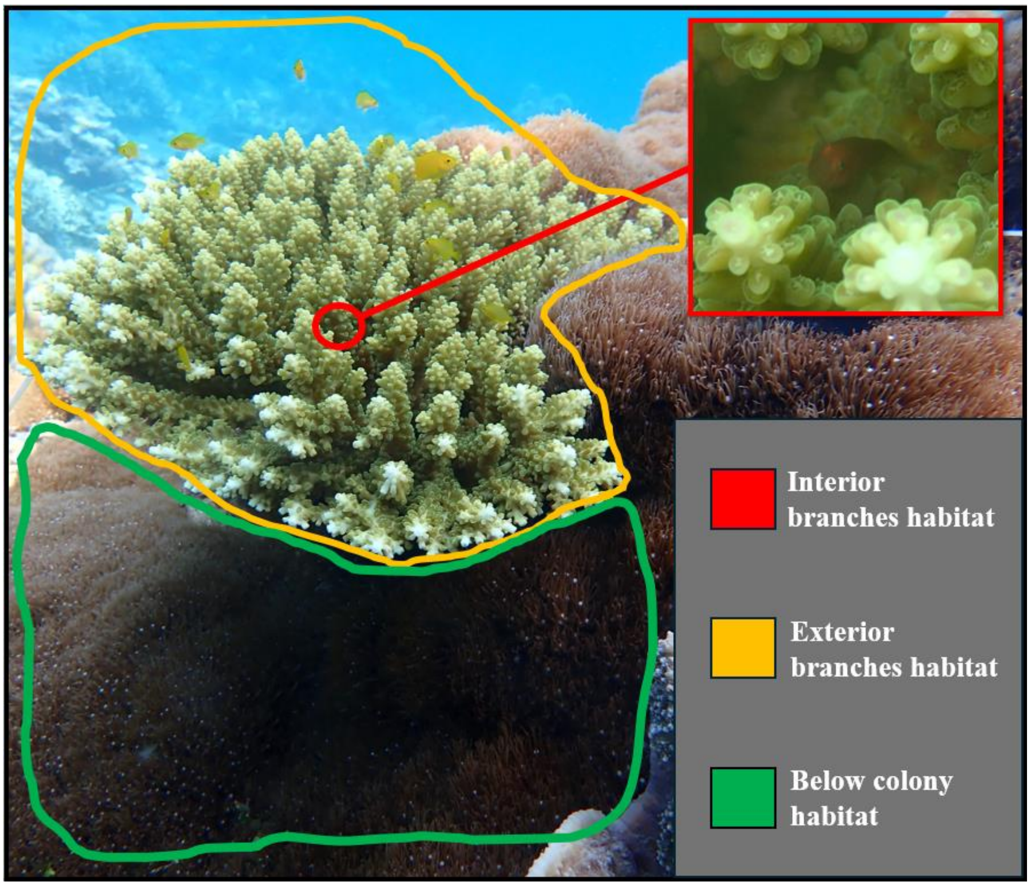

Figure 2: Branching *Acropora* with highlighted habitat zones. Photos by A. Duekilde

Stony corals have highly categorised morphological growth forms, such as massive, tabular, encrusting or branching. These confer specific ecological advantages and influences the role of the colony within the coral reef ecosystem (Zawada *et al*. 2019). Branching corals especially have significant effect on the recruitment of higher biodiversity as their high surface-area promotes rapid growth, making them quick colonisers of available substrate (NOAA, 2007; Zawada *et al*. 2019). Furthermore, they provide small scale habitats among their branches that are ideal refuges for the abundant small-bodied fish and invertebrates associated with coral reefs (Oh *et al*. 2024). These traits make branching corals ideal for coral restoration projects. Two of the most common genera used to that effect are *Acropora* and *Pocillopora* (Boström-Einarsson *et al*. 2020). *Acropora* is the most species-rich coral genus in the world and is named after their apical growth around an axial polyp. Other than this recognisable trait, however, they are not a very uniform group and display a wide range of branching morphologies and structural shapes (Wallace, 2011). *Pocillopora* is far less species rich but is increasingly widespread in the Indo-pacific. It has thick branches that are adorned with verrucae (small skeletal bumbs). They have high morphological plasticity and good environmental adaptability leading them to gradually become more dominant on some reefs as external stressors become more frequent with climate change (Gélin *et al*. 2017; Li *et al*. 2020). The branching structures of these two genera effect local flow dynamics inside and around the colonies, which in turn affects the transport of gases, nutrients and the dissipation of heat (Hossain & Staples, 2020). Branching corals therefore represent a microhabitat with an environment distinct from the larger reef, suitable for other life to utilise and inhabit.

Many cryptic species exist that are highly associated with these habitats living sheltered deep within their branches. Especially crustaceans take up this space, though it is also a typical habitat of cryptic fishes such as *Gobiodon* spp. (see Figure 2*)*. These are especially often found in *Acropora* corals (Patton, 1994). Further out by the exterior halves of the colony's branches is typically found a more fluid assemblage of less cryptic, small demersal fish. These likely use the coral as protection and may be associated with the specific colony, either refuging in or near it permanently or transiently. Most fish found here belong to four families: *Pomacentridae, Labridae, Apogonidae* and *Chaetodontidae* (Coker *et al.* 2013). Intuitively one would expect coral-feeding fish such as *Chaetodontidae* (Butterflyfish) to be strongly associated with live corals, however most fish found in these assemblages are planktivorous or omnivorous (Coker *et al.* 2013). Additionally, *Chaetodontidae* have been found to have larger home ranges than other coral reef fish of similar size which suggest that while they are dependent on live corals on a reef scale, they are likely less associated with specific singular colonies and only appear transiently in these individual microhabitats (Cowlishaw, 2014). Planktivorous *Pomacentridae*, conversely, have very small home ranges and are facultative or obligate coral dwellers. They are typically found feeding in the immediate water column around specific branching corals, quickly retreating when threatened (Coker *et al*. 2013; Cowlishaw, 2014; Pratchett *et al.* 2015a). They are also highly territorial, and their presence have been observed to reduce *S* locally (Dunkley *et al.* 2023). They might therefore be considered permanent residents of their individual microhabitats and have been documented to associate with the same coral colonies in observations across a whole year (Chase *et al.* 2024). *Apogonidae* (Cardinalfishes) are nocturnal meso-predators that often rest diurnally in the branching coral microhabitats and disperse to forage at dusk (Coker *et al.* 2013). They show strong site-fidelity and impressive homing abilities often returning to the same refuges again especially in specialist species. They are therefore semi-permanent within the individual colony microhabitat as they are shown to persist for up to several months but also leave for extended periods of time to forage (Gardiner & Jones, 2016). *Labridae* (Wrasses) is a species-rich and ecologically diverse group that ranges from large piscivores more than 100 kg in size to small ectoparasite predators like cleaner wrasses (Wainwright & Bellwood, 2002). Their association with the branching coral microhabitat is therefore highly species dependent as some might use it as refuge from predation whilst others represent those very predators from which smaller fish seek shelter and others again may not associate with branching corals at all. There is likely also an ontogenetic dependency in their level of association. The labrid fish *Thalassoma lunare* (See Figure 1) has, for instance, been observed refuging in branching coral microhabitats when juvenile (Wilson *et al.* 2010) and feeding on juvenile fish in those same habitats when adult (Holmes *et al*. 2012). Whilst there is a gap in the knowledge of coral colony association across developmental stages it is likely that juvenile fish (both labrid and in general) are less transient and more closely connected to the branching coral microhabitat as older, larger fish tend to have larger home-ranges (Coker *et al*. 2013; Cowlishaw, 2014).

Finally branching corals also offer another kind of refuge not within their branches but under them (Coker *et al*. 2013). *Acropora* corals especially can branch out horizontally instead of vertically. These colonies might be defined as tabular corals (though there is not a defined dimensional difference between “branching” and “tabular” growth forms) (Zawada *et al*. 2019). The shaded refuge under such colonies is open for larger fish species like *Serranidae* (Groupers), *Lutjanidae* (Snappers) or *Lethrinidae* (Emperors) (Kerry & Bellwood, 2015a). Large coral reef fish are unable to seek shelter in the narrow spaces between coral branches; however, these big sub-colony species may represent the highest fish biomass on coral reefs. How much of the fish assemblage beneath coral structures is made up by opportunistic fish as opposed to stable residents is not well-known, but there is evidence that large reef fishes show strong site fidelity (Khan *et al*. 2017). It is also suggested that it is the protection from UV-radiation from the sun, rather than from predation that is the main attraction of these shelters (Kerry & Bellwood, 2015b). Large reef fish appear to show a clear preference for canopy-like structures formed by tabular corals (as opposed to corals of more vertical branching morphologies or canopy structures formed by bummies or stone tunnels) (Kerry & Bellwood, 2014; Khan *et al*. 2017). Whether the space beneath a coral colony can be classified as belonging to the same microhabitat as that within is unclear. Even though they are both supported by the same colony structure, they differ greatly in environmental traits, inhabitant fish species and ecological effect. This disparity does, however, highlight the impactful overall ecosystem service a single branching coral colony can provide to the coral reef.

1.3 Ecology of fish coral-interactions

1.3.1 Predictors of fish assemblages on branching corals

SARs are a very commonly studied and applied phenomena in ecology. It assumes that an increase in area will lead to a related increase in *S* and has often been expressed as a power law. A similar phenomenon exists for *N* relating to individuals within a species or in an ecosystem (Abundance Area Relationship (AAR)) (Gaston & Blackburn, 2000; Ugland & Kraberg, 2021). It is therefore reasonable to assume that within the context of the branching coral microhabitat a similar relationship exists which might predict the metrics of the associated fish assemblage. SARs have, however, mainly been developed in terrestrial environments and even when applied in marine systems they are typically used for macroecological analysis and not on small scale studies (Ugland & Kraberg, 2021). The literature that explores colony size as a predictor for fish community structure appears to be very sparse, however since size can be associated with the age of a colony, understanding such a relationship could have important implications to gauge the temporal development of fish communities on restored reefs. Growth rates of *Acropora* and *Pocillopora* varies with species as well as many other factors and linear extensional growth (length of branches) has been found to be up to 37.2 cm $year^{-1}$ but often much less (Cresswell *et al*. 2020; Weil *et al*. 2020; Combillet *et al*. 2022; Dehnert *et al*. 2022). One key trait of marine environments is that more organisms can move three dimensionally as compared to terrestrial environments (Ugland & Kraberg, 2021). For the purposes of associating habitat size to community structure it might then be more meaningful to examine volume instead of area, however this is not typically how growth rates on branching corals are measured. Additionally, the main predictor of fish diversity on coral reefs have often been measures of structural complexity instead of environment size, both on small and large scale (Chittaro, 2002; Graham & Nash, 2012; Agudo-Adriani *et al*. 2016, Siqueira *et al*. 2023). Colony size has, however, repeatedly been found to positively influence fish assemblages on various corals (Agudo-Adriani *et al*. 2016; Komyakova *et al*. 2018). On a large scale the sum of colony heights has also been found to strongly correlate with fish density and biomass, in fact more so than structural complexity, however they were strongest correlated when analysed together (Fisher, 2023). Colony size has also been found to positively correlate with structural complexity in both *Acropora* and *Pocillopora* corals (Richardson *et al*. 2017; Million *et al*. 2021). Differentiating between these two metrics might therefore be redundant. Furthermore, such a correlation indicates that structural complexity might, similarly to colony size, serve as a temporal predictor on the development of fish assemblages on coral colonies. The importance of colony morphology on fish assemblage means by extension that coral species is also an important predictor as both growth rate and morphological complexity can vary greatly interspecifically (Richardson *et al*. 2017). Additionally, coral species have been shown to highly influence fish composition and certain fishes even show preference for single coral species (Pratchett *et al*. 2012; Komyakova *et al*. 2013, Komyakova *et al*. 2018). Conversely, the species of inhabiting fish also influence assemblage dynamics, as habitat use and levels of association can vary even among fishes within the same family (Chase *et al*. 2020, Siqueira *et al*. 2023). For instance, certain species of *Dascyllus* shows behaviours like algae farming or territoriality which affects *S* in their habitat (Ceccarelli *et al*. 2001; Chase *et al.* 2020; Dunkley *et al*. 2023). The association levels of fish might also depend on the ontogeny of the fish or the exposure to predation (Gauff *et al*. 2018). Fish populations on the larger reef might therefore affect the assemblages on singular colonies. The geographical structure of the whole reef could similarly be a factor (Chase & Hoogenboom, 2019). SARs have been found to change differently on continuous reefs compared to patch reefs with a higher *S* expected on patch reefs with isolated coral bummies at least on a small scale (Chittaro, 2002; Hattori & Shibuno, 2009). This could indicate that fish accumulate around coral patches to avoid the exposed open space between them. Finally, the condition of the coral colony has been shown to affect fish behaviour. Pomacentrid fish for instance show less or at least different association with bleached corals (Boström-Einarsson *et al*. 2018; Chase *et al*. 2020). However, the morphology of a colony has been shown to be more strongly associated with changes in fish assemblages than factors such as live coral tissue or algae cover, making it uncertain whether these are important predictors (Agudo-Adriani *et al*. 2016).

1.3.2 The ecological difficulty of investigating fish-coral interactions

Despite the well of knowledge that seemingly exists on coral reef fish species, there is still a lot of ambiguity surrounding the interactions between corals and coral reef fishes (Siqueira *et al*. 2023). Fish's use of coral reefs for shelter is well documented. Strong increases in fish density and biomass have repeatedly been found to correlate with increased coral rugosity (Graham & Nash, 2012). However, little is known as to whether it is the complexity or the presence of corals that increase fish populations. Siqueira *et al.* (2023) found that the fish population response to a loss of coral cover is heterogeneous and suggested a distinction between coral-associated and reef-associated fishes. Furthermore, only a small fraction of species typically associated with coral reefs, were found to be strongly associated with corals, even within families (See Figure 3). Similarly, Robertson (1998) found no substantial differences in relative *S* between reefs rich and poor in coral cover. Conversely, Komyakova *et al.* (2013) observed topographic complexity to be weakly associated with *N* and *S* whilst coral cover and especially coral species richness was significantly positively correlated. These contradictory findings indicate that fish-coral relationships are not straightforward and are subject to changes based on far more ecological and phylogeographic factors than the presence and structure of corals. The abundance of extant fish species on coral reefs alone makes it difficult to extrapolate any satisfactory models for population dynamics as the huge variety of reef fishes exhibit equally diverse patterns of association both with corals (Komyakova *et al*. 2013; Siqueira *et al*. 2023) and with each other (Choat & Bellwood, 1985; Jones, 1987; Hobson, 1991; Boaden & Kingsford, 2015). Additionally, the benthic fauna of a coral reef habitats is made up by far more structure forming organisms other than Scleractinian corals. Organisms like soft coral, ascidians, hydroids and sea sponges whose roles in fish population dynamics have been relatively neglected as a research topic when compared to stony corals. Sea sponges (*Porifera*) for instance appear to fulfil many similar ecological roles to corals, both offering ideal refuge and breeding sites and acting as a food source. Despite this they have seldom been considered in research that otherwise aims to explain the ecological importance of the benthic community with regards to fish assemblages

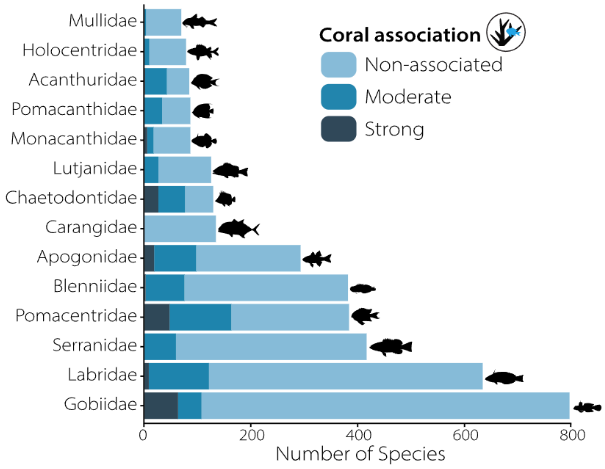

Figure 3: The distribution of association levels in common reef fish families. As seen in Siqueira *et al.* (2023)

(Coppock *et al*. 2022). Shima (2001) showed how fish recruitment patterns on coral reefs could be explained simultaneously by different factors when those factors were examined individually. This highlights the importance of taking a multifactorial approach in ecological studies and exemplifies how easily results can be refuted when omitting variables. However, as previously mentioned, coral reefs represent one of the richest and most diverse ecosystems in the world which equally enlarges the scope of potential variables to consider (Knowlton *et al.* 2012). This complexity issue was already acknowledged nearly 50 years ago where a "Chaos view" for colonisation of coral reef fish assemblages was proposed which suggested that a certain level of unexplainable randomness and chance might always be involved (Smith, 1978). Though research methods, technology and conservation interest have advanced far since then it still highlights the foundational issue with obtaining confident results from large scale research on coral reefs even when working with their most well studied organisms: corals and fish. Despite this, the majority of research on the relationship between these two groups appears to have been conducted on a large scale, considering the dynamics of the reef as a whole (Graham & Nash, 2012; Ménard *et al*. 2012; Komyokova *et al.* 2013; Wen *et al.* 2013; Dwita *et al.* 2022). Far less research can be found that investigate the individual microhabitats that exist within the reef, however Holbrook *et al*. (2002) did find that up to 60% of variation in fish species composition surrounding singular *Porites* colonies could be predicted by the available microhabitats provided by the structural composition of these colonies. The lack of such small-scale research makes it difficult to cross-examine these findings with other studies that focus on alternative explanatory factors (which as aforementioned often leads to contradictions on large scale studies). However, it is reasonable to expect fewer factors to be of importance on a localized study such as on a single colony. Examining the effect of coral structures in micro- rather than macro-habitats, such as on a single-colony scale (as is the aim of this study), could therefore be highly relevant to develop a foundation of more confident results, which in turn might increase understanding of the ecology on the reef as a whole.

1.4 Conservation of coral reefs

1.4.1 The global reduction of coral reefs

Coral reefs are suffering a multicausal decline worldwide. Global climate change has typically been deemed the primary threat to coral reef ecosystems due to its multitude of detrimental repercussions. Increased atmospheric carbon dioxide causes the pH of sea water to decline which acidifies the oceans causing desaturation of aragonite which is necessary for coral calcification (Hughes *et al.* 2017). Atmospheric temperature averages are rising which in turn warms the oceans causing elevated rates of photosynthesis by the *Symbiodinium* and thus elevated oxygen concentrations in the tissue of corals. This might force the corals to expel the *Symbiodinium* to avoid oxygen toxicity, which causes the corals to bleach (Lesser *et al*. 1990). Climate change also alters global weather phenomena causing more frequent extreme events like tropical storms which can destroy fragile coral structures and increase water sedimentation which smothers corals (US Department of Commerce, 2015). Local stressors also play a key role in the degradation of coral reefs. Overfishing and pollution can cause damage to a reef already stressed by global changes and might thus severely decrease its chances of natural recovery (Hughes *et al*. 2017). The first large scale bleaching event was witnessed in 1998 and after 2009 such events became continuously more recurring. In 2018 it was estimated that a 14% decline in average global coral cover had occurred in the previous two decades. The cover of algae on coral reefs increased by 20% concurrently, which could indicate a shift from coral to algae dominance in tropical reef communities (Souter *et al*. 2021). The biodiversity supported by coral reefs are also affected directly by the anthropogenic stressors that damages corals i.e. by temperature increases above species-specific thermal optima, higher chances of acidosis, and eutrophication-caused anoxia (Pratchett *et al.* 2015b; Wenger *et al*. 2015). But biodiversity is most severely affected indirectly through the loss of habitat as the complexity of the structural seascape on the reefs are reduced with coral loss, removing niche microhabitats that are the primary domain of specialist species (Pratchett *et al.* 2015b).

1.4.2 Management of coral reefs in the Philippines

Highly biodiverse coral reefs are more resilient towards environmental stressors and some of the healthiest reefs today therefore exist in the coral triangle (See Figure 4A) (Souter *et al*. 2021). The coral reefs of the Philippines are especially praised for having some of the highest diversity of corals and reef fishes in the world. There is 25000 km^2 of reef area surrounding the more than 7100 Philippine isles making it the third largest contributor to global coral cover in the world (Licuanan

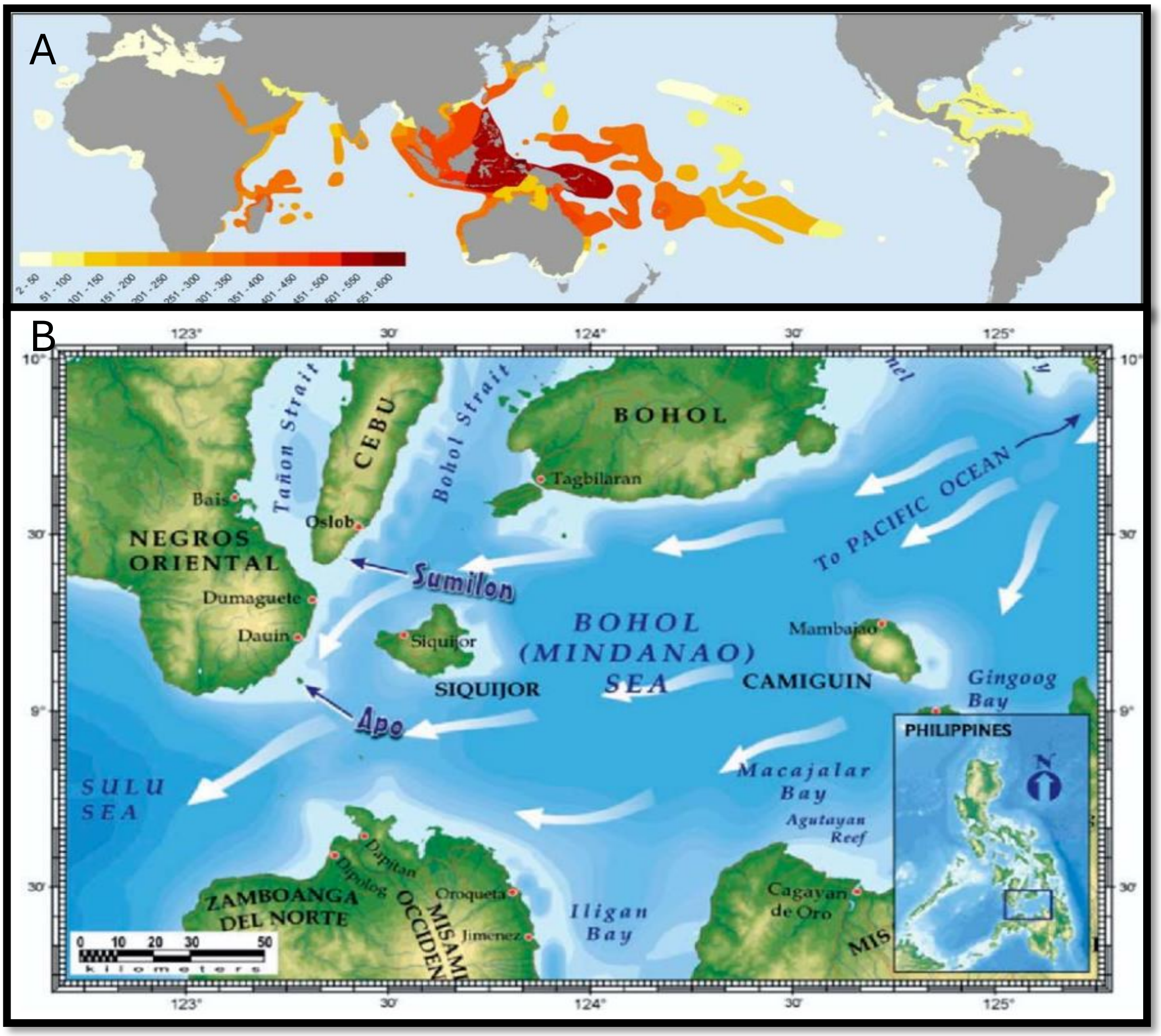

Figure 4: **(A)** Global biodiversity of Corals with *Symbiodinium* with the coral triangle in centre. Deeper reds indicate higher biodiversity. As seen in Veron *et al*. (2010). **(B)** Map shows the location of the first two no take marine reserves (later MPA's) in the Philippines. As seen in Alcala & Russ (2006)

et al. 2019). These reefs might have high probabilities for enduring and adapting to the changing conditions of the future and are therefore prime focus points for conservational success. Whilst reduction in hard coral cover and increase in macro algae growth is also occurring on Philippine reefs at an alarming rate there are several reefs where little to no change in these metrics have been recorded (Licuanan *et al*. 2019). Research into the success and decline of various Philippine reefs could therefore have important applications for improving future conservation efforts. The Philippines also have some of the highest reef-proximate population densities which are highly dependent on their fisheries for meeting dietary requirements (Institute for Marine Research, 2020). This greatly increases motivation for protection of the coastal environments and have meant that the country has historically been on the forefront of marine resource management initiatives (Matorres *et al*. 2024). Though the oldest marine sanctuary is the Hundred Islands National Park, which was established in the 1940's, the first real protection initiatives, that came as a response to witnessed ecological declines, began in the 1970's (Horigue *et al*. 2012). No take zones were implemented in the Southern Philippines around the small Islands of Sumilon and Apo which gradually developed into the marine protected areas (MPAs) that still exist today (See Figure 4B). The success of these inspired the deployment of more MPAs first in the nearby municipality of Dauin and since spreading to all regions of the Philippines (Alcala & Russ, 2006). Today there is well over 1000 MPAs in the country (Horigue *et al*. 2012). A key factor in the success of these MPAs is the allocation of management responsibilities to local communities instead of centralized government institutions as this secures more consistent and informed conservation efforts (Alcala & Russ, 2006). Non-government Organizations (NGOs) are an important component in marine conservation in the Philippines as they have more freedom and can work more goal-oriented whilst engaging the public and mediating communication with local governments (Horigue *et al*. 2012; Crossman, 2013). An exemplary NGO in this aspect is the Institute for Marine Research (IMR) which have conducted a long-term reef monitoring program on the MPAs of Dauin since 2019 and has as their mission "Using […] scientific evidence to educate, transform and encourage locally led marine conservation strategies within the Philippines" (Institute for Marine Research, 2020). NGOs like IMR represent experts responsible for undertaking a lot of the necessary research and data-collection to further improve future conservation efforts, but they are equally important as educators to inspire more funding and interest into marine conservation both locally and on a larger scale (Crossman, 2013). Promoting collaboration to increase the scale of success, for instance, could be very important for the future of Philippine coral reefs. Whilst the MPAs have been successful in achieving local conservation targets, they do not feature greater ecological connectivity which could be essential in establishing resilience towards climate change. Most of the MPAs are small and scattered and are subject to financial or governance constraints. Additionally, many (if not most) are poorly enforced (Horigue *et al*. 2012). There is therefore still a long way to go in the efforts of protecting the pristine coral reefs of the Philippines.

1.4.3 Coral restoration

Coral restoration is an emerging tool that can complement protection efforts (Matorres *et al*. 2024). As opposed to passive protection, coral restoration seeks to actively boost the ecosystem by manipulating the environment to increase the ecosystem services of corals. One of the most common methods is to utilise the asexual reproductive capabilities of corals to propagate and plant coral fragments unto available substrate (See Figure 5). There exists a whole sub-genre of methodologies for asexual coral reproduction. They are all, however, generally criticized for limiting genetic diversity, which, as already mentioned, is a key component in establishing resilient reefs (Boström-Einarsson *et al*. 2020). The oldest and most widely used restoration method in the Philippines is the deployment of ARs, however conversely to asexual propagation these were generally not implemented by academic institutions, but by the government to enhance fishery production (Matorres *et al*. 2024). The ecosystem enhancements provided by ARs is first and foremost additional substrate for settlement which can directly increase coral cover. The deployed structures themselves might also serve to increase seascape rugosity and thus increase biodiversity. Additionally, ARs might remove anthropogenic stress, caused by fishing and tourism, from the natural reefs (Higgins *et al*. 2022). The use of ARs as coral restoration tools has been criticized for the typical lack of clearly defined conservational objectives making it hard to assess their efficiency. It is furthermore suspected that ARs can introduce alien or even toxic materials into an ecosystem and that they might be a sink for fish and invertebrate biodiversity (Higgins *et al*. 2022). ARs have been deployed in the Philippines since the 1970s and regulated by local governments since 2000 (Matorres et al., 2024). While not originally intended for conservation or research, they may now serve those roles. Modern restoration often combines asexual propagation with ARs, leveraging the stability of ARs and the recruitment potential of propagated fragments (Matorres et al., 2024). This forms the basis of "coral nurseries," where fragments grow to sustainable sizes before being transplanted, or are grown directly on ARs if these serve as restoration sites (Boström-Einarsson et al., 2020). IMR also restores coral on an older AR in Dauin (see Figure 5), using asexual propagation and investigating experimental methodologies that would be difficult to conduct on natural reefs (Institute for Marine Research, 2020; McConnell & Waters, 2024).

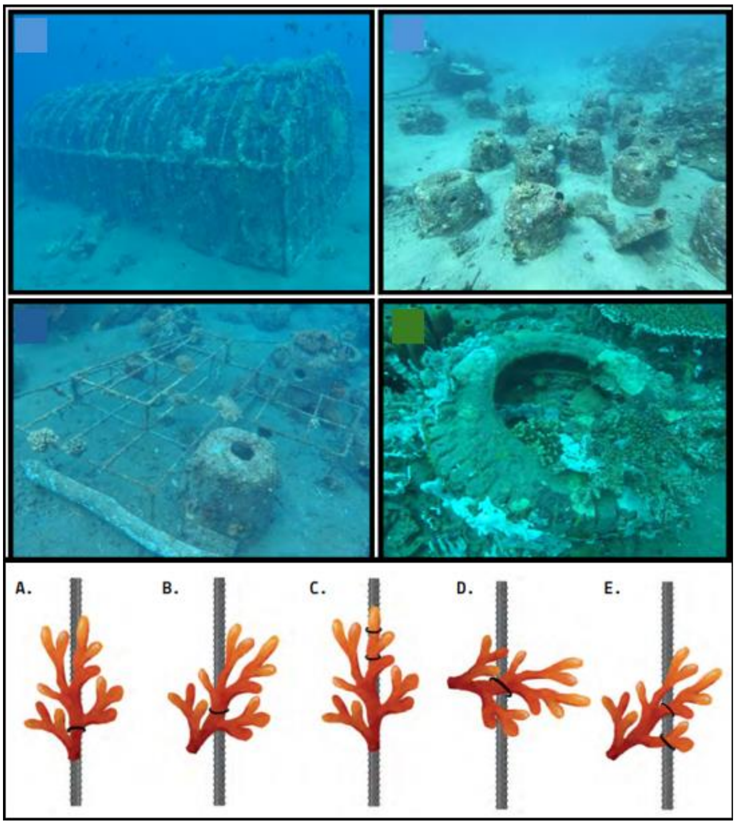

Figure 5: **(Top)** Examples of AR structures on Sahara reef, Dauin, Philippines. **(Bottom)** Example of coral propagation using small coral fragments. Ranked from good placement (A) to poor (E). Modified from Mcconnell & Waters (2024)

2. Methodology

2.1 Study area

All data was collected in October and November of 2024 at designated study sites along the coast of Dauin, Negros Oriental, Philippines. The data collection period thus coincided with the end of the typical wet season for the area. The wet season is characterized by slightly colder temperature averages, more frequent precipitation and higher chances of typhoons as compared to the dry season (PAGASA, n.d.). Data was collected from four sites spread over approximately eight kilometres of coastline: Ma'init, Poblacion, Maayong tubig and Sahara. These sites are four out of nine individual MPAs along the Dauin coastline the latest of which was established in 2005. They are marked by buoys and do not allow fishing, boat-traffic or unregulated diving (Bianchessi & Lumbab, 2012; Ferrandis, 2021). They are, however, popular dive sites for the abundant dive-tourism industry of Dauin and is each located near one or several well-visited dive resorts. All sites except Sahara represents natural coral reefs and are all part of IMR's standard survey sites (Institute for Marine Research, 2020). The sites were chosen partly as they were believed to have an abundance of the target coral genera and partly for their easy accessibility as compared to other potential sites. They further had the advantage of being distanced far apart such that the collected data represents relatively independent reefs along the full Dauin coastline.

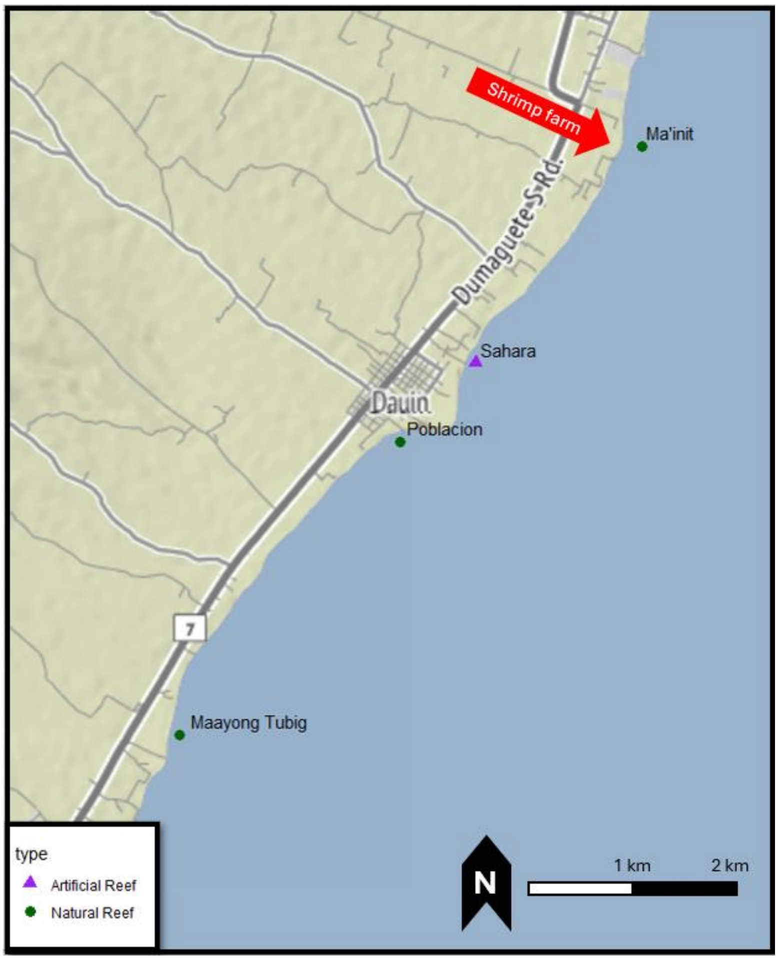

Figure 6: Map of the study area with the four reef sites. NRs are green dots. AR is purple triangle. Map generated in R using *ggmap*. Basemap tiles provided by Stadia Maps. Data © OpenStreetMap contributors (Kahle & Wickham, 2013; Stadia maps, n.d.)

The northernmost site is Ma'init which is located right off the coast of IMR's base of operations at Liquid Dive Resort. This reef mainly consists of bummies varying greatly in size with a few patches of larger continuous reef. The geographical shape of the coastline creates a phenomenon where the tidal currents are typically stronger here than along the rest of Dauin. In the survey period strong currents would typically occur with the rising afternoon tides. A shrimp farm is also located on the coast next to Ma'init which leads its wastewater via pipes directly into the MPA creating a consistent plume in the surface water near the coast (See Figure 6). This might make the water at Ma'init more eutrophicated than the other sites.

The second site is Poblacion which is located by the centre of the village of Dauin. It is therefore probably the most visited of the MPAs. Furthermore, there is heavy boat traffic right outside of the MPA as the beach there is sandy with no rocks and there is a small coastal tip to the north providing shelter from currents which makes it an ideal mooring site. The reef itself consists of a large and continuous main reef that stretches all the way from the coast down to past 20 meters depth, with a few scattered bummies surrounding it.

The southernmost site is Maayong tubig. This MPA also neighbours several large dive resorts. It is unique in having a distinct shallow reef that only extends to about 4 meters depth at high tide and a second deeper reef that starts at about 9 meters at high tide. The shallow reef is continuous and large whilst the deeper reef consists of closely scattered small bummies. Between the two reefs is a large patch of sandy bottom without solid structures.

The final site is named Sahara. This name is derived from the fact the site naturally features a sandy bottom habitat with hardly any solid structures for a reef to form on. However, in the late 2000s/early 2010s the first solid structures were placed there with the aim of turning it into an attractive dive site (Mcconnell & Waters, 2024). Today there are several fields of concrete bells and metal structures as well as two large rebar cages. Most of these structures acts as substrates for several coral colonies. It is seemingly a thriving reef with a large fish population, though the AR materials was left unattended for nearly a decade allowing natural ecosystem succession of biological growth which diminishes the amount of available substrate for coral recruitment. As a result, the hard coral cover is far lower than expected on Philippine reefs (Hughes *et al*. 2022). IMR is currently conducting trials to monitor how various restoration methods might improve the ecological condition of the AR. They aim to promote coral growth by replanting broken off coral fragments and conduct structural cleaning of AR materials to protect coral recruits from rapidly growing competitors such as macro-algae, sponges and cyanobacteria (Hughes *et al*. 2022; Mcconnell & Waters, 2024).

2.2 Survey methods

All field data were collected using SCUBA diving whilst adhering to standard PADI practices for safe recreational diving (Clent, 2023) and all field work was conducted exclusively by certified PADI dive masters. A total of 111 coral colonies were examined throughout the four sites. The target genera *Pocillopora* and *Acropora* was chosen for their branching morphology which makes them ideal fish habitats of the type that this study aims to investigate (Boström-Einarsson *et al.* 2020). At each site a minimum of 15 coral colonies of each genus was surveyed. To ensure a diverse size range the survey colonies were chosen in three size categories: Small (Less than 15 cm in width and height), medium (more than 15 cm in width or height but less than 30 cm in both) and large (more than 30 cm in width or height). This categorisation was estimated *in situ* using a ruler. Of each genus a minimum of five colonies in each size category was surveyed. This approach was used at Ma'init, Poblacion and Maayong tubig. At these three sites appropriate colonies were tagged before the data collection period using standard zip tags and colour coded electrical tape. Tags were placed with the purpose of distinguishing survey colonies such that repeated subsequent data collection of the same colony was possible. The colour codes were to distinguish between colonies of different size categories. Tags were placed securely and with as little damage to the colony as possible (see Appendix 1). Chosen colonies were only discriminated by size and genera. However, where possible it was also attempted to ensure that no two survey colonies were within three meters of each other to avoid the potential of two proximal colonies affecting the occurring fish populations on each other. This distance was determined by the average home range of some of the pomacentrids that were expected to be predominant on the coral colonies (Chase *et al.* 2020). Conversely colonies were also generally located within average visibility range (~10 meters) of at least one other survey colony such that locating them on repeated dives was made easier. When all data had been collected all tags were removed from the colonies and disposed of away from the ocean.

Sahara was surveyed with the objective of comparing potential trends observed on NRs with qualitative data from an AR. Therefore, only a few representatives of each colony category needed to be surveyed. The decision to sample less AR data was additionally made due to time constraints and the smaller size of the reef, making it harder to find enough suitable and appropriately distanced colonies. A minimum of two colonies in each size of each genus was surveyed. Furthermore, all data from each colony could be collected on a single dive negating the need for tagging at this site.

2.2.1 Measuring colony size and structure

Colonies were measured using the 3D modelling software RealityCapture (Capturing Reality, 2025). A series of photos were taken of each colony using an Olympus OM System tough TG-7 camera in a PT-059 underwater housing case (camera hereafter referred to as TG-7) (OM Digital Solutions, 2023a; OM Digital Solutions, 2023b). Each colony was photographed from several angles using the "Doming technique". The camera starts at a horizontal axis with the colony. The camera is then gradually moved all the way over the vertical axis down to the horizontal axis on the other side all whilst taking photographs of the colony at least once at every 30-degree angle change (minimum of 10 pictures per dome to ensure later alignment). This movement is then repeated perpendicular to the first dome such that the colony is thoroughly imaged from all sides (See Figure 7). RealityCapture was used to identify repeated control points on the photographs and align them to create a 3D point cloud of the colony. To make measures on the colony this point cloud was converted into a polygonal 3D representation. The model was scaled to

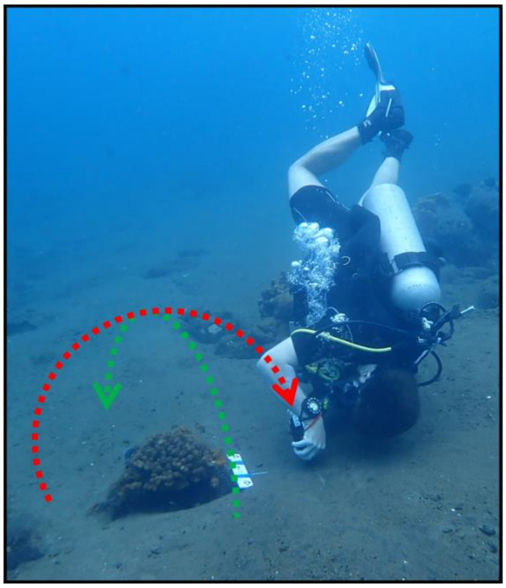

Figure 7: The doming technique used to 3D scan coral colonies. Photo by A. Lacson

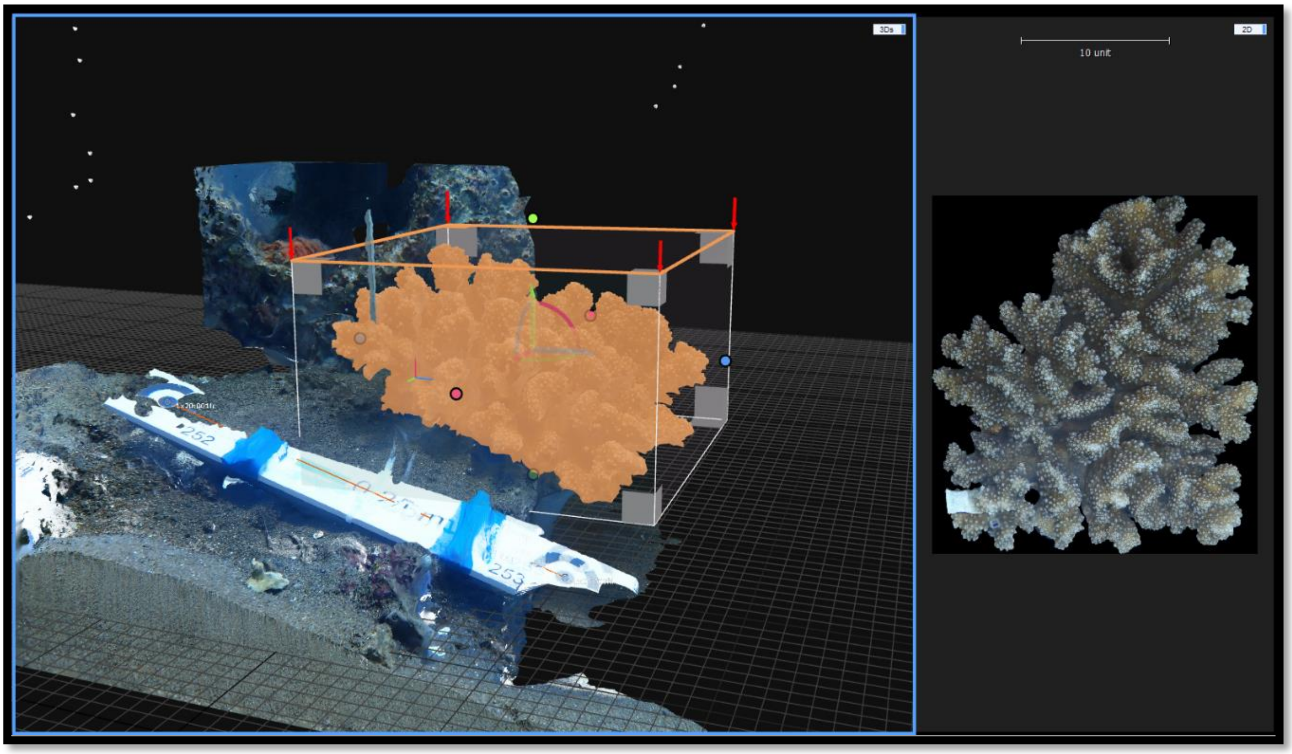

Figure 8*:* Screenshot from Realitycapture, showing the lassoed colony (PPL4 from Poblacion). **(Left)** Reconstruction area used to measure volume. **(Right)** Ortho projection of the lassoed polygons

accurate size by placing a coded scalebar next to the colony when it was photographed with two markers distanced 25 cm apart. RealityCapture recognises these markers as control points which can be used to estimate the accurate scale of every dimension of the colony. A few of the scanned colonies did not have sufficiently detailed photos of the scalebar to accurately detect the 25 cm markers. In these instances, the model was scaled by placing manual control points on certain identifiable aspects of the scale bar with known dimensions (See Appendix 2).

The advantage of creating 3D models of the colonies is that, if detailed enough, highly accurate measurements of various parameters can be conducted with the software *ex situ*, instead of with the time constraints and mechanic manipulations of doing it *in situ* on a dive. The size of the colonies was measured by creating an ortho projection of the specific polygons of the model environment that made up the surveyed colony. Polygons were selected with a lasso tool such that all else on the model was negated. The Ortho projection was created with the reconstruction area set as narrowly confined around the colony as possible. The volume was measured from the bottom of the reconstruction area to the surface of highlighted polygons (Called the "Cut volume" in RealityCapture). An accurate volume estimate of each colony was thereby calculated in cm^3 (See Figure 8).

The rugosity of the colonies was also estimated as this metric affects the potential space available between branches for fish to reside and hide in and might therefore influence fish assemblage. Rugosity can be measured by comparing surface area to volume; however, it was observed that the 3D models used in this study would "fill in" the deeper shaded parts of the branching coral structure, which had been sparsely photographed. This might cause differences in surface area between colonies to be minimised and unreliable. Instead, an alternative approach was conceived. Using the 3D model in full render for best reconstruction quality (called "sweet mode" in RealityCapture) the number of branches in each colony was counted. Furthermore, the average distance between branches was estimated by taking 10 measurements between randomly selected branches. The distance was measured between the axial polyps on Acropora colonies and the perceivable tips of the knobby branches on Pocillopora colonies. A rugosity index for each colony was then calculated as

$$Rugosity = \frac{N^2}{V * D} * e^{-SD/D}$$

Were N is the number of branches, V is volume in cm^3, D is the mean distance between branches and SD is the standard deviation of the mean distance. This formula was constructed to ensure that rugosity was decreased when a certain number of branches were situated on more space (volume) or had more space between them. It also penalises irregularity by adding the exponential decay term with *SD* such that colonies with irregular spacing appears less rugose as these are likely to have scattered open spaces within them and thus be less structurally dense.

2.2.2 Measuring colony environment

As the four survey sites displayed vastly different levels of reef connectivity, it was also relevant to investigate whether the surroundings of a coral colony affected the inhabiting fish population. The immediate area around the colony was therefore photographed for analysis. Four photographs were taken hovering above the sea floor at one meter height above the focal colony (A marked line-reel was used as height reference). Each photo was taken at a 90-degree angle to the previous one with the focal colony situated at the left-side edge of every photo. This method ensured that all four primary sides of the colony was recorded and that each photo had the focal colony as a reference point. The photos were taken directly down towards the substrate with the TG-7 set to the shortest focal length. They were subsequently analysed using ImageJ (Schneider *et al.* 2012). Each photo was comparted using a centred grid with 120000 $pixels^2$ $square^{-1}$ totalling 88 squares (See Figure 9). The number of squares featuring hard coral was counted (ignoring the focal colony). The number of squares featuring rugose structures not created by hard coral was counted as well. Coral and other rugose structures could coincide on the same squares. However, the number of uncovered squares was counted as the remaining squares that were devoid of any rugose structures. The total number of squares in each of those three substrate categories was added from all four photos and the full percentage of each in the surrounding environment was calculated for each colony.

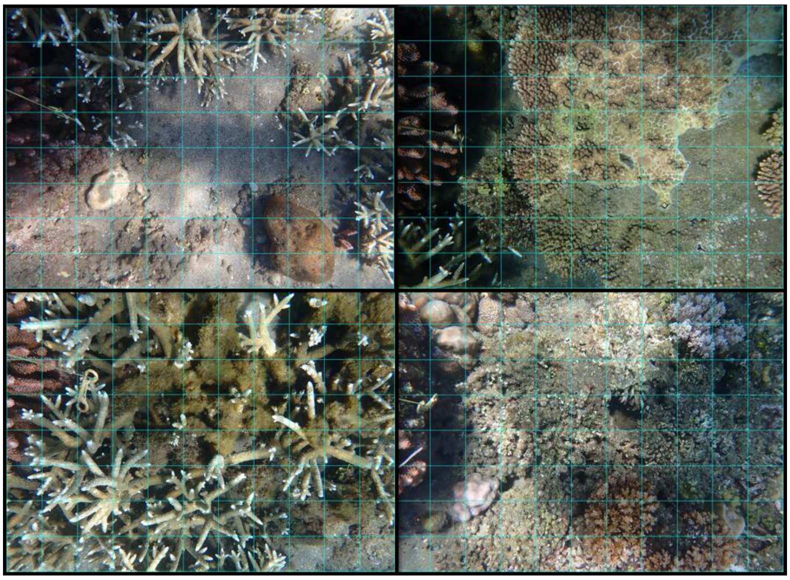

Figure 9: Example of colony environment analysis in ImageJ

2.2.3 Measuring fish abundance and diversity

Colonies were video-surveyed using a SCUBA-diver operated TG-7. One-minute videos were recorded of each colony. The number of videos recorded was determined by the apparent difficulty of estimating an accurate fish count of the colony, though they never exceeded three videos per colony. As the TG-7 battery depletes fast with prolonged video recording, it was necessary to use conservative footage requirements to maximise efficiency of each survey-dive. Typically, one video was recorded for colonies tagged as "small", two for "medium" and three for "large". This distinction was created since the size of the colony directly affected how difficult it was to record representative footage of the occurring fish assemblage. However, in cases where *N* appeared extraordinarily high on small or medium colonies the number of recorded videos were increased accordingly to decrease the chance of unrecorded individuals.

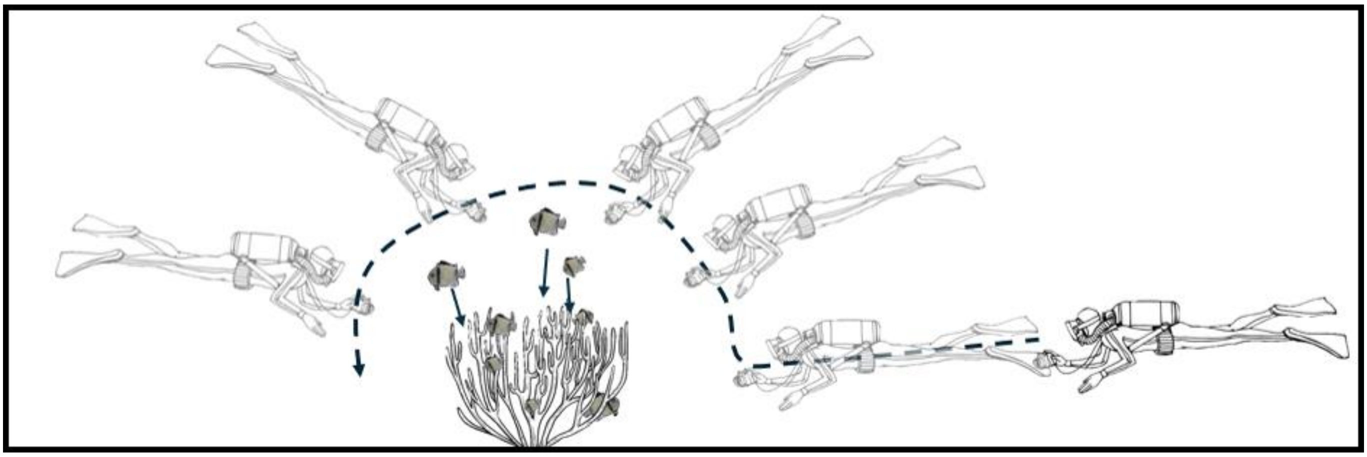

Figure 10: Movement pattern for recording video of fish assemblages on coral colonies: Created using images from Shutterstock (2025).

The time of day and water temperature was recorded at the onset of video-surveying each colony. Additionally, the depth of the colony was also recorded. All this data was collected from a Suunto Zoop Novo Dive computer (Suunto, 2025). The lunar phase at the time of the recording would retroactively be acquired from mDawod Inc. (2025). Each video was recorded with the shortest possible focal length on the TG-7 for a wide view. The movement pattern of the diver was consistent in each recording to ensure similar effect upon the behaviour of the fish. The presence and movements of the diver greatly affects fish behaviour. This was utilised to encourage refuging behaviour from the observed fish such that in areas with great pelagic fish activity it was possible to distinguish which individuals could be associated with the focal colony. Each recording was started at approximately five meters from the colony. At such distance the fish appeared unaffected by the diver and would venture further out from the colony making them more visible on the recording. The diver would continuously record whilst slowly approaching to a proximity no closer than to allow full camera view of the colony. The approach of the diver would typically encourage refuging behaviour in the fish concentrating them around the focal colony. The diver would then move in a circular pattern either going above or around the colony, such that the colony was recorded from all angles (See Figure 10). If several recordings were made of the same colony the diver would reset to a five-meter distance before the beginning of the next recording and approach the colony from a different angle. This recording pattern was used to the extent that the environment allowed it, however current or obstructions around the colony could enforce slight changes or adaptations to the method. After recordings had concluded the colony would be closely examined for cryptobenthic fish, which were counted *in situ*. To test the consistency of fish assemblages on the colonies secondary observations were made at a later date. Due to time constraints, it was not possible to do this on all coral colonies. Instead, the focus was to get repeated recordings on each coral colony category (size and genus) across all three NRs. A total of 52 colonies were recorded twice: 20 at Ma'init and 16 at both Maayong Tubig and Poblacion. The same recording method was used for secondary observations for consistency though not necessarily at the same time of day as the primary observations since field work had to be organized in cooperation with IMR's schedule.

Recordings were analysed in Capcut video editor (Bytedance, 2025), which allows for frame-by-frame video navigation. There are two main approaches often used to estimate fish counts from video-observations. N_{max} whereby N is estimated by the maximum number of individuals observed in a single frame of the full recording. And N_{mean} whereby N is estimated by averaging several N_{max}'s from shorter subdivisions of the full recording. Finally, a third, but more labour-intensive method is N_{total} where the N is estimated by identifying and counting each individual fish that appears in the whole recording (Stobart *et al.* 2015). As the purpose of this study was to investigate an environment that is actively used by fish as a refuge from predation the counting method had to take into consideration the likelihood that the whole fish population would not be in sight at any one time. Furthermore, there was the risk of recording transient fish who refuged momentarily (possibly due to the presence of the diver) but was otherwise not associated with the focal colony. Finally, the immediate water column surrounding the focal colony was often saturated with far more fish than ever observed refuging in the focal colony. For instance, if several branching colonies with their own associated assemblages was in near vicinity of the focal colony. This could cause overestimations of the actual associated *N*. To extrapolate as accurate a fish count as possible the videos were therefore analysed using a mix of the N_{mean} and N_{total} method. Each video was divided into four sections (approximately 15 seconds) and each individual was then counted in each of those four sections to yield a mean count of the whole video. If several recordings were made, the N_{mean}'s for each were averaged to obtain an overall mean count. To mitigate pelagic oversaturation, a fish was only counted if it was observed moving through, hiding under, or displaying refuging behaviour toward the focal colony at any point during the full recording. If the fish moved out of frame it was no longer considered present and would not be counted again unless it returned. This ensured fish could have a mean score of <1 which helped identify transient fish.

S was estimated by identifying fish to species level (when possible) using previous photo-data provided by IMR for comparison. Additionally, fish were divided into three size classes. To most accurately estimate fish size a stereo-video system (SVS) is needed (Harvey *et al.* 2002). However, this was not available for this study. Instead, the three size classes referred to the ontogenetic stage of the fish (1: Juvenile, 2: Intermediate, 3: Adult) and was estimated from the morphology of the fish and an approximation of their size (See Figure 11). The *N* of each fish type (species and size class) was counted and standard deviation calculated for the means.

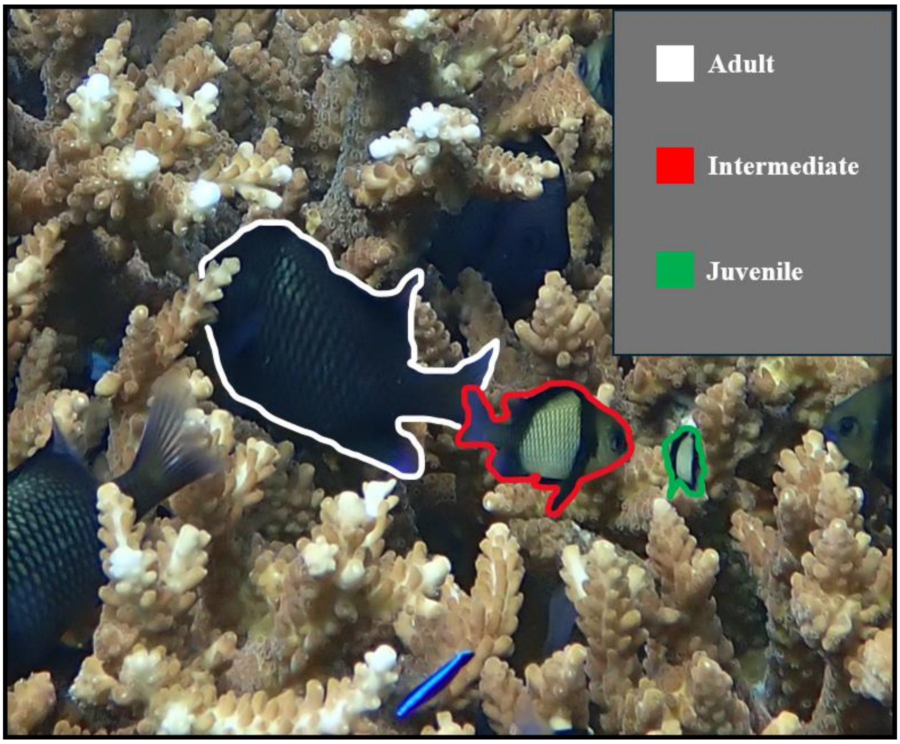

Figure 11: Example of size class estimations in Dascyllus reticulatus. This species grows darker as it matures and with more pronounced scales exemplifying how their ontogenetic stage can be approximated from their morphological appearance. Photo by A. Duekilde

2.3 Data management and statistical analysis

2.3.1 Data management

Roughly 500 gigabytes of video and image data were recorded and processed. All data were organised for further analysis in Microsoft office Excel version 2503 (Microsoft Corporation, 2025). Two overall data sheets were created. One organized in a wide format with one row per coral colony which summarised all metrics of that colony. And one organized in a long format which included the counts of all fish types on each coral colony. The data sheets were uploaded to Rstudio version 2024.12.1+563 "Kousa Dogwood" (Posit team, 2025) for statistical analysis using the "readxl" package (Wickham & Bryan, 2023). Data were mutated and organised further in Rstudio using packages "tidyverse", "tidyr" "lubridate", and "dplyr" (Grolemund & Wickham, 2011; Wickham *et al.* 2019; Wickham *et al.* 2023b; Wickham *et al*. 2024). Packages "igraph", "ggplot2", "ggpubr", "scales", "patchwork", "ggsignif", "gridExtra" and "RcolorBrewer" were used to visualise and plot data (Csárdi & Nepusz, 2006; Wickham, 2016; Auguie, 2017; Ahlmann-Eltze & Patil, 2021; Neuwirth, 2022; Kassambara, 2023; Wickham *et al.* 2023a; Pedersen, 2024; Csárdi *et al*. 2025).

2.3.2 Testing the effect of colony volume on fish assemblages

The two main response variables *S* and *N* were summarised as a collective count across all species and size classes but omitting any fish type with a mean count of <0.5 as these were considered transient and not reflective of actual colony inhabitants. The data was visualized to assess normality with a histogram and qq-plot (See Appendix 3) and tested with a Shapiro-Wilk test (P-values: $N = 1.2e^{-14}$; $S = 8.8e^{-11}$). Additionally, a linear model was fitted for each with the main relevant predictor variable being colony volume. This was done to test the data for heteroscedasticity with a Breusch-Pagan test (P-values: $N = 2.3e^{-4}$; $S = 0.2$) using the "lmtest" package (Zeileis & Hothorn, 2002). Colony volume was log10 transformed to improve model performance and stabilize variance since the raw values spanned nearly four orders of magnitude with a few outliers heavily right skewing the distribution. As assumptions for linear modelling was not met, generalised additive models (GAMs) were used instead with the package "mgcv" (Wood, 2017). GAMs allow for testing non-linear relationships by estimating the degrees of freedom (*edf*) and are thus better suited for evaluating complex ecological relationships. An initial visualisation of the relationship between the response variables and the various measured predictor variables had suggested that some relationships might not be linear (See Appendix 4). GAM can confirm this as *edf* close to 1 = linear relationship, whilst *edf* > 1 = higher complexity relationship.

To assess whether overdispersion was present in the data a GAM (family = Poisson) was fitted to each of the response variables using colony volume as the predictor variable. The Pearson residual sum of squares was calculated to quantify overdispersion. Both response variables exceeded the expected value of 1 under the Poisson assumption (Overdispersion statistic: $N = 6.8$; $S = 1.4$). Therefore, all subsequent GAMs were fitted using the Negative Binomial family, which accounts for over-dispersed data.

Several ecologically viable predictor variables that could be expected to influence fish assemblage had been recorded to create a multivariate model. Time variables (Date and Time of Day (ToD)) were grouped into categorical factors. Date was changed into weeks as a categorical factor to accommodate for the nature of field work typically grouping data from different sites on specific dates. ToD was divided into four categories: "Morning" (08:00 – 10:00), "Early midday" (10:00 – 12:30), "Late midday" (12:30 – 14:30) and "Afternoon" (14:30 – 17:30). This was done to reduce the number of levels and complexity in the model. Additionally, a correlation matrix was created between the numerical variables to assess multicollinearity as well as getting an initial impression of the effect of the predictor variables on the response variables (See Appendix 5). Multicollinearity can reduce the reliability of a model and add redundancy. Based on the correlation matrix it was decided to only include one of the three variables related to the surrounding colony environment. These were measured as percentages of the total surrounding area and were therefore highly correlated. The one included in the GAM was the measure of uncovered area as the other two variables could overlap and therefore infers less about the surrounding environmental structure on their own. Global GAMs were fitted for *N* and *S* with all remaining predictor variables included. A step-by-step Akaike information criterion (AIC) model analysis was performed to identify the most parsimonious model for each response variable and remove superfluous predictors to avoid overfitting. The final models were tested for optimization issues and model fit using the gam.check() function. Smooth plots were created to show the relationship structure of each continuous variable and to assess the nature of their influence on the response variables. To see if the colonies followed the typically assumed dynamics of SARs, and AARs (See section 1.3.1) they were fitted to a power law regression model:

$$y = a * x^b$$

Where *y* represents either *S* or *N*, *x* is colony volume, *a* is the baseline intercept and *b* is the scaling exponent. Finally, it was tested whether the effect of volumetric size differed between *Acropora* and *Pocillopora* colonies by inserting coral genus as an interaction term into the GAMs. Power law models were also fitted for each genus.

2.3.3 Testing the effect of colony rugosity

The AIC analysis previously mentioned revealed a difference in significance of colony rugosity's effect on *N* (not significant) and *S* (significant). Rugosity was completely removed as a predictor to create the most parsimonious GAM for volume vs *N*. This prompted further investigation into rugosity's influence especially since the measure of rugosity was calculated by a formula which included colony volume thus risking multicollinearity and the inclusion of one of these predictors overshadowing the effect of the other. A Pearson's product moment correlation test was performed between rugosity and volume (both raw and log10 transformed values). Additionally, a linear regression was fitted for *N* with volume and rugosity as independent predictor variables to calculate the variance inflation factor (VIF) between them using the "car" package (Fox & Weisberg, 2019). A GAM was fitted with rugosity as response variable and volume (as well as depth and surrounding uncovered area) as predictors. Furthermore, the GAM for *N* and *S* was refitted with rugosity included as a smooth term for both coral genera but omitting volume. Rugosity was also included as and interaction term with volume for both *N* and *S* to test how rugosity might influence the effect of volume on fish assemblages, and this relationship was plotted as layered smooth plots using the "itsadug" package (van Rij *et al*. 2022). Finally, a boxplot was made to gauge differences in colony volume and rugosity between *Acropora* and *Pocillopora* colonies and coral genus was added as an interaction term with rugosity in the GAM for volume. GAMs for *N* and *S* were fitted individually for *Acropora* and *Pocillopora* with rugosity interacting with volume. Layered smooth plots were made for visualisation.

2.3.4 Testing the effect of colony surroundings

Using the established GAMs for *N* and *S* the factors for surrounding colony environment was fitted as interaction terms to assess whether they affected the relationship between colony volume and fish assemblage. As previously mentioned, these were expressed as percentages of the whole surrounding area and was therefore highly correlated. Each factor was therefore fitted separately. Additionally, each factor was also introduced into the GAMs separately as smooth terms to gauge whether they had any direct effect on the colony fish assemblages. Smooth plots were made for each factor's effect on *N* and *S*.

2.3.5 Investigating other environmental variables

The aforementioned AIC step-by-step analysis had already revealed that several of the environmental variables had little predictive power on *N* and *S*. To summarize the relationships a GAM was fitted only including colony volume and each of the environmental variables (Colony depth, water temperature, lunar phase, time of day and week) as predictors for *N* and *S*. A table was made with the *edf*, AIC and p-values.

2.3.6 Investigating species interactions

A species index table was created. The Naïve Occupancy was calculated for each observed species across all sites combined and individually as well as for *Acropora* and *Pocillopora*. Naïve occupancy was calculated as

$$Na\ddot{i}ve\ Occupancy = \frac{n_o}{n_t}$$

Where n_o is the number of occupied colonies and n_t is the total number of colonies. Additionally, the mean size class and species-specific *N* as well as the *S* of associated colonies were also calculated with standard deviation. Finally, an inconsistency score was calculated for each species that had appeared on a colony with repeated observations. The standard deviation between repeated observations of the same species were calculated and standardized by dividing with the N_{mean} of those replicates — thus the score did not reflect the difference in direct fish counts but rather the proportional difference in the population of a species between two replicates. The average variation in *N* across all repeat colonies where a species had occurred was calculated and added to the species index.

The most abundant species (most individuals of the largest size class) on each colony were designated as the primary species. Since certain species are known to be territorial (Dunkley *et al.* 2023) the dominating presence of certain fishes could potentially influence the greater composition of a coral colonies fish assemblage. The primary species were therefore recorded, and the median *N* and *S* were plotted for their colonies as box plots and their frequency of dominated colonies as a bar plot. The GAM for *N* was fitted to include primary fish species as a categorical variable. Any primary fish species with less than three dominated colonies were considered rare occurrences and, for the purposes of reducing levels and model complexity, were grouped as "Rare species" in the

GAM. A post hoc pairwise comparison of the estimated marginal means was made to determine which primary species differed to each other in their relation to *N* and *S*. This was done using the "emmeans" package (Lenth, 2025) and was visualised with a pairwise plot of the estimated differences for visualisation.

Finally, it was investigated whether co-occurrence of any species could be expected by creating a species association network using the "vegan" package (Oksanen *et al*. 2025). The network was plotted and diagnostics on network structure, connectiveness and clustering were analysed.

2.3.7 Investigating fish size distribution

The proportionate *N* of each size class was calculated for each colony and expressed as a percentage of N_{total}. This was done to better compare distributions across colonies with highly varied *N*s. A Friedman test was performed to determine significant differences between the proportions of each size class. A post hoc pairwise Wilcoxon test was performed with the Bonferroni correction to counteract problems with multiple comparisons. This test helped determine which size classes differed. Non-parametric Friedman and Wilcoxon test were used due to the data being non-normal (percentages) and paired (a measure of each size class on the same colony). Wilcoxon tests were also performed to test for a difference in distribution in the three size classes between *Acropora* and *Pocillopora*. Finally, it was tested whether the distribution of fish sizes within the fish assemblage of a coral colony could be predicted by its volume or rugosity by fitting GAMs. First the three values for proportionate size distribution were summarised in a single weighted mean for colony fish size by multiplying the percentage *N* of each size class with their assigned categorical number (1, 2, 3). Similarly, Shannon's entropy index was calculated to gauge the evenness of the size classes using the following formula:

$$H' = \sum_{i=1}^{n} ((p_i + \in) * \log(p_i + \in))$$

Where *H'* is Shannon's entropy index (modified), p_i is the percentage of each size class and ∈ is an added pseudo count of 0.0001 to avoid zero values. Without this modification the formula could not distinguish between colonies were only two or one size class is represented. This formular yields higher entropy values for balanced colonies and lower for colonies dominated by fish in a single size class. The weighted size score and the entropy score was then fitted using the previously established GAM for *N* (family = Gaussian, since entropy and weighted scores are continuous).

They were harmonized with a step-by-step AIC analysis, ensuring that colony volume and rugosity remained as predictors. Smooth plots were made to visualise the relationship of the predictors on fish size distribution and evenness.

2.3.8 Testing fish community consistency

To gauge whether a single observation of a coral colony's fish community was representative Wilcoxon signed rank test was performed comparing both *N*, *S* and *N*% of all three size classes. Additionally, it was quantified how frequent a change in primary fish species occurred. Furthermore, Wilcoxon test was also performed to determine whether there was a difference in the changes between replicates in *Acropora* and *Pocillopora* colonies. Violin-plots were made to visually examine differences in the metrics and the colony specific change in *N* was plotted as well. Finally, a permutational test of variance (PERMANOVA) was performed using the "vegan" package (Oksanen *et al*. 2025). This was done on the long format species data to test if there was a deeper structural change in species composition between replicated observations. Bray–Curtis dissimilarities were calculated, and significance was assessed using 999 permutations. To account for potential non-independence among replicated observations from the same coral colony, permutations were stratified by colony identity.

2.3.9 Assessing differences between sites and comparing natural and artificial reefs

A key research question of this study was to compare and see if ecosystem trends on NRs were replicated on the AR at Sahara. All previously mentioned analyses were therefore made excluding the data from Sahara to ensure only natural trends were observed. Due to time constraints and the smaller scale of Sahara's reef there was a markedly lower amount of surveyed coral colonies (n = 14) compared to the three NRs ($n \approx 30$ per site). As a result, formal statistical comparisons involving the artificial reef were generally considered underpowered and thus not emphasized. It was instead elected to investigate qualitative comparisons with basic trends and models for visual assessments.

First a table was made with a summary of each site which was further divided into coral genera. This summary included the total *S* and *N* as well as the means colony^{-1} (including SD). It also detailed the percentage of observed colonies that were inhabited by fish and the most commonly observed species. Finally, Shannon's diversity index (*H'*), Simpson diversity index (*D*), and Pielou's evenness (*J'*) was also calculated using the "vegan" package (Oksanen *et al*. 2025) and included in the summary.

To assess whether the corals on ARs grew structurally different a box plot was made comparing colony volume and rugosity of *Acropora* and *Pocillopora* colonies respectively on each site. Additionally, "Site" was introduced as an interaction term with rugosity in the GAM that had previously been fitted to gauge the relationship between colony volume and rugosity. Similarly, "Site" was introduced as an interaction term in the GAM for colony volume vs *N* and *S* and finally in GAMs where it was interacting with the three surrounding environment variables fitted as fixed terms. Smooth plots were made for all these models. This was to investigate whether fish populations were interacting with coral colonies similarly on the AR as on the NRs and to gauge if the different environments would have a different impact.

Lastly, a PERMANOVA test was conducted, despite reservations about the statistical power of Sahara's fewer observations. This was done to provide a structured assessment of site differences in fish community composition, primarily to complement qualitative trends with statistical context and to visualize patterns via non-metric multidimensional scaling (NMDS) ordination. Bray–Curtis dissimilarities were calculated, and significance was assessed using 999 permutations. An ad hoc test for multivariate dispersion and difference in spread was also performed and a pairwise post hoc Tukey's honestly significant difference (HSD) test was used to compare differences between sites. A post hoc pairwise PERMANOVA was performed to identify sites with divergent species compositions. Additionally, a boxplot was made to assess inter-site differences in fish size composition. Finally, a Similarity Percentage (SIMPER) test was used to assess which fish types (species and size) mainly affected differences between sites. The aforementioned tests were made using the "vegan" and "pairwiseAdonis" packages in R (Martinez Arbizu, 2017; Oksanen *et al*. 2025).

3. Results

3.1 Interactions between coral colony morphology and fish assemblage

3.1.1 Colony volume

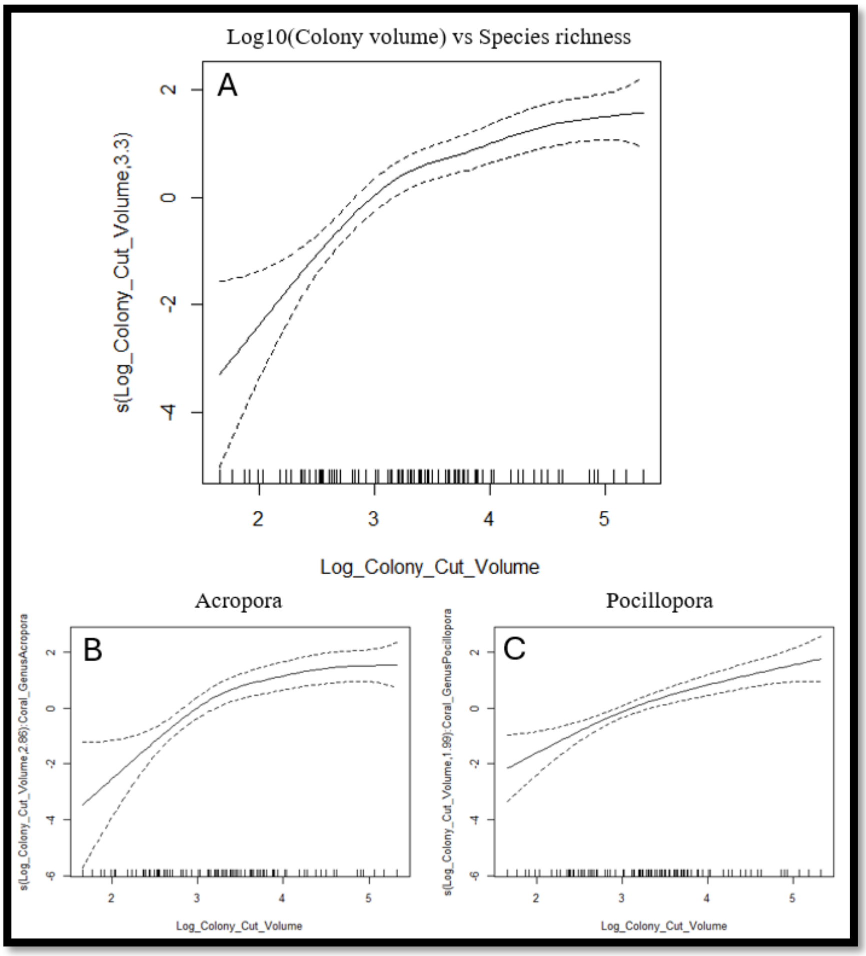

Figure 12: Smooth plots for the final GAM for colony volume vs *S*. **(A)**: All colonies combined. **(B & C)**: Separated by a coral genus interaction term with colony volume. X-axis shows the predictor variable. Y-axis shows the logarithmic partial effect of the predictor variable on the response variable. Solid line shows the smooth relationship estimate and dashed lines show the 95% confidence interval.

To achieve the highest level of parsimony the final GAM for volume vs *S* fitted after step-by-step AIC analysis included (aside from colony volume) rugosity, week factor, and coral genus as predictive variables (AIC = 278.5). The *edf* and p-value indicate that coral volume is significantly related to *S* in a non-linear manner when all colonies are grouped (p-value < $2e^{-16}$, *edf* = 3.3) (See Figure 12A). When introducing an interaction with coral genus (AIC =283.2) it is revealed that the relationship is significant for both, but closer to linear in *Pocillopora* (p-value = $1.8e^{-6}$, *edf* = 2.0) than in *Acropora* (p-value = $8.2e^{-7}$, *edf* = 2.9) (For full model calls and diagnostics see Appendix 6 & 7).

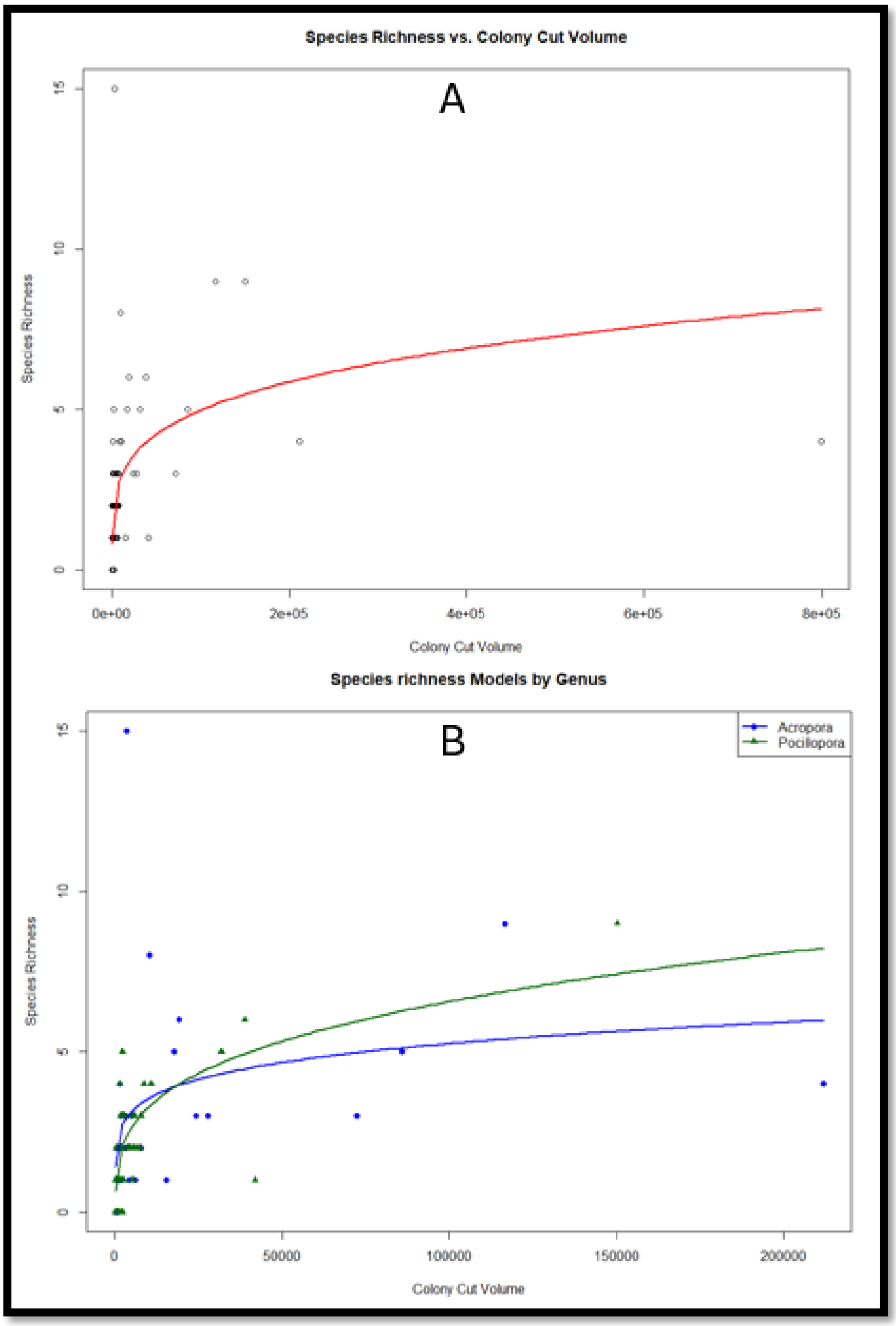

Figure 13: Power law regression plots of colony volume vs *S*. **(A)**: All colonies combined. **(B)**: Separated by coral genus. Green triangles and regression line indicate *Pocillopora* data, and blue dots and regression line indicate *Acropora*. Plotted with date from the error corrected data sheet

The relationship between colony volume and *S* was fitted to a power law regression. The model explained the relationship with a residual standard error (RSE) of 1.9 for all colonies combined and respectively 2.9 and 1.2 for *Acropora* and *Pocillopora* (For full model calls and diagnostics see Appendix 8 & 9). RSE indicates the typical deviation between the observed and expected values of the response variable (in this case *S*). The power law models for each were fitted as follows:

$S_{combined} = 0.20 * x^{0.295}$ (p-values: a = 0.01, b = 3.9e^-10^)

$$S_{combined} = 0.20 * x^{0.295} \quad (p\text{-values: } a = 0.01,\ b = 3.9e^{-10})$$

$$S_{Acropora} = 0.73 * x^{0.171} \quad (p\text{-values: } a = 0.24,\ b = 0.06)$$

$$S_{Pocillopora} = 0.20 * x^{0.301} \quad (p\text{-values: } a = 0.03,\ b = 1{,}4e^{-7})$$

Were *a* indicates the scaling factor at baseline intercept (practically colony volume = 1) and *b* is the scaling exponent (for base power law function see section 2.3.2). The models indicate that an increase in colony volume of one order of magnitude would result in *S* roughly doubling for the combined– and *Pocillopora*–model but only increase about 50% in *Acropora* corals. However, the coefficients' p-values exceeded the conventional threshold of significance (α = 0.05) in the *Acropora* model suggesting that this relationship is weak.

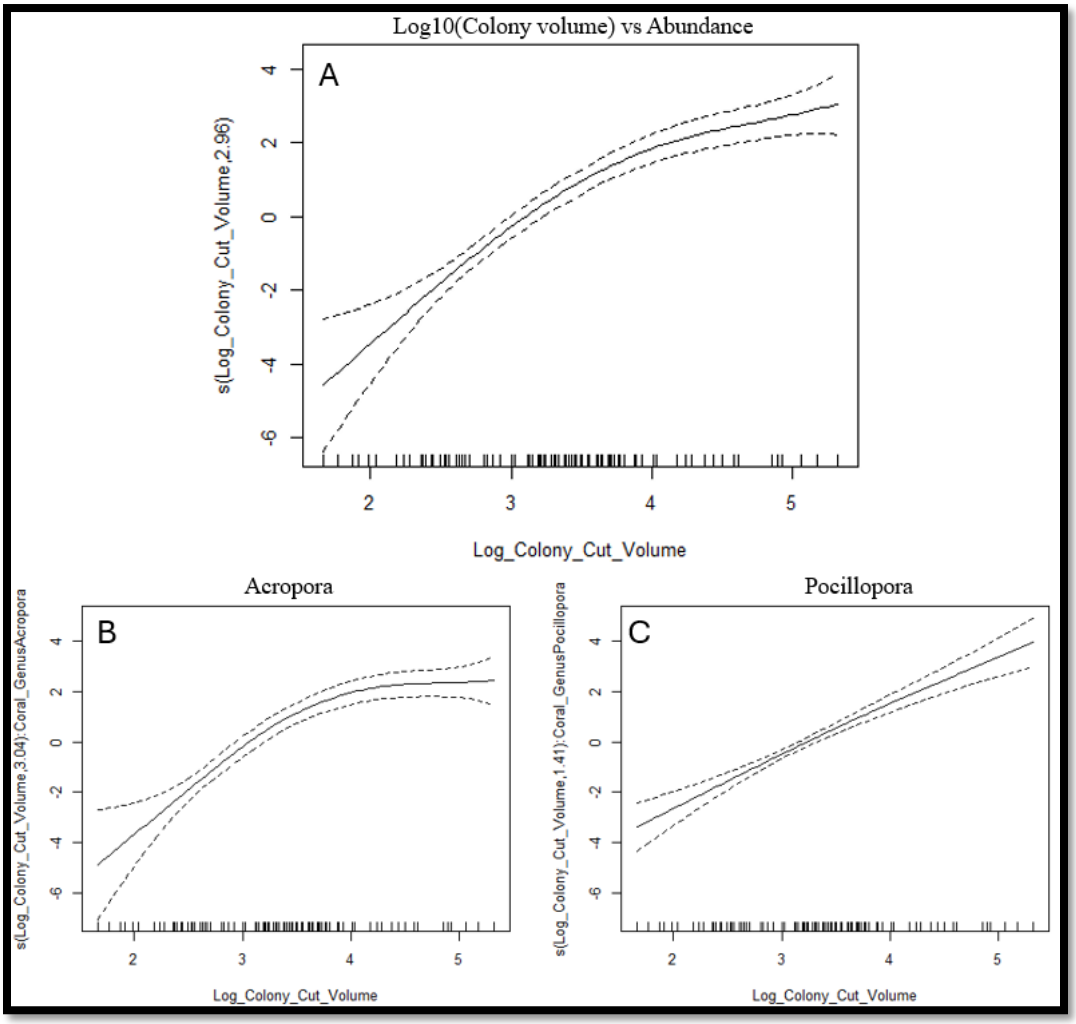

Figure 14: Smooth plots for the final GAM for colony volume vs *N*. **(A)**: All colonies combined. **(B & C)**: Separated by a coral genus interaction term with colony volume. X-axis shows the predictor variable. Y-axis shows the logarithmic partial effect of the predictor variable on the response variable. Solid line shows the smooth relationship estimate and dashed lines show the 95% confidence interval.

To achieve the highest level of parsimony the final GAM for volume vs *N* fitted after step-by-step AIC analysis included (aside from colony volume) colony depth, surrounding uncovered area percentage and water temperature as predictive variables (AIC = 434.8). The *edf* and p-value indicate that coral volume is significantly related to *N* in a non-linear manner when all colonies are grouped (p-value < $2e^{-16}$, *edf* = 3.0) (See Figure 14A). When introducing an interaction with coral genus (AIC =433.1) it is revealed that the relationship is significant for both, but closer to linear in *Pocillopora* (p-value = $2e^{-16}$, *edf* = 1.4) than in *Acropora* (p-value = $2e^{-16}$, *edf* = 3.0). (For full model calls and diagnostics see Appendix 10 & 11).

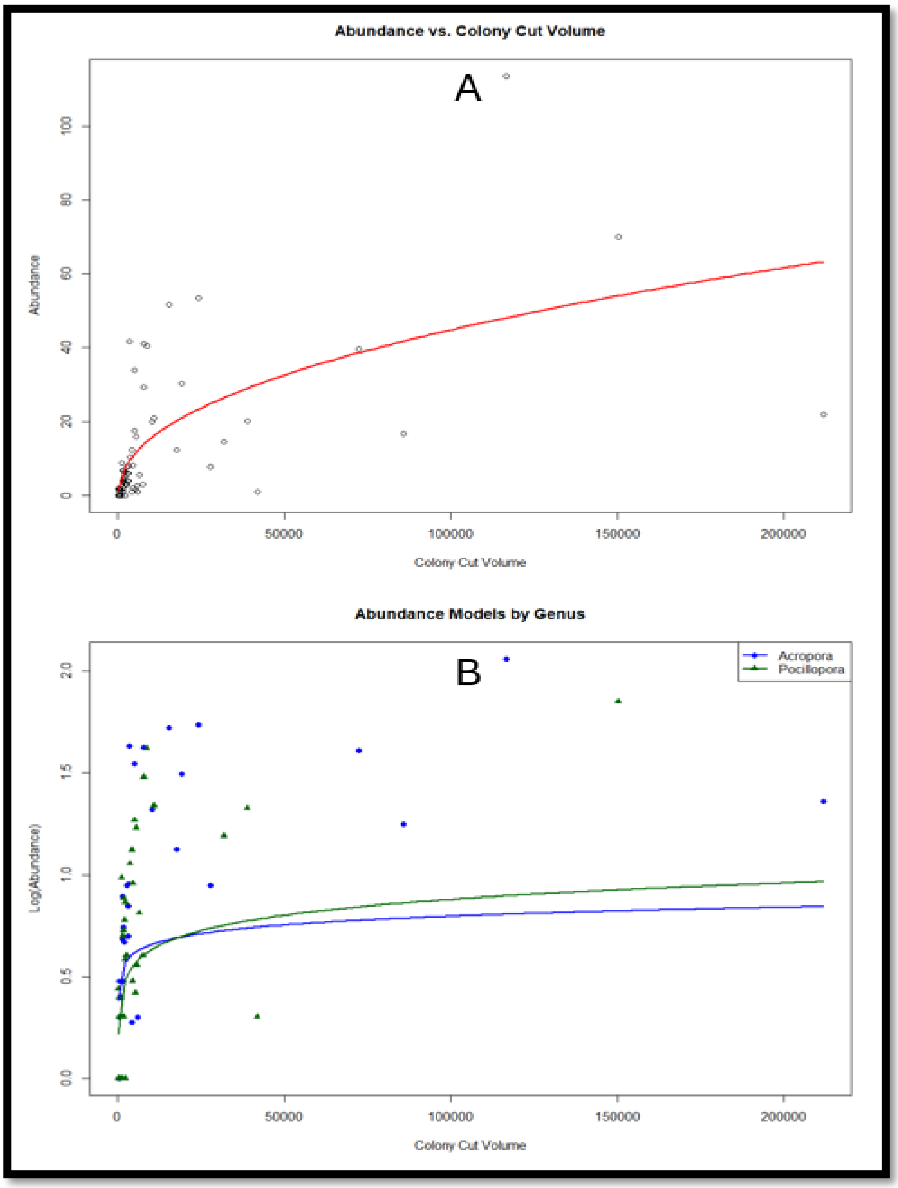

Figure 15: Power law regression plots of colony volume vs *N*. **(A)**: All colonies combined. **(B)**: Separated by coral genus. Y-axis has been log10 transformed for better visualization in B. Green triangles and regression line indicate *Pocillopora* data and blue dots and line indicate *Acropora*.

The relationship between colony volume and *N* was fitted to a power law regression. The model explained the relationship with a RSE of 13.0 for all colonies combined and respectively 20.0 and 9.2 for *Acropora* and *Pocillopora* (For full model calls and diagnostics see Appendix 12 & 13). The power law models for each were as follows:

$$N_{combined} = 0.22 * x^{0.460} \quad (p\text{-values: } a = 0.11,\ b = 4.26e^{-12})$$

$$N_{Acropora} = 0.75 * x^{0.356} \quad (p\text{-values: } a = 0.37,\ b = 1.8e^{-3})$$

$$N_{Pocillopora} = 0.05 * x^{0.593} \quad (p\text{-values: } a = 0.29,\ b = 6.1e^{-8})$$

The models indicate that an increase in colony volume of one order of magnitude would result in an expected increase of ≈ $N \times 3$ for the combined corals, ≈ $N \times 2$ in *Acropora* corals, and ≈ $N \times 4$ in *Pocillopora* corals. The p-value for coefficient *a* exceeds the conventional threshold of significance ($\alpha = 0.05$) in all three models however, which suggest that the estimated baseline intercept is unreliable.

3.1.2 Colony rugosity

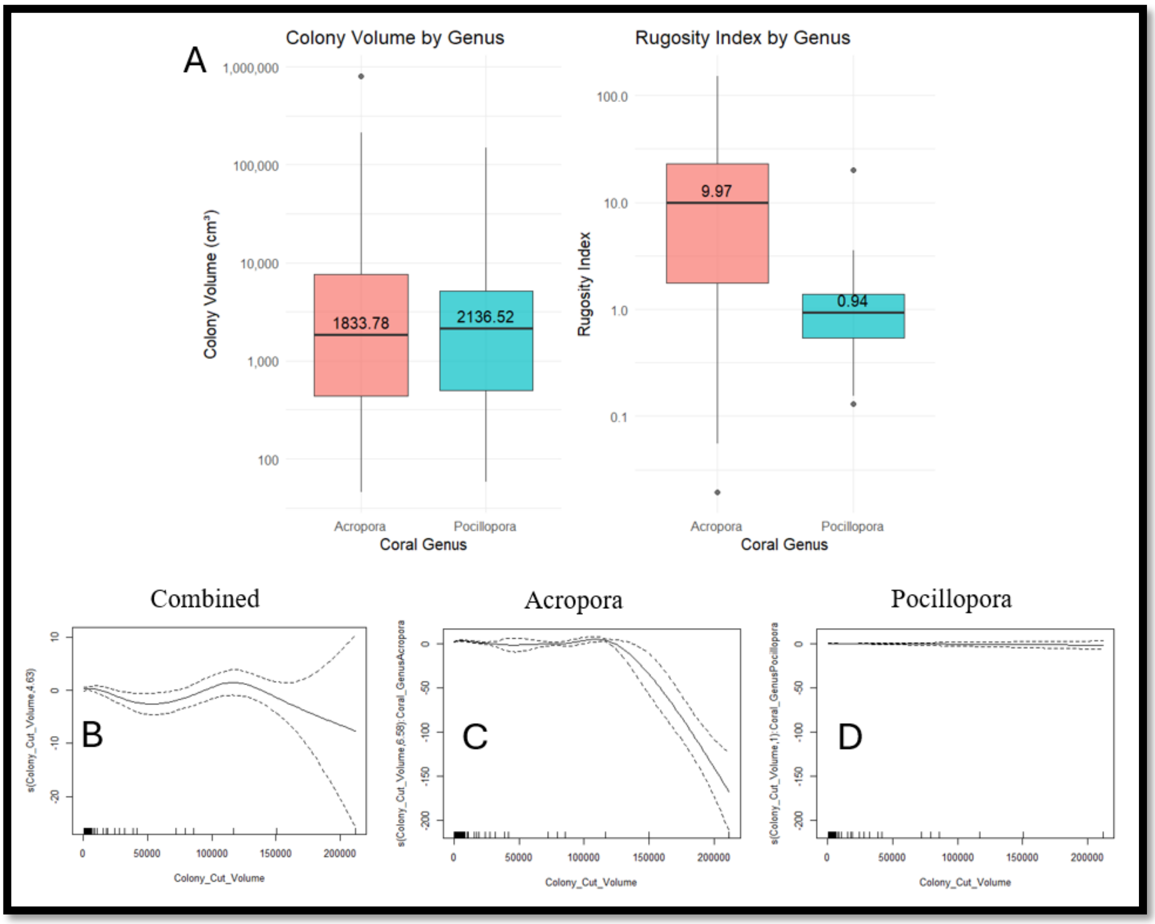

Figure 16: (A): Box plot of colony dimensions between coral genera with medians highlighted. Y-axis has been log10 transformed for better visualization. **(B – D)** Smooth plots of colony volume (raw values) vs rugosity. X-axis shows the predictor variable. Y-axis shows the logarithmic partial effect of the predictor variable on the response variable. Solid line shows the smooth relationship estimate and dashed lines show the 95% confidence interval.

The correlation test (≈ 0, p-value > 0.05) and the VIF (≈ 1) did not reveal any significant correlation between colony volume and rugosity (See Appendix 14 for full calls). Conversely, the GAM did find a significant nonlinear relationship between the two metrics (p-value = 0.03; *edf* = 4.6), however, when divided into the two genera, colony volume was not found to significantly predict an effect on rugosity for *Pocillopora* colonies (p-value = 0,4; *edf* = 1). The relationship for *Acropora* was significant and complex (p-value < $2e^{-16}$; *edf* = 6.6). The smooth plot (see figure 16C) reveals a nearly flat smooth around zero and then a sudden decrease. This suggests that volume only starts to have a negative effect on rugosity when *Acropora* corals reach a certain size.

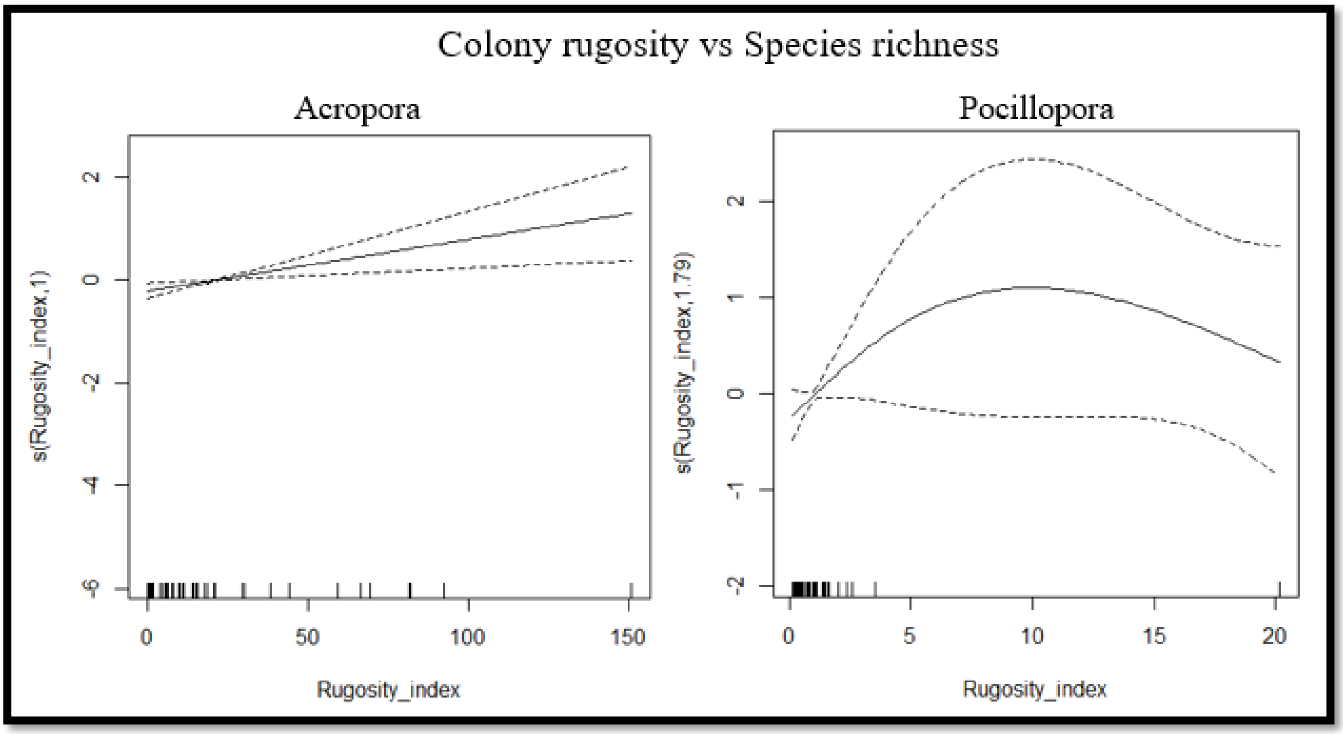

Figure 17: Smooth plots showing the direct effect of Rugosity on *S* without considering volume. X-axis shows the predictor variable. Y-axis shows the logarithmic partial effect of the predictor variable on the response variable. Solid line shows the smooth relationship estimate and dashed lines show the 95% confidence interval.

Rugosity was found to have a direct positive linear relationship with *S* on *Acropora* colonies (p-value = $5e^{-3}$, *edf* = 1) but not on *Pocillopora* colonies (p-value = 0.18, *edf* = 1.8). Higher rugosity appears to attract more species in *Acropora* colonies. While this relationship is not significant in *Pocillopora*, there is an indication of this same trend in the lower end of the data range where most data points are clustered. To further investigate this, it was attempted to log10-transform the x-axis for *Pocillopora*, which yielded a marginally significant positive relationship (See Appendix 15 for smooth plot and model summary with log10-tranformation).

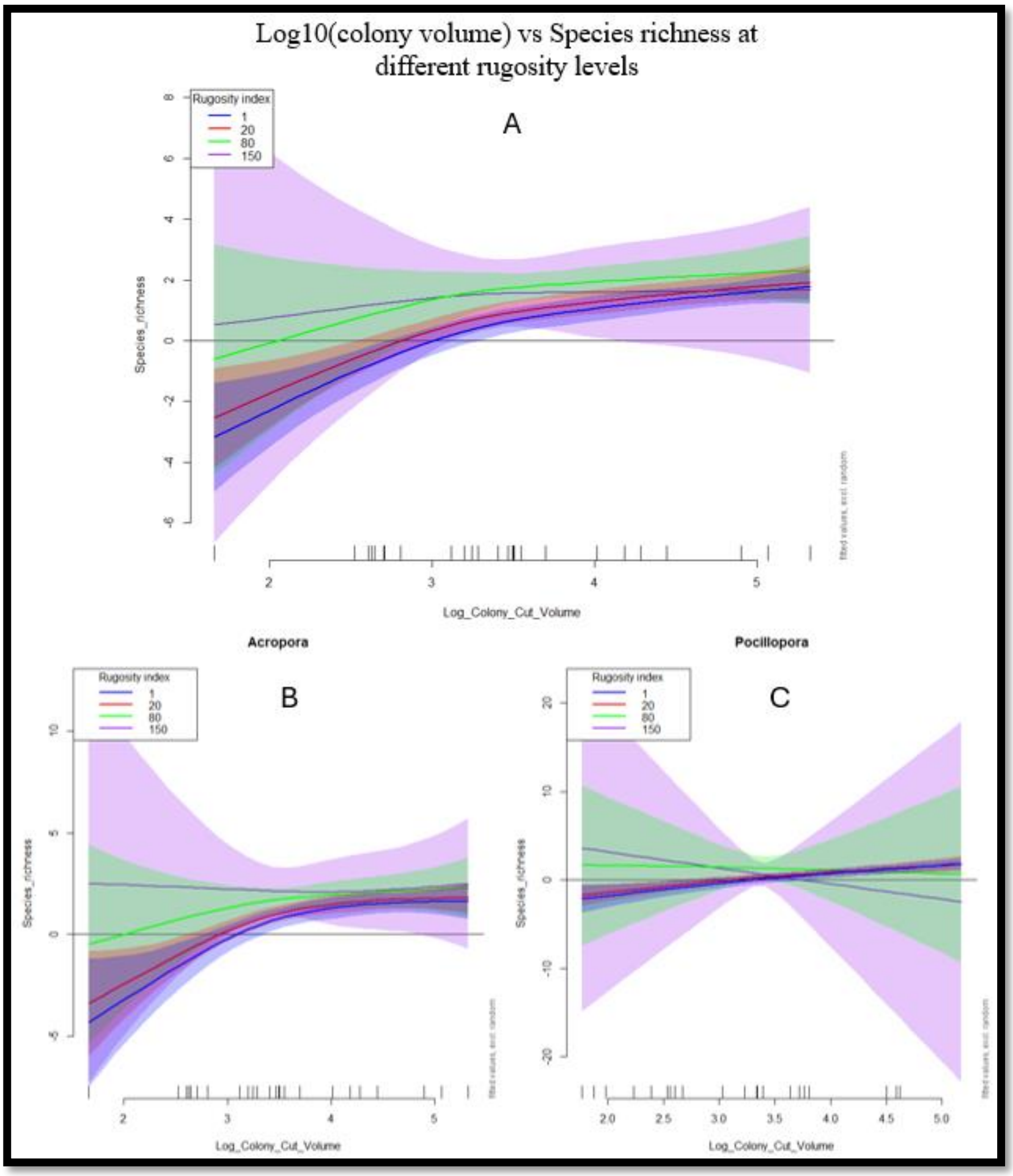

Figure 18: Layered smooth plots of volumes relationship with *S* at different rugosity levels. **(A)** all corals combined. **(B & C)** *Acropora* and *Pocillopora* respectively. Colour of smooth line and shaded area (95% confidence interval) aligns and represents rugosity level

Fitting a tensor interaction between colony volume and rugosity in the GAM for *S* was highly significant for each coral genus separate and combined (p-values: Combined $< 2e^{-16}$; *Acropora* $= 4.9e^{-6}$; *Pocillopora* $< 2e^{-16}$). This indicates that the rugosity of the coral colony significantly changes how many species can be expected to inhabit colonies of certain volumes. The layered smooth plots suggest that small colonies have much higher *S* at higher rugosities whilst the difference is less and the confidence interval greater in large colonies (See Figure 18). Generally higher rugosity levels also appear to cause wider confidence intervals. Including the tensor interaction slightly worsened model fit ($\Delta AIC = +2$).

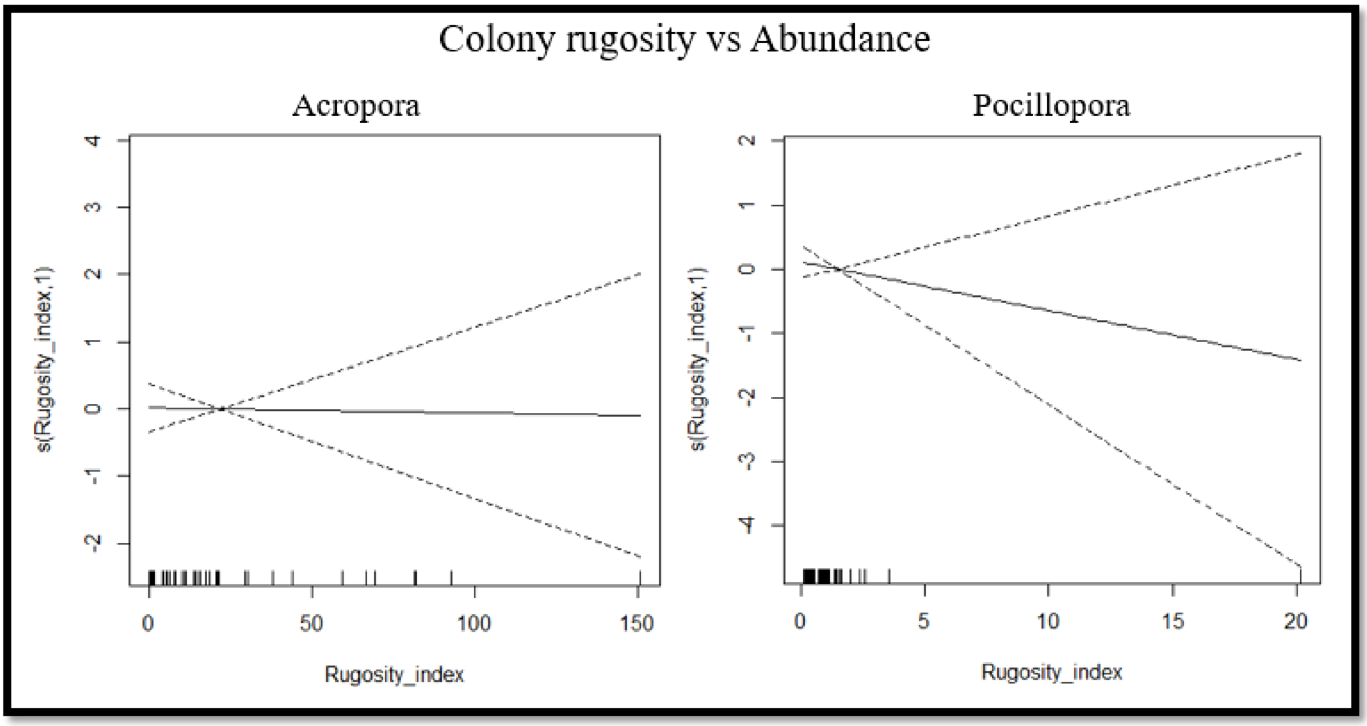

Figure 19: Smooth plots showing the direct effect of Rugosity on *N* without considering volume. X-axis shows the predictor variable. Y-axis shows the logarithmic partial effect of the predictor variable on the response variable. Solid line shows the smooth relationship estimate and dashed lines show the 95% confidence interval.

Rugosity was not found to have a direct relationship with *N* on either *Acropora* (p-value = 0.93; *edf* = 1) or on *Pocillopora* colonies (p-value = 0.38; *edf* = 1). Rugosity is therefore not a valuable predictor alone in estimating *N* on coral colonies. *Pocillopora* colonies does show a decreasing tendency suggesting that higher rugosity decreases *N* on these, however the uncertainty is very high. Log10-tranforming the X-axis yielded a marginally significant negative relationship (See Appendix 16 for smooth plot and model summary with log10-tranformation)

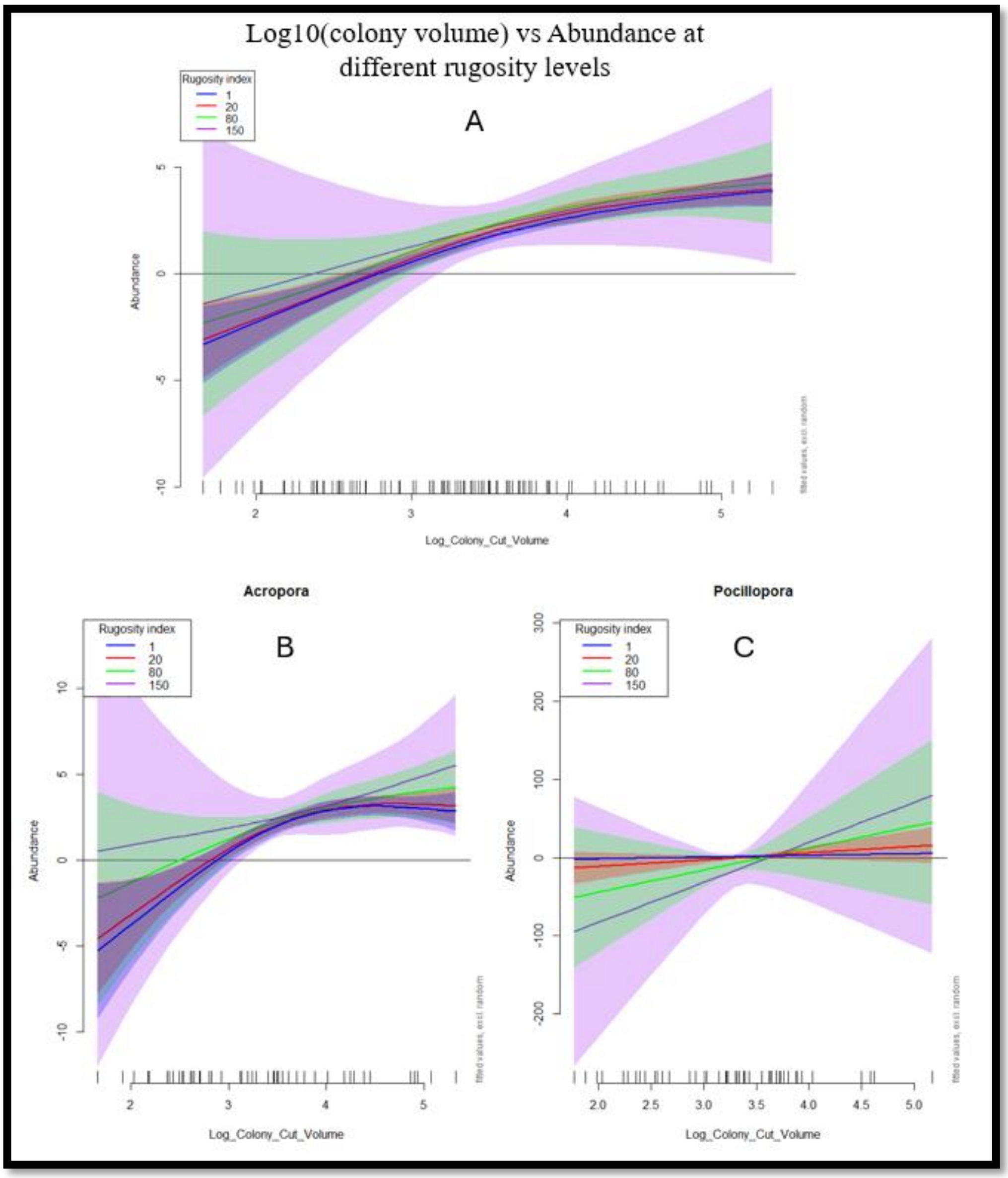

Figure 20: Layered smooth plots of volumes relationship with *N* at different rugosity levels. **(A)** all corals combined. **(B & C)** *Acropora* and *Pocillopora* respectively. Colour of smooth line and shaded area (95% confidence interval) aligns and represents rugosity level

Fitting a tensor interaction between colony volume and rugosity in the GAM for *N* was highly significant for each coral genus separate and combined (all p-values < $2e^{-16}$). This indicates that the rugosity of the coral colony significantly changes how many fish can be expected to inhabit colonies of certain volumes. The layered smooth plots suggest that small colonies have much higher *N* at higher rugosities whilst the difference is less and the confidence interval smallest in intermediate colonies. The difference in *N* gets wider again, as does the confidence interval, in larger colonies (See Figure 20). Generally higher rugosity levels also appear to cause wider confidence intervals. Including the tensor interaction worsened model fit (ΔAIC = +6.8).

3.2 Environmental effects on fish assemblage

3.2.1 Surrounding area effects

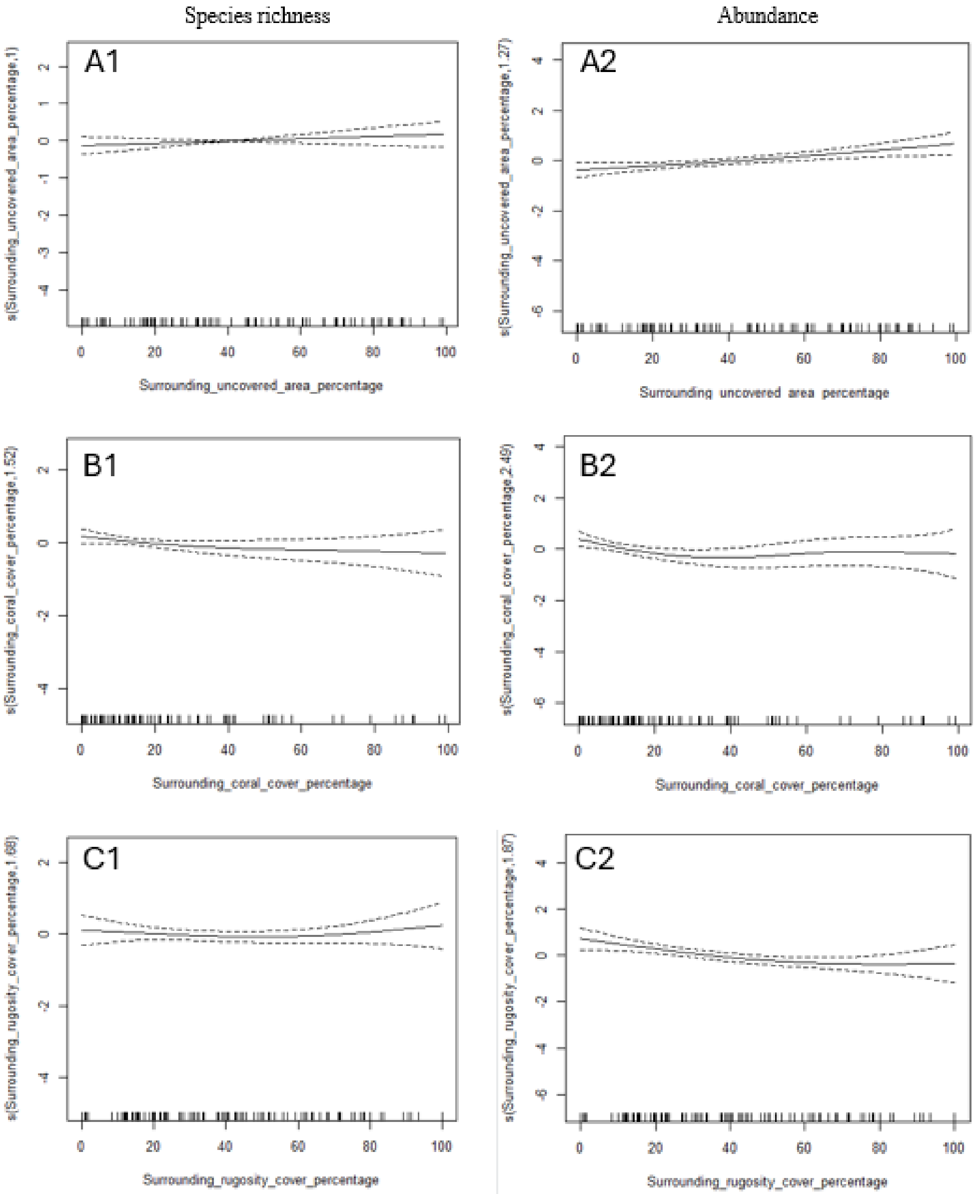

Figure 21: Smooth plots of the relationship between colony surroundings and *S* and *N*. **(A)**: shows uncovered area. **(B)**: shows coral cover. **(C)**: shows non-coral rugose structure cover. **(1)**: shows relationships with *S*. **(2)**: shows relationships with *N*. X-axis shows the predictor variable. Y-axis shows the logarithmic partial effect of the predictor variable on the response variable. Solid line shows the smooth relationship estimate and dashed lines show the 95% confidence interval.

None of the surrounding environment factors was directly related to changes in *S* (p-values: uncovered area = 0.31; coral cover = 0.22; rugose structures = 0.61), however, did seem to significantly predict *N* (p-values: uncovered area = $4.9e^{-3}$; coral cover = 0.06; rugose structures = $8.2e^{-3}$). The smooths suggest that higher levels of surrounding cover diminish the expected *N* on a coral colony. All surrounding area factors were highly significant when added as tensor interaction terms with colony volume both in predicting *N* and *S* (all p-values < $2e^{-16}$). The fish assemblage was therefore different in colonies of various volumetric sizes depending on their environment. While the p-values were similarly strong across models, the GAMs for *S* had the lowest AIC values ($S \approx 280$; $N \approx 437$), indicating a better overall fit. This suggests that the relationships between *S* and the environment have greater explanatory power than those for *N*. Including surrounding factors as either smooth terms or tensor interaction terms generally slightly worsened model fit compared to the original GAM for both *S* and *N* ($\Delta AIC \approx +2$).

3.2.2 Other environmental variables

Table 1: Summary of GAM relationships between environmental predictor variables and *N* and *S*

Response variable	Species richness				Abundance			
Predictor variables	*Numerical*				*Numerical*			
	Included in final model	EDF	p-value	AIC	Included in final model	EDF	p-value	AIC
Colony depth	No	3.2	0.09	284.4	Yes	1.5	1.7e^-4	445.6
Water temperature	No	1	0.11	286.5	Yes	1.8	0.39	458.9
Lunar phase	No	1.8	0.09	286.2	No	2.4	5.2e^-5	440.9
	Categorical				*Categorical*			
	Included in final model	levels	lowest p-value	AIC	Included in final model	levels	lowest p-value	AIC
Time of Day	No	4	Early midday = 0.13	289.8	No	4	Late midday = 0.35	459.7
Week	Yes	3	Week 43 = 0.02	285.1	No	3	Week 43 = 7.0e^-6	443.4

The remaining environmental variables generally appeared to be more significantly related to changes in *N* than *S*, however the GAMs for *S* appeared to be more accurate according to the AIC scores. Lunar phase was not included in the final model for *N* despite appearing significantly related in the simplified model. This suggests that, while a pattern may be present, its effect is likely overshadowed by confounding relationships with other variables. Conversely, water temperature was included. This indicates that water temperature may not be directly related to *N* but still improves model fit by accounting for underlying variability. Lastly while the temporal variables did not appear to have much effect on *S* and *N* overall, week 43 did deviate, at least marginally significantly, from the baseline comparison for either response variable. A plot of the medians revealed that both *S* and *N* was lower this week than the others (See Appendix 4).

3.3 Fish assemblage dynamics

3.3.1 Species metrics

Table 2: Part of the species index table featuring the six species with the highest overall naïve occupancy. All means are listed with SD's. For full table see Appendix 17

Species	Naïve Occupancy							Average			Inconsistency score
	Total	Maayong Tubig	Ma'init	Poblacion	Sahara	Acropora	Pocillopora	Size Class	Colony Abundance	Co-inhabting Species Richness	
Thalassoma lunare	0.44	0.36	0.44	0.40	0.71	0.46	0.43	1.61 ± 0.72	1.70 ± 1.81	6.18 ± 3.30	50.02
Dascyllus reticulatus	0.37	0.39	0.59	0.03	0.50	0.39	0.35	2.12 ± 0.77	28.50 ± 39.24	6.22 ± 3.66	21.01
Dascyllus trimaculatus	0.28	0.27	0.35	0.10	0.50	0.30	0.26	1.69 ± 0.64	2.98 ± 3.07	7.32 ± 3.50	23.37
Pseudocheilinus hexataenia	0.24	0.24	0.15	0.37	0.21	0.11	0.39	1.96 ± 0.63	1.01 ± 0.73	5.04 ± 2.85	64.30
Pomacentrus moluccensis	0.20	0.15	0.03	0.37	0.36	0.25	0.15	1.59 ± 0.66	5.74 ± 7.27	6.27 ± 3.45	38.15
Gobiodon spp.	0.14	0.06	0.09	0.27	0.14	0.19	0.07	1.29 ± NA	1.80 ± 1.90	4.00 ± 1.81	11.79

In all 111 coral colonies at least 59 different species of fish were observed with 56 identified to species level. These represented 16 different families (for full classification table see Appendix 18). All species were "least concern" on the IUCN red list, except *Plectroglyphidodon dickii* (Near threatened) (IUCN, 2025). More than half of all observed species belonged to either *Pomacentridae* (18) or *Labridae* (13). Species of these two families were also the most frequently observed with especially *Thalassoma lunare* and *Dascyllus reticulatus* appearing much more regularly on coral colonies than any other species. However, *D. reticulatus* have a much lower naïve occupancy at Poblacion compared to the other sites. *D. reticulatus* further stands out by being associated with the largest colony N_{mean} out of all species, though with a very large SD. This indicates the gregarious nature of *D. reticulatus. T. lunare* for comparison, have a much lower associated colony N_{mean}. Additionally, the inconsistency score for *T. lunare* is high, suggesting that they are solitary fish that change habitats frequently. All species not listed on table 2 (see Appendix 17) had a naïve occupancy of 0.1 or lower which suggests that most species in the branching coral microhabitat are rare. This included all four identified species of *Apogonidae*; the family with the third most observed species in the colonies. The generally low occurrence of most observed species may reflect the broader reef-wide species distribution or suggest that many coral reef species are only weakly associated with branching corals and thus appear only infrequently.

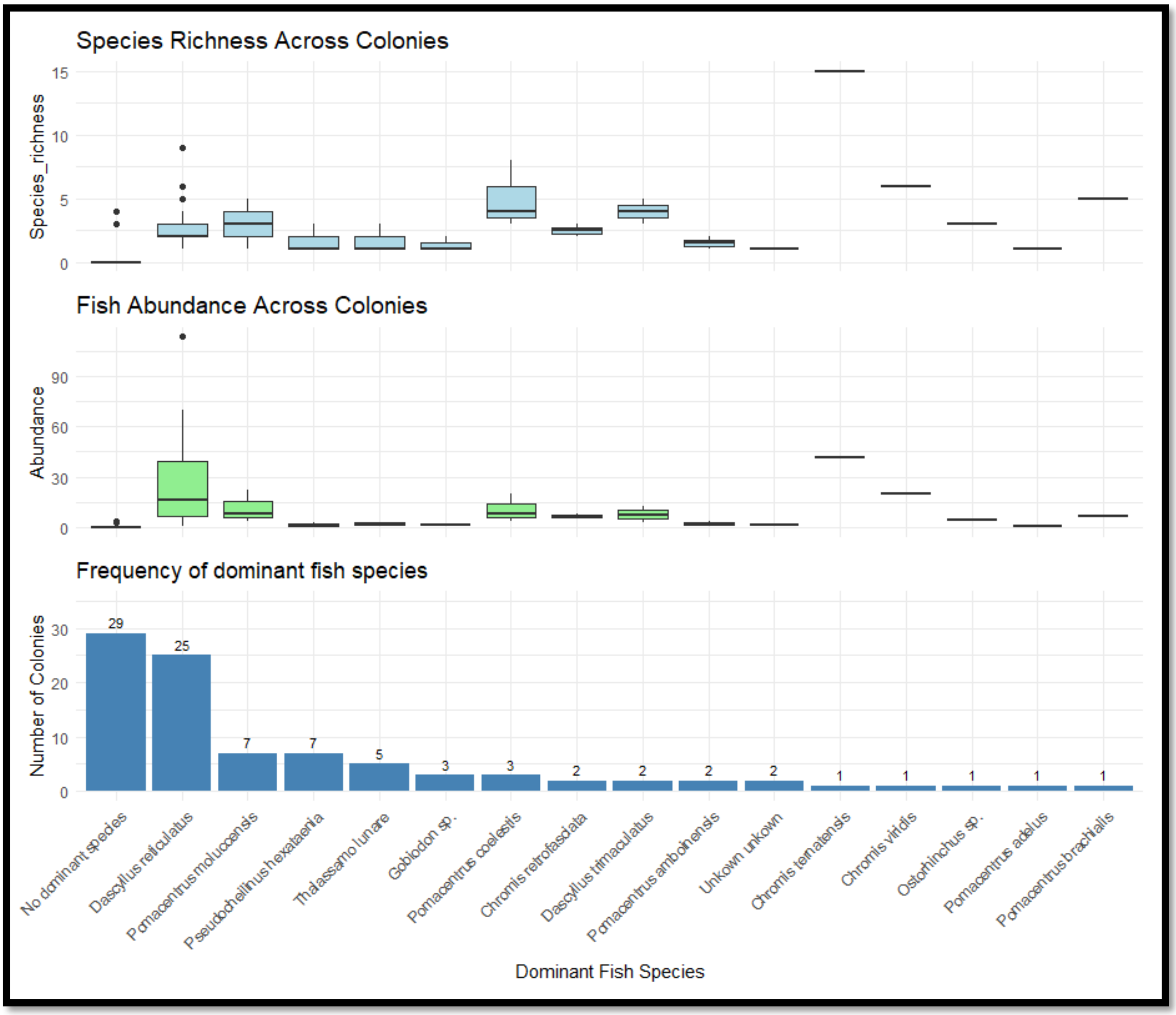

Figure 22: Plots showing frequency of colonies dominated by primary fish species as well as the median *S* and *N* on those colonies. For GAM analysis all species with a frequency of <3 dominated colonies were grouped together as "rare".

Colonies without any dominant fish occurred more frequently than any single species appeared dominant. Those colonies did however also include the 27 uninhabited colonies where *N* = 0. Adding primary fish species did improve the GAM for both *S* (ΔAIC = -5.1) and *N* (ΔAIC = -11.3) suggesting that accounting for the dominant species on a colony ads explanatory power in predicting the response variables. The only singular species to significantly be related to *N,* however, was *Pseudocheilinus hexataenia* (p-value = 2.4e^{-4}, est = -1.6). The grouped factor "Rare species" (p-value = 0,05, est = -0.5) as well as "No dominant species" (p-value = 1.1e^{-4}, est = -2.1) also indicated significant relationships. As the estimate for all these were negative, they are all associated with colonies with lower *N*s than expected. For *S* only *Pomacentrus coelestis* (p-value = 0.03, est = 0.7) and "Rare species" (p-value = 0.01, est = 0.5) showed significant relationships. The positive estimates indicates that *S* is higher than expected on their associated colonies. “No dominant species” were marginally significant according to the conventional threshold (p-value = 0.09, est = -0.8). This could be an indication that *S* was generally expected to be low on all colonies as the group that mainly represents uninhabited colonies did not have significantly less species. Post hoc pairwise comparisons (see Figure 23) exhibited significantly higher *N*s on coral colonies dominated by *D. reticulatus* compared to colonies with no dominant fish species (p = 5.6e^{-3}) and colonies dominated by *P. hexataenia* (p = 9.8e^{-3}). No significant pairwise differences were detected for *S* amongst any of the dominant fish species. Even though *P. coelestis* exceeded the expected reference group for *S* in the GAM, it did not differ markedly from other fish species in direct comparisons.

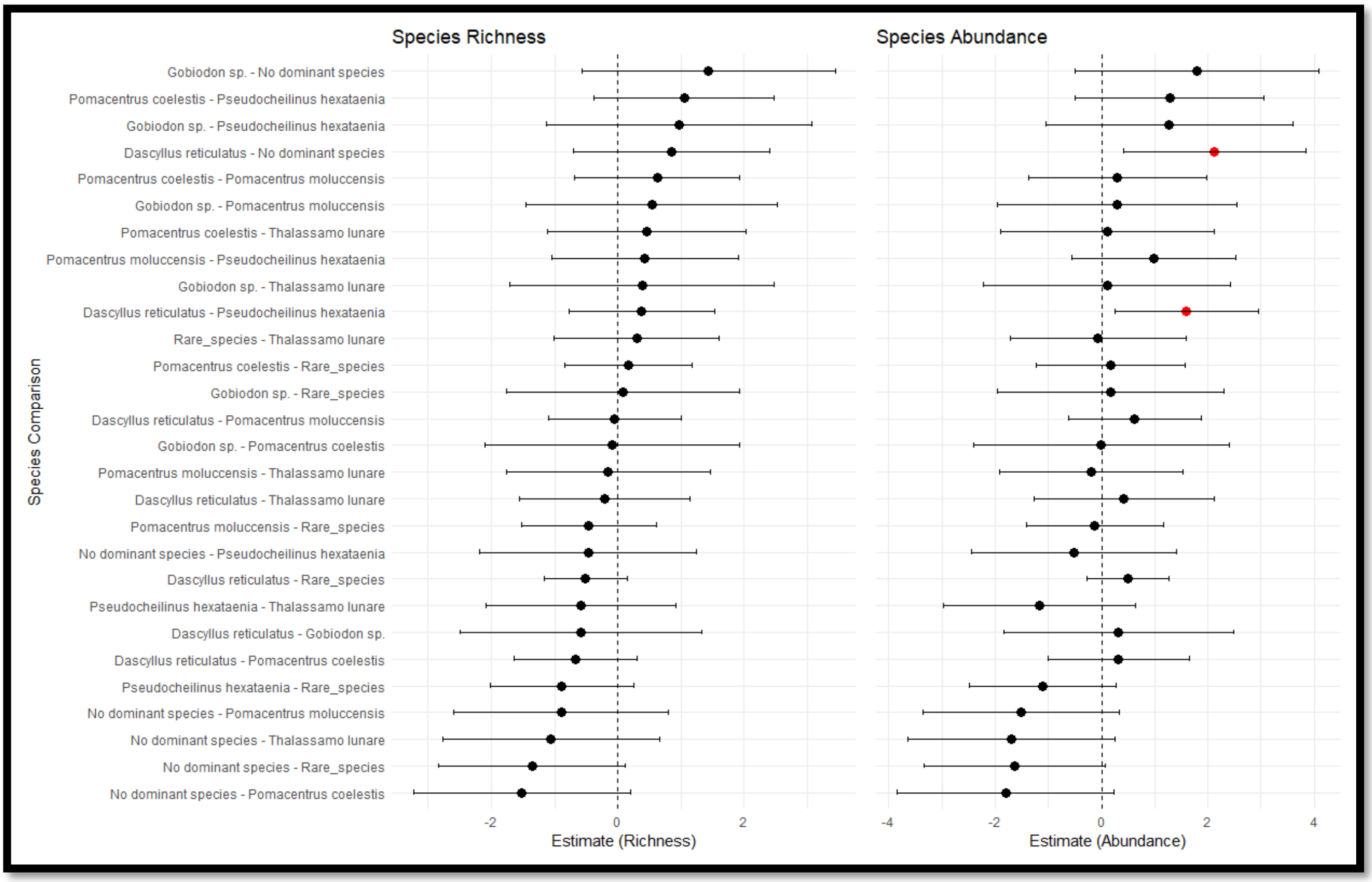

Figure 23: Plot of pairwise comparisons between dominant fish species. **(Left)** Comparisons of *S*. **(Right)** Comparisons of *N*. The points show the estimated difference. If significant (α = 0.05) the point is red. Points to the right indicate that the first listed species in the comparison has a higher *S/N* than the second. Horizontal lines show 95% confidence interval.

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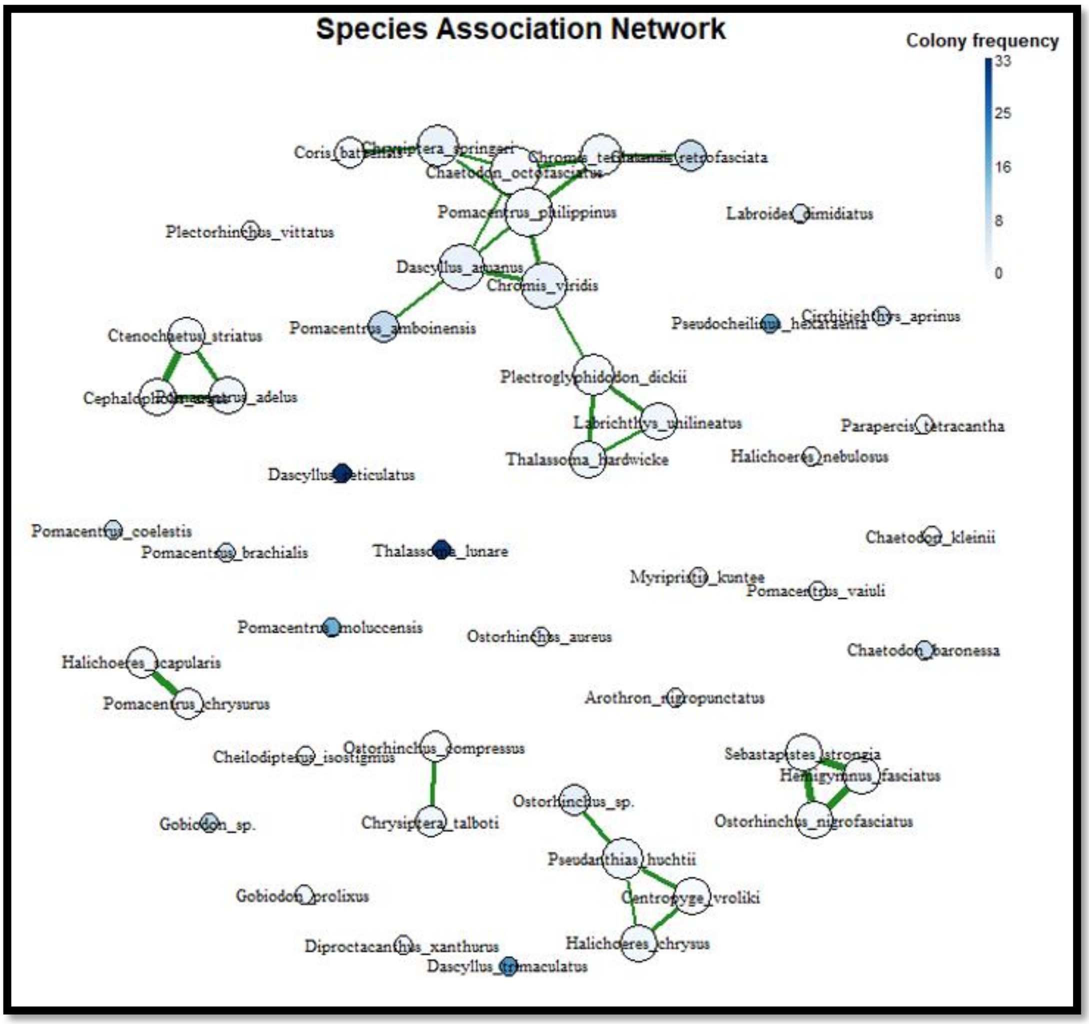

Figure 24: Species association network. Each node is a species. The size of the note shows the connectiveness of that species. The shade of the note shows the frequency. Lines are formed between significantly associated species (α = 0.05). Green lines are formed between species that positively correlate. Red lines are formed between species that negatively correlate.

The species association network has a low edge density (0.026) and a mean degree of 1.2 meaning that < 3% of all possible species-to-species associations exist and on average each species is connected to roughly one other species. There are 28 isolated components and the clusters that do exist have a small network diameter (longest ≈ 3). This all indicates that the species occur randomly with relation to each other and that they do not meaningfully associate. Furthermore, the species that are linked also generally have low frequency. That suggests that the detected associations may be artifacts of limited data and are thus not reliable. (For full species association statistics see Appendix 19).

3.3.2 Fish size metrics

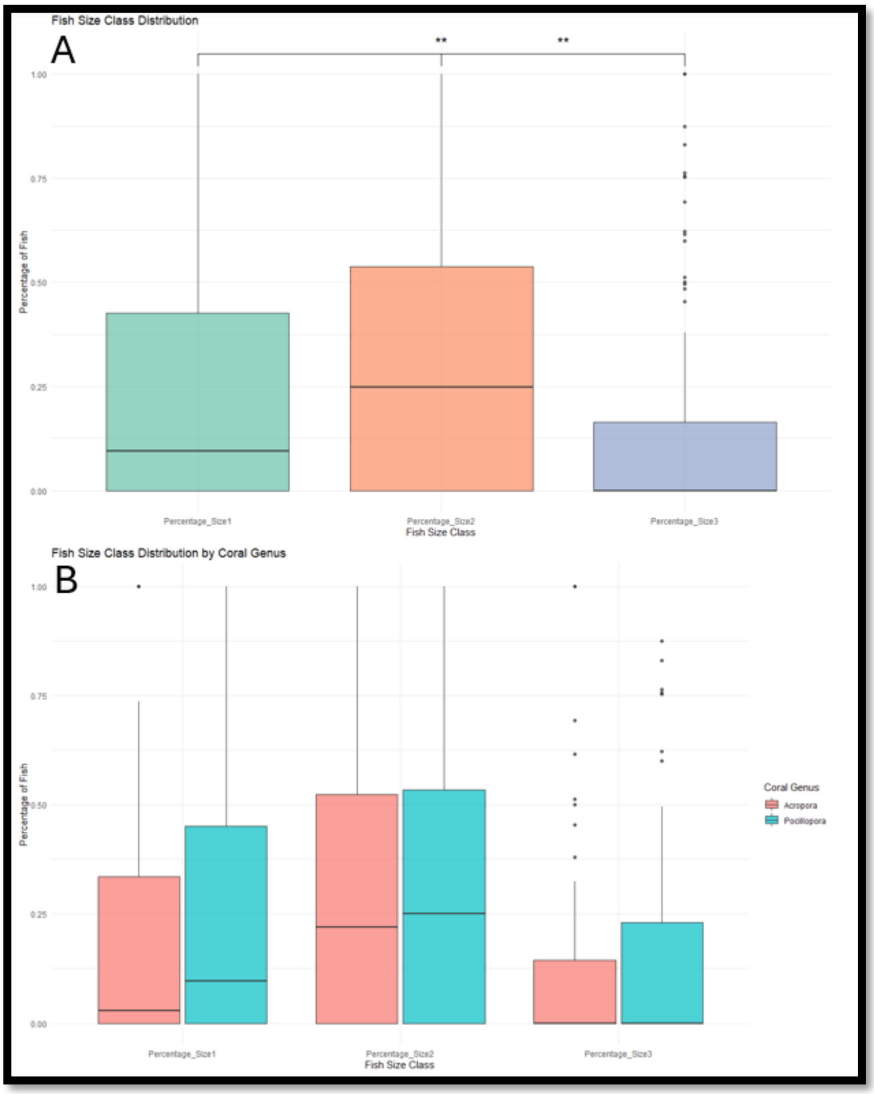

Figure 25: Boxplots showing the distribution of the different fish size classes. **(A)**: Median size distribution across all colonies combined with significance indicators showing meaningful differences in proportion. **(B)**: Median size distribution divided by coral genus. Red boxes are *Acropora*. Blue boxes are *Pocillopora*.

The Friedman test revealed that there is an uneven distribution across the three size classes (p-value = $3.5e^{-4}$) and closer inspection with a Wilcoxon test confirmed that the percentage of fish in size class 2 is significantly different compared to size class 3 (p-value = $8.4e^{-3}$) (See Figure 25A). No such difference was seen from either group when compared to size class 1, however it was marginally significant compared to size 3 (p-values: size1 vs size 2 = 0.8; size 1 vs size 3 = 0.09). This distribution appeared to be similar across both genera as no statistically significant differences were observed in any of the size classes (all p-values > 0.3). *Pocillopora* corals did appear to have more diversity, however, in their size class distribution as exemplified by the wider interquartile range in the boxplot (see figure 25B).

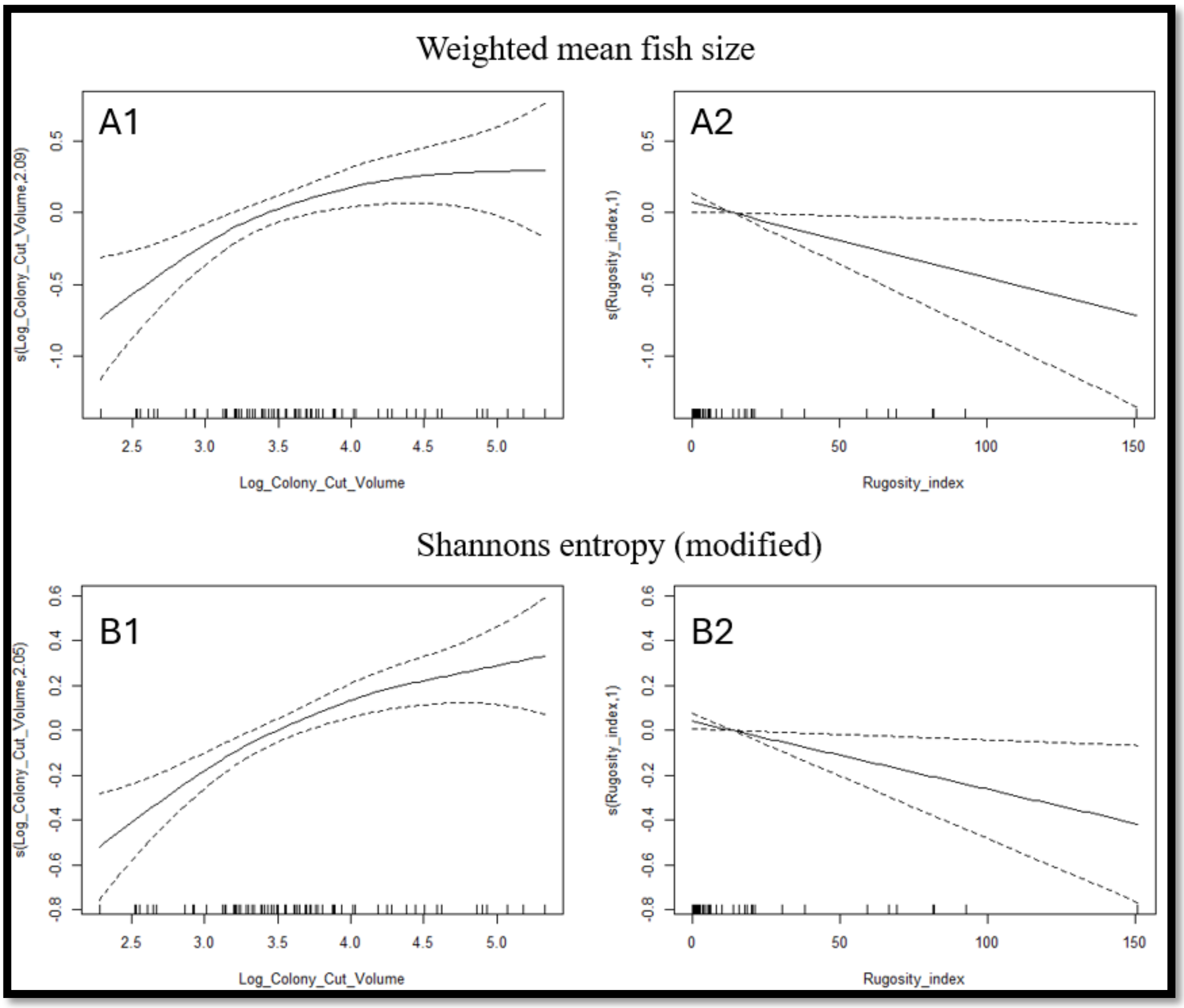

Figure 26: Smooth plots of the relationship between coral colony dimensions and the distribution of and evenness of fish sizes. **(A)**: show weighted fish score. **(B):** Show Shannon entropy (*H'*). **(1)**: is relationship with volume. **(2)**: is with rugosity. X-axis shows the predictor variable. Y-axis shows the logarithmic partial effect of the predictor variable on the response variable. Solid line shows the smooth relationship estimate and dashed lines show the 95% confidence interval.

Both coral colony volume and rugosity exhibited significant effects on fish size distribution and evenness, however very differently. Colony volume portrayed a strong nonlinear effect in both GAMS (Weighted fish size: p-value = $2.5e^{-3}$, *edf* = 2.1; *H'*: p-value = $1.9e^{-5}$, *edf* = 2.0). This suggests a saturating relationship between colony size and fish size or size class evenness, indicating that larger coral colonies support larger fish and more evenly size-distributed populations. But also, that the effect is less influential as colonies grow to higher volumes. Rugosity, conversely, exhibited significant negative linear effects in both GAMS (Weighted fish size: p-value = 0,03; *edf* = 1; *H'*: p-value = 0,02, *edf* = 1). Highly complex colonies therefore appear to be more exclusively inhabited by smaller fish.

3.3.3 Fish assemblage consistency

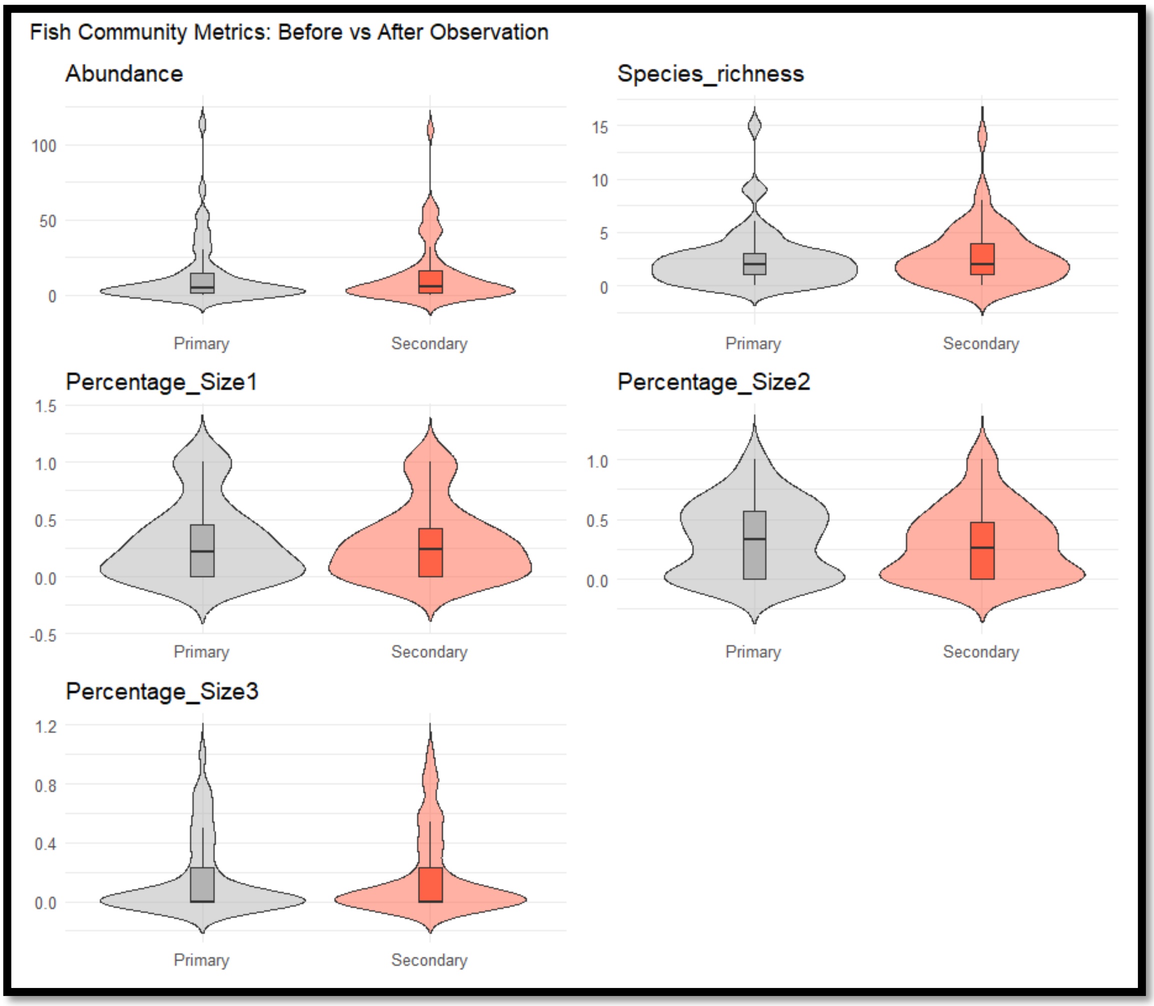

Figure 27: Violin plots comparing fish population metrics between primary and secondary observations. The shaded area shows data density at different values. Grey violins indicate primary observations. Orange violins indicate secondary observations.

Only 8 of the 52 repeatedly observed colonies had changed primary fish species between replicated observations (See Appendix 20 for full overview). The Wilcoxon signed rank test did not detect any significant differences between primary and secondary observations with respect to *S* or size distribution. However, *N* was found to change significantly between observations (p-value = 0.02). The general composition of a colonies fish assemblage therefore appears consistent; however, individuals may be transient thereby changing the *N* without changing *S* (if several individuals of the same species co-inhabit the colony). Changes appeared to generally result in both increases and decreases of *N* (see Figure 28). No significant differences were observed when comparing the change scores between coral genera, indicating that the change in *N* is happening in both *Acropora* and *Pocillopora* (For full test calls see Appendix 21). Conversely, the more detailed PERMANOVA test did not detect any differences in fish community composition between replicates of the same colony and additionally had very little effect size (p-value = 0.8; $R^2 = 3.1e^{-3}$) suggesting that the grouping factor (e.g. replicates) is not meaningfully explaining differences. This further supports that while the overall *N* might fluctuate the general composition of a coral colony's fish assemblage is consistent.

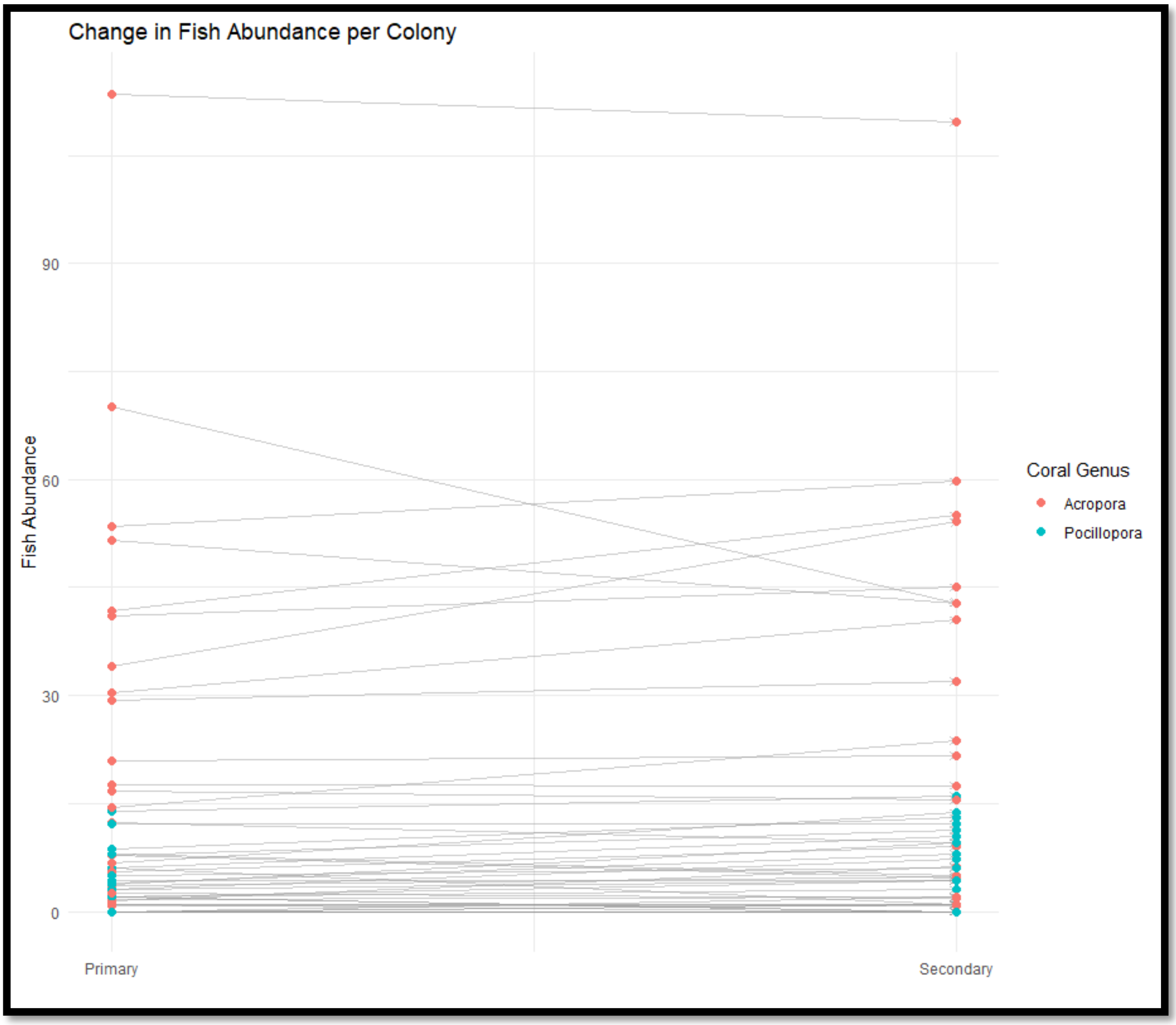

Figure 28: Line plot showing the difference in *N* between primary and secondary observation on all 52 repeated colonies. Red is *Acropora*, blue is *Pocillopora*.

3.4 Natural and Artificial reef site comparisons

3.4.1 Comparisons of site metrics

Table 3: Site summary table. *H'* stands for Shannon's diversity index. *D* stands for Simpsons diversity index. *J'* stands for Pielou's evenness

Site	Coral Genus	% Inhabited	Species richness	Mean Colony Richness	Total Abundance	Mean Colony Abundance	Most Common Fish Species	H'	D	J'
Ma'init	Acropora	61.11	15	1.33 ± 1.46	272	15.12 ± 21.92	Dascyllus reticulatus	0.56	0.36	0.34
	Pocillopora	87.50	20	2.56 ± 2.16	224	14.01 ± 19.11	Dascyllus reticulatus	0.75	0.45	0.42
	Total	73.53	24	1.91 ± 1.9	496	14.6 ± 20.34	Dascyllus reticulatus	0.66	0.4	0.39
Poblacion	Acropora	86.67	28	2.73 ± 3.77	116	7.74 ± 11.17	Pomacentrus moluccensis	0.93	0.53	0.56
	Pocillopora	66.67	11	1.07 ± 0.96	23	1.51 ± 1.58	Pseudocheilinus hexataenia	0.59	0.49	0.47
	Total	83.33	32	1.9 ± 2.83	139	4.63 ± 8.46	Pomacentrus moluccensis	0.78	0.5	0.52
Maayong Tubig	Acropora	70.59	27	2.59 ± 2.92	237	13.92 ± 27.91	Dascyllus reticulatus	0.75	0.39	0.42
	Pocillopora	75.00	17	2.19 ± 1.91	92	5.72 ± 5.74	Dascyllus reticulatus	0.8	0.49	0.49
	Total	72.73	36	2.39 ± 2.45	328	9.95 ± 20.55	Dascyllus reticulatus	0.77	0.44	0.46
Sahara	Acropora	85.71	10	3 ± 1.91	114	16.29 ± 13.04	Dascyllus reticulatus	0.79	0.43	0.49
	Pocillopora	85.71	9	2 ± 1.53	48	6.86 ± 8.58	Dascyllus reticulatus	0.59	0.42	0.42
	Total	85.71	11	2.5 ± 1.74	162	11.57 ± 11.68	Dascyllus reticulatus	0.69	0.43	0.46
Combined	Acropora	73.68	47	2.28 ± 2.73	739	12.96 ± 20.7	Dascyllus reticulatus	0.76	0.43	0.45
	Pocillopora	77.78	32	1.96 ± 1.79	386	7.16 ± 12.06	Dascyllus reticulatus	0.68	0.45	0.45
	Total	75.68	59	2.13 ± 2.32	1125	10.14 ± 17.22	Dascyllus reticulatus	0.8	0.69	0.58

D. reticulatus appears to be a dominant species in both *Acropora* and *Pocillopora* colonies across all sites except Poblacion. Poblacion additionally stands out by having both the lowest N_{total} and N_{mean}. However, it is the site with the second highest S_{total} and the second fewest uninhabited colonies. Conversely Ma'init has the highest N_{total} and N_{mean} but the lowest S_{total} of the three natural reefs. This indicates that the two reefs are quite different in their species composition with Ma'init having a few very common and numerous species, and Poblacion having more uncommon and less gregarious species. This is also suggested by the diversity indices which are all highest at Poblacion and lowest at Ma'init. Maayong tubig is in-between the other two sites in terms of diversity and mainly stands out by having the lowest percentage of inhabited colonies, yet the highest S_{total}, suggesting more species co-inhabit the colonies. Despite being an AR Sahara does not distinguish itself from the other sites in any values except having the highest percentage of inhabited colonies and the lowest S_{total} which might be artefacts of the lower total number of observed colonies. It is however noteworthy that despite fewer observations Sahara still has a higher N_{total} than Poblacion, which suggests that the AR is successful in attracting abundant fish communities. Finally, it is evident that *Acropora* corals support the larger and more diverse fish assemblages. Only at Ma'init does *Pocillopora* have a higher S_{total} than *Acropora*.

Figure 29: Box plot of colony dimensions between coral genera at each site with medians highlighted. Y-axis has been log10 transformed for better visualization. Red boxes are *Acropora*. Blue boxes are *Pocillopora*.

Acropora colonies were consistently more rugose than *Pocillopora* colonies at all sites despite them having equal median volumetric sizes. Sahara did have lower rugosity medians than any other site especially in *Pocillopora* colonies. Meanwhile, it was also the site with the highest median volume for *Pocillopora*. This does allude to *Pocillopora* colonies growing structurally differently than generally seen on the NRs. Maayong tubig also stood out by having the largest difference in volume medians between coral genera. It was additionally the only site with *Pocillopora* colonies being the largest. Maayong tubig also had a much lower median for *Acropora* rugosity compared to the other NRs and was more similar to Sahara. *Acropora* colonies therefore appeared to grow both smaller and less rugose at Maayong tubig compared to the other sites.

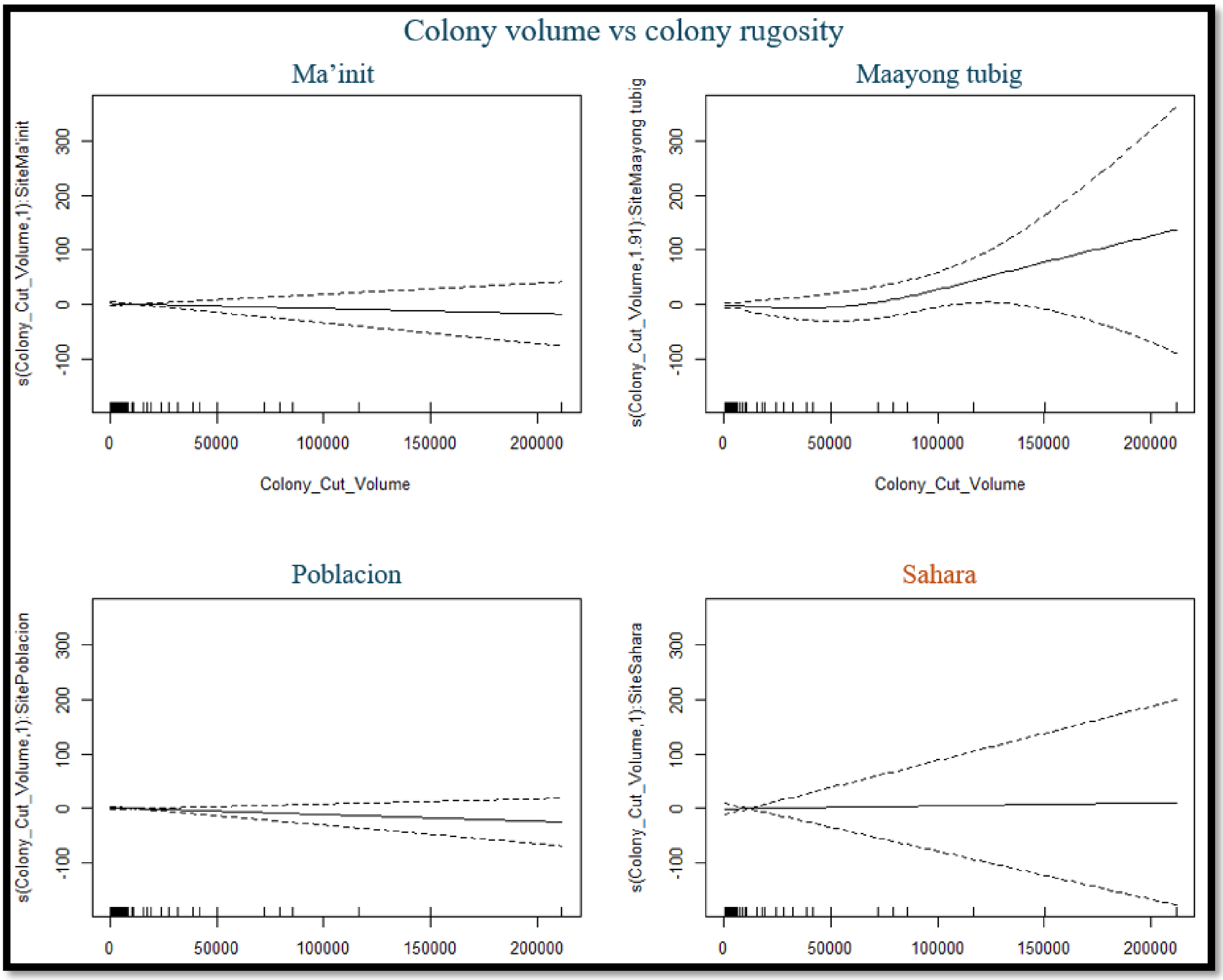

Figure 30: Smooth plots of the effect of colony volume (raw values) on colony rugosity at each site. X-axis shows the predictor variable. Y-axis shows the logarithmic partial effect of the predictor variable on the response variable. Solid line shows the smooth relationship estimate and dashed lines show the 95% confidence interval.

In none of the four sites were volume found to significantly affect rugosity at conventional threshold level, however Maayong tubig was borderline (p-value = 0.12; *edf* = 1.91). The other sites showed no indication of a relationship (p-value > 0.25; *edf* = 1). Sahara exhibits a wide confidence interval which indicates a lot of uncertainty in the estimation. The smooth plots suggest an expected increase in rugosity in larger colonies at Maayong tubig, however, also with high uncertainty.

3.4.2 Comparisons of ecological trends

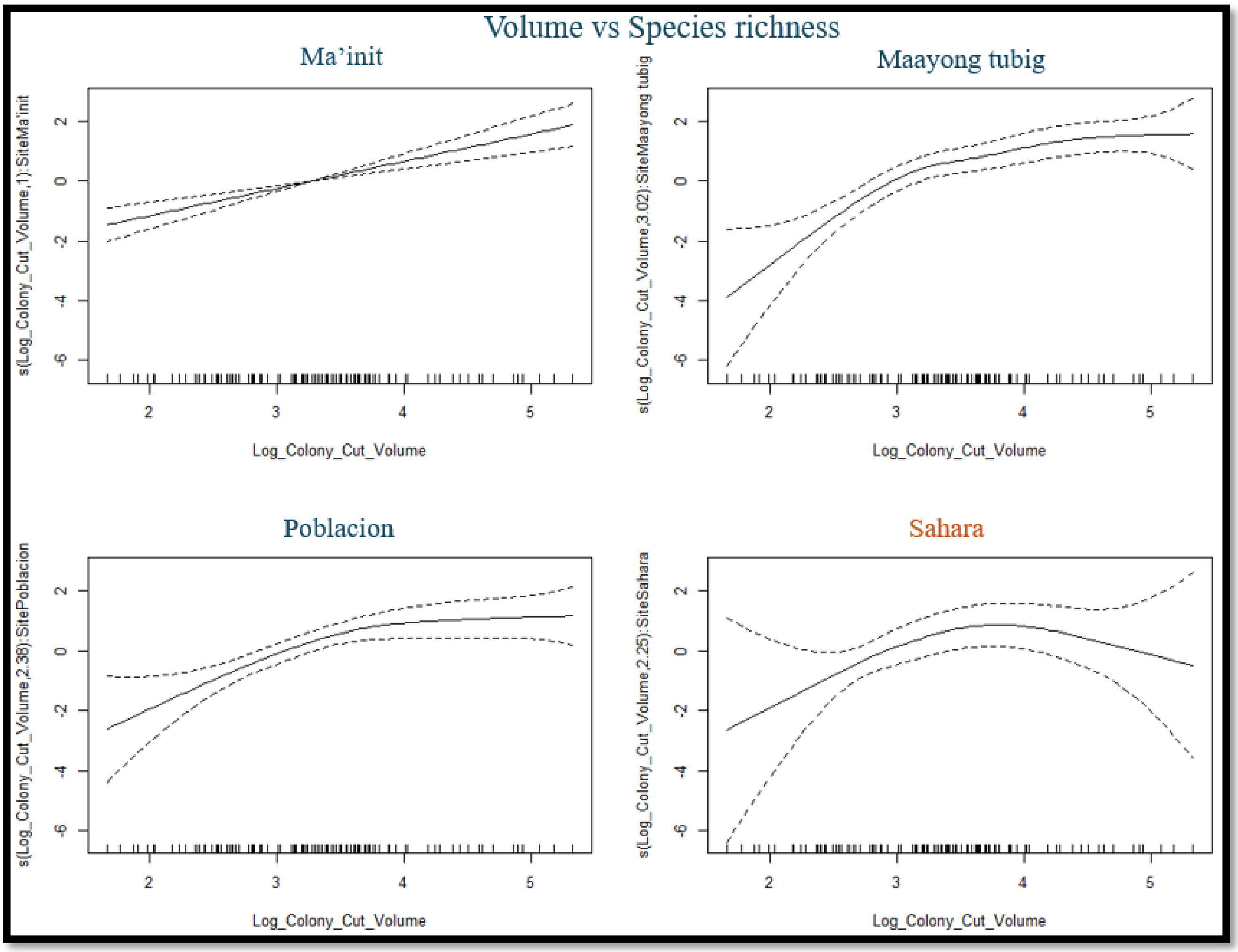

Figure 31*:* Smooth plots for the effect of colony volume on *S* at each site. X-axis shows the predictor variable. Y-axis shows the logarithmic partial effect of the predictor variable on the response variable. Solid line shows the smooth relationship estimate and dashed lines show the 95% confidence interval.

The previously established relationship between *S* and colony volume (see section 3.1.1) appears to be consistent on the NRs, however Ma'init deviates by the effect being linear (p-value = $5.0e^{-7}$; *edf* = 1.0). Maayong tubig (p-value < $2e^{-16}$; *edf* = 3.0) and Poblacion (p-value = $8.1e^{-5}$; *edf* = 2.4) are more akin to the overall relationship established with all NR data combined, however not quite as complex. Sahara (p-value = 0.09; *edf* = 2.3) also distinguishes itself by only exhibiting a marginally significant relationship, however the smooth plot does appear to follow a similar pattern both to Maayong tubig and Poblacion and the overall relationship. The added complexity of implementing "Site" as an interaction term greatly reduced model fit ($\Delta AIC = +58.6$). This suggests that the overall relationship between volume and *S* is better supported statistically than the individual relationships at each site.

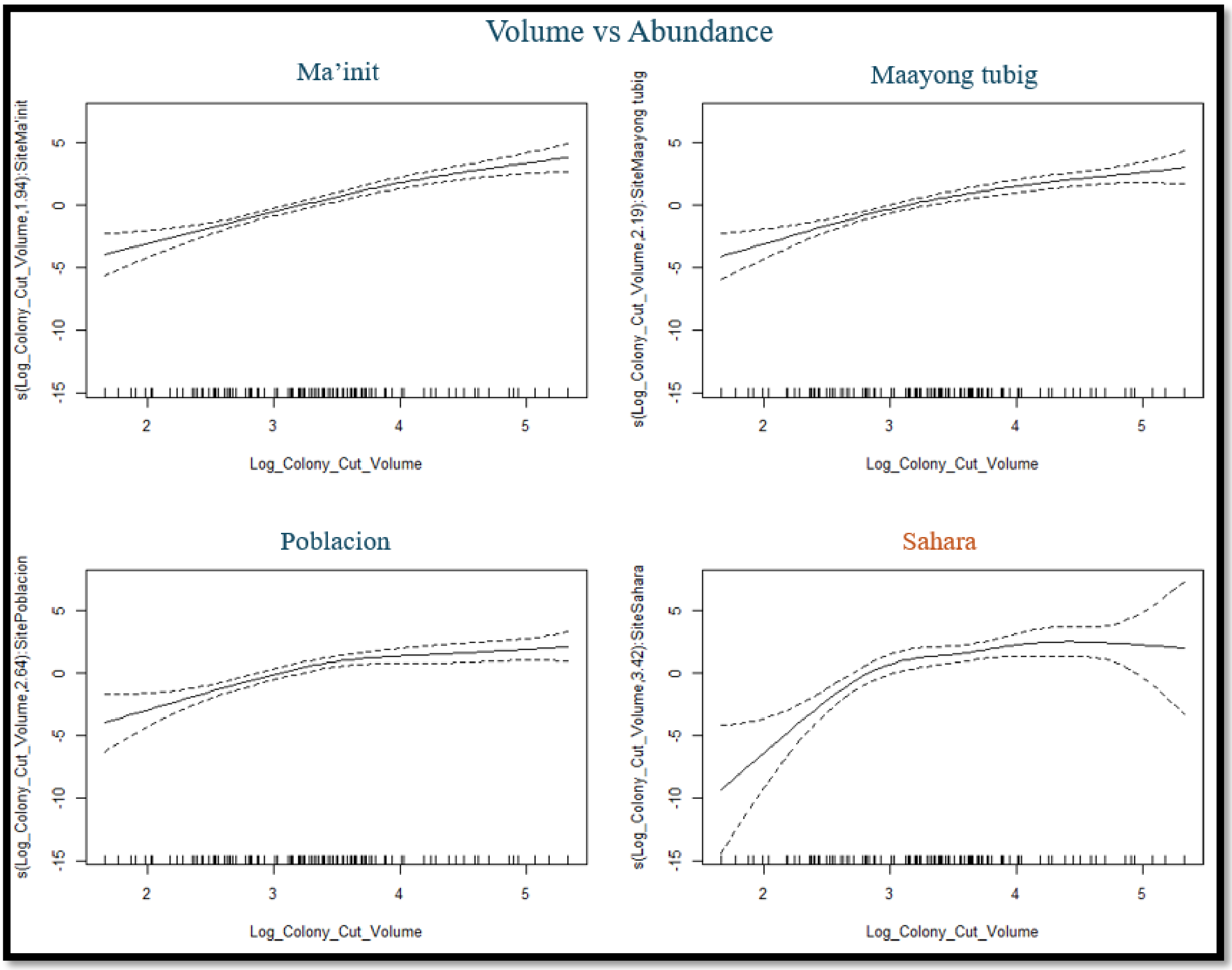

Figure 32*:* Smooth plots for the effect of colony volume on *N* at each site. X-axis shows the predictor variable. Y-axis shows the logarithmic partial effect of the predictor variable on the response variable. Solid line shows the smooth relationship estimate and dashed lines show the 95% confidence interval.

The previously established relationship between *N* and colony volume (see section 3.1.1) appears to be consistent on the NRs across all sites, though with varying levels of complexity. Ma'init (p-value $< 2e^{-16}$; *edf* = 1.9) followed by Maayong tubig (p-value $< 2e^{-16}$; *edf* = 2.2), Poblacion (p-value $< 2e^{-16}$; *edf* = 2.6) and finally Sahara (p-value $< 2e^{-16}$; *edf* = 3.4). Sahara exhibits a more complex effect of volume on *N* than the NRs both individually and combined (For combined smooth plot see Figure 14). However, uncertainty around the estimated smooth is also greater at Sahara, especially in both the extremes (See Figure 32). The added complexity of implementing "Site" as an interaction term severely reduced model fit (ΔAIC = +93.1). This suggests that the overall relationship between volume and *N* is better supported statistically than the individual relationships at each site.

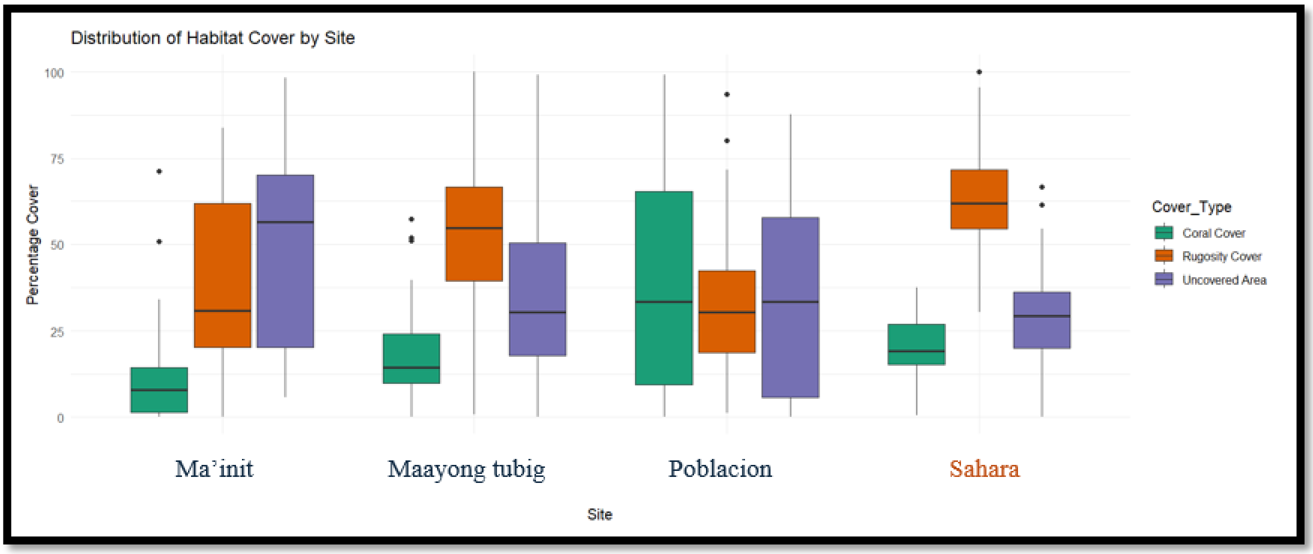

Figure 33: Boxplots showing the distribution of the different environmental surrounding factors at each site

Structural differences were observed in the surrounding reef at each site. Ma'init had a very low percentage of coral cover, and moderate amounts of other rugose cover. However, there was a lot of uncovered area which indicates that colonies were more isolated here. Maayong tubig had far less uncovered area and mostly rugose structures, yet somewhat low levels of coral cover. This indicates that whilst the reef was structurally complex around the colonies there were not large connective coral fields. Maayong tubig was the NR most similar to Sahara in surrounding area distribution (see Figure 33). Sahara had the highest level of non-coral rugose structures, however as most corals grew on complex artificial structures this was to be expected. Poblacion had the most even medians between the three metrics and most coral cover. This indicates that the reef was connective with uncovered patches and large coral fields.

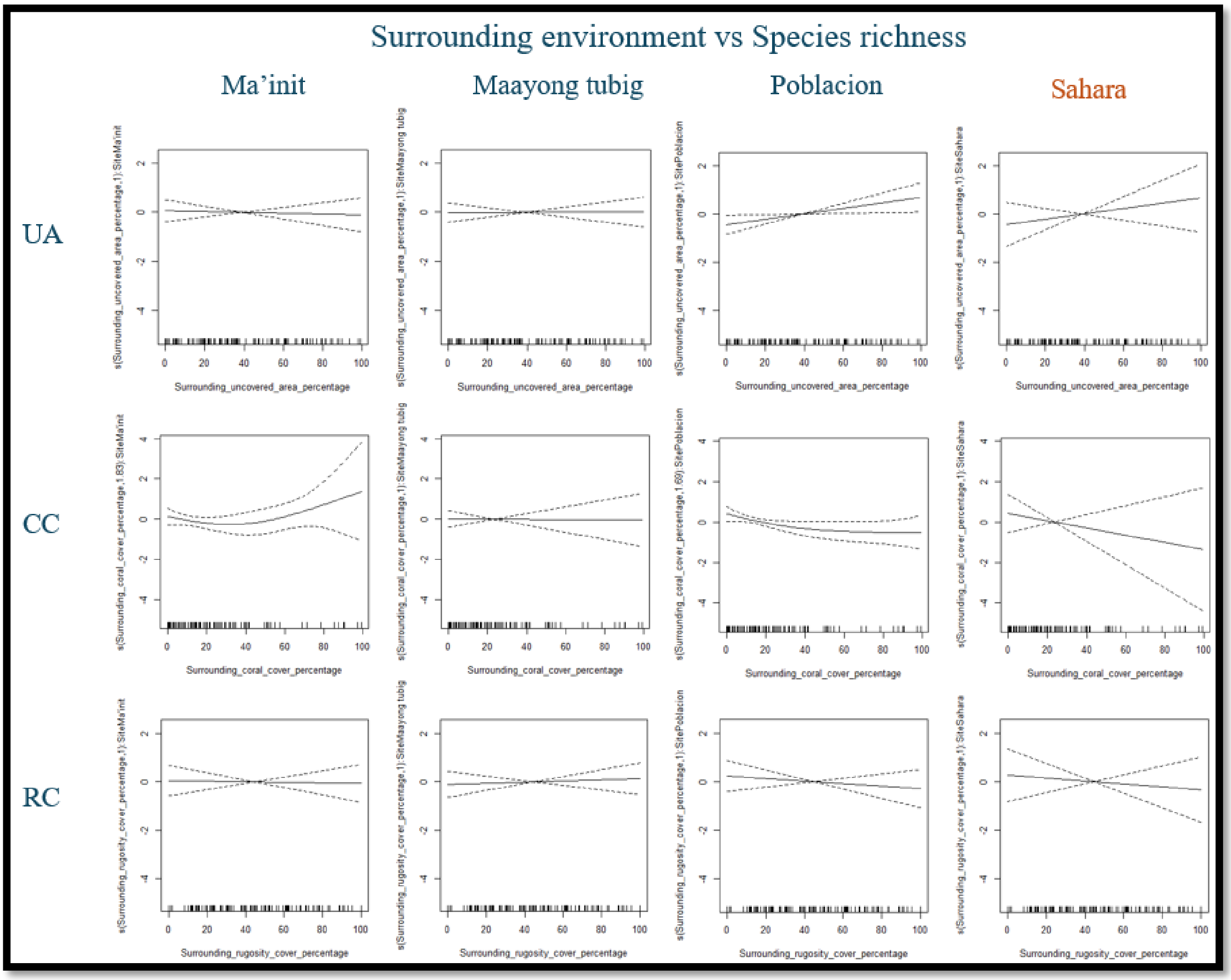

Figure 34: Smooth plots of the effect of the three surrounding environment factors, uncovered area (UA), coral cover (CC), rugose cover (RC) on *S* at each site. X-axis shows the predictor variable. Y-axis shows the logarithmic partial effect of the predictor variable on the response variable. Solid line shows the smooth relationship estimate and dashed lines show the 95% confidence interval.

None of the surrounding environment factors had significant effects on *S* at any sites except Poblacion. Here coral cover exhibited a marginally significant effect (p-value = 0.06; *edf* = 1.6). The smooth appears to stabilise just below zero suggesting that more coral cover results in fewer species on the colony. Uncovered area had a significant positive linear effect (p-value = 0.03; *edf* = 1.6) Coral cover was also the only metric that did not result in fully linear smooth plots. In Sahara and Poblacion there is an indication, though not significant, that more immediate uncovered area around the colony results in higher *S*, whilst the reverse is true for less isolated colonies.

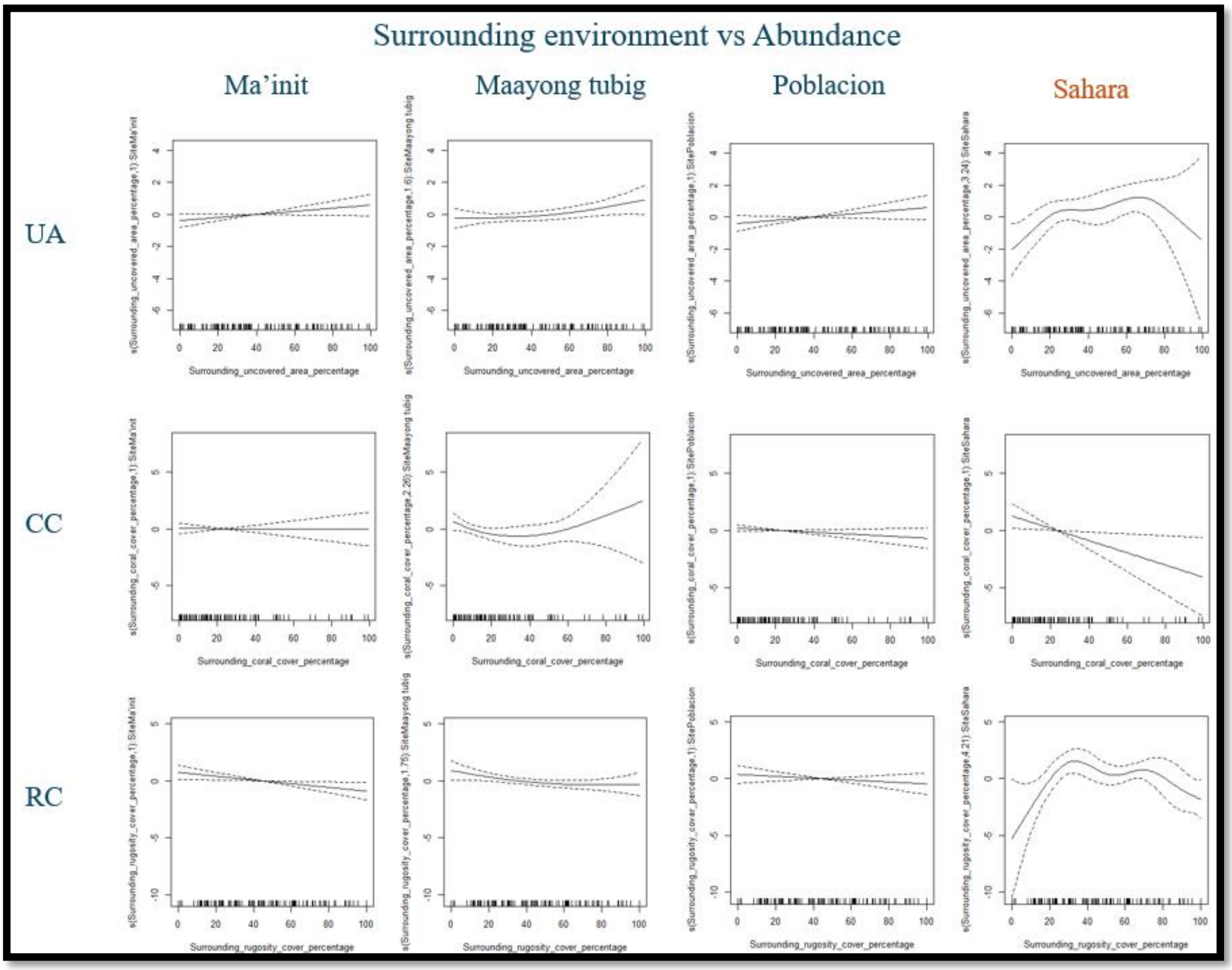

Figure 35*:* Smooth plots of the effect of the three surrounding environment factors, uncovered area (UA), coral cover (CC), rugose cover (RC) on *N* at each site. X-axis shows the predictor variable. Y-axis shows the logarithmic partial effect of the predictor variable on the response variable. Solid line shows the smooth relationship estimate and dashed lines show the 95% confidence interval.

All three surrounding environment factors had significant effects on *N* at Sahara. Uncovered area (p-value = $7.9e^{-3}$; *edf* = 3.3) and rugose cover (p-value = $3.3e^{-3}$; *edf* = 4.2) both displayed nonlinear relationships whilst coral cover had a negative linear relationship (p-value = 0.02; *edf* = 1). The high *edf* for uncovered area and rugose cover does, however, make it difficult to gauge any meaningful trends in these relationships. The other sites mostly displayed insignificant relationships between all three surrounding environment factors and *N* (p-value > 0.1), however in Ma'init increases in rugose cover had a significant negative effect on *N* (p-value =0.02; *edf* = 1). Conversely uncovered area had a positive effect (p-value = 0.05, *edf* = 1).

3.4.3 Comparisons of species composition

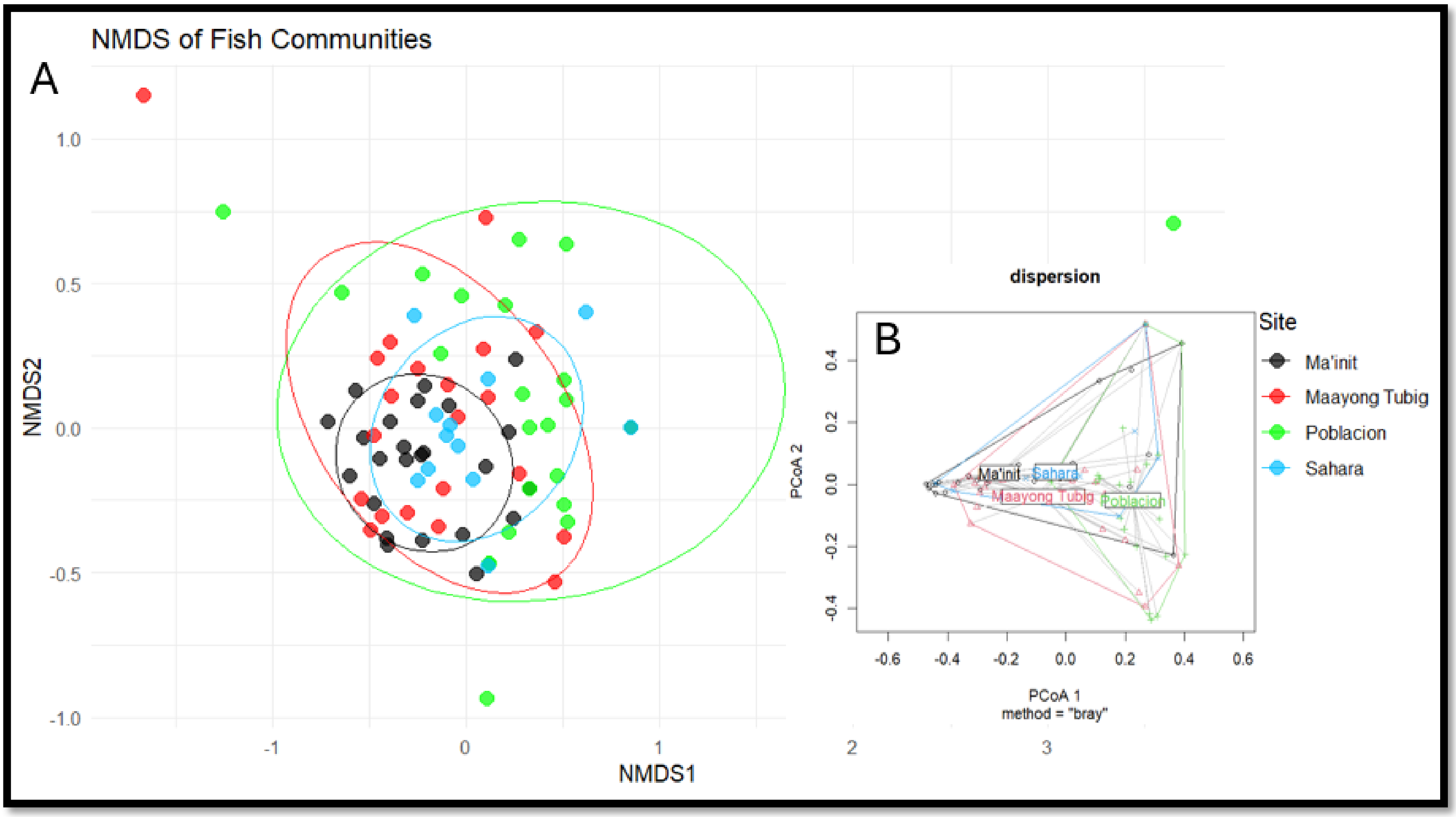

Figure 36: (A): NMDS ordination plot of species composition across the four sites. Axes represent ordination space dimensions (NMDS1, NMDS2), summarising variation. Points represent colonies (colour coded for Site). Distance between points represent similarity in species composition (closer = higher similarity). Ellipses represent 95% confidence intervals. **(B):** Dispersion plot of species composition within each site with convex hulls outlining the group spread. Site name tags represent the group centroid. Points represent colonies with lines connecting to their respective centroid indicating difference to the site mean.

The PERMANOVA test was significant (p-value = $1e^{-3}$) however a very small proportion of the variance is explained by the grouping variable "Site" (R^2 = 0.09). This suggest that intra-site differences in species composition are bigger than inter-site differences. The ad hoc test for dispersion differences in beta diversity was not significant at conventional thresholds (p-value = 0.1), though it was borderline. This suggests that some of the variance in species composition might be attributed to difference in spreads between sites, though most is likely driven by actual species shifts. The post hoc Tukey's HSD test did not find any significant pairwise differences in dispersion (p-values > 0.2) except a borderline difference between Poblacion and Ma'init (p-value = 0.1). The post hoc pairwise PERMANOVA further confirmed that the significant difference in species composition between sites could be attributed to Poblacion. Poblacion showed significant pairwise differences with both other NRs (p-values = $1e^{-3}$). Sahara conversely did not exhibit differences in species composition with any other site, except at borderline level with Poblacion (p-value = 0.01).

The proportion of variance explained by any of the pairwise groupings is very poor however (R^2 = 0.1 or less) (For full test calls see Appendix 22).

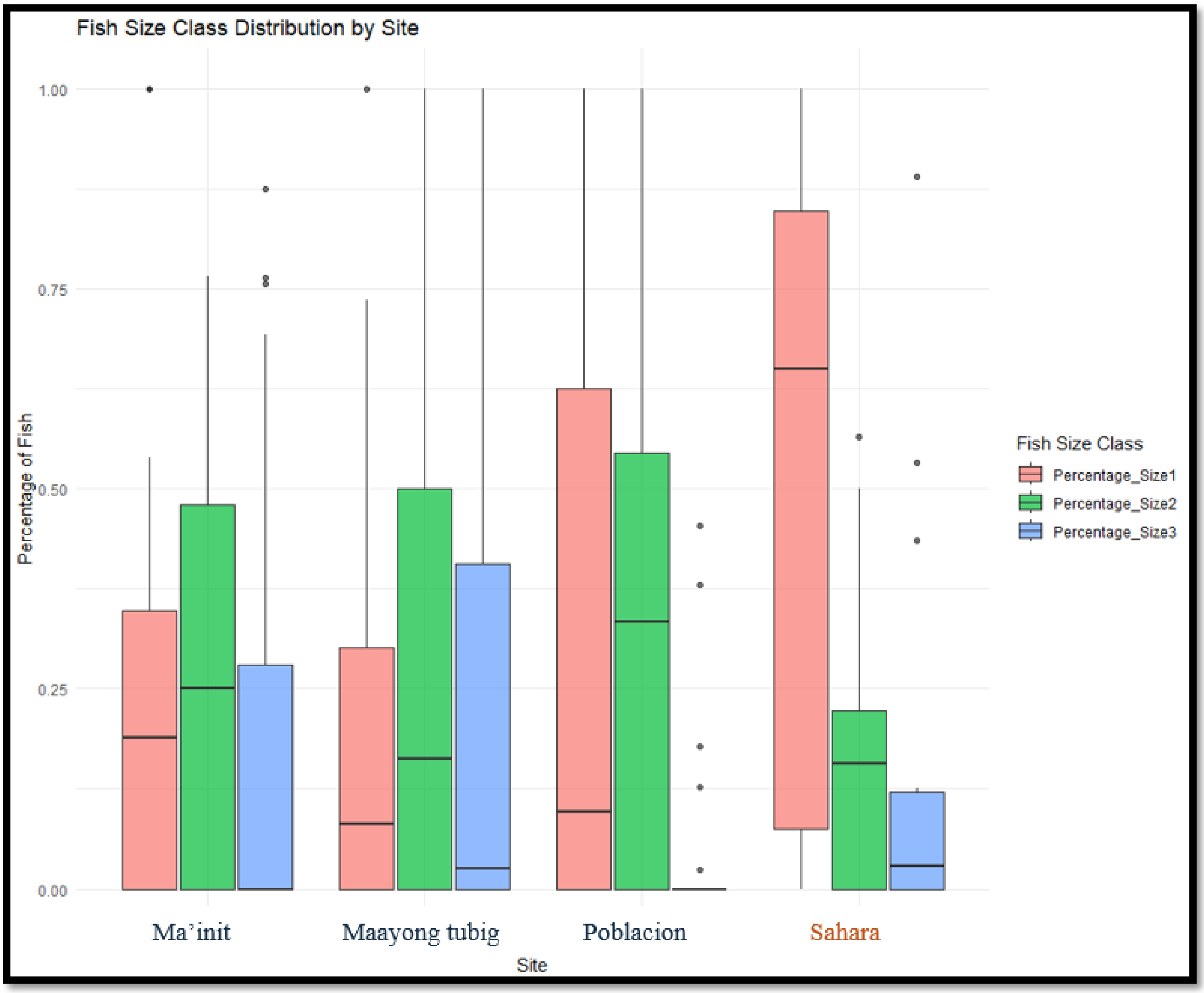

Figure 37: Boxplots showing the distribution of the different fish size classes at each site.

All NR sites generally follow the overall distribution of fish size classes (see Figure 25); however, Poblacion appears to have fewer large fish compared to the other sites and shows greater variation between size classes 1 and 2. Large fish are most predominant at Maayong Tubig among the NR sites. Sahara displays a markedly different distribution, with a higher proportion of small fish and a slightly higher median size for large fish than at any of the NR sites. The interquartile range for the two larger size classes is also quite narrow at Sahara, suggesting limited variability in their distribution.

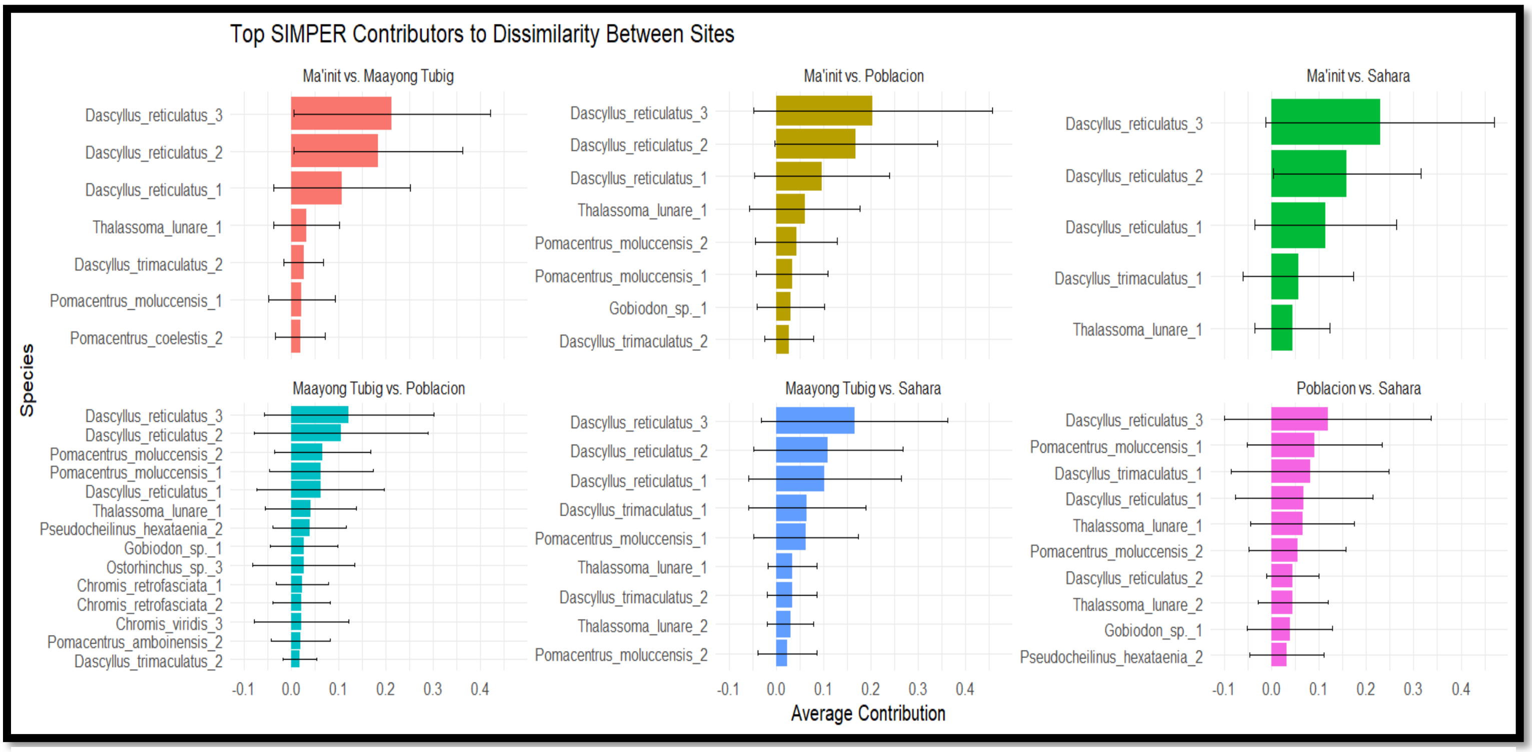

Figure 38: SIMPER test for species contribution to dissimilarity between pairwise sites. Only species contributing cumulatively up to 70% of the total dissimilarity are shown for clarity. X-axis shows the average contribution (%) to the overall Bray Curtis dissimilarity. Error bars indicate standard deviation.

D. reticulatus size class 3 consistently emerges as the top contributor in all pairwise comparisons, with the second and third highest contributors typically being other size classes of the same species. This pattern suggests that *D. reticulatus* is an ecologically central species driving community differences between sites, with variations especially pronounced in the *N* of larger individuals. The only other species to appear consistently among the top three contributors is *P. moluccensis*, specifically in comparisons involving Poblacion and either Maayong Tubig or Sahara. This indicates that *P. moluccensis* plays a particularly strong role in differentiating Poblacion from other sites. The only species to appear across all site comparisons are *D. reticulatus, D. trimaculatus*, and *T. lunare*, all of which seem to be common inhabitants of branching coral microhabitats. Their relative *N*s and size class distributions are likely key drivers of differences in fish assemblage composition across sites.

4. Discussion

4.1 Drivers of fish assemblage recruitment on branching corals

4.1.1 Larger corals accumulate more fish

Changes in *S* and *N* showed very similar interactions with coral colony volume, both displaying a significant non-linear increase that appears to reach a saturation point (See Figures 12 & 14). The observed increase in fish population with increasing coral colony size is consistent with previous research (Agudo-Adriani *et al*. 2016; Komyakova *et al*. 2018). When analysed by coral genus, *Pocillopora* exhibited a more linear relationship than *Acropora*. This suggests that, within the scope of the data collected in this study, *Acropora* demonstrates a clearer saturation point, beyond which additional increases in colony size yield diminishing returns in fish accumulation. However, more exceptionally large *Acropora* colonies were sampled than *Pocillopora* colonies. The *in-situ* sampling method, which classified any colony above 30 cm in height or length as “large,” did not impose an upper size limit. Consequently, “large” colonies in the dataset ranged from approximately 1500 cm^3 to over 200000 cm^3. Of the seven monitored colonies exceeding 50000 cm^3, only two were *Pocillopora*. The more linear pattern observed for *Pocillopora* may therefore reflect limited data at the upper size range, making it harder to determine when (or if) saturation occurs for this genus. It is possible that saturation infers a potential growth limit of the corals. If they seize to increase in size at a certain volume, then supposedly fish accumulation would halt as well. There is not much available literature on the size ranges of either genus, however studies in the Caribbean do indicate that *Acropora* colonies can grow a lot larger than any colony observed in this study even if colonies of such scale are rare (Hernández-Fernández *et al*. 2019; Weil *et al*. 2020).

Saturation is not unusual in ecology, at least in accumulation of species. SARs are commonly presumed to be asymptotic power laws (Tjørve & Tjørve, 2021). Species saturation can be attributed to several factors. For one thing the available number of potential colonizing species in the surrounding area (in this case the larger coral reef) might be relatively finite, meaning that the pool of new potential species gets smaller when the colony specific *S* increases. Furthermore, whilst an increase in size is expected to increase available ecological niches (Ugland & Kraberg, 2021), this effect diminishes over time. For instance, a coral colony needs to grow to a certain size before providing a sufficient habitat below the colony for large fish to seek refuge (See Figure 2) (Kerry & Bellwood, 2015a). However, once that habitat is created it does not change as the colony grows larger, except for in available space. In a relatively homogeneous environment, like that within the microhabitat of a branching coral, there is a limited number of ecological niches, which means that there are fewer opportunities for new species to occupy a certain role as the coral grows. Additionally, competition also increases as more species inhabit the colony, which further reduces the chance for new species to establish a presence. Similar attributes might explain saturation in *N* though AARs appears to generally be less discussed in population ecology, especially in aquatic systems and it is unknown if these tend to follow saturation curves. One study even found that the increase of area on subtropical coastal boulders had an exponentially positive effect on the size of mollusc communities (Londoño-Cruz & Tokeshi, 2007). Such a positive feedback loop does not, however, appear to be present in the *N* of coral associated fish assemblages, which on the contrary appears asymptotic. Intuitively it makes logical sense that more space contains more resources and thus has a higher carrying capacity. In a larger coral colony, there is more space to be utilized by fish as a refuge. Additionally, a larger colony has more immediate water column in which the inhabiting (often planktivorous) fish can feed without venturing too far away from safety. This establishes the basis for a linear relationship between colony volume and *N*. While the GAMs did detect a significant non-linear effect between those variables it was still less complex compared to the effect on *S* ($\Delta edf = -0.64$) indicating a less pronounced saturation point for *N*. This would suggest that coral colonies seize to accumulate species before they seize accumulating fish. Available ecological niches are likely filled before they reach the resource limits that constrain N_{total}. Considering the frequency of pomacentrid fish in this habitat, many of which are gregarious (especially *D. reticulatus*) this pattern is unsurprising (Parmentier & Frédérich, 2016). One social group of pomacentrids may inhabit and grow consistently with a colony whilst presenting competition that deters new species from being introduced. The apparent asymptotic relationship could occur because predation pressure and frequency of disease occurrences typically increase in larger populations, which inhibits growth rates. The effect on *N* might therefore be closer to a true asymptotic power law model: increased colony size continuously allows for a larger *N,* yet with diminishing effect, causing the slope to approach — but never fully reach — 0. The effect of colony volume on *S*, conversely, may be better described by a Michaelis–Menten-type model (Zou *et al.* 2023), where increasing coral size eventually ceases to generate new niches, leading to a true saturation point. The fact that this saturating trend remains evident even when colony volume is log-transformed further supports this interpretation. Michaelis-Menten models have successfully predicted *S* (but not *N*) on reef fish assemblages (Carminatto *et al.* 2025) so similar relationships on colony specific assemblages are likely.

4.1.2 Does fish assemblages scale with colony size according to a power law?

The power law regression models were fitted to further gauge if *S* and *N* interacted with changes in habitat size comparably to conventional SAR/AAR models. *S* was generally fitted more successfully with higher coefficient significance and lower RSE than *N*. However, the range of values for *S* was also much smaller (0-15) compared to *N* (0 – 113.6) so the relative RSE is actually very similar (11-13%). The coefficient *a* was only significant in the model for *S* (except for $S_{Acropora}$) which indicates that the estimated *N* at baseline volume (1 cm^3) was not meaningful. However, this is ecologically sensible given the fact that it is not meaningful to consider coral colonies as fish habitats at baseline size. The reason why *a* might still be significant in $S_{combined}$ and $S_{Pocillopora}$ is likely due to low variance and good model fit at the lower end of the data. *S* is additionally discrete so a value of 0.2 is ecologically meaningless. However, solving the models to estimate colony volume when either *S* or *N* equals 1 (which in both cases represents the first stable presence of fish) suggests that the model for *S* may be more reliable (S_1 = 273 cm^3; N_1 = 35.8 cm^3). S_1 is comparable to the smallest colonies observed with a fish presence (*Acropora* = 331.9 cm^3; *Pocillopora* = 190.2 cm^3) (See Figure 39). N_1 conversely is smaller than any observed corals. Therefore, while the coefficient *a* is not ecologically meaningful at baseline its significance still indicates a stronger predictive model.

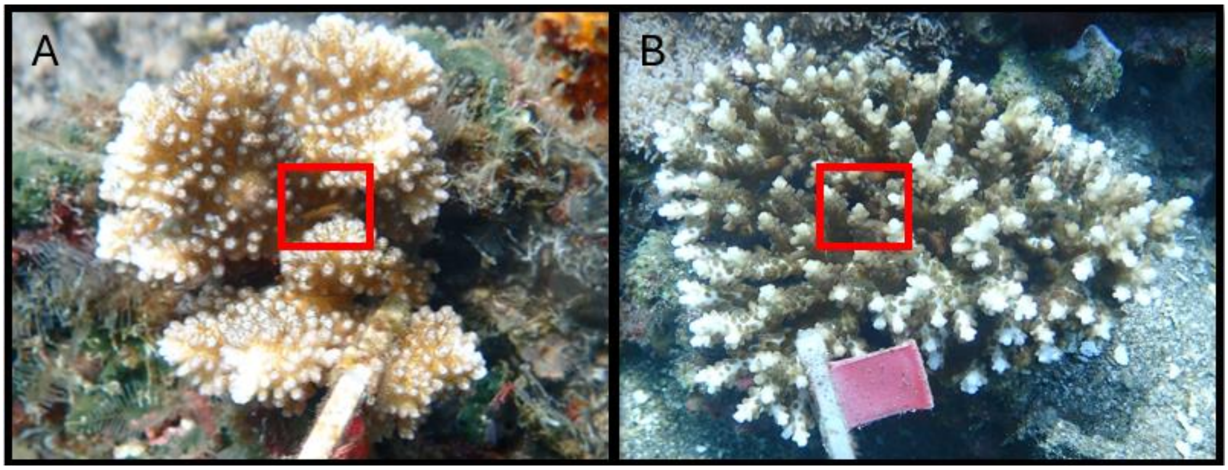

Figure 39: Smallest colonies observed with a fish presence. Red squares highlight fish. **(A)**: *Pocillopora* with *Thalassoma lunare*. **(B)**: *Acropora* with *Gobiodon* sp. Photos by A. Duekilde

The coefficient *b* was, however, significant in all models except $S_{acropora}$ suggesting that the estimated scaling in both *S* and *N* is generally reliable. It was also higher for *Pocillopora* in both models which indicates that proportional growth of the fish population occurs more rapidly in this genus. However, this is also dependent on differences in volumetric growth rates between *Acropora* and *Pocillopora*. Growth rates of branching corals are often measured as linear branch-length increase. Weil *et al*. (2020) found growth rates of *Acropora cervicornis* and *Acropora prolifera* to be up to 37 cm year^{-1}, however these were suggested to be unusually high and additionally these species do not inhabit the Indo-Pacific. Combillet *et al*. (2022) found much lower growth rates for small *Pocillopora* spp. in Culebra Bay ranging from 2 – 5 cm year^{-1}. It is not possible to extrapolate volumetric size increase from linear growth without knowing the radius and number of branches in the whole colony. However, in the data collection for this study it was observed that *Acropora* tended to have thinner and more abundant branches ($n \approx 100 - 1000$) compared to *Pocillopora* ($n \approx 20 - 100$). This morphological difference implies that even with similar or lower linear growth rates, *Acropora* colonies may achieve substantially greater volumetric growth due to their higher branch density. This does not align with the findings of Dehnert *et al.* (2022) though, who contrarily found volume of small colonies of *Pocillopora verrucosa* in a coral nursery in the Maldives to grow from 40 to 905 cm^3 in a one-year period whilst the highest observed volume increase of small *Acropora* spp. colonies was 36 to 390 cm^3. As these are expressed as volumetric growth they can be implemented in the power law models for *S* and *N*. These growth rates would yield an expected increase of 0.7 species and 3.1 fish over a one-year period in *Pocillopora* and 0.9 species and 2.7 fish in *Acropora* ($S_{acropora}$ is expected to have weak predictive power due to low significance of coefficients). This might not be representative for general fish assemblage progression on NRs though. There is much ambiguity in coral growth rates as they change depending on genus, species, environment and possibly also initial colony size (Cresswell *et al.* 2020; Dehnert *et al*. 2022). Furthermore, as demonstrated, it cannot be assumed that either *Acropora* or *Pocillopora* have higher growth rates in general. However, this calculation also exhibits that it is not unreasonable to expect a small coral, such as often used for propagation on ARs (Mcconnell & Waters, 2024), to grow large enough within a year to start sustaining a beginning fish population. It also highlights how these models have some predictive value that could be used in tangent with increased knowledge of coral growth to better maintain and develop ARs in the future to yield the most efficient growth in fish communities.

4.1.3 The effect of colony rugosity

The relationship between increased colony size and higher *S* and *N* is partially explained by the assumption that larger areas will offer more refuge opportunities. Refuges come, however, because coral colonies can be very complex and have a highly rugose structure. It is therefore logical to expect colony rugosity to be a key predictor of fish assemblage. Especially *S* might be influenced by differences in rugosity as more complex colonies likely have more ecological niches. Increased structural complexity has been found to positively influence both diversity and biomass of coral reef fish populations on a large scale (Graham & Nash, 2012), though studies on single colonies does not find the relationship to uniformly be positive (Agudo-Adriani *et al*. 2016; Komyakova *et al*. 2018). It is nonetheless expected that the structure of a coral affects the fish assemblage in some capacity. That aligns with the findings of this study. Rugosity was included as a predictive variable in the GAM for *S* (indicating some contribution to explained variance) and was found to have a direct significant positive relationship with $S_{Acropora}$ (and marginally with $S_{pocillopora}$ when using log10 transformed rugosity values). This indicates that more species can co-inhabit a more structurally complex colony, possibly because the added complexity creates more various niches. No direct significant relationship was found between rugosity and *N*, however, $N_{Pocillopora}$ had a marginal negative significant relationship when using log10 transformed rugosity values. This could indicate that dense and complex colonies have less available refuge space. However, *Pocillopora* colonies had a very narrow rugosity index span with all values ranging between 0.13 – 3.54 (except for one outlier at 20.13). If truly rugosity was expected to directly influence *N* it should be more obvious in *Acropora* colonies that ranged between 0.02 – 150.84 in rugosity index. It is possible that the effect of rugosity on *N* could be overshadowed by colony volume if these variables were confounding, however this did not appear to be the case. The GAM did detect a significant relationship between colony size and rugosity though little effect except in exceptionally large *Acropora* coral sizes were rugosity index dropped steeply (See Figure 16C). The complexity formula, used to calculate the rugosity index, penalizes larger colony sizes if the number of branches does not increase proportionally. However, it does not account for branch length. This observed drop in rugosity suggests that larger *Acropora* colonies may grow more through elongation of existing branches than through an increase in branch number. Branch length was not measured in this study, as no consistent method for accurate branch measurements of both *Acropora* and *Pocillopora* colonies was established. However, in future studies it might be included to more accurately assess rugosity especially of large corals.

While *N* may not be reliably predicted by rugosity alone, it was found to change in colonies of different volumes depending on their rugosity (See Figure 20). Higher rugosity consistently predicted a higher $N_{combined}$ and $N_{Acropora}$ across all volumes with the strongest differences occurring at the volume extremes. $N_{Pocillopora}$ in contrast, was lower for small, high-rugosity colonies but higher for large colonies with high rugosity. A similar pattern was observed for *S* (See figure 18). While $S_{combined}$ or $S_{Acropora}$ were not strongly affected by rugosity in larger colonies, small colonies showed a noticeable increase in richness with higher rugosity. Interestingly $S_{Pocillopora}$ exhibited an opposite trend to $N_{Pocillopora}$ increasing with rugosity in small colonies but decreasing in larger ones. This mirrors the trends seen in GAMS with log10 transformed rugosity values. These opposing trends suggest that fish assemblages on *Pocillopora* colonies interact with rugosity differently than on *Acropora*. This could be due to the limited range of rugosity observed in *Pocillopora*, which appear to maintain relatively consistent structural complexity as they grow. While the results support that rugosity influences fish assemblages — particularly in smaller colonies — colony size remains the more dominant factor. Combining structural complexity with colony dimensions has previously been shown to improve predictive strength (Fisher, 2023). However, in this case, the tensor interaction in the GAMs explained less variance, suggesting that other environmental or biological variables may be more influential.

4.1.4 The influence of a colony's environment

Several large-scale factors of the colony environment were measured to assess their influence on fish assemblage (See Table 1), however as they were secondary predictors the methodology had not specifically been designed to ensure a range of values. For instance, while the depth of observed colonies was measured, they were all relatively shallow, with the deepest colony found at 13.4 meters. Depth did exhibit a near-linear positive affect on *N* but no significant relationship with *S*. Depth stratification has recently been explored using eDNA (Zhao *et al.* 2025) which found distinctive fish species compositions at different depth intervals, though mainly when exceeding the sampled depths of this study. Interestingly, the highest biodiversity was observed at intermediate shallow zones (15 – 20m), which could align with the observed increase in *N* at deeper colonies of this study.

Water temperature and lunar phase influence fish metabolism and reproductive cycles (Sponaugle, 2015; Habary *et al*., 2016). Changes in these variables can therefore affect fish behaviour and potentially influence the observed fish assemblage. However, as with depth, there was limited variation in these parameters during sampling. Temperature remained relatively stable at 30 ± 2 °C and did not show a significant effect on fish assemblage. Interestingly, water temperature was included in the GAM for *N* with the lowest AIC, suggesting it contributes to explaining underlying variability. This may be due to a correlation between water temperature and depth, or it could reflect behavioural responses of fish to minor temperature shifts driven by changing weather conditions.

Lunar phase varied more than other factors, as sampling occurred over a month at random intervals based on the IMR schedule. While it showed no relationship with *S* it had a significant non-linear effect on *N* (For smooth plot and model diagnostics see Appendix 23). Ecologically, this may be explained by stronger tidal cues during the new and full moons, which can influence spawning and recruitment. For example, pomacentrid fish are known to spawn following lunar cycles (Lecchini *et al*. 2016), and increased activity may lead to higher observed *N* if individuals are less cryptic as a result. However, lunar phase was not included in the final GAM for either *S* or *N*, suggesting that its effect did not explain a large portion of the overall variability. Time of day was neither significant nor included in either model, suggesting that the observed fish assemblage remained stable throughout daylight hours. While coral reef fish often follow diurnal activity patterns — with notable behavioural peaks at dawn and dusk (Coker *et al*. 2013; Lecchini *et al*. 2016) — these transitional periods fell outside the sampling window. In contrast, the survey week did have an effect. Colonies observed during week 43 showed lower-than-expected *S* and particularly *N* (See Appendix 4). This may reflect an unrecorded weather event, such as a typhoon, that temporarily altered fish behaviour. Alternatively, the lower values may be explained by a higher proportion of small colonies surveyed that week.

The local environment primarily influenced *N* indicating that *S* is less responsive to the surrounding structure. The smooths indicate a slight positive effect of increased uncovered area, whilst more surrounding coral or rugose structures conversely appear to reduce *N* (See Figure 21). This suggest that fish tend to accumulate on isolated coral colonies more than on those situated on highly connective reefs. On the microhabitat scale a dilution effect seems to occur. Fish spread out more evenly when colonies are surrounded by structurally complex habitat, whereas isolated colonies act as aggregation points which causes clustering. This is further supported by the highly significant tensor interactions, which indicate that there is a difference in both the expected *S* and *N* on colonies of a given size depending on its surrounding environment. No immediate difference in the effects of coral cover as compared to simply rugose cover was observed. When each site was investigated individually, however, coral cover alone had a marginal negative effect on *S* at Poblacion, whilst it was only Ma'init that saw significant effects between uncovered area (positive) and rugosity cover (negative) on *N* (See Figure 35). This could indicate that the coral cover of a reef affects species composition, whilst the rugose structure of a reef affects fish distribution. Komyakova *et al.* (2013) found similarly that coral cover explains more variation in *S* (on a reef scale) than topographic complexity. It has previously been observed that patchy reefs support higher *S* than large connective reefs (Chittaro, 2002; Hattori & Shibuno, 2009). However, this does not align with the findings of this study. The most connective reef site (Poblacion) had a high S_{total} and a low N_{total} (See Table 3) which was contrary to the patchiest reef site (Ma'init). It does highlight, however, that coral colonies generally appear more effective at fish recruitment when they are not immediately adjacent to other refuge opportunities.

4.2 Dynamics of species composition on branching corals

4.2.1 Colonies are dominated by a few species and sub-adult fish

Of the 59 observed fish species only 6 appeared on more than 10% of all colonies (See Table 2). *Gobiodon* spp. represents gobies that could not confidently be identified to species level since getting high-quality photo data of these was exceedingly difficult. Each observed *Gobiodon* species therefore likely has a frequency below 10%. Of the remaining 5 species, 3 are pomacentrid and 2 are labrid fishes (See Figure 40). These are also the two most species rich families observed overall and can therefore be assumed to make up most of the associated fish assemblages on branching coral colonies in Dauin. The dominance of these two families aligns with findings from 50 meter transect surveys along Dauin's reefs (Institute for Marine Research, 2022), as well as with expected species composition from previous literature (Coker *et al*. 2013; Siqueira *et al*. 2023). This suggest that the fish inhabiting the corals reflect, to a degree, the overall fish population on the whole reef. Furthermore, it indicates that there is a very uneven distribution of species with the majority of the observed fish assemblages being comprised of only a few families and species. This is further supported by the low diversity indices (See Table 3). *Pomacentridae* generally appear to both be more gregarious and more consistent in their respective colonies than *Labridae*, especially the genus *Dascyllus*. There is plenty of research that confirms strong site fidelity, small home ranges and social groups in pomacentrid fish (Cowlishaw, 2014; Hattori & Casadevall, 2016; Chase *et al*. 2020; Chase *et al*. 2024), however the literature appears scarcer on these subjects regarding the relevant species of *Labridae*. This alone could suggest that they are less strongly associated with specific coral colonies and may change refuge more regularly.

The most frequently observed pomacentrid fish were *Dascyllus reticulatus*, *D. trimaculatus* and *Pomacentrus moluccensis*. Of these *D. reticulatus* was the most consistent, frequent and notably gregarious. *D. reticulatus* appeared to be the dominant species associated with *Acropora* and *Pocillopora* corals along the Dauin coastline. However, this trend shifted at Poblacion, where *D. reticulatus* was rare and *P. moluccensis* was significantly more common. A study from the Great

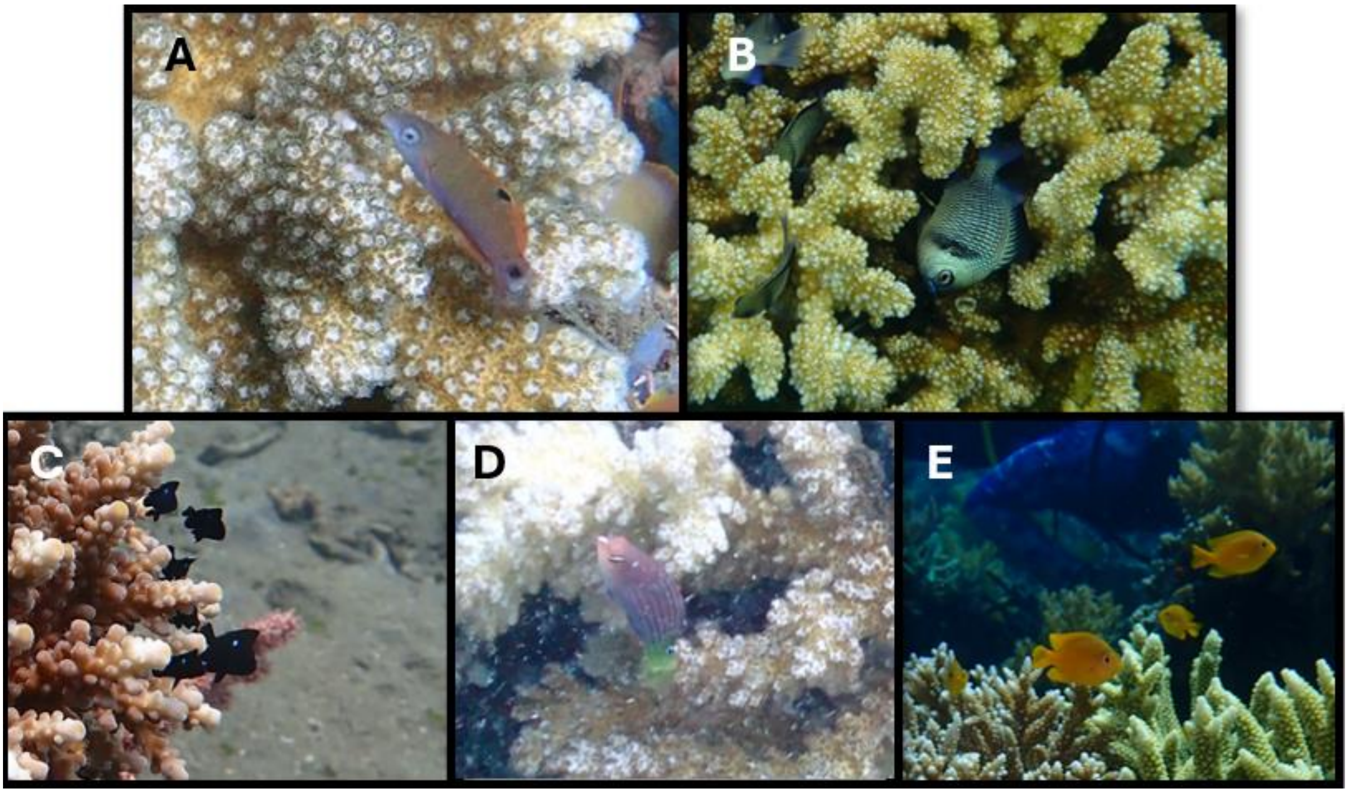

Figure 40: The 5 most observed fish species. **(A)** *Thalassoma lunare*. **(B)** *Dascyllus reticulatus*. **(C)** *Dascyllus trimaculatus*. **(D)** *Pseudocheilinus hexataenia*. **(E)** *Pomacentrus moluccensis*. Photos by A. Duekilde

Barrier Reef similarly found *P. moluccensis* to be a widespread inhabitant of coral colonies across habitats, while *D. reticulatus* was largely restricted to sand-patch areas (Chase & Hoogenboom, 2019). Pratchett *et al.* (2012) similarly found *P. moluccensis* to inhabit a much wider range of coral species than *D. reticulatus*. This suggests that *P. moluccensis* is a competitive generalist species that thrives in richer environments, whereas *D. reticulatus* may function more as a specialist, better suited to harsher or less contested habitats. The Dauin reefs are generally exposed and sloping, except at Poblacion where the coastline provides some shelter. The shift in dominant pomacentrids may therefore reflect the broader ecological influence of this geographical layout. This interpretation is further supported by higher diversity indices observed at Poblacion compared to other sites. Interestingly, previous reef scale research suggests that Poblacion should have a higher *N* than Ma'init (Institute for Marine Research, 2022) which contradicts the findings of this study. The coral colonies fish assemblage might therefore be less influential on the general fish population at richer sites. This also aligns with the aforementioned indication that isolated colonies attract more fish (See section 4.1.4) and could suggest that the individual coral colony represents a hotspot at a site like Ma'init, more so than at Poblacion. Additionally, Chase & Hoogenboom (2019) found colonies occupied by *P. moluccensis* to often be void of other species and have small assemblages, suggesting that this species is territorial and only partially gregarious. Their dominance at Poblacion could therefore also explain the lower *N*.

The most frequently observed labrid species were *Thalassoma lunare* and *Pseudocheilinus hexataenia*, both of which were commonly recorded across all four study sites. *T. lunare* had the highest naïve occupancy at nearly every site, suggesting it is a highly abundant and widely distributed species. It is also a species of commercial importance (Institute for Marine Research, 2022). While fished individuals are typically larger than those observed within the branching corals, the high prevalence of juveniles documented in this study may indicate a healthy and actively reproducing population. Most observed fish in general belonged to the smaller size classes, meant to represent juvenile and intermediate fish. This indicates an ontogenetic shift as fish mature where they associate less with the branching coral microhabitat as adults, which aligns with previous findings (Coker *et al*. 2013). Several species were observed with an average size class of ≈ 3 though these were generally species that were observed infrequently (Sometimes only once). Many of these were corallivores like *Chaetonidae* or large predators observed refuging beneath the colony (not within) like *Serranidae* who may be more transient than permanent coral dwellers. *D. reticulatus* was the only species with a high frequency that had an average size class above 2, indicating that they are lifelong coral dwellers which is consistent with the literature (Hattori & Casadevall, 2016).

The size and structure of the colonies exhibited significant effect on the expected distribution of size classes. Small or highly complex colonies would only support small fish, whereas larger and less complex colonies supported fish of all sizes. This validates the theory that large colonies offer more niche habitats. Previous research similarly suggest that highly complex habitats are mainly inhabited by small fish and that complexity across various scales is required for a heterogenous fish community (Halford & Bellwood, 1998; Nash *et al.* 2013). There were most fish observed in the 2nd size class. This could indicate that the coral colonies are a transitional habitat utilized between initial juvenile settlement and adulthood. Some coral reef fish are known to first settle on reef adjacent habitats like sea grass meadows or mangrove forest and then gradually move into the adult habitat (Sponaugle, 2015). However, it is also possible that this distribution is the result of “central tendency bias” — a tendency to prefer middle options on subjective rating scales. (Hollingworth, 1910). Given the lack of an SVS, size estimates were based on measurements made relative to other objects on the recordings as well as the morphology of the fish. This method was not foolproof, however, as poor video quality could often make estimates difficult. Prober SVS measurements are needed for a more thorough analysis of fish size distributions on branching corals.

4.2.2 Differences in species composition between *Acropora* and *Pocillopora*

Acropora colonies appeared to consistently support a higher *N* across all sites as well as a slightly higher *S* except at Ma'init. This is consistent with previous findings (Coker *et al.* 2013) and would suggest that more species associate with *Acropora* colonies. These likely have a more diverse structure with more available niches. Additionally, they might also have more space available for larger fish assemblages compared to *Pocillopora* within the same volumetric size. Alternatively, they simply grow to larger sizes and therefore has a higher N_{mean}. As previously mentioned, more exceptionally large *Acropora* colonies were sampled, which was mainly due to fewer large *Pocillopora* colonies sighted on the reefs. *Acropora* colonies were also found to have higher rugosity, which was shown to increase the expected *S* and *N*. Additionally, far more species of *Acropora* exist with more varied growth forms, meaning that the genus collectively has more varied niches and that there might be more fish strongly associated with specific *Acropora* species than *Pocillopora* species. Conversely, this also means that any one *Acropora* colony cannot be expected to always have a more diverse fish assemblage than comparable *Pocillopora* colonies. Chase & Hoogenboom (2019) found *A. intermedia* to have smaller hosts of pomacentrids than *P. damicornis* but *A. spathulata* to have a bigger host. High difference in proportional use of various *Acropora* species have previously been documented, indicating the importance of identifying *Acropora* colonies to species level to better predict the associated fish assemblage (Bonin, 2011). It is uncertain whether any observed fish species showed specific association with either coral genus. Although several species were recorded exclusively on one coral type, these were all rarely observed and thus likely not indicative of true habitat preference. *Gobiodon* spp. and *Pomacentrus moluccensis* have previously been suggested to prefer *Acropora* colonies (Patton, 1994; Bonin, 2011), which is partially reflected in their naïve association scores in this study. However, both species were only found on approximately 10% more *Acropora* colonies than *Pocillopora*. Among frequently observed species, *Pseudocheilinus hexataenia* showed the most uneven distribution, appearing predominantly on *Pocillopora* colonies. No documented habitat preferences exist for this species, but as a carnivorous fish that feeds on small invertebrates (Froese & Pauly, 2025) it may find more prey items in *Pocillopora* colonies. Pratchett *et al.* (2012) suggested that *P. damicornis* was the favourable habitat for coral dwelling organisms and potentially provide greater protection. Chase & Hoogenboom (2019) correspondingly saw a greater occupancy of *P. damicornis* by *Pomacentridae* than colonies of any other coral species. The proportion of inhabited *Pocillopora* colonies in this study was likewise higher than *Acropora* colonies. This may indicate that while

Acropora provides space and niche diversity to support more fish overall, *Pocillopora* may offer more advantageous refuge conditions, making it the preferred genus for many coral-dwelling species.

4.2.3 The effect of interspecies interactions on coral colony fish assemblages

There were no clear signs of any functional groups or species associations which could lend explanatory power to the variance seen in the fish assemblages or species compositions of different colonies. While the species association network did show a few minor clusters, further examination revealed that these could all be attributed to single co-occurrences of rare species (with the exception of the association between *Chromis retrofasciata* and *Chromis ternatensis* who co-occurred twice) (See Figure 41). These findings suggest that the fish species observed in this study tend to associate with coral colonies independently, and that no stable species groupings or functional associations exists which could predict co-occurrence patterns.

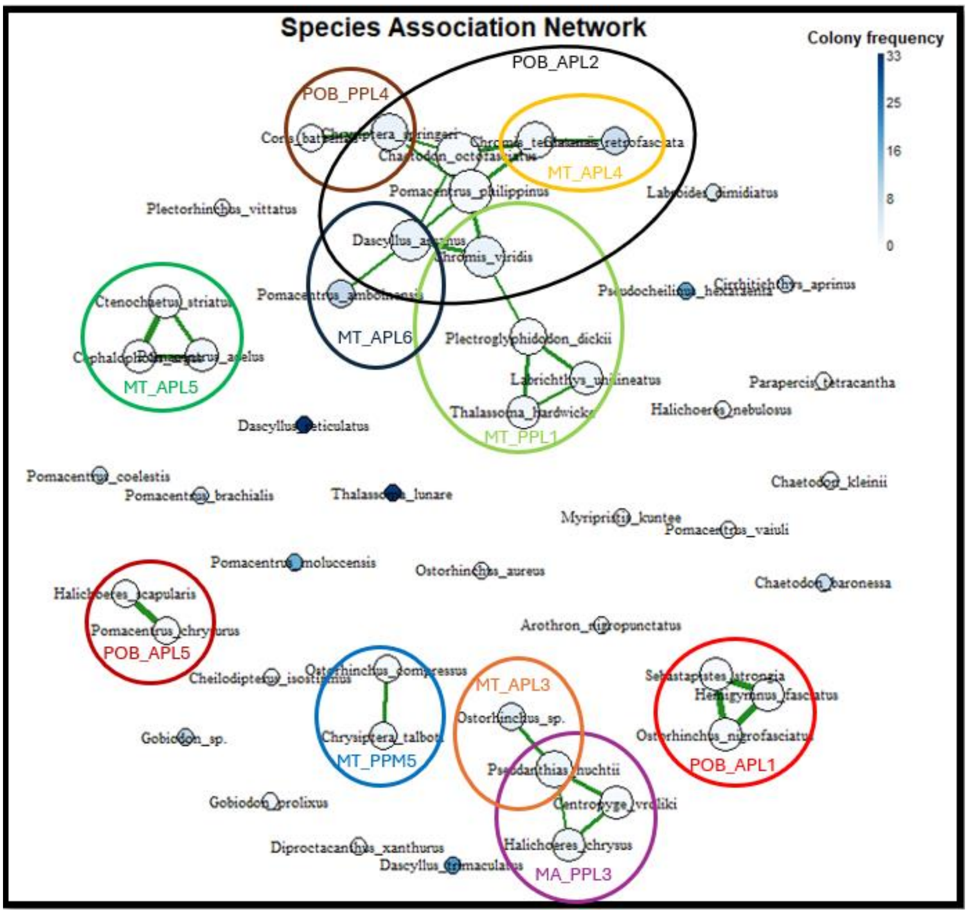

Figure 41: Species association network with each single occurrence association highlighted and marked with the site-specific colony ID (I.e. POB_APL2 stands for Poblacion *Acropora* Large 2)

One observed species, *Labroides dimidiatus*, is a mutualist known for cleaning parasites from other fish. Its presence has been shown to increase the *N* of *Pomacentridae* recruits at the reef scale (Sun *et al.* 2015). No such association was detected in this study, which may be due to the focus on individual coral colonies, where the influence of cleaner fish might be less apparent. Notably, *L. dimidiatus* occurred more frequently on *Acropora* colonies than on *Pocillopora* (naïve occupancy was 0.14 and 0.02, respectively). As previously noted, *Acropora* colonies generally supported larger and more diverse fish assemblages, which could in turn attract a parasite-cleaning species like *L. dimidiatus*. However, it is also plausible that causality runs in the opposite direction; That the presence of *L. dimidiatus* may attract other fish to *Acropora* colonies more than to *Pocillopora*. No previously documented coral genus-level habitat preferences were found for this species, however.

The most common family on the colonies, *Pomacentridae*, has conversely been found to be agonistic and negatively influence *S* (Dunkley *et al*. 2023) and is known to be territorial and aggressive especially against conspecifics within the *Dascyllus* genus (Chase *et al*. 2020). They have even been suggested to be keystone species due to their tight association with branching corals, their algae farming behaviour and their interactions with other fish and invertebrates, all of which shape the benthic community and species composition within their habitats (Ceccarelli *et al*. 2001). No negative associations with *Pomacentridae* were detected in this study, however. Neither in the species association network or when examining the specific *S* and *N* of those colonies where *Pomacentridae* were dominant. Conversely, the only dominant pomacentrid to cause significant deviation from expected values was *Pomacentrus coelestis* which positively affected *S*. While no research investigating sympatric species association of *P. coelestis* could be found, it has been suggested that this species have an unusually short lifespan and that they become more abundant after high-disturbance events (Kingsford *et al*. 2017). This could indicate that they are rapid opportunistic colonisers whose presence on colonies could indicate a less established – and less strongly associated – fish assemblage. More species might co-occur in such an environment where no clearly dominant species exist to dissuade new colonisers. This could also explain why the grouped “Rare species" factor similarly had a significant positive effect on *S* as these species might only appear as dominant on colonies where a more territorial and agonistic species have not yet established a firm presence. These species may indicate earlier succession stages in branching coral habitats, than species such as *Dascyllus reticulatus* and *Pomacentrus moluccensis*, though more research is required to confidently determine such a trend as this study only found three colonies with a primary population of *P. coelestis*. Furthermore, no direct comparisons between any dominant species indicated significant differences in *S*; Even when compared to the colonies without a primary fish species the majority of which (93%) were uninhabited. This could indirectly indicate the agonistic influence of pomacentrids in branching corals. Most colonies either had a dominant presence of pomacentrids (47%) or were uninhabited (29%). The fact that colonies void of fish did not have a significantly lower *S* than expected demonstrates a generally low *S* on all colonies. S_{mean} ranged from ≈1 to ≈2.7 species in the different coral genera at each site and the combined S_{mean} was ≈2 (all with nearly equivalent SD). If pomacentrids do discourage most new colonisers in their habitats then that would explain why corals (architects of one of the most diverse ecosystems on the planet) has such low internal diversity within their colonies. However, the observed low *S* also aligns with Siqueira *et al.* (2023) who suggested that only a small fraction of coral reef fish species is strongly associated with coral habitats (See Figure 3). It is therefore difficult to determine if the low observed *S* is a result of the high pomacentrid presence in the sampled colonies, or a general pattern to be expected in branching coral fish assemblages.

Both "Rare species" and "No dominant species" colonies had lower *N*'s than expected, which aligns with these being either uninhabited or having less established fish assemblages. Additionally, colonies dominated by *Pseudocheilinus hexataenia* also had lower *N*s. This might be attributed to this species seeking out more empty colonies rather than them actively decreasing the *N*, as they are described as shy (Froese & Pauly, 2025). The only species to be associated with significantly different *N*s in direct comparisons were *D. reticulatus* that dominated colonies with larger fish hosts. This, once again, highlights the highly gregarious nature of this species.

4.2.4 The consistency of the branching coral fish assemblage

Although some changes were observed in the colonies, the overall structure of the fish assemblages appeared stable over the 1–3 weeks that typically passed between repeated observations. Only 15% of colonies changed their primary fish species, and all these initially had small populations (<10 individuals), suggesting that colonies with fewer fish may be more prone to change. In most cases, the new dominant species had already been observed during the first survey, indicating that the shift was not due to competitive displacement but rather to coexisting species increasing at different rates. Notably, two of these changes involved a shift from *Thalassoma lunare* to *Pseudocheilinus hexataenia*—species known for high habitat inconsistency (see Appendix 17). Two additional shifts also involved these species. This suggests that colonies with small populations composed of species lacking strong site fidelity may account for most of the observed turnover.

No significant changes were detected in *S* or fish size distribution. Therefore, it can be inferred that single observations provide a fair representation of a colony's potential fish assemblage. This conclusion is supported by the PERMANOVA analysis, which found no significant differences in species-by-size-class counts between replicates. Previous studies have shown that *Dascyllus aruanus* can consistently inhabit *Pocillopora* colonies for up to a year (Chase *et al*. 2024); this study suggests similar stability generally applies to the overall fish assemblage of both *Acropora* and *Pocillopora* colonies.

Interestingly, despite the lack of compositional change detected by PERMANOVA, the cumulative *N* did vary between replicates. This implies that small, species-specific fluctuations occur regularly and can accumulate into noticeable differences in total assemblage size. These changes may result from recruitment or reproduction increasing population size, or from predation reducing it Additionally, while social groups — such as those formed by pomacentrids — may maintain stable associations with specific colonies, individuals or sub-groups may occasionally split off or join other groups in a fission–fusion dynamic. *D. aruanus* have been observed to move transiently between groups in *ex situ* experiments (Mann *et al*. 2014), indicating a precedent for this behaviour. This could account for the observed changes in *N* without affecting *S* and aligns with observations of both increases and decreases in *N* between replicates (see Figure 28).

4.3 Considerations on the Artificial reef "Sahara"

4.3.1 Ecosystem differences and similarities

Despite being an artificial reef Sahara shows considerable ecological similarity to the three natural reefs. Both the proportional occupation rate of colonies, S_{mean} and N_{mean}, and the diversity indices are comparable across all four sites. The similarity of the results at all four sites indicates both the confident reliability of these findings, and that knowledge acquired from observations on an NR can be useful in predicting trends on an AR. A meta-analysis review comparing fish community data from NRs and ARs across the world similarly concluded that ARs are typically comparable to NRs in fish community metrics such as fish density, biomass and diversity (Paxton *et al*. 2020). They did however find that tropical ARs tend to support lower fish densities compared to tropical NRs. Sahara did have a lower N_{total} and S_{total} than most of the NRs, but high means colony^{-1}. The seemingly smaller fish population is therefore likely a result of the fewer observed colonies. If approximately 30 colonies had been observed (like on the NRs) Sahara would have the second highest N_{total} with ≈ 350 fish (Assuming that the observed N_{mean} is consistent). Contrary to the findings of Paxton *et al.* (2020), the fish density at Sahara therefore appeared equal to the NRs, if not even on the higher end.

S, conversely, cannot be extrapolated up so easily as the overlap of species between colonies means it does not scale linearly. Paxton *et al*. (2020) saw an insignificant increase in *S* on tropical ARs, however this, once again, does not appear to be mirrored at Sahara. Interestingly, Sahara does have the highest S_{mean} colony^{-1} but a low S_{total} even compared to the smaller sample size. This means that while the colonies at Sahara seemingly can support a diverse fish assemblage, there is not much difference between the species observed on each colony. The only other site to have fewer observed species than colonies were Ma'init which also had the lowest diversity scores. While this technically means that Sahara's *S* is comparable to that of an NR, it does raise the question of whether Ma'init is representative of an undisturbed reef. Ma'init is more exposed to tidal currents and sedimentation than the other sites, it is routinely polluted by wastewater from the adjacent shrimp farm and based on visual assessment after repeated dives it seemingly is the most afflicted reef in terms of debris and garbage. While it is an MPA, it appears poorly enforced as much of the debris covering the reef is old fishing equipment such as nets, lines and hooks. It was in fact so noticeable during the study period that IMR and the local community lead frequent clean-up dives at this site specifically. Previous data also indicates higher levels of debris at Ma'init than any other site, followed by Sahara and with far less at Maayong tubig and Poblacion (Institute for Marine Research, 2019, 2020, 2022, 2023). If these pressures have a negative influence on the fish diversity, then Sahara's fish population cannot be claimed to be of equal diversity to a healthy NR, based on the findings of this study. Alternatively, it is possible that the reduced *S* is an indication of an earlier ecological successional stage at Sahara compared to the older NRs. The reef was established roughly 20 years ago and the presence of large hermatypic corals (including the second largest *Pocillopora* observed in the whole study) does indicate that it is at a later successional stage. McCarthy *et al.* (2025) suggest that the composition of hermatypic corals indicate proximity to a successional endpoint or "climax community" though without providing a clear definition of what such composition might look like. While this study only investigated two coral genera and therefore cannot determine Scleractinian diversity or cover at each site, it has been suggested by IMR that Sahara has less coral cover than expected on Philippine reefs (Hughes *et al.* 2022). This supports the theory that there might be a difference in successional stages, which could be reflected in the associated fish community.

4.3.2 Discussing the potential of geographic influence

Sahara and Ma'init share the geographical trait of both being positioned north of the coastal tip that protrudes just north of Poblacion (See Figure 6). While this feature is small it may still affect tidal current movements sufficiently to cause substantial changes in the ecosystem of the reefs on either side and could explain the similarity of the two aforementioned sites. This is not supported by the pairwise PERMANOVA, however, which found more differences in species composition between the two southern sites (Poblacion and Maayong tubig) than between either of the northern sites and Maayong tubig. Sahara, interestingly, does not differ significantly in species composition when compared to any of the sites (except at borderline with Poblacion). This indicates that even though there might be less species here, the ones that are present are generally among the most common species observed on all the other sites. This is supported by the naïve occupancy scores (See Appendix 17) and the similarity of species contribution to dissimilarity in the SIMPER test (see Figure 38). It also suggests that geographic location does not greatly affect fish recruitment within the eight kilometers span where the four sites were located, as Sahara might otherwise be expected to differ most in species composition from Maayong tubig (the furthest site). However, this pairing was the most similar according to p-values (See Appendix 22). Whilst knowledge of larval dispersal is ambiguous (Jones, 2015) this finding does not seem to contradict expected recruitment patterns.

4.3.3 Do coral-fish interactions differ on artificial structures?

Sahara mainly differed in one aspect compared to the NRs: The structural layout of the reef surrounding the colonies. There were more non-coral structures surrounding each colony at Sahara. As the colonies grew on artificial structures (Which were typically more complex than a naturally occurring rock face) this is not surprising. Paxton *et al*. (2020) found the substrate material of an AR to influence fish density, with concrete being positively associated. The reef at Sahara is made up of metal cages and hollow concrete bells that readily provide refuge for fish even before seeing any hermatypic coral growth. There is much ambiguity as to whether coral reef fish prefer live coral cover over abiotic or other types of refuges (Siqueira *et al*. 2023) and it is unknown if structural complexity on its own attracts fish. Should that be the case, however, then the nature of these artificial structures could explain the potentially high N at Sahara. However, the large presence of non-coral structures may also include elements that could reduce fish habitats. The artificial structures of Sahara have been found to increasingly be covered by benthic organisms that compete with corals, including the "coral killing sponge" *Terpios hoshinota* (Mcconnell & Waters, 2024). While the knowledge of fish-sponge interactions (or alternatively interactions with other benthic organisms) is sparce, it is generally assumed that they support smaller, less diverse fish assemblages than corals (Coppock *et al*. 2022). Similarly to what was observed across the NRs the surrounding environment of a coral colony at Sahara appears to influence the *N* of the colony, but not the *S*. However, the relationships were much more complex and non-linear which could indicate that the observed effects were coincidental and an artefact of the limited sample size (See Figure 35). It could also suggest a difference in the expected scale of associated fish assemblages depending on which AR structure the colony was situated on (concrete bell or metal cage). This variable was not considered for this study, and colonies were sampled at random across the whole AR. If for instance an increase of concrete structures positively influences *N,* but the reverse is true for an increase in metal structures, then that would explain the complexity of the relationship observed where these were grouped. Interestingly, the surrounding environment factors were less influential for the NR sites when investigated individually than combined, however this is likely due to less variation in habitat structure within each site. The coral colonies themselves appeared to generally grow structurally similar on the AR as on the NRs with no apparent association between colony size and rugosity and *Acropora* being more rugose than *Pocillopora*. The colonies observed at Sahara were generally large, but less rugose than at the other sites, however, and with smaller interquartile ranges (See Figure 29). This might suggest that there are fewer species of each coral genus present amongst the observed corals, and additionally that the present species grow larger — rather than more — branches. The influence of colony size on the associated fish assemblage does seem to be replicated at Sahara, though with less significance with respect to *S* and more complexity with respect to *N*. The more complex relationship could once again be attributed to the fewer data points at Sahara making it more difficult to calculate a smooth relationship. The less significant relationship with *S* could similarly be explained by fewer samples, though it might also be attributed to the smaller S_{total} observed on the site. Coral colonies will reach species saturation quicker if there generally are less species on the surrounding reef. So even though larger colonies were present at Sahara, they might not accumulate species as quickly as on the NRs and there may be niches left unoccupied. This would cause volume to appear as less influential on *S*. The key point, however, is that coral colony size does influence the associated fish assemblage on the AR, comparably to the NRs. This means it is possible to model how propagated colonies may affect reef fish populations over time.

4.3.4 A different sized fish assemblage

Fish assemblages on colonies at Sahara contained a higher proportion of small (juvenile) fish than those at any other site. Notably, the intermediate size class, which typically dominated assemblages across both coral genera and all NRs, did not constitute the majority at Sahara. This higher proportion of small fish is unexpected, given that they were found to usually be associated with smaller or more structurally complex colonies (See section 4.2.1); Features not typical of Sahara (See Figure 29). This could indicate a difference in recruitment or higher predatory pressure of intermediate individuals. Interestingly, the overall size distribution at Sahara more closely resembles that of broader reef-scale fish communities, where smaller species are more abundant (Kulbicki *et al*. 2015). This study's size classes, however, were not based directly on body length, but rather on estimated ontogenetic stages; size class 1 corresponds to juveniles. Thus, some fish considered "large" in this study could still be small-bodied species. On a reef scale, the expected dominance of small species therefore likely still holds, but this does not necessarily translate to colony-scale patterns.

One potential explanation for the size distribution at Sahara is a difference in pomacentrid community structure. Gregarious or social pomacentrids often form size-based hierarchies (Hattori & Casadevall, 2016), where social aggression might exclude smaller fish leading to an abundance of intermediate-sized fish and a few dominant large individuals. A reduced presence or shift in dominant pomacentrid species could alter this pattern. While 9 of 14 Sahara colonies were inhabited by pomacentrids, three were dominated by *Dascyllus trimaculatus*, which, unlike *D. reticulatus*, tends to associate less with coral colonies as adults (Hattori & Casadevall, 2016). This behavior could explain the dominance of juveniles and the scarcity of larger individuals in those colonies. Notably, *D. trimaculatus* was rarely dominant at other NRs, suggesting a site-specific population difference that may be driving the pattern. Supporting this, *D. trimaculatus* size class 1 was a key contributor to dissimilarity between Sahara and all the NRs (See Figure 38).

Two additional outliers likely influenced Sahara's size distribution due to the small sample size: one *Acropora* colony (APL3) with high structural complexity had many juveniles, consistent with expected rugosity-size relationships; another colony was inhabited solely by juvenile *Gobiodon* spp. These cases may exaggerate trends in Sahara's small dataset. With larger sample sizes, Sahara's assemblage patterns might converge with those of other sites. Nonetheless, if *D. trimaculatus* is genuinely more abundant at Sahara, the distinct size distribution may reflect a consistent, ecologically meaningful difference.

4.3.5 *Acropora* vs *Pocillopora*: Which is better for coral reef restoration?

The two focal genera of this study were chosen both for their abundance on the NRs and for their documented success in AR propagation efforts (Boström-Einarsson *et al*. 2020). They are also the most propagated corals at Sahara (Mcconnell & Waters, 2024). While promoting coral diversity is generally beneficial for ecosystem resilience, there are cases where a genus-specific propagation strategy may be advantageous, depending on the primary goal of the AR. For example, *Pocillopora* has shown higher survivorship than *Acropora* on Sahara (Mcconnell & Waters, 2024). If the purpose is simply to increase coral cover with the least effort this might be the better genus. *Acropora*, conversely, may have higher growth rates (though as previously stated this is not definite) and could thus be preferred if rapid coral expansion is the goal. The coral genus also influences fish assemblage structure, as exemplified by this study. The fitted power law models suggested that *Pocillopora* accumulates fish more efficiently as it grows and has a higher saturation level. Assuming *Acropora* grows faster it might be better for short term fish recruitment, but eventually a *Pocillopora*-dominated reef would host a larger more diverse fish population. These models are estimated from a scarcity of data in the upper size range, especially with regards to *Pocillopora*, so the suggested saturation level is not fully reliable. In fact, *Acropora* both had a higher S_{mean} and N_{mean} than *Pocillopora* in this study. As mentioned, the higher rugosity of *Acropora* likely means that they support more ecological niches, and the higher number of *Acropora* species could similarly increase the number of *Acropora* associated fish species. *Acropora* corals might therefore be necessary to support a more diverse fish community. As mentioned previously, there are certain *Acropora* species that grow tabular structures which creates shaded refuges preferred by larger fish (Kerry & Bellwood, 2015a). In contrast, *Pocillopora* tends to grow in dome-like forms, offering fewer such shelters. This is partially reflected in the observed species of this study. *Cephalopholis* spp., a genus of ecologically and commercially important predatory fish, was only seen on *Acropora* (though with a low naïve occupancy score of 0.2). Thus, while *Pocillopora* may efficiently recruit fish early on, *Acropora* appears to be important for sustaining long-term diversity and supporting larger species.

The stability and resilience of the chosen genus also influence the long-term viability of the AR. The reef at Sahara, for instance, is greatly affected by the aforementioned *Terpios hoshinota*. It is therefore important that the propagated corals are competitively viable. *Acropora* is known to be vulnerable to a range of threats: it is more susceptible to bleaching than *Pocillopora* (Pratchett *et al*. 2013), and it is affected by black- and brown-band diseases (Sisney *et al*. 2018) as well as outbreaks of corallivorous invertebrates such as *Drupella* spp. and *Acanthaster planci* — both of which have been reported in Dauin in recent years (Institute of Marine Research, 2023). As previously suggested *Pocillopora* colonies might act as the more advantageous habitat, maybe because they are more resilient. Thus, many of the observed fish species might compete to inhabit these sooner than *Acropora* colonies. This aligns with *Pocillopora* showing improved survivorship at Sahara. Chase *et al*. (2020) found that pomacentrids changed their association with coral colonies depending on how big a percentage of it was bleached, which suggest that susceptible corals might be less suitable to propagate unto ARs. Unfortunately, while some of the surveyed colonies for this study was impacted, this was not quantified due to time constraints. It is therefore unknown how this variable influences the associated fish assemblage.

The smallest observed colony to have any kind of fish host was a *Pocillopora* colony (190.2 cm^3) (See figure 39), which could suggest that these can recruit fish at smaller sizes. However, it was generally observed for both genera that the smallest corals that acted as fish refuges were ~350 cm^3. This suggests that coral colonies of either genera can begin influencing reef fish populations relatively quickly, depending on their initial size and growth rate. In summary, *Pocillopora* may be the better choice for enhancing survivorship and initial fish recruitment on an AR, while *Acropora* appears necessary to maintain long-term fish diversity and support a broader range of ecological functions.

4.4 Suggestions for future research

It could be valuable to model the relationship between coral colony volume and fish assemblage metrics using alternative approaches inspired by SARs, other than power law models. Michaelis–Menten models could particularly offer a better fit to predict *S* on growing colonies and to assess potential saturation points. However, more data from exceptionally large colonies are needed to reliably estimate at which size saturation might occur. Future fieldwork should therefore prioritize including more large-size categories when selecting target colonies.

Additionally, analyzing colony fish assemblages at the coral species level — rather than only at the genus level — could yield more precise insights, especially for *Acropora*. This was omitted in this study due to time constraints. While detailed imagery exists for each colony, reliable species identification often requires corallite or polyp-level morphological analysis or DNA sampling, neither of which were conducted in the current study. A more feasible alternative could be to categorize colonies by growth form (e.g. tabular, branching, encrusting) alongside genus. This would require defining dimensional criteria for each form, such as height-to-width ratios. Such additional morphological metrics could be extracted from the 3D models. Expanding the study to include other fish-associated coral genera beyond *Acropora* and *Pocillopora* would also be valuable.

The 3D models could also be used to measure average branch length and width which could help estimate volumetric growth rates from known linear growth rates. Additionally, such metrics could be integrated into the rugosity index formular to better account for branch size in addition to branch density. Alternatively, an improved *in situ* imaging method could be developed to capture more detailed data from shaded areas of the colonies, making surface area calculations from RealityCapture more accurate. This would allow rugosity to simply be estimated from a comparison of volume and surface area. Detailed 3D models could furthermore be used to assess the proportion of live, impacted or dead coral tissue, which was omitted in this study.

The use of an SVS to accurately measure fish size and estimate biomass could provide valuable insight into the actual contribution of branching coral habitats to the general fish population on coral reefs. Especially since so many of the observed fish were juvenile or small-bodied species. It could additionally help mitigate potential observers bias in fish size estimates.

Measures of tidal current strength and water sedimentation might provide valuable context, particularly for identifying colonies or sites that are more exposed to harsh conditions. Exposure appeared to influence species composition at both site and colony levels. Additionally, recording weather events could provide useful context for any temporal changes observed.

Finally, while AR colonies generally followed patterns similar to NR colonies, increasing the sample size and diversity of them would strengthen comparisons. Accounting for the AR material to which the colony is attached could additionally provide valuable context in predicting fish-colony interactions.

5. Conclusion

Coral colony size was found to be a strong predictor of associated fish assemblage metrics in both *Acropora* and *Pocillopora* colonies. Both *S* and *N* of associated fishes scaled with colony volume following asymptotic power-law relationships. However, a clear saturation point was less defined for *Pocillopora*, likely due to a limited number of large colonies in the dataset. Interestingly, both *S* and *N* increased more rapidly with colony growth in *Pocillopora* than in *Acropora*, despite this genus appearing to on average support smaller and less diverse fish assemblages. While power-law models provided satisfactory fits, a Michaelis–Menten model may better represent the relationship if fish assemblages indeed approach a true saturation point as colonies grow.

Model predictions aligned with field observations, suggesting that colonies with a volume of approximately 270 – 350 cm^3 can be expected to host fish. This volume might be attainable within a year's growth based on existing data on growth rates for both coral genera. Rugosity also influenced fish assemblages: colonies with higher structural complexity tended to support greater and more diverse fish assemblages, though this effect was dependent on colony volume and was less pronounced in *Pocillopora*. Higher rugosity and smaller colony size were both associated with greater numbers of juvenile fish.

The structure of the surrounding habitat also played a role. More isolated colonies tended to host larger assemblages, particularly when interacting with colony size. Depth and lunar phase were further suggested to influence *N*.

Across all the colonies surveyed, 59 fish species were recorded, though a few were clearly dominant. *Thalassoma lunare* and *Dascyllus reticulatus* were the most frequently observed, with the latter being highly gregarious and the most numerous overall. Most observed fish were juveniles or intermediates. *Acropora* colonies supported higher species diversity, whereas *Pocillopora* colonies were more frequently inhabited, suggesting a potentially advantageous habitat structure.

These ecological patterns were generally mirrored on the AR at Sahara, though with fewer observed species and a higher proportion of juvenile fish — possibly a result of smaller sample sizes. Nonetheless, the findings support the idea that fish assemblage development on propagated coral colonies can be extrapolated from known growth rates and comparisons to NR colonies. Both *Acropora* and *Pocillopora* appear to grow and recruit fish quickly, making them valuable candidates for coral reef restoration initiatives.

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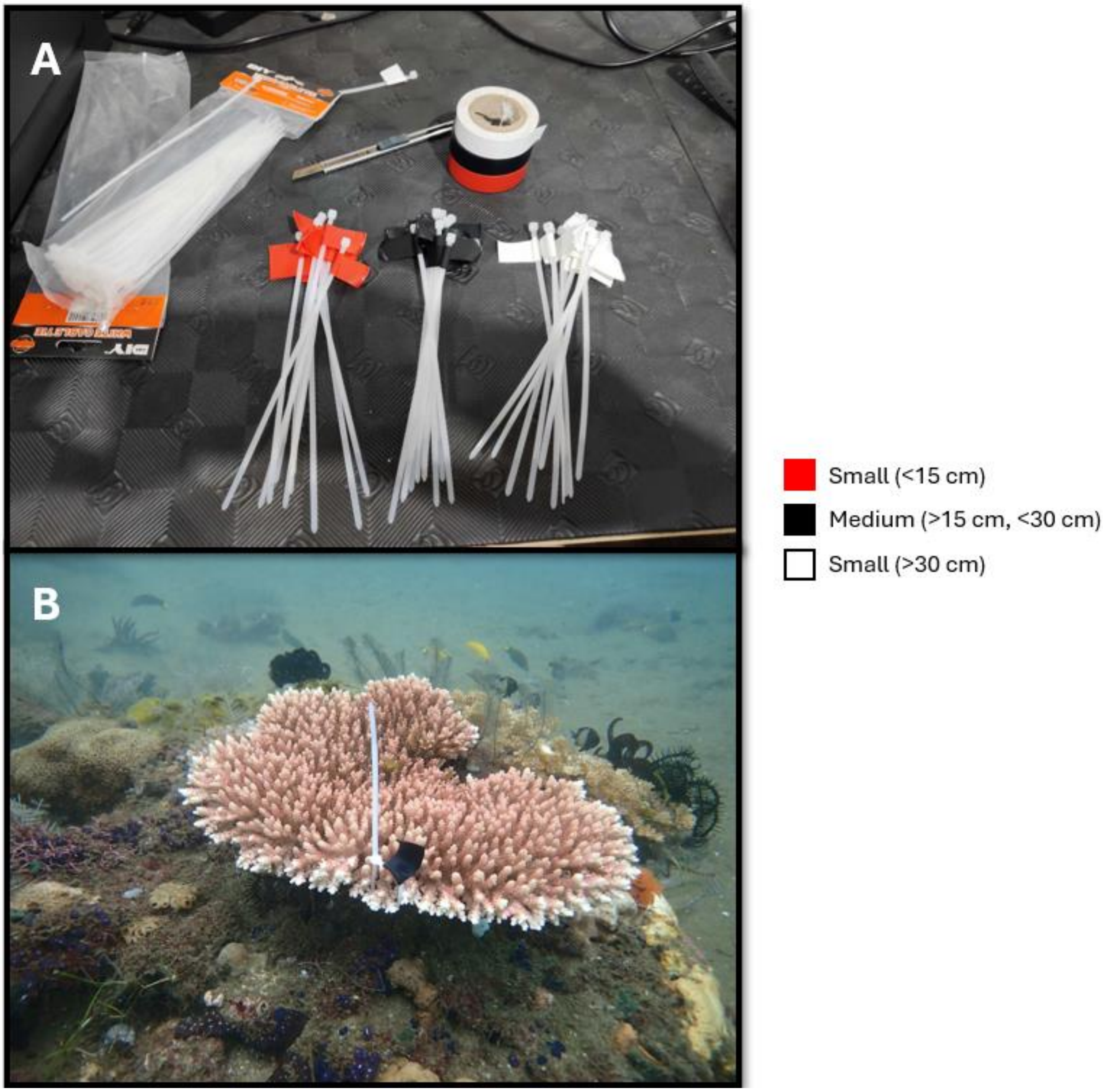
Appendix

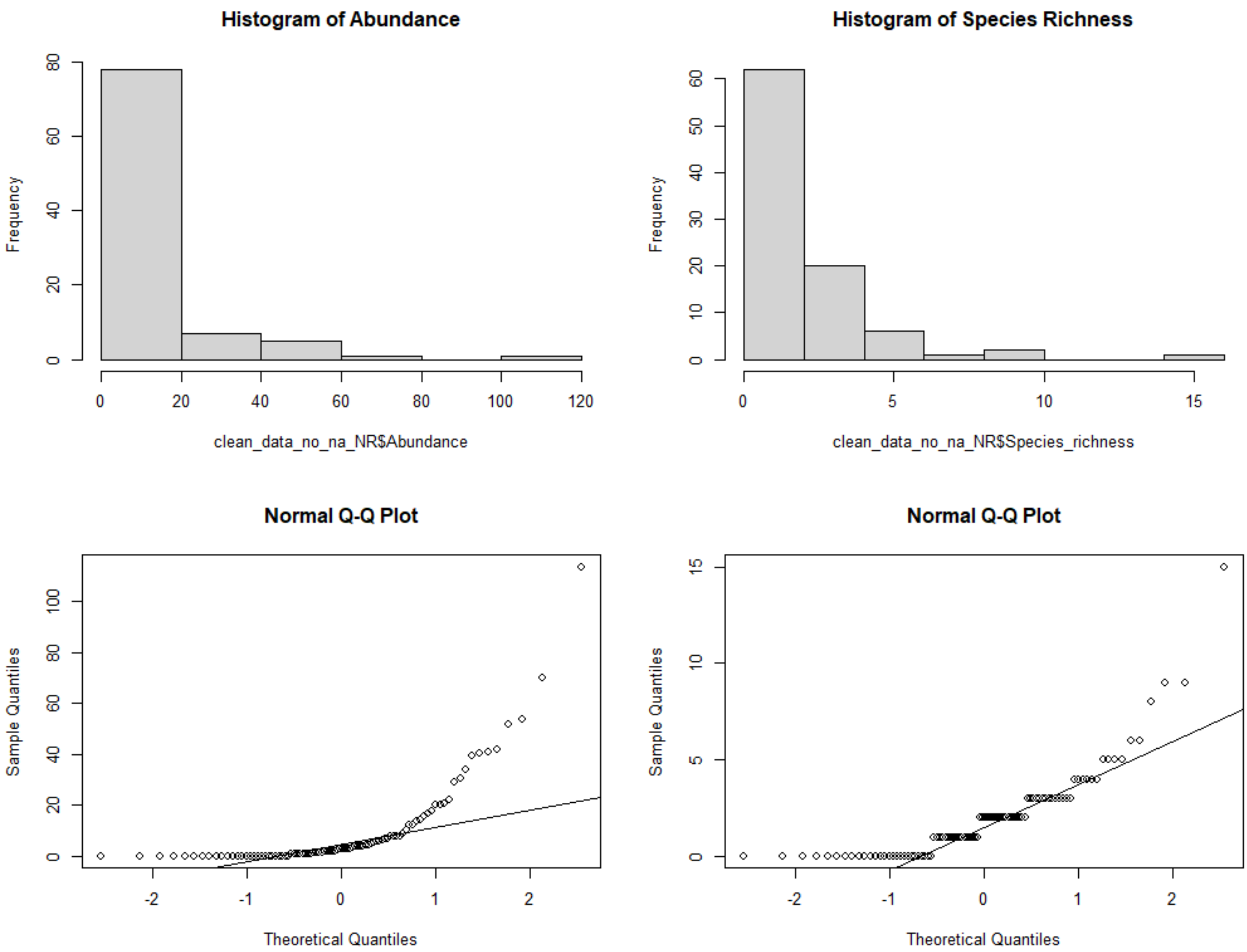
Appendix 1: Tags used to identify coral colonies.

(A): Tags made with electrical tape and zip-ties. **(B):** Example of placement on *Acropora* colony with minimal disturbance

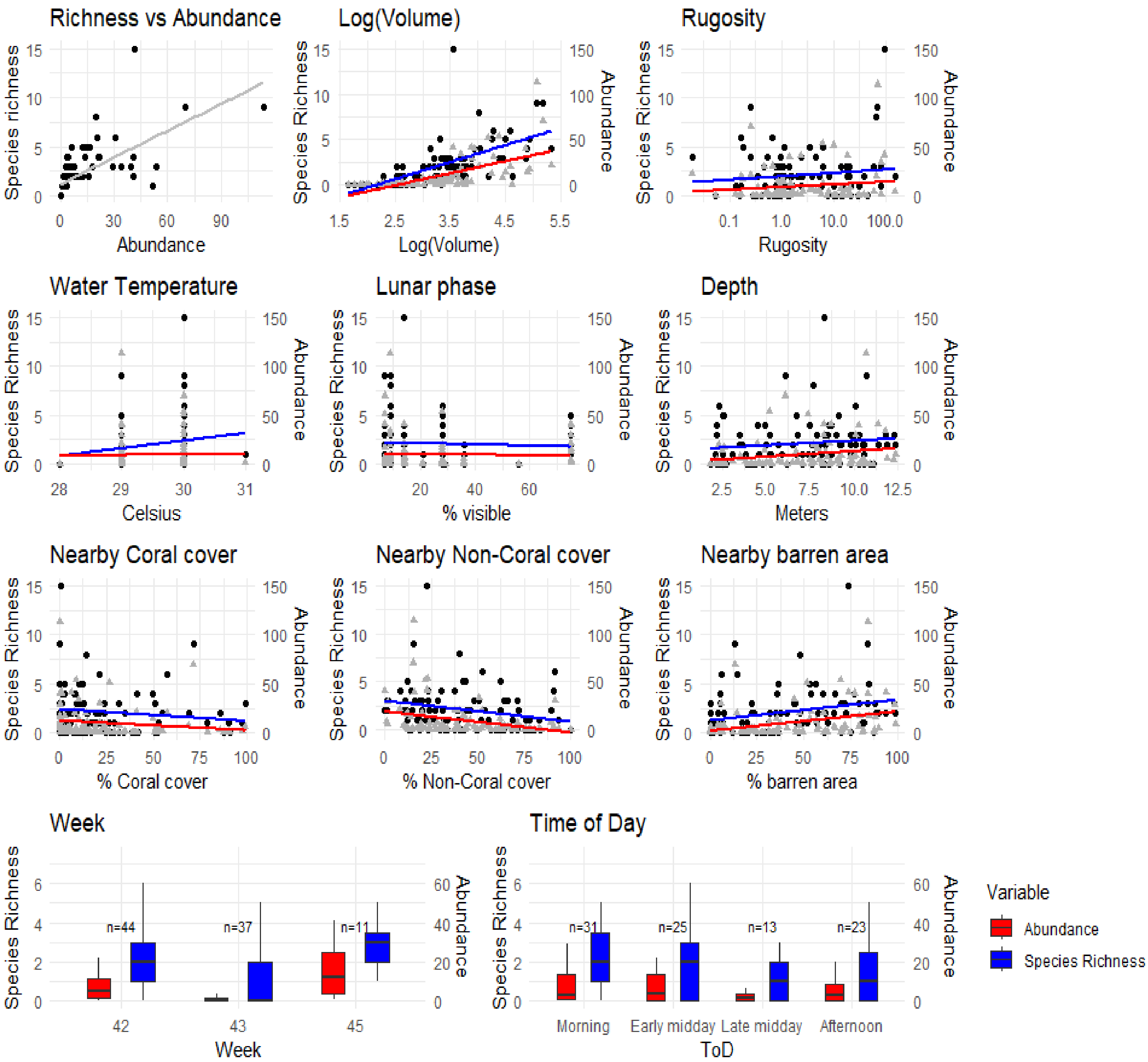


Appendix 2: Scale bar with dimensions

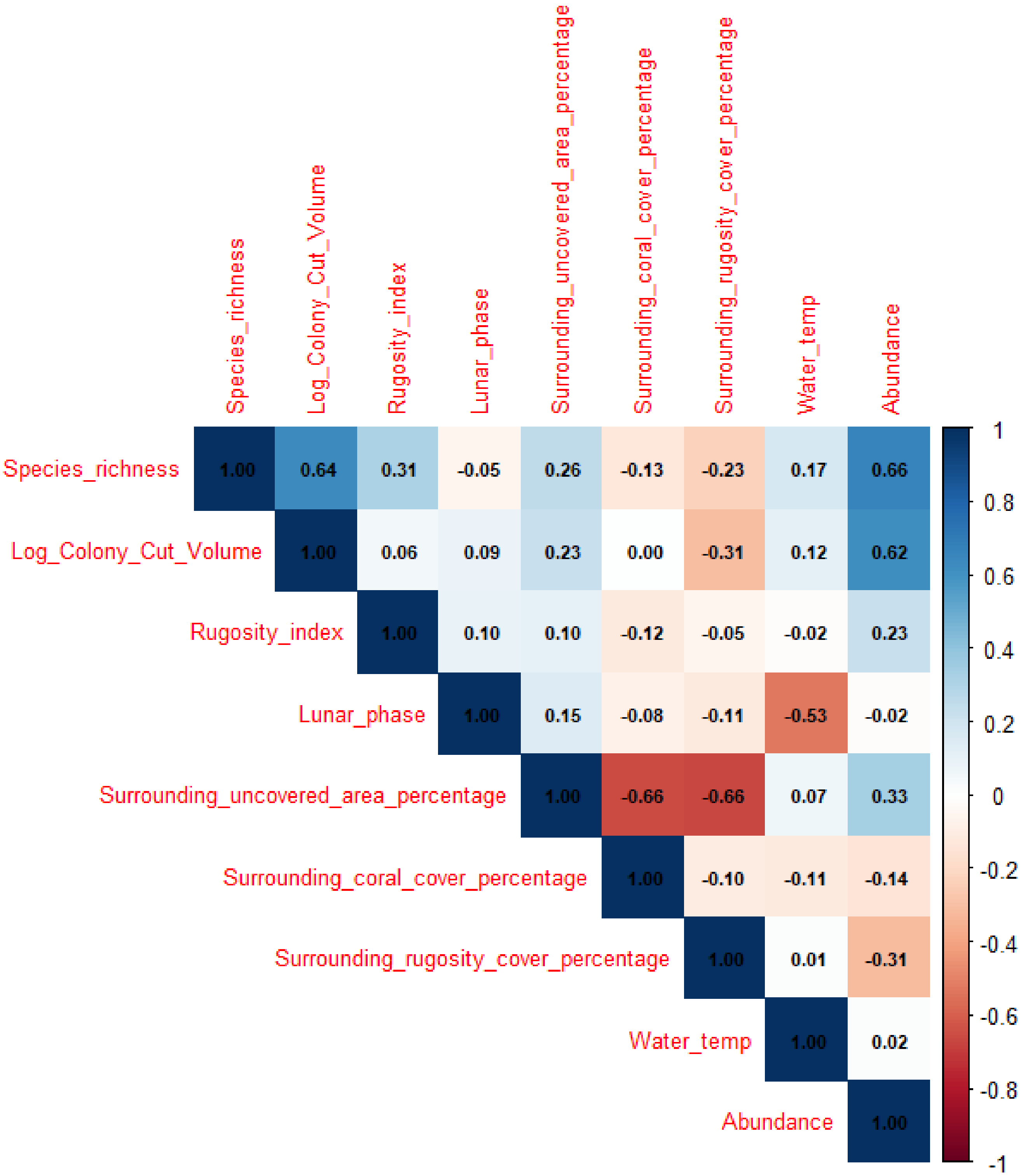
Appendix 3: Normality plots for Abundance and Species Richness



Appendix 4: All Variables plotted against N and S



Appendix 5: Correlation Matrix



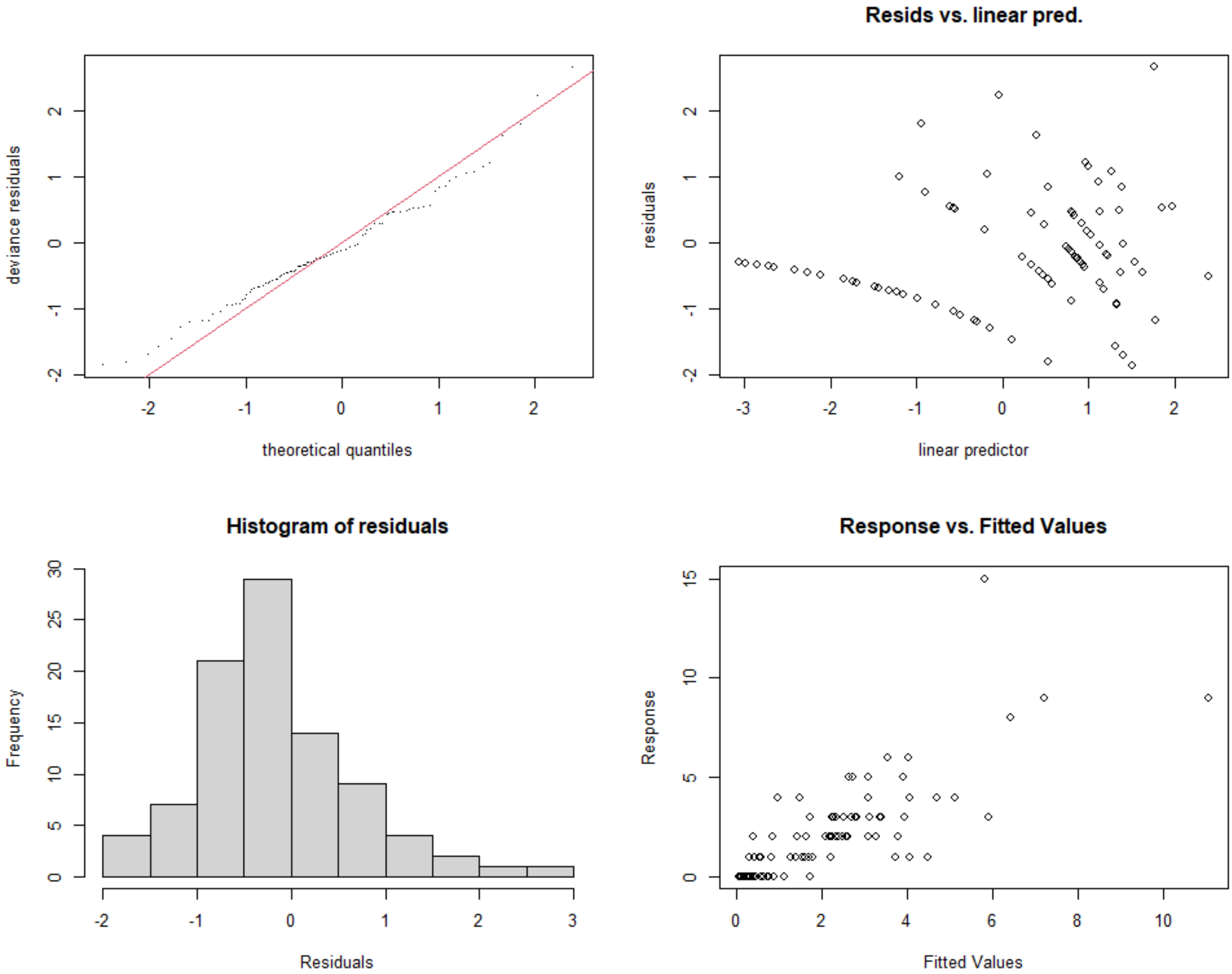
Appendix 6: Call and diagnostics Figure 12A

Summary

```
Family: Negative Binomial(19.923) 
Link function: log 

Formula:
Species_richness ~ s(Log_Colony_Cut_Volume) + s(Rugosity_index) + 
    Week_Factor + Coral_Genus

Parametric coefficients:
                        Estimate Std. Error z value Pr(>|z|)  
(Intercept)               0.1832     0.1802   1.017   0.3094  
Week_Factor43            -0.4175     0.2094  -1.994   0.0462 *
Week_Factor45            -0.3196     0.2340  -1.366   0.1720  
Coral_GenusPocillopora    0.3752     0.2019   1.858   0.0631 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                           edf Ref.df Chi.sq p-value    
s(Log_Colony_Cut_Volume) 3.295  4.121  63.75  <2e-16 ***
s(Rugosity_index)        1.916  2.323  12.24  0.0032 ** 
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =   0.57   Deviance explained = 67.5%
-REML =  139.4  Scale est. = 1         n = 92
```

gam.check

```
Method: REML   Optimizer: outer newton
full convergence after 6 iterations.
Gradient range [-2.112152e-05,-1.915355e-07]
(score 139.396 & scale 1).
Hessian positive definite, eigenvalue range [0.1415132,0.7155366].
Model rank =  22 / 22 

Basis dimension (k) checking results. Low p-value (k-index<1) may
indicate that k is too low, especially if edf is close to k'.

                           k'  edf k-index p-value
s(Log_Colony_Cut_Volume) 9.00 3.30    1.01    0.63
s(Rugosity_index)        9.00 1.92    0.98    0.61
```


deviance residuals
theoretical quantiles
Resids vs. linear pred.
residuals
linear predictor
Histogram of residuals
Frequency
Residuals
Response vs. Fitted Values
Response
Fitted Values

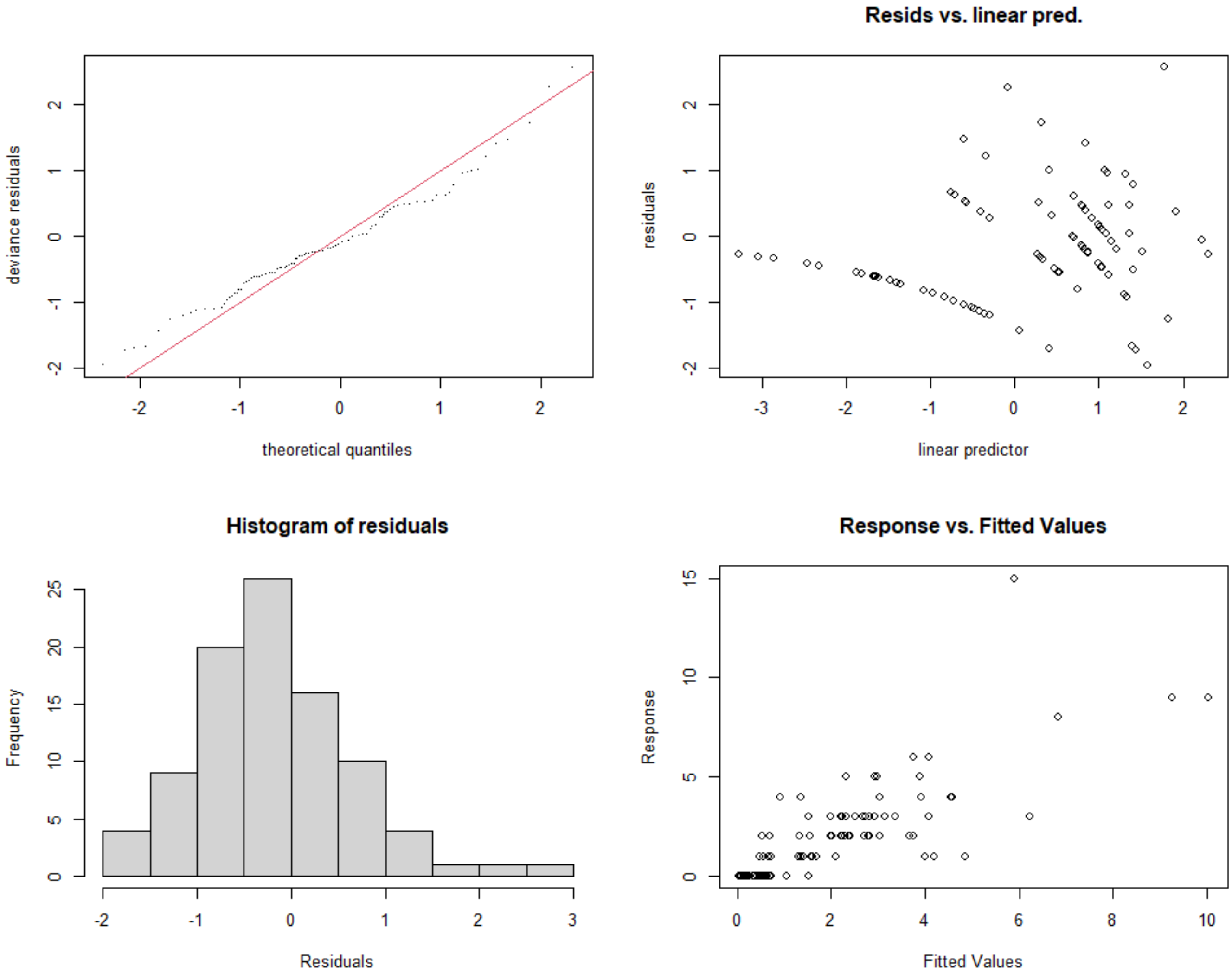
Appendix 7: Call and diagnostics Figure 12B/C

Summary

```
Family: Negative Binomial(17.321)
Link function: log

Formula:
Species_richness ~ s(Log_Colony_Cut_Volume, by = Coral_Genus) +
    s(Rugosity_index) + Week_Factor + Coral_Genus

Parametric coefficients:
                       Estimate Std. Error z value Pr(>|z|)
(Intercept)              0.1344     0.2190   0.613   0.5396
Week_Factor43           -0.4127     0.2077  -1.987   0.0469 *
Week_Factor45           -0.3015     0.2349  -1.284   0.1993
Coral_GenusPocillopora   0.5733     0.2736   2.096   0.0361 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                              edf Ref.df Chi.sq  p-value
s(Log_Colony_Cut_Volume):Coral_GenusAcropora    2.856  3.560  34.61 8.21e-07 ***
s(Log_Colony_Cut_Volume):Coral_GenusPocillopora 1.992  2.492  33.21 1.81e-06 ***
s(Rugosity_index)                               1.851  2.240  10.09  0.00792 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =   0.57   Deviance explained = 67.2%
-REML = 140.88  Scale est. = 1         n = 92
```

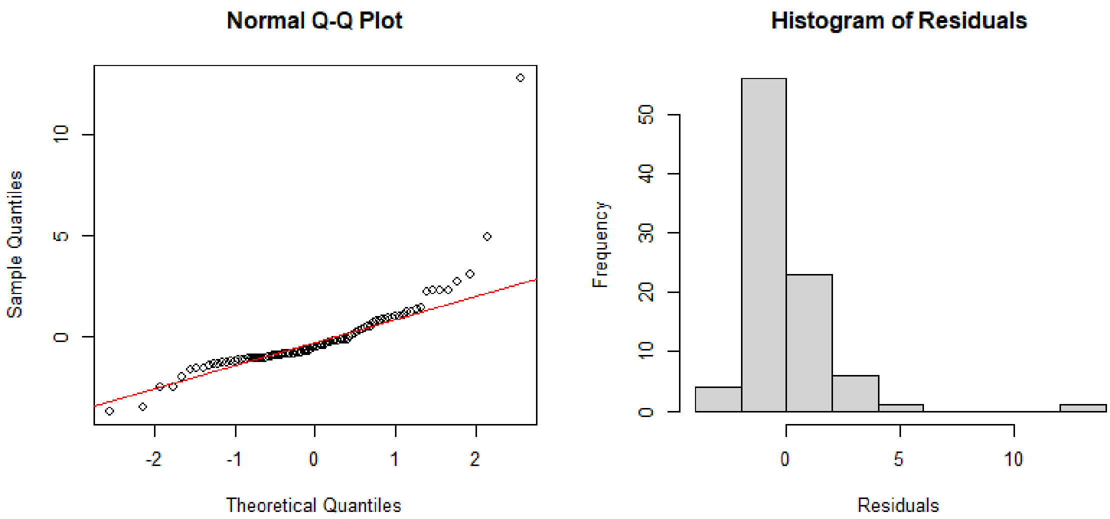
Gam.check

```
Method: REML   Optimizer: outer newton
full convergence after 6 iterations.
Gradient range [-4.709053e-06,1.398068e-08]
(score 140.8818 & scale 1).
Hessian positive definite, eigenvalue range [0.1624311,0.8307069].
Model rank =  31 / 31

Basis dimension (k) checking results. Low p-value (k-index<1) may
indicate that k is too low, especially if edf is close to k'.

                                                  k'  edf k-index p-value
s(Log_Colony_Cut_Volume):Coral_GenusAcropora    9.00 2.86    0.98    0.56
s(Log_Colony_Cut_Volume):Coral_GenusPocillopora 9.00 1.99    0.98    0.56
s(Rugosity_index)                               9.00 1.85    0.97    0.52
```


Resids vs. linear pred.
deviance residuals
theoretical quantiles
residuals
linear predictor
Histogram of residuals
Frequency
Residuals
Response vs. Fitted Values
Response
Fitted Values

Appendix 8: Call and diagnostics Figure 13A

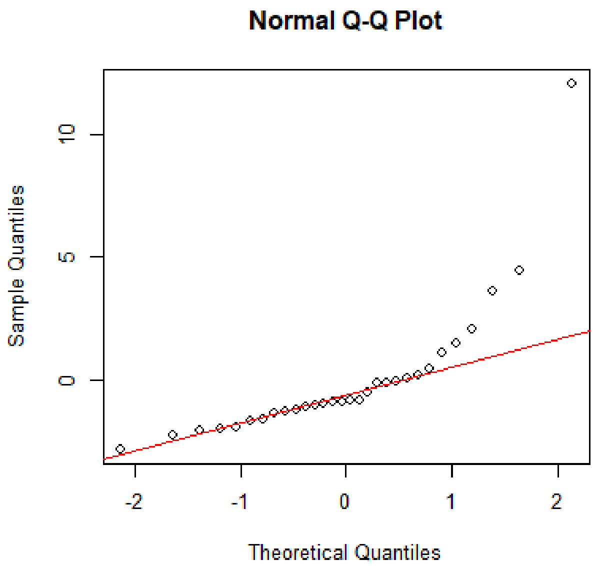
```
Formula: Species_richness ~ a * Colony_Cut_Volume^b

Parameters:
  Estimate Std. Error t value Pr(>|t|)
a  0.19979    0.08328   2.399   0.0185 *
b  0.29549    0.04199   7.037 3.91e-10 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 1.916 on 89 degrees of freedom

Number of iterations to convergence: 7
Achieved convergence tolerance: 5.216e-06
```

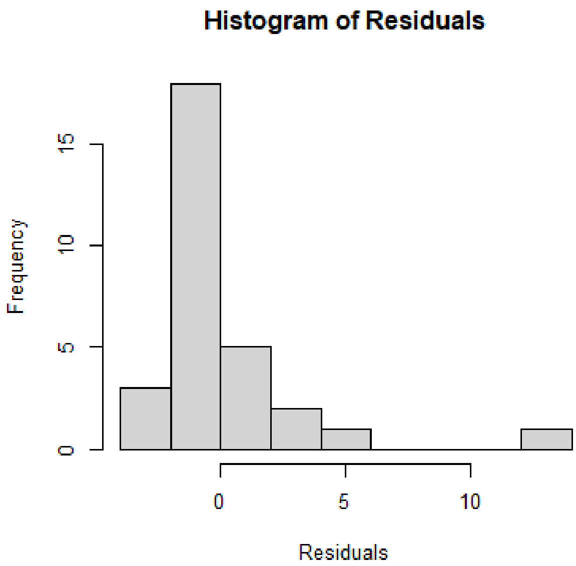


Appendix 9: Call and diagnostics Figure 13B

Acropora

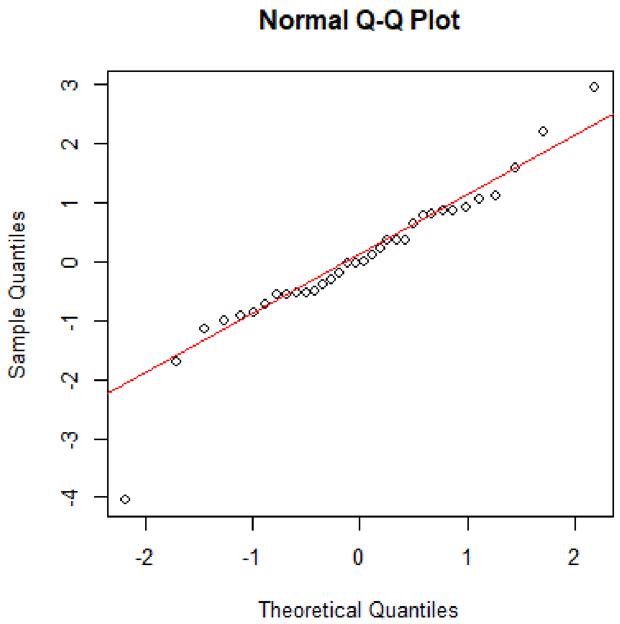
```
Formula: Species_richness ~ a * Colony_Cut_Volume^b

Parameters:
  Estimate Std. Error t value Pr(>|t|)
a  0.73410    0.61546   1.193   0.2430
b  0.17095    0.08603   1.987   0.0568 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 2.851 on 28 degrees of freedom

Number of iterations to convergence: 6
Achieved convergence tolerance: 1.458e-06
```

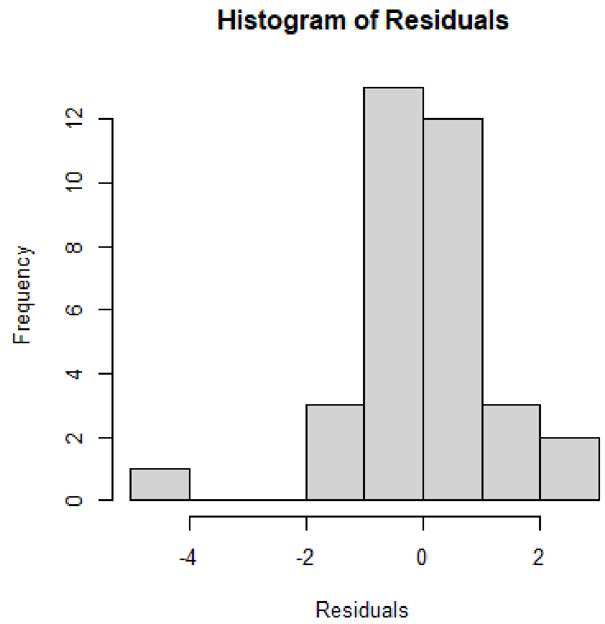




Pocillopora

```
Formula: Species_richness ~ a * Colony_Cut_Volume^b

Parameters:
  Estimate Std. Error t value Pr(>|t|)
a  0.20461    0.08883   2.303   0.0279 *
b  0.30128    0.04488   6.712  1.4e-07 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 1.228 on 32 degrees of freedom

Number of iterations to convergence: 4
Achieved convergence tolerance: 1.574e-06
```





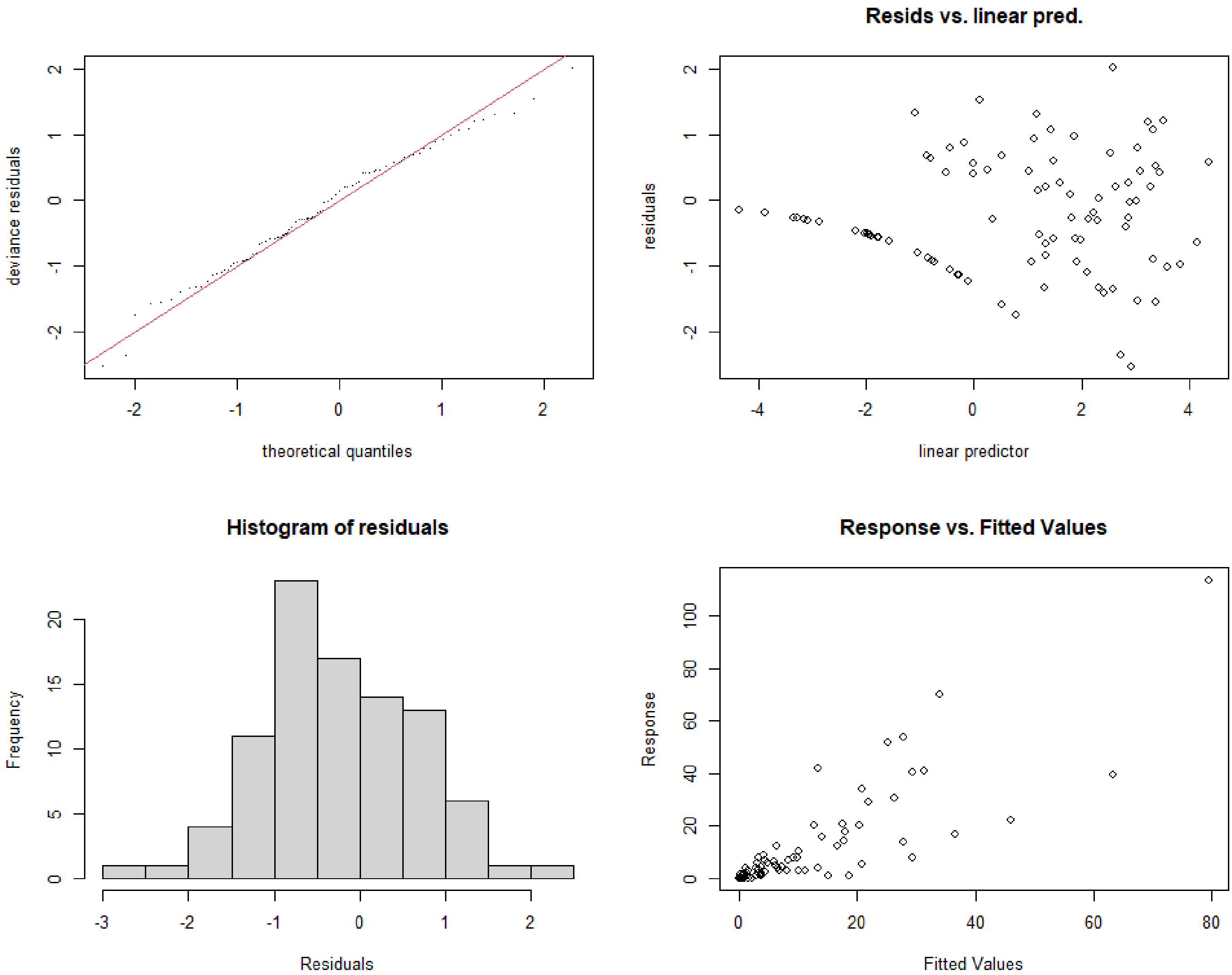
Appendix 10: Call and diagnostics Figure 14A

Summary

```
Family: Negative Binomial(2.326)
Link function: log

Formula:
Abundance ~ s(Log_Colony_Cut_Volume) + s(Colony_depth) + s(Surrounding_uncovered_area_percentage) +
    s(Water_temp, k = 4)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)   0.8689     0.1519    5.72 1.06e-08 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
                                          edf Ref.df  Chi.sq p-value
s(Log_Colony_Cut_Volume)                2.960  3.703 156.604 < 2e-16 ***
s(Colony_depth)                         1.000  1.001  13.571 0.00023 ***
s(Surrounding_uncovered_area_percentage) 1.263  1.475  11.277 0.00495 **
s(Water_temp)                           1.742  2.059   7.841 0.02195 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.675   Deviance explained = 81.6%
-REML =  218.1  Scale est. = 1         n = 92
```

Gam.check

```
Method: REML   Optimizer: outer newton
full convergence after 8 iterations.
Gradient range [-0.0001216607,3.523057e-05]
(score 218.0959 & scale 1).
Hessian positive definite, eigenvalue range [0.0001216438,17.41923].
Model rank =  31 / 31

Basis dimension (k) checking results. Low p-value (k-index<1) may
indicate that k is too low, especially if edf is close to k'.

                                           k'  edf k-index p-value
s(Log_Colony_Cut_Volume)                 9.00 2.96    0.89    0.28
s(Colony_depth)                          9.00 1.00    0.89    0.28
s(Surrounding_uncovered_area_percentage) 9.00 1.26    1.12    0.98
s(Water_temp)                            3.00 1.74    0.85    0.21
```



Resids vs. linear pred.
deviance residuals
theoretical quantiles
residuals
linear predictor
Histogram of residuals
Frequency
Residuals
Response vs. Fitted Values
Response
Fitted Values

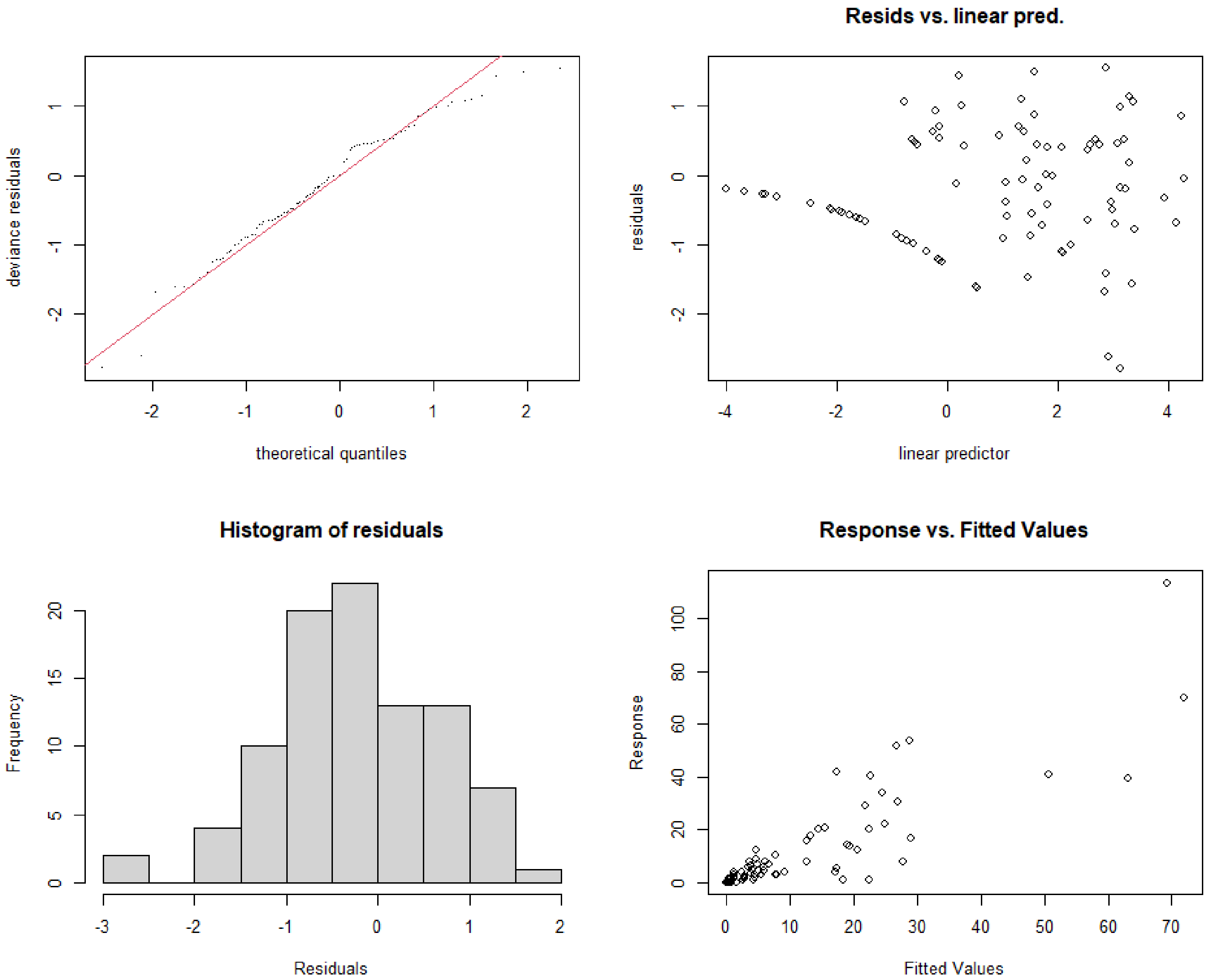
Appendix 11: Call and diagnostics Figure 14B/C

Summary

```
Family: Negative Binomial(2.568)
Link function: log

Formula:
Abundance ~ s(Log_Colony_Cut_Volume, by = Coral_Genus) + s(Colony_depth) +
    s(Surrounding_uncovered_area_percentage) + s(Water_temp,
    k = 4)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)   0.9382     0.1328   7.065  1.6e-12 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                                edf Ref.df  Chi.sq  p-value
s(Log_Colony_Cut_Volume):Coral_GenusAcropora    3.038  3.779 121.585  < 2e-16 ***
s(Log_Colony_Cut_Volume):Coral_GenusPocillopora 1.406  1.702  96.044  < 2e-16 ***
s(Colony_depth)                                 1.001  1.001  14.496 0.000142 ***
s(Surrounding_uncovered_area_percentage)        1.541  1.889  16.521 0.000805 ***
s(Water_temp)                                   1.634  1.986   3.467 0.150730
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.726   Deviance explained =   83%
-REML = 216.78  Scale est. = 1         n = 92
```

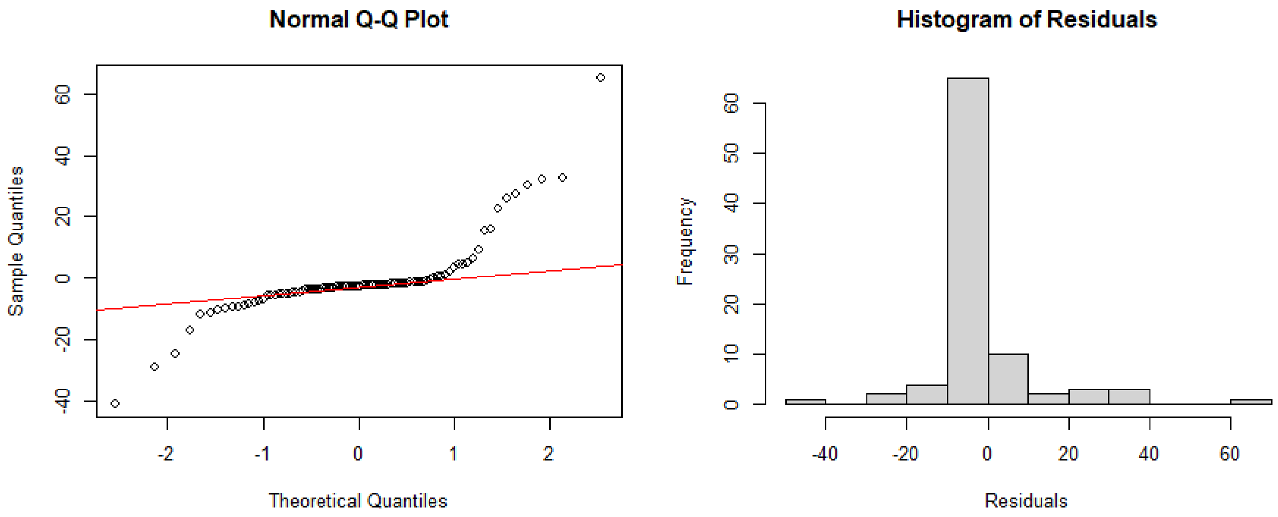
Gam.check

```
Method: REML   Optimizer: outer newton
full convergence after 8 iterations.
Gradient range [-9.913082e-05,2.370951e-05]
(score 216.7777 & scale 1).
Hessian positive definite, eigenvalue range [9.75751e-05,15.79371].
Model rank =  40 / 40

Basis dimension (k) checking results. Low p-value (k-index<1) may
indicate that k is too low, especially if edf is close to k'.

                                                  k'  edf k-index p-value
s(Log_Colony_Cut_Volume):Coral_GenusAcropora    9.00 3.04    0.94    0.43
s(Log_Colony_Cut_Volume):Coral_GenusPocillopora 9.00 1.41    0.94    0.49
s(Colony_depth)                                 9.00 1.00    0.89    0.28
s(Surrounding_uncovered_area_percentage)        9.00 1.54    1.12    0.99
s(Water_temp)                                   3.00 1.63    0.93    0.43
```


deviance residuals
theoretical quantiles
Resids vs. linear pred.
residuals
linear predictor
Histogram of residuals
Frequency
Residuals
Response vs. Fitted Values
Response
Fitted Values

Appendix 12: Call and diagnostics Figure 15A

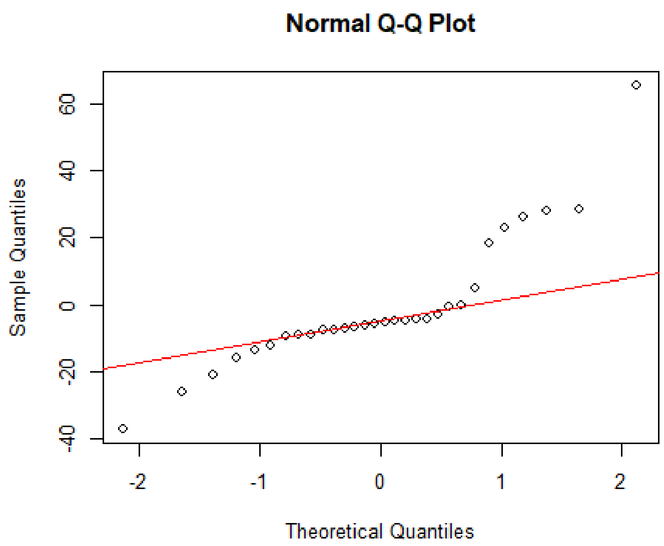
```
Formula: Abundance ~ a * Colony_Cut_Volume^b

Parameters:
  Estimate Std. Error t value Pr(>|t|)
a  0.22471    0.13979   1.607    0.111
b  0.46002    0.05747   8.004 4.26e-12 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 12.97 on 89 degrees of freedom

Number of iterations to convergence: 9
Achieved convergence tolerance: 4.621e-06
```

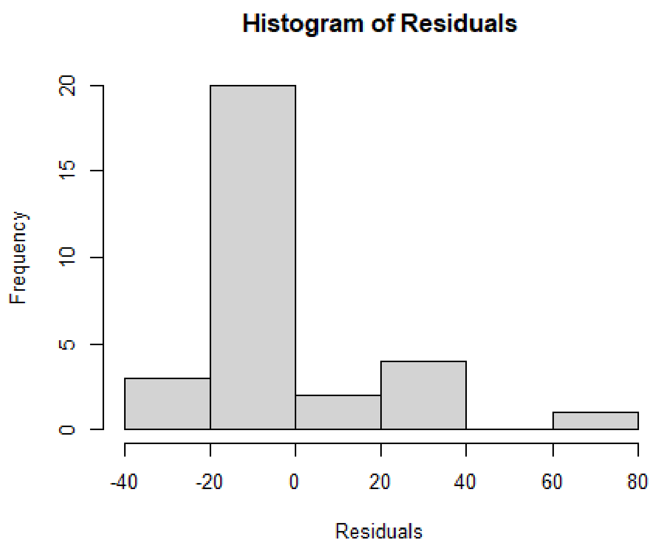


Appendix 13: Call and diagnostics Figure 15B

Acropora

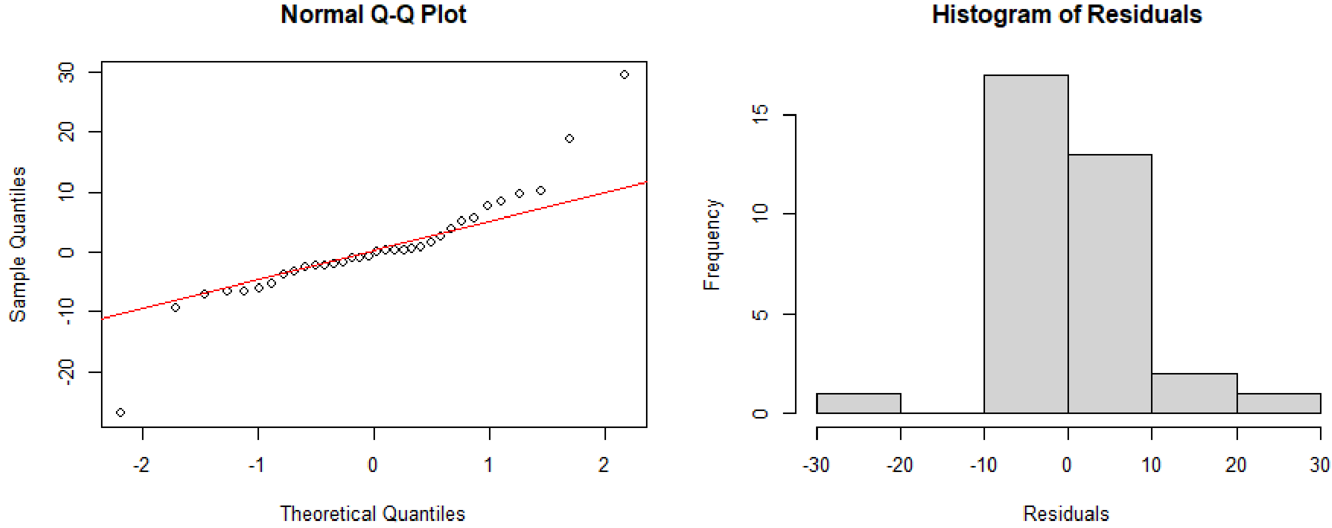
```
Formula: Abundance ~ a * Colony_Cut_Volume^b

Parameters:
  Estimate Std. Error t value Pr(>|t|)
a   0.7546     0.8348   0.904   0.3737
b   0.3558     0.1032   3.449   0.0018 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 19.99 on 28 degrees of freedom

Number of iterations to convergence: 12
Achieved convergence tolerance: 9.301e-06
```





Pocillopora

```
Formula: Abundance ~ a * Colony_Cut_Volume^b

Parameters:
  Estimate Std. Error t value Pr(>|t|)
a  0.05116    0.04739   1.079    0.288
b  0.59270    0.08459   7.007  6.1e-08 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 9.204 on 32 degrees of freedom

Number of iterations to convergence: 6
Achieved convergence tolerance: 5.518e-06
```



Appendix 14: Colony rugosity and volume correlation test

Raw volume data

```
	Pearson's product-moment correlation

data:  clean_data_no_na_NR$Colony_Cut_Volume and clean_data_no_na_NR$Rugosity_index
t = -0.17081, df = 90, p-value = 0.8648
alternative hypothesis: true correlation is not equal to 0
95 percent confidence interval:
 -0.2220013  0.1875063
sample estimates:
        cor 
-0.01800251 
```

VIF

```
Colony_Cut_Volume    Rugosity_index 
         1.000324          1.000324 
```

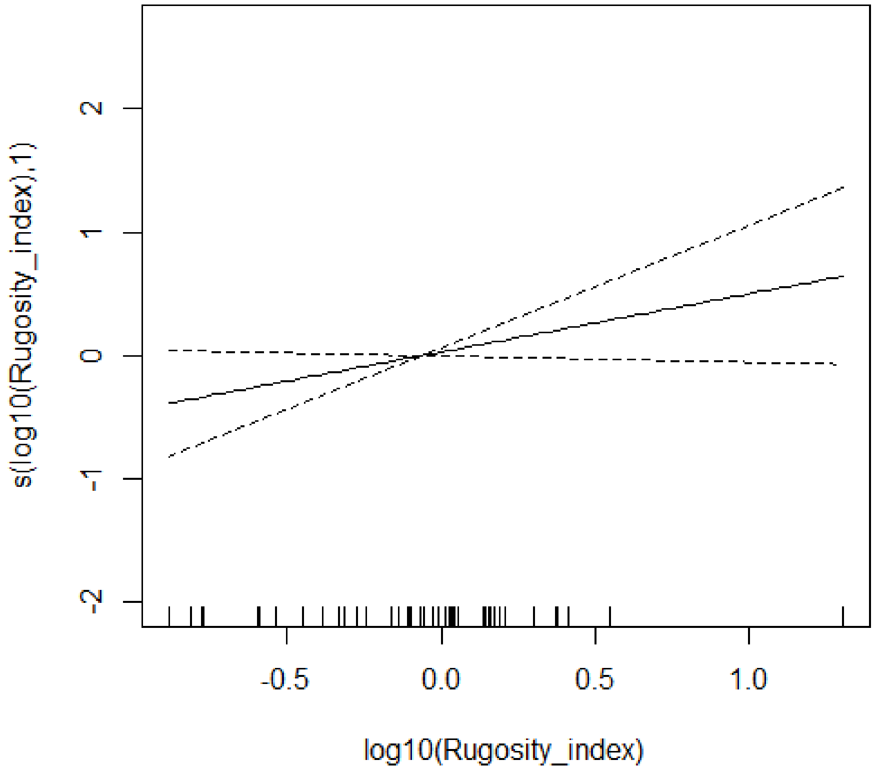
Log10 volume data

```
	Pearson's product-moment correlation

data:  clean_data_no_na_NR$Log_Colony_Cut_Volume and clean_data_no_na_NR$Rugosity_index
t = 0.65485, df = 90, p-value = 0.5142
alternative hypothesis: true correlation is not equal to 0
95 percent confidence interval:
 -0.1378992  0.2698742
sample estimates:
       cor 
0.06886317 
```

VIF

```
Log_Colony_Cut_Volume         Rugosity_index 
             1.004765              1.004765 
```

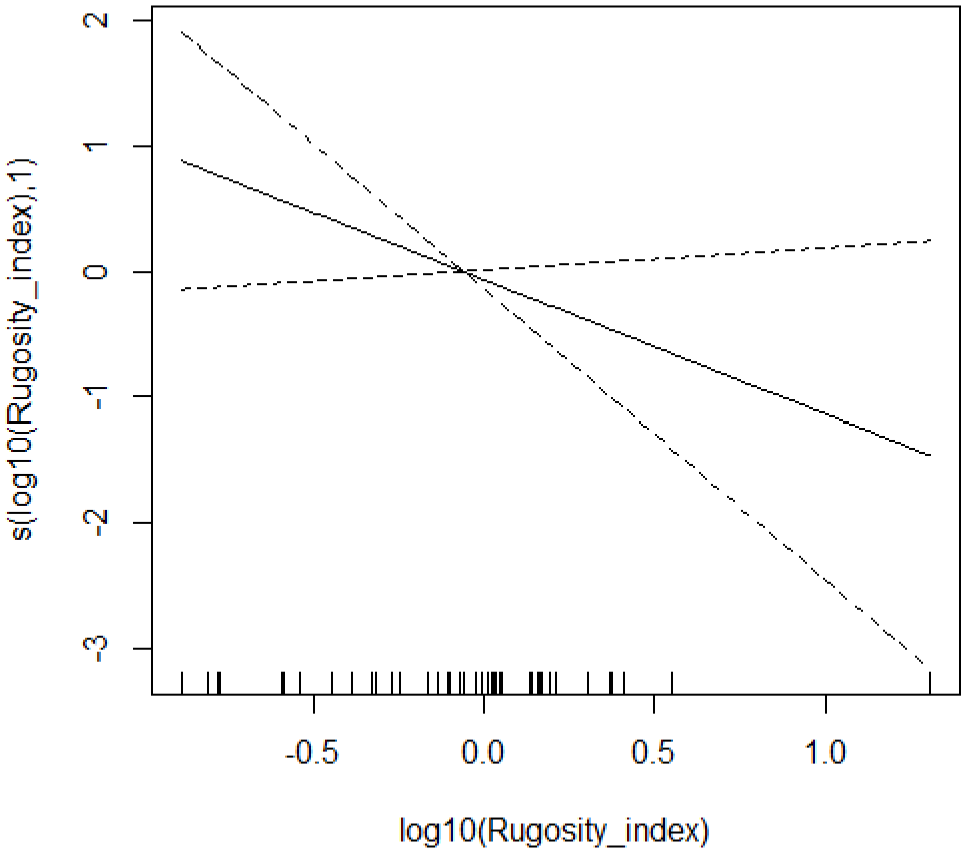
Appendix 15: log10(Rugosity) vs *S* in *Pocillopora*



Summary

```
Family: Negative Binomial(916102.681)
Link function: log

Formula:
Species_richness ~ s(Log_Colony_Cut_Volume) + s(log10(Rugosity_index)) +
    Week_Factor

Parametric coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)    0.53692    0.18229   2.945  0.00322 **
Week_Factor43 -0.40845    0.24367  -1.676  0.09370 .
Week_Factor45  0.06371    0.28510   0.223  0.82316
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
                         edf Ref.df Chi.sq p-value
s(Log_Colony_Cut_Volume)   1      1 39.257  <2e-16 ***
s(log10(Rugosity_index))   1      1  3.263  0.0709 .
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.667   Deviance explained = 63.4%
-REML = 65.914  Scale est. = 1         n = 45
```

Appendix 16: log10(Rugosity) vs *N* in *Pocillopora*



Summary

```
Family: Negative Binomial(0.462)
Link function: log

Formula:
Abundance ~ s(log10(Rugosity_index)) + s(Colony_depth) + s(Surrounding_uncovered_area_percentage)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)   1.8832     0.2281   8.256   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
                                          edf Ref.df Chi.sq p-value
s(log10(Rugosity_index))                    1  1.001  2.949   0.086 .
s(Colony_depth)                             1  1.000  0.980   0.322
s(Surrounding_uncovered_area_percentage)    1  1.000  1.506   0.220
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  -0.139   Deviance explained = 8.67%
-REML = 131.24  Scale est. = 1         n = 45
```

Appendix 17: Species index ranked by total naïve occupancy

Species	Naïve Occupancy							Average			Inconsistency score
	Total	Maayong Tubig	Ma'init	Poblacion	Sahara	Acropora	Pocillopora	Size Class	Colony Abundance	Co-inhabting Species Richness	
Thalassoma lunare	0.44	0.36	0.44	0.40	0.71	0.46	0.43	1.61 ± 0.72	1.70 ± 1.81	6.18 ± 3.30	50.02
Dascyllus reticulatus	0.37	0.39	0.59	0.03	0.50	0.39	0.35	2.12 ± 0.77	28.50 ± 39.24	6.22 ± 3.66	21.01
Dascyllus trimaculatus	0.28	0.27	0.35	0.10	0.50	0.30	0.26	1.69 ± 0.64	2.98 ± 3.07	7.32 ± 3.50	23.37
Pseudocheilinus hexataenia	0.24	0.24	0.15	0.37	0.21	0.11	0.39	1.96 ± 0.63	1.01 ± 0.73	5.04 ± 2.85	64.30
Pomacentrus moluccensis	0.20	0.15	0.03	0.37	0.36	0.25	0.15	1.59 ± 0.66	5.74 ± 7.27	6.27 ± 3.45	38.15
Gobiodon spp.	0.14	0.06	0.09	0.27	0.14	0.19	0.07	1.29 ± NA	1.80 ± 1.90	4.00 ± 1.81	11.79
Chaetodon baronessa	0.10	0.15	0.00	0.10	0.21	0.14	0.06	2.23 ± 0.59	1.00 ± 0.89	8.64 ± 3.70	0.00
Pomacentrus amboinensis	0.10	0.12	0.09	0.13	0.00	0.12	0.07	1.82 ± 0.52	2.39 ± 3.01	8.00 ± 3.44	28.87
Pomacentrus coelestis	0.09	0.09	0.18	0.03	0.00	0.11	0.07	2.06 ± 0.66	3.38 ± 2.81	9.80 ± 3.94	67.26
Cirrhitichthys aprinus	0.08	0.00	0.21	0.00	0.14	0.04	0.13	2.35 ± 0.68	0.94 ± 0.55	5.78 ± 3.77	50.68
Labroides dimidiatus	0.08	0.09	0.15	0.03	0.00	0.14	0.02	1.49 ± 0.64	1.28 ± 0.76	10.00 ± 3.71	30.30
Pomacentrus brachialis	0.08	0.12	0.09	0.00	0.14	0.12	0.04	1.85 ± 0.72	3.46 ± 4.42	8.67 ± 2.96	57.98
Chromis retrofasciata	0.07	0.15	0.00	0.10	0.00	0.11	0.04	1.63 ± 0.65	5.98 ± 4.98	9.25 ± 4.92	25.24
Unknown unknown	0.06	0.09	0.09	0.03	0.00	0.07	0.06	1.00 ± 0.00	1.13 ± 0.50	8.57 ± 5.26	
Ostorhinchus sp.	0.05	0.09	0.06	0.03	0.00	0.07	0.04	2.85 ± 0.45	3.44 ± 4.33	9.50 ± 4.81	25.89
Chromis ternatensis	0.04	0.06	0.00	0.03	0.07	0.07	0.00	1.87 ± 0.34	7.50 ± 11.70	12.50 ± 4.43	16.97
Chromis viridis	0.04	0.09	0.00	0.03	0.00	0.05	0.02	2.26 ± 0.75	8.00 ± 5.37	12.25 ± 3.86	40.48
Chrysiptera springeri	0.04	0.00	0.06	0.07	0.00	0.02	0.06	1.97 ± 0.17	0.73 ± 0.44	9.00 ± 4.83	28.28
Centropyge vroliki	0.03	0.03	0.03	0.00	0.07	0.04	0.02	3.00 ± 0.00	0.25 ± 0.22	12.00 ± 4.36	0.00
Chaetodon kleinii	0.03	0.03	0.03	0.03	0.00	0.05	0.00	2.13 ± 0.33	0.44 ± 0.48	9.67 ± 5.69	
Chrysiptera talboti	0.03	0.03	0.00	0.07	0.00	0.04	0.02	2.42 ± 0.82	0.53 ± 0.41	6.67 ± 2.08	
Dascyllus aruanus	0.03	0.06	0.00	0.03	0.00	0.04	0.02	1.86 ± 0.64	2.31 ± 1.56	11.33 ± 5.03	0.00
Gobiodon prolixus	0.03	0.00	0.09	0.00	0.00	0.04	0.02	1.25 ± 0.43	1.33 ± 0.58	5.33 ± 2.52	
Halichoeres chrysus	0.03	0.00	0.06	0.03	0.00	0.00	0.06	1.49 ± 0.50	1.36 ± 0.97	9.00 ± 5.57	38.57
Ostorhinchus aureus	0.03	0.06	0.03	0.00	0.00	0.05	0.00	3.00 ± 0.00	2.14 ± 1.76	11.33 ± 4.62	0.00
Thalassoma hardwicke	0.03	0.03	0.00	0.07	0.00	0.04	0.02	1.94 ± 0.97	0.94 ± 0.68	6.33 ± 1.15	
Pseudanthias hucthii	0.03	0.03	0.06	0.00	0.00	0.02	0.04	2.71 ± 0.55	6.93 ± 9.30	11.33 ± 5.51	99.80
Acanthurus leucocheilus	0.02	0.06	0.00	0.00	0.00	0.04	0.00	2.00 ± 0.00	0.42 ± 0.47	10.50 ± 4.95	
Canthigaster valentini	0.02	0.00	0.03	0.03	0.00	0.02	0.02	1.29 ± 1.48	0.29 ± 0.06	7.50 ± 4.95	
Halichoeres scapularis	0.02	0.00	0.03	0.03	0.00	0.02	0.02	1.00 ± 0.00	0.42 ± 0.12	6.00 ± 2.83	
Labrichthys unilineatus	0.02	0.03	0.00	0.03	0.00	0.02	0.02	1.25 ± 0.43	0.67 ± 0.47	6.50 ± 0.71	
Parapercis tetracantha	0.02	0.03	0.03	0.00	0.00	0.02	0.02	2.50 ± 0.50	1.00 ± 0.00	8.00 ± 5.66	
Plectorhinchus vittatus	0.02	0.00	0.03	0.03	0.00	0.04	0.00	3.00 ± 0.00	0.83 ± 0.24	9.00 ± 2.83	
Pomacentrus adelus	0.02	0.06	0.00	0.00	0.00	0.04	0.00	3.00 ± 0.00	1.62 ± 0.18	5.50 ± 4.95	7.86
Arothron hispidus	0.01	0.03	0.00	0.00	0.00	0.02	0.00	3.00 ± 0.00	1.00 ± NA	12.00 ± NA	
Arothron nigropunctatus	0.01	0.00	0.03	0.00	0.00	0.02	0.00	3.00 ± 0.00	0.25 ± NA	7.00 ± NA	
Cantherhines dumerili	0.01	0.00	0.03	0.00	0.00	0.00	0.02	3.00 ± 0.00	0.17 ± NA	15.00 ± NA	
Centropyge tibicen	0.01	0.03	0.00	0.00	0.00	0.02	0.00	3.00 ± 0.00	0.33 ± NA	14.00 ± NA	
Cephalopholis argus	0.01	0.03	0.00	0.00	0.00	0.02	0.00	3.00 ± 0.00	0.25 ± NA	9.00 ± NA	
Cephalopholis miniata	0.01	0.03	0.00	0.00	0.00	0.02	0.00	3.00 ± 0.00	0.08 ± NA	14.00 ± NA	
Chaetodon octofasciatus	0.01	0.00	0.00	0.03	0.00	0.02	0.00	2.00 ± 0.00	3.00 ± NA	16.00 ± NA	47.14
Cheilinus trilobatus	0.01	0.03	0.00	0.00	0.00	0.02	0.00	2.00 ± 0.00	0.17 ± NA	9.00 ± NA	
Cheilodipterus isostigmus	0.01	0.03	0.00	0.00	0.00	0.00	0.02	2.00 ± 0.00	1.00 ± NA	3.00 ± NA	
Coris batuensis	0.01	0.00	0.00	0.03	0.00	0.00	0.02	1.50 ± 0.50	2.00 ± NA	7.00 ± NA	0.00
Ctenochaetus striatus	0.01	0.03	0.00	0.00	0.00	0.02	0.00	3.00 ± 0.00	1.08 ± NA	9.00 ± NA	10.88
Diproctacanthus xanthurus	0.01	0.00	0.00	0.03	0.00	0.02	0.00	1.00 ± 0.00	2.00 ± NA	7.00 ± NA	0.00
Halichoeres nebulosus	0.01	0.00	0.03	0.00	0.00	0.00	0.02	2.00 ± 0.00	1.00 ± NA	5.00 ± NA	
Halichoeres sp.	0.01	0.03	0.00	0.00	0.00	0.02	0.00	1.00 ± 0.00	0.25 ± NA	7.00 ± NA	
Hemigymnus fasciatus	0.01	0.00	0.00	0.03	0.00	0.02	0.00	3.00 ± 0.00	0.25 ± NA	9.00 ± NA	
Myripristis kuntee	0.01	0.00	0.00	0.03	0.00	0.02	0.00	3.00 ± 0.00	3.00 ± NA	7.00 ± NA	47.14
Neoglyphidodon melas	0.01	0.03	0.00	0.00	0.00	0.02	0.00	3.00 ± 0.00	0.75 ± NA	14.00 ± NA	
Ostorhinchus compressus	0.01	0.03	0.00	0.00	0.00	0.00	0.02	1.00 ± 0.00	1.00 ± NA	5.00 ± NA	
Ostorhinchus nigrofasciatus	0.01	0.00	0.00	0.03	0.00	0.02	0.00	1.46 ± 0.50	2.17 ± NA	9.00 ± NA	10.88
Parapercis clathrata	0.01	0.00	0.00	0.03	0.00	0.00	0.02	2.00 ± 0.00	1.00 ± NA	7.00 ± NA	
Plectroglyphidodon dickii	0.01	0.03	0.00	0.00	0.00	0.00	0.02	3.00 ± 0.00	1.17 ± NA	7.00 ± NA	
Pomacentrus chrysurus	0.01	0.00	0.00	0.03	0.00	0.02	0.00	2.00 ± 0.00	2.00 ± NA	4.00 ± NA	0.00
Pomacentrus philippinus	0.01	0.00	0.00	0.03	0.00	0.02	0.00	1.80 ± 0.40	5.00 ± NA	16.00 ± NA	28.28
Pomacentrus vaiuli	0.01	0.03	0.00	0.00	0.00	0.02	0.00	2.00 ± 0.00	1.00 ± NA	7.00 ± NA	
Scorpaenopsis sp.	0.01	0.03	0.00	0.00	0.00	0.00	0.02	2.00 ± 0.00	1.00 ± NA	3.00 ± NA	
Sebastapistes strongia	0.01	0.00	0.00	0.03	0.00	0.02	0.00	2.00 ± 0.00	1.00 ± NA	9.00 ± NA	

Appendix 18: Species classification table

Color represents IUCN red list status: White = No status, Green = Least concern, Yellow = Near threatened, red = endangered or worse

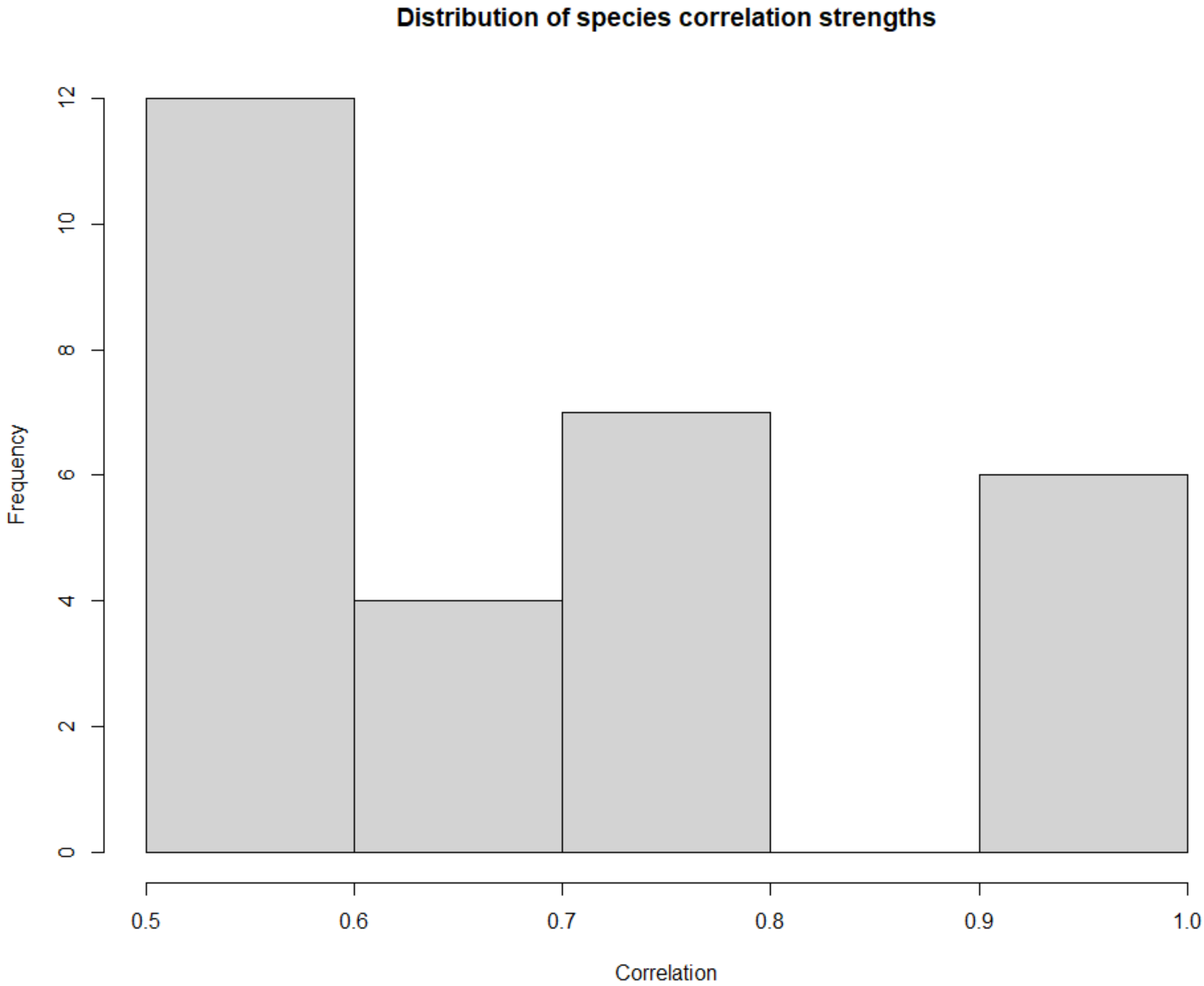
Family	Genus	Species
Acanthuridae	Acanthurus	Acanthurus leucocheilus
Acanthuridae	Ctenochaetus	Ctenochaetus striatus
Apogonidae	Cheilodipterus	Cheilodipterus isostigmus
Apogonidae	Ostorhinchus	Ostorhinchus aureus
Apogonidae	Ostorhinchus	Ostorhinchus compressus
Apogonidae	Ostorhinchus	Ostorhinchus nigrofasciatus
Apogonidae	Ostorhinchus	Ostorhinchus spp.
Chaetodontidae	Chaetodon	Chaetodon baronessa
Chaetodontidae	Chaetodon	Chaetodon kleinii
Chaetodontidae	Chaetodon	Chaetodon octofasciatus
Cirrhitidae	Cirrhitichthys	Cirrhitichthys aprinus
Gobiidae	Gobiodon	Gobiodon prolixus
Gobiidae	Gobiodon	Gobiodon spp.
Haemulidae	Plectorhinchus	Plectorhinchus vittatus
Holocentridae	Myripristis	Myripristis kuntee
Labridae	Cheilinus	Cheilinus trilobatus
Labridae	Coris	Coris batuensis
Labridae	Diproctacanthus	Diproctacanthus xanthurus
Labridae	Halichoeres	Halichoeres chrysus
Labridae	Halichoeres	Halichoeres nebulosus
Labridae	Halichoeres	Halichoeres scapularis
Labridae	Halichoeres	Halichoeres sp.
Labridae	Hemigymnus	Hemigymnus fasciatus
Labridae	Labrichthys	Labrichthys unilineatus
Labridae	Labroides	Labroides dimidiatus
Labridae	Pseudocheilinus	Pseudocheilinus hexataenia
Labridae	Thalassoma	Thalassoma hardwicke
Labridae	Thalassoma	Thalassoma lunare
Monacanthidae	Cantherhines	Cantherhines dumerili
Mullidae	Parapercis	Parapercis clathrata
Mullidae	Parapercis	Parapercis tetracantha
Pomacanthidae	Centropyge	Centropyge tibicen
Pomacanthidae	Centropyge	Centropyge vroliki

Pomacentridae	Chromis	Chromis retrofasciata
Pomacentridae	Chromis	Chromis ternatensis
Pomacentridae	Chromis	Chromis viridis
Pomacentridae	Chrysiptera	Chrysiptera springeri
Pomacentridae	Chrysiptera	Chrysiptera talboti
Pomacentridae	Dascyllus	Dascyllus aruanus
Pomacentridae	Dascyllus	Dascyllus reticulatus
Pomacentridae	Dascyllus	Dascyllus trimaculatus
Pomacentridae	Neoglyphidodon	Neoglyphidodon melas
Pomacentridae	Plectroglyphidodon	Plectroglyphidodon dickii
Pomacentridae	Pomacentrus	Pomacentrus adelus
Pomacentridae	Pomacentrus	Pomacentrus amboinensis
Pomacentridae	Pomacentrus	Pomacentrus brachialis
Pomacentridae	Pomacentrus	Pomacentrus chrysurus
Pomacentridae	Pomacentrus	Pomacentrus coelestis
Pomacentridae	Pomacentrus	Pomacentrus moluccensis
Pomacentridae	Pomacentrus	Pomacentrus philippinus
Pomacentridae	Pomacentrus	Pomacentrus vaiuli
Scorpaenidae	Scorpaenopsis	Scorpaenopsis sp.
Scorpaenidae	Sebastapistes	Sebastapistes strongia
Serranidae	Cephalopholis	Cephalopholis argus
Serranidae	Cephalopholis	Cephalopholis miniata
Serranidae	Pseudanthias	Pseudanthias huchtii
Siganidae	Diproctacanthus	Diproctacanthus xanthurus
Tetraodontidae	Arothron	Arothron hispidus
Tetraodontidae	Arothron	Arothron nigropunctatus
Tetraodontidae	Canthigaster	Canthigaster valentini

Appendix 19: Species association statistics

Degree refers to number of direct connections with other species. Betweenness refers to frequency of connecting components. Colony count is the number of colonies the species were observed on.

	species	degree	betweenness	colony_count
Dascyllus_reticulatus	Dascyllus_reticulatus	0	0	33
Dascyllus_trimaculatus	Dascyllus_trimaculatus	0	0	20
Thalassoma_lunare	Thalassoma_lunare	0	0	32
Gobiodon_prolixus	Gobiodon_prolixus	0	0	2
Plectorhinchus_vittatus	Plectorhinchus_vittatus	0	0	1
Pomacentrus_brachialis	Pomacentrus_brachialis	0	0	7
Pomacentrus_coelestis	Pomacentrus_coelestis	0	0	8
Chaetodon_kleinii	Chaetodon_kleinii	0	0	1
Cirrhitichthys_aprinus	Cirrhitichthys_aprinus	0	0	7
Labroides_dimidiatus	Labroides_dimidiatus	0	0	5
Arothron_nigropunctatus	Arothron_nigropunctatus	0	0	1
Pomacentrus_amboinensis	Pomacentrus_amboinensis	1	0	9
Gobiodon_sp.	Gobiodon_sp.	0	0	9
Centropyge_vroliki	Centropyge_vroliki	2	0	1
Halichoeres_chrysus	Halichoeres_chrysus	2	0	2
Ostorhinchus_sp.	Ostorhinchus_sp.	1	0	4
Pomacentrus_moluccensis	Pomacentrus_moluccensis	0	0	17
Pseudanthias_huchtii	Pseudanthias_huchtii	3	2	2
Parapercis_tetracantha	Parapercis_tetracantha	0	0	2
Halichoeres_nebulosus	Halichoeres_nebulosus	0	0	1
Pseudocheilinus_hexataenia	Pseudocheilinus_hexataenia	0	0	18
Chrysiptera_springeri	Chrysiptera_springeri	3	10	3
Chromis_retrofasciata	Chromis_retrofasciata	1	0	8
Chaetodon_baronessa	Chaetodon_baronessa	0	0	8
Chromis_ternatensis	Chromis_ternatensis	3	10	2
Ostorhinchus_aureus	Ostorhinchus_aureus	0	0	2
Cephalopholis_argus	Cephalopholis_argus	2	0	1
Ctenochaetus_striatus	Ctenochaetus_striatus	2	0	1
Pomacentrus_adelus	Pomacentrus_adelus	2	0	2
Chromis_viridis	Chromis_viridis	4	24	3
Dascyllus_aruanus	Dascyllus_aruanus	4	10	3
Pomacentrus_vaiuli	Pomacentrus_vaiuli	0	0	1
Labrichthys_unilineatus	Labrichthys_unilineatus	2	0	2
Plectroglyphidodon_dickii	Plectroglyphidodon_dickii	3	18	1
Thalassoma_hardwicke	Thalassoma_hardwicke	2	0	2
Cheilodipterus_isostigmus	Cheilodipterus_isostigmus	0	0	1
Chrysiptera_talboti	Chrysiptera_talboti	1	0	2
Ostorhinchus_compressus	Ostorhinchus_compressus	1	0	1
Hemigymnus_fasciatus	Hemigymnus_fasciatus	2	0	1
Ostorhinchus_nigrofasciatus	Ostorhinchus_nigrofasciatus	2	0	1
Sebastapistes_strongia	Sebastapistes_strongia	2	0	1
Chaetodon_octofasciatus	Chaetodon_octofasciatus	5	14	1
Pomacentrus_philippinus	Pomacentrus_philippinus	5	14	1
Myripristis_kuntee	Myripristis_kuntee	0	0	1
Halichoeres_scapularis	Halichoeres_scapularis	1	0	1
Pomacentrus_chrysurus	Pomacentrus_chrysurus	1	0	1
Diproctacanthus_xanthurus	Diproctacanthus_xanthurus	0	0	1
Coris_batuensis	Coris_batuensis	1	0	1



Distribution of species correlation strengths
Frequency
0
2
4
6
8
10
12
0.5
0.6
0.7
0.8
0.9
1.0
Correlation

Appendix 20: Overview of changes in primary fish species between replicated observations

	Site	Colony_ID	From	To	Abundance_Before	Abundance_After
	<chr>	<chr>	<chr>	<chr>	<dbl>	<dbl>
1	Ma'init	APM2	Pomacentrus coelestis	Dascyllus reticulatus	7.83	11.3
2	Ma'init	APM4	Dascyllus reticulatus	Thalassamo lunare	1	1
3	Ma'init	PPM4	Gobiodon sp.	Dascyllus reticulatus	2	3
4	Ma'init	PPS3	Thalassamo lunare	Pseudocheilinus hexata…	1.75	2
5	Poblacion	APL5	Pomacentrus moluccensis	Pomacentrus chrysurus	6	1
6	Poblacion	APM2	Pomacentrus moluccensis	Gobiodon sp.	6	10.4
7	Maayong tubig	PPL2	Pseudocheilinus hexataenia	Scorpaenopsis sp.	1	1
8	Maayong tubig	PPM1	Thalassamo lunare	Pseudocheilinus hexata…	2.58	1.83

Appendix 21: Wilcoxon signed rank test between replicates

Differences between replicates

	Metric	Test	p_value
1	Abundance	Wilcoxon signed-rank test	0.02359294
2	Species_richness	Wilcoxon signed-rank test	0.15045727
3	Percentage_Size1	Wilcoxon signed-rank test	0.89832850
4	Percentage_Size2	Wilcoxon signed-rank test	0.11377369
5	Percentage_Size3	Wilcoxon signed-rank test	0.29185611

	Metric	Changed	Total	Proportion_Changed
1	Primary_Genus	7	37	0.189
2	Primary_Species	8	37	0.216

Difference in change between coral genera

	Metric	Test	p_value
1	Abundance	Wilcoxon rank-sum	0.91898196
2	Species_richness	Wilcoxon rank-sum	0.87938573
3	Percentage_Size1	Wilcoxon rank-sum	0.05298664
4	Percentage_Size2	Wilcoxon rank-sum	0.09273332
5	Percentage_Size3	Wilcoxon rank-sum	0.50631912

Appendix 22: PERMANOVA test between sites with ad hoc and post hoc tests

PERMANOVA

```
Permutation test for adonis under reduced model
Permutation: free
Number of permutations: 999

adonis2(formula = comm_matrix ~ Site, data = meta_data, method = "bray")
         Df SumOfSqs     R2      F Pr(>F)    
Model     3    3.178 0.0932 2.6381  0.001 ***
Residual 77   30.919 0.9068                  
Total    80   34.097 1.0000                  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

POST HOC PAIRWISE PERMANOVA

```
                      pairs Df SumsOfSqs  F.Model         R2 p.value p.adjusted sig
1    Ma'init vs Maayong Tubig  1 0.6976581 1.809259 0.03949548   0.042      0.252    
2        Ma'init vs Poblacion  1 2.1971762 5.593815 0.11056323   0.001      0.006   *
3           Ma'init vs Sahara  1 0.6088577 1.660037 0.04655174   0.060      0.360    
4 Maayong Tubig vs Poblacion  1 1.1042373 2.573706 0.05647348   0.001      0.006   *
5    Maayong Tubig vs Sahara  1 0.4887339 1.180885 0.03558931   0.225      1.000    
6        Poblacion vs Sahara  1 0.9666987 2.286376 0.06479486   0.002      0.012   .
```

AD HOC BETADISPER

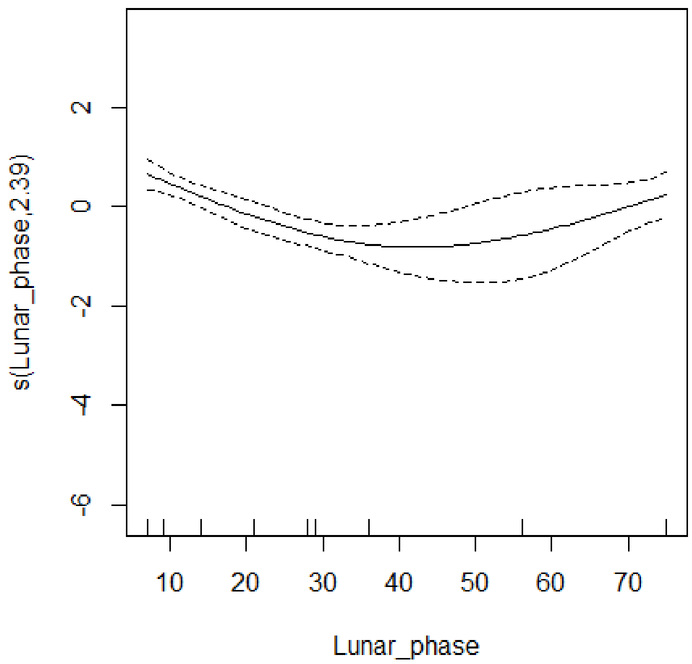
```
Analysis of Variance Table

Response: Distances
          Df  Sum Sq  Mean Sq F value  Pr(>F)  
Groups     3 0.08235 0.027450  2.1729 0.09799 .
Residuals 77 0.97272 0.012633                  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

POST HOC TUKEY HSD PAIRWISE

```
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = distances ~ group, data = df)

$group
                               diff          lwr        upr     p adj
Maayong Tubig-Ma'init    0.06397649 -0.023142226 0.15109520 0.2248120
Poblacion-Ma'init        0.07704723 -0.009077699 0.16317216 0.0959419
Sahara-Ma'init           0.03112430 -0.073228595 0.13547719 0.8618368
Poblacion-Maayong Tubig  0.01307075 -0.074949078 0.10109057 0.9797225
Sahara-Maayong Tubig    -0.03285219 -0.138774386 0.07307001 0.8474538
Sahara-Poblacion        -0.04592293 -0.151029287 0.05918342 0.6615254
```

Appendix 23: GAM for Lunar phase vs fish abundance

Smooth plot



Summary

```
Family: Negative Binomial(1.986)
Link function: log

Formula:
Abundance ~ s(Log_Colony_Cut_Volume) + s(Lunar_phase, k = 9)

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)   0.9162     0.1546   5.926  3.1e-09 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
                          edf Ref.df Chi.sq  p-value
s(Log_Colony_Cut_Volume) 2.973  3.732  149.9  < 2e-16 ***
s(Lunar_phase)           2.393  2.785   23.1 5.22e-05 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.622   Deviance explained = 78.7%
-REML = 221.82  Scale est. = 1         n = 92
```

Gam.check

```
Method: REML   Optimizer: outer newton
full convergence after 4 iterations.
Gradient range [3.597952e-07,1.589934e-05]
(score 221.8186 & scale 1).
Hessian positive definite, eigenvalue range [0.7551062,19.51479].
Model rank =  18 / 18 

Basis dimension (k) checking results. Low p-value (k-index<1) may
indicate that k is too low, especially if edf is close to k'.

                           k'  edf k-index p-value
s(Log_Colony_Cut_Volume) 9.00 2.97    1.05    0.90
s(Lunar_phase)           8.00 2.39    1.09    0.91
```