The Role of Coralliths in Coral Reef Recovery and Expansion

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Declaration

I, Nadia Jogee, declare the following:

(a) That the thesis has been composed by myself.

(b) That the work is my own.

(c) That the work has not been submitted for any other degree or professional qualification except as specified.

(d) That the included publications (data incorporated into Chapter 2) are my own work.

Signed

Nadia Jogee

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Abstract

In this thesis, I examined the ecological importance of a unique group of corals called coralliths and their role in reef recovery following disturbance events. Coral reefs are one of the most important habitats on Earth, supporting many ecosystem services essential to coastal communities in the tropics. However, they are threatened by human-induced and environmental disturbances, leading to increased degradation. These disturbances affect some of the most common species of coral present on reefs, but some more resilient species and morphologies can withstand these stressors. One such group of resilient corals are called coralliths. They are unattached, mobile corals moved passively by wave action and fish grazing. This movement means they encounter more environmental variation than sessile corals. This mobile lifestyle may precondition coralliths to be more tolerant of future climatic conditions. In this thesis, I investigated the key factors enabling corallith formation. Is it 1) a coral's ability to adapt to changes in the light environment or 2) the ability to recover quickly from physical damage? I also set out to understand the role coralliths may play in coral reef recovery post-disturbance and whether their resilience may mean they play a more significant role on coral reefs in the future.

Using PAM fluorometry, microscopy and CT scanning techniques in the lab, I found that a coral species' ability to recover from physical damage plays a more critical role in corallith formation than their ability to adapt to low light conditions. Using benthic surveys, I looked at changes in the coral community in the Caribbean over the last 40 years to discover that corallith-forming species (CFS) represent a larger-than-expected proportion of current Caribbean reefs. Looking more closely at the reefs of Utila and Tela, Honduras, I found that the proportion of CFS increased after local bleaching events. This suggests that CFS were benefitting from these otherwise harmful disturbance events. To learn whether this increase was restricted to the Caribbean, I used data collected in the Indian Ocean to look at the change in the CFS *Porites rus* after successive bleaching events. This species is found throughout the Indo-Pacific and is known to form huge encrusting colonies. However, despite their large size, they do not provide as much 3D structure as other coral species and, therefore, have fewer inhabitable niches. I showed that *P. rus* not only survived these events but increased its cover. The mechanism for this increase I show is through its

propensity to form coralliths and corallith formation is adaptive and not merely a morphological anomaly. Like *P. rus,* many CFS are encrusting and massive species of corals. A future reef with a higher proportion of CFS could provide less habitat for biodiversity, which relies on there being a variety of different ecological niches on reefs. This would directly impact the ecosystem services that coral reefs provide. By drawing conclusions on future reefs' community structure, we can better prepare communities to respond.

Lay Summary

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Coral reefs are one of the most important habitats on Earth, providing many key resources for nearly one billion people worldwide. However, due to human activities, they are being degraded and dying in many parts of the world. Not all species and forms of corals are susceptible to these disturbances, however, and one form of resilient coral is called a 'corallith'. Coralliths are mobile corals that get moved around by wave action; therefore, unlike immobile corals, they experience more daily pressures, such as being rolled around uneven surfaces, which damages their body. Yet coralliths can continue to survive and grow despite these harsh conditions. In the future, it is expected that environmental conditions on coral reefs will become harsher, and many immobile corals will not survive. Coralliths, however, are already used to extreme conditions, so they may be able to flourish on the coral reefs of the future.

In this thesis, I set out to try and understand why some coral species can form coralliths more easily than others. I found that how quickly a coral can recover from being broken and wounded seems more important than how it copes with changes in light intensity. I then looked at corallith-forming species of corals in the Caribbean and found that they represent a large proportion of the corals that exist today, which was not the case 40 years ago. This is likely because the Caribbean experienced many human-induced disturbances in this period, so the hardier corallith-forming species survived. I also looked at how corallith-forming species responded in real-time to disturbance events in the Maldives and found that not only did corallith-forming species survive, but they also increased in number. This means that in the future, we might see a larger proportion of corallith-forming species in the Indo-Pacific, just like we now see in the Caribbean. The impact this might have on reefs is something that we should continue to try and investigate.

Chapter 1. The importance of coral reefs, threats to their existence and the oddballs that call them home

In Chapter 1, I thoroughly appraised the current coral reef ecology literature, particularly the effect of disturbance events. I also introduce the reader to coralliths, the focus of my thesis. I then finish by outlining the overall aim of my thesis along with three main objectives that will aid in addressing this aim.

1.1 Coral Reef Ecology

1.1.1 The importance of corals and their biology

Tropical coral reefs are one of the world's most biodiverse habitats, providing a home for a plethora of species from all major classes of animal, plant and microbes (Roberts et al., 2002) despite the fact they occur in nutrient-poor waters. One resource that is not limited in tropical regions is light. One group of animals that has exploited this are the scleractinian corals belonging to the phylum Cnidaria. Many of these corals are formed from a colony of genetically identical clones (Peters, 2016). The individual animals that make up these structurally important colonies are polyps, which range in size from 1 mm to several centimetres in diameter (Peters, 2016). After fertilisation, coral larvae will settle on a suitable substrate and metamorphose into a primary polyp (Isomura and Fukami, 2018). This primary polyp then reproduces asexually to form genetic clones, which in turn produce more. As the number of polyps grows, they lay down an endoskeleton made from calcium carbonate ($CaCO_3$), providing the colony structure (Figure 1). For this reason, many scleractinian corals are called hermatypic, meaning they are reef-building. When corals die, their skeleton is integrated into the reef and continues to provide structural complexity, defined as the reef's three-dimensional organisation (Darling et al., 2017). It also provides a suitable substrate for future coral larvae to settle on. The structures provided by scleractinian corals create many niches for other taxa to inhabit, which is why corals are essential in terms of biodiversity (Gratwicke and Speight, 2005).

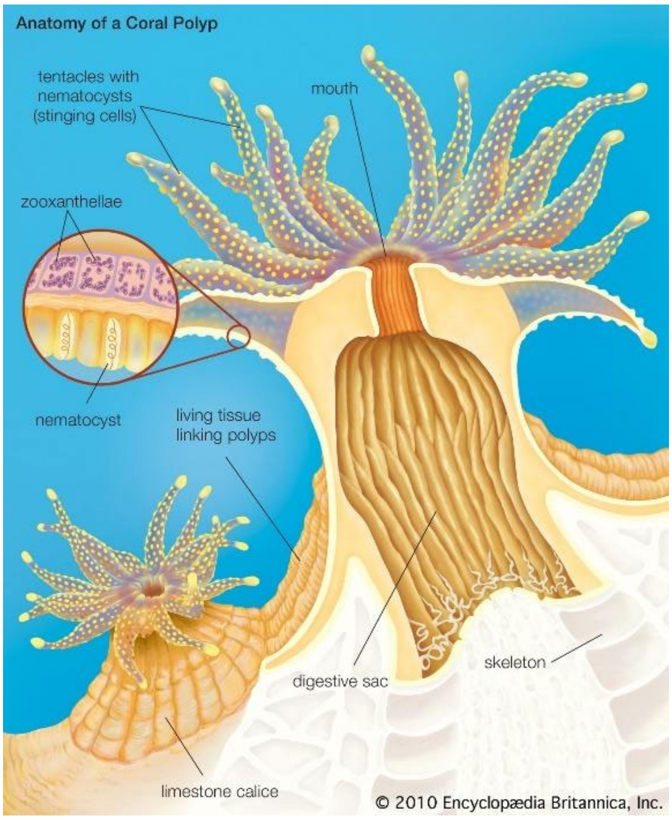


Figure 1. The anatomy of a coral polyp. The white, calcium carbonate skeleton supports genetically identical polyp clones. As the colony grows, the number of polyps can reach into the hundreds of thousands. The polyps can share nutrients through shared tissue, called the coenosarc. The tentacles of each polyp are lined with stinging cells called nematocysts that immobilise and capture prey. The tentacles then bring the food to the mouth of the polyp which moves the food through to the digestive sac. Waste is expelled through the mouth (Britannica, 2010).

Like most members of the phylum Cnidaria, the coral polyp is heterotrophic and uses nematocyst cells to capture prey (Sheppard et al., 2017). These stinging cells line the tentacles surrounding the polyp mouth and catch zooplankton, phytoplankton and other small particulate food that come into contact with them (Sheppard et al., 2017). However, for tropical, shallow reef corals, this only provides a small proportion of the food required by the coral and most of their food, in some cases up to 98%, is produced by endosymbionts called zooxanthellae that inhabit the gastrodermal tissue of the coral polyp (Baumann et al., 2018). Much of the energy produced from this food is utilised in mucous production, which is multifunctional and used by cnidarians for feeding, protection from xenobiotics, osmoregulation, reproduction, and competition for space, amongst others (Davies, 1991, Savoca et al., 2022). Zooxanthellae belong to the family *Symbiodiniaceae* and, along with their photosynthetic pigments, provide corals with their colour (LaJeunesse, 2020). The algae provide the coral with sugars and other essential nutrients required for normal metabolism, whilst the coral provides the algae with precursors to photosynthesis, such as ammonium (Sheppard et al., 2017, LaJeunesse, 2020). It is important to note that corals form close relationships with other microorganisms, and the coral-symbiont complex is often termed the 'holobiont', with new symbionts still being discovered. For example, Kwong et al. (2019) recently showed a close relationship between corals and apicomplexans, which they have named 'corallicolids'. Apicomplexans are generally parasitic, yet corallicolids appear to have no pathological impacts on corals. They have retained genes encoding for chlorophyll yet have no genes encoding for Photosystems. Their function is therefore unclear, whilst their prevalence appears indisputable, found in over 80% of samples tested (Kwong et al., 2019). Of all the relationships formed between coral and their symbionts, however, the photosynthetic properties of *Symbiodiniaceae* are most widely studied. We know them to be the main primary producers of healthy coral reefs, forming the foundation for a vast and complex food chain (LaJeunesse, 2020).

1.1.2 Disturbance as part of a healthy reef

Disturbance events, such as hurricanes, are considered a natural part of a coral reef ecosystem (Connell, 1978). On a healthy reef, disturbance can vary from persistent small-scale events, such as herbivory, to periodic large-scale events, such as hurricanes (Rogers, 1993). Although both can have a detrimental effect on the individuals present on the reef, disturbance also clears space for new colonisers, aiding a healthy pattern of regeneration (Connell, 1978). This is the central idea in the intermediate disturbance hypothesis, which helps explain the high biodiversity found on coral reefs.

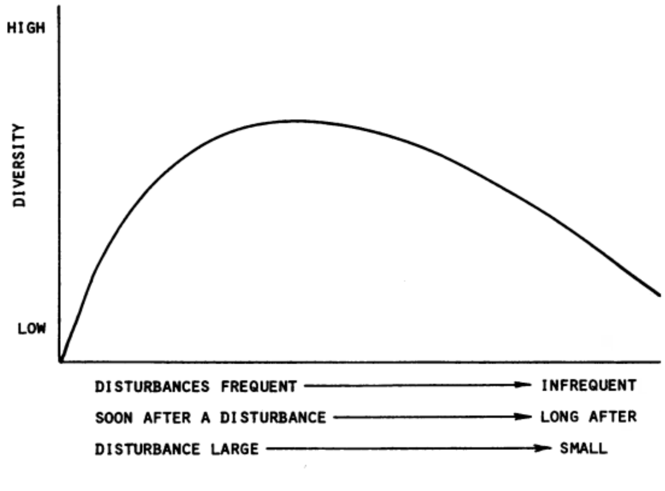


Figure 2. taken from Connell (1978), shows the theorised intermediate disturbance hypothesis and its classic 'humped' diversity pattern.

In the intermediate disturbance hypothesis, Connell (1978) describes how an ecosystem with few mild disturbance events will go through a process of succession, eventually reaching a climax community. He studied the coral reef around Heron Island, Australia, and observed that whilst the corals on the reef crest were both frequently and severely damaged during a hurricane, those corals in a nearby, more sheltered area were not (Connell, 1978). In this protected area, competitive exclusion by large, slow-growing species, either by overshadowing or direct aggression, meant that *Acropora cervicornis* was dominant (Connell, 1978). This meant that biodiversity in this area was low. When disturbance is severe and frequent, vast swathes of the reef can be damaged. In the centre of this disturbed area, only species with propagules that can travel and survive long distances can make it to the centre to colonise the area. One such group of benthic organisms that can do so are the macroalgae, which have been documented as being the main colonisers after certain disturbance events (Bruno et al., 2009). In this scenario, biodiversity will again be low due to few species being able to reach and colonise these disturbed areas. Therefore, Connell (1978) suggests that biodiversity will be highest when disturbance is intermediate in both frequency and severity (Figure 2). This theory has been tested many times since 1978, and although some debate on its merit remains (Fox, 2013, Sheil, 2013), many studies have found supportive evidence for it (Aronson and Precht, 1995, Hixon and Brostoff, 1983, Rogers, 1993).

1.1.3 Increased frequency and severity of disturbance

Over the last 30 years, disturbance events have become more frequent and severe (Baker, 2008, Hughes et al., 2018). We must aim to understand the effect these frequent disturbances have on coral reef community structure. It is thought to be algal species that capitalise on newly provided space after a disturbance event (Bruno et al., 2009). Still, there may also be opportunities for unexpected species or phenotypes to become dominant. Whilst the dominance of algae is generally thought to jeopardise the ecosystem services we rely on (Dudgeon et al., 2010, Hughes, 1994, Loya et al., 2001, Moberg and Folke, 1999, Norström et al., 2009), unexpected winners post disturbance might introduce novel services that we can use to our advantage. It is, therefore, essential to investigate which species are winners or losers after repeated disturbance events (Loya et al., 2001) and to understand how their newfound dominance or loss will affect ecosystem functioning. By doing so, we can make better decisions to aid in the protection of ecosystem services, which almost a billion people rely on globally.

One major cause for concern on tropical coral reefs is the rise in the frequency of mass-bleaching events (Brown et al., 2019, Lynn and Peeva, 2021, Thirukanthan et al., 2023). Coral bleaching is driven by a prolonged increase in sea surface temperatures, leading to the dissociation of zooxanthellae from the host coral tissues (Brown, 1997, Browne et al., 2019, Loya et al., 2001). Variation exists in corals' susceptibility and recovery rates to rising sea surface temperatures (Donner and Carilli, 2019, Loya et al., 2001, Roff et al., 2014). For example, *Acroporidae* and *Pocilloporidae* appear to be more vulnerable than *Porites spp.* and *Faviidae* (van Woesik et al., 2011). When corals die in large numbers, it has been shown that algae are often the first organisms to colonise the benthos, creating a very different landscape to the previously coral-dominated one (Bruno et al., 2009, Loya et al., 2001) (Bruno et al., 2009, Loya et al., 2001).

1.1.4 Phase shifts and stable states

Persistent changes in the reef environment can cause a ‘phase shift’ (Dudgeon et al., 2010). Coral reefs that experienced reduced water quality, overfishing, disease and hurricane damage (or a combination of these factors) can undergo radical changes resulting in a ‘phase-shift’ (Hughes, 1994). This is where a persistent environmental change causes a significant die-off of coral, and the remaining coral skeleton is covered with non-reef-building organisms, such as macroalgae, sponges or soft corals (Bell et al., 2013, Cruz et al., 2015, Done, 1992). Some of the most well-studied areas that have undergone phase shifts are Discovery Bay (Jamaica), Kāneʻohe Bay (Hawaii) and Moorea (French Polynesia) (Done, 1992). Phase shifts can negatively impact ecosystem services such as biodiversity, local food security and local financial provision through tourism, to name just a few (Dudgeon et al., 2010, Riegl et al., 2009). Phase shifts ultimately change the reef to the extent that recovery and reversal to scleractinian dominance may be unachievable in the foreseeable future unless the environmental change that triggered the phase shift is reversed. This does not mean that the new assemblage of species on the reefs has no economic importance, only that the services they provide might change.

A concept that is often confused with phase shifts is that of alternative stable states. This is where one set of environmental conditions can support more than one successional end-state (Dudgeon et al., 2010). The end-state achieved is down to the starting numbers of species (Dudgeon et al., 2010), as described in the Lotka-Volterra competition model (Petraitis and Dudgeon, 2004, Lotka, 1978). For an ecosystem to move from one stable state to an alternative stable state, there needs to be a large enough 'pulse perturbation' event that alters species numbers in the area whilst the environmental conditions remain essentially the same (Petraitis and Dudgeon, 2004, Lotka, 1978). One theoretical example of this could be a large-scale bleaching event killing many susceptible scleractinian species. Once the sea surface temperature returns to normal and the temperatures remain stable, this one-off bleaching event could be considered a pulse perturbation. The remaining species may be in different numbers, forming a different successional community.

1.2 Coral Bleaching

1.2.1 Causes of bleaching

The symbiosis between coral and zooxanthellae is fragile, and disruption to this relationship can rapidly lead to a dissociation of the two (Brown, 1997). Several factors can put stress on the relationship. Due to the algae providing colour to the coral, a dissociation of the two leaves the coral tissue transparent, revealing the coral's white calcium carbonate skeleton (Sheppard et al., 2017). It is for this reason that this process is called 'coral bleaching'. Corals have adapted to live within the upper reaches of their thermal tolerance, allowing photosynthesis to occur efficiently (Brown, 1997). This means that an increase in sea surface temperatures, as little as 1°C, can push that photosynthetic rate beyond this ideal maximum, putting pressure on the symbiotic relationship and causing coral bleaching (Brown, 1997). For example, during periods of elevated temperature and irradiance, a build-up of reactive oxygen species (ROS), produced due to increased photosynthetic rate and, in turn, aerobic respiration within the mitochondria, can cause severe damage to cells (Borek, 2004, Friedman et al., 2018, Seveso et al., 2018).

Reactive oxygen species are produced via the metabolism of oxygen during normal respiration, which includes superoxide radical ($O_2^\bullet$), hydroperoxyl radical (HO_2), hydrogen peroxide (H_2O_2) and hydroxyl radical ($^\bullet OH$) (Yu, 1994). These are damaging to cells in several ways, including compromising cell wall integrity and altering DNA structure (Friedman et al., 2018, Mydlarz and Jacobs, 2006). All organisms that respire aerobically produce ROS and are equipped with antioxidant defence mechanisms that mitigate the damage caused (Yu, 1994). These defences are acquired through either the diet of the organism, such as vitamin E, or metabolically produced, for example, antioxidant enzymes such as catalase (Borek, 2004). However, when sea surface temperatures increase, *Symbiodiniaceae* can quickly produce excessive ROS beyond the scope that the coral or algae can quench (Brown, 1997). To protect themselves from the harmful effects of ROS, the corals expel the algae from their tissue, causing them to bleach (Brown, 1997). Once the endosymbionts are lost, corals can starve to death in a matter of days if temperatures are not reduced, and the coral does not recover its endosymbionts (Brown, 1997).

1.2.2 Variability in bleaching susceptibility

However, it is important to note that there are both intra- and intergeneric differences in thermal tolerances in corals and within the family *Symbiodiniaceae* (Crabbe, 2009). These differences have been attributed to why we see a variation in coral susceptibility to bleaching both between species, within species and across spatial gradients (Baumann et al., 2018, Berkelmans and van Oppen, 2006, Brown, 1997, Crabbe, 2009, Diaz-Almeyda et al., 2017, Hennige et al., 2009, Hennige et al., 2011). For example, Hennige et al. (2010) found that the dominant *Symbiodinium* clade changed from clade C to D across a spatial gradient between optimal reef locations and marginal reefs in the Wakatobi Marine National Park, Indonesia. In these marginal reef habitats, temperatures regularly reach 34 °C and clade D is known to be more thermally tolerant than clade C (Hennige et al., 2008). However, it’s important to note that the clade alone does not infer how heat-tolerant a coral may be. For example, Guest et al. (2012) showed that long-term thermal history significantly impacts bleaching susceptibility. In their study, they observed that during a significant thermal anomaly in 2010 that affected much of Southeast Asia, corals in Singapore had a lower bleaching level than the same species in Pulau Weh (Guest et al., 2012). Historically, Singapore experienced seven times more degree heating weeks (a metric to measure sea surface temperature anomalies) than Pulau Weh during the 1998 bleaching event. It’s therefore thought that the corals in Singapore were pre-conditioned to withstand thermal stress more than those in Pulau Weh. Interestingly, some of the species in

Singapore that did not bleach were branching Acroporids, which are considered particularly susceptible to bleaching (Guest et al., 2012, Loya et al., 2001). Thermal tolerance of the symbionts present and the thermal history of the colony are just two contributing factors when assessing the susceptibility of corals to rising sea surface temperatures. When we discuss the future of coral reefs in a warming climate, we should be balanced in our approach and appreciate that although coral reefs are no doubt changing, they might not become lost entirely to climate change. Optimism for the future is essential if we are to drive the field of coral reef conservation forward.

1.2.3 Limiting environmental variation

Extreme environmental variation can be damaging to the normal functioning of coral colonies. One way in which corals limit the amount of variability that they experience and subsequently minimise the pressure put on the symbiotic relationship they rely on is by being sessile (Sheppard et al., 2017). By adopting a sessile lifestyle, the coral holobiont can acclimate to local environmental parameters, both diurnal and seasonal changes, and maximise photosynthetic output. Acclimation may occur in several ways, for example, through the strain of *Symbiodiniaceae* the coral hosts (Hennige et al., 2010) or through which photosynthetic pigments the *Symbiodiniaceae* produce (Hennige et al., 2008). A few exceptions exist where the colony is unattached to a fixed substrate and can be moved by wave action, such as *Fungia fungites.* However, these species are not considered hermatypic as they have a flattened disc-like shape and do not grow very large (< 20 cm diameter). These species are often described as 'large polyp corals' as the entire disc supports one large polyp (up to 25 cm in diameter) with longer tentacles, and they rely more on heterotrophic feeding than hermatypic corals. An understudied example of where a coral colony is unattached but where the coral species is hermatypic occurs when a corallith is formed, and these will be the focus of my thesis.

1.3 Coralliths and their biology

1.3.1 What are coralliths?

Despite being first described in 1880 (Great Britain. Challenger, 1880), coralliths are a much-overlooked morphology of corals, produced by only a handful of species (see Table 1 for complete list) (Capel et al., 2012, Glynn, 1974, Hennige et al., 2017, Hoeksema et al., 2017, Kersting et al., 2017, Roff, 2008, Scoffin et al., 1985, Tortolero-Langarica et al., 2016). Whilst most surviving coral larvae settle and develop on a stable solid substrate and are, therefore, sessile, coralliths are mobile. However, unlike *F. fungites* that are all free-living as adults, corallith-forming species (CFS) are not obligated to grow in this mobile, spheroidal or sub-spheroidal shape. Instead, coralliths are formed in one of two ways. Firstly, a coral larva will settle on a piece of dead coral rubble or small rock with suitable coralline crustose algae (CCA) growth upon its surface (Hennige et al., 2017). Once a larva has settled onto a mobile piece of substrate, the coral larva develops into a coral polyp and then, through asexual reproduction, forms a colony of polyps, creating tissue across the entire surface of the substrate (Figure 3) (Capel et al., 2012, Glynn, 1974). Formation through larval settlement has been observed in some areas to be the dominant formation process (Hennige et al., 2017, Glynn, 1974, Scoffin et al., 1985). Secondly, the fragmenting of an adult colony of CFS can lead to corallith formation (Roff, 2008). This can be through the growth of 'nodules' along the fringe of the colony, as we see in *Porites rus*. Once these nodules become too large to be supported by the colony, they become unattached. Otherwise, the adult colony can become fragmented by storm damage, erosion, grazing disturbance, wave action, fishing practices, irresponsible tourists kicking or hitting corals, burrowing animals and boats (Roff, 2008, Highsmith, 1982). When this fragmentation occurs, a CFS coral can heal over the point of breakage on the new fragment and then remain free-living.

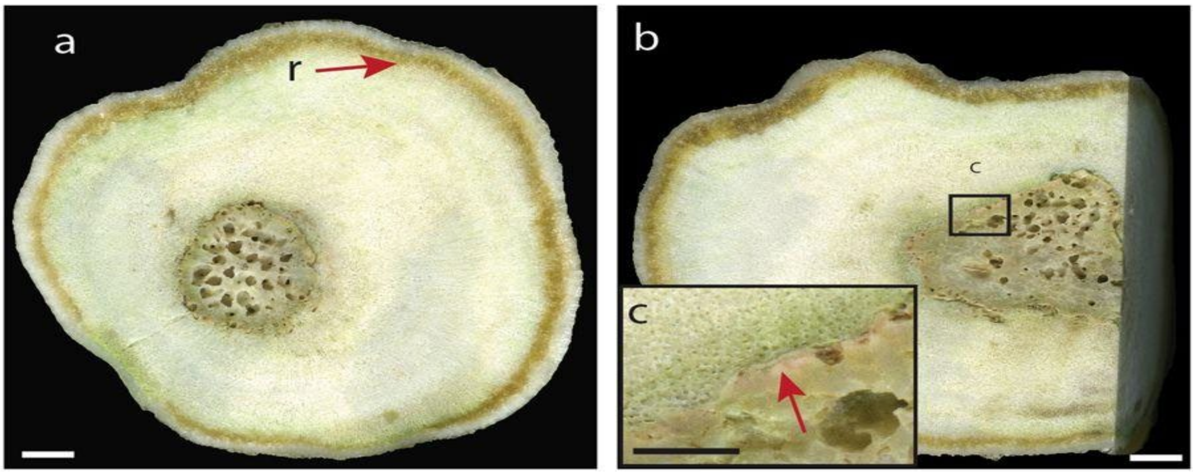


Figure 3. By cutting a corallith in half it is easy to see how a corallith forms through larval settlement. At the centre of the corallith is a small piece of coral skeleton. The outer tissue layer (r in the diagram a) has initially grown over this fragment and then laid down layer upon layer of calcium carbonate skeleton, forming a spheroidal ball. The red arrow in c shows the layer of crustose coralline algae that the larvae will have attached to. This crustose coralline alga is vital for larval settlement (Hennige et al., 2017). Scale bar is 0.5 cm in (a) and (b), and 0.2 cm in (c).

As small coral fragments are susceptible to movement by wave action or bioturbation caused by grazing fish (Glynn, 1974), non-branching coral morphologies are thought to be better suited to this passive lifestyle. For example, massive corals, which lay down layer upon layer of calcium carbonate skeleton to form large rounded colonies, are good candidates for corallith formation, and the majority of CFS described so far are from this group (Capel et al., 2012, Glynn, 1974, Hennige et al., 2017, Kersting et al., 2017, Roff, 2008, Scoffin et al., 1985, Tortolero-Langarica et al., 2016). This is because the irregular shape of branching morphologies makes them more likely to be broken when they are moved, because parts are more easily broken off. Also, the corallite (the calcium carbonate 'cup' within which the polyp sits) often protrudes in branching species such as *Acropora spp.* (Veron, 2016) whilst species such as *Porites spp.* have corallites that are 'sunken' and sit flush to the coral surface. This will minimise the damage done to sunken polyps and increase the damage done to protruding ones when they are rolled along the seabed.

1.3.2 Defining the term 'corallith.'

Coralliths have been infrequently documented over the last 150 years. Little attention was paid to coralliths at the turn of the century, the mid-1970s, again in the late 1980s, and then most recently in the past ten years (Table 1). In this time, the term 'corallith' has sometimes been misused to describe any coral found to be free-living and has also gone unused when incorrectly calling what is a corallith a 'fragment'. This confuses the subject of coralliths with asexual reproduction via fragmentation, a well-documented phenomenon. It is, therefore, important to clarify the differences between the two.

Table 1. A list of scleractinian coral species that have been described as coralliths, including their life-history strategy based on Darling et al. (2012) where sufficient data is available to assess. '*' denotes where the use of the term 'corallith' was not used, despite the

Species	**Reference**	**Location**	**Life History Strategy**
Acropora Formosa	Roff (2008)	Heron Reef, Australia	Competitive
Astreopora sp.	De Palmas et al. (2021)	Taiwan	Competitive
Cladocora caespitosa	Kersting et al. (2017)	Formentera, Mediterranean	Stress-tolerant
Cyphastrea chalcidicum	Richards (2013)	Kimberley, Western Australia	Stress-tolerant
Dipsastraea sp.	De Palmas et al. (2021)	Taiwan	
Goniastrea aspera	Roff (2008)	Heron Reef, Australia	Weedy
Goniopora stokesi	Pichon (1974)*	Madagascar	Stress-tolerant
Madracis cf. auretenra	Hoeksema et al. (2017)	Saba Bank, Dutch Caribbean	Generalist
Madracis decactis	Capel et al. (2012), Hoeksema et al. (2017)	South Atlantic; Saba Bank, Dutch Caribbean	Weedy
Millepora sp.	Richards (2013)	Kimberley, Western Australia	
Montipora digitata	Roff (2008)	Heron Reef, Australia	Competitive
Pavona clivosa	Glynn (1974)	Gulf of Panama	Stress-tolerant
Pavona gigantea	Glynn (1974)	Gulf of Panama	Stress-tolerant
Pavona varians	Glynn (1974) Scoffin et al. (1985)	Gulf of Panama; Rarotonga, Cook Islands	Stress-tolerant
Pavona venosa	Richards (2013)	Kimberley, Western Australia	Stress-tolerant
Platygyra lamellina	Roff (2008)	Heron Reef, Australia	Stress-tolerant
Pocillopora damicornis	Roff (2008)	Heron Reef, Australia	Weedy
Porites astreoides	Hoeksema et al. (2017), Rodriguez-Martinez and Jordan-Dahlgren (1999)	Saba Bank, Dutch Caribbean; Mexican Caribbean	Weedy
Porites divaricata	Hoeksema et al. (2017)	Saba Bank, Dutch Caribbean	Generalist
Porites evermanni	Boulay et al. (2014) *	Eastern tropical Pacific	Stress-tolerant
Porites furcata	Hoeksema et al. (2017)	Saba Bank, Dutch Caribbean	Weedy
Porites lutea	Hennige et al. (2017), Roff (2008), Scoffin et al. (1985)	The Maldives, Heron Reef, Australia; Madagascar	Stress-tolerant
Porites lobata	Tortolero-Langarica et al. (2016)	Isla Isabel, Central Mexican Pacific	Stress-tolerant
Porites panamensis	Glynn (1974)	Gulf of Panama	Weedy

Porites spp.	Great Britain. Challenger (1880) *	Indo-Pacific	
Psammocora profundacella	Richards (2013)	Kimberley, Western Australia	Stress-tolerant
Siderastrea radians	Hoeksema et al. (2017), Lewis (1989), Pichon (1974)	Saba Bank, Dutch Caribbean; Barbados, Caribbean; Madagascar	Stress-tolerant
Siderastrea siderea	Hoeksema et al. (2017)	Saba Bank, Dutch Caribbean	Stress-tolerant
Siderastrea stellata	Lima and Coutinho (2016) *	Arraial do Cabo, southeastern Brazil	Stress-tolerant
Stephanocoenia intersepta	Hoeksema et al. (2017)	Saba Bank, Dutch Caribbean	Stress-tolerant
Tubastrea coccinea	Dutra et al. (2023)	Brazil	
Tubastrea tagusensis	Dutra et al. (2023)	Brazil	

1.3.3 Corallith or fragment?

Asexual reproduction via fragmentation has long been observed in corals as a widely used mechanism allowing parent colonies to distribute their genotype across the reef (Highsmith, 1982). Fragmentation causes damage to the parent colony and effectively creates a wound, leaving the colony vulnerable to infection. If fragmentation was not adaptive, then selection should have caused the proliferation of morphologies that avoid such damage (Highsmith, 1982). Instead, many of the most essential hermatypic species of corals grow in a branching formation that is highly susceptible to breakage (Highsmith, 1982). Waves can passively move these newly broken fragments to new locations on the reef. They require resettlement elsewhere, often becoming lodged amongst other corals forming thickets, for example, *Acropora palmata* in the Caribbean (Aronson and Precht, 2001, Highsmith, 1982). These intricate structures create habitats and niches for many other species, which is why they are essential for increased biodiversity.

The breaking, moving and re-settling of corals far away from their parent colony allows for a more homogenous spread of genotypes and species across the whole reef, ultimately making the reef more resilient to threats such as infection (Highsmith, 1982). For example, one colony, species, or genotype may be highly susceptible to a pathogen (Aronson and Precht, 2001). Without the movement of individuals across the reef, vast areas of the reef could die off due to infection by a pathogen. A homogenous spread of genotypes would mean that whilst small pockets of coral may succumb to disease, the passing on of the pathogen could become disrupted, creating a healthier reef (Aronson and Precht, 2001, Highsmith, 1982). Secondly, if the parent colony dies from disease, small fragments resettled elsewhere may survive, continuing that genotype. This homogeneity occurs much quicker with fragmentation than with sexual reproduction. This is for several reasons. Firstly, larvae of some species do not travel very far before they settle (Ayre and Hughes, 2000). Secondly, fragmentation moves sections of corals that are large enough to function as a new parent colony, sometimes mature and large enough to sexually reproduce (Highsmith, 1982). Finally, fragmentation and re-settling is a constant process, whilst sexual reproduction only occurs periodically (Highsmith, 1982).

Vital to the process of reproduction by fragmentation is the resettlement of fragments. Prolonged movement of fragments makes them highly susceptible to further breakage (Burmester et al., 2017, DeFilippo et al., 2016, Shirur et al., 2016), tissue erosion (Burmester et al., 2017, DeFilippo et al., 2016, Shirur et al., 2016), shading from light (Glynn, 1974, Scoffin et al., 1985) and other detrimental abiotic factors. Resettlement allows the fragment to experience more stable conditions and acclimate to its new environment, maximising growth and allowing the process to continue. Conversely, coralliths do not need to resettle and can remain free-living. This separates them from coral fragments. Secondly, as previously mentioned, unlike *Fungia spp.* and other free-living corals, they are hermatypic. Therefore, herein, I use the term ‘corallith’ to refer to:

‘A mobile, hermatypic coral colony, whether formed through fragmentation or larval settlement, that remains unattached’.

1.3.4 Physiology of coralliths

Frequent movement means that all surfaces of a corallith are exposed to both optimum and sub-optimum environmental conditions (Hennige et al., 2017a, Scoffin et al., 1985, Tortolero-Langarica et al., 2016, Highsmith, 1982). It also means that they could experience a high level of physical trauma by being rolled over uneven and often hard surfaces. Polyps at the interface between coral and the substrate are expected to have a reduction in food and light availability. Yet, they have been observed to still be alive despite being bleached (Glynn, 1974, Great Britain. Challenger, 1880). Understanding the physiological responses to changes in the environment exhibited by CFS will be vital in deciphering why some coral species can remain free-living, which will be explored in my thesis. Knowing why some species can form coralliths could influence how we manage or restore reefs in the tropics. For example, restoration projects may choose to restore CFS species alongside commonly used species like *Acropora spp.,* because they may be more resilient to future climate conditions. Recreating rubble patches may also prove helpful so that larvae of the restored CFS have mobile substrates to attach to and expand the range of the restored area via a natural process. Evidence for this natural expansion of the reef and any other ecological roles performed by coralliths will be something I will be looking for in my thesis.

1.3.5 Adaptive plasticity

My thesis will examine the factors enabling corallith formation; one theory I will be testing is that it is adaptive plasticity to the light environment that is key. Movement by wave action and fish grazing means that coralliths experience changes in light availability (Glynn, 1974). For many coral species, this would be detrimental to their health, but CFS cope with these changes remarkably well (Glynn, 1974, Hoeksema et al., 2017, Kersting et al., 2017, Roff, 2008, Scoffin et al., 1985). This could be due to one of several reasons. Firstly, an increase in irradiance causes an increase in ROS; coralliths could be more efficient at upregulating their oxidative stress response than non-CFS (Dias et al., 2018). This would mean they are better equipped to quench ROS and combat the adverse effects they cause. A future study looking at CFS compared to non-CFS could reveal a greater difference between the two and show that CFS cope better with increased ROS under varying light conditions.

It would also be interesting to examine CFS's photosynthetic properties compared to non-CFS. One such difference could be the strain of *Symbiodiniaceae* they host both in the lab and *in situ* and their responses to changes in the light environment. For example, we might see better efficiency of photosynthesis in CFS or a difference in the photosynthetic pigments they possess demonstrated through measuring reflectance under suboptimal conditions. These may alter as a corallith is exposed to a change in the environment, supporting the theory that they have adaptive plasticity. When a CFS experiences changes in lighting, they may be able to reshuffle the dominant symbionts they host for more thermally tolerant species, or their symbionts may upregulate the production of different photosynthetic pigments that are more efficient at harvesting light in higher or lower PAR levels. Finally, the fact that polyps at the coral/substrate interface are often observed to be alive despite being pale or bleached is of interest. It could be that they are feeding more heterotrophically or can still capture some light. It has been shown that light can penetrate the tissue of corals and then scatter through the coral skeleton (Enriquez et al., 2017, Terán et al., 2010). This enables more light to be captured by algal symbionts within tissue that may not be in direct sunlight. This could mean that the surfaces of coralliths that are in contact with the coral sand bed could maintain a low level of photosynthesis as light might scatter through the sand.

1.3.6 Wound healing and pathogen exposure

Acroporidae and other branching species of coral need to become lodged on the reef relatively quickly to acclimate to their new surroundings compared to coralliths. This is partly because *Acroporidae* are known to have a very thin tissue layer compared to other coral genera (Loya et al., 2001). Abrasion can quickly damage the delicate coral tissue. Therefore, quickly becoming wedged amongst coral thickets minimises the amount of tissue damage they experience—their branching morphology aids in this process by acting like an anchor. I predict the tissue layer in some CFS species, such as *Siderastrea radians,* may be thicker than the average tissue thickness of branching corals. This could mean that the coenenchyme is not destroyed in the area of an abrasive wound. This will allow nutrients to continue to move around the coral colony between polyps and may speed up the healing process. However, like the *Acroporidae,* some CFS species, such as *Porites spp.* have a tissue layer that is considered thin. (Loya et al., 2001, Lough and Barnes, 2000). These species' immune responses could be more efficient by upregulating critical physiological processes, such as plug formation, speeding up the healing process.

Palmer et al. (2011) used histopathology to study the response of corals to wound infliction. They found that corals undergo the same four stages of wound healing that higher organisms experience. They observed an initial reduction in both zooxanthellae and melanin around the wound area, followed by a period of increase in both, forming a scab-like plug. van de Water et al. (2015) looked at the expression patterns for 15 immune genes involved in the Toll-like receptor pathway during wound healing under mild heat stress in *Acropora aspera*. They found that there was no significant upregulation. However, they did document a downregulation of NF-κB, which regulates the expression of antimicrobial peptides

(Takeda et al., 2003), possibly meaning this species is more susceptible to infection (van de Water et al., 2015). *Acropora aspera* is not one of the documented CFS. A study looking at the rate of wound healing and the gene expression patterns involved in the process of CFS could address whether CFS are better equipped to deal with wounds and pathogen exposure compared to non-CFS. This could help explain why CFS cope with increased levels of mechanical stress compared to non-CFS.

Due to their increased level of movement and subsequent mechanical stress and tissue abrasion, coralliths are likely to be at higher risk of infection than their static conspecifics. Organisms that come into regular contact with pathogens pay a cost both in terms of their pathogen load and their immune response (Zuk and Stoehr, 2002). Worth examining could also be the difference in the microbiome between the sea bed and the water column and the effect this has on pathogen exposure for coralliths vs sessile conspecifics. Regular pathogen exposure increases the chance of disease but also means a metabolic cost of upregulation, as synthesis of anti-microbial peptides requires energy and nutrients (Zuk and Stoehr, 2002). CFS may tolerate infections better than non-CFS, creating a trade-off between other life-history traits and immune responses. There are significant knowledge gaps in the immune response of corals, and investigating how more resilient species, like CFS, respond will further our understanding of how reefs will react to future events. As climate change predicts sea surface temperatures to increase, this may lead to newly emerging infectious diseases, understanding who will be the winners and losers (Donner and Carilli, 2019, Fabricius et al., 2011), in terms of who may be able to heal from wounds more rapidly, may help us to predict what the future reefs may look like. In my thesis, I will explore how CFS and non-CFS recover from breakage.

1.3.7 Life-history strategies of CFS

In order to view coral reefs using a mechanistic approach, ecologists are increasingly using a trait-based approach to classify species. Using this approach allows for a simplified view of a complex habitat whilst more easily identifying general and predictable rules for an ecosystem. Darling et al. (2012) used hierarchical clustering and random forests analyses to evaluate life-history strategies from species traits for scleractinia. They found that corals generally fall into one of four clusters, they named these clusters ‘competitive’, ‘stress-tolerant’, ‘weedy’ (ruderal) and generalist. The first three being in line with Grime (1988) who devised a way of classifying plants as one of these three life-history categories based on their traits known commonly as the CSR triangle.

Competitive corals tend to be of a plating or branching morphology, they have a fast growth rate, produce large colonies that shade out other corals can be found in shallow high light environments but are susceptible to coral bleaching. They are the species that would be expected to be present in low disturbance environments. Stress-tolerant species are slow growing, broadcast spawners with high fecundity, generally have a domed morphology with larger corallites and can be found in areas of higher disturbance, lower light or higher sedimentation. Ecological theory suggests that successful weeds reproduce faster and survive better than non-weedy species. Whilst the coral species that fit into the weedy cluster generally had a fast reproductive rate, such as short generation times, they didn't have high fecundity like other groups. However, their ability to brood and to reproduce via parthenogenesis might allow them to reproduce at low population densities on highly disturbed reefs. Finally, Darling et al. (2012) found that some corals presented traits that spanned these three life-history strategies. They classed this fourth group as generalists, but stated that as more information is gathered about this group then this name may change and the group be better defined.

I have taken the CFS that have so far been described in the literature and classified them into one of these four groups based on their traits. Some were used in Darling et al. (2012) and so their classification could be taken direct from this paper. Whilst the others I made a judgement based on information of these species on Corals of the World.com (Veron, 2016). I found that most CFS were classed as stress-tolerant corals (see Table 1). However, there were some instances of CFS being found to be competitive, generalists and weedy corals as well. This means that the traits required to be a CFS do not align with one of these clusters, and instead spans them. Another consideration is that CFS do not fit into one of these four clusters, but instead corallith formation is dictated by the environment. Roff (2008) described two coral species as CFS that are from the competitive cluster, which was to be somewhat unexpected. However, in the right conditions it could be that a small branching fragment of a competitive species is enabled to remain free-living and not rejoin the sessile community, therefore being a corallith.

1.3.8 Ecological role of coralliths

Coralliths are uniquely positioned to colonise areas that sessile corals cannot, such as areas of rubble, sand, or seagrass meadows. Hennige et al. (2017) studied coralliths in the Maldives and showed that coralliths get larger as the distance from the shore increases. Eventually, they become so large that only extreme weather conditions can move them (Hennige et al., 2017). At this point, any exposed skeleton they have is a suitable substrate for coral larvae to attach to and establish themselves as a new colony, creating a small coral 'bommie'. As this process continues and small amounts of the coral die off and become integrated into the reef framework, a small patch reef is formed. This area is expected to grow and merge with other corallith-driven patch reefs. Hennige et al. (2017) have called this the '*free-living stabilisation hypothesis*' (FLSH), which means that coralliths have the potential to stabilise their habitat (Figure 4).

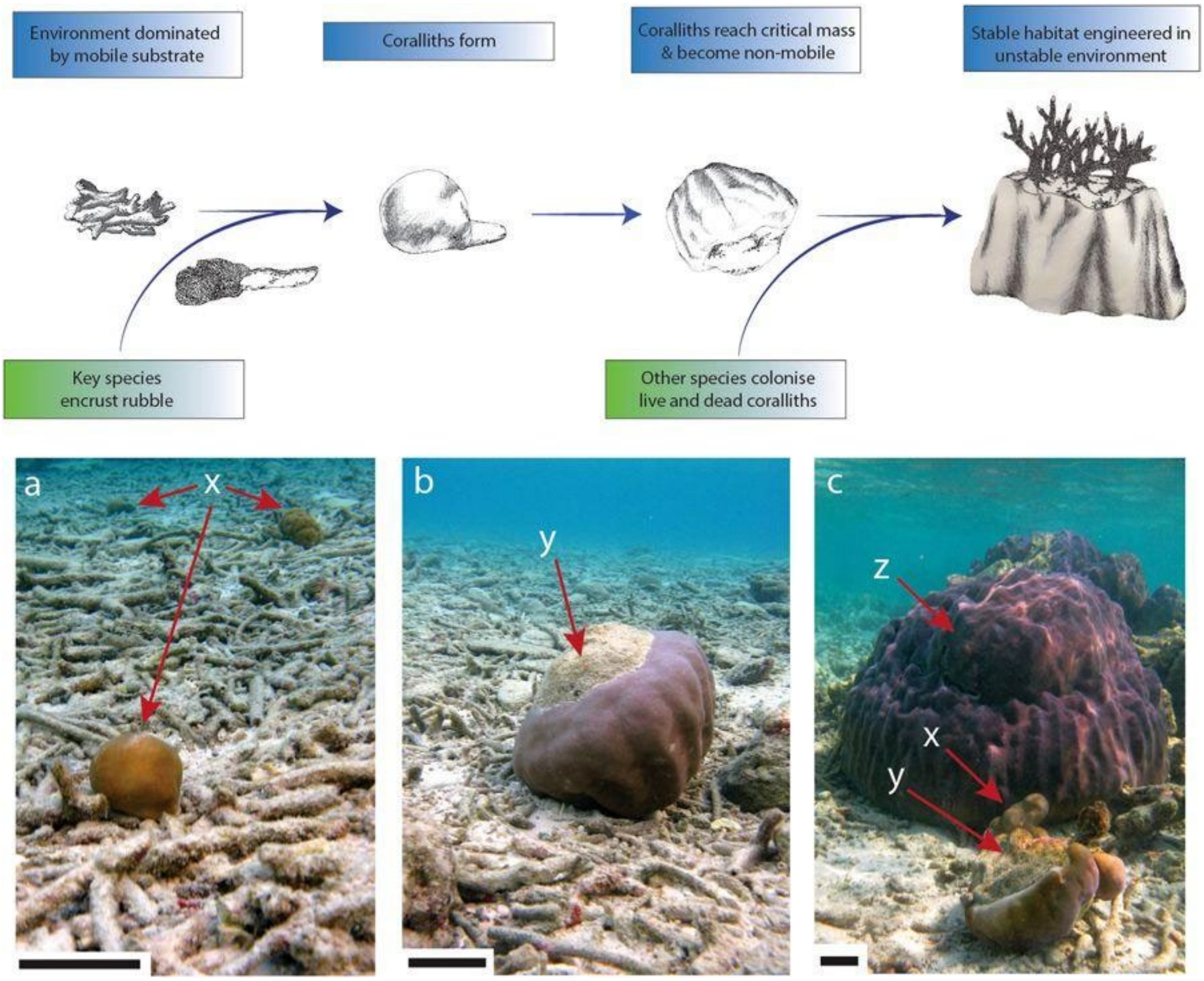


Figure 4. (a) In areas that have mobile rubble substrate, there are only a handful of massive coral species that can attach and develop into coralliths. (b) As coralliths grow in size they get moved by waves, which can cause damage to the tissue or expose areas that have no tissue coverage (y). (c) Eventually these coralliths become so large that they are unable to be moved by waves. Any exposed skeleton becomes suitable for other corals to attach to, forming a small patch reef (x, y). Figure taken from Hennige et al. (2017).

Patch reefs are common throughout the tropics and form a different biotope to the main reef framework. Here, competition is lower, but cover from predators is limited (Garrett et al., 1971). This leads to a different assemblage of fish and invertebrates associated with the corals than on a larger reef framework (Wallace, 1977). Although patch reefs have been widely documented and identified as essential components of coral reef ecology, the mechanisms behind their formation have not been as widely studied. To understand what substrate is at the heart of a patch reef, you would need to damage the structure, a practice that would be prohibited today for good reasons. However, Garrett et al. (1971) used dynamite to blast away portions of two reefs in Bermuda, Grid Reef and Make-Do Reef. They found that 50-70% of the total reef volume comprised corals or dead coral skeletons, with the other 30-50% being occupied by sediment-filled cavities. They found no trace of rock or stone. This poses the question of what was originally there for the coral larvae to attach to and establish the patch reef. I hypothesise that it may have been coralliths that began the process. This is an important question to investigate, as patch reefs constitute a large portion of coral reef habitat. For example, Bermuda has over 1500 patch reefs within its lagoon, varying in size from <10 m to >400 m in diameter (Garrett et al., 1971). The FLSH suggests that it could be coralliths that are expanding the range of the reef and forming a larger surface area to support the wider ecosystem. If coralliths have a key ecological role in developing new reef habitats, they need to be incorporated into reef management and not overlooked as mere curiosities.

1.3.9 Coralliths in the fossil record

Zapalski et al. (2022) recently described Devonian coralliths suspected to be of the species *Alveolites Tenuissimus* and *Favosites goldfussi* from the Holy Cross Mountains, Poland. Whilst most modern discoveries of coralliths have been in shallow waters, the coralliths they described were from relatively deeper depths, and they discounted the suggestion that they have been moved from shallow water to deeper water (Zapalski et al., 2022). They also drew similarities to a *Stylocoeniella guentheri* corallith found at ~28 m depth off Heron Island, Australia. The channel in which this relatively large corallith (~15 cm diameter) was found had a very flat topography and sandy bottom (Zapalski et al., 2022). Corals do not usually colonise these sandy substrates, yet coralliths can live on sand even at surprising depths.

Crame (1981) examined the formation of patch reefs in Kenyan Pleistocene reefs and found that initial patch reef formation was by massive species such as *Porites spp.,* which were the pioneer species that were regularly at the base of the patch reef (known as B horizon species), whilst thinner smaller species such as *Cyphastrea spp.* and *Montipora spp.* encrusted onto the basal species (also known as C horizon species) and extended the reach of the patch (Crame, 1981). It is possible that these basal *Porites spp.* individuals were coralliths that were able to colonise the sand, providing substrate for other species to attach to. This was also recognised by Hennige et al. (2017), who suggested this was free-living stabilisation.

1.4 Aims and Objectives

In this thesis, I address some of the knowledge gaps in corallith biology and ecology. Therefore, my overall thesis aim was:

To elucidate the factors enabling only some coral species to form coralliths and further understand the role coralliths play in coral reef ecosystems, particularly during and after periods of disturbance.

To achieve this, I had three main objectives, one being addressed in each of my three data chapters.

1) Does a coral species' ability to overcome physical or environmental light stress better enable it to produce a corallith?

In Chapter 2, I used lab techniques to put CFS and non-CFS under experimental stress to monitor how they respond to physical and light stress. By doing so, I aimed to detect differences that could explain why CFS can withstand the added stressors of a mobile life compared to non-CFS.

2) Is there evidence for FLSH in the Caribbean, where reefs have historically undergone dramatic changes due to disturbance?

In Chapter 3, I used field surveys to characterise the corallith community in Utila and Tela, Honduras. I looked for evidence that coralliths become larger as you move away from the shore, where they eventually stabilise and form patch reefs (FLSH). I also used pre-existing data sets to look at the change in CFS species over time and how historical disturbances have affected the corallith community in this region.

3) How do coralliths respond to repeated disturbances such as bleaching events?

In Chapter 4, I used pre-existing field survey data from The Maldives to look at the response of a CFS, *Porites rus,* to repeated bleaching events (one of the major threats to coral reefs today). *Porites rus* is known to be resilient to bleaching, and understanding its response may help us understand how other CFS might respond to repeated bleaching events.

Chapter 2: The acclimation and tolerance of corallith-forming species to suboptimal conditions caused by a mobile lifestyle

Coralliths experience added stress due to their mobile lifestyles, yet they can survive these pressures. Firstly, they will likely experience changes in the light environment more regularly than their sessile conspecifics. Secondly, they can endure the added pressure of mechanical stress from being moved around uneven surfaces, causing damage to both soft and hard tissue. In this chapter, I investigated why CFS can tolerate these sub-optimal conditions more than non-CFS.

2.1 Introduction

As described in Chapter 1, coralliths are unattached, free-living corals that are moved by wave action and fish grazing (bioturbation) (Glynn, 1974). Coralliths, therefore, are likely to experience a high level of physical stress (Glynn, 1974, Hoeksema et al., 2017). For example, being covered over by sand, silt or rubble or being rolled over uneven sea beds can cause damage to soft tissue as well as fracture and fragment skeletons. This would be fatal to many species of scleractinian corals (Highsmith, 1982), but coralliths can withstand this stress based on their existence in many systems. Being moved about also means that coralliths experience changes in their light environment. Firstly, when an individual corallith is rolled over, and there are changes in the orientation of the colony, different parts of the coral will be in brighter light whilst other parts will become shaded. Being in this orientation for a prolonged period can lead to the shaded part of the colony becoming bleached, which I observed in the field (Figure 1). Secondly, coralliths can be moved greater distances if they reach a steep area of reef and are rolled downhill, which can move them into lower light environments (Zapalski et al., 2022). These sometimes-drastic changes would be damaging to most coral species, yet coralliths can withstand this stress. This enables them to colonise areas that are uninhabitable to many coral species, such as rubble beds (Hennige et al., 2017, Kenyon et al., 2020). Once here, they can reach a critical maximum size and encrust and consolidate the substrate underneath (Hennige et al., 2017). In this way, they can create new habitat for other species (as described by FLSH). To date, only a handful of coral species have been described as able to form coralliths (see Chapter 1, Table 1 for a complete list of species). Understanding how these species can withstand the additional environmental pressure that comes with being mobile will help us to elucidate the factors enabling corallith formation. For example, do CFS recover from physical damage more quickly than non-CFS, or do they acclimate to high/low light more readily than non-CFS?

Figure 1. Photograph taken by Nadia Jogee at Sturch Bank, Utila, Honduras. The picture shows the underneath of a corallith that has been bleached due to its orientation facing the sand.

2.1.1 Causes of light stress

Scleractinian corals can exploit light via the symbiotic relationship they have with single-celled dinoflagellate algae (Berkelmans and van Oppen, 2006, LaJeunesse, 2020), collectively called zooxanthellae that live within the gastrodermis of the coral tissue (LaJeunesse, 2020). These symbionts can fix carbon dioxide via photosynthesis and provide the coral host with sugars and other secondary metabolites, providing a reliable food source in these otherwise nutrient-poor waters (LaJeunesse, 2020). To maximise the efficiency of this relationship, most corals have adapted to a sessile lifestyle. As larvae, they settle on solid, stable substrates and metamorphose into primary polyps, growing through asexual reproduction into the iconic vast structure we think of when we picture a tropical coral reef (Gleason and Hofmann, 2011). This sessile lifestyle means they only need to acclimate to daily and seasonal changes in the light environment, which does not have vast fluctuations in the tropics (Vermeij and Bak, 2002). Coralliths forgo this advantage of the sessile lifestyle and instead experience changes in the light environment in small time frames. For example, a corallith that is suddenly buried during a period of increased wave action will experience a sudden decrease in light availability (Glynn, 1974, Hoeksema et al., 2017, Roff, 2008, Scoffin et al., 1985). Whilst a corallith that is suddenly uncovered by wave action will experience a rapid increase in the available light.

2.1.2 Effects of light stress

Decreases in light availability will limit the amount of photosynthesis that can occur within the symbionts and, in turn, will reduce the amount of photosynthates they can produce (Comeau et al., 2013, Davies, 1991, Hennige et al., 2010, LaJeunesse, 2020). As many scleractinian corals rely on this as their primary food source, if this light reduction lasts for a prolonged period (a matter of days), they can starve to death (LaJeunesse, 2020, Loya et al., 2001). Consideration has been given to this in the literature, in particular corals in areas of high turbidity (Guest et al., 2016, Anthony and Larcombe, 2000, Brown et al., 2019, Browne et al., 2019, Hennige et al., 2008, Meesters et al., 2002, Rice and Hunter, 1992), living in the mesophotic zone (De Palmas et al., 2021, Eyal et al., 2019, Kahng et al., 2019, Lesser et al., 2009, Tamir et al., 2019) and to a lesser extent low light caused by burying (Rice and Hunter, 1992, Wesseling et al., 1999). Although all three cause low light conditions, they have unique accompanying challenges. High turbidity often comes with increased pollution; depth usually means a lower temperature, and burying means a higher risk of physical damage to soft tissues, which can all reduce photosynthesis. Although coralliths are at risk of low light caused by all three of these challenges, they are at a higher risk of burying due to their unattached position on the sea bed compared to their sessile conspecifics.

Photosynthesis is a highly complex process of chemical reactions driven by light. Photosynthesis can be divided into two major stages: the ‘light-dependent’ and the ‘light-independent’ reactions (Hall and Rao, 1999). During the light-dependent reactions of photosynthesis, which takes place in the thylakoid membranes of a chloroplast, a chlorophyll molecule in Photosystem II absorbs a photon of light (Hall and Rao, 1999). This sets off a chain of reactions whereby the electron is passed down to Photosystem I, and further reactions result in the production of both ATP and NADPH (Hall and Rao, 1999). These two molecules fuel the Calvin Cycle's reactions during the light-independent stage of photosynthesis, which produces photosynthates such as glucose (Hall and Rao, 1999). A reduction in the amount of available light, therefore, directly impacts the amount of food that the coral can attain from its symbionts (LaJeunesse, 2020). This can only be overcome by the symbiont community ‘reshuffling’ to a different dominant strain (Palacio-Castro et al., 2023) or physical acclimation to the new light environment (e.g. production of accessory pigments) whereby allowing for the maintenance of energy transfer rates (Iluz and Dubinsky, 2015).

Possible mitigations of light stress in coralliths

Corallith-forming species such as *Porites spp.* have been observed becoming buried *in situ*, yet they can be uncovered with their tissues intact and the coral is not entirely bleached (per comms. S.J. Hennige and own observations, see Figure 1). I hypothesise three possible reasons for this occurring. 1) It’s possible that observations in the field may be of coralliths that have only very recently been buried/covered over by substrates. Studies have shown that if corals are covered for a matter of hours, they can survive on their food reserves (Rice and Hunter, 1992, Lirman and Manzello, 2009). 2) CFS may acclimate more readily to low light conditions than non-CFS. 3) The substrates that coralliths become buried in will be formed through the erosion of coral skeletons on the reef. We know that coral skeletons can scatter light to maximise light harvesting by the coral (Enríquez et al., 2005). Therefore, the substrates covering the corallith may scatter enough light to allow photosynthesis to continue.

2.1.3 *Causes of physical stress*

Being moved over uneven substrates can cause damage to both soft tissues and skeletal structures (own observations in the field). All scleractinian corals are susceptible to breakage during periods of increased wave activity, such as storms and hurricanes, but coralliths experience this daily (Lugo et al., 2000, Rogers, 2019, Rogers, 1993). Coralliths can also be preyed upon by corallivores such as *Chaetodontids* (butterfly fish), or larger coralliths can be broken apart by species such as the Titan triggerfish (*Balistoides viridescens*). These large fish feed on burrowing animals that live within the skeletal structure of corals (Glynn, 1974). The movement caused by interactions with other animals has been termed 'bioturbation' (Glynn, 1974). All of these destructive processes cause damage to both the soft and hard tissues of corals, yet coralliths appear to be able to withstand the added pressures that physical damage causes.

2.1.4 Effects of physical stress

When a coral experiences damage to its soft tissues, it could first face increased exposure to pathogens (DeFilippo et al., 2016, Edmunds and Yarid, 2017, Palmer et al., 2011, Traylor-Knowles, 2016). A physical wound in the soft tissue becomes a point of entry for pathogens, which are numerous within the environment and can move freely within seawater (Mullen et al., 2004). Infection by a pathogen means that the coral must divert energy away from normal metabolic processes and instead put energy into fighting infection and healing the wound (Burmester et al., 2017, DeFilippo et al., 2016, Edmunds and Yarid, 2017, Palmer et al., 2011, Traylor-Knowles, 2016). A second effect of mechanical stress is damage to the underlying skeleton. If severe, this can mean fragmentation of the corallith into two or more smaller pieces (Highsmith, 1982). These newly formed fragments have one of two fates. 1) They can heal the wound at the site of fragmentation, 're-sheet' the surface of the substrate with new tissue and continue to grow as a corallith (Glynn, 1974, DeFilippo et al., 2016, Roff et al., 2014, Sheppard, 2020), or 2) they are unable to overcome these challenges and perish. The size of the fragments will play a significant role in the outcome of this scenario. A larger fragment might have a larger surface area of intact tissue to continue photosynthesis and, therefore, have enough energy to recover. A smaller fragment might have less available energy to recover and be more susceptible to burying, causing more light and physical stress.

2.1.5 Possible mitigations of mechanical stress in coralliths

Although some critical factors in survival after physical damage are out of the corallith's control, such as the subsequent size of fragments post-breakage, there are some physiological processes that CFS may be better at upregulating than non-CFS. Firstly, CFS may be able to re-sheet more quickly across exposed skeleton (DeFilippo et al., 2016, Roff et al., 2014, Sheppard, 2020) through either intratentacular budding (a polyp splits itself into two or more daughter polyps) or extratentacular budding (where a new, smaller polyp is formed next to a parent polyp and grows larger over time) than non-CFS (Haddon, 1883). It has also been observed in some CFS, such as *Porites spp*., that whole colonies can recover in a process known as the 'phoenix effect' (DeFilippo et al., 2016, Jogee, 2021, Roff et al., 2014, Sheppard, 2020). The phoenix effect is a phenomenon whereby seemingly dead coral can regenerate from remnant tissue existing on the surface or, in more notable cases, deeper within the coral's skeleton (Jogee, 2021, Krupp, 1992, Roff et al., 2014). Secondly, CFS may be able to heal the point of breakage and re-sheet the newly exposed skeleton while maintaining skeletal growth elsewhere in the coral better than non-CFS, which may need to divert energy to healing first before continuing growth elsewhere.

2.1.6 Advances in testing physiological responses: PAM fluorometry

The rate of photosynthesis has long been a measure of coral health, but the methods for testing this metric have historically been both invasive and destructive. They required covering the whole coral colony or removing a portion of the coral and moving to a lab environment to measure O_2 production (Osinga et al., 2012). Since the invention of the diving-PAM underwater fluorometer, this is no longer the case (Consalvey et al., 2005). When chlorophyll molecules absorb light energy, it has one of three fates: 1) it can drive photosynthesis, also known as photochemical quenching; 2) be re-emitted as light at a longer wavelength, known as fluorescence, or 3) be emitted as heat energy, also known as non-photochemical quenching (though this is a small amount in comparison to 1 and 2) (Baker, 2008, Consalvey et al., 2005, Kromkamp and Forster, 2003). These three pathways compete, so as photochemical quenching increases, fluorescence decreases and vice versa

(Hall and Rao, 1999). Therefore, measuring fluorescence gives us information about the photosynthetic rate. Modulated Diving PAM fluorometers allow for the non-invasive measurement of photosynthesis *in situ* and in the laboratory, without the need for dark-adaptation of the sample before measurement (Consalvey et al., 2005, Hennige et al., 2008).

2.1.7 Advances in testing physiological responses: Computer tomography of live corals

Computed tomography (CT scanning) of corals has been widely used to look at the structure of dead corals but has only been successfully used once previously to scan live corals (Laforsch et al., 2008). Computer tomography uses sequential X-ray scans to build up a 3D picture of a structure using cross sections, or slices, of the object. These slices can be stacked together to produce a 3D image. Each slice is a grey value of the object's density, corresponding to the X-ray beam's average attenuation. Laforsch et al. (2008) used CT scanning methods to measure the surface area of live scleractinian corals. Whilst they do not explicitly say how long the corals survived for post-scan, they did scan each coral three times to look at the method's reproducibility. This method has not been repeated in other studies looking at live corals, yet its application could give us great insight into the growth of corals. To date, growth rate studies look at overall volume change and linear extension rates, but detailed CT scans will enable us to not only measure volume changes but also to visualise where the growth has taken place.

2.2 Aims and Objectives

In this chapter, I aimed to elucidate some of the factors enabling corallith formation. I had three main objectives;

1) Using PAM-fluorometry techniques, I compared the photosynthetic capabilities of CFS with non-CFS when they were buried in two different substrates (one light-scattering, one non-light-scattering) to assess:
    a) Whether CFS and non-CFS could maintain normal photosynthetic rates in light scattering substrates.
    b) Whether CFS performed better at lower and higher light levels (light stress conditions) than non-CFS.

2) Using microscopy, I examined the tissue recovery at the site of breakage to assess whether:
    a) CFS heal more rapidly at the site of breakage than non-CFS.

3) Using CT scanning methods, I looked at the growth rate and visualised the skeletal accretion of live CFS compared to non-CFS to assess:
    a) Whether CFS accreted new skeleton more quickly than non-CFS, despite being recently wounded.
    b) Whether there was an uneven distribution of newly accreted skeleton in CFS and non-CFS.

2.3 Methods

2.3.1 Photosynthetic ability whilst being buried

Samples

Three coral species were chosen for this study due to their differing morphologies, the fast that one is CFS and the other two are not, but mainly due to their availability. This study took place during the height of the 2020 UK lockdown and acquiring corals was not possible so the corals that were used were what was available to me in the coral lab. Firstly, *Porites cylindrica* was selected as it is a CFS with a branching morphology when mature but with an encrusting base. The polyps of *P. cylindrica* are ~1 mm in diameter. Secondly, *Stylophora pistillata*, which has similar-sized polyps to *P. cylindrica*, is branching and non-CFS. Finally, *Platygyra sp.* was used as it is a massive coral, like many CFS, but to date, it has not been observed to form coralliths. In contrast with the other two species in the study, it has large polyps with variable size but approximately 10 mm at the broadest measure. *Platygyra spp.* are hard to identify to species level, though *Platygyra pini* is a common species in the aquarium trade, through which these specimens were obtained. However, for this study, we will refer to it as *Platygyra sp*. All corals were fragmented to create ten nubbins of each species that were 1.5 -2.5 cm long. For *P. cylindrica* 10 nubbins were cut from 3 larger coral colonies. It is likely however, that these were the same genotype as they had been propagated in the university's coral lab. For *S. pistillata,* 10 nubbins were cut from 4 larger colonies, these were more recently obtained from Tropical Marine Centre. They were cultured in captivity and there is no way of knowing if they were all from the same genotype or not. Similarly for the *Platygyra sp.* 10 nubbins were cut from 3 larger colonies that had been recently obtained from Tropical Marine Centre, and knowing if they were the same genotype or not was not possible. Although I recognise that this is a flaw in the methodology of this study, it is important to note that acquiring corals in the UK where you know the provenance and genotype is not common. The importation of corals is highly restricted in order to protect natural reefs, so many suppliers have turned to captive culture of corals. This is ultimately better for the environment, but means that studies in the UK are going to become more limited. If I was to perform this study again, I would take DNA samples and sequence them, to establish the relatedness of the corals used. Long-term, it would be a positive step to try and catalogue corals in captivity in this way, so that future studies could benefit from avoiding this for of pseudoreplication. Corals were fragmented two weeks before commencing the study to give them time to recover. All corals had been within our care for a minimum of six months and were acclimated to the experimental tank for one month before the start of the study.

2.3.2 Experimental Set-Up

Due to tank space, five of each species were allocated to one of two treatment groups: coral sand or black sand. Although this is a small sample size, it was thought that given available space in the lab and time permitted in the lab that this sample size would be manageable and also give some meaningful results based on other published studies such as Dias et al. (2019). Limpopo black sand was chosen because it does not scatter light like coral sand. The coral sand used in this study is natural medium coarse coral sand from the Tropical Marine Sand range (Figure 2) obtained through Tropical Marine Centre UK. The black sand used in this study was Unipac Limpopo black sand (Figure 2), with a small grain size of 1-2 mm and made of an inert quartzo-feldspathic gneiss (Chinoda et al., 2009). Fifteen 100 ml plastic beakers were half-filled with coral sand, whilst 15 were half-filled with black sand. Five nubbins of each species were placed into each of the two treatments. The beakers were then arranged in a 100-litre aquarium tank and evenly spaced into six rows of five (Figure 3). I chose not to use a random layout for this study but instead used a repeated pattern. This was because the position and direction of the light meant that the light dissipated towards the edges of the tank, creating an uneven level of PAR across the tank. A random layout would risk one species being grouped towards the lower light level, whereas a repeated pattern allowed each species to have an equal spread across the entire light range. Each beaker was labelled with treatment and numbered 1-15. Each coral nubbin was then covered with corresponding treatment sand, enough so no tissue was visible.

Figure 2. Photographs of the two substrates used in this study: Limpopo black sand (left) and medium coarse coral sand (right).

The aquarium was filled with artificial seawater mixed up using Red Sea aquarium salt and kept at 35 ppt for the duration of the study. This salinity was maintained via GHL Profilux and an auto-top-up system that pumped reverse osmosis water when the salinity rose above 36 ppt. A 10% water -change was performed the day before the start of the study to ensure good water quality before commencing. A 10% water change was then performed once per week to maintain conditions. Lighting was provided by 1 Ecotech Marine Radion G5 Pro, mounted as per the manufacturer’s guidelines. In-tank powerheads were installed in the tank to create water flow. Tanks overflowed to a sump filled with live rock; water passed through fine filter floss to remove particulate waste before entering the sump. Finally, the tank was fitted with an Aqua Medic protein skimmer to remove excess organic waste from the water. For the duration of the study, a black-out fabric surrounded the tank so that the only light the corals received was from the provided lights (Figure 3).

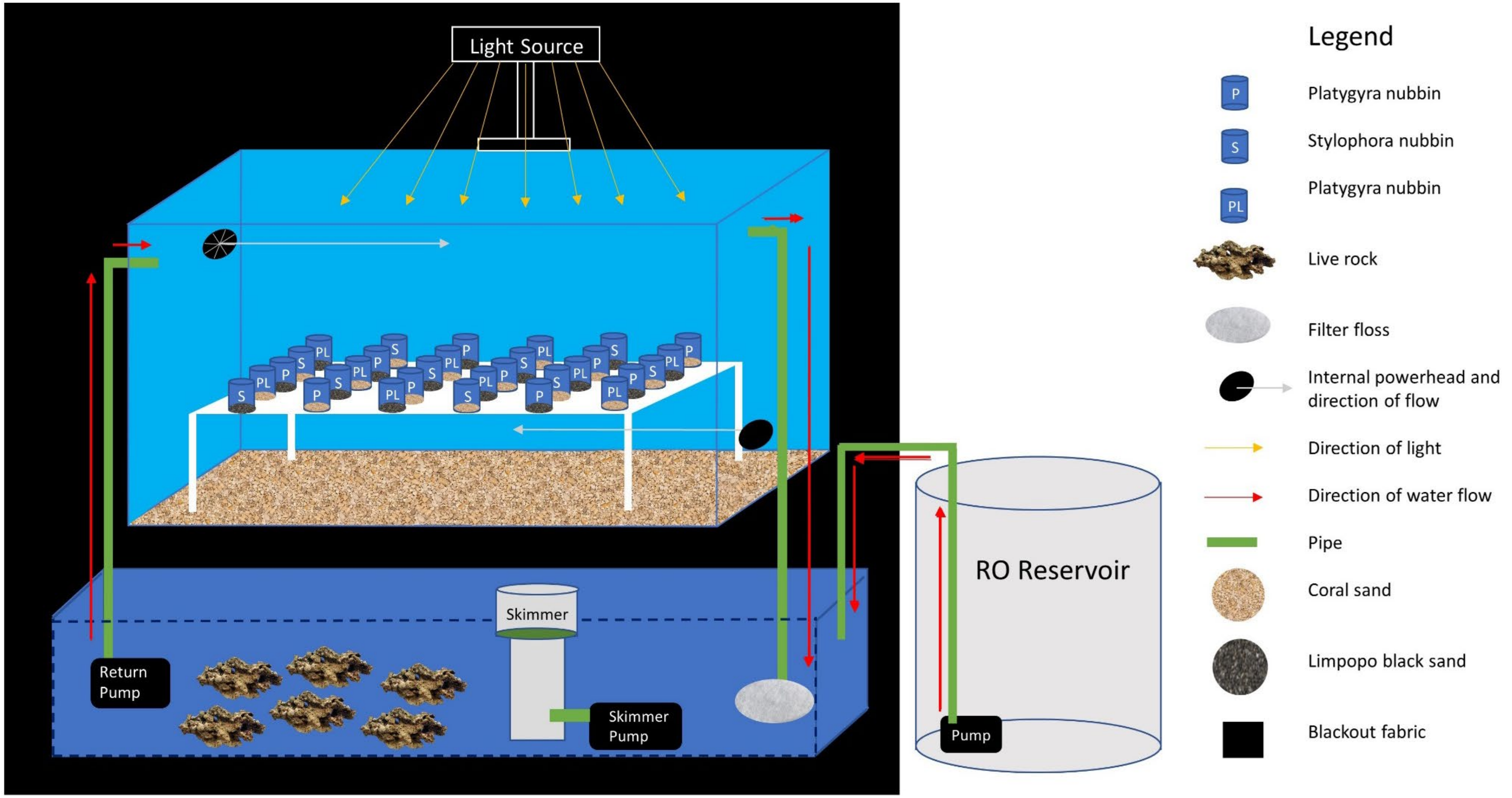


Figure 3. Schematic diagram of experimental set up.

2.3.3 Pam Fluorometry Measurements (Y)

A Diving-Pulse Amplitude Modulation (Diving-PAM II) fluorometer (Heinz-Walz) was used for all quantum yield measurements (*Y*) , also termed Fq'/Fm'; see Hennige et al. (2008) and Baker (2008) for further details on measurements and calculations of yield. All measurements were taken as close to the coral as possible without actual contact to avoid damage to the soft tissue. The samples in this study were not fully dark-adapted because once the coral was uncovered from beneath the sand, it was exposed to ambient light before the measurement was taken. Each coral nubbin was gently uncovered in turn, using a 'wafting' motion of the hand to remove the substrate from the surface of the nubbin whilst avoiding touching it with hands. Quantum yield measurements were taken, and the corals were covered in their respective treatment substrate. This study was carried out over 20 days. Three *Y* were taken for each coral on Day 1, and an average *Y* for each nubbin was calculated. From Day 3, *Y* measurements were then taken daily at 2 p.m. until Day 7. Due to limitations imposed on this study that were outside my control, measurements were taken every 3 to 4 days for a further 13 days.

Table 1. Parameters and definitions, adapted from Kromkamp and Forster (2003) and Baker (2008). Unless stated otherwise, all units are in instrument-specific values (fluorescence yields) or dimensionless (fluorescence ratios).

Parameter	Definition	Equation
F′	Steady-state fluorescence	-
F0′	Minimum fluorescence	-
Fm′	Maximum fluorescence	-
Fv	Variable fluorescence yield when dark-adapted	$(\mathrm{Fm} - \mathrm{F0})$
Fv′	Variable fluorescence yield under actinic light	$(\mathrm{Fm}' - \mathrm{F0}')$
Fq′	Fluorescence quenched	$(\mathrm{Fm}' - \mathrm{F}')$
Fv/Fm	Dark-adapted maximum photochemical efficiency of exciton energy transfer to PSII reaction centres, also called maximum quantum yield.	$\frac{(\mathrm{Fm} - \mathrm{F0})}{\mathrm{Fm}}$
Fq′/Fm′	Effective photochemical efficiency of PSII photochemistry, or effective quantum yield (Y)	$\frac{(\mathrm{Fm}' - \mathrm{F}')}{\mathrm{Fm}'}$
E	Actinic light intensity (PAR)	-
rETR	Relative electron transport rate (rETR, µmol electrons m^{-2} s^{-1}). This is the rate at which electrons move linearly through the electron transport chain, as electrons are given off by PSII and accepted by PSI.	$\mathrm{rETR} = \frac{\mathrm{Fq}'/\mathrm{Fm}}{2} \mathrm{~x~E}$
NPQ	Non-photochemical quenching is a mechanism to alleviate stress caused by high light intensity. It dissipates excess excitation energy as heat. As light intensity increases, we expect NPQ to increase.	$\frac{(\mathrm{Fm} - \mathrm{Fm}')}{\mathrm{Fm}'}$
qP	Photochemical operating efficiency of PSII under actinic light, also termed photochemical quenching. This is when excitation energy is used in photosynthesis. As light intensity increases, we would expect this to decrease.	$\mathrm{Fq}'/\mathrm{Fv}'$
E_k	The light saturation coefficient (µmol photons m^{-2} s^{-1}) describes the transition between light-limited and light-saturated photochemical efficiency.	-

2.3.4 Rapid Light Curves

On Day 1, 13-step rapid light curves (RLC) were performed on each coral. The corals in their beakers, along with water, were removed from the tank to carry out the RLC due to the need for the optic measuring sensor to be mounted on a clamp stand. Initial fluorescence measurements were taken in the absence of actinic light, but with ambient light in the room, this was followed by an increasing series of 13 actinic light steps from 1 to 2350 µmol photons m^{-2} s^{-1} delivered from an 8 V halogen bulb within the Diving-PAM via the fibre optic cable. Each actinic irradiance level was delivered for 20 seconds, and the entire light gradient was performed over 160 seconds. The fibre optic probe was always placed on the uppermost coral surface parallel to the water surface and kept in place using a clamp stand. After the RLC was complete, the corals were replaced in the tank. From the data gathered by the RLC non-photochemical quenching (NPQ), photochemical quenching (qP), the saturation irradiance for electron transport (E_k) and the relative electron transport rate (rETR) were calculated using equations outlined in Hennige et al. (2008) (see Table 1 for details of parameters). As the absorptance for each species is unknown, the constant for this parameter was set to 1 in my calculations, hence why I give the rETR and not ETR. To account for variation between the species, E/E_k was calculated, where E is the actinic light intensity (PAR), and E_k is the light saturation coefficient or the minimum saturation irradiance. All other parameters were then plotted against E/E_k.

2.3.5 Tissue recovery from fragmentation

The data collection was conducted with the help of another student. We cut five coral nubbins from three larger colonies of *P. cylindrica*, five nubbins from four colonies of *Platygyra sp*. and five nubbins cut from two larger *S. pistillata* colonies to a size of approximately 3 cm at their widest point. Corals were then photographed daily at the same point along the cut edge at 8 x magnification for 20 days. However, the *S. pistillata* nubbins had severe tissue damage by Day 3 and had more than 60% necrotic tissue, so they were excluded from the rest of the study. The tissue growth over the cut was measured using Fiji open source software and tissue growth rate was calculated in mm per day.

2.3.6 Skeletal growth

The same ten coral nubbins used to examine the tissue recovery detailed above were used to investigate the skeletal growth after breakage. All nubbins were mounted on milliput for ease of positioning in the acrylic cylinder that they were scanned in. The milliput was given a clear notch so that the same surface of coral could be identified and images could easily be compared over time. Coral nubbins were then scanned two days after cutting and then once a month for a further three months to look at growth over time. However, the *S. pistillata* nubbins did not survive after the first scans, so they were excluded from the rest of the study.

Coral nubbins were scanned in clear acrylic tubes with tank water in them. All nubbins were given 48 hours to recover from the stress of being cut before being scanned. This study uses the µCT scanner, a cone-beam system built at the University of Edinburgh. It comprises a 10–160 kV Feinfocus dual transmission and reflection source, aMicos UPR-160-air rotary table and a Perkin Elmer 0822 amorphous silicon flat panel X-ray detector with a terbium doped gadolinium oxysulfide scintillator. Each 3D volume is comprised of 2000 radiograms (exposure time: 2 s) captured during a full 360° rotation. A 0.8 mm aluminium filter was used during the scans to reduce the measurement noise and beam hardening effect. The source-sample and sample-detector distances were 37 mm and 549.5 mm, respectively. The X-ray source voltage and current were 120 kV and 500 µA, respectively. The X-ray spot size is 5 µm. Reconstructed 3D images have a voxel resolution of 13.25 µm. The shared 3D images are in 8-bit format. These images were rescaled (after reconstruction in Octopus23) with offset and slope of 0 and 7.84 × 10−3, respectively.

The resulting slices were then processed using Fiji open-source software. Each nubbin was imported as an image sequence (stack). The contrast was enhanced and the image was binarised. Then, using the threshold tool, images were segmented so that only the coral skeleton and not the milliput were visible, and this thresholding was applied to the whole stack (Figure 4). Using a macro plugin, total volumes for each nubbin were calculated in cm^3.

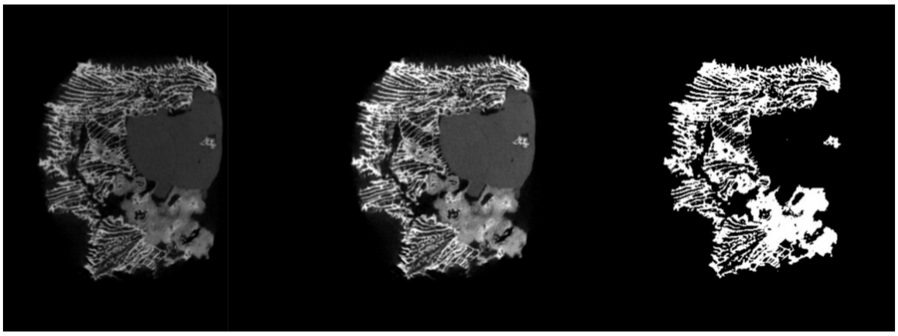


Figure 4. Images were taken from the segmentation process in Fiji open-source software. Raw 8-bit grayscale image of a *Platygyra sp.* slice with both coral skeleton and milliput visible (left). Enhanced contrast (centre). Images were binarised and milliput were removed using the threshold tool (right).

2.3.7 Data Analysis

All data were plotted in R using the package ggplot (Wickham, 2016). Segmented piecewise analyses were used to detect breakpoints in the rETR for each species. A generalised linear model with a gamma distribution was used to test the effect of E/E_k and species on NPQ. As the values for qP are bounded by 0 and 1, a beta regression was used to test the effect of E/E_k and species on qP. Linear models were used to test the effect of Day on daily mean *Y* values for each species in each treatment and then each treatment as a whole. Linear models were also used to test the effect of substrate on the difference in mean *Y* at the start and the end of the study for each species. The tissue extension rate over the newly exposed coral skeleton was measured in mm day^{-1} using Fiji open source software.

2.4 Results

Observations made on each measurement day from Day 5 onwards showed substantial necrotic tissue across all species (Figure 5). This was especially true of the black sand treatment, where all but three nubbins had perished by Day 7. By Day 20, only 1 *P. cylindrica* nubbin survived in the black sand treatment. Tissue loss was not as severe in the coral sand treatment, where 11 coral nubbins survived until Day 20 of the study.

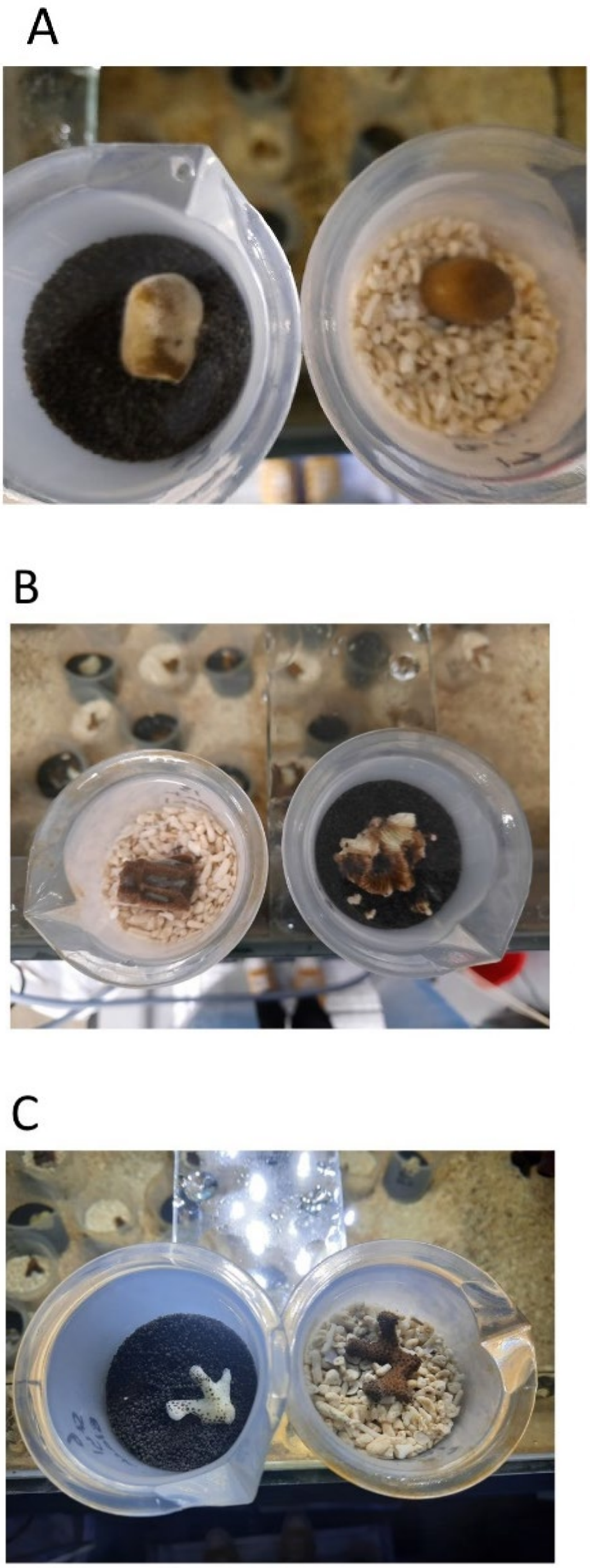
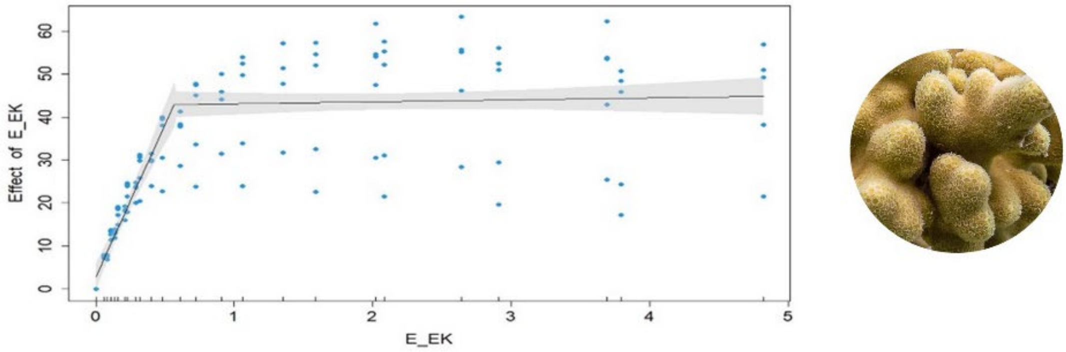


Figure 5. Photographs taken on Day 5 of the study showed extensive tissue loss across A) *P. cylindrica,* B) *Platygyra sp.* and C) *S. pistillata* coral nubbins in black sand, whilst nubbins in coral sand were all visibly healthy.

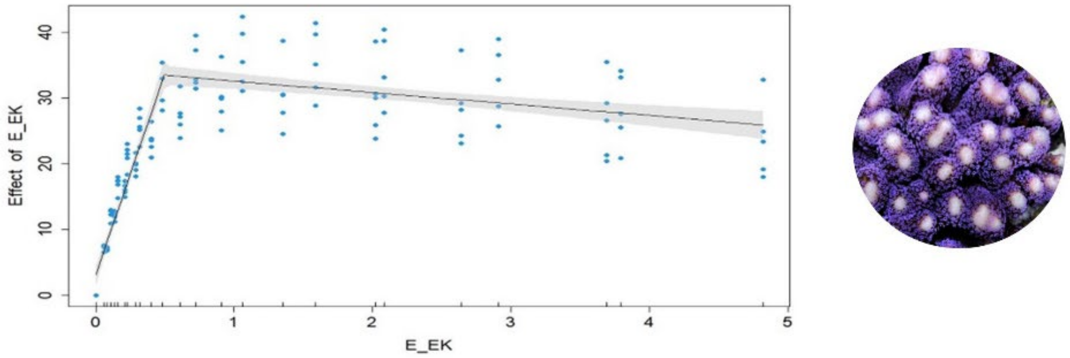
2.4.1 Relative electron transport rate

In *P. cylindrica,* the rETR rose quickly until E/E_K of 0.57 (breakpoint detected), at which point it plateaued. The slope before this point was 70.7, and after this point, the slope was only 0.5, the intercept for the breakpoint was rETR = 42.7 (see Table 2 and Figure 6). In *S. pistillata,* the rETR rose quickly until an E/E_K value of 0.49 (breakpoint detected), after which point it plateaued. The slope before this point was 61.5; after this point, the slope was weakly negative at -1.7. The intercept at the breakpoint was rETR = 34 (Table 2 and Figure 6). The rETR for *Platygyra sp.* rose quickly until an E/E_k value of 0.48 (breakpoint detected), after which point it plateaued. The slope before this point was 69, whilst, after this point, it was weakly negative at -0.06. The intercept at this point was rETR = 36 (Table 2 and Figure 6).

A



B



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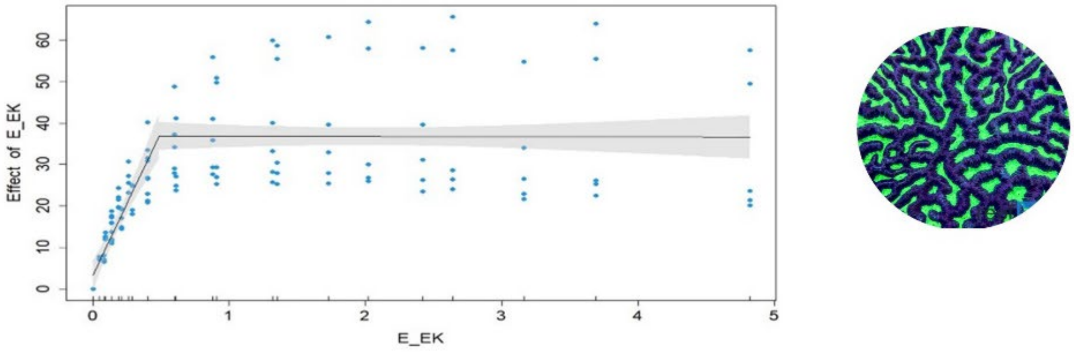


Figure 6. The effect of E/E$_k$ on rETR for *Porites cylindrica* (A), *Stylophora pistillata* (B) and *Platygyra sp.* (C). Line shows the mean effect on rETR and the shaded area indicates 95% CI.

Table 2. Results of the segmented piecewise analysis.

Species	Breakpoint E/E$_k$	Slope before breakpoint	Slope after breakpoint	Intercept at breakpoint (rETR)
Porites cylindrica	0.57	70.7	0.5	42.7
Stylophora pistillata	0.49	61.5	-1.17	34
Platygyra sp.	0.48	69	-0.06	36

2.4.2 Non-photochemical quenching

E/E$_K$ had a weakly positive effect on the NPQ of *Platygyra sp*. and a smaller effect overall than its effect on both *P. cylindrica* and *S. pistillata* (Figure 7). The data was not normally distributed with a strong positive skew. Therefore, a generalised linear model with Gamma distribution was used to test the effect of E/E$_k$ and species on NPQ (See Table 3).

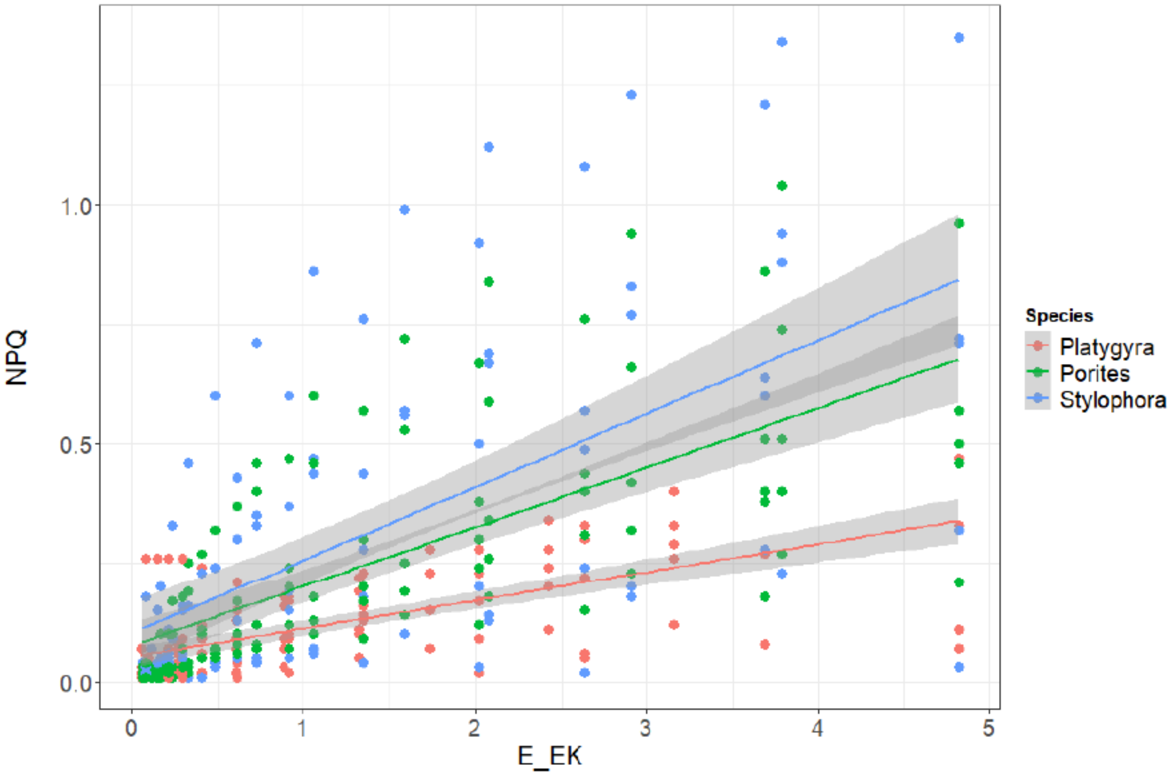


Figure 7. The effect of E/E$_k$ on non-photochemical quenching for *Platygyra sp., P. cylindrica,* and *S. pistillata*. Lines show the mean NPQ for the three species, and the shaded area shows the 95% CI.

Table 3. Results from the generalised linear model with Gamma distribution examining the effect of E/E_K and species on qP.

Coefficient	Estimate	SE	t-value	p-value
Intercept	-2.89	0.10	-29.23	<0.0001
E/E_k	0.53	0.04	14.02	<0.0001
P. cylindrica	0.52	0.12	4.20	<0.0001
S. pistillata	0.76	0.12	6.27	<0.0001

2.4.3 Photochemical Quenching

Overall, *P. cylindrica* had a higher qP than both *Platygyra sp.* and *S. pistillata* (Figure 8). A beta regression used to test the effect of E/E_k on qP showed that both species and E/E_k had a negative effect on qP (Table 4).

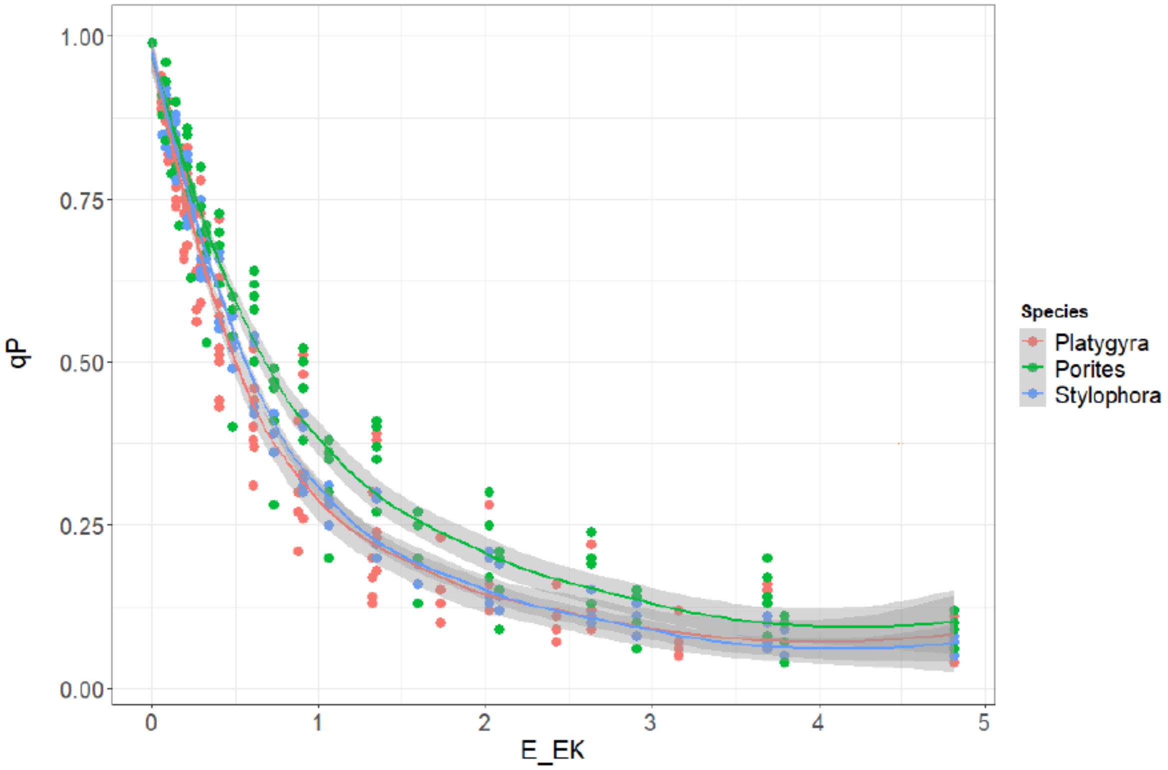


Figure 8. The effect of E/E_K and species on qP. Lines show the mean qP, and the shaded area shows the 95% CI.

Table 4. Results from the beta regression examining the effect of E/E_K and species on qP.

Coefficient	Estimate	SE	z-value	p-value
Intercept	1.2	0.1	16.1	<0.0001
E/E_K	-1.16	0.03	-30.8	<0.0001
P. cylindrica	0.2	0.09	2.6	0.01
S. pistillata	0.08	0.09	0.9	0.4

2.4.4 Daily Y (Fq'/Fm')

The use of a linear model showed no effect of day on *Y* for *P. cylindrica* in coral sand ($t_{44} = -1.47$, p = 0.15). A breakpoint was detected at 6.69 days for *P. cylindrica* kept in black sand. The slope before this breakpoint was -0.07; after this point, it was 0.02. However, this was based on only one nubbin surviving after this breakpoint. Removal of this individual and use of a linear model to test the effect of day on *Y* showed that day had a strong negative effect on *Y* ($t_{22} = -7.6$, p <0.001) (Figure 9).

One *S. pistillata* individual continued providing *Y* readings until the end of the study. However, there was a slightly visible film of algae growing on this nubbin, so any readings were likely an artefact of the algae, and the coral itself was likely dead. Removal of this individual and use of a linear model showed no effect of day on *Y* for *S. pistillata* in black sand ($t_{32} = -1.12$, *p* = 0.24) (Figure 9).

Use of a linear model showed no effect of day on *Y* for *Platygyra sp.* in coral sand ($t_{43} = -1.4$, p = 0.17). Use of a linear model showed that there was a strongly negative effect of Day on mean *Y* for *Platygyra sp.* in black sand ($t_{22} = -7.0$, *p* = <0.0001) (Figure 9).

Removal of the three coral nubbins that survived past Day 7 and the use of a linear model showed that day had a strong negative effect on *Y* overall for corals kept in black sand ($t_{70} = -11$, p <0.0001). Whilst day had a weak negative effect on *Y* for corals kept in coral sand ($t_{134} = -3.4$, p <0.0001) (Figure 9).

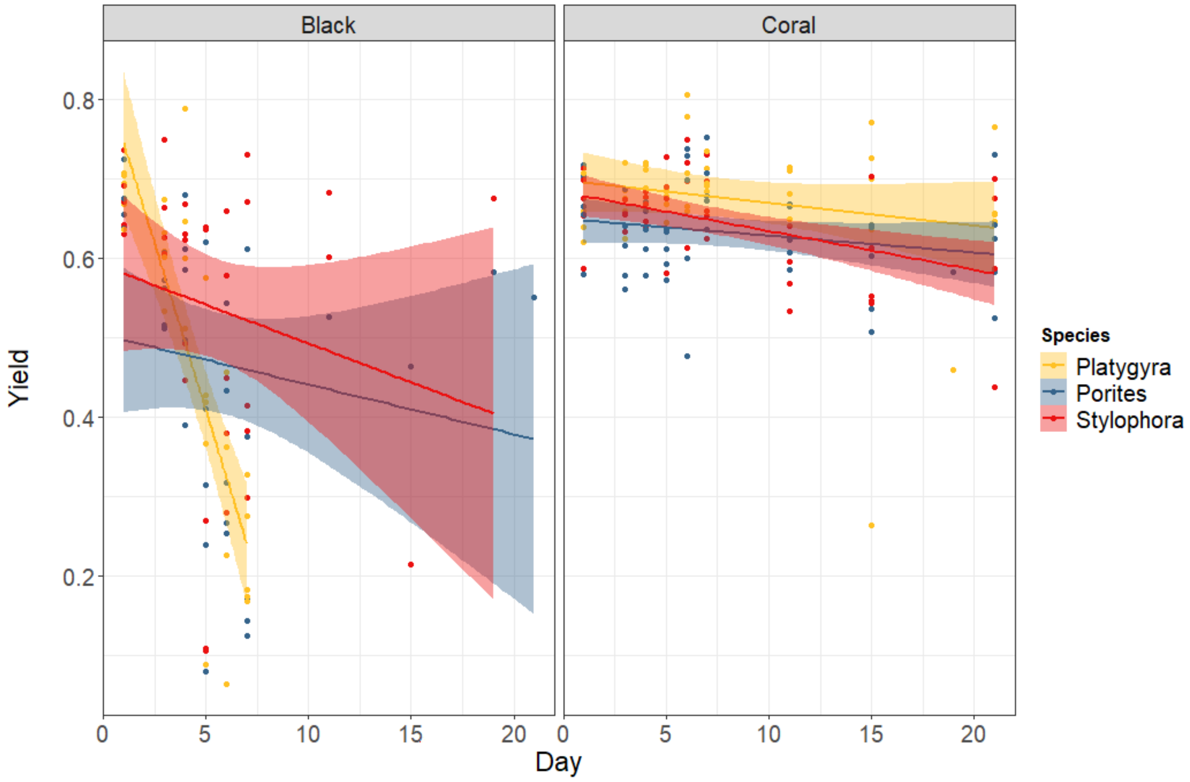


Figure 9. Scatterplot showing the effect of day on *Y*. Lines are extracted from linear models, and coloured areas show the 95% confidence interval of the fitted line.

The use of linear models showed that for *P. cylindrica,* there was an effect of substrate on the difference in mean *Y* from the start to the end of the study, with black sand having a strongly negative effect ($F_{1,8}$ = 15.41, *p* = <0.004) (Figure 10). The use of linear models showed that for *Platygyra sp.,* there was an effect of substrate on the difference in mean *Y* from the start to the end of the study, with black sand having a strongly negative effect ($F_{1,8}$ = 305.3, *p* = <0.0001) (Figure 10). There was no effect of substrate on the difference in mean *Y* between the start and the end of the study for *S. pistillata* (Figure 10).

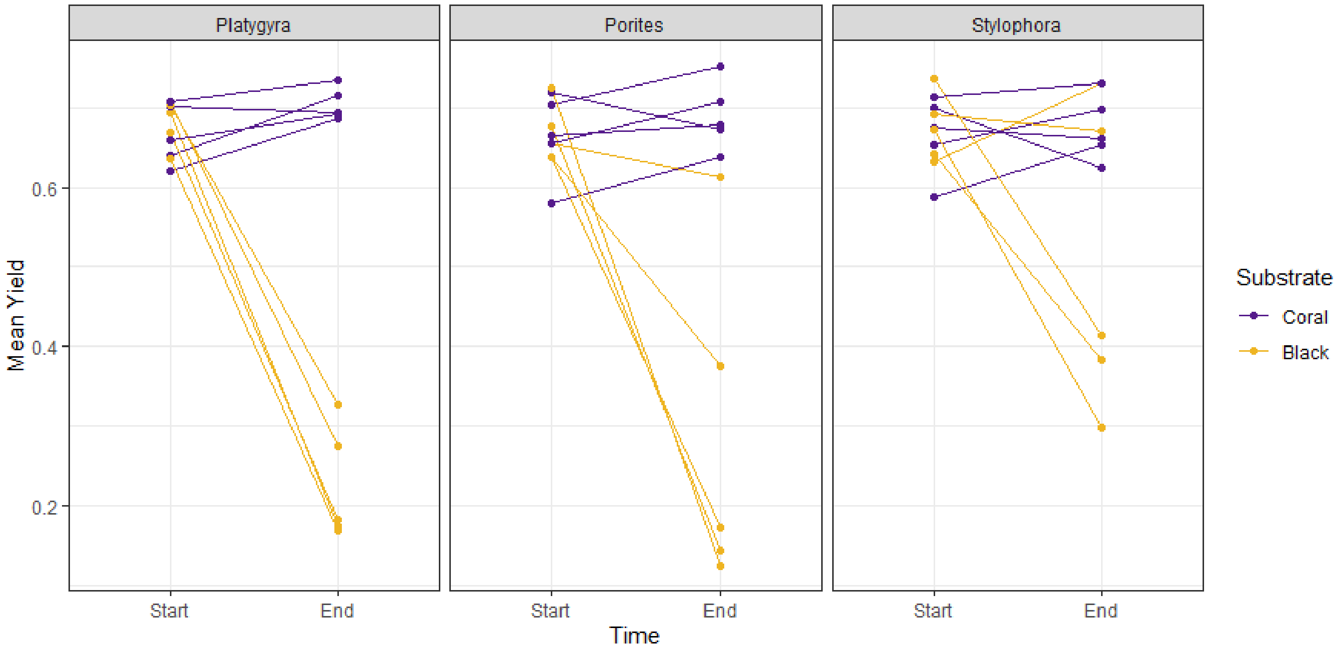


Figure 10. Mean *Y* (Fq′/Fm′) at the start and end of the study for five nubbins of each species: *Platygyra sp.* (left), *P. cylindrica* (centre) and *S. pistillata* (right). In the two different substrates (coral sand = purple line, black sand = yellow line). Whilst all individuals of *Platygyra sp.* and *P. cylindrica* showed similar patterns of either a decrease in black sand or a slight increase in coral sand, there was more variation in the response of *S. pistillata.* While some individuals in the coral sand decreased their mean *Y*, others increased, and the same was true in the black sand.

2.4.5 Tissue recovery at the point of breakage

Over the 20-day study, all corals healed along the cut edge (Figure 11). *Platygyra sp.* visibly healed the existing polyps, whilst *P. cylindrica* grew new ones. The rate of recovery across the 20 days was not significantly greater in *P. cylindrica* (mean ± S.E. = 0.12 mm day^{-1} ± 0.02) than in *Platygyra sp.* (0.08 mm day^{-1} ± 0.01), paired t-test: t_{78} = 1.528, p = 0.131. However, the initial rate of recovery between days 0-3 was 79% greater in *P. cylindrica* (0.34 mm day^{-1} ± 0.04) than in *Platygyra sp*. (0.19 mm day^{-1} ± 0.01), paired t-test: t_8 = 4.012, p= 0.004.

After the initial cut, the endolithic tissue layer was recognisable by the line of endolithic algae present within the skeleton of *P. cylindrica.* This tissue layer protected the newly exposed surface from becoming fouled by biofilm. The endolithic tissue then appeared to establish itself on the surface quickly and developed new polyps by Day 6.

2.4.6 Skeletal volume

There was no effect of Month on skeletal volume for *Platygyra sp.,* whilst Month had a strong positive effect on skeletal volume for *P. cylindrica* (t_{14} = 4.01, *p* = 0.001) (Figure 13).

However, although not statistically significant, it was interesting biologically to note that all individuals lost skeletal density (-0.86% in *P. cylindrica* and -7.5% in *Platygyra sp.)* in the first month post-cutting and then gained volume in the subsequent two months. Also worth noting was the appearance of gaps in the skeleton of *P. cylindrica* where the skeleton was cut. The coral grew over this cut, leaving a gap or 'scar' in the skeleton (Figure 14).

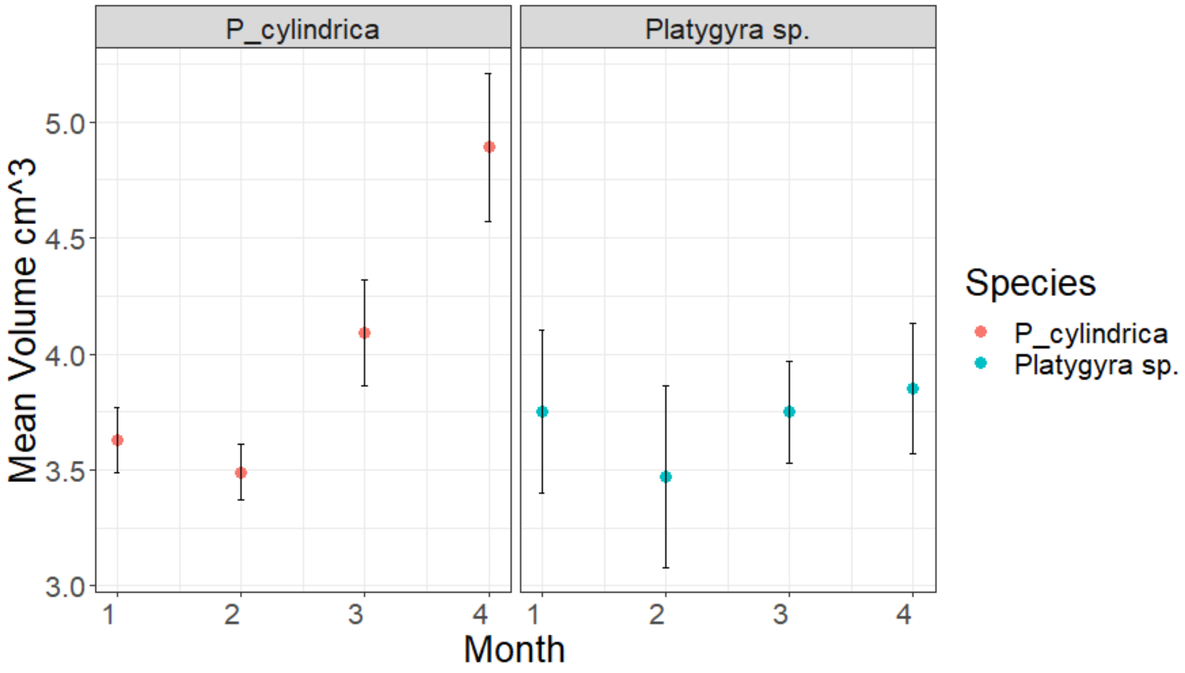


Figure 13. Skeletal volume in cm^3 over time for *P. cylindrica* (left) and *Platygyra sp.*(right). Error bars show SEM. *n* = 5 per species.

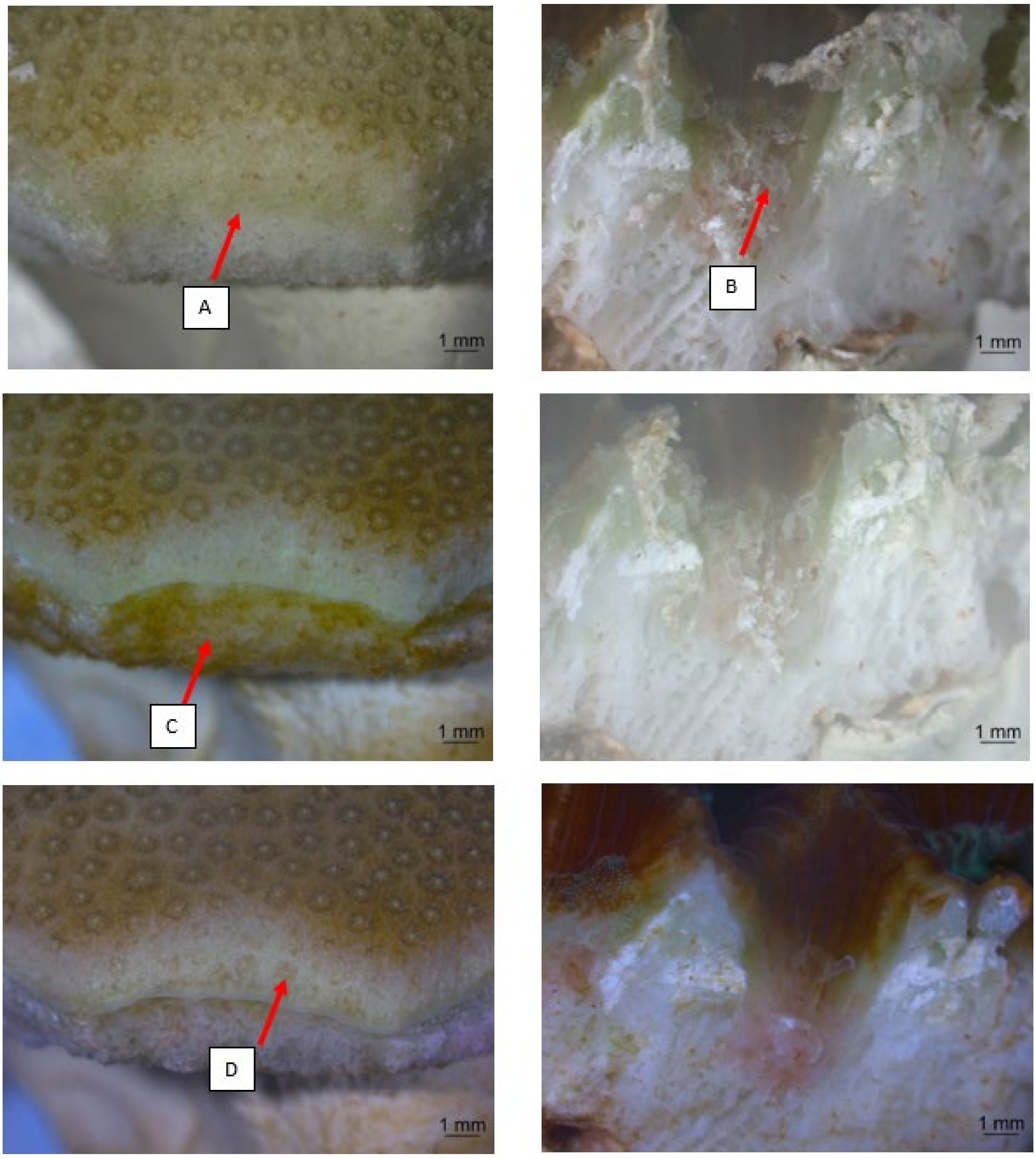


Figure 14. Images taken at 8 x magnification of the cut edge of one *P. cylindrica* (left column) and *Platygyra sp.* (right column), taken on Day 1 (top), Day 3 (middle) and Day 6 (bottom). In the top two and middle images of *P. cylindrica,* a clearly defined band of endolithic tissue is marked by the line of endolithic algae (A). This portion of the cut edge did not get any biofilm growing over it, unlike the exposed skeleton without endolithic tissue (C). This endolithic tissue appears to inhibit the growth of any biofilm and established itself on the newly exposed surface. By Day 6, I saw new polyps forming (D). In the same period in *Platygyra sp.* I did not see the same progression of new tissue growth but instead saw only the healing of the wound, which was extensive enough to expose mesenterial filaments (B). I also observed biofilm growing across the whole surface of the newly exposed skeleton, seen as mottle brown/green patches across the exposed skeleton.

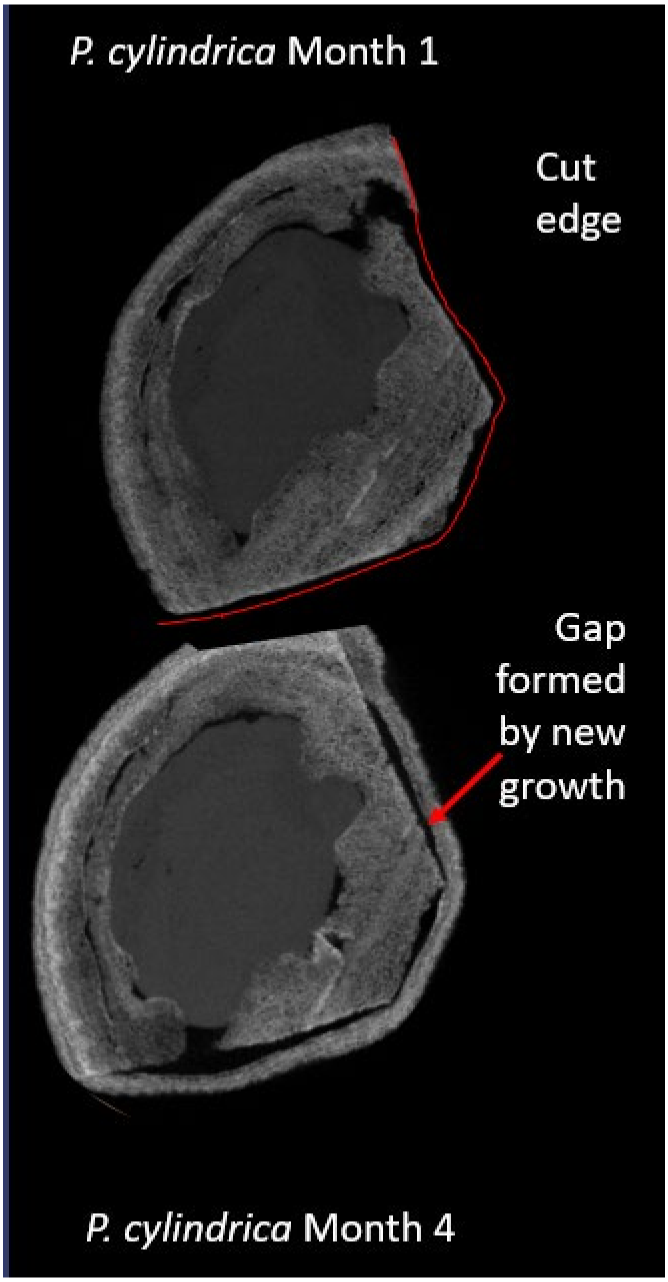


Figure 14. orthosclices of *P. cylindrica* on month 1 (top) versus month 4 (bottom). The red line indicates the cut edge of the nubbin. There is a clear gap formed over the cut edge by Month 4.

2.4.7 Signs of disease

After the *S. pistillata* nubbins were cut for the tissue growth and skeletal growth portion of this study, they quickly died within six days with visible signs of tissue necrosis (Figure 15). Historically, we have had similar issues in the lab with tissue sloughing in *Acropora spp., Pocillopora spp.* and other species of *Stylophora,* such as *S. hystrix.* The repeated nature of the same pathological signs suggests there might be a pathogen present in our study tanks, which could have caused the death of the *S. pistillata* nubbins, which is known to be more susceptible to conditions such as rapid tissue necrosis (RTN).

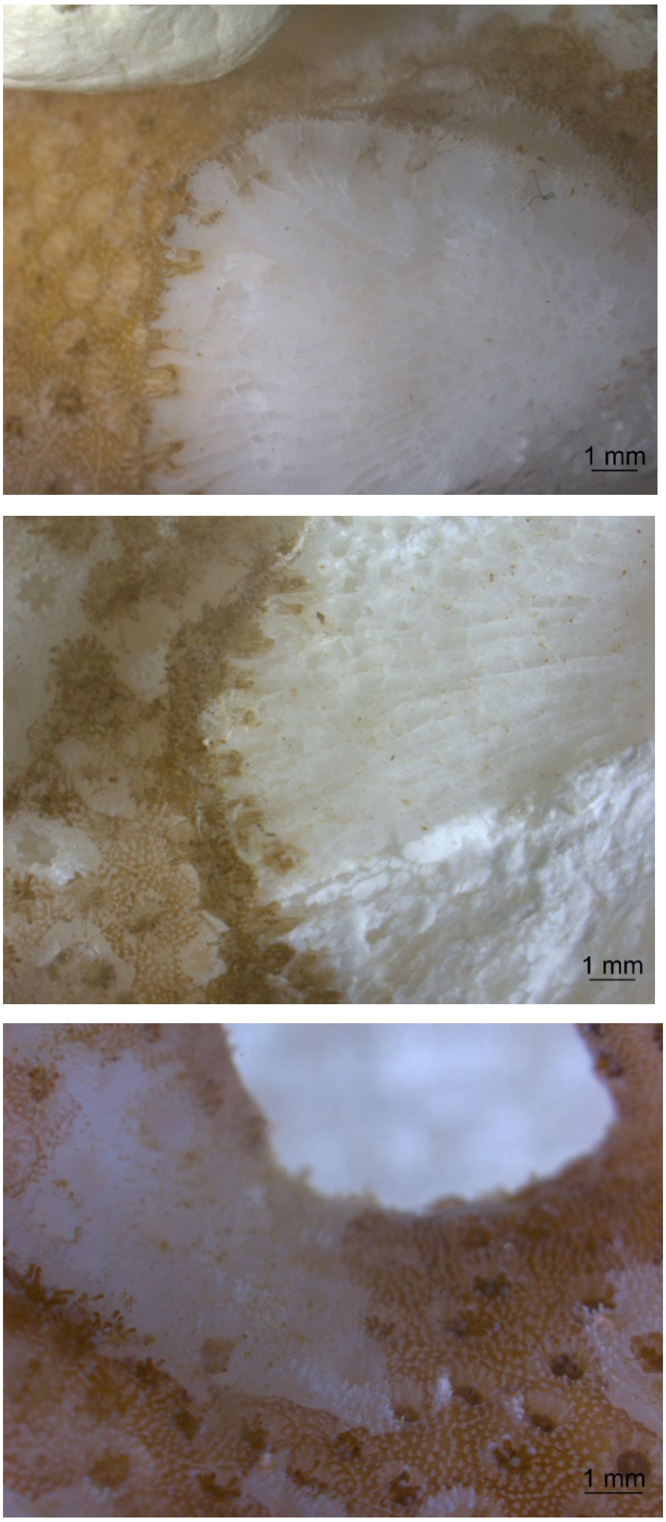


Figure 15. The top and centre images show the same cut face of a *S. pistillata* nubbin on Days 1 (top) and 2 (centre). The centre image shows clear signs of tissue erosion. Bottom image shows a photograph taken of the same nubbin on Day 2 but away from the cut edge, indicating that the tissue necrosis had spread to other areas of the colony.

2.5 Discussion

The results of this study suggest that *P. cylindrica* is more of a generalist species than either *S. pistillata* or *Platygyra sp*. It neither appeared to acclimate quickly to low light and being buried nor did it struggle to the extent of dying. *Porites cylindrica* also healed rapidly from wounds and had steady skeletal accretion across the four months of CT scans. *Stylophora pistillata* could divert energy into NPQ at higher light intensities but did not do well after physical stress and died during the study. *Platygyra sp.* did not cope well with the higher light levels during the RLC and could not divert as much excess energy into NPQ as the other two species and died in the black sand treatment, but did well whilst buried in the coral sand. It also had steady tissue recovery over the 20 days of study and grew new skeleton over the four months of scans, although not a significant amount.

2.5 1 Light Stress Responses

Rapid light curves are a quick and relatively easy method for testing the efficiency of photosynthesis at varying light levels and allow the level of light intensity required for photoinhibition (the point at which rETR plateaus) to be calculated. Whilst both *S. pistillata* and *Platygyra sp*. had a similar E/E_K at the point of photoinhibition (0.49 and 0.48, respectively), *P. cylindrica* reached photoinhibition at an E/E_K of 0.57, suggesting that it can tolerate higher light intensities than the other two species. Albeit only a slightly better performance, this means that *P. cylindrica* coralliths might be able to withstand the added pressure of suddenly being in brighter light conditions than the other two species in this study. *Stylophora pistillata* and *P. cylindrica* were better at diverting excess energy into NPQ at high light intensities than *Platygyra sp*., which suggests that they are better adapted to these higher light levels and can protect themselves against cellular damage caused by excess excited electron energy. Again, this means that coralliths of these two species might be better equipped to deal with brighter light conditions than *Platygrya sp.* As expected, all three species reduced the amount of energy they used in qP as E/E_k increased, but *P. cylindrica* could still quench more of the excited electron energy via photosynthesis. These results suggest that *P. cylindrica* and *S. pistillata* can cope well at high light intensities, although *P. cylindrica* did marginally better at maintaining photosynthetic efficiency.

These results mean that a fragment of either *S. pistillata* or *P. cylindrica* would cope marginally better at moving into an area of higher light than *Platygyra sp.* in the short term. The death of many of the nubbins before the end of the study meant that the RLC could not be reliably repeated at the end of the study. This meant we could not compare the species at the end and look for any low-light adaptation. Repetition of the study using a larger sample size and buried in just coral sand should allow for this comparison to be conducted. Another aspect of the light environment that was not tested here was the change in the spectral composition when buried. It would be expected that different wavelengths of light are reaching the colonies when buried compared to when not buried. This could change how the corals harvest light, for example by producing accessory pigments (LaJeunesse, 2020).

The daily *Y* measurements revealed that coral sand provided a light environment still conducive for photosynthesis, whilst black sand prohibited this in almost all nubbins. One limitation of this study was the difference in grain size between the coral sand and the black sand. The black sand was much finer than the coral sand, meaning nubbins were more compactly buried in the black sand. This would mean that the nubbins in the black sand had much lower movement of water around them than in the coral sand. The larger grain size in the coral sand also means that some small particulate food could have been moved through the coral sand, which could have aided heterotrophy in this treatment. The compact burial of *Platygyra sp*. could have been particularly problematic for this species as it has large polyps (~ 10 mm across), which could have become irritated by the finer sand. However, what is evident from this study is that all corals in the coral sand maintained a good rate of photosynthetic ability across the study and did not become bleached. It is hard to say how long this would have lasted. A repeat of the study should have continued to take measurements until signs of death in the coral sand treatment. These results show that photosynthetic abilities were maintained, and enough light was scattered through the coral sand, reaching the coral nubbin. This means that fragments of coral that become buried *in situ*, where the substrate will be composed primarily of coral sand, can continue the photosynthetic process, at least in the short term.

From the light stress portion of this study alone, we can think about how these three species would cope with being moved to high and low light conditions and buried. Although

Platygyra sp. performed marginally worse at higher light intensities, all three species appear to be able to cope with changes in light levels and with being buried in coral sand in the short term, so this does not seem to be a limiting factor in their ability to form coralliths. What does seem to have a significant impact on their survival rate is being buried in finer sediments. Sedimentation (depositing fine sediments on the coral surface) is one of the most damaging human-induced stressors on coral reefs. It is increasing on reefs worldwide (Tuttle et al., 2020). An extensive review of the literature on the effects of sedimentation on corals by Tuttle and Donahue (2022) describes several impacts. Some of these, including decreased fertilisation, lower larval survival and mortality of coral recruits, will have little direct impact on corallith and or fragment survival (although impacts on recruit survival will impact initial corallith formation). Factors described in Tuttle and Donahue (2022) that are of importance for this study are reduced photosynthetic efficiency of adults, bleaching of adults, decreased growth rate of adults and death of adult colonies. All these factors are ultimately linked to increased light attenuation caused by the sediment's obstruction of the light from the coral. Their review also showed that high sedimentation would select for a community composed of branching colonies of coral, as they are better at shedding sediments from their tissue than non-branching or plating colonies. Our study showed that *S. pistillata* survived marginally longer than *Platygyra sp*. in the black sand, supporting Tuttle et al. ’s findings. However, overall, the results of the present study indicate that high sedimentation and/or burial in fine-grain sediments are as damaging to CFS as non-CFS.

2.5.2 Mechanical Stress Response

The initial rapid rate of recovery in *P. cylindrica* could have been due to the endolithic tissue within the upper layer of the *P. cylindrica* skeleton, which we visibly saw establishing on the surface by raising from the skeleton rather than growing linearly down the face of the skeleton (Figure 12). Once the coral was cut and a newly exposed surface received suitable levels of PAR for symbiont colonisation, we observed increasing colouration of this endolithic tissue over the first four days likely caused by an increase in the zooxanthellae present in this tissue. These newly established symbiont cells could then aid in regenerating upper tissue layers by providing required photosynthates. By Day 8, we could see new coral polyps forming along the cut face. This was in contrast to the recovery of tissue in *Platygyra sp*., which appeared to seal the edge of the wound and then slowly grow tissue down the newly cut face. The ability of endolithic tissue to quickly establish on the skeleton's surface after fragmentation would increase the survival rate of *P. cylindrica* post-fragmentation by sealing the wound quickly and reducing the risk of infection.

2.5.3 The role of endolithic tissue

Since many *Porites spp*. have large, massive and sub-massive morphologies, their fragments are likely to have a relatively large surface area of exposed skeleton compared to a thin broken branch of a branching species. By endolithic tissue rising to the surface and then 're-sheeting' this skeleton with new soft tissue, which I observed in this study, the coral fragment can re-establish a large surface area for photosynthesis with minimal energy being diverted to calcification. This is unlike other species of coral, such as those with branching morphologies, which need to invest in skeletal growth to maximise tissue surface area. I also propose that endolithic tissue could contribute to the 'phoenix effect'. Whilst Sheppard (2020) described how massive corals recovered from shaded wreaths of surviving polyps, I suggest that corals may also be able to recover from endolithic tissues recolonising the skeletal surface. Thus, partially killed *Porites spp*. colonies and their coralliths may have a higher survival rate and be more successful at re-establishing themselves than many other species.

2.5.4 Heterotrophy aids recovery

All species in this study can feed through heterotrophy (Veron, 2016), which will aid in their recovery via the supplementation of nutrients alongside photosynthetic activity of the zooxanthellae. *Platygyra sp*. recovered well from being cut, with all nubbins surviving and continuing to grow. *Platygyra sp.* has large polyps (~10 mm across) (Veron, 2016), which can consume larger, energy-packed foods through heterotrophy (Houlbreque 2009). *Porites spp*. have small polyps (<2 mm across) (Veron, 2016) and have been observed to have their tentacles extended for feeding throughout the day and night, which would also aid them in their more rapid initial recovery. *Stylophora pistillata* has been used in several studies (Houlbrèque and Ferrier-Pagès, 2009) looking at heterotrophy and has been shown to utilise pico- and nanoplankton food sources. It is unlikely that their death was related to them not feeding as well as the other two species in this study, as they were provided with the same supplemented food in the same tank as the other two species. Instead, I think that their rapid tissue loss and ultimate death were caused by a disease such as RTN due to the visible signs of tissue necrosis that I saw.

2.5.5 Disease susceptibility

Rapid tissue necrosis is a disease associated with the presence of the bacterium *Vibrio harveyi* and causes 'peeling' and loss of tissue, resulting in the death of the coral colony. In this study, all nubbins of *S. pistillata* died after being cut. The tissue of all individuals was seen to be peeling and dying at a rapid rate, and all nubbins were dead or had over 80% tissue loss by Day 3. The presence of any infectious diseases could have been felt more acutely in *S. pistillata* than in *Platygyra sp*. or *P. cylindrica,* as this species is known to be more susceptible (Luna et al., 2007). This will affect the ability of this species to recover from breakage in the wild. Corals from the family *Pocilloporidae* are up to 5 times more susceptible to diseases such as skeletal eroding band disease than *Poritids* (Page and Willis, 2008). Nakamura and van Woesik (2001) suggest that coral morphology plays a significant role in susceptibility to disease. They state that simpler forms, such as massive species, are better equipped to expel toxic metabolites formed by pathogens via waste transfer at the solid-water interface. Diaz & Madin (2011) suggest that polyp size may impact disease susceptibility. They found that corals with larger polyps are more disease-resistant. These factors combined could explain why the *S. pistillata* in my study might have been more susceptible to a pathogen present in this study than both the *P. cylindrica* and *Platygyra sp.*

2.5.6 Skeletal scars

It has been recognised in the literature for some time that *Porites* corals can form scars within their skeleton. X-radiographs and CT scans looking at coral skeletons sometimes show high-density stress bands, which are thought to indicate high or low temperatures causing partial mortality (Hendy 2003). The resulting patch of dead coral can be enclosed by adjacent living tissue growing back over the skeleton and leaves behind a scar. As this study is the first time that corals have been repeatedly CT scanned over a prolonged period, it is the first recorded incident where these scars have been formed by damage to the tissue and not temperature anomalies. When these scars are formed through fragmentation, abrasion or grazing, the resulting scars are expected to be relatively small compared to those caused by temperature anomalies. The results of this study should be considered when future studies look at the reconstruction of past climate conditions using coral skeletons, as any detected scars may not be from temperature anomalies unless they are significantly large.

2.5.7 Skeletal volume

Porites cylindrica grew rapidly after cutting, similar to what has been shown to occur through ‘microfragmentation’. This is an approach used by coral restoration projects whereby cutting the fragments of coral to be restored to a small size causes them to grow more rapidly and establish a more extensive coverage of the reef than if cut larger (Page et al., 2018). This ability to grow rapidly will aid *P. cylindrica* in producing coralliths. The quicker a newly formed fragment can grow large and increase the surface area that can photosynthesise, the better its chances of survival.

Although not significant an interesting result biologically was the initial decrease in skeletal volume after being cut in the first month. It is unclear from our information here why this might have occurred. However, I speculate that there may be some loss of mineral content at the cut face when exposed to the water, which could have caused an initial loss of volume until the surface was resealed by tissue. Corals alter the pH at the coral tissue skeleton interface to aid in calcification (McCulloch et al., 2012). Once this tissue is lost and the skeleton exposed, it may be susceptible to erosion by seawater. The loss was greater in *Platygyra sp.* which has a more porous, matrix-like skeleton than P. cylindrica, which has a tightly porous, dense skeleton. Water could have eroded the skeleton more quickly in this species by entering skeletal cavities more easily. More in-depth, controlled studies looking at the mineral content of the skeleton and water after cutting could indicate whether this is the case.

2.5.8 Conclusion

In this study, I have looked at two possible factors enabling the formation of coralliths: recovery from light stress and physical stress. It appears that none of the species were limited by burial in coral sand, at least in the short term. *Porites cylindrica* is the only CFS used in this study, and its responses during the RLC and the burial study were not too dissimilar to the responses of *S. pistillata.* Therefore, I believe that the more critical enabling factor concerning corallith formation is a species' response to physical stress, particularly its ability to recover quickly from wounds and skeletal damage. Although there are some species of coral, such as *Porites spp.,* which can both quickly recover from tissue damage and are more resistant to diseases, and therefore able to form coralliths in most environments, it does not mean that all coral species' cannot form coralliths given the right conditions. For example, species such as *S. pistillata* might also be able to exist in a mobile unattached form if movement is low enough to avoid constant abrasive damage but enough to keep it from reattaching to the reef and if disease prevalence is low. Admittedly, these conditions are rare and likely to become rarer with the onset of climate change, increasing disease prevalence and wave energy through events such as storms (Lynn and Peeva, 2021). Although there are some unexpected *Acropora spp.* already documented as forming coralliths (Roff, 2008)

Chapter 3. Corallith community structure and ecological role in Utila, Honduras, and the wider Caribbean.

In the previous chapter, I tested whether CFS can withstand being buried in the sand compared to non-CFS and what their skeletal growth responses to being broken were. I found that CFS could better withstand these stressors ex-situ than non-CFS. In this chapter, I set out to see whether some of the findings from both my lab studies and previous work in the Indian Ocean by Hennige et al. (2017) translate ecologically to coralliths on Caribbean coral reefs.

3.1 Introduction

Previous studies of coralliths in the field show that they perform ecosystem functions such as stabilising and forming reef bommies, as described in Chapter 1 (Hennige et al., 2017). This study was conducted on Vavvaru Island, The Maldives, a research island with limited human activity. There are no fishing pressures in Vavvaru and minimal human-generated nutrient input from the island (per comms. S. J. Hennige). The reef at Vavvaru Island can be considered to be near-pristine. This starkly contrasts the reefs of the Caribbean, which have undergone many human-induced changes over the last century (Precht et al., 2019). Understanding if the ecological role of coralliths observed in Vavvaru is an anomaly or whether they perform similar or different roles in other regions will highlight if they should be considered in future coral reef management.

3.1.1 Species diversity in the Caribbean

The Caribbean has a much lower overall coral species richness, with a reported 51 species, compared to the Indo-Pacific, which has almost 700 (Roff, 2020). This is partly due to the sea level histories of the two regions (Gischler, 2015). Space is a limiting factor in coral growth and subsequent speciation. The Indo-Pacific has a longer history of stable sea levels 1-2 m above modern sea level (Gischler, 2015, Lutzenkirchen et al., 2023). This means that

Indo-Pacific reefs have historically had more vertical space to grow. The Indo-Pacific is also a vast, highly connected region, allowing extensive gene flow. In contrast, the Caribbean is a semi-enclosed sea with limited connectivity with other oceans. This limits gene flow into and within the Caribbean (Foster et al., 2012), reducing speciation opportunities. Finally, the Caribbean is a region impacted frequently by climatic disturbances, such as hurricanes, limiting species diversity to those that can withstand these disturbances, as described in the intermediate disturbance hypothesis (Connell, 1978). The Caribbean region has, therefore, favoured large, slower-growing species, such as *Acropora cervicornis*, which rely more heavily on asexual reproduction rather than sexual (Lugo et al., 2000). A reduction of sexual reproduction limits the amount of gene transfer and, therefore, reduces speciation.

3.1.2 Coral diseases in the Caribbean

Recent disease outbreaks have decimated coral populations in the Caribbean. Most notably, white band disease in the 1970s dramatically reduced the *Acropora spp.* populations (Aronson and Precht, 2001), and most recently, stony coral tissue loss disease (SCTLD) is causing the decline of massive coral species (Alvarez-Filip et al., 2022). Stony coral tissue loss disease was first reported in 2014 and has spread across the Caribbean in the last nine years (Alvarez-Filip et al., 2022). Of the 51 species of coral present in this region, 22 are susceptible to SCTLD and are primarily members of the *Meandrinadae* family and *Faviinae* subfamily (Williamson et al., 2022). These large stony corals currently represent a large proportion of the scleractinian corals present in the Caribbean. Whilst it has been suggested that their loss could allow for the regeneration of the previously dominant *Acropora cervicornis* and *A. palmata* (Alvarez-Filip et al., 2022), it could also lead to the further expansion of macroalgae as more surface becomes available. The spread of this disease is thought to be exacerbated by human activity, with ballast water from boats acting as a vector for the pathogen (Rosenau et al., 2021)

3.1.3 Overfishing in the region

Overfishing of herbivorous fish and the loss of other grazers (Williams and Polunin, 2001) led to a rise in the sponge population (Loh et al., 2015) and macroalgae cover by the 1970s (Bruno et al., 2009). These keystone species were initially temporarily replaced by echinoid herbivores (Bodmer et al., 2021). Urchins, although voracious eaters of algae are more destructive feeders than herbivores fish. Whilst herbivorous fish, such as the parrotfish, *Scarus vetula*, act as grazers and only scrape away algae on the surface of reef structures, urchins, such as *Diadema antillarum*, remove considerable amounts of calcium carbonate from both the consolidated reef structure and from the dead coral skeleton as they feed on algae on the surface (Bodmer et al., 2021). This means they are considered 'erosive agents' on Caribbean reefs. However, their function as the main herbivores on these reefs was short-lived, as a disease wiped out over 80% of the urchin population across the region in the mid-1980s (Bodmer et al., 2021). The subsequent rise in macroalgae meant that new coral recruitment was limited due to the competition from fast-growing algae.

3.1.4 Pollution and algal growth

Pollution is a significant stressor in the Caribbean (DeGeorges et al., 2010). Runoff from agricultural land, coastal development and other human-related sources has negatively affected the coral community of the Caribbean (DeGeorges et al., 2010). Nutrient availability, water and light are limiting factors to photosynthesis. In tropical shallow reefs, water and sunlight are abundant, so the only factor limiting algal growth is nutrient load. Nutrient input can cause phytoplankton blooms (Siung-Chang, 1997), which prevents light penetration and reduces photosynthesis in shallow-dwelling corals. Excessive nutrient load also increases the growth rate of macroalgae attached to the reef framework. This rapid growth can smother coral recruits. Herbivorous fish, whilst important grazers, are selective in their feeding, preferring early successional turf algae (Burkepile et al., 2022). This means that even in areas with a healthy population of herbivores, a high nutrient load has led to a rise in algal cover in the Caribbean.

3.1.5 The Caribbean 'phase shift'

The coral reefs of the Caribbean have been described as having undergone a 'phase shift' (Mumby, 2021). This is where human-induced contributing factors, such as disease outbreaks, overfishing, pollution and climate change, have led to a rapid overall shift in the community structure and composition from a coral-dominated state to an algal-dominated state (Dudgeon et al., 2010). Over time, the death and breakdown of corals and the replacement with soft macroalgae have led to a reef with reduced 3D structure. Many species of fish and invertebrates rely on the 3D structure provided by scleractinian coral, so their loss has led to an overall reduction in biodiversity (Darling et al., 2017). One sub-region which has undergone a phase shift is the Mesoamerican Barrier Reef (MBR).

3.2 Aims and Objectives

In this chapter, I aimed to assess the abundance and species richness of the corallith community on the reefs of Utila and to look for evidence of the FLSH and/or other ecological processes that coralliths are performing in this region. I did this by:

1) Carrying out surveys of unattached corals and their size at four sites at varying distances from the shore off the island of Utila to
    a) Look for evidence of the FLSH occurring here.
    b) Document the corallith community species composition in the region.
    c) Look for the overall prevalence of coralliths in differing reef habitats.

2) Using the information gleaned from these surveys, coupled with data sets provided by Operation Wallacea and the Atlantic and Gulf Rapid Reef Assessment (AGRRA), and a meta-analysis of the literature, I looked at the responses over time of CFS at Utila, Tela Bay and the wider Caribbean region to assess:
    a) Whether CFS abundance has been stable, increasing or decreasing in recent decades.
    b) Whether changes in the corallith community coincide with local or regional disturbances.

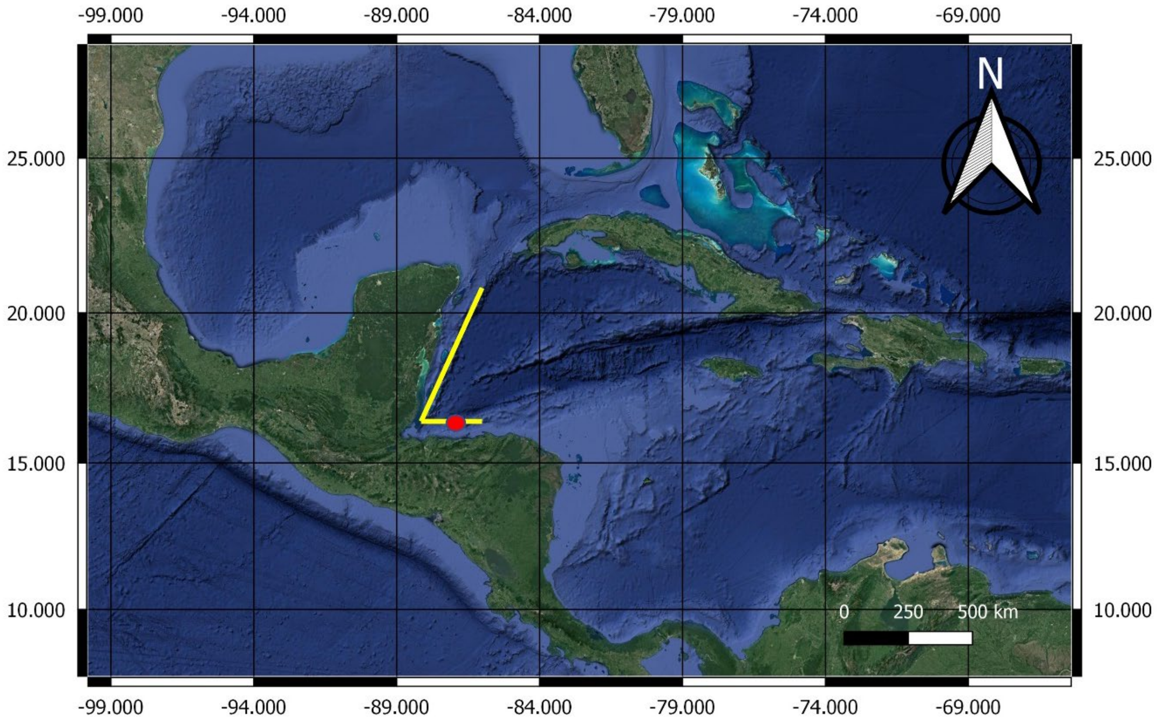
3.3 Methods

The following methods pertain to data collected during this study.

3.3.1 Study site

Utila, Honduras, is one of the three Bay Islands located on the southern boundary of the MBR and is part of the Bay Island National Marine Park. Utila is situated in the Caribbean Sea, approximately 36 km from the mainland of Honduras (Figure 1). The island is about 13 km long, 4.5 km at its widest point and has a population of around 4,000 people, most of whom live on the southwards-facing coastline. The island is a popular location for recreational diving and fishing; commercial fishing also occurs around the island. This coastline was chosen for this study during the field season of June 15th until August 6th, 2019. The reef along this coastline forms a spur-and-groove reef formation, which slopes down to a sandy bottom with patch reef formations. These patch reefs are found up to ~45 m deep. However, all sites used in this study were shallow reef sites with a maximum depth of 8 m. Four sites were used in total (Figure 2). Preliminary dives were conducted to identify four sites suitable for the present study. Sites were chosen that had large reef flat areas, working under the assumption that locations with steep drops would not hold coralliths as they would roll downhill to deeper inaccessible points

A



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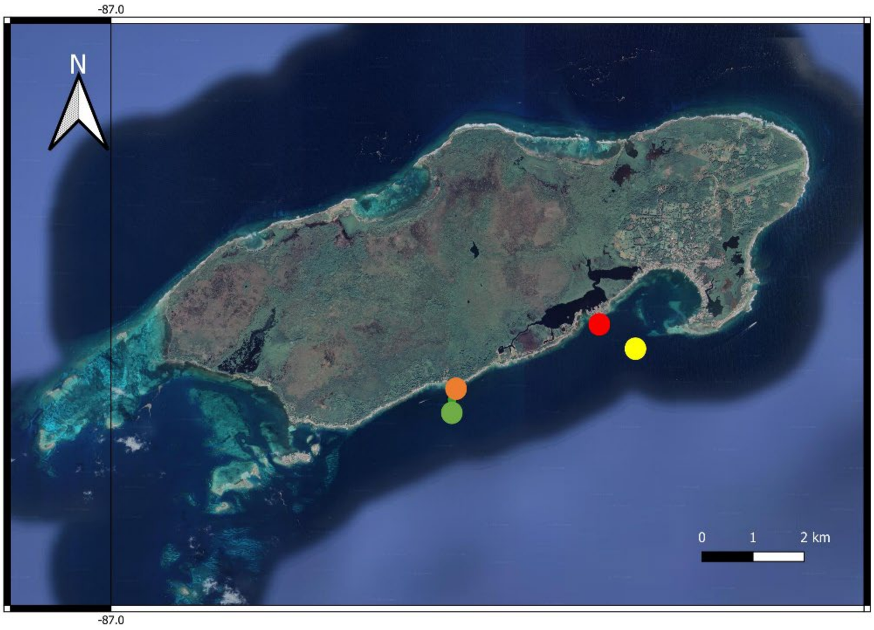
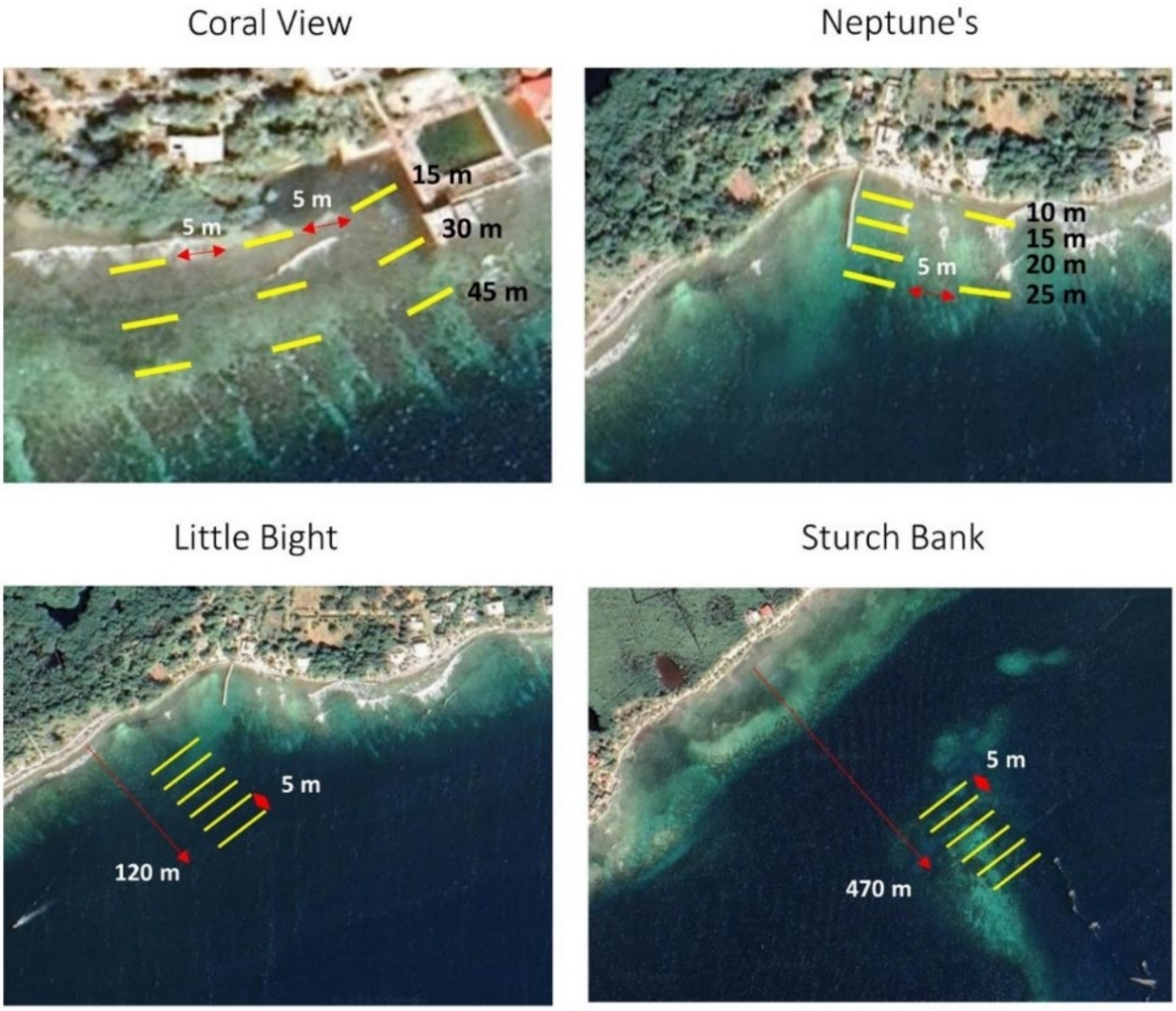


Figure 1. Satellite image from Google Earth of the western Caribbean Sea, showing A) The extent of the MBR demonstrated by the yellow line. The red circle denotes the location of the island of Utila, the smallest of the three Bay Islands, and B) a closer view of Utila and the location of the four sampling sites – red circle = Coral View, yellow circle = Sturch Bank, orange circle = Neptune's Beach and green circle = Little Bight.

Two snorkel sites, Neptune's Beach, 16°04'49.1"N 86°55'44.7"W, and Coral View, 16°05'20.6"N 86°54'40.4"W, representing near-shore (<45 m from the shore) were used. Two dive sites representing far-shore sites were used. They were Little Bight, 16°04'45.4"N 86°55'45.9"W, which is located approximately 120 m from the shore and Sturch Bank, 16°05'22.6"N 86°54'12.6"W, which is located about 470 m from the shore.

3.3.2 Field surveys

The data were collected during a single field season in the summer of 2019 between 29/06/19 and 14/07/19 by the same two divers using SCUBA. For all sites 50 m transects were laid out following the natural bathymetry of the site, but where the depth did not vary by more than 2 m up or downwards from the starting point. Due to ease of access, nine transects were sampled at Coral View. Three were at 15 m from the shoreline, three were at 30 m, and a final three were at 45 m from the shore, all at least 5 m apart horizontally. At Neptune's Beach, only six were to be conducted due to restricted access further along the shoreline and due to more uneven bathymetry. Two were sampled at 10 m, one at 15 m, one at 20 m and two from 25 m from the shore. For Little Bight and Sturch Bank, a total of 6 transects were surveyed. On the first dive, data collectors swam from the boat parallel to the shore until a location that was relatively flat in bathymetry and around 3-5 m in depth from the surface was found. A transect was then laid out in a direction that was deemed to be generally parallel to the shore. On subsequent dives, transects were laid out at least 5 m further than the previous transect and at a suitable location.



Coral View

Neptune's

Little Bight

Sturch Bank

Figure 2. Satellite images were obtained from Google Earth of all four data collection sites with yellow lines to show each location's schematic layout of transects. Data at Coral View and Neptune's Beach were collected via snorkelling, whilst data for Sturch Bank and Little Bight were collected via SCUBA.

An average depth for the whole transect was calculated by taking depth measurements from the same dive computer at 5 m intervals, and a mean was calculated for each transect. For each diver, 1 m was measured starting at the fingertips to the opposite shoulder. They then swam along the transect, keeping this point on the shoulder in line with the transect and the opposite arm outstretched. Any unattached corals that fell under this area were recorded. Videos of each transect were taken using an Apeman 4k 20mp camera so they could be referred back to later. The data from the near-shore transects were collected using a snorkel, whilst the far-shore sites were sampled using SCUBA. Temperatures were taken in the water using the same dive computer for each transect on the day of data collection.

Corals were classed as unattached if they were easily moved by hand. To do this, the data collectors tried to move the corals gently but with not so much force as to damage them, and for the largest ones, they were assessed whether they were encrusted back on the reef at their base. For each unattached coral, it was established whether it was a corallith or a fragment. This was judged based on whether there was a clear breakage point. If so, it was assumed that this was a newly broken coral and therefore, a fragment. If the coral was growing on a mobile piece of substrate, was a complete ball of coral, or if the breakage point had been fouled with algae or otherwise appeared aged (indicating it had been unattached for some time since fragmenting off), it was classed as a corallith. The species for most corals were identified in the field, but any unidentifiable were photographed from several angles and identified back on land. For every coral, the maximum length of living tissue was measured. If the coral was a corallith and attached to a piece of mobile substrate, the maximum length of the substrate and the width at the midpoint of this length were also measured (Figure 3). The percentage coverage of the living tissue on the mobile substrate was visually estimated.

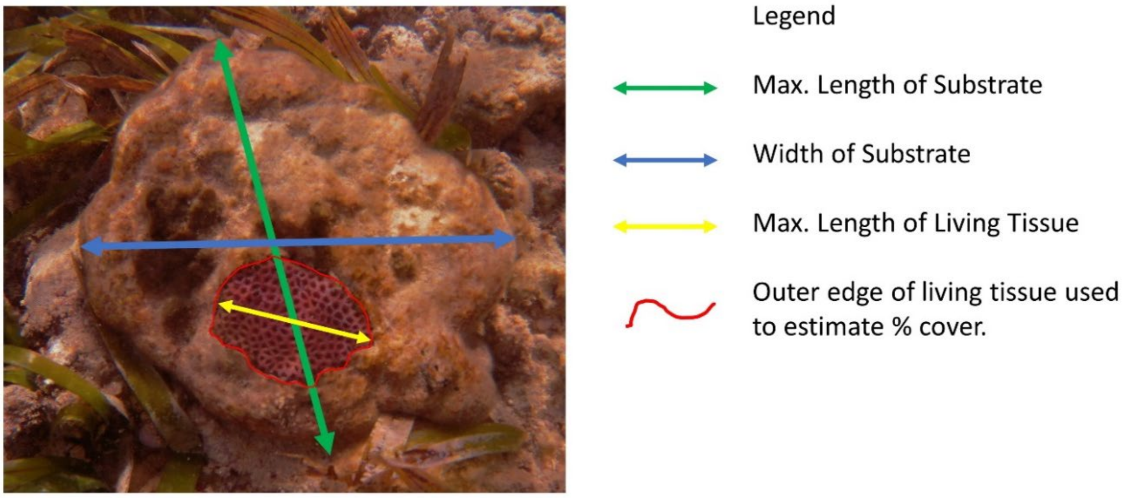


Figure 3. The schematic shows how the measurements were taken for each corallith. In this example, the percentage cover of tissue was estimated to be approx. 15%. This would therefore classify the corallith as ‘encrusting’.

Finally, the morphology of the coral was assessed. Corals with a complex 3D structure were either ‘branching’ or ‘plating’ depending on how branchlike, flattened, or plate-like they were (Figure 4). Corals with an encrusting morphology were classed as either ‘encrusting’, ‘enveloping’ or ‘sub-spheroidal’. These reflected the varying stages of corallith development, from recruit on a mobile piece of substrate to covering the entire surface. ‘Encrusting’ indicates the living tissue was covering less than 50% of the substrate to which it was attached. An ‘enveloping’ morphology was when the coral was encrusting on a substrate beyond a 2-dimensional plane and covered between 50 and 85% of the substrate. When the tissue covered 85-100% of the substrate, these were classed as ‘sub-spheroidal’. The depth at which each coral was found was measured and noted using the data collector's dive computer. For corals identified as fragments, all the same data was collected, aside from the length of the substrate as fragments by their definition were not attached to substrate.

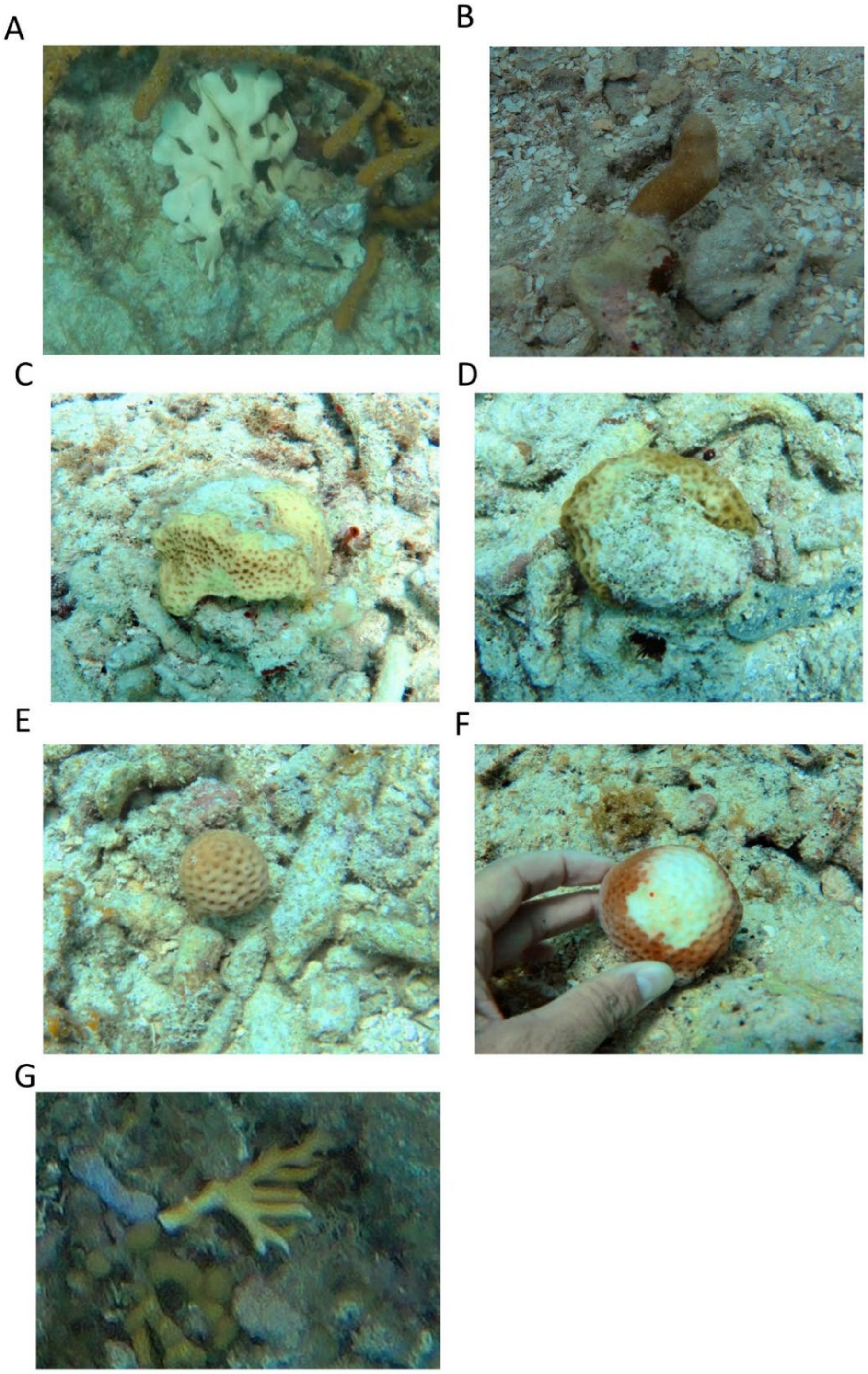


Figure 4. Images of corals documented in the field show the seven morphologies of coralliths and fragments. A) a plating *(Millepora sp.* hydrocoral and not scleractinian coral) fragment, B) a branching corallith, *Porites porites,* C) an 'encrusting', *A. humilis* corallith, with tissue that covered less than 50% of the substrate surface, D) an 'enveloping' *A. humilis* corallith with tissue covering between 50 % and 80 % of the substrate surface. The underside of this corallith was covered in living tissue. E) a spheroidal *S. siderea* corallith, with tissue covering the entire surface of the substrate. F) the underside of a spheroidal corallith showing the bleaching of tissue due to being sat on the sea bed, and G) a branching fragment of *A. cervicornis* with an apparent straight, neat white breakpoint showing that it was recently fragmented and not free-living for an extended period.

A detailed benthic survey data set provided by Operation Wallacea was used to assess the coral species present and substrate type at a 5 m depth contour at both Little Bight and Sturch Bank. The results were used to determine whether all species present were forming coralliths or just a subset of them. The Operation Wallacea data were collected along 50 m transects at 5 m depth, following the natural bathymetry of the site. Videos were taken of the transects using GoPro Hero 5's, and the footage analysed back on land using point intercept technique. Every 25 cm, the video was paused, and the benthic components underneath the transect line were categorised. Where the benthic component was a living organism, it was identified to the highest taxonomic level possible, including species levels for corals. From the data in this current study, coralliths found at Little Bight and Sturch Bank at depths > 3 m were selected, and the species composition was compared to the Operation Wallacea coral coverage data.

3.3.3 Historical coral cover

A thorough literature search was conducted using Web of Knowledge and Google Scholar to obtain literature using the search term 'coral cover AND Caribbean' between 01/01/1900 and 01/01/1980. The papers were reviewed, and the main species or genera of scleractinian observed in the study, the depth at which they were found, and the year and the location were captured in a table.

The following methods pertain to pre-existing data.

3.3.4 Coralliths in the wider Caribbean

Data obtained from Operation Wallacea were plotted to examine the proportional abundance of scleractinian coral species between 0 and 8 m depth for both Utila and Tela between 2012 and 2019. Tela Bay, like Utila, is a popular diving location in Honduras. The Banco Capiro Reef, which is located 8 km offshore in the mainland bay of Tela (Bodmer et al., 2015), has unusually high scleractinian coral cover for the Caribbean, with up to 62% cover and only 7% algal cover (Bodmer et al., 2017), making it one of the healthiest reefs in the Caribbean. Coralliths species identified from the field surveys in Utila were highlighted in the plots.

Using the coral cover down to species level and scaled dataset available from the summary products of the Atlantic and Gulf Rapid Reef Assessment database (AGRRA), the proportional abundance of scleractinian species was plotted between 2007 and 2014. In the field surveys, coralliths were only identified from 0 to 8 m depth ranges, so only transects between 0 and 8 m depth were chosen from the AGRRA database. Transects were divided into ecoregions, and only regions with at least four years of data were included in the plot.

3.3.5 Statistics

To test if the FLSH is occurring in Utila, several predictors of size were tested in a statistical model. The experimental design was hierarchical, with transects within sites. Linear mixed-effects models were used to test the effect of species, morphology, substrate length, distance from the shore and temperature, set as fixed effects, on the maximum tissue length. Because the three morphologies encrusting, enveloping and sub-spheroidal reflect the developmental stage of corallith formation and are therefore strongly correlated with tissue length, they were grouped under ‘encrusting’ for the linear mixed-effect model. Depth and substrate width were excluded from the analysis as they were strongly correlated with distance from shore and substrate length, respectively. Site and transect were both set as random effects. The data was not normally distributed, so the maximum tissue length (cm) was log-transformed. All continuous predictor variables were scaled and centred for ease of interpretation of the results.

All statistical analysis was performed in R (R, Core Team 2019) using the ‘lme4’ (Bates D, 2015), ‘dplyr’ (Wickham, 2019b) and ‘tidyr’ (Wickham, 2019a) packages. P values were obtained for the linear mixed effect model using the ‘VCVglmm’ package (Brown, 2019). Data was explored and plotted using the R package ggplot2 (Wickham, 2016).

3.4 Results

3.4.1 The coral community of Utila

Using the data provided by Operation Wallacea, in the field season of 2019, there is a broad range of 25 hermatypic coral species present across both Little Bight and Sturch Bank at 5 m depth (Figure 4). Unfortunately, benthic coverage data is unavailable for Neptune’s Beach and Coral View. The overall coverage of hermatypic corals at Little Bight was more than double that at Sturch Bank, with 312 observations at Little Bight versus 131. When the coral cover is compared with the coralliths present in these two sites (Figure 5) it is clear that only a handful of species present are forming coralliths. Although the hermatypic coral coverage is higher at Little Bight, the number of coralliths is vastly higher at Sturch Bank. The most abundant species of hard coral at Little Bight was *Orbicella annularis,* whilst the most abundant corallith species was *Porites porites* and at Sturch Bank, *A. cervicornis* had the highest coral coverage, but the most frequent corallith species was *Sidereastrea siderea.*

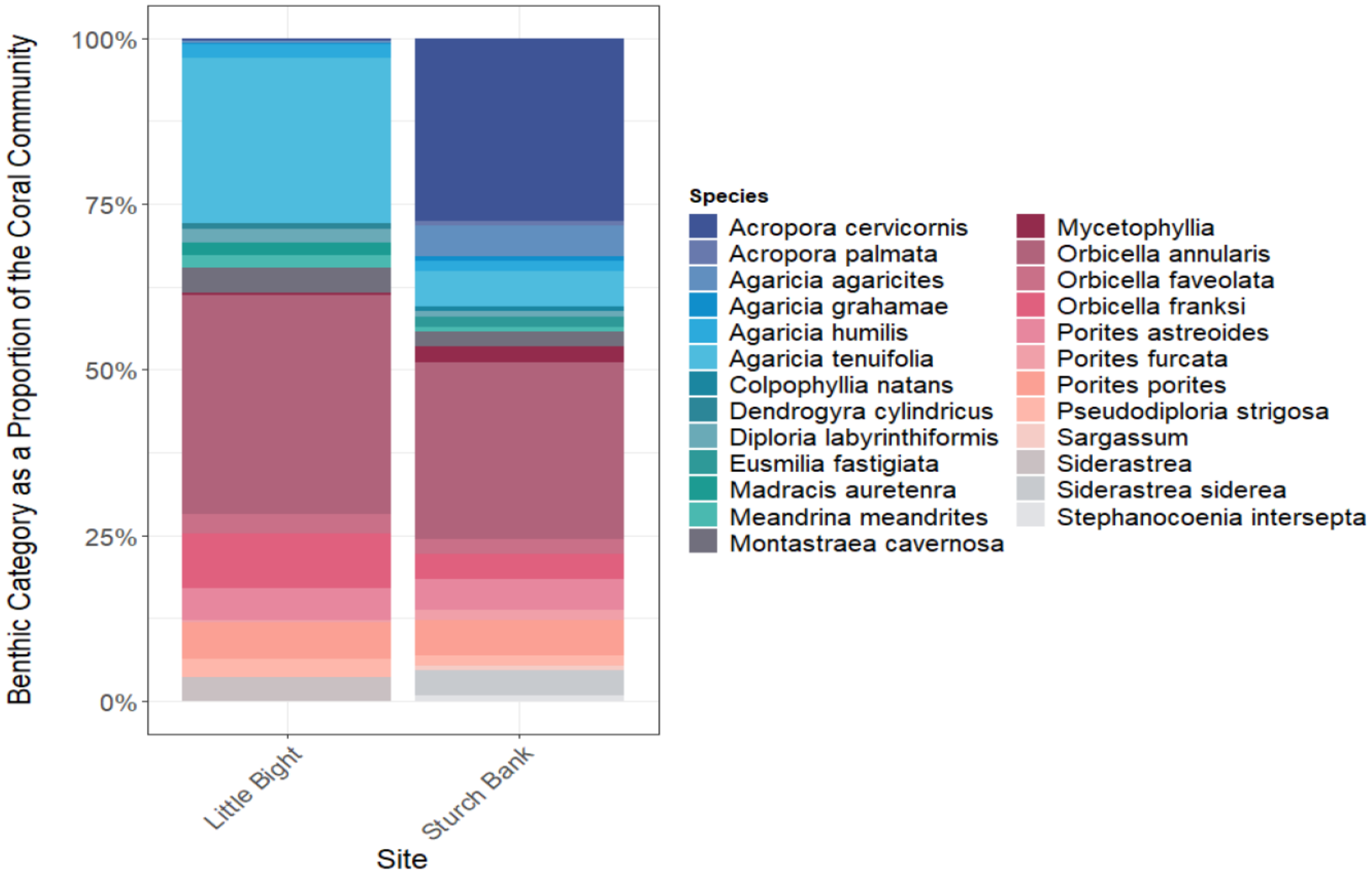


Figure 5. Proportion of coral species at Little Bight and Sturch Bank. Abundance of live coral was more than double at Little Bight ($n = 312$) compared to Sturch Bank ($n = 131$), although proportional representation at both sites was similar, with the key difference being the presence of *A. cervicornis* at Sturch Bank being much higher than at Little Bight and *Agaricia tenuifolia* being much more abundant at Little Bight than at Sturch Bank.

3.4.2 Corallith diversity and abundance

Coralliths were found at all four sites, *n* = 562 (Figure 6), with maximum living tissue lengths ranging from 0.5 cm up to 65 cm. All measurements were rounded to the nearest whole cm for the statistical analysis. The mean± standard deviation tissue length was 6.37± 7.80. Coralliths were found in very shallow waters at Coral View on transects that had an average depth of only 23 cm. Coral View had the highest abundance of coralliths overall, with *n* = 301 individuals documented at this site, whilst Little Bight had the fewest with only *n = 21* (Figure 6). In total, 11 species were found to be forming coralliths at identified sites (Figure 6). In descending order, the three most abundant corallith species were *Sidereastrea radians, Porites divaricata* and *S. siderea.* Four corallith species identified were *Colpophylia natans* coralliths (*n* = 10, 8, 6 and 3, respectively). *Colpophylia natans, O. annularis* and *D. strigosa* are massive coral species and formed some of the largest coralliths found, with maximum tissue lengths ranging from 2 to 65 cm, with half being over 30 cm. More than half of these large coralliths were found at Neptune's Beach. *Colpophylia natans* had the largest range in tissue length, ranging from 6 to 65 cm.

To summarise the diversity and evenness of the corallith communities at all four sites, Shannon-Weiner, Pielou's evenness and Simpson's diversity indices were calculated. All four sites had generally low CFS diversity, indicated by the low *H* values, and were fairly evenly spread, indicated by the high *J* and *D* values. Coral View had the lowest diversity and lowest evenness and Little Bight had the highest evenness and also having the highest diversity (Table 1).

Table 1. Shannon-Weiner, Pielou's and Simpson's biodiversity indices were calculated for the CFS communities at all four sites.

Site	*Shannon-Weiner*		*Pielou's*	*Simpson's*
	H	*H*Max	Equitability (*J*)	*D*
Neptune's	1.44	1.79	0.8	0.76
Coral View	1.14	1.95	0.59	0.62
Little Bight	1.63	1.79	0.91	0.82
Sturch Bank	1.48	2.08	0.67	0.67

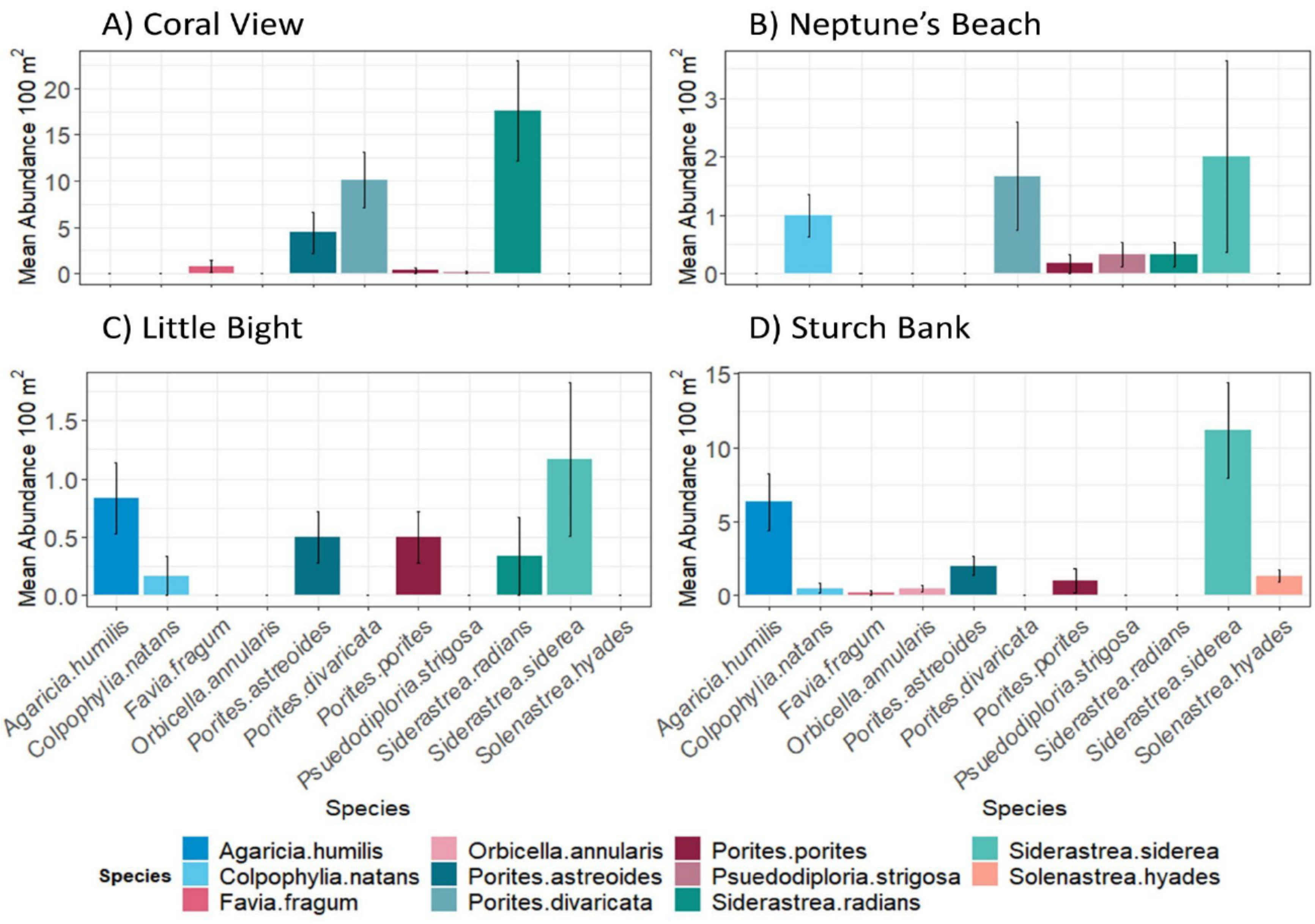


Figure 6. Mean corallith abundance per 100 m^2. Coral View had the highest abundance of coralliths (n = 301), whilst Little Bight had the fewest. Sturch Bank had the second highest abundance and also had the highest species richness (n = 8).

3.4.3 Substrate provision

Substrate provision at Little Bight and Sturch Bank differed (Figures 7 and 8). Little Bight had a more varied substrate type present, and almost a third of the substrate was sand. At Sturch Bank, there was less open space than at Little Bight, but of the present substrate, nearly two-thirds was rubble, and the rest was either exposed rock or rock with crustose coralline algae growing over it (Figure 7). Operation Wallacea collected this data, which was unavailable for Coral View or Neptune's Beach. Figure 8 shows images taken from the four sites offering a typical view of the substrate. In these images, we can see that the substrate at Neptune's Beach was much more solid hard bedrock with macroalgae, whilst Coral View had a lot of rubble and seagrass.

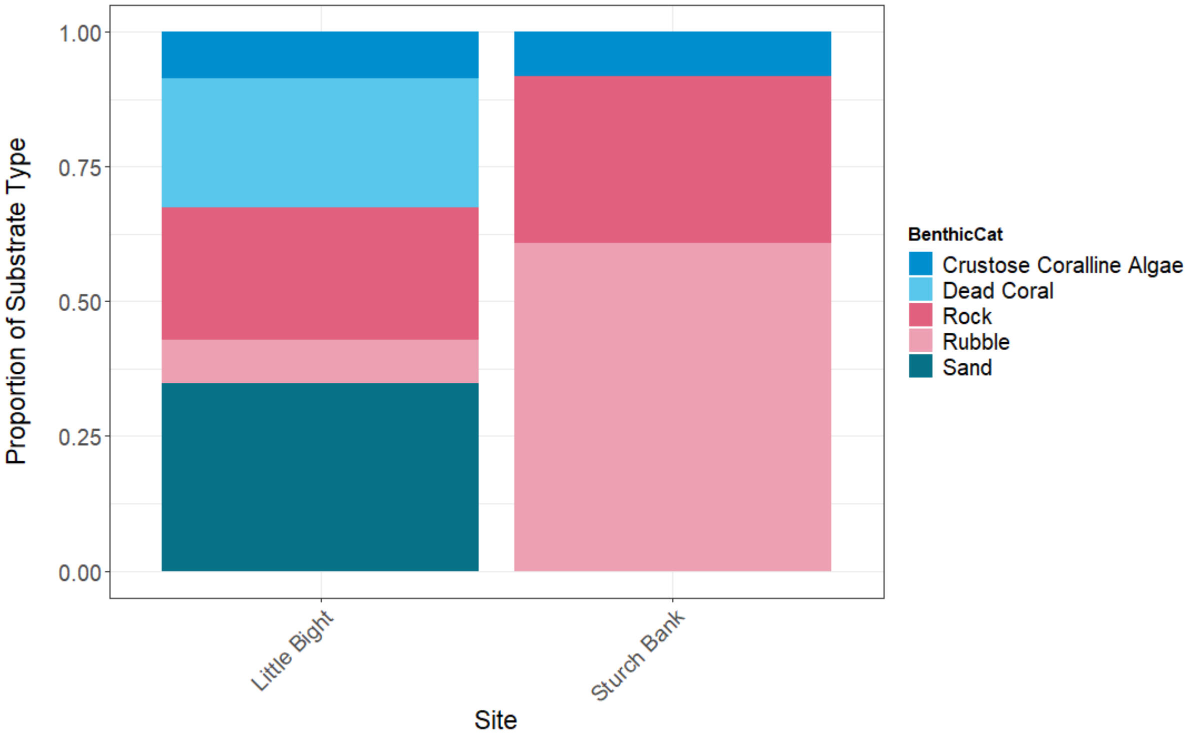


Figure 7. Abiotic benthic categories (substrate type) at Little Bight and Sturch Bank. Bars represent the proportion of each substrate type present. The abundance of rubble is much higher at Sturch Bank than at Little Bight.

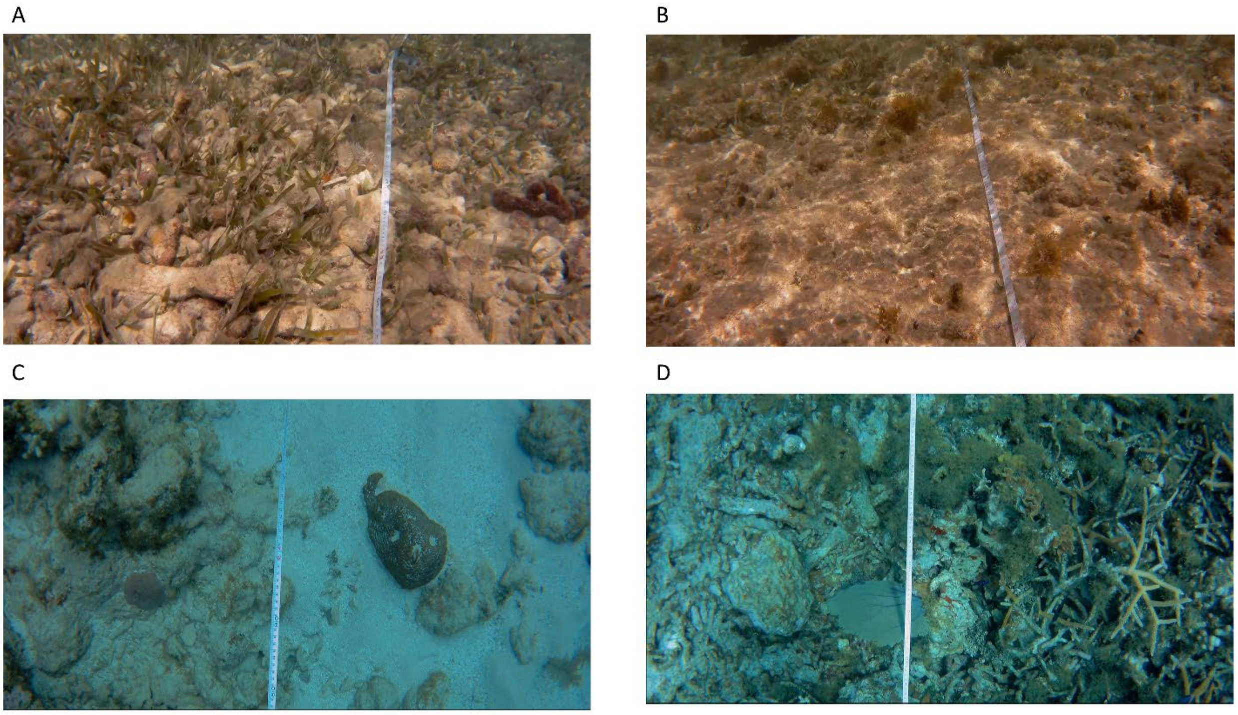


Figure 8. Shots were taken along a transect from each of the four sites in Utila. A) Coral View shows that this area typically had a high cover of rubble and seagrass, whilst my second near-shore site, B) Neptune's Beach, had a much rockier seabed with clumps of macroalgae. Of my two sites further from the shore, C) Little Bight had a much higher prevalence of sandy patches with rockier patches and D) Sturch Bank had a high density of rubble and broken fragments of coral interspersed with macroalgae.

3.4.4 Testing for the free-living stabilisation hypothesis

The linear mixed-effect model showed the distance from shore, and the water temperature did not affect the tissue length with $p > 0.05$. The smallest coralliths found had the longest length of living tissue of 1 cm, whilst the largest had a longest living tissue length of 65 cm. There were several species (*S. radians, P. divaricata, P. porites, P. astreoides, S. siderea* and *F. fragum*) that were these smallest of sizes. Whilst the two largest coralliths found were *S. siderea* and *C. natans*, both had the longest living tissue length of 65 cm. *Porites divaricata* was arbitrarily set as the baseline for the species predictor variable. *Siderastrea radians, F. fragum* and *P. porites* were not significantly different in size compared to *P. divaricata,* whilst all other species were markedly larger, with *C. natans* having the largest effect on size (see Table 2). For morphology, 'branching' was set as the baseline, and encrusting had a strong negative effect on size compared to branching (t = - 3.87 and p = <0.0001). Substrate length had a strong positive effect on maximum tissue length (t =6.70 and p = <0.0001). Temperature did not affect maximum tissue length.

Table 2. Results of the linear mixed effects model. Significance level was set at 0.05.

Fixed Effects	Estimates	Standard Error	*t* Statistic (*p* value)
Intercept	1.66	0.20	8.34 (<0.0001)
Species *S. radians*	0.13	0.10	1.28 (0.1)
C. natans	1.46	0.24	6.12 (<0.0001) *
D. strigosa	0.79	0.36	2.23 (0.01) *
F. fragum	0.15	0.23	0.64 (0.2) *
P. astreoides	0.45	0.13	3.58 (0.0002) *
P. porites	0.16	0.19	0.83 (0.2)
S. siderea	0.68	0.16	4.23 (<0.0001) *
A. agaricites	0.54	0.17	3.14 (0.0009) *
O. annularis	1.03	0.37	2.79 (0.0027) *
S. hyades	0.39	0.25	1.56 (0.06) *
Distance	0.03	0.19	0.14 (0.4)
Substrate Length	0.26	0.03	6.70 (<0.0001) *
Morphology Encrusting	-0.42	0.11	-3.87 (<0.0001) *
Temperature	0.02	0.04	0.50 (0.3)

3.4.5 Evidence for expansion after disturbance

Using data provided by Operation Wallacea, between 2013 and 2019, the corallith abundance in Tela increased, particularly between 2013 and 2014, from 14% to 36%. Whilst in Utila, the corallith abundance stayed relatively steady between 2012 and 2019 (Figure 10).

3.4.6 Corallith abundance in the Caribbean

Using data obtained through AGRRA, CFS now account for more than 50% of the hard coral community across three regions of the Caribbean between 2007 and 2014 (Figure 11).

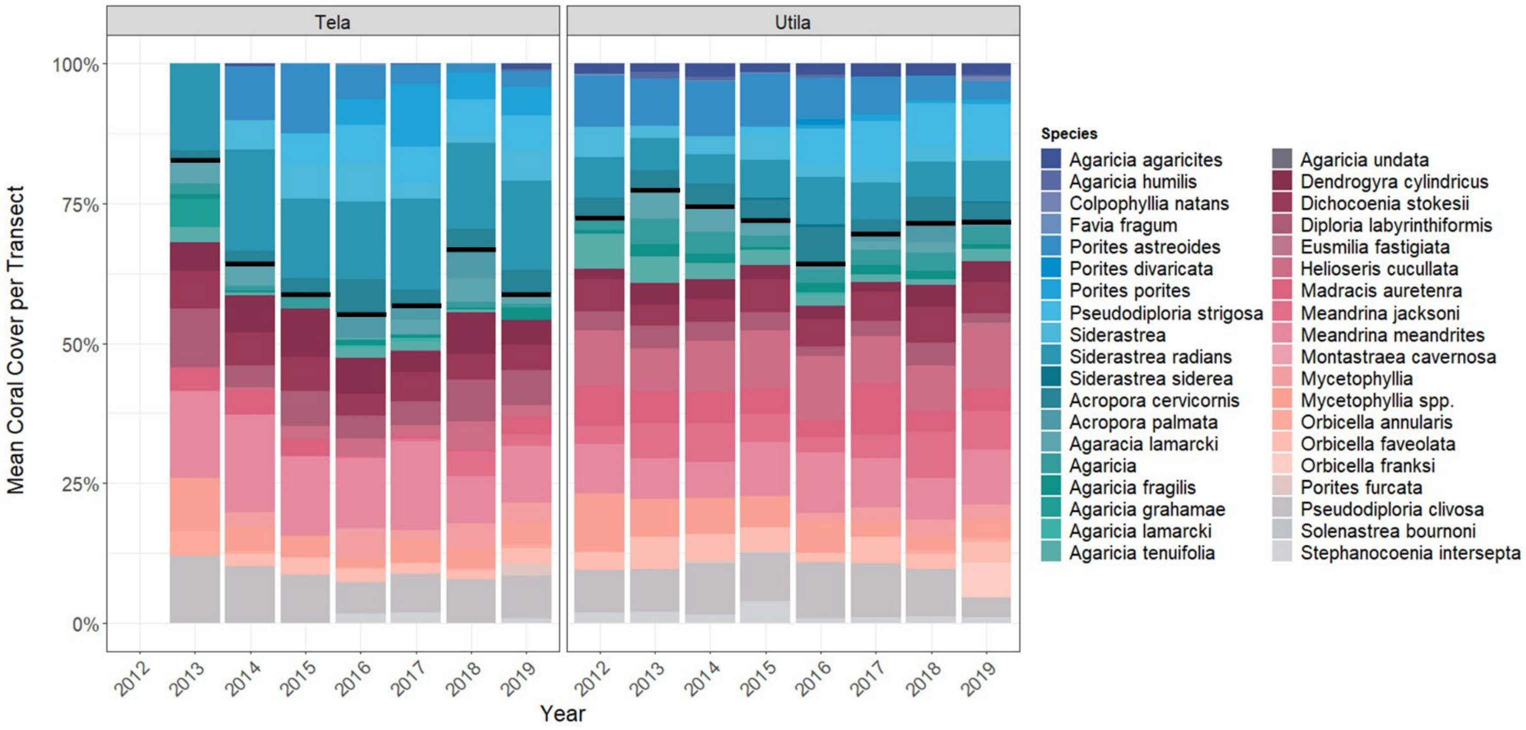


Figure 10. Hard coral community composition for Tela and Utila, Honduras, between 2012 and 2019. All species above the black line are corallith forming species, whilst all those below have not been documented to form coralliths to date.

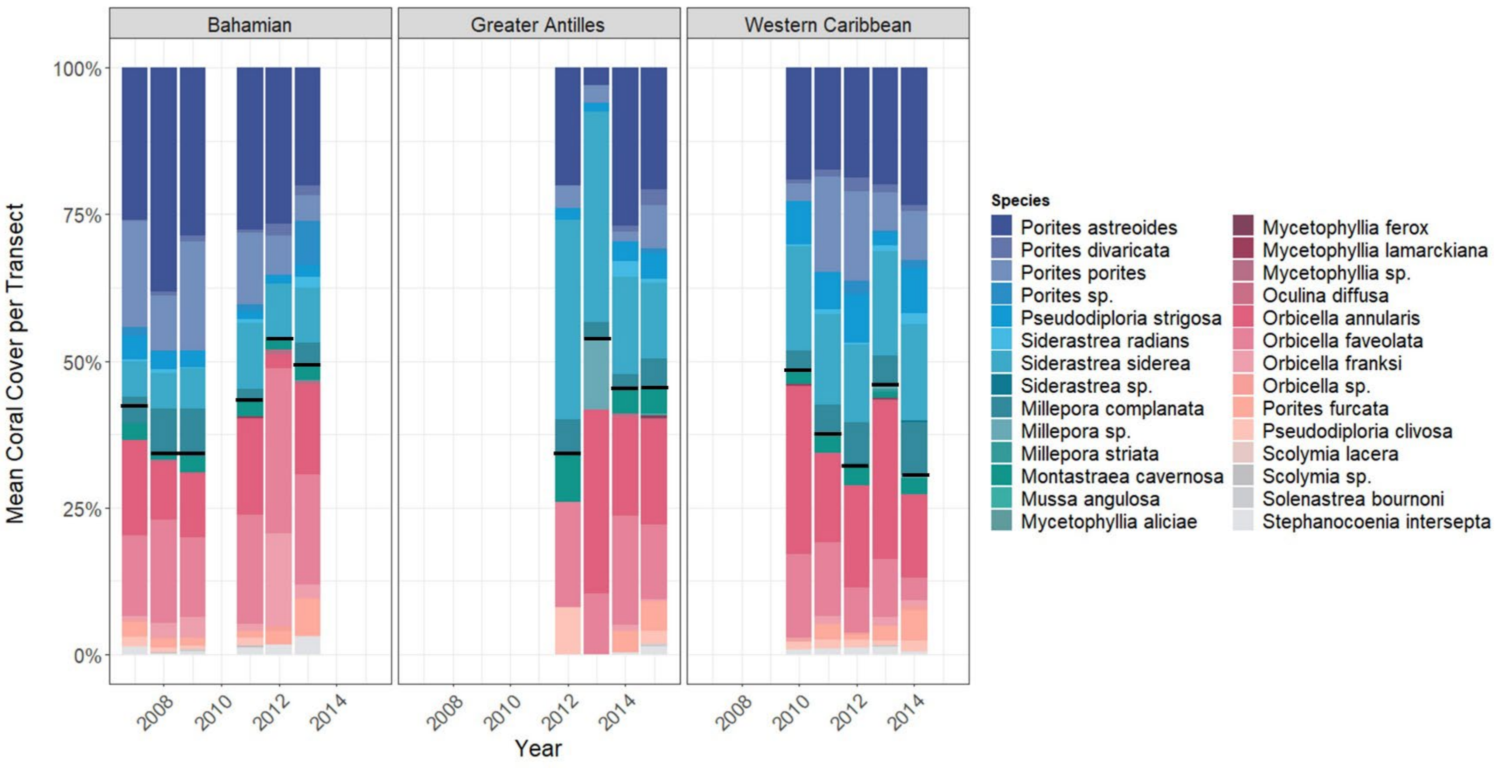


Figure 11. Hard coral community composition for Bahamian, Greater Antilles and Western Caribbean regions. All species above the black line are corallith forming, whilst those below the line have not been documented to form coralliths to date.

3.4.7 Historical coral cover

The earliest paper gleaned from the literature search was from 1959. Between 1959 and 1980, the literature shows that large, branching species, such as *Acropora palmata*, *P. porites*, and *A. cervicornis*, and large boulder species, such as *O. annularis*, dominated the coral reefs surveyed across the Caribbean (Table 3).

Table 3. Literature sourced describing Caribbean scleractinian cover, pre-1980. Asterisks denote where coralliths (or unattached living colonies) were identified.

YEAR PUBLISHED	AUTHOR	LOCATION	DEPTH	DOMINANT SCLERACTINIA
1959	Goreau (1959)	Jamaica	Shore Zone	*A. palmata, O. annularis, M. cavernosa*
			Lagoon	*O. annularis, P. porites*
			Rear of crest	*O. annularis, D. strigosa, M. cavernosa*
			Reef flat	*A. palmata*
			Reef Wall	*A. agaricites*
			Fore reef	*A. cervicornis*
1962	Kornicker (1962)	Mexico	< 9 m	*A. cervicornis, A. palmata, O. annularis, D. strigosa*
1965	Kissling (1965)	Florida Keys	< 1 m	*P. porites, P. astreoides, S. siderea, S. radians*
1968	Adams (1968)	St. Vincent	< 6 m	*P. porites, A. palmata*
1972	Porter (1972)	Panama	< 5 m	*A. palmata*
1976	Goodwin et al. (1976)	Grenada	< 12 m	*P. porites, P. astreoides, O. annularis, S. siderea*
1977	Bak (1977)	Dutch Antilles	Shallow reef	*D. clivosa, S. radians*
			Crest	*A. palmata*
			Wall < 8 m	*O. annularis, M. cavernosa, S. siderea, A. agaricites*
1973	Glynn (1973)	Puerto Rico	Reef flat	*P. furcata*
			Seaward slope	*A. palmata*
1974	Porter (1974)	Panama (Atlantic coast)	Shallow reef flat	*P. furcata*

1976	Macintyre (1976)	Panama	Intertidal reef flat	*S. radians*
			< 4 m	*S. siderea, P. astreoides, P. furcate, F. fragum,* *A. palmata*
			4-6 m	*Agaricia spp. S. siderea*
1980	Bak (1980)	Curaçao	10 m	*O. annularis*
1980	Antonius (1980)	Venezuela	< 1 m	*P. porites*
			3-7 m	*S. siderea*

3.5 Discussion

This study constitutes the first extensive survey of coralliths across the MBR. It also highlights previously unknown CFS, such as *A. humilis.* The corallith community varied across sites in terms of both species richness and corallith morphology. However, coralliths in Utila did not appear to stabilise and form patch reefs like the coralliths found around Vavvaru Island, Maldives (Hennige et al., 2017). Across the wider Caribbean, I found that CFS constitute a surprisingly large proportion of the hard coral community and theorise that this could be due to the Caribbean-wide phase-shift favouring CFS.

3.5.1 Coralliths in the intertidal shallow zone

Branching coralliths were most common at Coral View due to the high abundance of *P. divaricata* in shallow waters. Few Caribbean coral species are adapted to live in such shallow water, where daily temperatures can vary by over 15 °C (own observations in the field), corals can become exposed to the air at low tide, and there is a high amount of wave action. Despite the conditions at this site, Coral View had the highest abundance of coralliths. *Porites divaricata* and *S. radians* are two species that are common in this relatively hostile environment. These two species' ability to form coralliths and their skeletal structure may aid in their ability to survive in shallow habitats. Being mobile means periodically, different parts of the coral structure will be exposed to air, buried by sand, in direct light or shade. This constant rotation means that the part of the coral experiencing stress will periodically change. This could lead to a pattern of stress and recovery across the coral surface, which in turn means that no one part is experiencing stress long enough for that area of tissue to perish. Both species also have sunken corallites (Veron, 2016), meaning that the polyp's soft tissue is well protected from damage when rolled and partially buried.

Sturch Bank had a higher prevalence of rubble and coralliths than Little Bight (Figure 7). As coralliths can be formed through larval settlement on mobile substrate, the provision of rubble likely aids corallith formation. Although this data was not available for Coral View and Neptune's Beach, my observation in the field was that Coral View had the vast majority of its sea bed composed of rubble, whilst Neptune's Beach had a higher proportion of rocky substrate (Figure 7). Compared to Neptune's Beach, the substrate type and seagrass density at Coral View may contribute to the increased number of coralliths at Coral View. The seagrass density at Coral View was observed to be much higher here than at other sites. As documented in Kersting et al. (2017) and as proposed in Chapter 1, coralliths may benefit from high macroalgal or seagrass presence by reduction of abrasive surfaces, reduction of movement and shading and/or protection when the tide is out. Future work could look at the prevalence and survival of coralliths within seagrass meadows vs outside of these areas.

3.5.2 Coralliths further from the shore

Of the two sites surveyed further from the shore, Sturch Bank had the highest abundance of coralliths. At both locations, both *A. humilis* and *S. siderea* were the most common corallith species, but Sturch bank had ~10 times more coralliths in total than Little Bight (Figure 2). This is likely due to the presence of large rubble beds at Sturch Bank. Whilst Little Bight had a significant presence of sand, Sturch Bank had none documented in this study (Figure 3). Rubble is an ideal substrate for the production of coralliths. Corallith-forming species have been observed and shown to be more resilient to life in rubble beds (Hennige et al., 2017, Kenyon et al., 2020), whilst it has not yet been shown that sand is suitable for any hermatypic coral. This is possibly due to the smothering and unstable nature of sand, along with the inability of coral to cement and re-sheet sand. Rubble, whilst potentially more abrasive, provides spaces allowing for water flow around more of the corallith and is a stable enough substrate for coralliths to both cement rubble together and then re-sheet the newly formed larger surface (Figure 12). This can speed up the time taken for a coral to reach a larger size, which in turn can increase the survivorship of the coral (Lizcano-Sandoval et al., 2018).

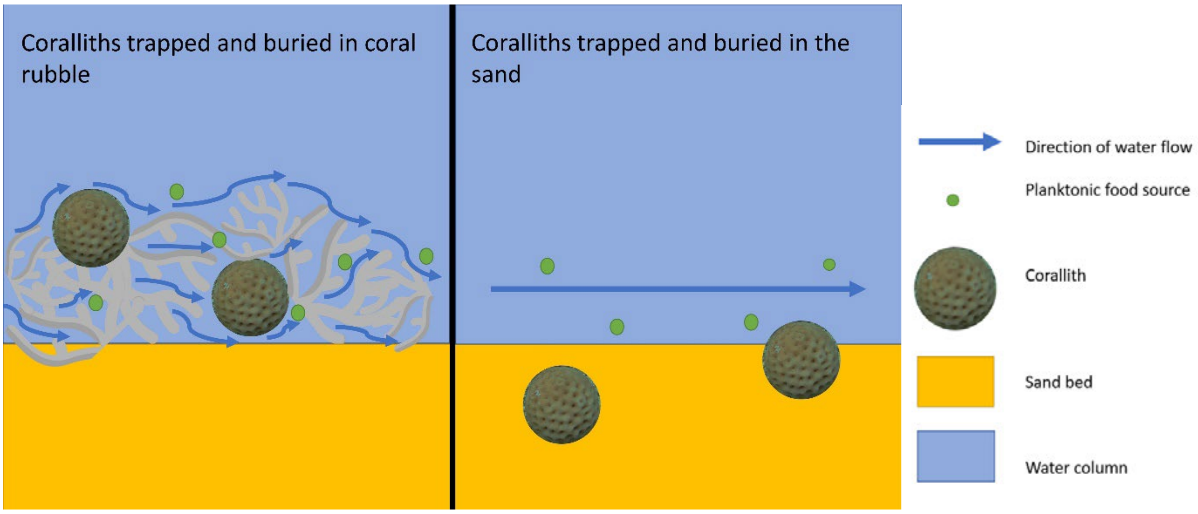


Figure 12. Schematic showing coralliths buried in rubble sat on the sand bed vs coralliths trapped and buried in the sand. In the rubble, there is movement of water through the rubble, and with it, the possibility of obtaining food through heterotrophy. This food provision is limited when buried in sand.

There was no observed increase in size with distance from the shore (Table 2), as seen in The Maldives (Hennige et al., 2017); however, other investigated variables did impact size. Some species had a positive impact on size, whilst others had a negative impact. The largest coralliths found were *S. siderea* and *C. natans* and were likely large broken-off fragments from a nearby larger colony, likely during a storm or hurricane. Whilst the smallest coralliths were coral recruits living on rubble. Amongst these coral recruits, many of the smaller (< 10 cm) coralliths were *S. siderea,* suggesting that some species have higher survival and/or growth rate as a recruit on rubble than others. Future investigations that look at the provision of rubble and its impact on corallith size could reveal another mechanism for FLSH. For example, in Utila, which has a groove and spur reef formation with offshore patch reefs, distance from shore may not be a suitable metric for predicting the size of corallith as there is a lack of a large lagoon with calmer water. However, based on what was observed in this study, the provision and size of rubble substrate might instead provide a mechanism for FLSH and patch reef and reef bommie formation.

3.5.3 Effect of size of substrate

The size of the substrate had a positive impact on the length of living tissue (Table 2). Once a recruit has settled on a piece of substrate, it can encrust tissue across the entire surface of the substrate. This process is called “re-sheeting” and has been observed in several studies (Jordan-Dahlgren, 1992, Lescinsky, 2012, Roff et al., 2014). Jordan-Dahlgren (1992) described a process of recovery in *A. palmata* where recruits that settle on a dead conspecific’s skeleton can grow to a larger surface area more rapidly and acquire any morphological benefits that the now-dead coral once had. A similar process of re-sheeting can also occur when coral recruits settle on mobile substrate, albeit the benefits are somewhat different. Firstly, the benefits observed by Jordan-Dahlgren (1992) were that the recruit could capitalise on the light-harvesting structure created by the now-dead coral. Here, the benefits are that the coral recruit can form a mobile corallith, which, although causes the coral to experience harsher conditions, may increase resilience to these through pre-conditioning (Carilli et al., 2012). Secondly, the recruit will be able to encrust over the substrate in a sheet-like manner to gain a larger surface area more rapidly than a coral recruit that must invest energy in producing a skeleton to support a growing surface area. The larger the piece of rubble that the recruit settles on, the larger the surface area it can obtain before laying down a metabolically costly skeleton. This was reflected in our findings that larger substrate positively impacted the longest length of living tissue.

3.5.4 Corallith forming species prevalence

Some species of scleractinian, whilst making up a relatively small portion of the sessile community, produce coralliths more readily than other hermatypic corals. When the abundance of corallith species at Sturch Bank and Little Bight was compared with the sessile species present in Operation Wallacea’s data for 2019 (Figure 1), it’s clear that of the sessile species present, only a handful are producing coralliths. *Siderastrea siderea* and *A. humilis,* the two most abundant corallith species at Little Bight and Sturch Bank, only make up a small percentage of the sessile community (both < 5%). This suggests that not all scleractinian species are suited to life as coralliths, or at least not in the conditions present at these two sites. For example, *A. cervicornis* was very common at Sturch Bank but was never found as a corallith, although that’s not to say this species could never form one. In another region, with different tides, light environment, depth, temperature or other environmental factors, *A. cervicornis* could perhaps form a corallith. *Acroporids* are possibly unlikely candidates for corallith formation due to their thin tissue, cupped corallites and sensitivity to changes in light and temperature. However, if conditions are right, all scleractinian corals could possibly form coralliths (as described in Chapter 2, section 2.5.8), with some *Acroporids* having been observed to form coralliths in Australia (Roff, 2008).

3.5.5 CFS vs non-CFS

Species such as *P. divaricata* and *S. radians* were only ever found in the shallows, whilst *O. annularis* was only ever found in deeper water (>4 m depth). We found coralliths and fragments of various species at depths where the species are known to be found, according to other zonation studies (Goreau, 1959, Bak, 1977). This suggests that coralliths and fragments do not journey far from their parent colony. However, what is interesting is when we look at which species are forming coralliths and which are forming fragments, specific patterns emerge. There were some species found at the same depths that, when unattached, were only ever found as coralliths and others that were only ever observed to be fragments. One example is two species from the same genus, *A. humilis* and *A. tenuifolia. Agaricia humilis* was only observed to form coralliths when unattached, whilst *A. tenuifolia* was only ever observed to be fragments. In corallith form, all of the *A. humilis* coralliths were either encrusting or rounded in morphology and attached to mobile substrate. This suggests that they were formed via larval settlement on mobile substrate rather than fragmentation of an adult colony. *Agaricia humilis* appears to have a high survival rate when larvae of this species settle on mobile substrate. However, these findings also suggest that adult colonies of this species either do not fragment often or have a low survival rate when they do fragment. This is evidenced by the lack of any *A. humilis* fragments found in this study. Unlike *A. tenuifolia,* which appears to have a high fragmentation rate, but no evidence of corallith-forming ability.

All of the *A. tenuifolia* fragments were either branching or plating in morphology, confirming that they were likely formed through fragmentation of an adult colony and not through larval settlement. All had a clear breakage point that had not fully healed, so they were classified as fragments and not yet coralliths. Whether any of these did go on to heal and form a free-living branching corallith is unknown. The alternative to this is that the fragments became lodged elsewhere on the reef and re-joined the sessile community, or they perished. Both *A. humilis* coralliths and *A. tenuifolia* fragments were often found next to one another at the same site and depths, with the same environmental parameters. This raises questions about what allows some species to form coralliths and not others. Here, I believe morphology comes into play. *A. tenuifolia* may be able to encrust onto mobile substrate to a certain extent, but it will eventually start branching out into the characteristic leaf-life plates that this species forms. Once this happens, any movement of the mobile substrate will put the coral at risk of breakage and tissue damage. This could potentially cause enough stress to prohibit complete corallith formation and ultimate death in this species. However, *A. humilis* is known to form small, rounded, massive shaped colonies, which are more suited to being rolled. Further work should look at the role that morphology plays in corallith formation. It would be particularly interesting to observe a species such as *Agaricia agaricites,* which has a very varied morphology. Although not identified on any of my transects, this species was observed to form coralliths on the reefs around Utila on recreational dives. What environmental factors trigger this species to adopt a more rounded encrusting morphology when forming a corallith, rather than branching out, would help elucidate why some species form coralliths when others do not.

3.5.6 Coralliths across Utila and Tela Bay

Corallith-forming species have increased their overall cover at Tela Bay but stayed fairly steady in their cover at Utila (Figure 5). The reef at Tela Bay is an unusual reef system within the MBR. It has high coral cover, relatively high sedimentation and starts at greater depths than many reefs in the MBR, meaning it exists in a lower light environment. What is of particular interest is the large increase in corallith cover in the year 2013, just after a bleaching event was documented at this site (per comms. A. Borcsok). Corallith-forming species, known to be reasonably tolerant of bleaching events (Loya et al., 2001), appear to have capitalised on the reduced cover of competitive species. Further studies of this phenomenon could give insight into the changes on reefs in the face of climate change as bleaching events are predicted to become more common.

While an increase in CFS does not damage the overall total coral cover at Tela Bay, it may, in time, cause a shift in the quality of available habitat. Currently, Tela Bay has a high coverage of structurally complex species, such as *A. cervicornis*, *A. palmata* and *A. tenuifolia*. Suppose the identified CFS continue to capitalise on any future bleaching events. In that case, this community composition may shift to species of lower rugosity, such as *A. humilis*, *S. siderea* and *P. astreoides*. Some corallith species with branching morphology were identified, such as *P. porites* and *P. divaricata*. However, a *P. divaricata* is unlikely to survive at the depths that Tela Bay is found at (>15 m depth), and a shift to a monoculture of *P. porites* would create a reef that is less resilient to disturbance. For example, if a pathogen that *P. porites* is susceptible to were to infect the area, then vast swathes of the reef could be lost.

3.5.7 Coralliths across the Caribbean: present and past

To investigate if there were any significant increases in corallith cover across the Caribbean, I looked at the abundance of scleractinian corals across the Caribbean using the comprehensive dataset available from The Atlantic and Gulf Rapid Reef Assessment (AGRRA). I observed that CFS made up a much larger proportion of the benthic community than I observed in Utila and Tela Bay; for the three ecoregions analysed, coralliths comprised over 50% of the coral community. This is much higher than was observed in The Maldives. To investigate whether this level of cover was present before the phase shift that the Caribbean underwent over the last 30 years, I looked at papers published pre-1980 that described the coral cover around the Caribbean region. It is evident that before the phase shift, the dominant species in the MBR and the wider Caribbean at < 10 m depth were *A. cervicornis, A. palmata* and *O. annularis.* The data provided by AGRRA shows that *P. porites*, *P. astreoides*, and *O. annularis* are currently the dominant three species. This is a significant shift in the coral community, and all three dominant species can form coralliths.

My findings show that CFS now represent a larger proportion of the coral community after a phase shift. This phase shift has caused a large increase in algal cover in the Caribbean, with vast areas of what was once coral cover now dominated by algae. Two potential explanations for this high cover of CFS exist: 1) CFS maintained their previous cover whilst other corals perished, causing them to have a higher proportional representation in the community, and 2) whilst other species of coral perished, CFS both survived and expanded their cover. It is difficult to say which of these is the case as one would need detailed benthic survey data to say what the previous corallith species abundance was and compare that to what it currently is to see if their cover has increased or stayed the same. Either way, what is clear is that any return to high coral cover depends more on CFS, as these are now the dominant scleractinian species. If, in a hypothetical scenario where algal cover is reduced in the Caribbean, and reefs were able to increase in coral cover via natural recruitment, it would be the corals present in the system that would seed the reefs of the future. This would lead to a reef of high coral cover but low rugosity.

3.5.8 Conclusion

This detailed study of coralliths in the Caribbean has revealed two key findings: 1) corallith formation is highly dependent on the provision of rubble, and 2) CFS appear to capitalise on severe and frequent disturbance events. These two facts could lead to irreversible changes on coral reefs as we see climate change causing more disturbances, such as bleaching events, which reduce non-CFS competition and ultimately create more rubble.

Chapter 4. An investigation into the global trend of increasing encrusting corals on reefs and the driving mechanism behind it

In the previous chapter, I investigated the community structure and the ecological role of coralliths in Honduras and the wider Caribbean. The major disturbances that occurred in the Caribbean caused a phase shift in the 1980s. I found that CFS were increasing in cover post-disturbance, and now represent over 50% of the coral community in the Caribbean. This leaves the question of what is occurring on reefs that have yet to undergo a phase shift fully but are experiencing repeated and severe disturbances. This was my focus in Chapter 4.

4.1 Introduction

Tropical coral reefs are one of Earth's most biodiverse and economically important habitats (Woodhead et al., 2019). They house the highest density of marine species and provide many crucial ecosystem services to almost a billion people (Woodhead et al., 2019, Moberg and Folke, 1999). These include food security (Foale et al., 2013), coastal protection from erosion (van Zanten et al., 2014), sources of income through fisheries (Teh et al., 2013) and tourism (Spalding et al., 2017), as well as being a source of medical compounds (Cooper et al., 2014). Many of these services can be attributed to high biodiversity, which in turn is largely due to the structural complexity of the reef itself (Graham and Nash, 2013, Newman et al., 2015). By providing many niches, structural complexity enables a high number of species to coexist (Gratwicke and Speight, 2005); complexity also helps to mediate ecological processes such as predation (Steele, 1999), competition and recruitment (Holbrook and Schmitt, 2002, Graham and Nash, 2013, Richardson et al., 2017). A critical process that keeps niches opening up and preventing the reef from reaching a climax community is disturbance.

4.1.1 Disturbance on coral reefs

In the last 30 years, however, disturbance events are becoming more frequent and severe (Baker et al., 2008, Hughes et al., 2018). Coral reefs are complex and dynamic in nature, and disturbances can push the system to a new extreme, such as total phase shifts (Hughes, 1994), impacting biodiversity and the ecosystem services reefs support. The primary line of thought is that algal species capitalise on newly provided space after a disturbance event (Bruno et al., 2009), but there may also be opportunities for unexpected species to become dominant (Norström et al., 2009). Unexpected winners post-disturbance might introduce novel outcomes that we can use to our advantage. For example, Robinson et al. (2022) have shown that coral reef fishes from climate-induced regime-shifted reefs are enriched with key micronutrients such as zinc, which benefits human health. It is, therefore, important to investigate which species are winners or losers after repeated disturbance events (Loya et al., 2001) and understand their effect on ecosystem functioning. One major disturbance event that is increasing in frequency and severity on tropical coral reefs is mass-bleaching events (Brown et al., 2019).

4.1.2 Porites rus, a CFS and resilient to bleaching

It has been documented that massive and sub-massive coral species, such as *Porites spp.* are more resilient to bleaching events, at least in the short term (van Woesik et al., 2011). What has so far been overlooked is the ability of many of these species to form coralliths. (Glynn, 1974, Roff et al., 2014). One such species, *Porites rus,* found throughout the Indo-Pacific, forms sub-massive, encrusting or undulating, connected, short branches (Veron, 2016) and often forms vast colonies that are commonly over five metres in diameter (Veron, 2016). *Porites rus* reproduces both sexually and asexually through polyp budding and through fragmentation (Veron, 2016). *Porites rus* coralliths experience and are resilient to a high level of physical and physiological stress because they frequently encounter changes in the abiotic environment, get buried in sand or shaded by other sessile colonies (Glynn, 1974, Roff, 2008, Capel et al., 2012, Hoeksema et al., 2017, Hennige et al., 2017). Once coralliths are large enough to no longer be moved or have their movement impeded, they can reattach to stable substrate and re-join the sessile community (Hennige et al., 2017).

One area where *P. rus* is seemingly increasing in cover, according to local observations, is The Maldives. This is despite repeated mass-bleaching events in The Maldives, which have led to a rise in the degradation of reefs in some areas, resulting in higher algal cover, increased dead coral framework and more extensive rubble beds (Kenyon et al., 2020). An increase in *P. rus* and subsequent decline of structural complexity may have a detrimental effect on the functioning of these reefs as local fish and invertebrate species may not be adapted to this low-lying habitat.

4.2 Aims and Objectives

It is unclear whether CFS merely survive bleaching events or whether they are increasing in cover and, if so, what mechanism allows for this increase. I had two main objectives:

1) I conducted a meta-analysis of the published literature reporting the response of scleractinia post-bleaching from across the globe. This was to assess
    a) Whether there is a directional response of CFS to bleaching events.

2) I then utilised detailed point-line survey data from the North Malé Atoll, The Maldives, to look at the response of two reefs post-bleaching, particularly changes in the percentage cover of *P. rus.* This was to assess:

    a) Whether there is evidence for the locally reported increase in *P. rus* (per. Comms. Dr. S Newman)
    b) Whether CFS increase their cover post-bleaching or maintains their previous cover.
    c) If there is an increase in *P. rus* cover post-bleaching, what is the mechanism and timescales behind the reported increase in the percentage cover *of P. rus* in the Maldives?

3) I also used point-line surveys looking at both coralliths and sessile corals from the same area to assess:
    a) Which species are CFS in this area?

b) Does a high abundance of sessile CFS conspecifics lead to a higher abundance of coralliths, or were coralliths evenly distributed around the islands?

4.3 Materials and Methods

4.3.1 Coralliths post-disturbance on a global scale

Firstly, to obtain an exhaustive list of CFS, I conducted a search of the literature using Google Scholar and Web of Science. Initially, the term 'corallith' was included as a search term. Then subsequent terms that have been used to describe mobile unattached corals were searched for, including 'circumrotary + coral', 'rhollolith' and 'unattached + coral'. Species that were described as coralliths, or that fit the description of a corallith, yet the term wasn't used, were compiled into a list of CFS (see Chapter 1 Table 1.).

To evaluate the changes in coral cover occurring on coral reefs globally, data on changes in total hard coral and CFS cover throughout bleaching events were collected from existing studies through literature searches. A sensitive search was conducted to recall relevant studies, after which the search was made more specific with additional keywords to exclude irrelevant studies (Aromataris and Riitano, 2014). The search term "corallith" was entered into the Google Scholar search engine and Web of Science. Further search terms were added, including "cover" and "presence", as well as specific regions, such as "Maldives". Next, a new search was started, using the search term "coral + cover", with variable additions of more specific terms, including "bleaching", "recovery", and particular regions. The steps undertaken followed a standardised methodology of an exhaustive review with selective citation (Randolph, 2009).

Studies were selected from this collection if they reported (a) percentage cover of live hard coral and CFS, (b) with replicated measurements, and (c) lasted before, during and after a bleaching event within the same site. All values were converted to a percentage of total area for ease of comparison. Four different methods were used in assessing benthic cover on reefs in this dataset: line-intercept transects, video-transects, photo quadrats, and *in-situ* assessed quadrats. To minimise the bias risk, consistency across incorporated study methodologies was ensured. Only published literature was considered, and no limits to dates were applied. Where available, species-specific corallith data was noted.

4.3.2 Maldives study site

Situated in the central Indian Ocean, The Maldives archipelago is a double chain of atolls, extending from 0°34′ S to 6°57′ N (Naseer and Hatcher, 2004). Within the central and eastern side of the atoll chain is the North Malé Atoll, within which the two study sites Vabbinfaru (4.3096° N, 73.4235° E) and Ihuru (4.3067° N, 73.4161° E) can be found (Figure 1). Both islands are formed of carbonate platforms. The main human activities on and around these islands are tourism-related (e.g. diving), with zero local fishing pressures (Moritz et al., 2017). Both islands have fringing reef formations, with Ihuru having a reef flat ranging from ~ 50-180 m from shore to reef crest. Vabbinfaru has a more extensive reef flat zone, which ranges from ~50-400 m from shore to reef crest. The monsoon season extends from May - October each year. Sea surface temperatures stay within a narrow range in non-bleaching years (28.5°C - 30°C). Outside the monsoon season, the waters are calm, with a maximum wind velocity of 6.6 m s^{-1} originating from the north (Morgan and Kench, 2012). This increases to 14 m s^{-1} during the monsoon when wave energy is predominantly from the west (Morgan and Kench, 2012). Surveys were carried out by the Banyan Tree research team each year between September and October from 2015 until 2019 inclusive. This timing is crucial to assess survivorship post-bleaching, which occurs during April and May when temperatures peak.

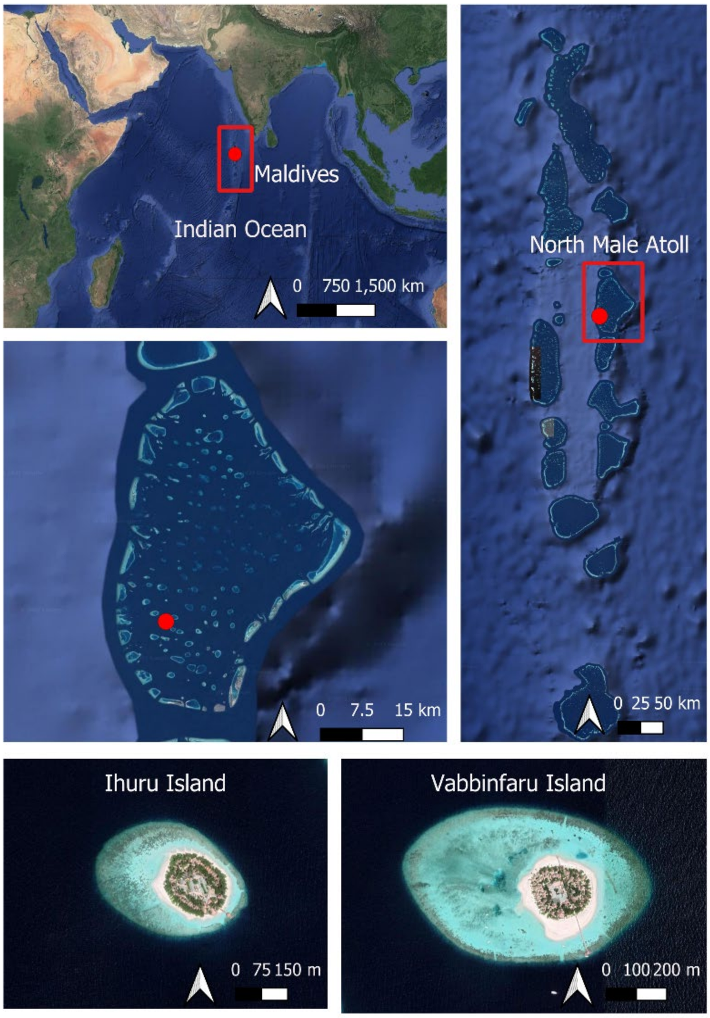


Figure 1. The location of Vabbinfaru and Ihuru islands in North Malé Atoll, Maldives. Image: Google Earth (2021).

4.3.3 Bleaching events

There were two significant bleaching events during this five-year study. The first was in April/May 2016 and the second was in April/May 2019. Both occurred 5-6 months before the data were collected for those years, which was key in assessing true declines in cover post-bleaching. The bleaching event in 2016 was widespread throughout the Maldives, with temperatures exceeding 31 °C for at least 12 weeks on these two reefs in particular (per comms. Newman). El Niño Southern Oscillation (ENSO)-induced warm SST anomalies caused extensive coral bleaching and mortality across The Maldives (Ibrahim et al., 2017). Increased SST persisted above the regional bleaching threshold of ~30.9 degrees Celsius for around three months, from late March to mid-May 2016. According to NOAA’s Coral Watch 2019, from April to mid-May, coral bleaching alert levels went from ‘warning’ to ‘Alert level 2', their highest alert level.

4.3.4 Benthic surveys

Data were collected between September and October each year from 2015 until 2019 inclusive. Surveys were carried out as part of a yearly monitoring project. Four 20 m line transects were fixed at 1 m (top reef) and 5 m (upper slope) depth contours at four locations around each island (north, south, east and west). This gave a total of 32 transects per island each year. Transects were all a minimum of 10 m apart to ensure independence. The benthos was categorised every 50 cm, giving a total of 40 observations per transect. The substrate was categorised as either sand, rubble, rock or dead coral framework. The benthos was categorised as either turf algae, macroalgae, cyanobacteria, crustose coralline algae (CCA), sponge, soft coral, or hard corals. Hard corals were further categorised by morphology as solitary, plating, branching, boulder, finger or encrusting (see S2 for more details). *Porites rus* was additionally classified to species level in 2016-2019 after encountering few other encrusting species. To aid comparison, we considered all 2015 encrusting records to be *P. rus*. I then further categorised the substrate type into 'recruitable substrate', which is substrate that coral larvae can settle upon, and 'non-recruitable', which they cannot. Recruitable consisted of rock, crustose coralline algae, dead framework and turf algae, whilst non-recruitable consisted of sand, sponges, solitary corals, soft corals and cyanobacteria.

4.3.5 Corallith surveys

In 2017, surveys were conducted by S.J. Hennige to characterise the corallith community around the two islands. Three 20 x 2 m belt transects were positioned at all four cardinal points around Vabbinfaru and on the east and west coastline of Ihuru due to accessibility. Coralliths were classified as any unattached scleractinian coral not from the family *Fungiidae* that had tissue growing across the entire surface of the skeleton. All coralliths were identified to species level where possible. To assess whether coralliths were of high or low mobility, all sessile conspecific corals found within the 40 m^2 area were also recorded.

4.3.6 Statistics

All statistical analyses were performed, and plots were created in R version 4.1.0 (R, Core Team 2019). Differences in the benthic community composition between years were assessed visually by plotting the data. Changes in mean abundance of hard coral cover (excluding *P. rus)* and *P. rus* cover alone, along with percentage cover for each, were calculated.

Mean and standard errors for corallith species abundance were calculated. The mean abundance per transect of *P. rus* coralliths and static colonies for each cardinal point was calculated and plotted. One-way ANOVAs were performed along with Tukey posthoc tests to identify any difference between abundances of coralliths and sessile conspecifics at the cardinal points. Linear regression was used to assess the relationship between sessile *P. rus* abundance and corallith *P. rus* abundance. All plots were made, and analyses were performed using R (R, Core Team 2019) using the package 'ggplot2' (Wickham, 2016).

4.4 Results

4.4.1 Worldwide response of CFS post-bleaching

The literature search yielded 12 separate studies that reported coral cover changes from nine different countries or regions across the globe (Figure 2). Overall, there was a decrease in total coral cover post-bleaching, which was as expected. However, papers that reported changes in genera or species and not just total coral cover showed that CFS increased post-bleaching for nine of the 12 studies. CFS cover was often seen to increase to a greater extent than other scleractinian coral cover. No clear geographic relationship in trends was identified (Figure 2). We acknowledge that this is a small sample of studies and that the trend is not always observed. For example, in Singapore, Guest et al. (2016) observed that CFS species declined more than the *Acroporids*. Whilst in one study by Pratchett et al. (2004), CFS did not increase, although overall coral cover was recovering.

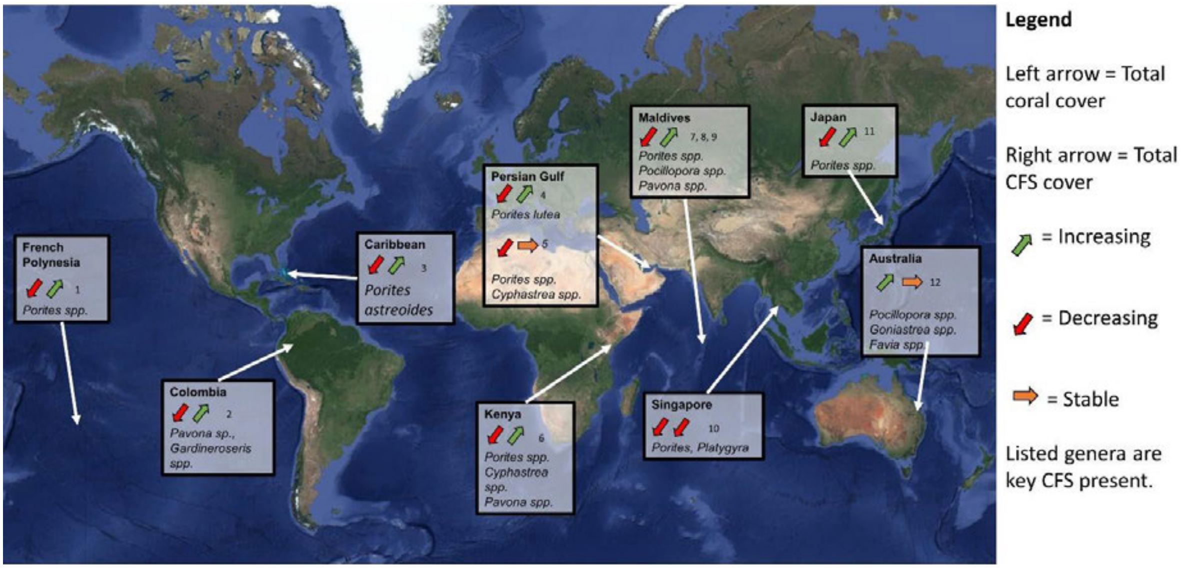


Figure 2. Generated from the literature search conducted to look at the global response of reefs post-bleaching events. The left arrow and its colour denote whether the total coral cover was reported to be increasing or decreasing post-bleaching, whilst the right shows the same for the CFS alone. The key CFS genera driving the response are listed. Numbers in superscript refer to a corresponding citation found in S1. In almost all cases, there was a steep decline in total coral cover post-bleaching, yet CFS cover increased in nine cases out of the 12 studies included.

4.4.2 Examining the mechanism for Porites rus expansion

Total coral cover was more than halved (-53%) across the two islands from 2015 to 2019. All morphological groups, except *P. rus,* reduced in cover after the 2016 mass-bleaching event (Figure 3). Branching and plating corals declined by 99% and 100% of their cover, respectively (Figure 3A). Finger corals made a slight recovery in 2018, only to succumb to the second bleaching event in 2019, resulting in a final loss of 70% from 2015 (Figure 3A). Boulder corals suffered fewer losses with less severe decreases in cover post-disturbance. Despite all other coral morphologies decreasing in abundance over the course of the study, *P. rus* increased its cover across the two islands by 455% in just one year from 2015 to 2016 (Figure 3). This was a change from 2% cover to 14% cover. By 2018, this had fallen to 5% cover but again increased to 10% five months after a second bleaching event in April/May 2019. Overall, this was a 344% increase from its original cover in 2015. *Porites rus* accounted for 24% of the scleractinian coral cover that remains in 2019 (Figure 3). Despite an initial reduction in 2016 of the recruitable substrates available due to a rapid increase in macroalgae, this later increased by 2018 to near 2015 levels. Finally, there was a significant increase in the abundance of rubble. In 2015, rubble only comprised 13% of all observations but accounted for 29% in 2019 (Figure 3A). This is likely due to the breakdown of the dead coral framework, which decreased over time.

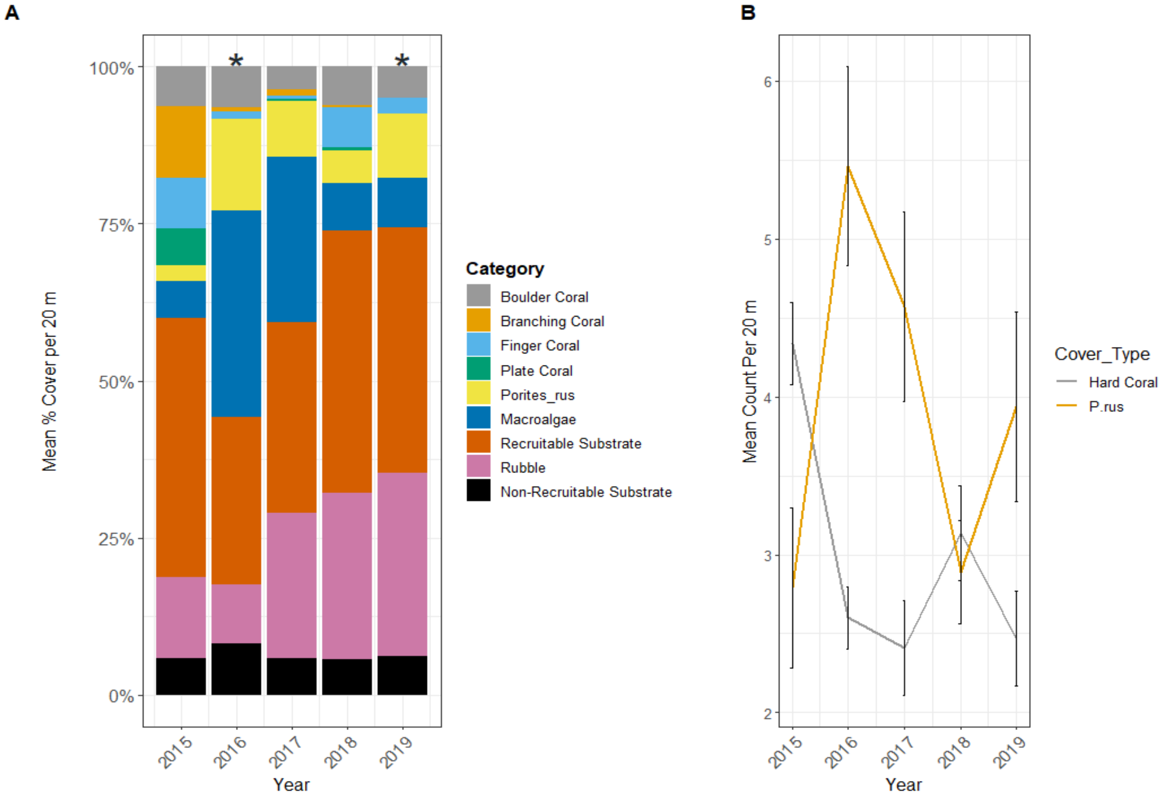


Figure 3 A) Proportional community composition of the entire reef flat benthos from 2015-2019 for both islands n=64 transects per year. Asterisks denote years with bleaching events. B) Grey line = Mean count per 20 m transect for hard coral and orange line = Mean count per 20 m transect for *P. rus* for both islands combined.

Rubble had the greatest increase on both islands by 2019 from its original cover in 2015 (Figure 4). Total coral cover decreased around Vabbinfaru, but whilst there were fluctuations between years at Ihuru, overall hard coral cover recovered by 2019 to similar values in 2015. *Porites rus* increased in cover in 2016 from 2015, then decreased again over the next three years around both islands and then rose again in 2019 after the second bleaching event, but more noticeably around Ihuru.

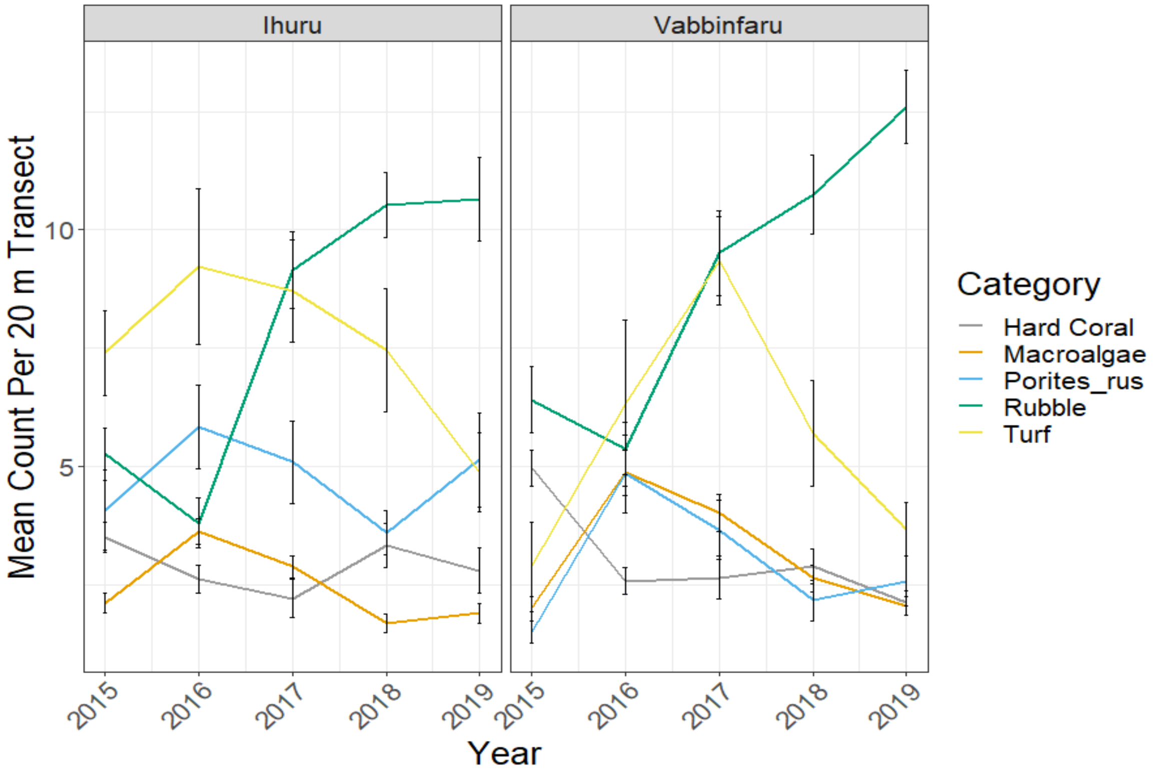


Figure 4. Change over time in mean abundance of Hard Coral, Macroalgae, *P. rus*, Rubble and Turf. Error bars = SEM *n* = 32 per island per year.

4.4.3 Corallith abundance

In total, 1012 coralliths were recorded across all 18 transects around the two islands. Three species of these were easily identifiable: *P. rus, Porites cylindrica*, and *Porites lutea.* All other coralliths were grouped as 'Other Scleractinia'. They ranged in size from 1 cm to 183 cm. 678 coralliths were 10 cm or less in diameter, whilst only 14 exceeded 100 cm in diameter. *Porites rus* accounted for 71% of all coralliths found. The mean ± SE abundance of *P. rus* coralliths per 40 m^2 was 21.6 ± 4.2. There were, however, differences between the abundance of *P. rus* coralliths at the four cardinal points ($F_{3, 14} = 12.8$, $p < 0.001$) (Figure 5). A Tukey posthoc test showed that abundances in the north differed from the south (adjusted $p = 0.03$) and the west (adjusted $p < 0.001$), and abundances in the east differed from the west (adjusted $p < 0.001$). There were also differences between the abundance of static *P. rus* colonies at the four cardinal points ($F_{3, 14} = 8$, $p = 0.002$) (Figure 5). A Tukey posthoc test showed that similar to corallith abundances, the north differed from the south (adjusted $p = 0.03$), the west (adjusted $p = 0.006$), and the east differed from the west (adjusted $p = 0.01$). The south and west had higher abundances of both static colonies of *P. rus* and *P. rus* corallith, whilst the north had the fewest (Figure 5).

A linear regression showed that there was a strong positive relationship between the abundance of sessile colonies of *P. rus* and the abundance of *P. rus* coralliths ($t_{13} = 4.83$, $p < 0.001$) (Figure 5).

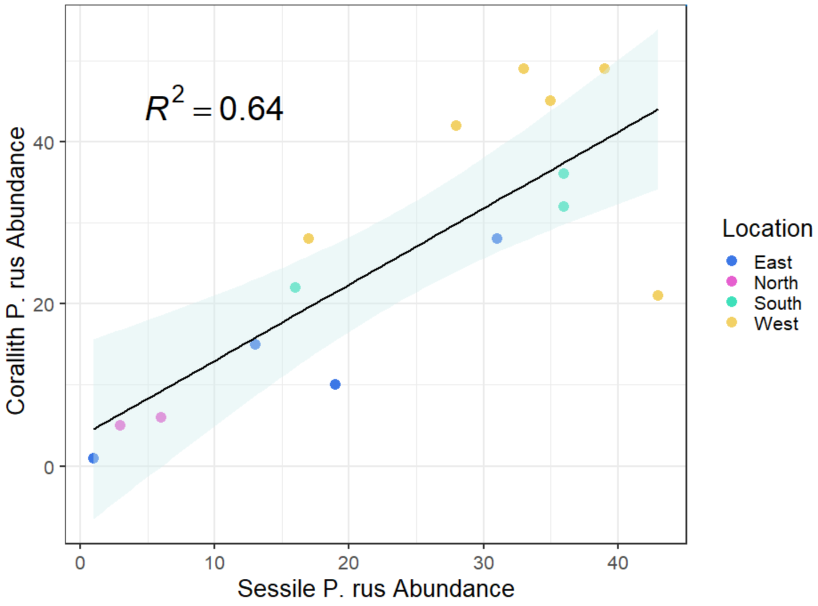


Figure 5. Relationship between the abundance of sessile colonies of *P. rus* and the abundance of *P. rus* coralliths *n* = 18. Points are coloured by cardinal point. The black line shows the regression line taken from the linear model.

4.4.4 Changes in fish functional groups

Corallivores steadily decreased in biomass over the five-year study from 15 kg per 100 m^2 in 2015 to less than 5kg per 100 m^2 (Figure 4). Invertivores suddenly increased to 8.75 kg in 2019 after remaining under 1.25 kg from 2015 to 2018 (Figure 4). Piscivores remained above 30 kg per 100 m^2 until 2018, when biomass started to decrease and was 16 kg per 100 m^2 (Figure 4). Herbivores were the most abundant functional group and steadily increased from 400 kg after 2015 until 2018 when there was a reduction in biomass, but they did not drop below the initial abundance measured in 2015 (Figure 4).

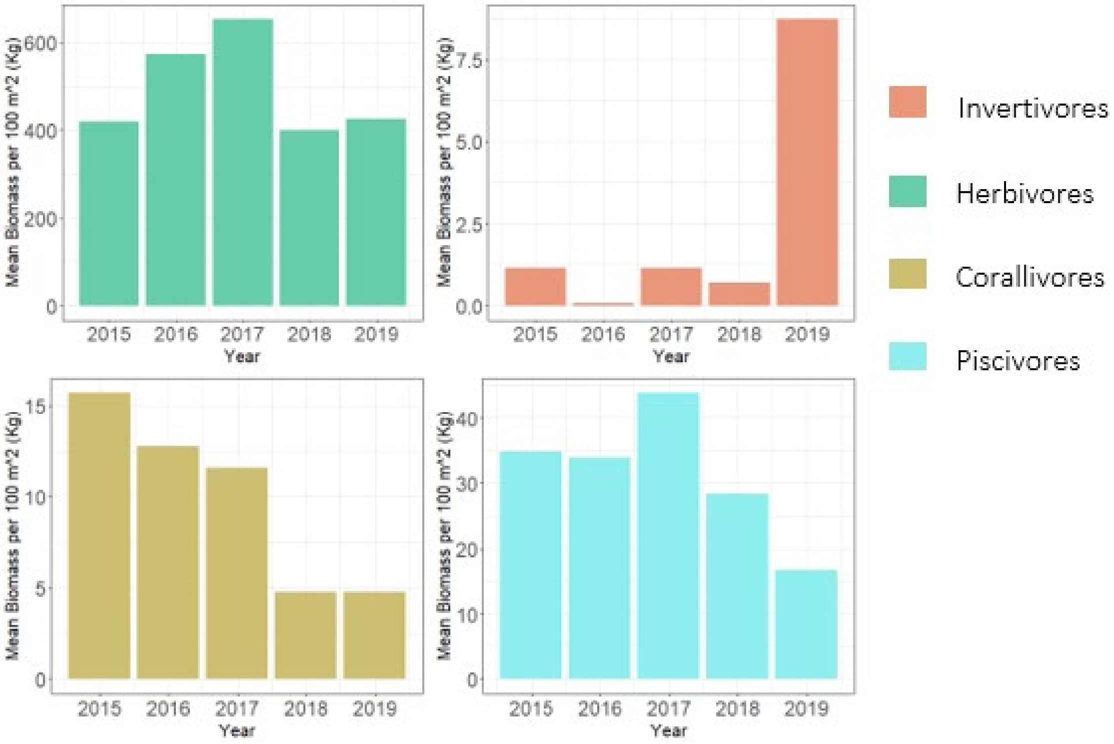


Figure 4. Mean biomass of fish functional groups per 100 m^2 over time.

The nMDS analysis (Figure 5A) showed a distinct difference in community composition despite the overlap between years with disturbance and years without. Years with bleaching events had less variation than years without and were characterised by more herbivorous fish. Macroalgae correlates most strongly with herbivores (Figure 5B) and characterised sites from years with disturbance. Branching, finger corals and dead framework were positively associated with piscivores and corallivores, which characterised sites from years without disturbance.

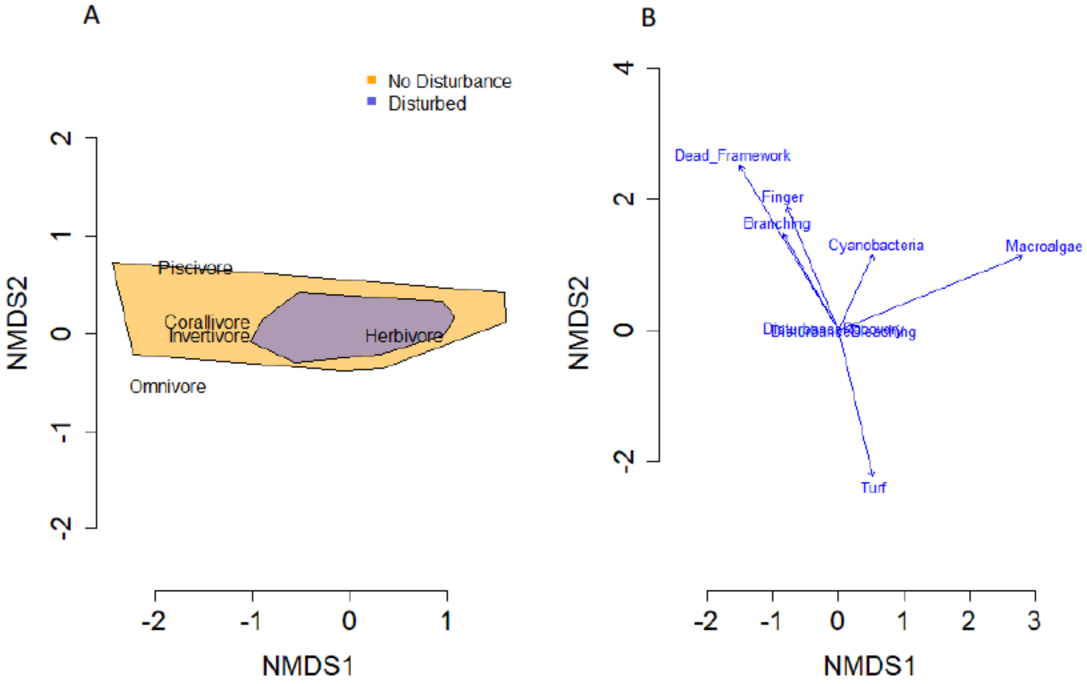


Figure 5. Ordination plot showing the results of the nMDS. A) Transects were allocated as being in a year with or without disturbance, and corresponding hulls were drawn around the sites. The functional group was plotted to show their influence on sites. B) Environmental drivers that significantly correlated with species were fitted using envfit() and plotted.

4.5 Discussion

A meta-analysis of the published literature found that CFS are not only resilient to bleaching events but are also increasing their percentage cover post-bleaching across multiple geographical regions (Figure 2). It has previously been documented that CFS are more resilient to bleaching events (van Woesik et al., 2011), but resilience alone does not explain this sometimes-rapid increase in cover. I, therefore, investigated in detail the changes occurring on two reefs in The Maldives across a five-year period and multiple bleaching events. I observed a rapid 455% increase in the cover of *P. rus* after the bleaching event in 2016. The subsequent reduction in *P. rus* cover in 2017 and 2018 could be attributed to an *Acanthaster planci* (crown of thorns starfish) outbreak that was noted in the area (per comms. S. Newman). Although this corallivore prefers to feed on *Acroporid* corals, when the abundance of these corals was reduced after the 2016 bleaching event, they likely opted to feed on the now-abundant *P. rus.* This outbreak of *A. planci* decreased between 2016 and 2018, possibly due to a reduction in their food or because they moved onto another nearby reef. Other corallivores would have likely had a similar response. Although I acknowledge that reefs are highly complex systems and there may be undocumented factors at play, this unprecedented increase of *P. rus* cover between 2015 and 2016, I believe, is due to its propensity to form coralliths and is key to the mechanism for *P. rus'*s expansion.

4.5.1 Coralliths on a healthy reef

A healthy reef has a high cover of scleractinian coral, so competition between sessile corals and CFS will be high (Figure 6). Due to this competition, coralliths on healthy reefs will have fewer opportunities to reattach to the benthic substrate. The coralliths of *P. rus* in The Maldives may be restricted to rubble beds during this time. Observations made by surveyors in the present study and by Kenyon et al. (2020) showed that *P. rus* was common in these areas. Whilst in rubble beds, coralliths will be moved by wave action more consistently, causing tissue damage via physical abrasion from coarse substrates. Constant rotation prevents the time needed for coralliths to remain immobile long enough for re-attachment to the substrate to occur. These factors combined mean that although *P. rus* can survive these conditions (Kenyon et al., 2020), it may not be able to expand its percentage cover amongst the benthos when the reef is diverse and healthy.

4.5.2 Coralliths in algal beds

During a bleaching event, *P. rus,* which is resilient to bleaching (Lenihan et al., 2008), can capitalise on the provision of new space and reduced competition (Figure 6). We can also see from the presented data that macroalgae becomes much more widespread after bleaching events. Macroalgae might have the effect of impeding the movement of coralliths without causing severe tissue damage. Algae may therefore improve corallith health and aid in re-attachment to the substrate. Similar observations were made in the Mediterranean (Kersting et al., 2017), where coralliths of the species *Cladocora caespitosa* were observed to be living in high densities amongst macroalgal beds (Kersting et al., 2017). This could be an effect of higher mobility outside of the algal bed, causing more significant tissue damage whilst the algal protects the corallith from tissue damage. When reefs become degraded, algal cover might protect coralliths and give them more opportunities to re-establish themselves as part of the stable benthic community.

4.5.3 Coralliths amongst rubble beds

Porites rus and other CFS may also benefit from the increased abundance of rubble, which has steadily accumulated across the five-year study (Figures 3A and 4). In 2015, rubble comprised 13% of the benthic surveys; by 2019, it accounted for 29% (Figures 3A and 4). Kenyon et al. (2020) have demonstrated that *P. rus* fragments have a higher survival rate amongst rubble beds compared with other corals. These coral fragments, by definition, are actually coralliths. Once coralliths start growing within the rubble bed, they may be able to consolidate the rubble by encrusting onto the rubble, growing tissue across the surface of the rubble and filling in spaces between pieces, cementing them together. The tissue growth across the surface of pre-existing rubble would more quickly make a larger colony than through calcification and skeletal growth alone. This larger colony would have a higher chance of survival due to an increased surface area for photosynthesis. We also know from Hennige et al. (2017) that larger coralliths have reduced rotation from wave action and are more likely to stabilise. Together, the reduction in movement by increased algae, the reduction in competition through mortality of other scleractinia and the consolidation of rubble means that coralliths of *P. rus* could aid in the rapid increase in cover of the species in relatively short time frames (e.g. one year).

4.5.4 A natural form of microfragmentation?

The process of small fragments of *P. rus* breaking off from a larger colony, then growing rapidly amongst rubble beds, is akin to ‘microfragmentation’, used in restoration projects in the Caribbean. It has been documented that when larger colonies of massive coral are cut to ~1 cm^2 microfragments, the growth rate is up to 25 times faster than the growth rate seen in larger fragments (Page et al., 2018), which have been more traditionally used in restoration efforts. Restoration efforts have adopted microfragmentation as it allows for the production of many transplant-ready colonies in a shorter space of time (Ceccarelli et al., 2020). These fragments, being genetic clones, can fuse together when planted close by so that you quickly get a large colony capable of reproduction (Page et al., 2018). What we see in The Maldives could be a natural form of microfragmenting. As *P. rus* is fragmented by wave action or fish grazing, these small fragments exist in high numbers amongst the rubble bed, as we saw from our corallith surveys (Figure 5). These might have faster initial growth after fragmentation and be able to fuse with genetic clones. We saw that where there is a high cover of sessile *P. rus,* there is also a high abundance of *P. rus* coralliths (Figure 5). This suggests that the coralliths do not travel very far from the parent colony, so there is an increased likelihood of genetic clones fusing. This again could aid in *P. rus* forming vast colonies.

4.5.5 A mechanism for CFS expansion

I have identified a positive feedback mechanism influenced by bottom-up dynamics (Figure 6). Norström et al. (2009) pointed out that whilst coral-macroalgal shifts are caused by a reduction in top-down control through loss of keystone species, shifts to a dominance of corallimorpharian are caused by bottom-up dynamics. What we see in our present study is not an isolated event. We see that between 2015 and 2017, there was a steep rise in *P. rus* percentage cover, which was reduced by 2018 with only a small per cent increase from its original cover in 2015, with this reduction likely being due to corallivores, such as *A. planci*. Without a second bleaching event, this trajectory might have continued. This explains why we have not seen a conversion to a *P. rus*-dominated landscape on reefs that have had just one bleaching event. Multiple factors, such as corallivore abundance and rubble provision, are also key. However, when there are repeated bleaching events, and the number of corallivores is not elevated, the mechanism we have identified repeats, as we see occurring in 2018-2019. It could also be that a certain percentage cover of *P. rus* needs to be present initially for our identified mechanism to cause an ongoing positive increase. If bleaching events continue to increase in frequency and severity and corallivore levels are not elevated, we will see a shift towards a *P. rus*-dominated reef as the baseline cover of *P. rus* increases between events.

Concept Figure

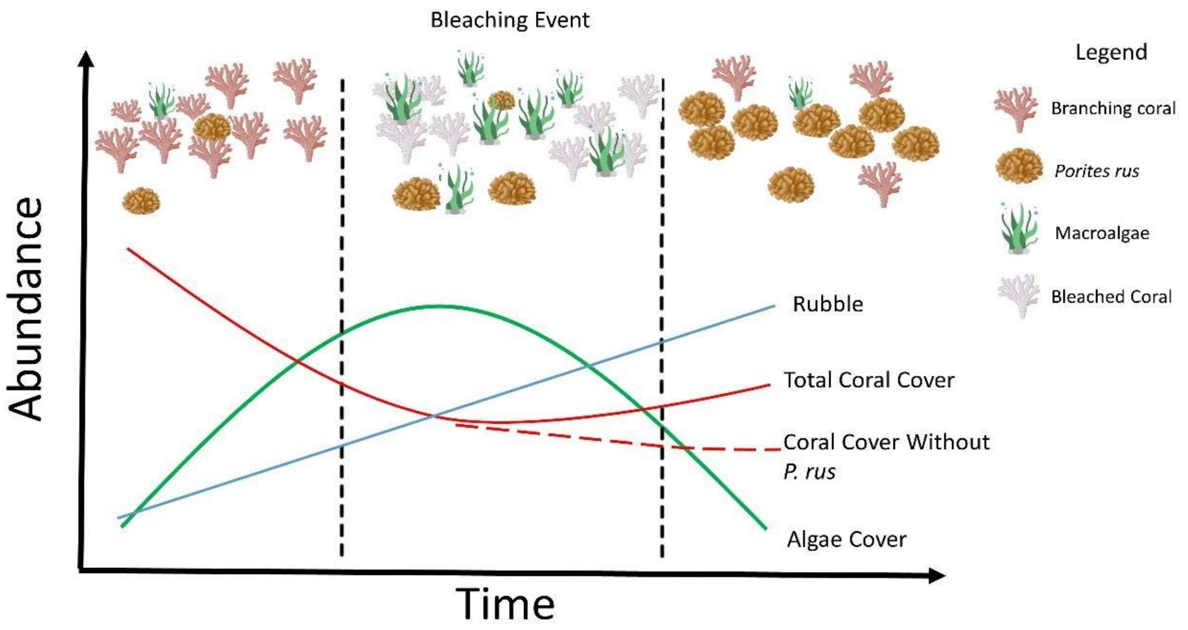


Figure 6. Concept figure showing the progression of the benthic community over time. Pre-bleaching, we see that branching colonies of scleractinia dominate the community. During a bleaching event, total coral cover is quickly reduced by more than half. At the same time, macroalgae take advantage of the reduction in coral cover and provision of space by rapidly increasing cover. Within the scleractinian community, we see that *P. rus* is resilient to the effects of the warming sea surface temperature (depicted at the top). Post-bleaching total coral cover has increased a small amount, and macroalgal cover has been reduced back to pre-bleaching levels. However, as illustrated in the figure, the composition of the remaining coral cover is no longer dominated by branching colonies; instead, it has a large proportion of *P. rus.* This is emphasised by the dotted line, which shows coral cover excluding *P. rus.* Amongst the substrate, we see a steady increase in rubble across all three years. This is likely due to the dead coral skeleton, which has increased due to the bleaching event, steadily breaking down into rubble. This provides new substrate for *P. rus* larvae to form new coralliths.

4.5.6 Increased CFS and a loss of rugosity

An increase in CFS on reefs could potentially mask habitat degradation by increasing overall total coral cover (a metric used in all studies yielded in the meta-analysis) while simultaneously decreasing habitat complexity and creating a low-relief reef (Figure 6 for concept figure). Corallith-forming species are generally massive, sub-massive, or encrusting species of coral. Only a few fast-growing, branching species have been found to grow and survive as a corallith morphology (Roff, 2008), and these were documented in one location at Heron Reef (Southern Great Barrier Reef), Australia. This means that an increase in CFS post-bleaching could reduce rugosity on reefs, reducing habitat provision for fish and other invertebrates. These findings highlight that using total coral cover as a metric for coral reef recovery post-bleaching may not be the best practice. Where possible, surveyors should strive to identify benthic species to the lowest possible level of identification. Where this is not possible, identifying morphological groups, as was done here, could also be done. This gives a better overall picture of how reefs respond to bleaching events. Coral cover may be recovering, but it may be creating a different reef than before. As with my study, also considering the available recruitable substrate vs non-recruitable substrate helps to assess the capacity for the reef to recover. From our meta-analysis, in studies where reefs were classed as recovering post-bleaching that also reported individual species responses, we saw that CFS increased to a higher degree than other scleractinia. This added to an overall high level of recovery in total coral cover but said little about the recovery of reef complexity.

Although a reef dominated by encrusting and massive, low-lying corals does not necessarily support high biodiversity, CFS may act as a ‘place-holder’ for more structurally complex species. By prohibiting macroalgae growth across the newly formed space, CFS might allow other species of coral to re-establish. Hennige et al. (2017) showed that when coralliths form patch reefs, any skeleton exposed during events such as storms or grazing is a suitable substrate for other coral larvae to settle upon. This means that post-bleaching, the newly expanded cover of CFS might eventually provide suitable substrate to support new recruits of more structurally complex coral species. Whilst in instances where we do not see an increase of CFS, we might be more likely to see a community dominated by algae, and a return to the previously complex habitat may be harder to establish. We have seen this in the Caribbean, where loss of keystone species, disease and hurricanes have formed the main disturbance events; space is now occupied mainly by macroalgae (Hughes, 1994). A return to a complex scleractinian community in these degraded areas has been a slower and, in many cases, still an absent process. Identifying if some disturbance events, such as bleaching events, leave behind a community that is more able to re-establish a complex community than others may help focus conservation efforts.

4.5.7 Impact of increased CFS on biodiversity

Of utmost importance for future studies will be to understand how the changes on reefs impact the associated fish communities. Fish provide essential ecosystem services; for example, they are a vital source of protein for many coastal communities (Eddy et al., 2021, Holmlund and Hammer, 1999). Here, I present some preliminary results showing how the fish community has changed over time and how this might relate to the changes in the coral community. Some caution needs to be made with the use of rapid fish surveys. For example, the surveys were carried out by different observers between years, who have varying abilities to identify fish during rapid assessments. This could explain the sudden increase in invertivores in 2019. For example, if a grouper was unidentified to species, it was classed as a piscivore. In 2019, there may have been a new observer that could identify a specific grouper to species and knew that it was an invertivore. This could explain the sudden increase in invertivores and decrease in piscivores in 2019. Despite this and the potential overlapping of functional groups, these surveys do suggest that, overall, there was a small rise in total fish biomass between 2015 and 2017. Still, that abundance returned to 2015 levels by 2019, suggesting the fish community is relatively stable.

When I looked in more detail at the fish functional groups, I saw variation between the functional groups. Firstly, there was a steady decrease in corallivores in the first three years of the study. Corallivores can be either obligate or facultative corallivores. When coral makes up more than 80% of their diet, they are classified as obligate corallivores (Cole et al., 2008). Most obligate corallivores belong to the family *Chaetodontidae* and show a strong preference for branching coral species belonging to the genera *Acropora*, *Porites* and *Pocillopora* (Cole et al., 2008). In the present study, there was a steady decline in corallivores in line with the decrease of branching corals and the increase of *P. rus.* The abundance of corallivores is often used as an indicator of reef health, and our study supports that their abundance can be used as a proxy for branching coral abundance and, therefore, reef complexity. Secondly, herbivorous fish increased initially between 2015 and 2017, coinciding with the increase in macroalgae (Figure 3A). Once macroalgae cover decreased in 2018, herbivores did, too. Finally, piscivorous fish saw a small increase in 2017 (Figure 4), followed by a decline to more than 50% of their original abundance. This could be explained by the decrease in corallivorous and herbivorous fish, upon which the piscivorous fish will predate.

This study misses observations on cryptic fish species, which are difficult to monitor in these types of surveys, yet they could be significantly affected by the rise in *P. rus.* Cryptic species rely on using the small spaces between corals and within the reef framework to hide from predators. *Porites rus* can encrust over these small spaces and, therefore, displace cryptic individuals. This process will be true for cryptic invertebrates as well as fish. Improvements in methods for surveying reefs could help to elucidate the effects of increased *P. rus.* For example, using eDNA analysis could help quantify the abundance of cryptic species (Gelis et al., 2021).

However, it is essential to recognise that the overall stability of fish biomass shouldn't be accepted as an ongoing trend. If *P. rus* continues to increase its cover after each successive bleaching event, which are set to continue, the reef might be flattening. This could lead to a shift in the fish community composition as those adapted to lower rugosity may prosper, which in turn could lead to a more permanent phase shift. Currently, the nMDS indicates that fish from the piscivore and corallivore groups are most closely correlated with an abundance of branching and finger corals. A loss of these corals could lead to a loss of these fish. The alternative could be that *P. rus* acts as a safeguard against the invasion of macroalgae. We have seen severe phase shifts in regions like the Caribbean, where algae dominate the reefs. In the Maldives, *P. rus* could act as a 'place-holder', prohibiting the growth of macroalgae long enough for other species of coral, such as branching species, to re-establish.

In the future, what we consider a healthy reef will no doubt change as baselines continue to slide. We will likely see the emergence of a new alternate stable state where massive encrusting species of coral, like *P. rus,* might be the dominant morphotype. This would have its own unique associated community, which in turn could provide limited or new ecosystem services. It is important to note that the associated fish and invertebrate community will be key in mediating the progression of phase shifts towards algal dominance via herbivory (Hughes et al., 2007). Managing fish stocks after bleaching events will be crucial in aiding reef resilience. So, too, will be the identification of the associated fish assemblages to a reef dominated by CFS. Are herbivores as abundant on these reefs as previously, or are predatory fish more prevalent and are corallivore numbers stable? An increase in CFS might encrust over the spaces on the reef relied upon by cryptic species, which predators can capitalise upon (Almany, 2004). Surveys like the one conducted here should be expanded to more reefs to investigate whether the mechanism for CFS expansion we have identified is occurring elsewhere and what the associated fish assemblages on these new reefs look like.

4.5.8 Conclusion

In conclusion, I have demonstrated that after bleaching events, CFS are generally increasing in their percentage cover on reefs worldwide, and I have suggested a mechanism for this increase. Coralliths can encrust onto the reef when competition is low, and macroalgae abundance is higher. They can then consolidate and stabilise coral rubble and rejoin the sessile benthic community. I recommend that reefs be monitored in areas where successive disturbance events occur and that CFS be noted in these surveys.

4.5 Chapter 4 Supplementary Data

S1. Table of references included in the meta-analysis.

Reference number	**Study**	**Location**	**Coral cover post-disturbance**	**Corallith cover post-disturbance**	**Species-specific**	**Comments**
1	Mehdi et al. (2002)	French Polynesia	Decrease	Increase	*Porites spp., Pocillopora spp., Montipora spp.*	All species declined post-bleaching except *Porites sp.*, which increased.
2	Zapata (2017)	Colombia	Decrease	Increase	*Pavona sp.* *Gardineroseris sp.*	All sites saw a steep decline except the deep sites where *Pavona sp.* were common.
3	Green et al. (2008)	Caribbean	Decrease	Increase	*Porites astreoides*	Surveys in Grenada and Barbados suggest increases in absolute cover of Porites astreoides have occurred.
4	Burt et al. (2008)	Dubai	Decrease	Increase	*Porites lutea*	*Porites sp.* dominated an area that was dominated by *Acropora sp.* before the mass-bleaching event. Rubble beds are more common.

5	Bargahi et al. (2020)	Persian Gulf	Decrease	Stable	*Porites spp.* *Cyphastrea spp.*	Massive declines were observed in the shallow staghorn zones, but no decline was reported amongst CFS-dominated zones.
6	McClanahan et al. (2001)	Kenya	Decrease	Increase	*Porites spp.* *Cyphastrea spp.* *Pavona spp.*	CFS in the unprotected area increased, whilst in the protected area, they did not.
7	Perry and Morgan (2017)	Maldives	Decrease	Increase	*Porites spp., Pocillopora spp.*	CFS increased in relative abundance, but also amongst recruits, CFS were larger in size than *Acropora spp.*
8	McClanahan (2000)	Maldives	Decrease	Increase	*Porites spp.* *Pavona spp.*	CFS dominates recruits. In 1958, the reefs were largely dominated by *Acropora spp.* but in 1999, *Porites* spp. was the dominant genus
9	Zahir (2000)	Maldives	Decrease	Increase	*Porites spp.*	CFS increased in relative abundance by surviving the bleaching event.
10	Guest et al. (2016)	Singapore	Decrease	Decrease	*Porites lobata* *Porites rus*	Contrary to our findings, CFS decreased.
11	Loya et al. (2001)	Japan	Decrease	Increase	*Porites lutea,* *Porites lobata,* *Porites rus*	CFS increased their relative abundance.
12	Pratchett et al. (2004)	Great Barrier Reef	Decrease	Stable	*Pocillopora spp.* *Goniastrea spp.,* *Favia spp.*	Corallith species did not decline in cover.

S2. Table of benthic categories and how organisms were categorised.

Benthic Categories	**Description**
Hard coral	Separated by growth form: Branching, finger, boulder, plate, encrusting and solitary corals
Sponge	Any member of the Phylum Porifera
Soft coral:	Any Octocorallia, Zoantharia or colonial anemone
Macroalgae:	Any algae bigger than 3 cm in length/height
Turf:	Any algae smaller than 3 cm in length/height
CA:	Coralline algae, primarily *Halimeda spp.* or other algae that contribute towards sand after death
Cyanobacteria:	Fine hair like algae-looking substance. If you wave your hand, it detaches from the substrate.
Rock:	All rock on the reef is dead coral. This category refers to rock that cannot easily be identified as coral growth form.
Rubble:	Pieces of rock less than 15 cm in length.
Sand:	If you pick it up, it sinks.
Silt:	It stays suspended in the water for a short while if you pick it up.
Other:	Anemones, trash, tunicates, etc

Chapter 5. General Discussion & Conclusions

In this chapter, I discuss my general findings from the previous three data chapters. I draw these conclusions together, offering the key messages contributing to coral reef ecology and the biology of coralliths. I also provide recommendations for future work and outline gaps in our knowledge that I believe will further the field.

5.1 Summary of Results

In this thesis, I set out to investigate the factors enabling some species of coral to form coralliths and the role that coralliths play in coral reef ecology. In Chapter 2, I found that when put under low light conditions due to being buried, all three species (1 known CFS and two non-CFS) maintained their photosynthetic abilities over a 20-day study in coral sand. Coral kept in black (non-light scattering) sand mostly died. From the coral sand work, I found variation between species in recovery from physical stress. *Porites cylindrica,* a CFS, recovered from tissue damage and healed the wound more rapidly than *Platygyra sp.* (non-CFS). *Porites cylindrica* could also accrete new skeleton over the subsequent three months faster than *Platygyra sp.* These results indicate that a coral species' ability to respond and recovery from physical stress had a greater impact on whether it can form a corallith than its ability to adapt to a changing light environment.

In Chapter 3, I set out to observe and document the corallith community in Utila, Honduras. There was no evidence of the FLSH occurring at this site. I observed coralliths being buried in rubble substrates yet surviving (although some had bleached undersides). I observed three species that, to date, had not been documented as corallith-forming. Through analysis of pre-existing data, I found that, in Tela, Honduras, a reef with a very high overall coral cover for the Caribbean, recent bleaching events favour CFS when looking at the community composition post-disturbance. I also found through a review of historical data and data provided by AGRRA that CFS form a substantial proportion of the coral community in Utila and across the Caribbean, and this shift appears to have coincided with the Caribbean-wide phase shift.

In Chapter 4, I investigated the idea that CFS are resilient to bleaching events and may increase their cover. Through a literature review, I found that reports of coral cover post-bleaching appear to show that CFS are increasing globally. I investigated this in greater detail using a pre-existing data set from the Maldives. I found that a CFS, *Porites rus*, not only is resilient to bleaching but expanded its cover by 455% in one year following the bleaching event. This unprecedented increase can only be possible if the coral is already present before the bleaching event in the form of coralliths, which can then encrust back onto the reef when competition is reduced and re-join the sessile community.

5.2 Synthesis

The findings from my thesis have contributed to the field of coral reef ecology in several vital ways. The conditions in which corals can survive are possibly broader than we thought. In the literature, we are concerned about increased sedimentation smothering corals, yet I've demonstrated that at least some corals can survive burial in the short term. I have also advanced analytical techniques and shown that corals can be repeatedly CT scanned over a period of months to look at the skeletal growth in detail. With some refinement, these methods can be used to better understand corals' growth patterns. I have also shown that repeated disturbance events favour CFS globally and that the mechanism behind CFS increased cover is their ability to form coralliths.

To re-evaluate where CFS belong in the matrix of life-history strategies as defined by (Darling et al., 2012), I have considered the findings in my data chapters along with my initial findings in Chapter 1 where I allocated the currently described CFS to one of Darling et al. (2012) groupings. My findings from Chapter 2, that CFS recover quickly from breakage and can tolerate low light levels, suggests that CFS align with stress-tolerant life-history strategies. However, five of the eleven CFS I found in Honduras, along with the prolific CFS, *Porites rus,* found in Chapter 4 belong to the weedy category. The fact that Caribbean CFS have a higher proportion of weedy species than CFS in the Indo-Pacific could possibly be because the Caribbean has had more frequent disturbances than areas of the Indo-Pacific. High rates of disturbance leads to the selection of species that have faster reproduction rates. However, although the weedy category includes mostly brooding corals, another strategy for rapid reproduction not considered by Darling et al. (2012) is asexual reproduction via the production of coralliths allowing a coral species to establish in a highly disturbed reef. Just as ruderal species of plants can reproduce rapidly via the regeneration from small fragments (Ramesh, 2023), so too can CFS. Whilst many corals can reproduce via fragmentation, these need to become lodged and re-join the sessile community and are rarely found thriving in rubble or sand beds. Corallith-forming species can colonise highly disturbed areas with a high cover of rubble and/or sand by forming coralliths from their fragments.

From my findings, I therefore suggest that CFS are placed in the generalist life-history strategy, as CFS spans several of the other three clusters. However, I think that a revision of the weedy group needs to be addressed to consider other traits which allow for rapid growth and reproduction.

This thesis details that coralliths are not simple morphological oddities but that the ability to produce coralliths is an adaptive trait. The production of coralliths allows a species to colonise areas otherwise inhospitable and act as a way of existing in an overcrowded reef, taking advantage of any reduced competition when the opportunity arises. Without these abilities, a species would be restricted in its cover by the present substrate, and it may be able to withstand sudden disturbances, but it would not be able to expand its cover. Both of these abilities have the result of the coral being able to take up a larger proportion of the benthic cover and by doing so increases its potential reproductive success. A large surface area means better resource gathering, which enables better gamete production. Therefore, forming coralliths is on par with a coral’s ability to reproduce asexually through fragmentation. As coralliths tend to be more resilient than coral fragments, we may see more coralliths on coral reefs than we previously saw before.

This could have significant implications for the future of coral reefs. As we know from a large body of published work, including the most recent IPCC report, we can expect disturbances on coral reefs to continue increasing in severity and frequency. This is an alarming fact for the future of most coral reefs. Undoubtedly, the future reefs will be unlike the coral reefs we observed only 50 years ago. However, many reports in the peer-reviewed literature and the mainstream media have suggested that coral reefs may become a thing of the past. From my work and reading the published literature, I believe it is unlikely that we will see entire losses of coral reefs, but we should expect significant changes. Perhaps they will have a higher proportion of CFS like we now see in the Caribbean. Therefore, the challenge is to continue trying to understand what future reefs might look like. There is already a large body of work with published findings of recovery and resilience to climatic disturbances (Baker et al., 2008, Hughes et al., 2010, Nyström et al., 2000, Roff and Mumby, 2012), as well as discoveries of new reef complexes unlike what we once thought of as a typical reef habitat (Mazzei et al., 2017). These discoveries will aid in our understanding of coral reefs in a changing ocean.

Coral reefs are highly complex and dynamic systems, and I do not doubt that other factors will affect the future of coral reefs. Still, if we take coralliths independently and look at potential future scenarios, we could see a much more flattened reef. This is because of the encrusting nature of many CFS. They would also encrust over many of the intricate gaps in the reef matrix, which are vital to the survival of many smaller prey species and cryptic species. This will impact the wider food chain and likely reduce overall biodiversity. However, some species could benefit from this new landscape. When we look at terrestrial habitats that have undergone a general flattening of the landscape, we can see that not all biodiversity is lost. For example, palm oil plantations in Africa offer a much-reduced canopy cover and less diverse landscape than the forest cleared to form them. Although overall biodiversity is much reduced, some species, such as wild pigs and leopard cats, have adapted to the new landscape and are benefitting (Harich and Treydte, 2016). This is still a devastating blow to the biodiversity crisis, but it does offer a glimmer of hope that species can adapt.

We should, therefore, continue to reduce our global emissions to try and combat a warming climate. Still, we must also accept some of the inevitable changes already occurring on reefs and attempt to either reverse them or aid species to adapt to them. For example, many restoration projects in the Caribbean are working admirably to restore species such as *Acroporids,* which have historically provided a lot of 3D structure on the reef and, as a result, increased biodiversity. However, including species such as *P. porites*, which are branching (albeit to a much lesser extent), more resilient to bleaching, and also a CFS may be wiser. Restoration of CFS alongside non-CFS could have the added benefit of consolidating substrates more rapidly after disturbances and help create new habitats suitable for natural coral recruitment.

5.3 Limitations and Future Recommendations

There were several fundamental limitations to this thesis. In Chapter 2, the substrate grain size differed between the black sand and the coral sand. I would repeat this study with just coral sand over varying grain sizes. I would also use a much larger sample size and try to obtain more reliable RLC data from the end of the study to look for any acclimation to the low-light environment. This would help elucidate whether the coral sand scatters light sufficiently enough to continue normal photosynthesis or whether the corals have acclimated. I would also repeat the CT scans with a holder that enables the exact repeat positioning of the coral for the scans each month. This would mean scans could be overlaid, which was not possible with the scans that I had. This would allow us to visualise the exact locations of skeletal accretion and not just overall volume changes. This could give interesting results about how corals grow: 1) do they extend linearly at an equal rate to how they thicken branches? 2) Do encrusting corals grow outwards whilst thickening at a similar rate? 3) Is there a reduction of skeletal accretion at the cutting site compared to the rest of the colony? I would also use a larger sample size to see whether the initial reduction in skeletal volume is an actual significant fact of coral growth post-cutting or just a chance observation in this study.

I would also have liked to do more detailed fish surveys in Chapter 4 using a more reliable identification approach, such as underwater cameras or eDNA sampling. This could help eliminate any observer bias and help look at any actual impacts of the increase of *P. rus* on the fish community.

Generated Publications

Published

‘*Endolithic Tissue Aids Rapid Recover from Wounds in Porites Cylindrica: the 'Phoenix Effect' in Action’* published in Reef Encounters using data from Chapter 2.

In Review

"Winners of bleaching events may cause an overall loss of coral reef complexity" has been sent out for review by Nature Communications in Earth and Environment. This paper was written using data from Chapter 4.

In Preparation

"Phase shift and bleaching induced expansion of corallith forming species in the Caribbean" is being written using data from Chapter 3.

"*Methods for long-term CT scanning of live corals shines new light on coral skeletal accretion"* is being written using data from Chapter 2.

"*Synthesis paper"* – yet to be formally titled, will be a 'Trends in Ecology and Evolution' style paper bringing together the current published literature along with data from Chapters 3 and 4 from my thesis. This paper will aim to describe corallith biology and give the wider field an understanding of the role coralliths play in coral reef ecology and how future scenarios might impact this role.

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