MARINE BIOLOGY ESSAY | Faculty of Science and Engineering

Algal turfs negatively impact coral health

I.C. Stanca† |

‡Groningen Institute for Evolutionary Life Sciences (GELIFES), Faculty of Science and Engineering, University of Groningen, The Netherlands

ABSTRACT

Coral reefs have been vulnerable and declining as a repercussion of natural disturbances and anthropogenic pressure. As coral abundance is declining, turf algae are taking over the reefs. Loss of herbivore species and decreased coral cover have led to an immense rise in algal abundance. The shift from a coral-dominated reef to an algal-dominated reef has been seen mostly in the Carribean. Algae can become a coral stressor and pathogen inducer leading to coral death. Algal induced stress has many mechanisms of affliction such as competition (abrasion, shading) , algal-coral contact, allelopathy. Through these mechanisms, algae can cause both direct and indirect effects that can lead to coral decline. As such, the rise of turf algae in coral reefs might impact the health of the corals. Disruption of the potential chances of recovery for bleached corals and reducing coral settlement rates have a big impact on future coral generations. The facilitation of invasion by pathogenic bacteria at the coral-algal interface could have a higher negative impact than other competitive mechanisms. The main indirect algal-coral contact effect is a microbiome shift. An insight into the effects algal abundance has on corals can mitigate future approaches in understanding coral mortality and assessment of management options. This essay explores the effects of algal-induced stress, the impact on coral fitness and microbiome, changes at an ecosystem level as well as measures to control high algal abundance.

KEYWORDS: algal-coral competition, algal abundance, algal-induced stress, coral fitness, coral decline, microbiome shifts, pathogen, negative impact.

Supervisors: S.E.T van der Meij, P.G. Boute

INDEX

1. INTRODUCTION

From 1957-2007 coral reefs worldwide have been in decline due to global warming and anthropogenic activity such as overfishing, trawling, and pollution (Eddy et al., 2021). These activities have exposed corals to various forms of stress, however the biggest impact on coral decline is heat stress caused by global warming. Heat stress in corals has been studied by many scientists over the years (Pandolfi et al., 2003; Muñiz-Castillo et al., 2019; Evans et al., 2020) to seek solutions to coral decline and find effective conservation measures to promote recovery of the lost coral cover. Effects of heat stress in corals have been studied the most in the Caribbean because it is characterized by high variations in terms of thermal patterns (Muñiz-Castillo et al., 2019).

Due to different and constant stress factors, the proportion of coral reef covered surface is declining, therefore the ecosystem is experiencing rapid ecological transitions (Pandolfi et al., 2003). Reef changes have been manifesting through eutrophication causing changes in macroalgae cover and their interactions with herbivore species. Keystone species, such as the sea urchin *Diadema antillarum* (Philippi, 1845) and herbivore fish kept the balance between algal and coral cover in a reef. Because of major changes in the ecosystem chain such as overfishing of herbivores and the disappearance *of D. antillarum* (Philippi, 1845), algal cover began to take over the reefs in the Carribean (fig.1). Algal cover began overshadowing the corals struggling to recover from disease (Reverter et al., 2022). Nonetheless, this shift from a coral-dominated reef to an algal-dominated reef can lead to the demise of the reef structure, as scleractinian corals are the foundation of reef-based ecosystems.

Fig.1 Peyssonnelid algal crusts overgrowing star coral near the Caribbean Island of St. John (Credit: Peter Edmunds)

Several studies show that, to improve coral cover and assist coral recovery by recruitment, it is important to understand the effects of algal stress regarding coral fitness and the impact of increased algal cover in coral reefs (Evans et al., 2020; Speare et al., 2019; Wells et al., 2022). The structure and composition of turf algae is important in order to asses the mechanisms through which it negatively impacts the coral cover. Therefore, in this essay, I aim to find answers to the following questions by reviewing case studies:

Chapter 3 and 4:

- What are the effects of stress caused by algae on coral health, in particular on coral fitness and microbiome?

Chapter 5:

- How does algal abundance impact the reefs at an ecosystem level?
- Is there a way to control algal abundance in reefs in order to facilitate coral recovery?

2. ALGAE TURF STRUCTURE AND COMPOSITION

2.1. Turf algae composition and function in the ecosystem

Algal turfs (TA) are composed of a variety of groups including diatoms, cyanobacteria, *Chlorophyta*, *Rhodophyta*, and *Phaeophyta* (Connell et al., 2014). The term “turf” is used to describe a dense accumulation of algal thalli less than 15 cm tall. Because they are composed of multiple groups, their morphological plasticity is considerable. Turfs can be filamentous, foliose, or calcareous articulated, and depending on their growth rate they can either be solitary or form aggregations. Algae that can form turfs are sometimes found in loose aggregations or as individuals, however, they can be distinguished from algal turfs by the density. As such, because of a high level of morphological plasticity the level of disturbance and stress they project on the environment also varies. Algal turf composition in reefs is usually determined based on grazing pressure and sedimentation (Connell et al., 2014).

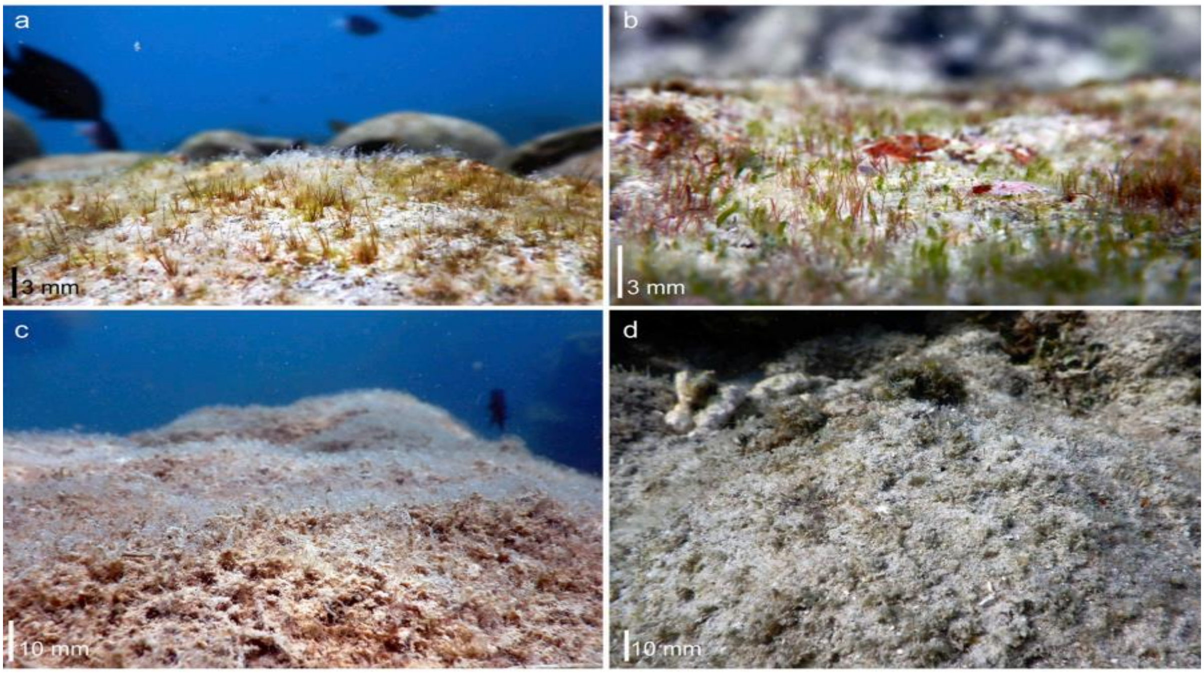

Fig. 2: a),b) Short productive algal turfs with lack of sediment (photographs R.P. Streit); c),d) long sediment-laden algal turfs (Tebbett & Bellwood, 2019)

When the grazing pressure is high, the algal turfs have a short but productive cover (Fig. 2.a.) however when sedimentation loads are high it can produce a shift in the algal community turning them from short and productive communities to long sediment-laden turfs (Fig. 2.b; 2.d). Long algal turfs are less preferred by herbivorous fishes, as such the accumulation of algal communities in reefs is higher. They can trap and retain particulate sediment, making the reefs a less preferable area for coral larvae to settle by imposing a physical barrier (Arjunwadkar et al., 2022). Increased levels of sedimentation favor the growth of algal turfs because of their higher tolerance and reduce the recruitment of corals and crustose coralline algae (Fong & Paul, 2011). Apart from sedimentation, the cover percentages of reef turf algae are influenced by seasonal upwelling. Differences in algal abundance influenced by seasonality are possible due to an influx of nutrients brought by seasonal upwelling and by changes in water temperature (Diaz-Pulido & Garzón-Ferreirab, 2002).

2.2. Effect of turf algae composition in coral settlements

Algal turfs are an important part of coral reef's ecosystem by being primary producers and providing nutrient retention, and recycling. Algae represent a key member of vital ecological functions of a reef (Fong & Paul, 2011). Algal nutrient retention and recycling contribute to overall productivity and provide trophic support for a diverse range of consumers found in coral reefs. For example, crustose coralline algae (CCA) (Silva & Johansen, 1986), is an essential type of algae that provides most of the calcium carbonate which adds to the low amounts produced by corals and other species. Furthermore, coralline algae form intertidal ridges at the highest points of the reefs to protect the more delicate coral species and invertebrates from the force of the waves (Fong & Paul, 2011).

Nonetheless, in a high abundance algae can have negative impacts on coral reefs. One major negative impact is on coral larvae settlement by providing unfavorable environmental conditions (Connell et al., 2014). It has been found that in proximity to filamentous algal turfs, there is a reduced settlement response in *Acropora millepora* (Ehrenberg, 1834) (Birrell et al., 2005; Fong & Paul, 2011). Consequently, Arjunwadkar et al. (2022) found that coral larvae are able to settle among algal turfs. It depends, however, on the algal turf type suggesting that turfs cultivated under different grazing pressure can have a different impact on coral settlement. Their results suggest that a sediment-free substrate is one of the most important factors for settlement of *Acropora* sp. . Even though algae can provide multiple benefits to coral reefs, it can also act as a coral stressor when it is found in large quantities by initiating algal-coral competition (Arjunwadkar et al., 2022).

3. ALGAE AS A CORAL STRESSOR

3.1. Main stress factors associated with algae

With low levels of coral coverage due to disease outbreaks, turf algae has taken over. The impact of this shift from a coral-dominated reef to an algal-dominated reef leaves little to no space for corals to recover due to the stress imposed by the algae. Shifts in the benthic cover of corals have been researched by Wild et al. (2014). With an increase in algal-coral contact, the coral cover is seeing a stress increase. However, not all algal-coral contacts have a negative impact. Wild et al. (2014) discovered that on average 50% of scleractinian corals have been overgrown by algae with 39% of encounters having no effects on the health of the corals. The most damage noticed from algal-coral contact (35%) was caused by filamentous turf algae (Wild et al., 2014). By looking at the bar graph (fig.3) we can observe the differences in algal cover due to the disappearance of the sea urchin *D. antillarum* that controls the abundance of algal turfs (Wild et al., 2014).

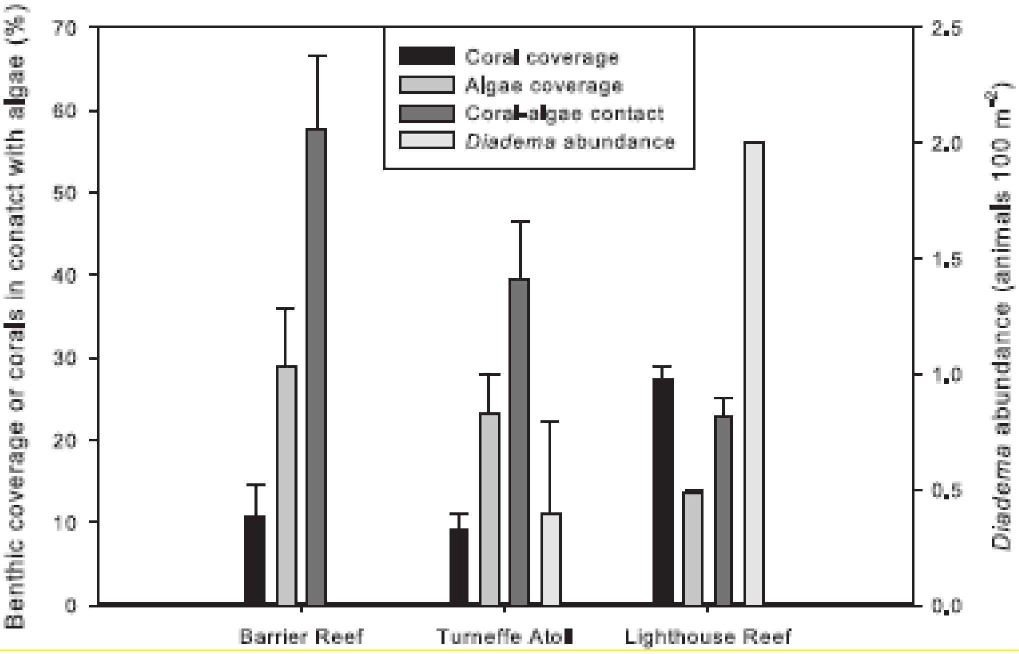

Fig.3 Abundance of scleractinian corals, algae and their contact frequency, and abundance of *D. antillarum* (per 100m^{-2} seafloor area at the three reefs (Credit: Barrier Reefs, Turneffe Atol, and Lighthouse Reef; Wild et al., 2014).

Algal-coral contact is one of the most common stress factors imposed by algae. Through direct contact algae can affect corals by abrasion, smothering, and overgrowing leading to depigmentation and resulting in tissue damage. In some cases, due to physical contact algae can trigger disease in corals. Nugues et al. (2004) studied the effects of physical contact between the macroalga *Halimeda opuntia (L.* 1816*)* and the coral Orbicella favaeolata (Ellis and Solander, 1786). Direct algal-coral contact with *H. opuntia* can trigger white plague type II disease in O. faveolate. It is unclear how the disease is transmitted or if the alga is the vector. *H. opuntia* has been repeatedly found near or growing on corals suffering from the white syndrome. Based on experiments, the pathogenic potential of the algae can be observed in contact with healthy corals. After a month of being in contact with the algae, 55% of the healthy coral colonies with algal contact had developed the white plague (Nugues et al., 2004).

Other stress factors by which algae can influence corals are shading and allelopathy. Through shading, turf algae blocks the sunlight required for coral's endosymbionts to do photosynthesis. Allelopathy is the algae capacity to produce chemical compounds that can potentially influence the growth, survival, and development of corals. Rasher & Hay (2010) studied the effects of seaweed allelopathy on corals, discussing the impact seaweed algae has on the ecosystem and corals. A rise in algae means a rise in polar metabolites which can accumulate and potentially harm corals.

Fig.4 Porites coral suffering tissue loss after being in contact with the algae *Lobophora variegate* (J.V.Lamouroux, 1817) for 20 days (Rasher & Hay, 2010).

Through microbially mediated effects and low oxygen flux mediated through allelopathy, algae can promote anoxia in corals. Depending on the chemical compounds released by the algae the effects of allelopathy are different. Seaweed effects are associated with microbial growth and coral bleaching (fig. 4) (Rasher & Hay, 2010). In the case of the genus *Lobophora* sp. (J.V.Lamouroux, 1817) through allelopathic stress caused by a variety of compounds, corals begin to bleach and their photosynthetic efficiency is suppressed (Vieira et al., 2016). However, the stress effect on corals may be produced by secondary metabolites that have antimicrobial properties influencing the microbiome of the corals. Through microbiome manipulation the expulsion of the zooxanthellate endosymbionts of corals can be triggered and lead to a bleaching effect. It is yet unclear if the chemical compounds are targeting the polyps or the endosymbiont *Symbiodinium* sp. (Freudenthal, 1962) (Vieira et al., 2016).

3.2. Algal-coral competition for space and coral settlement limitations

Corals and algae are the main competitors for space on coral reefs. Algae-dominated reefs consist of species that are normally present on coral reefs however in low densities such as turf algae, calcareous encrusting algae, turf algae, macroalgae such as *Halimeda* sp (J.V.Lamouroux, 1812). After disturbances such as white syndrome disease or yellow-band disease, algae gains the opportunity to cover the dying corals and spread rapidly. This creates a shift in the reef from a coral-dominated reef to an algae-dominated reef. The shift depends on a few critical factors favoring a rise in algal abundance illustrated in figure 5. Environmental conditions such as upwellings, atmospheric transport and storms promote nutrient increase. High levels of nutrients promote algal growth and diminish coral growth due to eutrophication (fig.5).

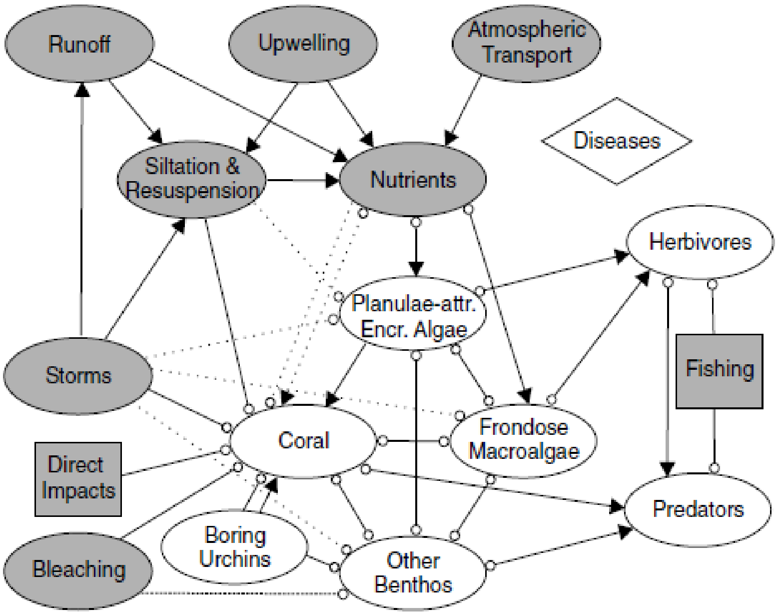

Fig.5 A conceptual model of major factors involved in coral-algal phase shifts with exogenous factors shaded, and anthropogenic factors represented in rectangles. Diseases have been omitted from this model. Circles represent losses, dashed lines represent weak links and arrows represent touching components (McManus & Polsenberg, 2004).

The first factor of importance in reef shifts is the ratio of coral to algae, a reduction in coral abundance doesn't necessarily mean the reef is undergoing a phase shift, however, if the coral cover continues to lower (e.g. due to disease), algae tend to overgrow and fill the reef leaving little to no space for the remaining healthy corals (McManus & Polsenberg, 2004). When corals are weakened, algae tend to colonize them and due to their high morphological plasticity, they are successful in growing in contact with coral tissue. Turf algae can stress, compete with and overgrow the coral *Orbicella* sp. (Dana, 1846) by changing their morphological structure facilitating stability to the algal assemblage (Cetz-Navarro et al., 2015). By settling on coral tissue the algae is participating in phase shifts and contributing as a stress factor by shading and sediment entrapment illustrated in fig 6.

Fig.6 Turf algae projecting in the coral tissue of *Orbicella sp*. with entrapment of sediment (a) and (b) deposition of sediment and shading of the coral tissue (Cetz-Navarro et al., 2015),(photo credit: J. Espinoza-Avalos).

A potentially important factor in reef shifts is nutrients. For corals to grow certain levels of nutrients are needed, however, excessive levels can inhibit new coral settlements (McManus & Polsenberg, 2004). On the other hand, an increase in nutrients promotes algal growth. The balance between coral and algae on a reef is maintained by herbivores that reduce the algal cover. Coral reefs are very similar to a chain reaction, algae is kept at bay by herbivores such as the surgeonfish *Acanthurus coeruleus* (Bloch & J. G. Schneider, 1801), which are reduced by predators (McManus & Polsenberg, 2004). At the same time, some predators feed on corals such as parrot-fish species. Therefore, any perturbation, such as overfishing of herbivorous species, can create a cascading effect and lead to an increase of nutrients in the water and induce a coral-algal phase shift. Vermeij et al. (2010) studied the effects of nutrient enrichment and the impact of herbivore abundance to determine whether these factors promote the coral-algal phase shift. Their experiments showed that in a nutrient-rich environment turf algae became superior and overgrew corals at a rate of 0.34mm 3 wk^{-1} compared to the control where no nutrients were added and the overgrowth rate was 0.12 mm 3 wk^{-1}. When herbivores were excluded, turf algae was still the superior competitor with a growth rate ranging from 0.36 mm 3 wk^{-1} to 0.44 mm 3 wk^{-1}. In the case of CCA presence in reefs, coral fitness is facilitated, the growth rates of corals (1.5-2.5 cm yr^{-1}) are higher than that of CCA. These results promote the idea that slowly but surely with continuous nutrient-enriched water, turf algae can overgrow corals fast even when herbivorous species are present. The presence of turf algae on reefs inhibits the fitness of neighboring corals, as such algal presence in reefs is a key component to the success of coral abundance. Some of the effects exerted by algal turfs in reefs are not visible now, but they will have a high impact on future coral settlements by lowering the fitness of the species when they are in close proximity (Vermeij et al., 2010).

Successful settlement and coral recruitment are crucial for a coral-dominated reef as disease outbreaks are occurring more frequently. Sediment and TA-free environment promotes a healthy and successful coral settlement however in most reefs both algal abundance and sedimentation levels have increased dramatically (Birrell et al., 2005). Birrell et al. (2005) tested the impact of algal turfs and sedimentation on coral settlements depending on algal turf type and presence, and the presence of sediment on *A. millepora*. Their findings show major differences between different turf algal assemblages and whether sediment is present. The two types of turf algae tested were different by means of density and height. Coral-larval settlement showed distinctive differences when sedimentation was added. In the case of denser non-grazed turf the coral settlement rates were extremely low, reaching values of 0. In comparison with grazed algal turf the effects on the settlements were smaller, but when sedimentation was added the rate of larval settlement was reduced whether algae was present or not (figure 7). Taking into consideration the results of Birrell et al. (2005), we can assume that TA does impact coral settlement, however, the fact that it`s capable of sediment entrapment is creating a barrier for coral reproduction.

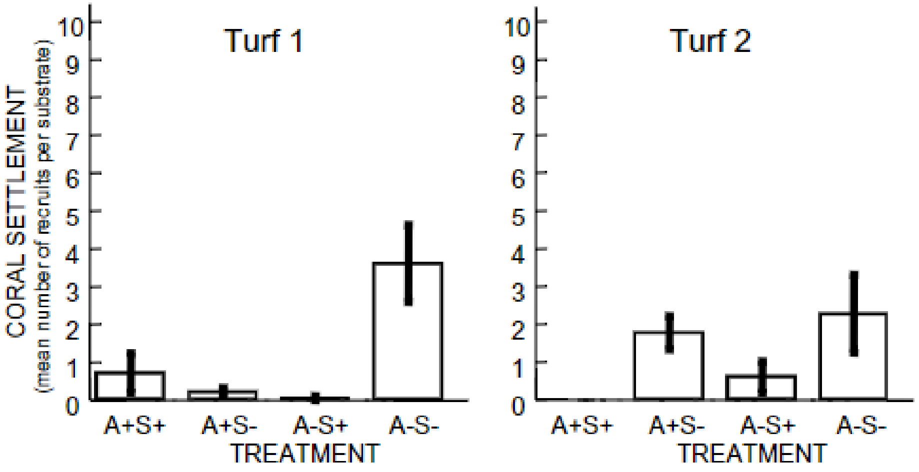

Fig. 7 Experimental settlements of *A. millepora* larvae with different algal turfs (Turf 1 and Turf 2). Graph shows treatments when algal turfs are present (A+) or removed (A-), when sediment was present (S+) or removed (S-) (Birrell et al., 2005).

Speare et al. (2019) shows a negative correlation between abundance in juvenile corals and turf algae cover when sedimentation is present. When no sedimentation is present, there seems to be no relationship between the species abundance. This doesn't necessarily mean that TA has no impact on coral settlement, as multiple studies suggest that they can be suppressed through reducing light, increasing sediment levels (Arjunwadkar et al., 2022), smothering (Fong & Paul, 2011) and allelopathy (Vieira et al., 2016).

4. CORAL DISEASES AND DISEASE INDUCTION:

4.1. Coral health in correlation with algal abundance

White Mat Syndrome (WMS) and Caribbean Yellow-Band Disease (CYBD) are two of the main infectious outbreaks that cause coral mortality in the Caribbean. Over the last decade, these diseases have led to a regional collapse of coral cover. The effects of the disease had negative impacts not only on the coral cover but on an ecosystem level reaching lower numbers of reef inhabitants Sweet et al. (2013). A number of contributing factors lead to these diseases including nutrient pollution, and high ocean temperatures that facilitate infection spread across multiple coral colonies. CYBD is caused by a mix of gram-negative *Vibrio* bacteria and affects corals by causing degradation of their chlorophyll pigments and deformation of the endosymbionts leading to discolored tissue (Vu et al., 2009). Studies showed that overfishing herbivore species has led to an increase in the abundance of reef algae(Wilson et al., 2019). While scleractinian corals are still battling with the disease, algae "helps" by acting as pathogen reservoir or as vectors promoting disease spread (Sweet et al., 2013) and by increasing Dissolved Organic Carbon (DOC) concentrations (Neilan M. Kuntz et al., 2005).

Vu et al. (2009) tested the effects of macroalgae in relation to O. *faveolata* (Ellis and Solander, 1786) affected by yellow-band disease. Their findings show that in the presence of macroalgae the diseases aren't influenced or exacerbated and don`t have an effect on the coral`s fitness. However in the case of WMS, the correlation between the disease and algae has been documented scarcely. The coral *Porites heronensis* (Veron, 1985) found in Japan, suffered outbreaks of WMS that occured during the peak of summer when temperatures are higher. During high temperatures, the macroalgae *Gelidium elegans* (Kützing, 1868) is at its highest abundance suggesting that it could act as a reservoir for WMS pathogens under high temperatures (Heitzman et al., 2022).

Sweet et al. (2013) looked at both diseases in the Caribbean and Indo-Pacific waters in correlation with benthic algae to assess whether the algae can exacerbate the effects of the disease or act as a potential pathogen. Their results show several pathogenic bacteria found in diseased corals are also found in algae, such as *Vibrio sp., Aeromonas sp., Aerobacter sp., Clostridium sp., Pseudoalteromonas sp. Vibrio sp.* was found in thin turf algae and *Dictyota* sp (J.V.Lamouroux, 1809). However, only one species of the genus is associated with triggering yellow-band disease which is not found in healthy coral tissue. Therefore, turf algae could be considered a vector for coral disease. The authors conclude that the majority of bacterial diversity found in corals is similar to the algal bacteria, however, it is probable that in some cases the bacteria residing in corals haven`t yet become pathogenic. In contrast to their findings, ciliated protozoans were detected in algae as well as in the lesions found in corals suffering from the white disease. The protozoan species belonging to the genus *Philaster* sp. *(*Fabre-Domergue, 1885), *Euplotes* sp (O.F. Müller, 1786), and *Varistrombidium* sp. (Xu, Sun, Clamp, Ma & Song, 2011) are capable of ingesting algal symbionts of corals and therefore triggering WMS (Sweet & Bythell, 2012). These results show that algae can be both a vector for disease and a pathogen by transferring pathogenic bacteria to healthy corals.

Algal overgrowth is capable of influencing the health state of corals as well using the same mechanisms to algal-coral contact. Due to already lower immunity caused by diseases, corals can be easily colonized by turf algae and macroalgae. A study by Thinesh et al. (2019) determined the impacts of algal colonization and coral susceptibility to the competitive effects of algae. Their results show that out of 5 coral species found in reefs on the southeast coast of India, only one genus, namely *Porites* (Link, 1807) show tissue lesions and discoloration caused by constant contact with the algae *Halimeda* sp. (J.V.Lamouroux, 1812). *Acropora* sp. (Oken,1815) as well as *Favites sp*. (Link,1807) experienced tissue discoloration at the algal-contact zone. The effects of algal settlement on corals seemed to have no impact on *Symphylia* and *Platygyra (*Ehrenberg, 1834) as seen illustrated in the bar graph (Fig.8).

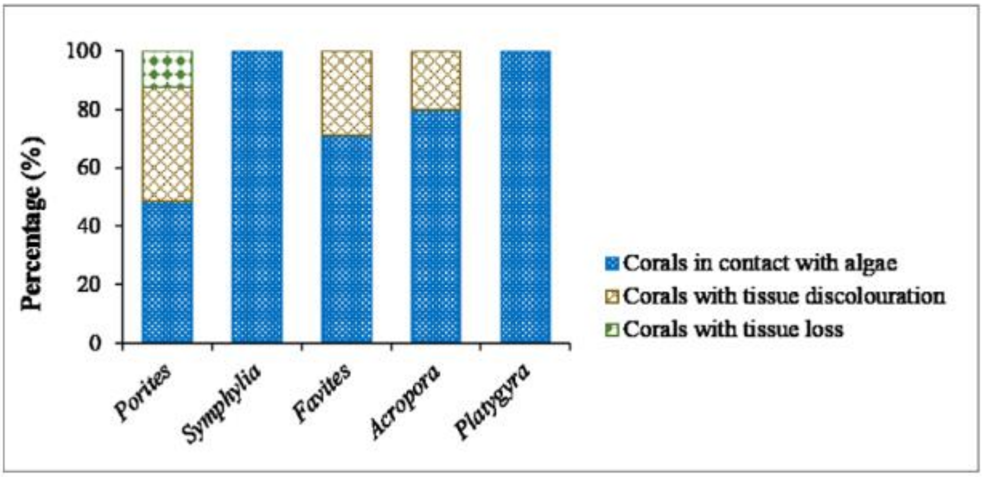

Fig. 8 Halimeda contact and tissue loss in 5 species of corals found in the southwest India coast (Thinesh et al., 2019).

We can therefore assume that the susceptibility for lesions due to algal contact is strictly dependent on algal type as well as coral type. *Porites* colonies left in contact with *Halimeda sp*. most likely experienced tissue loss due to the fact that the algae was shading it, preventing photosynthesis and the coral`s ability to feed. The authors conclude that in absence of herbivorous species to control *Halimeda sp*. distribution, *Porites* corals could become highly vulnerable (Thinesh et al., 2019).

4.2. Indirect effects of algal abundance on corals

The effects of algal abundance in coral reefs have more than just visible effects such as tissue damage and discoloration. The main key to algal-induced mortality in corals is at a microscopic level. Algal contact can trigger microbiome-induced mortality by increasing microbial activity leading to coral stress. In other cases, expulsion or alteration of the composition of their symbiotic microorganisms responsible for photosynthesis (Smith et al., 2006). Smith et al. (2006) studied the effects of algae-mediated, microbe-induced mortality when algae is placed in close proximity to corals. They tested whether algal presence can reduce coral health or induce coral mortality and if the effects are mediated by microbial activity. Their results show that *Pocillopora verrucosa* (Ellis and Solander, 1786) placed in close proximity to the green algae *D. cavernosa* (Forsskål) Børgesen, 1932) experiences major physiological differences reaching 100% coral mortality within 2 days (fig.9).

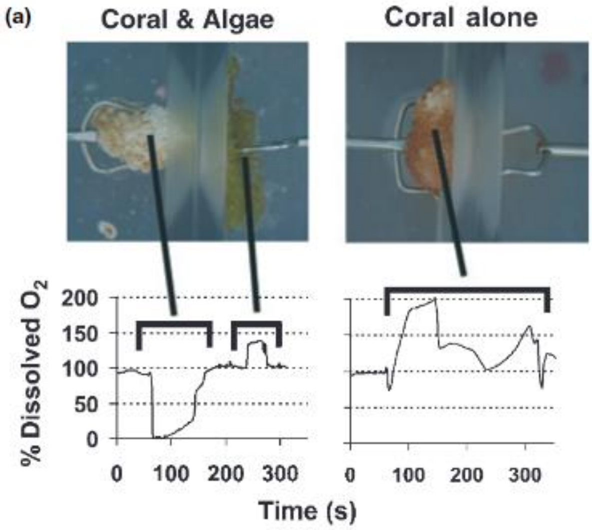

Fig. 9 Algal-coral pair in experimental chambers, Graph showing oxygen microprobe data taken along transects of the organismal surfaces (Smith et al., 2006).

Indirect effects of algal presence near corals include a major reduction in their photosynthetic capacity and due to algal presence, dissolved oxygen levels increase in the water (110-224%). Increased levels of dissolved oxygen lead to a state of stress and malfunction of the photosystem II of their endosymbionts. In contrast, when ampicillin antibiotics were added to the tanks there were no visible effects of reduced coral health. The photosynthetic efficiency was higher compared to the tanks with no antibiotics added (Smith et al., 2006). It can be assumed that it is enough for algae to only be situated near corals in order to initiate stress symptoms.

Pratte et al. (2018) promote the idea that the diversity of bacteria found in healthy coral tissue and at 5 cm away from the algal turf is ~50% less diverse than turf microbiome including turf-coral contact. Furthermore, the bacterial diversity found in turf-algal contacts was very similar to turf microbiome. This suggests that contact with TA can alter the microbiota of corals whereas the algae remain unaffected. The fact that the coral microbiome shifts but the algal microbiome remains the same could mean a potential transfer of turf microbes to the coral.

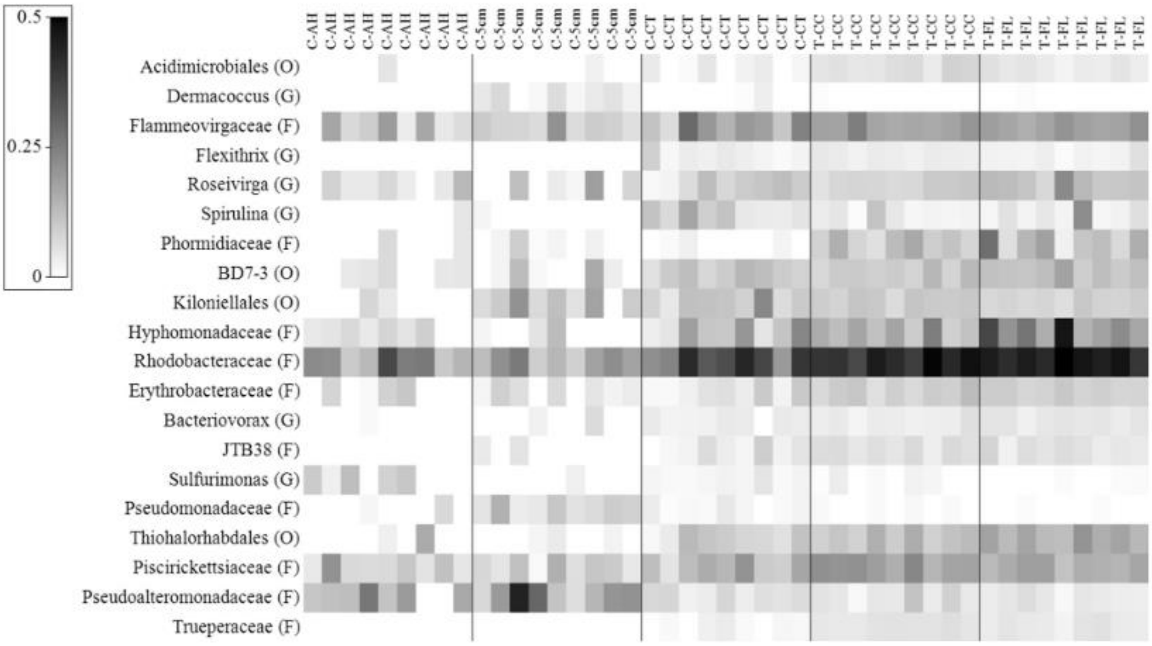

Fig.10 Microbial genera predictive in sample type. On Y axis bacteria is identified at genus level (G), identified at family level (F) or order (O). Treatments found on X axis: C-AH (apparently healthy coral); C-5cm (coral 5cm from the turf); C-CT (coral contacting turf), T-CC (turf contacting coral); T-FL (free-living turf) (Pratte et al., 2018).

In turf algae, *Rhodobacteraceae* family is highly abundant (fig 10) and has been associated with coral disease and bleaching (Roder et al., 2014). In the cases of coral-algal contact, the bacteria has been transferred to corals illustrated in fig.10, showing a major difference in *Rhodobacteraceae* abundance in healthy corals compared to turf-coral contact. A rise in *Rhodobacteraceae* in corals can mean a decline in health at the contact point. Samples of healthy corals and corals kept 5 cm away from turf algae had the same microbial composition when compared, therefore it can be assumed that in order to alter the microbial communities in corals, contact is necessary (Pratte et al., 2018).

4.3. Changes in coral-associated bacteria under algal pressure

Algal pressure can be categorized as a potential pathogen for corals due to triggering significant shifts in microbial diversity at the contact point with corals and acting as a vector for potential pathogenic species. As previously pointed out by Pratte et al. (2018) in order to change bacterial community composition in corals, algal touch is required. Briggs et al. (2021) show that in response to algal contact, 85% of microbial families found in coral's microbiota are changing in abundance. In response to both algal contact and abundance in site-level macroalgal cover 6/40 families showed shifts in abundance (Fig.11). Turf algae had a lower impact than macroalgae, however, 75% of families still exhibited the same response.

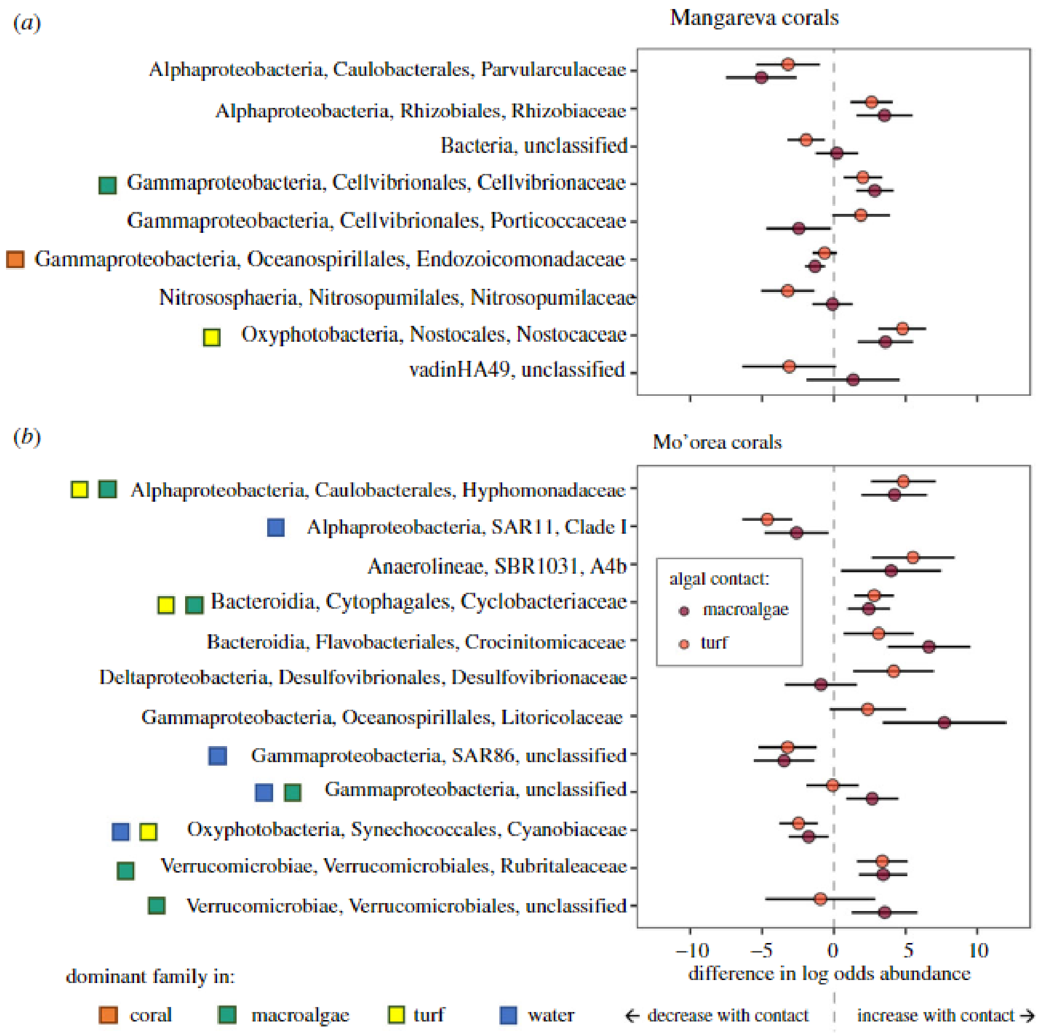

Fig.11 Microbial families that changed in response to algal contact (Briggs et al., 2021).

Lu et al. (2022) looked at the trends in bacterial diversity from three coral genera. The corals (fig.12) had healthy tissue (HH) and areas of algal growth (AA). Their results show differences in microbial communities and abundance between HH, AA, and coral-algae contact point (HA). Bacterial communities are known to influence the growth, development, and reproduction of corals, however, due to algal contact their community structure can change. The differences found between the HH and HA samples showed significant differences both in diversity and species richness from normal coral-associated bacteria (fig.12) (Lu et al., 2022).

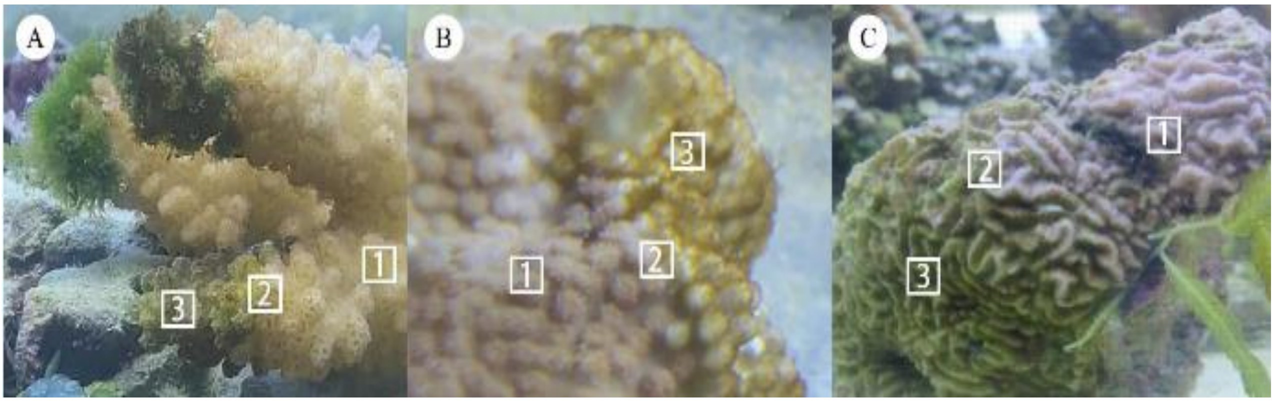

Fig. 12 (A) *Pocillopora sp* (B) *Montipora sp.* (C) *Pavona* sp (incorrectly identified as Platygyra), 1- HH; 2- HA; 3- AA (Lu et al., 2022).

The differences in diversity and richness were similar between coral genera however the degree of change to the bacterial communities was different suggesting a species-specific stress response. In HH corals *Proteobacteria* had a high relative abundance (fig.13) compared to the samples of algae (AA), with *alphaproteobacteria* being the most abundant. Previous studies show that high levels of *Proteobacteria* are consistent with stress factors (Pratte et al., 2018). High abundances in *Rhodobacteraceae* are lower in HH samples than in HA or AA samples, this can indicate an increase in stress under algal contact. As it was previously discussed *Rhodobacteraceae* can trigger the white syndrome. The family *Alteromonadaceae,* which has previously been linked to white plaque disease (WPD) (Sunagawa et al., 2009) was found more abundant at the contact point between the algae and the coral and in the AA samples. Consequently, the authors conclude that increased levels of *Rhodobacteraceae* and *Alteromonadaceae* favor algal pressure and growth leading to opportunistic colonization (Lu et al., 2022).

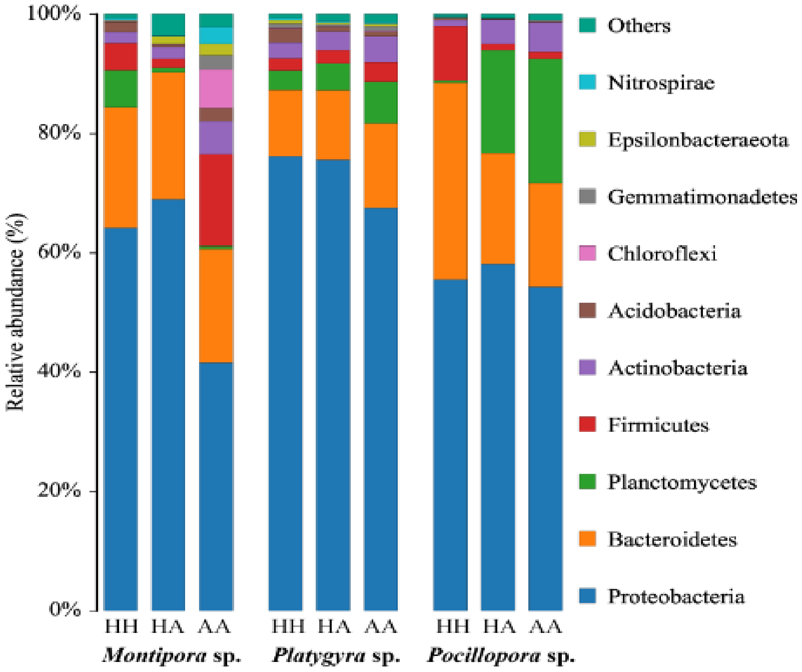

Fig. 13 Abundance (%) of major bacterial communities of corals sampled (Lu et al., 2022).

Similarly, to the results of Pratte et al. (2018), an increase in bacterial diversity at the contact point is shown by Roach et al. (2020) where the bacterial groups found at contact-level had their own unique functional taxonomic and metabolic profiles. The groups found at the algal-coral contact point were however much closer to an algal microbiome than a coral one with a high level of abundance in *Bacteroidetes* and *Firmicutes* which are commonly found in algae. The authors conclude that exhibiting high levels of the two bacterial groups can be a significant predictor of whether the coral is going to lose the battle for space against its algal competitor (Roach et al., 2020).

5. IMPORTANCE AND CONSERVATION MEASURES

5.1. Changes in the reef ecosystem due to coral decline.

Corals are the foundation of reefs with scleractinian corals being the major contributors to reef structure. Due to the coral cover decline that has been ongoing for a long time and facilitated by algal competition, coral reefs are heading to habitat loss and a decline in biodiversity (Pandolfi et al., 2003). In fish, response to coral loss varies between species, however herbivores, carnivores, and planktivores seem to have a higher response than corallivores (Pratchett et al., 2014). Consequently, a rise in herbivores has been noticed in reefs following a major coral loss event (Fig. 14).

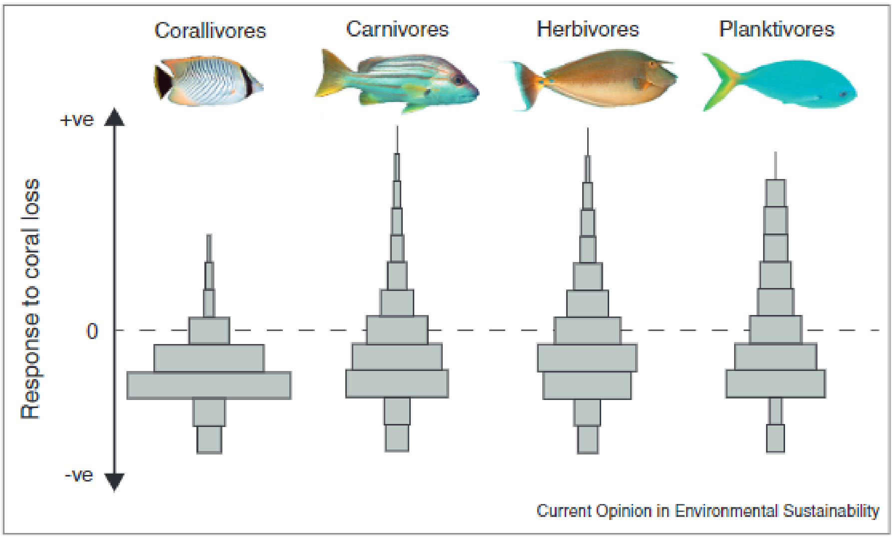

Fig. 14 Response in diversity within primary functional groups of fishes in reefs based on disturbances that cause >10% decline in coral cover (Pratchett et al., 2014).

Cheal et al. (2008) looked at responses of reef fish communities in correlation with coral decline on the Great Barrier reef. Their results show a decrease (8%) in species that feed on corals and in coral-dependent species (20.19%). However, 79% of species that declined in abundance were not coral-dependent, hence coral loss can affect a wider range of species that possibly use the reef as a nursery.

Similarly, to Pratchett et al. (2014), herbivores are noticed to increase in abundance in accordance with the rise of algal abundance. Migratory species are not heavily affected by the coral decline, but site-attached species such as damselfishes are impacted on a greater scale by coral loss showing 64% differences in worst-case reefs examined by Pratchett et al (2014).

5.2. Introduction of sea urchin *Diadema antillarum*

Due to the high increase in algal cover in reefs, it is important to look at conservational measures in order to protect or facilitate coral recovery. The sea urchin *Diadema antillarum* (Philippi, 1845), a keystone species that feeds on reef algae has seen major abundance declines due to disease(Lessios, 1988).

Williams (2022) looked at ways to restore sea urchins in reefs as a method of control for algal abundance. The species were grown in the lab and reintroduced in four reefs in Puerto Rico. The sites before *D. antillarum* was introduced showed no possibility for coral recruitment due to high levels of sedimentation and abundant turf and macroalgae. The results show a promising effect after the reintroduction of the sea urchin by reducing macroalgal cover by 88% (fig.15) in two months and showing positive effects for coral recruitment. During their study, coral recruitment didn't show much improvement however three small recruits were observed in one coral that was previously covered by macroalgae. The author hypothesized that by reintroducing the keystone species, the likelihood of survival for coral recruits could increase.

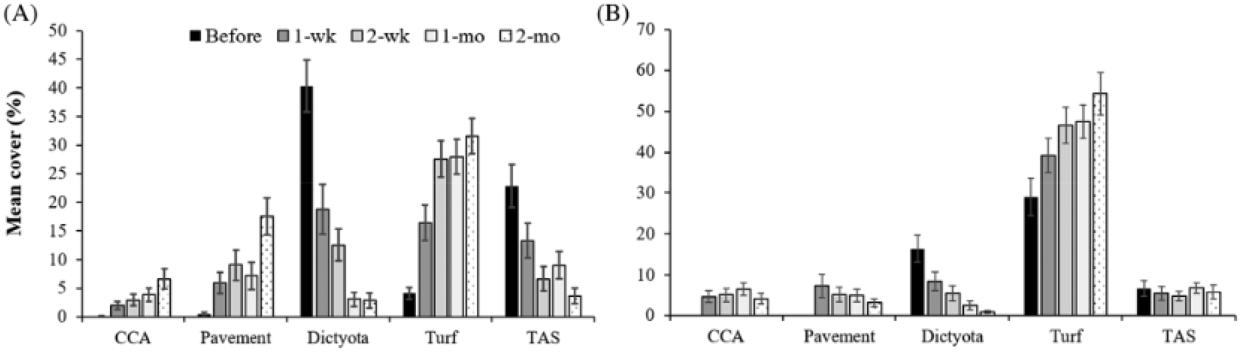

Fig. 15 Mean cover of benthic substrate inside the corals with *D. antillarum* throughout sampling time in (A) El Coral reef and (B) Mario reef in La Parguera, Purto Rico. Turf algae have sediment present (Williams, 2022).

6. DISCUSSION AND CONCLUSIONS

Coral cover has suffered a major decline, either due to natural stressors, diseases such as yellow-band disease, white mat syndrome, or white-band disease and because of global warming the rates of disease expansion will continue. This literature review shows that turf algae can become either a coral pathogen or a vector for pathogens.

Turf algae and macroalgae have always been in competition for space with corals, and because the coral abundance is in decline, they have the opportunity to shift the reefs and become the dominant species (de Carvalho & Villaça, 2021). The reef`s ability to shift to an algal dominated reef is also dependable on external factors such as rainy and dry season that increase nutrient levels. During the rainy seasons, the reefs in Columbian Carribean were dominated by algal turfs (43% cover) with very low macroalgae cover (<20%). However, during the upwelling periods (August and February) macroalgae predominated with 44% cover. It is important to take into account algal abundance differences due to seasonality in order to assess their impact on coral reefs (Diaz-Pulido & Garzón-Ferreirab, 2002).

Depending on the mechanism of affliction, algae can trigger different symptoms in corals. In table 1 are presented all mechanisms and effects reviewed in this essay. It can be noted that however there are many ways for algae to negatively impact coral health, only in the case of coral *O. faveolata* with YBD, algae abundance didn't exacerbate the disease (Vu et al., 2009). At the same time, it doesn't leave any space for recovery. Algal contact has an impact on coral health, however, it has been proven (Smith et al., 2006) that in some cases the algae doesn't have to have direct contact to initiate a stress response.

Table 1. Impact of different algal species on corals with their main affliction mechanism and corresponding direct and indirect effects with study source.

Algal species	**Coral species**	**Mechanism of affliction**	**Direct effect**	**Indirect effect**	**Reference**
Turf algae, Macroalgae	**Scleractinian corals**	• Competition	• Shift to an algal dominated reef	• Loss of coral species and biodiversity in reefs	(McManus & Polsenberg, 2004)
Turf algae, red algae brown algae Seaweed	**Most scleractinian corals and octocorals**	• Abrasion through algal-contact	• Tissue lesions and depigmentation	• Microbial growth and coral bleaching	(Rasher & Hay, 2010)
H. opuntia (J.V.Lamouroux, 1816)	**O. faveolata** (Ellis and Solander, 1786)	• Direct algal	• White plague type II	• Restricting photosynthetic capacity	(Nugues et al., 2004)
Lobophora sp. (J.V.Lamouroux, 1817)	**Porites** (Link, 1807)	• allelopathy	• Expulsion of endosymbionts leading to • coral bleaching	• Secondary metabolites with antimicrobial properties affecting coral microbiome	(Vieira et al., 2016)
Turf algae	**Orbicella sp.** (Dana, 1846)	• Overgrowth	• Shading • Colonization • Algal-coral contact • Sediment entrapment and deposition	• Low chances of recovery or new coral settlements.	(Cetz-Navarro et al., 2015)
Turf algae	**Acropora millepora** (Ehrenberg, 1834)	• Sediment deposition	• Low chances of successful settlements	• Shading and tissue damage	(Birrell et al., 2005; Speare et al., 2019)
Macroalgae	***Orbicella faveolata*** (Ellis and Solander, 1786***)*** **with YBD**	• No interference	• No effect	• No effect	(Vu et al., 2009)
Halimeda sp. (J.V. Lamouroux, 1816)	**Acropora sp. (**Oken, 1815) **Favites sp.** (Link, 1807)	• Direct algal contact	• Tissue discoloration at the contact point	• No effect	(Thinesh et al., 2019)

D. cavernosa ((Forsskål) Børgesen, 1932)	**P. verrucosa** (Ellis and Solander, 1786)	• Algal presence in proximity to coral	• Bleaching • Microbiome induced mortality	• Bacterial community shifts in both diversity and abundance • Reduction of photosynthetic capacity	(Smith et al., 2006)
Algae growing on the coral	**Pocillopora sp.** (Lamarck, 1816) **Montipora sp.** (Blainville, 1830) **Pavona sp.** **(**Lamarck, 1801) **(Platygyra sp. in the paper)**	• Overgrowth • Algal contact	• Depigmentation at contact point	• Shifts in bacterial diversity, coral microbiome very similar to algal microbiome instead of healthy coral microbiome.	(Lu et al., 2022)
Turf algae	**Diploria strigosaor** (Dana, 1846) **Orbicella faveolate** (Ellis and Solander, 1786)	• Algal-coral contact	• Potential trigger of WPD by increase of Alteromonadaceae • Potential trigger or WS due to increase in Rhodobacteraceae	• Increase in Rhodobacteraceae at the contact point • Increase in Alteromonadaceae • Both families favor algal growth and opportunistic colonization	(Pratte et al., 2018)

Most algal species negatively impact corals, however, turf algae has been noticed to have a bigger impact because it uses multiple mechanisms of affliction. Most common negative impact (table 1) is through direct algal-coral contact through which the coral experiences tissue discoloration or lesions. In some cases, turf algae can trigger WPD or WS in corals through contact. Algal presence can interfere with coral endosymbionts by reducing their photosynthetic capacity (Smith et al., 2006). Through high abundance and sediment deposition, turf algae restricts the capacity of reproduction and the development of new coral settlements (Birrell et al., 2005).

Algae`s ability to shift the microbiome diversity or transfer bacterial communities to the coral is a possible research outlook into indirect effects of algal abundance. Perturbances in the normal microbiota of corals can happen due to natural disturbances as well, such as high temperatures (Bourne et al., 2009). After algal-coral contact, the microbial diversity of corals becomes more similar to an algal microbiome than a healthy coral microbiome (table 1). By increasing the abundance of bacterial families or introducing families that aren`t commonly found in coral microbiota, algae can potentially be a vector for disease. Determining which pathogenic bacteria is transferred to corals during algal-coral contact could improve our understanding on engineering disease resistant coral species.

To conclude, understanding the mechanisms and effects of disease induction through algal vectors is important in order to effectively manage the remaining healthy coral reefs. By undestanding the factors that promote disease outbreaks, future research can be directed towards disease-resistant coral species. Meanwhile, a measure of protection and reef management for algal abundance control is the reintroduction of keystone species such as *D. antillarum* or other herbivore fish.

7. REFERENCES

1. Arjunwadkar, C. v., Tebbett, S. B., Bellwood, D. R., Bourne, D. G., & Smith, H. A. (2022). Algal turf structure and composition vary with particulate loads on coral reefs. *Marine Pollution Bulletin*, *181*. https://doi.org/10.1016/j.marpolbul.2022.113903
2. Birrell, C. L., McCook, L. J., & Willis, B. L. (2005). Effects of algal turfs and sediment on coral settlement. *Marine Pollution Bulletin*, *51*(1–4), 408–414. https://doi.org/10.1016/j.marpolbul.2004.10.022
3. Bourne, D. G., Garren, M., Work, T. M., Rosenberg, E., Smith, G. W., & Harvell, C. D. (2009). Microbial disease and the coral holobiont. In *Trends in Microbiology* (Vol. 17, Issue 12, pp. 554–562). https://doi.org/10.1016/j.tim.2009.09.004
4. Briggs, A. A., Brown, A. L., & Osenberg, C. W. (2021). Local versus site-level effects of algae on coral microbial communities. *Royal Society Open Science*, *8*(9). https://doi.org/10.1098/rsos.210035
5. Cetz-Navarro, N. P., Quan-Young, L. I., & Espinoza-Avalos, J. (2015). Morphological and community changes of turf algae in competition with corals. *Scientific Reports*, *5*. https://doi.org/10.1038/srep12814
6. Cheal, A. J., Wilson, S. K., Emslie, M. J., Dolman, A. M., & Sweatman, H. (2008). Responses of reef fish communities to coral declines on the Great Barrier Reef. *Marine Ecology Progress Series*, *372*, 211–223. https://doi.org/10.3354/meps07708
7. Connell, S. D., Foster, M. S., & Airoldi, L. (2014). What are algal turfs? Towards a better description of turfs. In *Marine Ecology Progress Series* (Vol. 495, pp. 299–307). https://doi.org/10.3354/meps10513
8. de Carvalho, L. L., & Villaça, R. C. (2021). Effect of fine-scale habitat differences on algal colonisation in a coral-dominated subtropical reef. *Anais Da Academia Brasileira de Ciencias*, *93*(3). https://doi.org/10.1590/0001-3765202120191191

9. Eddy, T. D., Lam, V. W. Y., Reygondeau, G., Cisneros-Montemayor, A. M., Greer, K., Palomares, M. L. D., Bruno, J. F., Ota, Y., & Cheung, W. W. L. (2021). Global decline in capacity of coral reefs to provide ecosystem services. *One Earth*, *4*(9), 1278–1285. https://doi.org/10.1016/j.oneear.2021.08.016

10. Evans, R. D., Wilson, S. K., Fisher, R., Ryan, N. M., Babcock, R., Blakeway, D., Bond, T., Dorji, P., Dufois, F., Fearns, P., Lowe, R. J., Stoddart, J., & Thomson, D. P. (2020). Early recovery dynamics of turbid coral reefs after recurring bleaching events. *Journal of Environmental Management*, *268*. https://doi.org/10.1016/j.jenvman.2020.110666

11. Fong, P., & Paul, V. J. (2011). Coral reef algae. In *Coral Reefs: An Ecosystem in Transition* (pp. 241–272). Springer Netherlands. https://doi.org/10.1007/978-94-007-0114-4_17

12. G. Diaz-Pulido a, & J. Garzón-Ferreirab. (2002). Seasonality in Algal Assemblages on Upwelling-influenced Coral Reefs in the Colombian Caribbean. *Botanica Marina , Vol. 45*, 284–292. https://doi.org/https://doi.org/10.1515/BOT.2002.028

13. Heitzman, J. M., Caputo, N., Yang, S. Y., Harvey, B. P., & Agostini, S. (2022). Recurrent disease outbreak in a warm temperate marginal coral community. *Marine Pollution Bulletin*, *182*, 113954. https://doi.org/10.1016/J.MARPOLBUL.2022.113954

14. Lessios, H. A. (1988). Mass Mortality of Diadema Antillarum in the Caribbean: What Have We Learned? In *Source: Annual Review of Ecology and Systematics* (Vol. 19). https://www.jstor.org/stable/2097159

15. Lu, C., Zhang, Q., Huang, Q., Wang, S., Qin, X., Ren, T., Xie, R., & Su, H. (2022). Significant Shifts in Microbial Communities Associated with Scleractinian Corals in Response to Algae Overgrowth. *Microorganisms*, *10*(11), 2196. https://doi.org/10.3390/microorganisms10112196

16. McManus, J. W., & Polsenberg, J. F. (2004). Coral-algal phase shifts on coral reefs: Ecological and environmental aspects. In *Progress in Oceanography* (Vol. 60, Issues 2–4, pp. 263–279). https://doi.org/10.1016/j.pocean.2004.02.014

17. Muñiz-Castillo, A. I., Rivera-Sosa, A., Chollett, I., Eakin, C. M., Andrade-Gómez, L., McField, M., & Arias-González, J. E. (2019). Three decades of heat stress exposure in Caribbean coral reefs: a new regional delineation to enhance conservation. *Scientific Reports*, *9*(1). https://doi.org/10.1038/s41598-019-47307-0

18. Neilan M. Kuntz, David I. Kline, Stuart A. Sandin, & Forest Rohwer. (2005). Pathologies and mortality rates caused by organic carbon and nutrient stressors in three Caribbean coral species. *MARINE ECOLOGY PROGRESS SERIES*, *294*, 173–180. https://doi.org/doi:10.3354/meps294173

19. Nugues, M. M., Smith, G. W., van Hooidonk, R. J., Seabra, M. I., & Bak, R. P. M. (2004). Algal contact as a trigger for coral disease. *Ecology Letters*, *7*(10), 919–923. https://doi.org/10.1111/j.1461-0248.2004.00651.x

20. Pandolfi, J. M., Bradbury, R. H., Sala, E., Hughes, T. P., Bjorndal, K. A., Cooke, R. G., McArdle, D., McClenachan, L., Newman, M. J. H., Paredes, G., Warner, R. R., & Jackson, J. B. C. (2003). Global trajectories of the long-term decline of coral reef ecosystems. *Science*, *301*(5635), 955–958. https://doi.org/10.1126/science.1085706

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

22. Pratte, Z. A., Longo, G. O., Burns, A. S., Hay, M. E., & Stewart, F. J. (2018). Contact with turf algae alters the coral microbiome: contact versus systemic impacts. *Coral Reefs*, *37*(1), 1–13. https://doi.org/10.1007/s00338-017-1615-4

23. Rasher, D. B., & Hay, M. E. (2010). Seaweed allelopathy degrades the resilience and function of coral reefs. *Communicative & Integrative Biology*, *3*(6), 564–566. https://doi.org/10.4161/cib.3.6.12978

24. Roder, C., Arif, C., Bayer, T., Aranda, M., Daniels, C., Shibl, A., Chavanich, S., & Voolstra, C. R. (2014). Bacterial profiling of White Plague Disease in a comparative coral species framework. *ISME Journal*, *8*(1), 31–39. https://doi.org/10.1038/ismej.2013.127

25. Smith, J. E., Shaw, M., Edwards, R. A., Obura, D., Pantos, O., Sala, E., Sandin, S. A., Smriga, S., Hatay, M., & Rohwer, F. L. (2006). Indirect effects of algae on coral: Algae-mediated, microbe-induced coral mortality. *Ecology Letters*, *9*(7), 835–845. https://doi.org/10.1111/j.1461-0248.2006.00937.x

26. Speare, K. E., Duran, A., Miller, M. W., & Burkepile, D. E. (2019a). Sediment associated with algal turfs inhibits the settlement of two endangered coral species. *Marine Pollution Bulletin*, *144*, 189–195. https://doi.org/10.1016/j.marpolbul.2019.04.066

27. Speare, K. E., Duran, A., Miller, M. W., & Burkepile, D. E. (2019b). Sediment associated with algal turfs inhibits the settlement of two endangered coral species. *Marine Pollution Bulletin*, *144*, 189–195. https://doi.org/10.1016/J.MARPOLBUL.2019.04.066

28. Sunagawa, S., Desantis, T. Z., Piceno, Y. M., Brodie, E. L., Desalvo, M. K., Voolstra, C. R., Weil, E., Andersen, G. L., & Medina, M. (2009). Bacterial diversity and white Plague disease-associated community changes in the caribbean coral montastraea faveolata. *ISME Journal*, *3*(5), 512–521. https://doi.org/10.1038/ismej.2008.131

29. Sweet, M., & Bythell, J. (2012). Ciliate and bacterial communities associated with White Syndrome and Brown Band Disease in reef-building corals. *Environmental Microbiology*, *14*(8), 2184–2199. https://doi.org/10.1111/j.1462-2920.2012.02746.x

30. Sweet, M. J., Bythell, J. C., & Nugues, M. M. (2013). Algae as Reservoirs for Coral Pathogens. *PLoS ONE*, *8*(7). https://doi.org/10.1371/journal.pone.0069717

31. Tebbett, S. B., & Bellwood, D. R. (2019). Algal turf sediments on coral reefs: what's known and what's next. In *Marine Pollution Bulletin* (Vol. 149). Elsevier Ltd. https://doi.org/10.1016/j.marpolbul.2019.110542

32. Thinesh, T., Jose, P. A., Ramasamy, P., Meenatchi, R., Selvan, K. M., & Selvin, J. (2019). Differential coral response to algae contact: Porites tissue loss, praise for Halimeda interaction at southeast coast of India. *Environmental Science and Pollution Research*, *26*(17), 17845–17852. https://doi.org/10.1007/s11356-019-05024-1

33. Ty N.F. Roach, Mark Little, Milou G.I. Arts, Joel Huckebae, Andreas F. Haasf, Emma E. Georgeh, & Robert A. Quinn. (2020). A multiomic analysis of in situ coral-turf algal interactions. *117*. https://doi.org/10.1073/pnas.1915455117/-/DCSupplemental

34. Vermeij, M. J. A., van Moorselaar, I., Engelhard, S., Hörnlein, C., Vonk, S. M., & Visser, P. M. (2010). The effects of nutrient enrichment and herbivore abundance on the ability of turf algae to overgrow coral in the Caribbean. *PLoS ONE*, *5*(12). https://doi.org/10.1371/journal.pone.0014312

35. Vieira, C., Thomas, O. P., Culioli, G., Genta-Jouve, G., Houlbreque, F., Gaubert, J., de Clerck, O., & Payri, C. E. (2016). Allelopathic interactions between the brown algal genus Lobophora (Dictyotales, Phaeophyceae) and scleractinian corals. *Scientific Reports*, *6*. https://doi.org/10.1038/srep18637

36. Vu, I., Smelick, G., Harris, S., Lee, S. C., Weil, E., Whitehead, R. F., & Bruno, J. F. (2009). Macroalgae has no effect on the severity and dynamics of Caribbean yellow band disease. *PLoS ONE*, *4*(2). https://doi.org/10.1371/journal.pone.0004514

37. Wells, C. D., Ngela Martínez-Quintana, • A. Tonra, K. J., & Lasker, H. R. (2022). Algal turf negatively affects recruitment of a Caribbean octocoral. https://doi.org/10.1007/s00338

38. Wild, C., Jantzen, C., & Kremb, S. G. (2014). Turf algae-mediated coral damage in coastal reefs of Belize, Central America. *PeerJ*, *2014*(1). https://doi.org/10.7717/peerj.571

39. Williams, S. M. (2022). The reduction of harmful algae on Caribbean coral reefs through the reintroduction of a keystone herbivore, the long-spined sea urchin *Diadema antillarum*. *Restoration Ecology*, *30*(1). https://doi.org/10.1111/rec.13475

40. Wilson, S. K., Robinson, J. P. W., Chong-Seng, K., Robinson, J., & Graham, N. A. J. (2019). Boom and bust of keystone structure on coral reefs. *Coral Reefs*, *38*(4), 625–635. https://doi.org/10.1007/s00338-019-01818-4