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# The Fate of Corals: Will They Overcome Competition with Algae and Cyanobacteria in a Changing Environment?

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## Abstract

Coral reefs provide substantial ecological and economic services to coastal communities in the tropics. Hence, there is a great concern about the permanence of these ecosystems and the consequent loss of the economic, ecological and social services coral reefs provide due to their susceptibility to natural and anthropogenic threats. Large-scale processes such as strong El Niño Southern Oscillation events, global warming and ocean acidification represent significant challenges for coral reefs. Benthic cyanobacteria and seaweed have substantially increased in reef areas, facilitated by excessive nutrient input, reduction in herbivore populations and global warming. This review briefly describes the currently known aspects of coral, algae and cyanobacterial interactions, as well as the local and global environmental and ecological aspects that have caused the increase of algae and cyanobacteria in detriment to reef corals. Reef communities will keep changing in the light of large-scale events and anthropogenic influences. As short-term measures, ambitious programs for grazer reintroduction could help curb population growth of algae and cyanobacteria. Medium- to long-term measures should be oriented at limiting nutrient input to water bodies.

**Keywords:** cyanobacteria, algae, coral reefs, competition, phase changes

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## 1. Introduction

Coral reefs constitute one of the most important, diverse and productive ecosystems in the planet. These ecosystems provide a great number of goods as well as economic and ecological services. Coral reefs protect coastal areas such as seagrasses and mangroves from erosion [1–3].

Coral reefs supply different food sources to coastal communities and also provide habitat for fish, molluscs and crustaceans of commercial interest [4–6]. Coral reefs also harbor a large diversity of microorganisms, algae and invertebrates that have provided researchers, the pharmaceutical, nutraceutical and cosmeceutical industries with many interesting bioactive molecules [7, 8].

Currently, the oceans are suffering remarkable changes evidenced by the increase and intensity of diseases, mass mortalities and blooms of several photosynthetic organisms. All these events have occurred in both disturbed and undisturbed areas around the globe (reviewed in [9]). Among some of the causes that have been linked to these events are global warming, increased UV radiation, overfishing, pollution and coastal eutrophication and oxygen depletion. However, some of all these factors may act in a synergistic manner rather than in isolation, considering that there are large spatial and temporal scales involved in all those processes [9–11].

Degradation of coral reefs has increased considerably world-wide, at least for which there are records of the phenomenon, since there is no consensus of what a pristine reef is [12]; therefore, it is very hard to assess the magnitude of changes and impacts compared to “base line” conditions [13]. Reef degradation has been linked to human activities and impacts; hence, there is a great concern about the permanence of these ecosystems and the consequent loss of the economic, ecological and social services coral reefs provide [14–16]. Moreover, large-scale processes such as the incidence of strong El Niño Southern Oscillation [ENSO] events, global warming and ocean acidification represent an enormous challenge for coral reefs to survive and remain as we know them today [17].

## 2. Cyanobacteria in reefs

Cyanobacteria are eubacteria with photosynthetic capabilities considered as “primitive microalgae” for a long time. These are ancient organisms dating back to 3.5 billion years as evidenced by their fossil record, particularly in stromatolites [18]. Recent molecular data have revealed that cyanobacteria are a polyphyletic group, and taxa, traditionally grouped by having similar morphologies, have different phylogenetic affiliations [19–22]. Cyanobacteria have a wide distribution in terrestrial and aquatic environments. Some taxa are involved in close symbiotic relationships with diatoms, sponges, corals, lichens and plants such as water ferns and cycads [23–26]. Many cyanobacteria are able to fix atmospheric nitrogen, making a significant contribution of this element into environments where it is usually limiting [27–30].

Marine benthic cyanobacteria thrive in a wide variety of habitats including rocky coastlines, sandy beaches, mangroves, marshes and swamps. The distribution of cyanobacterial mats is influenced by sediment type, tidal exposure and wave energy [31]. In coral reefs, given their abundance at certain times and locations, cyanobacteria may play a similar role to algae in terms of primary production and interactions with herbivores [32].

Cyanobacteria have long been regarded as regular elements of tropical marine communities and for that reason included in floristic lists from a number of tropical regions worldwide [33–35]. However, blooms of marine benthic cyanobacteria have become frequent in coastal areas receiving significant nutrient input from runoff and groundwater, as well as a result of large-scale climatic and hydrological changes [10, 11, 26, 36, 37]. Cyanobacterial blooms, toxin production and derived health risks are currently considered a public health hazard [38–43].

Blooms of marine benthic cyanobacteria grow on the substrate forming dark flimsy mats, usually red, purple, brown or black. There are several reports of marine benthic cyanobacteria blooms in several sites in the Pacific, in the island of Guam [44–46], in some Micronesian atolls and also in the Hawaiian Islands [50]. In the Atlantic, cyanobacterial blooms are a recurrent event strongly subject to seasonality in the state of Florida [51, 52]. In the Caribbean, there are reports from Puerto Rico [53], the Bahamas, Belize and the Virgin Islands [52], and the Colombian Caribbean [35, 54, 55]. Cyanobacterial blooms not only occur in coral reefs but also in seagrass meadows [56–58], mangroves [56, 57], estuaries and coastal lagoons [59].

Blooms in Guam and Australia, due to their extension, persistence and toxicity, have caused mass mortalities of fishes, as well as significant economic losses and health problems in residents or visitors to coastal areas. Marine turtles and manatees are also impacted by these blooms due to toxin exposure [60, 61]. Additionally, benthic cyanobacteria are often the dominant organisms that colonize coral skeletons after bleaching events [62]. Although several species of cyanobacteria grow in microbial mats, these tend to be dominated by a single species, although the reasons by which a species dominates over the other(s) are not yet entirely clear [63]. Additionally, cyanobacteria and turf algae may prevent or inhibit the settlement of coral larvae [50, 64–67]. The increasing occurrence, frequency and intensity of benthic cyanobacterial blooms, is now considered a great threat to coral reefs around the world [51]. Benthic cyanobacteria most commonly linked to bloom formation are included in the orders Chroococcales and Oscillatoriales, with the most common genera being *Schizothrix*, *Hormothamnion*, *Oscillatoria* and *Lyngbya* [68]. *Lyngbya*, in particular, is probably the most studied genus for which there is a great number of bloom reports and whose chemistry and chemical ecology are better documented [44, 45, 69–75]. However, recent studies have reassessed the phylogenetic affiliation of this genus finding that it is a rather diverse complex of species now reassigned into the genera *Moorea*, *Okeania* or *Lyngbya*, which may explain the vast chemical complexity of what used to be considered a single genus [19–22]. Although the taxonomy of the group has changed substantially, for the purpose of this review, I will refer to the names that were originally assigned in the papers where they were described.

Blooms of benthic cyanobacteria develop fast, covering vast areas in a period of few weeks. In those events, cyanobacteria grow on the substrate forming mats that can smother benthic organisms. As the bloom progresses, it can turn adjacent sediment and waters anoxic [49]. Cyanobacterial detachment from the sediment, either by flotation or wave action, may promote their dispersion [49, 68].

### 3. Algae in reefs

Algae are very important members of reef communities where they provide food and refuge to many organisms. They are also the basis of the reef food web [76]. Due to their different phylogenetic affiliations, varying forms and functions, algae are classified into three large functional groups based on growth form and size, ecological characteristics, toughness, susceptibility to herbivores and photosynthetic abilities. Functional groups are used to characterize algal communities in coral reefs and to understand their distribution and responses to environmental factors [76].

Filamentous and small algae with fast growth rates are included in the turf algae category. Multispecies assemblages of turf algae can be very abundant in reefs despite their low biomass. They are an attractive food source for several herbivores, preventing their overgrowth. Cyanobacteria are also included in this category [76]. The next category, fleshy macroalgae, is commonly known as seaweeds and includes the most well-known forms. Seaweed can be very abundant in reefs and have several adaptations to avoid herbivory [77–79]. A third category, coralline or crustose algae, secretes calcium carbonate and is important in cementing the reef framework but also in attracting coral recruits [80, 81].

### 4. Factors favoring the growth of algae and cyanobacteria in reefs

Competition for light and space between benthic algae and corals affects coral resilience and is essential when assessing the degree of reef health [65, 76]. In healthy coral reefs, reduced nutrient availability and high grazing pressure are the most important factors controlling the growth of algal turf and fleshy algae [82]. Phase shifts or phase changes are evident by a decrease in the cover and recruitment of corals compared to the colonization and substrate cover by turf algae, seaweed and cyanobacteria [14, 65, 83]. Phase shifts are common in many degraded reefs due to disparity in coral-algal interactions [15, 76, 86]. Under stressful conditions, favored by bleaching events, partial mortality or reduced grazing pressure, algae and cyanobacteria become competitively superior to corals, eventually overgrowing and killing them [15, 87].

Alleged causes linked to cyanobacterial blooms in fresh and brackish waters have been thoroughly studied (reviewed in [88]). However, blooms of marine benthic cyanobacteria are not understood that well. Normally, they occur in shallow waters, and environmental factors such as high temperatures, reduced wave action and the availability of phosphorus, nitrogen and iron have been linked to their formation [48, 49, 66, 89, 90]. Individual strains of cyanobacteria vary greatly in their bloom dynamics, which in some cases may be controlled by physical disturbances rather than nutrient availability or competition with macroalgae [91]. Several studies, however, have established correlations between bloom formation and mild wave action and increases in water temperature, phosphate levels and/or iron bioavailability. Bloom persistence, however, has been correlated to the low palatability of cyanobacteria to most generalist herbivores [45, 50, 70, 88, 92, 93].

Algal and cyanobacterial blooms may be difficult to explain because as multispecies consortia (at least in the case of cyanobacterial blooms) the dynamics in bloom formation may be a result

of species-specific adaptations or preferences (reviewed in [94]). Also, the resulting increased growth may be a result of nutrient loading and/or reduction or absence of grazing [94]. Hence, food web dynamics may be important to understand this phenomenon. However, it is a no-brainer that the removal of large and small herbivores [12] has certainly favored the growth of cyanobacteria and algae, which have taken advantage of the increased nutrient availability and decreased grazing pressure.

## 5. Water temperature and cyanobacterial blooms

Sustained water temperatures over 28°C, alterations of flow and time of residence, decrease in water viscosity, large-scale mixing processes and small-scale turbulence are physical factors that correlate with cyanobacterial bloom formation [10, 88, 89, 95].

Thorough monitoring of *Lyngbya majuscula* blooms in the coasts of Puerto Rico from September 1998 until February 2000 showed that during September 1998 and September 2000 to December 2000, *Lyngbya* achieved the greatest cover coinciding with the highest temperatures recorded. While mean cover values ranged between 7 and 82% year-round, *Lyngbya* cover reached up to 100% during the warmest periods [53]. In Rosario Islands, Colombia, a similar pattern was observed in September 2010 and 2011, where the cover of cyanobacterial mats reached a 100%, concurring with sustained water temperatures above 30°C [93].

In Australia, benthic cyanobacterial blooms are recognized as an environmental health hazard [47, 49, 96]. Monitoring of *L. majuscula* mats in eastern Australia during 2005 showed that during the cool winter months blooms did not develop, but between the months of October and November, when water temperature increased, there was a fast development of *Lyngbya* mats. Blooms began gradually at the end of October, when total bottom cover of *L. majuscula* did not surpass 10% in an area of 49 hectares. During November, the total bottom cover of *L. majuscula* reached values close to 40% in an approximate area of 329 hectares. At the same time, water temperature increased from 23.5°C in October to 30.8°C in December. By the end of December, the bloom covered almost a 100% of the total available substrate in an area of 529 hectares [89]. I calculated an approximate wet biomass of 5000 Tons when the bloom reached its peak. As temperature decreased, so did *Lyngbya* cover. Similar patterns were registered in the Colombian Caribbean. Mats of *L. majuscula* and *L. sordida* covered extensions close to a 100% of the available reef substrate in Rosario Islands in September 2010 when the water temperature surpassed 30°C [93]. Also, mats of *Symploca hydrinoides* and *Phormidium submembranaceum* were very conspicuous in Old Providence Island during October 2009 and July 2010. Again, those blooms took place during the warmest months recorded in the San Andres Archipelago [above 28°C] [55, 93].

## 6. Nutrient input favors the growth of algae and cyanobacteria

Water quality degradation as a result of increased nutrient input promotes the development and persistence of algal blooms and is one of the reasons that explains their expansion

worldwide [94]. Although assessing the influence of nutrients is far more complicated than correlating these with increased water temperatures, experts agree that nutrients play a significant role in favoring blooms. Regular or pulsed nutrient delivery promotes bloom development; the overall composition—not just concentration—of nutrient input impacts blooms and high-biomass blooms may be partly sustained by exogenous nutrient sources [94].

Several studies have shown that cyanobacterial blooms are stimulated by the increase in nutrient concentration in water bodies. Nutrient increase may be a result of sewage disposal, animal husbandry or agricultural activities [26, 41, 49, 56, 57, 88, 89, 95, 97]. Rains also stimulate bloom formation due to increased runoff and river flow providing extra amounts of nutrients from terrestrial environments to coastal areas [49, 55, 98]. Groundwater and atmospheric deposition may also influence bloom formation and dynamics [94]. Nutrients that do have a stimulating growth effect on cyanobacteria are iron, phosphorus and nitrogen [26, 36, 49, 57, 89, 90, 99]. In the Colombian Caribbean, I have detected an apparent synergistic effect of high temperatures, the onset of rainy seasons and nutrient increase with incidence of marine cyanobacteria blooms at various sites [55, 93].

Anthropogenic activities such as the use of fertilizers and the dumping of urban and industrial waste waters provide significant amounts of nutrients into water bodies [26]. The input of key nutrients favor the growth of phototrophic organisms such as plants, algae and cyanobacteria, largely controlling aquatic primary production in marine environments where nitrogen is usually limiting. These blooms, with oxygen consumption during the hours of darkness, generate anoxia and consequent mortality of fish and other aquatic organisms [56].

## 7. The effect of cyanobacteria and algae on corals

There is significant evidence that reef degradation has increased on a global scale. Just in the Caribbean region, at least 20% of live coral coverage has been lost per decade [6]. This loss has been attributed to the increase in human population, dumping of waste water, soil erosion and subsequent sediment input by rivers, eutrophication, imbalance of food chains, proliferation of macroalgae [65, 100, 101], diseases and climate change [101, 102], as well as the removal or decimation of top predators and large herbivores [12].

Competition is a process that determines the structure, composition and diversity of benthic communities in coral reefs [5, 103–107]. In coral reefs, competition between sessile organisms such as benthic algae and corals has become very significant for the resilience of corals due to the dominance and vast cover of algae and cyanobacteria in affected coral reefs [65]. Reef deterioration has caused a significant replacement of live coral cover by cyanobacteria and macroalgae [59, 83, 108].

The strong competition for space between coral, algae and marine cyanobacteria can determine the structure, composition and abundance of these three groups in coral reefs [59, 109]. Overgrowth of algae or cyanobacteria on corals can cause deleterious effects on their health [50, 54, 55, 66, 110]. The vast occurrences of benthic algae and cyanobacteria in coral reefs are certainly an indication of the prevalent ecological conditions and may serve as indicators of coral reef health and local ecological imbalances [51, 111].

Coral reefs have a great diversity of herbivores that can exert a strong pressure on communities of primary producers such as macroalgae and cyanobacteria [2, 15]. In tropical areas, the most important herbivores in terms of consumption and impact on macroalgae are fish and sea urchins [70, 72, 77]. These herbivores can consume between 60 and 100% of the algal biomass daily [112–114]. Herbivory and nutrient input are two more determinant factors that define the relationship between algae and corals in reefs [85, 115] and the success of algae in other coastal ecosystems [116].

However, the generalized decrease in the populations of reef herbivores is an indirect cause of the increase in algal coverage and consequent phase shifts [2, 15, 50, 83]. Overfishing in reef areas has decimated the populations of herbivorous fish causing imbalances in the populations of macroalgae and their consequent overgrowth on corals and other substrates [2, 83, 84]. Occasionally, other herbivores such as sea urchins can sometimes increase in response to the decrease in herbivorous fishes and control algal populations. In the Caribbean basin, however, mass mortalities of sea urchins, particularly *Diadema antillarum*, triggered an excessive increase of algae in Jamaica and other locations [83].

Benthic cyanobacteria are efficient colonizers in a wide array of substrates such as coral skeletons, live coral, sand and even macroalgae. Cyanobacteria increase the magnitude of the phase shifts [51]. Benthic cyanobacteria, as well as macroalgae, are favored by bottom-up (increase in nutrients in the water bodies) and top-down effects (such as the decline of herbivores in reefs) [85]. Various studies have shown that the most important factor in controlling algae populations in coral reef areas is herbivory and the lack of it increases the consequences of phase changes more so than eutrophication, especially in the Caribbean [117].

Seaweed or macroalgae, compared to terrestrial plants, are mostly foliage, lacking dense structural material such as lignin, cellulose and hemicellulose, being more susceptible to herbivore consumption [118]. Benthic cyanobacterial mats strongly resemble macroalgae because they may exhibit large biomass and could become a potential food source for reef herbivores [44]. During blooms, cyanobacteria can surpass macroalgae in terms of available biomass [44, 72, 93].

Herbivory in reef areas generates a strong pressure on macroalgae and cyanobacteria. In “healthy” reefs, grazing rates may reach 100% of the produced biomass [77, 85, 112, 119]. Macroalgae and cyanobacteria, however, minimize grazing by means of spatial or temporal escapes, tolerating herbivory by compensating tissue loss with fast growth rates or investing in structural or chemical defenses [77–79, 113]. The production of feeding deterrent compounds, in particular, is well documented in these groups and plays an important role against grazing, enabling the growth and persistence of algae and cyanobacteria in coral reef areas [78, 119]. Besides deterring herbivores, chemically defended cyanobacteria could be favored by selective fish and urchin grazing over palatable macroalgae, removing potential competitors and favoring their growth and expansion in reef areas [26].

Massive colonization of hard substrates by algae and benthic cyanobacteria can determine competitive networks, structure, composition and abundance of these three groups locally [51, 109]. In events where the abundance of cyanobacteria or macroalgae greatly increases, there is also an increase in overgrowth interactions with corals. The overgrowth of cyanobacteria and



algae over corals may cause deleterious effects on their health [50, 66, 110]. In the Colombian Caribbean, the growth of benthic cyanobacterial mats over different species of scleractinian corals and soft corals eventually results in the death of the coral tissue that underlies those mats [54, 93] (**Figure 1**). In the Florida Keys, [50] determined that the brown seaweeds *Dictyota* and *Lobophora*, as well as several species of *Lyngbya*, not only inhibited the larval settlement of the hard coral *Porites astreoides* and the soft coral *Briareum asbestinum*, but also showed increased recruit mortality when the larvae came into direct contact with these organisms. Hence, seaweed and cyanobacteria may be considered competitively superior to corals not just by taking up space but also by inhibiting their recruitment.

Competition through allelopathic mechanisms by benthic marine cyanobacteria causes harmful effects on corals and soft corals. This has been observed in the field and tested in laboratory experiments in various sites such as the Bahamas, Belize, Florida and Panama [52], Florida [120], Hawaii [121] and the Colombian Caribbean [54, 93]. Experiments have been performed over coral embryos and larvae [50, 66] or adult corals [110].

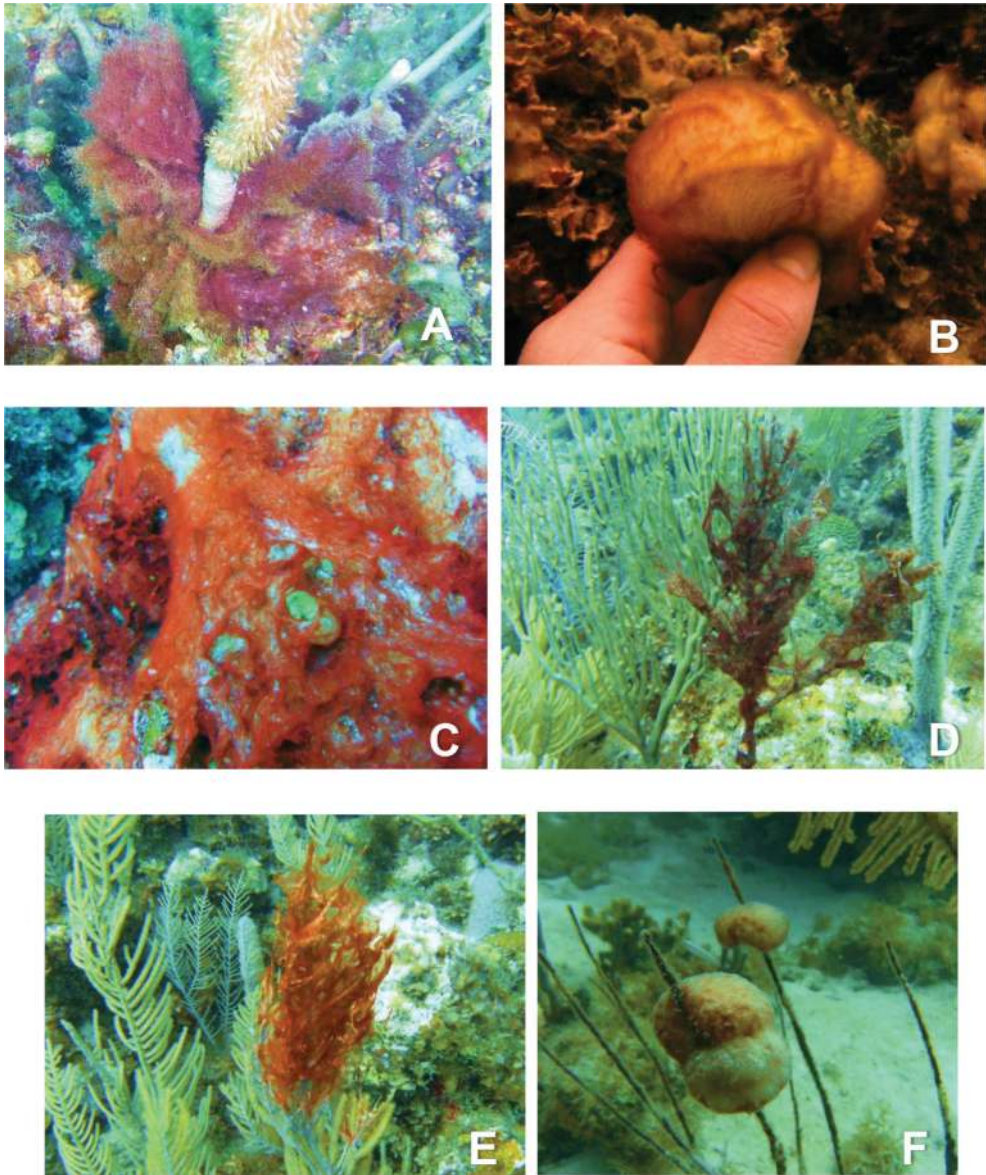
[66] compared the recruitment and survival of embryos of the hard corals *Pocillopora damicornis* and *Acropora surculosa*, in the presence of the cyanobacterium *L. majuscula*. Coral embryos got tangled in the dense *Lyngbya* filaments and died. Cyanobacterial mats may trap coral embryos but also promote sediment deposition and accumulation surrounding benthic microbial mats [122]. Under these mats, anoxic conditions may develop, which may favor nitrogen fixation but are potentially deadly to the very sensitive coral embryos [66]. Since recruitment is a key process in the maintenance and recovery of coral reef ecosystems [50, 123], any alteration in this process has negative implications and will affect the persistence and resilience of corals.

The fact that allelopathy is so hard to prove experimentally does not mean that it does not occur in reef environments. Cyanobacteria, in particular, while being in direct contact with corals, could release allelopathic compounds as a result of abrasion by water motion with consequent cell rupture. Many studies have shown that toxin release from cyanobacteria is a result of cell lysis due to abrasion, stress and cell death [124–126]. Additionally, environmental factors such as temperature may elicit active toxin liberation in these microorganisms [124, 126].

Competitive interactions between the hard coral *Porites lutea*, a brown alga *Dictyota dichotoma* and the cyanobacterium *Lyngbya bouillonii* were evaluated in Sesoko Island, Japan. While coral growth is compromised by direct contact and abrasion by the alga, mats of the cyanobacterium *L. bouillonii* are able to kill live coral tissue upon direct contact [110].

Interactions between cyanobacteria, a hard coral and a soft coral in Rosario Islands, Colombian Caribbean, were evaluated *in situ* in order to identify deleterious effects potentially related to allelopathic mechanisms. Cyanobacterial extracts were incorporated into Phytigel™ gels and these were placed in direct contact with the hard coral *Porites porites* and the soft coral *B. asbestinum* [127]. HPLC chromatographic profiles of zooxanthellae in coral tissues were evaluated after 24, 48 and 72 hours of exposure. Extracts from *Lyngbya* spp. showed a clear effect on the zooxanthellae chromatographic profiles evidenced by an increase in pheophytin, a degradation product from chlorophyll. The effect was greater with longest exposure time. These results suggest that cyanobacteria may compete against corals due to their fast growth rates, defenses against herbivory and allelopathic mechanisms. Further evidence was





**Figure 1.** Benthic cyanobacteria from Colombian Caribbean reefs. (A) Mats of *Moorea producens* growing at the base of a *Eunicea* soft coral. The soft coral retracts its polyps due to abrasion and possibly to avoid contact with the mat. Rosario Islands, 2016. (B) Filamentous mats of *Caldora* sp. This cyanobacterium grows profusely over various kinds of seaweeds. Old Providence Island, 2008. (C) Unidentified red filamentous mats overgrowing hard corals and green algae. Old Providence Island, 2008. (D and E) Multispecies cyanobacterial mats overgrowing soft corals, causing polyp necrosis and tissue death. The remaining gorgonin skeletons continue to be colonized by other cyanobacteria and filamentous algae. Old Providence Island, 2016. (F) Puffs of filamentous cyanobacteria may overgrow live corals causing bleaching and/or necrosis. In this case, they are growing over gorgonin skeletons. Old Providence Island, 2016. Photos A, D–F: Monica Puyana; B–C: Julian Prato.

obtained while testing the potential allelopathic effects of two organic extracts from marine cyanobacteria over live corals. Organic extracts from two different microbial consortia, a consortium of *S. hydroides* and *P. submembranaceum* and a consortium of *Lyngbya cf. semiplena*, *L. majuscula*, *Oscillatoria nigroviridis* and *O. margaritifera*, were tested at 0.002 ppm and 0.011 ppm, both below their natural concentration. In order to do so, fragments of the hard coral *Madracis mirabilis* were placed in individual containers, and once acclimated, with their polyps fully expanded, cyanobacterial extracts were resuspended in ethanol and seawater and coral behavior was registered. Both extracts generated the retraction of coral polyps with variable speed and intensity. Ethanol controls, on the other hand, presented a rapid recovery and a minimum shrinkage of polyps. Fragments exposed to cyanobacterial extracts showed 80 to 99% of polyp retraction, whereas solvent controls did not exceed 25% of polyp retraction. No extract proved to be lethal, and after 20 hours, corals extended their polyps displaying full recovery [93].

In another assay, the toxicity of four cyanobacterial extracts to embryos of *Montastrea annularis*, obtained during the mass spawning event in Rosario Islands in September, 2011, was evaluated. In this assay, we assessed embryo mortality 6, 18 and 24 hours after acute exposure to cyanobacterial extracts in concentrations of 1000, 500, 100 and 10 ppm. All tested extracts were toxic at concentrations of 500 and 1000 ppm, causing 100% embryo mortality within 6 hours. Controls with seawater and ethanol did not affect coral embryos. The extract that showed greater toxicity was obtained from a mixed *Lyngbya* assemblage, causing a 90% embryo mortality at the lowest concentration tested (10 ppm) after only 6 hours of exposure.

In summary, competition between corals, cyanobacteria and/or algae may take place either against coral embryos or larvae or during their adult stages. Some of the mechanisms include allelopathic inhibition on adult corals and embryos, negative effects of abrasion by direct physical contact, drastic decrease in oxygen levels near and under cyanobacterial mats, reduction of available space in reef substrates affecting larval recruitment and mortality of embryos entangled in cyanobacterial mats. All these effects strongly suggest that blooms of algae and benthic cyanobacteria pose a risk for the recruitment and development of reef builders and other reef organisms such as soft corals [50, 51, 66, 93, 110, 120, 121].

## 8. Climate change, ocean acidification and future of reefs

Resilience or the ability to withstand and recover from the negative phenomena affecting coral reefs is an essential role for their persistence. Recovery after each disturbance involves the re-establishment of coral coverage, the growth of surviving coral fragments, reproductive success and the subsequent settlement and survival of coral embryos and larvae [16, 123]. However, the recovery process in coral reefs is nowadays more difficult because the substrate in these ecosystems is frequently dominated by algae and cyanobacteria. These photosynthetic organisms efficiently colonize available substrates following disturbances and become dominant in degraded reefs [15, 65, 83, 123], reducing the resilience of coral reefs overall

[2, 15]. Algal dominance can become a serious bottleneck for the re-establishment of corals, depending on the characteristics of the dominant algal assemblages in each place [65, 123].

Large-scale hydrological disturbances and environmental changes due to global warming and ocean acidification are recognized as growing threats to coral reefs worldwide [17, 123, 128–130]. Global warming is also believed to facilitate the development, frequency and expansion of cyanobacterial blooms [10, 11, 26, 37]. These large-scale disturbances may have a more direct effect on corals, either by reducing growth rates and calcification regimes under acidic seawater conditions or by the onset of bleaching events under warmer conditions [17, 123]. Unless there is a significant reduction in CO<sub>2</sub> atmospheric levels, reefs with reduced populations of grazers and increased nutrient input are predicted from shift from predominantly coral-dominated to predominantly algal-dominated states [17, 130]. This pattern has been recognized for some time now, particularly in the Caribbean and the Eastern Pacific [131–135]. Management options such as restoring herbivore populations and limiting nutrient input to reef areas may only be effective under controlled CO<sub>2</sub> input to seawater [17, 123, 130]. Sea urchins are important grazers of noxious algae [136]; therefore, restoration of grazers such as urchins is believed to alleviate the problem of excessive algal biomass in coral reefs. In Hawaii, juveniles of the local urchin *Tripneustes gratilla* are raised in hatcheries and reintroduced in reef areas in order to remove excessive biomass of invasive algal species and restore the natural ecosystem function [137]. However, control of cyanobacterial populations by grazers seems very unlikely [26].

Approximately two-thirds of coral reefs in the Caribbean are threatened by human activities such as coastal development, wastewater and sediment input, pollution and overfishing [138]. The economic impact of coral bleaching, coral diseases and cyanobacterial blooms has not been quantified, but it is clear that these have caused significant changes in Caribbean reef communities [138]. Therefore, it is important to assess the impact of cyanobacterial blooms at local scales in order to understand their causes and consequences in order to address significant monitoring and management measures. The relationships between nutrient input and bloom formation are obscured by changes in food webs, habitat alterations and climate change. Nutrient enrichment has several effects in food webs, predator-prey interactions and overall nutrient dynamics. However, experts agree that management of nutrient inputs to watershed may be the most important measure to prevent excessive growth of algae and cyanobacteria [26, 94]. The Australian government, for instance, has invested significant funds to reduce nitrogen inputs into Moreton Bay to prevent blooms of *L. majuscula* [90].

## 9. Conclusions

In order to answer the question whether corals will overcome competition with algae and cyanobacteria in environments, the evidence shows that reef communities have changed over time and will keep changing in the light of large-scale events and anthropogenic influences. Algae and cyanobacteria are thriving as the total bottom cover of reef corals is reduced. So even if corals survive, their communities will not be the same. We do need to gain a better

understanding of causes, at local and regional scales, that support bloom formation. Also, it is crucial to convince managers that only long-term studies and periodic surveys will help to understand and manage algae and cyanobacteria in reefs and other marine ecosystems. As short-term measures, ambitious programs for grazer reintroduction could help curb population growth of algae and cyanobacteria. Medium- to long-term measures should be oriented at limiting nutrient input to water bodies.

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