

Review Article

Cyanobacteria in Coral Reef Ecosystems: A Review

L. Charpy,¹ B. E. Casareto,² M. J. Langlade,¹ and Y. Suzuki²

¹ Mediterranean Institute of Oceanography (MIO), IRD, UR235 Center of Tahiti, BP 529, 98713 Papeete, French Polynesia

² Graduate School of Science and Technology, Shizuoka University, 836 Ohya, Suruga-ku, Shizuoka 422-8529, Japan

Correspondence should be addressed to B. E. Casareto, casaretobe@aol.com

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Cyanobacteria have dominated marine environments and have been reef builders on Earth for more than three million years (myr). Cyanobacteria still play an essential role in modern coral reef ecosystems by forming a major component of epiphytic, epilithic, and endolithic communities as well as of microbial mats. Cyanobacteria are grazed by reef organisms and also provide nitrogen to the coral reef ecosystems through nitrogen fixation. Recently, new unicellular cyanobacteria that express nitrogenase were found in the open ocean and in coral reef lagoons. Furthermore, cyanobacteria are important in calcification and decalcification. All limestone surfaces have a layer of boring algae in which cyanobacteria often play a dominant role. Cyanobacterial symbioses are abundant in coral reefs; the most common hosts are sponges and ascidians. Cyanobacteria use tactics beyond space occupation to inhibit coral recruitment. Cyanobacteria can also form pathogenic microbial consortia in association with other microbes on living coral tissues, causing coral tissue lysis and death, and considerable declines in coral reefs. In deep lagoons, coccoid cyanobacteria are abundant and are grazed by ciliates, heteroflagellates, and the benthic coral reef community. Cyanobacteria produce metabolites that act as attractants for some species and deterrents for some grazers of the reef communities.

1. Cyanobacteria

Cyanobacteria are oxy-photosynthetic bacteria. One of the characteristics of cyanobacteria is their thylakoids, the seats of photosynthesis, respiration, and in some species, molecular nitrogen fixation. One of the earliest signs of life on Earth was the formation of stromatolite reefs, which exist now as fossil structures in the oldest rocks known [1]. This cyanobacterial fossil record is among the oldest of any group of organism, possibly reaching back to 3500 million years (myr) ago. Throughout the succeeding 3000 myr, many shallow reefs arose and provided a habitat for cyanobacteria. Modern corals are a relatively recent phenomenon; indeed, scleractinian corals first appeared 230 myr ago in the Triassic [2]. Although cyanobacteria have been supplanted to an extent by eukaryotic algae on modern coral reefs, especially by the dinoflagellate *Symbiodinium* sp. (zooxanthellae) and coralline red and green algae, they play an essential role in the ecology of modern reefs. Nowadays, cyanobacteria are present in the benthos and plankton compartments of coral reef ecosystems. In this paper, we discuss the contribution of cyanobacteria to photosynthetic biomass and their role in coral reef ecosystems.

2. Benthic Cyanobacteria

2.1. Microbialites. Microbialites are organosedimentary deposits of trapped benthic microbes and detrital sediment and/or mineral precipitation [3]. Thus, microbialites may display various degrees of mineral induration. Based on their internal structure, Burne and Moore [4] divided microbialites into stromatolites characterized as sedimentary structures containing lithified laminae [5], thrombolites (clotted texture), cryptic microbialites (vague, mottled or patchy texture), oncolites (concentric lamination), and spherulitic microbialites (spherular aggregates).

Microbialites may represent a major structural component of the reef. Microbialites consist exclusively of millimetre- to centimetre-thick thrombolite crusts. In the barrier reef-edge of Tahiti, they may form 80% of the rock by volume and reflect at least 13,500 years of continuous reef formation. However, the development of microbialites in the cryptic niches of the reef framework ceased about 6000 years ago when the sea level approached its present level [6].

Soft, biscuit-shaped, internally finely laminated stromatolitic structures, with substantial quantities of fine grain (micritic) carbonate, have been discovered in a lagoon on

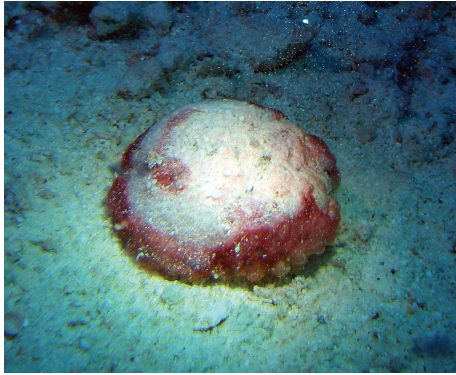


FIGURE 1: Stromatolitic structures built by filamentous, sheathed, non-heterocystous cyanobacteria recognized as two new species of *Phormidium*. Ahe lagoon, 25 m depth (Tuamotu Archipelago).

Tikehau atoll (Tuamotu Archipelago, French Polynesia) at depths of 15–23 m [7]. These modern stromatolites cover large areas of the lagoon floor and are especially numerous around patch reefs (Figure 1). They consist of filamentous, sheathed, non-heterocystous cyanobacteria recognized as two new species of *Phormidium* [3]. The constructional elements of carbonate precipitates fall into two categories characterized by distinctive forms and size ranges: micrometre-sized (0.5–2.0 μm) mineral fibres, rounded (0.1–0.2 μm) bodies, and grape-like clusters [3]. The growth of modern marine stromatolites represents a dynamic balance between sedimentation and intermittent lithification of cyanobacterial mats [8].

2.2. Endolithic Cyanobacteria. Carbonate skeletons of hermatypic corals harbour diverse populations of microboring organisms. Skeletons of live colonies are bored from the inside outward by Chlorophyta, while dead and denuded parts of coral skeletons are colonized at the surface and bored inward by a succession of euendoliths, starting with Chlorophyta and followed by cyanobacteria, to establish a stable Chlorophyta-dominated endolith community within 2 years [9].

The distribution of boring cyanobacteria generally depends on light level and depth; however some other factors may also influence their distribution. In Jamaica, in clear water, the boring cyanobacteria community structure changes below 20–30 m [10]. Boring cyanobacteria can also infest shells. In French Polynesia, infestations of cyanobacteria identified as *Hyella*, *Mastigocoleus*, and *Plectonema* destroy the commercially valuable shells of the black oyster *Pinctada margaritifera* [11].

In the carbonate cycle, cyanobacteria play an important and sometimes decisive role. Cycling of carbon and carbonate is linked to biological processes: some build up specific carbonate structures, some destroy carbonate substrates, and others do both simultaneously [12]. The photosynthetic activity of cyanobacteria, their extracellular polymeric substances, and possibly also their adherent heterotrophic bacteria are responsible for the construction of various carbonate structures and the ability to penetrate carbonate

material [13]. The boring activity of euendoliths results in biological corrosion and disintegration of carbonate surfaces. Grazing organisms on carbonate surfaces colonized by epi- and endolithic cyanobacteria produce specific biokarst forms and specific grains that can contribute to near-shore sedimentation [14]. Biological corrosion and abrasion together constitute bioerosion.

Endolithic phototrophs (cyanobacteria and Chlorophytes) are one of the major primary producers in dead coral substrates in a wide range of coral reef environments [15]. In an investigation of the photosynthetic activity and N_2 fixation rates of coral rubble endoliths in fringing reefs at La Reunion Island (France) and Sesoko Island (Okinawa, Japan), the main endolith flora was composed of the cyanobacteria *Hyella* (cf.) *caespitosa*, *Plectonema* (cf.) *terabrans*, *Mastigocoleus testarumin*, and *Scytonema* (cf.) *conchophyllum* (the last two species with heterocysts). Their primary production rate varied seasonally between 1.6 and 4.8 $\mu\text{g C } \mu\text{g chl}^{-1} \text{ day}^{-1}$ and were comparable to those of scleractinian corals [16].

2.3. Symbiotic Cyanobacteria. Marine sponges can host a variety of cyanobacterial and bacterial symbionts. For example, the filamentous cyanobacterium *Oscillatoria spongilae* is found in the sponge *Dysidea* on the Great Barrier Reef (Australia) and also in three species of *Dysidea* found around Guam [17]. In the Western Central Pacific reefs from Taiwan to the Ryukyu Archipelago, the encrusting sponge *Terpios hoshinata* is associated with unicellular cyanobacteria first described as *Aphanocapsa raspagellae* [18, 19] and later reclassified using molecular tools as closely related to *Prochoron* sp. [20]. In the shallow waters of the Caribbean Sea, the encrusting sponges *Terpios manglaris* and *T. belindae* are associated with the cyanobacterium *Hypheothrix* sp. (Oscillatoriales, Schizotrichaceae) [18, 19]. The sponge *Terpios* sp. aggressively competes for space by killing and overgrowing live corals and is responsible for devastating wide areas of coral reef. Phylogenetic analyses of 16S rRNA sequences of sponge-associated cyanobacteria have shown them to be polyphyletic. Many sequences are affiliated with *Synechococcus* and *Prochlorococcus* species [21, 22]. Cyanobacteria fill the cortical region of the sponge and penetrate inward into the choanosomal region [23]. Microbial symbionts may produce many of the pharmaceutically active compounds isolated from marine sponges [24, 25]. These compounds can serve a variety of ecological functions, from predator and competitor deterrence and resistance to malignant microbial infections. Because cyanobacterial symbionts can also overgrow and kill their host sponge, it is not known whether sponges can actively regulate their symbiont populations [26].

2.4. Epiphytes. Benthic marine species of *Phormidium* with narrow trichomes and *Plectonema* are common epiphytes on cyanobacteria and algae. These organisms attach externally onto sheaths of other cyanobacteria, while *Spirulina* tend to crawl inside their sheaths. Small coccoid epiphytic cyanobacteria (<0.8 μm diameter), which attach to sheaths of large

Lyngbya majuscula ($>80\ \mu\text{m}$), illustrate the enormous cell size range of marine cyanobacteria [27].

Cyanobacteria are frequently observed as epiphytes of seagrass on the Great Astrolabe Reef, Fiji [28], and on the Great Barrier Reef, Australia [29], as well as epiphytes of algal turf on Virgin Island [30] in French Polynesia [31].

2.5. Microbial Mats. Microbial mats are associations of organisms dominated by cyanobacteria in association with photosynthetic bacteria, sulphur bacteria, and other microorganisms. They generally form flat, extensive mats of several millimetres in thickness on sand or mud. In coral reef ecosystems, microbial mats are found in soft muddy floors of lagoons comprised alternatively by different gliding filamentous cyanobacteria. The diversity of cyanobacterial mats inhabiting different environments has been the focus of several recent studies that applied molecular methods to natural populations. To explore the identity and distribution of natural populations of benthic marine cyanobacteria, polyphasic approaches have been used on Tikehau atoll (French Polynesia) [32], in New Caledonia [33], in the western Indian Ocean in Zanzibar (Tanzania) [34], in La Reunion Island, and in Okinawa [36]. These studies identified three types of organosedimentary structures that regularly occur on the lagoon floor: horizontally spreading mats, cobweb-like soft gelatinous masses, and hemispherical to spherical domes. These structures differ in appearance, species composition, mode of growth, and in their relationship to the substrate.

For example, on Tikehau Atoll, mats were dominated by *Hydrocoleum cantharidosmum*, *H. coccineum*, *Spirulina subsalsa*, *Symploca hydnoidea* (Figure 2), and various species of *Phormidium* [32], whereas those in New Caledonia were dominated by heterocystous (*Nodularia harveyana*) and non-heterocystous (*Hydrocoleum cantharidosmum*, *H. lyngbyaceum*) [33]. In Page reef, Zanzibar, mats were dominated by filamentous non-heterocystous genera such as *Lyngbya*, *Microcoleus*, *Spirulina*, and *Oscillatoria* as well as by genera within Pseudanabaenaceae. Unicellular taxa were also represented, while heterocystous taxa were encountered only rarely [34]. In Broward County, Florida, USA, the blooms were dominated by *Lyngbya polychoa* [35]. Finally, on La Reunion Island and Sesoko Island, *Anabaena* sp. among heterocystous (Figure 3) and *Hydrocoleum majus* and *Symploca hydnoidea* among non-heterocystous cyanobacteria occurred in microbial mats at both sites, whereas *Oscillatoria bonnemaisonii* and *Leptolyngbya* spp. occurred only on La Reunion Island, and *Hydrocoleum coccineum* and *Phormidium laysanense* dominated on Sesoko Island. Mats dominated by *Hydrocoleum lyngbyaceum* and *Trichocoleus tenerrimus* occurred at lower frequencies [16, 36].

Biological N_2 fixation performed by cyanobacteria provides these organisms and microbial mat communities with a particular advantage when growing under N-limited conditions, which are most common in marine environments. Biological N_2 fixation by cyanobacteria appears to make a major contribution to N supply in coral reef ecosystems [36]. Not all cyanobacteria can fix atmospheric nitrogen.



FIGURE 2: Tufts dominated by *Symploca hydnoidea* in Mayotte lagoon at 10 m depth.

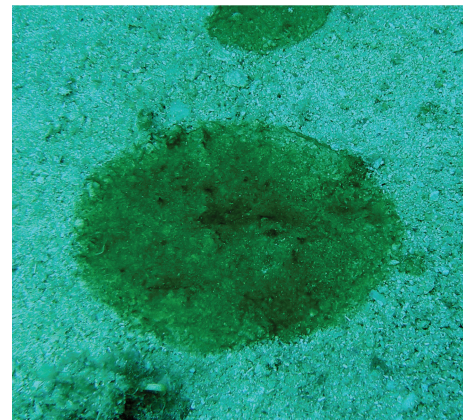


FIGURE 3: Cyanobacteria mats dominated by *Anabaena* sp. (heterocystous) in Mayotte lagoon at 14 m depth.

The process is oxygen-sensitive and energetically expensive, which constrains its implementation in oxygenic cyanobacteria; these bacteria separate the processes of carbon and nitrogen fixation either in space (i.e., heterocyst) or time [37].

The contribution of N_2 fixation to that required for primary production is between 2% and 21% in Tikehau atoll lagoon [38] and New Caledonia [33]. Casareto et al. [16] compared N_2 fixation rates of three different subenvironments (coral rubbles, microbial mats, and sandy bottoms) on La Reunion and Sesoko Islands. They found that N_2 fixation rates of microbial mats are one order of magnitude higher than that of other subenvironments and can contribute up to 95% of their primary production [16].

2.6. Harmful Effects. Cyanobacteria are becoming increasingly prominent on declining reefs, as these microbes can tolerate strong solar radiation [39]. Changes in land use or seabird distribution that lead to alter dissolved organics, iron, and phosphorus input enhance proliferation of noxious blooms of cyanobacteria [40]. The production of deterrent secondary metabolites by benthic cyanobacterial and similar microbial assemblages facilitates the formation of cyanobacterial blooms on coral reefs [41].

Kuffner et al. [42] found evidence that algae and cyanobacteria use tactics beyond space occupation to inhibit coral recruitment. On reefs experiencing phase shifts or temporary

algal blooms, the restocking of adult coral populations may be slowed due to recruitment inhibition by cyanobacteria, thereby perpetuating reduced coral cover and limiting coral community recovery. Cyanobacterial mats act as a poison for scleractinian corals and are able to kill live coral tissue [43]. About 30 diseases of corals have been recognised since they were first discovered more than 30 years ago. Little is known of the causes and effects of coral disease, although they can be caused by bacteria, fungi, algae, worms [44], and viruses [45–47].

Black band disease (BBD) of corals is caused by a pathogenic microbial consortium that exists as a horizontally migrating, laminated microbial mat. The consortium is structurally directly analogous to the cyanobacterial mats found in many illuminated, sulfide-rich benthic environments such as hot spring outflows and sediments of hypersaline lagoons, but is unique in that the entire mat community migrates across the surface of coral colonies, completely degrading coral tissue. BBD is one of a number of coral diseases believed to play an important role in the observed decline of coral reefs. The black band microbial consortium is dominated by *Phormidium corallyticum* [48] in the Caribbean, but other cyanobacteria species were described in Palau reefs [49] and in the Red Sea where a new cyanobacterium species, *Pseudoscillatoria coralii* gen. nov., sp. nov., dominates the BBD consortium on *Favia* sp. corals [50]. *P. corallyticum* can perform oxygenic photosynthesis in the presence or absence of sulfide but cannot conduct anoxygenic photosynthesis with sulfide as an electron donor. This species is not capable of fixing N₂ [51]. Recent discoveries [52, 53] indicate that different species and strains of BBD cyanobacteria, which can occur in the same BBD infection, may contribute to BBD pathobiology by producing different types and amounts of toxins at different stages of the disease process. Understanding the interactions between coral larvae and benthic bloom-forming cyanobacteria may be important in managing coral reef ecosystems [54].

2.7. Benthic Cyanobacteria Grazing. Cyanobacteria are generally considered to be a poor food source due to toxicity, low nutritional value, or a morphology that makes ingestion difficult. Despite these factors, there are grazers that are adapted to feeding on cyanobacteria [55].

Lyngbya majuscula constitutes a major portion of the diet of a Pomacentrid damselfish on Davies Reef, Australia [56], and on Orpheus Island, Australia [57]. Many cyanobacteria, including species of *Calothrix*, *Lyngbya*, *Oscillatoria*, and *Phormidium*, have been found in the plate of fish *Hemiglyphidodon plagiometopon* [58].

During the life of the coral, the endoliths are protected from grazers, but in dead coral skeletons endolith cyanobacteria are exposed to grazing by molluscs, echinoderms and scarid fish [9]. The importance of epiphytic cyanobacteria as a food source for heterotrophs in coral reef ecosystems was also reported by Yamamuro [28]. Thacker et al. [59] found that coral reef fishes can learn to avoid defensive secondary metabolites, but that this learning does not occur when access to food is limited. This strategy may indicate

that the effectiveness of the chemical defences of an alga or cyanobacteria is dependent on the state of the consumer and the defences of other prey in the environment. Thacker et al. [60] observed selected grazing on the cyanobacteria of Guam coral reefs, stressing the critical role of herbivory in determining coral reef community structure.

Some tropical benthic cyanobacteria are preferred foods for specialized consumers in the size range of mesograzers. Therefore, a diverse fauna may depend on cyanobacterial mats. Tropical mesograzers exploit considerably different food resources, with some species adapted to consume cyanobacterial mats. Benthic cyanobacteria may play important roles as food and shelter for marine consumers and may indirectly influence local biodiversity through their associated fauna [61, 62]. The cyanobacterial genus *Lyngbya* includes free-living, benthic, filamentous cyanobacteria that form periodic nuisance blooms in lagoons, reefs, and estuaries. *Lyngbya* spp. are prolific producers of biologically active compounds (metabolites). *Lyngbya majuscula* produces a wide variety of secondary metabolites, as well as lyngbyatoxin A (LTA). LTA production varies in different locations worldwide [63]. Specific metabolites produced by *Lyngbya majuscula* act as both feeding attractants to the specialist herbivore *Stylocheilus longicauda*, and as effective feeding deterrents to the generalist fishes [64]. One species, identified as *Lyngbya* cf. *confervoides*, produces a diverse array of bioactive peptides and depsipeptides [65].

Opisthobranchs may also play a role in top-down control of toxic cyanobacterial blooms, as was demonstrated for toxic *Lyngbya* by Capper and Paul [66].

Microbial mats can also be ingested by filter feeders. Identification of homoanatoxin-a from benthic marine cyanobacteria (*Hydrocoleum lyngbyaceum*) samples collected in Lifou (Loyalty Islands, New Caledonia) was recently reported [67]. This cyanobacterium was suspected to cause giant clam (*Tridacna maxima*) intoxications.

3. Planktonic Cyanobacteria

Planktonic cyanobacteria found in coral reef plankton are mainly filamentous and unicellular.

3.1. Planktonic Filamentous Cyanobacteria. Large blooms of *Trichodesmium*, a filamentous nitrogen-fixing cyanobacterium, are observed frequently in coral reef ecosystems [68]. They have been documented in the eastern Indian Ocean and western Pacific [69], in the central region of the Great Barrier Reef [70–73], in the Gulf of Thailand [74], and in the south-western Tropical Pacific [75]. *Trichodesmium* spp. have been described to be nontoxic, sometimes toxic, or always toxic to a range of organisms [76–81]. Recent studies have provided unprecedented evidence of the toxicity of *Trichodesmium* spp. from the New Caledonia lagoon [82], demonstrating the possible role of these cyanobacteria in ciguatera fish poisoning.

Trichodesmium is the most well-studied marine N₂-fixing organism and perhaps one of the most important. The rate of nitrogen fixation by *Trichodesmium* species in surface

waters is close to $2 \text{ pmol N trichome}^{-1} \text{ h}^{-1}$ [83]. It is difficult to quantify the importance of *Trichodesmium* diazotrophy because of the stochastic nature of the blooms. However, it is estimated that *Trichodesmium* contributes about 0.03–20% of the total CO_2 fixation in the coastal surface waters of Tanzania [84].

The pelagic harpacticoid copepod *Macrosetella gracilis* is usually found in association with blooms of *Trichodesmium* in tropical and subtropical waters. This copepod is one of the few direct grazers of these often toxic cyanobacteria [79, 85].

The study of Villareal [86] in the Belizean barrier reef showed significant grazing of *Trichodesmium* by the coral reef community.

3.2. Planktonic Unicellular Cyanobacteria. Oligotrophic waters surrounding coral reef ecosystems and lagoons are dominated by the small coccoid unicellular cyanobacteria *Synechococcus* and *Prochlorococcus* [87–95]. In coral reef waters, *Synechococcus* has a size of $1 \mu\text{m}$ and an abundance ranging from 10×10^3 to $500 \times 10^3 \text{ cells mL}^{-1}$, while *Prochlorococcus* has a size of $0.6 \mu\text{m}$ and an abundance ranging from 10×10^3 to $400 \times 10^3 \text{ cells mL}^{-1}$.

The contribution of unicellular cyanobacteria to phytoplankton biomass and production varies according to the ecosystem. In Tuamotu lagoon (French Polynesia), *Synechococcus* is the predominant group in terms of abundance and carbon biomass and has the highest planktonic primary production among lagoons. As it is generally scarce in deep water with limited light availability, its biomass contribution is reduced in deep lagoons. In very shallow lagoons, no general trend has been observed, as the dominant group appears to depend on the water residence time within the lagoon [89–96]. In Tuamotu lagoon and Miyako Island (Okinawa) picoplankton primary production represents 65–80% of total phytoplankton production [97, 98].

In the Great Astrolabe Reef lagoon (Fiji), *Synechococcus* is the most abundant group (85–95%), followed by picoeukaryotes (5–10%) and *Prochlorococcus* (<4%) [90]. Picoplankton primary production makes up 53.2% of the total phytoplankton production [90].

Ayukai [99] reported that on the Great Barrier Reef, the average abundance of cyanobacteria (*Synechococcus*) is 0.16 – $2.41 \times 10^4 \text{ cells mL}^{-1}$. Later, Crosbie and Furnas [92], using a flow cytometer, observed that *Synechococcus* was more abundant and had a greater biomass than *Prochlorococcus* at most inshore and mid-shelf sites in central regions (17°S) and at all shelf sites in southern areas (20°S) of Great Barrier Reef. Moreover, *Synechococcus* and *Prochlorococcus* abundance was better correlated with salinity, shelf depth, and chlorophyll *a* concentration than with nutrient concentrations.

At Sesoko Island (Okinawa), Tada et al. [100] found that picoplankton dominated the phytoplankton community with an average contribution to the total chlorophyll-*a* biomass of 52%. At Miyako Island (Okinawa, Japan), the contribution of picophytoplankton to total phytoplankton biomass is 45–100% [101]. In another study, Ferrier-Pagès and Furla [96] found that the picophytoplankton contribution to total chlorophyll was 32–73%. *Prochlorococcus*,

Synechococcus, and picoeukaryote abundance was on average 64 ± 11 , 12 ± 2 , and $4 \pm 0.7 \times 10^3 \text{ cells mL}^{-1}$, respectively. Their contribution to picoplankton biomass was 10, 49, and 41%, respectively, and the contribution of picoplankton primary production to total phytoplankton production is 65%. On Miyako Island, Okinawa (Japan), *Synechococcus* spp. represented 65% of the chlorophyll (< $3 \mu\text{m}$), 53% of autotrophic carbon, and 67% of the nitrogen [101]. In Mayotte (south-western Indian Ocean), particles < $10 \mu\text{m}$ accounted for 74% of the chlorophyll-*a* concentration and for 47% of the total living carbon [102].

In one study in New Caledonia's coral lagoon, unicellular diazotrophic cyanobacteria of 1 – $1.5 \mu\text{m}$ were found along a nutrient gradient using whole-cell hybridization with specific Nitro 821 probes [103]. Their abundance ranged from 3 to 140 cells mL^{-1} . These cells may contribute to N_2 fixation (from the < $10 \mu\text{m}$ size fraction) which was estimated to be 4.4 – $8 \text{ nmol N}^{-1} \text{ d}^{-1}$.

Very few studies have investigated grazing of unicellular cyanobacteria in coral reef waters [101, 102]. In Tikehau lagoon (Tuamotu), González et al. [104] showed that phagotrophic nanoflagellates were the major grazers of picocyanobacteria. Ciliates and heterotrophic dinoflagellates appeared to be grazing mostly on nanoplankton, both autotrophic and heterotrophic cells, showing the important contribution of coccoid cyanobacteria to the microbial food web.

In Takapoto (Tuamotu), the grazing rates of < $200 \mu\text{m}$ protozoa on cyanobacteria represented 74% of their growth rates [105]. In the lagoonal waters of the two largest atolls of French Polynesia (Rangiroa and Fakarava), 75% of the cyanobacteria production was consumed by < $10 \mu\text{m}$ fractions, equal to 0.05 – $0.5 \times 10^4 \text{ cyanobacteria mL}^{-1} \text{ h}^{-1}$ [96]. In the water over a fringing coral reef at Miyako Island (Japan), 30–50% of picocyanobacteria production was grazed by heterotrophic flagellates and ciliates, which themselves were grazed (50–70% of the production) by higher trophic levels [101].

On Conch Reef, Florida Keys, sponges are a net sink for picocyanobacteria [106]. In the Gulf of Aqaba, Red Sea, measurements of depletion of phytoplankton cells and pigments over coral reefs have revealed that *Synechococcus* contributes >70% of the total depleted carbon in summer. The grazing of cyanobacteria appears to be an important component of benthic-pelagic coupling in coral reefs [102, 107]. Another study by Yahel et al. [108] demonstrated that sponges removed significant amounts of picocyanobacteria but suggested that DOC may play a major role in the trophic dynamics of coral reefs. In Caribbean coral reef communities, gorgonian corals do not appear to graze significantly on picocyanobacteria [109].

4. Conclusions

Cyanobacteria are ubiquitous in coral reef ecosystems:

- (i) as a part of the reef (Microbialites),
- (ii) inside (endoliths) and above (epiliths and epiphytes) the coral reef,

- (iii) as symbionts of sponges,
- (iv) covering soft bottoms as microbial mats,
- (v) in the water column.

In addition, they have the following.

- (i) They help build and erode the reef.
- (ii) They are important primary producers.
- (iii) They represent an organic source for planktonic and benthic heterotrophic organisms.
- (iv) They enrich the ecosystem with nitrogen.

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