

Spatial scale of cyanobacterial blooms in Old Providence Island, Colombian Caribbean

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Abstract

Cyanobacterial blooms have increased in coastal waters worldwide, facilitated by excessive nutrient input and apparently global warming. They exert negative consequences in marine ecosystems, communities and habitats. Although reports of these events are frequent, their spatial extent and affected habitats are not completely recognized, hence restricting regional management actions. We examined the presence, spatial scale and cover of cyanobacterial blooms in different habitats of the reef systems off Old Providence Island, and identified the main bloom forming taxa. Cyanobacteria were registered in four different ecosystems, six geomorphological zones and nine habitats. Benthic cyanobacteria reached 18 to 72 % of the total cover in five habitats, particularly at the northwest, east and southeast portions of the island. These blooms consisted of complex consortia belonging to the genera *Okeania*, *Lyngbya*, *Symploca*, *Phormidium*, *Oscillatoria* or *Spirulina*. A bloom of planktonic cyanobacteria was dominated by *Trichodesmium* and developed on the fore reef of the island (NW), following heavy rains. These results suggest a potential new stressor for the island's reef complex. Future research should focus on the environmental factors that enable cyanobacterial blooms and their local impact on ecosystems and services.

Keywords: cyanobacteria; geomorphological zones; habitat; microbial consortia; reef system; Caribbean.

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Introduction

In the Caribbean region, at least 80 % of the total coral cover has been lost since the seventies (Mumby & Steneck 2008). Factors that explain this loss are coastal development and increased human population, sewage runoff, sediment input, eutrophication, overfishing and alteration in food chains, proliferation of fleshy and turf algae (McCook et al. 2001, Burke & Maidens 2004, Hughes et al. 2010, Vermeij et al. 2010), diseases and climate change (Aronson & Precht 2006, Mora 2008). Reef degradation is a consequence of reduction in coral cover and coral recruitment, as well as an increase in substrate colonization by macroalgae and cyanobacteria (River & Edmunds 2001, Kuffner & Paul 2004, Kuffner et al. 2006, Hughes et al. 2010, Rasher & Hay 2010, Vermeij et al. 2010, Charpy et al. 2012).



Blooms of benthic cyanobacteria appear to be on the rise on a global scale (Paul 2008, Paerl & Paul 2012). There are reports of these events in the Pacific Ocean (Becerro et al. 2006, Smith et al. 2008), Micronesian atolls and Hawaiian Islands (Kuffner et al. 2006), the Indian Ocean (Charpy et al. 2012), the Baltic Sea (Paerl 2002, Conley et al. 2009), and the Atlantic Ocean (Hayes et al. 2001, Paul et al. 2005).

Cyanobacterial blooms often develop in coastal zones with significant nutrient input (reviewed in Ahern et al. 2008, Paerl & Huisman 2009) as well as in highly populated and degraded areas (Hawser et al. 1992, Butler 1995, Ritson-Williams et al. 2005). However, there are also reports of these events in isolated places such as the Fijian Islands (Yamamuro 1999), Guam (Pennings et al. 1997, Nagle & Paul 1998, Thacker & Paul 2001, Becerro et al. 2006) and French Polynesia (Charpy et al. 2012). Besides occurring in shallow waters, factors such as high temperature, low wave action, increased nitrogen, phosphorus, and iron availability are related to bloom formation (O'Neil et al. 2000, Kuffner & Paul 2004, Albert et al. 2005, Ahern et al. 2007b, Ahern et al. 2008). While the causes for CyanoHABs (harmful algal blooms) in fresh and brackish waters have been thoroughly studied (reviewed in Paerl et al. 2011, Leão et al. 2012, Paerl & Paul 2012), blooms of marine cyanobacteria are less understood.

Many species of freshwater and marine cyanobacteria have been involved in harmful algal blooms (Cyano-HABs) (Havens 2008, Paerl & Paul 2012). These have direct or indirect negative consequences in planktonic and/or benthic communities, but in particular in organisms they have close contact with (Hallock 2005). In those events, cyanobacteria grow on the substrate, forming mats that affect benthic organisms (Ritson-Williams et al. 2005). Toxins produced by bloom-forming cyanobacteria can also affect sea turtles, mammals (including humans), fishes or invertebrates due to their neurotoxic, cytotoxic or hepatotoxic effects (Sivonen 1996, Sellner 1997, Chorus & Bartram 1999, Metcalf & Codd 2004, Arthur et al. 2008, Humpage 2008, Miller et al. 2010). They also exert a negative impact, as a result of chemical processes such as accumulation and liberation of hydrogen sulfide in

microbial mats or oxygen consumption as blooms recede and decompose (Hallegraeff 1993, Frias-Lopez et al. 2003, Havens 2008). Cyanobacterial blooms affect aquatic communities at various scales (Sellner 1997), competing for light, resources, or substrate (Sivonen 1996, Huisman & Hulot 2005). In coral reefs, cyanobacteria may play similar roles to those of macroalgae in terms of primary production and interactions with herbivores, given their local and seasonal abundance (Paul et al. 2001). For the aforementioned reasons, blooms are considered an important event in reef areas and consequently, there is a strong need to provide basic information on cyanobacteria to reef managers.

Cyanobacteria have fast growth rates and are unpalatable to most generalist herbivores (Thacker et al. 1997, Nagle & Paul 1999, Thacker & Paul 2004, Kuffner et al. 2006, Paerl et al. 2011, Paul et al. 2011), thus achieving high biomass (Ritson-Williams et al. 2005) and covering large areas in different marine ecosystems and habitats in periods of few weeks. Cyanobacterial blooms are seasonally recurrent in reef areas (Paul et al. 2001, Kuffner & Paul 2004, Ritson-Williams et al. 2005, Kuffner et al. 2006), seagrass meadows (Paerl 2002, Pittman & Pittman 2005, Conley et al. 2009), mangroves (Paerl 2002, Pittman & Pittman 2005), estuaries and coastal lagoons (Charpy et al. 2012). In the literature however, there are few detailed descriptions of the presence and coverage of benthic cyanobacteria among different habitats in reef complexes.

Currently, there is a major concern that large scale hydrological disturbances and environmental changes due to global warming facilitate development, frequency, dispersion and expansion of cyanobacterial blooms (Albert et al. 2005, Paerl & Huisman 2008, Paul 2008, Paerl & Huisman 2009). Herein, we report the occurrence of cyanobacteria blooms in Old Providence Island, in order to address their spatial scale, the habitats where they develop and the extent they achieve in different marine habitats. We provide the first detailed marine habitat map for the island and include some information on the main bloom forming taxa in the region. Understanding the incidence, spatial distribution and extension of cyanobacterial blooms may help to propose monitoring and management measures in the Caribbean region.

Materials and methods

Study area

Old Providence Island is part of the Archipelago of San Andrés, Old Providence and Santa Catalina, a group of oceanic islands, submerged banks and atolls located approximately 300 km off the Mosquito coast of Nicaragua (CORALINA-INVEMAR 2012, Bolaños & Acosta 2013). The archipelago is part of the Seaflower Biosphere Reserve established by UNESCO in 2000, a protected area that encompasses roughly 10% of the Caribbean Sea.

Old Providence is an island of volcanic origin (Miocene), with an emerged area of 20 km². The shallow reef complex in Old Providence has a total area of 285 km² and is characterized by the development of different coral formations (Geister 1977, 1986, Díaz et al. 2000). A 32 km long reef barrier runs along the eastern side of the island (García et al. 2003). The dominant associations in the barrier are associations of milleporids and zoanthidians (in the barrier reef and pinacles), patch reefs where predominant taxa are *Montastraea* spp., *Porites astreoides* and *Diploria* spp. and fringing reefs surrounding Kathleena island (Santa Catalina) and the northeast portion of Old Providence. These are characterized by massive corals such as *Siderastrea siderea*, *Diploria* spp. and *Montastraea* spp., along with *Porites* spp. On the western side of the island, the fore-reef terrace is characterized by the dominance of octocorals, macroalgae and corals such as *Dendrogyra cylindrus* (Acosta & Acevedo 2006), *Porites* spp. and *Diploria* spp. (Sánchez 1998, Díaz 2005, Acosta et al. 2011, Bernal-Sotelo & Acosta 2012).

The archipelago has a wet-dry tropical climate, with two major weather seasons: dry (January to April) and wet (June to December), with maximum peaks of rain between October and November (266-301 mm) (González & Hurtado 2012). May is considered a transitional month between seasons (Díaz et al. 1996). The warmer months of the year range between May to late September (Vivas-Aguas et al. 2012). Water temperature varies between 28.2°C ± 1.26 SD (Range: 24-32 °C; Vivas-Aguas et al. 2012). Surface salinity shows average values of 34.8 ± 1.62 (Range: 26-37; Vivas-Aguas et al. 2012). Variations in temperature and salinity between the dry and wet seasons are mostly related to precipitation levels (INVEMAR-REDCAM

2013). It also receives seasonal discharge of fresh water streams (sediments and organic matter input) from the island outwards to the sea (Geister & Diaz 1997).

Prevailing winds from the east and northeast (influence of the northeast trade winds) divide Old Providence Island in a dry eastern side and a western humid side. The months with low current action due to decreased wind speed are May, September and October (Realpe et al. 2012, González & Hurtado 2012). Tides are semi-diurnal but narrow. The western portion of the island is occasionally affected by strong swells.

In the archipelago, nitrate and phosphate concentrations exhibit great variation, with high values surpassing those of other Caribbean locations. Nutrient concentrations vary depending on sites, time of the year and distance to human dwellings (Gavio et al. 2010). In Old Providence island, greater nutrient levels during the wet season are correlated with increased fresh-water runoff by temporary streams or gullies, untreated sewage discharge, landfill leachates, organic and inorganic residues from animal husbandry practices and mangrove leaf litter inputs from the Mc Bean Lagoon area (Vivas-Aguas et al. 2012). Dissolved organic nitrogen values from Old Providence island are on average 74.38 ± 39.43 µg/L (Range: 2.7-281 µg/L), while phosphate concentrations are on average 88.9 ± 183.7 µg/L (Range: 1.8-1352 µg/L; Vivas-Aguas et al. 2012).

Sampling

Field surveys of cyanobacteria were performed in Old Providence Island in three moments. The first set of surveys was performed during the rainy months of October-November 2009 and July 2010, at three reef sites at the western portion of the island (Pinnacles, Felipe's Place and El Planchón). In these surveys we evaluated the cover of benthic cyanobacteria using belt transects covering an area between 30 and 60 m² at each site. We also registered signs such as tissue mortality, overgrowth or direct competition between corals, gorgonians and cyanobacteria. The second set of surveys was performed between October-November 2012. In these, a detailed assessment of benthic and planktonic cyanobacterial blooms on different substrates at the shallow reef complex of Old Providence, between 1 and 15 m depth, was carried out

(Figure 1). In these surveys, a Quickbird Satellite image from 2012 was used to identify and locate habitats and their main benthic components. The satellite image

domain ($13^{\circ}18'-13^{\circ}24'N$ and $81^{\circ}19'-81^{\circ}25'W$) was processed by georeference with field data. Atmospheric correction was performed using the module FLAASH

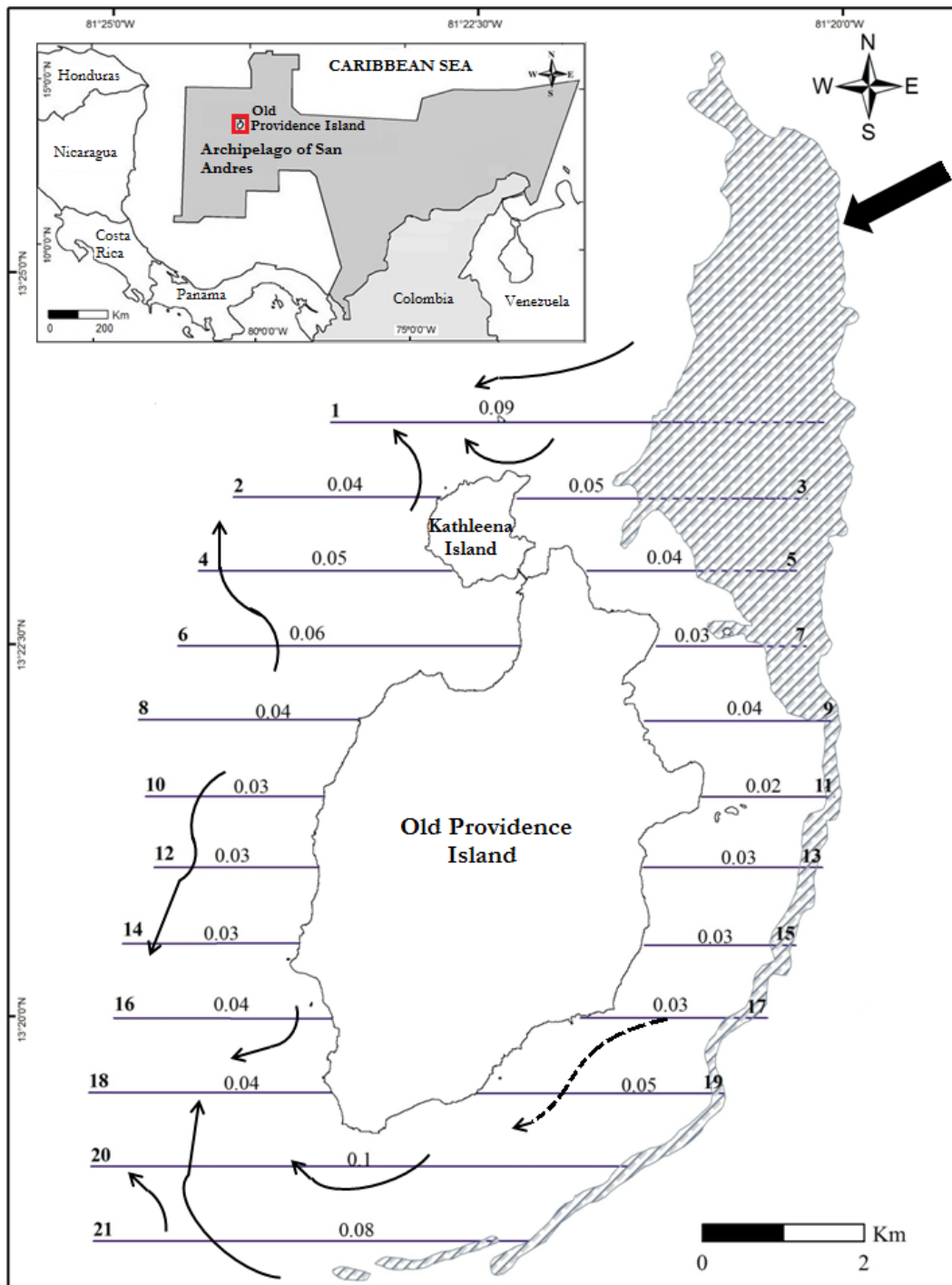


Fig. 1. Study area sampled at Old Providence Island during October 2012. Straight lines around the island represent the sampling transects evaluated by Manta Tow. Bold numbers at the beginning of each transect indicate transect number. Values in the middle of each line show the sampling area of each transect in km^2 . All transects had the same width (0.015 km), but length was variable (transect 1 = 6 km, transect 20 = 7 km, transect 21 = 5 km, transects 3 and 6 = 4 km, transects 2, 4, 5, 8, 16, 18 and 19 = 3 km, transects 7, 9, 10, 11, 12, 13, 14, 15, transect 17 = 2 km). Striped areas along the east portion of the island represent the barrier reef. Bold black arrows show the general pattern of marine currents around the island (Prah 1983). Map system projection is WGS84.

ENVI 5.0 and deglint following Hedley et al. (2005). Application of Lyzenga's (1981) depth invariant index, allowed reducing the interference from the water column and its variable depth following Mumby and Edwards (2000). Twenty one, 15 m wide transects, perpendicular to the coast, were examined to register cyanobacteria presence and relative coverage. Transects were separated from each other by roughly 930 m (30 s; Fig. 1). Transect length varied depending at which side of the island they were placed. Transects on the western side of the island spanned from the shore until the beginning of the reef slope (< 15 m depth), whereas transects on the eastern side of the island spanned from the shore until the beginning of the barrier reef. The Manta Tow technique was applied along each transect, where two divers were tethered to the boat with a 10 m rope and towed over the water surface at a speed of 1-2 knots. Within each transect, we recorded the type and frequency of the different habitats observed and estimated the relative area covered by cyanobacteria. We also recorded and geopositioned (± 3 m), the beginning and the end of each habitat type along each transect. Hence, the extent of each habitat category in the space was considered a "point". All habitat types, reordered

in the sampling, were later used to classify and validate the satellite image (Bernal et al. unpub. data). We registered a total of 550 points that covered different habitat types. Each habitat category was defined by the type and relative cover of its most prominent benthic components, including cyanobacteria. Occasionally, either water depth or turbidity impeded an adequate identification of the main benthic components, so divers descended to take either pictures or samples to correctly identify those features. We recorded blooms either by underwater photographs or video footage (Suppl. 1).

Habitats were classified according to the relative coverage of benthic components following similar studies in the region (Díaz et al. 2000, Benfield et al. 2007, Madden et al. 2008, Walker et al. 2008). Each unit was labeled by initially naming the geomorphologic area where it was located (Figure 2), followed by abbreviations of the main benthic components according to their relative dominance (higher to lower). Components with coverage $\leq 5\%$ were excluded from the habitat label. When elements had similar coverage (difference $\leq 3\%$), the elements were

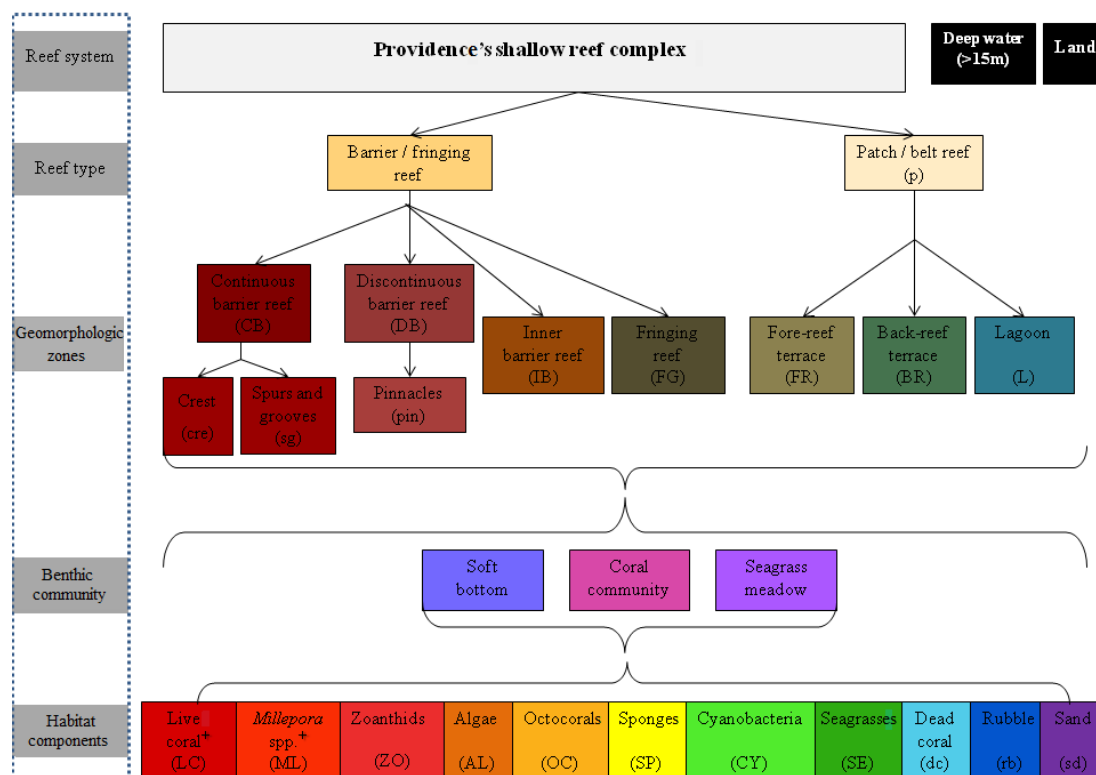


Fig. 2. Scheme of the reef classification, geomorphological zones, benthic communities and components used to categorize and name habitats in the Old Providence Island reef complex.

separated by a hyphen (-), always placing the dominant element in first place. Habitats with presence but very low live coral cover ($\leq 5\%$) were marked with an asterisk (*). The image was segmented into objects using Berkeley Image Segmentation software. Then, each segment was assigned to a category of habitats, following field surveys, visual interpretation of the image and the pattern of spectral signatures. The image was then validated with 152 points referenced in the field (following Chuvieco 2008), resulting in an overall accuracy of 94 % and a 0.94 Kappa coefficient (Mumby & Edwards 2000). Finally, we generated a map of the habitats where cyanobacteria were found as well as the area (km²) occupied by each unit and the area occupied by cyanobacteria within the unit.

Additionally, we used DIVA-GIS 7.4.0 software to generate a map representing the frequency in which cyanobacteria were recorded in georeferenced field points. The map was divided into spatial cells of 270 x 270 m (0.073 km²) in which we identified cyanobacteria density or the number of points with cyanobacteria (absolute record frequency). Each cell was identified with a specific color according to the frequency of points (white= 0 points, blue= 1 point, turquoise= 2 points, yellow= 3 points; red= 4 points, where the minimum registered value per cell was 0 points and the maximum registered value per cell was 4 points).

The third set of surveys was performed during December 2012. In these, we assessed the accumulation of drifting cyanobacteria on Old Providence beaches.

We do not perform long term assessments of environmental parameters such as nutrients, salinity or temperature in any of our surveys. During underwater surveys, a small sample of cyanobacterial mats (10 to 20 g) was collected and preserved in 4% formalin in seawater, to identify the main bloom forming species. To identify the different cyanobacterial morphotypes, three portions of each sample were analyzed under a Nikon optical microscope. The microscope was connected to a digital camera. The captured images were analyzed using NIS-Elements Br 2.30 Nikon Imaging Software, which allows performing the necessary measurements of each morphological attribute under several magnifications up to 100X. Characters considered for species identification were trichome width, cell length, presence of calyptrae, filament isopolarity, shape of apical cells, presence

of intertabular constrictions and presence of mucilaginous cases (Komárek & Anagnostidis 2005). Taxonomic identification of cyanobacteria has been traditionally performed on the basis of morphological parameters, especially in those belonging to the order Oscillatoriales due to their large cell size (Thacker & Paul 2001, Charpy et al. 2010, Engene et al. 2010). For the purposes of this paper we report the most common taxa found during field surveys after Komárek & Anagnostidis (2005) and Engene et al. (2013b). During the period between 2011 and 2014 there has been a profound reevaluation of the group systematics beyond genera reassignment, showing great genetic diversity, and wide morphological and chemical variation (Thacker & Paul 2004, Engene et al. 2010, Engene et al. 2011, Engene et al. 2012, Engene et al. 2013a, Engene et al. 2013b). Blooms of marine benthic cyanobacteria are not monospecific and “accurate” species identification involves molecular and chemotaxonomical analyses. However, there are still many sequences that can only be resolved at a genus level. Therefore, a species list of bloom forming cyanobacteria with their mean abundances or maps indicating their spatial distribution was not performed.

Data analysis

Data coverage (%) of each benthic component, as well as the coverage of benthic cyanobacteria (km²), were compared between habitats applying the non-parametric Kruskal-Wallis test since data did not adjust to a normal distribution (Kolmogorov-Smirnov test for coverage data: $n= 184$, $p < 0.05$ and Shapiro-Wilk test for area occupied by cyanobacteria: $n= 9$, $p < 0.05$), or were not homoscedastic (Levene test for coverage and area: $n= 184$ and $n = 9$, $p < 0.05$).

Results

Cyanobacterial mats were complex microbial consortia always composed by several cyanobacteria “species” (Figure 3). The most frequent mats were dominated by *Okeania* cf. *erythroflocculosa* (Engene et al. 2013b) and appeared as thick red mats overgrowing sand, rubble and macroalgae over hard substrates. We also found a great abundance of thick, puff-like mats composed by *Symploca hydroides* (Kützinger ex Gomont 1892) and *Phormidium submembranaceum* (Ardissonne et Straforello 1877 ex Gomont 1892). Those mats were particularly abundant



Fig. 3. (a, b) An assemblage of *Okeania* spp. overgrowing the base of a sea rod *Eunicea* sp. Bleaching and tissue damage became apparent after the cyanobacterial mat was removed. (c, d) An assemblage of *Symploca hydroides* and *Phormidium submembranaceum* growing over a *Montastrea franksi* colony. Tissue death was evident after the cyanobacterial mat was removed. (e) Red encrusting biofilms (assemblages of *Oscillatoria* spp., *Phormidium gracile* and *Lyngbya* spp.) rapidly overgrew gorgonian corals exposing the gorgonin matrix which was rapidly fouled. (f) Drifting mats of *Trichodesmium* entangled in a *Dendrogyra cylindrus* column. Prolonged contact with cyanobacteria caused bleaching and signs of white syndromes in the coral.

at the Pinnacles NE of the island and developed over the locally abundant *Turbinaria* and *Dictyota* macroalgae. Thin red or brown films were very common over well illuminated sandy substrates. These mats were composed by complex assemblages of *Oscillatoria* spp., *Lyngbya* spp. and *Phormidium* spp. in varying proportions. On the other hand, vertical mats growing under ledges or large corals, were only found at the Pinnacles NE of the island.

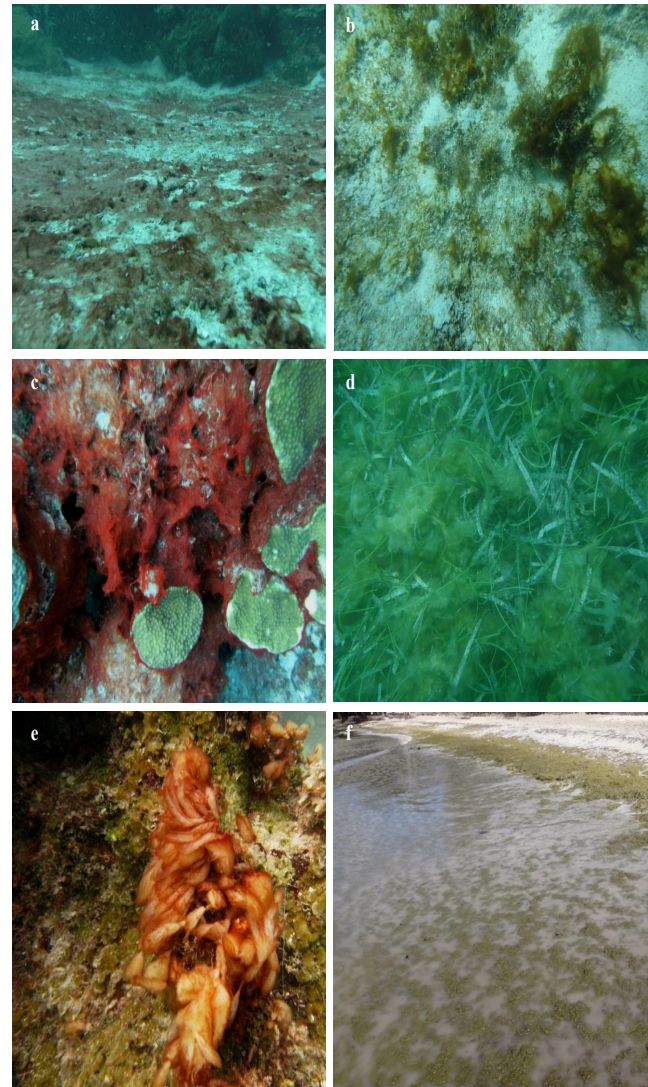


Fig. 4. Ecosystems and habitats in the Old Providence Island reef complex with extensive cyanobacteria cover (a) sandy bottoms, (b) calcareous algae and sand, (c) coral dominated reefs (d) Seagrasses (*Thalassia-Syringodium*), (e) macroalgae over dead coral, (f) accumulation of cyanobacteria at Southwest Bay beach after a three-day period of storms in November 2012. (Photo: Jim Robinson Martinez) The event also took place in December 2013.

These were composed of long red strands of *Oscillatoria* cf. *acuminata* (Gomont 1892) interspersed with few *Spirulina subsalsa* (Oersted ex Gomont 1892) filaments. Additionally, very thin red biofilms were sporadically found overgrowing gorgonians, displacing live tissue and exposing the gorgonin matrix (M. Puyana, unpub. data). These particular mats were complex microbial consortia of *Oscillatoria* spp., *Phormidium* (= *Leptolyngbya*)

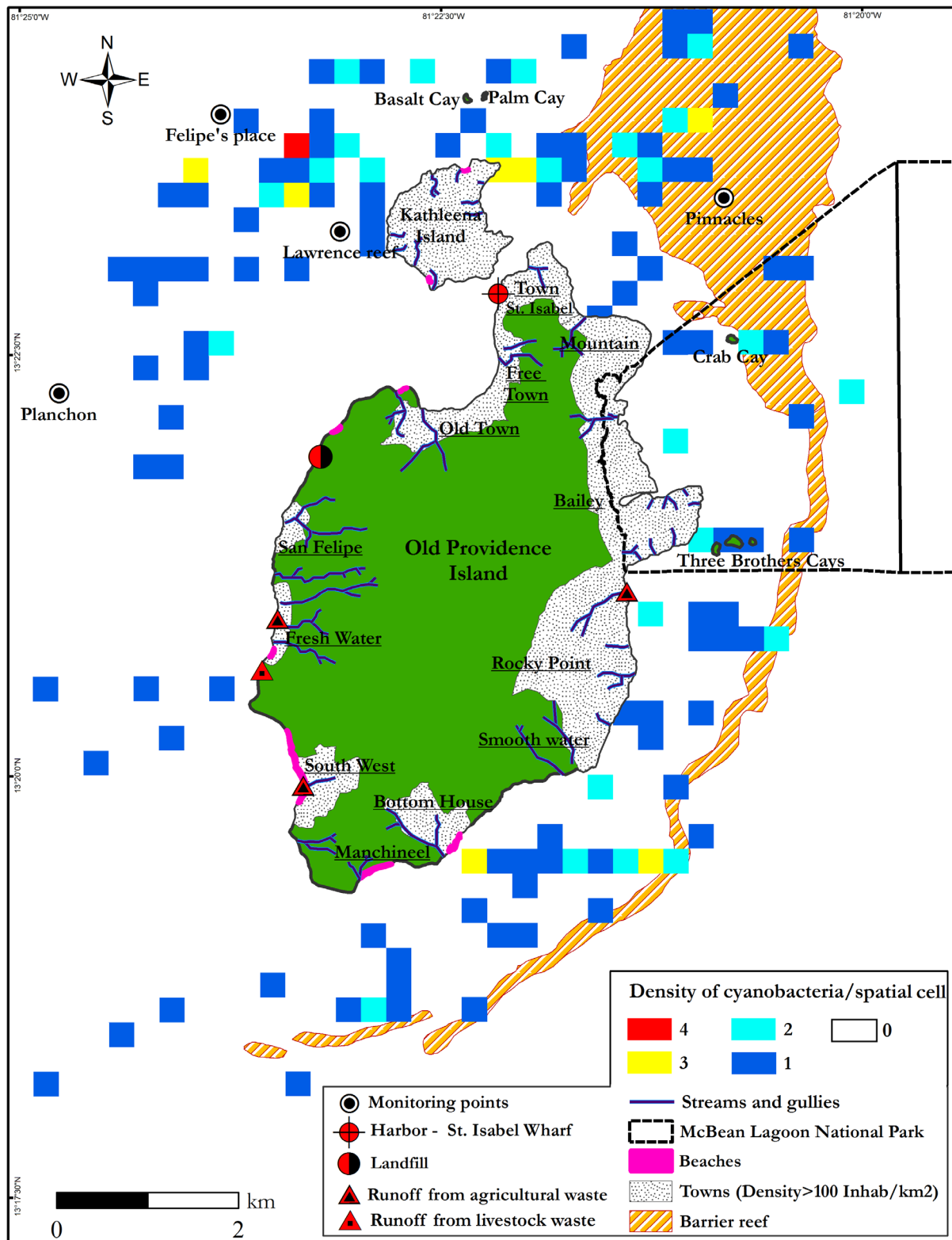


Fig. 5. Cyanobacterial density (frequency of field points) in the Old Providence Island shallow reef complex. The area was divided in 270 x 270 m spatial cells (0.073 km²). Note red and yellow spatial cells (north-west) with the greatest number of sampling points with presence of cyanobacteria. In white spatial cells, cyanobacteria were not recorded. Main pollution sources are shown following Vides & Sierra-Correa (2003): Streams and gullies, population density of main towns, harbor, landfill and runoff sources from livestock and agricultural waste activities. Names of the main towns are underlined. The borders of the Old Providence McBean Lagoon National Park are indicated in the map. Monitoring sites from 2009 to 2010 are also shown.

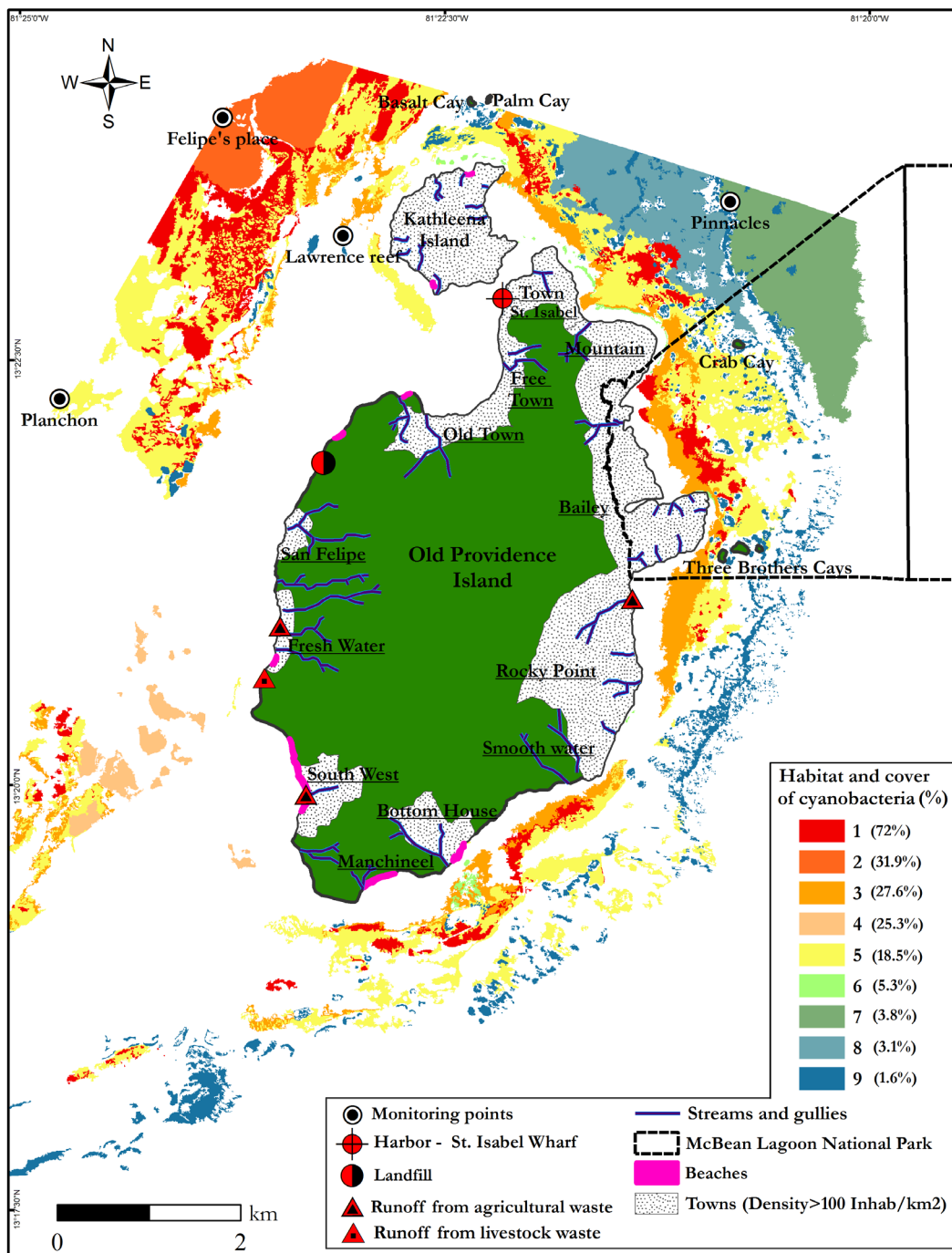


Fig. 6. Spatial distribution and cyanobacteria cover in different marine habitats in the Old Providence Island shallow reef complex. Note that the island was surrounded by cyanobacteria, but with the highest cover (red to yellow spatial cells) towards the north-west and north east portions. Numbers from 1 to 9 represent habitat code organized from those with highest (1) to lowest (9) cyanobacteria cover. Total benthic cyanobacteria cover >15% was considered high. Habitats: 1. FR-BR-L: Cyanobacteria and sand. 2. FR: Cyanobacteria, algae-dead coral and mixed coral-octocoral-sand. 3. L: Seagrasses, cyanobacteria and sand. 4. L: Sand, cyanobacteria and octocoral. 5. FR-BR-L: Sand and cyanobacteria. 6. FG-Lp: Algae, mixed coral, seagrass and dead coral-sand. 7. DBpin: Algae, sand and dead coral-*Palmythoa* spp.-*M. complanata**. 8. Lp: Sand, algae and dead coral*. 9. BRp-Lp: Algae and sand-dead coral-rubble*. BR=Back-reef terrace. BRp=Patch reef of the back-reef terrace. DBpin=Pinnacles of the discontinuous barrier reef. FG=Fringing reef. FR=Fore-reef terrace. FRp=Patch reef of the fore-reef terrace. L=Lagoon. Lp=Patch reef of the lagoon. Habitats marked with an asterisk (*) had a live coral cover ≤ 5%. Main pollution sources are shown following Vides & Sierra-Correa (2003): Streams and gullies, population density of main towns, harbor, landfill and runoff sources from livestock and agricultural waste activities. Names of the main towns are underlined. The borders of the Old Providence McBean Lagoon National Park are indicated in the map.

gracile (Meneghini ex Gomont, Anagnostidis 2001) and occasionally *Lyngbya* spp. Field surveys revealed signs of coral bleaching or tissue necrosis upon direct contact between benthic cyanobacteria and hard and soft corals (Figure 3). Moreover, the complex assemblages of thin red biofilms overgrowing gorgonians displaced live tissue, leaving behind the exposed gorgonin matrix, which was in turn rapidly fouled by algae and hydroids (Figure 3).

In late October 2012 (wet season), we recorded a massive shallow (1-15 m) bloom of planktonic cyanobacteria (Suppl. 1) and ctenophores at the NW portion of the island (13°22'47.8" N-81°23'57.3"W). Unlike previous findings (Quintana 2011; Prato 2013) the bloom thrived at various levels in the water column (calm water, no currents) considerably hindering horizontal visibility (< 15 m). The bloom accumulated as thick (40 cm) drifting mats over the reef bottom (Suppl. 1) and by November 2012, it had spread over a large area. Microscopical analyses revealed that the bloom was dominated by *Trichodesmium* interspersed with some *Lyngbya* filaments. *Dendrogyra* corals were affected by these planktonic blooms (Figure 3). As cyanobacterial mats drifted over the corals, they got entangled in the column structure and promoted the onset of white syndromes and partial death.

In Old Providence Island blooms of benthic and planktonic cyanobacteria developed in four ecosystems: benthic blooms over sandy bottoms, seagrasses and coral reefs (Figure 4), and planktonic blooms in the pelagic zone (Suppl. 1). Benthic cyanobacteria were also present in six geomorphological zones (Back-reef terrace, Patch reefs, Pinnacles, Fringing reefs, Fore-reef terrace and Lagoon) and nine habitats. While the planktonic bloom occurred only in the Fore-reef terrace and in one habitat (FR: cyanobacteria -60 %, dead coral -30 %, and live mixed coral 10 % cover).

The presence of benthic cyanobacteria was observed all around the island (Figure 5). Those blooms were more prevalent at the NW portion of the island (Felipe's Place, Lawrence Reef and El Planchón; Figure 5), where the highest live coral cover remains 14.1 ± 3.9 % on average. Only 6.3 % of the spatial cells had high densities of cyanobacteria (3 or 4 points with cyanobacteria; 5.5 % with three points, 0.8 % with four points), mainly in the N portion of the island, where most spatial cells (270 x 270 m) had 3 or 4 points with cyanobacteria (Figure 5). Most (> 90 %) spatial cells; however, had low cyanobacteria density (between 1 and 2 points where cyanobacteria were present: 74 % with one point, 19.7 % with two points; total cells with cyanobacteria = 127; Figure 5).

Table 1. Relative cover of benthic cyanobacteria and total area sampled in marine habitats at Old Providence Island shallow reef complex. Symbols represent the habitat code assigned in maps and other figures. Habitats were organized from those with highest (1) to lowest (9) cyanobacteria cover. Habitats marked with an asterisk (*) had a live coral cover ≤ 5 %. HB=Habitat. The first letters in each habitat are abbreviations indicating the geomorphologic zones where they were located: BR=Back-reef terrace. BRp=Patch reef of the back-reef terrace. DBpin=Pinnacles of the discontinuous barrier reef. FG=Fringing reef. FR=Fore-reef terrace. FRp=Patch reef of the fore-reef terrace. L=Lagoon. Lp=Patch reef of the lagoon. Other components in the habitat names are listed in descending order of benthic coverage.

Symbol	Habitat	Depth interval (m)	Total HB area (Km ²)	Area covered by cyanobacteria/HB (km ²)	Cyanobacteria cover (%)
1	FR-BR-L:Cyanobacteria and sand	0.4-15.3	2.6	1.89	72
2	FR:Cyanobacteria, algae-dead coral and mixed coral-octocoral-sand	3.6-15.3	1.1	0.35	31.9
3	L:Seagrass, cyanobacteria and sand	0.4-13.1	2.1	0.57	27.6
4	L:Sand, cyanobacteria and octocoral	0.4-13.1	0.5	0.13	25.3
5	FR-BR-L:Sand and cyanobacteria	0.4-15.3	7	1.29	18.5
6	FG-Lp:Algae, mixed coral, seagrass and dead coral-sand	0.5-7.7	0.1	0.01	5.3
7	DBpin:Algae, sand and dead coral-Palythoa spp.-M. complanata*	0.6-8.9	2.1	0.08	3.8
8	Lp:Sand, algae and dead coral*	0.4-13.1	1.6	0.05	3.1
9	BRp-Lp:Algae and sand-dead coral-rubble*	1.2-9.1	2.1	0.03	1.6
Total			19.2	4.4	

Blooms of benthic cyanobacteria developed as mats that varied in extension, color and thickness. They also varied on the types of habitat they were found. A large scale analysis revealed that nine of the 25 habitats registered on the shallow reef complex of Old Providence Island, (Table 1) had a relative coverage of cyanobacteria >1 %, at the fore reef (NW), pinnacles (NE), reef flat and lagoon (E) of the island. The total area of these nine habitats represents 30 % of the shallow reef complex, spanning an area of 64.3 km². During cyanobacterial blooms, five of the nine habitats (55.5 %) had high cyanobacteria cover, reaching 18 to 72 % of the total cover, particularly at the northwest, east and southeast portions of the island. Cyanobacteria covered over 4.2 km² of the reef complex (from 64.3 km² sampled; Figure 6) particularly in those habitats with low live coral cover and high coverage of sand, macroalgae, dead coral or seagrasses.

The habitat dominated by cyanobacteria that achieved the greatest extension was 5 (FRBRL: Sand and cyanobacteria; Table 1), spanning an area of 7 km². However, the greatest cyanobacteria cover (72 %) was registered in habitat 1 (FRBRL: Cyanobacteria and sand). This habitat was the second in extension covering an area of 2.6 km² and spanning around the island's contour, especially towards the NW. Habitats with cyanobacteria coverage between 18 and 32 % (2 - FR: Cyanobacteria, algae-dead coral and mixed coral-octocoral-sand, 5 - FRBRL: Sand and cyanobacteria), stretched around the reef complex. Habitats with cyanobacteria coverage lower than 6 % (6 - FG-Lp: Algae, mixed coral, seagrass and dead coral-sand; 9 - BRp-Lp: Algae and sand-dead coral-rubble; Table 1) were registered all along the eastern side of the island, from South to North, particularly at the NE end of the complex (Figure 6). Within the protected area of McBean Lagoon National Park (PNN McBean) and its surroundings, we also detected foci with high cover of cyanobacteria (>70 %; Figure 6).

Overall, in habitats 5, 1, 3, 7 and 9 (BRp-Lp: Algae and sand-dead coral-rubble*) the area covered by cyanobacteria was >2 km², whereas in the other four habitats, the area covered by cyanobacteria was lower (Figure 7A; Table 1). However, there were no significant differences in the area covered by cyanobacteria within all nine habitats (H: p>0.05,

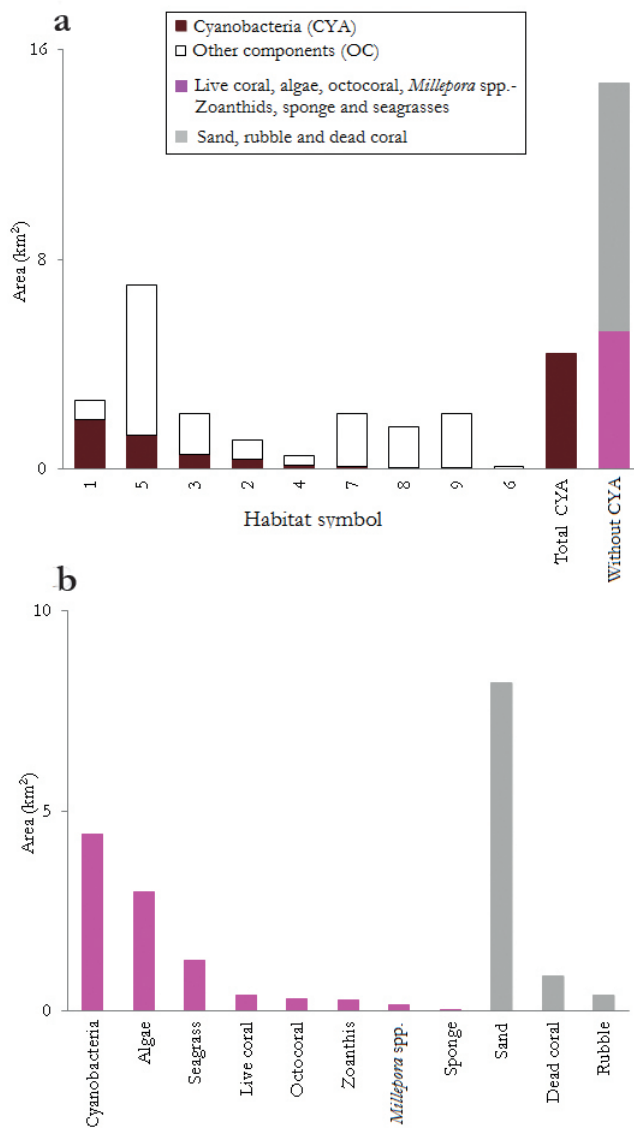


Fig. 7. (a) Total area covered by cyanobacteria in each habitat related to cover of live organisms and other substrate components. (b) Total area covered by live organisms and substrate components in all nine habitats. Other components include the sum of all organisms and substrate types. 1. FR-BR-L: Cyanobacteria and sand. 2. FR: Cyanobacteria, algae-dead coral and mixed coral-octocoral-sand. 3. L: Seagrasses, cyanobacteria and sand. 4. L: Sand, cyanobacteria and octocoral. 5. FR-BR-L: Sand and cyanobacteria. 6. FG-Lp: Algae, mixed coral, seagrasses and dead coral-sand. 7. DBpin: Algae, sand and dead coral-*Palythoa* spp.-*M. complanata**. 8. Lp: Sand, algae and dead coral*. 9. BRp-Lp:Algae and sand-dead coral-rubble*. BR=Back-reef terrace. BRp=Patch reef of the back-reef terrace. DBpin=Pinnacles of the discontinuous barrier reef. FG=Fringing reef. FR=Fore-reef terrace. FRp=Patch reef of the fore-reef terrace. L=Lagoon. Lp=Patch reef of the lagoon.

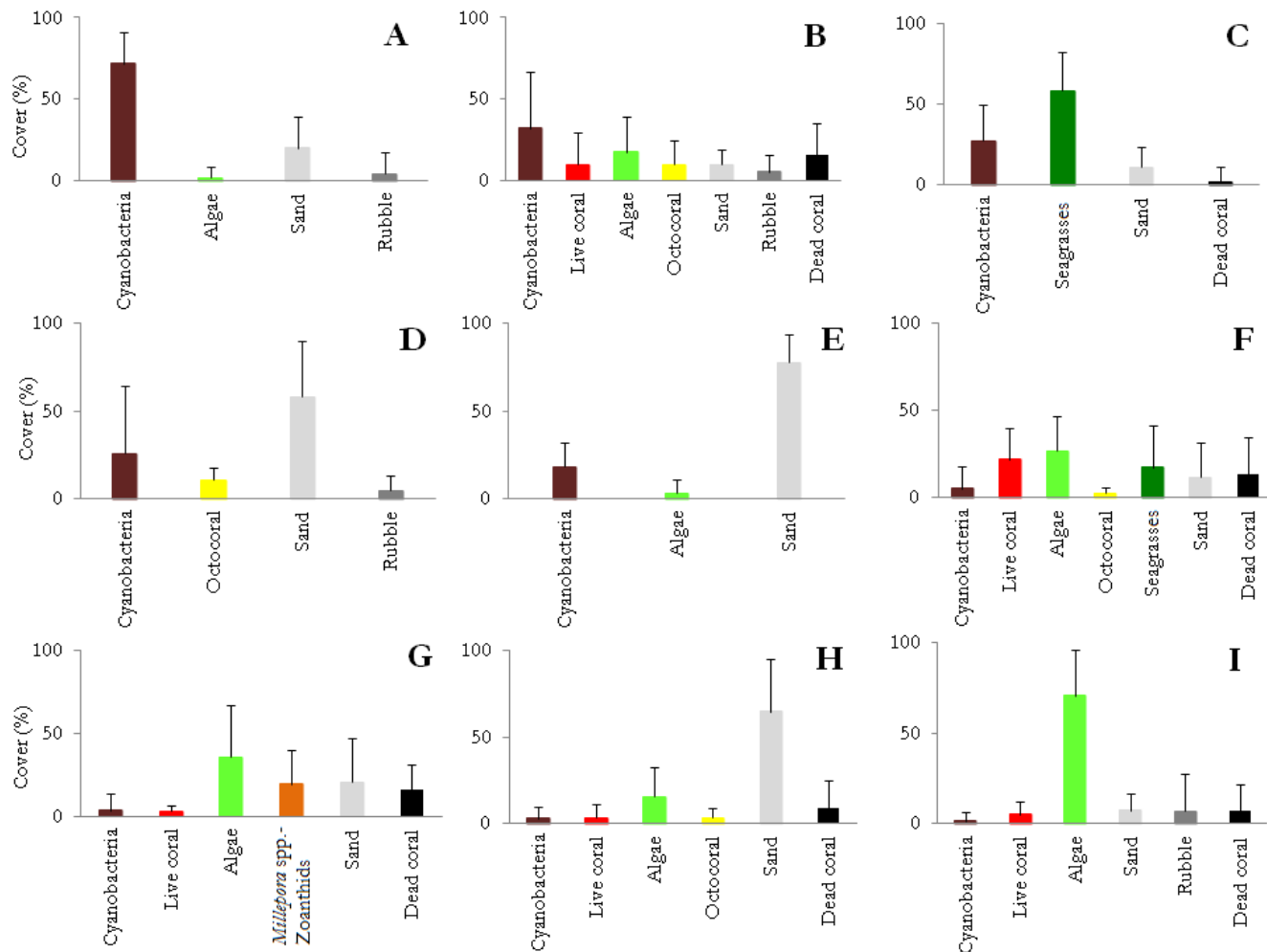


Fig. 8. Relative cover (%) of live organisms and other substrate components in the different habitats where cyanobacteria were registered. 1. FR-BR-L: Cyanobacteria and sand (a) 2. FR: Cyanobacteria, algae-dead coral and mixed coral-octocoral-sand (b) 3. L: Seagrasses, cyanobacteria and sand (c) 4. L: Sand, cyanobacteria and octocoral (d) 5. FR-BR-L: Sand and cyanobacteria (e) 6. FG-Lp:Algae, mixed coral, seagrasses and dead coral-sand (f) 7. DBpin: Algae, sand and dead coral-*Palythoa* spp.-*M. complanata** (g) 8. Lp: Sand, algae and dead coral* (h) 9. BRp-Lp: Algae and sand-dead coral-rubble* (i). BR=Back-reef terrace. BRp=Patch reef of the back-reef terrace. DBpin=Pinnacles of the discontinuous barrier reef. FG=Fringing reef. FR=Fore-reef terrace. FRp=Patch reef of the fore-reef terrace. L=Lagoon. Lp=Patch reef of the lagoon.

n=9). Therefore, the intensity of cyanobacteria was homogeneously distributed in all nine habitats, around the island. The total area covered by cyanobacteria in all habitats (4.4 km²) was 0.89 km² less than the total area covered by live organisms (algae, seagrasses, live coral, octocorals, zoanithids, *Millepora* and sponges; 5.3 km²; Figure 7A).

Within living components, cyanobacteria had the greatest coverage in all habitats followed by algae (2.96 km²) and seagrasses (1.25 km²). The remaining categories occupied less than 0.4 km² each (Figure

7B). Sandy bottoms covered an area of 8.21 km², half of it was covered by cyanobacteria (Figure 7B).

The average coverage of live components and other substrates was significantly different among all habitats (H: n=184, p<0.05). In most habitats though, categories with the greatest coverage were, aside from cyanobacteria, sand, algae, seagrasses and dead coral (Figure 8). Only in habitat 6 (FG-Lp: Algae, mixed coral, seagrasses and dead coral-sand) we registered a live coral coverage >20 % whereas in habitats 7 and 8 (7=DBpin: Algae, sand and dead coral-*Palythoa* spp.-*M.*

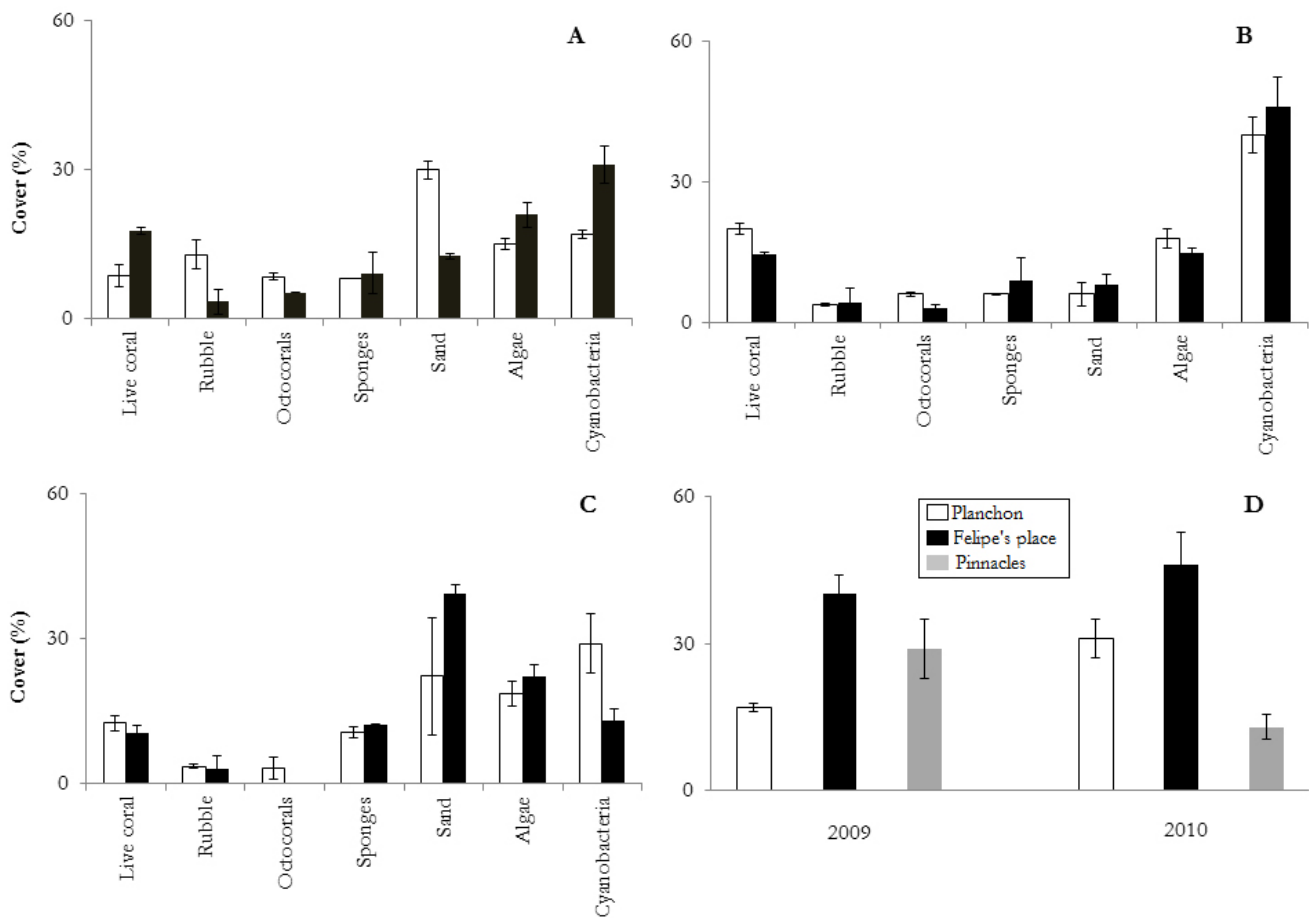


Fig. 9. Spatial and temporal comparison of the relative cover (average \pm SE) of benthic cyanobacteria and other components at three different sites: (A) Planchón, (B) Felipe's Place, and (C) Pinnacles in Old Providence Island during the wet season, (D) cyanobacteria coverage in October-November 2009 (white bars) and July 2010 (black bars). White bars: Planchón; Black bars: Felipe's Place; Gray bars: Pinnacles.

*complanata**, 8=Lp: Sand, algae and dead coral*) live coral cover never exceeded 4 %. Extensive cyanobacteria cover was observed associated to sandy bottoms, rubble, dead coral, seagrasses (*Thalassia-Syringodium*), macroalgae and mixed corals (Figure 8; Table 1).

We have witnessed high benthic cyanobacterial cover off Old Providence Island over the years. In 2009 and 2010, cyanobacteria cover was greater than 15 %, of the total benthic cover in most cases (Figure 9), surpassing live coral cover. Cyanobacteria coverage increased from 2009 to 2010, except for the Pinnacles area.

As a general trend, blooms of benthic cyanobacteria developed during the wet season and warmer months of the year from July to late October, while drifting cyanobacteria developed on October-November after periods of heavy rains. In both scenarios, blooms also developed during episodes of calm water conditions due to decreased wind speed and low current action.

Discussion

Blooms of marine benthic cyanobacteria have been recorded in the Caribbean region (Hayes et al. 2001,

Paerl 2002, Ritson-Williams et al. 2005, Littler et al. 2006). These are now common in Puerto Rico (Stielow & Ballantine 2003), the Bahamas, Belize and St. John in the US Virgin Islands (Paul et al. 2005, Ritson-Williams et al. 2005), as well as in Mexico (Escobar & Machain 2005), Costa Rica (Muñoz-Simon 2012), and Florida (Paul et al. 2005). In the southern Caribbean, Prato (2013) noted bloom of benthic cyanobacteria in the continental and oceanic islands of Colombia. To date, however, there are no reports of marine cyanobacterial blooms in the Colombian Caribbean (particularly planktonic blooms), although several species have been recorded in floristic lists in the region (Díaz-Pulido & Díaz-Ruíz 2003, Reyes et al. 2013). Benthic cyanobacterial mats in Old Providence, consisted of complex consortia belonging to the genera *Okeania*, *Lyngbya*, *Symploca*, *Phormidium* and *Oscillatoria* which have also been reported in other tropical areas (Hamisi et al. 2004, Thacker & Paul 2004, Charpy et al. 2010, Engene et al. 2013a, b). At Old Providence Island, as well as in other Colombian Caribbean reefs off the continental shelf such as Rosario Islands and Barú, cyanobacteria have become more conspicuous, frequently surpassing live coral cover (Puyana M & Acosta A, unpub. data). However, the impacts of benthic cyanobacteria in the Colombian Caribbean were only recently addressed in studies aimed at understanding their distribution and ecological interactions (Prato 2013) as well as their natural product's chemistry (Bayona 2011, Quintana 2011). Nonetheless, the apparent cyclic nature of cyanobacterial bloom onset over diminished coral cover has not been assessed.

We observed that cyanobacteria affected four marine ecosystems (soft bottom, seagrasses, coral reefs and the pelagic zone), most geomorphological reef zones and several marine habitats. Paul et al. (2005) and Engene et al. (2013b) have also found that benthic cyanobacteria grow and develop over various kinds of substrates.

Oceanic and continental Colombian reefs were once dominated by corals. Nowadays, however, other benthic components such as cyanobacteria or macroalgae, are much more conspicuous. We do not know if high cyanobacterial coverage represents a real tendency, or only reflects the fact that we are currently acknowledging their presence. We also ignore whether they are a permanent or temporal component of

the benthos. This demands thorough monitoring efforts. Of the twenty five habitats recognized in the Old Providence reef complex, 30 % of them had cyanobacteria coverage > 18 %. Hence cyanobacteria have become important and obvious benthic components, surpassing in many cases, live coral. Such was the case of habitat 1 (FRBRL: Cyanobacteria and sand), habitat 2 (FR: Cyanobacteria, algae-dead coral and mixed coral-octocoral-sand), habitat 3 (L: Seagrass, cyanobacteria and sand) habitat 4 (L: Sand, cyanobacteria and octocorals) and habitat 5 (FRBRL: Sand and cyanobacteria). These results indicate that cyanobacteria can reach significant coverage in habitats dominated by live organisms such as corals, macroalgae, seagrasses or octocorals.

Of particular interest are the potential effects of these blooms on habitats with live coral cover, because cyanobacteria may be aggressive space competitors, diminishing the availability of adequate substrates for larval settlement and affecting the recruitment of juvenile corals (Paerl 2002, McCook et al. 2001, Kuffner et al. 2006, Prato 2013). Cyanobacteria also developed on macroalgae. According to our observations, macroalgae seem to provide substrate for cyanobacteria since filaments get entangled in the algae, thus preventing detachment by water motion. As algae become more abundant in coral reefs, they may potentially harbor more cyanobacteria. We have not addressed any effects (negative or positive) of cyanobacteria growing over algae, but we cannot discard the notion that they might compete for the same resources, such as substrate, light and/or nutrients (Paul et al. 2005, Paul et al. 2011). In Old Providence island, seagrasses were not exempt of cyanobacteria growth. Seagrasses act as sediment and nutrient traps, providing substrate and resources for cyanobacterial growth (Stielow & Ballantine 2003, Hamisi et al. 2004, Albert et al. 2005). We have witnessed how profuse growth of benthic cyanobacteria, eliminated, in a few month period, a patch of *Thalassia* and *Syringodium* in San Andres Island, after continuous exposure of wastewater discharged by a hotel directly into the sea (Acosta A, unpubl. data). According to Miller (2009) the dominance of cyanobacteria and fleshy macroalgae on seagrass beds in St. Barthelemy Island is an indicator of elevated land-based sources of nutrient pollution such as run-off from coastal development, septic tank leakage and sewage input.

In our surveys, cyanobacteria were more widespread and frequent over shallow (1-15 m) sandy substrates and over dead corals. Greater light availability and low rugosity could favor the development of microbial mats over sandy bottoms. These hypotheses however, require further testing. Another advantage of growing on sandy bottoms and dead corals could be related to the lack of competitive interactions with other benthic organisms such as cnidarians that may pose some kind of resistance to cyanobacterial growth at various levels (Kuffner et al. 2006). Low perturbation by grazers in sandy bottoms, and a low herbivory regime over dead coral, may also facilitate the formation of cyanobacterial mats on benthic habitats (Fenchel 1998).

Sites with the greatest density of cyanobacteria, as well as habitats with the highest cyanobacteria coverage, were located at the NW portion of the island. This area is subject to several anthropic influences and pollution sources such as the Santa Isabel pier, the sanitary landfill, two of the main towns of the island (Old Town and Free Town, which have more than 100 inhabitants/km²), and fresh water discharge from agricultural and livestock activities through temporary and permanent gullies (Figures 5 and 6; Vides & Sierra-Correa 2003, CORALINA-INVEVAR 2012). In addition, at the NW portion of the coral reef complex, there is a convergence of local currents in the island (Prahl 1983; Figure 1), which may help concentrate the cyanobacteria as well as the resources they require to grow.

A high cyanobacteria percent coverage was found at the NW of Providence over several habitats (18 -72 %). Similar values have been reported in other tropical areas. Stielow and Ballantine (2003) monitored blooms of *Lyngbya majuscula* off the coasts of Puerto Rico from September 1998 until February 2000. Total coverage of cyanobacteria ranged between 7 % and 82 %, occasionally reaching a 100% cover. Likewise, Ahern et al. (2007b) mapped and described the temporal dynamics of a *Lyngbya majuscula* bloom in Australia. The bloom was seasonal, ranging from a cover of less than 10 % (49 hectares) up to 40 % (329 hectares). Once the bloom reached its highest peak, it covered almost 100 % (529 hectares) of the bottom. Although the total coverage of benthic cyanobacteria in Old Providence Island never reached 100 % in any habitat or ecosystem, the observed patterns in coverage of

benthic cyanobacteria correspond well to those values reported in the literature for degraded reefs.

In our study, the habitats surveyed with cyanobacteria –as a major component– covered an area equivalent to 19.2 km². Roughly 23 % of this area (4.4 km²) had a cyanobacteria cover > 18 %. Of the total area covered by cyanobacteria, 96 % (4.3 km²) had a coverage >18 %. We propose that cyanobacteria coverage >15 % could be used as a threshold level to indicate adverse reef health in Old Providence Island.

In Old Providence Island a massive bloom of planktonic cyanobacteria was also registered at the NW portion of the island. This bloom increased turbidity and restricted light penetration in the water column (Suppl. 1). Planktonic cyanobacterial blooms affect water quality, planktonic and benthic communities (Kuffner et al. 2006, Paerl & Paul 2012). Drifting cyanobacteria eventually sink, producing a thick cyanobacterial mat covering the reef for some weeks. Some of the competitive mechanisms between cyanobacteria against corals, octocorals or algae include anoxia, overgrowth or allelopathic effects via the production and exudation of toxins or allelochemical compounds (Hawser et al. 1992, Paerl 2002, Kuffner & Paul 2004, Codd et al. 2005, Ritson-Williams et al. 2005, Kuffner et al. 2006, Littler et al. 2006, Titlyanov et al. 2007), which cause polyp retraction, bleaching, tissue loss or mortality (Ritson-Williams et al. 2005, Littler et al. 2006, Smith et al. 2008, Hauri et al. 2010). Additionally, several authors have indicated that cyanobacteria and turf algae may prevent or inhibit the settlement of coral larvae (Edmunds & Carpenter 2001, McCook et al. 2001, Kuffner & Paul 2004, Kuffner et al. 2006, Vermeij et al. 2010), or favor the transport or settlement of potential pathogens that induce coral diseases. Recent studies in Old Providence Island (Acosta et al. 2011, Bernal-Sotelo & Acosta 2012) show that less than 10 % of live coral cover remains, whereas two decades earlier live coral occupied up to 35-40 % of the reef hard substrates (Acosta & Martínez 2006). Low live coral cover and relatively low recruitment rates (Acosta et al. 2011) could be further reduced by the onset and development of cyanobacterial blooms which can occupy the substrate for several weeks or months, forming patches of dwindling size (M. Puyana, pers. obser.), limiting the natural recovery of the reef ecosystem. These are some of the reasons why we

consider cyanobacterial blooms as a new stressor for reef communities. Sellner (1997), Howarth et al (2000) and Gilby et al (2011) indicate that cyanobacterial blooms exert negative changes in the composition, structure and interactions in benthic (medium to long-term) and planktonic communities, altering food webs as well. It is also important to mention that several benthic cyanobacteria produce toxins that can cause liver damage, gastrointestinal or skin disorders in humans exposed to them (Golubic et al. 2010, El-Shehawy et al. 2012). To date, however, there are no reports of toxicity to humans in the Colombian Caribbean as a result of contact with marine benthic cyanobacteria.

Cyanobacterial blooms could be temporal or permanent stressors for the reef complex of Old Providence Island, depending on several factors such as the local hydrographic regime (major current heading SW), that may play an important role in the attenuation, export or temporary elimination of cyanobacteria. Becerro (2006) indicated that wave surge, storms and intense tidal flow or currents, may export large amounts of cyanobacterial biomass either to the open sea or towards other neighboring ecosystems including the seashore. We witnessed a significant accumulation of cyanobacteria at Southwest Bay (Figure 4), after a three-day period of storms. This process may eventually release the pressure in the affected ecosystems by reducing direct interactions and competition between cyanobacteria and corals, macroalgae and seagrasses.

In Old Providence Island, Prato (2013) observed high cover of benthic cyanobacteria, especially during some of the warmer months of the year (June to August), where the mean water temperature was >29 °C. We observed a similar pattern in July but extended to October-November where cyanobacteria coverage was also high. Vivas-Aguas et al. (2012) indicated May to late September as the warmer months of the year (between 28.2 °C \pm 1.26 SD, with a maximum temperature of 32 °C). Although the temperature slightly decreases in October-November, it remains high until January. This usually high temperatures at the end of the year could favor the continuity of cyanobacteria blooms. Different studies have shown that there is a positive correlation between temperature increase and cyanobacterial growth (Thacker & Paul

2001, Watkinson et al. 2005, Ahern et al. 2007b, Paerl & Huisman 2008). The effect of temperature on increased cyanobacteria cover was documented by Ahern et al. (2007a). The authors mapped the distribution of *Lyngbya majuscula* off the eastern coast of Australia in 2005 and quantified bloom coverage over time. While the authors did not find *L. majuscula* during the winter and early spring months, as water temperature increased (from 23 °C to 30 °C), *Lyngbya* coverage rapidly increased, reaching 40 % of the substrate equivalent to an area of 329 hectares. When water temperature surpassed 32 °C, the bloom had occupied an area of 529 hectares. Then, cyanobacteria coverage diminished as the water cooled down in the fall.

The bloom of planktonic cyanobacteria in Old Providence Island, on the other hand, developed following peaks of heavy rains (October-November, after periods of drought). González & Hurtado (2012) mentioned average precipitation values for Old Providence Island of 301 mm in October and 266 mm in November, corresponding to 34 % of the total annual rainfall for the island. The bloom was also observed under low wind speed conditions (flat seas, no surge) which in turn may increase the time of residence of warm water masses, particularly in the lagoon (E of the island) and shallow terraces (N, NW). González & Hurtado (2012) stated that October (10.1 km/h) is after September (9.1 km/h), the month with lowest wind speed. December and January are the windiest months of the year (15.6, 15.1 km/h, respectively).

Reports of marine cyanobacterial blooms are on the rise (Paerl & Paul 2012) and probably will be more prevalent and intense with climate change. Several chemical, physical and biological, natural or anthropogenic factors are linked to the onset and development of cyanobacterial blooms, their interaction, however, is complex (O'Neil et al. 2012). For example, the expansion of urban centers on coastal areas and the consequent contribution of wastewater increase nutrient input, affect the predominant N/P relation, reduce salinity and increase water temperature (Dennison et al. 1999, Osborne et al. 2001, Watkinson et al. 2005).

An increase in water temperatures (above 28 °C), alterations of flow and time of residence, decrease in water viscosity, large scale mixing processes or small

scale turbulence are physical factors that correlate with bloom formation (Paerl 2002, Watkinson et al. 2005, Ahern et al. 2007a, Paerl & Huisman 2008, Paerl et al. 2011). Moreover, blooms of marine benthic cyanobacteria have been linked to an increase in nitrate, phosphate, ammonia or iron concentrations (Sellner 1997, O'Neil 2012, Zhang et al. 2012), and low salinity (Conley et al. 2009). Most of those stressors co-occurred in Old Providence Island, and may help to explain the underlying physical and chemical mechanisms behind cyanobacterial blooms. Historical records generated by the monitoring network of the quality of marine and coastal waters of Colombia-REDCAM (INVEMAR-REDCAM 2013), reported in Old Providence Island, from 2001 to 2012, increased concentrations of dissolved inorganic nitrogen (DIN) and orthophosphate with values of $74.4 \pm 39.43 \mu\text{g/L}$ (281 $\mu\text{g/L}$ max.) and $88.9 \pm 183.7 \mu\text{g/L}$, respectively (1352 $\mu\text{g/L}$ max.). Similar values were also reported by Vivas-Aguas et al. 2012). However, greater nutrient levels are invariably registered during the wet season (Vivas-Aguas et al. 2012). Nutrient peaks at the stations Santa Isabel, San Felipe and McBean, have been associated to the vicinity of human settlements and tourism (especially in the Santa Isabel wharf), leachates from the landfill at sector of San Felipe and the input of organic and inorganic residues from agricultural activity, animal husbandry and mangrove areas in the watershed of McBean Lagoon (Figure 5, 6; Vivas-Aguas et al. 2012). The current levels of DIN and phosphates surpass, in an order of magnitude, those considered standard for oligotrophic reef waters 14 $\mu\text{g/l}$ (= 1 μM) for DIN and 3.1 $\mu\text{g/l}$ (= 0.1 μM) for soluble phosphorus (Fabricius 2005). Greater nutrient levels promote algal development, which may help to explain the observed blooms. Further nutrient increase affects coral growth, reproduction and recruitment (Fabricius 2005).

The literature indicates that cyanobacterial blooms have consequences at various ecological scales (landscape, ecosystem, community, population and individual). Considering the extension and the apparent pulsing nature of cyanobacterial blooms in Old Providence Island, part of a UNESCO's Biosphere Reserve, it is important to mitigate the potential causative agents of these events. There is a strong need to further study the frequency, scale and duration of these events, and to understand the

consequences of blooms related to the biodiversity and the environmental services the affected areas provide. For these reasons, there is a strong need to establish a long term monitoring program in the region in order to understand and follow this new stressor. From a practical standpoint, we propose that the cover ratio between live coral and cyanobacteria could be used as an indicator of reef degradation. A threshold value of benthic cyanobacteria cover greater than 15 % could be indicative of degradation in coral reef ecosystems.

Conclusion

In conclusion, in Old Providence Island, blooms of benthic and planktonic cyanobacteria developed in four ecosystems (sandy bottoms, seagrasses, coral reefs and the pelagic zone), six geomorphological zones (Back-reef terrace, Patch reefs, Pinnacles, Fringing reefs, Fore-reef terrace and Lagoon) and nine habitats. The prevalence of cyanobacteria around Old Providence was very high. During cyanobacterial blooms, five of the nine habitats had high cyanobacteria cover (from 18 to 72 %). Blooms covered over 4.2 km² of the reef complex, particularly in those habitats with low live coral and high coverage of sand, macroalgae, dead coral or seagrasses. Cyanobacterial blooms are considered a new stressor in reef communities in the island and have an apparent pulsing nature. Therefore, it is important to understand the local conditions favoring these events in order to mitigate potential causal agents. We propose that benthic cyanobacteria cover greater than 15 % can be used as an indicator of degradation in coral reef ecosystems.

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Conflict of Interest

Alberto Acosta, as editor of *Universitas Scientiarum*, declares a conflict of interest. Therefore, the entire review process and approval of the manuscript was handled and edited by Luz Teresa Valderrama (co-editor of *Universitas Scientiarum*).

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Escala espacial de afloramientos de cianobacterias en la Isla de Old Providence, Caribe colombiano

Resumen. Los afloramientos de cianobacterias han incrementado en las zonas costeras de todo el mundo, favorecidos por el exceso de nutrientes y el aparente calentamiento global. Estos tienen consecuencias negativas sobre los ecosistemas, comunidades y hábitats marinos. Aunque los reportes de estos eventos son frecuentes, la extensión y los hábitats afectados aún no han sido completamente caracterizados, lo cual limita las acciones de manejo. En este estudio examinamos la presencia, escala espacial y cobertura de afloramientos de cianobacterias en diferentes hábitats del complejo arrecifal de la isla de Old Providence, e identificamos los principales taxa que generan afloramientos. Las cianobacterias fueron registradas en cuatro ecosistemas, seis zonas geomorfológicas y nueve hábitats. Las cianobacterias bentónicas cubrieron entre el 18 y el 72 % del sustrato en cinco hábitats, particularmente en el noroeste, este y parte sur de la isla. Tales afloramientos estuvieron conformados por consorcios complejos pertenecientes a los géneros *Okeania*, *Lyngbya*, *Symploca*, *Phormidium*, *Oscillatoria* o *Spirulina*. El afloramiento de cianobacterias planctónicas estuvo dominado por *Trichodesmium* y se desarrolló en la terraza prearrecifal (NO), tras un periodo de fuertes lluvias. Los resultados sugieren un nuevo estresor potencial para el complejo arrecifal de la isla. La investigación futura debería concentrarse en los factores ambientales que facilitan los afloramientos de cianobacterias y en el impacto local sobre los ecosistemas y sus servicios.

Palabras clave: cianobacterias; zonas geomorfológicas; hábitat; consorcio microbiano; sistema arrecifal; Caribe.

Escala espacial de afloramientos de cianobactérias na ilha Old Providence, Caribe colombiano

Resumo. Os afloramentos de cianobactérias têm aumentado em águas costeiras de todo o mundo, devido à entrada de nutrientes excessivos e também aparentemente ao aquecimento global. Estes afloramentos exercem efeitos negativos nos ecossistemas, comunidades e habitats marinhos. Embora os relatórios destes eventos sejam frequentes na literatura, a extensão e os habitats atingidos não são completamente conhecidos, o que implica a restrição das ações de gestão. Neste estudo analisamos a presença, escala espacial e cobertura dos afloramentos de cianobactérias em diferentes habitats marinhos do complexo recifal da ilha Old Providence, e identificamos as principais taxas que geram afloramentos. As cianobactérias foram registradas em quatro ecossistemas, seis zonas geomorfológicas e nove habitats. Durante os afloramentos bentônicos, as cianobactérias atingiram entre 18 a 72 % da cobertura total em cinco habitats, particularmente no noroeste, este e sudeste da ilha. Tais afloramentos são consórcios complexos pertencentes aos géneros *Okeania*, *Lyngbya*, *Symploca*, *Phormidium*, *Oscillatoria* e *Spirulina*. O afloramento de cianobactérias planctónicas foi dominado por *Trichodesmium* e se desenvolveu no terraço prearrecifal da porção noroeste da ilha, depois de chuva intensa. Os resultados sugerem um novo “estressor” potencial para o complexo recifal da ilha. As investigações futuras devem se concentrar nos fatores ambientais que facilitam o afloramento e no seu impacto local nos ecossistemas e serviços.

Palavras-chave: cianobactérias; zonas geomorfológicas; habitat; consorcios microbianos; sistema de recife.