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Benthic cyanobacterial bloom impacts the reefs of South Florida (Broward County, USA)

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Abstract Benthic cyanobacteria of the genus *Lyngbya* can form prominent mats and blooms in tropical and subtropical coral reef and seagrass habitats worldwide. A *Lyngbya* bloom on the reef tract offshore of Broward County, Florida, was first noted in 2002, and although it is seasonally variable in its distribution and abundance, it has persisted and spread over the past 3 years. In this study, the most abundant species of *Lyngbya* found in the blooms have been identified and compared to other species of *Lyngbya* by morphological and molecular methods. The most common species of *Lyngbya* is consistent with the properties of *Lyngbya confervoides* C. Agardh. The 16S ribosomal DNA sequence shares 88–92% identity with other known *Lyngbya* sequences, suggesting that this bloom consists primarily of a new, previously unsequenced species of *Lyngbya*. The second most common *Lyngbya* in the bloom is consistent with *Lyngbya polychroa*. This persistent bloom is a concern because it smothers octocorals and other invertebrates and negatively impacts these southeastern Florida reefs.

Keywords Cyanobacterial bloom · Benthic cyanobacteria · Florida reef tract · *Lyngbya*

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Introduction

A major concern on coral reefs worldwide is massive overgrowth by macroalgae and benthic cyanobacteria (Done 1992; Hughes 1994; McCook 1999). The increasing occurrence of benthic cyanobacteria (blue-green algae), which are usually grouped with turf algae in monitoring and ecological studies, has largely been overlooked. Benthic cyanobacteria are often early colonizers of dead coral and disturbed substrates (Tsuda and Kami 1973; Littler and Littler 1997; Diaz-Pulido and McCook 2002), but they can also form periodic blooms and replace eukaryotic algae in benthic turf communities (Paerl 1996; Dennison et al. 1999; Abed et al. 2003; Armitage and Fong 2004). Since cyanobacteria produce nitrogenous secondary metabolites that serve as chemical defenses against herbivores (Pennings et al. 1997; Nagle and Paul 1998, 1999; Paul et al. 2001), selective browsing by herbivorous fishes on macroalgae can remove potential competitors and favor the establishment of unpalatable, benthic cyanobacteria in reef habitats (Tsuda and Kami 1973; Thacker et al. 2001).

Here, we report an extraordinary proliferation of cyanobacteria on the reef-associated communities of South Florida stretching from southern Palm Beach County southward through Broward County. We identify the most common species of *Lyngbya* found in the bloom and compare this to other species of *Lyngbya* by morphological and molecular methods.

Methods

The reef system of southeast Florida is a northward continuation of the Florida Keys reef tract and extends approximately 126 km northward. Offshore of Broward County there are approximately three shore-parallel reef lines separated by sand deposits, although in the southern portion of the county there are multiple reef patches. The inner reef, approximately

1.2 km offshore, crests in 3–4 m of water depth; the middle reef, 1.9 km offshore, in 6–8 m; and the outer reef, 2.4 km offshore, in 15–21 m depth. Shoreward of the inner reef, a series of hard ground ridges occur. This ridge complex represents lithified Pleistocene shoreline deposits.

The biological communities were described by Goldberg (1973) and Moyer et al. (2003) and consist of a diverse coral reef community including various stony corals, gorgonians, sponges, and algae. The inner reef is sparsely colonized by small octocorals and algae. The reef structure is built of an internal *Acropora palmata* framework. Stony coral species (3% cover) with flat growth forms (*Diploria clivosa*, *Meandrina meandrites*) occur. The middle reef has more structural relief. Octocorals are conspicuous with some areas containing 30 per m^2. Stony corals include *Montastraea cavernosa*, *Siderastrea siderea*, and *Porites astreoides*. Coral coverage averages approximately 4% (Moyer et al. 2003). The outer reef often has stronger vertical relief and exhibits the highest diversity, abundance, and average coverage of sessile reef organisms. Octocorals and large barrel sponges (*Xestospongia muta*) are conspicuous. The reef framework consists of *A. palmata* in thick accumulations

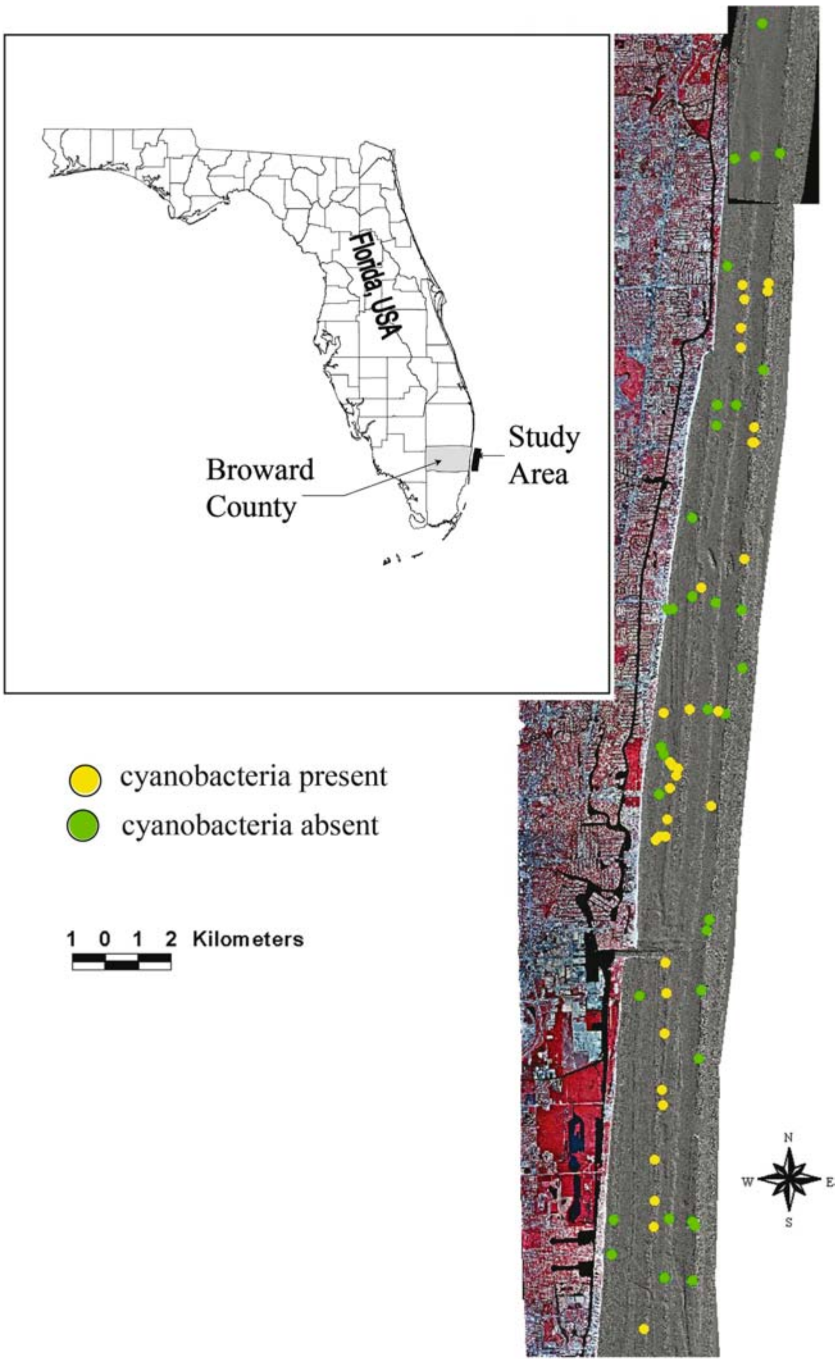

Fig. 1 *Shaded relief image* of seafloor created from high-resolution bathymetry of Broward County, Florida ("*Study Area*" in inset) superimposed with the presence or absence of *Lyngbya* cf. *confervoides* from 2003 to 2004

(Lighty 1977). Coral coverage averages approximately 4% (Moyer et al. 2003).

One of us (KB) has been diving on reefs in Broward County for 15 years and first observed *Lyngbya* spp. during the summer months in the early 1990 s. However, it was not until 2002–2003 that cyanobacteria persisted through the winter months and became abundant year round. Anecdotal presence and absence data were collected from the local dive community beginning in the summer of 2003. A questionnaire was distributed to the dive community through presentations to local dive clubs and the local dive boat operators' organization. Web posting of the questionnaire by a local environmental organization, Ocean Watch, also facilitated distribution. Photos of *Lyngbya* spp. were provided with the survey. The intent of the survey was to determine GPS locations where cyanobacteria were present and absent. Ten members of the dive community responded to the survey. ArcView (ESRI GIS) shape files were created with the information obtained from the survey and laid over surface images of the reef created from high-resolution laser bathymetric data.

Samples taxonomically examined by morphological and molecular methods were collected by scuba diving at Abby Too Reef (26°16.408′N, 80°03.8330′W, depth of reef crest 15 m) in Broward County in December 2003. Additional samples examined morphologically were collected by scuba diving at the same site on September 27, 2003 and from the third reef near Hillsboro Inlet (26°15.134′N, 80°03.908′W, depth of reef crest 17 m) on July 31, 2004.

We amplified and sequenced 16S ribosomal DNA from field collections of this cyanobacterium, hereafter referred to as *Lyngbya* cf. *confervoides*, following previously established techniques (Nübel et al. 1997; Thacker and Paul 2004). PCR products were cloned using the pGEM T-Easy Vector System (Promega), and representative clones were sequenced at the UAB DNA Sequencing Core Facility. Sequences were assembled using Sequencher 4.1 (GeneCodes, Ann Arbor, MI); potential chimeric sequences were examined using Chimera Check (Cole et al. 2003). Sequences were aligned to reference sequences using GenBank's BLAST algorithm and the Ribosomal Database Project's Sequence Match algorithm (Cole et al. 2003). Reference sequences included *L. confervoides* PCC7419 (GenBank accession number AJ000714), *L. confervoides* from Guam (AF510980), *Lyngbya aestuarii* (AJ621838), *Lyngbya bouillonii* (AF510970), *Lyngbya hieronymusii* (AF337650), *Lyngbya majuscula* from Guam (AF510976), *L. majuscula* from Jamaica (AY599503), *Lyngbya polychroa* (AF510979), and *Oscillatoria sancta* (AF132933). Likelihood ratio tests comparing hierarchical models of DNA substitution were evaluated by Modeltest (Posada and Crandall 1998). A maximum likelihood phylogenetic tree was generated in PAUP* (Swofford 1999) using the likelihood settings calculated by Modeltest in a heuristic search with ten random stepwise-addition sequences. Support for each node was evaluated with 100 bootstrap replicates of a fast stepwise-addition search.

Results and discussion

A distribution map based on presence and absence data from the Broward County dive community indicates that the middle reef tract (*d*(14 m) showed the greatest presence of cyanobacterial cover (Fig. 1). The outer tract (*d*(17 m), the inner tract (*d*(8 m), and the nearshore hardbottom (*d*(5 m) were sparsely covered in 2003, but by the summer of 2004 the overgrowth had spread to the other reef tracts (Fig. 2a). Proliferation of unidentified cyanobacteria (probably also *L.* cf. *confervoides*) on reefs off of Boynton Beach, FL (Palm Beach County), from 2002 to 2004 has been previously reported (Tichenor pers. comm.).

The samples collected in December 2003 consisted of four cyanobacteria of the family Oscillatoriaceae, all rich in phycoerythrin and two of them common *Lyngbya* spp. The most abundant species was in the size range of

Fig. 2 **a** *Lyngbya* cf. *confervoides* on Abby Too Reef, Broward County, Florida. **b** Microscopic view (400×) of *L.* cf. *confervoides* filaments, with cells arranged in linear trichomes within an extracellular sheath

10–15 μm in cell width and 3–5 μm in cell length (Fig. 2b). Collections made on September 27, 2003 had filaments 15.57 ± 1.07 (mean ± SD) μm in diameter ($n = 55$) and cells 12.00 ± 0.97 μm wide ($n = 55$) and 3.85 ± 0.41 μm long ($n = 25$). Samples collected on July 31, 2004 had similar measurements with filaments 14.38 ± 0.81 (mean ± SD) μm in diameter ($n = 44$) and cells 11.17 ± 0.64 μm wide ($n = 44$) and 3.91 ± 0.74 μm long ($n = 17$), indicating that the major species in the bloom was the same over time. This species of *Lyngbya* is consistent with the properties of *L. confervoides* C. Agardh (Littler and Littler 2000) with a few distinctions: the sheaths are firm but thin; externally smooth, rather than multilayered and externally rough; and the color is distinctly red due to high phycoerythrin content, rather than olive to blue-green, as in the original description (Gomont 1892). These properties may depend on particular ecological conditions: the pigmentation may be modified in response to ambient light, whereas the thickness and roughness of the sheath may depend on nutrient balance (Otero and Vincenzini 2004; Potts 2004). The fact that this growth is sudden and massive suggests that it may be a new genotype (or even a new species); however, very little is known about genetic variability within and among species of benthic cyanobacteria (Thacker and Paul 2004). The second most common *Lyngbya* in the bloom was found in distinct mats at some sites in Broward County in July 2004, and collections made on July 31, 2004 had filaments 40.41 ± 3.36 (mean ± SD) μm in diameter ($n = 34$) and cells 31.72 ± 3.82 μm wide ($n = 36$) and 4.05 ± 0.92 μm long ($n = 18$), consistent with *L. polychroa* (Meneghini) Rabenhorst 1847 (Synonym: *Lyngbya sordida* Gomont 1892) (Littler and Littler 2000).

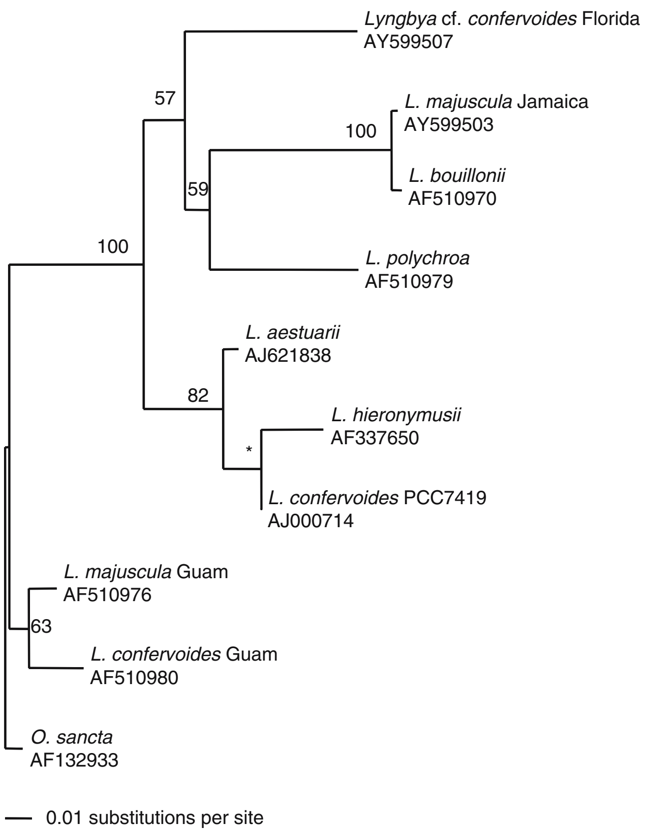

Fig. 3 Maximum likelihood phylogram of *Lyngbya* species and their relationship to *Lyngbya* cf. *confervoides* constructed from the alignment of 16S rDNA sequences. Numbers at each node represent percentage bootstrap support; an *asterisk* indicates <50% bootstrap support

PCR amplification and sequencing of *L.* cf. *confervoides* yielded a 1,331 bp fragment of 16S ribosomal DNA that has been deposited in GenBank under accession number AY599507. This sequence shares 88–92% identity with other known *Lyngbya* sequences, suggesting that this bloom consists primarily of a new, previously unsequenced species of *Lyngbya*. Hierarchical models of DNA substitution indicated that a general time-reversible model that included both the proportion of invariable sites and heterogeneous rates of substitution among variable sites best fit the data obtained. Estimated model parameters included the substitution rate matrix (A - C = 0.974, A - G = 1.283, A - T = 0.963, C - G = 0.180, C - T = 2.404, and G - T = 1.000), the proportion of invariable sites (I = 0.624), and the gamma distribution shape parameter (G = 0.774). This model generated a maximum likelihood tree with a likelihood score of 3,697.457; bootstrap analyses provided strong support for only three of seven nodes in this tree (Fig. 3). The three collections morphologically classified as *L. confervoides* were placed in separate clades, indicating that morphologically similar species of *Lyngbya* can show dramatic genetic differentiation.

The cyanobacterial bloom currently found in Broward County likely represents the emergence of a previously unknown species of *Lyngbya*. Such events may be precipitated by the increasing nutrient enrichment of coastal waters, facilitating the establishment of species that were previously rare and unreported (Glibert et al. 2004; Elmetri and Bell 2004). Ongoing studies include observations of the spread of this bloom as well as studies of growth and toxin production in response to nutrients. This bloom and other emerging threats may impinge on the health of Florida reefs in the years to come.

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