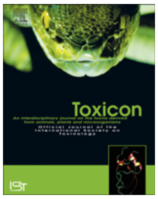
Toxicon 56 (2010) 836–841

Contents lists available at ScienceDirect

Toxicon

journal homepage: www.elsevier.com/locate/toxicon



# Marine toxic cyanobacteria: Diversity, environmental responses and hazards

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ARTICLE INFO

*Article history:*
Received 8 June 2009
Received in revised form 6 July 2009
Accepted 21 July 2009
Available online 29 July 2009

*Keywords:*
Benthic cyanobacteria
Ciguatera
*Hydrocoleum*
*Lyngbya*
*Oscillatoria* cf. *bonnemaisonii*
Marine
Molecular techniques
Toxicity
*Trichodesmium*

ABSTRACT

Toxic cyanobacterial blooms have been a primary concern predominantly in the plankton of freshwater bodies. Recently, however, the toxicity of benthic cyanobacteria is increasingly attracting attention of the scientific community and environmental agencies. The occurrence of toxic strains in benthic cyanobacteria is intimately linked to our understanding of the diversity and ecological responses of these organisms under field conditions. To that effect, we are engaged in combined morphotypic and genotypic characterization (polyphasic) of benthic natural populations of cyanobacteria in tropical lagoons and coral reefs, with the objective to provide a reliable reference for further comparative work. The methods of identification based on phenotypic properties and those based on molecular tools for genotypic identification are correlated. The approach is based on identifying the occurrences of cyanobacterial benthic blooms, tested for purity and analyzed by application of molecular tools. The questions addressed include the distinction between marine and freshwater taxa, between populations in geographically separate regions as well as between their potential vs. expressed toxicity.

## 1. Cyanobacteria in marine environments

Cyanobacteria in freshwater environments have been long known for their environmental impact, especially in conjunction with explosive reproduction of toxic strains in plankton blooms (Whitton and Potts, 2000). Many of these cyanobacteria represent hazard to humans (Bell and Codd, 1994) and domestic animals (Gunn et al., 1992; Negri et al., 1995). Formation of cyanobacterial blooms is associated with eutrophication and pollution in lakes and rivers. Similar imbalance in nutrient supply when transferred to marine environments is less predictable, where coastal eutrophication is often causing red tides, which are usually dominated by dinoflagellates (e.g. Lobel et al., 1988).

The nutrient overload that shifts the roles of nutrient limitation for primary producers from phosphorus to nitrogen often favors cyanobacteria that are able to fix atmospheric nitrogen (Schindler, 1977). Staal et al. (2003) observed that nitrogen-limited open ocean would theoretically favor heterocystous cyanobacteria, which occur in the

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0041-0101/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.toxicon.2009.07.023

plankton of the epicontinental Baltic Sea, but not in the open ocean. They suggested that high temperature requirement makes *Trichodesmium* competitive and, thus prevalent in tropical oceans, but could not explain the lack of occurrence of heterocystous cyanobacteria in pelagic realms at higher latitudes. The reason why heterocystous cyanobacteria did not occupy pelagic niches may have to do with their life cycle, which involves differentiation of akinetes, resting stages that survive in the sediment, from where they return to the plankton upon germinating next season. Benthic dependency on survival has been documented even for *Microcystis*, a plankton bloom-forming coccoid cyanobacterium without morphologically distinct resting stages (Brunberg and Blomqvist, 2002). Such alternate use of benthic and planktonic habitat is not available over abyssal depths. The composition of cyanobacterial picoplankton does depend on nutrient composition (Stockner, 1988; Urbach et al., 1998) but these organisms do not seem to form blooms (Stockner et al., 2000), although some of them have the ability to fix nitrogen. Thus, various *Trichodesmium* populations are the main contributors to plankton blooms in tropical oceans. The bloom formation and nitrogen fixation capacity of *Trichodesmium* may also further be nutrient-limited by iron (Berman-Frank et al., 2001).

In contrast, both heterocystous and non-heterocystous cyanobacteria occur in marine benthos of all latitudes, but, like other organisms, benthic cyanobacteria exhibit the highest diversity in tropical lagoons and coral reefs, where they form compact mini-blooms, characterized by local exponential growth of mats and coherent colonies (Abed et al., 2003a,b). Heterocystous cyanobacteria of the genus *Nodularia* and non-heterocystous ones of the genus *Hydrocoleum* contribute significantly to nitrogen fixation (Charpy et al., 2007). *Hydrocoleum* proved to be very close to *Trichodesmium* regarding 16S rRNA gene sequences suggesting a common origin of these most frequently observed benthic and planktonic non-heterocystous cyanobacteria in tropical oceans (Abed et al., 2006). However they differ in structure and function sufficiently to justify a separate generic identity. *Trichodesmium* cells contain packages of gas vesicles, which are lacking in the benthic *Hydrocoleum*. *Trichodesmium*, like *Nodularia* exhibits a spatial separation between cells performing carbon (photosynthesis) vs., nitrogen fixation, with the maximum yield output by day, when solar energy is available, whereas *Hydrocoleum*, similar to *Lyngbya majuscula* and other non-heterocystous cyanobacteria, fix nitrogen by night (Lundgren et al., 2002), using the energy accumulated the day before (Charpy et al., 2007).

Benthic cyanobacteria are rare in healthy coral reef environments; they occur on damaged surfaces and coral rubble, but prefer to form loose mats and colonies over sandy sediments or epiphytically on sea grass. They include opportunistic settlers, able to colonize newly available grounds within 24 h. Their continuing growth is contingent on competition with eukaryotic algae and sedentary animals.

## 2. Link between cyanobacterial bloom development and ciguatera fish poisoning syndrome

Poisoning by eating fish caught in tropical reef environments called ciguatera is a serious problem, usually caused by dinoflagellates, such as *Gambierdiscus toxicus* (Lehane and Lewis, 2000) causing characteristic neurological symptoms (Peaern, 2001). The toxins are transferred and concentrated along food chains, affecting especially carnivorous fish. There is recent evidence of poisoning derived from consumption of fish and clams originating from benthic cyanobacteria, with symptoms similar but more severe than those in typical ciguatera fish poisoning (Laurent et al. 2008). As early as the 1950s, Randall (1958) suspected that a benthic organism, most-likely a blue-green alga, was the source of the toxin of ciguatera fish poisoning (CFP). Halstead (1967), based on the presence of benthic cyanobacterium *L. majuscula* (Fig. 1) in the gut of a large number of poisonous fishes, hypothesized that these cyanobacteria might serve as a primary source of ciguatoxins (CTXs) or their progenitors. Observations by Hahn and Capra (1992) and Endean et al. (1993) that typical CFP signs of intoxication (quiescence, piloerection, diarrhoea, lachrymation, cyanosis, dyspnoea, convulsive spasms and death within 24 h stemming from respiratory failure) have been demonstrated in mice injected intraperitoneally with extracts of both *Trichodesmium* (*Oscillatoria*) *erythraeum* and mollusks, are coherent with this hypothesis. Furthermore, Banner (1967) was the first to

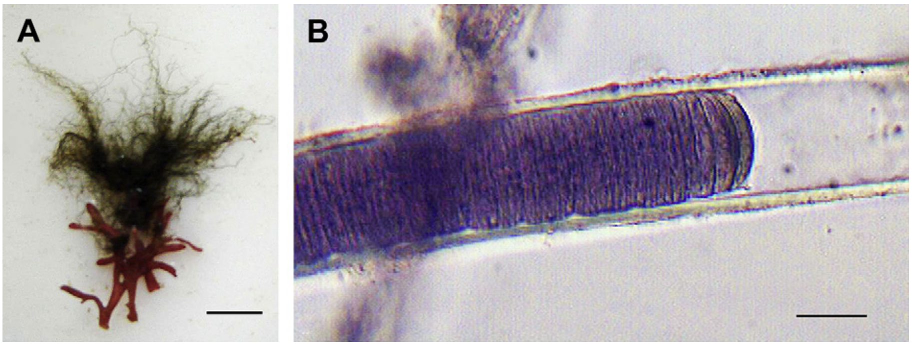

**Fig. 1.** *Lyngbya majuscula*. A) Entangled filaments epiphytic on a red alga. Filaments are often loose, carried by currents. B) Single trichome within its thick sheath. The latter is often overgrown by bacteria. Scale bar in A is 1 cm, in B is 20 μm long.