



Palatability and chemical defences of benthic cyanobacteria to a suite of herbivores



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ABSTRACT

Nuisance blooms of toxic cyanobacteria are a common occurrence in many tropical and subtropical locations. Benthic marine cyanobacteria of the genera *Lyngbya*, *Okeania*, and *Moorea* are frequently observed in both Florida and throughout the Caribbean, sometimes forming large mats, and are prolific producers of bioactive secondary metabolites that often act as feeding deterrents to generalist herbivores. Little is known regarding the ecological roles of the secondary metabolite chemistry and the palatability of benthic cyanobacteria to grazers. This study examines the palatability of benthic cyanobacterial species from Florida (IRL1, IRL2, IRL3 and *Okeania erythroflocculosa*) and Belize (BEL1, BEL2) to a range of macro- and mesograzers in Florida and Belize. Pair-wise feeding assays using artificial diets of *Gracilaria tikvahiae* or fish food coated with cyanobacterial extracts and a control were used to determine palatability of extracts to Floridian and Belizean generalist grazers. The extracts of IRL1, IRL2, IRL3 and *O. erythroflocculosa* from Florida did not deter feeding by invertebrate grazers. Reef fish, however, were deterred by the non-polar extracts of IRL1, IRL3 and *O. erythroflocculosa*. *Stylocheilus striatus* was stimulated to feed on IRL2 extracts and non-polar extracts from IRL3. Non-polar extracts of BEL1 stimulated feeding in *S. striatus*; however, no significant difference was observed between BEL2 extracts and the control. Most generalist invertebrate grazers, sympatric and non-sympatric, appear indifferent to cyanobacteria extracts whilst reef fish are more likely to be deterred by cyanobacterial extracts, which may affect species interaction within communities with fluctuating or dominating benthic cyanobacterial blooms.

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1. Introduction

Cyanobacteria are a ubiquitous component of all aquatic ecosystems. The family Oscillatoriaceae consists of more than 800 species with many species producing secondary metabolites that are of interest both ecologically and pharmaceutically (Engene et al., 2013a). One genus that sparked a wealth of research in these areas over the past five decades is *Lyngbya*. However, recent taxonomic reclassification of this polyphyletic group has yielded several phylogenetically distinct lineages including *Okeania* and *Moorea* (Engene et al., 2012; Engene et al., 2013a, 2013b). *Lyngbya*, *Okeania* and *Moorea* are abundant and globally

distributed genera in tropical and subtropical marine benthic environments (Engene et al., 2012; Engene et al., 2013a, 2013b).

Cyanobacterial blooms appear to be increasing in frequency and severity at a number of locations around the world (Albert et al., 2005; Paerl and Huisman, 2009; Paerl and Paul, 2012; Paul et al., 2005) and as such, they can have significant economic impacts upon recreational activities and fisheries (Abal et al., 2001). Benthic cyanobacteria are commonly found in Florida (Arthur et al., 2009; Burns, 2008; Engene et al., 2013b; Paul et al., 2005; Sharp et al., 2009) and have been observed in Belize on a number of occasions (Gunasekera et al., 2008a; McClanahan et al., 2007). Blooms can be prevalent during the summer and fall and are often exacerbated by warm water temperatures (>24°C) in relatively calm, shallow waters (Watkinson et al., 2005; pers. obs.). The Oscillatoriaceae family of benthic cyanobacteria have great plasticity allowing them to survive and thrive on a wide variety of substrates including sand, seagrass, algae, mangrove roots and coral reefs (Engene et al., 2013b; Paul et al., 2005).

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Species of *Lyngbya*, *Moorea* and *Okeania* are prolific secondary metabolite producers (Blunt et al., 2010; Blunt et al., 2012; Engene et al., 2012, 2013a; Liu and Rein, 2010). Why such huge arrays of compounds are produced and why they often vary geographically is unknown, but genetics (Sharp et al., 2009), local physico-chemical conditions (Paerl, 1996), nutrient availability (Arthur et al., 2009) and grazer interactions (Hay and Fenical, 1988; Paul et al., 2001) have all been suggested as driving factors. Many of these secondary metabolites act as feeding deterrents to a range of generalist grazers such as crabs (Pennings et al., 1996), sea urchins (Capper et al., 2006a; Nagle et al., 1996) and fish (Capper et al., 2006b; Nagle and Paul, 1998); often allowing blooms to proliferate when environmental conditions are favourable (Paerl and Paul, 2012; Paul et al., 2007; Thacker and Paul, 2001).

Given the vast array of cyanobacterial compounds that can vary both temporally and spatially, it is very difficult to compare palatability responses for generalist herbivorous grazers. Sensitivity to compounds and palatability can vary between grazers (Capper et al., 2006a), and prior exposure to 'local' compounds may acclimate local grazers but deter grazers in other geographic locations. Capper et al. (2006a) hypothesised that *Lyngbya* compounds are likely to be locally rather than broadly deterrent across a geographical range. However, this was not found to be the case when a crude extract was tested against sympatric and allopatric grazers in two geographic locations, Guam and Australia. Deterrence was observed in most consumers regardless of geographic origin or prior exposure to 'local' compounds. The major compound isolated during this study was the highly toxic lyngbyatoxin A (LTA). It is not known whether benthic cyanobacteria with less 'potent' toxins would be equally deterrent to grazers in different geographical locations. Thus far, collections of benthic cyanobacteria from Florida and Belize have not yielded LTA (Engene et al., 2013a, 2013b; Kwan et al., 2010; Sharp et al., 2009).

While benthic cyanobacteria blooms often play host to a range of macro- and mesograzers (Cruz-Rivera and Paul, 2002), the majority of these grazers appear to be opportunistic rather than specialists (Cruz-Rivera and Paul, 2002, 2006; Watkinson et al., 2005). Even for specialist grazers, sensitivity to crude extracts or specific compounds can vary both within and among species of cyanobacteria. The 'specialist' grazer *Stylocheilus striatus*, an opisthobranch mollusc, can be stimulated to feed in the presence of specific compounds (Arthur et al., 2009; Capper et al., 2005; Nagle et al., 1998). Nagle et al. (1998) found that malylgamides and majusculamides increased feeding at lower concentrations, but inhibited feeding at higher concentrations. While *S. striatus* may be able to bioaccumulate *Lyngbya* compounds with no apparent detrimental impact (Capper et al., 2005; Pennings and Paul, 1993a), sensitivity to, and thus avoidance of different species of benthic cyanobacteria may ultimately increase animal fitness. In palatability and associated biomass increase assays, *S. striatus* showed a preference for *L. polychroa* (now known as *Okeania erythroflocculosa*, Engene et al., 2013b) over *L. cf. confervoides* and attained a greater biomass on a monospecific diet of *L. polychroa* (Capper and Paul, 2008).

To further investigate deterrence of cyanobacteria to generalist and specialist consumers, the palatability of a range of benthic cyanobacteria and an unknown consortium of cyanobacterial species in sub-tropical Florida and tropical Belize was examined. Feeding experiments with a range of cyanobacterial extracts were conducted to test the adaptability and tolerance of diverse consumers that feed on chemically defended prey.

2. Materials and methods

2.1. Study sites and organisms

Grazers and cyanobacteria were collected and tested in Belize or Florida; however, it is important to note that both are broadly

distributed across the Florida and Caribbean region (Engene et al., 2012, 2013a, 2013b; Paul et al., 2005). Repeated collections of cyanobacteria from the same locations in both these regions over the years means they can readily be identified based on morphology and secondary metabolites, which are characteristic for each species (Engene et al., 2013a and b Sharp et al., 2009). Choosing these two locations therefore, allowed an assessment of a broad array of cyanobacteria-grazer interactions.

2.1.1. Florida collections

Blooms of cyanobacteria were observed at two sites in the Indian River Lagoon (IRL) at Jensen Beach in St. Lucie County during August 2004 with a different morphology collected at each location: 'filamentous' (IRL1) and 'slimy' (IRL2) (Table 1). Although previously both morphotypes were labelled as *Lyngbya cf. majuscula* (Dobretsov et al., 2010; Kwan et al., 2011), a recent phylogenetic study has now classified them as distinct from *Lyngbya* spp. based on phylogenetic analysis of 16SrRNA genes (Clade IV in Engene et al., 2013a). Other benthic cyanobacteria can be less conspicuous in the IRL; however, a fortuitous finding of one cyanobacterial mat consortium (covering approx. 3 m²) attached to a *Cladophora* species was collected in November 2004 (IRL3) at a small island located to the south of the Smithsonian Marine Station at Fort Pierce (SMSFP). Unfortunately, the composition of this particular cyanobacterial mat was not confirmed. *Okeania erythroflocculosa* (previously known as *Lyngbya polychroa* (red), Sharp et al., 2009) was collected in Broward County, Florida and maintained as above. All collections were returned to the SMSFP and maintained in 5 gal buckets of seawater at 35 ppt at 24°C with aeration and a 12 h light and dark cycle. Water was changed every 24 h. *Gracilaria tikvahiae* was obtained from Harbor Branch Oceanographic Institute and freeze-dried for use in palatability assays to test the effect of chemical extracts on feeding.

Sea hares (*S. striatus*) were collected from the blooms of *O. erythroflocculosa* and *Lyngbya cf. confervoides* in Broward County and maintained in small aquaria (1 L) at SMSFP on a diet of their host algae. Sea urchins (*Echinometra lucunter*) and crabs (*Pachygrapsus transversus*) were collected from the rocky shores adjacent to SMSFP and maintained in 5 gal buckets. Salinities were kept between 34 and 36 ppt and temperature consistent with ambient (24°C) with 12 h light and dark cycles. Water was changed every 24 h.

2.1.2. Belize collections

Two benthic cyanobacteria were collected during the spring of 2005. The first was identified as BEL1, red in colour (formerly *Lyngbya cf. polychroa*, but now called *Moorea producens*, Engene et al., 2012) and found in large quantities on mangrove roots at Twin Cays, Belize. Filament width was 27.78 μm ± 0.83 μm SE (n = 10) with a cell width of 25.28 μm ± 0.83 μm SE and length of 15 μm ± 0.00. The second was green in colour, BEL2 (formerly *Lyngbya cf. majuscula*, BEL2) and was collected from mangrove roots in the Pelican Cays. Filament width was 27.44 μm ± 0.64 μm SE (n = 10) with a cell width of 22.44 μm ± 0.64 μm SE and length of 5.0 μm ± 0.00. Collections were returned to the Smithsonian laboratory at Carrie Bow Cay (CBC) and maintained in 5 gal buckets of seawater at 35 ppt at ambient temperature (27°C) with aeration with 12 h light and dark cycles.

Sea urchins (*Diadema antillarum*) and crabs (*Pitho aculeata* and *Mithraculus sculptus*) were collected locally on the reef surrounding CBC. The sea hare *S. striatus* was not observed in any cyanobacterial collections in Belize and therefore could not be utilized in assays at CBC. Sea urchins were maintained in 5 gal buckets with flow-through seawater. Mesograzers were maintained in individual plastic containers with seawater changed every 24 h. All animals were kept at ambient temperatures with 12 h light and dark cycles. In-situ fish assays were carried out on Golden Reef close to CBC.

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