Effects of *Lyngbya majuscula* blooms on the seagrass *Halodule wrightii* and resident invertebrates

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ABSTRACT

Cyanobacterial blooms have been increasing worldwide due to increased nutrients associated with urban, industrial, and agricultural development. Blooms that occur in the Indian River Lagoon (IRL), Florida may be increased by nutrient-laden runoff from storm water and non-point sewage pollution due to alterations to the watershed. In the IRL, during the summer of 2006, extensive blooms of the marine cyanobacterium, *Lyngbya majuscula,* were observed forming mats throughout beds of the seagrass *Halodule wrightii* in Fort Pierce, Florida. The effects of cyanobacterial blooms were compared to artificial shading of *H. wrightii* to assess the shading potential of *L. majuscula*. The combined effects of *L. majuscula* removal and artificial shading showed increases in the below ground biomass of *H. wrightii*. However, leaf length increased in the presence of *L. majuscula*. In response to artificial shading, *H. wrightii* decreased in density, but showed similar leaf elongation. A common bivalve in our study area, *Macoma constricta,* increased in density when *L. majuscula* was removed. Therefore, when *L. majuscula* blooms occur, light limitation is one of the mechanisms altering *H. wrightii* density and leaf lengths in the IRL. Loss of *H. wrightii* biomass due to shading from cyanobacterial mats may further damage the diversity and habitat value of the IRL.

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1. Introduction

In coastal ecosystems, seagrass foundation species form habitat and stabilize local conditions (Dayton, 1972; Dawes et al., 1995; Bruno and Bertness, 2001; Duffy, 2006). They provide valuable ecosystem services, including acting as nursery habitat and refugia, providing a food source, recycling nutrients, and are highly productive (Dawes et al., 1995; Williams and Heck, 2001; Duarte, 2002; Heck et al., 2003; Duffy, 2006; van Tussenbroek et al., 2006). Worldwide seagrasses are declining due to a series of natural and anthropogenic stressors that have created poor conditions for seagrass success (Short and Wyllie-Echeverria, 1996; Orth et al., 2006; Waycott et al., 2009). It is estimated that 29% of the known areas of seagrasses have disappeared, and continue to decline at a rate of 7% per year (Waycott et al., 2009).

Anthropogenic pressures on coastal ecosystems are increasing worldwide (Halpern et al., 2008), which is one of the primary causes of seagrass losses (Orth et al., 2006; Waycott et al., 2009). Global increases in human populations have increased the frequency and magnitudes algal, phytoplankton, and cyanobacterial blooms, including harmful algae blooms (HABs) as a result of increased eutrophication (Hallegraeff, 1993; Anderson et al., 2002; Heisler et al., 2008). The occurrence and density of blooms can depend on the type of nutrients, availability of nutrients, density of grazers or suspension feeders, and local hydrodynamics (Cloern, 2001; Pittman and Pittman, 2005; Ahern et al., 2006, 2007; O'Neil et al., 2012; Lapointe et al., 2015). HABs have produced deleterious effects on seagrasses by overgrowing and smothering of seagrasses that lead to reduced light availability and inhibited gas exchange, ultimately decreasing photosynthetic rates (Watkinson et al., 2005; O'Neil et al., 2012; Lapointe et al., 2015; Morris et al., 2015). Therefore, the severity of the HABs is strongly related to seagrass losses.

Lyngbya majuscula is a potential HAB-forming species in marine ecosystems that has been increasing in frequency since the early 2000s (Paul et al., 2005; Paul, 2008; O'Neil et al., 2012). It is a

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filamentous benthic cyanobacteria found growing attached to sediment, seagrasses, and corals (Albert et al., 2005; Paul et al., 2005; Arthur et al., 2006; Ahern et al., 2007; Martín-García et al., 2014; O'Neil et al., 2012). The extensive benthic mats can become detached and blanket large areas due to oxygen bubbles trapped in their filaments following active photosynthesis (Albert et al., 2005; O'Neil et al., 2012). Toxicity of secondary compounds produced by *L. majuscula* have been shown to have adverse effects on humans, with severe skin and eye irritations and hampered respiratory functions (Osborne et al., 2001; Watkinson et al., 2005; O'Neil et al., 2012). Effects of *Lyngbya* spp. on coral reefs are also primarily a function of toxicity rather than shading by the cyanobacterial mats (Titlaynov et al., 2007). In animal communities, *L. majuscula* produces compounds that act as strong feeding deterrents (Osborne et al., 2001; Paul et al., 2005; Paul, 2008). When *L. majuscula* grows epiphytically on seagrasses, animals, such as green sea turtles (*Chelonia mydas*), are negatively impacted by exposure to potentially harmful toxins when ingesting *L. majuscula* with seagrass leaves (Arthur et al., 2006, 2008). Fish and meiofaunal communities (i.e. nematodes, copepods, polychaetes) abundances decreased in the presence of *L. majuscula* (Pittman and Pittman, 2005; García and Johnstone, 2006). Infaunal species also altered their sediment depth distribution, although this effect was less prominent in polychaete species (García and Johnstone, 2006).

Anthropogenic nutrient loading can cause algal blooms which in turn lead to dramatic decreases in seagrass abundance and distribution (Dennison et al., 1989; Hauxwell et al., 2001, 2003; McGlathery, 2001; Lamote and Dunton, 2006; Lapointe et al., 2015; Morris et al., 2015). When algae grows in epiphytic associations with seagrass species, their presence can result in reduced light absorption, nutrient absorption, and gas exchange by seagrasses (Brush and Nixon, 2002; Drake et al., 2003; Brodersen et al., 2015; Costa et al., 2015). Bloom scale events have also lead to decreases in maximum depth limits, coverage, and stability (McGlathery, 2001; Lapointe et al., 2015; Breininger et al., 2016) and can exacerbate the negative effects of other stressors such as grazing (Maciá, 2000). *Lyngbya majuscula* blooms have caused declines in seagrass biomass, attributable to light reduction, although the extent of decline is highly variable between seagrass species (Watkinson et al., 2005). These reductions in light can be a key factor affecting seagrass distribution (Duarte, 1991; Ralph et al., 2007; Steward et al., 2005, Choice et al., 2014). Due to their high light requirement, seagrasses can be sensitive to shading from algal and cyanobacterial blooms (Duarte, 1991; Orth et al., 2006; Ralph et al., 2007). Duarte (1991) estimated that seagrasses had an average minimum light requirement of 11% of surface light. However, light requirements are highly variable among species due to morphological and physiological differences, ranging from 4.4 to 29.4% of surface light (Dennison et al., 1993). The physical presence of *L. majuscula* may create barriers that alter light availability and photosynthetic potential for seagrasses, particularly when attached to seagrass leaves (Arthur et al., 2006; Ahern et al., 2007; O'Neil et al., 2012; Fabbri et al., 2015). This light reduction impedes photosynthetic activity of seagrasses (Duarte, 1991; Ralph et al., 2007) resulting in reduced growth and biomass (Tomasko, 1992; Czerny and Dunton, 1995; Shafer, 1999; Biber et al., 2009).

The Indian River Lagoon (IRL) is diverse estuary in Florida that extends 251 km from Ponce Inlet to Jupiter Inlet (Gilbert and Clark, 1981; Zimmermann and Montgomery, 1984; Dawes et al., 1995; Steward et al., 2005). The IRL watershed has drastically changed due to rapid urbanization and population growth and creation of canals that increased the amount of freshwater input into the estuary (Kim et al., 2002; Duncan et al., 2004). As a result, eutrophication of this shallow estuary increased due to the presence of land-based sources of nutrients (Sigua et al., 2000; Sigua and Tweedale, 2003; Lapointe et al., 2015). Point-source

sewage pollution was eliminated by 1996 as per the Indian River Lagoon Act of 1990 (*sensu* Lapointe et al., 2015) to protect the estuary. However, nutrient inputs remain, primarily sourced by storm water and non-point sewage pollution (Belanger et al., 2007; Lapointe et al., 2012, 2015). Residency time of water in the lagoon can be extensive, greater than one year, particularly in the northern IRL which has restricted water exchange (Smith, 1993). As a result recent evidence of nutrient accumulation in the IRL has been linked non-point sewage pollution, leading to increases in algal blooms (Phlips et al., 2002, 2010, 2011, 2015; Lapointe et al., 2015). Blooms in the IRL are indicative of these eutrophication events (Benz et al., 1979; Virnstein and Carbonara, 1985) and have resulted in decreases in seagrass abundance and distribution as a result of reduced light availability in the IRL (Lapointe et al., 2015; Morris et al., 2015). Recently, approximately 45% of seagrasses in the northern IRL have been loss since a series of algal and phytoplankton blooms in 2011 and subsequent years (Morris et al., 2015).

One of the dominant seagrass species in the IRL is *Halodule wrightii* Ascherson, a pioneer seagrass species, found in shallow intertidal and sub-tidal waters (Dawes et al., 1995; Steward et al., 2005). As a foundation species, seagrasses like *H. wrightii* strongly influences community composition, including benthic infauna abundance (Orth et al., 1984; Coen and Heck, 1991; Omena and Creed, 2004; Johnson and Heck, 2007). *Halodule wrightii* is also considered to have relatively broad environmental tolerances to factors such as salinity (up to 65 PSU) and temperature (2 °C–39 °C), compared to other seagrass species (McMillan, 1979, 1984; Björk et al., 1999; Koch et al., 2007; Mazzotti et al., 2007). As a result *H. wrightii* is known as a swift colonizer, particularly after stressors, compared to other species (De Oliveria et al., 1983). However, light requirements of *H. wrightii* are relatively high, at $20 \pm 14\%$ surface photosynthetic active radiation (PAR) (Steward et al., 2005). As a result, *H. wrightii* is known to have rapid responses to light attenuation as observed by changes in morphological traits, reductions in biomass and increased mortality (Tomasko, 1992; Czerny and Dunton, 1995; Shafer, 1999; Biber et al., 2009). In the IRL, *H. wrightii* abundance has been negatively impacted by series of algal, phytoplankton, and cyanobacterial blooms since 2011 and recovery has been slow (Morris et al., 2015). However, impacts of algal and cyanobacterial blooms on *H. wrightii* and its associate communities are still largely unknown.

The objective of this study was to test if *L. majuscula* affects *H. wrightii* communities and if those effects are a result of shading by *L. majuscula* mats on seagrass beds. This will provide insight into seagrass persistence in response to blooms. We hypothesize that (i) the presence of *L. majuscula* will reduce seagrass size and abundance, (ii) artificial shading will cause similar seagrass responses as the effect of *L. majuscula* presence and (iii) the abundance of macroinfaunal species (the bivalve, *Macoma constricta*, and two polychaetes *Clymenella mucosa* and *Nereis succinea*) will respond negatively *L. majuscula* presence and artificial shading. These infauna species are abundant bioturbators in *H. wrightii* meadows and are considered to have a random distribution (Coen and Heck, 1991; Omena and Creed, 2004).

2. Materials and methods

2.1. Study area

In the summer of 2006 (April to August), widespread blooms of *L. majuscula* occurred in the central IRL and were observed from Fort Pierce Inlet (27°28′22.002N, 80°17′16.691W) to Vero Beach (27°35′13.176N, 80°21′50.068W), Florida (Capper and Paul, 2008; personal observations). Our field experiment was established at