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Mussel-derived stimulation of benthic filamentous algae: The importance of nutrients and spatial scale

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ABSTRACT

The reoccurrence of benthic filamentous algal (FA) blooms in the Great Lakes, without associated increases in phosphorus loading, has stimulated renewed interest in determining the causes of Great Lakes benthic algal blooms. We investigated the potential roles of invasive mussels and nutrient limitation with experimental substrata within inner Saginaw Bay. FA abundance on live mussel substrata was typically significantly greater than that on inert (empty shell or rock) substrata. Nutrient addition (from an artificial source) significantly increased FA abundance on inert substrata. These results suggest that: 1) mussel nutrient excretion could be a primary stimulatory mechanism; 2) mussel-mediated stimulation may be even stronger in other, more oligotrophic, Great Lakes nearshore zones; and 3) increased nutrient loading to inner Saginaw Bay may exacerbate existing FA blooms. FA abundance on inert substrata was not affected, even in close proximity to mussels, indicating that the observed stimulatory effect of mussel-derived P on live mussels attenuated at very small spatial scales, on the order of centimeters or less.

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Introduction

Historically, excessive benthic algal growth and shoreline fouling events in the Laurentian Great Lakes have largely been a consequence of anthropogenic eutrophication (Auer, 1982; Bootsma et al., 2004; Herbst, 1969). Phosphorus (P) abatement programs ameliorated much of these historical problems (Auer et al., 2010; Bootsma et al., 2004; Higgins et al., 2008a), but now benthic filamentous algae (FA) blooms have returned to many areas of the Great Lakes, despite allochthonous P inputs remaining relatively steady (Bootsma et al., 2004, 2006; Cha et al., 2010; Malkin et al., 2010; Stow et al., 2014). Thus, the ecology underlying the causes of benthic algal blooms and associated wash-up of algal detritus requires attention (Auer et al., 2010; Bootsma et al., 2015; Hecky et al., 2004), as a firm understanding of ecology can indicate potential management solutions.

Modification of Great Lakes coastal ecosystems by invasive mussels may contribute to benthic algal blooms. In North America, dreissenid mussel invasion has greatly altered the ecology and biogeochemistry of aquatic ecosystems (Strayer, 2009). Benthic FA biomass commonly increases after dreissenid invasion (Higgins and Vander Zanden, 2010), and mussel-invaded aquatic ecosystems tend to shift from

planktonic towards benthic production (i.e., the “benthification” of Mills et al., 2003).

The mussel-related habitat modifications of increased nutrient, light, and hard substratum availability are likely drivers of increased FA biomass caused by dreissenid mussels. Through their filter feeding and excretion, dreissenid mussels can move pelagic P to benthic habitats (Hecky et al., 2004) and increase P bioavailability (Higgins et al., 2012). Stoichiometric FA surveys (Bootsma et al., 2004; Higgins et al., 2008a; Winslow et al., 2014), FA responses to point source nutrient inputs (Higgins et al., 2008b), and experimental P enrichments (Francoeur et al., 2015; Pillsbury et al., 2002) all indicate that FA biomass in the Great Lakes is often constrained by P availability; therefore mussel-derived P supplied to benthic habitats could increase FA growth. Mussel filter-feeding reduces phytoplankton abundance and abiotic turbidity, thereby increasing water clarity (see review by Higgins and Vander Zanden, 2010), which in turn increases light penetration to the benthos. Following dreissenid invasion of the Great Lakes, increased benthic light availability appears to have allowed benthic FA to grow at depths that were too poorly illuminated to support FA growth prior to dreissenid mussel invasion (e.g., Lowe and Pillsbury, 1995; Winslow et al., 2014). Mussels also add additional hard substrata (shells; Bially and MacIsaac, 2000; Vanderploeg et al., 2002) to the lakebed. Shells of living and dead dreissenid mussels now cover appreciable amounts of soft-sedimented lakebed within the Great Lakes

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(e.g., Berkman et al., 2000; Coakley et al., 1997; Dermott and Munawar, 1993). Because many FA taxa grow preferentially on hard substrata (John, 2003), dreissenid mussel shells could provide critical FA habitat in areas of soft lakebed sediments, analogous to the way native unionid mussel shells function as “islands” of suitable FA habitat in silty lakebeds (e.g., Francoeur et al., 2002). Whereas the above three effects of mussels are the most commonly cited, Armenio et al. (2016) have also proposed that mussel respiration may enhance FA growth by supplying additional inorganic carbon to FA.

The functioning and relative importance of aforementioned mussel-mediated processes in stimulating FA algal growth in Great Lakes nearshore zones are likely to be contextual and to vary across spatial scales. For example, rapid (relative to phytoplankton doubling time) mixing of epilimnetic water spatially integrates the filtering action of individual mussels, as the water cleared by the filtering activity of an individual mussel does not remain directly above that mussel. Thus, mussel-induced increases in water clarity should reflect the aggregate of mussel filtering activity over large spatial scales, on the order of kilometers. However, rapid uptake of mussel-derived nutrients by adjacent FA likely results in a nutrient effect at small spatial scales (on the order of centimeters) surrounding individual or clumps of mussels, analogous to local nutrient supply by plumes of excreta from individual zooplankters to phytoplankton (Lehman and Scavia, 1982) and from chironomid larvae to adjacent benthic algae in streams (Mooney et al., 2014; Power, 1991). Similarly, the effects of mussel-derived hard substrata should act at small (cm) spatial scales, as the provision of FA habitat by the shell substratum is limited to the shell itself.

The functioning and importance of mussel-related factors affecting FA may also vary temporally over the course of a growing season. The magnitude and importance of mussel-derived nutrient supply and water clarity should change over time, as mussel filtering and excretion rates respond to temporal changes in factors such as temperature and food availability (e.g., Bootsma and Liao, 2014; Johengen et al., 2014), or as alternative sources of nutrients and turbidity cause seasonal shifts in nutrient and light availability (e.g., Fahnenstiel et al., 1995). The ability of FA to respond to favorable nutrient, light, or substratum conditions can also vary temporally, for example as altered temperature affects algal physiological performance (e.g., Graham et al., 1982).

Inner Saginaw Bay provides an ideal context in which to investigate the relative importance of mussel-derived mechanisms for stimulating FA abundance; in particular, the light-poor and P-rich conditions relative to many other Great Lakes nearshore habitats (Fig. 1) present an opportunity for a conservative test of the existence and importance of mussel-mediated P stimulation of FA. If mussel-derived nutrients are important in light-poor and P-rich inner Saginaw Bay, then they should be at least equally important in other, more oligotrophic Great Lakes nearshore habitats. Additionally, inner Saginaw Bay currently experiences benthic FA blooms and shoreline fouling (Bull, 2015; Francoeur et al., 2014; Stow et al., 2014), and should be a reasonable model for other shallow, relatively eutrophic areas of the Great Lakes (e.g., the western Basin of Lake Erie), allowing for both direct application of Saginaw Bay-specific results to an existing management challenge and straightforward extension of such results to other eutrophic Great Lakes habitats currently experiencing similar problems.

The goal of this study was to examine the mechanisms by which mussels may stimulate FA abundance by empirically investigating the importance of mussel-derived nutrient supply and shell habitat on benthic FA abundance at small (cm) spatial scales in a low-light, high-nutrient context. This study therefore does not address potential stimulatory effects at large spatial scales, in which beds of mussels may affect algal growth conditions over larger areas. Specifically, we examined if: 1) the type of hard substrata (live mussels vs. inert empty shells or rocks) affected FA growth, 2) additional nutrient supply stimulated FA growth, and 3) mussels provided sufficient nutrients to influence FA growth on themselves and adjacent substrata.

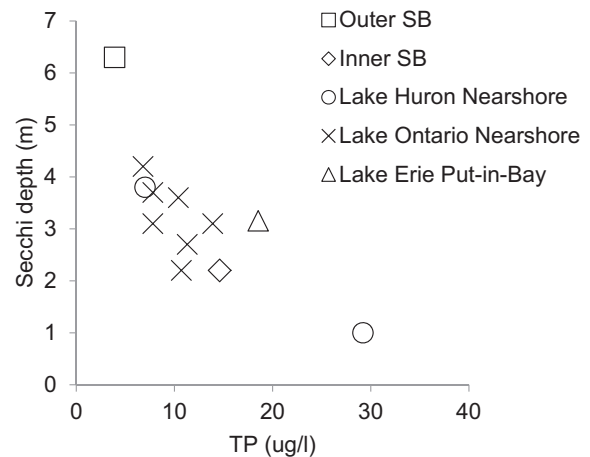


Fig. 1. Relationship of Secchi depth and total phosphorus at selected sites in the Great Lakes. Locations, sample sizes, time periods and data sources are: Inner and Outer Saginaw Bay, $n = 32-95$, May–October 2008–2010, Stow et al. (2014); two Lake Huron nearshore sites, $n = 141-150$, May–September 2010, Howell et al. (2014); seven Lake Ontario nearshore sites, $n = 20-74$, May–August 2008, Higgins et al. (2012); Put-in-Bay Lake Erie, $n = 18$, May–September 1995, Beeton et al. (1996). Values are means (Beeton et al., 1996; Stow et al., 2014), or weighted means (Higgins et al., 2012; Howell et al., 2014). Secchi depths for Lake Ontario and Lake Huron sites were estimated from published turbidity data using the “all lakes” regression equation of Koenings and Edmundson (1991).

Methods

Study site

Three in-situ experiments were performed from 2010 to 2012 within inner Saginaw Bay, approximately 2.7 km offshore from Linwood, Michigan, USA, adjacent to a previously-established survey site (the 3 m-deep station on survey transect 13, see Skubinna et al., 1995 and Francoeur et al., 2014). The study site ($43^{\circ}44'34.6''$ N $83^{\circ}54'58.0''$ W) was ~3 m deep, with a sandy (~50–60%) rocky (~25–30%) lakebed. FA (mean 9.26 g DM m^{-2} , maximum 50 g DM m^{-2} ; predominantly *Cladophora*, *Oedogonium*, *Spirogyra*, *Mougeotia*, and *Zygnema*), charophyte algae, and dreissenid mussels (~1600 mussels/m²) were common at this site (Francoeur et al., 2014), and FA were often observed growing upon mussels.

Survey of environmental conditions

On each site visit, we measured Secchi depth, downwelling irradiance (Li-Cor LI-192) and water temperature. In 2011, water samples were collected from ~0.5 m below the surface, filtered (0.7 μm glass fiber) and frozen in acid-washed bottles for later analysis of PO_4 , NO_3 , and NH_4 , using a Seal Discrete Nutrient Analyzer and EPA-approved methods (Seal Analytical, 2015). Water samples for TP measurements were collected and frozen without filtering, then digested with potassium persulfate prior to analysis.

In order to characterize benthic irradiance and estimate the potential for FA light saturation, we obtained hourly solar flux ($\text{J m}^{-2} \text{ h}^{-1}$) measurements from the nearby Linwood, Michigan, meteorological station (<http://www.agweather.geo.msu.edu/mawn/>) for the 21-day period immediately prior to each sampling event. We converted hourly solar flux to irradiance ($\mu\text{mol m}^{-2} \text{ s}^{-1}$), and applied the light extinction coefficient (k_d , calculated from downwelling irradiance measured over the 0–2 m interval) from the corresponding sampling date to calculate benthic irradiance (see Winslow et al., 2014). We then compared the maximum hourly benthic irradiance for each day (daily peak irradiance) to the lowest saturating irradiance (I_k) value reported for FA from inner Saginaw Bay ($101 \mu\text{mol m}^{-2} \text{ s}^{-1}$; Winslow et al., 2014) to determine if FA potentially experienced saturating irradiance for at

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