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Stimulation of Saginaw Bay charophyte photosynthesis by phosphorus

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ABSTRACT

Like many other benthic algae, charophytes can attain high abundance in shallow waters, thereby affecting benthic ecology and nutrient cycling, and their subsequent death, detachment, and shoreline deposition contribute to beach fouling within the Laurentian Great Lakes. In-situ nutrient enrichment experiments and stoichiometric analyses have shown that other types of Great Lakes benthic algae are frequently phosphorus (P)-limited, but comparable information is lacking for charophytes. This study coupled short-term P enrichment of charophytes collected from inner Saginaw Bay with fluorometric estimates of algal photosynthesis to assess potential nutrient limitation. Benthic irradiance at the experimental sites was frequently sufficient to saturate charophyte photosynthesis, and charophyte photosynthesis was stimulated by experimental P enrichment, suggesting that these algae were P-limited under natural conditions. Reduction of P loading may be an effective charophyte control measure, even in relatively light-poor and nutrient-rich areas of the Great Lakes.

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Introduction

The ecology and biogeochemistry of North American lake ecosystems have been greatly altered by dreissenid mussel invasion (Strayer, 2009). Mussel filter-feeding reduces phytoplankton abundance and abiotic turbidity, thereby increasing water clarity and light penetration to the benthos (Higgins and Vander Zanden, 2010). Through their filter feeding and excretion, dreissenid mussels can move pelagic P to benthic habitats (Hecky et al., 2004) and increase P bioavailability (Ozersky et al., 2009). Benthic producer biomass commonly increases after dreissenid invasion (Karatayev et al., 1997; Higgins and Vander Zanden, 2010), resulting in “benthification” of lake ecosystems (sensu Mills et al., 2003, see also Mayer et al., 2014). These changes have led to a renewed interest in the ecology of lentic benthic algae, in order to better understand and manage these altered lake ecosystems.

In the Laurentian Great Lakes, most attention has been focused on the filamentous green alga *Cladophora*, due to a resurgence of benthic filamentous green algal blooms and subsequent beach fouling (Auer et al., 2010; Bootsma et al., 2004; Higgins et al., 2008a). Field observations and simple modeling have concluded that mussel-induced increases in benthic light availability have extended the depth distribution of benthic filamentous green algae (Skubinna et al., 1995; Winslow et al., 2014). Stoichiometric analysis of filamentous algae (Bootsma et al., 2004; Higgins et al., 2008b; Winslow et al., 2014) and in-situ nutrient enrichment experiments (Francoeur et al., 2015, 2017; Pillsbury et al., 2002) indicate that filamentous algae such as *Cladophora* remain P-limited in

many areas of the Great Lakes, despite potentially increased benthic P availability resulting from mussel invasion. Similar conclusions have been reached by *Cladophora*-specific modeling exercises (Auer et al., 2010). Widespread filamentous algal P-limitation indicates that further reductions in P loading could be an effective control strategy, as has been the case for historical Great Lakes filamentous algal blooms (e.g., Auer et al., 2010; Bootsma et al., 2004; Higgins et al., 2008a).

Some nearshore zones in the Great Lakes are dominated by charophyte algae, not green algal filaments. Charophytes are macroscopic benthic algae with large, plant-like thalli and root-like rhizoids, which anchor them in lakebed sediments (John, 2003). They are present in the earliest records of Great Lakes benthic algae (e.g., Pieters, 1894, see also Stewart and Lowe, 2008). Charophytes are important members of aquatic ecosystems, strongly affecting lentic nutrient cycles and providing both food and habitat, but their biomass can accrue to nuisance levels (Schneider et al., 2015). Although data are scarce, it appears that charophytes have also increased in abundance in the Great Lakes following dreissenid mussel invasion (Skubinna et al., 1995; Stewart and Lowe, 2008). Within inner Saginaw Bay, charophyte biomass can exceed that of filamentous green algae (Francoeur et al., 2014; Skubinna et al., 1995), and charophytes contribute moderate amounts of material to local beach fouling (Bull, 2015). In other areas of Lake Huron, charophyte contributions to beach fouling (~30% of stranded material) greatly exceeded their relative abundance in local nearshore zones (Barton et al., 2013).

Nutrient limitation of charophyte algae has only rarely been investigated, and has never been examined in the Laurentian Great Lakes. Early culture-based experiments (Forsberg, 1964, 1965) suggested that moderate levels (8–30 μg SRP/l) of P inhibited charophyte growth; from this,

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it was inferred that high concentrations of P excluded charophytes from P-rich lakes due to direct toxicity. More recent experimental work has failed to find any evidence for charophyte P toxicity (e.g., [Blindow, 1988](#); [Kufel and Ozimek, 1994](#)), and the scarcity of charophytes in P-rich lakes is now generally attributed to light limitation (e.g., [Blindow, 1988, 1992](#)) or potential toxicity from very high nitrate concentrations ([Lambert and Davy, 2011](#)). Charophytes originally collected from a meso-eutrophic (52 µg TP/l) Polish lake displayed P-limited growth in laboratory mesocosms ([Kufel and Ozimek, 1994](#)); however, [Hough and Putt \(1988\)](#) reported occasional N limitation (but never P limitation) of charophyte photosynthesis in a mesotrophic (20–25 µg TP/l) Michigan lake.

Inferring charophyte P limitation in the Great Lakes based upon frequent P limitation of Great Lakes filamentous algae may be inaccurate. Algal taxa differ in their specific nutrient requirements, and can thus be limited by different nutrients under the same environmental conditions (e.g., [Borchardt, 1996](#); [Fairchild et al., 1985](#); [Tilman et al., 1982](#)). Furthermore, charophytes and filamentous algae can potentially utilize different sources of nutrients. Like filamentous algae, charophyte thalli take up dissolved nutrients directly from lakewater, however charophyte rhizoids can also take up nutrients from sediment pore-water, which can then be translocated to the rest of the thallus (e.g., [Littlefield and Forsberg, 1965](#); [Vermeer et al., 2003](#)). In contrast, filamentous green algae cannot directly access the pool of sediment nutrients, and thus they must rely only upon dissolved nutrients. Use of different nutrient sources increases the likelihood that charophyte and filamentous green algae may potentially display differential patterns of nutrient limitation.

The goal of this study was to investigate the potential for P limitation of charophyte algae within inner Saginaw Bay, a relatively light-poor and nutrient-rich area of the Laurentian Great Lakes with abundant charophyte meadows ([Francoeur et al., 2014](#)). Potential P limitation of charophytes was assessed by measuring charophyte photosynthetic responses to experimental P enrichments at three occasions during the growing season. In-situ light sufficiency was estimated from measures of solar flux, water clarity, and charophyte photosynthesis-irradiance (PI) curves. The light-poor and P-rich conditions of inner Saginaw Bay, relative to many other Great Lakes nearshore habitats, present an opportunity for a conservative test of the existence and importance of charophyte P limitation. If P availability limits charophytes in turbid, nutrient-rich inner Saginaw Bay, then P limitation could be equally important in other, more oligotrophic, Great Lakes nearshore habitats where light is more abundant and P is less available.

Methods

Study site

Charophyte algae were collected from two locations within inner Saginaw Bay. The first site (Site 13, 43°44.638' N 83°54.928' W) was approximately 2.7 km offshore from Linwood, Michigan, USA, and the second site (Site 11, 43°48.610' N 83°53.540' W) was approximately 7.6 km north of site 13. Sites 11 and 13 were previously visited as sampling stations in a wider survey of Saginaw Bay benthos across a range of depths, specifically, they correspond to the 3 m-deep sampling stations on [Francoeur et al.'s \(2014\)](#) survey transects 11 and 13, respectively. Both sites were ~3 m deep, with sandy (~55–70%) rocky (~25%) lakebeds; charophytes, filamentous algae, and dreissenid mussels (~1300–1600 mussels/m²) were common at both sites ([Francoeur et al., 2014](#)).

Field sampling and environmental measurements

On 24 June, 28 July, and 1 September 2015, charophytes were collected from both sites, held in site water, and transported to the laboratory in a cooler. Sub-samples were preserved via air-drying or by immersion in 2% glutaraldehyde for subsequent taxonomic identification;

the remaining charophyte material was used for experimentation. Secchi depth, downwelling irradiance (Li-Cor LI-192) and water temperature were measured at both sites on each sampling visit. Water samples were collected in acid-washed bottles, transported to the laboratory on ice, and filtered (0.7 µm glass fiber) for subsequent experimental use (see below) and nutrient analysis. Samples for nutrient analysis were frozen in acid-washed bottles for later analysis of SRP (automated molybdenum blue method with ascorbic acid reduction, read at 880 nm), NO₃ (automated Cd reduction-azo dye approach), and NH₄ (automated phenate method, with the addition of sodium nitroprusside), according to standard methods ([APHA, 2012](#)) using a Bran + Leubbe (Seal) AA3 autoanalyzer. Water samples for TP measurements were collected and frozen without filtering, then digested offline in an acid-persulfate reagent under autoclave conditions (120C, 20 psi, 45 min). The resulting digestate was analyzed for SRP as detailed above.

Potential light limitation was assessed using the procedure of [Francoeur et al. \(2017\)](#). Briefly, hourly terrestrial solar flux measurements (J m⁻² h⁻¹) were obtained from the nearby Linwood, Michigan, meteorological station (<http://www.agweather.geo.msu.edu/mawn/>) and converted to PAR irradiance (µmol m⁻² s⁻¹) as described in [Winslow et al. \(2014\)](#). Benthic irradiance at each site was estimated for the 21-d periods prior to sampling dates by combining terrestrial irradiance and site-specific measurements of *k_d* on the corresponding sampling date. Maximum hourly benthic irradiance for each day (i.e., daily peak irradiance) was compared to the mean *I_k* value of non-nutrient-enriched charophytes from each site on the corresponding sampling date (see next section for determination of *I_k*) to determine if charophytes potentially experienced saturating irradiance for at least 1 h of that day. The number of days with potential light saturation and the mean daily peak irradiance for the 21-day periods preceding each sampling event were calculated in order to summarize in-situ benthic light availability and provide a reasonable indication of whether the charophytes at a site could have been light-saturated in the period immediately preceding P enrichment experiments.

Photosynthetic response to P enrichment

The charophyte P-limitation assay relies upon the regulation of light-saturated algal photosynthetic rates by internal P content. Suboptimal P content results in lower rates of light-saturated photosynthesis in algae ([Senft, 1978](#); [Smith, 1983](#)), and provision of a limiting nutrient can rapidly restore algal photosynthetic performance ([Geider et al., 1993](#)). The details of the assay were based on a rapid physiological technique for measuring *Cladophora* nutrient stress (I.R. Davison; Central Michigan University, Michigan and K.H. Wyatt; Ball State University, Indiana, personal communication 2014). In brief, they exposed both nutrient-replete and nutrient-limited *Cladophora* to ambient or elevated nutrient concentrations for 3–12 h, and then measured algal photosynthetic performance using pulse amplitude-modulated (PAM) fluorometry rapid light curves. Nutrient-replete algae had consistently high rETR_{max} (analogous to P_{max} of a typical PI curve) values; in contrast, the low baseline rETR_{max} values of nutrient-limited algae were greatly elevated by experimental nutrient addition.

Charophyte P-limitation assays were initiated on the same day as sample collection. After arrival at the laboratory, macroinvertebrates and filamentous algal epiphytes visible to the naked eye were removed from charophytes using forceps. Individual 3–5 cm lengths of the apical ends of charophyte thalli were placed into acid-washed 50-ml vials (*n* = 12 for each site on each date). Each vial was filled with 50 ml of filtered site water. Half of the vials were then amended with Na₃PO₄ (enrichment of 600 µg P/l, final concentration). Vials were then incubated on a rotary table (30 rpm) in a growth chamber (±1 °C from site water temperature, 25 µmol PAR m⁻² s⁻¹) for 11–14 h. Following incubation, each charophyte thallus was subjected to a rapid light curve (sequential exposures to each of 9 fixed light intensities [0, 71, 140, 243, 344, 440, 661, 884, 1314 µmol PAR m⁻² s⁻¹];

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