THE INFLUENCE OF LIGHT AND NUTRIENTS ON BENTHIC FILAMENTOUS ALGAL GROWTH: A CASE STUDY OF SAGINAW BAY, LAKE HURON

By

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ABSTRACT

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In order to develop effective management strategies to alleviate shoreline-fouling events caused by nuisance-level filamentous benthic algal growth throughout the Great Lakes, we need to understand what is controlling benthic algal growth. By focusing on the benthic filamentous algae linked to shoreline-fouling in Saginaw Bay, Lake Huron, I examined how nutrient and light limit benthic algae biomass, and how this limitation varies across gradients of light and nutrient availability. Using active fluorometry and benthic algal internal nutrient content, the benthic algal community was found to be both light and nutrient limited over a large spatial range along the southwest region of Saginaw Bay in the summer of 2009. In addition, active fluorometry indicated that algal health decreased as site distance from the Saginaw River increased. Further, photosynthetic efficiency decreased as depth decreased, suggesting shallower depths are less conducive to growth than more protected, deeper depths. Analysis of light saturation indicated that light availability close to the river is sporadic and relatively constant at further distances. Furthermore, internal phosphorus significantly decreased as distance from the river increased along a 3.0 m depth contour, supporting the existence of a phosphorus gradient. My research sheds light on the degree to which key factors limit benthic algae growth in Saginaw Bay, and how their role varies along gradients common in systems with nuisance beach algae.

Dedicated to my mother and father, who saw me through the ups and downs, the tears, the late nights, the many requests for home-cooked meals and fresh laundry, and somehow knew that I would make it to the end. I could not have done it without you.

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This work is part of a multi-agency project to address multiple-stressor issues in Saginaw Bay. Benthic algae is recognized as a large concern by managers, with fisheries issues and harmful algal blooms also key areas of research. Institutions involved with this project include the Michigan Department of Natural Resources and Environment, NOAA Great Lakes Environmental Research Laboratory, CILER, seven universities (including Michigan State University), and Limno-Tech, Inc.

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INTRODUCTION

Excessive benthic algal growth has impacted the Great Lakes since the 1950s, leading to offensive shoreline fouling events and the appearance of poor nearshore water quality (Bootsma *et al*. 2004). Research from 1960 – 1980 identified phosphorus as the key controlling factor in nuisance-level benthic algal growth and pointed to the eutrophication of the Great Lakes as the overarching cause (Gerstein 1965, Beeton 1966, Davis 1969, Wong and Clark 1976, Auer and Canale 1982, Neil and Jackson 1982, Bootsma *et al.* 2004). Subsequently, a multi-state phosphorus ban was established in the 1970s and 80s to reduce benthic algal growth and alleviate shoreline-fouling events (Bierman *et al*. 1984); the phosphorus program led to a drop in benthic biomass and was declared the solution for the shoreline fouling problem (Bootsma *et al*. 2004, Higgins *et al.* 2008a, Auer *et al.* 2010). However, benthic algal biomass is returning to pre-abatement levels, yet allochthonous phosphorus inputs have remained near or below target levels set in the 1970s (Bootsma et al. 2004, Bootsma et al. 2006, Malkin et al. 2008). This resurgence of the detrital wash-up in the past decade has researchers revisiting the ecology behind nearshore nuisance-level benthic algal growth (Malkin *et al.* 2010).

One area where shoreline fouling is particularly problematic in the Great Lakes is Saginaw Bay, Lake Huron. Of particular concern for Saginaw Bay beach-goers and local landowners, the detritus has been impacting the housing market and economy of the area due to its offensive odor and appearance (Higgins et al. 2008b). Because the problem is strongly pronounced in summer months, beaches that were historically popular for public recreation and tourism are experiencing drops in use. Furthermore, landowners with beachfront properties must invest time and money into removing the deposits from their property fronts.

Few detailed historical observations exist about the composition of shoreline detritus in Saginaw Bay. A Michigan Department of Natural Resources (MDNR) memorandum issued in August 1961 described the wash-up as a “grey-black substance” composed of zooplankton (primarily ostracods and cladocerans), aquatic plant material, *Fragillaria* pieces, and *Cladophora* (Fetterolf 1961). Similar observations were made in an additional MDNR memorandum in September 1978 (Kenaga 1978). However, evidence suggests that the benthic algal detritus washing up on Saginaw Bay beaches in more recent decades is not dominated by *Cladophora*, a benthic algae species that attributed to cause beach fouling in many other regions in the Great Lakes. Instead, Saginaw Bay detritus appears to be composed primarily of decomposing metaphytonic chlorophytes (benthic autotrophs), including *Zygnematales*, *Oedogonium*, diatoms, and *Cladophora*, and vascular hydrophytes (macrophytes) (Pillsbury *et al.* 2002, Peters pers. obs.).

According to Saginaw Bay residents, shoreline fouling events have worsened in the last few decades (Dziekan *et al.*, unpubl.). It has been hypothesized that this change is related to the increase in water clarity caused by the invasion of the filter feeders, the zebra mussel (*Dreissena polymorpha*) and the quagga mussel (*Dreissena rostriformis bugensis*) (Auer *et al.* 2010). Bridgeman *et al.* (1995) found that phytoplankton abundance and productivity plummeted around the time of peak zebra mussel densities during the initial invasion in Saginaw Bay, which led to an increase in light penetration and potential decrease in competition for nutrients in the benthos. Lowe and Pillsbury (1995) suggested that this increased light penetration has created a shift in primary production from a planktonic- to a benthic-dominated system; increased water clarity caused by mussel filtration extended littoral zones, creating conditions favoring benthic algal growth and enhancing benthic primary productivity. This shift from a plankton-dominated to a benthic-dominated system has been termed "benthification," and the effects of such a shift may be dramatic, extending throughout aquatic food webs (Lowe and Pillsbury 1995, Nalepa and Fahnenstiel 1995). Benthification reallocates nutrients and energy sources to the benthos, making them unavailable to planktonic organisms and thereby enhancing benthic productivity (Fahnenstiel *et al.* 1995b, Nalepa and Fahnenstiel 1995, Cecala *et al.* 2008). Furthermore, the additional light may be favoring a benthic community dominated by genera uncommon in the system in the past; specifically that of green algae, which require higher light environments than other algal groups, such as diatoms and cyanobacteria (Pillsbury *et al*. 2002). This additional benthic biomass associated with benthification may be causing the increased benthic algal detritus seen in recent shoreline fouling events.

Literature describing the benthic algal community of Saginaw Bay is sparse. The first bay-wide biological survey took place in the 1990s as part of a study to monitor potential changes in periphyton community composition and nutrient limitation during the invasion of the *Dreissena polymorpha* (Lowe and Pillsbury 1995, Pillsbury *et al.* 2002). Litteral *et al.* (1995) completed a similar study, assessing how increased light levels from *D. polymorpha* filtration may have impacted the periphyton community. Likewise, Skubinna *et al*. (1995) quantified changes in bay-wide macrophyte community composition and distribution in response to increased water clarity, while also measuring the relative abundance of benthic filamentous algae. These few studies encompass nearly all that is known (prior to the beginning of this study) about the benthic algal community of Saginaw Bay.

Nevertheless, these studies have described several important shifts in the benthic community composition. Prior to the invasion of the dreissenid, algal communities were composed primarily of diatoms (Litteral *et al.* 1995). Following the invasion, increases in water clarity due to mussel filtration caused shifts in the benthic algal community to filamentous greens, with *Cladophora*, *Mougeotia*, *Spirogyra*, and *Zygnema* appearing as the dominant species (Litteral *et al.* 1995, Skubinna *et al.* 1995, Pillsbury *et al. 2002*). Litteral *et al.* (1995) suggested that benthic chlorophytes were light-limited prior to the dreissenid invasion, thereby explaining the drastic increase in filamentous green algae growth following increased light penetration in the bay. When water clarity decreased in 1994, the benthic algal community composition again favored diatom species and a decrease in filamentous biomass was observed (Litteral *et al.* 1995, Pillsbury *et al.* 2002); between 1993 and 1994, biomass of filamentous green algae decreased from 93% to just 29% of the total algal biomass (Litteral *et al.* 1995). However, anecdotal evidence and my preliminary observations in 2008 suggest that the benthos has now shifted back to primarily metaphytonic filamentous greens, specifically *Cladophora*, *Oedogonium* sp. and *Spirogyra* sp. (Litteral *et al.* 1995, Pillsbury *et al.* 2002, Peters pers. obs.).

Additional cause for concern rests on recent research: studies have found that algal detritus harbors potentially harmful pathogens, including *Escherichia coli* and enterococci (Byappanahalli *et al.* 2003, Rose *et al.* 2007, Verhougstraete *et al.* 2010). Algal wash-up protects the micro-organisms from weather, allowing them to reproduce to levels above recommended health standards. Then, when the detritus is disturbed by strong wind or wave action, these microorganisms can be released into the water column causing potential public health issues (Verhougstraete *et al.* 2010).

My study is designed to better understand the ecology of benthic filamentous algae in Saginaw Bay. Specifically, the motivation for this work was to assess the interaction of light and nutrients on benthic algal growth, particularly along light and nutrient gradients in the southwest region of Saginaw Bay. The overarching goals are twofold: to better understand the growth of benthic algae in Saginaw bay in order to (1) elucidate factors affecting beach fouling throughout out the Great Lakes and (2) inform managers in Saginaw Bay of the conditions that lead to or control benthic algal growth. Saginaw Bay presents a particularly good study system because it offers the ability to study benthic growth across multiple light, nutrient, and substrate gradients. By better understanding this growth dynamic, especially across gradients of conditions, future research can be focused on potential control methods to aid in alleviating the nuisance-level growth, both in Saginaw Bay and in other areas of the Great Lakes.

My thesis addresses the interaction of light and nutrients in limiting benthic algal growth along predicted light and nutrient gradients in the southwestern portion of Saginaw Bay. I used pulse-amplitude-modulated fluorometry to measure photosynthesis as well as the maximum fluorescence yield, which has been shown to indicate nutrient stress (Kolber *et al.* 1988, Falkowski and Kolber 1995). Furthermore, I measured the cell internal nutrient content and a variety of water quality parameters (i.e., water column total phosphorus and SRP concentrations, pelagic chlorophyll *a*) in relation to distance from the Saginaw River and water-column depth to understand basic growth parameters of the benthic algal community.

My research has provided insight on how light and nutrients influence benthic algal growth. Furthermore, findings from my study supports that benthic algae adapt to varying conditions, thereby complicating the factors controlling benthic algal growth. However, this better understanding of growth allows for more focused research to aid in predicting and managing nuisance benthic algae. Further, my results will inform models that are being developed as part of the larger project in Saginaw bay to describe benthic algae growth and its transport to shoreline. My research also documents where the algae is growing, which can help managers employ physical strategies (i.e. barriers) to reduce beach fouling. These findings further the understanding of a problem that has proliferated the Great Lakes. With this in mind, we hope to help guide managers on how to mediate shoreline fouling events.

CHAPTER I

Nutrient and Light Limitation of Benthic Algae along Predicted Light and Nutrient Gradients Saginaw Bay, Lake Huron

INTRODUCTION

The Great Lakes have a long history with nuisance-level benthic algal growth. Associated with eutrophication, the nuisance-level growth elicited a multi-state phosphorus ban during the 1970s, which led to a substantial drop in benthic filamentous biomass (Higgins *et al.* 2008b). However, reports of shoreline fouling began reappearing during the 1990s even though allochthonous phosphorus inputs remained near target levels (Nicholls *et al*. 2001, Higgins *et al*. 2008b, Malkin. *et al.* 2010).

Recent research suggests that the introduction of the invasive filter-feeders, the zebra mussel (*Dreissena polymorpha)* and the quagga mussel (*Dreissena rostriformis bugensis*), is responsible for this resurgence of benthic algal growth (Higgins *et al*. 2008b, Malkin. *et al.* 2010) by altering the habitat in favor of high productivity in the benthos. Dreissenids significantly altered the physical and chemical characteristics of the benthos by clearing the water column, engineering additional hard substrate, and shunting pelagic phosphorus to benthic primary producers (Johannsson *et al.* 2000, Hecky *et al.* 2004, Higgins *et al.* 2008b, Ozersky *et al.* 2009, Auer *et al.* 2010, Malkin *et al.* 2010). With this increase in benthic productivity, target phosphorus inputs set in the past may no longer be enough to control benthic algal growth throughout the Great Lakes (Auer *et al.* 2010).

Recent research has elucidated the seasonal patterns of benthic algal growth leading up to the algal detritus deposition events (Bootsma *et al.* 2004, Higgins *et al.* 2008a). With enough light and nutrients, facilitated by mussels, a filamentous algal community establishes on available hard substrate and around macrophyte beds throughout the benthos. Using the spring influx of phosphorus, the benthic community rapidly increases in biomass and spatial extent. Then, as the summer growing season progresses and water temperatures increase, conditions become unfavorable to growth; the filaments become highly epiphitized and are subject to the effects of self-shading (Higgins *et al.* 2008a). This progression inevitably leads to senescence and death of the community, which causes detritus. This detritus is then brought on shore with wind or storm events (Bootsma *et al.* 2004). Nevertheless, although our understanding of shoreline fouling is increasing, there is much that is not well understood concerning the role of the major factors, light and nutrients, which limit benthic algae growth.

A particular case of shoreline fouling is seen in Saginaw Bay, Lake Huron. Compared to other parts of the Great Lakes, Saginaw Bay is a relatively shallow, eutrophic estuary with less wave action and a high susceptibility to local weather changes (Danek and Saylor 1977). Therefore, it is expected that different patterns of benthic algal growth exist compared to other Great Lakes bays. Furthermore, although shoreline fouling events are similar in composition and frequency to other lakes, Saginaw Bay growth is relatively heterogeneous over space, which is less common in other Great Lakes. These unique conditions of Saginaw Bay provide the opportunity to examine benthic algae across gradients of limiting factors, to pinpoint the conditions that limit benthic algae growth, and investigate if management can alleviate the wash-up.

The objective of my study was to increase understanding about basic questions concerning the ecology behind shoreline fouling in Saginaw Bay, Lake Huron. Specifically, what is the limiting factor of benthic filamentous algal growth: light, nutrients, or an interaction of the two? Furthermore, do these limitations change across predicted light and nutrient gradients? I conducted a survey of the benthic algal community at 19 sites in the southwest region of Saginaw Bay to characterize growth conditions (e.g. nutrient availability, light), community composition, bay substrate, and overall algal health. I used pulse-amplitude-modulated (PAM) fluorometry and cell nutrient measurements along predicted light and nutrient gradients extending from the mouth of the Saginaw River and across depth. PAM fluorometry was used to measure light requirements of multiple samples of benthic algae and compare these to the light availability to assess light limitation for individual samples. Measuring internal nutrients allowed me to compare individual benthic algal samples to literature derived thresholds of nutrients to understand the level of nutrient limitation throughout the sampling area. I then analyzed cell phosphorus content and parameters of fluorometry across distance from the river, depth of the water column, and substrate type to assess the potential for patterns of algal health characteristics within the zone of high benthic biomass. I compared these values to published values to determine if light and nutrients were limiting.

MATERIALS AND METHODS

Overview

The goal of this study was to determine if light or nutrients, or both, limit benthic algal growth in Saginaw Bay and examine light and nutrient limitation patterns as a function of predicted gradients. A key element of my study was examining algae over a large portion of the Inner Bay to include environmental gradients that were predicted to affect algae growth, thereby spanning a large range of benthic conditions. I examined limitation along gradients to understand how limitation can potentially change or switch throughout different portions of a habitat. I measured cell nutrients and *in situ* algal health and estimated photosynthetic parameters throughout the benthic algal community in the southwest region of Saginaw Bay during the summer of 2009. These measurements were made on benthic algal samples collected across predicted light and nutrient gradients extending from the mouth of the Saginaw River to measure potential light and nutrient limitation patterns within the algal community over a range of conditions. Because water column parameters and substrate availability play a key role in benthic algal growth, I also collected surface water samples and made observations of the benthos with the help of SCUBA divers.

Study Site

This study took place in the nearshore zone (< 10 km of shore) of the inner bay of Saginaw Bay, Lake Huron. The inner bay is a eutrophic, well-mixed system with a mean depth of 5.1 m and a dominant counterclockwise, weak circulation pattern (7 cm/s) highly influenced by local wind changes (Sloss and Saylor 1975, Nalepa *et al*. 2002, Nalepa *et al*. 2003). Bottom substrates include silt/mud, cobble, and rock, and display great spatial heterogeneity (Nalepa *et al.* 1995). The hydraulic retention time for the inner bay is approximately 120 days and is highly influenced by flow from the Saginaw River, which makes up about 70% of the total flow into Saginaw Bay (Nalepa *et al.* 1995). The Saginaw Bay watershed receives extensive agricultural, industrial, and urban runoff (Millie 2006). It has been labeled an "Area of Concern" by the International Joint Commission due to excessive eutrophication, toxic substance and bacterial contamination, and the impact of other environmental stressors caused by Saginaw River eutrophication and runoff inputs (Nalepa and Fahnenstiel 1995, Nalepa et al. 2002, Millie et al. 2006).

When choosing the location of sampling sites, a goal was to quantify limitation in areas of dense growth and areas with a high potential for limitation (e.g., at the boundaries of growth). Based on preliminary observations in 2008 and early 2009, a large region (approximately 50 km^2) of benthic algae growth was identified in the southwestern quadrant of the inner bay close to the Saginaw River. Moving parallel to the shoreline, both toward and away from the river, little or no algal growth occurred beyond this large region of growth. Sampling (e.g. physical collection of algae) only took place where filamentous algal growth was present, which was limited to the 2.0 – 4.0 m depth zone. Algae was examined up to these algal growth boundaries across depth and distance from the Saginaw River in order to examine algae in areas with potentially degrees of limitation. Sites were also chosen along a 3.0 m depth contour in this region of growth to quantify light and nutrient limitation at the depth where algal growth was most commonly observed (Peters pers. observ.). Furthermore, light measurements were taken in areas beyond the extent of algal growth where light limitation was expected. In total, I chose 19 sites for physical collection of benthic algae within these distance and depth growth boundaries, 9 of which were at 3.0 m.

A previous study by Skubinna *et al.* (1995) examined many sites around the entire bay and, where possible, I chose sites that coincided with this previous work. My numbering scheme for transects and sampling sites reflected that of Skubinna *et al.* (1995). See Figure 1 for a map of all sampling site locations and Appendix A for coordinates.

Field Methodology

Benthic Algae

Benthic algae site selection

At each sampling site, divers would collect two bags of filamentous algae from each substrate type, which included *Chara*, mussels, and miscellaneous. For instance, if filamentous algae was observed growing on rocks and around *Chara*, two samples would be collected from two separate rocks and two additional samples would be collected from two separate *Chara* beds. Sites did not always have algal growth on each of the three substrate types. Samples were then brought onto the boat, placed out of the sun, and processed immediately to prevent photoadaptation to conditions different from the benthic light environment. After collection, all visible detritus and non-algal material was removed to leave a homogenous, clean sample of filamentous algae.

All fluorometry measurements were then taken immediately, including dark-adapted maximum photosynthetic efficiency measurements (Fv/Fm) and rapid fluorescence light-response curves (RLCs). Dark-adapted Fv/Fm, or the ratio of variable fluorescence to maximal fluorescence, is used to evaluate algal health in response to a variety of environmental parameters and has been shown to indicate nutrient stress (Kolber et al. 1988, Falkowski and Kolber 1995, Schreiber 2004, Kruskopf and Flynn 2006). RLCs are used to estimate photosynthetic performance at different light levels, which provides insight on optimal light regimes (Schreiber 2004). Since the apically-growing *Cladophora* was expected to be a dominant algal species within the samples, only the apical ends of filaments were used for active fluorescence analysis, to avoid biasing photosynthesis measurements by inclusion of dying or senescent cells (Hiriart-Baer *et al.* 2008). See Table 1 for a summary all active fluorometric measurements taken at each sampling site.

Active fluorescence measurements were made using a chronological methodology. First, using a Diving-PAM fluorometer (Heinz Walz, Effeltrich, Germany), an RLC was taken on each algal sample. RLCs were constructed by exposing algae to 9 increasing light levels (range 0 - ~2250), with an exposure time of 30 s prior to measurement of photosynthetic performance (i.e. light-adapted Fv/Fm) at an individual light level. The samples were then placed in a light-exclusion box and dark-adapted for at least 15 minutes. Dark-adapted algal material was then loaded into the measuring chamber strictly by touch to prevent actinic light from effecting sample fluorescence, and dark-adapted Fv/Fm measurements were taken. At all times prior and during fluorometric measurements, algal material was held in lake water to prevent desiccation. After all active fluorometry measurements were taken, the algal samples were removed from the dark box and stored on ice in a dark cooler until further lab analysis (of cell C, N, P, and species identification). Active fluorometry measurements were only made between the hours of 9:00 and 15:00 EST to limit potential diel fluctuations in Fv/Fm (Schreiber 2004, S. Francoeur, pers. comm.). See Table 1 for a summary all active fluorometric measurements taken at each sampling site and the lab.

Benthic Algae Tissue Nutrient Analyses

In order to capture a representative measure of internal benthic algal nutrient content, the filamentous algal samples collected by divers were blended into a homogeneous slurry by pulse-blending each sample 8-10 times with a 2-speed hand blender (Hamilton Beach, Washington, NC, USA). The slurry was then filtered onto pre-combusted filters (GF/F; Whatman; AMD Manufacturing Inc., Mississauga, ON, Canada) for internal carbon and nitrogen assay and on acid washed filters (GF/F) for internal phosphorus assay and frozen until analysis. I pre-combusted filters for C:N analysis by drying them at 450˚C for 2 hours and rinsing with DI water. Filters for internal P were acid washed in 10% HCl for at least 2 hours and pre-rinsed with DI water. A subsample of the slurry was also taken and preserved in 2% gluteraldahyde for later algal community identification (R. J. Stevenson pers. comm.).

Cell carbon and nitrogen were determined by thawing and acidifying frozen filters with 1 M HCL, and then drying the filters at room temperature for 4 hours. Measurements were made with a Perkin Elmer (model 2400) CHN elemental analyzer (PerkinElmer; Waltham, MA, USA). Tissue P measurements were determined by modifying typical total phosphorus methodology (e.g. Lind 1985) to account for the acid-washed filters. First, the sample filters were autoclaved for 30 min in a 100% potassium persulfate solution (Hiriart-Baer *et al*. 2008). The digestant was then filtered to remove filter particles. Finally, a 50% dilution of the filtrate was analyzed for total phosphorus following Lind (1985), with measurements made on a SEAL A2Q+ Discrete Analyzer (SEAL Analytical; Mequon, WI, USA).

I used two methods to determine nutrient limitation based on tissue nutrient measurements. First, I calculated percent tissue phosphorus (in mg P/g dwt) and compared to the published threshold value of 0.16% P, determined by Wong and Clark (1974) as the internal phosphorus content at which P becomes limiting. Second, I calculated the molar ratios of C:P, N:P, and C:N and compared the ratios against the literature-derived threshold 550:30:1, which is the known molar ratio for benthic marine plants and macroalgae (Atkinson and Smith 1983; Hiriart-Baer *et al*. 2008).

Benthic Algae Photosynthesis Parameters: Pulse-Amplitude-Modulated Fluorometry

I used rapid light curves to calculate photosynthetic parameters to understand the light requirements and long-term light habitats of the benthic algal samples in a variety of conditions throughout our study site. A rapid light curve consists of the irradiances emitted by the PAM fluorometer vs. the electron transport rate (ETR) at each irradiance, where the ETR is derived from light-adapted maximum photosynthetic efficiency measurements. The rapid light curve is then used to derive parameters of photosynthesis, including the initial slope of the curve (alpha), the maximum electron transport rate (ETR_{MAX}), and the light saturation index (E_K).

Fv/Fm is a measure of algal health and has been shown to indicate nutrient stress (Kolber and Falkowski 1995). Fv/Fm is used to calculate the curve used to derive the photosynthetic parameters of interest. α is the initial slope of the RLC curve (or P-E curve). It is a measure of how rapidly photosynthesis will increase if light is increased from low to slightly higher levels. The alpha parameter alone can be used to indicate the light availability for an algal sample; a high alpha typically indicates a low light environment while a low alpha indicates a high light environment. Alpha has been hypothesized to have a direct opposite correlation with nutrient availability, with low values indicating low availability and vice versa (Schreiber *et al.* 2004, Higgins *et al.* 2008a). The light saturation index (E_K) gives the light intensity at which further increases in light no longer cause increased photosynthesis and was calculated as ETR_{MAX}/alpha. If the E_K of a sample of algae is below the average light level in which that algae grows, the algal sample is light limited. If a sample is in a light environment well above their E_K, the samples have sufficient light and are limited by another factor. Both alpha and E_K can be used to better understand the light environment available to benthic algal samples.

ETR_{MAX}, alpha, and E_K were derived from the rapid light curves calculated via PAM fluorometry. The electron transport rate (ETR) was calculated to construct each RLC using the following equation:

$$ETR = Fv/Fm \times E \times 0.5 \times 0.82$$

where Fv/Fm is the light-adapted photosynthetic yield of the sample at a particular light intensity, E is irradiance/light intensity, 0.5 accounts for the assumption that 50% of photons are absorbed by each photosystem (Schreiber 2004), and 0.82 as the proportion of PAR absorbed by the average green leaf (Bjorkman and Demmig 1987). With the ETR calculation, photosynthetic parameters were derived by plotting the calculated ETR vs. the light intensity irradiances produced by the Diving-PAM to construct the RLC. I then parameterized the RLC by fitting the curve with a two-parameter photosynthesis model,

$$ETR = ETR_{MAX} * \tanh((alpha*E)/ ETR_{MAX})$$

developed by Jassby-Platt (1976), where ETR_{MAX} is maximum photosynthesis, alpha is the initial slope of the curve (see details below), and E is irradiance/light intensity. When photoinhibition was present in the RLC, the data points after the initial maximum were removed because the light values at which photoinhibition was observed were higher than any benthic light measurements made over the course of the summer. SAS version 9.2 statistical software was used for all PAM curve fitting.

Water Chemistry

A series of water quality and chemistry measurements were made at each site. A Secchi disk reading and a temperature, dissolved oxygen (DO), and pH profile of the water column were taken using a Hydrolab DS5 SONDE, calibrated daily for DO (luminescent DO probe, Hach Hydromet, Loveland, CO, USA). Light measurements were taken at the surface and 1.0 m depth using a LI-192 unidirectional (downwelling) light meter (LI-COR, Lincoln, NE, USA). A 1 L water sample was collected 0.5 m below the surface in an acid-washed polyethylene bottle pre-rinsed with sample water. Water samples were stored at 4˚C in the dark and processed within 24 hours.

Whole water samples were measured for total phosphorus and filtered to measure water column chlorophyll *a*, soluble reactive phosphorus, and particulate C:N ratios. Total phosphorus was determined calorimetrically after sample digestion with 5% potassium persulfate in an autoclave for 30 min (Menzel and Corwin 1965). To measure C:N ratios of filtered water column samples, filters were frozen until analysis, then thawed, acidified with 1 M HCL, and dried at room temperature for 4 hours. C:N measurements were made with a Perkin Elmer (model 2400) CHN elemental analyzer. All nutrient concentrations were analyzed at the Great Lakes Environmental Research Laboratory, Ann Arbor, MI.

Chlorophyll *a* concentrations were determined following Welshmeyer (1994). Frozen filters were extracted with 95% cold (refrigerated) ethanol for ~12 hrs. Samples were then read on a Turner Fluorometer. Concentrations were given as µg/L chlorophyll *a.* All chlorophyll *a* concentrations were analyzed at Michigan State University, East Lansing, MI.

Benthic Light Calculations

The benthic light was calculated at each site for each day the site was sampled as a means of assessing the light available to the benthic algal community. The benthic light calculations were based on k_{PAR} measurements taken at each site at the time of sampling. I also calculated midday averaged benthic light based on meteorological station data at each site for each day sampled to decrease potential variability caused by changes in cloud cover.

k_{PAR} was calculated using the formula:

$$k_{PAR} = \log(I_1 - I_0)/(\Delta z)$$

where I_1 is irradiance at 1.0 m depth, I_0 is the surface irradiance, Δz is the change in depth between the two irradiance measurements. Using the water column light measurements, I calculated instantaneous benthic light (IBL) with the formula:

$$I_z = I_0 \exp(-z * k_{PAR})$$

where I_z is irradiance at depth z, I_0 is irradiance at the surface of the water column, and k_{PAR} is the light extinction coefficient. I_z is reported in µmol/m^2-sec.

Additionally, I calculated the benthic light for sites where I predicted extreme light limitation, so much so that no benthic growth was ever observed. The benthic light calculations for these sites were made off of the light measurements I took outside of the range of growth where I expected light to be the primary limiting factor of algal growth. Results are reported in μmol/m^2-sec.

Midday averaged light was calculated using surface shortwave radiation (W/m^2-hr) measurements taken by the Linwood, Michigan, Meteorological station. The meteorological station records surface shortwave radiation measurements at the end of every hour. To calculate the midday average of these measurements, the recorded measurements taken from 9:00 to 15:00 EST were averaged for each sampling day. Since shortwave radiation is given in kJ/m^2-hr, I needed to convert the measurements to μmol/m^2-sec. These conversions were made by (1) multiplying shortwave radiation by the constant 5.03 to convert shortwave energy to quanta (Wetzel 2001), and then (2) multiplying by 0.46 to account for the proportion of PAR in shortwave radiation, according to Kirk (1994) (Hiriart-Baer *et al.* 2008). Once converted to μmol/m^2-sec, these averaged surface measurements were then set as the I_0 in the equation above and k_{PAR} values remained the same as in the calculation of IBL. This sequence of calculations produced the midday average benthic light (MBL).

The level of light limitation in a sample was examined by comparing E_K to MBL, where E_K is an intrinsic measure of the light required by individual samples and MBL is the amount of light available to the benthic community. To determine the absolute difference in the light environment required by the organism versus the light environment experienced, I analyzed the difference between the light required by the algal sample (E_K) and the average light environment available to it (MBL).Using this comparison, the farther E_K was below the available benthic light (MBL), the more light was limiting growth. Furthermore, in order to provide an understanding of what light levels were closest to benthic algal E_K measurements, I plotted (MBL - E_K) versus MBL.

Also, it must be considered that benthic algae has the ability to adapt to their light environment (Hill 1996). To understand the degree of adaptation, I compared E_K calculations to MBL. If no adaptation strategies were utilized, E_K would remain constant regardless of the level of environmental light.). If adaptation is present, E_K will fluctuate with the available light environment. Adaptation can also manifest itself in the plot of (MBL – E_K) versus MBL. If no adaptation strategies were utilized, then no relationship should develop between (MBL – E_K) and MBL. However, if adaptation is present, a relationship between the two parameters will be observed.

Statistical Analysis

All statistics were run using SAS statistical software, version 9.2 (SAS Institute Inc., Cary, NC, USA). Prior to analysis, benthic algal samples were averaged across replicate and water quality samples were averaged across site location, by date. All variables were tested for normality using the Shapiro-Wilk goodness-of-fit test and transformed when necessary. Internal phosphorus was log transformed and Fv/Fm was cube transformed. Throughout the statistical analysis, I report significance when p-values were 0.05 or less.

Benthic Algal Parameters

Aikaike's Information Criterion, corrected for small sample size (AIC_C), was used to determine the best-supported model for all benthic algal measurements (maximum photosynthetic efficiency, E_K, alpha, and internal P), with distance from the Saginaw River, water column depth, and substrate type as possible independent variables. Substrate type included three groups: *Chara*, mussels, and miscellaneous. R^2 and adjusted R^2 were also calculated for each potential model. I considered any model with a $\Delta AIC_C \leq 2$ to be equally plausible (Burnham and Anderson 2002). AIC weights were also calculated. All AIC information for each potential model and dependent variable combination can be found in Tables 5 and 6. Once the best-supported model (or models) was chosen for the benthic algal dependent variables, I ran a regression of the dependent and independent variables included, and reported the model strength (p-value). Models with $p>0.05$ were not used in further analysis. All best-supported models, including p-values, parameter estimates, R^2, and adjusted R^2, can be found in Table 1.

The effect of distance on internal phosphorus and Fv/Fm was also analyzed on a subset of the sampled set representing all sites at a site that was measured more intensively, 3.0 m, in order to reduce potential variability introduced by depth. The 3.0 m depth contour was chosen because it represents the depth at which growth was most commonly found. Conclusions drawn from this analysis could then be extrapolated to the larger region of growth since it represents an area of high biomass, as opposed to concentrating on the boundaries of limitation only. All AIC information for each potential model and dependent variable combination can be found in Tables

7 and 8. All best-supported models, including p-values, parameter estimates, R^2, and adjusted R^2, can be found in Table 2.

Analysis of both the full dataset and subdata was necessary to assess potential variability introduced by depth, which could hide underlying patterns with other parameters. If parameter significance differed between the two datasets, the results of both datasets will be presented and an explanation for future research given. If the same independent variables were found to be significant in both datasets, only the larger dataset will be discussed.

Water Quality Parameters

To determine the existence of light and nutrient gradients extending from the mouth of the river and across depth, I ran a simple regression with water-column depth and distance from the river as independent variables for each water quality dependent variable (k_{PAR}, SRP, TP, and Chlorophyll *a*). I then ran a multiple regression with both independent variables included. Models with a significance of $p>0.05$ were not used in further analysis.

Water quality variables are subject to a large amount of variability from daily stochastic events. Nevertheless, I expected to see the light and nutrient gradients reflected in the effect of distance and depth on each water quality independent variable. On the contrary, benthic algal variables are less stochastic than water quality variables. Because of the difference in timescales captured by water quality variables versus benthic algae variables, I did not expect the water quality variables to provide explanatory power to the benthic algal variables. Therefore, I did not measure a potential relationship between the two sets of variables.

RESULTS

Benthic Algae Tissue Nutrient Analysis

Comparison to Literature-Derived Threshold Values to Determine Nutrient Limitation

Percent tissue phosphorus ranged from 0.032 – 0.223 mg P/g dwt, with an average of 0.096 ± 0.009 mg P/g dwt (n=27). These internal nutrient measurements were generally lower than literature-derived thresholds for nutrient limitation, indicating severe phosphorus limitation across the entire benthic community. 38 of the 43 observations fell below 0.16 mg P/g dwt, the threshold value established by Wong and Clark (1974) for *Cladophora* sp. at which P is limiting, thereby deeming a majority of the samples to be P-limited (Fig. 2). Additionally, 11 samples were considered severely P-limited, falling below the tissue quota of 0.06% required for growth (Auer and Canale 1982; Fig. 2).

Similar results were found concerning P-limitation with the nutrient molar ratios. The mean C:P ratio was 765 ± 240, with 15 of the 19 samples measured above the 550:1 threshold value determined by Atkinson and Smith (1983) as the onset of P-limitation for benthic marine plants and macroalgae (Fig. 3.). 18 of the 19 samples were also above the threshold N:P of 50:1 (also from Atkinson and Smith, 1983), with an average of 61 ± 17 (Fig. 4).

Finally, all of the samples were well below the 18.33 threshold for C:N molar ratios at which N is limiting in benthic marine plants and macroalgae (Atkinson and Smith 1983; Fig. 5). Therefore, we did not find N to be a limiting factor for any algal samples.

Spatial Gradient in Tissue Phosphorus

Variation in distribution of tissue phosphorus was best explained by five models, including distance (p=0.10), distance + mussels (p=0.14), distance + depth (0.17), depth (p=0.39), and mussels (p=0.23) (Table 1). Assessing model strength for each of these five best-supported models resulted in non-significant models with p-values above 0.05 (> 0.1), indicating that tissue phosphorous was independent of depth, distance from the river, and substrate type. There was a single model that best described the effect of distance from river on internal phosphorus along the 3.0 m depth contour. It indicates that internal phosphorus significantly decreased with increasing distance from the river (n=15; p= 0.015; Fig. 6).

The Effect of Distance, Depth, and Substrate on Benthic Algae Photosynthesis Parameters to Determine Light Limitation across Gradients

Maximum photosynthetic efficiency (Fv/Fm) ranged from 0.093 – 0.64, with an average of 0.46 ± 0.022. The three best-supported models for the maximum photosynthetic efficiency parameter included depth of the water column + *Chara*, with an adjusted $R^2 = 0.21$, depth of the water column + mussels (adjusted $R^2 = 0.17$), and depth alone ($R^2 = 0.16$). In each of the three best-supported models, maximum photosynthetic efficiency significantly increased with increasing water-column depth ($p \leq 0.02$ for all models) No effect of distance was found for any of the models containing the entire dataset. In contrast, when effect of distance was analyzed on the 3.0 m depth contour subset of data, Fv/Fm significantly decreased as distance from the river increased and was found to be one of the best-supported models for the benthic algal parameter at 3.0 m depth (p=0.003; Fig. 7).

Alpha ranged from 0.041 – 0.23, with an average of 0.14 ± 0.0065 (n=37). The best supported models for the alpha parameter included depth + distance (adjusted $R^2 = 0.24$) and distance alone ($R^2 = 0.25$). Alpha significantly decreased ($p < 0.008$ for all models, Table 1) as distance from the river increased in all three of the best-supported models (Fig. 8 for distance alone). Depth alone was a marginally significant explanatory variable for alpha, where alpha increased as depth increased ($R^2 = 0.095$, p=0.064). None of the four best supported models along the 3.0 m depth contour were significant for α ($p > 0.3$ for all models, Table 2).

The light saturation index (E_K) ranged from 216.6 – 549.6 μmol/m^2-sec, with an average of 380 ± 12 μmol/m^2-sec (n=36). A single model best supported best described variation in E_K that included distance from the river, water-column depth, and *Chara* (adjusted $R^2 = 0.27$). E_K significantly decreased as water column depth increased (p=0.022, Figs. 9 and 10). E_K was also significantly higher when found on *Chara* as opposed to the two other substrate types (p-value=0.0086). When assessing E_K along the 3.0 m depth contour, a total of three models were deemed best-supported, including *Chara* ($R^2 = 0.20$), miscellaneous substrate types ($R^2 = 0.11$) and distance ($R^2 = 0.05$). However, only the model containing *Chara* elicited a significant relationship, where E_K was higher on *Chara* than other substrates, as seen when including all depths (p = 0.047). The other models were not significant (Table 8), and therefore the subdata do not support a significant relationship with distance.

(MBL – E_K) did not have a significant relationships with depth (R^2=0.013, p=0.40) or distance from the river (R^2=0.032, p=0.20), but did significantly increased with increasing MBL (MBL parameter estimate = 0.74, R^2 = 0.56, p<0.0001; Fig. 11). No data points fell lower 77 µmol/m^2-sec, suggesting that irradiances lower than 77 µmol/m^2-sec do not sustain growth. Furthermore, the onset of light saturation was observed beginning near 400 µmol/m^2-sec as samples begin to reach an irradiance above their light requirements. However, the few samples found to be in a light environment above E_K were close to the threshold of MBL – E_K = 0, so was not possible to determine if these samples were, in fact, light saturated.

MBL was below the 75 lower light threshold recognized in the previous analysis for all areas explored in regions I predicted the absence of algae growth was due to light limitation. At 5.0 m depth, approximately 22 km from the mouth of the river, benthic light was estimated to be between 10 µmol/m^2-sec in late July to 34 µmol/m^2-sec in mid August. In addition, at a site approximately 5 km from the river, an area assumed to be too turbid to allow growth due to proximity to the river, benthic light was estimated to be 26 µmol/m^2-sec at 2.0 m depth and 79 µmol/m^2-sec at 3.0 m depth.

Water Quality Analysis to Support Light and Nutrient Gradients

The mean and range for all measured water quality variables (k_{PAR}, SRP, TP, and chlorophyll *a*) are presented in Table 3. No combination of distance or depth produced a significant model ($p<0.05$). See Table 4 for all models, the number of observations included in each (n), R^2, adjusted R^2, and model p-values.

DISCUSSION

Both light and phosphorus were found to limit benthic algal growth. Across a majority of the samples, benthic algal tissue P content was far below reported thresholds for P saturation, with many samples near the amount simply required for growth. All 19 sites, which were located throughout the southwestern portion of Saginaw Bay from 2 – 4 m depths, exhibited evidence of phosphorus limitation in the benthic algal community. Furthermore, the light saturation coefficient (E_K) was well above typical benthic light levels experienced by algae, thereby suggesting overall light limitation. Additionally, evidence of light adaptation was noted across depth of the water column, which complicates the ability to predict the importance of each factor.

Verification of Light and Nutrient Gradients

My study was designed to examine processes over predicted nutrient and light gradients extending from the Saginaw River. Results of the surface water samples showed no evidence of a gradient with distance from the river. However, this is not evidence against the predicted gradients. Instead, these results indicate that the gradients are not strong enough to be seen on a daily basis. The parameters are subject to daily stochasticity, which added enough variability to hide any potential underlying patterns. My measurements of algal internal phosphorus and fluorescence parameters indicate that these gradients are present, but in order to obtain a more detailed measurement of the presence of each gradient, daily water column sampling is necessary to calculate weekly or monthly averages, which could then be compared across spatial gradients.

Light as a Limiting Factor

When comparing Saginaw Bay to other bays and shallow regions (e.g. shorelines) in the Great Lakes with abundant filamentous algal growth, algal growth ends at a much shallower depth than elsewhere. Lake Erie and Lake Ontario have reports of growth to at least 10 m depth and upwards of 20 m in Lake Michigan (Bootsma *et al.* 2005, Higgins *et al.* 2005, Malkin *et al.* 2008). This shallower growth boundary is likely due to light limitation being greater within Saginaw Bay. Although this boundary depth is much different across these different Great Lakes habitats, the light conditions at the boundary of growth are similar. I found that algae growth was limited to depths less than approximately 4 to 4.5 meters. According to Lorenz *et al*. (1991), the minimum daily light requirement for *Cladophora* is 27 μmol/m^2-sec, which he confirmed with a series of laboratory experiments and field observations in Lake Erie. Based on his calculations, a Saginaw Bay surface irradiance of 807 μmol/m^2-sec and a mean light attenuation coefficient of 0.697 m^{-1} (based on my light attenuation dataset), the maximum depth of colonization for Saginaw Bay should be approximately 4.85 m, as this is where the mean summer light environment is 27 μmol/m^2-sec. Therefore, even though the deepest sampling point was 4.0 m, it was close to the theoretical maximum depth of colonization, suggesting that the light environment at this depth is similar to other Great Lakes systems with benthic filamentous algae. Although the light environments near the boundaries of growth are similar, the extreme difference in the depth of growth in Saginaw Bay then elsewhere is consistent with my findings that light limitation may be an issue throughout the benthos of Saginaw Bay, outlined next.

The premise of the study was to determine the extent to which nutrients and light conditions influence benthic algal health and resulting growth. When assessing the effect of light, the light saturation index (E_K) calculations suggest that a majority of the community is in a light environment below what would be saturating; therefore, they are light limited. 90% of the samples analyzed were found in a light level below their E_K, indicating that they were in sub-saturating, or limiting, light environments. The 10% of samples found in light environments above their E_K were within 50 µmol/m^2-sec of this threshold, which made it impossible to evaluate the status of limitation. Overall, nearly the entire community was found to be light limited.

Phosphorus as a Limiting Factor

Using a combination of measurements, it was determined that (1) filamentous algae far from the river are persistently strongly limited by P, and (2) that benthic communities are acclimated to this limitation. All of the phosphorus measurements indicate an extreme level of phosphorus limitation is present throughout the benthic community. 88% of the tissue P samples fell below the requirement needed for P-saturation, according to Wong and Clark (1976), with almost 30% of those samples falling below the level required for growth established by Auer and Canale (1982). The fact that samples had P concentrations lower than the amount required for growth suggests that these samples were not growing. The algal samples were likely depleting the stores of phosphorus beyond the amount required for growth, yet were still viable. No pattern was observed among the samples to provide a cause for why the phosphorus stores were relatively low.

With P-limitation present throughout the community, dark-adapted maximum photosynthetic efficiency and benthic algal tissue P measurements could have a positive linear relationship since dark-adapted maximum photosynthetic efficiency have been found to indicate nutrient stress (Parkhill *et al.* 2001, Higgins *et al.* 2008a, Hiriart-Baer *et al.* 2008). Dark-adapted Fv/Fm is a measure of the photosynthetic capabilities of a sample and is highly affected by any limitation on the photosynthetic machinery within the sample in question (Kruskopf and Flynn 2006). However, a relationship between Fv/Fm and internal phosphorus was not found in my study. Analysis of the results on phosphorus limitation with internal phosphorus and maximum photosynthetic efficiency, in combination, indicate that phosphorus far from the river is persistently low and that benthic communities have become acclimated to this low level. Recent research suggests that when algal communities become acclimated to nutrient-limited environments, their Fv/Fm measurements do not provide a reliable indicator of nutrient stress (Parkhill *et al.* 2001). In fact, it has been found that phosphorus replete algal samples and samples from algal communities acclimated to low phosphorus had the same high Fv/Fm values (Fv/Fm = ~0.65; Parkhill *et al*. 2001). Only when the nutrient replete samples were deprived of phosphorus did a relationship with Fv/Fm exist. Therefore, the lack of a relationship between Fv/Fm and internal P suggests that the community is likely acclimated to the P-limiting nutrient levels.

Light vs. Phosphorus Limitation across Gradients of Light and Nutrient Availability

Light and phosphorus limitation of the benthic filamentous algae was observed to change across expected light and nutrient gradients extending from the Saginaw River. Alpha significantly decreased as distance from the river increased (Table 1). Along the 3.0 m depth contour, internal phosphorus and Fv/Fm also significantly decreased as distance from the river increased (Table 2). However, the significant relationship between alpha and distance dissolves when analyzing the 3.0 m subdata, indicating that distance may have an effect on alpha, but additional research is necessary to confirm this relationship. Nevertheless, these patterns in benthic algal growth parameters illustrate the importance of examining the heterogeneity and potential gradients within benthic habitats to achieve a full understanding of benthic light environment.

The change in the benthic algal parameters also suggests that the benthic community is exposed to gradients of light over time and space. Specifically, a high alpha indicates that the uptake of light is occurring at a rapid rate, inferring that light is not consistently available over time (Schreiber 2008). A low alpha measurement indicates a slow uptake of light, suggesting a more consistent or reliable source of light availability (Schreiber 2008). Therefore, the relationship between alpha and distance from the river suggests that close to the river, light availability is sporadic, while farther from the river, light availability is more constant over time.

Variations of E_K provide a deeper understanding of the level of light limitation across Saginaw Bay and may even suggest that the algal community is employing adaptation strategies to the low light availability. I predicted that E_K and (MBL - E_K) would vary as a function of light level in the benthos, which would decrease as a function of depth and proximity to the river. I could not evaluate the relationship between (MBL – E_K) and distance from the river. However, the results indicate no effect of depth on (MBL – E_K), suggesting that the benthic samples were adapted to the low-light environment. To clarify, E_K is an intrinsic measure of the light required by individual samples. E_K significantly decreases with depth, thereby suggesting that algae at deeper depths inherently require less light to survive than shallow depths; this suggests that the algae at deeper depths have acclimated to a lower light environment than algae at shallower depths. Moreover, the lack of a relationship between (MBL - E_K), and depth suggests that intrinsic needs of the algae parallel the environmental light available to those individual samples. Therefore, the E_K findings suggest that the community is light limited and provide more information about the level of light limitation and potential adaptation.

The effect of distance on the benthic algal parameters provides additional insight into phosphorus availability and the influence of the Saginaw River outputs. The negative relationship between internal phosphorus and distance from the river suggests that near the mouth of the river, phosphorus is more readily available than sites far from the river. This relationship between phosphorus and proximity to the river indicates that the Saginaw River has a significant effect on benthic growth requirements, which may help to guide local management efforts for future research and development of effective policy. The 3.0 m depth contour data also indicates that conditions near the mouth of the river produce algae that is relatively healthier, or less stressed by its environment, then sites farther away from the river, thereby suggesting that conditions closer to the mouth of the river are more amenable to benthic filamentous algal growth (assuming enough light is available for growth). The basis for this gradient with distance and algal health is found in the effect of distance from the river on Fv/Fm. A number of conditions could cause this gradient to develop, including (but not limited to) differences in light availability, phosphorus, nitrogen, habitat type, or water movement (Hill 1996). In a larger sense, the relationship with health and proximity to the river suggests that inputs from the river have a substantial effect on algal growth, which can be helpful when designing effective management strategies to alleviate the benthic algal growth.

CONCLUSION

This study indicates that the entire region of filamentous benthic algal growth in the southwestern portion of Saginaw Bay is both light and phosphorus limited. Furthermore, this study illustrates that important relationships exist between benthic algal parameters and expected light and nutrient gradients in Saginaw Bay and also shows that the Saginaw River as a key influence on algal health. In a larger context, this study aided in the understanding of how benthic algal growth parameters can change along gradients throughout a particular study system. With this result in mind, researchers can now work toward identifying the factors (light or nutrients, or both) that have the greatest effect on benthic growth in many areas of a heterogeneous environment. This detailed assessment of a benthic ecosystem can then be used to guide management efforts in controlling growth and subsequential shoreline fouling events. Although reducing phosphorus may seem to be the easy solution given historic successes, the Great Lakes benthos has become more complex and unpredictable, making research more vital than ever to understand how to protect and manage these crucial freshwater systems.

APPENDICES

APPENDIX A – Figures and Tables for Chapter I

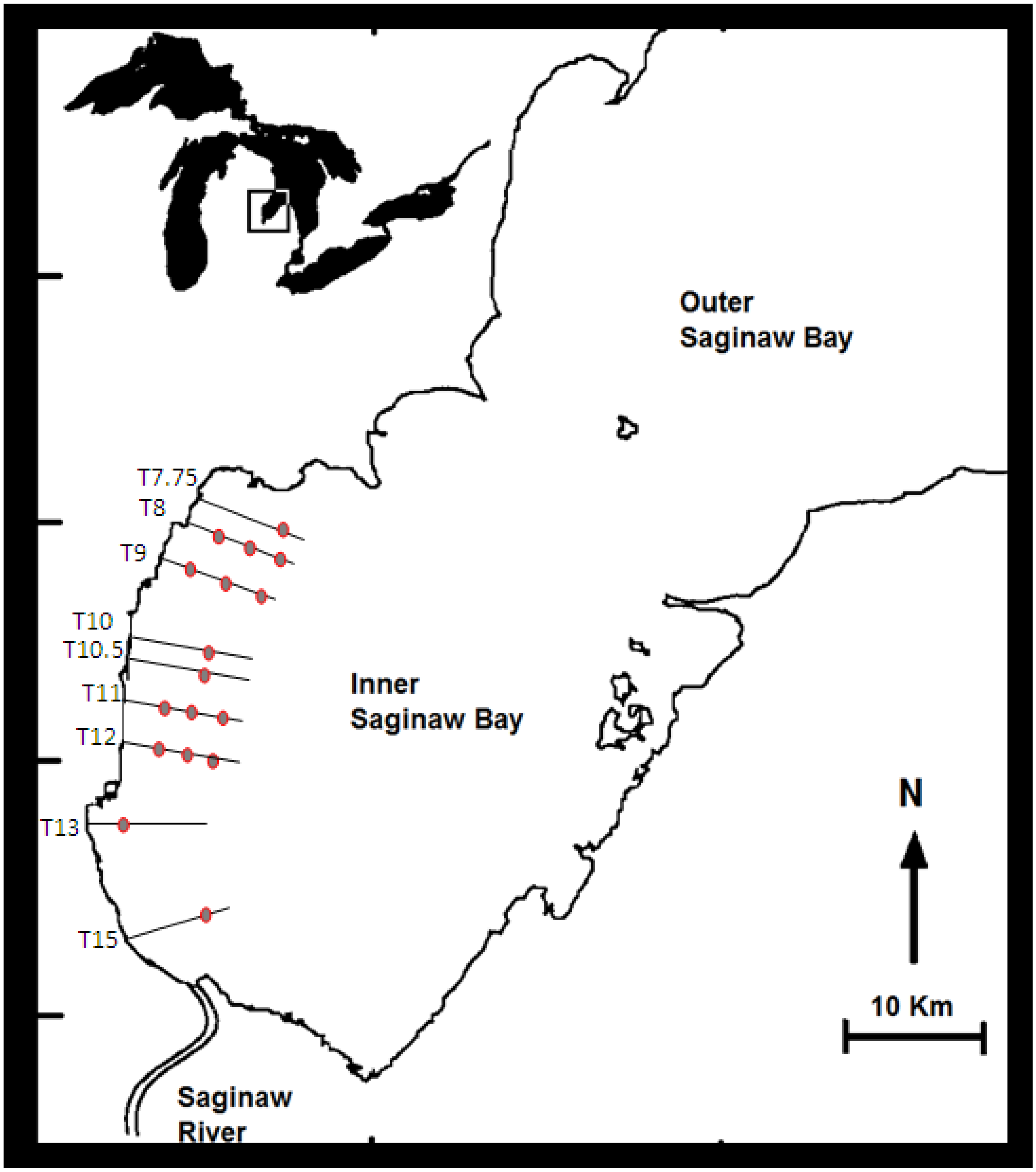

Figure 1 – A map of the inner bay of Saginaw Bay, Lake Huron demarcating sampling sites and transects. The numbering scheme is based off of Skubinna *et al.* (1995).

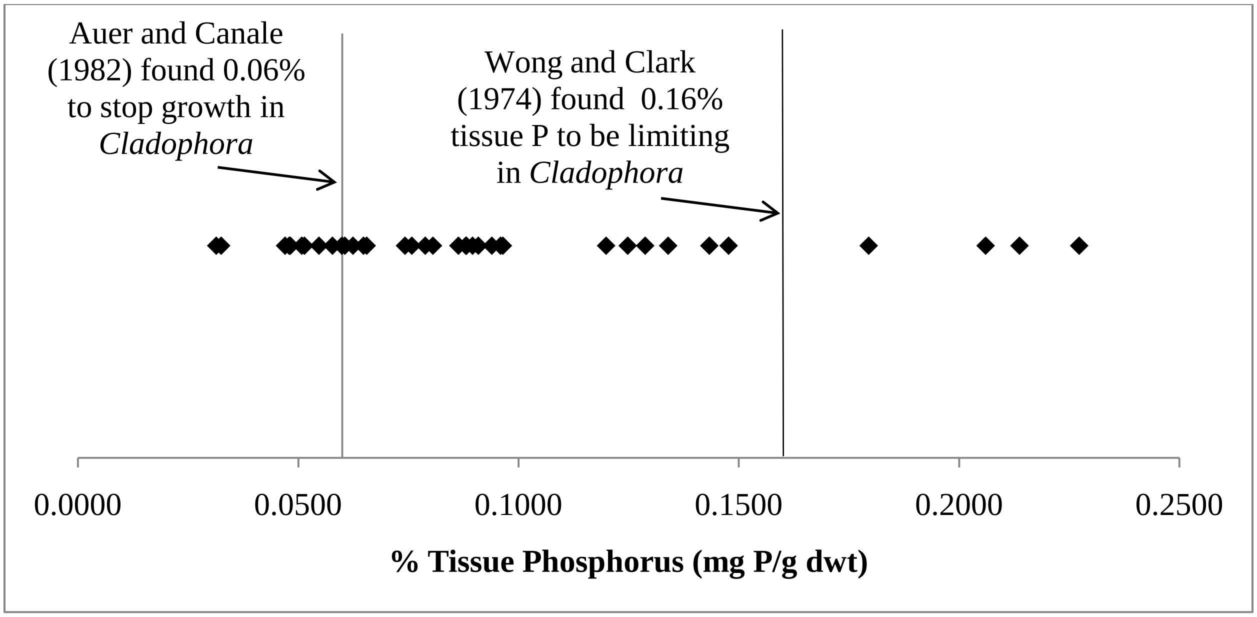

Figure 2. % Tissue phosphorus (mg P/g dwt) of benthic filamentous algae in the inner bay of Saginaw Bay, Lake Huron compared to published values of phosphorus limiting tissue concentrations (n = 27).

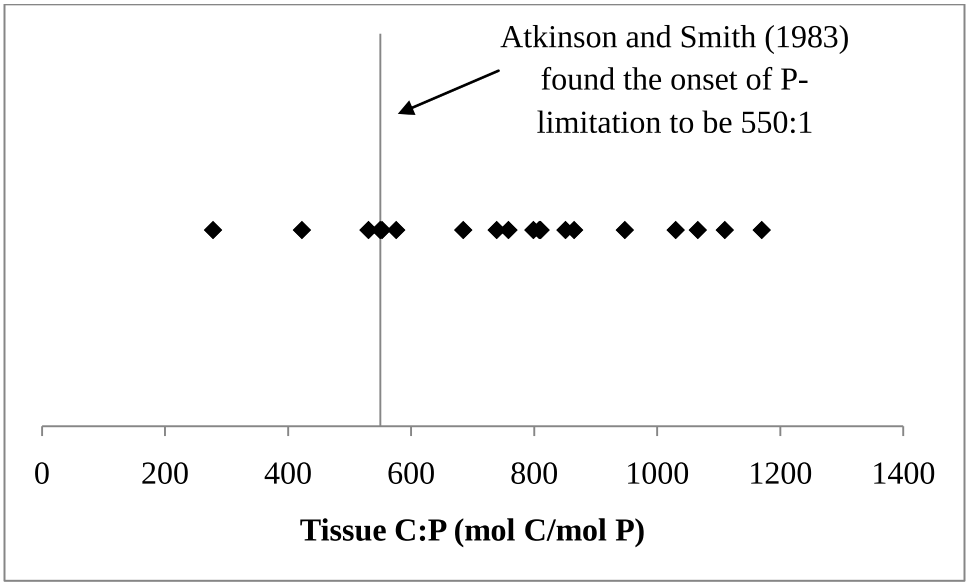

Figure 3. Tissue Carbon:Phosphorus (mol C/mol P) of benthic filamentous algae in the inner bay of Saginaw Bay, Lake Huron compared to published values of phosphorus-limiting tissue concentrations (n = 19).

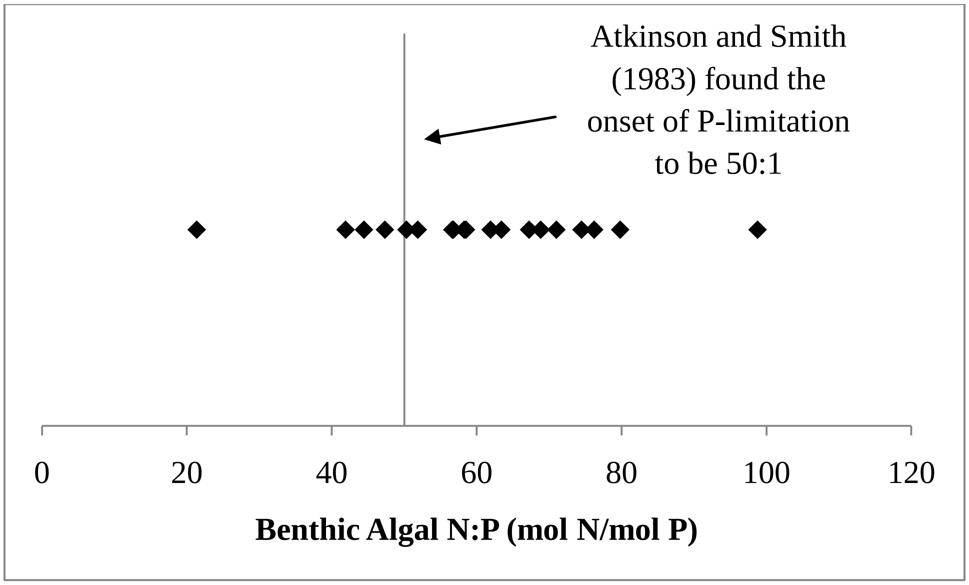

Figure 4. Tissue Nitrogen:Phosphorus (mol N/mol P) of benthic filamentous algae in the inner bay of Saginaw Bay, Lake Huron compared to published values of phosphorus-limiting tissue concentrations (n = 19).

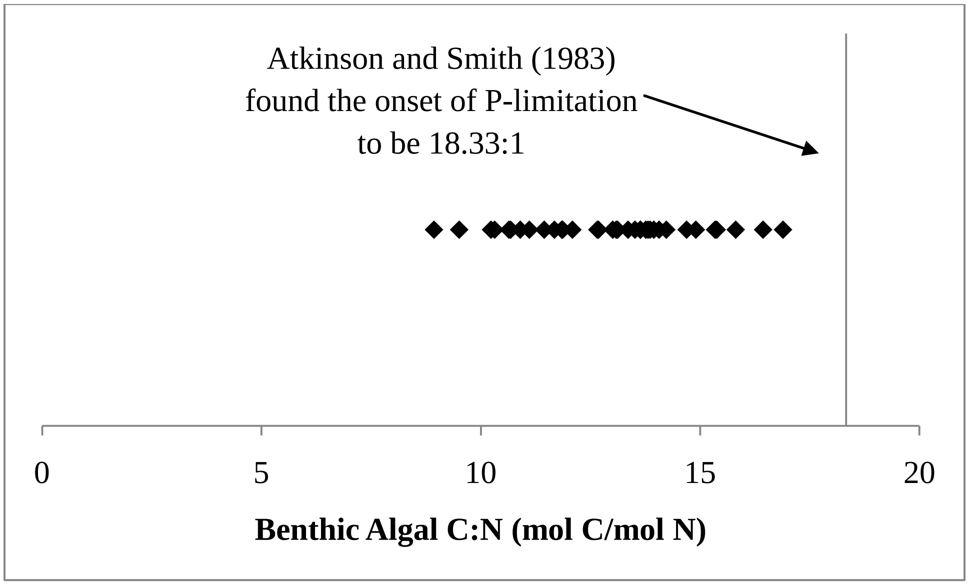

Figure 5. Tissue Carbon:Nitrogen (mol C/mol N) of benthic filamentous algae in the inner bay of Saginaw Bay, Lake Huron compared to published values of nitrogen-limiting tissue concentrations (n = 35).

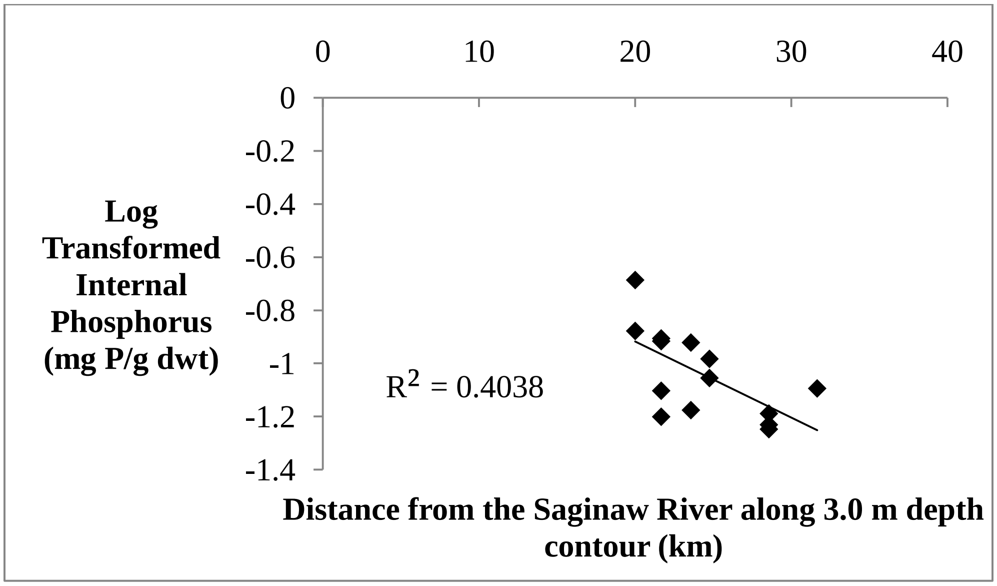

Figure 6. Internal phosphorus (log transformed, mg P/g dwt) of benthic filamentous algae in the inner bay of Saginaw Bay, Lake Huron over distance from the Saginaw River (km) along a 3.0 m depth contour (n=15).

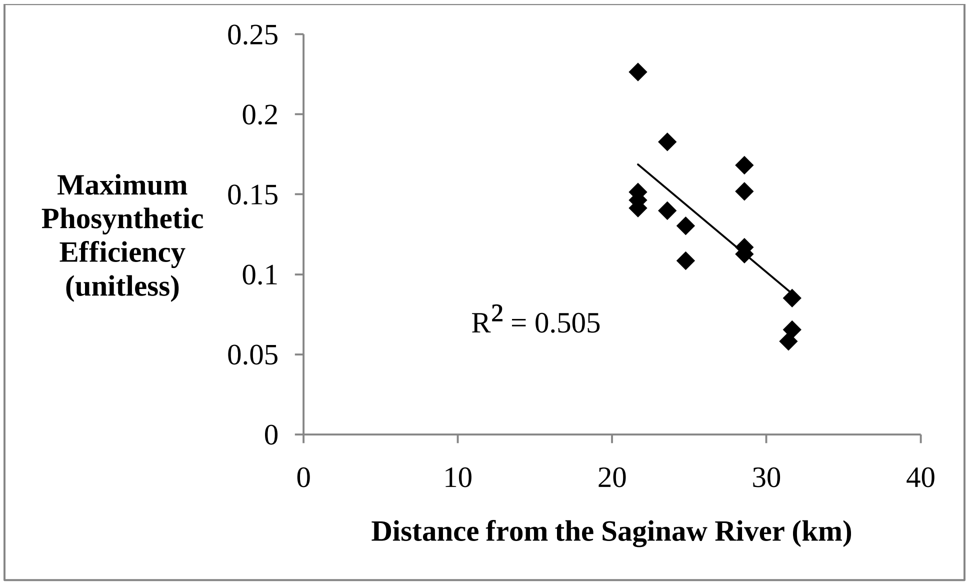

Figure 7. Maximum photosynthetic efficiency (cube transformed; unitless) of benthic filamentous algae in the inner bay of Saginaw Bay, Lake Huron over distance from the Saginaw River (km) along a 3.0 m depth contour (n=19).

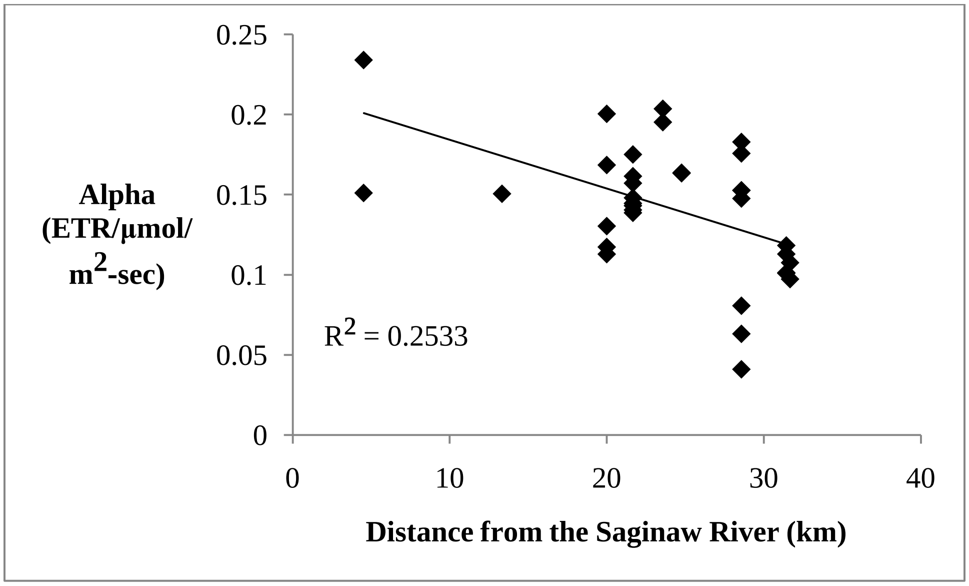

Figure 8. Alpha (ETR/µmol/ m^2-sec) of benthic filamentous algae in the inner bay of Saginaw Bay, Lake Huron over distance from the Saginaw River (km) for the best supported model including distance only (n=34).

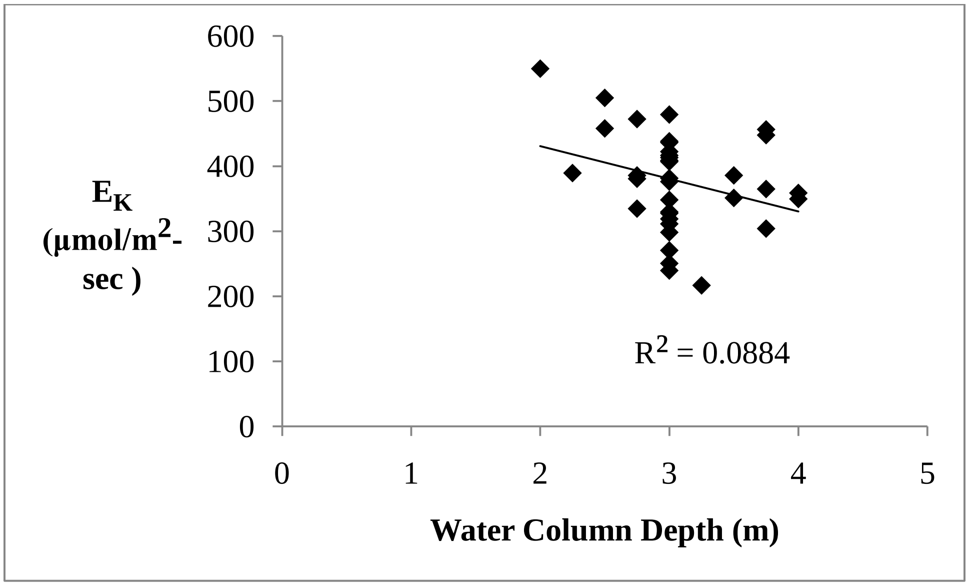

Figure 9. Light saturation index (E_K; µmol/ m^2-sec) of benthic filamentous algae in the inner bay of Saginaw Bay, Lake Huron over depth of the water column (m) for the best supported model including depth of the water column (m), distance from the Saginaw River (km), and the substrate type *Chara* (n=34).

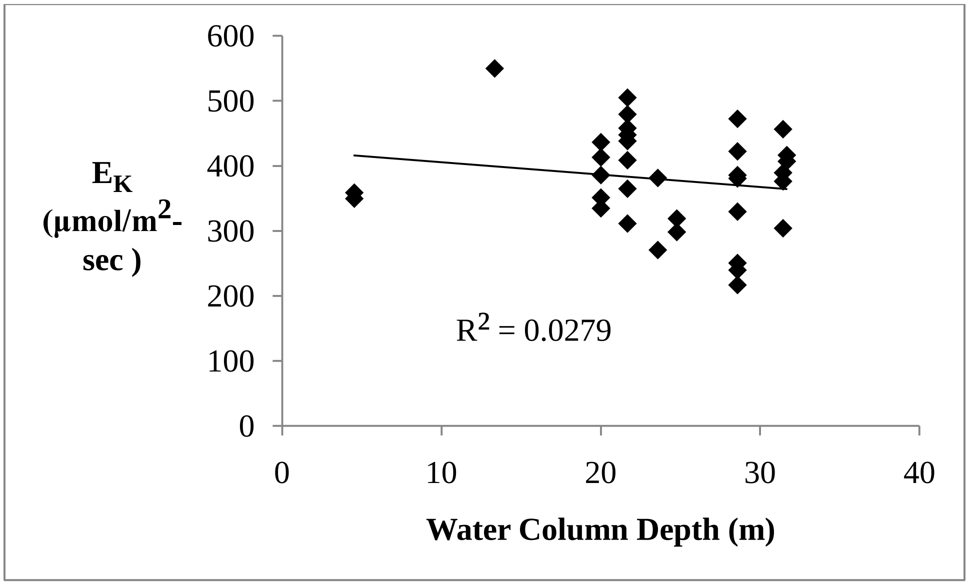

Figure 10. Light saturation index (E_K; µmol/ m^2-sec) of benthic filamentous algae in the inner bay of Saginaw Bay, Lake Huron over distance from the Saginaw River (km) for the best supported model including depth of the water column (m), distance from the Saginaw River (km), and the substrate type *Chara* (n=34).

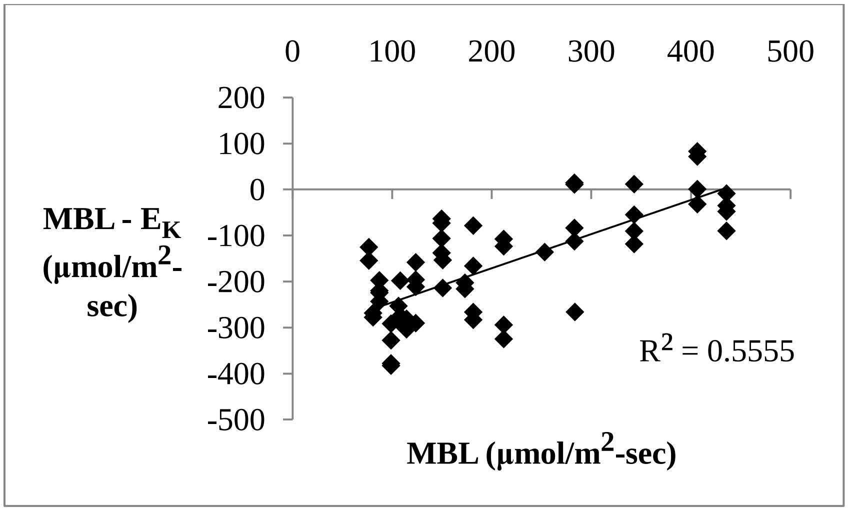

Figure 11. Midday averaged benthic light (MBL; µmol/ m^2-sec) minus the light saturation index (E_K; µmol/ m^2-sec) of benthic filamentous algae in the inner bay of Saginaw Bay, Lake Huron over the midday averaged benthic light (n=59).

TABLE 1. Table of best-supported models for all benthic algal dependent variables

Benthic Algae Parameter	**Models**	**Model p-value**	**Coeff. Var**	**R^2**	**Adj. R^2**	**Distance Parameter Estimate**	**Depth Parameter Estimate**	**Chara Parameter Estimate**	**Mussels Parameter Estimate**
Internal Phosphorus	Distance	0.10	-16.54	0.11	--	-0.015 (p=0.10)	--	--	--
	distance + mussels	0.14	-16.41	0.17	0.09	***-0.015*** ***(p=0.084)***	--	--	-0.086 (p=0.25)
	distance + depth	0.17	-16.59	0.15	0.07	-0.014 (p=0.12)	0.085 (p=0.36)	--	--
	Depth	0.39	-18.94	0.03	--	--	0.08922 (p=0.39)	--	--
	Mussels	0.23	-18.66	0.06	--	--	--	--	-0.099 (p=0.23)
Fv/Fm	depth + chara	***0.026***	49.77	0.20	0.15	--	***0.055*** ***(p=0.02)***	-0.02556 (p=0.2152)	--
	depth	***0.016***	50.22	0.16	--	--	***0.058*** ***(p=0.016)***	--	--
	depth + mussels	***0.020***	49.34	0.22	0.17	--	***0.05206*** ***(p=0.029)***	--	0.03125 (p=0.15)
Alpha	Distance	***0.0024***	25.18	0.25	--	***-0.0030*** ***(p=0.0024)***	--	--	--
	distance + depth	***0.0053***	25.00	0.29	0.24	***-0.0027*** ***(p=0.0078)***	0.017 (p=0.23)	--	--
E_K	distance + depth + chara	***0.0058***	17.29	0.34	0.27	-4.05 (p=0.313)	***-62.91*** ***(p=0.022)***	***65.50*** ***(p=0.0086)***	--

TABLE 2. Table of best-supported models for all benthic algal dependent variables along a 3.0 m depth contour

Benthic Algae Variable	**Model**	**Model p-value**	**Coeff. Var**	**R^2**	**Distance Parameter Estimate**	**Chara Parameter Estimate**	**Mussels Parameter Estimate**	**Misc Parameter Estimate**
IP (3.0 m)	distance	***0.015***	-12.74	0.40	***-0.029 (p=0.015)***	--	--	--
Fv/Fm (3.0 m)	distance	***0.003***	24.29	0.51	***-0.0081 (p=0.003)***	--	--	--
Alpha (3.0 m)	misc	0.297	21.02	0.06	--	--	--	-0.017 (p=0.30)
	mussels	0.316	21.07	0.06	--	--	0.016 (p=0.32)	--
	distance	0.363	22.31	0.06	-0.0019 (p=0.36)	--	--	--
	chara	0.986	21.68	0.00	--	-0.00026 (p=0.99)	--	--
E_K (3.0 m)	misc	0.157	18.97	0.11	--	--	--	-52.3 (p=0.16)
	chara	***0.047***	17.94	0.20	--	***62.2 (p=0.047)***	--	--
	distance	0.366	19.99	0.05	-4.09 (p=0.37)	--	--	--

TABLE 3. Summary table of all water quality variables measured (n=number of water column samples analyzed)

Water Quality Variable	Transformed?	Range (after transformation)	Units	Shapiro-Wilk p-value	Mean	Median	n
Alpha	No	0.1 - 0.23	ETR/μmol/m^2-sec	0.88	0.143	0.148	37
Chlorophyll a	No	4.03 - 12.32	μg chl*a*/L	0.49	7.47	7.91	21
E_K	No	216.6 - 549.57	μmol/m^2-sec	0.9995	377.15	380.83	36
K_{PAR}	Yes - Cubed	0.07 - 0.82	m^{-1}	0.29	0.43	0.47	19
Midday Benthic Light	Yes - Log	1.88 - 2.64	μmol/m^2-sec	0.2183	2.22	2.18	18
Fv/Fm	Yes - Cubed	0.0008 - 0.27	(unitless)	0.53	0.12	0.13	35
SRP	No	0.17 - 1.5	μg P/L	0.14	0.96	0.93	19
Total Phosphorus	No	6.73 - 16.72	μg TP/L	0.45	10.62	11.03	17

TABLE 4. Summary table of all water quality variables of models including water column depth and/or distance from the Saginaw River.

Water Quality Variable	Model	Model p-value	Coeff. Var	R^2	Adj. R^2	Distance Parameter Estimate	Depth Parameter Estimate
Chlorophyll a	depth	0.42	29.59	-0.02	--	--	-0.87 (p=0.42)
	distance	0.68	31.45	-0.05	--	0.033 (p=0.68)	--
	distance + depth	0.72	31.93	-0.08	35.82	0.024 (p=0.78)	-0.81 (p=0.50)
k_{PAR}	depth	0.44	56.17	-0.03	--	--	-0.093 (p=0.44)
	distance	0.72	57.97	-0.06	--	0.0032 (p=0.72)	--
	distance + depth	0.73	58.95	-0.09	-43.70	0.0022 (p=0.81)	-0.089 (p=0.49)
Total Phosphorus	depth	0.71	20.33	-0.06	--	--	0.52 (p=0.71)
	distance	0.19	20.98	0.05	--	-0.11 (p=0.19)	--
	distance + depth	0.42	21.00	-0.01	31.33	-0.12 (p=0.21)	-0.37 (p=0.81)
Soluble Reactive Phosphorus	depth	0.89	32.20	-0.07	--	--	-0.027 (p=0.89)
	distance	0.15	31.92	0.07	--	0.018 (p=0.15)	--
	distance + depth	0.34	32.82	0.02	-36.60	0.020 (p=0.15)	0.093 (p=0.67)

TABLE 5. Table of all possible models in the best-model selection for internal phosphorus and maximum photosynthetic efficiency variables

	Internal P				Maximum Photosynthetic Efficiency			
Models	R^2	Adj. R^2	AIC_C	w_i	R^2	Adj. R^2	AIC_C	w_i
depth + distance + chara + misc	0.2223	0.0667	-77.393	0.008	0.2718	0.1598	-167.995	0.012
depth + distance + chara + mussels	0.2223	0.0667	-77.393	0.008	0.2718	0.1598	-167.995	0.012
depth + distance + misc + mussels	0.2223	0.0667	-77.393	0.008	0.2718	0.1598	-167.995	0.012
depth + distance + chara	0.1591	0.0389	-78.948	0.017	0.2706	0.1896	-171.044	0.055
depth + distance + misc	0.1786	0.0613	-79.538	0.023	0.2167	0.1296	-168.832	0.018
depth + distance + mussels	0.2112	0.0985	-80.547	0.038	0.2438	0.1598	-169.927	0.031
depth + chara + misc	0.1056	-0.0222	-77.408	0.008	0.2624	0.1804	-170.696	0.046
depth + chara + mussels	0.1056	-0.0222	-77.408	0.008	0.2624	0.1804	-170.696	0.046
depth + misc + mussels	0.1056	-0.0222	-77.408	0.008	0.2624	0.1804	-170.696	0.046
distance + chara + misc	0.1716	0.0533	-79.325	0.021	0.1466	0.0518	-166.177	0.005
distance + chara + mussels	0.1716	0.0533	-79.325	0.021	0.1466	0.0518	-166.177	0.005
distance + misc + mussels	0.1716	0.0533	-79.325	0.021	0.1466	0.0518	-166.177	0.005
depth + chara	0.0554	-0.0305	-79.199	0.020	*0.2619*	*0.2092*	-173.538	0.191
depth + mussels	0.0975	0.0155	-80.342	0.035	0.2231	0.1676	-171.947	0.086
depth + misc	0.0691	-0.0156	-79.565	0.024	0.2001	0.143	-171.044	0.055
distance + depth	0.1466	0.069	-81.738	0.070	0.2105	0.1541	-171.451	0.067
distance + chara	0.1245	0.0449	-81.098	0.051	0.1355	0.0738	-168.638	0.016
distance + mussels	0.165	0.0891	-82.283	0.092	0.1293	0.0671	-168.414	0.015
distance + misc	0.1354	0.0568	-81.414	0.059	0.0705	0.0041	-166.390	0.005
chara + mussels	0.0443	-0.0425	-78.909	0.017	0.1038	0.0398	-167.520	0.009
chara + misc	0.0443	-0.0425	-78.909	0.017	0.1038	0.0398	-167.520	0.009
mussels + misc	0.0443	-0.0425	-78.909	0.017	0.1038	0.0398	-167.520	0.009

TABLE 5 (cont’d)

Models	Internal P				Maximum Photosynthetic Efficiency			
	R^2	Adj. R^2	AIC_C	w_i	R^2	Adj. R^2	AIC_C	w_i
depth	0.0442	0.0027	-81.763	0.071	*0.1881*	*0.1601*	-173.232	0.164
distance	0.1126	0.0741	-83.621	0.179	0.0703	0.0382	-169.031	0.020
chara	0.0103	-0.0327	-80.892	0.046	0.0962	0.065	-169.907	0.031
mussels	0.0404	-0.0013	-81.665	0.067	0.0693	0.0372	-169.000	0.020
misc	0.0156	-0.0272	-81.025	0.049	0.0042	-0.0302	-166.903	0.007

TABLE 6. Table of all possible models in the best-model selection for alpha and light saturation coefficient variables

	Alpha				Light Saturation Coefficient			
Models	R^2	Adj. R^2	AIC_C	w_i	R^2	Adj. R^2	AIC_C	w_i
depth + distance + chara + misc	0.2878	0.1896	-217.012	0.010	0.3537	0.2646	292.4782	0.091032
depth + distance + chara + mussels	0.2878	0.1896	-217.012	0.010	0.3537	0.2646	292.4782	0.091032
depth + distance + misc + mussels	0.2878	0.1896	-217.012	0.010	0.3537	0.2646	292.4782	0.091032
depth + distance + chara	0.2875	0.2163	-219.965	0.045	0.3372	0.2709	290.3688	0.261371
depth + distance + misc	0.2871	0.2158	-219.945	0.045	0.2651	0.1916	293.8767	0.04524
depth + distance + mussels	0.2878	0.2166	-219.978	0.046	0.1824	0.1006	297.5038	0.007378
depth + chara + misc	0.1121	0.0234	-212.483	0.001	0.2322	0.1554	295.3693	0.021449
depth + chara + mussels	0.1121	0.0234	-212.483	0.001	0.2322	0.1554	295.3693	0.021449
depth + misc + mussels	0.1121	0.0234	-212.483	0.001	0.2322	0.1554	295.3693	0.021449
distance + chara + misc	0.2572	0.1829	-218.548	0.022	0.2094	0.1304	296.3617	0.013059
distance + chara + mussels	0.2572	0.1829	-218.548	0.022	0.2094	0.1304	296.3617	0.013059
distance + misc + mussels	0.2572	0.1829	-218.548	0.022	0.2094	0.1304	296.3617	0.013059
depth + chara	0.1111	0.0538	-215.206	0.004	0.2244	0.1744	292.9467	0.072021
depth + mussels	0.1021	0.0442	-214.864	0.004	0.1121	0.0548	297.5461	0.007223
depth + misc	0.1074	0.0498	-215.065	0.004	0.1622	0.1081	295.5708	0.019393
distance + depth	0.2871	0.2411	-222.707	0.179	0.1627	0.1087	295.5501	0.019595
distance + chara	0.2539	0.2057	-221.159	0.082	0.2073	0.1562	293.6877	0.049723
distance + mussels	0.257	0.2091	-221.303	0.089	0.071	0.0111	299.0832	0.003349
distance + misc	0.2548	0.2067	-221.2	0.084	0.0887	0.0299	298.4293	0.004644
chara + mussels	0.0157	-0.0478	-211.741	0.001	0.1475	0.0925	296.162	0.01443
chara + misc	0.0157	-0.0478	-211.741	0.001	0.1475	0.0925	296.162	0.01443
mussels + misc	0.0157	-0.0478	-211.741	0.001	0.1475	0.0925	296.162	0.01443

TABLE 6 (cont'd)

Models	Alpha				Light Saturation Coefficient			
	R^2	Adj. R^2	AIC_C	w_i	R^2	Adj. R^2	AIC_C	w_i
depth	0.1011	--	-217.406	0.013	0.0932	0.0648	295.683	0.018335
distance	0.2533	--	-223.712	0.295	0.0279	-0.0024	298.0447	0.005629
chara	0.0149	--	-214.291	0.003	0.1465	0.1198	293.6218	0.051389
mussels	0.0089	--	-214.087	0.002	0.0384	0.0083	297.6777	0.006763
misc	0.0013	--	-213.825	0.002	0.0481	0.0183	297.333	0.008035

TABLE 7. Table of all possible models in the best-model selection for internal phosphorus and maximum photosynthetic efficiency variables along a 3.0 meter depth contour in Saginaw Bay, Lake Huron

	Internal P				Maximum Photosynthetic Efficiency			
Models	R^2	Adj. R^2	AIC_C	w_i	R^2	Adj. R^2	AIC_C	w_i
distance + chara + misc	0.4449	0.2784	-45.035	0.013	0.5137	0.381	-90.862	0.011
distance + chara + mussels	0.4449	0.2784	-45.035	0.013	0.5137	0.381	-90.862	0.011
distance + misc + mussels	0.4449	0.2784	-45.035	0.013	0.5137	0.381	-90.862	0.011
distance + chara	0.4447	0.3438	-49.696	0.136	0.5137	0.4326	-95.529	0.109
distance + mussels	0.4232	0.3183	-49.163	0.104	0.5091	0.4273	-95.388	0.102
distance + misc	0.4126	0.3058	-48.908	0.092	0.5068	0.4246	-95.319	0.098
chara + mussels	0.0608	-0.1099	-42.339	0.003	0.0378	-0.1226	-85.294	0.001
chara + misc	0.0608	-0.1099	-42.339	0.003	0.0378	-0.1226	-85.294	0.001
mussels + misc	0.0608	-0.1099	-42.339	0.003	0.0378	-0.1226	-85.294	0.001
distance	0.4038	0.3542	-52.520	0.559	0.505	0.4669	-99.082	0.645
chara	0.0583	-0.0202	-46.120	0.023	0.0007	-0.0762	-88.544	0.003
mussels	0.0367	-0.0435	-45.802	0.019	0.0261	-0.0488	-88.931	0.004
misc	0.0069	-0.0758	-45.376	0.016	*0.025*	*-0.05*	-88.914	0.004

TABLE 8. Table of all possible models in the best-model selection for alpha and light saturation coefficient variables along a 3.0 meter depth contour in Saginaw Bay, Lake Huron

Models	Alpha				Light Saturation Coefficient			
distance + chara + misc	R^2	Adj. R^2	AIC_C	w_i	R^2	Adj. R^2	AIC_C	w_i
distance + chara + mussels	0.0923	-0.1171	-105.297	0.007	0.1881	0.0007	154.5527	0.010246
distance + misc + mussels	0.0923	-0.1171	-105.297	0.007	0.1881	0.0007	154.5527	0.010246
distance + chara	0.0923	-0.1171	-105.297	0.007	0.1881	0.0007	154.5527	0.010246
distance + mussels	0.0562	-0.0786	-108.755	0.040	0.1849	0.0685	150.4975	0.077825
distance + misc	0.0834	-0.0475	-109.252	0.052	0.0858	-0.0448	152.4486	0.029339
chara + mussels	0.0775	-0.0543	-109.142	0.049	0.1101	-0.017	151.99	0.0369
chara + misc	0.0424	-0.0944	-108.508	0.036	0.1491	0.0275	151.2289	0.053988
mussels + misc	0.0424	-0.0944	-108.508	0.036	0.1491	0.0275	151.2289	0.053988
distance	0.0424	-0.0944	-108.508	0.036	0.1491	0.0275	151.2289	0.053988
chara	0.0555	-0.0075	-112.228	0.229	0.0549	-0.0081	149.5272	0.126425
mussels	0	-0.0666	-111.259	0.141	0.1442	0.0872	147.8391	0.294035
misc	0.028	-0.0368	-111.741	0.179	0.0309	-0.0338	149.9539	0.102135
	0.0296	-0.0351	-111.769	0.182	0.0667	0.0044	149.3141	0.14064

APPENDIX B – GPS COORDINATES OF SAMPLING SITES AND TRANSECTS

Transect	Depth (m)	Latitude	Longitude
T7.75	3.00	43.54.192N	83.51.385W
T8	2.25	43.53.867N	83.52.824W
T8	3.00	43.53.627N	83.52.086W
T8	3.75	43.53.365N	83.51.200W
T9	2.75	43.52.325N	83.53.184W
T9	3.00	43.52.103N	83.52.172W
T9	3.25	43.52.045N	83.51.959W
T10	3.00	43.50.782N	83.51.884W
T10.5	3.00	43.49.643N	83.52.550W
T11	2.50	43.48.634N	83.53.710W
T11	3.00	43.48.628N	83.53.545W
T11	3.75	43.48.633N	83.53.110W
T11.5	3.00	43.49.670N	83.53.177W
T12	2.75	43.47.671N	83.54.190W
T12	3.00	43.47.636N	83.53.842W
T12	3.50	43.47.623N	83.53.800W
T12.5	3.00	43.46.204N	83.54.691W
T13	2.00	43.44.580N	83.55.514W
T15	4.00	43.41.383N	83.51.325W

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