Investigating the influence of land use, water chemistry, invasive species, and spatial patterns on the production of algae along the south-east shoreline of Lake Huron

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ABSTRACT

In Lake Huron, oligotrophication of the offshore waters and periodic algal blooms in the nearshore have raised questions as to the relative importance of recent changes in land use and the introduction of invasive species on water quality and algae production. Our project examines the influence of water chemistry, land use, spatial patterns, and invasive species on nearshore algae production in Lake Huron using extensive surveys collected by the Ontario Ministry of Environment and Climate Change. We found that local lake nutrient levels, shoreline development, watershed land use, and invasive dreissenid mussels explain the most variation in algae production. Our results were consistent with the nearshore shunt hypothesis, stressing the role that dreissenid mussels are playing in the growth of benthic algae in Lake Huron. Our findings highlight the need to incorporate spatial patterns and invasive dreissenid mussels in water quality and benthic algae production modelling.

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GENERAL INTRODUCTION

Eutrophication was recognized as a major problem in the Great Lakes of North America in the 1960s and early 1970s due to increased nutrient inputs (Nicholls et al., 2001). Eutrophication is a major threat to river and lake ecosystems, with increases in the growth of phytoplankton and other algae having negative impacts on water quality and aesthetics, wildlife, and human health (Carpenter et al., 1998; Smith and Schindler, 2009; Howell et al., 2014). Eutrophication of lakes can arise due to increasing accumulation of nutrients, such as phosphorus in the water column (Schindler et al., 1974; Bennett et al., 2001; Carpenter et al., 2008). Following legislation to counteract eutrophication, including the Great Lakes Water Quality Agreement of 1972, there were successful reductions in nutrient loading into the Great Lakes by the 1980s. However, in the last 20 years, a resurgence of benthic algae in the Great Lakes, including Lake Huron, has raised concern in the scientific community as to what drives these changes (Kuczynski et al., 2016).

Similar to the other Great Lakes (i.e. Lakes Erie, Ontario, and Michigan), Lake Huron is also afflicted by nuisance benthic algae along the shoreline (Barton et al., 2013; Howell et al., 2014). Lake Huron is uniquely characterized by both oligotrophic waters offshore, and contrastingly poor nearshore water quality that is highly influenced by fluxes in nutrient inputs (Howell et al., 2014). During a study of phosphorus levels in the Great Lakes, it was observed that seasonal total phosphorus (TP) concentrations were different between sites, but were consistent on a yearly basis (Nicholls et al., 2001). Despite an seeming decreasing trend in long term TP concentrations in Lake Huron, there was no observed trend in TP concentrations over the past 20 years (Nicholls et al., 2001). Prior to the year 2000, beach fouling by algae was not a big concern in Lake Huron (Barton et al., 2013). However, after extensive surveys by Barton et al., (2013), it was found that benthic algae coverage of sites along the shoreline of Lake Huron increased eight-fold from 1977 to 2007 (Barton et al., 2013). The accumulation of benthic algae along the shoreline was not evenly distributed and exhibited high spatial variation, with certain species accumulating in particular areas (Barton et al., 2013). The degradation of water quality in the nearshore of Lake Huron has been attributed to two main ecosystem changes: the invasion of non-native species and land use change.

Invasive species

Invasive species pose a great threat to native ecosystems and biodiversity (Vitousek et al., 1990; Vitousek et al., 1996). Through the direct or indirect control of resources (Jones et al., 1994; Jones et al., 1997), invasive species can act as ecosystem engineers and can impact other organisms by indirectly changing the flow of energy within an ecosystem (Alper, 1998; Jones et al., 1994). Ecosystem engineers can alter habitats in two main ways: 1) they transform ecosystems through their own growth and become an important part of the changed environment; 2) they alter the physical structural environment (Alper, 1998; Jones et al., 1994). Through changes in ecosystem structure and function, invasive ecosystem engineer species can impact other biota. For example, through habitat alterations, the invasive grass *Phragmites* can modify sediments and macrofauna in the invaded habitat (Talley and Levin, 2001), and through changes in food-web structure, smallmouth bass can negatively impact native fish species (Vander Zanden et al., 1999). In addition, the invasive freshwater zebra mussel (*Dreissena polymorpha*) can impact the growth and biomass of submersed macrophytes by altering the light regime in invaded lakes (Skubinna et al., 1995).

Following the invasion of zebra and quagga mussels in the Great Lakes, water clarity has increased due to their filter feeding activity (Fishman et al., 2009). This change has been documented to impact the quantity of solids in the water column (Fishman et al., 2009). A main concern associated with the invasion of filter-feeding mussels, is their ability to filter large amounts of water, impacting water clarity, light regimes, and the distribution of nutrients (Hecky et al., 2004). The invasion of dreissenid mussels, including both zebra and quagga mussels, may have serious impacts on nearshore productivity through the nearshore shunt hypothesis (Hecky et al., 2004). The nearshore shunt hypothesis has been proposed as a mechanism in which dreissenid mussels redirect nutrients from the pelagic zone into the littoral zone, contributing to increased nutrients in the nearshore, and possibly the excessive growth of benthic algae (Hecky et al., 2004). There are growing concerns as to whether these changes in ecosystem state in the Great Lakes have led to the increase in growth of benthic filamentous algae, such as *Cladophora* (Barton et al,. 2013). In addition, dreissenid mussels may be creating more ample habitat, including hard substrate in the form of their shells, for benthic algae to attach and grow upon (Hecky et al., 2004; Arnott and Vanni, 1996).

Round gobies (*Neogobius melanostomus*) have been proposed to have a top-down impact of trophic cascades on benthic algae production (Barton et al., 2013). Round gobies may be contributing to changes in nearshore benthic algal growth by reducing the number of grazing benthic invertebrates (Barton et al., 2013). Stomach content analysis indicated that the round goby diet consists of mussels as well as macroinvertebrates (Barton et al., 2005). Benthic invertebrates are an essential part of lake ecosystems. A loss in species diversity can disturb the lake community, with benthic invertebrates being important in the cycling of nutrients in water bodies, by converting live plant and dead organic matter into food items for larger predators (Covich et al., 1999). McNickle et al., (2006) observed that following the zebra mussel invasion in Lake Huron, the nearshore communities of benthic invertebrates became more homogenous (McNickle et al., 2006). There was also a decreasing trend in macroinvertebrate taxa from 1970-2000, and from 2000-2003 in Lake Huron (Nalepa et al., 2007).

Land use change

The second environmental stressor that is proposed to alter the water quality of the nearshore of Lake Huron is a change in land use. Changes in land use of surrounding watersheds have been associated with alterations in lake water quality, resulting from sewage treatment plant effluents, leaching from septic tank systems, lawn fertilizers, runoff from agricultural lands and other sources of runoff (Reckhow and Simpson, 1980). Nutrients can enter a lake via precipitation, runoff, and groundwater inputs, and the levels of these nutrients that enter the lake are dependent on the geology of the adjacent land, land use, lake morphology, soil type, and anthropogenic disturbance (Dillon et al., 1993). Different types of land use practices lead to different changes in water quality (Arbuckle and Downing, 2001). Land use change in the form of agriculture has been attributed to increases in nutrient loading to lakes, as a consequence of the large accumulation of phosphorus that occurs in agricultural soils (Bennett et al., 2001), facilitating the growth and production of primary producers (Hofmann, 2009). Nutrients such as phosphorus and nitrogen from livestock manure contribute to the problem of eutrophication by increasing algal growth (Hofmann, 2009). In addition, agricultural activities (such as livestock and row crop production) and human development (sewage) were found to be strong predictors of algal community composition in lakes (Hall et al., 1999). Shoreline development can also influence nutrient loading in lakes. The majority of phosphorus entering lakes with moderate to high levels of shoreline development came from sewage disposal systems, and these systems contributed to increased phosphorus levels (Dillon et al., 1994). Sources of phosphorus enter Lake Huron via rivers connected to agricultural lands, waste water treatment plants, and septic systems, greatly contributing to the excessive growth of *Cladophora* (Auer et al., 1982). In addition, approximately 2-37% of nitrogen and 31-84% of phosphorus from annual precipitation that fell on the surrounding watershed of northwestern Lake Huron was carried to the lake (Manny and Owens, 1983), stressing the importance of investigating the impacts of land use change on the productivity in this Great Lake.

Objectives

There are a multitude of factors that influence lake productivity, including land use change (Auer et al., 1982; Arbuckle and Downing, 2001; Auer et al., 2010), local water chemistry (Schindler et al., 1974), and invasive species (Hecky et al., 2004; Malkin et al., 2008). There has been much debate however, on which factors contribute most to the deteriorating water quality along the shoreline of Lake Huron, as well as the spatial scale at which these factors are influencing water quality. The research questions we aim to answer are two-fold: 1) What is the relative influence of land use, local water chemistry, and spatial patterns on primary production along the southeast shoreline of Lake Huron? ; and 2) Are invasive species contributing to enhanced benthic algae production along the south-east shoreline of Lake Huron?

By addressing these questions, we hope to better understand the factors influencing primary production along the shoreline of Lake Huron in order to make informed management decisions.

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Chapter 1

Investigating the drivers of pelagic chlorophyll patterns along the south-east shoreline of Lake Huron using spatially-explicit models

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SUMMARY

In recent years the occurrence of shoreline fouling by algae in the southeast region of Lake Huron has been attributed to changes in surrounding land use and lake water chemistry. This study investigates the amount of variation explained in chlorophyll *a* patterns along the shoreline of Lake Huron by land use, water chemistry, and spatial patterns. We used water chemistry data collected by the Ontario Ministry of the Environment at 46 sites for the Inverhuron region, and 47 sites for the Point Clark region of south-eastern Lake Huron. Land use classification data was collected at the watershed and shoreline level for these regions by ASL Environmental Sciences Inc. We developed linear models and used a variation partitioning framework to quantify the amount of variation in chlorophyll *a* concentrations explained by land use and water chemistry, as well as the different spatial scales that these processes may be influenced by. Our results suggest that total phosphorus is the most important predictor of chlorophyll *a*, explaining between 62-99% of the variation, with both nutrient and chlorophyll concentrations showing spatial structure at the mouths of tributaries and in close proximity to development along the shoreline. Land use explained less than 5% of the total variation in chlorophyll *a*. Spatial patterns explained as much as 29% of the total variation in chlorophyll *a*. Our findings also suggest that nutrients and algae are both spatially and temporally structured along the shoreline, which highlights the need to include temporal and spatial variability in water quality monitoring techniques and decision making. This study demonstrates that nutrients and algae are spatially contingent, which highlights the need to include spatial variability in water quality monitoring techniques and management decision making.

INTRODUCTION

Lake Huron is an oligo-mesotrophic system undergoing a process of oligotrophication (Barbiero et al., 2012) that is sometimes afflicted by nuisance benthic algae washing up along the shoreline (Barton et al., 2013; Howell et al., 2014). Prior to 2000, beach fouling by algae was not prevalent (Barton et al., 2013), but recent surveys have revealed an increase in periphyton and other filamentous species along the shoreline within the last 10 years (mid-May and mid-August) (Barton et al., 2013). The accumulation of periphyton algae is not evenly distributed, with certain species accumulating in particular areas, exhibiting high spatial variation (Barton et al., 2013). For example, benthic algal growth has been observed to be higher near the mouths of some tributaries, where nutrient fluxes were higher (Howell et al., 2014). In particular, the growth of *Cladophora* in the nearshore region has been associated with increased phosphorus loading (Auer et al., 2010). Such external inputs of biologically available phosphorus can induce a strong biological response in the nearshore regions of lakes (Howell et al., 2014), and can impose a spatial structure that can allow for prediction of future lake eutrophication patterns. Additional factors that can impose a similar spatial structure to benthic algal growth include consequent alterations to light regimes and redirection of nutrients to the benthic habitat by dreissenids (Hecky et al., 2004). In this study, we will focus on understanding the influence of land use on algal production along the shoreline of Lake Huron.

Land use change and nutrients

Land use change can influence lake nutrient levels and primary production through two main mechanisms. Land used for agricultural practices can influence the amount of nutrients being loaded into a lake and facilitate the growth and production of primary producers

(Hofmann, 2009), as well as increase the amount of impervious surfaces within the surrounding catchment (Carpenter et al., 1998). Agriculture and urban development increase impervious surface area (Carpenter et al., 1998; Soranno et al., 1996), erosion, disturbance, and fertilizer application (Soranno et al., 1996) in the landscapes surrounding lakes. Dillon and Kirchner (1975) found that the annual average export of total phosphorus from watersheds that included both pasture and forest was significantly greater than the export of total phosphorus from watersheds that were forested. Agriculture and urbanization greatly increase the amount of total phosphorus exported from a watershed (Dillon and Kirchner, 1975). Nutrients such as phosphorus and nitrogen from livestock manure contribute to the problem of eutrophication by increasing algal growth (Hofmann, 2009). Lake Huron shoreline productivity is primarily limited by phosphorus, making it particularly sensitive to changes in phosphorus inputs (Howell et al., 2014). Phosphorus levels can be used to accurately predict algal standing crop production (Schindler, 1978). Nutrients can enter a lake via precipitation, runoff, and groundwater inputs, and the levels of these nutrients that enter the lake are dependent on the geology of the surrounding land, land use, lake morphology, soil type, and human activities (Dillon et al., 1993). In Lake Huron, sources of phosphorus are carried via rivers derived from agricultural lands, waste water treatment plants, and septic systems, and greatly contribute to the excess growth of *Cladophora* (Auer et al., 1982). A large percentage of the accumulation of phosphorus occurs in agricultural soils (Bennett et al., 2001). In addition, approximately 2-37% of nitrogen and 31-84% of phosphorus from annual precipitation that fell on the surrounding watershed of northwestern Lake Huron was carried to the lake (Manny and Owens, 1983), stressing the importance of investigating the impacts of land use change on the productivity in this Great

Lake. In order to control algal blooms of *Cladophora*, phosphorus loading in the nearshore regions associated with anthropogenic activities must be controlled and total phosphorus levels in nearshore water must be monitored (Higgins et al., 2012). Previous work in ecology has demonstrated the importance of incorporating the influence of spatial processes on lake communities. Due to the spatial structure of land use along the shoreline, and in the broader watershed region, we would expect these to impact spatial processes such as the production of algae and the distribution of nutrients within the nearshore region of the lake. It is important to further investigate the influence of spatial patterns on the production of algae.

Impacts of spatial scale

Spatial patterns in limnological data can arise from spatial dependency of environmental data and/or community processes that drive these patterns (Dray et al., 2006; Borcard and Legendre, 2002). Thus, it has become increasingly important for researchers to incorporate spatial scale in their studies of ecological processes (Borcard and Legendre, 2002). Depending on the spatial scale that is being studied, some variables may come out as being more important than others in explaining changes in a response variable. In fact, spatial variables have been found to account for nearly 50% of the variation in community composition (Cottenie 2005), demonstrating the importance of including space in studies of community structure The scale at which a study is conducted also influences the importance of certain variables. For example, large-scale studies have a tendency to focus on broad scale environmental variables and how they impact community structure can often find stronger relationships between these variables than can smaller-scale studies (Jackson et al., 2001). These studies emphasize the importance of incorporating multiple spatial scales in the study of community composition, and allow for researchers and ecosystem managers to identify spatial scales of greatest importance when designing management strategies that address environmental problems like the increasing occurrence of nuisance algae production.

Research Objectives

Here, we explore the diverse and potentially interacting factors that can influence lake primary production using the shoreline of Eastern Lake Huron as a study site. There has been much debate as to which factors are contributing to the deteriorating water quality in this region in addition to questions about what spatial scales are relevant to water quality management. Specifically, we quantify the relative influence of land use and water chemistry on algal production in Lake Huron, and investigate the insights that can be gleaned by determining the role of spatial structure. We predict that local processes will be the most important variables in structuring chlorophyll *a* concentrations because this is a highly heterogeneous environment where nearshore/offshore patterns and tributary inputs may be structuring patterns in nutrients as well as chlorophyll *a* along the shoreline. To test these hypotheses, we examined the spatial and temporal patterns in chlorophyll *a* and phosphorus over the nearshore region, as well as extending offshore in order to understand variations within this dynamic system.

METHODS

Site Descriptions

The Inverhuron and Point Clark study areas are located along the southeast shoreline of Lake Huron (Fig 1). These two regions have 15 separate drainage basins (6 in Inverhuron and 9 in Point Clark) that discharge to the shoreline (Howell et al., 2014).

The shorelines of both the Inverhuron and Point Clark study areas are developed. In the Point Clark study, the shoreline consists of cottages and permanent residences that rely on septic systems. The total surface area drained by the Point Clark study region is approximately 196 km^2. This region also contains the Pine River Watershed, the largest drainage basin, which drains an area of over 160 km^2 of the surrounding land. The total surface area drained by the Inverhuron study region is 114 km^2. The shoreline of Inverhuron is largely characterized by the Bruce Nuclear Generating Station, which comprises approximately 40% of the shoreline of the Inverhuron study region (Howell et al., 2014). To the south of the nuclear generating station is Inverhuron Bay, which contains both parkland and residential properties. North of the generating station is the Baie du Doré, an area that is largely comprised of wetlands. A large area of the Inverhuron region is drained by the Little Sauble River Basin, which extends approximately 43 km^2 inland. The watersheds of Inverhuron and Point Clark are composed primarily of rural lands with limited forest cover. Land cover is predominantly in the form of various croplands, pastures, and cleared lands. (Howell et al., 2014).

Data acquisition

Water chemistry

Both Point Clark and Inverhuron study regions were sampled in 2010 during the spring (May 12 & 13), summer (August 10 & 11) and fall (September 29 & 30) seasons. Water chemistry data were acquired from the Ontario Ministry of the Environment and Climate Change (OMOECC) Monitoring and Reporting Branch. Near shore (≥ 3 m), mid shore (1-3 m) and shoreline (< 2 m) sites were sampled. Nutrient and water chemistry data were collected and include the following variables: alkalinity (mg/L $CaCO_3$), total phosphorus (TP; µg/L), filtered total phosphorus (µg/L), chlorophyll *a* (µg/L), conductivity (µmho/cm^2), chloride (mg/L Cl^-), dissolved inorganic carbon (mg/L C), dissolved organic carbon (mg/L C), magnesium (mg/L), potassium (mg/L), sodium (mg/L), ammonia (µg/L N), nitrate (µg/L N), nitrite (µg/L N), pH, phosphate (µg/L P), suspended solids (mg/L Cl^-), reactive silicate (mg/L Si), sulfate (mg/L), turbidity (FTU), total inorganic nitrogen (µg/L N), total organic nitrogen (µg/L N), total nitrogen (µg/L N), and N:P ratio (Table 1). For more detailed information on how the data were collected, refer to Howell et al., (2014). Chlorophyll *a* concentrations were also used as a proxy for phytoplankton biomass to assess algal production along the shoreline. Chlorophyll levels were chosen as they have been established as an important indicator of phytoplankton biomass in freshwater ecosystems (Carlson, 1977; Smith, 1979). Trace levels of nutrients were recorded during sampling, with values taken near or below the detection limits, which may affect reliability of water chemistry data.

Weather conditions

Precipitation and wind data were collected by Environment Canada (http://climate.weather.gc.ca) at the Goderich, ON weather station on Lake Huron, located just south of the study regions (approximately 40 km south of the Point Clark study region, and approximately 60 km south of the Inverhuron study region). Data were collected for 3-day and 10-day intervals prior to the sampling date in order to test for the influence of seasonal weather patterns on algae production and temporal patterns.

Land use

Land use classification data were obtained from ASL Environmental Sciences Inc., by OMOECC (copyrighted, ASL Environmental Sciences Inc., 2013). Land use classification was surveyed over the two main study regions, Inverhuron and Point Clark. The surveys collected data on land use variables from the surrounding watersheds (WS) and shoreline units (SU). Shoreline units were characterized as 1-km wide polygons delineating the near-shore area of the study area. Inverhuron consists of six watersheds, three remnant watersheds and 18 shore units, with a total area of 113.88 km^2. Point Clark consists of nine watersheds, five remnant watersheds, and 14 shoreline units, with a total area of 19,625 ha (196.25 km^2). Land use classification information was collected for variables such as proportion of area not in natural state, area of row crop (ha), area of treeless land not in row crop (ha), area of tree covered land (ha), number of commercial structures, number of residential dwellings, cumulative length of surface water courses (m), cumulative length of roads (m), and cumulative area of roads (ha). Land use data was joined to the water chemistry data using the join and proximity analysis in Arc GIS 10.1 (ESRI, 2011).

Spatial Variation

Moran Eigenvector Maps (MEMs) are tools for incorporating spatial scale in ecological data, and were used to quantify how distances between sampling sites influence patterns in algal biomass along the shoreline of Lake Huron after accounting for water chemistry and land use variables. They are used to detect and quantify symmetric spatial patterns, which do not imply directionality in data over a wide range of scales (Borcard and Legendre, 2002). MEM variables were constructed by creating a distance matrix from the Euclidean distances between sampling sites, measured as the straight-line distance between sampling points in Euclidean space (Fig. S1). A threshold was then defined for the matrix, and any values under this threshold were assigned a value of four times the threshold, producing a neighbour matrix. A principal coordinates analysis was then conducted on the neighbour matrix (Borcard and Legendre, 2002; Sharma et al., 2011). Two-thirds of the resulting eigenvalues will be positive. These values are the MEM variables and represent the spatial structure in the dataset (Sharma et al., 2011). The first MEM variables represent broad spatial structures, with the succeeding MEMs representing finer spatial structures. The last MEM variables represent the fine-scale spatial patterns (Borcard and Legendre, 2002; Borcard et al., 2004). Linear patterns in the chlorophyll *a* data were evaluated, and chlorophyll *a* was not detrended in order to keep broad spatial patterns that were significant. Linear trends may be indicative of spatial patterns acting at a broader scale than the sampling scope. If there is a linear trend present it may mask other spatial patterns in the data set that could be better modelled by the MEM variables. A distance variable was also calculated as the distance from each site to the shoreline (measured in decimal degrees) and was used as a spatial variable in the regression models to further account for spatial variation.

Data analyses

Linear models were developed in conjunction with variation partitioning to quantify the variation in chlorophyll *a* explained by land use, water chemistry, and spatial variables (MEMs). To develop the linear models, a forward selection procedure with a dual-criterion ($\alpha = 0.05$ & adjusted R^2) was used to identify significant predictor variables (Blanchet et al., 2008). An adjusted coefficient of determination (R^2_{adj}) was calculated to evaluate model fit. This provides an unbiased measure of the variation of the response variable explained by the predictor variables (Peres-Neto et al., 2006). Models were created for Inverhuron and Point Clark within each of the three seasons (May, August, and September 2010). Because of the high correlation between TP and dissolved phosphorus ($r = 0.3$-0.9), separate chlorophyll models were developed to test model strength, and it was determined that TP models explained more variation in chlorophyll *a*. Models were then subsequently generated to understand the amount of variation in total phosphorus patterns (the most important predictor of chlorophyll *a*) explained by land use, water chemistry, and spatial patterns to better understand the key drivers of both increased nutrient levels and algal production.

Prior to analyses, environmental and land use variables were log transformed as necessary to meet normality assumptions. Multicollinearity was found to be low among environmental and land use predictor variables. ‘Depth of sample’ and ‘depth of site’ were tested as model covariates, but were not found to be statistically significant predictors ($p>0.05$). Therefore, a composite dataset was used in the analyses and for constructing models. All analyses were performed in the R-language environment (R Development Core Team, 2015). Mapping was performed using ArcGIS 10.1 (ESRI, 2011).

RESULTS

Patterns in chlorophyll a

Chlorophyll *a* varied spatially as well as seasonally at the two study regions, Inverhuron and Point Clark (Fig. 2), with Inverhuron sites containing lower chlorophyll than the Point Clark sites, as well as higher chlorophyll in the summer and fall seasons. In the Inverhuron study region, chlorophyll *a* concentrations ranged between 0.2-3.1 µg/L ($\bar{x}$= 0.52 µg/L) in May, 0.3-4.4 µg/L ($\bar{x}$= 1.4 µg/L) in August and 0.4-3.6 µg/L ($\bar{x}$= 1.02 µg/L) in September (Fig. S2 a,b,c, respectively). At the Point Clark study region, chlorophyll *a* concentrations ranged between 0.2-20.8 µg/L ($\bar{x}$= 2.4 µg/L) in May, 0.3-50 µg/L ($\bar{x}$= 7.02 µg/L) in August, and 0.4-44.7 µg/L ($\bar{x}$= 6.2 µg/L) in September (Fig. S3 a,b,c, respectively). Chlorophyll *a* concentrations were greater closer to the shore for both study regions and over the three sampling periods (Fig. S2, S3).

Relative influence of water chemistry, land use and spatial variables

Inverhuron

At Inverhuron, over the three sampling seasons, local water chemistry explained the most variation in chlorophyll *a* (between 50-68%), and spatial scale explained the second most amount of variation (between 10-20%) (Fig. 3a).

Seasonal chlorophyll models differed in the amount of variation explained by water chemistry, land use and spatial scale. A total of 70% of the variation in chlorophyll *a* was explained by water chemistry (TP) and spatial variables at the Inverhuron study sites in May, with 50% of the total variation being explained by TP uniquely. Approximately 20% of the total variation was explained by spatial variables (Fig. 4a). Spatial variables included MEM1 (Table

2), which represents broad spatial patterns (Fig. 6). Patterns in total phosphorus appear to be associated with calcium and distance from sample site to the shoreline (Fig. 4a; Table 3).

A total of 94% of variation in chlorophyll *a* was explained by water chemistry, land use and spatial variables at the Inverhuron study sites in August (Fig. 3a; Table 2). Water chemistry variables, which include both TP (67% of variation) and pH (4% of the variation) explained the majority of variation in chlorophyll *a* levels, with spatial patterns and land use explaining 19% and 2% of the variation, respectively (Fig. 4b). Water chemistry and spatial variables explained approximately 2% with shared variation. Water chemistry, land use and spatial variables explained approximately 3% with shared variation (Fig. 4b). Broad spatial patterns were the most important spatial structures in predicting chlorophyll *a* in August, followed by intermediate and fine spatial structures (Fig. 6). Total phosphorus in Inverhuron was related to calcium, broad, intermediate, and fine scale spatial patterns and the proximity to the shoreline (Fig. 4b, Table 3).

In September, a total of 72% of the variation in chlorophyll *a* was explained by water chemistry (TP) and spatial variables at the Inverhuron study sites (Fig 3a). Total phosphorus explained 62% of the variation, uniquely (Fig. 4c). Broad and fine scale spatial patterns (Fig. 6) explained 10% of the total variation, uniquely. Water chemistry was the most important driver of patterns in total phosphorus, followed by spatial patterns and the length of surface water courses in the watershed (Fig. 4c, Table 3).

Point Clark

As was the case for Inverhuron, local water chemistry was the most important driver of chlorophyll *a* levels over the three sampling seasons in Point Clark. Specifically, May models explained 91% of the variation in chlorophyll *a* (Fig. 3b), 89% of which was explained by water chemistry (TP: 84%; Calcium: 4%). An additional 2% of the variation in chlorophyll *a* was explained by intermediate and broad spatial patterns Fig. 5a; Table 2). Patterns in total phosphorus at Point Clark appear to be driven by spatial patterns (Table 3.). Spatial structures include distance from shoreline, broad and intermediate spatial patterns (Fig. 6).

At the Point Clark study sites in August, a total of 90% of the variation in chlorophyll *a* is explained by total phosphorus concentrations uniquely (Fig. 3b; Fig. 5b). Total phosphorus appeared to be influenced by calcium, disturbance, and the distance from shoreline (Fig. 5b; Table 3), with a large amount of shared variation being explained by both calcium and spatial variables.

In September, a total of 84% of the variation in chlorophyll *a* was explained by water chemistry and spatial variables at the Point Clark study sites (Fig. 3b). Total phosphorus explained 52% of the total variation, uniquely. Broad scale spatial patterns explained 4% of the total variation, uniquely (Fig 6). Variation shared between total phosphorus and broad spatial patterns explained 28% of the total variation (Fig. 5c). Total phosphorus appeared to be influenced by spatial variables, including the distance from the shoreline and intermediate spatial structures (Fig. 5c; Table 3).

Weather patterns

Total precipitation was higher in the months of May and September compared to August for the Inverhuron study region (Fig. S4a). At the Point Clark study region, total precipitation was higher in the month of September compared to May and August, although statistical tests did not find a significant difference in total precipitation over the three sampling seasons (Fig. S4b). Wind speed was higher in May and September compared to August in the Inverhuron and Point Clark study region over the three days prior to sampling (ANOVA; $p<0.05$) (Fig. S5a and S5b, respectively).

DISCUSSION

While spatial scale and land use were important in structuring patterns in chlorophyll *a* along the shoreline of Lake Huron, local water chemistry, specifically total phosphorus concentrations, was distinctively the most important driver in structuring patterns in chlorophyll *a*. Chlorophyll *a* is a spatially contingent variable that showed distinctive nearshore/offshore patterns as well as indirect tracers of catchment land use. Spatial patterns structuring chlorophyll *a* along the shoreline were more apparent and prominent in the spring and fall seasons of sampling, contingent upon regional weather conditions, as evidenced by higher precipitation events.

Chlorophyll a at Point Clark and Inverhuron

The Point Clark study region had consistently higher concentrations of chlorophyll *a* along the shoreline (May-Sept) compared to the Inverhuron study region. This pattern has been previously documented in Howell et al., (2014), with higher chlorophyll levels observed in Point Clark. The shoreline of both study regions is developed with both seasonal and permanent houses, which rely on septic systems for waste disposal (Howell et al., 2014), but the Point Clark study region has approximately double the year round population within the drainage basin relative to Inverhuron (Howell et al., 2014). Point Clark also has a larger drainage basin area, in which most of the land use practices are agricultural. This may also contribute to increased loading of nutrients to the nearshore region of Point Clark, with Point Clark mean summer TP concentrations found to be over six times the mean summer TP concentrations at Inverhuron (Howell et al., 2014; Sorrano et al., 1996; Sorrano et al., 2015).

Local water chemistry and nutrients

Local water chemistry was the predominant driver of chlorophyll *a* concentrations at sampling sites along the shoreline of the Inverhuron and Point Clark sampling regions. Important water chemistry parameters included total phosphorus, calcium, and pH. Of the three, total phosphorus was the most important predictor of chlorophyll *a* levels, and therefore, algal biomass along the shoreline of Inverhuron and Point Clark. This coincides with previous knowledge that algal growth in Lake Huron is limited by phosphorus (Howell et al., 2014). Calcium concentrations slightly contributed to the amount of variation explained in the chlorophyll models. Calcium concentrations in the lake may be indicative of dilution from the surrounding watershed. The importance of calcium in predicting both chlorophyll *a* and total phosphorus levels along the shoreline may be indicative of land use practices and groundwater seepage.

Spatial contingency of chlorophyll a

Our results indicated three types of spatial structures (broad, intermediate, and fine) that were important in explaining patterns in chlorophyll *a* within the Point Clark and Inverhuron study regions.

The broadest spatial structure that was important in structuring both algal biomass and total phosphorus concentrations along the shoreline appeared to be a nearshore/offshore spatial pattern. The distance from shore influenced chlorophyll concentrations, with the nearshore regions containing higher levels of chlorophyll *a* compared to the offshore regions. This coincides with previous research on nutrient and algal conditions in Lake Huron; offshore open-water nutrient and algal conditions suggest oligotrophy (Barbiero et al., 2012), however, the nearshore region is characterized by spatially variable levels of phosphorus and chlorophyll *a* along the shoreline (Howell et al., 2014).

Physical characteristics of the Great Lakes may also influence broad scale spatial structures in chlorophyll *a*. Thermal bars create thermal habitats within the nearshore region of lakes that could account for differences in nearshore versus pelagic water quality conditions (Stroemer, 1978). The nearshore region of a lake receives warmer, nutrient-rich water from tributaries and is separated from the cold pelagic water of the offshore region. This creates suitable habitat for the proliferation of algae (Stroemer, 1978). Mixing along the shoreline due to nearshore currents are also expected to influence water quality variability in Lake Huron (Yurista et al., 2012). Longshore circulation is a physical process by which currents within the nearshore region move nutrients and particulates parallel to the shoreline and cause a homogenizing effect on nutrient inputs (Yurista et al., 2012). Although the effects of mixing may make the direct connection between the land and the lake unclear, the nearshore region of the lake associated with a specific land use characteristic will tend to display a stronger land use signature than sites offshore, as mixing, dilution, and transport occur (Yurista et al., 2012).

Intermediate spatial scale patterns indicate that chlorophyll *a* may be structured around the mouths of tributaries, with higher concentrations of nutrients and chlorophyll in close proximity to the mouths of tributaries. There is a strong linkage between lakes and their watersheds through the transport of materials carried by surface runoff (Müller et al., 1998). Many studies have demonstrated that land use can influence nutrient availability and therefore nutrient loading to lakes at the watershed scale (Sorrano et al., 1996; Sorrano et al., 2015).

Loading from nonpoint sources represents a major external source of nutrients that assist in supporting high levels of primary productivity in culturally eutrophic lakes (Sorrano et al., 1996). Variability in the range of total phosphorus exported may be a reflection of the intensity of land use (Dillon and Kirchner, 1975). Therefore, our results may demonstrate patterns in chlorophyll *a* that are indirectly related to land use through connections with the proximity to major tributaries.

Pollutants can also enter lakes through groundwater seepage and can come from different sources, including nutrients and bacteria from septic systems or sewage lines (Crowe and Meek, 2009). Pollutants that enter a lake through groundwater seepage generally stay within the nearshore of the lake, and do not travel out from the shoreline (Crowe and Meek, 2009).

Intermediate spatial patterns that were important in structuring chlorophyll *a* indicate both direct and indirect impacts of land use. Land use was also related to changes in water quality through shoreline development. Shoreline development has been found to impact nutrient levels in lakes through leaching from sewage disposal systems (Dillon et al., 1994). The shoreline of Point Clark and Inverhuron has become highly developed with seasonal and year-round residential properties that rely on septic systems, which may be contributing to increased nutrient inputs in the nearshore region (Howell et al., 2014).

The drivers of fine scale spatial processes that were important in structuring chlorophyll *a* were difficult to determine. These may be indicative of the effects of variables that were not captured in our data (such as local water chemistry data that was not measured) or internal lake processes that were not quantified. The presence of invasive species in the nearshore could be contributing to increased suitable habitat for the proliferation of benthic algae. The invasion of both dreissenid mussels and round gobies can have serious impacts on nearshore productivity through two main mechanisms: the nearshore shunt hypothesis (Hecky et al., 2004) and trophic cascades (Barton et al., 2013). Future studies should consider investigating the impacts of dreissenid mussels on primary production patterns in the nearshore of Lake Huron.

Temporal patterns in Chlorophyll a

The influence of spatial structures on patterns in chlorophyll *a* is more evident in the spring and fall seasons, when precipitation and wind are higher. Sorrano et al., (1996) found that the watershed land use that contributes most of the loading to freshwater systems is highly dependent on precipitation (Sorrano et al., 1996). Large amounts of phosphorus can be transported to aquatic systems following precipitation events, as well as following the conversion of agricultural land to residential development (Bennett et al., 2001). In Lake Ontario, weather events have been found to increase tributary discharge into the lake which may result in increased input of nutrients from the surrounding land (Howell et al., 2012). Higher levels of chlorophyll *a* were also observed in the summer and fall seasons for the two study regions, which may be indicative of the influence of temperature on productivity. Increasing surface water temperatures may result in earlier spring growth of benthic algae such as *Cladophora* (Malkin et al., 2008). The influence of seasonal variability in both nutrient transport ability and temperature may be contributing to temporal signatures in the production of chlorophyll *a* along the shoreline of Lake Huron.

Implications

Freshwater systems are directly threatened by anthropogenic-associated stressors through nutrient loading, with coastal regions being especially vulnerable due to their proximity to land use practices for recreational, agricultural, and industrial purposes (Niemi et al., 2007). For this reason, it has become increasingly important for Great Lakes research to include coastal regions and watershed influences in order to assist in management of eutrophication (Niemi et al., 2007). The coastal region of the Great Lakes presents a dynamic system at the boundary of land and lake, where these two systems interact and influence one another (Niemi et al., 2007). Despite recorded decreases in open-water lake nutrient levels and oligotrophication (Barbiero et al., 2012), shoreline surveys suggest nutrient enrichment from the surrounding land and possibly increased sensitivity to enrichment due to the invasion of zebra mussels (Hecky et al., 2004). Management strategies for lake ecosystems impacted by land use development should include the development of houses set-back from the shoreline and to minimize the amount of shoreline development while also increasing the riparian buffer zones of lakes (Garrison and Wakeman, 2000), as well as monitoring surveys that are specific to shoreline/nearshore nutrient levels, especially near tributary out-falls.

Conclusions

Local nutrient levels in the nearshore region of Lake Huron are important in structuring algal biomass, but the level of nutrients and chlorophyll *a* show considerable spatial and temporal variability. This study highlights the need for water resource assessment strategies that are sensitive at both the temporal and spatial scales of these problems. This study also highlights the complexity of the nutrient and water quality dynamics, with possible interacting drivers influencing nutrient levels and water quality along the shoreline of Lake Huron.

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TABLES

Table 1: Monthly mean (with standard deviation in parentheses) of water chemistry variables measured at sites in the Inverhuron and Point Clark study regions in 2010, Lake Huron, Ontario. TP= total phosphorus, DP= dissolved phosphorus, DIC=dissolved inorganic carbon, DOC= dissolved organic carbon, TIN= total inorganic nitrogen, TON= total organic nitrogen, TN= total nitrogen, and n= number of samples.

	Inverhuron			Point Clark		
	May 13 (n=43)	Aug 11 (n=46)	Sept 30 (n=49)	May 12 (n=41)	Aug 10 (n=47)	Sept 29 (n=44)
Chlorophyll *a* (µg/L)	0.5 (0.5)	1.4 (1.2)	1.02 (0.7)	2.3 (3.8)	7.0 (9.4)	6.2 (7.2)
TP (µg/L)	3.1 (2.2)	6.0 (8.5)	11.6 (27.6)	16.8 (29.6)	36.9 (59.8)	34.2 (43)
DP (µg/L)	1.2 (0.9)	2.7 (4.8)	4.9 (14.6)	2.7 (2.9)	4.0 (5.1)	7 (10.4)
Alkalinity (mg/L $CaCO_3$)	86.6 (21.4)	87.5 (27.0)	90.3 (34.2)	99.9 (44.9)	114.0 (57.5)	118.3 (60.7)
Calcium (mg/L)	27.6 (5.7)	27.3 (7.3)	29.4 (10.5)	33.9 (16)	38.8 (20.4)	38.1 (21.5)
Chloride (mg/L)	7.6 (2.3)	8.4 (5.2)	7.8 (3.6)	9.3 (7.2)	9.8 (5.5)	10.3 (5.5)
Conductivity (umho/cm^2)	222.1 (47.3)	230.6 (63.5)	232.6 (69.4)	255.9 (110.2)	294.2 (146.5)	294.8 (155.4)
DIC (mg/L)	19.7 (4.6)	21.1 (6.5)	21.8 (7.9)	23.1 (10.5)	27.5 (14.5)	28.5 (14.3)
DOC (mg/L)	1.7 (0.4)	1.8 (0.9)	1.8 (1.1)	2.2 (1.3)	2.3 (1.7)	2.2 (1.4)
Hardness (mg/L $CaCO_3$)	102.6 (22.6)	103.6 (30.9)	109 (38.8)	123.5 (54.5)	142.3 (71.5)	140.2 (78.9)
Potassium (mg/L)	1 (0.1)	1.1 (0.7)	1.2 (0.7)	1.2 (0.4)	1.3 (0.7)	1.5 (0.8)
Magnesium (mg/L)	8.2 (2.1)	8.7 (3.1)	8.7 (3.1)	9.4 (3.7)	11.0 (5.5)	11 (6.5)
Sodium (mg/L)	4.8 (1.1)	5.0 (2.6)	4.8 (1.6)	5.8 (4.8)	6.4 (4.6)	6.1 (4.3)
Ammonia (µg/L)	20 (15.6)	27.4 (9.2)	21.4 (6.1)	22.6 (25.4)	14.8 (11.4)	7.9 (9.3)
Nitrite (µg/L)	3.7 (2)	4.0 (1.4)	4.1 (3.5)	4 (1.6)	6.9 (3.7)	7.2 (5.5)
Nitrate + Nitrite (µg/L)	484 (256)	288.1 (138.2)	346.9 (304.1)	491.7 (313.3)	556.8 (755.2)	1106 (1716.1)
Kjeldahl N (µg/L)	140.7 (51.5)	256.3 (117.9)	224.1 (158.9)	261.9 (223.6)	397.4 (431.3)	565 (562.3)
pH	8.3 (0.05)	8.5 (0.12)	8.3 (0.06)	8.3 (0.07)	8.4 (0.11)	8.3 (0.08)
Phosphate P (µg/L)	0.7 (0.3)	2.4 (2.0)	4 (13.9)	1.3 (0.9)	4.9 (4.2)	8.2 (8.2)
Suspended solids (mg/L)	1 (0.9)	2.1 (2.5)	2.9 (5)	10.3 (18)	24.6 (44.3)	33.3 (45.4)
Silicate (mg/L)	0.7 (0.2)	0.8 (0.3)	0.9 (0.6)	0.5 (0.4)	1.3 (0.9)	1 (1.03)
Sulfate (mg/L)	16.5 (1.4)	15.8 (1.1)	15.8 (1.2)	19.4 (9.2)	23.4 (32.9)	18.7 (33.1)
Turbidity (FTU)	0.5 (0.5)	1.1 (1.8)	2.3 (6.2)	5.1 (8.4)	15.3 (22.6)	18.3 (22.2)
TIN (µg/L)	504.1 (254.4)	315.5 (140.6)	368.4 (307.8)	514.3 (313.2)	571.6 (754.4)	1113.8 (1720.6)
TON (µg/L)	120.7 (52.4)	228.9 (113.2)	202.6 (154.6)	239.4 (224.5)	382.6 (431.2)	557.1 (560.2)
TN (µg/L)	624.7 (290.4)	544.4 (221.6)	571 (452.9)	753.7 (460.8)	954.2 (924.6)	1671 (1958.6

Table 2: Summary of regression models predicting chlorophyll *a* concentrations (in µg/L) at both the Inverhuron and Point Clark study regions during the months of May, August and September, 2010. Multiple regression models include predictor variables for chlorophyll *a* and were selected using a forward selection procedure. Predictors selected include total phosphorus (TP), water chemistry, land use, and spatial variables. The adjusted coefficient of determination (R^2_{adj}) was used to evaluate model performance, and the *p*-value was used to evaluate significance of models.

			Multiple regression		
Study Region	Month	Response variable (µg/L)	Predictor variables	R^2_{adj}	*p*
Inverhuron	May	Chlorophyll *a*	TP – MEM1	0.70	1.33e-11
Inverhuron	August	Chlorophyll *a*	TP + pH – unpaved roads +MEM1+MEM11–MEM13 – MEM20	0.94	< 2.2e-16
Inverhuron	September	Chlorophyll *a*	TP – MEM1 + MEM3 + MEM12	0.72	1.41e-12
Point Clark	May	Chlorophyll *a*	TP + calcium + MEM1 – MEM6	0.91	< 2.2e-16
Point Clark	August	Chlorophyll *a*	TP	0.90	< 2.2e-16
Point Clark	September	Chlorophyll *a*	TP + MEM2	0.84	< 2.2e-16

Table 3: Summary of regression models predicting total phosphorus concentrations (in µg/L) at both the Inverhuron and Point Clark study regions during the months of May, August and September, 2010. Multiple regression models include predictor variables for total phosphorus and were selected using a forward selection procedure. Predictors selected include calcium, water chemistry, land use, and spatial variables. The adjusted coefficient of determination (R^2_{adj}) was used to evaluate model performance, and the *p*-value was used to evaluate significance of models.

			Multiple regression		
Study Region	Month	Response variable (µg/L)	Predictor variables	R^2_{adj}	*p*
Inverhuron	May	Total phosphorus	Calcium – distance	0.48	8.8e-07
Inverhuron	August	Total phosphorus	-Distance + Calcium – MEM16 + MEM11 –MEM5 – MEM3 –MEM19 + MEM21	0.88	< 2.2e-16
Inverhuron	September	Total phosphorus	Calcium –distance + surface water courses + MEM9	0.79	2.17e-15
Point Clark	May	Total phosphorus	-Distance – MEM2 + MEM6 – MEM7	0.83	4.94e-14
Point Clark	August	Total phosphorus	Calcium - distance	0.87	< 2.2e-16
Point Clark	September	Total phosphorus	-Distance + MEM8	0.91	< 2.2e-16

FIGURES

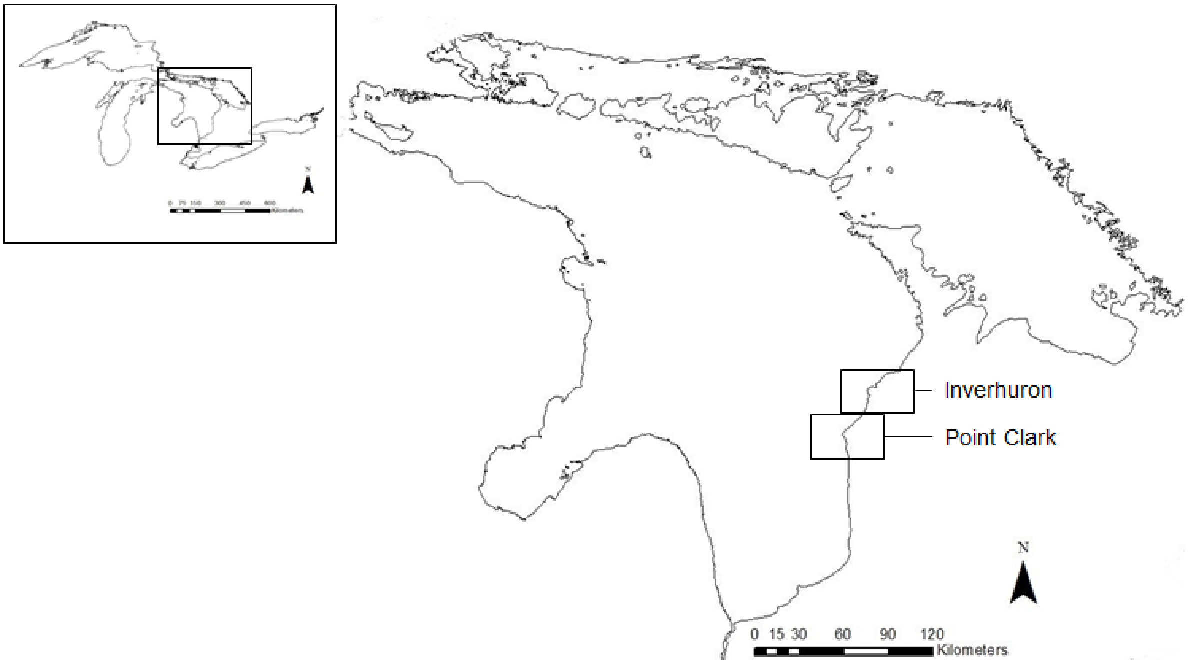


Figure 1: Map of the locations of the two study regions, Inverhuron and Point Clark in Lake Huron, Ontario.

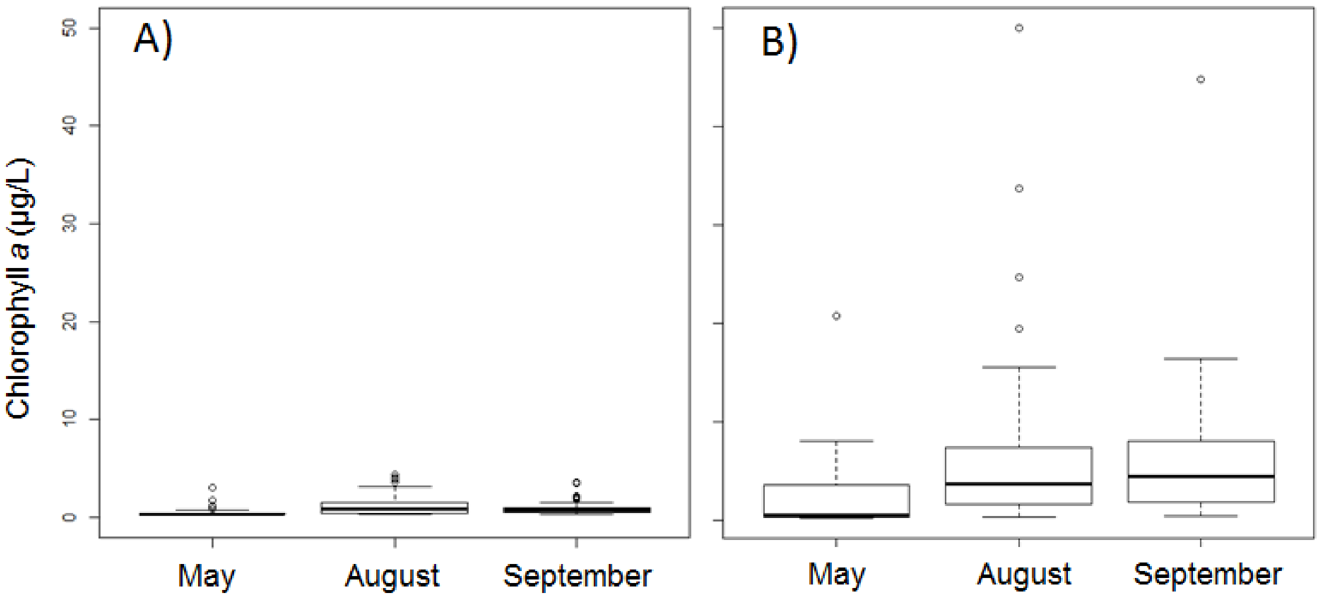


Figure 2: Ranges in Chlorophyll *a* levels at the Inverhuron (A) and Point Clark (B) study sites over the sampling months of May, August and September, 2010.

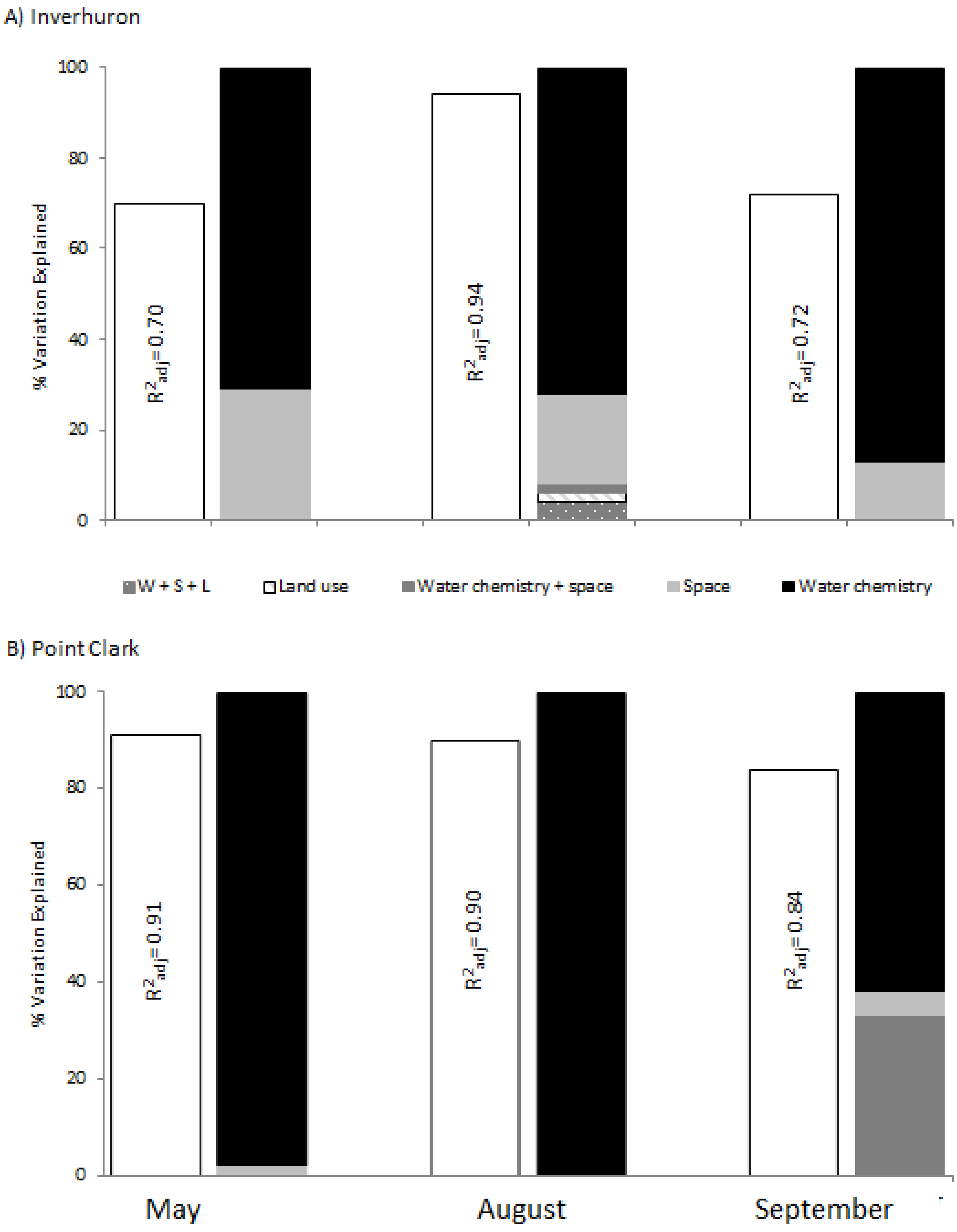


Figure 3: Percent total variation explained (open bars) and contributors of explained variation in chlorophyll *a* concentrations (filled bars) at A) Inverhuron and B) Point Clark for the months of May, August and September, 2010. The adjusted coefficient of variation (R^2_{adj}) was used to evaluate model performance and significant predictor variables were chosen through forward selection.

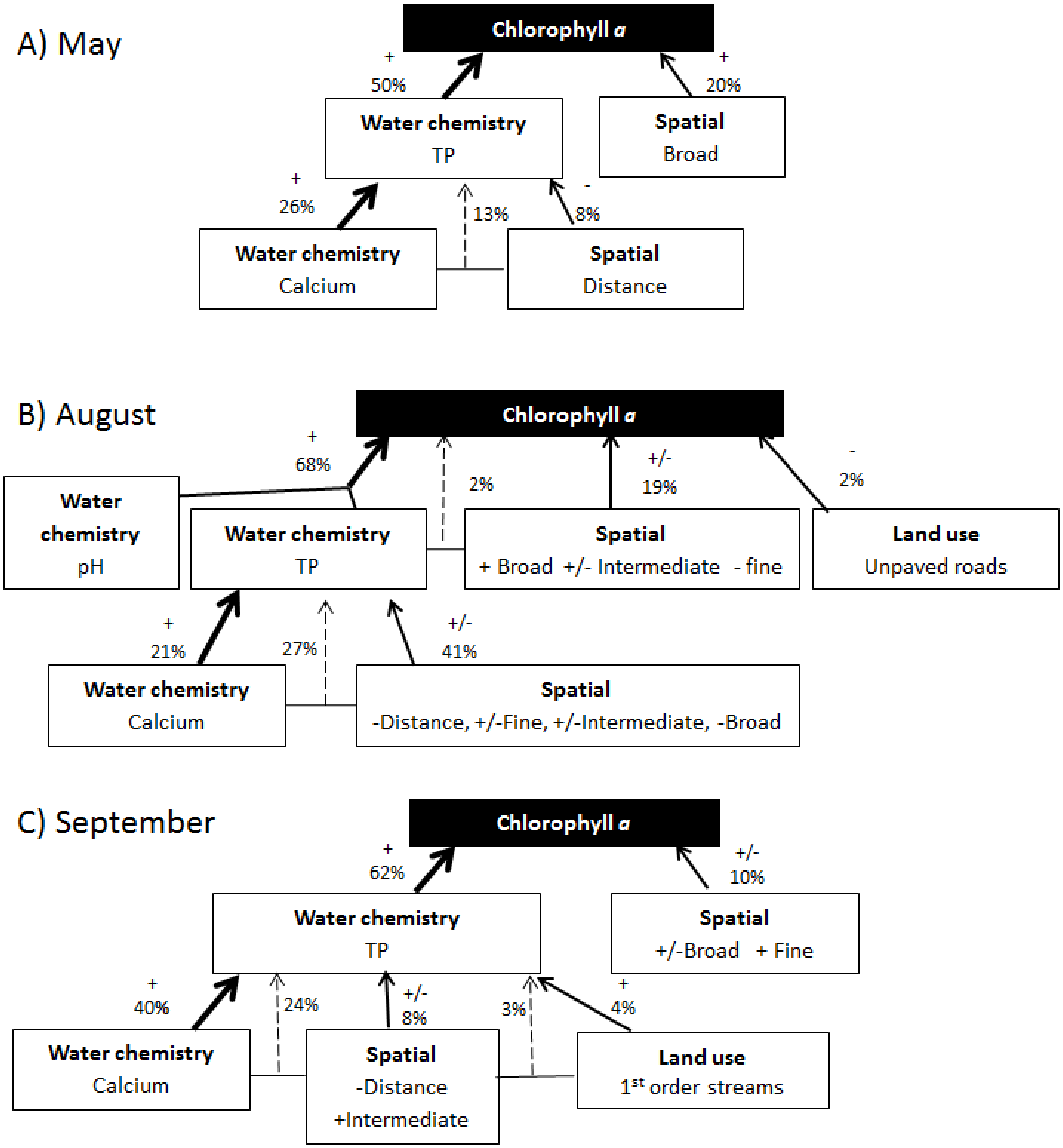


Figure 4: Inverhuron models of chlorophyll *a* for A) May, B) August and C)September sampling periods. Predictors include total phosphorus (TP), pH, land use variables (area of unpaved roads in watershed), spatial variables (fine, intermediate and broad scales). Total phosphorus models were also constructed using land use (length of 1st order streams in watershed), water chemistry (calcium) and spatial variables (distance from shoreline, fine, intermediate and broad scales). Amount of variation explained by predictor variables are included, as well as the relationship between these variables (+/-) and the response variables. The amount of shared variation is represented by the dashed line.

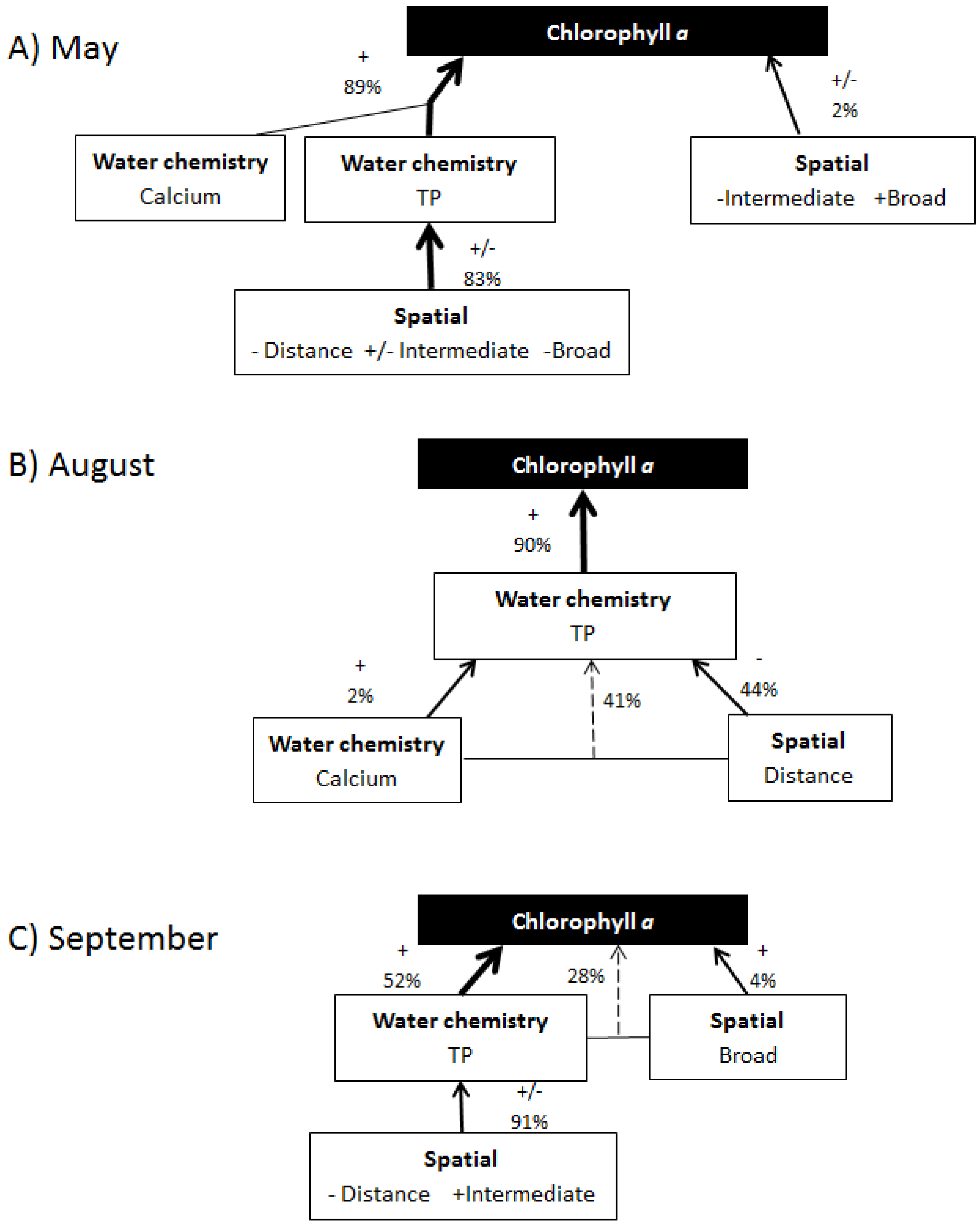


Figure 5: Point Clark models of chlorophyll *a* for A) May, B) August and C) September sampling periods. Predictors include total phosphorus (TP), calcium, and spatial variables (distance from shoreline, fine, intermediate and broad scales). Total phosphorus models were also constructed using water chemistry (calcium) and spatial variables (distance from shoreline, fine, intermediate and broad scales). Amount of variation explained by predictor variables are included, as well as the relationship between these variables (+/-) and the response variables. The amount of shared variation is represented by the dashed line.

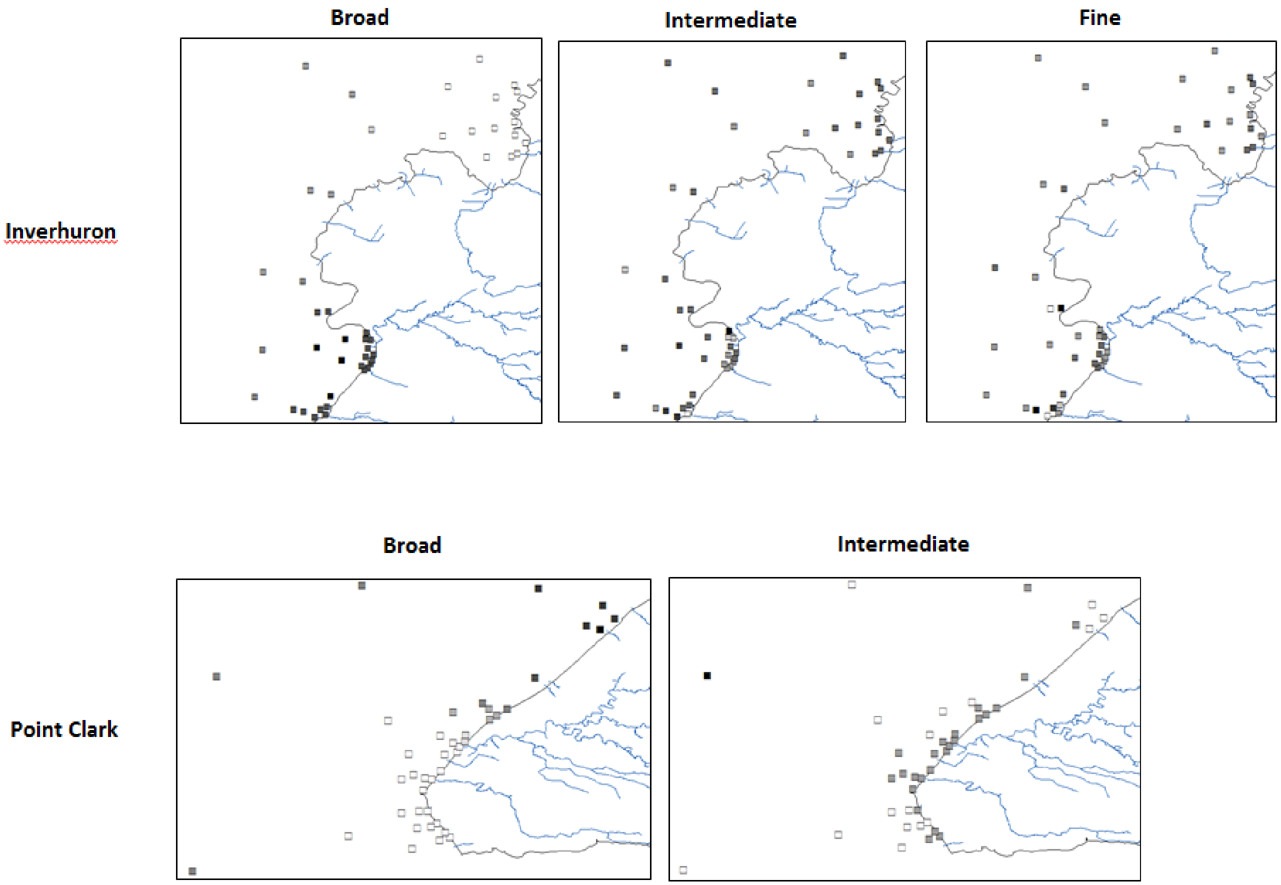


Figure 6: Maps of broad (MEM 1), intermediate (MEM 11) and fine (MEM 20) scale spatial patterns along the shoreline of the Inverhuron study region and broad (MEM 1) and intermediate (MEM 6) scale spatial patterns at the Point Clark study region. These spatial patterns were important in structuring chlorophyll *a* levels at sites sampled along the shoreline of Lake Huron, Ontario.

SUPPORTING INFORMATION

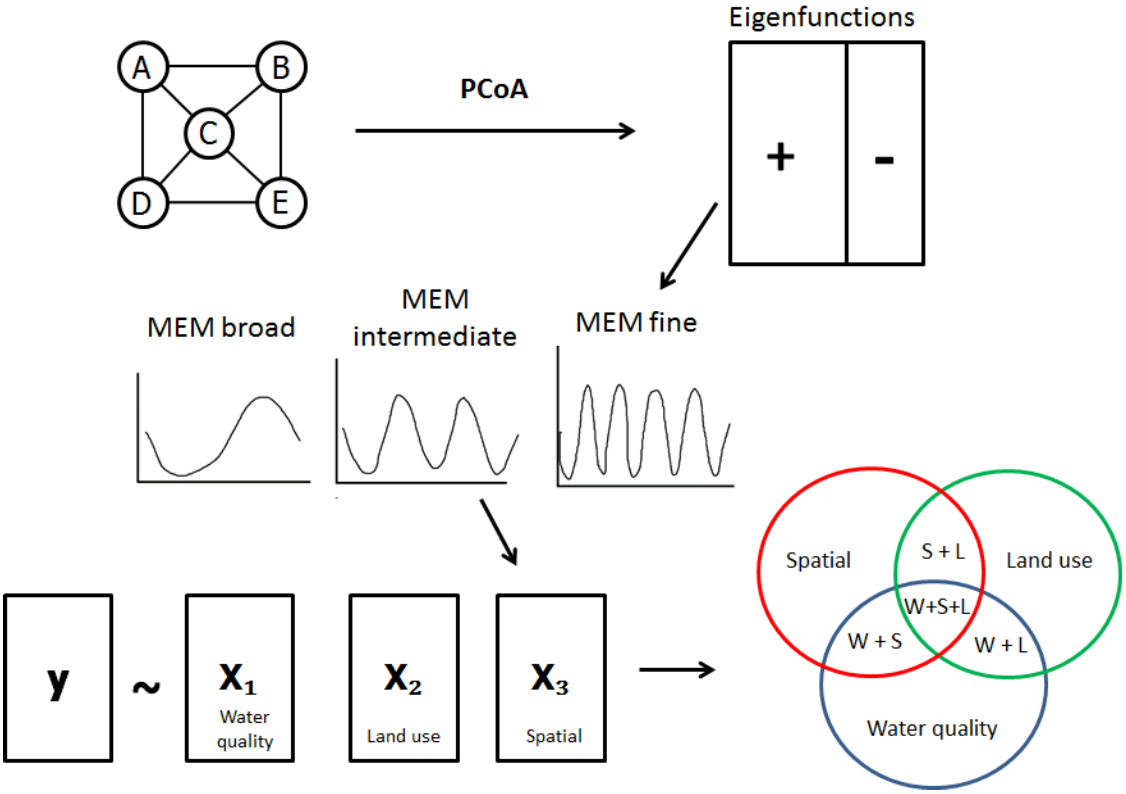
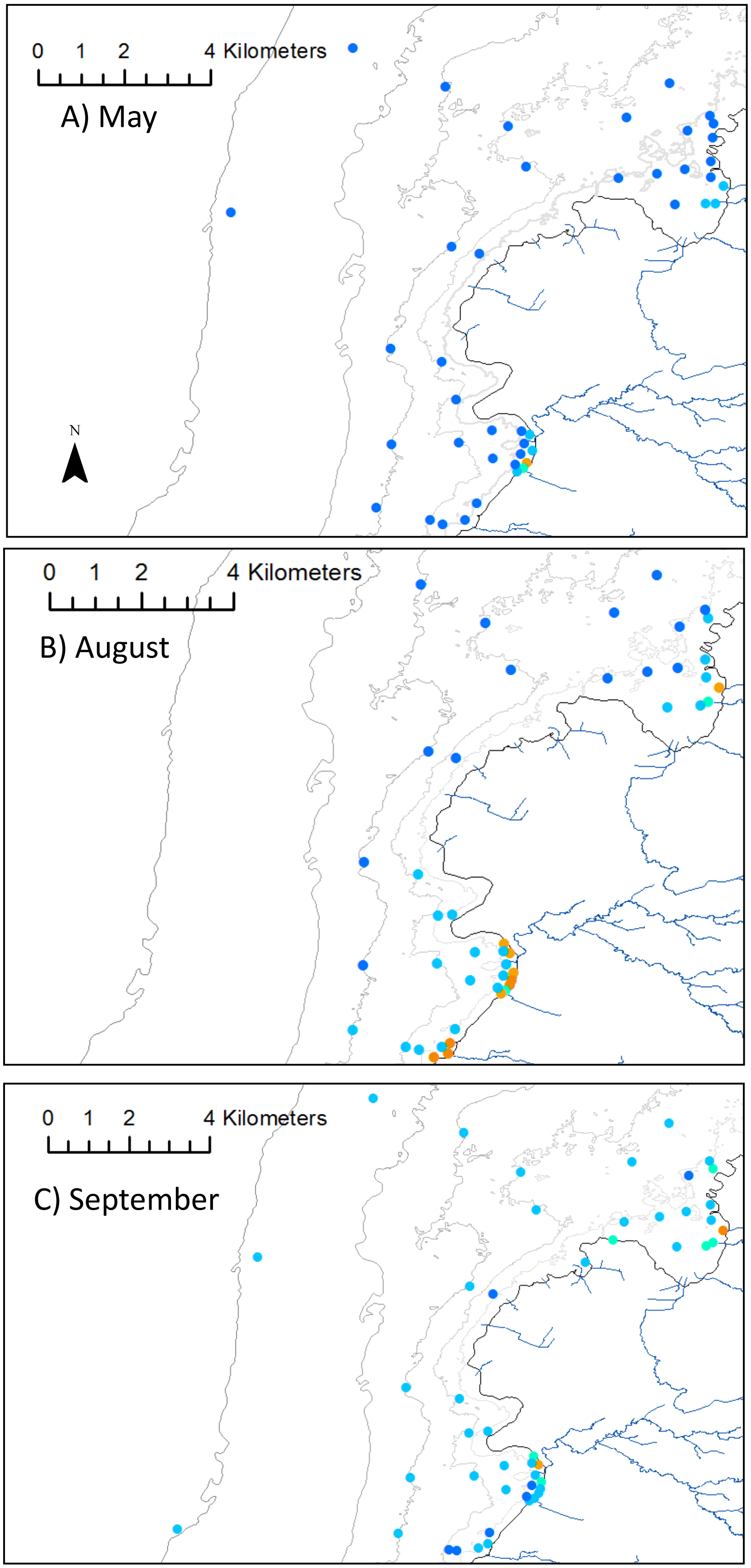


Figure S1: Overview of the steps used in order to incorporate MEMs into a linear regression model. The first step to a PCNM is to create a distance matrix from the Euclidean distances between sites. A neighbour matrix is then produced and a principal coordinates analysis (PCoA) is conducted on the neighbour matrix. The resulting positive eigenfunctions are referred to as MEM variables and are used to represent the spatial structure in the dataset. In the final step, a linear analysis is performed on the response data with a set of predictor variables, including the MEM variables and environmental variables, and a variation partitioning framework is used to partition the unique and shared variation. Modified from Borcard and Legendre (2002).



Chlorophyll *a* (µg/L)

- ● 0.2 - 0.5
- ● 0.5 - 1.5
- ● 1.5 - 2.5
- ● 2.5 - 3.5
- ● 3.5 - 5.0
- ● 5.0 - 10.0
- ● 10.0 - 20.0
- ● 20.0 - 30.0
- ● 30.0 - 40.0
- ● 40.0 - 50.0

Figure S2: Maps of chlorophyll *a* concentrations at the Inverhuron study region of Lake Huron for the three sampling seasons A) May, B) August and C) September.

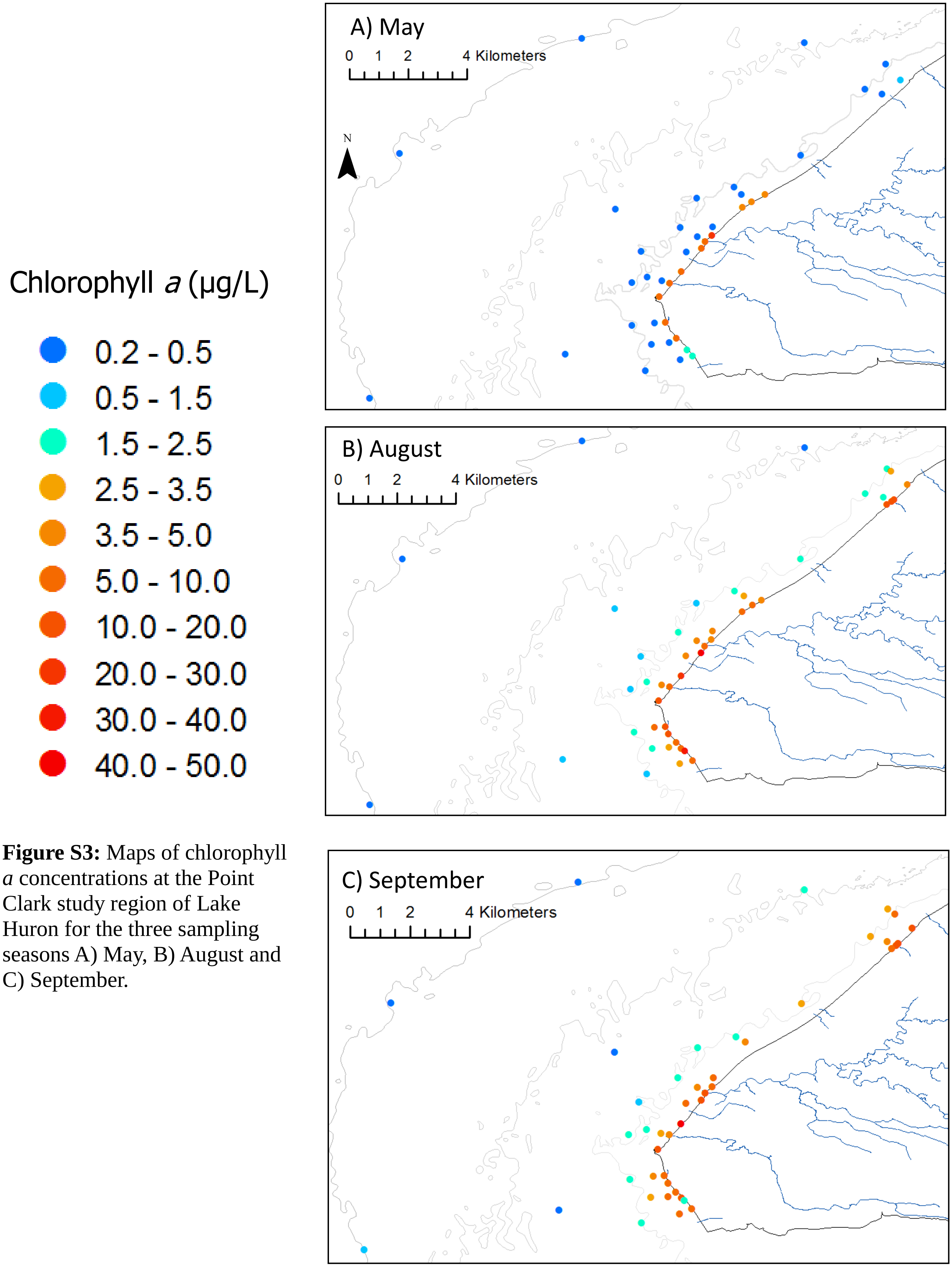


Figure S3: Maps of chlorophyll *a* concentrations at the Point Clark study region of Lake Huron for the three sampling seasons A) May, B) August and C) September.

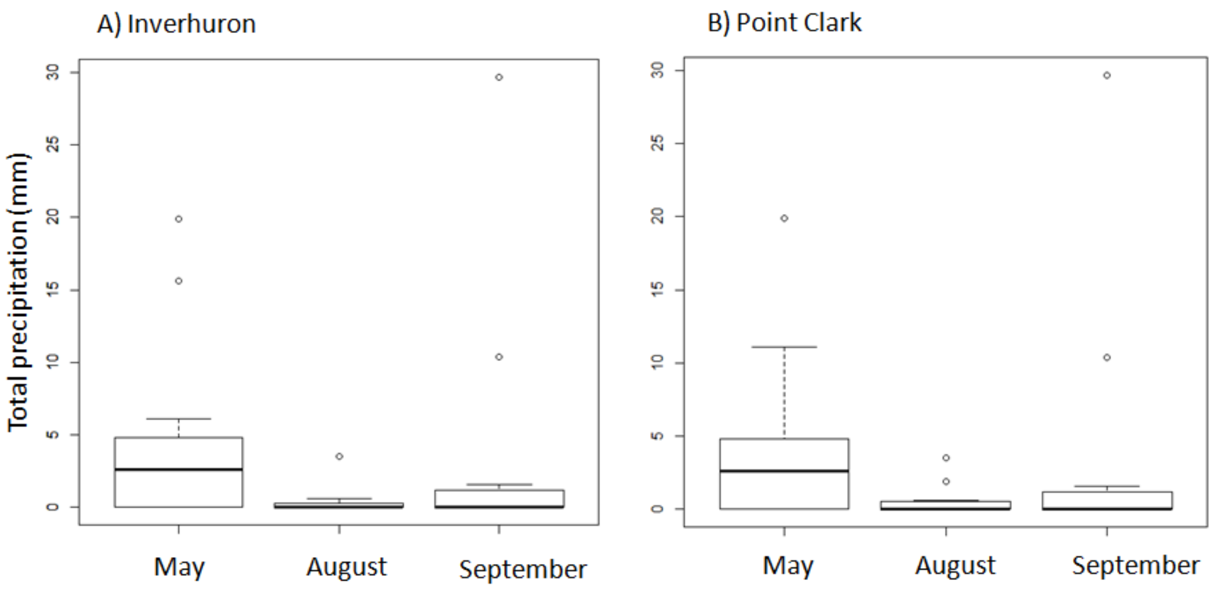


Figure S4: Range of total precipitation over the ten day sampling interval prior to the water quality surveys for the May, August and September sampling seasons for A) Inverhuron and B) Point Clark, Lake Huron, Ontario.

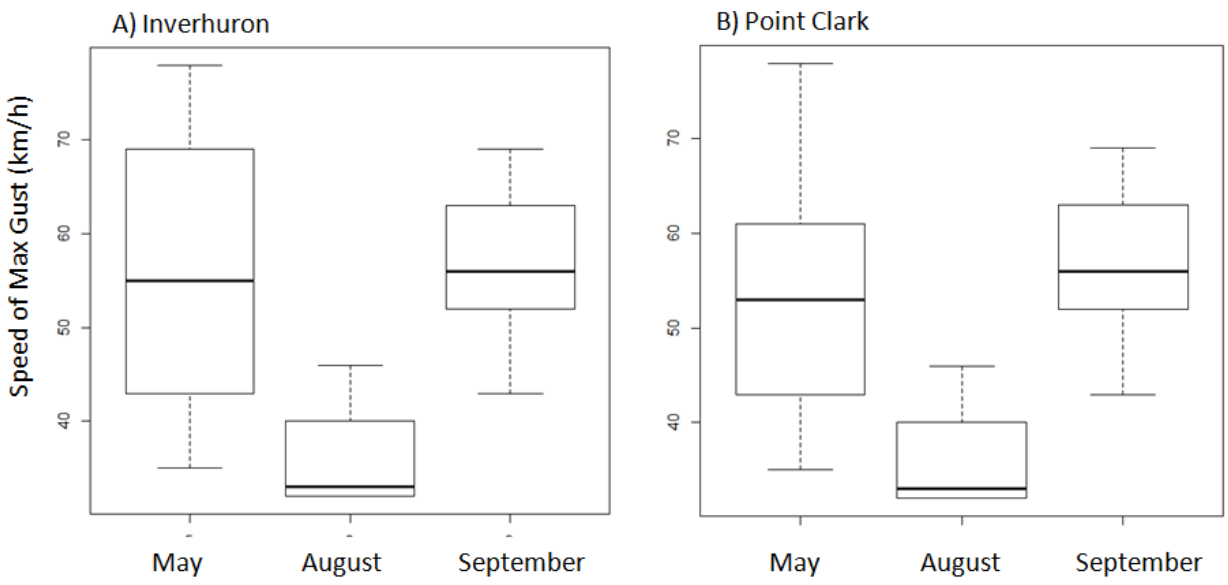


Figure S5: Range in wind speed over the ten day sampling interval prior to the water quality surveys for the May, August and September sampling seasons for A) Inverhuron and B) Point Clark, Lake Huron, Ontario.

Chapter 2

Invasive species, spatial patterns, and benthic algae production along the south-east shoreline of Lake Huron: Can benthic algae 'mussel' their way into the nearshore?

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Keywords: benthic algae, *Cladophora*, Lake Huron, dreissenid mussels, spatial patterns, algae production, ecosystem engineers

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SUMMARY

The resurgence of benthic algae, including *Cladophora*, in the Great Lakes despite efforts to reduce phosphorus loading, has attracted scientific interest to investigate the drivers of these changes. The occurrence of shoreline fouling may be linked to the introduction of invasive dreissenid mussels, but few empirical studies have been conducted to test this hypothesis. Here we investigate the influence of dreissenid mussels on benthic algae production along the south-east shoreline of Lake Huron. Using benthic algae and invasive species data collected by the Ontario Ministry of the Environment and Climate Change, we developed multiple regression models and used Moran Eigenvector Maps to determine the relative influence of invasive species, chlorophyll levels, and spatial patterns on the production of benthic algae, including *Cladophora*, along the south-east shoreline of Lake Huron. Dreissenid mussels, including zebra and quagga mussels, were the most important predictors of benthic algae production in our models, explaining between 14-52% of the variation. Spatial patterns explained between 8-48% of the variation. Our results are consistent with the nearshore shunt hypothesis, with higher algae production at sites with higher mussel density and biomass. Future modeling of benthic algae production in both inland and Great Lakes should consider the impacts of dreissenid mussels and their engineering abilities, as well as spatial patterns that are important in structuring the distribution of benthic algae along the shoreline.

INTRODUCTION

In the 1960s and 1970s, the growth of algae, including benthic algae such as *Cladophora,* reached nuisance conditions in the Great Lakes as a result of increasing nutrient loading (Auer et al., 1982). Following legislation to reduce phosphorus loading into the Great Lakes, there were documented decreases in open water phosphorus levels (De Pinto et al., 1986), and a decrease in concern of nuisance growth of benthic algae, including *Cladophora* in the Great Lakes (Auer et al., 2010). However, recent shoreline and water quality surveys in the Great Lakes, including Lake Huron, have found an increase in the occurrence of shoreline fouling with benthic algae species, including *Cladophora glomerata, Chara vulgaris,* and a mixture of periphyton (Barton et al., 2013; Howell et al., 2014). This "resurgence" of nuisance benthic algae in the early 21st century has led to increased attention on water quality in the Great Lakes (Auer et al., 2010; Kuczynski et al., 2016).

Cladophora is a filamentous green alga that is present in the Great Lakes, including Lake Huron, and grows attached to solid substrates (Auer et al., 1982; Dodds and Gudder, 1992). The growth of *Cladophora* in lakes and streams is common in North America, however, the nuisance growth of *Cladophora* in the Great Lakes has been connected to cultural eutrophication (Auer et al., 1982). The growth of benthic algae can become a nuisance during the die off period in mid- to late- summer, as water temperatures reach a seasonal high and algae can become detached from the lake bottom and wash up along the shoreline following high wind events (Howell et al., 2004). The extensive growth of *Cladophora* and other benthic algae can foul beaches and water intakes, affecting the aesthetics, economics, human and wildlife health (Byappanahalli et al., 2003; Byappanahalli and Whitman, 2009), and other ecosystem services provided by the lake (Howell et al., 2004; Higgins et al., 2008; Brooks et al., 2015). The observed patchy distribution of *Cladophora* along the shoreline may be associated with localized nutrient inputs. For example, in the upper Great Lakes, the nuisance growth of *Cladophora* has been connected to point source nutrient enrichment and discharges (Auer et al., 1982). In Lake Huron, historical nutrient levels were not sufficient to support extensive growth of *Cladophora* (Auer et al., 1982; Howell, 2004). However, since the mid-1990s, the return of nuisance growth of *Cladophora* in the Great Lakes has not been attributed solely to increased nutrient loading, but could also be associated with the ecosystem changes associated with the introduction of invasive species, including dreissenid mussels (Higgins et al., 2008; Brooks et al., 2016).

The reappearance of nuisance *Cladophora* blooms in the early 21st century has led to increased attention on this issue in the Great Lakes (Auer et al., 2010). In Lake Huron, an oligo-mesotrophic system, offshore open-water regions are currently undergoing oligotrophication (Barbiero et al., 2012), which makes shoreline fouling with benthic algae puzzling. The return of nuisance growth of *Cladophora* in the Great Lakes has not been attributed to increased nutrient loading, but rather the ecosystem changes associated with the introduction of invasive species, including dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*) (Higgins et al., 2008). Following the invasion of zebra mussels (*Dreissena polymorpha*), there have been documented increases in water clarity (Lowe and Pillsbury, 1996), increases in suitable habitat for the growth of benthic algae in the form of shells (Arnott and Vanni, 1996), and proposed changes in the cycling of nutrients, such as phosphorus, termed the “nearshore shunt hypothesis” (Hecky et al., 2004). These ecosystem alterations as a result of the dreissenid invasion are believed to benefit the growth of benthic algae in the nearshore (Lowe and Pillsbury, 1995). Since the invasion of zebra mussels in the Great Lakes, *Cladophora* growth rates are becoming more sensitive to P loading due to the ability of these mussels to transform particulate phosphorus to soluble forms that are more available to *Cladophora* (Higgins et al., 2012). In parts of Lake Ontario, dreissenid mussels could excrete soluble reactive phosphorus in amounts large enough to sustain populations of *Cladophora* (Ozersky et al., 2009). In Lake Erie, *Cladophora* growth was influenced by soluble reactive phosphorus concentrations and the light regime (Higgins et al., 2006; Auer et al., 2010), and higher photosynthetic rates have been observed in communities with dreissenids, compared to communities lacking dreissenids (Davies and Hecky, 2005).

Alternatively, changes in benthic algae growth may be attributed to the invasion of the round goby (*Neogobius melanostomus*) due to their top-down influence on benthic invertebrates. Round gobies may be reducing the number of grazing benthic invertebrates, and therefore decrease the grazing pressure on benthic algae (Barton et al., 2013). In Lake Michigan, invertebrate density decreased in the presence of round gobies, resulting in an increase in chlorophyll *a* concentrations (Kuhns and Berg, 1999). Observed changes in benthic invertebrate communities were also found following the invasion of zebra mussels, raising concern as to the interacting impacts that round gobies and mussels may have on benthic algae production. McNickle et al., (2006) observed that following the zebra mussel invasion in Lake Huron, the nearshore communities of benthic invertebrates became more homogenous (McNickle et al., 2006). In addition, there has also been a decreasing trend in macroinvertebrate taxa from 1970-2000, and from 2000-2003 in Lake Huron (Nalepa et al., 2007). Thus far, there have been few lake ecosystem studies to investigate the impacts of both of these invasive species on benthic algae production.

Due to the highly variable spatial distribution of benthic algae along the shoreline (Barton et al., 2013; Howell et al., 2014), we were also interested in looking at the spatial signatures that were important in structuring the patchiness of algae in the nearshore environment. Spatial processes that are derived from dependency on environmental characteristics and/or from community processes, can structure ecological communities (Dray et al., 2006; Borcard and Legendre, 2002). Particularly in limnology, incorporating spatial scales can provide insight into fine-scale (e.g., substrate, fine-scale habitat), watershed (e.g., influence of tributaries and land use), and regional processes (e.g., climate) interacting with measured predictor and response variables that may be missed otherwise (Jackson et al., 2001; Mikulyuk et al., 2011; Sharma et al., 2012). In the Great Lakes, despite decreases in nutrient loading, there have been observed spatially-variable growth of *Cladophora* and other benthic algae (Malkin et al., 2010; Barton et al., 2013; Howell et al., 2014). Thus, it is important to investigate what spatial scale is structuring this variability in order to better understand the causes of peaks in benthic algae growth.

Research Objectives

Here, we investigate the relative influence of invasive species, including dreissenid mussels and round gobies, and spatial variability on the production of benthic algae, including *Cladophora*, *Chara*, and other periphyton, along the shoreline of Lake Huron. We hypothesize that ecosystem alterations by invasive species may be contributing to the increase in benthic algal production along the shoreline. Specifically, we explore whether invasive species are associated with higher production of benthic algae along the south-east shoreline of Lake Huron. If dreissenid mussels alter the nearshore environment to promote the growth of benthic algae, it is expected that a larger amount of algae would be found at sites with these invasive species present. We believe that including invasive dreissenid mussels in empirical water quality models will assist with our understanding of the complex interacting drivers impacting nearshore water quality in the Great Lakes.

METHODS

Data acquisition

Benthic algae, invasive dreissenids, and invasive round goby data were acquired from the Ontario Ministry of the Environment and Climate Change (OMOECC) Monitoring and Reporting Branch. Data were collected in mid to late July 2010 along the south-east shoreline of Lake Huron in two major study regions: Inverhuron and Point Clark. Sites were chosen based on depth, and corresponded to depths of 1, 3, 6, 10, and 20 m (Figure 1). Sampling was conducted by divers at the bottom of the lake at each study site.

In each study region, 15 sites were sampled, and measures of benthic algae production were taken from 0.15 m^2 randomly placed quadrats for *Cladophora*, *Chara*, and other periphyton (hereinafter called periphyton). Three replicate quadrats were assessed at each site. Specifically, data were collected for: *Cladophora* biomass (g/m^2 dry weight); cover (%) and thickness (stand height in cm); *Chara* biomass (g/m^2 DW) and cover (%); and periphyton cover (%) and thickness (height in cm). The larger filamentous algae, including *Cladophora* and *Chara* were observed by divers, cover and thickness were measured, and samples were removed by hand from the bottom of the lake. Samples were then put into a mesh bag for identification on the boat deck and freeze-dried to determine dry weight at a later time. Periphyton data were collected using a periphyton piston sampler which was targeted on flat rock surfaces lacking dreissenid mussels in order to prevent obstruction of the sampler seal and to improve the efficiency of the sampler. As a result, periphyton samples lacked *Cladophora* and *Chara* species. Periphyton was defined for this paper separate from larger filamentous algae as it consisted mostly of diatom microalgae. Half of the periphyton samples were used for measurement of chlorophyll *a*, and the other half preserved for weighing at the OMOECC laboratory (Table 1).

Metrics of dreissenid mussels, including cover (%), shell cover (%), abundance (number), density (number/m^2), biomass (g/m^2), and total soft tissue biomass (g/m^2) were collected by divers from 0.15 m^2 randomly placed quadrats for zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*). After collection, samples were frozen, and later weighed for comparison of soft tissue and shell biomass (Table 1). Round gobies (*Neogobius melanostomus*) were observed by divers and by underwater video and goby density was estimated visually and categorized as: 0, not observed; 1, rare; 2, common; 3, abundant (Table 1), a similar method to the one used by Barton et al., (2013).

Data Analyses

Moran Eigenvector Maps (MEMs) were used to infer spatial patterns that were important in explaining the variation in *Cladophora*, *Chara*, and periphyton (benthic algae) production in the nearshore region of Lake Huron. MEMs were constructed using a distance matrix based on Euclidean distances (i.e., straight line distance) between sites (Borcard and Legendre, 2002). A series of sine waves with decreasing periods are generated from a Principal Coordinates Analysis on the distance matrix. These sine waves represent the MEM variables. MEM variables (MEM1-MEM8) each represent patterns at different spatial scales, ranging from broad spatial patterns to fine spatial patterns (Borcard and Legendre, 2002; Borcard et al. 2004).

Multiple regression models were developed for benthic algae production. A variation partitioning framework was used to quantify the unique and shared variation in benthic algae explained by invasive species and spatial patterns. To develop the linear models, a forward selection procedure with a dual-criterion ($\alpha = 0.05$ & R^2_{adj}) was used to identify significant predictor variables (Blanchet et al., 2008). Regional benthic algae models were created for both regions (Inverhuron and Point Clark) for each type of benthic algae (*Cladophora*, *Chara*, and periphyton), as well as global benthic algae models, which included data from both study regions. Sample site depth and goby rank abundances were tested as model covariates, but neither significantly improved model performance ($p>0.05$), and were therefore not included in the benthic algae models. Variables were transformed to meet normality assumptions. All analyses were performed in the R language environment (R Core Development Team, 2015). Mapping was performed using ArcGIS 10 (ESRI, 2010).

RESULTS

Both Inverhuron and Point Clark had high percent cover of periphyton, ranging from 53-100% in Inverhuron (Figure 2a) and 45-100% in Point Clark (Figure 2b). *Cladophora* had the second highest percent cover among groups of benthic algae, where mean cover in Inverhuron was 10.5% and in Point Clark was 18.8%. In addition, the average *Cladophora* biomass was 3 g/m^2 DW at the Inverhuron study region, and 7 g/m^2 DW at the Point Clark study region (Figure 3). Samples in the Point Clark study region found *Cladophora* biomass to be as high as 50 g/m^2 DW. *Chara* had low percent cover in both regions ranging from 0% to 9% in Inverhuron and 0% to 8% in Point Clark (Figure 2).

Regional benthic algae models

In Inverhuron, *Cladophora* percent cover ($R^2_{adj} = 0.52$) was predicted entirely by zebra mussel density ($R^2_{adj} = 0.52$), with no spatial variables entering the model as statistically significant (Table 2). In Point Clark, the model for *Cladophora* biomass ($R^2_{adj} = 0.88$) was predicted by broad (MEM2; R^2_{adj}=0.48; Figure 4) and fine (MEM6; R^2_{adj}=0.21; Figure 4) scale spatial patterns, zebra mussel soft tissue biomass (R^2_{adj}=0.2), and shared variation attributed to zebra mussel biomass and spatial patterns (R^2_{adj}=0.17) (Table 2).

In Inverhuron, no variables emerged as predictive of *Chara* percent cover. In Point Clark, *Chara* percent cover ($R^2_{adj} = 0.33$) was predicted by intermediate (MEM5; $R^2_{adj} = 0.33$; Figure 4) scale spatial patterns. Dreissenid density did not enter the *Chara* percent cover model in Point Clark (Table 2).

In Inverhuron, periphyton percent cover ($R^2_{adj} = 0.57$) was predicted by quagga mussel biomass ($R^2_{adj} = 0.29$), and fine (MEM6; $R^2_{adj} = 0.28$; Figure 4) scale spatial patterns (Table 2). For Point Clark, no variables emerged as significantly predictive of periphyton percent cover.

Round goby relative abundance was not a significant predictor variable in any of the regional benthic algae models. This may be because of the coarse and qualitative sampling method of round gobies, which may not be a good estimate of their impacts on benthic algae production.

Global benthic algae models

For the global benthic algae models, *Cladophora* percent cover ($R^2_{adj}= 0.55$) was predicted by zebra mussel biomass ($R^2_{adj}= 0.42$), and broad (MEM2; $R^2_{adj}= 0.13$; Figure 4) scale spatial patterns (Table 3). *Cladophora* thickness ($R^2_{adj}= 0.63$) was predicted by zebra mussel density ($R^2_{adj}= 0.36$), broad (MEM2; $R^2_{adj}= 0.12$), and fine (MEM6; $R^2_{adj}= 0.08$ and MEM7; $R^2_{adj}= 0.08$; Figure 5) scale spatial patterns (Table 3)

Chara biomass ($R^2_{adj}= 0.23$) was predicted by broad scale spatial patterns (Table 3; Figure 5).

Periphyton percent cover ($R^2_{adj}= 0.38$) was predicted by quagga mussel density ($R^2_{adj}= 0.14$), broad (MEM2; $R^2_{adj}= 0.12$; Figure 5), and fine (MEM5; $R^2_{adj}= 0.12$; Figure 5) scale spatial patterns (Table 3). Periphyton maximum thickness ($R^2_{adj}= 0.51$) was predicted by quagga mussel biomass ($R^2_{adj}= 0.41$), fine (MEM6; $R^2_{adj}= 0.10$; Figure 5) scale spatial patterns, and shared variation ($R^2_{adj}= 0.14$) between quagga mussels and spatial patterns (Table 3). Periphyton mean thickness ($R^2_{adj}= 0.41$) was predicted by quagga mussel biomass ($R^2_{adj}= 0.23$), broad (MEM3; $R^2_{adj}= 0.08$; Figure 5) and fine (MEM5; $R^2_{adj}= 0.10$; Figure 5) scale spatial patterns (Table 3).

DISCUSSION

Dreissenid mussels were the most important predictors of benthic algae cover along the shoreline of Lake Huron. As much as 52% of the variation in benthic algae percent cover was explained by invasive dreissenid mussels, highlighting the importance of dreissenid mussels in modelling benthic algae production in Lake Huron. In addition, spatial patterns along the shoreline of Lake Huron were important in structuring benthic algae production, explaining between 8-48% of the variation. These spatial patterns may be indicative of shoreline features such as the mouths of tributaries, substrate differences that can impact the growth and attachment of benthic algae, in addition to mussel beds. This project highlights the impacts of the "nearshore shunt hypothesis" as a result of the dreissenid mussel invasion on benthic algae production in an oligotrophic system.

Great Lakes benthic algae production

Despite observed oligotrophic conditions in the offshore region of Lake Huron (Barbeiro et al., 2012), we have found localized sites along the shoreline of Lake Huron that exhibit nuisance conditions of *Cladophora* growth. A study by Depew et al., (2011) found no nuisance conditions of benthic algae growth in Georgian Bay and the main basin of Lake Huron in 2005 (Depew et al., 2011). Approximately, five years after the study by Depew et al., (2011), we have found nuisance conditions of *Cladophora* biomass (>50 g/m^2 dry weight) at some sites in the Point Clark study region, emphasizing the change in benthic algae production over a short amount of time. Over approximately the past 30 years, planktonic primary production has declined, and benthic algae production has increased in Lake Huron, causing a shift from pelagic to benthic primary production (Brothers et al., 2016). Currently in Lake Huron, up to half of the lake primary production may be benthic (Brothers et al., 2016). In addition, the percentage of submerged aquatic vegetation in the nearshore of Lake Huron was estimated at approximately 15% (Brooks et al., 2015). The remaining Lower Great Lakes are also experiencing similar shifts in lake primary production, with all of the Lower Great Lakes experiencing decreases in planktonic primary production, and increases in benthic primary production in all lakes, except Lake Erie (Brother et al., 2016). Similar shifts in algae production have occurred in other inland lakes, including Lake Simcoe, where there has been a decrease in phytoplankton production as a result of the dreissenid invasion (Kim et al., 2015).

Dreissenid mussels and benthic algae

Dreissenid mussels were found to be important drivers of benthic algae biomass and cover in Lake Huron. Dreissenid mussel percent cover and biomass were important determinants of benthic algae, including *Cladophora* and periphyton along the shoreline of Lake Huron. For example, zebra mussel density was the most important driver of *Cladophora* percent cover in Inverhuron, explaining 52% of the variation. Dreissenid mussels have been demonstrated to impact aquatic habitats, including increases in hard substrate and light, as well as alter biotic interactions, which can impact water quality and food webs (Wilson et al., 2006). Dreissenid mussels have been proposed to impact benthic algae production through the "nearshore shunt hypothesis" (Hecky et al., 2004). By filtering large quantities of water, dreissenid mussels redirect nutrients from pelagic to benthic areas, which can help contribute to benthic algae growth in nearshore regions (Hecky et al., 2004). The presence of zebra mussels provides ample habitat for the growth of benthic algae, by recycling nutrients and excreting nutrients in the benthic zones (Arnott and Vanni, 1996) in the form of either feces or pseudofeces, by providing hard substrate in the form of shells for filamentous algae to attach to, and by reengineering nutrient cycling in the littoral zone in the form of redirecting nutrients from the pelagic zone (Hecky et al., 2004). Dreissenid excretion can also increase phosphorus levels in the near-bottom environment where benthic algae colonize, forming a concentration boundary layer (Dayton et al., 2014). Bioavailable phosphorus concentrated at the lake bottom can be at levels that are sufficient to support *Cladophora* growth over the growing season (Dayton et al., 2014; Ozersky et al., 2009). In addition, dreissenid mussels can increase water clarity in invaded systems by filtering particles from the water column and reducing the amount of total suspended solids (Fishman et al., 2009), and this in turn changes the light regime of the littoral zone and increases the depth of the photic zone (Auer et al., 2010). These changes are proposed to favour the growth of benthic algae (Hecky et al., 2004). An increase in availability of light has been demonstrated to favour the growth of benthic alga such as *Cladophora* (Auer et al., 2010), as well as other periphytic algae (Hansson, 1991). In Lake Huron, there was an increase in light penetration, biomass of benthic algae, concentrations of chlorophyll, and the rate of benthic primary productivity following the invasion of zebra mussels (Lowe and Pillsbury, 1995). It has been predicted that any increases in phosphorus in the nearshore region may cause an increase in *Cladophora* growth due to increased water clarity and subsequent increases in light penetration (Malkin et al., 2008). Our results indicate that dreissenid mussels are associated with higher algae production along the south-east shoreline of Lake Huron, which coincides with predictions from the nearshore shunt hypothesis.

Spatial patterns

The patchy distribution of observed benthic algae along the shoreline (Howell et al., 2004) has raised interest into the spatial processes that may be driving the nuisance growth of *Cladophora.* In our study, the distribution of benthic algae in the nearshore region of Lake Huron was found to be spatially contingent. Spatial patterns explained between 8-48% of the variation in benthic algae biomass and cover along the south-east shoreline of Lake Huron. Broad-scale spatial patterns were important in describing the distribution of *Cladophora* along the shoreline of the Point Clark study region, explaining as much as 48% of the variation in benthic algae production. This spatial pattern indicates a depth gradient along the shoreline, with higher mussel and *Cladophora* abundance at deeper sites. In Lake Ontario, there were observed increases in proportions of quagga mussels with lake depth, as well as quagga mussels occupying sites with softer substrates (Mills et al., 1993). Due to the increases in water clarity as a result of dreissenid mussel filter-feeding, benthic algae species have been able to colonize deeper sites in the Great Lakes (Kuczynski et al., 2016). The broad scale spatial patterns evident in our models may be suggesting the influence that dreissenid mussels are having on the maximum depth of colonization for benthic algae.

Intermediate-scale spatial patterns in the Point Clark study region were important in structuring the distribution of benthic algae along the shoreline of Lake Huron, explaining as much as 33% of the variation in *Chara* percent cover along the shoreline. Intermediate scale spatial patterns may be indicative of the tributaries draining the large Pine River watershed, which is an area primarily used for agricultural practices (Howell et al., 2014). Tributaries draining agricultural land could be contributing excess nutrients to the nearshore region, and these fluxes in nutrients can have impacts on primary production, as Lake Huron has become more sensitive to fluxes in nutrient levels (Howell et al., 2014).

Fine-scale spatial patterns were also important in explaining the distribution of benthic algae along the shoreline of Lake Huron, explaining as much as 28% of the variation in benthic algae production, including *Cladophora* biomass and periphyton percent cover. Fine scale spatial patterns may be indicative of differences in substrate types along the shoreline. The attachment of benthic algae requires different substrate types as well as the attachment of mussels. Substrate type is important in the distribution of *Cladophora*. *Cladophora* colonizes many different types of substrate, including rocks and clams (Dodds and Gudder, 1992). In addition, substrate type has also been found to be an important variable in explaining the pattern in abundance and distribution of zebra and quagga mussels (Mellina and Rasmussen, 1994; Mills et al., 1993). While zebra mussels have been found to occupy areas with harder substrate (Nalepa et al., 1995; Mellina and Rasmussen, 1994), quagga mussels have been observed at deeper depths, on bedrock and cobble substrates (Wilson et al., 2006), as well as on softer substrate types such as sand (Mills et al., 1993). *Cladophora* can use the shells of dreissenids as a point of attachment and this has been observed in the nearshore of Lake Ontario (Wilson et al., 2006). Therefore, fine scale spatial patterns influencing algae production may be attributed to the impact of available substrate on both the distribution of dreissenid mussels and the ability of algae to attach to the shells of dreissenid mussels.

Conclusions and Implications

With the majority of variation in benthic algae biomass and cover being explained by dreissenid mussels, we highlight the importance of including mussels in water quality management strategies and water quality modelling. In addition, spatial patterns, from broad to fine, were important in structuring the distribution of along the shoreline, including the impacts of depth, water clarity, and substrate type. In particular, we highlight the importance of broad scale spatial patterns in explaining the proliferation of benthic algae at deeper sites in response to ecosystem changes as a result of the dreissenid mussel invasion. These spatial patterns are important to take into consideration when planning benthic algae monitoring surveys, and modelling benthic algae production in the Great Lakes.

This study examined the relative influence of spatial patterns and invasive species, including dreissenid mussels and round gobies, on benthic algae biomass and cover along the shoreline of Lake Huron. The objective was to assess whether there was an association between benthic algae production and aquatic invasive species, and if they displayed any important spatial structures. We provide some of the first empirical modelling evidence for the impacts of invasive species, specifically dreissenid mussels, on benthic algae biomass and cover in Lake Huron, with our results being consistent with the 'nearshore shunt hypothesis' (Hecky et al., 2004). Dreissenid mussels were the most important drivers of patterns in benthic algae biomass and cover along the shoreline of Lake Huron, potentially due to their role as ecosystem engineers altering the distribution of nutrients, providing substrate for benthic algae to attach to, and increasing water clarity. With this information, it may help managers understand how the nearshore regions of the Great Lakes, in the presence of dreissenid mussels, may become more sensitive to shoreline inputs of nutrients such as phosphorus via rivers and point sources. Understanding the role of invasive dreissenid mussels as ecosystem engineers and their impacts on algal production is important, and their impacts on lake benthic algae production must be accounted for in management planning (Wilson et al., 2006). The appropriate target for management of Great Lakes benthic algae production remains with sources of phosphorus (Dayton et al., 2014; Brooks et al., 2015). In addition, spatial patterns along the shoreline may help our understanding of the distribution of benthic algae in the nearshore of Lake Huron and calls for the consideration of spatial patterns in water quality modelling and management strategies in the future.

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TABLES

Table 1: Mean (with standard deviation in parentheses) of biological variables measured at sites in the Inverhuron and Point Clark study regions in 2010, Lake Huron, Ontario. *D.poly= Dreissena polymorpha*, *D.bug= Dreissena bugensis,* n= number of samples.

	Inverhuron (n= 15)	Point Clark (n= 15)
Cladophora cover (%)	10.5 (9.6)	18.8 (20.6)
Cladophora thickness (cm)	2.8 (1.6)	2.1 (1.8)
Cladophora biomass (g/m^2 DW)	3 (3.3)	7.4 (10.8)
Chara cover (%)	1.1 (2.7)	0.9 (2.1)
Chara biomass (g/m^2 DW)	0.8 (2.1)	1.5 (3.6)
Periphyton cover (%)	84.4 (15)	82.9 (17.9)
Periphyton max thickness (cm)	2.4 (2)	2.5 (2.2)
Periphyton average thickness (cm)	1.6 (0.9)	1.5 (1.2)
Dreissenid cover (%)	12.2 (9)	5.7 (5.8)
Dreissenid shell cover (%)	8.9 (7.1)	9.4 (7.3)
Dreissenids (number/ m^2)	964 (861.6)	558.7 (813.2)
Dreissenids total biomass (g/m^2)	251 (213.8)	133.8 (161.5)
Dreissenids soft tissue biomass (g/m^2)	16 (13.2)	10.2 (13.5)
D. poly (number/ m^2)	154.2 (135.2)	94.2 (129)
D. poly total biomass (g/m^2)	46.8 (37.4)	37.3 (47.7)
D. poly soft tissue biomass (g/m^2)	1.4 (1.1)	1.3 (1.6)
D. bug (number/ m^2)	809.8 (747.8)	464.4 (698.2)
D. bug total biomass (g/m^2)	204.3 (180.7)	96.5 (117.4)
D. bug soft tissue biomass (g/m^2)	14.6 (12.4)	8.9 (12.1)

Table 2: Summary of regression models predicting benthic algae production at both the Inverhuron and Point Clark study regions in July, 2010. Multiple regression models include predictor variables that were selected using a forward selection procedure. The adjusted coefficient of determination (R^2_{adj}) was used to evaluate model performance, and the *p*-value was used to evaluate significance of models.

		Multiple regression			
Study Region	Response variable	Predictor variables	R^2_{adj}	Total R^2_{adj}	Model significance (*p*)
Inverhuron	*Cladophora* cover (%)	+ Zebra mussel density (no./m^2)	0.52	0.52	0.002
Inverhuron	Periphyton cover (%)	- Fine (MEM5)	0.28	0.57	0.002
		+ Quagga mussel biomass (g/m^2)	0.29		
Point Clark	*Cladophora* biomass (g/m^2)	+ Broad (MEM2)	0.48	0.88	7.36e-6
		+ Fine (MEM6)	0.21		
		+ Zebra mussel biomass (g/m^2)	0.20		
		+ shared variation between MEMs and zebra mussels	0.17		
Point Clark	*Chara* cover (%)	+ Intermediate (MEM5)	0.33	0.33	0.02

Table 3: Summary of global benthic algae regression models. Multiple regression models include predictor variables that were selected using a forward selection procedure. The adjusted coefficient of determination (R^2_{adj}) was used to evaluate model performance, and the *p*-value was used to evaluate significance of models.

	Multiple regression			
Response variable	Predictor variables	R^2_{adj}	Total R^2_{adj}	Model significance (*p*)
Cladophora cover (%)	Zebra mussel biomass (g/m²)	0.42	0.55	7.41e-06
	Broad (MEM2)	0.13		
Cladophora mean thickness (cm)	Zebra mussel density (no./m²)	0.36	0.63	4.99e-06
	Broad (MEM2)	0.12		
	Fine (MEM6)	0.08		
	Fine (MEM7)	0.08		
	Shared between zebra mussels and space	0.15		
Chara biomass (g/m²)	Broad (MEM2)	0.23	0.23	0.004
Periphyton cover (%)	Quagga mussel density (no./m²)	0.14	0.38	0.001
	Broad (MEM2)	0.12		
	Fine (MEM5)	0.12		
Periphyton max thickness (cm)	Quagga mussel biomass (g/m²)	0.41	0.51	2.78e-05
	Fine (MEM6)	0.10		
	Shared between quagga mussels and space	0.14		
Periphyton mean thickness (cm)	Quagga mussel biomass (g/m²)	0.23	0.41	0.001
	Fine (MEM5)	0.10		
	Broad (MEM3)	0.08		

FIGURES

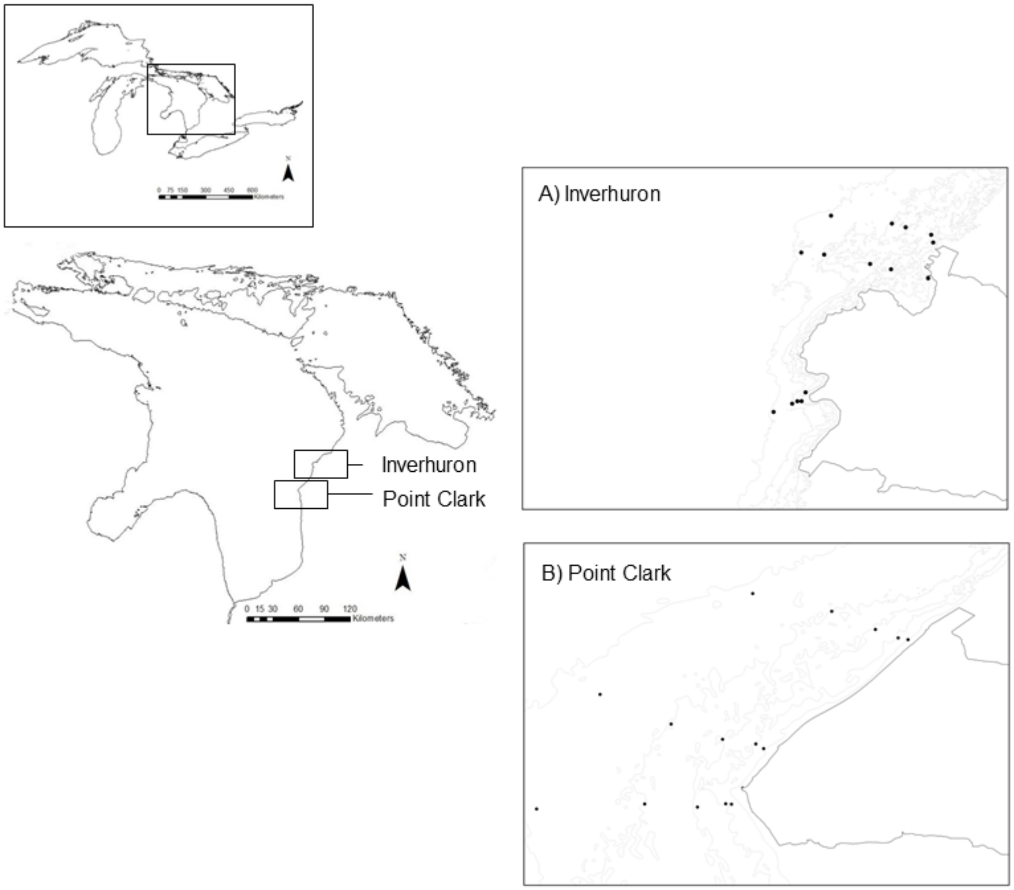

Figure 1: Sampling sites at depths of 1, 3, 6, 10 and 20 m depth in the A) Inverhuron and B) Point Clark regions.

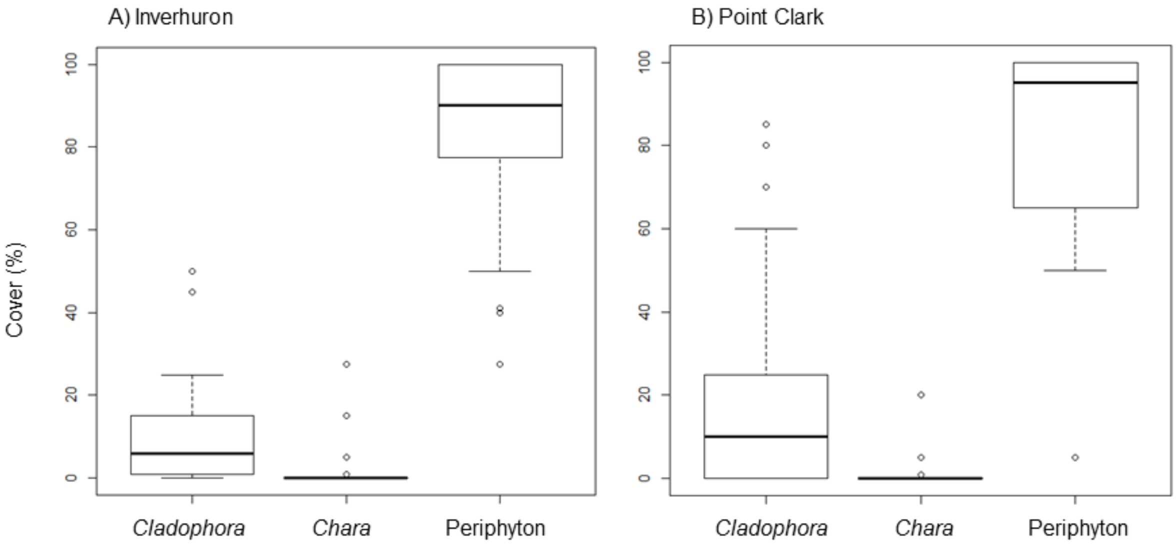

Figure 2: Percent cover of *Cladophora*, *Chara*, and periphyton within the 0.15 m² quadrat sampling area for the sites at A) Inverhuron and B) Point Clark.

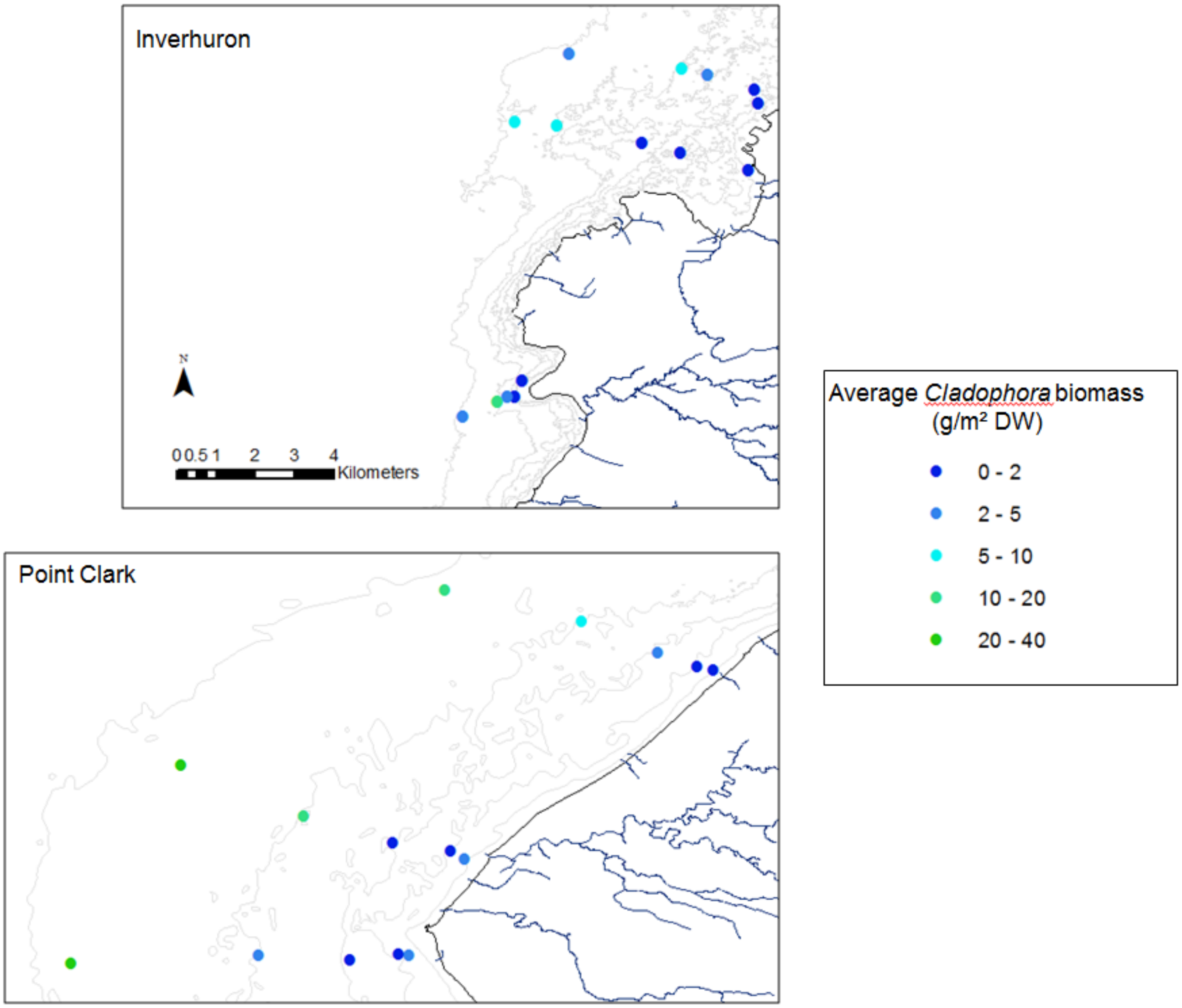

Figure 3: Average *Cladophora* biomass (g/m^2 dry weight) along the shoreline of the Inverhuron and Point Clark study regions.

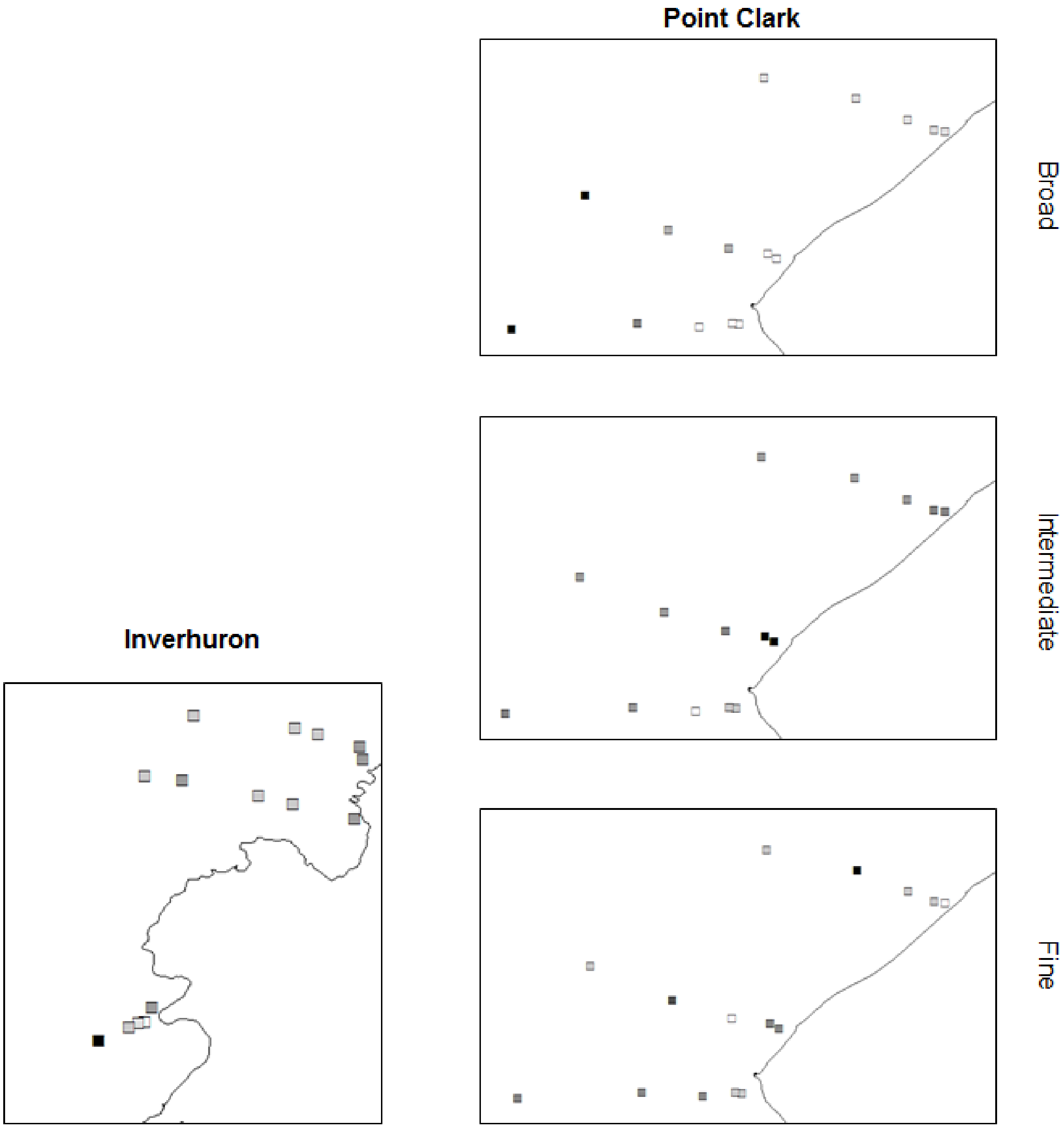

Figure 4: Maps of MEMs important in predicting benthic algae production at the Inverhuron and Point Clark study regions from the regional benthic algae models. MEMs include broad (MEM2), intermediate (MEM5) and fine (MEM6) spatial structures along the shoreline of Point Clark, and fine (MEM5) spatial structures along the shoreline of Inverhuron.

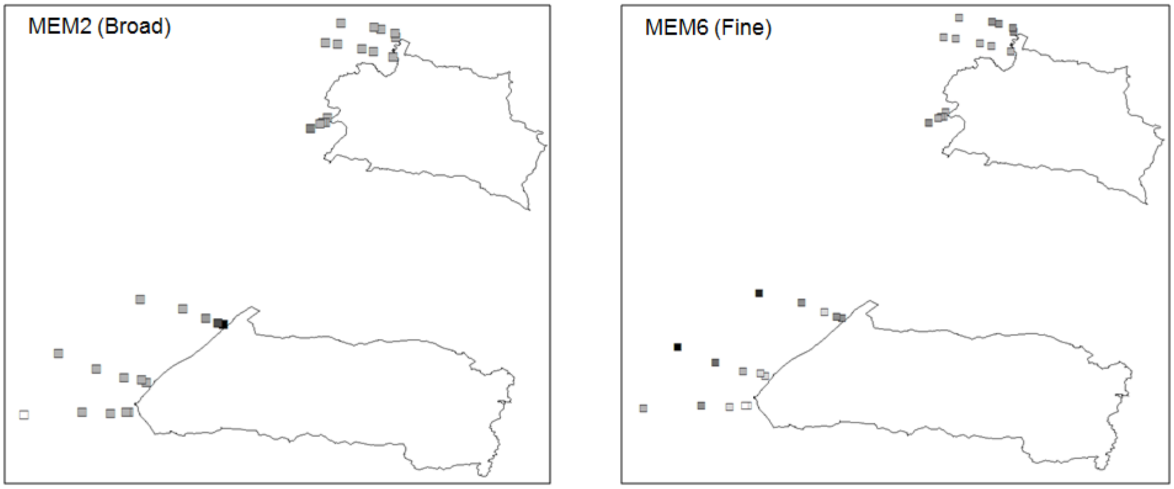

Figure 5: Maps of MEMs important in predicting benthic algae production for the global models. MEMs include broad (MEM2), and fine (MEM6) spatial structures along the south-east shoreline of Lake Huron.

SUMMARY AND CONCLUSIONS

We investigated the main drivers of changes in water quality and benthic algae production along the south-east shoreline of Lake Huron, using water chemistry, land use, invasive species, and benthic algae data collected by the Ontario Ministry of the Environment and Climate Change. Although the offshore of Lake Huron is oligotrophic (Barbiero et al., 2012), we found localized areas along the shoreline of Lake Huron that exhibited nuisance algae growth. Algae production along the south-east shoreline was associated with elevated nutrient levels (Chapter 1) and the presence of invasive dreissenid mussels (Chapter 2).

We found that water quality (measured as chlorophyll *a*) was driven primarily by total phosphorus levels along the shoreline, which is expected, as primary production in the Great Lakes is limited by phosphorus (Howell et al., 2014). However, we also observed spatial patterns along the shoreline are important in structuring the distribution of algae, and these patterns varied by season. In the spring and fall seasons, high precipitation and runoff were associated with spatial patterns around the mouths of tributaries due to runoff. In the summer, water quality was associated with shoreline development of residential properties that rely on septic systems for waste disposal (Chapter 1).

We found empirical evidence for the nearshore shunt hypothesis (Hecky et al. 2004) in Lake Huron, with higher algae production in regions with higher dreissenid mussel cover and density. Interestingly, there was no evidence for the nearshore shunt hypothesis when Lake Huron was sampled in 2005, although it was observed in Lakes Erie and Ontario (Depew et al., 2011). However, by 2010, the production of benthic algae, including *Cladophora*, the predominant alga fouling the shoreline of Lake Huron, was primarily driven by dreissenid mussels, and spatial patterns that were important in structuring algae production were associated with lake bottom substrate type (Chapter 2).

Despite recorded decreases in open-water lake nutrient levels and oligotrophication (Barbiero et al., 2012), shoreline surveys suggest nutrient enrichment from the surrounding land and possibly increased sensitivity to nutrient enrichment due to the invasion of zebra mussels (Hecky et al., 2004). This study highlights the complexity of the nutrient and water quality dynamics, with possible interacting drivers influencing water quality along the shoreline of Lake Huron and the need for water resource assessment strategies that are sensitive at both the temporal and spatial scales of these problems. Management strategies for lake ecosystems impacted by land use development should include: the development of houses set-back from the shoreline, minimizing the amount of shoreline development, increasing the riparian buffer zones of lakes (Garrison and Wakeman, 2000), and monitoring surveys that are specific to shoreline/nearshore nutrient levels, especially near tributary out-falls. In the presence of dreissenid mussels, nutrient inputs in the nearshore of Lake Huron may need to be monitored and controlled more stringently, with the management of phosphorus loading remaining as the most feasible option for controlling algae production along the shoreline of Lake Huron.

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