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## Commentary

## Commentary: The need for model development related to *Cladophora* and nutrient management in Lake Michigan

Harvey A. Bootsma<sup>a</sup>, Mark D. Rowe<sup>b,\*</sup>, Colin N. Brooks<sup>c</sup>, Henry A. Vanderploeg<sup>b</sup><sup>a</sup> University of Wisconsin-Milwaukee, School of Freshwater Sciences, 600 Greenfield Avenue, Milwaukee, WI 53204, USA<sup>b</sup> NOAA Great Lakes Environmental Research Laboratory, 4840 S State Rd., Ann Arbor, MI 48108, USA<sup>c</sup> Michigan Tech Research Institute, Michigan Technological University, 3600 Green Court, Ann Arbor, MI 48104, USA

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## ABSTRACT

In the past 10 to 15 years, excessive growth of *Cladophora* and other attached algae in the nearshore regions of Lake Michigan has re-emerged as an important resource management issue. This paper considers the question, “What information is needed to predict the response of *Cladophora* production in Lake Michigan to management variables, such as nutrient loading, and to additional environmental variables that are outside of management control?” Focusing on Lake Michigan, while drawing on the broader literature, we review the current state of information regarding 1) models of *Cladophora* growth, 2) models that simulate the physical environment, 3) models that simulate nearshore and whole-lake nutrient dynamics, with a specific focus on the role of dreissenid mussels, and 4) monitoring of *Cladophora* abundance. We conclude that while substantial progress has been made, considerable additional research is required before reliable forecasts of *Cladophora* response to nutrient loads and other environmental variables are possible. By providing a detailed outline of this complex, multidisciplinary problem, we hope that this paper will aid in coordinating collaborative research efforts toward the development of useful predictive models.

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## Introduction

Excessive growth of *Cladophora* and other filamentous algae has several negative impacts on Great Lakes ecosystems and the beneficial uses derived from these systems. Shoreline fouling reduces the esthetic quality of beaches and confounds the conventional use of fecal bacteria as water quality indicators (Whitman et al., 2003), making decisions related to beach closings uncertain. *Cladophora* mats also harbor organisms that are pathogenic to humans, including *Shigella*, *Campylobacter*, and *Salmonella* (Verhoughstraete et al., 2010). Water intakes are frequently fouled by sloughed algae. The economic impact of this fouling can be significant. For example, electrical power generation plants on both Lake Michigan and Lake Ontario have experienced partial or complete shutdowns due to fouling of cooling systems, resulting in costs of millions of dollars per year. Other economic impacts include the loss of business revenue and decreased property values (Limburg et al., 2010). Ecosystem health is also affected. *Cladophora* on beaches can harbor toxin-producing *Clostridium botulinum* (Chun et al., 2013), and decomposition of sloughed *Cladophora* within the lake may promote anoxic, nutrient-rich conditions in the benthos that favor the growth of *C. botulinum*. This in turn may contribute to outbreaks of avian botulism

(Lafrancois et al., 2011). Increased abundance of *Cladophora* after the 1990s has been concurrent with several other major ecosystem alterations including the establishment of invasive species such as dreissenid mussels and the round goby, and a shift from pelagic primary production to nearshore, benthic primary production (Fahnenstiel et al., 2010; Turschak et al., 2014). However, the interactions between *Cladophora* and other biotic components, and its role in trophic dynamics remain uncertain.

The primary, and perhaps only, remedial action that may address nuisance *Cladophora* growth is control of phosphorus loading, but there is uncertainty about the efficacy and system-wide consequences of such action. For example, in Lake Ontario there is some evidence that *Cladophora* may respond to local inputs of nutrients, especially phosphorus, in which case local efforts to reduce phosphorus loading may lead to measurable improvements (Higgins et al., 2012). At the same time, satellite imagery and direct sampling indicate that *Cladophora* is abundant in parts of Lake Michigan that are not near large nutrient inputs (Shuchman et al., 2013), suggesting that control of phosphorus concentrations at the whole-lake level may be required to reduce nuisance algal biomass (Bootsma and Liao, 2013). In either case, an understanding of the relationship between *Cladophora* growth and nearshore phosphorus dynamics is required to guide decisions related to nutrient management. In addition to reducing *Cladophora* growth, management actions may be taken to limit the negative

\* Corresponding author.

E-mail address: [mark.rowe@noaa.gov](mailto:mark.rowe@noaa.gov) (M.D. Rowe).

impacts of *Cladophora*, which generally follow massive sloughing events. These may include water intake designs that help to exclude sloughed *Cladophora* from intake water, such as the porous dikes that have been installed by some power plant operators, and removal of *Cladophora* after it has accumulated on the shore. Decisions related to these actions may be guided by knowledge of when and where sloughed *Cladophora* will become stranded on the shore.

The Great Lakes Water Quality Protocol of 2012 commits the United States (in the case of Lake Michigan) to develop programs, practices and technology necessary for a better understanding of the Great Lakes Basin Ecosystem, and to eliminate or reduce, to the maximum extent practicable, environmental threats to the Waters of the Great Lakes. The Protocol specifies Lake Ecosystem Objectives, which include maintaining algal biomass below the level constituting a nuisance condition, and maintaining an oligotrophic state in the open waters of Lake Michigan. To achieve the Lake Ecosystem Objectives, the Protocol specifies the need to establish Substance Objectives for phosphorus concentrations, and to develop phosphorus loading targets required to achieve these objectives. These objectives are similar to those established by the 1978 Great Lakes Water Quality Agreement (GLWQA). However, in recognition of the large changes that have occurred in the nearshore community, and the potential consequences of these changes for chemical and biological processes at the whole-lake level, the 2012 Protocol specifically addresses the need to establish phosphorus and algal objectives for nearshore waters.

### The need for models

The 1978 GLWQA relied on numerical models to establish P concentration objectives for each of the Great Lakes, and the P loading rates required to achieve these objectives (Chapra, 1977; Chapra and Sonzogni, 1979). Parameterization of the models was based on measurements of specific processes in the lakes' carbon and phosphorus cycles, including loading and mass transfer coefficients. To meet the objectives of the 2012 Protocol, a similar approach is needed. Specific questions that models can help to address include: 1) the relationship between land-management practices and nutrient loads; 2) the relationship between nutrient loads and in-lake nutrient concentrations, with consideration for both pelagic and nearshore waters; 3) the phytoplankton and benthic algal response to in-lake nutrient concentrations, taking into account additional environmental variables that control algal growth and biomass, including sub-surface light and loss processes such as grazing; 4) the relationship between meteorology, hydrodynamics, sloughing, and fouling of shorelines and water intakes.

The resurgence of *Cladophora* in Lake Michigan appears to be primarily due to increased light penetration and interaction with dreissenid mussels (Auer et al., 2010; Brooks et al., 2014; Hecky et al., 2004; Higgins et al., 2008). Dreissenid mussels provide solid substrate for attachment, increase light penetration by filtering particulate material from the water column, and excrete bioavailable, dissolved phosphorus directly into the *Cladophora* canopy (Bootsma and Liao, 2013; Dayton et al., 2014; Ozersky et al., 2009). The fact that P loading has remained constant, or even decreased (Dolan and Chapra, 2012) while *Cladophora* biomass has remained high raises the question of how *Cladophora* growth and abundance might respond to any further reductions in phosphorus loading. While reduced phosphorus loading may result in lower dissolved P concentrations, it may also lead to lower phytoplankton concentrations and further increases in water clarity. Conversely, greater phytoplankton abundance that might result from increased P loading might lead to greater consumption and P recycling by dreissenids, but it could also negatively affect *Cladophora* growth by decreasing water clarity. While existing models appear to reliably simulate the direct response of *Cladophora* growth to temperature, light and dissolved phosphorus concentration (Higgins et al., 2005; Tomlinson et al., 2010), the physical and biogeochemical mechanisms linking P loading, phytoplankton

production, dreissenid mussel grazing, and *Cladophora* growth are currently not well enough understood to reliably predict the *Cladophora* response to changes in P loading. For example, both soluble nutrient (N and P) excretion and particulate nutrient egestion by dreissenids respond in a complex way to seston abundance and nutrient stoichiometry (Bootsma and Liao, 2013; Johengen et al., 2013). In the case of particulate (biodeposit) egestion, the long-term fate of egested material is not well understood; is it recycled and made bioavailable, or is it buried and permanently lost from the system? The same can be asked about P that is incorporated into dreissenid shells. Models will help to define the key processes that need to be parameterized, and further research into these key processes will help to structure and calibrate the models. These models can then be used to estimate *Cladophora* production on a lakewide scale, and ultimately help to predict potential trajectories in response to management actions that result in altered nutrient loads.

### Spatial resolution

Models are needed on various spatial scales, including lakewide (km scale), nearshore (m scale), and the benthic boundary layer (cm scale). Lakewide physical/biogeochemical models are needed to set boundary conditions for nearshore models. With regard to *Cladophora* distribution in the nearshore, some guidance on the necessary spatial scale is provided by comparison of satellite images at varying resolution. MODIS images (1000 m) resolve only the largest patches. MERIS (300 m) and Landsat (30 m) images reveal significant structure at smaller scales, and appear to be more appropriate for assessing *Cladophora* distribution (Shuchman et al., 2013). It may be possible to simulate *Cladophora* growth on a lakewide scale using biophysical models with resolution of ~0.5 km if appropriate sub-grid-scale parameterizations are developed, but if the objective is to assess local effects of inflowing rivers, lake currents, or local nutrient loads, higher resolution may be needed. Transport and mixing in the near-bottom layer, which includes mussels and a *Cladophora* mat of varying thickness, is a critical process that likely regulates mussel filter feeding and the fate of nutrients excreted by mussels (Bootsma and Liao, 2013). Explicit resolution of near-bottom processes in models requires a vertical resolution on the scale of cm, or a sub-grid-scale boundary layer parameterization.

### Temporal resolution

Models are needed at various temporal resolutions. Simulation of *Cladophora* growth in response to dynamic transport, light, and nutrient concentrations in the benthic boundary layer requires hourly resolution or higher. For physical models, temporal resolution will generally be scaled to spatial resolution, with ranges from seconds (near-bottom layer) to hours (whole-lake). The temporal resolution of biogeochemical (phosphorus dynamics) models will vary with the process and location being modeled, and will vary from seconds to days.

### Uncertainty and management targets

Predictive uncertainty of models should be sufficient to establish whether management objectives will be met. In earlier work conducted by Canale and Auer (1982b) on Lake Huron, it was found that beach esthetics were significantly improved when average *Cladophora* biomass was reduced from 150 to 75 g dry weight (DW) m<sup>-2</sup>. Whether or not this is an appropriate target for Lake Michigan is uncertain. Unlike the nuisance growth in the 1970s, which was localized and supported to a large degree by point nutrient sources, the current problem is widespread. Increased water clarity has also resulted in expansion of the *Cladophora* growth zone to greater depths, and so for a given areal density, the amount of *Cladophora* per meter of shoreline has likely increased, and densities of less than 50 g DW m<sup>-2</sup> may still lead to large accumulations of algae. Currently, peak summer *Cladophora* biomass in Lake

Michigan frequently exceeds  $200 \text{ g DW m}^{-2}$  (Bootsma et al., 2005). Even when peak summer biomass is  $\sim 100 \text{ g DW m}^{-2}$ , as it was in the summer of 2009 in the Milwaukee region of Lake Michigan, beach fouling is significant. Based on these observations, and the earlier observations of Canale and Auer (1982b) on Lake Huron, a reasonable biomass target of  $50 \text{ g DW m}^{-2}$  seems appropriate for Lake Michigan, in which case a predictive uncertainty of  $\leq 25 \text{ g DW m}^{-2}$  is desirable.

An alternate criterion that may be more relevant to shoreline fouling would be *Cladophora* biomass integrated from nearshore to offshore across the *Cladophora* growth zone, which would be expressed as biomass per unit shoreline length; this metric would capture the variation in the total area of *Cladophora* habitat with varying light penetration and nearshore bottom slope. Such a criterion would require a moderate increase in model complexity in comparison to modeling a specific depth (e.g. Tomlinson et al., 2010). However, monitoring of multiple depths across the *Cladophora* growth zone might require a significant increase in field sampling effort, depending on the method of sampling (see below). If a single depth is selected for monitoring, then a depth between 50% and 75% of the photosynthetic compensation depth would likely be most appropriate, as light at this depth is sufficient to support significant growth, while the confounding influence of turbulence and sloughing is less severe than at shallow depths.

## Existing models

### *Cladophora* growth models

The Great Lakes *Cladophora* Model (GLCM) is a mechanistic model that incorporates light, temperature, and phosphate (operationally defined as soluble reactive phosphorus, SRP) concentration to model *Cladophora* growth. The GLCM was first published in a series of papers in a 1982 special issue of Journal of Great Lakes Research on Ecology of Filamentous Algae (Auer and Canale, 1982; Canale and Auer, 1982a, 1982b), and was recently updated through comparison to additional field data from Lake Michigan (Auer et al., 2010; Tomlinson et al., 2010). The GLCM uses site-specific characteristics, including water depth, and requires input of environmental variables including incident photosynthetically active radiation (PAR), a vertical PAR extinction coefficient ( $K_e$ ), ambient SRP concentration, and water temperature. It is particularly helpful for understanding the impacts of varying SRP concentration on *Cladophora* growth, including the amount of biomass that will be produced at different depths. Several adaptations of this model, with slight differences in structure and parameters, have been used to simulate *Cladophora* dynamics in other regions of the Great Lakes (Higgins et al., 2005; Malkin et al., 2008; Painter and Jackson, 1989).

### *Dreissenid* mussel metabolism models

Numerous studies have highlighted the important role of dreissenids in Great Lakes nutrient dynamics (reviewed in Bootsma and Liao (2013)). However, while several studies have measured and modeled dreissenid bioenergetics (e.g., Madenjian, 1995; Stoeckmann, 2003), there has been limited inclusion of dreissenids in nutrient dynamic models. Several ecosystem models have accounted for nutrient cycling by dreissenids, but there is limited data on which to base the parameterization of these models (Bierman et al., 2005; Canale and Chapra, 2002; Madenjian, 1995; Padilla et al., 1996; Schneider, 1992; Zhang et al., 2008). An empirical model has been developed for Lake Michigan nearshore quagga mussels that simulates dissolved P excretion as a function of temperature, mussel size, and food concentration (Bootsma, 2009). The model and its supporting empirical data indicate that temperature has a large influence on mussel metabolism and nutrient excretion (Bootsma and Liao, 2013).

## Biophysical models

Biophysical models attempt to simulate the physical, chemical, and biological systems that control the response of *Cladophora* production to changes in environmental variables, including those that are specifically targeted by management, such as phosphorus concentration. These interactions are complex. Ambient water-column bioavailable P concentration is one of several variables that influence *Cladophora* growth, and the response of bioavailable P concentration to changes in total P load is not straightforward, as bioavailable P is actively taken up and excreted by various members of the ecosystem. Concurrent changes to the physical environment may retard or enhance the response of *Cladophora* to changes in nutrient loads. For example, the increase in light penetration associated with the dreissenid mussel invasion appears to have offset some of the gains that were achieved through reductions in P loading from the 1970s to the 1990s (Auer et al., 2010).

Biophysical models on the scale of an entire Great Lake have not had the spatial resolution to simulate the nearshore zone where *Cladophora* occurs. The LM3-Eutro model of Lake Michigan has been used to simulate the response of lakewide mean P concentration and phytoplankton to total P loads, and to evaluate the GLWQA P-loading targets under pre-dreissenid conditions (Pauer et al., 2008, 2011). More recent comparisons of model simulations with empirical data suggest that dreissenid grazing has increased the apparent settling velocity of total P, resulting in more efficient removal of P from Lake Michigan and other Great Lakes (Chapra and Dolan, 2012). The spatial resolution of LM3-Eutro (5-km rectilinear grid) provides for limited resolution of the nearshore zone. A Saginaw Bay water quality model has simulated the role of dreissenid mussels in triggering cyanobacterial blooms (Bierman et al., 2005). More recently, Verhamme et al. (2013) have updated this model by including *Cladophora* and constructing a nested hydrodynamic model, with a high-resolution grid (500 m) inside the bay and boundary conditions provided by a coarse-resolution, hydrodynamic model of Lake Huron. In addition, Leon et al. (2012) described an implementation of the ELCOM-CAEDYM hydrodynamic-water quality model for Lake Ontario with a nested nearshore grid at 100-m resolution covering 9 km of shoreline near Pickering, Ontario. This model simulated many of the variables that control nearshore *Cladophora* growth, and could be expanded to simulate *Cladophora* in future work.

### Nutrient loading models

Estimates of historical nutrient loads are required for calibration and validation of biophysical models, but the load estimates themselves must be regarded as a model product. Tributary nutrient loads (units of mass per time) are calculated as the product of volumetric discharge and nutrient concentration, integrated over time. Estimates are required for point sources (e.g. wastewater treatment plants) and for non-point sources (rivers and streams). Point source loads are reported by regulated sources, and are compiled in USEPA Permit Compliance System (PCS) and Integrated Compliance Information System (ICIS) databases. Load estimates for rivers and streams rely on discharge data, much of which is available through the US Geological Survey stream gage network. Nutrient concentration measurements, which are made by federal, state, and local agencies, are much less abundant. In some cases, concentration measurements are compiled in the USEPA STORET database, but many isolated databases exist which makes estimates of lakewide nutrient loads a challenging and labor-intensive task. Further capture and integration of these disparate data sources are clearly needed.

Empirical models are used to fill temporal and spatial data gaps in order to estimate historical nutrient loads. Nutrient concentrations vary in a complex manner as a function of hydrologic variables, so empirical models are used to construct concentration-discharge relationships in order to make loading calculations. Dolan and Chapra (2012) estimated lakewide phosphorus loads for Lake Michigan for 1994–2008 using a

stratified Beale ratio estimator method to construct concentration–discharge relationships, and a unit area load method to estimate contributions from unmonitored areas. They also used models to estimate inter-lake transfer. Robertson and Saad (2011) estimated a long-term annual mean total P and total N load to Lake Michigan, using regression models of concentration–discharge relationships and the SPARROW model to estimate loads from unmonitored areas.

Predictive nutrient loading models vary from empirical regression-based models to mechanistic simulation models. The SPARROW model is a regression-based model that represents transfer of nutrient loads down a stream network, modified by point and non-point source contributions in stream segments. A SPARROW model was calibrated for the US portion of the Great Lakes, and is capable of predicting the response of long-term annual mean nutrient loads to changes in land use and point sources (Robertson and Saad, 2011). The SPARROW model focuses on the effect of land use variables, and is not capable of predicting temporal variation in loads in response to hydrologic variables. Mechanistic simulation models have the capability to predict runoff and nutrient loads at the watershed scale at annual, monthly, and daily time scales. Several popular models, including SWAT, HSPF, and DWSM were reviewed by Borah and Bera (2004); when properly calibrated, the models simulated annual and monthly nutrient and sediment loads reasonably well, but were challenged to simulate daily loads or extreme events. Other models that have been used by and are available through the EPA include the Loading Simulation Program in C++ (LSPC), which is tailored for determining TMDLs, the Storm Water Management Model (SWMM) which is applied primarily to urban areas, the Watershed Assessment Model (WAM), and the Watershed Analysis Risk Management Framework (WARMF). At finer spatial scales, field-specific phosphorus runoff from agricultural land can be estimated using the Phosphorus Index, which is calculated based on soil P content, soil type, cultivation practices, and land slope (e.g., Good et al., 2012). Watershed models vary greatly in their constructs, which often limits their applicability to specific spatial and temporal scales. For example, models that work well on the field scale or for single events may not estimate annual loads or basin-scale loads well, and vice-versa (Daniel et al., 2011). Watershed models of all types require detailed data on land cover, agricultural practices, point sources, as well as nutrient concentrations and loads, for calibration, validation, and predictions, which makes monitoring a necessity for the production of both historical and predicted nutrient loads.

#### Remote sensing

Satellite remote sensing has been applied to estimate the recent and historical distribution of *Cladophora*, information that is required for calibration and validation of lakewide biophysical models. Retrieval of *Cladophora* abundance from satellite-based spectral radiance observations is itself a product of a complex model of light transmission through the atmosphere and water column, and reflectance off the lake bottom. *Cladophora* mapping of the nearshore, optically visible zones of the lower four Laurentian Great Lakes has been completed using recent Landsat satellite imagery (Shuchman et al., 2013). While the vegetation identified in satellite imagery consists primarily of *Cladophora*, it may also include localized areas of vascular plants, other filamentous macroalgae, and diatoms, and so it is referred to as submerged aquatic vegetation (SAV). Extensions from this work enabled mapping and analysis of changing extent of SAV from c. 1975 to c. 2010 at five year intervals (Brooks et al., 2014). Fig. 1 shows an example of the *Cladophora*/SAV mapping results for all of Lake Michigan. The map, which has a 30-m resolution, was generated using Landsat satellite data from 2008 to 2011 collected during the vegetative growing season (late April–

September). SAV can be seen in northern Lake Michigan, with generally lower amounts mapped in the southern portion of the lake. The total area of optically shallow water mapped was approximately 4390 km<sup>2</sup>, of which 28% was mapped as SAV. Similar maps are available for all the optically visible areas of the lower four Great Lakes (Michigan, Huron, Erie, and Ontario, [www.mtri.org/cladophora.html](http://www.mtri.org/cladophora.html); Brooks et al., 2014). *Cladophora* is not currently a significant issue in Lake Superior.

Satellite remote sensing offers the advantage of wide areal coverage of the Great Lakes; however, accurate quantification of *Cladophora* biomass and fine temporal resolution remain a challenge. Both Shuchman et al. (2013) and Brooks et al. (2014) demonstrated how reasonable values of *Cladophora* dry-weight-per-square-meter can be linked to remote sensing aerial extents to estimate SAV biomass. In Shuchman et al. (2013) a Lake Michigan analysis was completed using an average of 50 g DW m<sup>-2</sup> with an assumption that 90% of the total biomass was visible to create a nominal estimate of the dry weight biomass of the SAV at 67 metric kilotons. In Brooks et al., 2014, these methods were extended by using the 50 g DW m<sup>-2</sup> as the nominal biomass estimate and 100 g DW m<sup>-2</sup> as an upper bound based on published and unpublished data. The Great Lakes *Cladophora* Model (GLCM) was used to estimate that the percentage of annual net production of *Cladophora* that is observable by Landsat is 90% or greater with a bottom detection depth limit (BDDL) of 20 m and similar (80%) with other BDDL values seen in the Great Lakes; scaling can account for areas beyond the Landsat BDDL. With these input values, dry biomass estimates of SAV for the current (c. 2011) time period were calculated for Lake Michigan at 61 metric kilotons, Lake Huron at 33 kt, Lake Erie at 8 kt, and Lake Ontario at 16 kt.

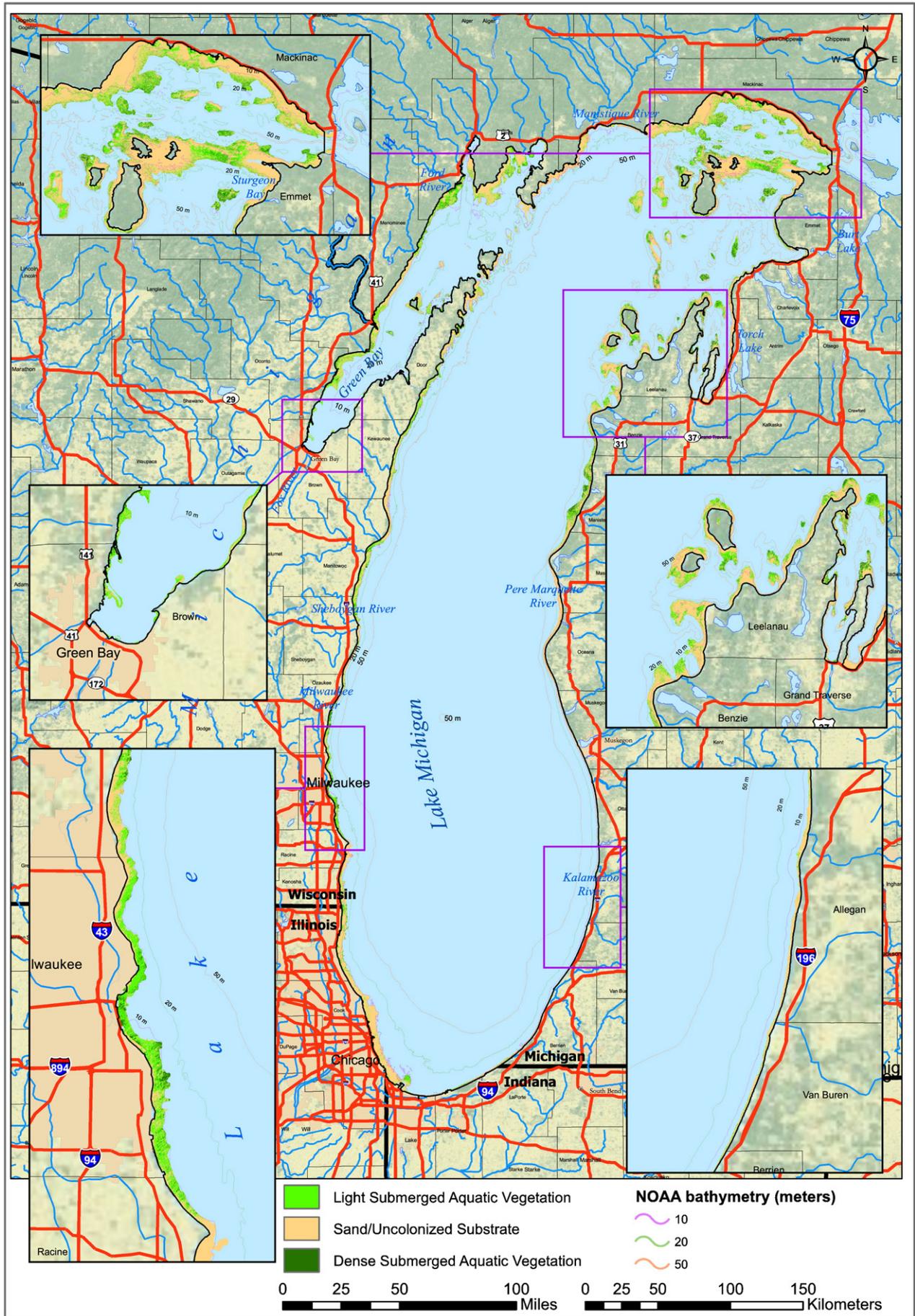
These estimates, however, are only as useful as the input values used to determine them, such as the nominal per unit area biomass values, fraction of SAV detected, GLCM model input values, and a Secchi disk transparency to BDDL relationship. Additional in situ monitoring is needed to test and improve the reliability of the remote sensing to biomass estimation relationship. Remote sensing products do not eliminate the need for in situ monitoring, but they extend the value of these observations and help fill in extent information for time periods and locations when in situ data were not available.

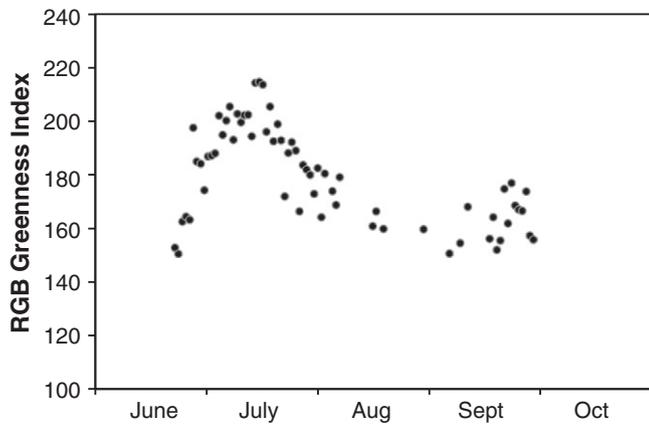
In-lake sensing methods offer the potential for greater spatial resolution than satellite remote sensing. Depew et al. (2009) evaluated the potential of a high-frequency echo-sounder for quantification of *Cladophora* distribution. Commercially-available automated signal processing software was found to give poor results over uneven bottom substrate, but interpretation by an analyst produced more accurate results. The method was successful in detecting presence of *Cladophora* at a nuisance-level, with a detection limit of ~7.5 cm bed height, or about 40% detection rate at 100 g m<sup>-2</sup> biomass (their Fig. 5). More recently, Bootsma et al. (unpubl.) have used in situ time lapse imagery to monitor *Cladophora* biomass at one-hour intervals throughout the growing season. Additional benthic samples are required to calibrate these images, but a simple analysis of image color indicates that this approach holds promise for monitoring benthic algal biomass (Fig. 2).

#### Modeling opportunities

##### *Cladophora* growth models

As outlined above, a number of models have been developed to simulate *Cladophora* dynamics in Lake Michigan and the other Great Lakes. These models work reasonably well when supported with empirical measurements of light, temperature and dissolved P concentration. However, they have not been linked to whole-lake biophysical models,





**Fig. 2.** Lake bottom “greenness” as determined by analysis of the red, green and blue bands in digital images. Images were collected with a digital SLR camera (50 mm lens) positioned approximately 1 m above the lake bottom (9 m depth), pointed downward at an angle of  $\sim 30^\circ$  below horizontal. One mid-day image was used for each day, and images collected on high-turbidity days were removed from the analysis.

and so there remains uncertainty about how *Cladophora* will respond to changes in external nutrient loading or internal nutrient cycling. At the whole-lake scale, models will need to account for profundal dreissenid mussels, which appear to be an important conduit for energy flow and nutrient cycling (Vanderploeg et al., 2010). Several processes will need to be quantified and parameterized, including grazing rates, dissolved nutrient excretion, nutrient egestion (as feces and pseudofeces), the long-term fate of nutrients in feces and pseudofeces, and the exchange of particulate and dissolved nutrients between the hypolimnion and epilimnion.

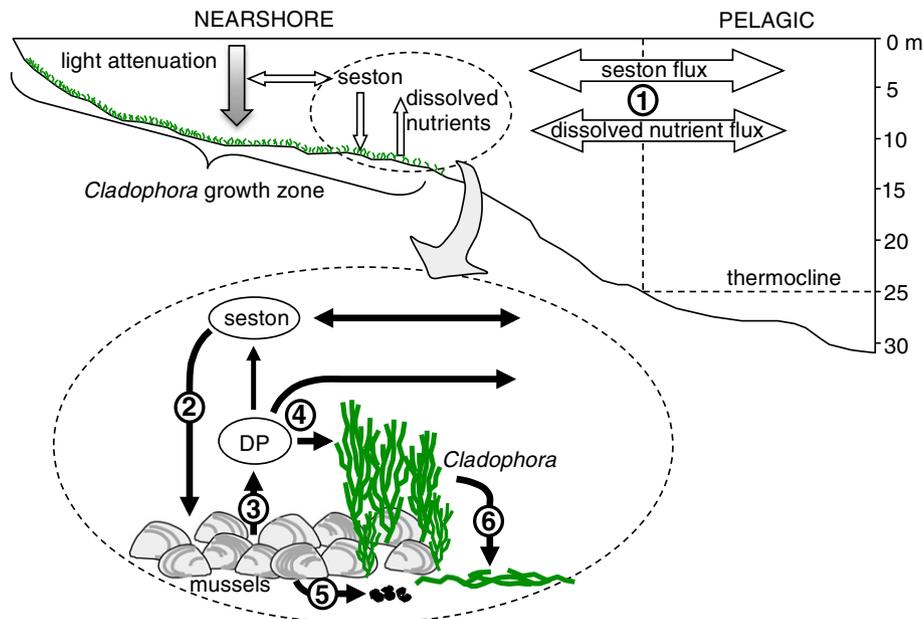
Within the nearshore zone, it will be necessary to develop a biogeochemical model that accounts for the major carbon and phosphorus cycling processes in this zone (Fig. 3). A first step might be to expand the *Cladophora* model to include SRP and irradiance as state variables. *Cladophora* itself may be an important regulator of nearshore SRP concentration, and so models that simulate the *Cladophora* response to changes in P loading and P concentration will need to account for

any feedbacks between phosphorus concentration and *Cladophora*. Inclusion of SRP as a state variable will also require accounting for P excretion by dreissenids, and the modulation of the dreissenid – *Cladophora* nutrient link by near-bottom mixing (see below). Simulation of benthic irradiance will require that the processes affecting light attenuation, including sediment resuspension and phytoplankton growth, be included in models.

The timing and magnitude of *Cladophora* sloughing have significant implications for beach esthetics, the clogging of water intakes, and in-lake biological processes, which may include outbreaks of avian botulism (Lafrancois et al., 2011). Current models use several approaches to simulate sloughing, with the process being driven by some combination of *Cladophora* standing biomass, turbulence (determined from wind speed and depth), water temperature, and algal physiological condition (Canale et al., 1983; Higgins et al., 2005, 2006; Tomlinson et al., 2010). Accurate simulation can be challenging, in part because it is difficult to design lab experiments to observe sloughing, and because there are limited in situ data that accurately record the timing and magnitude of sloughing as well as the multiple variables that may influence this process. In addition to modeling of the sloughing process, there is a need to account for the transport and fate of *Cladophora* after sloughing. In some parts of the lake, *Cladophora* likely represents a significant fraction of total biomass and nutrients, and the long-term fate of this material may have implications for whole-lake nutrient cycling and trophic dynamics (Turschak et al., 2014).

#### Remote sensing

Remote sensing can provide inputs to *Cladophora* growth models, including spatial locations of suitable habitat, water clarity, and temperature, which can be used to predict *Cladophora* production under different P concentration scenarios (Shuchman et al., 2013). Bathymetric water depth values can also be calculated using satellite imagery (Lyzenga et al. 2006) and LiDAR (Light Detection and Ranging) data (Irish et al., 2000), which can improve biomass modeling by providing depth values at higher resolution than historical bathymetry data. The production rate of *Cladophora* is the appropriate model output variable because it is production, not standing crop, that leads to accumulation on beaches (Auer et al., 2010). In combination with hydrodynamic modeling, growth



**Fig. 3.** Conceptual model of nearshore carbon and nutrient dynamics. Specific processes of importance include: 1. Exchange of dissolved and particulate nutrients between the nearshore and pelagic; 2. Seston grazing by mussels, with influence on light attenuation; 3. Dissolved P excretion by mussels; 4. Fate of excreted dissolved P (uptake by *Cladophora* vs dilution in water column); 5. Formation and long-term fate of mussel biodeposits; 6. *Cladophora* sloughing and fate of sloughed *Cladophora*.

models forced by remote sensing inputs can help to reveal the origin and destination of sloughing events. Continued monitoring of SAV (most often *Cladophora*) by remote sensing will provide an opportunity to evaluate the impacts of any future P control interventions (Brooks et al., 2014). Successful detection of changes over time by remote sensing will depend on the magnitude of changes relative to the accuracy of remote sensing data products. Ongoing in situ monitoring is needed to confirm remote sensing observations.

#### Biophysical models

Biophysical models have previously worked reasonably well to simulate pelagic nutrient and plankton dynamics, but there is evidence that these models now need to be revised to account for dreissenid impacts on the phosphorus cycle (e.g., Chapra and Dolan, 2012). Models that attempt to simulate the relationship between P loading and *Cladophora* production will need to account for several critical processes: 1) Nearshore–offshore exchange, 2) turbulence in the benthic boundary layer, 3) stratification and vertical mixing in the water column, and 4) nutrient processing by profundal dreissenid mussels (Fig. 3).

Hydrodynamic mixing between the nearshore and offshore has a controlling influence on nearshore nutrient concentrations. Nutrients entering the lake must first pass through the nearshore zone. Retention times within this zone will determine the extent to which *Cladophora* responds directly to nutrient loads. Modeling of nearshore nutrient dynamics in Lake Ontario indicates that local nutrient loading can result in brief periods of localized, high nutrient concentrations that *Cladophora* may be able to take advantage of (Leon et al., 2012), which is supported by the spatial *Cladophora* patterns observed by Higgins et al. (2012). At the same time, *Cladophora* biomass is high throughout much of Lake Michigan, even in areas remote from river mouths. For example, *Cladophora* biomass in the nearshore waters of Sleeping Bear National Lakeshore in northern Lake Michigan, including South and North Manitou Islands, can exceed 200 g DW m<sup>-2</sup> (Bootsma, unpubl.). Without a major local nutrient input, *Cladophora* growth in these regions must rely on a supply of P from pelagic waters. The degree of reliance on river nutrient loading vs. recycling within the lake will determine the time scales and magnitude of *Cladophora* response to any changes in external P loading, and this will be influenced primarily by nearshore–offshore exchange rates, especially during May–July, when most *Cladophora* growth occurs.

The ability to resolve nearshore hydrodynamic processes in whole-lake hydrodynamic models may be improved through the use of unstructured grid hydrodynamic models, such as the Finite Volume Coastal Ocean Model (FVCOM). FVCOM uses an unstructured triangular mesh grid that allows for realistic representation of the coastline and higher spatial resolution in the nearshore while maintaining coarser resolution offshore for computational efficiency (Luo et al., 2012). The FVCOM model package includes an online-coupled ecological model, and has been linked offline to biogeochemical water quality models, including CE-QUAL-ICM (Khangaonkar et al., 2012) and RCA (Xue et al., 2012). FVCOM was combined with a 1-D biological model to simulate the impact of quagga mussels on the spring phytoplankton bloom in Lake Michigan (Rowe et al., 2015).

When incorporating *Cladophora* models into larger ecosystem models that account for mussel nutrient cycling and plankton dynamics, it will also be necessary to account for vertical mixing throughout the entire water column in the nearshore zone as this will influence the delivery rate of food particles to mussels (Ackerman et al., 2001; Boegman et al., 2008), which in turn will affect mussel nutrient excretion and supply to *Cladophora*. Hydrodynamic simulations in Lake Michigan have largely focused on general circulation and the summer thermal structure of offshore waters (e.g., Beletsky et al., 2006). Less attention has been focused on simulation of thermal structure in the nearshore zone. Stratification within this zone is more variable than in the open waters of Lake Michigan; the water column may be stratified or mixed to the bottom in the summer at depths <30 m, depending on downwelling,

upwelling, wind-driven mixing, and internal waves. In winter, stratification can develop when surface temperature drops below 4 °C, but the weak stratification that results is more easily eroded than the stronger summer stratification (Rowe et al., 2015). During the summer stratified season, internal waves cause the location of the intersection of the thermocline with the bottom to oscillate, subjecting benthic organisms to large temperature fluctuations (Wells and Parker, 2010). Internal waves are responsible for much of the near-bottom turbulence during the stratified period (Hawley, 2004). To simulate the nearshore physical environment in which *Cladophora* and dreissenid mussels live, hydrodynamic simulations will require greater focus on nearshore phenomena than in the past, with sufficient spatial resolution to resolve the nearshore. Associated nearshore monitoring data will be required for nearshore model development at all months of the year.

Near-bottom mixing is important in determining nutrient concentrations within the *Cladophora* canopy, and also for delivery of food particles to dreissenid mussels. While dreissenids are major recyclers of nutrients in Lake Michigan and the other Great Lakes, the degree to which *Cladophora* can access these nutrients depends on near-bottom mixing. The time scale of vertical mixing versus that of *Cladophora* nutrient uptake determines whether mussel-excreted nutrients are assimilated by *Cladophora* or mixed into the water column (Bootsma and Liao, 2013; Dayton et al., 2014). In addition to accounting for this relationship, models should ideally be able to simulate near-bottom turbulence as a function of easily measured variables, which may include wind speed, wave height, and current speed. Bottom roughness and density of the *Cladophora* mat may also be important. Dayton et al. (2014) measured vertical profiles of SRP concentration in the benthic boundary layer over a *Cladophora* colonized mussel bed in northern Lake Michigan, and developed a 1-dimensional model to simulate SRP concentration within 1 cm of the bottom; such models could provide the basis for a benthic boundary layer parameterization within a larger 3-dimensional water quality model.

#### Need for observational data to support modeling

Observational data are needed to provide calibration and validation data sets, and model input variables. A significant data gap is the lack of an ongoing in situ *Cladophora* monitoring program in Lake Michigan. Apart from remote sensing (Brooks et al., 2014), there are currently three sites where monitoring is conducted with varying degrees of intensity: Atwater Beach near Milwaukee (University of Wisconsin-Milwaukee), Sleeping Bear Dunes National Lakeshore (National Park Services and UW-Milwaukee), and Keweenaw (Wisconsin Department of Natural Resources). Continuous monitoring of *Cladophora* biomass at multiple, representative, sites in Lake Michigan would be invaluable for ongoing development of modeling and remote sensing tools. In regional and lake-wide models, measurements of the critical variables for *Cladophora* growth are needed to drive and evaluate the models, including depth-dependent PAR, dissolved and particulate P concentrations, water temperature, currents, and wave height. Mapping of bottom habitat suitable for mussel and *Cladophora* growth is required to establish the maximum possible spatial extent of *Cladophora* colonization. Measurements of gross and net photosynthesis, *Cladophora* biomass, and *Cladophora* tissue P content are required for validation of *Cladophora* growth models (Auer et al., 2010). It is important to quantify the conditions of benthic shear stress and *Cladophora* growth status under which sloughing occurs in order to include this phenomenon in biophysical models. Because sloughing is a complex process that is difficult to test experimentally, in situ observations of *Cladophora* biomass and environmental variables with high temporal resolution are required to improve the sloughing component of models. To simulate interaction with dreissenid mussels, monitoring of mussel biomass distribution is needed in addition to process variables including the biomass-specific filtering rates of mussels, and excretion of SRP and other forms of nutrients. In addition, it is necessary to quantify the

dynamics of SRP concentration in the benthic boundary layer and within the *Cladophora* canopy. It may be possible to characterize some of these processes through experimentation, but in situ observations that account for the full physical and biogeochemical complexity of the natural environment will be necessary to validate model parameterizations derived from experiments.

These measurements, as well as turbidity, in situ irradiance, phytoplankton concentration, currents, waves and meteorological variables can also be made with in situ sensors. However, field sampling and laboratory analyses are also critical, especially for ambient nutrient concentrations, biomass of *Cladophora* and other benthic biota, and *Cladophora* P content. Other less conventional measurements may also be useful. For example, stable carbon isotope ratios may serve as an index of algal growth rate (MacLeod and Barton, 1998), and stable nitrogen isotopes may provide insights regarding the sources of nutrients that support algal growth (Lapointe, 1997). Ideally, monitoring should be conducted at sites representing a range of chemical and physical conditions, with priority given to sites where impacts on human uses or ecosystem function are particularly severe.

## Conclusions

Achieving the objectives of the Great Lakes Water Quality Protocol of 2012 for Lake Michigan will require an improved understanding of nutrient dynamics within the nearshore zone, and how nearshore processes affect the lake as a whole. Hecky et al. (2004) have highlighted several processes that need to be better understood to achieve these goals. These include the direct transfer of dissolved P between mussels and *Cladophora*, the long-term fate of dreissenid biodeposits, potential negative effects of *Cladophora* on dreissenid grazing, and the fate of sloughed *Cladophora* within the context of nutrient cycling and trophic dynamics. From a management perspective, there are several broader questions that we would add, and which models can help to address:

1. Should phosphorus target concentrations be the same for the nearshore and pelagic zones? The decline in plankton abundance in the pelagic zone has implications for the entire food web. Planktivorous fish abundance has declined over the past decade, although the extent to which this is linked to dreissenid mussels and nutrient loads is not clear (Bunnell et al., 2009, 2013). While reduced P loads may have a positive effect in controlling nearshore *Cladophora* growth, they may exacerbate the declines in plankton abundance and pelagic fish species. Previously, reduced nutrient loads benefited the entire ecosystem. Now, managers are faced with a conundrum, as there may not be a P loading target that is ideal for both the nearshore and pelagic zones.
2. What are the phosphorus loads that correspond with target concentrations? There is evidence that the relationship between loading and concentration has changed for the pelagic zone (Chapra and Dolan, 2012). Less is known about long-term phosphorus trends in the nearshore zone, and how nearshore phosphorus concentrations are influenced by proximity to river mouths, nearshore currents, and nearshore-offshore mixing.
3. If both nearshore and pelagic phosphorus targets cannot be achieved with the same phosphorus load, how will phosphorus and algae concentrations within each of these zones respond to various phosphorus loading scenarios? Managers may need to make difficult decisions that require compromise between pelagic and nearshore objectives. Models may help to guide these decisions.
4. What will the long-term, steady state conditions be with regard to nearshore and pelagic phosphorus concentration, phytoplankton production, *Cladophora* production, and mussel biomass? Lake Michigan continues to be in a state of transition. Mussel biomass in shallow waters may be declining, while deeper populations continue to grow (Nalepa et al., 2010). If nearshore populations decline, what are the

implications for *Cladophora*? With a phosphorus residence of 5 years or longer, the lake can be expected to exhibit a delayed response to changes in external loading and internal cycling.

For the past five decades, the conventional response to nuisance algal growth has been nutrient management, with the lake being considered as a single, uniform system. This approach has been largely successful. However, Lake Michigan and the other lower Great Lakes appear to be functioning under a new paradigm. We now know that there are fundamental differences between the nearshore and pelagic with regard to nutrient cycling and energy flow. The previous reductions in P loading have come with a significant cost, and further reductions are likely to be more expensive. A quantitative prediction of the response of both nearshore *Cladophora* and pelagic phytoplankton to P load reductions is necessary to determine whether acceptable *Cladophora* growth is achievable, and if so, at what cost. Further research is needed to understand this new paradigm, and numerical models will help to translate this new understanding into tools that are useful for managers.

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