

**Water Quality Management Options
to Control *Cladophora* Growth in the Milwaukee Region
of Lake Michigan**

Final Report

**MMSD Contract M03002P15
Amendment No. 1**

Harvey A. Bootsma¹, Erica B. Young²,
and John A. Berges²

¹Great Lakes WATER Institute
University of Wisconsin-Milwaukee
600 E. Greenfield Ave.
Milwaukee, WI 53204

²Department of Biological Sciences
University of Wisconsin-Milwaukee

For the Milwaukee Metropolitan Sewerage District

May 6, 2008

Table of Contents

Terminology	3
1. Executive Summary	5
2. Purpose	7
3. Spatial variation of <i>Cladophora</i> in relation to river P loading	8
3.1 Background and methods	8
3.2 Results	11
3.3 Discussion and conclusions	23
4. Phosphorus supply from dreissenid mussels	27
4.1 Experimental methods.....	27
4.2 Results	29
4.2.1 Effect of mussel size on P recycling	29
4.2.2 Effect of food supply and food quality on mussel P recycling	31
4.2.3 Effect of temperature on mussel P recycling	35
4.2.4 Quagga mussel P excretion model application.....	37
4.2.5 Putting mussel phosphorus excretion into perspective.....	39
5. A <i>Cladophora</i> model.....	44
5.1 Factors responsible for the resurgence of <i>Cladophora</i>	47
5.2 Can <i>Cladophora</i> be managed through phosphorus control?	52
6. Conclusions.....	61
7. Literature cited	64
Appendix I. The new <i>Cladophora</i> model: development, testing, and application to Lake Michigan	66

Acknowledgments

The data presented in this report was collected through field and laboratory studies conducted with the support of a number of students and technicians. We are particularly grateful for the assistance of Mr. Geoff Anderson, Ms. Stacey Faude, Ms. Lori Pansch, Ms. Rebecca Tucker, and Mr. Kendrick Wall, all of whom were a pleasure to work with. Mr. Chris Magruder and Mr. Eric Waldmer kindly provided historic water quality data from MMSD. This report benefited greatly from constructive reviews by Mr. Chris Magruder.

Terminology

Phosphorus is a nutrient that plays a critical role in the dynamics of *Cladophora* and other algae in Lake Michigan. Therefore an understanding of the *Cladophora* problem requires an understanding of phosphorus dynamics. Phosphorus occurs in numerous forms in aquatic ecosystems. In the literature, the nomenclature for these different forms is not always consistent, and this can lead to confusion when comparing different reports. Below is a summary of the phosphorus terminology used in this report, with a definition of each term.

Phosphorus (P). A nonmetallic element with a molecular weight of 30.97 g mol^{-1} . It is required by all bacterial, plant and animal life. In many temperate lakes, including Lake Michigan, phosphorus is the nutrient that is present in the lowest concentration relative to the demand by algae. Therefore phosphorus is referred to as a “limiting nutrient” in these lakes.

Total Phosphorus (TP). This includes all forms of phosphorus. From both a functional and an analytical perspective, total phosphorus can be divided into two main categories – particulate and dissolved.

Particulate Phosphorus (PP). This is the phosphorus present in particulate material that is collected on a filter. The definition of “particulate” depends on the pore size of the filter that is used. In this study, all filtration was done using Whatman GF/F glass fiber filters, which have a nominal pore size of about $0.7 \mu\text{m}$. Particulate phosphorus may include organic phosphorus within organic detritus, mineral phosphorus resulting from precipitation (often with iron or calcium), and phosphorus that is adsorbed onto the surfaces of particles. PP is measured by combusting filtered samples, followed by digestion in acid to convert all P to PO_4^{3-} (orthophosphate), which is measured using the molybdate method.

Total Dissolved Phosphorus (TDP). For the purpose of this study, TDP is all phosphorus that passes through a filter with a $0.7 \mu\text{m}$ pore size. It includes both dissolved organic phosphorus and dissolved inorganic phosphorus. TDP is measured by photo-oxidizing water samples under acidic conditions in the presence of peroxide, which converts all P to PO_4^{3-} . Total dissolved phosphorus is sometimes referred to simply as **dissolved phosphorus (DP)**.

Soluble Reactive Phosphorus (SRP). This is dissolved phosphorus that is measured by reaction with molybdate (the reaction produces a blue color, which is measured using a spectrophotometer). This method was designed to measure the orthophosphate ion (PO_4^{3-}), which is the form of phosphorus that is most directly available to algae. However, the analytical procedure may result in the hydrolysis of some organic phosphorus to PO_4^{3-} , which can result in an overestimate of the PO_4^{3-} concentration. Therefore, while the method is believed to provide an estimate of the amount of dissolved phosphorus that is directly available to algae, in practice it is more correct to refer to the measured form of phosphorus as soluble reactive phosphorus.

Dissolved Organic Phosphorus (DOP). Dissolved organic phosphorus may include a large suite of phosphorus-containing molecules that either leach from or are excreted by biota, including nucleic acids, phosphoproteins, phosphate esters, and nucleotide phosphates (ADP, ATP). Some algae, including *Cladophora*, are capable of utilizing DOP by producing an enzyme, **alkaline phosphatase**, which hydrolyses organic phosphorus to produce PO_4^{3-} , which is then taken up and assimilated. DOP concentration is usually determined indirectly, by subtracting the SRP concentration from the TDP concentration.

Tissue Phosphorus. This refers to the phosphorus concentration within algae tissues, sometimes called the internal P content. It is a useful measurement because it directly controls algae growth rates. It is usually presented with units of $\mu\text{g P mgDW}^{-1}$, where mgDW is the milligrams of dry weight of *Cladophora*. Some literature uses units of %. The % P content is equal to $\mu\text{g P mgDW}^{-1}$ divided by 10. Tissue phosphorus is sometimes referred to as the **cell phosphorus quota**, designated as **Q**.

1. Executive Summary

This report contains the results of Phase II of a study to determine causes of, and potential management options for excessive growth of the filamentous green algae, *Cladophora* sp., in the Milwaukee region of Lake Michigan. In addition to assessing the factors that influence *Cladophora* growth and biomass, this study included the development of a quagga mussel (*Dreissena bugensis*) model that simulated soluble reactive phosphorus (SRP) excretion by mussels as a function of water temperature, mussel size, and food concentration (the model focuses on the quagga mussel because this species has now largely replaced the zebra mussel, *Dreissena polymorpha*, in Lake Michigan). In addition, a *Cladophora* model was parameterized for Lake Michigan, and a graphical user interface was developed which allows for simple data entry and manipulation of the model to test management scenarios. Both the mussel model and *Cladophora* model were validated with in situ measurements made in Lake Michigan, and both models appear to simulate *in situ* conditions reasonably well.

Phase I of this study confirmed that *Cladophora* growth and biomass are controlled to a large degree by the availability of soluble reactive phosphorus, and therefore management of *Cladophora* requires knowledge of the sources of phosphorus to the lake's nearshore zone, and how phosphorus is cycled within this zone. In Phase II of this study, laboratory and field studies indicate that soluble reactive phosphorus (SRP) excretion by quagga mussels depends both on food supply and water temperature, with excretion rates rapidly increasing when temperature exceeds 12°C (59°F). As a result, moderate increases in nearshore temperatures in summer may result in large increases in P excretion by mussels. The mussel P excretion model was used, along with data on mussel size distribution, mussel densities, and nearshore distribution, to estimate the P loading to the Lake Michigan nearshore zone resulting from mussel metabolism. For the Wind Point to Fox Point stretch of shoreline, it is estimated that mussels excrete SRP at a rate more than 4 times greater than the loading rate from the mouth of the Milwaukee River. Therefore, efforts to control *Cladophora* growth through the reduction of nearshore P concentrations must consider reducing the availability of food for mussels. This food is provided both as particulate material that enters the lake directly from rivers, and as plankton which grows in offshore waters and is mixed into the nearshore zone. The relative importance of these two pathways is not yet known, but it will determine the rate at which phosphorus concentrations and *Cladophora* biomass in the nearshore zone respond to decreased nutrient load.

While quagga mussels are the major source of SRP for most of the nearshore zone, our study of the spatial distribution of algal phosphorus content and alkaline phosphatase activity indicates that, in close proximity (less than 5 km [3 miles]) to river mouths, river loading of P has a significant impact on *Cladophora*, and therefore reduced P loads should have an immediate, if modest, impact on *Cladophora* abundance near river mouths. Long-shore transect surveys suggest that nutrient discharge from the Milwaukee Harbor is rapidly dispersed and will likely only stimulate *Cladophora* growth in areas less than 2.5 km from the harbor outlets.

Historic (pre-mussel) and recent data were used as input to the *Cladophora* model to determine which factors are responsible for the *Cladophora* increase. The model indicates that increased nearshore dissolved phosphorus concentration is partly responsible for increased algal abundance, but the most important factor has been the increase in water clarity resulting from filter feeding by zebra and quagga mussels. Increased clarity has resulted in increased light intensities on the lake bottom, allowing for more *Cladophora* growth at shallow depths and for a 2-fold increase in the depth range of *Cladophora*, from a maximum depth of about 5 m prior to the mussel invasion to a current maximum depth of 11 to 12 m. It is this depth extension that is primarily responsible for increased algal biomass per unit of shoreline.

Although increased water clarity is the primary cause of increased *Cladophora* abundance, the only practical management option is to reduce in-lake dissolved phosphorus concentrations. In moderate to high-nutrient areas (i.e. where SRP concentrations are frequently greater than $1.0 \mu\text{g L}^{-1}$), such as nearshore areas close to river mouths, a 50% decrease in soluble reactive phosphorus concentrations will likely result in modest *Cladophora* biomass reductions of 25% or less. In nearshore areas where soluble reactive phosphorus concentrations are already relatively low (less than $1 \mu\text{g L}^{-1}$), a 50% decrease may result in *Cladophora* biomass reductions of as much as 74%, depending on depth, with greater proportional reductions occurring at deeper depths.

Because many of the obvious steps to reduce phosphorus loads have already been taken over the past three decades, further reductions will be a challenge. Agricultural sources can best be managed by focusing on “hot spots” where phosphorus concentrations are high and/or runoff and erosion are excessive. For the Milwaukee River there are also significant industrial point sources of phosphorus that can be considered. Much of the phosphorus uptake by *Cladophora* occurs between May and early July, and therefore phosphorus reduction efforts will be most effective if they focus on the April – June period. While *Cladophora* in areas near river mouths may respond quickly to any changes in river nutrient loads, large reductions in *Cladophora* abundance will only occur when the rate of phosphorus flow through the mussel filter feeding – excretion pathway (the nearshore “phosphorus shunt”) is attenuated. This pathway is controlled by offshore plankton production and physical nearshore – offshore exchange rates, which are currently not well quantified. Because plankton production is influenced by dissolved phosphorus concentrations in offshore waters, and because these concentrations respond slowly to changing river loads, there will be a lag time of 5 to 10 years between decreased phosphorus loads and significant *Cladophora* response.

2. Purpose

The Milwaukee Metropolitan Sewerage District (MMSD) has recently completed its Facility Planning effort for the year 2020. This planning effort is utilizing a comprehensive watershed-based approach to evaluate questions and provide answers regarding the impacts to water quality and the benefits of potential improvements to the MMSD's wastewater collection, conveyance, treatment and watercourse systems. The 2020 Facility Planning effort needs answers to questions that deal with a broad range of water quality issues, including those of nuisance algal growth in area waterways. Currently there is public concern regarding nuisance growth of the filamentous green alga, *Cladophora* sp., along Milwaukee's lakeshore. Excessive growth of this algae results in aesthetic degradation of beaches and other shorelines, potential health risks, clogging of water intakes, and alteration of the Lake Michigan nearshore ecosystem.

An initial study of the *Cladophora* problem was conducted by the University of Wisconsin-Milwaukee Great Lakes WATER Institute in 2005/06 with the objectives of providing quantitative data on in-lake *Cladophora* biomass and its distribution in relation to nearshore currents, and assessing the potential role of the zebra mussel (*Dreissena polymorpha*) in promoting *Cladophora* growth. The main findings of that study were that *Cladophora* growth in Lake Michigan is phosphorus-limited, although temperature and underwater irradiance also influence algal growth. Since the early 1990s, increased water clarity, an increase in average summer nearshore water temperatures along the Wisconsin coast, and a possible increase in phosphorus loading from some rivers, have all contributed to the increase in *Cladophora* biomass. An approximate comparison of *Cladophora* phosphorus demand with phosphorus input from rivers suggested that rivers do not provide enough phosphorus to meet all of the *Cladophora*'s growth requirements, and that there must be an internal source of phosphorus within the lake to meet this demand, the most likely candidate being phosphorus recycling by dreissenid mussels (zebra and/or quagga mussels).

Based on the 2005/06 study, several major needs were identified for the formulation of a *Cladophora* management strategy. These included:

1. A quantitative assessment of the role of river input versus dreissenid mussel nutrient recycling as potential sources of phosphorus for *Cladophora*.
2. An evaluation of the potential impact of the more recent invasive species, the quagga mussel (*Dreissena bugensis*) as a source of phosphorus.
3. The development of a *Cladophora* growth model, to be used as a management tool in which the results of various management options can be numerically simulated.

To address these needs, a second study phase was initiated in 2006, with the above needs set as the primary study objectives.

3. SPATIAL VARIATION OF *CLADOPHORA*

The objectives of the work presented in this section was to determine whether spatial patterns of *Cladophora* abundance and nutrient content in the nearshore region of Lake Michigan near Milwaukee indicates an influence nutrient discharge from Milwaukee harbor and/or mussel excretion on *Cladophora* photosynthetic and growth potential.

In relation to benthic algae (chiefly *Cladophora*) in nearshore Lake Michigan close to Milwaukee, we can consider two hypotheses:

Hypothesis 1: If inputs of nutrients (chiefly P) from Milwaukee harbor are the major factor driving growth of benthic algae, we would expect to observe a strong gradient in *Cladophora* photosynthesis, growth, and internal P content in relation to proximity to Milwaukee harbor outflows to Lake Michigan.

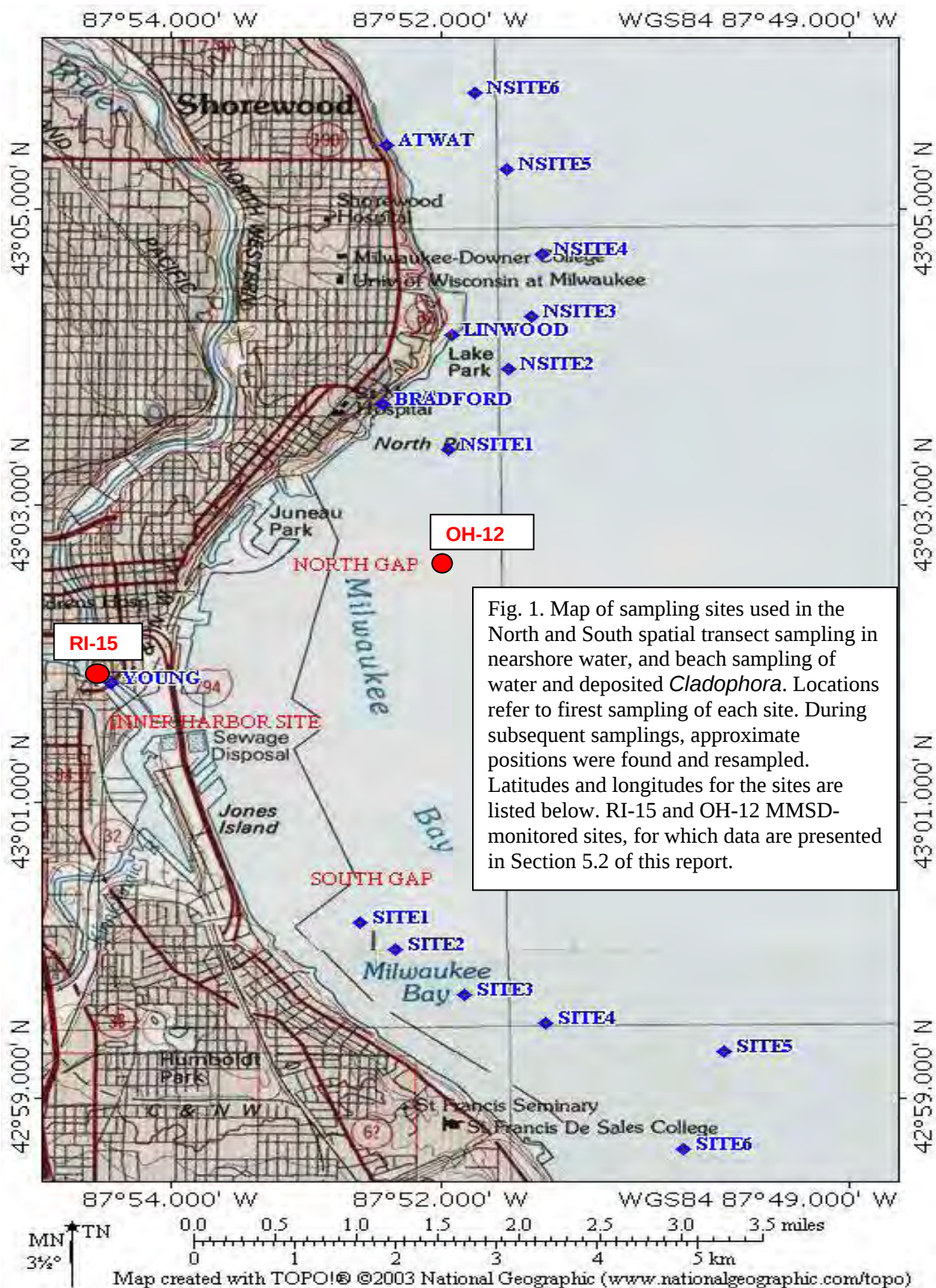
Hypothesis 2: If P excretion by dreissenid mussels is the major factor driving growth of benthic algae, we would not expect to see a strong spatial variability in relation to proximity to Milwaukee harbor, and we will expect to see expression of enzyme indices which indicate use of organic P sources, including those excreted by dreissenid mussels.

3.1 Background and Methods:

Surveys conducted in Phase I of this study indicated that **1)** Phosphorus (P) is the limiting nutrient for growth of *Cladophora* attached to the benthos at < 15 m water depth and **2)** the internal P content of *Cladophora* in nearshore Lake Michigan tends to be greater south of Milwaukee than to the north of the city. Because the prevailing water flow that enters the lake from the harbor is frequently to the south, this suggests that river input of P and other nutrients may be partly responsible for increased *Cladophora* growth. However, because samples were limited with regard to temporal coverage, it is uncertain whether this spatial pattern is persistent over time. In addition, nutrient inputs to the lake from the harbor are large enough that their influence may be over a very large area north and south of Milwaukee.

Spatial transects

To resolve this uncertainty, a series of spatial sampling exercises were conducted focusing on the area south of Milwaukee harbor between South Gap and Cudahy, which was sampled at three timepoints over the growing season, and a northern transect between points offshore from Bradford and Atwater Beaches sampled at a single timepoint was used as a comparison. We collected benthic algal samples from 6 sites over the transects. The south transect was between site 1 which was just south of the South Gap break in the outer harbor wall, and site 6 which was off Cudahy (see map Fig. 1). The north transect was from off Bradford beach, to off Atwater beach (Fig. 1). All sites were all between 9 and 10.5 m depth. Benthic algal samples were collected using a ponar grab which allowed all sites to be sampled in one day. Light attenuation profiles were measured using an upwards-facing 4pi type light meter (Li-cor, Lincoln NE) lowered over the sunny-side of the boat, and irradiance reading recorded every 1 m and at the bottom. Surface water samples were collected and stored on ice.



Exact positions of sampling sites shown on map in Fig. 1.

Northern Transect Sites: Atwater - Bradford

Nsite6 43° 05.788' N 87 ° 51.765'W
Nsite5 43° 05.272' N 87 ° 51.530'W
Nsite4 43° 04.699' N 87 ° 51.257'W
Nsite3 43° 04.279' N 87 ° 51.348'W
Nsite2 43° 03.923' N 87 ° 51.505'W
Nsite1 43° 03.373' N 87 ° 51.949'W

Beach Sampling Sites

Atwater beach 43 05.434' N 87 ° 52.403'W
Linwood Beach 43° 04.153' N 87 ° 51.924'W
Bradford Beach 43° 03.681' N 87 ° 52.434'W
Young St Bridge 43° 01.801' N 87 ° 54.446'W

Southern Transect Sites: South Gap - Cudahy

Site1 43° 00.191' N 87 ° 52.600'W
Site 2 43° 00.011' N 87 ° 52.351'W
Site3 42° 59.700' N 87 ° 52.351'W
Site4 42° 59.509' N 87 ° 51.241'W
Site5 42° 59.314' N 87 ° 49.922'W
Site6 42° 58.664' N 87 ° 50.218'W

Cladophora was sampled at ~ 0.5 - 1 km intervals along the North and South transects, measurements of water column light penetration were made, and surface water samples collected and analyzed for available dissolved phosphate using standard nutrient analysis methods (Parsons et al. 1984). *Cladophora* samples were analyzed for phosphorus content using an HCl digestion (Stainton et al. 1974) and activity of the enzyme alkaline phosphatase. Production of alkaline phosphatase activity (APA) in algae has been shown to be a good index of phosphorus limitation in a range of phytoplankton and macroalgal species (Beardall et al. 2001) and demonstrates a capacity of algae to utilize dissolved organic P (DOP) sources, which are excreted by dreissenid mussels. Our research in summer 2004 showed that in *Cladophora* from Lake Michigan, APA was present in field samples and was rapidly suppressed when excess phosphate was supplied (Young et al. 2005). APA is thus a reliable measure of P limitation in Lake Michigan *Cladophora* and may be related to DOP use by benthic algae. APA was measured using 4-methylumbelliferone-P as a fluorometric substrate (Fernley and Walker 1965). To extend this analysis, nearshore Milwaukee *Cladophora* was compared with *Cladophora* collected from nearshore Lake Michigan at the Indiana Dunes State Park, Indiana. This site is within several km of major discharges associated with the industrial area of Gary, Indiana.

To further investigate the use of organic P sources by benthic algae, and predict use of DOP excreted by dreissenid mussels, we tested the effect of supplying DOP and SRP on production of APA and internal P content of *Cladophora*. *Cladophora* from nearshore Lake Michigan is usually covered with microscopic algal epiphytes (predominantly diatoms) which form a dense community around each *Cladophora* filament. Most APA assays assess activity on the community as a whole so it was necessary to determine how much of the APA was due to these epiphytes, and whether *Cladophora* also produced APA. Localization of APA was done using a fluorometric localization technique using an enzyme-linked fluorescence (ELF-97TM) kit (Molecular Probes).

Growth of *Cladophora* in relation to spatial distribution was not assessed due to logistic constraints and boat access, but internal P content of the *Cladophora* was determined and can be used to predict growth rate, using the growth model (see section 5). However, photosynthetic capacity is an index of the potential growth rate of *Cladophora*. Measurements of photosynthetic capacity from some of the *Cladophora* samples were made *in situ* using an underwater pulse-amplitude modulated (PAM) fluorometer (Walz GmbH, Germany). This instrument provides a non-invasive means of determining the photosynthetic behavior of algae *in situ* (Young and Beardall 2003) and was used to construct photosynthesis vs irradiance (P vs I) curves to determine the saturation irradiance for *Cladophora* photosynthesis, to compare with the measured benthic irradiance at each of the transect sites. From the P vs I curves, one can determine the light intensity required by the algae to saturate photosynthesis. This saturation irradiance can be compared with the light measured *in situ* on the surface of the *Cladophora* bed at different depths to determine if the photosynthesis of *Cladophora* is limited by light.

3.2 Results

Light Attenuation at Sites. A visual examination of samples collected with the ponar grab suggested that there was less *Cladophora* biomass growing on mussels at the sites closest to South Gap, than at Green Can and Cudahy. Increasing water clarity with distance from South Gap was observed across the spatial transect with more light reaching the benthos at Green Can and Cudahy sites (Fig. 2). The sites seemed to fall in three groups: The South Gap site was clearly the most turbid, with the lowest irradiance reaching the benthos. The next 3 most turbid sites were sites 2 – 4 (between South Gap and Green Can), and the Green Can and Cudahy sites were the least turbid, and had higher irradiance reaching the benthos.

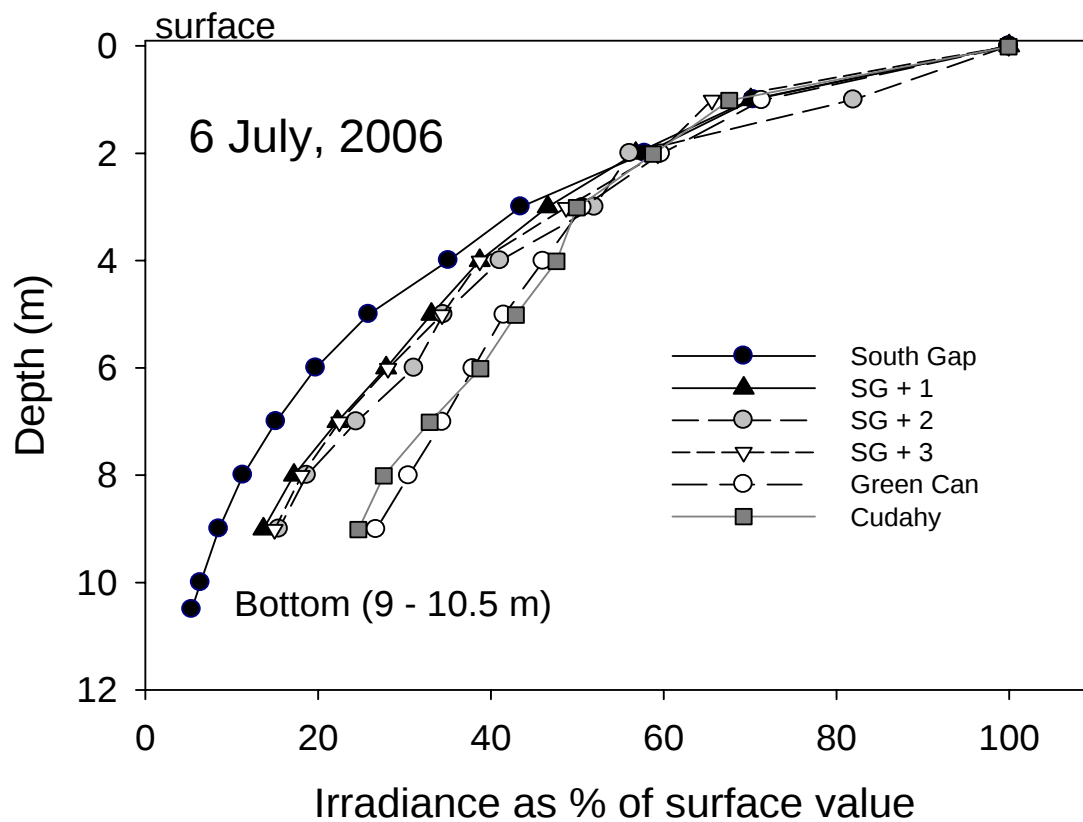


Fig. 2. Light attenuation through the water column at sites on a transect along the 10 m isobath between South Gap and Cudahy, plotted relative to the surface irradiance (6 July, 2006). See Fig. 1 for site reference.

Bottom Irradiance at each site ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$) on 6 July 2006.

South Gap site 1 : ~95
 Site 2 : ~200
 Site 3: ~210
 Site 4 : ~220
 Green Can Site 5 : ~410
 Cudahy Site 6 : ~420

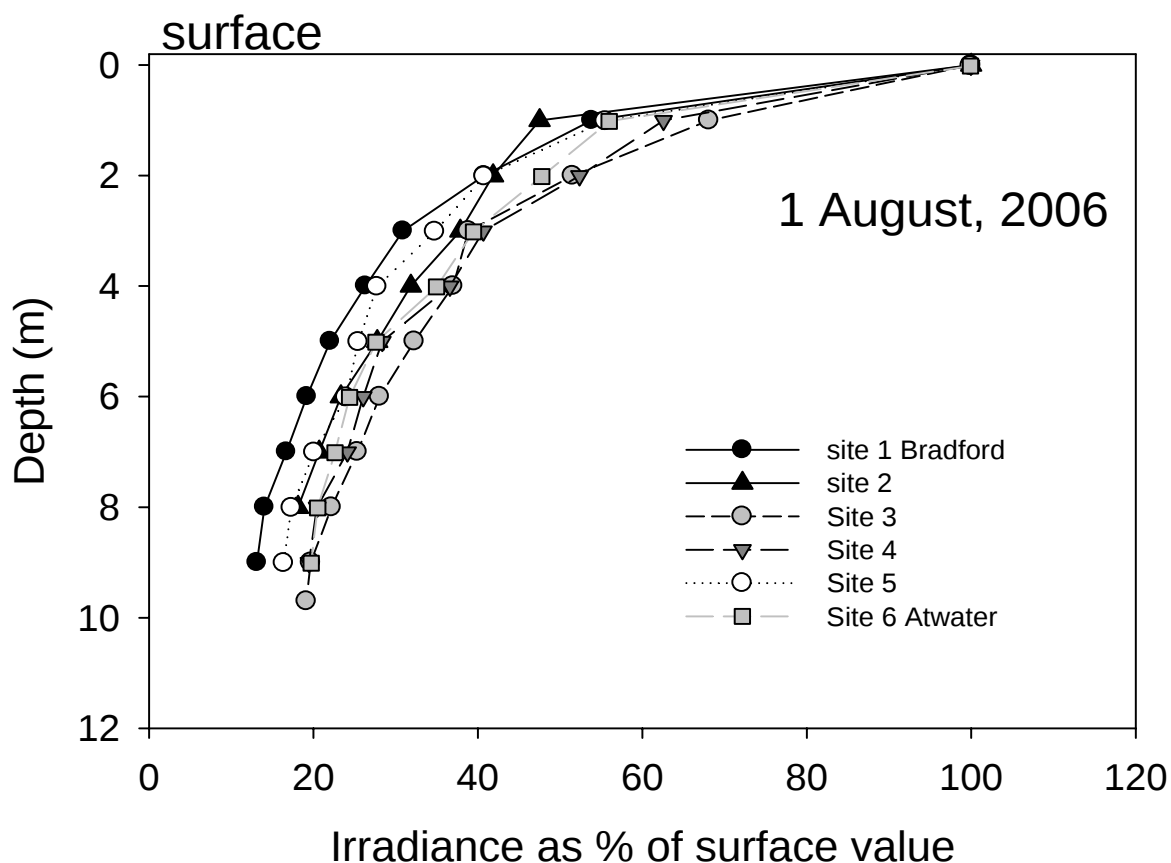


Fig. 3. Light attenuation through the water column at sites on a transect along the 10 m isobath between points off Bradford and Atwater Beaches, plotted relative to the surface irradiance (1 August, 2006). See Fig. 1 for site reference.

Bottom Irradiance at each site ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$) on 1 August 2006.

Bradford site 1 : ~370
 Site 2 : ~470
 Site 3: ~430
 Site 4 : ~478
 Site 5 : ~440
 Atwater Site 6 : ~524

Although the site off Bradford beach showed slightly higher light attenuation through the water column (Fig. 3). There was much less variation in light penetration between sites on the northern transect, and the northern sites showed higher light penetration to the benthos than the sites near South Gap, but lower light penetration than the most southerly sites, Green Can and Cudahy (Figs. 2 and 3).

Photosynthesis of *Cladophora* assemblages from spatial transects. To estimate whether light reaching the benthos was limiting for photosynthesis of *Cladophora*-epiphyte assemblages, photosynthesis capacity measurements were made on samples collected from the sites along the transect, using pulse-amplitude modulated (PAM) fluorometry. Photosynthesis-irradiance relationships were measured using 'rapid light curves' to determine maximum photosynthesis rate ($P_{\max}$) and the irradiance required to saturate photosynthesis (see Fig. 4).

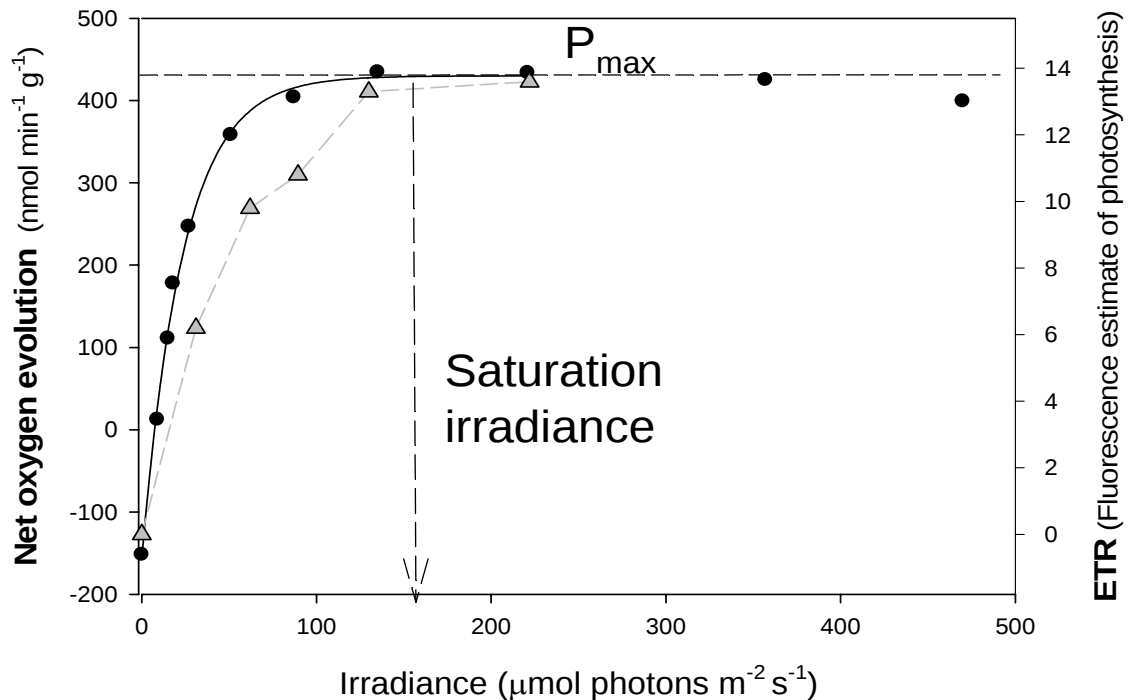


Fig. 4. Photosynthesis-irradiance relationships in *Cladophora*-epiphyte assemblages. Photosynthetic capacity measured by PAM fluorometry is expressed as relative 'electron transport rate' or ETR plotted in gray triangles (right axis). In some cases, photosynthetic oxygen evolution was also measured on the same samples, and is plotted in black circles (left axis). Determination of the irradiance required to saturate photosynthesis is shown (in this case $\sim 160 \mu\text{mol photons m}^{-2} \text{s}^{-1}$).

Maximum photosynthesis rates showed no clear differences in samples collected over sites from South Gap to Cudahy, in the July or August sampling time (Fig. 5). The irradiance required for saturation was slightly lower in the samples collected nearest to South Gap, suggesting that the benthic algae in this site is acclimated to lower irradiance, which is consistent with the light profiles measured at this site (Fig. 2). In the northern transect sites, the algae showed higher $P_{\max}$ at the Bradford and Atwater sites, although overall, the relative $P_{\max}$ values were lower than in *Cladophora* collected from the south transect (Fig. 6). Irradiance required for saturation was lower in the northern sites than the southern sites, which is consistent with the higher light penetration to the benthos seen in most of the northern sites (Figs 2 and 3).

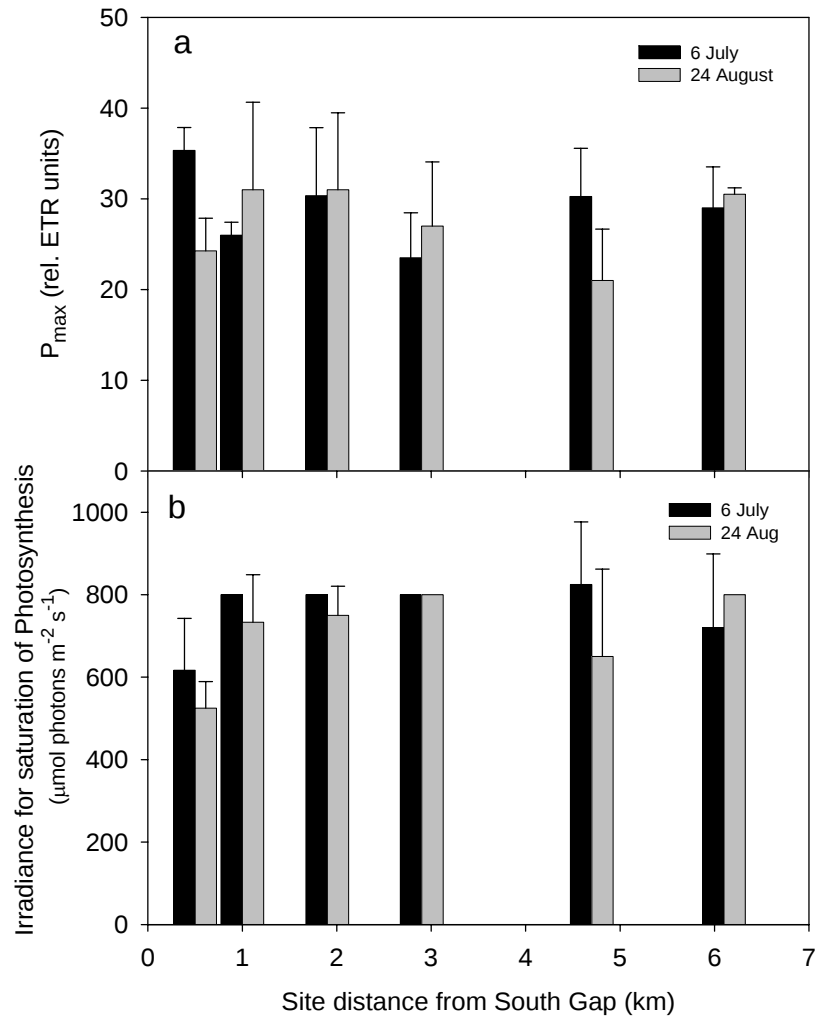


Fig. 5. Photosynthesis in *Cladophora*-epiphyte assemblages collected along a transect from South Gap to Cudahy. a. Relative maximum photosynthesis rate (P_{max}) measured by PAM fluorometry. b. estimates of the irradiance required for saturation of photosynthesis. Bars are means + standard deviation, $n \geq 2$.

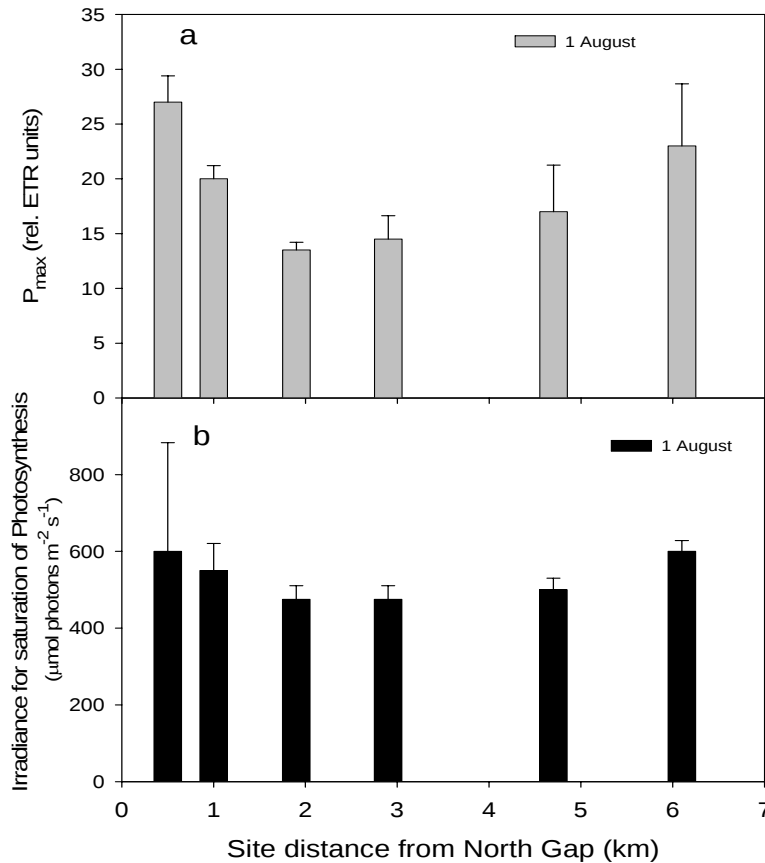


Fig. 6. Photosynthesis in *Cladophora*-epiphyte assemblages collected along a transect from North Gap to Atwater. a. Relative maximum photosynthesis rate (P_{max}) measured by PAM fluorometry. b. estimates of the irradiance required for saturation of photosynthesis (bottom). Bars are means + standard deviation, $n \geq 2$.

Internal P content of spatial samples. There was a significant difference in total internal P content of *Cladophora*-epiphyte assemblages sampled along the spatial transect from South Gap to Cudahy. On three of the sampling dates (6 Jul, 8 and 24 Aug) there was a significant decline in *Cladophora* P content with distance from South Gap, although this relationship was less evident in the samples collected on 8 August (Fig. 7). For samples collected on 6 July, the P content was significantly higher at the most northerly two sites than at Green Can and Cudahy sites (1-way ANOVA, $p < 0.05$). *Cladophora* samples collected from Indiana Dunes site on 12 July had much higher internal P content, $3.89 \pm 0.3018 \text{ mg g}^{-1}$, which was nearly double the highest internal P content measured in samples collected close to South Gap on 24 August. Samples from the northern transect had overall lower internal P content, which did not vary consistently along the transect (Fig. 7 bottom).

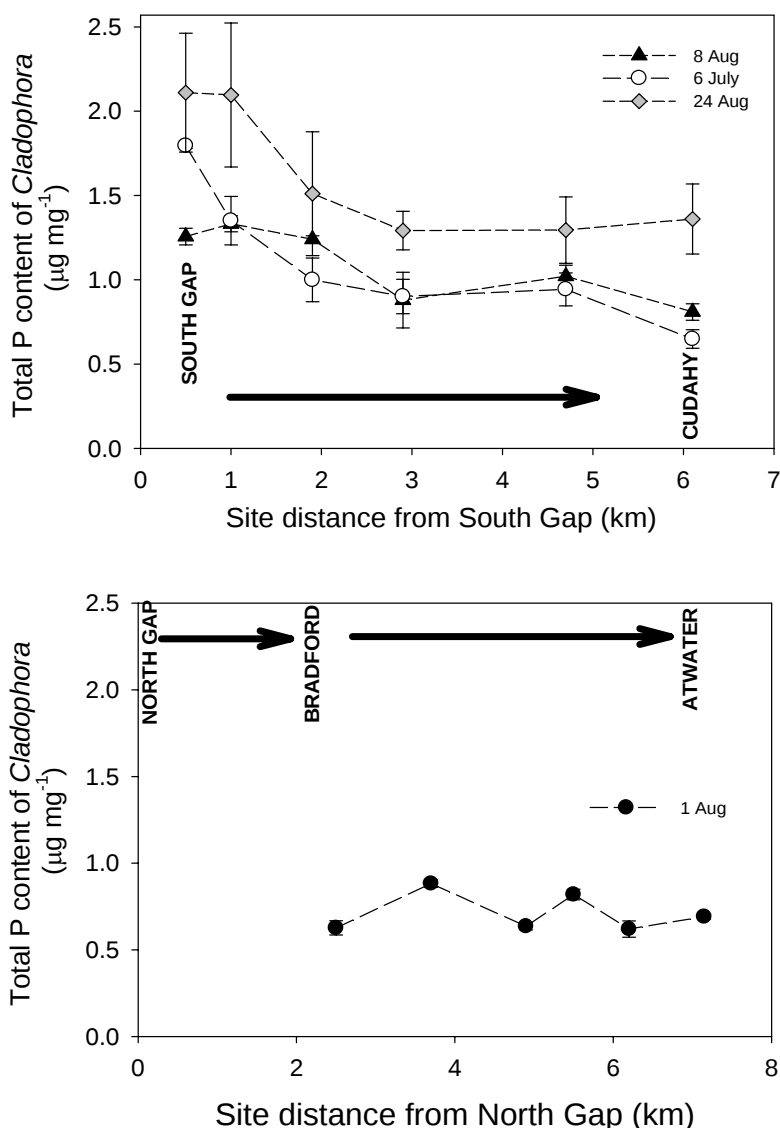


Fig. 7. Total P content in samples of *Cladophora*-epiphyte assemblages collected by ponar-grab along a transect following the 10 m isobath from South Gap to Cudahy (top), and North Gap to Atwater (Bottom), summer 2006. Points are means $\pm$ standard deviation of 6 samples. Note same y axis scales used for both graphs.

Alkaline phosphatase (APA) in spatial samples. The internal P content of *Cladophora*-epiphyte assemblages was well correlated with alkaline phosphatase activity (APA), as in spatial samples, those with higher P content, showed lower APA and those samples more distant from South Gap, which had lower P content, generally showed higher APA (Fig. 8). After extensive testing of different preparation methods and washing procedures for ELF-APA localization technique, APA was observed in both *Cladophora* filaments and the diatom epiphytes (Fig. 9). This activity was shown to be regulated in response to P availability (Fig. 10).

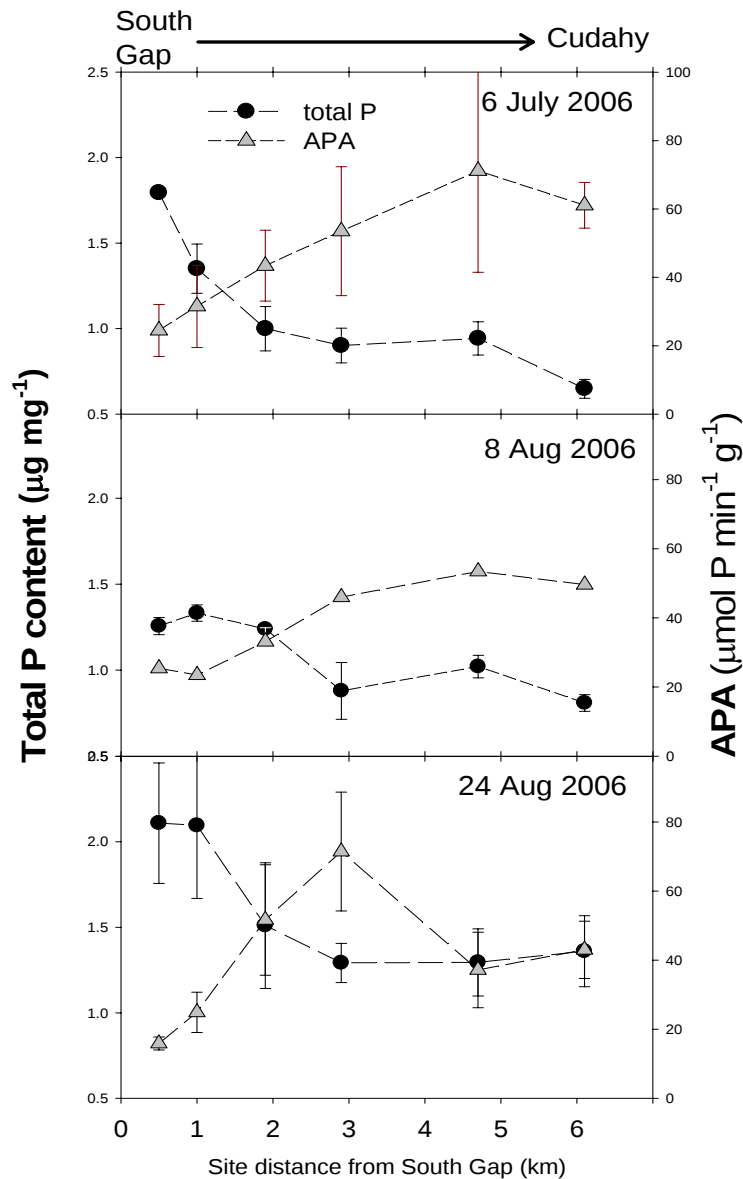


Fig. 8. The relationship between total P content and Alkaline phosphatase activity (APA) in *Cladophora*-epiphyte assemblages collected along a spatial gradient from near South Gap to Cudahy on 6 July, 8 and 24 August 2006. The inverse relationship between total P content and APA is evident. Points are means $\pm$ standard deviation of >5 samples.

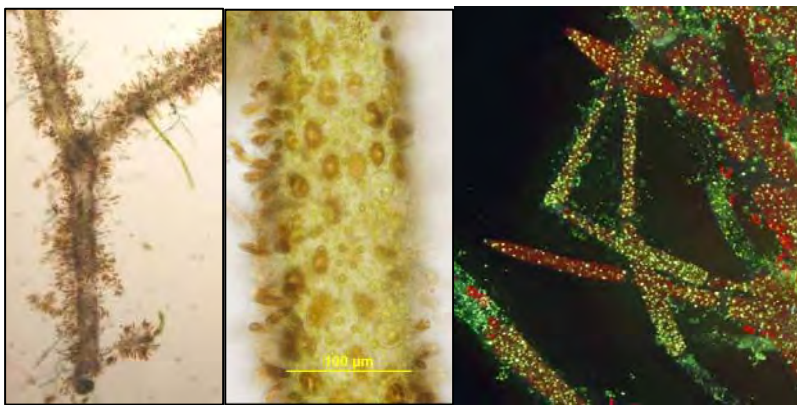


Fig. 9. *Cladophora*-epiphyte assemblages collected from nearshore Lake Michigan showing a dense coverage of epiphytic diatoms over the *Cladophora* filament. The right picture shows an epifluorescence picture with labeling of APA using ELF indicated by the green dots - present on the *Cladophora* filament tips, and on epiphytic algae. Images copyrighted.

Cladophora-epiphyte assemblages has considerable alkaline phosphatase activity (APA) indicating a well developed ability to use organic P in the water column or release from the benthos (Fig. 10A). There was only a slight suppression of APA in the algae when exposed to extremely higher SRP enrichment. When supplied with organic P (glycerol-phosphate), the algae were readily able to take up and incorporate the P for use in growth (Fig. 10C). The algal assemblages produced APA in excess of requirements to support required P uptake, and excess SRP was released into the water as a result of cleavage of SRP from the organic P source (Fig. 10B).

SRP availability. SRP concentrations in surface water showed no significant spatial variability over the transect from South Gap to Cudahy, although surface water collected at the entrance to the inner harbor had higher SRP concentration (Fig. 11). Therefore there was no strong signal in dissolved SRP input from riverine inputs to nearshore Lake Michigan, which was effectively diluted in the passage through the outer harbor. These low surface SRP concentrations of $< 3 \mu\text{g L}^{-1}$ can also be compared with >10 times higher concentrations measured over the season in the lower Milwaukee river ($30 - 70 \mu\text{g L}^{-1}$) and at beach sites (see Fig. 12).

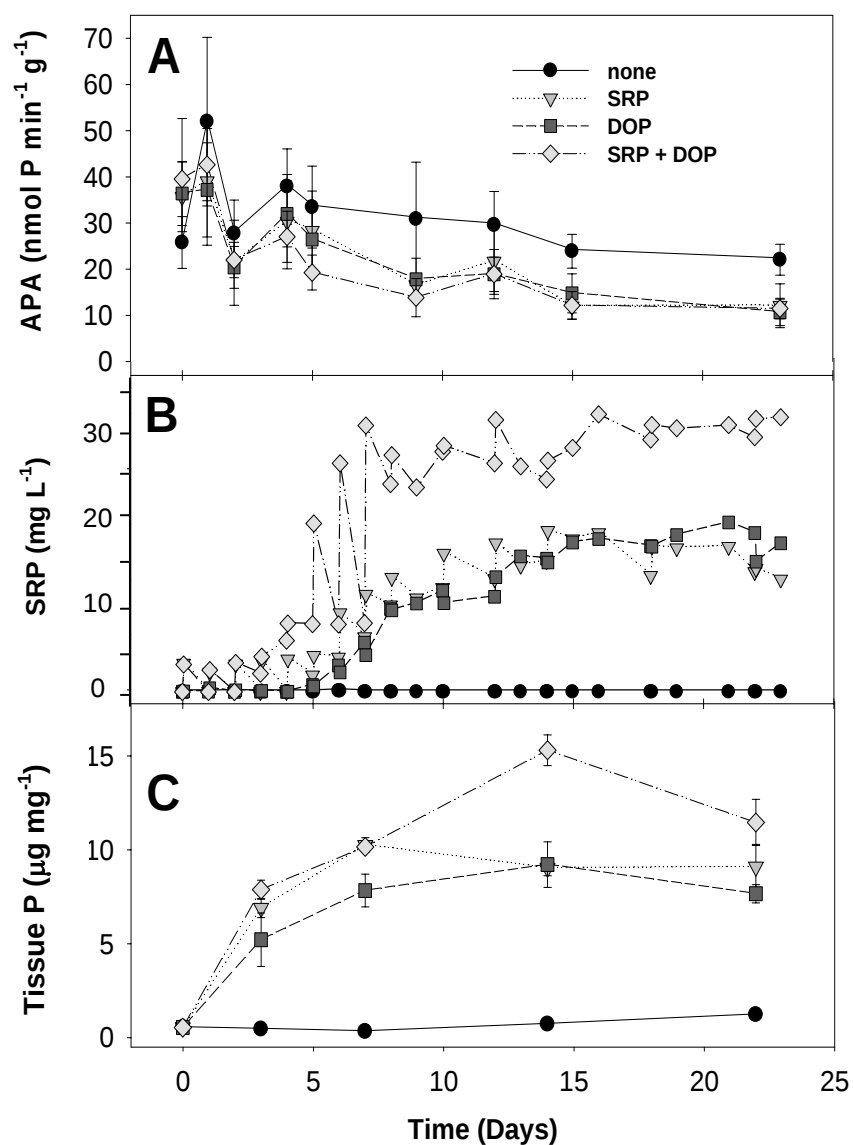


Fig. 10. Effect of inorganic and organic P enrichment on AP activity and internal P content in *Cladophora*–diatom assemblages over 24 days in laboratory culture. Treatments were control with no P enrichment, dissolved organic P (DOP; glycerol-P), soluble reactive P (SRP), or both P sources. **A.** AP activity (n=8), **B.** SRP concentration in growth medium (n=1) and **C.** total P content in *Cladophora*-diatom assemblage (n=2). Points are means $\pm$ standard deviation (for A and C).

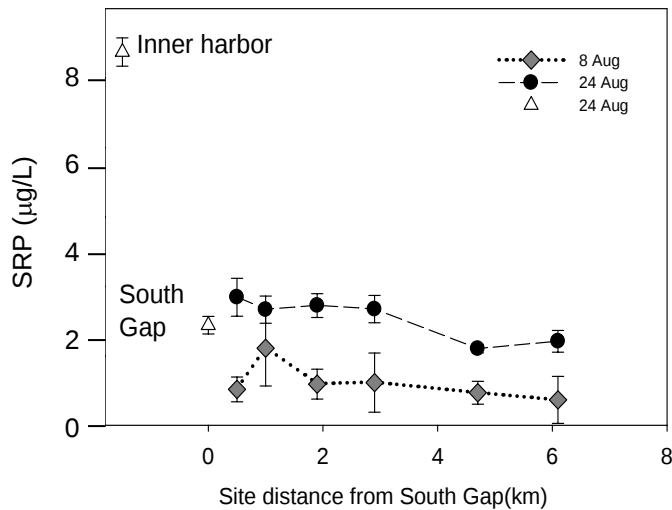


Fig. 11. SRP in surface water at sites along the transect from South Gap to Cudahy. SRP concentrations in samples collected from just inside South Gap and from at the entrance to the inner harbor on 24 Aug (open triangles) are added for comparison. Points are means $\pm$ standard deviation of ≥ 2 samples.

Seasonal Sampling of water and *Cladophora* on Milwaukee Beaches

Nearshore water nutrients fluctuated over the period June - Nov 2006. There was little clear change in SRP and SiO₂ except for slightly lower concentrations between late June and September (Fig. 12), which coincided with lower total internal P content of algae (Fig. 13, lower). Nutrient concentrations were 3-4 times higher in the Milwaukee River than on the beach wash throughout the seasons. APA in algae became less variable over the season and declined after mid September.

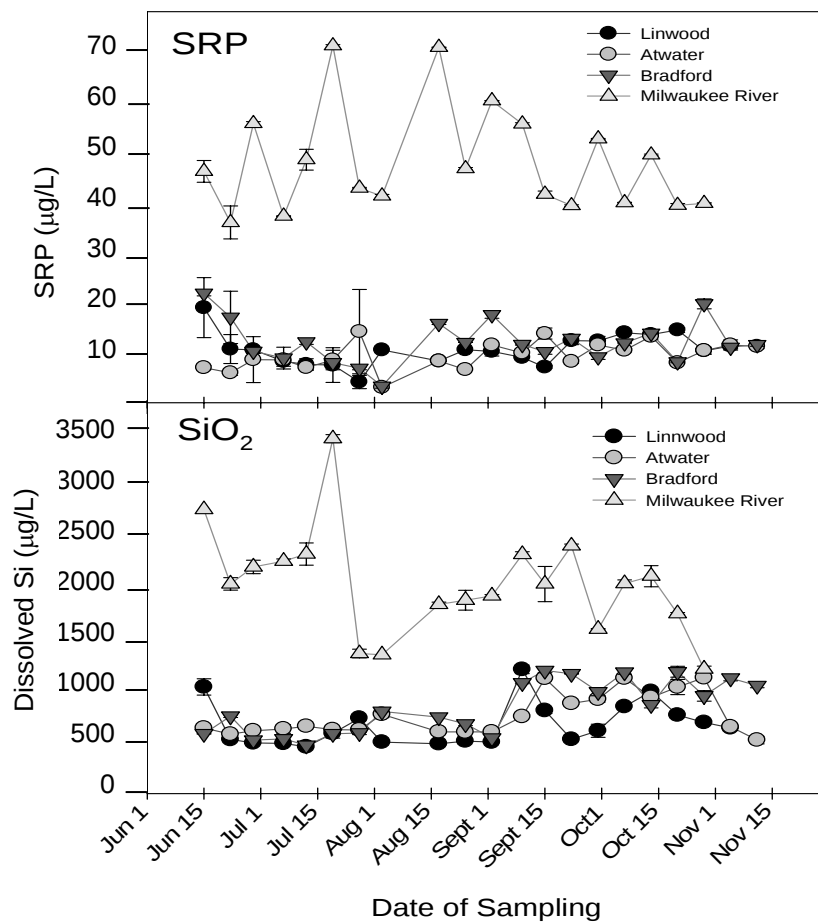


Fig. 12. Dissolved nutrients in nearshore water collected from beaches over 2006. Top SRP bottom SiO_2 . The 3 beach sites were sampled direct from the shore, and the Milwaukee River site was sampled from the Young St bridge, close to the confluence with the Kinnickinnic River. Points are means of 2 - 4 replicates $\pm$ standard deviation.

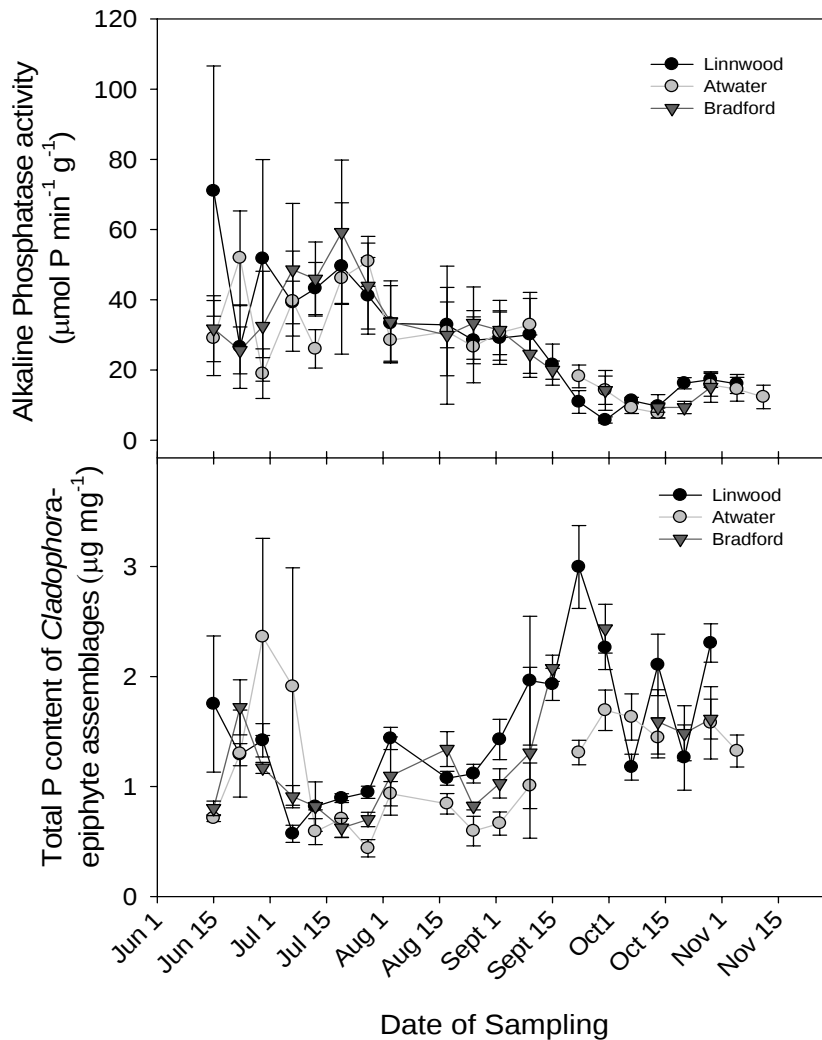


Fig. 13 Alkaline phosphatase activity (APA) and total P content of *Cladophora*-epiphyte assemblages collected from algae floating in shallow water at Milwaukee beach sites over 2006. Points are means $\pm$ standard deviation of > 6 samples.

3.3 Discussion and Conclusions

If riverine P inputs are the most significant influence on *Cladophora* growth, we expected to observe a gradient of *Cladophora* nutrient status, with algal internal P content and APA decreasing with distance from the river and harbor outlet at South Gap. However, if P supply from mussels is the dominant source of P for *Cladophora*, then no gradient should be observed. As a strong spatial gradient in *Cladophora* internal P content was observed in relation to proximity to Milwaukee harbor outflow at South Gap, this suggests that nutrients discharged into Lake Michigan are probably influencing total internal P content of *Cladophora*. However, turbidity also declined with distance from South Gap, influencing the

light environment for benthic algae along that gradient. The light availability was lower at the sites closest to South Gap, probably imposing greater light limitation on the algae growing close to South Gap. When *Cladophora* growth is limited by light, the available P is retained in the algal tissue and less quickly 'diluted' into new growth which could explain the higher internal P content of samples collected close to South Gap. Although we chose a constant depth (10 m) to sample, the effect of light attenuation and irradiance at the benthos may have complicated the interpretation of these results.

Although the effect of nutrient discharge from Milwaukee Harbor probably contributes to the gradient in *Cladophora* internal P content along the transect from South Gap to Cudahy, the effect of harbor nutrients seems to be diluted rapidly, with no effect of nutrients evident at greater than 2.5 km from the outer harbor outlet. In contrast to the south transect, the *Cladophora* collected along the north transect showed no significant spatial relationship to dissolved nutrient release from the Milwaukee harbor via North Gap, and overall the internal P content of samples from the northern sites was lower than south of the harbor. Measurements of nearshore current dynamics (Bootsma et al. 2005a) and models of Milwaukee harbor water plume discharge (H. Bravo and S. McLellan unpublished) suggest that harbor water can be carried both north and south of the harbor, depending on wind patterns, and conservative tracer experiments suggest rapid dilution or dispersal of this riverine water outside the outer harbor. The lack of spatial relationship between proximity to the harbor and *Cladophora* internal P content in site sampled north of the city can be explained by the rapid dispersal of harbor water, and the distribution of algal biomass. *Cladophora* biomass attached to the benthos is minimal within 3 km of North Gap in the northerly direction, because the substratum is unsuitable for *Cladophora* attachment (summarized in Fig. 14). **The combined observations of the north and south transects suggest that nutrient discharge from the Milwaukee Harbor is rapidly dispersed and will likely only stimulate *Cladophora* growth in areas less than 2.5 km from the harbor outlets.** This is consistent with rapid dilution reported in models of *E. coli* dispersal rates for the same area (Scopel & McLellan 2006).

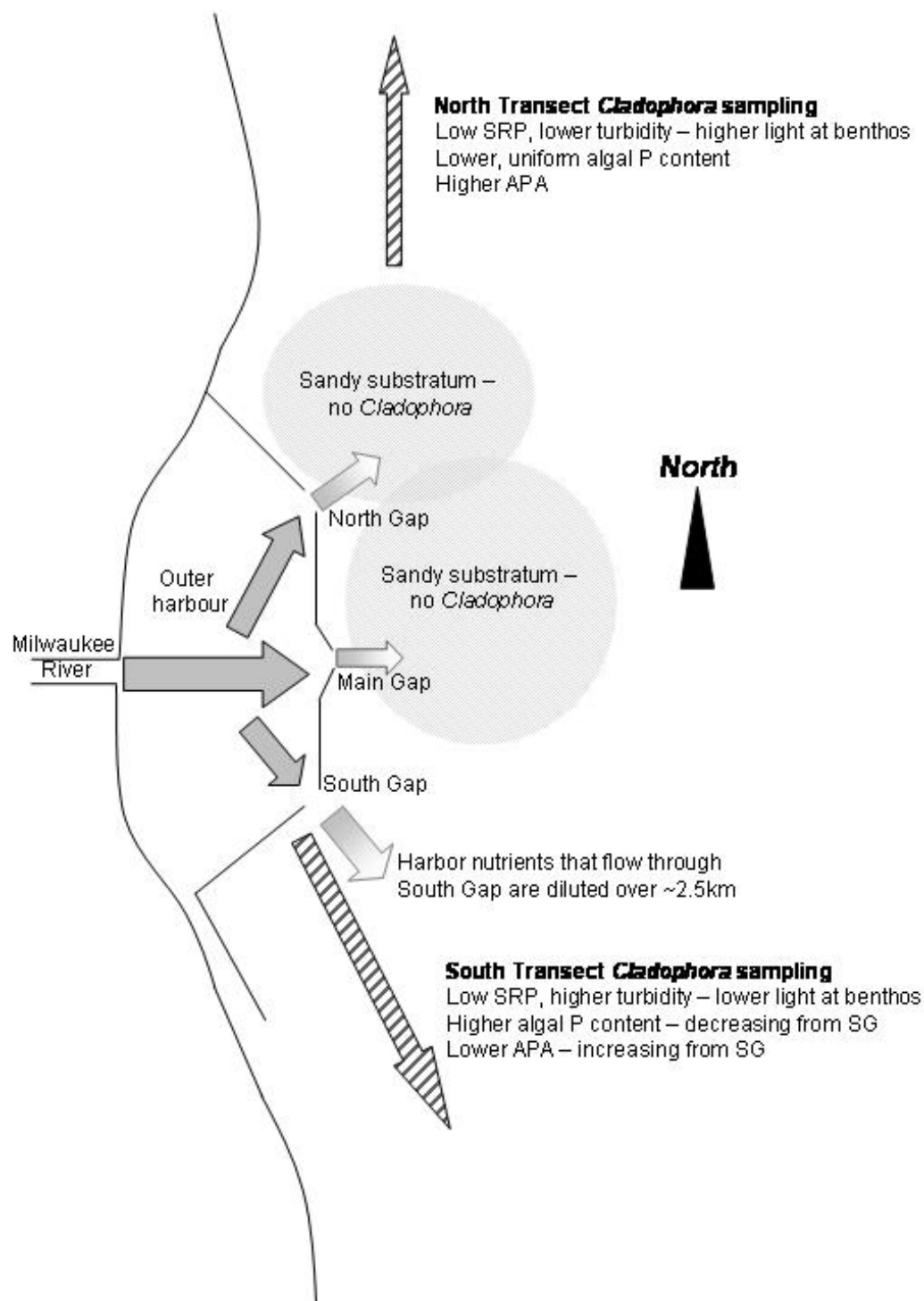


Fig. 14. Conceptual diagram of estimated nutrient dispersal and *Cladophora* sampled in Milwaukee nearshore region of Lake Michigan north and south from the outer harbor. *Cladophora* sampled in the south transect (South Gap to Cudahy) showed some influence of inputs from the harbor with a gradient of internal P content, whereas the *Cladophora* sampled in the northern transect were outside the region of clear influence from inputs from the Milwaukee harbor.

The SRP availability showed no significant spatial trend outside the outer harbor, although concentrations in the Milwaukee river and the inner harbor were several times higher. This suggests that a large proportion of the inorganic P in river water is effectively precipitated or taken up within the inner and outer harbor, and not released to the nearshore region where it can be taken up by benthic and pelagic algae. This supports earlier findings about total P 'capture' by the Milwaukee harbor (Bootsma et al. 2005b). The low SRP may also indicate rapid uptake by benthic and pelagic organisms close to South Gap. Organic P sources dissolved in riverine water could also be used to support growth of the *Cladophora*-epiphyte assemblages in nearshore Lake Michigan.

Probably a more significant source of dissolved organic P to benthic algae is excretion by abundant dreissenid mussels. Significant production of alkaline phosphatase activity (APA) suggests that the algae certainly can use and rapidly incorporate P supplied as a SRP or a dissolved organic form, such as can be excreted by mussels. The lack of a suppression of APA by SRP enrichment suggests these algae are well adapted to chronic P stress due to low SRP, and can continuously access P from organic P sources to support total P requirements. All of the samples collected from the north and south transect sites had P content lower than the 2.5 mg P/g dry mass estimated requirement to saturate growth (Auer and Canale 1982). **This suggests that although riverine inputs may be supplying some P to support *Cladophora*, growth is still limited by P supply, which means that any additional P release to the nearshore region, or increased availability through altered P cycling, could further stimulate *Cladophora* growth.** Certainly *Cladophora* has the capacity to take up and store higher concentrations than we typically find in nearshore regions close to Milwaukee. *Cladophora* collected from a high light (i.e. not light limited) site in Indiana, had P contents close to double the highest concentrations we observed in samples from close to South Gap. Dreissenid mussels could provide a significant amount of P required to support growth of *Cladophora*. However, as there was no evidence that mussel densities were higher around the sites we sampled south of South Gap compared with along the northern transect, the difference in P content between these two regions must be related to riverine nutrient sources.

Conclusion: Growth of *Cladophora*-epiphyte assemblages in nearshore regions of Lake Michigan near Milwaukee is supported by nutrient outflow from the Milwaukee harbor (including both riverine inputs and Jones Is WWTP) and internal lake P recycling, in which mussels play a dominant role. The proportion of these in supplying P to benthic algae varies spatially, with sites close to South Gap showing an elevated nutrient content consistent with supply from riverine outflow. However, the spatial extent of this effect is limited to a small area within 2-3 km of South Gap.

4. Phosphorus Supply from Dreissenid Mussels

During Phase I of this study, the zebra mussel (*Dreissena polymorpha*) was the dominant dreissenid in Lake Michigan. However, in 2006 the quagga mussel (*Dreissena bugensis*) displaced zebra mussels as the dominant dreissenid in the lake, and therefore this study focused on the role of the quagga mussel as a potential source of phosphorus to *Cladophora*.

4.1 Experimental Methods

Experiments were conducted both in the lake and in the laboratory to investigate P supply from quagga mussels. There were two main objectives of these experiments: 1) To quantify the magnitude of P supply from mussels within the lake, and compare this supply rate to river P loading rates; 2) To determine how environmental variables (temperature, food supply, food quality, mussel size) affect mussel P recycling rate, with the goal of developing an empirical model that simulates the role of mussels in the nearshore phosphorus cycle. This model can then eventually be coupled to the *Cladophora* model.

To test the effect of temperature, mussels were first left in 11°C filtered lake water for 48 hours to evacuate their gut contents. They were then placed in incubation chambers at three different temperatures: 10°C, 15°C, and 22°C. Within each temperature treatment, mussels were fed four different food concentrations: 0, 0.1, 0.5 and 2.0 mg ml⁻¹ dry weight of a green algae mixture (*Chlorella*, *Scenedesmus*, and *Selenastrum*) that was grown in the laboratory. Mussels were acclimated to each temperature-food combination for a period of three weeks, after which 3 mussels from each temperature-food combination were placed in clean chambers with filtered lake water. Subsamples were then collected at 0, 6, 12, 24, and 48 hour time points and analyzed for soluble reactive phosphorus (SRP). Following the experiment, mussel tissues were dried and weighed, so that phosphorus excretion rates could be normalized to mussel mass. Excretion rates were calculated by performing a linear regression of weight-adjusted SRP against time.

To test for the effect of food quality, the green alga *Scenedesmus* sp. was grown in the laboratory in growth medium until stationary phase was reached (the phase at which rapid reproduction ceases). At this point, it was assumed that dissolved P concentrations were low, due to uptake by *Scenedesmus*. This *Scenedesmus* culture was then transferred to five smaller aquaria. To these, various amounts of phosphate stock solution were added to produce phosphate incremental concentrations of 1, 20, 50, 100 and 200 µg L⁻¹. Algal cultures were left for one day, to allow algae to take up available dissolved P, resulting in algal cultures with various cellular P concentrations. Water from these aquaria were then pumped through 500 ml acclimation chambers, each containing six mussels similar in size, at a rate of 2.0 ml min⁻¹ and a temperature of 20 to 23°C. During pumping, aquaria were bubbled to prevent settling of algae. Mussels were left in acclimation chambers for 2.5 days. At the end of the acclimation period, subsamples were collected from the aquaria, filtered, and analyzed for particulate

carbon, nitrogen and phosphorus concentration. For the purpose of this experiment, food quality was defined by the algal C:P ratio. Following the acclimation period, mussels were placed into 150 ml incubation chambers. For each treatment (i.e. algal cellular P content), three replicate incubation chambers were set up, each containing two mussels. Incubation chambers were subsampled for soluble reactive phosphorus (SRP) and total dissolved phosphorus (TDP) at regular intervals, and SRP and TDP excretion rates were calculate as the change in dissolved P concentration divided by the time span of the incubation interval. After incubations, mussel lengths and dry tissue weight were measured, and P excretion rates were normalized to these measurements.

To determine the effect of mussel size on P recycling, an experiment similar in design to the food quality experiment was conducted, but mussels of various sizes were acclimated over 3 days to a single food concentration consisting of Milwaukee Harbor water with a particulate P concentration of $6.9 \mu\text{g P}$ per liter. Following acclimation, mussel P excretion was measured at 20°C in chambers filled with filtered lake water, as described above. For each mussel size, 3 replicate chambers were used.

To quantify mussel P excretion rates in the lake, and to determine how applicable lab-measured P excretion rates are to the natural environment, experiments were conducted in the lake on three separate days to measure P flux from mussel beds. For each experiment, incubation chambers were placed over mussels growing on large rocks. Chambers were cylindrical, 15 cm diameter and 8 cm tall. The base of each chamber was fitted with a neoprene skirt, which was sealed against the rock by placing a circular iron shot-filled neoprene sock over the skirt (Fig. 14). Following placement, chamber contents were gently stirred using a manual stir bar fitted in the chamber top. Chambers were then left to settle for several minutes, after which an initial water sample was drawn from the chamber using a 60 ml syringe and needle that were inserted

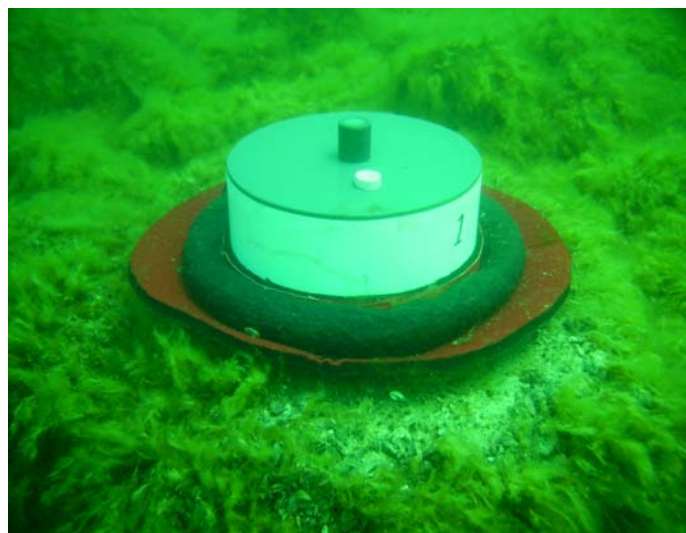


Fig. 14. Chamber used to make *in situ* measurements of mussel phosphorus recycling rates.

through a rubber stopper in the chamber top. Chambers were then left for approximately one hour, after which a second water sample was taken. Chambers were then removed, and all mussel under the chamber were collected and returned to the laboratory for measurement of numbers, lengths, and dry weights. Water samples were filtered immediately on return to the laboratory, and analyzed for SRP and TDP. SRP and TDP excretion rates were calculated both in aerial units ($\text{mg P m}^{-2} \text{ hr}^{-1}$) and mussel-normalized units ($\text{mg P mussel}^{-1} \text{ hr}^{-1}$). In all lab and field experiments, measured TDP excretions rates were very similar to SRP excretion rates, and therefore only the SRP excretion results are presented below.

4.2 Results

4.2.1 Effect of mussel size on P recycling. As expected, larger mussels have higher SRP excretion rates. In the mussel size experiment, mussel lengths ranged from 11 mm to 30 mm. Mussels in the 11 mm size class excreted soluble reactive phosphorus at a mean rate of $0.17 \mu\text{g P mussel}^{-1} \text{ hr}^{-1}$, while the mean excretion rate for 30 mm mussels was $0.51 \mu\text{g P mussel}^{-1} \text{ hr}^{-1}$. However, if P excretion rate is normalized to mussel mass, smaller mussels have a greater specific excretion rate than large mussels (Fig. 15). The observed relationship can be fitted with a power function, which explains 86% of the variance in specific P excretion rate at a given temperature and food supply (Fig. 15). To our knowledge, there are no other studies relating P excretion to mussel size for the quagga mussel. However, Mellina et al. (1995) have examined this relationship for the zebra mussel. A comparison of their P excretion vs. mussel weight relationships with ours suggests that quagga mussels have a higher specific P excretion rate than zebra mussels (Fig. 16). However, a direct comparison is difficult, because they did not report the concentration of food that mussels were exposed to in their

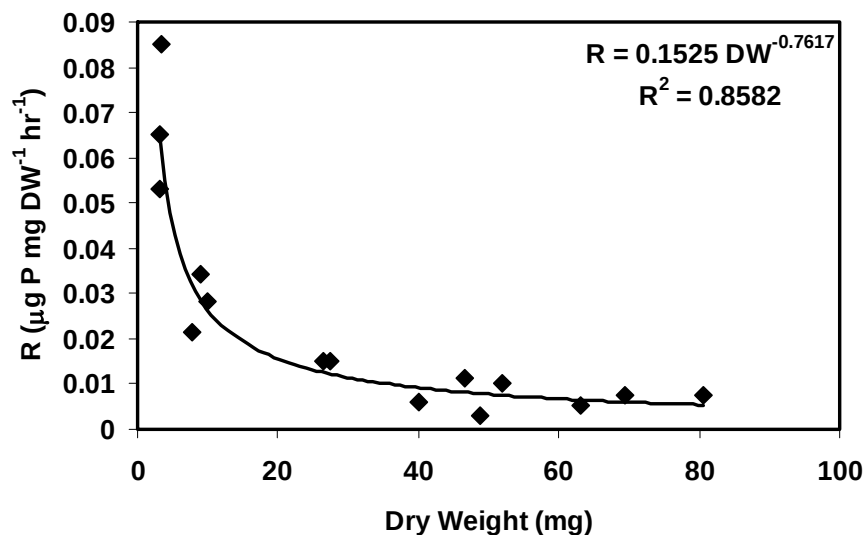


Fig. 15. Relationship between mussel tissue dry weight and weight-specific phosphorus excretion rate at a temperature of 23°C and a food concentration of $6.9 \mu\text{g P L}^{-1}$. R is the weight-specific phosphorus excretion rate of mussels.

experiments. The data of Mellina et al. (1995) indicates that a 16 mm mussel exposed to Oneida Lake plankton concentrations at 22°C should excrete P at a rate of 0.01 $\mu\text{g P mg}^{-1} \text{ hr}^{-1}$. In our study, 16 mm quagga mussels excreted P at rates greater than this, and only approached this low rate after three days with no food. Therefore, while the data for comparison are limited, they do suggest that quagga mussels may excrete more P than zebra mussels at a given temperature and food concentration.

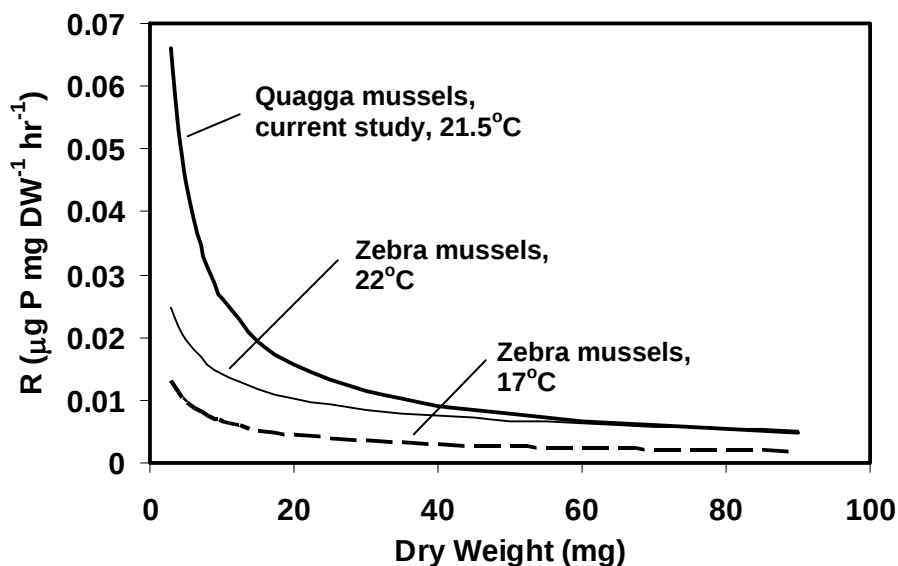


Fig. 16. Comparison of the quagga mussel weight - P excretion relationship observed in this study with that reported by Mellina et al. (1995) for the zebra mussel. Mussels in the study of Mellina et al. were collected from Oneida Lake (New York), but they did not report food concentration.

The relationship between mussel size and SRP excretion rate indicates that mussel population size structure can have a strong influence on P recycling rates. For a fixed mass of mussels, P excretion rates will be much greater if those mussels are small than if they are large. Figure 15 demonstrates that mass-specific P excretion rates are much greater for mussels below 10 mg than those above 10 mg. Based on our measurement of the length-weight relationship of quagga mussels from the Atwater station (Fig. 17), the 10 mg weight threshold is equivalent to a 16 mm length threshold. Size-frequency analysis of mussels from the Atwater station (Fig. 18) indicates that a significant proportion of mussels are smaller than 16 mm in length, highlighting the importance of accounting for both mussel densities and population size structure in any mussel P excretion simulation models.

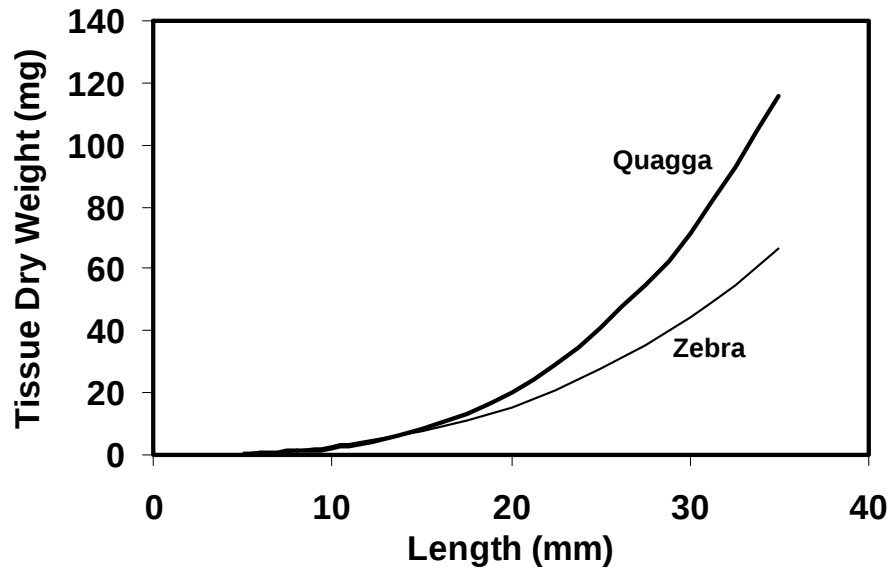


Fig. 17. Observed length-weight relationship for quagga mussels at the Atwater station, Lake Michigan, 2006. The curve is based on the measurement of mussels used in P excretions experiments. $W = 0.0018 L^{3.11}$, $r^2 = 0.95$. For comparison, the length-weight relationship for zebra mussels from Oneida Lake (Mellina et al. 1995) is also shown ($W = 0.00622 L^{2.61}$, $r^2 = 0.95$).

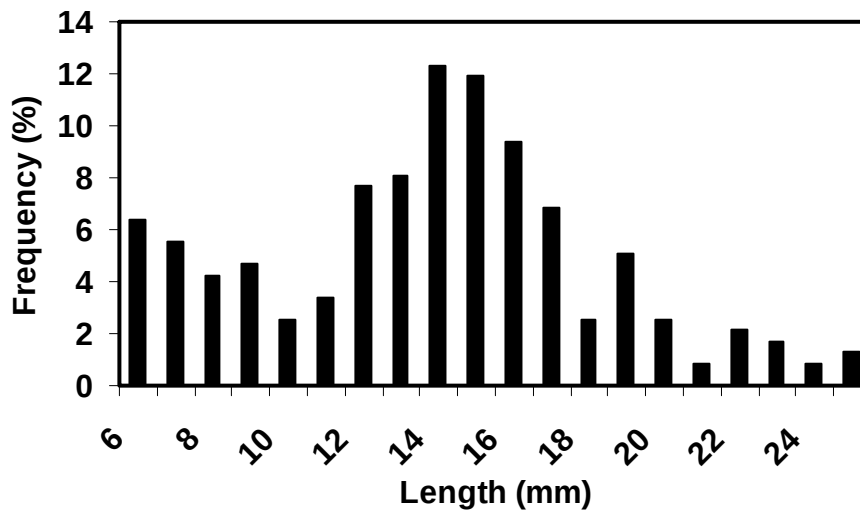


Fig. 18. Length-frequency relationship of quagga mussels collected from the Atwater station, October 20, 2006.

4.2.2 Effect of Food Supply and Food Quality on Mussel P Recycling. Results from the experiment in which mussels were fed *Scenedesmus* with different cellular P concentrations were analyzed to determine whether food quantity (measured as particulate organic carbon concentration), food carbon : phosphorus ratio, or food phosphorus content had the greatest influence on mussel P excretion rate. The analyses shows that each of these variables affects P excretion rate to some degree. Excretion rate generally increased with increasing particulate organic carbon concentration (Fig. 19), and showed an inverse relationship with food C:P ratio (Fig. 20).

However, the strongest relationship was between particulate phosphorus concentration and P excretion rate (Fig. 21). This suggests that the excretion of phosphorus by quagga mussels is a function of both the food concentration and the food C:P ratio.

In the food quantity / quality experiment, the food phosphorus concentration ranged from 142 to 363 $\mu\text{g L}^{-1}$. In contrast, the food P concentration in the mussel size experiment (Fig. 15) was 6.9 $\mu\text{g L}^{-1}$. Yet in both experiments the lowest P excretion rate was slightly less than 0.01 $\mu\text{g P mgDW}^{-1} \text{ hr}^{-1}$. Why this low rate was observed in the food quality experiment is uncertain. However, the food provided in this experiment (*Scenedesmus* culture) would be expected to be of higher quality than that in the harbor water, which would include a large proportion of non-living particulate matter. Because the organic carbon in this harbor material may be more difficult for mussels to assimilate (due, for example, to lack of vitamins or essential amino acids), the ingested phosphorus may be recycled (excreted) rather than assimilated. Other studies (Madon et al. 1998) have found that dreissenid assimilation efficiency is lower with a food supply typical of that found in turbid rivers than that found in lakes. This decrease in assimilation efficiency may be accompanied by an increase in the proportion of ingested food that is recycled. Therefore, when using measurements of particulate P in lake water to predict mussel P excretion rates, it may be necessary to know the composition of the particulate material, and what proportion is plankton versus resuspended detritus. One possible measurement that may serve as an index of particulate composition is the carbon : chlorophyll a ratio, which can provide an approximation of the proportion of particulate material that is made up of phytoplankton. Another measurement, which Madon et al. (1998) found to be useful is the inorganic : organic ratio in suspended particulate material, which is a relatively simple measurement to make.

Dreissenid mussels have a gut residence time no longer than several hours, and therefore their metabolism may be expected to respond quickly to changes in food supply. This was confirmed by making a time series of P excretion measurements following acclimation to a food supply. As shown in Fig. 22, P excretion rates for all mussel sizes were highest immediately after mussels were separated from their food supply, and decreased over time. Most mussels achieved a “basal” P excretion rate after about one day without food, although the smallest mussels in the experiment (11 mm) appeared to take about two days to reach a basal rate. Therefore, to accurately predict P excretion by mussels in the lake, data on food availability will be required on a daily basis. While this is difficult to achieve using conventional manual sampling methods, it may be possible to use continuous measurements of *in situ* chlorophyll fluorescence (e.g. with a monitoring sonde) as a proxy for food availability within the lake.

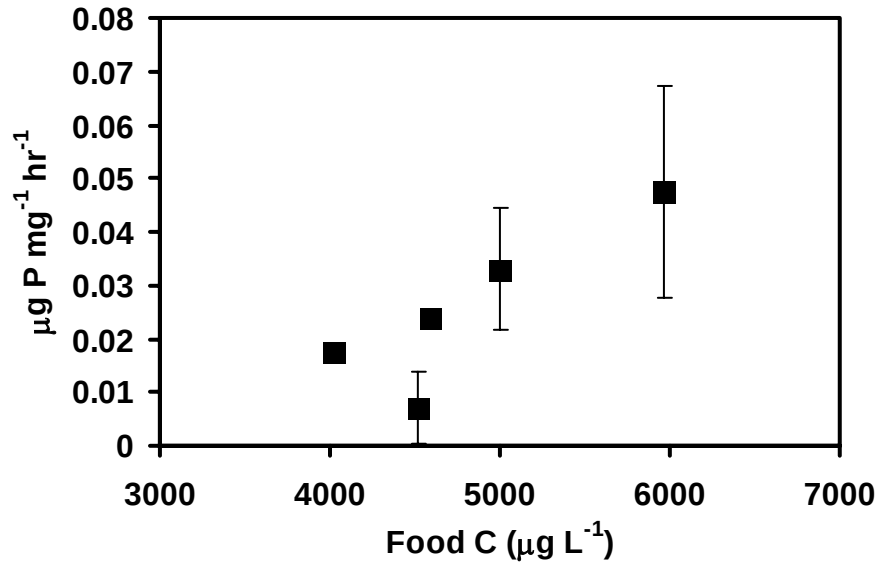


Fig. 19. Influence of food (*Scenedesmus* sp.) concentration, measured as particulate organic carbon concentration, on quagga mussel P excretion rate at 22°C. Mean mussel length for these experiments was 20 mm.

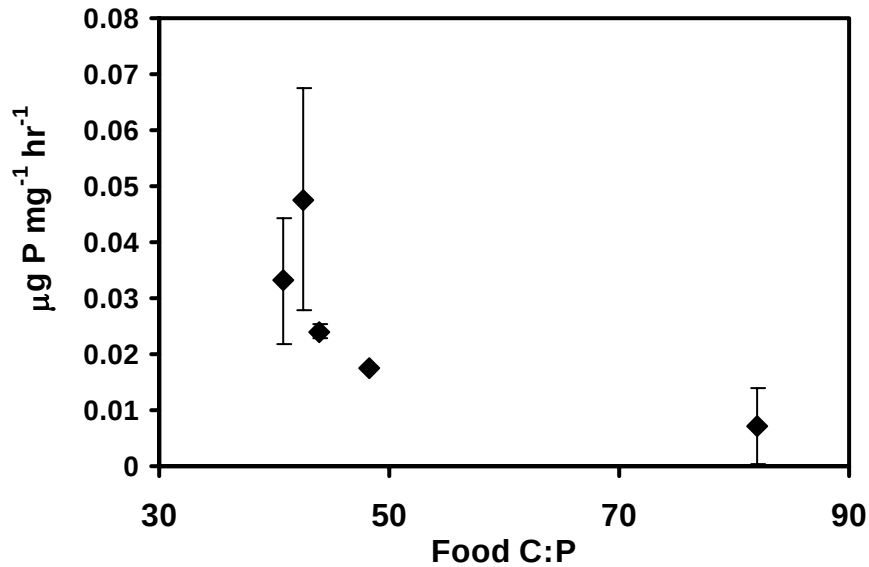


Fig. 20. Influence of *Scenedesmus* molar carbon : phosphorus ratio on quagga mussel P excretion rate at 22°C.

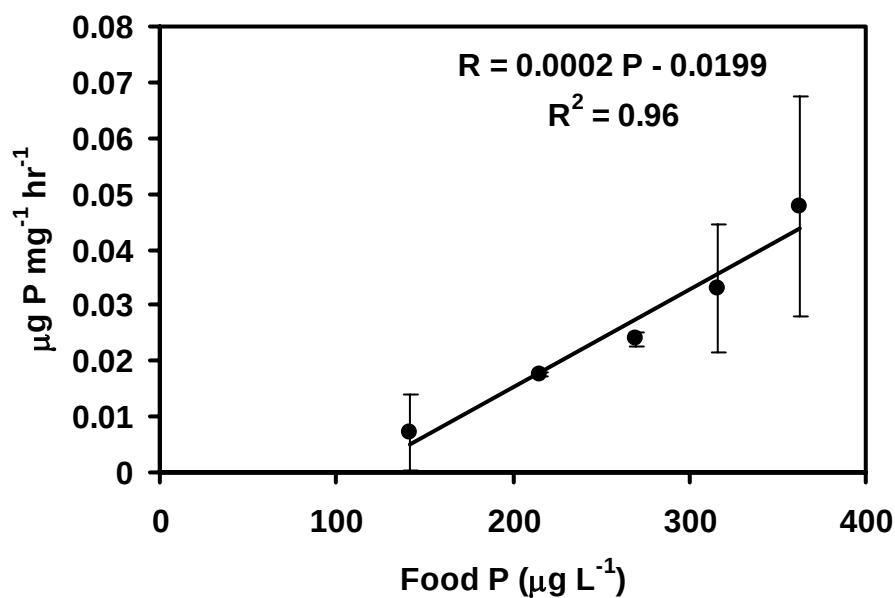


Fig. 21. Relationship between particulate phosphorus (as *Scenedesmus* sp.) concentration in acclimation water to quagga mussel P excretion rate at 22°C.

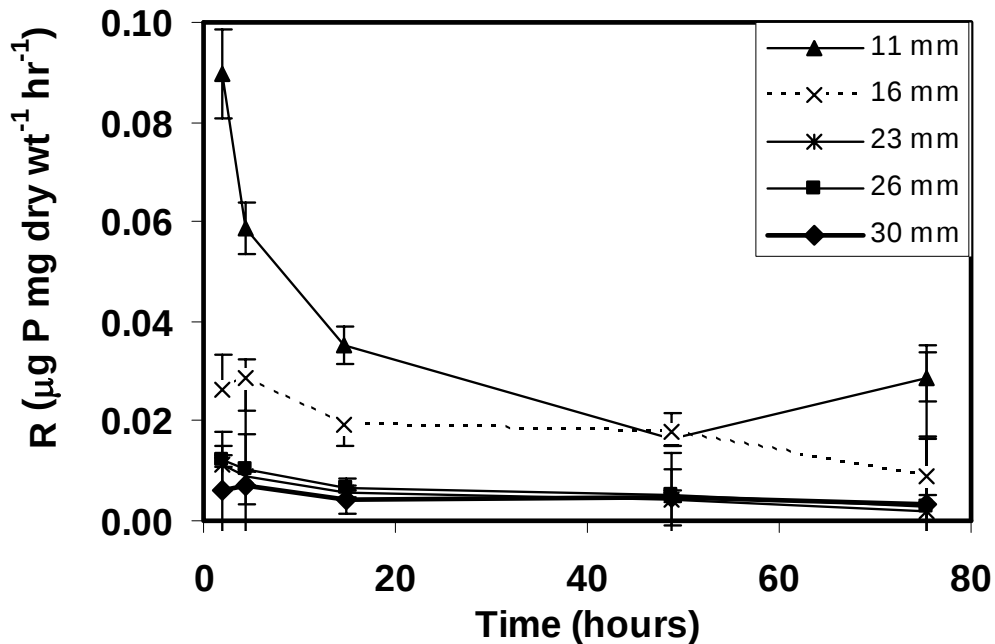


Fig. 22. Time response of mussel P excretion following removal from food source. Mussels of various sizes were acclimated in Milwaukee Harbor water (particulate P concentration = $6.9 \mu\text{g L}^{-1}$) for 3 days prior to P excretion measurements.

4.2.3 Effect of Temperature on Mussel P Recycling. A second experiment used a factorial design to examine the combined effect of temperature and food supply on mussel P excretion. In this experiment, mussels 20 mm in length were acclimated at three different temperatures, and at each temperature mussels were provided with four different food concentrations, one of which was a control (no food). As shown in Fig. 23, there was a positive curvilinear relationship between food supply and mussel P excretion rate. However, temperature had a much stronger influence on P excretion rate. Between 10 and 15°C, there was a modest increase in P excretion rate, but a temperature increase from 15°C to 22°C resulted in approximately a 4-fold increase in P excretion rate. The temperature range of 15°C to 22°C is one that characterizes Lake Michigan nearshore waters for much of the summer. As described in the Phase I report, mean June-August nearshore water temperatures for the Milwaukee nearshore region have increased by 3 to 4°C (5 to 7°F) over the past 30 years. During the June – August 2006 period, the mean temperature at the Atwater site (depth = 9 m) was 14°C (minimum = 6°C, maximum = 22°C), and on 31 of those days water temperatures exceeded 17°C. Because internal waves and upwelling events can cause large temperature fluctuations in the nearshore zone over short time periods, mussel SRP excretion can be expected to vary on a day to day basis, and **if nearshore warming trends continue, mussels can be expected to become a more significant source of phosphorus to the nearshore zone.**

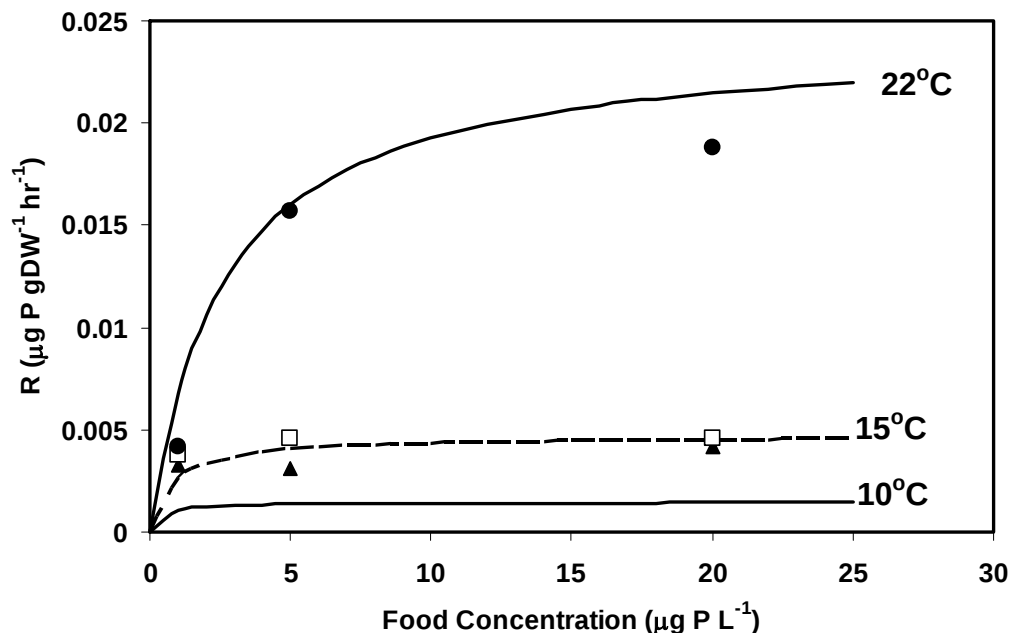


Fig. 23. Temperature response of P excretion rate (**R**) in quagga mussels acclimated to four different food concentrations. Mean mussel length was 20 mm, and food supply was a culture of green algae (*Chlorella* sp.). Points represent measurements made at 10°C (▲), 15°C (□), and 22°C (●). Curves show model simulation results.

Data from the temperature / food supply experiment were used to construct a model simulating the effect of these two variables on P excretion. To construct the model, the food – excretion relationship at each temperature was first fitted to a Michaelis-Menten type model:

$$R = \frac{V_{max} [S]}{K_m + [S]} \quad (1)$$

Where R = P excretion rate ($\mu\text{g P mgDW}^{-1} \text{ hr}^{-1}$), V_{max} is the maximum excretion rate, S is the food concentration (measured as $\mu\text{g particulate P L}^{-1}$), and K_m is the half-saturation constant. The fitted model parameters, V_{max} and K_m , were then plotted as a function of temperature. This revealed exponential relationships between these parameters and temperature, which were described by:

$$V_{max} = 0.0001 e^{0.241T}, r^2 = 0.998 \quad (2)$$

$$K_m = 0.0668 e^{0.166T}, r^2 = 0.973 \quad (3)$$

As a result, for any combination of temperature and food concentration, P excretion rate can be estimated. First, equations (2) and (3) are used to determine V_{max} and K_m , for a specific temperature, and these parameters are then used in equation (1), along with the known food concentration $[S]$, to estimate the excretion rate, R . This model was used to simulate P excretion over a range of temperatures for two food concentrations, $1.2 \mu\text{g P L}^{-1}$ and $6.1 \mu\text{g P L}^{-1}$. These concentrations were chosen because they are close to the observed lower and upper concentrations of particulate P at the Atwater station. The results of the simulation, along with experimentally measured rates at the two food concentrations, are shown in Fig. 24. The modeled results generally agree well with observations, although the model slightly underestimates P excretion at low temperatures, and slightly overestimates excretion at high temperature and low food concentration. It should be pointed out that the data used to construct this model were collected from experiments with 20 mm mussels. The model may still be applicable to mussels of other sizes (lengths), but in that case the calculated P excretion rates will need to be adjusted based on the length – excretion relationship described above (Fig. 15 and Fig. 16). The simplest approach to length correction is to first use the model to estimate P excretion based on ambient temperature and food concentration, and then multiply the derived rate by a length-correction factor. Using the observed weight – P excretion relationship (Figs. 15 and 16) and the length – weight relationship (Fig. 17), the relationship between P excretion rate (R) and mussel length is expressed as:

$$R = 0.1525 (0.0018 L^{3.11})^{-0.7617} \quad (4)$$

where R is the excretion rate ($\mu\text{g P mgDW}^{-1} \text{ hr}^{-1}$) and L is mussel length (mm). The above equation can be used to determine the mass-specific P excretion rate (R) for a given size of mussel. The ratio of the rate at a given size to the rate at 20 mm is then determined as:

$$F = 1207.8 L^{-2.3689}$$

(5)

So for example, the correction factor (**F**) for a mussel 15 mm in length is calculated as 1.98, and therefore the modeled P excretion rate is multiplied by 1.98 to determine the excretion rate for a 15 mm mussel.

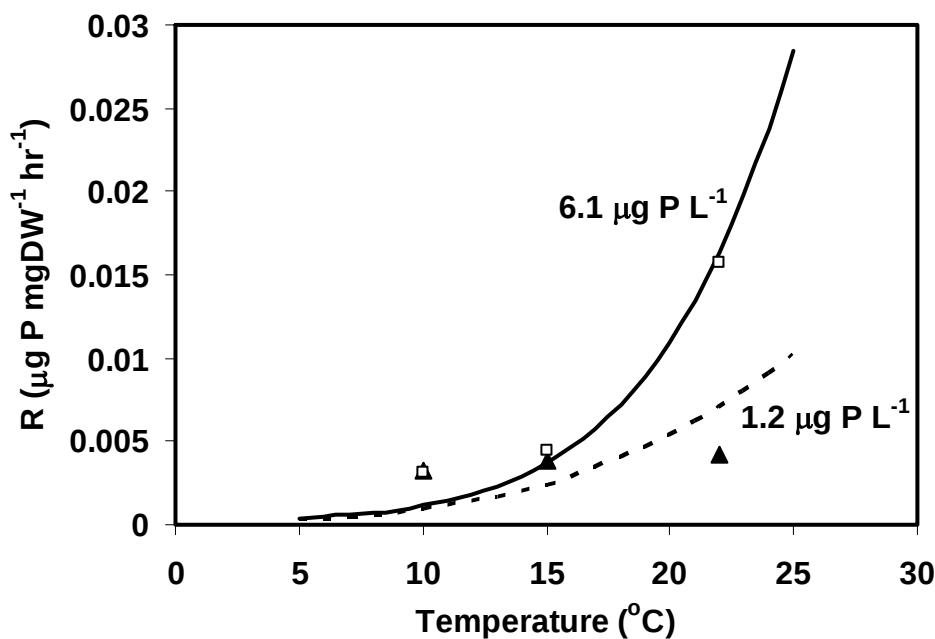


Fig. 24. Modeled relationship between P excretion rate and temperature for 20 mm quagga mussels at two different food concentrations. Open squares represent measured rates at a food concentration of $6.1 \mu\text{g P L}^{-1}$; Solid triangles represent measured rates at a food concentration of $1.2 \mu\text{g P L}^{-1}$.

4.2.4 Quagga Mussel P Excretion Model Application. The model described above was used to simulate mussel P excretion during the *Cladophora* growth period, May to October. The model was driven by environmental data collected from the Atwater station. These data included continuous water temperature measurements, particulate phosphorus measurements (representative of food supply), and data on mussel size distribution. Particulate phosphorus measurements were made weekly through most of this period, but less frequently in the first and last months. Mussel size distribution was measured on six occasions. The model was run with daily time steps, with daily values for food concentration and mussel size being interpolated from measured values.

The results of the simulation are shown in Fig. 25. Because temperature is the primary variable that drives mussel metabolism, the temporal fluctuations of modeled P excretion are somewhat similar to nearshore temperature patterns. Food supply may also play an important role, but during the 2006 study period, nearshore particulate phosphorus concentrations did not vary greatly among dates (mean = $2.28 \mu\text{g L}^{-1}$, std. dev. = 0.81).

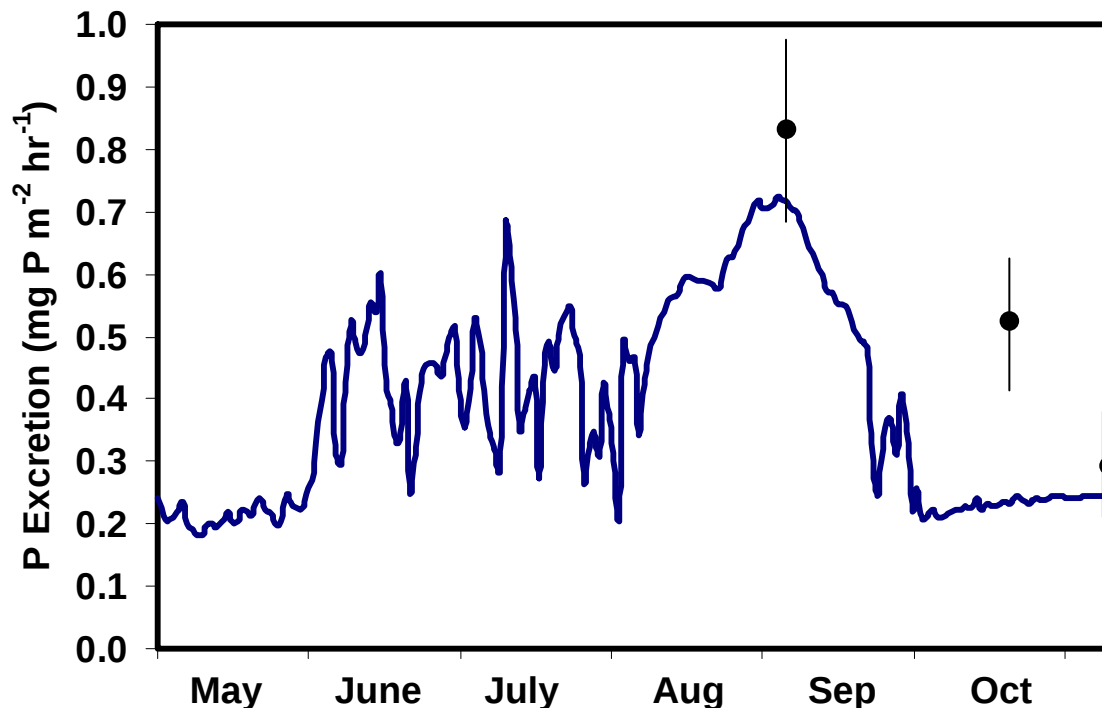


Fig. 25. Results of a model simulation of quagga mussel phosphorus excretion between May and October. Filled circles show benthic P flux rates measured *in situ*. Vertical bars show standard deviations. Measured benthic fluxes include mussels plus all other benthic organisms, such as bacteria, amphipods, and isopods.

On three days in late summer / fall of 2006, *in situ* measurements of benthic P flux were made using benthic chambers. The rates measured on these days are shown as filled circles in Fig. 25. The *in situ* rates measured on September 5 and November 9 are reasonably close to the modeled rates. For one date – October 20 – the simulated rate was significantly lower than the measured rate. There are several possible causes of this difference, including a possible underestimate of mussel biomass, and P release from detritus, including feces and pseudofeces, in the *in situ* incubation chambers. Laboratory experiments indicate that a large fraction of food consumed by quagga mussels can be egested as feces and pseudofeces (Maybruck 2007). The phosphorus recycling rate from this particulate material is not rapid, but if sufficient amounts accumulate on the lake bottom, especially during calm periods, its decomposition may make a significant contribution to the dissolved phosphorus pool. This potential P source is not accounted for in the model.

Despite the discrepancy between measured and modeled rates for the October 20 date, the comparison between measured rates and simulated rates is generally good considering the small number of validation points (further experiments are planned to complete this validation). The discrepancy in October may be due to the fact that, near temperatures of 10°C, the fitted model underestimates P recycling rate (see Fig. 3). The fact that modeled rates are consistently lower than measured rates may also reflect

the fact that organisms other than mussels can contribute to benthic P recycling in the lake. But the close agreement between measured and modeled values for the highest and lowest P recycling rates indicates that the empirical mussel P excretion model has utility in determining how phosphorus supply from quagga mussels will respond to changes in environmental conditions such as temperature, food supply, and mussel abundance. **For example, nearshore temperatures increased about 3°C between 1975 and 2000. If this rate of temperature increase continues, the model predicts that P excretion rates would be nearly 50% greater in 2025.** Conversely, if mussel abundance declines due to predation, disease or some other factor, the model can be used to determine the effect of such a decline on P excretion.

4.2.5 Putting Mussel Phosphorus Excretion into Perspective. Using the mussel excretion model, it is possible to estimate the potential role of mussels as a source of phosphorus to *Cladophora* in the nearshore zone if information on mussel distribution, mussel size, water temperature and food supply is available. In addition, an estimate of the *Cladophora* phosphorus demand is required. The net accumulation of phosphorus in *Cladophora* tissue can be determined by multiplying *Cladophora* biomass in 2006 (Fig. 26) by *Cladophora* P content to determine the areal concentration of *Cladophora* P (Fig. 27). If it is assumed that *Cladophora* biomass is negligible prior to spring (an assumption supported by the observed low biomass in late fall), then the accumulation of phosphorus within *Cladophora* during the growing season is equal to the maximum areal concentration of *Cladophora* tissue P. In 2006, this was 183 mg P m⁻². This approach assumes that all *Cladophora* growth accumulates as biomass between spring and the time of maximum biomass; i.e. any *Cladophora* that is lost to sloughing during this period is not accounted for. Because some *Cladophora* loss to sloughing likely occurs even during the accumulation period, this approach will result in a conservative estimate of *Cladophora* phosphorus demand. For example, in the Phase I report (Bootsma et al. 2006) we estimated *Cladophora* P demand based on *Cladophora* growth rates, rather than *Cladophora* accumulation, and the resultant estimated P demand was three times greater than that estimated here. In reality, the *Cladophora* P demand will be somewhere between these two estimates. This uncertainty does not affect the conclusions discussed below.

In addition to comparing mussel P excretion to *Cladophora* P demand, it is also instructive to consider mussel excretion relative to river P loading. A realistic comparison requires that both fluxes be expressed per unit area, and therefore an area must be delineated for this comparison. The area between Wind Point (south of Milwaukee) and Fox Point (north of Milwaukee), confined between the shore and a depth of 10 m, was chosen for this comparison. This area was selected because the Milwaukee Harbor is the only major source of water that drains into it², and the two points are physical barriers beyond which river-influenced coastal waters may be deflected to the open lake. The surface area of this zone is approximately 190 km². In the report for Phase I of this project, the calculations to determine phosphorus loading from the Milwaukee Harbor were presented as approximately 249 kg day⁻¹.

² The only other significant tributary is Oak Creek, for which the P loading rate is approximately 2.1% of that for the combined Milwaukee, Menomonee and Kinnickinnic Rivers. Therefore, it is not included in these calculations.

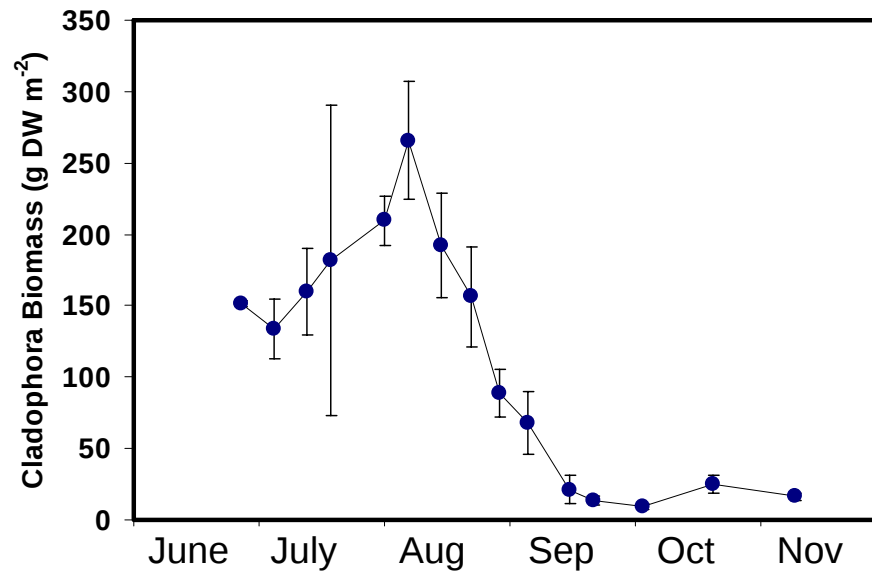


Fig. 26. *Cladophora* biomass (measured as dry weight of *Cladophora* per square meter of lake bottom) at a depth of 8 – 9 m, Atwater station, June to November 2006. All measurements are the means of 4 replicate samples.

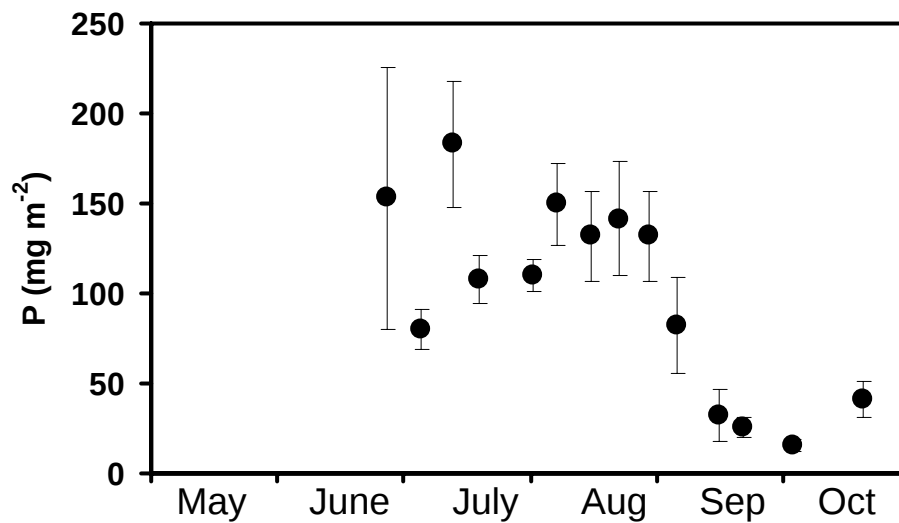


Fig. 27. Areal concentration of phosphorus within *Cladophora* tissue at the Atwater station (depth = 8 – 9 m), 2006. Values were determined as the product of *Cladophora* biomass and *Cladophora* tissue P content.

Over the 190 km² nearshore region this is equivalent to 1.31 kg km⁻² day⁻¹. To determine P supply from mussels, it is necessary to determine the proportion of lake bottom within this area that is covered with mussels, and what the mussel density is within that proportion. High resolution aerial photographs (acquired through a separate project funded by the Wisconsin Coastal Management Program) proved suitable for classifying bottom substratum to a depth of approximately 8 m. Using these images, the average proportion of lake bottom within the area of interest that is rocky bottom was determined as 65%. It was assumed that this value applies to the 8 m – 10 m portion of the lake bottom that is not visible in the images. It was also assumed that mussel density on all hard substratum is equal to that measured at the Atwater site, which averaged 5,500 per square meter.

Using these values, the excretion of P by mussels for the *Cladophora* growth period (set as May 1 to June 31) averaged 5.5 kg km⁻² day⁻¹. For the period May 1 to July 31, this represents a total flux of 906 mg P m⁻². A comparison of *Cladophora* P demand, river (harbor) P loading, and mussel P excretion (Table 1) suggests that, within the Wind Point to Fox Point nearshore region, mussel excretion provides 4 times more phosphorus than river inputs do, and mussel P excretion is more than that required by *Cladophora*. As pointed out above, the estimate of *Cladophora* P demand is conservative. However, considering the large difference between estimated *Cladophora* P demand and mussel P excretion, it seems unlikely that algal P demand exceeds the supply from mussels.

While the comparisons in Table 1 may suggest that river input of P plays a minor role compared to excretion of P by mussels, the two sources of P are not mutually exclusive. Much of the P entering the lake from rivers is in particulate form, and it is likely that mussels ingest and recycle at least some of this particulate P. In this case, the P excretion by mussels may ultimately be driven to some degree by P loading from rivers. In addition, a proportion of the P excreted by mussels will support the growth of plankton, which in turn may be consumed by mussels. In this case, mussel P excretion does not represent a net input of P to the nearshore ecosystem. Rather, the mussels serve as a catalyst to promote the recycling of dissolved P (DP) and the conversion of particulate P (PP) to a soluble form (DP) that is utilizable by *Cladophora*.

Table 1. A comparison of phosphorus supply and demand within the 190 km² nearshore zone between Wind Point and Fox Point, for the time period May 1 to July 31, 2006. All fluxes are normalized to the total area of 190 km². *Cladophora* and mussel fluxes were normalized by multiplying measured or modeled areal rates by 0.65, because 65% of the lake bottom in the specified area is hard substratum.

P Source / Sink	P Flux (mg m ⁻² d ⁻¹)	Flux for May 1 – July 31 (mg m ⁻²)	Total P for May 1 – July 31 (metric Tons)
<i>Cladophora</i> uptake		119	22.6
Input from Milwaukee Harbor	1.3	120	22.8
Mussel Excretion	5.5	506	96.1

The degree to which mussels feed on organic material derived from river inputs, as opposed to organic material derived from open-lake phytoplankton, will ultimately determine how quickly the nearshore ecosystem responds to any decrease in P loading from rivers. If mussel P excretion is driven primarily by food inputs from rivers (referred to as the nearshore phosphorus loop; Fig. 28), then the nearshore system will respond quickly to a decrease in river P loading. But if mussel metabolism is driven primarily by food supply from offshore plankton (offshore phosphorus loop, similar to what has been referred to by others (Hecky et al. 2004) as a “nearshore phosphorus shunt”), then the nearshore response to phosphorus abatement will be much slower. This is because Lake Michigan contains a huge standing stock of phosphorus with a relatively long residence time, which results in a slow response to external inputs. For example, according to the phosphorus model developed as part of the Lake Michigan Mass Balance Program (which uses data collected in 1994-95), if the concentration of P in inflowing rivers was reduced by 50%, it would take approximately 10 years for concentrations in the lake to be reduced by 50%. If the offshore loop is an important pathway by which P is made available to the nearshore zone, then it will take a similar length of time for nearshore processes, such as *Cladophora* growth, to respond to phosphorus abatement.

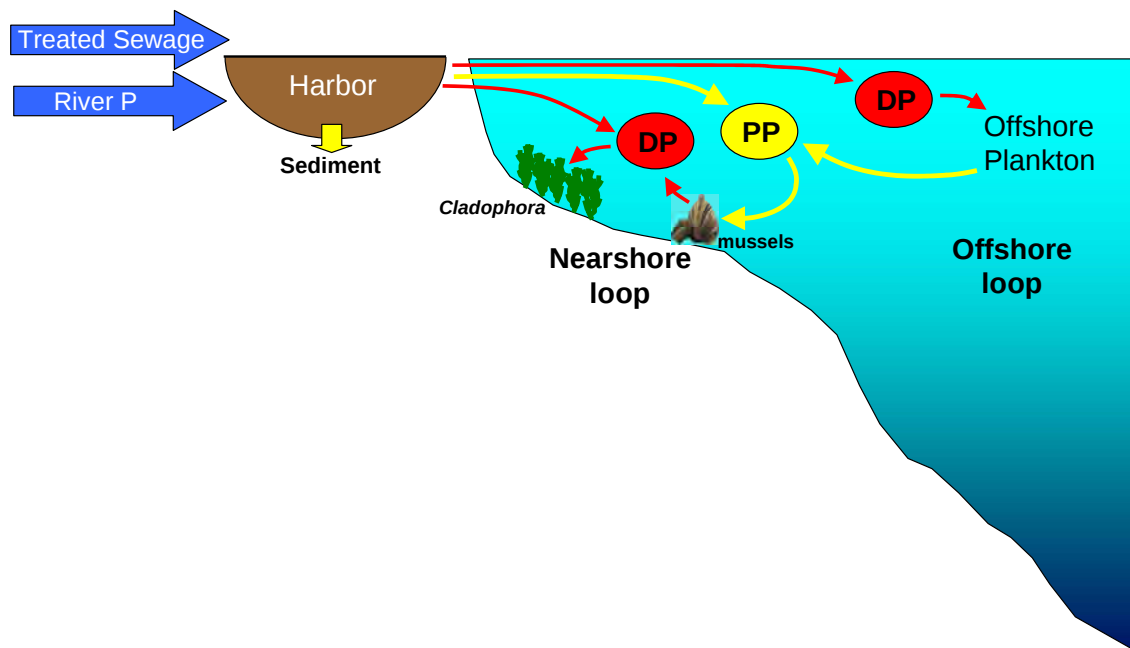


Fig. 28. Conceptual model of the nearshore phosphorus cycle. DP = dissolved phosphorus; PP = particulate phosphorus.

Currently, the relative importance of the nearshore loop versus the offshore loop is not known. Ultimately, it depends on hydrodynamics and the physical exchange rates between nearshore and offshore waters. Quantifying these rates would not only help to determine the nearshore response time to nutrient management strategies, but it would also allow for an assessment of the hypothesis that consumption of plankton by mussels in the nearshore zone is the main factor responsible for recent observed decreases in the abundance of plankton-eating fish such as alewife and rainbow smelt in the offshore zone.

The direct impact of river P loads on *Cladophora* will depend on the proximity to river mouth. In the above comparison, we selected a 40 km (25 mile) stretch of shoreline as the area of impact. If a smaller area was selected for the analysis, the relative impact of river load would be greater, whereas the impact would be less for a larger area. This influence of area on the relative impact of river loading can be demonstrated with a simple diffusion model, in which areal mussel P excretion rate is kept constant while the area-normalized river loading rate decreases as the area (length) of shoreline increases. As shown in Fig. 29, the direct influence of P loading from the Milwaukee Harbor to the lake can be expected to be significant within a distance of about 5 km (3 miles) north and south of the harbor. Beyond 15 km (9 miles) north or south of the harbor, river P loading is less than 10% of the total P supply (i.e. from river loading plus mussel excretion). This is in agreement with the spatial patterns of *Cladophora* biomass and tissue P content that we have observed (see section 3 in this report, and section 4.2 in the 2006 report of Bootsma et al.).

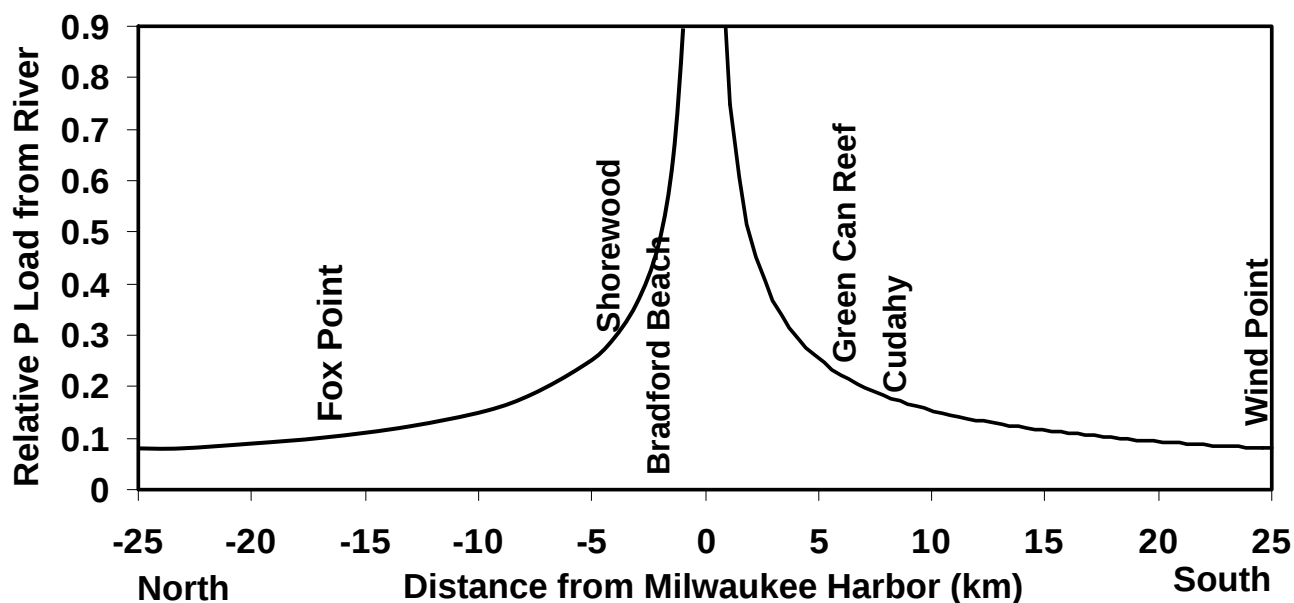


Fig. 29. Results of a diffusion model demonstrating the relative importance of river loading versus phosphorus excretion by mussels as sources of phosphorus to the Lake Michigan nearshore zone in which *Cladophora* grows. At a distance of 15 km or greater from the Milwaukee Harbor, mussels are responsible for greater than 90% of the phosphorus supply.

5. A *Cladophora* Model

A numerical model of *Cladophora* has several useful applications. First, it allows for the analysis of the effects of multiple environmental variables (temperature, irradiance, phosphorus concentration) on *Cladophora*. These variables interact in complex ways that may not be apparent if they are considered individually. A model accounts for this complexity. Second, a numerical model allows the testing of conceptual models of how the nearshore ecosystem functions, i.e. it indicates whether hypotheses about ecosystem functioning are valid, or if they are unrealistic. Third, a model is a powerful management tool that allows for exploration of various scenarios, whether they be management interventions or naturally occurring events such as climate change. This is especially useful with regard to management, as models allow for an assessment of the potential efficacy of various management options, which can then be weighed against the costs of those options.

An initial *Cladophora* model was developed in the early 1980s (Auer et al. 1982). That model was specifically developed for Lake Huron, under environmental conditions that were different from current conditions in Lake Michigan (e.g. there were no dreissenid mussels in the Great Lakes in the early 1980s). One of the objectives of this study was to collect data on *Cladophora* and environmental conditions in Lake Michigan to assess, and if necessary modify, the original *Cladophora* model. This was augmented with laboratory studies to examine the photosynthesis – irradiance relationship for *Cladophora* and how it is influenced by temperature and *Cladophora* P content.

In addition to revising the model, a graphical user interface (GUI) was developed. Advantages of the GUI include:

- 1) It simplifies the application of the model, so that users do not require programming experience.
- 2) It allows for easy adjustment of key model parameters.
- 3) It allows for adjustment of *in situ* phosphorus concentrations, which provides a quick view of the modeled response of *Cladophora* to changes in phosphorus loading.
- 4) It provides a visual display of model results along with any *in situ* observations, which allows for a visual assessment of model performance.
- 5) It provides quantitative information on the relative importance of temperature, light, phosphorus, and carrying capacity as factors limiting *Cladophora* growth.

A complete description of the revised *Cladophora* model is provided in Appendix 1. The main findings related to the modeling exercise are presented below.

Initial runs of the model for Lake Michigan indicated that simulated *Cladophora* biomass tended to be significantly lower than observed values. A comparison of model parameters with the results of our laboratory experiments indicated that the specific respiration rate of 0.44 day^{-1} used in the initial model is high. (The specific respiration rate is the proportion of gross photosynthesis that is respired; a value of 0.44 indicates

that the respiration of carbon as CO₂ is 44% of the gross carbon uptake by algae). In our laboratory experiments where algal carbon metabolism was measured over a range of light intensities, we found that specific respiration rates were generally less than 0.44 day⁻¹, with a mean of 0.23 day⁻¹. When this value was used in the model, simulated biomass values agreed well with measured values during the *Cladophora* accumulation period of June to July (Fig. 30).

Following the *Cladophora* biomass peak in early August (Fig. 30), there was a one to two week delay between the observed biomass decline and the modeled decline. This is probably because the observed decline was due to sloughing, a process which is not simulated by the model because the environmental factors that control sloughing are not well understood. The lack of sloughing within the model also explains the sustained moderate level of biomass through September and October, which were greater than the actual observed biomass values during that period. Currently, a sloughing coefficient can be applied in the model simply by entering a value in the GUI. However, this is a simplistic, and probably unrealistic approach to the sloughing problem, and a more complete understanding of the sloughing process will be necessary before this process can be adequately simulated within the model.

Although the sloughing process is not accounted for in the current model, from a management perspective it is more critical that the model is able to simulate the growth process, and that the maximum model biomass is similar to the observed maximum. This is because the management objective is not to control sloughing, but to control

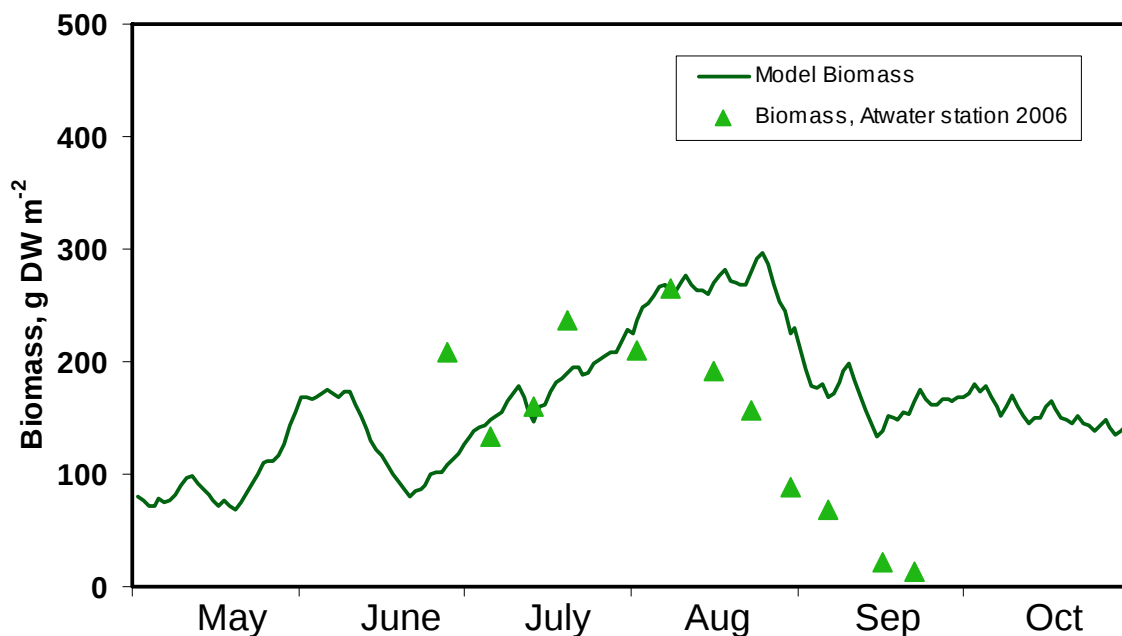


Fig. 30. Comparison of modeled (—) and measured (▲) *Cladophora* biomass for the period May – October, 2006, 9 m depth, Atwater Station. Model input included in situ temperature measurements, in situ light measurements, and soluble reactive phosphorus measurements.

Cladophora growth and biomass accumulation. Figure 30 demonstrates that the model simulates both biomass accumulation and maximum biomass quite well, suggesting that the model can be used with some degree of confidence to explore various scenarios by adjusting the model drivers of water temperature, light (which is a function of both atmospheric irradiance and water clarity), and dissolved phosphorus concentration.

A useful output of the model is a quantification of the relative importance of the various growth limiting factors. A plot of these factors against time (Fig. 31) is included as part of the model output. Figure 31 illustrates that, at a depth of 9 m, *Cladophora* growth is strongly limited throughout the summer by suboptimal temperature and light conditions, moderately limited by phosphorus, and limited very little by carrying capacity. This agrees with the Phase I observations, which showed that *Cladophora* growth becomes minimal at depths beyond 12 to 13 m, due to low light. Figure 31 also illustrates that phosphorus has a relatively strong influence on *Cladophora* growth at 9 m, while carrying capacity has a small influence (i.e. *Cladophora* biomass is usually well below the maximum possible biomass).

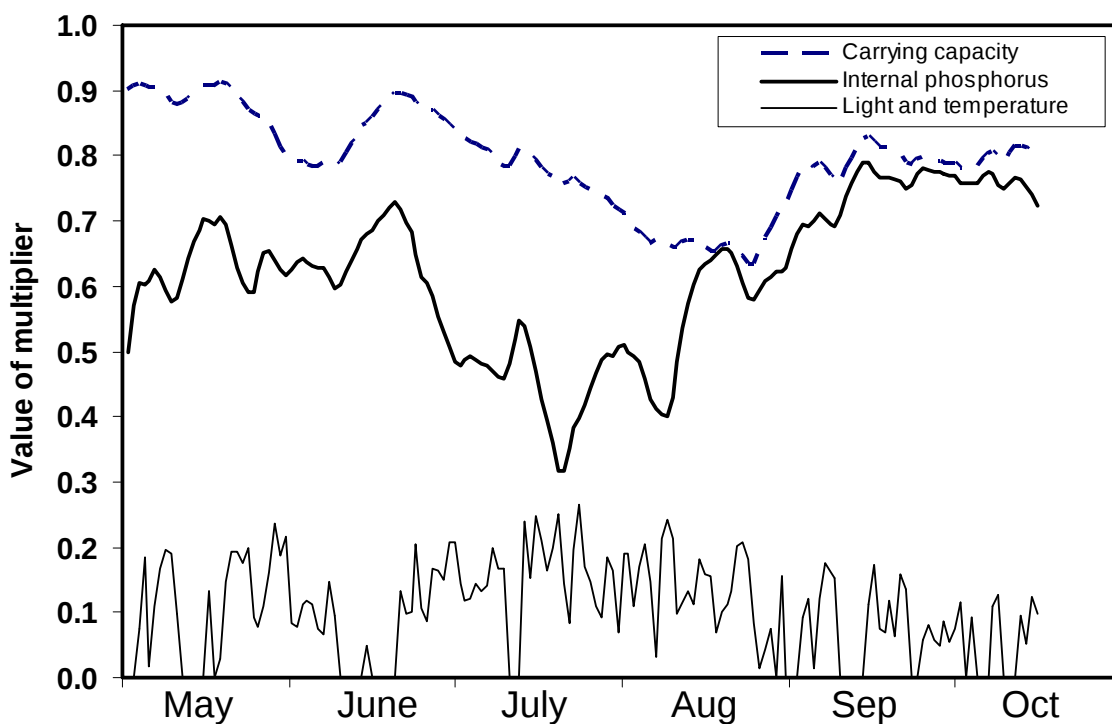


Fig. 31. Temporal dynamics of growth-limiting factors at a depth of 9 m at the Atwater station, summer 2006. A value near 1.0 indicates that the factor is nearly saturated, and a further increase will have minimal influence on *Cladophora* growth. A low value indicates the factor is well below saturation, and *Cladophora* growth will respond strongly to a change in this factor.

The calibrated model was used to address two critical *Cladophora* management questions:

1. What factors are responsible for the recent resurgence of *Cladophora* in Lake Michigan?
2. How will *Cladophora* respond to reductions in soluble reactive phosphorus concentration?¹

5.1 Factors Responsible for the Resurgence of *Cladophora*

To address the first question, the model was run using water clarity, soluble reactive phosphorus¹ and temperature data for the pre-dreissenid (pre-1990) and post-dreissenid (current) time periods. Atmospheric irradiance was kept constant, using data for 2006. Historic trends of water clarity, dissolved P and temperature for the Lake Michigan nearshore zone in the Milwaukee region are shown in Figs. 32 – 34.

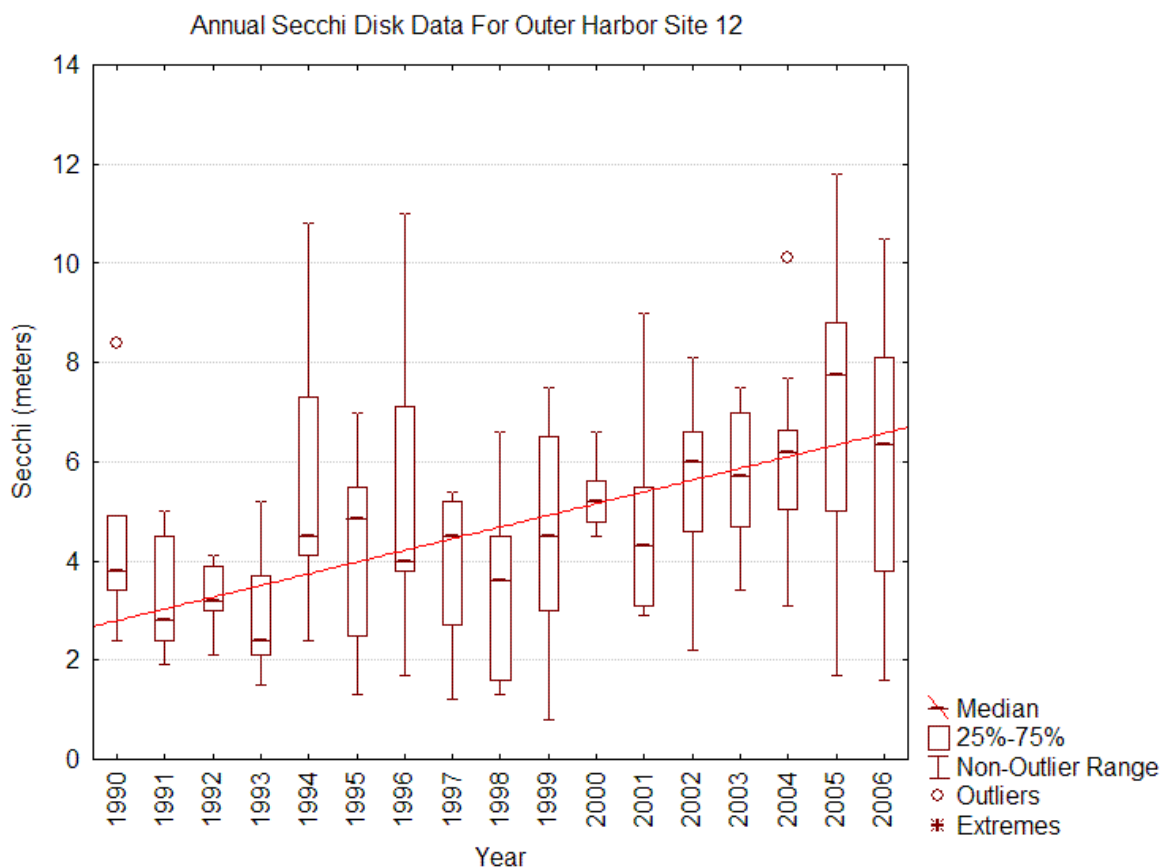


Fig. 32. Temporal trend of secchi disk depths measured just south of Milwaukee, 2 km offshore ($Z_{\max} = 10$ m). Data provided by Milwaukee Metropolitan Sewerage District.

¹ Management strategies are generally designed to achieve total phosphorus concentration targets, but the *Cladophora* model is driven by soluble reactive phosphorus. A comparison of historic SRP and TP concentrations for Lake Michigan tributaries and nearshore waters indicates these two variables are strongly correlated, and therefore reduction of TP concentrations can be expected to result in SRP reduction.

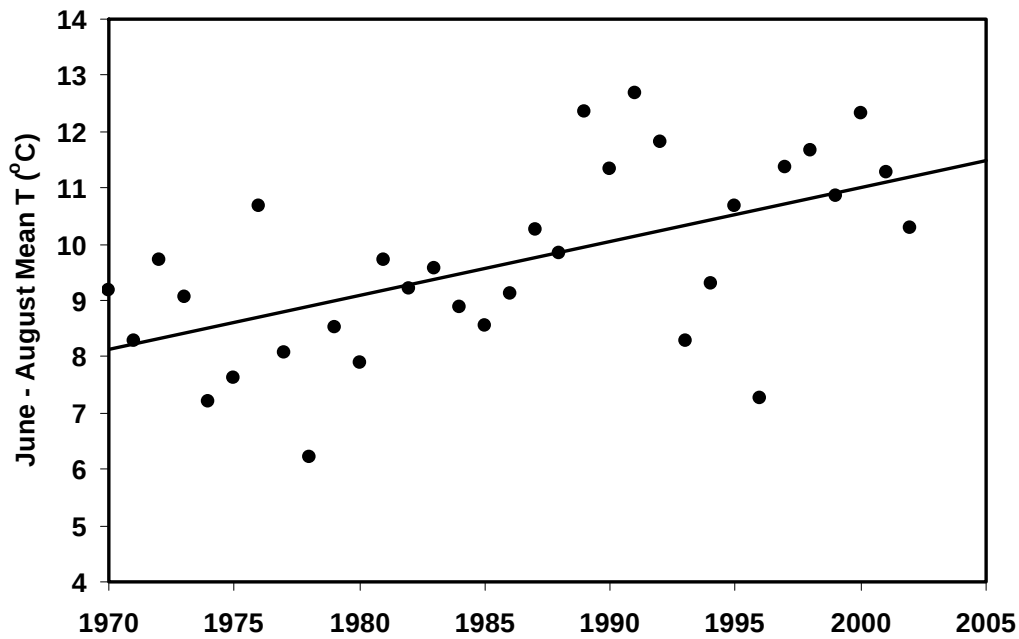


Fig. 33. Historic trend of average summer (June – August) nearshore water temperatures. Data are from the Linnwood water intake, which is positioned at a depth of 15 m.

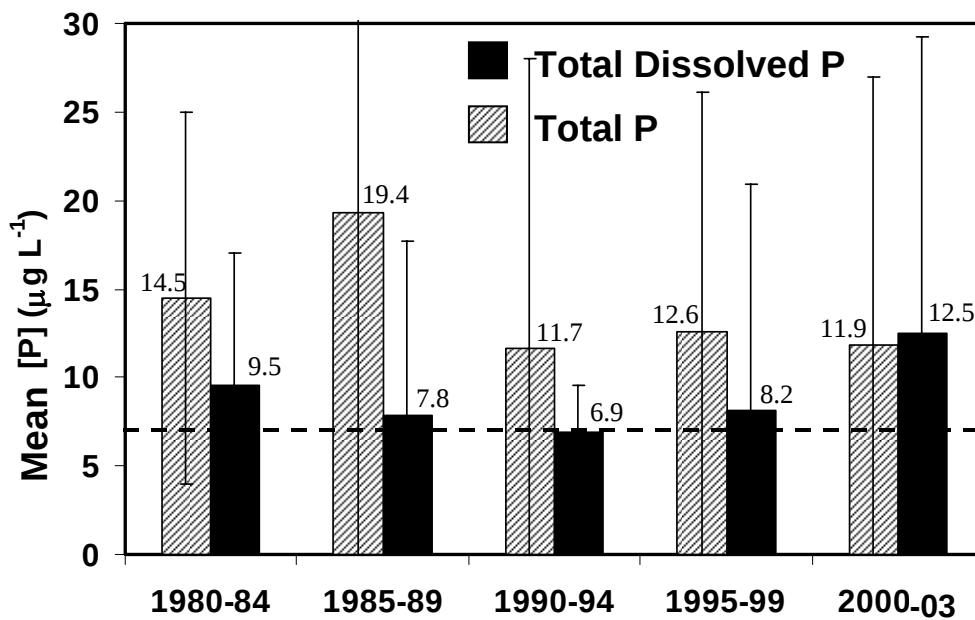


Fig. 34. Historic trend of near-bottom mean total dissolved phosphorus and total phosphorus concentrations at MMSD nearshore station OH-12 (located approximately 1 km offshore of the north gap of the Milwaukee Harbor wall, in about 13 m of water). Data provided by MMSD. Dashed line shows the target level of $7 \mu\text{g L}^{-1}$ total P set for open waters of Lake Michigan under the Great Lakes Water Quality Agreement.

Based on the trends shown in these figures, values for water clarity (light extinction coefficient), water temperature, and SRP (see footnote on page 47) were selected to represent current conditions and conditions prior to the establishment of dreissenid mussels (1985-89). These values are presented in Table 2. Current (2006) values are means for the Atwater station during the period of May 1 – July 31, because this is the primary growth period (sloughing begins in early August). Pre-mussel values were calculated as the daily values recorded in 2006 at the Atwater station multiplied by the mean pre-mussel : 2006 ratio (7.8 : 12.5) for each variable at MMSD's station OH-12. This approach was taken because the OH-12 data set provides an indication of historic trends, while the Atwater data is likely to be more representative of nearshore conditions over the lake as a whole.

Table 2. Water clarity, temperature and dissolved phosphorus values used as model input to determine the effects of historic changes in these values on *Cladophora* biomass in the Milwaukee region of Lake Michigan. 2006 values are means for the period May 1 – July 31, 2006. The model used actual daily values.

Period	Light Extinction Coeff. (m^{-1})	Temperature ($^{\circ}\text{C}$)	SRP ($\mu\text{g L}^{-1}$)
Current	0.325	10.2	0.58
Pre-mussel	2006 values X 2 = 0.65	2006 values – 2.5	2006 values X 0.62 = 0.35

Initial simulations using the above values indicated that the long-term change in nearshore temperatures has likely had a minimal effect on *Cladophora* biomass. Temperature has a strong influence on *Cladophora* metabolism, but because both the gross photosynthetic rate and the respiration rate increase with temperature, the effect on net photosynthesis and growth in the 10 – 20 $^{\circ}\text{C}$ temperature range is small. As shown in Fig. 35, the model suggests that the 2.5 $^{\circ}\text{C}$ temperature increase since the mid 1970s has resulted in slightly higher biomass in spring and early summer, and slightly lower biomass in late summer and fall, with very little effect on maximum biomass.

Because of the apparent small effect of temperature change on *Cladophora* biomass over the past several decades, the model was used to test the effects of temporal changes in water clarity and soluble reactive phosphorus (SRP). Using the values in Table 2, the annual *Cladophora* accumulation was determined under four scenarios: 1) pre-mussel conditions of water clarity, temperature and SRP concentrations; 2) The same as scenario 1, but with current SRP concentrations; 3) The same as scenario 1, but with current water clarity; 4) current (2006) conditions for water clarity and SRP concentrations. For all simulations, water temperatures and atmospheric irradiance measurements for 2006 were used. *Cladophora* growth was simulated for depths ranging from 2 m to a depth at which net biomass accumulation was 0, and the resulting biomass values were integrated over depth. It was assumed that biomass accrual was insignificant at depths of less than 2 m, due to wave action.

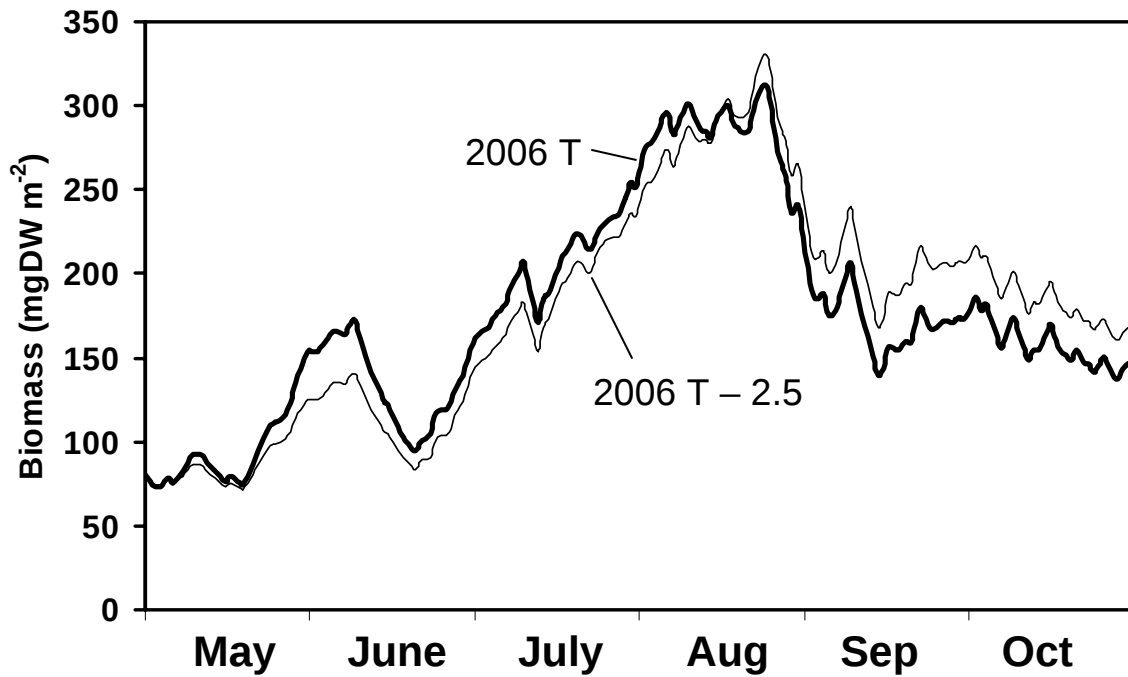


Fig. 35. Simulated *Cladophora* biomass at a depth of 9 m, showing the effect of a 2.5°C temperature increase between the mid-1970s and 2006 on algal biomass.

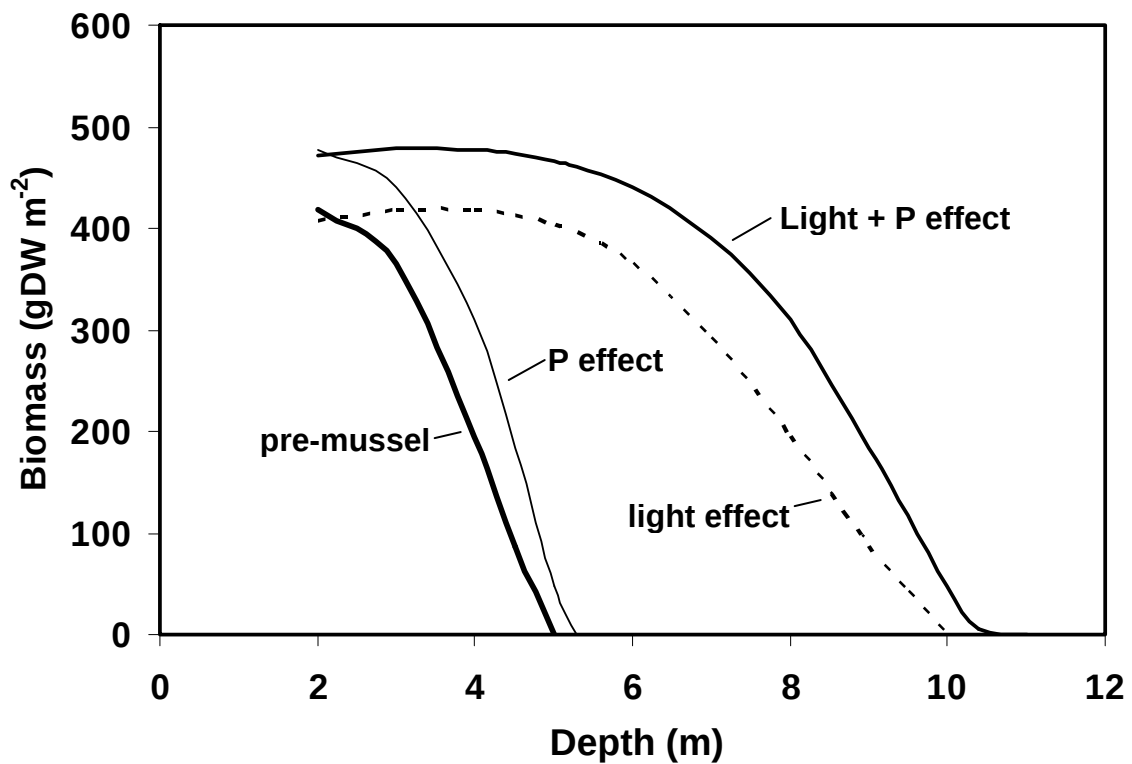


Fig. 36. Modeled effects of changes in water clarity (light effect) and soluble reactive P concentration on the depth distribution of *Cladophora* biomass. All simulated results are for August 7, the day on which maximum biomass was measured in 2006.

The results of these simulations are presented in Fig. 36. **While the increase in nearshored dissolved phosphorus concentration has resulted in a small increase in *Cladophora* biomass, it appears that the primary cause of increased biomass is the increase in nearshore water clarity.** The estimated increase in nearshore mean SRP concentration from a May-July mean of $0.35 \mu\text{g L}^{-1}$ in 1980-84 to $0.56 \mu\text{g L}^{-1}$ in 2000-03 results in a 37% increase in depth-integrated biomass, from 266 to 365 kg per m of shoreline (Fig. 37). This increase is due primarily to increased growth at each depth, with little change in the maximum depth of growth. By contrast, the increase in water clarity alone over the same time period results in more than a 3-fold increase in depth-integrated biomass. This is a result of the fact that: 1) the increased water clarity results in an increase in biomass at shallow depths, and 2) the depth range over which *Cladophora* can grow has doubled. Under pre-mussel water clarity conditions, the model indicates that the maximum depth at which net positive growth occurred was approximately 5 m. This has increased to almost 11 m in the post-mussel period (Fig. 36).

While numerical models such as the one presented here are useful in understanding complex ecological processes, model results must be used with caution, especially when applied to conditions outside of those for which the model is calibrated and validated. Nutrient dynamics and algal growth in the nearshore zone of Lake Michigan are complex processes, and no model can capture all of the factors that contribute to this complexity. The Lake Michigan *Cladophora* model was validated primarily with data from a depth of ~9 m. At shallower depths, the model indicates that biomass will increase, due to increased light availability. However, at shallower depths turbulence resulting from currents and wave action will also be greater, and this can be expected to have a negative impact on biomass that may counter the effects of increased light to some degree. Indeed, *Cladophora* biomass depth transects measured in 2005 (presented in Fig. 15 of the phase I report for this project) indicated that biomass at 5 m was equal to that at 9 m. Therefore the biomass values shown for depths shallower than 8 to 9 m in Fig. 36 are more likely to be overestimates than underestimates, as are the depth-integrated biomass values in Fig. 37. However, while this may affect the calculated magnitude of the increase in total *Cladophora* biomass following the establishment of dreissenid mussels, it does not alter the conclusion that the primary cause of this increase is increased water clarity, which has led to an increased depth range of the algae.

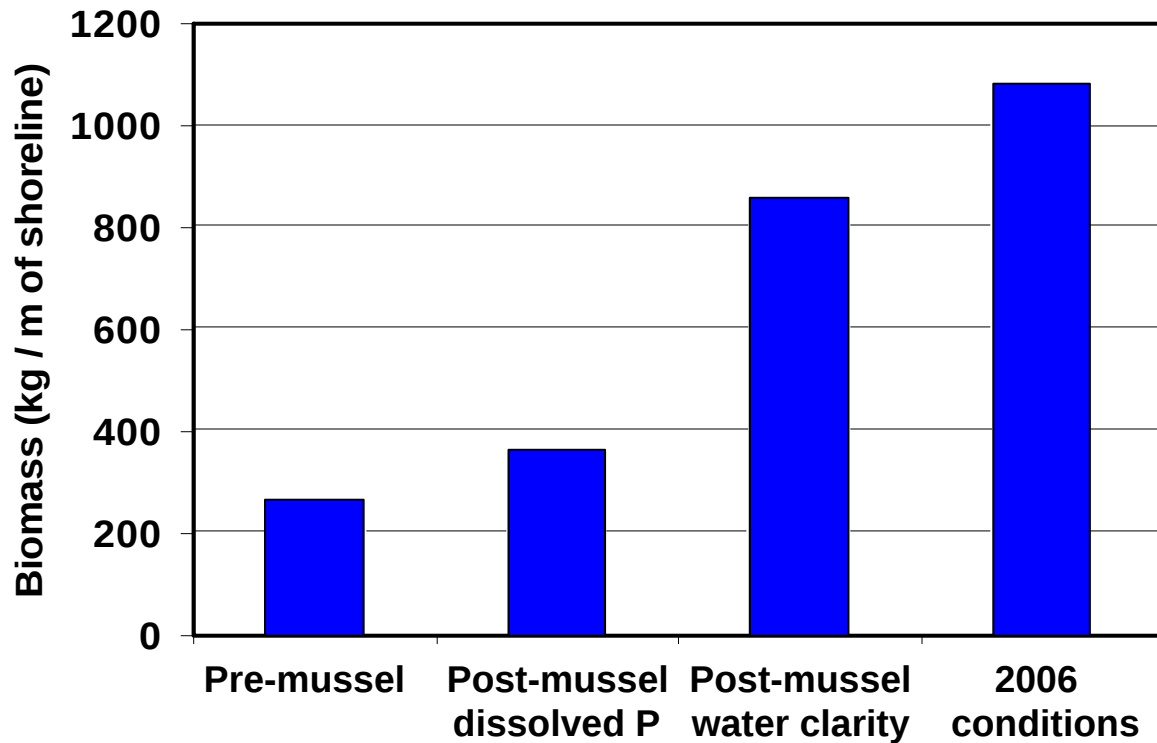


Fig. 37. Modeled maximum *Cladophora* accumulation under the four phosphorus / light scenarios used for Fig. 36, illustrating the effects of long-term changes in water clarity and dissolved phosphorus concentrations on *Cladophora* biomass in the Milwaukee region of Lake Michigan. Depth-integrated biomass was calculated using a nearshore lake bottom slope of 1:250, determined from bathymetric maps of the Milwaukee region of Lake Michigan.

5.2 Can *Cladophora* be Managed Through Phosphorus Control?

Although increased water clarity is a primary cause of the recent increase in *Cladophora* abundance, managing water clarity in Lake Michigan is not a viable option. The only potential management option is to counter the effects of increased water clarity by decreasing phosphorus loading from rivers. The obvious question is: how much would phosphorus concentrations need to be decreased, and is it feasible?

Just as the model can be used to assess the influence of recent changes in environmental conditions on *Cladophora* growth, so it can be used to assess the expected impact of phosphorus control. In Figures 38 and 39, the modeled *Cladophora* response to reductions in soluble reactive phosphorus (SRP) concentrations are shown. The response varies with depth. For example, a SRP reduction of 50% is predicted to result in a biomass reduction of 85% at 9 m, and 27% at 5 m.

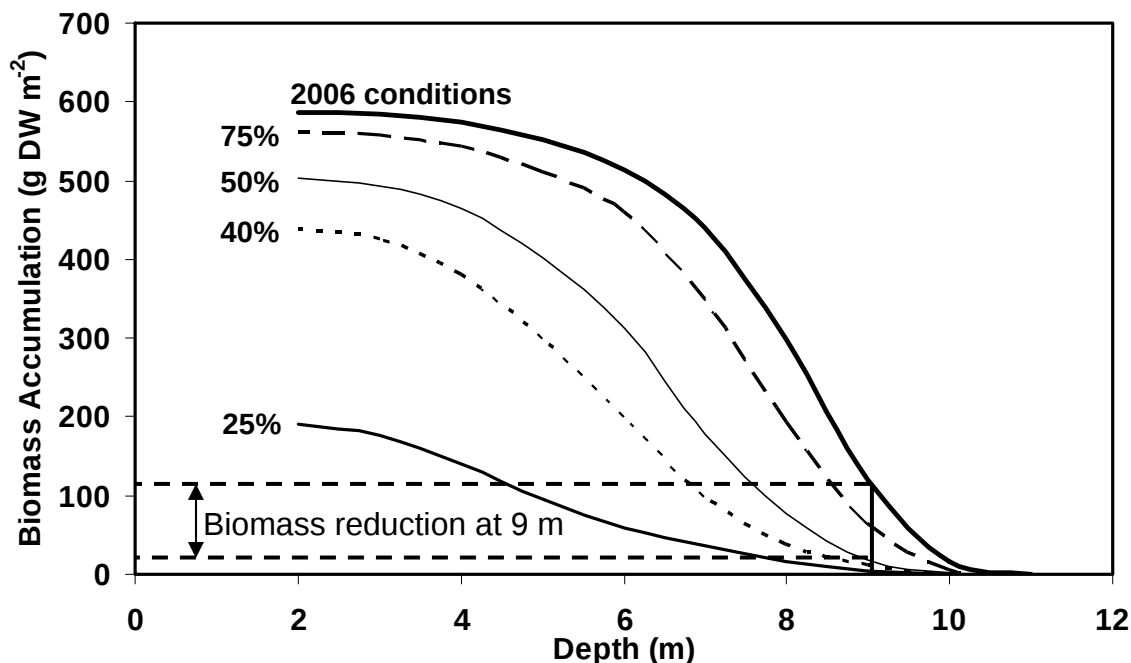


Fig. 38. Depth distribution of *Cladophora* biomass under various soluble reactive phosphorus reduction scenarios. Simulations were done using SRP, temperature and light data collected at the Atwater station in 2006. For each depth, the model shows maximum biomass prior to August 7. Initial biomass used for all simulations was 20 g m⁻² dry weight. Plotted values represent biomass increment above the initial 20 g m⁻². Percent values for each curve represent SRP concentrations relative to measured 2006 values. Mean 2006 SRP concentration was 0.58 µg L⁻¹ for the May-July growth period, and 0.92 µg L⁻¹ for the entire May – November monitoring period.

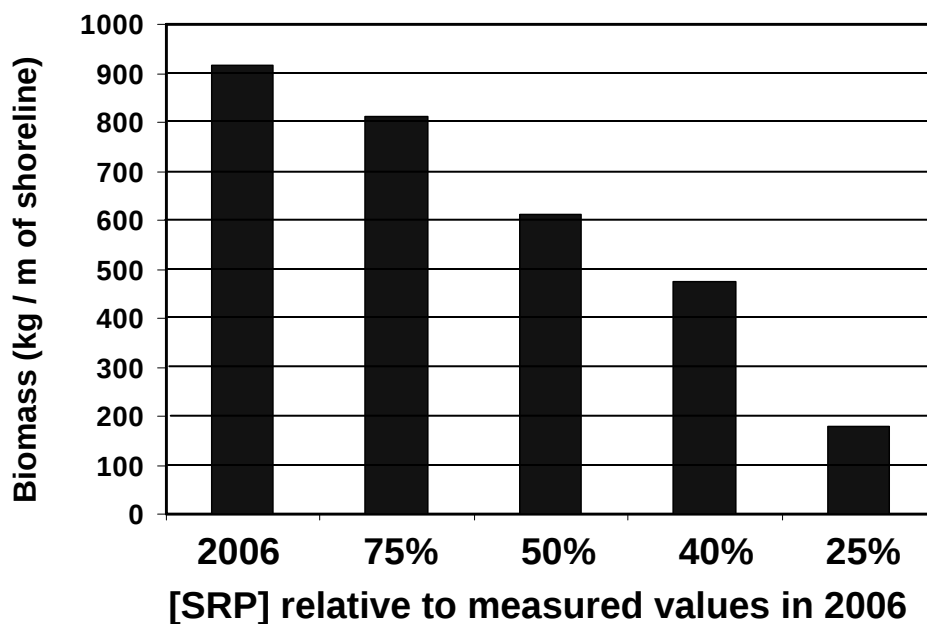


Fig. 39. Response of depth-integrated maximum *Cladophora* biomass to reductions in soluble reactive phosphorus concentrations. Details as for Fig. 38.

The amount of phosphorus reduction required to reduce *Cladophora* biomass to an acceptable level will vary with location, according to water clarity and availability of hard substratum. In regions with little hard substratum for the algae to grow on, a biomass density of 150 gDW m⁻² may be tolerable, whereas a lower biomass may be required in regions where the lake bottom is predominantly rocky. In a study near Harbor Beach, Lake Huron, Canale and Auer (1982a) found that beach aesthetics were significantly improved when average *Cladophora* biomass was reduced from 150 to 75 gDW m⁻², and the biomass maximum was reduced from nearly 300 gDW m⁻² to ~160 gDW m⁻². This corresponded to a reduction in mean soluble reactive P concentration from 40 µg L⁻¹ to 10 µg L⁻¹. Currently, nearshore TDP concentrations in Lake Michigan waters immediately offshore of Bradford Beach are greater than 12 µg L⁻¹ (Fig. 34). However, even if they were as low as the 10 µg L⁻¹ concentration that Canale and Auer found acceptable for Lake Huron in 1979, there would still be a *Cladophora* problem in Lake Michigan. The reason is that current water clarity in Lake Michigan is much greater than that in nearshore Lake Huron in 1979. Using the data provided by Canale and Auer (1982b), the estimated extinction coefficient for photosynthetically available radiation (PAR) in Lake Huron was approximately 1.7, while that for the Lake Michigan nearshore in 2006 was 0.325. As a result, the current depth range of *Cladophora* in Lake Michigan (11 to 12 m) is much greater than it was in Lake Huron in 1979 (~2 m).

The current model likely overestimates *Cladophora* biomass at shallow depths, so the biomass reductions shown in Figures 38 and 39 are probably conservative; i.e. actual depth-specific biomass levels would probably be less than those shown in Fig. 38. The model indicates that, at a depth of 9 m, a 50% reduction in SRP concentration would result in the maximum biomass being reduced from 115 gDW m⁻² to 20 gDW m⁻². As discussed above, previous measurements have indicated that biomass is not significantly greater at shallow depths than at 8 to 9 m, and therefore biomass response to phosphorus reductions may be similar across depths. If this is the case, then it is not unrealistic to expect that a 50% decrease in SRP concentration may result in biomass reductions of 50% or greater at all depths.

The question remains as to whether a 50% reduction in nearshore SRP concentration is achievable. As shown above (Fig. 34), **nearshore total dissolved P (TDP) concentrations near Milwaukee Harbor in the past have actually been as low as 55% of current concentrations.** The *Cladophora* model is driven by soluble reactive P (SRP) rather than TDP. However, a comparison of SRP and TDP data for Lake Michigan indicates the two are significantly correlated ($\text{TDP} = 1.69 \text{ SRP} + 1.56$, $r^2 = 0.67$). Therefore it is likely that SRP historic trends are similar to those for TDP shown in Figure 34, and SRP concentrations will respond to changing TP loads. **The cause of the recent increase in nearshore TDP is uncertain.** There is some evidence for a modest increase in P loading from the Milwaukee River over the past decade (see Fig. 24 in Phase I report). In addition, there has been an upward trend in the TDP : TP ratio in the Milwaukee River (Fig. 40), meaning that more of the P entering the lake is likely available for uptake by *Cladophora* and other algae. Potential sources of this TDP include agricultural soils, in which P content has increased by more than 50% in the last three decades, and municipal water (which is amended with phosphate for corrosion

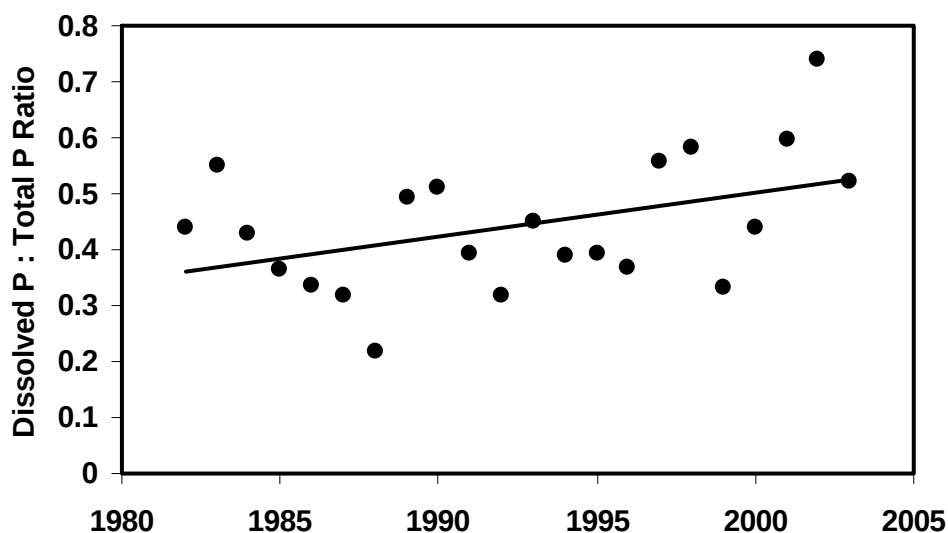


Fig. 40. Historic trend of the ratio of soluble reactive P : total P at MMSD station RI-15 on the Milwaukee River (located immediately upstream of the point where the river enters Milwaukee Harbor; see Fig. 1).

control) that does not pass through a wastewater treatment plant. A comparison of TDP and TP trends in the lake suggests that the TDP : TP ratio in the nearshore zone has also increased (Fig. 34). **While this may be due in part to the increased TDP:TP ratio for river loading, it is likely that dreissenid mussels have also contributed.** By consuming particles and excreting dissolved P, mussels can increase the TDP:TP ratio and convert particulate P into a dissolved form that is more available to *Cladophora*. Bivalves, including dreissenids, have been shown to be effective in converting particulate P to dissolved P in other systems (Heath et al. 1995; Arnott et al. 1996). The net result is that, even if P loads have not increased, more of the P entering the lake is made available for use by *Cladophora*. **Therefore, the nutrient parameter that needs to be managed is not soluble reactive phosphorus (SRP; sometimes referred to as orthophosphate, the most abundant inorganic form of phosphorus), but total phosphorus. *Cladophora* growth is directly driven by SRP concentration, but SRP in turn is ultimately controlled by total phosphorus loading.**

Phosphorus supply to the Lake Michigan nearshore region, in which *Cladophora* grows, is from two sources: direct allochthonous inputs from rivers and land surface runoff, and exchange between nearshore and offshore waters. Lake Michigan currently has a phosphorus standing stock of approximately 17,000 metric tonnes. In comparison, the most recent estimate of P loading to the lake is approximately 2,300 tonnes per year (see EPA presentaion: http://www.epa.gov/med/grosseile_site/LMMBP/LMMBP_Nutrients.pdf). This is reduced to about 1,600 tonnes per year if the loading from the Fox and Menominee Rivers is

excluded, as most of this loading is retained within Green Bay. Hence **the pool of P stored in Lake Michigan is more than 10 times the annual P load from rivers.** While the lake's standing stock of P is ultimately a function of loading rates, **within any given year phosphorus dynamics within the lake's open waters are controlled more by internal cycling processes than by external loads.** Whether or not this is the case for nearshore waters is uncertain. Nearshore waters are more directly influenced by river loads, as revealed by longshore trends in nutrient concentrations that match spatial trends of river loads (Garrison and Greb, 2005). However, through horizontal mixing the nearshore zone can also receive particulate P from the offshore zone, and this particulate P can be trapped in the nearshore zone as a result of filter feeding by zebra and quagga mussels. The relative importance of these two P sources – river loads and flux from the offshore to the nearshore – will determine the rate at which nearshore phosphorus concentrations and *Cladophora* biomass respond to decreased phosphorus inputs. If the nearshore zone is well mixed with the open lake, then total phosphorus concentration in the nearshore zone will respond to P loading reductions in the same manner as the whole lake. Figure 41 illustrates how the whole lake would respond to a 50% reduction in P loading. Following a reduction in P loading, it would take about 10 years for the lake to reach a new steady state. This reflects the lake's phosphorus residence time (calculated as total P pool divided by loading rate), which is about 10 years.

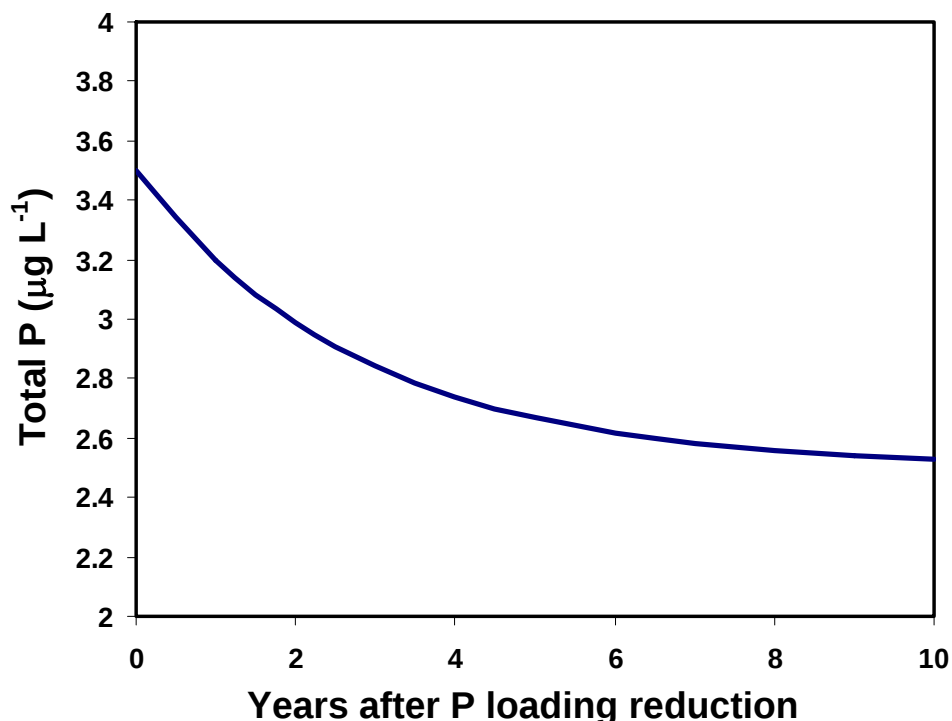


Fig. 41. Expected trend of whole-lake total phosphorus concentration following a 50% reduction in river phosphorus loads. Based on phosphorus model parameters derived as part of the Lake Michigan Mass Balance Study (1995).

If mixing between the open lake and the nearshore zone is slow, then the response of the nearshore zone to phosphorus loading reduction will be more rapid. This is illustrated by comparing the P residence time in the nearshore zone with that for the whole lake. The nearshore P residence time is calculated as the instantaneous mass of P divided by the P load. The instantaneous mass is a product of the concentration and the total volume. Garrison and Greb (2005) reported mean nearshore total P concentrations of 6 and 9 $\mu\text{g L}^{-1}$ for two longshore cruises between Door and Racine counties in 2004. During the present study, the mean total P measured at the Atwater station was 4.4 $\mu\text{g L}^{-1}$ (std. dev. = 1.6). Near river mouths, concentrations will be greater. For example, the 2000-05 mean near-bottom concentration at MMSD's OH-12 station offshore of the north gap of Milwaukee Harbor (see Fig. 1 for location), was 12.5 $\mu\text{g L}^{-1}$ (Fig. 34). Using 6 $\mu\text{g L}^{-1}$ as a representative value, and setting a depth of 15 m as the outer edge of the nearshore zone (*Cladophora* does not grow beyond this depth), the mass of P in the nearshore zone between Wind Point (near Racine) and the northern tip of the Door Peninsula is 53.4 metric tonnes. Using loading rates measured by the Lake Michigan Mass Balance Study and Phase I measurements made in 2005, the river P load to this same stretch of shoreline is approximately 284 tonnes per year. Therefore, the nearshore P residence time is a little more than 2 months – a very short time in comparison to the total lake P residence time of 10 years. If there were absolutely no mixing between nearshore and offshore waters, the nearshore zone would respond very rapidly to P loading reductions.

Over an annual cycle, there will always be complete mixing between the nearshore and offshore zones, and therefore average nearshore phosphorus concentrations will probably respond to load reductions over a time scale similar to that for the whole lake – i.e. about a decade. However, within an annual cycle mixing between the two zones will vary from week to week. During storm events or downwelling events caused by onshore winds, mixing will be rapid. But under calm conditions, or when winds promote longshore currents, horizontal mixing will be reduced and nearshore nutrient concentrations will be strongly influenced by river inputs. A critical time of year is the May – June period. The results of our studies over the past several years indicate that most of the P uptake by *Cladophora* is during this period, when light and temperature conditions are becoming optimal for the algae. Much of the algae growth through the rest of the summer is supported by the P that is assimilated during these months. Therefore, if river P loading is high during or immediately before this period, *Cladophora* growth may be greater than would be expected based on average annual P loads. Conversely, *Cladophora* growth will likely be much reduced if river P loading is reduced during this period. Therefore, while reductions of annual average nearshore P concentration will take many years (assuming loads are reduced), a more immediate response may be realized if P loading in the spring and early summer months is reduced. Unfortunately, this is a time of year when both river discharge and river P load can be high (Figs. 42 and 43). Although it will be a challenge to reduce P loads during these months, especially in years with heavy rainfall, it is likely that a greater benefit (in terms of *Cladophora* reduction) per unit cost will result from focusing on P reduction in these months rather than attempting to reduce total annual loads by 50%.

Based on current estimates made by the Milwaukee Metropolitan Sewerage District (MMSD) and the Southeastern Wisconsin Regional Planning Commission (SEWRPC) in 2006, the Jones Island Wastewater Treatment Plant contributes about 15% of the combined Milwaukee / Menomonee / Kinnickinnic total P load (with an additional 1.4% coming from combined sewer overflows), and about 33% comes from industrial point sources, with the other major contributor being agricultural non-point loading (29%). Reducing P loads from any one of these sources will likely have a moderate effect on nearshore P concentrations and *Cladophora* abundance. However, if each of these sources was reduced by 50%, that would result in a total P load reduction of about 40%. The impact of such a reduction on nearshore phosphorus concentrations and *Cladophora* abundance in the Milwaukee region of Lake Michigan is difficult to precisely determine. Relationship between P loading and nearshore P concentrations depends on nearshore hydrodynamics, nearshore-offshore exchange, and P uptake kinetics of *Cladophora*, none of which are currently well quantified. However, within the Milwaukee Outer Harbor region, nearshore total P concentrations (as shown in Fig. 34) are higher than in offshore waters, which indicates that nearshore-offshore exchange is slow enough that nearshore waters are significantly influenced by external P load. Therefore, it is not unreasonable to assume that a 40% reduction in P load might reduce outer harbor total P concentrations from the 2000-05 mean of $11.9 \mu\text{g L}^{-1}$ to a value in the range of 7 to $9 \mu\text{g L}^{-1}$ (the current mean TP concentration in the open waters of Lake Michigan is $\sim 3.5 \mu\text{g L}^{-1}$). The *Cladophora* model was used to determine what effect this decrease in total P concentration might have on *Cladophora*. Prior to running the model, total P concentrations were converted to soluble reactive P concentrations, assuming a SRP:TP ratio similar to that measured at the Atwater station (0.13). This resulted in SRP concentrations of 1.63 and $1.04 \mu\text{g L}^{-1}$. Using these values as input, and a depth of 9 m, the model predicts that a decrease in SRP concentration to $1.04 \mu\text{g L}^{-1}$ would result in approximately a 17% decrease in the average and maximum summer *Cladophora* biomass, with the average decreasing from 190 to 155 gDW m^{-2} (18%). These results are relevant to the nearshore region in the immediate vicinity of Milwaukee Harbor, which includes Bradford Beach.

The above scenario demonstrates how *Cladophora* near Milwaukee Harbor would respond to a 40% decrease in SRP concentration. If a similar reduction in loading is applied to more oligotrophic waters with P concentrations similar to those observed at the Atwater station, the reduction in average summer *Cladophora* biomass is predicted to be about 35%, and the reduction in maximum biomass would be about 45%. **The greater *Cladophora* response at such sites is due to the fact that *Cladophora* growth becomes more sensitive to changes in P concentration as P concentrations decrease**, i.e. the change in biomass per unit change in P concentration is greater at low P concentrations than at high P concentrations. However, the lower the dissolved P concentration, the more difficult it is to produce further decreases in concentration, because natural P recycling processes in the lake will always maintain P concentrations above a minimum threshold. During 2006, the mean total P concentration at the Atwater station was $4.4 \mu\text{g L}^{-1}$ (std. dev. = 1.6). Phosphorus modeling done as part of the Lake Michigan Mass Balance Study suggests that, if there was no river P loading to the lake, the steady state total P concentration in

the Lake would be about $2.2 \mu\text{g L}^{-1}$. If the SRP:TP ratio of 0.13 is applied to this value, the resulting SRP concentration would result in minimal growth of *Cladophora* at depths greater than 7 m, and a reduction in maximum summer biomass of 55% at a depth of 6 m. This is obviously an unrealistic scenario, but it provides some boundaries within which realistic management goals can be set.

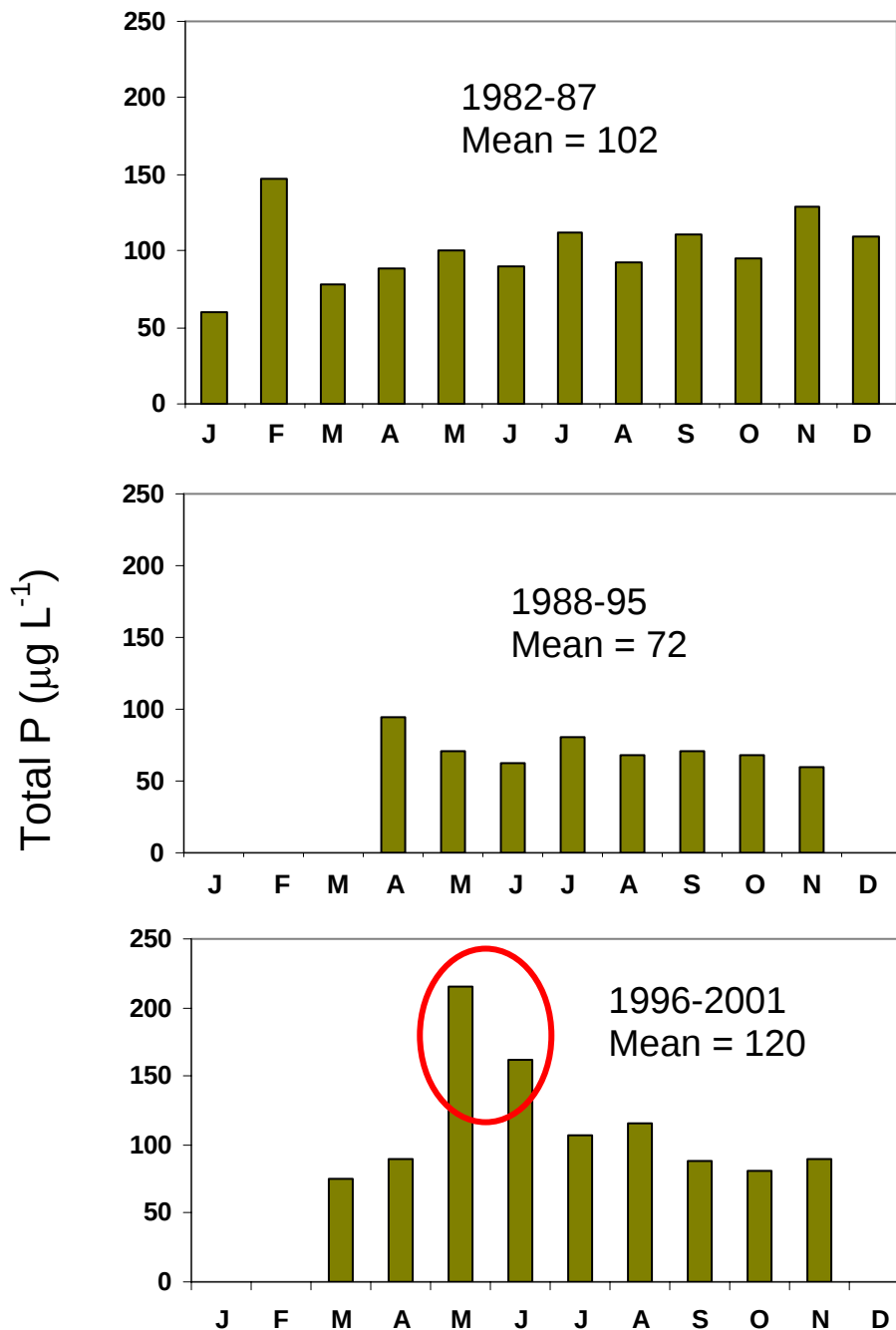


Fig. 42. Seasonal distribution of total phosphorus concentration in the Milwaukee River for three different multi-year time periods. Data provided by MMSD. The red circle highlight the time of year when *Cladophora* assimilated and stores P to support growth during summer.

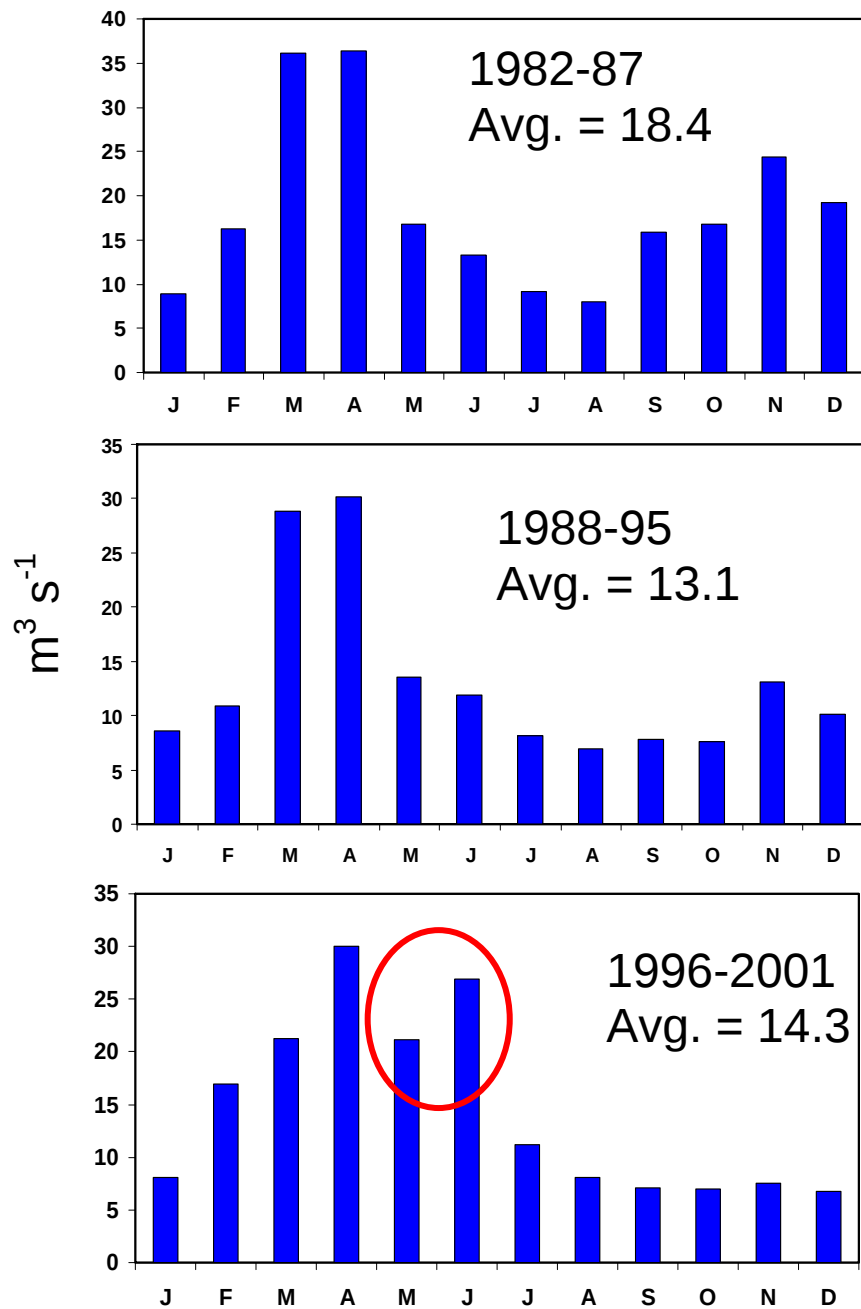


Fig. 43. Seasonal distribution of Milwaukee River discharge for three different multi-year time periods. Data provided by USGS.

6. Conclusions

- While there is some evidence that phosphorus loading to Lake Michigan has increase in the last decade, and that nearshore total phosphorus concentrations have increased (at least within the Milwaukee region), **the primary cause of increased *Cladophora* abundance is greater nearshore water clarity.**
- Increased water clarity is a result of mussel filtration in the nearshore zone. As a result, *Cladophora* at depths of less than 5 m is more productive than it was in the past, and more importantly, **the depth range of *Cladophora* has doubled**, so that there is now a much greater biomass per unit of shoreline.
- Although phosphorus loads do not appear to be the main cause of the increase in *Cladophora*, **a reduction in nearshore phosphorus concentrations is the only means by which *Cladophora* abundance might be reduced.**
- Total phosphorus concentrations in the pelagic (open) waters of Lake Michigan are below the target concentration of $7 \mu\text{g L}^{-1}$ set as part of the Great Lakes Water Quality Agreement. However, **as a result of the increase in water clarity, phosphorus target concentrations may need to be reconsidered, at least for nearshore waters.**
- **Nutrient cycling by dreissenid mussels (zebra and quagga mussels) represents a major challenge for the reduction of phosphorus concentrations in the nearshore zone.** At the regional scale (e.g. Wind Point to Fox Point), mussels provide dissolved P at a rate several times faster than it enters from rivers. Therefore, any reduction in nearshore dissolved P concentrations will require not only a reduction in the direct loading of dissolved P from rivers to the nearshore zone, but a reduction in the supply of food to mussels, which can be in the form of particulate P entering the nearshore zone both directly from rivers, and from offshore waters in the form of plankton.
- The amount of plankton provided to the nearshore zone is determined by pelagic plankton production, which is ultimately driven by external P loads. However, due to the long residence time of P in Lake Michigan, pelagic plankton production will respond slowly to changes in P loads. **Reducing river P loads will have some beneficial local effects in the short term, but the maximum benefits of reduced P loads will be realized over longer periods of 5 to 10 years.** In the short term, maximum benefits will be seen if P loads are minimized in the April – June period, when most P uptake by *Cladophora* occurs.
- During the current study (2006), the mean total P concentration measured at the Atwater station was $4.4 \mu\text{g L}^{-1}$. In comparison, the total P concentration in the open waters of Lake Michigan has steadily declined from $6.0 \mu\text{g L}^{-1}$ in 1996 to $3.5 \mu\text{g L}^{-1}$ in 2005 (Barbiero et al. 2002; Bootsma 2006). These concentrations are the lowest that have ever been measured since a regular monitoring program

began in the early 1970s. This would appear to make further reductions a difficult task. However, based on the available data, **P loading rates are still relatively high**. Therefore the low total P concentrations in the lake are likely not the result of reduced loading. Rather, they may be due to effective P scavenging by mussels, which release P in particulate form (feces and pseudofeces) that remains trapped in lake sediments, and in dissolved form that can be taken up by *Cladophora*.

- **Ultimately, the P excretion rate of mussels and the growth of *Cladophora* are controlled by the supply of phosphorus, not the ambient concentration.** Mussel filtration effectively keeps particulate P concentrations low, while high *Cladophora* photosynthetic rates resulting from high water clarity keep dissolved P concentrations low. As a result of these two processes, lake total P concentrations do not reflect P loading rates (supply).
- If Lake Michigan nutrient cycles were still functioning in the way they did prior to the establishment of dreissenid mussels, it would be very difficult to attain total P concentrations lower than $4.4 \mu\text{g L}^{-1}$ (the average at the Atwater station during this study). But if, as the evidence suggests, mussels have altered the phosphorus cycle in a way that reduces the ambient concentration : loading ratio, then **it should be possible to reduce nearshore total P concentration to a level similar to the current open water concentration of $3.5 \mu\text{g L}^{-1}$ through a reduction in total P loading.**
- Presently, there are insufficient quantitative data on key nutrient cycling processes (e.g. nearshore-offshore exchange rates; the fate of mussel feces and pseudofeces) to predict precisely how in-lake phosphorus concentrations will respond to changing loads (current Lake Michigan nutrient cycling models do not account for the effects of mussels and the “nearshore shunt”). The response will depend on current P loading rates. **In nutrient-rich areas such as Milwaukee Harbor and Bradford Beach, moderately large reductions in P loading will result in only modest reductions in *Cladophora* biomass.** For example, model results suggest that a 50% reduction in industrial point sources, agricultural non-point sources, and wastewater treatment sources would reduce nearshore SRP concentration by approximately 40%, and the maximum *Cladophora* biomass by about 17%.
- **In most nearshore areas, where total phosphorus concentrations are less than half of those near Milwaukee Harbor, *Cladophora* will be more responsive to reductions in P loading** because the sensitivity of *Cladophora* growth to dissolved P concentration increases as P concentration decreases. For example, at a depth of 8 m at the Atwater station, a 50% reduction in the concentration of soluble reactive P (the P form that is most available to algae, and that is used as input to the *Cladophora* model) would result in a 74% reduction in *Cladophora* biomass. Currently it is difficult to determine to what degree P loading would need to be reduced to achieve a targeted reduction in

nearshore total P concentration, because nearshore P cycling dynamics are not well understood.

- In the past 30 years much has been done to reduce the loading of P to Lake Michigan and the other Great Lakes. **Reducing loads further, even by another 25%, will be a challenge and will require focusing on sources where reductions can be achieved with the greatest cost effectiveness.** For agricultural sources, this will likely mean focusing on phosphorus “hot spots”, rather than applying blanket strategies to broad areas. Even then, reductions will come slowly, as agricultural soils contain a huge store of phosphorus with a very slow turnover time (Carpenter 2005). Advances in identifying and managing phosphorus hot spots is currently being made through programs such as the UW-Extension Discovery Farms Program and the Wisconsin Buffer Initiative. Within urban areas, sources of diffuse loading will need to be identified, as will industrial point sources.

As mentioned above, nutrient dynamics in Lake Michigan have changed over the past decade, making nutrient models that were developed as part of the Lake Michigan Mass Balance Study in the mid 1990s unrealistic. The nearshore zone has become much more important with regard to energy flow and nutrient dynamics. As a result, there are key processes which are important to understand in order to better predict the response of *Cladophora* and other organisms to nutrient loading. This study has addressed several of these, including the recycling of phosphorus by dreissenid mussels, and the influence of phosphorus, light and temperature on *Cladophora* growth and biomass.

The most urgent need is to better understand the links between phosphorus inputs from rivers and nearshore total phosphorus concentration, so that realistic loading targets can be set. The next steps toward improving our predictive capacity with regard to nutrient loads and *Cladophora* response are:

- 1) Determine the fate of riverine particulate P, which makes up approximately one third of P input from rivers, and is a food source for mussels. Is it retained in the nearshore zone? Is it consumed by mussels and recycled as biologically available dissolved inorganic P?
- 2) Quantify nearshore – offshore exchange of phosphorus; How effective is the nearshore phosphorus “shunt”, and how does it modify the relationship between P loading and nearshore algal growth?
- 3) Determine how depth influences *Cladophora* sloughing; Does increased light availability result in greater *Cladophora* biomass at shallower depths, or does sloughing offset the advantage of higher irradiance and cause *Cladophora* at shallow depths to respond to phosphorus concentrations in the same manner as deep *Cladophora*?

7. Literature Cited

- Arnott, D.L., and M. Vanni. 1996. Nitrogen and phosphorus recycling by the zebra mussel (*Dreissena polymorpha*) in the western basin of Lake Erie. *Can. J. Fish. Aquat. Sci.* 53:646-659.
- Auer, M.T., and Canale, R.P. 1982a. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 2. Phosphorus uptake kinetics. *J. Great Lakes Res.* 8:84-92.
- Auer, M.T., and Canale, R.P. 1982b. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 3. The dependence of growth rates on internal phosphorus pool size. *J. Great Lakes Res.* 8:93-99.
- Auer, M.T., R.P. Canale, H. C. Grundle, and Y. Matsuoka. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron : 1. Program description and field monitoring of growth dynamics. *J. Great Lakes Res.* 8: 73-83.
- Barbiero, R.P., M. Tuchman, G. Warren, and D. Rockwell. 2002. Evidence of recovery from phosphorus enrichment in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 59(10):1639-1647.
- Beardall, J. Young, E. and Roberts, S. 2001. Interactions between nutrient uptake and cellular metabolism: approaches for determining algal nutrient status. *Aquatic Sciences.* 63: 44-69.
- Bootsma, H.A. 2006. Naturally occurring chemicals: nutrients. Plenary presentation, State of the Lakes Ecosystem Conference 2006, Milwaukee, WI.
http://www.epa.gov/solec/solec_2006/plenary/day2/nutrients.pdf
- Bootsma H.A., E.G. Young, and J.A. Berges. 2005. Temporal and spatial patterns of *Cladophora* biomass and nutrient stoichiometry in Lake Michigan. Proceedings of a workshop "*Cladophora* Research and Management in the Great Lakes", Great Lakes Water Institute Dec. 8, 2004.
http://www.glwi.uwm.edu/research/aquaticecology/cladophora/page_report.php
- Bootsma, H.A., E.B. Young, and J.A. Berges. 2006. *Cladophora* abundance and physical / chemical conditions in the Milwaukee region of Lake Michigan. Great Lakes WATER Institute Technical Report No. 2005-02, submitted to the Milwaukee Metropolitan Sewerage District.
- Canale, R.P., and Auer, M.T. 1982a. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 5. Model development and calibration. *J. Great Lakes Res.* 8:112-125.
- Canale, R.P., and Auer, M.T. 1982b. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 7. Model verification and system response. *J. Great Lakes Res.* 8:134-143.
- Carpenter, S.R. 2005. Eutrophication of aquatic ecosystems: bistability and soil phosphorus. *Proc. Nat. Acad. Sci.* 102(29):10002-10006.
- DiToro, D.M. 1980. Applicability of cellular equilibrium and Monod theory to phytoplankton growth kinetics. *Ecol. Model.* 8:201-218.
- Droop, M.R. 1973. Some thoughts on nutrient limitations in algae. *J. Phycol.* 9:264-272.
- Fernley, H.N. and Walker, P.G. 1965. Kinetic behaviour of calf-intestinal alkaline phosphatase with 4-Methylumbelliferyl phosphate. *Biochem. J.* 97, 95.

- Garrison, P., and S. Greb. 2005. Systematic survey of *Cladophora* and water quality on the Wisconsin Lake Michigan shoreline. In, H.A. Bootsma, E.T. Jensen, E.B. Young, and J.A. Berges (eds.), *Cladophora* research and management in the Great Lakes; Proceedings of a workshop held at the Great Lakes WATER Institute, University of Wisconsin-Milwaukee, December 8, 2004.
http://www.glwi.uwm.edu/research/aquaticceology/cladophora/page_report.php
- Graham, J.M., M.T. Auer, R.P. Canale, and J.P. Hoffmann. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 4. Photosynthesis and respiration as functions of light and temperature. *J. Great Lakes Res.* 8(1):100-111.
- Gray, I.M. 1984. Study of *Cladophora* dynamics in Lake Ontario. Contract Report NWRI, CCIW, Burlington, Ontario, Canada.
- Heath, R.T., G.L. Fahnenstiel, W.S. Gardner, J.F. Cavaletto, and S.-J. Hwang. 1995. Ecosystem-level effects of zebra mussels (*Dreissena polymorpha*): An enclosure experiment in Saginaw Bay, Lake Huron. *J. Great Lakes Res.* 21:501-516.
- Hecky, R.E., R.E.H. Smith, D.R. Barton, S.J. Guildford, W.D. Taylor, M.N. Charlton, and T. Howell. 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. *Can. J. Fish. Aquat. Sci.* 61(7): 1285-1293.
- Higgins, S.N., Hecky, R.E., and Guildford, S.J. 2005. Modeling the growth, biomass, and tissue phosphorus concentration of *Cladophora glomerata* in eastern Lake Erie: Model description and field testing. *J. Great Lakes Res.* 31:439-455.
- Higgins, S.N., Hecky, R.E., and Guildford, S.J. 2006. Environmental controls of *Cladophora* growth dynamics in eastern Lake Erie: Application of the *Cladophora* growth model (CGM). *J. Great Lakes Res.* 32(3):629-644.
- Madon, S.P., D.W. Schneider, J.A. Stoeckel, and R.E. Sparks. 1998. Effects of inorganic sediment and food concentrations on energetic processes of the zebra mussel, *Dreissena polymorpha*: implications for growth in turbid rivers. *Can. J. Fish. Aquat. Sci.* 55: 401-413.
- Maybruck, B.T. 2007. The role of dreissenids and the associated heterotrophic microbial community in carbon dynamics and nutrient cycling. Ph.D. thesis, University of Wisconsin-Milwaukee. 175 pp.
- Mellina, E., J.B. Rasmussen, and E.L. Mills. 1995. Impact of mussel (*Dreissena polymorpha*) on phosphorus cycling and chlorophyll in lakes. *Can. J. Fish. Aquat. Sci.* 52:2553-2573.
- Painter, D.S., and Jackson, M.B. 1989. *Cladophora* internal phosphorus modeling: Verification. *J. Great Lakes Res.* 15:700-708.
- Parsons T., Maita, Lalli C. 1984. A manual of chemical seawater analysis. Pergamon Press.
- Scopel C.O. and McLellan S.L. 2006. Sources and nearshore transport of *Escherichia coli* at Lake Michigan beaches. *J. Great Lakes Res.* 32:543-552.
- Stainton, M.P., Capel, M.J. and Armstrong, F.A. 1974. The chemical analysis of fresh water. *Can. J. Fish. Mar. Serv. Misc. Spec. Publ.* 25.
- Whitton, B.A. 1970. Biology of *Cladophora* in freshwaters. *Water Research* 4:457-476.
- Young, E. and Beardall, J. 2003. Photosynthetic function in *Dunaliella tertiolecta* during a nitrogen starvation and recovery cycle. *Journal of Phycology* 39: 897-905.

Appendix I

The New *Cladophora* Model: Development, Testing, and Application to Lake Michigan

L.M. Tomlinson and M.T. Auer
Michigan Technological University
Department of Civil and Environmental Engineering

Submitted to Harvey Bootsma of the Great Lakes WATER Institute
March 7, 2007

TABLE OF CONTENTS

LIST OF TABLES AND FIGURES	68
INTRODUCTION.....	69
MODEL DEVELOPMENT	69
Model Components.....	69
Biomass.....	69
Internal Phosphorus	73
External Phosphorus	75
TESTING MODEL PERFORMANCE.....	77
Model Inputs	77
Model Performance - 1979	78
Model Performance - 1980	81
Summary of Performance Testing	84
APPLICATION OF THE NEW <i>CLADOPHORA</i> MODEL TO LAKE MICHIGAN	84
Inputs.....	84
Model Simulations	85
<i>CLADOPHORA</i> MODEL SUMMARY	88

List of Tables and Figures

Figure 1. Maximum phosphorus uptake rate as a function of internal phosphorus concentration. Dashed line (- -) is the Auer and Canale (1982a) uptake function; bold line represents an improved fit to the data from Auer and Canale (1982a) and is used in the current model.....	75
Figure 2. Seasonal variation in nearshore water temperature at Harbor Beach, Lake Huron in 1979. Data from Canale and Auer, 1982b	77
Figure 3. Measured and calculated seasonal variation in Cladophora standing crop at Harbor Beach, Lake Huron in 1979.	79
Figure 4. Measured and calculated seasonal variation in Cladophora standing crop at Harbor Beach, Lake Huron in 1979.	79
Figure 5. Seasonal dynamics of growth-limiting factors at Harbor Beach, Lake Huron in 1979. Growth is limited by light and temperature at this site, and phosphorus is available in excess....	80
Figure 6. Seasonal dynamics of measured soluble reactive phosphorus at Harbor Beach, Lake Huron in 1979.	81
Figure 7. Seasonal dynamics of measured soluble reactive phosphorus at Harbor Beach, Lake Huron in 1980.	82
Figure 8. Measured and calculated seasonal variation in Cladophora standing crop at Harbor Beach, Lake Huron in 1980.	82
Figure 9. Measured and calculated seasonal variation in internal phosphorus at Harbor Beach, Lake Huron in 1980.	83
Figure 10. Seasonal dynamics of growth-limiting factors at Harbor Beach, Lake Huron in 1980. Growth is limited by light and temperature at this site, and the decline in phosphorus loading has led to an increase in phosphorus limitation of Cladophora growth.	83
Figure 11. Seasonal variation in water temperature at the Atwater station, Lake Michigan in 2006.	85
Figure 12. Seasonal dynamics of soluble reactive phosphorus at Atwater station, Lake Michigan in 2006.	85
Figure 13. Seasonal variation in Cladophora standing crop at Atwater station, Lake Michigan in 2006, depth = 9 m.	86
Figure 14. Seasonal variation in internal phosphorus at Atwater station, Lake Michigan in 2006. Depth = 9 m.	87
Figure 15. Seasonal dynamics of growth-limiting factors at Atwater station, Lake Michigan in 2006. Depth = 9 m.	87
Table 1. Polynomial expressions for gross photosynthesis and respiration response surfaces. The third order polynomials are given below (x_1 = light at depth, $\mu\text{E m}^{-2} \text{s}^{-1}$, x_2 = temperature, $^{\circ}\text{C}$) together with the values of their coefficients.....	70
Table 2. Summary of model variables and coefficients.	76

Introduction

The use of mathematical models to predict the growth of *Cladophora* began with a series of papers published in 1982, where Canale and Auer described the development and application of a mechanistic model for Lake Huron (termed the CAM). Their model described the growth of *Cladophora* associated with a point source of phosphorus and satisfactorily predicted growth in adjacent shallow (less than 2 meters) waters. Painter and Jackson (1989) modified the Canale and Auer (1982b) model to predict the growth potential of *Cladophora* for conditions of soluble reactive phosphorus, temperature, and light extinction at specific sites in Lakes Ontario, Erie, Huron, and Simcoe. Higgins et al. (2005, 2006) modified the CAM framework, developing the *Cladophora* Growth Model (CGM) and applying it over a wider range of depths and phosphorus conditions in Lakes Erie and Ontario.

There has been no modeling of *Cladophora* in Lake Michigan to date. Here, we revisit the Canale and Auer (1982b) framework in order to develop a mechanistic model for application in Lake Michigan. Changes made to the original CAM by Painter and Jackson (1989) and Higgins et al. (2005, 2006) were evaluated and applied in the new model as appropriate. This updated model, which reflects the current understanding of *Cladophora* ecology, was calibrated and confirmed using the Auer/Canale data set from Lake Huron and then used to predict *Cladophora* growth in Lake Michigan in 2006.

Model Development

Model Components

The model framework includes three state variables, *Cladophora* biomass and phosphorus (the limiting nutrient) present in the water (dissolved P) and in the algae (internal P). Their dynamics are simulated using expressions that describe their relationship amongst one another and with the physical and chemical environment, i.e. phosphorus availability and the presence of suitable conditions of light and temperature. The requirement of substrate suitable for attachment is not modeled explicitly here, but is accommodated in field measurements of biomass and can be included in model projections. Thus, the variables of interest for this model are *Cladophora* biomass and stored internal phosphorus.

Biomass

Changes in *Cladophora* biomass reflect the net result of gains through growth and losses to respiration and sloughing (a physical detachment process). Growth is mediated by conditions of light and temperature, internal phosphorus concentration, and carrying capacity. Biomass losses, respiration and sloughing, are governed by light/temperature and wind speed, respectively.

Cladophora grows attached to a fixed substrate and is lost only through respiration and sloughing. A biomass can therefore be calculated using a mass balance developed for the biomass state variable, where the change in biomass with respect to time is described by:

$$\frac{dX}{dt} = [\mu - R - L]X \quad (1)$$

where: X = *Cladophora* biomass (g DW m⁻²)
 μ = gross specific growth rate coefficient (hr⁻¹)
 R = respiration rate coefficient (hr⁻¹)
 L = sloughing rate coefficient (hr⁻¹)

The gross specific growth rate is a function of light, temperature, internal phosphorus concentration and carrying capacity. The gross specific growth rate is expressed as the product of dimensionless multipliers, each varying from 0 → 1, which account for the potentially limiting processes outlined above. This relationship can be expressed mathematically as:

$$\mu = \mu_{\max} [M_{LT} \cdot M_P \cdot M_X] \quad (2)$$

where: μ = gross specific growth rate coefficient (hr⁻¹)
 $\mu_{\max}$ = maximum gross specific growth rate coefficient (hr⁻¹)
 M_{LT} = growth multiplier for light and temperature (dimensionless)
 M_P = growth multiplier for internal phosphorus (dimensionless)
 M_X = growth multiplier for carrying capacity (dimensionless)

The gross specific growth rate coefficient for *Cladophora* at varying levels of light and temperature and under optimal nutrient conditions has been reported by Graham et al. (1982). In general, these results show *Cladophora* has an optimum temperature range for growth between 13°C and 17°C, depending upon light intensity. Maximum growth in the optimum temperature range occurs under light intensities between 300 and 600 $\mu\text{E m}^{-2} \text{ s}^{-1}$. Respiration generally increases with increasing light and temperature. Net photosynthesis decreases with departure from the optimum due to photorespiration (high light) and light limitation (low light). Graham et al. (1982) fit these relationships to three-dimensional surfaces with specific growth and respiration rates, light, and temperature as coordinate directions. Values for the growth or respiration rate can then be determined for any combination of light and temperature values.

Here, we fit the original laboratory measurements of Graham et al. (1982) to new surfaces for gross photosynthesis and respiration, generating rate coefficient multipliers (M_{LT} and R_{LT} ; range 0 → 1) that vary with light and temperature. Rate coefficients are then determined as the product of the surface-derived multipliers and specific rates of gross photosynthesis maximum specific rates for gross photosynthesis and respiration developed for field populations on a site-specific basis. The polynomials and coefficients used to generate these surfaces are presented in Table 1.

Table 1. Polynomial expressions for gross photosynthesis and respiration response surfaces. The third order polynomials are given below (x_1 = light at depth, $\mu\text{E m}^{-2} \text{ s}^{-1}$, x_2 = temperature, °C) together with the values of their coefficients.

Gross photosynthesis:	$M_{LT} = a_1 + a_2x_1 + a_3x_2 + a_4x_1^2 + a_5x_1x_2 + a_6x_2^2 + a_7x_1^3 + a_8x_1^2x_2 + a_9x_1x_2^2 + a_{10}x_2^3 + a_{11}x_1^3x_2 + a_{12}x_1^2x_2^2 + a_{13}x_1x_2^3$
-----------------------	--

Respiration:	$R_{LT} = b_1 + b_2x_1 + b_3x_2 + b_4x_1^2 + b_5x_1x_2 + b_6x_2^2 + b_7x_1^3 + b_8x_1^2x_2 + b_9x_1x_2^2 + b_{10}x_2^3 + b_{11}x_1^3x_2 + b_{12}x_1^2x_2^2 + b_{13}x_1x_2^3$		
where:	$a_1 = -3.10189820044715E - 02$ $a_4 = -2.99494257852711E - 06$ $a_7 = 1.6875291852178E - 09$ $a_{10} = 5.41146607284034E - 06$ $a_{13} = 7.18690371326443E - 08$	$a_2 = 1.21097828989578E - 03$ $a_5 = 2.87556463159981E - 04$ $a_8 = -2.59743951456656E - 07$ $a_{11} = 8.94172679669356E - 11$	$a_3 = 3.12062696338505E - 02$ $a_6 = -1.06206957408835E - 03$ $a_9 = -8.88202634153844E - 06$ $a_{12} = 2.67412430299216E - 09$
	$b_1 = 9.57964430724275E - 02$ $b_4 = -4.72010300767978E - 07$ $b_7 = 7.87726632078466E - 11$ $b_{10} = 2.33853164223086E - 05$ $b_{13} = 3.03917511652015E - 08$	$b_2 = 5.90365507708485E - 04$ $b_5 = 1.90990816538341E - 05$ $b_8 = -2.51393854052121E - 08$ $b_{11} = 4.20154521630618E - 11$	$b_3 = 2.25715188890411E - 02$ $b_6 = -1.16739190002568E - 03$ $b_9 = -1.94496751357286E - 08$ $b_{12} = -1.90416382375698E - 09$

The light term in the response surface polynomials is the PAR (photosynthetically available radiation) at depth. PAR in the water column varies over the day (photoperiod) and with depth (attenuation) and water transparency. Available light varies as a function of the depth at which *Cladophora* is growing, and is attenuated according to a measured vertical extinction coefficient. The light available at depth is calculated by:

$$I = I_o e^{-K_e \cdot z} \quad (3)$$

where: I = PAR light at depth ($\mu E \text{ m}^{-2} \text{ s}^{-1}$)
 I_o = surface PAR light intensity ($\mu E \text{ m}^{-2} \text{ s}^{-1}$)
 K_e = vertical extinction coefficient (m^{-1})
 z = depth of *Cladophora* (m)

The effect of photoperiod on PAR at depth is accommodated by basing calculations on hourly incident light values. This is in contrast to previous modeling efforts (Higgins et al. 2005, 2006) that utilized photoperiod average PAR, an approach that over predicts *Cladophora* growth. The reason for this is the non-linear nature of the light response surface. Photoperiod average photoperiod PAR values typically fall near the optimum for *Cladophora* growth. Application of such a value suggests optimal light conditions for the entire photoperiod. In actuality, light conditions are sub-optimal both in the morning/evening (too low, limitation) and at mid-day (too high, inhibition). The hourly approach applied here, thus more accurately describes the relationship between incident light and *Cladophora* growth.

As an attached alga, *Cladophora* requires solid substrate and may be limited by the availability of such surfaces. Given suitable substrate and optimal conditions of light, temperature and nutrients, biomass will approach a maximum value. This level, its carrying capacity, serves to mimic negative feedback on growth from self-shading and space limitation. Within the model,

the growth of *Cladophora* may be limited by the carrying capacity term, which is described mathematically as:

$$M_x = 1 - \left[\frac{X}{X_{\max}} \right] \quad (4)$$

where: M_x = growth multiplier for carrying capacity (dimensionless)
 X = *Cladophora* biomass density (g DW m⁻²)
 $X_{\max}$ = maximum *Cladophora* biomass density (g DW m⁻²)

In an effort to accommodate potential self-shading effects, the CGM (Higgins et al. 2005) allows the maximum biomass to vary as a function of mean daily PAR at depth. Thus, the value of $X_{\max}$ varies with depth. This method is not adopted here, as light at depth is already accounted for in the light and temperature polynomials. Instead, the Canale and Auer (1982b) constant for maximum biomass is retained, where $X_{\max} = 800$ g DW m⁻². This number was determined by field measurement and both model calibration at the Lake Huron site and examination of *Cladophora* samples gathered at the Harbor Beach site.

Respiration is one of two loss processes invoked in the *Cladophora* model. Two forms of respiration are recognized: that in the light (light-enhanced respiration) where changes in respiration track changes in PAR and temperature and that in the dark (basal respiration) which varies only with temperature (Graham et al. 1982). Light-enhanced respiration (R , calculated hourly) is determined as the product of a maximum respiration rate coefficient ($R_{\max}$) and the dimensionless multiplier generated by the response surface polynomial:

$$R = R_{\max} \bullet R_{LT} \quad (5)$$

where: R = specific respiration rate coefficient (hr⁻¹)
 $R_{\max}$ = maximum specific respiration rate coefficient (hr⁻¹)
 R_{LT} = respiration multiplier for light and temperature (dimensionless)

Basal respiration was assumed to vary in a linear fashion with temperature in the CAM (Canale and Auer 1982b). Here, we also assume a linear relationship between temperature and basal respiration, but utilize the respiration measurements by Graham et al. (1982) at light levels below the compensation point to develop the function:

$$R_B = 1.25E-4 \bullet T + 8.29E-4 \quad (6)$$

where: R_B = basal specific respiration rate coefficient (hr⁻¹)
 T = temperature (°C)

The choice of using R or R_B over the hourly cycle is established through inclusion of logic statements in the code.

The second loss process, sloughing, is influenced by turbulence (wind velocity) and biomass levels. The empirical relationship relating wind speed, biomass and sloughing developed by Canale and Auer (1982b) has been retained here:

$$L = S \cdot L_{\max} \cdot \frac{\omega}{\omega_{\max}} \cdot \frac{X}{X_{\text{factor}}} \quad (7)$$

where:

- L = sloughing loss rate coefficient (hr^{-1})
- S = shear stress correction factor (3.4, dimensionless)
- $L_{\max}$ = maximum sloughing loss rate coefficient (0.176 hr^{-1})
- ω = daily wind speed (mph)
- $\omega_{\max}$ = maximum seasonal wind speed (11.1 mph)
- X = biomass (g DW m^{-2})
- X_{factor} = biomass sensitivity factor, equal to a site-specific maximum biomass density (433 g DW m^{-2})

Canale and Auer (1982b) treated S, $L_{\max}$, and $X_{\max}$ as constants, determined experimentally (S, laboratory flume), through field measurement ($X_{\max}$) and by model calibration ($L_{\max}$). The shear stress correction factor was calculated using velocity measurements in an experimental flume, while the maximum sloughing loss rate was obtained by optimization of the fit of calculated and measured sloughing rates. The maximum biomass density used in the sloughing calculation is a direct measurement of *Cladophora* biomass, and is used to normalize the sloughing rate, as is the maximum seasonal wind speed value. Sensitivity analyses by Canale and Auer (1982a) demonstrated that average seasonal sloughing rates at the study site on Lake Huron are suitably approximated using seasonal average wind speeds.

It should be noted, however, that the sloughing is a complex phenomenon, related both to the physical stresses placed on filaments and to the alga's physiological state as might be influenced by environmental variables such as water temperature (Whitton 1970). The CGM (Higgins et al. 2006) forces sloughing events based upon a 10-day metabolic balance performed on cells lying at the base of the *Cladophora* filaments, i.e. sloughing is a function of light and temperature. Their approach does not take physical stress (turbulence) into account. While we applaud this effort to adopt a mechanistic approach that accommodates algal physiology, we have elected to reduce model complexity by retaining the wind stress driven approach of Canale and Auer (1982a).

Internal Phosphorus

In the CAM, growth limitation by nutrients is driven by the amount of phosphorus stored internally by the alga. The Droop Model (1973) describes this relationship:

$$M_P = 1 - \left[\frac{Q_o}{Q} \right] \quad (8)$$

where:

- M_P = growth multiplier for internal phosphorus (dimensionless)
- Q_o = minimum internal phosphorus concentration (P as % DW)

Q = internal phosphorus concentration (P as % DW)

The value for the minimum internal phosphorus concentration ($Q_0 = 0.05\%P$) was determined through field observation at the site on Lake Huron (Auer and Canale 1982) and proved useful in subsequent modeling analysis. Field measurements of internal phosphorus made on Lake Michigan at Milwaukee (Bootsma 2006) support this value.

The internal phosphorus concentration is calculated as the mass of phosphorus stored in the algae divided by the algal biomass:

$$Q = \frac{s}{X} \quad (9)$$

where: s = mass of stored phosphorus (g P m^{-2})

The mass of phosphorus stored in the alga is increased by uptake from the water and reduced by losses to respiration. The mass balance on phosphorus stored in *Cladophora* is given by:

$$\frac{ds}{dt} = \rho \bullet X - R \bullet s \quad (10)$$

where: ρ = phosphorus uptake rate ($\% \text{ P hr}^{-1}$)

In this mass balance, uptake as a source of stored phosphorus varies as a function of the water column soluble reactive phosphorus concentration and the internal phosphorus concentration (a feedback mechanism):

$$\rho = \left[\frac{P}{K_m + P} \right] \bullet 0.0745 \bullet Q^{-1.5963} \quad (11)$$

where: ρ = phosphorus uptake rate ($\% \text{ P d}^{-1}$)
 P = soluble reactive phosphorus concentration ($\mu\text{g P L}^{-1}$)
 K_m = half-saturation constant for uptake as a function of soluble reactive phosphorus concentration ($\mu\text{g P L}^{-1}$)

Phosphorus uptake is governed, in the classic Michaelis-Menten fashion, by water column phosphorus levels (P) and rates are attenuated as internal phosphorus concentrations increase. This relationship is based upon laboratory measurements conducted on field populations of *Cladophora* by Auer and Canale (1982). The feedback function (second term in Equation 11) has been modified and refit to better accommodate the suppression of uptake at high internal phosphorus levels (Figure 1).

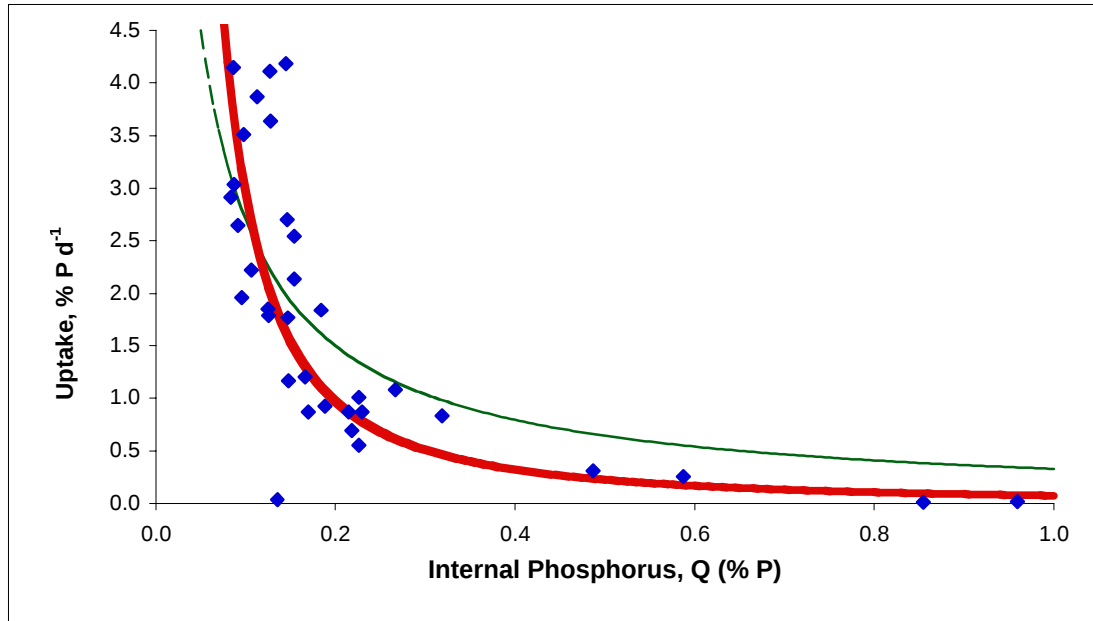


Figure 1. Maximum phosphorus uptake rate as a function of internal phosphorus concentration. Dashed line (---) is the Auer and Canale (1982a) uptake function; bold line represents an improved fit to the data from Auer and Canale (1982a) and is used in the current model.

Painter and Jackson (1989) modified the uptake function utilized in the CAM to include the effects of temperature as described by Gray (1984), who found rates to be lowered by 23% from the optimum for a 10°C reduction in temperature; a temperature increase of 10°C reduced the phosphorus uptake rate by 41%. However, this adjustment has little impact on the calculation of stored phosphorus levels due to the different time scales of uptake and other physiological processes (local equilibrium; cf. DiToro 1980). Thus, a temperature modification for uptake is not adopted here.

Note that the utilization of a mass balance on stored phosphorus (s in Equation 10) with subsequent calculation of the internal phosphorus concentration (Q in Equation 9) separates the effects of partitioning phosphorus reserves among new growth (X in Equation 1) and losses to respiration (R in Equation 1). It is necessary to separate the processes because respiration has no effect on internal phosphorus concentration (both s and X are lost, Equation 10) and growth has no effect on the mass of stored phosphorus (Equation 10). This approach and that utilized by Canale and Auer (1982b) are numerically equivalent, but the presentation adopted here provides a clearer description of the phenomenon.

External Phosphorus

In the nearshore area, soluble reactive phosphorus concentrations are regulated by loadings (i.e., point sources) and are subject to depletion from a given area by advective and dispersive transport. Phosphorus uptake by *Cladophora* provides an additional means of depletion of phosphorus from the water column, although the loss of dissolved phosphorus due to uptake is

usually small compared with the loading and transport components. A mass balance equation for ambient soluble reactive phosphorus in a given water column segment is described by:

$$V \frac{dP}{dt} = W_i + a_{ij}P_j - \rho X A_i \quad (12)$$

where: W_i = phosphorus loading to segment i (mg P hr⁻¹)
 a_{ij} = advective and dispersive transport between cells i and j (m³ d⁻¹)
 P_j = soluble reactive phosphorus concentration in cell j (µg P L⁻¹)
 A_i = areal distribution of *Cladophora* in segment i (m²)
 ρ = phosphorus uptake rate (% P d⁻¹)
 X = *Cladophora* biomass density (g DW m⁻²)

In the current model framework, the external phosphorus concentrations are site-specific inputs based upon actual measurements taken at intervals throughout the season. As such, soluble reactive phosphorus values are daily values that serve to drive the growth of *Cladophora*; however, management applications of the model will utilize a user-specified loading of phosphorus to predict growth potential in the nearshore region.

Table 2. Summary of model variables and coefficients.

Quantity	Definition	Units	Value	Source
$\mu_{\max}$	Maximum gross specific growth rate	d ⁻¹	1.53	Auer and Canale, 1982b
$R_{\max}$	Maximum specific respiration rate	d ⁻¹	0.285	Auer and Canale, 1982b
$X_{\max}$	Maximum biomass density	g DW m ⁻²	800	Canale and Auer, 1982b
K_m	Half saturation constant for uptake as a function of external phosphorus concentration	mg P m ⁻³	125	Auer and Canale, 1982a
Q_o	Minimum cell quota for phosphorus	% P	0.05	Auer and Canale, 1982b
z	Depth of <i>Cladophora</i>	m	-	Direct measurement
K_e	Light extinction coefficient	m ⁻¹	-	Direct measurement
Temperature	-	°C	-	Direct measurement
P	Soluble reactive phosphorus	µg P L ⁻¹	-	Direct measurement
ω	Wind speed	mph	5.7	Canale and Auer, 1982a

Testing Model Performance

The *Cladophora* model previously described can be used to simulate seasonal dynamics in *Cladophora* biomass and internal phosphorus concentration. Here, performance of the revised model is examined for two years (1979 and 1980; Canale and Auer 1982a) differing in the magnitude of the phosphorus loading to the system.

Model Inputs

Model inputs required for the updated model include water temperature, hourly average PAR, extinction coefficient and soluble reactive phosphorus concentration. A seasonal plot of water temperature for Harbor Beach was published by Canale and Auer (1982b); the software package UN-SCAN-IT 6.0 was used to generate daily water temperatures based on this plot. Figure 2 shows water temperature at Harbor Beach in 1979.

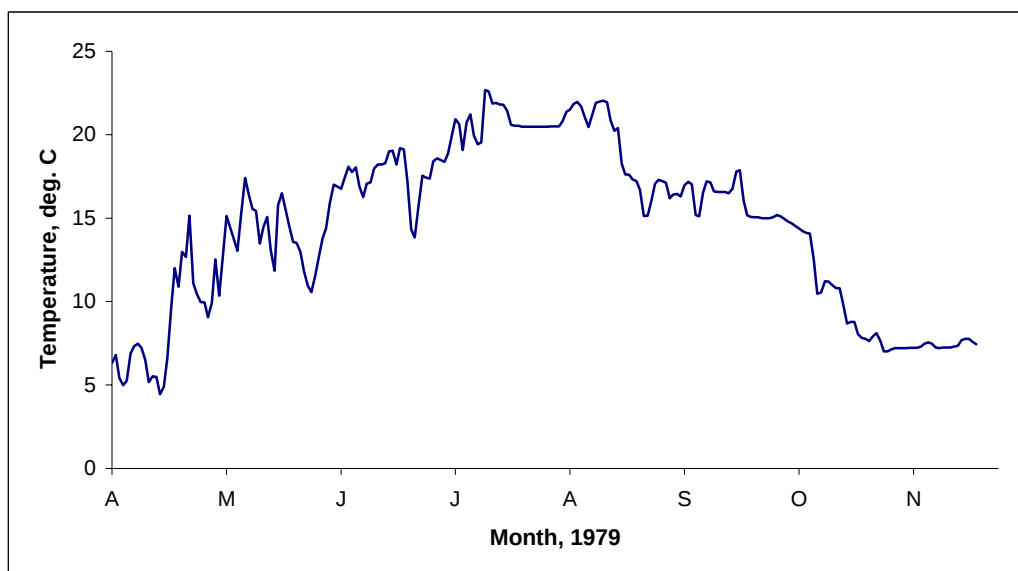


Figure 2. Seasonal variation in nearshore water temperature at Harbor Beach, Lake Huron in 1979. Data from Canale and Auer, 1982b.

The model also requires values for the maximum specific gross growth rate and respiration rate coefficients. Auer and Canale (1982b) conducted laboratory experiments with field populations from the Lake Huron study site to establish values for these coefficients. Rates measured in the laboratory (under sub-optimal conditions of light and temperature) were normalized to optimal conditions using the response surfaces of Graham et al. (1982). Here, the normalization process was repeated, using the newly-developed response surfaces described above, yielding values for the maximum specific rate coefficients for net photosynthesis, respiration, and gross photosynthesis of 1.24, 0.285, and 1.53 d⁻¹, respectively.

A light extinction coefficient (1.367 m⁻¹; constant over the season) was determined for the Lake Huron study site using light at depth data published by Canale and Auer (1982b). The soluble reactive phosphorus concentration was measured periodically during 1979 and 1980 and reported

by Canale and Auer (1982a). Representative hourly incident PAR values were obtained for a latitude comparable to the Lake Huron study site from the Upstate Freshwater Institute (1994; unpublished data). Canale and Auer (1982a) did not report the sampling depth at the study site which the biomass and internal and dissolved phosphorus data represent. The study site was generally less than 2 meters in depth and a depth of 1.5 m is used here, consistent with a program where sampling was not supported by SCUBA.

Model Performance - 1979

A model run simulating *Cladophora* biomass and internal phosphorus concentration at the Lake Huron study site were simulated for the 30-May to 16-August interval in Harbor Beach in 1979. Figure 3 and Figure 4 show the predicted biomass and internal phosphorus from 30-May to 16-Aug. These dates were chosen based on the dates of samples reported by Canale and Auer (1982a). These samples represent conditions where point source phosphorus inputs were unregulated and both internal phosphorus and *Cladophora* biomass levels at the study site were at their maximum. Model inputs and coefficients were as described above and presented in Table 2.

Model output generally tracks the time course of development (early and mid-June) and maximum standing crop (July) of *Cladophora* biomass. However, the model does not capture the late August decline of biomass measured at Harbor Beach. This decline is generally believed to occur as a result of enhanced respiration (warmer temperatures). As shown in Figure 5, light and temperature conditions (M_{LT}) are less favorable in August, but this change is not of the magnitude necessary to produce the decline in biomass observed. This shortfall suggests a need to re-visit limitation due to light and temperature, and is possibly affected by the response surface polynomial fit at higher light and temperature values.

It is also worthy to note that the occurrence of a wind-induced sloughing event in late August may also contribute to the observed decline in measured biomass. This model simulation utilized an approach in which a seasonal average wind speed (and therefore sloughing rate) and thus a single sloughing event would not be captured by the model. Again, uncertainties with regard to the sloughing phenomenon of *Cladophora* and the triggers of such an event warrant further investigation.

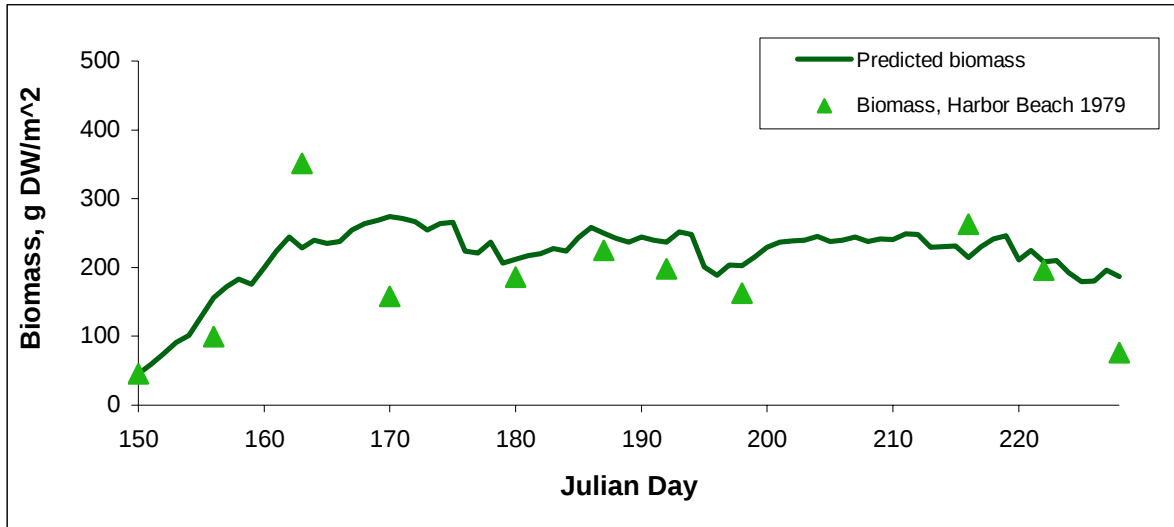


Figure 3. Measured and calculated seasonal variation in *Cladophora* standing crop at Harbor Beach, Lake Huron in 1979.

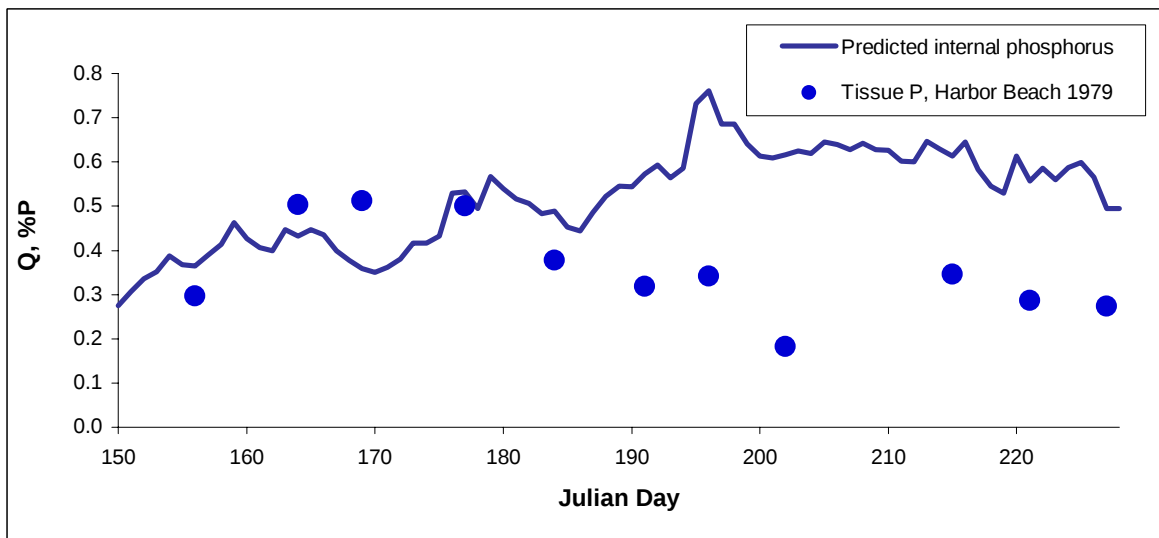


Figure 4. Measured and calculated seasonal variation in *Cladophora* tissue P content at Harbor Beach, Lake Huron in 1979.

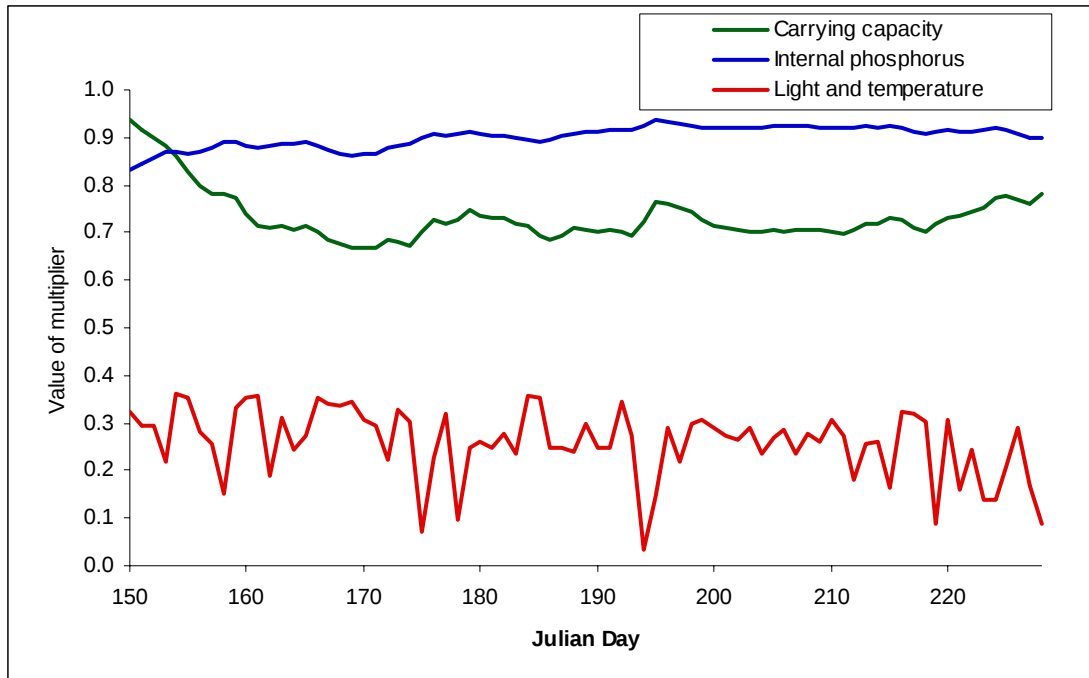


Figure 5. Seasonal dynamics of growth-limiting factors at Harbor Beach, Lake Huron in 1979. Growth is limited by light and temperature at this site, and phosphorus is available in excess.

Model-predicted internal phosphorus concentrations for 1979 are of the same magnitude as those observed in the field (Figure 4. Measured and calculated seasonal variation in *Cladophora* tissue P content at Harbor Beach, Lake Huron in 1979.). The internal phosphorus levels predicted here track temporal variation in measured SRP concentrations (the driving force; Figure 6. Seasonal dynamics of measured soluble reactive phosphorus at Harbor Beach, Lake Huron in 1979.) and are of an appropriate magnitude for these rather high soluble phosphorus concentrations. Fine structure in the internal phosphorus output is due to the effects of growth dilution. These observations suggest that model constructs relating dissolved and internal phosphorus are performing appropriately. Model output is less successful in tracking seasonality in observed internal phosphorus concentrations, i.e. under-prediction in June and over-prediction in July. Because the model seems to handle the dissolved P – internal P coupling well, this shortfall in model performance calls into question the validity of the SRP data set. The study site lies adjacent to the discharge of a phosphorus-rich point source, but is also strongly influenced by wind-driven exchange with phosphorus-depleted offshore waters. It is not clear that the original sampling effort appropriately described spatial and temporal variability in SRP concentrations at the scale required to reproduce observed trends in internal phosphorus concentrations.

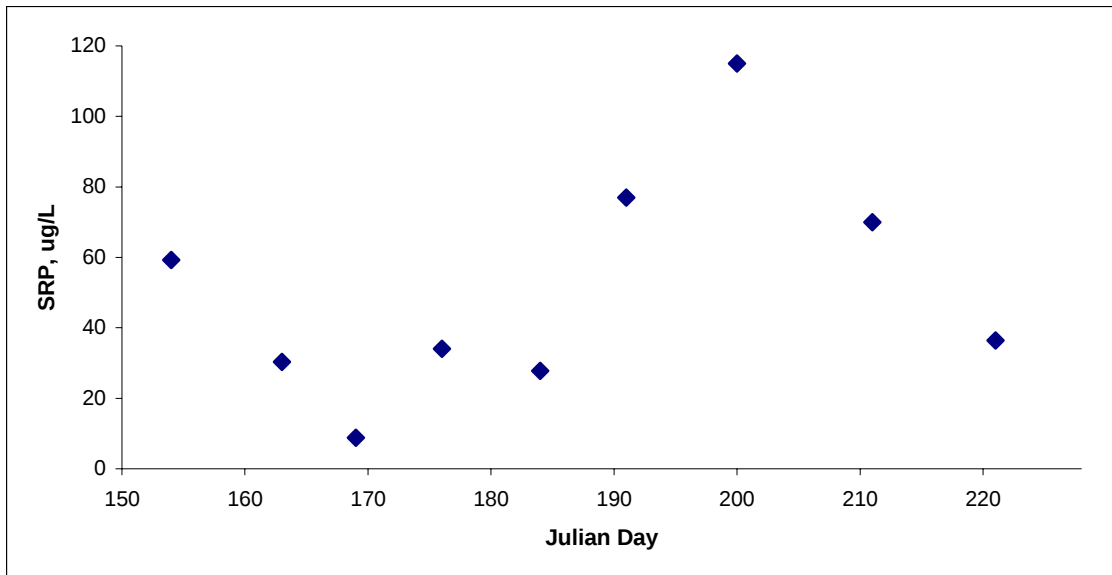


Figure 6. Seasonal dynamics of measured soluble reactive phosphorus at Harbor Beach, Lake Huron in 1979.

Model Performance - 1980

A second simulation was performed for the 26-May to 16-August interval of 1980, the period in the Canale and Auer (1982a) study where phosphorus removal was applied at the point source and both phosphorus and *Cladophora* biomass levels at the study site were lower than in 1979. Soluble reactive phosphorus values were those measured in 1980 (Figure 7). All other model inputs and coefficients, including conditions of light and temperature, were as for 1979 (no temperature data are available for that year).

Model output for *Cladophora* biomass (Figure 8) successfully tracks both the magnitude and temporal structure of field observations. As with the 1979 simulation, the model fails to capture the decrease in biomass observed in late July. The causes of that shortfall are difficult to determine due to the lack of temperature measurements. The model captures the (lack of) seasonal structure in internal phosphorus concentrations (Figure 9), but tends to over-predict measured concentrations (as did the Canale and Auer 1982a simulation). This again calls into question the degree to which the original sampling program appropriately characterized SRP levels in this dynamic nearshore region.

The nature of the model output appropriately reflects the response to reductions in point source phosphorus loading. The response is manifested in both model-predicted and measured internal phosphorus reserves (compare Figure 4 and Figure 9) where levels are reduced from 0.18-0.50% P, in 1979 (model-predicted ~0.50% P) to 0.06-0.28% P in 1980 (model-predicted 0.30% P). The response is also reflected in the degree of phosphorus limitation (compare Figure 5 and Figure 10). The behavior of the model in this regard affirms the utility of the underlying physiological constructs.

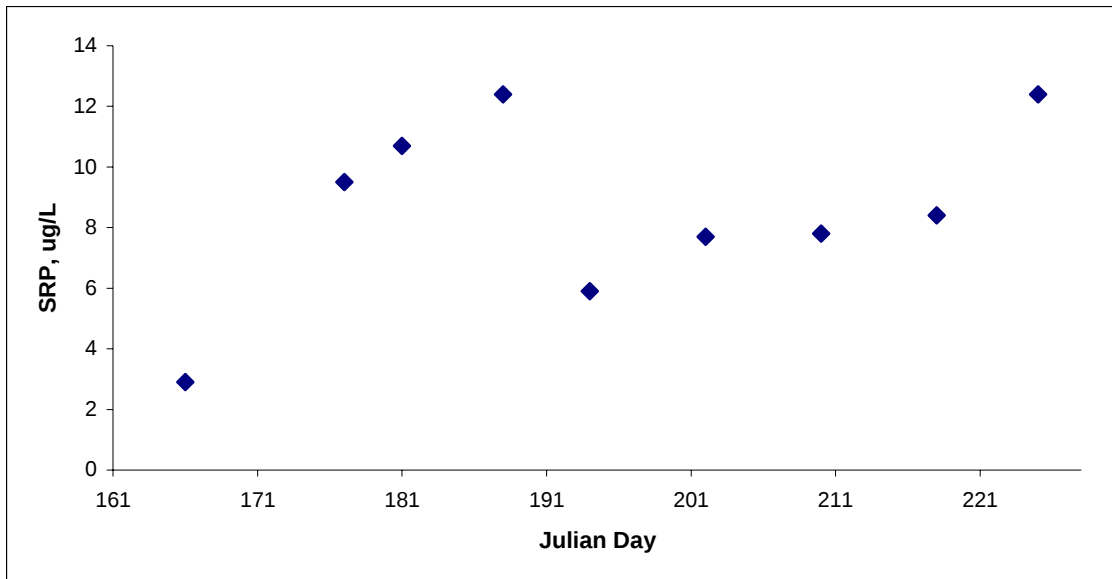


Figure 7. Seasonal dynamics of measured soluble reactive phosphorus at Harbor Beach, Lake Huron in 1980.

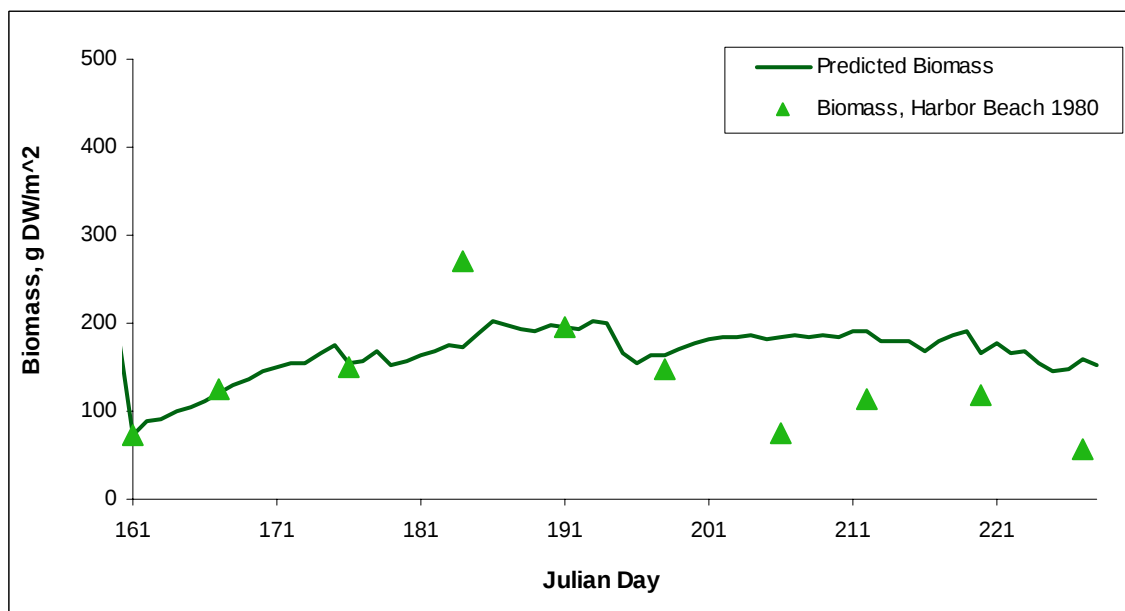


Figure 8. Measured and calculated seasonal variation in *Cladophora* standing crop at Harbor Beach, Lake Huron in 1980.

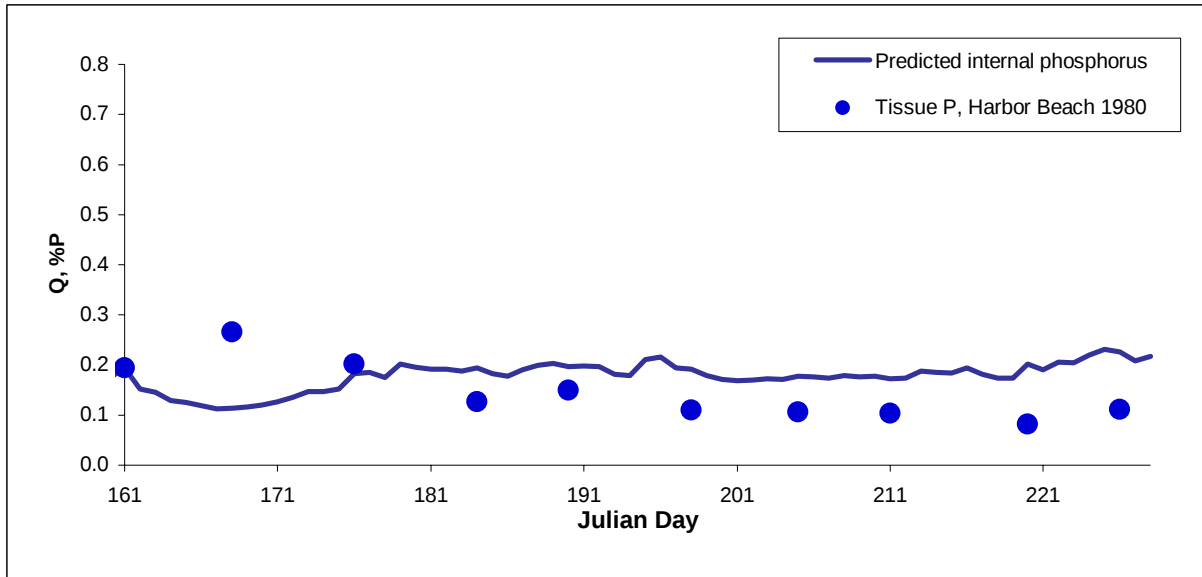


Figure 9. Measured and calculated seasonal variation in internal phosphorus at Harbor Beach, Lake Huron in 1980.

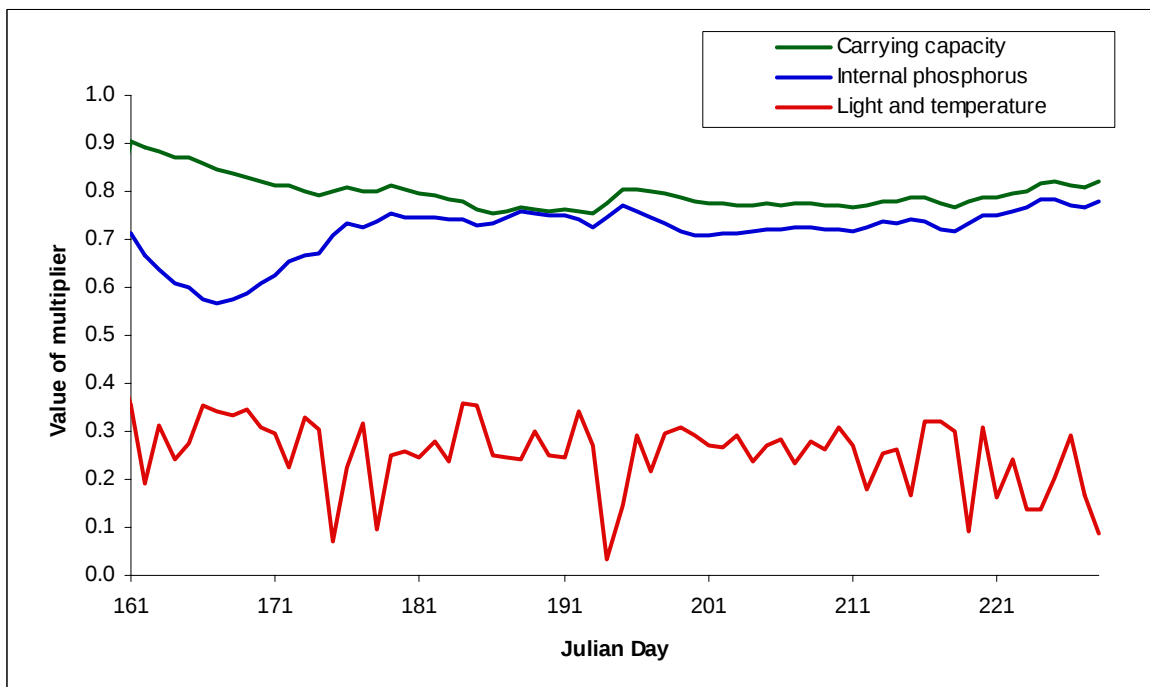


Figure 10. Seasonal dynamics of growth-limiting factors at Harbor Beach, Lake Huron in 1980. Growth is limited by light and temperature at this site, and the decline in phosphorus loading has led to an increase in phosphorus limitation of *Cladophora* growth.

Summary of Performance Testing

The revised *Cladophora* model has been tested using the data sets simulated in the original study (Canale and Auer 1982a). Model output successfully tracks the time course of development and magnitude of algal biomass for both years, with the exception of the period of decline late in the season. Simulations of internal phosphorus concentration respond appropriately to changes in ambient SRP levels, but on occasion fail to track temporal structure (1979) and magnitude (1980). Thus, the current *Cladophora* model, as tested using Lake Huron data reported by Canale and Auer (1982a), may be expected to appropriately predict internal phosphorus levels and biomass density given a particular set of environmental conditions.

Application of the New *Cladophora* Model to Lake Michigan

The Lake Michigan study site at Atwater Beach, Wisconsin presents an environment that differs considerably from that of the Lake Huron effort. The sampling location is much deeper (9 m), light availability is greater (less extinction due to zebra mussel filtering effects) and SRP concentrations are lower ($<1.5 \mu\text{g L}^{-1}$; 2006), essentially reflective of offshore conditions. The revised *Cladophora* model is applied here to simulate *Cladophora* biomass and internal phosphorus concentrations over the 5-July to 7-September interval of 2006.

Inputs

Environmental conditions required as input and field measurements used in evaluating model performance were provided by Harvey Bootsma of the Great Lakes WATER Institute. *In situ* measurements were made at 9 meters depth at the Atwater station. Variations in water temperature were recorded by a data logger (Figure 11). Soluble reactive phosphorus concentrations (Figure 12) were measured at regular intervals throughout the summer. Daily extinction coefficients were calculated based on *in situ* light measurements and rooftop incident light measurements (data collected on the rooftop of the WATER Institute). Extinction coefficients were generally stable, near an average value of 0.25 m^{-1} , but some excursions were not, perhaps reflecting the occurrence of resuspension events.

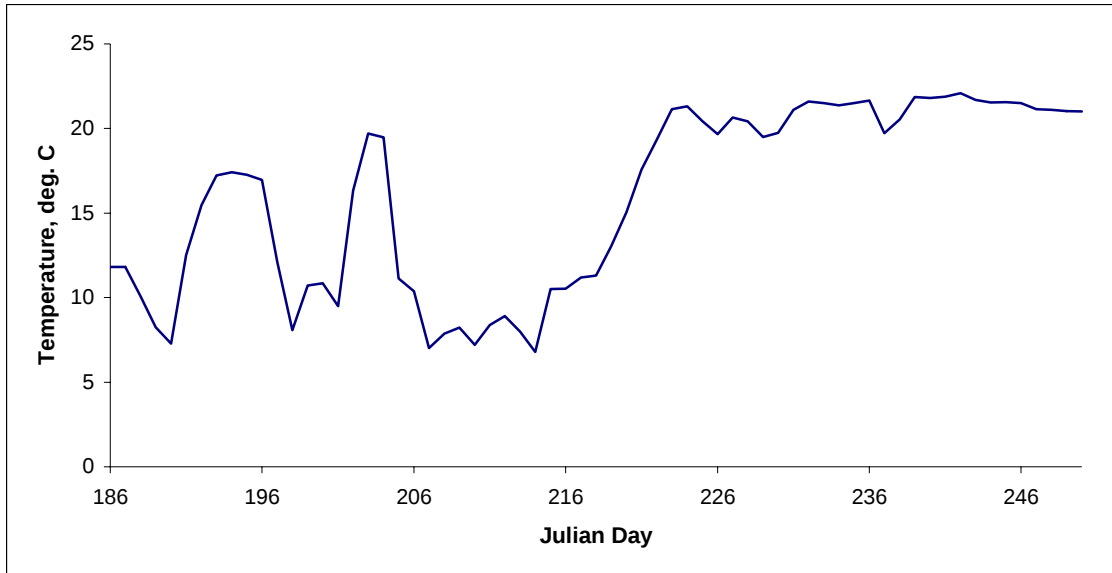


Figure 11. Seasonal variation in water temperature at the Atwater station, Lake Michigan in 2006.

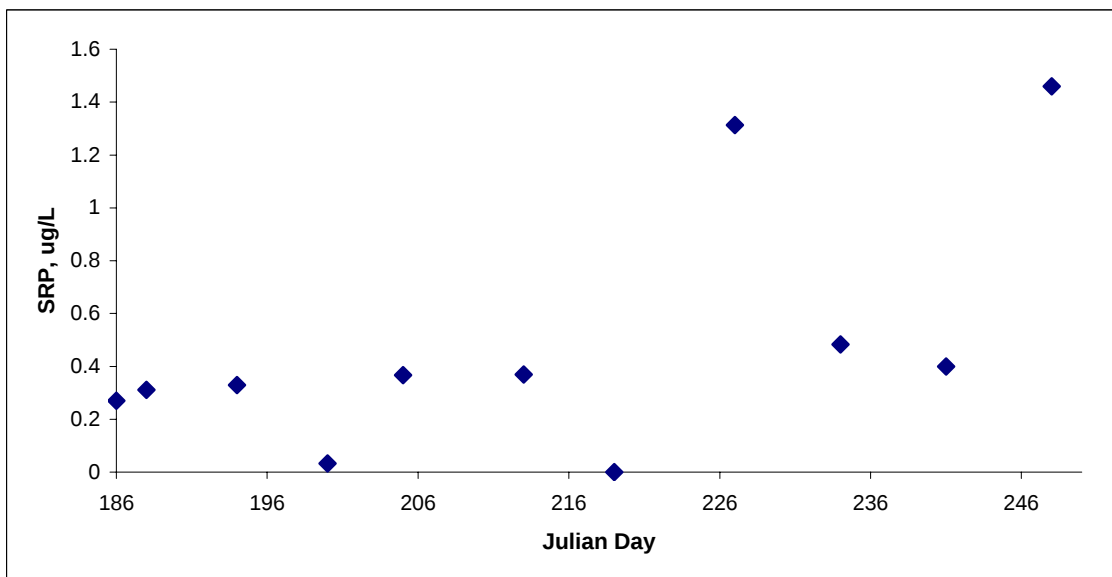


Figure 12. Seasonal dynamics of soluble reactive phosphorus at Atwater station, Lake Michigan in 2006.

Model Simulations

The model was run for environmental conditions (light, temperature, soluble reactive phosphorus concentration) measured for the site on Lake Michigan. Model coefficients were unchanged from those determined for the Lake Huron study site.

Model output successfully tracks the magnitude and time course of development of *Cladophora* standing crop (July) and the peak midsummer standing crop in early August of field observations. (Figure 13) As with the 1979 and 1980 Lake Huron simulations, the model fails to capture the magnitude of the decrease in biomass observed in mid- to late-August. This may be due, in part, to the rise in SRP concentrations measured in August and input to the model. Figure 15 indicates a decrease in internal phosphorus limitation during this time period, which may exacerbate over-prediction from the response surface polynomials. Additionally, in this simulation the sloughing rate is equal to zero, reflecting the depth attenuation of shear stresses due to wind. Thus, loss of biomass is due only to respiration; however, if a sloughing event were to occur in August, it is probable that model predictions may more closely track observed measurements of biomass.

The model captures the somewhat seasonal structure in internal phosphorus concentrations (Figure 14) and also the magnitude of measurements of internal phosphorus. Again, internal phosphorus predictions track that of the available SRP, resulting in the predicted spike in August of internal phosphorus. It should be noted, however, that the model responds appropriately (with both predicted biomass and internal phosphorus concentrations) to a significantly lower external phosphorus concentrations than those seen at the study site in Lake Huron. This once again affirms the utility of the underlying physiological constructs in the model, particularly in regards to internal phosphorus predictions.

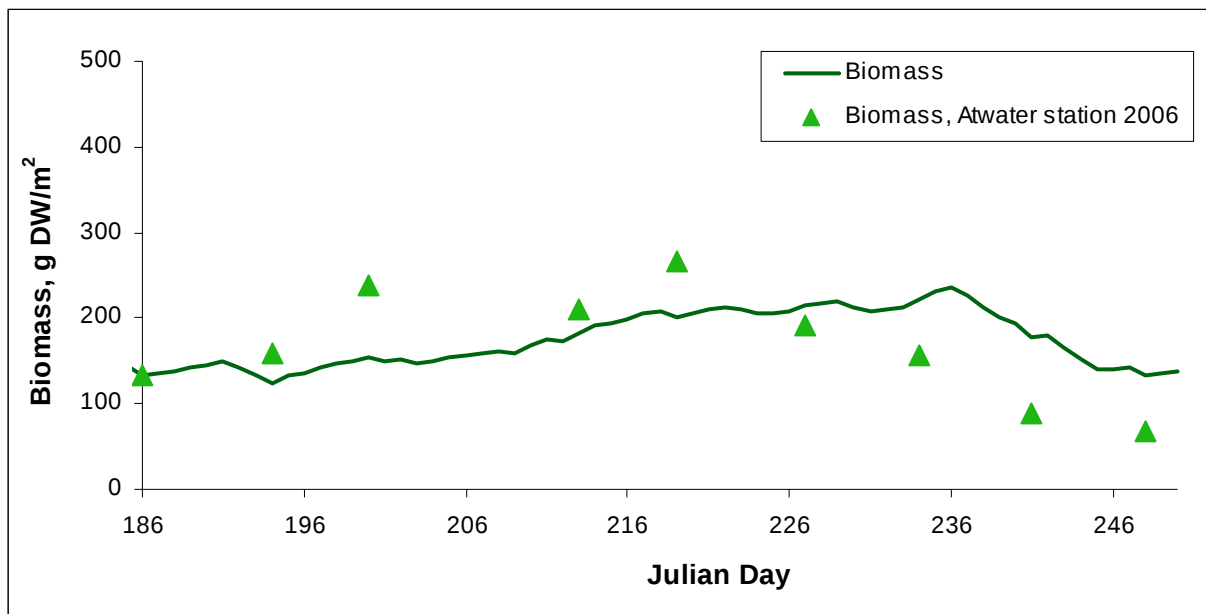


Figure 13. Seasonal variation in *Cladophora* standing crop at Atwater station, Lake Michigan in 2006, depth = 9 m.

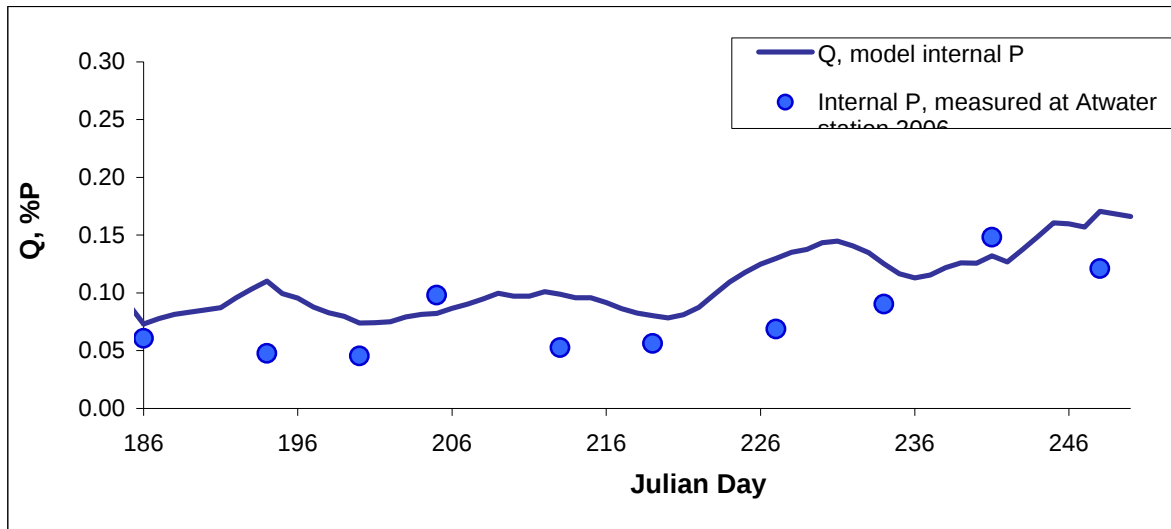


Figure 14. Seasonal variation in internal phosphorus at Atwater station, Lake Michigan in 2006. Depth = 9 m.

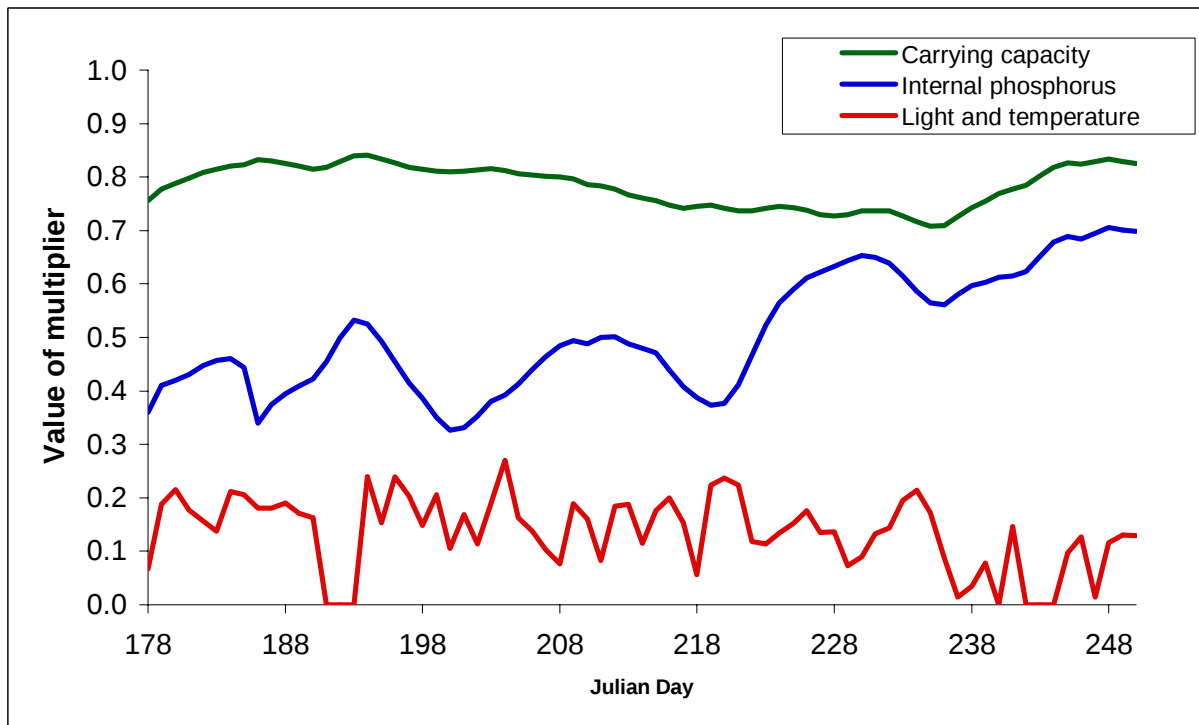


Figure 15. Seasonal dynamics of growth-limiting factors at Atwater station, Lake Michigan in 2006. Depth = 9 m.

Cladophora Model Summary

A new *Cladophora* model was developed following the framework of Canale and Auer (1982b) and updated to reflect current understanding of *Cladophora* ecology. The new model features open-source code and a user-friendly graphical user interface, allowing site-specific input of environmental conditions and physiological rates. Model performance was evaluated using data from Lake Huron (Harbor Beach study site, 1979 and 1980) and suggests that the underlying physiological constructs suitably predict biomass and internal phosphorus during development of the midsummer standing crop. The failure of the model to capture the measured decline in biomass in late summer is potentially due to the fit of the response surface polynomials and warrants further investigation. Application of the model to a much deeper station in Lake Michigan (Atwater Beach, 2006) confirms the ability to predict appropriate internal phosphorus concentrations based on ambient SRP concentration and to sustain growth in a variety of environmental conditions, further supporting the utility of the model as a tool for *Cladophora* management.