Environmental Controls of Cladophora Growth Dynamics in Eastern Lake Erie: Application of the Cladophora Growth Model (CGM)

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ABSTRACT. The Cladophora growth model (CGM) was used to estimate the importance of light, temperature, phosphorus, and self-shading on the spatial and temporal variability of Cladophora growth rates and biomass accrual in eastern Lake Erie during 2002. The CGM predicted that Cladophora growth was highly sensitive to spatial and temporal variations in soluble phosphorous concentration (SRP). Specifically the CGM predicted that: 1) Site-to-site differences in SRP concentration resulted in a 2× difference in depth-integrated biomass; 2) maximum growth rates were strongly influenced by SRP concentrations during periods of rapid biomass accrual (mid-June to mid-July); 3) inter-annual differences in SRP concentration during the spring period (~1 µg/L) could result in up to a 3.5× difference in depth integrated biomass; 4) Spatial variations in water clarity could result in a 2× difference in depth-integrated biomass between sites, with variations between sites occurring primarily between 2–6 m depth; 5) the mid-summer sloughing phenomenon likely resulted from self-shading by the algal canopy; and 6) the seasonal growth pattern of Cladophora was strongly regulated by temperature.

INDEX WORDS: Cladophora, Lake Erie, coastal eutrophication, benthic algae.

INTRODUCTION

Cladophora glomerata is a filamentous green alga that grows attached to hard surfaces in alkaline freshwaters at temperate and tropical latitudes (Sheath and Cole 1992). While the distribution of C. glomerata is ubiquitous, nuisance bloom formations are most often attributable to anthropogenic eutrophication (e.g., Neil and Owen 1964, Whitton 1970, Pitcairn and Hawkes 1973, Parker and Maberly 2000). From 1995 to 2002, widespread Cladophora blooms were documented along the rocky coastlines of eastern Lake Erie (Higgins et al. 2005b). Cladophora blooms have also been recently reported in Lake Ontario (T. Howell, Ontario Ministry of the Environment, pers. com.), the western shoreline of Lake Michigan (Byappanahalli et al. 2003), and isolated locations of Lake Huron (personal observation). The presence of widespread algal blooms in the coastal zones of these lakes (or lake basins), all of which are considered oligotrophic to meso-oligotrophic by offshore total phosphorus concentrations, may be symptomatic of fundamental shifts in water quality caused by the invasive zebra and quagga mussels (Dreissena polymorpha and D. bugensis, respectively) (Hecky et al. 2004, Higgins et al. 2005b).

Cladophora blooms were a significant ecological phenomenon in the lower Laurentian Great Lakes during the 1960s through to the early 1980s (Bellis and McClarty 1967, Herbst 1969, Shear and Konasewich 1975, Auer et al. 1982, Millner and Sweeney 1982). During the late 1970s a significant effort to understand the dynamics of Cladophora growth and biomass accrual resulted in the development of a mathematical growth model specific to Cladophora (Auer and Canale 1980; Auer et al. 1982; Canale et al. 1982; Canale and Auer 1982a, b; Auer and Canale 1982a, b; Graham et al. 1982). The “Auer and Canale” model, which related growth and biomass accrual to several dynamic parameters including light, temperature, dissolved phosphorus, and carrying capacity, was successfully validated on field populations of Cladophora in proximity to a sewage treatment outfall in Lake Huron (Canale and Auer 1982b). The “Canale and Auer” model was recently revised and verified on field populations of Cladophora in eastern Lake Erie (Higgins et al. 2005a). In the remainder of this
manuscript the revised model is referred to as the *Cladophora* growth model (CGM). The CGM simulations in this manuscript are made using environmental data from the five sites where the model was validated (Higgins *et al.* 2005a) and model validation results for each of the five sites are presented therein. While the previous study (Higgins *et al.* 2005a) was concerned with model development and testing, in this study we have applied the CGM to estimate the influence of natural environmental variability on the seasonal and spatial dynamics of *Cladophora* growth rates and biomass accrual in eastern Lake Erie. Specifically, we have used the CGM to investigate the sensitivity of *Cladophora* growth and biomass accrual to seasonal and site-to-site variability in surface irradiance, water clarity, temperature, and phosphorus. In addition we have used the CGM to investigate the underlying causes of the mid-summer sloughing phenomenon that is a common feature of dense *Cladophora* mats in the Laurentian Great Lakes and elsewhere.

**METHODS**

**Study Area and Environmental Variables**

The lake bottom of eastern Lake Erie’s northern littoral zone, from Port Dover to Fort Erie, consists of bedrock shelves (~80%) interspersed with smaller areas of sand and glacial till (Rukavina and St. Jacques 1971, St. Jacques and Rukavina 1973). The area of lake bottom and suitable substratum within each 1-m depth contour (from 0–10 m) is provided in Higgins *et al.* (2005b). The northern shoreline is highly exposed to waves generated from the predominant southwesterly winds. Water clarity is controlled by suspended particulate material (Higgins *et al.* 2005a, b), which is, in turn, controlled by turbulent particle re-suspension and settling velocities (Bloesch 1982, Weidman 2003, Higgins *et al.* 2005a). The bedrock areas were heavily colonized by *Dreissena bugensis* (Quagga mussel) in 2002 with densities between 4,000–11,000 individuals/m² (Patterson *et al.* 2005). A survey of 24 littoral zone sites from 1995 to 2002 (Higgins *et al.* 2005b) indicated that by mid-July > 90% of the rocky lake bottom (0–5 m) was overlain with *Cladophora* with a median biomass of 170 g/m² of dry mass (DM).

A detailed description of how environmental input variables were collected or estimated is available in Higgins *et al.* (2005a, b). In general, surface photosynthetically active radiation (PAR) was estimated from total solar radiation data collected from an Environment Canada meteorological buoy moored offshore of Long Point and an empirical relationship between total solar radiation and PAR for eastern Lake Erie (Higgins *et al.* 2005a). Simulated 100% cloud-free and 70% cloud-free surface PAR was generated for eastern Lake Erie (42°47'N, 79°59'W) using an atmospheric coefficient of 0.325 and the computer programs of Fee (1990). The reflectance of PAR from the water surface was assumed to remain constant at 10% of incident irradiance. Daily estimates of water column PAR extinction (kPARwc) were determined using an empirically derived relationship between kPAR and turbidity, and site-specific relationships between wave height and turbidity (Bloech 1982, Howick and Wilhm 1985, Higgins *et al.* 2005a). The extinction of PAR through *Cladophora* mats of varying density (kPARmat) was measured using field collected *Cladophora* in an outdoor incubator under direct sunlight. Attenuation of PAR was measured using a small flat plate collector of a Diving PAM fluorometer (Heinz Walz GmbH) within varying densities of *Cladophora*. The amount of PAR available at the base of the mat (PARmat) is described as:

\[
\text{PAR}_{\text{mat}} = (\text{PAR}_0 * e^{-k\text{PAR}_{\text{wc}} * Z_{\text{wc}}}) * e^{-k\text{PAR}_{\text{mat}} * Z_{\text{mat}}} \quad (1)
\]

Where \(\text{PAR}_0\) represents the amount of PAR available immediately below the water surface, kPARwc represents the water column extinction coefficient for PAR, Zwc represents the depth from the water surface to the top of the *Cladophora* mat, kPARmat represents the extinction coefficient of the mat, and Zmat represents the depth from the surface of the mat where PAR is to be modeled (modified from Wetzel 1983).

Wind speed and wave height were recorded from Environment Canada meteorological buoys moored offshore of Long Point and Port Colbourne for the duration of this study (01 May 02–31 Oct 02). Water temperature was recorded at each of the five sites at 2 m lake depth, 30 cm from the lake bottom, at 30-minute intervals using tidbit® temperature loggers (Onset corporation). Daily mean temperature values were used as model input. Due to the loss of some temperature loggers during autumn storms we were unable to obtain direct measurements of temperature from Rock point and Rathfon point after 08 Oct 02, and from Peacock point after 21 Oct 02. For the remaining portions of the model run, until 31 Oct 02, we estimated temperature at sites using the mean temperature of remaining sites. Water samples were from northern littoral zone
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sites (< 20 m station depth) and were filtered through a 0.45 µM GF/F filter in the field and frozen until analysis. Samples were analyzed for soluble reactive phosphorus (SRP) by the National Laboratory for Environmental Testing (NLET) using the stannous chloride-molybdate blue technique with a minimum detection limit of 0.2 µg/L (Charlton et al. 1999).

**Model Simulations**

All model simulations were conducted using the Cladophora growth model (CGM) (Higgins et al. 2005a). The CGM describes tissue phosphorus concentrations, growth, biomass accrual, and sloughing of Cladophora on the basis of mechanistic and empirically determined mathematical relationships with light, temperature, wind speed and direction, and soluble reactive phosphorus (SRP) (Higgins et al. 2005a). The CGM was incorporated into a computer simulation model using Stella modeling software (High Performance Systems Inc. 2001), and is available from the corresponding author of this manuscript. The CGM was verified on field populations of Cladophora at five sites in eastern Lake Erie (Higgins et al. 2005a) at shallow depth (2 m), and one site at deeper depths (5 m and 10 m) during 2002 (Higgins et al. 2005a). We used the median values of site-specific environmental data (Table 1) from these five sites, combined with non-site specific environmental data (Table 2) to establish conditions for a site that we refer to as the “median site.” We used the CGM to simulate Cladophora growth and biomass accrual over a range of depths (0–10 m) and report the results over a depth gradient, integrated over depth (in the case of biomass accrual), or as mean value over depth (in the case of specific growth rates). Depth integrated data are reported in two ways: 1) as a value that does not account for lake bathymetry and assumes that 1 m² of surface area is available for each 1 m depth contour, and 2) as a value that accounts for the bathymetry and substratum availability along the northern shoreline of Lake Erie’s eastern basin. We employ the first method of depth integration for assessing the effects of varying environmental parameters on Cladophora biomass without the confounding influence of bathymetry or substratum availability. We employ the second method for assessing how shifting model parameters will affect the total Cladophora biomass produced along the northern littoral zone of eastern Lake Erie accounting for bathymetry and substratum availability.

**RESULTS AND DISCUSSION**

**Model Verification**

The CGM was verified at the 5 sites used in this study (Fig. 1) during the same study year (Higgins et al. 2005a). The CGM predicted both the seasonality and magnitude of growth, tissue phosphorus, and biomass accrual of Cladophora across the five sites, which encompassed the expected range of ecological conditions in eastern Lake Erie, and direct comparisons between model simulations and measured data are presented in Higgins et al.
**TABLE 2. Non site-specific environmental data collected during 2001–2003 in eastern Lake Erie.**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Units</th>
<th>Year</th>
<th>Seasonal Range</th>
<th>Spring-Summer mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>PAR²</td>
<td>µM/m²/s</td>
<td>2001</td>
<td>35–1,209</td>
<td>824</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2002</td>
<td>79–1,237</td>
<td>869</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2003</td>
<td>78–1,344</td>
<td>803</td>
</tr>
<tr>
<td></td>
<td></td>
<td>100% Cloudless</td>
<td>712–1,123</td>
<td>1,114</td>
</tr>
<tr>
<td></td>
<td></td>
<td>70% Cloudless</td>
<td>498–786</td>
<td>780</td>
</tr>
<tr>
<td>Photoperiod</td>
<td>h</td>
<td>2001–2003</td>
<td>10.4–15.3</td>
<td>14.9</td>
</tr>
<tr>
<td>Wind Speed</td>
<td>m/s</td>
<td>2001</td>
<td>0.1–16.2</td>
<td>4.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2002</td>
<td>1.9–13.2</td>
<td>4.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2003</td>
<td>1.8–13.6</td>
<td>4.5</td>
</tr>
<tr>
<td>Wave height</td>
<td>m</td>
<td>2001</td>
<td>0.0–4.3</td>
<td>0.36</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2002</td>
<td>0.1–2.1</td>
<td>0.42</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2003</td>
<td>0.1–2.1</td>
<td>0.42</td>
</tr>
</tbody>
</table>

Notes: 1. Seasonal range for all data represents the period 01 May to 31 October, while the spring-summer mean value represents the period 01 May 02–24 July 02; 2. PAR data represents mean PAR during the photoperiod.

**FIG. 1.** Map of the eastern Lake Erie’s northern shoreline. Numbers refer to site locations where environmental data were collected and the model was validated (Higgins et al. 2005a). Site locations are as follows: 1. Peacock Point, 2. Hoover Point, 3. Grant Point, 4. Rock Point, and 5. Rathfon Point.
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The following sections describe the application of the CGM to estimate the response of Cladophora growth and biomass accrual to natural and anthropogenic induced variability in environmental parameters.

Seasonal Variability of Growth and Standing Crop

The seasonal pattern of biomass accrual (Fig. 2a) represents the integrated response of Cladophora to numerous, and highly dynamic, environmental variables (Tables 1, 2) that control growth and loss processes. The rate of biomass accrual, or loss, can be defined as:

\[ \frac{dx}{dt} = [\mu - R - L] \times X \] (2)

where \( \frac{dx}{dt} \) represents the change in biomass over time (g/m²/day), \( \mu \) represents the gross specific growth rate (day⁻¹), \( R \) represents the specific respiration rate (day⁻¹), \( L \) represents the specific loss rate due to sloughing (day⁻¹), and \( X \) represents the biomass or standing crop (g/m²). The CGM was developed and validated without the inclusion of additional loss terms such as grazing (Higgins et al. 2005a). Cladophora filaments are generally considered as poor food quality and not heavily grazed (Canale and Auer 1982a). The seasonal pattern of depth-integrated biomass accrual, and its subcomponents, was simulated using the CGM using the median data from five sites in eastern Lake Erie (Fig. 2a). During the spring (01 May 02–16 Jun 02) the growth rates were maximal and remained positive with the exception of a 2-day period during mid-May (12–13 May, 2002) when dense cloud cover reduced surface irradiance (Fig. 2b). From mid-June until mid-August the net specific growth rates declined to seasonally low values, which were < 0.05 day⁻¹. From July to October the mean net specific growth rate was 0.032 day⁻¹. During autumn (08–31 Oct 02) the balance of net specific growth rates became slightly positive allowing for some biomass accrual to occur. During the period of most rapid biomass accrual (15 Jun 02–24 Jul 02) specific growth rates had declined substantially from spring values and were well below optimal values (Fig. 2b).

The CGM calculates the net specific growth rate (\( \mu_{NET} \)) as a function of three multipliers (Higgins et al. 2005a) that account for the influence of light and temperature (\( P_{NET} \times a \)), internal phosphorus concentration (\( M_P \)), and self-shading (\( M_X \)) on the maximum net specific growth rate (\( \dot{\mu}_{NET} \)) (Equation 3).

\[ \mu_{NET} = \dot{\mu}_{NET} \times (P_{NET} \times a) \times M_P \times M_X \] (3)

Each multiplier is dimensionless and varies from 0–1, while \( \dot{\mu}_{NET} \) is a constant with a value of 0.6 day⁻¹ (Higgins et al. 2005a). We compared the seasonal variability of these multipliers and \( \mu_{NET} \) using the CGM and median data from five sites in eastern Lake Erie during 2002 (Fig. 2c). The simulation (Fig. 2c) was constrained to depths less than 4 m, where 87% of the depth-integrated biomass occurred. The general seasonal pattern in \( \mu_{NET} \) was controlled by the parameter “\( P_{NET} \times a \),” indicating the importance of temperature and available PAR (Fig. 2c). Temperature controlled the general seasonal pattern of “\( P_{NET} \times a \),” while rapid oscillations were controlled by strong cloud-cover or high turbidity events that reduced available PAR. The rapid day-to-day fluctuations in \( \mu_{NET} \) were also largely dependent on variations in the amount of PAR available at depth, which were caused by variable cloud cover early (01 May 02–15 Jun 02) and late in the growing season (15 Sep 02–31 Oct 02) and fluctuations in water clarity during the rapid growth phase (16 Jul 02–14 Sept 02). As biomass approached its seasonal peak value the parameter for self-shading (\( M_X \)) also became quantitatively important, reducing depth integrated production by an additional 20%. The growth multiplier for self-shading (\( M_X \)) is calculated as:

\[ M_X = 1 - \frac{X}{X_{MAX}} \] (4)

where \( X \) represents the areal biomass of Cladophora (g/m²), and \( X_{MAX} \) represents the maximum areal biomass (g/m²) and is dependant on available PAR at the mat surface (Higgins et al. 2005a). Phosphorus concentrations within Cladophora tissues were below optimal growth requirements for the duration of this study (01 May 02–31 Oct 02). Within the CGM tissue P values are assessed using variations in the parameter \( M_P \), the growth multiplier for tissue phosphorus. Within the CGM the value for \( M_P \) is calculated as:

\[ M_P = 1 - \frac{Q_0}{Q} \] (5)

Where Q is the tissue P concentration (% DM), and \( Q_0 \) is the minimum tissue P concentration (0.05% DM) required for growth (Wong and Clark 1976, Auer and Canale 1982b). The median tissue P value
FIG. 2. Cladophora growth model (CGM) estimates for the seasonal dynamics of a) biomass accrual, b) net specific growth rate, and c) Cladophora growth model multipliers. In panel A the depth integrated biomass calculations are per meter of shoreline assuming 1 m$^2$ of surface area for each 1 m-depth contour (see Methods). Values for the net specific growth and multipliers were calculated to represent depths 0–4 m where >90% of Cladophora biomass occurred during 2002. Multipliers vary from 0–1 and refer to the effects of available light and temperature ($P_{\text{net}} \times a$, solid line), internal phosphorus concentration ($M_P$, dotted line), and carrying capacity ($M_X$, dashed line).
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(Q) from the 5 sites in eastern Lake Erie ranged from 0.09–0.25% DM during 2002, forcing \( M_P \) to vary from 0.43–0.80 (i.e. realized growth rates were 43–80% of optimal values based on light and temperature conditions) (Fig. 2c). Rapidly declining values for tissue P (Q) during May forced \( M_P \) to decline from 0.80 to 0.44 by June. From June to August, the period of rapid biomass accrual, \( M_P \) stabilized and had a mean value of 0.46 (Fig. 2c) and the CGM predicted that realized growth rates were 46% of those obtainable based on ambient water temperatures and available PAR.

Vertical Distribution of Growth and Standing Crop

Cladophora biomass predicted by the CGM was in close agreement with observed data, with the exception of the shallowest depths (< 1.5 m) (Fig. 3). This comparison was based on the median environmental data from 5 sites in eastern Lake Erie (Table 1) and non-site-specific data (Table 2). Under high PAR intensities (> 600 \( \mu M/m^2/s \)) and summer water temperatures (15–24°C), the CGM predicted that reduced growth rates would occur at shallow depths in response to increased light enhanced respiration (Graham et al. 1982). Translating these results to field conditions, however, is problematic. The Cladophora mats at shallow depths (< 1 m, where PAR may exceed 600 \( \mu M/m^2/s \)) are dense and the mean mat thickness was near 10 cm (Higgins et al. 2005b). While light enhanced respiration may occur near the surface of the mat \textit{in situ}, maximum PAR values (1,100 \( \mu M/m^2/s \)) at the mat surface are attenuated to levels below 600 \( \mu M/m^2/s \) within the upper 1.5 cm of the mat structure. Therefore, even under the highest PAR intensities the effects of light enhanced respiration or photoinhibition would be diminished within a short distance into the mat. While the CGM accounts for reductions in growth due to self-shading it does not account for the positive effects of self-shading under conditions where PAR at the surface of the mat exceeds optimal values. Secondly, the photosynthetic response of Cladophora collected from eastern Lake Erie during 2002 showed no reduction in maximum photosynthesis at PAR intensities between 600–1,200 \( \mu M/m^2/s \) (Higgins 2005), and this result is similar to that reported by Lester et al. (1988) for Cladophora from Lake Michigan. Therefore, in eastern Lake Erie the CGM will over-predict the influence of light enhanced respiration or photoinhibition on mat growth rates and biomass accrual at shallow depths (< 1 m) where PAR intensities often exceed 600 \( \mu M/m^2/s \) at the mat surface. Therefore, we constrained PAR values to 0–600 \( \mu M/m^2/s \) at the mat surface, and under these conditions the CGM predictions for biomass accrual at shallow depths (< 2 m) are more similar to measured values than the unconstrained CGM, and are identical to the unconstrained CGM predictions at deeper depths (> 2 m) (Fig. 3). For the remainder of the simulations in this manuscript we have used the constrained CGM (i.e., removed the effects of light enhanced respiration or photoinhibition).

Self-shading and Midsummer Sloughing

An important component of the seasonal pattern of Cladophora growth and biomass accrual, under bloom conditions, is the mid-summer sloughing event (Fig. 2a). During the mid-summer period, typically mid-July to early August in Lake Erie...
filaments become detached from their holdfasts and create large drifting mats. The mid-summer detachment phenomenon has been documented in a variety of lakes and rivers (e.g., Wong et al. 1978, Bellis and McLarty 1967, Whitton 1970), however the underlying mechanisms causing the sloughing have not been adequately described or modeled. Previous efforts to model the detachment process as a function of metabolic imbalance (Canale et al. 1982) predicted that the onset of sloughing would occur when the *Cladophora* mat approached zero (or negative) growth. Other researchers noted that the metabolic imbalance hypothesis was improbable since, in their study, excess photosynthetic products (starch) were found accumulated within *Cladophora* tissues immediately prior to the onset of sloughing, and suggested other factors such as nutrient limitation as potential causes of the sloughing (Mantai 1987, 1989). Numerous studies also mention the potential for temperature to exert some control over the midsummer-sloughing event (see Whitton 1970 for review) however a wide discrepancy remains between the temperature tolerances determined under laboratory conditions and field observations of the temperature at which the sloughing event occurs. For example, laboratory studies have demonstrated that positive growth may occur at temperatures between 25–30°C (Bellis 1968, Graham et al. 1982, Lester et al. 1988, Higgins 2005), while field studies in the Laurentian Great Lakes region report deterioration of the algae and sloughing to occur at temperatures < 24°C (e.g., Wong et al. 1978, Auer et al. 1982, Higgins et al. 2005b). During 2002 the sloughing event in eastern Lake Erie occurred as water temperatures approached 22.5°C (Higgins et al. 2005a). Photosynthesis-Irradiance (P vs. I) experiments conducted on *Cladophora* tissues in eastern Lake Erie during 2002 (Higgins 2005) revealed no obvious differences in photosynthetic capacity prior to, during, or after the sloughing event. The results of these experiments cast doubt on the hypothesis that temperature alone is responsible for the sloughing phenomenon. Further, the sloughing phenomenon in eastern Lake Erie was noted to occur at sites where tissue phosphorus concentrations were maintained at high levels due to proximity to a local nutrient source (Higgins et al. 2005b). This result casts doubt on the hypothesis that phosphorus limitation alone is responsible for the sloughing phenomenon.

In the CGM simulations the net specific growth rates of the mat did not display obvious signs of prolonged metabolic imbalance prior to the sloughing event (Fig. 2b). The CGM, however, integrated growth rates over the entire vertical structure of the mat and the results did not necessarily reflect the potential for metabolic imbalance to have occurred at the base of the mat where the physical detachment of the filaments generally occurred. To elucidate whether self-shading could induce metabolic imbalance at the base of the mat we modeled the specific growth rates at the top and bottom of the mat independently (Fig. 4). The quantity of PAR available to the upper and lower mat surfaces were estimated using Equation 2, and the light extinction within the mat (kPAR\text{mat}) was calculated using the relationship between kPAR\text{mat} and mat density. At shallow depths (0–4 m) the growth rates at the surface of the mat were positive throughout the simulation period, while at the base of the mat growth rates became consistently negative after 04 July 02 until the sloughing event. These simulation results suggest that a prolonged period (14–20 days) of negative growth occurred at the base of the mat prior to the sloughing event, which occurred be-

![FIG. 4. The seasonal variability of net specific growth rates at the surface and base of the *Cladophora* mat during 2002 as predicted by the *Cladophora* growth model (CGM). Data represent the mean specific growth rates between 0–4 m. The solid line represents rates at the upper mat surface, while the dashed line represents rates at the base of the mat.](image-url)
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Between 24–29 Jul 02. In these model simulations the difference in growth rates between the upper and lower mat surfaces was completely driven by available PAR, and negative growth rates at the base of the mat occurred irrespective of tissue P concentration (data not shown). Ambient water temperatures (22–25°C), which increased respiratory rates, further exacerbated the metabolic imbalance at the base of the mat. However, the CGM predicted that at PAR values below 25 µM/m²/s growth rates are negative at all temperatures between 0–35°C (Graham et al. 1982).

During the 10-day period immediately prior to the sloughing event simulated growth rates at the base of the mat were negative at depths less than 5 m, and slightly positive at depths below 5 m (Fig. 5). The increase in growth rates at the base of the mat with increases in lake depth may appear counter-intuitive, as the exponential declines in PAR through the water column might be expected to exert control over the amount of PAR reaching the base of the algal mat. While the quantity of PAR reaching the mat surface is important, the attenuation of PAR through the mat structure is rapid when algal densities are high (Fig. 6). At high mat densities, such as those found at depths between 0–4 m, the PAR extinction coefficients of the mat (kPARm = 25–30 m⁻¹) are nearly two orders of magnitude higher than that of the water column (kPARwc = 0.5 m⁻¹). As a result of the declining height and density of the mat with lake depth, sufficient PAR reached the base of the mat to maintain positive growth at depths 7–10 m.

As predicted by the CGM, we hypothesize that the underlying cause of the midsummer-sloughing event in eastern Lake Erie was the prolonged metabolic imbalance at the base of the Cladophora mat during mid-summer. The CGM simulations also indicated that growth rates at the mat surface, while positive, were strongly P-limited. These results are also consistent with observations that Cladophora can grow at higher temperatures (25–30°C) in both field and laboratory settings (e.g., Graham et al. 1982, Whitton 1970, Higgins 2005). In fact, Cladophora harvested from the same sites modeled in this study displayed no reduction in its photosynthetic capacity throughout the sloughing period (Higgins 2005). In this study the CGM predicted

**FIG. 5.** The vertical distribution of PAR and net specific growth rates at the surface (solid lines) and base (dashed lines) of Cladophora mats at the “median” site in eastern Lake Erie as predicted by the CGM. Daily mean PAR values represent mean values during the photoperiod. Both daily mean PAR and net specific growth rates are mean values for the 10-day period (14–24 July) immediately preceding the midsummer-sloughing event. The solid vertical line in panel A represents the minimum PAR requirement for growth (~30 µM photons/m²/s).
that the metabolic imbalance was caused primarily by low light conditions at the bottom of a dense algal mat, exacerbated by moderately high water temperatures (~23°C).

In our original formulation of the CGM (Higgins et al. 2005a) we were unable to define a mathematical relationship between metabolic imbalance of the mat and the sloughing phenomenon, and therefore modeled the sloughing phenomenon based solely on temperature. As the ambient water temperature exceeded a set threshold, 22.5°C for eastern Lake Erie, the sloughing event was induced. However, we considered the use of temperature as unsatisfactory since it did not explain the underlying causes of the sloughing event and also because other field studies showed that deterioration and eventual sloughing of the mat occurs once the accumulated growth rates exceed a pre-defined threshold (e.g., 40% of the biomass is lost through respiration). Each of these assumptions will require testing under a wide range of field conditions and it is likely that these calculations will be modified as the decay and sloughing phenomenon within field populations of Cladophora are more thoroughly understood.

The Effects of Parameter Variability on Growth and Biomass

In the previous sections the general seasonal and spatial patterns of Cladophora in eastern Lake Erie were discussed in relation to several environmental variables including light, temperature, and dissolved phosphorus. In this section we use the CGM to investigate how inter-site and seasonal variability in these environmental parameters affect Cladophora distribution, growth, and standing crop.

PAR

To estimate the effects of inter-annual variability in cloud cover on Cladophora growth rates and biomass, PAR data collected during 2002 was substituted with data collected from 2001 and 2003, and with simulated 70% and 100% cloud-free PAR data generated using Fee’s (1990) computer program. The variability in PAR values between 2001–2003 resulted in only a 5–6% difference in the depth-integrated standing crop and had a negligible effect on the depth distribution (data not shown). The CGM predicted that 100% cloud-free conditions would increase the depth-integrated biomass by 37% (from 2002 conditions), with 70% of the difference occurring between 1–5 m depth. Depth-integrated biomass modeled using the 70% cloud-free conditions (1–10 m) was 3% higher than CGM predictions under 2002 measured PAR conditions. These results indicated that inter-annual variability
in the amount of PAR received at the surface of the lake likely has only a minor role in controlling year-to-year differences in standing crop.

**kPAR**

During 2002 the mean kPAR values ranged from 0.36–0.71 m\(^{-1}\) between sites, with the median site having a value of 0.45 m\(^{-1}\) (Table 1). The CGM predicted that site-to-site differences in kPAR would cause large differences in the depth distribution of biomass and the total depth-integrated biomass between sites. The effects of water clarity on depth-integrated biomass and the depth distribution of biomass were modeled using water clarity data from the most turbid site (Peacock point) and the least turbid site (Rathfon point), while constraining all other variables to site-median values (Fig. 7). Under the most turbid conditions the depth-integrated biomass was 380 g/m (i.e., per meter of shoreline) with > 90% of the biomass occurring at depths < 3 m. Under the least turbid conditions the depth-integrated biomass was 860 g/m, and 90% of the biomass occurred at depths < 6 m. Approximately 70% of the difference in depth-integrated biomass between these two simulations occurred between 2–6 m depth. These results demonstrate that the natural range in water clarity between sites in eastern Lake Erie can have a strong influence on the depth-integrated biomass and the depth distribution of biomass. Further, shifts in water clarity have relatively little effect at depths < 2 m where growth is light saturated, and the most effect on biomass at intermediate depths (2–6 m). These simulation results also suggest that the depth-integrated biomass would increase toward the eastern end of the basin where mean water clarity was highest (Table 1).

During the spring-summer growing period (01 May 02–24 July 02) mean kPAR values at the median site, modeled using site dependant relationships with wave height (Higgins *et al.* 2005a), ranged from 0.43–0.45 m\(^{-1}\) (Table 1). The CGM predicted that a depth-integrated biomass of 645 g/m and 652 g/m during 2001 and 2002 respectively, and that the depth-distribution was similar between years (data not shown). While these results suggest that year-to-year differences in water clarity were small compared to site-to-site differences kPAR data were generated using wave height data from meteorological buoys (Higgins *et al.* 2005a) and therefore do not reflect potential variability in kPAR due to other factors such as spring runoff or variability in the influence of rivers. Overall, this result suggests that site-to-site differences in the propensity for sediment resuspension are more important drivers of variations in water clarity than changes in surface meteorological conditions (wind speed, wave height) alone.

**Temperature**

The CGM predicted that site-to-site variability in depth-integrated biomass, 580–740 g/m, based solely on temperature was relatively low compared with other factors. Our analysis does not, however, include the potential interaction of temperature with upwelling events that may be associated with higher dissolved nutrient concentrations.

**Phosphorus**

Previous studies have demonstrated the importance of available phosphorus in controlling the growth rates and biomass accrual of *Cladophora* in Lake Erie (Neil and Jackson 1982; Higgins *et al.* 2005a, b), Lake Ontario (Painter and Kamaitis...
In eastern Lake Erie mean SRP concentrations during the spring-summer growing period of 2002 ranged from 0.9–3.5 µg/L at our five nearshore sites (Table 1). One of these sites (Rock Point) is frequently influenced by the plume of the Grand River, maintains higher SRP concentrations throughout the summer period, and is not considered representative of other areas along the northern shoreline of eastern Lake Erie (Higgins et al. 2005b). Excluding the Rock Point site, the mean SRP during the spring-summer period ranged from 0.9–2.1 µg/L at the remaining four sites. While constraining other parameters to the “median” site values we used the CGM to simulate Cladophora growth based on SRP concentrations at the four remaining sites (Fig. 8).

Based on the site-to-site differences in SRP the peak depth-integrated biomass ranged from 390–800 g/m. While the lowest mean SRP concentration during the spring-summer period occurred at Rathfon point (Table 1), the CGM predicted that the lowest depth-integrated biomass would occur at Grant Point (Fig. 8). The difference in model predictions between these sites illustrates the importance of the SRP concentration during the period of rapid biomass accrual (July). At the Rathfon Point site the SRP concentrations were lower initially; however, they increased and remained near 1 µg/L during July (data not shown). At the Grant Point site SRP concentrations were higher initially, but declined rapidly to very low concentrations (< 0.2 µg/L) during July. Because the change in biomass (Equation 1) is based on the net specific growth rate multiplied by the biomass, differences in the specific growth rates between sites during periods of high biomass (e.g., July) will have a much larger effect on biomass accrual than during periods of low biomass (e.g., May). As a consequence, the site-to-site differences in SRP during July had a large influence on differences in the net specific growth rates, biomass accrual, and peak standing crop of Cladophora between sites in eastern Lake Erie.

The CGM was used to examine the influence of inter-annual differences in SRP concentration on the peak standing crop of Cladophora at the “median” site (Fig. 9). Inter-annual differences in spring SRP concentrations in the offshore waters of eastern Lake Erie varied by ~1 µg/L during post- Dreissena years (Table 3). SRP concentrations in nearshore waters of eastern Lake Erie were assumed to display at least the same degree of inter-annual variability as the offshore waters. We varied SRP by ± 0.5 µg/L from median conditions during 2002, constraining the minimum SRP concentration to 0.2 µg/L (Fig. 9).

To determine the influence of these changes in SRP on basin wide Cladophora biomass (northern shoreline) the influence of bathymetry and substratum availability were included in the calculations. In these calculations the areal biomass for each 1 m depth interval at the “median” site is multiplied by the total amount of available substratum for that depth contour. Using this method the CGM predicted that peak depth-integrated biomass along the northern shoreline of eastern Lake Erie would have been approximately 10,000 tonnes DM during 2002, which is similar to estimates of 11,000 tonnes made using field-collected biomass data from 1995–2002 (Higgins et al. 2005b). Further, the CGM predicted that increases of 0.5 µg/L SRP from 2002 “median” conditions would result in a total depth-integrated biomass of 15,600 tonnes, a 1.5x increase from biomass estimates during 2002 (Fig. 9). Conversely, the CGM predicted that a reduction
of 0.5 µg/L SRP from 2002 “median” conditions would result in a maximum standing crop of 4,700 tonnes, a 54% decrease from biomass estimates during 2002. These results illustrate the sensitivity of *Cladophora* biomass accrual in eastern Lake Erie to ambient SRP concentration. The CGM also predicts that the timing of the sloughing event would be altered by variability in SRP concentration of 0.5 µg/L (Fig. 9). As previously discussed, the CGM predictions for the timing of the sloughing event were based on metabolic imbalance at the base of the algal mat. Under increased SRP conditions (+ 0.5 µg/L) the mat density increased rapidly, reducing the amount of PAR reaching cells at the base of the mat below minimum requirements, and the sloughing event was triggered approximately 9 days earlier (Fig. 9). When SRP concentrations were reduced by 0.5 µg/L from 2002 “median” conditions the CGM predicted that the algal mat would not reach a sufficient density to trigger the mid-summer sloughing.

**TABLE 3. Offshore SRP concentrations (µg/L) in eastern Lake Erie (1991–2003).** Minimum, maximum, and mean values were calculated by averaging monthly basin-wide mean values for “n” years. Data provided by M. Charlton (NWRI, Environment Canada).

<table>
<thead>
<tr>
<th></th>
<th>June</th>
<th>July</th>
<th>August</th>
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<tbody>
<tr>
<td>Minimum</td>
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<tr>
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**SUMMARY**

The CGM predicted that *Cladophora* growth and biomass accrual in eastern Lake Erie was phosphorus limited and highly sensitive to variability in dissolved phosphorus concentrations during the study period (Fig. 9, Higgins *et al.* 2005b). Spatially, the CGM predicted that site-to-site differences in SRP would result in a 2X difference in depth-integrated biomass. Temporally, the CGM predicted that both seasonal and year-to-year variability in SRP concentrations were important factors in controlling variability in growth rates and biomass accrual.

CGM simulations indicated that *Cladophora* growth was most responsive to elevated SRP concentrations during the period of maximum biomass accrual (mid-June to mid-July; Fig. 2). Monthly mean SRP concentrations (post *Dreissena*) varied by ~1.0 µg/L between years (Table 3), and CGM predictions indicated that such differences would result in a 3.5× change in depth-integrated biomass (Fig. 9). These CGM predictions support previous assertions (Higgins *et al.* 2005b) that managing phosphorus will be effective at controlling *Cladophora* blooms in eastern Lake Erie. The widespread *Cladophora* blooms in eastern Lake Erie were not necessarily associated with point source nutrient discharges and were considered governed by basin-wide P availability (Higgins *et al.* 2005b).

Further research efforts should focus on gaining a more complete understanding of the phosphorus sources to the littoral zones, including the importance of Dreissenids in modifying the bioavailability of phosphorus.

The CGM predicted that, in addition to phosphorus, variations in water clarity were important controls on the spatial variability in growth rates and biomass accrual of *Cladophora* in eastern Lake Erie post-*Dreissena*. The CGM predicted that vari-
ations in water clarity were responsible for up to a 2x difference in depth-integrated biomass between sites. Further, the differences in water clarity affected the depth distribution of biomass with largest differences between sites occurring between 2–6 m depth. Previous Cladophora studies have generally limited themselves to depths < 3 m and would have missed the importance water clarity plays in controlling site-to-site differences in depth integrated biomass.

The deterioration and physical detachment of Cladophora filaments from their holdfasts (sloughing) is an important feature of the seasonal growth cycle of Cladophora (Fig. 2). A variety of potential mechanisms including temperature stress (Bellis and McClarty 1967, Whitton 1970, Dodds and Gunder 1992), nutrient stress (Mantai 1987, 1989), or a combination of factors inducing cellular deterioration (Canale et al. 1982), have been proposed as causes of the sloughing phenomenon. These hypotheses, however, have treated the Cladophora mat as a single unit. Our CGM simulations suggest that the attenuation of light through dense Cladophora mats induce negative growth rates and cellular deterioration toward the base of the mat, even under high light conditions at the mat surface. The inability of cells toward the base of the mat to maintain positive metabolic balance is likely exacerbated by other factors including high temperatures, thick coatings of epiphytes (Lowe et al. 1982, Stevenson and Stoermer 1982, Dodds 1991), and low nutrient concentrations. Cellular deterioration at the base of the Cladophora mat can occur while cells toward the surface of the mat are still actively growing, and growing under different growth limiting conditions. The lack of intercellular organelles or plasmodesmata suggests that intercellular transport of nutrients or metabolites within Cladophora filaments is low and metabolites or nutrients acquired by cells at the surface of the algal mat are not effectively transported to cells toward the base of the mat. Cladophora filaments harvested from identical sites and time periods as in this study, and incubated at ambient lake temperatures, showed no decline in photosynthetic capacity throughout the sloughing period (Higgins 2005). This result is in agreement with our CGM model predictions and suggests that the sloughing phenomenon in eastern Lake Erie was not a direct physiological response to temperature, but a community level response to self-shading in combination with other factors.

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REFERENCES


———, and Auer, M.T. 1982b. Ecological studies and mathematical modeling of Cladophora in Lake
Environmental Controls on Cladophora Growth


Stevenson, R.J., and Stoermer, E.F. 1982. Seasonal


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