

## Modeling the growth response of *Cladophora* in a Laurentian Great Lake to the exotic invader *Dreissena* and to lake warming

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### Abstract

A *Cladophora* growth model (CGM) is calibrated and validated here to simulate attached and sloughed *Cladophora* biomass in daily time-steps in an urbanized location of Lake Ontario, using two years of collected input data and independent measurements of *Cladophora* biomass. The CGM is used to hindcast *Cladophora* growth using multiplicative factors of seasonal minimal tissue phosphorus concentrations ( $Q_P$ ) and seasonal mean nearshore light attenuation ( $K_{dPAR}$ ) of the early 1970s and 1980s relative to modern data. The possible effects of climate on growth are also forecast using additive temperature increases. *Cladophora*  $Q_P$  in Lake Ontario has declined in parallel with decreasing pelagic P concentrations, resulting in reduced *Cladophora* biomass at all depths in the euphotic zone.  $K_{dPAR}$  has also declined, most strongly since the mid-1990s, following *Dreissena* mussel invasion, driving an increase in biomass between 3.5- and 10-m depth. Combining these effects, the CGM predicts that biomass along shorelines today is lower in Lake Ontario than in the 1980s. However, any increases in  $Q_P$  in this post-dreissenid-mussel period will result in greater *Cladophora* proliferation than in previous decades due to increased nearshore water clarity. *Cladophora*  $Q_P$ , while still currently lower than in the early 1980s, may be rising due to P supply to the littoral zone by the invasive mussels. The surface water temperature of Lake Ontario indicates warming of  $0.96^\circ\text{C decade}^{-1}$  from 1980 to 2006. With increasing surface water temperatures, the CGM predicts an earlier spring growth but only a marginal increase in peak *Cladophora* biomass.

Eutrophication continues to be among the most critical and pervasive issues facing coastal waters—marine and freshwater alike (Rabalais and Nixon 2002; Smith et al. 2006). Blooms of annual or ephemeral attached macroalgae are symptomatic of nutrient enrichment in littoral zones underlain by hard substrata and are typically indicative of degraded ecosystem health (Raven and Taylor 2003; Smith et al. 2005; Worm and Lotze 2006). High biomass of the globally distributed filamentous green alga, *Cladophora*, in particular, is regarded as a sentinel of eutrophication in alkaline systems (Dodds and Gudder 1992; Lembi 2003). Nuisance densities of *Cladophora* have been reported from estuaries (Gordon and McComb 1989; Valiela et al. 1997), inland seas (Kiirikki 1996; Curiel et al. 2004), and hard-water rivers and lakes with moderate energy (Power 1992; Parker and Maberly 2000). In the Laurentian Great Lakes, *Cladophora* is a nuisance throughout Lakes Ontario, Erie, and Michigan, where hard substrate is available, and in

isolated areas near nutrient point sources in Lake Huron (Herbst 1969).

There is a widespread perception that since the establishment of invasive dreissenid mussels (i.e., the zebra mussel [*Dreissena polymorpha*] and the quagga mussel [*D. bugensis*]) over the past 15 yr, *Cladophora* biomass has resurged in the lower Great Lakes (Mills et al. 2003; Hecky et al. 2004; Bootsma et al. 2005). The degree to which this perception is accurate, however, is unclear. Due to their high biomass in these lakes (e.g., up to 150 g shell-free DM  $\text{m}^{-2}$ ; Fleisher et al. 2001), dreissenid mussels have been credited with reengineering nutrient distributions by removing suspended particulate matter through filter-feeding, then excreting dissolved regenerated nutrients as well as generating organic waste as feces and pseudofeces in the benthos (Hecky et al. 2004). This process, recently termed “benthification” (Zhu et al. 2006), has been implicated in shifting pools of matter with attendant nutrients from the pelagia to the benthos and increasing the solar radiant flux to the littoral benthos. Mussels can be an important source of nutrients to overlying flora (Kahlert and Pettersson 2002) and, furthermore, may remove competitive demands for nutrients via filtration of plankton (Holland et al. 1995). In the Great Lakes, long-term pelagic total P concentrations have been declining since the 1970s due in part to nutrient abatement strategies (e.g., Nicholls 2001; Millard et al. 2003) while currently, dreissenid mussels may be increasing supply of P to benthic flora (Hecky et al. 2004). The decadal-scale response of *Cladophora* tissue P quota ( $Q_P$ ) to these counteracting pressures in the Great Lakes is not known. The lower Great Lakes have additionally experienced a significant increase in light penetration since dreissenid mussel establishment (Howell et al. 1996) in response to decreased seston

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concentration (Millard et al. 2003) and, in Lake Ontario, possibly a reduced frequency of whiting events (Barbiero et al. 2006). The resulting increase in euphotic depth may have increased the biomass of *Cladophora* occurring at previously light-limited depths and increased its areal extent of coverage (Zhu et al. 2006).

The effects of climate change on the limnology of the Great Lakes may also have important consequences for macroalgal blooms. Direct effects of epilimnetic temperature increases on macroalgae include increases in photosynthetic and respiration rates. An early hypothesis proposed that supraoptimal temperatures cause a metabolic imbalance in *Cladophora* beds, giving rise to a commonly observed mid-summer senescence and detachment (Graham et al. 1982). However, evidence has supported the converse; *Cladophora* effectively acclimates to high temperatures (Mantai 1987), such that temperature optima for net primary production can be as high as 28–31°C (Lester et al. 1988). Summer temperature increases in Lake Ontario may be expected based on increasing temperature and decreasing duration of ice cover in lakes in the Great Lakes region (Jensen et al. 2007). Whether an increase in surface water temperature due to climate change may exacerbate the magnitude of *Cladophora* blooms has not yet been investigated.

Testing hypotheses about the relative effects of historical changes to nutrient supply and light penetration on benthic algal biomass accrual is limited by scant direct measures of *Cladophora* biomass over decadal scales. In the absence of direct measures, a numeric model that predicts *Cladophora* growth rate and biomass accumulation seasonally, in response to known environmental drivers including light, temperature, and nutrient concentrations, provides a framework for assessing the seasonally and depth-resolved accumulation of *Cladophora* biomass. Through sensitivity analyses of the model, the effects of changes in water transparency, nutrient concentration, and surface-water temperature can be assessed.

The goal of this study is to quantitatively assess the effects of decadal-scale changes in Lake Ontario on nuisance macroalgal biomass. Our first objective is to calibrate and validate a growth model for an area on the north shore of western Lake Ontario, an area that has received an increasing No. of public complaints of macroalgal shoreline fouling over the past decade (The Regional Municipality of Halton, pers. comm.), using direct measurements of *Cladophora* biomass collected over two growing seasons that experienced very different meteorology. The second objective is to apply the model to predict the independent and combined effects of decadal-scale changes in  $K_{dPAR}$  and *Cladophora*  $Q_P$  on *Cladophora* biomass accumulation. Two decades are chosen for hindcasting: the early 1970s, which preceded P-abatement strategies, and the early 1980s, which followed P-abatement but preceded dreissenid mussel establishment, which was first ecologically detectable in western Lake Ontario in 1991 (Nicholls 2001). The third objective is to use the model to forecast the direct effects of climatic warming on the seasonality and magnitude of *Cladophora* growth, based on a near linear trajectory of increasing surface water

temperature in Lake Ontario. In these sensitivity analyses, we employ the two modern years (2004 and 2005) of meteorology in order to predict a range of outcome scenarios. The limnological and meteorological data from the two modern years are referred to as the baseline data.

## Methods

*Site description*—Field sampling for this study was conducted on Lake Ontario in Oakville, Ontario, Canada (43.44°N, 79.66°W). The site is underlain by boulders and cobble and supports up to 100% *Cladophora* coverage at 2.0-m depth during midsummer. The species identified throughout the Laurentian Great Lakes, using molecular markers, is *C. glomerata* (L.) Kützing (K. Muller, U. Waterloo, pers. comm.).

*Measurements of Cladophora biomass*—*Cladophora* biomass estimates were made by snorkellers deploying 0.25-m<sup>2</sup> quadrats at 2.0-m depth. Five replicate quadrats were harvested. The percentage of attached algal coverage, bed height, and filament length were measured in each quadrat. All *Cladophora* biomass was harvested with scraping tools from the quadrats and collected in mesh bags. The product of bed height and algal coverage, the “stand volume,” was correlated, independently on each day, with algal biomass (mean  $\pm$  SD of all days: 7.5  $\pm$  2.6 g DM L<sup>-1</sup> stand volume). In 2004, biomass was estimated either by direct harvests or using the stand volume correlation. In 2005, all biomass was estimated from direct harvests. In the lab, harvested material was rinsed in mesh sieves (pore size ~1 mm) and picked clean with forceps to remove larger debris and macrofauna. The rinsing process also had the effect of removing the majority of the finer filamentous alga, *Ulothrix zonata*, which was abundant early in the spring prior to *Cladophora* dominance and in late summer between *Cladophora* seasonal cohorts, but was otherwise a marginal fraction of the macroalgal biomass. The cleaned *Cladophora* material was examined under dissecting microscope to confirm that the filamentous algae were almost exclusively *Cladophora*.

*Measurements of tissue phosphorus concentrations*—Tissue P concentration ( $Q_P$ ) was measured of randomly sampled *Cladophora* harvested in triplicate weekly to biweekly during the growing season at 2.0-m depth. Samples were collected on 13 dates in 2004 and on 15 dates in 2005. Dried *Cladophora* tissue was combusted at 450°C for 1 h and then autoclaved for 30 min in distilled water with 4% potassium persulphate solution added to a final concentration of 0.16%. Following digestion, solubilized P was measured spectrophotometrically using the molybdate blue method (American Public Health Association 1998).

*Cladophora growth model*—To construct seasonally resolved estimates of *Cladophora* biomass, the *Cladophora* growth model (CGM) was used. Previous versions of the model described here have successfully been validated to

predict *Cladophora* biomass at discrete distances from a sewage treatment plant in Lake Huron (Canale and Auer 1982), and to predict *Cladophora* seasonal growth from 2 m to 10 m depth in the agriculturally dominated, oligotrophic eastern basin of Lake Erie (Higgins et al. 2005a).

Daily time steps of *Cladophora* were predicted as attached or as sloughed (i.e., detached) biomass. The sum of these components, the “cumulative” biomass, was also quantified. The CGM was run using the visual interactive modeling package Stella, version 7.0.2 (2001; High Performance Systems).

The CGM predicts daily specific growth rate ( $\mu$ ;  $d^{-1}$ ) as

$$\mu = (GPP - R - S) \cdot X \quad (1)$$

where GPP is the daily specific gross primary production ( $d^{-1}$ ), R is the daily specific respiration rate ( $d^{-1}$ ), S is the daily specific sloughing rate ( $d^{-1}$ ), and X is the attached *Cladophora* biomass ( $g \text{ DM m}^{-2}$ ). GPP is the product of the gross primary production during the day ( $GPP_{\text{day}}$ ) and the photoperiod.  $GPP_{\text{day}}$ , in turn, is the sum of the net primary production during the day ( $NPP_{\text{day}}$ ) and the respiration during the day ( $R_{\text{day}}$ ). R is the sum of  $R_{\text{day}}$  multiplied by the photoperiod, and the respiration during the night ( $R_{\text{night}}$ ) multiplied by the dark period of the day (1-photoperiod).  $NPP_{\text{day}}$  and  $R_{\text{day}}$  are calculated as

$$NPP_{\text{day}} = NPP_{\text{max}} \cdot M_{\text{LT-NPP}} \cdot M_{\text{P}} \cdot M_{\text{X}} \quad (2)$$

$$R_{\text{day}} = R_{\text{max}} \cdot M_{\text{LT-R}} \cdot M_{\text{P}} \cdot M_{\text{X}} \quad (3)$$

where  $NPP_{\text{max}}$  and  $R_{\text{max}}$  are the maximum  $NPP_{\text{day}}$  and  $R_{\text{day}}$  under ideal conditions;  $M_{\text{LT-NPP}}$  and  $M_{\text{LT-R}}$  are multipliers representing the effects of irradiance and temperature on NPP and R, respectively;  $M_{\text{P}}$  is the multiplier representing the effects of *Cladophora*  $Q_{\text{P}}$ ; and  $M_{\text{X}}$  is the multiplier representing the effects of self-shading. All multipliers are dimensionless and expressed as proportions from zero to unity.  $NPP_{\text{max}}$  was set to 0.60 ( $d^{-1}$ ; Higgins et al. 2005a) and  $R_{\text{max}}$  was set to 0.44 ( $d^{-1}$ ; Canale and Auer 1982).

The  $M_{\text{LT}}$  multipliers for  $NPP_{\text{day}}$  and  $R_{\text{day}}$  were determined in steady-state conditions as the interactive effects of irradiance and temperature on the respective metabolic rates and expressed as polynomial functions of irradiance and temperature (Graham et al. 1982).  $R_{\text{day}}$  was measured as the dark respiration rate of *Cladophora* that had been immediately previously acclimated to a given light level.  $R_{\text{night}}$  was calculated as the dark respiration rate measured in dark-acclimated *Cladophora* and was a function of temperature alone (Graham et al. 1982). The  $M_{\text{P}}$  multiplier was based on the Droop growth model in which P is the limiting resource

$$M_{\text{P}} = 1 - Q_0 \cdot Q_{\text{P}}^{-1} \quad (4)$$

where  $Q_0$  is the minimal cell quota (%P, as a fraction of dry mass).  $Q_0$  was set to 0.05% (Auer and Canale 1982). The  $M_{\text{X}}$  multiplier is a function of the attached crop of *Cladophora* which acts as a surrogate for light attenua-

tion through the *Cladophora* canopy.  $M_{\text{X}}$  was calculated as

$$M_{\text{X}} = 1 - X \cdot X_{\text{max}}^{-1} \quad (5)$$

where  $X_{\text{max}}$  is the maximum attached biomass attainable and took the constant value of  $500 \text{ g DM m}^{-2}$ , based on the highest biomass recorded in the Oakville region (Kamaitis 1984). Setting the maximum biomass to a constant value was an update to earlier CGM configurations, which previously allowed it to vary with depth (Higgins et al. 2005a). This amendment was made because  $X_{\text{max}}$  is a function of substrate roughness which was not observed to vary with depth.

The continuous sloughing function was computed as

$$S = S_{\text{max}} \cdot M_{\text{shear}} \cdot V_{\text{east}} \cdot V_{\text{max}}^{-1} \cdot X \cdot X_{\text{max}} - 1 \quad (6)$$

where  $S_{\text{max}}$  is the maximum sloughing rate ( $d^{-1}$ );  $M_{\text{shear}}$  is an empirically derived dimensionless multiplier related to wave-induced shear stress as a function of depth (Higgins et al. 2005a);  $V_{\text{east}}$  is the wind speed weighted to the east, the direction of greatest fetch; and  $V_{\text{max}}$  is the maximum easterly weighted wind speed, which was set to  $14 \text{ m s}^{-1}$ . Because of the depth-dependence of wave-induced shear stress, sloughing estimates were greatest at the shoreline and decayed with depth.

An additional catastrophic detachment function was also added to the model. This function removed 75% of the attached biomass in one time step, triggered when the product of  $M_{\text{shear}}$ ,  $V_{\text{east}}$ ,  $V_{\text{max}}^{-1}$ , and X exceeded a threshold ranging from 150 to 200 ( $g \text{ DM}$ ). This threshold range was based on a catastrophic detachment that occurred in 2004 during a storm. Because only a single event was available to set the threshold, we suggest that the absolute values be employed with due caution when applied to a new situation.

*Input data parameterization, calibration, and validation of the Cladophora growth model*—All data were input as diel averages or interpolations, or in the case of surface irradiance, as diurnal averages. Input requirements to the CGM are summarized in Table 1.

Daily  $Q_{\text{P}}$  values were interpolated from weekly to biweekly samples by fitting a cubic function, the curve of best fit, to the measured  $Q_{\text{P}}$  values.

To calculate photosynthetically active radiation (PAR) at the depth of growth ( $E_z$ ;  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ), surface irradiance ( $E_0$ ;  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) and daily estimates of the PAR extinction coefficient ( $K_{\text{dPAR}}$ ;  $\text{m}^{-1}$ ) were required.  $E_0$  was calculated from measurements of shortwave radiation dose ( $W \text{ m}^{-2} 10^{-1} \text{ min}$ ) collected with a pyroheliometer on the roof of Canada Centre for Inland Waters (Burlington, Ontario, Canada). The calculation of PAR fluence rate ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) was accomplished by multiplying the radiation dose by three constants: (1) 1.667 to account for the conversion of the integration time; (2) 5.03, the estimated conversion from shortwave radiative energy to quanta (appendix 2; Wetzel 2001); and (3) 0.46, the estimated proportion of PAR in shortwave radiation (Kirk 1994). Each measure of  $E_0$  was corrected for surface solar

Table 1. Input parameters to the *Cladophora* growth model.

Input parameter	Method of measurement	Source
Temperature (°C)	Surface measurements reported hourly, from which daily means were calculated.	Environment Canada buoy C45139
Surface irradiance ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Diurnal mean PAR was calculated from the mean of 10-min shortwave radiation doses measured with a rooftop pyroheliometer.	Canada Centre for Inland Water
Wind speed and direction ( $\text{m s}^{-1}$ )	Reported hourly from station buoy, from which daily means weighted from the east, were calculated.	Environment Canada buoy C45139
$K_{d\text{PAR}}$ , modern ( $\text{m}^{-1}$ )	Daily mean values were calculated from wind velocity weighted from the east. Wind data were reported hourly.	Environment Canada buoy C45139
$K_{d\text{PAR}}$ , historical ( $\text{m}^{-1}$ )	Seasonal mean values were calculated from historical nearshore secchi depths using a correlation between modern seasonal mean nearshore secchi depth and $K_{d\text{PAR}}$ at 2 m.	Environment Canada nearshore Sta. 5, and this study
$Q_{\text{P}}$ , modern (% DM)	Directly measured from triplicate samples collected weekly to biweekly. Daily values were interpolated from a curve fit to the seasonal data.	This study
$Q_{\text{P}}$ , historical (% DM)	Seasonal minimum $Q_{\text{P}}$ was measured directly. Daily values were calculated as a proportional fraction to modern $Q_{\text{P}}$ .	Owens 1972 and Kamaitis 1984

reflectance as a function of solar azimuth (Walsby 1997), then averaged to compute the diurnal mean.

On 24 occasions, PAR profiles were taken at 2-m depth using a spherical quantum sensor (Li-Cor), from which  $K_{d\text{PAR}}$  values were calculated. To estimate daily  $K_{d\text{PAR}}$ , an empirical relationship was derived as a function of wind speed and direction. Light attenuation in the shallowest depths is attributable to wind-induced resuspension, so wind speed weighted from the direction of greatest fetch, east, was correlated with  $K_{d\text{PAR}}$ . Weighting was accomplished as follows:

$$V_{\text{east}} = V_{\text{absolute}} \cdot (0.5 \cdot \sin(\text{wind direction}) + 1) \quad (7)$$

where north is 0°. Winds blowing for extended periods of time were assumed to drive greater resuspension than shorter gusts, so weighted wind speeds were averaged over 3-hr intervals and the maximum value was correlated with measured  $K_{d\text{PAR}}$ . This correlation ( $r = 0.747$ ) was higher than all others calculated with weighting from all other cardinal directions and unaveraged wind speeds. Wind speed and direction were recorded hourly from a surface buoy on western Lake Ontario (C45139; Environment Canada).

Temperature was measured hourly from the same surface buoy as was used for wind speed and direction (C45139; Environment Canada), from which unweighted daily mean averages were computed.

For input to the sloughing algorithm, hourly windspeed weighted from the east ( $V_{\text{east}}$ ) was averaged over each day.

The initial starting date of the model run was set to day 125 (04 May 2004 or 05 May 2005); a day when *Cladophora* biomass was evident but had not yet come to dominate the periphyton community at 2.0-m depth. An initial date based on a threshold temperature did not result in a better model fit, measured as sum of squared errors between predicted and measured biomass during exponential phase growth. An initial seed biomass of 2.0 g DM  $\text{m}^{-2}$  yielded the best model fit.

The CGM was first calibrated at 2.0-m depth using input data from 2004 and then validated with data from 2005. The daily attached biomass output was compared with seasonal biomass collected at 2.0 m. To extend the biomass predictions of the CGM to other depths, we constructed a relationship between  $Q_{\text{P}}$  and depth. An exponential increase in  $Q_{\text{P}}$  with depth was determined, following the form

$$Q_{\text{P}(Z)} = (Q_{\text{P}(2)} - a) + ae^{b(Z-2)} \quad (8)$$

where  $Q_{\text{P}(Z)}$  and  $Q_{\text{P}(2)}$  are the  $Q_{\text{P}}$  values at a given depth ( $Z$ ) and at 2.0 m, respectively. Using samples collected from the same study site during midsummer 2006 (A. Houben, U. Waterloo, unpubl. data),  $a$  and  $b$  were calculated to be 0.00366 and 0.3388 respectively (Fig. 1). Additionally,  $K_{d\text{PAR}}$  was assumed to decrease with depth (Higgins et al. 2005a). In order to report a depth-integrated biomass ( $\text{kg DM m}^{-1}$  shoreline), the areal biomass predicted by the CGM at 0.5-m depth increments was multiplied by the mean area of each depth contour in the Oakville region (Viriden et al. 2000).

The maximum potential error in predicted peak biomass at the calibration depth, 2 m, was assessed by sensitivity gradient analysis. Four major measured input parameters (surface temperature,  $K_{d\text{PAR}}$ , wind speed, and  $Q_{\text{P}}$ ) were varied independently from -20% to +20% and plotted against the percentage change in peak attached biomass. Using these sensitivity gradients, and estimated coefficients of variation for each input parameter, the magnitude of the sources of variability in estimates of peak attached biomass were quantified.

*Hindcasting: Changes in  $K_{d\text{PAR}}$ ,  $Q_{\text{P}}$ , and temperature*—The sensitivity of the CGM to historical  $K_{d\text{PAR}}$  and  $Q_{\text{P}}$  was assessed for each factor independently and interactively. Because historical daily estimates of these variables were not available, two different approaches were taken to

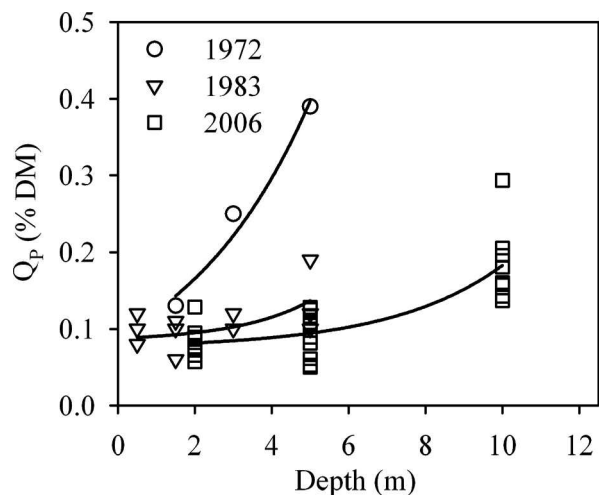


Fig. 1. The relationship between *Cladophora* tissue phosphorus ( $Q_P$ ) and depth between decades. The exponential rise in  $Q_P$  with depth decreases in each progressive decade, indicating that the switch from P-limitation to light-limitation is occurring at deeper depths than historically. Directly measured data (symbols) with exponential curves of best fit.

employ historical  $K_{d_{PAR}}$  values and historic  $Q_P$  in the CGM. For  $K_{d_{PAR}}$ , a seasonal mean historic value was used as a constant input into the model. Using a seasonal mean  $K_{d_{PAR}}$ , instead of a daily variable, yielded differences in peak biomass of <10% compared with the calibration dataset output. Historic  $K_{d_{PAR}}$  was estimated based on secchi depths collected from 1966 to 2005 from a nearshore north western buoy (Environment Canada Sta. 5: 43.42°N, -79.66°E). These secchi depth data were used because they comprised the largest proximal dataset available (STAR database; Environment Canada). Data collected between June and August, the main *Cladophora* growing season, were used. These data were collected from a median depth of 24 m. Data were subdivided into 3 time periods: a period prior to dreissenid mussel invasion and substantive reductions in pelagic P concentrations, 1966–1980 ( $n = 24$ ); a period prior to dreissenid establishment and following large pelagic P reductions, 1981–1990 ( $n = 10$ ); and the modern period which is characterized by dreissenid mussel establishment and low pelagic P concentrations, 1991–2001 ( $n = 4$ ). Secchi depth (m) was converted to  $K_{d_{PAR}}$  ( $m^{-1}$ ) as

$$K_{d_{PAR}} = c \cdot (\text{secchi depth})^{-1} \quad (9)$$

where  $c$  is a constant. Using the relationship between mean  $K_{d_{PAR}}$  for 2004 and 2005 ( $0.454 \text{ m}^{-1}$ ) and the most recent secchi depths,  $c$  was calculated to be 2.37.

For historical  $Q_P$ , a seasonal constant was inappropriate. Instead, a ratio between the historical seasonal minimum value and the modern seasonal minimum, termed the  $Q_P$ -factor, was calculated. Historical daily  $Q_P$  values were calculated as the product of the daily baseline  $Q_P$  values and the decade-specific  $Q_P$ -factor. Historical minimum *Cladophora*  $Q_P$  from Lake Ontario were obtained from previous *Cladophora* surveys conducted in 1972 and again

in 1982 and 1983 (Owens 1972 (reported in Kamaitis 1984); Kamaitis 1984; Painter and Kamaitis 1987). These surveys targeted the dates of peak *Cladophora* biomass and correspondingly to seasonal minimum  $Q_P$ . No comparable datasets were available from this study area from the 1990s.

The combined effects of historical  $K_{d_{PAR}}$  and  $Q_P$  were assessed using seasonal mean  $K_{d_{PAR}}$  and  $Q_P$ -factors for each of the two time periods (1972 and 1982–1983). The relationship between  $Q_P$  and depth was different between time periods (Fig. 1). Consequently, for the sensitivity analyses of the combined effects of  $K_{d_{PAR}}$  and  $Q_P$ , exponential relationships between  $Q_P$  and depth (Eq. 8), specific to each time period, were used. The relationships were calculated based on  $Q_P$  values reported in Kamaitis (1984). For 1972,  $a$  and  $b$  were 0.09209 and 0.2922 and for 1982–1983  $a$  and  $b$  were 0.00406 and 0.5146, respectively.

To assess the potential effect of changes in surface water temperature, an ecologically relevant scale of change was first defined. Climate change models, based on global circulation models, so far, have not been constructed with the spatial resolution necessary to directly predict the water temperature in the Great Lakes expected in the coming decades (Schertzer and Crowley 1999). Instead, we plotted the surface water temperature in Lake Ontario from the earliest available records to construct the surface water trend from 1966 to 2006, using data from July to September, inclusive. Data from 1966 to 1990 were taken from lake-wide surface-water temperature data collected during surveillance cruises, from an airborne radiometer, or satellite data (Schertzer 2003). Years for which there were <4 data points available during the season of interest were excluded. Data from 1991 to 2006 were collected hourly from a western Lake Ontario buoy (C45139; Environment Canada). Trends in temperature over time were made by linear regression analysis in SPSS version 14.0.

The direct effects of rising temperatures on the peak biomass of attached *Cladophora* were assessed with the CGM using additive increases to baseline temperature. Seasonal surface temperature was increased by increments of  $0.5^\circ\text{C}$  for successive model runs.

For all sensitivity analyses, the CGM was run from day 125 to day 208, the day of catastrophic detachment in 2004. No catastrophic detachment events were allowed in these model predictions because of the unpredictable episodic trigger for these events.

## Results

*Contemporary Cladophora growth and seasonal biomass accumulation*—The two years used to calibrate and validate the *Cladophora* growth model (CGM) were very different meteorologically, as evident from the differences in the spring warming and in mean surface irradiance between the 2 yr (Fig. 2). The contrast in seasonal growth patterns of *Cladophora* at 2.0-m depth is made obvious by comparing the timing of peak measured biomass, which was a full month earlier in 2005 relative to 2004 (Fig. 2A).

The CGM adequately predicted the timing and magnitude of attached *Cladophora* biomass at 2.0-m depth

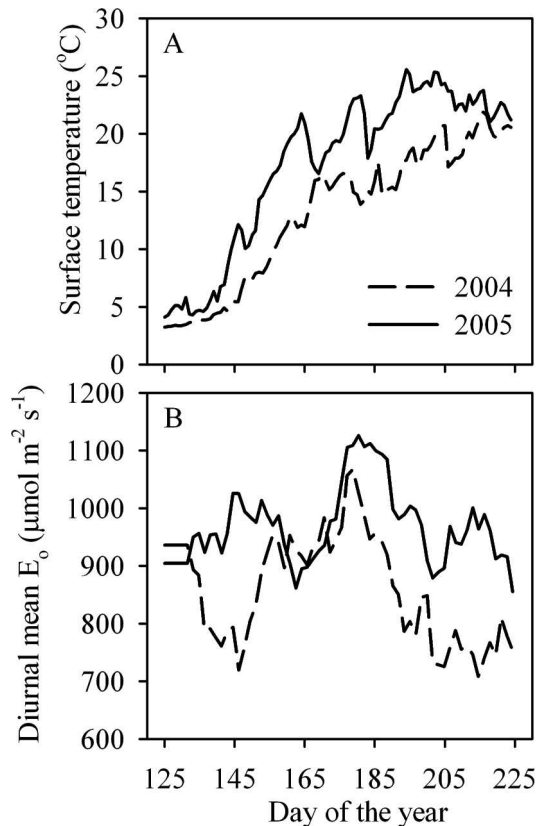


Fig. 2. Baseline data input to *Cladophora* growth model (CGM). (A) illustrates the faster rate of spring warming and the higher peak temperature of 2005. (B) shows the higher mean surface irradiance ( $E_0$ ) in 2005. For clarity, the daily mean  $E_0$  in this figure was smoothed with a nearest-neighbor running average.

(Figs. 3A, B). Peak predicted biomass as a percentage of peak measured biomass was 90% in 2004 and 113% in 2005. Due to heterogeneity in physical structure at the 1-m<sup>2</sup> scale, there was inherently high variability in attached *Cladophora* biomass measured with quadrats. The mean coefficient of variation in measured biomass averaged across the season was 52% ( $n = 5$ ) and standard error for each date ranged from 1.3 g m<sup>-2</sup> to 23.4 g m<sup>-2</sup> (mean SE or all dates = 9.3 g m<sup>-2</sup>).

Error around the model-predicted peak biomass using the calibration dataset was dominated by the model's sensitivity to  $Q_P$  input (Fig. 4).  $Q_P$  had a coefficient of variation of 20.0% (between replicates, within sampling days). Variation in  $Q_P$  of +20% and -20% resulted in an average of +75% and -79% variation in peak biomass predictions, respectively (Fig. 4). Changes in all other input parameters by  $\pm 20\%$  resulted in peak biomass variation of  $< \pm 20\%$ . The large error created by variation in  $Q_P$  is due to the hyperbolic relationship between  $Q_P$  and growth rate, and the very low concentrations of  $Q_P$  currently measured in Lake Ontario. The difference in  $Q_P$  between decades, however, is approximately an order of magnitude greater than the CV between modern replicates.

A major storm event on day 208 (24 Jul 2004) caused a synchronous detachment of *Cladophora* that resulted in

extensive shoreline fouling in the region of study and caused blockage of the cooling water intake at Pickering Nuclear Generating Stations, ~80 km to the east of the study site. By contrast, loss of attached biomass in 2005 was always gradual, and no single storm event caused massive detachment (Figs. 3A, B).

The seasonal peak in total attached *Cladophora* biomass integrated through 12.0-m depth was similar in 2004 and 2005 (46.0 kg DM m<sup>-1</sup> shoreline in 2004 vs. 55.5 kg DM m<sup>-1</sup> shoreline in 2005; Figs. 3C, D). The cumulative depth-integrated biomass, the sum of sloughed and attached material, on the day when attached biomass was at its peak, was also similar between years (54.3 kg DM m<sup>-1</sup> shoreline in 2004 vs. 65.1 kg DM m<sup>-1</sup> shoreline in 2005).

The depths of peak attached biomass were the same or deeper than the depth of peak cumulative biomass (Table 2), due to the depth dependency of sloughing. Taking the mean from the two calibration years, peak attached biomass was estimated at  $2.5 \pm 0.3$ - (SD) m depth. The depth beyond which no growth occurred during the season was estimated at  $10.4 \pm 0.4$ -m depth, which experienced mean irradiance of  $2.9 \pm 0.2$ -mol m<sup>-2</sup> d<sup>-1</sup>.

*Hindcasting Cladophora biomass using historical light attenuation ( $K_{dPAR}$ ) and tissue P concentrations ( $Q_P$ )*—The seasonal mean  $K_{dPAR}$  was 0.43 m<sup>-1</sup> in 2004 and 2005, 0.68 m<sup>-1</sup> for the period that encompassed 1982–1983, and 0.76 m<sup>-1</sup> for the period that encompassed 1972. The mean seasonal minimal  $Q_P$  for the baseline years was 0.050% and the  $Q_P$ -factors (ratio of historical minimum seasonal  $Q_P$  to baseline seasonal minimum  $Q_P$ ) were 1.78 for 1982–1983 and 2.57 for 1972. The independent effects of changing  $K_{dPAR}$  and  $Q_P$  led to opposing model outputs. Analyses using historical  $K_{dPAR}$  alone yielded peak attached biomass predictions that were  $42\% \pm 3\%$  in 1982–1983 and  $36\% \pm 3\%$  in 1972 of the 2004–2005 peak attached biomass (Figs. 5A, B). Using historical  $K_{dPAR}$ , the attached biomass at depths deeper than 2.0 m were predicted to be lower than in 2004–2005 (Figs. 6A, B). The depths beyond which no seasonal growth was predicted were  $10.4 \pm 0.4$  m in 2004–2005,  $6.7 \pm 1.1$  m during the 1982–1983 period, and  $5.2 \pm 1.1$  m during the 1972 period (Table 2). Peak attached biomass predictions using historical  $Q_P$  alone yielded 286%  $\pm$  26% in 1982–1983 and 344%  $\pm$  29% in 1972, relative to 2004–2005 peak attached biomass (Figs. 5C, D). Using historical  $Q_P$ , the depth of peak attached biomass was 1.0 m deeper than in 2004–2005, due to greater sloughing at the shallowest depths (Fig. 6C, Table 2).

Using historical  $K_{dPAR}$  and  $Q_P$  together, peak attached biomass was predicted to be higher and to occur earlier in the season relative to 2004–2005 (Figs. 5E, F). At depths shallower than 3.5 m, peak attached and cumulative biomass was predicted to be higher in 1982–1983 and 1972, relative to 2004–2005 (Figs. 6E, F). Conversely, at depths  $> 3.5$  m, peak attached and cumulative biomass was predicted to be lower in 1982–1983 and 1972, relative to modern years (Figs. 6E, F). The overall result was that peak attached biomass for 1982–1983 was  $1.40 \pm 0.16$  times higher than 2004–2005 and cumulative biomass was

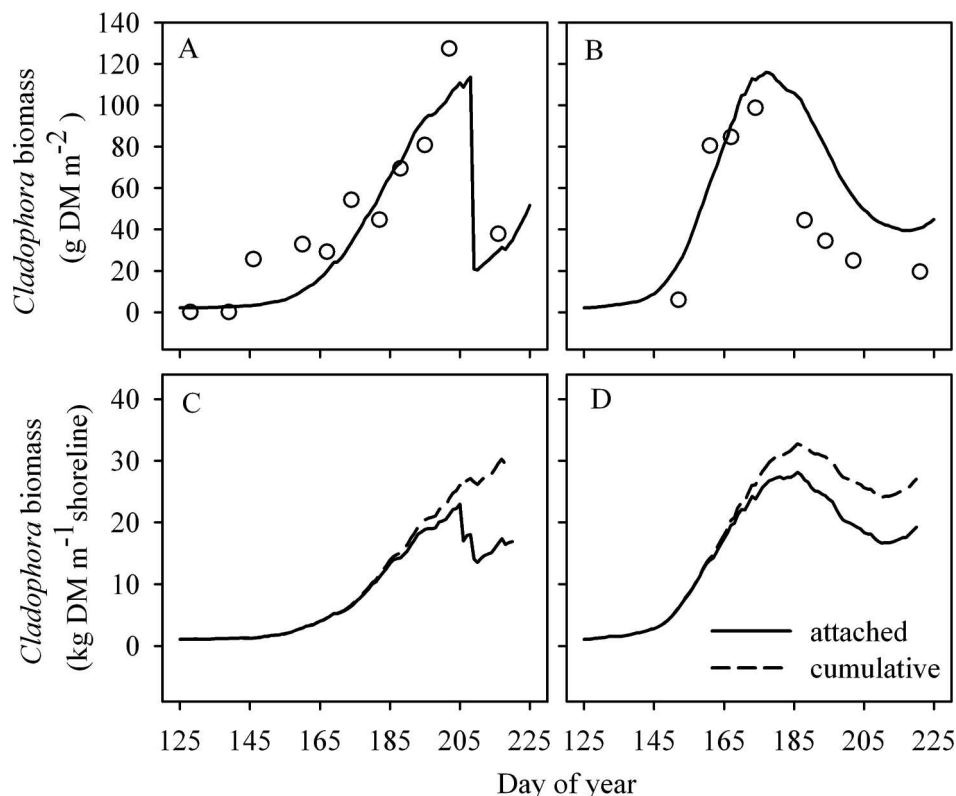


Fig. 3. Measured (circles) and *Cladophora* growth model predicted (lines) biomass of *Cladophora glomerata* at 2.0-m depth at Oakville, Lake Ontario, in (A) 2004 and (B) 2005. Predicted depth-integrated *Cladophora* biomass in (C) 2004 and (D) 2005. Biomass was predicted at 0.5-m increments, between 0.5-m to 12.0-m depth. Cumulative biomass was calculated as the sum of attached and sloughed *Cladophora* biomass.

$2.04 \pm 0.06$  times higher (Table 2). For 1972, peak attached biomass was  $1.6 \pm 0.17$  times higher than 2004–2005 and cumulative biomass was  $2.66 \pm 0.20$  times higher (Table 2).

**Forecasting *Cladophora* biomass at increasing temperatures**—Data records of the mean surface water temperature from Lake Ontario averaged over July–September (d 182–273) from 1966 to 2006 indicate an overall increase at a rate of  $0.049^\circ\text{C yr}^{-1}$  determined by linear regression analysis (Fig. 7). A warming trend appears to commence around 1980; linear regression analysis from 1980 to 2006 indicates an increase in surface temperature of  $0.096^\circ\text{C yr}^{-1}$ .

The dominant predicted direct effect of increased temperatures was an earlier onset of exponential growth (Figs. 8A, B). There was a marginal increase in peak biomass with increasing temperature (Figs. 8C, D). The greatest increase in biomass was achieved with a  $1.0^\circ\text{C}$  increase over baseline temperatures (at  $0.5^\circ\text{C}$  resolution), resulting in  $7.7\% \pm 2.5\%$  increase in peak attached biomass.

## Discussion

Proximal and global anthropogenic pressures, such as exotic species invasions and global climate change, have led to major changes to the limnology of the Laurentian Great

Lakes over the last several decades. Yet, in the absence of continuous historical records, quantifying the effects of these perturbations on ecosystem processes remains a major challenge. Sensitivity analyses employing calibrated numeric models offer a practicable means to assess the response of a system to historic anthropogenic stressors, and furthermore, to predict future responses to environmental changes. In this study, we addressed the response of nuisance macroalgal biomass accumulation to decadal-scale ecosystem level changes. We analyzed the effects of decreased light attenuation in the nearshore due to dreissenid mussels, changes in tissue phosphorus concentration ( $Q_P$ ) due to the opposing forces of decreasing pelagic P concentrations and potentially increasing benthic P supply from mussels, and increasing summer-lake water temperatures on attached and sloughed *Cladophora* biomass in Lake Ontario. Because *Cladophora* is the dominant component of the summer littoral flora on hard substrata in the lower Laurentian Great Lakes, knowledge of its production and seasonal growth dynamics is a prerequisite to constructing nearshore nutrient and carbon budgets, and, by extension, essential to assessing the relative importance of the benthos to nearshore or whole system processes.

*The Cladophora growth model and contemporary biomass*—Attached *Cladophora* biomass measured in Lake

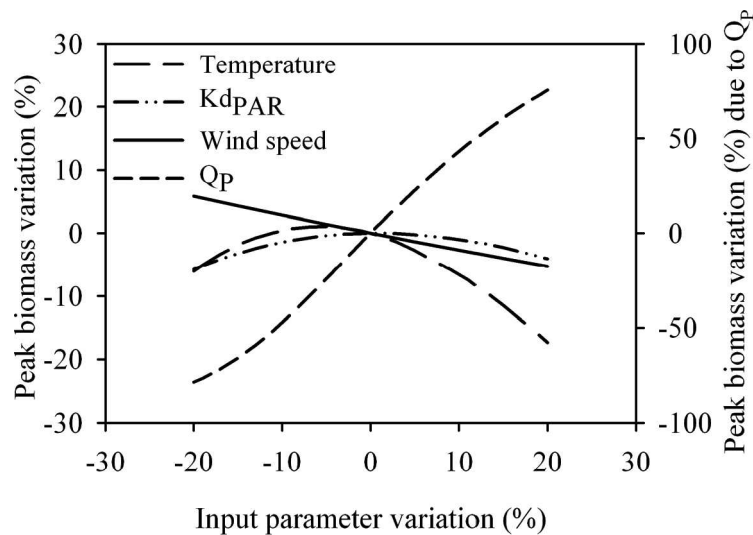


Fig. 4. The variation in peak attached biomass in 2004 and 2005 at 2.0-m depth due to variation in the main measured input parameters. The left ordinate axis relates to all parameters except  $Q_P$ .

Ontario at 2.0-m depth peaked at 99 g DM  $m^{-2}$  and 130 g DM  $m^{-2}$  in 2004 and 2005, respectively. These values are near the range of direct measurements obtained in 2002 from five sites in eastern Lake Erie (range of maximum biomass measurements: 100–243 g DM  $m^{-2}$ ; median: 152 g DM  $m^{-2}$ ), with the highest *Cladophora* density found in proximity to the nutrient-rich effluent of the Grand River (Higgins et al. 2005b). The largest deviation in attached *Cladophora* biomass between estimates predicted by the *Cladophora* growth model (CGM) and directly measured values occurred in 2005 following the summer biomass peak. This deviation may reflect an underestimation of one or both of the attached biomass loss terms, sloughing and respiration, during senescence. Sloughing rates are recognized as the most difficult parameter to quantify accurately (Canale and Auer 1982). More likely, *Cladophora* respiration rates may have been underestimated for senescing *Cladophora* because metabolic-rate algorithms were based on measurements of vigorously growing *Cladophora* filaments (Graham et al. 1982). The metabolic demands

of cellular repair may increase as *Cladophora* ages, leading to higher respiration following peak biomass.

In this version of the CGM, biomass loss is comprised of three components: daily respiration, daily sloughing, and a massive detachment triggered by a storm event. In 2005, respiration and sloughing alone adequately accounted for the biomass decrease of the first seasonal cohort of growth. In contrast, in 2004, these processes could not account for the rapid loss of *Cladophora* that occurred in synchrony along the north shore of Lake Ontario. Catastrophic loss events have been observed previously in the Great Lakes (e.g., Whitton 1970), but an algorithm describing the mechanism of this loss has been lacking. Therefore, we added a strictly physical mechanism to describe a catastrophic detachment of *Cladophora* related to attached biomass, a correlate of algal filament length, and storm magnitude, a correlate of shear stress imposed by waves. One consequence of a massive detachment event is an increase in irradiance and ambient nutrient concentrations relative to the remaining *Cladophora* filaments, potentially

Table 2. Results of sensitivity analyses testing the independent and combined effects of historical light attenuation coefficients ( $K_{dPAR}$ ) and historical *Cladophora* tissue P concentrations ( $Q_P$ ) relative to the mean of 2004 and 2005. Mean averages and standard deviations are computed from two model runs using each baseline year separately. Maximal attached and cumulative (attached plus sloughed) *Cladophora* biomass integrated from 0.5-m to 12.0-m depth (kg DM  $m^{-1}$  shoreline) was predicted using the *Cladophora* growth model (CGM). Maximum depth (m) is defined as the depth at which no net positive growth was predicted for any day during the model run.

		Peak attached biomass	Peak cumulative biomass	Depth of peak attached biomass	Depth of peak cumulative biomass	Max. depth
Kd <sub>PAR</sub> effects	2004, 2005 (baseline)	55±3	66±5	2.5±0.3	2.5±0.1	10.4±0.4
	1982–1983	24±3	32±4	1.6±0.0	1.6±0.1	6.7±1.1
	1972	20±3	27±3	1.5±0.1	1.4±0.1	5.2±1.1
Q <sub>P</sub> effects	1982–1983	157±4	274±28	3.5±0.4	2.0±0.2	11.3±0.3
	1972	189±4	356±33	3.5±0.4	1.8±0.3	11.6±0.2
Kd <sub>PAR</sub> and Q <sub>P</sub> effects	1982–1983	77±4	173±16	2.1±0.4	1.4±0.1	8.1±1.4
	1972	88±4	236±12	2.1±0.2	1.2±0.1	6.5±0.7

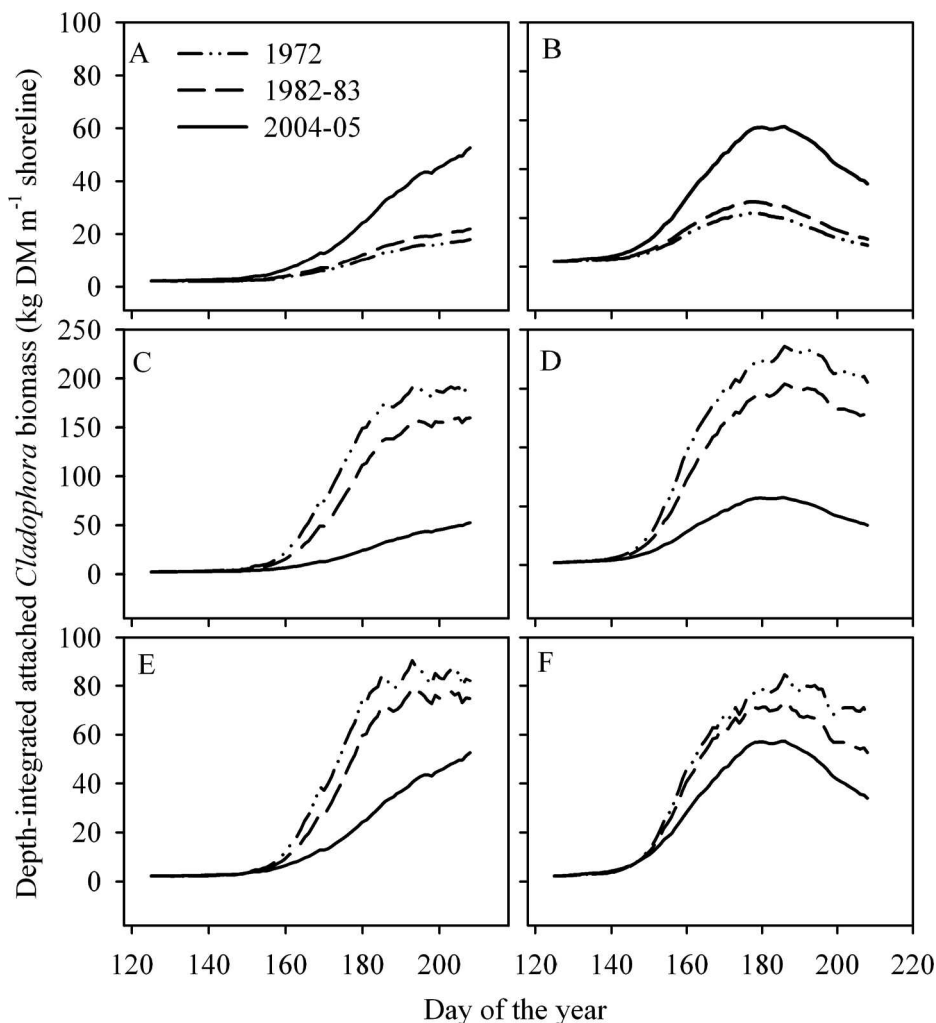


Fig. 5. *Cladophora* growth model (CGM) predictions of depth-integrated attached *Cladophora* biomass and the independent effects of historical  $K_{dPAR}$  using (A) 2004 and (B) 2005 baseline data; the independent effects of historical  $Q_P$  with (C) 2004 and (D) 2005 baseline data; the combined effects of historical  $K_{dPAR}$  and  $Q_P$  using (E) 2004 and (F) 2005 baseline data. Note the differences in ordinate axis scales.

serving to enhance growth. The mechanism of detachment, therefore, could affect total seasonal biomass accrual. The implication is that with increasing frequency and magnitude of storm events predicted as a consequence of climate change in the Laurentian Great Lakes region (Kunkel et al. 1999), total seasonal *Cladophora* productivity may increase.

The CGM, originally constructed to predict macroalgal biomass density in relation to a high-concentration nutrient point-source in Lake Huron (Canale and Auer 1982), and then validated in a rural shoreline in the oligotrophic eastern basin of Lake Erie, was herein validated in a very different limnological setting. We applied the model in an urbanized location which experiences both a higher and more complex nutrient supply regime than the Lake Erie site, with numerous nutrient-rich point sources (including, e.g., storm water drains and a wastewater treatment plant ~6 km distal to our study site). The Lake Ontario study site also allowed us to assess the capacity of the model to accurately predict *Cladophora* biomass in response to

temperature differences, for use in predicting *Cladophora* biomass under future temperature scenarios. While Lake Erie is a shallow lake that warms quickly, Lake Ontario is deep and strongly stratified; the north shore experiences frequent upwelling (i.e., see frequent cooling intervals during the warming season in Fig. 2). By validating the CGM in this new environment, we gained confidence that it can be applied to other systems that experience seasonal macroalgal blooms (e.g., other Great Lakes with different temperature and nutrient regimes, the Baltic Sea, fluvial lakes of the St. Lawrence Seaway, etc).

*Cladophora growth model under historic and forecast scenarios*—In this study, we collected *Cladophora* biomass and determined  $Q_P$  over 2 yr that experienced contrasting meteorology. The differences in the rate of spring warming and the maximum seasonal temperatures provided a good range of conditions to assess the effects of the target variables:  $Q_P$ , light attenuation ( $K_{dPAR}$ ), and

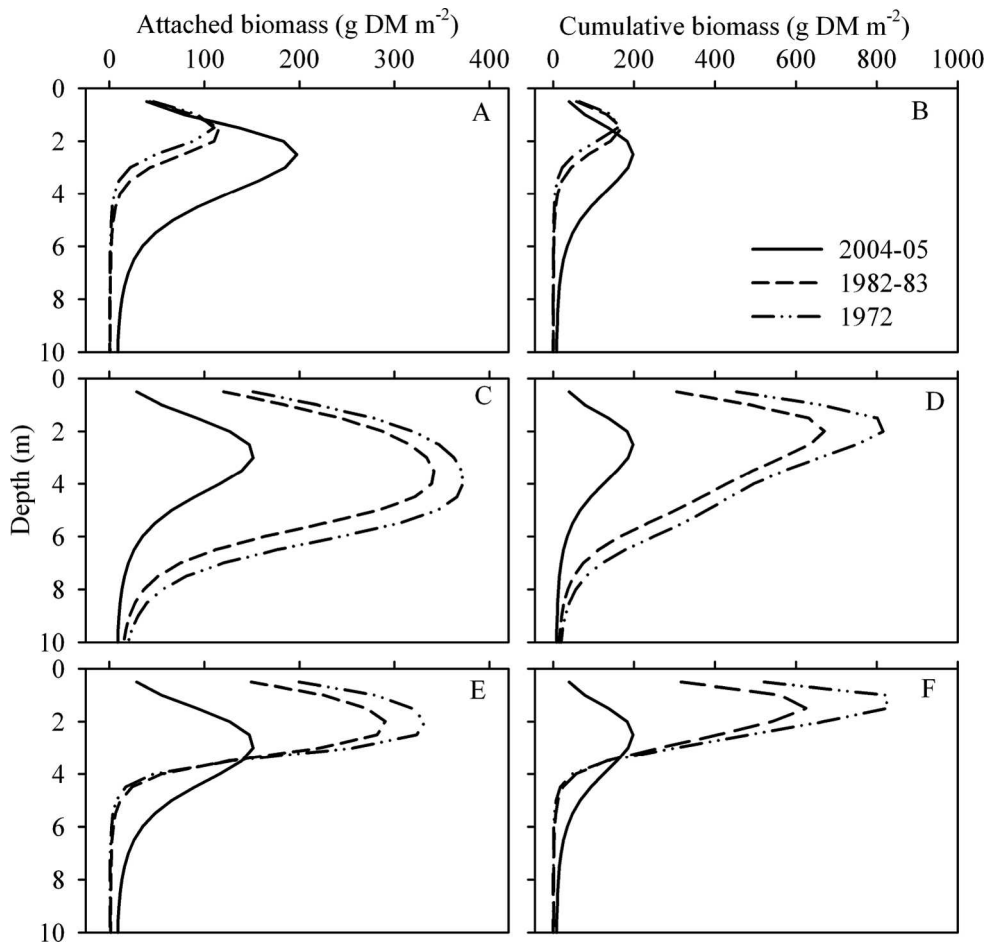


Fig. 6. On the dates of peak biomass, *Cladophora* growth model predicted depth distribution of *Cladophora* biomass density. The independent effects of historical light attenuation ( $K_{dPAR}$ ) on (A) attached biomass density and (B) cumulative biomass density; the independent effect of historical tissue P concentrations ( $Q_P$ ) relative to modern concentrations on (C) attached biomass and (D) cumulative biomass; the combined effects of historical  $K_{dPAR}$  and  $Q_P$  on (E) attached and (F) cumulative biomass.

surface water temperature. *Cladophora*  $Q_P$  declined from 1972 to 1982 (Painter and Kamaitis 1987), a period marked by declining dissolved P concentrations in Lake Ontario (Nicholls 2001). Seasonal minimal *Cladophora*  $Q_P$  in modern years are lower still than 1982 levels. Anecdotal evidence of increasing macroalgal shoreline fouling and water intake clogging since the early 1990s supports the possibility that the seasonal mean *Cladophora*  $Q_P$  was lower in the late 1980s, prior to mussel establishment, than today. If this is true, we may be currently witnessing an increase toward concentrations measured in the early 1980s. However, only continued monitoring will resolve the direction of trajectory of an interannual change in *Cladophora* biomass.

The effects of lower  $Q_P$  and higher  $K_{dPAR}$  observed over the past three decades operate in opposing directions on seasonal *Cladophora* density and depth distribution. Biomass at depths down to 3.5 m is lower in modern years than in the early 1970s and 1980s (due to lower  $Q_P$ ) while biomass at depths  $>3.5$  m is now higher (due to higher  $K_{dPAR}$ ). The overall result is a lower total depth-integrated

attached and cumulative *Cladophora* biomass in contemporary biomass relative to the early 1970s and 1980s. The consequence of the increased areal extent of growth, however, is that if  $Q_P$  rises to levels that were found in previous decades, due to allochthonous nutrient sources or autochthonously through nutrient regeneration by mussels, the accumulation of biomass will exceed the historical biomass previously produced at a given P concentration.

*Cladophora* biomass was measured in 1982 and 1983 at three depths in Oakville on weeks estimated to be the seasonal peak (Kamaitis 1984). The magnitude and depth-distribution of the peak *Cladophora* biomass predicted for 1982 and 1983 at Oakville were very similar to those measured (Fig. 9), demonstrating that the CGM was adequately parameterized for historical  $Q_P$  and  $K_{dPAR}$ . Historical mean seasonal  $K_{dPAR}$  was estimated from the relationship between modern secchi depth at 25 m and light attenuation measured at 2 m. This assumption that an increase in secchi depth at 25 m is proportional to the increase in water clarity at a much shallower site leads to a conservative estimate of nearshore  $K_{dPAR}$  (i.e., minimal

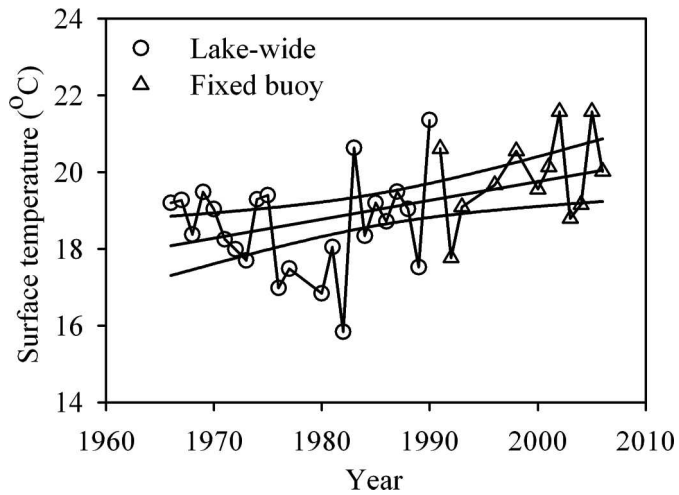


Fig. 7. Mean surface water temperature from July to September in Lake Ontario, collected from lake wide methods (Schertzer 2003), or from a fixed buoy (C45139; Environment Canada). Linear regression for 1966 to 2000: mean surface temperature ( $^{\circ}\text{C}$ ) =  $0.0494(\text{yr}) - 79.00$ ;  $r^2 = 0.21$ . A warming trend appears to begin in 1980. Linear regression from 1980 to 2006: mean surface temperature ( $^{\circ}\text{C}$ ) =  $0.0961(\text{yr}) - 172.24$ ;  $r^2 = 0.30$ . The line of best fit and 95% confidence intervals about the regression are shown.

interdecadal change is estimated) because the influence of dreissenid filtration is greater in shallow waters where the water column is smaller and particle resuspension is greater. But, the relationship between  $K_{d\text{PAR}}$  and secchi depth between decades may also be affected by changes in the particle size spectrum due to size-selective filtration by the mussels and, consequently, changing scattering characteristics of particles in the nearshore. Despite these potential uncertainties, the  $K_{d\text{PAR}}$  value used as model input for 1982–1983 simulated the observed depth–distribution of *Cladophora* biomass with remarkable accuracy (Fig. 9). Direct measurements of *Cladophora* biomass lie between the predicted attached and cumulative *Cladophora* biomass, indicating that sloughing may be overestimated at depths shallower than 2 m. No comparable data are available at Oakville in 1972 because biomass was measured immediately following a major detachment event.

Changes in global climate are expected to decrease the ice cover and increase the No. of nearshore ice-free days in Lake Ontario, resulting in increased temperatures and a loss of spring turnover (Schertzer and Croley 1999). Modeling these effects on *Cladophora* biomass will require linking the CGM to a hydrodynamic model to assess the influence of not only temperature, but also nutrient circulation, in the littoral zone. In this study, we limited

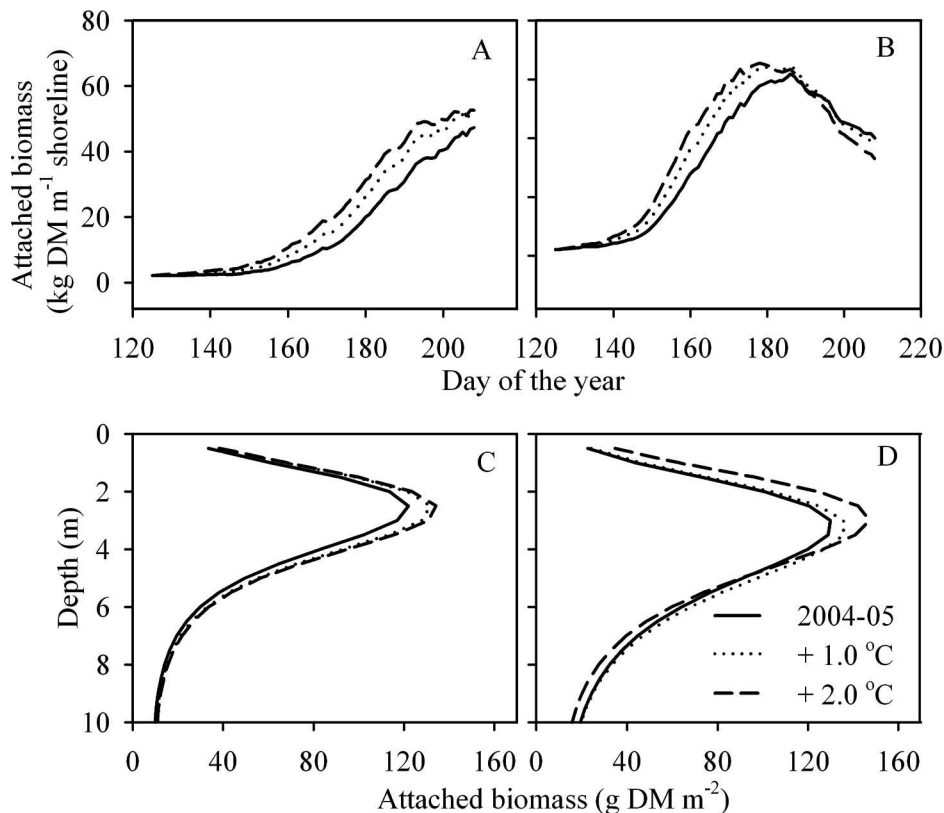


Fig. 8. The effects of increasing temperature on the seasonality of *Cladophora* growth using (A) 2004 and (B) 2005 baseline data. The effects of temperature on the depth distribution during peak biomass using (C) 2004 and (D) 2005 baseline data. There was no further increase in depth-integrated peak attached biomass above a  $2.0^{\circ}\text{C}$  increase in temperature (at  $0.5^{\circ}\text{C}$  resolution).

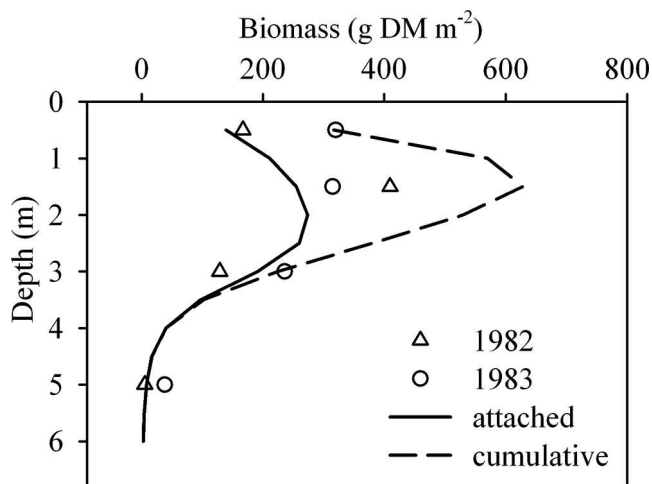


Fig. 9. Historical direct measures of *Cladophora* biomass in 1982 and 1983 relative to model predictions for attached biomass and cumulative biomass on the date of peak predicted biomass.

our assessment to the direct effects of increasing temperatures on spring growth and peak summer biomass. As we have demonstrated, summer peak biomass is limited by available P and light. Consequently, higher temperatures are predicted to strongly influence only the timing of growth, rather than biomass accumulation. Surface temperature has increased at an average rate between 0.5°C and 0.9°C decade<sup>-1</sup> over the past 2–3 decades in Lake Ontario, slightly less than the increase measured in Lake Superior from 1979 to 2006 (1.1 ± 0.6°C decade<sup>-1</sup>; Auston and Colman 2007). The CGM predicts a modest 7.7 ± 2.5% and 7.2 ± 6.3% increase over modern years in depth-integrated peak attached *Cladophora* biomass for a 1.0°C and 2.0°C increase in temperature, respectively. That temperature largely affects the seasonality rather than total biomass accumulation is also illustrated by the similarity in total biomass accumulation predicted using the two baseline datasets. The summer surface-water temperature of 2004 was, on average, 4.2°C colder than in 2005, yet peak measured and predicted biomass were very similar between years. Thus, predicting peak *Cladophora* biomass in the future will continue to depend primarily on P supply and nearshore optical properties.

Two shortcomings of the application of the CGM should be noted. First, while the change in  $Q_P$  with depth is accounted for in predicting *Cladophora* biomass at depths beyond 2 m, we predict biomass accumulation at depths that are up to 2 m deeper than the deepest direct measurements of  $Q_P$ . This extrapolation of the  $Q_P$  versus depth relationship, however, can generate only a marginal error in biomass estimates because the growth rates at these depths are constrained almost entirely by irradiance, rather than by  $Q_P$ . Secondly, we calibrated the CGM at 2.0-m depth, and then implicitly assumed that the accuracy of the model's output would be similar at all depths. The generality of the CGM is demonstrated in this study, and as a corollary, we suggest the application of the CGM to depths beyond 2.0 m at this site is well-justified.

*Implications for dreissenid mussels and eutrophication*—This study demonstrates, using historical data in a contemporary model, that critical environmental factors that are changing as a result of human activity (e.g., dreissenid mussel establishment) could result in proliferation of noxious amounts of *Cladophora* biomass equal to, or in excess of, levels reached during the decades prior to P control. It has been suggested that P loading restrictions be relaxed in the lower Laurentian Great Lakes as a means to enhance fisheries yields (e.g., Stockner et al. 2000); yet the establishment of abundant benthic filter feeders has shifted the effects of eutrophication (in terms of high algal biomass) towards the nearshore and especially to the littoral zone (Hecky et al. 2004; Zhu et al. 2006). Dreissenid mussels effectively clear the water column through filter-feeding and, thus, reduce the effects of eutrophication as indicated by water clarity and suspended chlorophyll concentration (e.g., Holland et al. 1995, Budd et al. 2001). However, we demonstrate how these benthic grazers, by enhancing light availability and possibly by focusing nutrients to the benthos in the littoral, enhances other undesirable effects of eutrophication, specifically, an overabundance of benthic macroalgal biomass. Other studies have similarly demonstrated that other adverse effects of nutrient enrichment, such as the frequency of (potentially toxic) cyanobacterial blooms, are not ameliorated, and perhaps even amplified, by the addition of benthic filter-feeders (Sarnelle et al. 2005; Caraco et al. 2006).

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