REVIEW
AN ECOLOGICAL REVIEW OF *CLADOPHORA GLOMERATA* (CHLOROPHYTA) IN THE LAURENTIAN GREAT LAKES[1]

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Cladophora glomerata (L.) Kütz. is, potentially, the most widely distributed macroalga throughout the world's freshwater ecosystems. *C. glomerata* has been described throughout North America, Europe, the Atlantic Islands, the Caribbean Islands, Asia, Africa, Australia and New Zealand, and the Pacific Islands. *Cladophora* blooms were a common feature of the lower North American Great Lakes (Erie, Michigan, Ontario) from the 1950s through the early 1980s and were largely eradicated through the implementation of a multibillion-dollar phosphorus (P) abatement program. The return of widespread blooms in these lakes since the mid-1990s, however, was not associated with increases in P loading. Instead, current evidence indicates that the resurgence in blooms was directly related to ecosystem level changes in substratum availability, water clarity, and P recycling associated with the establishment of dense colonies of invasive dreissenid mussels. These results support the hypothesis that dreissenid mussel invasions may induce dramatic shifts in energy and nutrient flow from pelagic zones to the benthic zone.

Key index words: Cladophora ecology; dreissenid mussels; exotic species; macroalgal blooms

Abbreviations: APA, alkaline phosphatase activity; DM, dry mass; DO, dissolved oxygen; DOC, dissolved organic carbon; *P–I*, photosynthesis–irradiance; TP, total phosphorus; WWTP, wastewater treatment plant

Through the late 1990s and into this century, coastal municipalities and their water utilities on the lower Laurentian Great Lakes (Ontario, Erie, Michigan) received an increasing frequency of complaints about the fouling of beaches (Fig. 1) by decaying organic material (L. Moore, Ontario Water Works Research Consortium, personal communication). The rotting beached material produced a foul odor that discouraged the public from enjoying the lakes and was at times so offensive in sight and smell as to be confused for raw sewage. The bulk of this material was almost entirely composed of a single filamentous algal species, *Cladophora glomerata*, and associated epiphytes. *C. glomerata* blooms are not unique to the Great Lakes region and have been reported in lakes, rivers, and estuaries associated with nutrient enrichment from human
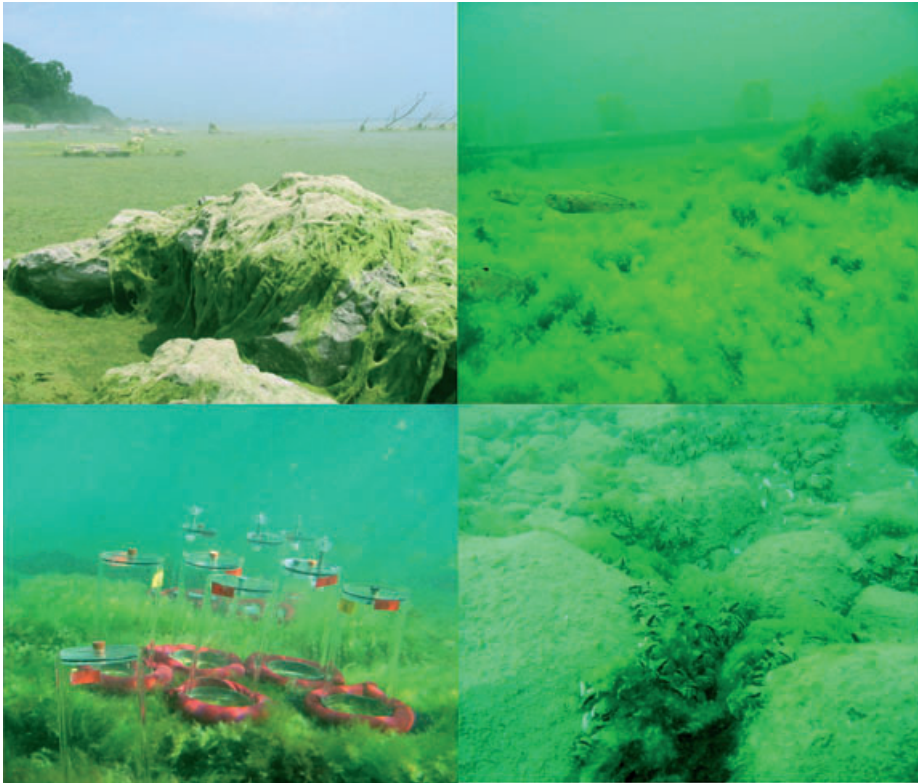
Fig. 1. Cladophora in the Laurentian Great Lakes. Clockwise from top left: Shoreline fouling by *Cladophora* in the waters and shoreline adjacent to Rock Point Provincial Park, eastern Lake Erie (22 June 2006); *Cladophora* bloom (2.0 m depth) and round gobies in eastern Lake Erie (6 August 2003); *Cladophora* associated with dreissenid mussels (3.0 m) in Lake Huron (25 August 2006); *Cladophora* with sampling chambers (1.5 m depth) in Lake Ontario (5 July 2006).

activities (Whitton 1970, Planas et al. 1996, Orlova et al. 2004a,b).

The return of widespread *C. glomerata* blooms in the lower Great Lakes from 1995 to 2006 was not associated with increased total phosphorus (TP) loading or ambient TP concentrations. Indeed, there was no detectable trend of increasing ambient TP concentrations in the offshore waters of the Great Lakes from the 1990s to 2006 (Fig. 2). The notable increase in shoreline fouling by *Cladophora* in the lower Great Lakes was, however, coincident with the establishment of dense communities of invasive zebra and quagga mussels (*Dreissena polymorpha* and *D. bugensis*, respectively), which occurred during the early to mid-1990s (Vanderploeg et al. 2002; Table 1). Dreissenid mussel invasions have often been associated with dramatic changes in the physical, chemical, and biological properties of the invaded habitats, including shifts in primary production and energy transfer from pelagic to benthic pathways (Lowe and Pilsbury 1995, Skubinna et al. 1995, Vanderploeg et al. 2002, Hecky et al. 2004, Higgins 2005). Widespread blooms of *C. glomerata* within oligotrophic (L. Ontario, L. Michigan) and mesotrophic (L. Erie) lakes represent a troubling phenomenon. The information provided here, though focused on the Great Lakes, may serve as a case study for the responses of *C. glomerata*, other macroalgae, and associated food web interactions to dreissenid mussel invasions that are occurring throughout North America, the Baltic Sea, and Europe (Ram and McMahon 1996, Orlova et al. 2004a,b).
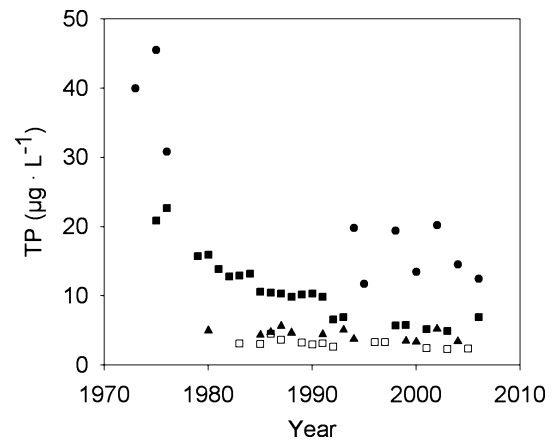

Fig. 2. Spring (April–May) offshore (>20 m station depths) total phosphorus (TP) concentrations in the epilimnion (0–20 m) of Lake Superior (open squares), Lake Huron (closed triangles), Lake Erie (closed circles), and Lake Ontario (closed squares), 1974–2006. Unpublished data, Water Quality Monitoring and Surveillance Division, Environment Canada.

TABLE 1. A history of *Cladophora* research and key ecological changes in the Laurentian Great Lakes.

Date	Lake	Description	References
1820	E	Earliest known description of nuisance algae fitting description of *Cladophora*: ''confervae [filamentous algae] that are washed ashore in times of wind, and emit disagreeable effluvia''	Taft and Kishler (1973)[a]
1820	E, O	Erie Canal and Welland Canal connects Lakes Erie and Ontario	Sly (1985)
1847–1848	E, H, M, O	Earliest formally published report of *C. glomerata* in the Great Lakes	Taft and Kishler (1973)[a]
1871	S	*Cladophora* spp. on bottom sandy sediments in ''immense quantities''	Taft and Kishler (1973)[a]
1880–1881	E, H, M, O	Taxonomic assessments and natural history inclusion of *C. glomerata* in Great Lakes	Taft and Kishler (1973)[a]
1900	E, O	Human population: 3–4 million people in each catchment	Botts and Krushelniki (1995)
1915	O	Published note on *Cladophora* sp. from deep waters	Kindle (1915)
1930	E, O	Human population: 6–7 million people in each catchment	Botts and Krushelniki (1995)
1933	E, O	Start of complaints linked to excessive beachings of *Cladophora*	Neil and Owen (1964)
1940	E	Suitable conditions established for excessive growth of *Cladophora* in the western basin	Taft and Kishler (1973)[a]
1950	E, O,	Human population: 8–9 million people in each catchment	Botts and Krushelniki (1995)
1960	O, GL	Opening of St. Lawrence Seaway to ocean shipping (and to foreign species invasions)	Sly (1985)
1957–1958, 1961	E, O	Increase in complaints linked to excessive *Cladophora*. Initiation of first intensive scientific and ecological studies of this species	Ontario Water Resources Commission (1968)
1963	GL	Abundant *Cladophora* growth reported at various sites in all Great Lakes	Neil and Owen (1964), Herbst (1969)
1970s	E	Ohio State University studies of *Cladophora* in the Ohio Islands region	Taft and Kishler (1973)
1970	E, O	Human population: 11–12 million people in each basin	Botts and Krushelniki (1995)
1972	M	The *People of the State of Illinois v. the City of Milwaukee* Lake Michigan pollution court case partially decided on presence of *Cladophora* blooms at sites ''downstream'' of point sources. US$2.9 billion in wastewater treatment plant (WWTP) upgrades ordered	Mortimer (2004)
1972	GL	Initiation of phosphorus reduction and development of phosphorus loading objectives (GLWQA)	Nicholls et al. (2001)
1980	H	Decline in *Cladophora* biomass by 80% at a site in western Lake Huron. Directly associated with P abatement at a wastewater treatment facility	Canale and Auer (1982b)
1983	O	Apparent decline in *Cladophora* biomass from 1970s levels, attributed to lake-wide total phosphorus (TP) reduction	Painter and Kamaitis (1987)
1985	E, O	Human population: 13–14 million people in each catchment	Botts and Krushelniki (1995)
1990s	GL	Establishment of *Dreissena* species in all Great Lakes	Vanderploeg et al. (2002)
1991–1993	H	Increased macrophyte and benthic algal production following dreissenid mussel invasion in Saginaw Bay	Lowe and Pilsbury (1995), Skubinna et al. (1995)
1995–present	E, O, M	Apparent resurgence of *Cladophora* blooms and increase in complaints	Dejong (2000), Bootsma et al. (2005), Higgins et al. (2005b)

Erie = E, Huron = H, Ontario = O, Michigan = M, Superior = S.
[a] Taft and Kishler (1973) and references therein.

History of Cladophora *in the Great Lakes. C. glomerata* was first described in the Great Lakes in 1848, although it was probably present during or before the early 1800s (Table 1). During the late 1950s, increasing public complaints about beach fouling prompted the Ontario Water Resources Commission (1968), now the Ontario Ministry of the Environment, to initiate studies on the ecology of *Cladophora* in Lake Erie and Lake Ontario. Reports by Neil and Owen (1964) and Herbst (1969) indicated that by the early 1960s, *Cladophora* blooms occurred in all five (Erie, Huron, Michigan, Ontario, Superior) of the Great Lakes. *Cladophora* blooms were identified as a significant problem in the lower Great Lakes (Erie, Michigan, Ontario) from the 1950s through the 1970s by the International Joint Commission (IJC 1980) and were recognized in the Great Lakes Water Quality Agreement (1978) between Canada and the United States. During 1972, *People of the State of Illinois v. the City of Milwaukee*, a Lake Michigan pollution court case on the impacts of untreated ''raw'' sewage emitted from the City of Milwaukee to Lake Michigan, was partially decided on the abundance of *Cladophora* at sites ''downstream'' of Milwaukee wastewater treatment plants (WWTP), and $2.9 billion in WWTP upgrades were ordered (Mortimer 2004).

Numerous studies were conducted during the 1970s and early 1980s to better understand the ecology of *C. glomerata* and provide the information necessary for successful management, many of which are reported in four benchmark publications (Shear and Konasewich 1975, Taft 1975, Wong and Clark 1976, Auer 1982). These studies identified the role of temperature, light, macronutrients (C, N, P), and micronutrients in constraining *Cladophora* growth rates and biomass accrual. They provided a scientific consensus that elevated concentrations of soluble phosphate associated with cultural eutrophication were ultimately responsible for the bloom occurrences.

Reductions in TP concentrations in the lower Great Lakes from the 1970s to the mid-1990s (Fig. 2), brought about through significant restrictions on point sources of TP loading to the Great Lakes basin (Charlton et al. 1999), were primarily designed to reduce eutrophication in the offshore waters of the lakes and deep-water anoxia in Lake Erie (Vallentyne and Thomas 1978, IJC 1980). These reductions in loading and ambient TP concentrations, however, also reduced *Cladophora* biomass (e.g., by ~80% within an area of shoreline directly influenced by a sewage treatment outfall in Lake Huron [Canale and Auer 1982b] and by ~60% at seven sites across Lake Ontario [Painter and Kamaitis 1987]). While spatial surveys were not reported for Lake Erie or Lake Michigan, it is reasonable to conclude that biomass followed a similar response to declining P concentrations. In Lake Ontario and Lake Erie, spring TP concentrations continued to decline until the early to mid-1990s (Fig. 2). Based on spring TP concentrations in offshore waters (Fig. 2), these lakes would now be considered oligotrophic (Ontario, Huron, Michigan) and mesotrophic (Erie). During the time period 1984–1993, few incidents of beach fouling by *Cladophora* were reported, and we are not aware of any quantitative in situ surveys. In 1994, public complaints of algal beach fouling in the eastern basin of Lake Erie prompted the Ontario Ministry of the Environment (OME) to initiate in situ surveys for *C. glomerata* in Lake Erie (Higgins et al. 2005b). Subsequent public complaints in Lake Ontario and eastern Lake Huron prompted shoreline observational surveys and some in situ surveys by the OME (Table 2). In eastern Lake Erie, where *Cladophora* shoreline fouling was extensive, recent (1995–2006) surveys indicated that biomass at depths ≤0.5 m was 30%–60% lower than during 1979–1980, but at depths of 1.0–2.0 m, biomass was similar (Fig. 3). At seven sites in Lake Ontario, biomass at 0.5–1.5 m depth was 30%–60% lower than in 1982–1983 and was similar at 3.0 m depth (Fig. 4). Compared with the early 1970s, however, biomass at all depths (0–3 m) in 2006 (Lake Ontario) was 12%–25% lower (Fig. 4). While these survey data only report values 0–3 m depth, modeling efforts (Higgins et al.

TABLE 2. Tissue nutrient concentrations for carbon (Q_C), nitrogen (Q_N), and phosphorus (Q_P) measured during the period of peak biomass in Lake Huron, eastern Lake Erie, and Lake Ontario during 2006 (S. N. Higgins, unpublished data).

Lake	Depth (m)	n	Q_C (% DM)	Q_N (% DM)	Q_P (% DM)
Huron	0.5	4	25.1 ± 2.3	2.9 ± 0.50	0.18 ± 0.10
	1.5	1	10.7 ± n/a	0.8 ± n/a	0.06 ± n/a
	2.0	4	20.9 ± 6.8	1.9 ± 1.3	0.08 ± 0.07
	3.0	1	21.2 ± n/a	1.5 ± n/a	0.04 ± n/a
Erie (east)	0.5	4	29.1 ± 2.7	2.0 ± 0.43	0.07 ± 0.04
	1.0	4	29.2 ± 3.2	1.8 ± 0.40	0.06 ± 0.01
	1.5	4	30.3 ± 2.7	2.3 ± 0.65	0.11 ± 0.04
	2.0	4	32.0 ± 1.4	2.2 ± 0.43	0.09 ± 0.03
Ontario	0.5	4	28.4 ± 2.8	2.4 ± 0.56	0.08 ± 0.03
	1.5	7	29.2 ± 2.7	1.9 ± 0.53	0.07 ± 0.03
	3.0	7	27.2 ± 1.7	1.8 ± 0.29	0.07 ± 0.04

Values are reported as % of dry mass (DM) ± 1 SD. Lakes Ontario, Erie data sources: see captions of Figures 2–3.
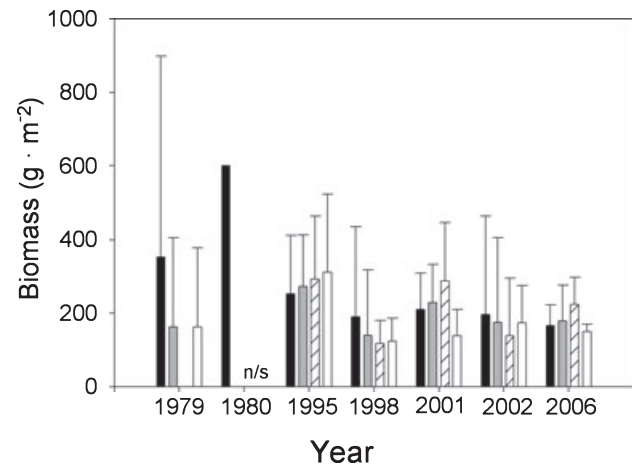

FIG. 3. *Cladophora* biomass at shallow (0–2 m) depths in eastern Lake Erie, 1979–2006. Depth intervals of 0.5 m (solid bar), 1.0 m (gray bar), 1.5 m (hatched bar), and 2.0 m (open bar) are included. Data sources: Millner et al. (1982), Neil and Jackson (1982), Higgins et al. (2005b), Table 2.

2005b, Malkin et al. 2008) have estimated that increases in water transparency caused by invasive dreissenid mussels had resulted in significant changes to the depth distribution and total biomass integrated over the depth of the euphotic zone.

Taxonomy and biogeography. *C. glomerata* is widely distributed throughout freshwater and estuarine ecosystems of the world, including North America, Europe, the Atlantic Islands, the Caribbean Islands, Asia, Africa, Australia and New Zealand, and the Pacific Islands (Guiry and Guiry 2007). In North America, *C. glomerata* occurs in all biomes except the tundra (Sheath and Cole 1992). Recent efforts to validate the morphologically determined species identifications utilizing nucleotide sequences from the internal transcribed spacer (ITS) region of the nuclear ribosomal cistron have demonstrated that
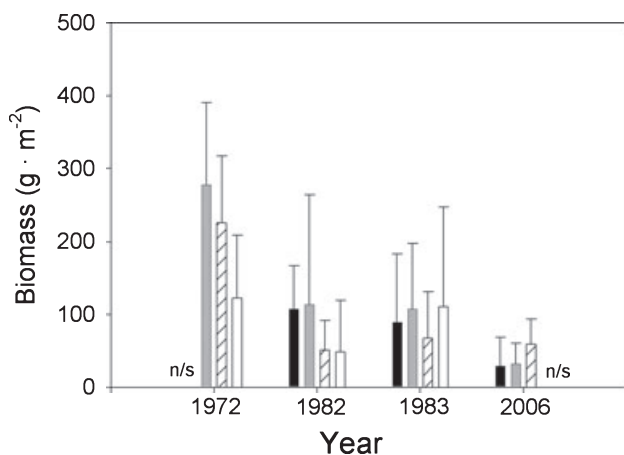
Fig. 4. *Cladophora* biomass at shallow (0–5 m) depths at seven sites spanning the north shore of Lake Ontario, 1972–2006. Note the different biomass scale to that for Lake Erie (Fig. 3). Samples were collected from 0.5 m (solid bar), 1.5 m (gray bar), 3.0 m (hatched bar), and 5.0 m (open bar). Data sources: Painter and Kamaitis (1987) and reports therein. Data from 2006 (Table 2) were collected from the same seven sites as Painter and Kamaitis (1987) using similar methods.

freshwater *Cladophora* comprise few, possibly one, species (Marks and Cummings 1996). Similar efforts to delineate *Cladophora* species in North America, including the Great Lakes region, using molecular markers and intersimple sequence repeats (ISSRs) indicated that populations had <1% nuclear sequence divergence in the ITS region between the ribosomal genes (Ross et al. 2006). These results suggest that one cosmopolitan species of *Cladophora* dominates North American freshwaters, including the Great Lakes (Marks and Cummings 1996, Ross et al. 2006). However, Ross et al. (2006) noted that the presence of two distinct freshwater species (i.e., *C. glomerata* and *C. fracta*) cannot be ruled out, and that further studies utilizing microsatellites would assist in resolving this question. We have applied the current taxonomic understanding of the biogeography of *Cladophora* in the Great Lakes, and the terms *Cladophora* and *C. glomerata* are used interchangeably.

Physiological requirements. *Cladophora glomerata* requires a hard surface for attachment, a relatively high light environment, warm waters, ambient pH between 7 and 10, and some degree of water motion (Whitton 1970). While *Cladophora* may be present in oligotrophic to eutrophic systems, excessive growths of *Cladophora* are generally associated with eutrophic waters (Herbst 1969, Whitton 1970, Planas et al. 1996). In lakes, *Cladophora* is associated with the eulittoral and sublittoral zones of exposed shorelines (Whitton 1970). *Cladophora* may grow attached to plant material (epiphytic), rock surfaces (epilithic), or to the surfaces of animals (epizootic) including the opercula of fish or the shells of gastropods or bivalve mussels (Whitton 1970, Higgins

et al. 2005b). Within the lower Great Lakes, *Cladophora* distribution is restricted by the availability of suitable substrata for attachment (Higgins et al. 2005b).

Light requirements: The photosynthetic response of *Cladophora* follows a hyperbolic, or similar, response to irradiance. The photosynthesis–irradiance (*P–I*) curve can be defined using several parameters, including P_M (maximal rate of photosynthesis), α (slope of the ascending linear portion of the curve), β (slope of the declining portion of curve due to photoinhibition or light-enhanced photorespiration), I_{CR} (critical irradiance required to maintain positive net photosynthesis), and I_K (the half-saturation irradiance for maximal photosynthesis = P_M/α). Maximal rates of net photosynthesis (P_M [NET]) of *Cladophora* from the Great Lakes are generally reported normalized to dry mass (DM) and, based on a photosynthetic quotient of 1.1 (Davies and Hecky 2005), ranged from 13.4 to 38.4 mg C · g $DM^{-1} \cdot h^{-1}$ (Adams and Stone 1973, Mantai 1974, Wood 1975, Lester et al. 1988). Maximal areal rates of P_M (NET) of 197 mg $O_2 \cdot m^{-2} \cdot h^{-1}$, or 66 mg C · $m^{-2} \cdot h^{-1}$, have been described for in situ populations of *Cladophora* in eastern Lake Erie (Davies and Hecky 2005). Reported values of α ranged from 0.11 to 0.26 mg $O_2 \cdot$ mg $DM^{-1} \cdot h^{-1}$ (µmol photon · $m^{-2} \cdot s^{-1})^{-1}$ for *Cladophora* from Lake Huron (recalculated from figs. 11–16 in Graham et al. 1982) and Lake Michigan (Lester et al. 1988). Values of I_K for Great Lakes *Cladophora* have been reported to range between 15 and 600 µmol photons · $m^{-2} \cdot s^{-1}$ (Graham et al. 1982, Lester et al. 1988, Higgins 2005).

Values of I_{CR} are reported to range 6–44 µmol photons · $m^{-2} \cdot s^{-1}$ (Graham et al. 1982, Lester et al. 1988, Lorenz et al. 1991, Necchi 2004), and these values have been used to estimate the depth distribution of *Cladophora* in lakes (Lorenz et al. 1991, Higgins et al. 2005b). Using the approach of Lorenz et al. (1991) and the lower limits of light attenuation (K_d) generally found in these lakes ($K_d \sim 0.18$ m^{-1}), the expected maximum colonizable depth would be ~30 m. Field studies have recently reported *Cladophora* patches at 20 m depths in some locations of Lake Ontario (Wilson et al. 2006) and Lake Michigan (Bootsma et al. 2005). The maximum depth of colonization, and depth-integrated biomass, are expected to vary considerably based on highly variable coastal water clarity and available substratum for attachment. In addition to the effects of variable water-column light attenuation on *Cladophora* growth and distribution, large gradients in light and photosynthesis are expected through the vertical structure of *Cladophora* beds (Dodds et al. 1999). At *Cladophora* bed densities commonly observed in the Great Lakes, K_d values within the bed are ~30 m^{-1} (Higgins et al. 2006), which are nearly two orders of magnitude larger than water-column K_d values. As

with other dense macroalgal beds, self-shading controls the maximum potential standing crop (Hill and Boston 1991, Dodds et al. 1999). Therefore, the maximum areal standing crop will vary over depth and with variations in water clarity. Toward the base of the *Cladophora* bed, self-shading may result in light intensities falling below minimum critical requirements for extended periods (weeks), leading to cellular deterioration, weakening filament strength, and increasing susceptibility to physical detachment (Higgins et al. 2006).

While low ambient light intensities control the depth distribution of *Cladophora*, and may be an important factor in controlling seasonal sloughing, high light intensities have been demonstrated to induce photoinhibition and light-enhanced photorespiration in some studies (e.g., Graham et al. 1982, Ensminger et al. 2005), although not in others (e.g., Lester et al. 1988, Necchi 2004, Binzer et al. 2006). The influence of photoinhibition and light-enhanced photorespiration has been incorporated into models of population growth (Canale and Auer 1982a, Graham et al. 1982, Higgins et al. 2005a). These models predict reductions in growth and biomass accrual at shallow depths where ambient light intensities are high. The incorporation of photoinhibition or light-enhanced photorespiration, measured during physiological experiments on small portions of filaments (phytoelements), into models of in situ population growth, is problematic for several reasons. *Cladophora* beds often flourish at shallow depths, including the splash zone, suggesting that physiological and/or population level mechanisms can reduce potential negative effects of high-light environments. Physiological acclimation to high-light environments in *Cladophora* include low chl *a* concentrations, low chl *b/a* ratios, low maximal rates of photosynthesis, low values of α (i.e., the initial linear slope of *P–I* curves), the presence of active bicarbonate uptake mechanisms (proton pump), and the possession of a xanthophyll cycle to protect PSII from oxidative stress related to ultraviolet-B (UVB) radiation (Choo et al. 2005). Population-level responses to photoinhibition, or light-enhanced photorespiration, are related to the positive effect of self-shading on limiting the potential effects of photoinhibition to the upper few millimeters to centimeters of the algal or plant canopy (Hill and Boston 1991, Dodds et al. 1999). In a study of *P–I* relationships in 190 aquatic vascular plant and macroalgal communities, including *C. glomerata*, Binzer et al. (2006) determined that photoinhibition did not occur in a single incidence when experiments were conducted at the population level and concluded that the absence of photoinhibition was completely attributable to self-shading.

Temperature: Minimum temperature requirements for the initiation of vegetative growth of *C. glomerata* are near 5°C (Graham et al. 1982). Several authors have suggested that cool spring temperatures limit the growth potential of *Cladophora* in Lake Superior, and while small amounts are found in various locations around the lake (Sheath and Cole 1992), including offshore reefs (Jackson et al. 1990), larger growths are restricted to thermal effluents and warm harbors (Herbst 1969, Parker and Drown 1982). Studies assessing the influence of thermal effluents on *Cladophora* growth in Lake Erie have indicated that growth was initiated earlier in the season within the warm effluent plumes; however, the magnitude of the summer standing crop remained unaffected (Moore 1978). Reported temperature optima and thresholds for the growth of *C. glomerata* vary widely among studies. For *C. glomerata* isolated from the Great Lakes, region optimal temperatures for growth have been reported to range from 13°C to 31°C, and reported maximum threshold temperatures have been reported to range between 30°C and 35°C (Bellis 1968, Gerloff and Fitzgerald 1976, Graham et al. 1982, Lester et al. 1988). A number of studies have invoked high midsummer lake temperatures as the cause of the midsummer sloughing phenomenon (see Whitton 1970 for review). However, in the Great Lakes, the midsummer sloughing period tends to occur as lake temperatures reach 22°C–24°C (Canale and Auer 1982a, Higgins et al. 2005b), which is ~10°C cooler than critical temperatures determined within in vitro experiments. Lester et al. (1988) reported that maximum photosynthetic rates for *Cladophora* from Lake Michigan occurred between 28°C and 31°C. Similarly, in a study on *Cladophora* from eastern Lake Erie, maximum photosynthetic rates remained unchanged before and during the midsummer sloughing period (S. N. Higgins, unpublished data), which occurred at lake temperatures near 24°C. These results do not support the hypothesis that temperature alone is responsible for the midsummer sloughing phenomena in the Great Lakes.

Nutrient limitation: Reports of N-limited *Cladophora* growth from freshwater systems are few, and a majority of studies indicate P as the limiting nutrient for growth. Perhaps the most definitive example of P limitation of *Cladophora* in the Great Lakes comes from the ecosystem-level experiments by Auer and colleagues (Auer 1982), where the introduction of tertiary P removal at a municipal wastewater treatment facility on Lake Huron was demonstrated to reduce in situ *Cladophora* biomass by ~80% (Canale and Auer 1982b). A similar, although more indirect, study of the relationship between P loading and *Cladophora* biomass in Lake Ontario showed a 60% reduction in biomass from 1972 to 1982–1983 in response to the strict P-abatement strategies implemented within the Great Lakes basin (Painter and Kamaitis 1987). A similar response of *Cladophora* to P abatement was noted on Lake Windermere, England, where biomass was

reduced ~90% from 1992 to 1997 through reductions in basin-wide soluble P concentrations (fig. 6 in Parker and Maberly 2000).

The P-uptake kinetics for *C. glomerata* have been described by Gerloff and Fitzgerald (1976), Auer and Canale (1982a,b), Rosemarin (1982), and Planas et al. (1996). P uptake is a function of external phosphate concentrations, the cell quota for P (Q_P), and temperature and can be described using the function

$$\rho = \rho_{max} \cdot \tau \cdot [P/(K_m + P)] \\ \cdot \{K_q/[K_q + (Q_P - Q_{P0})]\} \quad (1)$$

where ρ equals P uptake (% $P \cdot d^{-1}$), ρ_{max} equals the maximum P-uptake rate (% $P \cdot d^{-1}$), τ is a temperature-dependent coefficient (dimensionless) for P uptake (Gray 1984 *in* Painter and Jackson 1989), P equals the external phosphate concentration ($\mu g \ P \cdot L^{-1}$), K_m equals the half-saturation constant for uptake as a function of external phosphate concentration ($\mu g \ P \cdot L^{-1}$), K_q equals the constant relating uptake to Q_P, and Q_{P0} is the minimum cell quota for P required to maintain positive growth (Auer and Canale 1982b). Values of ρ_{max} and K_m are dependent on Q_P and are the highest when Q_P approaches Q_{P0} (Auer et al. 1983). The relationship between K_m and Q_P has been defined as

$$K_m = 246 \times Q_{P0}/Q_P \quad (2)$$

by Auer and Canale (1982a); however, we are unaware if similar relationships between ρ_{max} and Q_P have been quantified. Under conditions of P limitation, and constant temperature, values of Q_P approach Q_{P0}, the portion of equation 1 $\{K_q/[K_q + (Q_P - Q_{P0})]\}$ approaches 1, and ρ is linearly dependent P (at locations where $P < K_m$).

The Q_P of *Cladophora* tissues is a direct function of P uptake and the dilution of P through growth. In addition, the relationship between Q_P and growth potential in *Cladophora* has also been quantified (Gerloff and Fitzgerald 1976, Wong and Clark 1976, Auer and Canale 1982b). Growth potential follows a Droop model response to changes in Q_P (Auer and Canale 1982b; Fig. 5). At Q_P values >0.16% DM, potential growth rates are relatively insensitive to small variations in Q_P, and additional P uptake is considered "luxury" consumption (Lohman and Priscu 1992). In the Great Lakes, Q_P values between 0.16% and 0.83% DM have generally been reported during the early spring period (Higgins 2005), in proximity to point sources of P (Canale and Auer 1982a, Jackson and Hamdy 1982), or at locations (i.e., at greater depths or areas of high turbidity) where growth is light limited (Bootsma et al. 2005, Higgins et al. 2005b). During the peak growth period, however, Q_P values at most shallow sites (<3 m) are ≤0.11% DM (Table 2). As Q_P values fall below
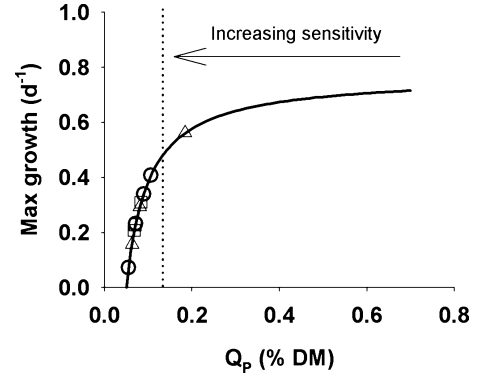

FIG. 5. The Droop relationship between growth potential and tissue phosphorus concentration (Q_P) (Auer and Canale 1982b). Measured values of Q_P from Lake Erie (open circle), Lake Ontario (open squares), and Lake Huron (open triangles) during the time of peak biomass in 2006 (Table 2) are reported. The dashed vertical line represents a Q_P of 0.16% dry mass (DM), below which growth becomes increasingly sensitive to variations in Q_P.

0.16% DM, growth rates become increasingly sensitive to small variations in Q_P (Fig. 5). At Q_P values below 0.05%–0.06% DM, which are considered to be the minimum cell quota (Q_{P0}), growth cannot be maintained (Gerloff and Fitzgerald 1976, Wong and Clark 1976, Auer and Canale 1982b). Declines in Q_P through the growing season indicate that the dilution of P through growth exceeds P uptake and that growth becomes increasingly P limited over time. However, as leaching of nutrients during senescence may occur, interpretations of Q_P as an estimate of growth potential (as in Fig. 5) during periods of senescence should be considered with caution. Exploiting the relationship between Q_P and growth potential, P-limited *Cladophora* growth has recently been demonstrated within Lakes Ontario, Erie, Michigan, and Huron (Table 2; Bootsma et al. 2005, Higgins et al. 2005b).

P limitation of *Cladophora* growth has also been demonstrated using the alkaline phosphatase activity (APA) assay (Mantai 1978, Mantai et al. 1982, Freeman 1986), where the expression of the alkaline phosphatase enzyme is expected to occur under low Q_P concentrations. In these studies, however, the relationships between Q_P and APA were often complex. In some experiments, low Q_P was directly associated with high APA (Freeman 1986). However, in other studies, declines in Q_P during rapid vegetative growth (following a nutrient pulse) were associated with large short-term (1–3 d) increases in APA, but then returned to low levels despite persisting low Q_P values (Mantai 1978).

Using similar approaches to that for Q_P, cell quotas for nitrogen (Q_N) have been used to assess the potential for N-limited growth in *Cladophora*, with critical Q_N values (Q_{N0}) near 1.1% DM (Gerloff and Fitzgerald 1976). Using these criteria, the potential

for N limitation was demonstrated at two sites in eastern Lake Erie during 1979 (Millner et al. 1982). In western Lake Erie, Q_N values approached the 1.1% critical concentration; however, the C/N ratio within *Cladophora* tissue remained relatively stable, and neither N nor P appeared to limit growth (Lorenz and Herdendorf 1982). In general, reported Q_N concentrations, including recent surveys of Lake Ontario, Erie, and Huron (Table 2), indicate that N limitation is rare in the Great Lakes region (Neil and Owen 1964, Neil and Jackson 1982, Bootsma et al. 2005, Higgins et al. 2005b).

Carbon (C) limitation of benthic algal photosynthesis can result from increased boundary layer conditions restricting CO_2 and bicarbonate exchange with surrounding waters (Cheney and Hough 1983, Turner et al. 1994). Within the boundary layer, C limitation may be exacerbated by shifts in C speciation to nonutilizable forms caused by increases in pH associated with photosynthesis. However, studies utilizing C isotopes have indicated that variable boundary layer thickness had little effect on C acquisition in *Cladophora* and that HCO_3^- was readily used as a source (Raven et al. 1982, 1994). *C. glomerata* possesses carbonic anhydrase within its periplasm, which can rapidly catalyze the dehydration of HCO_3^- to CO_2, promoting the passive diffusion of CO_2 into the cells. In addition, *C. glomerata* possesses an active bicarbonate-uptake mechanism (i.e., a proton pump) that is activated during periods of C limitation (Choo et al. 2002, 2005). The active uptake mechanism in *C. glomerata*, and its ability to utilize bicarbonate, may explain its success in waters with relatively high pH and low ambient CO_2 concentrations (Choo et al. 2002). The absence of *Cladophora* from quiescent waters may, however, reflect the inability of these processes to overcome increased boundary layer conditions, or reductions in advective mixing, that reduce gas exchange with the surrounding waters. In more turbulent locations, the importance of short-term (seconds to hours) reductions in C fixation on growth, when measured on timescales relevant to the cell doubling time (days), may be limited when other elements such as P are in low supply and ultimately growth limiting.

Life cycle and population dynamics. The life cycle of *C. glomerata* has been reviewed by Bellis and McLarty (1967) and Whitton (1970). In general, *C. glomerata* reproduces asexually through the development of biflagellate or quadriflagellate zoospores (Van den Hoek 1963, Bellis and McLarty 1967). The development of zoosporangia and formation of zoospores have been correlated with short photoperiods (Van den Hoek 1963, Hoffmann and Graham 1984), although in field populations, zoosporangia can be noted throughout the vegetative growth period (Bellis and McLarty 1967). Each zoosporangium may contain several hundred zoospores, and upon release, the zoospores attach to hard substratum at their anterior end by affixing their flagella to the substratum (Bellis and McLarty 1967). Given favorable environmental conditions, germination and vegetative growth can begin shortly after the zoospores become attached (Bellis and McLarty 1967, Whitton 1970). As vegetative growth proceeds, upright filaments are produced, and branching from the main filament may occur. The degree to which branching and sub-branching occurs has often been related to water velocity or turbulence (Dodds and Gudder 1992, Bergey et al. 1995). The loss of branches has been associated with the bursting of zoosporangia (Bellis and McLarty 1967). Growth may occur in an intercalary or apical manner (Whitton 1970); however, branched forms have lower intercalary growth than unbranched forms (Bellis and McLarty 1967). In branched forms of *Cladophora*, growth is typically acropetal, where apical cells elongate vertically, while subapical cells elongate horizontally and produce lateral branches through the process of budding (Van den Hoek 1963). In this manner, the youngest branches are those closest to the apex. *C. glomerata* may overwinter as thick-walled akinete cells that remain tightly adhered to the substratum (Whitton 1970), and given favorable conditions, vegetative growth can begin as temperatures approach 5°C (Graham et al. 1982).

In north temperate lakes and rivers, *Cladophora* generally follows a two-node seasonal growth pattern, with a midsummer biomass peak followed by a period of widespread detachment of filaments (i.e., sloughing), a period of low growth, and then an autumn biomass peak that may be smaller or larger than the summer peak (Bellis and McLarty 1967, Whitton 1970, Higgins et al. 2005b). Under optimal conditions, measured in vitro, vegetative growth may be rapid with maximum net specific growth rates near 0.7–0.8 d^{-1} (Auer and Canale 1982b, Rosemarin 1982). However, these high rates are rarely achieved in natural settings due to suboptimal environmental conditions and negative feedback mechanisms, such as self-shading and reductions in dissolved gas and nutrient exchange within dense canopies (Hill and Boston 1991, Dodds et al. 1999, Choo et al. 2002). Specific growth rates are generally highest during the spring period when availability of limiting nutrients are at seasonal maxima and self-shading is minimal (Canale and Auer 1982b, Higgins et al. 2006). Thereafter, specific growth rates decline with seasonal declines in limiting nutrients and the effects of self-shading. While specific growth rates decline with increases in biomass, given otherwise favorable environmental conditions, areal growth rates increase, and population growth proceeds into an exponential growth phase (Fig. 6). Where *Cladophora* growth is extensive, the midsummer biomass peak is generally followed by a major sloughing event when weakened filaments are torn from their holdfasts or broken along the filament
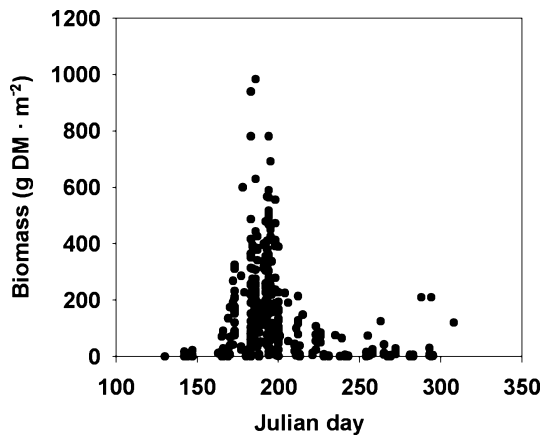
F$_{IG}$. 6. Seasonal changes in *Cladophora* biomass in eastern Lake Erie over multiple years, 1979–2006. All sites, depths (0–3 m), years included. (See Fig. 3 legend for data sources.) DM, dry mass.

axis, by the shear stress associated with water turbulence (Bellis and McLarty 1967, Whitton 1970, Canale and Auer 1982a, Higgins et al. 2005a,b). There are several proposed mechanisms causing the weakening of filaments and their susceptibility to detachment. These mechanisms include temperature stress (Bellis and McLarty 1967, Whitton 1970, Dodds and Gudder 1992), nutrient deficiency (Mantai 1978, 1987), metabolic imbalance of the *Cladophora* stand (e.g., depth-integrated growth) caused by a variety of factors (Canale and Auer 1982b), or metabolic imbalance of cells at the base of the stand caused primarily by self-shading (Higgins et al. 2006).

Once detached, the *Cladophora* filaments, which are neutral to negatively buoyant (but may float in surface mats due to entrained gas bubbles or surface tension), are susceptible to resuspension and horizontal transport. Floating and entrained *Cladophora* mats have been implicated in the fouling of commercial fishing nets, beaches, and industrial water intakes and are considered a major public nuisance (Taft 1975). A majority of the filaments, however, are transported to low energy depositional areas where they overlay sediments and begin to decompose. Some filaments may escape the initial detachment process; however, the biomass of these remaining filaments declines through the midsummer (August–September) period (Fig. 6). This period of low growth has been explained as a function of high ambient water temperatures and limiting nutrients leading to a metabolic imbalance (Whitton 1970, Canale and Auer 1982b, Higgins et al. 2006) and may also relate to other aspects of their life cycle, such as zoospore formation, dispersion, and recolonization. In the Great Lakes, the autumn biomass peak is generally lower than the spring-summer peak (Fig. 6), and growth models predict that autumn regrowth is restricted to shallower depths than during the spring growth period due to

reductions in water clarity and photoperiod (S. N. Higgins, unpublished data).

Community and ecosystem interactions. Biogeochemical cycling: Rapidly growing *Cladophora* beds have large capacities for nutrient and gas exchange, with the potential to alter biogeochemical cycling dramatically. During exponential population growth, *Cladophora* beds act as a nutrient sink, removing ecologically significant quantities of macronutrients (C, N, P) from the water column. For example, *Cladophora* beds along a 100 km stretch of shoreline in eastern Lake Erie were estimated to have removed ~15 tonnes of P over a 31 d period during May–June 2002, yet their tissues remained unsaturated and growth rates became increasingly P limited over time (Higgins et al. 2005b). As per measured tissue stoichiometry from eastern Lake Erie (Table 2), these *Cladophora* populations removed ~3,000 tonnes of C and ~230 tonnes of N over the spring growth period. During the senescence phase, *Cladophora* acts as a nutrient source to the water column. In a study of decomposition and nutrient release rates in *Cladophora* from the Baltic Sea, Paalme et al. (2002) noted that decomposition rates and N-release rates were similar, with declines in each of ~50% over a 14 d period under aerobic or anaerobic conditions. Release rates of P, however, were dependent on the dissolved oxygen (DO) concentration. Under anaerobic conditions, loss rates were rapid, with ~50% of initial P stores lost from tissues within 7 d and 80% lost over a 30 d period (Paalme et al. 2002). Under aerobic conditions, however, loss rates were much slower, with no significant loss of P from tissues within 14 d, and ~40% loss over a 30–35 d period (Paalme et al. 2002).

Microbes: Macroalgae may exude large quantities of fixed C as dissolved organic carbon (DOC) during their growth phase. For example, *C. fracta* from Shoe Lake, Michigan, was demonstrated to release 0%–90% of its daily fixed C (Cheney and Hough 1983). The released DOC, in turn, may stimulate the microbial food web (Valiela et al. 1997), which aggregates DOC into amorphous particles that may be utilized by higher trophic levels (Alber and Valiela 1994).

Microbes such as *Escherichia coli* and human pathogenic organisms (Shiga toxin producing *E. coli, Salmonella, Shigella, Campylobacter*) have been found adhered to both living and decomposing filaments of *Cladophora* along the shorelines of Lake Michigan (Byappanahalli et al. 2003, Whitman et al. 2003, Ishii et al. 2006, Olapade et al. 2006). *E. coli* and enterococci were present on 97% of *Cladophora* samples collected from 10 beaches on the Wisconsin, Illinois, Indiana, and Michigan shorelines of Lake Michigan (Whitman et al. 2003). Furthermore, *E. coli* and enterococci survived for >6 months in sun-dried *Cladophora* mats stored at 4°C and grew readily after rehydration (Whitman et al. 2003).

E. coli and total coliforms are commonly used as indicators of fecal contamination, and the increased potential for the presence of pathogenic bacteria, at public bathing beaches on the Great Lakes. However, little information currently exists on the relationship between pathogenic and non-pathogenic bacterial strains on *Cladophora* filaments, or on the importance of *Cladophora* as a source of these contaminants to beaches compared with other potential sources. Recent studies (Whitman et al. 2003, Ishii et al. 2006) indicate that *Cladophora* is capable of providing the necessary environmental requirements for the survival, and potentially the growth, of these bacteria. Due to the widespread occurrence of indicator bacteria in *Cladophora* mats, the presence of pathogenic bacteria in *Cladophora* mats near point sources, and the potential for *Cladophora* to act as a transport vector to areas of increased human contact, further studies should be undertaken to understand the interactions between *Cladophora* and bacteria and the implications to human health.

Epiphytes: Filaments of *C. glomerata* represent a large surface area and are often heavily colonized by epiphytic algae (Lowe et al. 1982, Sheath and Morison 1982, Stevenson and Stoermer 1982, Dodds 1991). The dominant epiphytes on *Cladophora* in the Great Lakes region are *Phormidium diguetti, Leibleinia epiphytica,* and *Chamaesiphon incrustans,* all cyanobacteria, comprising 53%–90% of the cell density, with most of the remainder being composed of diatoms, primarily *Cocconeis pediculus* and *Rhoicosphenia curvata* (Sheath and Morison 1982). Strong seasonality in epiphytic diatom assemblages and the proportion of epiphytic biomass to the total algal biomass were noted on *Cladophora* filaments from Lake Huron (Stevenson and Stoermer 1982). During May, the epiphytic diatom community comprised ∼30% of the total algal biomass. During the early to midsummer (June–July), *Cladophora* growth exceeded that of epiphytes, and the epiphytic diatom biomass was reduced to ∼20% of the total algal biomass. As *Cladophora* growth rates declined through the autumn period, the proportion of epiphytic diatoms to total algal biomass increased, reaching >60% by November (Stevenson and Stoermer 1982). Epiphytes may compete with *Cladophora* for resources, such as limiting nutrients or light (Dodds 1991), and Stevenson and Stoermer (1982) postulated that dense assemblages of epiphytes may accelerate the sloughing process. Thick coatings of epiphytes can exacerbate light limitation of *Cladophora* growth, especially toward the base of the algal bed where light already reaches levels near or below minimum requirements. Epiphytes may also compete for growth-limiting nutrients (Dodds 1991, Dodds and Gudder 1992) and therefore reduce the growth rates of *Cladophora.* Stevenson and Stoermer (1982) suggest that larger internal P-storage capabilities in *Cladophora* allow for relatively higher growth rates during periods of low external concentrations or when nutrients are received in pulses.

Competition with other macroalgae: In addition to *C. glomerata,* several other species of benthic macroalgae are common throughout the Great Lakes, and in some cases, these species dominate benthic algal assemblages. The red alga *Bangiadulcis (Bangia) atropurpurea,* an invader to the Great Lakes, was shown to inhabit the splash zone, where it competed with *Ulothrix zonata* (Weber et Mohr) and, to a lesser extent, *Cladophora* (Blum 1982). In Lake Superior, while total benthic algal biomass was low, *U. zonata* and an unidentified *Ulothrix* sp. dominated the shallow littoral periphyton communities (Gerloff and Fitzgerald 1976, Jackson et al. 1990). These species are more tolerant of cooler ambient water temperatures than *Cladophora,* and in the lower Great Lakes, they were dominant during the early spring before *Cladophora* growths were extensive (Kirby and Dunford 1981, Auer et al. 1982, Blum 1982). In Georgian Bay and the North Channel of Lake Huron, Sheath et al. (1988) noted that while 15 macroalgal species were found, only *Cladophora* (92%) and *Chara globluaris/vulgaris* (7%) contributed significantly to the total macroalgal standing crop. Other species, primarily *Phormidum retzii, U. zonata, Zygnema* spp., and *Spirogyra* spp. contributed ≤1% to the total macroalgal standing crop (Sheath et al. 1988). In recent years, shoreline fouling along eastern Lake Huron, though initially thought to be *Cladophora,* was determined to be primarily caused by *Chara* spp. (E. T. Howell, personal observation). While *Chara* grows in cobble beds and is not thought to compete directly with *Cladophora* for space, the recent shoreline fouling by *Chara* suggests that increased in situ growth may be caused by similar mechanisms that have influenced *Cladophora* growth. In Saginaw Bay of Lake Huron, hard substrata at intermediate depths (2.5–5.5 m), previously dominated by diatoms, became heavily colonized by the filamentous green algae *Spirogyra* and *Mougeotia* immediately following the invasion of dreissenid mussels (Lowe and Pilsbury 1995). These species may represent a transitional assemblage, and their initial success is due to rapid dispersion (Lowe and Pilsbury 1995). Blooms of *Spirogyra* were also noted during the summer period (July) of 2002 in eastern Lake Erie and June 2007 in Lake Ontario (S. N. Higgins, personal observation), where filaments grew as loosely attached metaphyton overtop of the thick (≥10 cm) *Cladophora* beds. These *Spirogyra* blooms persisted for days to weeks during relatively calm weather, before being dislodged by wind-induced turbulence. This finding suggests that *Spirogyra,* and other loosely attached macroalgae, may not successfully compete in the exposed shorelines of the Great Lakes where strong winds and >2 m waves are common and water turbulence is often high.

Invertebrates: *Cladophora* beds provide habitat for a diverse group of invertebrates including tubificids,

gammarids, cladocerans, tricopterans, mollusks, and crayfish (Taft 1975, Chilton et al. 1986, Dodds 1991, Dodds and Gudder 1992). In eastern Lake Erie, the most common macroinvertebrates associated with *Cladophora* were amphipods, primarily *Gammarus fasciatus,* and a diverse assemblage of chironomids (Szabo 2004). *Cladophora* beds were the preferred habitat for *G. faciatius,* though not the exotic invader *E. ischnus* (Van Overdijk et al. 2003). Stomach content and stable isotope analysis revealed that both *G. fasciatus* and chironomid species fed on epiphytic diatoms when abundant, and a controlled laboratory experiment demonstrated that *G. fasciatus,* but not *E. ischnus,* grazed directly on *Cladophora* filaments (Szabo 2004). Analysis of gut contents from in situ populations of macroinvertebrates and fish in Lake Huron, however, indicated that predation represented negligible losses to the standing crop (Canale and Auer 1982a).

Dreissenids: Dramatic increases in macrophyte and benthic algal biomass, including *Cladophora,* have occurred concurrently with successful invasions by *D. polymorpha* and *D. bugensis* (zebra and quagga mussels, respectively) within lakes, rivers, and estuaries (Lowe and Pilsbury 1995, Skubinna et al. 1995, Orlova et al. 2004a, Higgins et al. 2005b, Zhu et al. 2006). Increased *Cladophora* growth in dreissenid-infested waters may occur by several mechanisms. First, dreissenids increase the three-dimensional surface area, the tortuosity, of the lake bottom and thereby increase the colonizable area for zoospores and akinetes. Increases in the initial growing stock of *Cladophora* may increase areal growth rates and nutrient sequestering, particularly during the spring period when ambient nutrient concentrations are at their maxima. Higher initial standing stocks of vegetative cells, and higher total areal P storage by *Cladophora* during the spring, would result in a higher likelihood that the maximum potential standing crop would be reached by midsummer. In addition, the ability of *Cladophora* akinetes and zoospores to attach directly to dreissenid shells allows *Cladophora* to colonize areas where the substratum would otherwise be marginal (Wilson et al. 2006) and therefore reduce patchiness and increase the total available habitat. Second, dreissenid mussels often increase water clarity dramatically (Holland 1993, Fahnenstiel et al. 1995, Howell et al. 1996) and thereby increase the colonizable depth, the depth of light-saturated growth, and depth-integrated biomass of benthic algae (Higgins et al. 2005b, 2006, Malkin et al. 2008). Third, dreissenid mussels directly increase the bioavailability of P by consuming seston and releasing metabolic waste, feces, and pseudo-feces (Arnott and Vanni 1996, Orlova et al. 2004a, Conroy et al. 2005). Because *Cladophora* filaments overlay the dreissenid beds, and reduce mixing with the water column, *Cladophora* probably has a competitive advantage over phytoplankton in accessing nutrients

released from dreissenids. Fourth, dreissenids may reduce phytoplankton concentrations through grazing (Nicholls and Standke 1997, Barbiero et al. 2006), thereby reducing competition for P and reducing losses of bound P (seston) to the hypolimnion (Hecky et al. 2004). Makarewicz et al. (2000) reported significant increases ($\sim$1 $\mu g \cdot L^{-1}$) in springtime (April–May) soluble reactive P concentration in each of Lake Erie's basins over the *Dreissena*-invasion period. Fifth, the release of CO_2 and consumption of O_2 by dreissenid respiratory processes may reduce the potential for C limitation or O_2 inhibition of *Cladophora* growth (Hecky et al. 2004).

Ecological models. Ecological models that incorporate physiological, population, community, and ecosystem level interactions have been successfully used to predict *Cladophora* growth dynamics in the Great Lakes (Auer 1982, Higgins et al. 2005a) and elsewhere (Gordon and McComb 1989, Parker and Maberly 2000). The models used may be quite simple, as in the case of two regression-based models used by Parker and Maberly (2000) to predict peak *Cladophora* biomass in Lake Windermere, England. The Parker and Maberly model predicted the magnitude of the summer standing crop on the basis of winter soluble phosphate concentrations or the Julian day where soluble phosphate concentrations fell below 1 mg $\cdot$ m^{-3}. These purely empirical models were useful for forecasting *Cladophora* biomass and setting targets for P control, and for hindcasting biomass estimates for years where direct measurements were unavailable.

The first theoretical *Cladophora* growth model proposed for the Great Lakes was that of Storr and Sweeney (1971). The Storr and Sweeney model described the two-node seasonal growth dynamics of *Cladophora* on the basis of ambient water temperature and photoperiod. During 1979–1980, a mechanistically structured *Cladophora* growth model (Auer and Canale 1982a,b, Auer et al. 1982, Canale and Auer 1982a,b, Canale et al. 1982, Graham et al. 1982) was developed to evaluate the relative importance of environmental factors in controlling growth rates and evaluate management strategies to control nuisance blooms. The Auer and Canale model, in its simplest form, is given by the equation

$$\mathrm{d}X/\mathrm{d}t = [\mu - R - L] \cdot X \qquad (3)$$

where X = biomass (g DM $\cdot$ m^{-2}), μ = the gross specific growth rate (d^{-1}), R = the specific respiration rate (d^{-1}), L = the specific loss rate due primarily to sloughing (d^{-1}; Canale and Auer 1982a). The Auer and Canale model provided the conceptual framework (Fig. 7) to incorporate the mechanistic and empirical relationships between the following: (i) μ and light, temperature, the cell quota for phosphorus (Q_P), and self-shading; (ii) R and light and temperature; and (iii) L and wind-speed and algal density. As a result, while equation 3 is quite simple,
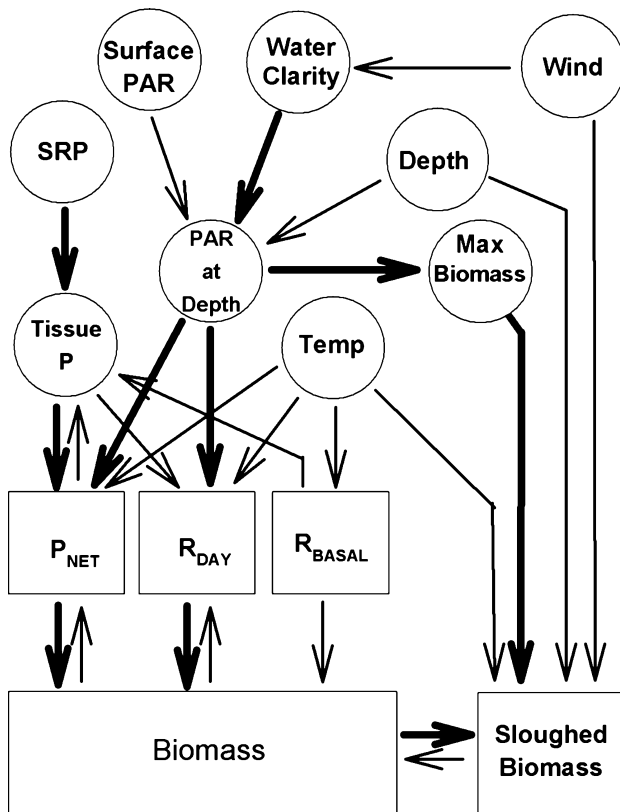
FIG. 7. Conceptual diagram of Auer and Canale *Cladophora* growth model modified from Higgins et al. (2005a). Thickened arrows represent model components influenced by invasive dreissenid mussels (see text). SRP, soluble reactive phosphorus; P_{NET}, net photosynthesis; R_{DAY}, respiration during daylight hours; R_{BASAL}, basal respiration (nocturnal).

the complexity of the model arises in the 30 or more equations required to derive these four primary variables. Since the environmental input data (Fig. 7) in coastal regions are often highly variable both spatially and temporally, the model is a useful tool for estimating the relative importance of these variables on growth and losses of *Cladophora* over space and time, and for assessing P-abatement scenarios while incorporating the natural variability in other important parameters. The Auer and Canale model was developed and calibrated at site in direct proximity to a WWTP in western Lake Huron during 1979 (Canale and Auer 1982a) and was validated in 1980 (Canale and Auer 1982b). This model successfully predicted the response of *Cladophora* growth to declines in soluble P resulting from the implementation of tertiary treatment at the WWTP, demonstrating both the model's utility and the efficacy of P-abatement programs.

The Auer and Canale model was subsequently revised (Higgins et al. 2005a, 2006) and field tested in eastern Lake Erie postdreissenid invasion. These revisions were primarily associated with adapting the model structure to function over a larger depth range, reducing input data requirements, and

adding a subroutine to calculate the effects of self-shading on multiple vertical layers within the mat structure. A sensitivity analysis of the model (Higgins et al. 2006) for eastern Lake Erie revealed that *Cladophora* growth was highly sensitive to ambient phosphate concentrations and that interannual differences in phosphate ($\pm 0.5 \, \mu g \cdot L^{-1}$) could cause a $3.5 \times$ difference in depth-integrated biomass, and that spatial variations in water clarity were responsible for up to a 2-fold difference in depth-integrated biomass between sites. In addition, the model results indicated that self-shading was the underlying cause of the midsummer sloughing event in eastern Lake Erie (Higgins et al. 2006).

The revised Auer and Canale *Cladophora* growth model (Higgins et al. 2005a, 2006) was recently applied in Lake Ontario to hindcast growth rates based on historical changes in Q_P and water clarity (Malkin et al. 2008). The modeling results estimated that the current maximum standing crop of *Cladophora* is 34% and 29% lower than that during the early 1970s and early 1980s, respectively, and that these declines were primarily the result of reductions in Q_P. However, model simulations indicate that depth-integrated biomass postdreissenid invasion (1995–present) was probably higher than during the immediate preinvasion period (1984–1994) due to both increased P availability and increased water clarity (Higgins 2004 and S. N. Higgins, unpublished data).

In addition to their utility for *Cladophora* management, such models provide a framework for the development and testing of ecological hypotheses and can focus research efforts to areas of *Cladophora* ecology that remain poorly understood. For example, the failure of initial formulations of *Cladophora* growth models (Auer 1982, Higgins et al. 2005a) to predict the midsummer sloughing event indicated that the underlying mechanisms responsible were poorly understood. Subsequent studies indicated that self-shading promoted prolonged (weeks) metabolic imbalance toward the base of the *Cladophora* beds and was the most likely cause of the sloughing event within Lake Erie; model formulations were then updated (Higgins et al. 2006). Since in situ surveys of *Cladophora* biomass were not undertaken on the Great Lakes during the 10-year period prior to dreissenid invasion (1984–1994), the importance of dreissenids as a cause of the "resurgence" of *Cladophora* blooms has not been directly quantified. While model hindcasts cannot prove dreissenids as the cause of the resurgence, they can provide probabilities based on the implications of dreissenid-induced changes in water clarity, ambient phosphate, and availability of hard substratum. Recent attempts to quantify the effects of dreissenid mussels on *Cladophora* growth have indicated that dreissenid-induced increases in soluble P and water clarity have increased the depth distribution and depth-integrated biomass of *Cladophora* over

predreissenid years and are the most probable cause of the resurgence in bloom formations (Higgins 2004, Malkin et al. 2008). Further improvements in model estimates would be gained by the addition of a dreissenid bioenergetics model, estimating P efflux from dreissenids based on dreissenid density and various water-column parameters (e.g., water velocity, turbidity, temperature, seston stoichiometry); fractioning dreissenid P efflux into feces, pseudofeces, and dissolved organic and inorganic fractions; and quantifying the ability of *Cladophora* to access these fractions. In addition, as coastal zone processes in large lakes and estuaries are often spatially and temporally complex, the full complement of required input data is often difficult to measure directly using field programs. Therefore, the inclusion of *Cladophora* growth models into validated hydrodynamic and biological models that predict the necessary input parameters on a fine spatial scale, and that include point (WWTP, tributary, storm water drains, thermal effluents) and nonpoint (mixing with offshore waters, dreissenids, resuspension, upwelling) sources of P, turbidity, and temperature would be a useful improvement for managing blooms in these complex coastal systems.

Summary and management implications. Despite dramatic reductions in *Cladophora* bloom occurrences from the 1970s to the 1990s, brought about through stringent, and expensive, P-abatement programs, changes in substratum availability (Hecky et al. 2004, Wilson et al. 2006), water clarity (Holland 1993, Fahnenstiel et al. 1995, Howell et al. 1996), and P availability (Arnott and Vanni 1996, Makarewicz et al. 2000, Conroy et al. 2005) associated with the establishment of dense dreissenid mussel colonies have caused a renewed proliferation of this nuisance macroalga in the lower Great Lakes. Quantitative assessments of the total depth-integrated biomass over this time period will require the use of calibrated *Cladophora* growth models and environmental input data from predreissenid years. Due to the apparent influence of dreissenids on *Cladophora* growth, given similar anthropogenic P-loading rates, depth-integrated *Cladophora* biomass is expected to covary with spatial and interannual variations in dreissenid population density. Previous P management in the Great Lakes has focused primarily on controlling pelagic zone P concentrations to reduce phytoplankton blooms at a lake or basin scale (Vallentyne and Thomas 1978, IJC 1980). Successful management of *Cladophora* blooms will require an improved understanding of the sources and retention of both particulate P (i.e., that can be recycled by dreissenids) and soluble P to the littoral zone, improved monitoring and forecasting of dreissenid population density, improved monitoring of *Cladophora* populations over a gradient of human and dreissenid influence, and further improvements in our understanding *Cladophora* ecology and capacity to model the complete seasonal growth cycle and transport and fate of detached filaments.

Several aspects of *Cladophora* ecology remain poorly understood, including (i) the relative importance of dreissenid-induced changes in water clarity, P, and habitat availability on the resurgence of *Cladophora* blooms in the lower Great Lakes; (ii) the underlying mechanisms governing the deterioration and sloughing of *Cladophora* filaments; (iii) the transport and fate of sloughed filaments and their effect on benthic organisms within depositional areas; (iv) the relative importance of environmental factors or life-cycle phenomena that control the period of low vegetative growth during the midsummer period; (v) the factors controlling, and importance of, DOC exudation on growth rates, biogeochemical cycling, and stimulation of microbial activity; (vi) the interactions with indicator bacteria (i.e., *E. coli*) and potential human pathogens by *Cladophora*; and (vii) the importance of *Cladophora* to littoral zone biogeochemical cycling and food webs.

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