Appendix 1.

An Ecological Review of Cladophora in the Laurentian Great Lakes


Abstract

Cladophora glomerata is a filamentous green alga that grows attached to hard substrata in the littoral zone of alkaline waters, and has a widespread distribution across the globe. Recent reports of widespread C. glomerata blooms, and associated problems, in the lower Laurentian Great Lakes and the Baltic Sea have prompted a renewed scientific interest in the ecology this species. Cladophora blooms were a major problem in these lakes from the 1950’s through to the 1970’s, and were largely eradicated through the implementation of strict phosphorus (P) controls within the Great Lakes basin. While the total P loading, or P concentrations, have not increased substantially in recent years, the resurgence in Cladophora is coincident with the establishment of dense populations of invasive dreissenid (Dreissena polymorpha, D. bugensis) mussels that create additional habitat, exert strong controls over water clarity, and increase the recycling rates and bioavailability of P in the littoral zone. Increased substratum provided by dreissenids may have reduced the patchiness of Cladophora beds and increased growth in areas where substratum was previously marginal, improvements in water transparency have shifted the depth distribution and maximum extent of colonization, and increased P supply from retention and recycling has increased growth rates and the maximum standing crop. Phosphorus remains the primary limiting nutrient for Cladophora growth in the Laurentian Great Lakes, and depth integrated biomass is highly sensitive to small variations in soluble phosphorus concentrations and water transparency. Widespread nitrogen limitation has not been demonstrated for Cladophora from the Great Lakes. Carbon limitation may become important in rapidly growing, and dense, Cladophora beds. Adaptation and acclimation to high light environments by Cladophora suggest light enhanced respiration or photoinhibition will not exert strong controls over population growth. Cladophora is often heavily colonized by epiphytes, and provides habitat and refugia for macroinvertebrates and some littoral fish. Cladophora is also colonized by bacteria including potential human pathogens. The causes of cellular deterioration and detachment, and the fate of detached material remain largely unknown.
Introduction
Widespread blooms and shoreline fouling by the benthic filamentous alga *Cladophora glomerata* (Chlorophyta) have recently (1995-present) been reported throughout the lower Laurentian Great Lakes (Michigan, Erie, Ontario) and within geographically isolated areas of Lake Huron (Howell 1998, Bootsma et al. 2005, Higgins et al. 2005b, Wilson et al. 2006). *Cladophora* blooms were identified as a significant problem in these lakes during the 1950’s through the 1970’s by the International Joint Commission (IJC 1980) and the Great Lakes Water Quality Agreement (1978) between Canada and the United States. Numerous studies were conducted during the 1970’s and early 1980’s in order to better understand the ecology of this species and provide the information necessary for successful management, many of which are reported in several benchmark publications (Shear and Konasewich 1975, Taft 1975, Wong and Clark 1976, Auer 1982). These studies identified several key factors including temperature, light, photoperiod, self-shading, and several macro and micro-nutrients that were important in constraining *Cladophora* growth rates. These studies provided a scientific consensus that elevated concentrations of soluble phosphorus (SRP) associated with cultural eutrophication were ultimately responsible for the increase in bloom formations. The reductions in total phosphorus (TP) concentrations in the lower Laurentian Great Lakes (Figure 1) brought about through the significant reductions in P loading (Charlton et al. 1999) were primarily designed to reduce eutrophication in the offshore waters of the lakes and deep water anoxia problems in Lake Erie (Vallentine and Thomas 1978, IJC 1980).

![Figure 1. Spring (April-May) offshore (>20 m station depths) TP concentrations in the epilimnion (0-20m) of Lake Superior (open squares), Lake Huron (closed triangles), Lake Erie (closed circles), and Lake Ontario (closed squares) 1974-1976. Data provided by NWRI, Environment Canada.](image)

However, the reductions in loading and TP concentrations also reduced *Cladophora* biomass 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 7 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 these systems. In Lake Ontario and Lake Erie spring TP concentrations continued to decline until the early-mid 1990’s (Figure 1). At current spring TP concentrations these lakes would be considered oligotrophic (Ontario, Huron, Michigan) to mesotrophic (Erie). During this time, few incidents of beach fouling by *Cladophora* were reported, and in situ surveys were not conducted. In 1994, public complaints of algal beach fouling in eastern basin of Lake Erie prompted the Ontario Ministry of the Environment (OME) to initiate in situ surveys in Lake Erie (Howell 1998, Higgins et al. 2005b). Subsequent public complaints in Lake Ontario and eastern Lake Huron prompted shoreline observational surveys and some in situ surveys (Howell, unpublished data).

In eastern Lake Erie, where *Cladophora* blooms appear the most extensive, recent (1995-2006) surveys indicated that biomass at depths ≤ 0.5 m was 30-60% lower than during 1979-80, and similar at depths 1.0-2.0 m (Figure 2). A similar general response was noted at seven sites in Lake Ontario, where biomass at 0.5-1.5 m depth was 30-60% lower than values reported during 1982-83, but similar at 3.0m depth. Compared with the early 1970’s, however, biomass at all depths in 2006 (Lake Ontario) was 12-25% lower (Figure 3). While these survey data only report values 0-3m depth, modeling efforts (Higgins et al. 2005b, Tomlinson et al. 2006, Malkin et al. in prep) have estimated that increases water transparency caused by invasive dreissenid mussels (*Dreissena polymorpha, D. bugensis*) had resulted in significant changes to the depth distribution and depth integrated biomass. Increases in benthic algal and macrophyte growth associated with dreissenids have been reported in the Laurentian Great Lakes (Lowe and Pilsbury 1995, Skubinna et al. 1995, Hecky et al. 2004, Higgins et al. 2005b, 2006), and elsewhere (e.g. Zhu et al. 2006).

The recent resurgence of widespread *Cladophora* blooms (Figure 2-3, Bootsma et al. 2005, Higgins et al. 2005b), which are the most commonly observed forms of coastal eutrophication in the Great Lakes, presents two potential conundrums. First, if P loading rates have generally remained below GLWQA targets and offshore phosphorus concentrations remain low in the lower Great Lakes why has there been the resurgence *Cladophora* blooms and shoreline fouling in recent years? Second, If a strong relationship between *Dreissena* and *Cladophora* exists can *Cladophora* and other benthic algae be successfully managed in dreissenid infested waters? The purpose of this article is to review the current state of knowledge regarding the ecology of *C. glomerata* in the Laurentian Great Lakes, to explore the causes of the recent *Cladophora* blooms including potential interactions with dreissenid mussels, and to identify knowledge gaps that preclude a more thorough ecological understanding and successful management. While this review of *Cladophora* ecology is geographically focused on the Laurentian Great Lakes, where we have the most experience and insights, much of this information applies to other freshwater systems where *Cladophora* blooms also occur and to the general response of macroalgae and macrophytes to dreissenid mussel invasions.
Figure 2. *Cladophora* biomass at shallow (0-2m) depths in eastern Lake Erie 1979-2006. Depth intervals of 0.5m (solid bar), 1.0m (grey bar), 1.5m (hatched bar), and 2.0m (open bar) are included. Data sources: Millner and Sweeney (1982), Neil and Jackson (1982), Higgins (2005b). Data from 2006 were collected as part of this report from 4 sites (Peacock, Grant, Rock, Rathfon) using the same methods and site locations as Higgins et al. (2005b).

Figure 3. *Cladophora* biomass at shallow (0-5m) depths at seven sites spanning the north shore of Lake Ontario 1972-2006. Samples were collected from 0.5m (solid bar), 1.5m (grey bar), 3.0m (hatched bar), and 5.0m (open bar). Data sources: Painter and Kamaitis (1987) and reports therein. Data from 2006 were collected as part of this report from the same 7 sites as Painter and Kamaitis (1987) using similar methods.
**Taxonomy and Biogeography**

The genus *Cladophora* contains approximately 120 species (Bakker et al. 1994), including 11 freshwater and brackish water species (Van den Hoek 1963; Whitton 1970). The high morphological plasticity of *Cladophora* and overlapping morphological characteristics between species has made identification to the species level difficult using traditional morphological indicators (Bellis and McLarty 1967; Whitton 1970; Bakker et al. 1994). *C. glomerata* is widely distributed worldwide, and in North America is found in all biomes except the tundra (Sheath and Cole 1992). Recent efforts to validate the morphologically determined species identifications and discern the biogeography of *Cladophora* species and varieties in North America through the use of molecular markers and intersimple sequence repeats (ISSR’s) indicate that North American populations have <1% nuclear sequence divergence in the ITS (internal transcribed spacer) region between the ribosomal genes (Ross 2006). These results suggest that one cosmopolitan species of *Cladophora* dominates North America including the Laurentian Great Lakes (Ross 2006). This manuscript applies the current taxonomic understanding of the biogeography of *Cladophora* in the Laurentian Great Lakes and the terms *Cladophora* and *C. glomerata* are used interchangeably.

**Physiological Responses**

*C. glomerata* requires a hard surface for attachment, a relatively high light environment, warm alkaline waters, ambient pH values between 7-10, 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 conditions (Herbst 1969, Whitton 1970; Planas et al. 1996). In lakes *C. glomerata* 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; Dodds and Gudder 1992, Higgins et al. 2005b). In the Laurentian Great Lakes *Cladophora* has been observed to commonly grow attached to the shells of dreissenid mussels (Higgins, personal observation). Within the lower Great Lakes *Cladophora* distribution is restricted by the availability of suitable substratum for attachment (Higgins et al. 2005b). While human-made structures such as breakwalls and piers may be colonized these areas represent only a small fraction of the surface area compared with the extensive bedrock shelves and cobble areas present in the lakes.

**Light**

The minimum, or critical, light requirements (E<sub>cr</sub>) for growth are reported to range between 25-44 µmol photons m<sup>-2</sup> s<sup>-1</sup> (Graham et al. 1982; Lester et al. 1988; Lorenz et al. 1991), 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<sub>d</sub>) generally found in these lakes (K<sub>d</sub> ~0.18) the expected maximum colonizable depth would be approximately 20 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. For example, reductions in water clarity to mean $K_d$ values near 0.5 m$^{-1}$, which are often found in coastal areas susceptible to particle resuspension, would reduce the maximum depth to ~7 m. Strong gradients in light and photosynthesis are expected through the vertical structure of Cladophora beds. At Cladophora bed densities commonly found in the Laurentian Great Lakes $K_d$ values within the bed are ~30 m$^{-1}$ (Higgins et al. 2006), nearly two orders of magnitude larger than water column $K_d$ values. As with other macro-algal beds self-shading controls the maximum areal biomass achievable (Dodds 2003, Higgins et al. 2006), therefore maximum biomass will vary over depth and with variations in water clarity. Towards the base of the Cladophora bed self-shading may result in light intensities falling below minimum critical requirements for extended time periods (weeks), leading to cellular deterioration, the weakening filament strength, and increasing the susceptibility of filaments 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 photo-inhibition and enhanced photorespiration in some studies (e.g. Graham et al. 1982, Ensminger et al. 2005), though not others (e.g. Lester et al. 1988, Higgins et al. in prep). The influence of photoinhibition and light enhanced photorespiration has been incorporated into models of population growth (e.g. Canale and Auer 1982a, Graham et al. 1982, Higgins et al. 2005a), which predict reductions in growth and biomass accrual at shallow depths where ambient light intensities are high. The incorporation of photoinhibition or light enhanced respiration terms, measured during physiological experiments, to estimates of population growth is problematic for several reasons. Cladophora beds often flourish at shallow depths, including the splash zone, suggesting physiological and/or population level adaptations to high light and high UVR environments. Adaptations to high light environments in Cladophora include low Chlorophyll a concentrations, low Chl b/a ratios, low maximal rates of photosynthesis, low values of $\alpha$, the presence of active bicarbonate uptake mechanisms (proton pump), and the possession of a xanthophyll cycle to protect photosystem II from oxidative stress related to UV-B (Choo et al. 2005). In addition to these physiological adaptations to high light environments, self-shading by the algal canopy reduces potentially inhibiting or damaging irradiances to the upper few cm of the algal assemblage (Dodds 2003, Higgins et al. 2006), and therefore provides additional photo-protection to cells below the canopy surface. Further, short term reductions (minutes to hours) in carbon fixation by light enhanced photorespiration that do occur would not necessarily exert strong influence over growth rates at time scales related to cell doubling time (days) when other elements, such as phosphorus, are in low supply and are ultimately limiting to daily growth.

Temperature
Minimum temperature requirements for the initiation of vegetative growth of C. glomerata are near 5 ºC (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 1980, Auer and Canale 1981), including offshore reefs (Jackson et al. 1990), larger growths are
restricted to thermal effluents and 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 was unaffected (Moore 1978). Reported temperature optima and thresholds for the growth of *C. glomerata* vary widely among studies. For *C. glomerata* isolated from the Laurentian Great Lakes region optimal temperatures for growth have been reported to range from 13-31°C, and reported maximum threshold temperatures have been reported to range between 30-35°C (Bellis 1968; Adams and Stone 1973; Graham et al. 1982; Lester et al. 1988). A number of studies have invoked high mid-summer lake temperatures as the cause of the midsummer sloughing phenomenon (Whitton 1970). However, in the Laurentian Great Lakes the midsummer sloughing period tends to occur as lake temperatures reach 22-24°C (Canale and Auer 1982a; Higgins et al. 2005b), which is approximately 10 °C cooler than critical temperatures found within in vitro experiments. Lester et al. (1988) found that maximum photosynthetic rates, for *Cladophora* harvested from Lake Michigan, occurred between 28-31°C. Similarly, in a study on *Cladophora* from eastern Lake Erie maximum photosynthetic rates were unchanged before and during the mid-summer sloughing period (Higgins et al. in prep), which occurred at lake temperatures near 24 °C. These studies suggest that temperature alone is not responsible for the midsummer sloughing phenomena.

**Nutrient Limitation**

Most macroalgal blooms, including those formed by *Cladophora*, result from nutrient enrichment within the photic zones of aquatic systems (Valiela et al. 1997). Throughout the world’s marine and estuarine environments macroalgal blooms are most often considered nitrogen limited (e.g. Valiela et al. 1997, Charlier and Lonhienne 1996, Fletcher 1996). However, as discussed below, reports of nitrogen limited *Cladophora* growth from freshwater systems are few, and the majority of studies indicate phosphorus as the limiting nutrient for growth. Perhaps the most definitive example of P-limitation of *Cladophora* in the Laurentian Great Lakes comes from the ecosystem level experiments by Auer, Canale, Graham 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, though more indirect, study of the relationship between phosphorus loading and *Cladophora* biomass in Lake Ontario showed a 60% reduction in biomass from 1972 to 1982-3 in response to the strict P-abatement strategies implemented within the Laurentian Great Lakes basin (Painter and Kamaitis 1987).

The direct relationship between internal tissue phosphorus (ITP) concentration, external soluble reactive phosphorus (SRP) concentration, and P-uptake in *Cladophora* has been quantified by several researchers (Auer and Canale 1982a,b, Rosemarin 1982, Planas et al. 1996). In addition, the relationship between ITP concentration and growth potential in *Cladophora* has also been quantified (Gerloff and Fitzgerald 1976, Wong and Clark 1976, Auer and Canale 1982b), and growth potential follows a Droop model response (Figure 4) to changes in ITP concentration. As noted in Figure 4, at ITP concentrations above
0.16% of dry mass (DM) the potential growth rates are relatively insensitive to variability in ITP concentrations, and under these circumstances growth rates are not limited by phosphorus. As ITP concentrations fall below 0.16 % DM growth rates become increasingly sensitive to variations in ITP concentration. At ITP concentrations below 0.05-0.06 %DM, which are considered to be the minimum cell quota, positive growth cannot be maintained (Gerloff and Fitzgerald 1976, Wong and Clark 1976, Auer and Canale 1982). During the growth period ITP values are a balance between P uptake and the dilution of ITP through growth (Auer and Canale 1982a), and during senescence additional ITP may be lost through leaching. Spatially, increases in ITP may be found in proximity to nutrient sources (Canale and Auer 1982a) and in areas where growth is light limited, such as at depths below 2-4 m or in shallower areas with low water clarity (Bootsma et al. 2005, Higgins et al. 2005b). Temporally, declines in ITP through the growing season indicate that the dilution of P through growth exceeds P uptake and that growth becomes increasingly P-limited over time. As leaching of nutrients during the senescence period may occur interpretations of ITP concentration during periods of senescence should be considered with caution. Exploiting the relationship between ITP concentration and growth, P-limited Cladophora growth has recently been demonstrated within Lakes Ontario, Erie, Michigan, and Huron (Table 1, Bootsma et al. 2005, Higgins et al. 2005b). P-limitation of Cladophora growth in Lake Erie has also been

Figure 4. The Droop relationship between growth potential and internal phosphorus concentrations within Cladophora tissues (Auer and Canale 1982b). ITP concentrations from Lake Erie (open circle), Lake Ontario (open squares) and Lake Huron (open triangles) from 2006 (Table 1) are reported.
demonstrated using the alkaline phosphatase assay (APA), however the APA response was complex and did not always correspond with ITP concentrations (Mantai et al. 1982, Hiriart-Baer et al. submitted).

While P-limitation of *Cladophora* growth and bloom formation has been well documented in the Laurentian Great Lakes and elsewhere, in some circumstances other nutrients, including nitrogen, carbon, or micronutrients may limit growth in freshwater systems. Using similar approaches to that for ITP, internal tissue nitrogen (ITN) concentrations have been used to assess the potential for nitrogen limited growth in *Cladophora*, with critical ITN values near 1.1% of dry mass (Gerloff and Fitzgerald 1976). Using these criteria, the potential for nitrogen limitation has been demonstrated at two sites in eastern Lake Erie during 1979 (Millner et al. 1982), and in the Wisconsin river (Dodds 2003). In western Lake Erie, ITN values were found to approach the 1.1% critical concentration, however, the authors noted that the C/N ratio within tissues remained relatively stable, and concluded that neither nitrogen nor phosphorus limited growth (Lorenz and Herdendorf 1982). In general, reported ITN concentrations, including our recent surveys of Lake Ontario, Erie, and Huron (Table 1), indicate that N-limitation is rare in the Laurentian Great Lakes region (Neil and Owen 1964, Neil and Jackson 1982, Bootsma et al. 2005, Higgins et al. 2005).

Carbon (C) limitation of benthic algal photosynthesis can result from increased boundary layer conditions restricting CO$_2$ and bicarbonate exchange with surrounding waters (e.g. Turner et al. 1994). Within the boundary C limitation may be exacerbated by shifts in carbon speciation to non- utilisable forms caused by increases in pH associated with photosynthesis. The potential for carbon to limit *Cladophora* growth is not well understood. *C. glomerata* possesses carbonic anhydrase within its periplasm, which rapidly catalyses the dehydration of HCO$_3^-$ to CO$_2$. As well, *C. glomerata* possesses active bicarbonate uptake mechanisms (i.e. a proton pump) that are activated during periods of carbon limitation (Choo et al. 2002, 2005). The active uptake mechanisms in

### Table 1. Internal tissue carbon, nitrogen, and phosphorus measured during the period of peak biomass in Lake Huron, eastern Lake Erie, and Lake Ontario during 2006. Values are reported as % of dry mass ± 1 standard deviation. Lakes Ontario, Erie data sources: see captions of Figure 2-3. Lake Huron data collected offshore of Southampton, Goderich, and Collingwood.

<table>
<thead>
<tr>
<th>Lake</th>
<th>(m)</th>
<th>n</th>
<th>ITC (%DM)</th>
<th>ITN (%DM)</th>
<th>ITP (%DM)</th>
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</thead>
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<td>2.9 ± 0.5</td>
<td>0.18 ±0.10</td>
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<td>1</td>
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<td>20.9 ± 6.8</td>
<td>1.9 ± 1.3</td>
<td>0.08 ± 0.07</td>
</tr>
<tr>
<td></td>
<td>3.0</td>
<td>1</td>
<td>21.2 ± n/a</td>
<td>1.5 ± n/a</td>
<td>0.04 ± n/a</td>
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<tr>
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<td>2.0 ± 0.43</td>
<td>0.07 ± 0.04</td>
</tr>
<tr>
<td></td>
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</tr>
<tr>
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<tr>
<td></td>
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<td>2.2 ± 0.43</td>
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</tr>
<tr>
<td>Ontario</td>
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<td>2.4 ± 0.56</td>
<td>0.08 ± 0.03</td>
</tr>
<tr>
<td></td>
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<td>29.2 ± 2.7</td>
<td>1.9 ± 0.53</td>
<td>0.07 ± 0.03</td>
</tr>
<tr>
<td></td>
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<td>27.2 ± 1.7</td>
<td>1.8 ± 0.29</td>
<td>0.07 ± 0.04</td>
</tr>
</tbody>
</table>
C. glomerata may explain its success in waters with relatively high pH and low ambient CO₂ 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. Presumably, increased boundary layers and diffusive gradients would also occur in detached and entrained Cladophora filaments compared with attached filaments where current velocities and turbulence would increase mixing through the vertical structure of the algal bed. As previously mentioned, the importance of short term (seconds to hours) reductions in carbon fixation on growth, when measured on timescales of cell doubling time (days), may be limited when other elements such as phosphorus are in low supply and ultimately growth limiting.

Population Dynamics
In north temperate lakes and rivers Cladophora generally follows a two-node seasonal growth pattern, with a mid-summer biomass peak followed by a period widespread detachment (or sloughing), a period of low growth, and then an autumn biomass peak that may be smaller or larger than the summer peak (Bellis and McClarty 1967, Whitton 1970; Higgins et al. 2005b). Under optimal conditions vegetative growth may be rapid with maximum net specific growth rates near 0.7-0.8 day⁻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 or reductions in dissolved gas and nutrient exchange within dense canopies (Choo et al. 2002, Dodds 2003). Specific growth rates are generally highest during the spring period when availability of limiting nutrients are at seasonal maxima, and self-shading is minimal. Thereafter, specific growth rates decline with seasonal declines in limiting nutrients and the effects of self-shading (Canale and Auer 1982b, Higgins et al. 2006). 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 (Figure 5). Where Cladophora growth is extensive the midsummer biomass peak is generally followed by a major sloughing event where weakened filaments are torn from their holdfasts by the shear stress associated with water turbulence (Bellis and McClarty 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, most of which are described in previous sections. These mechanisms include temperature stress (Bellis and McCarty 1967, Whitton 1970, Dodds and Gudder 1992), nutrient deficiency (Mantai 1987, 1989), 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). While these mechanisms are similar to those proposed for other freshwater, estuarine, and marine macroalgae (Valiela et al. 1997), insufficient information on the circumstances under which certain mechanisms will dominate precludes accurate assessment of their importance (Higgins et al. 2006).
Once detached the *Cladophora* filaments, which are neutral to negatively buoyant (though 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 (e.g. Taft 1975). The 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 (Figure 5). 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 dispersion and re-colonization. In some locations the autumn re-growth has resulted in an autumn biomass peak of similar or larger magnitude to the mid-summer peak. In the Laurentian Great Lakes, however, the autumn biomass peak is generally lower than the spring-summer peak (Figure 5), and growth models predict that autumn re-growth is restricted to shallower depths than during the spring growth period due to reductions in water clarity and photoperiod (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 dramatically alter biogeochemical cycling. During the exponential
population growth phase *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 phosphorus over a 31 day period during May-June, 2002 and yet their tissues remained unsaturated and growth rates became increasingly P-limited over time (Higgins et al. 2005b). Based on measured algal stoichiometry from eastern Lake Erie (Table 1) these *Cladophora* populations removed ~3000 tonnes of carbon, and ~230 tonnes of nitrogen during this same 31 day 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 nitrogen release rates were similar, with declines in each of ~50% over a 14 day period under aerobic or anaerobic conditions. Release rates of phosphorus, however, were dependant on the dissolved oxygen (DO) concentration. Under anaerobic conditions loss rates were rapid with ~50% of initial P stores lost from tissues within 7 days, and 80% lost over a 30 day period (Paalme et al. 2002). Under aerobic conditions, however, loss rates were much slower, with no significant loss of P from tissues within 14 days, and ~40% loss over a 30-35 day period (Paalme et al. 2002).

In some locations, the nutrient efflux from macroalgal beds during the senescence phase has been associated with an increase in phytoplankton production (Valiela et al. 1997), however it is unknown whether this is a significant feature of the relatively exposed littoral areas in the Great Lakes. Large gradients in DO have been noted in macroalgal beds in response to gradients in light and photosynthesis combined with low advective mixing (Dodds 2003), and similar responses should be expected in dense *Cladophora* beds. In addition, during periods of calm weather and high light *Cladophora* beds may have a large effect on DO concentrations within the overlying water column. For example, on a calm day in July of 2002 photosynthetic O2 evolution by *Cladophora* at 1-2m depth caused ambient DO concentrations to reach >200% saturation in an exposed area of shoreline in eastern Lake Erie (Higgins, unpublished data). While O2 associated with photosynthesis may increase ambient DO concentrations during the day, at night O2 consumption by *Cladophora* and other macroalgae and macrophytes has been implicated in reducing ambient DO below required concentrations for some fish species.

**Microbes**

While it remains unstudied in *Cladophora*, some macroalgae fix carbon in excess and exude large quantities of dissolved organic carbon (DOC) during their growth phase, which may be incorporated within the microbial foodweb (Valiela et al. 1997). In turn, microbes aggregate DOC into amorphous particles that may be utilized by higher trophic levels (Alber and Valiela 1994), and microbial activity may largely contribute to the biological oxygen demand within nutrient enriched waters (Valiela et al. 1997).

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). As *Cladophora* is prone to detachment, it may act as a transport vector for these bacteria to other shoreline areas where the potential for human contact is increased. *E. coli* not associated with human pathogens may also adhere to, and become transported by, detached *Cladophora* filaments.

**Epiphytes**

Filaments of *C. glomerata* represent a large surface area and are often heavily colonized by epiphytic algae (e.g. Lowe et al. 1982; Stevenson and Stoermer 1982a,b; Dodds 1991; Johnson 2004). 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 1982a). During May the epiphytic diatom community comprised approximately 30% of the total algal biomass. During the early to mid-summer (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. As discussed above, 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, and therefore may result in more rapid deterioration and sloughing of the *Cladophora* filaments. Epiphytes may also compete for growth limiting nutrients with *Cladophora* (Dodds 1991; Dodds and Gudder 1992), and therefore reduce the growth rates of *Cladophora*. However, the importance of nutrient competition between *Cladophora* and its epiphytes is not fully understood. The results of Stevenson and Stoermer (1982), however, suggest that larger internal P storage capabilities in *Cladophora* allows 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 Laurentian Great Lakes and in some cases these species dominate benthic algal assemblages. The red alga *Bangia atropurpurea*, an invader to the Laurentian Great Lakes, inhabits the splash zone, where it competes with *Ulothrix zonata* and, to a lesser extent, *Cladophora* (Blum 1982). In Lake Superior, while overall benthic algal biomass is low, *U. zonata* and *Ulothrix* sp. dominate the shallow littoral periphyton communities (Gerloff and Fitzgerald 1976; Jackson et al. 1991). These species are more tolerant of cooler ambient water temperatures than *Cladophora*, and in the lower Great Lakes they are sometimes found dominating during the early spring period before *Cladophora* growths are extensive (Kirby and Dunford 1981, 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* and *Chara globularis/vulgaris* contributed significantly to the standing crop. Other species, primarily *U. zonata*, *Zygnema* spp. and *Spirogyra* spp. contributed little to the overall biomass (Sheath et al. 1988). In recent years reports of shoreline fouling along the eastern Lake Huron shoreline, though initially
thought to be primarily *Cladophora*, were found to be dominated by *Chara spp*. While *Chara* grows in cobble beds and is not thought to compete directly with *Cladophora* for space, the recent shoreline fouling by *Chara* suggests increased *in situ* growth that 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 alga *Spirogyra* and *Mougeotia* immediately following the invasion of dreissenid mussels (Lowe and Pillsbury 1995). The authors noted that these species may represent a transitional assemblage and attributed their initial success to their ability for rapid dispersion (Lowe and Pilsbury 1995). Blooms of *Spirogyra* were also noted during the summer period (July) of 2002 in eastern Lake Erie (Higgins, personal observation), where filaments appeared to grow as loosely attached metaphyton overtop of the thick (> 20 cm) *Cladophora* beds. These *Spirogyra* blooms persisted for 4-5 days during a period of relatively calm weather, before being dislodged by wind induced turbulence. The inability to withstand moderate turbulence suggests that this alga, and other loosely attached algae, 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 high.

Invertebrates

*Cladophora* beds provide habitat for a diverse group of invertebrate species including tubificids, gammarids, cladocerans, tricopterans, mollusks, and crayfish (Taft 1975; Chilton et al. 1986; Dodds 1991; Dodds and Gudder 1992; Johnson 2004). In eastern Lake Erie the most common macroinvertebrates associated with *Cladophora* were amphipods, including *Gammarus fasciatus* and the exotic invader *Echinogammarus ischnus*, and a diverse assemblage of chironomids (Johnson 2004). Some studies indicated that *Cladophora* beds were preferred habitat for *G. faciatus*, though not the exotic invader *E. ischnus* (Ricciardi et al. 2001, Van Overdijk 2003; Johnson 2004). As *G. fasciatus* densities declined in response to competition with *E. ischnus*, *Cladophora* may have provided some refugia for the native species. Stomach content and stable isotope analysis revealed that both *G. faciatus* and chironomid species fed on epiphytic diatoms when abundant on the *Cladophora* filaments, and a controlled laboratory experiment demonstrated that *G. fasciatus*, but not *E. ischnus*, would graze directly on *Cladophora* filaments (Johnson 2004).

Dreissenids

Dramatic increases in macrophyte and benthic algal biomass, including *Cladophora*, has been demonstrated to occur concurrently with successful invasions by *Dreissena polymorpha* and *D. bugensis* (zebra and quagga mussels respectively) within lakes, rivers, and estuaries (Lowe and Pillsbury 1995, Skubinna et al. 1995; Orlova et al. 2004, Higgins et al. 2005b, Zhu et al. 2006). Increases in *Cladophora* growth in dreissenid-infested waters may occur by several mechanisms. First, dreissenids increase the three-dimensional surface area, or tortuosity, of the lake bottom, and therefore 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 nutrients are generally at their maxima. Higher initial standing stocks of vegetative cells, and higher total areal P storage by *Cladophora*
during the spring period, would result in higher areal growth rates and a higher likelihood that the maximum peak biomass would be reached. In addition, the ability of *Cladophora* akinetes and zoospores to attach directly to dreissenid shells may allow *Cladophora* to colonize areas where the substratum would otherwise be marginal (Wilson et al. 2006), and therefore reduce patchiness and increase the available habitat. Second, a large number of studies (e.g. Holland 1993, Fahnenstiel et al. 1995, Howell et al. 1996) have demonstrated the ability of dreissenid mussels to dramatically improve water clarity, and therefore increase the colonizable depth and the depth of light saturated growth (Higgins et al. 2005b, 2006). Third, dreissenid mussels directly increase the bioavailability of phosphorus by consuming seston and releasing metabolic waste, feces, and pseudo-feces (Arnott and Vanni 1996, Orlova et al. 2004, Conroy et al. 2005). Because *Cladophora* filaments overlay the dreissenid beds, and reduce mixing with the water column, *Cladophora* likely has a competitive advantage over phytoplankton in accessing nutrients released from dreissenids. Fourth, dreissenids may reduce phytoplankton concentrations (e.g. Nicholls and Standke 1997, Barbiero et al. 2006) thereby reducing competition for phosphorus and loss of bound P (seston) to the hypolimnion (Hecky et al. 2004). Makeriwickz et al. (2000) reported significant increases (~1 µg/L) in spring time (April-May) soluble reactive phosphorus 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 carbon limitation or O$_2$ inhibition of *Cladophora* growth (Hecky et al. 2004).

**Summary and Management Implications**

Dramatic reductions in *Cladophora* bloom occurrences from the 1970’s to the 1990’s, brought about through stringent, and costly, P-abatement programs in the Great Lakes basin have now been partially offset by ecosystem level 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 phosphorus availability (Arnott and Vanni 1996, Conroy et al. 2005, Makarewicz et al. 2004) associated with the establishment of dense dreissenid mussel colonies in these systems. *Cladophora* biomass, from shallow depths (0-2 m), during post-dreissenid years is similar (eastern Lake Erie) or lower (Lake Ontario) than values reported during the 1970’s and early 1980’s (Figure 2), however these data do not report depth integrated biomass and do not represent the 10 year period (1984-1994) immediately prior to dreissenid invasion. 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 pre-dreissenid years.

The use of ecological models to estimate *Cladophora* growth and predict it’s response to changing environmental conditions has been relatively successful in the Laurentian Great Lakes (Auer and Canale 1982a,b, Canale and Auer 1982a, b, Graham et al. 1982, Higgins et al. 2005a, 2006, Malkin et al. in prep). However, several aspects of *Cladophora* ecology remain poorly understood, including: 1) the relative importance of dreissenid induced changes in water clarity, soluble phosphorus, and habitat availability on the resurgence of *Cladophora* blooms in the lower Laurentian Great Lakes, 2) the underlying mechanisms governing the deterioration and sloughing of *Cladophora* filaments, 3) the transport and fate of sloughed filaments, and their effects on the transport of potentially
harmful bacteria, biogeochemical cycling, and on benthic organisms within depositional areas, and 4) the relative importance of environmental factors or life-cycle phenomena that control the period of low vegetative growth during the mid-summer period and the size of the autumn biomass peak.

*Cladophora* growth from shallow depths (≤3m) are highly sensitive to variations in phosphorus availability (Higgins et al. 2006, Table 1). *Cladophora* growth at depths below 2-4 m becomes increasingly light limited (Higgins et al. 2005b, 2006) and spatial and temporal variations in growth at these depths, and depth integrated biomass, will correspond with changes in water transparency (Higgins et al. 2006). Dreissenid mussel beds, which often underlay *Cladophora* beds, release SRP (e.g. Arnott and Vanni 1996, Orlova et al. 2004, Conroy et al. 2005), improve water clarity (e.g. Holland 1993, Fahnenstiel et al. 1995, Howell et al. 1996), and increase habitat suitability (Hecky et al. 2004, Higgins et al. 2005b, Wilson and Howell 2006). Therefore, given similar anthropogenic P-loading rates, depth integrated *Cladophora* biomass should be expected to co-vary with spatial and inter-annual variations in dreissenid population density. Previous P-management in the Laurentian Great Lakes has focused primarily on controlling pelagic zone P concentrations in order to reduce phytoplankton blooms (Vallentine and Thomas 1978, IJC 1980). Successful management of *Cladophora* 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 improvements in several aspects of *Cladophora* ecology.

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