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Cladophora Resurgent and Revisited: A Brief
Literature Review

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CLADOPHORA RESURGENT AND REVISITED: A BRIEF LITERATURE REVIEW

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ABSTRACT

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ABSTRACT

Three decades ago, blooms of *Cladophora* sp. were common along the shores of Lakes Erie, Ontario, Michigan and Huron (more localized). Links to excess inputs of phosphorus to these lakes were established and phosphorus abatement strategies imposed by the 1972 Great Lakes Water Quality Agreement successfully reduced bloom occurrences. In the recent years, excessive growth of *Cladophora* has once again become a common feature of the shorescapes of these lakes and while the P control target concentrations for pelagic waters are being met. In this paper, our current state of knowledge of the taxonomy, morphology, biology and general ecology of *Cladophora* is reviewed and the possible causal links to the current resurgence of *Cladophora* algal blooms in the Great Lakes is discussed, specifically, the potential links to the invasion of exotic species, climate change and population growth.

NWRI RESEARCH SUMMARY

Plain language title

Literature Review on Shoreline Algae Problem

What is the problem and what do scientists already know about it?

Shoreline algae detaches from the lake bottom and makes a smelly mess - this seems to have intensified in recent years. Nutrients are thought to be the culprit although the reasons for the resurgence of the problem now are under investigation.

Why did NWRI do this study?

There was a need to consolidate known information for partners in research to use.

What were the results?

Much is known about the physiology of *Cladophora* algae, less is known of its taxonomy and little is known about why Lake Ontario has the problem now.

How will these results be used?

They will be used by researchers working on the shoreline algae problem.

Who were our main partners in the study?

University of Waterloo, Ontario Ministry of the Environment.

RETOUR DE ET SUR *CLADOPHORA* : BRÈVE REVUE DOCUMENTAIRE

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RÉSUMÉ

Il y a environ 30 ans, les proliférations de l'espèce *Cladophora* n'étaient pas rares le long des rives des lacs Érié, Ontario, Michigan et Huron (plus circonscrites sur ce lac). On a établi des liens entre ce phénomène et les rejets excessifs de phosphore dans les lacs, et des stratégies de réduction du phosphore, imposées par l'Accord de 1972 relatif à la qualité de l'eau dans les Grands Lacs, ont permis de réduire efficacement l'apparition des proliférations. Au cours des dernières années, des poussées de *Cladophora* ont une fois encore envahi le littoral des Grands Lacs alors même que les objectifs de réduction des concentrations en phosphore pour les eaux pélagiques étaient atteints. Dans cet article, on fait le point des connaissances sur la taxinomie, la morphologie, la biologie et l'écologie générale de *Cladophora* et on traite des causes possibles de la résurgence actuelle de *Cladophora* dans les Grands Lacs et, plus particulièrement, des liens possibles avec l'invasion d'espèces exotiques, les changements climatiques et la poussée démographique.

Sommaire des recherches de l'INRE

Titre en langage clair

Analyse documentaire sur le problème des algues du littoral

Quel est le problème et que savent les chercheurs à ce sujet?

Les algues du littoral des lacs se détachent du fond et forment un boursier malodorant - phénomène qui semble s'intensifier depuis quelques années. Les nutriments semblent être en cause dans la prolifération des algues, mais on cherche les raisons de la résurgence actuelle du problème.

Pourquoi l'INRE a-t-il effectué cette étude?

Il était nécessaire de compiler les connaissances acquises pour que les partenaires de cette recherche puissent les utiliser.

Quels sont les résultats?

Les connaissances abondent sur la physiologie de l'algue *Cladophora*, mais la taxinomie de l'espèce reste lacunaire. On ne sait pas pourquoi le lac Ontario est maintenant aux prises avec le problème.

Comment ces résultats seront-ils utilisés?

Les résultats serviront aux chercheurs qui travaillent sur le problème des algues du littoral.

Quels étaient nos principaux partenaires dans cette étude?

Université de Waterloo, ministère de l'Environnement de l'Ontario.

Three decades ago, blooms of *Cladophora* sp. were common along the shores of Lakes Erie, Ontario, Michigan and Huron (more localized). Links to excess inputs of phosphorus to these lakes were established and phosphorus abatement strategies imposed by the 1972 Great Lakes Water Quality Agreement successfully reduced bloom occurrences. In the recent years, excessive growth of *Cladophora* has once again become a common feature of the shorescapes of these lakes and while the P control target concentrations for pelagic waters are being met. In this paper, our current state of knowledge of the taxonomy, morphology, biology and general ecology of *Cladophora* is reviewed and the possible causal links to the current resurgence of *Cladophora* algal blooms in the Great Lakes is discussed, specifically, the potential links to the invasion of exotic species, climate change and population growth.

Index words: *Cladophora*, Great Lakes, nutrients, climate change, dreissenids

TAXONOMY AND MORPHOLOGY

The species of the macroalgae *Cladophora* are distributed worldwide inhabiting a wide range of habitats, from arctic to tropical climates and freshwater to marine environments (Dodds and Gudder 1992, Marks and Cummings 1996, Sheath and Cole 1992). As many as 38 species of *Cladophora* have been identified, 11 of which are considered freshwater species (van den Hoek 1963). The most common freshwater species are *Cladophora glomerata*, *C. fracta* and *C. rivularis* (Whitton 1970). The physiological requirements of most freshwater species restrict their distribution to relatively eutrophic conditions where high nutrient concentrations and relatively alkaline conditions are found (van den Hoek 1963; Robinson and Hawkes 1986). The taxonomic delineation of the various freshwater species of *Cladophora* is often visually difficult because of their high phenotypic plasticity, their morphological adaptability to varying environmental conditions and the structural changes that occur due to plant age (Bellis and McClarty 1967, Bergey et al. 1995, Parodi and Cáceres 1991, Prescott 1951, van den Hoek 1963; Wilson et al. 1999). Ideally, taxonomic discrimination can be based on morphometric characteristics such as the extent of filament branching and the size of filaments and cells. Some typical morphological traits of *Cladophora* include, multinucleate cells, barrel shaped cells typically much longer than wide with thick cell walls (Canter-Lund and Lund 1995). However, within one species, some of these morphometric parameters can be very variable rendering inter-species differentiation a difficult task (e.g. apical cell diameter: *C. rivularis*, 19 - 45 μm ; *C. fracta* 16 - 27 μm ; van den Hoek 1963). As such *Cladophora* plants are rarely identified to the species level complicating our abilities in addressing certain fundamental questions on the evolution and ecology of this taxon (Marks and Cummings 1996).

Another approach to identifying different species and perhaps even biogeographical isolates is the analyses of genetic material. These types of analyses will help elucidate species boundaries and patterns of endemism (i.e. distinguishing between local populations which may

have genetically adapted to a particular locations or conditions) (Bakker et al. 1992). While the external morphology of *Cladophora* is quite adaptable, fundamental cellular processes and genetic traits are more conservative and less susceptible to environmental influences (Graham 1982). This type of molecular data can help discriminate between genetic divergence and ecological plasticity thereby furthering our understanding of how *Cladophora* sp. can occupy such a wide range of habitats (Marks and Cummings 1996). The sequencing of internal transcribed spacers (ITS) is one approach to phylogenetic analysis. Specifically it is the ITS regions located within rDNA cistrons that are of interest. These regions are virtually free of functional constraints, therefore they evolve at a faster rate demonstrating a number of substitutions and well-documented length variations between biogeographic isolates (Bakker et al. 1992). Numerous studies of phylogenetic relationships between algal species have been successfully attempted in marine systems (e.g. Bakker et al. 1995, Bot et al. 1989), however, only one study to date has attempted a similar approach in freshwaters with limited success (Marks and Cummings 1996). The differences in geographical scale and geological age between marine and freshwater systems may require additional genetic analyses from a multitude of DNA loci to successfully differentiate between species and biogeographic isolates of freshwater *Cladophora*.

CLADOPHORA AND ITS ENVIRONMENT

Cladophora is a ubiquitous macroalgae found in a wide range of habitats from freshwater lakes and streams and brackish estuaries to marine coastal environments (Dodds and Gudder 1992, van den Hoek 1963). Although this genus is found in a wide range of environments, it does have some fundamental physico-chemical requirements for successful population establishment and proliferation. These basic environmental pre-requisites as well as their influence on growth, photosynthesis and reproduction are discussed below.

Basic physical requirements

Substrate—*Cladophora* sp. are found in association with a wide range of substrates. Some species are intrinsically free floating (*C. fracta* var. *fracta*), some are usually found attached to a substrate but can survive as floating mats (*C. rivularis*), while others can form spherical aggregates, commonly referred to as 'lake balls' (*C. aegagropila*) (van den Hoek 1963, Niyama 1989). Most freshwater species, however, are inherently sessile spending most of their life cycle attached to hard substrates (van den Hoek 1963). The typical naturally occurring hard substrate used by *Cladophora* sp. ranges from coarse gravel, to boulders and bedrock (Neil and Owen 1964). However, this macroalgal genus is also found growing on man-made structures (e.g. break walls, piers) and/or debris (e.g. wood, iron) (Neil and Owen 1964, Bellis and McLarty 1967). With the appearance of dreissenid mussels in the Laurentian Great Lakes, *Cladophora* has adopted another type of substrate readily attaching itself to mussel shells (personal observation). The dreissenids may also be significantly increasing substrate availability by increasing water clarity, thereby increasing the potential depth of *Cladophora* habitation.

The chemical composition of the preferred substrate is not well understood. *Cladophora* sp. have been found on sandstones and limestone but zoospores of *C. glomerata* have been shown to avoid calcareous rocks, an unexpected phenomenon considering this species high

requirement for calcium (see below) (Whitton 1970 and references therein). While the limitations of growth of *Cladophora* imposed by substrate type are unclear, some of the factors thought to be important are slope, surface roughness, chemical composition, stability and hydrodynamic forces (Dodds and Gudder 1992).

Flow—Almost a century ago, observations were made noting that stagnant water bodies were virtually devoid of Cladophoraceae algae (Fritsch 1906). Later investigations clearly identified a link between the presence of *Cladophora* sp. and water movements (e.g. Dodds and Gudder 1992, Neil and Owen 1964). The main hypothesis for flow requirements of *Cladophora* sp. likely relates to its cellular structure and how that influences nutrient and waste exchange at the plant-water boundary. The cell wall of *Cladophora* is made up of three distinct layers: 1. inside layer of cellulose, 2. adjacent layer of pectin and 3. a final insoluble possibly chitin-based layer (Cronshaw et al. 1958, Rani and Bharathan 2000). The insolubility of the outermost layer may be a limiting factor in the molecular diffusion of substances across the cell wall. Since molecular diffusion is a gradient driven process, steep gradients generated by high water velocities likely favor rapid nutrient and waste exchange at the cell surface (Herbst 1969, Dodds 1989). Convincing evidence of an 'inherent current demand' by freshwater algae was first presented by Whitford and Schumacher (1961), showing increased uptake of phosphorus (^{32}P) in moving compared to static waters. The erosion of the boundary layer at the plant/water interface under swift flowing conditions allows *Cladophora* sp. to make more efficient use of available nutrients (Whitford and Schumacher 1961, Adams and Stone 1973). This may be particularly relevant to areas where nutrient concentrations are marginally limiting yet high turbulence still allows for growth (Neil and Owen 1964). While in rivers and streams an inherent unidirectional water motion is present, in the lacustrine littoral zones water movements are a result of waves and currents. While wave action is important, currents are likely more important in generating enough turbulence for *Cladophora* sp. growth (Neil and Owen 1964). Particularly, long shore currents can be significant contributors of water motion often reaching speeds of $15 \text{ cm} \cdot \text{s}^{-1}$ (Neil and Owen 1964). In fact, velocities of $15 \text{ cm} \cdot \text{s}^{-1}$ and greater are thought to be needed to produce relatively steep diffusion gradients at the interface between sessile organism and the surrounding water (Whitford and Schumacher 1961). While not yet clearly understood, physiological rates such as growth and photosynthesis of freshwater algae have been linked to current velocity, as such it becomes important to understand this aspect of *Cladophora* sp. ecology from a management perspective.

Temperature—Temperature tolerances and optimum requirements for survival, growth and/or reproduction are thought to be some of the most important variables limiting the geographical distribution of *Cladophora* sp. (Breeman et al. 2002). Particularly, in the Laurentian Great Lakes, temperature is thought to be one of the important variables influencing *Cladophora* growth and senescence cycles (Herbst 1969, Moore 1975). While there seems to be a consensus in the literature that temperature exerts a significant control over the growth of this macroalgae, it is still unclear which temperatures lead to maximum growth. *Cladophora glomerata* sampled in Sweden could grow vigorously between 7 and 15EC (Waern 1952 as cited in Herbst 1969), while this same species sampled in Green Bay, Lake Michigan showed optimum photosynthetic temperatures between 28-31EC (Lester et al. 1988). In Lake Erie, *Cladophora* has been found to

begin rapid growth at temperatures of 10 or 11EC (Moore 1977 and references therein) The wide range of reported optimum temperatures may be due to a number of reasons, such as differences in nutrient levels used in the various experiments, but also and maybe more importantly, due to possible physiological ecotypes from different geographical regions (Hoffman and Graham 1984, Wong et al. 1978). However, on average, *Cladophora* sp. demonstrate good growth between 15 and 25EC (e.g. Bellis 1968a, Hoffman and Graham 1984, Wong et al. 1978).

In temperate climates, *Cladophora* frequently has two annual peaks in biomass, the first occurring in the spring (May/June) and a second often reduced peak in the fall (September/October) (Bellis and McLarty 1967, Wong et al. 1978). During the summer months there is typically a rapid reduction in *Cladophora* biomass (die-off) which is commonly thought to be directly associated with increases in temperature (Graham et al. 1982, Whitton 1970), although some evidence disputes the involvement of temperature in the summer die-offs in Lakes Erie (Mantai 1987) and Michigan (Lester et al. 1988). From a phylogenetic point of view, a summer die-off due to high water temperatures is likely given that natural selection pressures can lead to colder thermal tolerance, but this at the expense of a tolerance to higher temperatures (Breeman et al. 2002). It is crucial that the direct effects of temperature on *Cladophora* and the likely interactions with parameters such as nutrients and light that ultimately determine growth rates and biomass be elucidated. The high densities that *Cladophora* stands can reach by midsummer may also reduce water circulation and turbulent flow required to maintain these dense stands possibly contributing to die off at such times. Such investigations would shed some light on the general ecology of this macroalgal genus and identify the presence or absence of ecotypes which will be critical in the management of *Cladophora* sp. in the Laurentian Great Lakes basin.

Light—As primary producers *Cladophora* sp. are obligate photoautotrophs, and they cannot maintain vegetative stands without light. Different autotrophs require different levels of light to reach and maintain optimum photosynthesis and by extension growth rates. *Cladophora* sp. vary in their ability to thrive in high and/or low light conditions, *C. basiramosa* is shade-loving while *C. glomerata* thrives in high light environments (van den Hoek 1963). In the last four decades there have been numerous studies on the minimum and saturating light requirements of *Cladophora* sp. (e.g. Adams and Stone 1973, Lester et al. 1988, Leukart and Hanelt 1995, Lorenz et al. 1991). There has been some debate in the past on the light requirements of *Cladophora* (Mantai 1974, Wood, 1975), and more recent studies do not clearly reconcile these differences (e.g. Lester et al. 1988, Lorenz et al. 1991). For example, Lester et al. (1988) reported minimal light requirements ranging from 44 to 104 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for Lake Michigan *C. glomerata* incubated in closed chambers under constant flow conditions. Graham et al. (1982), on the other hand, reported minimum light requirements between 25 and 35 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for cultured *C. glomerata*, originally from Lake Huron, and maintained at temperatures ranging from 5-20EC. However, at temperatures above 25EC minimum light requirements ranged between 35 and 75 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Graham et al. 1982). Overall, field studies have reported minimum light requirements ranging between 28 and 190 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ while laboratory studies find minimum requirement ranges between 29 and 75 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Graham et al. 1982, Lester et al. 1988, Leukart and Hanelt 1995, Lorenz et al. 1991). The large variability in reported light requirements could be related to the

experimental methods (e.g. estimating growth by filament length extension, O₂ evolution, or ¹⁴C fixation) and incubation periods (less than 1 h to multiple weeks) utilized. For example, Wood (1975) pointed out that experiments using ¹⁴C as a tracer of photosynthesis may well underestimate these rates if the change in pH and associated precipitation of carbonates (i.e. Ca¹⁴CO₃ and Mg¹⁴CO₃; *see below*) is not taken into account. It is likely that the minimum light requirement for *Cladophora* sp. is near 30 :mol•⁻²•⁻¹, a conclusion based on the field study conducted by Lorenz et al. (1991). These authors visually investigated the depth range of *C. glomerata* in western Lake Erie, measuring the diffuse light attenuation at each site and back-calculating an average daily light intensity requirement of 28 :mol•⁻²•⁻¹. This inherent light requirement can be very useful in lake management practices, e.g. locating depths for water intake pipes where *Cladophora* are not likely to interfere (Lorenz et al. 1991) or locating depths for sewage treatment outflow pipes which are not likely to supply phosphorus directly to *Cladophora* sp. beds. Historically, in Lake Erie *Cladophora* sp. are not known to grow significantly below 4 m while in Lake Ontario, the much clearer waters between Toronto and Hamilton have tended to support growths up to 7.6 m depth (Neil and Owen 1964). The extent to which light will penetrate a water body will inevitably influence the area which can be colonized by *Cladophora* sp. and thereby the quantity of macroalgae that can be produced (Neil and Owen, 1964). Finally, the role of light in influencing *Cladophora* sp. is not limited to its intensity but is also related to the duration of exposure, i.e. the photoperiod (Hoffman and Graham 1984, Storr and Sweeney 1971).

Recent increases in transparency in nearshore areas of the Great Lakes because of high dreissenid mussel filtration capacity may have extended the depth of light penetration over hard substrates and contributed to more extensive and denser stands of *Cladophora* (Fahnenstiel et al. 1995). Also *Cladophora* as with other green algae (Donahue et al 2003) may have a high tolerance to ultraviolet (UV) light which lets them flourish in shallow transparent environments. Recent increases in UV-B and water clarity due to dreissenid filtration may be selectively favoring *Cladophora* over other algal groups.

Basic chemical requirements

Major ions and pH—Particularly hard and alkaline waters are the environments generally occupied by *Cladophora* (Neil and Owen 1964, Whitton 1970). The requirement for calcium (Ca) and possibly magnesium (Mg) may be the main reason for the restriction to hard waters. While the Ca and Mg requirements for survival (1.2 mg•L⁻¹ Ca and 0.7 mg•L⁻¹ Mg) of *Cladophora glomerata* are below trace levels (ca. 5 mg•L⁻¹), the needs for growth (i.e. branching) and sporulation are much higher (64.0 mg•L⁻¹ Ca and 108.5 mg•L⁻¹ Mg) (Bellis 1968b). In addition to the basic cellular Ca (e.g. elongation and division of cells) and Mg (e.g. cofactor for internal phosphatase activity) requirements, *Cladophora* has an elevated demand for Ca in its cell wall (Lin 1977, Sikes 1978). In healthy growing cultures, over 95% of the total Ca found in association with *Cladophora* is loosely bound (i.e. exchangeable) to the pectinic layer of the cell walls (Sikes 1978). Some forms of pectin (i.e. low methoxyl (LM) pectin) are inherently dependent on Ca for their gelling properties and the higher the Ca content the stronger the gel

that is formed (Hoejgaard 2002). While, to our knowledge, there is no evidence on the type of pectin found in *Cladophora* cell walls, the above normal need for Ca suggests that LM pectin could be the main pectin in the cell walls of this macroalgae. It has also been suggested that *Cladophora* precipitate carbonates (Ca- and MgCO_3) which could then be used as a pH buffering system during reductions in pH incurred through respiration (Wood 1975). Silicon has also been demonstrated as an essential nutrient for *Cladophora* with a structural role as well (Moore and Traquair 1976). Silicon deficiency (measured as germanium (specific inhibitor of silicic acid metabolism) toxicity) results in incomplete cross walls production and stunted cell division. A very high requirement for sulfur and boron has also been identified but the reasons for these above average needs are yet unknown (Gerloof and Muth 1984). Silicon concentrations having been rising in the lower Great Lakes since P management began but the dense growths of *Cladophora* which occurred under low Si conditions prior to P reduction suggest that Si was not limiting *Cladophora*.

In terms of alkalinity, *Cladophora* are typically restricted to waters with a pH between 7 and 9 (Bellis 1968b, Whitton 1970). It is still unclear what the physiological reasons are for this pH restriction but it may be related to the form of inorganic carbon available at different pHs (Sheath and Burkholder 1985). With respect to carbon availability, the main species of dissolved carbon between pH 7 and 9 is bicarbonate (HCO_3^-). While *Cladophora* can utilize HCO_3^- through the activity of carbonic anhydrase, not all aquatic plants can, many require carbon as dissolved CO_2 for carbon fixation (Raven et al. 1982, Sikes 1978). The lower physiological pH limit of *Cladophora* could be a manifestation of competition with other macroalgae and macrophytes while the higher physiological pH limit of *Cladophora* may be related to the Ca requirements of this macroalgae. At higher pH, Ca readily precipitates as CaCO_3 and may become biologically unavailable. Moreover, as for all other organisms, high pH in the surrounding environment can lead to ammonium (NH_4^+) toxicity (Robinson and Hawkes 1986) as well as other physiological disturbances.

Macronutrients (N and P)—It has been suggested that while seasonal differences in *Cladophora* productivity is likely related to variations in temperature and perhaps light availability, productivity within and between water bodies during the growing season are likely related to different nutrient levels (Adams and Stone 1973). Some studies have demonstrated nitrogen limitation of growth in both marine and freshwater *Cladophora*, at least temporarily during the growing season (Mason 1965, Peckol et al. 1994, Planas et al. 1996). However, most studies have identified phosphorus as the first and foremost rate limiting nutrient for *Cladophora* growth in freshwater ecosystems (e.g. Auer and Canale 1980, Herbst 1969, Painter and Kamaitis 1987, Wong and Clark 1976). Typically, *Cladophora* sp. tend to be restricted to waters approaching eutrophic conditions (van den Hoek 1963). Not surprisingly, relationships between phosphorus concentrations in the water and the predominance of *Cladophora* have been demonstrated on more than one occasion (e.g. Auer and Canale 1980, Chételat et al. 1999, Painter and Jackson 1989, Painter and Kamaitis 1987). The identification of which nutrient is actually limiting growth in natural systems is not a simple task. Plant tissue critical nutrient requirements can be determined and used as thresholds for identifying nutrient limitation. Early studies have determined these minimum requirements for *Cladophora* and minimum cell quotas of 0.5-1.6

mg·g⁻¹ dry wt and 11-15 mg·g⁻¹ dry wt have been reported for P and N, respectively (Auer and Canale 1982a,b, Gerloff and Fitzgerald 1976 in Millner et al. 1982, Wong and Clark 1976). Relationships between external P and internal tissue P concentrations have been demonstrated (Lorenz and Herdendorf 1982, Wong and Clark 1976), however, the variability in external concentrations cannot reliably and consistently be related to the nutritional status of macroalgae such as *Cladophora* which are known to accumulate surplus levels of luxury P during time of plenty for use during times of deficiency (Lin 1971). Furthermore, instantaneous measurements of dissolved nutrient levels may not necessarily reflect recent past conditions, on which *Cladophora* biomass stands and growth rates may be more dependent (Dodds 1991b).

The concentrations of P found in plant tissue are much more stable and representative of average P supply in a particular location (Auer and Canale 1980). Nuisance growth of *Cladophora* have often been associated with urban areas, specifically, their proximity to nutrient sources such as water and sewage treatment plant effluent pipes or river mouths (e.g. Herbst 1969, Neil and Owen 1964, Painter and Kamaitis 1987). Internal P concentrations have been clearly shown to mirror the distance from a nutrient source and be related to urbanization (Lin 1971, Painter and Kamaitis 1987). Internal P concentrations can also reflect pulse inputs of P which can occur following rainfall events (Lin 1971, Hiriart-Baer et al. in preparation). During such storm events, storm sewers can overflow, wastewaters can by-pass water treatment plants and river discharge can increase significantly leading to relatively large pulse inputs of phosphorus now available for macroalgal growth (Lin 1971). Dreissenids may have increased the supply of P available in the nearshore areas of the lower Great Lakes as they harvest planktonic organisms and regenerate nutrients benthically (Hecky et al. submitted). While *Cladophora* abounds in the Lower Great Lakes, other issues aside from phosphorus surround the success of this macroalgae in this Great Lakes. Its reproductive and overwintering capacity (see REPRODUCTION section below) also plays a major role in the success of *Cladophora* (Rosemarin 1985).

Vitamins—Most organisms require vitamins for normal growth and development including *Cladophora*. Some of the important vitamins that have been recognized in the *Cladophora* literature are vitamins B₁ (or thiamine) and B₁₂ (or cobalamin). Direct requirements for vitamin B₁ have been demonstrated whereby increases in thiamine concentrations elicited increases in growth rates (Moore and McLarty 1975). Similar essential requirements for vitamin B₁₂ have also been shown (Gerloff and Muth 1984, Hoffmann 1990). Only microorganisms such as bacteria and phytoplankton can synthesize these B vitamins *de novo*. As such, thiamine and cobalamin must be supplied externally. In addition to microbial sources in natural waters, sewage and soil runoff can be significant inputs of these vitamins and increased concentrations by such means have been suggested as possible contributors to excessive growth of *Cladophora* (Moore and McLarty 1975). The increased bacterial activity associated with biodeposits of dreissenids may not insure a good supply of these essential compounds in nearshore rocky areas where dreissenids and *Cladophora* are prominent.

CLADOPHORA BIOLOGY AND ECOLOGY

Growth and Photosynthesis

Freshwater *Cladophora* sp. in temperate environments typically undergo a conspicuous bloom, senescence and second bloom growth cycle starting in the spring (May/June) and ending in the fall (September/October) each year (Lorenz and Herdendorf 1982, Neil and Owen 1964, Whitton 1970). In streams this growth cycle has been related to flow hydrology, with winter promoting spring blooms in *Cladophora* through the systematic removal of primary consumers (Power 1992). While this may be a controlling factor in some streams and rivers, in lakes this annual growth cycle is more likely related to factors such as temperature and light. Storr and Sweeney (1971) developed a theoretical seasonal growth curve for *Cladophora* in Lake Ontario. This analysis was based entirely on water temperature and seasonal photoperiod and these two variables clearly predicted two distinct peaks in growth (June and September). The commonly observed summer decline was also depicted but was strictly related to temperature. Although this might suggest an overwhelming role of water temperatures in the traditional summer die off of *Cladophora* other factors may also play a role. For example, the production of zoospores and their subsequent expulsion leads to brittle filaments which may lead to this mid-summer sloughing/die-off (Dodds and Gudder 1992, Hoffman and Graham 1984). Alternatively, a development of ammonia toxicity due to increases in pH during levels of high growth (i.e. photosynthesis) could partly explain the summer drop in standing crop (Robinson and Hawkes 1986).

Under favorable conditions, growth rates can be relatively high and a maximum rate of 1.08 d^{-1} has been experimentally determined (Auer and Canale 1982b). Under natural conditions, the determination of growth rates is not an easy task, so very few studies report *in situ* rates. One study on the marine *C. vagabunda* reported maximum *in situ* growth rates of ca. 0.10 d^{-1} (Peckol et al. 1994). Although significantly lower, it is not surprising that in their natural environment, *Cladophora* do not consistently encounter optimum growing conditions allowing growth rates in the order of 1.08 d^{-1} . Even at reduced growth rates, *Cladophora* standing crops can be very high and biomass levels in the excess of $200 \text{ g dry wt} \cdot \text{m}^{-2}$ are not uncommon given sufficient nutrients and light (Auer and Canale 1980, Auer et al. 1982a, Kirby and Dunford 1981, Lorenz and Herdendorf 1982, Mantai et al. 1982).

The productivity, i.e. biomass, of *Cladophora*, although the end result, is inevitably controlled at the physiological level by photosynthetic rates that can be achieved during the growing season (Mantai 1974). Many studies have experimentally determined photosynthetic rates and significant variations in the data exist (Adams and Stone 1973, Jackson 1966, Mantai 1974, Wood 1975). Most laboratory derived photosynthetic rates have reported maximum values spanning ca. 10 to $50 \text{ mg C} \cdot \text{g dry wt}^{-1} \cdot \text{h}^{-1}$ (e.g. Adams and Stone 1973, Lester et al. 1988, Mantai 1974). This inconsistency reported in the literature may be related to the difficulty in measuring photosynthetic rates in organism like *Cladophora* which tend to sink and clump (Mantai 1974) or may be complicated by factors such as pH which can alter significantly during active photosynthesis resulting in carbonate precipitation (Wood 1975). Furthermore, varying degrees of acclimation, differences in nutrient levels, variations in light exposures and the possibility of ecotypic adaptations may all lead to disparate results. While *in situ* photosynthetic

experiments are likely to be the most informative, as for growth rates, the determination of such rates are not simple. Only one study to our knowledge has produced such rates and carbon fixation rates for *C. fracta* (Shoe Lake, Michigan) ranged between 0.26 to 5.39 mg·g⁻¹·h⁻¹ (Cheney and Hough 1983). This study measured seasonal rates of photosynthesis with peaks occurring in the spring and fall with summer rates being characteristically low.

Photosynthetic rates depend on temperature and light availability (Graham et al. 1982). Temperatures between 13 and 17°C are thought to elicit maximum photosynthetic rates although optimum temperatures of 28-31°C have been reported (Graham et al. 1982, Lester et al. 1988). While there has been some debate as to the light utilization efficiency of *Cladophora*, it is generally accepted that this genus photosynthesizes well under high light conditions (van den Hoek 1963). Light levels which seem to elicit maximum photosynthetic rates are in the order of 300-600 μmol·m⁻²·s⁻¹ but, similar to temperature, values as high as 790 and ca. 1000 μmol·m⁻²·s⁻¹ have been reported (Graham et al. 1982, Lester et al. 1988, Rivers and Peckol 1995). However, values as low as ca. 30 μmol·m⁻²·s⁻¹ have been shown to saturate photosynthesis (Leukart and Hanelt 1995), but photosynthetic light saturation levels are known to be temperature dependent (Doods and Gudder 1992). The interaction between temperature and light levels are study poorly understood and need further study as does the genetic constitution of the different isolates of *Cladophora* used in these comparisons.

Reproduction

The success of the *Cladophora* genus in such a wide range of habitats is partly related to its reproductive strategy. It can function as a perennial by successfully overwintering vegetatively in cold climates and can extend its growth reach by asexual reproduction through zoospore production (Rosemarin 1985). The perennial growth success is achieved by the production of resistant spores called akinetes. Although not well understood, the production of these thick-walled perennial structures is related to unfavorable environmental conditions. Specifically, some of the environmental cues thought to trigger akinete production in the Cladophorales *Pithophora oedogonia* are low temperatures, short photoperiods, nutrient depletion and dessication (Lembi and Spencer 1981, Spender et al. 1980). Overwintering akinetes in this species remain attached to rocks awaiting more favorable conditions, typically germinating in the spring when water temperatures reach 15°C (Spencer et al. 1980).

In lakes that freeze during the winter, akinetes are effectively dislodged by the scouring action of the ice sheet and not available as seed populations for *Cladophora* in the shallow nearshore zones. The depth of this akinete-free zone will of course depend on the thickness of the ice sheet which varies from year to year and lake to lake. It follows that most of the initial spring growth of *Cladophora* is located at depth leaving a band of shallow waters initially free of this macroalgae and typically colonized by other species such as *Ulothrix* and *Bangia*, in the early spring months in the Laurentian Great Lakes (Garwood 1982, Lorenz and Herdendorf 1982). In the months following akinete germination, sporulation begins increasing the population size at depth as well as contributing to the recolonization of the ice-scoured shallow zones of lakes (Hällfors et al. 1975, Rosemarin 1985). Similar to akinete production, zoosporogenesis and the

extent of sporulation is thought to be regulated by environmental parameters such as temperature (15-20EC), short photoperiods (8L:16D), low light intensity ($<100 \text{ } \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) and vitamin (B₁ and B₁₂) deficiencies (Hoffman and Graham 1984).

With the exception of the winter of 2002/2003, the Laurentian Great Lakes, in the last five years, have seen a trend in diminishing ice cover (Wisby 2002). Whether the reduction in ice-scouring in the Great Lakes is resulting in increased akinete winter-survival and thereby contributing to more rapid early spring growth of *Cladophora*, remains to be determined. But it should be noted that although nutrient availability plays an important role in the amount of *Cladophora* growth in the lower Great Lakes, its life cycle plays a significant role in its dominance in this region (Rosemarin 1985).

Biological Interactions

Biological interactions are inevitable in natural systems. Aquatic plants may have to compete with other species for resources, can function as a substrate or provide refuge for other organisms and are susceptible to predation by grazing organisms. Interspecific competition can occur through the indirect exploitation of resources, such as space or nutrients, or by direct interferences through allelochemical interactions and suppression (Wetzel 2001). In the case of *Cladophora* sp., few studies have looked at direct competition but results suggest that this macroalgae are capable of allelochemical interferences (Dodds 1991a). Interspecific competition has also been observed. In the Great Lakes, *Cladophora* sp. compete mainly with *Bangia atropurpurea* and *Ulothrix zonata*. *Ulothrix* is a cold water species (0-15EC) co-dominating the shallow waters (<1 m) with *Bangia* during the spring (Garwood 1982). As water temperatures rise above 10EC, *Cladophora*, which until then is found only in deeper waters (>1 m), starts displacing both *Ulothrix* and *Bangia*. While *Bangia* has a wide temperature tolerance range (2-26EC), the rapid growth rates of *Cladophora* quickly outcompete this species for space. During the summer months, *Bangia* finds refuge on rocky shores subject to heavy wave action, something *Cladophora* is unable to withstand (Garwood 1982).

Cladophora must also interact with the microscopic organisms that settle on its filaments. These organisms form a complex community of bacteria and microalgae. These epiphytes can create an environment where nutrients and light are competed for, although empirical evidence suggests otherwise (Dodds 1991a). The diversity of the algal epiphyte species composition varies between lake systems but the main algal groups found on *Cladophora* in the Laurentian Great Lakes are diatoms (e.g. *Cocconeis pediculus*), blue-green (e.g. *Lyngbya diguetii* and *Fischerella muscicola*) and red algae (*Chroodactylon* sp. a.k.a. *Asterocytis* sp.) although green algae (*Ulothrix* sp.) can also occur (Stevenson and Stoermer 1982, Sheath and Morison 1982, Lowe et al. 1982). The epiphytic biomass and its distribution on *Cladophora* tufts will partly depend on the water movement regime. Fast moving waters limit the colonization capability of epiphytes (cf Bergey et al. 1995). Similarly, epiphytic biomass measured as chlorophyll *a*, tends to decrease as you move from the basal to the apical portions of the *Cladophora* tufts (Dodds 1991c). Current velocity is significantly reduced in the basal portions of the tufts compared to the apical wave swept parts of the plant (Dodds 1991c). Nutrient concentrations can also influence *Cladophora*

epiphytes, particularly the structure of the epiphytic species composition responds to nutrient availability (Marks and Power 2001). Compared to the other macroalgae in the Great Lakes, *Cladophora* is a particularly suitable host for epiphytes, a quality attributable to its cellulose wall (Lowe et al. 1982). On the other hand the mucilaginous cell walls of *Bangia*, *Ulothrix* and *Stigeoclonium* result in little colonization by epiphytic organisms. While epiphytes may not always be beneficial to *Cladophora*, they do play a significant role in littoral habitat food webs. They are significant prey to grazers such as mayfly nymphs, caddis fly larvae and snails, which in turn are prey for other organisms such as fish (Dodds 1991a, Sarnelle et al. 1993). Grazing of epiphytes may actually stimulate growth in *Cladophora* by supplying nutrient through regeneration processes or simply by reducing epiphytic biomass thereby minimizing the competition between host and epiphyte (Sarnelle et al. 1993). Less well known is the extent to which other periphyton for example the microalgal epilithon can compete with *Cladophora* for nutrients. The obvious advantage of the architecture of *Cladophora* growth allows it grow out of the boundary layer on the rocky surfaces which can limit nutrient and carbon dioxide availability to the epilithon (Hecky and Hesslein 1995). Buoyant filamentous growth allows *Cladophora* to access the overlying waters and to reduce the boundary layer through turbulent action in the wave zone and from longshore currents. Microalgal epilithon will not be able to take advantage of excess nutrients and carbon dioxide in the same manner and their growth can eventually be limited by *Cladophora* shading in dense stands.

Cladophora itself, is not a preferred food source, because it's cell wall composition is likely a deterrent to primary consumers not adapted to feeding on large coarse materials. Some stream organisms are well adapted morphologically and behaviorally to effectively graze upon this macroalgae, for example, some caddisfly larvae (e.g. *Tinodes waeneri* and *Agapetus celatus*) and crayfish species (e.g. *Pacifastacus leniusculus* and *Orconectes propinquus*) (Creed 1994, Duddley and D'Antonio 1991, Guan and Wiles 1998, Harrison and Hildrew 2001). Waterfowl may also graze *Cladophora* (L. F. Moore, OWWRC, personal communication). While significant grazing may occur in streams, significant reductions in biomass due to grazing has not been demonstrated for lake systems.

THE PAST, PRESENT AND FUTURE OF *CLADOPHORA* IN THE LAURENTIAN GREAT LAKES

The Laurentian Great Lakes are not foreign to instances of eutrophication, localized or widespread. In the 1960s, Lakes Erie and Ontario supported significant productions of both planktonic and benthic algae, clear signs of eutrophication of these fresh waters. Nearshore waters were dominated by *Cladophora* sp. resulting in vast accumulations of plant material on lake shorelines during the summer months. Both littoral and pelagic primary production were largely a consequence of excess nutrient inputs, specifically phosphorus from wastewater discharge. In 1972, P abatement strategies recommended by the International Lake Ontario - St. Lawrence River Water Pollution Board (ILOWPB) were implemented through legislation by the government of Canada, reducing the allowable phosphate content of household detergents down to 5% (Stevens and Neilson 1987). In that same year, the Great Lakes Water Quality Agreement (GLWQA) was signed and wastewater treatment plants were now required to upgrade their treatment facilities to achieve effluent total P concentrations of no more than 1 mg TP·L⁻¹. By

the early 1980s, both Lakes Erie and Ontario showed clear signs of recovery from eutrophication. The legislated reductions in P had been successful, and excessive algal blooms had all but disappeared. In the 1990s, however, the proverbial tide had turned. Nearshore benthic algal blooms were once again increasing in frequency, abundance and spatial scale. In 2002, the nearshore waters of Lakes Erie, Ontario, Michigan and Huron were all showing signs of excess nutrient inputs, supporting large benthic algal blooms (REF; Bob you mentioned you might have a reference here?). *Cladophora* had returned.

The causal factors of this resurgence, however, are unclear. Phosphorus loadings to the lakes have significantly improved since the 1960s. The loadings to Lakes Huron, Superior and Michigan were consistently below target levels (4300, 3400 and 5600 metric tonnes \cdot y $^{-1}$) between 1981 and 1992 and the loadings for Lakes Ontario and Erie were at or below targets (7000 and 11000 metric tonnes \cdot y $^{-1}$) during that same period (Neilson et al. 1995). Given this apparent stability of P loadings to the Great Lakes, the search for the causal factors of increased littoral algal production remains elusive. During the last decade, the lower Laurentian Great Lakes have experienced ecological destabilization following the arrival of a number of exotic species, notably the zebra and quagga mussels, in addition to human population expansion and changing land use activity practices. These large lake systems, in particular, Lakes Ontario, Erie and Michigan are deemed lakes in transition, adjusting to changing chemical and biological processes. Currently, investigations into the role of dreissenid mussels on phosphorus cycling in nearshore waters of Lake Erie are underway. Dreissenid mussels were first spotted in Lake St-Clair in 1988, and today mussel populations are well established all around Lakes Erie, Ontario, Michigan and Huron (Charlton 2001). It has been proposed that dreissenid mussels can lead to the eutrophication of nearshore waters in lacustrine systems (Hecky et al submitted). The re-organization of lake food web structures and re-partitioning of critical nutrients (eg. phosphorus) between the pelagic and littoral lake habitats has been hypothesized as one way dreissenid mussels can transform freshwater ecosystems (Strayer et al. 1999). While nutrient loadings may not have changed in the lower Great Lakes since the invasion of dreissenid mussels, the sequestering of nutrients in shallow waters by these benthic organisms may effectively be fertilizing nearshore shallow waters and resulting in increased benthic algal growth. Furthermore, the filtration activities of these mussels may be favoring benthic primary production by *Cladophora* by increasing water clarity and uv penetration which reduces viable benthic habitat for many benthic algal species but may favour green algae like *Cladophora* (Donohue et al 2003).

Lake internal processes are not the only changes that have been occurring in the last few decades. Reduced ice cover, longer growing seasons and erratic storm patterns, all reflections of global variability and possibly indicative of climate change, may all also be contributing to the recent increases in benthic plant productivity in the Great Lakes. As previously discussed, *Cladophora* sp. overwinter in the form akinetes firmly attached to hard substrates. The presence of ice on lakes can effectively remove these perennial structures in the zone scoured by a gently moving ice sheet thereby reducing the amount of ready to bloom biomass. The thickness, persistence and extent of movement of the ice sheet will undoubtedly influence the extent of the akinete free zone in the nearshore waters. It is no surprise that there exists interannual variability in the degree of ice cover, however, the extent and duration of ice cover over the Great Lakes has

decreased extensively in the last decade (Wisby 2002). Reduced winter ice scouring and the associated reduced akinete dislodgement may be allowing a jump start in spring growth over a larger area of the nearshore zone. Changes in the frequency and severity of storms may also have a significant impact on the nutrient loading patterns to the Great Lakes and particularly storm sewer discharges and consequently on our decisions of resource allocations for controlling inputs to the lakes. Currently, storm water management infrastructure is limited, however, awareness of the significant inputs of nutrients that can occur through storm water runoff is increasing.

Alternatively, there are concerns that population growth rates are exceeding the gains achieved by improved wastewater treatment and control measures that only address concentrations at end of pipe rather than total loadings. This combination of circumstances may be leading to localized eutrophication. Simply considering population growth, P inputs can significantly increase over time if guidelines remain unchanged during that same period. Estimates of municipal (human derived) P inputs from Toronto are presented in Table 1. Population growth alone in Toronto has significantly increased P loading estimates to Lake Ontario with 2002 estimates reaching 1953 levels. This clearly demonstrates the importance of bridging the gaps between water and wastewater treatment plant infrastructure updates, effluent guidelines and population growth rates (Chambers et al. 2001). However, P concentrations in open waters are still meeting the GLWQA guidelines of $< 10 \mu\text{g} \cdot \text{L}^{-1}$, the open water nutrient dynamics currently seem to be unaffected by the increased nearshore loadings of nutrients.

Controlling the excessive growth of *Cladophora* in the new millennium is a foreseeable challenge given the complexity of change the Laurentian Great Lakes are experiencing. Many individual, yet, ultimately interacting issues need to be investigated for the development of optimum and enduring management solutions. For example, the role of dreissenid mussels in altering the nearshore environment of the Great Lakes must be understood. While present in the Great Lakes since the late 1980s, the consequences of their presence for the nearshore environment through their re-engineering of nutrient distributions and cycling (Hecky et al submitted) may only be coming apparent now. The consequences of this re-engineering of P fluxes between the pelagic and littoral lake habitats may effectively be fertilizing nearshore shallow waters resulting in increased benthic algal growth. Furthermore, the filtration activities of these organisms may be increasing the available benthic habitat of *Cladophora* by increasing water clarity. These are some ways in which mussels may be transforming these freshwater ecosystems (Hecky et al submitted; Strayer et al. 1999). We must also understand how current land use practices and climate change are impacting point and non-point sources of nutrients to these large lakes. Is population growth significantly increasing the total load of nutrients to the nearshore? Are less frequent but more severe storms altering the contribution of non-point nutrient inputs to the overall nearshore nutrient budget? Understanding the relative contribution of the point and non-point sources of nutrients and the transformation of the internal lake processes by dreissenids will allow the development proper management decisions. Do funding resources need to be diverted to the construction of storm water management infrastructure or should they be directed towards research and development of technology for improved nutrient removal processes? Last but not least, the taxonomy of *Cladophora* needs to be elucidated if we are to understand the ecology of this filamentous green macroalgae in the Great Lakes. We must answer the questions: Are there are different *Cladophora* ecotypes in the Great Lakes? If so,

what are their individual ecological requirements? If there are among and between lake differences in *Cladophora* requirements, these must be taken into consideration from a management perspective. The elucidation of the role of these various internal and external lake influencing processes are only a few of the questions that need to be addressed if we are to provide long term solutions to manage the luxurious growth of *Cladophora* in the Laurentian Great Lakes.

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TABLE 1. Estimates of P inputs to Lake Ontario from Toronto over time.

Year	Population (x10 ⁶)	Water Use ^a (L•capita•d ⁻¹)	P in effluents ^b (mg•L ⁻¹)	Total input (tonnes•d ⁻¹)
1912	0.5	343	4.3	0.74
1953	1.2	343	4.3	1.77
1991	3.9	343	1	1.34
1996	4.3	343	1	1.47
1998	4.6	343	1	1.58
1999	4.7	343	1	1.61
2000	4.8	343	1	1.65
2001	4.9	343	1	1.68
2002	5.0	343	1	1.72

^asource: <http://cbc.ca/news/indepth/background/groundwater2.html>

^bPrior to 1972, a conservative estimate of P inputs from municipal waste of 4.3 mg•L⁻¹ was derived from the estimated value of 540 gP•capita•y⁻¹ (Sly 1976). Post 1972, the environmental effluent guideline value of P concentrations is used.

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