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# Environment Canada

## Water Science and Technology Directorate

Direction générale des sciences et de  
la technologie, eau  
**Environnement  
Canada**

***CLADOPHORA* RESURGENT AND  
REVISITED:  
A BRIEF LITERATURE REVIEW**

V.P. Hiriart-Baer, L.M. Campbell, S.N. Higgins,  
M.N. Charlton, L.F. Moore, S.J. Guldorf and  
R E. Hecky

WSTD Contribution No. 07-252

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***Cladophora* resurgent and revisited:  
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by

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### **NWRI RESEARCH SUMMARY**

#### **Plain language title**

Update on the knowledge of *Cladophora* ecology in the Great Lakes

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

In recent years *Cladophora* nuisance growth in the Laurentian Great Lakes has shown a resurgence. In the 1960s and 1970s nuisance growth levels of *Cladophora* were a symptomatic response to lake eutrophication. Nutrient abatement strategies successfully curbed these nuisance benthic algal blooms. With lake-wide nutrient targets being attained in most of the Great Lakes, the cause of the resurgence of *Cladophora* is perplexing. This manuscript briefly reviews the ecophysiology of *Cladophora* known to date in efforts to bring our knowledge of this macroalgae up to date.

#### **Why did NWRI do this study?**

1. To bring our level of knowledge of *Cladophora* up to date in the context of the resurgence of nuisance blooms of this macroalgae despite lake wide phosphorus targets being met.

#### **What were the results?**

A review of the literature shows that *Cladophora* management may require a nearshore waters nutrient management approach.

#### **How will these results be used?**

The results will be published to update our knowledge of the ecophysiology of *Cladophora* in the Great Lakes.

#### **Who were our main partners in the study?**

University of Waterloo, Ontario Water Works Research Consortium and Ontario Clean Water Association

#### **Abstract**

Three decades ago, blooms of *Cladophora* sp. were common along the shores of Lakes Erie, Ontario, Michigan and Huron. Links to excess inputs of phosphorus to these lakes were established and phosphorus (P) 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 even 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, in regards to the invasion of exotic species, climate change and population growth.

## **Nouveaux épisodes de prolifération de *Cladophora* : survol de la littérature**

Véronique P. Hiriart-Baer, Linda M. Campbell, Scott N. Higgins, Murray N. Charlton, Laurence F. Moore, Stephanie J. Guildford et Robert E. Hecky

### **Sommaire des recherches de l'INRE**

#### **Titre en langage clair**

Mise à jour des connaissances sur l'écologie de la *Cladophora* dans les Grands Lacs.

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

Au cours des dernières années, la prolifération de *Cladophora* dans les Grands Lacs laurentiens est redevenue problématique. Dans les années 1960 et 1970, la prolifération de *Cladophora* était reliée à l'eutrophisation des lacs. Les stratégies qui ont alors été mises sur pied pour réduire la présence de nutriments ont permis de freiner la prolifération d'algues benthiques. Les niveaux cibles de nutriments étant atteints dans la plupart des Grands Lacs, la nouvelle prolifération de *Cladophora* soulève plusieurs questions. Le présent document permet de mettre à jour nos connaissances sur la *Cladophora* en résumant les données actuelles sur l'écophysiologie de cette macroalgue.

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

Il nous permet également de mettre à jour nos connaissances dans le contexte d'une nouvelle prolifération de cette macroalgue, et ce, malgré l'atteinte des niveaux cibles de phosphore.

#### **Quels sont les résultats?**

Un survol de la littérature nous montre qu'une approche axée sur la gestion des nutriments présents à proximité du rivage pourrait être nécessaire afin de maîtriser la croissance de la *Cladophora*.

#### **Comment ces résultats seront-ils utilisés?**

Les résultats seront publiés afin de mettre à jour nos connaissances sur l'écophysiologie de la *Cladophora* dans les Grands Lacs.

#### **Quels étaient nos principaux partenaires dans cette étude?**

L'Université de Waterloo, l'Ontario Water Works Research Consortium et l'Agence ontarienne des eaux.

#### **Résumé**

Il y a trois décennies, les épisodes de prolifération des différentes espèces de *Cladophora* étaient fréquents le long des rives des lacs Érié, Ontario, Michigan et Huron. Des liens ont alors été établis avec l'apport excessif de phosphore. Des stratégies de réduction, adoptées dans le cadre de l'Accord de 1972 relatif à la qualité de l'eau dans les Grands Lacs, ont permis de limiter les épisodes de prolifération. Dans les dernières années, les problèmes de prolifération excessive de *Cladophora* sont redevenus fréquents aux abords des rives, même

après avoir atteint les objectifs de concentration en phosphore. Dans le présent document, les connaissances actuelles sur la taxonomie, la morphologie, la biologie et l'écologie générale de la *Cladophora* sont passées en revue. Les causes possibles de sa prolifération actuelle dans les Grands Lacs sont aussi analysées, particulièrement en lien avec l'invasion d'espèces exotiques, les changements climatiques et l'accroissement de la population.

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## 1 INTRODUCTION

The genus *Cladophora* are a group of Chlorophyta macroalgae of which both marine and freshwater species are found. In fresh waters, large blooms of *Cladophora* are typically reflections of nutrient enrichment often resulting in local fouling of beaches and waterfront properties. Three decades ago, large mats of decaying plant material were a common sight in the North American Great Lakes. While nutrient management strategies drastically decreased algal blooms in the 1980s to mid 1990s, recent years have seen renewed incidence of *Cladophora* blooms. However, the causal nature of this renewed growth remains unclear. This paper reviews our current state of knowledge of the biology and ecology of these high nutrient organisms in order to better understand the etiology of this resurgence.

## 2 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 interspecies differentiation a difficult task (e.g. apical cell diameter: *C. rivularis*, 19 - 45  $\mu\text{m}$ ; *C. fracta* 16 - 27  $\mu\text{m}$ ; van den Hoek 1963). Consequently, *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 two studies to date has attempted a similar approach in freshwaters (Marks and Cummings 1996; Ross et al. 2006). 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*. However, new techniques such as intersimple sequence repeats (ISSR) have recently been success in differentiating a North American Great Lakes *Cladophora* clade from north American group of samples (Ross et al. 2006). Furthermore, within the Great Lakes clade, two genetically distinct groups were identified: 1) a Lake Erie and Ontario group and 2) a Lake Huron and Michigan group. The significance of this finding in terms of management control remains to be determined.

### 3 *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.

#### 3.1 Basic physical requirements

##### 3.1.1 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).

### 3.1.2 Flow

Almost a century ago, observations were made noting that stagnant water bodies were virtually devoid of *Cladophoraceae* (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. an outer 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 ( $^{32}\text{P}$ ) 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 cm/s (Neil and Owen 1964). In fact, velocities of 15 cm/s 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.

### 3.1.3 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 15°C (Waern 1952 as cited in Herbst 1969), while this same species sampled in Green Bay, Lake Michigan showed optimum photosynthetic temperatures between 28-31°C (Lester et al. 1988). In Lake Erie, *Cladophora* has been found to begin rapid growth at temperatures of 10 or 11°C (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 perhaps 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 25°C (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 genus' general ecology and identify the presence or absence of ecotypes which will be critical in the management of *Cladophora* sp. in the Laurentian Great Lakes basin.

#### 3.1.4 Light

*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  $\mu\text{E}/\text{m}^2/\text{s}$  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  $\mu\text{mol}/\text{m}^2/\text{s}$  for cultured *C. glomerata*, originally from Lake Huron, and maintained at temperatures ranging from 5-20°C. However, at temperatures above 25°C minimum light requirements ranged between 35 and 75  $\mu\text{mol}/\text{m}^2/\text{s}$  (Graham et al. 1982). Overall, field studies have reported minimum light requirements ranging between 28 and 190  $\mu\text{mol}/\text{m}^2/\text{s}$  while laboratory studies find minimum requirement ranges between 29 and 75  $\mu\text{mol}/\text{m}^2/\text{s}$  (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,  $\text{O}_2$  evolution, or  $^{14}\text{C}$  fixation) and incubation periods (less than 1 h to multiple weeks) utilized. For example, Wood (1975) pointed out that experiments using  $^{14}\text{C}$  as a tracer of photosynthesis may well underestimate these rates if the change in pH and associated precipitation of carbonates (i.e.  $\text{Ca}^{14}\text{CO}_3$  and  $\text{Mg}^{14}\text{CO}_3$ ; see below) is not taken into account. It is likely that the minimum light requirement for *Cladophora*

sp. is near 30  $\mu\text{mol/m/s}$ , 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  $\mu\text{mol/m/s}$ . 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 (Hoffman and Graham 1984, Storr and Sweeney 1971). *Cladophora* dry weight production has been shown to increase significantly at optimal temperatures with an increase in photoperiod (12 to 14hr) (Storr and Sweeney 1971). On the other hand, reduced photoperiods, due to seasonal changes or unfavorable shaded environments, have been shown to increase zoospore production, a possible strategy to establish new growth in more favorable environments (Hoffman and Graham 1984).

Recent increases in transparency in nearshore areas of the Great Lakes because of high dreissenid 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.

## 3.2 Basic chemical requirements

### 3.2.1 Major ions and pH

Particularly hard and alkaline waters are the chemical 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 Ca and 0.7 mg/L Mg) of *Cladophora glomerata* are below levels found in most freshwater environments (ca. 5 mg/L), the needs for growth (i.e. branching) and sporulation are much higher (64.0 mg/L Ca and 108.5 mg/L 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  $\text{MgCO}_3$ ) 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).

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 ( $\text{HCO}_3^-$ ). While *Cladophora* can utilize  $\text{HCO}_3^-$  through the activity of carbonic anhydrase, not all aquatic plants can and many require carbon as



dissolved CO<sub>2</sub> 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<sub>3</sub> and may become biologically unavailable. Moreover, as for all other organisms, high pH in the surrounding environment can lead to ammonium (NH<sub>4</sub><sup>+</sup>) toxicity (Robinson and Hawkes 1986) as well as other physiological disturbances.

### 3.2.2 *Macronutrients (N and P)*

It has been suggested that while seasonal differences in *Cladophora* productivity are 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 dry wt and 11-15 mg/g 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* has 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 known 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. unpublished). 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 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 high phosphorus concentrations may contribute to the success of this macroalgae in the Great Lakes. Its reproductive and overwintering capacity (see Reproduction section below) also plays a major role in the success of *Cladophora* (Rosemarin 1985).

### 3.2.3 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 B<sub>1</sub> (or thiamine) and B<sub>12</sub> (or cobalamin). Direct requirements for vitamin B<sub>1</sub> have been demonstrated whereby increases in thiamine concentrations elicited increases in growth rates (Moore and McLarty 1975). Similar essential requirements for vitamin B<sub>12</sub> 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 insure a good supply of these essential compounds in nearshore rocky areas where dreissenids and *Cladophora* are prominent.

## 4 CLADOPHORA BIOLOGY AND ECOLOGY

### 4.1 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 flooding promoting spring blooms in *Cladophora* through the systematic removal of stream invertebrates (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  $1.08 \text{ d}^{-1}$  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.  $0.10 \text{ d}^{-1}$  (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  $1.08 \text{ d}^{-1}$ . Even at reduced growth rates, *Cladophora* standing crops can be very high and biomass levels in the excess of  $200 \text{ g dry wt/m}$  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 dependent at the physiological level on net 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 net photosynthetic rates have reported maximum values spanning, on average, between  $5$  and  $20 \text{ mg C/g dry wt/h}$  (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, photoperiod 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 net photosynthetic carbon fixation rates for *C. fracta* (Shoe Lake, Michigan) which ranged between  $0.26$  to  $5.39 \text{ mg C/g dry wt/h}$  (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  $17^{\circ}\text{C}$  are thought to elicit maximum photosynthetic rates although optimum temperatures of  $28$ - $31^{\circ}\text{C}$  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  $300$ - $600 \mu\text{mol/m}^2/\text{s}$  but, similar to temperature, values as high as  $790$  and ca.  $1000 \mu\text{mol/m}^2/\text{s}$

have been reported (Graham et al. 1982, Lester et al. 1988, Rivers and Peckol 1995). However, light saturation parameters ( $I_k$ ) as low ca. 30  $\mu\text{mol/m/s}$  have been reported for *Cladophora glomerata* (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 poorly understood and need further study as does the genetic constitution of the different isolates of *Cladophora* used in these comparisons.

#### 4.2 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 ice 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

(15-20°C), short photoperiods (8L:16D), low light intensity (<100  $\mu\text{E}/\text{m}^2/\text{s}$ ) and vitamin ( $\text{B}_1$  and  $\text{B}_{12}$ ) 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* especially in very shallow depths, 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, especially nuisance growths and die offs, its life cycle plays a significant role in its dominance in this region (Rosemarin 1985).

#### 4.3 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 (0-15°C) co-dominating the shallow waters (<1 m) with *Bangia* during the spring (Garwood 1982). As water temperatures rise above 10°C, *Cladophora*, which until then is found only in deeper waters (>1 m), starts displacing both *Ulothrix* and *Bangia* in shallow waters. While *Bangia* has a wide temperature tolerance range (2-26°C), the rapid growth rates of *Cladophora* quickly allow it to 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 grazer 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 to 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 light and nutrients in 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*. While significant grazing may occur in streams, significant reductions in biomass due to grazing has not been demonstrated for lake systems.

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

All the Laurentian Great Lakes have experienced eutrophication, either localized or widespread. In the 1960s, Lakes Erie and Ontario supported significant standing crops 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. By the early 1980s, the legislated reductions in P had been successful, and excessive algal blooms had all but disappeared. In the 1990s, however, 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 have been reported as supporting large benthic algal blooms, signs of excess nutrient inputs.

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/y) between 1981 and 1992 and the loadings for Lakes Ontario and Erie were at or below targets (7000 and 11000 metric tonnes/y) 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 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 nutrient enrichment 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 and transformation 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 moving

ice sheets thereby reducing the amount of overwintering 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 higher initial spring seed biomass 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. 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 the end of the pipe rather than total loadings to the environment. This combination of circumstances may be leading to localized nutrient enrichments. Considering population growth in the Greater Toronto Area (GTA) in combination with improved P removal treatments and strategies to reduce water effluent flows, P loadings to the aquatic environment have decreased since 1991 (Table 1). However, assuming the most current (2000) estimates of per capita P inputs have remained constant for the past 2 years, population growth alone may be reversing the gains achieved in the last decade. While effluent guidelines are continually being met and bettered by all but a few plants in the GTA, total loads may still be on the rise. Furthermore, if population growth occurs as it is expected without further improvements of P removal strategies, in 2021 P loadings to Lake Ontario by the GTA may attain pre-GLWQA levels. This exercise clearly demonstrates the importance of bridging the gaps between water and wastewater treatment plant infrastructure modernization, effluent guidelines and population growth rates (Chambers et al. 2001). However, P concentrations in open waters are still meeting the GLWQA guidelines of  $< 10\mu\text{g/L}$ , the open water nutrient dynamics currently seem to be unaffected even if nearshore loadings have increased.

Controlling the excessive growth of *Cladophora* in the new millennium is an unforeseen, yet perhaps not unexpected, 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. We must also understand how current land use practices and climate change also are impacting point and non-point sources of nutrients to these large lakes. 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 excess growth of *Cladophora* in the Laurentian Great Lakes.

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**Table 1. Estimates of P inputs to Lake Ontario from the Greater Toronto Area over time. Regions included in the calculations are: Halton, Peel, York, Durham and Metro Toronto.**

Year	Population (x10 <sup>6</sup> )	P in effluents (mg/L)	Total input (tonnes/d)	P per capita (g/capita/day)
1912	0.5	4.3 <sup>a</sup>	0.74 <sup>c</sup>	1.47
1953	1.2	4.3 <sup>a</sup>	1.77 <sup>c</sup>	1.47
1991	3.9	0.71 <sup>b</sup>	1.71	0.44
1996	4.3	0.61 <sup>b</sup>	1.44	0.33
1998	4.6	0.70 <sup>b</sup>	1.36	0.30
2000	4.8	0.68 <sup>b</sup>	1.29	0.27
2001	4.9	n.d.	1.32 <sup>d</sup>	0.27 <sup>e</sup>
2002	5.0	n.d.	1.34 <sup>d</sup>	0.27 <sup>e</sup>
2021*	6.5	n.d.	1.75 <sup>d</sup>	0.27 <sup>e</sup>

n.d.: no data available

<sup>a</sup>Prior to 1972, a conservative estimate of P inputs from municipal waste of 4.3 mg/L was derived from the estimated value of 540 gP/capita/y (Sly 1976).

<sup>b</sup>Annual effluent P concentration averages for all the Greater Toronto Area (GTA) wastewater treatment plants. Data obtained from the Ontario Ministry of the Environment.

<sup>c</sup>Calculated by assuming a 343 L water use and discharge per capita. Source: <http://cbc.ca/news/indepth/background/groundwater2.html>.

<sup>d</sup>Calculated using phosphorus discharge per capita estimates for 2000.

<sup>e</sup>Assumed phosphorus discharge per capita standards for 1998 are maintained and not improved in 2001, 2002 and 2021.

\*source: <http://www.ryerson.ca/news/2000/20000302.html> for projected population in 2021 for the GTA.

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