Modeling the growth dynamics of *Cladophora* in eastern Lake Erie

by

Scott Neil Higgins

A thesis
presented to the University of Waterloo
in fulfillment of the
thesis requirement for the degree of
Doctor of Philosophy
in
Biology

Waterloo, Ontario, Canada, 2005

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required revisions, as accepted by my examiners.

I understand this thesis may be made electronically available to the public.

Abstract

Cladophora glomerata is a filamentous green alga that currently forms extensive blooms in nearshore areas of Lake Ontario, eastern Lake Erie, Lake Michigan, and isolated locations in Lake Huron. The biomass, areal coverage, algal bed characteristics, and tissue phosphorus concentrations of *Cladophora glomerata* were measured at 24 nearshore rocky sites along the northern shoreline of Lake Erie's eastern basin between 1995-2002. Midsummer areal coverage at shallow depths (≤5m) ranged from 4-100 %, with a median value of 96%. Peak seasonal biomass ranged from <1 to 940 g m^{-2} dry mass (DM), with a median value of 171 g m^{-2} DM. Tissue phosphorus varied seasonally, with initial high values in early May (0.15 to 0.27 % DM; median 0.23 % DM) to midsummer seasonal low values during peak biomass (0.03 to 0.23 % DM; median 0.06 % DM). A numerical *Cladophora* growth model (CGM) was revised and field-tested at 5 sites in eastern Lake Erie during 2002. The CGM is useful for: 1) Predicting *Cladophora* growth, biomass, and tissue phosphorus concentrations under non-point source P loading with no depth restrictions; 2) providing estimates of the timing and magnitude of the midsummer sloughing phenomenon; 3) determining the contribution of *Dreissena* invasion to the resurgence of *Cladophora* in eastern Lake Erie; and 4) developing management strategies for *Cladophora* abatement. The CGM was applied to investigate how the spatial and temporal patterns of *Cladophora* growth were influenced by the natural variability in environmental parameters in eastern Lake Erie. Seasonal patterns in *Cladophora* growth were strongly influenced by temperature, and peak depth-integrated biomass was strongly influenced by both available light and phosphorus. The photosynthetic capacity of field collected *Cladophora* was a poor predictor of the mid-summer sloughing phenomenon. The CGM, however, predicted that self-shading within the dense *Cladophora* mats would have caused negative growth rates at the base of the dense mats for 14 days prior to the sloughing event. The metabolic imbalances at the base of the *Cladophora* mats were driven primarily by the availability of light and were exacerbated by intermediate water temperatures (~23°C). The excellent agreement between model simulations and field data illustrates the ability of the CGM to predict tissue P and growth over a range of sites and depths in eastern Lake Erie and suggests potential for the model to be successfully applied in other systems.

Acknowledgements

I would like to acknowledge the thoughtful advice and scientific insight of my co-advisors Dr. Robert Hecky and Dr. Stephanie Guildford. All aspects of this thesis, from the identification of research questions to the final draft, greatly benefited from their vast experience and knowledge. Bob, thank you for sharing your knowledge and enthusiasm. Stephanie, thank you for your wonderful advice and critical reviews. I would like to thank my committee members Drs. William Taylor, Ralph Smith, Todd Howell. Bill, your door was always open and your help with all manner of questions including time-series analysis was, and is, greatly appreciated. Ralph, this thesis was conducted under the auspices of the Lake Erie Strategic grant in which you devoted much time and effort and the research I have conducted strongly benefited from the team approach that you fostered. In addition I thank you for your understanding when I put that little dent in the MNR boat engine. Todd, your assistance throughout this project has been extremely rewarding for me. From your initial comments at our first meeting in Port Dover "…If you are going to work in the nearshore you better be ready to take on the challenge…", to sharing your *Cladophora* survey data for Chapter 2, and to asking the direct and difficult questions that needed answers at my committee meetings…I thank you for investing your time, effort, and thoughtfulness in my research.

The field aspects of this thesis could not have been completed without the assistance of Paul Weidman, Griffin Cobb, Reagan Johnson, and Lyndsey Ackroyd. The nearshore of Lake Erie was a challenging natural laboratory to work in and we took our successes with our inevitable bruises. We spent many an hour under the water observing and collecting samples and many late nights in our converted field laboratory/garage sifting through the samples and conducting experiments. Thank you for your help and friendship. I would also like to thank Ngan Diep for her field assistance on several occasions, especially the grueling diel survey that she so wonderfully volunteered her time and efforts for. I would also like to acknowledge the efforts of Dave Depew for coordinating many of the field aspects and also conducting the particulate nutrient analysis. Thank you to Luis Leon for his assistance with mapping and GIS, and to Sairah Malkin for reviewing the manuscript form of Chapter 2. I would also like to acknowledge my fellow graduate students and members of the University of Waterloo Aquatic Ecology group. It has been a pleasure to work with you and your friendship is very much appreciated. Special thanks to my officemates Patricia Ramlal and Margaret Vogel, and my roommates Jane Almond and Mohamed Mohamed, for tolerating my antics. Most importantly, thank you to my family for your love and support every step of the way.

I would also like to acknowledge the Ontario Ministry of Natural Resources (Port Dover), Ontario Ministry of the Environment, Environment Canada, the National Sciences and Engineering Council of Canada, the Ontario Graduate Scholarship Program, and the University of Waterloo for logistical and financial support. I would also like to acknowledge Ontario Parks who facilitated shoreline access the to the waters adjacent to Rock Point provincial park.

Table of Contents

List of Figures

.

List of Tables

Chapter 1 General Introduction

1.1 Taxonomy and biogeography

The genus *Cladophora* contains approximately 120 species (Bakker et al. 1994), including 11 freshwater and brackish water species (Van der Hoek 1963; Whitton 1970). The high morphological plasticity of *Cladophora* and overlapping morphological characteristics between species has made identification to the species level difficult using traditional morphological indicators (Bellis and McClarty 1967; Whitton 1970; Bakker et al. 1994). In the Laurentian Great Lakes the majority of studies have identified *Cladophora* as *C. glomerata* (e.g. Bellis and McClarty 1967; Taft 1975; Millner et al. 1982; Lorenz and Herdendorf 1982), and samples of *Cladophora* reported from this study were readily identified as *C. glomerata* (Van Den Hoek 1963). Current efforts to validate the morphologically determined species identifications and discern the biogeography of *Cladophora* species and varieties in the Laurentian Great Lakes through the use of molecular markers and microsatellites are ongoing (Ross et al. 2005). This thesis applies the current taxonomic understanding of the biogeography of *Cladophora* in the Laurentian Great Lakes and the terms *Cladophora* and *C. glomerata* are used interchangeably.

1.2 Overview of Life Cycle and Physiological Requirements

The life cycle of *C. glomerata* has been reviewed by Bellis and McClarty (1967) and Whitton (1970). In general, *C. glomerata* reproduces asexually through the development of biflagellate or quadriflagellate zoospores (Van Den Hoek 1963; Bellis and McClarty 1967). The development of zoosporangia and formation of zoospores has been correlated with short photoperiods (Van Den Hoek 1963; Hoffman and Graham 1984), although in field populations zoosporangia can be noted throughout the vegetative growth period (Bellis and McClarty 1967). Each zoosporangium may contain several hundred zoospores, and upon release the zoospores attach to hard substratum at their anterior end by affixing their flagella to the substratum (Bellis and McClarty 1967). Given favorable environmental conditions, germination and vegetative growth can begin shortly after the zoospores become attached to the substratum (Bellis and McClarty 1967; Whitton 1970). As vegetative growth proceeds upright filaments are produced and branching from the main filament may occur. The degree to which branching and sub-branching occurs has often been related to water velocity or turbulence (e.g. Dodds and Gudder 1992; Bergey et al. 1995). The loss of branches has been associated with the bursting of zoosporangia (Bellis and McClarty 1967). Growth may occur intercalary and apically (Whitton 1970), however branched forms have relatively low intercalary

growth compared with unbranched forms (Bellis and McClarty 1967). In branched forms of *Cladophora* growth is typically acropetal, where apical cells elongate vertically while sub-apical cells elongate horizontally and produce lateral branches through the process of budding (Van Den Hoek 1963). In this manner the youngest branches are those closest to the apex. *C. glomerata* may over-winter as thick walled akinete cells that remain tightly adhered to the substratum (Whitton 1970), and given favorable conditions vegetative growth can begin as temperatures approach 5°C (Graham et al. 1982).

The physical and chemical requirements for *C. glomerata* have been described in detail elsewhere (e.g. Bellis 1968; Whitton 1970; Neil 1975; Gerloff and Fitzgerald 1976; Wong et al. 1978; Hoffman and Graham 1984). In general, *C. glomerata* requires a hard surface for attachment, a relatively high light environment, warm alkaline waters, ambient pH values between 7-10, and some degree of water motion (Whitton 1970). Excessive growths of *Cladophora* are generally associated with eutrophic waters (Whitton 1970; Planas et al. 1996; Herbst 1969). In lakes *C. glomerata* is associated with the eulittoral and sublittoral zones of exposed shorelines and is typically absent from quiescent waters (Whitton 1970). *Cladophora* may grow attached to plant material (epiphytic), rock surfaces (epilithic), or to the surfaces of animals (epizootic) including the opercula of fish or the shells of gastropods or bivalve mussels (Whitton 1970; Dodds and Gudder 1992, Chapter 2). The minimum light requirements for growth are generally reported to range between 29-44 μM m-2 s-1 (Graham et al. 1982; Lester et al. 1988; Lorenz et al. 1991), and these values have been used to estimate the depth distribution of *Cladophora* in lakes (Lorenz et al. 1992; Chapter 2). Reported temperature optima and thresholds for the growth of *C. glomerata* vary widely among studies. For *C. glomerata* isolated from the Laurentian Great Lakes region optimal temperatures for growth have been reported to range from 13-31°C, and reported threshold temperatures have been reported to range between 30-35°C (Bellis 1968; Adams and Stone 1973; Graham et al. 1982; Lester et al. 1988). Although many factors are important for constraining growth rates (Herbst 1969; Whitton 1970; Canale and Auer 1982a) phosphorus is generally considered as the nutrient that limits excessive growths and nuisance blooms (e.g. Neil and Owen 1964; Pitcarin and Hawkes 1973; Wong and Clark 1976; Canale and Auer 1982b; Freeman 1986; Painter and Kamaitis 1987; Chapter 2). Carbon limitation in benthic algae has been demonstrated in various studies (e.g. Turner et al. 1994), however the potential for carbon limitation of *Cladophora* growth is not well understood. *C. glomerata* possesses carbonic anhydrase within its periplasm for the dehydration of HCO3- to CO2, and possesses active carbon uptake mechanisms during periods of carbon limitation (Choo et al. 2002). The active uptake mechanisms in *C. glomerata* may explain its success in waters with relatively high pH and low ambient CO2

concentrations (Choo et al. 2002). In general, nitrogen has not been found to limit *Cladophora* growth in the Laurentian Great Lakes region (Neil and Owen 1964; Wong and Clark 1976; Chapter 2), however enrichment experiments including both nitrogen and phosphorus showed increased growth over trials using only phosphorus (Neil and Owen 1964).

1.3 Population and community dynamics of *Cladophora*

In north temperate lakes and rivers *Cladophora* generally follows a two-maxima seasonal growth pattern, with a larger mid-summer peak followed by a period of low growth and then a smaller autumn biomass peak (Bellis and McClarty 1967, Whitton 1970; Chapter 2,4). Under optimal conditions vegetative growth may be rapid with maximum net specific growth rates near 0.7 day^{-1} (Auer and Canale 1982b; Rosemarin 1982). Increases in areal biomass and density may reduce water exchange within the mat and increase competition for limiting resources including light and growth limiting nutrients (Choo et al. 2002; Chapter 4,5). Where *Cladophora* growth is extensive the midsummer biomass peak is generally followed by a major sloughing event (Bellis and McClarty 1967, Whitton 1970; Canale and Auer 1982b, Chapter 2). Various studies have suggested that the mid-summer sloughing phenomenon is related to ambient water temperatures (e.g. Bellis and McClarty 1967; Whitton 1970; Dodds and Gudder 1992). However, in the Laurentian Great Lakes region the sloughing event occurs at temperatures near 23°C (Wong and Clark 1976; Canale and Auer 1982b; Chapters 2-5), which is approximately 10°C below threshold values for positive growth as determined through *in vitro* physiological experiments (Bellis 1968; Graham et al. 1982; Lester et al. 1988; Chapter 5). Other studies have suggested that the sloughing event is triggered by numerous factors contributing to a negative metabolic balance of the *Cladophora* mat (Canale and Auer 1982b), however this hypothesis has been challenged by Mantai (1987, 1989) who noted that excess photosynthetic products were noted in the tissues of *Cladophora* immediately prior to the sloughing event. In Chapter 4 of this thesis I present an amendment to the metabolic imbalance hypothesis of Canale and Auer (1982b) that indicates the potential of metabolic imbalance at the base of *Cladophora* mats to be the underlying cause of the mid-summer sloughing phenomenon in eastern Lake Erie and perhaps elsewhere.

Filaments of *C. glomerata* represent a large surface area and are often heavily colonized by epiphytic algae (e.g. Lowe et al. 1982; Stevenson and Stoermer 1982a,b; Dodds 1991; Johnson 2004). Strong seasonality in epiphytic diatom assemblages and the proportion of epiphytic biomass to the total algal biomass were noted on *Cladophora* filaments from Lake Huron (Stevenson and Stoermer

1982a). During May the epiphytic diatom community comprised approximately 30% of the total algal biomass. During the early to mid-summer (June-July) *Cladophora* growth exceeded that of epiphytes and the epiphytic diatom biomass was reduced to ~20% of the total algal biomass. As *Cladophora* growth rates declined through the autumn period the proportion of epiphytic diatoms to total algal biomass increased, reaching >60% by November (Stevenson and Stoermer 1982). The epiphytic diatom community structure was dominated by sessile *Fragilaria spp.* and *Amphora perpusilla* during May, and *Cocconeis pediculus* from June-August (Stevenson and Stoermer 1982). Diversity dramatically increased during September-October until the diatom community became numerically dominated by *Rhoicosphenia curvata* during November (Stevenson and Stoermer 1982). Epiphytes may compete with *Cladophora* for resources such as limiting nutrients or light (Dodds 1991), and Stevenson and Stoermer (1982) postulated that dense assemblages of epiphytes may accelerate the sloughing process. At the base of dense stands of *Cladophora,* where the detachment of filaments generally occurs, ambient light levels can reach levels near or below minimum requirements for *Cladophora* growth (Chapter 4,5). In these locations the further reduction in light due to 'thick coatings' of epiphytes could exacerbate light limitation and result in more rapid deterioration and sloughing of the *Cladophora* filaments. Closer to the mat-water surface, where light intensities are high, epiphytic diatoms may increase photosynthetic rates by reducing photoinhibition (Dodds 1991). Epiphytes may also compete for growth limiting nutrients with *Cladophora* (Dodds 1991; Dodds and Gudder 1992), and therefore reduce the growth rates of *Cladophora.* However, the importance of nutrient competition between *Cladophora* and its epiphytes is not fully understood, and the results of Stevenson and Stoermer (1982) suggest that *Cladophora* may out-compete diatoms for limiting nutrients during periods of rapid growth.

In addition to providing habitat for epiphytes, dense *Cladophora* stands also provide habitat for numerous invertebrates (Chilton et al. 1986; Dodds 1991; Dodds and Gudder 1992; Johnson 2004). In eastern Lake Erie the most common macroinvertebrates associated with *Cladophora* were amphipods, including *Echinogammarus ischnus* and *Gammarus fasciatus,* and a diverse assemblage of chironomids (Johnson 2004). Stomach content analysis revealed that both amphipods and chironomids fed on epiphytic diatoms when abundant, and a controlled laboratory experiment demonstrated that *G. fasciatus* could graze directly on *Cladophora* filaments (Johnson 2004).

During the early 1990's dense colonies of *Dreissena polymorpha* (zebra mussel) became established in Lake St. Clair, Lake Erie, Lake Ontario, and Lake Michigan (e.g. Howell et al. 1996; Holland 1993; Napela et al. 1995). Very little is known about the direct interactions between

Cladophora and *Dreissena.* Dreissenid mussels may increase *Cladophora* productivity by increasing the available surface area for the attachment of filaments, increasing the water clarity and thereby increasing the photosynthetic compensation depth and maximum depth of colonization, and increasing the availability of dissolved phosphorus, nitrogen and carbon (Hecky et al. 2004). In Saginaw Bay of Lake Huron, where the immediate effects of *Dreissena* colonization on water quality parameters were intensively studied (JGLR Special Issue 21(4), 1995), significant increases in macrophyte biomass (Skubinna et al. 1995) and benthic algal biomass and productivity (Lowe and Pillsbury 1995) were noted after *Dreissena* colonization.

1.4 *Cladophora* and the Laurentian Great Lakes

Cladophora was first identified in the Laurentian Great Lakes in 1848 (Taft 1975). From the 1950's through to the mid-1980's extensive *Cladophora* growths were noted in Lakes Ontario, Erie, Michigan, and localized portions of Lake Huron (Kishler 1967; Taft and Kishler 1973; Shear and Konansewich 1975; Ontario Ministry of the Environment 1982; Canale and Auer 1982a). These nuisance algal blooms restricted recreational uses of beaches and nearshore areas, created problems for industrial and municipal water intakes, fouled the nets of commercial fishermen, caused taste and odor problems, reduced property values, and required costly clean up measures (Milner & Sweeney 1982; Dodds & Gudder 1992; DeJong 2000; Ormerod 1970). During the 1970's the International Joint Commission identified large blooms and beach accumulations of *Cladophora* in the lower North American Great Lakes as a major problem (Shear & Konasewich 1975). Due to the large public interest, influence on fisheries and local industries, and biological implications numerous studies were undertaken to determine how to control these massive nuisance algal growths. In general, most studies reported that elevated phosphorus concentrations were responsible for bloom formations of *Cladophora* (e.g. Neil & Jackson 1982; Planas et al. 1996; Wong & Clark 1976). The implementation of strict phosphorus controls in the Laurentian Great Lakes during the 1970's was successful in reducing *Cladophora* tissue phosphorus concentrations and biomass at 7 sites along the northern shoreline of Lake Ontario (Painter and Kamaitis 1987), and along a 2 km stretch of shoreline in Lake Huron where nuisance growths of *Cladophora* were directly associated with a municipal water treatment facility (Auer et al. 1982). While *Cladophora* surveys at other sites in these and other Laurentian Great Lakes were either not conducted or reported during the 1980's it is probable that reductions in tissue phosphorus concentrations and biomass were a general phenomenon across lakes Ontario, Erie, Michigan, Lake Huron. Recently, however, widespread *Cladophora* blooms and beach foulings have been reported in Lake Ontario (Campbell et al. submitted; personal observation),

eastern Lake Erie (Chapter 2), and Lake Michigan (Byappanahalli et al. 2003). Beach foulings by *Cladophora* have also been reported in isolated locations along the eastern shoreline of Lake Huron (S. Guildford, University of Waterloo, pers. comm.). The resurgence of *Cladophora* in these oligotrophic to oligo-mesotrophic lakes, or lake basins, is troublesome and may be indicative of fundamental changes in water clarity and nutrient cycling caused by *Dreissena* (Lowe and Pillsbury 1995; Hecky et al. 2004; Chapter 2).

1.5 Thesis Overview

The overall objectives of this thesis were: 1) To assess the seasonal and spatial distributions of *Cladophora* in eastern Lake Erie *post Dreissena,* 2) to determine the ecological factors currently responsible for the recent bloom occurrences, 3) to develop or revise a *Cladophora* growth model for eastern Lake Erie, and 4) to determine the contribution of *Dreissena* (zebra and quagga mussels) to the *Cladophora* resurgence. This thesis is divided into four independent data chapters (Chapters 2-5), and each chapter deals with a specific aspect of my overall research objectives. At the time of thesis submission Chapter 2 and 3 have been accepted for publication in the Journal of Great Lakes Research.

Chapter 2 presents an assessment of the spatial and temporal dynamics of *Cladophora* growth in eastern Lake Erie during 1995, 2001, and 2002 using datasets collected by Dr. Todd Howell (Howell 1998; Howell unpublished data) and myself. In general Dr. Howell's datasets dealt primarily with the spatial dynamics of *Cladophora* growth during the peak biomass season of 1995 and 2001, while my datasets were collected on a smaller number of sites over the ice-free season (May-November 2001, 2002). Combined, these datasets were the most extensive surveys of *Cladophora* in eastern Lake Erie to date and provided a unique opportunity for assessing both the seasonal and spatial dynamics of *Cladophora*. Chapter 2 is important and relevant for several reasons. Firstly, Chapter 2 quantifies the biomass, distribution, and tissue phosphorus and nitrogen concentrations of *Cladophora* across the eastern basin of Lake Erie and places these values in historical context. Secondly, the presence of widespread *Cladophora* blooms along the shorelines of eastern Lake Erie is a visible sign of coastal eutrophication in an otherwise oligo-mesotrophic lake basin. Widespread *Cladophora* blooms have recently been reported in Lakes Ontario and Michigan and the resurgence of *Cladophora* in these three Laurentian Great Lakes is likely not coincidental. Therefore, the information provided in Chapter 2 may prove useful in understanding the seasonal and spatial dynamics of *Cladophora* in

these other systems. Thirdly, Chapter 2 provides a preliminary assessment of the contribution of *Dreissena* to the resurgence of *Cladophora.*

In Chapter 3 the numerical description of a revised *Cladophora* growth model (CGM) and the results of field-testing in eastern Lake Erie are presented. The numerical model (CGM) relies heavily on the *Cladophora* growth model designed by M. Auer, R. Canale, J. Graham and colleagues (1982 JGLR spec. issue 8(1): 73-143) on Lake Huron. In general, the results of field-testing demonstrate that the model can predict the seasonal and spatial dynamics of *Cladophora* growth, biomass accrual, and tissue phosphorus concentration with reasonable accuracy. While it is expected that the model will be re-visited as knowledge and modeling requirements increase, the successful application of the CGM in eastern Lake Erie suggests it may also prove useful in other Laurentian Great Lakes systems.

In Chapter 4 the CGM is applied to investigate the sensitivity of *Cladophora* growth to seasonal and spatial variations in water quality parameters in eastern Lake Erie. Specifically the CGM is used to evaluate how spatial and temporal variability in water temperature, surface irradiance, water clarity, and dissolved phosphorus affects the distribution and biomass accrual of *Cladophora.* These modeling scenarios are useful for understanding how natural variability in environmental parameters affects the seasonal and spatial dynamics of *Cladophora* in eastern Lake Erie. This chapter also addresses the implications of increases or decreases in available phosphorus on *Cladophora* biomass and distribution while constraining other environmental variables. Such an approach is useful for ascertaining the potential success of managing *Cladophora* growths through nutrient control, or contrarily, for assessing the implications of potential increases in limiting nutrients on *Cladophora* growth and biomass. In addition, Chapter 4 presents a potential mechanism for the mid-summer sloughing phenomenon that is consistent with the results of previous studies.

Chapter 5 reports the results of *in vitro* photosynthesis vs. irradiance experiments conducted on *Cladophora* collected from 5 sites in eastern Lake Erie from May-October, 2002. These experiments provide insights into the physiological condition and growth patterns of field populations of *Cladophora* in eastern Lake Erie. Specifically the data from this chapter is useful for interpreting the CGM predictions, especially in those cases where CGM predictions contrast with data obtained directly from field surveys. Finally, Chapter 6 presents a general summary and key results of each data chapter (Chapters 2-5).

1.6 Literature cited

Adams, M. S. and W. Stone. 1973. Field studies on photosynthesis of *Cladophora* glomerata (Chlorophyta) in Green Bay, Lake Michigan. Ecology 54: 853-62.

Auer, M. T., and R. P. Canale. 1982. Ecological and mathematical modeling of *Cladophora* in Lake Huron: 3. The dependence of growth rates on internal phosphorus pool size. J. Great Lakes Res., 8: 93-99.

Bakker, F. T., J. L. Olsen, W. T. Stam, and C. Van Den Hoek. 1994. The *Cladophora* complex (Chlorophyta): New views based on 18S rRNA gene sequences. Mol. Phylogenet. Evol. 3: 365-382.

Bellis, V. J. 1968. Unialgal cultures of *Cladophora glomerata* (L.) Kutz. I. Response to temperature. J. Phycol. 4: 19-23.

Bellis, V. J., and D. A. McLarty. 1967. Ecology of *Cladophora glomerata* (L.) Kütz. In southern Ontario. J. Phycol., 3: 57-63.

Bergey, E. A., C. A. Boettiger, and V. H. Resh. 1995. Effects of water velocity on the architecture and epiphytes of *Cladophora glomerata* (Chlorophyta). J. Phycol. 31: 264-271.

Byappanahalli, M. N., D. A. Shively, M. B. Nevers, M. J. Sadowsky, and R. L. Whitman. 2003. Growth and survival of Escherichia coli and enterococci populations in the macro-alga *Cladophora* (Chlorophyta). FEMS Microbiology Ecology 46: 203-211.

Campbell, L, M., M. N. Charlton, V. P. Hiriart-Baer, S. Higgins, S. Malkin, S. J. Guildford, R. E. Hecky, T. Howell, D. Dejong, and L. F. Moore. Then and now: Historical overview of the nuisance green alga, *Cladophora glomerata* in the Laurentian Great Lakes. Submitted to the J. Great Lakes Res.

Canale, R. P., and M. T. Auer. 1982a. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 5. Model development and calibration. J. Great Lakes Res., 8: 112-125.

Canale, R. P., and M. T. Auer. 1982b. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 7. Model verification and system response. J. Great Lakes Res., 8: 134-143.

Chilton, E. W., R. L. Lowe, and K. M. Schurr. 1986. Invertebrate communities associated with Bangia atropurpurea and *Cladophora glomerata* in western Lake Erie. J. Great Lakes Res. 12: 149-153.

Choo, K., P. Snoeijs, and M. Pedersen. 2002. Uptake of inorganic carbon by *Cladophora glomerata* (Chlorophyta) from the Baltic Sea. J. Phycol. 38: 493-502.

Dejong, D. 2000. The growth and distribution of the green alga *Cladophora* at Presqu'ile Provincial Park: Implications for management (Ontario). MES Thesis. Wilfrid Laurier University. 92p.

Dodds, W. K. 1991. Factors associated with dominance of the filamentous green alga *Cladophora glomerata.* Wat. Res., 25: 1125-1132.

Dodds, W. K., and Gudder 1992. The Ecology of *Cladophora.* J. Phycol. 28: 415-427.
Dolan, D. 1993. Point source loadings of phosphorus to Lake Erie: 1986-1990. J. Great Lakes Res. 19: 212-223.

Freeman, M. C. 1986. The role of nitrogen and phosphorus in the development of *Cladophora* glomerata (L.) Kutzing in the Manawatu river, New Zealand. Hydrobiologia 131: 23-30.

Gerlof, G. C., and G. P. Fitzgerald. 1976. The nutrition of Great Lakes *Cladophora.* Ecological Research Series EPA-600/3-76-044. Duluth, Minnesota: U. S. Environmental Protection Agency, Office of Research and Development.

Graham, J. M., M. T. Auer, R. P. Canale, and J. P. Hoffmann. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 4. Photosynthesis and respiration as functions of light and temperature. J. Great Lakes Res., 8: 100-111.

Hecky, R. E., R. E. H. Smith, D. R. Barton, S. J. Guildford, W. D. Taylor, M. Charlton and T. E. Howell. 2004. The near shore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Submitted to Can. J. Fish. Aquat Sci. 61: 1285-1293.

Herbst, R. P. 1969. Ecological factors and the distribution of *Cladophora glomerata* in the Great Lakes. Am. Midl. Nat. 82: 90-98.

Hoffmann, J. P., and L. E. Graham. 1984. Effects of selected physiochemical factors on growth and zoosporogenesis of *Cladophora glomerata* (Chlorophyta). J. Phycol., 20: 1-7.

Holland, R. E. 1993. Changes in planktonic diatoms and water transparency in HatcheryBay, Bass Island area, western Lake Erie, since the establishment of zebra mussels. J. Great Lakes Res. 19: 617-624.

Howell, T. E., C. H. Marvin, R. W. Bilyea, P. B. Kauss, and K. Somers. Changes in Environmental conditions during *Dreissena* colonization of a monitoring station in eastern Lake Erie. J. Great Lakes Res. 22(3): 744-756.

Johnson, R. 2004. The benthic food web on nearshore hard substrates at Peacock Point, eastern Lake Erie. M.Sc. Thesis. University of Waterloo, Waterloo, Ontario, Canada.

Kishler, W. J. 1967. A quantitative study of *Cladophora glomerata* (L) Kuetzing in the island region of Western Lake Erie. M.Sc. Thesis. Ohio State University, Columbus, Ohio.

Lester, W. W., M. S. Adams, and A. M. Farmer. 1988. Effects of light and temperature on photosynthesis of the nuisance alga *Cladophora glomerata* (L.) Kutz from Green Bay, Lake Michigan. New Phytol., 109: 53-58.

Lorenz, R. C., and C. E. Herdendorf. 1982. Growth dynamics of *Cladophora glomerata* in western Lake Erie in relation to some environmental factors. J. Great Lakes Res 8(1): 42-53.

Lorenz, R. C., M. E. Monaco, and C. E. Herdendorf. 1991. Minimum light requirements for substrate colonization by *Cladophora glomerata.* J. Great Lakes Res. 17(4): 536-542.

Lowe, R. L., and R. W. Pillsbury. 1995. Shifts in benthic algal community structure and function following the appearance of Zebra Mussels (*Dreissena polymorpha)* in Saginaw Bay, Lake Huron. J. Great Lakes Res. 21: 558-566.

Lowe, R. L., B. H. Rosen, and J. C. Kingston. 1982. A comparison of epiphytes on *Bangia atropurpurea* (Rhodophyta) and *Cladophora glomerata* (Chlorophyta) from Northern Lake Michigan. J. Great Lakes Res. 8: 164-168.

Mantai, K. E. 1987. Energy relations in *Cladophora glomerata* from Lake Erie. J. Great Lakes Res. 13: 279-284.

Mantai, K. E. 1989. Commentary: Rebuttal to comment by M. T. Auer and J. M. Graham. J. Great Lakes Res. 15: 371-372.

Millner, G. C., and R. A. Sweeney. 1982. Lake Erie *Cladophora* in perspective. J. Great Lakes Res. 8: 27-29.

Nalepa, T. F., J. A. Wojcik, D. L. Fanslow, and G. A. Lang. 1995. Initial colonization of the zebra mussel (Dreissena polymorpha) in Saginaw Bay, Lake Huron: population recruitment, density, and size structure. J. Great Lakes Res. 21: 417-434.

Neil, J. 1975. Physical and chemical requirements. *In: Cladophora in the Great Lakes.* H, Shear and E. E. Konasewich (eds.). International Joint Commission. 179p.

Neil, J. H., and M. B. Jackson. 1982. Monitoring *Cladophora* growth conditions and the effect of phosphorus additions at a shoreline site in northeastern Lake Erie. J. Great Lakes Res. 8: 30-34.

Neil, J. H., and G. E. Owen. 1964. Distribution, environmental requirements and significance of *Cladophora* in the Great Lakes. *In:* Proc. 7th Conference on Great Lakes Research, pp. 113-121.

Ontario Ministry of the Environment. 1982. Observations on *Cladophora* growth in some nearshore areas of Lake Huron and Southern Georgian Bay. Field Work 1981. Water Resources Assessment Unit, Southwestern Region.19p.

Ormerod, G. K. 1970. The relationship between real estate values, algae and water levels. Lake Erie Task Force, Department of Public Works, Canada.

Painter, D. S., and G. Kamaitis. 1987. Reduction of *Cladophora* biomass and tissue phosphorus in Lake Ontario, 1972-83. Can. J. Fish. Aquat. Sci. 44: 2212-2215.

Pitcairn, C. E. R., and H. A. Hawkes. 1973. The role of phosphorus in the growth of *Cladophora.* Water Research 7: 159-171.

Planas, D., S. C. Maberly, and J. E. Parker. 1996. Phosphorus and nitrogen relationships in Cladophora glomerata in two lake basins of different trophic status. Freshwater Biology 35: 609-622.

Prescott, G. W. 1962. Algae of the western Great Lakes area. W. C. Brown Co. Dubuque Iowa. 977p.

Rosemarin, A. S. 1982. Phosphorus nutrition of two potentially competing filamentous algae, *Cladophora glomerata* (L.) Kutz. and *Stigeoclonium tenue* (Agardh) Kutz. from Lake Ontario. J. Great Lakes Res. 8: 66-72.

Ross, S., R. Sheath, and K. Muller. 2005. Molecular phylogeography and species discrimination of freshwater *Cladophora* (Cladophorales, Chlorophyta) in North America. In: *Cladophora* research and management in the Great Lakes, Proceedings. H. Boostma, E. Jenson, E. Young, and J. Berges (eds.). University of Wisconsin at Milwaukee, Great Lakes Institute. 105p.

Shear, H. and E. E. Konasewich. 1975. *Cladophora* in the Great Lakes. International Joint Commission. 179p.

Skubinna, J. P., T. G. Coon, and T. R. Batterson. 1995. Increased abundance and depth of submersed macrophytes in response to decreased turbidity in Saginaw Bay, Lake Huron. J. Great Lakes Res. 21: 476-488.

Stevenson, R. J., and E. F. Stoermer. 1982. Luxury consumption of phosphorus by five *Cladophora* epiphytes in Lake Huron. Trans. Am. Microsc. Soc. 101: 151-161.

Taft, C. E. 1975. History of *Cladophora* in the Great Lakes. In: *Cladophora* in the Great Lakes. H. Shear and D. E. Konasewich (eds.). International Joint Commission. Pp. 5-16.

Taft, C. E. and W. J. Kishler. 1973. *Cladophora* as related to pollution and eutrophication in western Lake Erie. Water Resources Center Project Completion Report No. 332x, 339x. Ohio State University. Ohio.

Turner, M. A., E. T. Howell, G. G. C. Robinson, P. Cambell, R. E. Hecky, and E. U. Schindler. 1994. Roels of nutrients in controlling growth of epilithon in oligotrophic lakes of low alkalinity. Can. J. Fish. Aquat. Sci. 51: 2784-2793.

Van den Hoek, C. 1963. Revision of the European species of *Cladophora,* E. J. Brill, Leiden. 248 pp.

Whitton, B. A. 1970. Biology of in freshwaters. Water Research 4: 457-476.

Wong, S. L., and B. Clark. 1976. Field determination of the critical nutrient concentrations for *Cladophora* in streams. J. Fish. Res. Board Can. 33: 85-92.

Wong, S. L., B. Clark, M. Kirby, and R. F. Kosciuw. 1978. Water temperature fluctuations and seasonal periodicity of *Cladophora* and *Potamogeton* in shallow rivers. J. Fish. Res. Board Can. 35: 866-870.

Chapter 2

The wall of green: The status of *Cladophora glomerata* on the northern shores of Lake Erie's eastern basin, 1995-2002.

2.1 Abstract

The biomass, areal coverage, algal bed characteristics, and tissue phosphorus concentrations of *Cladophora glomerata* were measured at 24 near shore rocky sites along the northern shoreline of Lake Erie's eastern basin between 1995-2002. Midsummer areal coverage at shallow depths (≤5m) ranged from 4-100 %, with a median value of 96%. *Cladophora* biomass began accumulating at most sites during early May, and achieved maximum values by mid-July. Peak seasonal biomass ranged from <1 to 940 g m^{-2} dry mass (DM), with a median value of 171 g m^{-2} DM. Nearshore water concentrations of TP were lower than during pre-phosphorus abatement years, however *Cladophora* biomass levels are similar to reported values in those years. The midsummer 'die off' occurred shortly after the biomass peak, when water temperatures neared 22.5°C. Areal coverage declined after die-off to <10%, mean filament lengths declined from 33 cm to <1 cm, and mean biomass declined to < 1 g DM m^{-2}. Tissue phosphorus varied seasonally, with initial high values in early May (0.15 to 0.27 % DM; median 0.23 % DM) to midsummer seasonal low values during peak biomass (0.03 to 0.23 % DM; median 0.06 % DM). *Cladophora* biomass is sensitive to changes in phosphorus and light availability, and reductions in biomass previously achieved through phosphorus control may now be reversed because of increased water transparency and phosphorus availability to the benthos following establishment of dreissenids.

2.2 Introduction

Cladophora glomerata is a filamentous green alga widely distributed throughout lentic and lotic freshwaters of the world (Blum 1956, Dodds 1991; Sheath and Cole 1992). In general, *C. glomerata* grows attached to hard substrates in nutrient rich alkaline freshwaters, and was first described in Lake Erie in 1848 (Taft 1975). The biology and ecology of *C. glomerata* have been reviewed elsewhere (see Whitton 1970, Dodds and Gudder 1992; Hiriart-Baer et al. submitted). Although high morphological plasticity makes classification to species level difficult (Bellis and McClarty 1967), the vast majority of researchers have identified *Cladophora* in the Laurentian Great Lakes region as *C. glomerata*. For the remainder of this paper all references to *Cladophora* infer *C. glomerata*. During the 1960's through to the early 1980's severe nuisance blooms of *Cladophora* were described throughout the rocky shorelines of Lake Ontario and Lake Erie, and in localized portions of Lake Michigan and Lake Huron (Herbst 1969; Shear and Konasewich 1975; Auer et al. 1982; Millner and Sweeney 1982; Campbell et al. submitted). Large blooms and subsequent 'die-off' events of *Cladophora* severely reduced the aesthetic value of the near shore waters where they occurred (Taft 1975). Beach accumulations of *Cladophora* were at times measured in tonnes of fresh material (Neil and Owen 1964; Shear and Konasewich 1975; Taft 1975). In the early stages of decay *Cladophora* releases noxious odours that deterred the recreational uses of beaches and shorelines (Shear and Konasewich 1975; DeJong 2000). Property values decreased in the areas where beach wash-ups occurred, and severe economic impacts were incurred by businesses in the tourism and recreational sectors (Taft 1975, DeJong 2000). When free-floating in the water column these filaments clogged fishing nets reducing their efficiency and increasing their down time when they must be cleaned, and caused problems for municipal and industrial water intakes (Taft 1975). Recent evidence indicates that shoreline mats of decaying *Cladophora* in Lake Michigan supported high concentrations of *Escherichia coli* (Byappanahalli et al. 2003).

Although the total socio-economic costs of the '*Cladophora* problem' have never been fully assessed in any of the Great Lakes (though see Taft 1975), the indication of *Cladophora* as a 'serious problem' by the International Joint Commission led to a series of focused studies aimed at understanding the factors that promoted growth and bloom occurrences (see Shear and Konasewich 1975; and J Great Lakes Res. 8(1), 1982). These studies led to the conclusion that although several important factors (e.g. light, temperature, phosphorus, nitrogen, CO_2) could be responsible for controlling growth rates (Canale and Auer 1982; Hoffman and Graham 1984), that elevated concentrations of soluble phosphorus were generally responsible for the bloom occurrences (Herbst

1969; Gerloff and Fitzgerald 1976; Auer and Canale 1980). Because *Cladophora* blooms and shoreline fouling occurred at the lake margins they were perhaps the most obvious signs of the extent of cultural eutrophication in Lake Erie from the 1960's through to the 1980's. Large public outcries about 'the *Cladophora* problem', in part, led to the multi-billion dollar investments in sewage treatment plant upgrades and the removal of phosphates from detergents to reduce phosphorus loadings. Total phosphorus concentrations in the offshore and near shore zones of the Laurentian Great Lakes responded dramatically to the reduction of phosphorus loading (Stevens and Neilson 1987; Nicholls et al. 2001). While total phosphorus concentrations in the near shore zones also decreased or remained unchanged after *Dreissena* colonization (Nicholls and Standke 1997; Nicholls et al. 1999), spring SRP concentrations have increased in all basins of Lake Erie post-*Dreissena* (Makarewicz et al. 2000). Unfortunately, very little data exists on *Cladophora* in the Laurentian Great Lakes from 1983-1990, the period where phosphorus concentrations were dramatically reduced in the lower Great Lakes but prior to the invasion of *Dreissena polymorpha* (zebra mussel) and *D. bugensis* (quagga mussel). The little information that does exist for this period suggests that, at least in Lake Ontario, tissue phosphorus concentrations and bloom occurrences of *Cladophora* were somewhat reduced. In their study Painter and Kamaitis (1987) indicated that mean tissue phosphorus declined from 0.49% AFDM to 0.20% AFDM from 1972-1983, a 59% reduction. Furthermore, over these same years mean biomass declined from 205.8 g DM m^{-2} to 85.9 g DM m^{-2}, a 58% reduction (Painter and Kamaitis 1987).

Beginning in 1995 and through to 2002, the period following *Dreissena* establishment, a series of surveys for the investigation and surveillance of *Cladophora* shoreline fouling were undertaken in Lake Erie by the Ontario Ministry of the Environment (Howell 1998). Throughout the 1995-2000 period nuisance blooms were a regular occurrence in Lake Erie, and in 2001-2002 an intensive effort was undertaken to determine the seasonal and spatial distribution and physiological status of *Cladophora* in the eastern basin of Lake Erie. I bring together these datasets with the objective of assessing spatial and seasonal distribution, biomass, and nutrient status of *Cladophora* along the northern shoreline of Lake Erie's eastern basin. I also estimate the total amount of phosphorus taken up by *Cladophora*, discuss its significance to littoral zone and basin wide phosphorus dynamics, and provide preliminary estimates of how *Dreissena*-induced increases in water clarity influence *Cladophora* growth and biomass on a basin scale.

2.3 Methods:

2.3.1 1995 and 2002 spatial surveys:

Cladophora samples were collected from 0.0625 m^2 quadrats over four depth zones (0-0.5 m, 0.5-1.0 m, 1.0-1.5 m, 1.5-2.0 m) at 20 sites during mid-summer (Table 2.1). At each survey location (Figure 2.1) the percentage cover, and minimum, median, and maximum height of the *Cladophora* beds were determined for 5 randomly placed quadrats within each depth zone. For each site the data reported are the mean from all quadrats taken from 0-2 m depth, therefore at most sites a total of 20 quadrats was observed. In 1995, areal biomass was estimated using a semi-quantitative approach that combined limited quantitative sampling for biomass with the results of the visual survey. At each site, 5 of the quadrats were cleared by hand of *Cladophora* and material was retained for determination of dry weight. A conversion factor was calculated for each site to convert estimated mean areal volume (percent cover x median thickness x quadrat area) into biomass, and was determined by dividing the dry mass in a sample quadrat by the volume of *Cladophora* in the quadrat. In 2002, three 0.0625 m^2 quadrats were cleared of *Cladophora* in each depth zone, rinsed of debris, placed in bags and stored on ice. The frozen samples were freeze dried and analyzed for loss-on-ignition (LOI), and total tissue phosphorus (% DM).

2.3.2 2001-2002 seasonal surveys:

Five sites that allowed shore access and were distributed across the northern shoreline were selected to sample the seasonal variability in biomass, tissue phosphorus, and algal bed characteristics. The seasonal sites are identified in Table 2.1 with (s) following the site name. At each site, algae was collected at 2 m depth, and at one of these sites (Peacock point) samples were collected at 2 m, 5 m, and 10 m depths. These same sites were also part of a separate study assessing seasonal growth rates and the contribution of *Dreissena* to *Cladophora* resurgence (Chapters 3-5). Two other sites, Lowbanks and Point Abino (sites 22 and 36 in Table 2.1), were sampled in 2001 using the same methods. Samples were collected from three randomly placed 0.25 m^2 quadrats using SCUBA and an underwater airlifting device described by Barton and Hynes (1978). Prior to removing the biomass in each quadrat the percent cover was estimated visually, and the bed height and maximum filament lengths were measured with a ruler at three locations within the quadrat and then averaged. *Cladophora* was collected using the airlifting device under very low suction into a 250 μm mesh bag. Algal material was washed of debris and placed in whirl Pac bags and kept cool until return to the laboratory (1-4 h).

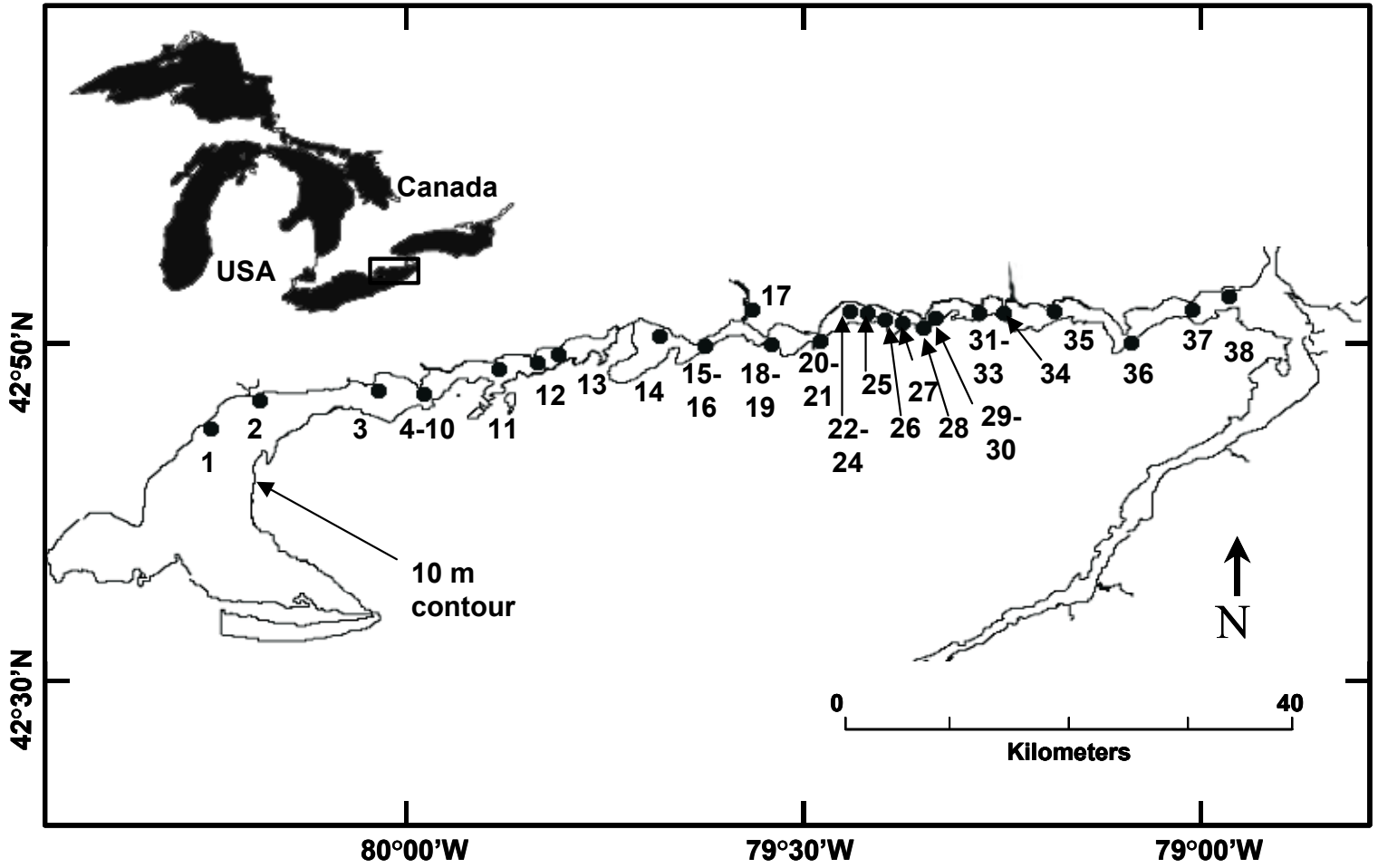

Figure 2.1. Map of the northern shoreline of Lake Erie's eastern basin. Site numbers refer to locations of sites as indicated in Table 2.1

Table 2.1. *Cladophora* bed characteristics for surveys in Lake Erie's eastern basin, 1995-2002. For sites with depth indicated as 0-2m tissue P samples are the mean of 4 replicate samples, while remaining sites report the mean value of 3 replicate samples. Site names with (S) refer to locations where the 2002 seasonal survey was conducted (see text).

Station name	Site-depth #	Depth (m)	Date sampled	n	% cover	Median Bed Height (cm)	Biomass (g DM m^{-2})	Tissue P (% DM)
Port Ryerse	1	2	1-Jun-01	3	100	6.5	99	n/s
Port Dover	2	0-2	19-Jul-95	20	92	5.9	92	0.114
Nanticoke	3	0-2	19-Jul-95	20	73	7.4	49	0.065
Peacock Point (S)	4	0-2	17-Jul-95	20	100	12.0	320	0.043
	5	2	1-Jun-01	3	100	9.0	307	0.065
	6	2	8-Jul-02	3	100	15.7	156	0.040
	7	5	25-Jul-01	3	78	7.0	68	0.230
	8	5	8-Jul-02	3	97	4.4	68	0.120
	9	10	1-Jul-01	3	73	3.0	10	n/s
	10	10	14-Jun-02	3	10	1.0	0.74	0.200
Hoover Point (S)	11	2	8-Jul-02	3	100	10.3	185	0.050
Sandusk Creek mouth	12	0-2	19-Jul-95	20	99	11.0	150	0.050
Featherstone Point	13	0-2	13-Jul-95	20	99	19.0	600	0.045
West of Low Point	14	0-2	13-Jul-95	20	93	7.7	360	0.036
Grant Point (S)	15	0-2	13-Jul-95	20	96	14.0	440	0.062
	16	2	15-Jul-02	3	100	8.1	337	0.063
Splatt Bay (G. River)	17	0-2	12-Jul-95	20	98	18.0	180	0.095
Rock Point (S)	18	0-2	12-Jul-95	20	75	6.2	71	0.052
	19	2	8-Jul-02	3	100	11.6	162	0.230
Mowhawk Point	20	0-2	12-Jul-95	20	93	9.8	310	0.028
	21	0-2	2-Jul-02	20	100	15.0	319	0.063
Lowbanks	22	2	1-Jun-01	3	96	7.9	90	0.060
	23	5	1-Jun-01	3	100	7.3	28	0.129
	24	10	1-Jun-01	3	100	3.0	5	0.140
Long Beach	25	0-2	2-Jul-02	40	43	4.0	38	0.120
Grabel Point (west side)	26	0-2	2-Jul-02	20	4	1.0	1	0.061
Grabel Point (east side)	27	0-2	2-Jul-02	20	82	8.0	99	0.072
Morgans Point (west side)	28	0-2	2-Jul-02	20	24	2.0	<1	0.057
Morgans Point (east side)	29	0-2	11-Jul-95	20	87	7.9	390	0.060
	30	0-2	2-Jul-02	20	97	16.0	419	0.048

Rathfon Point (S)	31	0-2	11-Jul-95	20	87	8.0	220	0.040
	32	0-2	2-Jul-02	20	67	9.0	78	0.073
	33	2	8-Jul-02	3	100	11.6	52	0.098
Sugar Loaf Point	34	0-2	11-Jul-95	20	94	6.7	220	0.048
Whitemans Point	35	0-2	17-Jul-95	20	90	4.6	360	0.048
Point Abino	36	2	1-Jun-01	3	100	n/s	135	0.078
Windmill Point	37	0-2	17-Jul-95	20	93	6.5	330	0.046
Bertie Bay	38	0-2	10-Jul-95	20	91	5.7	340	0.045

Algal material was spun in a salad spinner for 20 s and the fresh mass (FM) determined. Sub-samples were taken for identification. Approximately 10 g FM was dried at 60°C for 24 h then reweighed to obtain the dry mass (DM) and the FM to DM conversion ratio. The dried material was then ground to a fine powder using a ball grinder, and a sub-sample was ashed at 440°C for 1 h and the Ash Free Dry Mass (AFDM) calculated. Ashed material was analyzed for tissue phosphorus using the methods of Planas et al. (1996) for phosphorus extraction, and Stainton et al. (1977) for soluble reactive phosphorus (SRP) measurement. Dried algal tissues were analyzed for tissue C and N using a CE-440 Elemental Analyzer (EAI).

Nearshore water samples were collected at each site 1 m above the *Cladophora* bed using a Van Dorn sampler or while SCUBA diving and swimming up current from the sampling location (to minimize the potential for re-suspended material being collected in sample). The north shore 10-m bathymetry contour is typically 1.5 to 5.0 km from shore. Temperature was logged at each site, 0.1 m above the lake bottom, using HOBO tidbit temperature loggers (Onset Corporation) at 30 min discrete intervals for the majority of the ice-free season. Light extinction coefficients (kPAR) were calculated directly from profiles using a LICOR flat plate collector (Wetzel and Likens 1979), or from transmissometer deployments (during non-daylight hours) and a derived relationship between light extinction coefficients and transmissivity. 'Offshore' Eplimnetic water samples were collected at multiple stations, ranging from 11m to 65m lake depth, throughout the eastern basin from the CSS Limnos. Soluble reactive phosphorus (SRP) and total phosphorus from unfiltered samples (TP) were sampled using the protocols of Charlton et al. (1999) and analyzed by the National Laboratory for Environmental Testing (NLET) at the National Waters Resource Institute (Environment Canada 1979).

Digitized bathymetric maps of Lake Erie (NOAA 1998) and bottom substratum composition (Rukavina and St. Jacques 1971; St. Jacques and Rukavina 1973) were used to calculate the area of

rocky lake bottom within the 0-10 m contours of the eastern basin's northern shoreline. These maps were also used to calculate the volume of overlaying water in the 0-10 m depth zone (north shore only), and the 11-67 m depth zone (offshore). In the offshore zone the upper 20 m of the water column was used for subsequent calculations of nutrient budgets for the epilimnion.

2.4 Results

2.4.1 Physical and chemical environment:

The northern shoreline of Lake Erie's eastern basin is dominated by bedrock (~80 %), with smaller areas of glacial till and sand (Rukavina and St. Jacques 1971; St. Jacques and Rukavina 1973). All sites were located on rocky lake bottoms and shallow depths (0.5-10 m). The near shore rocky lake bottoms are typically large, flat expanses of limestone of low slope interspersed with smaller areas of cobbles and boulders. These shallow (≤10 m) rocky lake bottoms in the eastern basin currently have mean densities of *D. bugensis* between 4,000-11,000 ind. m^{-2} (Patterson et al. submitted). *Cladophora* typically grew attached to either rocky surfaces or living mussel shells, and was absent in small patches where the accumulation of sediment or dead shell material precluded their attachment to a hard, stable surface.

The northern shoreline of Lake Erie's eastern basin is a highly dynamic environment. The predominant winds are from the southwest with a resulting fetch exceeding 80 km. South-westerly winds of 10-15 km/h with corresponding 1-2 m waves are common, 15-25 km h^{-1} winds are not unusual, and physical forcing processes result in the re-suspension of organic and inorganic particles and a reduction in light penetration. As such, variability in light extinction coefficients (kPAR) increases at shallower depths due to increased potential for sediment resuspension (Figure 2.2). Secchi depth readings were highly correlated to kPAR (Figure 2.3). Seasonal epibenthic water temperatures fluctuated from near 0°C (winter) to approximately 25°C in August, then began declining in September (Figure 2.4).

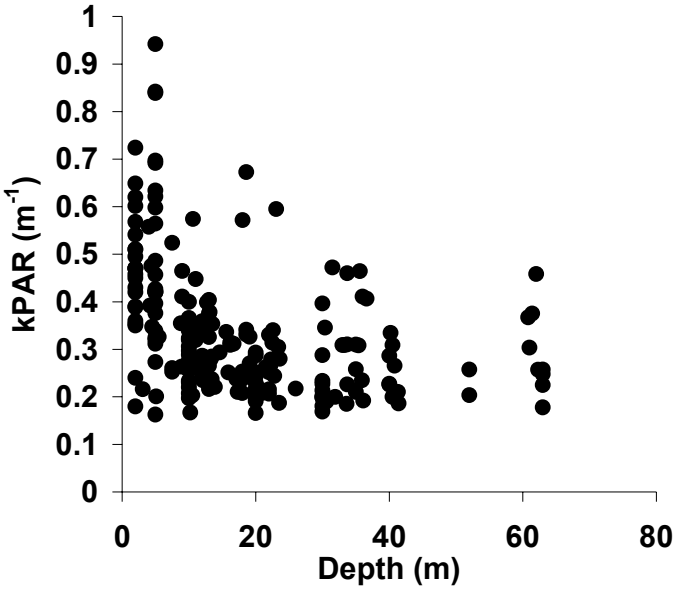

Figure 2.2. Variability in light extinction coefficients (kPAR) with station depth. All measurements were conducted *in situ* during 2001-2002 (May-November) in the eastern basin of Lake Erie. The majority of near shore measurements (<10 m lake depth) are from the Peacock Point to Hoover Point reach of shoreline, while offshore measurements (≥10 m lake depth) were made at numerous sites throughout the basin.

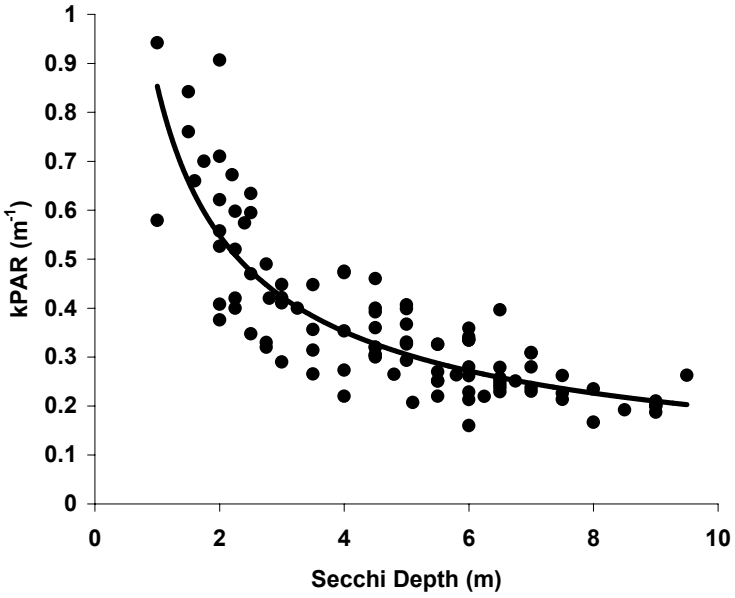

Figure 2.3. Extinction coefficients (kPAR) vs. secchi depth (m) measured in eastern Lake Erie during 2001-2003 (kPAR = 0.12 + (0.84 *(Secchi)$^{-1}$), R^2 = 0.79, Fit Standard Error = 0.073, n = 228).

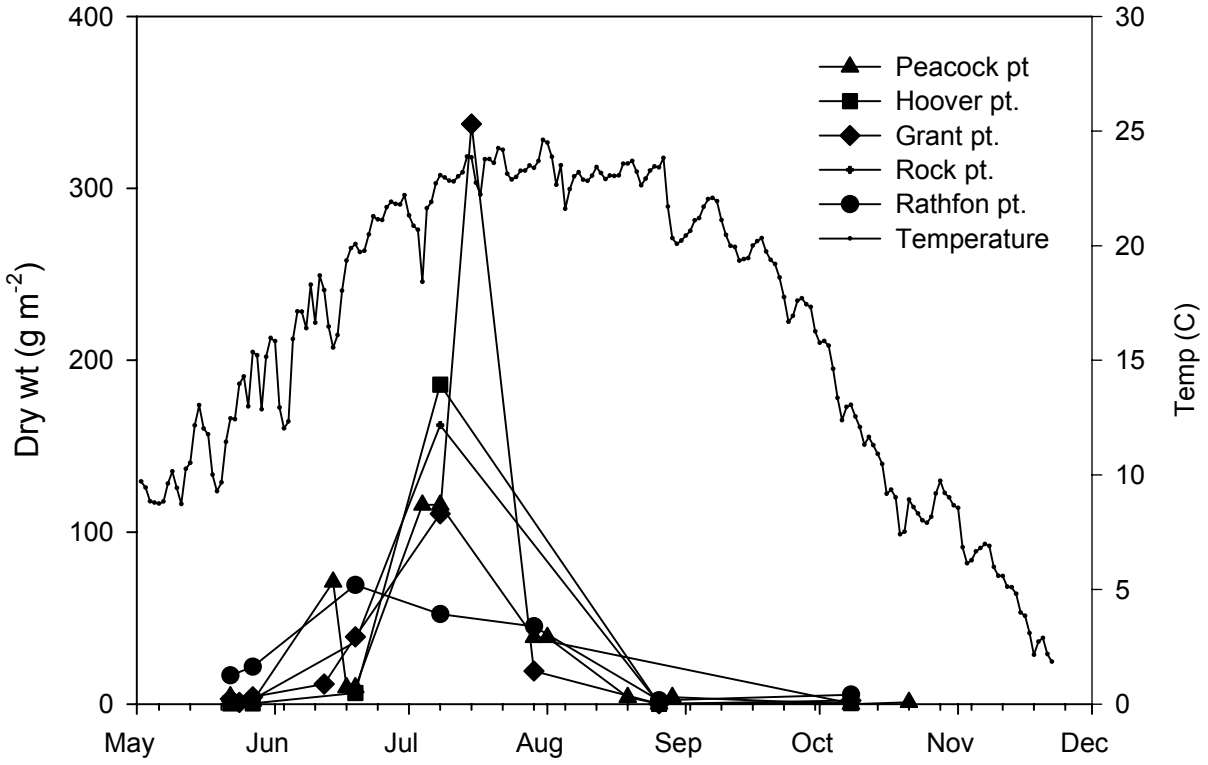

Figure 2.4. Seasonal changes in water temperature and *Cladophora* biomass at 5 sites in the eastern basin of Lake Erie during 2002. All sites were at 2 m depth. At peak biomass the standard error ranged from 6-42% of the mean biomass at each site. Reported daily mean temperatures were recorded using *in situ* Tidbit© temperature loggers at 0.25 m from the lake bottom and averaged among the 5 sites.

Mean SRP concentrations in north shore and offshore waters were high in spring (6-8 μg L^{-1}), and declined to seasonal low values (below the 0.2 ug L^{-1} limit of detection) in September, then increased in the autumn (~3 μg L^{-1})(Table 2.2). The north shore depth zone (0-10 m), and the epilimnion of the offshore zone (11-67 m), have water volumes of 1.3 km^3 and 94 km^3 respectively. Total SRP ranged from 0.25 to 7.8 tonnes P in the north shore waters, and 18 to 700 tonnes in the offshore waters (Table 2.2). Mean TP, from unfiltered samples, ranged from 7.4 to 12.5 ug L^{-1} in the north shore waters, and 7.0 to 13.6 μg L^{-1} in offshore waters. Total TP ranged from 9.3 to 15.8 tonnes in the north shore waters, and from 650 to 1300 tonnes in offshore waters (Table 2.2).

Table 2.2 Ambient phosphorus concentrations in north shore and offshore waters in the eastern basin of Lake Erie during 2002.

	North shore (0-10 m)							Offshore (11-65 m)						
Month	n	Mean SRP ($\mu g\ L^{-1}$)	sd	Total SRP Nshore (tonnes)	Mean TP ($\mu g\ L^{-1}$)	sd	Total TP Nshore (tonnes)	n	Mean SRP (ug/L)	sd	Total SRP Offshore (tonnes)	Mean TP ($\mu g\ L^{-1}$)	sd	Total TP Offshore (tonnes)
Apr	11	6.21	2.89	7.83	12.5	1.55	15.8	18	7.59	2.02	701	13.6	1.23	1256
May	8	2.34†	0.75	2.94	10.46†	1.38	13.2	8	4.56†	2.57	421	12.31†	1.43	1137
Jun	11	1.70	0.98	2.14	9.1	1.90	11.4	16	1.36	0.65	125	9.7	2.19	896
Jul	11	1.20	0.30	1.51	7.4	2.37	9.3	16	1.19	0.69	110	7.0	2.08	647
Aug	3	0.93	0.12	1.18	9.7	3.59	12.2	4	1.28	0.25	118	8.9	1.16	823
Sept	10	nd	n/a	0.25	9.8	4.16	12.3	15	nd	n/a	18	9.1	2.14	844
Oct	9	2.82	1.29	3.55	10.7	2.47	13.5	13	2.96	1.68	274	10.2	0.86	944

2.4.2 *Cladophora* distribution and bed characteristics

Seasonally, the areal coverage of *Cladophora* achieved its maximum by mid June to early July 2002 at sites of shallow depth (≤2 m). This maximum areal coverage was maintained until the mid-summer die-off period (between the July 15 and July 29 sampling dates) when areal coverage began to decline. By August 26, areal coverage had declined from nearly 100% at most sites to 2-5 %, then increased once again at most sites by September. Combining our 1995, 2001 and 2002 data *Cladophora* had a median areal coverage estimate of 95% across the rocky near shore sites during the peak-growing season (data from Table 2.1). Some sites, particularly those in shallow zones (≤2 m) on the west sides of peninsulas (sites 26 and 28 in Table 2.1), had reduced areal coverage. My sampling design did not allow us to empirically determine the causes of this phenomenon, however algal coverage in these shallow westerly facing littoral zones may be lower due to the prevalent southwesterly winds that increase turbulence and sloughing. At depths 2 m or greater I saw no effects of water turbulence on early summer coverage patterns, although I noted qualitatively that areal coverage less than 100% occurred primarily where small (cm^2) or large (m^2) patches of previously sedimented material (including shells of dead *Dreissena*) on the lake bottom that prevented the attachment of filaments. Areal coverage at most of the 5 and 10 m sites was at or near 100 % by early summer (Table 2.1).

The maximum filament lengths at all sites during 2002 followed a similar pattern to coverage, increasing throughout the spring until the end of July, when much of the algal material had been sloughed. *Cladophora* at 2 m sites achieved maximum filament lengths of approximately 30-35 cm by mid July 2002 (data not shown). After the sloughing period, *Cladophora* at some sites showed increasing filament lengths in the autumn, although little biomass accumulated during that time (Figure 2.4). Maximum filament lengths declined greatly with increasing depth beyond 2 m, such that at 10 m only 0.5-2 cm filaments were present at My sites. The median height of the *Cladophora* bed from the lake bottom was 8.0 cm at depths ≤2 m during the peak-growing season (Table 2.1).

2.4.3 Areal Biomass

Seasonally, biomass at most of my 2 m sites (2002) increased slowly until late June, then rapidly until mid July (Figure 2.4). These sites showed a range of seasonal maximum biomass from 78 g DM m^{-2} at Rathfon point to 337 g DM m^{-2} at Grant point (Figure 2.4). Biomass declined dramatically after

daily averaged water temperatures reached 22.5°C (Figure 2.4), and by July 29 all sites had biomass values <50 g DM m^{-2}. The importance of short sampling intervals is highlighted by my increased sampling effort at the Grant point site. The *Cladophora* biomass at Grant point tripled within seven days in mid July to reach a maximum value of 340 g DM m^{-2} (Figure 2.4). Because other sites were not sampled as frequently, I likely did not observe the maximum biomass present at these sites, and biomass values presented in Table 2.1 possibly under-represent true seasonal maximum values. The midsummer sloughing event began between July 15 and July 29 as water temperatures approached 22.5°C. By the end of July areal biomass was reduced to levels <45 g DM m^{-2} and had decreased even further to <2 g DM m^{-2} by September (Figure 2.4). Although filament length increased during the autumn, there was only a small increase in biomass (Figure 2.4) because of low areal coverage. Highest biomass levels were reported from the Featherstone to Grant Point (site-date #'s 13-16), Morgans Point (#29-30), and Whitemans Point (#35) shorelines (Table 2.1). Overall, 21 of the 32 shallow water site-date combinations had biomass values over 100 g DM m^{-2} by midsummer, and 13 of these sites had over 300 g DM m^{-2} (Table 2.1). *Cladophora* biomass declined with increasing depth and, although coverage was often high, very little biomass existed at 10 m at any of the sites during the season (Table 2.3).

Table 2.3 The depth distribution, biomass, and algal bed characteristics of *Cladophora* during the peak growth period in the eastern basin of Lake Erie during 2001-2002. 'n' refers to the number of stations where *Cladophora* parameters were sampled and averaged. n/s refers to 'no sample' available for analysis.

				Biomass (g DM m^{-2})						
Depth (m)	n	Areal cover (%)	Median Bed ht (cm)	Max	Min	Mean	Median	Std dev	%N	%P
0.5	12	62	8.2	939.2	<1	196.1	113.9	268.4	n/s	n/s
1	12	94	9.2	780.8	<1	175.3	70.6	230.8	1.9	0.063
1.5	12	88	9.3	486.7	<1	138.5	69.6	156.3	n/s	n/s
2	15	100	10.3	341.7	52.8	146.4	122.8	83.7	2.5	0.070
5	6	96	7.4	111.1	25.4	54.4	53.8	34.4	2.1	0.129
10	5	73	2.9	4.7	0.5	1.9	0.5	2.4	3.1	0.230

The mean seasonal peak biomass for each depth stratum (Table 2.3) was highly correlated with estimates of daily mean PAR reaching each depth (Figure 2.5). PAR values at depth were calculated using surface irradiance values generated for 1 July 2002, which was approximately the midpoint

during the peak growing period (Figure 2.4), under cloudless conditions (Fee 1990), and a negative linear relationship between light extinction and station depth from 0-12 m (Figure 2.2).

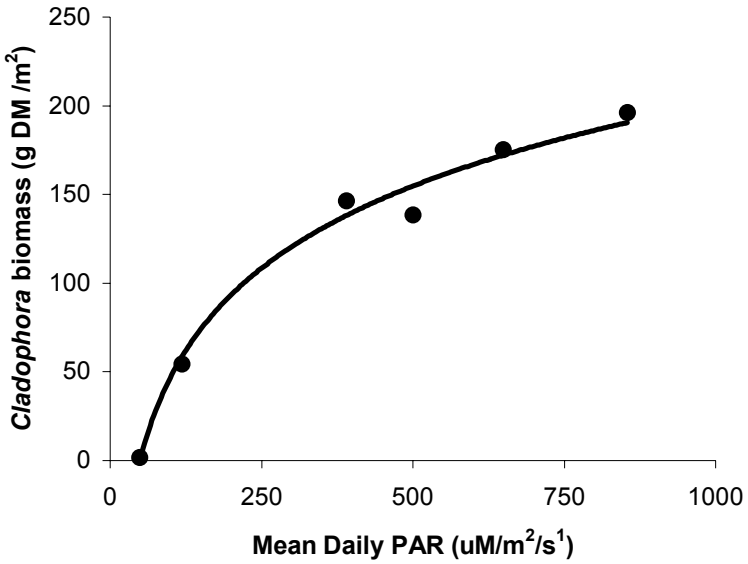

Figure 2.5 Maximum *Cladophora* biomass in eastern Lake Erie as a function of mean daily PAR. *Cladophora* biomass values are mean values from Table 2.3. See text for calculations of mean daily PAR at depth. The regression *Cladophora* biomass and PAR (Biomass (g DM m^{-2}) = 66.82 Ln(Mean Daily PAR) – 260.53 (R^2 = 0.99, n = 6)) was fitted using the least squares method.

2.4.4 Tissue phosphorus, Tissue nitrogen, and Potential Growth

Seasonally, tissue phosphorus concentrations were high during the spring (0.20-0.35 % DM), and then decreased as the biomass increased until the midsummer die-off event. (Figure 2.6). Following the midsummer die-off event, tissue phosphorus concentrations increased to 0.16-0.25 % DM, and then declined to 0.10-0.16 % DM by mid-August. The exception to this general trend at my seasonal sites was Rock Point, a site that is adjacent to the outlet of the Grand River and is often enriched by its high nutrient and sediment-laden plume (T. Howell, Ontario Ministry of the Environment, unpublished data). *Cladophora* at Rock Point maintained high tissue phosphorus concentrations throughout the 2002 growing season, and exhibited the highest total areal phosphorus values of the 5 seasonal sites (Figure 2.7). At all seasonal sites other than Rock point, tissue phosphorus declined to 0.05-0.1 % DM (Figure 2.6) by early July. The low midsummer tissue phosphorus concentrations indicated by the seasonal surveys are similar to values reported in my larger mid-summer spatial dataset (Table 2.1).

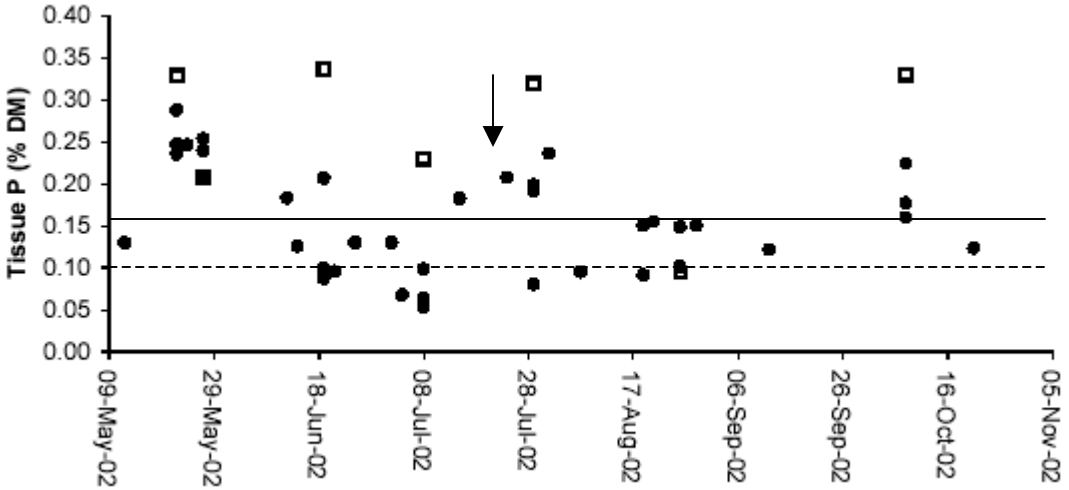

Figure 2.6 Seasonal changes in internal P concentrations in Cladophora tissues measured at 5 shallow (2 m) sites (closed circles) in the eastern basin of Lake Erie during 2002. The Rock Point site (open squares) is located adjacent to the outlet of the Grand River and is considered to be enriched site (see text). The arrow indicates the approximate date when the major sloughing, or 'die-off', period began. The upper solid line represents the tissue P concentration (0.16 % DM) where P limitation of growth begins (Wong and Clark 1976). The lower dashed line represents the tissue P concentration (0.10 % DW) where severe P limitation is expected (see text).

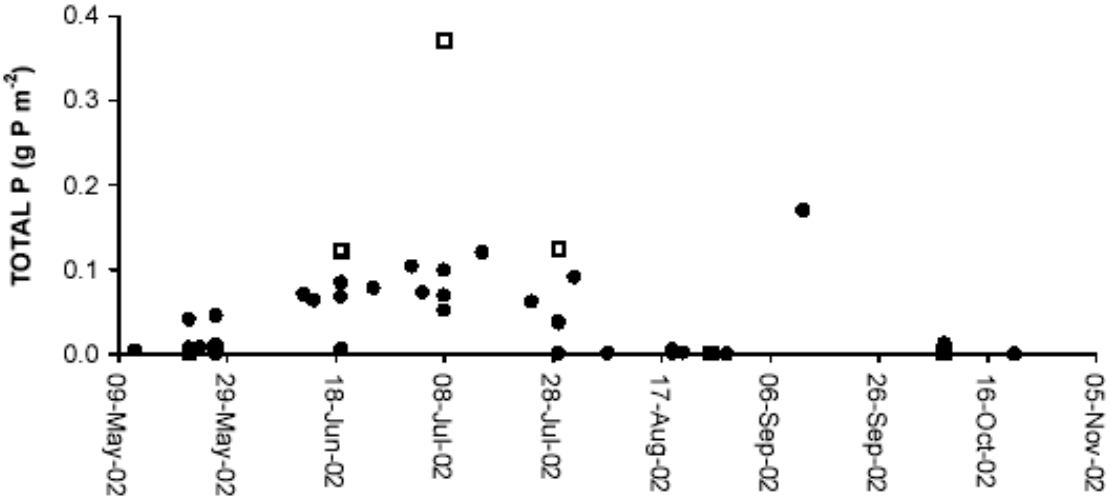

Figure 2.7 Seasonal changes in areal P of *Cladophora* tissues at 5 shallow (2 m) sites (closed circles) in the eastern basin of Lake Erie during 2002. The Rock Point site (open squares) is located adjacent to the outlet of the Grand River and is considered to be nutrient enriched (see text). The arrow indicates the approximate date when the major sloughing, or 'die-off', period began.

The mean midsummer tissue phosphorus concentration at shallow depths (1 m) was 0.06 % DM, increasing to 0.23 % DM at my deepest sites (10 m). Seasonally, tissue nitrogen concentrations

did not follow a consistent pattern between sites (data not shown). However, tissue nitrogen concentrations were always in excess of the 1.1% critical concentration reported by Gerloff and Fitzgerald (1976). During the midsummer period when N limitation might be expected, mean tissue nitrogen concentrations ranged from 1.9 to 3.1 % DM (Table 2.3).

The relationship between tissue phosphorus and specific growth of Lake Huron strains of *Cladophora* has been determined under laboratory conditions, and maximal rates are approximately 0.77 day^{-1} (Auer and Canale 1982). The Droop equation has been used to model specific growth as a function tissue phosphorus concentration (Auer and Canale 1982), and the resulting curve has an inflection point at a tissue phosphorus value near 0.10 % DM. Therefore, at tissue phosphorus concentrations below 0.10 % DM the model predicts that specific growth becomes increasingly sensitive to small shifts in internal phosphorus stores. Wong and Clark (1976) indicate that phosphorus-limited growth begins below 0.16 % DM. The critical concentration of tissue phosphorus required for positive growth is 0.05 % DM (Gerloff and Fitzgerald 1976; Auer and Canale 1982). Using this approach of relating tissue phosphorus concentrations to potential growth, I considered tissue phosphorus concentrations below 0.06 % DM to be 'critically' phosphorus limited, concentrations between 0.05-0.10 % DM to be 'severely' phosphorus limited, concentrations between 0.10-0.16 % DM to be 'moderately' phosphorus limited, and values exceeding 0.16 % DM to be 'non-phosphorus' limited. In general, my seasonal data show two distinct patterns: high tissue phosphorus concentrations in the spring where specific growth rates would not be strongly affected by internal phosphorus stores, and low midsummer tissue phosphorus concentrations where maximum potential growth rates would be reduced and strongly affected by small shifts in internal phosphorus (Figure 2.6). At my seasonal sites 'non-phosphorus' limited growth occurred in the early spring period prior to the onset of rapid growth, and immediately after the midsummer die-off event (Figure 2.6). 'Moderate' phosphorus-limitation occurred between 14 June 2002 and 4 July 2002, and growth was then considered 'severely' phosphorus limited until the midsummer die-off event that occurred between the 20-29 of July. 'Moderate' phosphorus limitation persisted from early August through to early October. *Cladophora* tissues from Rock Point did not follow the general trends outlined above and growth, with the exception of one date in late August, was non-phosphorus limited throughout the season (Figure 2.6).

Tissue phosphorus data were collected from 31 shallow water (≤2 m) sites sampled during mid-summer (Table 2.1). Twenty-eight of these sites had tissue phosphorus values below the 0.10 % DM inflection point, indicating 'severe' phosphorus limitation. The median specific growth rate from

the overall mid-summer dataset (Table 2.1), as predicted from tissue phosphorus via the Droop model, is 0.11 day^{-1}. This value is only 14 % of the maximum specific growth rate of 0.77 day^{-1} (Auer and Canale 1982), and suggests that low tissue phosphorus concentrations can dramatically reduce the upper limit to growth during the midsummer period. Furthermore, *Cladophora* at 17 of these shallow (≤2 m) sites had tissue phosphorus concentrations below the 'critical' value of 0.06 % phosphorus (DM) and would not be expected to exhibit any positive growth during this midsummer period (Table 2.1). The only shallow (≤2 m) sites that did not show 'severe' phosphorus limitation in the midsummer were Port Dover, Rock Point, and Long Beach. *Cladophora* tissues from deeper (5 and 10 m) sites indicated either 'moderately' phosphorus limited or 'non- phosphorus' limited growth.

2.5 Discussion

2.5.1 Distribution

Perhaps the most obvious and important observation of my surveys is that dense stands of *Cladophora* are now a consistent feature across eastern Lake Erie's northern shoreline. My sites encompassed a wide geographical distribution, and for all years sampled (1995, 2001, 2002) areal coverage approached 100 % in shallow (≤5m) rocky zones by early summer. The spatial distribution of *Cladophora* was limited by the availability of hard substrata for attachment, and therefore dominated on exposed rocky peninsulas and shorelines rather than in depositional zones (deep embayments or sand beaches) where hard lake bottoms were overlain by eroded materials (Rukavina and St. Jacques 1971; St. Jacques and Rukavina 1973). In general, the sites that showed the least areal cover were either from very shallow depths (0.5 m) on shorelines exposed to the predominant southwesterly winds where high turbulence and scour likely increased sloughing rates, or that included deposits of unconsolidated material (sand, or empty *Dreissena* shells) that overlaid suitable substratum. In the 1-5 m depth zone it was rare to find suitable substratum that was not completely overgrown by early summer. The midsummer areal biomass (≤5 m) was highly variable among sites, with mean values near 100 g DM m^{-2} (Table 2.3), and was almost always above 50 g DM m^{-2} (Table 2.1). Maximum biomass, up to 940 g DM m^{-2}, was associated with the shallowest depth zone (Table 2.3), and may indicate localized nutrient enrichment. These biomass levels are similar to those in Lake Erie during the 1970's (Table 2.4) when *Cladophora* blooms were deemed a 'serious problem' by the International Joint Commission (Shear and Konasewich 1975).

Table 2.4 Peak seasonal biomass in Lake Erie 1967-2002 (0-3 m depths). Maximum, minimum and median values are from n number of sites indicated within the study. References are as follows 1. Mantai et al. 1982, 2. Neil and Jackson 1982, 3. Kishler in Taft 1975, 4. Lorenz & Herdendorf 1982, and 5. Monaco 1985.

			Biomass (g DW m^{-2})				
Location	Year	n	Max	Min	Median	Std Dev	Reference
L. Erie (east basin)	1977	1	420	420	420	n/a	1
	1979	11	983	4	65	300	2
	1995	58	781	24	280	165	This study
	2001	4	307	28	117	118	This study
	2002	42	939	0	84	205	This study
L. Erie (west basin)	1967	15	268	55	111	58	3
	1979	2	102	100	101	1	4
	1980	2	214	184	199	21	4
	1982	14	235	15	63	60	5

2.5.2 Phosphorus Limitation

Although a number of factors have contributed to the success and dominance of *Cladophora* in the Laurentian Great Lakes, the majority of studies conducted in the 1970's indicated that the high dissolved phosphorus concentrations had promoted high growth rates and bloom occurrences (e.g. Shear and Konansewich 1975; Gerloff and Fitzgerald 1976; Canale and Auer 1982; Lorenz and Herdendorf 1982; Neil and Jackson 1982). By the early 1980's the aggressive phosphorus abatement strategies initiated in the 1970's had significantly reduced phosphorus loading and offshore total phosphorus concentrations in the lower Great Lakes (Dolan 1993; Charlton et al. 1999), and significant declines in both tissue phosphorus concentrations and areal biomass of *Cladophora* were noted in Lake Ontario (Painter and Kamaitis 1987). Although there is a lack of published studies on *Cladophora* from the other lower Great Lakes, presumably tissue phosphorus and biomass of *Cladophora* declined in these systems as well. However, as early as 1995 (Initial survey of T. Howell) *Cladophora* had once again reached nuisance levels in Lake Erie. *Cladophora* blooms and shoreline fouling have recently been noted in Lake Ontario (Campbell et al. submitted), Lake Michigan (Byappanahalli et al. 2003), and localized shorelines of Lake Huron (T. Howell, Ontario Ministry of the Environment, unpublished data). Despite the large reductions in phosphorus loadings and concentrations it is troubling to note that large stands of *Cladophora* are currently widespread in the lower Great Lakes, especially in oligotrophic systems such as the eastern basin of Lake Erie.

Although a significant modeling effort is ongoing to discern which variables were most important to growth, and the relevance of *Dreissena* to the 'resurgence' of *Cladophora*, my present data indicate that increases in spring soluble phosphorus concentrations and shifts in water clarity may be largely responsible for the overall increase biomass post *Dreissena*.

The widespread nature of dense *Cladophora* stands (> 50g DM m^{-2}) across my sites indicates that phosphorus concentrations in the north shore waters (Table 2.2) were sufficient to produce bloom occurrences. Furthermore, the majority of tissue phosphorus was accumulated by mid-June (Figure 2.7), prior to the rapid growth phase that began in mid-June and continued to early July (Figure 2.4), indicating that spring and early summer phosphorus concentrations were most important to growth. With only a few exceptions, tissue phosphorus concentrations were drawn down to extremely low values by early summer (Table 2.1, Figure 2.6) at all my shallow sites (≤2 m). These tissue phosphorus values were generally well below the 0.16 % DM value where growth becomes increasingly sensitive to internal phosphorus stores (Planas et al. 1996), and often close to the critical 0.06 % DM value required for positive growth. Such low tissue phosphorus concentrations indicate that growth likely became strongly phosphorus-limited as stands approached peak biomass.

2.5.3 Light Limitation

While *Cladophora* at shallow water sites showed signs of phosphorus limitation by early summer, those at depths of 5 m or greater maintained high tissue phosphorus concentrations, and had lower areal biomass, indicating that other factors potentially controlled growth at these deeper depths. The potential for photosynthetically active radiation (PAR) to limit growth and accumulated biomass was investigated by assessing photosynthetic light response curves of *Cladophora* vs. estimates of available PAR *in situ* in the same fashion as Lorenz et al. (1991). The photosynthetic response to light in *Cladophora*, as with other algae, follows a hyperbolic (or similar) response to increasing irradiance (e.g. Graham et al. 1982). At low light levels, growth is directly proportional to PAR and growth is considered light limited. As PAR increases past the inflection point (Ik) of the photosynthesis vs. PAR curve, photosynthesis becomes light saturated and increasing PAR has little positive effect on growth rates. Because PAR declines exponentially with depth, the degree to which can be determined from measured PAR extinction coefficients (kPAR), at some depth photosynthetic rates are linearly dependent on available PAR and are termed light limited. The depth (Z_{lim}) where light limitation of *Cladophora* will occur can be estimated using the equation:

$Z_{lim} = (\ln I_0 - \ln I_k)/ kPAR$

where I_0 is the mean surface irradiance during daylight hours, I_k is the inflection point of the photosynthesis vs. PAR curve, and kPAR is the extinction coefficient of PAR through the water column. Due to the high variability in kPAR along the north shore of Lake Erie (Figure 2.2), I chose to estimate Z_{lim} over a range of kPAR values that encompassed most of the variability noted *in situ* (0.2-0.6 m^{-1}), and a mean surface irradiance (I_0) of 807 uE m^{-2} s^{-1} determined by Lorenz et al. (1991) for 39 cloud-free days (April-November) over western Lake Erie. I_k values for naturally growing *Cladophora* at my seasonal sites had a mean value of 205 uM m^{-2} s^{-1} (n=35, sd =175; Chapter 5). These I_k values are below those determined by Graham et al. (1982) for Lake Huron strains of *Cladophora*, where I_k values were approximately 300 uM m^{-2} s^{-1}. Using my estimate of Ik, we estimate Z_{lim} to be 6.9 m, 3.4 m, and 2.3 m at kPAR values of 0.2 m^{-1}, 0.4 m^{-1}, and 0.6 m^{-1} respectively. Because *in situ* kPAR values are typically between 0.4-0.6 m^{-1} (Figure 2.2), the depth of Z_{lim} would generally be expected to fall between 2.3-3.4 m depth, below which growth rates would be light limited. Using the I_k value of Graham et al. (1982) Z_{lim} would fall between 1.6-2.5 m at kPAR values 0.4-0.6 m^{-1}.

The seasonal peak biomass of *Cladophora* over depth (Table 2.3) was highly correlated to estimates of available PAR (Figure 2.5), and allowed us to estimate: 1) the areal biomass of the *Cladophora* beds, and the total P contained within them, at depths other than those I directly sampled; and 2) how shifts in water clarity (i.e. kPAR) could affect the depth distribution and biomass of *Cladophora* across the northern shoreline (Table 2.5). Because sloughing (Canale et al. 1982) and potentially grazing by *Gammarus fasciatus* (Szabo 2004) can be significant loss terms and my estimates of areal phosphorus are based only on the standing crop and the amount of phosphorus contained therein, the estimates presented should be conservative. Overall, by early summer, the *Cladophora* beds along eastern Lake Erie's northern shoreline would have a total mass of approximately 12000 tonnes by dry mass (Table 2.5). This biomass of *Cladophora* would have contained approximately 15 tonnes of phosphorus, most of which would have been removed from the water over a 31 d period (12 May 2002 - 12 June 2002, Figure 2.7) at a mean rate of 0.49 tonnes day^{-1}. The mass removal rate of SRP by *Cladophora* (8 tonnes) during May exceeds the nearshore decline in SRP (6 tonnes) during this period, and is likely an important factor in causing the large SRP gradient between nearshore and offshore (Table 2.2, Student T-test, p = 0.03). The amount of SRP contained within the north shore water mass, however, would have been insufficient to maintain

the P demand by *Cladophora* over the 30-d period, and additional phosphorus from underlying *Dreissena* beds, from surface runoff, or from the offshore water mass would be required.

Table 2.5 The biomass and P content of *Cladophora glomerata* along the northern shoreline of Lake Erie's eastern basin pre and post *Dreissena* colonization. Pre-mussel conditions were assumed to represent an increase in mean kPAR by 0.08 m^{-1} from current, post-mussel conditions (see text).

					Estimated Biomass (tonnes/N shore)				Estimated Phosphorus (tonnes/N shore)			
Depth strata (m)	Total Area (km^2)	Bedrock Area (km^2)	Est Kd Pre-Mussels	Est Kd Post-Mussels	Pre Mussels	Post Mussels	Difference	Difference (% of total)	Pre-Mussels	Post-Mussels	Difference	Difference as % of total
0-1	20.3	18.0	0.64	0.56	3381	3429	48	1.8	2.70	2.74	0.04	0.8
1-2	13.2	13.0	0.62	0.54	1907	2011	104	4.0	1.53	1.61	0.08	1.7
2-3	16.7	15.0	0.59	0.51	1638	1839	200	7.6	1.59	1.78	0.19	3.9
3-4	20.0	16.0	0.56	0.48	1207	1506	299	11.4	1.85	2.31	0.46	9.2
4-5	23.8	18.0	0.53	0.45	815	1248	433	16.4	1.71	2.62	0.91	18.2
5-6	25.9	18.0	0.51	0.43	339	868	529	20.1	0.72	1.84	1.12	22.4
6-7	25.4	18.0	0.48	0.40	0	554	554	21.0	0.00	1.19	1.19	23.7
7-8	22.3	19.5	0.45	0.37	0	332	332	12.6	0.00	0.72	0.72	14.3
8-9	26.5	19.3	0.42	0.34	0	134	134	5.1	0.00	0.29	0.29	5.8
9-10	32.7	19.2	0.40	0.32	0	2	2	0.1	0.00	0.00	0.00	0.0
Total	226.8	174.0			9287	11924	2637		10.10	15.10	5.00	

By June however, both nearshore and offshore water masses had low SRP concentrations (<2 ug L^{-1}) that were not significantly different from one another (Table 2.2, student T-test, p = 0.28). It is during this period (June to July) when *Cladophora* tissue phosphorus concentrations declined rapidly to values considered 'severely limiting' to growth (Figure 2.6a).

The invasion and proliferation of *Dreissena* within the Laurentian Great Lakes has resulted in environmental conditions that are conducive to the growth of *Cladophora*. In the somewhat isolated bays of lakes Huron, Ontario, and Erie, where water quality parameters were studied intensively before and after *Dreissena* colonization, large increases in water clarity and ambient phosphorus were noted. For example, declines in kPAR over *Dreissena* invasion were approximately 0.3 m^{-1} in western Lake Erie (Holland 1993) and between 0.4-0.8 m^{-1} in Saginaw Bay of Lake Huron (Fig. 9b in Fahnenstiel et al. 1995). In the north shore waters of eastern Lake Erie, where current mean mussel densities are 4 x 10^3 to 11 x 10^3 individuals m^{-2} (Patterson et al. submitted), I calculated a decline in kPAR of 0.08/m over the invasion period based on the increase in secchi depth (4-6 m) noted by Howell et al. (1996) and the relationship between secchi depth and kPAR (Figure 2.3). Howell et al.'s (1996) measured increases in water transparency should be conservative since they were taken at a 10 m index station, and *Dreissena* should have a larger effect on water clarity at shallower depths with a reduced overlying water column. The relationship between *Cladophora* biomass and available PAR (Figure 2.5, Equation 2.1):

Peak Biomass = 66.82 Ln (Mean daily PAR) – 260.53 (R^2 = 0.99, n = 6) (Eq. 2.1)

can be used estimate how shifts in mean daily PAR would affect the seasonal peak biomass of *Cladophora* at different depths. Mean daily PAR at each depth is a function of daily mean surface irradiance, depth, and kPAR. To simplify the calculations, and negate the potential effect of different atmospheric conditions before and after *Dreissena*, I considered surface irradiance under cloudless conditions, using a constant value pre and post *Dreissena*. kPAR values for each depth were calculated from the relationship between kPAR and water depth (Figure 2.2) and then increased by 0.08 m^{-1} to represent pre-*Dreissena* conditions. Because this approach is based solely on shifts in water transparency, it would not be expected to provide accurate predictions of how *Cladophora* biomass would change where light does not limit growth (i.e. above I_k or approximately 3 m). Previous studies on Lake Erie (see Table 2.4 for references) limited their surveys to ≤ 3m and my model suggests that, based on an increase in kPAR of 0.08 m^{-1} from current conditions, depths >3 m would have contained 25% of the depth

integrated biomass pre-*Dreissena* (Table 2.5). My surveys indicate that *Cladophora* below 3 m now contributes approximately 40% of the depth-integrated biomass (Table 2.5). Furthermore, when I modeled depth-integrated biomass by shifting kPAR over a range conditions seen in other systems, I noted that although biomass at depths <3 m were not strongly affected (light saturated under most likely scenarios), biomass at depths >3 m was strongly influenced by shifts in kPAR equal to that caused by *Dreissena* in Lake Erie and other systems (Figure 2.8).

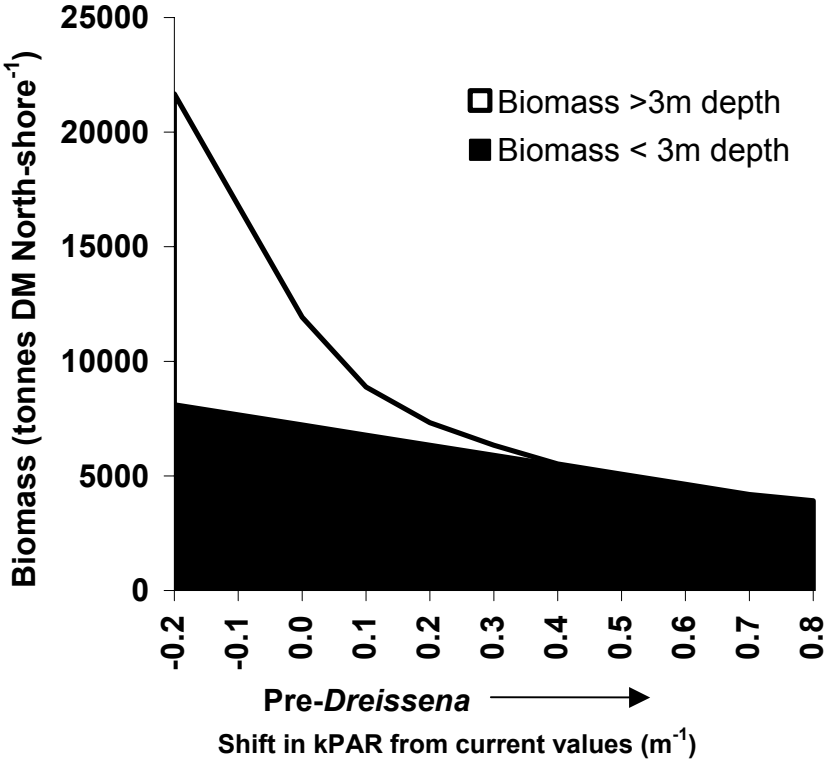

Figure 2.8 Dependence of maximum standing *Cladophora* biomass along eastern Lake Erie's northern shoreline on deviation of mean kPAR from current conditions. Current kPAR values (0) are depth dependent and are presented in Figure 2.2.

2.5.4 Management Implications

Increases in overall water clarity and spring concentrations of SRP attributed to *Dreissena* (Howell et al. 1996; Makarewicz et al. 2000) have undoubtedly increased the habitat and overall biomass of *Cladophora* in eastern Lake Erie. Increases in benthic algal production post-*Dreissena* were also noted in Saginaw Bay of Lake Huron (Lowe and Pillsbury 1995). Unfortunately, my assessment of *Cladophora* in the

western and central basins of Lake Erie is hampered by a lack of data on biomass and distribution. *Cladophora* blooms were a serious problem in the western basin of Lake Erie from the late 1960's to the early 1980's (Table 2.4), however I expect that these blooms subsided in the 1980's, as was the case in Lake Ontario (Painter and Kamaitis 1987), as SRP concentrations were reduced through phosphorus abatement. Increases in water clarity (Holland 1993) and SRP (Makarewicz et al. 2000) in the western basin post-*Dreissena* would likely have a similar positive effect on *Cladophora* distribution and biomass as noted in the eastern basin.

Previous *Cladophora* surveys in Lake Erie during the late 1970's restricted their observations to depths ≤3 m, and my current estimates of biomass within this depth range are similar (Table 2.4). During the 1970's and early 1980's, as management strategies were being designed to control *Cladophora* biomass, there was no reason to expect increases in near shore water clarity. While my data indicate that phosphorus remains the key nutrient controlling bloom occurrences, the increases in water clarity due to *Dreissena* have increased the overall habitat of *Cladophora*, which is now found growing at much deeper depths (Table 2.5). The potential for management of *Cladophora* biomass will ultimately depend on controlling available phosphorus during the spring and early summer. While *Dreissena* have likely increased available phosphorus (to the benthos) through metabolic wastes, feces and pseudofeces production (Hecky et al. 2004), the rapidly declining tissue phosphorus concentrations of *Cladophora* from May-July (Figure 2.6) indicate that phosphorus from *Dreissena* and the overlying water column was insufficient to overcome the growth dilution effect and maintain high growth rates during this time period. Other researchers (Makarewicz et al. 2000) have noted significant increases in spring SRP in all basins of Lake Erie post-*Dreissena* invasion. I hypothesize that mixing of nearshore waters with offshore waters during the early spring (April-May), when a large SRP gradient exists, provides most of the phosphorus required by the *Cladophora* and is therefore critical to controlling biomass accrual. During the period of maximum growth (mid-June to mid-July) the offshore waters had low SRP concentrations (1.2-1.4 $\mu g\ L^{-1}$), and the SRP gradient that had existed between the near-shore and offshore waters during April and May had disappeared (Table 2.2). At most of the shallow water sites tissue phosphorus values are near the critical concentration required for positive growth by early summer (Table 2.1) suggesting that further reductions in dissolved P would reduce *Cladophora* biomass. Conversely, due to the increase in habitat and depth of light saturated growth, increases in local or basin-wide ambient P could accentuate the '*Cladophora* problem' even further.

The offshore zone of the eastern basin of Lake Erie is oligo-mesotrophic (Table 2.2, Wetzel 1983), however the widely distributed nearshore blooms of *Cladophora* indicate that the northern coastal areas are experiencing severe eutrophication. The underlying causes of this eutrophication remain unclear, but appear linked to increased water clarity and bioavailability of phosphorus attributable to the dense communities of *Dreissena*. The implications of the *Cladophora* blooms, and their subsequent die-off and decomposition, are wide ranging and include those discussed for years prior to phosphorus abatement. Also highly important, although largely unknown, are the implications of these widespread blooms to nutrient cycling, and to the density and diversity of nearshore food web members; and the implications of the die-off, transport, and decomposition of the large amounts of organic material to rates of hypolimnetic oxygen consumption, the deep water anoxia phenomena noted in the central basin of Lake Erie, and the use of *Escherichia coli* as an indicator of fecal bacteria in locations where *Cladophora* accumulates on shorelines (Byappanahalli et al. 2003).

2.6 Literature cited

Auer, M. T., and R. P. Canale. 1980. Phosphorus uptake dynamics as related to mathematical modeling of *Cladophora* at a site on Lake Huron. J. Great Lakes Res., 6: 1-7.

Auer, M. T., and R. P. Canale. 1982. Ecological and mathematical modeling of *Cladophora* in Lake Huron: 2. Phosphorus uptake kinetics. J. Great Lakes Res., 8: 84-92.

Auer, M. T., R. P. Canale, H. C. Grundler, and Y. Matsuoka. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 1. Program description and field monitoring of growth dynamics. J. Great Lakes Res. 8: 73-83.

Bailey, R. C., L. Grapentine, T. J. Stewart, T. Schaner, M. E. Chase, J. S. Mitchell, and R. A. Coulas. 1999. Dreissenidae in Lake Ontario: Impact assessment at the whole lake and Bay of Quinte spatial scales. J. Great Lakes Res., 25: 482-491.

Barton, D. R., and H. B. N. Hynes. Wave-zone macrobenthos of the exposed Canadian shores of the St. Lawrence Great Lakes. J. Great Lakes Res. 4: 27-45.

Bellis, V. J., and D. A. McLarty. 1967. Ecology of *Cladophora glomerata* (L.) Kütz. In southern Ontario. J. Phycol., 3: 57-63.

Blum, J. L. 1956. The ecology of river algae. Bot. Rev. 22: 291-341.

Byappanahalli, M. N., D. A. Shively, M. B. Nevers, M. J. Sadowsky, and R. L. Whitman. 2003. Growth and survival of Escherichia coli and enterococci populations in the macro-alga *Cladophora* (Chlorophyta). FEMS Microbiology Ecology 46: 203-211.

Campbell, L, M., M. N. Charlton, V. P. Hiriart-Baer, S. Higgins, S. Malkin, S. J. Guildford, R. E. Hecky, T. Howell, D. Dejong, and L. F. Moore. Then and now: Historical overview of the nuisance green alga, *Cladophora glomerata* in the Laurentian Great Lakes. Submitted to the J. Great Lakes Res.

Canale, R. P., and M. T. Auer. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 5. Model development and calibration. J. Great Lakes Res., 8: 112-125.

Canale, R. P., M. T. Auer, and J. M. Graham. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 6. Seasonal and spatial variation in growth kinetics. J. Great Lakes Res., 8: 126-133.

Charlton, M. N., R. Le Sage, and J. E. Milne. 1999. Lake Erie in transition: the 1990's. *In*: State of Lake Erie (SOLE) – Past, present, and future. M. Munawar, T. Edsall & I. F. Munawar (eds.). pp 97-123.

Dejong, D. 2000. The growth and distribution of the green alga *Cladophora* at Presqu'ile Provincial Park: Implications for management (Ontario). MES Thesis. Wilfrid Laurier University. 92p.

Dodds, W. K. 1991. Factors associated with dominance of the filamentous green alga *Cladophora glomerata*. Wat. Res., 25: 1125-1132.

Dodds, W. K., and Gudder 1992. The Ecology of *Cladophora*. J. Phycol. 28: 415-427.
Dolan, D. 1993. Point source loadings of phosphorus to Lake Erie: 1986-1990. J. Great Lakes Res. 19: 212-223.

Environment Canada. 1979. Analytical Methods Manual. Inland Waters Directorate, Ottawa, Ontario.

Fahnenstiel, G. L., G. A. Lang, T. F. Nalepa, and T. H. Johengen. 1995. Effects of zebra mussel (Dreissena polymorpha) colonization on water quality parameters in Saginaw Bay, Lake Huron. J. Great Lakes Res., 21: 435-448.

Fee, E. J. 1990. Computer programs for calculating in situ phytoplankton photosynthesis. Rep. 1740. Central and Arctic Region, Department of Fisheries and Oceans, Winnipeg, Manitoba.

Gerlof, G. C., and G. P. Fitzgerald. 1976. The nutrition of Great Lakes *Cladophora*. Ecological Research Series EPA-600/3-76-044. Duluth, Minnesota: U. S. Environmental Protection Agency, Office of Research and Development.

Graham, J. M., M. T. Auer, R. P. Canale, and J. P. Hoffmann. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 4. Photosynthesis and respiration as functions of light and temperature. J. Great Lakes Res., 8: 100-111.

Hecky, R. E., R. E. H. Smith, D. R. Barton, S. J. Guildford, W. D. Taylor, M. Charlton and T. E. Howell. 2004. The near shore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Submitted to Can. J. Fish. Aquat Sci. 61: 1285-1293.

Herbst, R. P. 1969. Ecological factors and the distribution of *Cladophora glomerata* in the Great Lakes. Am. Midl. Nat. 82: 90-98.

Hiriart-Baer, V. P., L. M. Campbell, S. N. Higgins, M. N. Charlton, L. F. Moore, S. J. Guildford, and R. E. Hecky (submitted). *Cladophora* resurgent and revisited: A brief literature review. J. Great Lakes Res.

Hoffmann, J. P., and L. E. Graham. 1984. Effects of selected physiochemical factors on growth and zoosporogenesis of Cladophora glomerata (Chlorophyta). J. Phycol., 20: 1-7.

Holland, R. E. 1993. Changes in planktonic diatoms and water transparency in Hatchery Bay, Bass Island area, Western Lake Erie since the establishment of the zebra mussel. J. Great Lakes Res., 19: 617-624.

Holland, R. E., T. H. Johengen, and A. M. Beeton. 1995. Trends in nutrient concentrations in Hatchery Bay, western Lake Erie, before and after *Dreissena polymorpha*. Can. J. Fish. Aquat. Sci., 52: 1202-1209.

Howell, T. 1998. Occurrence of the alga *Cladophora* along the north shore of Eastern Lake Erie in 1995. Ontario Ministry of the Environment. ISBN 0-7778-8172-1. PIBS 3716E. 37p.

Howell, E. T., C. H. Marvin, R. W. Bilyea, P. B. Kauss, and K. Somers. 1996. Changes in environmental conditions during *Dreissena* colonization of a monitoring station in eastern Lake Erie. J. Great Lakes Res. 22: 744-756.

Szabo, R. 2004. The benthic food web on nearshore hard substrates at Peacock Point, eastern Lake Erie. M.Sc. Thesis. University of Waterloo, Waterloo, Ontario, Canada.

Lorenz, R. C., and C. E. Herdendorf. 1982. Growth dynamics of *Cladophora glomerata* in western Lake Erie in relation to some environmental factors. J. Great Lakes Res 8: 42-53.

Lorenz, R. C., M. E. Monaco, and C. E. Herdendorf. 1991. Minimum light requirements for substrate colonization by *Cladophora glomerata*. J. Great Lakes Res. 17: 536-542.

Lowe, R. L., and R. W. Pillsbury. 1995. Shifts in benthic algal community structure and function following the appearance of Zebra mussels (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron. J. Great Lakes Res. 21: 558-566.

Makarewicz, J. C., P. Bertram, and T. W. Lewis. 2000, Chemistry of offshore surface waters of Lake Erie: Pre- and Post-*Dreissena* introduction. (1983-1993). J. Great Lakes Res. 26: 82-93.

Millner, G. C., and R. A. Sweeney. 1982. Lake Erie *Cladophora* in perspective. J. Great Lakes Res. 8: 27-29.

Neil, J. H., and M. B. Jackson. 1982. Monitoring *Cladophora* growth conditions and the effect of phosphorus additions ant a shoreline site in northeastern Lake Erie. J. Great Lakes Res., 8: 30-34.

Neil, J. H., and G. E. Owen. 1964. Distribution, environmental requirements and significance of *Cladophora* in the Great Lakes. *In*: Proc. 7th Conference on Great Lakes Research, pp. 113-121.

Nicolls, K. H., and S. J. Standke. 1997. Effects of zebra mussels on chlorophyll, nitrogen, phosphorus, and silica in north shore waters of Lake Erie. Ministry of Environment and Energy, Toronto. ISBN 0-7778-6707-9, PIBS 3856E.

Nicolls, K. H.,G. J. Hopkins, S. J. Standke, and L. Nakamoto. 2001. Trends in total phosphorus in Canadian near-shore waters of the Laurentian Great Lakes: 1976-1999. J. Great Lakes Res. 27: 402-422.

Nicolls, K. H., S. J. Standke, and G. J. Hopkins. 1999. Effects of dreissenid mussels on nitrogen and phosphorus in north shore waters of Lake Erie. In: State of Lake Erie (SOLE) – Past, present, and future. M. Munawar, T. Edsall & I. F. Munawar (eds.). pp 323-336.

NOAA. National Oceanic and Atmospheric Administration. 1998. Bathymetry of Lake Erie and Lake St. Clair. CD-ROM, National Geophysical Data Center, GLERL, Office of Oceanic and Atmospheric Research. http://www.ngdc.noaa.gov/mgg/greatlakes/

Painter, D. S., and G. Kamaitis. 1987. Reduction of *Cladophora* biomass and tissue phosphorus in Lake Ontario, 1972-83. Can. J. Fish. Aquat. Sci. 44: 2212-2215.

Patterson, M, W. R., J. J. H. Ciberowski, and D. R. Barton. Submitted. The distribution and abundance of *Dreissena* species (Dreissenidae) in Lake Erie, 2002. J. Great Lakes Res.

Planas, D., S. C. Maberly, and J. E. Parker. 1996. Phosphorus and nitrogen relationships in *Cladophora* glomerata in two lake basins of different trophic status. Freshwater Biology 35: 609-622.

Rukavina, N. A. and D. A. St. Jacques. 1971. Lake Erie nearshore sediments Fort Erie to Mohawk point, Ontario. Proc. 14th Conf. Great Lakes Res. 387-393.

Shear, H. and E. E. Konasewich. 1975. *Cladophora* in the Great Lakes. International Joint Commission. 179p.

Sheath, R. G. and K. M. Cole. 1992. Biogeography of stream macroalgae in North America. J. Phcol. 28: 448-460.

St. Jacques, D. A. and N. A. Rukavina. 1973. Lake Erie nearshore sediments – Mohawk point to Port Burwell, Ontario. Proc. 16th Conf. Great Lakes Res. 454-467.

Stainton, M. P., M. J. Capel, and F. A. J. Armstrong. 1977. The chemical analysis of freshwater. Can. Fish. Mar. Serv. Misc. Spec. Publ. 25, 180p.

Stevens, R. J., and M. A. Neilson. 1987. Response of Lake Ontario to reductions in phosphorus load, 1967-82. Can. J. Fish. Aquat. Sci., 44: 2059-2068.

Systat Software Inc. 2002. Table Curve 2.1. Version 5.01.

Taft, C. E. 1975. History of *Cladophora* in the Great Lakes. In: *Cladophora* in the Great Lakes. H. Shear and D. E. Konasewich (eds.). International Joint Commission. Pp. 5-16.

Van Den Hoek, C. 1963. Revision of the European species of *Cladophora*. E. J. Brill., Leiden, Netherlands, 248p.

Wetzel, R. G. Limnology. 2nd Edition. Harcourt Brace College Publishers, Toronto. 767p.

Wetzel, R. G., and G. E. Likens. 1979. Limnological Analyses. W. B Saunders Company. Toronto. 357p.

Whitton, B. A. 1970. Biology of *Cladophora* in freshwaters. Water Research 4: 457-476.

Wong, S. L., and B. Clark. 1976. Field determination of the critical nutrient concentrations for *Cladophora* in streams. J. Fish. Res. Board Can. 33: 85-92.

Chapter 3

Modeling the growth, biomass, and tissue phosphorus concentration of *Cladophora glomerata* in eastern Lake Erie: Model Description and Field Testing

3.1 Abstract

Cladophora glomerata is a filamentous alga that currently forms extensive blooms in nearshore areas of Lake Ontario, eastern Lake Erie, Lake Michigan, and isolated locations in Lake Huron. During the late 1970's an extensive effort was put forward to model *Cladophora* growth and biomass accrual based on several highly dynamic ecological variables including: PAR, SRP, water temperature, and carrying capacity (Canale and Auer 1982a). The original 'Canale and Auer' model was developed and validated in proximity to a sewage treatment outfall in Lake Huron and predicted *Cladophora* growth and biomass over a range of SRP concentrations, at shallow depths (0-3m), with reasonable accuracy. I present a revised version of the 'Canale and Auer' model, that we refer to as the *Cladophora* growth model (CGM), which expands its utility to greater depths and to areas of non-point source P loading while reducing the quantity of input data required. The revised model was tested over a single growing season at 5 sites, and 3 depths (2, 5, 10m), that represented a wide geographical distribution and expected range in ecological conditions in eastern Lake Erie. The revised model predicted growth, biomass, and tissue phosphorus concentrations with reasonable accuracy. The revised model is useful for: 1) Predicting *Cladophora* growth, biomass, and tissue phosphorus concentrations under non-point source P loading with no depth restrictions; 2) providing estimates of the timing and magnitude of the midsummer sloughing phenomenon; 3) determining the contribution of *Dreissena* invasion to the resurgence of *Cladophora* in eastern Lake Erie; and 4) developing management strategies for *Cladophora* abatement.

3.2 Introduction

Cladophora glomerata (L.) Kütz is a filamentous green alga that is widely distributed throughout alkaline lakes and rivers at temperate and tropical latitudes (Herbst 1969; Whitton 1970; Sheath and Cole 1992). *Cladophora* growth and bloom formation is greatest in shallow water around lake margins, and due to this conspicuous location *Cladophora* blooms continue to be the most visible sign of cultural eutrophication in the North American Great Lakes. Nuisance growths of *Cladophora* were a common feature of Lakes Ontario, Erie, Michigan and localized zones of Huron and Superior during the 1960's through to the early 1980's (Shear and Konansewich 1975; Taft 1975; Campbell et al. submitted). *Cladophora* blooms were so extensive they warranted special mention by the International Joint Commission (Shear and Konansewich 1975), led to several large research initiatives aimed at understanding the biology and ecology of this organism (e.g. Special Issue JGLR 8(1) 1982), and contributed to the implementation of strict phosphorus controls on sewage treatment facilities and on the removal of phosphates from detergents. Although the majority of research and monitoring of *Cladophora* in the Great Lakes halted from the early 1980's to the mid 1990's, there is sufficient qualitative evidence to suggest that the problem blooms of *Cladophora* had subsided as a result of declining P availability (Painter and Kamaitis 1987; Campbell et al. submitted). However, in 1995 a *Cladophora* survey by the Ontario Ministry of the Environment (OME) revealed that large nuisance blooms were a common feature of the Canadian shorelines of Lake Erie's eastern basin (Howell 1998) and Lake Ontario (Howell pers. comm.). With assistance from several agencies, including the OME, the Ontario Ministry of Natural Resources, and Environment Canada, I implemented a program in 2001 to study the ecology and model the growth of *Cladophora* in eastern Lake Erie.

Phosphorus availability is generally recognized as the key factor controlling *Cladophora* blooms in the Laurentian Great Lakes (Herbst 1969; Gerloff and Fitzgerald 1976; Auer and Canale 1982b; Painter and Kamaitis 1987). Spatial or temporal shifts in water clarity can also have a large effect on the total depth-integrated biomass produced along a reach of shoreline. For example, in Chapter 2 I noted that changes in water clarity attributed to the strong filtering capacity of *Dreissena polymorpha* (zebra mussel) and *D. bugensis* (quagga mussel) increased the habitat of *Cladophora* and caused an increase in depth-integrated biomass by a factor of 1.3. In addition to phosphorus and light, other dynamic parameters including temperature and carrying capacity constrain growth rates and biomass accrual (Auer and Canale 1980; Canale and Auer 1982b; Dodds 1991). Using these parameters, *Cladophora* growth and biomass

were successfully modeled at shallow depths (0-3m) in Lake Huron during the late 1970's (Auer and Canale 1980; Auer and Canale 1982a,b; Auer et al. 1982; Canale and Auer 1982 a,b; Canale et al. 1982; Graham et al. 1982), and portions of the model were applied to Lake Ontario to estimate the potential for *Cladophora* bloom formation during the 1980's (Painter and Jackson 1989). While the 'Canale and Auer' model simulated growth, biomass accrual, and sloughing (Canale and Auer 1982b) it required significantly more input data than the 'Painter and Jackson' model whose focus was to estimate only the potential for *Cladophora* blooms to occur, not to predict biomass (Painter and Jackson 1989). For clarity we refer to these as the 'Canale and Auer' and the 'Painter and Jackson' models respectively.

There are numerous benefits in modeling *Cladophora* growth dynamics in the Laurentian Great Lakes. Firstly, portions of Lakes Erie, Ontario and Michigan are currently experiencing a resurgence of *Cladophora* blooms along with the associated environmental, aesthetic, and economic costs. Modeling is a useful tool for understanding the importance of highly dynamic ecological variables that constrain growth rates. The 'Canale and Auer' model, in particular, is useful for evaluating *Cladophora* management scenarios such as localized or lake wide phosphorus control while accounting for the variability in other important parameters. Secondly, mounting evidence from these lakes has indicated that *Dreissena polymorpha* and *D. bugensis* invasions have led to dramatic changes in water quality that are beneficial to benthic algal growth (Fahnenstiel et al. 1995; Lowe and Pillsbury 1995; Pillsbury et al. 2002; Hecky et al. 2004). Since very little data on *Cladophora* biomass were collected during years immediately preceding *Dreissena* invasion, there is no direct way to ascertain the impact of *Dreissena* on the *Cladophora* 'resurgence' in Lakes Ontario, Erie, and Michigan. The application of a robust and field tested *Cladophora* growth model that incorporates *Dreissena* induced changes in water quality would be a useful tool for hind-casting and determining the contribution of *Dreissena* invasion to the *Cladophora* resurgence. Thirdly, a *Cladophora* growth model may offer some insights and predictive capacity to the mid-summer sloughing phenomenon by identifying the factors causing metabolic imbalance (Canale et al. 1982). And fourthly, the modeling process itself is highly useful for identifying areas where our current understanding of the mechanisms controlling growth, biomass accrual, and sloughing is insufficient. Considering the magnitude of current *Cladophora* problems in eastern Lake Erie (Chapter 2), Lake Ontario (Campbell et al. submitted), and Lake Michigan (Byappanahalli et al. 2003), directed research efforts are needed to understand the causes and solutions to the extensive bloom formations.

When applying the 'Canale and Auer' model directly to eastern Lake Erie I noted several confounding problems that required model modifications. The purpose of this manuscript is to provide a numerical description of the modified model, to describe the model modifications in detail, and to demonstrate the model's performance in eastern Lake Erie. Subsequent chapters will address management implications for *Cladophora*, and the contribution of *Dreissena* in causing the *Cladophora* resurgence.

3.3 Methods

3.3.1 Site Description

The littoral zone of eastern Lake Erie's northern shoreline provides ample habitat for *Cladophora*. Approximately 80% of the shoreline, from Port Dover to Fort Erie (Figure 3.1), consists of bedrock shelves of low slope (Rukavina and St. Jacques 1971; St. Jacques and Rukavina 1973). Areal estimates of bedrock for each depth stratum (0-10m) are presented in Higgins et al. (Chapter 2). The areal coverage of *Cladophora* over hard substratum and at shallow depths (0-5m) is approximately 95% by early summer (Chapter 2). Most of the shoreline, with the exception of several small isolated bays, is exposed to the predominant southwesterly winds with fetches exceeding 100 km. The eastern basin of Lake Erie is considered oligotrophic with mean total phosphorus concentrations ranging from 7-14 $\mu g\ L^{-1}$, and mean SRP concentrations ranging from below analytical detection limits (0.2 $\mu g\ L^{-1}$) to 8 $\mu g\ L^{-1}$, during the ice free season (Chapter 2).

In 2002 I collected data required to model *Cladophora* growth from one site (Peacock Point) at 3 depths (2m, 5m, 10m), and 4 additional sites (Hoover, Grant, Rock, Rathfon) at 2m depths only (Figure 3.1). All sites consisted of bedrock shelves with few rocks or boulders, and nearly all rocky surfaces were colonized by *D. bugensis*. Current density estimates for *D. bugensis* along the north shore of eastern Lake Erie are 4,000 to 11,000 individuals per square meter (Patterson et al. submitted). *Cladophora* filaments were found attached to rock surfaces or directly to shells of living *Dreissena*. Patches of dead *Dreissena* shells, ranging from cm to m in diameter, were occasionally noted at the sites. These patches overlaid suitable hard surfaces for the attachment of *Cladophora* filaments, and *Cladophora* did not colonize the individual shells forming these patches.

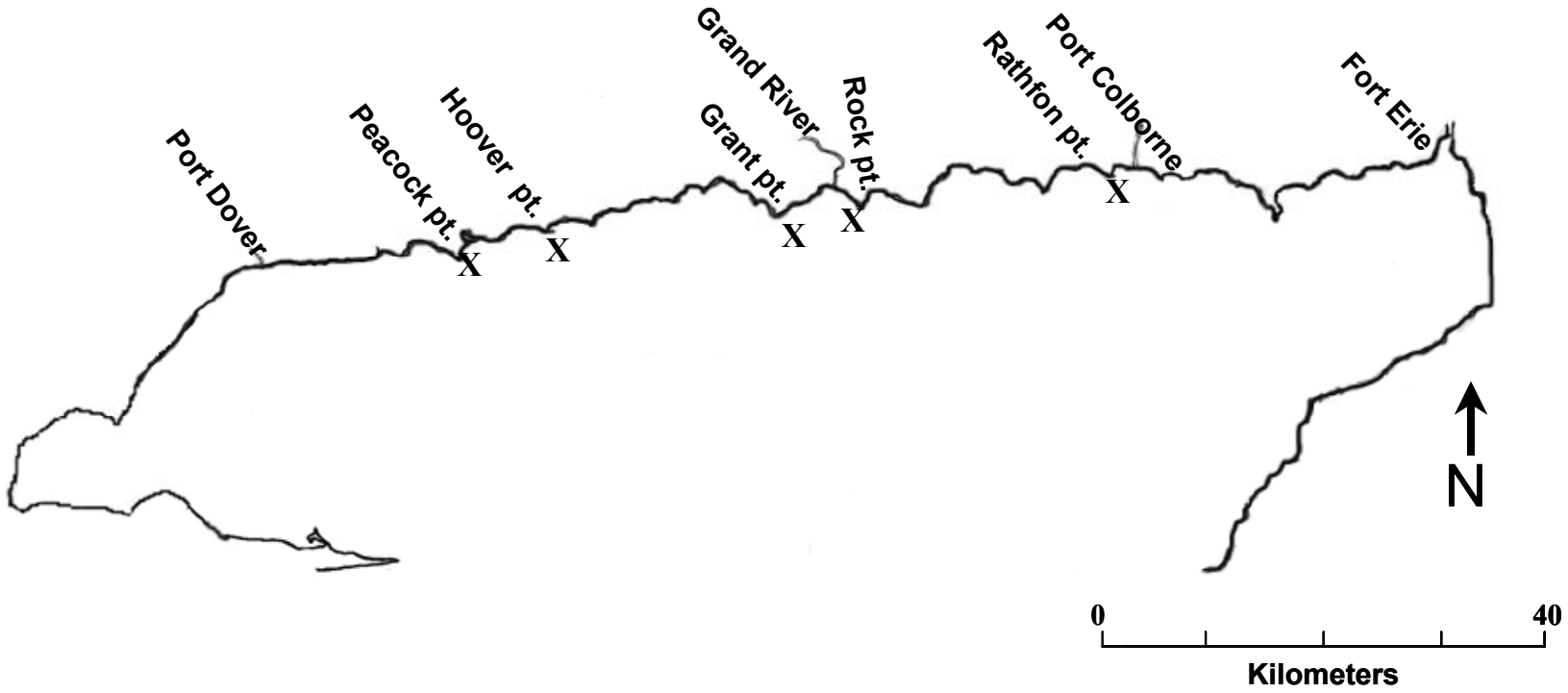

Figure 3.1 Map of the northern shoreline of Lake Erie's eastern basin. Sites names are indicated adjacent to locations where data was collected for *Cladophora* model input and verification. Approximate site locations are identified with an 'X'.

3.3.2 Sampling Methodology

Surface meteorological data, including total solar radiation, wind speed and direction, and wave height were collected and recorded at 30 min intervals, over the duration of our model simulations (22 May 02 to 31 Oct 02), by Environment Canada meteorological buoys moored offshore of Long point and Port Colbourne (buoy #c45142). Surface photosynthetically active radiation (PAR) data was also collected hourly, over a 5-day cloud free period, from the roof of the MNR Port Dover facility, approximately 100m from the Lake Erie shoreline, using a LICOR flat plate collector and data logger. At all sites (2m depth) ambient water temperature was collected using temperature loggers (Tidbit ©, Onset corporation) at 30 min intervals beginning on 16 May 02. Daily mean temperature values were used as model input. Due to the loss of some temperature loggers during autumn storms I was unable to obtain direct measurements of temperature from Rock point and Rathfon point after 08 Oct 02, and from Peacock point after 21 Oct 02. For the remaining portions of the model run, until 31 Oct 02, I estimated temperature at these sites using the mean temperature of remaining sites.

At each site water-samples were collected weekly or bi-weekly from a surface vessel, or using SCUBA, approximately 1m above the *Cladophora* mat using methods described in Chapter 2. Unfiltered water samples were analyzed for turbidity using an HF Instruments DF100 turbidometer. One to 2 L whole water samples were filtered through a pre-weighed, pre-combusted, 0.45 um GF/F filter. The mass of the total suspended solid material within the water sample was calculated as the change in mass of the dried filter before and after filtration, divided by the volume filtered. Filtered water samples were frozen and stored until SRP analysis could be completed. At one site (Peacock point, 5m depth) a moored transmissometer was used to generate estimates of total suspended solids at 10-minute intervals (Weidman 2004) from 07 Jun 02 to 20 Aug 08 02. SRP was analyzed using the molybdate blue method (Stainton et al. 1977) on a Cary 100 Bio spectrophotometer using a 10 cm quartz cuvette.

3.4 Results and Discussion

3.4.1 General Model Description

The model described in this manuscript is based on the 'Canale and Auer' model developed by R.P. Canale, M. T. Auer, L. Graham and colleagues during the late 1970's and presented as six papers in a special issue of the Journal of Great Lake Research focused on the ecology of filamentous algae (JGLR 8(1), 1982). Conceptually, the growth model is based on several dynamic variables including: light,

temperature, phosphorus, and carrying capacity (Figure 3.2). The standing crop, or biomass, is a function of growth and loss (respiration and sloughing) terms. The model predicts specific growth by subjecting an empirically determined maximum specific growth rate, based on available light and temperature, to forcing functions that account for *in situ* conditions that are, most often, sub-optimal. Model variables and coefficients are defined in Table 3.1.

During the initial attempts to validate the 'Canale and Auer' model in eastern Lake Erie I noted that some model coefficients were highly dynamic over the larger depth range in this study and model simulations showed large differences in relation to collected data. Further, the model was designed under conditions of point source phosphorus loading where ambient SRP concentrations did not approach non-detectable limits (Auer et al. 1982). Evidence from our previous *Cladophora* surveys in eastern Lake Erie (Chapter 2) indicated that *Cladophora* blooms were wide spread and associated primarily with non-point source loading. SRP concentrations in eastern Lake Erie also approached levels near or below detection limits during our study, and below concentrations in which the model was validated (Canale and Auer 1982b). In order to ensure the model would accurately predict *Cladophora* growth and biomass accrual in eastern Lake Erie we modified the 'Canale and Auer' model in several ways. These modifications are as follows: 1) Revisions to the equations for net growth and diurnal respiration to account for concerns noted by Painter and Jackson (1989) and to ensure they functioned over the larger depth range within this study; 2) a revision to the equations for carrying capacity, including a dynamic self shading term that is a function of both algal density and available PAR; 3) the inclusion of parameters to account for the high spatial and temporal variability of water clarity; 4) the inclusion of forcing functions to ensure the decline in wind induced sloughing with increases in depth; 5) the inclusion of forcing functions that relate the mid-summer sloughing phenomenon to water temperature; 6) the inclusion of subroutines that allow growth rates to be calculated based on SRP or tissue P concentrations; 7) the inclusion of subroutines to calculate phosphorus storage within accumulated biomass and sloughed material; and 8) the exclusion of point source P loading and transport functions (not shown in Figure 2). Further, we incorporated the revised 'Canale and Auer' numerical model into a user-friendly computer simulation model using Stella © software (Stella 2001) which is available upon request from the corresponding author of this manuscript.

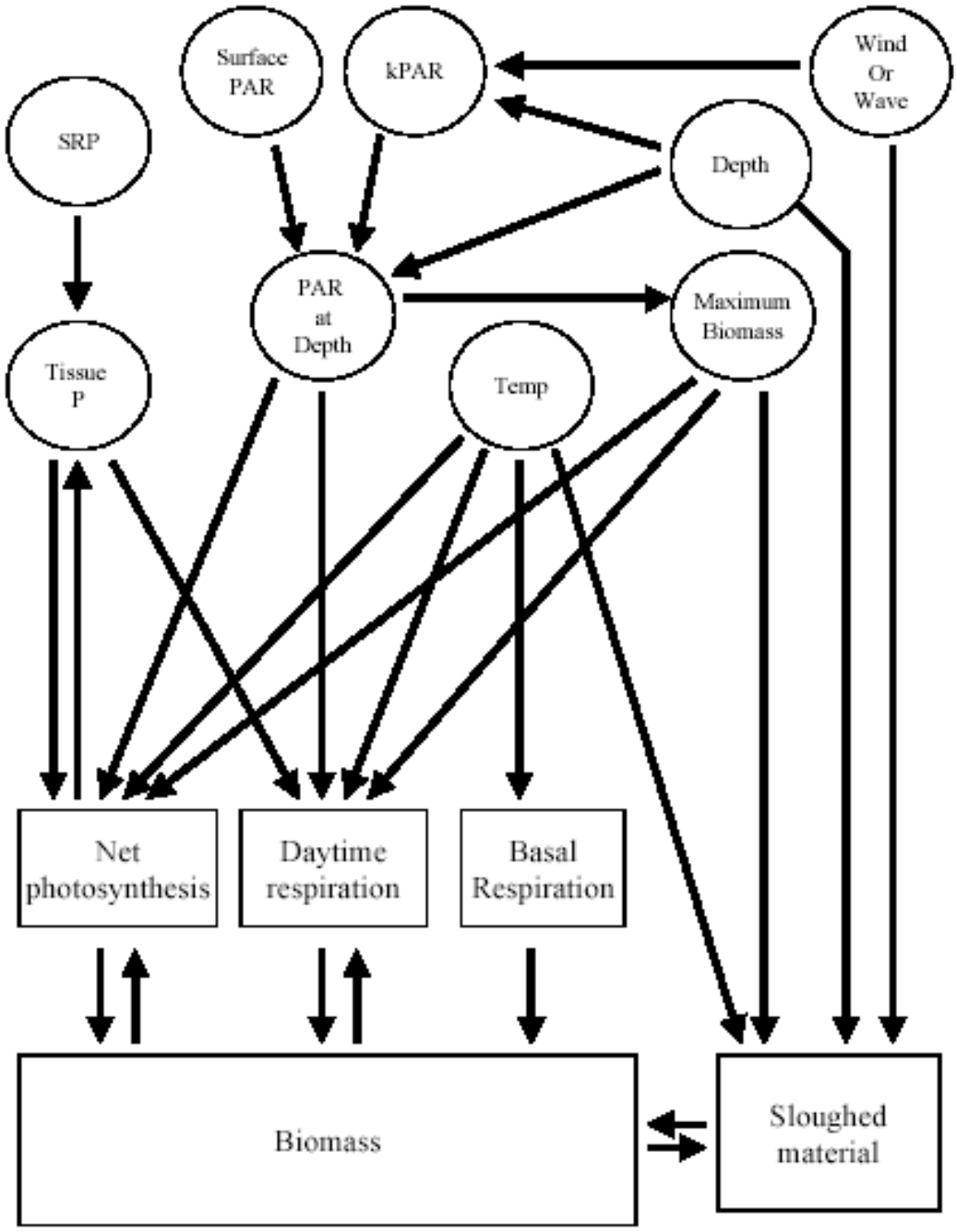

Figure 3.2 A simplified diagram of the modified 'Canale and Auer' *Cladophora* growth model. Model variables and coefficients are described in Table 1.

Table 3.1 Model variables and coefficients for the *Cladophora* growth model (CGM). Asterisks (*) indicate model variable is dynamic and dependant on other model variables. Dashes (-) indicate that the units are dimensionless.

Model Variable	Definition	Units	Value	Source
μ	Gross specific growth rate	Day^{-1}	*	Canale and Auer (1982a)
μ_{NET}	Net specific growth rate	Day^{-1}	*	This study
$\hat{u}_{NET}$	Maximum net specific growth rate	Day^{-1}	0.60	Chapter 5
P_{NET}	Net specific growth polynomial	Day^{-1}	*	Graham et al. (1982)
a	Scaling factor for P_{NET}	-	5.43	This study (see text)
R	Diurnal specific respiration rate	Day^{-1}	*	Canale and Auer (1982a)
R_{DAY}	Daytime specific respiration rate	Day^{-1}	*	Graham et al. (1982)
R_{MAX}	Maximum daytime specific respiration rate	Day^{-1}	0.44	Canale and Auer (1982a)
P_{RLT}	Daytime respiration polynomial	Day^{-1}	*	Graham et al. (1982)
b	Scaling factor for P_{RLT}	-	4.52	This study (see text)
R_B	Specific basal respiration rate	Day^{-1}	*	Canale and Auer (1982a)
PP	Photoperiod	-	0 to 1	Canale and Auer (1982a)
M_P	Multiplier for internal P limitation	-	0 to 1	Canale and Auer (1982a)
Q	Internal P concentration	% P (DM)	*	Canale and Auer (1982a)
Q_0	Minimum internal P concentration	% P (DM)	0.05	Auer and Canale (1982b)
p	P uptake rate	% P day^{-1}	*	Auer and Canale (1982a)
p_{MAX}	Maximum P uptake rate	% P day^{-1}	4.5	Auer and Canale (1982a)
τ	Variation of p_{MAX} with temperature	-	*	Painter and Jackson (1989)
SRP	Soluble reactive phosphorus concentration	ug L^{-1}	*	Auer and Canale (1982a)
Km	Half saturation constant for P uptake as a function of external P concentration	ug L^{-1}	125	Auer and Canale (1982a)
Kq	Half saturation constant for P uptake as a function of internal P concentration	% P (DM)	0.07	Auer and Canale (1982b)
p_D	Growth dilution of internal P	% P	*	Canale and Auer (1982a)
P	Standing stock of P within *Cladophora* bed	g m^{-2}	*	This study (see text)
M_X	Multiplier for carrying capacity	-	0 to 1	Canale and Auer (1982a)
X	Biomass	g DM m^{-2}	*	
X_{MAX}	Maximum biomass density	g DM m^{-2}	*	This study
L	Specific sloughing rate	Day^{-1}	*	Canale and Auer (1982a)
L_{MAX}	Maximum specific sloughing rate	Day^{-1}	*	This study
ω	Wind speed	Km h^{-1}	*	Canale and Auer (1982a)
ω_{MAX}	Maximum wind speed	Km h^{-1}	17.9	Canale and Auer (1982a)
S	Shear stress correction factor	-	*	This study
t_{coeff}	Turbidity coefficient	-	*	This study
t_{MIN}	Site specific minimum turbidity	NTU	*	This study
t	Turbidity	NTU	*	This study

3.4.2 Numerical Model Description

The change in *Cladophora* biomass over time is defined as the gross specific growth rate, minus respiration and other losses, multiplied by the current biomass (Canale and Auer 1982a). Numerically, the change in biomass (g DM day^{-1}) function is described as:

$$dX/dt = [\mu - R - L] * X \qquad \text{(Eq. 3.1)}$$

Where, μ = Gross specific growth rate (day^{-1}),

R = Diurnal specific respiration rate (day^{-1}),

L = Specific loss rate (day^{-1}),

X = *Cladophora* biomass (g DM m^{-2}).

The gross specific growth rate (μ) is a function of the net specific growth rate and the net specific respiration rate modified by several parameters to take into account sub-optimal growth conditions, and is described by the following equation:

$$\mu = [(\mu_{NET} + R_{DAY}) * M_P * M_X] * PP \qquad \text{(Eq. 3.2)}$$

Where, μ_{NET} = Net specific growth rate based on available PAR and temperature only (day^{-1}),

R_{DAY} = Daytime specific respiration rate based on available PAR and temperature only (day^{-1}),

M_P = Growth multiplier for tissue phosphorus (dimensionless),

M_X = Growth multiplier for carrying capacity (dimensionless).

PP = Photoperiod (dimensionless).

The parameters μ_{NET} and R_{DAY} (Equation 3.2) replace parameters M_{LT} (growth multiplier for light and temperature) and μ_{MAX} (maximum gross specific growth rate under optimal P) from the 'Canale and Auer' model. The replacement of these parameters was made to correct model errors under low ambient irradiance values (originally noted by Painter and Jackson (1989)) that occur at shallow depths in response to short term reductions in water clarity or at deeper depths as ambient PAR declines. In our revision (Equation 3.2), the maximum gross specific growth rate (unmodified by M_P or M_X) is calculated from μ_{NET} (Equation 3.3) and R_{DAY} (Equation 3.4), which are maximal rates under a given set of light and temperature conditions, unmodified by M_P and M_X. The value for $\hat{u}_{NET}$, 0.6 day^{-1}, was lower than the

value used by Canale and Auer (1982a), and was set as the maximal net specific growth rate noted in photosynthesis vs. irradiance experiments on *Cladophora* from Lake Erie during 2002 (Chapter 5).

$$\mu_{NET} = \hat{u}_{NET} * [P_{NET} * a] \quad \text{(Eq. 3.3)}$$

Where, $\hat{u}_{NET}$ = Maximum net specific growth rate (0.6 day^{-1})
P_{NET} = Polynomial for net photosynthesis (dimensionless),
a = Scaling factor for net growth (5.43, dimensionless),

$$R_{DAY} = R_{MAX} * [P_{RLT} * b] \quad \text{(Eq. 3.4)}$$

Where, R_{MAX} = Maximum daytime specific respiration rate (0.44 day^{-1})
P_{RLT} = Polynomial for daytime respiration (dimensionless),
b = scaling factor for light respiration (4.52, dimensionless).

Painter and Jackson (1989) noted that errors in the 'Canale and Auer' model resulted from the use of dissimilar scaling factors for daytime respiration in calculations of the gross specific growth rate and the diurnal respiration rate. My modifications split the gross specific growth rate into it's constituent parameters, μ_{NET} and R_{DAY}, and scaling factors are applied to each value independently (Equations 3.3 and 3.4). The use of independent scaling factors for P_{NET} and P_{RLT} simplifies the model structure, ensures that R_{DAY} is identical in calculations of μ (Equation 3.2) and R (Equation 3.8), and corrects the model errors noted by Painter and Jackson (1989) at low irradiance values. The scaling factors used in Equation 3.3 and 3.4 force the polynomial equations for net specific growth (P_{NET}) and daytime specific respiration (P_{RLT}) to vary from 0-1. These values are then multiplied by $\hat{u}_{NET}$ and R_{MAX} such that μ_{NET} and R_{DAY} represent optimal rates under a given set of light and temperature conditions. Using the polynomial equations of Graham et al. (1982) the maximum achievable value for P_{NET} is approximately 0.184 day^{-1}, occurring at PAR and temperature values of 400 uE m^{-2} s^{-1} and 14.5 °C respectively. The scaling factor (a) required to force P_{NET} to vary from 0-1 is 5.43. The maximum achievable value for P_{RLT} using Graham et al.'s (1982) equations is approximately 0.221 day^{-1}, occurring at PAR and temperature values of 1200 uE m^{-2} s^{-1} and 17 °C respectively. The scaling factor (b) to force P_{RLT} to vary from 0-1 is 4.52.

The forcing function M_P incorporates the relationship between internal phosphorus concentrations and the gross specific growth rate as determined by Auer and Canale (1982b) and is defined by the following equation:

$$M_P = 1 - [Q_0/Q] \qquad \text{(Eq. 3.5a)}$$

Where, Q_0 = Minimum cell quota for internal phosphorus (% DM),
Q = Internal phosphorus concentration (% DM).

As in the original 'Canale and Auer' model, Q is calculated as the difference between P uptake and dilution through growth (Canale and Auer 1982a). P uptake (p) is calculated as:

$$p = p_{MAX} * \tau * (SRP/(Km+SRP)) * (Kq/(Kq+Q-Q_0)) \qquad \text{(Eq. 3.5b)}$$

Where, p_{MAX} = maximum specific P uptake velocity (day^{-1}),
τ = Temperature dependant coefficient for P uptake (dimensionless),
Km = Half saturation constant for uptake as a function of external SRP concentration ($\mu g\ L^{-1}$),
SRP = Soluble reactive phosphorus concentration ($\mu g\ L^{-1}$),
Kq = Half saturation constant for uptake as a function of internal P concentration (%P DM).

The coefficients p_{MAX}, Km, and Kq, remain identical to those determined by Auer and Canale (1982a,b) and are presented in Table 1. The τ value used by Painter and Jackson (1989) was applied since it was based on experiments using *Cladophora* (Gray 1984), while the τ value used by Canale and Auer (1982a) was based on experiments using *Scenedesmus* (Rhee and Gotham 1981).

In the 'Canale and Auer' model the growth dilution of phosphorus within *Cladophora* tissues is calculated by multiplying Q by the gross specific growth rate. We noted that the use of the gross specific growth rate would tend to overestimate the effect of growth dilution of tissue phosphorus (P_D) since actual growth, and therefore growth dilution, is also dependant on diurnal respiration (R) (i.e. is dependant on Net growth). Painter and Jackson (1989) noted a similar effect and also included R in calculations of growth dilution. Dilution of tissue phosphorus (P_D) through growth is calculated as:

$P_D = Q /(\mu NET + 1) * X$ (Eq. 3.5c)

In Chapter 2 one of my overall objectives was to determine the importance of *Cladophora* in the P dynamics of Lake Erie's eastern basin. As a partial solution I included a subroutine within the model to calculate the standing stock of phosphorus contained within the *Cladophora* mat throughout the growing season (Equation 3.5d).

$P = X * (Q / 100)$ (Eq. 3.5d)

Where, P = Standing stock of phosphorus within the *Cladophora* mat (g m^{-2})

In previous efforts to evaluate the importance of *Cladophora* to the P dynamics of eastern Lake Erie I solved Equation 3.5d. at peak seasonal biomass (Chapter 2), however Equation 3.5d does not account for P associated with sloughed material and will underestimate the amount of P sequestered by *Cladophora* over a growing season. The total amount of P uptake by *Cladophora* can be determined using Equation 3.5b, however this may overestimate the importance of *Cladophora* in whole lake P cycles since it does not account for P regenerated from sloughed material. Therefore, values generated using equations 3.5b and 3.5d provide upper and lower boundaries for P sequestered by *Cladophora*.

In addition to light, temperature, and phosphorus, the Canale and Auer (1982a) included a forcing function to account for carrying capacity (M_x), determined by the following equation:

$M_X = 1 – [X/X_{max}]$ (Eq. 3.6)

Where, X = *Cladophora* biomass (g DM m^{-2}),

X_{max} = Maximum *Cladophora* biomass (g DM m^{-2}).

Conceptually, the forcing function for carrying capacity (M_X) is important because it accounts for the strong attenuation of light through *Cladophora* mats of varying density. Canale and Auer (1982a) considered X_{max} to be a fixed value for each study location that needed to be determined through direct field observation. I found that using a fixed value of X_{max} over a larger depth range, as was used in my study area (0-15m), to be inappropriate since the degree of light attenuation through the *Cladophora* mat

will be determined by the density of the mat and the quantity of PAR available to the mat surface. Secondly, fixed values of X_{MAX} are generally difficult to ascertain for sites where growth conditions are sub-optimal and the potential maximum biomass is never achieved. In eastern Lake Erie, I noted strong relationships between maximum biomass and available PAR. Maximum biomass was determined by sampling 24 nearshore sites at 6 depths (0.5m - 10m) during 1995, 2001, and 2002 (Chapter 2). Mean available PAR at each depth was calculated using the mean surface irradiance measured for 39 cloud free days over western Lake Erie (Lorenz et al. 1991) and mean kPAR values for each depth as described Chapter 2. As depth increases and available PAR declines the maximum biomass also declines (Figure 3.3).

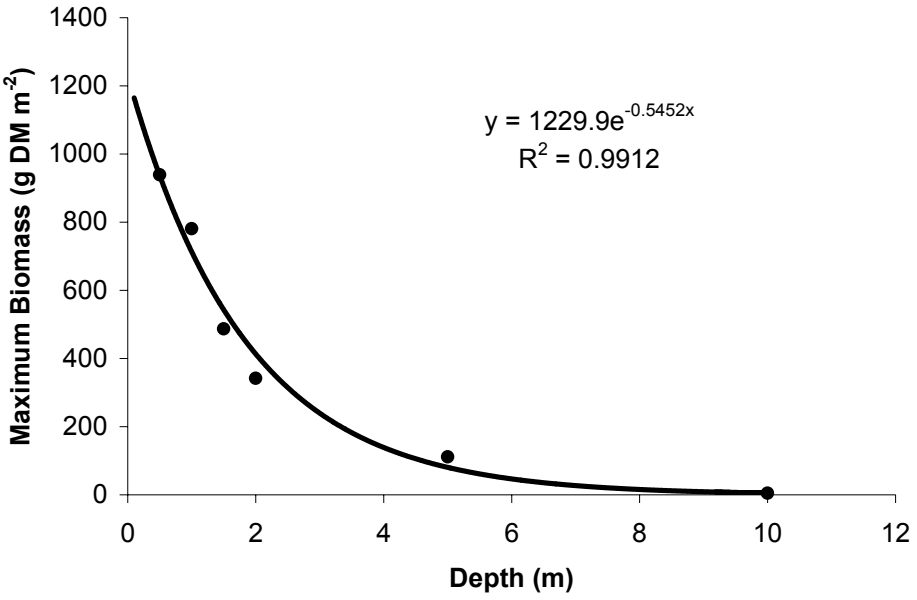

Figure 3.3 The maximum biomass of *Cladophora glomerata* vs. depth. Samples were collected at 28 sites along the northern shoreline of Lake Erie during 1995, 2001, and 2002 over six depths (0.5-10m) by Howell (1998) and Higgins et al. (submitted).

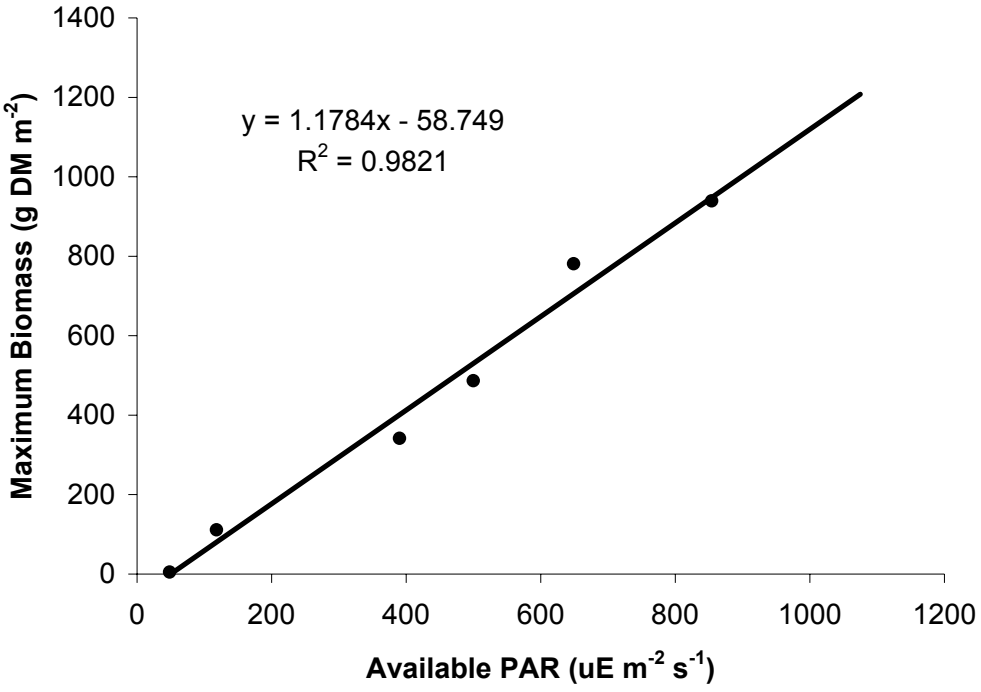

Figure 3.4 The maximum biomass of *Cladophora glomerata* vs. PAR. Samples were collected at 28 sites along the northern shoreline of Lake Erie during 1995, 2001, and 2002 over six depths (0.5-10m) by Howell (1998) and Higgins et al. (submitted).

The decline in maximum biomass over depth is highly correlated to the availability of PAR (Figure 3.4). We used the empirical relationship between X_{MAX} and mean daily PAR (Equation 3.7) in a similar fashion to Lorenz et al. (1991) and Chapter 2.

X_{MAX} = 1.18 * Mean Daily PAR – 58.7 (Eq. 3.7)

In the littoral zones of eastern Lake Erie the mean Daily PAR available to *Cladophora* mats is highly variable both spatially and temporally (Chapter 2). Because X_{MAX} is dependant on available PAR the maximum sustainable biomass (X_{MAX}) is also highly variable. The use of a dynamic variable to account for the carrying capacity is a distinct advantage to the model since it incorporates changes of *in situ* light conditions that may occur on daily, seasonal, or annual scales, and on spatial scales such as between sites and over a range of depths. The use of the dynamic X_{MAX} variable based on ambient PAR also allows the

model to be applied to locations where X_{MAX} cannot be measured directly due to sub-optimal growth conditions.

While equations 3.2-3.7 dealt exclusively with parameters required to solve the gross specific growth rate (u), the calculation of biomass (Equation 1) requires the incorporation of loss terms including respiration and sloughing. The diurnal specific respiration rate (R) is a function of both daytime respiration rate (R_{DAY}), which is modified by forcing functions for internal phosphorus and biomass, and basal respiration occurring at night (Equation 3.8).

$$R = (R_{DAY} * M_P * M_X * PP) + (R_B * (1-PP)) \quad \text{(Eq. 3.8)}$$

Where, R_{DAY} = Daytime respiration rate (day^{-1}),

M_P = Forcing function for internal phosphorus (dimensionless),

M_X = Growth mulitplier for carrying capacity (dimensionless),

PP = Photoperiod (dimensionless, 0-1),

R_B = Dark or basal specific respiration rate (day^{-1}).

Although Canale and Auer (1982a) included M_P and M_X in the calculation of the gross specific growth rate (μ), which included daytime respiration, their model did not include these forcing functions when daytime respiration was used in the calculation of diurnal respiration. The inclusion of M_P and M_X in the calculation of R is, however, required to ensure consistency in the daytime respiration terms used in the growth (μ) and diurnal respiration (R) portions of equation 3.1, otherwise estimates of net production would be skewed (i.e. Daytime respiration would always be higher in the calculation of R than μ). While daytime respiration rates (R_{DAY}) are a function of both light and temperature, basal respiration rates (R_B) are modeled solely a function of temperature (Canale and Auer 1982a). I have retained Canale and Auer's (1982a) function, without modification, for determining basal respiration rates (Equation 3.9).

$$R_B = 0.151 * (0.025\ T + 0.1) \quad \text{(Eq 3.9)}$$

Where, T = Daily mean water temperature (C).

The 'Canale and Auer' model also includes a loss term to account for sloughing and is based on surface wind conditions, shear stress, empirically determined maximum sloughing rates, and biomass (Equation 3.10).

$$L = (S) * (L_{MAX}) * (\omega / \omega_{MAX}) * (X/X_{MAX}) \quad \text{(Eq. 10)}$$

Where, L represents the specific loss or sloughing rate (day^{-1}), S represents the shear stress correction factor (dimensionless), L_{MAX} represents the maximum sloughing rate (day^{-1}), ω represents the daily wind speed (km h^{-1}), ω_{MAX} represents the maximum daily windspeed (17.9 km h^{-1}), X represents the *Cladophora* biomass (g DM m^{-2}), and X_{MAX} represents the maximum *Cladophora* biomass (g DM m^{-2}).

Canale and Auer (1982a) considered S, L_{MAX}, and X_{MAX} to be static, having values of 3.4, 0.176 day^{-1}, and 433 g DM m^{-2} respectively. The shear stress correction factor (S) was calculated using velocity measurements in an experimental flume (Canale and Auer 1982b). The maximum sloughing rate (L_{MAX}) was determined by curve fitting calculated and measured sloughing rates (Canale and Auer 1982b), and X_{MAX} was determined through direct observation. Over the larger depth range in this study, however, these values would tend to overestimate sloughing at deeper depths where wind induced turbulence and shear stress would be greatly diminished. To account for the decline in meteorologically forced sloughing at deeper depths we forced S and L_{MAX} to decay exponentially with depth until no wind induced sloughing occurred at 10m depth, using the following equations:

$$S = 5.031\ e^{(-0.3918 * Z)} \quad \text{(Eq. 3.11)}$$

$$L_{MAX} = 0.242\ e^{(-0.3187 * Z)} \quad \text{(Eq. 3.12)}$$

As the northern shoreline of Lake Erie is directly exposed to winds from only southerly directions we corrected observed wind speed values by applying correction factors to account for wind direction. Winds from 135 to 225 degrees (ESE to WSW) were multiplied by a factor of 1, winds from 90 to 135 (E to ESE) and 225 to 270 (W to WSW) were multiplied by a factor of 0.75, and winds from all northerly directions were multiplied by a factor of 0. For calculations of sloughing (Equation 3.10), I modeled X_{MAX} as a function of depth rather than available PAR (as in Equation 3.7) since short-term declines in water clarity would have un-realistically induced major sloughing events within the model.

While functions 9 through 11 relate sloughing to shear stress and biomass, there is a general recognition that the mid-summer sloughing phenomenon is related to high ambient water temperature (Bellis and McClarty 1967; Whitton 1970). Canale and Auer (1982b) acknowledge that their model did not account for the mid-summer sloughing phenomenon, and simulated autumn biomass was therefore much greater than measured *in situ* biomass. As a result, autumn growth rates were also greatly inflated since they were, in part, dependent on the standing crop (Equation 3.1). While it would be a distinct advantage to model the sloughing phenomenon as a relationship between the deterioration of cells and environmental variables, we are currently unable to define such a relationship mathematically. We therefore have included a subroutine that forces the major sloughing event to occur at 22.5°C, which was the temperature at which sloughing occurred in eastern Lake Erie during our study. The subroutine for temperature induced sloughing includes logic functions that force 90% of the biomass to be sloughed per day at temperatures above 22.5°C to a minimal value of 0.1 g DM m^{-2}. In other studies in the Laurentian Great Lakes region the timing of the sloughing events tend to occur at temperatures 22-25°C (Wong and Clark 1978; Lorenz and Herdendorf 1982). While this method of determining the timing of the mid-summer sloughing is not completely satisfactory, it more accurately predicts post sloughing biomass and the autumn growth peak than the unmodified 'Canale and Auer' model.

3.4.3 Measurement and Calculation of Model Input Parameters

Calculations of P_{NET} and P_{RLT} polynomials (Graham et al. 1982) are based on ambient PAR and temperature. The quantity of PAR at depth (I_Z) is calculated using the equation (modified from Wetzel 2001):

$$I_Z = I_0 * r * e^{(-kPAR * Z)} \qquad \text{(Eq. 3.13)}$$

Where, I_0 = Surface PAR (uM m^{-2} s^{-1}),
r = Coefficient accounting for reflection (0.9, dimensionless),
kPAR = Water column extinction coefficient for PAR (m^{-1}),
Z = depth (m).

Surface PAR (I_0) values were determined from the relationship between PAR, measured from the rooftop of the Port Dover laboratory, and total solar radiation measured from an Environment Canada MET buoy

(Figure 3.5). Sunny days were chosen to ensure that both sensors received similar solar irradiance, and comparisons were not influenced by different cloud conditions between locations. Measures of total solar radiation from Environment Canada's MET buoy and PAR measured at the Port Dover station were highly correlated ($r^2 = 0.9128$) (Figure 3.5) indicating that PAR could be reasonably estimated from continuous measurements of total solar radiation.

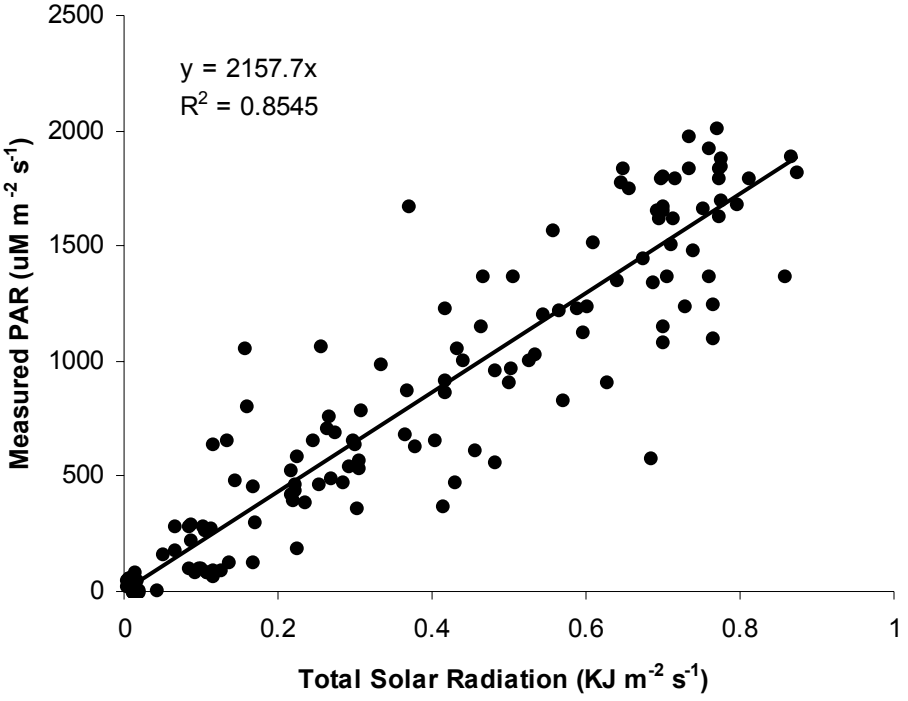

Figure 3.5 Total solar radiation vs. PAR measured over a 4-day period in eastern Lake Erie (see text). N = 143.

Because the relationship between total solar radiation and PAR was only conducted during sunny days it does not take into account cloudy or hazy conditions that could potentially affect the spectral distribution of incoming solar radiation, and therefore the relationship between total solar radiation and PAR. However, in a direct study comparing total solar radiation to PAR it was found that cloudy or hazy conditions did not significantly alter this relationship (Morel and Smith 1974). Daytime mean PAR (I_0) was then determined by averaging hourly PAR estimates over the duration of the photoperiod for each day. These calculations were conducted prior to their introduction into the simulation model.

The 'Canale and Auer' model used daily secchi disk measurements and a derived relationship between secchi transparency and kPAR (Auer and Canale 1982a). During my initial surveys I noted that variability in water column extinction coefficients were primarily driven by the resuspension of particulate material into the water column due to meteorological events. Because particle resuspension is, in part, dependent on water depth, measured kPAR values were generally much higher and more variable in shallower locations (Bloesch 1982; Chapter 2). The modeling requirements included daily kPAR data for each site and depth, which could not, practically, be achieved through point sampling or linear interpolations between sampling dates that were sometimes more than a week apart. Strong empirical relationships between kPAR values and measures of suspended solids (Figure 3.6- 3.7), and the relationship between kPAR vs. station depth (Chapter 2), reduced the data requirements to daily turbidity or TSS measurements at a single depth for each site.

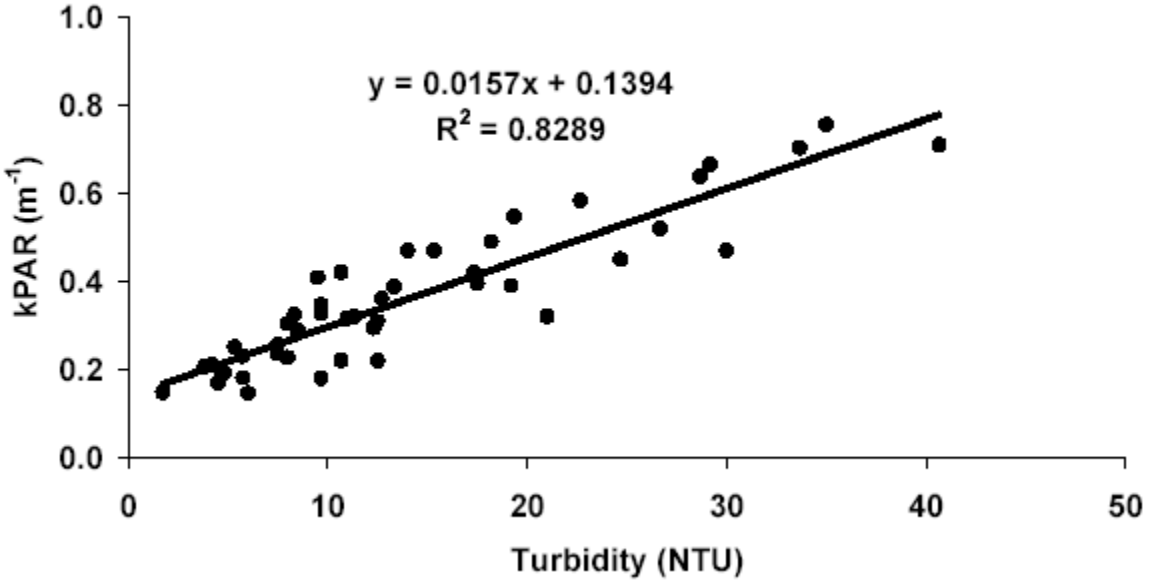

Figure 3.6 Vertical PAR extinction coefficients vs. turbidity measured in the vicinity of Peacock point (see Figure 1) during 2002 and 2003. N = 66.

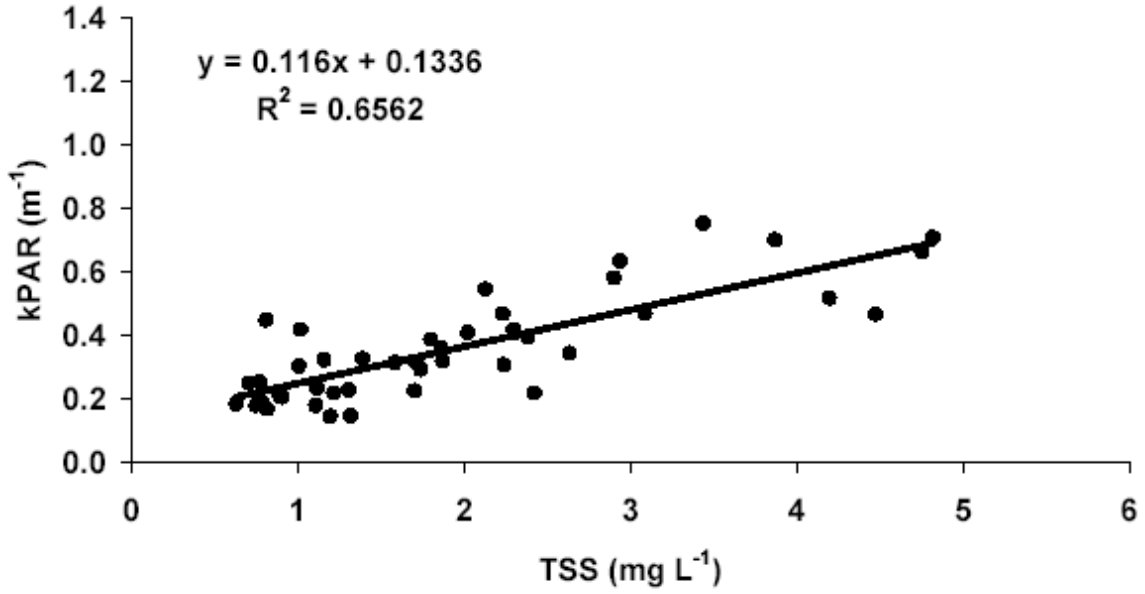

Figure 3.7 Vertical PAR extinction coefficients vs. total suspended solids measured in the vicinity of Peacock point (see Figure 1) during 2002 and 2003. N= 47.

At our primary site, Peacock point, a moored transmissometer was deployed at 5m depth to capture the temporal variability in particulate material (Weidman 2003). To obtain continuous estimates of water clarity at our remaining sites we derived relationships between wave height and water column turbidity (Figure 3.8) in a similar fashion to Howick and Wilhm (1985). To simplify the relationship between turbidity and wave height, we used calculated turbidity coefficients rather than measured turbidity values (Equation 3.14).

$$t_{coeff} = 1 - [t_{MIN} / t] \qquad \text{(Eq. 3.14)}$$

Where, t_{MIN} = site specific minimum turbidity (NTU)
t = turbidity (NTU)

The use of the turbidity coefficients ensured all sites had the same range in turbidity (0 to 1). Turbidity resulting from wave-induced resuspension was a function of wave height and duration. The cumulative 3-day wave height was calculated in an identical fashion to Howick and Wilhm (1985) using an exponential decay factor of 0.693. Overall, the empirical relationship between wave height and turbidity

(Figure 3.8), and the relationship between turbidity and kPAR (Figure 3.6), allowed for daily estimates of kPAR at each site based on meteorological data. These equations, however, are not expected to function in locations or times where meteorological induced resuspension does not exert strong control over water clarity, such as in close proximity to river mouths or during early spring runoff.

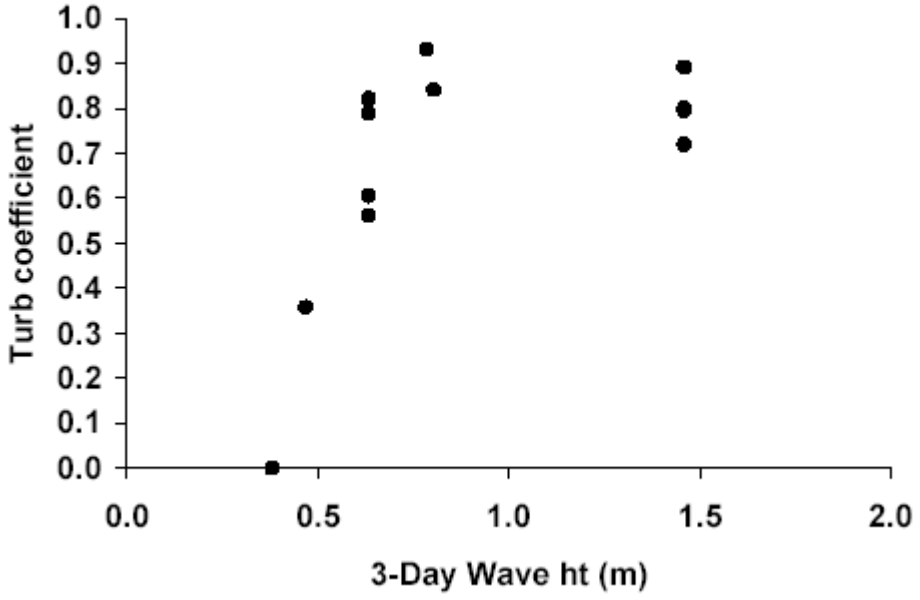

Figure 3.8 Turbidity coefficients vs. wave heights for 4 sites in eastern Lake Erie (Figure 1, except Peacock point). Wave heights are calculated using a 3-day exponential decay function in identical fashion to Howick and Wilhm (1985). Turbidity coefficient values were forced to vary from 0 to 1 and account for site specific ranges in turbidity (see text for calculations).

The simulation model also requires daily estimates of SRP or tissue phosphorus concentration. Ambient SRP concentrations in the northern littoral zone of eastern Lake Erie during 2002 ranged from springtime values of 8 μg L^{-1} to values below detection (0.2 μg L^{-1}) (Chapter 2, 5). In general, SRP concentrations declined until early July, then increased immediately prior to the major sloughing event (29 July 02) when SRP concentrations became highly variable. During the intensive *Cladophora* growth period (01 Jun 04 to 20 Jul 04) SRP values were generally below 4 μg L^{-1} (Chapter 2,5). Continuous estimates of SRP were determined by linear interpolating between sampling dates. Tissue phosphorus concentrations also showed a distinct seasonal trend of declining concentrations until the midsummer-sloughing period, when concentrations in the remaining *Cladophora* increased dramatically (Chapter 2).

Continuous estimates of tissue P were also determined through linear interpolation between sampling dates.

3.4.4 Model Performance

The simulation model was designed such that growth rates could be calculated based on measured or modeled tissue phosphorus concentrations. Modeled tissue P concentrations were determined as the difference between P uptake (Equation 3.5b) and the dilution of P within the plant tissue (Equation 3.5c). When the simulation model was run, modeled tissue P concentrations were compared with measured tissue P values (Figures 3.9, 3.10). In general, model estimates for tissue P were similar to measured values (Figures 3.9, 3.10). However, during the initial days of the simulation the model predicted rapid declines in tissue P that were often not evident in measured values. As a result, modeled growth rates based on SRP concentrations were generally lower than rates based on measured tissue phosphorus at the beginning of the simulation. Overall simulated biomass accrual, based on measured or simulated tissue phosphorus, tracked changes in measured biomass values closely at all sites and depths. The CGM predictions poorly predicted the maximum biomass at two sites, Grant Point and Rathfon Point, during 2002 (Figure 3.9). At Grant point the CGM under-predicted the maximum biomass due to the under-prediction of tissue phosphorus concentrations. The CGM over-predicted the maximum biomass at Rathfon point, however the available data do not provide sufficient information to deduce the cause.

Although the equation for calculating sloughing during the growing season (Equation 3.10) is identical to that of Canale and Auer (1982a) at shallow depths, and was validated in Lake Huron, my revisions to how sloughing is calculated at deeper depths remains un-validated. The inclusion of a function to determine the onset of the midsummer-sloughing period was based solely on temperature and reasonably predicted the timing and post-sloughing biomass. While the relationship between sloughing and temperature for each new system can easily be incorporated into the model, the inclusion of sloughing functions based on the physiological deterioration of the alga would be a distinct improvement.

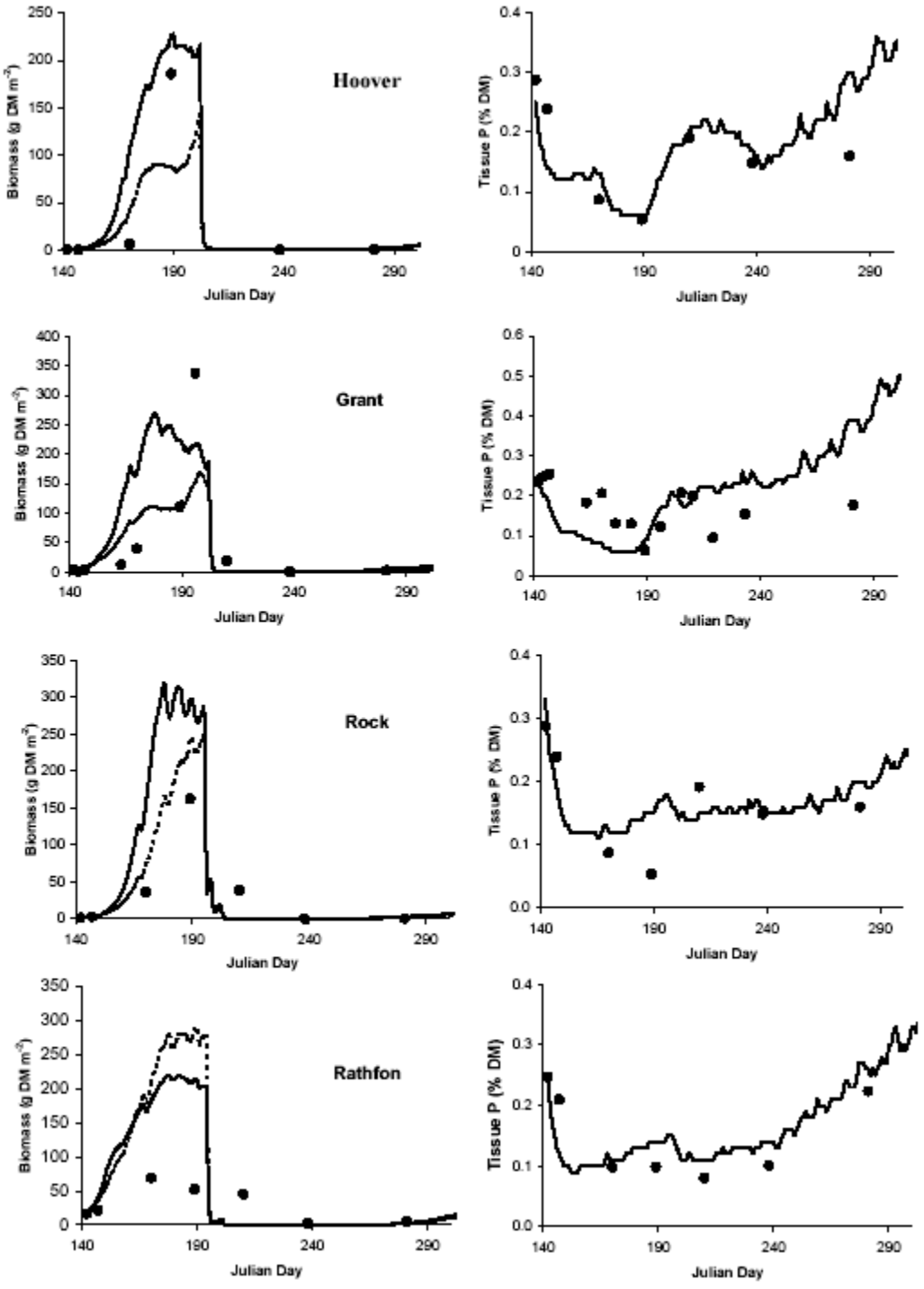

Figure 3.9 Model simulations for biomass and tissue P vs. collected data for 4 sites in eastern Lake Erie (2m depth) during 2002. Biomass simulations were conducted using SRP (dashed lines) and measured tissue P (solid lines). Measured values are reported as solid circles. Note differences in Y-axis scales among sites.

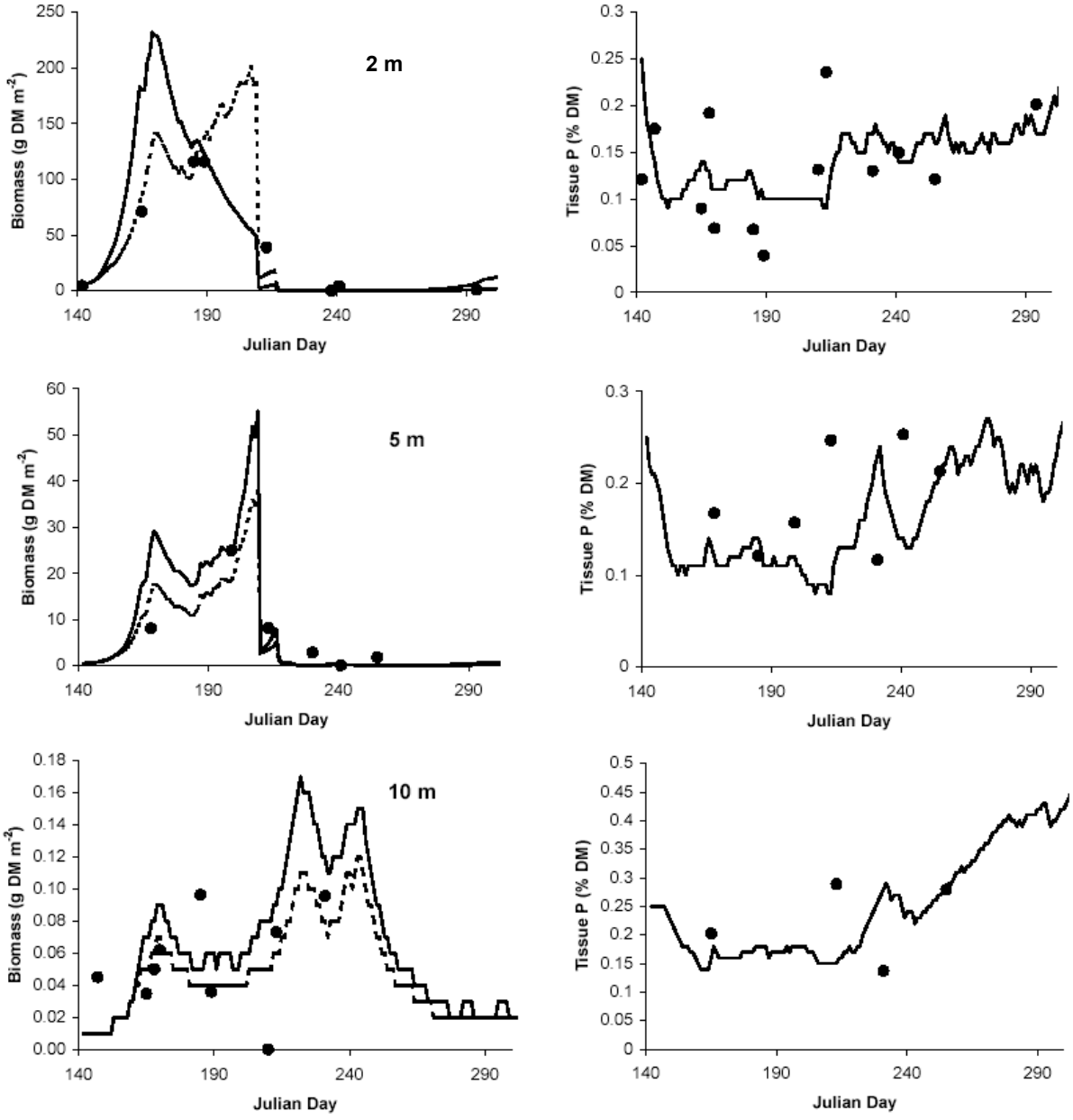

Figure 3.10 Model simulations for biomass and tissue P vs. collected data for Peacock point, eastern Lake Erie, at 3 depths (2, 5, 10 m) during 2002. Biomass simulations were conducted using SRP (dashed lines) and measured tissue P (solid lines). Measured values are reported as solid circles. Note differences in Y-axis scales between depths.

3.5 Conclusion

The 'Canale and Auer' *Cladophora* model, from which the simulation model (CGM) was based, was successfully developed, calibrated, and validated in Lake Huron in relation to point source phosphorus loading and at relatively shallow depths (0-3m). In eastern Lake Erie we required the model to function over a greater range of depths (0-15m), and in the absence of point source phosphorus loading, where SRP concentrations approached analytical detection limits. During my initial attempts to validate the 'Canale and Auer' model directly to eastern Lake Erie I noted that some model coefficients that were held static, including k_{PAR} and X_{MAX}, were highly dynamic over the larger depth range and model simulations showed significant errors in relation to collected data. The modifications to the 'Canale and Auer' model were primarily concerned with ensuring the model functioned appropriately over the larger depth range. Of these modifications, I consider the inclusion of a dynamic term for the maximum potential biomass (X_{MAX}) to be the largest improvement to the model. In the 'Canale and Auer' model the X_{MAX} term, which accounts for the attenuation of light in *Cladophora* mats as density increases, was static and had to be determined through direct field observation (Canale and Auer 1982a). The maximum potential biomass is, however, not static betweens sites or depths and direct field observations are not possible when sub-optimal growing conditions prevent biomass from reaching maximum potential values. Therefore, the inclusion of a dynamic X_{MAX} parameter, based on the relationship between available PAR and field observations of maximum biomass, provides a distinct advantage since it allows the model to function in locations where X_{MAX} cannot be directly ascertained. An additional benefit is a significant reduction in the amount of field data required to ascertain X_{MAX} when applying the model at multiple sites and depths. Modifications were also made to how u_{NET} and R_{DAY} terms were scaled to field rates, ensuring the model did not predict positive growth rates under low light scenarios (as noted by Painter and Jackson 1989). When the 'Canale and Auer' model is restricted to shallow depths in systems of high water clarity such low values of PAR during the photoperiod are likely never encountered. Because the model to was required to function at depths where PAR was often below values required to sustain positive growth rates, such modifications were critical to ensure positive growth did not occur indefinitely as depth increased.

Model simulations for biomass and tissue phosphorus concentration showed reasonable agreement with collected field data at a range of sites and depths that reflected the range of environmental conditions in eastern Lake Erie. If model predictions for tissue P are poorly estimated the model can be run based on linear interpolations between collected tissue P data for the entire season, or the portions of

the season. The agreement between model simulations and field data illustrates the ability of the revised *Cladophora* model to predict tissue P and growth over a range of sites and depths in eastern Lake Erie and suggests potential for the model to be successfully applied in other systems.

3.6 Literature cited

Auer, M. T., and R. P. Canale. 1980. Phosphorus uptake dynamics as related to mathematical modeling of *Cladophora* at a site on Lake Huron. J. Great Lakes Res., 6: 1-7.

Auer, M. T., and R. P. Canale. 1982a. Ecological and mathematical modeling of *Cladophora* in Lake Huron: 2. Phosphorus uptake kinetics. J. Great Lakes Res., 8: 84-92.

Auer, M. T., and R. P. Canale. 1982b. Ecological and mathematical modeling of *Cladophora* in Lake Huron: 3. The dependence of growth rates on internal phosphorus pool size. J. Great Lakes Res., 8: 93-99.

Auer, M. T., R. P. Canale, H. C. Grundler, and Y. Matsuoka. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 1. Program description and field monitoring of growth dynamics. J. Great Lakes Res. 8: 73-83.

Bellis, V. J., and D. A. McLarty. 1967. Ecology of *Cladophora glomerata* (L.) Kütz. In southern Ontario. J. Phycol., 3: 57-63.

Bloesch, J. 1982. Inshore-Offshore sedimentation differences resulting from resuspension in the eastern basin of Lake Erie. Can. J. Fish. Aquat. Sci. 39: 748-759.

Byappanahalli, M. N., D. A. Shively, M. B. Nevers, M. J. Sadowsky, and R. L. Whitman. 2003. Growth and survival of Escherichia coli and enterococci populations in the macro-alga *Cladophora* (Chlorophyta). FEMS Microbiology Ecology 46: 203-211.

Campbell, L, M., M. N. Charlton, V. P. Hiriart-Baer, S. Higgins, S. Malkin, S. J. Guildford, R. E. Hecky, T. Howell, D. Dejong, and L. F. Moore. Then and now: Historical overview of the nuisance green alga, *Cladophora glomerata* in the Laurentian Great Lakes. Submitted to the J. Great Lakes Res.

Canale, R. P., and M. T. Auer. 1982a. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 5. Model development and calibration. J. Great Lakes Res., 8: 112-125.

Canale, R. P., and M. T. Auer. 1982b. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 7. Model verification and system response. J. Great Lakes Res., 8: 134-143.

Canale, R. P., M. T. Auer, and J. M. Graham. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 6. Seasonal and spatial variation in growth kinetics. J. Great Lakes Res., 8: 126-133.

Dejong, D. 2000. The growth and distribution of the green alga Cladophora at Presqu'ile Provincial Park: Implications for management (Ontario). M.ES. Thesis. Wilfrid Laurier University. 92p.

Dodds, W. K. 1991. Factors associated with dominance of the filamentous green alga *Cladophora glomerata*. Wat. Res., 25:125-1132.

Fahnenstiel, G. L., G. A. Lang, T. F. Nalepa, and T. H. Johengen. 1995. Effects of zebra mussel (Dreissena polymorpha) colonization on water quality parameters in Saginaw Bay, Lake Huron. J. Great Lakes Res., 21: 435-448.

Gerlof, G. C., and G. P. Fitzgerald. 1976. The nutrition of Great Lakes *Cladophora*. Ecological Research Series EPA-600/3-76-044. Duluth, Minnesota: U. S. Environmental Protection Agency, Office of Research and Development.

Graham, J. M., M. T. Auer, R. P. Canale, and J. P. Hoffmann. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 4. Photosynthesis and respiration as functions of light and temperature. J. Great Lakes Res., 8: 100-111.

Gray, I. M. 1984. Study of *Cladophora* dynamics in Lake Ontario. Contract report NWRI., CCIW, Burlington Ontario, Canada.

Hecky, R. E., R. E. H. Smith, D. R. Barton, S. J. Guildford, W. D. Taylor, M Charlton and T. E. Howell. 2004. The near shore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Submitted to Can. J. Fish. Aquat Sci., 61: 1285-1293.

Herbst, R. P. 1969. Ecological factors and the distribution of *Cladophora glomerata* in the Great Lakes. American Midland Naturalist 82: 90-98.

Hoffmann, J. P., and L. E. Graham. 1984. Effects of selected physiochemical factors on growth and zoosporogenesis of Cladophora glomerata (Chlorophyta). J. Phycol., 20: 1-7.

Howell, T. 1998. Occurrence of the alga *Cladophora* along the north shore of Eastern Lake Erie in 1995. Ontario Ministry of the Environment. ISBN 0-7778-8172-1. PIBS 3716E. 37p.

Howick, G. L., and J. Wilhm. 1985. Turbidity in Lake Carl Blackwell: Effects of water depth and wind. Proc. Okla. Acad. Sci., 65: 51-57.

Hudson, J. J., W. D. Taylor, and D. W. Schindler. 2000. Phosphate concentrations in lakes. Nature 406: 54-56.

Lester, W. W., M. S. Adams, and A. M. Farmer. 1988. Effects of light and temperature on photosynthesis of the nuisance alga *Cladophora glomerata* (L.) Kutz from Green Bay, Lake Michigan. New Phytol., 109: 53-58.

Lorenz, R. C., and C. E. Herdendorf. 1982. Growth dynamics of *Cladophora glomerata* in western Lake Erie in relation to some environmental factors. J. Great Lakes Res 8: 42-53.

Lorenz, R. C., M. M. Monaco, and C. E. Herdendorf. 1991. Minimum light requirements for substrate colonization by *Cladophora glomerata*. J. Great Lakes Res., 17: 536-542.

Lowe, R. L., and R. W. Pillsbury. 1995. Shifts in benthic algal community structure and function following the appearance of Zebra Mussels (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron. J. Great Lakes Res. 21: 558-566.

Morel, A., and R. C. Smith. 1974. Relation between total quanta and total energy for aquatic photosynthesis. Limnol. Oceanogr. 19: 591-600.

Painter, D. S., and M. B. Jackson. 1989. *Cladophora* internal phosphorus modeling: Verification. J. Great Lakes Res. 15: 700-708.

Painter, D. S., and G. Kamaitis. 1987. Reduction of Cladophora biomass and tissue phosphorus in Lake Ontario, 1972-83. Can. J. Fish. Aquat. Sci. 44: 2212-2215.

Patterson, M, W. R., J. J. H. Ciberowski, and D. R. Barton. Submitted. The distribution and abundance of *Dreissena* species (Dreissenidae) in Lake Erie, 2002. J. Great Lakes Res.

Pillsbury, R. W., R. L. Lowe, Y. D. Pan, and J. L. Greenwood. 2002. Changes in the benthic algal community and nutrient limitation in Saginaw Bay, Lake Huron, during the invasion of the zebra mussel (*Dreissena polymorpha*). J. N. Am. Benthol. Soc., 21: 238-252.

Rhee, G-Y., and I. J. Gothman. 1981. the effect of environmental factors on phytoplankton growth: Temperature and the interactions of temperature with nutrient limitation. Limnol. Oceanogr. 26: 635-648.

Rigler, F. Radiobiological analysis of inorganic phosphorus in lakewater. Verh. Int. Verin. Theor. Angew. Limnolo. 16: 465-470.

Rukavina, N. A. and D. A. St. Jacques. 1971. Lake Erie nearshore sediments Fort Erie to Mohawk point, Ontario. Proc. 14th Conf. Great Lakes Res. 387-393.

Shear, H. and E. E. Konasewich. 1975. *Cladophora* in the Great Lakes. International Joint Commission. 179p.

Sheath, R. G., and K. M. Cole. 1992. Biogeography of stream macroalgae in North America. J. Phycol. 28, 448-460.

St. Jacques, D. A. and N. A. Rukavina. 1973. Lake Erie nearshore sediments – Mohawk point to Port Burwell, Ontario. Proc. 16th Conf. Great Lakes Res. 454-467.

Stainton, M. P., M. J. Capel, and F. A. J. Armstrong. 1977. The chemical analysis of freshwater. Can. Fish. Mar. Serv. Misc. Spec. Publ. 25, 180p.

Stella research and education software. 2001. High performance systems, Inc. http://www.hps-inc.com.

Taft, C. E. 1975. History of *Cladophora* in the Great Lakes. In: *Cladophora* in the Great Lakes. H. Shear and D. E. Konasewich (eds.). International Joint Commission. Pp. 5-16.

Weidman, P., 2003. In situ particle clearance rates of Quagga mussels in eastern Lake Erie. M.Sc. Thesis. University of Waterloo, Canada. 99p.

Wetzel, R. G. 2001. Limnology: Lake and River Ecosystems. 3rd edition. Academic Press. New York. 1006p.

Whitton, B. A. 1970. Biology of *Cladophora* in freshwaters. Water Research 4: 457-476.

Wong, S. L., and B. Clark. 1976. Field determination of the critical nutrient concentrations for *Cladophora* in streams. J. Fish. Res. Board Can. 33: 85-92.

Chapter 4

Cladophora growth model simulations: The spatial and temporal variability in growth dynamics of Cladophora in eastern Lake Erie

4.1 Introduction

Cladophora glomerata is a filamentous green alga that grows attached to hard surfaces in alkaline freshwaters. *C. glomerata* is found in most temperate biomes of North America (Sheath and Cole 1992), and nuisance bloom formations are generally attributable to anthropogenic eutrophication (e.g. Neil & Owen 1964; Whitton 1970; Pitcairn & Hawkes 1973; Parker & Maberly 2000). From 1995 to 2003 widespread *Cladophora* blooms were documented along the rocky coastlines of eastern Lake Erie (Chapter 2). *Cladophora* blooms have also been recently reported in Lake Ontario (T. Howell Ontario Ministry of the Environment, pers. com., Hiriart-Baer et al. submitted, S. Malkin, University of Waterloo, unpublished data), the western shoreline of Lake Michigan (Byappanahalli et al. 2003), and isolated locations of Lake Huron (S. Guildord, University of Waterloo, pers. com.). The presence of widespread algal blooms in the coastal zones of these lakes (or lake basins), all of which are considered oligotrophic by offshore total phosphorus concentrations, are highly troublesome and may be symptomatic of fundamental shifts in water quality caused by the invasive zebra and quagga mussels (*Dreissena polymorpha* and *D. bugensis* respectively) (Hecky et al. 2004; Chapter 2).

Cladophora blooms were a significant ecological phenomenon in the lower Laurentian Great Lakes during the 1960's through to the early 1980's (Bellis and McClarty 1967; Herbst 1969; Shear and Konasewich 1975; Auer et al. 1982; Millner and Sweeney 1982). During the late 1970's a significant modeling effort to understand the dynamics of *Cladophora* growth and biomass accrual resulted in the development of a mathematical growth model specific to *Cladophora* (Auer and Canale 1980; Auer et al. 1982; Canale et al. 1982; Canale and Auer 1982a, b; Auer and Canale 1982a, b; Graham et al. 1982). The 'Canale and Auer' *Cladophora* growth model, which related growth and biomass accrual to several dynamic parameters including light, temperature, dissolved phosphorus, and carrying capacity was successfully validated on field populations of *Cladophora* in proximity to a sewage treatment outfall in Lake Huron (Canale and Auer 1982b). The 'Canale and Auer' model was recently revised and verified on field populations of *Cladophora* in eastern Lake Erie (Chapter 3) and in the remainder of this manuscript the revised model is referred to as the *Cladophora* growth model (CGM). The revisions to the CGM were primarily associated with ensuring the model functioned over a larger depth range, and under conditions of non-point source phosphorus loading where concentrations of soluble reactive phosphorus reached non-detectable limits (Chapter 3). We have applied the CGM to investigate the influence of light,

temperature, and phosphorus on the seasonal and spatial dynamics of *Cladophora* growth and biomass accrual in eastern Lake Erie. My overall objective was to analyze the sensitivity of *Cladophora* growth rates and biomass accrual to variability in these environmental parameters, and provide a scientific framework for management.

4.2 Methods

4.2.1 Study area and environmental variables

The lake bottom of eastern Lake Erie's northern littoral zone (Figure 1), from Port Dover to Fort Erie, consists of bedrock shelves (~80%) interspersed with areas of sand and glacial till (Rukavina and St. Jacques 1971, St. Jacques and Rukavina 1973). The area of lake bottom and suitable substratum within each one-meter depth contour (from 0-10m) is provided in Chapter 2 (Table 2.5). The northern shoreline is highly exposed, with few quiescent bays, to waves generated from the predominant southwesterly winds. Water clarity is controlled by suspended particulate material (Chapter 2,3), which is, in turn, controlled by turbulent particle re-suspension and settling velocities (Bloesch 1982, Weidman 2004, Chapter 3). The bedrock areas are heavily colonized by *Dreissena bugensis* (Quagga mussel) with current densities near 11,000 individuals $\cdot$ m^{-2} (Patterson et al. submitted). A survey of 24 littoral zone sites from 1995 to 2002 (Chapter 2) indicated that by mid-July 95% of the rocky lake bottom (0-5m) was overlain with *Cladophora* with a median biomass of 170 g DM m^{-2}.

A detailed description of how environmental input variables were collected or estimated is available in Chapters 2 and 3. In general, surface photosynthetically active radiation (PAR) was estimated from total solar radiation data collected from an Environment Canada meteorological buoy moored offshore of Long Point (Figure 3.1) and an empirical relationship between total solar radiation and PAR for eastern Lake Erie (Chapter 3, Figure 3.5). Simulated 100% cloud-free and 70% cloud-free surface PAR was generated for eastern Lake Erie (42°47 N, 79°59 W) using an atmospheric coefficient of 0.325 and the computer programs of Fee (1990). The reflectance of PAR from the water surface was assumed to remain constant at 10% of incident irradiance. Daily estimates of water column PAR extinction (kPAR) were determined using an empirically derived relationship between kPAR and turbidity, and site-specific relationships between wave height and turbidity (Bloech 1982; Howick and Wilhm 1985; Chapter 3). The extinction of PAR through *Cladophora* mats was measured using field collected *Cladophora* in an outdoor incubator under direct sunlight. Attenuation of PAR was measured

using a small flat plate collector of a Diving PAM fluorometer (Heinz Walz GmbH) within varying densities of *Cladophora.* The amount of PAR available at the base of the mat (PARm) is described as:

$$PARm = (PAR_0 * e^{-kPARwc * Zwc}) * e^{-kPARm * Zm} \quad \text{(Equation 4.1)}$$

Where PAR_0 represents the amount of PAR available immediately below the water surface, kPARwc represents the water column extinction coefficient for PAR, Zwc represents the depth from the water surface to the top of the *Cladophora* mat, kPARm represents the extinction coefficient of the mat, and Zm represents the depth from the surface of the mat where PAR is to be modeled (modified from Wetzel 1983).

Wind speed and wave height were recorded using standard Environment Canada meteorological buoys moored offshore of Long Point and Port Colbourne (Figure 3.1) for the duration of this study (01 May 02 – 31 Oct 02). Water temperature was recorded at each of the 5 sites at 2m lake depth, 30 cm from the lake bottom, at 30-minute intervals using temperature loggers (Onset corporation). Daily mean temperature values were used as model input. Due to the loss of some temperature loggers during autumn storms we were unable to obtain direct measurements of temperature from Rock point and Rathfon point after 08 Oct 02, and from Peacock point after 21 Oct 02. For the remaining portions of the model run, until 31 Oct 02, we estimated temperature at sites using the mean temperature of remaining sites. Water samples were from northern littoral zone sites (<20m station depth) and were analyzed for soluble reactive phosphorus (SRP) by the National Laboratory for Environmental Testing (NLET) (Charlton et al. 1999).

4.2.2 Model Simulations

All model simulations were conducted using the revised *Cladophora* growth model (CGM) as described Chapter 3. The CGM describes internal phosphorus concentrations, growth, biomass accrual, and sloughing on the basis of mechanistic and empirically determined mathematical relationships with light, temperature, wind speed and direction, and soluble reactive phosphorus (SRP) (Figure 3.2). The model has been verified on field populations of *Cladophora* at the 5 sites in eastern Lake Erie (Figure 3.1) at shallow depth (2m), and one site at deeper depths (5m and 10m) during 2002 (Chapter 3). I used the median values of site-specific environmental data (Table 4.1) from these 5 sites during 2002, combined

with non-site specific environmental data (Table 4.2) to establish conditions for a site that we refer to as the 'median site'. Site-specific SRP data was supplemented with SRP data collected at other northern littoral zone sites (Table 2.2, Figure 4.1). I used the model to simulate *Cladophora* growth and biomass accrual over a range of depths (0-10m) and report the results over a depth gradient, integrated over depth (in the case of biomass accrual), or as mean value over depth (in the case of specific growth rates). Depth integrated data are reported in two ways: 1) as a value that does not account for lake bathymetry and assumes that 1 m^2 of surface area is available for each 1m depth contour, and 2) as a value that accounts for the bathymetry and substratum availability along the northern shoreline of Lake Erie's eastern basin. I employ the first method of depth integration for assessing the effects of varying environmental parameters on *Cladophora* biomass without the confounding influence of bathymetry or substratum availability. I employ the second method for assessing how shifting model parameters will affect the total *Cladophora* biomass within the northern littoral zone of eastern Lake Erie accounting for bathymetry and substratum availability.

Table 4.1 Site-specific environmental data collected during 2002 at 5 sites in eastern Lake Erie.

	kPAR (/m)[1]		Water Temperature (C)		SRP (ug L^{-1})	
Site	Range[2]	Mean[3]	Range[2]	Mean[3]	Range[2]	Mean[3]
Peacock	0.10 - 2.46	0.71	5.9 - 24.3	13.0	0.2 - 4.0	1.2
Hoover	0.22 - 0.87	0.42	5.9 - 24.9	14.6	<0.2 - 7.9	2.1
Grant	0.25 - 0.86	0.50	5.9 - 24.6	14.6	<0.2 - 5.1	1.1
Rock	0.25 - 0.74	0.47	5.9 - 25.0	14.9	1.6 - 6.6	3.5
Rathfon	0.21 - 0.50	0.36	5.9 - 25.6	15.3	0.3 - 8.6	0.9
Median (2002)	0.22 - 0.86	0.45	5.9 - 24.6	14.7	0.2 - 3.1	1.1
2001	0.23 - 1.57	0.43				
2003	0.23 - 1.27	0.45				

Notes: 1. kPAR data represent values for 2m depth. kPAR at other depths are calculated within the model framework based on empirical relationships between station depth and kPAR for eastern Lake Erie (Chapter 2,3); 2. Seasonal Range (01 May 02 to 31 October 02); 3. Mean data for spring-summer growing period (01 May 02 - 24 July 02); 4. Median data represent median values between sites, with the exception of SRP where site median data was supplemented with SRP data from additional sites (< 10m depth) along the northern coastline of eastern Lake Erie (Chapter 2).

Table 4.2 Non site-specific environmental data collected during 2001-2003 in eastern Lake Erie.

Parameter	Units	Year	Seasonal Range[1]	Spring-Summer mean[1]
PAR[2]	uM m^{-2} s^{-1}	2001	35-1209	824
		2002	79-1237	869
		2003	78-1344	803
		100% Cloudless	712-1123	1114
		70% Cloudless	498-786	780
Photoperiod	h	2001-2003	10.4-15.3	14.9
Wind speed	m s^{-1}	2001	0.1-16.2	4.4
		2002	1.9-13.2	4.7
		2003	1.8-13.6	4.5
Wave height	m	2001	0.0-4.3	0.36
		2002	0.1-2.1	0.42
		2003	0.1-2.1	0.42

Notes: 1. Seasonal range for all data represent the period May 01 to October 31, while the spring-summer mean value represents the period 01 May 02 - 24 July 02; 2. PAR data represent mean PAR during the photoperiod.

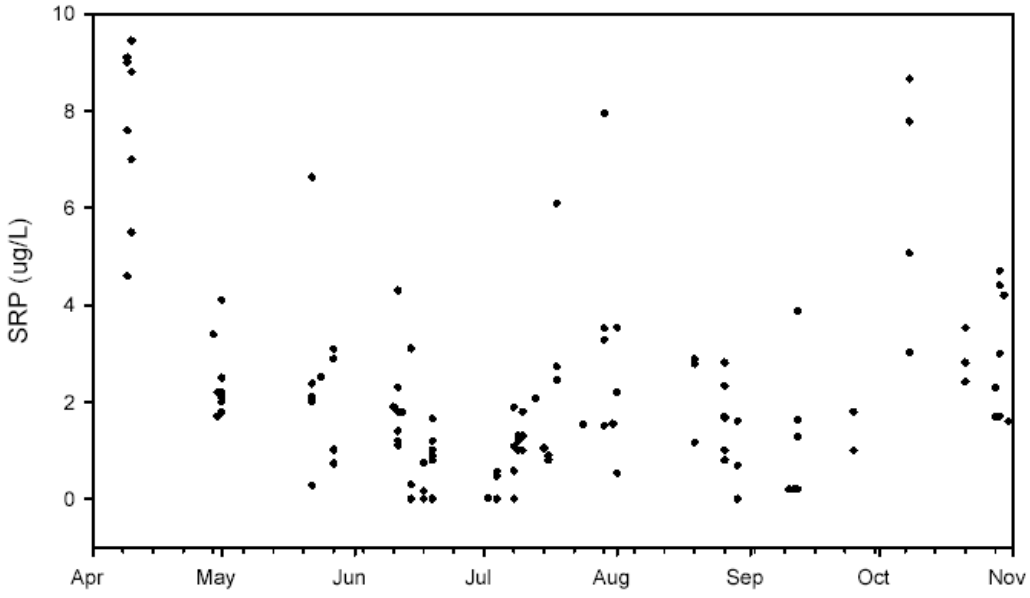

Figure 4.1 Soluble reactive phosphorus (SRP) concentrations at nearshore (<10m) sites in eastern Lake Erie during 2002.

4.3 Results & Discussion

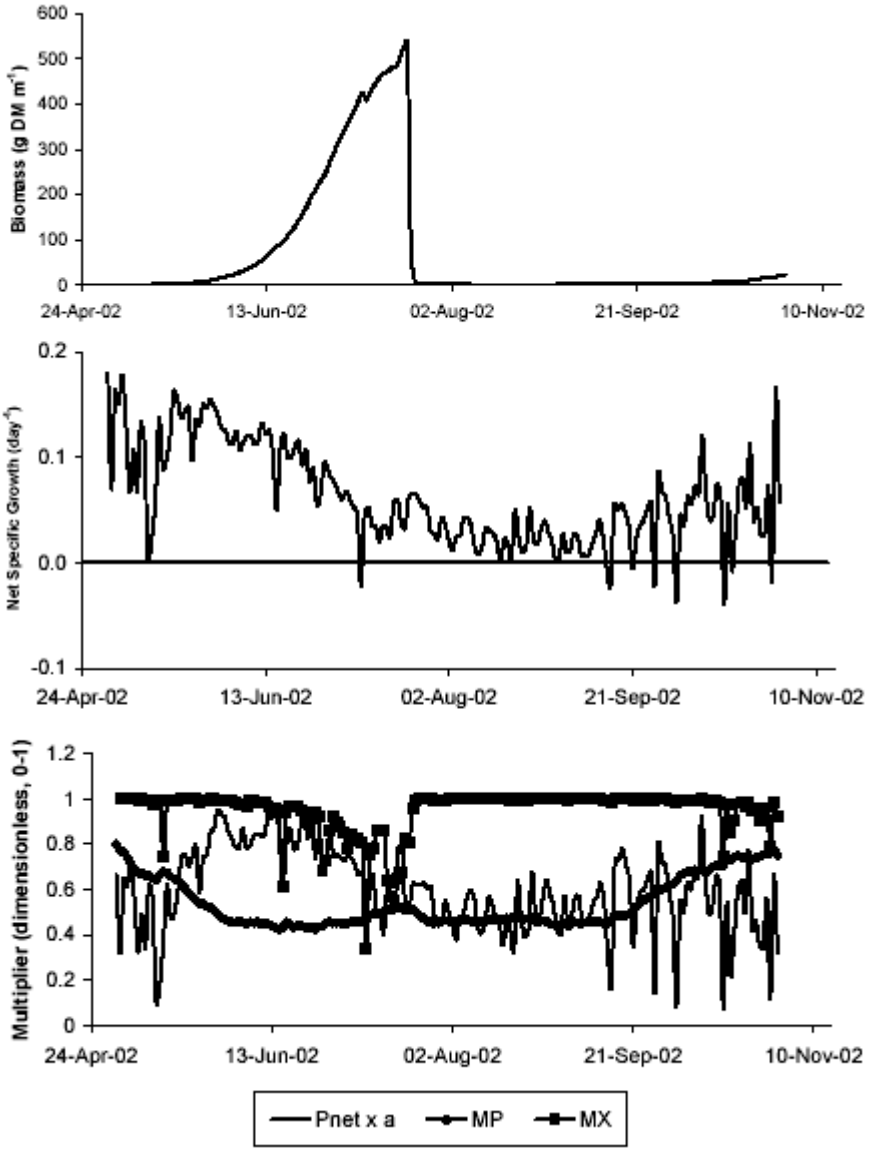

Figure 4.2 Seasonal dynamics of a) biomass accrual, b) net specific growth rate, and c) *Cladophora* growth model multipliers. In panel A the depth integrated biomass calculations are per meter of shoreline assuming 1m^2 of surface area for each 1m-depth contour (see methods). Values for the net specific growth and multipliers were calculated to represent depths 0-4m where >90% of *Cladophora* biomass occurred during 2002.

4.3.1 Seasonal variability of growth and standing crop

The seasonal pattern of biomass accrual (Figure 4.2a) represent the integrated response of *Cladophora* to numerous, and highly dynamic, environmental variables (Table 4.1, 4.2) that control growth and loss processes. The rate of biomass accrual, or loss, can be defined as:

$$Dx/dt = [\mu - R - L] * X \qquad \text{(Equation 4.2)}$$

where dx/dt represents the change in biomass over time (g DM m^{-2} day^{-1}), μ represents the gross specific growth rate (day^{-1}), R represents the specific respiration rate (day^{-1}), L represents the specific loss rate due to sloughing (day^{-1}), and X represents the biomass or standing crop (g DM · m^2). The seasonal pattern of depth-integrated biomass accrual, and its subcomponents, was simulated using the CGM using the median data from 5 sites in eastern Lake Erie (Figure 4.2a). During the spring (01 May – 16 June) the growth rates were maximal and remained positive with the exception of a two-day period during mid-May (May 12-13, 2002) when dense cloud cover reduced surface irradiance (Figure 4.2b). From mid-June until mid-August the net specific growth rates declined to seasonally low values, which were <0.05 day^{-1}. From July to October the mean net specific growth rate was 0.032 day^{-1}. During autumn (October 08-31, 2002) the balance of net specific growth rates became slightly positive allowing for some biomass accrual to occur. During the period of most rapid biomass accrual (15 Jun 02 – 24 Jul 02) specific growth rates had declined substantially from spring values and were well below optimal values (Figure 4.2b).

The CGM calculates the net specific growth rate (μNET) as a function of three multipliers (Chapter 3) that account for the influence of light and temperature (Pnet * a), internal phosphorus concentration (M_P), and self-shading (M_X) on the maximum net specific growth rate (ûNET) (Equation 4.3).

$$\mu NET = \hat{u}NET * (Pnet * a) * M_P * M_X \qquad \text{(Equation 4.3)}$$

Each multiplier is dimensionless and varies from 0-1, while ûNET is a constant with a value of 0.6 day^{-1} (Chapter 3). We compared the seasonal variability of these multipliers and μNET using the CGM and median data from 5 sites in eastern Lake Erie during 2002 (Figure 4.2c). The simulation was constrained to depths less than 4m, where 87 % of the depth-integrated biomass occurred. The general seasonal pattern in μNET was controlled by the parameter 'Pnet * a', indicating the importance of temperature and

available PAR (Figure 4.2c). Temperature controlled the general seasonal pattern of 'Pnet * a', while rapid oscillations were controlled by strong cloud-cover or high turbidity events that reduced available PAR. The rapid day-to-day fluctuations in μNET were also largely dependent on variations in the amount of PAR available at depth, which were caused by variable cloud cover early and late in the growing season and fluctuations in water clarity during the rapid growth phase. As biomass approached its seasonal peak value the parameter for self-shading (M_X) also became quantitatively important, reducing depth integrated production by an additional 20 %. The growth multiplier for self-shading (M_X) is calculated as:

$$M_X = 1 - X/Xmax \qquad \text{(Equation 4.4)}$$

where X represents the areal biomass of *Cladophora* (g DM m^{-2}), and Xmax represents the maximum areal biomass (g DM m^{-2}) and is dependant on available PAR at the mat surface (Chapter 3). Phosphorus concentrations within *Cladophora* tissues were below optimal growth requirements for the duration of this study. Within the CGM tissue P values are assessed using variations in the parameter MP, the growth multiplier for tissue phosphorus. MP is dimensionless and varies from 0-1. Values below 1 represent a departure from optimal tissue phosphorus values and growth rates are affected proportionally (Equation 4.3). Within the CGM the value for M_P is calculated as:

$$M_P = 1 - Q_0/Q \qquad \text{(Equation 4.5)}$$

Where Q is the tissue P concentration (% DM), and Q_0 is the minimum tissue P concentration (0.05 % DM) required for growth (Wong and Clark 1976, Auer and Canale 1982b). The median tissue P value from the 5 sites in eastern Lake Erie ranged from 0.09-0.25 % DM during 2002, forcing MP to vary from 0.43-0.80 (i.e. realized growth rates were 43-80 % of optimal values based on light and temperature conditions) (Figure 4.2c). Rapidly declining values for tissue P during May forced M_P to decline from 0.80 to 0.44 by June. From June to August, the period of rapid biomass accrual, M_P had a mean value of 0.46 (Figure 4.2c) indicating that realized growth rates were 46 % of those obtainable based on ambient water temperatures and available PAR.

4.3.2 Vertical distribution of growth and standing crop

Measured and CGM predicted values for the vertical distribution of *Cladophora* biomass during the peak standing crop are presented in Figure 4.3. With the exception of the shallowest depths (<1m) the CGM, using the median environmental data from 5 sites in eastern Lake Erie, predicted the general pattern of biomass over the range of depths within this study (0-10m)(Chapter 3, Figure 3.9, 3.10).

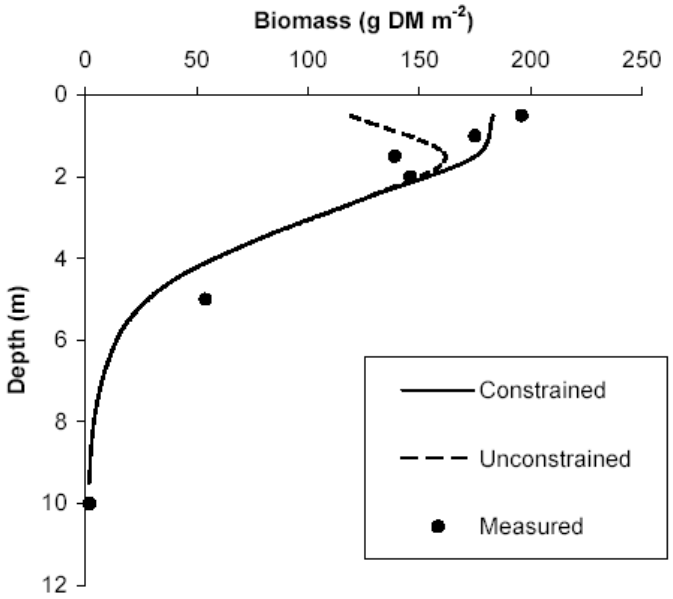

Figure 4.3 *Cladophora* growth model (CGM) predictions vs. measured values for the standing crop of *Cladophora glomerata* in eastern Lake Erie. Constrained CGM predictions were made by eliminating the effects of enhanced photorespiration at PAR values >600 uM photons m^{-2} s^{-1} (see text). Measured biomass values represent the mean biomass data from 1995-2002 (Table 2.3).

Under high PAR intensities (>600 uM m^{-2} s^{-1}) and summer water temperatures (15-24°C), the CGM predicted that reduced growth rates would occur at shallow depths in response to increased light enhanced respiration (Graham et al. 1982). Translating these results to field conditions, however, is problematic. While light enhanced respiration may occur near the surface of the mat *in situ,* maximum PAR values (1100 uM m^{-2} s^{-1}) at the mat surface are attenuated to levels below 600 µM m^{-2} s^{-1} within the upper 1.5 cm of the mat structure. The *Cladophora* mats at shallow depths (<1m, where PAR may exceed 600 uM m^{-2} s^{-1}) are dense and the mean mat thickness was near 10cm (Chapter 2). Therefore, even under the highest PAR intensities the effects of light enhanced respiration would be diminished within a short distance into the mat. While the CGM accounts for reductions in growth due to self-shading it does not account for the positive effects of self-shading under conditions where PAR at the surface of the mat exceeds optimal

values. Secondly, the photosynthetic response of *Cladophora* collected from eastern Lake Erie during 2002 (Chapter 5) showed no reduction in maximum photosynthesis at PAR intensities between 600-1200 uM m^{-2} s^{-1}, and this result is similar to that reported by Lester et al. (1988) for *Cladophora* from Lake Michigan. Therefore, in eastern Lake Erie the CGM will over-predict the influence of light enhanced respiration on mat growth rates and biomass accrual at shallow depths (<1m) where PAR intensities often exceed 600 uM m^{-2} s^{-1} at the mat surface. We constrained PAR values to 0-600 uM m^{-2} s^{-1} at the mat surface, and under these conditions the CGM predictions for biomass accrual at shallow depths (<2m) are more similar to measured values than the unconstrained CGM, and are identical to the unconstrained CGM predictions at deeper depths (>2m) (Figure 4.3). For the remainder of the simulations in this manuscript we have used the constrained CGM.

4.3.3 Self-shading and midsummer sloughing

An important component of the seasonal pattern of *Cladophora* growth and biomass accrual, under bloom conditions, is the mid-summer sloughing event (Chapter 2, 3, Figure 4.2a). During the mid-summer period, typically mid-July in Lake Erie (Mantai 1987; Chapter 2), *Cladophora* filaments detach from their holdfasts and create large drifting mats. The mid-summer detachment phenomenon has been documented in a variety of lakes and rivers (e.g. Wong et al. 1978; Bellis and McLarty 1967; Whitton et al. 1970), however the underlying mechanisms causing the sloughing have not been adequately described or modeled. Previous efforts to model the detachment process as a function of metabolic imbalance (Canale et al. 1982) predicted that the onset of sloughing would occur when the *Cladophora* mat approached zero (or negative) growth. Other researchers noted that the metabolic imbalance hypothesis was improbable since, in their study, excess photosynthetic products were found accumulated within *Cladophora* cells immediately prior to the onset of sloughing, and suggested other factors such as nutrient limitation as potential causes of the sloughing (Mantai 1987, 1989). Numerous studies also mention the potential for temperature to exert some control over the midsummer-sloughing event (see Whitton 1970 for review), however there remains wide discrepancy between the temperature tolerances determined under laboratory conditions and field observations of the temperature at which the sloughing event occurs. For example, laboratory studies have demonstrated that positive growth may occur at temperatures between 25-30°C (Bellis 1968; Graham et al. 1982, Lester et al. 1988; Chapter 5), while field studies in the Laurentian Great Lakes region report deterioration of the algae and sloughing to occur at temperatures < 24°C (e.g.

Wong et al. 1978; Auer et al. 1982; Chapter 2). During 2002 the sloughing event in eastern Lake Erie occurred as water temperatures approached 22.5°C (Chapter 2).

In the CGM simulations the net specific growth rates of the mat did not display obvious signs of prolonged metabolic imbalance prior to the sloughing event (Figure 4.2b). The CGM, however, integrated growth rates over the vertical structure of the mat and the results did not necessarily reflect the potential for metabolic imbalance to have occurred at the base of the mat where the physical detachment of the filaments generally occurred. To elucidate whether self-shading could induce metabolic imbalance at the base of the mat I modeled the specific growth rates at the top and bottom of the mat independently (Figure 4.4). The quantity of PAR available to the upper and lower mat surfaces were estimated using equation 4.2, and the light extinction within the mat (kPARm) was calculated using the relationship between kPARm and mat density (Figure 4.6).

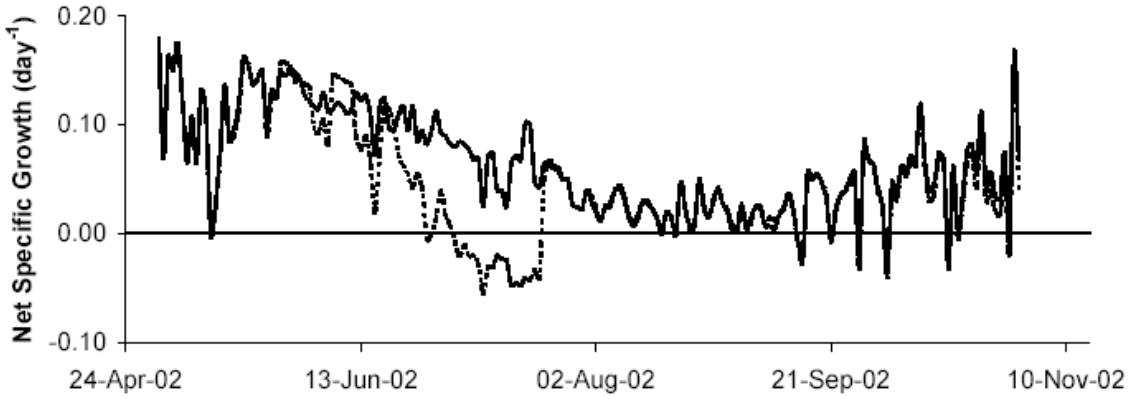

Figure 4.4 The seasonal variability of net specific growth rates at the surface and base of the *Cladophora* mat during 2002 as predicted by the *Cladophora* growth model (CGM). Data represent the mean specific growth rates between 0-4m. The solid line represents rates at the upper mat surface, while the dashed line represents rates at the base of the mat.

At shallow depths (0-4m) the growth rates at the surface of the mat were positive throughout the simulation period, while at the base of the mat growth rates became consistently negative after 04 July 02 until the sloughing event. These results suggest that a prolonged period (14-20 days) of negative growth occurred at the base of the mat prior to the sloughing event, which occurred July 24-29, 2002. In model simulations the difference in growth rates between the upper and lower surfaces was completely driven by available PAR, and negative growth rates at the base of the mat occurred irrespective of modeled internal

P concentration (data not shown). High ambient water temperatures, which increased respiratory rates, further exacerbated the metabolic imbalance at the base of the mat. However, the CGM predicts that at PAR values below 25 uM m^{-2} s^{-1} growth rates are negative at all temperatures between 0-35°C (Graham et al. 1982).

During the 10-day period prior to the sloughing event growth rates at the base of the mat were negative at depths less than 5m, and slightly positive at depths below 5m (Figure 4.5).

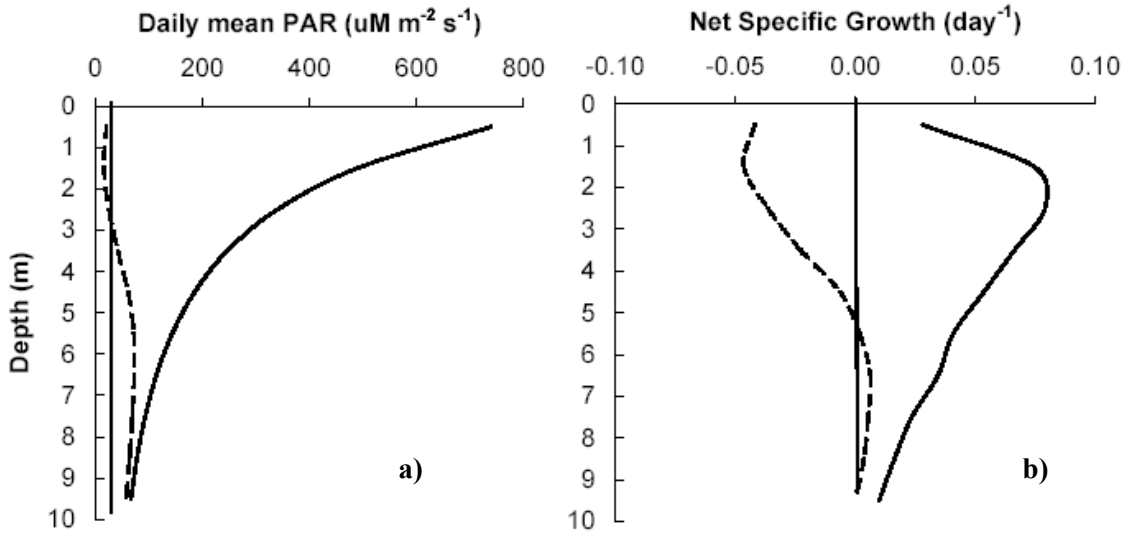

Figure 4.5 The vertical distribution of PAR and net specific growth rates at the surface (solid lines) and base (dashed lines) of *Cladophora* mats at the 'median' site in eastern Lake Erie as predicted by the CGM. Daily mean PAR values represent mean values during the photoperiod. Both daily mean PAR and net specific growth rates are mean values for the 10-day period (July 14-24) immediately preceding the midsummer sloughing event. The solid vertical line in panel A represents the minimum PAR requirement for growth (~30 uM photons m^{-2} s^{-1}).

The increase in growth rates at the base of the mat with increases in depth may appear counter-intuitive, as one might expect the exponential declines in PAR through the water column to exert control over the amount of PAR reaching the base of the mat. While the quantity of PAR reaching the mat surface is important, the attenuation of PAR through the mat structure is rapid when algal densities are high (Figure 4.6). At high mat biomass, such as those found at depths between 0-4m, the PAR extinction coefficient of the mat (kPARm, 25-30 m^{-1}) is nearly two orders of magnitude higher than that of the water column (kPARwc, 0.5 m^{-1}) and light is attenuated rapidly. As a result of the declining height and density of the

mat with lake depth, and although the quantity of PAR at the surface of the mat was reduced, sufficient PAR reached the base of the mat to maintain positive growth at depths 7-10m.

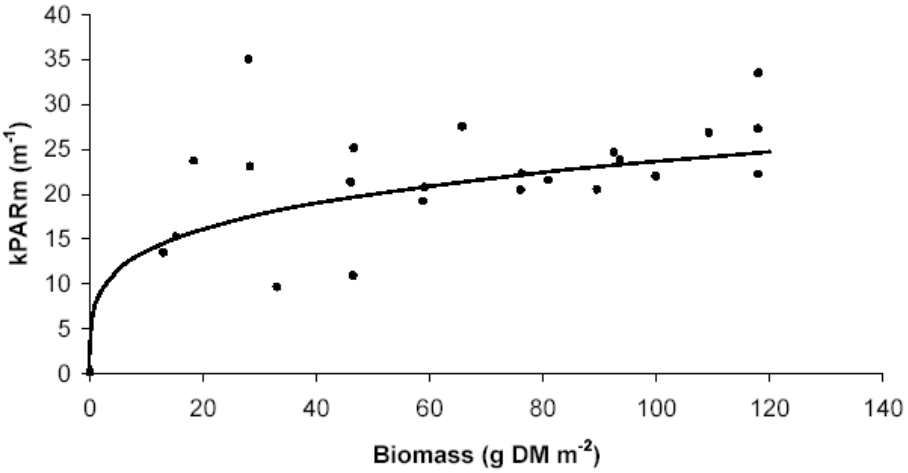

Figure 4.6 The extinction coefficients of PAR through *Cladophora* mats of varying areal biomass (kPARm). The line of best fit was chosen using Tablecurve 2D (Systat 2001), and was represented by the equation: kPARm = 7.84 * Biomass^0.24, R^2 = 0.75, Std Error = 4.26, n = 26.

The underlying cause of the midsummer-sloughing event in eastern Lake Erie is hypothesized to be the prolonged metabolic imbalance at the base of the *Cladophora* mat as predicted by the CGM. Also noted were that growth rates at the mat surface, while positive, were strongly P-limited. The disparity between growth conditions at the surface and base of dense *Cladophora* mats may account for the occurrence of starch found in tissues prior to the sloughing event in the study of Mantai (1987). While I did not analyze *Cladophora* tissues for starch it is probable that cells near the surface of the mat contained starch (a potential indicator of nutrient limitation; Mantai 1987) while cells near the base of the mat would have very low starch concentrations (light limited). These results are also consistent with observations that *Cladophora* can grow at higher temperatures (25-30°C) in both field and laboratory settings (e.g. Graham et al. 1982; Whitton 1970; Chapter 5). In fact, *Cladophora* harvested from the same sites modeled in this study displayed no reduction in its photosynthetic capacity throughout the sloughing period (Chapter 5). In this study the metabolic imbalance was caused primarily by low light conditions at the bottom of a dense algal mat, exacerbated by moderately high water temperatures (~ 23°C). If mat densities were lower it is probable that positive growth rates could have been sustained to higher temperatures, and the sloughing event delayed. Conversely, if water temperatures were higher the CGM

predicts that maximum sustainable densities would be lower and the sloughing event would have occurred earlier in the season.

In my original formulation of the CGM (Chapter 3) I was unable to define a mathematical relationship between metabolic imbalance of the mat and the sloughing phenomenon, and therefore modeled the sloughing phenomenon based solely on temperature. As the ambient water temperature exceeded a set threshold, 22.5° for eastern Lake Erie, the sloughing event was induced. However, despite the inclusion of this aspect in the CGM I considered the use of temperature as unsatisfactory since it did not explain the underlying causes of the sloughing event and also because other field studies showed that deterioration and sloughing of *Cladophora* occurred over a range of temperatures (Wong et al. 1978, Auer et al. 1982; Mantai 1987; Chapter 2). I have therefore included a subroutine in the CGM that predicts the sloughing event based on the metabolic balance at the base of the *Cladophora* mat. If the accumulated growth (at the base of the mat), summed over a 10-day period, exceeds a pre-determined threshold the sloughing event is induced. Based on CGM simulations at the 5 nearshore sites I found that setting a threshold value of 0.4 (i.e. over the 10-day period 40 % of the biomass would be lost through respiration) predicted the sloughing event to occur within our field observations (24-29 July 02). The CGM subroutine to predict the sloughing event is based on the following assumptions: 1) that the attenuation of light through the *Cladophora* mats is adequately described under field conditions, 2) that the mid-summer sloughing event is triggered by a prolonged period (≥10 days) of metabolic imbalance, 3) that the deterioration and eventual sloughing of the mat occurs once the accumulated growth rates exceed a pre-defined threshold (e.g. 40% of the biomass is lost through respiration). Each of these assumptions will require testing under a wide range of field conditions and it is likely that these calculations will be modified as the decay and sloughing phenomenon within field populations of *Cladophora* are more thoroughly understood.

4.3.4 The effects of parameter variability on growth and biomass

In the previous sections the seasonal and depth distribution of *Cladophora* in eastern Lake Erie in relation to several environmental variables including light, temperature, and dissolved phosphorus were discussed. In this section I discuss how inter-site and inter-seasonal variability in these environmental parameters affect *Cladophora* distribution, growth, and standing crop.

4.3.4.1 PAR

To estimate the effects of inter-annual variability in cloud cover on *Cladophora* growth rates and biomass, I substituted PAR data collected during 2002 with data collected from 2001 and 2003, and with simulated 70% and 100% cloud-free PAR data generated using Fee's (1990) computer program. The variability in PAR values between 2001-2003 resulted in only a 5-6% difference in the depth-integrated standing crop and had a negligible effect on the depth distribution (data not shown). The CGM predicted that 100% cloud-free conditions would increase the depth-integrated biomass by 37 % (from 2002 conditions), with 70% of the difference occurring between 1-5m depth. Depth-integrated biomass modeled using the 70 % cloud-free conditions (1-10m) was 3 % higher than CGM predictions under 2002 measured PAR conditions. These results indicated that inter-annual variability in the amount of PAR received at the surface of the lake likely has only a minor role in controlling year-to-year differences in standing crop. Further, when measured PAR data is unavailable the use of simulated 70% cloud-free PAR data is acceptable, causing only minor errors in predicted depth-integrated biomass. While dense cloud-cover was not prevalent over the lake during the mid-summer period of 2001-2003, prolonged cloud-cover during the mid-summer could cause additional stress to cells at the base of the mat and be important in the timing of the sloughing event.

4.3.4.2 kPAR

During 2002 the mean kPAR values ranged from 0.36-0.71 m^{-1} between sites, with the median site having a value of 0.45 m^{-1} (Table 4.1). The CGM predicted that site-to-site differences in kPAR would cause large differences in the depth distribution of biomass and the total depth-integrated biomass betweens sites. The effects of water clarity on depth-integrated biomass and the depth distribution of biomass were modeled using water clarity data from the most turbid site (Peacock point) and the least turbid site (Rathfon point), while constraining all other variables to site-median values (Figure 4.7). Under the most turbid conditions the depth-integrated biomass was 380 g DM m^{-1} with >90% of the biomass occurring at depths <3m. Under the least turbid conditions the depth-integrated biomass was 860 g DM m^{-1}, and 90% of the biomass occurred at depths <6m. Approximately 70% of the difference in depth-integrated biomass between these two simulations occurred between 2-6m depth. These results demonstrate that the natural range in water clarity between sites in eastern Lake Erie can have a strong influence on the depth-integrated biomass and the depth distribution of biomass. Further, shifts in water clarity have relatively little effect at depths <2m where growth is light saturated, and the most effect on biomass at intermediate

depths (2-6m). These results also suggest that the depth-integrated biomass would increase towards the eastern end of the basin where mean water clarity was highest (Table 4.1).

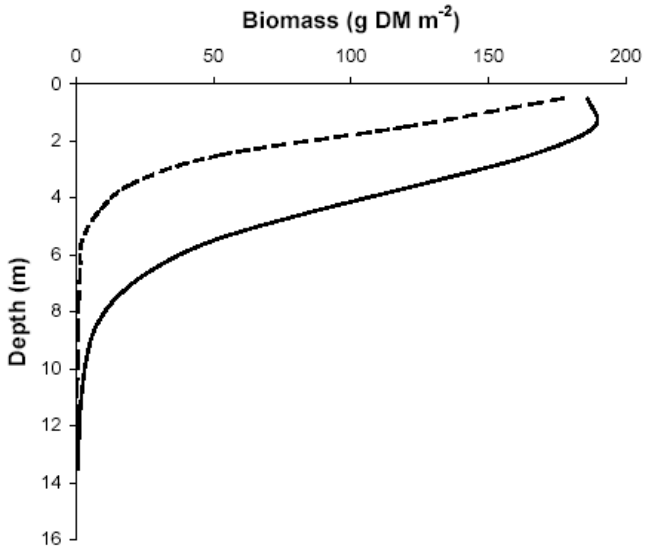

Figure 4.7 The variation in peak *Cladophora* biomass vs. depth based on maximum site-to-site variations in water clarity (kPAR) during 2002. The CGM predictions were based on 'median' site data and water clarity data for the site with the highest mean kPAR value (Peacock point, dashed line) and lowest mean kPAR value (Rathfon point, solid line).

During the spring-summer growing period (01 May – 24 July) from 2001-2003 mean kPAR values at the median site, modeled using site dependant relationships with wave height (Chapter 3), ranged from 0.43-0.45 m^{-1} (Table 4.2). The CGM predicted that the resulting inter-annual variability in depth-integrated biomass between years of highest (2001) and lowest (2002) water clarity would be small. Specifically, the CGM predicted that a depth-integrated biomass of 645 g DM m^{-1} and 652 g DM m^{-1} during 2001 and 2002 respectively, and that the depth-distribution was similar between years (data not shown). While my data suggests that year-to-year differences in water clarity are small compared to differences between sites it should be noted that our kPAR data were generated using wave height data from meteorological buoys (Chapter 3) and therefore do not reflect potential variability in kPAR due to other factors such as spring runoff or variability in the influence of rivers.

4.3.4.3 Temperature

The mean water temperature during the spring-summer growing period (01 May 02 – 24 Jul 02) varied from 13.0 – 15.3°C between the 5 nearshore sites (Table 4.1). Westerly sites (Peacock point, Hoover Point) experienced episodic cool-water upwelling events that persisted for 4-7 days, and decreased ambient temperatures 1-10°C. Eastern sites (Rock, Rathfon) did not have strong upwelling events and mean water temperatures during the spring-summer growing period were 0.3-2.3°C warmer. The CGM was used to assess the impact of inter-site variability in temperature on the seasonality and depth distribution of the standing crop. Model simulations were conducted using daily mean water temperatures from each site and used site-median values for the remainder of the environmental input data (Table 4.1). The CGM predicted that depth-integrated biomass would range from 580-740 g DM m^{-1} on the basis of temperature differences between the sites, and that these effects were consistent across the range of depths (0-10m).

4.3.4.4 Phosphorus

Previous studies have demonstrated the importance of available phosphorus in controlling the growth rates and biomass accrual of *Cladophora* in Lake Erie (Neil and Jackson 1982; Chapter 2, 3), Lake Ontario (Painter and Kamaitis 1987; Painter and Jackson 1989), Lake Huron (Canale et al. 1982), and other systems (e.g. Wong and Clark 1976; Parker and Maberly 2000). In eastern Lake Erie mean SRP concentrations during the spring-summer growing period of 2002 ranged from 0.9 – 3.5 μg L^{-1} at our 5 nearshore sites (Table 4.1). One of these sites (Rock point) is frequently influenced by the plume of the Grand River, maintains higher SRP concentrations throughout the summer period, and is not considered representative of other areas along the northern shoreline of eastern Lake Erie (Chapter 2). Excluding the Rock point site, the mean SRP during the spring-summer period ranged from 0.9-2.1 μg L^{-1} at the remaining 4 sites. While constraining other parameters to the 'median' site values I used the CGM to simulate *Cladophora* growth based on SRP concentrations at the 4 remaining sites (Figure 4.8).

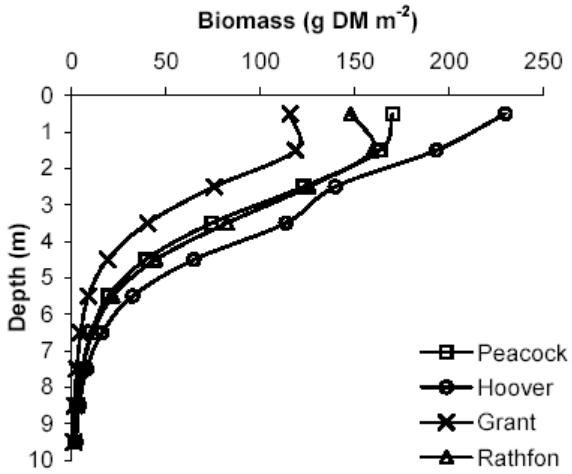

Figure 4.8 CGM predictions for the peak *Cladophora* standing crop vs. depth. Simulations were based on 'median' site data and SRP data from 4 sites in eastern Lake Erie during 2002.

Based on the site-to-site differences in SRP the peak depth-integrated biomass ranged from 390-800 g DM m^{-1}. While the lowest mean SRP concentration during the spring-summer period occurred at Rathfon point (Table 4.1), the CGM predicted that the lowest depth-integrated biomass would occur at Grant point (Figure 4.8). The difference in model predictions between these sites illustrates the importance of the SRP concentration during the period of rapid biomass accrual (July). At the Rathfon point site the SRP concentrations were lower initially; however, they increased and remained near 1 μg L^{-1} during July (data not shown). At the Grant point site SRP concentrations were higher initially, but declined rapidly to very low concentrations (< 0.2 μg L^{-1}) during July. Because the change in biomass (Equation 4.1) is based on the net specific growth rate multiplied by the biomass, differences in the specific growth rates between sites during periods of high biomass (e.g. July) will have a much larger effect on biomass accrual than during periods of low biomass (e.g. May). As a consequence, the site-to-site differences in SRP during July had a large influence on differences in the net specific growth rates, biomass accrual, and peak standing crop of *Cladophora* between sites in eastern Lake Erie.

The CGM was used to examine the influence of inter-annual differences in SRP concentration on the peak standing crop of *Cladophora* at the 'median' site (Figure 4.9). Inter-annual differences in spring SRP concentrations in the offshore waters of eastern Lake Erie varied by ~ 1 μg L^{-1} during post-*Dreissena* years (Table 4.3).

Table 4.3 Offshore SRP concentrations (μg L^{-1}) in eastern Lake Erie (1991-2003). Minimum, maximum, and mean values were calculated by averaging monthly mean values for 'n' years. Data provided by M. Charlton (NWRI, Environment Canada).

	June	July	August
n	10	9	7
Min	0.27	0.36	0.53
Max	1.76	1.09	1.41
Mean	0.83	0.65	0.92

SRP concentrations in nearshore waters of eastern Lake Erie were assumed to display at least the same degree of inter-annual variability as the offshore waters. I varied SRP by +/- 1 μg L^{-1} from median conditions during 2002, constraining the minimum SRP concentration to 0.2 μg L^{-1} (Figure 4.9, 4.10).

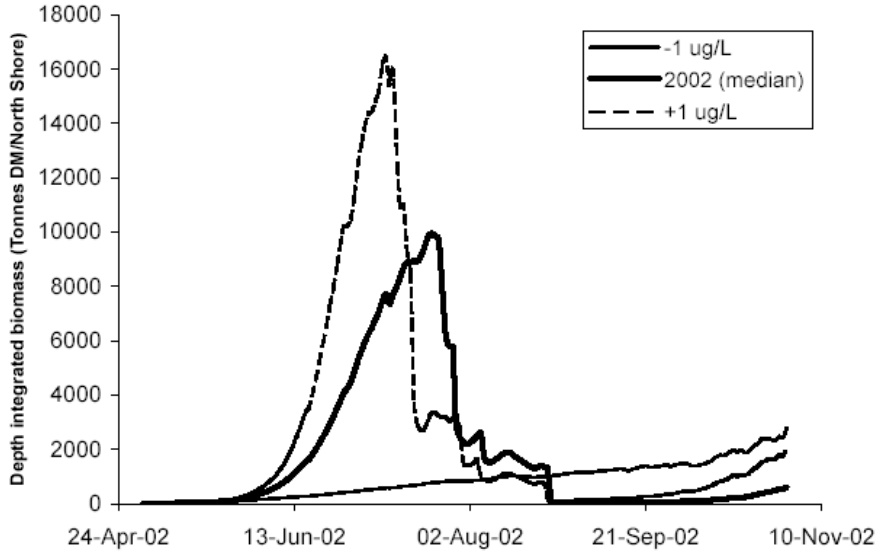

Figure 4.9 The effect of SRP variability on the total depth-integrated *Cladophora* biomass along the northern shoreline of eastern Lake Erie as predicted by the CGM. The 2002 simulation was based on the median environmental data from 5 sites in eastern Lake Erie during 2002 (Table 4.1, 4.2). The remaining two simulations were conducted by varying the 2002 median SRP data by +/- 1 μg L^{-1}, while holding other variables constant at 2002 median values.

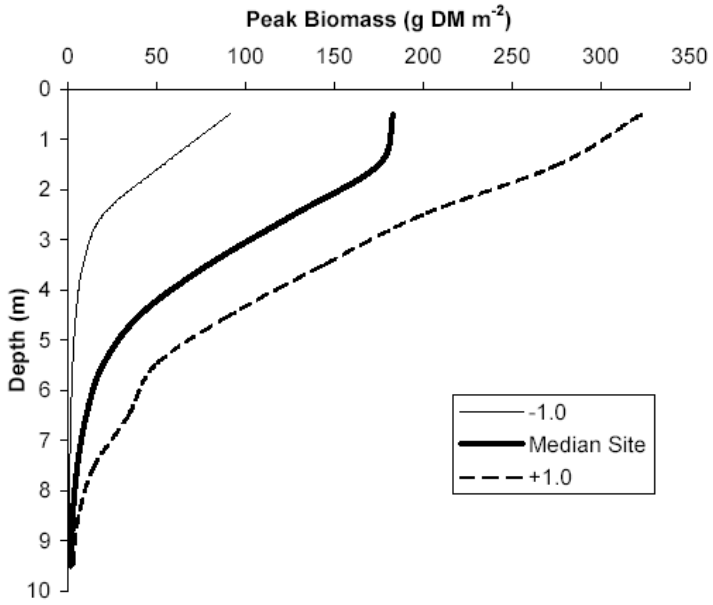

Figure 4.10 The effect of SRP variability on the depth distribution of peak *Cladophora* biomass in eastern Lake Erie based on CGM model simulations. Model simulations were conducted using 2002 median data, and modifying SRP by +/- 1 ug L-1 from 2002 values.

To determine the influence of these changes in SRP on basin wide *Cladophora* biomass (northern shoreline) the influence of bathymetry and substratum availability were included in the calculations. In these calculations the areal biomass for each 1m depth interval at the 'median' site is multiplied by the total amount of available substratum for that depth contour (Table 2.5). Using this method the CGM predicted that peak depth-integrated biomass along the northern shoreline of eastern Lake Erie would have been approximately 10,000 tonnes DM during 2002, which is similar to estimates of 11,000 tonnes DM made using field-collected biomass data from 1995-2002 (Chapter 2). Further, the CGM predicted that increases of 1 μg L^{-1} SRP from 2002 'median' conditions would result in a total depth-integrated biomass of 18,000 tonnes DM, a 79% increase from biomass estimates during 2002. Conversely, the CGM predicted that a reduction of 1 μg L^{-1} SRP from 2002 'median' conditions would result in a maximum standing crop of 3000 tonnes DM, a 71% decrease from biomass estimates during 2002. These results illustrate the sensitivity of *Cladophora* biomass accrual in eastern Lake Erie to ambient SRP concentration and suggest that reductions of 1 μg L^{-1} would cause a substantial decrease in total *Cladophora* biomass. The CGM also predicts that the timing of the sloughing event would be altered by variability in SRP concentration of 1 μg L^{-1} (Figure 4.9). As previously discussed, the CGM predictions

for the timing of the sloughing event were based on metabolic imbalance at the base of the algal mat. Under increased SRP conditions the mat density increased rapidly, reducing the amount of PAR reaching cells at the base of the mat below minimum requirements, and the sloughing event was triggered approximately 14 days earlier (Figure 4.9). When SRP concentrations were reduced by 1 μg L^{-1} from 2002 'median' conditions the CGM predicted that the algal mat would not reach a sufficient density to trigger the mid-summer sloughing. The CGM also predicted that the vertical distribution of *Cladophora* biomass would be altered by +/- 1 μg L^{-1} shifts in SRP from 2002 conditions (Figure 4.10).

4.4 Conclusions

The growth and biomass accrual of *Cladophora* represents an integrated response to numerous and highly dynamic environmental variables. The *Cladophora* growth model (CGM) provides a useful tool to examine the influence of environmental variability on growth rates both spatially and temporally. The CGM was applied to investigate the role of light, temperature, and phosphorus on the seasonal and spatial dynamics of *Cladophora* growth in eastern Lake Erie during 2002. The model simulations were based on environmental data collected at 5 sites in eastern Lake Erie that represented the expected range of environmental conditions found in eastern Lake Erie (Chapter 2) and indicated the following:

1) The seasonal pattern of *Cladophora* growth in eastern Lake Erie during 2002 was strongly influenced by ambient water temperature.

2) Dense cloud cover reduced daily growth rates to very low levels, however dense cloud cover generally persisted for only 1-2 day periods and inter-annual variability in surface PAR between 2001-2003 had only a minor impact on the resulting standing crop. Further, the use of simulated 70% cloud-free PAR caused only a 3-4 % difference in standing crop from measured PAR data (2001-2003).

3) The depth distribution of *Cladophora* in eastern Lake Erie was strongly influenced by site-to-site differences in water clarity. The CGM predicted that inter-site differences in kPAR would result in 2X difference in standing crop between sites with the highest and lowest water clarity.

4) Inter-annual variability in kPAR from 2001-2003 had only a minor effect on the standing crop.

5) The CGM predicted that a prolonged period (~14 days) of negative growth occurred at the base of the *Cladophora* mat immediately prior to the sloughing event. The metabolic imbalance was primarily caused by low light availability, and exacerbated by intermediate water temperatures (22-24°C).

6) The CGM under-predicted biomass accrual at shallow depths (≤1.5m) in eastern Lake Erie. This resulted from over-predicting the effects of photorespiration at high light intensities (600-1200 uM m^{-2} s^{-1}) and not accounting for the positive effects of self-shading.

7) The growth and biomass accrual of *Cladophora* in eastern Lake Erie was highly sensitive to available phosphorus. Tissue P concentrations were below optimal values for the duration of the 2002 growing season. Site-to-site differences in SRP concentration were responsible for up to a 2X difference in depth-integrated biomass.

8) The CGM predicted that inter-annual variability in SRP concentration of +/- 1 μg L^{-1} from 2002 median levels would strongly influence the depth-integrated biomass of *Cladophora* in eastern Lake Erie. For example, reductions in soluble reactive phosphorus by 1 μg L^{-1} from 2002 'median' conditions would result in a 70% reduction in the standing crop at the 'median' site, while and increase of 1 μg L^{-1} would result in a 80% increase in the standing crop at the 'median' site.

4.5 Literature cited

Auer, M. T., and R. P. Canale. 1980. Phosphorus uptake dynamics as related to mathematical modeling of *Cladophora* at a site on Lake Huron. J. Great Lakes Res., 6: 1-7.

Auer, M. T., and R. P. Canale. 1982a. Ecological and mathematical modeling of *Cladophora* in Lake Huron: 2. Phosphorus uptake kinetics. J. Great Lakes Res., 8: 84-92.

Auer, M. T., and R. P. Canale. 1982b. Ecological and mathematical modeling of *Cladophora* in Lake Huron: 3. The dependence of growth rates on internal phosphorus pool size. J. Great Lakes Res., 8: 93-99.

Auer, M. T., R. P. Canale, H. C. Grundler, and Y. Matsuoka. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 1. Program description and field monitoring of growth dynamics. J. Great Lakes Res. 8: 73-83.

Bellis, V. J. 1968. Unialgal cultures of *Cladophora glomerata* (L.) Kutz. I. Response to temperature. J. Phycol. 4: 19-23.

Bellis, V. J., and D. A. McLarty. 1967. Ecology of *Cladophora glomerata* (L.) Kütz. In southern Ontario. J. Phycol., 3: 57-63.

Bloesch, J. 1982. Inshore-Offshore sedimentation differences resulting from resuspension in the eastern basin of Lake Erie. Can. J. Fish. Aquat. Sci. 39: 748-759.

Byappanahalli, M. N., D. A. Shively, M. B. Nevers, M. J. Sadowsky, and R. L. Whitman. 2003. Growth and survival of Escherichia coli and enterococci populations in the macro-alga *Cladophora* (Chlorophyta). FEMS Microbiology Ecology 46: 203-211.

Canale, R. P., and M. T. Auer. 1982a. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 5. Model development and calibration. J. Great Lakes Res., 8: 112-125.

Canale, R. P., and M. T. Auer. 1982b. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 7. Model verification and system response. J. Great Lakes Res., 8: 134-143.

Canale, R. P., M. T. Auer, and J. M. Graham. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 6. Seasonal and spatial variation in growth kinetics. J. Great Lakes Res., 8: 126-133.

Charlton, M. N., R. Le Sage, and J. E. Milne. 1999. Lake Erie in transition: the 1990's. *In:* State of Lake Erie (SOLE) – Past, present, and future. M. Munawar, T. Edsall & I. F. Munawar (eds.). pp 97-123.

Fee, E. J. 1990. Computer programs for calculating *in situ* phytoplankton photosynthesis. Rep. 1740. Central and Arctic Region, Department of Fisheries and Oceans, Winnipeg, Manitoba.

Graham, J. M., M. T. Auer, R. P. Canale, and J. P. Hoffmann. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 4. Photosynthesis and respiration as functions of light and temperature. J. Great Lakes Res., 8: 100-111.

Hecky, R. E., R. E. H. Smith, D. R. Barton, S. J. Guildford, W. D. Taylor, M. Charlton and T. E. Howell. 2004. The near shore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Submitted to Can. J. Fish. Aquat Sci. 61: 1285-1293.

Herbst, R. P. 1969. Ecological factors and the distribution of *Cladophora glomerata* in the Great Lakes. American Midland Naturalist 82: 90-98.

Hiriart-Baer, V. P., L. M. Campbell, S. N. Higgins, M. N. Charlton, L. F. Moore, S. J. Guildford, and R. E. Hecky (submitted). *Cladophora* resurgent and revisited: A brief literature review. J. Great Lakes Res.

Howick, G. L., and J. Wilhm. 1985. Turbidity in Lake Carl Blackwell: Effects of water depth and wind. Proc. Okla. Acad. Sci., 65: 51-57.

Lester, W. W., M. S. Adams, and A. M. Farmer. 1988. Effects of light and temperature on photosynthesis of the nuisance alga *Cladophora glomerata* (L.) Kutz from Green Bay, Lake Michigan. New Phytol., 109: 53-58.

Mantai, K. E. 1987. Energy relations in Cladophora glomerata from Lake Erie. J. Great Lakes Res. 13: 279-284.

Mantai, K. E. 1989. Commentary: Rebuttal to comment by M. T. Auer and J. M. Graham. J. Great Lakes Res. 15: 371-372.

Millner, G. C., and R. A. Sweeney. 1982. Lake Erie *Cladophora* in perspective. J. Great Lakes Res. 8: 27-29.

Neil, J. H., and G. E. Owen. 1964. Distribution, environmental requirements and significance of *Cladophora* in the Great Lakes. *In:* Proc. 7th Conference on Great Lakes Research, pp. 113-121.

Painter, D. S., and M. B. Jackson. 1989. Cladophora internal phosphorus modeling: Verification. J. Great Lakes Res. 15(4): 700-708.

Painter, D. S., and G. Kamaitis. 1987. Reduction of *Cladophora* biomass and tissue phosphorus in Lake Ontario, 1972-83. Can. J. Fish. Aquat. Sci. 44: 2212-2215.

Parker, J. E., and S. C. Maberly. 2000. Biological response to lake remediation by phosphate stripping: control of *Cladophora.* Freshwater Biology 44: 303-309.

Patterson, M, W. R., J. J. H. Ciberowski, and D. R. Barton. Submitted. The distribution and abundance of *Dreissena* species (Dreissenidae) in Lake Erie, 2002. J. Great Lakes Res.

Pitcairn, C. E. R., and H. A. Hawkes. 1973. The role of phosphorus in the growth of *Cladophora.* Water Research 7: 159-171.

Rukavina, N. A. and D. A. St. Jacques. 1971. Lake Erie nearshore sediments Fort Erie to Mohawk point, Ontario. Proc. 14th Conf. Great Lakes Res. 387-393.

Shear, H. and E. E. Konasewich. 1975. *Cladophora* in the Great Lakes. International Joint Commission. 179p.

Sheath, R. G., and K. M. Cole. 2002. Biogeography of stream macroalgae in North America. J. Phycol. 28: 448-460.

St. Jacques, D. A. and N. A. Rukavina. 1973. Lake Erie nearshore sediments – Mohawk point to Port Burwell, Ontario. Proc. 16th Conf. Great Lakes Res. 454-467.

Weidman, P., 2003. In situ particle clearance rates of Quagga mussels in eastern Lake Erie. M.Sc. Thesis. University of Waterloo, Waterloo, Ontario, Canada. 99p.

Whitton, B. A. 1970. Biology of *Cladophora* in freshwaters. Water Research 4: 457-476.

Wong, S. L., and B. Clark. 1976. Field determination of the critical nutrient concentrations for *Cladophora* in streams. J. Fish. Res. Board Can. 33: 85-92.

Wong, S. L., B. Clark, M. Kirby, and R. F. Kosciuw. 1978. Water temperature fluctuations and seasonal periodicity of Cladophora and Potamogeton in shallow rivers. J. Fish. Res. Board Can. 35: 866-870.

Chapter 5

Photosynthesis and respiration of *Cladophora*: *In vitro* experiments with *Cladophora* harvested from 5 sites in eastern Lake Erie (2002)

5.1 Introduction

Recent increases in benthic algal productivity and biomass accrual in the lower Laurentian Great Lakes are considered linked to changes in water clarity and available phosphorus caused by invasive zebra and quagga mussels (*Dreissena polymorpha and D. bugensis respectively*) (Lowe and Pillsbury 1995; Hecky et al. 2004; Chapter 2). The benthic alga *Cladophora glomerata* currently forms extensive blooms in Lake Ontario (Campbell et al. submitted), eastern Lake Erie (Chapter 2), Lake Michigan (Byappanahalli et al. 2003), and isolated locations of Lake Huron (T, Howell pers. com.). By other measures of lake trophic status, for example offshore total phosphorus concentration, these lakes or lake basins are oligotrophic to oligo-mesotrophic (Wetzel 2001; Chapter 2). In eastern Lake Erie the massive shoreline blooms of *Cladophora* are not necessarily associated with point sources of nutrients, and most of the rocky lake bottom (>90%) between 0-5m depth is blanketed with *Cladophora* by early summer (Chapter 2).

Response curves generated using algal photosynthesis vs. irradiance (P-I) experiments are often used to model *in situ* growth rates or assess the physiological condition of the algae (e.g. Graham et al. 1982; Fee 1990; Henley 1993; Litchman et al. 2003; Behrenfeld et al. 2004). The shape of the P-I curve is generally assessed using a hyperbolic, or similar, function (e.g. Baly 1935; Jasby and Platt 1976; Bannister 1979; Platt et al. 1980). Three parameters are generally used to define the P-I response curve including: α, which is the slope of the ascending portion of the P-I response; Pm, which is the maximum rate of photosynthesis; and R_d, which is the rate of respiration in the dark (e.g. Baly 1935; Jasby and Platt 1976). If declines in Pm are noted at high irradiance then a fourth parameter, β, is often included to characterize the downward slope of the P-I response (e.g. Platt et al. 1980). Previous studies have noted that these P-I variables may vary according to the experimental methodology (Wood 1968; Mantai 1987; Henley 1993) or physiological status of the algae (Henley 1993; Turner et al. 1994; Litchman et al. 2003;

Behrenfeld et al. 2004). Experimental conditions may affect the P-I response curves in several ways including: self-shading, carbon limitation, and the length of the incubation (Wood 1968; Mantai 1987; Henley 1993). The P-I response may also be affected by nutrient stress, previous light history, concentration of photosynthetic pigments, or other factors that influence the physiological condition of the algae (e.g. Henley 1993; Litchman et al. 2003; Behrenfeld et al. 2004).

Based, in part, on the P-I response of *Cladophora* isolated from Lake Huron a *Cladophora* growth model was developed to investigate and predict how changes in environmental parameters would affect *in situ* growth rates and biomass accrual (Canale and Auer 1982; Graham et al. 1982). A revised version of the *Cladophora* growth model (Chapter 3) was field tested at 5 sites in eastern Lake Erie and used to assess the importance of environmental variability on the spatial and temporal patterns of growth and biomass accrual (Chapter 3, 4). At most sites the CGM predicted the seasonal growth patterns and maximal biomass of *Cladophora* with reasonable accuracy, however in some cases the model performed poorly. Specifically, the CGM predictions often underestimated biomass at shallow depths (< 1m) compared with the results from my biomass surveys (see Chapter 4). Also, the timing of the sloughing event was not well predicted by earlier versions of the CGM (Canale and Auer 1982; Chapter 3) that were based primarily on the physiology of the algae and did not include population level interactions such as self-shading by the algal canopy. In this study I present the results of P-I experiments on *Cladophora* from 5 sites in eastern Lake Erie during the 2002 ice-free season. Such physiological experiments were useful for interpreting population level dynamics noted during my field surveys (Chapter 2), and for assessing the validity of predictions for *Cladophora* growth and biomass accrual made using the *Cladophora* growth model (Chapter 3, 4). The main objectives of this study were to determine if the spatial and temporal growth patterns of *Cladophora* in eastern Lake Erie could be adequately described

by its photosynthetic capability, specifically in those instances where the CGM predictions contrasted field observations.

5.2 Methods

5.2.1 Site Description

Experiments were conducted *in vitro* on *Cladophora* harvested from 5 sites in eastern Lake Erie during 2001-2002 (Figure 3.1). These sites were also locations where a *Cladophora* growth model (CGM) was revised and field-tested (Canale and Auer 1982; Chapter 3,4), and were part of a larger network of sites where seasonal and spatial surveys for biomass, tissue phosphorus, and water chemistry were conducted (Howell 1998; Chapter 2). The substratum at all sites primarily consisted of bedrock shelves of low slope (<10°). All sites were heavily colonized by the invasive mussel *Dreissena bugensis*, and *Cladophora* filaments were found attached to the mussel shells or directly to the rock surfaces. During 2002, densities of *D. bugensis* in this region of eastern Lake Erie ranged from 4,000-11,000 individuals m^{-2} of lake bottom (Patterson et al. submitted).

5.2.2 Water sampling and algal collections

A detailed description of sampling methodology for water chemistry is provided in Chapter 2. Briefly, triplicate water samples were collected in 1 L rigid and opaque polyethylene bottles approximately 1m above the surface of the *Cladophora* mat using SCUBA and swimming up current to minimize the potential for re-suspended material to be collected in the sampling vessels. Water samples were analyzed for turbidity using an HF Instruments DF100 turbidometer. Water column extinction coefficients (kPAR) were determined from the relationship between turbidity and kPAR (Chapter 3). Water temperature was

measured to 0.1°C in situ using both an alcohol thermometer, and using *in situ* Tidbit © temperature loggers (Onset Corporation).

Cladophora was collected from 3 x 0.25m^2 quadrats using SCUBA and an underwater airlifting device under low suction (Barton and Hynes 1978; Chapter 2) and retained in 250 um mesh bags. Upon return to the surface the algal material from one of the quadrats was placed into a 10 L polyethylene carboy half-filled with lake water and kept in the dark at lake temperature. This algal material was to be used for the physiology experiments. The algal material from the remaining two quadrats was stored in ziplock bags, kept cool and in the dark until return to the laboratory where it was used for biomass estimations, tissue nutrient analysis, and taxonomic identification. Analysis of *Cladophora* tissues for phosphorus content is described in Chapter 2.

5.2.3 *In vitro* P-I experiments

Sufficient algal material for the experiments was removed from the 10 L carboy and placed in a sampling tray with lake water. Debris and visible macro-invertebrates were picked from the *Cladophora* filaments. No efforts were made to remove epiphytes and P-I experiments were assumed to represent community metabolism. For each of the sites 12 x 128 mL glass bottles were filled with lake water from each site screened through a coarse nitex mesh to remove large debris then a 47 mm GF/F filter, with a nominal pore size of 0.7 μm, to remove seston. Approximately 0.08 g DM of *Cladophora* was placed in each of the 11 bottles, with two bottles serving as initials that were immediately fixed with Winkler reagents (see below), and one additional bottle serving as a control for planktonic net O_2 exchange. All of the preceding steps were conducted under low ambient light. Two of the bottles containing *Cladophora* filaments were completely opaque and were used to estimate dark respiration. All bottles were placed in a temperature-controlled incubator under PAR values ranging between 0-1200 uM m^{-2} s^{-1}. A 150 W

metal halide lamp and a 150 W sodium halide lamp were situated together overhead one end of the incubator and capped bottles were inverted and positioned at various distances from the light source to provide a light gradient. PAR was measured beside each bottle using a spherical light sensor (Biospherical QSL 100). P-I incubations were conducted at temperatures within 0.5°C of the median lake temperature between all sites. Incubation times were restricted to ~ 45 min to reduce the potential for carbon limitation, O_2 inhibition of photosynthesis, or photoinhibition (Henley 1993). Values of dissolved inorganic carbon (DIC) in eastern Lake Erie were high (~23 mg L^{-1}) relative to rates of carbon assimilation noted in these experiments. The maximum carbon assimilated in the experiments was calculated to be <20 % of the DIC contained within the incubation vessel (27 May 02 experiments), however in the majority of experiments maximum carbon uptake was <8 % of DIC contained within the incubation vessel. The potential for self-shading to have occurred within the incubation vessels, and the implications to the results, are discussed in later sections. Dissolved O_2 concentrations were measured in initial and final samples by Winkler titration (Stainton et al. 1977) and O_2 exchange was determined as the difference between samples after incubation and the mean of 2 samples that were fixed prior to the incubation (initials).

5.2.4 The influence of algal density on self-shading

The influence of algal density on self-shading was determined under controlled *in vitro* conditions. A 1.7 L plexiglass chamber was situated directly beneath a 150 W metal halide lamp such that irradiance at the upper surface of the *Cladophora* mat would be approximately 1200 uM m^{-2} s^{-1}. With the exception of the overhead incubator light the experiments were conducted under dim and indirect room lighting. *Cladophora* filaments were placed into the chamber and allowed to settle to the bottom and the height of the resulting algal mat was recorded. The intensity of PAR was measured at the top and base of the algal

mat using a small PAR sensor associated with a diving-PAM fluorometer (Heinz Waltz Gmbh). The extinction coefficient of the *Cladophora* mat (kPARm) was calculated as:

$kPARm = (\ln I_0 - \ln Iz)/z$ (Wetzel 1983)

Where I_0 is the PAR at the mat surface ($\mu M\ m^{-2}\ s^{-1}$), Iz is the PAR at the base of the mat ($\mu M\ m^{-2}\ s^{-1}$), and z is the depth of the mat (m). The algal material was then collected placed in a drying oven at 60°C, for 24 hours, then weighed for dry weight. The experiment was repeated 26 times over a range of algal biomass (13-120 g DM m^{-2}) and density (0.3-11.8 g DM m^{-3}).

5.2.5 The influence of algal density on net photosynthesis

An experiment to determine the influence of self-shading on net photosynthesis for relatively thick algal mats (2-15 cm) was conducted on 11 Sept 02. The experiment was conducted in an outdoor water bath at mid-day and surface irradiance values were approximately 1700 uM $m^{-2}\ s^{-1}$. Algal material was collected from the Peacock point site and transported to the lab at lake temperature (~20°C). Algal material was placed in the 1.7 L plexiglass chambers at densities ranging from 60-1000 g DM m^{-2} and allowed to incubate for 0.75-1.2 hours at 20°C. Plexiglass disks fitted with two rubber gaskets could be fitted into the top and bottom of the chamber to provide a gas tight incubation vessel. The upper disk was fitted with a manual stirring device and ports for sampling. When water samples were taken from the chamber the upper disk would slide inward ensuring no changes in pressure inside the sampling vessel, and the corrected chamber volume could be calculated. Three replicate chambers for each algal density (60, 240, 480, 960 g DM m^{-2}) were sampled for O_2 exchange before and after the incubation. Chambers were stirred before initial and final samples were taken and at 10 minute intervals during the experiment. Water samples (55 mL) were slowly removed from the chambers using a 60 mL plastic syringe to prevent

bubble formation. The volume in each syringe was then adjusted to 50mL and fitted with a rubber stopper. Winklers reagents were injected directly into the syringe and mixed by inverting several times until no flocculent remained. The contents of the syringe were slowly ejected into a 150 mL Erlenmeyer flask and titrated using 0.5N sodium thiosulphate (Stainton et al. 1977). The maximum change in DIC within the chambers was calculated to be <7 %.

5.2.6 Data analysis and modeling *in situ* photosynthesis

Photosynthesis vs. irradiance data were fitted to the hyperbolic tangent equation of Jasby and Platt (1976) using commercially available curve fitting software (Systat Software Inc. 2000, Table curve 2D). No evidence was found for significant photoinhibition at experimental irradiance values (0-1200 uM m^{-2} s^{-1}) and a beta term was not included. For each experiment the goodness of fit was assessed using the degrees of freedom adjusted R^2 value. In cases where the degrees of freedom adjusted R^2 value was below 0.9 the data was rejected and not used in subsequent analysis. The parameters generated from the *In vitro* PI experiments (Table 1) were used to generate estimates of net photosynthesis (P_{NET}) using the equation (Jasby and Platt 1976):

$$P_{NET} = ((Pm * Tanh (\alpha * Iz/Pm) - R_d) \qquad \text{(Equation 5.1)}$$

where, Pm is the maximum gross rate of photosynthesis (mg O_2 g DM^{-1} h^{-1}), α is the light limited portion of the P-I curve (mg O_2 · mg DM^{-1} · uM photons^{-1} · m^{-2}), Iz is the irradiance at depth z, and R_d is the rate of dark respiration (mg O_2 g DM^{-1} h^{-1}). The net specific growth rate (μNET) was then calculated using the equation:

$$\mu NET = ((P_{NET} * 24 /1000) * PP) - ((Rd*24/1000) *(1-PP)))/(C * \theta) \qquad \text{(Equation 5.2)}$$

where PP is the photoperiod (0-1, dimensionless), C is the mean carbon content (37.5 mg C/ 100 mg DM) (Auer and Canale 1982b), and θ is the photosynthetic quotient (12 mg C/ 32 mg O_2) (Auer and Canale 1982b). The initial steps in Equation 5.2, Pm* 24/1000 and Rd * 24/1000, were required to convert units from mg O_2 g DM^{-1} h^{-1} to mg O_2 mg DM^{-1} day^{-1}. To estimate the importance of self-shading on growth rates the *Cladophora* mat was modeled as 10 layers of equal thickness, and μNET was calculated for each mat layer. The photosynthetic response variables Pm, α, and Rd were assumed to remain constant between mat layers and μNET for each layer was calculated based on changes in available PAR. Daily estimates of production were presented as rates over mat depth, or as a depth integrated value.

Table 5.1 Photosynthetic parameters of *Cladophora glomerata* collected from 5 sites in eastern Lake Erie during 2002 and measured *in vitro*. Measured data were fitted to the equation of Jasby and Platt (1976). Data are reported for experiments where measured values were fitted to the Jasby and Platt equation with an $R^2 > 0.90$. The term 'Icr' represents the critical PAR intensity where net photosynthesis equals zero. The term 'Ik' = Pmax(Gross)/alpha and represents the inflection point on the gross photosynthesis vs. irradiance curve.

Site	Date	Depth (m)	Pmax (Net) (mg O_2 • g DM^{-1} h^{-1})	Alpha (mg O_2 mg DM^{-1} uM photons^{-1} m^{-2})	Respiration (mg O_2 • g DM^{-1} h^{-1})	Icr (uM m^{-2} s^{-1})	Ik (uM m^{-2} s^{-1})	R^2
Peacock	27-May-02	2	4.35	0.0124	0.98	80	430	0.98
	14-Jun-02	2	2.47	0.0732	3.38	53	80	0.97
	17-Jun-02	2	3.82	0.0411	1.77	45	136	0.92
	04-Jul-02	2	7.23	0.0599	1.45	25	145	0.97
	08-Jul-02	2	2.92	0.0243	1.13	48	166	0.93
	29-Jul-02	2	6.85	0.0461	1.36	31	178	0.96
	01-Aug-02	2	8.51	0.0389	2.17	57	275	0.99
	01-Aug-02	5	4.60	0.0335	1.24	38	174	0.96
	19-Aug-02	5	7.01	0.0127	1.8	145	696	0.96
Hoover	27-May-02	2	11.56	0.0238	4.18	180	660	0.94
	19-Jun-02	2	4.19	0.0511	1.96	40	120	0.95
	08-Jul-02	2	1.76	0.0327	1.35	45	95	0.91
	29-Jul-02	2	6.26	0.0393	0.77	20	179	0.95
Grant	27-May-02	2	7.19	0.0343	3.32	101	306	0.95
	25-Jun-02	2	8.34	0.0520	2.7	53	212	0.93
	02-Jul-02	2	3.89	0.0453	2.27	53	136	0.94
	08-Jul-02	2	7.46	0.0457	1.58	35	198	0.96
	15-Jul-02	2	4.85	0.0450	0.67	15	123	0.91
	24-Jul-02	2	11.29	0.0654	0.98	16	188	0.92
	29-Jul-02	2	5.96	0.0861	5.52	70	133	0.94
Rathfon	27-May-02	2	6.82	0.0797	3.06	40	124	0.96
	08-Jul-02	2	13.15	0.0827	1.75	22	180	0.95
	29-Jul-02	2	7.35	0.0529	1.81	35	173	0.97
	08-Oct-02	2	3.45	0.0204	1.27	64	231	0.97
Rock	27-May-02	2	22.99	0.0924	4.7	52	300	0.98
	19-Jun-02	2	6.52	0.0805	1.52	20	100	0.92
	08-Jul-02	2	9.96	0.0774	1.6	21	149	0.96
	29-Jul-02	2	9.28	0.0661	0.89	14	154	0.96

5.3 Results

5.3.1 Spatial and temporal variability of photosynthetic parameters

Maximum net and gross photosynthetic rates were highly variable both spatially and temporally (Table 1, Figures 5.6-5.16). Highest Pm (Net) values occurred during the spring (27 May 02) at the Rock point (23.0 mg O_2 g DM^{-1} h^{-1}) and Hoover point (11.6 mg O_2 g DM^{-1} h^{-1}) sites. These sites were both turbid and had high tissue phosphorus concentrations on 27 May 02 compared to other sites and dates (Chapter 2). For the remainder of the sampling dates (June-October) values of Pm (Net) ranged from 1.8-13.1 mg

O_2 g DM^{-1} h^{-1} with a mean value of 6.4 mg O_2 g DM^{-1} h^{-1}. During the sloughing period (24-29 July 02) values for Pm (Net) ranged between 6.0-11.3 mg O_2 g DM^{-1} h^{-1}, and values were within the range of values reported during the spring and early summer period (Table 1). Values for Pm (net or gross) were poorly correlated to water clarity, temperature, biomass, or tissue phosphorus concentrations. The slope of the light limited portion of the photosynthesis vs. irradiance curve (α) ranged from 0.01-0.09 mg O_2 · mg DM^{-1} · uM $photons^{-1}$ · m^{-2}, with a mean value of 0.05 mg O_2 · mg DM^{-1} · uM $photons^{-1}$ · m^{-2} across all sites and dates (Table 1). Values for α did not display any strong seasonal trends, and were not strongly correlated to water clarity, temperature, biomass, or tissue phosphorus concentrations. During the late spring to mid-summer period (14 Jun 02 – 29 Jul 02) Pm and α tended to covary (Figure 5.1; R = 0.72, n = 19). During the early spring (27 May 02) and late summer to autumn (01 Aug 02 to 08 Oct 02) the relationship between Pm (Gross) and α was less consistent (Figure 5.1). The light saturation parameter, Ik = Pm/α (Talling 1957), varied from 80-660 uM m^{-2} s^{-1} during the ice-free season (Table 5.1). High values of Ik (≥300 uM m^{-2} s^{-1}) were associated with experiments conducted early in the growing season (27 May 02, Table 5.1). During the remainder of the season Ik varied from 80-231 uM m^{-2} s^{-1} with a mean value of 154 uM m^{-2} s^{-1}. The critical irradiance (Icr) where net photosynthesis is equal to zero, Icr = Rd/α (Henley 1993), varied from 14-180 uM m^{-2} s^{-1}. Critical irradiance values >100 uM m^{-2} s^{-1} were associated with the first sampling date (27 May 02) from sites where little biomass had accumulated. For the remainder of the growing season values of Icr ranged from 14-70 uM m^{-2} s^{-1} with a mean value of 36 uM/m^2/s. Evidence of photoinhibition at high irradiance (600-1200 uM m^{-2} s^{-1}) was not detected in any of our *in vitro* photosynthesis vs. irradiance experiments (Figures 5.6-5.16).

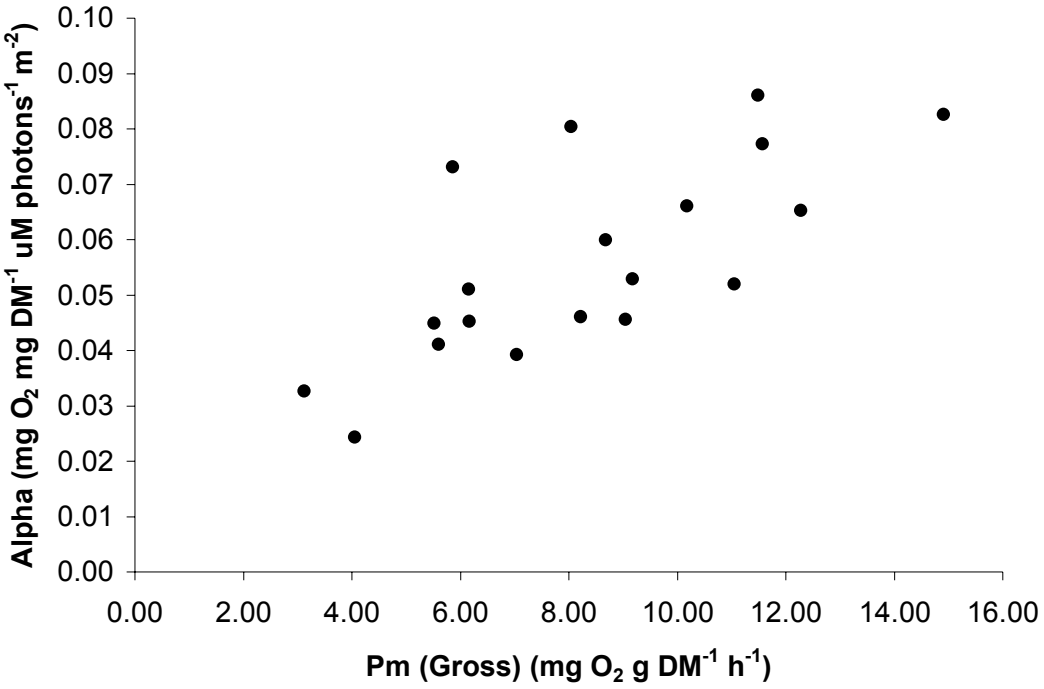

Figure 5.1 The relationship between maximum gross photosynthesis and alpha (α) in *Cladophora* sampled during the late-spring early summer (14 Jun 02 – 29 Jul 02) and measured *in vitro*. R = 0.72, n = 19.

5.3.2 Effects of self-shading on P-I parameters

Numerous authors have discussed the potential for self-shading to occur in natural communities or within *in vitro* incubations of *Cladophora* (e.g Wood 1968; Mantai 1987). Under *in situ* conditions *Cladophora* can grow to thick mats (>0.5 m) in which light is attenuated quickly (Chapter 4), and self-shading undoubtedly occurs. It is highly probable that some degree of self-shading occurs during the majority of *in vitro* photosynthesis incubations even when the amount of algal material used is small and clumping of filaments is reduced. A theoretical examination of the effect of self-shading on the interpretation of P-I curves is presented in Appendix A. In general, as self-shading increases the slope and convexity of the light limited portion of the P-I curve decreases, and the values of Ik and Icr increase. When self-shading

is severe photosynthetic rates do not reach light saturation (i.e. the P-I curve does not plateau) and Pm values cannot be reliably estimated. So long as self-shading is not severe, i.e. PAR sufficient to saturate photosynthesis penetrates to the bottom of the mat, Pm values are identical under varying degrees of self-shading. The effects of algal density on the light attenuation coefficient (kPARmat) of an algal mat are described in Figure 5.2.

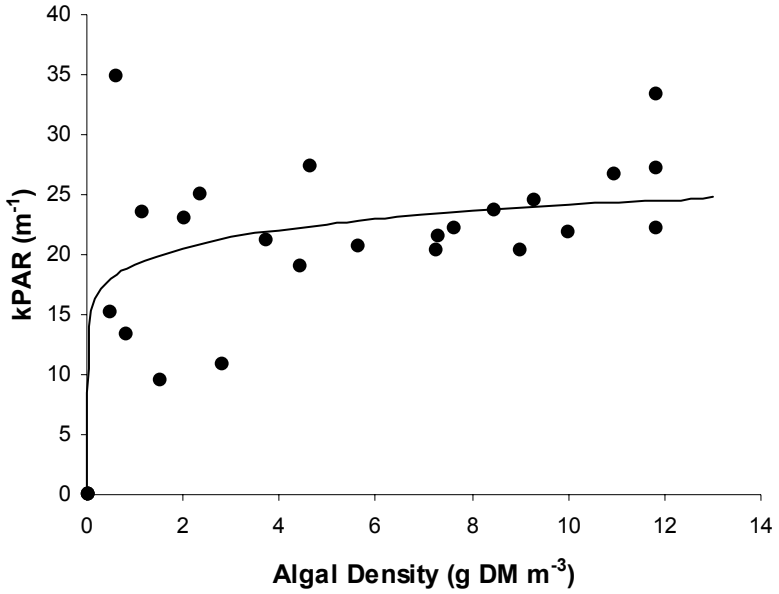

Figure 5.2 Extinction coefficients of PAR vs. *Cladophora* mats density. The data points were fitted with a power function, kPARmat = 19.213 * Mat density^(0.0989), R^2 = 0.064, n = 26.

As the algal density increases from zero light is rapidly attenuated within the algal mat. Algal density during *in vitro* incubations reported in this study was approximately 4 g DM m^{-3}, the height of the algal mat was <1 cm in thickness, and the extinction coefficient of the mat (kPARmat) was approximately 20 m^{-1}. Based on these values and using the approach outlined in Appendix 1, the effect of self-shading would increase the reported Ik and Icr values by ~10%, decrease the α value by ~10%, and have no influence on the reported value of Pm.

Under *in situ* conditions algal mats can become very dense and light penetration is strongly attenuated (Figure 5.2). As mat thickness increases the proportion of algae growing under light limited conditions also increases. We simulated the influence of algal density on biomass specific photosynthesis and areal photosynthesis (Figure 5.3) in an experiment conducted in 1.7 L chambers, in an outdoor incubator under full sunlight and maintained at 20°C. As the areal biomass increased the biomass specific growth rate rapidly declined due to self-shading. Under the range of *in situ* areal biomass estimates for eastern Lake Erie (0-1000 g DM m^{-2}; Chapter 2) the biomass specific growth rate could vary by one order of magnitude due to the effects of self-shading (Figure 4.6). Areal growth rates increased with increases in areal biomass under the range of biomass values in this experiment (Figure 5.3). The initial rise in net photosynthesis with increased areal biomass was rapid, however, the slope of the relationship between net photosynthesis and areal biomass was always less than 1, which is consistent with the effects of self-shading (i.e. increases in areal biomass cause declines in biomass specific growth rates).

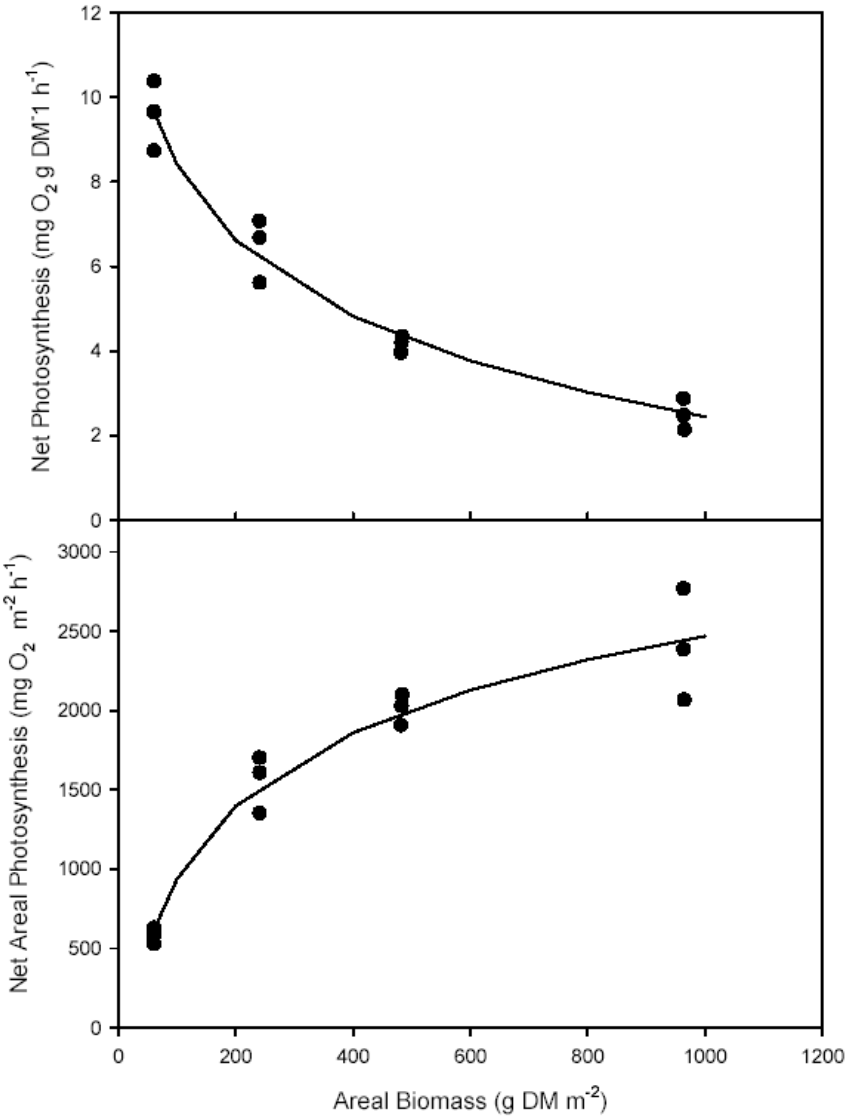

Figure 5.3 Net photosynthetic rates of *Cladophora* normalized to dry mass and area of substratum vs. Areal *Cladophora* biomass.

5.3.3 Modeling *in situ* growth rates

Seasonal values of μNET, based on *in vitro* P-I experiments and integrated over mat depth, varied from -0.002 to 0.297 day^{-1} with a mean value of 0.075 day^{-1}. Values of μNET were highly variable between sites, remained positive from spring (27 May 02) to mid-summer (01 Aug 02), and displayed no obvious

declining trend prior to the mid-summer sloughing period (24-29 Jul 02). Because these values of μNET are integrated over mat depth they represent the total mat growth rate, and do not reflect growth at any specific portion within the mat. Although the integrated values of μNET were positive through the sloughing period, values for μNET at the base of the algal mat were negative during the two sampling dates (15 Jul 02 and 24 Jul 02) prior to the sloughing event (Figure 5.4). Growth rates in the upper portions of the mat remained positive through the mid-summer sloughing period. Modeled growth rates (integrated over mat depth) declined during August and October sampling dates due to a combination of factors including a reduction in day length, a reduction in mean daily PAR due to increased cloud cover, increased water column turbidity, and low values for Pm and α (Table 5.1, Figures 5.6-5.16).

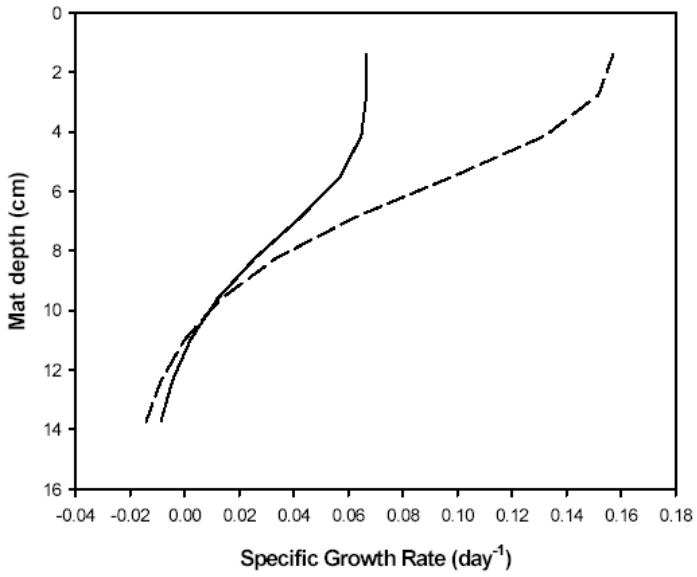

Figure 5.4 Net specific growth rate of *Cladophora* vs. mat depth on 15 Jul 02 and 24 Jul 02 at Grant point, eastern L. Erie. The solid line represents growth rates on 15 Jul 02 and the dashed line represents growth on 24 Jul 02.

Seasonal values for μNET (*in vitro*) were compared to values of μNET estimated using the *Cladophora* growth model (CGM) (Chapter 3) under identical surface irradiance, water clarity, water temperature, biomass, and tissue phosphorus (Figure 5.5). Values of μNET (CGM) were initially higher than μNET (*in vitro*) during June, however during July CGM predicted values for each depth and site were similar or below those predicted by the *in vitro* experiments. Overall, the values of μNET (*in vitro*) and μNET (CGM) were poorly correlated (R^2= 0.07, n = 28, p = 0.16).

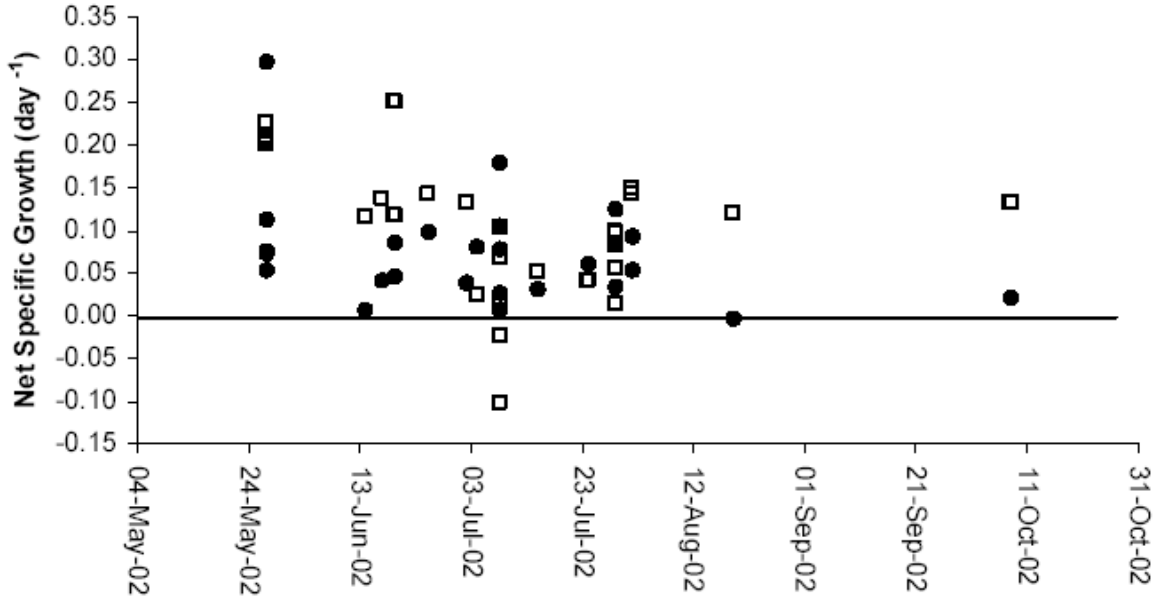

Figure 5.5 Daily specific growth of *Cladophora glomerata* at 5 sites, 2m depth, in eastern Lake Erie, 2002. Growth rates are estimated by *in vitro* experiments (closed circles) and the *Cladophora* growth model (CGM) (Open squares).

5.4 Discussion

The maximum value of Pm (Net) reported in this study, 24.0 mg O_2 g DM^{-1} h^{-1} (Table 1), was slightly below values of Pm (24-40 mg O_2 g DM^{-1} h^{-1}) reported in other studies of *Cladophora* from the Laurentian Great Lakes (Lester et al. 1988, Mantai 1974). The mean value of Pm (Net) reported in this study was 7.1 mg O_2 g DM^{-1} h^{-1} (n = 28, s.d. = 4.19) was similar to values of Pm reported by Graham et

al. (1982) and Adams and Stone (1973) for *Cladophora* from Lake Huron and Lake Michigan respectively. Previous researchers have commented on the potential for differences in methodology, particularly self-shading and carbon limitation, to cause differences in maximum photosynthetic rates noted between studies (e.g. Wood 1968, 1975; Mantai 1974; Mantai and Haase 1977). In this study the effects of self-shading and carbon-limitation on Pm were estimated to be small and not responsible for the low values of Pm (relative to optimum Pm values). The photosynthetic rates presented in this study were normalized to biomass in order to facilitate estimates of biomass accrual and comparisons with *Cladophora* growth model (CGM) predictions. Mantai (1987) reported that chlorophyll concentrations in *Cladophora* from Lake Erie, normalized to biomass, varied by 3x over a 1-2 day period. Variability in cellular chlorophyll concentrations were not assessed in this study, however may be largely responsible for the variations in reported photosynthetic rates (normalized to biomass) noted between studies, especially those conducted on field collected *Cladophora* under a wide range of light histories and nutrient limitation. Values of Pm (gross) and α were correlated during the late-spring early-summer (14 Jun 02 – 29 Jul 02) period (Figure 5.1), and this co-variation may indicate nutrient stress (Behrenfeld et al. 2004). Although no relationship was found between Pm or α and tissue P during the late-spring early-summer period, tissue P values were generally below 0.2 % DM where growth rates of *Cladophora* become increasingly sensitive to internal P concentration (Wong and Clark 1976; Auer and Canale 1982; Plannas et al. 1996). The low maximum rates of photosynthesis found in this study did not appear to be related to self-shading or carbon limiting conditions within the experiments, and were indicative of the physiological status of *Cladophora*.

Graham et al. (1982) reported declines in maximum net photosynthetic rates at irradiance values >600 μM m^{-2} s^{-1} caused by concomitant increases in light enhanced respiration. As a result, the *Cladophora* growth model (CGM), which is based on the equations of Graham et al. (1982), predicts a

decline in growth rates and biomass accrual at shallow depths (<2m) where light intensities often exceed 600 μM m^{-2} s^{-1}. In eastern Lake Erie the CGM under-predicted areal biomass at shallow depths (<2m) compared to estimates of areal biomass from field collections (Chapter 4). Maximal photosynthetic rates of *Cladophora* collected during this study maintained high photosynthetic rates between 600-1200 μM m^{-2} s^{-1} (Figures 1-11). Lester et al. (1988) also reported no decline in net photosynthetic rates at irradiance values 600-1600 μM m^{-2} s^{-1}. These results indicate that net growth rates of *Cladophora* are not necessarily inhibited at high irradiance values and that the CGM can underestimate biomass accrual where PAR intensities exceed 600 μM m^{-2} s^{-1}.

Numerous studies have attempted to relate the midsummer-sloughing phenomenon to relationships between the physiological response or condition of *Cladophora* tissues and environmental parameters (e.g. Bellis 1968; Wong et al.1978; Mantai 1987, 1989, Lester et al. 1988). Field studies, however, have generally indicated that the alga was physiologically capable of growth within the environmental conditions prevailing in the field prior to and during the commonly observed sloughing events (e.g. Canale and Auer 1982b; Mantai 1987; 1989). In this study the photosynthetic capacity of *Cladophora*, as estimated by the variables Pm and α, were poor predictors of the mid-summer sloughing event that occurred in eastern Lake Erie between July 24-29, during 2002. The sloughing event, however, was preceded by negative growth rates occurring at the base of the algal mat (Figure 5.4). In the model simulations illustrated by Figure 5.4, the variables Pm and α were assumed to remain constant through the mat layers and did not account for the physiological adaptation of *Cladophora* to low light intensities. The attenuation of PAR through the dense and thick algal mats, however, reduced intensities to well below the minimum light requirements (29-35 μM m^{-2} s^{-1}) predicted in this and other studies (e.g. Graham et al. 1982; Lester et al. 1988; Lorenz et al. 1991). At algal densities over 4 g DM m^{-3} (equivalent to ~65 g DM m^{-2}) approximately 90% of PAR incident at the mat surface is attenuated within the upper 10cm of

the mat. PAR values in the bottom layer of the algal mats during the 15 Jul 02 and 24 Jul 02 experiments were 9.5 and 10.9 μM m^{-2} s^{-1} respectively, and these PAR values would decrease as mat thickness and density continued to increase. Therefore, while increases in water temperature, low tissue P concentrations, and declining day length were important factors in the overall decline of overall mat growth rates (Chapter 4), the results presented in this study indicate that the most probable cause of the midsummer-sloughing event in eastern Lake Erie was the inability to maintain metabolic balance within cells at the base of the algal mat due to self-shading.

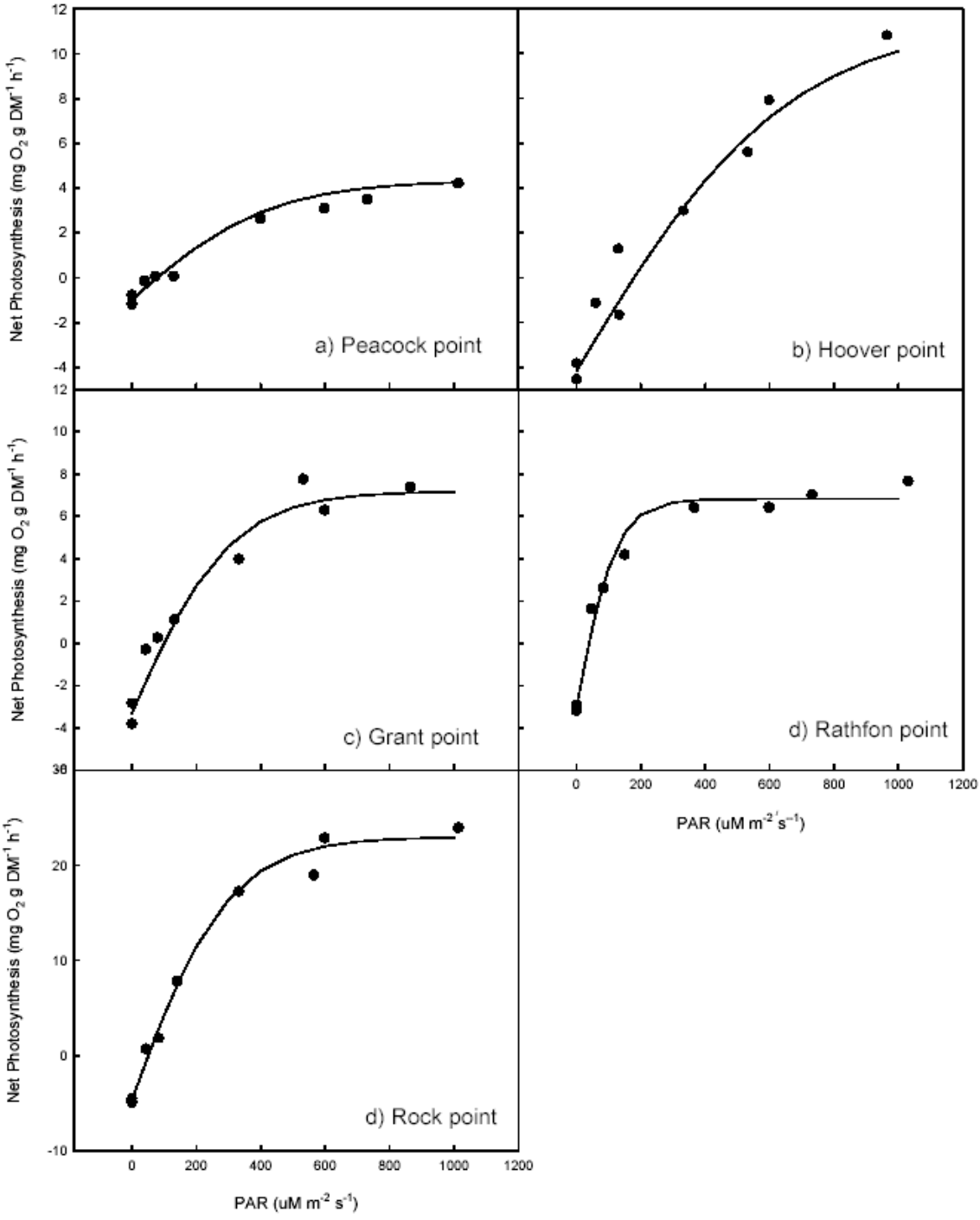

Figure 5.6 The photosynthesis vs. PAR response curves for *Cladophora* harvested at 5 nearshore sites in eastern Lake Erie on 27 May 02. Measured values are fitted using the Jasby and Platt (1976) equation. Values for photosynthetic parameters are located in Table 5.1.

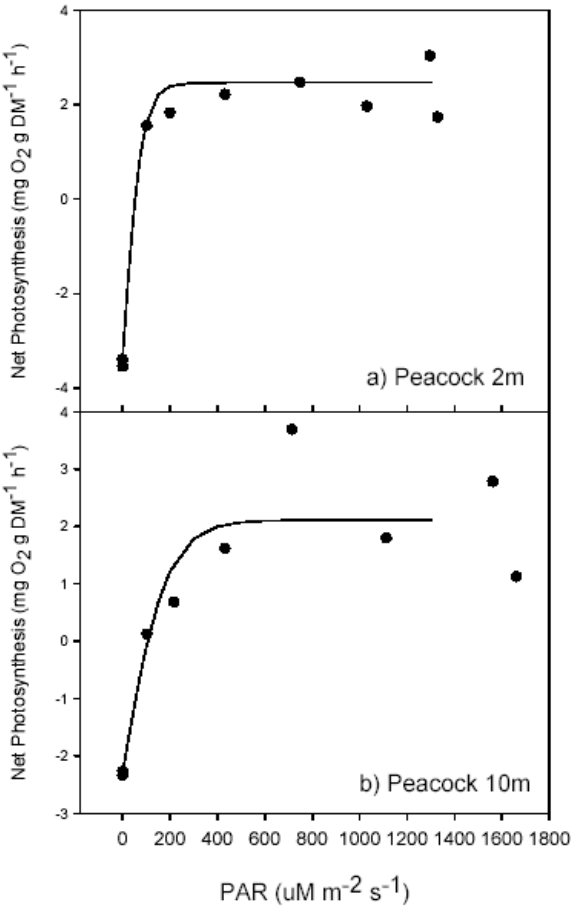

Figure 5.7 The photosynthesis vs. PAR response curves for *Cladophora* harvested at 2m and 10m depths Peacock point, eastern Lake Erie on 14 Jun 02. Measured values are fitted using the Jasby and Platt (1976) equation.

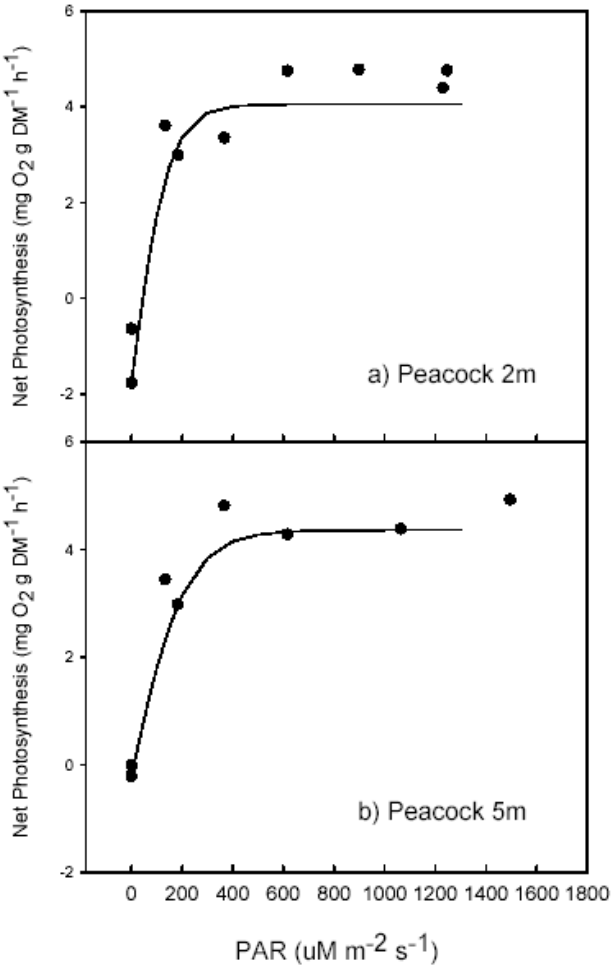

Figure 5.8 The photosynthesis vs. PAR response curves for *Cladophora* harvested at 2m and 5m depths Peacock point, eastern Lake Erie on 17 Jun 02. Measured values are fitted using the Jasby and Platt (1976) equation. Values for photosynthetic parameters are located in Table 5.1.

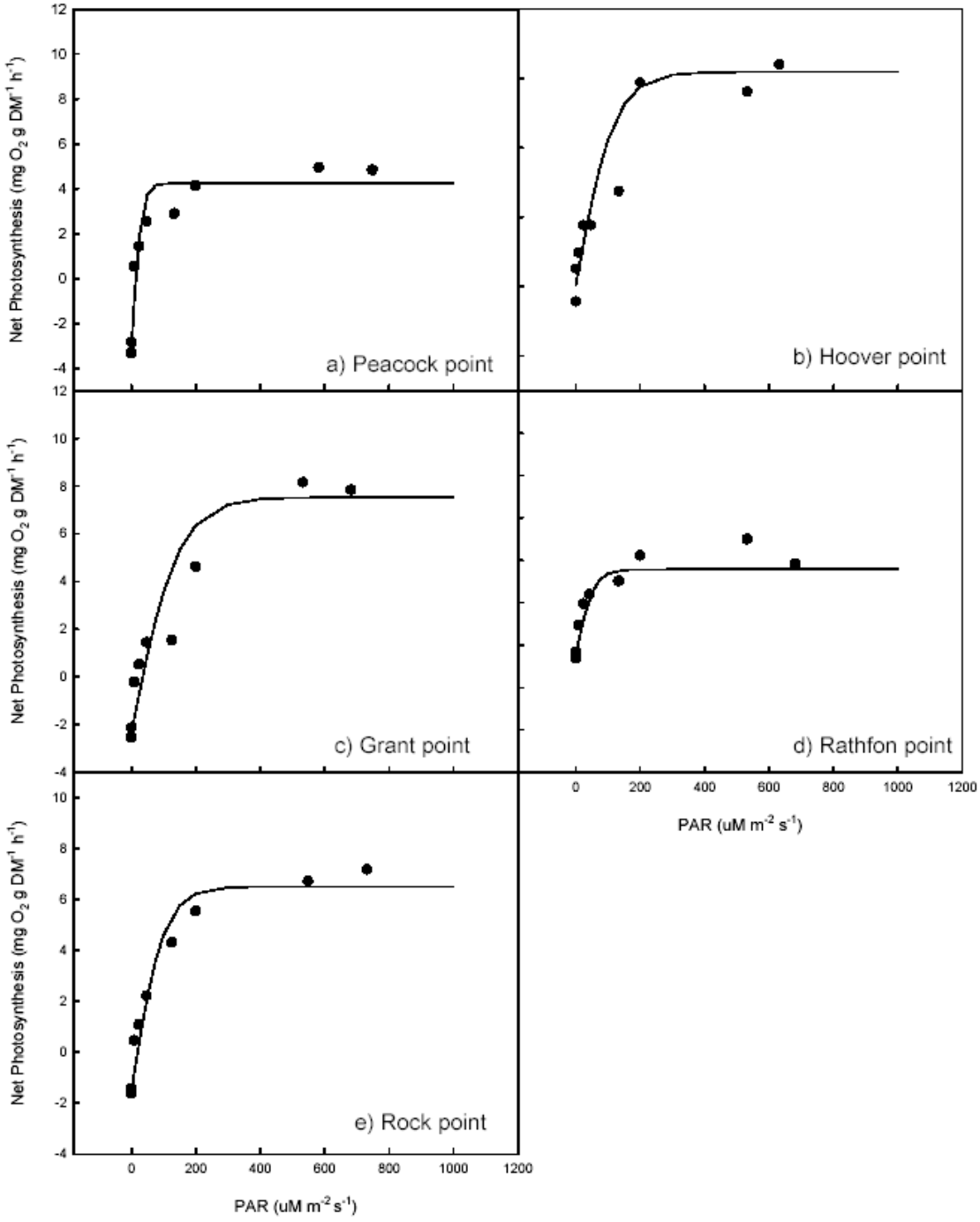

Figure 5.9 The photosynthesis vs. PAR response curves for *Cladophora* harvested at 5 nearshore sites in eastern Lake Erie on 19 Jun 02. Measured values are fitted using the Jasby and Platt (1976) equation. Values for photosynthetic parameters are located in Table 5.1.

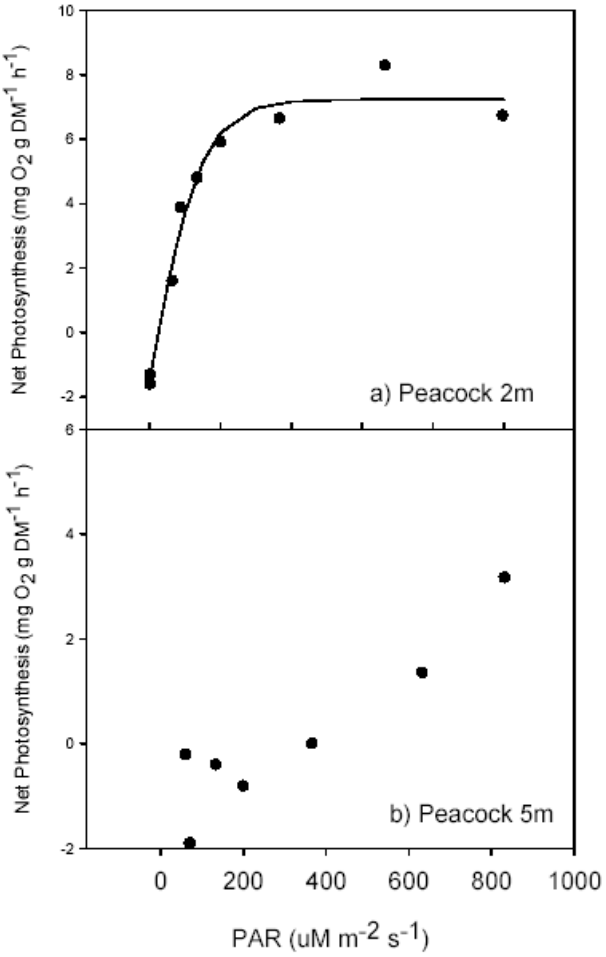

Figure 5.10 The photosynthesis vs. PAR response curves for *Cladophora* harvested at 2m and 5m depths Peacock point, eastern Lake Erie on 04 Jul 02. Measured values are fitted using the Jasby and Platt (1976) equation. P-I data from *Cladophora* from 5m depth had low R^2 value (<0.90) when fit to the Jasby and Platt (1976) equation and data were not used in subsequent calculations. Values for photosynthetic parameters for *Cladophora* from 2m depth are located in Table 5.1.

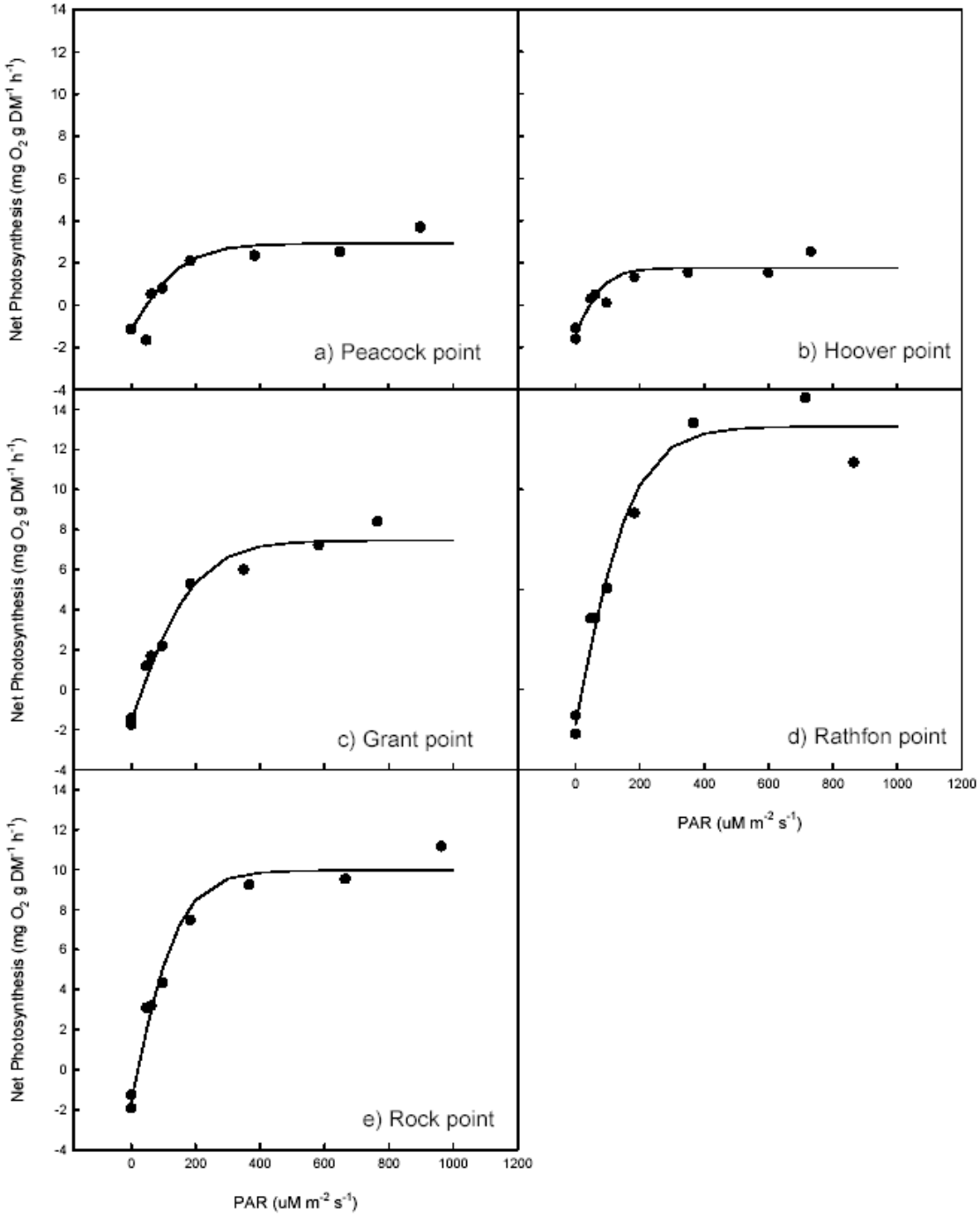

Figure 5.11 The photosynthesis vs. PAR response curves for *Cladophora* harvested at 5 nearshore sites in eastern Lake Erie on 08 Jul 02. Measured values are fitted using the Jasby and Platt (1976) equation. Values for photosynthetic parameters are located in Table 5.1.

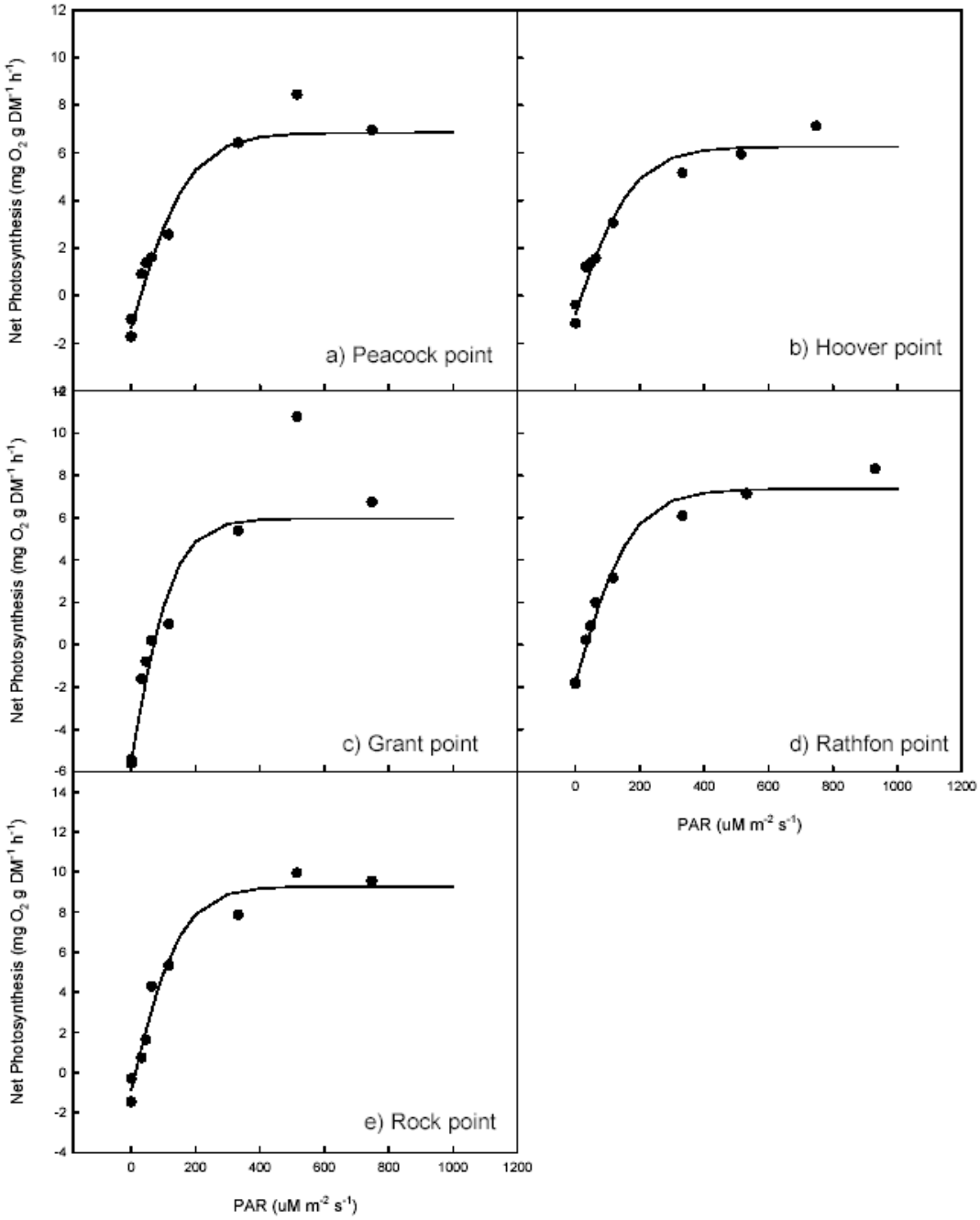

Figure 5.12 The photosynthesis vs. PAR response curves for *Cladophora* harvested at 5 nearshore sites in eastern Lake Erie on 29 Jul 02. Measured values are fitted using the Jasby and Platt (1976) equation. Values for photosynthetic parameters are located in Table 5.1.

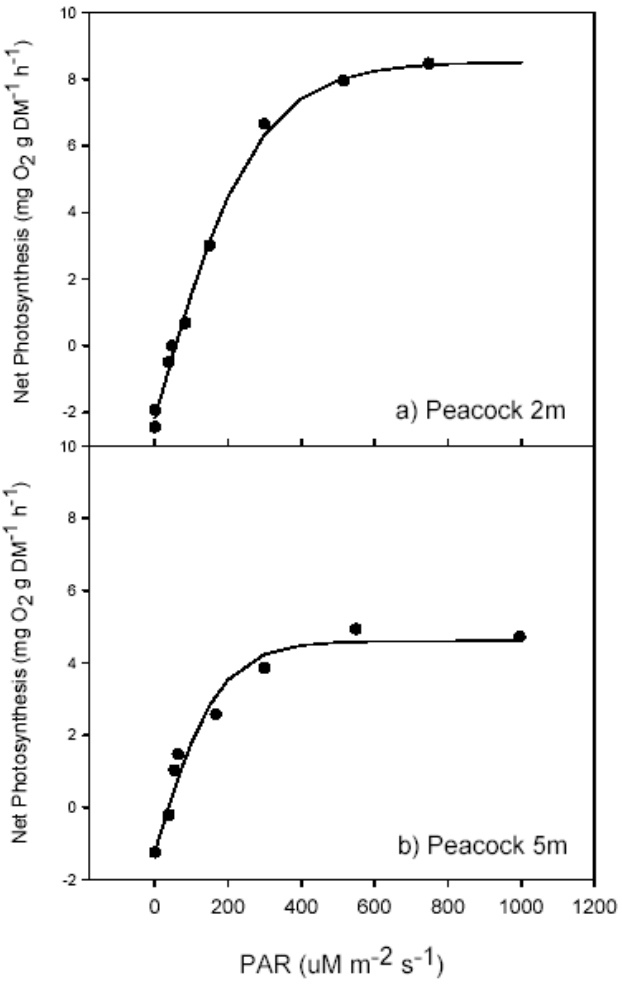

Figure 5.13 The photosynthesis vs. PAR response curves for *Cladophora* harvested at 2m and 5m depths Peacock point, eastern Lake Erie on 01 Aug 02. Insufficient algal material was available at 10m depth for P-I incubations. Measured values are fitted using the Jasby and Platt (1976) equation. Values for photosynthetic parameters are located in Table 5.1.

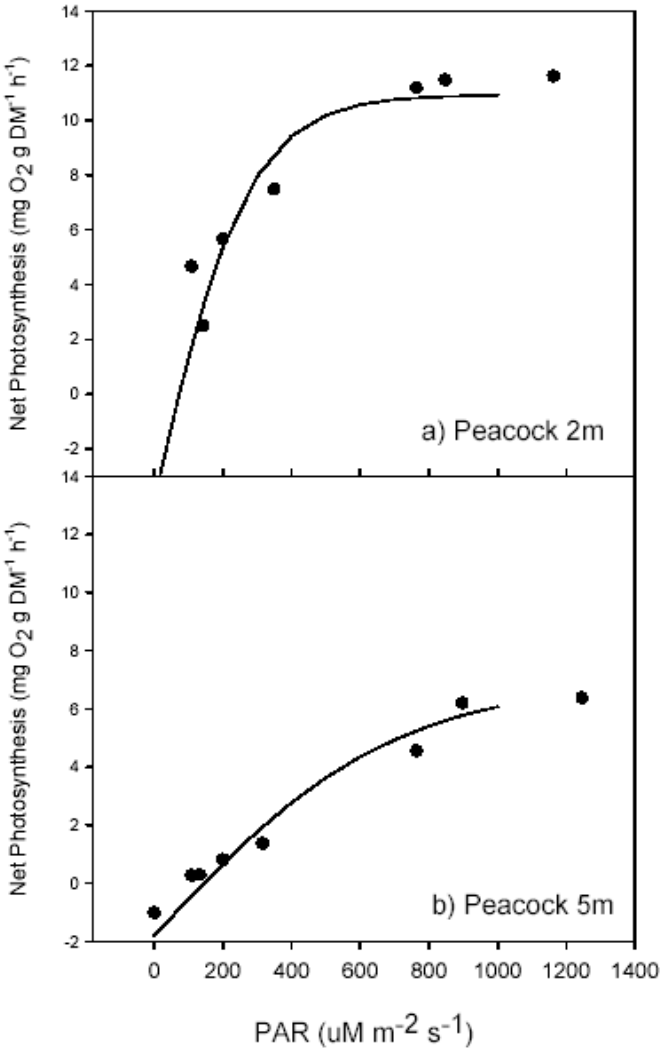

Figure 5.14 The photosynthesis vs. PAR response curves for *Cladophora* harvested at 2m and 5m depths Peacock point, eastern Lake Erie on 19 Aug 02. Insufficient algal material was available at 10m depth for P-I incubations. Measured values are fitted using the Jasby and Platt (1976) equation. Values for photosynthetic parameters are located in Table 5.1.

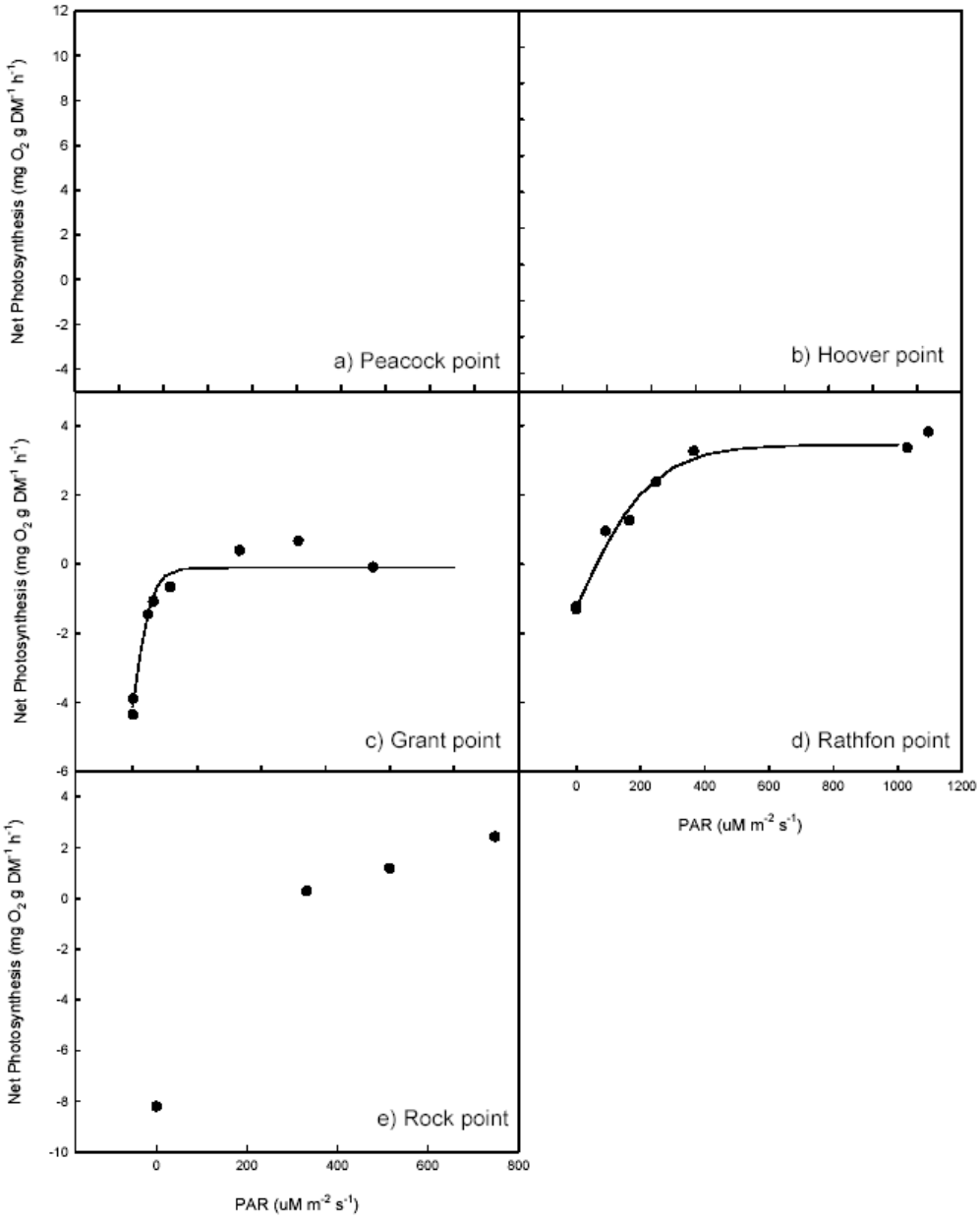

Figure 5.15 The photosynthesis vs. PAR response curves for *Cladophora* harvested at 3 nearshore sites in eastern Lake Erie on 08 Oct 02. *In situ Cladophora* coverage and biomass was low at all sites sampled, and there was insufficient biomass at Peacock point and Hoover point for photosynthesis experiments. At Rock point there was only sufficient algal biomass to conduct photosynthesis experiments at 4 light levels. Due to a lack of photosynthetic data at intermediate irradiance values at the Rock point site the fitted curve showed significant error from measured data, and photosynthetic parameters were not calculated. Measured values are fitted using the Jasby and Platt (1976) equation. Values for photosynthetic parameters are located in Table 5.1.

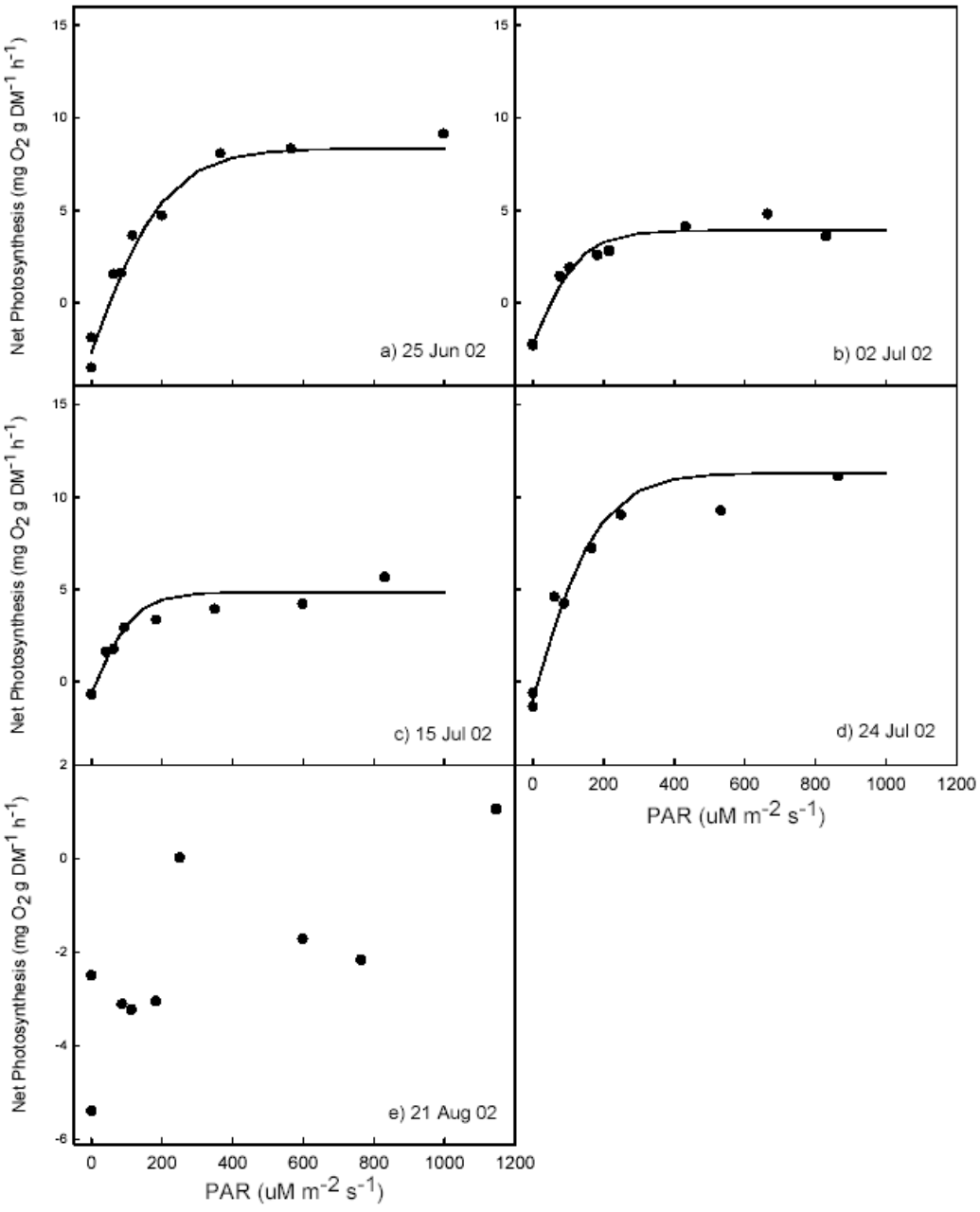

Figure 5.16 The photosynthesis vs. PAR response curves for *Cladophora* harvested at Grant Point, eastern Lake Erie on dates other than reported in Figures 5.6-5.15. Measured values are fitted using the Jasby and Platt (1976) equation. The fitted Jasby and Platt (1976) curve on 21 Aug 02 showed significant error from measured data, and photosynthetic parameters were not calculated. Values for photosynthetic parameters on the remaining days are located in Table 5.1.

5.5 Literature cited

Auer, M. T., and R. P. Canale. 1982. Ecological and mathematical modeling of *Cladophora* in Lake Huron: 3. The dependence of growth rates on internal phosphorus pool size. J. Great Lakes Res., 8: 93-99.

Baly, E. C. C. 1935. The kinetics of photosynthesis. Proc. R. Soc. Lond. B. 117-218-39.

Bannister, T. T. 1979. Quantitative description of steady state, nutrient-saturated algal growth, including adaptation. Limnol. Oceanogr., 24: 76-96.

Barton, D. R., and H. B. N. Hynes. Wave-zone macrobenthos of the exposed Canadian shores of the St. Lawrence Great Lakes. J. Great Lakes Res. 4: 27-45.

Behrenfeld, M. J., O. Prasil, M. Babin, and F. Bruyant. 2004. In search of a physiological basis for covariations in light-limited and light-saturated photosynthesis. J. Phycol. 40: 4-25.

Bellis, V. J. 1968. Unialgal cultures of Cladophora glomerata (L.) Kutz. I. Response to temperature. J. Phycol. 4: 19-23.

Byappanahalli, M. N., D. A. Shively, M. B. Nevers, M. J. Sadowsky, and R. L. Whitman. 2003. Growth and survival of Escherichia coli and enterococci populations in the macro-alga *Cladophora* (Chlorophyta). FEMS Microbiology Ecology 46: 203-211.

Campbell, L, M., M. N. Charlton, V. P. Hiriart-Baer, S. Higgins, S. Malkin, S. J. Guildford, R. E. Hecky, T. Howell, D. Dejong, and L. F. Moore. Then and now: Historical overview of the nuisance green alga, *Cladophora glomerata* in the Laurentian Great Lakes. Submitted to the J. Great Lakes Res.

Canale, R. P., and M. T. Auer. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 5. Model development and calibration. J. Great Lakes Res., 8: 112-125.

Fee, E. J. 1990. Computer programs for calculating in situ phytoplankton photosynthesis. Rep. 1740. Central and Arctic Region, Department of Fisheries and Oceans, Winnipeg, Manitoba.

Graham, J. M., M. T. Auer, R. P. Canale, and J. P. Hoffmann. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 4. Photosynthesis and respiration as functions of light and temperature. J. Great Lakes Res., 8: 100-111.

Hecky, R. E., R. E. H. Smith, D. R. Barton, S. J. Guildford, W. D. Taylor, M. Charlton and T. E. Howell. 2004. The near shore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Submitted to Can. J. Fish. Aquat Sci. 61: 1285-1293.

Henley, W. J. 1993. Measurement and interpretation of photosynthetic light-response curves in algae in the context of photoinhibition and diel changes. J. Phycol. 29: 729-739.

Howell, T. 1998. Occurrence of the alga *Cladophora* along the north shore of Eastern Lake Erie in 1995. Ontario Ministry of the Environment. ISBN 0-7778-8172-1. PIBS 3716E. 37p.

Jasby, A. D. and T. Platt. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceanogr., 21: 540-547.

Lester, W. W., M. S. Adams, and A. M. Farmer. 1988. Effects of light and temperature on photosynthesis of the nuisance alga Cladophora glomerata (L.) Kutz from Green Bay, Lake Michigan. New Phytol., 109: 53-58.

Litchman, E, D. Steinter, and P. Bossard. 2003. Photosynthetic and growth responses of three freshwater algae to phosphorus limitation and daylength. Freshwater biology 48: 2141-2148.

Lorenz, R. C., and C. E. Herdendorf. 1982. Growth dynamics of *Cladophora glomerata* in western Lake Erie in relation to some environmental factors. J. Great Lakes Res 8: 42-53.

Lowe, R. L., and R. W. Pillsbury. 1995. Shifts in benthic algal community structure and function following the appearance of Zebra Mussels (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron. J. Great Lakes Res. 21: 558-566.

Patterson, M, W. R., J. J. H. Ciberowski, and D. R. Barton. Submitted. The distribution and abundance of Dreissena species (Dreissenidae) in Lake Erie, 2002. J. Great Lakes Res.

Platt, T., C. L. Gallegos, and W. G. Harrison. 1980. Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. J. Mar. Res. 38: 687-701.

Mantai, K. E. 1974. Some aspects of photosynthesis in *Cladophora glomerata*. J. Phycol., 10: 288-291.

Mantai, K. E. 1987. Energy relations in *Cladophora glomerata* from Lake Erie. J. Great Lakes Res. 13: 279-284.

Mantai, K. E. 1989. Commentary: Rebuttal to comment by M. T. Auer and J. M. Graham. J. Great Lakes Res. 15: 371-372.

Mantai, K. E., and C. Haase. 1977. Some factors affecting photosynthesis and respiration measurements in Cladophora glomerata. J. Great Lakes Res., 3: 191-195.

Planas, D., S. C. Maberly, and J. E. Parker. 1996. Phosphorus and nitrogen relationships in Cladophora glomerata in two lake basins of different trophic status. Freshwater Biology 35: 609-622.

Stainton, M. P., M. J. Capel, and F. A. J. Armstrong. 1977. The chemical analysis of freshwater. Can. Fish. Mar. Serv. Misc. Spec. Publ. 25, 180p.

Talling, J. F. 1957. Photosynthetic characterisitics of some freshwater plankton diatoms in relation to underwater radation. New Phytol. 56: 29-50.

Turner, M. A., E. T. Howell, G. G. C. Robinson, P. Cambell, R. E. Hecky, and E. U. Shindler. 1994. Roles of nutrients in controlling growth of epilithon in lakes of low alkalinity. Can. J. Fish. Aquat. Sci. 51: 2784-2793.

Wetzel, R. G. 2001. Limnology: Lake and River Ecosystems. 3rd edition. Academic Press. New York. 1006p.

Wong, S. L., and B. Clark. 1976. Field determination of the critical nutrient concentrations for *Cladophora* in streams. J. Fish. Res. Board Can. 33: 85-92.

Wong, S. L., B. Clark, M. Kirby, and R. F. Kosciuw. 1978. Water temperature fluctuations and seasonal periodicity of *Cladophora* and *Potamogeton* in shallow rivers. J. Fish. Res. Board Can. 35: 866-870.

Wood. K. G. 1968. Photosynthesis of Cladophora under unnatural conditions. In Algae, Man and the Environment, Ed. D. F. Jackson, pp 121-133. New York: Syracuse Univ. Press.

Wood, K. G. 1975. Photosynthesis of *Cladophora* in relation to light and CO_2 limitation; $CaCO_3$ Precipitation. Ecology 56: 479-484.

Chapter 6
Overall Summary and Conclusions

6.1 General Comments

The preceding chapters have described my research on the ecology of *Cladophora* in eastern Lake Erie. Each chapter attempts to address a particular aspect of *Cladophora*. In this chapter I summarize the objectives and major conclusions of each of the preceding data chapters (chapters 2-5).

6.2 Chapter 2 Summary

Chapter two reported the combined results of *Cladophora* surveys conducted by myself, and Dr. Todd Howell of the Ontario Ministry of the Environment (Howell 1998), in the eastern basin of Lake Erie during 1995, 2001, and 2002. Dr. Howell's surveys dealt primarily with the spatial distribution of *Cladophora* during peak biomass at 15 sites along the northern shoreline of eastern Lake Erie, and were restricted to depths between 0.5m and 2m. My surveys dealt primarily with the seasonal dynamics of *Cladophora* distribution at 5 sites distributed along the northern shoreline of eastern Lake Erie, and were conducted at depths 2m, 5m, and 10m. Our combined datasets, 24 sites in total, form the most extensive survey of *Cladophora* that had been conducted in eastern Lake Erie to date and provide a unique opportunity to assess the spatial and temporal dynamics of *Cladophora* post *Dreissena* colonization. The main objectives of Chapter 2 were an assessment of the spatial and temporal distribution, biomass, and nutrient status of *Cladophora* in eastern Lake Erie, and a preliminary assessment of the role of dreissenid mussels in the *Cladophora* resurgence. A secondary objective was to estimate the importance of *Cladophora* to the phosphorus dynamics of the eastern basin of Lake Erie. The main conclusions of chapter two were as follows:

1. *Cladophora* was widely distributed along the northern shoreline of eastern Lake Erie during our study period, 1995-2002. Across the 24 sites, and at depths <5m, the median areal coverage was 96%. Qualitatively, it was noted that coverage less than 100% generally occurred due to the presence of previously sedimented material, including empty and unattached shells of *Dreissena*,

which overlaid suitable substratum and prevented the attachment of filaments. The 24 sites in this study represented only areas that were associated with exposed rocky substratum and these areas comprised approximately 80% of available surface area along the northern coastline. *Cladophora* requires hard surfaces for attachment and it was not expected that it would be found, to any large extent, in the remaining areas of lake bottom that are dominated by glacial till and sand. The distribution of *Cladophora* at shallow depths was limited by the availability of hard substratum. The vertical distribution of *Cladophora*, however, was empirically related to the mean daily PAR available at depth and therefore dependant on water clarity. *Cladophora* was distributed to at least 10m depth at the sites sampled during the survey.

2. The seasonal growth pattern of *Cladophora* included a strong mid-summer biomass peak, followed by a lengthy period of low growth, then a relatively small autumn biomass peak. Visible algal growth began in early May, followed by a period of rapid biomass accrual during June and July. Between 24-29 July 2002 a major sloughing event occurred and filaments were dislodged from their holdfasts and drifted throughout the littoral zone, onto beaches, and were lost from the sites under study within only a few days. From August to October re-growth was noted by increased filament lengths and areal coverage, however relative to the midsummer peak little biomass had accumulated by 31 October 02 at any of the sites.

3. The areal biomass of *Cladophora* was depth dependant, with highest biomass occurring at the shallowest depths. At depths ≤2m the peak biomass was highly variable, ranging from <1 g DM m^{-2} to 940 g DM m^{-2} with a median value of 171 g DM m^{-2}. Sites with low biomass were often associated with the west sides of peninsulas exposed to the predominant southwest winds and it was hypothesized these areas had an increased propensity for sloughing and sand scour that precluded biomass accrual. Sites with high peak biomass may have represented locations of point source nutrient enrichment. The decline in mean biomass with depth was correlated with available PAR. At a depth of 10 m the median peak biomass was 0.5 g DM m^{-2}.

4. The widespread and ubiquitous distribution of dense *Cladophora* mats across the northern shoreline of eastern Lake Erie indicated that phosphorus concentrations in the north shore waters were sufficient to produce bloom occurrences. However, at shallow depths (≤2m) the seasonal declines in tissue P concentrations of *Cladophora* indicated that *Cladophora* was strongly P-

limited by early summer. The decline in tissue P concentrations from spring (median value of 0.23% DM) to midsummer (median value of 0.06% DM) indicated that the dilution of tissue P through growth exceeded P uptake. The midsummer tissue P concentrations at all shallow water sites (≤2m) were below the 0.16% DM concentration where growth became increasingly sensitive to internal P stores. The median midsummer tissue P value (0.06 %DM) at the shallow water sites (≤2m) was equivalent to the critical P concentration required to maintain positive growth. At 5m and 10m depths the median midsummer tissue P concentrations were 0.13 %DM and 0.23% DM respectively, and *Cladophora* at these depths were predominantly light limited. Tissue nitrogen concentrations displayed no evidence of N limitation.

5. The invasion and proliferation of dreissenid mussels in eastern Lake Erie has resulted in alterations of water quality conducive to the growth of *Cladophora*. Dreissenid induced increases in mean water clarity were estimated to have caused a 25% increase in depth integrated *Cladophora* biomass. Increases in water clarity have also caused shifts to the depth distribution of *Cladophora* biomass, where depths ≥3m contained ~40% of the total depth integrated biomass compared with 25% prior to dreissenid colonization.

6. During peak biomass *Cladophora* tissues across the northern shoreline of eastern Lake Erie contained approximately 15 tonnes of phosphorus, most of which was removed from the water column over a 31 day period (12 May 02 – 12 Jun 02) at a rate of 0.49 tonnes/day. The mass removal rate of SRP from the water column by *Cladophora* represented only a small proportion of the SRP flux in the epilimnion of offshore waters (<6 %) during May-June 2002. However, P uptake by *Cladophora* during May exceeded the decline in littoral zone SRP concentrations, and was likely an important factor in causing significantly lower SRP concentrations in nearshore vs. offshore waters. The rapid decline in tissue P concentrations during June and July 2002 corresponded with basin wide declines in SRP during that period. The rapidly declining tissue P concentrations indicated that phosphorus from *Dreissena* and the overlying water column were insufficient to overcome the growth dilution effect and maintain high growth rates.

6.3 Chapter 3 Summary

While the field surveys, that comprised the data for Chapter Two, were being conducted other efforts were ongoing to collect data required to model the growth, biomass accrual, and tissue phosphorus concentration of *Cladophora* at the 5 reference sites in eastern Lake Erie. Several highly dynamic factors including available PAR, SRP, temperature, and carrying capacity were important constraints on the growth and biomass accrual of *Cladophora*. The purpose of Chapter Three was to describe a revised *Cladophora* growth model (CGM) and the results of field-testing in eastern Lake Erie. A brief description of the major modifications and the results of the field-testing are as follows:

7. In eastern Lake Erie the CGM was required to function at depths where light would often fall below the minimum requirement for positive growth. The revisions made to the Canale and Auer model simplified the pre-existing model structure, and ensured the model would function accurately at depth

8. The CGM included the use of a dynamic Xmax term (maximum obtainable biomass) that had several distinct advantages over the use of a fixed Xmax term. Firstly, the use of a dynamic Xmax term incorporated spatial and temporal differences in available PAR such as between sites of differing water clarity, over a range of depths, or at a single site where water clarity was highly variable. Secondly the incorporation of an Xmax term based on available PAR reduced the requirement for direct observations at each specific site and depth, a requirement that often cannot be met if growth conditions are sub-optimal.

9. The CGM required daily estimates of water clarity for each site and depth under study. In Lake Erie my field studies revealed that changes in water clarity were driven by the resuspension of particulate matter due to surface meteorological conditions, and water clarity was highly variable between sites and across the range of depths within this study. Direct daily measurements of water clarity at each site and depth could not practically be achieved within the limitations of my study. However, empirical relationships between water clarity and station depth, and between water clarity and measures of suspended solids (turbidity or total suspended solids), reduced the data requirement to daily estimates of turbidity (or total suspended solids) at a single depth for each site. Site-specific empirical relationships between wave heights and turbidity were derived and used to calculate water clarity for each site, depth, and time-step within the model structure.

The use of these relationships was a distinct advantage since they accounted for the high spatial and temporal variability in water clarity in eastern Lake Erie.

10. In eastern Lake Erie the CGM was required to function at depths (≥10m) where the effects of wind-dependent sloughing would be greatly diminished. In the absence of empirical data I derived a theoretical relationship that forced the effects of wind dependent sloughing to decline exponentially with depth, such that at 10m no wind dependent sloughing would occur. While this theoretical relationship corrected potential errors associated with wind induced sloughing at deeper depths it remains to be field-tested.

11. In eastern Lake Erie the CGM was forced to function at ambient SRP concentrations below those for which the model was originally developed and validated. It was noted that as SRP approached seasonal minimum values that tissue P concentrations were often over estimated. In my study tissue P was only overestimated for a short duration and therefore growth rate estimates continued to predict biomass accrual with reasonable accuracy. However, it was recognized that extended periods of low SRP could cause more significant errors in model predictions. For this reason the CGM was designed such that it could function using either measured SRP or measured tissue P values. I encourage potential users to validate the prediction of tissue P values within the model, especially under conditions where SRP approaches non-detectible concentrations.

12. The CGM is a series of mathematical equations that can be used in any modeling platform. I used the commercially available modeling software Stella© (Stella 2001). The use of Stella© greatly simplified the use of the model and allowed for numerous simulations to be conducted with relative ease. Furthermore, the model or the user interface can be easily updated or modified to suit the users current needs. The Stella© version of the CGM is most useful for predicting the growth, tissue P, and biomass accrual of *Cladophora* for a small number of independent sites. Attempts to model *Cladophora* over a larger spatial area will require the use of modeling platform more suitable for that objective.

13. The CGM was field tested in eastern Lake Erie and predictions were compared with measured values of tissue P and biomass at 5 sites and 3 depths (2m, 5m, 10m). The model predicted the seasonal dynamics of tissue P and biomass with reasonable accuracy.

6.4 Chapter 4 Summary

Chapter four describes the application of the CGM in eastern Lake Erie with the overall objective of assessing how ecologically relevant variability in the parameters that control *Cladophora* growth could affect its distribution, biomass, and tissue phosphorus concentrations. The application of the CGM was useful in ascertaining how highly dynamic ecological variables would influence the growth rates and biomass accrual of *Cladophora* over space and time. Perhaps the most interesting were the occurrences where the CGM poorly predicted *in situ* conditions. Specifically the CGM did not accurately predict biomass at shallow depths (≤1.5m), or the timing of the midsummer-sloughing event. The erroneous CGM predictions highlighted some specific areas where additional research and knowledge was required, and led to a new hypothesis on the factors that control the midsummer-sloughing event. Overall, the conclusions of Chapter four were as follows:

14. The general seasonal pattern of *Cladophora* growth in eastern Lake Erie was strongly influenced by ambient water temperature. Increases in spring water temperatures, to optimal values in June, caused an increase in specific growth rates during that period. Ambient water temperatures during July and August exceeded optimal values for growth and specific growth rates declined. During October water temperature decreased and specific growth rates increased, however the reduced photoperiod and increased cloud-cover did not allow for significant biomass accumulation.

15. Dense cloud cover reduced daily growth rates to very low levels, however dense cloud cover generally persisted for only 1-2 day periods and inter-annual variability in surface PAR between 2001-2003 had only a minor impact on the resulting standing crop. Further, the use of simulated 70% cloud-free PAR caused only a 3-4 % difference in standing crop from measured PAR data (2001-2003).

16. The depth distribution of *Cladophora* in eastern Lake Erie was strongly influenced by water clarity. The CGM predicted that inter-site differences in kPAR would result in 2X difference in standing crop between sites with the highest and lowest water clarity. The changes in the depth

distribution of biomass between sites with the highest and lowest water clarity occurred primarily at depths of 3-6m.

17. Inter-annual variability in kPAR from 2001-2003 had only a minor effect on the standing crop at our 'median' site, which is expected to represent the average growing conditions in eastern Lake Erie.

18. Attenuation of PAR through dense *Cladophora* mats is rapid. The CGM predicted that a prolonged period (~14 days) of negative growth occurred at the base of the *Cladophora* mat immediately prior to the sloughing event. The metabolic imbalance was primarily caused by low light availability, and exacerbated by reductions in growth due to intermediate water temperatures (22-24°C).

19. Previous laboratory experiments (Graham et al. 1982) demonstrated a reduction in net growth under high irradiance conditions (>600 uM m^{-2} s^{-1}) due to light enhanced respiration. These experiments, however, were not consistent with experiments conducted on *Cladophora* from this study (Chapter 5) or studies on Cladophora from Lake Michigan (Lester et al. 1988). Furthermore, the CGM did not account for the positive effects of self-shading within dense *Cladophora* mats, and the CGM may over-predict the influence of light enhanced respiration at shallow depths (<1m) where ambient PAR often exceeds 600 uM m^{-2} s^{-1}.

20. The growth and biomass accrual of *Cladophora* in eastern Lake Erie was highly sensitive to available phosphorus. Tissue phosphorus concentrations were below optimal concentrations throughout the growth period (May-Oct, 2002). Site-to-site differences in SRP concentration were responsible for up to a 2X difference in depth-integrated biomass.

21. The CGM predicted that inter-annual variability in SRP concentration of +/- 1 μg L^{-1} would strongly influence the depth-integrated biomass of *Cladophora* in eastern Lake Erie. For example, reductions in soluble reactive phosphorus by 1 μg L^{-1} from 2002 'median' conditions would result in a 70% reduction in the standing crop at our 'median' site, while and increase of 1 μg L^{-1} would result in a 80% increase in the standing crop at our 'median' site.

6.5 Chapter 5 Summary

Chapter Five reported the results of *in vitro* photosynthesis vs. irradiance experiments from the 5 reference sites in eastern Lake Erie during 2002. These experiments provided insights into the physiological condition of *Cladophora* and were useful for interpreting *in situ* growth patterns. The main objective of this chapter was to determine if the spatial and temporal patterns of *Cladophora* growth in eastern Lake Erie could be adequately described by its photosynthetic capacity, specifically in those instances where the CGM predictions contrasted field observations. The main conclusions of Chapter Five were as follows:

22. The photosynthetic parameters Pm and α were highly variable between sites and over the 2002 growing season in eastern Lake Erie. Photosynthetic rates were normalized to biomass and did not account for potential changes in the concentration of photosynthetic pigments.

23. The values of maximum photosynthesis reported in Chapter 5 were generally 3x lower than optimal rates reported in other studies. Values of Pm and α co-varied during the spring-summer growth period. Both low values of Pm and the co-variation of Pm and α suggest growth rates were strongly nutrient limited.

24. Maximal rates of photosynthesis did not display evidence of enhanced photorespiration or photoinhibition at PAR intensities between 600-1200 μM m^{-2} s^{-1}. CGM predictions generally underestimated growth and biomass accrual at shallow depths (≤1.5m) where PAR intensities often exceeded 600 μM m^{-2} s^{-1}.

25. Seasonal variations in photosynthetic parameters were not useful predictors of the mid-summer sloughing event even though the experiments were conducted on *Cladophora* from the *in situ* populations under study. The field-collected *Cladophora* tissues retained photosynthetic capacity through the mid-summer sloughing period.

26. The inclusion of a simple model to estimate the in situ growth rates of *Cladophora* at different depths within the *Cladophora* mat revealed strong light limitation at the lower portions of mat caused negative growth rates in the weeks prior to the sloughing event. It was hypothesized that

the inability to maintain positive net photosynthesis at the base of the *Cladophora* mat was the cause of the mid-summer sloughing event in eastern Lake Erie during 2002.

Appendix A: The influence of self-shading on interpretations of P-I parameters from *in vitro* and *in situ* experiments on *Cladophora*.

The influence of self-shading on *in vitro* photosynthesis-irradiance response curves can be examined using a theoretical approach. In the following scenario there are 4 layers of algae each identical in their physiological response to light (i.e. photoadaptation has not occurred). The values of maximum photosynthesis (Pm) and the slope of the light limited portion of the P-I response curve (α) have been set to maximal values reported during this study (Chapter 5). These values are also similar to those reported for *Cladophora* from Lake Michigan (Lester et al. 1988). Pm (gross) value is 28 mg O_2 m^{-2} h^{-1}, α is 0.092 mg O_2 uM $photons^{-1}$, and the value for respiration is 4.7 mg O_2 m^{-2} h^{-1}. These values were used to construct P-I response curves (Figure 7.1) for the 4 mat layers using the Jasby and Platt (1976) equation. Incident PAR at the upper mat surface was varied from 0-1600 uM photons m^{-2} s^{-1}. Each mat layer was assumed to attenuate 20% of the light incident on its upper surface. Overall the lowest layer received approximately 40% of the irradiance received by the top layer.

This theoretical exercise reveals several relevant points on how self-shading affects the interpretation of P-I response curves. Firstly, as long as Pm is attainable at the lowest mat layer the effects of self-shading are more prevalent on the light limited portion of the P-I response curve (α) than on maximal photosynthetic rates (Pm) (Table 7.1). As a result, the variation in Pm and alpha are independent of one another, and variations in Icr (Icr = Rd/ α) and Ik (Ik= Pm/ α) will be strongly dependant on changes in α. Secondly, as self-shading increases the values of α decrease, and the values of Icr and Ik increase. Thirdly, under conditions of intense self-shading the P-I response will not asymptote and Pm cannot be ascertained with any reasonable degree of certainty. And fourthly, if light saturation is reached at the bottom layer then values of Pm are similar between mat layers.

Table A 1. The theoretical effects of self-shading on P-I response curves. The P-I response curves are generated for 4 overlaying mat layers of equal thickness. Each mat layer is set to attenuate 20% of the PAR incident to its upper surface. Photosynthetic parameters are held constant between mat layers and assume no photoadaptation (see text). The units for PAR, Icr, and Ik are uM photons m^{-2} s^{-1}. The units P_{NET}, Pm are mg O_2 g DM^{-1} m^{-2}.

Layer 1		Layer 2		Layer 3		Layer 4	
PAR	P_{NET}	PAR	P_{NET}	PAR	P_{NET}	PAR	P_{NET}
0	-4.70	0	-4.70	0	-4.70	0	-4.70
10	-3.78	8	-3.96	6.4	-4.11	5	-4.23
25	-2.41	20	-2.86	16	-3.23	13	-3.52
50	-0.14	40	-1.04	32	-1.77	26	-2.35
100	4.18	80	2.50	64	1.10	51	-0.03
200	11.44	160	8.80	128	6.43	102	4.38
400	19.53	320	17.21	256	14.52	205	11.73
800	23.01	640	22.48	512	21.43	410	19.75
1600	23.30	1280	23.29	1024	23.23	819	23.04
Pm	23.3		23.3		23.2		23.0
Alpha	0.092		0.074		0.059		0.047
Icr	51		64		80		100
Ik	253		315		393		489

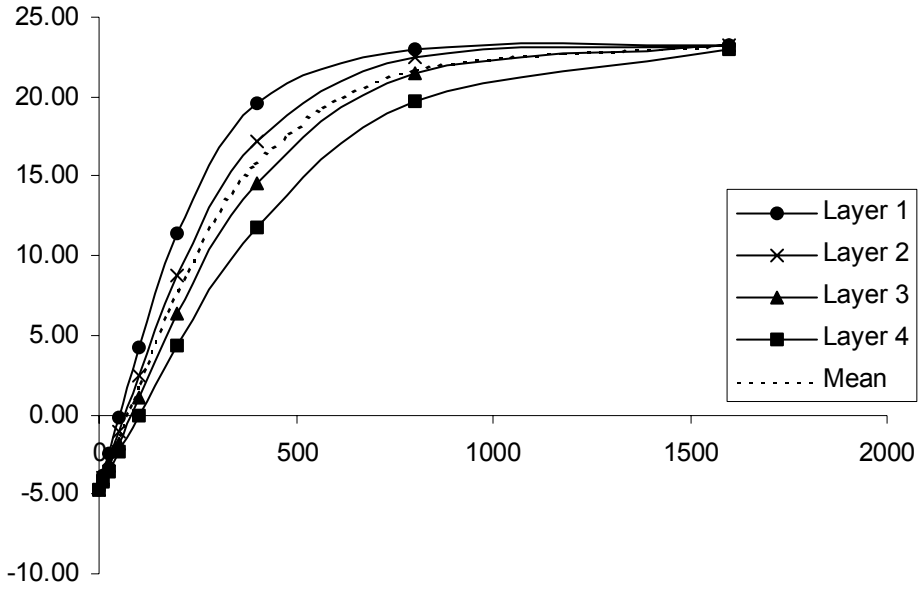

Figure A 1 The theoretical effects of self-shading on P-I response curves. The P-I response curves are generated for 4 overlaying mat layers of equal thickness. Each mat layer is set to attenuate 20% of the PAR incident to its upper surface. Photosynthetic parameters are held constant between mat layers and assume no photoadaptation (see text).