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MODELING CANOPY EFFECT IN THE GREAT LAKES CLADOPHORA MODEL

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MODELING CANOPY EFFECT IN THE GREAT LAKES *CLADOPHORA* MODEL

By

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Dedicated to my dad, Ankur Bakshi, who taught me everything in life, inspired me to follow my dreams and believed in me. To my mom, Sarvjeet Bakshi, for giving me the wisdom in doubt and for being my biggest strength, my (motherlike) sister, Aanchal, for being my guardian angel, my brother-in-law, Vivek, for showing confidence in me and my best friend, Avi, for always being there through ups and downs of my life.

Table of Contents

List of Figures v

Abstract viii

1 Introduction 1

2 Objective and Approach 4

3 Modeling Methods 7

3.1 Light & Temperature Mediation Factors 8
3.1.1 Mediation Factor for Photosynthesis Growth 8
3.1.2 Basal Respiration and Mediation Factor for Light-Enhanced Respiration 11

3.2 Canopy Modeling 11

4 Results and Discussion 16

4.1 Photosynthesis Response Surfaces 16

4.2 Light-Enhanced Respiration Response Surface 19

4.3 Net Growth Response Surface 23

4.4 Canopy Results 24

5 Model Application and Future Work 32

6 References 33

Appendix A.1: MATLAB code to generate 2D photosynthetic growth, light-enhanced respiration and net growth response surfaces 37

Appendix A.2. Light and Temperature Mediation Factors (f_μ (I, T) and f_R (I, T)) and Basal Respiration VBA code in the GLCM v3 40

List of Figures

Figure 1. Graham et al. (1982) photosynthesis growth rate (d^{-1}) measurements of Cladophora over the light and temperature gradients 5

Figure 2. Generalized Platt function for a specific temperature showing the relationship between growth rate and light intensity, mediated by the ascending (α) and descending (β) limbs of the plot with the onset of photoinhibition (P_{max}) 9

Figure 3. Idealized temperature dependence functions of P_{max}, α and β 10

Figure 4. Box and arrow diagram showing the steps taken towards generating normalized 2D photosynthesis response surfaces $f\mu I,T$ 10

Figure 5. Generalized exponential and logistic growth model curves 12

Figure 6. Illustration to show the effect of self-shading on the net growth of the layers in the canopy due to light attenuation 14

Figure 7. Box and arrow diagram showing a snapshot of one-day canopy model simulation 15

Figure 8. Examples of Platt equation fit to Graham photosynthesis growth measurements at 20 ^{o}C (top) and 25 ^{o}C (bottom) 16

Figure 9. Temperature dependence function fit for the Platt coefficient α 17

Figure 10. Temperature dependence function fit the Platt coefficient β 17

Figure 11. Temperature dependence function fit the Platt coefficient P_{max} 18

Figure 12. Normalized light and temperature growth mediation factor surface (dimensionless). 0 represents unfavorable light & temperature conditions for growth progressing to 1 which represents most favorable conditions. 19

Figure 13. Basal respiration function fit (line) to Graham et al (1982) experimental basal respiration data (points) at light intensities 10 (grey) & 25 (black) $\mu E \cdot m^{-2} \cdot s^{-1}$ 20

Figure 14. Examples of Platt equation fit to Graham's light-enhanced respiration measurements (minus RB) at 15 ^{o}C (top) and 20 ^{o}C (bottom) 21

Figure 15. Temperature dependence function fit for the Platt coefficient $RLTmax$ 22

Figure 16. Temperature dependence function fit for the Platt coefficient α_R..... 22

Figure 17. Normalized light and temperature respiration mediation factor surface (dimensionless). 0 represents unfavorable light & temperature conditions for light enhanced respiration progressing to 1 which represents most favorable conditions..... 23

Figure 18. Net Growth Response Surface showing the effect of light and temperature with μmax = 1.08 d^{-1} and $Rmax$ = 0.44 d^{-1} (Auer and Canale, 1982) and fQ = 1 24

Figure 19. Model runs to show the effect of different $Xmax$ values on the net biomass model output (Figure 19.a: $Xmax$ = 800 $gDM.m^{-2}$; Figure 19.b: $Xmax$ = 600 $gDM.m^{-2}$; Figure 19.c: $Xmax$ =450 $gDM.m^{-2}$ and Figure 19.d: $Xmax$ = 300 $gDM.m^{-2}$)..... 25

Figure 20. Model output with canopy algorithm showing the effect of environmental factors (light attenuation in the canopy) in leveling off the biomass without forcing it an artificial maximum biomass value 26

Figure 21. The inverse of the slope of the line fit (i.e. areal biomass density, $Xlayer$) for biomass density vs bed height was calculated to be 9 $gDM{\cdot}m^{-2}{\cdot}cm^{-1}$..... 26

Figure 22. An illustration showing the decrease in the net growth (μnet) with light attenuation. For the darkest part of canopy (where I = 0), μnet becomes negative 27

Figure 23. Daily biomass (X) prediction with canopy sub-model, varying light intensity and temperature (top). Corresponding daily μnetoutput driving biomass production..... 28

Figure 24. μnet profile with canopy depth at noon. In the presence of sunlight, the μnet for top layers is positive and negative for self-shaded bottom layers 29

Figure 25. Hourly μnet breakdown corresponding to hourly light and daily temperature at two different days. For solid line, the aggregation of positive μnet is more than negative μnet resulting in a positive net growth for that day. For dotted line, negative μnet takes over the day-time μnet resulting in a negative μnet for the day..... 30

Figure 26. The variation in the realized maximum biomass with canopy light attenuation factor (k_{alg})..... 31

Figure 27. GLCM v3 growth simulation output, incorporating canopy algorithm, showing seasonality in Lake Michigan along with 2006 observational data points 31

Abstract

Cladophora glomerata is a filamentous green alga native to the Great Lakes. However, its nuisance growth in phosphorus rich waters negatively affects the lakes' aesthetic and water quality. The Great Lakes *Cladophora* Model (GLCM) v1, developed in 1982, was the first mechanistic model to simulate *Cladophora* growth basing phosphorus availability and environmental conditions followed by *Cladophora* Growth Model and GLCM v2. In this study, the light and temperature mediation factors for *Cladophora* net growth are revised as a necessary step prior to the development of a self-shading algorithm. The concept of a fixed-value, maximum achievable biomass (carrying capacity) employed in the previous models is replaced by an approach where the maximum realized biomass is determined mechanistically. The canopy (self-shading) algorithm, incorporated in the GLCM framework, models the effects of light attenuation within the algal mat on the net biomass production of *Cladophora*. The resultant GLCM v3 is more mechanistic and eliminates the need of an overly deterministic carrying capacity term.

1 Introduction

The filamentous green alga *Cladophora* glomerata grows attached to solid substrate to the depth of light penetration in the Great Lakes. *Cladophora* is native to the Great Lakes but reaches nuisance levels in phosphorus (P) rich waters. With the advent of urban development and intensification of agricultural practices near and surrounding the shores of Great Lakes, the lake water became P-rich. *Cladophora* became a subject of concern in mid 1950s because of unpleasant odor and accumulation on the beaches (Shear and Konasewich, 1975). The investigative studies conducted thereafter indicated a correlation between the incidence of nuisance growth of *Cladophora* and sources of phosphorus enrichment (Shear and Konasewich, 1975). Initially identified in association with locally enriched areas, nuisance growth ultimately became lake-wide fertility where heavy *Cladophora* growth can be supported by all suitable substrate (Shear and Konasewich, 1975). The Great Lakes Water Quality Agreement (GLWQA), originally signed in 1972, was amended in 1978, imposing a ban (limits) on phosphorus soaps and detergents and regulations on wastewater treatment plant phosphorus discharge (IJC, 1978).

The reduction of P concentrations in wastewaters in this Post P-management period led to a decline in total phosphorus levels in the Great Lakes (Dove and Chapra, 2015) as well as concentrations of soluble reactive phosphorus, SRP (orthophosphate; form of fully and freely available phosphorus (Reynolds, 2006) that autotrophs can assimilate to grow (Correll, 1999)) (Dove and Chapra, 2015). This led to reductions in stored P in *Cladophora* (Painter and Kamaitis, 1987), limiting growth and resulting in a decline of *Cladophora* nuisance growth, indicating management success albeit for a brief period.

Even before the effect of P management could be fully understood in the context of *Cladophora* growth, light penetration and phosphorus cycling in the Great Lakes ecosystem was altered by the introduction of invasive zebra and

quagga mussels (*dreissenids*) (Hebert et al., 1989) through discharges of international ship ballast water from Baltic Sea. Mussels feed on detritus and phytoplankton, enhancing P cycling by converting particulate phosphorus (PP) to excreted SRP and fecal pellet. (Hecky et al., 2004). There was a resurgence in *Cladophora* nuisance growth conditions (Kuczynski et al., 2016) associated with the invasion of mussels, despite the fact that P management was successful in reducing the stored P content of *Cladophora* (Kuczynski et al., 2016), this resurgence was a result of increased lake clarity due to the presence of *dreissenids*, which filter phytoplankton, making the water more transparent. With more transparency, the sunlight could penetrate more deeply thereby increasing the maximum colonizable depth by *Cladophora* by a factor of five and ultimately resulting in a six-fold increase in the *Cladophora* production potential. (Kuczynski et al., 2016).

The resurge of *Cladophora* in the *dreissenids* period, despite successful P management, raised concern and need to have a standardized and mechanistic growth model for *Cladophora*. The initial *Cladophora* Model was developed by Canale and Auer (1982). The model was based on SRP, stored P and biomass mass balance applied on Lake Huron to a location near point source of phosphorus loading. The effects of light and temperature (I/T), phosphorus loading, internal P coupled with wind and sloughing effects were modeled in this first version of Great Lakes *Cladophora* Model (GLCM). Tomlinson et al. (2010), updated the GLCM, (re-fitted (I/T) polynomials, readjusted respiration function & stored P, eliminated temperature dependence on P uptake and revised sloughing algorithm) leading to the next version of GLCM (v2). This version was validated for 1979 Lake Huron dataset and then for 2006 Lake Michigan data set.

Higgins et al., (2005, 2006) and Malkin et al., (2008) used initial GLCM framework to build a new *Cladophora* Growth Model (CGM). The development of this model focused on eliminating GLCM's static X_{max}, (maximum biomass) term in carrying capacity (accounting for attenuation of light within *Cladophora* mat).

Higgins et al., (2005) stated that the X_{max} value used in GLCM was directly taken from field observations that cannot be static between different sites, depth and in case of sub optimal growing conditions, instead X_{max} changes as light attenuates within *Cladophora* mat due to self-shading and introduced a dynamic X_{max} term. However, the dynamic X_{max} function presented by Higgins et al., (2005) was developed from field observations which contradicted their statement of X_{max} having site, depth and environmental condition dependence. Kuczynski (2017), recognizing the fact that the X_{max} in CGM relied on field data and poorly-constrained tuning coefficients, developed a more mechanistic approach to model self-shading.

Cladophora self-shading (aka canopy effect) is analogous to a canopy of trees in a forest. In a forest canopy, the tall emergent trees receive ample sunlight to grow, however, as we move down within the canopy, the light attenuates and becomes less available for shrubs and bushes on the forest floor. Similarly, the growth of *Cladophora* is affected by the light attenuation within its canopy. Higgins et al., (2005) and Malkin (2007) also supported this concept of compromised growth of algal cells at the bottom of canopy. Kuczynski (2017), used a complex light averaging algorithm (Simpson's 1/3 rule), accounting for light attenuation within the canopy, to apply to the overall canopy growth equation. Although this approach is more mechanistic and eliminates location specific, poorly constrained X_{max} term, the averaging could over or under predict *Cladophora* growth.

Therefore, this report presents the research work done to eliminate X_{max} and develop a new mechanistic algorithm to model canopy effect. The underlying work done to revise photosynthesis and respiration surfaces (dependent on light and temperature), is also presented as a necessary step in working with the canopy model.

2 Objective and Approach

The research presented here supports the development of the Great Lakes *Cladophora* Model v3 (Kuczynski, 2017). More specifically, this work seeks to improve the performance of the 2-dimensional (light, temperature) growth and respiration response surfaces that drive *Cladophora* growth. Next, the surfaces are incorporated within a canopy sub model accommodating self-shading as a negative feedback on carrying capacity. The objective of this report is to revisit and enhance these two major features of GLCM v3:

1) Refitting the light & temperature algorithms (response surfaces) that drive the growth model.

2) Introducing a new self-shading algorithm, canopy effect, to mechanistically simulate carrying capacity.

Graham et al., (1982) did laboratory experiments to measure photosynthesis (Figure 1) and respiration rates of *Cladophora* over gradients of lights and temperature. The photosynthesis-irradiance (P-I) measurements were done over a temperature range of 1-35 ^{o}C and photosynthetic active radiation range of 10-1235 ($\mu E \cdot m^{-2} \cdot s^{-1}$). Graham et al. (1982) and then Tomlinson et al. (2010), fit the above measurements to 2-dimensional polynomial surfaces. However, the coefficient complexity of the polynomial surfaces and poor prediction over some regions of the surface, led Kuczynski (2017) to refit those surfaces. Kuczynski (2017) used new equations to develop light and temperature surfaces for photosynthesis and light enhanced respiration.

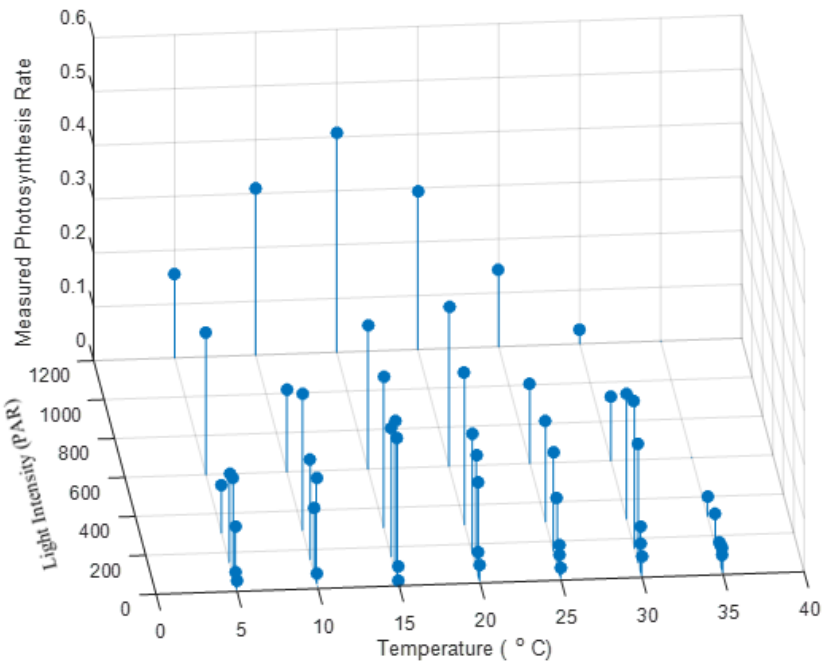

Figure 1. Graham et al. (1982) photosynthesis growth rate (d^{-1}) measurements of *Cladophora* over the light and temperature gradients

In this work, Kuczynski's (2017) data fitting equations were fine-tuned, replacing interpolation of values with functions, and incorporated in a sub module in GLCM v3. Net growth was calculated by applying a mediation factor of light and temperature obtained by continuous response surfaces of light and temperature (I/T) for photosynthesis and respiration. The resultant photosynthesis I/T surface also exhibits the phenomenon of photoinhibition (reduction in photosynthetic capacity due to higher light intensity) which was not evident in previous v3 development (Kuczynski, 2017).

The centerpiece of the report, however, is the development of an algorithm to model the effect of self-shading or canopy thickness on net growth of *Cladophora*. As the alga continues to grow, it creates a dense algal mat at the bottom of the lake. The canopy of algae prevents light penetration through the mat and introduces a negative feedback to the overall *Cladophora* growth. Earlier models accommodated negative feedback employing a maximum possible

biomass (X_{max}), i.e. the logistic population growth model. This approach is not truly mechanistic as the use of X_{max} forces the model to stop algal growth.

Therefore, the need to have a mechanistic approach to model the self-shading effect led to the development of new canopy modeling algorithm. The algorithm divides the *Cladophora* canopy in to layers, considering the light attenuation through each centimeter layer. The light attenuation through water (k_e) coupled with attenuation in the canopy (k_{alg}) alters the algal growth in each layer. The net growth is then calculated for each individual layer, per hour, ultimately aggregating to the overall biomass prediction per day for the entire model run period.

3 Modeling Methods

The Great Lakes *Cladophora* Model v3.0 (Kuczynski 2017) calculates change in biomass (X) density as described in Equation (1):

$$\frac{dX}{dt} = (\mu_{net} - L) * X \quad (1)$$

where μ_{net} is the net specific growth rate (d^{-1}) and L is the rate of sloughing (the phenomenon of detachment of the algae from the substrate due to physical stresses; not treated in this report). μ_{net} is determined as described in Equation (2):

$$\mu_{net} = \mu_{max} * f_{\mu}(I,T) * f(Q) - R_{max} * f_R(I,T) - R_B \quad (2)$$

where μ_{max} is the maximum gross specific growth rate (d^{-1}), $f_{\mu}(I,T)$ is light and temperature mediation factor (dimensionless) for photosynthetic growth, $f(Q)$ is a function (dimensionless) describing algal stored phosphorus mediation of growth represented by Equation (3) (Droop, 1968), R_{max} is the maximum light-enhanced respiration rate (d^{-1}), $f_R(I,T)$ is a light & temperature mediation factors (dimensionless) for light-enhanced respiration and $R_B$is the basal respiration (d^{-1}).

$$f(Q) = 1 - \frac{Q_{min}}{Q} \quad (3)$$

where Q_{min} ($gP \cdot gDW^{-1}$, as %) is the minimum stored P required to sustain the algal cell structure and basal metabolism and Q is the stored P of the alga.

The functions $f_{\mu}(I,T)$ & $f_R(I,T)$ represent the mediation of rates of gross growth (μ) and respiration (R) by light and temperature (as visualized by 2D response surfaces). Prior to the development of the canopy sub-model, it is necessary to ensure the photosynthesis (used interchangeably with growth) and respiration response surfaces have the best possible fit to the original laboratory

measurements of Graham et al., 1982. With the response surfaces fit, we then divide the canopy into vertical layers and apply Equation (2) to each layer, integrating over the canopy for the total growth effect. The following sections describe in detail the approach taken to revise (re-fit) the light & temperature functions and the development of an algorithm to replace the carrying capacity function used in previous versions of the GLCM with a canopy sub-model providing negative feedback on growth (self-shading).

3.1 Light & Temperature Mediation Factors

In the Great Lakes, growth of *Cladophora* starts in May and extends until early October, responding to seasonal patterns in temperature and light intensity. Additionally, the lake bottom light climate varies among sites due to differences in the vertical light extinction coefficient and within sites due to depth. The mediation factors ($f_\mu(I,T)$ & $f_R(I,T)$), accommodate those difference.

3.1.1 Mediation Factor for Photosynthesis Growth

In this revision of the GLCM, the 2D photosynthesis response surface was refit by applying the Equation (4) (Platt et al. (1980)) over the range of light conditions and discrete temperatures used by Graham et al. (1982) in making laboratory measurements.

$$P = P_{max} * \left(1 - e^{-\frac{-\alpha.I}{P_{max}}}\right).e^{-\frac{-\beta.I}{P_{max}}} \quad (4)$$

where P = gross specific photosynthetic rate (d^{-1})

P_{max} = model fitting parameter equivalent to maximum gross specific photosynthesis rate when $\beta = 0$ (d^{-1})

I = Photosynthetically active radiation (PAR) ($\mu E \cdot m^{-2} \cdot s^{-1}$)

α = model fitting parameter mediating the ascending limb of the curve ($\mu E \cdot m^{-2} \cdot s^{-1}$)

β = model fitting parameter mediating the descending limb of the curve ($\mu E \cdot m^{-2} \cdot s^{-1}$)

The Platt et. al (1980) function (referred to as Platt function in this report) includes an ascending limb (α) which describes the response of the alga to light, a max (P_{max}) above which photoinhibition begins and a descending limb describing the photoinhibition. The general nature of the Platt function (Equation (4)) is presented in Figure 2.

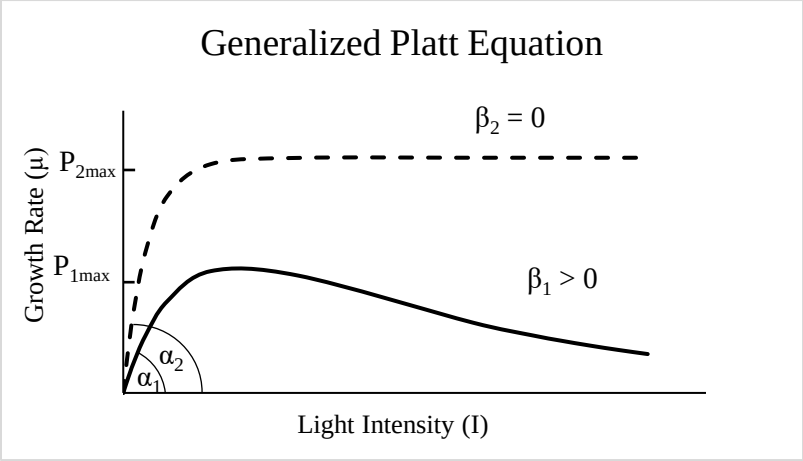

Figure 2. Generalized Platt function for a specific temperature showing the relationship between growth rate and light intensity, mediated by the ascending (α) and descending (β) limbs of the plot with the onset of photoinhibition (P_{max})

We adjusted the Platt function coefficients to achieve a best fit of measured (Graham et al. 1982) to modeled rates of photosynthesis over a range of light intensities at each discrete temperature. We developed a family of curves describing the temperature dependence each of the Platt coefficients (α, β and P_{max}; presented in idealized form in Figure 2). The approach illustrated by Figures 2 and 3 is then used for (I,T) pairs specified at 0.1 intervals of light and temperature to generate a 2D surface (Appendix A.1). The maximum modeled value of μ is located on the 2D surface and applied to normalize that surface, so $f_{\mu}(I,T)$ ranges

from 0 → 1. The process leading to a normalized response surface is illustrated in Figure 4. In application to the GLCM v3, an (I,T) pair of interest is specified and its position located on the normalized 2D surface. That normalized value of $f_\mu(I,T)$, is then multiplied by a user-specified (measurements, literature, calibration) value of the maximum gross specific growth rate (μ_{max}, d^{-1}) in Equation 2 (Appendix A.2).

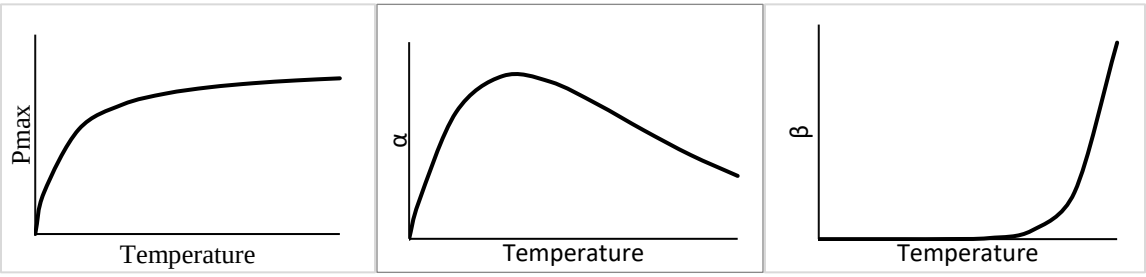

Figure 3. Idealized temperature dependence functions of P_{max}, α and β

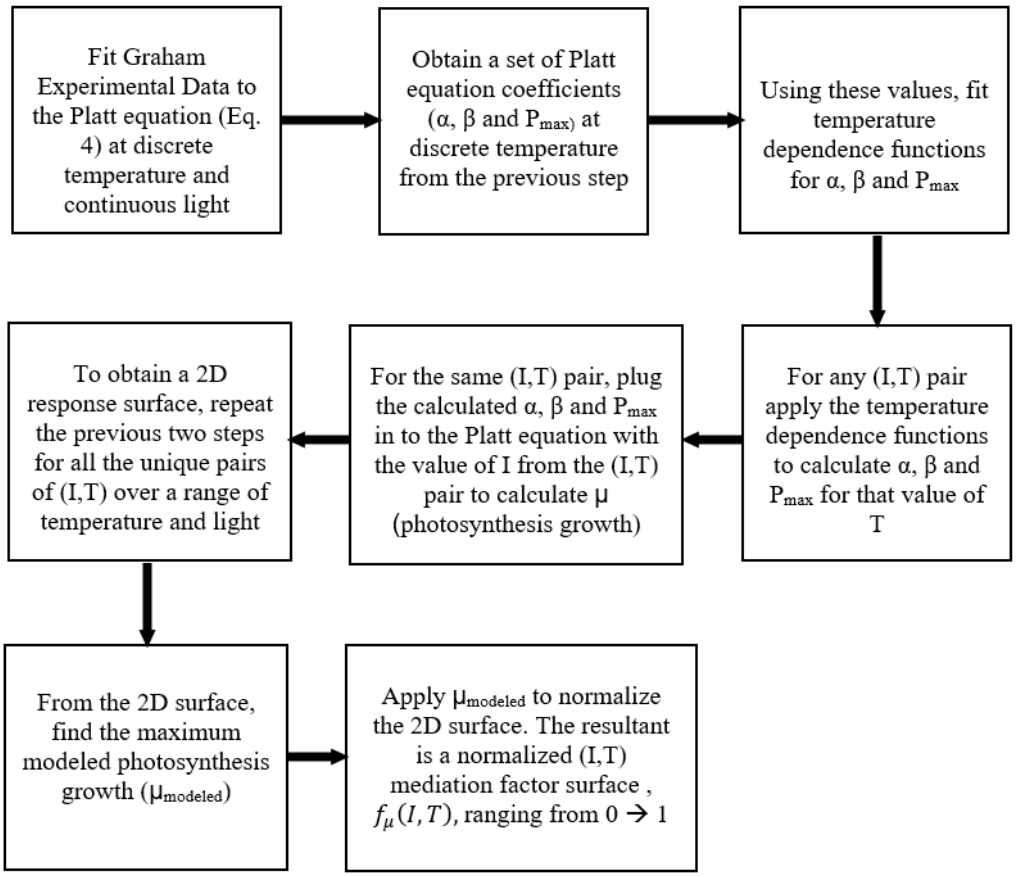

Figure 4. Box and arrow diagram showing the steps taken towards generating normalized 2D photosynthesis response surfaces $f_\mu(I,T)$

3.1.2 Basal Respiration and Mediation Factor for Light-Enhanced Respiration

Respiration (R) is a sink term in the net growth rate calculation (Equation 2) and is equal to the sum of light enhanced respiration ($R_{max} * f_R(I,T)$) and basal respiration (R_B) as described in Equation (5).

$$R = R_{max} * f_R(I,T) + R_B \quad (5)$$

Basal respiration is continuous, supporting resting state cell function, while light enhanced respiration varies with both light and temperature. A normalized 2D response surface is developed here as described above for gross photosynthesis (Figure 2-4) and a value of R_{max} is user defined. The only difference being that there is no evidence of photoinhibition in the light-enhanced response surface. Therefore, the descending limb of Platt equation is absent, i.e. β = 0. Basal respiration varies only with temperature, described here using a simplification of the Arrhenius equation (Equation 5; Chapra, 1997).

$$R_B = \mathrm{R_{B,20}} * \theta^{T-20} \quad (6)$$

3.2 Canopy Modeling

The point of departure in population growth modeling is the exponential model, where the specific growth rate coefficient is a constant, i.e. its ability to drive growth is unchanged regardless of the size of the population.

$$\frac{dX}{dt} = \mu_{max} * X \quad (7)$$

where X is the population size (biomass for *Cladophora*) and μ_{max} is the growth rate. This modeling approach is not intuitive, however, since resources in nature are limited and may support only a finite population; the exponential growth

model predicts infinite growth. The logistic growth model (Equation 8) accommodates this limitation by introducing a carrying capacity term (X_{max}) with the realized growth rate asymptotically approaching zero as $X \rightarrow X_{max}$. The two models are compared in Figure 5.

$$\frac{dX}{dt} = \mu_{max} * \frac{X_{max}-X}{X_{max}} * X \quad (8)$$

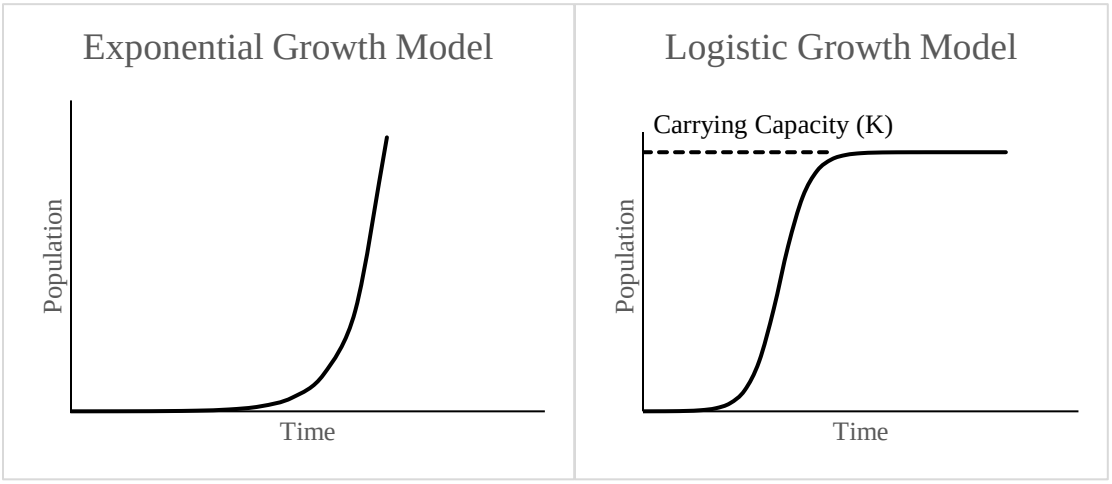

Figure 5. Generalized exponential and logistic growth model curves

The logistic growth equation was incorporated in the previous versions of the Great Lakes *Cladophora* Model (Canale and Auer, 1982; Tomlinson et al., 2010), basing the value of X_{max} on field observations. Empirically-derived values of 'maximum biomass' (X_{max}) may vary considerably from location to location, having been reported to as reach 600 gDM/m^2 (dry mass per square meter) in Lake Erie (Higgins et al. 2005) but are more commonly observed to be in the range 100-300 gDM/m^2. In Lake Huron, Michigan and Ontario (Canale and Auer, 1982; Tomlinson et al., 2010 and Malkin et al. 2007). In the absence of an agreed upon 'global' value of X_{max}, the overly deterministic nature of the logistic model leads to adjustment of model coefficients (e.g. μ_{max} and R_{max}) beyond accepted ranges or mechanistically unconstrained tuning of X_{max} to make the model fit the

data. X_{max} approach does not evolve from an understanding of the self-shading mechanism as applied to *Cladophora.*

In this work, we move away from the idea of a fixed-value, maximum achievable biomass (carrying capacity), toward an approach where the maximum realized biomass is determined more 'organically' as a mechanistic mass balance that includes a source term (the maximum specific growth rate coefficient, μ_{max}) and a suite of sink terms (R_{max}, R_B) and environmental mediation factors ($f(I,T)$, $f(Q)$), i.e. Equation 2 absent the logistic growth model term. We conceptualize the sink term and mediation factors collectively as environmental friction, which plays against μ_{max} to determine the maximum realized biomass. All of these terms are incorporated in a canopy sub-model which accommodates both local (vertically within the canopy, i.e. self-shading) and global, vertically across the canopy (e.g. incident light, water column light extinction, phosphorus availability) sources of environmental friction. Here, algal growth does not simply shut down as biomass approaches an empirically-derived value of X_{max}. Instead, as growth extends the algal canopy above the bottom, net growth continues at the canopy surface but an increasing proportion of the canopy becomes self-shaded and lies within a sub-optimal light environment where basal respiration predominates. Eventually, as more and more of the canopy is placed in near or complete darkness, respiration in the lower canopy balances net photosynthesis near the canopy surface and net canopy growth ceases; a 'maximum realized' biomass is achieved (Figure 6). It is noted that the magnitude of that maximum realized biomass is also influenced by canopy-global features that vary seasonally, with depth and among study sites.

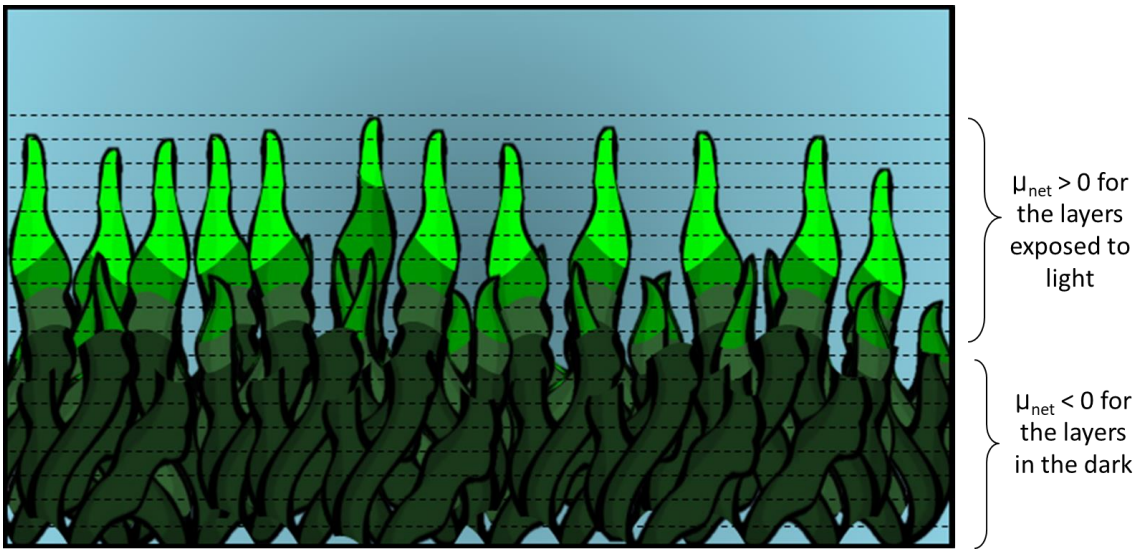

Figure 6. Illustration to show the effect of self-shading on the net growth of the layers in the canopy due to light attenuation

To mechanistically model the canopy effect, we first empirically determine the constant areal biomass density (i.e. the amount of biomass that can be accrued in a centimeter of the canopy), X_{layer} (gDM/m^2·cm) (Malkin bed height VS biomass 2003 data via Kuczynski's (2017) personal communication). The user-specified initial total canopy biomass is then divided by the areal biomass density (X_{layer}) to calculate the initial number of cm-thick layers. Biomass remaining after accommodating the user-specified biomass in the calculated number of layers is added to an additional top layer. For each layer, the availability of light ($I_{z,layer}$) is a factor of both light attenuation through the water column (k_e) and attenuation within the canopy (k_{alg}) (Higgins et al., 2005, Malkin, 2007):

$$I_{z,layer} = I_o * e^{-k_e * z} * e^{-k_{alg} * d_{mat}} \quad (9)$$

where I_o = incident water surface photosynthetically active radiation (PAR) (μE · m^{-2} · s^{-1})

k_e = light extinction coefficient through water column (m^{-1})

z = water column depth (m)

k_{alg} = light extinction coefficient through the algae mat (m^{-1})

d_{mat} = depth of the layer within the canopy mat (0 → bed height) (m^{-1})

The sub-model consists of a family of nested loops first calculating biomass accrual according to Equation 1 and 2 for each layer per hour at each water column depth, aggregating all the layers' biomass at the end of the hour which serves as an initial condition for the next (hourly) step. The process is repeated for each layer, each hour for the entire model simulation period which, when summed, yields a daily time series of *Cladophora* biomass for the entire period.

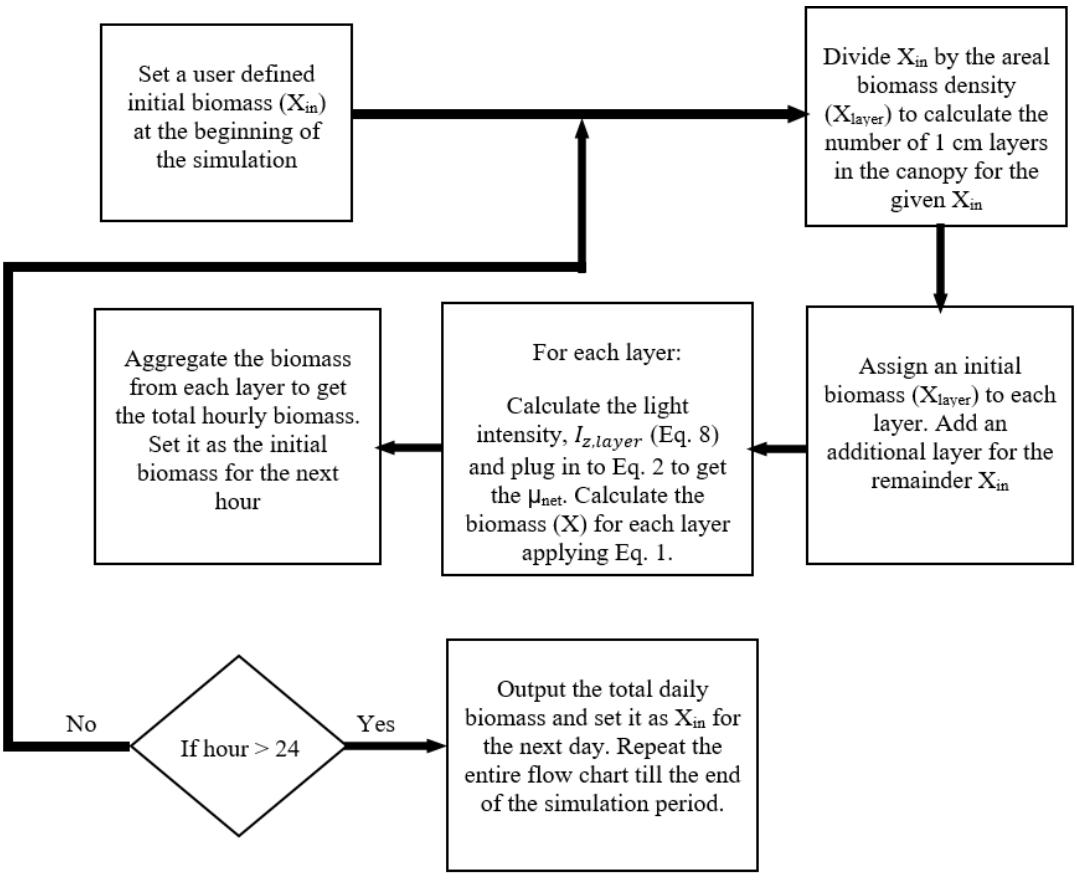

Figure 7. Box and arrow diagram showing a snapshot of one-day canopy model simulation

4 Results and Discussion

4.1 Photosynthesis Response Surfaces

As discussed in the previous section, the first step towards the development of the 2D photosynthesis response surface is to fit the Graham et al. (1982) photosynthesis data to the Platt equation (Equation 4).

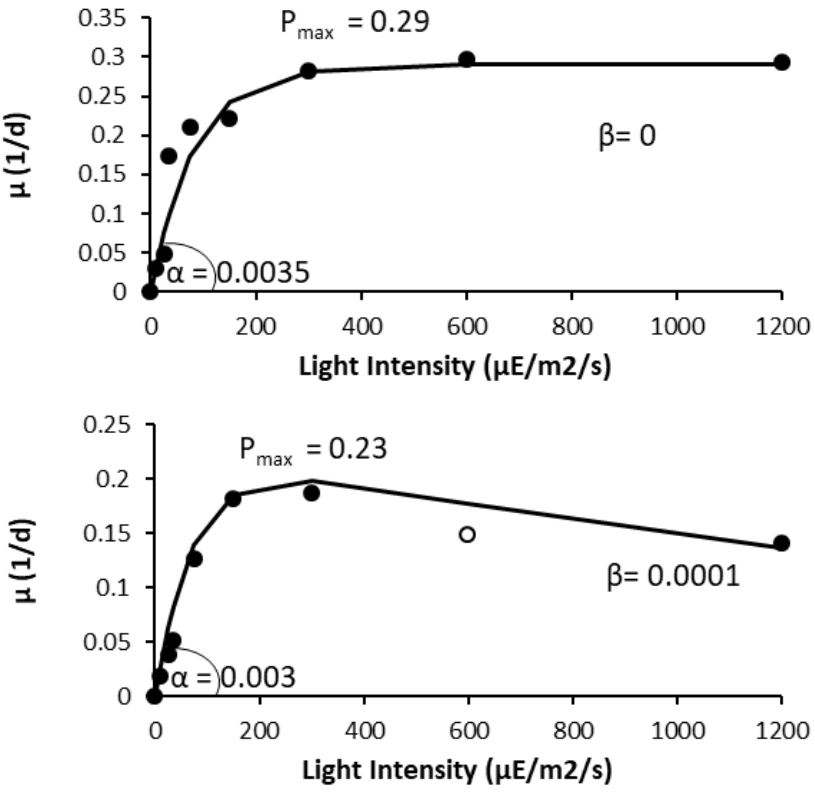

Figure 8. Examples of Platt equation fit to Graham photosynthesis growth measurements at 20 ^{o}C (top) and 25 ^{o}C (bottom)

Similar curves were fit to the photosynthesis growth data available at 1, 5, 10, 30 and 35 ^{o}C resulting a family of temperature dependent Platt coefficients (α, β and P_{max}).

The ascending limb (α), the descending limb (β) and the point above which photoinhibition begins (P_{max}) were fit to the following temperature dependence functions:

$$\alpha = 0.55 * \left(1 - e^{\frac{-0.001\,T}{0.55}}\right) * e^{\frac{-0.048\,T}{0.55}} \quad (10)$$

$$\beta = 1.0E-17 * T^{9.3} \quad (11)$$

$$P_{max} = 0.34 * \frac{T}{T+3.1} \quad (12)$$

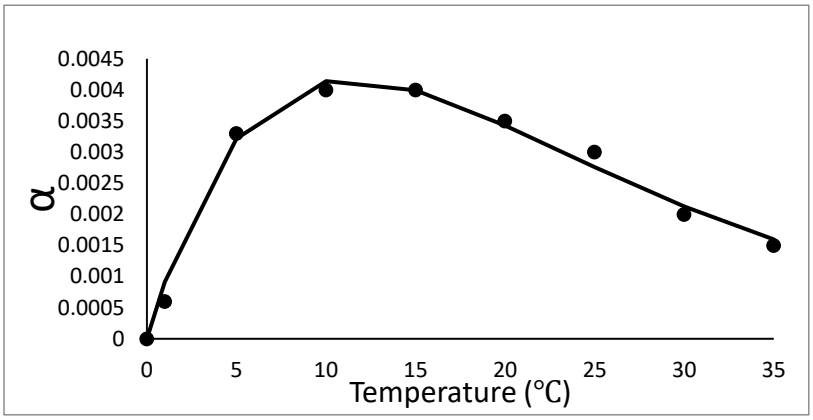

Figure 9. Temperature dependence function fit for the Platt coefficient α

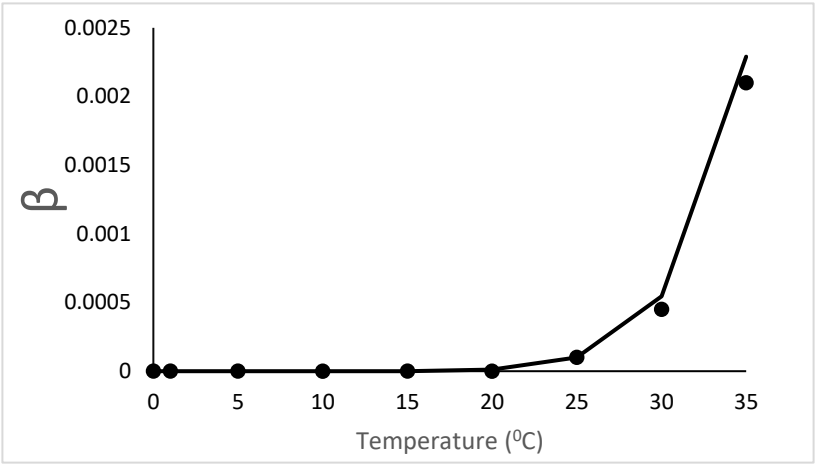

Figure 10. Temperature dependence function fit the Platt coefficient β

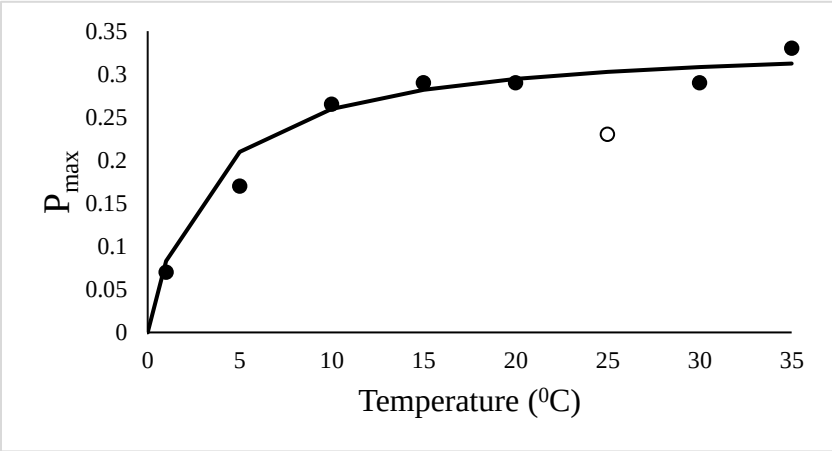

Figure 11. Temperature dependence function fit the Platt coefficient P_{max}

For any given pair of light and temperature (I,T), the Platt coefficients govern the temperature dependence, which when plugged into Platt Equation (4) along with the corresponding light, give the photosynthesis growth (μ). To generate a 2D photosynthesis response surface, a MATLAB code is written that calculates growth (μ) for a range of temperature (0-35 ^{o}C) and light (0-1200 μE.m^{-2}.s^{-1}). (Appendix A.1). The surface is then normalized with the highest predicted μ ($\mu_{modeled}$ ≈ 0.29 d^{-1}), resulting in a mediation factor ($f_{\mu}(I,T)$) surface (Figure 12). $f_{\mu}(I,T)$ is multiplied by the literature reported value of maximum specific growth rate, μ_{max}, (μ_{max} = 1.08 d^{-}1, Canale and Auer (1982); μ_{max} = 1.53 d^{-1}, Tomlinson et al., 2010; μ_{max} = 0.6 d^{-1}, Higgins et al., 2005 and Malkin et al. 2008) which gives the photosynthetic *Cladophora* growth (Equation 2), mediated by light and temperature.

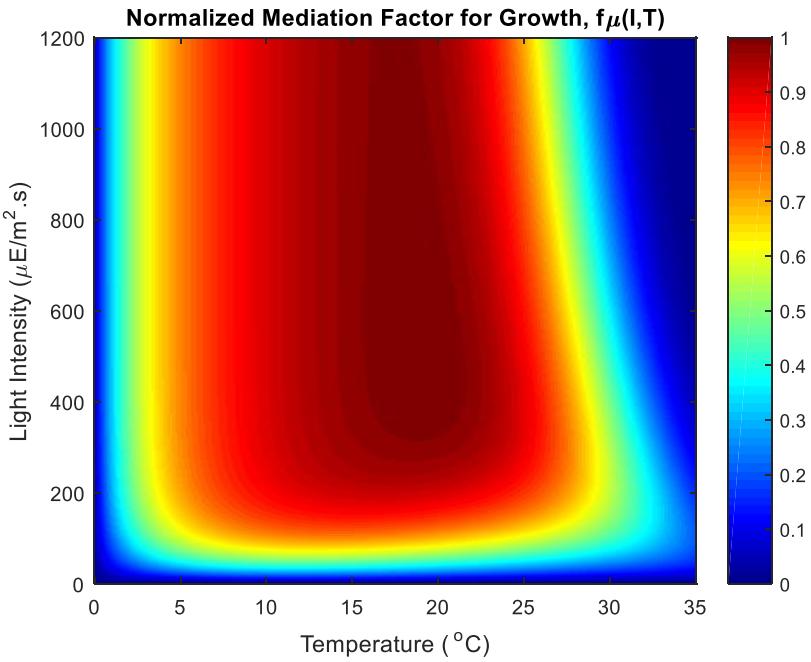

Figure 12. Normalized light and temperature growth mediation factor surface (dimensionless). 0 represents unfavorable light & temperature conditions for growth progressing to 1 which represents most favorable conditions

In Figure 12, photoinhibition (i.e. reduction in photosynthesis potential of the alga) can be observed at higher light intensities which was not evident in the previous GLCM v3 development.

4.2 Light-Enhanced Respiration Response Surface

The minimum average daily light intensity required by *Cladophora* to grow is 27 μE·m^{-2}·s^{-1} (Lorenz et al., 1991). Below this threshold, the alga only respires, sustaining the resting state cell function. So, the Graham et al. (1982) experimental measurements available for 10 and 25 μE·m^{-2}·s^{-1} have been utilized to develop the basal respiration equation (Figure 13). Earlier versions of the GLCM used either a linear fit (Tomlinson et al., 2010) or an exponential equation (Kuczynski, 2017) to define R_B. In this report, R_B shows a better fit with the Arrhenius equation (Equation 5; Chapra 1997) (Equations 6, 13).

$$R_B = \mathrm{R}_{\mathrm{B},20} * \theta^{T-20} \quad (13)$$

where θ = 1.04 (dimensionless)

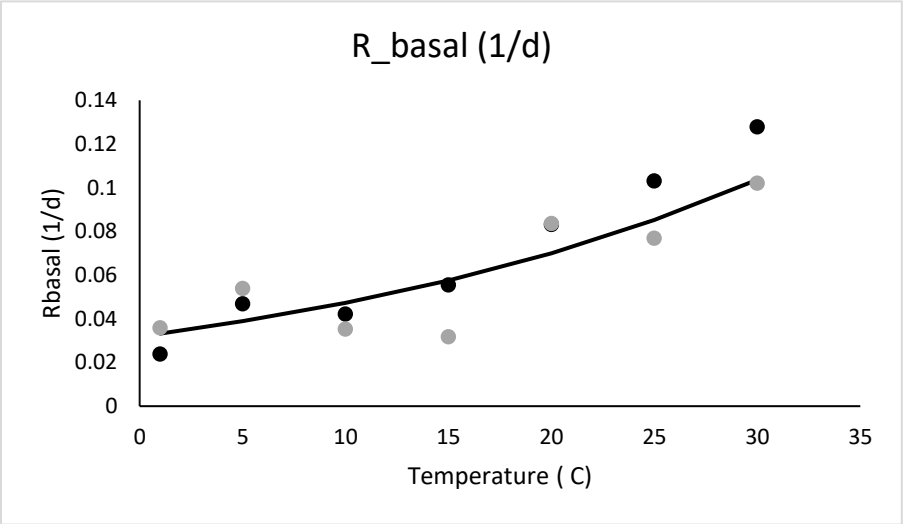

Figure 13. Basal respiration function fit (line) to Graham et al (1982) experimental basal respiration data (points) at light intensities 10 (grey) & 25 (black) $\mu E \cdot m^{-2} \cdot s^{-1}$

The data for the development of the 2D light-enhanced respiration surface is calculated by subtracting R_B from the total respiration measurements (Graham et al., 1982). Then a Platt function with β = 0 is applied to the data at discrete temperature, to obtain the functions of temperature dependent coefficient (Equations 14 and 15) ($R_{LT_{max}}\ and\ \alpha_R$). The 2D light-enhanced response surface is generated by applying Platt equation to all the combinations of (I,T) for a range of temperature and light (similar to the photosynthesis 2D surface), which is then normalized by the highest modeled R ($R_{modeled}$ ≈ 0.12 d^{-1}) to get the mediation factor $f_R(I,T)$ for light-enhanced respiration. In the context of the GLCM application, the $f_R(I,T)$ mediation factor is multiplied with a maximum specific rate of light-enhanced respiration (R_{max} = 0.44 d^{-1}, Auer and Canale 1982, Higgins et al., 2005, Malkin et al., 2008; R_{max} = 0.287 d^{-1}, Tomlinson et al., 2010) to calculate the light-enhanced respiration rate.

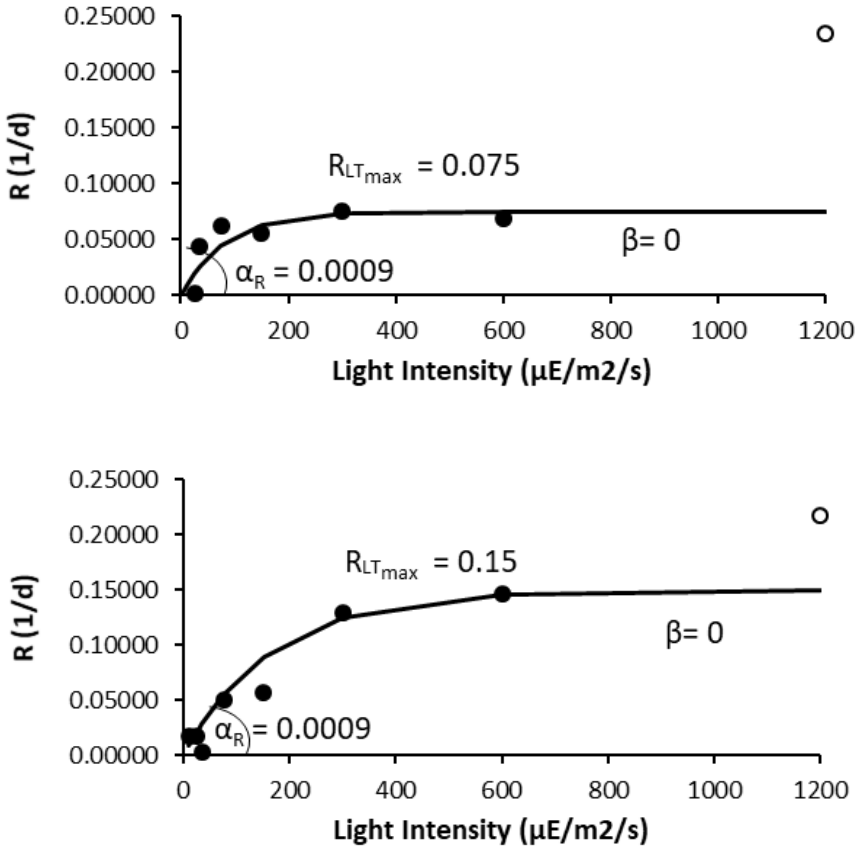

Figure 14. Examples of Platt equation fit to Graham's light-enhanced respiration measurements (minus R_B) at 15 °C (top) and 20 °C (bottom)

The Platt coefficients as a function of temperature are as follows:

$$R_{LT_{max}} = 0.08 * \theta^{T-20} \; with \; \theta = 1.03 \text{ (dimensionless)} \qquad (14)$$

$$\alpha_R = 0.00095 * \frac{T}{T+1.4} \qquad (15)$$

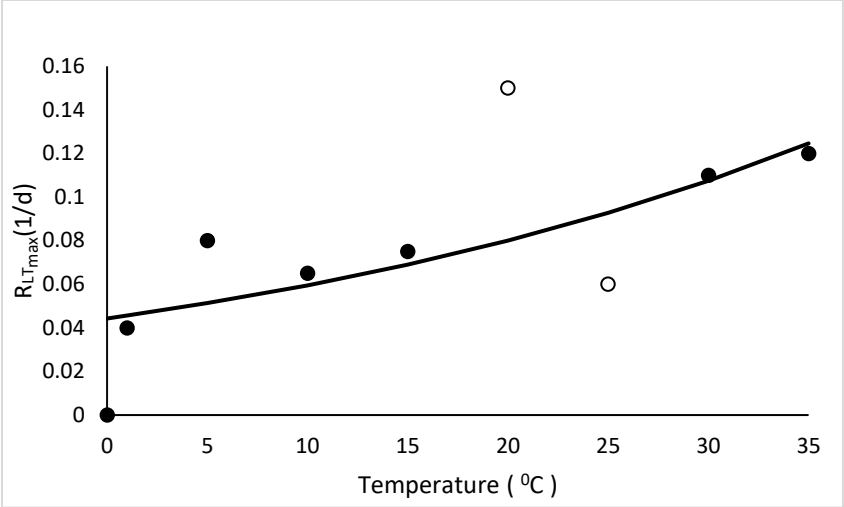

Figure 15. Temperature dependence function fit for the Platt coefficient $R_{LT_{max}}$

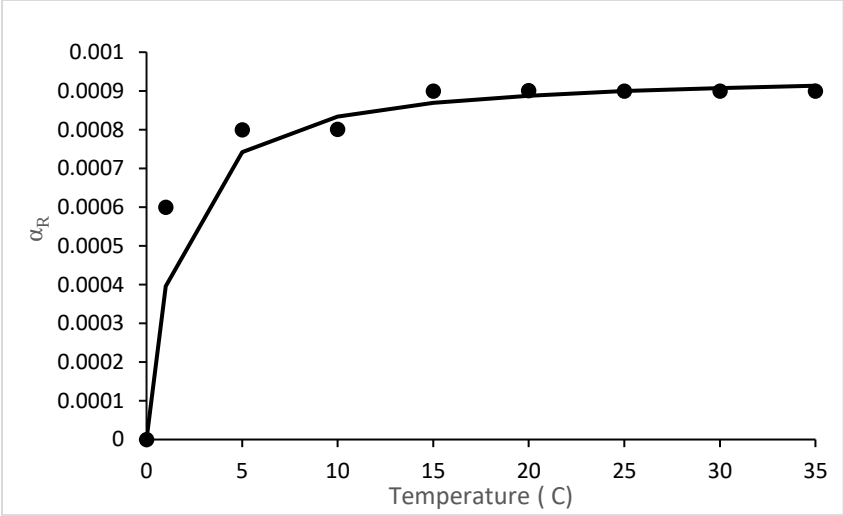

Figure 16. Temperature dependence function fit for the Platt coefficient α_R

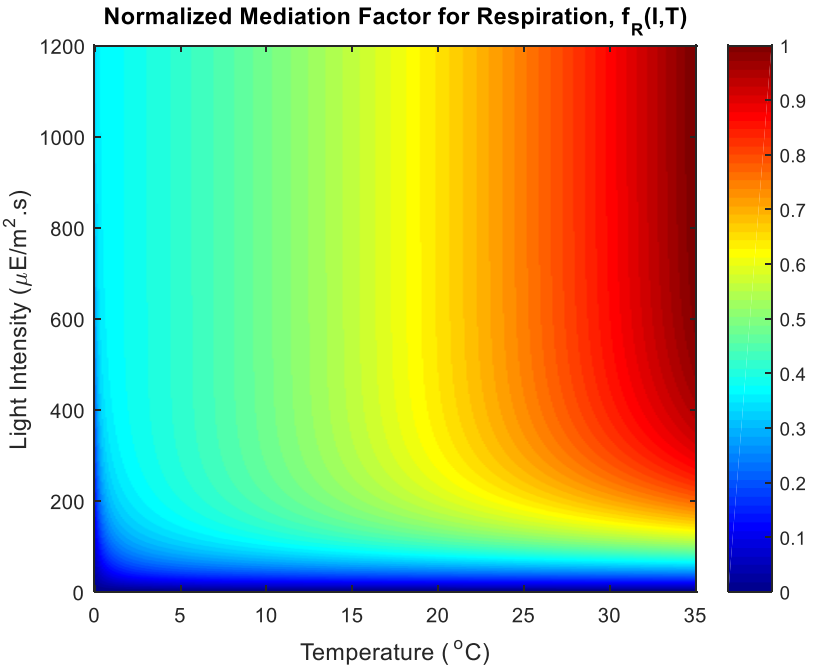

Figure 17. Normalized light and temperature respiration mediation factor surface (dimensionless). 0 represents unfavorable light & temperature conditions for light enhanced respiration progressing to 1 which represents most favorable conditions

4.3 Net Growth Response Surface

The net growth (Equation 2) response surface is visualized by subtracting the total respiration surface (light enhanced + basal) from the photosynthetic growth surface (Figure 18). To observe only the effect of light and temperature environmental conditions on the net growth, $f(Q)$ is set to 1 in Figure 18 (i.e. there is no nutrient limitation affecting the net growth).

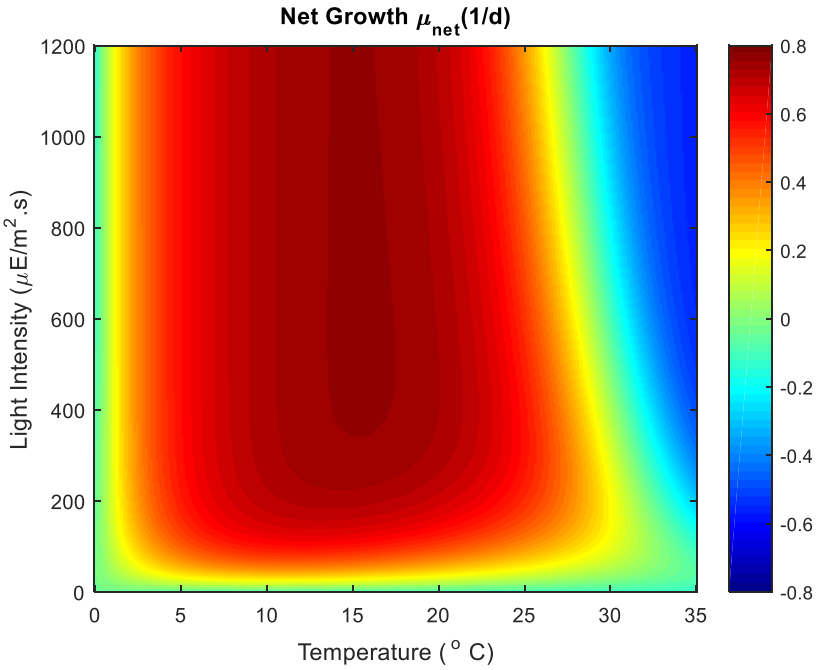

Figure 18. Net Growth Response Surface showing the effect of light and temperature with μ_{max} = 1.08 d^{-1} and R_{max} = 0.44 d^{-1} (Auer and Canale, 1982) and $f(Q)$ = 1

The dark red zone on the surface is the optimal light and temperature combination (also informally referred to as a sweet spot) where the net growth (μ_{net}) is maximum.

4.4 Canopy Results

The net growth dictates the rate of biomass production depending on the environmental factors of light, temperature and nutrient availability (Equation 2). The model would be an exponential growth model (Figure 5) if it had only net growth and nothing to put a cap on it. The earlier models (GLCM v1 and GLCM v2) used an overly deterministic value of X_{max} which stops the biomass production once it reaches X_{max} (like the logistic growth model, Figure 5). Tomlinson et. al 2010 stated that the maximum biomass density (X_{max}) cannot be practically achieved, hence remains undetermined. Canale and Auer (1982) used an X_{max} value of 800 gDM/m^2 to calibrate their model for Lake Huron data. To illustrate how

the hardwired X_{max} value can affect the biomass prediction output, we ran the model with different X_{max} values keeping all the other environmental factors (light = 500 μE.m^{-2}s^{-1}, temperature = 15 ^{o}C and nutrient availability, $f(Q)$=1) constant.

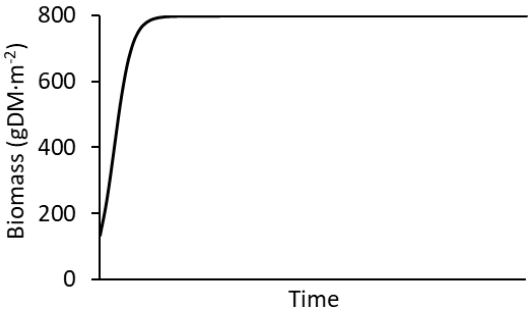

Figure19. a

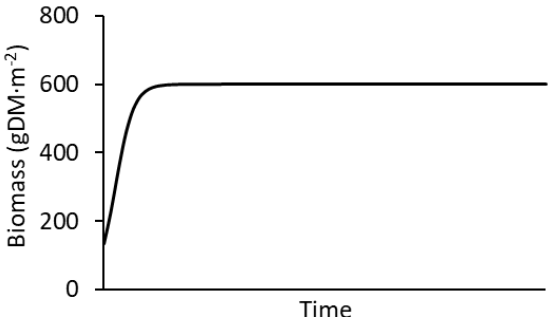

Figure 19. b

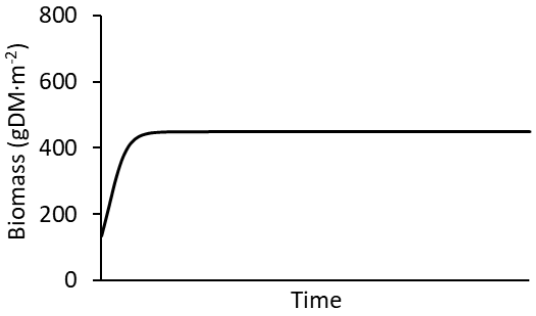

Figure 19. c

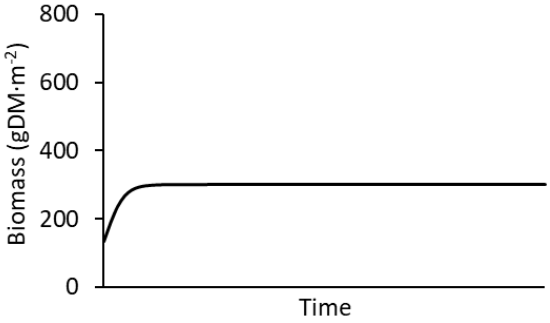

Figure 19. d

Figure 19. Model runs to show the effect of different X_{max} values on the net biomass model output (Figure 19.a: X_{max} = 800 gDM.m^{-2} ; Figure 19.b: X_{max} = 600 gDM.m^{-2} ; Figure 19.c: X_{max} =450 gDM.m^{-2} and Figure 19.d: X_{max} = 300 gDM.m^{-2})

Unlike the above hardwired X_{max} approach, the limitation on biomass production in the canopy model is a manifestation of how net growth is affected by light attenuation due to self-shading and is more ‘organic’. To show the organic nature of the model, the above model was re-run with the same environmental conditions, replacing the hardwired X_{max} value with the mechanistic canopy algorithm.

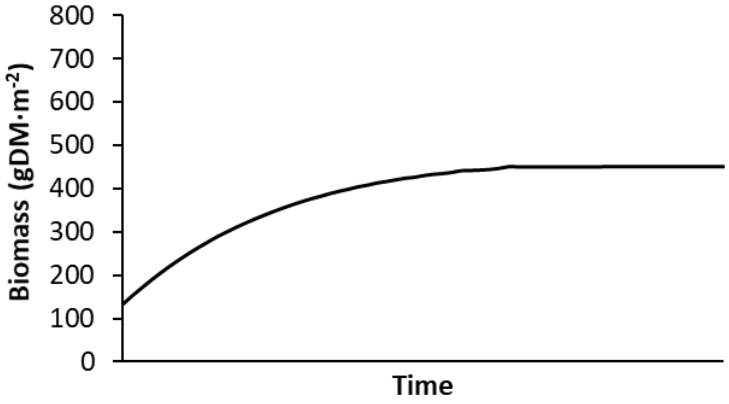

Figure 20. Model output with canopy algorithm showing the effect of environmental factors (light attenuation in the canopy) in leveling off the biomass without forcing it an artificial maximum biomass value

The canopy algorithm divides the *Cladophora* bed height into 1 cm layers. The light attenuation within the canopy (k_{alg}) is a manifestation of how many layers are there for a given biomass (Equation 9). To calculate the number of layers, the biomass is divided by the areal biomass density (X_{layer}) of *Cladophora*. X_{layer} i.e. how much biomass can fit in a cm layer is the inverse of the slope of the line fitting biomass versus bed height data (Figure 21), whose value is calculated to be 9 gDM.m^{-2} cm^{-1}. The pairwise measurements of bed height and biomass density was obtained by Kuczynski (2017) from Malkin (via personal communication).

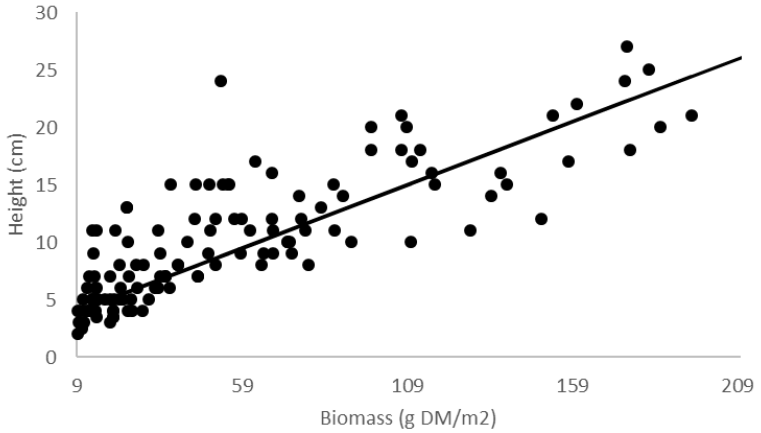

Figure 21. The inverse of the slope of the line fit (i.e. areal biomass density, X_{layer}) for biomass density vs bed height was calculated to be 9 gDM·m^{-2}·cm^{-1}.

(Note that the biomass density values below 9 gDM.m^{-2} were not used for the linear fit because there is no canopy effect for the biomass less than the areal biomass density)

In the canopy, the net growth (μ_{net}) of the layers exposed to light is positive whereas the layers are in dark only respire resulting in a negative μ_{net} (Figure 22). As the *Cladophora* grows, the bed height increases, and more layers are at the bottom are in darkness. Ultimately, a state of equilibrium is attained when the overall μ_{net} becomes zero (the μ_{net} of top layers is balanced by the negative μ_{net} of the bottom layers) and the biomass doesn't grow any further.

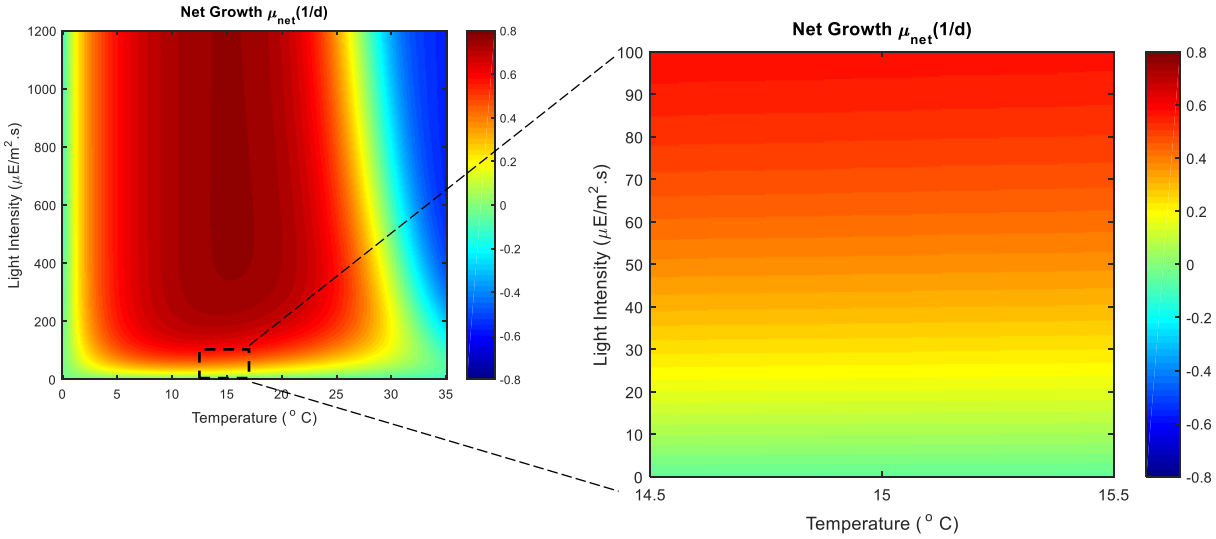

Figure 22. An illustration showing the decrease in the net growth (μ_{net}) with light attenuation. For the darkest part of canopy (where I = 0), μ_{net} becomes negative (Note: To understand the effect of light, $f(Q)$ is set as 1 for this figure. In the environment, $f(Q)$<1 which means that the photosynthetic growth is less than what is used for the above illustration, thereby making μ_{net} more negative for I = 0)

To demonstrate the effect of light and temperature variation coupled with the canopy effect on net biomass (X) and corresponding net growth (μ_{net}), the GLCM with only canopy sub-model (no nutrient limitation or sloughing effect) was run for field observed hourly light intensity and daily temperature for 65 days of

summer (same data was used to calibrate GLCM v2 for Lake Huron; for site information refer to Tomlinson et al., 2010).

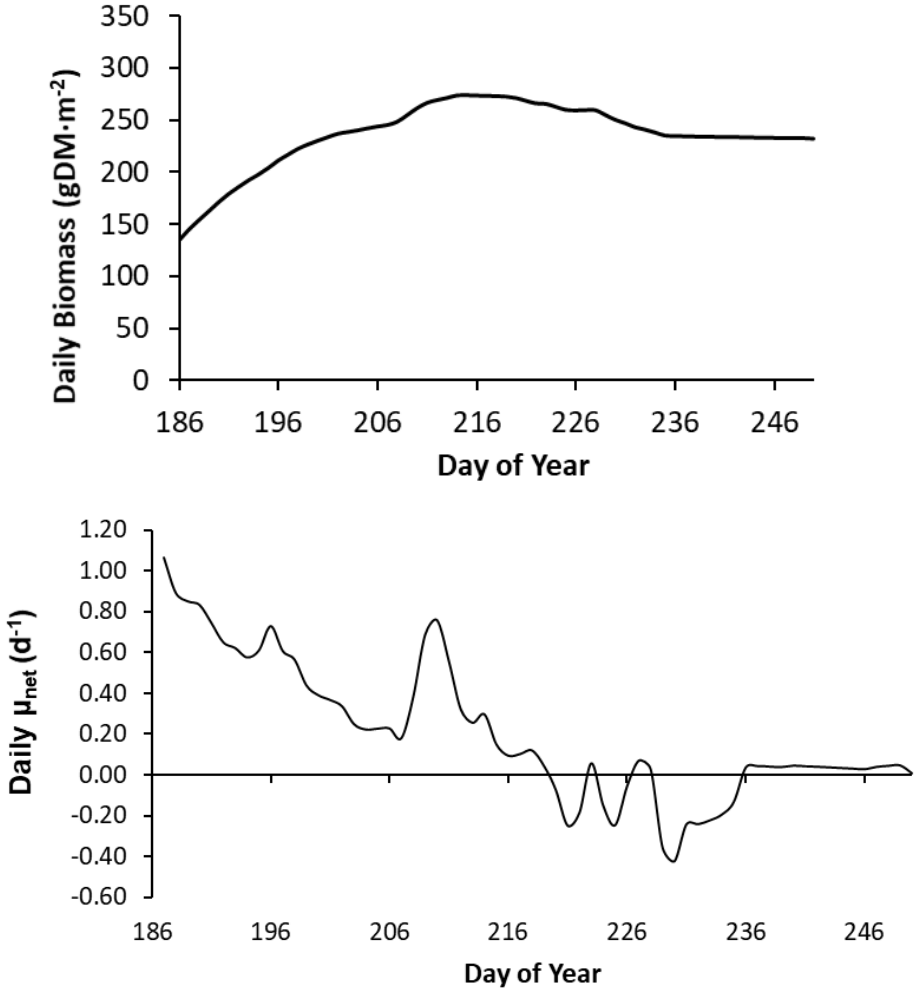

Figure 23. Daily biomass (X) prediction with canopy sub-model, varying light intensity and temperature (top). Corresponding daily μ_{net}output driving biomass production (bottom)

The daily μ_{net} output drives the slope of daily biomass (X) prediction curve. When the μ_{net} is large and positive, the biomass grows quickly, while a negative μ_{net} corresponds to a negative slope i.e. decrease in biomass. The daily μ_{net} is an aggregation of hourly net growth rates at each layer in the canopy manifested by hourly light intensity and daily temperature values. During the day, the top sunlight exposed layers of the canopy experience positive μ_{net} while the self-shaded layers

only perform basal respiration resulting in a negative μ_{net} (Figure 24). The peaks in daily μ_{net} (Figure 23, bottom) show optimal light and temperature combinations resulting in a higher magnitude of day-time μ_{net} for the top layers which is difficult to be balanced by day-time self-shaded layers' basal respiration and overall night-time respiration (Figure 25). While on other colder and cloudy days, the positive μ_{net} magnitude isn't big enough to completely take over the sink term. Additionally, as the biomass grows over time, the number of layers increase in the canopy i.e. more and more filaments are self-shaded. The top layers cannot compensate for the self-shaded layers' negative feedback (Figure 25), resulting in negative trough in Figure 23. This organic negative feedback due to interplay between light, temperature and the canopy eliminated the need of a carrying capacity term.

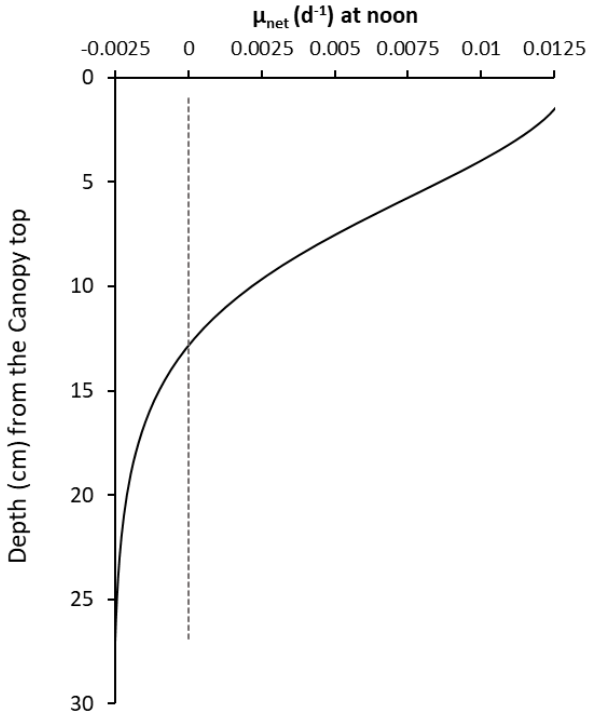

Figure 24. μ_{net} profile with canopy depth at noon. In the presence of sunlight, the μ_{net} for top layers is positive and negative for self-shaded bottom layers

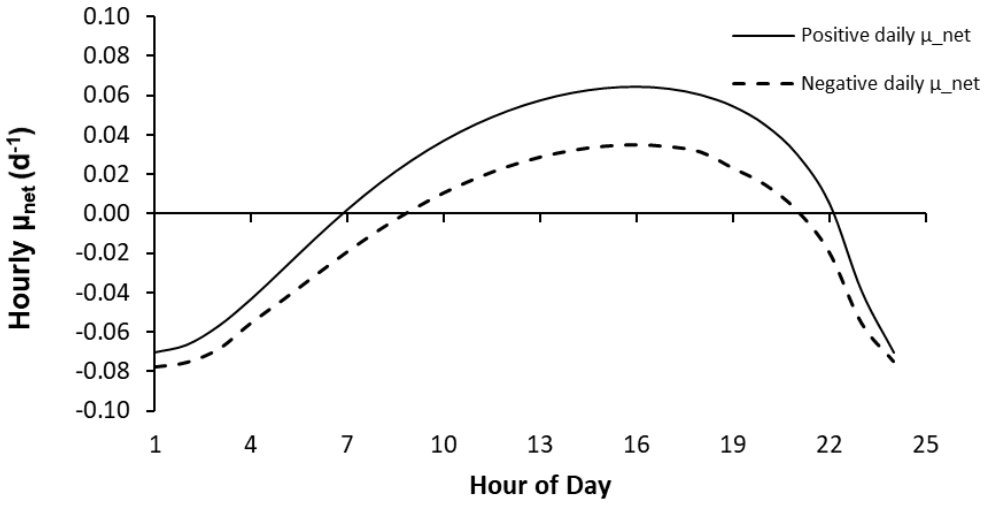

Figure 25. Hourly μ_{net} breakdown corresponding to hourly light and daily temperature at two different days. For solid line, the aggregation of positive μ_{net} is more than negative μ_{net} resulting in a positive net growth for that day. For dotted line, negative μ_{net} takes over the day-time μ_{net} resulting in a negative μ_{net} for the day.

The light received by each layer in the canopy is a function of attenuation through water (k_e) and algal mat (k_{alg}) (Equation 9). k_e is well understood and measured for different Great lakes, ranging from 0.1-1.2 m^{-1} (Lakeaccess.org). However, the attenuation of light through algal mat had been measured for a wide range of riverine and lacustrine *Cladophora*. Flynn (2014) measured an average of 47 ± 34 m^{-1} for riverine *Cladophora*. Higgin (2005) used an average value of 21 ± 3.3 m^{-1} by an X function to describe k_{alg} (k_{alg} = 7.84 * $X^{0.24}$) while Malkin et al. (2008) averaged k_{alg} to be around 24.1± 3.3 m^{-1} for the lacustrine *Cladophora*. Riverine *Cladophora* tends to be form a denser algal mat since they are pushed together due to the downstream flow. However, in lacustrine environment, the filaments can be long and standing. Therefore, we suggest a value range of 21 ± 3.3 m^{-1} (by Higgins et al, 2005) for light attenuation in the canopy for the Great Lakes *Cladophora* Model v3. Figure 23 demonstrates the sensitivity of the model for this range of k_{alg}.

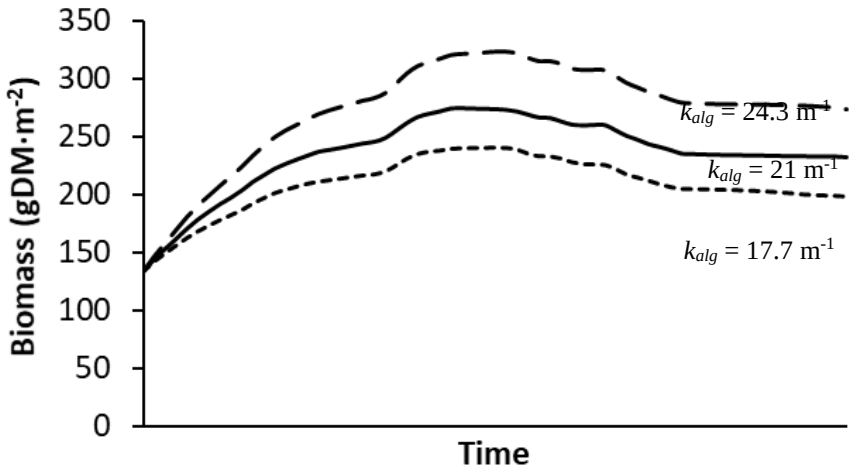

Figure 26. The variation in the realized maximum biomass with canopy light attenuation factor (k_{alg})

The canopy algorithm was finally incorporated in GLCM v3 (under development) to calibrate the model with real field observational data. Lake Michigan *Cladophora* data was used to demonstrate the results presented in Figure 23. The data was collected in 2006 and was used to calibrate the GLCM v2 model by Tomlinson et al (2010). The model parameters used for Figure 27 are: μ_{max} = 1.53 d^{-1}, R_{max} = 0.287 d^{-1} (Tomlinson et al. 2010), Q_{min} = 0.04 %P, ke = 0.2 m^{-1}, kalg = 21 m^{-1} with an initial biomass value of 134 gDM/m^2.

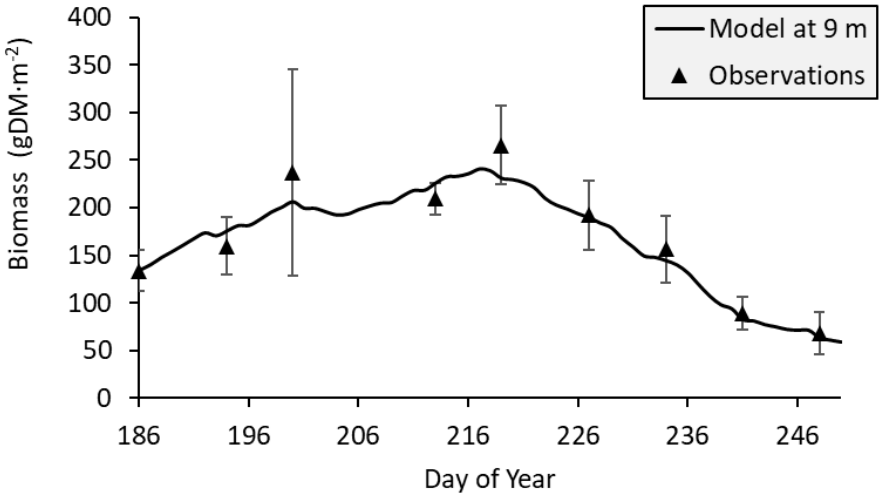

Figure 27. GLCM v3 growth simulation output, incorporating canopy algorithm, showing seasonality in Lake Michigan along with 2006 observational data points

5 Model Application and Future Work

The research presented in this report focuses on the development of a mechanistic canopy sub-model, eliminating the overly deterministic modeling parameter X_{max}. It also presents the necessary steps to revise the light and temperature based net growth mediation factors prior to the development of the sub-model. The algorithm is incorporated with the other *Cladophara* modeling elements (namely phosphorus uptake rate, stored phosphorus limitation and sloughing) in the third version of the Great Lakes *Cladophora* model. The GLCM v3 has future *Cladophora* management applications in predicting the nuisance algal growth in the Great Lakes. Although presently there is no defined nuisance *Cladophora* levels for the Great Lakes, field observations and studies could contribute towards its quantification. Once the limits are set, the GLCM v3 can be used to predict near and offshore water quality basing *Cladophora* growth and provide P-management solutions coupled with hydrodynamic and ecological models.

In the future, more field observations and investigations should be conducted relating *Cladophora* biomass to the canopy height to better understand the constant areal biomass density. Similar to riverine *Cladophora,* which tends to form a denser mat because of being pushed closer by the downstream flow, wind and wave stresses can mediate the light attenuation within the algal mat (k_{alg}) in the lucustrine *Cladophora*, however the effects are unknown. Investigations to study external stresses can also be applied to model a more mechanistic sloughing algorithm. Future work can be done to couple the canopy sub-model with a sloughing sub-model to study the effects on the tensile strength of the filaments due to self-shading, impacting the onset of sloughing. All these enhancements will contirubte towards a more accurate and mechanistic Great Lakes *Cladophora* Model.

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Appendix A.1: MATLAB code to generate 2D photosynthetic growth, light-enhanced respiration and net growth response surfaces

```
clear all
close all
%% Initialize
Temp_range = 35;
Light_range = 1200;
dT = 0.1;
dL = 0.1;
Pmax_a = 0.34;
Pmax_b=3.1;
u_alpha_a = 0.55;
u_alpha_b=0.001;
u_alpha_c=0.048;
u_alpha_const = 0;
u_beta_a=1.00E-17;
u_beta_b=9.3;
R_a= 0.08;
R_Theta =1.03;
R_T = 20;
R_alpha_a = 0.00095;
R_alpha_b =1.4;
R_basal_a = 0.07;
R_basal_Theta =1.04;
R_basal_T =20;
prompt = 'What is the value of umax?';
u_max=input(prompt);
prompt = 'What is the value of Rmax?';
R_max=input(prompt);

%% Matrix
temp_axis = 0:dT:Temp_range;
light_axis = 0:dL:Light_range;
[~,s_t] = size(temp_axis);
[~,s_l] = size(light_axis);
Pmax=zeros(1,s_t);
u_alpha = zeros(1,s_t);
u_beta =zeros(1,s_t);
P= zeros(s_l,s_t);
Rmax =zeros(1,s_t);
R_alpha = zeros(1,s_t);
Rb = zeros(s_l,s_t);
R =zeros(s_l,s_t);
```

```
42
43      %% Calculate Growth
44 -    for T = 2 : s_t
45 -        Pmax(T) = Pmax_a*(temp_axis(T)/(temp_axis(T)+Pmax_b));
46 -        u_alpha(T) = (u_alpha_a*(1-exp(-u_alpha_b*temp_axis(T)/u_alpha_a))...
47                      *exp(-u_alpha_c*temp_axis(T)/u_alpha_a))+u_alpha_const;
48 -        u_beta(T) =u_beta_a*temp_axis(T)^u_beta_b;
49
50 -        for I = 2 : s_l
51
52 -            P(I,T) = Pmax(T) * (1 - exp(-u_alpha(T) * light_axis(I)/Pmax(T)))...
53                      * exp(-u_beta(T) * light_axis(I)/Pmax(T));
54 -        end
55 -    end
56      %% Calculate Respiration
57 -    for T = 1 : s_t
58 -        Rmax(T) = R_a* R_Theta^(temp_axis(T)-R_T);
59 -        R_alpha(T) = R_alpha_a* (temp_axis(T)/(temp_axis(T)+R_alpha_b));
60
61 -        for I = 1 : s_l
62 -            Rb(I,T) =R_basal_a* R_basal_Theta^(temp_axis(T)-R_basal_T);
63 -            if Rmax(T)==0
64 -                R(I,T) = 0;
65 -            else
66 -            R(I,T) = Rmax(T) * (1 - exp(-R_alpha(T) * light_axis(I)/Rmax(T)));
67 -            end
68 -        end
69 -    end
70      %% normalise
71 -    umax_modeled= max(max(P));
72 -    f_u = P/umax_modeled;
73 -    Rmax_modeled = max(max(R));
74 -    f_R = R/Rmax_modeled;
75
76      % if no max values are known, use modeled values
77 -    if u_max == 0
78 -        u_max = umax_modeled;
79 -    end
80 -    if R_max == 0
81 -        R_max = Rmax_modeled;
82 -    end
```

```
83
84      %% Net growth
85 -    unet = (u_max* f_u  -R_max * f_R - Rb);
86
87      %% Normalised surfaces
88 -    figure(1)
89 -    imagesc(temp_axis,light_axis,f_u);
90 -    set(gca,'YDir','normal')
91 -    colormap jet
92 -    xlabel('Temperature (^o C)');
93 -    ylabel('Light Intensity (\muE/m^2.s)')
94 -    title('Normalised Gross Growth Surface (f_u(I,T))');
95 -    colorbar
96
97 -    figure(2)
98 -    imagesc(temp_axis,light_axis,f_R);
99 -    set(gca,'YDir','normal')
100 -   colormap jet
101 -   xlabel('Temperature (^o C)');
102 -   ylabel('Light Intensity (\muE/m^2.s)')
103 -   colorbar
104 -   title('Normalised Light Enhanced Respiration Surface (f_R(I,T))');
105
106     %% Net growth
107 -   figure(5)
108 -   imagesc(temp_axis,light_axis,unet);
109 -   set(gca,'YDir','normal')
110 -   colormap jet
111 -   xlabel('Temperature (^o C)');
112 -   ylabel('Light Intensity (\muE/m^2.s)')
113 -   colorbar
114 -   caxis([-0.8,0.8])
115 -   title(['Net Growth \mu_n_e_t(1/d)']);
```

Appendix A.2. Light and Temperature Mediation Factors (f_{μ} (I, T) and f_R (I, T)) and Basal Respiration VBA code in the GLCM v3

```
Function PhotoRateNew(I As Variant, T As Variant) As Double

'fu(I,T) equations aka PhotoRateNew:

'Equation Coefficients
Pmax_a = 0.34
Pmax_b = 3.1
u_alpha_a = 0.55
u_alpha_b = 0.001
u_alpha_c = 0.048
u_beta_a = 1E-17
u_beta_b = 9.3

umax_modeled = 0.28778


' calc gross growth parameters
Pmax = Pmax_a * (T / (T + Pmax_b))
u_alpha = u_alpha_a * (1 - Exp(-u_alpha_b * T / u_alpha_a)) * Exp(-u_alpha_c * T / u_alpha_a)
u_beta = u_beta_a * T ^ u_beta_b


PhotoRateNew = (Pmax * (1 - Exp(-u_alpha * I / Pmax)) * Exp(-u_beta * I / Pmax)) / umax_modeled


End Function


Function RespRateNew(I As Variant, T As Variant) As Double

'fR(I,T) equations aka RespRateNew:

'Equation Coefficients
R_a = 0.08
R_Theta = 1.03
R_T = 20
R_alpha_a = 0.00095
R_alpha_b = 1.4


Rmax_modeled = 0.1246

'calc total respiration
Rmax = R_a * R_Theta ^ (T - R_T)
 R_alpha = R_alpha_a * (T / (T + R_alpha_b))

RespRateNew = (Rmax * (1 - Exp(-R_alpha * I / Rmax))) / Rmax_modeled


End Function
```

```
Function Rb(T As Variant) As Double

'Basal Respiration at T

Rb_a = 0.07

Rb_Theta = 1.04

Rb = Rb_a * Rb_Theta ^ (T - 20)

End Function
```