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Light limitations to algal growth in tropical ecosystems

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SUMMARY

1. Spatial and temporal variations in algal concentrations are controlled in many aquatic ecosystems by the availability of solar irradiance, rather that nutrients or grazing. In such light limiting conditions, changes in the optical or hydrological characteristics of the water column will directly impact biomass concentrations. Here we develop and test an approach based on the relationship between available solar irradiance within the mixed layer and algal biomass concentrations.

2. As with most nutrient/biomass relationships, an increase in available solar energy favours an increase in biomass when light limitation prevails. The ratio between light/biomass is then used to determine a critical light requirement that can be used to estimate critical depth and compensation irradiance and open the way to exploring how changes in mixing depth and vertical attenuation may influence algal biomass concentrations.

3. This approach is used to describe real conditions in two disparate algal communities; the phytoplankton community in Lake Victoria, East Africa and the microphytobenthos community in the lacustrine system of Esteros del Iberá (South America).

4. Differences in the critical light requirement were used to examine the relative efficiency of the algal communities in their use of available solar energy. The tropical phytoplankton community showed similar energetic requirements to theoretical estimates and were found to be less efficient when compared with the phytobenthos community.

Keywords: critical depth, lakes, light limitation, phytobenthos, phytoplankton

Introduction

Patterns of abundance in algal biomass provide a fundamental tool in understanding the driving forces in ecosystem productivity in relation to changing environmental forcing functions. Aquatic autotrophs have nutritional and energetic requirements for their photosynthetic carbon fixation and growth. Attempts to describe resource control of algal carrying capacities have followed two general approaches, a population dynamics approach based on the modelling of growth and loss processes (e.g. Weissing & Huisman, 1994; Siegel, Doney & Yoder, 2002), and a resource based approach in which relationships between algal concentrations and available resources are directly used to estimate the supportive capacities of ecosystems (e.g. Reynolds & Maberly, 2002). This latter approach has often been used to explore eutrophication phenomena related to phosphorus loads (e.g. Vollenweider, 1976; Reynolds, 1992; Reynolds *et al.*, 2000), using regression models of algal biomass and nutrients. Maximum biomass concentrations have been found to be a predictable function of the available resources. In most cases, a linear relation or accelerating increase of chlorophyll with nutrients (e.g. Scheffer, 1998) is found. However, such an approach has rarely been used to explore the relationship between solar energy and algal biomass. This may partly be due to the complexity in modelling light availability in aquatic environments

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[spatio-temporal variability of light within the water column, the competition for light with abiotic components (e.g. suspended sediment) and the negative feedback of algal auto-shading].

As with most nutrient/biomass relationships, an increase in available solar energy favours an increase in biomass concentrations in light limited conditions. In the present work, we relate solar irradiance in the mixed layer to algal biomass concentrations to determine an ecosystem specific ratio between available energy and stored energy. This relationship is used to describe real conditions in two disparate algal communities; the phytoplankton community in Lake Victoria, East Africa and the microphytobenthos community in the lacustrine system of Esteros del Iberá (South America).

Methods

Integrated irradiance in the water column

According to the Lambert–Beer law, the irradiance of a single wavelength will be attenuated exponentially in a homogenous medium in relation to the quantity and quality of the attenuating components within the pathlength. Assuming that this is also valid for the entire photosynthetic available radiation wavelength band (PAR waveband, PUV 514, Biospherical Instruments, San Diego, CA, U.S.A.) (only approximately true) and that the overall attenuation can be considered to be the sum of the attenuating components, the total column attenuation coefficient is the sum of the attenuation because of the phytoplankton biomass (ω, mg m^{-3}) and a non-phytoplankton 'background' attenuation (K_{bg} m^{-1}). The resulting equation can be used to determine the solar irradiance at depth 'z' (I_s mol photon m^{-2}day^{-1}).

$$I_s = I_o\, e^{-(k\omega + K_{bg})z} \qquad (1)$$

where k is the specific light attenuation coefficient for phytoplankton (m^2 mg^{-1}) and I_o (mol photon m^{-2} day^{-1}) is the incident solar irradiance just below the surface of the water. By integrating irradiance (eqn 1) over the mixing depth (z_{mix}), the resulting equation for the total column integrated irradiance (Q_t mol photon m^{-2} day^{-1} m) is

$$Q_t = \int_0^{z_{mix}} I_s\, dz = \frac{I_0}{(k\omega + K_{bg})}\left(1 - e^{-(k\omega + K_{bg})z_{mix}}\right) \qquad (2)$$

Note that the column integrated irradiance considers the attenuation because of biomass concentrations, where increasing concentrations reduce the total irradiance available throughout the water column. A similar relationship (without separating attenuation components) is used in Talling's seminal work on integral photosynthesis Talling, 1957a,b as 'light division-hours k_m^{-1}, (kilolumens m^{-2} h^{-1} m).

To determine the total daily exposure for all cells within a perfectly mixed water column, we can utilise the incident irradiance above the water surface and an albedo factor (related to solar declination) to determine the below surface daily irradiance (I_o). Consequently for a water column with a surface area of 1 m^2 (and a known mixing depth), it is possible to estimate the depth-integrated solar irradiance available to the phytoplankton community during a single day. In the same manner, it is possible to integrate the volumetric concentrations of biomass over the mixed depth. The resulting depth integrated biomass ($W = \int_0^{z_{mix}} \omega\, dz$, mg chl *a* m^{-2}) is the most appropriate dimension to relate with the depth integrated solar irradiance.

Steady state light requirements

When a population is at steady state with its limiting resource, the biomass concentrations should exactly balance the resource availability, where a change in the latter will directly modify the former, in a predictable manner. In the present approach, we denominate the relationship between the available irradiance and the light limited algal biomass concentrations as the 'critical light requirement' or the energy necessary to maintain a fixed biomass in equilibrium. The critical light requirement ($\psi = Q_t/W$ mol photon m mg chl a^{-1} day^{-1}) links available energy (no. of photons) to stored biomass in a similar manner as quantum yield, without considering the chemical energy associated to the photosynthetic process.

At first glance, the critical light relationship ($Q_t = W\psi$) would appear to show an unlimited increase in (light limited steady state) biomass with increasing column irradiance (Q_t). However, increases in biomass will increase attenuation ($k\omega$), thereby reducing Q_t. This negative feedback prevents unlimited phytoplankton growth. In the case of phytobenthos, the unlimited increase of biomass with Q_{tb} is inappropriate as the carrying capacity for active layer of phytobenthos reaches a plateau when the bottom is

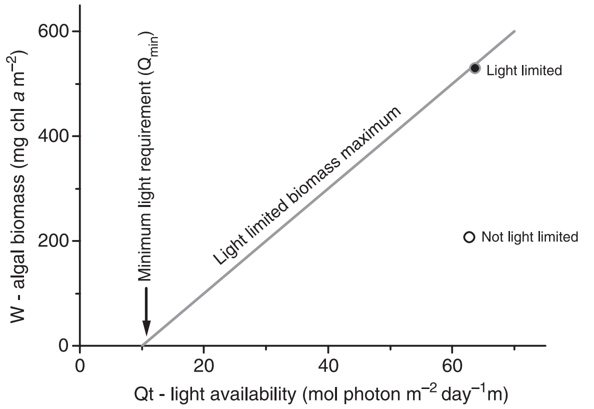

Fig. 1 The relationship between depth integrated irradiance (daily) and algal biomass per unit area (mg chl *a* m^{-2}) in light limiting conditions in a perfectly mixed water column. The slope of the upper limit corresponds to the ratio between energy stored in the ecosystem as biomass and the energy available. The intercept is the minimum light requirement to permit algal biomass ($Q_{\min}$). Sites located on the upper limit are in light limited steady state, while sites located below are limited by another factor or have not reached steady state.

covered, thereby suggesting a logarithmic relationship.

In real ecosystems, light limited conditions are difficult to determine and many sites may be far from steady state or limited by other resources (or grazing). However, if a significant number of sites are examined, those sites which are limited only by light will constitute an upper limit when plotted against available irradiance, while those sites which are limited by other factors will have lower relative concentrations (Fig. 1). This upper limit represents the light limited steady state biomass concentrations or the carrying capacity of the system under different irradiance conditions. Similarly, the x intercept (abscissa) can be considered as the minimum light requirement ($Q_{\min}$ mol photons m^{-2} day^{-1} m) necessary for a positive biomass, making $\psi = (Q_t - Q_{\min})/W$. By solving for the depth integrated biomass (W) and including the full eqn 2 for the integrated daily irradiance Q_t:

$$W = 1/\Psi\left[\frac{I_o}{(k\omega + K_{bg})}(1 - e^{-(k\omega + K_{bg})z_{mix}}) - Q_{\min}\right] \quad (3)$$

In this manner, it is possible to determine an expected biomass concentration on the basis of information on irradiance and water optical conditions. Additionally, applying eqn 3 over a large data set, it is possible to determine where light limitation exists as well as what may result from changes in overall column attenuation or mixing depth.

Estimating community parameters

Having identified biomass concentrations in light-limited conditions, it is then possible to estimate a number of important community variables, in particular the critical depth and the compensation irradiance (Ryther, 1956; Talling, 1957a). Most importantly, these community variables are determined *in situ* or from remotely observed measurements.

Critical depth is defined as the depth at which the column integrated productivity and column integrated loss rates are equal. Following Sverdrup (1953), at light limited steady state biomass concentrations, the depth of the mixed layer will define the critical depth ($z_{\text{mix}} = z_c$). Having identified the critical light requirement (ψ), it is possible to determine the critical depth (z_c) as a function of available irradiance (Q_t), providing interesting information for the *in situ* estimation of productivity and losses (Falkowski & Raven, 1997).

Compensation irradiance is the irradiance at which local net production equals the local loss rate. Assuming that losses are depth independent, compensation irradiance (I_c) can be defined in terms of the critical depth (z_c) as $I_c = I_o/(Kz_c)(1 - e^{-Kz_c})$ where K is the overall attenuation coefficient (Siegel *et al.*, 2002). Separating the attenuation coefficient, one can define the compensation irradiance as:

$$I_c = \frac{I_o}{(k\omega + K_{bg})z_c}(1 - e^{-(k\omega + K_{bg})z_c}) \quad (4)$$

Considering the critical light requirement at a light limited steady state (eqn 3 with $z_{mix} = z_c$), it is possible to define the compensation irradiance in terms of the biomass per area, the critical light requirement and the critical depth as:

$$I_c = (W\psi + Q_{\min})/z_c \quad (5)$$

Having information on the critical light requirement (ψ), it is also possible to determine Huisman & Weissing's critical light intensity (I^*_{out}) (Huisman & Weissing, 1994; Weissing & Huisman 1994; Huisman, 1999). The latter, defined as the column leaving irradiance when total integrated growth and losses are in equilibrium, can be estimated by using the power relationship between the attenuation coefficients and critical depths of those sites found to be light limited.

Field sampling

The present biomass/resource approach was used to explore two extremely different algal communities, the tropical phytoplankton community of the Lake Victoria inshore waters (East Africa) and the subtropical microphytobenthos community of the lacustrine system of Ibera wetland (South America). Three surveys (2002–2004) were performed along the Ugandan and Kenyan coast of Lake Victoria (within 15 km from the coast) for a total of 277 sampling sites covering all major types of inshore areas. In the lacustrine system of Ibera wetland, six sites (mean depth, 2.0 m) were sampled regularly in nine dates during a seasonal cycle (1999–2000). Incident solar PAR was measured 3 m above the water surface (LiCor LI190SZ). Vertical profiles of temperature (Hydrolab Datasonde 4, Hach Company, Loveland, CO, U.S.A.) and solar radiation were measured at each sampling site. Water samples were taken at 0.5 and 1.5 m (only in Ibera). Chlorophyll *a*, total phosphorous, total nitrogen, dissolved organic matter and soluble reactive silicon concentrations were measured. In Ibera wetland, sediment samples (30 cm^2 × 1 cm) from the first centimetres of the lake bottom were measured for chlorophyll *a* concentrations and percentage of organic matter.

Data and sample analysis

Mixing depth was defined graphically by the intersection of trend lines fitted to the thermal profiles, one through the upper part of the epilimnion and the second through the metalimnion (Wetzel, 1975). Chlorophyll *a* concentrations were measured using a calibrated portable fluorometer (Turner Design, Sunnyvale, CA, U.S.A.) in Lake Victoria and using standard spectrophotometric methods in Ibera (Strickland & Parsons, 1972). The vertical light attenuation coefficient (K) was determined using the irradiance profiles in Lake Victoria and indirectly from Secchi disk and chlorophyll *a* concentration measurements in the Ibera wetland (Scheffer, 1998). In the sediment samples, chlorophyll *a* analysis included centrifugation after the pigment extraction in acetone. Nutrient analyses (phosphorus, nitrogen and silicon) were performed through spectrophotometry following standard methods of APHA, American Public Health Association (1992). Dissolved organic matter was estimated using the 272 nm-absorbance of filtered samples (GV Millipore 0.22-μm filter, Millipore S.A., Molsheim, France) and gravimetric calibration (Bracchini *et al.*, 2004).

Results

Light utilisation

The algal concentrations at different solar irradiances for the pelagic environment of Lake Victoria (Fig. 2a) and the benthic ecosystem of the lakes of the Ibera wetland are shown (Fig. 2b). The carrying capacity for each system was derived from points located at the upper limits of the scatterplot, representing the highest

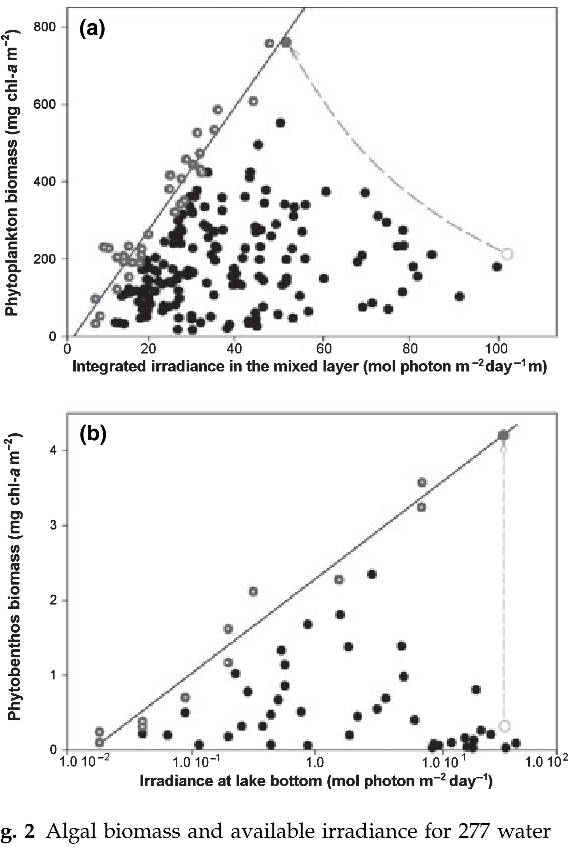

Fig. 2 Algal biomass and available irradiance for 277 water samples obtained in the mixed layer of (a) Lake Victoria and (b) 54 sediment samples in the shallow lakes of the Iberá wetland. The lines were fitted by least-square regression to determine the upper limits for each data set. The distance from the upper limit considers the reduction in available irradiance due to induced attenuation by phytoplankton biomass in the water column.

concentrations measured at specific irradiance conditions. For the tropical phytoplankton community, the critical light requirement was determined to be 0.067 mol photon m day^{-1} mg chl a^{-1} ($R^2 = 0.9224$, $P < 0.001$). For the subtropical microphytobenthos, ψ was found to be 0.016 mol photon m day^{-1} mg chl a^{-1} ($R^2 = 0.9537$, $P < 0.001$). Minimum light requirements were found to be 1.2 and 0.01 mol photon m^{-1} day^{-1}, respectively. As expected, benthic algae showed a higher efficiency and lower minimum light requirement compared with pelagic algae (Carrick, Aldridge & Schelske, 1993).

Many sampling sites in both Lake Victoria and Ibera wetland are located below the light limited biomass maximum (Fig. 2a). This divergence from the upper biomass limit indicates conditions where nutrient limitation or grazing are more important than light limitation. While sites far from the carrying capacity may not necessarily be more nutrient limited, there was a higher probability of finding elevated concentrations of excess nutrients, in particular phosphorus and silica, in those sites in Lake Victoria closest to the upper biomass limit (Fig. 3a). As phytobenthos communities have a direct access to nutrients released by the sediment, we used the percentage of organic matter in the sediment as a general indicator of the available nutrient flux. Once again, the sites further from the carrying capacity showed a lower percentage of organic matter in the sediment (Fig. 3b).

Compensation irradiance

Riley (1957) suggested a community level compensation irradiance of 3.5 mol photon m^{-2} day^{-1} while Siegel *et al.* (2002) reports values from 1.0 to 1.8 mol photon m^{-2} day^{-1} for North Atlantic open waters. Our values for phytoplankton in Lake Victoria ranged from 2.5 to 10 mol photon m^{-2} day^{-1}, with the largest values present in the shallower coastal waters.

The measurements of $I^{*\text{out}}$ were found to be 2.1 (1.6) μ mol photon m^{-2} s^{-1} for Lake Victoria which are similar to those values reported by Huisman (1999) for microcosm experiments using monocultures (1–10 μ mol photon m^{-2} s^{-1}).

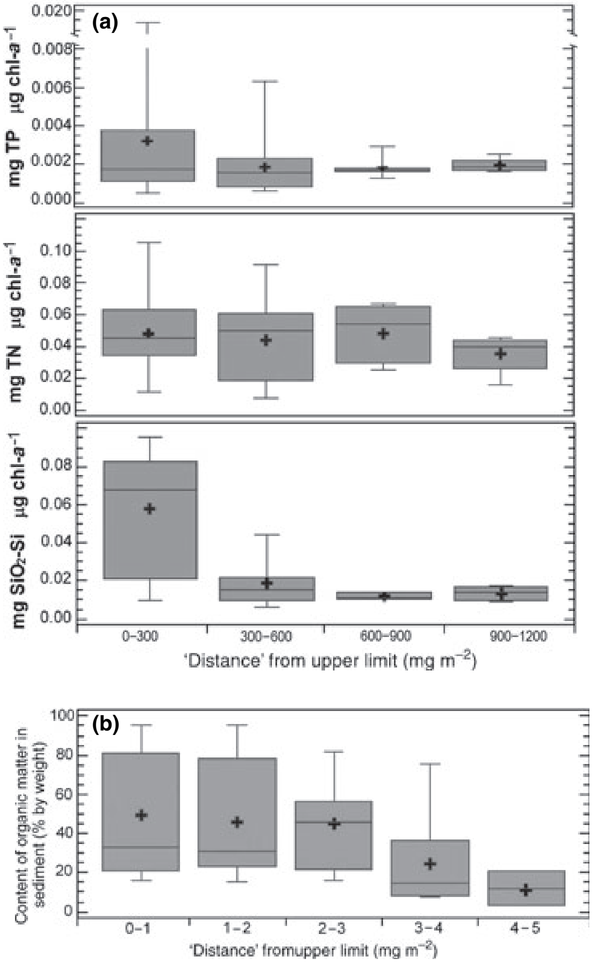

Fig. 3 (a) Concentrations of nutrients in sampling sites located at different 'distances' from the light-controlled upper limit of phytoplankton biomass in Lake Victoria inshore waters. (b) Percentages of organic matter in sediment in sampling sites located at different 'distances' from the light-controlled upper limit of microphytobenthos biomass in lakes of the Ibera wetland. The term 'distances' indicates the difference in biomass per unit area (mg m^{-2}) from upper limit line, as shown in Fig. 2. Distributions in each difference range are represented by Box-and-Whisker plots. Within each plot, the cross delineates arithmetic average, while each box is divided by the statistical median and extends to the quartiles. The lines extend to encompass the farthest points. Silica, phosphorus and organic matter concentrations show a negative trend between lower and higher distances from the upper limit ($P \le 0.10$).

Discussion

This resource based approach presented here provides a new tool for interpreting the impacts of changes in optical and hydrodynamic conditions on algal biomass. It has particular relevance in the understanding the timing and location of algal blooms and their relation to mixing depth, background turbidity and daily irradiance. As mixed layer deepening can lead to catastrophic changes in tropical lakes (Talling, 1966; MacIntyre, Romero & Kling, 2002;

O'Reilly *et al.*, 2003), the use of this approach to explore the potential effects of environmental change on algal biomass can provide new insights into the study of these important ecosystems.

The relationship between available irradiance and biomass concentrations in light limiting conditions is controlled by the hydrological structure (mixing depth) and optical conditions of the water column. Both of these variables change over space and time and are intimately connected to climate and catchment characteristics. Using the critical light intensity (eqn 3), it is possible to relate optical and hydrological conditions of the water column with its expected equilibrium biomass concentrations (*W*).

Waters with a high background attenuation (K_{bg}) will have a lower available irradiance (Q_t) allowing them to support a lower steady state biomass concentration per unit area (*W*) with respect to areas where K_{bg} is less. Critical depth will also be lower as background attenuation creates a reduced energy environment which negatively influences overall productivity. Further reductions in Q_t should correspond to a lower *W* as the system moves to a new steady state along the biomass/resources line.

The depth of the mixed layer directly influences the equilibrium biomass concentrations. When there is a reduction in the mixing depth in a light limited system, initially surplus solar energy becomes available, as the critical depth is greater than the mixed depth ($z_c > z_{mix}$). Subsequently, biomass concentrations (volumetric) will increase, increasing attenuation and reducing the available energy in the water column. This increase in volumetric biomass will continue until a new steady state is reached where critical depth and mixing depth are again balanced (Fig. 4). Note than while volumetric biomass concentrations have increased, biomass concentrations per area (*W*) will be lower (Fig. 5). Conversely, an increase in mixing depth would initially lead to a lower attenuation ($k\omega$) as the biomass becomes more diluted within a larger volume (Reynolds, 1984). The increased Q_t would permit a higher depth integrated biomass (*W*) until new steady state light limiting conditions are achieved. It is important to note that the volumetric biomass (ω, mg chl *a* m^{-3}) at this second steady state will be lower (increased mixing depth clearly does not increase volumetric biomass concentrations) while the depth integrated biomass will be higher. The positive relationship of increasing *W* with increasing mixing depth will continue until background attenuation (K_{bg}) becomes dominant.

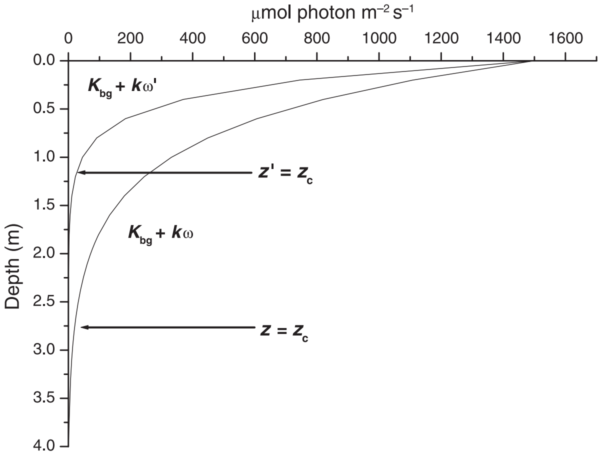

Fig. 4 Irradiance profiles for steady state conditions where mixing depth and critical depth coincide (solid line). Changes in mixing depth from *z* to *z'* lead to conditions where surplus energy is available. As biomass increases in the new mixed layer (*z'*) to utilise this available energy, total attenuation increases until a new light limited biomass (volumetric) concentration (ω') is reached. At this new steady state condition, a new critical depth results (broken line).

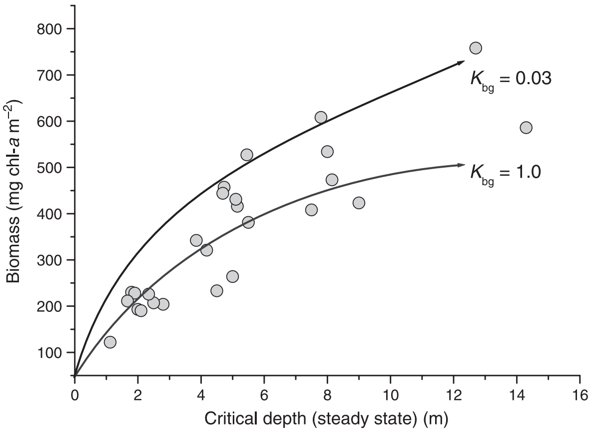

Fig. 5 The relationship between critical depth and phytoplankton biomass at sites where light limitation occurs in Lake Victoria. Critical depth and column integrated phytoplankton biomass (mg chl *a* m^{-2}) show a positive relationship as decreasing mixing depths will lead to a reduction in available depth integrated solar radiation and consequently a lower column integrated biomass at steady state. This relationship will be modified by the background attenuation coefficient (K_{bg}), where higher attenuation will lead to lower steady state biomass concentrations per area.

The present resource based relationship differs from most primary productivity models (Behrenfeld & Falkowski, 1997) in that parameters are determined from a large number of *in situ* data, lessening the need to extrapolate from single species or single station data of photosynthesis–light relationships. Having identified the correlation between biomass and available irradiance (critical light requirement), it is then possible to (i) estimate how changes in hydrodynamics and optical conditions will influence algal biomass concentrations; (ii) delineate areas where biomass concentrations are limited by something other than light; (iii) estimate key community parameters. All three uses of this approach can be made based on data obtained *in situ* or from remote platforms.

Differences in the critical light requirement (ψ) can be utilised to compare the relative efficiency of a specific algal community in its use of available solar energy. While it is an oversimplification to extend this energy based ratio to estimate of photosynthetic fixation, one can convert critical light requirement (mol photon m day^{-1} mg^{-1}) to a minimum quantum requirement (mole photons mole^{-1} of CO_2 converted) at a fixed depth (e.g. 1 m). The results for the Lake Victoria phytoplankton community (16.3 moles photons mole^{-1} CO_2) compare well to estimates determined by Kirk (1994) (10–12 moles photons mole^{-1} CO_2, assuming a daily biomass turnover. As any calculation of conversion efficiency, there will be a variation with depth (resource availability).

It should be noted that the present approach is based on several important assumptions, firstly that optical properties throughout the mixing depth are uniform, secondly that the attenuation of the PAR waveband follows the Lambert–Beer law and thirdly, that all phytoplankton cells present in the mixed layer are exposed to the same daily average irradiance. This final assumption is the most critical and represents the model's main limitation. In clear deep waters, a vertical distribution of phytoplankton is common, leading in most cases to variations in the exposition of phytoplankton cells according to depth. However, in shallow and estuarine ecosystems a complete mixing permits this assumption to be made.

A disadvantage of this approach is that it follows an indirect method to determine community parameters rather than directly measuring production and loss rates. Little insight is gained regarding the processes that determine net productivity. Finally such a method requires a significant number of observations to be able to determine those concentrations which are limited by light.

In many ecosystems, nutrient concentrations are such that they do not limit growth. In fact, the spatial and temporal variations in phytoplankton concentrations are often controlled by the availability of solar irradiance within the mixed layer. In such cases, the optical or hydrological conditions of the aquatic environment will determine the carrying capacity of the ecosystem. Modifications in the concentrations of dissolved organic matter, tripton and phytoplankton will change the energy environment, leading to a new steady state with different biomass concentrations. Changes in the mixing depth, caused by modifications in the water/atmosphere heat exchange and wind conditions as well as changes in water level will have similar effects. In such dynamic conditions, modelling the algal carrying capacity becomes quite challenging. The present approach links available solar irradiance to stored biomass to examine the variability of algal carrying capacity as well as key community parameters. Used with a sufficient number of sampling sites, this approach represents a potentially powerful tool for interpreting ecosystem limits.

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