Nordic Hydrology, 20, 1989, 53-72

The Importance of Phytoplankton Photoadaptation in Influencing Estimates of Integral Photosynthesis

Paper presented at the Nordic Hydrological Conference
(Rovaniemi, Finland, August – 1988)

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The rates of light limited (α^B) and light saturated ($P\max^B$) photosynthesis per unit chlorophyll often showed significant differences between samples collected from the top and the bottom of the mixed layer in Lake Erken (59° 51′ N). The importance of these vertical variations to the photosynthetic rate of the lake as a whole was examined by systematically changing the vertical weighting given to the biomass specific photosynthetic rates associated with each depth, when calculating integral photosynthesis. These simulations, carried out over the 3 month period from July to September of 1987, suggest that vertical variations in rates of biomass specific photosynthesis could account for at most a 24 to 36 percent change in monthly rates of integral photosynthesis. this variance in integral photosynthesis was similar to that which could result from inaccurate estimates of integral biomass, but was less than the measured temporal variability in integral photosynthesis. It was not possible to identify the specific processes responsible for the vertical variations in biomass specific photosynthesis, but evidence does suggest that photoinhibition of the surface phytoplankton was partially responsible, particularly when biomass increased at the surface in the presence of blue-green algae. Simulations which increasingly redistributed the total integral biomass to the upper 1-4 m of the water column suggest that while the upward migration of blue-green algae may lead to enhanced levels of photoinhibition, the effect on integral photosynthesis may be partially offset by increased concentrations of biomass at surface light intensities.

Introduction

Rates of aquatic photosynthesis are a function of light, the total biomass within a body of water, and the rate of photosynthesis per unit of biomass (biomass specific photosynthesis). Since the influx of light to aquatic ecosystems is highly variable in time, it would be desirable to estimate changes in photosynthesis on scales of similar temporal resolution. Unfortunately, measurements of the amount and distribution of biomass, as well as rates of biomass specific photosynthesis are both time comsuming and costly to obtain. When estimating rates of integral water column photosynthesis (*i.e.* mgC m^{-2} d^{-1}), it has therefore been necessary to develop methods which extrapolate less frequent estimates of these biologic variables over the shorter time scales characteristic of measurements of solar radiation. Rates of biomass specific photosynthesis are variable over smaller scales of time and space than can be conveniently described by the sampling and analysis necessary to measure this parameter. Consequently, small scale variability in the rates of biomass specific photosynthesis adds a degree of uncertainty to attempts to estimate rates of integral photosynthesis.

Within a body of water the dimensions of time and space are inseparably linked by the rate of water movement (Harris 1980a). If changes in the rates of biomass specific photosynthesis occur over shorter time scales than those characteristic of diffusion over a given horizontal or vertical scale, spatial variations in this parameter will result (Lewis *et al.* 1984). Thus, one result of short term variations in biomass specific photosynthesis will be the vertical variability of this parameter. The purpose of this paper is to estimate the variance in integral photosynthesis which results from vertical differences in biomass specific photosynthesis, and to compare this variability in integral photosynthesis to that occurring through time, or that which might result from changes in either the total amount or vertical distribution of algal biomass.

Changes in biomass specific photosynthesis from a variety of processes which can be collectively grouped under the heading of photoadaptation. Common to all photoadaptive processes is that they are initiated by changes in the phytoplanktons *in situ* light climate that remain constant over the time scales necessary for changes in biomass specific photosynthesis to occur. Photoadaptive processes occur over a range of time scales (Harris 1980a, Falkowski 1984, Lewis *et al.* 1984), with processes ranging from rapid (minute to hourly) photoinhibitory reductions brought about by changes in electron transport and chloroplast structure, to longer term (hourly to daily) changes brought about by changes in factors such as photosynthetic pigment concentration or intercellular chemistry, and finally to successional changes (daily to monthly) brought about by species specific variations in biomass specific photosynthesis.

The influence of photoadaptation on biomass specific rates of photosynthesis is related to both the process involved, and the time scale of the process relative to

time scale of hydrodynamic variability (Lewis *et al.* 1984, Cullen and Lewis 1988). For example, exposure to high light intensities near the waters surface can lead to rapid photoinhibition and declines in photosynthesis over relatively short time periods. As a result, investigations of this process (Neal and Richerson 1987, Elser and Kimmel 1985, Vincent *et al.* 1984) have concluded that increases in the rate of surface mixing will generally increase the rates of integral water column photosynthesis by limiting the effects of photoinhibitory light exposure. On longer time scales, thermal stratification of the water column leads to a more stable and heterogeneous hydrodynamic environment in which reduced rates of vertical mixing permits photoadaptation to the prevailing light intensities within relatively stable portions of the seasonal "mixed" layer. Such photoadaptation leads to the so called shade adaptation, and eventually to species differentiation in areas such as that above a deep seasonal thermocline where the influences of surface induced vertical mixing will be limited to periods of relatively high winds. Therefore, over greater scales of time and space, studies such as that by Tilzer and Goldman (1978) have reported that algal photoadaptation during stratified conditions leads to more effective utilization of the available light and enhanced rates of integral photosynthesis.

To determine rates of biomass specific photosynthesis a single water sample is incubated over a range of light intensities and the measured rates of photosynthesis fit to an impirical relationship between light intensity and the rate of photosynthesis. For this purpose I have used the equation suggested by Jassby and Platt (1976).

$$P^B(I) = P^B_{max} \tanh(\alpha^B I / P^B_{max}) + R^B \quad (1)$$

where

- P^B = biomass specific photosynthesis ($mgC(mgChl)^{-1} h^{-1}$)
- I – light intensity ($\mu Em^{-2}s^{-1}$)
- P^B_{max} = the rate of light saturated biomass specific photosynthesis ($mgC(mgChl)^{-1} h^{-1}$)
- α^B – the rate of light limited biomass specific photosynthesis ($mgC(mgChl)^{-1} E^{-1} m^2$) or the slope of the initial linear portion of the curve
- R^B – the Y intercept of the equation which in theory should represent the phytoplanktons dark respiration. In practice this was small and could not be determined with good accuracy

The form of this relationship is illustrated by Fig. 1. Using data such as in Fig. 1, rates of light limited (α^B) and light saturated ($Pmax^B$) photosynthesis can be estimated (Gallegos and Platt 1981), allowing actual rates of biomass specific photosynthesis (P^B) to be estimated from measurements of light intensity.

During the summer of 1987 a series of algal biomass and biomass specific photo-

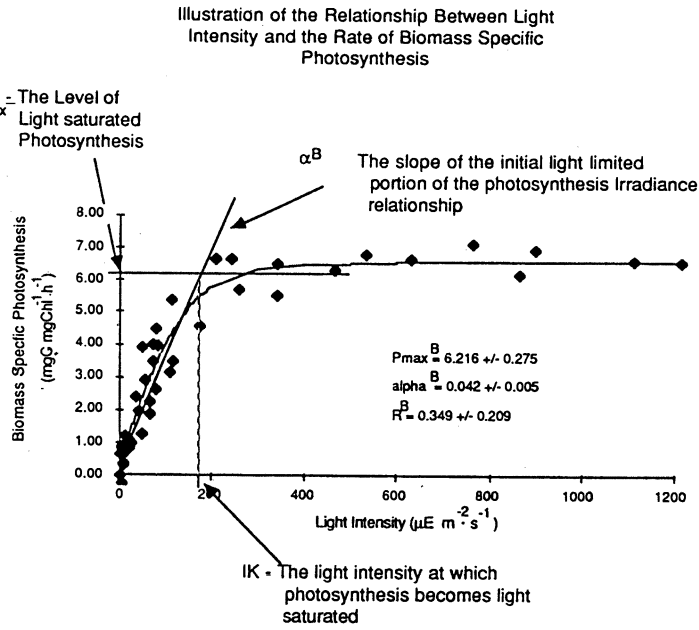

Fig. 1. An example of the relationship between biomass specific photosynthesis and light intensity. The curved line in this figure is calculated from Eq. (1), after the values of $P\max^B$, α^B and R^B have been optimized to minimize the squares of the residuals between predicted and measured rates of photosynthesis. IK is the light intensity at which photosynthesis first becomes light saturated, and is calculated as the quotient of $P\max^B$ divided by α^B

synthesis measurements were obtained from Lake Erken, a mesotrophic lake located in central Sweden. The lake has a surface area of 23.7 km^2, a mean depth of 9 m and a maximum depth of 21 m. A detailed description of the lake can be found in Håkanson (1978) and Nauwerck (1963). Measured values of $P\max^B$, α^B, and chlorophyll *a* obtained from the top and bottom of the seasonal mixed layer (Fig. 2), often showed significant variations with depth. When vertical differences in the photosynthetic parameters $P\max^B$ and α^B exist, they may result from any of the previously described processes of photoadaptation, and it is impossible to say which, if either of the two depths in Fig. 2 are representative of the water column as a whole.

In order to examine the potential effect of vertical variations in rates of biomass specific photosynthesis on estimates of intergral photosynthesis, I have run a number of simulations in which the vertical weighting of the top and bottom measurements of $P\max^B$ and α^B (Fig. 2) were varied in the equations used to estimate integral photosynthesis as will be described in the following section. This was done to gain maximum estimates of the changes in integral photosynthesis

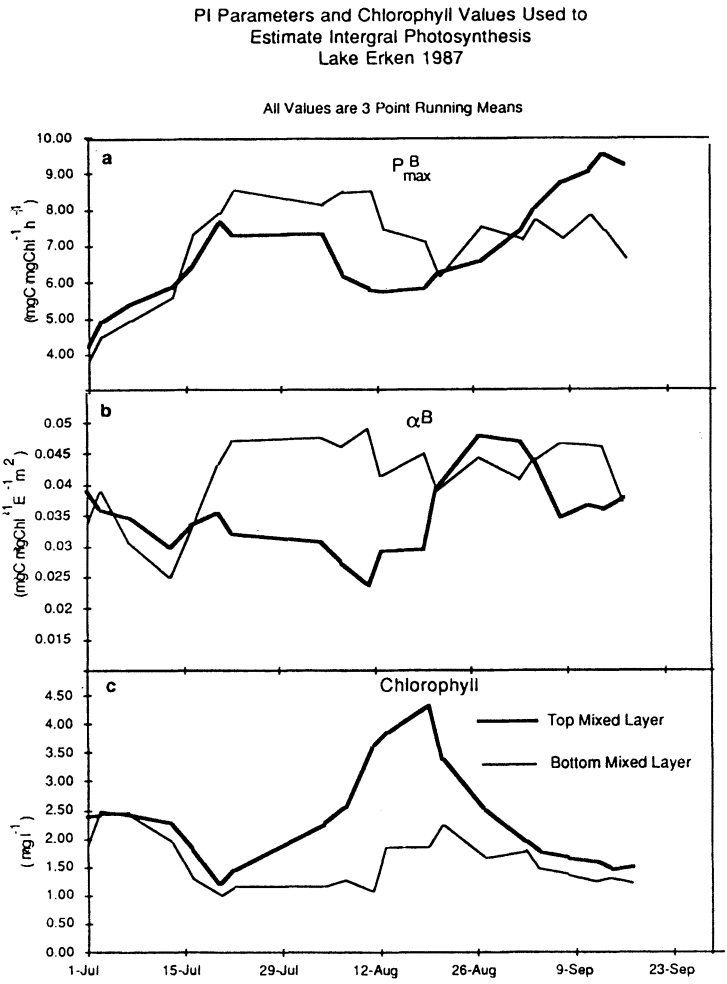

Fig. 2. The values of $Pmax^B$, α^B, and chlorophyll used to estimate rates of integral photosynthesis. All data shown here have been smoothed through time by use of a 3 point running mean. Values of R^B are not shown since they were usually not statistically different from zero, and showed no seasonal or vertical trends.

which could result from vertical variability in rates of biomass specific photosynthesis. The magnitude of these estimated variations in integral photosynthesis are compared with:

- Changes in the rates of integral photosynthesis which occurred through time as a result of the measured temporal changes in biomass, biomass specific photosynthesis and light.

- Changes in the rates of integral photosynthesis which were simulated by redistributing the same total integral chlorophyll *a* so that progressively greater quantities of the chlorophyll *a* were in the upper metres of the water column.
- Changes in the rates of integral photosynthesis which were simulated by increasing the total integral water column chlorophyll *a* concentration. Increases in integral chlorophyll *a* were made in a manner which might result from inaccurate calculations based on an inadequate description of the vertical distribution of chlorophyll *a*.

These comparisons allow the relative importance of vertical variations in biomass specific photosynthesis in influencing rates of integral photosynthesis to be accessed, and will aid in future decisions regarding the temporal and spatial sampling resolution needed to accurately estimate rates of integral photosynthesis. The manipulations made in these comparisons are not however, truly representative of the changes that would occur in nature. For example, it is impossible to simply increase algal biomass without concurrent changes in species composition, which would probably also lead to changes in the rates of biomass specific photosynthesis. It is best that the results presented here be viewed as a simple analysis of the errors which may result from inaccurate measurements of the parameters used to estimate rates of integral photosynthesis.

Methods

Photosynthesis *vs* irradiance (*PI*) relationships were obtained by incubating a single ^{14}C enriched lake water sample at a large number of light intensities using the short term (20 min) photosynthetron (PSTRON) incubation method of Lewis and Smith (1983). Samples were enriched with ^{14}C (as sodium bicarbonate) to give a final sample concentration of 0.5-1.0 μCi ml^{-1}. In addition to 43 light exposed 5 ml PSTRON aliquots, 6 blanks were obtained by immediately poisoning 5 ml aliquots with 100 μl of formalin, and 3 total count samples were obtained by directly injecting 20 μl of enriched sample into 10 ml of counting cocktail containing 200 μl of 2-phenoletheylamine. Sample collection was carefully carried out to minimize light shock to the phytoplankton. Samples were collected with an opaque Van Dorn bottle and then transferred to opaque acid washed plastic bottles. In the lab, samples were processed in dim light immediately after returning from the field. Experience has shown it to be practical to begin a PSTRON incubation (lights on) within 20-30 min after a sample is removed from the lake. Alkalinity was determined by titration (APHA 1975), and these values were converted to total dissolved inorganic carbon concentrations using the equation of Gächter *et al.* (1984).

The *in vivo* fluorescence of chlorophyll *a* was measured using a Turner 111 fluorometer, after samples had been dark adapted for a period of 10-30 min.

Fluorescence first was measured for untreated water (F) and then measured again (F_D) after the addition of DCMU [3-(3,4-dichlorophenyl)-1,1-diemethylurea] added in an ethanol solution to give a final concentration of 10^{-5} M. These two measurements of chlorophyll *a* fluorescence were then expressed as a ratio of the relative fluorescence increase after the addition of DCMU [$(FD\text{-}F)/FD$] (Öquist *et al.* 1982).

To determine the waters chlorophyll *a* concentration, samples were filtered onto Whatman GFF glass fiber filters and immediately extracted in 10 ml. of 90 % acetone. After an extraction of 24-36 hours in the dark and at 4°C, the chlorophyll *a* concentration in the extract was measured fluorometrically according to the methods given in Strickland and Parsons (1972). Experiments have shown that grinding of the filters did not significantly increase the measured chlorophyll *a*.

Estimation of Integral Photosynthesis

Total incoming solar radiation (300-3,000 nm) was measured using an Epply pyranometer which was calibrated against an Ångströms pyrheliometer at the Swedish Agricultural University, Ultuna, Sweden. These data (watts m^{-2}) were subsequently converted to photosynthetically active radiation (PAR), using the conversion factors of Tilzer (1983). PAR is defined as the radiation between 400 and 700 nm, and is measured in quanta $m^{-2}\,s^{-1}$. The vertical extinction of PAR through the water column was measured using an Li-Cor underwater photometer and PAR quantum sensor. The average surface light intensity during profile measurement was estimated from a regression of the log of irradiance *vs* depth, and an extinction coefficient was then calculated by substituting the estimated surface irradiance (I_0) and a measured sub surface irradiance (I_z) into Eq. (2).

$$I_z = I_0 e^{-kz} \tag{2}$$

where

k – the vertical attenuation coefficient for radiation (m^{-1})
I_0 – surface light intensity
I_z – light intensity at depth z

A final value for the extinction coefficient was calculated as the mean of the extinction coefficients obtained from $I_z$measurements, made at one metre intervals, between 2 and 9 m (Wetzel 1983). Using Eq. (1) and hourly averages of surface light intensity (I_0) hourly underwater irradiance fields were estimated between 0 and 8 m (usually $I_8 < 1\,\% \; I_0$) at a depth interval of 0.5 m. The values of the extinction coefficents used to estimate underwater light were changed half way through the time between measurements of underwater light profiles, which were made at 5-10 day intervals.

To measure rates of biomass specific photosynthesis samples were collected twice weekly from the top and the bottom of the seasonal mixed layer from 1 July

to 17 September, except during the interval from 23 July to 3 August when analytical difficulties prevented accurate estimates of ^{14}C uptake. For each individual water sample the rates of photosynthesis per chlorophyll *a* measured by the PSTRON incubations were fit to the impirical *PI* relationship (Eq. (1)) using a non linear estimation procedure (SAS Institute 1985). Minimizing the squares of the residuals allowed optimized estimates of P^Bmax, α^B, *and* R^B (*PI* parameters) to be obtained.

The measured vertical variability in the *PI* parameters should adequately reflect that which results from photoadaptive processes operating over similar or longer time scales than the twice weekly sampling frequency used here. Namely, those resulting from inter-species changes in physiology that occur over the time scale of cell division, or longer term changes that occur as a result of changes in species composition. Photoadaptive processes operating over shorter time scales, such as photoinhibition or those leading to diurnal variations in photosynthesis (*e.g.* MacCaull and Platt 1977, Rivkin and Putt 1988), may have a relatively noisy signal due to an inadequate sampling frequency relative to that of photoadaptive variability. This noise could either underestimate or overestimate actual vertical variability in biomass specific photosynthesis as a result of sample aliasing which may occur under such a situation (see Fig. 2 in Legendre and Demers (1984) for an illustration of aliasing). To reduce this noise the *PI* parameters and chlorophyll *a* concentrations have been smoothed through time using a three point running mean, and all calculations of integral photosynthesis made in this paper are based on the smoothed data. Given the temporal limitations of the data, the running means may best represent the longer term (1-2 weeks) trends in vertical variability of the *PI* parameters, which result from photoadaptive processes operating over all time scales.

Using estimated values of the *PI* parameters, it is possible to estimate hourly profiles of the rates of biomass specific photosynthesis (P^B) by entering individual values of I_z(estimated from (Eq. 2) into Eq. (1)). To calculate rates of integral photosynthesis the vertical values of biomass specific photosynthesis (P^B) occurring at light intensity (I_z) were multiplied by the chlorophyll *a* concentration at that depth (B_z) and the results were then summed over the 8 m depth used in these simulations, as shown by Eq. (3). As with the extinction coefficient data, the *PI* parameters and chlorophyll *a* concentrations were changed half way through the time interval between sampling dates.

$$P = \sum_{z=i}^{j} P^B_z \, B_z i \qquad (3)$$

where

P – integral water column photosynthesis (mgC m^{-2} h^{-1})
P^B_z – estimated biomass specific photosynthesis (mgC(mgChl)$^{-1}$ h^{-1})at depth

z, calculated from Eq. (1)
B_z – the chlorophyll *a* concentration at depth z ((mgChl)m^{-3})
j – the maximum depth to which calculations were made. In this case 8 m
i – the depth interval for the calculations in this case 0.5 m

This method of simulating rates of integral photosynthesis is essentially the same as that described by Fee (1973) except a different empirical expression (Eq. (1)), has been used to describe the photosynthesis *vs* irradiance relationship.

The importance of vertical variations in the *PI* parameters in affecting estimates of integral photosynthesis was estimated when calculating the hourly profiles of biomass specific photosynthesis. This was accomplished by varying the depth to which the *PI* parameters associated with the top and bottom samples were used, when substituting these parameters into Eq. (1). Since the measured vertical differences in the *PI* parameters could result from any of a number of photoadaptive processes, which characteristically occur at different depths, it was impossible to determine the depth to which either sample should be used to provide a accurate representation of the actual vertical variability in biomass specific photosynthesis. It was therefore, felt best to estimate the maximum variability in integral photosynthesis which could result from vertical variations in the *PI* parameters. To do so, all possible one metre interval combinations of top and bottom *PI* parameters were considered: *i.e.* top not used, bottom used 0-8 m; top used 0-1 m, bottom used 1-8 m ... top used 0-8 m, bottom not used. So that only the effects of varying vertical distributions of the *PI* parameters would influence the resulting estimates of integral photosynthesis. All chlorophyll *a* concentrations (B_z) used in these simulations were set to the mean of the top and bottom samples.

The effect of redistributing the biomass within the water column, while holding the total water column biomass constant was investigated as illustrated by Fig. 3a. For these simulations the total integral biomass was set to the mean of the top and bottom concentrations integrated over the 8 m depth, as was the case for the first set of simulations described above. The water column chlorophyll *a* was then redistributed so that the surface concentrations (Fig. 2) were used to a progressively greater depth, while the lower concentrations were progressively reduced so that the integral biomass remained constant. This simulation would be analogous to the upward migration of buoyant bluegreen algae during periods of low vertical mixing; a phenomenon often observed in Lake Erken during the summer. To simulate the effects of increasing concentrations of integral chlorophyll *a* on estimates of integral photosynthesis, the top chlorophyll *a* concentration was progressively used to greater depths in Eq. (3) as shown by Fig. 3b. Such a simulation is representative of the types of errors which may result from inaccurate estimates of integral biomass. Unlike biomass specific photosynthesis, the vertical variability in chlorophyll *a* could be clearly associated with a particular process; the accumulation of buoyant algae at the lake surface. It was therefore possible to limit the range

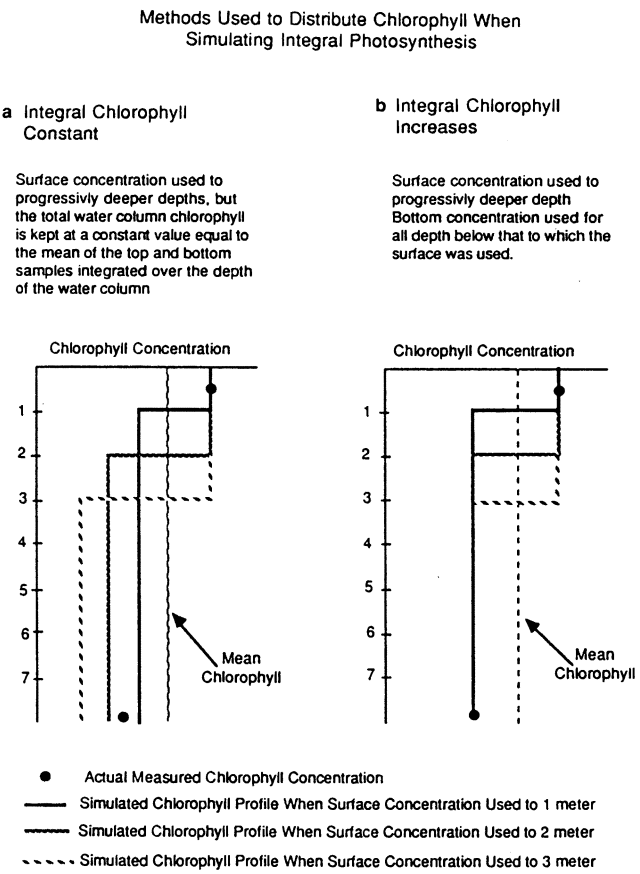

Fig. 3. Graphical representation of the methods by which chlorophyll was vertically distributed when estimating integral photosynthesis in the second and third of simulations. For the first set of simulations the mean chlorophyll concentration was used at all depths.

of depths over which chlorophyll *a* simulations were made, so that the depth to which the surface concentrations were used in Eq. (3) was varied between 1 and 4 m. It would have been clearly unrealistic to use the surface chlorophyll *a* concentrations to greater depths. The difference between these two methods of varying the chlorophyll *a* concentrations is that in the second method (Fig. 3b) the integral biomass is allowed to increase, while in the first (Fig. 3a) the integral biomass is held constant by reducing the chlorophyll *a* concentrations below the depth to which the top samples concentration is used. For all chlorophyll *a* simulations the *PI* parameters were set to the mean of the values estimated for the top and bottom samples.

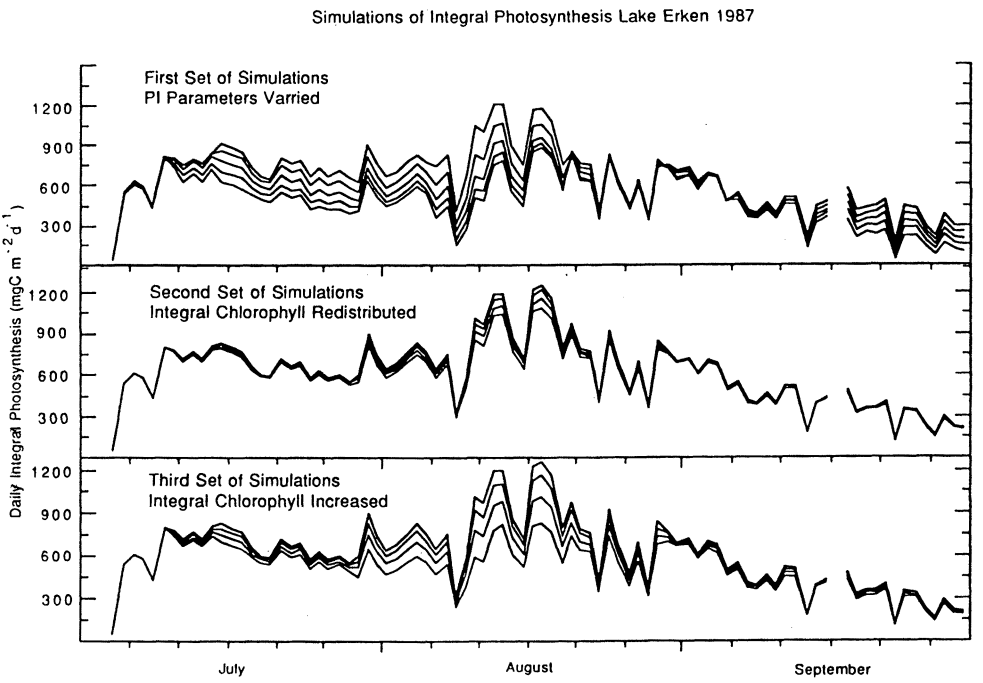

Fig. 4. Daily rates of integral photosynthesis calculated for the 3 sets of simulations. These data allow the variance associated with the different simulations, as represented by the differences between the lines, to be compared with the estimated temporal changes in integral photosynthesis. For the first set of simulations only runs 1,3,5,7, and 9 are plotted. The gap in the data during mid September is the result of missing light data.

Results and Discussion

All simulated rates of daily integral photosynthesis are summarized in Table 1, and selected runs from each set of simulations are plotted in Fig. 4. The first set of simulations (runs 1-9 Table 1) examined the effect that vertical variability in biomass specific photosynthesis might have on estimates of integral photosynthesis. They show that differences in the vertical stratification of the *PI* parameters could cause maximum monthly variations in estimates of integral photosynthesis of 24 to 36 percent. During July and August the simulated integral photosynthesis decreased as the top *PI* parameters were used to greater depths when calculating integral photosynthesis, while in September the opposite trend occurred. Some indication of the processes responsible for the vertical variability in biomass specific photosynthesis may be gained by examining the direction of these changes in simulated integral photosynthesis.

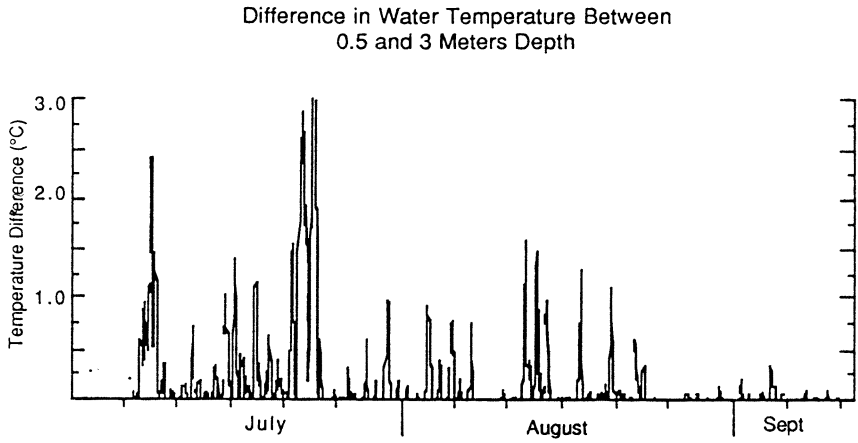

Fig. 5. Measured difference in water temperature between the depths of 0.5 and 3.0 m. From the first week in July water temperatures were recorded at 30 minute intervals.

During July and August the lake was thermally stratified, and some degree of thermal stratification was often noticeable within the upper 3 m of the water column (Fig. 5). This suggests that relatively low rates of vertical mixing in the upper water column when combined with sufficiently high surface light intensities, led to the photoinhibition of the surface phytoplankton. It therefore, seems reasonable to largely attribute the relatively low surface values of α^B and $P\max^B$ to the effects of photoinhibition. Naturally, if the surface phytoplankton were photoinhibited, giving these data increasing weight in the calculation of integral photosynthesis would decrease the final values obtained.

The lake lost all thermal stratification and completely mixed during the first days of September, after which any thermal stratification which occurred was weak and present only episodically at the waters surface (Fig. 5). Under such conditions it is unlikely that effects of photoinhibition would be noticeable at the surface water. The fact that the surface *PI* parameters now increased relative to the those at the bottom of the mixed layer (now taken as an arbitrary depth of 16 m), certainly suggests this was the case. The relative increase in the surface *PI* parameters probably results from vertical differences in the physiology and species composition which resulted from successional changes in the phytoplankton community at this time. In Fig. 6 the ratio $(F_D\text{-}F)/F_D$ is plotted for the top and bottom samples as

Table 1 – Estimates of integral photosynthesis. See text for a description of the different simulations. Rates of integral photosynthesis are expressed as monthly means of the rates calculated over a daily time span. The simulated variability is also shown by the percent change between the first run and each subsequent run in a given set of simulations.

First Set of Simulations
Vertical Stratification of PI Parameters Changed

Simulation Run	Depth Top PI Used to	July Mean Daily Integral Photosynthesis ($mgC \cdot m^{-2} \cdot d^{-1}$)	August Mean Daily Integral Photosynthesis ($mgC \cdot m^{-2} \cdot d^{-1}$)	September Mean Daily Integral Photosynthesis ($mgC \cdot m^{-2} \cdot d^{-1}$)	July Percent Change From Run 1	August Percent Change From Run 1	September Percent Change From Run 1
1	0	705.7	781.2	325.0			
2	1	691.1	741.7	343.3	-2.1	-5.1	5.6
3	2	672.5	704.9	358.8	-4.7	-9.8	10.4
4	3	650.0	673.4	372.5	-7.9	-13.8	14.6
5	4	625.7	648.9	386.0	-11.3	-16.9	18.8
6	5	601.7	630.1	399.8	-14.7	-19.3	23.0
7	6	578.3	614.8	413.9	-18.1	-21.3	27.4
8	7	556.4	601.5	428.4	-21.2	-23.0	31.8
9	8	534.5	589.2	442.9	-24.3	-24.6	36.3

Second Set of Simulations
Chlorophyll Redistributed to the Upper Water Column – Integral Chlorophyll Constant

Simulation Run	Depth Top Chlorophyll Used To	July Mean Daily Integral Photosynthesis	August Mean Daily Integral Photosynthesis	September Mean Daily Integral Photosynthesis	July Percent Change From Run 10	August Percent Change From Run 10	September Percent Change From Run 10
10	1	630.7	720.9	390.4			
11	2	639.9	753.4	395.6	1.5	4.5	1.3
12	3	648.3	780.7	400.0	2.8	8.3	2.5
13	4	655.0	800.5	403.2	3.9	11.0	3.3

Third Set of Simulations
Integral Chlorophyll Increased

Simulation Run	Depth Top Chlorophyll Used To	July Mean Daily Integral Photosynthesis	August Mean Daily Integral Photosynthesis	September Mean Daily Integral Photosynthesis	July Percent Change From Run 14	August Percent Change From Run 14	September Percent Change From Run 14
14	1	584.1	586.0	367.2			
15	2	613.5	679.7	382.8	5.0	16.0	4.2
16	3	637.2	750.7	394.6	9.1	28.1	7.5
17	4	655.0	800.5	403.2	12.1	36.6	9.8

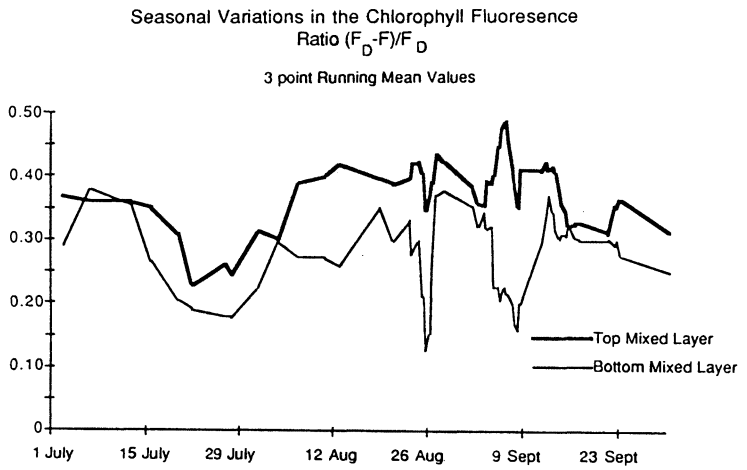

Fig. 6. Measurements of the relative increase in chlorophyll fluorescence after the addition of DCMU. The vertical differences in this figure could only occur if phytoplankton populations were physiologically different at the two depths, indicating the seasonal mixed layer was rarely well mixed from top to bottom. This parameter which was determined more frequently than those used to simulate integral photosynthesis. The pronounced declines in the bottom fluorescence ratio in late August and early September are probably the result of the accumulation of senescent phytoplankton from the declining surface population.

was done for the *PI* parameters and chlorophyl *a* in Fig. 2. During September this ratio showed two dramatic declines at the bottom of the mixed layer. Changes in the fluorescene ratio, which have been suggested to be a relative indicator of photosynthetic capacity (Samuelsson and Öquist 1977), can result from a variety of factors such as changes in the growth and nutrient limitation of the phytoplankton, or rapid photoinhibitory effects which are closely linked to light exposure at the surface (Roy and Legendre 1979, Harris 1980b). In this case, the declines in DCMU induced fluorescence at the bottom of the mixed layer, which corresponded to the decline in surface chlorophyll *a*, seems to indicate that the relative reduction in the bottom *PI* parameters was a result of the accumulation of a senescent population of phytoplankton, which was sinking out of the upper water column. The fact that increasing the weight of the upper samples *PI* parameters increased calculated integral photosynthesis during September therefore, results from reductions in the bottom *PI* parameters caused by the accumulation of senescent phytoplankton.

During late July and August populations of buoyant bluegreen algae often accumulated in the upper metres of the water column as indicated by the high surface chlorophyll *a* concentrations in Fig. 2. This seems to have enhanced the relative decline in the surface values of $P\max^B$ and α^B but may have also led to a

compensating situation where decreases in integral photosynthesis brought about by photoinhibition of the surface phytoplankton were offset by increases in biomass at the higher irradiances. To test this possibility, a second set of simulations (runs 10-13 Table 1) were made which increased the proportion of biomass in the upper water column in a manner analogous to the vertical migration of a motile species of phytoplankton (Fig. 3a). The results of these simulations showed maximum increases in integral photosynthesis of 11 percent during August when the contrast between top and bottom chlorophyll *a* was greatest. As a result, it can be concluded that the decreases in integral photosynthesis caused by reductions in biomass specific photosynthesis in the upper water column, could be partially offset by simultaneous increases in the concentrations of the apparently photoinhibited phytoplankton.

Two qualifications should be made regarding the above simulations. First, the simulations did not reduce the light penetration to the lower water column as would result from the greater concentrations of biomass at the surface. This would have the effect of slightly overestimating integral photosynthesis. However, concentrations of surface biomass (Fig. 2) were not so high as to cause appreciable self shading. Secondly, for increases in surface biomass to be effective in increasing integral photosynthesis, the biomass moving to the surface must come from a light level below *IK* (Fig. 1), so that photosynthesis was not already light saturated. Values of *IK* generally ranged between 200-300 $\mu E\ m^{-2}\ s^{-1}$, which would make biomass specific photosynthesis light saturated to a depth of approximately 3-4 m during cloud free mid-day periods. This suggests that in increases in integral photosynthesis brought about by the redistribution of biomass to the upper water column are greatly constrained by the light saturated nature of the photosynthesis irradiance relationship. During periods of high surface light, nearly 50 percent of the photic zone is already light saturated. Under these conditions only the upward movement of biomass from the bottom half of the photic zone will have any effect on integral photosynthesis. The 15 percent increase in integral photosynthesis simulated by the upward redistribution of biomass was therefore largely the result of photosynthesis occurring during periods of lower surface light intensities, when photosynthesis would be light saturated to shallower depths. This is illustrated in Fig. 7 where the rate of daily integral photosynthesis (run 13 Table 1) has been divided by total daily light to yield overall estimate of the efficiency of integral photosynthesis. Examination of these data show that greater amounts of carbon were fixed per mole of PAR when the daily PAR influx was lowest.

The final set of simulations (runs 14-17 Table 1) were done to examine the sensitivity of estimates of integral photosynthesis to changes in integral chlorophyll *a*. The purpose of these simulations was to illustrate the magnitude of errors which could occur when attempting to estimate integral photosynthesis using chlorophyll *a* data of limited vertical resolution. In these simulations the total integral chlorophyll *a* was allowed to increase by progressively using the surface chlorophyll

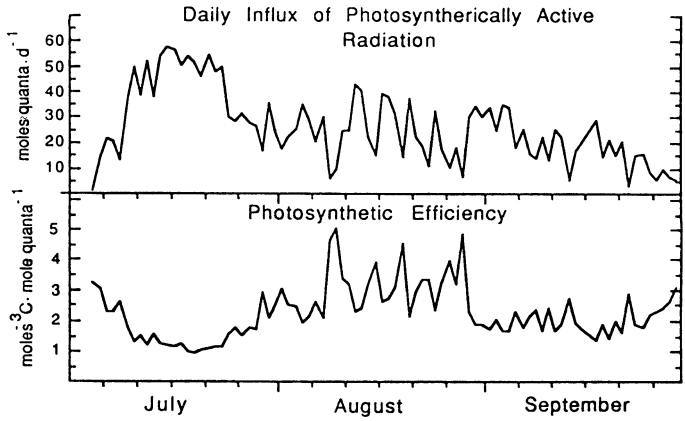

Fig. 7. Total daily PAR influx (moles quanta $m^{-2} d^{-1}$), and the ratio of daily integral photosynthesis ($moles^{-3}(m^{-2} d^{-1})$) divided by the PAR influx. This ratio shows changes in the relative amount of carbon fixed per mole of quanta, and therefore can be seen as a measure of the efficiency of photosynthesis. The values of daily integral photosynthesis used are from simulation run 13. Photosynthetic rates were converted to molar units so that a dimensionless ratio would result.

a concentrations to deeper depths in Eq. (3), as illustrated by Fig. 3b. Consequently, integral chlorophyll *a* was sensitive to the differences in the chlorophyll *a* concentrations between the two depths. These simulations showed integral photosynthesis could increase by up to 36 percent depending on the weighting given to the surface chlorophyll *a* data (Table 1). These simulations suggest that effort should be spent on obtaining accurate estimates of the vertical distribution of chlorophyll *a*, particularly when buoyant bluegreen species are present.

Conclusions

Vertical differences in the rates of biomass specific photosynthesis were a common occurrence in Lake Erken, particularly under periods of thermal stratification when there were large vertical differences in chlorophyll *a* concentration. Estimates of the variance in integral photosynthesis which could result from hypothetical differences in the vertical distribution of the measured photosynthetic parameters α^B and $P\max^B$, suggests that vertical variations in the rates of biomass specific photosynthesis could have a significant impact on estimates of integral photosynthesis. Calculations made on a monthly basis, found maximum estimates of the variance in integral photosynthesis, attributable to vertical variations in biomass specific photosynthesis, to range between 24 and 36 percent of mean daily integral

photosynthesis. This variance is similar to that which might occur as a result of inaccurate estimates of integral chlorophyll *a*. The variance in integral photosynthesis, derived from vertical variations in biomass or rates of biomass specific photosynthesis, was not however as great as that occurring through time as a result of temporal changes in these biologic factors and incoming light. Daily rates of integral photosynthesis commonly varied by as much as 50 percent over periods of 1-2 weeks (Fig 4).

The potential variability in integral photosynthesis brought about by variations in integral chlorophyll *a* were more easily constrained to certain periods in time, since variability in estimates of integral chlorophyl *a* were attributable to a single process; the upward migration of bluegreen algae. In the case of biomass specific photosynthesis, evidence suggests that vertical differences in this parameter were the result of a number of different photoadaptive processes operating at different depths in the water column, and over different scales of time. The variability in integral photosynthesis simulated as resulting from vertical variations in biomass specific photosynthesis was temporally more persistent than that associated with differences in integral chlorophyll *a* (Table 1 Fig. 4). This was partly a result of the rates of biomass specific photosynthesis showing greater vertical variations over longer periods of time than was the case for chlorophyll *a* (Fig. 2), but also results from an inability to restrict the differences in biomass specific photosynthesis shown in Fig. 2 to certain portions of the water column. For example, the greatest vertical differences in biomass specific photosynthesis occurred between Mid-July and Late-August. During this time, frequently measured temperature differences (Fig. 5) in the upper water column, suggest that rates of vertical mixing were low, and that the depressed surface values of $P\max^B$ and α^B were largely the result of photoinhibition. If this were so, estimates of the variance in integral photosynthesis could be substantially reduced by using the surface *PI* parameters only in the upper portion of the water column when calculating rates of integral photosynthesis. Effort would therefore, be well spent on identifying the specific processes leading to vertical variations in biomass specific photosynthesis, and in quantifying the relative contribution of each process to total vertical variations such as those shown in Fig. 2. This would allow both more realistic estimates of the variance associated with calculations of integral photosynthesis to be made, and would also identify the time scales which estimation procedures must be able to resolve in order to reduce the variance associated with different photoadaptive processes.

Acknowledgements

Thomas Hellström made many valuable suggestions, particularly regarding the methods used to calculate integral photosynthesis. I also thank Kurt Pettersson, Ulf Lindqvist, and Björn Mattsson of the Erken Laboratory for assistance with the

field and laboratory work. The comments of an anonymous reviewer led to substantial improvements in the original manuscript.

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Received: 13 February, 1989

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