Donald C. Pierson

Effects of Vertical Mixing on Phytoplankton Photosynthesis and Phosphorus Deficiency
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Doctoral dissertation to be publicly examined in Lecture Hall 1022 Trädgårdsgatan 18, Uppsala, on 7 December 1990 at 10:15 A.M., for the Degree of Doctor of Philosophy. Professor Egil Sakshaug, University of Trondheim, Norway will be the external examiner approved by the Faculty. The discussion will be held in English.

Abstract

Variability in the frequency and depth of vertical mixing influences the productivity of aquatic ecosystems by regulating the availability of light and nutrients. Several specific effects of vertical mixing on rates of algal photosynthesis and phosphorus deficiency are investigated in this thesis. Measurements made during summer stratification in Lake Erken (central Sweden) show vertical variations in light limited (aL) and light saturated (Fm,max) photosynthesis per unit of chlorophyll a. Depressed photosynthesis in the upper water column is attributed to photoinhibition, and variations in species composition caused by the vertical migration of buoyant blue-green algae, processes which can only occur in the absence of rigorous vertical mixing. Simulations examining the importance of vertical variations in biomass specific photosynthesis suggest a relatively small effect on areal photosynthesis. Maximum variations in monthly rates of areal photosynthesis of 24-36 percent were estimated, which are small relative to normal temporal variations in areal photosynthesis.

Internal phosphorus loading occurs in Lake Erken as a result of: 1) Transport of phosphorus across the thermocline during stratification. 2) Increases in the thermocline depth, which results in the entrainment of hypolimnetic water and exposure of larger areas of bottom sediment to the epilimnion water. 3) The migration/transport of phosphorus rich Gloeotrichia echinulata colonies from the sediments. In spite of a relative long and stable period of thermal stratification in 1988, extreme levels of phosphorus deficiency were measured for only 2 weeks following the onset of thermal stratification. Afterwards, phosphorus deficiency decreased while biomass and productivity increased, indicating that phosphorus was diffusing through the thermocline. In 1987-1989 the blooming of G. echinulata coincided with declines in mixing depth to below 10 meters, which led to increases in internal phosphorus loading and an increased transport of resting phosphorus rich G. echinulata colonies to the epilimnion. Because of their large size G. echinulata have low rates of biomass specific photosynthesis. Their blooming therefore, caused seasonal declines in whole water measurements of biomass specific photosynthesis.

Predictions of photosynthesis based on incubator derived measurements of biomass specific photosynthesis and in situ measurements of irradiance, may be in error if spectral differences between the incubator and in situ irradiance are not considered. These errors can vary greatly with depth, and on other spatial and temporal scales depending on the optical characteristics of the water and phytoplankton assemblage. Estimation of the magnitude of such errors shows that aL can be underestimated by as much as 40 percent, or overestimated by as much as 120 percent at the base of the euphotic zone. Errors at the surface are however small, and consequently maximum errors in areal photosynthesis are on the order of +/- 20 percent.

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Preface

This thesis is based on the following papers which will be referenced to in the text by their Roman numerals (I-V)


Introduction

Photosynthesis is a fundamental biological process in aquatic ecosystems, the rate of which sets overall constraints on flows of material and energy. As a result, it is a subject which has been intensively studied in both freshwater and marine environments, especially after the introduction of the $^1$C-based methods to measure photosynthesis (Steemann Nilsen 1952). The nature of the relationship between photosynthesis and irradiance (PI), is a fundamental parameter in all models which attempt to predict aquatic photosynthesis (eg. Fee 1969, 1973, Jitts et al. 1976, Platt & Gallegos 1980, Field & Effler 1983, Harrison et al. 1985, Herman & Platt 1986). Since rates of biomass specific photosynthesis (ie. carbon uptake normalized to chlorophylla) set upper limits on the rate of phytoplankton growth, the PI relationship also provides a measurable means to examine phytoplankton adaptation to environmental change. The importance for examining the factors regulating biomass specific photosynthesis is obvious. The literature on this subject is vast and has been reviewed in many articles (eg. Harris 1978, 1980a, 1980b, 1984, Falkowski 1980, Kirk 1983, Richardson et al. 1983, Talling 1984, Harding et al. 1987).

The present work is an attempt to examine the effects of vertical mixing on measurements of biomass specific photosynthesis. It was strongly influenced by research which suggested the importance of hydrodynamic processes as potential regulators of biomass specific photosynthesis. In particular, the review articles of Harris (1980a) and Legendre and Demers (1984) influenced the work described here. In the case of lakes, it can be stated that as a result of much greater density differences (during thermal stratification), and due to the rapid vertical attenuation of light, gradients in light, temperature and nutrients are much greater in the vertical than the horizontal dimension. This research focuses on examining the effects of vertical mixing on rates of biomass specific photosynthesis. Two avenues of investigation are followed. One deals with the effect of vertical mixing on photoadaptive processes. The other examines the effect of vertical mixing on phytoplankton nutrient deficiency, on the premise that changes in cellular nutrient levels will influence rates of biomass specific photosynthesis. A general framework of the influences of vertical mixing on rates of aquatic photosynthesis is presented in figure 1. The numbered pathways in this figure are described below.

1 Vertical mixing — Nutritional Status

One of the most obvious effects of vertical mixing on lake phytoplankton dynamics is its effect on algal nutrient status. While relationships between increasing nutrient concentration and lake turnover are frequently given in the literature, data on the inputs of nutrients to the epilimnion by gradual diffusion through the thermocline, or as the result of episodic upwelling events are less often reported. The most common attempt towards estimating nutrient inputs from hypolimnetic sources during thermal stratification is to estimate vertical diffusion coefficients from a passive tracer such as temperature, and then from the vertical concentration gradients of a given nutrient to estimate its flux to the epilimnion (Jassby & Powell 1975, Hesslein & Quay 1973, Li 1973).
Figure 1. A flow chart which emphasizes the influences of vertical mixing on rates of biomass specific photosynthesis. Major influences are exerted through the effect on in situ light and photoadaptation, and through effects caused by changes in algal nutrient deficiency.

2 Algal Nutritional Status — Biomass Specific Photosynthesis
Nutrient status is one of the potential regulators of biomass specific photosynthesis. Variations in rates of biomass specific photosynthesis occur as a result of changes in intracellular concentrations of a limiting nutrient. Nutrient quota vs. photosynthesis relationships have only sparsely been reported in the literature for natural phytoplankton assemblages (Sneft 1978 and Heyman 1986). To date such relationships have been most successfully obtained in phytoplankton cultures maintained in a stable environment (Sneft 1978 Smith 1983a).
3 Photoadaptation/Photoinhibition — Biomass Specific Photosynthesis

Vertical mixing by controlling the magnitude and duration of past light exposure influences both photoadaptive and photoinhibitory processes. Rates of biomass specific photosynthesis show responses to changes in irradiance (e.g., Beardall & Morris 1976), which are assumed to allow the phytoplankton to utilize in situ light more efficiently. High light exposures however, may also lead to photoinhibitory decreases in rates of biomass specific photosynthesis (Neale 1987). The importance of photoinhibitory processes, or photoadaptive processes in affecting rates of biomass specific photosynthesis varies in accordance with the time scale examined.

4 Algal Nutritional Status — Biomass

It has been clearly demonstrated that in most freshwater lakes total phosphorus concentration is the major determinate of the algal biomass (Schindler 1974), and that total phosphorus concentration can be used as a useful predictor of algal biomass (Dillon & Rigler 1975, Vollenweider 1968) or to predict volumetric rates of photosynthesis (Smith 1979). The relationship between total phosphorus concentration and areal or volumetric rates of photosynthesis is however, far from a constant one (Heymann & Lundgren 1986), largely as a result of other factors which regulate rates of biomass specific photosynthesis (see points 2 and 3 above).

5 Biomass — Biomass Specific Photosynthesis

There is often an inverse relationship between standing crop biomass and rates of biomass specific production (Kalff & Knoechel 1978, Rodhe et al. 1956). This relationship results from a positive relationship between biomass and algal size (Kalff & Knoechel 1978, Malone 1980), and an inverse relationship between rates of biomass specific photosynthesis and size (Taguchi 1976, Malone 1980, Cote and Platt 1983). Therefore, as biomass increases, biomass specific production decreases as a result of shifts in species composition which favor large algae with low rates of biomass specific photosynthesis.

6 Vertical Mixing — Light Available for Photosynthesis

Both light intensity and spectral composition vary greatly with depth. Consequently, the depth and rates of vertical mixing have direct influences on photosynthesis by regulating both the quality and quantity of light impinging on the phytoplankton.

7 Changes in Surface light

Temporal variations in surface irradiance occur over a number of scales ranging from short time scales due to factors such as cloudiness, to diurnal time scale, and finally to seasonal time scales. This adds an additional source of variation to the in situ light climate, and will therefore influences rates of areal and biomass specific photosynthesis.

Figure 1 is presented to allow the reader to place the goals and results of the individual investigations undertaken in this thesis into a larger framework of the factors regulating aquatic photosynthesis. Of all the pathways in figure 1, the three that directly affect rates of biomass specific photosynthesis (2, 3, and 5) are discussed in more detail below. After this the results from the individual investigations are summarized.
Figure 2. An example of the relationship between biomass specific photosynthesis and irradiance. Photosynthesis initially increases linearly with irradiance with a slope of $\alpha^B$. At an irradiance of approximately $I_K$ photosynthesis reaches the light saturated rate $P_{\text{max}}^n$. At even higher irradiance a decline $\beta$ may occur due to photoinhibition.

The Effect of Light Exposure on Biomass Specific Photosynthesis

Figure 2 illustrates the general features of the relationship between photosynthesis and irradiance (PI), and is typical of the PI curves measured in the research at Lake Erken. Initially, rates of biomass specific photosynthesis increase linearly with increasing irradiance, but as higher irradiances are approached photosynthesis becomes light saturated and independent of irradiance. The slope of the initial light limited portion of the PI relationship is known as $\alpha^B$, whereas the light saturated rate of photosynthesis is known as $P_{\text{max}}^n$. The approximate irradiance at which photosynthesis becomes light saturated is termed $I_K$, which is calculated as the quotient of $P_{\text{max}}^n/\alpha^B$. Detailed descriptions of the biochemical reactions involved in aquatic photosynthesis are available in Prezelin (1981), Kremer (1981), and Kirk (1983). The reactions occurring in-
(1981), Kremer (1981), and Kirk (1983). The reactions occurring in photosynthesis are generally divided into two groups: The light and the dark reactions. The light reactions, as their name suggests, are dependent on the absorption of light by the photosynthetic pigments. Light energy is used to remove hydrogen from water which, after passing through a series of intermediate steps, combines with NADP so that NADPH\textsubscript{2} is formed and O\textsubscript{2} is evolved. Also as part of the light reactions, a closely coupled (photophosphorylation) reaction results in inorganic phosphorus uniting with ADP to form ATP. In the dark reactions NADPH\textsubscript{2} along with the chemical energy fixed in ATP is used to reduce CO\textsubscript{2} and form carbohydrates (carboxylation).

The light reactions occur at two reaction centers within the chloroplasts, each of which is characterized by a distinct combination of photosynthetic pigments and proteins. These reaction centers or photosystems are associated with a large number of non reaction center light harvesting pigment molecules. Excitation energy generated by absorption of light by the light harvesting pigments is transferred to the photosystem I and II reaction centers, where it drives the light reactions. A simple functional entity, the photosynthetic unit (PSU), is often defined. It is composed of the reaction centers of photosystems I and II and all of the accessory light harvesting pigments and proteins associated with these reaction centers (Prezelin 1981). It is therefore, a composite of all the components needed to collect light and drive the light reactions of photosynthesis.

The rate of light limited biomass specific photosynthesis ($\alpha^n$) is a measure of the light reactions, and can be considered to be a function of two factors (Bannister 1974, Platt & Jassby, 1976).

$$\alpha^n = \frac{a_{ph}^* \phi}{4 > (1)}$$

where: $\alpha^n =$ The slope of the initial light limited portion of the photosynthesis vs. irradiance relationship ie. [

[mg C (mg Chl)$^{-1}$ h$^{-1}$] [mole quanta m$^{-2}$ s$^{-1}$]

$a_{ph}^* =$ The absorption cross section of cellular chlorophyll\textsubscript{a} ie. (m$^2$ mg Chl$^{-1}$)

(Morel, 1978 Kishino et al., 1986)

$\phi =$ The quantum efficiency of carbon assimilation ie. [mg C (mole quanta)$^{-1}$]

Thus $\alpha^n$ is function of both efficiency by which light is captured by chlorophyll\textsubscript{a} ($a_{ph}^*$), and the efficiency by which this captured light is utilized to fix carbon ($\phi$). Kiefer & Mitchell (1983) suggest that $\phi$ is relatively independent of nutrient limitation, but varies as an inverse function of
irradiance with maximum values occurring at low irradiances. Sakshaug et al. (1989) define the relationship between $\phi$ and irradiance as a function of absorption cross section and turnover time of photosystem II, such that $\phi$ decreases when the incident photon flux saturates the processing capacity of the photosystem. The value of $a_{ph}^*$ varies as a result of changes in the cellular distribution or packaging of the intracellular chlorophylla. In general, $a_{ph}^*$ will be maximal when the intracellular chlorophylla is highly dispersed, so that increases in chlorophylla /cell, cell size, and cell sphericity, will all tend to decrease the value of $a_{ph}^*$ (Kirk, 1975, 1976, 1983 Morel & Bricaud 1981). Also since $a_{ph}^*$ is normalized to chlorophylla, the presence of other light harvesting pigments and changes in their relative composition can lead to changes in $a_{ph}^*$.

The rate of light saturated photosynthesis ($P_{\text{max}}$) is a measure of the dark reactions in photosynthesis (e.g. Platt & Jassby, 1976 Harris, 1978). These reactions are not directly dependent on light capture, but are dependent on the concentration and activity of enzymes which catalyze the reduction of $CO_2$ to carbohydrates. The value of $P_{\text{max}}$ also depends on the maximal potential rate at which the light reactions can deliver the NADPH and ATP intermediates which feed the dark reactions. This is in turn controlled by number of the PSUs, and the concentration of enzymes and electron transfer molecules used in the light reactions.

Both photoadaptation and photoinhibition are the result of changes in biomass specific photosynthesis which are brought about by changes in the rate at which phytoplankton absorb photons. This is in turn a function of: The correspondence between the spectral distribution of in situ irradiance and the absorption spectra of the phytoplankton, the intensity of the irradiance, and the time interval over which the exposure occurs. Neither photoadaptation nor photoinhibition are processes in themselves, but they result from the combined effects of one or more of a number of different physiological and ecological processes (see below). Photoadaptation can be defined as changes in photosynthesis which result in the phytoplankton being better able to utilize their present light climate. Photoinhibition differs from photoadaptation in that it always results in decreases in the rate of biomass specific photosynthesis. It is induced by exposures to high irradiance, and it always occurs over relatively short (minute to hour) time scales. It might be concluded that photoinhibition is detrimental to the phytoplankton, since it results in reduced photosynthetic rates; however, it is also possible that photoinhibition is a protective mechanism, which reduces photosynthesis when the phytoplankton are faced with irradiances greater than those which they can effectively utilize.
The processes responsible for photoadaptation and photoinhibition operate over a number of temporal and spatial scales (Harris 1980a). Below is a list of some of the most important of these processes which is compiled from the reviews of Harris (1978) and Falkowski (1980). They are listed in order of their reaction time, beginning with those occurring over the shortest time scales, and ending with the longest ones.

- Electron transport in the light reactions
- Chloroplast size and distribution within the cell
- Total pigment concentration
- Ratios of different light harvesting pigments
- Photosynthetic enzyme concentrations
- Respiration rate
- Cellular chemical composition
- Cell size and shape
- Colony Size and Shape
- Species Composition

At this point, it would be satisfying to describe the changes in biomass specific photosynthesis that would occur as a result of a shift between two irradiances over a given time interval. The time scale of the perturbation would determine the adaptive processes involved, and from a knowledge of the above processes the nature of the response could be deduced. Unfortunately, a number of complications make such a simple analysis impossible. For one thing, the kinetics of photoadaptation often show a distinct hysteresis if the effects of opposing shifts in irradiance are compared. For example, the rate of photoadaptation as a result of a shift from low to high irradiance is often much more rapid than when the reverse of this shift occurs, and the phytoplankton are returned to low irradiance (Harris 1980a check 80, Cullen & Lewis 1988, Sakshaug et al. 1987). Also, the processes listed above do not only depend on irradiance exposure, but may be affected by such things as nutrient availability, temperature or the composition of the phytoplankton community. For example, changes in species composition, with resulting changes in size, shape and adaptation strategy, are influenced by more than irradiance. Factors such as grazing pressure, the need to minimize or maximize rates of sinking or floating, or even historical factors such as the presence or absence of sediment resting stages may be of importance. These types of complications are discussed in more detail in paper IV, in regards of the influence of the large colonial blue-green alga Gloeotrichia echinulata.

Photoadaptation.

As a result of the problems in determining a universal causative relationship between irradiance exposure and any of the specific adaptive processes listed above, Photoadaptational strategies are most often consi-
dered in terms of the PSUs, and two general adaptational strategies have been identified: Strategies leading to changes in the size of the PSUs, and strategies leading to changes in the numbers of the PSUs. The result of these two strategies on the PI relationship is considered in detail by Prezelin (1981), and Richardson et al. (1983). The strategies can be briefly described as follows. Increases in the size of the PSUs, or the ratio of light harvesting pigments to reaction centers, would increase \( \alpha \), when normalized on a cellular basis, since the increased light harvesting pigments would more effectively collect light and transfer it to the reaction centers. Changes in \( \alpha^a \) (normalized to chlorophylla), will however, decrease as a result of the increased pigment concentration. Increasing the size of the PSUs would not have any effect on \( P_{\text{max}} \) since when photosynthesis is saturated it is the number of reaction centers and their turnover time that determines the photosynthetic rate. Consequently, \( P_{\text{max}} \) per cell will be unaffected by changes in PSU size, but due to increased pigment concentrations \( P^a_{\text{max}} \) will decrease. Increases in the number of PSUs will increase \( \alpha \) per cell, since a greater number of PSUs, will more effectively harvest light on a cellular basis. Values of \( \alpha^a \) will not however, change since increases in the number of PSUs will be accompanied by increases in pigmentation (assuming PSU size is constant). On a cellular basis, \( P_{\text{max}} \) will increase in response to increases in the number of PSUs. \( P^a_{\text{max}} \) will not change since, as was the case for \( \alpha^a \), increase in PSU number also results in increased pigment concentration.

Adaptation strategies based on the PSU concept are useful in that they provide a relatively simple (modelable) explanation of a complicated series of physiological events. However, for the PSU adaptation strategies to function as described above, a number of somewhat unrealistic assumptions must be fulfilled. Perhaps most importantly it is assumed that either PSU size or number changes. It is not clear why these two strategies should operate independently of one another. For example, it could be envisioned that increases in the number of PSUs would occur concurrently with a decrease in PSU size. Under such a scenario, \( P_{\text{max}} \) normalized to both cell number and chlorophylla would increase. There are also problems when considering the response of \( P^a_{\text{max}} \) or \( \alpha^a \) which are normalized to chlorophylla. For the responses of the chlorophylla specific PI parameters to be as described above the ratio of chlorophylla : total pigments must remain constant as PSU size or number changes. This is an unrealistic assumption, as changes in pigmentation is a known adaptive response to changes in irradiance (eg. Falkowski 1980, Yentsch 1980, Perry et al. 1981). Finally, the rate of photosynthesis will not only depend on the size and number of PSUs, but also on the rates at which the light reactions can process the absorbed photons, or the dark reactions can process the products of the light reactions. This will in turn be dependent on the concentrations of electron transfer molecules, and the concentration and activity of photosynthetic enzymes (Kirk 1983).
Photoinhibition.

As was the case for the description of photoadaptation above, the research and literature on photoinhibition is far too large to describe here. What follows is a brief description of the phenomenon which is compiled from the review articles by Richardson et al. (1983) and Neale (1987). Photoinhibition results in declines in the value of $P_{\text{max}}^a$ and $\alpha^a$ as a result of exposure to high irradiance (Neale 1987). Photoinhibitory reductions in photosynthesis are not well understood, but it does appear that interruption of electron transport through photosystem II is primarily responsible. Irradiance of shorter wavelength, particularly in the UV range, has a greater potential to induce photoinhibition (Smith et al. 1980). However, most measurements of photoinhibition are made with respect to photosynthetically active radiation (PAR), which is a broadband measurement of irradiance between the 400-700 nm wavelengths. The data of Neale (1987), suggest that the photoinhibition may be brought about by irradiances ranging from between 100 $\mu$Em$^{-2}$s$^{-1}$ - 4000 $\mu$Em$^{-2}$s$^{-1}$. Richardson et al. (1983) find that even lower irradiances of 75 $\mu$Em$^{-2}$s$^{-1}$ - 80 $\mu$Em$^{-2}$s$^{-1}$ may be sufficient to induce photoinhibition, when the effects of photoinhibition are measured on growth rather than photosynthesis. Harris (1980b) suggests a value of approximately 200 $\mu$Em$^{-2}$s$^{-1}$ is necessary to induce photoinhibition, and that up to 60 percent reductions can occur in the value of $P_{\text{max}}^b$.

As a result of the short time scale involved, and the requirement for a high irradiance exposure, declines in photosynthesis brought about by photoinhibition are evident only in the upper water column. This is a very common feature of in situ photosynthesis incubations, where sample bottles suspended near the surface often show lower rates of photosynthesis than those somewhat deeper. Harris (1978) and Harris (1980b) reviewed studies of in situ photosynthesis, and in Harris (1980b) the depression in surface bottle photosynthesis ($P_{\text{surface}}/P_{\text{max}}$) is shown to be dependent on surface irradiance. In situ incubations do not demonstrate that photoinhibition is a common or important phenomenon, since containment by sample bottles may significantly increase light exposure, relative to freely circulating conditions. Measurements of in vivo chlorophyll fluorescence, made on uncontained samples (Vincent et al. 1984, Elser & Kimmel 1985, Neale & Richerson 1987), also show surface photoinhibition during periods of low vertical mixing, suggesting that photoinhibition may also be of significance under natural unconstrained conditions. The PI incubation method used here (I, IV, V, Lewis & Smith 1983) allows estimations of $P_{\text{max}}^a$ and $\alpha^a$ over sufficiently short time intervals (20 min.) that photoinhibition by the incubation irradiance will not be significant. This allowed vertical variations in $P_{\text{max}}^a$ and $\alpha^a$, which are independent of containment effects, to be examined (I).
Figure 3. A simple experiment showing the potential decreases in photosynthesis which can result from photoinhibition under conditions typical of *in situ* measurements of photosynthesis. A sample was collected from the surface in the morning. Part of this was used to produce the Time 0 PI curve, another subsample was suspended at 0.5 m for 4 h after which the second PI curve was measured. Confinement at the surface during high mid-day irradiances led to significant reductions in both $P_{\text{max}}$ and $\alpha$. 
The effects of photoinhibition on the PI relationship is often described as resulting in a decline in photosynthesis to values below $P_0^{\text{max}}$ at irradiances greater than $I_K$. Platt et al. (1980), define the slope of this decline as $\beta$ (fig. 2), and have formulated a mathematical description of the PI relationship which includes $P_0^{\text{max}}$, $\alpha^b$, and $\beta$ as variables. Of over 330 PI curves which were measured at Lake Erken, a $\beta$ decline in photosynthesis was measured on less than 10 occasions. The photosynthesis incubators had maximum irradiances of between 1000 and 1200 $\mu$E m$^{-2}$ s$^{-1}$, while underwater irradiances in Lake Erken rarely exceed 1000 $\mu$E m$^{-2}$ s$^{-1}$. Consequently, $\beta$ type declines in photosynthesis are of little importance in Lake Erken. The values of $P_0^{\text{max}}$ and $\alpha^b$ do however, decline as a result of exposures to high irradiance. This can be illustrated by the simple experiment shown in figure 3, where both $P_0^{\text{max}}$ and $\alpha^b$ underwent significant and large declines in a sample suspended at 0.5 meters for 4 hours. It can be deduced from the data in figure 3 that a PI curve based on a 4 hour $\textit{in situ}$ incubation would show a $\beta$ decline at high irradiances; however, from the short term incubations it can be seen that the decline in photosynthesis above the $\beta$ threshold irradiance is due to a decrease in $P_0^{\text{max}}$ at all irradiances greater than $I_K$. These data therefore, illustrate the importance of time scale considerations when examining the $\textit{in situ}$ photosynthetic characteristics of the phytoplankton. When $\beta$ reductions were evident during the short term incubations in Lake Erken, it was always for samples collected at the bottom of the euphotic zone. This suggests that photoadaptive changes which increase light harvesting capacity (ie. increases in pigments and changes in pigment composition) make the phytoplankton particularly sensitive to photoinhibition.

The Effects of Nutrients on Rates of Biomass Specific Photosynthesis.

The availability of limiting nutrients has been shown to regulate growth in experimental phytoplankton cultures (eg. Droop, 1973, Rhee 1978, Rhee & Gotham 1981), and in natural populations there is a good relationship between the concentration of a limiting nutrient and biomass (eg. Vollenweider 1968, Dillon & Rigler 1975, Heyman & Lundgren 1988). It would therefore be expected that nutrients will also regulate rates of photosynthesis, even though the processes regulating growth are more numerous than those regulating photosynthesis. ATP, ADP, and NADPH are critical compounds used in the photosynthetic process, and all photosynthetic pigments are bound by protein which makes up approximately 57 percent of the chloroplasts. Consequently, phosphorus and nitrogen deficiency can directly influence the phytoplankton’s ability to photosynthesize. Senft (1978) and Smith (1983a) have shown that a relationship exists between $P_0^{\text{max}}$ and the cellular phosphorus concentrations, and that this relationship takes the same form as the specific growth relationship of Droop (1973). The relationship between nutrient limitation and $\alpha^b$ is not considered by either Senft (1978) or Smith (1983a), and
parameters directly describing nutrient limitation are absent from mechanistic descriptions of photosynthesis such as those by Bannister (1979), Kiefer & Mitchell (1983), and Sakshaug et al. (1989). However, $\alpha^a$ will be related to nutrient availability, if nutrient availability affects light harvesting capacity. Laws & Bannister (1980), Kiefer & Mitchell (1983), and Sakshaug et al. (1989) show the ratio of cellular chlorophyll to carbon to be related to nutrient availability, supporting this contention. In addition to physiological processes, nutrient availability also acts on the ecological processes which may influence rates of biomass specific photosynthesis. Changes in the ratios of available nutrients have been shown to affect the selection of species which dominate the phytoplankton community (Kilham & Tilman 1977, Tilman et al. 1982) which can in turn, influence rates of biomass specific photosynthesis (see below and IV).

The Effects of Species Composition and Phytoplankton Size on Rates of Biomass Specific Photosynthesis.

There is an often observed negative relationship between increases in algal cell size and the values of both $P_{\text{max}}^a$ and $\alpha^a$. (Taguchi, 1976, Malone 1980, Cote & Platt, 1983). A mechanistic explanation for this relationship is most obvious for $\alpha^a$ where the affects of chlorophyll packaging on $a_{\text{ph}}^*$ (Kirk 1975, 1976, 1983, Morel & Bricaud 1981) would lead to the obtained negative relationship. In the case of both $\alpha^a$ and $P_{\text{max}}^a$, variations in the ratio of surface area/volume, resulting from changes in size, are suggested to cause reduced rates of photosynthesis by influencing nutrient or CO$_2$ uptake (Taguchi, 1976, Cote & Platt, 1983, Paerl 1983). In large colonial algae such as G. echinulata, cells are so closely packed that it is possible that significant portions of the internal cells are shaded and have no chance to photosynthesize. Under such circumstances reductions in both $\alpha^a$ and $P_{\text{max}}^a$ would occur, since some chlorophyll extracted from the colonies would be from shaded cells. Paerl (1983) makes a similar argument in regards to carbon limited photosynthesis. He demonstrates, by autoradiographic methods, that only the outer layers of large (100 µm - 200 µm) Microcystis aeruginosa colonies actively photosynthesize under ambient carbon concentrations, and that the addition of both CO$_2$ or HCO$_3^-$ increased the rate of photosynthesis in the inner portions of the colonies. A similar mechanism could also explain the reduced rates of $\alpha^a$ and $P_{\text{max}}^a$ as a result of diffusion limited transport of phosphorus and nitrogen into large colonial algae.

Hydrodynamic Regulation of Biomass Specific Photosynthesis.

Hydrodynamic processes are expected to influence biomass specific photosynthesis both by affecting the stability of the environment, and the availability of growth limiting factors such as light, temperature and nutrients. In terms of limiting factors, one of the most obvious consequen-
ces of variations in the mixing regime will be the effect on light availability. Reductions in vertical mixing which coincide with the onset of thermal stratification, can greatly affect the availability of light. Rates of biomass specific photosynthesis have been shown to increase as a function of increasing irradiance (e.g. Steemann Nilsen et al. 1962, Beardall & Morris 1976 Cullen & Lewis 1988), as long as the irradiance is below photoinhibitory levels. Increases in irradiance exposure brought about by the formation of a thermally stratified mixed layer, will therefore be expected to lead to increased rates of biomass specific photosynthesis. Indeed, spring increases in biomass specific photosynthesis, which coincided with the onset of thermal stratification, were observed in Lake Erken (IV), and are commonly reported in other lakes (e.g. Jewson 1976, Heyman 1986, Tilzer and Beese 1988).

In can be hypothesized that rates of biomass specific photosynthesis will be limited by the stability of the environment relative to the adaptive rate of the phytoplankton. Biomass specific photosynthesis will reach maximum levels, as determined by ambient levels of light, nutrients, and temperature as long as the environment is stable over a time interval that is long enough for adaptation to occur. However, if adaptation proceeds at a rate which is less than that of environmental change, adaptation will be out of phase with the present environment, and photosynthesis will be below optimal levels. Since the major factor regulating the stability in the aquatic environment is hydrodynamics (Legendre & Demers 1984), hydrodynamic variability, particularly in vertical mixing, can be seen as a major factor regulating rates of biomass specific photosynthesis. Harris et al. (1980) put forth this hypothesis to explain lower levels of measured biomass in Hamilton Harbor (Lake Ontario), than would be predicted by phosphorus vs. biomass relationships. They suggest that a high frequency of vertical mixing limited the ability of the phytoplankton to adapt to their current environment, with the result of reduced rates of biomass specific photosynthesis, and growth.

Falkowski (1983) examined the relationship between hydrodynamics and adaptation in a slightly different manner to explain the presence, or absence of vertical differences in the size of algal PSUs. He showed that when the rate of vertical mixing was less than the rate of adaptation vertical differences in PSU size existed, while when mixing rates exceeded adaptation rates PSU profiles were uniform. Lewis et al. (1984a) developed a model which characterizes the relationship between adaptation and mixing in more rigorous mathematical terms, and later (Lewis et al. 1984b) showed vertical differences in the rate of light saturated photosynthesis to be related to vertical mixing as predicted by the model.

A distinction should be drawn between the results of Harris et al (1980), and that of Falkowski (1983) or Lewis et al. (1984a 1984b). In fact these represent two related, but different issues. In the first case Harris et al. (1980) suggest that variability in vertical mixing limits productivity, where in the second case it is shown that spatial patterns brought about
by adaptation will only be evident when the environment is segregated into hydrodynamically stable regions. The second view does not specifically suggest that production is limited by hydrodynamic changes, as long as the mixing regime is stable enough so that adaptation has time to occur. It should however, be realized that adaptation can only bring production up to the limits set by ambient levels of light, temperature, and nutrients. Therefore, even shifts between stable mixing regimes can affect productivity through changes in the availability of factors limiting phytoplankton growth.

*The Importance of Scale.*

Phytoplankton adaptation occurs over a range of temporal and spatial scales, depending on the rate of the adaptive process relative to the rate of water movement. Harris (1980b) provides a hierarchical description of adaptation which links the time scales of adaptive processes to spatial scales over which the adaptation would be noticeable. When environmental change is rapid only physiological adaptation will have time to occur, and the results of this adaptation will be noticeable only over small spatial scales. Seasonal changes in the environment occur over sufficiently long time scales to bring about changes in species composition and community structure, and will be evident over much larger scales. In the case of lakes, this scale may encompass the entire lake basin.

The perceived influence of adaptation on photosynthesis may be highly dependent on the time scales over which observations are made. For example, exposure to high light intensities near the water surface can lead to rapid declines in photosynthesis due to the effects of photoinhibition. Consequently, water column stability often leads to declines in photosynthesis at the surface (Vincent et al. 1984, Elser & Kimmel 1985, Neale & Richerson 1987) and it is concluded that increases in vertical mixing will increase rates of areal photosynthesis by limiting photoinhibitory light exposure. This has been confirmed by both mathematical simulations (Platt & Gallegos 1980, Gallegos & Platt 1982, Gallegos & Platt 1985) and by experimental studies which artificially induced vertical circulation (Jewson & Wood 1975, Marra 1978, Joiris & Bertels 1985, Nixdorf et al. 1990). Over longer time scales, increases in the thermal stability of the water column can lead to decreased rates of vertical mixing, and as a result a spatially more heterogeneous and stable environment. Such an environment, will increase productivity since more extensive adaptation, which can occur over longer time scales, will allow the phytoplankton to utilize the available resources more effectively (Harris 1980). Tilzer & Goldman (1978) reported that algal photoadaptation during stratified conditions leads to more effective utilization of the available light, and enhanced rates of integral photosynthesis. Therefore, over longer time scale decreases in vertical mixing can lead to increased rather than decreased rates of biomass specific photosynthesis.
Results of the Investigations Included in this Thesis

The major part of the research contained within this thesis was carried out on Lake Erken, a moderately eutrophic lake located in central Sweden. The lake has a surface area of 23.7 km², a mean depth of 9 m, and a maximum depth of 21 m. Detailed descriptions of the lake can be found in Nauwerck (1963) and Håkanson (1978). Research was carried out over three years (1987-1989), beginning at the onset of thermal stratification, and ending in the fall, after the lake had turned over. From automated recordings of water temperature estimates of the vertically mixed layer, and other features concerning the development of thermal stratification were made. Automated measurements of surface irradiance, and occasional estimates of the vertical extinction coefficient of downwelling irradiance, allowed the irradiance at different depths, and the average irradiance within the mixed layer to be determined. Measurements of photosynthesis, dissolved nutrients, and phosphorus deficiency which are more tedious and time consuming to complete, were made at 3 to 7 day intervals. Samples for these analyses were usually collected from 0.5 and 3 meters, and at the base of the epilimnion. A more detailed description of sampling and methods is given in the individual papers I-IV.

Paper I examines the vertical variability in rates of biomass specific photosynthesis during 1987, and the potential impact of this variability on estimates of areal photosynthesis. Papers II and III deal with the factors regulating the transport of phosphorus from the hypolimnion to epilimnion during thermal stratification in 1988, and the effect of internal phosphorus loading on indices of phosphorus deficiency. In paper IV data from all years was used in order to examine the factors regulating seasonal variations in biomass specific photosynthesis. Paper V was based on a research project begun at the Friday Harbor Laboratory of the University of Washington. This paper estimates the potential errors which may occur when incubator based measurements of biomass specific photosynthesis are used to predict photosynthesis in situ. Such errors occur due to spectral differences between incubator and in situ irradiance. The results from this investigation are therefore applicable to the photosynthesis measurements made at Lake Erken.

The Importance of Phytoplankton Photoadaptation in Influencing Estimates of Integral Photosynthesis (I).

In paper I the question of the potential importance of photoadaptation and/or photoinhibition in affecting estimates of areal photosynthesis is considered. In doing so two separate issues are taken up. First, the occurrence and magnitude of vertical variations in rates of biomass specific photosynthesis are examined. And secondly, the potential importance of these vertical variations in influencing estimates of areal photosynthesis is calculated.
Figure 4. Measurements of $P^B_{\text{max}}$ and $\alpha^B$, chlorophyll $a$ made at 0.5 meters and at the base of the epilimnion during 1987. Vertical variations in biomass result from the presence of blue-green algae. Vertical differences in the PI parameters were greatest in mid-August when there were also large vertical differences in chlorophyll $a$. All data is smoothed through time with a 3 point running mean.
Previous work had documented that photoinhibition was a relatively common occurrence in tropical lakes (Vincent et al. 1984, Neale and Richerson 1987) and in a mid-latitude reservoir (Elser and Kimmel 1985). However in Lake Erken the potential vertical variations in photosynthesis resulting from short term (small scale) photoinhibition were less certain due to lower surface irradiances at this northern location (60°N) and the fact that the lake is often subjected to wind induced vertical mixing. Seasonal trends in $\alpha^\alpha$, $P_{\text{max}}^\alpha$ and chlorophyll $a$ showed that vertical differences in photosynthetic rates were common, and correlated with vertical variations in biomass (fig. 4). For such differences to exist the rate of vertical mixing must have been lower than the rate of photoadaptation (Lewis et al. 1984a). Indeed, temperature measurements showed relatively large (0.5-3.0 °C) differences developed in the upper 3 meters of the water column between periods of wind induced mixing (fig. 5). These temperature differences alone however, did not prove to be a reliable predictor of the timing and magnitude of photoadaptation. The largest vertical differences in rates of biomass specific photosynthesis occurred after the period of maximum thermal stability, at times of maximum biomass corresponding to the blooming of colonial bluegreen algae. Since large colonial algae would be expected to have lower rates of biomass specific photosynthesis (see also IV), their migration to the surface during calm periods complicates interpretations of vertical differences in biomass specific photosynthesis, which would suggest photoinhibition. Consequently, it was impossible to attribute the reductions in surface PI parameters specifically to photoinhibition.

**Figure 5.** Measured difference in water temperature between the depths of 0.5 and 3.0 m. These data show that vertical mixing occurs intermittently in the surface waters during the summer, and that large ephemeral temperature gradients can form during calm periods.
While the actual photoadaptive process (photoinhibition vs. species differentiation or other photoadaptive processes) could not be identified, it is clear that significant vertical differences in the rates of biomass specific photosynthesis are common in Lake Erken. To access the potential importance of these variations on estimates of areal photosynthesis, a series of simulations were run which systematically varied the weighting given to the PI parameters measured at the top and bottom of the mixed layer. The results suggest that vertical variations in rates of biomass specific photosynthesis could account for at most a 24 to 36 percent change in the calculated rates of areal photosynthesis. This is a range in error that is comparable to errors that might occur from inaccurate determinations of areal biomass, but which is less than temporal variations in areal photosynthesis resulting from the measured variations in $\alpha^e$, $P_{\text{max}}$, and chlorophyll $a$.

**Effects of Vertical Mixing on Phytoplankton Phosphorus Deficiency (II, and III).**

Internal phosphorus loading, from hypolimnion to epilimnion during thermally stratified conditions, is influenced by seasonal changes in the rate and depth of vertical mixing. In paper II the hydrodynamic factors affecting internal phosphorus loading, and the resulting changes in indices of algal phosphorus deficiency are examined. This analysis is continued in paper III, and the relative merits of different indicators of phosphorus deficiency are compared.

Internal phosphorus loading occurs in Lake Erken as the consequence of: transport of soluble reactive phosphorus (SRP) across the thermocline, the deepening of the mixed layer which results in the entrainment of hypolimnic water and exposure of the lake sediments, and biologically mediated transport resulting from the migration of *G. echinulata* from the lake sediments to the epilimnion. Comparison of hypolimnetic SRP and water temperature measurements made in 1988 and 1989, show a relationship between increased hypolimnetic temperatures and SRP concentrations (fig 6). While the mechanism behind this hypolimnetic temperature - SRP relationship is unclear, the implication is that the timing of the onset of thermal stratification may play an important role in regulating internal phosphorus loading. The actual diffusive transport across the hypolimnion is controlled by episodes of vertical mixing. Examination of the 1988 temperature data in figure 6, shows that there was an increase in hypolimnetic temperature throughout the period of thermal stratification. As these temperature measurements were made at a depth of 15 meters, the temperature rise must result from the exchange of colder phosphorus rich hypolimnetic water with warmer water from the epilimnion. Direct solar warming can not be responsible since less than 0.05 percent of the surface radiation penetrates to this depth. The stepwise nature of the hypolimnetic temperature increase suggests that individual
Figure 6. Seasonal variations in hypolimnetic temperature, and soluble reactive phosphorus concentrations. All measurements were made at the 15 meter depth. The increases in hypolimnetic temperatures during stratification suggests epilimnion - hypolimnion exchange.
mixing events are responsible for the majority of the phosphorus transport. Predictions of the phosphorus loading associated with individual storm events will however, be greatly complicated by both interannual and seasonal variations in concentrations of hypolimnetic SRP.

The transport of phosphorus to the epilimnion as a result of the migration of phosphorus rich *G. echinulata* colonies is suggested by two lines of evidence. First, measurements made in this work (II), and by Ulen (1971) both show the initially emerging *G. echinulata* colonies to be rich in phosphorus, and that the phosphorus concentration of these algae declines with time. Since \(^{32}\)P uptake measurements show that *G. echinulata* can not compete with the other pelagic phytoplankton for phosphorus (Istvanovics et al. 1990), these algae must depend on internally stored phosphorus for growth. Secondly, there is a distinct lag between the rise in surplus phosphorus associated with the original appearance of *G. echinulata*, and the subsequent *G. echinulata* biomass maximum (II). This sequence of events would be consistent with the initial seeding of the epilimnion with phosphorus rich colonies, which later divide and increase in biomass until their surplus phosphorus stores were depleted.

Temporal trends in indices of phytoplankton nutrient deficiency were consistent with the described mechanisms of internal phosphorus loading. Turnover times (TT) of \(^{32}\)P were relatively short in June, but increased in early July at a time corresponding to the first stepwise increase in hypolimnetic temperature. Other indicators of phosphorus deficiency also showed similar temporal trends. Total alkaline phosphatase activity (TAPA), the biomass specific rate of maximum phosphorus uptake \((V_{\text{max}}^n)\) and the phosphorus deficiency index (PDI, calculated as \(P_{\text{max}}/V_{\text{max}}^n\)), Lean and Pick 1981) all suggested severe rates of phosphorus deficiency in June. Phosphorus deficiency later declined to moderate or low levels by mid July, and then remained low until the end of September. Although phosphorus was transported across the thermocline, it was rapidly taken up by the phytoplankton, since epilimnetic SRP concentrations remained low while indicators of phosphorus status suggested declining phosphorus deficiency. Indexes of phosphorus deficiency were therefore, much more sensitive indicators of internal phosphorus loading than were concentrations of SRP.

Vertical differences in TT were consistently greater at the base of the epilimnion, further suggesting that SRP was continually diffusing through the thermocline. *G. echinulata* became dominant at the same time as the second peak in TT, which followed the seasonal decline in epilimnetic nitrate. Since these algae are nitrogen fixers, and since decreasing N/P ratios appear to favor blue-green algae (Schindler 1977, Smith 1983b, 1986), one could hypothesize that increased internal phosphorus loading favored *G. echinulata* dominance. However, it is equally possible that the seasonally increasing epilimnion depth, may have resulted in a greater transport of resting *G. echinulata* colonies to the epilimnion. Since these algae are large and rich in phosphorus, their migration to the epilimnion would naturally reduce TT. Consequently, it is not clear whether reduced
phosphorus deficiency and a shift from phosphorus to nitrogen limitation, causes the increasing dominance of *G. echinulata*, or if the shift in nutrient limitation is in itself a result of the *G. echinulata* migration from the sediments. In fact it is probably a combination of increased SRP transport giving *G. echinulata* a competitive advantage in terms of nutrient conditions, and an increased inoculation giving them an advantage in terms of numbers.

Comparison of TT, biomass specific surplus phosphorus (SP), biomass specific TAPA, the ratio of particulate nitrogen to phosphorus (PN:PP), and PDI showed all of these to be useful indicators of phosphorus deficiency in Lake Erken. However PN:PP and specific SP suffered from potential bacterial interferences, and specific TAPA was influenced by cyanophyte phosphatases which are not necessarily indicative of phosphorus deficiency (Pettersson 1980). PDI was a superior indicator of phosphorus deficiency since it was not influenced by either bacterial or detrital material, and not dependent on measurements of phosphatases. Correlations were obtained between PDI and specific TAPA, TT, and the turnover time of surplus phosphorus (SP/Vmax).

**Temporal Changes in Biomass Specific Photosynthesis During the Summer: The Regulation by Environmental Factors and the Importance of Phytoplankton Succession (IV).**

In (IV) measurements of photosynthesis, phosphorus limitation, and thermal structure which were made during the summers of three years (1987-1989) are examined. The relationship between thermal structure and internal phosphorus loading found in 1988 (II and III) was also found when comparing estimates of nutrient deficiency and thermal stability between years. Internal phosphorus loading was greatest in 1989 as a result of greater hypolimnetic SRP concentrations (fig 6), and a less stable and more deeply mixed water column (fig 7). Epilimnetic SRP and chlorophylla concentrations were highest in this year, and both P/C and N/P ratios suggested low levels of phosphorus deficiency. In 1988 a stable and long lasting period of thermal stratification occurred (fig 7). Stratification set in earlier and lasted nearly a month longer in 1988 than in either of the other two years. In spite of the greater stability of the water column, only slightly higher levels of phosphorus deficiency were measured as a result of internal phosphorus loading (II and III).

Differences in thermal stability and phosphorus loading led to clear yearly differences in biomass and species composition. Most dramatic were the changes seen in 1989. In mid July of this year *G. echinulata* reached the highest biomass measured in any year (mean epilimnion chlorophylla 21.2 mg m-3) and completely dominated the pelagic phytoplankton (90% by biomass). Following the decline of *G. echinulata* in 1989, a second greater bloom of large centric diatoms occurred after the breakdown of thermal stratification. In 1987 and 1988 the maximum levels of biomass...
Figure 7. The summer thermal structure of Lake Erken as shown by 2 °C isotherms. Note the differences in the time scales. Instrument failure in 1989 prevented data from being collected after the second week in August.
Figure 8. Normalized plots of $P_{\text{max}}^B$, $\alpha^B$ and the ratio of chlorophyll $a$ to particulate carbon. The value of these parameters are expressed as a percentage of the maximum value measured in each year. Time in days is expressed relative to the maximum measure blue-green algal biomass. This maximum (day 0) corresponded with the maximum surface chlorophyll $a$ concentrations in 1987 and 1988, and the first major chlorophyll $a$ peak in 1989.
were measured when *G. echinulata* dominated the phytoplankton community. In all years increases in *G. echinulata* biomass coincided with a deepening of the epilimnion to depths of at least 10 meters. At this depth the lake's accumulation sediments (Håkanson 1981, 1982), which would be rich sources of nutrients and resting *G. echinulata* colonies, become exposed to the epilimnentic waters. As a result, increased SRP loading, and an inoculation of resting colonies into the epilimnion, appears to initiate the *G. echinulata* blooms.

Seasonal trends in $P_n^{\max}$ and $\alpha^a$ were most clearly related to changes in the dominance of *G. echinulata* (fig 8). In fact the relationship between *G. echinulata* and these photosynthetic parameters was the only common seasonal (week-month) trend that could be found for all years. Over shorter (day-week) time scales, changes in $\alpha^a$ were related to changes in mean epilimnentic light exposure (Tilzer & Beese 1988), which was calculated from the cumulative irradiance measured on the day of sampling, prior to sample collection. This relationship was however, variable in time as it was superimposed upon longer term trends controlled by changes in species composition. Lower values of both $P_n^{\max}$ and $\alpha^a$ during the dominance of large (100$\mu$m - 200$\mu$m) colonial blue-green algae is caused by reductions in the ratio of surface area to volume which limits rates of nutrient uptake, $CO_2$ uptake, and light absorption by cells located in the interior of the colonies. For $\alpha^a$ large size and high chlorophyll content would reduce the absorption cross section of chlorophyll a as a result of pigment packaging effects. Indeed, comparison of the greater than 12$\mu$m chlorophyll a size fraction with $\alpha^a$ shows a negative relationship between these two parameters (fig 9). Presumably, the disadvantages incurred by *G. echinulata* due to decreased rates of biomass specific photosynthesis are offset by higher rising velocities, which allow the algae to spend on average more time at higher irradiances in the upper euphotic zone.

**Size Fractionated Chlorophyll and Alpha 1989**

![Figure 9](image.png)

**Figure 9.** Temporal variations in the proportion of total chlorophyll a passing through a 12 $\mu$m filter, and the rate of light limited photosynthesis ($\alpha^a$). Detailed chlorophyll a size fractionation data was only available in 1989.
The results in IV illustrate the importance of phytoplankton size and species composition in controlling seasonal variations in rates of biomass specific photosynthesis. In Lake Erken, temporal changes in rates of biomass specific photosynthesis are not easily predictable from measurements of temperature, nutrient deficiency, or irradiance. Attempts to relate changes in $\alpha^p$ or $\Phi^p_{\text{max}}$ to variations in temperature, or chlorophyll $a$ specific measurements of phosphorus (PP, SP, TAPA) and nitrogen (PN) were complicated by temporal changes in the composition of the phytoplankton community. Even though short term changes in $\alpha^p$ were related to changes in irradiance exposure over longer time scales this relationship was also affected by changes in the phytoplankton community. Therefore, a better understanding of the seasonal trends in biomass specific photosynthesis will depend on a better understanding of the seasonal succession of the phytoplankton. It is however hopeful that simple analogs to detailed measurements of species composition, such as filter fractionated chlorophyll $a$ concentrations, have proved useful in predicting changes in $\alpha^p$ (fig 9). This suggests that phytoplankton size, and simple measurements of it, are parameters of algal community structure that should be included in further investigations of phytoplankton photosynthesis, and would be important parameters in models of phytoplankton photosynthesis and photoadaptation.

Comparison of PAR and PUR Based Estimates of Photosynthesis: An Illustration of the Errors Associated With Spectral Variations in Irradiance (V).

To make predictions of areal photosynthesis over time periods longer than a few hours, requires that measurements of photosynthesis be normalized to variations in surface irradiance. The most common means to accomplish this is to develop a relationship between photosynthesis and irradiance, and then to use this relationship with frequent measurements of surface irradiance to predict temporal variations in photosynthesis. Such methods have been described in detail by others (eg. Fee 1969, 1973, Jitts et al. 1976, Platt and Gallegos 1980, Field and Effler 1983, Harrison et al. 1985, Herman and Platt 1986), and have been applied at Lake Erken (I). The PI relationship can be derived either from incubations made at different depths in situ, or from measurements made in an incubator where the irradiance intensity is varied by neutral density filters. Incubator based measurements are often preferred since in the laboratory it is possible to expose more samples to a larger range in irradiance over a shorter time interval. The shorter incubation time limits photoadaptation to the incubation irradiances, and allows more detailed investigations to be undertaken. The larger sample number permits the PI relationship to be more accurately defined. The disadvantage of incubation methods is that while variations in irradiance intensity occurring within the euphotic zone can be accurately reproduced, it is impossible to reproduce variations in
can be accurately reproduced, it is impossible to reproduce variations in the spectral composition of irradiance, which varies greatly as a function of water depth. Photosynthetically active radiation (PAR) is the measurement of irradiance most often employed to predict photosynthesis in calculations such as those described above. It is calculated as an integral of the downwelling irradiance between 400 nm and 700 nm.

\[
\text{PAR} = \int_{400}^{700} \text{Ed}(\lambda) \, d\lambda
\]

where: \( \text{Ed} = \) downwelling irradiance (\( \mu \text{moles quanta m}^2 \text{ s}^{-1} \text{ nm}^{-1} \))

\( \lambda = \) wavelength (nm)

Because of its broad bandwidth PAR is insensitive to spectral variations in irradiance composition. Consequently, equal PAR irradiances in an incubator and in situ may have different spectral compositions, which may in turn induce different photosynthetic responses. A spectral mismatch between incubator and in situ irradiance may therefore lead to errors in estimating in situ rates of photosynthesis, both at specific depths, and when making calculations on an areal basis. The purpose of paper V was to estimate these potential errors.

One means to eliminate these errors is to estimate the proportion of the incident photon flux (PAR) actually absorbed by the phytoplankton. Photosynthetically usable radiation (PUR, Morel 1978) is an estimate of the rate of algal photon absorption, which is calculated as the product of downwelling irradiance and the chlorophyll \( a_{\text{ph}} \) specific absorption coefficient integrated over the PAR bandwidth.

\[
\text{PUR} = \int_{400}^{700} \text{Ed}(\lambda) \, a^*_{\text{ph}}(\lambda) \, d\lambda
\]

(3)

where: \( a^*_{\text{ph}} = \) the absorption coefficient of the phytoplankton normalized to chlorophyll \( a \) (ie. \( m^2 \text{ mmole chl} a^{-1} \))

When photosynthesis is light limited its rate will be directly proportional to the proportion of the total photon flux which is absorbed by the phytoplankton. This is defined by the ratio of PUR/PAR, and is known as the absorption cross section of chlorophyll \( a^* \). The value of \( a^*_{\text{ph}} \) is dependent on the spectral composition of the irradiance striking the phytoplankton, which varies as a function of the light source (ie. solar vs. artificial), and the attenuation of the light due the depth and optical
properties of the water in situ, or due to variations in incubator design. From equation 1 it can be seen that changes in the value of \( a_{ph}^* \) will lead to changes in \( \alpha^o \), the slope of the light limited PI relationship. Estimates of \( \alpha^o \) will be in error if spectral differences between in situ and incubator irradiance cause the in situ absorption cross section of chlorophyll \( [a^*(z)] \) to be different from that within the incubator \( [a_{ph}^*(inc)] \). In paper V it is shown that this error can be defined in terms of these two chlorophyll absorption cross sections.

\[
\Delta^*(z) = \frac{\bar{a}_{ph}^*(inc)}{a_{ph}^*(z)} - 1
\]

The magnitude of the \( \Delta^* \) error is strongly dependent on the depth and optical characteristics of the water, which influence the attenuation of light in situ, particularly between the wavelengths where the phytoplankton absorb most strongly (400-550nm). This can be illustrated by measurements which allowed the values of \( \Delta^* \) to be estimated at two sites with different biomass. One site, Parks Bay had a moderate areal chlorophyll concentration of 70 mg m\(^{-2}\), while the other, East Sound, was in the midst of a bloom of the dinoflagellate *Gymnodinium spp.*, and as a result had a high areal biomass of 370 mg chlorophyll a m\(^{-2}\). These two sites showed differing values of \( \Delta^* \) which can be related to the greater phytoplankton biomass at East Sound, and its consequent influences on the attenuation of in situ irradiance. At both sites \( \Delta^* \) was slightly negative in the upper 4 meters of the water column (fig 10), suggesting a slight potential underestimation of the in situ photosynthesis at these depths, since the in situ irradiance spectra was slightly richer in blue-bluegreen irradiance (400-550nm) than the incubator light source. For depths greater than 4 meters \( \Delta^* \) became positive, with this increase being much more pronounced at East Sound, where the maximum value of \( \Delta^* \), at 15 meters, indicates that in situ estimates of photosynthesis could be overestimated by up to 80 percent. Proportionally greater absorption due to chlorophyll at East Sound, resulted in a more rapid decline in the blue and a more distinct shift to the green wavelengths relative to the spectral shift occurring at Parks Bay (fig. 11). This narrowing of the irradiance spectrum with depth reduced the levels of PUR and the value of \( a_{ph}^*(z) \), which had the effect of increasing the \( \Delta^* \) error (eq 4).

Simulations which calculated \( \Delta^* \) in response to large variations in areal biomass and concentrations of gelbstoff (dissolved organic matter), confirmed the results described above. Increasing the concentration of either of these constituents resulted in a shift in the in situ irradiance peak towards the green wavelengths, and a progressive increase in the \( \Delta^* \) error. The simulations show maximum overestimations in photosynthesis, found at the bottom of the euphotic zone in waters with large gelbstoff (440 nm
Figure 10. Vertical variations in the maximum potential $\Delta^*$ errors. At both sites a small potential underestimation of photosynthesis is possible in the upper 2-3 meters of the water column. Below 4 meters overestimations of photosynthesis will occur, with up to 80 percent errors possible at East Sound. The greater $\Delta^*$ errors at East Sound is the result of the greater narrowing of the East Sound irradiance spectra as was illustrated in the next figure.

Despite the large potential errors in estimating photosynthesis at specific depths, errors in estimating daily rates of areal photosynthesis ($\Delta_{\text{areal}}$) were relatively small, with the maximum simulated errors varying by only $+/-$ 20 percent. This results from the fact that large portions of areal photosynthesis occurs in the upper water column where $\Delta^*$ errors are low (fig. 10), and where photosynthesis often occurs at the light saturated rate ($P_{\text{sat}}$) which is not affected by the spectral considerations which lead to the $\Delta^*$ errors in light limited photosynthesis. The factors determining the $\Delta_{\text{areal}}$ errors are the same as for $\Delta^*$, the only difference being that the potential
magnitude of $\Delta_{\text{areal}}$ is less. Accordingly, the trends describing variations in
the magnitude and direction of $\Delta^*$, also apply to $\Delta_{\text{areal}}$. Biomass stratification
affected the magnitude of the $\Delta_{\text{areal}}$ error, by determining the relative
proportions of the areal biomass that photosynthesized at light limited and
light saturated rates. Subsurface chlorophyll $a$ maxima increased the
amount of biomass at subsaturating irradiances, and could thereby
increase the potential error in estimating areal photosynthesis by a
maximum of 10-15 percent.

Figure 11. Irradiance spectra from the 1 and 15 meter depth at each field
site. These spectra are normalized to the maximum value of $Ed(\lambda)$ measured in each spe-
ctra. The spectra are similar at 1 meter, but at 15 meter the East Sound Spectra is
considerably narrower.

The results of this paper suggest that incubation methods using
quartz halogen light sources, may lead to large errors in estimating rates
of light limited photosynthesis ($\alpha^*$) at specific depths. The magnitude and
direction of these errors will depend on the concentrations of phytoplank-
ton and gelbstoff, and the depth within the water column, making the exact
prediction of these errors difficult. The seriousness of such errors will
depend on the use to which the photosynthesis measurements are put. In
the worse case, estimates of the rate of photosynthesis of a specific layer
deep in the euphotic zone, could be greatly in error. Comparisons of $\alpha^*$
between samples collected from the surface and deep within the euphotic
zone, as were made in paper I, will also be affected. In the case of paper I,
in situ values of $\alpha^*$ at the bottom of the mixed layer will be overestimated
so that the apparent decrease in $\alpha^*$ at the surface in figure 4 may be
exaggerated. However baring any major chromic adaptation by the
phytoplankton, such errors in estimating in situ values of $\alpha^*$ will largely
result from vertical differences in the spectral composition of irradiance,
which is influenced most strongly by the concentration of biomass and
gelbstoff, rather than by phytoplankton physiology ($\alpha_{\text{phy}}$). Incubations
using a light source of constant spectral quality may therefore, provide
useful comparative values of $\alpha^*$, when the physiological adaptation of the
phytoplankton is of interest. Errors in estimations of areal photosynthesis will not be seriously affected since $A^*$ errors are small in the surface water where the majority of areal photosynthesis occurs.

**Summary**

The major results of the work presented in this thesis can be summarized as follows:

- Vertical mixing occurred infrequently enough, and at low enough rates to permit significant vertical variations in $\alpha^p$, $P_{\text{max}}^p$ and chlorophyll $a$ to occur during periods of thermal stratification in Lake Erken. Two mechanisms are identified as leading to these differences at times of low vertical mixing: Photoinhibition in the upper water column, and the upward migration of buoyant colonial blue-green algae, which photosynthesize at low rates due to their large size.

- Vertical variation in $\alpha^p$ and $P_{\text{max}}^p$ exert a relatively small potential influence on estimates of areal photosynthesis. Monthly rates of areal photosynthesis were estimated to vary by a maximum of 24-36 percent as a result of vertical variations in rates of biomass specific photosynthesis. These variations are similar to ones which would occur from an inadequate description of the vertical distribution of chlorophyll $a$, and are less than normal seasonal variations in areal photosynthesis.

- Measurements made by several different methods, typically suggested moderate - low phosphorus deficiency during thermal stratification in Lake Erken. As external loading of phosphorus is low (Pettersson 1985), internal phosphorus loading must be of major importance to the pelagic phytoplankton. Three mechanisms of phosphorus loading are identified: 1) Transport of phosphorus across the thermocline. 2) The entrainment of hypolimnetic water and exposure of the lake sediments resulting from a seasonal increase in the thermocline depth. 3) The migration of phosphorus rich *G. echinulata* colonies from the sediments to the epilimnion.

- The phosphorus deficiency index (PDI, Lean and Pick 1981) proved to be a superior means to estimate phytoplankton phosphorus deficiency. PDI was not influenced by bacterial or detrital interferences as were surplus phosphorus and particulate nutrient ratios, or by the presence of cyanophyte phosphatases as were measurements of alkaline phosphatase activity.

- Temporal variations in biomass specific photosynthesis during the period of summer stratification were most clearly related to the blooming of the colonial blue-green algae *G. echinulata*, which because of its large size had relatively low rates of biomass specific photosynthesis. The blooming of this species resulted in declines in whole water measurements of biomass specific photosynthesis. Over shorter (daily) time scales changes in $\alpha^p$ were related to calculations of the average irradiance exposure within the epilimnion.
When estimating rates of photosynthesis from incubator derived photosynthesis vs. irradiance curves and in situ measurements of irradiance, spectral differences in light quality can potentially lead to large errors if irradiance is measured as PAR. These errors will be greatest deep within the euphotic zone, where to 40 percent underestimations and 120 percent overestimations of in situ photosynthesis are possible. Such errors are of minor significance when estimating areal photosynthesis, since errors in the upper water column are small.

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References


List of Symbols and Abbreviations

PI  Photosynthesis vs. Irradiance relationship.

\( P_{\text{max}} \)  The rate of light saturated photosynthesis when expressed as a rate per volume of water \((\text{mgC m}^{-3} \text{ h}^{-1})\).

\( P_{\text{Bmax}} \)  The rate of light saturated photosynthesis when expressed as a rate normalized to the chlorophyll\( \alpha \) concentration of water ie. \(\text{mgC mgChl}^{-1} \text{ h}^{-1}\). Such rates, which are normalized to chlorophyll\( \alpha \), are often referred to biomass specific rates.

\( \alpha \)  The slope of the light limited portion of the PI curve when photosynthesis is measured as a volumetric rate \(\left[(\text{mgC m}^{-3} \text{ h}^{-1})\left(\mu E \text{ m}^{-2} \text{ s}^{-1}\right)\right]^{-1}\).

\( \alpha^B \)  The slope of the light limited portion of the PI curve when photosynthesis is measured as a chlorophyll\( \alpha \) specific rate. ie. \(\left[(\text{mgC mgChl}^{-1} \text{ h}^{-1})\left(\mu E \text{ m}^{-2} \text{ s}^{-1}\right)\right]^{-1}\).

\( \phi \)  The quantum efficiency of photosynthesis (mmoles C mmoles photons absorbed\(^{-1}\)).

\( a_{\text{ph}}^* \)  The absorption cross section of chlorophyll\( \alpha \). This parameter relates \( \phi \) to \( \alpha^B \) and is calculated as the ratio of PUR/PAR \((\text{m}^2 \text{mmoleChl}^{-1})\).

\( R_B \)  The \( Y \) intercept of the photosynthesis vs. irradiance relationship. This value should represent the dark uptake of \( \text{CO}_2 \), and should be slightly negative. When expressed as a biomass specific value its units are \(\text{mgC m}^{-3} \text{ h}^{-1}\).

\( I_K \)  The approximate irradiance where photosynthesis becomes light saturated. Calculated as \( P_{\text{Bmax}}/\alpha^B \left(\mu E \text{ m}^2 \text{ s}^{-1}\right)\).

\( \beta \)  The slope of the decline in photosynthesis to below the light saturated rate that may occur as a result of photoinhibition. \(\left[(\text{mgC mgChl}^{-1} \text{ h}^{-1})\left(\mu E \text{ m}^{-2} \text{ s}^{-1}\right)\right]^{-1}\).

\( P \)  The volumetric rate of photosynthesis calculated as occurring at a given irradiance

\( P_B \)  The chlorophyll\( \alpha \) specific rate of photosynthesis calculated as occurring at a given irradiance.
The chlorophyll-specific rate of photosynthesis calculated as occurring at a given irradiance when irradiance is measured as PAR. This is in fact the same as $P_{\text{B,PAR}}$ above, but in paper V it is specifically stated that PAR was the measurement of irradiance.

The chlorophyll-specific rate of photosynthesis calculated as occurring at a given irradiance when irradiance is measured as PUR.

UV Ultraviolet radiation

$\lambda$ Wavelength (nm)

$E$ Einstein a measure of radiation equal to one mole of photons

PAR Photosynthetically available radiation. The integral photon flux between the wavelengths of 400-700 nm ($\mu$E m$^{-2}$ s$^{-1}$).

PUR Photosynthetically useable radiation. The proportion of PAR absorbed per unit of chlorophyll (mmoles photons mmole chl$^{-1}$ h$^{-1}$).

$E_d$ Downwelling underwater irradiance. This notation was used in paper V, where measurements had a fine spectral resolution ($\mu$E m$^{-2}$ s$^{-1}$ nm$^{-1}$).

$I$ Irradiance measured as PAR. Used in all papers except V.

$K_d$ The vertical attenuation coefficient of downwelling PAR irradiance (m$^{-1}$).

$K_d(\lambda)$ The vertical attenuation coefficient of downwelling irradiance at wavelength $\lambda$ (m$^{-1}$).

$a_{ph^*}(\lambda)$ The absorption coefficient due to phytoplankton at wavelength ($\lambda$). This coefficient is normalized by the chlorophyll concentration of the phytoplankton material (m$^2$ mmole Chl$^{-1}$)

$c$ The beam attenuation coefficient at 660 nm (m$^{-1}$).

PSU Photosynthetic unit.

$\Delta^*$ Estimated error in $\alpha^B$ (paper V).
\( A_{\text{areal}} \) Estimated error in calculations of areal photosynthesis (paper V).

\( T_T \) Turnover time of orthophosphate (min.)

\( T_{sp} \) Turnover time of surplus phosphorus (min.)

\( \text{TAPA} \) Total alkaline phosphatase activity (nmole ptase l-1 min-1).

\( \text{SP} \) Algal surplus phosphorus (\( \mu \)gP l-1).

\( v \) The uptake velocity of phosphorus determined by radiochemical methods

\( V_{\text{max}} \) Maximum phosphate uptake velocity (\( \mu \)gP l-1 h-1).

\( V_{B_{\text{max}}} \) Maximum phosphate uptake velocity normalized to chlorophylla (\( \mu \)gP \( \mu \)gChl l-1 h-1).

\( \text{PDI} \) Phosphorus deficiency index (Lean and Pick 1981). Calculated as \( P_{\text{max}}/V_{\text{max}} \).

\( K \) The apparent half saturation constant of phosphorus uptake (\( \mu \)g P l-1)

\( S \) The orthophosphate concentration of the water estimated from experimental measurements of \( ^{32}\text{P} \) uptake (\( \mu \)g P l-1).

\( \text{SRP} \) Soluble reactive phosphorus (\( \mu \)g P l-1).

\( \text{DIN} \) Dissolved inorganic nitrogen (\( \mu \)g N l-1).

\( \text{PN} \) Particulate nitrogen (\( \mu \)g N l-1).

\( \text{PP} \) Particulate phosphorus (\( \mu \)g P l-1).

\( Z \) Depth (m)

\( Z_m \) Depth of the mixed layer or epilimnion (m).

\( Z_{\text{max}} \) Maximum depth of the lake (m).

\( Z_{\text{photo}} \) Depth of the euphotic zone which is defined as the depth where irradiance is 1% of surface PAR (m).