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The seasonal productivity cycle of phytoplankton and controlling factors in Lake Constance[1]

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ABSTRACT

Annual phytoplankton productivity in Lake Constance is about 300 g C m^{-2}, a value typical for meso-eutrophic lakes. Seasonal variations in phytoplankton biomass and productivity are exceptionally great because of a sequence of factors controlling the production process: During winter productivity is controlled by low energy inputs and high respiratory losses due to deep water column mixing. Biomass is low and water transparancy high. The spring phytoplankton growth is triggered by the thermal stabilization of the water column. The summer phytoplankton biomass maximum mainly depends on phosphorus availability. However, biomass yields comprise only 15–20% of values to be expected from the Redfield ratio because large proportions of POM are detritus and non-algal biota. Moreover, sedimentation during the second half of the year removes biomass from the euphotic zone. Water transparency and thus vertical distribution of algal photosynthesis is highly dependent on phytoplankton biomass. Self-shading causes considerably smaller seasonal variations in areal biomass and photosynthetic rates than in volume-based values. By light-shade adaptation effects of seasonal fluctuations in mean daily surface radiance fluxes on algal photosynthesis can to a significant extent be compensated for. At any given level of biomass daylength is the major determinant of daily production rates.

1. Introduction

Over the past twenty years enormous progress has been made in the study of the functioning of freshwater ecosystems (e.g. [1]). Numerous case-studies exist in which thorough year-round investigations were performed (e.g. [2] and [3]). The understanding of general principles that govern the seasonality of the lacustrine communities, however, is far from sufficient to draw generalized conclusions. Several reasons can be given for this:

(1) Every lake has individual features created by morphometry, hydrology, climate and biotic composition which hampers generalization. (2) The temporal course of events is caused by complex interactions of physical, chemical, and biological factors which undergo steady seasonal and diel changes. (3) The biological responses to physical and chemical driving forces is delayed to varying degrees, thereby creating disequilibria on a short time scale [4]. This does not preclude long-term homiostasis [5]. Nevertheless, there is growing consensus among limnologists that in principle deterministic concepts of lake ecosystem functioning can be developed, based upon few well-studied systems, which can be extrapolated to other lakes. An important pre-

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[1] Dedicated to Professor Elster on his 80th birthday.

requistite for determinism within communities is the notion that species selection is governed by resource availability and competition for resources (e. g. [6]). Historic aspects of species invasion are presumed to play only a minor role. In analyses of the phytoplankton species periodicity [7, 8] and zooplankton community structure (9) truly deterministic perspectives begin to emerge.

The analysis of the primary production process of phytoplankton as a whole in many respects is simplistic because an assemblage which may consist of 100 or more species is treated as one functional unit. However, successes of predictive productivity models based on relatively few and simple assumptions are clear indications that determinism can be successful also for the community as a whole [10, 11, 12, 13, 14].

In Lake Constance phytoplankton are highly variable both with respect to species composition and total biomass. In a series of papers Sommer has analyzed the factors controlling the seasonal species periodicity of phytoplankton and controlling factors [15–19]. Moreover, the effect of biomass changes on the production potential [20], factors controlling photosynthesis-light relationships [21] and the fate of newly produced organic matter [22, 23, 24] have been studied. It is the aim of the present paper to describe and to evaluate important factors governing the seasonal course of phytoplankton productivity. Special emphasis will be on the effects of incident radiance and on the underwater light field. Finally, different procedures to estimate annual phytoplankton productivity will be compared.

List of symbols, units and definitions (listed in the order as they appear in the text)
PAR, mmol $m^{-2}h^{-1}$, or μmol $m^{-2}s^{-1}$: photosynthetically active radiation (400 – 700 nm). Mean energy content assumed to be 218 kJ mol^{-1}.
I_o, mmol $m^{-2}h^{-1}$ or μmol $m^{-2}s^{-1}$: quantum flux of PAR immediately below water surface. Reflexion losses assumed to be 10 %.
I_z, mmol $m^{-2}h^{-1}$ or μmol $m^{-2}s^{-1}$: underwater quantum fluence of PAR at depth Z.
z_{eu}, m: euphotic depth, defined by light level where PAR is 1 % of value immediately below water surface. It is assumed that below z_{eu} the net carbon balance over 24 hrs. is negative.
Z_s, m, Secchi depth
k, ln-units m^{-1}: vertical light attenuation coefficient, mean value over spectrum of PAR, here related to scalar underwater quantum fluence.
k'_w, ln-units m^{-1} background vertical light attenuation coefficient, mean value over spectrum of PAR, here related to scalar underwater quantum fluence.
$\bar{k}_c$, m^2 mg^{-1} Chl $\underline{a}$: absorption cross-section of algal cells in vivo, normalized to chlorophyll $\underline{a}$, mean value over spectrum of PAR
A, mg Cm^{-3} h^{-1}: photosynthetic rate, hourly mean value during the incubation period (usually 4 hrs)
A_{max}, mg $Cm^{-3}h^{-1}$: photosynthetic rate, highest value within profile, as above
P, mgC (mg Chl$\underline{a}$)h^{-1}: photosynthetic rate, normalized to chlorophyll $\underline{a}$, hourly mean value over incubation period
P_{max}, mgC (mg Chl$\underline{a}$)$^{-1}h^{-1}$: maximum chlorophyll-specific photosynthetic rate, also termed 'photosynthetic capacity'.
α^B, mgC (mg Chla mmol PAR) $^{-1}m^2$: slope of the light-limited P versus irradiance curve, obtained by linear regression analysis.

I_k, mmol $m^{-2}h^{-1}$, or μmol $m^{-2}s^{-1}$: irradiance at onset of light saturation, obtaned by graphical evaluation.

Z_{I_k}, m: depth where irradiance has declined to intensity at onset of light saturation (I_k).

Z_i, m: depth where irradiance has declined to value half-saturating to photosynthesis (0,5 I_k) here obtained by solving ey. 7.

(O. D.), dimensionless: depth interval defined by decrease in underwater irradiance by 50%. Thus Z (O. D.) = Z (m) · k/ln2.

$\bar{I}_z$, mmol $m^{-2}h^{-1}$, or μmol $m^{-2}s^{-2}$: underwater PAR, mean value over mixed water column

Z_m, m: depth of mixing

Z_c, m: citical depth of mixing, beyond which phytoplankton growth no longer is possible

Az, $mgCm^{-3}h^{-1}$; photosynthesis at depth Z.

R_z $mgCm^{-3}h^{-1}$: respiratory carbon losses at depth Z

r, dimensionless: respiration losses, expressed as proportions of light-saturated photosynthesis over a 24-hr period.

2. Materials and methods

Between early May 1980 and mid-July 1983 daily primary productivity was estimated at 141 dates in Überlinger See, a fjordlike bight stretching 18 km from the main basin of the lake to the northwest. The numbers of dates of measurement per year were as follows: 1980: 28; 1981: 55; 1982: 39; 1983: 19. Samples were collected by non-metallic Van Dorn bottles from the following depths within the uppermost 20 m: 0, 1, 2, 3, 4, 5, 6, 8, 10, 12.5, 15, 17.5, 20 m. Sometimes samples were also taken from 7 m. Photosynthetic rate measurements were performed in situ [25, 26]. The depths of incubation were variable depending on the water transparency during the day of measurement and were adjusted so that the deepest incubations were performed at a light level of approximately 0.5% of surface iradiance. As a spot-check of water transparancy which is a function of the highly variable chlorophyll concentration in Lake Constance (see eq. 3 and 4), Secchi readings were performed prior to each sampling. Secchi depth in Lake Constance was found to be related to euphotic depths by

$$Z_{eu} = 4.71\, Z_s^{0.57}.\ r^2 = 0.85; p < 0.001 \qquad (1)\ [27].$$

Near the lake surface incubation racks were spaced every 0.5 m and samples for two neighboring depths were withdrawn from the same sampler which had a height of 70 cm. The contents of the Van Dorn samplers were poured into pre-rinsed plastic carboys of 25 liter volume which were immediateley transferred to the cabin of the boat for further sample processing to protect the phytoplankton from exposure to excessive doses of light.

Photosynthetic rate estimates were based on a modified radiocarbon technique [25, 26]. Duplicate 120-ml B. O. D. bottles were incubated in their respective sampling depths in a horizontal position. At each depth also one dark bottle was incubated, the C-uptake rate in which was substracted from the mean values of the light uptake rates. In order to minimize light exposure of the incubation flasks, they were covered with black cloths on deck during handling whenever possible. The samples were labeled with a sodium-14C bicarbonate solution of 4–8.10^4 Bq per sample. Incubations lasted for approximately 4 hrs symmetrically around solar noon. After retrieval of the incubation bottles, 1.00 ml of sample was withdrawn by a precision syringe for the measurement of the added activity in Unisolve Gel (Zinsser Frankfurt/M.). Filtration of the samples onto 0.8 μm membrane filters was completed within 1 hr after the end of the incubation. After careful rinsing with distilled water the filters were dissolved in 3.5 ml of dioxane-PPO coctail (Riedel de Haen No. 24224). Radioactivity was measured in a Beckman LS 7500 liquid scintillation counter. Counting efficiency was determined by internal toluene standards of known activity. Daily production rates were calculated by using Talling's light-division hours (see eq. 22).

Data on daily surface radiation were kindly provided by the Konstanz weather station and were based on Star pyranometer readings of energy inputs in the range of 300–3000 nm [28]. Flux of energy was converted to quanta by assuming a mean energy content of photosynthetically active radiation (PAR) of 218 kJ mol^{-1}. Thus 1 kJ of total short-wave radiation was converted to 2.11 mmol of PAR by assuming that PAR equals 46% of total short-wave radiation [10]. Underwater irradiance gradients were determined within 1 hr around solar noon by lowering an underwater quantum scalar irradiance meter (QSP 200 Biospherical Instruments, San Diego). Underwater readings were corrected for variations of surface irradiance during the measurements by using a reference sensor (QSR-240) on deck. Surface reflection and backscattering losses were assumed to comprise 10% of incident radiance.

Water temperatures were measured by a thermistor probe (Züllig, Rheineck, Switzerland). Chlorophyll concentrations were determined spectrophotometrically from hot ethanol extracts by using the monochromatic equations by Lorenzen [29], pheopigments were corrected for by acidification using the procedure by Moed and Hallegraeff [30] and Nusch [31]. For further details see [20].

3. Results and discussion

3.1 *General background and characteristics of the plankton community*

Lake Constance is a large (surface area ca. 500 km^2) deep (mean depth 100 m, maximum depth 254 m) lake of glacial origin situated at the northern fringe of the alps. Its immediate surrounding is both heavily populated (ca. 470 km^{-2}) and used for recreation and agriculture (general description in Kiefer [32]). The previously oligotrophic lake has undergone accelerated eutrophication since 1950, mainly due to domestic sewage influx [33–35]. Sewage diversion has led to slowing increases in winter SRP concentrations since 1975 and a gradual decline since 1981 [36].

The lake freezes over only about every 80 years (last in 1963) and thus in general is warm-monomictic. Thermal stratification begins in mid-March and reaches its maximum stability in late July. An irregular temperature gradient extends from the surface to 30–40 m. Autumnal mixing begins in October and reaches about 50 m by the

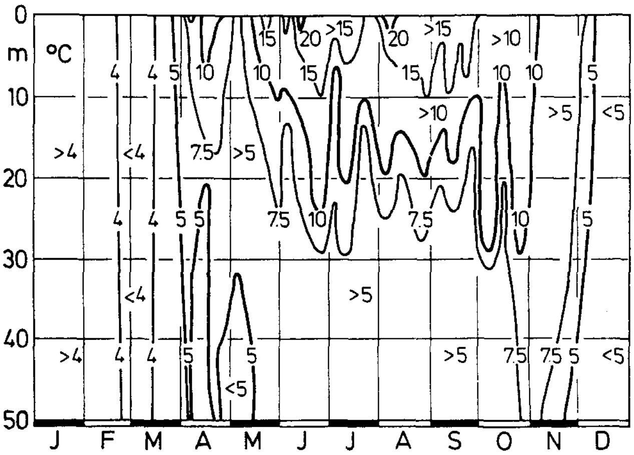

Figure 1. Temperature isopleths in the uppermost 50 m of Lake Constance/Überlinger See in 1981. Only minor seasonal temperature variations occur below 50 m depth. The maximum depth of Überlinger See is 147 m.

end of the year. Mixing progresses until early March but does not reach the deepest strata of the main lake basin every year. However, Überlinger See (maximum depth of 147 m) is mixed down to the bottom every year (Fig. 1, Fig. 14).

The phytoplankton community is characterized by extreme variations both in total biomass and species composition. The spring bloom which is dominated by small phytoplankton species is terminated by excessive grazing by daphnids ("clear-water phase") [37, 38]. Later during the year larger species dominate which are less susceptible to grazing but exhibit slower growth [15]. Overall, interspecific competition for nutrients and differential losses due to grazing and sedimentation are the single most important factors controlling species succession during summer. During winter large diatoms prevail [8].

3.2 *The underwater light field*

The daily sum of solar irradiance depends both on daylength and mean daily quantum flux. At the latitude of Lake Constance the daylength varies by a factor of c. 2 seasonally due to the variation of solar height. The mean quantum flux depends on the cosine of the mean zenith angle which controls the pathlength of the light through the atmosphere and the quantum flux density at any horizontal plane (Fig. 2, bottom). At Lake Constance mean daily quantum fluxes vary by a factor of 2.5 seasonally. They are always lower than to be anticipated for this altitude and latitude [39, 40], probably mainly due to cloudiness (Fig. 2, center). Because daylength and average daily quantum flux density varies synchronously, the effects of both are multiplicative leading to a variation of total daily incident light by a factor of 5 over the course of the year (Fig. 2, top).

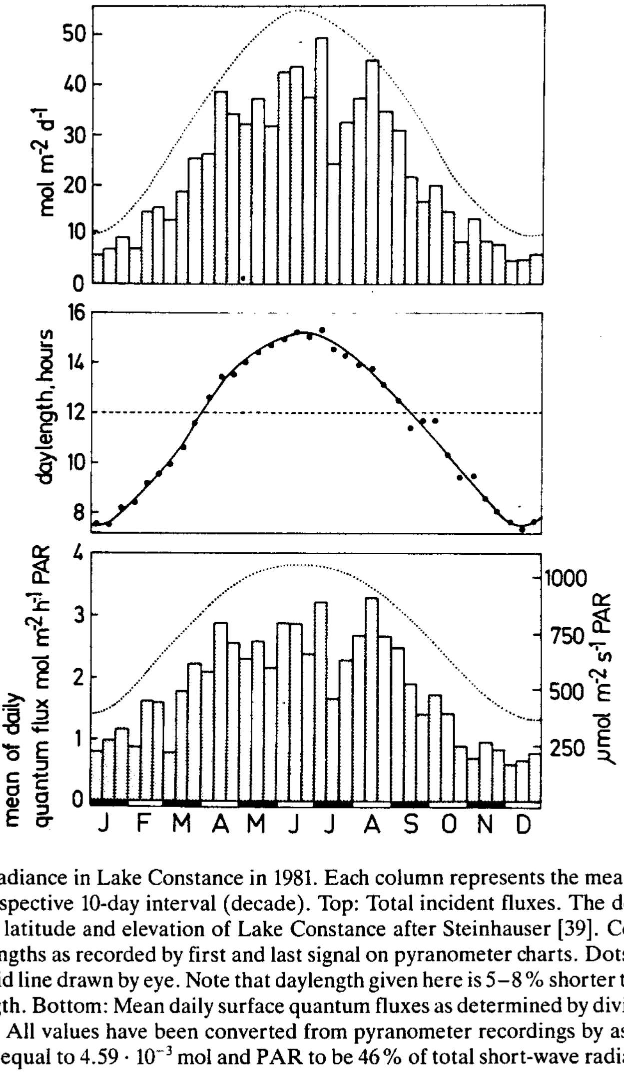

Figure 2. Surface irradiance in Lake Constance in 1981. Each column represents the mean value of daily recordings during respective 10-day interval (decade). Top: Total incident fluxes. The dotted line gives theoretical value for latitude and elevation of Lake Constance after Steinhauser [39]. Center: Seasonal fluctuations of daylengths as recorded by first and last signal on pyranometer charts. Dots: Observed 10-day mean values, solid line drawn by eye. Note that daylength given here is 5–8 % shorter than astronomically defined daylength. Bottom: Mean daily surface quantum fluxes as determined by dividing daily total inputs by daylength. All values have been converted from pyranometer recordings by assuming 1 kJ of PAR to be equal to $4.59 \cdot 10^{-3}$ mol and PAR to be 46 % of total short-wave radiation.

3.2.1 Seasonal course of euphotic cholorophyll concentration and water transparency

Over the course of the year both euphotic depths (as defined by the depth at which 1 % of surface quantum flux density occurs) and Secchi depths vary widely. During the study period (measurements on 141 days) euphotic depth was found to vary between 4.8 m and 22.5 m, Secchi depth between 1.4 m and 14.7 m [20, 27]. During the same period, mean euphotic concentrations of chlorophyll a (corrected for pheopig-

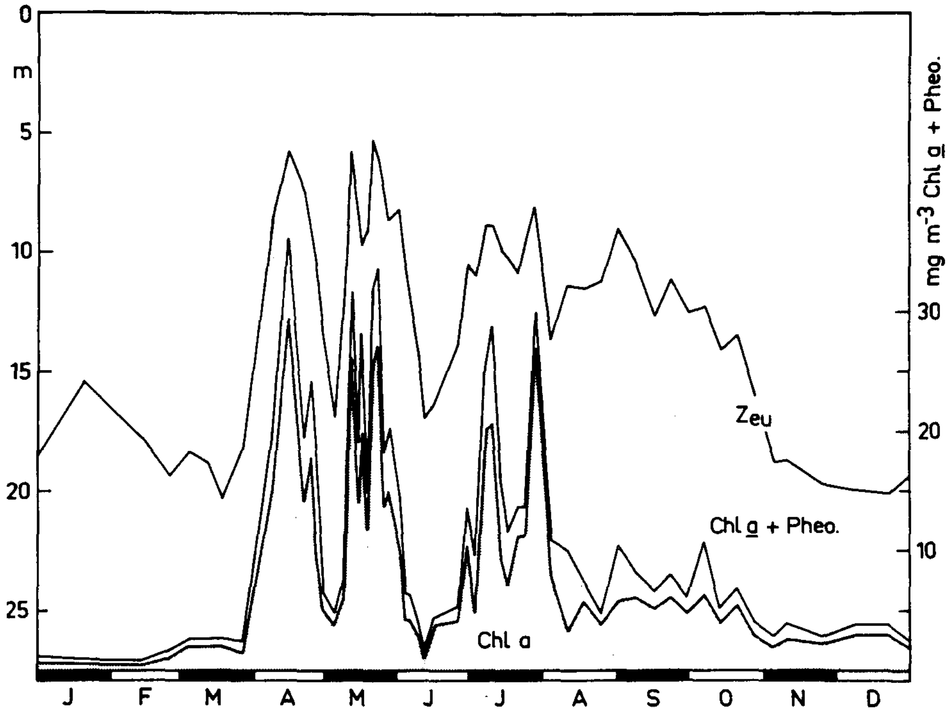

Figure 3. Seasonal variations of the euphotic depth (Z_{eu}) as defined by the 1-% surface irradiance level (left scale) and mean euphotic concentration of photosynthetic pigments (shaded: chlorophyll a) in 1981. The mean contribution of pheopigments in total pigments within the euphotic zone was 27.4 ± 8.2%.

ments) ranged from 0.36 to 29.6 mg m^{-3}. The proportion of pheopigments in total pigments (chla + pheopigments) within the euphotic zone was relatively constant (mean 27.4 ± 8.2%) [20].

The seasonal course of water turbidity and chlorophyll concentration show good agreement (Fig. 3). During the winter months euphotic chlorophyll concentrations are usually less than 1.2 mg m^{-3} and euphotic depths are in excess of 15 m. The phytoplankton spring bloom begins with the establishment of thermal stratification. Because vertical density gradients then still are small, windy weather frequently leads to destratification and dilution of newly developed phytoplankton. The clear-water phase following the spring bloom was less pronounced in 1981 (shown in Fig. 3) than in other years. In 1980 and 1982 minimum euphotic Chla concentrations in June were 0.68 and 0.51 mg m^{-3}, and euphotic depths were 15.0 and 18.3 m, respectively.

The summer maximum of Chla concentration is of a similar magnitude as the spring maximum. It is accomplished by species with lower Chla: cell volume ratios than the spring phytoplankton. Both the late summer minimum and the small autumnal chlorophyll maximum occur regularly every year (Fig. 3).

3.2.2 Vertical light attenuation and euphotic chlorophyll

Vertical light attenuation coefficients were determined from relative measurements of underwater quantum flux:

$$k = [1/(Z_2 - Z_1)] \cdot \ln (I_{Z_2}/I_{Z_1}), \tag{2}$$

Because near the lake surface wavebands that are poorly transmitted are still abundant, the overal gradient of PAR is usually steeper than at greater depths where only the most penetrating spectral components prevail [41, 42]. Although the spectrum of PAR is dramatically narrowed with depth in Lake Constance to green light with maximum fluxes around 550 nm, the tendency of vertically declining k_z is small ([43], and own data). However, vertical varations in light attenuation coefficients do occur due to vertical changes in chlorophyll concentration [20], similar as observed in Lake Zurich by Schanz [44].
A regression analysis of vertical light attenuation (y) versus pigment (chlorophyll plus pheopigment) concentration (x) yielded the linear relationship

$$y = 0.015\,x + 0.27; r^2 = 0.81, p < 0.001 \tag{3}$$

Talling [41], Bindloss [45], Jewson [46], and Dubinsky & Berman [42] have used this procedure to quantify the effects of phytoplankton pigments on transmission of monochromatic light whereas Berman [47], Tilzer [48], Megard et al. [49], Schanz [44], and others have analyzed phytoplankton pigment effects on the attenuation of PAR. The influence of pigment concentration and background light attenuation on water transparancy can be expressed by

$$k = \bar{k}_c \cdot (\mathrm{Chl}\underline{a} + \mathrm{Pheo}) + k'_w \tag{4}$$

This relationship can be used to predict the vertical extent of the euphotic zone from pigment concentration by

$$Z_{eu} = \ln 100/k = 4.605/[\bar{k}_c (\mathrm{Chl}\underline{a} + \mathrm{Pheo}) + k'w] \tag{5a}$$

Because in Lake Constance pheopigments on the average comprise 27.4% of total pigments (Chla + pheopigments) with relatively little variation, we can predict the euphotic depth from concentrations of viable Chla. If p is the ratio of live Chl$\underline{a}$ to total pigments (0.726 in the case of Lake Constance, see [20]) total vertical light attenuation is

$$k = (\bar{k}_c/p) \cdot \mathrm{Chl}\underline{a} + k'_w \tag*{(eq. 4)}$$

Following eq. 3 the euphotic depth in Lake Constance is related to concentrations of viable Chl$\underline{a}$ by

$$Z_{eu} = 4.605/(0.02/\mathrm{Chl}\underline{a} + 0.27). \tag{5b}$$

However, both vertical and temporal variations in the chlorophyll-specific light attenuation coefficient ($\bar{k}_c$) are likely in Lake Constance, as in other lakes: Since green light is transmitted best, $\bar{k}_c$ can be expected to decrease with depth [51]. Because small particles absorb light more efficiently than large ones do [52], in Lake Constance $\bar{k}_c$ should be at maximum in spring when small-sized phytoplankton dominate.

The euphotic depth exhibits a hyperbolic relationship to chlorophyll concentration. The agreement between the data points and the prediction based on eq. 5 is reasonable at chlorophyll concentrations higher than 5 mg m^{-3}. However, maximum observed euphotic depths exceed highest values predicted under the assumption of a constant background attenuation by as much as 35%. Background light attenuation is affected by water molecules, Gelbstoff and non-photosynthetic particles [46]. For nearby Lake Zurich Schanz [44], based on Smith and Baker [50] has estimated that the attenuation coefficient for pure water between 0 and 20 m is c. 0.12 m^{-1}. If this value is applied to Lake Constance, 56% of the mean background light attenuation (0.27 m^{-1}) should be due to substances other than water. Lake Constance has an average concentration of Gelbstoff of c 1.8–2.0 mg l^{-1} (H. H. Stabel, U. Möser-Scheffel, pers. comm.) whith little seasonal variation. However, turbidity due to particulate material is highly variable. Total organic weight (POM) closely follows phytoplankton biomass (Fig. 7). Both allochthonous minerogeneous particles and autochthonous calcite formed by decalcification exhibit concentration maxima during summer when phytoplankton density is high. When phytoplankton concentrations are low, background light attenuation coefficients are around 0.20 m^{-1} (Fig. 4). About 40% of light attenuation then can be attributed to Gelbstoff and detritus.

The relationship between euphotic chlorophyll concentration and vertical light attenuation can also be used to predict the total chlorophyll content within the euphotic zone. Integral euphotic chlorophyll is Chla Z_{eu}. From Eq. 5 it follows that

$$\sum_{0}^{Z_{eu}} \mathrm{Chl}a\,\Delta Z = \frac{\ln 100}{\bar{k}_c \cdot \mathrm{Chl}a/p + k'_w}$$

and , consequently

$$\sum_{0}^{Z_{eu}} \mathrm{Chl}a\,\Delta Z = \frac{\ln 100}{(\bar{k}_c/p) + (k'_w/\mathrm{Chl}a)} \qquad (6a)$$

For Lake Constance this relationship can be expressed by

$$\sum_{0}^{Z_{eu}} \mathrm{Chl}a\,\Delta Z = \frac{4.605}{0.02 + (0.27/\mathrm{Chl}a)} \cdot \qquad (6b)$$

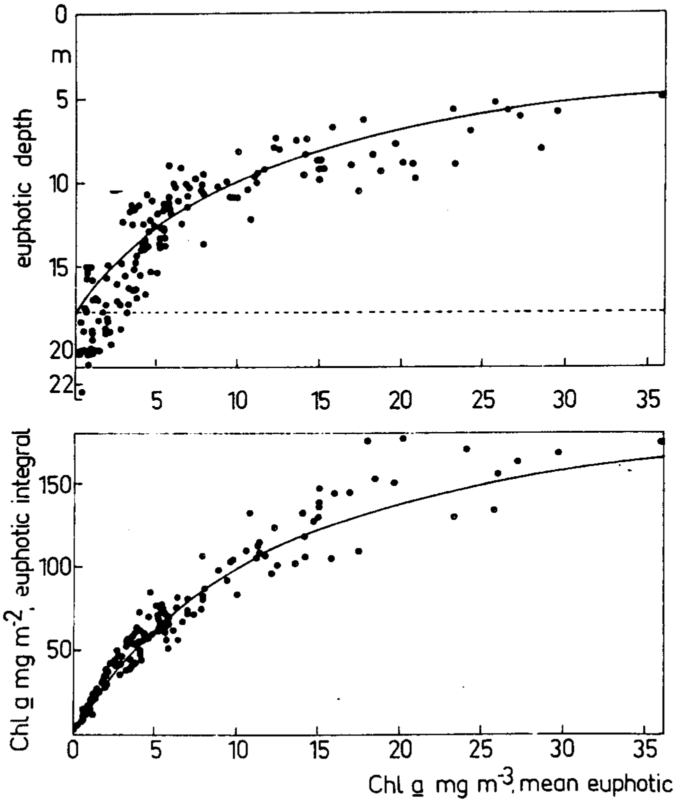

Figure 4. Relationships between mean euphotic chlorophyll a concentration and euphotic depth (top), and with integral euphotic pigment content (bottom). The curvelinear relationship between Z_{eu} and Chla in the top panel was derived from equation 5. The relationship between integral euphotic chla and mean euphotic chlorophyll concentration in the bottom panel was predicted by equation 6. The broken line in the upper panel defines the upper limit of the euphotic depth in the absence of chlorophyll as predicted from equation 5. Note that in reality euphotic depths at low phytoplankton exceed this value because of lower-than-average non-algal seston concentrations.

Fig. 4 bottom shows good agreement between predicted and observed values. The theoretical upper limit of Chla within the euphotic zone which would be reached if virtually all light would be absorbed by photosynthetic pigments is never approached.

The lower the background light attenuation and the higher the absorption cross-section of algal cells, the more phytoplankton is within the euphotic zone at any given chlorophyll concentration. In shallow and wind-exposed Lough Neagh with high concentrations of suspended solids, high non-algal turbidity restricts the euphotic chlorophyll content [46].

During periods of maximum biomass, substantial fractions of chlorophyll are below the euphotic zone and thus do not contribute to the production process (Fig. 5).

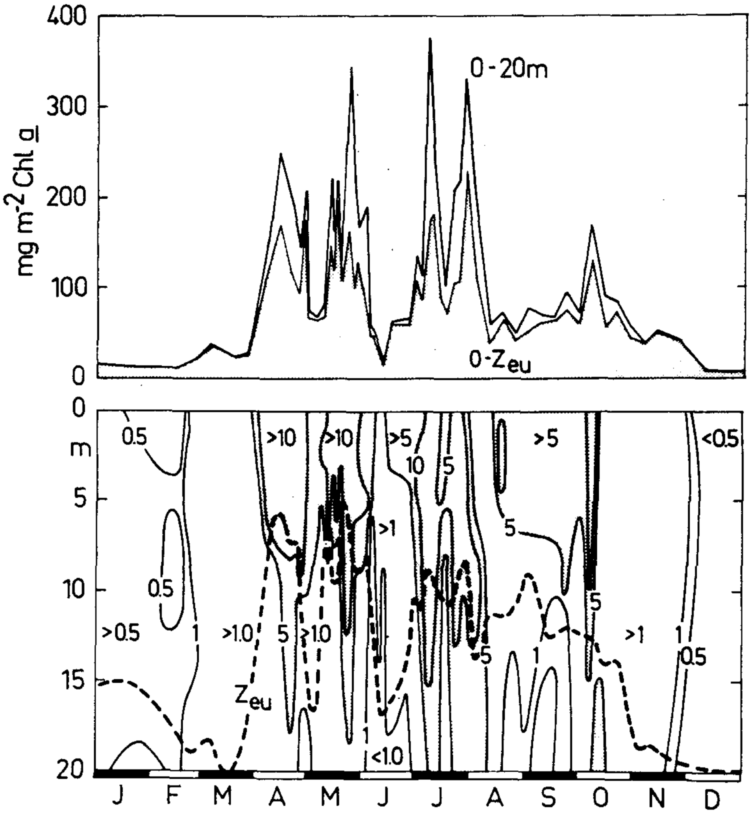

Figure 5. Seasonal and vertical distribution of chlorophyll a, corrected for pheopigments in Lake Constance, 1981. Top: Vertical pigment integral within the euphotic zone (shaded) and in the uppermost 20 m which is the maximal vertical extent of the euphotic zone. Bottom: Depth-time distribution of chlorophyll a, broken line: Euphotic depth shaded: Concentrations exeeding 5 mg m^{-3}.

3.2.3 The Seasonal distribution of the underwater quantum flux

During winter, early spring and late autumn when phytoplankton are scarce and have only negligible impact on water turbidity, the depth-time distribution of underwater irradiance reflect the variations at the water surface. During the growing season, however, the irradiance underwater at any given depth is to a greater extent controlled by water transparency changes than by variations in surface irradiance (Fig. 6).

3.3 *Euphotic seston and phosphorus*

If biomass inceases, concentrations of dissolved nutrients decline because nutrients are incorporated into phytoplankton [53]. For truly reciprocal patterns between

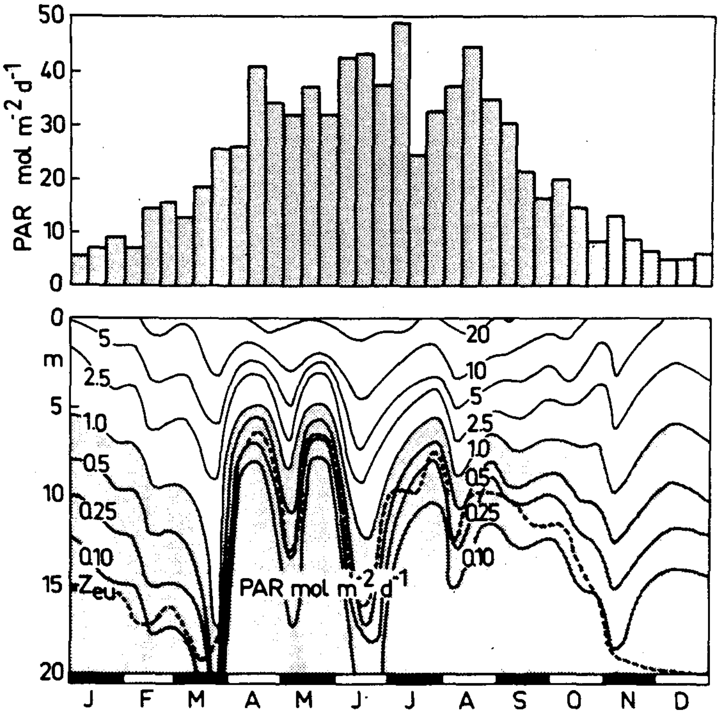

Figure 6. Seasonal and vertical distribution of photosynthetically active radiation (PAR) in 1981. Top: Incident daily fluxes, mean values for the respective 10-day intervals. Bottom: Depth-time distribution of underwater quantum fluxes. Shaded: Daily fluxes below 1 mol m^{-2}. Broken line: Lower boundary of the euphotic zone.

biomass and nutrient concentrations within the euphotic zone three conditions have to be met: (1) Negligible quantities of dissolved nutrients enter or leave the euphotic zone during the growing season via the tributaries and the outlet, respectively. (2) Minimal losses of biomass occur by settling fluxes. (3) The elemental composition of biomass does not change. Because nutrients in excess of demand are accumulated in the biomass pool by luxury consumption [54–57], condition (3) is only met for a nutrient that continues to be limiting to phytoplankton growth yield throughout the stratified season.

In Lake Constance truly reciprocal patterns between dissolved and incorporated phosphorus only appear during the first half of the growing season. If scales of dissolved reactive phosphorus and particulate carbon are standardized according to the Redfield ratio [58] it moreover becomes obvious that major proportions of particulate phosphorus are not incorporated in phytoplankton biomass. Phytoplankton biomass and total POC vary in remarkable synchrony (Fig. 7). Phytoplankton carbon on the average contributes 15–20 % to the total particulate organic carbon pool [59]. The rest of the POC-pool is comprised of detritus, bacterioplankton and zooplankton. Considerable seasonal variation of this percentage does exist, however. During winter phytoplankton contribute 6 %–20 % to the total POC-pool, in July at maximum 40 %–50 % of POC consists of phytoplankton. The significant correlation between phytoplankton carbon and total POC (1981: $r^2 = 0.61$, $p < 0.001$) and the synchrony in the temporal variation of phytoplankton and POC suggest that the turnover of newly formed particulate organic carbon is rapid. The decline in total POC and phytoplankton biomass in late April was caused by a temporary increase in mixing depth. Thereby SRP entered the euphotic zone and POC was lost from the euphotic zone by mixing beyond the euphotic depth. Decreasing POC and phytoplankton in late May and early June, by contrast, are caused by excessive grazing mainly by cladocera which also regenerate nutrients.

Between mid-June and mid-winter both POC and phytoplankton concentrations are much lower than to be expected if all euphotic SRP were incorporated into POM. This discrepancy could be explained in three fashions: (1) enhanced P-content of POM, (2) nutrients other than P limit phytoplankton growth yield, and (3), large proportions of P are lost from, rather than regenerated within, the euphotic zone.

The first hypothesis can be clearly dismissed: The P-content of POM would have to increase sixfold as compared to the Redfield ratio (C : P 106, atomic) in order to explain the observed time-course of POC and SRP. Enhanced P-content in phytoplankton, however, could only be expected early in the year while P is still in excess. The second hypothesis can at best explain the lack of reciprocity in July and August when large diatoms obviously are Si-limited. In fact, silicon depletion ultimately leads to the decline of diatom populations [60, 17, 8].

The best explanation for decreasing SRP values without reciprocal POC increase in late summer and autumn is sedimentation of POM of the euphotic zone. During the first half of the year flagellates dominate the phytoplankton which decompose within the euphotic zone, whereas later in the year sedimentary losses of phytoplankton are significant and SRP is absorbed to settling particles [7, 36, 59, 61].

3.4 *Photosynthesis-irradiance relationships*

In Lake Constance both total phytoplankton biomass and species composition exhibit unusually large seasonal variations which lead to a wide array of profile-shapes [20]. The vertical integral of photosynthesis and thus productivity per unit lake surface area is a function of fractional light absorption, that is, the proportion of underwater PAR that is absorbed by active photosynthetic pigments [62, 49, 20].

In Lake Constance the theoretical productivity maximum, on the condition that all underwater light is absorbed by photosynthetic pigments, is never reached [20]. However, in hyper-eutrophic lakes [63, 64] and littoral cyanobacterial mats [65] areal production rates close to the upper limit [62] are observed.

At any given chlorophyll concentration (and thus water transparency) and surface irradiance, integral photosynthesis is controlled by the photosynthetic responses of algae to light. In Lake Constance photosynthesis versus irradiance curves (“P vs. I curves”) exhibit a wide variety (Fig. 8). Disregarding surface light inhibition, two

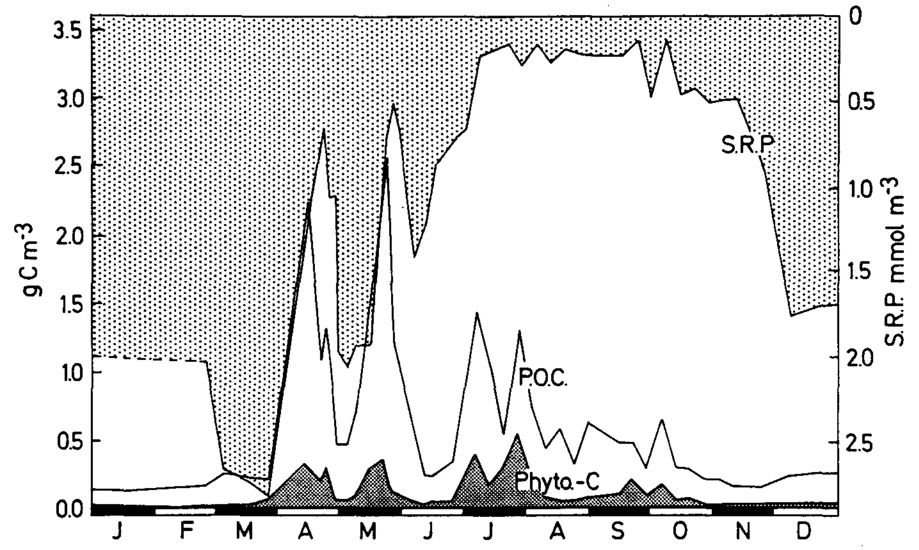

Figure 7. Seasonal course of POC and phytoplankton carbon (dark shade), as well as soluble reactive phosphorus (SRP, stippled) in 1981. The scales (left: Carbon from bottom to top, right: SRP from top to bottom) have been adjusted to each other according to C : P atomic ratio of 106 (Redfield ratio). Changing POC concentrations should lead to reciprocal changes in SRP concentrations and vice versa by transitions of P-pools from the dissolved to the organic particulate fraction and back. Note that until early June POC and SRP concentration changes can be explained by pool transitions alone, whereas later in the year POC is lower by a factor of 6 than anticipated from euphotic SRP concentrations.

parameters suffice to describe P vs. I curves [66]: The initial slope of the limited portion of the curve (α^B) and the light-saturation plateau or photosynthetic capacity (P_{max}). The initial slope of the light-limited portion of the P vs. I curve (α^B) is a function of the maximum quantum yield of photosynthesis and the absorption cross-section of photosynthetic pigments, whereas the light-saturation plateau is controlled by the potential of the photosynthetic units to generate reductant [67–70].

In Lake Constance the initial slope of P vs. I curve has been determined by regression analysis. The intersection with the plateau of light-saturation (P_{max}) characterizes the "light intensity at onset of light saturation", I_k. In Lake Constance α^B and P_{max} are not correlated with each other. Quantum fluxes at which photoinhibition becomes apparent, appear to be related to I_k (Fig. 8).

Variations in photosynthetic responses to light can be attributed either to changing species composition, light-shade adaptation in populations of individual species, or, most likely, both. Whereas the initial slope (α^B) exhibits a consistent pattern with high winter values and low summer values, the photosynthetic capacity shows three maxima, of which the early summer peak (late May/early June) has been the most consistent between the years of observation (Fig. 9).

The photosynthetic capacity is predominantly temperature-controlled in Lough Neagh whose phytoplankton species composition varies relatively littel with season [72]. Findenegg's [73] contention that light-saturated photosynthetic rates are

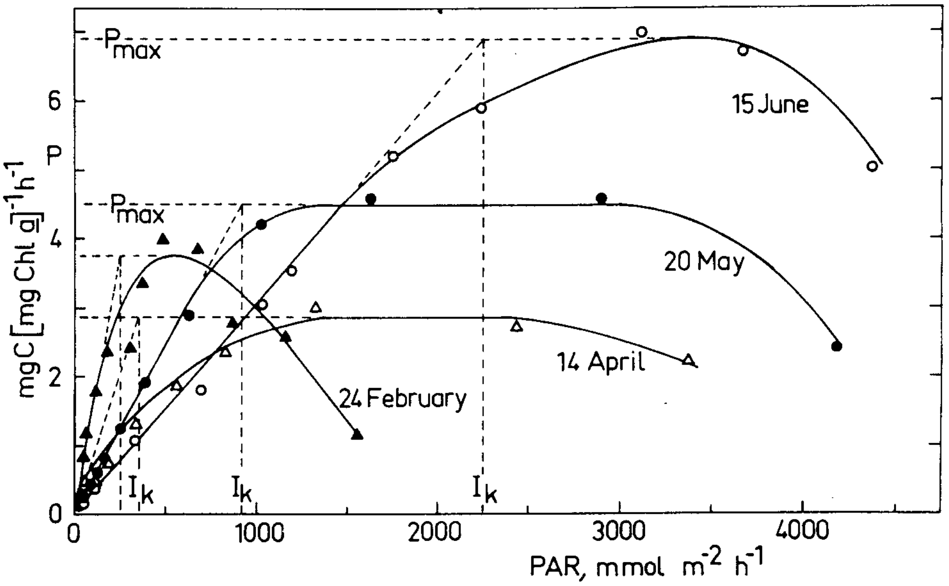

Figure 8. Dependence of photosynthesis per unit of chlorophyll a from underwater radiance at 4 dates in 1981. The quantum fluxes at onset of light saturation (I_k) have been determined by linearly extrapolating the light-limited portion of the P vs. I curve as determined by linear regression analysis to chlorophyll-specific photosynthetic rates at saturating light levels (P_{max}).

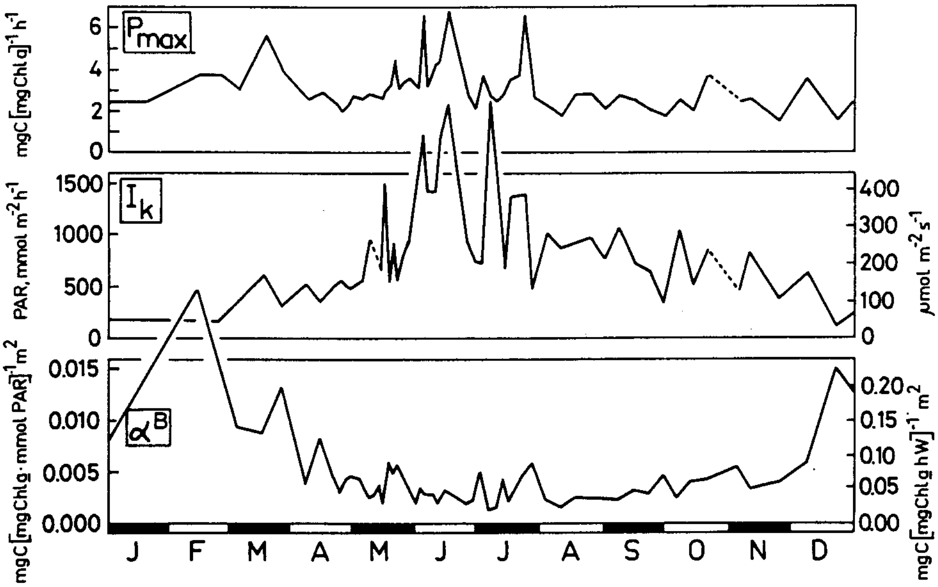

Figure 9. Seasonal course of light-saturated chlorophyll-specific photosynthesis (photosynthetic capacity P_{max}), quantum flux at onset of light saturation (I_k) and the slope of the light-limited portion of the P vs. I curve (^{B}). P_{max} and ^{B} are truly independent from eachother whereas I_k is given by P_{max}/α^B.

affected by nutrient supply have only been supported in cultures by Senft [74].
In Lake Constance, a rather irregular pattern of variations in photosynthetic capacity is observed. Concomitant photosynthetic measurements in an incubator under saturating light and constant temperature conditions suggest that alterations in light-saturated photosynthetic rates are mainly related to mean cell volumes of the assemblage. Variations due to changes in species compositions mask possible temperature effects. The consistently high light-saturated assimilation numbers in June can be explained by the combination of relatively high temperatures and small species [75].

Part of the variation in P_{max} could also be explained by light-shade adaptation which can act in two dimensions: Over the course of the year algae should adapt to daily mean quantum fluxes as a function of solar height and depth of mixing. During lake stratification algae should moreover adapt to prevailing quantum fluxes at any given depth as a function of surface irradiance and vertical light attenuation [76, 77]. In Lake Constance both temporal and vertical shifts in light-shade adaptation are likely.

Temporal shifts in photosynthetic light responses can in part compensate for seasonal variations in incident quantum fluxes. If relative photosynthesis as a fraction of maximal photosynthesis is plotted, effects by varations in biomass and photosynthetic capacity can be eliminated [78] (Fig. 10). In plots of relative photosynthetic rates versus actual depth, variations in the vertical distribution are considerable because water transparency changes as a function of biomass (Fig. 10, top). If relative photosynthetic rates are plotted versus levels of underwater irradiances, however, the isopeths shift in parallel with surface irradiance (Fig. 10, bottom). This suggests that the algae are capable of in part compensating for variations in surface irradiance. Fig. 10 is based on data during the incubation period around noon. Sesonal variations in daylength, therefore, are not accounted for.

Vertical shifts in light-shade adaptation are also to be expected in Lake Constance whose upper water column does not exhibit homothermy during summer. Observed vertical shifts in quantum yields of light-limited photosynthesis whenever the water column is thermally stratified, point into that direction [21].

3.5 *Estimates of annual primary producitivity*

Annual primary productivity figures are of fundamental importance for determining the trophic status of a lake [73, 78, 79]. In conjunction with the transfer efficiency within the food web they determine maximum attainable fish yields [80–82]. Nevertheless, good estimates of annual primary productivity exist only for a limited number of lakes [83]. Because photosynthetic measurements cannot be performed daily, extrapolations from a restricted number of measurements covering all seasons have to be attempted. Moreover, measurements over the entire light period usually but not always yield lower estimates of daily production rates than 2–3 consecutive short incubations during the same light period [84–86]. Therefore, also day-rate estimates of primary production are usually based on extrapolations of values obtained during a period covering only a fraction of the entire day.

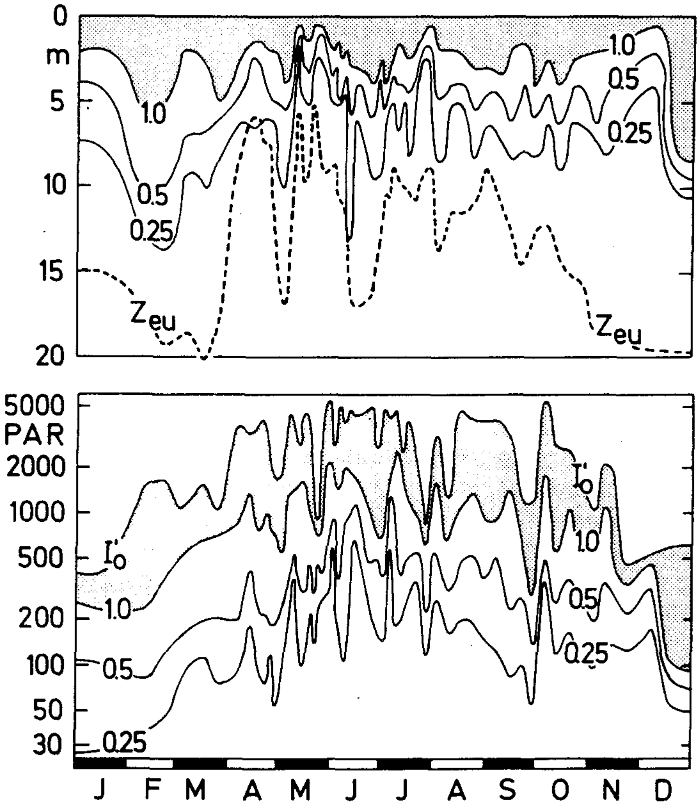

Figure 10. Depth-time distribution of relative photosynthetic rates during mid-day incubations (expressed as fractions of light-saturated photosynthesis) in 1981. Photosynthesis in the top panel is plotted versus actual depth, in the bottom panel versus under water irradiance during the incubation period. The lower boundary of the euphotic zone is given in the top panel. Note that light levels at which a certain relative photosynthesis is reached varies roughly in parallel with incident quantum fluxes.

3.5.1 Daily primary production rates

In this study Talling's [10, 41] method of extrapolation from 4-hr to day-rate estimates has been used. This method assumes that the physiological responses of phytoplankton to irradiance does not change within one day although evidence to the contrary does exist, also for Lake Constance [21]. In the simplest form the vertical integral of photosynthesis can be expressed by

$$\sum_{0}^{Z_{eu}} A_Z \, \Delta Z = A_{max} \cdot Z_i \qquad (7)$$

where Z_i is the depth where half-saturated photosynthesis is observed [10]. If in the light-limited portion of the P vs. I curve a linear relationship between underwater irradiance and photosynthesis exists, Z_i is defined by

$$Z_i = \ln(I'_o / 0.5\, I_K) / k \tag{8}$$

In this study, unlike in Talling's model, the vertical photosynthesis integral was determined from in-situ measurements at 15 depths by trapezoidal integration. It was assumed that the photosynthetic rate measured at any given depth (A_z) represented a reasonable average for the layer between the two adjacent layers ($A_z \cdot \Delta Z_n$). The depth interval ΔZ_n thus was calculated by

$$\Delta Z_n = \frac{Z_{n+1} + Z_n}{2} - \frac{Z_{n-1} + Z_n}{2} \tag{9}$$

where Z_n is the sampling depth considered, Z_{n+1} and Z_{n-1} are the sampling depths immediately below and above. The depth Z_i was determined from the ratio $\Sigma A/A_{max}$ which yielded results that did not differ significantly from estimates based on graphical determinations of I_k. Talling used the depth Z_i in units of optical depth, that is, divided by the depth interval within which underwater radiance decreases to 50 % of its original value, which he termed light-divisions L. D.:

$$[L.\,D.] = Z_i\,[O.\,D.] = \ln(I_o/0.5\, I_k) / \ln 2 \tag{10}$$

Because light-divisions take into account the exponential decline of light with depth and the physiological responses of the phytoplankton assemblage at hand to light, their time-integral represents a convenient proportionality factor for integral photosynthesis as a function of surface irradiance, termed light division-hours, [L. D. H.]:

$$[L.\,D.\,H.] = [L.\,D.] \cdot \Delta t = [\ln(I_o/0.5\, I_k) / \ln 2] \cdot \Delta t \tag{11}$$

Photosynthesis during the incubation period was expressed on an hourly basis and $[L.\,D.\,H.]^{inc}$ was determined by using the mean surface irradiance during the incubation period. For the entire day light-division-hours were based on the mean value of hourly surface irradiance during the entire day, multiplied by the daylength in hours. Daily integral photosynthesis then was determined by

$$\sum_{0}^{Z_{eu}} \sum_{0}^{\Delta t_d} A_Z \Delta Z \Delta t_d = \sum_{0}^{Z_{eu}} A_Z \Delta Z[h^{-1}] \cdot [L.D.H.]^d / [L.D.H.]^{inc} \tag{12}$$

3.5.2 Procedures of extrapolation for annual productivity estimates

For realistic estimates of annual productivity we need day-rate estimates of integral photosynthesis on a sufficient number of dates. The question how many day-rate estimates are required is open to dispute and cannot be resolved in general. Unexplained dramatic day-to-day variations of integral daily photosynthesis have been observed [87]. In Lake Constance daily photosynthetic rates exhibit wider short-term fluctuations than do both incident irradiances and vertical light attenuation. However, mean euphotic chlorophyll concentrations show a similar variability (Table 1). Although in Lake Constance vertical light attenuation is strongly dependent on phytoplankton abundance (chlorophyll concentration), a significant proportion of turbidity is independent of phytoplankton and probably relatively stable. Day-to-day variations in production rate estimates moreover to some extent depend on patchiness of biomass and lateral advection rather than on waxing and waning of biomass.

Table 1: Short-term variations in daily production rates in Lake Constance together with important controlling variables, May 1981.

Date	I_0 mol $m^{-2}d^{-1}$	k* m^{-1}	chla* mg m^{-3}	P g C $m^{-2}d^{-1}$
4	20.9	0.27	3.8	1.06
8	37.8	0.39	5.9	1.19
11	21.6	0.81	26.4	–
14	33.2	0.55	14.1	2.63
15	49.1	0.48	20.8	2.92
18	0.51	11.7	2.80	
20	46.1	0.89	25.7	3.94
22	50.6	0.77	27.2	0.57
25	14.8	0.61	13.6	1.31
27	20.1	0.54	15.0	2.41
C.V.%	42.6	33.2	50.9	52.6

* mean value within the euphotic zone

In lakes that exhibit wide variations in phytoplankton biomass, more frequent estimates of production rates will be required. As a general rule, primary productivity should be estimated sufficiently often to allow reasonable monthly mean values which then can be used as a basis for estimates of annual productivity. In most lakes a flexible sampling schedule (more frequent measurements in spring and summer than in late fall and winter) is recommended.

However, even if frequent measurements are performed, extrapolations will be necessary. Ideally these extrapolations should take into consideration all variables that control algal photosynthesis: The environmental variables incident irradiance, vertical light attenuation and temperature, variations in biomass, and the variables which control the intrinsic porperties of the P vs. I curve. Megard et al. [14] have demonstrated how the interaction of environmental and instrinsic profile parameters might operate but in general available information is insufficient for accurate predictions.

In Table 2 results of four methods of calculating monthly mean values of daily production rates and thus annual productivity are compared:

(1) *Averaging of daily areal production rates:* The simplest and probably most commonly applied method is to calculate monthly mean values of daily production rates by forming arithmetic mean values. This method assumes that irradiances and integral photosynthesis during the days of measurement are representative for the respective months. Fig. 11 upper panel shows that estimates of monthly means of daily irradiance based on the days of photosynthetic measurements in reality can differ greatly from true monthly mean values even if frequent measurements are performed.

Table 2: Four different estimates of monthly mean values of daily primary production rates (as g $m^{-2}d^{-1}$) and of annual sums (as g $m^{-2}yr^{-1}$) for 1981 in Lake Constance.
Daily rates were estimated from 4-hour incubations around noon by using Talling's light-division-hour method (eq. 12). Monthly mean values were calculated by forming arithmetic means of measured values (1), by correcting for deviations between monthly mean values in surface irradiance on days of measurement and true mean irradiance values by using quotient (linear interpolation, 2), as well as by using ratio of light-division-hours (3), and based on a simplified Fee-model from mean values of irradiance, water transparency, and photosynthesis – versus irradiance curve, which were determined for each ten-day-interval.

Month	n*	(1) arithmetic mean value	(2) corrected linearly	(3) corrected logarithmically	(4) integrated P vs Icurve
January	1	0.05	0.16	0.16	0.14
February	2	0.27	0.17	0.22	0.26
March	2	0.31	0.66	0.41	0.60
April	6	2.03	2.07	2.05	2.85
May	9	2.09	2.20	2.15	2.20
June	8	1.32	1.13	1.21	1.15
July	7	1.76	2.11	1.94	2.94
August	5	0.82	1.04	0.91	0.84
September	4	0.85	1.01	0.91	0.65
October	4	0.57	0.49	0.54	0.68
November	3	0.25	0.25	0.25	0.24
December	2	0.04	0.06	0.06	0.02
Annual sum	53	316	347	330	385

* number of incubations per month

Here two procedures to correct for actual variations in the daily incident irradiances in lieu of the irradiances observed on the days of measurement are compared (methods 2 and 3):

(2) *Linear correction for variations in surface irradiance:*

Here A_d is the arithmetic mean value of all daily production rate estimates during the month of observation. $I_{o\ obs}$ is the surface irradiance on the days of observation and $I_{o\ act}$ is the true monthly mean value of daily surface irradiances:

$$A_{dcorr} = A_d \cdot \bar{I}_{0act} / I_{0obs}. \tag{13}$$

(3) *Light-division-hour method:* This method uses the daily light-division hours as proportionality factor:

$$\sum A_{\mathrm{dcorr}} = \sum A_d \cdot [\mathrm{L.D.H.}]^d_{\mathrm{act}} / [\mathrm{L.D.H.}]^d_{\mathrm{obs.}} \tag{14}$$

$[\mathrm{L.\,D.\,H.}]^d{}_{\mathrm{obs}}$ is the mean value for daily light-division-hours based on the days of photosynthetic measurements and $[\mathrm{L.\,D.\,H.}]^d{}_{\mathrm{act}}$ is the true monthly mean value of daily light-division-hours. The latter method should yield a more realistic estimate of monthly mean values of daily production rates. In reality, however, the differences are rather small (Table 2, Fig. 11, bottom).

(4) *Extrapolation from mean environmental and profile variables:* The procedure adopted here is a simplification of the first version of Fee's model [12, 13] which uses surface irradiance, vertical light attenuation and photosynthesis versus irradiance relationships. At first, true mean values of surface irradiance and average measured values of k, Chla concentration, α^B and $P_{\max}$ were determined. These values then were used to determine a simplified pattern of the depth-time distribution of daily photosynthesis (Fig. 12, bottom). Vertical integrations were performed by subdividing the photosynthesis-depth profile into two portions: From the surface down to the depth where I_k occured, a constant rate of light-saturated photosynthesis was assumed to occur:

$$A_Z = P_{\max}\,\mathrm{Chla} = \mathrm{const.} \tag{15}$$

At depths where underwater irradiance was less than I_k photosynthesis was assumed to be

$$A_Z = \alpha^B I_Z \cdot \mathrm{Chla}. \tag{16}$$

Vertical integration was performed by

$$\sum_{0}^{Z_{cu}} A_Z\,\Delta Z = \mathrm{Chl\underline{a}}\left(P_{\max} \cdot Z_{I_K} + \int_{Z_{I_k}}^{Z_{eu}} \alpha^B\,I_Z\,dz\right).$$

Because if

$$Z > Z_{I_k}, \qquad \int_{Z_{I_k}}^{Z_{cu}} A_Z\,dz = \mathrm{Chl\underline{a}} \int_{Z_{I_k}}^{Z_{cu}} \alpha^B\,I_k \cdot e^{-kz}\,dz,$$

the vertical photosynthetic integral can be expressed by

$$\sum_{0}^{Z_{cu}} A_Z\,\Delta Z = \mathrm{Chl\underline{a}}\left(P_{\max} \cdot Z_{I_K} + \alpha^B\,I_K \cdot \frac{1 - e^{-k(Z_{cu} - Z_{I_k})}}{k}\right). \tag{17}$$

This method disregards surface light inhibition and the curvature of the transition zone between light-saturated and light-limited photosynthesis and thus should yield overestimates of integral photosynthesis (Fig. 12, top). However, surface inhibition has a rather small impact on integral photosynthesis [11] and may be overestimated

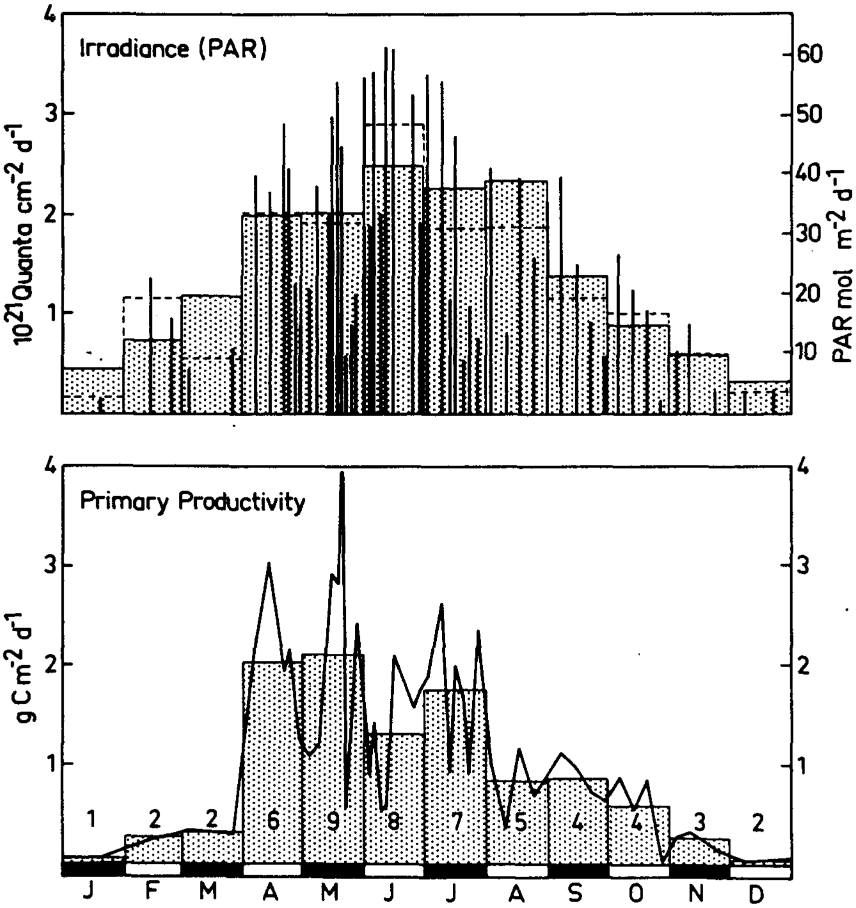

Figure 11. Seasonal courses of incident PAR (top) and daily photosynthetic rates in 1981 (bottom). The solid vertical lines in the upper panel represent daily quantum fluxes on the days of photosynthetic measurements, the stippled columns represent true monthly mean values of surface irradiance, broken lines monthly mean values based on dates where primary production rates were measured. The solid line in the bottom panel connects daily integral photosynthetic rates on the days of measurement. The stippled columns represent monthly mean values of production rates as determined by equation 14 by taking into consideration the discrepancy between true monthly mean values of daily quantum fluxes and mean values based on days of photosynthetic measurements. Numbers of photosynthetic measurements during the respective months are given.

in incubations where phytoplankton are held at fixed depths [88]. Annual productivity estimates by method (4) are 22 % higher than the most unrealistic estimates using uncorrected monthly mean values of daily pruduction rates and 11 % to 17 % higher than the estimates correcting for variations in daily sums of surface irradiance. Comparisons of the estimates of monthly mean values (Table 2) show that the variability of results becomes smaller as the number of individual measurements rises. Each extrapolation technique, also those which make more elaborate assumptions,

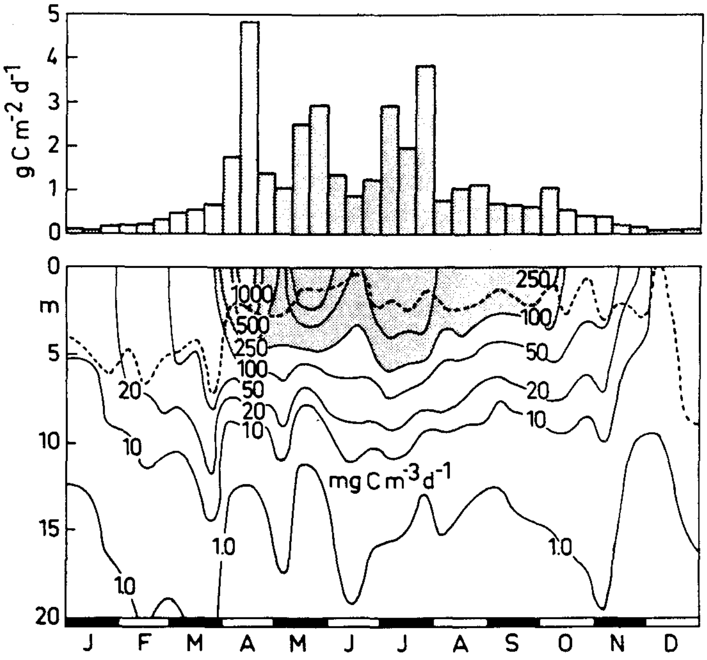

Figure 12. Seasonal and vertical distribution of daily primary production rates in Lake Constance. Top: Ten-day mean values of daily integral production rates as determined by using mean daily irradiances, vertical light attenuation coefficients and profile parameters by equation 16. Bottom: Depth-time distribution, based on ten-day mean values of relevant parameters as determined by equations 14 and 15.

suffer from remarkable inaccuracies which cannot be accounted for by correction procedures. From this we conclude that the best and most accurate strategy for estimating annual productivity is to make as many in situ measurements as possible rather than to increase the sophistication of the calculation procedure.

3.6 *Seasonal variations in biomass and productivity*

The primary production process is driven by inputs of radiance and nutrients. The biomass yield moreover depends on the net balance of production rates minus loss rates. There is overwhelming evidence now that "metabolic losses", that is, respiration and release of dissolved organic matter, are the single most important in the majority of phytoplankton communities [89, 21, 90, 91].

Whole-community studies are indispensable if mass and energy budgets of lakes are to be attempted. With few exceptions, studies of species periodicity only yield data on net changes in population densities and thus do not give a true picture of the flow of matter. Mass balance studies on the population level are only feasible if true population growth rates can be determined by the analysis of division stages [92–95]. This extremely laborious approach obviously cannot be applied on a routine basis.

3.6.1 The effect of incident radiance and mixing depth

The unusually wide fluctuations in both species composition and total biomass of Lake Constance phytoplankton indicates that the ratio of production rates to loss rates are highly variable over the course of the year.

Daily light inputs at the surface of Lake Constance vary about five-fold seasonally due to variations in day length (1:2) and mean daily irradiances as a consequence of variations in solar angles (1:2.5, Fig. 2). However, the quantity of light a phytoplankter actually receives moreover is controlled by the vertical gradient of underwater light and the mixing depth of the water column. The effect of the interaction of these factors on the phytoplankton has been treated by two concepts which in essence attempt to predict the net energy balance of the entire community.

Common to both concepts is the contention that beyond a certain depth of mixing the algae receive insufficient quantities of light to maintain a positive net energy balance. Riley [96] has calculated the mean quantity of light the algae receive by averaging the underwater light fluxes over the mixed water column. We can write

$$\bar{I}_Z = \frac{1}{Z_m} \int_0^{Z_m} I_Z \, dZ = \frac{1}{Z_m} \int_0^{Z_m} I'_0 \cdot e^{-kZ} \, dZ \tag{18}$$

[76]. Riley [96] has used

$$\bar{I}_Z = I'_0 \frac{1 - e^{-kZ_m}}{kZ_m} \tag{19a}$$

which has been termed "effective light climate" [97], where I'_0 is the irradiance immediately below the water surface and Z_m the mixing depth. Since at large mixing depths $e^{-kZm} << 1$ we can can simplify this equation to

$$\bar{I}_Z \approx \frac{I'_0}{kZ_m} \tag{19b}$$

Riley observed beginning spring growth of marine phytoplankton at an effective light climate of 0.03 cal cm^{-2} min^{-1} which is roughly equivalent to a quantum flux of 44 μmol m^{-2} s^{-1} of PAR, or a daily input of ca. 1.8 mol m^{-2} of PAR. In two Swedish lakes chrysophytes appear to be able to grow above 44 μmol m^{-2} S^{-1} but not below 22 μmol m^{-2} S^{-1} [97].

In Lake Constance the spring bloom begins at an effective light climate exceeding about 2 mol m^{-2} d^{-1} which is in good agreement with Riley's and Ramberg's findings (Fig. 13). However, during periods of both low or absent stability and stratification, potential growth rates vary widely, and are counterbalanced by concomitant losses [22]. Overall, the effective light climate appears to have a stronger influence on the velocity of carbon turnover than on biomass growth and decline, respectively.

The second concept of determining the net energy balance of phytoplankton was developed by Sverdrup [98] for the ocean and was later applied to lakes [41, 99]. It

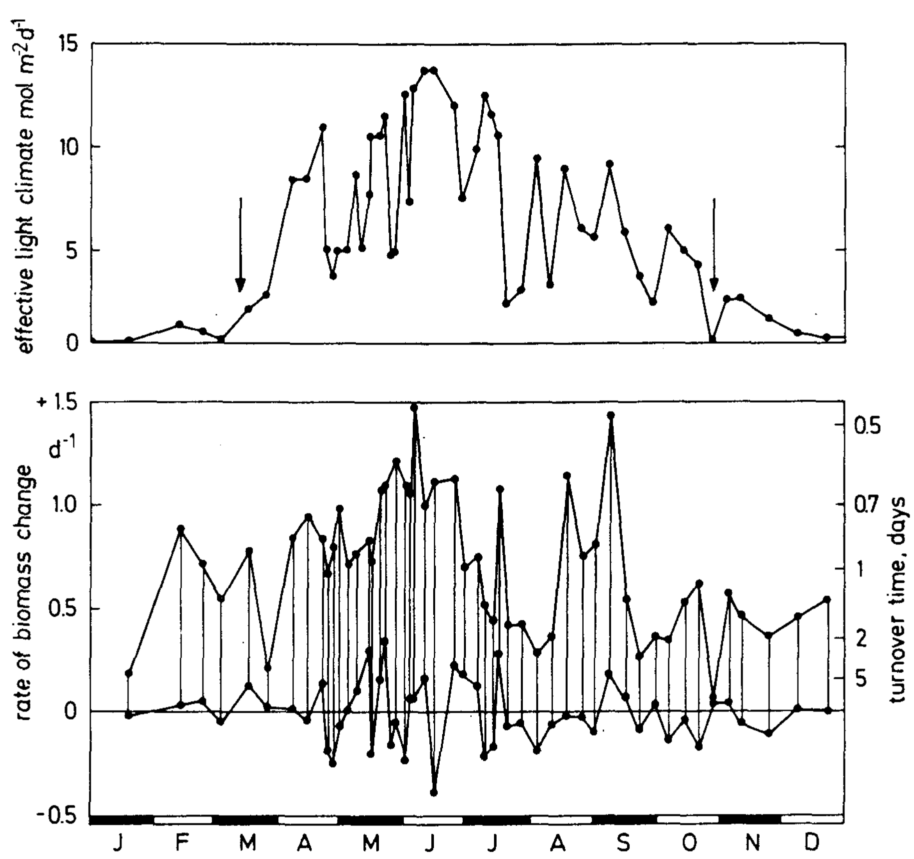

Figure 13. Seasonal variations in the effective light climate (calculated by using equation 19, top panel) and rates of potential and actual daily community biomass change (ln-units d^{-1}, bottom panel). The discrepancy between potential rates of growth (upper curve) to be expected from photosynthetic rates, and observed rates of change (lower curve) are attributed to losses 22. The right scale given carbon turnover times corresponding to potential growth rates. During mixing the effective light climate is controlled by incident PAR, vertical light attenuation and mixing depth. During thermal stratification the effective light climate was assumed to correspond to the mean irradiance over the euphotic water column, or 21 % of the irradiance immediate below the lake surface. The vertical arrows designate the beginning and end, respectively, of the period with a thermal gradient within the water column.

defines a mixing depth ("critical depth of mixing") Z_c, beyond which population growth its no longer possible because then the vertical integral of respiration exceeds the vertical integral of photosynthesis. Talling and Grobbelaar in turbid systems found that the critical depth of mixing corresponds two 5–6 times the euphotic depth. Lake Constance is rather clear during winter when thermal stability is low or absent with a euphotic depth of about 20 m. The critical depth of mixing during that time should be 100 m–120 m and should be exceeded for a period of 4–6 weeks each winter.

Any model defining the critical depth of mixing should not only incorporate surface irradiance and changes in the optical properties of the water body concerned, but also variations in the photosynthetic light requirements of the algae. In Lake Constance, photosynthetic profile parameters are highly variable over the course of the year (Figs. 8–10). It has frequently been assumed that respiration is constant over depth in a mixed water column and can be expressed as a fraction of light-saturated photosynthesis:

$$R_Z = r\,A_{max} \tag{20}$$

In a mixed water column the vertical integral of hourly photosynthesis can be expressed by

$$\Sigma A_Z\,\Delta\,Z = (A_{max}/k)\,\ln\,(I_o/0.5\,I_K) \tag{21a}$$

[10, 41]. This equation can be transformed to

$$\Sigma P \Delta Z = (A_{max} \cdot \ln 2/k) \cdot [\mathrm{L.\,D.}] \tag{21b}$$

[41]. Daily photosynthesis then is

$$\sum_{0}^{Z_{eu}} \sum_{0}^{At_d} A_Z\,\Delta\,Z\,\Delta t = (A_{max}\,\ln 2/k) \cdot [\mathrm{L.D.H.}]^d \tag{22}$$

where daily light division hours L. D. H.^{d} are the time-integral of hourly light-divisions L. D. based on the mean surface irradiance and mean I_k value.

$$[\mathrm{LDH}]^d = [\mathrm{LD}] \cdot \Delta td \qquad \text{(cf. eq. 11).}$$

The hourly vertical integral of respiration has to be calculated for the entire mixing depth because algae travel from the water surface to the depth of mixing (Z_m) and back:

$$\sum_{0}^{Z_m} R_Z\,\Delta\,Z = rA_{max} \cdot Z_m \tag{23}$$

The daily integral of respiration in a mixed water column is

$$\sum_{0}^{Z_m} \sum_{0}^{24} R_Z\,\Delta\,Z\,\Delta\,t_t = 24r\,A_{max} \cdot Z_m. \tag{24}$$

When it is assumed that algal respiration is constant over the entire 24-hr period the critical depth of mixing is reached if

$$\sum_{0}^{Z_m} \sum_{0}^{\Delta t_d} A_Z \Delta Z \Delta t_d = \sum_{0}^{Z_m} \sum_{0}^{24} R_Z \Delta Z \Delta t \tag{25}$$

Since then

$$(A_{max} \ln 2/k) [L.D.H.]^d = 24 r A_{max} \cdot Z_m,$$

we can define the critical depth of mixing ($Z_m = Z_c$) by solving the above equation:

$$Z_c = [L.D.H.]^d \ln 2/24 kr = [L.D.H.]^d/35 kr \tag{26}$$

This equation takes into consideration changes in the photosynthetic characteristics of the algae but requires information on the ratio between light-saturated photosynthesis and the 24-hour average of dark respiration (Fig. 14).

Overall losses from the phytoplankton have been estimated indirectly by comparing potential rates of community growth as calculated from production rates, with observed rates of biomass change. If losses due to grazing, sedimentation and in dissolved form (extracellular release, autolysis) are taken into account, we can indirectly estimate that during a 24-hour interval, 30%–50% of daily gross photosynthesis are lost by respiration [89, 21, 90, 91]. We can use this value to calculate the range of relative respiration rates as a fraction of light-saturated photosynthesis ($r = R_z/A_{max}$) on an hourly basis for the light period. This model assumes that respiration does not change over the diel cycle. Although this is not likely to be true, this simplifying assumption is necessary here to relate light-saturated photosynthesis to respiration. During the light period, hourly integral photosynthesis can be expressed by

$$\Sigma A \Delta Z = A_{max} \cdot Z_i \text{ (eq. 7).}$$

During the same time-interval the depth integral of respiration in a stratified water column over the euphotic zone is

$$\Sigma R \Delta Z = r A_{max} Z_{eu} \tag{27}$$

If the respiratory losses within the euphotic zone during a 24-hour period comprise 30%–50% of integral gross photosynthesis, the range of respiratory losses during the entire light period should be about 10%–30% of daily gross photosynthesis depending on changing ratios of light to dark periods. Provided that light-saturated photosynthesis and respiration are assumed to remain constant during the day, hourly respiration and photosynthesis are related to each other by

$$r A_{max} \cdot Z_{eu} = (0.1 \ldots 0.3) A_{max} Z_i. \tag{28}$$

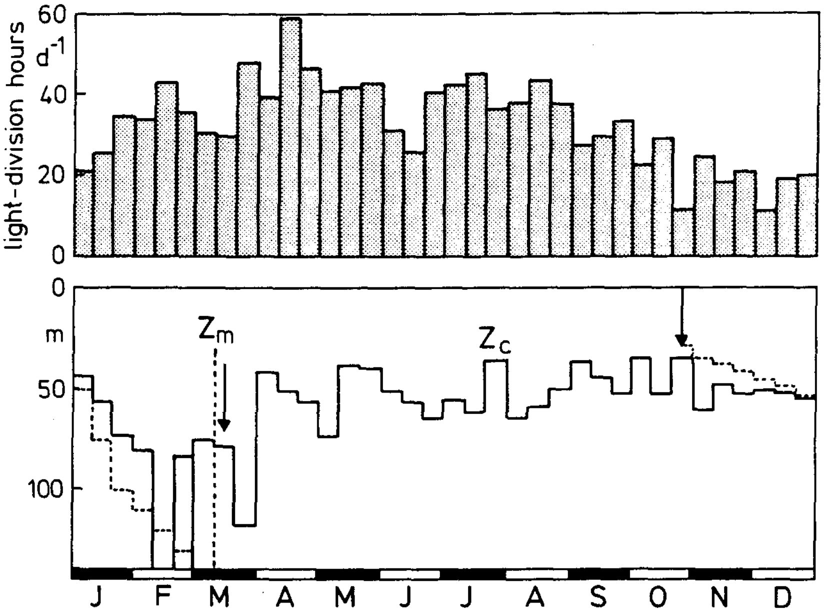

Figure 14. Ten-day mean values of daily light-division-hours (top), and critical (solid lines) and actual (broken lines) depths of mixing. Mixing depth was assumed to correspond with homothermy. Daily light-division-hours were determined by equation 11 and represent a proportionality factor of integral photosynthesis as controlled by mean surface irradiance, daylength, and photosynthetic light requirements of the phytoplankton assemblage. The critical depth of mixing was determined by using equation 26 by assuming r = 0.045 which is a lower estimate assuming a daily integral respiration of ca. 30% of daily integral gross photosynthesis. The vertical arrows designate the beginning and end, respectively, of the period with a thermal gradient within the water column.

If the intrinsic shape of the photosynthesis-depth curve is known, hourly respiratory losses during day can be expressed as fractions of the concomitant light-saturated photosynthetic rate by solving eq. 28 for r.

In Lake Constance the light level at depth Z_i on the average corresponds to 12.5% of surface irradiance, [20]. Thus, the average ratio of $Z_{eu} : Z_i = 2.2$ and the range of r is

$$r = 0.043 - 0.13$$

It has been mentioned earlier that phytoplankton by light-shade adaptation can to a large extent offset effects caused by variations in mean daily incident radiance. Light-division hours provide a proportionality factor for the control of integral photosynthesis by irradiance which accounts for changes in the photosynthetic light requirements of the phytoplankton community. In fact, in Lake Constance daily light division hours only vary by a factor of 3 whereas incident radiance varies fivefold over the course of the year (Fig. 14, top) (Daily mean irradiance varies by a factor of 2.5, Fig. 2).

Critical depths of mixing exceed the actual mixing depth till the end of the year if it is assumed that integral respiration comprises 30% of integral gross photosynthesis. Phytoplankton actually decreases slowly during this period, perhaps mainly by dilution. Only between January and March our model predicts that the lake mixes beyond the critical depth (Fig. 14, bottom). Respiration rates in fact probably are variable both with time and depth. This is also suggested for Lake Constance where overall losses are significantly correlated with production rates [22].

The onset of thermal stratification of the lake is associated with rising light-division hours. Both lead to a dramatic increase in biomass. During mid-summer algae are adapted to maximum light levels and consequently are most sensitive to changes in the light climate created either by decreasing surface radiances, increasing mixing depths, or both. Periods of growth can be followed immediately by periods of biomass decline and are controlled by subtle shifts in the balance between growth and losses rather than by the absolute magnitude of either process [22]. If the balance only slightly tilts in either direction for an extended period (say, 2–3 weeks) we can expect dramatic changes in total biomass.

3.6.2 Regular seasonal patterns of productivity changes

In large lakes such as Lake Constance it can be assumed that nutrient inputs from the watershed to the euphotic zone during the period of thermal summer stratification are negligible for the overall nutrient budget. The input of nutrients during deep winter mixing, therefore, determines the maximum attainable biomass for the ensuing summer [100]. Our investigations were performed during a period when winter concentrations of soluble reactive phosphorus were rather stable (about 2.7 μ mol 1^{-1}). (Since 1981 nutrients have decreased as a consequence of sewage diversion.)

Although the study period was too short to distinguish random from regular events with certainty, a few recurrent patterns emerge (Fig. 15).

(1) Biomass exhibits three peaks, the spring bloom (early April–late May) the summer maximum (early July–mid-August), and the autumnal maximum which shifted from mid-October in 1980 to mid-September in 1982. The summer peak is more pronounced with respect to biomass whereas the spring peak is higher with respect to chlorophyll indicating a significant shift in C: Chl$\underline{a}$ ratios. The clear-water phase regularly occurred in early June but was variable in its extent. It was most pronounced in 1980 and 1982 but less so in 1981 and 1983. In 1984 and 1985 the clear-water phase was delayed and less pronounced (unpubl. data).

(2) Daily production rates exhibit a less regular pattern than biomass. The photosynthesis minimum during the clear-water phase is less pronounced than is the biomass minimum. The highest daily production rates are reached in spring.

(3) Turnover rates (biomass-specific photosynthetic rates) lack a consistent seasonal pattern except for the pronounced maximum during the clear-water phase which is associated with highest maximum assimilation numbers (Fig. 9). The summer biomass maximum coincides with a minimum in biomass-specific photosynthesis.

Despite these marked year-to-year variations, annual productivity figures were

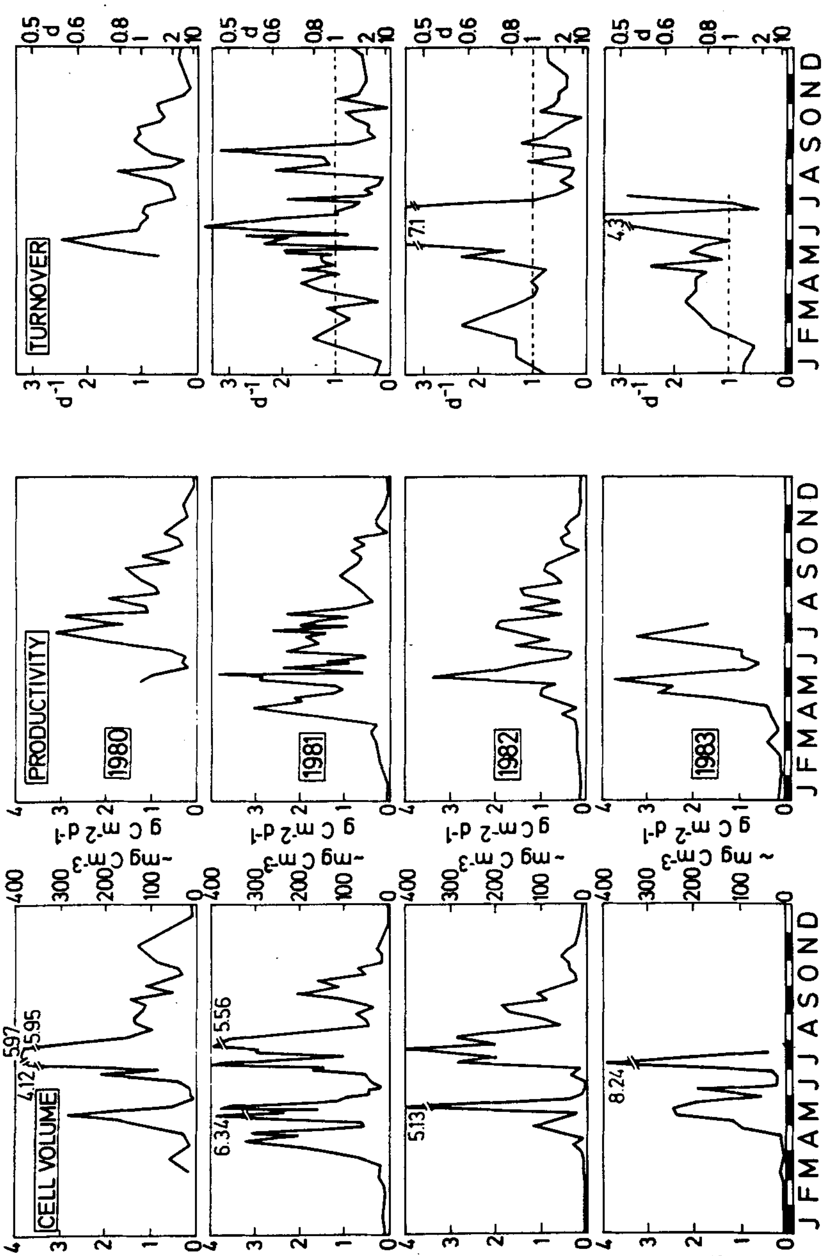

Figure 15. Year-to-year variations in the seasonal course of the mean euphotic phytoplankton cell volume (left), daily primary production rates (center) and phytoplankton carbon turnover (right) which was calculated as described in [22].

rather consistent during the study period (Table 3). This conclusion can be drawn although in 1980 and 1983 productivity estimates did not cover the entire year.

Table 3: Estimates of annual primary productivity in Lake Constance between 1980 and 1983. Values are based on monthly mean values of measured production rates. Values in parentheses were obtained by extrapolating day-rate estimates of photosynthesis to monthly mean values by using true mean monthly irradiances and light-division hours (procedure 3). In 1980 productivity estimates were not conducted between January and April, in 1983 estimates are missing between August and December. To allow a rough estimate of annual productivity the fractions of productivity during these time intervals to annual productivity was assumed to be the same as in 1981 (Jan.–April 1980: 26% of annual) and in 1983 (August–December: 36% of annual), respectively.

Year	g cm^{-2} year^{-1}
1980	ca. 280
1981	316 (330)
1982	237 (269)
1983	ca. 290

4. Conclusions

The seasonal cycles of photosynthesis and biomass development, both with respect to total biomass and species composition, can be regarded as integral expressions of all the factors controlling the primary production process. It is obvious that all factors controlling the seasonal periodicity of the phytoplankton acting at the population level are also responsible for events at the community level, however, to varying degrees.

In production biology the phytoplankton community as a whole can be viewed at as a functional unit which harvests radiant energy and nutrients and produces organic matter that can, or can not, be utilized by the subsequent consumer food web. The efficiency of resource utilization by a community is dependent on external and internal factors.

By *"external factors"* we can understand the availability of the resources in question within the environment. In a critical analysis Talling [101] has shown that the issue of resource utilization efficiency as a function of resource availability is not as clear as one should anticipate from the massive volume of data available. It appears beyond any doubt that for resource availability Liebig's minimum factor concept as expanded by Blackman is universally applicable: Responses in growth rates and yields are a function of the ratio between the availabilities of different resources to each other. And so is resource utilization efficiency. This means that the resource in shortest supply controls the overall response of the community either by controlling its growth rate or crop yield, or both. The resource in shortest supply thereby is utilized with maximum efficiency. The situation is complicated in four respects:

(1) In multispecies systems different species can be controlled by different resources. In such situations it is impossible to identify one single limiting resource for the community as a whole [4, 6, 16].

(2) In some instances considerable time is required for the establishment of an

equilibrium between community responses and resource availability. If the time-constant of resource availability shifts is more rapid than the time-constant of equilibrium formation, no clear pattern can emerge in the response of a community to the availability of a certain resource [4, 16, 102–104].

(3) In phytoplankton different resources can be responsible for growth rate and growth yield. Instantaneous growth rates frequently are controlled by energy availability whereas maximum attainable yields are controlled by nutrient availability [105].

(4) Apparent changes in total biomass and biomass composition are the net result of processes controlling growth (resources) and losses (sinks). Because growth follows the Law of the Minimum, at any given time only one factor is important, whereas losses are controlled by several factors acting concomitantly [106].

By *"internal factors"* controlling resource utilization efficiency, I understand physiological properties of the organisms involved. With respect to nutrients specific nutrient requirements as well as capabilities of nutrient uptake and storage systems are important [55, 56]. With respect to light, specific light requirements of different algal species or groups and the capability for light-shade adaptation have to be considered [68, 71].

The understanding of the seasonal productivity cycle of the phytoplankton is confounded by the complexity of factor interactions. When compared with other lakes, Lake Constance is characterized by unusually large variations in total biomass, species composition and production rates [106]. This variability can best be explained by the seasonal amplitude of both the availability of various resources, and of the factors leading to losses.

In winter the situation is characterized by scarce radiant energy inputs, deep mixing and ample nutrients. Biomass yield is restricted not only by low inputs of energy but also by metabolic losses.

The spring bloom undoubtedly is triggered by the establishment of stratification, however weak it is in the beginning. Abundant nutrients permit rapid growth that at times is interrupted by brief mixing events. Mixing then has a two-fold effect: It dilutes the phytoplankton over a deeper layer of water, and increases respiratory losses. Nutrients at this time are efficiently utilized by the community because only negligible proportions of organic matter are lost by sedimentation.

The end of the spring bloom is brought about neither by nutrient axhaustion within the euphotic zone nor by increasing ratios of integral respiration to integral photosynthesis. The latter can be excluded because in Lake Constance the euphotic zone is thermally stratified and no well-mixed epilimnion exists. The reason for the sudden end of the spring bloom is overgrazing by *Daphnia* populations which can efficiently feed upon the small species available at this time of the year [37, 38, 108, 15]. However, the extent and lately also the timing of the clear-water phase varies. The causal relationships are not fully understood. Zooplankton grazing causes considerable nutrient regeneration leading to increases in euphotic phosphorus concentrations. Favorable light conditions and possibly the dominance of photosynthetically highly active species cause the shortest phytoplankton carbon turnover times of only 4–8 hours during that period [21].

The ensuing summer maximum of biomass is composed of larger more highly grazer-resistant species with lower cellular pigment concentrations. As a consequence, photosynthetic activity is distinctly lower than during spring. Considerable proportions of biomass now are lost by sedimentation which exhibits brief maxima, especially in diatoms if nutrients become depleted. The species composition is controlled by sequential elimination of populations by nutrient depletion, Sommer [8] has proposed that diminished thermal stability coupled with high-light requirements caused the sudden decline of the summer phytoplankton. Photosynthesis and light data do not fully support this view because light requirements of photosynthesis begin to decrease prior to the collapse of the bloom (Fig. 9).

The brief autumnal phytoplankton growth pulse is likely to be triggered by nutrient infusions from the underlying hypolimnion. Efficient nutrient uptake does not allow increasing concentrations of SRP in the euphotic zone, however. The diminished effective light climate by the combined effects of declining dayly radiance inputs and increasing mixing depths leads to the gradual decrease in biomass toward the end of the year.

Reynolds et al. [91] have stressed that photosynthetic rates merely are a measure of the capacity for growth, rather than actual growth, as major proportions of carbon initially fixed do not show up as biomass. In view of our findings this statement should be specified: The photosynthetic activity determines the turnover *velocity* of organic carbon. The amount of carbon that is available to the subsequent consumers depends on the product of biomass multiplied by turnover rates. Thus, the effective availability of radiant energy which ultimately drives the turnover of carbon, together with the supply of nutrients which determines the quantity of accumulated biomass, in the end control how much organic matter can be transferred to the consumers. Losses due to respiration affect the transfer efficiency of carbon and energy along the pelagic food web.

5. Summary

Lake Constance is a large (540 km^2) deep (mean: 100 m) warm-monomictic lake. The phytoplankton assemblage is characterized by unusually wide fluctuations in biomass and daily production rates.

Water transparency is strongly influenced by phytoplankton abundance (chlorophyll concentration) with euphotic depths ranging from 4.8 to 22.5 m. Due to self-shading, the chlorophyll content within the euphotic zone varies considerably less (1:16) than mean concentrations (1:100). The phytoplankton are predominantly phosphorus-limited. However, the maximum biomass comprises only 15–20% of the value to be expected in case of complete incorporation of soluble reactive phosphorus (SRP) into phytoplankton biomass from the Redfield ratio. The remaining phosphorus is stored in particulate organic matter (POM, detritus, bacteria and zooplankton) which varies concomitantly with phytoplankton biomass. However, reciprocal matching patterns of POM and euphotic SRP only occur during the first half of the year. Thereafter, large proportions of phosphorus are lost from the euphotic zone by sedimentation.

Photosynthetic responses of phytoplankton to light exhibit a considerable variation with season. The slope of the light-limited portion of the photosynthesis *versus* irradiance curve shows highest values in winter and minima during summer. The light-saturated maximum assimilation numbers show irregular variations. However, consistently high values are observed in June when phytoplankton biomass is low due to grazing by daphnids. It is suggested that assimilation numbers are mainly influenced by species composition (mean cell size) whichs masks temperature effects. Light-shade adaptation is the most likely mechanism by which light-limited photosynthetic rates are affected. The irradiance at onset of light saturation, which is a function of both light-limited and light-saturated photosynthetic rates, shows low values in winter and maxima during summer. Susceptibility of photosynthesis to inhibition by high irradiances is inversely related to irradiances at onset of light saturation.

The vertical distribution of photosynthesis is a function of incident irradiance, the vertical gradient of underwater light which in turn is controlled by phytoplankton abundance, and photosynthesis-irradiance relationships. Seasonal variations in light-shade adaptation can compensate for variations in daily mean incident photon fluxes but not for changes in water transparency. As a consequence, daily primary production rates vary considerably less than daily inputs of irradiance.

The seasonal cycle of primary productivity is strongly dependent on the mean quantity of light the algae recieve as a function of surface irradiance, vertical light attenuation and the depth of water column mixing. It is likely that the "critical depth of mixing" beyond which a positive net photosynthetic balance no longer can be maintained, is exceeded during approximately 10 weeks between early January and mid-March. Nevertheless the decline of biomass during that time is rather slow. During most of the year the mean irradiance to which the algae are exposed within the water column to a greater extend control rates of carbon turnover (that is, photosynthesis per unit of biomass) than actual rates of biomass change which mainly depend on overall loss rates.

Annual primary productivity of Lake Constance as estimated by four different procedures in parallel ranges from 240–384 g C m^{-2}, values typical for meso-eutrophic lakes. During winter limited radiant energy supply and high respiratory losses due to deep mixing lead to low production rates. The spring bloom is triggered by the establishment of a temperature gradient of surface waters. At the end of the spring bloom small and photosynthetically active phytoplankters are eliminated by grazing. During the summer high phytoplankton biomass is comprised of large grazer-resistant species with low photosynthetic activities. During autumn a third biomass maximum is made possible by low-light requirements of phytoplankton coupled with the infusion of nutrients from the aphotic zone as mixing of the upper layer deepens.

ZUSAMMENFASSUNG

Der Bodensee ist ein großer (540 km^2) tiefer (im Mittel 100 m) warm-monomiktischer See. Die Photoplanktonlebensgemeinschaft ist durch ungewöhnlich weite Schwankungen der Gesamtbiomasse und täglichen Produktionsrate gekennzeichnet.

Die Lichtdurchlässigkeit des Wassers ist stark durch die Phytoplanktonbiomasse (Chlorophyllkonzentration) beeinflußt mit euphotischen Tiefen zwischen 4,8 m und 22,5 m. Infolge von Selbstbeschattung

schwankt der Gesamtgehalt der euphotischen Zone an Chlorophyll wesentlich weniger (1:16) als mittlere Chlorophyllkonzentrationen inerhalb der euphotischen Zone (1:100). Das Phytoplankton ist überwiegend phosphor-begrenzt. Dennoch erreicht die maximale Biomasse nur 15%–20% des Wertes der bei vollständiger Inkoporation des im Winter vorhandenen gelösten reaktiven Phosphor nach der Redfield ratio (C:P = 106:1) zu erwarten wäre. Der verbleibende Phosphor ist in der partikulären organischen Substanz (POM, Detritus, Bakterien und Zooplankton) enthalten, die gleichzeitig mit der Phytoplanktonbiomasse schwankt. Allerdings verhält sich die Gesamt POM und die euphotische Phosphatkonzentration nur während der ersten Hälfte des Jahres reziprok. Danach geht ein großer Anteil des Phosphors durch Sedimentation aus der euphotischen Zone verloren.

Die photosynthetische Antwort des Phytoplanktons auf Licht zeigt beträchtliche jahreszeitliche Unterschiede. Der Anstieg des lichtbegrenzten Abschnittes der Photosynthese-Strahlungskurve zeigt höchste Werte im Winter und Minima während des Sommers. Die lichtgesättigten maximalen Assimilationszahlen zeigen unregelmäßige jahreszeitliche Variationen. Höchste Werte wurden stets im Juni festgestellt, wenn die Phytoplanktonbiomasse infolge starken Zooplanktonfraßes niedrig ist. Es ist wahrscheinlich, daß Assimilationszahlen in erster Linie durch die Artenzusammensetzung beeinflußt werden (mittlere Zellgröße), welche Temperatureffekte überdeckt. Hell-Dunkeladaptation ist der wahrscheinlichste Mechanismus, durch welchen lichtbegrenzte Photosynthesearten beeinflußt werden. Die Strahlung am Beginn der Lichtsättigung, welche eine Funktion sowohl der lichtbegrenzten als auch der lichtgesättigten Photosynthese ist, zeigt niedrige Werte im Winter und maximal während des Sommers. Die Empfindlichkeit der Photosynthese gegen Hemmung durch hohe Strahlung verhält sich umgekehrt proportional zur sättigenden Lichtintensität.

Die Vertikalverteilung der Photosynthese ist eine Funktion der einfallenden Strahlung, des vertikalen Unterwasserlichtgradienten, welcher selber durch Phytoplanktonbiomassedichte gesteuert wird, sowie den Photosynthese-Strahlungsbeziehungen. Jahreszeitliche Schwankungen der Hell-Dunkeladaptation können Schwankungen der mittleren täglichen Strahlung teilweise ausgleichen, nicht aber Unterschiede in der Lichtdurchlässigkeit des Wassers. Infolgedessen schwanken tägliche Produktionsraten wesentlich weniger als tägliche Strahlungsenergieinputs.

Der Jahreszyklus der Primärproduktion hängt sehr stark von der mittleren Lichtmenge ab, welche die Algen als Folge der Oberflächeneinstrahlung, der vertikalen Lichtattenuation und der Durchmischungstiefe der Wassersäule erhalten. Es ist wahrscheinlich, daß die «kritische Durchmischungstiefe», jenseits welcher eine positive Photosynthese-Nettobilanz nicht mehr aufrecht erhalten werden kann, während etwa 10 Wochen zwischen Anfang Januar und Mitte März überschritten wird. Trotzdem ist die Biomasseabnahme während dieser Zeit langsam. Während der meisten Zeit dieses Jahres kontrolliert die mittlere Strahlung, der die Algen innerhalb der Wassersäule ausgesetzt sind, zu einem größeren Maß die Umsatzgeschwindigkeit des Kohlenstoffs (d. h. Photosynthese pro Biomasseeinheit) als die tatsächliche Rate der Biomasseänderung, welche in erster Linie von den Gesamtverlusten abhängt.

Die Jahresproduktion des Phytoplanktons im Bodensee wurde durch vier verschiedene Berechnungsverfahren errechnet. Sie schwankt zwischen 240 und 384 g C m^{-2}, ein Wert, der typisch für meso-eutropische Seen ist. Während des Winters führen geringer Strahlungsenergieinput und hohe Atmungsverluste infolge von tiefer Durchmischung zu geringen Produktionsraten. Die Frühjahrsblüte wird durch Ausbildung eines Temperaturgradienten in oberflächennahen Wasserschichten ausgelöst. Am Ende der Frühjahrsblüte werden kleine und photosynthetisch aktive Phytoplanktonarten durch Zooplantionfraß weitgehend eliminiert. Während des Sommers wird die dichte Phytoplanktonbiomasse durch photosynthetisch wenig aktive Arten gebildet, die aufgrund ihrer Größe durch das Phytoplankton nur relativ wenig eliminiert werden. Während des Herbstes wird ein drittes Biomassemaximum durch geringe Lichtansprüche des Phytoplanktons gemeinsam mit der Zufuhr von Nährstoffen aus tieferen Wasserschichten infolge einer Zunahme der Durchmischungstiefe ermöglicht.

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REFERENCES

1 Le Cren, E. D., and Lowe-McConnell, R. H. (eds.): The Functioning of Freshwater Ecosystems. International Biological Programme. Cambridge Univ. Press 1980.

2 Developments of Hydrobiology. A monograph Series. W. Junk.

3 Monographiae Biologicae. Elsevier.

4 Richerson, P. J., Armstrong, R., and Goldman, C. R.: Contemporaneous disequilibrium, a new hypothesis to explain the paradox of the plankton. Proc. Nat. Acad. Sci *67* (4), 1710–1714 (1970).

5 Kilham, P. in preparation.

6 Tilman, D.: Resource competition between planktonic algae: An experimental and theoretical approach. Ecology *58*, 338–348 (1977).

7 Reynolds, C. S.: Phytoplankton periodicity: The interactions of form, function and environmental variability. Freshwat. Biol. *14*, 11–142 (1984).

8 Sommer, U.: Seasonal succession of phytoplankton in Lake Constance. Bio Science *85*, 351–357 (1985).

9 Lewis, W. M. Jr.: Zooplankton community analysis. Studies on a tropical system. Springer Verlag 1979.

10 Talling, J. F.: The phytoplankton population as a compound photosynthetic system. New Phytol. *56*, 133–149 (1957).

11 Vollenweider, R. A.: Calculation models of photosynthesis-depth curves and some implications regarding day rate estimates in primary production measurements. Mem. Ist. Ital. Idrobiol./Suppl. *18*, 425–457 (1965).

12 Fee, E. J.: A numerical model for the estimation of photosynthetic production, integrated over time and depth, in natural waters. Limnol. Oceanogr. *14*, 906–911 (1969).

13 Fee, E. J.: A numerical model for determining integral primary production and its application to Lake Michigan. J. Fish. Res. Bd. Can. *30*, 1447–1468 (1973).

14 Megard, R. O., Tonkyn, D. W., and Senft, W. H.: Kinetics of oxygenic photosynthesis in planktonic algae. J. Plankton Res. *6*, 325–337 (1984).

15 Sommer, U.: The role of r- and k-selection in the succession of phytoplankton in Lake Constance. Acta Oecologia/Oecol. Gener. *1981* (2), 327–342 (1981).

16 Sommer, U.: Nutrient competition between phytoplankton species in multispecies chemostat experiments. Arch. Hydrobiol. *96*, 399–416 (1983).

17 Sommer, U.: Sedimentation of principal phytoplankton species in Lake Constance. J. Plankton Res. *6*, 1–15 (1984).

18 Sommer, U.: Population dynamics of three planktonic diatoms in Lake Constance. Holarct. Ecol. *7*, 257–261 (1984).

19 Sommer, U.: Light, stratification and zooplankton as controlling factors for the spring development of phytoplankton in Lake Constance. Schweiz. Z. Hydrol. *45*, 394–404 (1984).

20 Tilzer, M. M.: The importance of fractional light absorption by photosynthetic pigments for phytoplankton productivity in Lake Constance. Limnol. Oceanogr. *28*, 833–846 (1983).

21 Tilzer, M. M.: The quantum yield as a fundamental parameter controlling vertical photosynthetic profiles of phytoplankton in Lake Constance. Arch. Hydrobiol./Suppl. *69*, 169–198 (1984).

22 Tilzer, M. M.: Estimation of phytoplankton loss rates from daily photosynthetic rates and observed biomass changes in Lake Constance. J. Plankton Res. *6*, 309–324 (1984).

23 Geller, W.: Production, food utilization and losses of two coexisting ecologically different *Daphnia* species. Arch-Hydrobiol. Beih. Ergebn. Limnol. *21*, 67–79 (1985).

24 Simon, M., Tilzer, M. M.: Bacterial responses to seasonal changes in primary production and phytoplankton biomass in Lake Constance. J. Plankton Res. *9*, 535–552 (1987).

25 Stemann-Nielsen, E.: The use of radioactive carbon (^{14}C) for measuring organic production in the sea. J. Cons. Int. Explor. Mer. *18*, 117–140 (1952).

26 Sakamoto, M., Tilzer, M. M., Gächter, R., Rai, H., Collos, Y., Tschumi, P., Berner, P., Zbären, D., Dokulil, M., Bossard, P., Uehlinger, U., and Nusch, E. A.: Joint field experiment for comparisons of measuring methods of photosynthetic production. J. Plankton Res. *6*, 365–383 (1984).

27 Tilzer, M. M.: Secchi dish-chlorophyll relationships in a lake with highly variable phytoplankton biomass. Hydrobiologia (in press).

28 Sauberer, F.: Empfehlungen für die Durchführung von Strahlungsmessungen an und in Gewässern. Mitt. int. Ver. Limnol. *11*, 1–77 (1962).

29 Lorenzen, C. J.: Determination of chlorophyll and phaeopigments: Spectrophotometric equations. Limnol. Oceanogr. *12*, 343–346 (1967).

30 Moed, J. R., and Hallegraeff, G. M.: Some problems in the estimation of chlorophyll *a* and phaeopigments from pre- and post-acidification spectrophotometric measurements. Int. Rev. ges. Hydrobiol. *63*, 787–800 (1978).

31 Nusch, E. A.: Comparison of different methods for chlorophyll and phaeopigment determination. Arch-Hydrobiol./Beih. Ergebn. Limnol. *14*, 14–36 (1980).

32 Kiefer, F.: Naturkunde des Bodensees. 2nd Ed. Jan Thorbecke Verlag 1972.

33 Wagner, G.: Simulationsmodelle der Seeneutrophierung, dargestellt am Beispiel des Bodensee-Obersees. Teil II: Simulation des Phosphorhaushaltes des Bodensee-Obersees. Arch-Hydrobiol. *78*, 1–41 (1976).

34 Elster, H. J.: Der Bodensee. Bedrohung und Sanierungsmöglichkeiten eines Ökosystems. Naturwiss. *64*, 207–215 (1977).

35 Elster, H. J.: Neuere Untersuchungen über die Eutrophierung und Sanierung des Bodensees. gwf, wasser–abwasser *123*, 277–287 (1982).

36 Stabel, H. H.: Impact of sedimentation on the phosphorus content of the euphotic zone of Lake Constance. Ver. int. Ver. Limnol. *22*, 964–969 (1984).

37 Lampert, W., and Schober, U.: Das regelmäßige Auftreten von Frühjahrs-Algenmaximum und «Klarwasserstadium» im Bodensee als Folge von klimatischen Bedingungen und Wechselbeziehungen zwischen Phyto- und Zooplankton. Arch. Hydrobiol. *82*, 364–386 (1978).

38 Schober, U.: Kausalanalytische Untersuchungen der Abundanzschwankungen des Chrustaceenplanktons im Bodensee. Ph. D. Thesis, 162 pp. Univ. of Freiburg i. Br. 1980.

39 Steinhauser, F.: Die Zunahme der Intensität der direkten Sonnenstrahlung mit der Höhe und die Verteilung der «Trübung» in den unteren Luftschichten. Met. Z. *56*, 172–181 (1939).

40 Hutchinson, G. E.: A Treatise on Limnology. I. Geography, Physics, and Chemistry. John Wiley 1957.

41 Talling, J. F.: The underwater light climate as a controlling factor in the production ecology of freshwater phytoplankton. Mitt. int. Ver. Limnol. *19*, 214–243 (1971).

42 Dubinsky, Z., and Berman, T.: Seasonal changes in the spectral composition of downwelling irradiance of Lake Kinneret (Israel). Limnol. Oceanogr. *24*, 652–663 (1979).

43 Jewson, D. H., Talling, J. F., Dring, M. J., Tilzer, M. M., Heaney, S. I., and Cunningham, C.: Measurements of photosynthetically available radiation in freshwater: Comparative tests of some current instruments used in studies of primary production. J. Plankton Res. *6*, 259–273 (1984).

44 Schanz, F.: Vertical light attenuation and phytoplankton development in Lake Zurich, Limnol. Oceanogr. *30*, 299–310 (1985).

45 Bindloss, M. E.: The light climate of Loch Leven, a shallow Scottish lake, in relation to primary production of phytoplankton. Freshwat. Biol. *6*, 501–518 (1976).

46 Jewson, D. H.: Light penetration in relation to phytoplankton content of the euphotic zone of Lough Neagh, N. Ireland. Oikos *28*, 74–83 (1977).

47 Berman, T.: Light penetrance in Lake Kinneret. Hydrobiologia *49*, 41–48 (1976).

48 Tilzer, M. M.: Predictions of productivity changes in Lake Tahoe at increasing phytoplankton biomass. Verh. int. Ver. Limnol. *20*, 407–413 (1979).

49 Megard, R. O., Combs, W. S. Jr., Smith, P. D., Knoll, A. S.: Attenuation of light and daily integral rates of photosynthesis attained by planktonic algae. Limnol. Oceanogr. *24*, 1038–1050 (1979).

50 Smith, R. C., and Baker, K. S.: The bio-optical state of ocean waters and romote sensing. Limnol. Oceanogr. *23*, 247–259 (1978).

51 Atlas, D., and Bannister, T. T.: Dependence of mean spectral extinction coefficient of phytoplankton on depth, water color, and species. Limnol. Oceanogr. *25*, 157–159 (1980).

52 Kirk, J. T. O.: Light and Photosynthesis in Aquatic Ecosystems. Cambridge Univ. Press. 1983.

53 Pechlaner, R.: The phytoplankton spring outburst and its conditions in Lake Erken (Sweden). Limnol. Oceanogr. *15*, 113–130 (1970).

54 Fuhs, G. W., Demmerle, S. D., Canelli, E., and Chen, M.: Characterization of phosphorus-limited plankton algae (with reflections on the limiting nutrient concept). In: Likens, G. E. (ed.): Nutrients and Eutrophication: The Limiting Nutrient Controversy. Spec. Symp. Amer. Soc. Limnol. Oceanogr. *1*, 113–133 (1972).

55 Droop, M. R.: The nutrient status of algal cells in continuous culture. J. Mar. Biol. Ass. U. K. *55*, 541–555 (1974).

56 Rhee, G. Y.: Effect of N:P atomic ratios and nitrate limitation on algal growth, cell composition and nitrate uptake. Limnol. Oceanogr. *23,* 10–25 (1978).

57 Rhee, G. Y.: Continuous culture in phytoplankton ecology. In: Droop, M. R., and Jannasch, H. W. (eds.): Advances in Aquatic Microbiology, vol. 2. Academic Press 1980.

58 Redfield, A. C.: The biological control of chemical factors in the environment. Amer. Scient. *4*b, 205–221 (1958).

59 Stabel, H. H.: The role of plankton biomass in controlling fluctuations of suspended matter in Lake Constance. Hydrobiologia *140,* 173–181 (1986).

60 Sommer, U., and Stabel, H. H.: Silicon consumption and population density changes of dominant planktonic diatoms in Lake Constance. J. Ecol. *73,* 119–130 (1983).

61 Stabel, H. H., and Geiger, M.: Phosphorus adsorption to riverine suspended matter: Implications for the P-budget of Lake Constance. Water Res. *19,* 1347–1352 (1985).

62 Bannister, T. T.: Production equations in terms of chlorophyll concentration, quantum yield, and upper limit to production. Limnol. Oceanogr. *19,* 1–12 (1974).

63 Robarts, R. D., and Zohary, T.: *Microcystis aeruginosa* and underwater light attenuation in a hypereutrophic lake (Hartbeespoort Dam, South Africa). J. Ecol. *72,* 1001–1017 (1984).

64 Robarts, R. D.: Hypertrophy, a consequence of development. Intern. J. Environmental Studies *25,* 167–175 (1985).

65 Revsbech, N. P., Jorgensen, B. B., Blackburn, I. H., and Cohen, Y.: Microelectrode studies of the photosynthesis and O_2, the H_2S and pH profiles of a microbial mat. Limnol. Oceanogr. *28,* 1062–1074 (1983).

66 Jassby, A. D., Platt, T.: Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceanogr. *21,* 540–547 (1976).

67 Stemann-Nielsen, E., and Jorgensen, E. G.: The adaptation of plankton algae. I. General part. Physiol. Plant *21,* 401–413 (1968).

68 Falkowski, P. G.: Light-shade adaptation and assimilation numbers. J. Plankton Res. *3,* 203–216 (1981).

69 Prézelin, B. B.: Light reactions in photosynthesis. In: Platt, T. (ed.): Physiological Bases of Phytoplankton Ecology, pp. 1–46 1981.

70 Perry, M. J., Talbot, M. C., and Alberte, R. S.: Photoadaptation in marine phytoplankton: response of the photosynthetic unit. Mar. Biol. *62,* 91–101 (1981).

71 Richardson, K., Beardall, J., and Raven, J. A.: Adaptation of unicellular algae to irradiance. An analysis of strategies. New Phytol. *93,* 157–191 (1983).

72 Findenegg, I.: Produktionsbiologische Untersuchungen an Ostalpenseen. Int. Rev. ges. Hydrobiol. *49,* 381–416 (1964).

73 Jewson, P. H.: The interaction of components controlling net phytoplankton photosynthesis in a well-mixed lake (Lough Neagh, Northern Ireland). Freshwat. Biol. *6,* 551–576 (1976).

74 Senft, H. W.: Dependence of light-saturated rates of algal photosynthesis on intracellular concentrations of phosphorus. Limnol. Oceanogr. *23,* 709–718 (1978).

75 Tilzer, M. M.: Distinction between light-mediated and light-independent variations of photosynthesis in Lake Constance. Hydrobiologia (in press).

76 Tilzer, M. M., and Goldman, C. R.: Importance of mixing, thermal stratification and light adaptation for phytoplankton productivity in Lake Tahoe (California-Nevada). Ecology *59,* 810–821 (1978).

77 Falkowski, P. G.: Light-shade adaptation in marine phytoplankton. In: Falkowski, P. G. (ed.): Primary Productivity in the Sea, pp. 99–120, 1980.

78 Rodhe, W.: Standard correlations between pelagic photosynthesis and light. Mem. Ist. Ital. Idrobiol. Suppl. *18,* 365–381 (1965).

79 Rodhe, W.: Crystallization of eutrophication concepts in Northern Europe. In: Eutrophication: Causes, Consequences, Correctives, pp. 50–64. Nat'l. Acad. Sci., Washington D. C., 1969.

80 Oglesby, R. T.: Relationship of fish yield to lake phytoplankton standing crop, production and morphoedaphic factors. J. Fish. Res. Bd. Can. *34,* 2271–2279 (1977).

81 Hecky, R. E. and Fee, E. J.: Primary production and rates of algal growth in Lake Tanganyika. Limnol. Oceanogr. *26,* 532–547 (1981).

82 Hecky, R. E.: African lakes and their trophic efficiencies: A temporal perspective. In: Meyers, D. G., and Strickler, J. R. (eds.): Trophic Interactions within Aquatic Ecosystems. AAAS Selected Symp. *85,* 405–448 (1984).

83 Wetzel, R. G.: Limnology, 2nd Ed. Samders 1983.

84 Vollenweider, R. A., and Nauwerck, A.: Some observations on the C-14 method for measuring primary production. Ver. int. Ver. Limnol. *14,* 134–149 (1961).

85 Tilzer, M. M., Hillbricht Ilkowska, A., Kowalczewski, A., Spodniewska, I., and Turczynska, J.: Diel phytoplankton periodicity in Mikolajskie Lake, Poland, as measured by different methods in parallel. Int. Rev. Ges. Hydrobiol. *62,* 279–289 (1977).

86 Tilzer, M. M., and Horne, A. J.: Diel patterns of phytoplankton productivity and extracellular release in ultra-oligotrophic Lake Tahoe. Int. Rev. ges. Hydrobiol. *64,* 157–176 (1979).

87 Rodhe, W., Vollenweider, R. A., and Nauwerck, A.: The primary production and standing crop of phytoplankton. In: Buzzati-Traverso, A. A. (ed.): Perspectives in Marine Biology, pp. 299–322. Univ. of California Press 1958.

88 Jewson, D. H., and Wood, R. B.: Some effects on integral photosynthesis of artificial circulation of phytoplankton through light gradients. Verh. int. Verein Limnol. *19,* 1037–1044 (1975).

89 Peterson, B. J.: Radiocarbon uptake: Its relation to net particulate production. Limnol. Oceanogr. *23,* 179–184 (1978).

90 Forsberg, B. R.: The fate of planktonic primary production. Limnol. Oceanogr. *30,* 807–819 (1985).

91 Reynolds, C. S., Harris, G. P., and Gouldney, D. N.: Comparisons of carbon-specific growth rates of cellular increase of phytoplankton in large limnetic enclosures. J. Plankton Res. *7,* 791–820 (1985).

92 Elbrächter, M.: Population dynamics of *Ceratium* in coastal waters of the Kiel Bay. Oikos. Suppl. *15,* 43–48 (1973).

93 Pollingher, U., and Serruya, C.: Phased division of *Peridinium cinctum* f. *westii* (Dinophyceae) and development of the Lake Kinneret (Israel) bloom. J. Phycol. *12,* 162–170 (1976).

94 Heller, M. D.: The phased division of the freshwater dinoflagellate *Ceratium hirundinella* and its use as a method of assessing growth in natural populations. Freshwat. Biol. *7,* 527–533 (1977).

95 Sommer, U., Wedemeyer, C., and Lowski, B.: Comparison of potential growth rates of *Ceratium hirundinella* with observed population density changes. Hydrobiologia *19,* 159–164 (1984).

96 Riley, G. A.: Phytoplankton in the North Central Sargasso Sea, 1950–52. Limnol. Oceanogr. *2,* 252–270 (1957).

97 Ramberg, L.: Relations between phytoplankton and light climate in two Swedish forest lakes. Int. Rev. ges. Hydrobiol. *64,* 749–782 (1979).

98 Sverdrup, H. U.: On conditions for the vernal blooming of phytoplankton. J. Cons. Explor. Mer. *18,* 287–295 (1953).

99 Grobbelaar, J. U.: Phytoplankton productivity in turbid waters. J. Plankton Res. *7,* 653–663 (1985).

100 Vollenweider, R. A.: Advances in defining critical loading levels for phosphorus in lake eutrophication. Mem. Ist. Ital. Idrobiol. *33,* 53–83 (1976).

101 Talling, J. F.: Factor interactions and implications for the prediction of lake metabolism. Arch. Hydrobiol./Beih. Ergebn. Limnol. *13,* 96–109 (1979).

102 Kilham, S. S.: Silicon and phosphorus growth kinetics and competitive interactions between *Stephanodiscus minutus* and *Synedra* sp. Verh. int. Verein. Limnol. *22,* 435–439 (1984).

103 Sommer, U.: The paradox of the plankton: Fluctuations of phosphorus availability maintain diversity of phytoplankton in flow-through cultures. Limnol. Oceanogr. *29,* 633–636 (1984).

104 Sommer, U., and Kilham, S. S.: Phytoplankton natural community experiments: A re-interpretation. Limnol. Oceanogr. *30,* 436–440 (1985).

105 Tilzer, M. M.: Environmental and physiological control of phytoplankton productivity in large lakes. In: Tilzer, M. M., and Serruya, C. (eds.): Functional and Structural Properties of Large Lakes, Science Tech. Publishers Inc., Madison (in preparation).

106 Tilzer, M. M.: The productivity of phytoplankton and its control by resource availability. A review. In: Kumar, H. D. (ed.): *Phycotalk,* Banaras Hindi University, Varanasi, India (in press).

107 Tilzer, M. M.: Dynamik und Produktivität von Phytoplankton und pelagischen Bakterien in einem Hochgebirgssee (Vorderer Finstertaler See, Österreich). Arch. Hydrobiol. Suppl. *40,* 201–273 (1972).

108 Geller, W.: Stabile Zeitmuster in der Planktonsukzession des Bodensees. Verh. Ges. Ökologie *8,* 373–382 (1980).

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