LIGHT PENETRANCE IN LAKE KINNERET

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Abstract

The characteristics of light penetrance in Lake Kinneret, Israel, were observed over the years 1970 to 1973. Light measurements were made concurrently with those of algal speciation and biomass, chlorophyll α concentrations and primary production. Vertical extinction coefficients of 'green' light (filter VG9), the most penetrating spectral component, ranged from 0.15 (August 1970) to 0.93 ln units m^{-1} (April 1970), reflecting the large differences between algal standing crops in non-bloom and bloom seasons. During the dinoflagellate bloom *(Peridinium cinctum fa westii)* from February through June, the increment of extinction coefficient per unit increase of chlorophyll α concentration was 0.006 ln units mg^{-1} m^2. The uneven vertical distribution of algae at this period caused irregularities in the depth curves of light penetrance. At other times, when the phytoplankton cells were more homogeneously dispersed with depth, regular light penetrance curves were observed; however, as previously noted (Rodhe, 1972), attenuation of algal photosynthetic activity often appeared to be regulated by the blue spectral component (filter BG 12). Ratios of absorbed to scattered light in the upper water column ranged from 85:15 to 75:25.

Introduction

Of all environmental conditions, the most necessary for primary production is light. In this paper, I present data pertaining to the seasonal fluctuations of light penetrance in the waters of Lake Kinneret (Sea of Galilee), Israel, in relation to characteristics of the phytoplankton, such as chlorophyll concentration and photosynthetic activity.

In an earlier study of this lake, Rodhe (1972) has given some information on the penetrance of downwelling irradiation. He suggested that, for at least part of the year, although green light is the most penetrating component

of the spectrum, the blue wave lengths of light (i.e. passing through a BG 12 filter, from about 380 to 465 nm) are determining the photosynthetic gradient in the water column. This finding contrasts with results from other lakes, in which the most penetrating component of the light appeared to determine the attenuation of photosynthesis with depth (Rodhe 1965).

Most previous work on light penetrance has been carried out in waters where there was (or was assumed to be) a more-or-less homogeneous vertical distribution of algae and particulate matter throughout the water column. Unfortunately, this situation frequently does not obtain in lakes and oceans (Baker & Brook, 1971; Strickland, 1968) and therefore, in the present study, we determined the standing crops of the phytoplankton, chlorophyll concentrations and photosynthetic carbon fixation concurrently with the light measurements.

Methods

Initially, all measurements of *in situ* light penetrance were made with a simple 'cross' photometer (Aberg & Rodhe 1942, p. 13), equipped with a single selenium cell covered by a diffuser plate. Standard limnological light filters (Schott filters BG 12, VG9 and RG2 with mean optical midpoints at 430, 530 and 635 nm respectively) were used with this instrument. From August 1972, we used a Whitney LMT 8B illuminance meter which has a selenium light cell giving a linear response with the visible light spectrum. This instrument has an on-deck sensor (calibrated in foot candles) and in-water sensors measuring both downwelling and upwelling irradiance. Therefore, we could also obtain information concerning the ratio of scattered to absorbed light in the water column. Neither

of the photometers permitted the measurement of absolute values of light energy in situ, and therefore, the data for light penetrance were always expressed relative to the light intensity determined at the water surface.

The results of an ongoing study with an ISCO radiometer of the spectral distribution of light energy in this lake, which will supplement the present report, will be published later.

Techniques for the determination of the phytoplankton biomass, chlorophyll and photosynthetic carbon assimilation have been previously described (Berman & Pollingher, 1974). Data on net surface radiation were kindly made available by F. Mero and U. Isaac of Tahal Co. I am also grateful to the Israel Meteorological Service for data on percentage of cloud cover.

Results

Net surface radiation
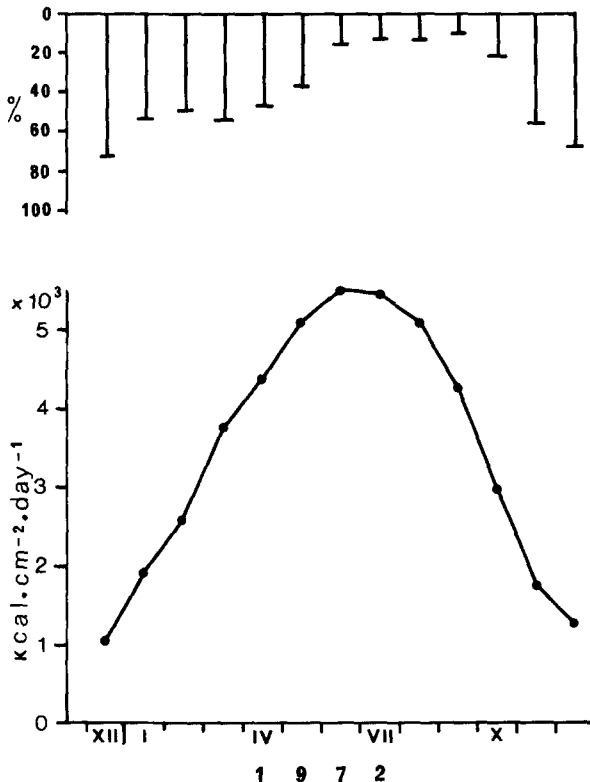
Daily net radiation ranged from a maximum of about

Fig. 1. Daily net solar radiation in the Lake Kinneret region and percentage of noontime cloud cover.

$5800 \text{ k cal m}^{-2} \text{ day}^{-1}$ in June-July to a minimum of $430 \text{ k cal m}^{-2} \text{ day}^{-1}$ on an overcast day in December (Fig. 1). These net radiation values (i.e. total minus reflected irradiance) measured at Ginnosar, close to the western lake shore, are somewhat incorrect for the open lake waters but give an accurate picture of the annual pattern of radiation. In comparison, for a typical temperate zone, daily radiation averages about $2200 \text{ k cal m}^{-2} \text{ day}^{-1}$ (Odum, 1971). Unfortunately, due to lack of suitable instrumentation, values of subsurface light intensity in the lake, I_0' (Talling, 1957), in energy terms were unavailable for this study. Monthly averages of the percentage of cloud cover, estimated at noon at Degania, on the SW lake shore, are also shown in Fig. 1. Clouds are generally important only from November through April in this region.

Seasonal fluctuations of in situ light penetrance

Four typical profiles of light penetrance measured with the Whitney photometer (without color filters) are given in Figs. 2, 3, 4 and 5. These figures also show relative photosynthetic carbon assimilation, concentrations of chlorophyll, percentage composition of the phytoplankton biomass, and Secchi disc depths. In January (Fig. 2), when the lake was completely thermally mixed, and prior to the annual dinoflagellate bloom (Berman & Pollingher, 1974), the algae were more-or-less homogeneously distributed throughout the water column. In this instance, a classical curve of light penetrance was obtained for the upper 20-25 m. The attenuation of primary productivity followed that of light except for higher intensities (above 3 m) and for the lowest (30 m). The latter phenomenon appears in most of the graphs and may be due either to relatively high photosynthetic efficiencies in dim light (Goldman, 1969; Dubinsky & Berman, in preparation) or to an artifact of the ^{14}C method which makes it impossible to determine true compensation points, or both.

During the early peak of the *Peridinium* bloom (Fig. 3), the light attenuation curve was strongly influenced by the dense algal population, which, on this occasion, was concentrated very close to the surface.

From 5 m downwards, a constant extinction coefficient was obtained. Graphs determined during the bloom show several deviations from a constant vertical exponential attenuation of light and photosynthesis curves. Such deviations may be explained by the heterogeneous dispersion of the phytoplankton, which results from vertical movements of the dinoflagellates during the incubation period of the productivity runs. Another graph (Fig. 4)
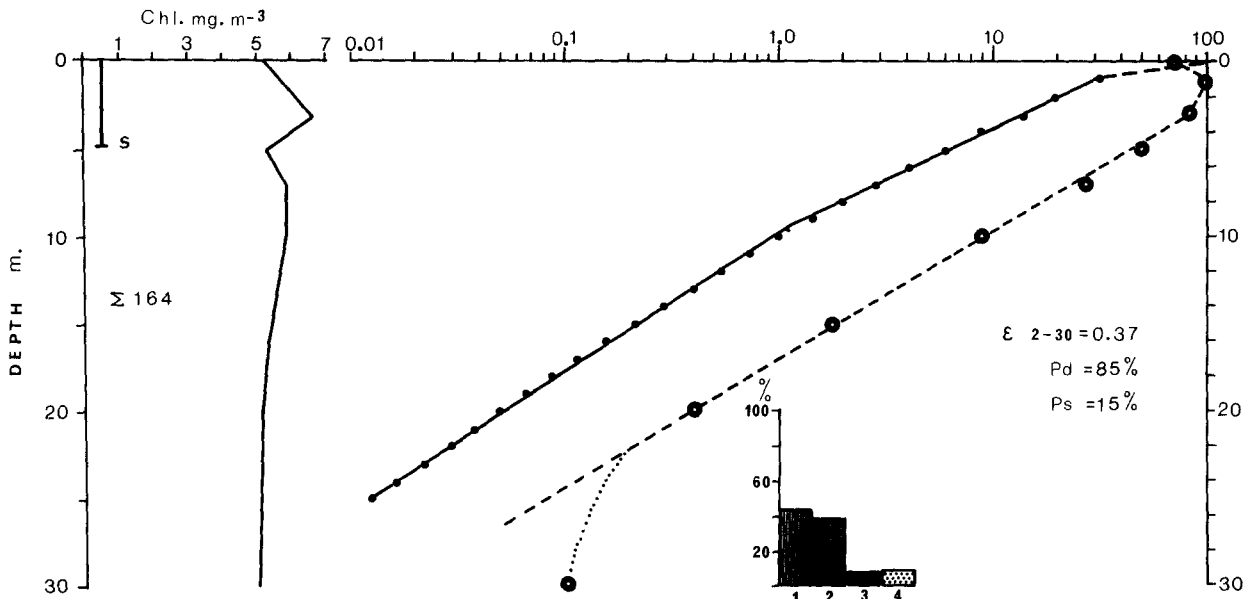
Fig. 2. Profiles of downwelling irradiation (actually photocell response, see text, p. 4) (. _. _.); relative photosynthesis as percent of maximum rate (___); chlorophyll α concentrations and percentage algal biomass composition (1 - Pyrrophyta, 2 - Chlorophyta, 3 - Cyanophyta, 4 - Chrysophyta). Also given are Secchi disc readings (S), total chlorophyll standing crop in the trophogenic zone (Σ) in mg m^{-2}, extinction coefficients for indicated depths, and percentages of light energy absorbed (Pd) and scattered (Ps) by water at indicated depths. 10 January 1973.
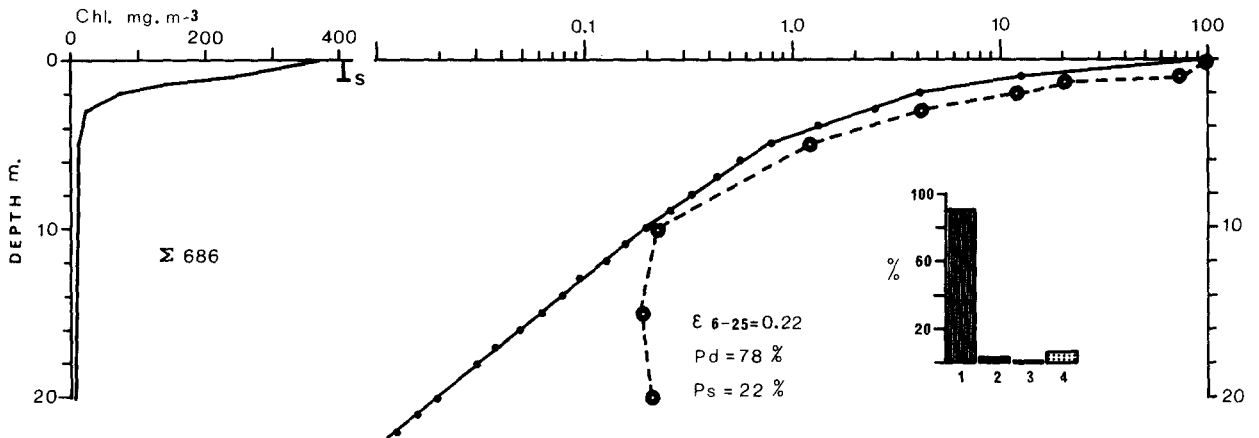

Fig. 3. As Fig. 2, 21 March 1973.

from the late phase of the *Peridinium* bloom showed increasing turbidity of the water compared to the earlier date (Fig. 3), despite a lower total standing crop of chlorophyll. This was possibly caused by an increase in suspended detrital material from senescent or dead algal cells. In this instance, it should be noted that what appears to be light inhibition of photosynthesis in the surface waters is really due to a decrease in the algal standing crop. However, true light inhibition of primary productivity in surface samples was observed on other occasions (Fig. 2, 5 and 7). The final profile in the series (Fig. 5) is representative of those obtained after the disappearance of the *Peridinium* bloom, when the lake is fully thermally stratified, and algal populations are more diverse. An increase
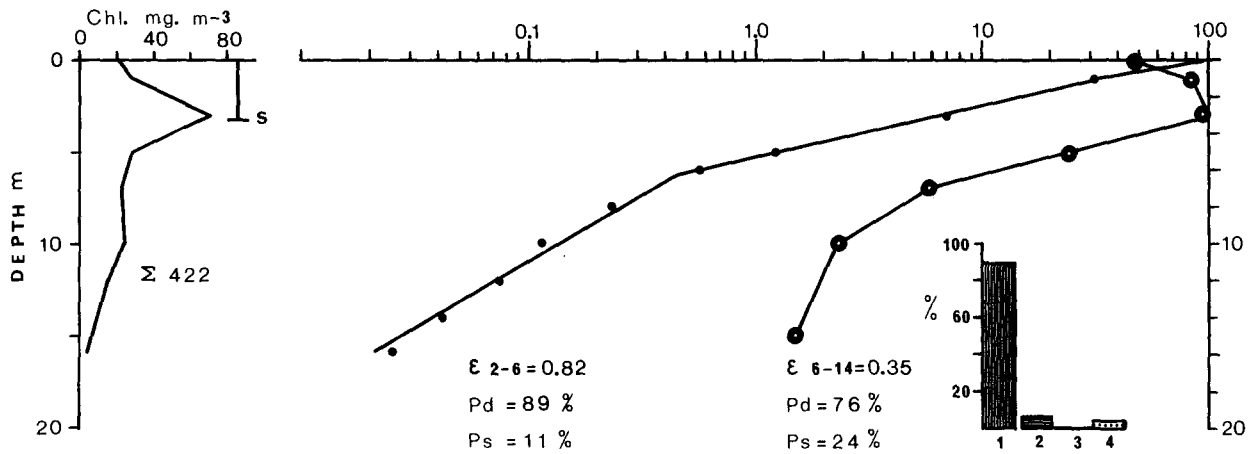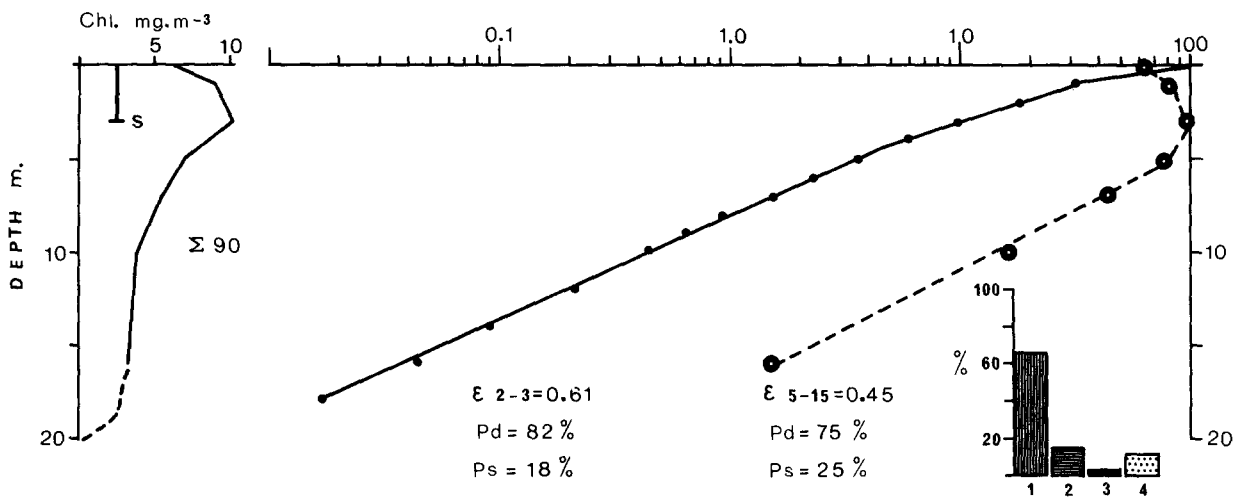
Fig. 4. As Fig. 2, 9 May 1973.

Fig. 5. As Fig. 2, 15 August 1973.

in light penetrance below 20 m (not shown in Fig. 5) was probably due to the absence of algae in the hypolimnic waters.

In Figs. 2 to 5, I have also indicated the ratios of absorbed to scattered light (Whitney, 1938) as determined by the Whitney photometer. For the main upper water column, this ratio ranged from 85:15 to 75:25. It was highest in the profile measured on 10 January 1973, even though algal standing crop was not very different from that of 15 August 1972, when the lowest value (75:25) was found. As yet, little is known about the non-living particulate matter or dissolved colored compounds in this lake, but clearly these, together with living particulate matter, will determine the above ratios (Hutchinson, 1957). For a number

of Wisconsin lakes, Whitney (1938) determined ratios ranging from 96.8:3.2 to 76:24, and Aberg & Rodhe (1942) found ratios of 94.8:5.2 to 93.2:6.8 in two Swedish lakes.

Figs. 2 to 5 also show that at 1% level of photocell response to incident surface light, often taken as the limit of the trophogenic zone, significant photosynthetic carbon incorporation still took place. Indeed, discernible light dependent ^{14}C fixation occurred at levels as low as 0.1% of incident light. However, the ^{14}C method is not very reliable for measuring true compensation points, and care must be taken to avoid a relatively high artifactual count on filters with low activity (Williams et al. 1972).

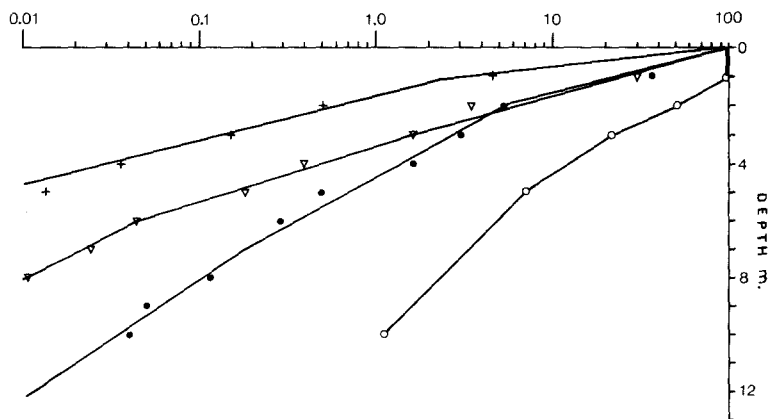In general, the attenuation of algal photosynthetic activity followed that of downwelling light, as recorded by

Fig. 6. Underwater light penetrance measured with Whitney photometer with filters RG2 (+), BG12 (▽) and UG9 (.), and relative photosynthetic rates (o-o-o). 4 April 1974.

the sensor of the Whitney photometer without filters (Figs. 2 to 5). The penetration of light was also measured with this instrument using three conventional color limnological filters (Figs. 6 and 7). Although photosynthesis usually paralleled the green (most penetrating) component of downwelling light during the period when *Peridinium* was dominant in the phytoplankton (Fig. 6), at other times, photosynthetic carbon assimilation more closely followed the gradient of blue light. This feature of

the algal response to downwelling light in Lake Kinneret was first noted by Rodhe (1972). This point has been questioned by Talling (see Discussion in Rodhe, 1972), who pointed out that it is difficult to ascribe a blue light effect which is unrelated to a spectral band in the red region, and that vertical homogeneity of the algal population must be shown to exist. This latter condition often does occur during the post-bloom season in Lake Kinneret (Figs. 2 and 7). Rodhe (personal communication) has
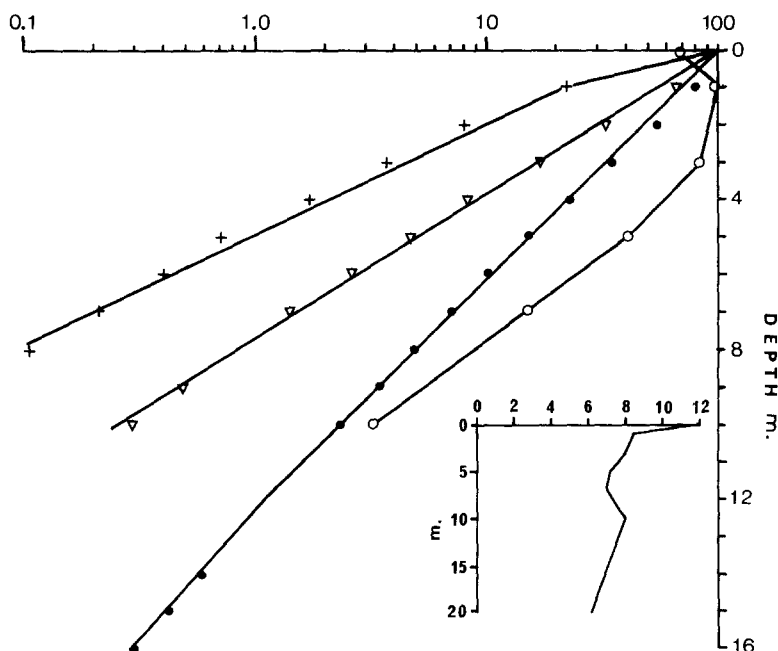

Fig. 7. As Fig. 6, 26 December 1973.
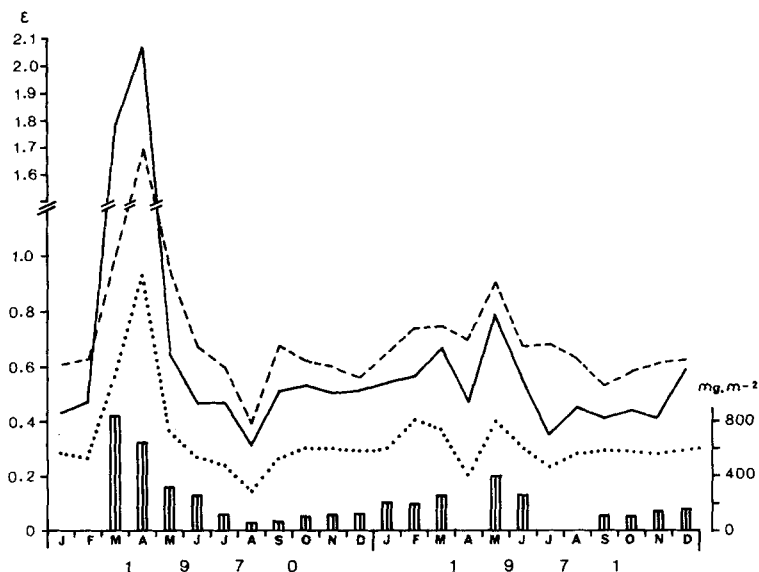Insert shows depth profile of chlorophyll α (mg m⁻³).

45

Fig. 8. Average monthly extinction coefficients measured with Aberg-Rodhe photometer with filters RG2 (____), BG12 (___), VG9 (.......). Average monthly chlorophyll α contents in trophogenic zone (mg m^{-2}) are shown by histograms. The trophogenic zone was taken as the water column to 30 m during homothermy, and the epilimnic layer (15 to 20 m) during stratification (Berman & Pollingher, 1974).

found that irradiation with blue light (BG 12) gives maximal rates of photosynthesis for *Peridinium*, but this effect has yet to be investigated for the major algal species present in the lake during the summer and fall. It also should be noted that the color filters used in this and previous studies have a fairly broad spectral transmittance. Ongoing work with a scanning radiometer will provide more accurate information on the relationship between actual light energy fluxes at defined wave lengths and phytoplankton photosynthesis.

Annual and seasonal fluctuations of vertical extinction coefficients

A measure of the efficacy of light penetration is given by the vertical extinction coefficients of light attenuation (ϵ) in the water column. Monthly average values of this parameter and concentrations of chlorophyll α in the trophogenic zone for the years 1970, 1971, and from August 1972 to December 1973 are shown in Figs. 8 and 9. In the former years, measurements were made with the Aberg-Rodhe 'cross' photometer with color filters (RG2, BG2 and VG9) and average ϵ values for each broad color band are given (Fig. 8). Unfortunately, readings with this instrument in 1972 were unreliable, and subsequently, from August 1972, measurements were made with the Whitney photometer, usually without filters.

Clearly, when the vertical distribution of phytoplankton or other particulate matter is not homogeneous, as is normally the case in Lake Kinneret during the *Peridinium* bloom, the vertical extinction coefficient will vary widely throughout the trophogenic zone (e.g. Fig. 3). The data shown in Figs. 8 and 9 were based on averaged values for vertical extinction coefficients over the upper 10 m of the water column, and give only a generalized idea of the actual range of values for these parameters.

A consistent annual pattern was observed, although it should be emphasized that the absolute values of ϵ in 1972-1973 are not directly comparable with previous results, because two instruments with presumably different sensor characteristics were used. However, since most of the penetrating light energy after the first few meters of water is confined to a wave band with a peak at 550 nm (Dubinsky & Berman, in preparation), the penetrance characteristics of the 'green light' (ϵ_g) are probably fairly close to that measured by the 'broad spectrum uncovered' sensor of the Whitney instrument. Talling (1957) found that multiplication of the extinction coefficient of the most penetrating component of light by a factor of 1.33 approximated the value of an 'effective' extinction coefficient used in calculations of primary production (Talling, 1972).

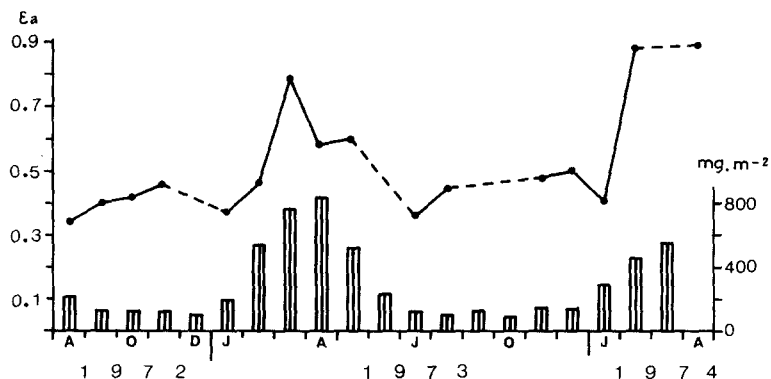For Kinneret waters, the minimum penetrance of light

46

Fig. 9. Average monthly extinction coefficients (ϵ) measured with a Whitney photometer without filters. Histograms show average monthly chlorophyll α concentrations in trophogenic zone (mg m^{-2}).

occurred during the annual dinoflagellate bloom. The greatest range of monthly averaged values for ϵ_g were observed in 1970, when this parameter varied from 0.15 (August) to 0.93 ln units m^{-1} (April). In 1971, when the lowest standing crops of *Peridinium* developed, the fluctuations in ϵ values were more limited (ϵ_g maximum to minimum 0.49 to 0.21 ln units m^{-1}). From August 1972 to December 1973, the average monthly extinction coefficient ranged from 0.31 (February 1973) to 0.88 ln units m^{-1} (May 1973). These observations, which were made at a central lake station, were probably only slightly affected by inflows of silt and detritus resulting from winter rains. The annual variations in minimum vertical extinction coefficients in Lake Kinneret are much greater than those recorded for lakes such as Lake Victoria, where the phytoplankton populations are generally stable and less dense throughout the year (Talling, 1965).

As in many lakes, 'green light' was the most penetrating component of downwelling irradiation, usually followed by 'blue' and 'red'. Occasionally, when very high concentrations of *Peridinium* cells were located near the surface, blue light was absorbed to a greater extent than red.

The increment of extinction coefficient with a unit increase of chlorophyll concentration, ϵ_s (in ln units mg^{-1} m^2), is a parameter of some ecological interest, as it is a measure of the 'self-shading' characteristics of an algal population, and can be used to predict maximum areal concentrations of chlorophyll. Talling (1972) found average ϵ_s values of 0.02 for *Asterionella* in Lake Windermere, but observed an ϵ_s of 0.01 for a dense population of the dinoflagellate *Ceratium hirundinella* in Esthwaite water. Of course, the vertical extinction coefficient measured in natural waters is not only a function of the chlo-

rophyll concentration, but also of other dissolved and particulate materials present. Nevertheless, in Lake Kinneret, I found the following significant linear correlation between the vertical extinction coefficient and chlorophyll α concentraton

$$(\epsilon) = 0.006 \text{ (chlorophyll } \alpha) + 0.46$$
$$(r = 0.79, n = 45, p < 0.001)$$

Thus, the ϵ_s value here, 0.006 ($\pm$ 0.0015), is still lower than that reported for *Ceratium*. Average chlorophyll content of *Peridinium* was determined as 0.23 ng chlorophyll α per cell. Talling (1972) found 0.25 ng chlorophyll α per cell for *Ceratium*. The low ϵ_s value above would imply a maximum chlorophyll α concentration of about 730 mg/m^2 and helps to explain the extremely dense standing crops of *Peridinium* which develop during the bloom in Lake Kinneret (Berman & Pollingher, 1974). In addition, the capacity of the dinoflagellates to swim actively throughout the water column (Berman & Rodhe, 1971) alleviates problems of self-shading and permits, in effect, a deepening of the trophogenic zone.

The data presented in this paper indicate two distinct seasons in respect to the light penetrance characteristics of Lake Kinneret. When *Peridinium* do not dominate the phytoplankton, light penetrance is very comparable to that reported for many other lakes (e.g. Rodhe, 1965). At this time, because the algae are fairly evenly dispersed vertically, models relating integral photosynthetic activity with incident light energy (Talling, 1957, 1972; Rodhe, 1972) can be successfully applied. Such models break down with the increase of *Peridinium*, when the vertical distribution of algae becomes very heterogeneous and unstable.

47

Summary

1. Profiles of light penetrance at a central deep station in Lake Kinneret were measured from 1970-1973, at first with an Aberg-Rodhe 'cross' photometer, with color filters VG9, BG12 and RG2, then from 1972 with a Whitney photometer, usually without filters. Concurrently, phytoplankton biomass, chlorophyll and primary productivity were also determined.

2. The dominant feature affecting light penetrance in the lake water was the presence or absence of the annual dinoflagellate bloom of *Peridinium*. When these organisms dominated, their patchy vertical distribution resulted in very uneven light penetrance. At other seasons, normal attenuation curves of downwelling light were found.

3. Although light inhibition of photosynthesis in the upper water layers was sometimes actually due to lower algal concentrations (Fig. 4), on other occasions (Figs. 2, 5 and 7), the relatively strong irradiance near the surface did appear to limit primary productivity.

4. In Lake Kinneret, as elsewhere, significant photosynthetic carbon fixation occurred below the 1% level of photometer sensor response.

5. During the non-bloom period, when the phytoplankton cells were often fairly homogeneously dispersed with depth, the attenuation of photosynthetic response often seemed to follow the extinction of blue light (filter BG12), as previously noted by Rodhe (1972). At other times, the decline of photosynthetic activity was parallel to the attenuation of the most penetrating light component (green filter VG9).

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