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Temporal and vertical variation of chlorophyll *a* concentration, phytoplankton photosynthetic activity and light attenuation in Lake Kinneret: possibilities and limitations for simulation by remote sensing

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The relationship between chlorophyll a (Chl a) and primary productivity (PP) in the uppermost water layer and the water column-based (0–15 m) integral values of those variables were examined using measurements taken in Lake Kinneret (Israel) from 1990 to 2003. In 81% of all Chl a profiles examined, the distribution was fairly uniform within the entire 0–15 m water column, and 12.3% of instances showed a prominent subsurface maximum, when the lake phytoplankton was dominated by the dinoflagellate Peridinium gatunense. Chl a can be reliably estimated by remote sensing techniques in the productive and turbid water of Lake Kinneret, since Chl a concentration at surface layers can be extrapolated to the entire water column. Light vertical attenuation coefficient average for wavelengths from 400 to 700 nm, K_d, ranged from 0.203 to 1.954 m^{-1} and showed high degree of temporal variation. The maximal rate of photosynthetic efficiency, P_B^{opt} [average 3.16 (±1.50)], ranged from 0.25 to 8.85 mg C m^{-3} h^{-1} mg Chl a^{-1}. Using measured data of Chl a, P_B^{opt}, and light as an input, a simple depth-integrated PP model allowed plausible simulation of PP. However, a lack of correlation between photosynthetic activity and temperature (or other variable with remotely sensed potential) renders the use of models that require input of photosynthetic efficiency to calculate integrated PP of little value in the case of productive and turbid Lake Kinneret.

INTRODUCTION

Consistent long-term monitoring is conducted in relatively few lakes and reservoirs worldwide due to the economical burden. If a long-term monitoring program does exist, most of the measurements have been taken at a fixed station and with a relatively long interval (days or weeks) between samplings. In recent years, however, major developments have taken place in the development of the means for monitoring, in terms of both temporal and spatial variation. Of these, remotely operated sensors, carried onboard aircrafts and satellites, are doubtless the most comprehensive means exploited for spatial coverage, and they are extensively used for monitoring of the distribution of important ecological variables in inland water bodies, such as chlorophyll *a* (Chl *a*) concentration and water temperature (Millie *et al.*, 1992; Jupp *et al.*, 1994; Mayo *et al.*, 1995; Lindell *et al.*, 1999). Since the signals recorded by the remotely positioned sensors are indirect information for the variables of concern for ecologists (Chl *a* concentration and other

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phytoplankton pigments, concentration of total suspended matter or temperature), the point measurements that were so far the hard core of the monitoring programs are an essential database for the parameterization and calibration of the sophisticated modern instruments and models employed. Productive waters, and particularly inland water bodies, are definitely less important than oligotrophic marine water bodies in terms of global mass balance (with relation to carbon cycling and other major elements), but the paramount significance of lakes and reservoirs as source of potable water makes the capability to monitor those water bodies on a large spatial scale or frequent temporal scale an important assignment.

As remotely sensed information on Chl *a* distribution is intrinsically limited to the uppermost water layer, it is important to explore the relationships between the phytoplankton standing stock in that layer and the entire euphotic water layer phytoplankton content. The pattern of the vertical distribution of phytoplankton determines to a large extent the potential for primary productivity (PP) and also determines to a large extent the pattern of light penetration within the water column. A fairly uniform distribution of phytoplankton in the euphotic zone of the water column is often assumed in PP models (Behrenfeld and Falkowski, 1997). In those models, information on the vertical distribution of phytoplankton, or in most cases actually Chl *a* concentration, is instrumental for reliable interpretation of the surface acquired data collected by remotely operated sensors. While that assumption is probably largely valid in transparent, oligotrophic, mainly marine waters, it often does not apply to productive waters (Wetzel, 2001).

Phytoplankton density and productivity are monitored systematically in Lake Kinneret (Israel) for more than three decades, along with other physical, chemical and biological characteristics. Chl *a*, PP and light are measured in Lake Kinneret at fixed depths throughout the entire period of the monitoring programs (Berman *et al.*, 1995). In publications summarizing Lake Kinneret monitoring, we mostly used the integrated value of Chl *a* and PP in the euphotic water column. In the current summary, integrated data are presented for the sake of characterization of the lake phytoplankton characteristics and for comparison of the multiannual record. The large database of detailed information on the vertical variation of Chl *a*, PP and available light in the water column is used for the study of the relationships between variable values at the surface and within the entire euphotic water column. The elucidation of those relationships is used to explore the possibilities and limitations of remotely sensed information and information acquired by automatically operating instruments to increase the monitoring capability in Lake Kinneret, as a case study of inland, turbid and productive water body.

Limnological background

Lake Kinneret is a warm monomictic lake with a surface area of 170 km^2 and mean and maximum depths of 24 and 43 m respectively. Homothermy occurs between late December and early March with minimum water temperatures usually <15°C. The lake is strongly stratified from about April to December with maximum epilimnetic temperatures reaching 29–30°C. With the onset of stratification, the hypolimnion rapidly becomes anoxic with high concentrations of sulfide (130–250 μM) and ammonia (~30–100 μM N–NH_4^+). The dominant phytoplankton from February through May is often the dinoflagellate *Peridinium gatunense* Nygaard, which forms dense blooms, with up to 400 g m^{-2} wet weight algal biomass, and comprises >90% of the algal biomass during the bloom and 59–90% on an annual basis (Berman *et al.*, 1995; Zohary, 2004). In the recent decade, however, this bloom has not always occurred, and other algae were prominent in the phytoplankton assemblage,for example, *Microcystis*, *Ankistrodesmus*, *Carteria*. Nanoplanktonic forms of chlorophytes, diatoms, cyanophytes and dinoflagellates normally dominate the assemblage from June through January in Lake Kinneret. A detailed description of the lake phytoplankton was recently published (Zohary, 2004).

METHODS

Water samples were taken from eight depths: 0, 1, 2, 3, 5, 7, 10 and 15 m, between 08:00 and 09:00 h local time (GMT + 2 h), with a 5-L Aberg-Rodhe sampler at a pelagic sampling station located in the central part of the lake and transferred immediately to polyethylene carboys kept in dark. Duplicated 50-mL subsamples were transferred to polycarbonate 60-mL bottles for carbon uptake measurement with a modified ^{14}C technique (Steemann-Nielsen, 1952; Berman and Pollingher, 1974). A spike of ~3×10^5 Bq of [^{14}C] bicarbonate was added to each bottle. The bottles were incubated *in situ* for the determination of carbon assimilation, at the respective depths of the samples' origin. After incubation for ~3 h, the samples were filtered onto polyacetate 25 mm 0.45 μm membrane filters under light vacuum (~100 mg Hg), rinsed with filtered lake water and left overnight in the presence of HCl vapor to eliminate any remaining traces of inorganic ^{14}C. Control samples poisoned by Lugol's solution at zero time were run in each experimental series to compensate for non-biological absorption to filters. The total added

^{14}C was checked for each sampling series by counting 0.1-mL portions withdrawn directly from each of the incubated bottles. Total radioactivity in the particulate fraction retained on the filters was determined by liquid scintillation with quench correction. The average difference between duplicates was ~12%.

For the determination of Chl *a*, samples were processed in the laboratory ~1 h after collection. Particulate matter was collected by filtration of water samples onto glass-fiber filters (Whatman GF/C), ground in 90% acetone and left overnight at 4°C in the dark. Chl *a* concentration was determined fluorometrically (Holm-Hansen *et al.*, 1965), following clarification of the extract by centrifugation for 3 min at 1100×*g*.

Areal PP and Chl *a* content were calculated by integrating the weighed measurements at the eight discrete samples over a water column of 0–15 m. The values representing the upper most layer of the water column were derived of the average between the samples from 0- and 1-m depths. The daily PP was calculated by multiplying the hourly average by the appropriate photoperiod. A full complement of eight measurements of both Chl *a* and PP was available on most dates, but on two occasions, the PP set was not complete and therefore eliminated from the calculations.

Light profiles were taken at the water sampling location with a LI-192 (Licor, Lincoln, NE, USA) underwater quantum sensor. The instrument is cosine corrected and measures the vector irradiance in the 400–700 nm waveband, that is, the photosynthetically active radiation (PAR) range of the electromagnetic spectrum. Light measurements were taken at the water surface, 0.5 m below the surface, and then at 1-m intervals down to the depth where light intensity had declined to a value of <1 μmol photon m^{-2} sec^{-1}. The vertical attenuation coefficient of downwelling irradiance, K_d, was calculated separately for each measured interval and also as an average of a larger scale as

$$K_d = -[\ln(E_{z1}/E_{z2})]/z, \mathrm{m}^{-1} \quad (1)$$

where E_{z1} is the downwelling irradiance at depth z_1, E_{z2} the downwelling irradiance at depth z_2 and z the vertical interval between the measured layers. The averaged K_d for the interval 0.5–2.5 m was used for a temporal comparison, due to reasons specified in *Results*.

The areal Chl *a* and daily integral PP up to 1993 have been published on several occasions (Berman and Pollingher, 1974; Pollingher and Berman, 1977, 1982; Berman *et al.*, 1992, 1995, 1998). In the current study, a particular use is made of the vertical data for the time interval from 1990 to 2003, in which systematic measurement of the PAR was conducted.

RESULTS

Chlorophyll and PP: integrated measurements

The monthly averages of the areal Chl *a* content for the period from 1990 through 2003 showed a high degree of variation in the interval from January to June and relative stability from July to December (Fig. 1a). The multiannual monthly average of integral Chl *a* ranged from 115 to 584 mg m^{-2} and was 223 mg m^{-2} with a coefficient of variation [CV = 100(SD/average)] of 40%. The average for January–June period (Winter–Spring, WS) was 320 mg m^{-2} with CV of 52%, and for the July–December (Summer–Autumn, SA), it declined both in intensity and in variability to 127 mg m^{-2} and CV of 18%. The variability of the monthly average of PP showed smaller differences between the maximum value in May (2674 mg C m^{-2} day^{-1}) and the minimum in December (872 mg C m^{-2} day^{-1}) than Chl *a*

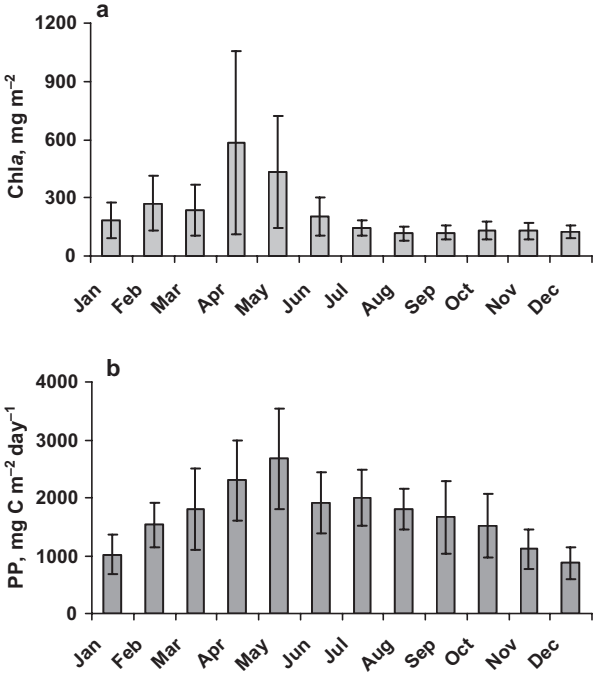

Fig. 1. Monthly average and SD of phytoplankton variables, based on the integration of data from the water column from 0 to 15 m. The calculation is based on data collected in the years 1990–2003, in 358 experiments. Bars, average; lines, SD. (**a**) Areal chlorophyll *a* (Chl *a*) content; (**b**) daily primary productivity (PP).

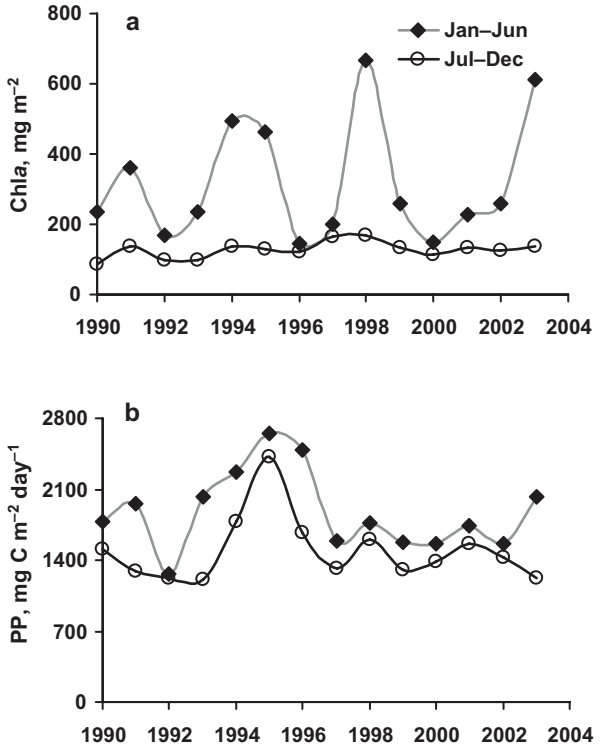

Fig. 2. Semi-annual average of phytoplankton variables, based on the integration of data from the water column from 0 to 15 m. The calculation is based on the data collected in the years 1990–2003, in 358 experiments. (**a**) Areal chlorophyll *a* (Chl *a*) content; (**b**) daily primary productivity (PP).

concentrations, and the difference between WS and SA was relatively small (Fig. 1b). The multiannual monthly average of PP was 1686 mg C m^{-2} day^{-1} and CV of 19%, for the WS period it was 1876 mg C m^{-2} day^{-1} and CV of 20% and for the SA period it was 1496 mg C m^{-2} d^{-1} and CV of 21%.

Partition of the averages into semi-annual averages clearly demonstrates the relatively high temporal variability of Chl *a* areal content in the WS period and relative stability in the SA period (Fig. 2a). The conspicuously high records in the years 1994, 1995, 1998 and 2003 were caused by an extraordinary high growth of *P. gatunense*, which prevailed from February to May or even June. Multiannual variability of the semi-annual averages of PP is also evident (Fig. 2b), but in this case, the dynamics of the change with time in the two seasonal averages is fairly similar.

Chlorophyll and PP: vertical variation

The degree of the homogeneity/heterogeneity of the vertical distribution of Chl *a* was assessed using CV. The CV of vertical distribution of Chl *a* in the epilimnion ranged from 1 to 180%, with high numbers when *Peridinium* dominated the lake phytoplankton. The CV of Chl *a* measured from the surface down to 15-m depth was <15% in the SA period and in January, indicating a relatively homogeneous pattern of vertical distribution of Chl *a*. On the other hand, the CV of the vertical distribution of Chl *a* from February to June was >20% indicating heterogeneity in many profiles, which showed several patterns of distribution. Of the 358 Chl *a* profiles included in the current study, in 290 the CV of the vertical distribution of Chl *a* was <30%. In those profiles, the relationship between the Chl *a* concentration (mg m^{-3}) recorded in the uppermost layer (the layer residing between 0 and 1 m below surface) and the integrated Chl *a* concentration (mg m^{-2}) over the 0–15 m water column was as follows: Chl a_{int} = 12.64 Chl $a_{uppermost}$ + 23.7 (r^2 = 0.91, n = 290, P < 0.001). Most of the apparently heterogeneous distributions (44), recorded when *P. gatunense* dominated the phytoplankton, showed typical high concentrations and high variation in the upper part of the water column (0–5 m), which were sometimes an order of magnitude higher than the concentrations in lower water layers. The relationship between the uppermost layer and the integrated Chl *a* value was as follows: Chl a_{int} = 4.49 Chl $a_{uppermost}$ + 189.6 (r^2 = 0.84, n = 44, P < 0.001). The vertical distribution of *P. gatunense* changes diurnally, but it is rarely uniform any time, and during the photoperiod most cells concentrate close to the water surface (Pollingher, 1988). That pattern may be, however, changed by the force of wind acting on the water surface, which is capable of overwhelming the directional movement of the cells; therefore, not all profiles with *P. gatunense* dominance were highly heterogeneous.

In the case of another 14 conspicuously heterogeneous profiles, there was an abrupt decrease of Chl *a* concentration 7 or 10 m below the surface but a uniform distribution above. The rest (10) of the highly heterogeneous Chl *a* profiles showed different patterns of vertical distribution.

As most of the heterogeneous profiles occurred in the period when *Peridinium* dominated the lake, there was an apparent correlation between Chl *a* concentration and the degree of variation of the vertical distribution (Fig. 3). A prominent exception is the case of the large diatom *Aulecoseira* (*Melosira*) *granulata* that may dominate the phytoplankton in the WS period, but the vertical alignment of this species is pretty uniform. If it shows in large densities in the lake, it occurs in January and February. It is obvious that the average vertical distribution in January is not different from that of the SA period and only moderately higher in February, despite the higher average Chl *a* values.

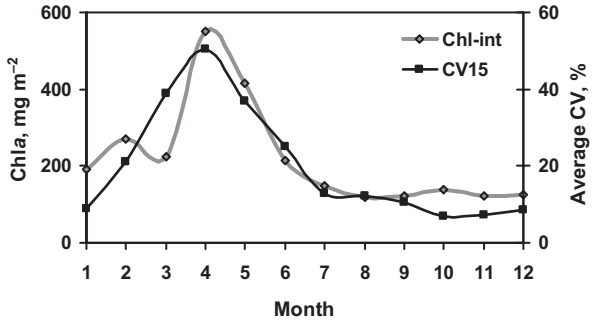

Fig. 3. Monthly average of areal chlorophyll *a* (Chl *a*) concentration and coefficient of variation (CV) of Chl *a* vertical distribution in the water column 0–15 m in Lake Kinneret from 1990 to 2003, in 358 experiments. The relationship between two variables was $y = 0.1086x$, $r^2 = 0.86$.

The average vertical profile of PP when *P. gatunense* dominated the lake phytoplankton showed a decrease from the uppermost layer toward the bottom (Fig. 4a). When other phytoplankton was dominant, a photoinhibitive effect was obvious, that is, the uppermost layer was on average less productive than the immediate layer beneath, but below the layer of maximum productivity, a consistent decline occurred in the downward direction. During the *Peridinium* period, ~56% of the PP was contributed by the 0–2 m layer, while otherwise it was restricted to 35%. The overall annual PP average of the uppermost layer was 41%. More than 95% of the PP occurred in the 0–7 m layer during the *Peridinium* period and in the water column of 0–10 m when other phytoplankton was dominant (Fig. 4b).

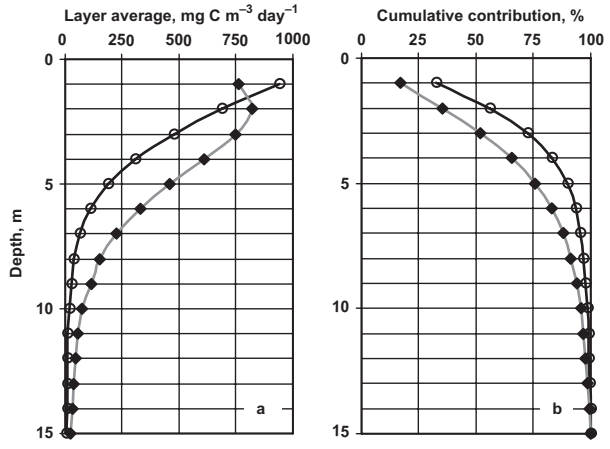

Fig. 4. (**a**) Average primary productivity segregated to water layers (0–1, 1–2,..., 14–15 m) in Lake Kinneret. Presented are averages based on all measurements taken in 1990–2003; averages ($n = 63$) when *Peridinium gatunense* was the dominant species (○) and measurements taken ($n = 295$) when other phytoplankton dominated the lake (◆). The actual value for the non-*Peridinium* cases was multiplied by 3. (**b**) Cumulative contribution of the 15 separate layers to the areal primary productivity.

Photosynthetic rates

In the period from 1990 to 2003, the depth of the maximal Chl *a* normalized productivity (optimal depth) ranged from 0 to 5 m, with an average of 1.35 ± 1.03 m, and the Chl *a* normalized productivity at that depth ranged from 0.25 to 8.85 mg C h^{-1} m^{-3} mg Chl a^{-1}, with a trend of higher values during the SA season (Figs 5 and 6). There was a conspicuous difference in the annual averages (Fig. 5), but the variability within each year was so high that a significant difference was observed only between the year with the highest average (1996) and the year with the lowest average (1998). The lowest monthly average was in April with 2.20 (±1.32) mg C h^{-1} mg Chl a^{-1} and the highest in September, with 3.93 (±1.72) mg C h^{-1} mg Chl a^{-1} (Fig. 6). There was only a slight variation in the overall average of the maximal Chl *a* normalized productivity, regardless of the depth where it occurred, with the exception of the case of optimal depth at 0 m (Table I). However, the average light measured at the depth of the maximal rate of PP decreased with depth, indicating radically different photosynthetic response of the dominant phytoplankton species to light input. The monthly averages of maximal rate of photosynthesis and the depth where it occurred moderately correlated positively, with the largest deviation from the regression line achieved in December and January (Fig. 7).

Downwelling attenuation coefficient—K_d

The coefficient of linear correlation, r^2, of the ln transposed light measurements against depth was mostly >0.99. Nevertheless, the variability of downwelling attenuation coefficient, K_d, was high when calculated for each 1-m interval of each one of the light profiles measured in this study. K_d was far more variable when *Peridinium* dominates the lake than otherwise, and most of the variability was apparent in the uppermost layer of the water column (Fig. 8). It is to say that the attenuation coefficient for a specific water layer may be conspicuously different from the average K_d based on the calculation over the entire euphotic zone. Therefore, the use of an average K_d for the entire epilimnetic water column may be misleading. In addition, there are some technical limitations (due to factors that were explicitly discussed by Kirk, 1994) pertained to the ability to measure light reliably, which force the uppermost layer to be measured below the surface of the water column. Consequently, for

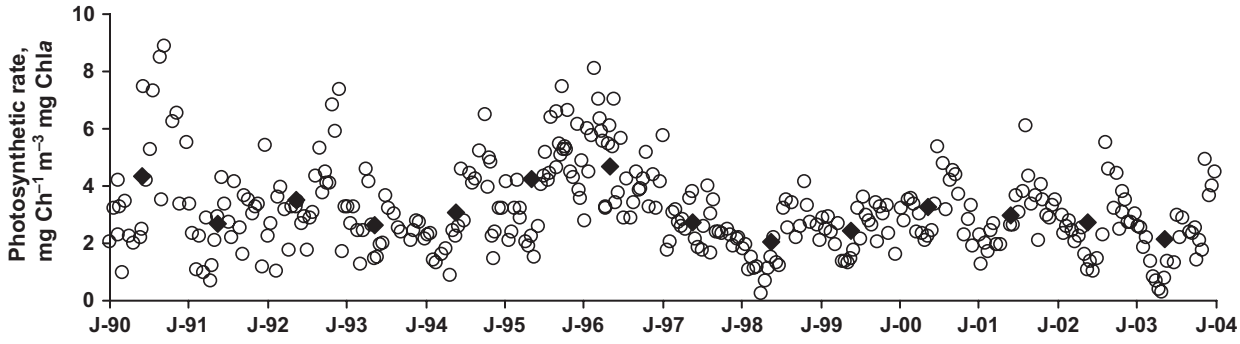

Fig. 5. Maximum Chl *a* normalized photosynthetic rate (mg C h^{-1} m^{-3} mg Chl a^{-1}) in Lake Kinneret in the years 1990–2003 (n = 358). *X*-axis intervals begin on January 1 of each one of the indicated years. Filled symbols (◆), annual average.

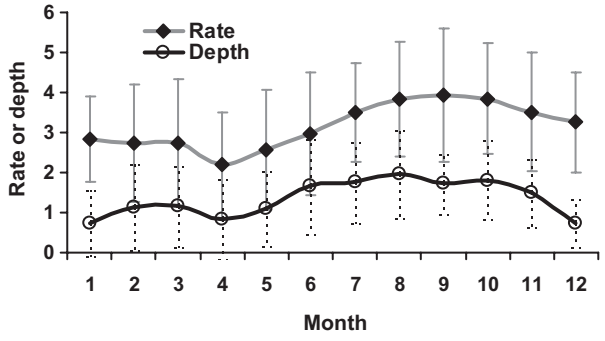

Fig. 6. Monthly average of the maximum Chl *a* normalized photosynthetic rate (mg C h^{-1} m^{-3} mg Chl a^{-1}) and the average depth (m) where it occurred in Lake Kinneret in the years 1990–2003, in 358 experiments. Vertical lines, SD.

Table I: The depth of the maximal rate of photosynthesis, the average (and SD) rate of photosynthesis at that depth (mg C h^{-1} m^{-3} mg Chl a^{-1}), the number of samples at the given depth and the average light (μM photon m^{-2} s^{-1}) available at the depth of maximal rate of photosynthesis in Lake Kinneret from 1990 to 2003

Depth, m	Average	SD	*n*	Average light
0	2.48	1.45	75	567
1	3.31	1.39	139	399
2	3.39	1.54	98	319
3	3.36	1.58	38	189
5	3.08	1.07	6	75

the sake of a temporal comparison K_d computed for the interval of 0.5–2.5 m is presented, which encompasses the water layer where most PP occurs.

The average K_d, in the 0.5–2.5 m water layer, varied from 1990 to 2003 within a relatively narrow limit, from 0.203 to 1.954 m^{-1}, but showing a high degree of temporal variation (Fig. 9). The average and SD were 0.627 and 0.231 m^{-1} (n = 333). The value was highest in April and lowest in July and August (Fig. 10), and the overall average for WS was higher than for SA, but all those averages were not different statistically. The plot of Chl *a* concentration in the uppermost layer of 0–1 m versus several K_d values showed a relatively low level of correlation when all data were used (Fig. 11a) and even lower if cases with Chl *a* concentration were >30 mg m^{-3} were omitted (Fig. 11b), that is, excluding samples dominated by *P. gatunense*. The slope of the regression of K_d versus Chl *a* concentration yields the value of the partial attenuation that is attributed to Chl *a*, K_c. In our case, it was 0.0031 for the overall database and 0.076 without the *P. gatunense* data, and varied saliently in different years and seasons.

Euphotic depth

Direct measurement of light intensity showed that it declined to 1% of its value at surface on an average depth of 9.27 (±2.18) m with a maximum and minimum of 15.17 and 1.86 m, respectively. The depth of light decimation to 10% of its surface value averaged 4.04 (±1.05) m with a maximum and minimum of 6.50 and 0.82 m, respectively. The light penetration parameters covaried temporarily (correlation coefficient of r^2 = 0.87, n = 333, $P < 0.001$) showing minimal values in April when mostly *Peridinium* dominated the lake phytoplankton (Fig. 12).

DISCUSSION

Lake phytoplankton

Phytoplankton composition, density and photosynthetical activity in Lake Kinneret showed a remarkable

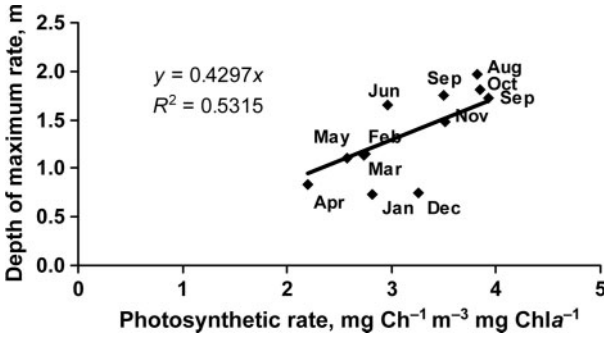

Fig. 7. The correlation of the monthly average of the maximum Chl *a* normalized photosynthetic rate (mg C h^{-1} m^{-3} mg Chl a^{-1}) and the average depth (m) where it occurred (optimal depth) in Lake Kinneret in the years 1990–2003, in 358 experiments.

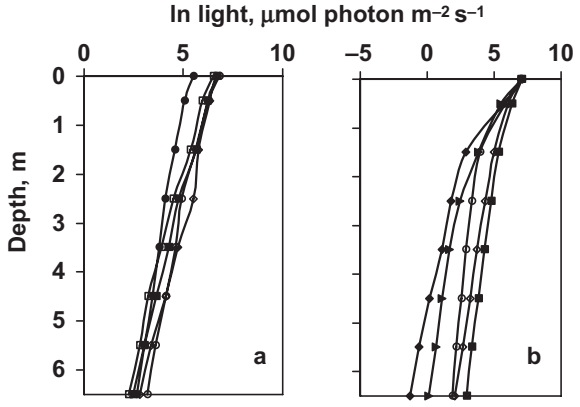

Fig. 8. Selected profiles of light (ln transformed values) versus depth in Lake Kinneret in 2003. (**a**) On dates with a fairly uniformly vertical dispersal of Chl *a* concentration; (**b**) on dates with a conspicuous subsurface Chl *a* maximum (*Peridinium*-dominated phytoplankton).

stability over the span of time of more than two decades. That stability has been explained about a decade ago by the control of availability of phosphorus, which is the limiting nutrient in the lake (Berman *et al.*, 1995). In the recent decade, only slight changes were recorded in phosphorus concentrations or its temporal dynamics, but major changes in phytoplankton occurred. The most conspicuous floristic signature of the lake phytoplankton was the formation of dense blooms of the large thecated dinoflagellate *P. gatunense*, mostly from February to June. This bloom was subsequently followed by a mixture of small dinoflagellates, chlorophytes and small diatoms that were the dominant components of the phytoplankton, in varying proportion throughout the rest of the year (Pollingher, 1986). That predictability of phytoplankton succession in the lake has been shattered in the recent decade, with the appearance of new dominant species of phytoplankton and the de-stabilization of *Peridinium* periodicity, phenomena described and discussed extensively by Zohary (Zohary, 2004). In 1994, 1995, 1998 and 2003, *Peridinium* densities were at least twice the average of 1972–1993 on one hand, and on the other hand less than half in the years 1997, 2000 and 2001. Although in the years of extremely low *Peridinium* concentrations other species took a relatively larger share in the total phytoplankton biomass, annual and WS Chl *a* concentrations in such years were low, and those with extremely high *Peridinium* concentrations were conspicuously high (Fig. 2a). The shift in phytoplankton succession in the lake did not have a conspicuous impact on the pattern of vertical distribution of Chl *a*, even when the dominant species was a cyanophyte, such as *Aphanizomenon ovalisporum* (Pollingher *et al.*, 1998). Despite the salient variation in Chl *a* concentrations, the fluctuations in PP were fairly small and not different from the temporal fluctuations recorded in the period 1972–1993, when the lake phytoplankton composition and density varied within a relatively narrow limit (Fig. 2b).

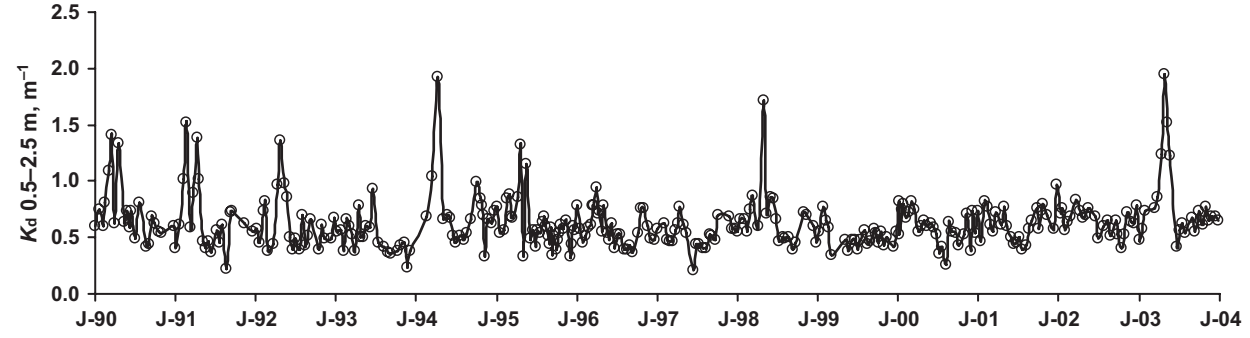

Fig. 9. Downwelling irradiance attenuation coefficient—K_d, average for wavelengths from 400 to 700 nm, in Lake Kinneret from 1990 to 2003 (n = 333). Based on measurements taken from 0.5 below surface down to 2.5 m.

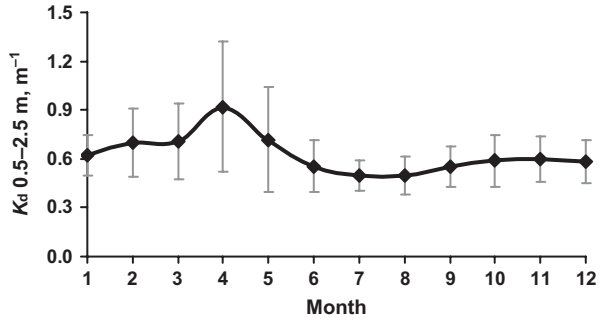

Fig. 10. Monthly average of irradiance downwelling attenuation coefficient—K_d. Based on measurements taken from 0.5 below surface down to 2.5 m in Lake Kinneret from 1990 to 2003, in 333 experiments. Vertical lines, SD.

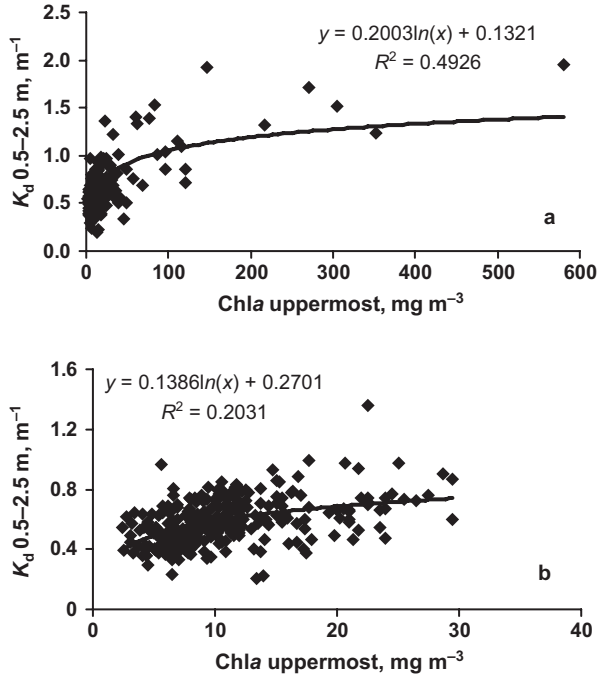

Fig. 11. The relationship between Chl *a* concentration in the uppermost layer (0–1 m) versus K_d calculated at the 0.5–2.5 m layer of the water column. (**a**) All comparisons (n = 333); (**b**) cases where Chl *a* concentration was <30 mg m^{-3} (n = 294). The trend line was fitted by the use of logarithmic regression.

Surface chlorophyll and the chlorophyll of the euphotic depth

The definition of relationships between the standing stock of phytoplankton and its photosynthetic activity in the 'surface' layer and within the entire water column is a key factor for the implementation of remotely operated sensors for water body monitoring. So far as the phytoplankton standing stock is considered, represented by Chl *a*, the lower boundary of the 'surface' is determined by the 'penetration depth', Z_{pd}, which is defined as the water layer where downwelling irradiance declined to $1/e \approx 0.368$ of the value at the surface (Morel and Berthon, 1989). Penetration depth has practical meaning as ~90% of the diffusely reflected radiance (the energy potentially recorded by remotely operated optical sensors) originates in that water layer (Gordon and McCluney, 1975). The overall penetration depth in Lake Kinneret was in average 1.77 m, and the average Chl *a* concentration within that layer was almost identical with the Chl *a* calculated for the uppermost layer. The degree of vertical variation of Chl *a* concentration in Lake Kinneret is mostly small enough to enable considering the uppermost layers as representative of the entire euphotic layer. Even if the vertical distribution is not uniform, when *Peridinium* forms thick crop, the relatively high correlation between Chl *a* concentration at the uppermost layer and the integral Chl *a* content makes the uppermost layer a fair representative of the euphotic layer.

The plausible correlation between the Chl *a* concentration within the penetration depth and the Chl *a* content in the euphotic water column may not exist in lakes where stable stratification allows formation of high chlorophyll concentration close to the compensation depth (Fee, 1976; Christensen *et al.*, 1995); but in the case of Lake Kinneret, light penetration at the compensation depth does not surpass the depth of mixing, which during stratification is usually located at ~15 m (Serruya, 1978).

Remote sensing of chlorophyll

Most of the information pertaining to remote sensing of Chl *a* was developed for oligotrophic waters, where detritus and inorganic particles are scarce or their concentrations correlate with phytoplankton density. The major goal of the studies conducted in Lake Kinneret on that subject was to develop robust algorithms for remote monitoring of Chl *a* density in turbid inland waters. The concept was based on the application of semi-analytical approach, which made use of the ranges with a maximal and minimal sensitivity of reflectance to change in chlorophyll concentration (Gitelson *et al.*, 1994; Yacobi *et al.*, 1995). We inferred from our work that the spectral requirements for Chl *a* estimation are restricted and the use of an instrument with several narrow (10–20 nm) spectral channels in the red and near infrared ranges should be sufficient. Based on that work, we reckoned that satellite-carried sensors are capable of providing the necessary information for the estimation of Chl *a* density in productive waters. The concept employed in Lake Kinneret was tested in a whole range of productive, inland and coastal water bodies and found appropriate for

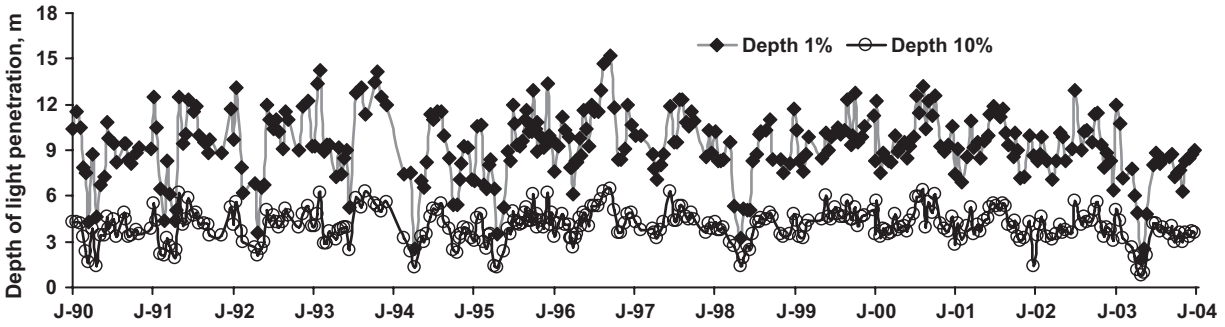

Fig. 12. The depth of 1 and 10% light penetration in Lake Kinneret from 1990 to 2003 (n = 333).

the construction of algorithms for Chl *a* estimation (Gitelson *et al.*, 2000). A further development for the use of the optical information in the red and near-infrared range of the electromagnetic spectrum, based on fieldwork in shallow lakes in Nebraska, USA, was recently presented (Dall'Olmo *et al.*, 2003).

Modeling of PP

In previous years, a relatively high linear correlation was found between Chl *a* concentration and PP in the uppermost layers of 0 and 1 m (Berman *et al.*, 1995). Since most of the PP is executed in those layers, we could hope for an easy first-order approach for the estimation of PP using Chl *a* surface concentration as the major input, as done for instance by Joint and Groom (Joint and Groom, 2000) in the case of the North Sea. However, using the data of 1990–2003, we realized that those correlations are not valid anymore, particularly for the WS period. During the 4 years with extremely high *Peridinium* crop, the concentration of cells near the surface became so large that the correlation between Chl *a* and PP at the uppermost layer significantly declined in comparison with previous years. Anyway, Chl *a* normalized photosynthetic efficiency is species dependent and depends on the physiological status of algae (Kruskopf and Flynn, 2006). It should, therefore, be rather an exceptional situation if surface Chl *a* concentration alone can be used as a predictor for PP in a natural environment.

The estimation of daily integrated PP is a more challenging task, as it requires a larger input for calculation. It has been successfully accomplished for ocean global coverage, using Chl *a* measurements acquired by satellite-carried sensor and a set of meteorological data (Behrenfeld and Falkowski, 1997). To test the feasibility of predicting PP in Lake Kinneret, daily integral PP was simulated using a simple model devised by Talling (Talling, 1957):

$$P_a = B \times P_B^{opt} \times \ln(E_0/0.5E_z)/K_d \quad (2)$$

where P_a = areal daily PP, B = phytoplankton biomass, P_B^{opt} = biomass-based maximal photosynthetic rate (optimal productivity), E_0 = light available at water surface, E_z = the light available at the depth of optimal productivity and K_d = the vertical attenuation coefficient of downwelling radiation.

The input data for the model were measurements taken in Lake Kinneret from 1990 through 2003. The phytoplankton biomass was the average Chl *a* concentration of the uppermost water layer (that of 0 and 1 m), assuming it is a fair representative of the entire euphotic layer, as described previously.

Comparison of the modeled daily integral PP to the actually measured data showed a plausible match in most cases, with the most extreme deviations when high crop of *P. gatunense* prevailed in the lake (Fig. 13). The linear regression between the two series was as follows: $PP_{simulated} = 1.00 \cdot PP_{measured} + 411$ ($r^2 = 0.63$, $n = 325$, $P < 0.001$). It is to say that one can simulate integral daily PP using actual measurements as the input data. If the input data are designed to derive from remotely operated sensors and/or by automatically recording instruments, phytoplankton biomass and light measurement (and calculation of K_d) are also feasible. The measurement of E_0 (light available at water surface) precisely, under field conditions, is technically impossible, but assuming that it is equal to 90% of the light recorded above surface in a meteorological station is probably a fair approximation, and even a change of that value to 95 or 85% changes the simulated result only slightly.

Vertical variability of K_d was noted in Lake Kinneret in the past (Dubinsky and Berman, 1981) and is also typical of other lakes (Schanz *et al.*, 1997). The vertical variability of K_d is strongly related to Chl *a* concentration when *Peridinium* dominates the lake phytoplankton, but otherwise it is not. We already have found that when

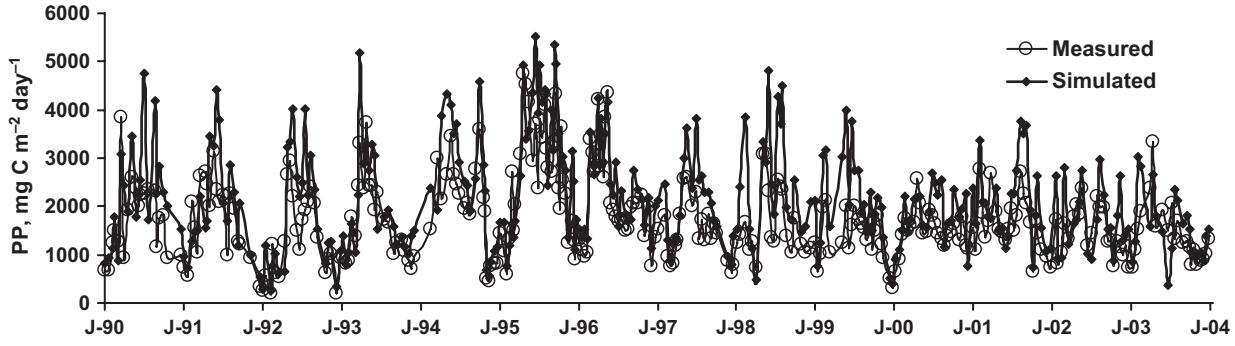

Fig. 13. Simulated and measured daily integral primary productivity (PP) from January 1990 through December 2003 in Lake Kinneret. The simulation was done using equation (2) (n = 333).

Peridinium dominates the lake phytoplankton, it is also the major component of the total seston, and therefore the concentration of Chl *a* covaries with the concentration of total suspended matter (Yacobi and Gitelson, 2000). Otherwise, Lake Kinneret is typical case 2 water where Chl *a* concentration and other water components that determine the optical properties of the water are not strongly correlated. The concentrations of the colored dissolved organic matter in the lake, measured in the range of 400–700 nm, are below our measuring capabilities; therefore, it can be safely stated that non-phytoplankton-suspended particles are the major components that determine the optical properties of the water besides phytoplankton pigments. Thus, the increase of light attenuation in December and January, during the overturn, is apparently affiliated with the increase of suspended sediment in the water, and not with the increase of Chl *a* concentration.

K_d is highly not uniform along the water column, but for modeling of PP, the uppermost 0.5–2.5 m provides an appropriate basis. In principle, it is possible to calculate K_d by using radiative transfer models, using reflectance emitted from the water surface (Morel and Berthon, 1989; Morel and Loisel, 1998) or by employing empirically derived relationship (Kutser *et al.*, 1995; Gons *et al.*, 1998). The latter requires frequent recalibration but is potentially useful for large water surfaces, following calibration at one or few points for each experiment separately. Alternatively, a simple technical solution for the determination of K_d is by using just two sensors located in the water column to obtain a fairly good estimation of the light attenuation in the uppermost part of the water column.

In models designed to calculate global ocean PP, temperature was used as a proxy for the estimation of maximum photosynthetic efficiency, taking into account the positive relationship between carbon assimilation and temperature and the negative relationships between nutrients and temperature (Balch and Byrne, 1994; Behrenfeld and Falkowski, 1997; Maranon *et al.*, 2003; Perez *et al.*, 2005). Jassby *et al.* (Jassby *et al.*, 2002) calculated the characteristic value of photosynthetic efficiency using measured values of PP and Chl *a* and subsequently used it in their model for assessing temporal and spatial variability of PP in the Sacramento-San Joaquin Delta system (California).

In the case of Lake Kinneret, the variation in P_B^{opt} is virtually independent of temperature (Fig. 14), although in average it is higher throughout the SA period (Fig. 6). Use of monthly or seasonal averages of P_B^{opt} yielded poor simulating results when introduced to equation (2) for the calculation of daily integral PP. A possible source of error in the calculation of correlation between maximal P_B^{opt} and temperature could have been caused by measurement in suboptimal irradiance conditions, as indicated by the exceptionally low average P_B^{opt} in the 0-m depth record (Table I). However, elimination of the data from the surface layer does not change fundamentally the relationships illustrated in Fig. 14.

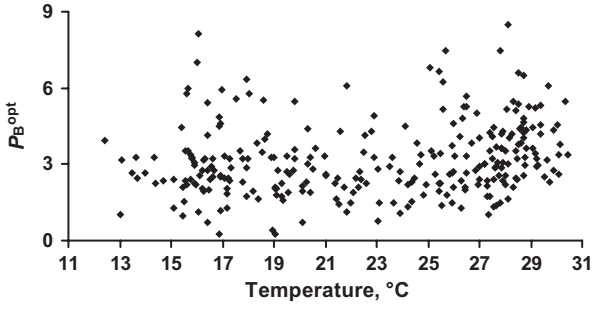

Fig. 14. The relationship between epilimnetic water temperature and maximum efficiency of photosynthetic activity in Lake Kinneret, 1990–2003 (n = 280).

It is expected that there is a positive correlation between temperature and P_B^{opt} as Calvin cycle enzymatic activity should increase with temperature elevation (Sukenik *et al.*, 1987). But, P_B^{opt} is dependent also on nutrients, cell size and light history (Falkowski, 1981). Nutrient concentrations in the epilimnion of Lake Kinneret are highest during the winter overturn, when temperatures are relatively low (Serruya, 1978), and in that respect the situation is not different from that found in oligotrophic waters. But complex interaction of nutrients with other abiotic and biotic factors in Lake Kinneret makes the capability to predict P_B^{opt} by a simple measurement not feasible. It is highly probable that the situation found in Lake Kinneret—a lack of correlation between temperature and P_B^{opt}—is common to other productive water bodies. The size spectrum of phytoplankton is mostly higher than in oligotrophic marine environments; the latter are often dominated by small cells, whereas in productive waters, it usually ranges at least one order of magnitude between the smallest dominant cells and the largest dominant forms. Another factor is the probability of opportunistic supply of nutrients to the euphotic layer of inland waters. While the enrichment of the nutrient deplete euphotic water column in pelagic marine environments is limited to the predictable event of thermal destratification, in inland waters accidental provision of nutrients by the way of terrestrial input or horizontal translocation from the littoral is not exceptional.

CONCLUSIONS

Chl *a* can be reliably estimated by remote sensing techniques, even in productive and turbid water like that of Lake Kinneret. A preparatory work both at water surface and using satellite-carried sensors was already finalized in the lake and enabled mapping of the spatial distribution of Chl *a* in the lake (Mayo *et al.*, 1995; Yacobi *et al.*, 1995). The finding that the assessment of Chl *a* at surface layers can be extrapolated to the entire water column indicates that remote sensing techniques can be used for the estimation of the phytoplankton Chl *a* standing stock. On the other hand, application of models for PP, in Lake Kinneret using remotely sensed data, is not feasible. The most crucial factor is the lack of capability to simulate P_B^{opt} by statistical dependence with an easily measured variable like temperature. A solution that seems plausible in the current status of knowledge is the use of *in situ* moored instrument that can provide information on maximum efficiency of photosynthetic activity (Wilhelm *et al.*, 2004) and use it as a source for the simulation of whole lake productivity.

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