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Optimal conditions for primary production in a polymictic tropical lake (Lake Xolotlán, Nicaragua)

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Abstract

From 1987 to 1993 we assessed the variation of phytoplankton biomass, underwater irradiance and primary production in Lake Xolotlán (L. Managua, Nicaragua). Chlorophyll-*a* averaged 65 mg m^{-3} and maximum and minimum concentrations were 120 and 30 mg m^{-3}, respectively. The variability over depths and weeks was low (CV $<$ 20%). There were strong correlations between particulate carbon and chlorophyll-*a* (the ratio $\approx$ 100: 1) and between particulate carbon and particulate nitrogen and phosphorus (the ratio $\approx$ 100: 11: 1). Gross primary production averaged 6.8 g C m^{-2} d^{-1} and was stable over the years (CV $\approx$ 10%). Algal cell growth was approximately 4–5 g C m^{-2} d^{-1}.

Productivity was limited only by the availability of underwater light and the depth of the photic zone was mainly regulated by the chlorophyll-*a* concentration. Therefore, areal photic zone chlorophyll-*a* was the only factor directly correlated to the integral photosynthetic activity but, contrary to theoretical models, the production did not increase in proportion to chlorophyll-*a*. Data from African lakes show a similar pattern.

Introduction

Primary production in warm tropical lakes is higher than in temperate lakes (Brylinsky & Mann, 1973; Melack, 1979; Brylinsky, 1980; Lemoalle, 1981; Lemoalle et al., 1981; Lewis, 1987; Kalff, 1991; Pollingher & Berman, 1991). The reason is that the maximum rate of photosynthesis per biomass and time (photosynthetic capacity) is a function of temperature (Harris, 1978). Higher incident irradiance and enhanced vertical mixing are additional factors promoting primary production in tropical lakes (Lewis, 1987). At comparable phytoplankton biomass within the photic zone, primary production in tropical lakes is in general two to three times higher than in temperate lakes, as shown by Lemoalle (1981) and Lemoalle et al. (1981). Lewis (1987) came to the same conclusion using global data on incident irradiance and water temperature, and assumptions of quantum yield and chlorophyll-*a* in the photic zone, according to Bannister & Wiedemann (1984) and Talling (1971), among others. Measured rates (IBP mean values) did, however, not show latitude differences of that magnitude. To explain this Lewis concluded that nutrient limitation must be of greater importance in tropical lakes than in temperate lakes. On the other hand, there is some evidence for increasing nutrient concentration and nutrient input with decreasing latitude (Schindler, 1978; Kalff, 1991). Nutrient dynamics and availability should also be favoured at low latitudes by high temperature due to its driving of turn-over rates (Brylinsky & Mann, 1973). Furthermore, data in Lemoalle (1981) and Lemoalle et al. (1981) indicate that tropical lakes with very high primary production had a production per biomass reduced close to that of temperate lakes (cf. Vareschi 1982), and these shallow, well mixed lakes were primary limited by light and less by nutrients (Ganf & Viner, 1973; Talling et al., 1973; Robarts, 1979).

The present study deals with the primary production of tropical Lake Xolotlán, Nicaragua, covering the period 1987–1993. The lake is situated at 12° N and 38 m above see-level. The surface area is close

to 1000 km^2 and mean depth is approximately 8 m. Wind speed over the lake is 5–10 m s^{-1} (Erikson et al., 1997). Water temperature is between 28 and 30 °C and is, like oxygen concentration, homogenous throughout the whole water column, with exception for rare windless occasions (PLX, 1987; Lacayo, 1991). The water content of inorganic carbon is approximately 150 mg l^{-1}, never being a limiting resource for primary production. Large quantities of sewage water from the city of Managua enter the lake via the southern basin. The lake is endorheic and accumulates nutrients. Further information on geology and physical and chemical properties of the lake is given in Lacayo (1991) and Erikson et al. (1997). The results presented here are part of a larger study of the productivity and organic carbon cycling in the lake. A previous paper (Erikson et al., 1997) dealt with results from 1985–1986 and showed that the level of primary production was as high as in the most productive warm tropical lakes. The present paper includes different methods to measure primary production and a more complete set of data on phytoplankton biomass, particulate organic matter and underwater light climate.

The aims of this paper are: (i) to describe the long-term variation of phytoplankton biomass and primary production, (ii) to compare the results of different methods measuring primary production, (iii) to evaluate the role of nutrients and underwater light as controlling factors, (iv) to compare the results with those from similar tropical lakes and with theoretical models of maximum primary production.

Methods

Sampling regime

Sampling and measurements were done at varying intervals during the period 1987–1993 at one station in the shallow, southern basin and one station in the deeper central basin (Figure 1), mainly at the end of the dry season (April) and at the end of the rainy season (Oct.–Nov.), sometimes also in between these periods. We often sampled for several days during a period of about one week, but from 1992 and onward most samplings were performed during one day. In 1991 and 1993 primary production was measured only at the end of the rainy season.

Samples for biomass parameters were collected with a Van Dorn sampler from three depths in the centre of the lake (0.5, 3, 10 m) and from two depths in the southern basin (0.5, 3 m). Sometimes we sampled for chlorophyll-*a*, phaeophytin and particulate carbon, nitrogen and phosphorus from each meter of the water column. An integrated water sample of the photic zone was used for primary production measurements. ^{3}H-adenine incorporation was assessed in water from 0.5 m depth and in different size fractions by filtering the water through cellulose acetate membrane filters of 3 μm and 1 μm pore-size under low pressure (manual pump and change of filters when pores became clogged). Underwater PAR transmission was measured at 0.25 m intervals directly within the photic zone.

Diurnal studies were performed in the central basin on 6–7 June 1987, 10–11 October 1988, 13–14 April 1989, 27–28 October 1989, and 3–4 April 1990. Samplings for biomass parameters were repeated at 4 h intervals and comprised the entire 24-hour cycles. Diurnal O_2 evolution was measured by series of short incubations from dawn to dusk, whilst measurements of ^{3}H-adenine incorporation (in Oct. 1989 and April 1990) were performed during the entire 24-hour cycles, repeatedly in 4 h intervals.

Analytical methods

Phytoplankton chlorophyll-a and phaeophytin were measured by filtration of lake water through GF/C glass fiber filter, followed by spectrophotometric analysis of ethanolic extracts before and after acidification (Nuch & Palme, 1975). Pigment extraction in acetone, as described in Ahlgren (1983), with grinding of filters and additional analysis of chlorophyll-*b* and chlorophyll-*c* was done for the comparison of methods. Particulate organic carbon (POC) and nitrogen (PON) were determined by filtering lake water onto pre combusted GF/C glass fiber filter and analysed with a Carbo Erba CHN analyser. Particulate phosphorus (PP) was determined directly by analysing lake water filtered onto cellulose acetate membrane filters (0.45 or 1.0 μm pore-size) or indirectly as a difference by analysing both unfiltered and filtered (GF/C) lake water. PP samples were analysed after digestion in a mixture of sulphuric, nitric and perchloric acids, using a modification of the Murphy & Riley (1962) method (Ahlgren & Ahlgren, 1976). Samples for dissolved organic carbon (DOC) were filtered through GF/C glass fiber filters and analysed with a Shimadzu TOC analyser.

Underwater irradiance of down-welling photosynthetically active radiation (PAR: 400–700 nm) was

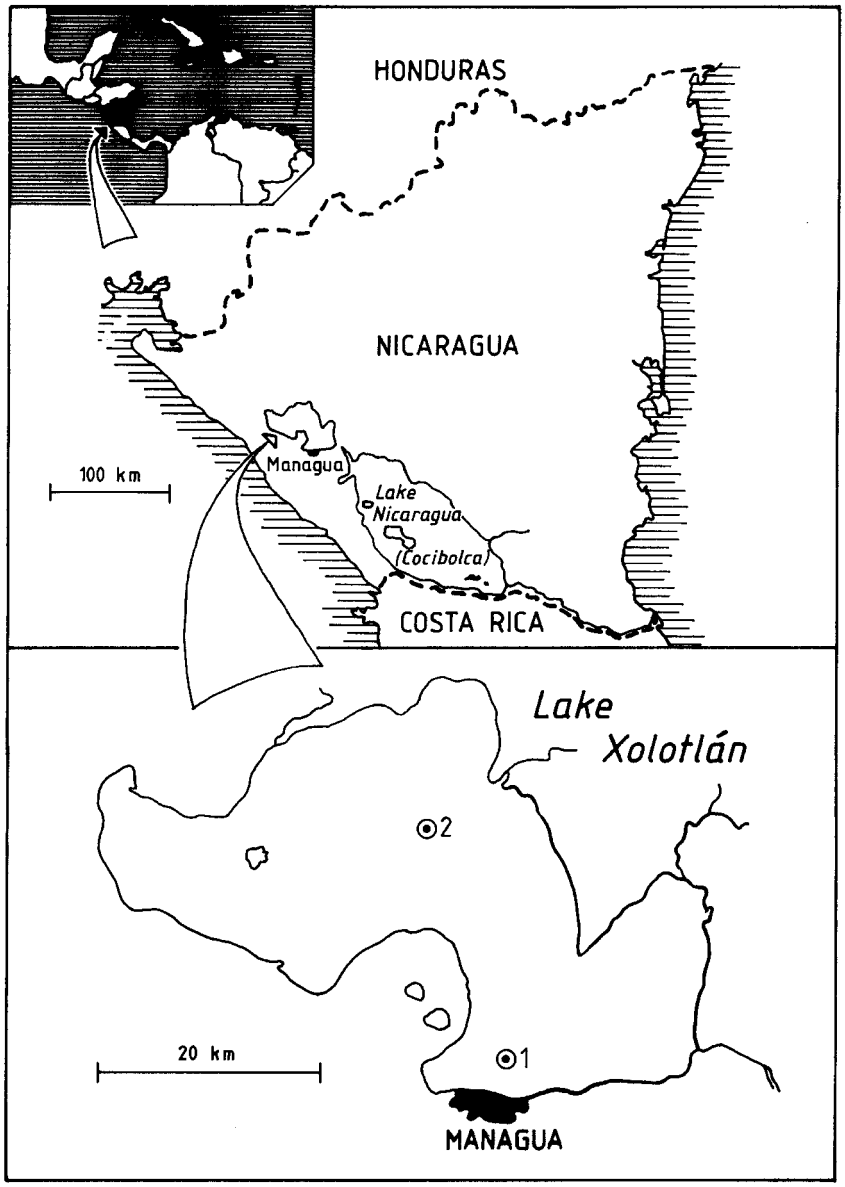

Figure 1. Lake Xolotlán and the sampling sites; 1 in the southern basin and 2 in the central basin.

measured with a LI COR 185 B quantum meter and a LI COR SB cosine corrected underwater quantum sensor. Transmission of light within the blue, green and red spectral regions was measured through Schott BG 12, VG 9 and RG 2 filters, with optical mid-points of 450, 535 and 650 nm respectively. Incident irradiance (I_o) was registered by an integrator connected to a second LI COR quantum sensor above the water surface. Records of the water level were obtained from the national institute for land surveying (INITER, Managua), as daily measurements of lake water surface in meters above sea level (m.a.s.l.) at the Carranza and Miraflores stations.

Primary production was measured as oxygen evolution in light bottles compared to dark bottles with an YSI 57 oxygen meter and flask probe. Eight pairs of light bottles were rapidly filled with an integrated water sample from the photic zone and immediately submerged at eight distinct levels (0.1–3 m). Three dark bottles were treated in the same way and sub-

merged below 3 m. After an incubation of 30 minutes oxygen concentration was measured in all bottles. Measurements by the ^{14}C method as described in Ahlgren (1988) were performed twice in November 1993. ^{14}C was also measured in the filtrates in order to detect DOC excreted by photosynthezising algae. The ^{14}C method was once used at the same time as the O_2-method, which on that occasion was assessed with both the oxygen meter and the Winkler technique.

Algal cell growth was measured as the difference between the rates of ^{3}H-adenine and ^{3}H-thymidine incorporation. The ^{3}H-thymidine method as described in Erikson et al. (this volume) was used to measure the heterotrophic activity of bacterioplankton. Both bacteria and algae incorporate adenine, but thymidine is incorporated only by bacteria (Riemann & Bell, 1990). Assays for adenine incorporation in unfiltred and filtered water were made in 20 ml glass scintillation vials and incubated in a water bath on board. Triplicate 10 ml samples and a formaldehyde killed blank (2% final conc.) of unfiltered water were incubated with 250 nM [methyl-^{3}H]adenine (24 Ci mmol^{-1}; Amersham) for four hours. Filtered water (3 μm and 1 μm) were incubated with 100 nM [methyl-^{3}H]adenine (24 Ci mmol^{-1}; Amersham). The optimum adenine concentration and incubation time was chosen by experience (Bell, pers. com.). The incubations were stopped by adding formaldehyde to a final concentration of 2%. Further analysis were performed as for ^{3}H-thymidine (Erikson et al., 1998). The coefficient of variation for triplicate determination was seldom higher than 10%.

Algal abundance was assessed in all ^{3}H-adenine samples in October 1989 and in twelve of the samples in April 1990. Unfiltered and filtered samples (< 3 μm and < 1 μm) for the enumeration of algae were placed in 20-ml plastic scintillation vials containing sterile formaldehyde (4% final conc.). 0.1–0.2 ml of sample was diluted to > 2 ml with sterile tap water, sonicated 1 min in an ice-bath with a Rapids 350 Ultrasonic Disintegrator at 20kHz and 100W, added to a Millipore funnel and filtered onto black 25 mm, 0.2-μm pore-sized Nuclepore polycarbonate filters. The filters were examined using a Nikon Labophot fluorescent microscope and filter set G1-B for autofluorescence.

Data handling

Long term trends were evaluated using average values calculated for all depths and days of each sampling period. Depth integrated data of primary production and underwater irradiance (see below) from adjacent days were treated in the same way. The variability at different depths and over short and long time scales were expressed as the coefficient of variation (CV; in figures as standard deviation) within and between such average values. Relationships were tested by means of regressions.

Vertical extinction coefficients (K) were estimated as the slope of the log transformed irradiance vs depth relationship. The vertical extinction coefficient for the spectral region that penetrated the deepest (K_{min}) was estimated likewise. Irradiance at any depth of the water column (I_z), or the depth (z) for any irradiance, was calculated as $I_z = I'_o \cdot e^{-Kz}$. I'_o is the irradiance just below the surface, which could not be precisely measured because of the permanent heavy sea, and was taken to be 90% of I_o. The depth of the photic zone (Z_p), at the depth of 1% of incident irradiance, is thus given by ln 100/K. The average light availability integrated over the water column under conditions of complete mixing (I_m) is calculated as $I_m = (I'_o/K \cdot z) \cdot (1–e^{-Kz})$, according to Riley (1957). The fraction of light absorbed by chlorophyll-*a* was calculated as $F_{abs} = k_c \cdot \text{Chla}/K_{min}$ (cf. Ganf, 1974), where k_c is the specific absorption coefficient for chlorophyll-*a* in the spectral region that penetrated the deepest. Long time average (normal) water level is close to 38 m.a.s.l. (IRENA, 1982). The entire water column is vertically mixed and at normal water level its depth is on average 10 m in the central basin and 5 m in the southern basin. Mixing depths (Z_m) in the two basins are thus given by the water level records (m.a.s.l.) subtracted by 28 and 33 m, respectively.

Differences between oxygen content in exposed and unexposed bottles were integrated planimetricaly over the depth of the photic zone to give gross primary production per square meter and hour. ^{14}C data were treated in the same way. Results from the two methods were compared by using the stoichiometric relationship between carbon and oxygen (12/32).

Incorporation rates of adenine were converted into carbon production according to the moles adenine incorporated, the mole% of adenine in DNA (25%), the mole wt of adenine (318; nucleotide average), the C:DNA ratio (50; Karl, 1981) and the fraction of DNA to other macro molecules (0.8; Bell, pers. com.). Thus, net primary production (g C m^{-2} h^{-1}) = (moles of ^{3}H-adenine – moles of ^{3}H-thymidine incorporated) $\cdot$ (318/0.25) $\cdot$ 50 $\cdot$ 0.8 $\cdot$ (1000 $\cdot$ water column depth in meters) $\cdot$ (60/incubation time in minutes).

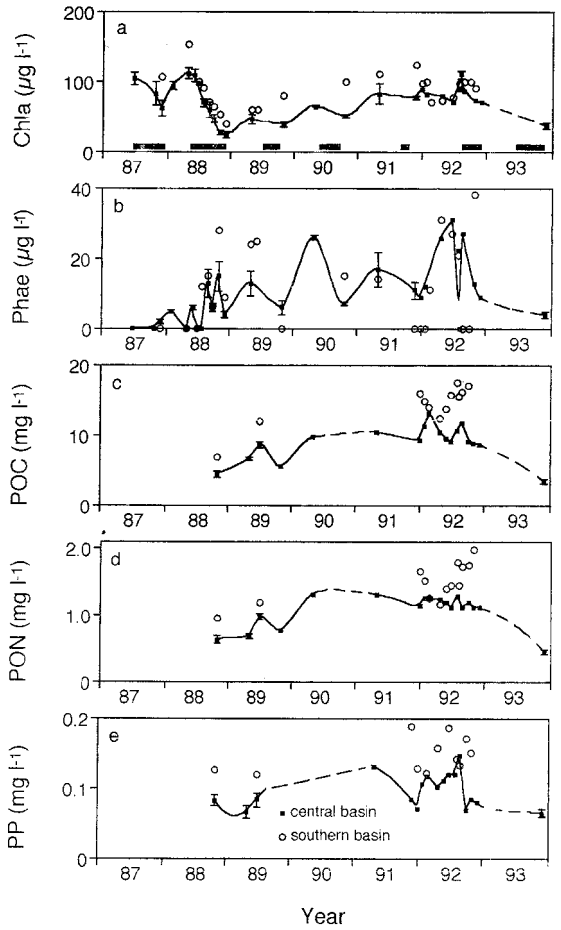

Figure 2. Temporal variability of mean column concentrations of (a) chlorophyll-*a*, (b) phaeophytin, (c) particulate organic carbon, (d) particulate organic nitrogen and (e) particulate organic phosphorus. Standard deviations (SD; vertical bars) are shown for averages that are composed of data from more than three depths and from adjacent days. Rainy periods are shown in Figure a (horizontal black bars) and symbols for central and southern basin in Figure e. Lines are interpolations on basis of data from the central basin.

Diurnal rates of gross production (O_2 evolution) and net production (^{3}H-adenine incorporation) were determined from planimetric integration of the time course curves.

Results

Algal biomass

The mean concentration of chlorophyll-*a* in the water column (Chla) of central Lake Xolotlán ranged between 30 and 120 μg l^{-1} (Figure 2a), with an

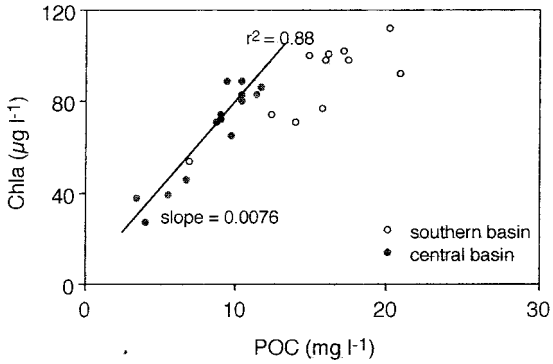

Figure 3. Relationship between concentrations of chlorophyll-*a* and particulate organic carbon.

average of 65 μg l^{-1}. The variation of Chla in the southern basin was similar to that in the centre, but concentrations were on average 45% higher (Figure 2a). The most significant change in Chla coincided with a period of storms and heavy rains, e.g. the tropical hurricane Juan in October 1988, when Chla dropped dramatically. Chla decreased also during regular rain periods (Aug.–Nov.) whereas during dry periods (Dec.–April) there was always an increase of Chla. The coefficient of variation (CV) of vertical and weekly averages was never more than 20% (Figure 2a).

The periodic averages of phaeophytin concentration in the water column (Phae) showed a higher CV (Figure 2b). Phae also exhibited greater seasonal variations than Chla at both sampling sites with values ranging from 0 to 38 μg l^{-1} (Figure 2b). Over the years the CV for Chla was 37% and for Phae 80% (data from the end of the rainy seasons and end of the dry seasons). The CV for the sum of Chla and Phae was however lower (31%). From 1987 to 1989, when Chla and Phae were assessed frequently within short intervals and during a period of great biomass changes, there was an inverse correlation ($p < 0.05$) between the two pigment concentrations. Sampling was relatively frequent also during 1992 and Chla and Phae from this period showed a similar inverse relationship (Figure 2a,b). Furthermore, despite much higher Chla in the southern basin than in the central, Phae was on average higher in the central basin than in the southern (14 and 12 μg l^{-1}, respectively).

POC averaged 15.2 mg l^{-1} in the southern and 8.5 mg l^{-1} in the central basin and differences were generally higher ($> 45\%$) than corresponding differences in Chla (Figure 2c). This was probably due to

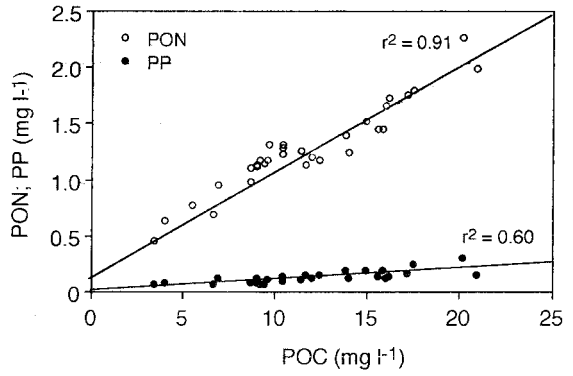

Figure 4. Relationships between concentrations of particulate nitrogen and phosphorus and particulate organic carbon.

detritus and bacteria of the sewage water that entered into the southern basin. A strong linear relationship between POC and Chla was obtained for the central basin, with an intercept indicating zero non-algal POC and a proportion of POC to Chla by weight of 130: 1 (Figure 3), whereas a weaker relationship was obtained in the southern basin.

Particulate organic nitrogen (PON; Figure 2d) averaged 1.3 mg l^{-1} and particulate organic phosphorus (PP) 0.12 mg l^{-1} (Figure 2e). PP showed a higher temporal variability than PON (CV = 41 and 30%, respectively). This was true also for adjacent days and depths. Still, both were strongly correlated to POC and the average ratio by weight of C: N: P in their particulate organic forms was 100: 11: 1, based on slopes of regression lines (Figure 4).

Light availability

During the dry and rainy periods I'_o at 9–10 a.m. was on an average 1450 and 1250 μmol Quanta m^{-2} s^{-1}, respectively. This agrees with other long term measurements of incident irradiance over the area (Fuente, 1986).

The vertical extinction coefficient (K) ranged between 1.84 and 4.11 m^{-1} in the centre of the lake, with decreasing light penetration during the dry period and increasing light penetration during the rainy period (Figure 5a). K was higher in the southern basin and variations did not always follow those in the centre, which probably was a result of the influence of the sewage water. Red light always penetrated deepest, i.e. had the minimum vertical extinction coefficient (K_{min}). Blue light was attenuated most rapidly. K and K_{min} (CV = 22%) were strongly correlated to Chla in the central basin, although the linear regression

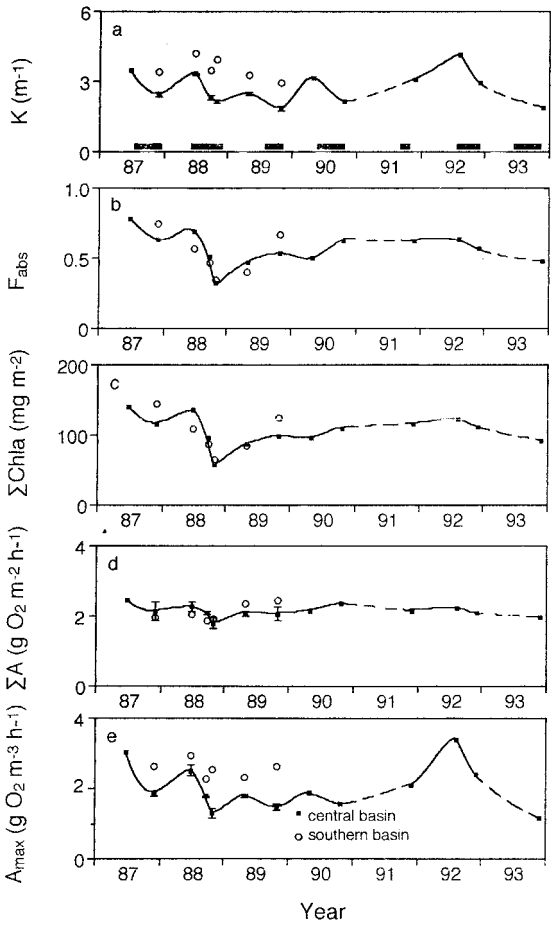

Figure 5. Temporal variability of (a) vertical extinction coefficient, (b) chlorophyll-*a* fractional light absorption, (c) chlorophyll-*a* in the photic zone, (d) depth integrated gross primary production and (e) production at optimum depth. Standard deviations, symbols for rainy periods and basins and interpolated lines as in Figure 2.

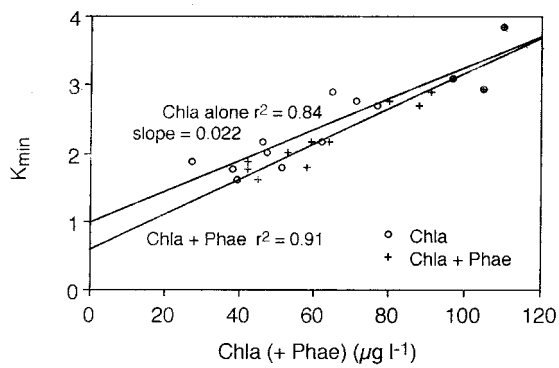

Figure 6. Relationship between the minimum vertical extinction coefficient and mean column concentrations of chlorophyll-*a*, with and without correction for phaeophytin in the central basin.

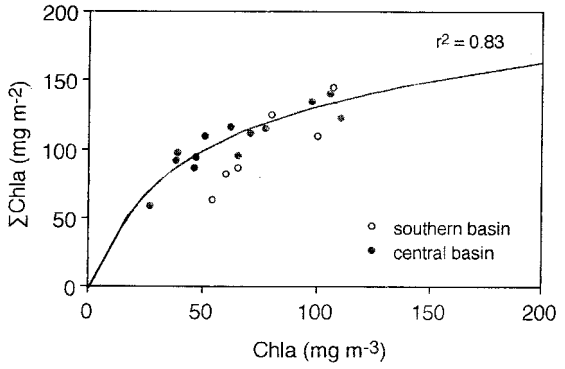

Figure 7. Relationship between chlorophyll-*a* in the photic zone and mean column concentration of chlorophyll-*a*.

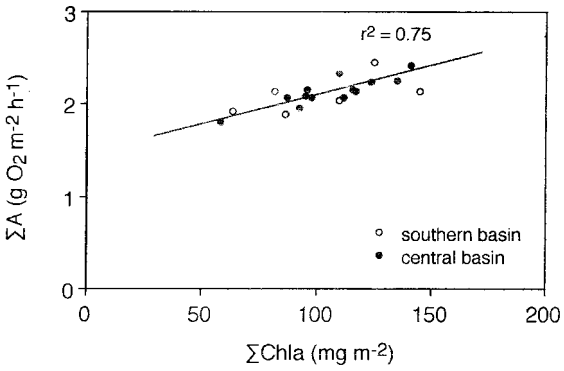

Figure 9. Relationship between depth integrated gross primary production and chlorophyll-*a* in the photic zone.

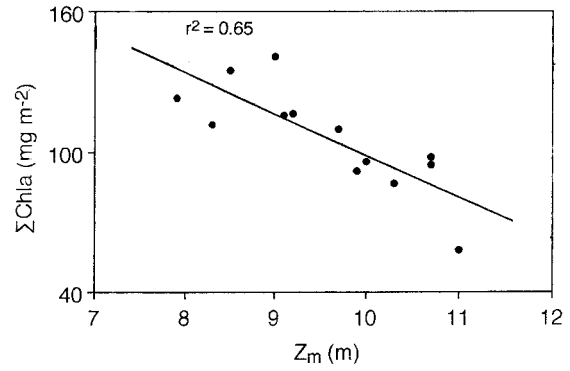

Figure 8. Relationship between chlorophyll-*a* in the photic zone and the mixing depth (i.e. the total water column) in the central basin.

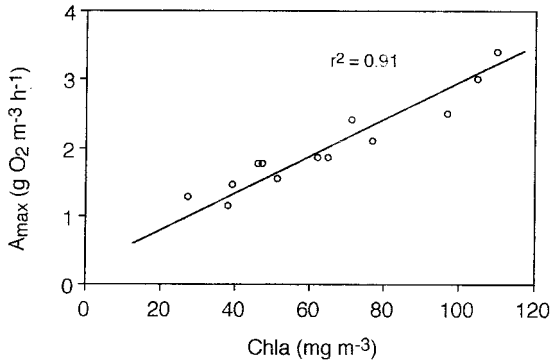

Figure 10. Relationship between primary production at optimum depth and mean column concentration of chlorophyll-*a*.

[K_{min} = 0.022 Chla + 0.98] demonstrated that a significant part (0.98 m^{-1}) of the light attenuation was due to agents other than Chla (Figure 6). Assuming that this part was constant the slope of the linear regression (k_c = 0.022; specific absorption coefficient) would give the actual increment of light attenuation with increasing Chla. However, K_{min} correlated more strongly to Chla + Phae than to Chla alone (Figure 6). According to that linear regression the attenuation by other agents, beside algal biomass, was lower (0.58 m^{-1}) and even more constant over years.

The fraction of light that was absorbed by Chla (F_{abs}) varied between 0.79 and 0.33 (CV = 21%; Figure 5b). F_{abs} was inversely correlated to Phae ($p > 0.05$), thus emphasising the reverse relationship between Phae and Chla. The mean light availability within the mixed water column (I_m) was temporally stable, at least in the central basin, where it was 2.2 mol Quanta m^{-2} d^{-1} (CV = 11%). There was an inverse relationship between the depth of the photic zone (Z_p) and Chla in the centre of the lake (see Figure 6 where $Z_p \approx \ln 100/K_{min}$). The same relationship was not found in the southern basin, which probably was due to the different kinds of turbidity. Differences between basins were reduced when biomass was expressed as chlorophyll-*a* integrated over Z_p (ΣChla; Figure 5c), but only data from the central basin showed an increase of ΣChla with Chla in the expected form of a saturation curve (Figure 7), which is the effect when F_{abs} approach unity (cf. Ganf, 1974). According to this curve, maximum biomass of the photic zone ($\Sigma Chla_{max}$) was reached at 150–175 mg Chla m^{-2}, which agrees very well with the theoretical calculation of $\Sigma Chla_{max}$ in Lake Xolotlán, which gives 168 mg Chla m^{-2} using the equation of Talling (1965) on our data. ΣChla was inversely correlated to Z_m in the central basin (Figure 8).

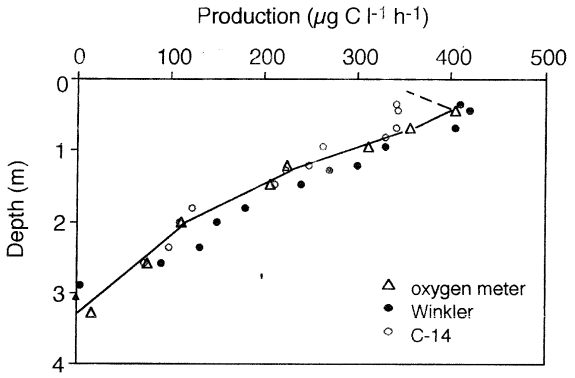

Figure 11. Depth profiles of gross primary production measured with different methods.

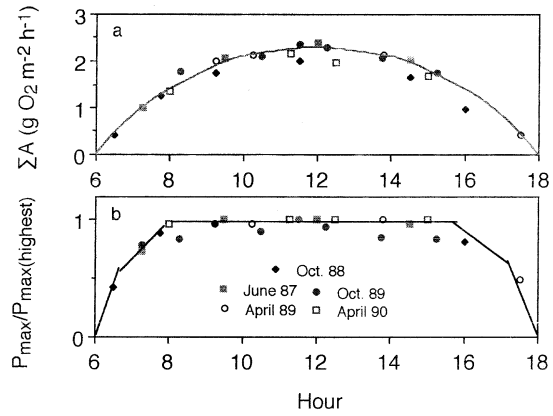

Figure 12. Daily variability of (a) depth integrated gross phytoplankton production and (b) photosynthetic capacity, expressed as the proportion between individual daily values and the highest value of the day.

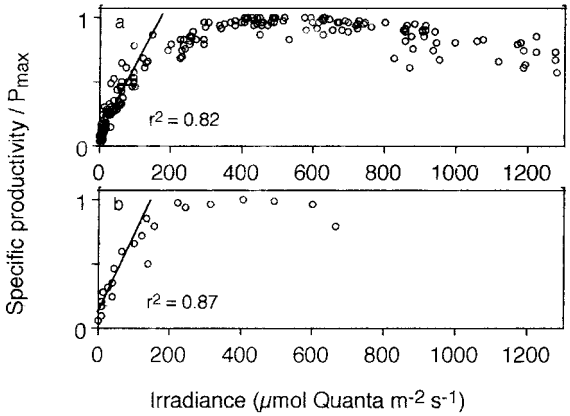

Figure 13. Relationships between production per biomass (specific production), measured by (a) the oxygen meter method and (b) the C-14 method, and underwater irradiance. In order to normalise specific production rates from different sampling periods to each other, they are expressed as proportions to their corresponding production per biomass at optimum depth (photosynthetic capacity).

Primary production

Gross primary production per surface area in the photic zone (ΣA) did not vary much over time and between basins (Figure 5d). In the central basin ΣA averaged 2140 mg O_2 m^{-2} h^{-1} (CV = 7%) and in the southern basin 2030 mg O_2 m^{-2} h^{-1} (CV = 10%). The low variability was true also for ΣA of adjacent days (Figure 5d). There was a strong relationship between ΣChla and ΣA (Figure 9), but weaker between Chla and ΣA. The variation of the production at optimum depth (A_{max}) (Figure 5e) was, however, a direct function of Chla (Figure 10). On the other hand, Z_p was inversely correlated to Chla and ΣA was therefore little affected from one period to another. Differences of primary production measured as ^{14}C assimilation and measured as O_2 evolution (especially that measured with oxygen meter) were small (CV = 9% for all methods and incubation depths simultaneously measured) except at optimum depth of production where the ^{14}C method gave about 15% lower values (Figure 11). Analysis for ^{14}C-labelled exudates in connection with measurements of ^{14}C-production gave very low values, showing no indication of a significant or persisting pool of DOC originating from algal excretion.

Diurnal primary production ($\Sigma\Sigma A$) during five sampling days were 19.3, 16.3, 18.9, 19.7 and 17.1 g O_2 m^{-2} d^{-1}, with an average value of approximately 18 g O_2 m^{-2} d^{-1} (Figure 12a). The two lowest values were recorded during October 1988 and April 1990 and coincided with periods of a high Phae in proportion to Chla (56 and 40%) and the resulting reduction of ΣChla. The average $\Sigma\Sigma A$ value is related to the 'mid-day' average ΣA (hourly rate, see above) by a factor of 8.5, which conforms fairly well with a general experience from tropical lakes (Talling, 1965, Lemoalle, 1981).

Photosynthetic capacity at optimum depth (P_{max}; $= A_{max}$/Chla) exhibited a low variability. Average P_{max} was 31.0 mg O_2 mg $Chla^{-1}$ h^{-1} (CV = 13%). P_{max} was generally at optimum before 09:00 and remained at that level throughout the day until after 15:00 (Figure 12b). P_{max} decreased with increasing biomass, more in relation to ΣChla ($Chla \cdot Z_p$; $p < 0.001$) and less to Chla alone ($p \approx 0.05$). The ratio of individual values of production normalised to Chla at each depth to the corresponding P_{max}, which was calculated in order to make different production profiles comparable,

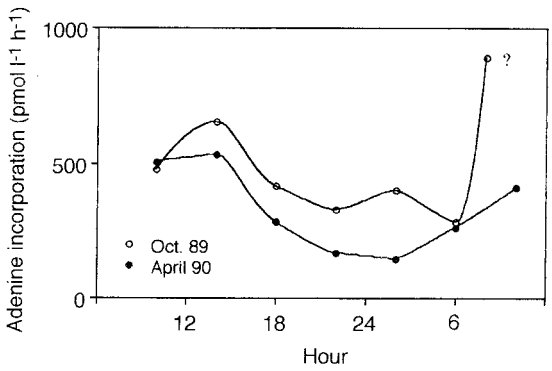

Figure 14. Diurnal variability of phytoplankton cell growth measured as incorporation of ^{3}H-adenine.

showed a similar relationship to under water irradiance on all occasions (Figure 13a). At low irradiance ($<$ 100 μmol Quanta m^{-2} s^{-1}) the relationship was linear. The irradiance indicating the onset of light saturation of photosynthesis (I_k), equivalent to the light intensity at with an extrapolation of the straight line would reach P_{max}, was 185 μmol Quanta m^{-2} s^{-1}. Actual P_{max} was found at a higher irradiance (I_s; average = 525 μmol Quanta m^{-2} s^{-1}, CV = 13%). At still higher irradiance near the surface productivity decreased as a result of photoinhibition. The slope of the initial linear section of the photosynthesis-irradiance curve is a measure of the photosynthetic efficiency (P_{eff}) and was 47 mg O_2 mg Chla^{-1} mol Quanta^{-1} m^2. Measurements of primary production with the ^{14}C method gave similar estimates of I_k and P_{eff} as with the O_2 method (Figure 13b).

Rates of ^{3}H-adenine incorporation into algae over two diurnal cycles (Figure 14) gave cell growth values of 5.4 and 3.9 g C m^{-2} d^{-1}. The ^{3}H-adenine incorporation rate by algae was at a maximum shortly after the peak of photosynthesis (see Figure 12a), but contrary to photosynthesis, it persisted also during the dark hours. The proportions of incorporation rates in the $<$ 3–μ m and $<$ 1–μm fractions to total rates were 33 and 12% on October 1989 and 3 and 1% on April 1990. Counts of algal cells gave corresponding numerical proportions of 21 and 5% on October 1989 and 15 and 1% on April 1990 in the two fractions respectively.

Discussion

Biomass and productivity

We checked the reliability of our pigment analyses by comparing the results of the ethanol and acetone extraction methods on four parallel samples. Chlorophyll-*a* concentrations were 40.1 μg l^{-1} (CV = 12%) and 37.5 μg l^{-1} (CV = 13%) and phaeophytin concentrations 3.9 μg l^{-1} (CV = 20%) and 2.7 μg l^{-1} (CV = 43%), respectively. Chlorophyll-*b* was 7.0 μg l^{-1} (CV = 9%) and chlorophyll-*c* 1.6 μg l^{-1} (CV = 27%), assessed by acetone extraction, but these pigments were never measured with ethanol extraction. On another occasion the proportions of chlorophyll-*b* and chlorophyll-*c* to chlorophyll-*a* were even lower (3 and 8%, respectively). Individual analyses of phaeophytin are known to be less precise, at least when concentrations are low (Lorenzen, 1967). However, Phae in this study were often high and composed of $>$ 30 measurements on 10 occasions during the periods (mainly from 1987 to 1989) from which the inverse relationship between Chla and Phae was demonstrated. If Phae in proportion to Chla is taken as an index of algal mortality, the trends of Chla and Phae are further confirmed by the variation of Z_m and repiratory losses in its dark portion (see; Erikson, this volume). The coupling between Z_m and algal biomass also explains the stable increase of approximately 20 μg l^{-1} of Chla during dry periods, because evaporation and the resulting decrease of Z_m was about the same each season. Precipitation and the increase of Z_m was, however, not always regular and the decrease of Chla during rainy periods was therefore more variable, shifting the over all level of Chla up or down from one year to another. There was a dramatic biomass decrease in 1988, but we believe it was an exceptional result caused by the rainstorms. More frequent sampling at this time did not reveal a regular pattern that was not detected during other periods with less frequent sampling. Instead, the low Chla variation of weekly averages demonstrated a stability of the algal biomass over short time periods.

In general our pigment estimates seem reliable, but small deviations from true concentrations are likely to be present, especially when Chla was low and Phae high. Such errors probably explain the unrealistic intercept of the POC vs Chla relationship, showing that all POC was associated to Chla in the central basin (Figure 3). In an other study, bacterial carbon in the central basin was estimated to be on average 8% of total POC (Erikson et al., 1998), i.e. approximately 0.7 mg l^{-1}. Additionally, carbon biomass of lysing algal cells, not yet decomposed, was also of significance, because POC correlated stronger to Chla + Phae than to Chla alone (r^2 = 0.91 and 0.88, respectively in the central basin). Phae was on average

14 μg l^{-1} and might represent a carbon concentration of about 1 mg l^{-1} (carbon/pigments ratios are discussed below). Taken into account also detritus, POC, that was not associated to Chla, would thus be at least 2 mg l^{-1} on average in the central basin. Still, the strong correlation between POC and Chla implies that most of POC was synonymous to algal carbon of active phytoplankton. The fact that the phytoplankton community always was dominated by the same few species of blue-greens and diatoms (Hooker et al., 1991; Erikson et al., 1997) may explain such a constant relationship between algal carbon and Chla. According to this relationship, and with corrections for non-algal POC, the ratio by weight between algal carbon and Chla would be about 100: 1 [(average POC of 8.5 mg l^{-1}-average non-Chla POC of 2.0 mg l^{-1})/average Chla of 0.065 mg l^{-1}]. This ratio is high compared to the average ratios found between algal carbon and chlorophyll-*a* ($\approx$ 50:1; Ahlgren, 1983), but other tropical lakes, similar to Lake Xolotlán (Lake George and Lake Nakuru), had the same C: Chla ratio of about 100: 1 (Viner, 1977; Vareschi, 1982).

All data associated to phytoplankton biomass demonstrate that algae in Lake Xolotlán were homogeneously distributed in depth (see SD in Figure 2). Of these, POC showed the lowest vertical variability (CV $<$ 10%) and was probably the parameter that was analysed with highest relative precision. We therefore conclude that the phytoplankton community of Lake Xolotlán was constantly and completely mixed throughout the entire water column. Minimal Coriolis effect, low maximum stability and the response of stability to change in heat content are factors at low latitudes, that facilitate the mixing of tropical lakes (Lewis, 1987). Strong trade winds, large wind fetch and shallow depth in relation to the area are additional factors that promote the constant and complete vertical mixing of Lake Xolotlán. The chlorophyll-*a* content of the whole water column during periods of high Chla was about 800 mg m^{-2}, because high Chla ($\approx$ 100 μg l^{-1}) coincided with low Z_m ($\approx$ 8 m), which can be deduced from Figure 7 and Figure 8. Phae was not a significant part of the biomass on those occasions (see Figure 6). Otherwise, when also Phae is taken into account, the sum of Chla and Phae was constantly of that same magnitude (on average 770 mg m^{-2}, CV = 20%; excluding Oct. 1988).

Z_m varied between 8 and 11 m in the central basin and was much greater than Z_p. Underwater light was therefore a scarce resource for the algae. The ratio between Z_p and Z_m (0.19; see Erikson, 1998) was of the same magnitude as the critical ratio (0.18–0.20) when light becomes the growth limiting factor (Talling, 1971; Grobbelaar, 1985; Alpine & Cloern, 1988). The mean light availability within Z_m (I_m = 2.2 mol Quanta m^{-2} d^{-1}) was similar to levels that have been reported to constitute the threshold for light limitation of phytoplankton in three subtropical lakes (Oliver, 1981; Geddes, 1984; Phlips et al., 1995). The constant I_m in Lake Xolotlán was therefore interrelated to the likewise constant total areal biomass (Chla + Phae). Light absorption by other agents, mainly DOC, that was 21 mg l^{-1} over time and sites (CV = 18%; data shown in Erikson et al., 1998), was temporally constant (Figure 6). Thus, the threshold for 'self-shading' (including shading by non-algal particles) was reached in the lake.

Gross primary production in Lake Xolotlán (2.1 g O_2 m^{-2} h^{-1}) was in the upper range of what previously has been reported from other tropical lakes (Melack, 1979; Lemoalle, 1981). It was also stable from one sampling period to another and between the two sampling sites and, although sampling was infrequent, it indicates that the average value was representative for all years. Two specific features of tropical lakes promote a high and stable photosynthetic production; incident solar irradiance that for most of the day and all year round exceeds the light saturation level for photosynthesis (Lewis, 1987) and high water temperature that enhances the specific production at optimum depth (Harris, 1978). Of these, temperature of the mixed layer, due to low altitude (see; Lewis, 1987), was comparably high in Lake Xolotlán (28–30 °C). The results of this study conform with the results of the previous investigation from the mid-eighties (Erikson et al., 1997). The average hourly rate of integral photosynthesis was, however, slightly higher ($\approx$ 12%) in the present study than in the previous. This might be an effect of much shorter handling and incubation times, thereby keeping methodological artefacts to a minimum. It is also possible that short incubation times made production rates measured by the ^{14}C method almost equal to the gross production measured by the O_2 method (Figure 11). Thus, the ^{14}C method can be considered measuring close to gross production during the 0.5 h incubation. The agreement between the two methods was also good in estimates of I_k and P_{eff} (Figure 13). In this case, the ^{14}C method was more sensitive when measuring low photosynthetic rates in the deep portion of Z_p. It seems reasonable to use a direct stoichiometric relationship between carbon and oxygen (12/32) and mean hourly

and daily gross primary production were therefore 0.8 g C m^{-2} h^{-1} and 6.8 g C m^{-2} d^{-1}, respectively.

We estimated the algal cell growth as the difference between ^{3}H-thymidine and ^{3}H-adenine incorporation, implying that adenine was incorporated by both bacteria and algae, whilst thymidine was incorporated exclusively by bacteria and not by algae. The proportions of incorporation rates and algal cell numbers in different size fractions corresponded fairly well and demonstrate that algal cell growth was rather accurately estimated by this method. Measurements were done only at the depth of 0.5 m, but vertical differences of ^{3}H-adenine incorporation into plankton were small in a later study of a similar nearby lake, which experienced the same winds and mixing (Erikson, unpublished data). Thus, the results indicated that a large part (61–73%) of the gross production was used for cell growth (4–5 g C m^{-2} d^{-1}) during both seasons. In contrast to this, total net biomass increase in the centre of the lake was only approximately 0.2 g C m^{-2} d^{-1} (see Figure 2a; $\Delta \approx 0.2$ mg Chla m^{-3} d^{-1}, algal C: Chla $\approx$ 100: 1 and $Z_m \cdot 10$ m) during dry periods and slightly negative during normal rainy periods, demonstrating that biomass losses were more or less in parity with biomass gains. Biomass changes were accordingly small from one day to another ($< 1\%$) and the renewal time for the phytoplankton biomass was long ($\approx$ 2 weeks, based on a mean column algal carbon $\approx$ 65 g C m^{-2} and cell growth $\approx$ 4.5 g C m^{-2} d^{-1}).

Optimal conditions and maximum production

Previously we found low or non-detectable levels of inorganic nutrients (Erikson et al., 1997) and argued that nutrients were recycled rapidly and never accumulated in the free water, as was observed in other eutrophic tropical lakes (Golterman, 1971; Lewis, 1987). Other studies in Lake Xolotlán (Erikson, 1998; Erikson et al., 1998; Ahlgren et al., 1997) show that most of the respiratory losses and bacterial decomposition of phytoplankton took place within the water column, which probably was an effect of high temperature and permanent mixing, thereby promoting recycling and availability of nutrients for growing algae.

By examining the inter-relationships of particulate organic carbon, nitrogen and phosphorus (POC, PON, PP) new information can be gained on the nutrient status of the phytoplankton population (Viner et al., 1981). The algal cell content (i.e. particulate matter) of both nitrogen and phosphorus was constant relative to cellular carbon over a five-fold range of biomass. POC was always related to PON by a factor of 9 and to PP (and to Chla) by a factor of 100. The correlation of POC vs. PP was not as strong as the correlation of POC vs. PON, probably due to the fact that most nitrogen is in protein whilst phosphorus can be stored in excess by algae. Due to such luxury consumption of phosphorus the cellular N/P – ratio decreases with increasing trophic level (Forsberg et al., 1978). The particulate N/P – ratio in Lake Xolotlán was on average 11, which is still within the range (10–15) that, according to Sakamoto (1966), indicates a balance between the nitrogen and phosphorus contents with what is required for the optimal growth of phytoplankton. It was also just below the critical ratio (12), proposed by Dillon & Rigler (1974), above which phosphorus tends to become the limiting nutrient. Furthermore, the relative uptake rates of nitrogen and phosphorus in algae are equal to their relative proportion in algal cells (Viner, 1977). This proportion was constant in Lake Xolotlán. We conclude therefore that phytoplankton were never nutrient limited.

The stability of P_{max} over a wide range of Chla also implies that phytoplankton production never was limited by nutrients. Over the hours of most intensive photosynthesis, nutrient depletion might occur and cause a decrease of P_{max} (Vollenweider, 1965; Ganf, 1975), but no such decrease was observed in Lake Xolotlán. The permanent vertical mixing is an additional factor for the constant and high productivity as it minimises long-lasting effects of surface photoinhibition (Neale & Richerson, 1987; Cullen & Lewis, 1988) and optimises productivity by a higher integral utilisation rate of the available light energy (Marra, 1978). As a result, both P_{max} and P_{eff} were extremely high in Lake Xolotlán, in fact close to or in parity with their supposed upper limits (Talling et al., 1973; Platt & Jassby, 1976; Robarts & Zohary, 1992). Furthermore, the fact that these values were assessed in bottle enclosures proves that our light exposure of the algae in fixed and static positions within the photic zone was not too long.

The maximum quantum yield (Q_{max}) for natural phytoplankton under optimal conditions of light and nutrients is expected to be about 0.06 mol C mol Quanta^{-1} (Bannister, 1974a,b). By definition P_{eff} (mg C mg Chla^{-1} mol Quanta^{-1} m^2) is constant from the depth corresponding to $0.5I_k$ and below (Talling, 1957). Within this sub-column, all light absorbed by Chla is used for photosynthesis and carbon fixation per quanta is at a maximum. Hence, the quantum yield ($= P_{eff} \cdot$ sub-column ΣChla) in Lake Xolotlán was

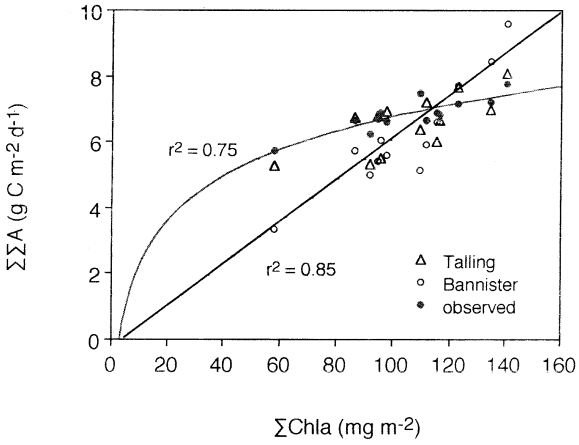

Figure 15. Relationship between diurnal primary production, estimated on basis of observed data and theoretical models, and chlorophyll-*a* in the photic zone. Diurnal primary production according to the model of Talling will increase non-linearly with chlorophyll-*a* in the photic zone, as for observed data, whilst the model of Bannister, which is built on fewer variables, predicts a linear increase.

0.063 mole C per mol Quanta absorbed (CV = 14%). The quantum yield is also given by P_{eff}/k_c (Platt & Jassby, 1976; Kirk, 1986). We estimated both P_{eff} and k_c by linear regressions and the relationship is therefore constant in this study and gives 0.067 mole C mol Quanta^{-1}. Thus, the quantum yield in Lake Xolotlán was at the theoretical maximum, probably a result of the vertical mixing that gave optimal conditions for the integral photosynthesis in terms of both nutrient availability and light utilisation.

Theoretical models of Talling (1965) and Bannister (1974a,b) for predicting the primary production under optimal conditions in lakes are presented in Table 1. They are also solved for average values from Lake Xolotlán. Compared to the observed production they show a remarkably good predictive accuracy for Lake Xolotlán, at least for typical rates. For particular sampling periods the accuracy was less uniform and some of our parameters might be questioned in one or two cases, where observed rates differed greatly from the predictions of both models (Figure 15). More important, however, was a general trend of differences, indicating that predicted rates, deduced by the model of Bannister, underestimated low and overestimated high observed rates. Primary production predicted according to Bannister increased linearly from the zero-zero intercept with ΣChla, whilst the same intercept, which should exist in a functional relationship between primary production and biomass within the photic zone, would imply a saturated increase for observed primary production. Thus, typical rates of primary production in Lake Xolotlán were at their optimum, but did not increase further in accordance to what is predicted as maximum rate.

Comparison with other tropical lakes

African lakes of different productivity show the same non-linear relationship between $\Sigma\Sigma A$ and ΣChla (Lemoalle, 1981; Lemoalle et al., 1981), as were found in Lake Xolotlán. By selecting the most productive African lakes and comparing them with Lake Xolotlán (Table 2) we show that the ratio between $\Sigma\Sigma A$ and ΣChla was higher ($\approx$ 0.17) for the lakes with a photic zone biomass of about 100 mg Chla m^{-2}, lower ($\approx$ 0.11) for the lakes with a photic zone biomass of about 200 mg Chla m^{-2} and lowest ($\approx$ 0.06) for the lake with a photic zone biomass of about 300 mg Chla m^{-2}. One lake, Lakes George, was exceptional, having an intermediate ΣChla, but a low $\Sigma\Sigma A$/ΣChla ratio ($\approx$ 0.08). All lakes in Table 2 were vertically mixed, either within an upper layer of the water column (L. Aranguadi and L. McIlwaine, when stratified) or throughout their entire depths (L. George, L. Nakuru, L. Kilotes and L. Xolotlán), if not equally frequent, at least on a diurnal basis (Ganf & Viner, 1973; Talling et al., 1973; Robarts, 1979; Vareschi, 1982). Cyanobacteria dominated in the lakes, with *Microcystis* and/or *Chroococcus spp.* in all except in L. Aranguadi and L. Nakuru, where *Spirulina platensis* was the only dominant. The Z_p/Z_m ratio and I_m were also similar in all lakes, demonstrating that they all were light limited with an algal biomass optimised to a level set by their respective Z_m (Table 2). Thus, the threshold for 'self-shading' (including shading by non-algal particles) was reached in all lakes. ΣChla and F_{abs} differed accordingly (Table 2).

Also P_{max} differed between the lakes in Table 2. One explanation for this, as well for the different $\Sigma\Sigma A$/ΣChla ratios, could be that biomasses were expressed differently. Chlorophyll-*a* was corrected for phaeophytin in lakes George, McIlwain and Nakuru (Ganf, 1974; Robarts, 1979; Vareschi, 1982), like it was in the present study, but was not in lakes Kilotes and Aranguadi (Talling et al., 1973), resulting in a relatively lower P_{max}. However, chlorophyll-*a* in Lake Xolotlán, not corrected for phaeophytin, would give a P_{max} of 26 mg O_2 mg Chla^{-1} h^{-1}, which is still much higher than in lakes Kilotes and Aranguadi and P_{max} in Lake Nakuru was the lowest of all, despite correc-

Table 1. Equations for theoretical $\Sigma\Sigma A$ and their solutions for average values from Lake Xolotlán (central basin). Most of the symbols are given in the text. Δh *(1)* and Δd *(2)* are daylengths in hours and days. 0.9 *(1)* is an empirical factor for the conversion of hourly to daily production rates. $0.9\Delta h = 9$ for tropical lakes (Lemoalle 1981). cf. *(1)* is the oxygen to carbon conversion factor and 12 *(2)* is the molar weight of carbon. Q_{max} is maximum quantum yield. F_{abs} *(2)* is the fractional absorption by Chla, calculated from $K_c\text{Chla}/K_{min} \cdot I'_o$ and $I_{0.7}$ *(2)* are daily average irradiance (mol Quanta m^{-2} d^{-1}). $I_{0.7}$ is the irradiance that gives a production of $0.7P_{max}$

Equation for theoretical $\Sigma\Sigma A$..	..and solved for average values from L. Xolotlán	
.. (1) according to Talling (1965):		
$[A_{max} / K] \cdot [\ln I'_0 – \ln 0.5\, I_k] \cdot 0.9\, \Delta h \cdot \text{cf}$	$= 2050/2.65 \cdot 2.68 \cdot 9 \cdot (12/32)$	$= 7.0$ g C m^{-2} d^{-1}
..(2) according to Bannister (1974a,b):		
$12 Q_{max}\, I_{0.7}\, F_{abs} \cdot \Delta d \cdot \int \sin h^{-1} (I'_0/I_{0.7})\, dt'$	$= 12 \cdot 0.067 \cdot 11.1 \cdot 0.59 \cdot 0.5 \cdot 2.55$	$= 6.7$ g C m^{-2} d^{-1}

Table 2. Data on photosynthetic characteristics for Lake Xolotlán (central basin) and five productive African lakes. Data on $\Sigma\Sigma A$, daily production (g O_2 m^{-2} d^{-1}), ΣChla, biomass of the photic zone (mg m^{-2}), Z_p, depth of the photic zone (m), and P_{max}, photosynthetic capacity (mg O_2 mg Chla^{-1} h^{-1}), for the African lakes, except for L. Nakuru, are compiled in Lemoalle (1981) and Lemoalle et al. (1981). ^{14}C data from L. McIlwaine was transformed by us to oxygen production using the factor $(1.2 \cdot 32/12)$. Z_m, mixing depth (m), for L. McIlwaine and L. Aranguadi were estimated from oxygen depth-time distribution diagrams and for the other lakes as mean depths of the basins. K_{min}, minimum vertical extinction coefficient (m^{-1}) and F_{abs} are accounted for in the references, except for F_{abs} in L. Kilotes and L. Aranguadi, which were calculated by us, using a k_c value, specific absorption coefficient (m^2 mg Chla^{-1}) of 0.016, according to Bannister (1974a,b). I_m, average light availability within Z_m (mol Quanta m^{-2} d^{-1}), for all lakes were calculated by us (see Methods)

Lakes (*study periods*) / (references)	$\Sigma\Sigma A$	ΣChla	Z_p	Z_m	P_{max}	K_{min}	F_{abs}	I_m
L. Xolotlán (*annual mean 1987–1993)*: (this study)	18	105	1.7	10	31	2.32	0.59	2.2
L. McIlwaine (*annual mean 1975–1976*): (Robarts, 1979)	14	95	2.1	13	26	1.76	0.53	2.1
L. George (*annual mean 1968–1970*): (Ganf, 1974, 1975; Ganf & Viner, 1973)	12	150	0.40	2.5	20	8.9	0.67	2.3
L. Kilotes (*maximum values, 3 March 1964*): (Talling et al., 1973)	21	190	0.45	2.6	21	7.9	0.83	2.2
L. Aranguadi (*maximum values, 15 Jan. 1966*): (Talling et al., 1973)	23	220	0.15	1.0	18	24.4	0.96	2.1
L. Nakuru (*annual mean 1972–1973*): (Vareschi, 1982)	18	335	0.35	2.2	14	17.8	0.95	2.0

tion for phaeophytin. Differences between the lakes can also be explained by difficulties in estimating correct production rates. Talling et al. (1973) explained the low P_{max} in Lake Aranguadi by a methodological underestimation of productivity due to high tension and loss of oxygen in the dense algal suspensions in the bottles. Incubations in vertical tubes, that encompassed the entire Z_p to avoid such complications, yielded however no or only moderately higher rates than corresponding incubation in fixed bottles (Talling et al., 1973; Vareschi, 1982; Grobbelaar, 1985). Additionally, there was no great differences in productivity between experiments manipulating the degree of oxygen tension or between successive measurements during short incubations in dense algal suspensions (Ganf, 1975; Vareschi, 1982). There could also have been an underestimation of P_{max} by simply missing the depth of highest rate with the discreet sample incubations used, which especially could occur in very condensed systems like Lake Aranguadi. The photic zone in Lake Xolotlán was not very condensed and we had the opportunity to adjust the depths of incubation between successive samplings, why average periodic P_{max} values in this study are likely of a correct order of

magnitude. In Lake George, which was stratified during the day, Ganf (1975) related the decrease of P_{max} to the depletion of available nutrients by photosynthesising algae. Harris (1978) proposed photoinhibition as an alternative explanation, as these algae were exposed to high light intensity for long periods. Vareschi (1982) explained the low specific productivity in Lake Nakuru, as an effect of severe self-shading. Algal cells in all lakes in Table 2 were, however, subjected to a similar vertical PAR gradient (see; Z_p/Z_m ratios and I_m) and differences in production per biomass between the lakes were not in general caused by different degrees of PAR-photoinhibition. Nor could self-shading effects have been of importance; all lakes were shaded to their upper limits and it would not matter if an algae was shaded by an other algae or by a non-algal particle within this light gradient.

During the same period as the measurements in bottle enclosures were conducted in Lake Aranguadi, the diurnal change of oxygen content in the water column of the lake indicated a yield of 43 mg O_2 m^{-2} d^{-1} (Talling et al., 1973), i.e. almost twice as high as the value we refer to (Table 2). Diurnal changes of oxygen in the water columns of lakes George, Nakuru and Kilotes did, however, not exceed the maximum estimates of primary production assessed with bottle enclosures (Talling et al., 1973; Ganf & Horne, 1975; Vareschi, 1982). After reviewing and controlling methods and results of studies in African lakes Vareschi (1982) came to the conclusion that maximum photosynthetic rates in tropical waters do not exceed 25–30 g O_2 m^{-2} d^{-1}. Robarts & Zohary (1992) assessed, via bottle enclosure measurements, the upper limit of phytoplankton production in a subtropical hypertrophic reservoir and recorded a few extremely high values ($\approx$ 10 of 300), but their bulk data (running mean) demonstrate that maximum rates, that occurred during periods of 'tropical conditions' in the lake, generally not exceeded 30 g O_2 m^{-2} d^{-1}.

Long-term variation of phytoplankton biomass in Lake Xolotlán was more or less predictable, with a slow and steady increase of chlorophyll-*a* per unit volume during dry periods and a decrease during rainy periods, that was more variabel, shifting the overall level of phytoplankton biomass up or down from one year to another. Chlorophyll-*a* per unit area was rather constant over all years, at least when also including degradation products into the total biomass. Gross primary production was high and temporally and spatially stable, which was a result of the permanent mixing of the water column, giving optimal conditions for photosynthesis in terms of nutrient availability and light utilisation. The oxygen and ^{14}C method gave similar estimates of gross primary production during short incubations and methodological artefacts were probably small. Still, the results from Lake Xoltotlán and other tropical lakes that show a reduced increase of primary production in relation to the increase of biomass, could be effects of methodological artefacts, but if true, primary production in tropical lakes would never reach levels that are predicted from theoretical models and achieved in other systems, as for example in algal mass cultures (Uhlmann, 1978).

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