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Algal respiration and the regulation of phytoplankton biomass in a polymictic tropical lake (Lake Xolotlán, Nicaragua)

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Abstract

Community respiration in tropical Lake Xolotlán, Nicaragua, was assessed seasonally and during diurnal cycles, via oxygen consumption in bottle enclosures. Results were analysed in relation to phytoplankton biomass, mixing depth, depth of photic zone and phytoplankton production. A great part of community respiration was associated with the heterotrophic activity of the phytoplankton biomass or its degradation by bacteria and 80% of the variability in oxygen consumption was explained by the variation of chlorophyll-*a*. Specific rate of respiration was 1.5 mg O_2 mg Chla^{-1} h^{-1} during diurnal cycles, which corresponded to less than 5% of the specific rate at optimum depth of production. Still, diurnal water column respiratory losses were always of the same magnitude as the total photosynthetic gains in the photic zone, since the mixing depth exceeded the depth of the photic zone. Total column net growth was zero at a ratio between depth of photic zone and mixing depth of 0.19. Water level variations however altered the mixing depth and affected this ratio and net growth. As a consequence, the phytoplankton biomass either increased or decreased until the ratio was re-established through changes of the photic zone depth, which was governed by the phytoplankton biomass itself through the chlorophyll-*a* light attenuation.

Introduction

The central role of mixing depth in phytoplankton dynamics and the effect of dark respiration on algal biomass was pointed out early by Sverdrup (1953) and Ryther (1954) and was further elaborated by Talling (1957a, 1971), Steele (1962) and others. But despite the early recognition of its importance, the problem was addressed in few studies during following years (e.g. Bannister, 1974; Ganf & Viner, 1973; Harris, 1978). A switch from O_2 measurements to ^{14}C techniques was one reason for this. Algal respiration could not be measured by the ^{14}C technique and total column net productivity was seldom discussed. In recent years, however, studies in shallow, turbid systems, like rivers and estuaries, once again have given attention to the role of dark respiration in a well mixed environment (Alpine & Cloern, 1988; Cloern, 1987; Cole et al., 1992; Lewis, 1988; Wofsy, 1983).

Lake Xolotlán is a large (≈ 1000 km^2), shallow (mean depth ≈ 8 m) and warm (≈ 29 °C) endorheic tropical lake (12 °N). The NE trade winds blow steadily during the entire year (5–10 m s^{-1}) and make the lake continuously mixed throughout its total depth (Erikson et al., 1997). Water column stratification does not generally occur, not even for short periods during the day (Montenegro, 1992). The lake is eutrophic (total phosphorus ≈ 150 μg l^{-1}) and turbid (secchi disc depth ≈ 0.4 m) with a high algal biomass (algal carbon ≈ 6 mg l^{-1}) of mainly blue-greens. Erikson et al. (1997, 1998a) also found that the algal biomass was homogeneously distributed in depth and that biomass per unit area was more or less equal at different sampling sites. Biomass per unit volume was, therefore, inversely related to the depth of the water column. Photosynthetic production was high (16–20 g O_2 m^{-2} d^{-1}) and limited only by light and not by nutrients, but there was rarely any corresponding rapid increase of phytoplankton biomass. Great losses of algal biomass could not be attributed to outflow, sedimentation or grazing, because the basin is closed, the water column is constantly mixed and the zooplankton biomass is low (≈ 1% of algal biomass; see Mangas & Garcia, 1991). Instead, high concentrations of phaeophytin were indications of a continuous degradation of biomass within the water column, where the vertical mixing kept the average algal cell in darkness for about 90% of the time. Therefore, respiratory losses of algal carbon must be of importance for the losses of algal biomass, which also was indicated by preliminary data on oxygen consumption.

Warm tropical, polymictic and eutrophic lakes are often very productive (Melack, 1979) and high metabolic rates can be measured by changes in concentrations of dissolved oxygen. In addition, phytoplankton and bacteria are the main respiring organisms in such systems (Ganf, 1974; Jensen et al., 1990; Schwaerter et al., 1988) and bacterial metabolism is greatly dependent on utilization of extra cellular products of photosynthetic origin (Larsson & Hagström, 1979, 1982). Therefore, phytoplankton productivity and community respiration should be coupled.

The purpose of this study is to determine whether the coupling between mixing depth and algal respiration regulates the phytoplankton biomass in Lake Xolotlán. The geology and the physical and chemical properties of the lake have been described elsewhere (Erikson et al., 1997; Lacayo, 1991).

Methods

Sampling regime

From June 1987 to November 1993 sampling was performed mainly at the end of the dry season (April) and at the end of the rainy season (October – November) in the southern basin (station 1; Figure 1) at about 9 a.m. and in the central basin (station 2; Figure 1) at about 10 a.m. Diel studies were performed in the central basin on 10–11 October 1988, 13–14 April 1989, 27–28 October 1989, and 3–4 April 1990. Sampling was begun at ca. 10 a.m., repeated at 4 h intervals and ending with a final sampling on the morning the second day. Water was collected from discrete depths with a Van Dorn sampler.

Community respiration was always measured at three depths, whereas photosynthetic pigments often were measured at each meter of the water column. Parallel samplings for phytoplankton production and number, incident irradiance, under water light penetration and bacterial production and number are described in Erikson et al. (1998a, b).

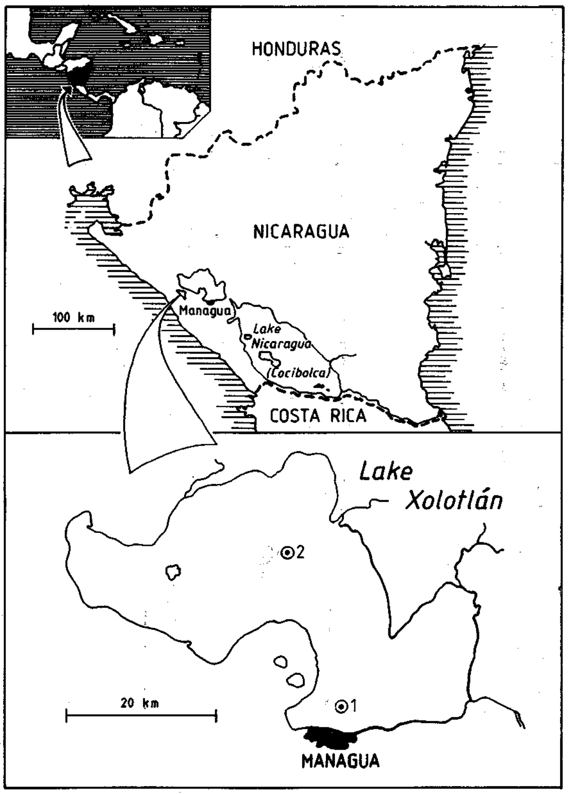

Figure 1. Lake Xolotlán, Nicaragua. 1 and 2 in the bottom panel are the sampling stations in the southern and central basin, respectively.

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.

Analytical procedures

Community respiration was measured with an YSI 57 oxygen meter and flask probe repeatedly (about every second hour) during several hours (≈ 8 h) as oxygen consumption in paired dark 125 ml BOD bottles. The probe forced out some of the water (≈ 1 ml) from the bottles, which were then refilled with the original water before closing the sample again. There were no differences in total oxygen consumption between bottles that were opened and closed several times and bottles that were kept closed until a final measurement.

The bottles were kept dark and at constant temperature (≈ 29°C) on board and later in the laboratory. Diel (24-h) studies were performed in the same way, but always on board. The oxygen meter was protected against direct sunshine and changes in air temperature. Assessments of phytoplankton chlorophyll-*a* and phaeophytin, photosynthetic activity, algal growth rate and number, incident irradiance , under water light penetration and bacterial production and number are accounted for by Erikson et al. (1998a, b).

Data handling

A plot of oxygen consumption versus time was basis for estimating community respiration, which was taken as the slope of the best straight line between the first 3 or 4 data points in the series of measurements (at least 4 hours of incubation). There was often a marked decrease in oxygen consumption with time and an extended series of data could not be fit by a single linear relationship. The variance in oxygen consumption between paired incubations was negligible compared to the variance between successive incubations. Mean water column respiration (R) was calculated on basis of data from all three depths, while respiration in the photic zone ($R_{0.5}$) was given directly by the data from 0.5 m.

Erikson et al. (1991) showed that the models of Talling (1965) accurately predicted observed hourly and daily rates of photosynthetic activity in Lake Xolotlán and that prevailing conditions in the lake met with the idealised requirements and assumptions of the models. Talling (1971) included assumptions on respiration in order to predict also the balance between total column photosynthesis and total column respiration. The equation can be written as:

$$q = \ln 2 \cdot \mathrm{LDH}/K \cdot 24r \cdot Z_\mathrm{m},$$

where q is the ratio between total column photosynthesis and total column respiration, K is the light extinction coefficient (m^{-1}), $24r$ is the specific rate of respiration as proportion of the specific rate of optimum production over the diel cycle and Z_m is the mixing depth (m). LDH (light division hours) is the time integral of irradiance and defines the total daily incident irradiance available for photosynthesis within the water column. It is approximated by $0.9\Delta t(\ln I'_0$-$\ln 0.5\ I_k)/\ln 2$ (Talling, 1957b). Δt is the day length in hour and in my calculations (and in most tropical lakes) equal to 10 (Erikson et al., 1998a; Lemoalle et al., 1981). I'_0 is the mean daily light intensity just below the surface and was 1250 μmol Quanta m^{-2} s^{-1} during the end of the rainy season and 1450 μmol Quanta m^{-2} s^{-1} during the end of the dry season (Erikson et al., 1998a; Fuente, 1986). I_k is the onset of light saturation of photosynthesis and was 185 μmol Quanta m^{-2} s^{-1} during all seasons (Erikson et al., 1998a). Accordingly, LDH in Lake Xolotlán was 34.0 and 36.0 during each season. No dial sampling day was totally over-cast.

Figure 2. Water level variations (meters above sea level) during the years of investigation.

Results

Mixing depth and phytoplankton biomass

The water level decreased approximately one meter during the dry period and increased 0 to 3 m during the rainy season (Figure 2). Abnormal heavy rains in 1988, when the hurricane Juan struck Nicaragua, led to extremely high water level. Rains were scarce from October 1991 to September 1992 and the entire period could be classified as a drought. Long term average 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.

There was an inverse non-linear correlation between Z_m and the phytoplankton biomass expressed as column mean concentration of chlorophyll-*a* (Chla) (Figure 3). Precipitation during the rainy period enlarged Z_m and Chla decreased, while evaporation during the dry period reduced Z_m and Chla increased. Evaporation was about the same for each year and therefore, abnormalities in precipitation affected Z_m and phytoplankton biomass for a long period onwards (see Figure 2a in Erikson et al., 1998a).

Chla was inversely related to Z_m also on a spatial scale and was on average 45% higher in the shallower

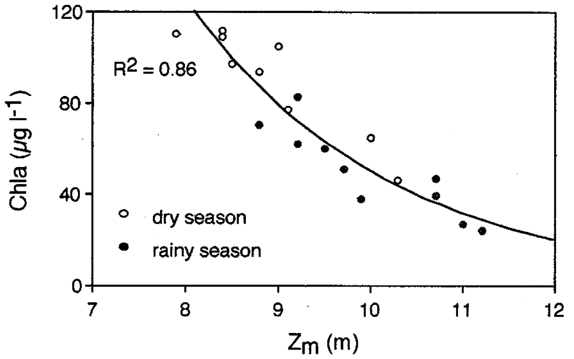

Figure 3. Relationship between mixing depth (Z_m) and mean column concentration of chlorophyll-*a* (Chla) in the central basin ($p < 0.001$).

southern basin compared to the deeper central basin (Erikson et al., 1998a). However, this spatial difference was subjected to seasonal variations. During the rainy period, the difference in Chla between the two basins was almost two-fold, whereas during the dry period, there was hardly any difference at all (Figure 4). Higher wind velocity during the dry season increased horizontal mixing and levelled out spatial differences in Chla. Chla decreased in the shallow parts and increased in the deep parts of the lake as a result of such mixing between the basins.

There was a significant relationship between Z_m and the ratio between column mean concentration of phaeophytin (Phae) and Chla (Figure 5). Phae in Lake Xolotlán might be seen as an indicative measure of dying algae in the water column, because vertical mixing and high metabolic rates will limit any accumulation of degradation products. Thus, the rate of mortality (i.e. proportion of dead algae to live algae) was enhanced by increasing Z_m.

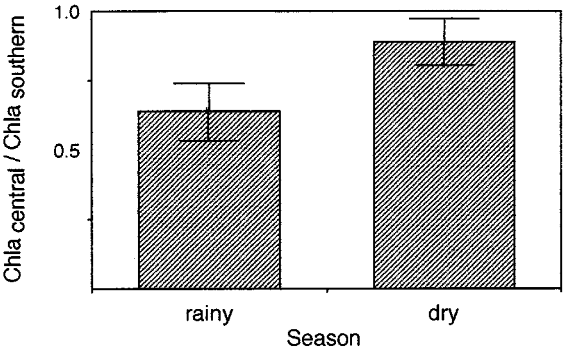

Figure 4. The proportion of mean column concentration of chlorophyll-*a* in the central basin ($\mathrm{Chla}_{\mathrm{central}}$) to mean column concentration of chlorophyll-*a* in the southern basin ($\mathrm{Chla}_{\mathrm{southern}}$) during rainy and dry seasons.

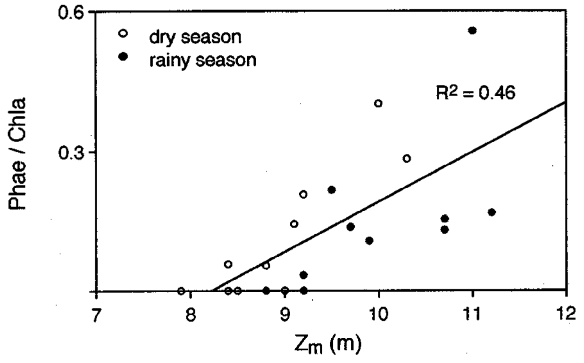

Figure 5. Relationship between mixing depth (Z_m) and mean column concentration of phaeophytin as proportion to mean column concentration of chlorophyll-*a* (Phae/Chla) in the central basin ($p < 0.01$).

Community respiration and algae

Mean community respiration of the water column (*R*) was significantly correlated to Chla (Figure 6) and 80% of the variability in *R* was explained by the variation of Chla. According to the slope of the linear regression the average specific rate of respiration was 1.5 mg O_2 mg Chla^{-1} h^{-1}. Community respiration at 0.5 m depth ($R_{0.5}$) was higher than at other depths, which means that respiration was enhanced in the photic zone. Compared to *R*, $R_{0.5}$ was less strongly correlated to Chla and more strongly correlated to the phytoplankton production at optimum depth ($A_{\max}$) (Figure 7).

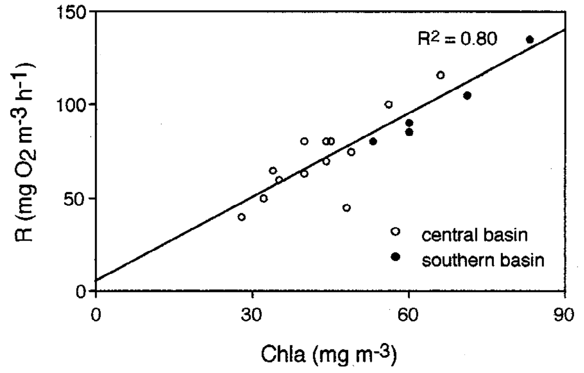

Figure 6. Relationship between mean column concentration of chlorophyll-*a* (Chla) and the mean column respiration (*R*) in the central and the southern basin ($p < 0.001$).

Table 1. Data from four diel sampling periods. Units are as follows: R (mg O_2 m^{-3} h^{-1}), Z_m (m), $\Sigma\Sigma A$ (g O_2 m^{-2} d^{-1}), A_{max} (g O_2 m^{-3} h^{-1}), K (m^{-1}), 24RZ_m (g O_2 m^{-2} d^{-1})

Diurnal sampling	R	Z_m	$\Sigma\Sigma A$	A_{max}	K	LDH	24RZ_m	$\frac{\Sigma\Sigma A}{24RZ_m}$	$\frac{\ln 2\ \mathrm{LDH}}{K24rZ_m}$
October 1988	55.5	11.0	16.3	1.28	2.14	34.0	14.6	1.12	0.95
April 1989	76.6	10.3	18.9	1.78	2.45	36.0	18.9	1.00	0.94
October 1989	70.6	10.7	19.7	1.45	1.84	34.0	18.1	1.08	1.13
April 1990	82.2	10.0	17.1	1.85	3.13	36.0	19.7	0.86	0.75

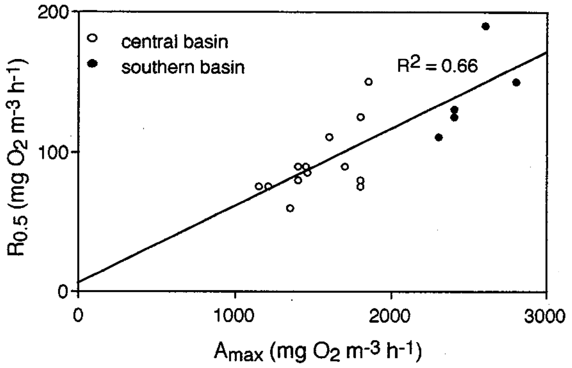

Figure 7. Relationship between primary production at optimum depth (A_{max}) and respiration at 0.5 m ($R_{0.5}$) ($p < 0.001$).

The coupling between respiration and photosynthesis was also apparent during the diel cycles (Figure 8). $R_{0.5}$ was enhanced during the day. Also respiration at depths below the photic zone was more or less affected, probably as a result of vertical mixing. Rates at 10 m in October 1988, which was a rather calm day until the wind started in late afternoon, were therefore unaffected for most of the day. The other days were all windy. During night, respiration became more or less uniform at all depths and was totally at a much lower level. The specific rate of respiration from midnight to 6 a.m. averaged 1.1 mg O_2 mg $Chla^{-1}$ h^{-1} in all four diel measurements. Average diel R values are given in Table 1.

The average specific rate of respiration as proportion of the specific rate of A_{max} (the ratio = r) was 0.048. The specific rate of A_{max} is the photosynthetic capacity (P_{max}) and averaged 31 mg O_2 mg $Chla^{-1}h^{-1}$ (CV = 13%; Erikson et al., 1998a). During an entire diel cycle r was even lower and averaged 0.044 (CV = 4%) (Table 1; R/A_{max} equals r under conditions of complete mixing).

Table 1 presents data on daily primary production ($\Sigma\Sigma A$), production at optimal depth (A_{max}), light extinction coefficient (K), LDH (see Methods), average diurnal R and Z_m from the four 24-h sampling periods. Data on $\Sigma\Sigma$ A, A_{max}, K, and I_0' and I_k (for the calculation of LDH) are accounted for and discussed in Erikson et al. (1998a). Data on R and Z_m are from this study. The product of $R \cdot 24 \cdot Z_m$ expresses diel water column respiration. The table also presents the quotients of $\Sigma\Sigma$ $A/24R \cdot Z_m$ and $\ln 2 \cdot \mathrm{LDH}/K \cdot 24r \cdot Z_m$ for the different periods. They both express, the first empirically and the second theoretically, the ratio between total column production and respiration.

Discussion

Respiration for maintenance and growth

Community respiration in Lake Xolotlán was enhanced during the day in the photic zone (see Figure 8), which probably was a coupling to the photosynthetic activity. A similar coupling between respiration and photosynthetic activity was found by Ganf (1974) in Lake George, Uganda, where blue-green algae also dominated phytoplankton. Raven & Glidewell (1975) and Langdon (1988) discuss dark respiration in terms of growth respiration and maintenance respiration. Growth respiration is associated to cell growth (growth rate) and maintenance respiration to basal metabolism (energy supply). Growth rate of blue-green algae is more influenced by the previous light history of the cell than is the growth rate of eukaryotic algae due to the more efficient internal homeostasis in eukaryotic cells (Foy et al., 1976). Thus, much of what is measured as diel change in dark respiration in blue-green algae may represent changes in growth respiration. After several hours in darkness, the growth rate ceases and growth respiration declines to a low maintenance respiration rate (Padan et al., 1971; Sentzova et al., 1975). This is seen in Lake Xolotlán as a covariation

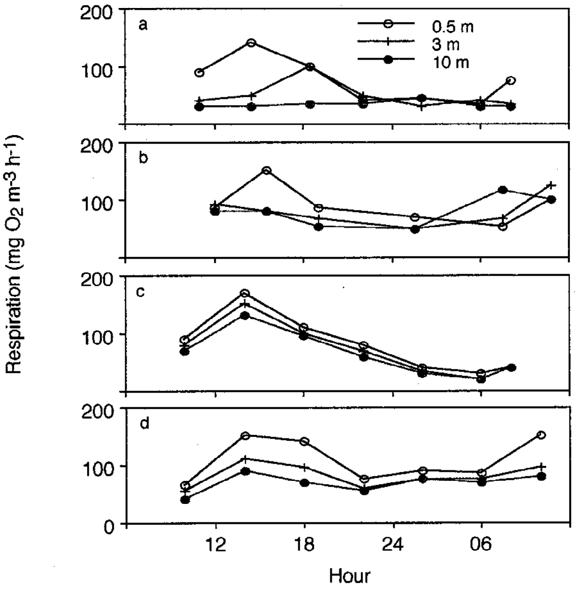

Figure 8. Respiration over the diurnal cycle at 0.5 m, 3 m and 10 m in (a) October 1988, (b) April 1989, (c) October 1989 and (d) April 1990.

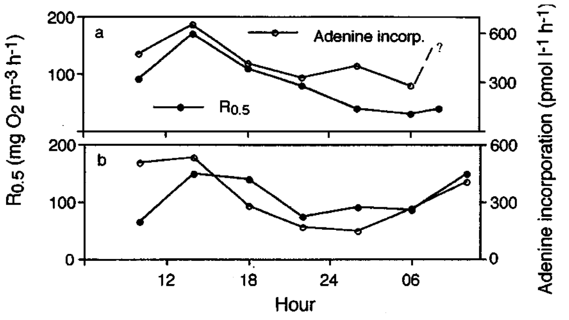

Figure 9. Covariance between respiration at 0.5 m ($R_{0.5}$) and algal cell growth at the same depth measured as incorporation of (^{3}H)-adenine (i.e. (^{3}H)-adenine incorporation minus (^{3}H)-thymidine incorporation; see Erikson et al., 1998a).

over the diel cycle between the phytoplankton growth rate at 0.5 m and $R_{0.5}$ (Figure 9). Thus, cell growth is made possible by light-induced reactions in the algae when passing the photic zone, but is in itself not light dependent. Growth and growth respiration, therefore continue after the algae are transported out of the photic zone by water mixing. Growth respiration, thus, is related more to phytoplankton production than to phytoplankton biomass.

The correlation between *R* and Chla in Figure 6. is based on respiration measurements in samples mainly from below the photic zone (e.g. 2 of 3 measurements) that were taken at 9–10 a.m. These rates were still close to the maintenance respiration of the night (see Figure 8). Thus, maintenance respiration was strongly correlated to phytoplankton biomass. If $R_{0.5}$ values are excluded from the column means, the average specific rate of maintenance respiration would be 1.2 mg O_2 mg Chla^{-1}h^{-1}, i.e. similar to the value of basal respiration during night estimated from the diurnal series of measurements (1.1 mg O_2 mg Chla^{-1}h^{-1}). In Lake George, Uganda, which presents conditions in many respects similar to those in Lake Xolotlán, the rate of basal respiration (maintenance respiration) was of the same magnitude (1 mg O_2 mg Chla^{-1}h^{-1}; Ganf, 1974).

A certain fraction of the community respiration must be bacterial respiration. Still, it is reasonable to consider community respiration in total when evaluating respiratory losses *versus* photosynthetic gains in Lake Xolotlán, at least in the centre of the lake. Total bacterial production was best correlated to Phae and bacteria respired organic matter released from phytoplankton cell lysis during degradation of algal biomass (Erikson et al., 1998b). Effects of allochthonous inputs of organic matter on bacterial production were seen only close to shore (Erikson et al., 1998b). The abundance's of pathogenic bacteria also decreased rapidly with distance from shore (Vargas et al., 1991). Sediment microbial activity was substrate limited and was only 6% of the pelagic heterotrophic activity (Ahlgren et al., 1997). The resuspension of sediments would therefore contribute little to the community respiration of the water column. Thus, by restricting the further discussion to the central basin, I expect a close coupling between community respiration and algal carbon metabolism and no great influences from sediments and allochthonous organic matter, which facilitates further analysis of the phytoplankton net growth.

Phytoplankton net growth

The empirical and theoretical mean ratios of total column production and respiration are both close to unity (1.02 and 0.94, respectively; see Table 1). Variations within the means are small (CV = 9 and 14%) and concurrent. Both observed and predicted values were thus in accord, indicating an algal net growth of almost zero. The difference from a quotient of exactly unity could be real or within the margin of error in the data. For example, the negative growth on April 1990 may be due to the high Phae/Chla ratio (0.40), that reduced the depth of the photic zone and the total column photosynthesis (numerator in the first equation) and increased light extinction (denominator in the second equation). However, similar conditions existed on October 1988 (Phae/Chla = 0.56), but growth was not seen to be affected negatively. On that occasion, total column respiration may have been underestimated due to an assumption of a too shallow Z_m (denominator in both equations). I estimated Z_m for sampling site 2 as the average depth of the central part of the lake and justify this by the horizontal mixing within the basin. The depth at the sampling site was, however, greater than surrounding depths. During days of least horizontal mixing there may be a reduced influence from surrounding areas on the apparent depth of the mixed water column at the sampling site. The sampling day of October 1988 was calmer than other days of sampling (cf. patterns of vertical mixing in Figure 8) and if Z_m was permitted to increase in the calculations with just 1 m ($\approx$ 10%), respiration would be even to production on that occasion too. Thus, due to the extension of the area which the sampling site is supposed to represent, Z_m will vary and strongly affect the result of the net growth balance. Unfortunately there is no way to decide objectively the functional Z_m for each occasion. Instead I will address the problem in another way.

Predicted Z_m, that will give zero net production, can be calculated by assuming the quotient $\ln 2 \cdot \mathrm{LDH}/K \cdot 24r \cdot Z_m$ being unity. In order to enlarge the data set for such an analysis I will use records on K from all periods of sampling (Erikson et al., 1998a) and the average r of 0.044. Such an analysis shows a significant correlation between predicted Z_m and observed Z_m of the central lake basin (Figure 10). However, it is notable that points from the dry and the rainy periods fall on separate sides of the common linear regression. Comparison of separate regression lines (Snedecor & Cochran, 1980) from the different periods reveals that the lines are significantly different regarding to the intercepts (p = 0.096, i.e. $p < 0.025$; Significance level corrected for two sequential test according to Bonferroni's test for inequalities), but not regarding to the slopes (p = 0.68). This implies that the increased horizontal mixing during the dry season was apparently reducing Z_m of the sampling site by enhancing influences from shallower parts of the lake (see Figure 4). During the rainy season, on the other hand, less horizontal mixing was apparently increasing Z_m towards the greater depth of the sampling site. If the values of observed Z_m in Figure 10 are corrected by a 1 m addition or reduction according to this, the slope of the linear regression becomes almost 1 : 1 (slope = 1.08) and the coefficient of correlation is made stronger (r^2 = 0.82).

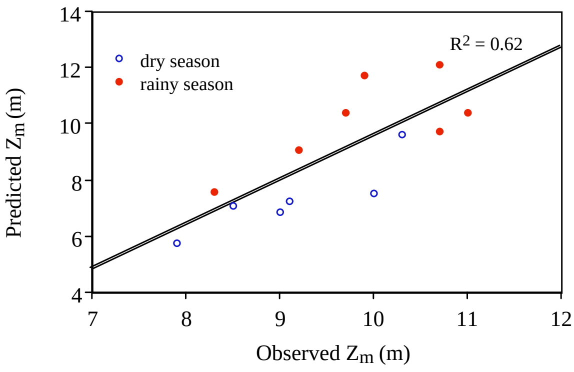

Figure 10. Relationship between observed mixing depth and theoretically predicted mixing depth in the central basin ($p < 0.001$).

Wind induced seasonal influences on phytoplankton biomass, demonstrated in Figure 4 and 10, are also evident in Figure 5. Most points below the linear regression represent samples from the rainy period and most points above represent the dry period. Thus, the rate of mortality of algae increased in the water of the central basin when it was mixed with water from shallower parts with higher Chla. The effect of wind induced horizontal mixing is also detectable in Figure 3; chlorophyll-*a* per unit area in the central basin was generally higher in the dry season than in the rainy season.

Regulation of biomass

Phytoplankton biomass in Lake Xolotlán was regulated in two ways. First, and most important, by the seasonal variation of Z_m. Second, and in addition, by the variation of Z_p, which was determined by K ($Z_p = \ln 100/K$) and was affected by the regime of horizontal mixing of turbid water. Data from the southern basin indicate that net growth was always positive (except on Oct. 1988) and biomass was produced in excess in shallow parts of the lake. Enhanced horizontal mixing therefore reduced Z_p in the central basin. This situation is similar to what phytoplankton experience in certain rivers where the ratio of the photic zone to the mixed depth (Z_p: Z_m) decreases along the way (Cole et al., 1992; Lewis, 1988).

The ratio of Z_p: Z_m in the central basin averaged 0.19 and was rather stable (CV = 19%; n = 13). According to the seasonal dynamics discussed above, values of the dry season were on the lower side of the range (0.16 ± 0.01) and values of the rainy season on the upper (0.21 ± 0.02). In an analysis of phytoplankton growth in another turbid, well-mixed environment, San Francisco Bay, Alpine & Cloern (1988) suggest that growth would be negative if the ratio Z_p: Z_m was <0.16. Grobbelaar (1985) concluded that the same critical ratio was 0.18 in subtropical Wuras Dam. The proportion of respiration to production (r) is of importance when determining such critical ratio. Cole et al. (1992) found, that along the tidal freshwater portion of Hudson River, the summer average Z_p: Z_m ratio of 0.2 demanded a r of 0.05 to explain the maintenance of algal biomass. As LDH in Lake Xolotlán was stable (seasonal variation $\approx$ 6%) and K was inversely related to Z_p, the equation of Talling (1971) can be written as $Z_p/Z_m = r \cdot 4.58$. Thus, a Z_p: Z_m ratio of 0.19 would imply a r of 0.042 when net growth is zero. This value is almost identical to the observed average value of 0.044.

Harris (1978) found a clear relationship between r and Z_p/Z_m for different lakes during different seasons. Compared to this relationship, the value of r in Lake Xolotlán was approaching an absolute minimum value and, as a consequence, so was Z_p /Z_m. This should exert a powerful selection pressure on species growing in the lake. A low value of r is the result of either low specific rate of respiration or high photosynthetic capacity. In terms of algal survival strategies, phytoplankton populations that can shift rapidly back to low maintenance respiration rates will be favoured together with those that can withstand photoinhibition and optimise production during short times under full light intensities. Blue-green algae match the first adaptive requirement (Harris, 1978) and blue-greens constituted the dominant algal group in Lake Xolotlán (Erikson et al., 1997; Hooker & Hernandez, 1991). This was also the case in Lake George (Ganf & Viner, 1973), where r was likewise low ($\approx$ 0.05; Ganf, 1974). On the other hand, some evidence suggests that diatoms are those best adapted according to the second requirement (Harris, 1978). In lakes where low Z_p: Z_m ratios last during short periods of spring circulation diatoms can resist photoinhibition, exhibit low r values and bloom (Harris, 1973; Talling, 1957a). In Lake Xolotlán diatoms constituted the second dominant group of algae and together the two algal groups made up 90% of total biomass. Furthermore, during all years of investigation the biomass was mainly represented by a few species; *Lyngbya contorta*, *Chroocoocus* sp., *Cyclotella* spp. and *Nitzschia* spp. (Erikson et al., 1997; Hooker & Hernandez, 1991). Other factors that normally regulate phytoplankton biomass were of minor importance in Lake Xolotlán. Losses by sedimentation and grazing were probably low (see above) and nutrients were never a scarce resource for growing algae (Erikson et al., 1998a).

In conclusion, seasonal water level variations had a definite impact on the total algal biomass in Lake Xolotlán. Increasing Z_m prolonged the time algae spent in darkness and enhanced respiratory losses and thereby the degradation of biomass. However, algal biomass governed the light penetration and, as a result of the reduction of biomass, Z_p increased subsequently. The same Z_p: Z_m ratio as before was re-established, but now at a lower biomass concentration. When Z_m decreased, the Z_p: Z_m ratio was re-established by lower respiratory losses and increasing biomass concentrations, which reduced light penetration and Z_p. Horizontal translocation of water masses of different biomass concentrations was an additional factor of importance in this dynamic. Consequently, algal species with minimum specific respiration were favoured in Lake Xolotlán.

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