VI.1d. Patterns of planktonic primary production and algal biomass

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Both physical and biological processes are important in controlling mean levels and fluctuations of primary production and algal biomass. Climatic factors drive production variation directly (e.g. through fluctuations in light) or indirectly through the regime of stratification (Richerson, this volume). Biotic processes, such as grazing and competition, affect biomass, the species composition of the biomass, and potentially overall rates of primary production. Biotic effects have a special opportunity to affect overall rates of production in a nitrogen limited system like Lake Titicaca (Wurtsbaugh *et al.*, this volume; Vincent *et al.*, this volume) if they affect the potential of N-fixing cyanobacteria to flourish. The relative importance of physical and biotic controls on phytoplankton primary production and biomass has recently been discussed extensively under the rubric of "top down" (biotic) versus "bottom up" (physical/chemical) hypotheses (Carpenter and Kitchell, 1984; Harris, 1986). Tropical lakes should show at least relatively more effects of "top down" control than higher latitude lakes because the muted seasonal cycle of the tropics reduces the variation in important physical drivers of phytoplankton variation, including light, temperature, and strength of stratification.

Description of studies and methods

Three studies of primary production and phytoplankton biomass of a year or more in duration have been conducted in the various basins of Lake Titicaca. Richerson *et al.* (1977), working in Lago Grande in 1973, conducted the first such study. This programme was maintained for another year for phytoplankton production and still longer for other parameters by the staff of the Instituto del Mar del Perú. Lazzaro (1981, 1982) conducted a similar study in Lago Pequeño (Huiñaimarca) in 1979–80. In 1981–82, Richerson *et al.* (1986) and Vincent *et al.* (1986) conducted parallel studies of production and biomass variation in Lago Grande and shallow, polymictic Puno Bay. All studies estimated phytoplankton biomass carbon by applying the regression

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equation of Mullin *et al.* (1966) to cell volume estimates (from enumerations) and used the *in situ* ^{14}C method to measure primary production. Except for deficient estimates of nitrogen and phosphorus in 1973, these three studies also measured a relatively complete suite of physical and chemical factors using standard methods. Details can be found in the original papers.

Thus, our understanding of patterns of variation in phytoplanktonic production processes in Lake Titicaca is restricted to four years for Lago Grande and even less for Puno Bay and Lago Pequeño. Some additional data exists for Lago Grande for the years 1984–5 (Alfaro Tapia and Roncal, personal communication) and 1985–8 (Iltis, this volume).

Lago Grande

Figure 1 shows profiles of primary production from 1973. Table 1 gives the basic statistics describing photosynthesis in Lago Grande for 1973 (annual means; for more detailed data see Richerson *et al.*, 1977). Figure 2 shows the pattern of primary production for 1973–5 and 1981–2.

The productivity of Lago Grande was moderately high in these years, averaging a little above 1 g C m^{-2} d^{-1}. Because the epilimnion of this large lake is deeper than the euphotic zone, the phytoplankton crop is diluted into a large volume of water. Thus production per unit volume of water is relatively low (5–30 mg C m^{-3} h^{-1}) and the depth of maximum photosynthesis is rather deep (3–10 m).

The variation of production during the year is modest compared to temperate lakes but the pattern of variation of production during the year is highly variable (see below for a statistical analysis). Given the highly regular pattern of variation in stratification and fairly regular variation in chemical parameters visible in Fig. 2, one might expect a more predictable seasonal pattern of primary production. We believe that there are several reasons for the irregular variations within years. First, the variation in insolation is quite modest, so this variable cannot impose a strong seasonal signal. Second, photosynthesis is usually nitrogen limited (Vincent *et al.*, 1984; Wurtsbaugh *et al.*, 1985; Carney, 1984; Wurtsbaugh *et al.*, this volume). This limitation leads to a highly variable incidence of nitrogen fixing cyanobacteria during the stratified season, resulting in unpredictable peaks of production, as in December 1973. At other times, less intense cyanobacterial fixation has resulted in broad plateaux of production, as in the February-May period of 1982. When N-fixing populations are not present, the stratified season often shows pronounced production minima, as in October 1973, January and February 1981, and the last 5 months of 1982. We have no explanation for these variations in cyanobacterial populations; they are often absent for prolonged periods even when nitrogen limitation is intense (Wurtsbaugh *et al.*, this volume). Episodes of intense denitrification, such as we observed in 1981 (Vincent *et al.*, 1984), might also impose considerable variation in

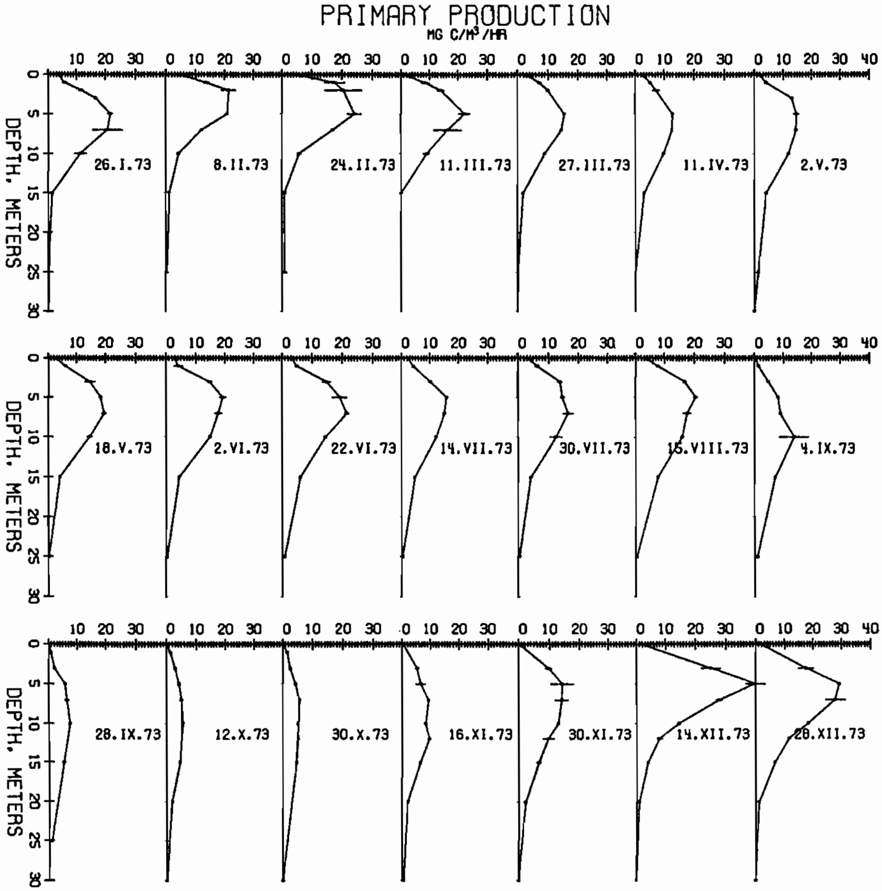
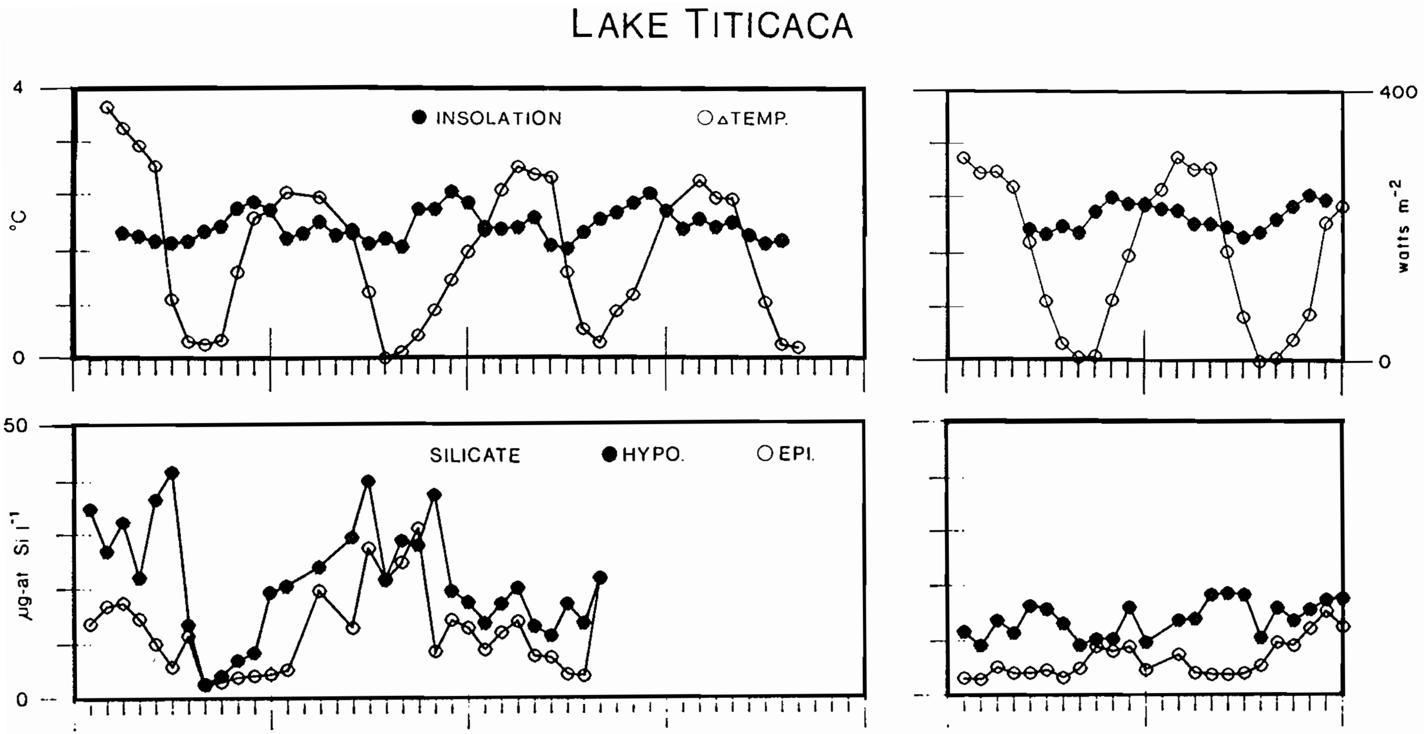


Figure 1. Vertical profiles of daily net ^{14}C (light minus dark bottle) uptake estimates of photosynthesis in Lago Grande in 1973. Bar shows the range of duplicate light bottles (Richerson *et al.*, 1977).

Table 1. Statistics describing primary production in Lake Titicaca. Θ is the rate of photosynthesis at Z_{opt}(averaging over the three maximum depths). Z_{mix} is the depth to the top of the main thermocline. Z_{cu} is the last depth at which light ^{14}C uptake exceeds that in the dark. Biomass was computed from algal counts using the method of Mullin *et al.* (1966). R was measured with a Belfort pyrheliometer at Lago Grande, but with a PAR sensor (n = 8 only) at Lago Pequeño. P_{cal} was computed assuming 10 kcal g C^{-1}.

ANNUAL MEANS									
Production (P) gC m^{-2} day^{-1}	Biomass (B) C m^{-2}	P/B day^{-1}	Θ hr^{-1}	Incident Radiation(R) kcal m^{-2} day^{-1}	P/B/R $X10^{-3}$ m^2 $kcal^{-1}$	P_{cal}/R %	Z_{opt} m	Z_{mix} m	Z_{eu} m
Lago Grande (1973)									
1.45	2.97	0.51	0.13	5086	0.10	0.29	6	50	17.7
Lago Pequeño (1979-80)									
0.56	2.52	0.22			0.19		5.3	24	25.2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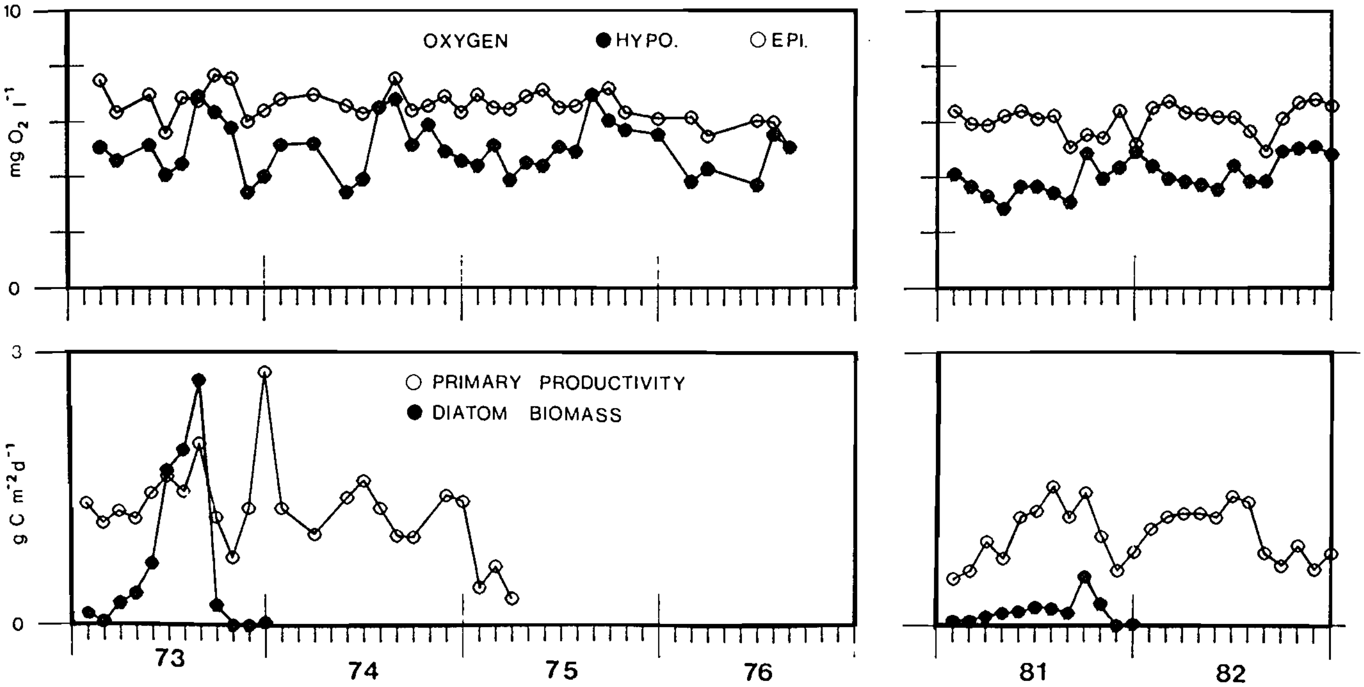

Figure 2. Monthly averaged series of basic limnological data from Lake Titicaca. Δ temp. is the difference between the temperature at 10 m and the deep hypoliminion temperatures at 150 m (Richerson *et al.*, 1986).

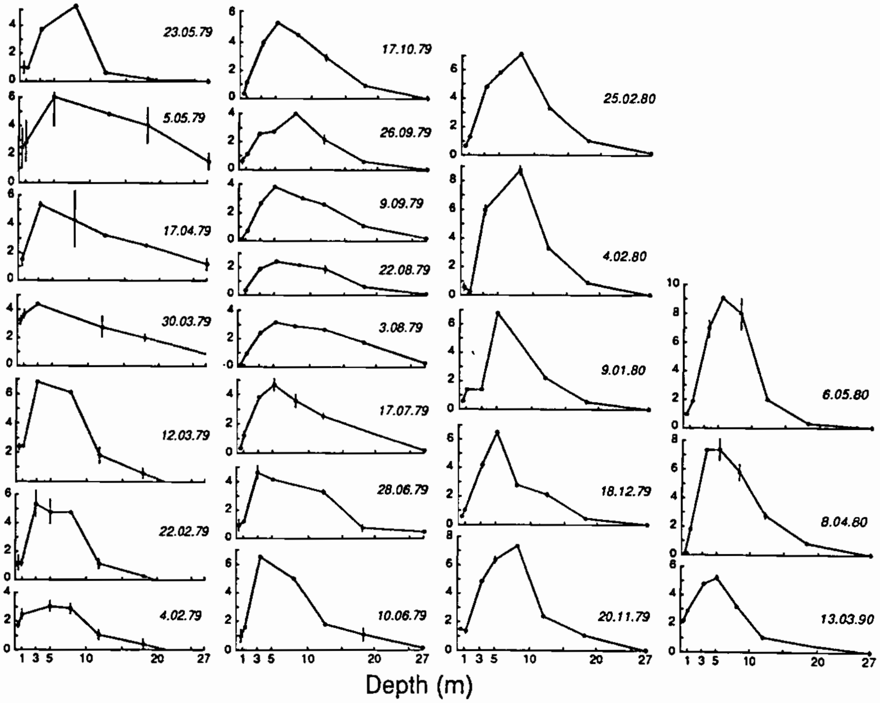

Figure 3. Profiles of estimated photosynthesis, as in Figure 1, for the Fosa de Chúa station in Lago Pequeño (Lazzaro, 1981). Vertical scale is mg c m^{-3} hr^{-1}.

production when mixing during isothermy is incomplete. Third, the impact of the deepening of the thermocline and isothermy during the dry season has only a modest and variable influence on production rates. Production peaks do generally occur in this period, but the effects of added nutrients tend to be offset by the deteriorating light climate caused by deep mixing of the phytoplankton crop.

Lago Pequeño

Figure 3 shows vertical profiles of primary production for the 40 m deep Fosa de Chúa station, and Figure 4 a similar plot for the 6 m deep Sukuta station. Figure 5 shows the pattern of variation at these two stations for production and related variables over the course of the study. Table 1 lists average statistics describing production at the Fosa de Chúa station.

There are interesting contrasts between the Lago Grande and Lago Pequeño data (Table 1). Mean primary production is much lower in Lago Pequeño, averaging just 0.56 g C m^{-2} d^{-1} in the most comparable relatively deep Chúa station, although the biomass (average 2.52 g C m^{-2}) differs little

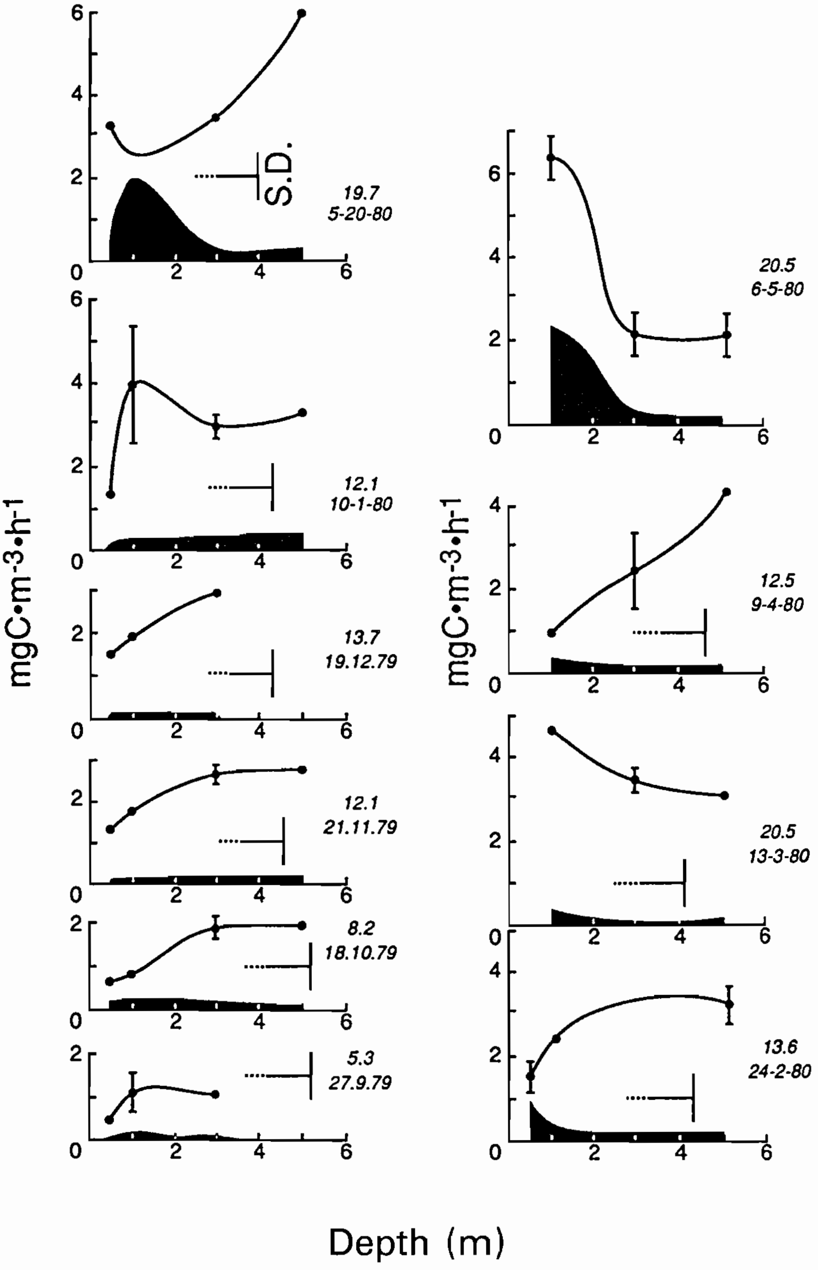

Figure 4. Vertical profiles of estimated photosynthesis at the shallow Sukuta station in Lago Pequeño. Dark bottle uptake is shown in black (Lazzaro, 1981).

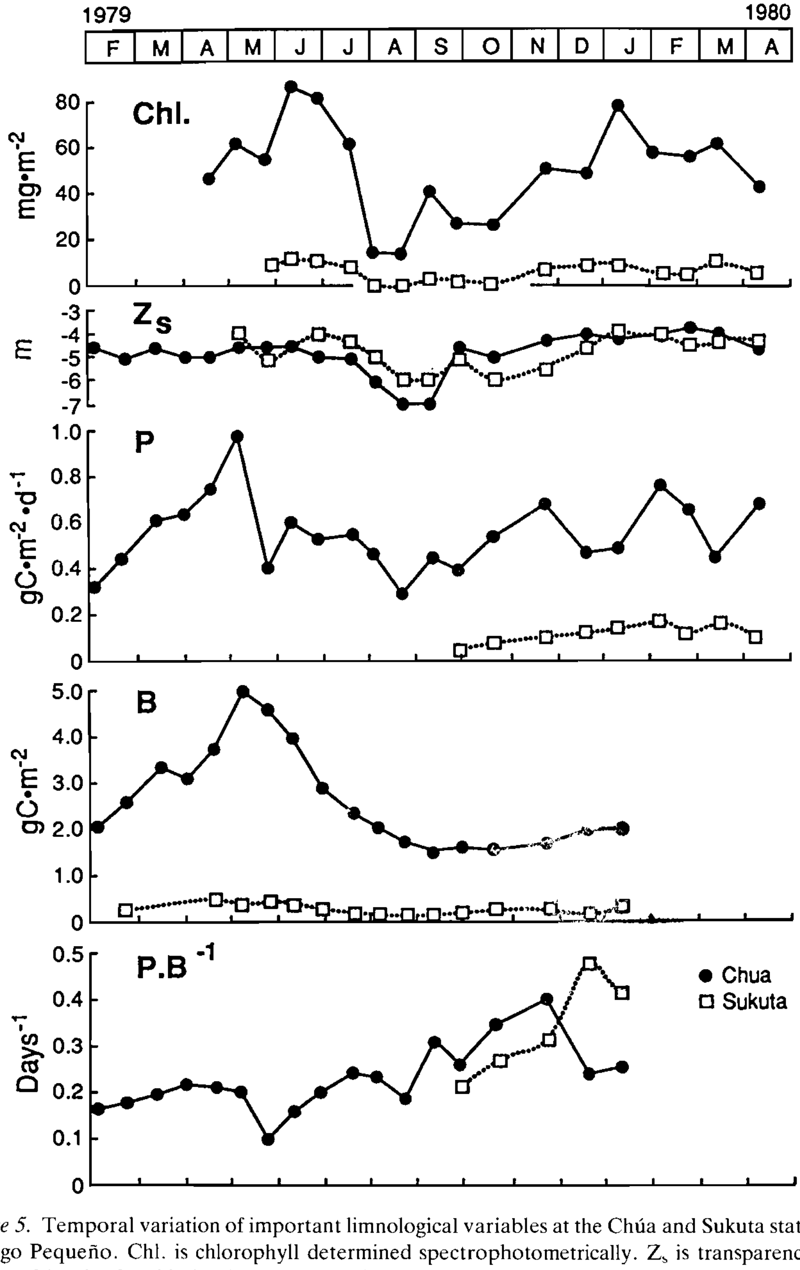

Figure 5. Temporal variation of important limnological variables at the Chúa and Sukuta stations in Lago Pequeño. Chl. is chlorophyll determined spectrophotometrically. Z_s is transparency as measured by the Secchi disk (Lazzaro, 1981).

from Lago Grande. As a result the P/B ratio at Chúa is less than half of that of Lago Grande (0.22 d^{-1}). Production was even lower in the shallow Sukuta station, but the P/B ratio was rather similar, indicating generally similar conditions for phytoplankton growth. The shape of the vertical profiles of primary production are very similar in Lago Grande and Lago Pequeño.

A number of hypotheses might explain the relatively low production in Lago Pequeño. Large areas of this shallow sub-basin are covered with macrophytes (Collot, this volume), which might compete with phytoplankton for nutrients. The sub-basin might receive less nutrient loading, due to its water budget being dominated by nutrient-depleted inflows of surface water from Lago Grande (Carmouze, this volume). However, the comparable phytoplankton biomass in the two sub-basins indicates roughly similar levels of total nutrients. The lack of nitrogen fixing cyanobacteria during the period of study, despite relatively low N:P in the hypolimnion of the Fosa de Chúa station, perhaps only means that the 1979–80 period studied by Lazzaro was one of unusually low production. Our limited knowledge of the variation in Lago Grande (see below) suggests that years with production as low as half of the mean reported in Table 3 do occur there. Finally, the shallow, well illuminated water column that characterizes so much of Lago Pequeño may deny grazing zooplankton a refuge from diurnal predation that is available to vertically migrating plankters in Lago Grande. Lower grazing rates in Lago Pequeño might therefore result in a lower turnover of biomass, and thus lower P/B. Further work is clearly required to solve this problem.

Lazzaro (1982) analysed the relationship between various measures of photosynthesis and physical parameters in Lago Pequeño. Table 2 summarises his results. These data can be used to test the validity of Talling's (1957) model of production in a vertically well mixed system. In this model, Z_i should estimate the depth at which production is half of Z_{opt}. The mean and 95% confidence interval for this relationship is 1.07 ± 0.27, indicating a good fit. Assuming that the model fits, I_k, the initial slope of the photosynthesis-irradiance curve, could be estimated. Because surface irradiance data (photosynthetically active portion of the spectrum) are available for only 4 dates, the 95% confidence interval for I_k is rather wide ($1.59 \leq I_k \leq 5.48\ J\ cm^{-2}\ h^{-1}$).

Bahía de Puno

Figure 6 shows the pattern of production observed in Bahía de Puno in 1981–2. Mean production for the two-year period was 0.82 g C m^{-2} d^{-1}, similar to the 1.02 g C m^{-2} d^{-1} recorded for the same period in Lago Grande. Vertical profiles of primary production closely resemble those for Fosa de Chúa and Lago Grande, with surface inhibition always present, a maximum at moderate depths (3–7 m), and increasingly severe light limitation below Z_{opt}. As shown in Figure 6, photosynthetic rates near the bottom of the 25 m

Table 2. Statistical relationships between primary production and physical variables in Lago Pequeño.

Depth of optimal production and Secchi transparency (Z_e), visual fits

$Z_{opt} = 1.06\ Z_e$ (Fosa de Chúa, $n=22$)
$Z_{opt} = 0.45\ Z_e$ (Sukuta, $n=8$)

Chlorophyll concentration (B_{chl}) and production at the optimum depth (P_{opt})

$\log P_{opt} = 0.46 \log B_{chl} + .54$ (Chúa + Sukuta, $n=26$, $r=.68$, $p<.001$)

Optimal specific production ($C_{opt} = P_{opt}/B_{chl}$) and B_{chl}

$\log C_{opt} = -0.53 \log B_{chl} + 0.54$ (Chúa + Sukuta, $n=26$, $r=.73$, $p<.001$)

Vertical dispersion of photosynthesis (Z_i = Hourly Production/P_{opt}) and secchi transparency and extinction coefficient (E)

$\log Z_i = 0.62 \log Z_e + 0.64$ (Chúa, $n=21$, $r=.42$, $p<.05$)
$Z_i = -76.8\ E + 31$ (Chúa, $n=5$, r-.93, $p<.001$)

deep station varied from zero to 40% of the maximum, depending upon transparency. Bahía de Puno is polymictic (Richerson, this volume) and is sometimes stratified within the euphotic zone. Vincent *et al.* (1986) showed that stratification sometimes led to the formation of a deep chlorophyll maximum in and below the stratified layer, and to higher production in the light-limited region than under unstratified conditions. On some dates in late 1982, the production curve was bimodal. These relatively clear-water conditions are reflected in Fig. 6 in the high production at 24 m from September through to November, 1982.

Vincent *et al.* (1986) examined nutrient and light controls on photosynthesis in Bahía de Puno. N:P ratios were below 10:1 during the period of the study, and, as in the main lake, nutrient bioassay experiments (Wurtsbaugh *et al.*, 1985; Carney, 1984) and physiological measures of nutrient limitation (Vincent *et al.*,1984a) generally showed nitrogen limitation of photosynthesis (see also Wurtsburgh *et al.* this volume). Consistent with this experimental evidence, the maximum and areal total photosynthesis responded quite strongly to an episode of nitrogen fixation (December 1981–June 1982). During this period, production approximately doubled relative to background values measured throughout most of 1981 and the latter half of 1982. As Fig. 6 indicates, areal production was closely correlated with surface light intensity in 1981 ($r = +0.85$, $p < .01$, one month lag), but the relationship is not significant in 1982 due to the N-fixation supported peak. There is no

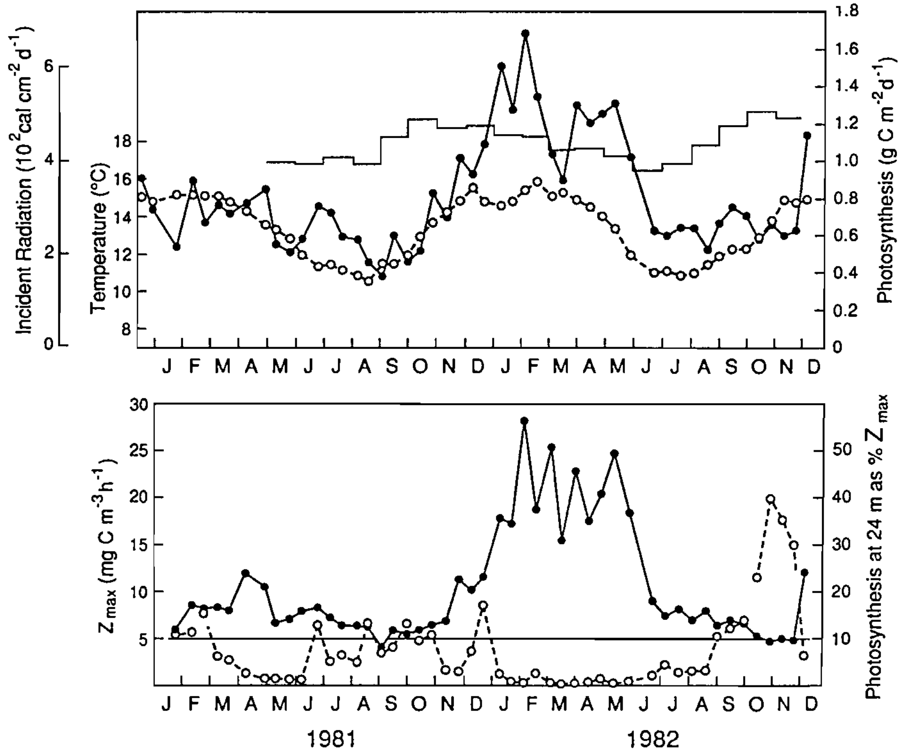

Figure 6. Photosynthesis and other important limnological variables in Bahía de Puno. (a) Daily production (closed circles), temperature at 4 m (open circles) and monthly average incoming radiation (thin line). (b) Maximum photosynthetic rate (Z_{max}, closed circles) and photosynthesis at 24 m as a percentage of Z_{max} (open circles). The horizontal line is drawn at 10% of Z_{max} (Vincent *et al.*, 1986).

indication in either year that the dry season circulation of Lago Grande had any effect on production in Bahía de Puno.

Comparative analysis of patterns of variation in production and related variables

The three sub-basins of the lake exhibit a good deal of independence of behaviour. Lago Pequeño is only connected to Lago Grande via the narrow Estrecho de Tiquina, and has somewhat different major ion composition from the main lake (Lazzaro, 1981; Carmouze, this volume). The connection between Lago Grande and Bahía de Puno is quite broad, and there are no marked differences in water chemistry. Nonetheless, patterns of production in the latter two systems at 0, 1, and 2 month lags are uncorrelated (Vincent *et al.*, 1986). The 1982 peak of production due to the presence of cyanobacterial N-fixation was present in both lakes, but with somewhat different timing. Production in Lago Grande appears to respond to deep circulation in that basin in many years, but Bahía de Puno did not apparently receive enough nutrients by advection or diffusion from the main basin to stimulate production in 1981 or 1982.

Richerson *et al.* (1986), Richerson and Carney, (1988) and Vincent *et al.* (1986) examined the seasonal and interannual patterns of variation in primary production and other variables in Lago Grande and Bahía de Puno with several different statistical approaches. These studies compared patterns of variation in Titicaca with those of other temperate and tropical lakes. Vincent *et al.* (1986) examined the relationship between variation in light intensity and variation in primary production in 12 tropical and 11 temperate systems. The tropical systems had a much higher variance in production relative to variation in light than did temperate lakes. Many, but not all, tropical lakes, including both Bahía de Puno and Lago Grande, had a variance in primary production several to many times higher than that for incident solar radiation (averaging 14.44). Temperate lakes showed a narrower range, this ratio averaging 1.8. Moreover, the overall correlation between monthly incident solar radiation and monthly primary production (scaled by the annual mean in each lake) for all temperate lakes was large and significant ($n = 160$, $= 0.57$, $p < 0.01$), whereas it was small and insignificant for tropical systems ($n = 150$, $r = +0.11$, $p > 0.05$). A more detailed look at the data confirmed this overall result. For 13 years of tropical data, 5 years showed significant lags ($p < 0.05$) at 0, 1 or 2 months lag. However, in only two of these years (including Bahía de Puno in 1981, as already mentioned) were the correlations positive. By contrast, 11 of 14 temperate lake years showed significant correlations for at least one lag, and only one of these was negative. In most temperate lakes, primary production is strongly entrained in the seasonal cycle of insolation, but as the amplitude of this cycle diminishes in the tropics, this effect appears to vanish.

Richerson *et al.* (1986) and Richerson and Carney (1988) tested the weak seasonality hypothesis with the multi-year time series of physical, chemical and biological data from Lago Grande (Fig. 2). Multi-year data sets were assembled for four comparison sets of data from other temperate and tropical lakes (lakes George, Leven, Washington and Tahoe). Monthly mean data were analysed using two-way Analysis of Variance to estimate variance due to fixed monthly (seasonality) and between-year effects. Richerson and coworkers also estimated autocorrelation functions for these time series. The results are quite striking. In the ANOVA analysis (see Table 3) Lago Grande showed a strongly seasonal pattern of physical variation, with months effects dominating the pattern. By contrast, chemical and biological variables (with the exception of diatom biomass) varied much less seasonally and usually not significantly. However, variation between years is large for such variables (again excepting diatom biomass). Richerson and Carney (1988) extended this analysis to biomass, diversity and measures of succession rate. Patterns

Table 3. Results of analysis of variance of data series from Lago Grande and some comparison with temperate and tropical lakes. One asterisk indicates a treatment effect significant at the .05 level, two asterisks at the .01 level. k/X is the coefficient of variation of treatment means (Richerson *et al.*, 1986).

LAKE	Latitude	N	df		Variance			k/X		Grand mean
			Months	Years	% Years	% months	Total	Years	Months	
George	0°									
1) Chlorophyll *a*		36	11	3	14	40	9581	0.09	0.15	411.5 mg Chl *a* m^{-2}
Titicaca	16°S									
1) Radiation		41	11	3	13**	76**	1101	0.05	0.10	251.8 watts m^{-2}
2) Difference of temperature		62	11	5	3	92**	0.131	0.11	0.67	1.55°C
3) Silicate in epilimnion		54	11	4	39**	8	45.8	0.43	0.20	9.69 μg-at l^{-1}
4) Silicate in hypolimnion		54	11	4	31**	19	78.9	0.27	0.21	18.14 μg-at l^{-1}
5) Oxygen in epilimnion		60	11	5	39**	13	0.300	0.06	0.03	6.38 mg l^{-1}
6) Oxygen in hypolimnion		60	11	5	26**	31*	0.97	0.11	0.12	4.62 mg l^{-1}
7) Primary production		49	11	5	29**	26	0.182	0.20	0.19	1.13 g C m^{-2} d^{-1}
8) Diatom biomass		25	11	2	17*	49*	0.101	0.41	0.82	0.256 ml m^{-3}
Tahoe	39°N									
1) Primary production		116	11	9	49**	22**	0.0046	0.24	0.16	0.196 g C m^{-2} d^{-1}
Washington	48°N									
1) Radiation		102	11	8	4	73**	7057	0.11	0.56	128 watts m^{-2}
2) Chlorophyll *a*		102	11	8	23**	47**	109.5	0.41	0.59	12.2 μg l^{-1}
3) Primary production		102	11	8	18**	63**	2.77	0.34	0.64	2.07 g C m^{-2} d^{-1}
Leven	56°N									
1) Primary production		43	11	3	9*	66**	13.48	0.28	0.76	4.82 g O^{2} m^{-2}

were similar; all variables showed large and significant variation between years. Only diversity showed a significant fixed 12-month effect, as a result of a tendency to low diversity during the middle of the stratified period in the three years of record. Richerson (unpublished data) has also examined the other major groups of algae, and diatoms are the only one to show significant months effect in the ANOVA. The biological data from comparison temperate lakes (Table 3) show highly significant monthly effects, which are higher than between years effects except for Tahoe, where cultural eutrophication and relatively sunny winters reduce the effect of seasonality.

The autocorrelation analyses confirm these results (Fig. 7). In highly seasonal time series, the autocorrelation function is significantly negative at 6 months lag (winter and summer are very different), while there is a significant positive peak at 12 months lag (one year is much like another). Physical variables in Lago Grande show the highly seasonal pattern, as do biological variables in classical temperate lakes like Loch Leven. By contrast, production in Lago Grande and chlorophyll in Lake George show no statistically significant sign of a seasonal pattern, although there is a hint of a 6 month cycle in both systems. For Lago Grande, a 6 month cycle is consistent with the weak tendency of production to peak either during maximum stratification (due to N-fixation occurring during this season), or during the period of minimum stratification (due to cycling of nutrients from the hypolimnion).

Figure 8 shows a similar general pattern for major algal groups. All groups except cryptophytes exhibit some patterning with significant positive autocorrelations for up to 3 months lag (Fig. 8b), reflecting the major episodes of abundance clearly visible in Fig. 8a. For Cyanophyceae and Chlorophyceae the autocorrelation function becomes significantly negative slightly after six months and then increases. This indicates moderate seasonality; there are fairly consistent patterns with mixing and stratification. No group, however, has a pattern of regular seasonality that repeats in subsequent years, as would be indicated by a distinct minimum autocorrelation at 6 months and maximum at 12 months.

An analysis of variance with biomass data of the major groups also indicates that interannual variability is quite significant, while regular seasonal variation within years is more modest. Variance between years is significant at $p < 0.01$ for all major groups (Cyanophyceae, Chlorophyceae, Bacillariophyceae, Dinophyceae), while the months effect is only significant for Bacillariophyceae.

Dominant phytoplankton species show generally similar patterns to the major groups (Fig. 9). The filamentous blue-green *Nodularia spumigena* shows one of the strongest seasonal signals we have detected among biological measures. This species regularly peaks during the stratified period and reaches minima during mixing. The filamentous green *Gloeotilopsis planctonica* and the centric diatom *Cyclotella andina* are more typical. They show significant lags, but virtually no hint of truly regular seasonality. Even though species like *C. andina* have only occurred during the cool season, the exact

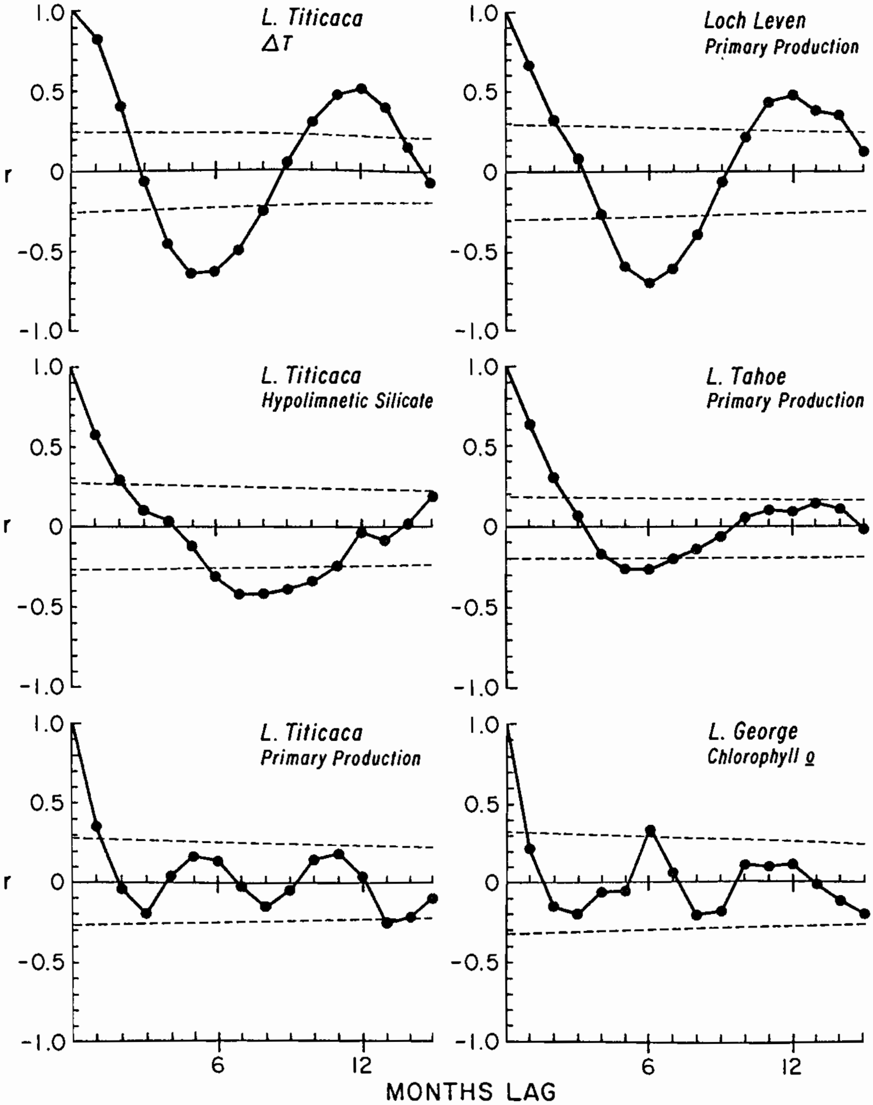

Figure 7. Autocorrelation functions for data series from Lago Grande and some comparison with tropical and temperate lakes. The vertical axis gives the value of the autocorrelation (r) as a function of months of lag on the horizontal axis. The near-horizontal dashed lines delimit the envelope in which 95% of the autocorrelations from a random series of the length of each data series should fall (Richerson *et al.*, 1986).

timing and magnitude of their maxima and minima is so variable as to fail to indicate a statistically significant seasonal cycle.

Principal components analysis is a useful technique to summarize the "seasonal" succession pattern of the whole community (Allen *et al.*, 1977).

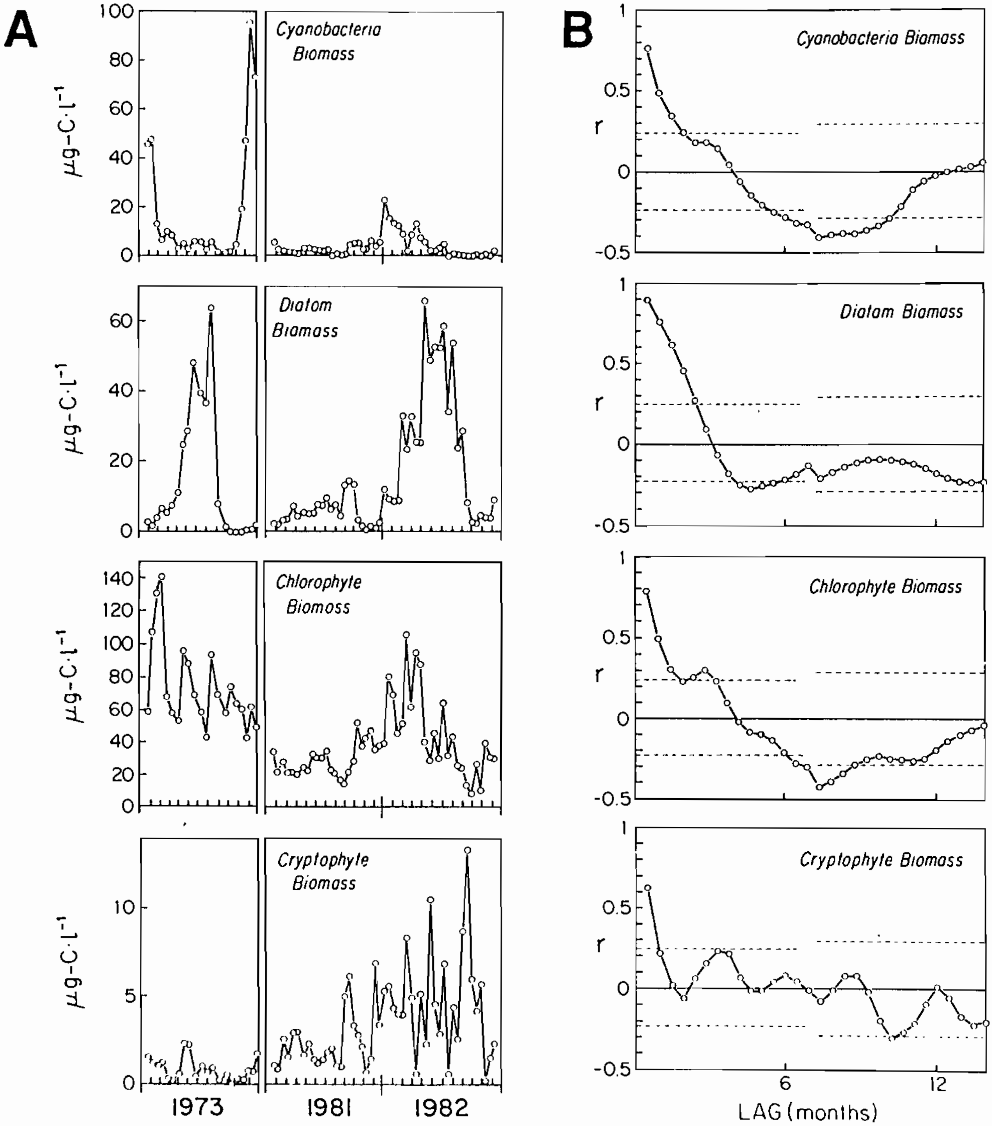

Figure 8. Biomass of the major algal groups for the three years of record (A). Autocorrelations for the major groups (B).

Figure 10 shows how the Lake Titicaca community changes during the three years; each point represents the composition of the community during a given month. The abundance of the 15 commonest species defines the axes of the multidimensional space of possible communities in this analysis. A large change in the community from one date to another is reflected by a

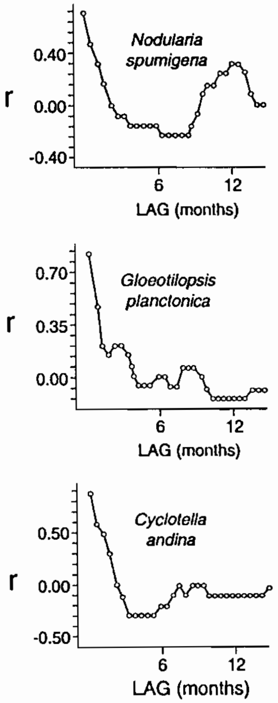

Figure 9. Autocorrelation functions for three species of algae.

large shift in position. A strong and regular seasonality would be indicated by a large circle or oval for a yearly trajectory. Each year would come close to mapping out the same trajectory of species composition as every other. Clearly, the Lake Titicaca phytoplankton do not exhibit this behaviour. During the three years for which we have data, the Titicaca community wanders about in a rather irregular pattern without any apparent tendency to form closed 12 month polygons (Fig. 10). These very irregular intra-year patterns, and substantial changes between years, are in sharp contrast to PCA results for north temperate lakes (Allen *et al.*, 1977).

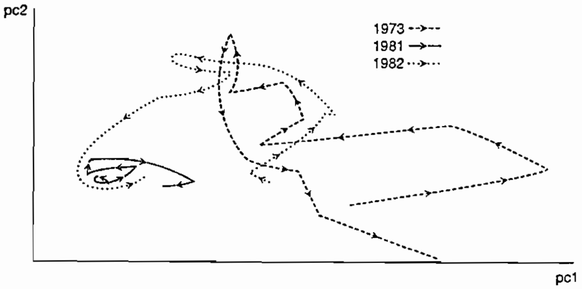

Figure 10. Plot of the first two principal components of monthly average phytoplankton biomass in Lake Titicaca.

In Lago Grande, a rather large proportion of the variation in many biological and chemical variables is unexplained by either months or years effects in the ANOVA, and shows up as significant autocorrelations at one or two months lags. In the two most typical temperate lakes in Richerson *et al.*'s comparison, seasonal plus between years effects accounts for a very large proportion of the variation in all series. This reflects the tendency of biological and physical variation in Titicaca to occur in "pseudoseasonal" events of 1–3 months duration. In any one year, this looks something like the familiar seasonal cycles of the temperate zone, but the patterns are not repeated in subsequent years.

We wish to end this section with a note of caution. It is clear from less complete and unpublished data from other years that Lake Titicaca varies outside the bounds of the data analysed above. Alfaro Tapia and Roncal (personal communication) and Iltis (personal communication) have observed a long episode of very low production and biomass, and high transparency, in Lago Grande during the years 1984–8. Both groups report large numbers of secchi depths exceeding 10 m with maxima of almost 20 m, whereas in earlier studies secchi depths exceeding 10 m were unusual. Both production and phytoplankton biomass were only a fraction of the averages based on the data shown in this paper. Our understanding of the interannual variability of both temperate and tropical lakes is still very incomplete. Longer and more complete time series of data are urgently required from lakes like Titicaca both to help in the management of local resources, and to understand basic questions regarding the effects of climate change and similar phenomena.

Surface inhibition of photosynthesis

As shown by the profiles in previous sections, primary production in all sub-basins of Lake Titicaca is usually characterized by surface inhibition, a maximum of production around 5 m, and an exponential decline below that depth. One problem posed by profiles with this shape is the significance and reality of the surface inhibition above Z_{max}. This effect is a result of high light intensities, and is termed photoinhibition. Photoinhibition takes some time to develop, and in experiments with moving bottles designed to mimic mixing in the epilimnion of lakes eliminate or greatly reduce the photoinhibition effect (Jewson and Wood, 1975; Marra, 1978). On the other hand, as described by Richerson (this volume), diurnal stratification in the top few metres of the water column, due to the same high light intensities that cause photoinhibition in fixed bottle experiments, also reduces mixing at shallow depths during daylight hours.

Vincent *et al.* (1984b) and Neale and Richerson (1987) used the poison DCMU, which blocks the reoxidation of Photosystem II intermediates, as a physiological measure of state of algal cells. When DCMU is administered,

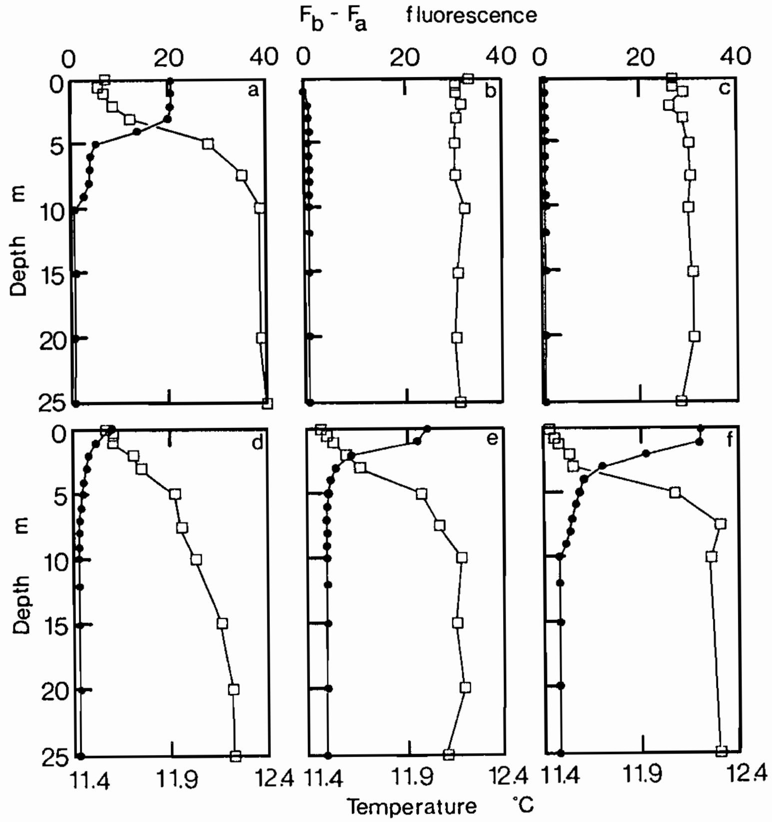

Figure 11. Diel cycle of temperature and fluorescence depression, 21–22 July, 1982, in Lago Grande. a) 16:30 21 July; b–f) 22 July; b) 05:30 h; c) 07:30 h; d) 09:30 h; e) 11:30 h; f) 13:30 h. Open box, F_{aft}–F_{bef}; solid circle, temperature (Vincent *et al.*, 1984b).

light cannot be used to produce electrons in the reaction centre and is instead lost by chlorophyll fluorescence. Thus DCMU generally enhances the fluorescence of living cells. However, when the PS II reaction centre is inactivated by photoinhibition, electrons are no longer produced, and DCMU ceases to increase fluorescence emission. In Lake Titicaca, there is minimal increase of *in vivo* fluorescence in near-surface algal populations upon addition of DCMU, but populations near Z_{max} show maximal DCMU enhancement. Thus, at the surface, DCMU does not increase fluorescence very much because photoinhibition has already resulted in the inactivation of Photosystem II. Figure 11 shows an example of the daily cycle of inhibition and recovery, measured by the difference between fluorescence before (F_{bef}) and after (F_{aft}) the administration of DCMU. Neale and Richerson conducted a series of experiments to quantify the dynamics of inhibition and recovery during the diurnal cycle in Lago Grande. On 8 different experimental days, short-term experimental incubations were conducted in which algae from shallow (3–5 cm) and deep (15–20 cm) in the euphotic zone were incubated at several different light intensities. These experiments showed that the inhibition of ^{14}C uptake closely parallels the decline in DCMU enhanced fluorescence. The inhibition process is quite rapid, with a time scale of a few minutes, whereas recovery is slow, requiring hours. Hence, the photosynthetic capacity of an algal cell declines to a level set by the highest light intensity to which it is exposed during the daily cycle, and does not significantly recover until after dark.

These results show that diurnal stratification, at least in Lake Titicaca, but probably in many other systems under bright light conditions, is easily strong enough to subject shallow phytoplankton populations to inhibiting light intensities. The traditional fixed bottle experiment is thus not misleading about the effects of photoinhibition. One might expect algal populations to adapt to high light intensities and eliminate the photoinhibition effect. However, the deep mixed layer of Lake Titicaca means that most cells experience suboptimal light on any given day. Nocturnal mixing (Richerson, this volume) prevents the community from segregating into high and low light adapted forms, as is possible with the sun and shade leaves of terrestrial plants. Thus, the photoinhibition of the plankton is perhaps an inevitable tradeoff caused by the need to adapt to the low average light conditions of planktonic environments.

Conclusion

Lake Titicaca exhibits a level and pattern of primary production that is basically tropical, although modified by its altitude. Brylinski and Mann (1973) estimated regression equations describing patterns of global production in lakes. Their simplest equation based only on latitude and altitude predicts ($r^2 = 0.49$; $n = 93$) that Titicaca production should be 0.90 g C m^{-2} d^{-1}. A second equation based on latitude, altitude, visible incident radiation, day length range, air temperature and precipitation ($r^2 = 0.58$; $n = 84$) predicts 1.26 g C m^{-2} d^{-1}. Measured values from Lago Grande (1.13 g C m^{-2} d^{-1}, 4 year average from Table 3), Lago Pequeño (0.56 g C m^{-2} d^{-1}), and Bahía de Puno (0.82 g C m^{-2} d^{-1}) are rather close to these predictions. Even the Lago Pequeño value is not so far off considering the inevitable noise inherent in such a broad comparison. The lake might be described as moderately eutrophic based on its total annual production compared to lakes on a worldwide basis. On the other hand, its position near the regression line given its physical situation (especially the long tropical growing season) suggests that the designation "mesotrophic" is more appropriate.

The pattern of temporal variation in Lake Titicaca is fascinating, especially if it turns out to be typical of large, deep tropical lakes. Despite the seasonal pattern of variation of physical factors, the low amplitude of physical variation appears to result in a failure to entrain biological processes in the seasonal cycle. Unlike the case in higher altitude lakes, seasonality in the sense of a regular 12 month cycle is essentially absent. Total variation is reduced somewhat, interannual variation is comparable, and the amount of variation unexplained by the factors analysed in this study is substantially higher, compared to temperate lakes. Two hypotheses seem worth pursuing in future studies. (1) Subtler physical and chemical mechanisms may control the variation in production and other biotic factors. (2) Biological interactions, such as predator-prey and competitive processes, may generate endogenous variation, perhaps of the chaotic sort. These ideas are closely related to the "top down" (biotic) versus "bottom up" (physical) hypotheses about the most important factors regulating processes in the plankton currently being actively investigated by temperate zone limnologists (Carpenter *et al.*, 1985; Harris, 1986). Richerson and Carney (1988) hypothesize that complex dynamics (e.g. chaos) may be responsible for a significant amount of the acyclical within-years and interannual variation in Lake Titicaca. Titicaca is an excellent place to study such effects. It has the three contrasting basins for comparison, and its mean temperatures are much like those of the better studied temperate lakes. It has easily detected physical forcing effects, but apparently not such a strong seasonal signal as to dominate biological and chemical processes. If biotic processes have free-running dynamics that generate their own patterns of variation, these might be convincingly separated from physical controls in such a lake. Workers are encouraged to develop the long-term data that would be so valuable from such a system to test these and similar ideas.

Understanding the causes of variation is, of course, also important for applied purposes in Lake Titicaca. The present evidence from Titicaca suggests that it is less variable than temperate lakes only in having little predictable seasonality. There is every reason to expect that year-to-year variation will be important to management of the lake's biotic resources. Our data only sample a few years and do not reflect the longer term variation that might be induced by lake-level changes and the like. We know some years have values of transparency, production and phytoplankton biomass outside the range of the data analysed here.

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