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Patterns of temporal variation in Lake Titicaca, a high altitude tropical lake. II. Succession rate and diversity of the phytoplankton

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With 2 figures and 1 table in the text

Introduction

A pattern of regular seasonality accounts for much of the variation in most limnological variables in typical temperate lakes due to the strong seasonal pattern in the primary physical forcing variables — insolation, temperature, and stratification. It is not yet clear how consistently tropical lakes depart from this pattern. MELACK (1979) showed that tropical lakes generally have a lower coefficient of variation of photosynthetic rate than temperate lakes, and described three patterns of variation. TALLING (1986) presented data from a variety of tropical systems showing examples of hydrologically and hydrographically controlled seasonality as well as examples of non-seasonal variation. RICHERSON et al. (1986) analyzed multiyear time series from Lake Titicaca, Lake George, and some comparison temperate lakes. They used autocorrelation and ANOVA techniques to isolate the component of the variation in several variables due to the regular 12-month seasonal cycle from non-seasonal sources of variation. In this paper, we extend the previous analysis of the Lake Titicaca time series to phytoplankton biomass, diversity, and succession rate. A similar analysis of patterns of succession of phytoplankton populations and major groups will be presented in a subsequent paper.

Lake Titicaca is a large (8,100 km^2, 273 m max. depth), high altitude (3,800 m asl) tropical (16 ° S) lake. The lake is cool (epilimnetic temperatures 11—15 °C), monomictic (± isothermal for a few weeks in July and August), and moderately productive (mean carbon fixation rate $1.13\,\mathrm{g\,C \cdot m^{-2} \cdot d^{-1}}$). It is a nitrogen-limited system (WURTSBAUGH et al. 1985, VINCENT et al. 1985, CARNEY 1984). For general limnological information, see RICHERSON et al. (1977, 1986), CARMOUZE & AQUISE (1981), LAZZARO (1981), and VINCENT et al. (1986). The species composition of the phytoplankton is discussed in CARNEY et al. (in press).

Our previous analysis of temporal patterns (RICHERSON et al. 1986) focussed on physical, chemical, and selected biological variables, including primary production and diatom biomass. Stratification and insolation are highly seasonal in Lake Titicaca, although the absolute magnitude of variation is small. Thus the hydrographic forcing of chemical and biological processes (TALLING 1986) is highly seasonal. Hydrological effects are small because of the large volume of the lake relative to its annual water budget. However, most chemical and biological variables showed little evidence of seasonal variation. Only diatom biomass and one chemical variable (hypolimnetic oxygen concentration) showed statistically significant evidence of regular seasonal fluctuations. For the most part, interannual variation was larger than regular seasonal variation, and irregular variations within years were an important feature of the chemical and biological series. Note that data from more than one year is required to distinguish irregular variation within years from a regular 12 month seasonal cycle. Thus, MELACK's (1979) classification of Lake Titicaca as seasonal on the basis of variations in primary production in 1973 is not strictly correct because the pattern of variation in that year was not repeated in subsequent years.

Methods

The data series we analyze here are based on phytoplankton enumerations from 1973 and 1981—1982. At approximately two week intervals, samples were collected from seven to nine

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depths in the epilimnion and preserved in LUGOL's. Slides prepared using the glutaraldehyde technique of DOZIER & RICHERSON (1975) were examined at 1250× and 500× using phase contrast microscopy. Smaller forms were counted only at the higher magnification. Water from all epilimnetic depths was mixed, three replicates were counted on each date, and the results converted to estimates of cell carbon per liter using the equations of STRATHMANN (1967) for diatoms and MULLIN et al. (1966) for all other species. Our techniques in 1973 differed slightly from 1981—82 (RICHERSON et al. 1977), but the epilimnetic averages for the two periods analyzed here are quite comparable.

Diversity was computed according to the SHANNON-WEAVER index using estimated phytoplankton biomass carbon as the measure of abundance. We computed three measures of succession rate according to the suggestions of ARMSTRONG (1969; see WILLIAMS & GOLDMAN 1975), JASSBY & GOLDMAN (1974), and LEWIS (1978). Each of these indices of the rate of community change is based on summing the changes in the contribution of a given species to a measure of community status, and dividing by the elapsed time between measurements. Thus, they are per day measures of the rate of community change. ARMSTRONG's index uses contributions to diversity as a basis for computing rate of change, while JASSBY's and LEWIS' use different measures of total biomass. The three indices are highly correlated in this data set (A—L, $r = 0.90$, A—J, $r = 0.80$; J—L, $r = 0.90$, $n = 72$).

We used two simple statistical techniques to detect pattern in the data. Autocorrelation estimates were made on linear interpolations of the raw data to give values with equal 14-day spacing. Lags up to 15 were computed separately for 1973 and 1981—82 and averaged. Lags from 16—30 were only computed using the 1981—82 data. Two-way analysis of variance was used to partition the variance of each series into fractions due to fixed monthly and between-years effects. Each month was represented by an average value for the month computed from linearly interpolated daily values. Computations were made using the Minitab statistical package.

Results

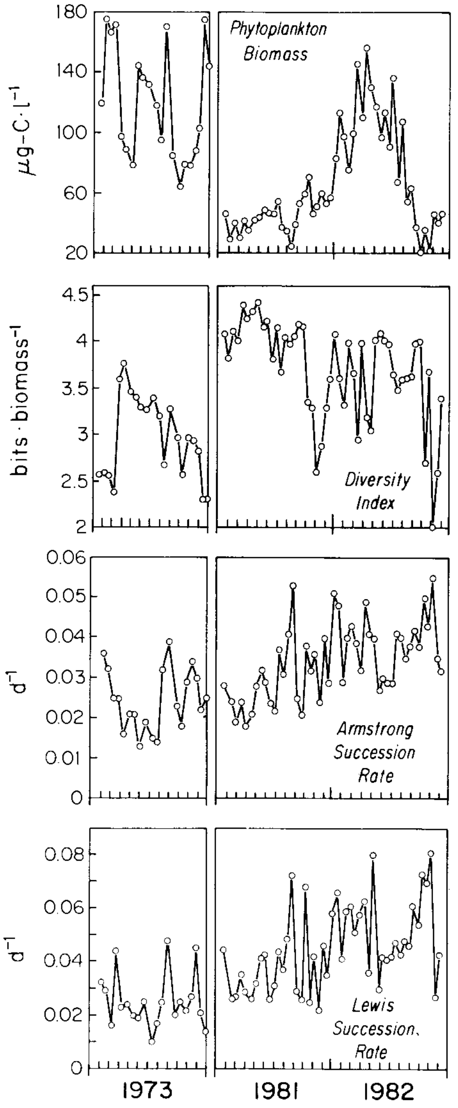
As the plots of standing crop, diversity and succession rate show (Fig. 1), the Lake Titicaca phytoplankton exhibit modest evidence of regular seasonal fluctuations and major between-year variations in succession rate and biomass. Much of the variation within years is apparently aseasonal. For example, there were four conspicuous peaks of phytoplankton biomass in 1973, but patterns in 1981 and 1982 show quite different patterns. There is no marked tendency for similar patterns of total biomass or succession rate to recur in the three years. There is a tendency for diversity to reach minima sometime during the period of strongest stratification.

In the autocorrelation function analysis (Fig. 2), strongly seasonal patterns would be manifest by significant minima at six months lag and a peak at twelve months lag. None of the autocorrelation analyses show evidence of a strong seasonal cycle. In all of the series, there is significant autocorrelation at short lags. In the biomass and diversity series, some significantly negative values occur near but not exactly at six months lag. In the succession rate series, LEWIS' and JASSBY's (not shown) indices have marginally significant negative values at lags near one year.

The analyses of variance confirm these general impressions of modest seasonality, and moderately large seasonal variation within and between years. Between-years variation is highly significant in all five series, but a seasonal effect is significant only in the diversity series. Significance levels aside, the between-years variation accounts for roughly half of the variance in these records, and, with the exception of diversity, monthly effects account for 25% or less of the total variance.

Discussion

These results are consistent with previous analyses of temporal variations in Lake Titicaca. Compared with typical temperate lakes, and with tropical lakes dominated by



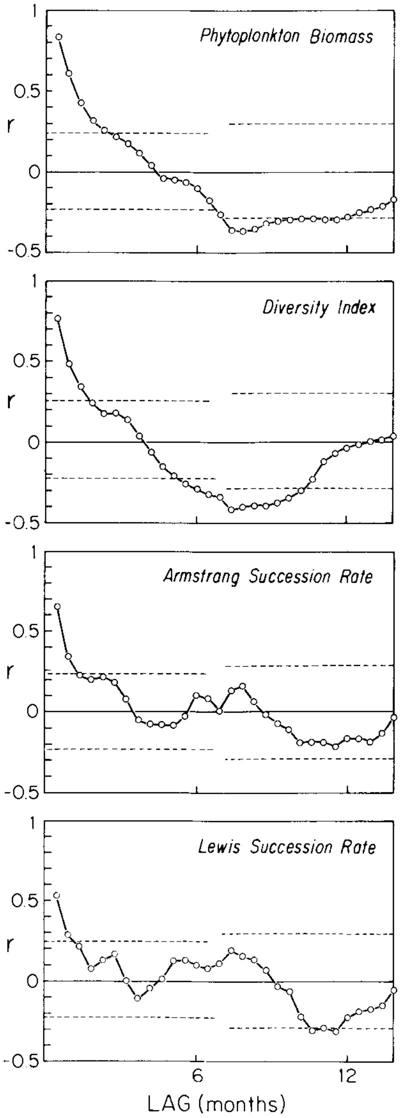


Fig. 1 (left). Biweekly interpolated time series plots of phytoplankton biomass (carbon), diversity, and succession.

Fig. 2 (right). Autcorrelation functions for the data series. The vertical axis gives the value of the autocorrelation (r) plotted against lag in months on the horizontal axis. The horizontal dashed lines delimit the envelope within which 95 % of the points derived from a random series are expected to fall (Chatfield 1980).

seasonal hydrology (Talling 1986), biotic processes in Lake Titicaca show weak to negligible effects of seasonality of hydrographic processes. A strongly seasonal pattern of stratification, in the absence a strongly seasonal light regime, temperature regime, or

Table 1. Results of analysis of variance of several phytoplankton time series. One asterisk indicates a treatment effect significant at the 0.05 level, two asterisks at the 0.01 level.

Variable	df		Variance	
	Months	Years	% months	% years
1. Mean Epilimnetic Biomass	11	2	14	56**
2. Diversity	11	2	35**	48**
3. Succession Indices				
a. Armstrong's	11	2	18	52**
b. Lewis's	11	2	9	71**
c. Jassby's	11	2	23	44**

hydrology, is apparently not sufficient to entrain most chemical and biological processes in a consistent pattern of seasonal fluctuation.

The rate of succession in Lake Titicaca is low relative to the maximum rates for temperate Clear and Castle Lakes among the examples given by Williams & Goldman (1975). Its rates are comparable to those they report for Lake Tahoe, which Titicaca resembles in morphometry. The maximum rates for Lake Titicaca measured by Jassby's index are 20—50% of the maximum values that Jassby & Goldman (1974) report for several summers in Castle Lake. By the measure of Lewis' index, succession rates in Lake Titicaca are roughly similar, especially in 1981—82, to those in Lake Lanao in mean value and range. Although the number of comparison are still small, stratified, hydrographically dominated tropical lakes appear to have low maximum succession rates compared to typical temperate lakes. Succession rates in Castle Lake are highly seasonal (Jassby & Goldman 1974 present data for three summers), so in this respect Lake Titicaca probably also differs from temperate lakes.

The non-seasonal biotic fluctuations that are so important in Lake Titicaca are potentially of great theoretical interest. Models show that biotic processes can fluctuate endogenously, even in the absence of external environmental fluctuations (e.g. May & Oster 1976, Powell & Richerson 1985). Such fluctuations may be important in aquatic systems (Murdoch & McCauley 1985, Carpenter et al. 1985, Steele & Henderson 1984). Low-seasonality tropical systems, where the effects of physical environmental variation on biotic processes are unusually small may be an excellent place to investigate this hypothesis.

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