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DYNAMICS AND SUCCESSION OF THE PHYTOPLANKTON IN A TROPICAL LAKE: LAKE LANA O, PHILIPPINES

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SUMMARY

(1) Phytoplankton dynamics in Lake Lanao, Philippines, were studied over a 16-month period on the basis of weekly abundance measurements for seventy species and a number of physical and chemical variables.

(2) An analysis of growth pulses and growth correlations in the major classes of phytoplankton provides evidence that the niche space is divided temporally on the basis of nutrient and light availability. Growth maxima of diatoms and cryptomonads occur during periods of relatively low light availability and high nutrient availability; pulses of green algae, blue-green algae and finally dinoflagellates occur successively towards the high light and low nutrient end of the spectrum.

(3) Variations in total autotroph biomass over the 16-month period were more closely related to factors affecting growth than to factors affecting loss of biomass. Loss control factors nevertheless influenced succession by their differential effects on individual species.

(4) Major factors controlling phytoplankton growth include light availability (computed from measurements of incident light, mixing depth and transparency) and nutrient availability (computed from measurements of nutrient concentrations, turbulence and change in depth of mixing). Individual species were arranged by statistical methods according to their growth patterns along gradients of these two factors. There is an identifiable taxonomic trend in the separation similar to that observed in the class-level analysis of succession, but a number of species showed divergent behaviour from others of their taxonomic group.

(5) Measurable factors governing loss of autotroph biomass include grazing rate (analysed on the basis of herbivore biomass) and sinking rate of cells (analysed on the basis of the mean Richardson Number over the euphotic zone). Individual phytoplankton species did not separate well on the basis of grazing intensity. Overall losses of autotroph biomass to grazing are quite low (< 7% per day), which probably accounts for the limited influence of grazing on succession. A good separation of species, however, was obtained on the basis of their different sinking rates along a gradient of turbulence. There is a strong tendency for diatoms and cryptomonads to thrive when turbulence is maximal, for blue-green algae and dinoflagellates to thrive when turbulence is minimal, and for green algae to occupy the broad middle range of conditions.

(6) Only the two species of *Melosira* showed any evidence of initiating growth pulses from meroplanktonic inocula; the role of the dormant phase in *Melosira* appears to be similar to that in temperate lakes.

(7) The surface/volume ratio of biomass units plays an important role in determining the position of a species on the factor gradients. The S/V ratio of a species is significantly correlated with its position on the gradients of nutrient availability and sinking rate. Since the different phytoplankton classes have substantially different mean S/V ratios, these correlations appear to underlie the tendency of species to segregate on the factor gradients in relation to taxonomic affinities.

(8) The overall pattern of succession in Lake Lanao shows some definite contrasts with that in temperate lakes. Phytoplankton succession can be regarded as a series of episodes initiated by abrupt changes in abiotic factors, and such episodes appear to be more numerous over a year in Lake Lanao than in most temperate lakes. Events within any given episode, however, are very similar in Lake Lanao and in typical temperate lakes. This hypothesis is supported by a statistical comparison of succession in Lake Lanao and Lake Erken, Sweden.

INTRODUCTION

The seasonal succession of phytoplankton species is an important and familiar aspect of the biology of temperate lakes, in which it usually bears some obvious relation to seasonal weather changes that affect the availability of light and nutrients in the water column. Tropical lakes likewise experience seasonal weather changes that induce physico-chemical changes of various kinds, although these changes differ in amplitude and periodicity from those of temperate lakes. Seasonal changes in phytoplankton abundance have been described for only a few tropical lakes (e.g. Gonzales 1961; Talling 1966; De Reyes 1972; Iltis 1974), yet it is already clear that succession can be quite dramatic in these lakes despite the reduced amplitude of seasonal weather changes. Only very shallow equatorial lakes seem to be exceptional in this respect, as the diurnal cycle may be dominant and the phytoplankton thus change little in the course of a year (Ganf 1974a).

Plankton communities offer great possibilities for the study of succession as a general biological phenomenon, since the events in the successional sequence occur at a convenient pace for observation and study, but in only a few instances (e.g. Margalef 1958; Allen & Koonce 1973; De Amezaga, Goldman & Stull 1972) have these possibilities been exploited. The study of phytoplankton succession involves a number of technical problems that may partly account for the slow progress in this field. The taxonomic complexity of phytoplankton communities creates particular difficulties. If the species are separated carefully, frequently it is at the expense of proper attention to the construction of a supporting data base that would provide the physico-chemical and ancillary biological information to support a penetrating analysis. In addition, plankton succession occurs with sufficient speed that any meaningful picture of dynamics is lost if the sampling interval is much longer than a week. Finally, even the ideal data base is so complex as to require computer reduction in several stages. It is this last difficulty, in particular, which seems to have stopped the pioneering students of succession at the most basic levels of interpretation (e.g. Birge & Juday 1922; Ruttner 1930; Pearsall 1932).

The present study of phytoplankton dynamics in Lake Lanao, Philippines, attempts to minimize the common faults of data collection, and to emphasize the analytical rather than the descriptive potential of data on plankton succession.

STUDY SITE AND METHODS

The major features of Lake Lanao, on the island of Mindanao in the Philippines, have already been described (Lewis 1978a), but some additional details are relevant to the present analysis.

Lake Lanao becomes isothermal each year during the last part of the cool season (December–January). At other times the lake is thermally stratified, but the stratification differs from that in a temperate lake of comparable size. The epilimnion is extremely thick (20–40 m), and during periods of calm weather lasting from a few days to several weeks

the wind cannot mix the entire epilimnion (Lewis 1973). A second thermocline therefore develops at a depth of 12–25 m. The uppermost of the two epilimnetic compartments typically contains the entire euphotic zone.

Organic material moves by sedimentation and migration into the lower compartment of the epilimnion, where decomposition occurs rapidly due to the high temperature. Depletion of oxygen and accumulation of nutrients within the lower compartment is ultimately interrupted by wind stress and heat loss associated with storms. Remixing of the entire epilimnion, and in certain cases also a thickening of the original epilimnion, recharges the euphotic zone with nutrients, thus stimulating primary production (Lewis 1974). This mixing of chemically divergent layers during the stratification period, which I have referred to as 'atelomixis' (Lewis 1973), permits high productivity to persist on a low nutrient base, and is the dominant non-seasonal factor affecting energy flow.

The phytoplankton analysis is based on integrated samples taken at weekly intervals with a plastic tube (Lewis 1978a), and on weather data, nutrient chemistry, productivity (^{14}C), light penetration, and zooplankton abundance data obtained by methods described elsewhere (Lewis 1973, 1974, 1977a). Abundances of all seventy species (listed in Lewis 1978a) at mid-lake stations 1 and 2 in 45 m of water (Lewis 1978a) were averaged to obtain the abundance estimate for a given week. Such averages can be considered reasonably representative of the entire lake (Lewis 1978b). Since the species were counted according to pre-set statistical criteria (Lewis 1978a), the data are of approximately uniform quality for the thirty most abundant species, but of slowly declining quality due to lower counts for the other species. For the thirty most abundant species, the standard error for an abundance estimate in a given week for a given species is 15–20% of the mean; this takes into account analytical variance due to technique, replicate variance for samples taken at a single station, and station variance due to differences between two stations 1 km apart (Lewis 1978b).

ENVIRONMENTAL FACTORS AND THEIR ASSESSMENT

Growth control factors

As indicated in Fig. 1, three separate factors deserve consideration as important mechanisms controlling the growth of phytoplankton: nutrient availability, light availability, and metabolic rate as affected by temperature. Nutrient and light availability are in turn controlled by a number of operational factors, the importance of several of which has already been shown (Lewis 1974); these are marked with an asterisk in Fig. 1.

Nutrient availability

Nutrient availability is markedly influenced by change in mixing depth (z_m), which is defined here as the surface layer over which nutrients and gases are freely redistributed within a 24-h span. With a stable thermocline at 20 m, the lake may become calm at midday and effectively stop mixing except in the top metre; an afternoon breeze frequently causes free mixing over the top 20 m once again, however. In this case, z_m is considered to be 20 m.

The depth of the mixed layer each week was determined from thermal and oxygen profiles. Figure 2 shows the depth of the uppermost thermocline, which usually marks the bottom of the mixed layer, although the mixed layer may occasionally not extend to the

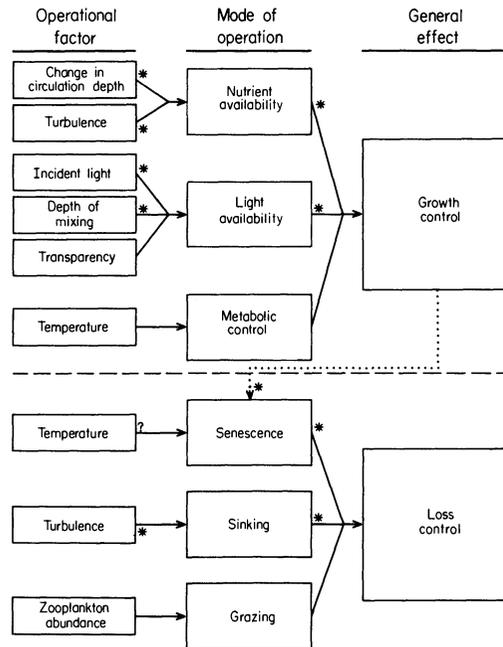
Phytoplankton succession in a tropical lake

FIG. 1. Diagram of the major factors controlling variations in phytoplankton biomass in Lake Lanao; feedback effects are not shown. Linkages considered to be the source of greatest variation are marked with an asterisk.

uppermost thermocline. Points below the mixed layer show considerable oxygen depletion. In Lake Lanao, respiration in the water column averages $3.4 \text{ mg C m}^{-3} \text{ h}^{-1}$ (95% limits over a year, $2.6\text{--}4.3 \text{ mg C m}^{-3} \text{ h}^{-1}$), so that in the absence of mixing the 24-h loss of oxygen below the euphotic zone would be *c.* 0.25 mg l^{-1} (Lewis 1974). Water layers showing oxygen concentrations $>0.25 \text{ mg l}^{-1}$ below saturation at mid-morning were thus considered to have been stagnant for more than 24 h. Similar corroborating deductions were made independently on the basis of uniformity in heat distribution in the upper water column.

A mixed layer may show oxygen concentrations below saturation if there has been a recent incorporation of anoxic water from below due to change in z_m . In this case, however, the mixed layer will be marked by uniformity in oxygen and thermal profiles, and this consideration overrides the oxygen depletion criterion in determination of z_m . Application of these techniques leaves very few ambiguous determinations of z_m for Lake Lanao.

The values of z_m for the week prior to each of the sixty-five plankton sampling dates form the basis of Fig. 3(e). From the z_m values, weekly change in z_m was calculated (Fig. 3(a)). Change in z_m is a critical factor in regulating nutrient supply. As long as z_m shows no change, which is the modal condition, nutrients that are incorporated into plankton biomass move from the mixed layer into the stagnant layer below, depleting the nutrient pool within the mixed layer. Increase in z_m thus represents improvement of nutrient supply by return of nutrients to the surface. The value of z_m may also decrease, of course, and this

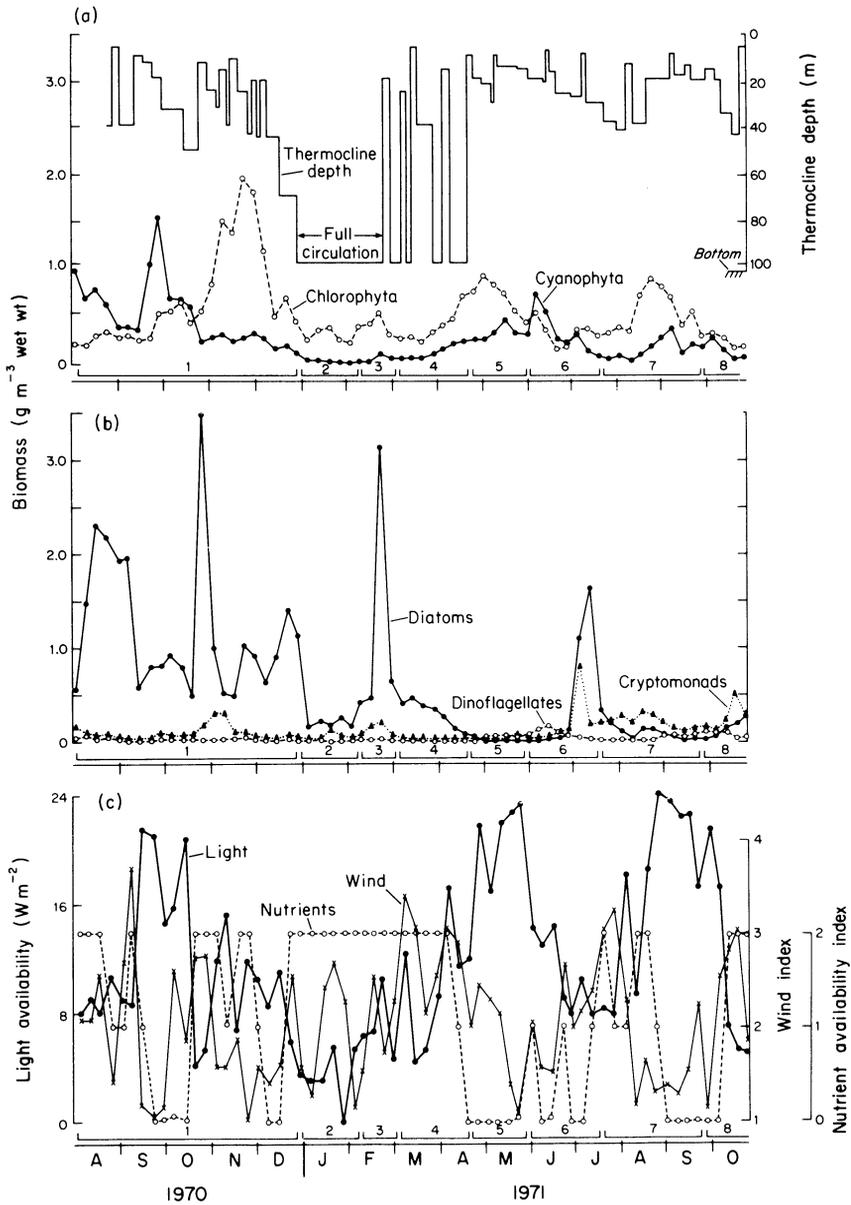


FIG. 2. Abundance of major phytoplankton groups in Lake Lanao over the study period, and values of some of the major environmental variables affecting their abundance; the numbers 1-8 along the abscissa refer to growth phases described in the text (p. 861-2). (a) Chlorophyta and Cyanophyta, with the depth of the uppermost thermocline superimposed; (b) diatoms, dinoflagellates and cryptomonads; (c) wind speed, nutrient-availability index and light availability (for methods of calculation, see text).

restricts nutrient supply by limiting the nutrient pool from which phytoplankton can draw, so that deficiencies occur more quickly. The value of z_m is never less than 12 m in Lake Lanao. As surface irradiance is usually reduced to 1% by 12–15 m depth, z_m is always equal to or greater than the thickness of the euphotic zone (z_{eu}). The modal value of z_m is only slightly greater than the average thickness of the euphotic zone, however (Fig. 3(e)).

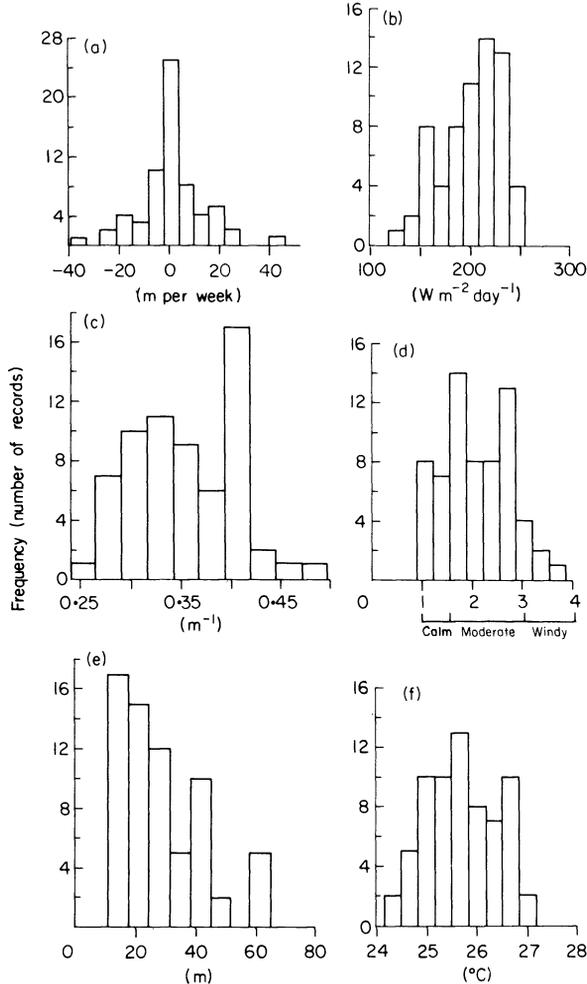


FIG. 3. Frequency distributions of weekly means of factors controlling phytoplankton growth in Lake Lanao over the study period. (a) Change in thickness of the mixed layer; (b) incident sunlight; (c) extinction coefficient, η ; (d) wind strength; (e) depth of the mixed layer, z_m ; (f) water temperature averaged between 1 and 15 m depth. The coefficients of variation of (a)–(f) are 20, 15, 14, 32, 48 and 3% respectively.

Turbulence also affects nutrient availability. Nutrient demand is unevenly distributed with depth, on account of the light optimum of photosynthesis. In a turbulent water column, nutrients are rapidly supplied to the zone of the light optimum from all parts of the mixed layer, but this is less true in a calm water column. Turbulence also facilitates nutrient uptake by renewing nutrient supply at sites of uptake on cell surfaces. This is the

presumed explanation for the increase in photosynthetic rates of phytoplankton in closed systems in response to turbulence (e.g. Ohle 1961; Pasciak & Gavis 1975).

Turbulence in the mixed layer is generated by wind, hence the average wind strength over a week is related to the degree of turbulence over the week. The frequency distribution of mean weekly wind strengths is shown in Fig. 3(d), and the pattern of changes over the study period appears in Fig. 2. The wind strengths are shown in the figures as arbitrary, linearly-scaled values between 1 and 4: in terms of actual wind velocities, 4 = 10 m s⁻¹ and 1 = 0 m s⁻¹.

In many lakes, nutrient input from the watershed is an additional factor affecting nutrient availability on a weekly basis. This is not the case for Lake Lanao, as the river water carries little more nutrient than the lake water into which it discharges (Lewis 1974), and the yearly river input is small relative to lake volume (flushing time = 6.5 years (Frey 1969)). River input is therefore disregarded here.

In order to quantify the mode of operation of the growth control factors, the boxes in the centre column of Fig. 1 must be represented in terms of some joint function of the relevant boxes in the left-hand column of Fig. 1. For nutrient availability, this is difficult. Concentrations of soluble nutrients at weekly or 2-weekly intervals are known over much of the study period (Lewis 1974), but direct use of these data to represent nutrient availability is not legitimate in view of the rapid changes in free nutrient levels during any given week. Nutrients added to the euphotic zone by deep mixing a few days prior to sampling may be removed by phytoplankton by the time samples are taken.

Nitrate-nitrogen frequently dropped below 1 µg l⁻¹, whereas reactive-phosphate and silicate were ordinarily not severely depleted (Lewis 1974). Nutrient limitation was therefore most likely to be caused by nitrogen depletion.

It is convenient to recognize three nutrient-availability states, based primarily on nitrate concentrations, and to assign each a number, as follows. Nitrate in the euphotic zone may be undetectable (< 1 µg l⁻¹ NO₃-N), present in trace amounts (*c.* 1 µg l⁻¹), or present in quantifiable concentrations (2–10 µg l⁻¹). These conditions are assigned nutrient-availability numbers (NA) of 0, 1 and 2 respectively. Since phytoplankton are capable of 'luxury consumption' of nutrients, nutrient availability to cells at a given instant is not always proportional to the concentration of soluble nutrient in the water (Eppley & Strickland 1968; Thomas 1970). This should not constitute a problem here, however, as the nutrient availability is judged on the basis of average concentration of soluble nutrients over a considerable period of time (7 days), and not at an instant in time. Since luxury consumption must be preceded by high concentrations of soluble nutrients in the water, average concentrations over a period of time should be related to average nutrient availability over the same period.

Continuous recordings of nutrient concentrations are obviously not available, but it is possible in Lake Lanao to estimate nutrient availability from depth of mixing (z_m) and change in depth of mixing (Δz_m) over a week interval. Comparisons of z_m and Δz_m with nitrate levels lead to the following conclusions.

(1) If $z_m > 40$ m, NA is always 2. this is explained by light limitation of photosynthesis due to deep mixing. Thus for the entire circulation period, except for brief periods of stability, NA = 2.

(2) If $\Delta z_m > 5$ m, then NA almost always reaches 2, but declines to 1 within a short period, usually 2–5 days, unless $z_m > 40$ m or unless there is another marked increase in z_m . The convention is adopted that NA for a given week should be assigned the value of 2 if

$\Delta z_m > 5$ m, even though the nitrate concentration by the end of the week when nutrient samples were taken had dropped below $2 \mu\text{g l}^{-1}$.

(3) If $\Delta z_m > 5$ m, generating an NA value of 2 for a given week, and if $z_m < 40$ m, then NA for the following week is assumed to be 1 unless a sample at the beginning of the week indicates that NA should be 0.

(4) High turbulence retards the decline of the NA value from 1 to 0 for longer periods following a high Δz_m . When wind strength is in the upper quartile (Fig. 3(d)), decline of NA from 2 to 0 following $\Delta z_m > 5$ m is assumed to occur over 2 weeks instead of 1 week unless nutrient data clearly indicate otherwise.

The above criteria are sufficient for assignment of an NA value of 0, 1, or 2 to each of the 65 weeks in the study (Fig. 2). Although this system is in appearance less precise than the raw nutrient concentration data, it provides a much more valid indication of availability of nutrients to cells and performs well in the analysis.

Light availability

Availability of radiant energy (referred to here as 'light') is the second major factor controlling phytoplankton growth. In Lake Lanao, variations in availability of light result from variations in incident light (I_0), depth of the mixed layer (z_m), and transparency.

Variation of incident light is less pronounced for Lake Lanao than for temperate lakes, but is nevertheless significant. Figure 3(b) shows the distribution of weekly means.

The depth of the mixed layer, which has already been discussed in connection with nutrient availability, varies between 12 and 60 m. On average, 99% of the incident light is absorbed in the upper 12 m, so the total range of variation in z_m represents an approximate 5-fold variation in availability of light. Inhibition of growth can therefore occur as a result of deep mixing even when the amount of incident light is high. This has been clearly demonstrated in a previous study (Lewis 1974).

Transparency is primarily affected by phytoplankton biomass. As indicated in Fig. 3(c), the vertical extinction coefficient for the 300–700 nm band varies between 0.25 and 0.48 (\ln units m^{-1}). These extremes correspond to 1% light levels at 18.4 and 9.6 m below the water surface.

Computation of light availability from the operational factors which affect it is not so difficult as computation of nutrient availability. The photosynthetically-available radiation (I_z) reaching any depth z is

$$I_z = I_0(0.95)(0.46)(\exp(-\eta z))$$

where I_0 is total irradiance, the two constants correct for reflectance and unusable wavelengths (Talling 1957), and η is the extinction coefficient for light (400–700 nm) in the water column. Over a week, if z_i is the depth of an individual cell at instant i , $E(z_i) \simeq z_m/2.0$, where z_m is the depth of the mixed layer and E indicates expectation. Thus the light to which an average cell is exposed is approximately

$$I_a = \frac{1}{z_m} \int_0^{z_m} I_z dz$$

The integral was evaluated numerically for each week and the results were expressed as $\text{W m}^{-2} \text{day}^{-1}$ (Fig. 2).

In addition to nutrients and light, temperature potentially affects metabolic rates and

thus growth (Fig. 1). Figure 3(f) shows the variation in mean temperature of the euphotic zone excluding the uppermost metre, where there is marked short-term change. The greatest thermal change in Lake Lanao occurs during seasonal mixing, which produces the values below 25 °C in Fig. 3(f). This seasonal thermal change is coincident with extreme light limitation caused by deep mixing, which must be considerably more important to the phytoplankton than the accompanying slight thermal change. At other times of the year the euphotic zone temperatures fall within a range of 2 °C.

The potential controlling role of temperature variation would appear to be much lower than in temperate lakes, as the range of variation is slight by comparison with variation of other factors. Productivity analysis confirms this supposition (Lewis 1974).

Loss control factors

The rate of loss of phytoplankton in Lake Lanao is obviously very great throughout the year, as biomass accumulations produced during periods of high productivity do not endure more than a few days (Fig. 4(a)). Mechanisms which control biomass loss are not so easy to separate as those which control growth. Losses must be attributed to grazing, sinking, and other unspecified factors, referred to in Fig. 1 as 'senescence.'

Grazing

The annual cycles of grazing zooplankton are shown in Fig. 4(b). Grazing zooplankton in the limnetic zone include two copepod species, seven rotifers, and three cladocerans (Lewis 1977a). All of the zooplankton groups to some degree reflect the changes in total autotroph biomass. Minimum zooplankton density occurred during the seasonal circulation when autotroph biomass was very low. Zooplankton density also climbed with major surges in phytoplankton biomass at various times of the year. This suggests that autotroph biomass exercises more control over zooplankton density than the reverse.

The contribution of the zooplankton to total rate of loss of autotroph biomass can be estimated by a method similar to that used in the analysis by Jassby & Goldman (1974) of grazing in Castle Lake, California. The method involved calculation of an upper limit on total volume of water filtered by the zooplankton, and comparison of this with the known loss rates of the phytoplankton. From a standard value for the conversion of wet biomass to dry biomass (11%, Sitaramaiah 1967) plus the abundance data and the individual weights, the total zooplankton biomass was calculated for each date. This total biomass value was then used in conjunction with an upper limit for filtration rates to determine the maximum possible loss of autotroph biomass. The upper limit used was 2000 ml per mg dry wt day⁻¹, as justified by Jassby & Goldman from the literature.

The results of the computations are given in Fig. 4(c) as the percentage loss per day to grazing, together with the net growth estimate for total autotroph biomass expressed in the same form. The grazing estimate is probably too high, because (1) the maximal filtration rates from the literature were used in the calculation, and (2) the zooplankton were assumed to exploit the food source in the euphotic zone continuously, when in fact many stages and species spend the day below the euphotic zone and only graze the more luxuriant upper layers at night.

Figure 4(c) shows that the maximum possible loss of autotrophs to grazing is always much less than the growth rate. The average replacement rate for autotroph biomass (i.e. net production divided by standing crop) is 80% per day, whereas the mean maximum possible loss to grazing is 6.8% per day. Loss mechanisms other than grazing are therefore

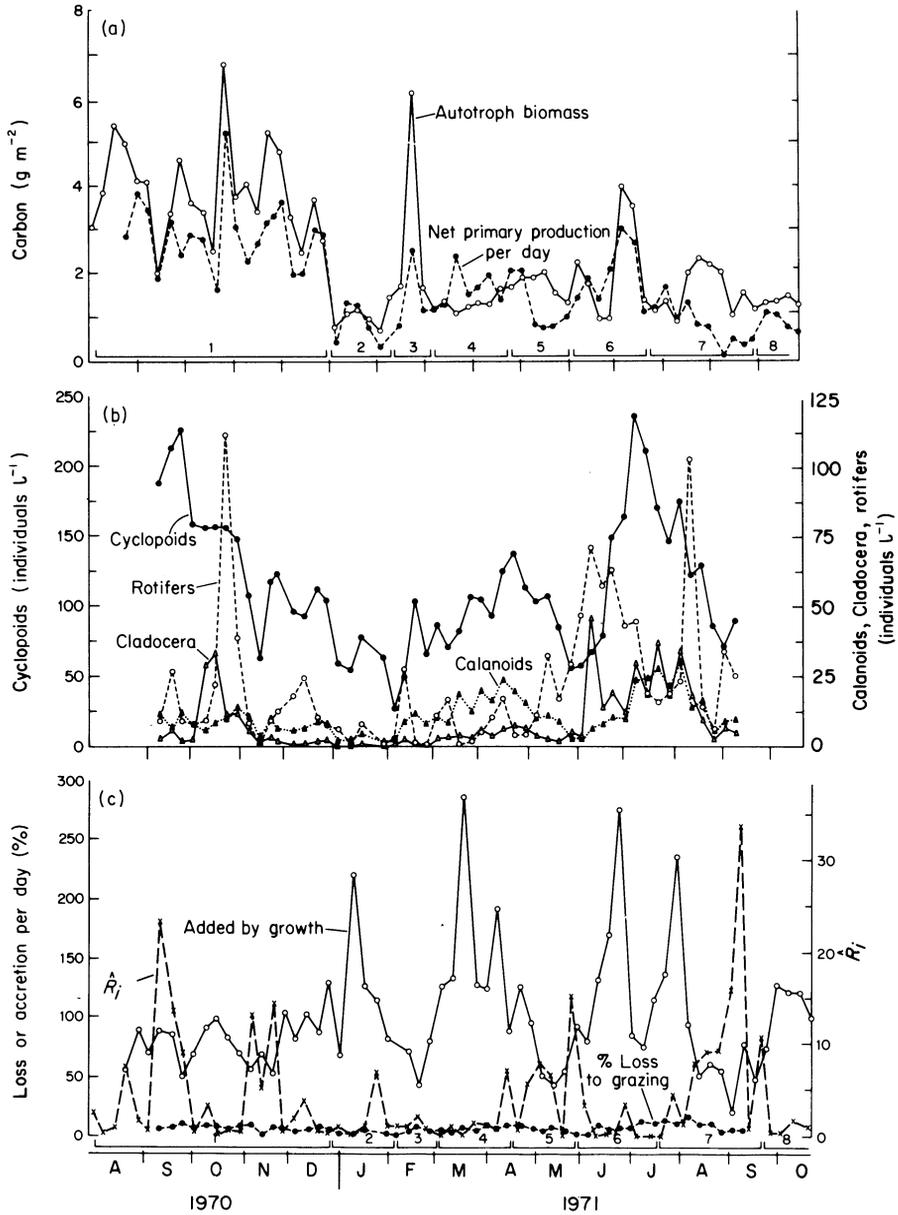


FIG. 4. Temporal changes in phytoplankton biomass and related variables in Lake Lanao over the study period; the numbers 1-8 along the abscissa refer to growth phases described in the text (p. 861-2). (a) Net primary production per day and autotroph biomass in the euphotic zone; (b) abundance of the major groups of grazing zooplankton; (c) replacement rate of autotroph biomass, estimated maximum possible loss to grazing, and mean Richardson Number (\bar{R}_i) for the euphotic zone.

more important in accounting for disappearance of autotrophs. A similar conclusion was reached by Jassby & Goldman (1974) for Castle Lake.

Although grazing does not repress autotroph biomass as a whole to any significant degree, it may affect succession if it is selective. A statistical study of succession rate (Lewis 1978c) showed that a small but identifiable portion of variation in succession rate is attributable to grazing.

Sinking

The importance of sinking as a mechanism of biomass loss is well documented. Sinking rate varies between species and between nutritional states of a single species (Hutchinson 1967; Smayda 1970). The principal environmental factor directly affecting sinking is turbulence, as indicated in Fig. 1.

Turbulence is controlled by wind speed (Figs. 2(c) and 3(d)), but the turbulence profile is also affected by the density profile of the upper water column. The relationship of the turbulence profile to wind speed and the density profile can be estimated from the Richardson Number, R_i .

$$R_i = g \left(\frac{1}{\rho} \frac{d\rho}{dz} \right) \left(\frac{du}{dz} \right)^{-2}$$

where g is acceleration due to gravity (981 cm sec^{-2}), ρ is density, z is depth, and u is current velocity. The development and significance of R_i are reviewed by Mortimer (1974).

The approach adopted here was similar to that of Ganf (1974b), who estimated the Richardson Number for Lake George, Uganda, as an indication of the role of turbulence in plankton distribution. It should be stressed that, although the computations are based on the Richardson Number, they do not produce a reliable estimate of true instantaneous R_i , for reasons to be given below.

Use of the formula for R_i requires data on the vertical density gradients and vertical (current) velocity gradients in the water column. The density gradients are easily derived from the temperature gradients. The current velocity gradients were not measured directly but were estimated as follows. (i) The assumption was made that surface current velocity (u_0) averages 2% of the mean wind velocity (W) (Hutchinson 1957a). (ii) The current-velocity profile was assumed to decrease exponentially within the mixed layer at such a rate that the current velocity at 15 m depth was one-tenth that of the surface current. Although decline of current velocity with depth is not always regular, this rule of computation is roughly representative of conditions in lakes of moderate size as summarized by Hutchinson (1957a). The relationship of surface current to currents at other depths is thus $u_z = u_0 e^{-0.153z}$, where z is the depth in metres. (iii) From assumptions (i) and (ii), the current at any depth z was calculated as: $u_z = 0.02 W e^{-0.153z}$, where the velocities are in cm s^{-1} and the depth is in metres.

From the density and velocity profiles, the values of \hat{R}_i in successive layers 2 m thick were calculated for each week in the year. The wind strength inserted in the formula was a mean for the week, and the density profile was that obtained at the end of the week. The value of $d\rho dz^{-1}$ was approximated by $\Delta\rho\Delta z^{-1}$ over a layer 2 m thick, and a similar approximation was made for $du dz^{-1}$. A mean value of \hat{R}_i was then obtained for each date by averaging the individual \hat{R}_i values from the surface to the bottom of the euphotic zone (15 m). These mean values of \hat{R}_i are given in Figs. 4(c) and 5(b).

The procedure by which \hat{R}_i values were obtained would clearly be inadequate for exacting studies of lake hydrodynamics. Estimation of the current velocity profile from wind, and use of a mean weekly wind value for computing surface current velocity are major sources of inaccuracy. Nevertheless, the R_i values computed in this way permit rational ranking of weeks on the basis of turbulence in the euphotic zone, since the computation is properly based on wind strength and density profile. This is sufficient for present purposes.

True values of R_i below 0.25 indicate significant growth of turbulence, whereas high values of R_i indicate negligible turbulence. The very lowest values occur when the density profile is nearly uniform, and under such conditions the approximation used here will produce good estimates of R_i , as the velocity profile becomes unimportant in the computation. Of the sixty-five weekly mean R_i estimates, fourteen were < 0.25 . Values of $R_i > 1$ indicate negligible turbulence (Ganf 1974b). Of the sixty-five values, forty-one exceed 1.0, although the computations are less trustworthy in these cases. The paucity of very low values of R_i is surprising, and suggests that sinking due to lack of turbulence could be a major influence in the community.

Although sinking may be a very important aspect of phytoplankton loss, it cannot account for the massive losses implied by the high turnover of biomass (annual average 1.24 days, $n=61$ (Lewis 1974)). This is particularly clear from vertical profiles of autotroph biomass taken in calm weather (Lewis 1978b). Amounts of phytoplankton biomass in deep water under such conditions are very small, which is not compatible with the hypothesis that the massive losses are accounted for mainly by sinking. As it has also been demonstrated that grazing accounts for only a small loss, some third factor or complex of factors must be operating. Figure 1 refers to this unknown factor as 'senescence'.

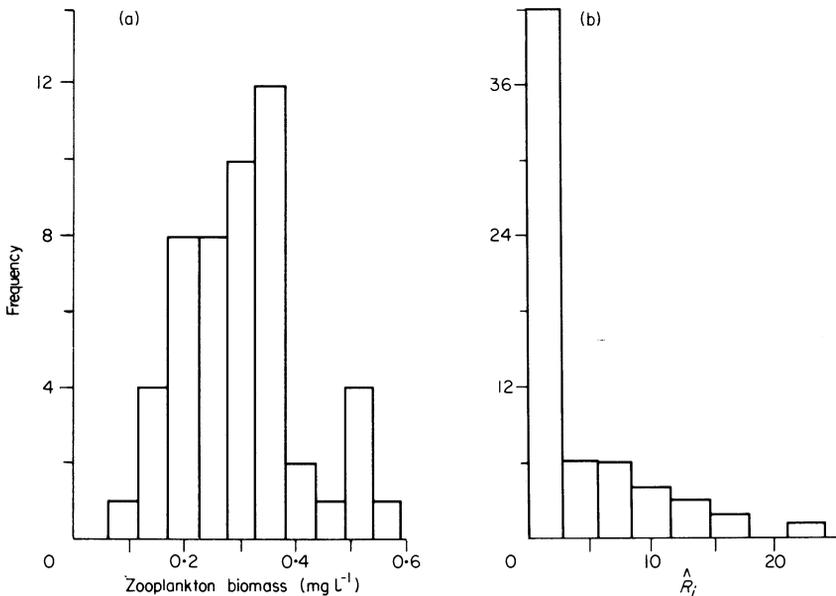


FIG. 5. Frequency distributions of weekly means of factors affecting loss of phytoplankton biomass. (a) Wet biomass of herbivorous zooplankton (mean for the entire water column, 0–4.5 m); (b) mean value of the Richardson Number, \hat{R}_i , in the euphotic zone. The coefficients of variation are 35 and 155% respectively.

Decomposition of dead cells must occur very rapidly, as very little detritus and few dead organisms are observed in the euphotic zone. Skeletal parts (e.g. frustules) are almost always visible among living cells, but not in large numbers. Phytoplankton die for unspecified reasons, perhaps in part through disease (Canter & Lund 1953; Shilo 1971). By analogy with terrestrial autotrophs, for which mechanisms behind such mortality are better known, it is postulated in Fig. 1 that this undescribed mortality is intimately related to the nutritional state of the population in question, that is, to growth control mechanisms.

TEMPORAL CHANGES IN TOTAL AUTOTROPH BIOMASS

The weekly changes of total phytoplankton biomass in Lake Lanao are illustrated in Fig. 4, together with the concurrent changes in net primary production. The correspondence between biomass and primary production is remarkably close (linear correlation, $r=0.77$, $P<0.01$). As the estimates were entirely independent methodologically, this close relationship inspires confidence in both estimates. The turnover of autotroph biomass is so rapid that even minor changes in primary production are quickly mirrored in the biomass of phytoplankton.

Biomass of phytoplankton at any fixed instant is determined by the balance between growth and loss rates. In Lake Lanao, net primary production has the greatest influence on the temporal pattern of autotroph biomass (Fig. 4(a)). The loss rate, although substantial in magnitude, is almost strictly proportional to biomass. A more independent loss rate, such as that which might be caused by grazing under some circumstances, would tend to uncouple primary production and biomass.

The study period can be divided into eight time intervals that are separated by shifts in growth control factors (Figs. 2 and 4). Analysis of these factors (Lewis 1974) has shown that phytoplankton growth is affected primarily by limitations on nutrients (mainly N) and light. The shifts in controlling factors and their relevance to total autotroph biomass can be summarized as follows.

Period 1. From August to December 1970, biomass was high due to sustained high primary production. Decreases in both production and biomass were caused by temporary nutrient depletion during calm weather. Enrichment of the euphotic zone by atelomixis occurred frequently during storms, which caused biomass and production always to increase again before falling to very low levels.

Period 2. Seasonal cooling caused a complete breakdown of stratification in late December. This charged the euphotic zone with nutrients, but the instability of the water column prevented biomass accumulation near the surface, and caused overall light limitation by allowing movement of the phytoplankton to great depths.

Period 3. The dramatic increase of production and autotroph biomass in February did not signal the end of the full circulation, but rather the onset of a short period of very calm weather during which the light limitation imposed on autotrophs by their continual removal from the surface was temporarily relieved. This calm period was too short to lead to the establishment of a new seasonal thermocline. The increase in autotroph biomass thus terminated when winds once again agitated the water column and re-established a severe light limitation.

Period 4. Instability of the water column continued into March and early April. The

end of this period was marked by transient stratification and brief peaks in primary production when the weather was calm.

Period 5. Nutrient depletion resulted from calm weather and the establishment of a stable, high-lying thermocline.

Period 6. Repression of phytoplankton growth by nutrient depletion was reversed in Period 6 by a series of storms, leading to atelomixis and a consequent rise in production and autotroph biomass.

Periods 7 and 8. Period 7 was similar to Period 5, as production was severely limited by nutrient depletion during calm weather. Period 8 recapitulated the events of Period 6.

In summary, phytoplankton growth was severely limited by light during Periods 2 and 4 and by nutrients during periods 5 and 7. Periods 1, 3, 6 and 8 were most favourable for growth, and were therefore marked by increasing autotroph biomass. Figure 4(a) shows that the close correspondence between biomass and primary production persists whether conditions for autotroph growth are optimal or very poor, and whether the principal limiting factor is light or nutrients.

SUCCESSION AT THE CLASS OR DIVISION LEVEL

Five major taxonomic groups at the class or division level contribute to the Lake Lanao phytoplankton. The abundances of these groups over the study period are illustrated in Fig. 2. A statistical analysis of abundances (Lewis 1977b) has shown that species within divisions are ecologically more similar than species chosen at random, and this provides a rationale for considering broad successional changes at the division level before proceeding to the analysis of individual species.

Figure 2 shows some definite patterns in the abundance of certain phytoplankton groups in relation to the depth of the mixed layer, which is related both to nutrient availability and light availability, as explained previously. Diatom peaks coincide almost perfectly with marked depressions of the thermocline, except during seasonal circulation. This is particularly clear in Period 1, where three separate episodes of thermocline depression are documented. Not only are the occurrences of diatom peaks coincident with deep mixing, but the duration of deep mixing seems to control the duration of the peaks. Talling (1966) has documented a similar pattern in Lake Victoria. When the thermocline disappears entirely, however, diatom growth is suppressed by light limitation, as is the growth of other groups.

Figure 2 shows that dominant diatoms of Lake Lanao grow rapidly only when the mixed layer is 25–50 m thick. When the mixed layer is 25–50 m thick, nutrients are generally available and turbulence is high. Turbulence and nutrient availability are difficult to separate, as they are strongly correlated in Lake Lanao. Inability of the Lanao diatoms to persist in calm weather may thus be due to their poor tolerance of low nutrient levels, to their rapid sinking rates, or to less obvious but correlated conditions. These distinctions are best made at the species level.

The growth pulses of blue-green and green algae also show some clear, but more complicated, relationships to depth of mixing. Both groups decline when conditions are favourable for diatom growth, i.e. during periods of deep mixing. Maxima occur when the mixed layer is thin, but the maxima are not coincident for the two groups. Blue-green algae appear to increase when nutrient depletion is pronounced, and green algae under less severe conditions (Fig. 2). The establishment of a high thermocline following nutrient

enrichment thus leads to marked growth of green algae, followed by a pulse of blue-green algae, as in Periods 4-5-6 and in Period 7 (Fig. 2). Pulses in Period 1 are more difficult to interpret. The green algae increased toward its end when intermittent instability of the upper water column prevented severe nutrient depletion. The maximum of blue-green algae in the middle of Period 1 is expected, but should have been preceded by a pulse of green algae if these really occupy an intermediate position in succession between diatoms and blue-green algae. The green algae of Lake Lanao increase slowly, however, and rapid nutrient depletion resulting from massive diatom growth early in Period 1 could have shortened the favourable period for growth to such an extent that the pulse of green algae did not occur.

The dinoflagellates and cryptomonads, though less abundant than the other three groups in terms of average biomass, are at times quantitatively important. High biomass of cryptomonads occurred only at times suitable for diatom pulses, as in Periods 1, 3 and 6 of Fig. 2. The dinoflagellates produced high biomass only during early Period 6, when nutrient depletion was more severe than at any other time during the study period.

On the whole, the interpretation of major pulses of the five phytoplankton groups is surprisingly straightforward. Division of niche space between major groups is summarized schematically in Fig. 6. A successional shift from one major group to another occurs as a result of a shift in controlling factors along one of the two axes shown in the figure. In a diagrammatically simple sequence during stratification, nutrient renewal by atelomixis would generate conditions falling within the diatom space in Fig. 6. Subsequent calm weather would result in more superficial mixing and incipient nutrient depletion, causing an evolution into the space occupied by green algae. Complete nutrient depletion would bring the habitat into the space occupied by blue-green algae, and thence to the dinoflagellate space. Usually this sequence is interrupted, or some portion of it is temporally contracted, so that it does not appear so prominently as expected.

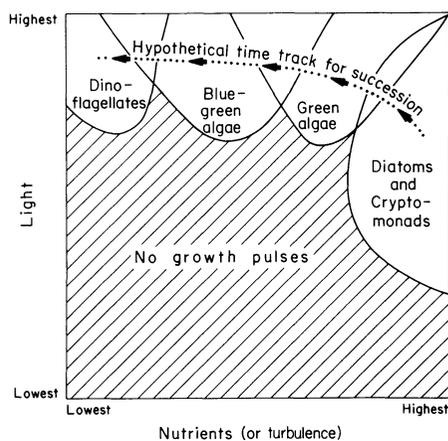


FIG. 6. Diagrammatic representation of the division of niche space between the major groups of phytoplankton in Lake Lanao, as deduced from the conditions under which growth pulses occur.

The above discussion applies specifically to growth pulses for major phytoplankton groups. As a great deal of the annual production is accounted for by these growth pulses, the merit of such an approach seems great. There is another possible analytical scheme, however, by which a different kind of insight may be achieved. If the phytoplankton

groups are compared statistically, their abundances may prove to be in some cases highly correlated and in other cases virtually independent, and ecological affinities can be judged on this basis. This approach differs from the previous analysis in that growth pulses are assigned no special significance in the statistical comparison. It is therefore possible for taxa whose pulses are coincident to correlate poorly in general if their resistance to unfavourable conditions differs substantially.

Table 1 gives correlation data for the major phytoplankton groups. The values in the table are Spearman rank correlation coefficients ($n=65$). Pearson product-moment coefficients were not used because several different kinds of transformations would have been required to normalize the data, and hence a uniform application of the non-parametric correlation is simpler to interpret. Above the diagonal in Table 1, the biomass of each group (B) is compared with the biomass of other groups over a 65-week period (the \mathbf{B} matrix). Below the diagonal, the rate of change in biomass ($\Delta B/\Delta t$) of each group is compared with rate of change in all others for successive 1-week periods (the $\Delta\mathbf{B}$ matrix). The \mathbf{B} matrix, above the diagonal, has the greatest descriptive power insofar as it represents the temporal coincidence in abundance of the groups. The analytical power of the \mathbf{B} matrix is limited, however, by the direct dependence of the biomass for a given week on the biomass of the previous week. The biomass value for any given week integrates back through time to an indefinite and variable extent, which means that it is a poor basis on which to judge the comparative growth response of algal groups to conditions prevailing over specific intervals of 1 week. For this purpose, the $\Delta\mathbf{B}$ matrix below the diagonal is more useful, as it shows the overall response of a group to growth and loss factors affecting the population over a specific interval of 1 week. The focus of interpretation should thus be on the correlations of the $\Delta\mathbf{B}$ matrix, but in some cases it will be useful to compare these with values from the \mathbf{B} matrix as well.

TABLE 1. Values of the Spearman rank correlation coefficient for pairwise comparisons of biomass (above the diagonal) and rate of change in biomass (below the diagonal) between major phytoplankton groups in Lake Lanao

	Diatoms	Green algae	Blue-green algae	Cryptomonads	Dinoflagellates
Diatoms		-0.02	0.18	0.05	-0.07
Green algae	0.26*		0.27*	0.03	-0.04
Blue-green algae	0.11	0.53*		-0.07	0.49*
Cryptomonads	0.17	0.39*	0.11		0.32*
Dinoflagellates	0.11	0.16	0.24*	0.07	

* Significant at $\alpha=0.05$

For diatoms, B is not significantly correlated with B of any other group, but ΔB for diatoms is significantly correlated with ΔB for green algae. The latter relationship fits well with the observed relationship between pulses of diatoms and green algae (Fig. 6): the green algae follow the diatoms closely in a successional sequence after nutrient enrichment, and the overlap is expressed by the correlation of biomass change in the two groups. That this is only an overlap in optima and not a coincidence of trends is indicated by the lack of significant correlation in B values.

For blue-green and green algae, the significant correlations in Table 1 also correspond with the interpretations of growth pulses as shown in Fig. 6. The correlation of ΔB values is quite high, and even the B values are significantly correlated. The green and blue-green

algae thus appear to be closer ecologically than the diatoms and green algae in Lake Lanao.

The successional sequence of Fig. 6 leads from blue-green algae to dinoflagellates, and hence a significant ΔB correlation between these two groups would also be expected, and does appear in Table 1.

For the three most important groups in terms of numbers or biomass (diatoms, green algae and blue-green algae), significant correlations in ΔB occur if and only if the groups being compared are adjacent in the successional sequence shown in Fig. 6. The general validity of the sequence formulated from pulse analysis is thus supported by the correlation analysis. The two minor groups, dinoflagellates and cryptomonads, do not fit the scheme quite so neatly, but are not really divergent from it. From the pulse analysis, cryptomonads would be expected to be correlated with diatoms, whereas in fact they are correlated only with green algae, which are adjacent to diatoms in the successional sequence. Pulse analysis is not easy for this group as biomass seldom reaches high levels; pulses that do occur are definitely coincident with diatom pulses, but not all diatom pulses are accompanied by significant rises in cryptomonad biomass (Fig. 2). The change in day-to-day biomass level, which in this group is much more important in determining annual mean biomass than are growth pulses, is more closely allied with changes in abundance of green algae. Cryptomonads thus occupy a successional border area between diatoms and green algae, which is in fact compatible with Fig. 6.

Dinoflagellates also present a slight interpretative problem. Abundance change (ΔB) of this group is strongly correlated with that of blue-green algae, as might be expected from its proposed position in the successional sequence (Fig. 6). Unexpectedly, the dinoflagellates also correlate with the cryptomonads. The correlation is limited to B and does not extend to ΔB , however. This suggests that the significant correlation is produced spuriously as a by-product of the common and steady rarity of these two groups, and not by any strong ecological affinities, which should be expressed as a positive relation in the ΔB values.

All of the significant correlations in Table 1 are positive. Although one group may compete best under specified circumstances and, when those circumstances prevail, usurp most of the resources, the competitive effect is not sufficiently strong to cause decline in the less well-adapted groups.

A general successional sequence passing from diatoms to green algae and then to blue-green algae in temperate lakes was recognized long ago (Pearsall 1932), and appears to be widely accepted, although much of the evidence is non-quantitative. In the temperate zone, the general pattern seems to apply equally well to very large lakes (Schelske & Stoermer 1972; Schelske *et al.* 1972) and very fertile lakes (e.g. Bush & Welch 1972). Dinoflagellates logically fit at the end of this successional sequence because of their nutritional flexibility, and perhaps also because of their motility (Hutchinson 1967).

The shift from diatoms to green algae in many lakes results from silicon depletion (Lund 1950; Lund, Mackereth & Mortimer 1963; Schelske & Stoermer 1971). In at least some lakes, however, the relationship between diatom growth and silicon availability is not so straightforward (Bailey-Watts 1976). In Lake Lanao, silicon concentration remains sufficiently high for other nutrients and turbulence to be implicated rather than silicon (Lewis 1974). The shift from green algae to blue-green algae generally follows nutrient depletion in temperate lakes, but the exact mechanism is still controversial. The most straightforward hypothesis, which would be highly applicable to Lake Lanao, is that the nitrogen-fixing capability of some blue-green algae gives them an advantage when

nitrogen sources are depleted (Lund 1965; Hutchinson 1967; Horne *et al.* 1972). This hypothesis does not explain the success of species not capable of fixing nitrogen, so that other group properties such as buoyancy regulation (Reynolds & Walsby 1975) or carbon uptake ability (Shapiro 1973) may be involved as well.

In summary, it has been possible to demonstrate quantitatively by pulse analysis and correlation analysis the existence of a successional sequence at the division and class level in the Lake Lanao phytoplankton. This sequence is essentially the same as that which occurs commonly in temperate lakes, and appears to be related primarily to gradients of nutrients and light. Absence of seasonal temperature cycles, which have been considered as one possible determinant of successional sequences in temperate lakes (Lund 1965; Hutchinson 1967) does not lead to the development of a notably different successional sequence in this tropical lake.

SUCCESSION AT THE SPECIES LEVEL

Figure 7 shows the seasonal patterns for eight of the most abundant phytoplankton species. Analysis of the trends in these and other species requires the identification of environmental factors that play important roles in succession, and the positioning of the growth optima of the individual species along gradients of these factors.

Identification of growth optima of individual species

Those weeks when the increase of individual species was optimal were identified, and related to environmental factors as follows.

(i) Time-periods favourable for the growth of each species were identified by use of a threshold criterion. By definition, favourable periods for a given species i must be accompanied by positive values of $db_i dt^{-1}$, where b_i is the biomass per unit surface area of the species. Empirically, all values of $\Delta b_i \Delta t^{-1}$ (with $\Delta t = 1$ week) exceeding 1.6 were considered to correspond with conditions favourable for the growth of a species. The choice of 1.6 as a threshold value is somewhat arbitrary, but higher values of $\Delta b_i \Delta t^{-1}$ occur so infrequently that the statistical information on the corresponding time-periods is too sketchy, whilst values of $\Delta b_i \Delta t^{-1}$ closer to 1.0 are difficult to discriminate statistically from a true steady state (1.0) or a slightly declining population. Values exceeding 1.6 were not admitted as real unless the number of counting units upon which Δb_i was based exceeded 18 per ml; this restriction is based on counting statistics (Lewis 1978b). Among the twenty-seven species used in the analysis, the mean number of weeks on which $\Delta b_i \Delta t^{-1} \geq 1.6$ was 9.4, or 14% of the sampling periods.

(ii) The environmental factors were tested for evidence of relationship to high values of $\Delta b_i \Delta t^{-1}$ in each species. If for the i th species, the number of weeks on which the value of $\Delta b_i \Delta t^{-1}$ meets the criteria described in (i) above is n_i , then it is possible to compute $\text{Var}(X_k, n_i)$ over the n_i dates, where X_k is a measure of the k th environmental variable. The value of $\text{Var}(X_k, 65)$ over all 65 weeks can also be computed. A statistic of the same form as the standard F statistic results:

$$F'_{n_i, 65} = \text{Var}(X_k, n_i) / \text{Var}(X_k, 65)$$

The theoretical frequency distribution of $F'_{n_i, 65}$ is not known, however.

(iii) The frequency distribution of $F'_{n_i, 65}$ was determined for all of the pertinent values

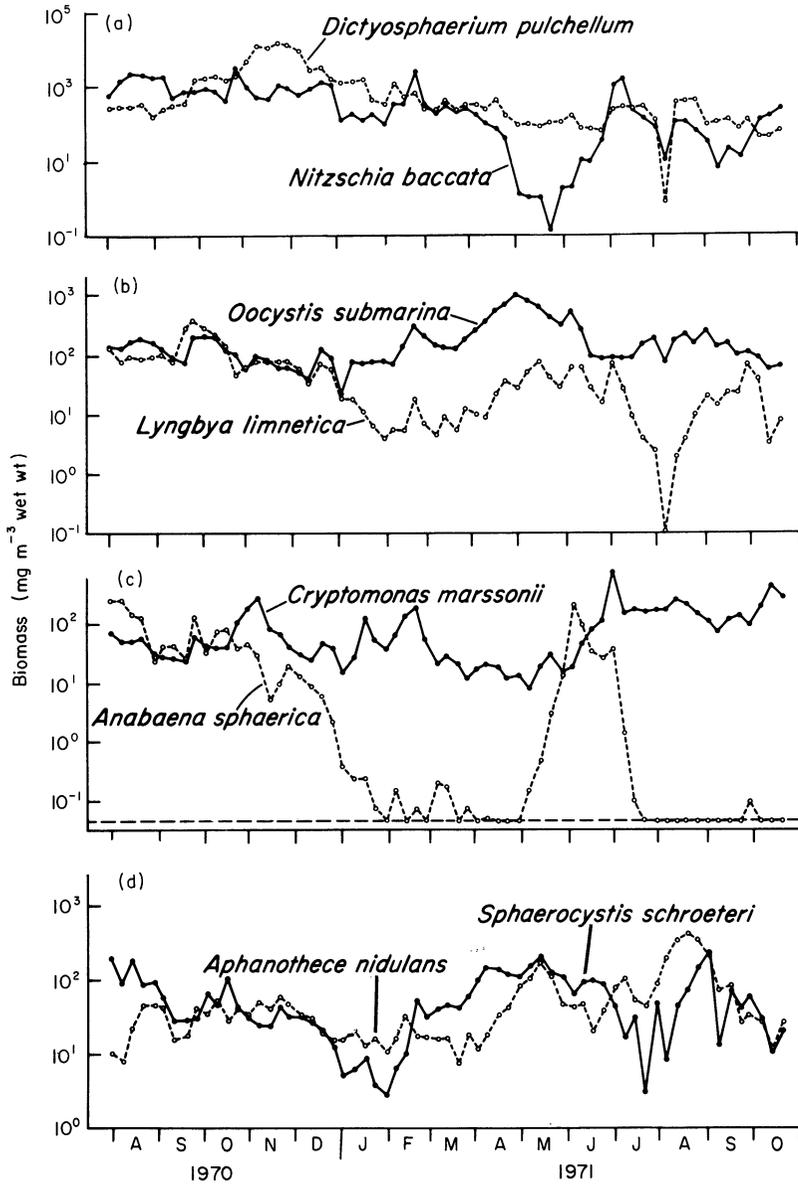


FIG. 7. Changes in biomass of the eight most abundant phytoplankton species in Lake Lanao over the study period. In (c) the pecked line indicates the detection limit of *Anabaena*.

of n_i (which range from 4 to 16) by use of a Fortran random-number generator, which selected, without replacement, a subgroup of size n_i from the sixty-five sample dates. The mean value of X_k was computed for each of the n_i dates thus selected, and from this the value of $F'_{n_i, 65}$ was computed. This process was repeated to generate frequency distributions of $F'_{n_i, 65}$ for all values of n_i and all operational variables (X_k).

(iv) The hypothesis was formulated that if factor k is important in controlling growth of species i , then occasions on which the value of $\Delta b_i \Delta t^{-1} \geq 1.6$ should be typified by a narrow range of values for X_k . That is, the value of $F'_{n_i, 65}$ under such circumstances should be smaller than could be explained by chance alone. The values of $F'_{n_i, 65}$ were thus computed for all twenty-seven species, and the values were compared with the frequency distributions of $F'_{n_i, 65}$ generated by random choice of the n_i dates.

Significance of growth control factors

For operational growth control factors (Fig. 1), the sample values of $F'_{n_i, 65}$ proved to be significant at $\alpha=0.05$ for an average of 5% of the species, regardless of the identity of the factor being tested. At the 5% probability level used, this is exactly what would be expected if none of the individual operational factors had any effect as determinants of biotic variation. This finding is reasonable ecologically, insofar as the operational factors affecting growth act in an interdependent, non-linear fashion. For this reason, successful growth models (e.g. Riley 1946; Riley, Stommel & Bumpus 1949) quantitatively interpret operational factors in terms of their mode of operation (Fig. 1), and only then attempt to predict growth and loss. Clearly the analysis of succession must proceed similarly.

The values of $F'_{n_i, 65}$ for nutrient and light availability, computed from the operational factors as already described, proved to be significant in 19% of the test cases. This is a substantial improvement over the 5% figure for unaltered operational factors. Although one might expect the 19% figure to be even higher for these two factors, their joint distribution does facilitate a good separation of species, as shown in Fig. 8. One reason for the relatively low percentage of significance is the fineness with which the species are tuned to the plankton environment, which by comparison makes the environmental data seem rather crude. Also the statistical test would be more powerful if the number of cases in which the $\Delta b_i \Delta t^{-1}$ criterion is met were greater. Obviously data covering 600 weeks would provide much better resolution than data covering 65 weeks.

Figure 8(a) shows the means of light and nutrient availability for the individual phytoplankton species. Means were computed for the i th species from the n_i dates on which $\Delta b_i \Delta t^{-1} \geq 1.6$. Figure 8 thus indicates the division of the habitat through time on the basis of sunlight and nutrients. The arrangement of species by taxonomic group is remarkably similar to that shown in Fig. 6, which was derived by a different method. For comparison, Fig. 8(b) shows envelope lines containing 95% of the means generated by random choice of n_i weeks (without replacement) from the 65 weeks of the study. Lines for $n_i=4, 8, 12$ and 16 are shown. (The mean value of n_i for the species in Fig. 8(a) is 9.4.)

Segregation of taxa is relatively clear in the nutrient-poor, light-rich portion of the spectrum. The dinoflagellate is a specialist, thriving under conditions of extreme nutrient poverty. Blue-green algae, with the exception of *Dactylococcopsis fascicularis*, do well under rather extreme conditions, and clearly succeed at times when the Chlorophyta cannot.

At higher nutrient levels in Fig. 8, species are more numerous and less clearly grouped. This is reasonable insofar as a combination of light and nutrient levels that is more

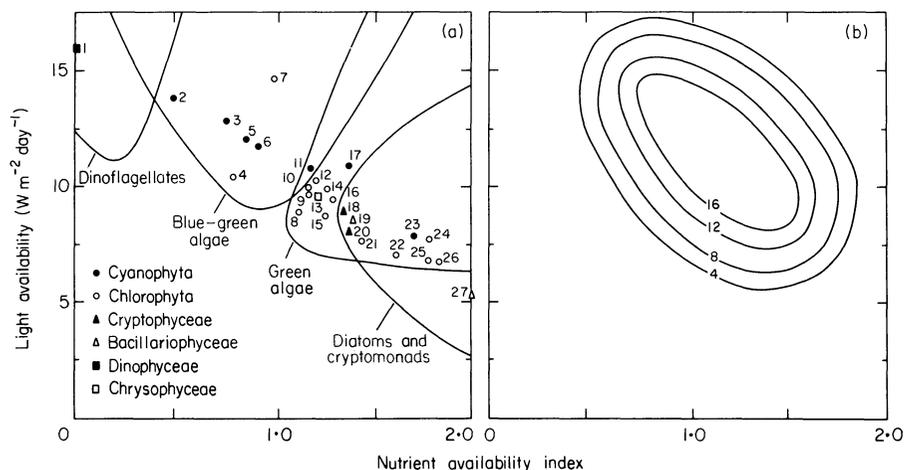


FIG. 8. (a) Positions of twenty-seven of the most abundant phytoplankton species in Lake Lanao along gradients of the two major growth control factors (nutrient availability and light availability). (b) Envelope lines containing 95% of the means for n_i samples selected by random sampling (without replacement) from the sixty-five dates on which phytoplankton samples were taken. Key to species (listed by genus if only one species is present): 1 = *Gymnodinium*, 2 = *Anabaena sphaerica*, 3 = *A. spiroides*, 4 = *Sphaerocystis*, 5 = *Lyngbya*, 6 = *Chroococcus*, 7 = *Selenastrum* sp. 1, 8 = *Oocystis submarina*, 9 = *Chodatella* sp. 1, 10 = *Ankistrodesmus setigerus*, 11 = *Dactylococcopsis wolterecki*, 12 = *Chodatella subsalsa*, 13 = *Chromulina*, 14 = *Oocystis lacustris*, 15 = *Tetraedron*, 16 = *Dimorphococcus*, 17 = *Aphanothece*, 18 = *Rhodomonas*, 19 = *Nitzschia baccata*, 20 = *Cryptomonas*, 21 = *Dictyosphaerium*, 22 = *Scenedesmus* sp. 1, 23 = *Dactylococcopsis fascicularis*, 24 = *Kirchneriella elongata*, 25 = *Coelastrum*, 26 = *Scenedesmus ecornis*, 27 = *Melosira granulata*.

generally optimal for photosynthesis would presumably lead to more intense biotic pressures, and consequent reduction of niche dimensions. The Chlorophyta first appear adjacent to the blue-green algae, but span an extensive range of conditions bounded by some apparently critical nutrient availability. The two cryptomonads and *Nitzschia* are closely grouped, and overlap with the chlorophytes in the region of high nutrient availability. *Melosira* occupies a distinct position, and is not allied ecologically to other species.

The general light requirements of the major taxa are difficult to sift from the literature. The model of Lehman, Botkin & Likens (1975) utilizes light optima for the major taxa based on a literature review. The order of major groups along the light axis of Fig. 8(a) for Lake Lanao does not accord with the I_{opt} relationships used for this model, however. This discrepancy may in part be due to the coupling of nutrient and light availability in nature, where these two factors frequently show a negative correlation (Fig. 2(c)). This negative correlation in effect prevents any group from simultaneously exploiting optima of the two factors.

The grouping of species in Fig. 8 is the same as would be expected from the class-level analysis of succession focusing on dominants. It is clear, however, that there is a considerable scatter of species within taxa, and that certain species are nonconformist.

Significance of loss control factors

The foregoing analysis has positioned individual species with respect to niche dimensions related to growth control. A similar and complementary approach is possible using

niche dimensions related to control of biomass loss (Fig. 1). Grazing intensity is approximated by zooplankton abundance, and sinking rate by the Richardson Number estimate outlined previously. Senescence, the indefinite third factor directly affecting loss, is not considered, as it cannot be adequately quantified. The effects of senescence on succession should be largely merged into the growth control analysis, however, if the proposed linkage between this variable and growth control mechanisms does exist (Fig. 1).

A total of 20% of the species showed significant values of $F'_{ni, 65}$ based on \hat{R}_i (sinking rate), but only 3% were significant based on herbivore biomass (grazing loss). The suspected importance of sinking rate as a factor in succession is thus supported. The failure of grazing intensity as a criterion for localizing growth optima of species in the annual successional sequence does not imply complete non-significance of grazing as a factor in succession; two other multivariate statistical studies (Lewis 1977c, 1978c) have shown that grazing contributes to succession, but that its effect is clearly subordinate to other effects. The low number of significant $F'_{ni, 65}$ values for individual species is due to the small range of variation in grazing intensities over the year in Lake Lanao (Fig. 5(a)), and to the small percentage of autotroph biomass that is lost to grazing. The effect of grazing is sufficiently great to be detected easily when statistical tests are made for all species, but not so when the attempt is made to position individual species with certainty on the grazing gradient.

Figure 9(a) shows the joint distribution of species with respect to sinking and grazing. As with the similar growth control plot, there is a remarkably clear arrangement of species by taxon. The arrangement is in this case dictated mainly by the position of species on the gradient of sinking rates (\hat{R}_i), as would be expected from the weakness of grazing intensity as a positioning criterion for individual species.

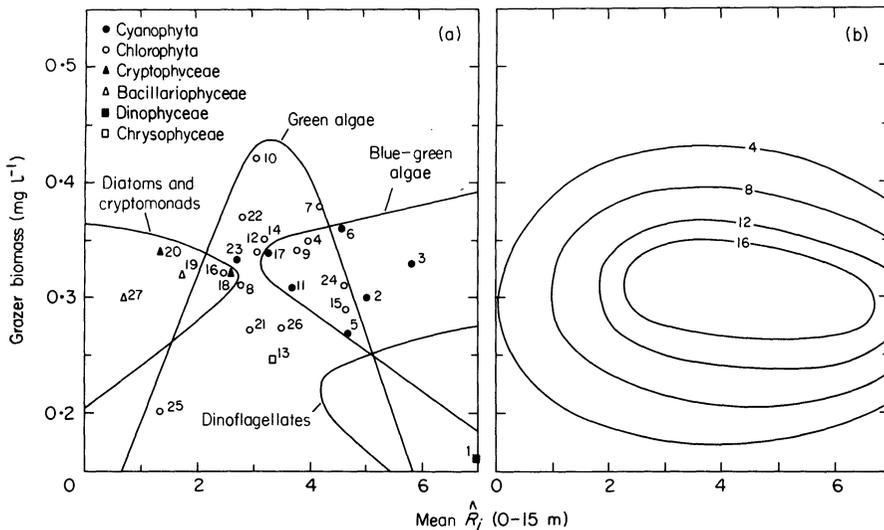


FIG. 9. (a) Positions of twenty-seven of the most abundant phytoplankton species in Lake Lanao along gradients of the two major factors controlling biomass loss—grazing by zooplankton (measured as herbivore biomass) and sinking rate (measured as the mean Richardson Number, \hat{R}_i). Key to species as in Fig. 8. (b) Envelope lines showing 95% confidence area for means of grazing and sinking rate on 4, 8, 12 or 16 sample dates picked at random (without replacement) from the sixty-five actual sample dates.

Diatoms and cryptomonads show an ecological alliance, as they did in the analysis of growth control factors, and are favoured by turbulent conditions and minimum sinking rates. Diatoms are large and are weighted by their frustules, so their need for turbulence seems obvious; this reasoning clearly does not apply to the cryptomonads, however. The cryptomonads are motile, and their position on the turbulence gradient in Fig. 9(a) suggests a manner in which their motility may be adaptively significant. At very high turbulences ($\hat{R}_i \simeq 0$), motility is of no value to the cryptomonads in maintaining position. This is clearly demonstrated by an analysis of vertical distributions of species under turbulent conditions (Lewis 1978b). There is a transition, however, from maximum turbulence to minimum turbulence over which the limited motility of a genus like *Rhodomonas* would be of value. In this transition area, turbulence would be sufficiently pronounced to move non-motile species into undesirable portions of the water column, but not powerful enough to override the limited powers of movement of a small flagellate. The cryptomonads of Fig. 9(a) occupy just such a transition area.

The green algae occupy the broad middle ground in Fig. 9(a), as they did in the analysis of growth control factors. Their adaptability to extremes of turbulence is clearly limited, however, and this provides the main basis for their separation from other taxa.

The blue-green algae overlap the green algae to an extent in Fig. 9, but are nevertheless quite distinct. The vacuolated blue-green algae (numbers 2, 3 and 6) are clustered to the extreme right of the diagram, indicating that vacuolation is of great value when turbulence is minimal. Buoyancy control is by far the most likely function of the vacuoles (Reynolds & Walsby 1975), but the manner in which buoyancy regulation is advantageous remains indefinite. In Lake Lanao the vacuolated blue-green algae apparently use buoyancy regulation to avoid shading in calm weather (Lewis 1978b). This fits well with their tendency to thrive when light availability is high (Fig. 8). Such an explanation, however, does not preclude the possibility that vacuolation confers other advantages such as the facultative movement between zones of high nutrients and high light availability.

The dinoflagellate species in Fig. 9(a) is distinct, just as it was in the growth factor analysis, and appears to compete poorly unless turbulence is minimal. Motility in this instance clearly has a different significance from that in the cryptomonads, which lack the great nutritional flexibility that is characteristic of the dinoflagellates. Motility is an effective defence against sinking, but must occur with other adaptations compensating for extreme nutrient scarcity if it is to be of value when turbulence is minimal. This is true of the dinoflagellates, but not of the cryptomonads. It is clear from this example that stereotypes of the ecology of flagellate species cannot be accurate, as motility has different adaptive significance in different taxa.

Relationship between growth control and loss control factors

Major factors affecting growth and loss in the phytoplankton populations have been treated separately so far, yet these factors are related. The tendency of high light availability and high sinking rates to occur together during calm weather, for example, introduces some difficulties in the separation of the two factors as a basis for phytoplankton succession. The degree of ambiguity in the interpretations is determined by the strength of association between factors (Table 2).

Table 2 shows that there is some potential confusion of the sinking rate effect with sunlight availability, as these two variables are significantly correlated. Since the two

TABLE 2. Pearson product-moment correlation coefficients showing the strength of association between major growth control and loss control factors

Loss control factors	Growth control factors	Nutrient availability	Light availability
		Grazing rate	-0.06
Sinking rate (\bar{R}_i)		-0.34*	0.54*

* $P < 0.05$

variables have very similar importances as criteria for localizing species on environmental gradients (Figs 8 and 9), and since the association between them is by no means perfect, it is very unlikely that the significance of either variable could be explained principally on the basis of the other. A similar but even stronger argument can be made for the relationship between sinking rate and nutrient availability (Table 2). Nutrient availability, sunlight availability, and sinking rate thus appear to have separate and direct effects on succession, as suggested in the analysis.

Figure 10 shows a schematic version of biotic and abiotic changes that occur in Lake Lanao during a complete successional sequence. The sequence is initiated by deep mixing, which (i) reduces light availability by carrying phytoplankton far below the surface, (ii) raises nutrient availability, and (iii) reduces sinking rate to a minimum. This deep mixing is followed by a calm period during which there is (a) a steady rise in light availability as heat accumulation in the upper water column retards mixing (decreasing transparency opposes this trend, but in Lake Lanao the effect of mixing depth generally predominates), (b) a steady depletion of nutrients within the euphotic zone, and (c) a steady increase in sinking rate as turbulence declines in response to surface heat accumulation. Trend (a) would be favourable to autotroph growth if other factors did not change, and trends (b) and (c) would be generally unfavourable to autotroph growth if other factors did not change (Fig. 10).

The joint effect of the three most important growth and loss control factors can be represented in terms of the suitability (as measured by net growth) for an average autotroph species growing without competition (Fig. 10). Individual species do differ in their exact optima for growth (Fogg 1965; Hutchinson 1967; Lehman, Botkin & Likens 1975), but in the absence of competition the optima are likely to lie near the upper range of nutrient and light availabilities found in Lake Lanao, and toward the lower range of sinking rates. It is important to note here that Fig. 10 does not represent a full range of imaginable conditions, but rather the conditions which actually occur in Lake Lanao. Average light availability in the euphotic zone, for example, seldom if ever becomes high enough to inhibit phytoplankton growth, and is most frequently below typical light saturation values, so an increase in light availability can be regarded as generally favourable. The same is true of nutrient availability and of euphotic zone turbulence (\bar{R}_i). Optimal circumstances for increase of phytoplankton biomass therefore occur when these three factors are jointly maximized. This assumes that the factors have equal influence over the full extent of their range of variability in Lake Lanao, which cannot be exactly true in nature but suffices as an approximation for present purposes. One exception must be made to this simplification, and this concerns the relative importance of light and other factors when light availability is at its minimum in the Lanao system. Full circulation limits available light to such an extent that even maximum nutrient availability and

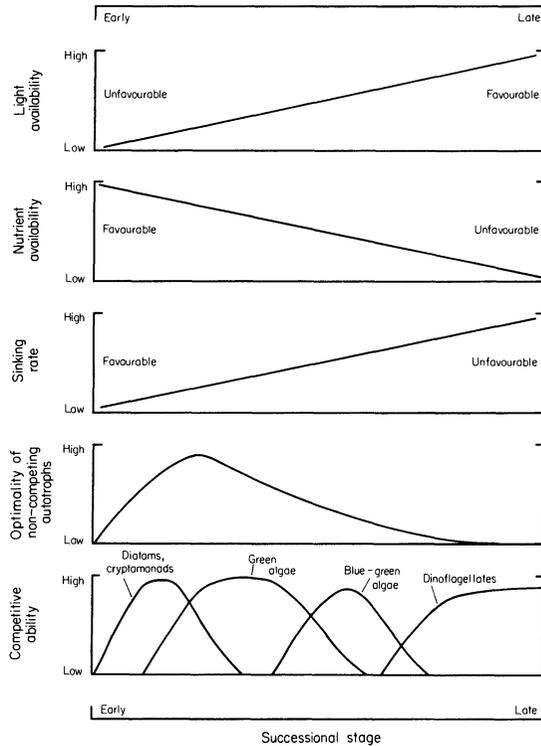


FIG. 10. Diagrammatic representation of the responses of the major phytoplankton taxa to gradients of the major growth control and loss control factors in Lake Lanao (see text for details).

minimum sinking rates are ineffective in generating increases in any species. The effect of light availability in these lowermost ranges is therefore greater than are any favourable effects of the other two major factors combined.

On the basis of the above rationale, Fig. 10 shows the change in overall suitability of the environment for autotrophs from early to late stages of the succession. The curve of suitability begins at a very low point because of the limitation on light availability, reaches a maximum, and then declines as nutrient availability and turbulent mixing move toward their minimum values. Individual species assume specific positions along this curve as determined by their differing competitive abilities (realized niches, Hutchinson 1957b; Levins 1968). Diatoms, cryptomonads and some green algae occupy the ideal positions, and thus dominate during periods of high to moderate productivity. Deterioration of overall conditions for autotrophs leads to a shift favouring species with special adaptations that compensate for changes in one or more of the growth control or loss control factors. In the blue-green algae, such adaptations include buoyancy regulation and nitrogen fixation, and in the dinoflagellates, mixotrophy and motility.

The taxonomic groupings depicted in Fig. 10 are of course not perfect in nature. The blue-green alga *Dactylococcopsis fascicularis*, for example, reacts similarly to an average green alga, and the green algae *Selenastrum* and *Sphaerocystis* react similarly to average blue-green algae.

Importance of meroplanktonic phases

Lund (1954, 1955) has demonstrated the existence of a special life-history strategy in the genus *Melosira*, by which a rapid spring bloom is derived from a large inoculum of dormant cells from the lake bottom. Talling (1966) also found that seasonal maxima of *Melosira* spp. in Lake Victoria coincided with periods of greatest turbulence, suggesting translocation of cells from refugia on the lake bottom. Hutchinson (1967) has suggested that significant inocula of other algal genera besides *Melosira* might originate from non-planktonic refugia, but this possibility has been little studied.

The two *Melosira* species of Lake Lanao flourished during the seasonal circulation period (Fig. 11). Most phytoplankton species declined in abundance during circulation because of the limitation on light availability. A few species maintained rather steady abundance, but *M. granulata* was the only species to show marked increase in abundance. The positive trend in *M. granulata* populations during December cannot, in fact, be accounted for by growth, and must, therefore, be explained by recruitment of pre-existing cells. The increase after December, however, can be accounted for mostly by growth of the inoculum. Growth occurred slowly until middle or late February, when there was a brief interruption in deep mixing and a rapid increase in *Melosira* population density, representing a doubling rate of *c.* 1.0 per day. Decline of the population occurred as stable stratification became established. This pattern indicates that *M. granulata* is favoured by high nutrients and light, but does not remain suspended in the absence of marked turbulence (Fig. 9). A minor increase in the population during the storm period of July is consistent with this interpretation.

Melosira agassizii followed the pattern of *M. granulata* but was less abundant (Fig. 11).

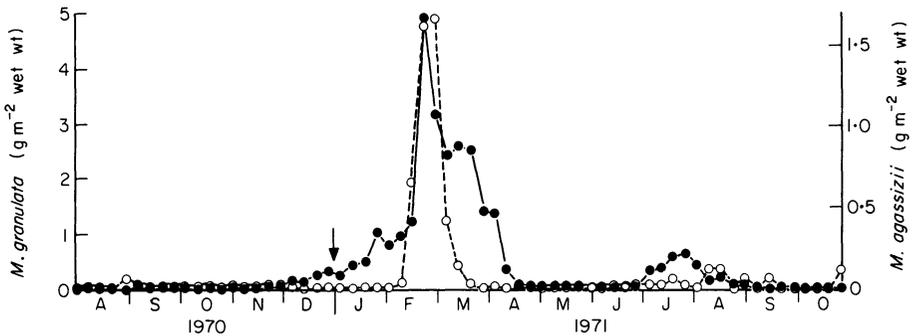


FIG. 11. Abundance patterns of *Melosira agassizii* (o - o) and *M. granulata* (●—●) in Lake Lanao over the study period, expressed as wet weight per unit area within the euphotic zone. The arrow marks the first date of complete seasonal circulation.

The species was below the detection limits (*c.* 0.5 cell ml⁻¹) until February, so the details of the early period of increase are not so clear as they are for *M. granulata*. The subsequent decline in *M. agassizii* was much more abrupt, probably because this species is considerably heavier than *M. granulata* and requires even more turbulence.

Melosira is the only important genus to show any evidence of reliance on meroplanktonic inocula. Some of the large and very rare species might well be supported by meroplanktonic inocula, as the demographic data on them are too weak to prove

otherwise, but among species accounting for 98% of annual biomass, *Melosira* appears to be unique.

Melosira lies at the uppermost end of the size spectrum among those species contributing 98% of the annual biomass. Other important species that are packaged in relatively large biomass units include the dinoflagellates and *Cryptomonas*, which are motile, *Anabaena spiroides*, which contains gas vacuoles, and *Coelastrum cambricum*, which varies enormously in size according to conditions. *Melosira* has clearly been able to join this group by heavy reliance on seasonal redistribution occurring after long periods of non-planktonic existence.

Morphology and succession

The arrangement of species along the environmental gradients in Figs 8 and 9 reflects the variation of physical and physiological traits among the phytoplankton. It should therefore be possible to extend the analysis of succession with a search for relationships between measurable traits of adaptive significance and the position of species on the factor gradients.

The measurable morphological trait of greatest potential adaptive significance in the phytoplankton as a whole is the surface/volume (=S/V) ratio. The volume of average plankton units for various species could also be tested, but is highly correlated with S/V ratio (for Lake Lanao, the Spearman Rank correlation coefficient is -0.84 , $P < 0.01$), and has no detectable significance in these analyses that is distinct from the S/V ratio, so the analysis is limited to the S/V ratio.

The mean volumes of plankton units for each species are known (Lewis 1978a). From geometric models, the surface area of a plankton unit having average volume was calculated for each of the twenty-seven common species shown in Figs 8 and 9. The surface/volume ratios were computed from plankton units, i.e. an association of cells found most frequently in nature, and not from the dimensions of a single cell (Lewis 1976).

The S/V ratio of phytoplankton species is potentially significant in relation to nutrient availability, an important growth factor, and to sinking rate, an important loss control factor. The S/V ratio of species was therefore compared to their positions on gradients of nutrient availability and sinking rate (Figs 8 and 9). Scatter diagrams of the variables are given in Fig. 12.

The scatter diagrams show that *Kirchneriella elongata* and *Aphanothece nidulans* (code numbers 24, 17) are highly divergent from the other species, with S/V ratios of 20.0 and 34.7 respectively. The cells of these two species are embedded in a bulky gelatinous matrix. As the outside of this matrix constitutes the surface of the unit, whereas only the cells themselves contribute to volume, the S/V ratio is very high. This may explain the high nutrient requirement of *Aphanothece* relative to other blue-green algae, despite the small size of its cells (see Fig. 8). *Aphanothece* and *Kirchneriella* do not occupy the absolute extreme of the nutrient gradient as would be expected from the S/V value alone, however. The gelatinous matrix probably does decrease the nutrient-uptake potential of the cells, but does not require the same quantities of nutrients as does the protoplasm. The S/V ratios of these two species are therefore not comparable to those of other species because of the matrix.

Gymnodinium (code number 1) is also divergent from other species in Fig. 12(a),

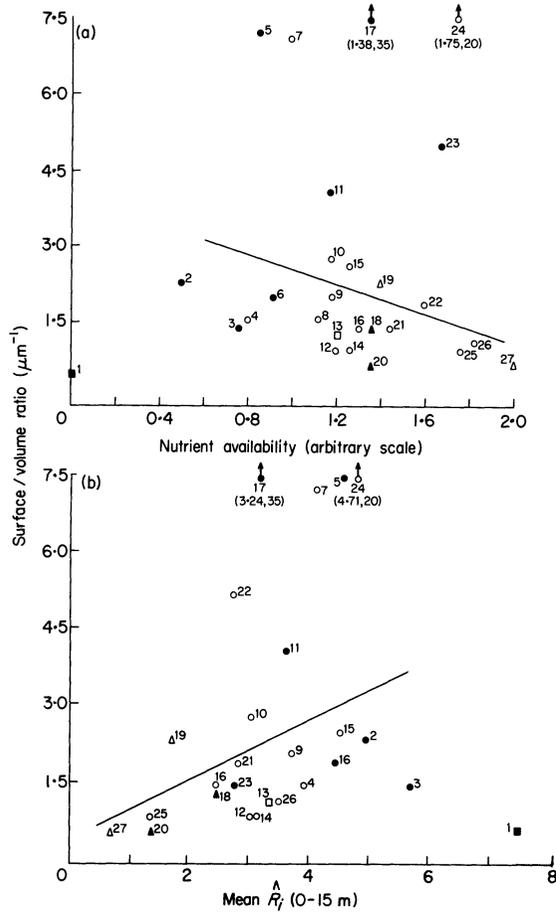


FIG. 12. Relation of the surface/volume ratio to the positions of individual phytoplankton species on the gradients of (a) nutrient availability and (b) sinking rate (mean Richardson Number, \bar{R}_i). Key to species as in Fig. 8. The lines show the best linear fit to the data after exclusion of *Kirchneriella* (24), *Aphanothece* (17) and *Gymnodinium* (1).

probably because of its mixotrophic nutritional capabilities, which would reduce the importance of the S/V ratio in determining its position on the nutrient gradient.

A correlation analysis on the data in Fig. 12(a) showed that the relationship between S/V ratio and position on the nutrient availability gradient was statistically significant. The Spearman rank correlation coefficient (r_s) is -0.46 ($P < 0.05$) if *Kirchneriella*, *Aphanothece*, and *Gymnodinium* are excluded from the analysis for the reasons given above. This relationship is surprisingly strong, and indicates that species with high S/V ratios predominate increasingly as succession proceeds and nutrients become scarce.

The nitrogen-fixing blue-green algae (code numbers 2 and 3) diverge only slightly from the main pattern in Fig. 12(a). Nitrogen-fixing ability, therefore, does not exempt species from at least some of the limitation imposed by the S/V ratio. The significance of the S/V ratio may be reduced to some extent by this adaptation, however, allowing the species to thrive at slightly lower nutrient availabilities than their S/V ratios would predict, as suggested in Fig. 12(a).

Margalef (1958, 1968) considers motility of flagellated phytoplankton as potential compensation for the poor nutrient-gathering ability of cells with low S/V ratio. Although special resistance to nutrient limitation does apparently occur in *Gymnodinium* (Fig. 12(a)), this is not typical of flagellates in general. The resistance of *Gymnodinium* thus would appear to relate more to its mixotrophic nutritional characteristics than to its motility.

A similar analysis was conducted on S/V ratio and the position of species on the turbulence gradient (\hat{R}_t , Fig. 12(b)). The potential significance of S/V ratio in this case is in the retardation of sinking, which varies in an inverse, albeit complex, manner with S/V ratio (Hutchinson 1967; Smayda 1970). Once again, the relationship is statistically significant ($r_s = 0.50$, $P < 0.01$), suggesting that part of the significance of S/V ratio is that it regulates the position of a species on a turbulence gradient during succession.

The position of a species on the nutrient-availability gradient is highly correlated with its position on the \hat{R}_t gradient ($r_s = -0.77$, $P < 0.01$). This close correlation essentially prevents separation of the effects of sinking and nutrition by means of partial correlation, so the causal interpretation of the significance of the S/V ratio in succession must be made cautiously. The S/V ratio is definitely important in the positioning of species along gradients of nutrient availability and turbulence, but the exact proportion of adaptive significance attributable to either factor individually cannot be specified here. It is clear, however, that the S/V ratio is an important determinant of the position of a species in the successional sequence.

Relationship of succession to changes in phytoplankton morphology has been studied by Margalef (1967), who suggests on the basis of a literature review (mainly marine) that an almost universal pattern of plankton autotroph succession is as follows, moving from early to late successional stages: (i) small-celled species with high S/V ratios; (ii) larger species with lower S/V ratios; (iii) flagellates. The Lake Lanao sequence is very different from this. Succession moves from low to higher S/V ratios as nutrients become scarce, and flagellates appear both early and late in succession. Either Margalef's conclusions are not well founded, or the Lanao system is different from the ones he has studied.

The relation between S/V ratio and position on the nutrient-availability and turbulence gradients explains at least part of the tendency for species of close taxonomic relationship to cluster along environmental gradients. The mean value of S/V for the blue-green algae (excluding *Aphanothece*) is 3.63, for green algae (excluding *Kirchneriella*) 1.95, and for diatoms 1.46. The arrangement of the groups along the nutrient gradient is thus expected, on the basis of S/V ratio alone, to be as indicated in Figs 8 and 9.

CONCLUSIONS

There are certain key differences between phytoplankton dynamics in Lake Lanao and in the intensively studied temperate lakes upon which our present understanding of succession is founded. The first of these differences is obvious, and might well have been deduced from very little evidence. Autotroph biomass in Lake Lanao varies less than one order of magnitude over a year (Fig. 4), whereas the annual variation in temperate lakes is typically much greater as a result of winter biomass losses. Similarly, the annual variation in biomass of the major individual phytoplankton taxa is relatively low in Lake Lanao (Fig. 2).

A second and more subtle contrast between Lake Lanao and the more familiar temperate lakes is visible in the successional patterns. In plankton environments generally, succession consists of a series of episodes of variable length (Margalef 1967). An episode is initiated by an abrupt change in physico-chemical conditions, which is followed by a sudden change in plankton composition. There is subsequently a continuous alteration in plankton composition caused by biotic alterations of the physico-chemical environment. The succession rate is at first high, but quickly declines (Lewis 1978c). Successional change continues until another abrupt externally-induced physico-chemical alteration initiates another successional episode. A major contrast between Lanao and most temperate lakes lies in the number of such episodes per year.

The changes in abundance of the major taxa (Fig. 2) give intuitive support to the hypothesis that there are more successional episodes over a year in Lake Lanao than in most temperate lakes. A more quantitative approach is possible through the use of Nauwerck's (1963) data on Lake Erken, which were collected in a manner very similar to that used for the Lanao data. Where a particular taxon occupies a specific position in the successional sequences of two lakes, the number of successional episodes over a year in the two lakes can be determined on the basis of the number of marked abundance changes in that taxon. The taxon used for the test must be one which appears early in a successional sequence or episode, as the average duration of episodes may vary in the two lakes. Diatoms and, to a lesser extent, cryptomonads meet these requirements. In both Lake Lanao and Lake Erken, these two groups typically appear early in a successional sequence initiated by sudden addition of nutrients to the euphotic zone.

For both lakes the mean biomass of diatoms was calculated for the first 12 months of the study period, and the number of occasions on which the diatom biomass line crossed the mean during the 12 months was then determined. This procedure is not affected by the rate of biomass change in any specific successional episode, nor by the differing average abundances of diatoms in the two lakes. For Lake Lanao, the number of intersections of the annual abundance trace with a line representing the mean was 14; for Erken it was 5. For cryptomonads, the corresponding numbers were 10 and 6. These results are consistent with the hypothesis that successional episodes are more numerous in Lake Lanao than in Lake Erken.

An extension of the above analysis shows that the number of times in a year that blue-green algal abundance intersects with a line representing the mean is about the same for Erken and Lanao. This means that the Lanao episodes are shorter in a successional sense, and frequently terminate before the successional sequence reaches the blue-green stage, which is toward the end of a sequence initiated by a nutrient pulse (Fig. 10). Thus the Lanao community is maintained on average in a more 'youthful' condition by early termination of successional episodes.

The contrasting pattern of succession in Lake Lanao with that in Lake Erken is not surprising in view of what is already known of the factors regulating autotroph growth in Lake Lanao. Variations in the supply of resources are much more irregular and numerous in Lake Lanao than in comparable temperate lakes (Lewis 1974), where seasonal events are the dominant control mechanism. In Lake Lanao, and perhaps in other lowland tropical lakes that undergo stratification, the much greater frequency of critical variations in the supply of resources drives succession faster and maintains a more youthful system, despite the similarity of events within any particular successional episode to those one might see in a temperate lake.

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