

## Phytoplankton Succession in Lake Valencia, Venezuela

William M. Lewis, Jr.

University of Colorado, Department of Environmental, Population and Organismic Biology, Boulder, CO 80309, U.S.A.

**Keywords:** seasonality, phytoplankton succession, tropical lakes, phytoplankton communities, phytoplankton abundance

### Abstract

Phytoplankton counts and supporting physical and chemical data were taken on Lake Valencia, Venezuela, over a five-year interval. The data are used to test the validity of a successional paradigm for class-level taxa. According to the paradigm, formulated from previous studies of Lake Lanao, Philippines, and from data on temperate lakes, the order of taxa from early to late succession is: diatoms, chlorophytes, blue-green algae, dinoflagellates. A successional episode is considered to begin when stability of a water column is restored after deep mixing. As the episode progresses, there is a steady decrease in concentration of the limiting macronutrient (in this case, N). In a test of the validity of the paradigm for Lake Valencia, dates of exceptional population increase or decrease were obtained for each taxon. Since nitrate concentration declines steadily as succession progresses, the entry of a given taxon into the successional sequence is indicated quantitatively by the mean nitrate concentration on dates of exceptional increase in population density, and exit from the successional sequence is indicated by mean nitrate concentration on dates of exceptional population declines. The successional position of each major taxon, bounded by its entry and exit in the sequence, can be mapped on the complete spectrum of nitrate concentrations observed in the lake. For Lake Valencia, the nitrate mapping procedure agrees exactly with the predictions based on the successional paradigm. Conformance of Lake Valencia phytoplankton with predictions made *a priori* suggests that there is a generalized pattern in the phytoplankton succession of the mixed layers of temperate and tropical lakes.

### Introduction

The sequential appearance of algal taxa in plankton environments has been termed phytoplankton succession, which is considered to have certain features in common with biological succession in other kinds of environments (Margalef, 1958, 1967). Despite general agreement on the importance of succession in phytoplankton communities, numerous aspects of phytoplankton succession are as yet not well understood (Hutchinson, 1967; Reynolds, 1980). Treatments of phytoplankton succession are too often largely descriptive and too often rely on *a posteriori* reasoning to explain associations and trends. While description is essential, analysis of

succession should incorporate more statistical and experimental approaches. For statistical approaches, it is especially desirable that *a priori* hypothesis testing be used to establish the validity of specific concepts related to succession. The present paper describes phytoplankton abundance patterns in Lake Valencia, Venezuela, and uses the information to test hypotheses formulated *a priori* concerning phytoplankton succession.

The Lake Valencia data span a five-year interval over which phytoplankton counts are available for all autotrophic taxa found in the growth zone of the lake. The phytoplankton data are supported by concurrent physical and chemical data. The present analysis focuses on the existence of patterns in the

abundance of class-level taxa. This type of analysis will yield a null result unless classes contributing to the phytoplankton have a certain amount of ecological coherence, i.e., unless species of a given class are more likely to respond in a similar manner than species of different classes. Ecological coherence is expected in view of the shared morphology and physiology of the members of a class, and has been demonstrated statistically for at least one lake (Lewis 1977).

## Methods

The phytoplankton samples were taken at a mid-lake station between January 1977 and October 1981 (Fig. 1). Samples were taken weekly in 1977 and 1978 and biweekly thereafter. On each sampling date, an integrating sampler of the type described by Lewis & Saunders (1979) was used to collect successive 5-m increments of water from the top to the bottom of the water column (35 m). This

sampling strategy assures that concentrated layers of phytoplankton will not be missed. Although the vertical distributions of the phytoplankton are known from counts of successive samples over the vertical profile, the present analysis deals only with the average abundance of phytoplankton between 0–15 m depth.

Phytoplankton samples were preserved in the field with Lugol's solution. Counts of each sample were made with an inverted microscope following sedimentation in a 5-ml chamber. Counting methodology was as described by Lewis (1978a). Care was taken to count all autotrophic cells regardless of size. Cells as small as  $0.7 \mu\text{m}$  in diameter were routinely counted. Fluorescence microscopy showed that all autotrophic cells were being counted by the inverted microscope method.

Individual cells were counted except for filamentous species, which were quantified by length, and a few colonial species with exceedingly high numbers of cells per colony, which were counted as colonies. Numerous measurements were made of

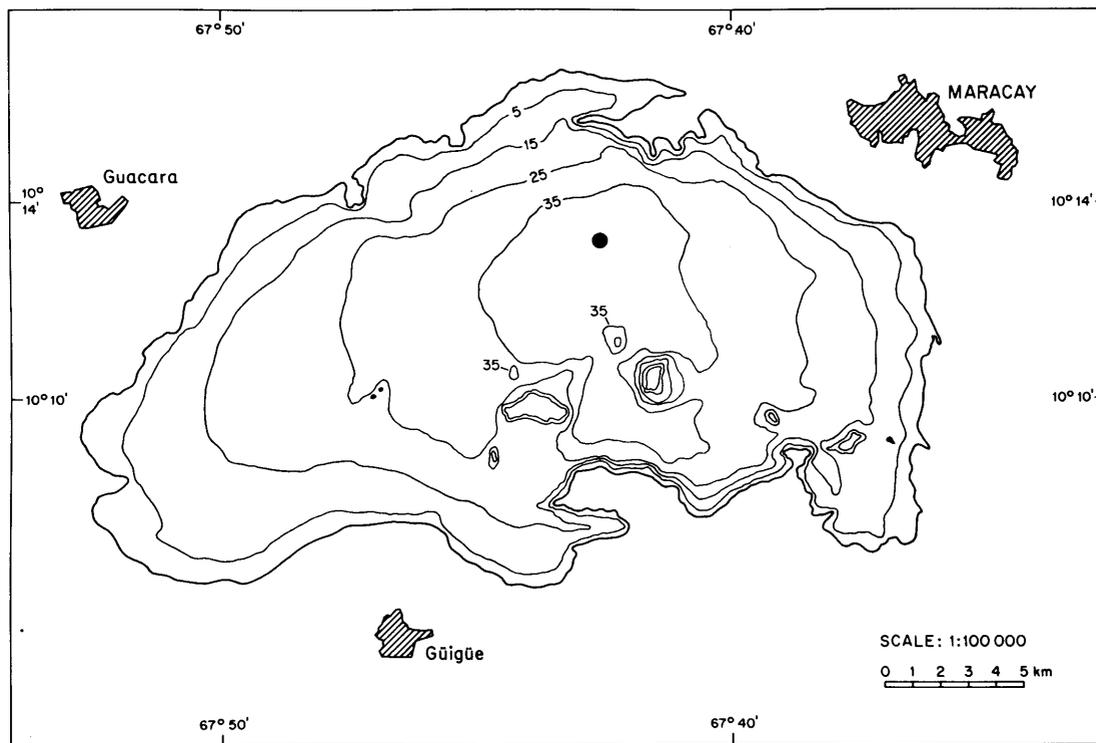


Fig. 1. Outline map of Lake Valencia showing the location of the main sampling station from which the phytoplankton samples were taken.

the dimensions of cells and colonies for each species. From these measurements, cell volumes and colony volumes were computed, as reported by Lewis & Riehl (1982). Also computed for each taxon on each date was the mean number of 'plankton units', which is the number of cells divided by the number of cells per filament, per colony, or per coenobium. The cell volume per unit volume of water (0–15 m) is the index of abundance of primary interest in the following analyses.

Although numerous environmental variables were measured, those of principal interest here include nitrate concentration and the thickness of the upper mixed layer. Nitrate was determined by cadmium-copper reduction of nitrate to nitrite followed by spectrophotometric determination of nitrite (Bendschneider & Robinson, 1952; Wood *et al.*, 1967). Thickness of the mixed layer was considered to be equal to the isothermal zone at the top of the water column early in the morning (prior to daytime heat accumulation). An analysis of seasonal changes in the mixed layer and other aspects of heat distribution has been presented elsewhere (Lewis, 1983a, 1984).

### Description of the Lake

Lake Valencia occupies a graben in north-central Venezuela. The lake (mean depth 19 m, maximum depth 37 m) appears to be very old, since the lacustrine sediment is more than 100 m thick (Bradbury *et al.*, 1981). The water level of the lake has fluctuated considerably over the last 10 000 years (Lewis & Weibezahn, 1981). The lake has not discharged water through its outlet since the 17th century, and has consequently become somewhat saline: specific conductance between 1977 and 1981 was 1900–2100  $\mu\text{S cm}^{-1}$  (at 25 °C) and pH was 8.5–9.5.

Studies of the chemistry of waters draining from a protected watershed in the Lake Valencia basin have shown that the lake probably was mesotrophic prior to the 17th century (Lewis & Weibezahn, 1983). However, extensive discharge of sewage into Lake Valencia has raised the nutrient loading substantially over the past 20 years. Lewis & Weibezahn (1983) computed that the natural background loading for the lake would be about 0.23  $\text{g m}^{-2} \text{y}^{-1}$  for phosphorus and 2.36  $\text{g m}^{-2} \text{y}^{-1}$  for

nitrogen. Principally because of sewage, the loading in 1977 and 1978 averaged 2.43  $\text{g m}^{-2} \text{y}^{-1}$  for phosphorus and 11.2  $\text{g m}^{-2} \text{y}^{-1}$  for nitrogen. Diversion of some additional sewage to lake resulted in a rise of phosphorus loading to 3.31  $\text{g m}^{-2} \text{y}^{-1}$  after 1978.

Because of high phosphorus loading, soluble reactive phosphorus (SRP) concentrations in the growth zone of Lake Valencia seldom reached undetectable concentrations during the course of the study (average, ca. 10  $\mu\text{g P l}^{-1}$ ). After prolonged stratification the SRP levels did decline to about 1  $\mu\text{g l}^{-1}$  in 1977 and 1978, but such low levels were not observed after the increase of phosphorus loading in 1979. In all 5 years of the study, pronounced nitrogen depletion was evident from the complete disappearance of nitrate (detection limit, 1  $\mu\text{g N l}^{-1}$ ) and ammonium (detection limit, 2  $\mu\text{g N l}^{-1}$ ) in the upper water column, from the response of the algal community to nitrogen enrichment in enclosure experiments (Lewis, 1983b), and from N fixation (Levine & Lewis, 1984; Lewis & Levine, 1984). Thus the phytoplankton community is primarily nitrogen-limited.

As might be expected from the high nutrient loading, chlorophyll levels in Lake Valencia were quite high. During the annual period of stratification, chlorophyll *a* averaged between 30 and 40  $\mu\text{g l}^{-1}$ .

Lake Valencia shows pronounced physical and chemical seasonality. The water column is thermally stratified without interruption between approximately March and November. During this seasonal stratification, the thickness of the upper mixed layer averages about 12 m (Lewis, 1983a). The thickness of the mixed layer is not stable, however. The upper mixed layer can be thickened suddenly by a period of windy, cool weather that allows erosion of the thermocline. This phenomenon, which has been called *atelomixis* (Lewis, 1973), is of great importance in changing the chemical environment of the phytoplankton during the stratification season (Lewis, 1974). In temperate lakes the mixed layer is not entirely stable, either, but repeated major changes in the thickness of the mixed layer are less likely than in tropical lakes, including Lake Valencia.

In Lake Valencia, seasonally increasing wind strength and decreasing minimum temperature cause declining stability of the water column in

November or December. This results in deeper mixing and ultimately in mixing of the entire water column, which typically occurs at the end of November but can occur slightly earlier or considerably later depending on the conditions in a particular year. Between the first day of overturn and the return of calmer weather with higher minimum temperatures in March or April, the stability of the water column is very low and complete mixing may occur on any day when wind strength is substantial. However, seasonal overturn can be interrupted by periods of calm weather.

Figure 2 shows the thickness of the mixed layer as determined by thermal profiles. The duration of the seasonal stratification is indicated for each of the five years. The end of the seasonal stratification in each year is the estimated date of first complete

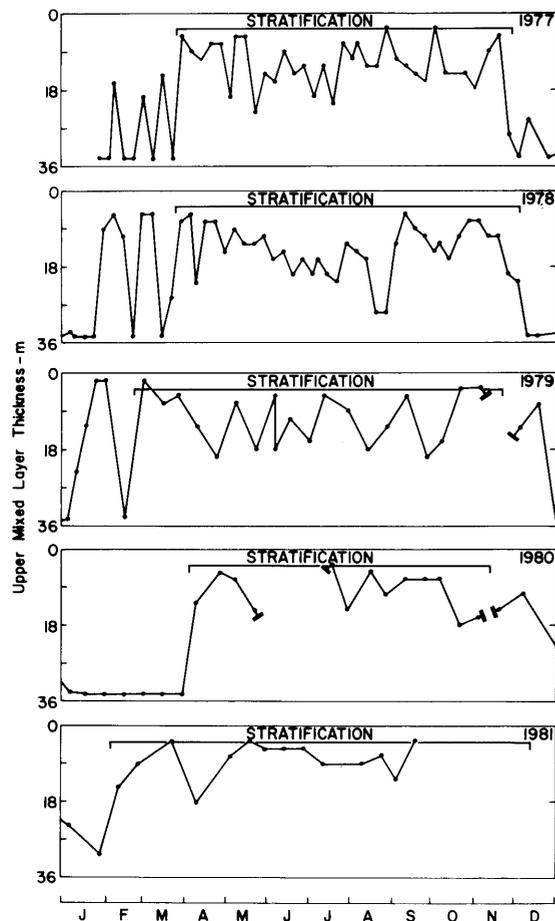


Fig. 2. Thickness of the upper mixed layer over the five-year study interval as determined by thermal profiles in the early morning.

mixing of the water column. Onset of complete mixing in November or December was typically followed by at least one interval of 2–4 weeks during which there was stratification. However, sustained (seasonal) stratification did not become re-established in any year until at least February; in 1980 it was delayed until early April.

Numerous episodes of atelomixis are evident from changes in the thickness of the mixed layer during the stratification season. The most dramatic of these occurred in August of 1978, when cool weather and strong winds depressed the thermocline to about 25 m for a period of 2 weeks, after which the situation was reversed by calm, sunny weather. Other such events of a less extreme nature can also be identified in the graphs.

Figure 3 shows the nitrate concentration in the

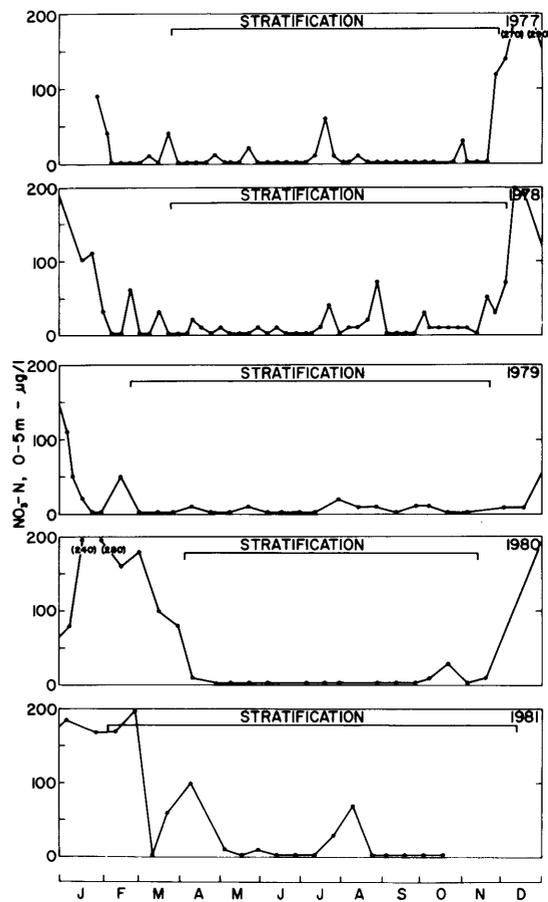


Fig. 3. Nitrate-nitrogen concentration in the upper 5 m of the water column over the five-year study interval.

upper 5 m of the water column. The nitrate concentration in the upper water column reflects the combined influence of strong biological demand for nitrate and of change in thickness of the mixed layer. As would be expected, nitrate concentrations were typically high during the seasonal overturn. However, when the water column stopped mixing, even for relatively short intervals, nitrate was depleted from a concentration of  $100 \mu\text{g l}^{-1}$  or more to undetectable levels within a matter of a few weeks. Ammonium showed a similar pattern, although maximum concentrations were well below those of nitrate and depletion occurred prior to nitrate depletion, as expected. During stratification, increases in mixed layer thickness brought up from the aphotic zone water rich in nutrients, thus increasing the surface inorganic nitrogen concentrations. The size of any specific increase is of course related to the amount of change in mixed layer thickness. The marked episode of atelomixis in August 1978 provides a good example of the effect of changes in mixed layer thickness on the amount of nitrate in the upper water column; the nitrate graph for 1978 shows a nitrate spike coincident with the depression of the thermocline at this time.

### Overview of phytoplankton composition and abundance

One hundred and forty-six species were identified for counting purposes. Taxonomy and morphometric features of the species are given by Lewis & Riehl (1982). Although individual species will not be discussed here, it is useful to mention the most common species and genera, which account for most of the observed class-level changes in abundance.

For the blue-green algae, both coccoid and filamentous forms were common. A small coccoid genus, *Synechocystis* (including *S. aquatilis* and an undescribed species), was the most common taxon both numerically and by volume among the blue-greens. *Microcystis* (mainly *M. aeruginosa*) and *Chroococcus* (including *C. dispersus* and *C. limneticus*) were also present in quantity. Common filamentous forms included very small species of *Lyngbya* (mainly *L. limnetica*) and *Oscillatoria* (*O. limnetica*). *Anabaena* was represented by several different species, including the abundant species

*Anabaena volzii* and *Anabaena spiroides*. *Anabaenopsis* was also common, as was *Cylindrospermum stagnale* (also called *Anabaenopsis raciborskii*; see Lewis & Riehl, 1982).

Among the green algae or chlorophytes, *Scenedesmus* (6 species) was common, and microalgae of the genera *Chlorella* and *Coccomyxa* were also occasionally very abundant. Many other genera were observed, including *Ankistrodesmus*, *Coelastrum*, and *Kirchneriella*.

Diatoms included a mixture of centric and pennate forms. There were several species of *Nitzschia* (*N. palea*, *N. amphibia*, *N. kutzingiana*), plus *Cyclotella meneghiniana*, occasionally *Melosira granulata*, and the very tiny centric *Thalassiosira guillardii*. Cryptophytes, represented almost exclusively by the genus *Cryptomonas* (*C. caudata*, *C. erosa*), were also occasionally abundant. Other major taxa were represented by generally small numbers of organisms. Countable numbers were observed of *Dinobryon* (mainly *D. sociale*) and *Peridinium inconspicuum* at some times, and euglenophytes (*Phacus*, *Trachelomonas*) appeared briefly in some years.

Figure 4 shows the time-averaged composition of phytoplankton in Lake Valencia both in terms of cell volume and number of individuals (plankton units per ml). The phytoplankton community of Lake Valencia is dominated by blue-greens, diatoms, and greens. Lake Valencia shows a pronounced dominance by blue-greens, although the greens and diatoms are significant components of phytoplankton cell volume.

Table 1 shows the changes in composition from year to year, expressed as percent of cell volume or as percent of plankton units per ml, for the seven classes of phytoplankton that made measurable contributions to the phytoplankton of Lake Valencia. Phytoplankton abundance was highest by volume in 1978 and 1980, although in numerical terms the four years were very similar except for 1977, which showed lower abundance. The percentage contributed by blue-green algae varied little among the five years, but the percentages contributed by other taxa shifted quite dramatically from one year to another. In the first, second, and fifth years, the diatoms were much more important than they were in the third and fourth years. The chlorophytes showed almost the mirror image of the diatom pattern. Cryptophytes were virtually ab-



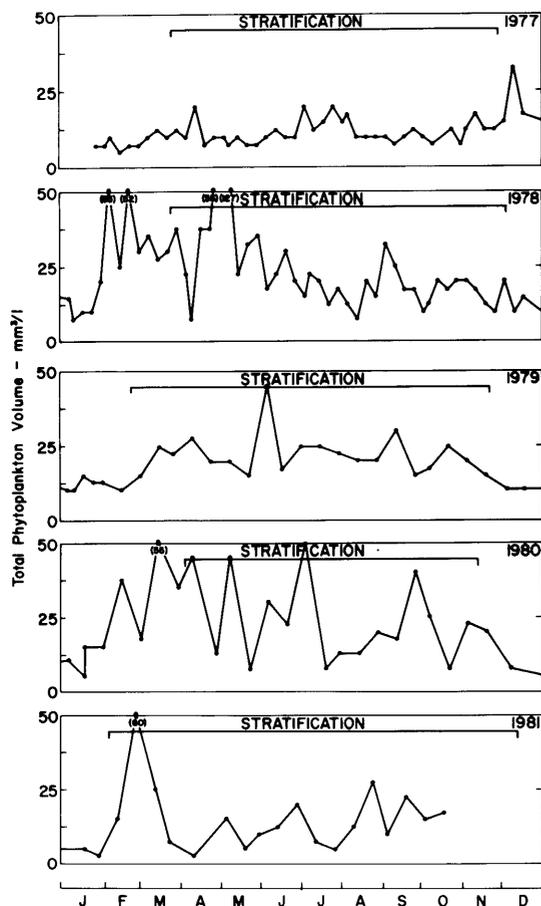


Fig. 5. Total phytoplankton abundance in terms of cell volume ( $\text{mm}^3 \text{l}^{-1}$  in the top 15 m) between 1977 and 1981.

Although large accumulations of biomass can be observed during overturn due to temporary stability of the water column, growth during this season is always interrupted by the resumption of complete overturn and the accompanying light limitation. With the first onset of seasonally stable stratification, however, biomass accumulation can occur over a longer interval, thus producing a strong maximum. Progress toward the maximum may be irregular because of changes in thickness of the mixed layer, which cause both dilution of phytoplankton biomass near the surface and short-term light deprivation. An example of this is March of 1978, when there was a sudden increase in the thickness of the mixed layer from about 7 m to about 20 m. In general, the maximum biomass tends to occur when the upper mixed layer is thin,

since the best light conditions occur at such times.

When the lake is stably stratified and the mixed layer is unchanging, decline from the biomass maximum is explained by nutrient depletion. This is suggested by a comparison of Fig. 5, which shows phytoplankton volume, and Fig. 3, which shows nitrate concentration in the upper water column, and is confirmed by enrichment experiments conducted in large containers *in situ* (Lewis, 1983b). Many of the irregularities in the phytoplankton volume curve can be explained by variations in nutrients, which are in turn controlled by changes in thickness of the mixed layer; grazing is of minimal importance because less than 10% of primary production is consumed by herbivores (T. Frost, unpublished grazing studies). A decline in phytoplankton volume may be slowed or reversed following a thickening of the mixed layer, which has the effect of replenishing depleted nutrient supplies. As the stratification period progresses, however, small changes in mixed layer thickness become less effective in renewing nutrient supply, since an increasing proportion of the total nutrient content is in the very deepest water that is not usually incorporated in the upper mixed layer except during the most drastic incidents of atelomixis. Thus there is a general seasonal trend toward greater nutrient stress over the stratification interval, but there is also a considerable amount of non-seasonal variation imposed on this trend by irregular changes in the mixed layer.

The main question of interest here is whether or not the trends in environmental factors and total phytoplankton biomass are accompanied by trends of a predictable nature in the abundance of class-level taxa. Plots of the abundance of the four most abundant taxa are given in Figs 6–9. Although all of the taxa show some tendency to respond to the best and the worst conditions in parallel with total phytoplankton biomass, differences in responses are very difficult to judge by simple examination of the graphs. There is a suggestion that the diatoms respond to mixing much more quickly and sharply than other taxa, and that they are less favored by stable high-lying thermoclines than the blue-greens. Both the chlorophytes and the cryptophytes are very different in their patterns from either the diatoms or blue-greens, but the exact nature of the differences is difficult to formulate from simple observation.

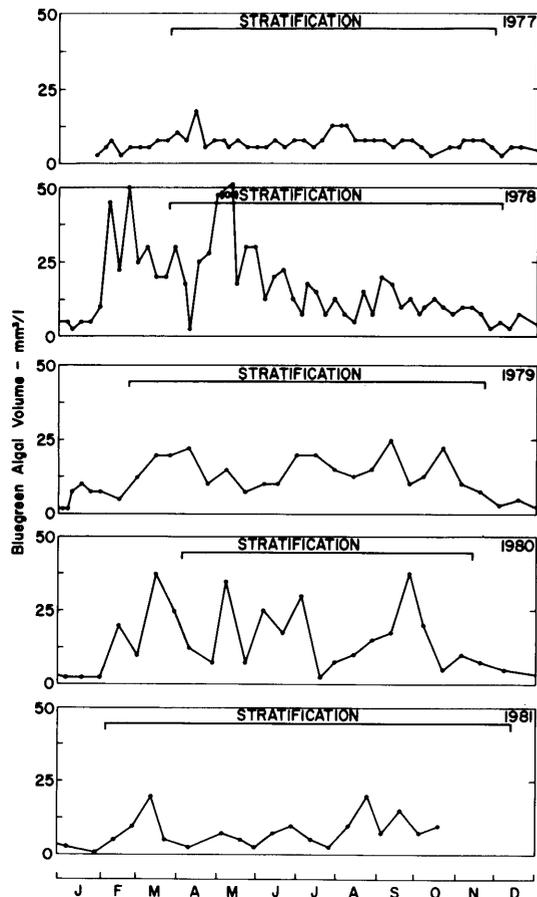


Fig. 6. Blue-green algal cell volume over the study period.

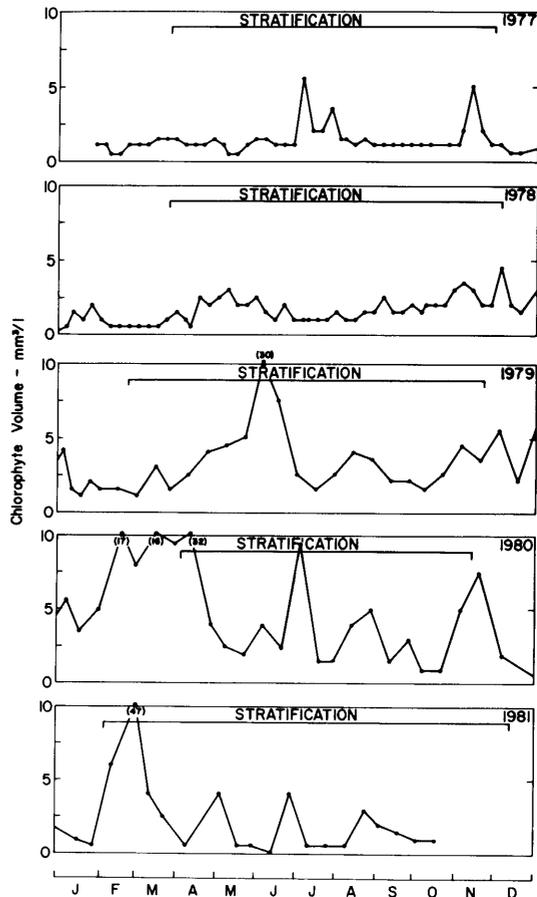


Fig. 7. Chlorophyte cell volume over the study period.

### A successional paradigm as the basis for hypothesis testing

In the upper mixed layer of lakes, changes in phytoplankton abundance can occur as the organisms modify their environment (e.g. by nutrient uptake). Such biotically driven change has been called autogenic succession. This terminology was introduced by Tansley (1935) for terrestrial plant communities and was subsequently revived by Odum (1971). Autogenic succession in deep lakes can be said to begin when deep mixing gives way to water column stability and to end when water column stability is disrupted by abiotic forces (Lewis, 1978c). The concept of successional time can be applied to autogenic succession: certain taxa tend to appear early in the autogenic sequence and others appear later. Changes in species composi-

tion can also occur as a direct result of drastic abiotic influences, such as mixing. Such changes in species composition have been called allogenic succession. This usage, also due to Tansley and then Odum, is perhaps unfortunate, since the concept of successional time is not relevant to abiotically induced change. For present purposes, succession will refer specifically to autogenic changes in the community, and allogenic changes will be treated as disruptions of the autogenic successional sequence. The emphasis here is on succession during the growing season in the upper mixed layers of lakes that stratify. Successional rules may also be applicable to lakes that mix continuously, to winter populations, and to metalimnetic populations, but the rules will be different and will not be considered here.

Temperate-zone data on phytoplankton during

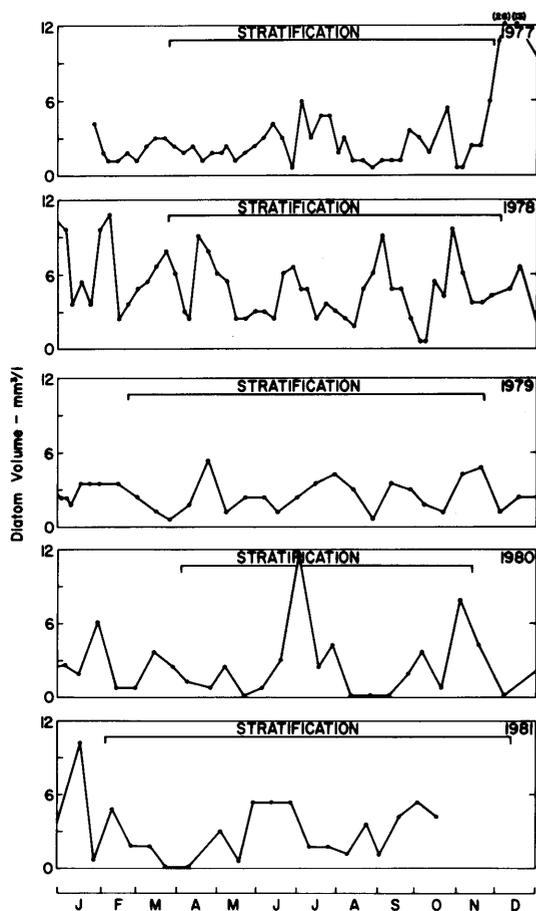


Fig. 8. Diatom cell volume over the study period.

the growing season in the mixed layer of lakes that stratify suggest a general successional paradigm for these communities. This paradigm was summarized as follows by Lewis (1978b) from the literature: (1) succession in the euphotic zones of lakes that show prolonged stratification consists of episodes whose beginning is marked by stratification of a mixed water column and whose termination is caused by remixing of the water column; (2) after stabilization of a water column, a successional pattern is dictated by autogenic changes; (3) the most important autogenic changes include decreases in nutrient availability and in transparency; (4) diatoms occur early in a successional episode, chlorophytes occur after diatoms, and blue-greens occur after chlorophytes. In temperate lakes, the stratification season often consists of a single successional episode that begins with spring layering and ends with

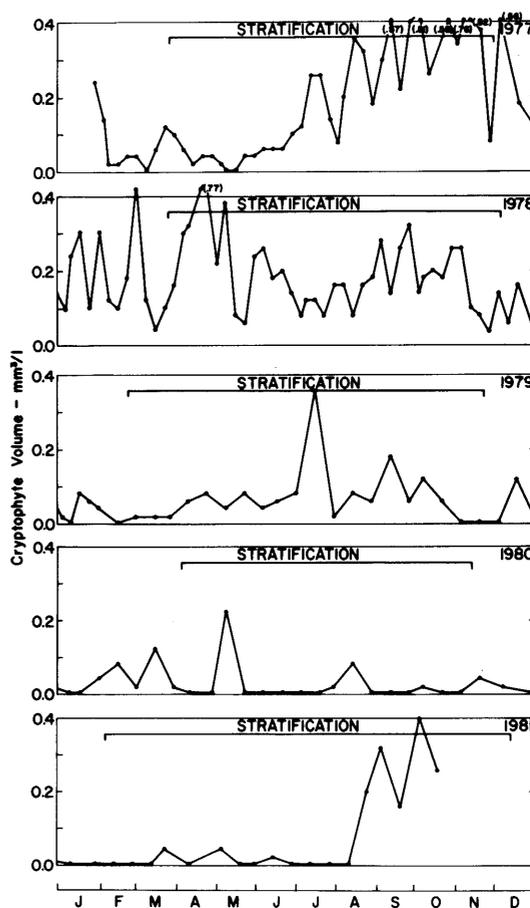


Fig. 9. Cryptophyte cell volume over the study period.

fall thermocline depression. Upwelling or thermocline movement can reset or retard succession in some temperate lakes, however (Reynolds, 1980).

Some lakes are strongly dominated by one taxon. This phenomenon can be accommodated within the framework of the successional paradigm if conditions in certain lakes, particularly those at the extremes of the trophic spectrum, are under the influence of such powerful allogenic influences that autogenic succession plays a less significant role. In effect, the positions of selected taxa on the environmental spectrum are temporally expanded under the influence of allogenic influences affecting nutrient supply or transparency.

If the key environmental factors underlying the successional paradigm are biotically labile factors of a general nature such as nutrient availability and transparency, then the paradigm should apply just

as well to tropical lakes as to temperate ones. In a test of this hypothesis, Lewis (1978b) made an analysis of the sequence of appearance of class-level taxa in the phytoplankton of Lake Lanao, a warm monomictic tropical lake. The analysis showed that the paradigm applied very well to Lake Lanao. Although Lake Lanao was indistinguishable from a temperate lake in the sequence of appearance of taxa, the number of successional episodes per year was greater than in temperate lakes because of occasional drastic changes in the thickness of the mixed layer. The number and duration of successional episodes was dependent on irregular variations in weather, which were in turn responsible for changes in the thickness of the mixed layer. In an analysis of succession rate, Lewis (1978c) showed that resource supply (mainly nutrients) was the dominant factor driving the autogenic sequence.

On the basis of the Lake Lanao study, Lewis (1978b) extended the paradigm somewhat by suggesting that dinoflagellates would come after blue-greens in successional time and that cryptophytes would precede blue-greens in the sequence, although the more exact position of cryptophytes could not be specified from the Lanao work. Chrysophytes and euglenophytes were not placed in the sequence, since these were virtually absent in Lanao.

### Testing the successional paradigm

Given the appropriate kind of environmental data and a long sequence of abundance measurements for the phytoplankton, it should be possible to devise a statistical test for the general validity of the successional paradigm in any given lake. The first requirement is a quantitative method for identifying the entry and exit of taxa in the successional sequence. Lewis (1978b) used peak abundances and correlation matrices to identify position in successional sequences and matched these up with environmental factors whose deviation from the mean was determined by Monte Carlo methods. For Lake Valencia, the long run of data allows the use of simpler methods.

Experience with the Lake Lanao data (Lewis, 1978b) shows that the most productive approach in analyzing succession is to consider the weekly changes in abundance of each taxon rather than the

abundances per se. Although the abundance matrix is an indicator of the suitability of conditions for particular taxa of algae, the change of abundance is an even more specific indicator because there is minimal lag between favorable or unfavorable environmental conditions and the corresponding change in abundance. Thus the increase or decrease in population size for all taxa of interest was calculated for every sampling interval over the study period for Lake Valencia.

There is some question as to whether or not it is best to express the change in abundance in absolute terms or in relative terms. For samples taken very close together (e.g. one day), it would probably be best to express change in abundance in relative terms as growth per individual of the population. Over longer intervals, however, the algae have ample opportunity to express the influence of factors affecting growth and loss. Thus for Lake Valencia, which was sampled either biweekly or weekly, absolute change in abundance is a suitable index for identifying exceptional growth or decline.

A frequency distribution was constructed for the change in abundance of each taxon. The mean change (which is always near zero), the standard deviation, and the standard error of the mean were computed. When this was completed, dates corresponding to positive changes in abundance more than one standard deviation above the mean were selected by computer and a similar selection was done for negative changes more than one standard deviation below the mean change for each taxon. The selection process thus identified the weeks during which conditions favoring growth or leading to mortality were well beyond the average. Excluded by the selection were all of the smaller changes in abundance clustered around the mean. These smaller changes are not likely to be informative for present purposes because they indicate populations that are near steady-state. The times of greatest increase will be assumed to indicate the entry of a particular taxon into the successional sequence, and the times of greatest decrease will be assumed to indicate the departure of that taxon from the successional sequence.

Running parallel to the abundance matrices for phytoplankton are matrices of environmental variables that are necessary for testing the successional paradigm. According to the formulation of the paradigm that was given in the preceding section,

mixed layer thickness would be the best physical guide to successional status of the phytoplankton. The best chemical guide would be the macro-nutrient in greatest demand, which in the case of Lake Valencia is inorganic nitrogen.

Consider first the times of exceptional increase in abundance. The mixed layer thicknesses and nitrate concentrations at the end of these time intervals were selected by computer and aggregated in the form of frequency distributions whose mean, standard deviation, and standard error were determined. This produced for each taxon a mean mixed layer thickness and a mean nitrate concentration corresponding to the periods of notable population increase for each taxon.

Since a successional episode is initiated and maintained in an autogenic mode by physical stability of the water column, we would expect to find that the mixed layer thickness is greatest for growth pulses of taxa appearing late in succession. Fig. 10 depicts the position for growth pulses of each of the seven major taxa found in Lake Valencia along the spectrum of mixed layer thicknesses encountered in Lake Valencia. For each taxon, both the mean and standard error around the mean are indicated. The top axis of the graph is a linear percentile axis. From this axis it is evident where growth of each taxon falls on the spectrum of values observed over the course of the five-year interval for Lake Valencia. The bottom axis of the graph converts the percentile axis to mixed layer thicknesses. Since the frequency of given mixed layer thicknesses is by no means uniform across the range of possible values (0–35 m), the arrangement of mixed layer thicknesses along the bottom axis is not line-

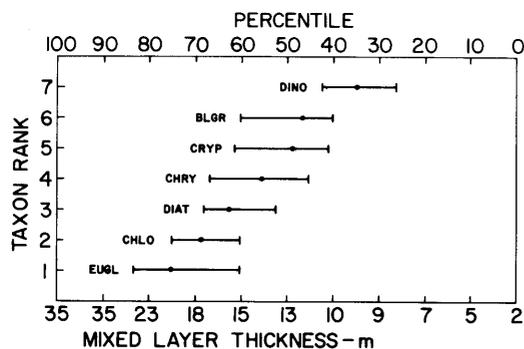


Fig. 10. Mean and standard error of mixed layer thicknesses corresponding to dates when the seven taxa showed increases in abundance greater than one standard deviation above the mean.

ar. For example, the percentile gap between mixed layer thicknesses of 23 and 35 m is the same as the percentile gap between mixed layer thicknesses of 2 and 5 m. Furthermore, a mixed layer thickness of 35 m, which occurs each year at the time of seasonal mixing, is represented in the frequency distribution sufficiently often that it takes up more than 10 percentage points even though it is a unique value.

Although Fig. 10 shows substantial overlap of standard errors, there are differences in the average mixed layer thicknesses corresponding to growth pulses for the different taxa. Except for the inversion of chlorophytes and diatoms in the sequence, the order of appearance is identical to the sequence proposed by the successional paradigm (diatoms, chlorophytes, blue-greens, dinoflagellates). This does not constitute a test of the paradigm, however, insofar as the successional order is determined not only by the time of appearance of a taxon but also by its time of decline, which will be taken up below.

In Fig. 10 the order of appearance of two taxa not included in the predictions made by the successional paradigm is also shown (euglenophytes, chrysophytes). The euglenophytes appear very early in the sequence, i.e., at times corresponding to a thick mixed layer, and chrysophytes appear slightly later, after the diatoms. Consistent with the Lanau work, cryptophytes appear prior to blue-greens.

Figure 11 shows the coincidence of growth pulses with nitrate concentrations in the upper water column. The graph is prepared in the same form as the graph for mixed layer thicknesses. The means are distributed over the left half of the graph (i.e.

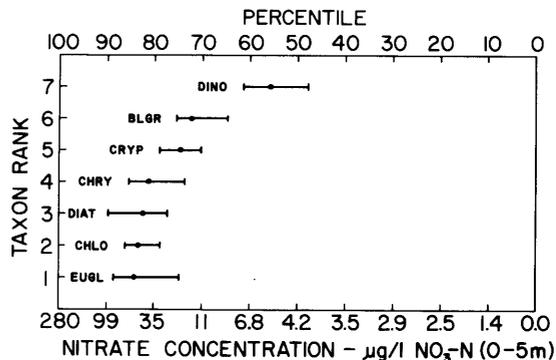


Fig. 11. Mean and standard error of nitrate concentration in the upper 5 m of the water column for dates coinciding with increases in population size more than one standard deviation above the mean.

above 50th percentile), where nitrate concentrations are above the annual average. This is not surprising, since phytoplankton organisms require substantial amounts of inorganic nitrogen for rapid growth. At the same time, the growth pulses do not extend to the very highest nitrate concentrations, which coincide with the period of seasonal mixing. When the lake is actively mixing, phytoplankton species are unable to take advantage of the very high nutrient concentrations because of light deprivation. Thus the growth pulses occur when the nitrate levels are high, but only after they already show some reduction from the maximum as a result of uptake in a stably stratified water column in which light conditions adequate for phytoplankton growth.

The order of appearance of taxa in the sequence of declining nitrate concentrations is identical to that observed for mixed layer thicknesses, but the means for the seven taxa are not distributed over such a wide proportion of the total range of values. The figure shows that euglenophytes, chlorophytes, diatoms and chrysophytes all increased under almost identical conditions. These taxa are able to take advantage of the highest nitrate concentrations coincident with sufficient irradiance for net growth. The growth pulses of cryptophytes occur at slightly lower nitrate concentrations, indicating a slightly later appearance in the autogenic successional sequence. The growth pulses of blue-greens are even further retarded, and the dinoflagellates are extreme in showing their growth pulses very far down the scale of nitrate values with respect to other taxa. Thus the nitrate data suggest that four of the seven taxa begin to enter the successional sequence almost simultaneously when the growth conditions are best, while the other three enter somewhat later when the nitrate concentrations are lower. However, all taxa enter the successional sequence when the nitrate concentrations are above the 50th percentile.

The nitrate concentrations corresponding to significant population declines mark the departure of taxa from the successional sequence. The nitrate concentrations corresponding to population decreases were first screened, however, by exclusion of values coinciding with mixed layer thicknesses changing by more than 5 m. The purpose of this screening was to exclude major disruptions by allo-genic factors as causes for decline and thus focus attention on the autogenic sequence. Fig. 12 shows

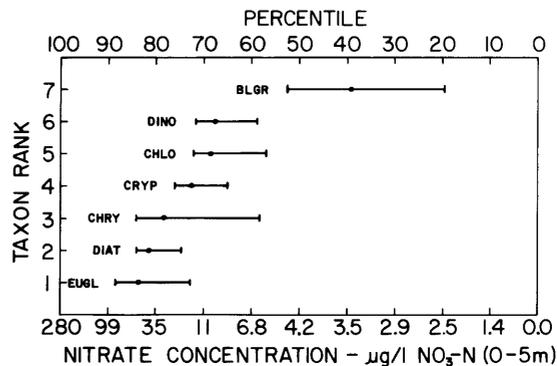


Fig. 12. Mean and standard error of nitrate concentration corresponding to decreases in abundance of the seven major taxa more than one standard deviation below the mean, after exclusion of dates with significant increase in mixed layer thickness (>5 m).

the nitrate data for population declines. As in Fig. 11, taxa are arranged in order from the upper to the lower end of the nitrate scale. The order in which taxa appear is different from the order in which they appeared in Figs 10 and 11, but there is some rough correspondence since euglenophytes, diatoms, and chrysophytes are among the first to decline, just as they were among the first to appear in the successional sequence. For all the taxa except dinoflagellates, the nitrate values corresponding to disappearance from the sequence (Fig. 12) are lower than the nitrate values corresponding to appearance in the successional sequence (Fig. 11). Obviously this must be the case if autogenic succession is accompanied by reductions in the critical macro-nutrient, as postulated. Dinoflagellates are expected to be exceptional in this respect, since their growth is not terminated by lack of nutrient but only by reversion of the autogenic successional sequence through physical events increasing the thickness of the mixed layer and restoring high nitrate levels. Even minor nutrient enrichment by slight increase in mixed layer thickness (<5 m) can reset succession in the dinoflagellate phase. This explains why the decline of dinoflagellates is associated with higher nitrate concentrations than is their increase.

Figure 13 shows the mean nitrate values corresponding to appearance and disappearance in the successional sequence as defined by the population changes discussed above. The taxa differ very great-

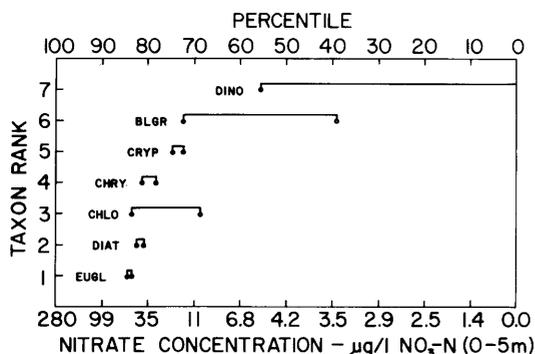


Fig. 13. Span of nitrate concentrations bridging the mean conditions for exceptional increase in abundance (successional entry) and exceptional decrease in abundance (successional exit) of each of the seven major taxa of phytoplankton.

ly in the breadth of the environmental spectrum that they occupy. The interval between favorable and unfavorable conditions in terms of percentiles is very narrow for euglenophytes, diatoms, chrysophytes, and cryptophytes. The interval for chlorophytes, blue-greens, and dinoflagellates is much broader, although the interval for the blue-greens and dinoflagellates extends into that region of the environmental spectrum that is well below optimum for the growth of photosynthetic organisms because of nutrient depletion. The chlorophytes are unique in growing over a very broad spectrum while simultaneously overlapping some of the most ideal conditions for growth. Environmental breadth of the Chlorophyta may be accounted for by the great taxonomic breadth of this group. Exceptional successional breadth for the chlorophytes was also noted by Lewis (1978b) in the study of Lake Lanao.

Since the position of a taxon in the successional sequence is determined both by its appearance in substantial numbers and by its subsequent decline, a reasonable quantitative estimate of the position of a taxon in a successional sequence is the mid-range of the mean values for major increases and major declines. The mid-ranges were thus calculated for the taxa shown in Fig. 13 and the taxa were arranged in order to form a successional sequence. The sequence is given in Table 2, along with the percentile of nitrate concentrations corresponding to the position of the taxon in the successional sequence and the breadth of the environmental range covered by each taxon.

As shown by Table 2, the order of appearance of

Table 2. Successional rank as determined by percentile mid-range between mean nutrient conditions for increase and mean conditions for decline, and percentile breadth between increase and decline.

Taxon	Successional Rank	Percentile Mid-range	Percentile Breadth
Euglenophytes	1	83.4	0.6
Diatoms	2	81.9	1.2
Chrysophytes	3	80.1	2.4
Chlorophytes	4	75.9	14.5
Cryptophytes	5	73.8	1.8
Blue-greens	6	56.3	33.1
Dinoflagellates	7	34.9	43.4

five of the major taxa is exactly as predicted by the successional paradigm. Taxa not included in the paradigm (euglenophytes and chrysophytes) are also positioned with respect to the other taxa. Since the taxa were positioned according to criteria developed earlier by Lewis (1978b), and since the order of appearance of the major taxa in the successional sequence was predicted from the paradigm before evaluation of the Lake Valencia data, it is appropriate to evaluate the validity of the conclusions by methods involving *a priori* probability. The hypothesis to be tested is that the four taxa specified with certainty by the paradigm (diatoms, chlorophytes, blue-greens, dinoflagellates) will appear in the exact order postulated by the successional paradigm. The probability of this happening by chance alone is equal to  $1/4!$ , which is 0.04, below the accepted 95% criterion for verification of an hypothesis.

From the information in Table 2 and the mean and peak abundance of each of the seven class-level taxa in the successional sequence, it is possible to construct in graphical form a generalized but quantitatively based picture of the successional sequence for Lake Valencia. This is given in Fig. 14. In preparing the figure, the mean abundance (cell volume) for each taxon was taken as the baseline abundance for that taxon. As an indication of the height to which each taxon rises in its periods of growth, the annual maxima were selected and then averaged. The position of the abundance peak on the X-axis was determined from Table 2. Position of the peak on the X-axis represents successional

time measured in terms of nitrate concentrations converted to percentiles. In addition, the breadth of each peak was determined from the information in Table 2. Thus the figure, while diagrammatic, is based on average and peak abundances, on the relative successional position of the taxa as determined by the foregoing analysis, and on the relative breadth occupied by each taxon in the successional sequence.

Figure 14 condenses in graphical form the points that have already been made from the tabular material and statistical analysis. In addition, Fig. 14 shows how a synopsis of the successional sequence could be incomplete without counts of relatively rare taxa. Since the baseline abundances in Lake Valencia are very different for the seven taxa, a complete picture of succession requires that very large numbers of cells be counted over long periods. If the counts are very extensive, it is possible to place even relatively rare taxa in the successional sequence, and to verify that they occupy a position specified by a successional paradigm, even though they do not contribute in a major way to average phytoplankton biomass. This is the strongest possible test of the successional paradigm. Even though the paradigm may be of general validity, determinants of the baseline abundance will dictate whether or not a given taxon makes a significant contribution to total phytoplankton biomass in a given lake.

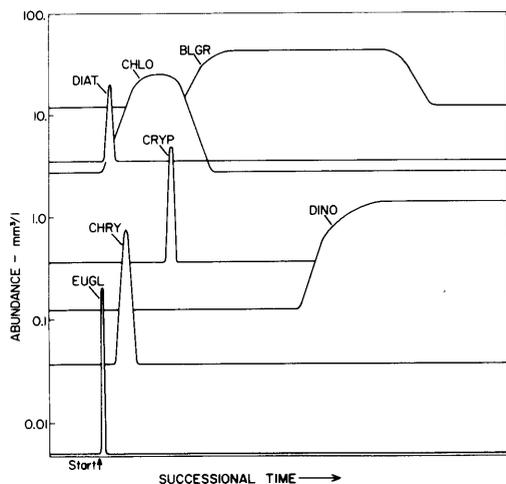


Fig. 14. Synopsis of succession in Lake Valencia based on average and maximum abundances, relative position in the successional sequence, and percentile breadth of position in the successional sequence.

## Conclusions

The conformance of Lake Valencia phytoplankton populations with predictions made by the successional paradigm offer some hope that there is a general successional rule applicable to many kinds of lakes. This pattern may be difficult to discern by simple examination of population data, since there are many instances in which autogenic succession may be reversed or may proceed at different speeds according to environmental conditions. Thus objective quantitative evaluation of the paradigm is essential.

The differing environmental breadths covered by the seven taxa in the successional sequence offer some interesting possibilities for extension of the successional paradigm to cover questions related to taxonomic composition of phytoplankton communities. If the breadths observed in the Lake Valencia study are conservative or semi-conservative properties of the major taxa, then these breadths might be used for predictive purposes in determining expected composition of lakes whose environmental conditions are known. However, studies on other lakes are essential before this possibility can be evaluated. Especially important is the quantitative determination of successional sequences using phosphorus as a macronutrient index in a lake that is phosphorus-limited, since the two presently available analyses are both based on lakes that are nitrogen-limited.

## Acknowledgments

This paper is a contribution to the joint Venezuelan-North American Study of the Lake Valencia. Financial support was provided by National Science Foundation Grants DEB 7604300, 7805324, and 8003883. The Fundación Eugenio Mendoza provided important logistical support. I am grateful to Linda Killan, Betsy Chronic, Diane Larson, Ronna Edgett, and Paul Zilis for counting the phytoplankton, and to reviewers and editors for comments.

## References

- Bendschneider, K. & R. J. Robinson, 1952. A new spectrophotometric method for the determination of nitrite in sea water. *J. Mar. Res.* 11: 87-96.

- Bradbury, J. P., B. Leyden, M. Salgado-Labouriau, W. M. Lewis, Jr., C. Schubert, M. W. Binford, D. G. Frey & D. R. Whitehead, 1981. Late quaternary environmental history of Lake Valencia, Venezuela. *Science* 214: 1299–1305.
- Hutchinson, G. E., 1967. A treatise on limnology. Vol. II. Wiley, New York.
- Levine, S. N. & W. M. Lewis, Jr., 1984. Diel variation of nitrogen fixation in Lake Valencia, Venezuela. *Limnol. Oceanogr.* 29: 887–893.
- Lewis, W. M. Jr., 1973. The thermal regime of Lake Lanao (Philippines) and its theoretical implications for tropical lakes. *Limnol. Oceanogr.* 18: 200–217.
- Lewis, W. M. Jr., 1974. Primary production in the plankton community of a tropical lake. *Ecol. Monogr.* 44: 377–409.
- Lewis, W. M. Jr., 1977. Net growth rate through time as an indicator of similarity among phytoplankton species. *Ecology* 58: 149–157.
- Lewis, W. M. Jr., 1978a. A compositional, phytogeographical and elementary structural analysis of the phytoplankton in a tropical lake. *J. Ecol.* 66: 213–226.
- Lewis, W. M. Jr., 1978b. Dynamics and succession of the phytoplankton in a tropical lake. *J. Ecol.* 66: 849–880.
- Lewis, W. M. Jr., 1978c. Analysis of succession in a tropical phytoplankton community and a new measure of succession rate. *Amer. Nat.* 112: 401–414.
- Lewis, W. M. Jr., 1983a. Temperature, heat, and mixing in Lake Valencia, Venezuela. *Limnol. Oceanogr.* 28: 273–286.
- Lewis, W. M. Jr., 1983b. Interception of atmospheric fixed nitrogen: an explanation of scum formation in nutrient-stressed blue-green algae. *J. Phycol.* 19: 534–536.
- Lewis, W. M. Jr., 1984. A five-year record of the thermal and mixing properties of a tropical lake (Lake Valencia, Venezuela). *Arch. Hydrobiol.* 99: 340–346.
- Lewis, W. M. Jr. & S. N. Levine, 1984. The light response of nitrogen fixation in Lake Valencia, Venezuela. *Limnol. Oceanogr.* 29: 894–900.
- Lewis, W. M. Jr. & W. Riehl, 1982. Phytoplankton composition and morphology in Lake Valencia, Venezuela. *Internat. Rev. ges. Hydrobiol.* 67: 297–322.
- Lewis, W. M. Jr. & J. F. Saunders III, 1979. Two new integrating samplers for zooplankton, phytoplankton, and water chemistry. *Arch. Hydrobiol.* 85: 244–249.
- Lewis, W. M. Jr. & F. H. Weibezahn, 1981. Chemistry of a 7.5-meter sediment core from Lake Valencia, Venezuela. *Limnol. Oceanogr.* 26: 907–924.
- Lewis, W. M. Jr. & F. H. Weibezahn, 1983. Phosphorus and nitrogen loading of Lake Valencia, Venezuela. *Acta Cientifica* 34: 345–349.
- Margalef, R., 1958. Temporal succession and spatial heterogeneity in phytoplankton. In A. A. Buzzati-Traverso (ed.), *Perspectives in marine biology*, pp. 323–349. Univ. of California Press, Berkeley.
- Odum, E. P., 1971. *Fundamentals of ecology*. 3rd ed. Saunders, Philadelphia. 574 pp.
- Reynolds, C. S., 1980. Phytoplankton assemblages and their periodicity in stratifying lake systems. *Holarctic Ecol.* 3: 141–159.
- Smayda, T. J., 1980. Phytoplankton species succession. In I. Morris (ed.) *The physiological ecology of phytoplankton*, pp. 493–570. Univ. Calif. Press, Berkeley.
- Tansley, A. G., 1935. The use and abuse of vegetational terms and concepts. *Ecology* 16: 284–307.
- Wood, E. D., F. A. J. Armstrong & F. A. Richards, 1967. Determination of nitrate in sea water by cadmium-copper reduction to nitrate. *J. Mar. Biol. Assoc. U.K.* 47: 23–31.