ANALYSIS OF SUCCESSION IN A TROPICAL PHYTOPLANKTON COMMUNITY AND A NEW MEASURE OF SUCCESSION RATE

WILLIAM M. LEWIS, JR.

Department of E.P.O. Biology, University of Colorado, Boulder, Colorado 80309

A quantitative measure of succession rate was recently introduced by Jassby and Goldman (1974b), who suggested that such a measure might correlate with various environmental variables. Jassby and Goldman applied the succession rate index to a plankton community, although their rationale would also apply to other community types if sufficient data could be collected.

The analysis of succession in complex communities typically takes the form of a bulky statistical or verbal description. Some more succinct extract of succession data is also necessary if communities are to be extensively compared. The succession rate concept put forth by Jassby and Goldman is therefore a significant step toward the development of suitable analytical tools.

The Jassby-Goldman (JG) index makes several assumptions in order to quantify succession rate. Although all assumptions are to a degree arbitrary, one critical assumption of the JG index involving the weighting of individual species contributions seems unnecessarily weak and may interfere substantially with the usefulness of the index. A similar index that does not require the assumption can easily be formulated and seems to perform better in an empirical test.

THEORY

The concept of succession in biological communities is widely used but loosely defined. In his attempt to identify the critical attributes of succession, Margalef (1968, p. 27) recognized that a concrete definition of succession could not be formulated without arousing differences of opinion. A rigid definition clearly would destroy the universal value of the succession concept, but quantitative studies cannot proceed without rigid definitions. The solution to this problem that has become traditional in similar cases involving such concepts as diversity, competition, and stability is that the noun itself continues to represent a very broad set of biological phenomena, while rigid definitions that may lack universal appeal are used in quantitative work.

Reasonable criteria for measurement of succession are (1) maximum simplicity consistent with reality and (2) concordance with the most widely accepted components of the succession concept. It is possible that more than one approach will meet these requirements. Although common usage of the term

"succession" does not suggest a rigid universal definition, two conceptual components do seem to be widely accepted: (1) succession constitutes a change in relative abundance of species in a community, and (2) this change is directional. The directional aspect of the succession concept derives originally from analysis of land plant communities (Cowles 1899, 1901; Clements 1916). Margalef (1958, 1968) has attempted to demonstrate a similar directional aspect of succession in plankton communities, but this is not yet well verified.

The directional aspect of succession, although widely accepted, obviously inhibits quantification, as the degree of change in community composition is much easier to quantify than its direction. An example illustrates the difficulties. A pulse of nutrients in a plankton system typically sets succession back to a pioneer stage analogous to the pioneer stages of terrestrial plant succession (Margalef 1967). Two major kinds of observations can be made on the community as succession proceeds from this pioneer stage. The first is rate of change in community composition (succession rate), which would in most cases probably be high at first and then decline. The second kind of observation would encompass any overall trends in quality of the community (succession direction). Margalef (1958) postulates that typical qualitative or directional changes include replacement of small by large species and of nonmotile by motile species as succession proceeds from the pioneer stage. If no such trends are in fact identifiable, then succession would have a negligible or weakly developed directionality, even though its rate would still be quite measurable. Rate and direction are clearly separate considerations, even though they may prove to be related statistically, and rate is the easier of the two to quantify.

The Jassby-Goldman succession rate index does not measure the directional aspect of succession, as it is calculated solely from rates of change in the abundance of species. The index is:

$$\sigma_j = \left[\sum_i (dc_i/dt)^2 \right]^{1/2},$$

where

$$c_i(t) = b_i(t) / \left[\sum_i b_i(t)^2 \right]^{1/2}$$

and $b_i(t)$ is the biomass of the ith species at time t. Separation of rate from direction is clearly necessary in the formulation of such an index and may even be desirable. The consequences of this separation deserve some preliminary consideration, however, as succession is commonly viewed as a directional phenomenon.

Succession in plankton communities is episodic. In a typical sequence, plankton autotrophs respond to a sudden increase in availability of limiting nutrients by an increase in overall growth rate and a shift in community composition favoring certain fast-growing species. As nutrients are depleted, there is a shift in relative abundance of species favoring species with adaptations to nutrient scarcity (e.g., Pearsall 1932; Margalef 1958; Nauwerck 1963; Planas 1973). If plankton succession has an identifiable direction, as Margalef

believes, then qualitative changes during this transition from high to low nutrients should be predictable and general. The successional trend may be interrupted at any time, however, by environmental perturbations leading to complete or partial restitution of higher nutrient levels and an abrupt shift back toward the former community composition. This constitutes a reversal of direction and onset of a new episode. An index of succession rate alone does not specifically recognize the onset of a new episode, and the transition to a new episode is treated as part of a continuous successional change, even though it might be more properly viewed for some purposes as the end of one sequence and beginning of another.

At least one textbook author has noted that not all succession is directional (Poole 1974). Odum (1971) clarifies the problem connected with direction by classifying succession as either autogenic, driven mainly by changes resulting from the action of the biota on the habitat, or allogenic, driven mainly by changes not originating in the biota. Autogenic succession is likely to be more strongly directional than allogenic succession. It would be possible to argue that only Odum's autogenic succession should be called succession and that his allogenic succession should be called something else. This would require some impossibly fine distinctions regarding the relative importance of changes having origins internal and external to the community, however. For present purposes it seems reasonable to accept the implicit assumption by Jassby and Goldman that the rate and directional aspects of succession can and should be separated for analytical purposes.

Any index of succession rate is likely to combine the changes in abundance of individual species. The principal question in formulation of an index is how the contributions of individual species to overall change should be weighted. According to the guideline of maximum simplicity consistent with reality (Occam's razor), the changes in all species should be weighted equally. This means that a loss or gain of one individual per unit time in species A should have the same effect on the index as a loss or gain of one individual per unit time in species B, regardless of the abundance or ecological roles of A and B. The reasoning behind this conclusion may not be immediately obvious, however.

There is some evidence showing that individuals of different species are not always equal in their effect on community dynamics (e.g., Paine 1969). This might suggest that species should be weighted unequally. If the species were weighted unequally, however, then some general hypothesis would have to be formulated which would relate a measurable species property to the relative influence of individual species on community dynamics. A general hypothesis of this type is clearly premature at present. The α matrix for a community, computed empirically (Levins 1968), might serve as a foundation for unequal weighting but would be impractical in most cases and especially so for phytoplankton because of the technical difficulties associated with the estimation of α values for such species. Since a general rationale for unequal weighting would be unfounded at present, and an experimental or observational rationale for unequal weighting seems impractical, rational unequal weighting is not a

possible foundation for a succession rate index, although it might well become
so in the future. This leaves arbitrary unequal weighting and equal weighting as
possible foundations for an index. By the rule of simplicity, arbitrary unequal
weighting is less justifiable than equal weighting.

Even if the species are all treated identically, there are two possible bases for
an index, as changes in a given species can be expressed as a proportion of the
abundance of that species or as a proportion of the entire community. Actually,
since succession is a community phenomenon, only the latter alternative is
defensible. The first alternative in effect weights species in inverse relation to
their abundance. A twofold increase in the rarest species would not be equated
by most observers with a twofold increase in the most abundant species.
Changes in abundance of species should therefore be expressed in relation to
the abundance of all species combined.

The JG index does not weight species equally and thus carries an implicit
and unwarranted hypothesis concerning the relative importance of species. A
simple example illustrates this point. Let a hypothetical community consist of
30 individuals and three species. All individuals have the same biomass, so it is
inconsequential whether abundance is measured as number or biomass. Let the
relative abundances of species change over a unit of time from 10, 10, 10 to 10,
8, 12 by a shift of two individuals from one species to another. The value of $\hat{\sigma}_j$ in
this case is .161 day^{-1} (values of the index are always > 0 and usually much
less than 1 for realistic examples). An identical numerical shift in abundances
when the species have different initial abundances produces a different index
value. For example, if the initial abundances are 1, 1, 28 and change to 1, 3, 26
over a unit of time by a shift of two individuals, the value of $\hat{\sigma}_j$ is .079 day^{-1}. A
given shift in abundance of species in a community of fixed size thus produces
an index value that is dependent on the initial abundances. In general, a shift in
a more equitably organized community produces higher values than the same
shift in a less equitably organized community. This is due to an arbitrary
unequal weighting of individuals belonging to species of differing abundance
and is not defensible without accompanying theory showing why individuals
from different species should not be weighted equally.

It is possible to formulate a simple succession rate index which shares the
desirable features of the JG index but weights changes in all species identically.
This index, which will be symbolized σ_s and called the summed difference (SD)
index, is:

$$\sigma_s = \sum_i |d[b_i(t)/B(t)]|/dt,$$

which is estimated over a short time interval as

$$\hat{\sigma}_s = \frac{\sum_i |[b_i(t_1)/B(t_1)] - [b_i(t_2)/B(t_2)]|}{t_2 - t_1},$$

where $b_i(t)$ is the abundance of the ith species at time t, and $B(t)$ is the size of the
community at time t.

The SD and JG indexes are similar in their insensitivity to change in the size
of a community without some accompanying change in relative abundance of

species. Both indexes yield a value of zero for any hypothetical community that is shrinking or expanding when all species are changing at an identical rate.

Jassby and Goldman have described their index in terms of a geometric model which helps clarify the formulation of the index, although the model is not really related to the biological validity of the index. They visualize all possible community compositions as falling on the surface of a hypersphere. The JG index is the rate of movement from one point to another on the hypersphere surface. The criticisms of the JG index can be restated in terms of this model. It is most convenient to think in terms of a community with three species, in which case the index is visualized as movement on the surface of a sphere. The convention is adopted that species are ordered in increasing abundance and correspond successively to the dimensions x, y, z. Communities with one strongly dominant and two relatively rare species will thus be situated near the pole of the sphere, and communities with species of nearly equal abundance will be near the equator. For communities occupying positions very near the pole of the sphere, a relatively large shift in abundance is required to cause appreciable movement across the sphere surface. For communities near the equator, an identical numerical shift produces much more movement and thus generates a higher index value. In the example already given, the shift from 1, 1, 28 to 1, 3, 26 occurs near the pole and thus generates a smaller index value than the shift from 10, 10, 10 to 10, 8, 12, which occurs in a community near the equator. According to the arguments concerning equal weighting, the rates should be the same for these two communities.

The disparity of succession rates illustrated by the example is explained in geometric terms by the curvature of the sphere surface. A hypervolume with plane surfaces circumvents this problem, and the SD index can in fact be visualized as based on an n-dimensional polygon. For both of the examples given above, the SD index generates the value $\hat{\sigma}_s = .133$ day^{-1}. In geometric terms, the community is initially resting on the surface of a plane. A change in composition moves the community out of the plane in dimension x some fixed distance according to change in species 1, another distance in dimension y corresponding to change in species 2, and finally a distance in dimension z for the third species, such that the community returns to the plane. The index then corresponds to the sum of the distances moved in the three dimensions and not to the distance between the initial and final resting places in the plane.

If one accepts the equal weighting of species in the quantification of succession, the SD index has a sounder theoretical base than the JG index. The JG index is closely related to the SD index but distorts succession rates of communities that have very high or very low equitability.

APPLICATION

Both the JG and SD indexes were computed for the phytoplankton of Lake Lanao, Philippines. Lanao is a large lake (365 km^2) of moderate depth (mean, 60 m) and unexceptional water chemistry (conductance, 105 μmho/cm at 25° C). There is a marked succession of species in conjunction with both
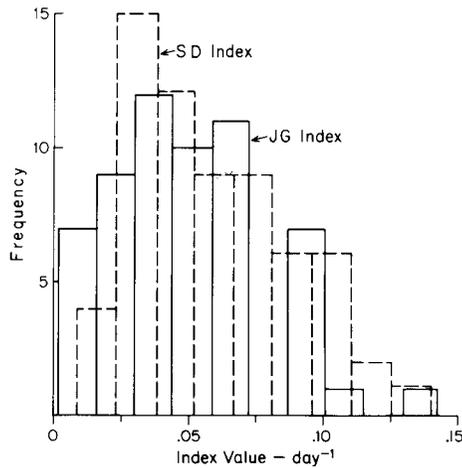
Fig. 1.—Frequency distribution for 64 different measurements of phytoplankton succession rate taken over a 65-wk period on Lake Lanao; JG = Jassby-Goldman index, SD = summed difference index.

seasonal and nonseasonal changes in the lake, as in temperate lakes (Lewis 1978).

The abundance data on phytoplankton span 65 wk with a constant interval of 1 wk between samples. The samples were taken in midlake from the euphotic zone (0–15 m) with an integrating sampler. Counts of all 70 autotrophic species were obtained with an inverted microscope. The counts produced an estimate of the number of independent biomass units (i.e., individuals) of each species. Depending on the species, a unit might be comprised of one or several cells. For example, the species *Scenedesmus ecornis* always occurs as groups of four attached cells, so for counting purposes an individual is considered to consist of such a group of four cells. For each species, the mean size of the individual biomass unit was used to convert numerical abundance to biomass abundance. The data set of interest here thus consists of weekly estimates of the abundance of 70 species reported as numbers of individuals per unit area or as weight per unit area within the euphotic zone over a period of 65 wk. Technical details of productivity and other measurements discussed below are given elsewhere (Lewis 1974, 1978) as is the seasonal physicochemical cycle of the lake (Lewis 1973).

Figure 1 shows the frequency distributions of the JG and SD indexes for the 65-wk study period. Both index values are distributed similarly with a slight skew to the right. By Kolmogorov-Smirnov criteria (Conover 1971), neither distribution differs from normality at $\alpha = .05$, but the P values are near significance and the skew would thus probably prove to be real if more data were available. The high values on the right tail in figure 1 correspond to brief periods when supply of resources is nearly optimal as indicated by marked pulses of net production and autotroph biomass (fig. 2). Transitions into and out of such periods result in high succession rates and high absolute values for
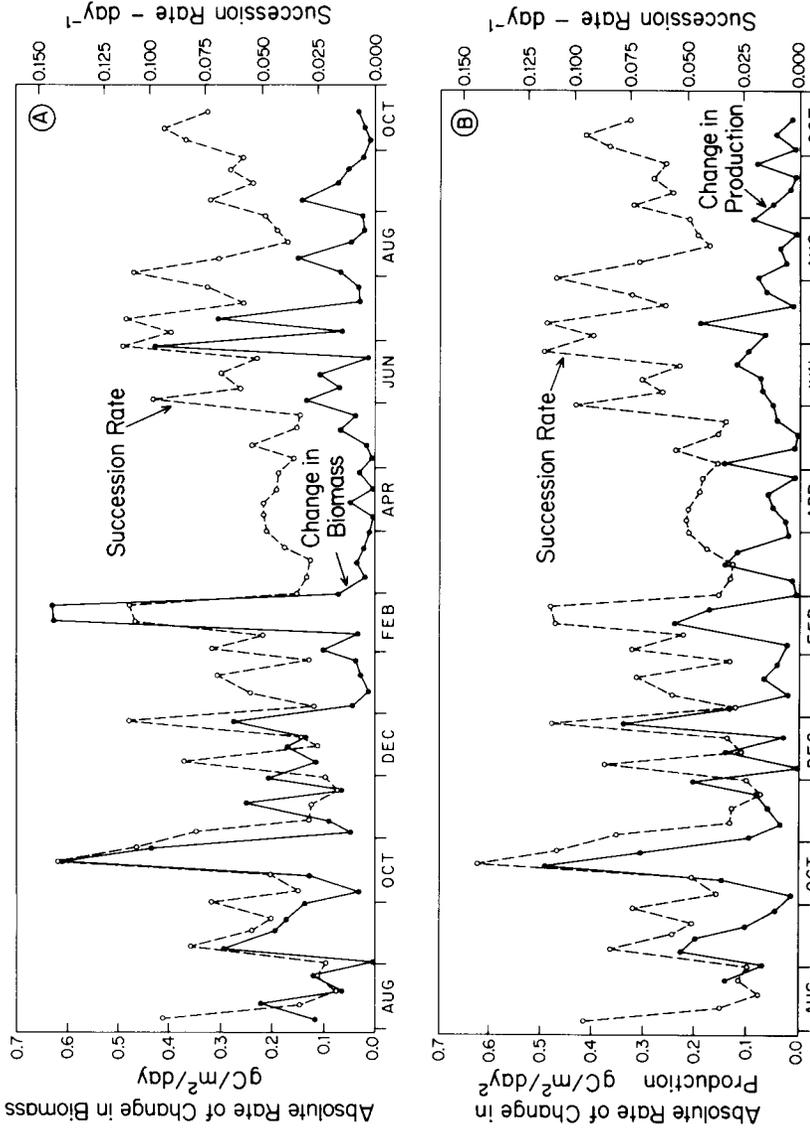
FIG. 2.— Pattern of succession rates, as measured by the summed difference succession rate index (based on biomass) compared with absolute values of the first derivatives of biomass and primary production with respect to time on Lake Lanao. A. Absolute value of rate of change (per day) in total autotroph biomass plotted with succession rate. B. Absolute value of rate of change (per day) in daily net primary production plotted with succession rate.

the rates of change in production and biomass. For this reason, high succession rate values commonly appear in pairs (fig. 2).

As succession is a response to environmental change, rate of succession should be related statistically to rate of environmental change. Measuring the rate of environmental change directly is difficult, as multiple factors of unknown relative importance are involved.

For Lake Lanao phytoplankton, it is convenient to break down aggregate environmental change into two categories: (1) change in factors affecting quantity or quality of resource supply to the phytoplankton (growth control mechanisms), and (2) change in quantity or quality of factors affecting phytoplankton attrition (loss control mechanisms). These two categories encompass all obvious sources of environmental change except temperature, which could affect both growth and loss but varies little and thus bears no detectable statistical relation to phytoplankton community dynamics in this lake (Lewis 1974).

The two most important growth control mechanisms are sunlight availability, which is the predominate controlling agent during the season when the lake is not thermally stratified, and nutrient availability, which is the predominate controlling agent during the season when the lake is thermally stratified (Lewis 1974). Phytoplankton biomass and primary production are strongly related to these two aspects of resource supply. In Lake Lanao, variation in phytoplankton biomass and primary production is much more influenced by irregularities in resource supply than by irregularities in attrition (Lewis 1978). Absolute rates of change in phytoplankton abundance and primary production therefore constitute a community bioassay of the rate of change in resource supply to the phytoplankton and should be statistically related to succession rate.

Loss control mechanisms include grazing and sinking. Grazing accounts for a small proportion of biomass loss (mean, $< 7\%$/day) but may nevertheless exercise a qualitative effect on community composition. Grazing variability must therefore be considered a potentially significant aspect of environmental change and should be tested for statistical relationship to succession rate. Sinking rate, another mechanism of biomass loss, varies in direct correlation with nutrient supply due to the common importance of turbulence to the two factors. The relationship of turbulence, which retards sinking, to succession rate should therefore emerge from the analysis of resource supply mechanisms discussed above.

The above arguments are intended to justify the conclusion that environmental change in Lake Lanao is well described by absolute rates of change in phytoplankton abundance and primary production measured over short time intervals and by grazing rates. If this conclusion is valid, then any defensible measure of succession rate should be related statistically to one or more of these variables.

Table 1 shows a correlation matrix for the JG and SD succession rate indexes and three major community variables plus their rates of change and their absolute rates of change: (1) autotroph abundance, (2) net primary

TABLE 1

CORRELATIONS OF THE JG AND SD SUCCESSION RATE INDEXES WITH
PLANKTON COMMUNITY PROPERTIES OF LAKE LANAO, PHILIPPINES

| | BIOMASS | | NUMBERS | |
VARIABLE	JG	SD	JG	SD
Autotroph abundance (no. 64):				
B_p	−.23	.00	−.09	−.06
$\Delta B_p/\Delta t$	−.05	−.05	−.05	.00
$\mid \Delta B_p\ \Delta t \mid$	.28*	.57**	.30*	.34**
Primary production (no. 60):				
PN_p	−.21	.02	−.01	−.05
$\Delta PN_p/\Delta t$	−.04	−.05	.15	.18
$\mid \Delta PN_p/\Delta t \mid$	.14	.44**	.35**	.32**
Grazer biomass (no. 50):				
B_g	.16	.29*	.26	.30*
$\Delta B_g/\Delta t$	−.12	−.10	−.05	−.05
$\mid \Delta B_g/\Delta t \mid$	−.13	.01	.01	.07

NOTE.—PN_p = net primary production, B_p = abundance of primary producers (phytoplankton), B_g = biomass of grazers. JG and SD index values under the biomass column were computed from changes in biomass of individual species. Under the numbers column the index values were derived from changes in numbers of individuals for each species.
* $P < .05$.
** $P < .01$.

production, and (3) grazer biomass. The table reports the Pearson product-moment correlations, but nonparametric correlations involving fewer statistical assumptions produce virtually the same result. Each of the variables was measured concurrently with succession rate over most or all of the 65-wk period. The SD and JG indexes of table 1 have been computed both on the basis of biomass and numbers of individuals, as the results sometimes differ for these two methods of computation.

There is no significant correlation between autotroph abundance (numbers or biomass) and either of the succession rate indexes, nor is there any correlation between the rate of change in autotroph abundance and either of the indexes. These are entirely reasonable results. The succession rate may be low when abundance is either high or low if environmental conditions are stable and may be high when abundance is either high or low if environmental conditions are unstable. It would therefore be surprising if abundance were related to succession rate. Also, over any appreciable length of time, the rate of change in abundance is negative approximately half the time and positive approximately half the time. This means that any correlation of succession rate with degree of change in abundance will be masked by the changing sign of the abundance derivative.

A positive correlation between succession rate and absolute value of the rate of change in autotroph abundance would be reasonable if the latter is an index of change in environmental conditions, as postulated earlier. In a typical

sequence, deep mixing brings nutrients to the surface, which leads almost immediately to a pulse in primary production and phytoplankton abundance and a shift toward diatom dominance. Without further nutrient input, the nutrient availability quickly declines, leading to a decline in phytoplankton abundance and primary production and a shift to chlorophytes and later to bluegreens and dinoflagellates (Lewis 1978). Shifts in resource availability thus result in shifts in phytoplankton abundance, production, and community composition after a short period incorporating only the growth lag of the phytoplankton. As will be demonstrated below, the growth lag is usually shorter than the sampling interval and is therefore of little practical concern in a correlation analysis.

The correlation between absolute rate of change in phytoplankton biomass and succession rate is in fact significant for both the JG and SD indexes of succession rate, but the correlation with the SD index is much stronger (table 1). This may be due to the weaker founding assumptions of the JG index. The SD index and absolute rate of change in autotroph biomass are plotted against time in figure 2A to show the relation indicated by the correlation. When autotroph abundance and succession rate are computed on the basis of numbers of individuals rather than biomass, both indexes show a significant correlation and the strength of the relationship is more nearly the same for the two indexes.

Primary production and the succession rate indexes are related in much the same way as autotroph abundance and the indexes. Contrary to the indication of table 1, one might expect that succession would proceed more rapidly at high than at low levels of production and that this would produce a positive correlation between succession rate and production. There are two major reasons why this does not occur. (1) Productivity varies much more than turnover rate, as autotroph biomass is strongly correlated with productivity. The proportions of various species may therefore change almost as rapidly at low productivity levels as at high productivity levels. (2) Changing environmental conditions are the driving force for succession, but the rate of change in conditions is more strongly related to the rate of change in productivity than to the level of productivity. The lack of correlation between productivity and succession rate is therefore not surprising (table 1).

The rate of change in primary production does not correlate with succession rate for precisely the same reason that rate of change in abundance does not, i.e., due to the change in sign of the derivative. The absolute value of the rate of change in productivity does correlate with succession rate, however, as it reflects the rate of change in environmental conditions, whether this change be repressive or stimulatory for phytoplankton growth. The correlation appears as expected for the SD index whether the index is computed on the basis of biomass or numbers of individuals (table 1). The JG index does not show the relationship when the index is computed from biomass but does show it when the computations are based on numbers of individuals.

Grazing rate is also a possible correlate of succession rate. Total biomass of grazers is considered for present purposes to be an index of grazing rate. When

grazer biomass is high, succession may be affected by grazing as a result of selection of food size or quality by grazers (Burns 1968; Wilson 1973; Infante 1973; Porter 1973). Certain factors minimize this effect in Lake Lanao, however. (1) The grazer populations tend to follow the autotroph populations, hence proportional loss of autotroph biomass to grazing is much more constant than grazer biomass itself. (2) The loss of autotrophs to grazing accounts for only a small proportion of net production. In 1970-1971, the average loss was 7%/day and the maximum loss at any time of year was 15%/day. Similar situations exist in other lakes (Nauwerck 1963; Jassby and Goldman 1974a). The fate of the ungrazed algal biomass in these lakes is still a matter for speculation.

Table 1 suggests a positive relationship between grazing rate and succession rate as measured by the SD index, although the coefficients are fairly low. This is difficult to interpret on the basis of table 1 alone, as grazing rate may be high at times when succession rate is high simply because the grazers peak in response to pulses of autotroph growth. Computation of partial correlation coefficients partly solves this interpretive difficulty. When grazer biomass (B_g) is controlled for autotroph biomass (B_p), the correlation of B_g with either of the succession rate indexes is almost identical to the uncontrolled values shown in table 1. This indicates that high grazing pressure does speed succession, although the magnitude of the effect is not so great as might be expected. Once again, the SD index is more sensitive to the effect than the JG index.

Absolute value of the rate of change in grazing is not correlated with succession rate. This variable probably does reflect environmental change, but only with a long and unpredictable lag caused by the slow demographic response of zooplankton and the relay of environmental changes through the first trophic level.

In general, table 1 shows that the JG index differs greatly in its relationship to community variables according to whether it is computed from numbers or biomass. Positive relationships are generally stronger when computations are based on numbers rather than biomass (table 1). The SD index does not show such a large disparity in relationships when the measure of abundance is switched from numbers to biomass. This difference between indexes is explained by the difference in species weighting strategies on which they are based. The SD index is sensitive only to changes in relative abundance of species, whereas the JG index is affected by the initial structure of the community as well as its rate of change. Since the structure of the community is different when it is expressed in terms of numbers than it is when expressed in terms of biomass, behavior of the JG index differs considerably according to the method of abundance measure. As indicated earlier, this particular sensitivity of the JG index is not based on ecological reasoning and is therefore undesirable.

The relationships between variables in table 1 could easily be affected by time lags. If the correlations are repeated with the incorporation of time lags, no significant positive correlations are obtained. Time lags must occur in nature, but the week between samples is sufficiently long to prevent the lag

TABLE 2

RESULTS OF LINEAR MULTIPLE REGRESSION ANALYSIS

Dependent Variable	% Accountable Variation $|\Delta B_p/\Delta t|$	% Additional Accountable (B_g)	% Additional Accountable $|\Delta PN_p/\Delta t|$	Overall Significance (P)
JG (biomass)	14.6	2.5	.0	.064
SD (biomass)	43.6	8.3	1.0	.001
JG (numbers)..........	38.7	6.4	.1	.001
SD (numbers)..........	35.4	9.3	.3	.001

NOTE.—The linear multiple regression analysis was done to determine the extent to which variation in the succession rate can be explained by variables discussed in the text. Variables were entered into the regression in the order indicated. Results are shown for analyses based on both numbers of individuals and biomass.

effect from appearing in the analysis. Average phytoplankton biomass turnover time in Lanao is 1.2 days, so adjustments in the autotroph component of the plankton occur very rapidly in response to any change in environmental variables.

A linear regression model was used as a supplement to table 1 so that the amount of variation in the indexes attributable to the separate factors could be compared (table 2). Table 1 suggests that only three of the nine variables considered above would constitute significant predictors of succession rate: (1) absolute rate of change in phytoplankton abundance, (2) absolute rate of change in net primary production, and (3) grazer biomass. The multiple regression confirms this and also shows that the inclusion of rate of change of primary production (2) does not add significantly to explained variance provided the other two variables have already been considered. The SD index in particular is well predicted by the linear regression and a large amount of the total index variance is explained. Table 2 shows that grazer biomass accounts for a distinctly separate component of variance than absolute rate of change in abundance. This supports the hypothesis that grazer biomass is significant as an index of the intensity of selective attrition, whereas the absolute rate of change in autotroph abundance is significant as an index of change in resource supply. These two factors appear to have effects which are separate and to a large extent additive.

SUMMARY

Succession entails changes in the relative abundance of species in a community. The Jassby-Goldman (JG) index of succession rate is affected by any change in the relative abundance of species but weights contributions from different species unequally. There is no apparent ecological foundation for this unequal weighting. A more defensible measure of succession rate can be derived from the summed change in abundances of all species, independent of sign, expressed as a proportion of the whole community. A new index of succession rate obtained in this way is named the summed difference (SD) succession rate index.

Analysis of succession in the plankton community of Lake Lanao, Philippines, shows that both the JG and SD succession rate indexes are positively correlated with three community variables: (1) absolute rate of change in autotroph abundance (numbers or biomass), (2) absolute rate of change in net primary production, (3) grazing rate. The first two variables are measures of the overall rate of change in resource supply to the phytoplankton, and grazing intensity is a measure of selective attrition. Positive relationships between these variables and succession rate are generally stronger if succession rate is measured by the SD index rather than by the JG index. A multivariate approach shows that the variance in succession rate attributable to change in resource supply is largely distinct from that attributable to selective attrition by grazing. According to a linear model, change in resource supply accounts for about 44% of variance in succession rate and grazing accounts for an additional 8%.

LITERATURE CITED

Burns, C. W. 1968. The relationship between body size of filter-feeding Cladocera and the maximum size of particle ingested. Limnol. Oceanogr. 13:675–678.

Clements, F. E. 1916. Plant succession: analysis of the development of vegetation. Carnegie Inst. Washington Pub. 242. 512 pp.

Conover, W. J. 1971. Practical nonparametric statistics. Wiley, New York. 642 pp.

Cowles, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Bot. Gaz. 27:95–117, 167–202, 281–308, 361–391.

———. 1901. The physiographic ecology of Chicago and vicinity. Bot. Gaz. 31:73–108, 145–181.

Infante, A. 1973. Investigations on the incorporation of different algae by some zooplankton-species. Arch. Hydrobiol. Suppl. 42:340–405.

Jassby, A. D., and C. R. Goldman. 1974a. Loss rates from a lake phytoplankton community. Limnol. Oceanogr. 19:618–627.

———. 1974b. A quantitative measure of succession rate and its application to the phytoplankton of lakes. Amer. Natur. 108:688–693.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, N.J. 120 pp.

Lewis, W. M., Jr. 1973. The thermal regime of Lake Lanao (Philippines) and its theoretical implications for tropical lakes. Limnol. Oceanogr. 18:200–217.

———. 1974. Primary production in the plankton community of a tropical lake. Ecol. Monogr. 44:377–709.

———. 1978. Dynamics and succession of the phytoplankton in a tropical lake. J. Ecol. (in press).

Margalef, R. 1958. Temporal succession and spatial heterogeneity in phytoplankton. Pages 323–349 in A. Buzzati-Traverso, ed. Perspectives in marine biology. University of California Press, Berkeley.

———. 1967. Some concepts relative to the organization of plankton. Oceanogr. Marine Biol. Annu. Rev. 5:257–289.

———. 1968. Perspectives in ecological theory. University of Chicago Press, Chicago. 111 pp.

Nauwerck, A. 1963. Die Beziehungen zwischen Zooplankton und Phytoplankton im See Erken. Symb. Bot. Upsalienses 17(5):1–163.

Odum, E. P. 1971. Fundamentals of ecology. 3d ed. Saunders, Philadelphia. 574 pp.

Paine, R. T. 1969. A note on trophic complexity and community stability. Amer. Natur. 103:91-93.

Pearsall, W. H. 1932. Phytoplankton in the English lakes. II. The composition of phytoplankton in relation to dissolved substances. J. Ecol. 30:241-262.

Planas, M. D. 1973. Composition, ciclo y productividad de fitoplancton del lago de Banyoles. Oecol. Aquatica 1:3-106.

Poole, R. W. 1974. An introduction to quantitative ecology. McGraw-Hill, New York. 523 pp.

Porter, K. G. 1973. Selective grazing and differential digestion of algae by zooplankton. Nature 244:179-180.

Wilson, D. S. 1973. Food size selection among copepods. Ecology 54:909-914.