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Among Phytoplankton Species**



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NET GROWTH RATE THROUGH TIME AS AN INDICATOR OF ECOLOGICAL SIMILARITY AMONG PHYTOPLANKTON SPECIES¹

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Abstract. Demographic data on 30 phytoplankton species of Lake Lanao, Philippines, are used to test some specific hypotheses relating ecological similarity of species to their phylogenetic relationship, mean abundance, size, surface:volume ratio, and morphology. Ecological similarity is quantified in terms of the correlation of weekly growth rates for species pairs over a 65-week period. About 1/3 of all 435 unique species pairs produce significant positive correlations. The frequency distribution of the correlation values is displaced to the right of zero to the extent that there are no significant negative correlations. This is interpreted as evidence against strong interspecific antagonisms such as those which might be produced by heteroantibiosis. The incidence of significant positive correlations is significantly higher among pairs belonging to the same taxonomic division or among pairs having the same morphotype than among pairs chosen at random. Species grouped by size, S/V ratio, or mean abundance are not significantly more similar to each other than to species chosen at random. On this basis phylogenetic relationship and morphotype appear to be of general (i.e., strategic) significance in community organization, whereas size and S/V ratio are of specific (i.e., tactical) significance because they are relevant in the reaction of species to certain environmental variables but not to others. Mean abundance, which is itself a manifestation of such specific characters as S/V ratio and morphology, fails as a grouping criterion because succession proceeds by shifts in both dominant and rare species. The greater similarities observed between species of common phylogenetic relationship or morphology, while statistically detectable, are quantitatively weak and thus suggest relatively poor coherence of species groups.

Key words: *Community organization; niche; Philippines; phytoplankton; succession.*

INTRODUCTION

Beginning with Charles Elton, ecologists have taken advantage of the principle that simple natural systems share many of the features of complex systems but are generally easier to study. Certain phenomena, however, may be properly studied only in complex systems. For example, a complex community might be most appropriate as a vehicle for some studies of community organization. Simple communities ordinarily occur in nature where abiotic stress is high, and this may distort the relative importance of the biotic interactions that ordinarily influence community structure.

Plankton systems are among the most tractable of complex biological units, and this accounts for their use as illustrative material for some important concepts in ecology (e.g., Hutchinson 1961, Margalef 1968). Unfortunately, most comprehensive plankton studies antedate the recent focus of ecological thought on competition as a determinant of community structure.

Spatial separation of species that is effected and maintained by competition is now a clearly documented feature of community organization among

vertebrates (MacArthur 1958, Schoener 1968, 1974, Cody 1974, Roughgarden 1974). In addition, most studies demonstrating spatial separation at least suggest the existence of other kinds of separation, especially temporal or dietary. Examples are the studies of Schoener (1968, 1975) and Pianka (1973) dealing with overlap in food habits among lizards. Spatial separation and other supplementary resource-partitioning mechanisms have also been documented for zooplankton species (Sandercock 1967, Miracle 1974, Mararewicz and Likens 1975, Lane 1975).

For the phytoplankton, spatial separation of species is not so prominent due to the absence of substrate and poor motility of the organisms involved. By analogy with the findings for vertebrates, particularly Schoener's (1975) most recent work, it is logical to suppose that inadequacy of the spatial separation mechanism in phytoplankton simply shifts the competitive interaction to other variables. This was in fact suggested by Hutchinson (1961) and is at least implicitly evident in subsequent commentary related to the plankton "paradox" (Richerson et al. 1970, Grenny et al. 1973, Titman 1976). However, further theoretical advances are difficult without considerably more information about phytoplankton community organization than has been available in the past. This deficiency is being remedied by a

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series of studies using statistical techniques to compare and group species (Margalef 1958, 1974, Levandowsky 1972, Allen and Koonce 1973, De Amezaga et al. 1973, Iltis 1974). Hypotheses that seek to explain phytoplankton community organization will rely heavily on such studies as a source of valid generalizations. The following analysis of plankton abundance data from Lake Lanao, Philippines, is also an attempt to explain community organization in terms of the characteristics of individual species.

RATIONALE OF ANALYSIS

In two previous studies, I have approached the problem of community organization in the Lake Lanao phytoplankton from two different perspectives. First I determined the coincidence of growth periods in individual species with the values for various physical and chemical variables. On this basis, I positioned species on environmental gradients by a rationale similar to that used for terrestrial plants (Whittaker 1967), except that the gradient analysis was based on variation through time rather than through space. The species segregated along gradients of nutrient and sunlight availability roughly according to phylogenetic relationship, with diatoms and cryptomonads occupying the low light/high nutrient portion of the spectrum, succeeded by greens, then by blue-greens, and finally by dinoflagellates in the extreme high light/low nutrient portion of the spectrum. Surface/volume ratio also proved to be a partial determinant of the position of species along the nutrient axis, as species with high S/V ratios most often occupy the low nutrient portion of the habitat space.

In a second study, I have compared the shape of the abundance frequency distributions between individual species (Lewis, *in press*). The coefficient of variation and skew of the distributions served as indicators of demographic strategy. The C.V. (coefficient of variation) and skew of the frequency distributions proved to be related to attrition rates for the phytoplankton community. Species characterized by highest C.V. and skew (i.e., *r*-selected species) flourish when all sources of attrition are minimal. This demographic strategy is observed in both common and in rare species. At the other extreme, when all sources of attrition are maximal, the species with lowest C.V. and skew (i.e., *k*-selected species) flourish. Grazing and nongrazing attrition have somewhat separate influences. The C.V. and skew of diatom species and of species with filamentous morphotype average above those of other groups, and these species tend to flourish during periods of low grazing attrition. The lowest C.V. and skew value are found among greens and blue-greens of colonial

or coenobial morphotype, and these species tend to flourish during periods of high grazing attrition.

What follows is a third approach to the community organization of the Lake Lanao phytoplankton. From the weekly abundance estimates of all species, the weekly rate of change in biomass (i.e., net growth) of each species can be approximated. If b_i is the biomass of the i^{th} species at time t , the true instantaneous growth rates of all n species at time t are:

$$db_1/dt, db_2/dt, \dots, db_n/dt.$$

The value of db_i/dt is approximated from the data as $\Delta b_i/\Delta t$, where Δt is 7 days. The value of $\Delta b_i/\Delta t$ for a given week will be called the "growth response" of species i for the week in question. The word "response" is included in order to stress the focus of the analysis on the effect of week-to-week changes in environmental variables on the net growth of individual species.

The growth responses of any two species, i and k , are compared by means of a correlation coefficient $r_{i,k}$. High values of $r_{i,k}$ indicate similar growth responses, which might in fact be equated with strong niche overlap. However, this terminology will be avoided here due to the rather specific meanings which have now been attached to this term where field data are concerned (e.g., Colwell and Fuytuma 1971, Pianka 1973).

Specific hypotheses are based on possible relationships between similarity of growth response in two species and their phylogenetic relationship, size, mean abundance, S/V ratio, and morphotype. This procedure is similar in effect but slightly different in analytical philosophy from a cluster analysis, in which the species would first be grouped, and then considered *a posteriori* in an attempt to explain the grouping on the basis of species characteristics (e.g., Allen and Koonce 1973).

Change in biomass, rather than biomass itself, is used in this analysis because biomass change integrates the response of a species to environmental change over a more specific time interval. Biomass itself integrates the response of a species to environmental conditions, but an uncertain amount of past environmental history is represented by a measure of biomass at a given instant. Change in biomass therefore provides a firmer foundation for the comparison of responses of species to prevailing conditions over a relatively short span of time.

The use of similarity in growth response as an indicator of ecological similarity between phytoplankton species is most defensible if the community is not in competitive equilibrium. Suppressive competitive effects between two very similar species become more probable as equilibrium is approached.

Lake Lanao specifically (Lewis 1973, 1974) and plankton environments in general (Hutchinson 1967) are unlikely to approach equilibrium closely due to the rapid change in critical environmental variables. However, a similar analytical approach has been used in terrestrial environments where equilibrium is more likely and has nevertheless been successful. Levins (1968) uses the "probability of co-occurrence alpha" to measure spatial overlap between species in much the same way that growth response similarity is used here to measure temporal concurrence in the growth of species. Other vertebrate ecologists have used similar techniques (Pianka 1973). In addition, Margalef (1974) has given arguments in support of the assumption that co-occurrence is a valuable measure of ecological similarity between phytoplankton species.

METHODS AND STUDY SITE

Lanao is a large natural lake located in the southern Philippines. Essential statistics, taken from Frey (1969) are: mean depth, 60 m; area, 357 km², latitude, 8° N; replacement time, 6.5 yr. The lake has moderately well-buffered water (methyl orange alkalinity, 51 mg/l; conductance at 25°C, 105 μ mho/cm), and is highly productive (620 gC · m⁻² · yr⁻¹ net, Lewis 1974). Lanao is not greatly affected by man at present. There is a seasonal thermal cycle with complete mixing in late December–March and stratification the rest of the year (Lewis 1973). Non-seasonal changes in depth of mixing can markedly influence nutrient availability in the upper water column and thus influence plankton succession.

The data to be used below consist of quantitative counts for all 70 autotroph species at weekly intervals for 65 consecutive weeks. Phytoplankton samples were taken from the euphotic zone (0–15 m) with an integrating tube sampler (Lund and Talling 1957) at two stations 1 km apart, preserved in Lugol's solution, and counted with an inverted microscope (560 ×). Special care was taken to separate species correctly and to count all species, including the smallest ones. Note was made of the average volumes of all species so that counts could be converted to biomass. Abundance of each species can thus be expressed in terms of biomass per unit volume of water or numbers of independent plankton units per unit volume of water. Independent units, or "individuals," may be colonies, cells, or filaments according to species, and will be referred to here as "plankton units." The surface/volume ratio for a plankton unit of average size was calculated for each species from composite geometric figures (Lewis 1976).

The 70 species of planktonic autotrophs in Lake Lanao of course vary greatly in average abundance. The rarest species were not even detected every

week. Owing to the statistical uncertainty of the counts for very rare species, analysis is limited to those species represented by nonzero counts on at least 61 of the 65 sampling dates. Thirty of the 70 species met this criterion. The criterion is not particularly restrictive as about 30,000 specimens per week were sorted for identity.

The 30 species included in the analysis belong to the Cyanophyta (5), Chlorophyta (19), Chryso-phyceae (1), Bacillariophyceae (2), Dinophyceae (1), and Cryptophyceae (2). For convenience these categories will be referred to here as divisions, although in fact they are a mixture of divisions and classes. The taxonomy and population dynamics of the species are discussed elsewhere.

Samples were counted to meet preset statistical standards. On the initial two transects across the counting chambers, all species were tabulated. After the first two transects, additional transects were added for species whose count had not exceeded 100 counting units. After each subsequent transect, those species for which 100 units had been tabulated were eliminated so that as the count proceeded attention was focused on increasingly rare species. An upper limit on total counting effort was set at 40 h for the two sampling stations combined. Statistical determination of variation between replicates and between stations demonstrated that the true difference between stations 1 km apart is statistically detectable but very low (average C.V. < 10%). Data for the two stations are consequently pooled in the following analysis.

A variance between counts was obtained for each species every week. Since the data from the two adjacent stations have been pooled, the variance of the count for a given species on a given week is an aggregate attributable to (1) counting and sub-sampling methods, (2) true difference between replicate samples at the same station, (3) true difference between the two stations 1 km apart. The first of these three components of variance is by far the largest.

A mean was taken of the 65 weekly variances for each species to obtain an estimate of the overall reliability of data on individual species. The mean standard deviations average 31% of the mean abundance for the 30 species (SD = 16%).

Correlation analysis of strongly autocorrelated data sets can be misleading (Denman 1975, Winkler and Hays 1975). The amount of autocorrelation in the $\Delta b/\Delta t$ matrix for the 30 species was therefore checked. Five lags were used for each species (1, 2, 3, 4, and 5 wk). A total of 22 of the possible 150 autocorrelations using these 5 lags were significant at $\alpha = .05$. The majority of these were borderline cases ($.25 < r < .30$). The highest instance of

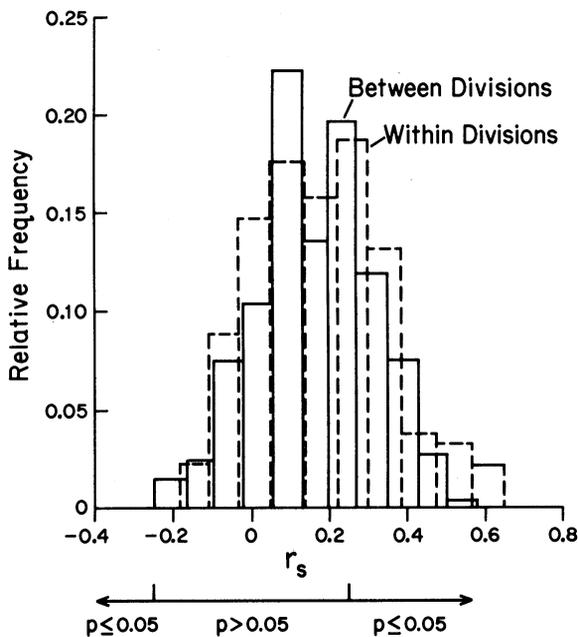


FIG. 1. Frequency distribution of r_s values for all 435 possible correlations of $\Delta b/\Delta t$ among the 30 phytoplankton species. The distribution is decomposed into correlations attributable to intradivision and interdivision species pairs.

autocorrelation was with a lag of 1 wk (9/30 significant at $\alpha = .05$).

Although autocorrelation is detectable for some species, the intensity of autocorrelation is generally so low that it will not be considered in the interpretation of data.

The frequency distribution of $\Delta b/\Delta t$ for most species is skewed to the right, and transformation is not uniformly satisfactory, so the Spearman rank correlation (r_s) is used in the comparisons of $\Delta b/\Delta t$ between species. The 30×30 correlation matrix contains 435 unique values of the type $r_{i,j}$, $i \neq j$.

RESULTS

The frequency distribution of r_s values for all possible distinct species pairs appears in Fig. 1. The r_s values are not symmetrically oriented around 0, as might be expected, but are displaced toward positive values of r_s . In fact there are no significant negative correlations of $\Delta b/\Delta t$ between species pairs, whereas $\approx 1/3$ of all correlations are significant and positive (Table 1).

The absence of significant negative correlations between species argues against any strong antagonism between species or between species groups. It is useful to distinguish between two types of competitive interaction to explain the absence of negative correlations. (1) With an improvement of re-

TABLE 1. Results of correlation analysis for values of $\Delta b/\Delta t$ among phytoplankton species meeting various criteria. Number of distinct species pairs is given, as well as the percentage of significant r_s values among these pairs. Asterisk marks significant departure by comparison with a species group of similar size chosen at random (chi-square)

Population	Number pairs	Significant relationships %
All 30 species		
All possible pairs	435	34
Intradivision pairs	183	37
Interdivision pairs	252	31
Intrafamily pairs	30	29
Interfamily pairs	397	34
Species grouped by abundance measured as biomass		
Most abundant 13 species		
All possible pairs	78	45*
Intradivision pairs	20	80*
Interdivision pairs	58	33
Least abundant 17 species		
All possible pairs	136	31
Intradivision pairs	79	32
Interdivision pairs	57	30
9 rare species with lowest count variance		
All possible pairs	36	47
Intradivision pairs	16	56
Interdivision pairs	20	40
Species grouped by abundance measured as number of plankton units		
Most abundant 13 species		
All possible pairs	78	37
Intradivision pairs	25	36
Interdivision pairs	53	38
Least abundant 17 species		
All possible pairs	136	30
Intradivision pairs	78	31
Interdivision pairs	58	29
Species grouped by size of plankton unit		
Largest 15 species, with each other	105	32
Smallest 15 species, with each other	105	36
Largest 15 with smallest 15	225	33
Species grouped by S/V ratio		
10 species with highest S/V ratio	45	29
15 species with lowest S/V ratio	105	39
10 highest with 15 lowest	150	33
Species grouped by morphology		
Flagellates with flagellates	6	67
Flagellates with non-flagellates	104	33
Colonial with colonial	15	53
Colonial with noncolonial	144	38
Single cell (nonflagellated) with same	28	39
Single cell (nonflagellated) with all others	176	35
Morphologically similar, all pairs	49	49*
Morphologically dissimilar, all pairs	320	34

* Significant at $\alpha = .05$.

source supply, competing species A and B may both increase in abundance, although the increase for A is much greater than for B. Similarly, with a deterioration of resource supply, both species may decrease, but A much less rapidly than B. In both cases, A is the best competitor, but the sign of $\Delta b/\Delta t$ is the same for both species. A change in conditions may, of course, reverse the roles of A and B. (2) An increase or decrease in the abundance of species A may be accompanied by the opposite trend in species B. If the species are using many of the same resources, as do the phytoplankton, this is most likely to occur when change in resource supply is nil or slight, bringing the community into a close approach to competitive equilibrium, or if there is a direct antagonism, such as heteroantibiosis, between the species. In addition, it is theoretically possible for one or both species of a species pair to show no significant net change in biomass over a 1-wk period. In reality this is an exceptional situation.

The distribution of r_s values indicates that competitive relations of type 2 are much less important in the Lanao phytoplankton than relations of type 1. It is clear from the basic physical, chemical, and biological data on Lake Lanao (Lewis 1974) that the supply of major resources (sunlight, nutrients) to the phytoplankton is almost always changing significantly. General improvement in resource supply causes increased abundance of most species and little change in the remainder, although the species complex taking the greatest proportion of resources is determined by specific environmental conditions. General deterioration in resource supply has similar effects of opposite sign. This scheme accounts for the large number of positive correlations between species and complete lack of negative ones.

Absence of demonstrable antagonisms is interesting in view of the possible role of biochemical interactions in plankton succession (Hutchinson 1967). While antibiosis and other direct mechanisms for competition may exist, their effect seems to be insufficiently strong to affect the biomass of target species on a regular basis. One possibility is that antibiotic effects are simply masked by the much more powerful effects of resource supply. Another possibility is that increases in biomass of a species exercising antibiotic effects are irregularly associated with the strength of the effect.

Phylogenetic relationship and interspecific similarity

One obvious hypothesis would connect phylogenetic relationship with demographic responses to environmental change. For example, the common pigments and intracellular organization of the

Cyanophyta, plus traits shared by many species in the group (e.g., nitrogen fixation), might reasonably cause a pair of species from this division to respond to environmental changes more similarly, on the average, than a species pair crossing divisional lines. If phylogenetic relationship at the division level and growth response are related, then species of the same division should show higher correlations of $\Delta b/\Delta t$ than species of different divisions. The hypothesis is tested by a comparison of the number of significant correlations of $\Delta b/\Delta t$ between species pairs (1) where both species are members of the same division, and (2) where the two species belong to different divisions.

The frequency distributions of r_s values for intradivision and interdivision species pairs are compared in Fig. 1. The distributions are very similar, but most of the very highest correlations are intradivisional. The number of significant values of r_s in the interdivision group is lower than in the intradivision group (Table 1). However, the value of chi-square computed from the number of significant and nonsignificant r_s values for the intradivision group (using all possible pairs to determine expected frequencies) is not significant at $\alpha = .05$.

Although the growth response similarity for the 30 species cannot be readily predicted from phylogenetic relationships at the division level, it is still possible that there is a detectably greater similarity among species of smaller taxonomic units. Seven families are represented by more than one species, and the r_s values for all possible interfamilial pairs can thus be compared with the r_s values for intrafamily pairs. Table 1 shows that growth response similarity between species drawn from the same family is no greater than similarity of species drawn at random.

Mean biomass abundance and interspecific similarity

Another possibility is that abundant species have either more or less similar growth responses than do abundant and rare species. In this section, biomass is used as the index of abundance. For analytical purposes it is useful to dichotomize the 30 species. The 13 most abundant species, which account for about 90% of the annual crop in Lake Lanao, will be considered common, and the other 17 will be considered rare. The 13 common species include members of the Cyanophyta (3), Chlorophyta (6), Bacillariophyceae (2), and Cryptophyceae (2). The proportion of significant correlations is significantly greater between common species than between species chosen at random (Table 1: chi-square, $p < .01$).

When the intradivision and interdivision relationships among the top 13 species are separated, the

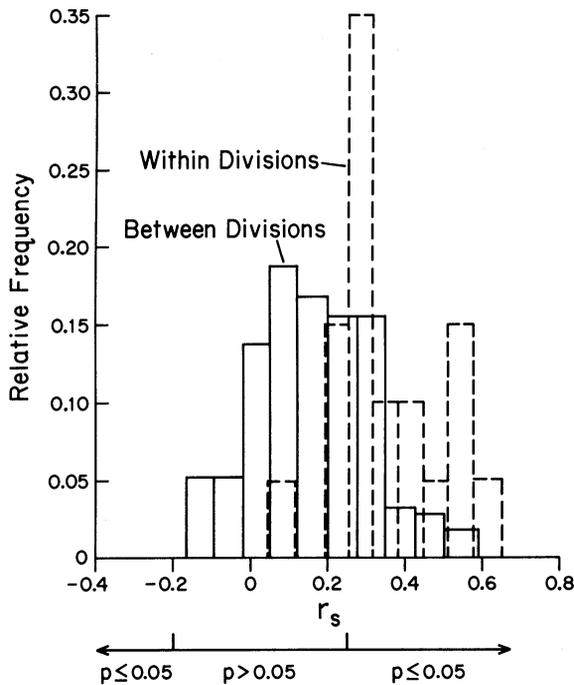


FIG. 2. Distribution of r_s values for $\Delta b/\Delta t$ among the 13 species having highest mean annual standing crop and 17 species having lowest mean annual standing crop.

source of the higher correlations becomes evident (Fig. 2, Table 1). For the abundant species group, a far greater percentage of intradivision pairs produce significant correlations than among the rare species group or the 30 species as a whole. For the 17 rare species, however, inter- and intradivision associations do not differ from each other, nor do they differ from interdivision associations in the common species (Table 1).

The failure of the 17 rare species to show a high percentage of significant intradivision correlations could be due either to ecological differences between rare and common species or to differences in the quality of the data on rare and common species. Despite the precautions that were taken to assure maximum uniformity of data, there is some difference in the error variance of the two data sets. The mean coefficient of variation (s/\bar{x}) for the replicate counts of the 13 most common species is 24% (SD, 10%), whereas for the 17 least abundant species it is 37% (SD, 17%). The greater amount of noise in the data on rare species could thus be responsible for the apparent difference between rare and common species.

The importance of data quality in affecting the percentage of significant relationships can be tested by discarding the rare species with greatest count variances until the rare species group is comparable in average variability to the common species group.

Discarding the eight species with greatest count variance produces a group of nine rare species with a mean coefficient of variation for replicate counts of 25%. This group of nine produces 36 unique r_s values, of which 47% are significant (Table 1). The percentage of significant r_s values is even higher for intradivision pairs among this group of nine (56%). This is considerably higher than the percentage for the original group of 17 rare species, although too few species are involved to make a sound statistical demonstration.

The foregoing analysis indicates that the closer relationship of intradivision pairs, which could not be demonstrated previously in the 30 species as a whole, does in fact exist but is masked in the rare species group and in the combination of all species by the error variance, because the relationship is rather weak. Mean abundance itself is not related to similarity of growth response.

Mean numerical abundance and interspecific similarity

Abundance in this section is measured in terms of the number of plankton units. When the relationships within the group of 13 numerically most abundant species or within the group of 17 numerically rarest species are compared with the entire group of 30 species, no large differences appear (Table 1). The proportion of significant relationships among abundant species is somewhat greater, but not significantly so. The intradivision and interdivision relationships are also homogeneous for both the abundant and rare groups. Thus there is no evidence of any relation between abundance and similarity of growth response. This is the same conclusion as for the analysis of abundance based on biomass. However, the intradivision relationships do not show up in this case as they did with the analysis of abundance based on biomass. The high-variance species are more equally distributed between common and rare species, and the intradivision relationship is therefore uniformly masked by statistical noise.

S/V ratio, size, morphology, and interspecific similarity

The surface:volume (S/V) ratios for 25 of the 30 species range between 0.5 and 7.3. Five species with bulky gelatinous matrices (e.g., *Aphanothece nidulans*, *Kirchneriella elongata*) are omitted because the matrix creates problems in the computation of S/V ratios (Lewis 1976). For analytical purposes, the 25 species can be divided into a group with a high S/V ratio and a group with a low S/V ratio. There is a natural break in the frequency distribution of S/V ratios between species ranking 10 and 11 in

descending order by S/V ratio. Therefore the 10 species with highest S/V ratios (range, 1.9–7.3) are used as the high S/V ratio group, and the other 15 species (range, .5–1.5) are used as the low S/V ratio group.

Correlations of $\Delta b/\Delta t$ among species in the high S/V group, the low S/V group, and between groups are summarized in Table 1. Although the percentage of significant correlations appears to be higher than expected for the low S/V group and lower than expected for the high S/V group, the differences from groups chosen at random are not significant.

A comparison between species can also be based on the average size of a plankton unit for individual species. Average wet weights of plankton units for the 30 species range between 1×10^{-8} mg (= $10 \mu\text{m}^3$ cell volume) to 2.5×10^{-6} mg. The smallest species include *Dactylococcopsis fascicularis*, *Chlorella* sp., and others which occur as tiny unicells. The largest species, such as *Melosira granulata*, *Coelastrum cambricum*, and *Gymnodinium* sp., occur either as aggregations of 2 to 15 large cells or as very large unicells. Some even larger species are present in the lake (*Pediastrum clathratum*, *Botryococcus braunii*), but were consistently very rare and do not belong to the group of 30 species analyzed here.

The group of 30 species is divided into the 15 largest and 15 smallest species for analytical purposes. The proportion of significant relationships within or between these groups is not significantly different from the 30 species as a whole (Table 1).

Another set of possible relationships involves morphological similarities between species. Morphological features that cross divisional lines include (1) flagella, (2) colonial growth habit, (3) unicellular, nonflagellated growth habit, and (4) filamentous growth habit. The first three features typify a sufficient number of Lanao species to warrant testing. Filamentous growth habit, although interesting, cannot be analyzed statistically in the Lanao data because an insufficient number of species show this morphotype.

Among the 30 species, four are motile by virtue of flagella (*Gymnodinium* sp., *Chromulina* sp., *Cryptomonas marssonii*, *Rhodomonas minuta*). These four species form six distinct pairs, of which four (67%) show significant r_s values for $\Delta b/\Delta t$. This proportion of significant relationships is much higher than for flagellates paired with nonflagellates, or for species chosen at random. However, the relatively small number of flagellate species involved in the test makes it impossible to say whether the contrast is due to chance.

Species whose biomass units routinely consist of more than four cells are classified as colonial. Included in this group are *Aphanothece nidulans*, *Dictyosphaerium pulchellum*, *Dimorphococcus luna-*

tus, *Coelastrum cambricum*, and other similar species. Filamentous species (*Lyngbya limnetica*, *Melosira granulata*) are excluded as belonging to a different morphotype. Also excluded are such species as *Scenedesmus ecoris*, that always consist of four or two cells. The colonial species as narrowly defined here account for 6 of the 30 Lanao species. The proportion of significant relationships within this group is higher than for species chosen at random (Table 1), but once again the number of pairs is too small to provide definite statistical evidence.

The third morphological category includes species whose biomass units consist of single, nonflagellated cells. In the Lake Lanao group, this applies to such species as *Dactylococcopsis fascicularis*, *Ankistrodesmus setigerus*, and *Nitzschia baccata*. Eight of the 30 species belong to this category. Once again the proportion of significant intragroup relationships is higher than for species chosen at random, but not sufficiently so to provide statistical evidence (Table 1).

A more general hypothesis based on morphology can be formulated if specific morphological types are not considered individually. Pairs of species can be classified as being (1) morphologically similar or (2) morphologically dissimilar. The first category lumps all of the morphologically similar pairings of flagellates, colonial forms, and single cell non-flagellates. The proportion of significant relationships is significantly higher for morphologically similar species than for species chosen at random (Table 1).

DISCUSSION

The foregoing analysis can be summarized as follows: (1) Species of the same division are significantly more similar in their growth responses than are species chosen at random. However, this trend is sufficiently weak that it can be demonstrated statistically only for species represented by counts with very low variances. (2) Species with a high mean standing crop are not detectably more similar to each other in growth response than species chosen at random. The same applies to species with a low mean standing crop. (3) Species grouped by S/V ratio or size are not detectably more similar to each other in growth response than species chosen at random. (4) Species of similar morphotype are more similar in growth response than species chosen at random.

These results complement the gradient analysis, in which the species were arranged on gradients of critical environmental variables. The difference is that the analysis of growth response is a measure of composite similarity which fails to identify the critical variables regulating growth, but in so doing

avoids the bias involved in the selection and weighting of critical variables.

Phylogenetic relationship emerges as a recognizable indicator of similarity in both the gradient analysis and the analysis of growth response. This suggests that phylogenetic relationship is a very broad determinant of similarity.

The existence of greater ecological similarity between species of close phylogenetic relationship partly vindicates the old and important practice of lumping the phytoplankton at the division level. Community dynamics in the phytoplankton are frequently explained in terms of changes in diatoms, bluegreens, greens, and other groups of divisional status. The motivation for this lumping is obviously the unrewarding task of giving a species-specific description of seasonal changes. The assumption that divisions are valid ecological groups does seem to have some ecological foundation, but the degree of similarity among species within a division is relatively weak even though it is detectable statistically. In an analysis based on spatial co-occurrence, Margalef (1974) has demonstrated a significant, predominantly positive, but quantitatively weak coincidence in the distribution of congeners in selected phytoplankton genera. The connection between phylogenetic relationship and ecological similarity thus seems to be very similar in Lake Lanao and in the marine environments treated by Margalef.

Mean abundance is one indicator of degree of dominance in the community and thus has considerable ecological significance. By analogy with terrestrial communities, it would be expected that a particular set of conditions should favor a few dominant species and in addition a cluster of less dominant species, and that both the abundant and rare species would change as the conditions change. From another perspective, however, it seems that the species with high mean abundance are those which compete best under conditions that are generally optimal for algal growth, i.e., when the total productivity of the community is high. These species might therefore share certain physiological attributes and thus tend to respond more similarly than species chosen at random. Although both of these two viewpoints probably contain elements of truth, the analysis suggests that the first is the more accurate for the Lake Lanao plankton community, as there is no detectably greater similarity among species grouped by abundance than among species chosen at random.

The S/V ratio is a determinant of position on the nutrient supply gradient, but is not related to similarity of growth response among species. The contradiction is only apparent. S/V ratio is significant specifically in gain and loss of materials through the cell boundary, but when other factors become

important, S/V ratio does not have an important bearing on growth, and under such conditions, species of similar S/V ratio may behave differently. This explains the insignificance of S/V ratio in the analysis of overall growth response despite its importance in the gradient analysis.

The absence of any detectable relationships between species based on size is, like the absence of relationships based on S/V ratio, attributable to the specificity of size as an adaptation. While size may be extremely important as a determinant of the position of a species on certain gradients (e.g., turbulence), size itself is not a sufficiently general character to account for a significant degree of similarity in the overall growth pattern of species.

The evidence for similarity of growth response between similar morphotypes is important in view of Margalef's extensive use of morphotype in describing plankton succession (Margalef 1958, 1968). Margalef's view of flagellates, for example, is that such species flourish under conditions of nutrient depletion by virtue of their motility. A corollary, which is actually more amenable to testing than Margalef's hypothesis, is that the demographic responses of flagellates to environmental change should be more similar to each other than to those of other morphotypes. The Lanao data support this corollary, although not so strongly as might be hoped. Further investigation will probably show that certain morphotypes are much more significant than others in dictating the growth optima of species. It appears from the Lanao data, for example, that flagellated species are much more similar ecologically than non-flagellated unicells, but statistical rigor is lacking here. To summarize, phylogenetic relationship and morphotype seem to have very general (i.e., strategic) significance, which leads to a greater average similarity in growth response, whereas size and S/V ratio have more specific (i.e., tactical) significance which cannot produce a detectably greater similarity in growth response. Mean abundance is itself a manifestation of such traits as S/V ratio and morphotype, but fails as a criterion for ecological grouping because succession proceeds by simultaneous shifts in both common and rare species.

The failure of close similarities in several instances where they might have been expected and the weakness of the relationships that do exist are among the most notable results of the analysis. A general weakness of statistical relationships between species has also been characteristic of other analyses attempting to group species according to various criteria of similarity (Allen and Koonce 1973, Margalef 1974). This suggests that individual species are very distinctive in their adaptations to the complex of environmental factors and are on a statistical basis well separated in time and space, even though many

species co-occur at a particular point in time and space. Ecological analysis based on groups of species may therefore be of limited value because of the poor coherence of the groups. The study of phytoplankton communities will probably be most successful if it can be based on a composite treatment of individual species, even though this is methodologically much more demanding than a treatment of species groups.

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