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for Coexisting Phytoplankton Species**



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## ECOLOGICAL SIGNIFICANCE OF THE SHAPES OF ABUNDANCE-FREQUENCY DISTRIBUTIONS FOR COEXISTING PHYTOPLANKTON SPECIES<sup>1</sup>

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**Abstract.** Abundance-frequency distributions for 31 phytoplankton species from Lake Lanao, Philippines, are constructed on the basis of 65 weekly samples. All of the distributions have a positive skew. The shapes of the distributions are quantified in terms of the coefficient of variation and a skew statistic. CV (the coefficient of variation) and skew are highly correlated for the 31 species and vary over approximately an order of magnitude between species. High CV and skew are interpreted as evidence of an opportunistic demographic strategy and low CV and skew as evidence of a conservative strategy. Relationships are tested between CV or skew and three sets of variables: (1) mean abundance measured as biomass or numbers, (2) morphofunctional properties such as size and surface:volume ratio, and (3) niche descriptors. Niche descriptors are variables which give the average position of a species on an environmental gradient when net growth of the species is positive. The results of the analysis on the 3 sets of variables are as follows. (1) The mean abundance of a species is not statistically related to the CV or skew of its frequency distribution. This indicates that rare species are as likely to have an opportunistic strategy as common species. (2) Three specific morphofunctional characteristics (volume, surface area, and S:V ratio) are not related to CV or skew, but two general morphofunctional characteristics (morphotype and taxonomic affinity) are related to CV and skew. Filamentous morphotypes and diatoms have the most opportunistic patterns (high CV and skew), while coenobial morphotypes and chlorophytes have the most conservative patterns. (3) Among 5 different niche descriptors, CV and skew are related only to those which incorporate some measure of attrition, especially grazing. Periods of high attrition correspond with success of conservative species, and periods of low attrition with success of opportunistic species. Attrition due to grazing is the mechanism by which the general morphofunctional variables (morphotype, taxon) are related to shape of the abundance-frequency distribution.

**Key words:** Community structure; niche; Philippines; phytoplankton; population dynamics; succession.

### INTRODUCTION

Studies of plankton environments frequently produce data describing the abundances of a large number of coexisting phytoplankton species. As it is not unusual for 50 or more phytoplankton species to be present in detectable numbers at any given time, the abundance data matrix may be quite large. The means for extracting maximum information from such data are not yet well developed, however. It is traditional to conduct some kind of correlation analysis based on time, comparing algal populations and physico-chemical variables or herbivore activity. In the past, this approach has dominated the analysis of algal abundance data (Hutchinson 1967).

Some significant attempts have been made to broaden the interpretation of phytoplankton abundance data by use of special statistical tools (Fager 1957), by ingenious application of standard statistical tools (Iltis 1974), and by multivariate techniques (Levandowsky 1972a; Allen and Koonce 1973; De Amezaga et al. 1973; Iltis 1974). These and other methods are necessary if the wealth of information in phytoplankton abundance matrices is not to be wasted.

Here I consider the interpretive value of the

abundance-frequency distributions for coexisting phytoplankton species. An abundance-frequency distribution can be obtained for each species represented in a phytoplankton abundance matrix if the abundances of the individual species are taken out of their temporal sequence and reordered in a frequency distribution. Abundance-frequency distributions have apparently not been used for interpretive purposes except to the extent that the mean abundance for a species, which is also the mean of its abundance-frequency distribution, is commonly computed and used in interpretation. Shapes of abundance-frequency distributions from nature seem to be generally unused in all branches of community ecology, although much theoretical work in ecology deals implicitly with the shapes of abundance-frequency distributions. This may be explained by a reluctance among ecologists to take abundance data out of their temporal sequence, which inevitably results in a loss of certain kinds of information. I hope to show here that this may nevertheless be a useful means of dealing with some aspects of community structure that have heretofore been largely the subject of theory alone.

### Description of the community

The phytoplankton abundance matrix used here is based on a 65-wk study of Lake Lanao, Philippines.

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Lanao is a large natural lake (357 km<sup>2</sup>) located on Mindanao (8°N, 124°E). Physical features of the lake are described by Frey (1969) and the physico-chemical cycles and productivity by Lewis (1973, 1974). Lanao has a mean depth of 60 m and a replacement time of 6.5 yr. Human population density in the watershed is low, and the lake itself is not yet greatly affected by man. The alkalinity averages 51 mg/l (methyl orange) and shows very little seasonal change. Conductance averages 105  $\mu$ mho/cm (25°C). The lake mixes completely in late December-March and is stratified the rest of the year. Nonseasonal changes in the depth of mixing cause abrupt shifts in the nutrient levels of the upper water column, which in turn lead to changes in productivity and plankton succession. The lake is highly productive (620 gC · m<sup>-2</sup> · yr<sup>-1</sup> net).

Successional patterns in the phytoplankton over the year of study have already been described (Lewis 1977a). In addition, special studies have been made of the similarity in growth patterns between species (Lewis 1977b) and of the rate of succession as compared with the rate of change in environmental variables (Lewis 1977c). The phytoplankton is comprised of 70 species, including Cyanophyta (12), Euglenophyta (4), Chlorophyta (44), Chrysophyceae (1), Bacillariophyceae (4), Dinophyceae (3), and Cryptophyceae (2). Diatoms contribute 37% of the mean autotroph biomass, chlorophytes 34%, and cyanophytes 19%. Diatoms and cryptomonads flourish when nutrients are plentiful and light availability is low, bluegreens and dinoflagellates dominate when nutrients are depleted and light availability is high, and greens occupy the middle portion of the nutrient and light availability spectra. Succession rate is quantitatively related to absolute rate of change in resource supply and to grazing rate.

#### METHODS

Two or 3 samples were taken weekly at each of 2 stations 1 km apart in midlake. A tube sampler of the type described by Lund and Talling (1957) was used to obtain integrated samples of the euphotic zone (0–15 m). Samples were preserved immediately in Lugol's solution and were later examined in a sedimentation chamber with an inverted microscope (560 $\times$ ).

Counts were made of all autotrophic organisms, and special care was taken to separate species correctly. For each sample, individuals of all species were tabulated from 2 full transects of a counting chamber. After 2 transects, those species represented by a count of 100 or more units were no longer tabulated. After each subsequent transect, other species whose counts had exceeded 100 were dropped from the tabulation. In this way, counting effort focused on increasingly rare species as the count proceeded. This continued up to a total effort of 40 man-h per weekly sample series.

The samples from the 2 different stations proved to be little different than replicates from the same station

(station effect <10% of mean abundance for an average species), so all samples on a given date are treated as replicates here. The counting procedure produced data of approximately uniform error variance in the top 19 species (ordered by numbers of individuals), and slowly increasing error variance with increasing rank beyond this. Thirty-one of the 70 species were selected for analysis, as the abundance data on the rarest species are statistically unreliable. These 31 species account for 98% of the annual mean biomass and span three orders of magnitude in mean abundance (Table 1). Mean coefficient of variation ( $s/\bar{x}$ ) for counts on replicate samples of the top 19 species is 28.3%, whereas for succeeding 12 species it is 41.1%.

Records were kept of the dimensions of all species so that counts could be converted to biomass by the use of geometric models (assuming protoplasm to have a density of 1.0 g/cm<sup>3</sup>).

#### RESULTS

##### *Variation in abundance of species*

The phytoplankton species of Lake Lanao differ markedly in their amplitudes of variation through time. Some species fluctuate wildly, while others maintain a remarkably constant population size. Figure 1A illustrates temporal variation in species from both extremes and the middle of the variability spectrum. To facilitate comparison, the plots all have the same relative scale.

If abundances for individual species such as those of Fig. 1A are arranged in frequency distributions, some additional facts about variability emerge (Fig. 1B). All frequency distributions are asymmetrical and skewed to the right, but the degree of skew varies greatly between species. The distribution for such species as *Chroococcus minutus* approaches symmetry, while the distribution for other species such as *Anabaena spiroides* is markedly skewed.

The above observations are best quantified in terms of statistics that describe the shape of the abundance-frequency distributions. Two such statistics were computed for each species: (1) the coefficient of variation ( $CV = S/\bar{X}$ ) and (2) a skewness statistic,  $SK$  (Glass and Stanley 1970):

$$SK = \left\{ \sum (x - \bar{x})^3/n \right\} / s^3$$

The skewness statistic is not affected by the size of the mean and is in this sense, like the CV, a "relative" measure.

Values of CV and  $SK$  for the Lanao species appear in Table 1. It is clear from the table that species with high coefficients of variation also tend to have the most pronounced skew. These 2 indicators of curve shape are in fact closely correlated for the data of Table 1 ( $r = .78$  after log transformation). This is a noteworthy aspect of the distributions, as a

TABLE 1. Thirty-one of the most important Lanao phytoplankton species and their characteristics. Measurements of abundance are from the surface to the bottom of the circulating layer (15 m). Abundance is expressed both as numbers of individuals and as biovolume. The mean sizes and S:V ratios were computed as indicated in the text

Taxon	Frequency distribution properties				Morphofunctional properties		
	Mean individuals/cm <sup>2</sup> (thousands)	Mean mm <sup>3</sup> /m <sup>2</sup>	CV (%)	SK	μm <sup>3</sup> /individual <sup>1</sup>	S:V ratio	Morpho-type
<b>Cyanophyta</b>							
<i>Chroococcus minutus</i>	341	955	62	.36	280	1.89	CE
<i>Aphanothece nidulans</i>	11,280	1,466	88	1.24	13	...	CO
<i>Dactylococcopsis fascicularis</i>	563	56	107	1.23	10	5.00	S
<i>D. wolterecki</i>	586	87	85	2.19	15	4.00	S
<i>Anabaena sphaerica</i>	621	1,527	202	2.70	246	2.25	FI
<i>A. spiroides</i>	37	369	316	5.49	1,000	1.41	FI
<i>Lyngbya limnetica</i>	9,343	2,242	114	1.79	24	7.25	FI
<b>Chlorophyta</b>							
<i>Tetraedron minimum</i>	382	95	53	.98	25	2.48	S
<i>Sphaerocystis Schroeteri</i>	284	1,365	115	2.92	480	1.47	CO
<i>Oocystis submarina</i>	1,712	2,397	81	2.37	140	1.43	CE
<i>O. lacustris</i>	69	346	102	1.69	500	0.90	CE
<i>Franceia droescheri</i>	100	29	178	2.76	30	1.82	S
<i>Chodatella subsalsa</i>	515	1,287	60	1.76	250	0.90	CE
<i>C. sp.</i>	170	67	103	3.22	40	2.00	CE
<i>Ankistrodesmus setigerus</i>	265	92	218	3.65	35	2.71	S
<i>Selenastrum minutum</i>	1,365	27	170	2.34	2	7.00	S
<i>Dictyosphaerium pulchellum</i>	848	4,239	195	3.00	500	1.32	CO
<i>Dimorphococcus lunatus</i>	126	881	65	1.10	700	1.34	CO
<i>Coelastrum cambricum</i>	55	1,371	90	1.66	2,500	0.87	CO
<i>Scenedesmus ecornis</i>	27	128	97	1.32	480	1.12	CE
<i>S. sp.</i>	53	53	113	2.15	100	1.85	CE
<i>Closterium sp.</i>	89	71	73	1.57	80	1.46	S
<i>Staurastrum paradoxum</i>	6	60	93	1.66	1,100	0.97	CE
<b>Chrysophyceae</b>							
<i>Chromulina sp.</i>	238	283	87	2.56	100	1.13	FL
<b>Bacillariophyceae</b>							
<i>Nitzschia bacata</i>	8,409	15,977	146	2.79	190	2.31	S
<i>Melosira granulata</i>	87	1,040	210	3.23	1,200	0.61	FI
<i>M. agassizii</i>	3	50	437	6.44	1,500	0.19	FI
<b>Dinophyceae</b>							
<i>Gymnodinium sp.</i>	43	515	103	1.93	1,200	0.51	FL
<i>Peridinium sp.</i>	12	136	133	1.51	1,150	0.46	FL
<b>Cryptophyceae</b>							
<i>Rhodomonas minuta</i>	1,029	720	97	1.82	70	1.35	FL
<i>Cryptomonas marssonii</i>	220	2,640	124	2.74	1,200	0.54	FL

randomly-constructed set of frequency distributions would not necessarily show such a relationship.

The coefficient of variation and skew can be interpreted ecologically. Species whose abundance-frequency distributions have a high CV and skew have marked powers of increase under a narrow range of favorable conditions but drop radically in abundance at other times. Such species thus fit the demographic profile of opportunistic weedy species (Hutchinson 1951) or *r*-selected species (Cody 1966; MacArthur and Wilson 1967; Pianka 1970). Species with a low CV and skew lack the ability to produce impressive growth surges but persist more effectively when conditions are unfavorable. Such species conform to the pattern of conservative nonweedy or *K*-selected species. Presumably a given autotroph species in Lake Lanao is genetically tuned to the physico-chemical environ-

ment, competing species, and grazers in this particular lake. As an average species passes through 294 generations per year in Lanao (Lewis 1974), the opportunity for such tuning is excellent. Since selection may act differently on the same species in another lake, generalizations about the demographic strategy of a species apply with certainty only to the Lake Lanao population of the species.

The skew of abundance-frequency distributions is created by the tendency of algal species to produce an occasional growth pulse which carries the abundance far above its modal level. Table 1 shows that this property is not restricted to species of a given morphotype or mean abundance, but is shared to some extent by all phytoplankton species in Lake Lanao. The demographic pattern of all phytoplankton species thus incorporates two rather separate components: (1) a per-

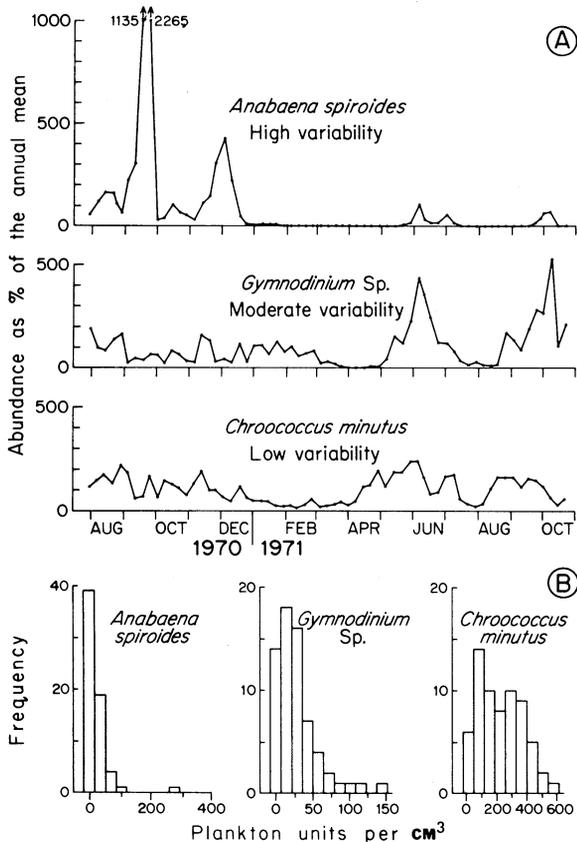


FIG. 1. Abundance data on three phytoplankton species from Lake Lanao over a 65-wk period. The 3 species were chosen to represent high variability (*Anabaena*), moderate variability (*Gymnodinium*), and low variability (*Chroococcus*). A. Abundance over time for the three species. B. Abundance-frequency distributions for the three species (note compressed scale for *Anabaena*).

sistence component, in which the abundance varies closely about the modal abundance, and (2) a bloom component, in which the species moves far above the modal abundance for a short time and then returns. The degree of difference between these two components is measured by the skewness and CV statistics.

The modal abundance for phytoplankton always lies well to the right of zero, as even the rare species are represented by very large absolute numbers of individuals in the plankton habitat as a whole. Very rare species or species that undergo strong seasonal declines in abundance merely become a part of what has been aptly called the "hidden flora" of a lake (Rahat and Dor 1968).

Since CV and skew of the abundance-frequency curve provide a means for ordering species according to their demographic strategies, it is possible to determine whether demographic strategy as measured by these criteria is related to other species properties of known or probable ecological significance. One wonders, for example, whether species of high mean

abundance are more variable in abundance than rare species, or whether large species are less inclined to bloom dramatically than small species. These and other possibilities can be tested statistically with the CV and skew statistics.

The CV and skew statistics are compared here with 3 groups of variables: (1) abundance descriptors, which give the annual mean abundance of species in terms of numbers or biomass; (2) morphofunctional descriptors, which give either metric or nonmetric characteristics that have morphological or functional significance; and (3) niche descriptors, which give the position of species on environmental gradients. Analysis of variables in each of these three classes is discussed below in detail. Variables in all classes were tested for correlation with CV or skew of abundance-frequency distributions. Correlation coefficients are reported in Table 2. All variables were first tested for normality by Kolmogorov-Smirnov criteria (Conover 1971). Variables which differed significantly from normality were transformed prior to correlation analysis. Variables that required transformation are so marked in Table 2. Simple logarithmic transformation in all cases normalized the nonnormal variables satisfactorily. The coefficients in Table 2 are for Pearson product-moment correlations. In some cases the simple correlation coefficient was supplemented with a first order partial controlling for potentially confounding variables from the list in Table 2. The table gives the simple bivariate correlation unless partial correlation proved to be of value in unmasking spurious or misleading simple correlations. Whenever a partial correlation is reported instead of a simple one, the coefficient in the table is followed by a list of the controlling variable number or numbers in parentheses.

*Shape of the abundance-frequency curve in relation to average abundance*

The first null hypothesis is that there exists no relation between the shape of the abundance-frequency curve for a species and its mean abundance. The abundance-frequency distribution for a species can be based either on biomass or on numbers of individuals, as either produces the same value for CV and skew. This is not true of mean abundance, however, as the species will clearly rank differently according to whether abundance is expressed as biomass or as numbers of individuals (Table 1). Separate determinations must therefore be made of the relation between CV or skew and the two possible measures of mean abundance.

One potential problem in the analysis of abundance descriptors is the increase in relative error variance in species of increasing rarity. This problem does not seem critical for two reasons. (1) The increase in error variance with decreasing mean abundance is not very great up to species of rank 31, as indicated previously. (2) The statistics used in the analysis are annual

TABLE 2. Correlations between various species characteristics and the coefficient of variation or skew of the abundance-frequency distributions. Simple bivariate correlations are reported except when partial correlation shows a substantially different relationship of variables. When partial correlations are reported, they are accompanied by a listing of the control variables (in parentheses). Variables that were log transformed are so marked

Variable name	Variable number	Correlation	
		Skew (log)	CV (log)
Abundance descriptors			
Mean abundance, as individuals (log)	1	-.11	-.21
Mean abundance, as biomass (log)	2	-.01	-.07
Morphofunctional descriptors <sup>1</sup>			
Volume per biomass unit (log)	3	.10	.16
S:V ratio per biomass unit (log)	4	-.22	-.20
Surface per biomass unit	5	.02	.10
Niche descriptors (Means for weeks on which $RG_i > 1.6$ )			
Mean nutrient index value (log)	6	.20	.13
Mean irradiance availability	7	-.11 (8)	-.14
Mean grazer biomass	8	-.37* (1)	-.37* (2)
Mean change in autotroph biomass ( $\Delta B_p$ )	9	-.21	-.40* (8)
Mean change in autotroph numbers ( $\Delta N_p$ )	10	-.17 (8)	-.35* (8)
Mean net primary production ( $PN_p$ )	11	-.10	.02
Mean change in primary production ( $\Delta PN_p$ )	12	-.11	-.17

<sup>1</sup> See Table 3 for two other morphofunctional descriptors.

\*  $P < .05$ .

means. As these means are computed from the entire 65 data points for each species, the error variance of the mean is of considerably less significance than the error variance of individual data points for a species.

Table 2 shows that there is no significant relation between CV or skew and either of the two abundance descriptors. This suggests that a given shape of abundance-frequency distribution is equally likely to occur in rare and common species. Thus while some species of high average abundance and high CV or skew form dramatic blooms that dominate the autotroph community at certain times of the year, some rare species behave in a demographically identical fashion much further down the abundance scale where their growth pulses are much less obvious. Similarly, certain rare species share with common species such as *Chroococcus minutus* the ability to hold a very steady abundance through the year. The forces which dictate mean abundance seem to be separate from those which dictate demographic strategy.

#### *Shape of the abundance-frequency curve in relation to morphofunctional traits*

Five morphofunctional descriptors were used in the analysis. Three of these are specific in that they represent a particular trait: (1) volume, (2) surface:volume (S:V) ratio, and (3) surface area. The other two morphofunctional descriptors are general, as they represent a number of specific traits: (1) morphotype and (2) taxon.

Table 1 gives the values for two of the specific morphofunctional descriptors, volume per biomass unit and S:V ratio. Surface area, the third specific descriptor, can easily be calculated from the other two and is consequently not listed in Table 1. These data

were obtained from composite geometric models for each species (Lewis 1976).

There is no significant simple or partial correlation of volume, S:V ratio, or surface area with CV or skew (Table 2). Although the variables are likely to be of great significance for the survival of species, they are governed by factors separate from those which determine the shape of the abundance-frequency distribution. These results are counterintuitive, as it would seem that very small species with a high S:V ratio and high growth potential could most readily live by an  $r$  type of strategy in the rapidly-changing plankton environment. Quite apart from the statistical demonstration, the raw data of Table 1 clearly indicate that this is not so.

The two general morphofunctional descriptors (morphotype, taxon) are not metric and thus cannot be subjected to a correlation analysis. Group comparison tests can be used to search for differences in the shapes of abundance-frequency curves for different morphotypes or taxa, however.

Table 1 lists five morphotypes: coenobial (CE), colonial (CO), single-cell nonflagellate (S), filamentous (FI), and single-cell flagellate (FL). Coenobial and colonial types are distinguished by the degree of uniformity in the number of associated cells. *Scenedesmus*, for which the number of joined cells is almost always four, is classified as a coenobium, whereas *Dictyosphaerium*, which has a highly variable number of cells, is considered a colony.

The morphotypes are contrasted with the null hypothesis that the CV and skew statistics of abundance-frequency curves are not different for different morphotypes. Table 3 summarizes the results of a Student-Newman-Keuls (SNK) multiple range test

TABLE 3. Mean CV and skew for species grouped by morphotype (cenobial, colonial, flagellate, single cell nonflagellate, filamentous) and by taxon (chrysophyte, cryptophyte, dinoflagellate, green, bluegreen, diatom). Dashed lines join groups that are not significantly different by SNK criteria

	Morphotype					Taxon					
	CE	CO	FL	S	FI	CH	CR	DN	GR	BG	DI
Mean CV	89	108	110	128	255	.87	1.10	1.18	1.13	1.39	2.64
Mean skew	1.81	1.98	2.11	2.18	3.93	2.56	2.28	1.72	2.13	2.14	4.15

(Sokal and Rohlf 1969) comparing the mean CV and skew values among the five morphotypes. The variables were log transformed prior to this analysis. The dashed lines in the table underscore groups that were mutually indistinguishable by SNK criteria at  $\alpha = .05$ . On this basis the filamentous morphotype has a significantly higher CV than the other four morphotypes, which are not mutually distinguishable. For skew, SNK is unable to distinguish any morphotype as distinct from the others.

The group comparison tests are not particularly powerful because of the small number of species in each group. Nevertheless, the presence of a considerable gradient in mean CV and skew between groups plus some statistically significant intergroup differences indicates a systematic variation of demographic strategy with morphotype. The explanation of this phenomenon is not obvious. The filamentous forms, which are distinctly opportunistic, include representatives of the filamentous bluegreens, whose capabilities for producing extraordinary growths at certain times of the year are notorious (Reynolds and Walsby 1975). It is more difficult to generalize from the literature about the coenobial types, which are distinctly conservative in Lanao.

Margalef (1958, 1968) has attributed to flagellates a special role in phytoplankton successional sequences on the basis of their motility, hence one might expect the flagellate morphotype to segregate more cleanly than it has here. Margalef believes that motility augments the nutrient gathering ability of flagellates to such an extent that they can tolerate the low nutrient levels characteristic of late successional stages. There is no necessary connection, however, between the position of a species in the successional sequence and its demographic strategy. This point is well demonstrated in the Lake Wingra studies (Allen and Koonce 1973). Motility functions as a unique advantage under ice (Nauwerck 1963; Tilzer 1972), but its exact significance under the continuous ice-free conditions of Lake Lanao is harder to specify. The data suggest that flagellate species play a variety of ecological roles in the Lanao plankton system.

The 31 species can also be grouped by taxon into six major groups which form logical ecological entities on functional and structural grounds. As with morphotype, the analysis must proceed by group compari-

son. The mean CV and skew values for the groups appear in Table 3. Statistical analysis is somewhat inhibited by the uneven distribution of species among taxa. The chrysophytes, cryptophytes, and dinoflagellates are omitted from the SNK analysis, as these groups contain fewer than three species. The SNK comparison between greens, bluegreens, and diatoms achieves a separation of diatoms as a distinct group both on the basis of CV and skew (Table 3). Greens and bluegreens are not separable from each other even though the group sizes are fairly large.

The overall analysis of morphofunctional variables suggests that specific morphofunctional characteristics (size, surface area, S:V ratio) are not related to demographic strategy, whereas more general morphofunctional characteristics (morphotype, taxonomic affinity) are related to demographic strategy. This difference can be explained in terms of the significance of specific and general morphofunctional traits for the success of a species. The significance of one specific trait is greatly modified by others. For example, the S:V ratio of a Lanao phytoplankton species is related to its position on a nutrient gradient (Lewis 1977a) and this partially determines the timing of growth pulses for the species. Other specific morphofunctional characteristics interact with S:V ratio to determine the size of these growth pulses and the degree of subsequent decline. Since organisms sharing one specific morphofunctional character do not necessarily share others, their abundance-frequency distributions may be shaped differently even though their responses on a nutrient gradient are qualitatively similar. General morphofunctional characters such as morphotype and taxon encompass a number of specific morphofunctional characters and are thus more likely to serve as good predictors of the overall similarity of abundance-frequency distributions between species. This explains the better relationship between general morphofunctional characters and the shapes of the abundance-frequency distributions.

*Shape of the abundance-frequency curve in relation to niche descriptors*

All phytoplankton increase and decrease in abundance over the course of a year. The periods of increase for a particular species correspond with the coincidence of certain favorable conditions which de-

fine the central portion of the niche for the species. The hypothesis to be tested here is that there is no correspondence between the demographic traits of a species, as indicated by the CV and skew of its abundance-frequency distribution, and the position of the species during its growth phases along one or more axes of the niche.

One practical problem arising from the hypothesis is the difficulty of measuring the variables which constitute the axes of the niche. Two approaches are possible here. (1) Three of the most important niche dimensions can be measured individually from the data at hand and are the basis for what will be called "simple" niche descriptors. (2) Data describing the overall rate of growth processes in the autotrophs can be used as composite indicators of a wide variety of unmeasurable environmental conditions and are the basis for what will be called "composite" niche descriptors.

#### *Simple niche descriptors*

The directly measurable niche dimensions include nutrient availability, light availability, and grazing pressure. Values for each of these three variables have been previously computed in connection with a gradient analysis and are extensively explained elsewhere (Lewis 1977a). The computations can be briefly described as follows. (1) Nutrient availability for a given week was assigned a value of 0, 1, or 2 according to whether inorganic nitrogen, which is the nutrient most commonly limiting (Lewis 1974), was completely depleted in the euphotic zone ( $< 1 \mu\text{g/l}$ ), in low supply ( $1-2 \mu\text{g/l}$ ), or readily available ( $>2 \mu\text{g/l}$ ) over the week. (2) Sunlight availability was assigned a value equal to the mean photosynthetically-available irradiance (Ph.A.R. 350-700 nm) reaching an average phytoplankton cell. This was computed from the incident irradiance, the depth of mixing, and the extinction coefficient of light in the water column (Lewis 1977a). (3) Grazing pressure was considered directly proportional to the biomass of grazers. Biomass of herbivores per unit surface area was computed from weekly zooplankton samples (for sampling methods, see Lewis 1975). These data provide a matrix of weekly values for the three variables spanning the entire study period.

In order to determine which of the values in the nutrient-sunlight-grazing matrix represent the central portion of the niche of a given species, it is necessary to use the weekly abundance estimates for the species. First, the periods of significant net growth must be identified for each species. If  $b_i(t)$  is the biomass of the  $i^{\text{th}}$  species at time  $t$ , the species is said to be increasing significantly during weeks for which net relative growth ( $RG_i$ ) exceeds a certain threshold. Net relative growth is:

$$RG_i = b_i(t_2)/b_i(t_1)$$

where  $t_1$  is the first day of the week and  $t_2$  the last.

For present purposes, the threshold for  $RG_i$  in all species is set at 1.6 with the provision that abundances below 25 individuals/cc cannot be considered because the error variance on such low counts is too great. The value 1.6 for  $RG_i$  is arbitrary and other values ranging between 1.2 and 2.0 give similar results in the analysis. The value 1.6 strikes a good balance between the need for (1) a sufficiently high  $RG_i$  that error variance could not produce spurious instances of apparent growth and (2) a value sufficiently low to be observed with reasonable frequency.

Using weekly  $RG_i$  values and the established threshold value (1.6), it is possible to identify a number of weeks during the 65-wk period when any given species meets the criterion for demographic success. Average values of the three variables (nutrient availability, light availability, grazing pressure) were obtained for these dates. This produced estimates of the location of a species on the gradients of nutrient, light, and grazing where the species succeeds in growing, i.e., an estimate of its position in the niche space. These estimates are the simple niche descriptors. Using the data for all 31 species, the simple niche descriptors for species are compared statistically with the CV and skew of their abundance-frequency distributions.

The problem of lag effects arises in connection with the computation of niche descriptors. It is possible for the behavior of the biota in a given time interval to reflect the conditions in a previous time interval, which would in turn affect the computation of any niche descriptor. This problem was investigated in a quantitative study of phytoplankton succession in Lake Lanao and proved to be inconsequential for phytoplankton demographic phenomena (Lewis 1977c). Lag effects certainly occur in the phytoplankton, but the lags are shorter than the sampling interval (7 days), so they do not have to be considered in the analysis. This is not surprising in view of the short mean turnover time for autotroph biomass in the lake (1.2 days), which allows rapid response to environmental changes.

The first two niche descriptors, which are based on resource supply (nutrients, sunlight), are not related to CV or skew of the abundance-frequency distribution (Table 2). The third niche descriptor, which is based on attrition (grazing), bears a significant negative relation to CV and skew. The partial correlation is reported in this case, because grazer biomass is related to autotroph abundance. More opportunistic species (i.e., those with high CV and skew) evidently cannot withstand grazing pressure and tend to flourish when it is minimal. The selection abilities of grazers must be important in explaining this trend, as the total daily removal by zooplankton is not great (mean, 7%). This relation between the position of a species on the grazing gradient and the shape of its abundance-frequency curve is in concordance with the general notion that

*r*-selected species are more poorly equipped to withstand biotic pressures than *K*-selected species (Dobzhansky 1950).

#### Composite niche descriptors

The first two composite niche descriptors measure the change in autotroph abundance in terms of biomass ( $\Delta B_p$ , variable 9) or numbers of individuals ( $\Delta N_p$ , variable 10) at weekly intervals. Change in autotroph abundance is a measure of the general condition of the water column for autotrophs and is determined by the sum of all variables affecting phytoplankton growth and attrition. Species which thrive when autotroph abundance is increasing rapidly obviously have different adaptations from species which thrive under conditions generally more adverse for autotrophs. Whether demographic strategy is one of the adaptations of significance in this context is tested by a procedure identical to that which was outlined for the simple niche descriptors.

There is a significant negative relation between CV and  $\Delta B_p$  or  $\Delta N_p$  niche descriptors. Skew does not show the relationship so strongly. The relation of the skew statistic with other variables is in fact typically weaker than for the CV statistic. This is probably due to the greater statistical uncertainty of the skew measurement, which is more markedly affected by one or two outlying measurements than is CV. It therefore does not seem justifiable to attribute any biological significance to the stronger relationship between CV and the niche descriptor in this case.

The significant relationship between the  $\Delta B_p$  or  $\Delta N_p$  niche descriptors and CV suggests that opportunistic species thrive when autotrophs as a whole do not. There are two mechanisms by which this might occur. (1) Opportunistic species may anticipate general increases in autotroph abundance by means of adaptations for very rapid growth in response to generally favorable conditions. This type of opportunism parallels the often-cited opportunism of early colonizers in secondary succession among land plants (Odum 1969). (2) In addition, opportunistic species may thrive due to some special physiological capability that becomes important only when conditions have deteriorated to an extent which renders ineffective the superior competitive abilities of the more conservative species. The filamentous bluegreens of Lake Lanao behave in this manner, as they flourish late in the successional sequence, possibly because of nitrogen-fixing capabilities.

The third and fourth composite niche descriptors are net primary production ( $PN_p$ , variable 11) and weekly change in net primary production ( $\Delta PN_p$ , variable 12). As with the other niche descriptors, growth periods for each species were identified and average values of  $PN_p$  and  $\Delta PN_p$  were obtained for these periods.

Table 2 shows that  $PN_p$  and  $\Delta PN_p$  niche descrip-

tors are unrelated to the CV or skew of the abundance-frequency distributions. Primary production on a given date is mainly controlled by rate of resource supply, as grazing is never sufficiently intense to act as an overall suppressant of autotroph growth (Lewis 1974, 1977a). It may seem surprising that the niche descriptors based on change in autotroph abundance should be significantly related to CV while the production-based descriptors are not. Abundance change reflects the balance of attrition and growth, but production is more purely related to growth, which is in turn under the control of resource supply. Since simple niche descriptors based on resource supply earlier proved to be unrelated to the CV and skew of species, it is only reasonable that composite niche descriptors based on production should also be unrelated. The implication is clear that sources of attrition are much more important in relation to the demographic strategy of species than are growth control mechanisms. This is confirmed by the independently-demonstrated relation between the simple niche descriptor for grazing intensity, a specific source of attrition, and the shape of abundance-frequency distributions.

#### OVERALL STATISTICAL CONSIDERATIONS

Up to this point in the analysis each variable in the lists from Table 2 and Table 3 has been treated as a separate statistical problem. This can be defended on the basis of *a priori* selection of variables and separate consideration of each variable in its biological context. Final evaluation of the overall variable list requires some additional precautions, however. In a random examination of 28 unrelated variable pairs using  $\alpha$  of .05, the expected number of significant results is  $.05 \times 24$ , or 1.2. The number of significant relationships observed in the study is six. The probability of six or more significant results occurring by chance alone is:

$$1 - \sum_{i=1}^5 \binom{28}{i} (0.95)^{28-i} (0.05)^i$$

which is .002. This computation is actually only approximate because of some multicollinearity in the independent variables (which was to a large extent compensated by partial correlation). Nevertheless it is very safe to assume that the significant results are not entirely due to chance. The probability that every one of the significant results is real is determined by Bonferroni criteria (Harris 1975), which are extremely stringent when large numbers of variables are involved. To assure at the .05 level that all six of the significant results are not due to chance, the individual coefficients would have to be significant at  $\alpha = .05/28$ , or .0018, which they are not. We can say with certainty only that most of the coefficients signify real biological relationships and that the expected number of falsely significant coefficients at  $\alpha = .05$  is 1.2.

However, the discussion thus far and some *a priori* tests to follow in the conclusions section show that the significant results are clustered around measures of attrition. Meaningful clustering has a very low probability of random occurrence, and thus increases substantially the statistical likelihood that the overall interpretation is correct.

#### CONCLUSIONS

The analysis supports five general conclusions. Shapes of abundance-frequency distributions are not related to (1) mean abundance, (2) specific morphofunctional characteristics, and (3) position of a species on gradients of growth control mechanisms (resource supply). Shapes of abundance-frequency distributions are related to (1) general morphofunctional characteristics (morphotype, taxon) and (2) position of a species on gradients of attrition control mechanisms.

The 3 negative conclusions are of course less certain than the 2 positive ones. The conclusion about mean abundance seems quite sound, however, as measurement of this variable is technically simple. Generalization about specific morphofunctional properties is based on the analysis of three such properties (size, surface area, S:V ratio). It is possible that other such properties not considered here would prove to be related to the shape of abundance-frequency distributions. The third negative conclusion, which denies any relationship between the shape of abundance-frequency curves and the position of a species on resource supply gradients, is intrinsically difficult to defend owing to the complexity of variables involved. The conclusion is strengthened here by the use of two independent assessments of resource supply: (1) direct measure of nutrient and light availability (simple niche descriptors) and (2) net production as a reflection of overall resource availability (composite niche descriptor).

The two positive conclusions appear to be quite distinct from each other, but might actually be explained by a common mechanism if there is some connection between the general morphofunctional characteristics and the position of a species along gradients of attrition factors. This possibility can be explored by comparisons of morphotype groups or taxonomic groups. The comparisons are based on niche descriptors which incorporate some measure of attrition. There are two such niche descriptors: (1) the simple niche descriptor based on grazing intensity (variable 8), and (2) the composite niche descriptor based on change in autotroph biomass (variable 9). The niche descriptor based on change in autotroph numbers (variable 10) could also be used but adds nothing to an analysis including variable 9. Variable 8 is affected by the response of a species to grazing attrition, whereas variable 9 is affected by the response of a species to both grazing and nongrazing attrition.

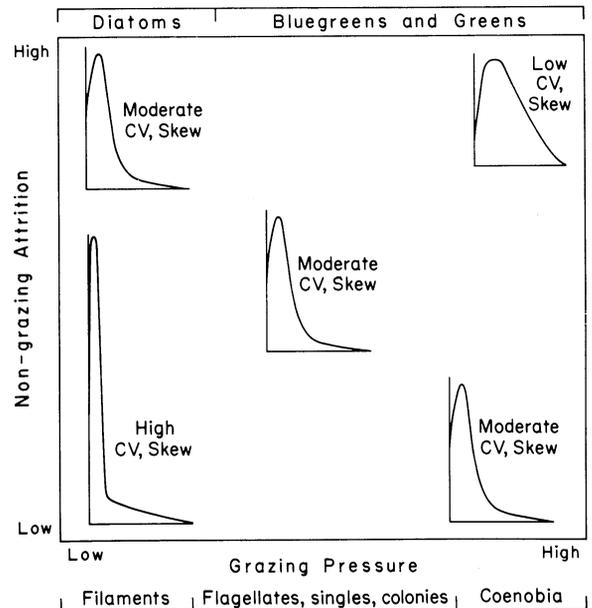


FIG. 2. Schematic representation of the overall interpretation suggested by the data analysis. Positions occupied on the axes by the various morphotypes or taxa indicate conditions under which these groups are most likely to increase in biomass. Positions inside the graph occupied by the different demographic strategies indicate conditions under which species having such strategies are most likely to increase in biomass.

The Student-Newman-Keuls multiple range test separates morphotypes on the basis of the grazing intensity niche descriptor. The separation at  $\alpha = .05$  splits the morphotypes into two overlapping groups: (1) FI-FL-CO and (2) FL-CO-CE-S. This suggests that a significant part of the observed difference between morphotypes occurs through the mechanism of grazing. Specifically, filamentous forms do not thrive in the presence of grazers.

Morphotype groups do not separate on the basis of the abundance change niche descriptor (variable 9). Nongrazing attrition is therefore not implicated as a mechanism explaining the demographic differences between morphotypes.

Taxonomic groups, like morphotype groups, separate on the basis of grazing intensity. This produces two overlapping groups: (1) DI-BG and (2) BG-GR. The diatoms thrive when grazing intensity is minimal. No separation is possible on the basis of the abundance change niche descriptor. In a manner similar to the morphotype analysis, the significance of taxon as a grouping criterion seems to derive directly from grazing, and not from other sources of attrition.

Figure 2 summarizes all of the relationships uncovered by the analysis. The figure indicates the dominance of what Levandowsky (1972b) has called "rarifying" aspects of the niche in determining demographic strategy. Levandowsky and Allen and Koonce

(1973) have argued on independent grounds that grazing in particular must be a primary determinant of phytoplankton strategy. The foregoing analysis confirms this and suggests that nongrazing attrition is important as well, but is much more independent of morphology or taxonomic affinity.

It remains to be seen whether relationships similar to those of Fig. 2 are typical of many plankton systems. If so, an important question is whether demographic strategy as revealed by the abundance-frequency distribution is a conservative species property or is highly malleable according to the environmental background. Aside from its basic importance to the understanding of plankton community structure, this is relevant to the analysis of water blooms developing from directional changes in lake nutrition. If shape of the abundance-frequency distribution is a conservative species property, alterations in relative abundance of phytoplankton species following nutrient enrichment may be accounted for by an increase in the mean abundance of certain species with highly skewed distributions. It is possible that potential problem species in a particular habitat could be forecast more meaningfully from the shapes of the abundance-frequency distributions than from the relative abundance of species. Moreover, species with characteristic types of abundance-frequency distributions could prove to be of value in paleolimnological interpretation, particularly as the factors associated with various kinds of distributions are better defined.

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