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Spatial Distribution of the Phytoplankton in a Tropical Lake (Lake Lanao, Philippines)¹

Abstract

The distribution of phytoplankton was studied in Lake Lanao, Philippines. In calm weather, the species segregate vertically with motile species and buoyancy-regulating species above other species in the water column. On a distance scale of 12.5 km, horizontal variability yields a coefficient of variation of 23.6% for total biomass, 30.2% for net primary production, and an average of 30.3% for individual species biomass after removal of error variances. Variabilities on a scale of 1 km are about half as large. Horizontal patchiness of individual species is not related to their abundance, surface to volume ratio, morphotype, or taxon, but is negatively related to their size.

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1. Introduction

Although phytoplankters are capable of only limited movement, they are distributed heterogeneously in lakes (LUND 1965, HUTCHINSON 1967). Vertical and horizontal spatial heterogeneity result from heterogeneity in the factors that control growth and attrition, and to a lesser degree from buoyancy regulation and active movement. Vertical variation is both more obvious and better documented than horizontal variation, but not necessarily more important. Complete understanding of plankton dynamics must be in part based on knowledge of the vertical and horizontal distributions of species, as variation in space and time may be functionally related (MARGALEF 1958, HUTCHINSON 1961, RICHERSON *et al.*, 1970, RILEY 1976).

The present analysis documents both vertical and horizontal variation in the distribution of the phytoplankton of Lake Lanao, Philippines. Phytoplankton com-

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position and succession in Lake Lanao have already been analyzed (LEWIS 1978 a, b). In the present analysis, particular emphasis is placed on the comparative distributions of individual species, as this aspect of spatial variation is potentially most important in understanding community structure and successional phenomena in the phytoplankton but has been studied much less than variation in total biomass or production.

2. Description of the Study Site

Lake Lanao is located on the island of Mindano at an altitude of 720 m (8° N, 124° E). The main physical features of the lake as given by FREY (1969) are: maximum depth, 112 m; mean depth, 60.3 m; area, 357 km²; replacement time, 6.5 yr.

Weather patterns and the corresponding features of the thermal regime in Lake Lanao have already been analyzed (LEWIS 1973). The main seasonal feature is a period of cool relatively dry weather lasting from December through March (mean temperature, 21.5–22.5 °C); rain, 150–200 mm month⁻¹). November and April are transition months with variable weather. The remaining six months are typically warmer and wetter (23.0–24.0 °C; 250–340 mm month⁻¹).

Since Lanao is a large lake with low shoreline development, wind-generated mixing is pronounced throughout the year. The thickness of the mixed layer is never less than 12 m, as daily convective air movement mixes the lake to this depth even if the lake is calm at midday. During the stratification season (April–November), the depth of the mixed layer varies from 12 to 45 m, with a mean of about 25 m. During the circulation period (December–January), the water column has no stable structure and deep mixing occurs frequently (LEWIS 1973). February and March are transition months when deep mixing alternates with stratification.

Lake Lanao has a conductance of 105 $\mu\text{mho cm}^{-1}$ at 25 °C, and an alkalinity of 1.02 meq l⁻¹. Nitrate-nitrogen averages only 9 $\mu\text{g l}^{-1}$ in the euphotic zone and is frequently undetectable (<1 $\mu\text{g l}^{-1}$, LEWIS 1974). Molybdate-reactive phosphorus is more concentrated (29 $\mu\text{g l}^{-1}$ PO₄-P, average) and appears to be less important than nitrogen as a limiting nutrient for autotrophs. Silicon averages 2.2 mg l⁻¹ Si

Table 1. List of the 27 species used in the studies of spatial distribution

Cyanophyta	Chlorophyta (continued)
<i>Chroococcus minutus</i> (KUTZ.) NAEG.	<i>Chodatella</i> sp. 1
<i>Aphanothece nidulans</i> P. RICHT	<i>Kirchneriella obesa</i> (W. WEST) SCHMIDLE
<i>Dactylococcopsis fascicularis</i> LEMM.	<i>Selenastrum minutum</i> (NAEG.) COLLINS
fa. <i>solitaria</i>	<i>Dictyosphaerium pulchellum</i> WOOD
<i>Dactylococcopsis woltrecki</i> BEHRE	<i>Dimorphococcus lunatus</i> A. BRAUN
<i>Lyngbya limnetica</i> LEMM.	<i>Coelastrum cambricum</i> ARCH.
<i>Synechococcus</i> sp. 1	<i>Scenedesmus ecornis</i> (RALFS) CHOD.
Euglenophyta	var. <i>polymorphus</i> CHOD.
<i>Trachelomonas bacillifera</i> var. <i>minima</i>	<i>Scenedesmus</i> sp. 1
PLAYF.	Unknown 28
Chlorophyta	<i>Chromulina</i> sp. 1
<i>Tetraedron minimum</i> (AL. BRAUN)	Bacillariophyceae
HANSGIRG	<i>Nitzschia bacata</i> HUST.
<i>Sphaerocystis schroeteri</i> CHOD.	<i>Melosira granulata</i> (EHRBG.) RALFS
<i>Oocystis submarina</i> LAGERHEIM	Cryptophyceae
<i>Oocystis lacustris</i> CHODAT	<i>Rhodomonas minuta</i> SKUJA var.
<i>Franceia droescheri</i> (LEMM.) G. M. SMITH	<i>nannoplantctica</i> SKUJA
<i>Chodatella subsalsa</i> LEMM.	<i>Cryptomonas marssonii</i> SKUJA

in the euphotic zone and is probably never sufficiently depleted to limit diatom growth completely.

Extensive studies of primary production have shown that Lake Lanao is highly productive (LEWIS 1974). The annual average net primary production is $1.7 \text{ gC m}^{-2} \text{ day}^{-1}$, and gross primary production averages $2.6 \text{ gC m}^{-2} \text{ day}^{-1}$. The lake is nevertheless quite transparent. The average depth to which 1% incident light penetrates is 12 m. High transparency despite high productivity is due to the exceptionally low amount of dissolved and nonliving suspended matter in the euphotic zone, the high production per unit of autotroph biomass, and the great amount of mixing and nutrient renewal in the upper water column.

Lake Lanao has no fixed horizontal thermal or chemical gradients which might affect horizontal phytoplankton distribution. The watershed is mostly timbered and the rivers are not rich in dissolved nutrients (LEWIS 1974). The lake has no isolated arms or bays which might promote horizontal plankton heterogeneity.

Lake Lanao contains 70 phytoplankton species. The analysis of individual species here is limited to 27 of the most abundant species (Table 1).

3. Methods

For the studies of vertical distribution, samples were taken at station 1 (Fig. 1) with a Van Dorn sampler, preserved with Lugol's solution, and counted with an inverted microscope (LEWIS 1978a). All species were separated in the counts. Two series were selected for complete analysis: (1) 25 December, 1970, representing a period of deep mixing and high turbulence, and (2) 23 July, 1970, representing a period of stable stratification and minimum turbulence. Thermal, oxygen, and C-14 productivity profiles were taken at the same time as the phytoplankton samples. The C-14 methods are given by LEWIS (1974). Temperature profiles were made with a thermistor and oxygen profiles by Winkler analysis.

Horizontal variation of phytoplankton was studied in two different ways. (1) At a time of approximately average phytoplankton biomass and primary production (12 March, 1971), a detailed multiple-station study was made of heterogeneity. This will be referred to here as the "intensive" study. Triplicate integrated phytoplankton samples were taken with a weighted plastic tube (0–15 m) at each of 8 stations along two transects crossing the lake (Fig. 1). Abundant species were counted with an inverted microscope in a 2 cc chamber and rarer species were counted in a 5 cc chamber by the same method (LEWIS 1978a). (2) Two replicate samples were taken weekly for 65 weeks at stations 1 and 2, 1 km apart, so that an annual average variability estimate on a scale of 1 km would be available to supplement the intensive study. This will be referred to as the "extensive" study.

In addition to the intensive and extensive studies of heterogeneity in autotroph biomass, there was a detailed multiple-station, multiple-date study of heterogeneity in primary production. The results of this study have been reported elsewhere (LEWIS 1974) but are recalled as necessary to broaden the interpretation of abundance data.

4. Vertical Distribution

Figure 2 illustrates the vertical distribution of total phytoplankton biomass in Lake Lanao during calm weather of the stratification season (23 July, Fig. 2a), and during windy weather just prior to seasonal circulation (25 December, Fig. 2b). Thermal and chemical profiles that were taken at the same time as the plankton samples provide a basis for interpretation of vertical biomass distribution. The anomalous bottom portion of the thermal profiles has been discussed elsewhere (LEWIS 1973).

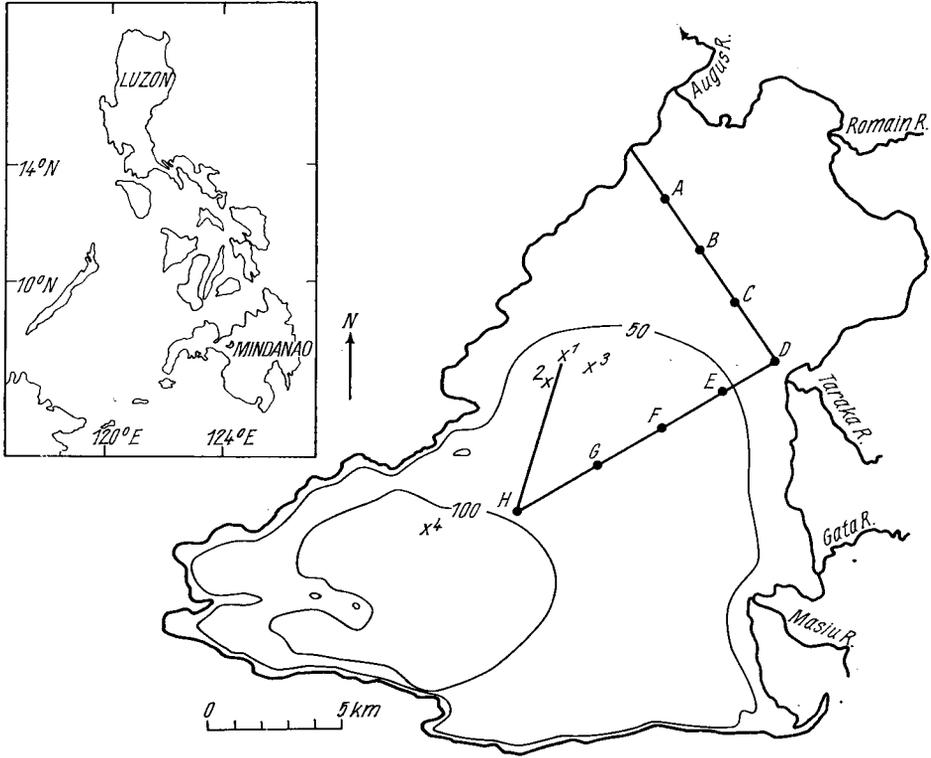


Fig. 1. Map of Lake Lanao showing stations.

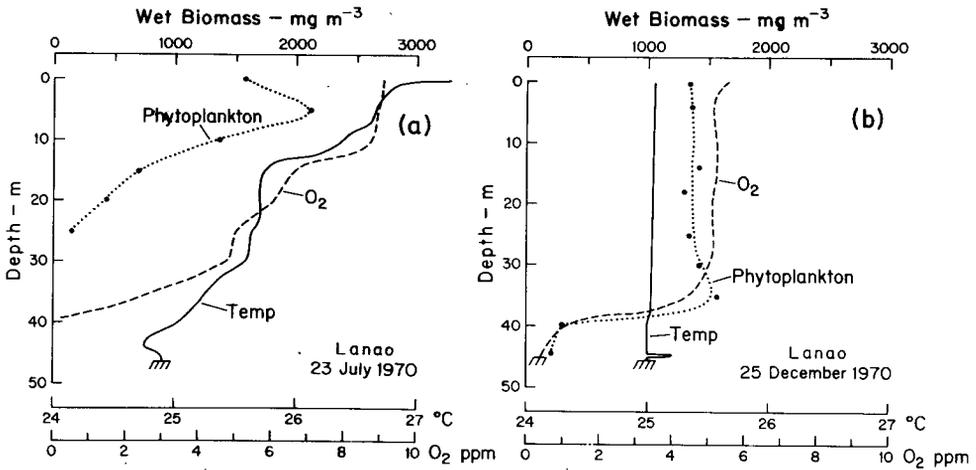


Fig. 2. Vertical distributions of total phytoplankton biomass, temperature, and oxygen in Lake Lanao. (a). Distributions during a period of calm weather. (b). Distributions during a period of deep turbulence.

The biomass distribution of phytoplankton during calm weather of the stratification period plainly reflects the vertical distribution of primary production (Fig. 2a). The surface suppression, maximum just below the surface, and exponential decline below 5 m which are visible in Fig. 2a are also typical of the primary production profiles for this period (LEWIS 1974). The temperature curve shows a secondary thermocline splitting the epilimnion at 15 m. This thermocline had been in existence for about a week prior to the date of sampling. The renewal time for biomass in the upper 15 m at this time was 1.5 days. The calm weather obviously permitted development of an uneven distribution of biomass that very precisely reflected the distribution of primary production over the previous day or more. Considering the uniformly high renewal rates of phytoplankton biomass in Lanao (mean, 1.24 days; range, 0.35–4.90 days, 0–15 m), a vertical distribution of biomass similar to that shown in Fig. 2a is a very likely result of any calm period lasting more than a few hours during daylight.

The rapid decline of biomass below 15 m in the calm-weather profile (Fig. 2a) suggests that sedimentation alone cannot keep pace with other factors causing disappearance of autotroph biomass. Fig. 2a shows that, despite the high rate of biomass renewal near the surface, some factor prevents accumulation of substantial biomass below the euphotic zone through sinking when turbulence does not actively transfer biomass to deeper water.

The effect of deep turbulence on biomass distribution is illustrated in Fig. 2b. The top 40 m was chemically and thermally uniform due to vigorous mixing throughout this layer, whereas the water column below 40 m had not yet been mixed. Vertical distribution of phytoplankton biomass was remarkably uniform in the top 40 m, even though active growth was limited to the top 12 m, which received 99% of incident radiation. Biomass renewal time in the upper 15 m on this date was 0.76 days. Despite this rapid renewal, which can be attributed to the movement of substantial nutrient supplies into the euphotic zone, new biomass was moved away from the lighted zone by turbulence at such a rate that a net decline in phytoplankton biomass occurred over the following weeks.

A simple measure of vertical distribution for individual species can be achieved by vertical summation of biomass to a depth at which the summation equals exactly half the total biomass per unit area. Thus if B_i is biomass per unit area of the i^{th} species, b_i is biomass per unit volume of the i^{th} species, and z is depth, there is a value of z , which can be called h , such that:

$$B_i = 2 \int_{z=0}^h b_i dz$$

This follows the precedent of RUTTNER (1937), who refers to h as the "Halbwerttiefe". This will be referred to here as the "biomass half-depth."

The frequency distributions of the biomass half-depth for important phytoplankton species of Lake Lanao appear in Fig. 3. The vertical distributions of species differ radically on the two dates, as might be expected from the previously-mentioned difference in distribution of total biomass.

Under calm stratified conditions (23 July, 1970), the species were narrowly clumped inside the euphotic zone. Despite these optimum conditions for vertical separation of populations, there were no outlying species resting either very near the surface or deep in the water column. Close inspection shows, however, that all of the flagellate taxa present on this date (*Rhodomonas*, *Cryptomonas*, *Gymnodinium*) had h values of 5 m or less and thus contributed heavily to the near-surface group shown in Fig. 3. In addition, the Nostocaceae (*Anabaena* spp.) plus *Lyngbya* and *Aphanothece* contributed to the near-surface group. All of the green algae and diatoms were deeper in the water column.

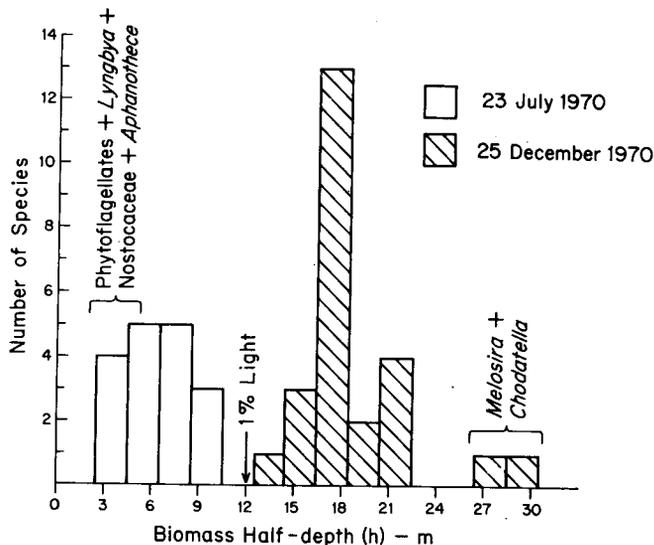


Fig. 3. Frequency distributions of the biomass half-depth (h) for important phytoplankton species in Lake Lanao. Distributions are shown for two different dates, one during a period of calm weather (23 July) and the other during a period of deep turbulence (25 December).

The phytoflagellates and the vacuolated bluegreens, notably *Anabaena*, have considerable capacity to regulate vertical position in the water column (HUTCHINSON 1967, REYNOLDS and WALSBY 1975). Also, a series of studies on mountain lakes provides convincing evidence that some of the phytoflagellates routinely move in a directed manner in order to increase overall photosynthetic efficiency (TILZER 1973; TILZER and SCHWARTZ 1976). Many studies have demonstrated clumping of phytoflagellates in certain portions of the water column in a manner suggesting directed movement (e. g. NAUWERCK 1963, BAKER 1970, TALLING 1971, BERMAN and RODHE 1971). Density regulation in both the filamentous and coccoid bluegreens is now known to be at least partially controlled by light (WALSBY 1969, MEFFERT 1971, REYNOLDS 1972, DINSDALE and WALSBY 1972). Evidence of buoyancy in field populations of tropical species has also been obtained for filamentous and for coccoid species (TALLING 1957, GANF 1974).

In Lake Lanao, the vacuolated bluegreens and the phytoflagellates apparently use their powers of movement to rise above the biomass maxima of other species during calm weather. The selective advantage of this tactic under conditions of high algal biomass probably derives from the shading of one population by others. The motile populations lie only slightly higher in the water than the non-motile ones, however. The region nearest the surface is unfavorable due to the very high light intensities there.

During the period of deep mixing, the majority of species had biomass half-depths approximately equal to half the circulating layer (i. e., ca. 18 m, Fig. 3). None of the motile or buoyant species showed any significant departure from this pattern. Turbulence must therefore have overwhelmed any tendency toward vertical segregation.

Two taxa, *Melosira* and *Chodatella*, are divergent from the main group of species shown in Fig. 3. The seasonal history of *Melosira* in temperate lakes is known to be profoundly affected by turbulence (LUND 1954, 1955). *Melosira* sinks rapidly and is

consequently not common in the plankton during stratification. During periods of turbulence, however, sinking is retarded by turbulence and a substantial planktonic *Melosira* population develops. The high biomass half-depth of *Melosira* on 25 December, 1970 (*Melosira* was absent on 23 July, 1970) is evidently explained by sedimentation losses from the upper water column even under conditions that maintain uniform distribution of other species. The deep population of *Chodatella* is less easily explained, as this species is extremely small and probably not vulnerable to rapid sedimentation. Since relatively small numbers of *Chodatella* individuals were observed at any depth, however, this particular observation is probably a sampling or counting artifact.

In summary, the distribution of total autotroph biomass seems to be related in a very straightforward manner to light penetration and turbulence. Under calm conditions, the biomass curve reflects the production curve, which is in turn under control of light penetration. Individual species segregate under these conditions, with the motile species above non-motile species. Deep turbulence generated by wind or thermal inversion masks the effects of light penetration, and smooths the vertical distribution of total biomass. Motile species cannot segregate from non-motile species under these conditions, although *Melosira* may accumulate toward the bottom of the water column because of its high sinking rate.

5. Horizontal Distribution

According to PLATT *et al.* (1970), total variation in counts (σ_t^2) is the sum of (1) variation due to counting technique, subsampling, and other analytical errors (σ_0^2), (2) true variation among replicate samples at a station (σ_1^2), and (3) true variation between stations (σ_2^2). These three components of variance serve here as a basis for analysis of analytical error and for a discussion of patchiness in the phytoplankton.

Since variability in the counting technique itself is relevant to the analysis of patchiness, a consideration of counting statistics is useful. For replicate samples taken at the same station, the standard deviation of an abundance estimate obtained with a 2-cc counting chamber averages 24% of the mean (i. e., the coefficient of variation is 24%). Since two replicates at each station are averaged to obtain abundance estimates for species counted in 2-cc chambers, standard error for an abundance estimate at a single station averages about 17% of the mean. The errors associated with counts on 5-cc chambers are slightly lower than these. Also, all counting errors increase for species having an abundance less than about 75 counting units per cc. The 27 most abundant species are typically above this threshold, however. The 17% standard error for an estimate of a single species at a single station includes analytical errors of all kinds (σ_0^2) and true variation between replicates 1 to 5 m apart at a single station (σ_1^2), which is typically very small.

a) Intensive Heterogeneity Study

On the date of the intensive study, the lake had been calm for 24 hours following an extended period of heavy winds. Productivity was $1.4 \text{ gC m}^{-2} \text{ day}^{-1}$, slightly below the annual average (LEWIS 1974), and the mean wet biomass of phytoplankton was 1413 mg m^{-3} (0–15 m), very near the annual average for the lake. The physico-chemical conditions at the index station are indicated in Fig. 4. Storms had during

the previous week mixed the lake to 48 m, the level of the primary thermocline, thereby relieving oxygen depletion below a previously-existing secondary thermocline at 20 m. By 12 March 1971, traces of a new secondary thermocline were already visible again at 20 m and wind-driven circulation had not extended below this level for at least two days. The weather on the sampling date was calm, as indicated by the high surface temperature (Fig. 4).

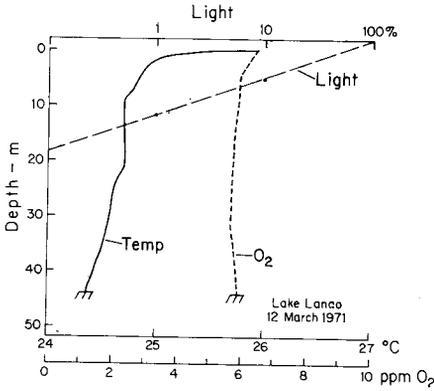


Fig. 4. Physical and chemical conditions at the index station (mid-lake) on 12 March 1971, the date of the intensive biomass heterogeneity study.

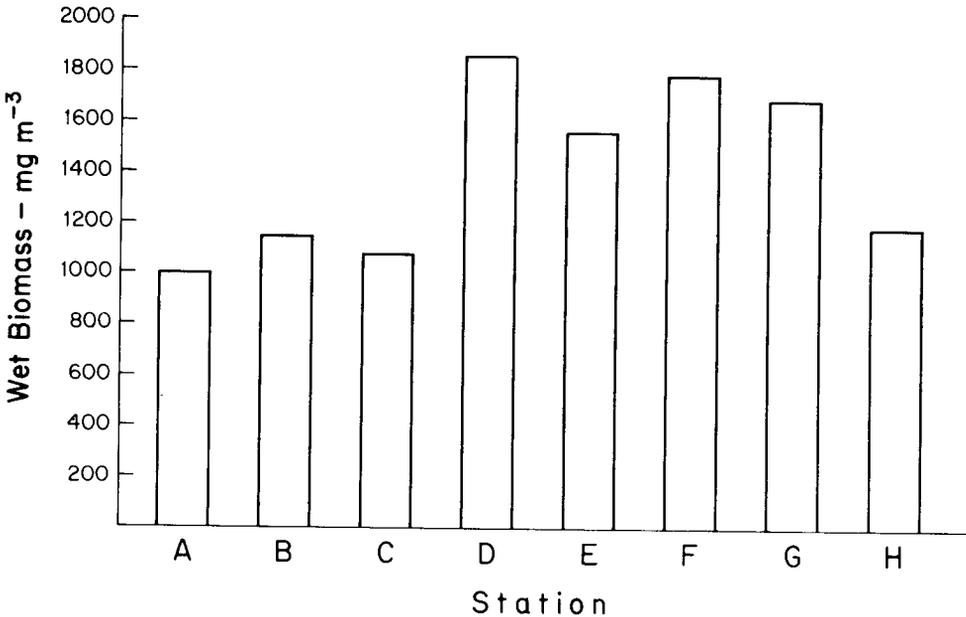


Fig. 5. Phytoplankton biomass at each of the 8 sampling stations on 12 March 1971. Locations of the stations are indicated on the map. Biomass is an average for the euphotic zone (0-15 m).

Variation of algal biomass between stations on 12 March is shown in Fig. 5. BARTLETT's test for homogeneity of variances between stations yielded a chi-square value of 11.4 (7 degrees of freedom), which is not significant at $\alpha = 0.05$. The stations therefore did not differ significantly in variability of replicates. This finding agrees with productivity studies, which also showed homogeneous variances between stations on a given date (LEWIS 1974). Homogeneity of biomass variances between stations is of ecological interest and also permits straightforward analysis of variance to test significance of differences in mean biomass between stations.

A one-way ANOVA with stations as treatments yielded an F value of 6.52 for total autotroph biomass, which is significant at $\alpha = 0.05$. The sampling transects probably give a conservatively high estimate of variability, as they included one point about 1 km from a river mouth and another about 1 km from shore (Fig. 5).

The components of variances can be separated by Model II criteria as follows (SOKAL and ROHLF 1969):

$$\begin{aligned}\text{within group variance} &= \sigma_0^2 + \sigma_1^2 \\ \text{among group variance} &= \sigma_0^2 + \sigma_1^2 + n\sigma_2^2\end{aligned}$$

where n is the number of replicates. From these equations, σ_2^2 , variation due to station alone is easily computed. The station effect is fairly small, even though it is statistically significant (Table 1).

The ANOVA allows separation of true variance between stations (σ_2^2) from variance due to other sources ($\sigma_0^2 + \sigma_1^2$, Table 2). The coefficient of variation for biomass replicates at a given station is 15.4% (Table 2). For productivity (C-14) replicates at a given station the comparable figure is 6.4%.

For purposes of discussion and further analysis, a special coefficient of variation was calculated from the station effect only (σ_2^2). This will be symbolized by CV_2 ($= \sigma_2/\bar{X}$). Since CV_2 is not affected by σ_0^2 and σ_1^2 , it is a truly comparative measure of patchiness.

The variance attributed to station differences alone (σ_2^2) yields a CV_2 of 23.6% for biomass (Table 2). For primary production the mean CV_2 on 7 different dates from Lake Lanao (LEWIS 1974) is very similar (30.2%).

The expected frequency distributions of biomass and primary production at randomly-selected stations on a given date can be constructed from the analysis of va-

Table 2. Statistical summary of horizontal heterogeneity for Lake Lanao under conditions of average autotroph biomass and primary production

Homogeneity of variances between stations (chi-square, <i>d. f.</i> = 7)	
Total autotroph biomass	11.4 +
Biomass of individual species, mean chi-square for 27 species	6.7 +
Equality of means between stations (F , <i>d. f.</i> = 7,8)	
Total autotroph biomass	6.5*
Biomass of individual species, mean F for 27 species	6.3*
Coefficient of variation between replicates at a station (CV_0 , %: includes error variance)	
Total autotroph biomass	15.4
Biomass of individual species, mean CV for 27 species	26.7
Primary production	6.4 ++
Coefficient of variation between stations (CV_2 , %: does not include error variance)	
Total autotroph biomass	23.6
Biomass of individual species, mean CV for 27 species	30.3
Primary production	30.2 ++

+ Not significant.

* Significant at $p = 0.05$.

++ Data from LEWIS (1974).

riance with certain assumptions and restrictions. First, the forms of the distributions must be approximated. Insufficient data are available for any good empirical test, but both biomass and primary production are "overdispersed" ($s^2/\bar{X} > 1$). Under these circumstances, the negative binomial or lognormal distributions are often good approximations of the empirical distributions (CASSIE 1962a, b). According to KOLMOGOROV-SMIRNOV criteria (CONOVER 1971), the negative binomial fits the Lanao data better than the lognormal. The distributions are therefore represented here as negative binomial for both production and autotroph biomass.

The biomass and productivity distributions are of the same type (negative binomial) and have very similar coefficients of variation based on station effects alone (24% biomass vs 30% productivity). Mean annual autotroph biomass is approximately 1500 mg wet wt m^{-3} (average, 0–15 m), or 1.5 $g m^{-3}$. Annual average primary production is 1.7 $g C m^{-2} day^{-1}$. The productivity and biomass means and coefficients of variation are so nearly equal that they can be considered for present purposes to represent identical distributions with means of 1.6 and coefficients of variation equal to 27%. Two variables with equal coefficients of variation and equal

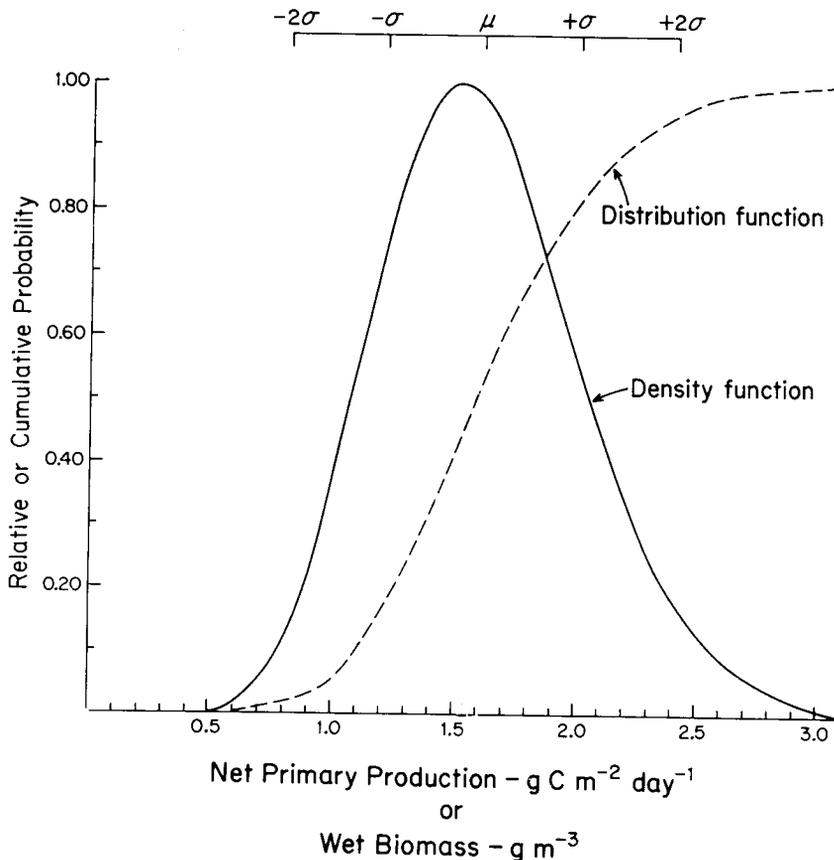


Fig. 6. Predicted frequency distribution (with no error variance) of autotroph biomass and primary production measurements at stations averaging 12 km apart on Lake Lanao during a period of average primary production and autotroph biomass.

means have equal variances, hence one curve represents both biomass and primary production (Fig. 6).

Fig. 6 represents a statistical population consisting of an infinite set of measurements of biomass or productivity at randomly-selected stations over the surface of Lake Lanao. The measurements are assumed to have been taken at a single instant in time on a day for which biomass and production were near average, and to be free of measurement error. The list of stations from which random selections were made is assumed to consist of all possible stations situated with respect to a single arbitrary reference point such that no station is closer than 2.5 km to any other station. The graph thus indicates heterogeneity on a distance scale of about 12 km, as the mean distance between randomly-paired stations from a complete list of possible stations meeting the minimum distance criterion is about 12 km.

The curve in Fig. 6 is subject to the following limitations. (1) The variance of productivity between stations changes some with the level of productivity (LEWIS 1974). Coefficients of variation between stations are highest at the highest levels of productivity. The same may be true of biomass, although this has not yet been proved. The curves of Fig. 6 represent the expected distributions under conditions of average biomass and production. The shapes of the curves would change some with time since the variances and means are correlated to some degree, and the curves would of course shift seasonally back and forth along the abscissa. (2) The ANOVAs for productivities were done on the basis of production per unit volume at the depth of maximum fixation (P_{\max}). In Fig. 5 the productivity is expressed as fixation per unit area, which is derived from the known relationship between P_{\max} and production per unit area (LEWIS 1974). Some additional variance is introduced along with this transformation. (3) For both biomass and productivity the original data were taken along a transect, and not at randomly-selected points. It is assumed that random selection would yield results close to those obtained by transect. (4) Areas of the lake closer than 1 km to shore are excluded from consideration.

The biomass of individual species can be treated as total biomass has been treated above. This demonstrates whether certain taxa are more or less heterogeneous in horizontal distribution than others.

At the time of the intensive heterogeneity study, the most abundant species in the lake was *Nitzschia bacata*, which contributed 44.0% of the total biomass. *N. bacata* was followed by *Melosira granulata* (15.3%), *Oocystis submarina* (6.6%), *Coelastrum cambricum* (6.4%), *Dictyosphaerium pulchellum* (4.9%), *Aphanothece nidulans* (4.1%), and about 40 other species of lesser importance. Statistical analysis was limited to those species for which the average number of recorded counting units was 5 or more per replicate sample. Attention is thus focused on 27 species. Included in this group are 6 bluegreens, 2 diatoms, 2 cryptomonads, 1 chrysophyte, 1 euglenophyte, and 15 greens (Table 1). The 27 species account for 98.2% of the total autotroph biomass.

The outcome of the statistical analysis on individual species is summarized in Table 2, which gives mean values for the 27 species. As with the analysis of total biomass, the first step was a test of homogeneity of variances between stations. Of the 27 species, only one, *Chroococcus minutus*, produced a chi-square value significant at the 5% level as a result of BARTLETT's test. This one significant value is borderline and is of no real interest, as 27 separate tests are expected to produce one incidence of type 1 error when all variances are homogenous. Individual phytoplankton populations are as variable at one station as at another, as is total biomass.

The ANOVA on individual species using stations as treatments produced F values ranging from 0.07 to 33.2 (Fig. 7). Of the 27 values, 11 are not significant at $\alpha = 0.05$. There is no obvious breakdown of F values along taxonomic lines. Although the two species with highest values are both bluegreens (*Lyngbya limnetica* and *Dactylococcopsis*

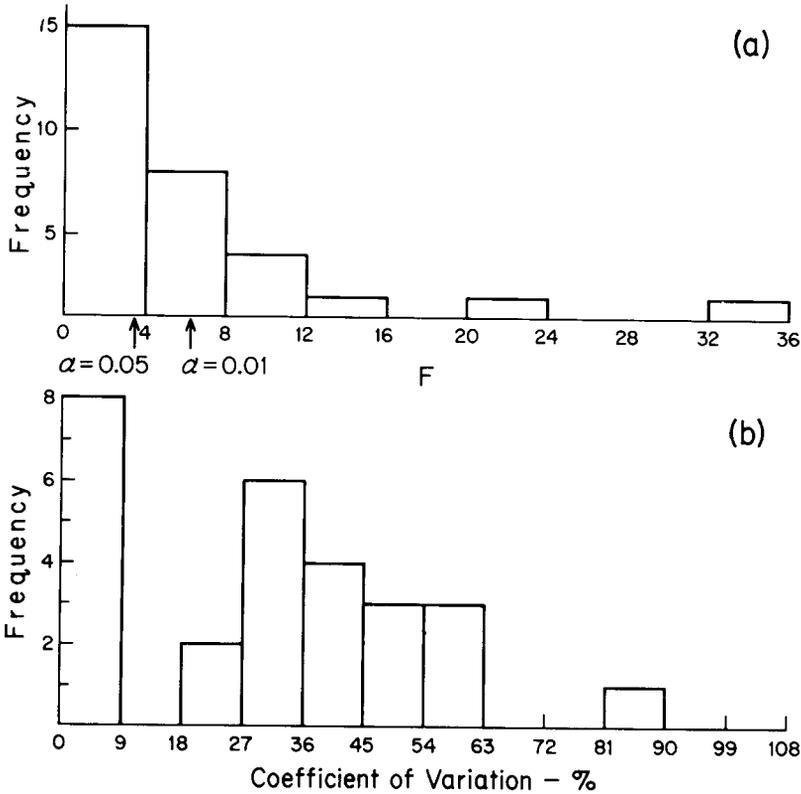


Fig. 7. Frequency distributions of statistics resulting from an analysis of variance for the biomass of 27 different phytoplankton species. (a). F values for a test of the hypothesis that biomass is homogeneous between stations ($d.f.=7, 8$). (b). Coefficients of variation of biomass between stations (error variance removed).

fascicularis), other bluegreens produced very low values of F . The average F value is in fact very close to the F value for total phytoplankton biomass (Table 2). Biomass of individual species, like total autotroph biomass, was heterogeneous to an extent just sufficient to allow statistical differences to appear in a routine ANOVA.

The relative variability between stations appears in Fig. 7b in terms of the coefficients of variation for the 27 species. Variability between replicates ($\sigma_0^2 + \sigma_1^2$) has been removed from the data in Fig. 7b, hence the figure gives an estimate of variability due to station effects only (CV_2). Variability between replicates, which is not shown in Fig. 7, is higher for individual species than for total biomass (Table 2). This is explained by the lower counting effort that is represented in estimates of the abundance of individual species than of total biomass. The values of CV_2 for the 27 species are distributed bimodally (Fig. 7). As with the F values, however, no obvious taxonomic breakdown is visible within the distribution.

The data of Fig. 7 permit statistical comparisons to be made between the patchiness of a species, as indicated by CV_2 , and other species traits. Five such comparisons were made.

(1) Patchiness *vs* size. The CV_2 and mean size of the plankton unit were compared by SPEARMAN rank correlation after log transformation of both variables. The correlation was significant ($r_s = -0.34$, $p = 0.04$).

(2) Patchiness *vs* abundance. The mean biomass abundance of each of the 27 species was computed for all transect stations. Rank correlation between biomass abundance and CV_2 proved non-significant ($r_s = -0.20$, $p = 0.15$). A similar result occurred when abundance was computed as numbers of plankton units ($r_s = 0.01$).

(3) Patchiness *vs* S/V ratio. The ratios of surface to volume for average plankton units of each species were computed from composite geometric figures (LEWIS 1976). There was no significant rank correlation between these ratios and CV_2 ($r_s = 0.20$, $p = 0.16$).

(4) Patchiness *vs* morphotype. The 27 species represent 5 different morphotypes: (1) flagellates, (2) unicells, (3) filaments, (4) colonies, (5) coenobia. Aggregations of cells were classified as colonial if the number of cells varied greatly (*Dictyosphaerium*) and as coenobial if the number was essentially constant (*Scenedesmus*). A KRUSKAL-WALLIS test (SOKAL and ROHLF 1969) was used to determine whether the morphotypes differed in average degree of patchiness. No significant differences were detected ($p \gg 0.05$).

(5) Patchiness *vs* taxon. Patchiness of bluegreens, greens, and diatoms proved to be the same in a KRUSKAL-WALLIS test comparing CV_2 in these major taxa ($p \gg 0.05$).

There have been no intensive efforts to find relationships between species properties such as size or S/V ratio and degree of patchiness. It is therefore difficult to put the results of the Lanao study into perspective.

Whereas a number of relationships might seem theoretically reasonable, the only significant relationship in the Lanao data is between size and patchiness. Smaller organisms are more patchily distributed than larger ones. This finding is compatible with some of MARGALEF's (1958, 1967) generalizations concerning phytoplankton heterogeneity and succession. Small species presumably produce more patchiness because they have less ecological inertia due to high biomass turnover. The trend is quantitatively rather weak, however, and does not apply to S/V ratio but only to size itself. Clearly most of the variation in patchiness remains to be explained by other factors. Factor interactions may be more important than single factors in determining patchiness, or the historical dimension of the patch phenomenon may not be adequately probed by the intensive heterogeneity study. Ideally, intensive studies should be repeated many times, but this will require very large amounts of manpower because of the large number of species.

The spatial variability for individual species averages almost exactly the same as for total autotroph biomass or productivity (Table 2). This implies little or no interdependence in the patchiness of individual species. This is contrary to the prediction of any straightforward application of competition theory to the plankton assemblage, and suggests that the relevance of patchiness to competition in the phytoplankton may be less than is often supposed.

b. Extensive Heterogeneity Study

The extensive study differs in two respects from the intensive study: (1) the data span the entire study period, and (2) the stations span a distance that is an order of magnitude less than those of the intensive study.

For total autotroph biomass, the mean coefficient of variation between stations is 10% (52 separate dates). This includes all three components of variance ($\sigma_0^2 + \sigma_1^2 + n\sigma_2^2$). The error component (σ_0^2) is minimal because of the high counting effort represented by the total biomass estimates. The true station component (σ_2^2) is not separable in this case but is obviously represented by a coefficient of variation less than 10%. This is considerably less than the between-station component on the longer distance scale of the heterogeneity study (24%, Table 2).

For individual species, the extensive study yielded an average coefficient of variation of 35% ($\sigma_0^2 + \sigma_1^2 + n\sigma_2^2$). The variability between replicates for this same group was 24% ($\sigma_0^2 + \sigma_1^2$). The segregated station effect yields a coefficient of variation of 18% (CV_2). This is considerably lower than the value for the longer distance scale of the intensive study (30%, Table 2).

The data of the extensive heterogeneity study generally support the conclusion of the intensive study that horizontal heterogeneity is not very great even though it is detectable statistically. The studies further suggest that really significant heterogeneity occurs only on a scale considerably greater than 1 km.

6. Discussion

The vertical distribution studies suggest that the placement of species in the water column can be understood and predicted according to rather simple rules based on turbulence in the water column and morphology or motility of the organisms. While it is well known that morphology or motility can affect vertical distributions of individual species, comprehensive studies of entire communities have not been undertaken to provide generalized community-level rules for the arrangement of species in the water column. The Lanao studies indicate that further inquiry along these lines might produce some powerful generalizations about vertical distributions.

Horizontal distributional studies of phytoplankton are not yet standardized, hence it is difficult to compare the Lanao findings with what is known from other water bodies. One of the best and most easily comparable studies of a non-oceanic waterbody is that of PLATT and FILION (1973) on Bedford Basin, Nova Scotia. Although Bedford Basin is a marine habitat and is subject to tidal influence, the methods of study were similar to those used on Lanao.

PLATT and FILION found that variance of autotroph abundance between stations, measured as chlorophyll, was about 12 times the within-station variance. For Lake Lanao, the comparable ratio is about 5 for autotroph biomass. The values for the two waterbodies are not greatly different although it does appear that Lake Lanao is less patchy. This is not surprising considering the greater probability of physico-chemical heterogeneity in Bedford Basin. A related study by PLATT *et al.* (1970) on a nearshore marine environment also demonstrated a degree of patchiness in chlorophyll that is similar to the patchiness of biomass in Lanao.

Methods are especially important in the study of heterogeneity. For example, PLATT and FILION took biomass samples at a single depth, whereas the Lake Lanao samples were integrated over the depth of the euphotic zone. Samples from one depth yield estimates of horizontal biomass heterogeneity that may be affected by vertical biomass distribution, whereas the integrated samples of the Lanao study are not influenced by vertical distribution. Also the heterogeneity of autotroph biomass and chlorophyll are not strictly comparable, as the ratio of chlorophyll to biomass may be heterogeneous just as is biomass itself.

The importance of analytical error is magnified if the ratio of within- and between-station variances is used as an index of heterogeneity as it is in the Bedford Basin study. Segregation of a true station effect as the basis for evaluation of patchiness seems to be a better approach, particularly if comparisons between different kinds of measurements are desirable.

RICHERSON *et al.* (1970) provide perhaps the only existing comparison of patchiness between individual phytoplankton species in lakes. They found statistically significant horizontal heterogeneity in about half of the species of Castle Lake, California. They proposed on this basis a concept of contemporaneous disequilibrium, which was

probably adumbrated previously by MARGALEF (1958, 1967). About half of the species cited by RICHEYSON *et al.* are not heterogeneously distributed, however, and this half includes 4 of the 5 most abundant species. The species list includes a number of taxa that are almost certainly not euplanktic. This is not surprising in view of the very small size of the basin (0.2 km²), which probably leads to mixing of littoral and limnetic floras, but is undesirable for validation of an hypothesis dealing specifically with the plankton. While this study is important as a prototype for heterogeneity studies of individual species, it does not seem to support a theory based on marked patchiness of individual species. The impression given by the Castle Lake data is in fact similar to that cited above for the Lake Lanao data. The phytoplankton at any moment contains a few species of clearly heterogeneous distribution, others of clearly homogeneous distribution, and a large number of borderline cases. In the Lake Lanao data at least, these categories are not easily separable on the basis of demographic or morphological statistics.

MARGALEF (1958) has made a convincing case for asynchrony of succession in the Ria of Vigo, a nearshore marine environment. Asynchronous succession clearly results in patches that differ both qualitatively and quantitatively in biota. The Ria of Vigo, however, is likely to be on the upper end of a heterogeneity spectrum due to its physical characteristics. In a plankton environment such as Lake Lanao, enclosure of the water mass and the absence of point sources of nutrients reduce the possible range of heterogeneity.

There has been an increasing tendency since the publication of HUTCHINSON'S (1961) "plankton paradox" paper to credit phytoplankton patchiness in lakes with considerable significance in explaining the community organization of phytoplankton. On the very large distance scales of marine environments, patchiness is of unquestionable importance (RILEY 1976). On the smaller distance scales of lakes, however, where internal mixing is promoted by physical boundaries to water movement, the significance of horizontal spatial heterogeneity is still far from clear. Statistical documentation of heterogeneity does not demonstrate or indicate any overall significance to community organization. In fact statistically detectable patchiness is almost a certainty given a strong data set, and the pressing biological questions revolve around the magnitude of this patchiness rather than its mere existence. Magnitude of phytoplankton patchiness in Lake Lanao is sufficiently small to burden severely any significant theoretical framework based upon it. While one cannot conclude that patchiness is trivial to community organization, considerably greater depth of analysis than is now available will be required to establish the connection with certainty.

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8. Summary

The vertical and horizontal distribution of phytoplankton was studied in Lake Lanao, Philippines, over a 16-month period. The distribution of total autotroph biomass and distribution of individual species are both considered in the analysis.

Vertical distribution of total phytoplankton biomass during calm weather closely reflects the vertical distribution of net primary production, with a maximum in the

upper euphotic zone. In windy weather phytoplankton biomass is entirely uniform over the mixed layer, even if the layer is very thick (45 m). In calm weather, motile species (phytoflagellates) and species with buoyancy control (Nostocaceae, *Lyngbya*, *Aphanothece*) uniformly overlie the other species, but only by a few meters. In windy weather no species shows good evidence of nonuniform distribution except *Melosira*, which apparently sinks with significant speed even in a turbulent water column.

Horizontal distribution was studied in a combination of intensive and extensive studies. On a distance scale of 12.5 km (mean distance between randomly-paired stations), the coefficient of variation for total phytoplankton biomass is 23.6% after removal of error variance. The comparable figure for primary production is 30.2%, and for 27 species studied individually the figure is 30.3%. On a distance scale of 1 km, the relative variabilities are about half as great.

The patchiness of individual species was statistically compared to their size, mean abundance, surface to volume ratio, morphotype, and taxon. The only significant relation is between size and patchiness, which are negatively related.

The small degree of horizontal heterogeneity in the phytoplankton, although statistically detectable, is interpreted as cause for skepticism regarding major relationships between patchiness and community organization.

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