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COMPARISON OF TEMPORAL AND SPATIAL VARIATION IN THE ZOOPLANKTON OF A LAKE BY MEANS OF VARIANCE COMPONENTS^{1, 2}

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Abstract. A standard 2-way analysis of variance is used to separate components of variance in zooplankton abundance data (individuals per unit area). The sampling design and interpretation, which are applied to Lake Lanao, Philippines, require that samples be (1) widely distributed over the limnetic zone, (2) representative of the full range of temporal variation, and (3) free of significant autocorrelation. Under these conditions the relative importance of spatial and temporal variation can be quantitatively compared for individual zooplankton species and developmental stages. The analysis yields variance components associated with (1) stations, (2) dates, (3) station-date interaction, and (4) error. The station component is interpreted as a quantitative measure of "fixed" spatial patchiness, which is caused by temporally stable differences between stations. The dates component is a quantitative measure of the variation in abundance through time, and the interaction component is a quantitative measure of "ephemeral" spatial patchiness. Ratios between these variance components provide a measure of their relative importance. The analysis shows that, among 16 zooplankton species and developmental stages, (1) there are radical differences between species in the relative importance of spatial and temporal variation, (2) the 2 spatial components of variance (fixed plus ephemeral) exceed the temporal component of variance for about half the species, (3) the ephemeral component of spatial variance is typically much greater than the fixed component of spatial variance, and (4) the spatial component of variance has a much greater relative importance in the large cladoceran species than in other zooplankton species. Interspecific differences in the relative importance of spatial and temporal patchiness may be related to differences between species in adaptive strategies for survival in the limnetic zone.

Key words: *Philippines, plankton community structure, spatial variation, temporal variation, tropical lakes, zooplankton.*

INTRODUCTION

Plankton biology is devoted in large part to the study of spatial and temporal variation of plankton populations. Field studies most often emphasize one or the other of these types of variation. There are some exceptions to this, including the work by Margalef (1958, 1967), attempting to integrate temporal and spatial variation within a successional framework. In general, however, the combined study of spatial and temporal variation often remains out of reach despite increased sophistication in sampling and analysis. For example, application of spectral analysis techniques to the study of spatial variation (Platt et al. 1970, Platt and Denman 1975, Powell et al. 1975) virtually precludes any simultaneous study of temporal variation except in variables subject to automated *in vivo* measurement (e.g., chlorophyll). For zooplankton, increasingly sophisticated information is available on patch structure at an instant in time (e.g., Wiebe 1970), but typically the temporal dimension is not fully treated because the data requirements for detailed description of patch structure are very great. Partly as a result of these practical difficulties, it is possible to read the entire literature on spatial and temporal variation in plankton without obtaining any firm intuitive grasp of the relation be-

tween the two, particularly of their relative magnitudes in plankton environments generally. The purpose of this paper is to compare spatial and temporal variation in a lacustrine plankton community by a method which could be routinely used in a wide variety of lakes. The method applies specifically to lakes because of their definite boundaries, but might also be adapted to marine plankton environments.

METHODS

A standard 2-way analysis of variance can be used to separate spatial and temporal variation and their interaction in zooplankton abundance data which span both time and space. Variance components resulting from this separation can then be compared to indicate the relative magnitudes of spatial and temporal variation. The method is applied here to zooplankton populations of Lake Lanao, Philippines.

Lanao is a large natural lake located on the island of Mindanao. Summary statistics, as given by Frey (1969), are: maximum depth, 112 m; mean depth, 60.3 m; area, 357 km²; replacement time, 6.5 yr. The lake mixes between January and February and is stratified the rest of the year, typically with a very thick epilimnion (Lewis 1973). Lanao is highly productive 620 g C·m⁻²·yr⁻¹ net, Lewis 1974) but concentrations of inorganic nutrients, especially nitrogen, are typically very low in the upper water column.

The Lake Lanao zooplankton is composed of 1 calanoid copepod species, 1 cyclopoid species, 3 clado-

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ceran species, 7 rotifer species, and 1 *Chaoborus* species (Lewis 1977). The present analysis is limited to the 2 copepod species and their developmental stages plus the 3 cladocerans and the single most common rotifer species. Other rotifers were too rare to warrant analysis. The mean abundance of zooplankton at the main sampling station (Station 1, Fig. 1) over an 18-mo study period was 175 individuals/litre, or 7.82×10^6 individuals/m². The species included in the analysis here accounted for >90% of zooplankton individuals present in the lake over the 18-mo study period.

The zooplankton samples were taken with a Clarke-Bumpus sampler (64 μ m mesh net) towed vertically from a point 0.5 m over the bottom to the surface. For each tow the flowmeter readings were recorded so that the amount of water filtered could be computed. The meter was calibrated separately for each set of replicate tows by raising the sampler through the water column without the net attached. Filtration efficiencies averaged $\approx 50\%$ and varied little between stations and dates. Capture efficiency of the Clarke-Bumpus after correction for filtration efficiency did not differ significantly from that of a Schindler-Patalas trap equipped with a 28 μ m mesh net.

The present analysis is based on duplicate samples taken at each of 9 stations on 5 different dates (Fig. 1). Organisms in each tow sample were tabulated according to species and developmental stage. Since the sample was integrated over the water column, variations in vertical spatial distribution are not considered. Use of the term "spatial variation" thus should be interpreted to mean "spatial variation in abundance beneath a unit of lake surface." Spatial variation in abundance beneath a unit of lake surface can be expressed on an area basis (divide numbers by area of net mouth) or volume basis (divide numbers by volume of water beneath area of net mouth) after correction for filtration efficiency. Implications of these 2 modes of data expression are discussed with the results.

RATIONALE FOR COMPARISONS

From the abundance matrix spanning time and space for a given species or developmental stage, it is possible to partition the sum of squares as follows:

Total SS = Stations SS + Dates SS + Interaction SS + Error SS. The components of the total sum of squares are then converted to mean squares as in an ordinary 2-way analysis of variance with random effects (e.g., Sokal and Rohlf 1969, p. 317). From the mean squares, the components of variance are computed as follows:

$$\begin{aligned}
 S_e^2 &= MS_e \\
 S_s^2 &= (MS_s - MS_i)/(N_d \cdot N_r) \\
 S_d^2 &= (MS_d - MS_i)/(N_s \cdot N_r) \\
 S_i^2 &= (MS_i - MS_e)/N_r
 \end{aligned}$$

where S^2 = variance, MS = mean square, N = num-

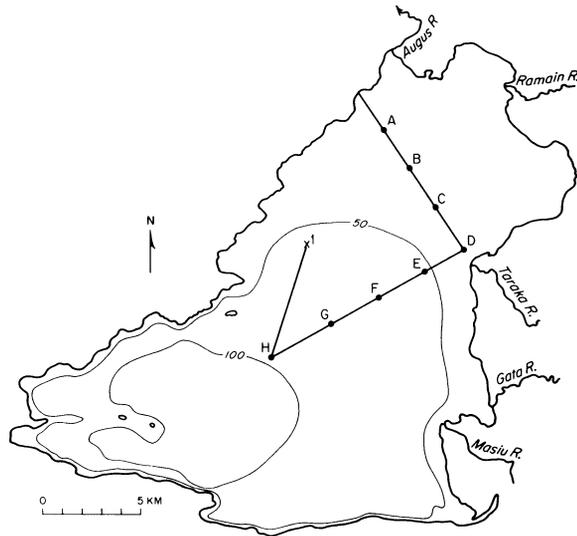


FIG. 1. Map of Lake Lanao showing the sampling stations and the 50- and 100-m contours.

ber of samples, e = error, s = stations, d = dates, i = interaction, and r = replicates. Each of the 4 components is then most conveniently expressed as a percentage of the total variance.

The component S_s^2 is associated with predictable unevenness between stations independent of date, and will be large whenever morphometric or hydrologic factors are responsible for persistent average differences in the capacity of different stations to produce or support plankton. The S_i^2 component is associated with patchiness which changes character from one date to the next and is thus ephemeral (the term "ephemeral" appears to have been first used in this context by Platt and Filion [1973]). Ephemeral spatial patchiness, which changes character through time, is most likely to be associated with turbulence and water movements of an unpredictable nature.

The ratios $S_s^2:S_d^2$ and $S_i^2:S_d^2$ can be computed from the list of variance components to provide measures of the relative importance of the 2 kinds of horizontal spatial variation as compared with temporal variation in the same habitat. The ratio $S_s^2:S_d^2$ weighs "fixed" spatial patchiness against temporal variation, and the ratio $S_i^2:S_d^2$ weighs "ephemeral" spatial patchiness against temporal variation. A composite ratio, $(S_s^2 + S_i^2):S_d^2$, compares the sum of both types of horizontal spatial variation with temporal variation.

The exact biological interpretation of the variance ratios depends greatly on the sampling design. The purpose here is to compare temporal variation over a full annual cycle with spatial variation over the entire limnetic habitat. In this respect the method is most easily applied to lakes, where the size of the habitat is limited. In oceans or very large lakes, it would be

TABLE 1. Conditions in Lake Lanao on the 5 sampling dates (data for Station 1, Fig. 1) during 1971

Date	Code	Net production (g C · m ⁻² · day ⁻¹)	Mixed layer (m)	O ₂ at 35 m (mg/l)	Zooplankton (individuals/litre)
25 Feb	1	1190	60	4.18	130
15 Apr	2	1440	25	5.08	280
13 May	3	770	15	4.15	190
10 Jun	4	1940	15	2.50	150
8 Jul	5	2530	30	3.00	310

necessary to circumscribe an area for study arbitrarily, although this seems quite reasonable.

Even with these sampling restrictions, the results may still depend on the distribution of samples through time. Additional requirements are thus helpful in maximizing the effectiveness of the analysis. One obvious possibility is to require completely random sampling, but this results in inefficiency in meeting the restriction that the full range of conditions be represented. Furthermore, sampling schemes are typically scheduled on a nonrandom basis for practical reasons. Instead, it suffices to require that the samples be far enough apart in time that they are not autocorrelated. Thus, the sample on date 1 gives no more statistical information about the sample on date 2 than about the sample on date 5. For Lanao zooplankton, 4 wk is a sufficiently long interval to prevent autocorrelation.

An analogous requirement for spatial variation is that the samples for a given date be located such that the distance between stations is not strongly correlated with their biological similarity. Given that zooplankton patches vary in size and are irregularly arranged (Cassie 1963, Hutchinson 1967), this condition is not very restrictive.

If the above conditions can be met, then it is possible to compute characteristic variance ratios as described above for individual habitats and compare them with ratios for other habitats. If the samples are too close together in space or time, however, the variances will be artificially reduced and the ratios will consequently have less comparative value.

Confidence limits for the components of variance were calculated according to the procedures outlined by Hicks (1964, p. 153) and Snedecor and Cochran (1967, p. 285). The limits on each value need not be reported here, as confidence limits for typical components are quite representative. The station component (S_s^2) averages $\approx 10\%$ of total variance, and the 95% confidence limits for a single estimate of 10% would be 3.5–36%. The dates component (S_d^2) averages $\approx 40\%$, for which 95% confidence limits would be 13–100% on a single estimate. The interaction component (S_i^2) averages $\approx 40\%$, for which 95% limits would be 21–77% on a single estimate.

RESULTS

Table 1 summarizes the conditions in Lake Lanao on the 5 sampling dates. The first date coincides with the last part of the circulation period and the other dates fall within the stratification period. Variations in O₂ and primary production are attributable to periodic deep mixing which irregularly stimulates the phytoplankton in the upper water column during the stratification season (Lewis 1974).

Table 2 shows the components of variance and the variance ratios for both volume-based and area-based abundances of zooplankton. For all species and stages the station and date factors and their interaction are statistically significant ($p \ll .01$) even though the components of variance attributable to these 3 sources may be very unequal. The error component of variance is generally quite small. The data in Table 2 can be summarized as follows.

1) The station component of variance, which represents fixed horizontal spatial variation, differs greatly according to whether abundance is measured on an area or a volume basis. When abundance is expressed on an area basis, the station component of variance never exceeds 10% of the total variance except for *Tropodiptomus* adult females, whose station component is only 15% of the total. When abundance is expressed on a volume basis, however, the proportion of the total variance accounted for by stations increases drastically for all species except the copepod *Thermocyclops*. All stages of *Thermocyclops* show uniformly low percentages of variance attributable to fixed spatial patchiness whether the abundance is expressed on an area or a volume basis.

The ratio $S_s^2:S_d^2$ shows that fixed spatial variation approaches or exceeds the magnitude of temporal variation only for volume-based *Tropodiptomus* adults and eggs, *Diaphanosoma*, and *Moina*.

2) The interaction component is in most cases considerably larger than the component of variance associated with stations. This indicates that ephemeral spatial variation is typically larger than fixed spatial variation. Advanced stages of *Tropodiptomus* are exceptional in this respect. The relative importance of ephemeral spatial variation is not greatly affected when abundance is expressed on a volume rather than an area basis.

The ratio $S_i^2:S_d^2$ shows that the ephemeral spatial variance component exceeds the size of the temporal variance component for $\approx 1/2$ of the species and developmental stages. The ratio also shows that the comparative importance of ephemeral spatial variation and temporal variation varies enormously between species. The ephemeral spatial component has greatest relative importance in the 2 large cladocerans (*Diaphanosoma*, *Moina*), whose adults and eggs generate ratios of $S_i^2:S_d^2$ in excess of 2 whether abundance is measured on an area or a volume basis.

TABLE 2. Mean abundances for zooplankton species and stages over the 5 dates and 9 stations of the study, plus the components of variance and component ratios discussed in the text

Species/stage	Abundance measure (V = vol basis A = area basis)	Code	Mean (V = individuals/litre A = thousands/m ²)	Percent of variance accounted for				Ratios		
				Stations	Dates	Inter-action	Error	$S_s^2:S_d^2$	$S_i^2:S_d^2$	$(S_s^2 + S_i^2):S_d^2$
<i>Thermocyclops hyalinus</i>										
Nauplii	V	1	108.9	5	76	13	6	.07	.17	.23
	A		4713	7	75	14	5	.09	.18	.27
Copepodids	V	2	33.1	3	45	41	11	.06	.91	.97
	A		1497	9	41	42	7	.22	1.02	1.25
♀ ♀	V	3	4.9	1	49	41	10	.02	.84	.85
	A		237	7	37	50	5	.20	1.33	1.53
Eggs	V	4	13.3	3	36	47	14	.08	1.28	1.37
	A		628	4	32	58	6	.14	1.81	1.95
<i>Tropodiatomus gigantoviger</i>										
Nauplii	V	5	7.5	14	37	45	5	.37	1.22	1.59
	A		282	0	54	40	5	.00	.74	.74
Copepodids	V	6	6.6	16	51	26	7	.30	.51	.82
	A		276	1	59	33	7	.02	.56	.57
♀ ♀	V	7	1.9	34	27	17	21	1.23	.64	1.87
	A		72	15	33	22	31	.44	.67	1.11
Eggs	V	8	3.1	28	34	23	15	.83	.68	1.51
	A		121	10	55	18	17	.18	.33	.52
<i>Conochiloides dossuarius</i>										
Adults	V	9	23.1	12	49	32	8	.25	.65	.90
	A		929	4	59	28	8	.07	.48	.55
Eggs	V	10	5.8	10	42	36	12	.23	.87	1.10
	A		230	2	52	33	12	.05	.64	.69
<i>Diaphanosoma modigliani*</i>										
Adults	V	11	7.3	25	17	55	4	1.49	3.31	4.81
	A		275	0	27	70	4	.00	2.43	2.32
Eggs	V	12	2.3	28	13	37	23	2.20	2.90	5.11
	A		83	4	22	48	26	.19	2.22	2.41
<i>Moina micrura</i>										
Adults	V	13	0.7	17	14	58	11	1.21	4.27	5.49
	A		25	0	17	69	13	.00	3.77	3.73
Eggs	V	14	0.3	0	10	72	18	0.00	5.92	5.80
	A		11	0	6	71	24	0.00	5.55	5.00
<i>Bosmina fatalis</i>										
Adults	V	15	2.2	8	58	30	4	.13	.53	.66
	A		81	2	75	19	4	.03	.25	.28
Eggs	V	16	0.7	19	54	19	7	.34	.36	.70
	A		24	5	77	9	10	.06	.11	.18

* Also includes some *D. sarsi*.

3) The composite ratio $(S_s^2 + S_i^2):S_d^2$, which indicates the relative importance of total spatial and total temporal variation, is very high for the 2 large cladocerans (*Diaphanosoma* and *Moina*) and very low for the small cladoceran (*Bosmina*) and the naupliar stages of the copepod *Thermocyclops*. For other species and developmental stages, temporal variation and total horizontal spatial variation are more nearly of equal importance.

DISCUSSION

The dependence of the fixed spatial (station) component of variance on the method of abundance expression is biologically revealing. The lake is suffi-

ciently deep that all stations have a complete euphotic zone (9–18 m based on 1% light), so the only difference between stations with regard to structure of the water column is in the thickness of the nonproducing zone. This would obviously vary from one station to another according to depth (Fig. 1). All of the zooplankton in Lanao migrate, and all except the rotifers migrate considerable distances (Lewis 1977). The zooplankton thus do have some direct biological dependence on the nonproducing layer. The data suggest that for any water column inside the 25-m isobath, the number of organisms that can be supported is much more dependent on surface area than depth. Thus, when abundance is expressed on a volume basis, the station vari-

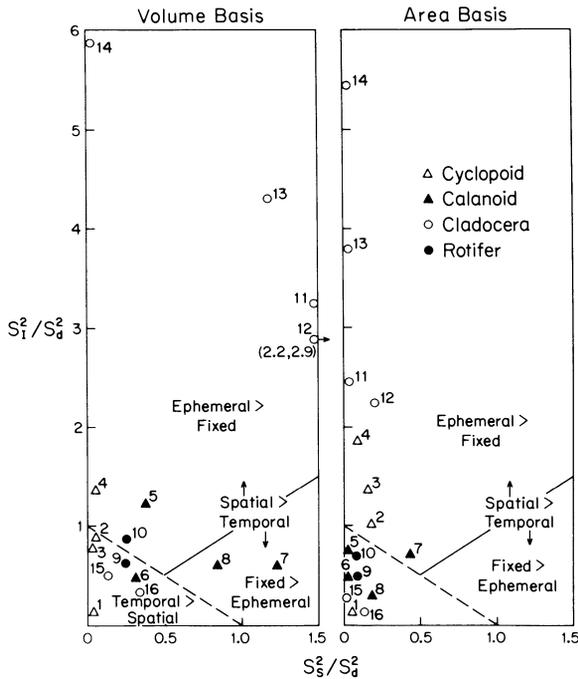


FIG. 2. Ratios of variance components mapped against each other to show relative importance of spatial variation (fixed or ephemeral) and temporal variation in zooplankton. Codes are from Table 2.

ance is exaggerated because the plankton are, in effect, forcibly distributed over the whole water column, while the top 25 m is far more important than deeper water in maintaining the population.

Thermocyclops at all developmental stages is an exception to these generalizations. Additional volume below a unit surface appears to contribute proportionally to the maintenance of the population, and this brings into balance the fixed spatial variance components associated with volume and area expression of abundance. The study of abundance gradients has, in fact, shown that *Thermocyclops* is the only species whose abundance per unit area increases toward deeper water (Lewis 1978). Factors which explain the value of additional water volume below a unit surface to *Thermocyclops* are not clear, but may be related either to predation or to resource supply.

Figure 2 illustrates the low relative magnitude of fixed spatial variance, especially when abundance is expressed on an area basis. If samples were allowed to span both the littoral and limnetic habitats, the points would presumably fall more to the right of Fig. 2, especially in a small lake with a high percentage of littoral habitat. Lakes with point sources of heterogeneity such as effluents or tidal input would also be likely to show greater fixed spatial variation, as would very large lakes where permanent physico-chemical gradients are more easily maintained. An extensive comparison of lakes by the method of variance com-

ponents would establish the general importance of fixed spatial gradients in plankton communities.

Figure 2 also illustrates the great difference between species with respect to relative importance of temporal and spatial variation. The especially high ephemeral patchiness of the 2 large cladocerans (*Diaphanosoma* and *Moina*) suggests that ephemeral patchiness may be extremely important to the survival of these species in the limnetic habitat. It will be especially critical to determine whether extreme ephemeral patchiness of this type is based mainly on differential reproduction, differential mortality, or behavior, and whether it is characteristic of certain taxa.

Predation is recognized as a major factor influencing the composition and structure of zooplankton communities (Hrbacek et al. 1961, Brooks 1968, Zaret 1975, Hall et al. 1976), and is likely to influence the distribution of herbivores in particular. Vertical distribution of species is probably related strongly to predation (Zaret and Suffern 1976), and some fixed horizontal spatial patterns in distribution of cladocerans are known to be maintained by predation (Zaret 1969, Kerfoot 1975). In addition, Lewis (1978) has demonstrated stable horizontal community structure gradients maintained by predation in the pelagic zone of a large lake. All of these observations suggest that the great differences in ephemeral patchiness between species shown in Fig. 2 might reflect the interplay between differential predation and prey adaptation in the zooplankton.

The copepod *Thermocyclops* shows an interesting trend toward increasing relative importance of ephemeral patchiness at progressive stages in the life history (Fig. 2), but no similar trend appears for the copepod *Tropodiptomus*. Such differences may well signify major differences in adaptive strategy between species.

Zooplankton adaptations associated with temporal variation in the limnetic environment have been much more extensively studied than adaptations associated with spatial variation. The comparison of horizontal spatial variation and temporal variation in Lake Lanao zooplankton suggests that adaptation specifically associated with horizontal spatial variation may be a major feature in some species but not in others. Further studies of this type may thus provide insight into the community structure of lake zooplankton. The separation of variance components provides a tool for comparing lakes and for comparing species within and between lakes.

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