55. Evidence for Stable Zooplankton Community Structure Gradients Maintained by Predation

William M. Lewis, Jr.

Abstract

Zooplankton were sampled on transects across Lake Lanao, a large tropical lake, on five different dates representing the full range of annual conditions. The sampling stations ranged in depth between 25 and 80 m. Regression analysis showed that abundance is linearly related to depth for almost all species and developmental stages and that the relation is quite stable through time. Herbivorous cyclopoid nauplii, copepodids, and adults showed a strong positive relation between abundance per unit area and depth, as did carnivorous *Chaoborus* larvae of all instars. All other herbivores, including calanoids, cladocerans, and a rotifer species, showed negative depth-abundance relationships, and thus decreased in areal abundance toward midlake. The gradients ranged in intensity but were especially strong for cladocerans. The hypothesis is formulated that herbivore abundance gradients are created and maintained by predation through *Chaoborus*, the dominant primary carnivore. The feeding rates, abundance-depth relation, and feeding selectivity of all four *Chaoborus* instars were used to calculate potential predation losses as a percentage of the stock of each prey type, assuming an average community structure. These losses were then regressed against depth and proved to have significant slope, thus yielding predation gradients for individual prey species. The predation gradients were compared to abundance gradients and showed a significant negative relationship. The evidence for maintenance of abundance gradients by predation is thus very strong. This mechanism is apparently responsible for maintenance of an unexpected amount of pattern in the zooplankton community structure of the limnetic zone, and for spatial diversification of the zooplankton.

It is now well established that competing species partition environmental resources, and that this partitioning is accomplished in large part by dietary, spatial, or temporal segregation (e.g. MacArthur 1958; Schoener 1974, 1975; Cody 1974; Roughgarden 1974). Mechanisms and strategic bases for separation of many kinds of organisms remain to be worked out, however. The major focus thus far has been on vertebrates and higher plants (Whittaker 1967), although a few comprehensive studies of invertebrate groups are also available (e.g. Green 1971; Lane 1975).

Mechanisms for partitioning of resources among plankton species have been of special interest since Hutchinson (1961) first pointed out the heuristic value of analyzing resource partitioning in a community which occupies an unstructured habitat. For phytoplankton, the mechanisms most likely to facilitate resource partitioning include temporal separa-

tions based on varying optima and tolerances for resource supply and attrition factors (e.g. Hutchinson 1967; Allen and Koonce 1973; Grenny et al. 1973; Titman 1976; Lewis 1977a), and spatial separation based on ephemeral horizontal spatial patchiness and possible vertical spatial variation as well (Margalef 1958; Richerson et al. 1970; Sandusky and Horne 1978). The relative importance of these mechanisms and their interaction have not yet been well established. For the zooplankton, which are capable of extensive vertical movement, there is evidence that vertical spatial separations interacting with temporal separations facilitate resource partitioning (Sandercock 1967; Miracle 1974; Lane 1975; Makarewicz and Likens 1975). Horizontal spatial patchiness has also been documented (e.g. Hutchinson 1967; Wiebe 1970; Mullin and Brooks 1976; Lewis 1978a), but its relative importance in separation of zooplankton species is not obvious at present.

The present study gives evidence for stable horizontal spatial gradients in the relative abundances of euplanktonic zooplankton species in a large lake. Horizontal spatial variation can be subdivided into a fixed component and an ephemeral component. In terms of an analysis of variance model, the fixed component is a main effect caused by differing average conditions between stations, whereas the ephemeral component is a space-time interaction resulting from patchiness of changing character caused by moving water masses. The separation of these components in Lake Lanao has been discussed elsewhere (Lewis 1978a). The separation technique showed that in Lake Lanao ephemeral horizontal spatial variation generally exceeds horizontal spatial variation in magnitude. Fixed horizontal variation will be the focus of the present discussion, however, because fixed variation proves to be of special interest in connection with zooplankton community structure in Lake Lanao. The relation of the fixed component of variation to other components is shown schematically in Fig. 1.

Fixed horizontal variation in a plankton population must be based on fixed features of the planktonic habitat. Two general kinds of fixed features seem to be worthy
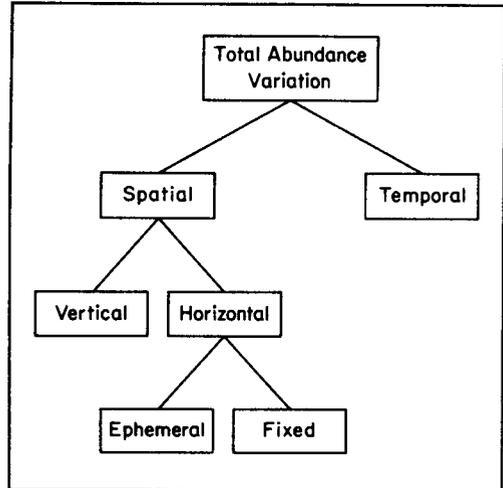

Fig. 1. Schematic organization of components of variance for plankton abundance in lakes.

of consideration: physicochemical gradients created and maintained by a point source of heterogeneity, such as a river, and depth. In the open ocean, both of these sources of variation are ordinarily absent (depth is functionally infinite), hence one would expect fixed spatial variation to be nil except over regions so large that climatic differences come into play. In lakes, persistent horizontal physicochemical gradients emanating from point sources are frequently not well developed, particularly if the flushing rate of the lake is low. Depth, however, provides a universal fixed gradient in lakes. In fact the depth gradient creates two major communities in lakes, the littoral and the limnetic. It is well known that these two communities differ in composition, complexity, and function from each other. The present study considers only the plankton community in the limnetic zone. The depth gradient extends across the limnetic zone, but crosses no obvious plankton ecozones, hence it is common to visualize the plankton zone as having essentially no stable community structure gradients. The qualitative composition of plankton is in fact typically uniform over the limnetic zone if ephemeral patchiness is averaged through time. The question to be tested here is whether the depth gradient in the limnetic zone is in fact associated with

subtle but important quantitative changes in the relative abundance of species. This line of inquiry is a logical extension of recent studies which have shown that horizontal gradients in morphology of species populations can be quite striking in some cases (Green 1967; Zaret 1972a; Kerfoot 1975). The same kinds of forces which maintain polymorphisms in species might also maintain community structure gradients, even in the largely unstructured limnetic zone.

Data collection and study area

The study of spatial variation was conducted on Lake Lanao, Philippines. Lanao is ideal for the study of fixed spatial variation associated with depth because it is large (360 km²), contains a substantial depth gradient (maximum depth, 112m; mean, 60 m), and lacks any detectable chemical gradients arising from point sources (flushing time, 6.5 yr). The physicochemical features and plankton biology of the lake have been thoroughly described (Frey 1969; Lewis 1973, 1974, 1977b). Herbivorous zooplankton in the limnetic zone include one cyclopoid copepod species, one calanoid copepod species, three cladoceran species, and seven rotifer species (Table 1). The present analysis excludes the six least abundant rotifer species, as these did not provide a firm statistical basis for analysis. The only planktonic carnivore is *Chaoborus*, which is represented by large populations of a single unnamed species (Eckstein Form 1; Lewis 1975).

Heterogeneity studies were made on five different dates spanning the full range of annual conditions (Table 2). On each date, samples were taken at eight stations, 2.5 km apart along two transects representing most of the lake inside the 10–m contour. The station depths ranged from 25 m to 80 m. Duplicate tows were taken at each station on each date with a calibrated metered net. The tows were later corrected for filtration efficiency using the meter readings. The transect was run in reverse order on alternate dates. A detailed comparison of metered net samples with Schindler-Patalas trap samples using a 35-μm net showed that los-

Table 1. List of euplanktonic zooplankton in Lake Lanao and mean abundances (entire water column, 0–45 m) at main sampling station (N = 52 weeks).

Species/Stage	Mean abundance indiv./liter
Copepoda	
Thermocyclops byalinus	
Adult	10.88
Copepodid	25.97
Nauplius	88.87
Tropodiaptomus gigantoviger	
Adult	2.13
Copepodid	4.04
Nauplius	3.56
Cladocera	
Diaphanosoma (modigliani/sarsi)	4.79
Moina micrura	0.43
Bosmina fatalis	1.50
Rotifera	
Conochiloides dossuarius	17.48
Hexarthra intermedia	4.27
Polyarthra vulgaris	0.81
Keratella procurva	0.68
Keratella cochlearis	3.96
Trichocerca brachyurum	0.26
Tetramastix opoliensis	4.33
Diptera	
Chaoborus (Eckstein 1)	0.160

ses through the net meshes for species discussed here were negligible (Lewis 1979). Samples were preserved in the field with Lugol's solution and counted later with a dissecting scope.

Analytical methods

For each species or developmental stage, the relation between abundance per unit surface area and depth was tested with a linear regression analysis. Potential compli-

Table 2. Conditions in Lake Lanao on the five sampling dates (data for main station in 45 m of water).

Date (1971)	Net production mg C/m²/day	Mixed layer (m)	O_2 at 35 m mg/liter	Zoo-plankton indiv./liter
25 Feb	1,190	60	4.18	130
15 Apr	1,440	25	5.08	280
13 May	770	15	4.15	190
10 Jun	1,940	15	2.50	150
8 Jul	2,530	30	3.00	310

Table 3. Relation of water depth to mean population size per unit area. Column 1 gives correlation coefficient derived from model I regression of abundance (No./m^2) and depth. Column 2 gives probability associated with regression slope. Column 3 gives numbers of individuals at a station 25 m deep, as determined by regression analysis. Column 4 gives expected slope of regression on assumption that each added meter of depth adds 1/25 of number at a station 25 m deep. Column 5 gives observed slope. Column 6 shows observed slope as a percentage of expected.

Species/Stage	(1, 2) Abundance vs. depth r	p	(3) Thousands indiv./m^2 @ 25 m	(4) Expected slope	(5) Observed slope	(6) Obs./Exp. × 100(%)
				thousands indiv./m^2/m depth		
Herbivores						
Cyclopoids—*Thermocyclops hyalinus*						
Nauplii	0.24	0.02	3,888	155.5	37.0	23.8
Copepodids	0.52	0.00	959	38.3	24.1	62.8
Adult ♀♀	0.45	0.00	112	4.5	5.63	125.9
Calanoids—*Tropodiaptomus gigantoviger*						
Nauplii	−0.19	0.05	336	13.5	−2.46	−18.2
Copepodids	0.09	0.21	—	—	—	0.0
Adult ♀♀	−0.33	0.00	91	3.63	−0.83	−23.0
Cladocera						
Diaphanosoma modigliani*	−0.26	0.01	355	13.8	−3.14	−22.7
Moina micrura	−0.31	0.00	34	1.36	−0.42	−31.9
Bosmina fatalis	−0.17	0.07	109	4.34	−1.22	−28.1
Rotifers						
Conochiloides dossuarius	−0.15	0.09	1,080	43.2	−6.81	−15.8
Predators						
Chaoborus						
Instar 1	0.37	0.00	0.161	0.0064	0.0081	125.8
Instar 2	0.42	0.00	0.150	0.0060	0.0036	60.0
Instar 3	0.33	0.00	0.128	0.0051	0.0035	68.0
Instar 4	0.54	0.00	0.000	0.0000	0.0302	∞

* Includes some *D. sarsi*.

cations were checked as follows. 1. Nonlinearity. A depth-abundance relation might exist in nonlinear form, so the analyses were repeated after semilog and log transformations. The transformations did not substantially change the results. The simple linear model was therefore retained.

2. Time-space interactions. As the analysis extended over five different dates, it would have been possible for depth-abundance relations to be time-dependent. Multiple regression controlling for time showed that this was not the case, so the simple regression was retained.

Results

Table 3 lists the species and stages included in the study and the results of regression analysis for each. The first column in the table gives the Pearson product-moment correlation coefficient abundance vs. depth as derived from the regression slope (model I regression: Sokal and Rohlf 1969) and the second column indicates the significance level of the regression slope. The depth-abundance relation is highly significant for most species and stages. No relation could be conclusively demonstrated for calanoid copepodids, and this group will be considered to show no relationship (it is quite likely that β error in the analysis is responsible for the failure of the demonstration here, in view of the demonstrated relationship in both younger and older stages). The relations for *Bosmina* and *Conochiloides* are borderline but will be retained for further analysis.

The relations in Table 3 leave much variance unaccounted for, even though they are for the most part significant statistically. This is because the ephemeral component of spatial variance (Fig. 1), which typically accounts for a major portion of total spatial variance (Lewis 1978*a*) is intentionally excluded from the analysis and thus appears as part of the error variance.

One important aspect of the regressions is that the cyclopoid groups all have positive slopes, indicating an increase in numbers per m^2 with increasing depth, while all other herbivore species show negative or zero slopes, indicating the opposite trend or no trend. The predator *Chaoborus* shows a trend similar to the cyclopoids.

Column 3 of Table 3 gives the average numbers of organisms at a station 25 m deep. These were computed from the regression lines (X = depth, Y = indiv./m^2) and compare closely in all cases with the mean numbers of organisms actually observed at the shallowest stations (25 m).

The fourth column in Table 3 is the expected slope of the depth-abundance relation. Expectation is based on the assumption that each meter of depth beyond the 25-m station will contribute 1/25 of the abundance

per unit area at the 25-m station. Expectation here provides a null hypothesis and not a prediction of reality, as will become apparent. Since the euphotic zone falls within the top 25 m (1% light = 9–18 m, depending on date), the expected slope basically assumes that a 1-m layer from the nonproducing zone of the lake is equivalent in its support capacity to a 1-m layer from the producing zone.

The observed slopes of depth vs. abundance, as derived from the regression analysis, are given in column 5 of Table 3. As might be anticipated, they are always lower than the expected slopes of column 4. The negative values for all species except *Thermocyclops* are counter-intuitive, however, as they suggest that addition of 1 m to the nonproducing zone detracts substantially from the support capacity of the producing zone (support capacity refers to the sum of growth and mortality control factors).

The last column in Table 3 shows the ratio of observed to expected slopes expressed as a percentage, which facilitates comparisons between species and stages. There are four possible results, all of which are shown in the table.

1. Percentage > 100% (cyclopoid adults, *Chaoborus* instars 1 and 4). This indicates that the addition of a meter of depth to the nonproducing zone increases the support capacity of the water column for this particular species or stage by more than an equal amount of depth in the producing zone. The remarkable avoidance of shallower water by large *Chaoborus* (zero abundance at 25 m) has been documented elsewhere (Lewis 1975) and appears to result from downslope movement necessitated by fish predation or by elimination of large individuals due to fish predation.

2. Percentage > 0 and < 100% (cyclopoid nauplii, copepodids, *Chaoborus* instars 2 and 3). Abundance per unit surface increases with addition of depth below 25 m, but only by a fraction of the amount expected from a straightforward extrapolation of numbers at the 25-m station.

3. Percentage 0% (calanoid copepodids). Adding depth below 25 m is inconsequential to the support capacity of the water column.

4. Percentage < 0% (all cladocerans, rotifers, two stages of calanoids). Adding depth below 25 m reduces the support capacity of the upper 25 m.

Discussion

The analysis shows that a fixed and temporally stable horizontal spatial varia- tion in the limnetic zone is statistically detectable for almost all species and devel- opmental stages, that the fixed spatial variation can be expressed in terms of linear relationships between abundance per unit surface area and depth, and that the nature of the fixed spatial variation is quite different between the coexisting
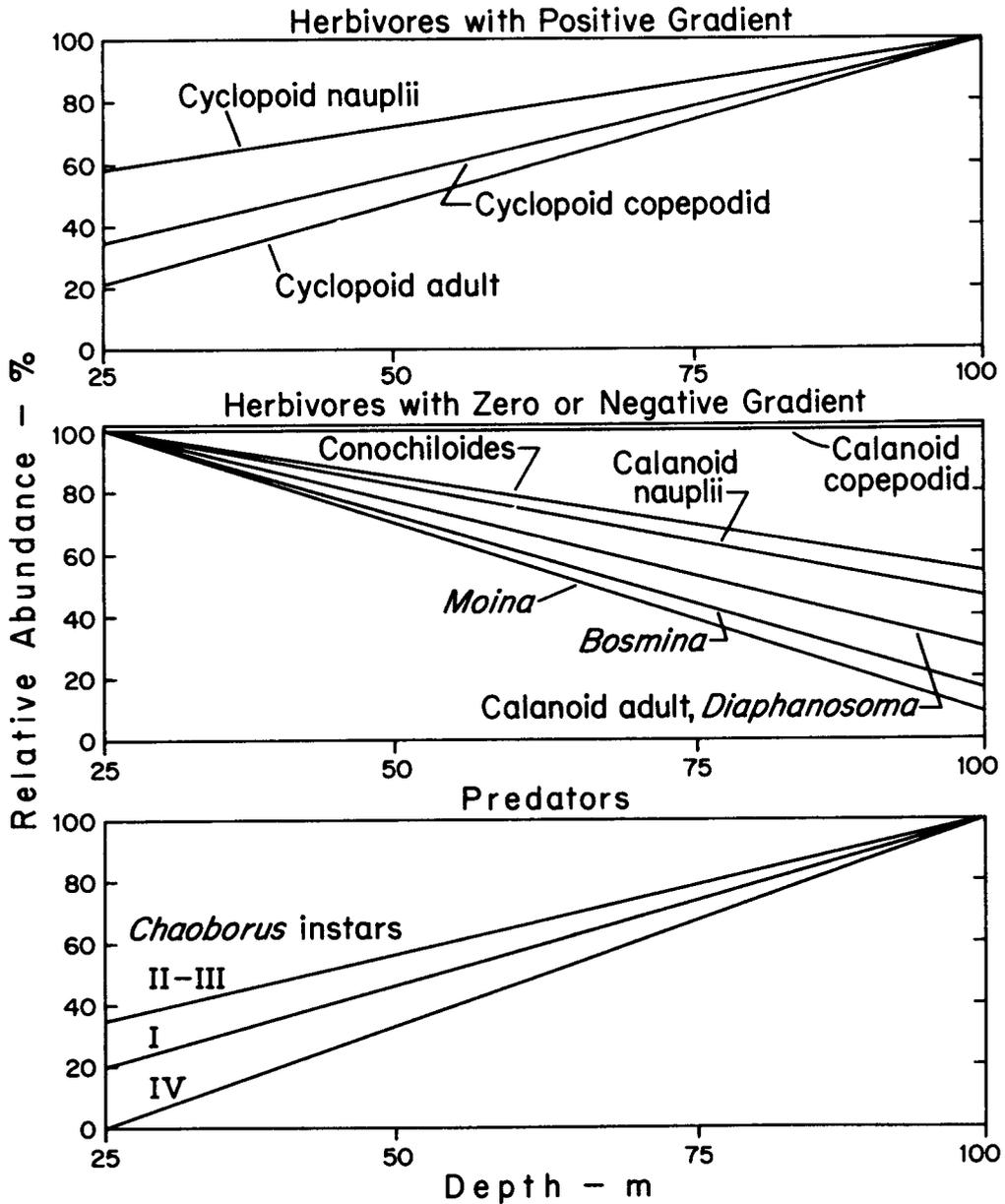

Fig. 2. Abundance gradients with depth in Lake Lanao shown as percentage of maximum abundance.

species. Figure 2 illustrates the spatial gradients that were detected in the analysis. In order to facilitate comparison, the abundance of each species in Fig. 2 is expressed as a percentage of its abundance at the depth where abundance is maximum. The changes shown in Fig. 2 take the form of clinal gradations in relative abundance of species rather than sharp transitions in abundance.

Simple ecological explanations for the herbivore gradients in Fig. 2 could be based on corresponding gradients of either the phytoplankton food resource or predation. Extensive studies of primary production and phytoplankton composition and distribution (Lewis 1974, 1978b) show that no comparable fixed gradients exist in the food resource. Thus predation is the most likely mechanism by which the gradients are maintained.

Chaoborus is by far the most important zooplankton predator in Lanao. The fish fauna is largely endemic and does not include efficient first-order planktivores of great abundance in the pelagic zone. The feeding habits of the *Chaoborus* population are known in considerable detail (Lewis 1977b, 1979), so it is possible to convert the *Chaoborus* abundance gradients of Fig. 2 to gradients of attrition for all prey species. This was done as follows.

1. The average dietary composition was obtained for each instar from a previous study (Lewis 1977b). This dietary composition reflects considerable feeding selectivity. Cladocerans and copepod copepodid/adults are major components of the diet. The cladocerans in particular are eaten in amounts far exceeding their relative abundance in the plankton.

2. Feeding rates were obtained for each *Chaoborus* instar by cohort analysis of the *Chaoborus* abundance data over an 18-month interval and approximations of growth efficiency (Lewis 1979). The food intake computed on this basis varies between 33 and 90% of body wt day^{-1}, depending on the age of the predator. These estimates were independently confirmed by measurements of herbivore loss rates.

3. The total potential loss of each food type to predation in terms of weight per unit surface area was calculated as follows:

$$L_{k,z} = \sum_{i=1}^{4} I_i \, W_{i,z} \, P_{i,k}$$

where $L_{k,z}$ is the predation loss of prey type k at a station in water of depth z to *Chaoborus* of all instars (mg/m^2/day, assuming initial community structure is as given in Table 1), I_i is the food intake rate of *Chaoborus* of instar i (fraction of body weight per day), $W_{i,z}$ is the weight per unit area at a station of depth z of *Chaoborus* instar i (mg/m^2), and $P_{i,k}$ is the proportion of prey type k in the diet of *Chaoborus* of instar i.

4. The predation loss of each prey type was then expressed as a percentage of the total stock of prey available (again assuming initial community structure as given in Table 1) to obtain relative loss:

$$RL_{k,z} = (L_{k,z}/B_k) \, N \, 100$$

where $L_{k,z}$ is the absolute daily loss as defined above, $RL_{k,z}$ is the relative daily loss of prey type k at a station of depth z (%/day), and B_k is the stock of prey type k (mg/m^2).

5. The values of $RL_{k,z}$ were then tested for linear regression with z. All relationships were highly significant (Fig. 3a). A regression line was obtained for each prey type and these are shown in Fig. 3a.

It should be noted that these computations leading to Fig. 3a are not intended to represent actual loss rates, but rather potential rates based on an average community structure as set forth in Table 1. In actuality the community structure responds to these predation gradients and thus the relative abundances are adjusted away from the average according to predator abundance and composition of a particular site. Figure 3a merely shows how this adjustment could be maintained by predation. In a situation approaching equilibrium, predation pressure on certain species and stages in excess of
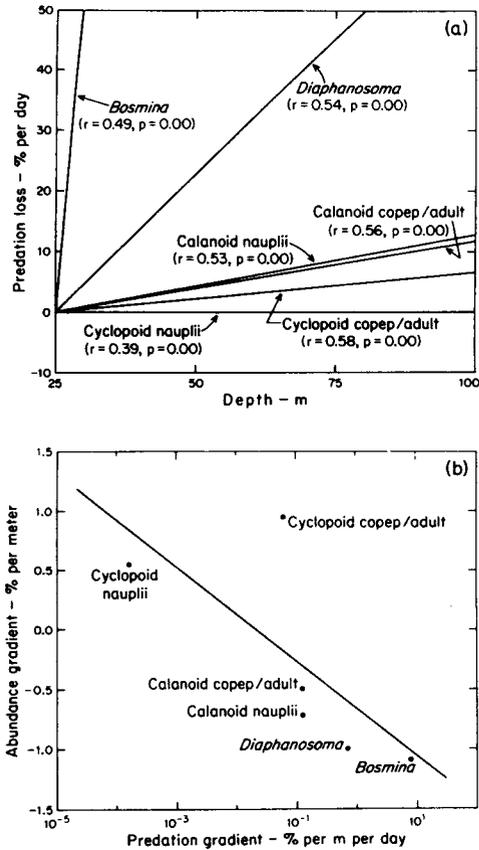
Fig. 3. a. Predation gradients with depth in Lake Lanao computed for a fixed community structure of prey (average annual abundance of all species at central sampling station in 45 m of water as shown in Table 1). Loss expressed as percentage of population per day eaten by all instars of *Chaoborus*. b. Relation of predation gradients to abundance gradients in Lake Lanao herbivores.

their growth capacity will cause drastic decline in abundance of these forms until the predator reduces its selectivity for them (Lewis 1977*b*).

The analysis leading to Fig. 3a omits *Moina* and *Conochiloides*. *Moina* is such a small proportion of the available prey that a predation analysis on the species is not possible, even though the abundance data are sound. *Conochiloides* lacks distinctive skeletal parts resistant to maceration in the crop of *Chaoborus* so that predation data based on crop analysis are not comparable

to the data for other species. In addition, the copepodid and adult stages are combined in Fig. 3a because they could not be distinguished in the crop analysis.

Figure 3a shows that considerable predation gradients exist in Lake Lanao and that the severity of the gradients varies greatly between species and stages. There is an overall increase in the severity of predation toward deep water, coincident with the increase in numbers of all *Chaoborus* instars toward deep water (Fig. 2). Because of the selective feeding on cladocerans, especially in larger *Chaoborus* instars, the gradients are very steep for *Diaphanosoma* and *Bosmina*. Nauplii of both copepods, by contrast, are seldom eaten by *Chaoborus* and thus experience very limited gradients.

If predation gradients (Fig. 3a) establish and maintain abundance gradients (Fig. 2), then the two should be quantitatively related. The relation will not be linear because the effect of a given predation gradient on a species will depend on the average production rate of the species and all other sources of mortality besides *Chaoborus* predation. The relationship is shown in Fig. 3b in a semilog format, which condenses the great range of predation gradients. It is clear that the predation and abundance gradients are related. The correlation of points shown in Fig. 3b is significant at $P = 0.05$ and accounts for 51% of the total variance in gradients ($r = 0.77$, $r^2 = 0.51$). The circumstantial evidence for maintenance of the abundance gradients by predation is therefore very strong.

Figure 3b has two general implications for the organization of the plankton community. First it is evident that a physically and chemically unstructured plankton environment can support an unexpected degree of stable pattern in community structure. While several cases of fixed horizontal pattern in a single species based on predation have been documented (Green 1967; Zaret 1972*a*; Kerfoot 1975). The existence of predation-maintained fixed patterns in the structure of entire limnetic zooplankton assemblages has apparently not been demonstrated.

It is presently clear that predation ac-

counts for many differences in herbivore composition between lakes (e. g. Hrbáček et al. 1961; Brooks and Dodson 1965; Brooks 1968; Dodson 1970; Zaret 1972b). The Lanao data suggest that predation plays a similar role within lakes, except that the influence is more subtle and affects the relative abundance of species rather than the species composition.

A second implication of the analysis is that predation helps maintain complexity in the lake zooplankton. While some generalized arguments and experimental evidence support this notion for some communities (Paine 1966), no demonstration has ever been given for lake zooplankton. The fixed predation gradients in Lake Lanao could easily account for the persistence of species that would be eliminated if predation were uniform or randomly variable over the lake. It thus seems possible that the gradients enhance the overall biotic diversity of herbivores.

If predation gradients can reasonably account for herbivore abundance gradients, then a second step toward the mechanistic explanation for fixed patterns in community structure would involve an analysis of the factors controlling the distribution of primary carnivores. Such an explanation would involve fish predation on *Chaoborus*. The behavior and distribution of *Chaoborus* both suggest that deep water offers refuge from predation, largely because of the daily retreat of larvae to water of low oxygen content (Lewis 1975, 1977b). Organization of the zooplankton thus in large part seems to be determined in a stepwise manner from the top trophic levels. Although one should not overlook the certainty that other mechanisms will affect the other components of variation (Fig. 1), the separation of variance components seems to simplify mechanistic approaches to community structure.

References

ALLEN, T. F., and J. F. KOONCE. 1973. Multivariate approaches to algal strategems and tactics in systems analysis of phytoplankton. Ecology 54: 1234–1246.
BROOKS, J. L. 1968. The effects of prey size selection by lake planktivores. Syst. Zool.

17: 272–291.
———, and S. I. DODSON. 1965. Predation, body size, and composition of the plankton. Science 150: 28–35.
CODY, M. L. 1974. Competition and the structure of bird communities. Princeton Univ. Press.
DODSON, S. I. 1970. Complementary feeding niches sustained by size-selective predation. Limnol. Oceanogr. 15: 131–137.
FREY, D. G. 1969. A limnological reconnaissance of Lake Lanao, Philippines. Int. Ver. Theor. Angew. Limnol. Verh. 17: 1090–1102.
GREEN, J. 1967. The distribution and variation in *Daphnia lumboltzi* (Crustacea:Cladocera) in relation to fish predation in Lake Albert, East Africa. J. Zool. Lond. 151: 181–197.
GREEN, R. H. 1971. A multivariate statistical approach to the Hutchinsonian niche: bivalve mulluscs of central Canada. Ecology 52: 225–229.
GRENNY, W. J., D. A. BELLA, and H. C. CURL. 1973. A theoretical approach to interspecific competition in phytoplankton communities. Am. Nat. 107: 405–425.
HRBÁČEK, J., M. DVOŘÁKOVA, V. KOŘÍNEK, and L. PROCHÁZKÓVA. 1961. Demonstration of the effect of fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. Int. Ver. Theor. Angew. Limnol. Verh. 14: 192–195.
HUTCHINSON, G. E. 1961. The paradox of the plankton. Am. Nat. 95: 137–146.
———. 1967. A treatise on limnology, v. 2. Wiley.
KERFOOT, W. C. 1975. The divergence of adjacent populations. Ecology 56: 1298–1313.
LANE, P. A. 1975. The dynamics of aquatic systems: a comparative study of the structure of four zooplankton communities. Ecol. Monogr. 45: 307–336.
LEWIS, W. M., JR. 1973. The thermal regime of Lake Lanao (Philippines) and its theoretical implications for tropical lakes. Limnol. Oceanogr. 18: 200–217.
———. 1974. Primary production in the plankton community of a tropical lake. Ecol. Monogr. 44: 377–409.
———. 1975. Distribution and feeding habits of a tropical *Chaoborus* population. Int. Ver. Theor. Angew. Limnol. Verh. 19: 3106–3119.
———. 1977a. Ecological significance of the shapes of abundance-frequency distribution for coexisting phytoplankton species. Ecology 58: 850–859.
———. 1977b. Feeding selectivity of a tropical *Chaoborus* population. Freshwater Biol. 7: 311–325.
———. 1978a. Comparison of spatial and temporal heterogeneity in lake plankton by means of variance components. Ecology 59: 666–671.
———. 1978b. Spatial distribution of the phytoplankton in a tropical lake. Int. Rev. Gesamten Hydrobiol. 63: 619–635.

——. 1979. A zooplankton community analysis. Springer-Verlag, New York.

MacARTHUR, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39: 599–619.

MAKAREWICZ, J. C., and G. E. LIKENS. 1975. Niche analysis of a zooplankton community. Science 190: 1000–1003.

MARGALEF, R. 1958. Temporal succession and spatial heterogeneity in natural phytoplankton, p. 323–349. *In* A. Buzzati-Traverso [ed.], Perspectives in marine biology. Univ. Calif. Press.

MIRACLE, M. R. 1974. Niche structure in freshwater zooplankton: a principle components approach. Ecology 55: 1306–1316.

MULLIN, M. M., and E. R. BROOKS. 1976. Some consequences of distributional heterogeneity of phytoplankton and zooplankton. Limnol. Oceanog. 21: 784–796.

PAINE, R. T. 1966. Food web conplexity and species diversity. Am. Nat. 100: 65–76.

RICHERSON, P., R. ARMSTRONG, and C. R. GOLDMAN. 1970. Contemporaneous disequilibrium, a new hypothesis to explain the "paradox of the plankton". Proc. Natl. Acad. Sci. 67: 1710–1714.

ROUGHGARDEN, J. D. 1974. Species packing and the competition function with illustrations from coral reef fish. Theor. Pop. Biol. 5: 163–186.

SANDERCOCK, G. A. 1967. Coexistence of calanoid copepods. Limnol. Oceanogr. 12: 97–112.

SANDUSKY, J. C., and A. J. HORNE. 1978. A pattern analysis of Clear Lake phytoplankton. Limnol. Oceanogr. 23: 636–648.

SCHOENER, T. 1974. Resource partitioning in ecological communities. Science 185: 27–39.

——. 1975. Presence and absence of habitat shift in some widespread lizard species. Ecol. Monogr. 45: 233–258 . . . .

SOKAL, R. R., and F. J. ROHLF. 1969. Biometry. Freeman.

TITMAN, D. 1976. Ecological competition between algae: experimental confirmation of resource-based competition theory. Science 192: 463–465.

WHITTAKER, R. H. 1967. Gradient analysis of vegetation. Biol. Rev. 42: 207–264.

WIEBE, P. H. 1970. Small-scale distribution in oceanic zooplankton. Limnol. Oceanogr. 15: 205–217.

ZARET, T. M. 1972*a*. Predator-prey interaction in a tropical lacustrine ecosystem. Ecology 53: 248–257.

——. 1972*b*. Predators, invisible prey, and the nature of polymorphism in the Cladocera (Class Crustacea). Limnol. Oceanogr. 17: 171–184.