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24. A relative increase in the density of NE terminals could result from a degeneration of the cellular elements in the affected areas with the NE terminals remaining intact. However, this possibility appears somewhat unlikely because we have evidence that other biochemical parameters, such as DA and serotonin levels, do not change in an analogous manner in the areas in question (unpublished observations). An absolute increase in the density of NE terminals could be due to several possible processes, such as faulty overdevelopment of the corresponding NE system or systems; failure of some NE terminals to regress, as part of a normal process, during postnatal development (analogous to the apparently normal decrease of the nigrostriatal DA during adolescence) [A. Carlsson and B. Winblad, *J. Neural Transm.* **38**, 271 (1976)]; or sprouting of NE nerve endings in response to damage of some other neuronal system or systems impinging on the same perikarya [G. Raisman, *Brain Res.* **14**, 25 (1969); R. Y. Moore, A. Björklund, U. Stenevi, *ibid.* **33**, 13 (1971)]. In this latter respect, the possibility of a primary damage of the neuron system containing γ-aminobutyric acid is especially provoking [E. Roberts, *Neurosci. Res. Program Bull.* **10**, 468 (1972)]. Any of these factors may confer on the afflicted brain regions the kind of special biological vulnerability that has been hypothesized as one of several possible factors predisposing the affected individual to schizophrenia [S. S. Kety, *Semin. Psychiatry* **4**, 233 (1972); W. Pollin, *Arch. Gen. Psychiatry* **27**, 29 (1972)].
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Zooplankton Niches and the Community Structure Controversy

In a recent report Makarewicz and Likens (*1*) interpret the results of their study of the zooplankton community in Mirror Lake, New Hampshire, as supporting the individualistic concept of natural communities (*2*). They state that "the finding parallels Ramensky's . . . and Gleason's . . . concepts of species individuality and community continuity." Ecologists have long argued about whether natural communities constitute highly structured entities. Pielou (*3*) has defined community structure as "the amount of interdependence among the species." Thus, the more biological interactions that occur in a given community, the stronger the statistical associations among species and the more definite the structure. Obviously, the degree of structure will vary with the taxonomic unit that is considered. For example, much of the support for the individualistic concept has come from studies of terrestrial plant communities (*4*). Zooplankton communities in lakes, however, exhibit a definite structure which invalidates the application of the individualistic concept as proposed by Makarewicz and Likens (*1*). My argument consists of two parts: why they did not find community structure, and how it can be found. Because the community structure controversy has important ecological implications, a careful evaluation of their interpretation is warranted.

Makarewicz and Likens (*1*) report on 48 productivity estimates of 15 zooplankton species. They collected nonreplicated samples at four depths each month for a year. They plotted isopleths (isolines) of these productivity values using two to four species per graph, with depth on the *Y* axis and time of year on the *X* axis. The isopleth representations are termed population response surfaces. Because mean monthly production values for the species are continuous and because the population response surfaces do not overlap greatly, Makarewicz and Likens conclude that "this intracommunity population structure is analogous to the extensive or intercommunity population continuum formed by communities in relation to habitat gradients." They do suggest, however, that the observed division of the niche space has resulted from species interactions.

The productivity estimates themselves are a valuable contribution to zooplankton ecology. My criticism concerns only the representation of the results and subsequent conclusions concerning community structure. Three central questions are (i) Do 48 environments (samples) per year adequately characterize the overlap patterns of a zooplankton community? (ii) Have the sets of species used to represent niche separation been appropriately chosen? (iii) Does the use of productivity values give a good estimate of species importance? The following remarks apply mostly to zooplankton communities: sweeping generalizations for all communities should be avoided until biological insights are better developed.

First, it is crucial in delineating community structure to select an appropriate spatial-temporal framework for the organisms in question. Makarewicz and Likens state that species with similar modes of feeding do not overlap very much. Species found together at a single time and depth, however, may not be overlapping greatly on a diurnal basis, and conversely species not found together at a single time and depth may be overlapping greatly on a diurnal basis. Using complex vertical migration patterns, zooplankton can select habitats to minimize effective overlap even though their depth ranges for a 24-hour period (or a single time period) are identical (Table 1). Zooplankton can also exhibit large overlaps over the diurnal period, although their depth ranges are discontinuous at a particular time period. Makarewicz and Likens base their annual analysis on 48 small samples, each representing 11.88 liters of water with a total volume sampled of less than 0.6 m^3 for the year. In my niche analysis of the zooplankton community of Gull Lake, Michigan, I sampled 40 to 80 time-depth environments for one station and diurnal period, each sample usually representing more than 1 m^3 of lake water (*5*). Overlap patterns for different time periods were often different. Makarewicz and Likens (*1*) selected their one time period at about noon, the time when most zooplankton populations overlap to the least extent. Makarewicz (*6*) determined only one set of migration patterns in August 1969, and he found that several species underwent vertical migration. However, he made no effort to evaluate the overlap patterns in regard to the migration results. Thus, I believe that the initial data base of Makarewicz and Likens (*1*) is inadequate for representing species overlap patterns, mainly because there are too few samples. Exaggerated niche separations can easily become an artifact of a scanty data set.

Second, a major problem with their analysis is the selections of species used to demonstrate small overlaps. Usually they place two to four populations on one graph [figure 1 of (*1*)], based on a criterion of feeding mode. There are several disturbing aspects of this procedure. The selection was accomplished on the basis of a few literature references, which in total do not constitute a thorough description of the feeding habits of the species under consideration. There is not good justification for the four categories used: predators, herbivorous macroconsumers, herbivorous microconsumers, and miscellaneous. Many species groupings appear handpicked to illustrate the least overlap. Biological cases could be made for the lumping of *Daphnia catawba* and *Bosmina longirostris*, *Cyclops scutifer* or *Asplanchna priodonta* and *Diaptomus minutus*, *Holopedium gibberum* and *Bosmina longirostris*, as well as many sets of rotifers (*5*). Often *B. longirostris*, *D. catawba*, and *H. gibberum* filter feed at similar rates on similar algal size classes (*5, 7*). *Diaptomus* and *Cyclops* species can seize the same prey species (*7, 8*). Some omnivorous species, especially calanoid copepods, can change their feeding mode several times in an annual period and can exhibit more than one mode in a diurnal period. Larger predators that might compete with *Mesocyclops edax* were ignored completely, and, in addition, they were probably sampled inaccurately. Table 3 in (*6*) lists densities of 20 of the 30 species found in the lake, of which several groups (*Tropocyclops prasinus*, copepodids, nauplii, *Epischura lacustris*), although numerous, are not mentioned in (*1*). Overlaps of these groups should be considered. There is also some confusion about whether adults or immature forms are evaluated, and more confusion about which species constitute one or more zooplankton communities. There is no standardization for the number of species per graph or of feeding types per graph. For example, microconsumers are represented on four graphs with two other groups. Although most attempts at classifying

Table 1. Overlap patterns of pairs of zooplankton species (the degree of joint use of the ecological space by a species pair) in Gull Lake in July and December 1972; overlap calculations are those used by Levins (*11*). Case 1: the overlap coefficients are low, but the mean amplitudes of the species pairs are almost completely overlapping. Case 2: the overlap coefficients are high, but the mean amplitudes of the species pairs do not overlap so much as in case 1.

Date	Species	Amplitude of 50% of the population over 24 hours		Percentage of overlap amplitude of 50% of the population	Overlap coefficients
		Upper depth (m)	Lower depth (m)		
		Case 1			
July	i = *Daphnia pulex*	9.4	21.2	83	α_{ji} = .34
July	j = *Daphnia longiremis*	9.8	19.6	100	α_{ij} = .57
July	i = *Diaphanosoma leuchtenbergianum*	4.8	21.7	93	α_{ji} = .49
July	j = *Daphnia dubia*	5.9	22.1	98	α_{ij} = .11
December	i = *Daphnia retrocurva*	5.0	17.0	100	α_{ji} = .37
December	j = *Daphnia pulex*	4.1	18.8	82	α_{ij} = .19
December	i = *Daphnia galeata*	7.5	22.5	75	α_{ji} = .41
December	j = *Daphnia pulex*	4.1	18.8	77	α_{ij} = .28
		Case 2			
July	i = *Daphnia galeata*	7.2	16.3	40	α_{ji} = .64
July	j = *Daphnia retrocurva*	2.5	10.8	43	α_{ij} = .65
July	j = *Bosmina longirostris*	12.5	16.6	0	α_{ji} = .62
July	i = *Diaptomus minutus*	5.5	10.8	0	α_{ij} = .57
December	i = *Bosmina longirostris*	10.2	15.8	100	α_{ji} = .60
December	j = *Daphnia galeata*	7.5	22.5	37	α_{ij} = 1.10
December	j = *Bosmina longirostris*	10.2	15.8	77	α_{ji} = .42
December	i = *Daphnia dubia*	11.5	20.0	51	α_{ij} = 1.18

Table 2. Mean niche values of the Gull Lake filter-feeding zooplankton species for 1972–1973. Annual mean values $\overline{X}$ and their coefficients of variation (C.V.) (in parentheses) are also given [see Levins (*11*) for equations]. Niche overlap (α_{ij}) measures the degree of joint use of the ecological space by a species pair. The mean value of community overlap patterns is $\overline{\alpha}$. Diversity (H) takes account of the number of species (N) and their relative abundance patterns. Species breadth (B_1) is a measure of the use of ecological space. Community niche breadth ($\hat{B}$) is the total niche breadth for all the coexisting species. The ratio $B_i/\hat{B}$ indicates how broad-niched a species is in regard to its community. The quantity D_i/K_i is the ratio of the density of species i to its carrying capacity, and $K_i/(B_i/B)$ is a measure of the carrying capacity of species i per unit of niche space. Dates are as follows: 1 = 3 July 1972, 2 = 5 August 1972, 3 = 16 September 1972, 4 = 26 October 1972, 5 = 14 December 1972, 6 = 10 February 1973, and 7 = 19 May 1973.

Niche value	Dates							$\overline{X}$	C.V.
	1	2	3	4	5	6	7		
$\overline{\alpha}$	.50	.58	.46	.55	.48	.47	.52	.51	(.09)
H	2.4	3.3	3.4	3.4	2.7	2.0	2.0	2.8	(.21)
$B_i/\hat{B}$	.56	.65	.54	.75	.48	.47	.54	.57	(.17)
D_i/K_i	.11	.10	.17	.15	.11	.15	.11	.13	(.21)
$K_i/(B_i/\hat{B})$	.92	.94	.93	.88	1.02	1.03	1.00	.96	(.06)

pelagic zooplankton by feeding type are to some degree arbitrary, it is probable that, regardless of the mode of classification, most species suffer from at least diffuse competition (*9*). If this is true, then overlaps should be represented in a more sophisticated way to include the effects of multiple species.

Third, it is debatable whether productivity as Makarewicz and Likens (*1*) have represented it is a good measure of species importance values, which can then be used to illustrate niche separation. If species importance is to be quantified, then the units have to be standardized. Some species are represented by one productivity isopleth, others by two to seven. In addition, Makarewicz and Likens do not graph the lower productivity values for the most productive species, and isopleth values on a given graph vary by a factor of 3 to 15. This gives the illusion that there is more niche separation than there really is. A great deal more justification is needed for using only the maximum productivity values as "adaptive centers." I have found that density and productivity are not always the best criteria of species well-being. Zooplankton can undergo large and sudden shifts in density and yet exhibit poor long-term survival. Frequency of occurrence in environments (*h*) is a useful criterion of success, since species that maintain themselves (regardless of their rarity) in a variety of habitats are often persistent. Yet in the analysis of Makarewicz and Likens a sudden increase in density ensures a well-defined adaptive center regardless of whether that increase is a capricious event or a normal fluctuation in an equilibrium community. Statements such as "the population response surface to the niche variables provides the best characterization of the niche" or "in relation to depth (at a given time), or in relation to time (at a given depth), the distributions of these species should form bell-shaped curves" are misleading and not validated in (*1*) or in papers of others. Thus, Makarewicz and Likens have not measured or represented the overlaps of their species very well, and their representation of niche separation is biased and unrealistic. The evidence they present should not be used as strong support for the individualistic concept (*2*).

Table 3. Comparison of zooplankton species and date effects for two niche ratios for four cruises in 1966 and seven cruises in 1972–1973; *F* values are given with probability estimates (in parentheses) and degrees of freedom (d.f.) for a two-way analysis of variation without interaction.

Statistic	D_i/K_i	$B_i/\hat{B}$	d.f.
	Filter feeders		
1966			
Species	7.35 (.001)*	14.38 (.001)*	8,27
Season	.59 (.999)	.50 (.999)	4,27
1972–1973			
Species	2.38 (.013)*	3.45 (.001)*	12,67
Season	.56 (.999)	2.69 (.021)*	6,67
	Seizers		
1966			
Species	16.55 (.001)*	7.65 (.004)*	3,12
Season	.32 (.999)	.61 (.999)	4,12
1972–1973			
Species	60.05 (.001)*	6.51 (.002)*	4,18
Season	.18 (.999)	.71 (.999)	6,18

*Significantly variable at the 5 percent level.

Community structure in nature has been difficult to identify and more difficult to quantify. The search for community structure is partially the search for macroscopic properties (*10*) at the community level. I have found some macroscopic properties that I term "consistent indices." These indices can be defined as measures that (i) vary less than the original variables, (ii) are characteristic of a type of community, (iii) vary among different types of communities so that their consistency is not a mathematical artifact, and (iv) have some intuitive meaning for the investigator. These consistent indices can best be delineated if one finds statistical ensembles derived from data on groups of highly interacting species that can be expected to exhibit community structure. Pelagic filter feeders are an example. I have used Levins's (*11*) equations to evaluate zooplankton community structure (*5*) and to find consistent indices. This analysis centers on several niche measures that are calculated from density values and distribution patterns for a set of coexisting species.

In the pelagic zone of Gull Lake, the zooplankton communities exhibit several consistent indices (Table 2). An individual species changes its niche values and underlying distribution patterns markedly throughout the year. Table 3 shows that species are significantly more variable, at the .001 to .013 probability level, than the community over season. Vertical migration patterns change unpredictably with date and year. Species come and go, and densities of individual species fluctuate over several orders of magnitude. Environmental heterogeneity is not the same for any pair of sampling dates; twice there was a severe hypolimnetic oxygen deficit, and once there was ice cover. The results in Tables 2 and 3, however, constitute documentation that natural communities do possess structure or integrity that cannot be obtained from an analysis of individual species in isolation.

In one sense, it is not fair to criticize Makarewicz and Likens for not identifying macroscopic community properties when they were not looking for them. In another sense, however, their niche analysis does not give (i) a realistic representation of zooplankton overlap patterns and (ii) valid conclusions concerning zooplankton community structure. In addition, throughout their report, terminology (importance values, community continuum) is borrowed freely from terrestrial plant ecology. This procedure is unwarranted. There is no particular reason why 1-mm aquatic animals should behave like 10-m trees, nor do carapaces possess the same chemical composition as bark. Yet Makarewicz and Likens try to force their data to fit the individualistic concept that was originally developed for large terrestrial plants.

Finally, I agree with their general conclusion that niche separation occurs with season and depth in zooplankton communities. This fact has been well documented in earlier studies (*12*). Actually the evidence for niche separation can be used to strengthen my arguments for community structure, in that the community remains consistent regardless of large fluctuations in density, changes in behavior patterns, and the presence or absence of particular species. It is fair to question, however, whether the limited data base that Makarewicz and Likens present for partial niche separation constitutes any support for the individualistic concept of community structure for zooplankton communities. In view of the intense efforts being given to studies of the structure of animal communities at the present time, it would be appropriate to reexamine the community structure controversy in more detail than presented here and in (*1*). Undoubtedly, lake zooplankton are not the only animal group that exhibits a substantial degree of community structure. Other groups should be identified and compared so that a more coherent theory of community structure can be formulated than has been possible thus far. Reductionist approaches, such as the individualistic concept, are of limited value in the study of animal communities.

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Lane is correct in stating that "Community structure in nature has been difficult to identify and more difficult to quantify" (*1*). Our approach (*2*) was an attempt to interrelate the activities of the limnetic species of zooplankton living together in Mirror Lake over a period of a year. Obviously, this is difficult to do. Using productivity as a measure of success in the environment, we have attempted to combine measures of zooplankton density and metabolism to gain some insight into how a community, as a living system of interacting species populations, is organized within the aquatic ecosystem. This certainly is not a reductionist approach.

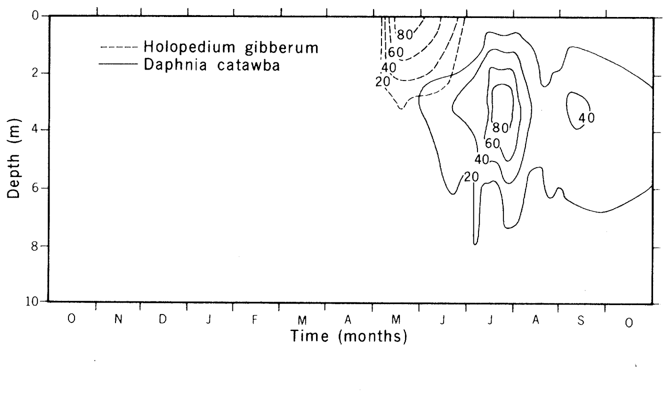
Ecologists mean by "structure" various characteristics of communities, including the amount of interdependence among the species (*3*), species occurrence, species diversity, growth form composition, biomass, distribution of species populations in space and time, dominance-diversity relationships, and especially the ways in which species both interrelate and differ in niche within the community (*4, 5*). Lane states (*1*) that our study was concerned with community structure with special reference to niche differentiation; however, her statement that we did not find any community structure is completely false. The community of zooplankton in Mirror Lake possessed a biomass, a species diversity, and an interdependence among species. In (*2*) we stated: "The niche structure of the zooplankton community should be conceived as an intensive or intracommunity population continuum corresponding to the niche hyperspace."

The principle of species individuality has been used to refer to intercommunity (habitat) distribution; we have noted an analogy to intracommunity (niche) species differences or individuality in (*2*). Lane (*1*) indicates that we applied the individualistic concept to our analyses and concludes that, since a zooplankton community possesses structure, this is an invalid procedure. First, we did not apply the individualistic concept to our data. We provided support for it. Second, Lane misinterprets (*1*) the implication of the individualistic concept for community structure. The principle of species individuality (*6*) may be stated as follows: "Each species is distributed in its own way, according to its own genetic, physiological, and life-cycle characteristics and its way of relating to both physical environments and interactions with other species; hence, no two species are alike in distribution" (*5*). The existence of structure or species interactions in a community does not invalidate the principle of species individuality. In fact, strong support for the principle of species individuality has come from studies on highly structured forest communities (*7*).

We cannot claim that our methods are perfect but we do think them adequate by current standards of limnological research and as bases for our published results. Some points on technique and interpretation follow.

1) We used a water bottle to collect water samples from Mirror Lake and then filtered this water through a Likens-Gilbert filter equipped with a mesh net (35 μm). This technique, criticized by Lane (*1*), has been carefully tested and compared with towed devices (for example, an Isaacs-Kidd sampler, a Clarke-Bumpus sampler, and a 0.5-m vertical tow net) in Mirror Lake (*8*).

Serious functional problems may occur in metered devices such as the Clarke-Bumpus sampler if fine mesh nets are used, giving inaccurate results (*9*). McNaught (*10*) recommended that nets



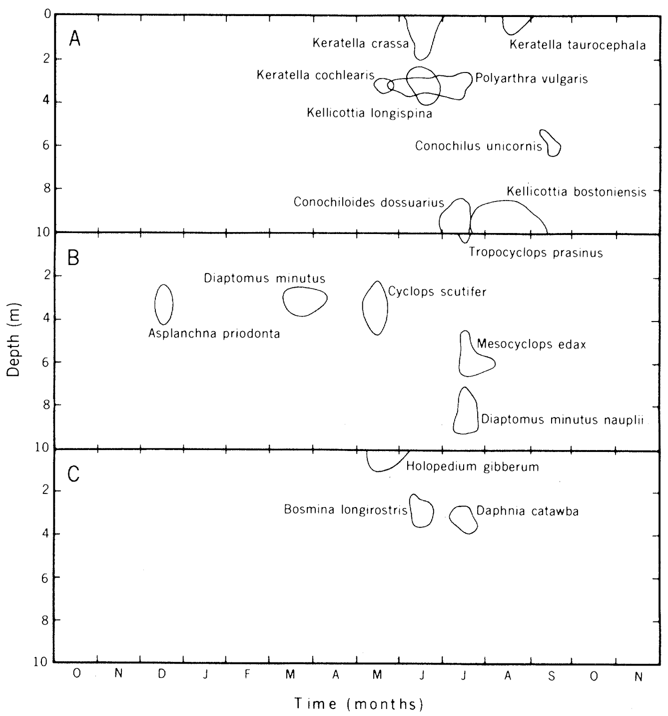


Fig. 1 (above). Population response surfaces of *Daphnia catawba* and *Holopedium gibberum*. Isolines represent the percentages of the highest daily production value of a species during a year. Isolines are drawn from production values calculated from each sampling date at depths of 0, 3, 6, and 9 m. Fig. 2 (right). Centers of niche response surfaces of limnetic zooplankton in Mirror Lake, New Hampshire. The area within the 15 percent isoline is plotted for each species and is taken as the niche center of the niche response surfaces presented in figure 1 of (*2*). The 15 percent isoline represents the percentage of the highest monthly production value of a species during a year. The 15 percent isoline is drawn from mean monthly production values calculated from depths of 0, 3, 6, and 9 m.

finer than 363-μm mesh (No. 2 net) should not be used on such devices in productive waters. Since Mirror Lake is unproductive and many researchers have used a 158-μm mesh net, we used a No. 10 (158-μm) net on the towed devices.

All species of zooplankton caught with the towed devices were found in the water bottle. The water bottle caught as many or more individuals of each species of zooplankton as did the other devices. What was particularly striking in our tests was the number of rotifers and nauplii missed with a No. 10 net (*8*). On the basis of our tests and the literature (*11*), we believe that our sampling technique was adequate and quantitative. Lane used a Clarke-Bumpus sampler equipped with a 120-μm mesh net in highly productive waters (*12*).

2) We considered the cladocerans, calanoid and cyclopoid copepods, and rotifers in our study of the zooplankton of Mirror Lake (*13*). Lane claims (*1*) that she is studying zooplankton community structure but she considers only calanoid copepods and cladocerans. Increasing evidence indicates that rotifers play a major role in energy transfer (*8, 11, 14*) and nutrient cycling (*8*) in lakes. Furthermore, the possibility of diffuse competition exists between herbivorous rotifers, cladocerans, and copepods (*1*). How can one determine zooplankton community structure by studying only a portion of the community?

3) Lane (*1*) criticizes our use of productivity as a key measure. Any measure of species success or well-being (for example, frequency of occurrence, density, or productivity) is arbitrary. We would agree that density is not the best way to compare populations of organisms of widely different sizes and metabolic rates. We chose productivity because it seemed most appropriate as a measure of the species role in the community, for it expresses the species use of resources for individual and population growth and permits a comparison of species of widely different size and metabolism on a single scale. We believe productivity is a less arbitrary measure of the fitness of a population in an aquatic ecosystem than frequency of occurrence.

4) In Lane's analysis of Gull Lake, Michigan, only four sampling dates, all from the summer, were examined. In her studies of Lake Michigan, Cranberry Lake, and Lake George, only two to three sampling dates, all from the summer, were used (*12*). At Mirror Lake we obtained weekly samples at four depths during the late spring, summer, and early autumn and sampled at monthly intervals during the late autumn, winter, and early spring. As Lane suggests, 48 samples per year would not fully characterize the zooplankton community of any lake (*1*), but neither do samples at only four sampling dates, all from one season, as Lane has done (*15*). Lane mistakenly believes that we used only 48 samples in our analysis (*1*); in fact, 84 samples were taken on 21 different dates. From these 84 samples, we calculated mean monthly productivity values for each depth. These values were used to construct the niche response surfaces (*2*).

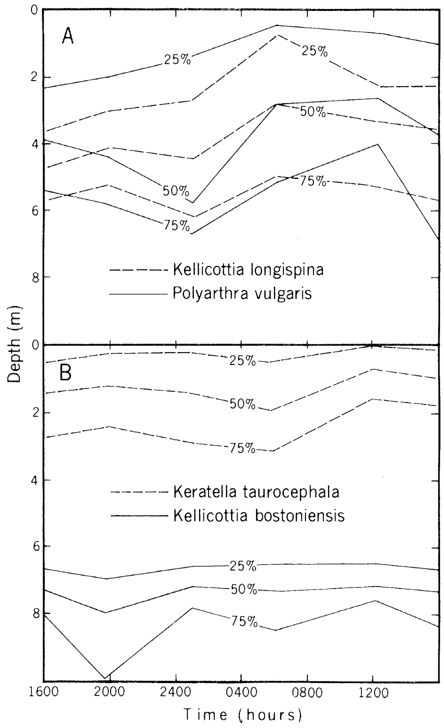


Fig. 3. Vertical migration patterns of selected zooplankton species in Mirror Lake during August. Migration patterns were determined by the quartile method of Pennak (*18*).

5) Lane criticizes our construction of the niche response surfaces (*1*). Isoline values must be chosen but different choices gave response surfaces of similar form for the two dominant species in the lake (Fig. 1) (*16*). Our statements on species niches are not affected by these choices.

In an effort to clarify this, we graph in Fig. 2, A through C, only the niche centers of each species. Species of zooplankton are grouped as suggested by Lane (*1*). As before (*2*), the niche centers of the niche response surfaces do not overlap, except for *Keratella cochlearis* and *Kellicottia longispina* whose niche centers overlap with *Polyarthra vulgaris*. The niches of these species appear to differ in feeding behavior (*17*).

6) Referring to the niche response surface, Lane concludes (*1*) that a sudden increase in density will ensure a well-defined niche center. Consider species with individuals that have long life-spans (for example, a year), such as *Mesocyclops edax*, *Cyclops scutifer*, and *Diaptomus minutus* in Mirror Lake. After hatching, there is a general decrease in population density throughout the year due in part to predation. During this period, there is considerable growth of an individual organism. The result is a niche response surface with a well-defined center during a period of decreasing population densities.

Similarly in species with a shorter life-span, the location of the niche response surface within the niche hyperspace and the intensity of the population's response are functions not only of population size but also of the growth of the individual organism and the duration of development of each species. Individual growth and duration of development are functions of temperature and food supply. Thus, the location of the niche response within the niche hyperspace and the intensity of the population response are, in part, functions of temperature and food. Furthermore, we believe that the positions of the niche response surfaces, the niche centers, and the intensity of the response result in part from trophic interactions such as competition, predation, and competitive displacement, as well as physical and chemical variables.

7) Lane indicates (*1*) that we did not evaluate vertical migration as a possible mechanism of niche separation. The broad overlap of the niche response surfaces of some species indicates that there is still some competition among species. Part of the overlap of niche response surfaces could be due to niche differences other than separation in time and space and feeding behavior, such as vertical migration (*2*).

However, our analysis of the vertical migration of rotifers in Mirror Lake indicates that this mechanism does not reduce competition or separate niches. For example, the niche response surfaces and the niche centers of *Keratella taurocephala* and *Kellicottia bostoniensis* are located in August on the time axis but are separated into the epilimnion and hypolimnion, respectively, on the depth axis. There is little overlap of the niche response surfaces of these two species (*2*). These species have a very limited vertical migration (Fig. 3A); thus, there is little overlap over a 24-hour period. Examination of *Polyarthra vulgaris* and *Kellicottia longispina*, two species whose niche centers are not located in the month of August but whose niche response surfaces do overlap during August, indicates a similar pattern of vertical migration (Fig. 3B). Competition between these species does not appear to be reduced by vertical migration in Mirror Lake. Instead, niches are separated and competition is reduced by the scattering of the niche response surfaces and their centers along the depth and time axes.

Our study of how the species in the limnetic community of Mirror Lake relate to one another has led us to conclude that each species has its own position or niche, with a central location that differs from those of other species. This division of the niche hyperspace now apparent in the zooplankton of Mirror Lake is a result of evolutionary processes including reduction of competition, predation, competitive displacement, and possible extinction of species in the past. We consider the limnetic zooplankton community of Mirror Lake to be structured as a system of interacting populations, whose niche centers have evolved toward dispersion in relation to the complex gradients of depth, time, and food within the ecosystem.

We believe that studies of the density, behavior, and metabolism of all zooplankton species interacting within the multitude of environmental variables in an aquatic ecosystem are required to unravel the complex relationships between organisms in a community. The macroscopic properties that Lane refers to (*1, 12*) express the occurrence of species in samples, not species interactions. At best, these measures may permit interesting comparisons of communities. We think that community research should, when it can, go beyond expressing only the apparent degree of structure and should investigate how communities are structured. We hope that our studies have contributed to that end.

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11. Similarly, D. W. Schindler [in *Productivity Problems of Freshwaters*, Z. Kajak and A. Hillbricht-Ilkowska, Eds., proceeding of the International Biological Program Unesco Symposium, Kazimierz Dolny, Poland, May 1970 (P.W.N./Polish Scientific Publishers, Warsaw, 1972), pp. 311–331] G. E. Likens and J. J. Gilbert [*Limnol. Oceanogr.* **15**, 816 (1970)] have noted that small mesh nets are needed to obtain quantitative samples of rotifers. H. H. Bottrell *et al.* [*Norw. J. Zool.* **24**, 419 (1976)] suggested that volume samples, such as obtained with water bottles, are probably the most accurate in that they give the highest densities of rotifers and crustaceans. A. Karabin [*Bull. Acad. Pol. Sci. Cl. 2 Ser. Sci. Biol.* **19**, 197 (1971)] observed that the density of *Leptodora kindtii* was up to eight times larger in a volume sampler than in net hauls.
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13. Our productivity measurements did include the naupliar, copepodid, and adult stages of all the copepods, except *Tropocyclops prasinus*, which was not included in (*2*) because it represented less than 0.2 percent of the total productivity of the zooplankton community (*8*). We have included this species in Fig. 2. *Epischura lacustris* was observed in a different location than our usual sampling point in a year prior to the reported study (*2*).
14. G. G. Winberg, in *Productivity Problems of Freshwaters*, Z. Kajak and A. Hillbricht-Ilkowska, Eds., proceedings of the International Biological Program Unesco Symposium, Kazimierz Dolny, Poland, May 1970 (P.W.N./Polish Scientific Publishers, Warsaw, 1972), pp. 363–382.
15. A seasonal periodicity of species occurrence, biomass, and productivity of zooplankton are well documented in the literature [(*8, 14*); see also G. E. Hutchinson, *Treatise on Limnology* (Wiley, New York, 1967), vol. 2]. As part of the succession of species populations of zooplankton with time, there would be different degrees of interactions with different species. For example, some omnivorous species can change their feeding mode several times in a year's time (*1*). Over an annual cycle, the composition and density of potential prey and competitors are continually changing with time. In general, biological, physical, and chemical components of the ecosystem produce a multitude of environmental variables integrated to form a functioning whole. Seasonally, species populations of the zooplankton community are subjected to and interact within a range of these environmental variables. To analyze niche division and community structure effectively, the sampling scheme must attempt to consider seasonal succession.
16. The bell-shaped distribution of niche response surfaces of zooplankton in Mirror Lake is similar to the bell-shaped distribution observed for the blue-gray gnatcatcher in oak woodlar [R. B. Root, *Ecol. Monogr.* **37**, 317 (1967)].
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19. We thank S. Levin and R. H. Whittaker for critical comments and discussion.

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