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Environmental Variables Affecting Small-Scale Distributions of Five Rotifer Species in Lancaster Lake, Michigan[1]

Abstract

The small-scale distributions of the rotifers *Polyarthra vulgaris*, *Synchaeta stylata*, *Conochilus unicornis*, *Hexarthra mira*, and *Asplanchna priodonta* were investigated in Lancaster Lake, Cheboygan County, Michigan, July 21, 1974. Measurements were taken for 13 depths (at 1-m intervals) and at 4 times of the day (1:00 AM, 7:00 AM, 1:00 PM, and 7:00 PM). In addition, the abundances of 6 crustacean, 2 planktonic dipteran, and 10 algal species, as well as temperature, light, oxygen, chlorophyll *a*, alkalinity, pH and free carbon dioxide were measured. Whereas abiotic factors appeared to control large scale occupation of the lake, and excluded most species from the deeper portions of the hypolimnion, small-scale distributional variation of the rotifers depended upon biotic interactions, particularly with the crustacean zooplankton.

Contents

1. Introduction

Although species distributions in the crustacean zooplankton have been well documented in a number of extensive lake studies, information concerning diurnal migration, vertical distribution and horizontal patchiness in the Rotatoria remains very incomplete. Notable contributions have been made by BERZINS (1958), CAMPBELL (1941), KOSICKI (1960), GILYAROV (1965), and DUMONT (1972), as well as LARSSON (1971), PEJLER (1957, 1965), RUTTNER-KOLISKO (1974, 1975a, 1975b), RUTTNER (1905, 1943), and GEORGE and FERNANDO (1969, 1970). However, these works have left unclear the relative effects of chemical and physical variables, and particularly of biotic interactions, upon small-scale rotifer distributions. The present study attempts to identify those variables and their correlations with the abundances of *Polyarthra vulgaris*, *Synchaeta stylata*, *Conochilus unicornis*, *Hexarthra mira*, and *Asplanchna priodonta*.

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[1] This paper represents a contribution from The University of Michigan Biological Station.

2. Materials and Methods

Lancaster Lake, Cheboygan County, Michigan (N 45° 37', W 84° 43'), possesses a distinct thermocline and clinograde oxygen curve during the summer months, and is colored with limno-humic acids, derived from drainage through adjacent cedar swamp vegetation. The light compensation depth is approximately 4 m. The lake is of ice block origin, having a single basin with maximum depth of 17.4 m and a surface area of 9.8 ha. In some years the lake displays meromixis, attributable to its low surface-to-volume ratio and wind sheltered location.

Samples for physicochemical measurements were collected with a 3-liter Kemmerer bottle at 1:00 AM, 7:00 AM, 1:00 PM, and 7:00 PM, July 21, 1974, at 1-m intervals to a depth of 12 m. Two hundred ml from each sample were preserved in Lugol's solution for phytoplankton enumeration. Temperature was measured with a standard resistance thermometer, and total light penetration was recorded with a submarine photometer equipped with a Weston cell. Dissolved oxygen was determined titriometrically by the ALSTERBERG (Azide) modification of the WINKLER method (APHA 1971). Total alkalinity was determined titriometrically (APHA 1971), pH obtained with a Beckman model N field pH meter, and free carbon dioxide calculated from the pH and alkalinity data with a nomagraph. Chlorophyll a concentrations were determined with a Turner Model III fluorometer (HOLM-HANSEN et al. 1965).

Zooplankton samples were obtained with a 12.8-liter SCHINDLER-PATALAS plankton trap. The zooplankton were anaesthetized with carbonated water and preserved with 5% buffered formalin.

Two counting techniques were employed for the zooplankton. Total counts of each sample were made of the less abundant species (*Daphnia pulex*, *Chaoborus* spp., *Bosmina longirostris*, *Asplanchna priodonta*, *Diaptomus reighardi*, *Tropocyclops prasinus*, *Mesocyclops edax*, *Cyclops bicuspidatus thomasi*) with the use of a modified BOGOROV counting chamber (GANNON 1971).

Polyarthra vulgaris, *Hexarthra mira*, *Synchaeta stylata*, *Conochilus unicornis* and the copepod nauplii were counted by first reducing all samples to 50 ml; three 1-ml subsamples were then extracted with an automatic pipet and combined in a plexiglass counting cell (STEMBERGER 1974). Two such pooled subsamples were used, resulting in coefficients of variation below 10% for all but the very small mean values.

Phytoplankton counts were performed with a .01-ml PALMER-MALONEY counting chamber (STEIN 1973). Samples were adjusted to 5.0 ml and enumerated under a compound microscope (430 X). Three, or occasionally two, subsamples were counted; coefficients of variation rarely exceeded 15%.

3. Results

The diel distributions of the plankton species studied (figs. 1 and 2) indicated that more than 90% of their abundances (with the significant exceptions of *Cryptomonas erosa* and the small flagellates *Chlamydomonas* and *Rhodomonas* spp.) existed in the upper 9 m of the water column. Values included in the data analysis (Tables 1 and 2) refer to samples taken from 0—9 m. All species abundances were log-transformed to improve normality.

Temperature, oxygen, and free carbon dioxide (fig. 3) were highly intercorrelated; a single principal component (PC) accounted for 91.5% of their observed variance (PC = .59 Temp. + .56 Oxy − .58 CO_2; eigen value = 2.744). Separate effects of these three variables could not be dissociated. The single resultant variable, however, is highly correlated with the relative exclusion of most plankton species from the deeper portions of the hypolimnion.

Most of the plankton species distributions were consistent with previous literature. *Daphnia pulex*, *Diaptomus reighardi* and the two species of *Chaoborus* (*C. flavicans*, *C. punctipennis*) all showed pronounced upward migration at night. The adult *Cyclops bicuspidatus thomasi* were consistently found in the hypolimnion; cyclopoid copepodids, in contrast, were largely found in the epilimnion and thermocline. Cope-
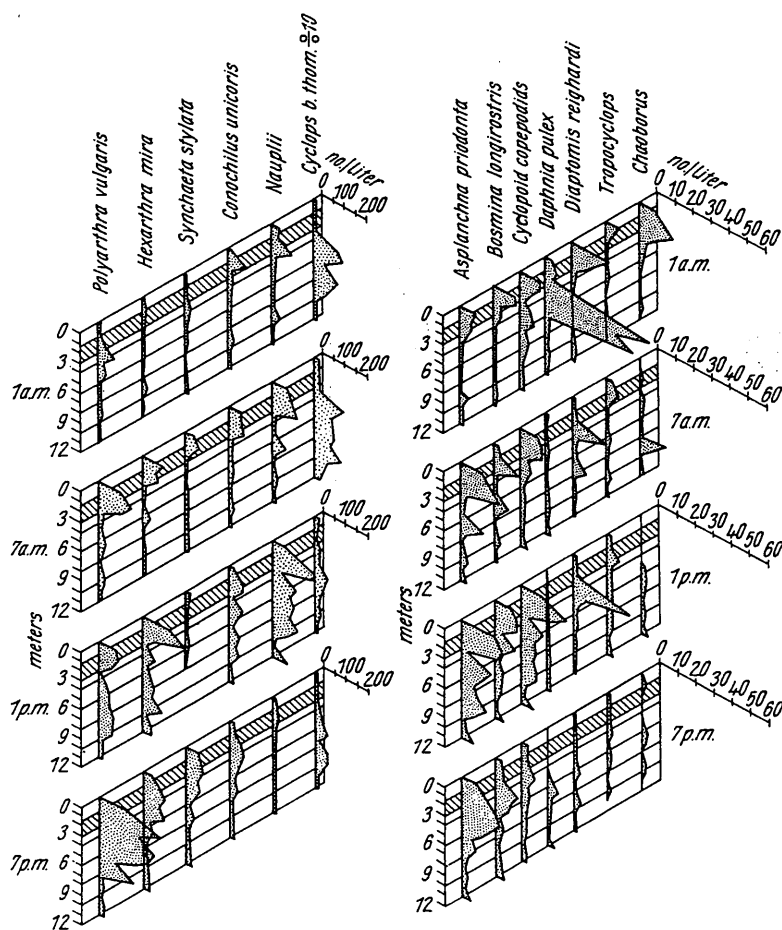
Fig. 1.   Abundances of the major zooplankton species for 13 depths and 4 times of the day in Lancaster Lake, Michigan, July 21, 1974. Termocline indicated with hatching.

pod nauplii were distributed, like the rotifers, in the upper portion of the water column.

The high concentrations of chlorophyll a in the hypolimnion (fig. 4), below light levels detectable by the Weston submarine photometer, are attributed to Cryptomonas erosa and Chlamydomonas and Rhodomonas spp., which are known facultative heterotrophs (HUTCHINSON 1967). Cryptomonas erosa was a major component of ILMAVIRTA's (1974) study of the diel periodicity of phytoplankton in Lake Pääjärvi, Finland. A marked downward migration during the daylight hours, similar to the pattern shown in the present study, was attributed to negative phototaxis. Most other algal species, particularly the diatoms, were concentrated at or above the bottom of the thermocline.

The distributions of the five rotifer species displayed considerable similarity (Table 1). A summation of the five species abundances for each sample was correlated with the distributions of the crustacean zooplankton and with physical/chemical variables (Table 2).

The small filter-feeding crustacea Bosmina longirostris, Tropocyclops prasinus, and the copepod nauplii similarly showed a high degree of intercorrelation. This
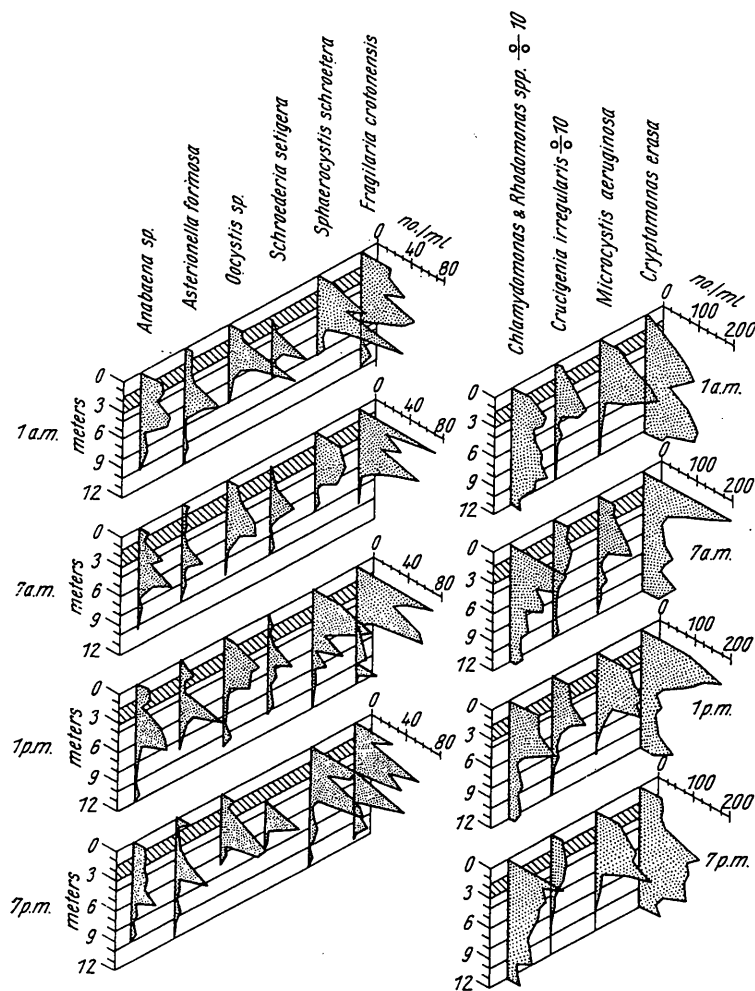
Fig. 2. Abundances of the major phytoplankton species for 13 depths and 4 times of the day in Lancaster Lake, Michigan, July 21, 1974. Thermocline indicated with hatching.

"small crustacean" community, consisting of the summed abundances of the three taxa, showed high correlation with the rotifers. Rotifer abundances also showed high, but less consistent, positive correlations with chlorophyll a and an inverse relationship with adult *Cyclops bicuspidatus thomasi* and *Diaptomus reighardi*. Whereas the small zooplankton species were highly associated in their distributions, the large crustacea were much less closely associated (fig. 4).

4. Discussion

The five rotifer species chosen for the study are all common components of freshwater lakes in North America. *Conochilus unicornis* displayed slight diurnal migration in lake 122 of the ELA lakes (SCHINDLER and NOVÉN 1971), with maxima both at the surface and at 4 meters. RUTTNER (1905) reported that the species rose to the surface
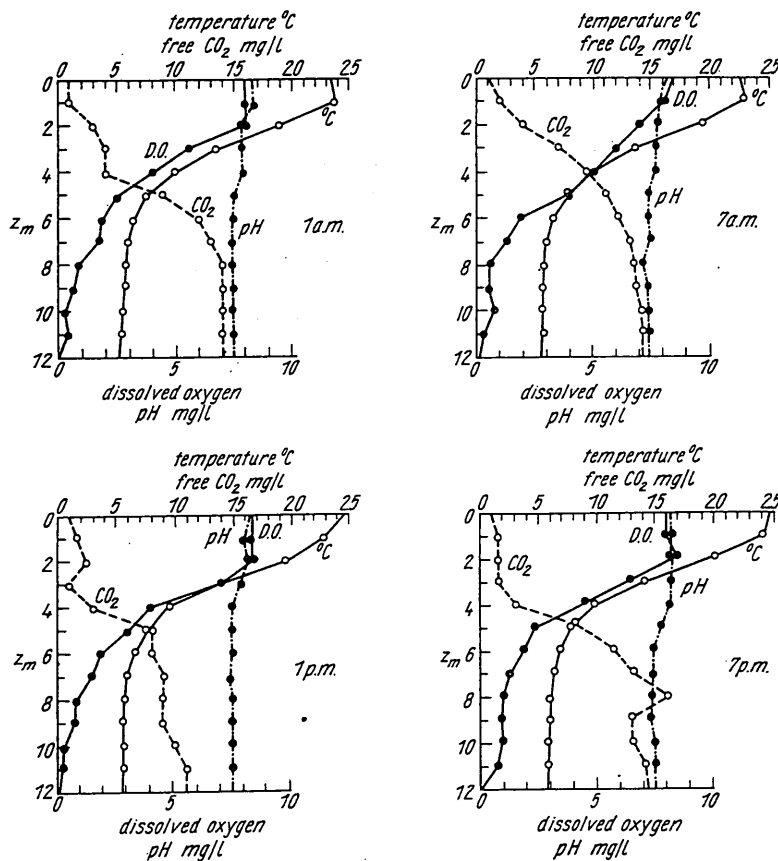
Fig. 3. Physical and chemical measurements taken concurrently with the plankton samples for 13 depths and 4 times of the day in Lancaster Lake, Michigan, July 21, 1974.

at night in the Grosser Plöner See. The species is a detritivore (NAUWERCK 1963) or nannoplanktivore, and possesses malleoramate trophi. The population in Lancaster Lake was concentrated near the surface at night, but was more uniformly distributed in the water column during the daylight hours.

SCHINDLER and NOVÉN (1971) reported that *Polyarthra vulgaris* occupied the lower depths (6—10 m) of lake 122 on June 21, 1968, and the top three meters on August 26, 1968. GEORGE and FERNANDO (1969) noted that the *P. vulgaris* population of Sunfish Lake, Ontario, remained in the hypolimnion during the months of June and July after stratification had occurred, but consistently occurred in the epilimnion during August and September. Oxygen depletion in the hypolimnion was the most probable cause for this change. They also observed that the species exhibited an early evening migration to the surface in June, July, August, and February, with subsequent sinking during the night, but a reverse pattern in March and April. They suggested that temperature, oxygen, and light regimes may have initiated this migratory behavior. PENNAK's (1944) study of five lakes in Colorado failed to uncover diurnal migration of any sort by the species. BERZIN's (1958: discussed in HUTCHINSON 1967) study of Lake Skarshultsjön described maxima in the epilimnion. PEJLER (1957) suggested that the species is more positively phototrophic than most planktonic roti-
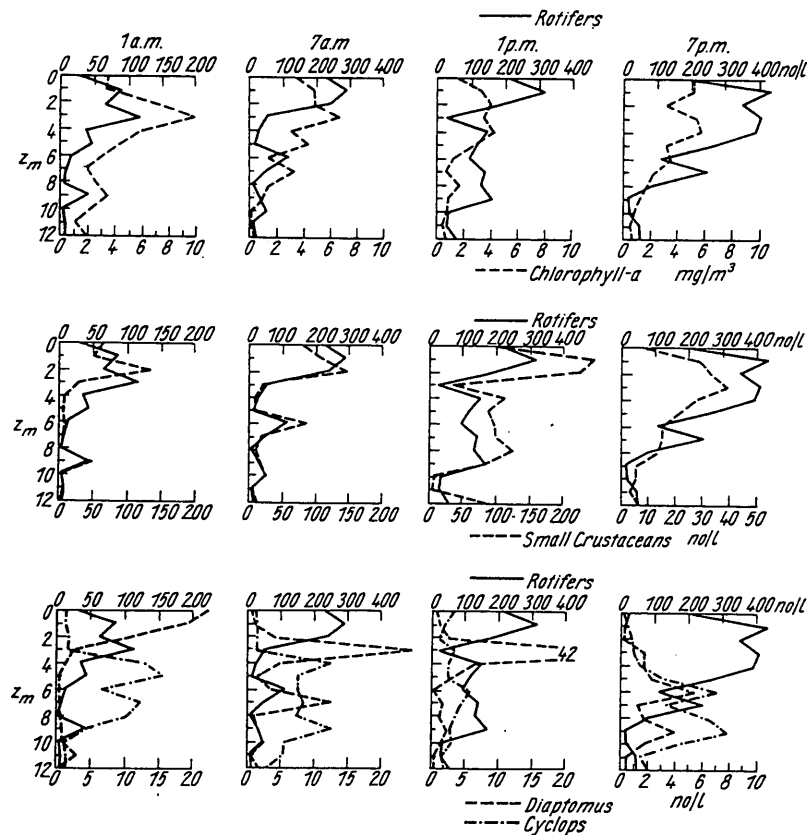
Fig. 4. Comparisons of the microdistribution of the rotifer community with chlorophyll a concentration, the distribution of the small crustacea, and the distributions of two dominant, large copepod species in Lancaster Lake, Michigan, July 21, 1974.

Table 1. Correlation matrix of log-transformed rotifer distributions, July 21, 1974, in Lancaster Lake. (Absolute values exceeding .402 indicate significance at $P < .01$)

	Polyarthra	Synchaeta	Hexarthra	Conochilus	Asplanchna	Total Rotifers
Polyarthra	1.000					
Synchaeta	.738	1.000				
Hexarthra	.813	.555	1.000			
Conochilus	.707	.437	.846	1.000		
Asplanchna	.759	.524	.913	.874	1.000	
Total Rotifers	.858	.635	.935	.895	.973	1.000

fers, and, like GEORGE and FERNANDO (1960, 1970), attributed its exclusion from the hypolimnion in late summer to oxygen depletion. Our data support GEORGE and FERNANDO's observations of a nighttime sinking. *P. vulgaris* is termed a specialist upon the larger cryptomonads (EDMONDSON 1965). Similar observations were made by POURRIOT (1965), who also cited the work of earlier authors. The high numerical abundance of *P. vulgaris* in Lancaster Lake at a time when *Cryptomonas erosa* was a dominant phytoplankter is considered significant. NAUWERCK (1963) has suggested that the species may utilize smaller particles as well.

Table 2. Correlation matrix of the rotifer community, crustacean species, and environmental variables. (Absolute values exceeding .402 indicate significance at $P < .01$)

	Total Rotifers	Diaptomus	Cyclops	Mesocyclops	Copepodids	Daphnia	Chaoborus	Bosmina	Nauplii	Tropocyclops	Chlorophyll a	Diss. Oxygen	Temperature	Free CO$_2$	Light
Total Rotifers	1.000														
Diaptomus	.124	1.000													
Cyclops	−.672	−.121	1.000												
Mesocyclops	.224	.737	−.101	1.000											
Copepodids	.526	.067	−.344	.263	1.000										
Daphnia	−.410	.026	.486	−.138	−.209	1.000									
Chaoborus	−.149	.260	.159	.076	−.145	.689	1.000								
Bosmina	.834	.356	−.569	.752	.579	−.326	−.032	1.000							
Nauplii	.732	.272	−.458	.461	.686	−.384	−.046	.760	1.000						
Tropocyclops	.729	.385	−.398	.417	.615	−.255	.005	.752	.883	1.000					
Chlorophyll *a*	.164	.175	−.439	.081	.113	.049	.106	.173	−.036	−.012	1.000				
Diss. Oxygen	.492	.236	−.641	.224	.442	−.235	.039	.493	.339	.339	.699	1.000			
Temperature	.549	.150	−.769	.145	.541	−.357	.007	.534	.453	.381	.552	.862	1.000		
Free CO$_2$	−.592	−.170	.753	−.169	−.568	.409	−.061	−.620	−.490	−.441	−.454	−.820	−.933	1.000	
Light	.499	−.161	−.527	.005	.514	−.616	−.417	.368	.462	.291	.165	.519	.717	−.712	1.000

THIENEMANN (1919) observed that *Hexarthra mira* exhibited a marked downward movement at nightfall in the Ulmener Maar. MIRACLE (1974) made reference to the colonization of the hypolimnion by this species during the summer months in Banyolas Lake, Spain. Diurnal migration for the species was not evident in Lancaster Lake. The species possesses malleoramate trophi similar to those of *Conochilus unicornis*, with which its distribution was also highly correlated.

HUTCHINSON (1967) describes *Synchaeta stylata* as a late summer species. The population in Lancaster Lake migrated 2–3 m downward at night, as did *P. vulgaris*. Both species possess virgate trophi, and their food selection might be expected to be similar. Three other species of the genus have been raised successfully on *Cryptomonas ovata* in the laboratory by POURRIOT (1965), who also mentions *Mallomonas* and centric diatoms as part of the Synchaetid diet.

Asplanchna priodonta exhibited reverse migration in Lake Donk (DUMONT 1972), probably a result of interspecific avoidance of the coexisting crustacean species. The species was concentrated at the surface at night in Lancaster Lake, with maximum concentrations several meters below the surface during the daylight hours. *A. priodonta* is a well known predator upon smaller rotifers such as *Keratella* and *Brachionus*, apparently capturing its prey by "random encounters" (POURRIOT 1965), but consumes a wide variety of large algal species, including *Peridinium* and some diatoms (NAUWERCK 1963) as well. The distribution of *A. priodonta* followed very closely that of the algivorous rotifers in Lancaster Lake.

Microdistributional variation in rotifer abundance was considerable in Lancaster Lake, as well as in previous lakes studied. Such variation is unexplainable solely in terms of such smoothly changing variables as temperature, oxygen, or light. RUTTNER-KOLISKO (1975a) has stated: "One gets the impression that the migration pattern is not specific for a particular species, but changes from one lake to the other, and also within one biotope, according to the momentary environmental situation." Our results suggest that such microdistributional variation may be a function of biotic interactions with other plankton species.

The microdistributional correlations between species in Lancaster Lake may imply a number of cause-effect relationships:

(1) Predators may be found together with their prey, but eliminate the prey species at very low rates, generating a high positive correlation. Such a relationship is hypothesized as the cause underlying the high positive, though inconsistent, relationship between the rotifers and phytoplankton biomass assessed as chlorophyll *a*. The work of NAUWERCK (1959) and ERMAN (1956) suggests that rotifers may filter about .001 ml of water per hour. Thus, even at the highest rotifer densities observed, reduction of algal standing crop would be minimal.

(2) Predators may be capable of locating their prey, but eliminate the prey species at sufficiently rapid rates to generate a high negative correlation. The high negative correlation of adult *Cyclops bicuspidatus thomasi* with the rotifer community in Lancaster Lake might be interpreted as such a relationship. Experimental studies of feeding rates by *C. bicuspidatus thomasi*, however, indicate an average rate of less than 1 (McQUEEN 1969) to as many as 6 (ANDERSON 1970) prey per predator taken per day, an amount hardly sufficient to account for high mortality in the rotifers, and not a sufficient explanation of the inverse correlation.

(3) Prey species may detect and avoid concentrations of potential predators. Implied by such a relationship are both the sensory perceptive capacities and motility for avoidance by the prey species. DUMONT (1972), in a study of the reverse migration of *Asplanchna priodonta* in the shallow eutrophic Lake Donk, Eastern Flanders, Belgium, suggested that the "stimulus [for reverse migration] might very well be within the organisms themselves, i. e., that the presence of one species in large numbers

might force the other to behave in an unusual way." DUMONT concluded that the avoidance reaction by *Asplanchna* was proportional to the "robustness" of the crustacean species. STRICKLER and BAL (1973) have demonstrated the existence of such mechanoreception and behavioral avoidance reactions in the crustacean copepods. The existence of similar sensory capacities appears highly plausible in most zooplankton species. The maximum rate of vertical migration of *P. vulgaris* has been calculated (GEORGE and FERNANDO 1970) at about .3—.4 m/hour. The fins of *Polyarthra* may permit escape from predators (ALLEN 1968). The appendages of *H. mira* may have a similar function. The extent to which escape velocities exceed normal swimming and the duration of such behavior are unknown, however. In a heterogeneous environment consisting, apparently, of very small patches, the avoidance capacities of even the relatively weak swimming rotifers and small crustacea is likely to be significant.

(4) Organisms may be correlated indirectly, either positively or negatively, by their mutual response to a third environmental variable. For example, whereas late instar *Chaoborus* larvae are known predators upon smaller *Daphnia* (FEDERENKO 1975a, b), the high positive correlation between them is better interpreted as a mutual response to light.

(5) Reproduction in the phytoplankton (VOLLENWEIDER 1969) and smaller zooplankton species (ALLAN 1976) may be important in determining large-scale variations in species abundances. Egg development time in *Hexarthra fennica* (RUTTNER-KOLISKO 1975b), for example, is halved with each 5 °C increase in temperature; assuming a similar relation in other rotifer species, reproductive capacity near the surface of Lancaster Lake may be more than four times as great as in the hypolimnion.

Reproduction related to temperature can be important in generating high correlations between species on a large scale, but is unsatisfactory in explaining microdistributional patchiness within a particular species. Differential reproduction due to differences in food availability is also too slow to account for diel microdistributional variation.

(6) Horizontal or vertical transport due to currents may induce significant correlations as a result of differential swimming ability of organisms desiring to maintain a preferred environmental condition such as temperature or light level. Because of Lancaster Lake's wind-sheltered location, the effects of wind-generated currents on distributions are probably minimal, especially below 2 m in the metalimnion.

The high positive and negative correlations between species abundances in Lancaster Lake (Figs. 1 and 2) suggest that biotic interactions may strongly modify basic behavioral responses to such physico-chemical conditions as light and oxygen concentration to the extent that future studies of vertical distribution must be synecological in approach, considering all major components of the plankton community.

5. Summary

The diurnal microdistributional patterns of 5 species of rotifers were examined in Lancaster Lake, Michigan on July 21, 1974. A total of 24 physical, chemical and biotic variables most relevant to the rotifer distributions were measured. The following conclusions emerge:

(1) Considerable patchiness, both horizontal and vertical, was evident for all plankton species.

(2) The large scale and microdistributions of the rotifers, including the predacious *Asplanchna priodonta*, were highly similar.

(3) The small crustacea (*Bosmina, Tropocyclops,* and the copepod nauplii) were highly correlated with the distribution of the rotifers.

(4) All of the small zooplankton species exhibited inverse correlations with the large crustacea, particularly the predatory copepod *Cyclops bicuspidatus thomasi*. They also showed positive, but inconsistent, correlations with phytoplankton concentrations.

(5) Whereas abiotic factors such as temperature and oxygen undoubtedly excluded the rotifers as well as other zooplankton species from the lower portion of the water column, microdistributional variation from the epilimnion to the upper waters of the hypolimnion could best be explained in terms of interactions between plankton species.

(6) Specifically, the reverse diurnal migration of rotifer species hypothesized by previous authors, which has been explained as a response to abiotic factors such as light, may be associated with avoidance of the larger crustacean species, and microdistribution should thus logically vary according to the constitution of the zooplankton community.

6. Acknowledgements

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