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THE INFLUENCE OF NATURAL PERTURBATION ON PROTOZOAN COMMUNITIES INHABITING ARTIFICIAL SUBSTRATES¹

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CAIRNS, J., JR., KAESLER, R. L., KUHN, D. L., PLAFKIN, J. L., YONGUE, W. H., JR. 1976. The influence of natural perturbation on protozoan communities inhabiting artificial substrates. *Trans. Amer. Micros. Soc.*, 95: 646-653. Polyurethane artificial substrates were positioned in a substrate-associated transect through littoral, sublittoral, and profundal sediments of Douglas Lake, Michigan. Substrates were also suspended in a vertical transect within the epilimnetic open water. Cluster analyses of species composition and statistical comparisons of species numbers indicated that distinct protozoan communities develop on each substrate, all manifesting characteristics of interactive equilibrium. The large differences in preoverturn species numbers and compositions between littoral-sublittoral sediments, profundal muds, and open waters clearly illustrate the distinctive nature of these environments in Douglas Lake. Following the major perturbation (autumnal overturn), there was a breakdown of competitive interactions with noninteractive colonization dynamics apparently determining the nature of each assemblage.

Thermal stratification in a lake causes a vertical zonation of the water column which can present a substantial physical boundry to the distribution of aquatic organisms, particularly microbes subject to passive dispersal. The breakdown of stratification as a result of the "turnover" of the water mass brings about a redistribution of certain materials and organisms within the larger system (Hofmann, 1975; Lund, 1971). Specific communities are exposed to a major change in chemical and physical conditions which can disrupt their functional integrity. Propagules may successfully colonize areas from which they might previously have been excluded. Lake basins also exhibit benthic zonation in which the designation of littoral, sublittoral, profundal, and pelagic zones is conventionally based on the physical dynamics, productivity, and species composition characteristic of each area. The purpose of this study was to investigate the distribution of protozoan species colonizing artificial substrates along a cross-sectional transect in Douglas Lake, Michigan, and determine any changes in this distribution associated with autumnal overturn.

METHODS AND PROCEDURES

On 18 July 1975, during the period of thermal stratification, a series of polyurethane foam substrates (PF units) identical to those used by Cairns & Yongue

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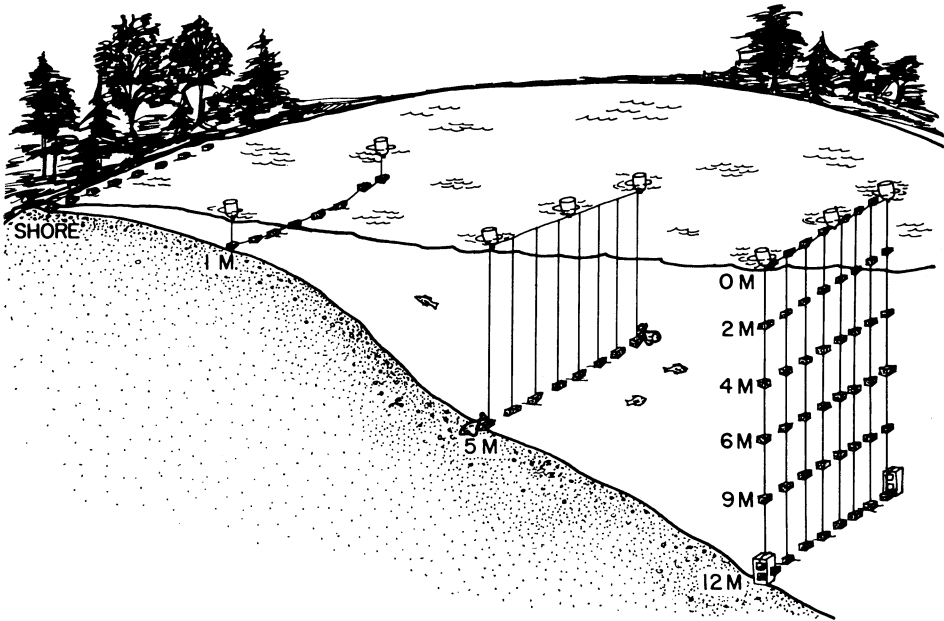


FIG. 1. Schematic diagram of substrate locations (SHORE, shore-water interface; 1 m, littoral sediments; 5 m, sublittoral sediments; 0, 2, 4, 6, 9 m, pelagic zone; 12 m, profundal sediments).

(1974) were placed in the pelagic zone of South Fishtail Bay, Douglas Lake, Cheboygan County, Michigan. Four PF units were harvested on days 1, 3, 6, 15, and 21 after initial placement and returned immediately to the laboratory. The PF units were then squeezed to extract as much material as possible. Four wet-mount slides were prepared from each sample and identifications were taken to species whenever possible using standard protozoology keys. Each slide was examined by systematically scanning from right to left from top to bottom, covering a 22×22 mm #2 coverglass, primarily with a "high dry" objective.

Additional PF units were positioned along eight transects in South Fishtail Bay, Douglas Lake on 16 August 1975. Each transect consisted of: (a) a vertical line suspended from surface floats and anchored in the sediments at a depth of 12 m; substrates were secured with string at the surface, 2 m, 4 m, 6 m, 9 m, and 12 m (bottom); (b) substrates were partially buried in the sediments at the shore-water interface, 1 m, and 5 m (see Fig. 1). The transects were aligned with the dominant epilimnetic current patterns (Gannon & Brubaker, 1969).

Four transects were harvested between 19 September and 21 September 1975. PF units were placed intact in wide-mouth, screw-capped jars, packed in insulating material, and shipped via air freight to Virginia Polytechnic Institute and State University. On arrival, PF units were squeezed and treated as previously described. All identifications of colonizing protozoa were completed within 48–60 hr of harvesting.

The fall 1975 overturn occurred in Douglas Lake on 29 October and the remaining four transects were harvested on 1 November and 4 November 1975. Harvesting, shipping, and identification procedures were the same as those for the preoverturn period. Again, all identifications were completed within 48–60 hr of harvesting.

TABLE I
Surface water chemistry on sampling dates

	Preovertum		Postovertum	
	12 Sep. 1975	21 Sep. 1975	2 Nov. 1975	4 Nov. 1975
Temp., C	15.8	16.0	10.5	10.3
Secchi M	3.2	3.25	3.75	3.75
DO mg/l	8.88	9.02	10.12	10.28
(% sat)	(91)	(93)	(93)	(94)
Alk (CaCO ₃) mg/l	117	117	121	122
Hard (CaCO ₃) mg/l	12	120	136	141
Conductivity μ umhos/cm 25 C	249	263	250	253
pH	8.55	8.48	8.37	8.37
Si μ g/l	1694	1709	1650	1640
Sol-P μ g/l	¹	9	3	3
Total-P μ g/l	12	12	11	11
NO ₂ + NO ₃ N μ g/l	26	6	7	3
NH ₃ -N μ g/l	12	39	37	22
Ca mg/l	29.09	29.35	29.85	29.66
Mg mg/l	11.20	11.05	10.84	11.02
K mg/l	0.63	0.65	0.71	0.70
Na mg/l	2.29	2.24	2.36	2.36
Cl mg/l	3.79	3.60	3.43	3.42

¹ Contaminated sample.

Because species number is a discrete variable, observations from each location for pre- and postoverturn were paired and averaged. The resulting data fits a normal distribution. These data were then analyzed with a two-way analysis of variance. All species were given a rank of 0.00, 0.25, 0.50, 0.75, or 1.00 at each sampling location, both pre- and postoverturn, depending on the number of samples in which they occurred (0, 1, 2, 3, or 4, respectively). A matrix of correlation coefficients was then computed in the Q-mode among all 18 samples from pre- and postoverturn. Three cluster analyses were computed from this matrix, all of them using the unweighted pair-group method with arithmetic averages (Sokal & Sneath, 1963). These cluster analyses were: (1) the nine sample groups (locations) from preovertum, (2) the nine sample groups from postoverturn, and (3) all 18 sample groups. These were computed separately to minimize distortion of similarity relationships. The coefficient of cophenetic correlation (r_{cc}) was used to assess the amount of distortion introduced due to averaging during the clustering process.

RESULTS

Thermal stratification of Douglas Lake was rather stable through 20 October 1975, when surface water temperature rapidly began to drop. During this time, the thermocline was located between 15–19 meters. On 29 October 1975, cold weather and high winds brought about overturn. Surface water chemistry for the sampling days is presented in Table I. There were significant differences in temperature and chloride concentration ($\alpha < .05$) between pre- and postoverturn. There was no sample evidence to indicate differences in the other parameters measured.

The number of species inhabiting the PF units differed significantly ($\alpha = .0001$) with location. Although overturn significantly increased ($\alpha = .0001$) overall numbers of species, the magnitude of its effect also varied significantly ($\alpha = .0002$) with location. Mean species numbers from each substrate location are listed in Table II. In order to further interpret this highly significant inter-

TABLE II
Mean species numbers at each substrate location

Location	Mean species numbers	
	Pre-overturn	Post-overturn
Shore-water interface	55.5	83.3
Littoral sediments	53.3	78.3
Sub-littoral sediments	47.8	70.8
Pelagic zone surface	49.3	60.0
2 meters	47.0	63.8
4 meters	37.3	58.0
6 meters	40.5	53.0
9 meters	35.5	60.8
Profundal sediments (12 meters)	29.5	13.1
OVERALL MEANS	43.9	60.1

action effect, single degree of freedom contrasts were performed separately on the pre- and postoverturn data. The results of these contrasts are summarized in Table III. PF units placed in the littoral and sublittoral sediments had significantly greater numbers of species ($\alpha < .0004$) than did the units placed in the open water, both pre- and postoverturn. Units placed in the sublittoral sediments at 5 m differed significantly ($\alpha = .0262$) from the units in the littoral sediments only after overturn. Surface and 2 m open water units were significantly different ($\alpha = .0016$) from the 4, 6, and 9 m units before overturn, but there was no difference between these after overturn. In addition, the units placed in the flocculent black ooze of the profundal zone (12 m) were significantly different ($\alpha = .0001$) from all of the other units.

The cophenetic correlation coefficients which measure introduced distortion in the clustering process were, in all instances, higher than 0.9. This indicates there was very little distortion in the clusters. The Q-mode dendrogram (Fig. 2) computed from all 18 sample groups shows good separation between the pre- and postoverturn samples. Species compositions of shore and 1 m sediments are more similar to all other locations after overturn than they were before overturn. Species such as *Trinema complanatum* Leidy, *Diffugia acuminata* Ehr., *D. urceolata* Carter, *Hyalosphenia papilio* Leidy, *Cyphoderia ampula* Ehr., for example, were found only in these littoral sediments. Although this dendrogram also shows that following overturn the profundal sediments are very different from

TABLE III
Statistical comparisons of substrate locations with respect to numbers of colonizing protozoan species

Location contrast	Preoverturn	Postoverturn
1. Sediments vs. open water	$\alpha = .0003$	$\alpha = .0001$
2. 0, 2 meter open water vs. 4, 6, 9 meter open water	$\alpha = .0016$	N.S. ¹
3. Shore, 1 meter sediment vs. 5 meter sediment	N.S.	$\alpha = .0262$
4. All vs. 12 meter open water (sediment)	$\alpha = .0001$	$\alpha = .0001$

¹ N.S. = no sample evidence to conclude a difference.

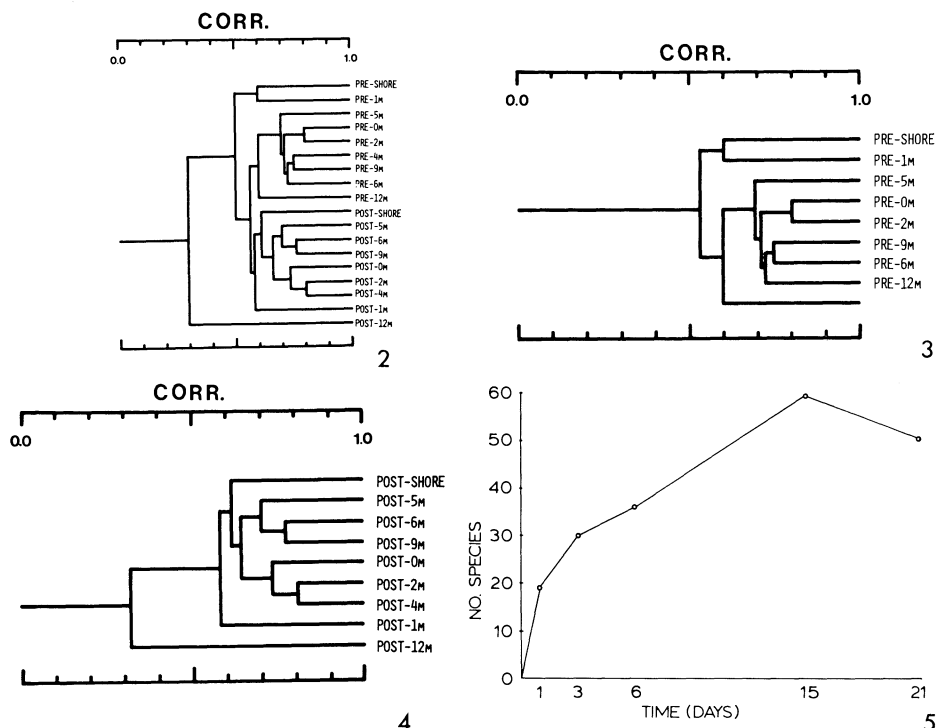


FIG. 2. Q-mode dendrogram prepared by the unweighted pair-group method with arithmetic average (UPGMA) from a matrix of correlation coefficients computed among samples from pre- and postoverturn; cophenetic correlation coefficient (r_{cc}) = 0.902. Fig. 3. Q-mode dendrogram (UPGMA) prepared from a matrix of correlation coefficients computed among samples from preoverturn; r_{cc} = 0.929. Fig. 4. Q-mode dendrogram (UPGMA) prepared from a matrix of correlation coefficients computed among samples from postoverturn; r_{cc} = 0.962. Fig. 5. Colonization curve of surface substrates during stratification.

every other location, this result is somewhat artificial, since the substrates were apparently covered by the flocculent sediments which became anoxic during stratification. The detectable presence of H_2S in the samples indicated that the overturn did not reoxygenate the portion of these sediments where the substrates were located. Of the few species found in these substrates, all were those generally classified as sapropelic or polysapropelic (Kahl, 1930-1935; Kudo, 1966) (*Chaenomorpha capucina* Blochmann, *Heteronema acus* Ehr., *Glaucoma scintillans* Ehr., *Cyclidium obliquum* Kahl, *Chaena limicola* Lauterborn).

The dendrogram for preoverturn samples (Fig. 3) shows there are distinct differences in composition among the various locations. There are four basic clusters having unique compositions: (1) shore-water interface; (2) 1 m, littoral sediments; (3) 12 m, profundal sediments; (4) all remaining locations. Within the fourth cluster there are three other clusters which can also be considered unique. These are the 5 m, sublittoral sediments, 0 and 2 m pelagic water, and the 4, 6, and 9 m pelagic locations. There is a distinct stratification in species composition in the pelagic water column. As indicated in Figure 4, these clusters change following overturn. Most importantly, there is a decrease in the similarity of all of the pelagic water locations, and the littoral sediments become more similar to the rest of the locations than they were prior to overturn.

The colonization of initially sterile PF units is shown in Figure 5. The number of species rises to a peak of 59 on day 15 and decreases to 50 on day 21.

DISCUSSION

The large differences in preoverturn species numbers and compositions between littoral-sublittoral sediments, profundal muds, and open water clearly differentiate these areas as distinct environments within the lake basin. These differences have generally been attributed to the greater spatial heterogeneity of the littoral zone (Wetzel, 1975), with bacteria (Olah, 1974), algae (Burns & Mitchell, 1974; Pieczynska, 1971), and other microorganisms (Neel, 1948) attaining their greatest diversities here.

Before overturn, there was no significant difference in species numbers between the littoral and sublittoral substrates. Each location had a highly unique species composition, but the sublittoral substrates most closely resembled PF units from the open water. Within the pelagic zone, there was a significant difference in species numbers above and below the 4 m line (Contrast 2, Table III); the composition clusters substantiated this demarcation. Unlike the communities of the littoral sediments, the *overall* compositional similarity of the pelagic substrates was quite high ($r = 0.71$).

The substantial differences in species numbers within the epilimnion before overturn could be considered the result of communities "fine tuning" to the subtle peculiarities of particular depths. (Potentially important environmental variables might be differential mixing due to subsurface currents and thermal seiches, the diminution in quantity and change in quality of solar energy with depth, etc.) These communities have undoubtedly had sufficient time (5 weeks) to develop the endogenous interactive mechanisms required for such adaptations (competition, predation). The colonization curve for surface substrates (Fig. 5) clearly illustrates this; utilizing the terminology of Simberloff & Wilson (1970), a non-interactive maximum species number (59) was reached by day 15 with the subsequent onset of the interactive phase of colonization marked by a reduction in species numbers. The fact that this maximum species number is equivalent to that attained by all pelagic substrates after overturn was probably not coincidental. These protozoan assemblages, having gained stability in physical space offered by the substrate, have very high reproductive rates relative to the period between major changes in the epilimnetic environment. As Hutchinson (1961) points out, such communities would be expected to exhibit competitive exclusion. Even without spatial constancy, however, Petersen (1975) has hypothesized that several phytoplankton species can exhibit true competitive equilibrium if they are collectively limited by an array of different nutrients.

Immediately after overturn, there was a highly significant increase in the number of species at all locations, with the exclusion of the profundal sediments. Cairns et al. (1971) observed a similar increase in species numbers after exposing established protozoan communities to dramatic physical disruption. Despite the increase, highly significant differences in species numbers between littoral-sublittoral sediments, profundal, and pelagic zones were retained.

Following overturn, the overall compositional similarity of the pelagic zone was substantially reduced (post $r = 0.64$; pre $r = 0.71$), with the preoverturn stratification in species numbers disappearing. The chemical-physical upheaval associated with overturn apparently disrupted the capability of these assemblages to differentially limit species numbers. One might speculate that ecological space again becomes available with this breakdown of competitive exclusion mechanisms, and noninteractive colonization dynamics take precedence in determining species numbers. All species are qualitatively equated with respect

to their capacities to occupy the newly available space. Species already inhabiting a particular substrate have the advantage accruing to pioneer occupants. Occupation of the remaining space is determined by a random draw from the available species pool (Gilroy, 1975). Cairns et al. (1976) noted a substantial reduction in compositional similarity among 10 replicate PF units from a single location following the 1974 fall overturn in Douglas Lake. Rapid changes in composition have also been observed to occur concomitantly with spring circulation and other catastrophic perturbations (Jassby & Goldman, 1974).

The disruption of competitive interactions also profoundly affects the species assemblages of the littoral and sublittoral sediments. Unlike the pelagic zone, the primary mechanisms of passive dispersal between the various areas of the sediments include differential sedimentation as well as turbulent mixing. The latter was probably the only important force affecting dispersal in the open water and would be essentially equivalent at all depths, particularly following overturn. Sedimentation, however, does tend to differentially deposit potential colonizers within the littoral and sublittoral sediments (Davis & Brubaker, 1973). Therefore, because potential colonists from other areas of the lake are deposited in greater abundances in these areas, sediment assemblages would be expected to exhibit quantitative differences in species numbers and become somewhat more similar to all other areas compositionally. This proves to be the case.

Of the sediment assemblages, those at the 5 m location most resemble those of the pelagic. In fact, they are included within the overall compositional cluster for the open water. The implication from preoverturn that the 5 m location exhibits characteristics of both the pelagic and benthic environments is thus reiterated. Finally, these conclusions imply that the profundal sediments would become inundated with a large number of species, primarily from the pelagic zone, which had been previously excluded. However, isolation of these substrates from the oxygenated water apparently eliminated any possibility of survival for all but the most specialized polysapropelic forms.

CONCLUSIONS

Protozoan communities developing on artificial substrates placed in lake sediments probably have competitive interactions similar to those of communities established on the surrounding natural substrate. Positioning of substrates in the open water, however, introduces an element of spacial stability unique within the pelagic environment. Assemblages of microorganisms which colonize these PF units are given the unusual opportunity to develop the types of endogenous interactive mechanisms required for "fine tuning" to the environmental variations at different depths.

In general, given areas which differ in environmental conditions (light availability, habitat diversity, etc.) and given that these conditions remain constant with respect to the reproductive rates of the organisms being considered, communities develop which adjust to these environmental differences by varying their species numbers and species compositions.

1. If these areas have different finite species pools and/or immigration pressures (number of species invading, number of individuals invading), then each can be considered a separate system. Shore, 1 m, and open water are thus distinct systems in this respect.

2. If the areas in question are contained within one system, then the communities that develop adjust to differing conditions by limiting species numbers. Species able to successfully compete for available resources will be retained—others will be excluded.

Drastic environmental perturbation such as lake overturn causes the partial or complete breakdown of interactive mechanisms. Simple functions of noninteractive colonization assume primary importance in determining the nature of particular assemblages.

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