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REALISM AND REPLICABILITY OF FRESHWATER LENTIC MICROCOSMS AS A FUNCTION OF WATER AGITATION

J. Harte, D. Levy, G. Lockett, J. Oldfather, J. Rees,
E. Saegebarth, and D. Schneider

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REALISM AND REPLICABILITY OF FRESHWATER LENTIC MICROCOSMS AS A FUNCTION OF WATER AGITATION

by

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April 1983

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INTRODUCTION

Microcosms can be defined as "experimental units designed to contain components of, and to exhibit important processes occurring in, a whole ecosystem" (Draggan & Reisa, 1980). Traditionally, microcosms have been used in chemical uptake studies (e.g., Wright, 1975), enrichment studies (e.g., Williams & Gray, 1970), and primary productivity measurements (e.g., Goldman, 1963). Such applications are typically of short duration (4-48 hrs.) and are carried out in small samples, of a few liters volume or less, from a natural system. More recently, larger microcosms have been proposed for use in longer term studies to determine effects of pollutants on ecosystem functions and species composition (Pilson, Oviatt, & Nixon, 1980; Giesy, 1980; NAS, 1981). A potential obstacle to such applications arises with the possibility that over longer time periods (weeks or months), microcosms may replicate poorly and their chemical and biotic behavior may diverge from the natural system from which they were derived. The results reported here contribute to the understanding of this obstacle.

In a series of experiments, we have been analyzing how the design of lentic freshwater microcosms and the conditions under which they are operated affect their replicability and realism (Harte, Levy, & Rees, 1983; Harte et al., 1981). A partial list of the factors that can affect lentic microcosm replicability and realism includes: container size and shape, light and temperature levels, rate of water agitation, rate of hydraulic flow-through, presence or absence of macroflora and macrofauna, and presence or absence of algal wall growth (Perez et al., 1977; Harte et al., 1981; Harte, Levy, & Rees, 1983). Perez et al. (1977) demonstrated that the degree of water agitation in estuarine microcosms effects significantly the degree to which these systems simulate the estuary from which they were derived. In the experiments described below, the ability of lentic freshwater microcosms to replicate well and to simulate accurately the pelagic epilimnion of a stratified reservoir is explored as a function of the degree of water agitation. Lessons learned from the previous studies concerning tank size, water temperature control, and the necessity for prevention of algal wall growth, are incorporated into the experimental design.

METHODS AND MATERIALS

General

Field. Briones reservoir, located in Contra Costa County, California, was used as the water source and field-comparison system for these experiments. Briones has an area of 2.8×10^6 m^2, a maximum depth of 70 m, and a volume of 8.4×10^7 m^3. Hydrologic input to this reservoir is from its watershed and via pipeline from Pardee Reservoir situated on the Mokelumne River in the foothills of the Sierra Nevada about 120 km to the east. The input replaces losses mainly due to evaporation. The average annual inputs from the watershed and from Pardee Reservoir are about 1% and 4% of the reservoir volume, respectively and thus, the reservoir is a relatively closed system. It is typically thermally stratified from spring through late autumn.

In 1981, an 8-week and a 6-week experiment were carried out. Experiment I (June 6, 1981 - August 20, 1981) used water taken in equal amounts from depths of 5 and 8 meters. During the course of the experiment the epilimnion depth was 8-10 meters and its depth-

integrated temperature increased from 18.5°C to ~20.5°C (Figure 1). Experiment II (October 21, 1981 - November 23, 1981) used water taken in equal amounts from 0, 5, and 10 meters. During this experiment the epilimnion depth was 15-20 meters and its depth-integrated temperature decreased from 17.6°C to 15° (see Figure 2). In both experiments, water was obtained approximately 100 meters from the nearest shore using a 12 liter Van Dorn bottle.

Laboratory. The water was placed in a large mixing tank in the laboratory, from which it was transferred by siphoning to each of the microcosms. Just prior to placement of the water in the mixing tank, the large zooplankton were removed by filtration (.75 mm mesh). These zooplankton were then added in equal amounts to each microcosm after the siphoning process was completed. Between the removal of the water from the reservoir and its installation in the microcosms, the elapsed time was less than four hours.

Macrofauna and macroflora were not included in the microcosms. Previous work has indicated that the inclusion of macrofauna in microcosms less than 10 m^3 volume reduces rather than increases the similarity of the microcosms to a pelagic system (Harte et al., 1980).

A benthic compartment was not included in the microcosms, because during times of stratification of a deep water reservoir such as Briones, the epilimnion is relatively isolated from the deep benthos. Furthermore, the influence of the littoral zone on the pelagic zone in Briones is slight (Harte et al., 1983). Nutrient

measurements in the reservoir were consistent with the notion that the epilimnion was relatively isolated during the course of experiments I and II.

All the microcosms were contained in cylindrical nalgene tanks (diameter = 33.0 cm; height = 70.5 cm), which were filled with 58 liters of water. Previous work has demonstrated that microcosms 50 liters, or larger best simulate pelagic surface water during times when that portion of the natural system was relatively isolated (Harte et al., 1981).

Each tank was housed in an insulated jacket of water. A water chiller was used to provide temperature control for each jacket of water. During the course of each experiment, the temperatures of the microcosms were maintained within $1^{o}C$ of the epilimnion depth-integrated temperature on a week by week basis (Figures 1 and 2).

Light was provided by high-output, full-spectrum, fluorescent tubes. The light:dark cycles were set to be commensurate with those experienced by the natural system, or 14h:10h for Experiment I and 11.5h:12.5h for Experiment II. Table 1 gives the light levels in the tanks for both experiments, as well as the midday light levels in the reservoir on August 3, 1981. By way of comparison, in Experiment I the light intensity was 2.4 watts/m^2 (PAR) for 14 hours/day at a depth of 18 cm in the tanks, while in the reservoir, the light intensity at midday was 37.5 watts/m^2 (PAR) at a depth of 5 m.

Build-up of surface growth in the tanks was prevented by transfer of the microcosm contents to a clean container each week.

Experimental Design

Three replicate tanks were used to study each level of agitation. In Experiment I, systems A were not agitated while systems D were agitated by pyrex stirring propellers (4 blades; r = 2.5 cm) inserted to a depth of 15 cm and rotated at ~600 rpm by standard stirring motors. Motors were on during light periods and off during dark periods. In Experiment II, systems A were not agitated. Systems B were agitated by air bubbling out of a capillary tube at a rate of 1 liter/min.; the tube extended 15 cm below the water surface. Systems C were agitated by slowly rotating (75 rpm) flat lucite paddles (20 cm x 7.5 cm x .5 cm) inserted to a depth of 23 cm. Systems D were agitated by rapidly rotating (600 rpm) teflon stirring propellers (3 blades, r = 2.2 cm) inserted to a depth of 23 cm. The stirring motors in systems C and D were on continuously.

Sampling and Measurement Procedures

Sampling was done weekly in the reservoir and in the microcosms. The two systems were sampled within a day of each other. In the reservoir, sampling was done from a small aluminum boat at approximately the same position from which the microcosm initiation water was obtained.

Field In Experiment I, samples were taken at 0, 5, 10, 15, 20, and 25 meters using a 1.7 liter Van Dorn bottle. Two samples were taken at each depth: one for zooplankton and large-phytoplankton counts and a second for small-phytoplankton counts and chemical meas-

urements. In Experiment II, reservoir samples were taken at 0, 5, 10, 15, 20, 25, and 30 meters using a 12 liter Van Dorn bottle. Again two samples at each depth were taken and their contents allocated as in Experiment I. The zooplankton and large phytoplankton water sample was immediately filtered through a plankton bucket fitted with a 64 μm Nitex straining net. The trapped organisms were rinsed from the net and preserved in Lugol's solution. From the water sample allocated for small phytoplankton counts, five cc subsamples were taken immediately and treated with Lugol's solution.

Laboratory For zooplankton and large-phytoplankton counts a 2 liter sample of water from each microcosm was filtered through the plankton bucket and the filtrate returned to the microcosm. The trapped organisms were treated with Lugol's solution as in the field. For small-phytoplankton counts and chemical measurements, a polyethylene tube was inserted into each microcosm to obtain a depth-integrated water sample. From this sample, subsamples for small-phytoplankton counts and chemical measurements were taken.

Measurements

The 5 cc phytoplankton samples were counted using a Leitz-Diavert inverted microscope and 5 cc counting chambers. Zooplankton samples were placed in 100 cc settling chambers and counted in a similar fashion. All phytoplankton and zooplankton samples were allowed to stand 24 hours before counts were made. Phytoplankton and zooplankton number and type (genus and species when possible) were recorded for the most abundant taxa.

Ammonia was determined by the indophenol reaction (Solorzano, 1969). Nitrate plus nitrite was determined by reduction and diazotization (Golterman, 1969). Dissolved silica was determined by the silico-molybate method (Strickland & Parsons, 1972), and dissolved oxygen was determined by the iodometric method (Wetzel & Likens, 1979). In the field, pH measurements were made with a Sargent-Welch (PBX) meter and matching electrode and in the laboratory with an Orion (601) meter and matching electrode. Total organic carbon was measured using a Dohrmann DC-80 TOC analyzer. Dissolved organic carbon (DOC) was defined as the total organic carbon content of filtrate obtained by filtering a sample of water through a rinsed Gelman, A/E, glass fiber filter (pore size $\simeq$ .3 μm).

The rate of gypsum dissolution was used as a measure of agitation levels (Perez et al., 1977) in the reservoir and in the microcosms. Small calcium sulfate (gypsum blocks) (~2.5 cm x 1.5 cm x .7 cm) were strung at various depths in the reservoir and tanks for periods of 23 to 48 hours. In the reservoir, the line with attached blocks was anchored to the bottom, while in the tanks it was suspended from above. The weights and dimensions of the blocks were noted before and after immersion. To carry out these measurements in the laboratory, the tanks were stocked with water from the reservoir epilimnion and their temperature maintained within 1°C of the depth-integrated temperature of the reservoir epilimnion.

Data Analysis

Tables 3, 4, 6, and 7 contain the taxonomic and chemical data from both experiments. In each experiment, data were averaged over two time intervals: Experiment I, weeks 1-5 and weeks 6-8; Experiment II, weeks 1-3 and weeks 4-6. For each variable and time interval, there are four entries in the tables. For the microcosms, $\bar{x}$ represents the average over time and over the three replicates within a given treatment system. For the reservoir, $\bar{x}$ represents the average over time and over the depths within the epilimnion from which the microcosms were initially stocked.

The second entry, σ^2, is related to the 90% confidence interval about $\bar{x}$ by

$$c.i.(90\%) = 3.3 \times \sigma.$$

For a specific variable, each data point was identified by the location (i) and time (α) it was taken. For the microcosms, i refers to a specific microcosm (within a replicate set) and in the reservoir i refers to a specific depth. The variance associated with each data point, $\sigma^2_{i\alpha}$, was determined using a combination of repeated measurements and assumed probability densities. For the chemical data guassian probability distributions were used while for the taxonomic data negative binomial probability distributions were used (Bliss & Fisher, 1953). The variance associated with an aggregated quantity (e.g., σ^2) is the sum of variances associated with individual data points used to construct the aggregate quantity, divided by the square of the number of data points summed over, or

$$\sigma^2 = \sum_{i=1}^{N} \sum_{\alpha=1}^{\gamma} \frac{\sigma_{i\alpha}^2}{(N \cdot \gamma)^2}$$

For the microcosms, the third entry, χ^2, is a measure of the replicability of data within each microcosm system. It is a chi-square statistic with N-1 degrees of freedom, where N is the number of replicates. It is defined by

$$\chi^2 = \sum_{i=1}^{N} \frac{(X_i - \bar{X})^2}{N \cdot \sigma^2},$$

where x_i is the time averaged value for the parameter of interest in the i'th replicate of a particular treatment system. For this statistic, the null hypothesis is that putative replicate microcosms are indistinguishable with respect to the variable being considered. For N=3, a $\chi^2 > 6.00$ would indicate rejection of this hypothesis at a significance level <.05. For the reservoir, χ^2, when given, is a chi-square statistic which indicates the variability with depth within the epilimnion.

For the chemical data, the fourth entry in the tables is an alternate measure of the replicability of the data within a given microcosm treatment system. It is the coefficient of variation, C.V., defined as

$$C.V. = \frac{\sqrt{\sum_{i=1}^{N} \frac{(X_i - \bar{X})^2}{N-1}}}{\bar{X}}$$

This method of assessing replicability is a reasonable alternative to the χ^2 method, when the standard deviation (σ) is small compared to variable's value (e.g., $\sigma / \bar{x} << .1$). For most of the chemical data this condition was satisfied, while it was not satisfied for the taxonomic data.

For the taxonomic data, the fourth entry, t, is a t-statistic. It characterizes the degree of similarity between a time-averaged variable's value averaged over a particular set of microcosms and averaged over depth in the reservoir epilimnion. This t-statistic has N-1 degrees of freedom and is defined by

$$t = \frac{(\bar{X}_R - \bar{X}_M)\cdot\sqrt{(N-1)}}{\sqrt{\sigma_R^2+\sigma_M^2}\cdot\sqrt{\chi_M^2}},$$

where the subscripts R and M refer to the reservoir and the microcosm system respectively. For this statistic, the null hypothesis is that the average value of a variable measured in a set of microcosms is indistinguishable from the depth-integrated value of the variable measured in the reservoir, and that within a given set, the microcosms are considered indistinguishable. For N=3, $|t| > 2.92$ would indicate rejection of this hypothesis at a significance level $<.10$ (two-sided test). This t-statistic was calculated for the chemical variables, but not listed in Tables 3 and 4 because in most cases it did not add information that was not obvious by inspection. Where needed in the results section, it is quoted directly in the text.

For either chemical or taxonomic data, two different sets of replicate microcosms can be compared using another t-statistic. It has 2(N-1) degrees of freedom and is defined as,

$$t = \frac{(\bar{X}_A - \bar{X}_B)\cdot\sqrt{2\cdot(N-1)}}{\sqrt{\sigma_A^2+\sigma_B^2}\cdot\sqrt{\chi_A^2+\chi_B^2}},$$

where the subscripts A and B refer to the two different sets of microcosms being compared. For this statistic, the null hypothesis is that the mean value of a variable measured in one set of microcosms is indistinguishable from the mean value measured in another set of microcosms, and that within a given set, the microcosms are considered indistinguishable. For N=3, $|t| > 2.13$ would indicate rejection of this hypothesis at a significance level $< .10$ (two-sided test).

Although the above statistics (χ^2 and the various t-statistics) are written down in terms of time-averaged quantities, they can also be used to compare variables observed at one time. The formulas remain unchanged except that the variables' values and their associated variances (σ^2's) at single times are substituted in the above formulas for the respective time-averaged quantities.

The rate of gypsum dissolution, K, was quantified using the expression

$$K = \frac{1}{2 \cdot T \cdot \rho_i^{1/3}} \cdot [W_i^{1/3} - W_f^{1/3}],$$

where T is the time period of immersion, ρ_i is the initial density of the gypsum block, and W_i and W_f are the initial and final weights, respectively, of the immersed block.

RESULTS

Table 2 contains the gypsum dissolution rates measured in the reservoir as a function of depth and measured in the microcosms as a function of different agitation levels. In both experiments, the dissolution rate in the most vigorously agitated microcosms, systems D, most nearly matched that measured in the reservoir epilimnion. The dissolution rate in the least agitated microcosms, systems A, was on the order of one-tenth that measured in the most agitated microcosms.

In both experiments, most of the chemical data (94% of data entries tables 3 and 4) exhibited good replication within a set of microcosms ($\chi^2 \leq 6.00$ and/or C.V. $\leq .10$). In the microcosms, the chemical variables in both experiments did not vary as functions of the level of agitation. As is seen in the tables, the differences measured in systems with different levels of agitation were small in magnitude and not systematic when considered as functions of agitation level. In particular, in Experiment I, differences between mean values of the chemical variables in the microcosms with different agitation levels were either < 1% or not statistically significant

($|t| < 1.50$, d.f. = 4). In Experiment II, differences between the chemical variables, except ammonia, in any two sets of microcosms with different agitation levels were < 3% or in the case of the nutrients < .2 μM. During weeks 4-6, the mean values of ammonia differed by ≤ 3 μM between any two treatments, but exhibited no systematic pattern with respect to agitation level.

Maximum differences in dissolved oxygen concentrations, DOC, TOC, and pH (Experiment II) between all sets of microcosms and the reservoir were small (<1.3 mg/liter, <100 μM(C), <100 μM(C), and < .18 respectively), non-systematic, and judged not to be of biological importance.

On the other hand, some of the other chemical variables did exhibit systematic differences between all sets of microcosms and the reservoir. In Experiment I, NH_4^+ and $NO_3^- + NO_2^-$ concentrations were systematically higher (7-10 μM(N); 3-8 μM(N) respectively) in the microcosms than in the reservoir, while pH values were lower ($|t| > 6.56$, d.f. = 2 for all the above variables). In Experiment II, NH_4^+ concentrations steadily increased in all sets of the microcosms, while remaining relatively constant in the reservoir. In the second time interval, the NH_4^+ concentrations were ≥5 μM(N) higher ($|t| > 3.75$, d.f. = 2) in the microcosms than in the reservoir. (Subsequent studies using deionized water have shown that an increase in NH_4^+ in the microcosms can be the result of airborn contamination in the laboratory. This contamination was eliminated in the deionized water studies by use of dust covers and an air filtration system.) During

Experiment II, dissolved silica concentrations in the reservoir epilimnion increased while remaining constant in all sets of the microcosms. In the second time interval, the dissolved silica concentration in the reservoir epilimnion was ~8 μM(Si) higher ($|t| > 46.7$, d.f. = 2) than in all sets of the microcosms. The increase in SiO_2 concentration in the lake epilimnion was accompanied by a decrease in hypolimnion SiO_2 concentration and a cooling trend in the epilimnion waters. Thus a source of SiO_2 was available to the lake epilimnion from the hypolimnion; no such source was available to the microcosms, which were initially stocked with epilimnetic water.

Table 5 displays the taxonomic groupings of the organisms counted. Only those taxa which were dominant with respect to volume density were tabulated. Unlike the chemical variables, some of the taxonomic variables in the microcosms did exhibit definite trends as a function of agitation method and level. The word "method" is used to distinguish agitation accomplished by mechanical means from agitation accomplished by bubbling or no agitation. "Level" refers to the rate of gypsum dissolution.

In both experiments, the taxonomic variables in sets of microcosms with no agitation (systems A) and agitation accomplished by bubbling (systems B) exhibited slightly better replication than did the mechanically agitated microcosms (systems C and D). In Experiment I, 67% of the taxonomic data entries for systems A exhibited good replication ($\chi^2 \leq 6.00$) compared to 50% in systems D (Table 6). In Experiment II, 93% and 100% of the taxonomic data entries in sys-

tems A and B respectively exhibited good replication compared to 75% in systems C and D (Table 7).

During the course of both experiments, cladoceran population densities in the mechanically agitated systems were lower than those in the unagitated or bubbled systems. In Experiment I, time-averaged cladoceran population densities in the mechanically agitated microcosms were ~1.8 times lower than those in the unagitated systems. The time-averaged number densities differed in the two systems by (3.3-7.0)/l ($|t| > 3.62$, d.f. = 4). Throughout Experiment II, time-averaged cladoceran population densities in the mechanically agitated systems were more than 6.4 times less than those in the unagitated and bubbled systems. The differences in the number densities were (1.2-3.0)/l ($|t| > 4.66$, d.f. = 4). Copepod and rotifer populations did not exhibit statistically separable patterns of dependence on method or level of agitation in either experiment.

In both experiments, diatom population densities exhibited systematic effects as a function of the method of agitation. During periods of constant or increasing populations, (weeks 1-5, Experiment I; weeks 1-3, Experiment II), both Stephanodiscus astraea and Fragilaria crotonensis time-averaged population densities were higher in the mechanically agitated systems than in the unagitated or bubbled systems. In Experiment I, the difference in number densities was 8.1 x 10^3/l ($|t| > 3.21$, d.f. = 4) for Stephanodiscus astraea and 278/l ($|t| > 5.03$, d.f. = 4) for Fragilaria crotonensis. In Experiment II, these two differences were (688-912)/l ($|t| > 2.62$, d.f. = 4) and

(241-419)/1 ($|t| > 2.65$, d.f. = 4) for Stephanodiscus astraea and Fragilaria crotonensis respectively. Assuming an average cell volume of 7.7×10^4 μm^3 for Stephanodiscus astraea and an average colony volume of 1.5×10^5 μm^3 for Fragilaria crotonensis, the above differences imply that the time-averaged volume density of diatoms in the mechanically agitated microcosms was (2-4)x higher than in the unagitated and bubbled microcosms.

In addition to these absolute differences in population levels, the ratio of the population levels of the two species was observed to depend on the method of agitation. The ratio of the time-averaged Stephanodiscus astraea number density to Fragilaria crotonensis number density was greater in the mechanically agitated systems than in the unagitated and bubbled systems. In both systems, no Stephanodiscus astraea was observed after the fifth week in the unagitated and bubbled microcosms, while it was present in the mechanically agitated microcosms throughout both experiments. Independent of the method or level of agitation, Fragilaria crotonensis was not observed in any set of microcosms after the seventh and fifth week in Experiments I and II respectively (Figures 1 and 2).

Unlike the diatoms, flagellates did not exhibit systematic or statistically separable patterns with respect to agitation treatment in either experiment. Also unlike the diatoms, they thrived throughout both experiments (Figures 1 and 2). Ceratium hirundinella was only observed in Experiment II. It did not exhibit any systematic or statistically separable pattern with respect to agitation

treatment. In all sets of microcosms, it decreased to low levels by the sixth week.

The taxonomic variables in the reservoir and one set of microcosms were plotted as functions of time for both experiments (Figures 1 and 2). These figures allow a qualitative comparison of trends observed in the reservoir and in the microcosms. In Experiment I, flagellates, Stephanodiscus astraea and Fragilaria crotonensis were the dominant by volume phytoplankton in the reservoir. Here, the most definitive trends with time of the taxonomic variables were a bloom of Fragilaria crotonensis and the steady increase of Stephanodiscus astraea during weeks 1-5. As exhibited in Figure 1, these same trends were observed in the mechanically agitated microcosms. Total diatom volume densities in these microcosms never differed from those in the reservoir at any time by more than a factor of two. In terms of the two species of diatoms, the major difference between the reservoir and the microcosms was that during the first five weeks, 50% of the total diatom volume in the reservoir was comprised of Fragilaria crotonensis compared to only 8% in the microcosms. Figure 1 shows that with the exception of the rotifers, all taxonomic variables in the microcosms followed the qualitative trends observed in the reservoir. Although not plotted, Stephanodiscus astraea in the unagitated microcosms tracked the reservoir very well during weeks 1-4.

During weeks 1-5 of Experiment I, the rotifer populations in both mechanically agitated and unagitated microcosms, experienced a

major (>10x increase) bloom not observed in the reservoir. This bloom was statistically indistinguishable ($|t| < .70$, d.f. = 4) week by week in the two sets of microcosms. During this bloom, flagellate population levels decreased identically in both sets of microcosms ($|t| < .75$ all weeks but the third).

In Experiment II, the dominant (by volume) phytoplankton in the reservoir were flagellates, Fragilaria crotonensis, and Ceratium hirundinella. In the reservoir, the most significant trends with time of the taxonomic variables were the decrease of Fragilaria crotonensis and the increase of rotifers (>10x). Fragilaria crotonensis in both the unagitated and bubbled microcosms exhibited the decrease observed in the reservoir (Figure 2). For the first 4-6 weeks and with the exception of the rotifers, all the taxonomic variables in the unagitated and bubbled microcosms tracked well the behavior of the same variables in the reservoir. With the exception of the most agitated microcosms, rotifers decreased in all sets of microcosms, while the rotifers in the reservoir experienced a bloom. In systems D, the rotifers did not appear to decrease, but poor replication does not allow a definitive statement about their behavior.

In all four sets of microcosms copepods and flagellates exhibited an inverse relationship. This is best illustrated by time averaging the data for weeks 5 and 6. For systems A, B, C, and D respectively, the time-averaged values for the copepod number densities are .59, .25, .17, and 0.00/l, while the corresponding time-averaged flagellate number densities are 5.06, 8.64, 9.37, and 13.42

x 10^5/l. The correlation coefficient between these two variables is -.971.

The time averaged values of the taxonomic variables were used to compare quantitatively each set of microcosms with the reservoir. A variable in a set of microcosms was considered to exhibit good tracking, if it both replicated well with the set ($\chi^2 \leq 6.00$), and if its mean value (averaged over the set of microcosms) was close ($|t| \leq 2.92$, d.f. = 2) to the depth-averaged value observed in the reservoir epilimnion. By these criteria, the taxonomic variables in Experiment I tracked poorly with only 17% of the taxonomic data entries satisfying them in the mechanically agitated systems. In Experiment II, the unagitated and bubbled systems tracked the reservoir quite well, while the mechanically agitated systems did not (the above tracking criteria were satisfied by 79%, 61%, 21%, and 14% of the taxonomic data entries in systems A, B, C, and D respectively). As Table 7 demonstrates tracking was better in the first three week interval than in the second.

In Experiment I, the same statistically significant connection between the chemical data and the taxonomic data was observed in both the reservoir and the microcosms. In systems with higher volume densities of diatoms, lower concentrations of SiO_2 were observed. Each microcosm in the experiment was utilized to establish a linear regression between total diatom volume density averaged over weeks 1-8 as a function of SiO_2 concentration averaged over weeks 6-8 (Table 8). The correlation coefficient was r = -.995 (d.f.=4).

Inserting the reservoir's SiO_2 concentration averaged over weeks 6-8 into this linear regression gives an estimate of the total diatom volume averaged over weeks 1-8 in the reservoir of 5.22×10^8 $\mu m^3/l$. The observed value was 5.28×10^8 $\mu m^3/l$, thus the relationship of SiO_2 concentration and total diatom volume was the same in the reservoir and microcosms. No other statistically significant relationships between the chemical and taxonomic data were observed in the reservoir or microcosms in either Experiment I or II.

DISCUSSION

The tracking criteria used in the previous section are very stringent. They require that a time-averaged taxonomic variable in a particular set of microcosms be statistically indistinguishable within that set as well as statistically indistinguishable from the depth-integrated value measured at one location in the reservoir. Sampling and measurement variance is accounted for, but no allowance is made for lateral or vertical variation of the variable in the reservoir. Inclusion of such variation would increase the range of values which characterize the reservoir, thus increasing the likelihood that the microcosm values fall with that range. Furthermore, relaxing the replication criteria would broaden the range of values a variable could have in a set of microcosms, further increasing the likelihood that this range of values would include the variable's value in the reservoir. We know of no microcosm work where this type of replication criteria is included in the standards set up for good tracking.

Even though a set of microcosms might be statistically distinguishable from the reservoir, it still could exhibit the significant trends observed in the reservoir, and hence would be a useful system

for studying biological or toxicological mechanisms. Figures 1 and 2 illustrate that for 4 to 6 weeks in both experiments and with the exception of the rotifers, the taxonomic variables in the treatment systems shown in the figures exhibited the same trends with time as were observed in the reservoir. Indeed, in Experiment I, this was true for both treatment systems, while in Experiment II, the cladoceran and diatom populations in the mechanically agitated systems were qualitatively different from those in the reservoir.

In addition, the same relationships between chemical and taxonomic data in the reservoir were observed in the microcosms. Most notably, in Experiment I, one linear expression derived solely from microcosm data accurately related total diatom volume densities to SiO_2 concentrations in each microcosm and the reservoir. Other chemical variables did not exhibit significant correlations with the taxonomic variables in the reservoir and this was also true in the microcosms.

The differences observed between the rotifer populations in the microcosms and the reservoir are difficult to explain in terms of the variables measured in these experiments. Possibly, the major food sources of the rotifers consisted of bacteria and organic materials not measured and which differed between microcosms and reservoir. Regardless of the reason, only in the first three weeks of Experiment II was tracking and replication acceptable; poor tracking or poor replication characterized all other periods of both experiments, and this is our most negative result. The applicability of lentic micro-

cosms to the study of rotifers will be of limited value if this problem persists in future experimental design.

The relation between rotifer population densities in the microcosms and the method of agitation poses another puzzle. In each of the six weeks of Experiment II, and in each of the last five weeks of Experiment I, the mean rotifer densities in the mechanically agitated tanks exceed that in the non-mechanically-agitated tanks. For some of these weeks, poor replication of the rotifer densities makes it impossible to distinguish statistically the population densities between the mechanically and non-mechanically agitated systems, but the effect nonetheless seems worth exploring in future experiments. Possibly, grazing pressure by the cladocera on either the rotifers or on the rotifer food supply was relieved in the mechanically-agitated microcosms; the evidence available from these experiments does not allow us to determine which, if either, of these possibilities is correct.

In Experiments I and II, mechanically-agitated systems had reduced cladoceran populations and enhanced diatom populations. Perez et al. (1977) observed a similar pattern in their estuarine microcosm investigations, with predatory copepod population densities correlating negatively with agitation level and phytoplankton population densities showing a positive correlation. At least two classes of mechanisms can be postulated to explain how the method of water agitation affected the microcosm diatom and cladoceran population densities. First, vigorous mechanical agitation may have directly

damaged the cladocera and/or interfered with their grazing and growth patterns. Second, it may have directly enhanced diatom growth and viability by reducing sinking and/or increasing nutrient availability and transport. If the diatoms in the microcosms were not grazed upon by the cladocera, then neither class of mechanism, alone, would be sufficient to explain the observed relative increases in diatom population densities and relative decreases in the cladocera population densities in the mechanically agitated microcosms. On the other hand, if diatoms were an important component of the cladocera diet, then direct damage to the cladocera by mechanical agitation would lead to relative increases in the diatom population densities in the mechanically agitated systems. Thus, under the postulate of significant grazing, the first class of mechanisms acting alone is not excluded by our results. Conversely, with the above grazing postulate, the supposition that the second class of mechanisms acted alone is excluded.

In another set of experiments, Perez et al. (1977) studied the effects of mechanical agitation on microcosms derived from one point in Narragansett Bay. The mechanical agitation was accomplished by rotating paddles whose direction was reversed every 30 seconds. The level of agitation present was evaluated by measuring the dissolution rates of hard crystalline sugar balls. The dissolution rates observed in the most vigorously agitated microcosms were close to those measured in the natural system. Comparisons of biological and chemical variables in microcosms with a range of agitation levels,

including some with no mechanical agitation, were made. The systematic effects they observed when comparing no agitation with the highest level of agitation were the same we observed. Namely, total grazer densities were decreased in the mechanically agitated microcosms as compared to the non-agitated microcosms and total phytoplankton cell densities were increased. These relative increases in total phytoplankton cell densities were greater in their late spring experiments, (9-18)x, than in their early summer experiments, (1.9-5)x. Since diatoms made up a larger fraction of their phytoplankton populations in the late spring than in the early summer, this is also consistent with our results that mechanical agitation increased diatom populations while not systematically affecting dinoflagellate and flagellate populations.

In the Narragansett work, the Bay at the site used to gather stocking water was compared directly with those microcosms with a $169cm^2$ benthic compartment, a 35 day turnover time, and the most vigorous agitation rate. The data presented also allow a comparison of the Bay in the late spring and early summer experiments with microcosms in the same configuration except with no direct mechanical agitation. For both experiments, the most vigorously agitated microcosms had total phytoplankton cell densities which were much higher (32x, late spring; 6.4x, early summer) than in the Bay, while the total grazer densities in these microcosms were statistically the same as in the Bay. In the late spring experiment, total phytoplankton cell densities in the non-agitated microcosms were close to those

in the Bay (2x), while total grazer densities were much higher (5x). In the early summer experiment, both the total phytoplankton cell density and total grazer density in the non-agitated microcosms, were essentially the same as in the Bay (1.3x and 1.1x respectively). In both experiments, the ratio of chlorophyll$_a$ concentration to phytoplankton cell density in the most vigorously mechanically agitated microcosms was significantly lower than this ratio observed in the Bay. This is suggestive of an altered planktonic physiological state in the mechanically agitated systems. This ratio in the non-agitated microcosms was close to that observed in the Bay.

Perez (personal communication) has concluded that the level of mechanical agitation in estuarine microcosms should be set to match the dissolution rate in the field system being investigated. This conclusion was based on the assumption that the matching of physical parameters, in particular the gypsum dissolution rate, is _a priori_ more important than achieving maximum realism of biological population densities. While we agree that the matching of lake or estuarine turbulence levels in microcosms is a desirable goal, we urge that some caution be exercised in interpreting gypsum dissolution rates too literally. In particular, water movement in the reservoir can be characterized by scales of motion ranging from small (e.g., small-scale turbulence) to large (e.g., wind driven currents). The dissolution rates of the tethered gypsum blocks measured in the reservoir may reflect increased dissolution due to large scale motion not present in the microcosms. Thus, by matching gypsum dissolution

rates, it is possible that microturbulence in the microcosms is set well above the value in the natural system.

CONCLUSION

We have carried out three microcosm tracking experiments using the Briones Reservoir epilimnion as a source of water and as the comparative natural system. In a previous summer experiment (Harte, Levy, & Rees, 1983) and in one of the experiments reported here (Experiment II), excellent tracking of both the dominant phytoplankton and zooplankton taxa were achieved for 4-6 weeks using microcosms which were non-agitated or were gently agitated by bubbling. In these two experiments, the dominant taxa in the microcosms were statistically not distinguishable from those measured in the reservoir. In the 1981 fall experiment (Experiment II), the mechanically agitated microcosms exhibited zooplankton and phytoplankton population densities quite different in magnitude and evolution over time from those in the reservoir, even though the water agitation level in these microcosms was close to that in the reservoir as determined by gypsum dissolution rates. In the 1981 summer experiment (Experiment I), most of the dominant phytoplankton and zooplankton taxa in both mechanically agitated and non-agitated microcosms could be statistically distinguished from the variables in the reservoir. Nonetheless, for five weeks the major population changes exhibited by the

dominant phytoplankton and zooplankton in the reservoir were well followed by these variables in the microcosms. A further indication that important relationships in the reservoir during Experiment I were also present in the microcosms is the fact that the identical functional and numerical relationship between SiO_2 concentrations and total diatom volume observed in the reservoir was observed in the microcosms.

In both the Narragansett work and this study, the only cases where phytoplankton and zooplankton were statistically indistinguishable from those in the natural system were with non-mechanically agitated microcosms. In each of these experiments, the dissolution rates of gypsum or hard crystalline sugar in these systems were less than the dissolution rates averaged over time in the natural system. These results suggest that matching gypsum dissolution rates in the microcosms and the natural system does not guarantee good tracking of all the relevant biotic variables.

We conclude that freshwater microcosms designed to mimic the pelagic epilimnion of a lentic body can be run for periods of three to six weeks with statistically acceptable replicability and realism. In most cases, gentle, non-mechanical, agitation is the most successful technique for insuring good tracking and replicability. Gypsum dissolution rates very likely do not provide a realistic measure of biologically-relevant turbulence.

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TABLE CAPTIONS

(1) Light intensities in the microcosms and the reservoir

(2) Gypsum dissolution rates in the microcosms and the reservoir.

(3) Time averaged chemical data for the microcosms and the reservoir in Experiment I.

(4) Time averaged chemical data for the microcosms and the reservoir in Experiment II.

(5) Dominant taxa present in the experiments.

(6) Time averaged taxonomic data for the microcosms and the reservoir in Experiment I.

(7) Time averaged taxonomic data for the microcosms and the reservoir in Experiment II.

(8) Total diatom volumes and SiO_2 concentrations in each microcosm and the reservoir in Experiment I.

TABLES

TABLE 1

Experiment I		Experiment II	
Tank depth (cm)	I(watts[PAR]/m^2)	Tank depth (cm)	I(watts[PAR]/m^2)
0	3.0	0	2.0
18	2.4	20	1.5
36	1.7	40	.7
Res. depth (m)		Res. depth (m)	
0	150.0		
5	37.5		
10	14.7		
15	4.0		
20	1.1		
25	.4		

TABLE 2

	Experiment I		Experiment II	
Res. depth (m)	K(cm/hr)	T(^{o}C)	K(cm/hr)	T^{o}(C)
0	.0140	18.0	.0050	14.2
5	.0078	18.0	.0042	14.0
10	.0058	15.0	.0042	14.0
15	.0051	12.0	.0040	14.0
20	.0050	11.5	.0039	14.0
25	.0042	11.5	.0035	12.0
30			.0035	12.0
Tanks				
A	.0010	19.0	.0005	15.0
B			.0012	15.0
C			.0031	15.0
D	.0081	19.0	.0047	15.0

TABLE 3

Experiment I

	weeks 1-5				weeks 6-8			
	$\bar{x}$	σ^2	χ^2	C.V.	$\bar{x}$	σ^2	χ^2	C.V.
				NH_4^+ (μM[N])				
A	10.4	.038	2.96	.04	12.9	.063	1.53	.03
D	10.6	.038	12.36	.08	12.9	.063	69.50	.20
Res.	3.3	.018			2.1	.016		
				$NO_3^- + NO_2^-$ (μM[N])				
A	7.7	.17	2.860	.11	13.3	.49	5.07	.15
D	7.1	.15	.019	.01	13.1	.48	.50	.05
Res.	4.0	.10			4.9	.18		
				SiO_2 (μM[Si])				
A	15.3	.0090	55.6	.06	13.5	.0098	35.8	.05
D	14.3	.0081	61.7	.06	9.3	.0057	1830.0	.43
Res.	15.6	.0120			10.9	.0110		
				O_2 (mg/l)				
A	8.57	.00067	7.90	.01	8.58	.0011	67.4	.04
D	8.64	.00067	44.10	.02	8.39	.0011	3.12	.01
Res.	9.80	.00130			8.85	.0021		

(table continued on next page)

Table 3 continued

Experiment I

	weeks 1-5				weeks 6-8			
	$\bar{x}$	σ^2	χ^2	C.V.	$\bar{x}$	σ^2	χ^2	C.V.
				pH				
A	7.93	.00006	4.36	.003	7.97	.0001	.33	.0009
D	8.00	.00006	2.73	.002	8.02	.0001	.33	.0009
Res.	8.65	.00100			8.62	.0017		

TABLE 4

Experiment II

	weeks 1-3				weeks 4-6			
	$\bar{x}$	σ^2	χ^2	C.V.	$\bar{x}$	σ^2	χ^2	C.V.
				NH_4^+ (μM[N])				
A	4.6	.022	2.57	.06	10.1	.049	112.80	.29
B	4.6	.022	0.08	.01	8.4	.041	5.55	.07
C	5.5	.027	0.18	.02	11.3	.055	3.41	.05
D	4.7	.023	5.22	.09	8.6	.041	16.17	.12
Res.	3.3	.016			3.0	.014		
				$NO_3^- + NO_2^-$ (μM[N])				
A	1.1	.017	.45	.10	1.8	.028	.33	.07
B	1.2	.019	.12	.05	2.2	.037	.45	.07
C	1.2	.020	.61	.12	1.9	.030	.12	.04
D	1.3	.020	.24	.07	2.0	.033	.09	.03
Res.	0.6	.014			1.0	.015		
				SiO_2 (μM[Si])				
A	3.5	.0017	2.29	.02	3.0	.00090	0	0
B	3.6	.0018	.32	.01	2.9	.00084	3.69	.02
C	3.5	.0017	2.29	.02	2.9	.00087	2.57	.02
D	3.5	.0017	0	0	2.8	.00083	2.13	.02
Res.	8.0	.0066			11.0	.00730		

(table continued on next page)

Table 4 continued

Experiment II

	weeks 1-3				weeks 4-6			
	$\bar{x}$	σ^2	χ^2	C.V.	$\bar{x}$	σ^2	χ^2	C.V.
				DOC (μM[C])				
A	1550	59	6.34	.02	1540	38	19.3	.02
B	1520	56	16.10	.02	1540	38	35.8	.03
C	1530	58	8.72	.02	1520	37	4.1	.01
D	1520	56	25.10	.03	1500	37	29.3	.03
Res.	1580	61			1600	41		
				TOC (μM[C])				
A	1630	66	2.62	.010	1620	41	.43	.003
B	1620	66	3.11	.010	1600	39	16.80	.020
C	1630	68	.33	.004	1620	41	1.19	.005
D	1650	69	6.77	.020	1620	41	74.10	.040
Res.	1630	67			1690	45		
				pH				
A	7.76	.0001	.33	.0009	7.37	.0001	4.59	.004
B	7.74	.0001	.33	.0009	7.54	.0001	.65	.001
C	7.75	.0001	.33	.0009	7.47	.0001	1.64	.002
D	7.78	.0001	.33	.0009	7.50	.0001	6.87	.004
Res.	7.92	.0009			7.44	.0009		

TABLE 5

Chrysophyta	
Stephanodiscus astraea	
Fragilaria crotonensis	
Pyrrhophyta	
Ceratium hirundinella	
Cryptophyta	"flagellates"
Chroomonas sp(p).	
Unidentified flagellates	
Rotifera	
Keratella cochlearis	
Keratella quadrata	
Polyarthra sp(p).	
Copepoda	
Calanoida	
Cyclopoida	
Cladocera	
Daphnia schødleri	
Alona spp.	
Bosmina spp.	

TABLE 6

Experiment I

	weeks 1-5				weeks 6-8			
	$\bar{x}$	σ^2	χ^2	t	$\bar{x}$	σ^2	χ^2	t
	flagellates (#/l) x 10^{-3}							
A	225	640	.39	7.96	603	1,570	77.1	.13
D	349	1,570	7.33	.86	658	8,070	11.4	.11
Res.	478	4,500	1.03		695	10,830	1.0	
	Stephanodiscus astraea (#/l) x 10^{-3}							
A	2.51	.053	12.6	.44	0.00	.013	0.0	∞
D	10.56	.572	27.6	-2.52	7.98	1.165	79.4	-.05
Res.	2.93	.092	34.6		7.50	.814	43.7	
	Fragilaria crotonensis (#/l)							
A	142	425	3.61	4.65	13.9	13.5	5.88	3.56
D	420	1,980	1.48	5.82	14.3	15.2	13.20	2.37
Res.	1,620	55,400	3.81		321.1	2,520.0	6.30	
	Rotifera (#/l)							
A	123.0	69.80	4.75	-7.64	4.78	.63	31.00	2.27
D	123.0	67.00	2.03	-11.81	101.00	111.00	82.90	-.90
Res.	22.7	3.59	6.58		37.00	12.30	1.19	

(table continued on next page)

Table 6 continued

Experiment I

	weeks 1-5				weeks 6-8			
	$\bar{x}$	σ^2	χ^2	t	$\bar{x}$	σ^2	χ^2	t
				Copepoda (#/l)				
A	3.77	.265	6.16	-1.67	.39	.038	1.15	4.61
D	2.10	.120	3.76	-.27	.22	.030	1.40	4.57
Res.	1.91	.138	.77		2.45	.310	11.22	
				Cladocera (#/l)				
A	16.10	2.00	.01	-116.00	7.34	.64	.82	-7.21
D	9.10	.63	.65	-9.82	4.06	.31	2.62	-1.46
Res.	3.65	.32	1.04		2.65	.40	5.45	

TABLE 7

Experiment II

	weeks 1-3				weeks 4-6			
	$\bar{x}$	σ^2	χ^2	t	$\bar{x}$	σ^2	χ^2	t
	flagellates (#/l) x 10^{-3}							
A	541	5,320	.98	-3.27	396	7,450	16.31	-.03
B	521	4,700	.05	-13.59	735	9,990	3.18	-2.47
C	383	2,300	.57	-1.06	779	14,500	12.26	-1.22
D	195	1,110	.49	5.45	1,150	19,600	6.85	-2.78
Res.	346	1,980	.44		386	2,500	.33	
	Stephanodiscus astraea (#/l) x 10^{-3}							
A	.156	.0068	4.63	-.70	.111	.0063	1.11	.49
B	.088	.0048	.21	-1.42	.111	.0057	2.28	.35
C	.844	.0228	4.70	-3.16	1.022	.0316	10.98	-1.96
D	1.000	.0300	4.23	-3.54	2.354	.0756	1.04	-10.80
Res.	.044	.0044	.90		.134	.0056	.53	
	Fragilaria crotonensis (#/l)							
A	385	2,220	1.34	.38	177.0	1,610	1.49	-2.26
B	532	3,610	1.11	-2.12	42.9	175	2.48	2.76
C	773	7,470	.54	-7.00	121.0	399	8.38	-.55
D	804	8,110	2.49	-3.43	274.0	1,600	7.05	-2.29
Res.	407	2,660	6.23		95.4	121	2.61	

(table continued on next page)

Table 7 continued

Experiment II

	weeks 1-3				weeks 4-6			
	$\bar{x}$	σ^2	χ^2	t	$\bar{x}$	σ^2	χ^2	t
				Ceratium hirundinella (#/l)				
A	38.5	56.0	.36	-1.97	38.5	151.0	1.51	-.43
B	34.1	44.5	1.89	-.40	5.1	17.1	.79	7.76
C	71.2	117.6	1.08	-4.53	38.5	51.8	7.12	-.31
D	46.5	66.3	2.12	-1.56	22.5	30.8	7.64	.82
Res.	30.8	29.5	5.71		33.6	17.1	1.97	
				Rotifera (#/l)				
A	4.22	.32	.54	-.95	.67	.050	.38	26.36
B	2.72	.19	4.21	1.33	.33	.033	1.77	12.43
C	7.11	.62	1.50	-4.20	2.17	.148	13.56	4.07
D	6.06	.52	9.35	-1.21	9.50	1.060	37.19	1.43
Res.	3.88	.17	13.58		23.06	3.750	.09	
				Copepoda (#/l)				
A	1.39	.085	.51	-4.95	.61	.045	2.23	2.40
B	.89	.058	5.25	-.63	.39	.038	2.60	3.22
C	1.34	.078	.24	-6.98	.56	.048	2.46	2.43
D	.73	.058	3.32	-.29	.06	.028	.22	17.18
Res.	.63	.008	17.05		1.23	.015	6.64	
				Cladocera (#/l)				
A	3.890	.293	3.46	1.80	3.560	.278	3.27	-2.59
B	1.500	.098	3.61	5.37	3.560	.253	1.93	-2.98
C	.275	.028	.90	15.78	.555	.043	1.92	4.94
D	.225	.035	.72	17.55	.225	.028	.89	9.86
Res.	5.595	.225	60.18		1.970	.043	39.75	

TABLE 8

	Total diatom volume: wks 1-8 ($\mu m^3/l$) x 10^{-8}	SiO_2: wks 6-8 $\mu M(Si)$
System	y	x
A1	.86	14.1
A2	1.30	13.6
A3	1.88	12.67
D1	13.46	5.17
D2	7.07	9.53
D3	2.83	13.07
Res.	5.28	10.90

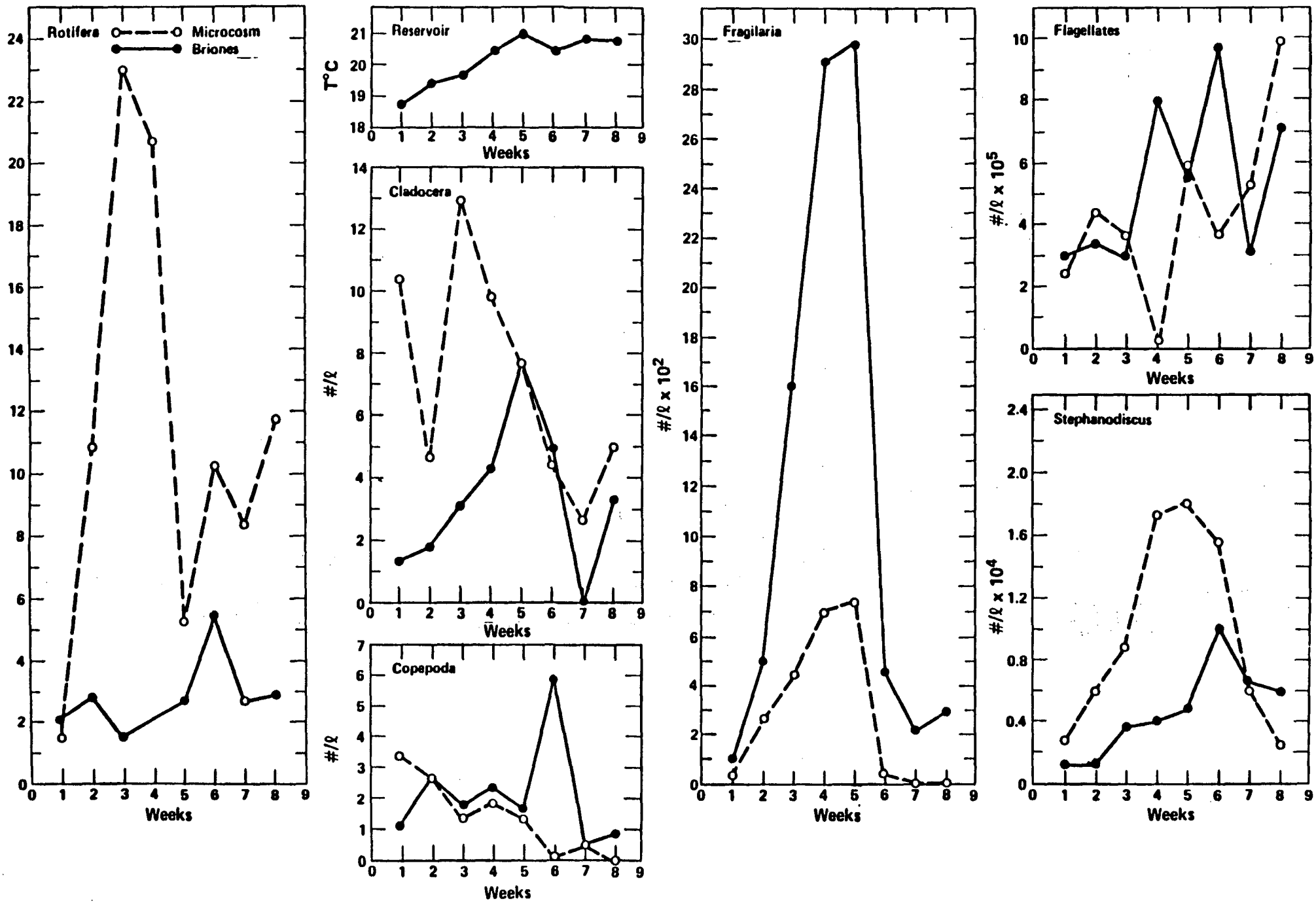
FIGURE CAPTIONS

(1) The dominant taxonomic variables in Experiment I are plotted as functions of time for the D microcosms and the reservoir.

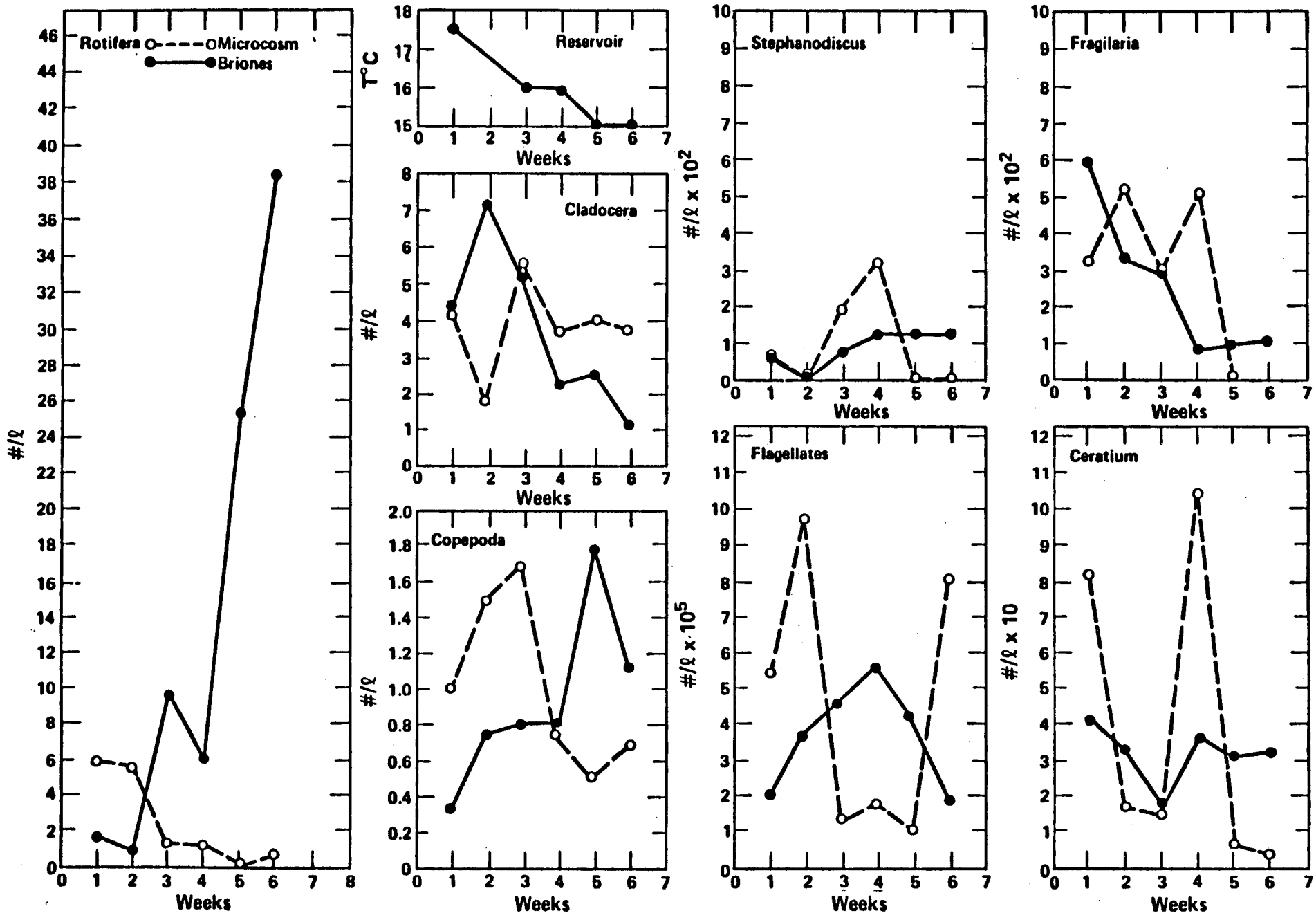
(2) The dominant taxonommic variables in Experiment II are plotted as functions of time for the A Microcosms and the reservoir.

FIGURES

EXPERIMENT I



EXPERIMENT II



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