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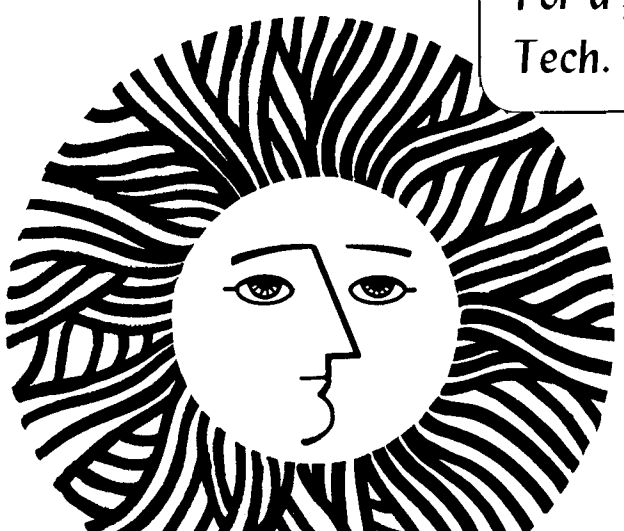

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DISCLAIMER

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ABSTRACT

A comparison is made of diatom population dynamics between 2 reservoirs in Central California and laboratory microcosm derived from each of the epilimnia of the reservoirs. Three experimental runs lasted from 8–13 weeks and embraced both the wet winter and dry summer seasons typical of the Mediterranean climate of the area. Microcosm diatom population dynamics most closely paralleled that found in reservoir epilimnion during the late spring--early summer at time of reservoir stratification. During times of winter overturn, the microcosm diatom population patterns diverged from those of the reservoirs within 24 days or less. In all three experiments, morphological changes involving what was believed to be gamete formation was observed when laboratory diatom numbers decreased by an order of magnitude. Similar morphological changes were not observed in the reservoir diatom populations.

INTRODUCTION

Diatoms contribute significantly to the primary productivity of the biosphere. Found in diverse habitats, from soils to benthic aquatic sediments to the photic pelagic zones of oceans and lakes, diatoms have been estimated to be responsible for 20-25 percent of the world net primary production (Werner, 1977). Diatoms are characterized by the possession of a uniquely beautiful silicious encasement, or frustule, on the structure of which the taxonomy of the group is based. Most forms are unicellular, although there are numerous multicellular aquatic species.

In aquatic habitats such as oceans or lakes, pelagic diatoms often constitute the most important algal component of the plankton. In particular, algal blooms in lakes not disturbed to a great extent by human activity usually consist primarily of diatoms. Reasons for fluctutions of diatom populations are varied, complex, and interrelated, and include light intensity (Rodhe, 1948; Talling, 1955), concentration of dissolved silica (Lund, 1950; Kilham, 1971; Schelske et al., 1972), competition with other algal species for nutrients such as phosphorus (Tilman; 1976), zooplankton predation (Schindler, 1971; Weers and Zaret; 1975; Nadin-Hurley and Duncan, 1976), and the amount of turbulence (Moss, 1969).

In the present experiments waters from two reservoirs in central California were brought into the laboratory, and diatom populations, as well as other biological and chemical parameters, were monitored simultaneously in laboratory microcosms and their parent reservoirs.

Our object was to use these data to assess the degree of similarity of diatom populations between the field and laboratory and to relate differences to conditions peculiar to the microcosm environment.

METHODS AND MATERIALS

General

Field.

Two local reservoirs within 30 km of the laboratory were utilized as "parent" water bodies: (1) Lafayette Reservoir, 5 km in circumference and 36 m maximum depth, and (2) Briones Reservoir 22 km in circumference and 70 m maximum depth. Hydrologic inputs to both these reservoirs are from their immediate watersheds and from the Pardee Reservoir on the Mokelumne River. The latter input is via pipeline. For Lafayette Reservoir, annual input from its watershed averages about 25 percent of the reservoir's volume, while annual input from Pardee Reservoir averages about 4 percent of the volume of Lafayette. For Briones Reservoir, annual input from its watershed averages about 1 percent of the reservoir's volume, while annual input from Pardee Reservoir averages about 4 percent of the volume of Briones. The actual inflows during the experimental periods were dependent on the time of year the experiments were performed. In California, a dry season generally extends from mid-spring through mid-autumn. More detailed information about actual hydrologic inputs during the experiments are described in the Results Section.

Water from the epilimnion of Lafayette was used to stock the microcosms of the first experimental run (19 October 1978–17 January 1979), while similar water from Briones reservoir was used for the second and third runs (20 April–5 July 1979; 14 November 1979–11 January 1980). Stocking water was taken a sufficient distance from

shore (~100 m) to insure that samples were from the pelagic zone of the reservoir. Water depth of both reservoirs at the sampling sites was greater than 20 m. Water was brought from the reservoirs in large containers and poured directly into the microcosms.

Laboratory.

Table 1 outlines the experimental conditions for the 3 runs on which our results are based. Laboratory microcosms stocked with water from the 2 local reservoirs were monitored simultaneously with their parent water body. Each experiment lasted from 8-13 weeks. All microcosms were 50 liter cylindrical nalgene containers. Since surface growth on container walls is know to have profound effects on the dynamics of the desired "pelagic" environment of our laboratory microcosms (Jassby et al., 1977; Dudzik et al., 1979), a simple strategy, that of transferring water weekly to clean containers, was adopted to prevent the build-up of algal growth on the tank walls. In runs 1 and 2 (Table 1) the water was poured, while in run 3, the water was siphoned. Each set of experimental tanks was run in triplicate. All microcosms were maintained in a temperature-controlled room at 19 ± 1°C. Illumination was provided by banks of 1.3 m, high-output flourescent lights on a 12h:12h light:dark cycle. Light irradiance on the water surface of the microcosms was 6 ± 1 watts/m^2. To simulate gentle turbulence, aeration was used in runs 1 and 2. The aeration was provided by gently passing air through a capillary tube which extended 15 cm below the water's surface. Air flow rate was about 1 liter/minute.

Measurements and Sampling Procedure

Field.

Field samples were taken at weekly intervals during times of our laboratory tracking runs. Reservoir samples were taken on the same day as laboratory microcosm samples. All field samples were taken from a small boat at the same site from which the microcosms were filled. Samples were taken with a 2-liter Van Dorn sampler at a depth of 1 m. Two samples were taken, one for zooplankton, a second for phytoplankton and water chemistry. Temperature was recorded with a thermometer as soon as water samples were taken. All field samples were treated in the same manner as microcosm samples with regard to measurement procedure, counting, and enumeration.

Laboratory

The following parameters relevant to this study were measured and monitored in laboratory microcosms: (1) phytoplankton genera and total volume, (2) zooplankton genera and total volume, (3) nitrate + nitrite and ammonia. Integrated phytoplankton samples were taken by inserting a polyethylene tube into the water column of the microcosm. A 5 ml sample was used for counting under a Leitz Diavert inverted microscope utilizing Utermoehl counting chambers. Initial zooplankton samples were taken with a premeasured 100 ml glass cylinder inserted into the microcosm. After initial data analysis it was decided that a larger zooplankton sample was needed. Accordingly, 1 liter zooplankton samples were taken in the "Briones, late fall--early winter" run and filtered through a plankton bucket (Wildco) fitted with a 64 μ Nitex

straining net. These samples were then filtered down and placed in 100 ml settling chambers for subsequent enumeration and counting. All phytoplankton and zooplankton samples sat 24 hrs before counting. Nitrate + nitrite determination was done by the method of Solorzano (1969) and ammonia, after Golterman (1969). For both of these chemical analyses a 10 ml sample of water was pipetted from each microcosm.

Presentation of Data

In Figures 1-3, diatom volume densities are shown as they evolved week by week for each experiment. For the laboratory systems, the range of values spanned by the three laboratory systems is indicated. In Tables 2-4, the time-averaged values for diatom volume densities and inorganic nitrogen levels are given.

There are two reasons to average data over time. First the jitter inherent in the parameters of the natural systems is smoothed out to some degree by this process. Secondly, it allows for sensible comparison between different systems which may differ from one another in one or more of their variables only by a phase difference in time. For example, two freshwater systems may both exhibit a similar diatom bloom but be slightly out of phase if the bloom in one precedes that in the other by a few days. The time-aggregated value for diatom volumes would be similar for both systems, whereas a day-by-day comparison of the diatom populations would yield different results. For our microcosms and lakes such phase differences were judged not to be biologically significant, and so we used time-aggregated quantities in our analyses. The time intervals over which the data were averaged

were selected such that major phytoplankton blooms were included within the interval. The endpoints of the intervals usually occurred at times when the systems were quiescent.

In Tables 2-4, x is the time-averaged value of the indicated parameter. For the laboratory systems, x is the average over the three replicates. The quantity δ is the error in determining the quantity x. The actual value of the indicated parameter is $x \pm \delta$ to a 90 percent degree of confidence. The quantity S is the square root of the experimental variance among replicate laboratory systems.

RESULTS

Run 1: Lafayette Reservoir (Late Fall--Early Winter, 92 Days)

Field.

During the first 47 days, the diatom population consisted almost entirely of Fragilaria (≥98.6 percent by volume). On day 57, Stephanodiscus appeared and one week later Asterionella. By day 91, Stephanodiscus and Asterionella comprised 99.4 percent of the total diatom population by volume. Total diatom volume density varied between 1.4×10^5 μ^3/ml and 5.5×10^6 μ^3/ml (Fig. 1, Table 2). By volume diatoms dominated the algal community except during days 0-7 and 47-61, when Ceratium volume densities were comparable ($(0.5\text{-}1) \times 10^6$ μ^3/ml and $(2\text{-}5) \times 10^5$ μ^3/ml respectively). Low levels of blue greens ($\leq 6 \times 10^5$ μ^3/ml) and flagellates ($\leq 1 \times 10^5$ μ^3/l) occurred sporadically. Ammonia levels increased from ~4 μM(N) to ~15 μM(N) over the first 78 days; they then decreased to 7 μM(N) by day 92 (Table 2).

Nitrate plus nitrite levels increased from ~3 μM(N) to 8 μM(N) over 92 days. Water temperature decreased from 15°C to 11°C during the experiment. The thermocline disappeared and windy conditions ultimately promoted vertical as well as horizontal mixing. During this experiment, input from the water shed was about 11 percent of the volume of the reservoir, while input from Pardee reservoir was <1 percent.

Laboratory.

The diatom Fragilaria remained at low levels compared with the field population. By day 26, it had disappeared (Fig. 1). After day 14, Ceratium and blue green algae had disappeared as compared with low-level appearances by these phytoplankton in the reservoir. During days 61-92, low levels of flagellates ($\leq 3 \times 10^5$ μ^3/ml) were present in contrast to none in the reservoir. Ammonia levels were generally significantly lower than in the reservoir, while nitrate plus nitrite levels were generally the same as in the reservoir (Table 2).

Run 2: Briones Reservoir (Late Spring--Early Summer, 77 Days)

Field.

For the first 56 days, Stephanodiscus was the only diatom present. Over the first 21 days, its volume density ranged between 0.5×10^6 μ^3/ml and 2.4×10^6 μ^3/ml, while after day 21 its density decreased significantly (Fig. 2, Table 3). On days 63-70, no diatoms were present, but by day 77, Synedra had appeared at a low volume density ($\sim 0.5 \times 10^5$ μ^3/ml). Through the first 28 days, diatoms were the dominant algae (by volume). During days 35-49, volume densities of Stephanodiscus and Ceratium (10^5 μ^3/ml) were comparable but relatively low. On days 56 and 63, flagellates ($\sim 5 \times 10^5$ μ^3/ml) were the dominant phyto-plankton by volume and by day 70, blue green algae ($\sim 2.7 \times 10^6$ μ^3/ml) were the dominant phytoplankton. Inorganic nitrogen levels were low and relatively constant (Table 3). The water temperature increased from 16°C to 22°C during the experiment, and the

reservoir remained stratified. There was insignificant water input to the reservoir from both rainfall and discharge from Pardee Reservoir.

Laboratory

Stephanodiscus was the only diatom present. The evolution in time of its volume density closely paralleled that found in the reserovir (Fig. 2, Table 3). Over the first 21 days its volume density ranged from 0.2 x 10^6 μ^3/ml to 1.8 x 10^6 μ^3/ml. As in the reservoir, Stephanodiscus was the dominant alga, by volume, for 28 days. After this it decreased significantly, and at a more rapid rate than did the Stephanodiscus in the reservoir. During days 35-56, very low levels of flagellates (0.5 x 10^5 μ^3/ml) were present. In two of the three laboratory systems high levels of Ulothrix (~10^6 μ^3/ml) were present. In one system this occurred on days 42-63 while in the other on days 63-77. Ammonia levels in the laboratory were very close to those in the reservoir (Table 3), while nitrate plus nitrite levels were slightly higher than in the reservoir.

Run 3: Briones (Late Fall--Early Winter, 59 Days)

Field.

During days 1-21, Stephanodiscus was the only diatom present. During days 29-50, Asterionella (2-7 percent of total diatom volume) and Fragilaria (6-28 percent of total diatom volume) also appeared (Fig. 3, Table 4). on day 59, a different species of Stephanodiscus appeared and made up 53 percent of the total diatom volume, while the original species of Stephanodiscus comprised 40 percent of the

total diatom volume. Total diatom volume density ranged from 0.8×10^5 μ^3/ml to 4×10^5 μ^3/ml.

Except on day 16, diatoms were the dominant algae by volume. On day 16, flagellate volume densities were high (~4.6×10^5 μ^3/ml) and exceeded diatom volume densities. Inorganic nitrogen levels were low and relatively constant (Table 4). The surface water temperature decreased from 14.5°C to 11°C during the experiment as the thermocline disappeared and vertical as well as horizontal mixing took place. During this experiment, input from watershed was ~1 percent of the reservoir volume while input from Pardee reservoir was <1 percent.

Laboratory.

Stephanodiscus was the only diatom present. On days 1-21, its volume density was close to that observed in the reservoir (Fig. 3, Table 4). After day 36, no diatoms were observed in the laboratory. Flagellate volume densities were comparable to the diatom volume densities on days 7-29 (~3×10^5 μ^3/ml). Subsequently, and in contrast to the reservoir, flagellates were the dominant phytoplankton, by volume during days 36-51. Inorganic nitrogen levels were comparable to those in the reservoir.

In all three experiments, morphological changes in diatom cell structure were observed which were not seen in the corresponding corresponding natural systems, particularily when diatom populations in the laboratory decreased significantly. The observed changes included what appeared to be dying cells, an increase in the number of empty frustules, and cellular inclusions which appeared to be gametic,

particularly in Stephanodiscus. Small spherical inclusions within individual cells seen at this time were interpreted to be sperm cells, and sexual reproduction is known to occur in diatoms at times of environmental change or stress (Drebes, 1977).

DISCUSSION

In two of the three experiments reported here, the degree of similarity in the measured parameters between the microcosms and the field was low, while in the third (Briones: late spring--early summer) it was high. Because diatoms are of such importance in fresh water systems our discussion is concentrated on them. We shall restrict our attention to genera of phytoplankton observed at volume densities $\geq 0.4 \times 10^5$ μ^3/ml in order to emphasize the dominant phytoplankton.

The following are among the more important conditions which have been implicated to some degree in influencing diatom population density: (1) light intensity and wavelength; (2) temperature; (3) antibiosis involving other planktonic algae; (4) grazing by zooplankton; and (5) import and export of biota and nutrients, to and from the water body of interest.

Light intensity levels, temperature, and competition from other algal species could each have been in part responsible for the disappearance of diatoms in the microcosms. That light intensity is important in the development of diatom populations is not in dispute, but quantitative data is scant and the effect of light intensity on diatom growth appears to be closely linked with temperature. Light levels at the water surface in the laboratory room housing our microcosms averaged one thirtieth that of average midday natural levels at this location, and this intensity was maintained for 12 hours, which would not be the case in a natural habitat. The field data of Talling

(1955) suggest that Asterionella divides at only slightly less than the maximum surface rate at a depth of 3 meters where the light levels were 25 percent of the intensity found at the surface. At 2.5 percent of the surface light intensity corresponding to a depth of 9 meters, cell division was negligible. Light levels may not have been intense enough to sustain viable diatom populations in our microcosms, although the high degree of tracking observed in run 2 suggests that light levels may not have been of major importance.

Temperature is an important factor in the growth and development of diatoms, but its effects appears species specific and dependent on geographical location (Hutchinson, 1967; Werner, 1977). Laboratory data on temperature tolerance of diatoms can be questioned, because at extreme temperature ranges the organisms may be persisting in a non-reproductive state in an unsuitable environment. Our microcosms were maintained at a constant temperature (19 ± 1°C), a temperature which may not be optimal for development of the diatom species present. Field data suggest that an optimal temperature range would be from 5-15°C (Hutchinson, 1967). In this regard, it is noteworthy that in the experiment in which microcosm diatom densities matched most closely those in the field, the microcosm water temperature was closest to that in the reservoir (Briones: late spring--early summer).

With regard to the third possible influence, antibiosis by other algae, allelopathic inhibition of diatom growth by blue-green algae

such as Anabaena has been demonstrated (Keating, 1978), but few blue-green algae were present in our microcosms.

Zooplankton numbers were generally too low to warrant statistical analysis, although certain patterns did emerge. In two of the three experiments (runs 1 and 2) zooplankton densities in the microcosms were considerably higher than in the field samples throughout most of the run. For example, in run 1 during days 13-41, Daphnia density in the microcosms averaged 3.7×10^6 μ^3/ml, while in the reservoir during this period Daphnia density remained below 1×10^4 μ^3/ml, while in the reservoir during this period, Daphnia were not recorded. In run 2, during days 28-49, Daphnia density in the microcosms average 1.6×10^6 μ^3/ml. In run 3, Daphnia densities in the microcosms during the period of diatom decline, days 16-29, were below 1×10^4 μ^3/ml. Using the observed Daphnia densities along with the diatom densities and size distributions in the microcosms, and using information about rates of Daphnia grazing on diatoms (Infante, 1973), we were able to estimate crudely the potential effect of grazing in our laboratory systems. In runs 1 and 2, the decline of the diatom populations could have been a consequence of grazing, while in run 3 grazing was unlikely to have played a major role.

Condition 5, the import or export of nutrients and biota from the sampling site, is likely to be of major importance. In run 2, which was carried out during a time of year when Briones Reservoir is stratified and also when there is relatively little inflow of water to the reservoir, the epilimnion is a well-isolated system. Influxes of

nutrients such as silica to the epilimnion are generally low during this period. Under such circumstances, it is not surprising that the microcosms, which were stocked from epilimnion waters, behaved similarly to the lake epilimnion. Neither the microcosms nor the field sampling site had their nutrients replenished during the course of the experiment. In contrast, in runs 1 and 3, where the diatom populations of the microcosms dropped sharply relative to those in the field, the field sampling site was not hydrologically isolated. In particular, lake overturn and watershed inputs linked the sampling site to external sources of nutrients, while the microcosms were effectively isolated water bodies during the run.

Results of chemical measurements in Briones in the fall and winter of the year subsequent to run 3 reinforce this conclusion. From November, 1980 to January, 1981, a turnover and mixing was observed in Briones, with concomitant increases in silicate concentration in the upper 15 meters of the surface waters from 27 μM(Si) prior to turnover to 44 μM(Si) after turnover. Since silica is crucial for the formation of diatom frustules these results are consistent with the relatively rapid decline of the diatoms in the field in run 2 and in all the microcosms.

Import and export of biota from the sampling sites is also a possibility. Our field sampling site, which was also the site of initial collection of reservoir water, was a single location near the center of the reservoir. Horizontal and vertical mixing within the lake could have brought diatoms to the site. In the late fall--early

winter experiments new species of diatoms appeared in the field samples while no new species appeared in the microcosms. Gusty wind conditions and subsequent horizontal and vertical mixing of the epilimnion prevailing at this time could have resulted in patchy distribution of reservoirs phytoplankton.

Although Moss (1969) concluded that turbulence was necessary for the proper suspension of Stephanodiscus rotula in the water column, it is unlikely that the discrepancy observed between diatom densities in the microcosms and the field in runs 1 and 3 resulted form the sinking of diatoms from the water columns in the microcosms. In particular, samples taken at intervals from material settling out on the bottoms of the microcosms did not reveal the presence of viable diatoms.

The microcosms, as presently designed and operated, were intended to mimic an isolated epilimnion, which was found to be the case. It is uncertain whether microcosms can be successful in maintaining essential diatom dynamics under other circumstances such as during periods of lake turnover.

Our microcosm design and sampling procedures are being modified to take into account the importance of diatom population dynamics in freshwater microcosms. We plan alterations in our microcosm design which will allow us to mimic more closely the parent natural water body, including lower temperatures and higher light intensities. Ambient silica concentrations, essential in diatom frustule formation and one of the more important limiting factors in diatom population development, will be more closely monitored. Both during initiation

of microcosms and subsequent monitoring of the natural system greater emphasis will be placed on vertical and horizontal distributions of lake biota. In these ways, we hope to extend the useful life of pelagic microcosms, and increase the range of conditions under which plankton succession patterns parallel closely those in the parent natural system.

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Table 1. Synopsis of experimental organization.

Experiment	Duration	Inclusive Experimental Dates	Container Sizes (L)	Number Replicates	Surface Growth Mitigation	Aeration	Tracking Lake	Parameter Sampling Interval
Lafayette: Late fall--early winter	13 weeks	19 Oct. 1978-17 Jan. 1979	50	3	Pour	+	Lafayette Reservoir	weekly
Briones: Late spring--early summer	11 weeks	20 Apr. 1979-5 July 1979	50	3	Pour	+	Briones Reservoir	weekly
Briones: Late fall, early winter	8 weeks	14 Nov. 1979-11 Jan. 1980	50	3	Siphon	-	Briones Reservoir	weekly

Table 2. Lafayette reservoir, late fall--early winter.

	Days 7-22			Days 22-56			Days 56-92		
	x	δ	S	x	δ	S	x	δ	S
				Diatoms ($x10^5$ μ^3/ml)					
		Fragilaria			Fragilaria Stephanodiscus			Fragilaria Stephanodiscus Asterionella	
Field	6.08	0.61		17.46	1.45		14.33	1.25	
Lab.	0.67	0.10	0.15						
				NH_4^+(μM(N))					
Field	3.68	0.38		7.9	0.41		13.41	0.53	
Lab.	6.8	0.53	0.9	4.1	0.27	2.0	4.5	0.28	2.1
				NO_3 + NO_2 (μM(N))					
Field	3.2	0.83		4.23	0.86		5.56	0.76	
Lab.	4.2	1.06	0.3	4.7	0.99	0.75	6.7	0.86	0.7

Table 3. Briones reservoir, late spring--early summer.

	Days 7-14			Days 14-56			Days 56-77		
	x	δ	S	x	δ	S	x	δ	S
				Diatoms ($x10^5$ μ^3/ml)					
				Stephanodiscus					
Field	15.1	1.82		3.6	0.23				
Lab.	14.0	1.76	2.2	2.08	0.17	0.47			
				NH_4^+ (μM(N))					
Field	5.15	0.53		3.29	0.25		2.95	0.25	
Lab.	5.1	0.53	0.4	5.2	0.30	0.4	3.5	0.32	1.56
				NO_3 + NO_2 (μM(N))					
Field	1.65	0.53		1.44	0.30		2.25	0.48	
Lab.	3.4	0.79	0.7	4.0	0.59	0.6	5.9	1.01	3.1

Table 4. Briones reservoir, late fall--early winter.

	Days 7-14			Days 14-56		
	x	δ	S	x	δ	S
Diatoms ($x10^5$ μ^3/ml)						
	Stephanodiscus			Stephanodiscus Fragilaria Asterionella		
Field	2.94	0.30		2.98	0.26	
Lab.	1.62	0.21	0.93	0.22	0.09	0.24
	Days 7-21			Days 21-59		
NH_4^+ (μM(N))						
Field	4.15	0.40		3.91	0.40	
Lab.	4.9	0.45	0.64	4.6	0.28	1.6
$NO_3 + NO_2$ (μM(N))						
Field	2.65	0.59		4.73	0.73	
Lab.	3.6	0.80	1.0	4.3	0.62	0.4

FIGURE CAPTIONS

Fig. 1. Lafayette reservoir: late fall--early winter, 1978-79. (a) Field temperature and (b) diatom populations for field and laboratory microcosms. Data for microcosms given as ranges. All laboratory diatoms are Fragilaria. The circles above each field data point represent relative abundances of the designated diatom species.

Fig. 2. Briones reservoir: late spring--early summer, 1979. (a) Field temperature and (b) diatom populations for laboratory microcosms. Data for microcosms given as ranges. All laboratory diatoms are Stephanodiscus. The circles above each field data point represent relative abundance of the designated diatom species.

Fig. 3. Briones reservoir: late fall--early winter, 1979-80. (a) Field temperature and (b) diatom populations for field and laboratory microcosms. All laboratory diatoms are Stephanodiscus. The circles above each field data point represent relative abundances of the designated diatom species.

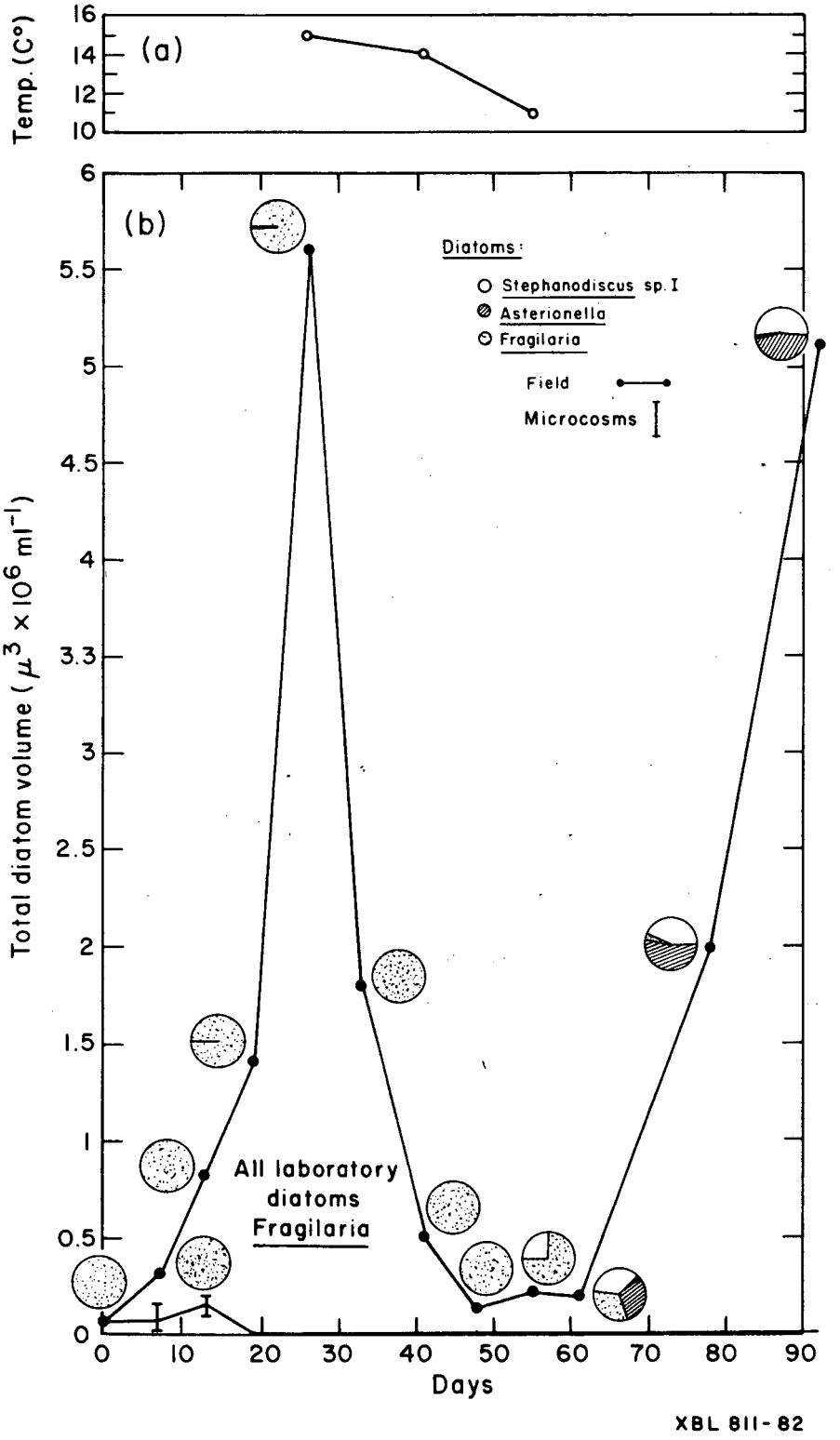

Fig. 1. Lafayette reservoir: late fall--early winter, 1978-79.

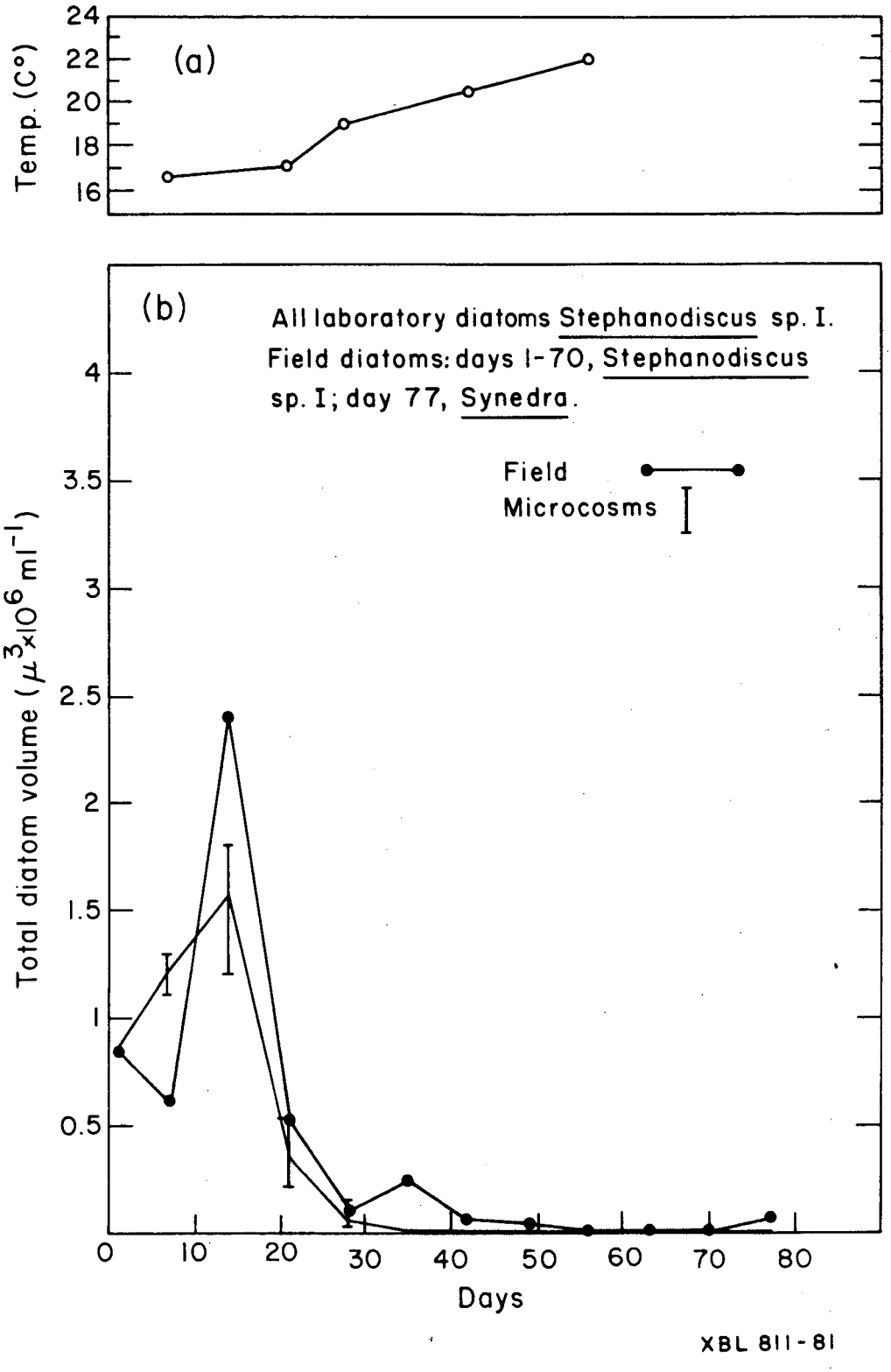

Fig. 2. Briones reservoir: late spring--early summer, 1979.

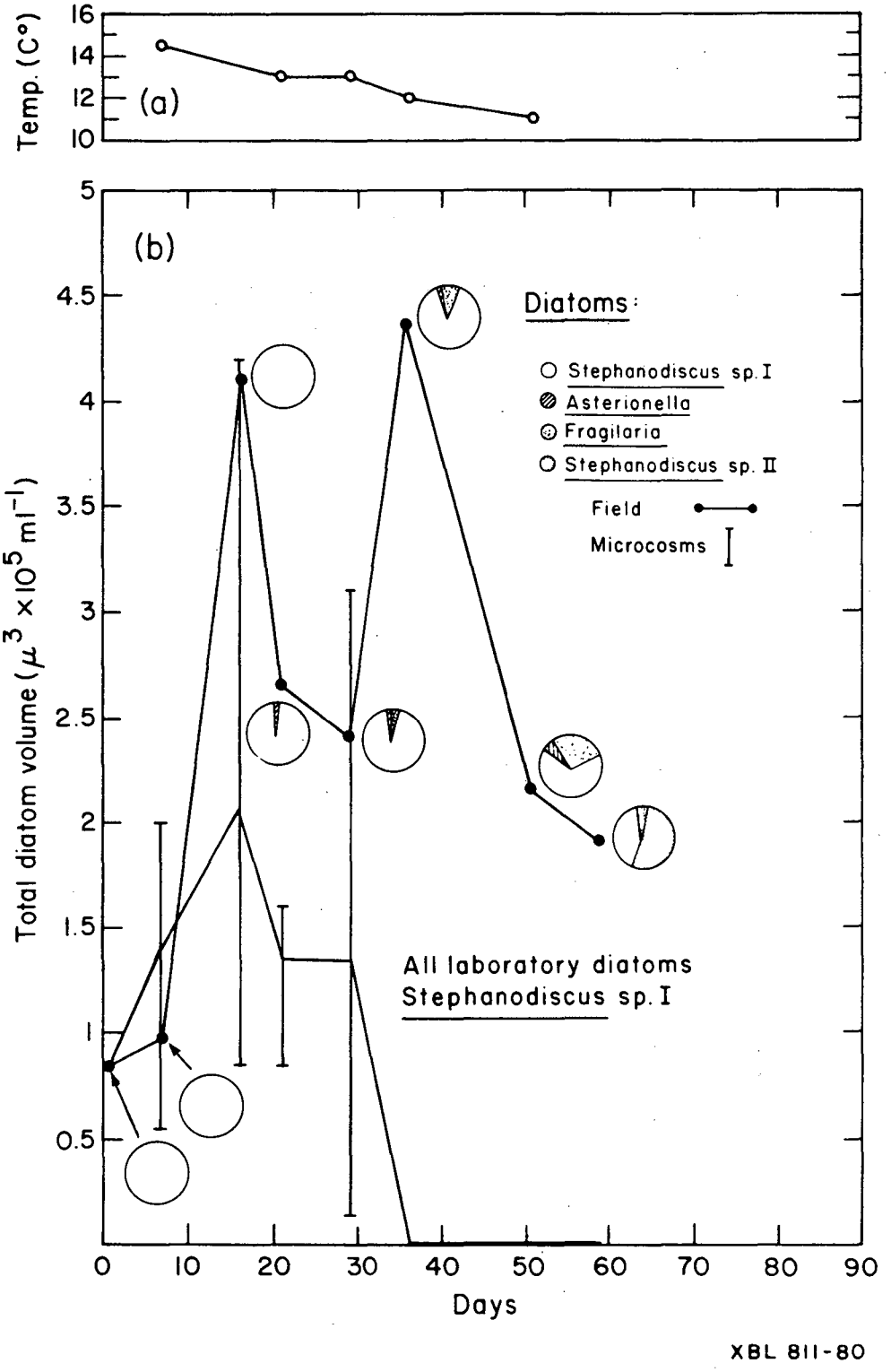

Fig. 3. Briones reservoir: late fall--early winter, 1979-80.

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