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COMMUNITY DEVELOPMENT IN FRESHWATER MICROCOSMS

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ABSTRACT

Two cylindrical freshwater microcosms with a volume of 700 ℓ were maintained under controlled laboratory conditions for 190 days. The two microcosms were identical with regard to initial chemical composition and biological inocula, with the exceptions that in one microcosm (designated Tank 2) mosquitofish (Gambusia) and herbivorous catfish (Placostomas) were added. Three distinct communities developed in the tanks: (1) a phytoplankton-zooplankton assemblage and (2) two periphyton-zoobenthos communities associated with the sides and bottom of the tank, respectively. Community development and successional patterns were similar in both tanks. Major differences between the tanks involved timing of succession of the zooplankton and zoobenthos, attributable to predation by fish, principally Gambusia. A major drawback for these microcosms as use for experimental analogs such as lakes was a luxuriant periphyton growth which eventually overwhelmed the biomass of the system. The tanks displayed a degree of successional replicability, a large number of species, and a diversity of community development. Microcosms of this size could find use as experimental systems for higher level trophic manipulation and observation of life cycles not amenable to field studies.

INTRODUCTION

Laboratory research in general, and freshwater microcosm research in particular, has recently emerged as an autonomous field (Cooke, 1971). While much is known of freshwater community and floral and faunal population structure (Hutchinson, 1967) attempts to study aquatic communities under controlled conditions in the laboratory are few (e.g., Neill, 1975). Many freshwater organisms have complex life cycles involving different stages inhabiting different environments at different times, and optimally one would want to be able to follow all developmental stages of a given species. In most lakes this is difficult due to size and environmental heterogeneity.

In the present study two microcosms of the same size (700 ℓ), initial nutrient composition, and organismal inocula, and maintained in a constant environment, are assessed individually and on a comparative basis with regard to community development. One tank was stocked with the mosquitofish Gambusia and the herbivorous catfish Placostomas, while the other was not. Although the most intensive studies involved the phytoplankton and zooplankton, occasional benthic sampling and general observation in all parts of the tanks provided an overall picture of community development. Due to their size and surface/volume ratio, the microcosms resembled small ponds. While having drawbacks discussed elsewhere (Jassby, et al., 1977b), these microcosms offered ease of manipulability and control of environmental conditions. Aims of this study were to analyze components of the microcosm, such as the phytoplankton, zooplankton, and zoobenthos, and ascertain any developmental similarities with natural systems.

Laboratory created analogs could have use as experimental freshwater ecosystems. Additionally, these microcosms could be useful for the study of community structure and trophic interaction.

In a previous analysis and discussion of microcosms of a similar size, Jassby, et al. (1977a,b), concluded the following with regard to their community structure: (1) a shift from larger to smaller zooplankters due to predation by fish (Gambusia) on larger zooplankters, (2) a concomitant increase in bacteria, phytoplankton, and rotifer number in those tanks with fish due to a decrease in the grazing pressure of the larger the zooplankters, and (3) an oscillating phytoplankton community which was controlled by abundance of larger zooplankters, notably Daphnia pulex. These findings were consistent with what is known to occur natural systems.

In some as yet unknown ways aquatic microcosm size affects every level of ecosystem development. The larger the microcosm size, the greater possibility for diverse community development and, it is suspected, the greater the time rate for community succession. While this paper describes a community development perhaps unique to only one size of microcosm, similarities between these and microcosms of different sizes should elucidate to what degree laboratory aquatic microcosm community structure and development can simulate to that of natural systems.

METHODS AND MATERIALS

The microcosm set-up is described in detail by Jassby, et al. (1977b) and will only be briefly outlined here. The microcosms were 2 cylinders 60.9 cm in radius and 75.8 cm in height, designated Tanks 1 and 2. Sand gravel 4 cm in depth was placed on the bottom of each tank as a benthic substrate. The systems were maintained in a temperature controlled room at 19 $\pm$ 1°C and were illuminated by 8 banks of fluorescent lights on a 12:12 light dark cycle. Water used to fill the tank was from the laboratory deionized water system. Chemical enrichment was made from stock solutions of a freshwater algal medium (Woods Hole MBL; Nichols, 1973).

Biological inoculation of each tank (assigned in time as day 0) consisted of 3.5 ℓ of well-mixed lake water taken from the littoral of the local Lake Anza. Faunal additions were made at irregular intervals (Table 1). Additions were identical in both tanks with the exceptions of the introduction of Gambusia (mosquitofish) and Placostomas (herbivorous catfish) into Tank 2.

The tanks were monitored for 190 days. Biological monitoring of the microcosms consisted of sampling the "pelagic" zone (the water column) and the "benthic" zone (the sides and bottom). Phytoplankton was sampled with a plastic tube the height of the water column and provided with one partially closed end for ease of sampling. The tubes provided an integrated sample. Three samples were taken at the center, middle, and perimeter of the tanks to compensate for patchiness. Phytoplankton were counted using a Sedgewick-Rafter cell and a Reichert Zetopan microscope equipped with phase contrast. Zooplankton sampling

was done with a Wildco plankton bucket outfitted with 64 μm Nitex nylon mesh. Sampling procedure was the same as for phytoplankton. Counting of protozoa was done in a similar manner as for the phytoplankton. All other zooplankton counting was done with a dissecting microscope and a gridded square plastic petri dish. Larger zooplankton, such as Daphnia and Simocephalus, were counted in size classes of 0.2 mm increments.

The sides and bottom of the tanks were examined periodically. Side samplers were constructed from plexiglas strips 79 cm in height, 7.5 cm in width, and 0.5 cm in thickness. Three sets of standard microscope slides (two in each set) were affixed with small dabs of silicone sealant at regular intervals to the plexiglas, such that a depth profile could be obtained. The four plexiglass strips were clamped to the sides at regular intervals around the periphery of each tank. The microscope slides were examined at intervals throughout the experiment. The plexiglas strips were taken from the tanks and slides removed by cutting the silicone sealant carefully with a scalpel. Three glass slides, one from each depth interval, were removed for each examination. After cleaning and drying the bottom of the slides and placing on top of a clean slide, examination was made under the microscope. Only attached flora and closely associated fauna could be observed by this method. To collect side fauna which would not necessarily be collected with the side samplers, a net, the leading edge form-fitted to the tank sides and outfitted with a 64 μm mesh net, was used. When drawn up the tank side, with minimum exposure to the "pelagic" zone of the tank, rotifers and crustaceans associated

with, but not necessarily attached to, the tank sides, were collected. The volume of water which passed through the net could be estimated, and the sample collected compared with an equivalent volume of a pelagic sample.

For bottom samples, collecting vials 5 cm in height and 2.5 cm in diameter were cut so as to make their height equal to the depth of the sand. A series of small holes were drilled in the sides to allow the passage of infauna in and out of the vials. A stainless steel wire loop positioned at the top of the vials provided a means to remove the vials from the tanks. A total of 16 bottom samplers were placed in each tank, arranged at regular intervals in radiating rows of 4 each, reaching from the center to the periphery of the tank, dividing the tank bottom into quadrants. Bottom samplers were examined at the same times as the side samplers. Four samples, from the center to the perimeter of each tank, were examined at one time. They were raised from the bottom of the tanks and examined by carefully spreading the sand grains in a fingerbowl and observing under a compound microscope.

Detailed general observations were made at weekly intervals on the tanks, and notes were made regarding to relevancies such as biological succession and general behavior of zooplankton. While generally qualitative in nature, such notes provided a valuable overview of general tank development.

RESULTS

General Tank Development

A general overview of the most outstanding aspects of community development within the tanks is given here to orient the reader (Figs. 1-4). General community development and structure was similar in both tanks. The presence of the fish, particularly Gambusia, effected timing, but not overall pattern, of succession. Both tanks had an initial phytoplankton peak dominated by diatoms and green algae at about the same time, Tank 1 on day 28 and Tank 2, day 35 (Fig. 1a,b). A reddish-brown species of Oscillatoria which appeared on the sides and bottom of both tanks by day 42 had disappeared by day 56 (Fig. 2a,b) Heavy algal growth was present on the tank sides by day 49, dominated by a small unidentified filamentous green algae and the diatom Navicula. There was an emergence of Tanytarsus adults by day 42, and many adult flies were present in the tank room (Fig. 3a,b) At this time also there were many Tanytarsus larval tubes on the sides of the tanks, and circular areas around the tubes indicated where the midge larvae had been eating the algae. By day 63 phytoplankton numbers had decreased and periphyton growth had decreased noticeably in vigor. Phytoplankton number decrease was thought due to grazing by zooplankton, particularly Daphnia pulex, which reached high densities in both tanks by day 56 (22-25 individuals ℓ^{-1}; Fig. 4a,b). D. pulex ephippia began to appear on the surface of the water by day 56, and by day 77 hundreds were present around the tank rims. On day 70 the macroalga Cladophora, which was soon to dominate algae growth on the tank sides, had appeared. The Cladophora strands grew quickly

and reached lengths of 30 cm or more by day 119 in Tank 1. By day 147, loose clumps of Cladophora were present in both tanks, reminiscent of Cladophora balls of temperate lakes (Smith, 1950). The gastropod Physa, which was introduced into the tanks on day 49, and achieved tremendous populations (≈10 cm^2) in Tank 1 by day 105, had by that time eaten much of the attached algae on the sides of the tanks with the exception of the Cladophora. Populations of Physa in Tank 2 were smaller and developed later, which was thought to be due to predation of newly emerged snails by Gambusia and Placostomas. The ostracod Cypridopsis achieved high population densities in both tanks after the lush development of Cladophora and were seen grazing the Cladophora strands, presumably feeding on epiphytic algae. At the end of the experiment the tank sides were dominated by Cladophora and Cypridopsis.

Phytoplankton Succession

There were two phytoplankton peaks in each of the tanks, apparently grazer controlled. When Daphnia pulex disappeared from the plankton of Tank 1 on day 154, phytoplankton levels had begun to increase by day 161. In Tank 2 the disappearance of D. pulex was brought about much sooner (day 98) due to predation by Gambusia, which were seen to actively seek out and eat the Daphnia. Phytoplankton numbers begin to increase by day 105 in Tank 2 after the disappearance of Daphnia from that tank (compare Figs. 1a,b with 4a,b).

Succession of types of phytoplankton was the same for both tanks. The first peak in both tanks was dominated by diatoms and green algae, although the greens dominated in both numbers and volume (Fig. 5a-d). Dominant species include the filamentous green Rhizoclonium,

the solitary Golenkenia, and a small round green nannoplankter, from 2-4 μm in diameter, possibly Chlorella. Dominant diatoms included Synedra and Cyclotella. The fact that all species of algae decreased after day 35 despite the presence of sufficient nutrients for growth (Jassby et al., 1977b, Fig. 1b) indicates that Daphnia pulex is an efficient and general grazer. The second peak in both tanks was dominated by the crytophyte Cryptochrysis, which reached much higher levels in Tank 2 than 1 (5.0 vs 2.0 $mm^3\ \ell^{-1}$) (Fig. 5e,f). During the initial phytoplankton peaks a total of 19 species was found (Table 2). A few of these species, such as Sphaerocystis and Treubaria, are considered euplanktonic and are not normally a component of the benthos.

The period of low phytoplankton biomass in both tanks was also a period of low diversity, from 2-5 species being found at a given time. The two most abundant species were LRGT's* (Chlorella?) and the cryptophyte Chroomonas. Euplankters such as Schroderia and Ankistrodesmus appeared sporadically.

Benthic Algae

Several differences were noted between the populations of phtyoplanktonic and benthic algae: (1) the species composition of the benthic algae differed from that of the phytoplankton, (2) the only alga encountered on the gravel bottom was the aheterocystic blue green

* LRGT is a general term to denote single unidentifiable round green algae cells from 2-10 μm in diameter. Some of these were quite possibly species of Chorella.

Oscillatoria, and (3) the tank sides, while exhibiting algal succession, eventually became overwhelmed by the macrophyte Cladophora.

By day 56 Rhizoclonium and a diatom (Navicula sp.) were found on the sides of Tank 1. It is noteworthy that living Rhizoclonium was found in the plankton of Tank 1 on day 63, indicating that this normally benthic alga was sloughing off the tank sides. Cladophora, which appeared in both tanks by day 70, was found in association with the same species of Oscillatoria encountered on the tank bottoms. By day 84 Cladophora had become dominant, with strands in Tank 2 up to 30 mm in length growing laterally from the tank sides. By this time the periphyton began to diversify, and the diatoms Navicula, Gomphonema, and the stalked Brébissonia were found on the tank sides. An unidentified diatom was present growing epiphytically on Cladophora. There was some vertical zonation of algae noted. Qualitatively more algae appeared to be growing on the top 1/3 of the tanks than the bottom 2/3, and the species showed relative differences in abundance. In Tank 1 on day 105 small round yellow-brown unicells (5 μm in diameter) were most abundant in the top 1/3 of the tanks and were progressively less abundant towards the tank bottom. Navicula was the most abundant alga, other than Cladophora, on the bottom 2/3 of the side. Whether this vertical zonation was due to a decrease in light intensity or differential grazing by the snail Physa is not clear. By day 105, Cladophora began to be found in dense growths and was, on occasion, cropped from the tanks.

Zooplankton and Zoobenthos Succession

In both tanks there was an initial rapid succession of protozoans (principally Pseudomicrothorax), rotifiers, and crustaceans (chiefly the cladoceran Daphia pulex and the copepod Cyclops vernalis) (Fig 6a,b). In Tank 2 the crustacean peak ended on day 98 due to predation by Gambusia, whereas in Tank 1 D. pulex was found in the plankton until day 154. In both tanks as phytoplankton numbers rebounded due to abated grazing pressure by the crustaceans, there was a second rotifier increase, but not a protozoan or crustacean increase. Thus, phytoplankton maxima in the tanks were thought to be controlled of grazing by crustaceans, chiefly D. pulex.

Zoobenthic succession was closely linked with periphyton growth, and in this sense simulated phytoplankton-zooplankton succession. Periphyton growth on the tank sides reached a visually observable maximum on day 49 in both tanks. Tanytarsus midge larvae were seen in large numbers ($\approx$1 larva/cm^2) on the tanks sides on this day, and reached a maximum in the water column (24 ℓ^{-1}) on day 63, these high numbers presumably reflecting the dense populations on the tanks sides. Simocephalus velulus, a benthic cladoceran, reached maximum numbers in the plankton (15 ℓ^{-1}) on day 49 in Tank 1. The ostracod Cypridopsis did not appear in Tank 1 until day 112 and in Tank 2 until day 147. The delay in development of ostracod populations in tank 2 was possibly due to predation by Gambusia. The relatively late appearance of Cypridopsis in both tanks may be due, in part, to their detritivorous habit and the subsequent later development of a particulate detrital pool, as speculated by Cooke (1967).

Protozoa

Protozoans, specifically the ciliate Pseudomicrothorax, were very abundant in the plankton of the tanks from days 14-21, up to 35,000 ℓ^{-1} in Tank 2 on day 21 (Fig. 6b). After this time their numbers dropped precipitously. It was thought that initial high protozoan numbers were due to unhindered feeding on phytoplankton. Their decrease in numbers may be explained by competition from phytoplankton feeding rotifiers. Greatest planktonic protozoan diversity was found in the first 35 days of tank observation. A euplanktonic heliozoan (Actinophrys) was found in low numbers (2-5 ℓ^{-1}) on day 35 in Tank 2. Microscopic examination of floating rafts of Oocystis on this day revealed the presence of a Paramecium, which was host for a symbiotic Chlorella-like alga, and species of Didinium and Stentor. Present in fluctuating low numbers (3-26 ℓ^{-1}) throughout the run were Pseudomicrothorax, a stalked Vorticella which readily became detached from its substrate, a Strombidium, and the zooflagellate Monas. Benthic protozoa included Euplotes and the stalked, arborescent Zoothamnion, recorded from Tanks 1 and 2 on days 84 and 105, respectively. Pseudomicrothorax may be a facultative plankter, as it was observed from side samples taken on days 84 and 105 in both tanks. The same species of Vorticella recorded from the plankton was observed attached to periphyton in Tank 1 on day 84.

Rotifera

Of the 9 rotifer species encountered in the tanks, 5 could be considered chiefly littoral and the remainder euplanktonic (Table 3). Littoral species were dominant during the first rotifer peak, while the

reverse was true during the second (Table 4). There was no correlation between any of the more abundant algal species sampled in the pelagic zone and any species of rotifer, as was the situation encountered by Edmondson (1965), so that the shift from one rotifer type to the other could not be explained on this basis. The relationship between Chroomonas and Keratella quadrata abundances in Tank 2 are compelling (Fig. 7 a,b), but a similar relationship was not so obvious in Tank 1. Follow-up experiments introducing K. quadrata to Chroomonas culture would be of value. Philodina and Lecane were periodically abundant on the tank sides, the latter being observed among the branches of Cladophora. Dicranophorus was observed ingesting whole cells of Oocystis in floating rafts of this alga on day 35. Maximum observed rotifer abundances ($400\ \ell^{-1}$) were within limits found in natural systems. Employing known rotifer filtration rates averaging 0.001 ml hr^{-1} (Blažka, 1971), and assuming a phytoplankton doubling time of one day, rotifer populations would have a negligible effect on phytoplankton abundances, which was observed to be the case.

Alona guttata

The cladoceran Alona guttata was observed to be primarily a littoral crustacean and spent the majority of time grazing on periphyton. Animals were occasionally seen moving away from the sides of the tank and swimming in the pelagic zone, but the data indicates that at a given time the majority of the population remained on the tank sides (Table 5). Abundance of A. guttata in the water column, which presumably reflected dense populations on the tank sides, peaked on days 42 (Tank 1) and 49 (Tank 2) respectively, which coincided with a peak in periphyton

abundance (Fig. 8 a,b). The greater abundances in Tank 1 vs Tank 2, (110 vs 39 ℓ^{-1}) could be a result of Gambusia predation. Growth rates of A. guttata appear high and the life span short. A resolution of the abundance curve in Tank 1 into two class sizes reveals a rapid succession of instars and a life span of 2-3 weeks (Fig. 9). A second abundance peak in Tank 1 on day 105 could be interpreted as a second generation yielding a generation time of 63 days.

Daphnia pulex

Daphnia pulex was observed to be a planktonic species. In culture no animals were seen to alight on the sides or bottom of containers. Although D. pulex presumably undergoes duirnal vertical migrations, as has been noted for other species of the genus Daphnia, lack of dark period sampling made such analysis impossible. Microcosms of this size would certainly lend themselves to depth interval sampling. Individuals were seen to congregate at times around the periphery of the tanks furthest from turbulence produced by aeration, and for this reason aeration was turned off for 10 minutes prior to sampling to permit a random distribution in the water column.

Both tanks demonstrated a similar pattern of development (Fig. 10). Initially females were more abundant, but by day 49 males had appeared and by day 56 had roughly equaled females in number (11-12 individuals ℓ^{-1} of each sex). Ephippia were first noted on the water surface by day 56. The greater percentage of males were present on day 63 (70%). Males had a smaller mean size than females and were not larger than 1.0 mm in carapace length. The smallest size of both sexes was 0.6 mm in length, while the largest females recorded were 2.2 mm

in length. Gradual population decreases after day 63 were suspected of being the result of food depletion due to intense grazing of phytoplankton (Jassby, et al., 1977b). Filtration rates of D. pulex in low algal concentrations may be quite high (30-90 mℓ day^{-1}) as has been found for Simocephulus vetulus (Sushtchema, 1958). None were found in Tank 2 after day 84, that tank stocked with Gambusia. Low numbers (2-10 $ℓ^{-1}$) were sampled in Tank 1 until day 147. Tank 2 appears to have had two generations, one peaking around day 42, and the second, day 77, while Tank 1 may have had as many as 3, peaking at days 49, 98-105, and 147.

The population dynamics presented here for Daphnia pulex are essentially those found for Cladocera in general in natural systems. After initial rapid growth and reproduction by parthenogenic females in "spring" conditions of high phytoplankton numbers, males appear, apparently due to effects of "crowding" by zooplankton other than Cladocera (Banta and Brown, 1939). Since rotifers numbers are highest in both tanks on day 28, and male D. pulex first appear on day 42 before maximum Daphnia population numbers are observed, high rotifer densities are suspect in providing a triggering mechanism for male production. Ephippial production by formerly parthenogenic females take place generally at the same time as production of males, but for different reasons, and is thought to be the result of a decreasing food supply (Slobokin, 1954). Phytoplankton numbers in both tanks had been decreasing since day 35 prior to ephippial appearance on day 56. Sexual reproduction culminating in formation of ephippia insures presence of an overwintering dispersal stage. Duration of

ephippial diapause is related to conditions of duration of exposure to light and temperature (Stross, 1966).

A curious but potentially important behavior pattern of Daphnia pulex was noted during times of low phytoplankton numbers. When faced with a low food supply in the water column, the Daphnia would aggregate arount the tank sides, and appeared to be feeding by applying their open valves to the periphyton and rapidly moving their appendages. On day 70, a time of low phytoplankton numbers in both tanks, greater numbers of Daphnia were found near the tank sides than in the water column (43 vs 15 ℓ^{-1}, respectively, in Tank 2). Such behavior may be species or population specific, and would have obvious adaptive advantages in small, shallow bodies of water.

Simocephalus vetulus

Simocephalus vetulus was observed to be a primarily a benthic cladoceran, and in culture preferred container sides as a substrate. Data for S. vetulus is too scant to make any but the most generalized statements with regard to its population dynamics within the tanks (Fig. 11). Fish predation could be a cause for the lower numbers found in Tank 2. The two population peaks in Tank 1 could indicate a generation time of about 60 days, about that found for Alona guttata and Daphnia pulex in these microcosms. Competition with A. guttata and Tanytarsus larvae could account in part for relatively low observed populations of S. vetulus. No ephippial production was seen by S. vetulus.

Tanytarsus sp.

The occurrence and abundance of the midge Tanytarsus in the microcosms present difficulties of interpretation. Originally introduced

as 5 larvae per microcosm on day 16, by day 42 large numbers of adults were present in the aquarium room (Table 6). In addition to being found on the sides of the tanks, usually oriented with antennae down towards the surface of the water, adults occurred in great numbers near the overhead bulbs used as a light source for the microcosms. Adults were phototropic and ephemeral and by day 49 few remained.

A peak of larval abundance occurred on the tanks sides on day 35. The midge larvae were observed to be grazers of periphyton, and peak abundances in the plankton occurred 2 weeks after the initially abundance growth of diatoms and small filamentous multicellular green algae on the tank sides (day 49). Circular areas free of algae marked the presence of midge larvae, as was observed in the laboratory by Cavanaugh for Tanytarsus similis (1930). Maximum larvae numbers occurred after the emergence of winged adults, and such large number of either were never again observed. The time differential involved indicates a generation time of 21 days. The reason for the lack of a second emergence of adults remains unexplained, as does the origin of the original emergence. In the latter case, relatively few numbers of adult females could be responsible for engendering the large number of observed emergent adults, but that would require the occurrence of 2 generations in 26 days, between days 16 and 42. Such a short generation time could reflect significant facets of the ecology of Tanytarsus, such as potentially very rapid growth rate of the midge larva.

Cyclops vernalis

Late copepodid and adult stages of Cyclops vernalis appeared to function as carnivorous predators, as are all those members of the genus which have been closely studied (Fryer, 1957a,b). Adult C. vernalis were seen to grasp immature ostracods (Cypriodopsis sp.) when these were presented to them in large numbers. In Tank 2, a large adult population of C. vernalis developed about 2 months after removal of the fish at the termination of the experiment (after day 190). The copepods were apparently capable of preventing a population of D. pulex from developing by feeding on the young instars. Adult female D. pulex introduced into the tank after the dense population of C. vernalis had developed were not prey items of C. vernalis. Their large size (up to 3 mm in carapace height) in comparison to C. vernalis (≈1.6 mm in length), may have been responsible for this; however, few young D. pulex were seen in that tank despite the presence of reproductive females.

Naupliar stages of C. vernalis were observed to be exclusively planktonic, while the copepodid stages were primarily benthic. Copepodid stages and adults, were, however, collected in routine plankton samples and observed swimming freely in the center of the tanks. The feeding habits of the naupliar stages are unknown, but are suspected of being herbivorous, as algal remains were seen in the guts of first and second naupliar stage animals. Copepodid stage and adults may also be capable of periodic exclusive herbivory. In a separate series of experiments in smaller (50 ℓ) microcosms dense populations (up to 600 ℓ^{-1}) of C. vernalis of all stages developed in the absence of other zooplankton.

Fecal pellets containing what appeared to be exclusively algal remains and examination of gut contents of adults revealed that at least part, and perhaps all, of their diet to be algae of the genus Cryptomonas. The feeding habits of C. vernalis may be variable depending on food supply. The species has not been studied thoroughly in the field with regard to its feeding habits (Fryer, 1957a). The possibility exists that there is a change in mode of feeding from herbivory to carnivory as development proceeds from nauplius to adult, as is suspected for C. ladakanus (Hutchinson, 1937).

Large populations of 1st and 2nd naupliar stages developed only in Tank 1, in densities up to 271 ℓ^{-1} (Fig. 12a,b). Older naupliar and copepodid stages were not found in as great abundance as the 1st stage nauplii in either tank, perhaps due to cannibalism (Fig. 13). The occurrence of a greater number of nauplii in Tank 1 than 2 could have been due to direct predation by fish, but observation did not support this view. Gambusia of an equivalent size to those in the tanks, exposed to high concentrations (200 ℓ^{-1}) of nauplii, were not seen to feed. Rather, fish predation of adult copepods, particularly females made more visible carrying egg sacks, seems a more likely possibility.

Cypridopsis sp.

Although ostracods form one of the most conspicuous and abundant invertebrate components of the benthos, they are virtually unknown as limnoplankters (Hutchinson, 1967). The presence and relative abundance of Cypridopsis in our tanks were associated with growth of the macrophytic alga Cladophora and predation by Gambusia (Fig. 4a,b). First

sampled in Tank 1 by day 84, relatively large numbers (19 $^{-1}$) occurred by day 147. The dark brown valves of the adults made them easily visible, although younger instars were noticeably lighter in color. Cladophora was first noted in both tanks, in strands up to 30 cm in length, by day 98. No Cypridopsis were seen in the water column of Tank 2 until day 140. In Tank 1 the Cladophora was seen to harbor relatively large populations of Cypridopsis, which grazed the epiphytic algae found on the Cladophora while leaving the Cladophora undamaged. The Gambusia were unable to penetrate the dense growth of Cladophora which had developed by day 147, allowing protection for the ostracods. There was a relationship between abundance of Cypridopsis on the tank sides and in the water column. Relatively large numbers were first noted in Tank 1 on the sides by day 140, and by day 147 significant numbers (19 $^{-1}$) were being found in the water column.

Physa sp.

Five 5-millimeter long specimens of the gastropod Physa sp. were placed in each tank on day 56, with the aim of reducing or eliminating algal growth on the tank sides. Snail population abundances and peaks differed between the 2 tanks. Snail populations reached a maximum first on day 105 in Tank 1, with as many as 100 snails 4 mm in length observed on a 100 cm^2 area of tank side (Table 7). Concomitant with this abundant population was a noticeable selective reduction of algal growth. While the snails were effective in removing unicellular and smaller multicellular algae, they were ineffective in cropping with the Cladophora which began to appear by day 98. Populations did not peak in Tank 2 until day 168. The staggered population peaks were

thought to be the result of fish predation on young snails. In a separate experiment, Gambusia of the same size as the fish in the microcosms were seen to readily feed on young snails which had recently emerged from their gelatinous egg capsules. With no fish present in Tank 1, snail populations quickly reached a maximum; however, in Tank 2, with Gambusia present, populations took longer to develop.

OTHER FAUNAL COMPONENTS

The oligochaete Pristina was found on days 84 and 112 in Tank 2 in examined bottom samples, living amoung sand grains. Specimens were occasionally found in plankton samples, but considering the reported behavior of naid oligochates to leave the benthos, occurrence in the plankton is not surprising (Pennak, 1953, p. 280). Two specimens of larval mites of an unknown species were collected from tank side samples taken on day 105 in Tank 2. Due to their interesting and complex life histories, an occurrence of mites in the microcosms could provide an opportunity for study of their life cycle. The mites were seen clinging to Cladophara. One unidentified nematode was collected in a bottom sample on day 98 of Tank 1.

The (Placostomas) catfish, initially introduced into Tank 2 to graze periphyton, had negligible observable effect. They appeared to be less efficient in algal grazing than the gastroped Physa, although they could conceivably have contributed to the lower Physa populations in Tank 2 by eating very young snails. The catfish were sluggish at temperatures at which the microcosms were maintained (19 $\pm$ 1^{o}C).

Discussion

Two possibilities emerge as uses for laboratory microcosms of this size: (1) as experimental systems in lieu of larger and less manageable naturally occurring freshwater bodies at the ecosystem level and (2) as systems for use in study of the biota at the community and population level. The first use depends on broad demonstrable analogies between the microcosm and naturally occurring systems, optimally at the ecosystem level. The second does not and requires

only that particular components of the system, notably at the community level, are able to thrive and reproduce, thus rendering themselves available for study. Two analogies between microcosms of similar size to those discussed here and natural water bodies have been forewarded previously (Jassby, et al., 1977a) viz., a shift in zooplankton type from large to smaller sizes in the presence of planktivorous fish and a grazer-controlled oscillating phytoplankton-zooplankton community. While not ruling out microcosms of a similar or smaller size as possibilities for laboratory experimental systems, the use of these microcosms as systems for community and organismal study will be stressed here. Only further experimentation with microcosm size, nutrient level, and period of observation (up to 2 years or more) under laboratory conditions, as are being planned in this laboratory, will further reveal the potential of microcosms for experimental systems.

Algal succession in freshwater systems, notably lakes, is thought to depend on a complex interaction of physical, biochemical, and biological factors (Hutchinson, 1967, p. 426). While the two phytoplankton peaks in both tanks are the result of grazing by zooplankton, the phytoplanktonic algal associations and successions were similar in both tanks, a diatom-green algal association in the first peak, followed by a period of low algal biomass, followed by a second peak dominated by the cryptophyte Cryptochrysis. These associations and successions were not typical of any known lakes, and the species composition was too low for the applicability of various phytoplankton indices (e.g., Nygaard, 1949), although the initial nutrient level would anticipate a mesotrophic algal composition. Pro- and

anti-biotic factors involved in algal succession, such as those found for blue-green algae in a pond (Keating, 1977) could avail themselves to analysis in a microcosm situation.

The microcosm side and bottom periphyton communities differed from each other in species composition and in turn differed from the phytoplankton community. There were, in effect, 3 floral communities present. Compared with our knowledge of phytoplankton, much less is known concerning the biology of attached algae. There was a filmy growth of Oscillatoria on the gravel of tank bottom by day 42, and a heavy periphyton growth on the tank sides by day 49. There was an initial peak of biomass of periphyton similar to that seen in the phytoplankton 2-3 weeks earlier. Similar spring periphyton peaks have been observed in natural systems (Moss and Round, 1967). Closer analysis of the relative timing, comparative biomass, and species succession of microcosm phytoplankton and periphyton could indicate patterns of primary production in natural systems.

Cladophora was the only macrophyte to establish itself in the tanks. Macrophytes, including Cladophora, are suspected of acting as nitrogen "sinks," limiting phytoplankton growth by competing for nitrogen (Fitzgerald, 1969). With an excess of nitrogen in the system, periphyton also occurs on macrophytes. A second phytoplankton bloom occurred despite the presence of the Cladophora, and epiphytic algae was observed on the Cladophora, indicating, as verified chemically, an excess of nitrates and nitrites during the experiment. Biflagellated swarmers, probably zoospores of Cladophora, were counted in low densities (2-3 ℓ^{-1}) in both tanks on days 168 and 175. An obvious potential was

present for in depth studies of life cycles of this important genus of fouling algae.

Zooplankton succession was similar in both tanks. A protozan peak on day 21 was followed by a rotifer peak (days 28-35) and a crustacean peak, dominated by Daphnia pulex, from days 49-77. A second rotifer peak (days 156-190) followed a second phytoplankton bloom. Replicability of successional phenomena for microcosms of this size appears possible, rendering such systems useful for studying successional alterations under a known perturbation. Ecological effects of organismal interactions at higher trophic levels, such as those reported by Parker (1961) and McQueen (1969) could be studied in these microcsms.

Of particular interest are the potentials for in depth life cycle studies of individual species of the plankton or benthos. Some species seemed particularly suited to this size microcosm. Crustaceans such as Daphnia pulex and Cyclops vernalis developed large, viable, reproducing populations. The food of the naupliar stages of cyclopoid copepods is not known, but is suspected to be algae. In some lakes cyclopoid copepods are the sole zooplankter (Hutchinson, 1937). Dipteran larvae such as Tanytarsus have a high rate of secondary production as evidenced by their rapid growth rates. In some lakes, such a Baikal, immense numbers of dipteran adults coat local trees during periods of emergence (Kozhov, 1963), indicating large and potentially productive larval populations.

Microcosms of the size described here (700 ℓ) appear to have potential as tools for ecological research both at the ecosystem and community level. With further research into the nature of the freshwater

microcosms as a biological entity, the components which can be considered analogous to natural systems and those which are inherent only to the microcosm will become better understood.

ACKNOWLEDGEMENTS

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REFERENCES

Banta, A. M. and L. A. Brown, 1939. Control of Male and Sexual-Egg Production in Studies on the Physiology, Genetics and Evolution of Some Cladocera. Carnegie Inst. Washington, Pub. 513, Paper No. 39, Dept. Genetics, x+285 pp.

Blažka, P., 1971. Laboratory Measurements of Processes Involved in Secondary Production, pp. 222-295. In: A Manual on Methods for the Assessment of Secondary Productivity in Freshwaters, W. T. Edmondson and G. G. Winberg, eds., IBP Handbook No. 17 Blackwell Scientific Publ., Oxford, xxiv+358 pp.

Cooke, G. D., 1967. The Pattern of Autotrophic Succession in Laboratory Microcosms. Bioscience 17:171-721.

Cooke, G. D., 1971. Aquatic Laboratory Microsystem and Communities, pp. 48-85. In: The Structure and Function of Freshwater Microbial Communities, J. Cairns, ed., Virginia Polytechnic Institute and State University.

Cavanaugh, W. J. and J. E. Tilden, 1930. Algal Food, Feeding, and Case-Building Habits of the Larvae of the Midge Fly, Tanytarsus dissimilis. Ecology 11:281-287.

Edmondson, W. T., 1965. Reproductive Role of Planktonic Rotifers as Related to Food and Temperature in Nature. Ecol. Monogr. 35:61-111.

Fitzgerald, G. P., 1969. Some Factors in the Competition or Anagonism Among Bacteria, Algae, and Aquatic Weeds. J. Physiol. 5:351-359.

Fryer, G., 1957a. The Feeding Mechanism of Some Fresh-Water Cyclopoid Copepods. Proc. Zool. Soc. London 129:1-25.

Fryer, G., 1957b. The Food of Some Freshwater Cyclopoid Copepods and Its Ecological Significance. J. Anim. Ecol. 26:263-286.

Hutchinson, G. E., 1937. Limnological Studies in Indian Tibet. Int. Revue ges. Hydrobiol. Hydrogr. 35:134-176.

Hutchinson, G. E., 1967. A Treatise on Limnology. II. Introduction to Lake Biology and the Limnoplankton. John Wiley and Sons, NY, 1115 pp.

Jassby, A., M. Dudzik, J. Rees, E. Lapan, D. Levy and J. Harte, 1977a. Trophic Structure Modifications by Plantivorous Fish in Aquatic Microcosms. Environmental Protection Agency Report, EPA-600/7-77-096, Washington, DC, 52 pp.

Jassby, A., J. Rees, M. Dudzik, D. Levy, E. Lapan, and J. Harte, 1977b. Production Cycles in Aquatic Microcosms, Environmental Protection Agency Report, EPA-600/7-77-097, Washington, DC, 18 pp.

Keating, K. I., 1977. Allelopathic Influence on Blue-Green Bloom Sequence in a Eutrophic Lake. Science 196:885-887.

Kozhov, Mikhail, 1963. Lake Baikal and Its Life, Monographiae Biologicae, Vol. XI, The Hague, Dr. W. Junk, vi+344 pp.

McQueen, D. J., 1969. Reduction of Zooplankton Standing Stocks by Predaceous Cyclops bicuspidatus thomasi in Marion Lake, British Columbia. J. Fish. Res. Bd. Canada 26:1605-1618.

Moss, B. and F. E. Round, 1967. Observations on Standing Crops of Epipelic and Epipsammic Algal Communities in Shear Water, Wilts. Brit. Phycol. Bull. 3:241-248.

Neill, W. E., 1975. Experimental Studies of Microcrustacean Competition Community Composition and Efficiency of Resource Utilization, Ecology 56:809-826.

Nichols, H. W., 1973. Growth Media-Freshwater, pp. 7-24. In: Phycological Methods, J. R. Stein, ed., Cambridge University, xii+448 pp.

Nygaard, G., 1949. Hydrobiological Studies of Some Danish Ponds and Lakes. Part II. The Quotient Hypothesis and Some New or Little Known Phytoplanktonic Organisms, Danske Vidensk, Selsk. Biol. Skr. 7:293.

Parker, R. A., 1961. Competition Between Eucyclops agilis and Daphnia pulex. Limnol., Oceanogr. 6:299-301.

Pennak, R. W., 1953. Fresh-Water Invertebrates of the United States. Ronald Press Co., NY, ix+769 pp.

Smith, C. W., 1950. The Fresh-Water Algae of the United States, McGraw-Hill, NY, Vol. vii+719 pp.

Slobodkin, L. B., 1954. Population Dynamics in Daphnia obtusa. Kutz Ecol. Monogr. 24:69-88.

Stross, R. G., 1966. Light and Temperature Requirements for Diapause Development and Release in Daphnia. Ecology 47:368-374.

Sushtchenia, L., 1958. Kolichestvennȳe dannȳe o fil'tratsionnom pitanii-planktonnykh rachkov. Nauch. Dokl. vȳssh. Shk., Biol. Nauki 1:241-260.

Table 1. Biota stocked in the microcosms, not present in the original inocula.

Group	Day	Number Introduced Into Each Tank
Cladocera		
Daphnia pulex	16	10 females
Simocephalus vetulus	16	5, sex unknown
Alona guttata	16	10, sex unknown
Copepoda		
Cyclops vernalis	16	1-3 adults, plus an undetermined number of naupliar and copepid stages
Annelida		
Pristina sp.	16	5 of various sizes
Insecta		
Tanytarsus sp.	16	5 larvae
Gastropoda		
Physa sp.	49	5, 0.25-0.50 cm in length
Pisces (Tank 2 only)		
Gambusia affinis	34	5, 1.2 cm in length
Placostomas placostomas	59	5, 1.5 cm in length

Table 2. Species of algae found during the first phytoplankton peak (days 28 and 35) in Tanks 1 and 2.

	Tank 1	Tank 2
CHLOROPHYCEAE		
Closterium sp.	-	+
Golenkenia sp.	+	+
*LRGT I (2-5 µm diam.)	+	+
**LRGT II (6-10 µm diam.)	+	+
Oocystis sp.	+	+
Sphaerocystis sp.	+	+
Rhizoclonium sp.	+	+
Scenedesmus bijuga	+	+
Schroderia sp.	+	+
Staurastrum sp.	+	-
Treubaria triappendicula	-	+
BACILLARIOPHYCEAE		
Coscinodiscus lacustris	+	-
Cyclotella Menenghiana	+	-
Navicula sp. (20 µm length)	+	+
Synedra radians I (50 µm length)	+	+
Synedra radians II (120 µm length)	+	-
Synedra ulna	-	+
CYANOPHYCEAE		
Spirulina sp.	-	+
CRYPTOPHYCEAE		
Chroomonas sp.	_	+

*This one most likely one or more species of *Chlorella*.
**These are probably disassociated cells of *Oocystis* or *Sphaerocystis*.

Table 3. Species of rotifers recorded in tanks with their observed habitat.

EUPLANKTONIC
Aneuropsis sp.
Keratella Cochlearis
Keratella quadrata
Polyarthra sp.
CHIEFLY "LITTORAL"
Dicranophorus sp.
Lecane sp.
Philodina sp.
Trichotria sp.
Voronkowia sp.

Table 4. Percentage composition of representative rotifers during the two rotifer peaks in the "pelagic" zone of the tanks.

		Tank 1 (%)	Tank 2 (%)
Peak 1 (day 28)	*Dicranophorus* sp.	0.43	0.69
	Lecane sp.	0.33	0.28
	K. cochlearis	0.01	0.01
Peak 2 (day 109)	*Polyarthra* sp.	0.62	0.99+
	Aneuropsis sp.	0.33	--
	K. quadrata	0.05	--

Table 5. Relative number of Alona guttata on the tank side vs the center column, day 70 (number ℓ^{-1}).

	Tank 1	Tank 2
Water column	0	2
*Near tank side	35	30

*"Near tank side" is considered here to mean within one cm of the side of the tank.

Table 6. Tanytarsus abundances in tanks. Larval numbers expressed in numbers ℓ^{-1} in plankton; adults, in numbers seen on tank sides. Data for both tanks is pooled.

Day	Larvae	Adults
42	0	20
49	1	none seen
56	17	none seen
63	24	none seen
70	7	none seen
77	1	none seen

Table 7. Physa populations on the tank sides. Numbers indicate day of run.

	Tank 1	Tank 2
Appearance of egg capsules	84	98
Appearance of young snails	98	140
Large population of snails present on tank sides	105 (≈60 ind/10 cm^2)	168 (≈10 ind/10 cm^2)

FIGURE CAPTIONS

Fig. 1. Phytoplankton abundance: (a) Tank 1, (b) Tank 2.

Fig. 2. (a) Periphyton growth, Tank 1.
(A) Spike with Lake Anza water.
(B) Oscillatoria sp. first noted from tank bottom.
(C) Heavy green algal (Chlorophyceae) growth first noted on tank side.
(D) Rhizoclonium sp., Navicula sp. present on tank sides.
(E) Oscillatoria sp. no longer present on tank bottom.
(F) Oscillatoria present; Cladophora sp. noted for first time.
(G) Oscillatoria sp. dominant; Navicula sp. present Rhizoclonium sp., Cladophora sp. present.
(H) Cladophora sp. present; Oscillatoria sp. present around bases of Cladophora sp.; Navicula sp.; Gomphonema sp. present.
(I) Several large clumps of Cladophora lying on tank bottom.
(J) Cladophora only algal species present, all others grazed by gastropod Physa.

Fig. 2. (b) Periphyton growth, Tank 2.
(A) Spike with Lake Anza water.
(B) Oscillatoria sp. first noted from tank bottom.
(C) Heavy growth of greel algae (Chlorophyceae) first noted on tank side.
(D) Oscillatoria sp. no longer present on tank bottom.
(E) Cladophora sp. appears for first time; Oscillatoria sp. present.
(F) Cladophora sp. dominant; Oscillatoria sp., Gomphonema sp., (Navicula sp. present.)
(G) Cladophora balls present.

Fig. 3. (a) Development of the zoobenthos, Tank 1.
(A) Spike with Lake Anza water.
(B) Tanytarsus sp. tubes present on tank sides, many adult flies present on tank rim.
(C) Daphnia pulex ephippia noted for first time on tank rim.
(D) Maximum number (≈160) Daphnia pulex ephippia recorded from tank rim.
(E) Maximum snail (Physa sp.) population attained (≈10/cm^2).
(F) Ostracod Cypridopsis sp. seen grazing tank sides; Daphnia pulex observed near sides of tank.
(G) Cypridopsis sp. population reaches maximum.
(H) Physa sp. population minimum.

Fig. 3. (b) Development of the zoobenthos, Tank 2.
(A) Spike with Lake Anza water.
(B) Tanytarsus sp. tube present on tank sides; many adult flies present on tank rim.
(C) Daphnia pulex ephippia noted for first time.
(D) Young snails (Physa sp.) recorded for first time.
(E) Ostracod Cypridopsis sp. recorded for first time grazing epiphytes of Cladophora.

Fig. 4. Abundance of Daphnia pulex: (a) Tank 1, (b) Tank 2.

Fig. 5. Abundance of green algae (Chlorophyceae) in water column:
(a) Tank 1, (b) Tank 2.
Abundance of diatomes (Bacillariophyceae) in water column:
(c) Tank 1, (d) Tank 2.
Abundance of cryptophytes (Cryptophyceae) in water column:
(e) Tank 1, (f) Tank 2.

Fig. 6. Zooplankton succession in (a) Tank 1 and (b) Tank 2 (from Jassby, et al., 1977b).

Fig. 7. (a) Abundance of cryptophyte Chroomonas in water column, Tank 2. (b) Abundance of rotifer Keratella quadrata in water column, Tank 2.

Fig. 8. Abundance of the cladoceran Alona guttata in the water column: (a) Tank 1, (b) Tank 2.

Fig. 9. Population structure of Alona guttata in Tank 1.

Fig. 10. Population structure of the cladoceran Daphnia pulex in Tanks 1 and 2. Each pip on the vertical axis represents two individuals. Black portions of histograms are males, straited, females; (*) indicates no data taken on these dates.

Fig. 11. Population structure of the cladoceran Simocephalus vetulus in Tanks 1 and 2. Each pip on the vertical axis represents 2 individuals.

Fig. 12. Abundance of the 1st naupliar stage of the copepod Cyclops vernalis: (a) Tank 1, (b) Tank 2.

Fig. 13. Distribution of developmental stages of the copepod Cyclops vernalis in Tank 1.

Fig. 14. Abundance of the ostracod Cypridopsis sp. in the water column: (a) Tank 1, (b) Tank 2.

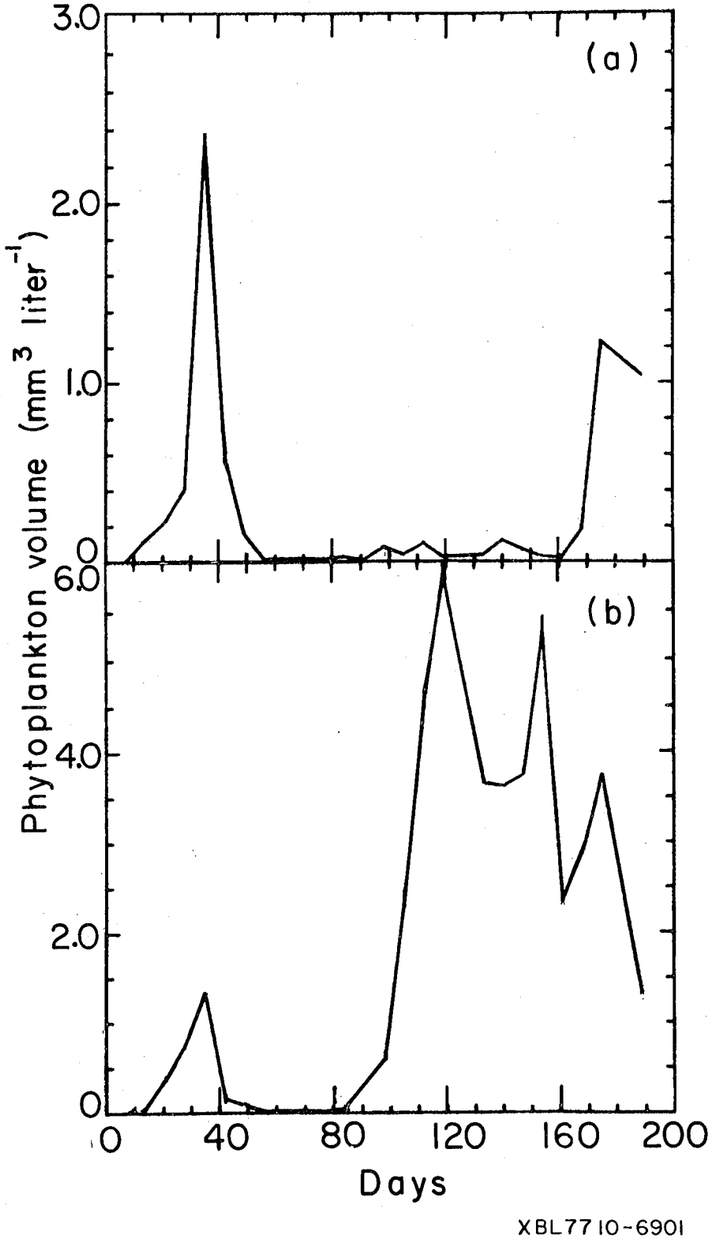
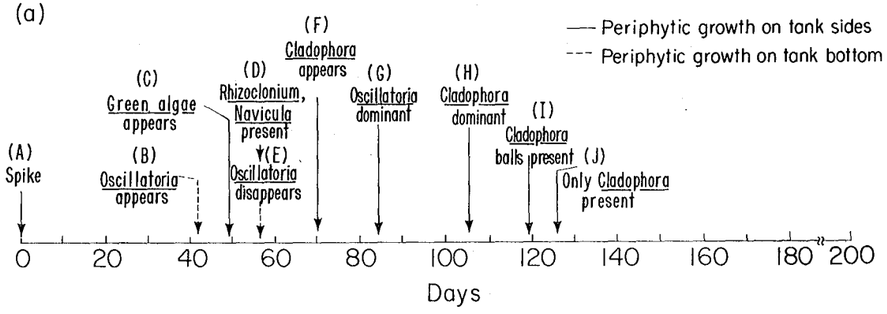


Fig. 1



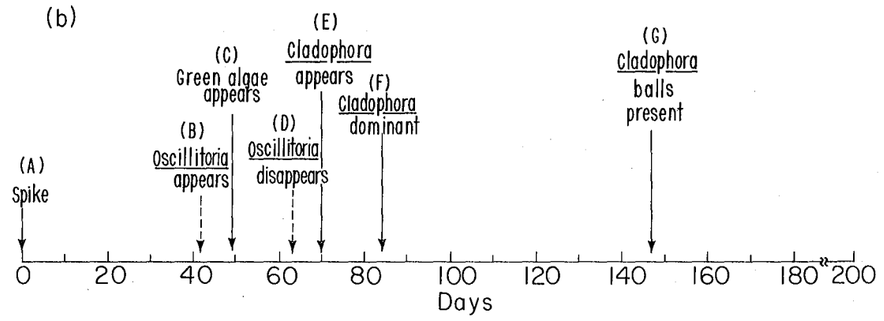


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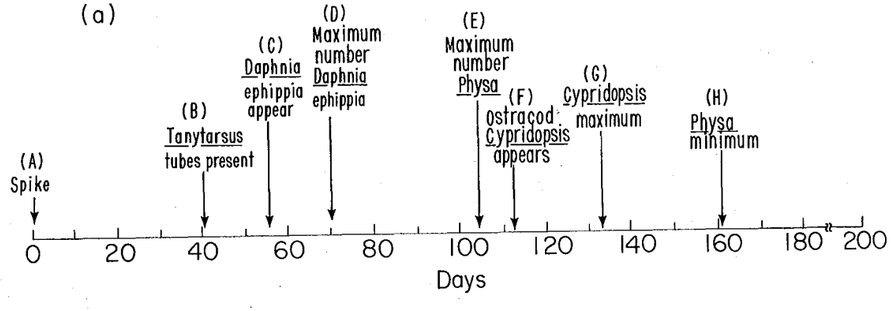
Fig. 2



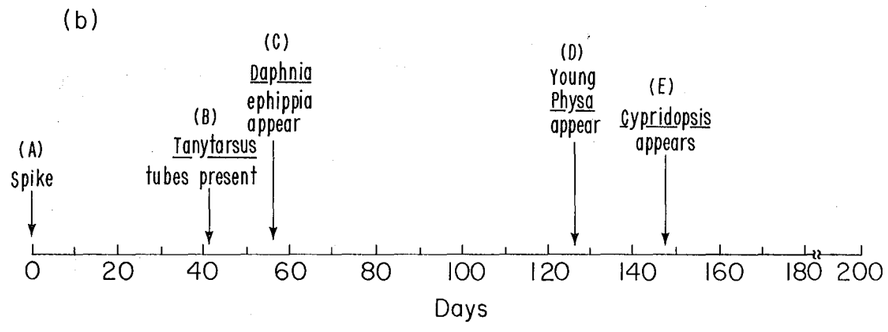


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Fig. 3

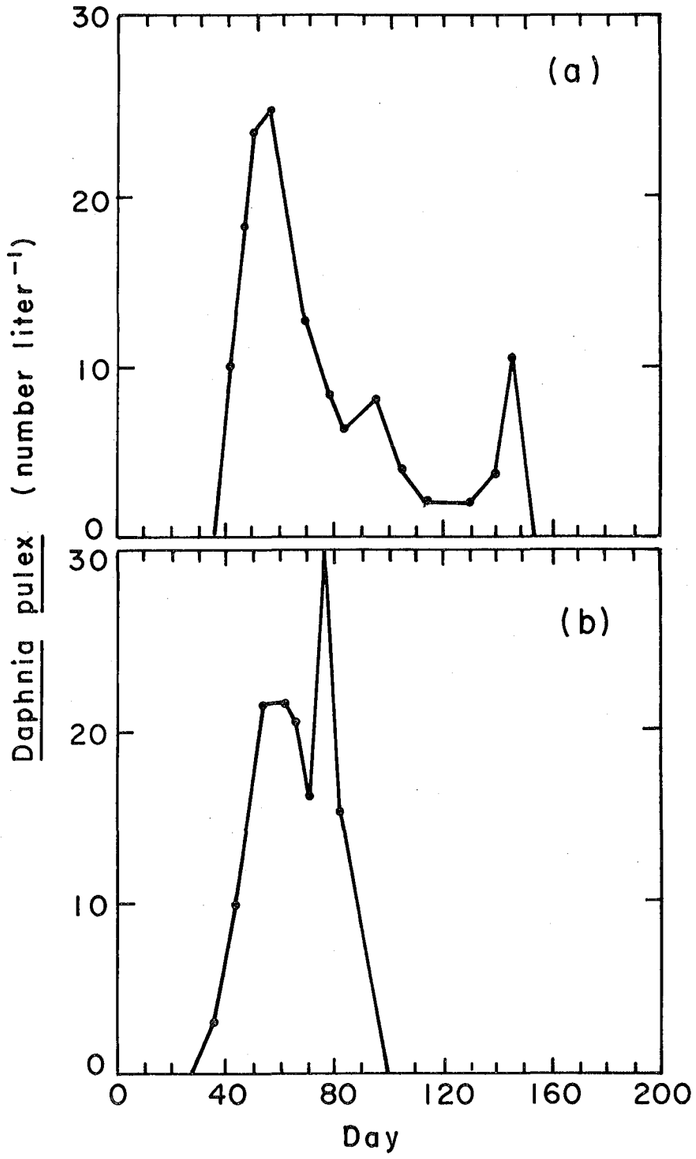

(a)
(b)
Daphnia pulex (number liter^{-1})
30
20
10
0
0
40
80
120
160
200
Day
XBL7710-6957

Fig. 4

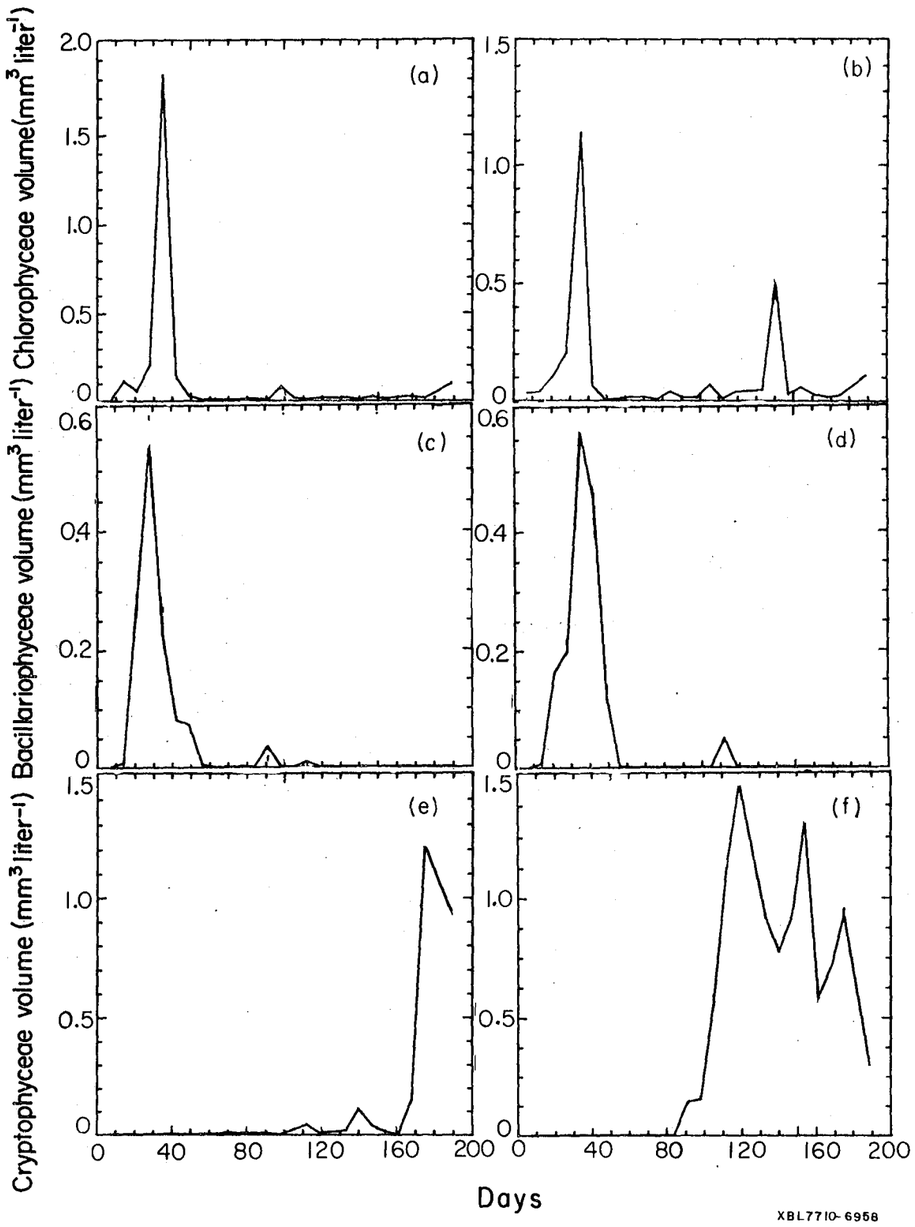
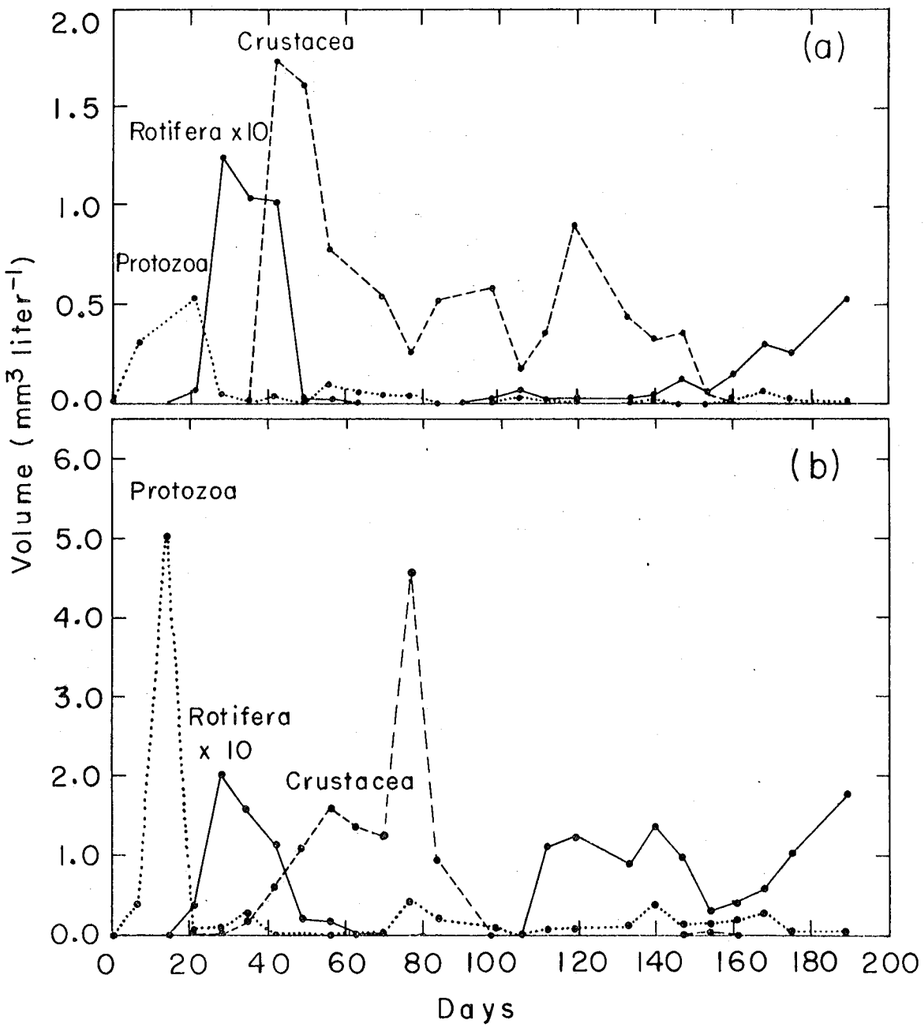


Fig. 5



XBL 7710-6905

Fig. 6

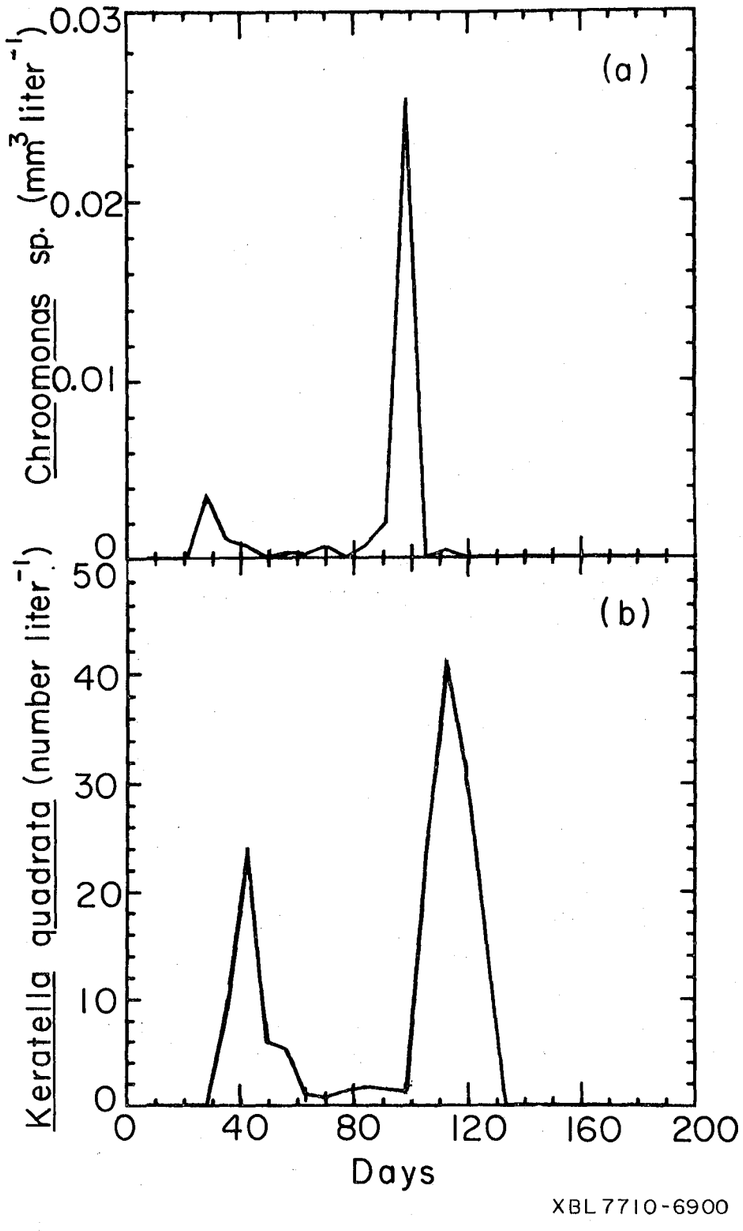


Fig. 7

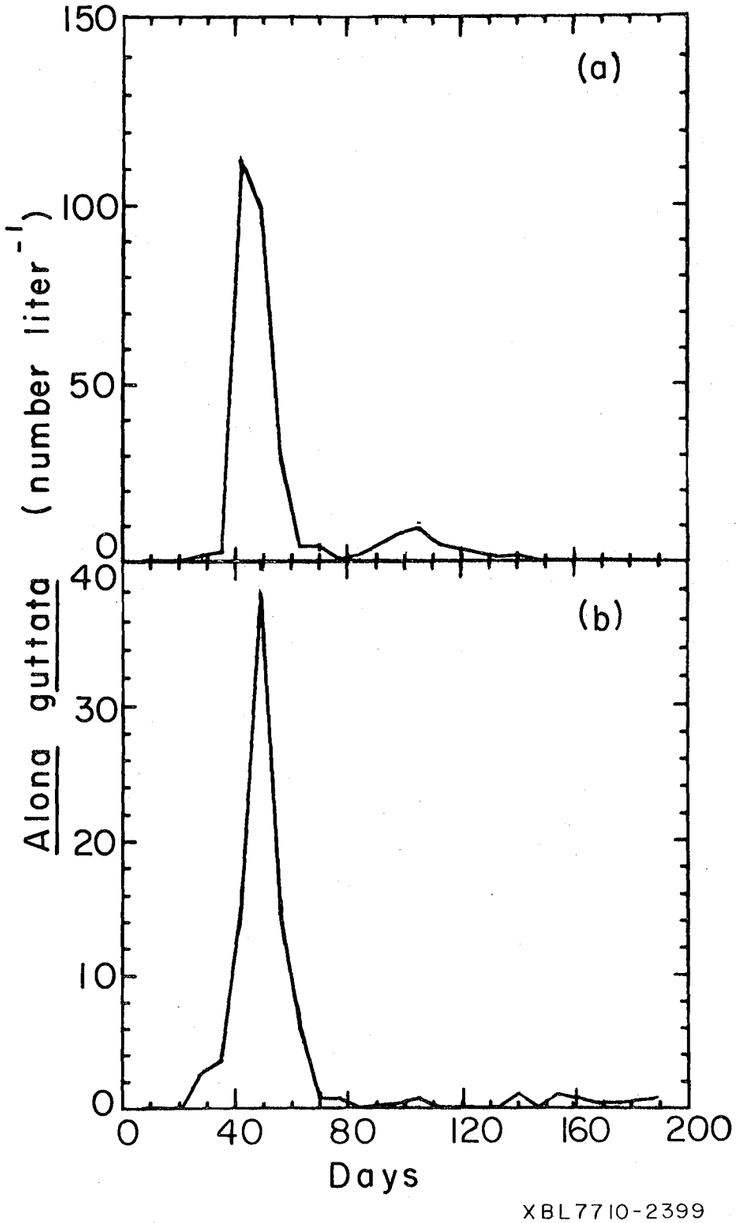

150
100
50
0
(a)
(number liter^{-1})
40
30
20
10
0
(b)
Alona guttata
0
40
80
120
160
200
Days
XBL7710-2399

Fig. 8

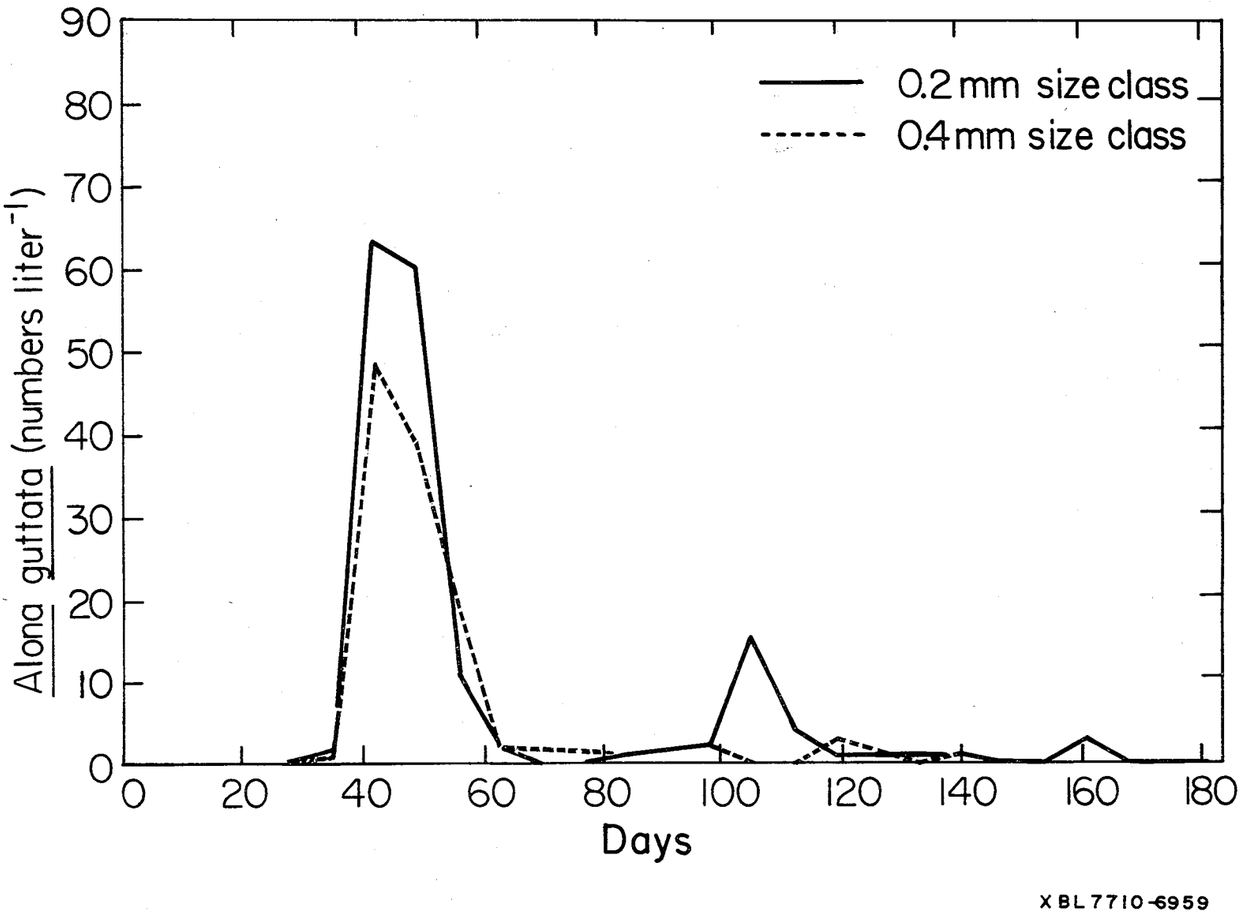

0.2 mm size class
0.4 mm size class
Alona guttata (numbers liter^{-1})
Days
0
10
20
30
40
50
60
70
80
90
0
20
40
60
80
100
120
140
160
180
XBL7710-6959

Fig. 9

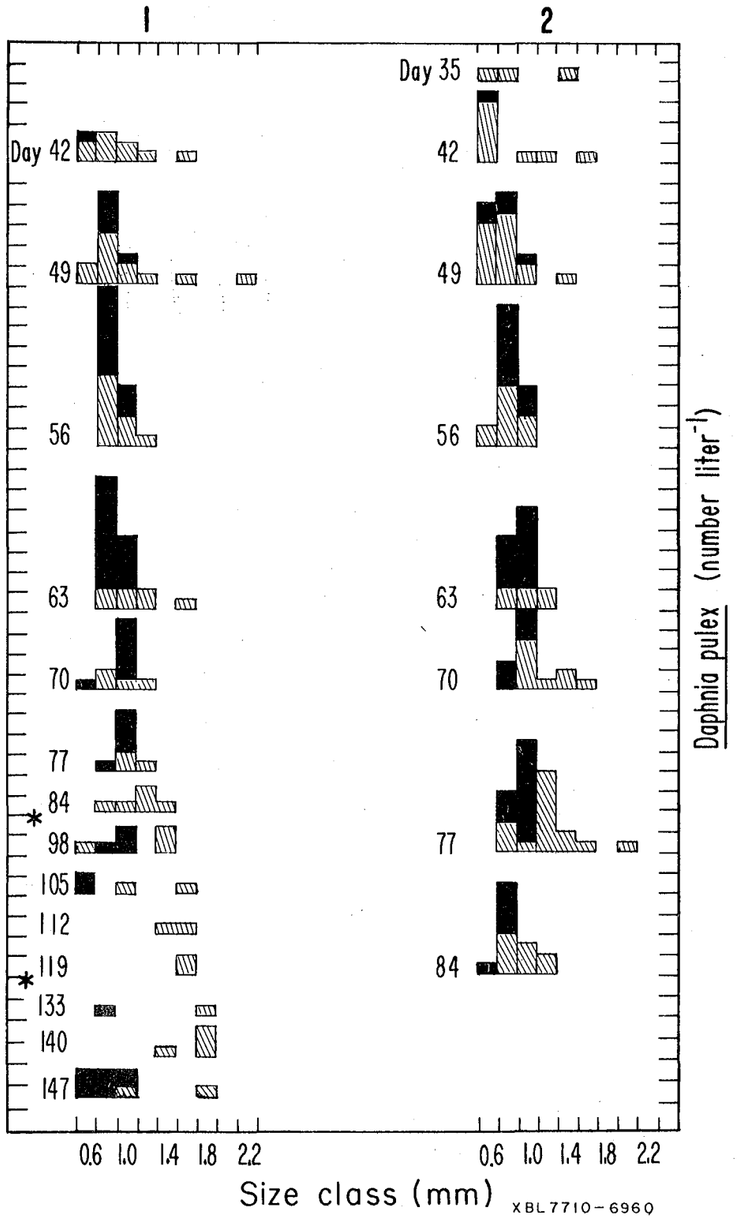
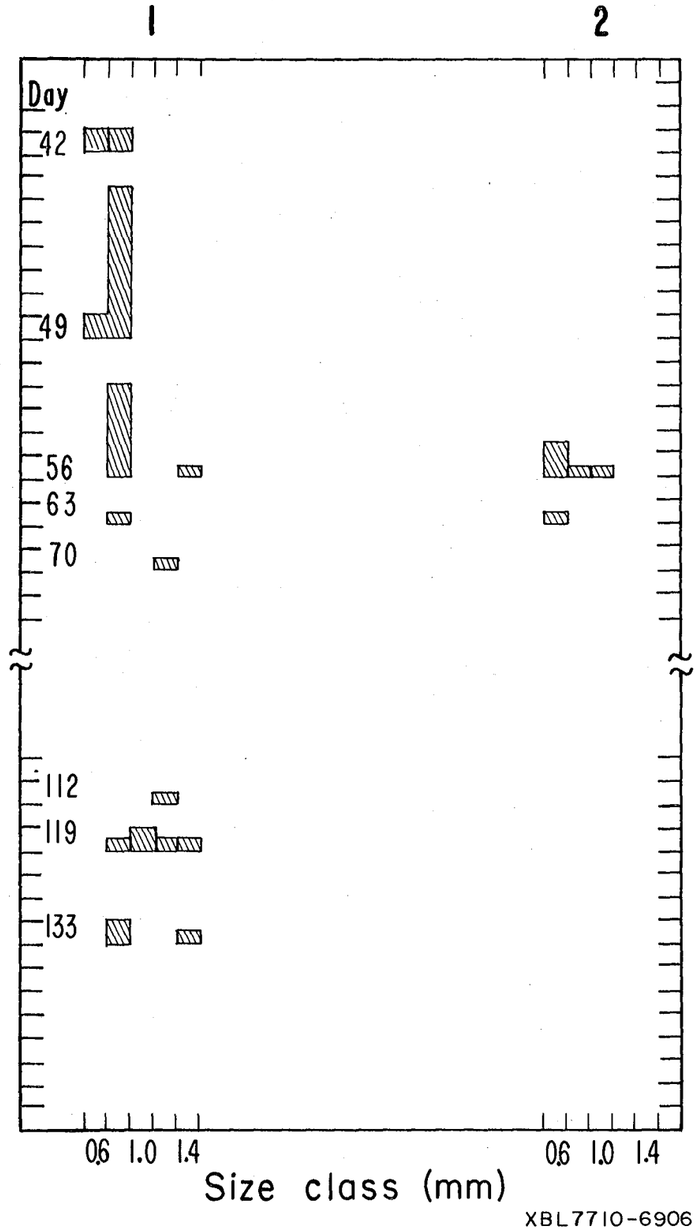

1
2
Day 35
Day 42
42
49
56
63
70
77
84
98
105
112
119
133
140
147
0.6 1.0 1.4 1.8 2.2
0.6 1.0 1.4 1.8 2.2
Size class (mm)
Daphnia pulex (number liter⁻¹)
XBL 7710-6960

Fig. 10



(Simocephalus vetulus (number liter^{-1})

Fig. 11

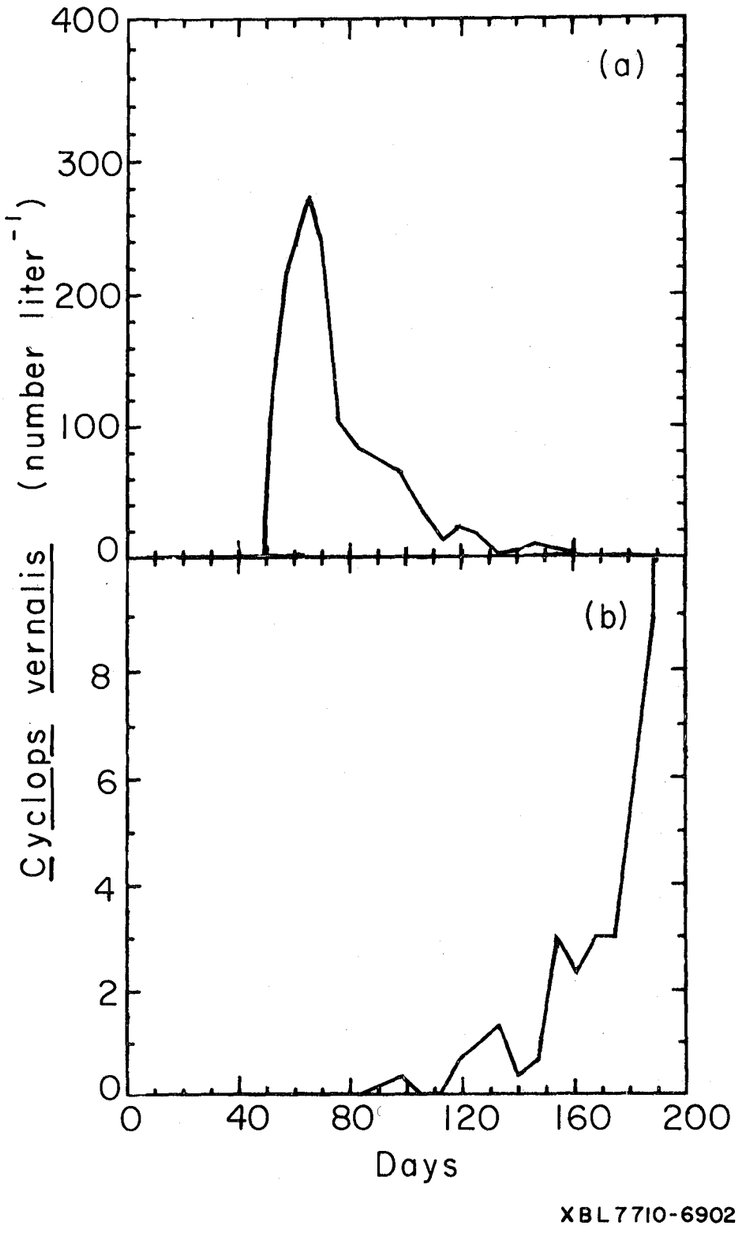

400
300
200
100
0
(a)
(b)
8
6
4
2
0
0
40
80
120
160
200
Days
Cyclops vernalis (number liter⁻¹)
XBL7710-6902

Fig. 12

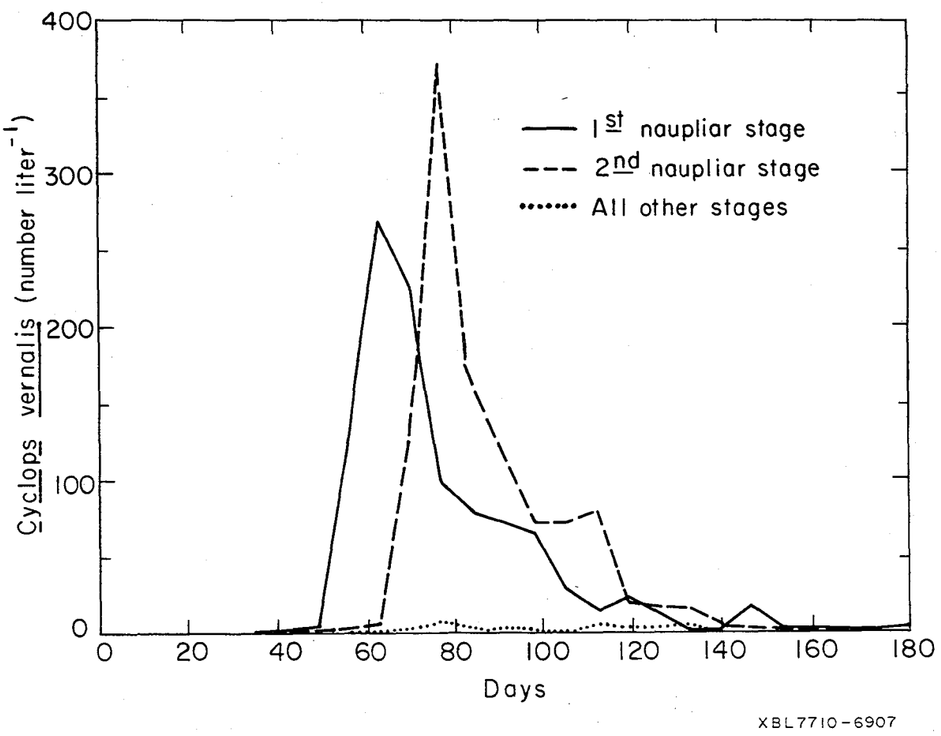

400
300
200
100
0
Cyclops vernalis (number liter⁻¹)
1st naupliar stage
2nd naupliar stage
All other stages
0
20
40
60
80
100
120
140
160
180
Days
XBL7710-6907

Fig. 13

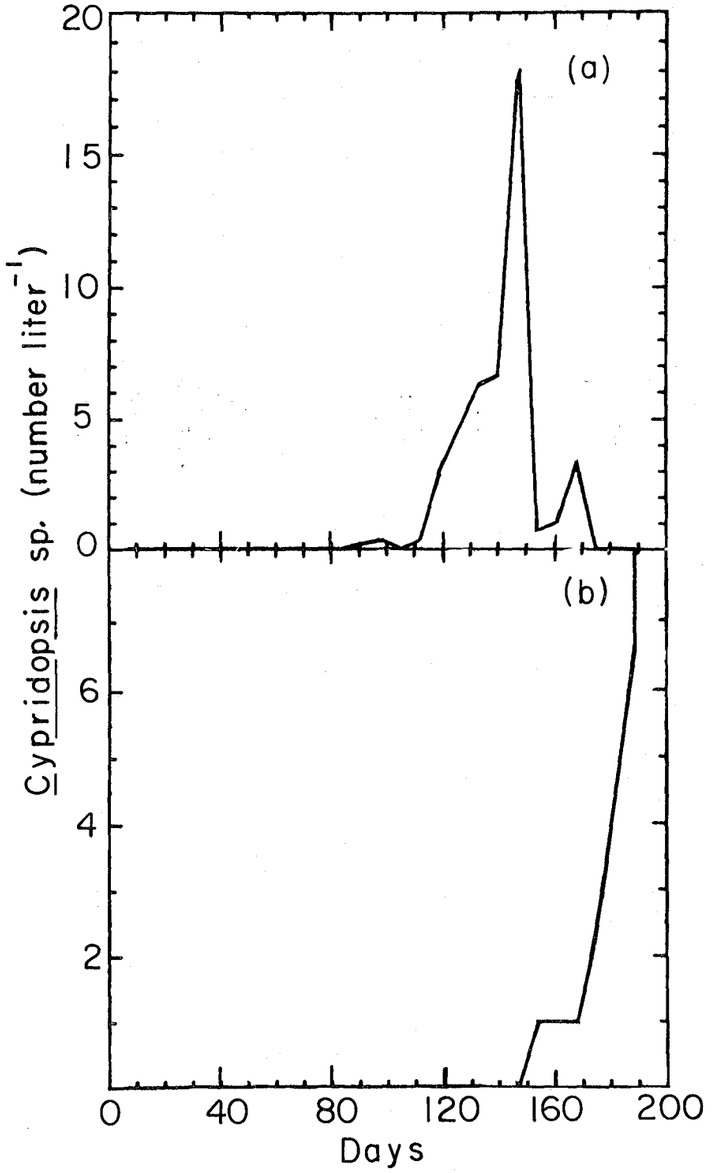

20
15
10
5
0
6
4
2
(a)
(b)
Cypridopsis sp. (number liter^{-1})
0
40
80
120
160
200
Days
XBL7710-6903

Fig. 14

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