THE UNIVERSITY OF MANITOBA

The response of planktonic crustacean communities in large enclosures to experimental acidification

by

Douglas James Ramsey

A Thesis

Submitted to the Faculty of Graduate Studies

in partial fulfillment of the requirements for the degree

of Master of Science

Department of Zoology

Winnipeg, Manitoba

January, 1985

THE RESPONSE OF PLANKTONIC CRUSTACEAN COMMUNITIES IN LARGE ENCLOSURES TO EXPERIMENTAL ACIDIFICATION

BY

DOUGLAS JAMES RAMSEY

A thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

Abstract

Large enclosures (10 m diameter and 2.0-2.5 m deep) installed in lake 302 of the Experimental Lakes Area were used to examine the responses of planktonic crustaceans to acidification with sulfuric acid. The effects of prolonged enclosure were also examined. Four enclosures were installed at the end of May in 1979 and the contained communities remained isolated from the lake for approximately 13.5 months. In 1979, two enclosures (A1 and A2) were acidified from pH 6.8 to 4.7 between June 21 and July 5 and maintained at mean pH levels of 4.80 (A1) and 4.84 (A2) for 15 weeks. Acidification was resumed on May 15, 1980 and continued to July 17 except for two interruptions (May 23-June 2 and June 19-25). For most of June, 1980, the pH of A1 was maintained between 4.7 and 5.0 while the pH in A2 was between 5.0 and 5.2. The second pair of enclosures (Ctrl 1 and Ctrl 2) were maintained as controls for the duration of the study. The zooplankton communities in the four enclosures and in the surrounding lake were sampled at approximately weekly intervals from June 5 to October 20, 1979 and from May 12 to July 17, 1980.

Crustacean plankton community abundance in the acid tubes was lower than in the controls in both years. The reduction was significant in both A1 and A2 in 1979, averaging 50% of control abundance, but was significant only in the more acid A1 in 1980. Acidification differentially

affected the Copepoda with no reductions of any cladoceran and with increased abundance of Diaphanosoma brachyurum and Ophryoxus gracilis in the acid enclosures in both years. Consequently, community structure was significantly altered. Five of the seven copepod species exposed to reduced pH in 1979 (Diaptomus minutus, Mesocyclops edax, Cyclops bicuspidatus thomasi, Acanthocyclops vernalis, and Eucyclops agilis) decreased in abundance. Tropocyclops prasinus mexicanus abundance was not affected but egg development was disrupted and the species' seasonal dynamics were altered by periodic reductions of cohort success and by a recruitment failure in the autumn. All four copepod species exposed to reduced pH in 1980 (D. minutus, Epischura lacustris, T. p. mexicanus, and M. edax) decreased in abundance, with greater reductions of T. p. mexicanus, M. edax, and calanoid nauplii accounting for the lower community abundance in A1.

The declines of the major copepod species were the product of physiological stress rather than an effect of alterations in food supply or predation intensity. The source of this stress was the increased hydrogen ion concentration and the mode of action of the pH toxicity was species-specific. D. minutus declined because of increased mortality below pH 5.0, M. edax because of recruitment failure, and T. p. mexicanus because of increased mortality and lower recruitment. The sensitivity of D. minutus to pH below 5.0 in this study is consistent with the geographic distribution of the species with pH among shallow lakes in

granitic basins. While previously considered to be the most acid tolerant zooplankter, the tolerance of D. minutus to pH below 5.0 appears to be limited to lakes in quartzite drainage basins and/or to lakes of sufficient depth for thermal stratification to develop in summer.

Although no cladoceran decreased in the acidified tubes, some species were stressed at lower pH. Bosmina longirostris survival decreased and Holopedium gibberum egg production ceased below about pH 5.0.

The major effect of enclosure was quantitative with significant increases in community abundance recorded in both years. B. longirostris, T. p. mexicanus, and M. edax increased because the invertebrate predators Leptodora kindtii and Chaoborus spp. were excluded from the enclosures. D. minutus increased because the enclosed copepodids were prevented from emigrating to the limnetic zone. Enclosure had but a minor effect on community structure and no effect on community diversity. All effects of enclosure were similar in the two years. In spite of these enclosure effects, the crustacean plankton communities which developed in the acidified enclosures were very similar to those observed in shallow culturally acidified lakes of comparable pH.

Acknowledgements

I am deeply indebted to my supervisor, Dr. K. Patalas, for his help, encouragement, and patience over the rather extended duration of this project. I would also like to thank the staff of the Experimental Lakes Area project for their tolerance of another grad student, the loan of their precious equipment, and their advice on how to use it. In particular, Dr. D. W. Schindler initially encouraged the project, secured funding, and made the facilities of the camp available. R. Nero, R. France, and S. Levine helped install the enclosures. Financial support from the Freshwater Institute, Department of Fisheries and Oceans, is gratefully acknowledged.

Finally, this project could not have been completed without the considerable help and unfailing support of my wife Susan, particularly for the exceptional quality of graphics she produced.

Table of Contents

List of Tables

Page

Page

Page

List of Figures

Page

Page

Page

List of Appendices

Introduction

Acid precipitation, the product of anthropogenic emissions of sulfur and nitrogen oxides, is responsible for the increasing acidity of many lakes in regions of sparingly soluble bedrock (Beamish and Harvey 1972; Conroy et al. 1975; Wright and Gjessing 1976). Assessment of the effects of this acidification on planktonic crustaceans has been hampered by the lack of pre-acidification data, with the result that investigations have generally been limited to surveys of lakes in and near acid-affected regions on the assumption of previously similar plankton communities. The validity of this assumption is known only in part, with similar zooplankton community composition and structure occurring among lakes with similar morphology in a particular geographic area (Patalas 1971). The natural variability of zooplankton abundance, both within a lake over time and among lakes in a given area, has been little studied but the available evidence suggests that it can be considerable. Among seven lakes in the Muskoka-Haliburton region of Ontario, mean ice-free season zooplankton abundance differed by factors of as much as 2 to 3 in a single year (Yan and Strus 1980). In a 12 year study of Esthwaite Water in the English Lake District, Smyly (1972) found that mean annual abundance of the major species varied by factors of 2-30 from year to year. Similarly, the seasonal dynamics of the common plankton species of the Canadian Shield have been found to vary

greatly between lakes (Schindler and Noven 1971; Hutchinson 1967). Consequently, only the qualitative effects of acidification on zooplankton communities can be confidently described with survey data and, of these, reduced community diversity (Hendrey et al. 1976; Leivstad et al. 1976; Almer et al. 1978; Confer et al. 1983) and altered community structure (Sprules 1975; Roff and Kwiatkowski 1977) are the most documented. In Ontario and Scandinavia these effects become apparent only below pH 5.3 (Roff and Kwiatkowski 1977) or 5.0 (Sprules 1975; Hendrey and Wright 1976) but in the Adirondack Mountains of New York and the White Mountains of New Hampshire the changes are a continuous function of pH (Confer et al. 1983).

Despite the tenuous nature of the underlying assumption, a few attempts at describing pH-related changes in zooplankton abundance have been made. Roff and Kwiatkowski (1977) found reduced maximum summer community abundance in lakes below pH 5.0 in the LaCloche Mountain region of Ontario and Confer et al. (1983) have correlated lower point in time community biomass with decreasing pH in 18 Adirondack Mountain lakes. In contrast, DeCosta (1975) found no relationship between zooplankton biomass and pH in Cheat Lake, Virginia. The available information on the seasonal variability of zooplankton communities in acidic lakes is very limited (Yan and Strus 1980; Roff and Kwiatkowski 1977; Janicki and DeCosta 1979).

To circumvent the interpretive problems associated with

survey data, several experimental studies have been undertaken to better quantify the chemical (Schindler et al. 1980a and b; Jackson et al. 1980) and biological (Yan and Stokes 1978; Muller 1980; Nero 1981; Malley et al. 1982) changes accompanying acidification. A short term (2 1/2 month) enclosure experiment (Lawrence 1980) confirmed the altered zooplankton community structure reported in the survey studies but the experiment did not resolve the question of acid-related reductions of abundance nor were life-history effects considered.

The purpose of this study is to examine the effects of a longer term experimental acidification on the species composition, community stucture, abundance, and life history of planktonic crustaceans using large (160 m^3) enclosures. Sulfuric acid was used as the acidifying agent because sulfate is the predominant anion in the precipitation in acid-affected regions of northeastern North America (Likens and Bormann 1974).

Enclosures, also called tubes, mesocosms, or limnocorrals, were selected as the technique for this experiment because they appear to offer a reasonable compromise between whole-lake studies and laboratory experiments by allowing manipulation of a natural assemblage of organisms and the associated interactions within and between trophic levels while affording the luxury of replication. Because the enclosed zooplankton communities are a subsample of a single lake community, enclosures also

provide the theoretical advantage of reducing or eliminating the spatial variation of community abundance and dynamics common to regional surveys and to the use of control and experimental lakes. Temporal variation of these parameters, as would occur in a before and after study of a treated or polluted lake, should also be eliminated because the experimental units are all exposed to the same climatic conditions. However, enclosure may impose some artificiality, hence an investigation of such enclosure effects is necessary for extrapolation to "natural" systems (Menzel and Case 1977; Steele 1979).

Despite the widespread use of enclosures for the experimental manipulation of zooplankton communities (Marshall and Mellinger 1980; Beers et al. 1977; Grice et al. 1977; Kuiper 1977; Smyly 1976, 1978; McLaren 1969), little effort has been directed toward determining the replicability of enclosed communities or to evaluating the effect of enclosure on crustacean plankton (Takahashi et al. 1975), particularly over the longer term; >30 days (Smyly 1976, 1978). Consequently, the second objective of this study is to determine the effects of enclosure on, and the replicability of, crustacean plankton communities in tubes.

In this experiment, four portions of the same zooplankton community were enclosed from late May, 1979 to mid-July of 1980. Two of the enclosures were maintained as controls and two were acidified from a pH of about 6.9 to a nominal pH of 4.75 from June 21 to October 20, 1979.

Acidification was resumed on May 15, 1980 and continued to July 17. The zooplankton communities in the four enclosures and in the lake were monitored from June 5 to October 20, 1979 to determine the initial responses of the communities to the treatments. Monitoring was continued from May 12 to July 17, 1980 with the purpose to determine if the early-season community responses changed with continued enclosure or acidification. However, due to the interruption of the acidification schedule on two occasions by evacuations from forest fires in the area, this goal was only partially realized. While the effects of enclosure could still be examined, the pH levels in the acidified tubes fluctuated too greatly during these periods for the acidification regime to be considered comparable to that imposed in 1979. These disruptions were also responsible for the pH levels in the two acidified enclosures being maintained at different levels for approximately one month. An interesting ancillary experiment consequently developed, with the resulting acidification regimes allowing examination of the responses of the zooplankton communitites to pH ranges immediately above, 5.0-5.5, and below, 4.5-5.0, the apparently critical value of 5.0.

Description of the study lake

The experiment was conducted in the south basin of lake 302 (L302 S), a small double-basin lake located in the Experimental Lakes Area (ELA) ($93^{o}45'W$, $49^{o}40'N$) of

Northwestern Ontario (Fig. 1). This basin had not been experimentally manipulated before this study but served as a control for a hypolimnion nutrient injection experiment conducted in the north basin of the lake from 1972 to 1976 (Schindler et al. 1980c).

The watershed of L302 is underlain by Precambrian acid granites and the extreme southerly end of the south basin has a thin overlay of glacial drift, consisting predominantly of sand and gravel composed of quartz, plagioclase, and K-feldspar; minerals which are poorly soluble in water (Brunskill and Schindler 1971). The watershed vegetation is typical of boreal subclimax forests with jack pine, black spruce, trembling aspen, and white birch as the dominant species (Brunskill and Schindler 1971).

With epilimnetic conductivity, Ca^{++} concentration, and alkalinity ranging from 14-31 uS cm^{-1}, 1.5-2.3 mg L^{-1}, and 50-70 eq L^{-1}, respectively, in recent years, L302 S falls in the category of being highly sensitive to acidic deposition (NRCC 1981).

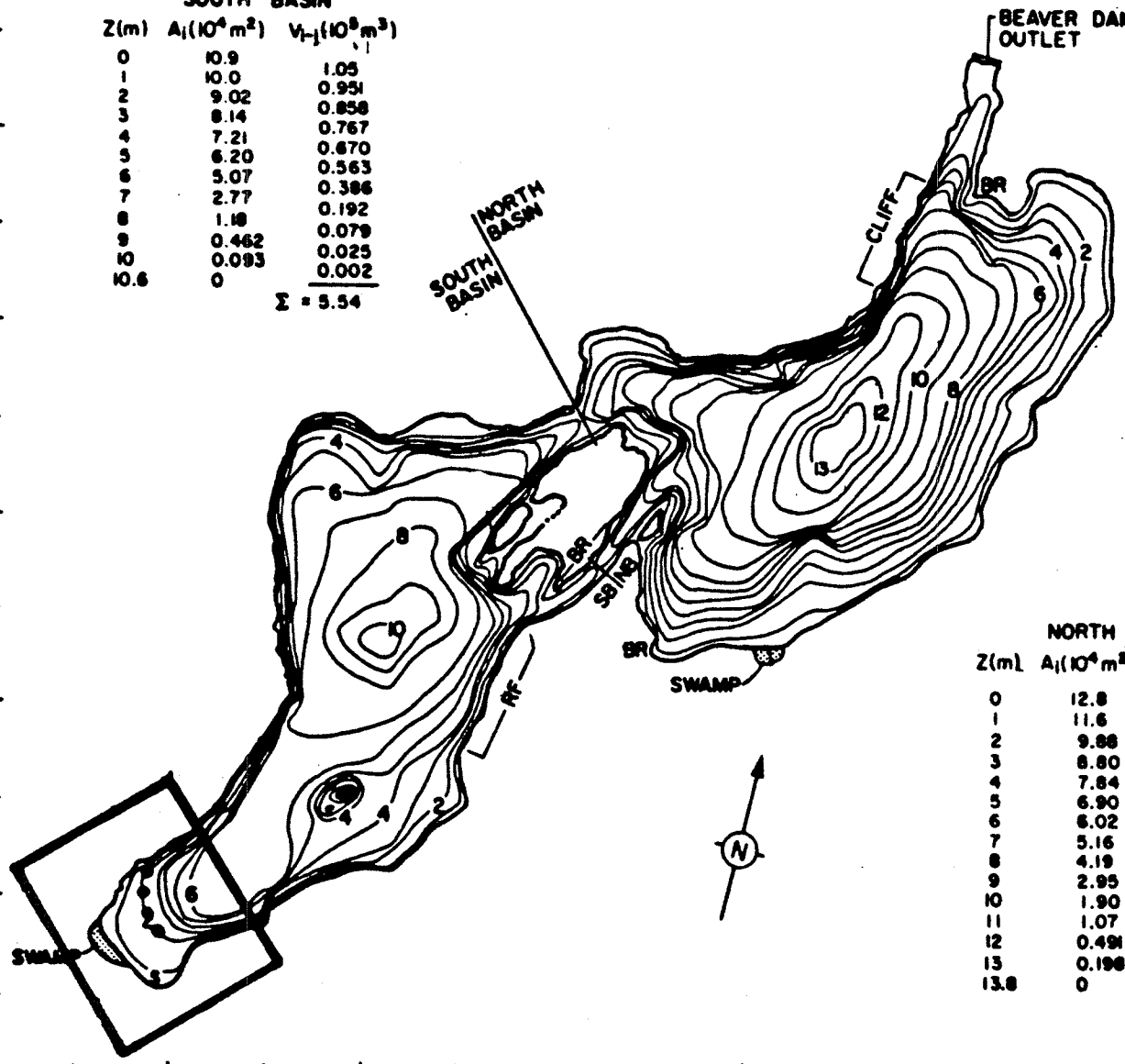
Materials and Methods

Tube location, construction, and preparation

Four tubes, approximately 10m in diameter and with bottoms open to the sediments, were used for the experiment. These were located in 2.0-2.5m of water at the extreme southerly end of the lake where the bottom material is predominantly sand of variable grain-size (Fig. 2a and b).

Figure 1. Bathymetric map of Lake 302, Experimental Lakes Area (from Brunskill and Schindler 1971), showing location of enclosures in the south basin. The outlined region is enlarged in Figure 2a.

LAKE 302



SCALE METERS
0 50 100 200

CONTOUR INTERVAL ONE METER
S = SAND
BR = BEDROCK
RF = ROCK FACE

SOUTH BASIN

Z(m)	$A_i(10^4 m^2)$	$V_{i-j}(10^3 m^3)$
0	10.9	
1	10.0	1.05
2	9.02	0.951
3	8.14	0.858
4	7.21	0.767
5	6.20	0.670
6	5.07	0.563
7	2.77	0.386
8	1.18	0.192
9	0.462	0.079
10	0.093	0.025
10.6	0	0.002
		$\Sigma = 5.54$

NORTH BASIN

Z(m)	$A_i(10^4 m^2)$	$V_{i-j}(10^3 m^3)$
0	12.8	
1	11.6	1.22
2	9.88	1.07
3	8.80	0.933
4	7.84	0.831
5	6.90	0.736
6	6.02	0.646
7	5.16	0.559
8	4.19	0.467
9	2.95	0.355
10	1.90	0.241
11	1.07	0.147
12	0.491	0.076
13	0.198	0.033
13.8	0	0.006
		$\Sigma = 7.32$

TOTAL LAKE

Z (m)	$A_i(10^4 m^2)$	$V_{i-j}(10^3 m^3)$
0	23.7	
1	21.6	2.27
2	18.9	2.03
3	16.9	1.79
4	15.0	1.60
5	13.1	1.41
6	11.1	1.21
7	7.93	0.945
8	5.36	0.658
9	3.41	0.434
10	2.00	0.266
11	1.07	0.148
12	0.491	0.076
13	0.198	0.033
13.8	0.	0.006
		$\Sigma = 12.9$

Figure 2. a. Enlarged view of tube location in L302 S indicating control and acidified enclosures and location of sampling stations in the lake for zooplankton (●) and water chemistry (O).
b. Photo of tubes on site.

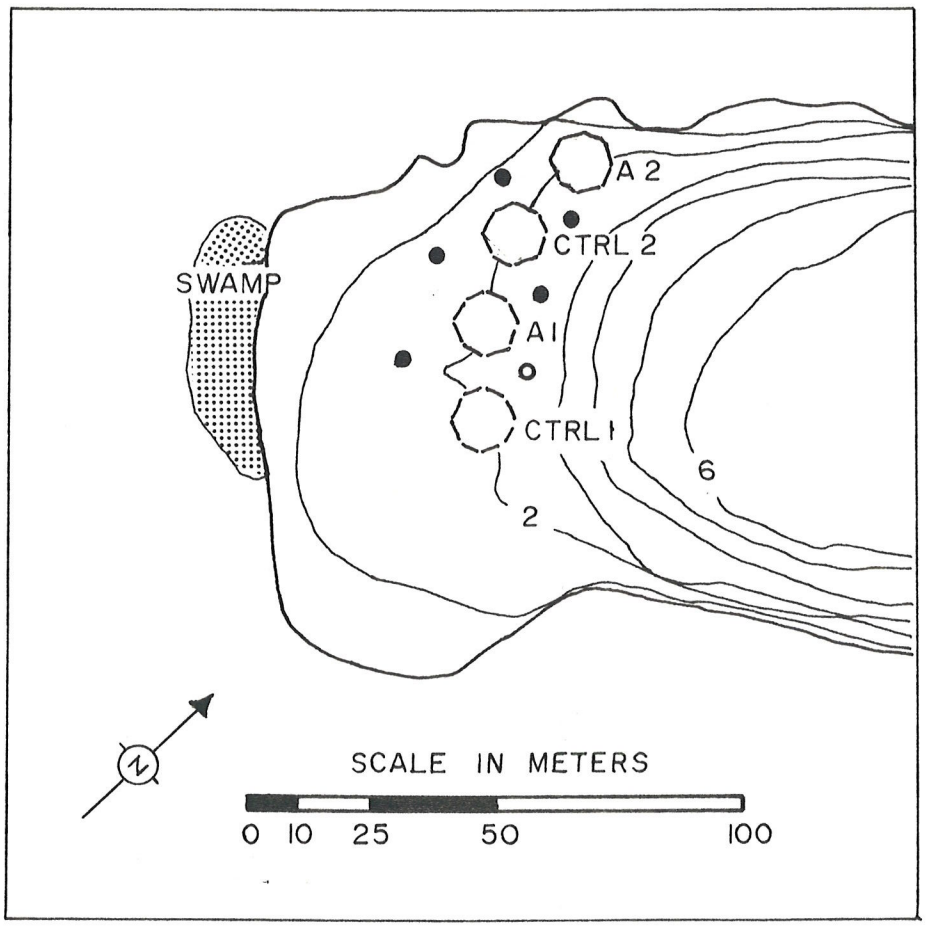
NOTICE/AVIS

PAGE(S) Figure 2 IS/~~ARE~~ EST/~~SONT~~ colour photo

PLEASE WRITE TO THE AUTHOR FOR INFORMATION, OR CONSULT THE ARCHIVAL COPY HELD IN THE DEPARTMENT OF ARCHIVES AND SPECIAL COLLECTIONS, ELIZABETH DAFOE LIBRARY, UNIVERSITY OF MANITOBA, WINNIPEG, MANITOBA, CANADA, R3T 2N2.

VEUILLEZ ECRIRE A L'AUTEUR POUR LES RENSEIGNEMENTS OU VEUILLEZ CONSULTER L'EXEMPLAIRE DONT POSSEDE LE DEPARTEMENT DES ARCHIVES ET DES COLLECTIONS SPECIALES, BIBLIOTHEQUE ELIZABETH DAFOE, UNIVERSITE DU MANITOBA, WINNIPEG, MANITOBA, CANADA, R3T 2N2.

a.



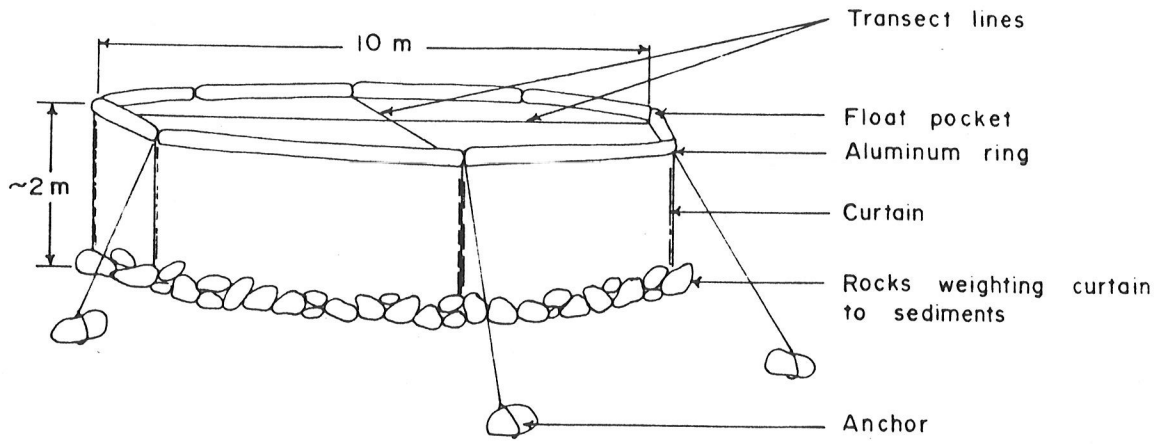
b.

The enclosures were constructed as described by Cruickshank et al. (1983) with each tube composed of a curtain and a structural ring (Fig. 3). Each curtain was made from a single, 3.0m x 31.5m, piece of translucent 10 mil reinforced polyethylene with a pocket, 66cm in circumference, of white reinforced vinyl sewn onto the top edge. Eight styrofoam blocks, each 15.2x15.2x122 cm, were fitted into the vinyl pocket for flotation. The octagonal structural rings were constructed with 3.66m long sections of 25.6mm, outside diameter (OD), aluminum conduit connected by 45^{o} elbows made from 46cm long pieces of 302mm, inside diameter (ID), stainless steel pipe. Plastic industrial cable ties attached the rings to the curtains.

The tubes had been used previously for a nutrient addition experiment. They were prepared for use in this study by scrubbing accumulated periphyton from the walls and by raising the curtains from the lake bottom to allow wind generated turbulence to flush the enclosures for two weeks prior to the experiment.

The curtains were sealed to the sediments by piling rocks along the lower edge, and each enclosure was held in position by six 30-45 kg anchors attached to the aluminum ring with plastic-coated steel aircraft cable. The curtain of control tube 1 (Ctrl 1) was sealed on May 28, 1979 while the curtains of control tube 2 (Ctrl 2), acid tube 1 (A1), and acid tube 2 (A2) were sealed on May 30, 1979. All four curtains remained sealed to the bottom until July 17, 1980,

Figure 3. Details of tube construction and installation.



TUBE INSTALLATION

the end of the study, as determined from frequent inspections by SCUBA diving.

Acidification regime

With four enclosures used for the study, a single level of acidification was selected. Considering that significant effects on zooplankton have been demonstrated only below pH 5.3 or 5.0, a slightly lower nominal value of pH 4.75 was chosen to ensure that some effects would be observed without creating unusually extreme conditions. Such levels of acidity are common among acidic lakes in Nova Scotia (Watt et al. 1979) and Ontario (Beamish and Harvey 1972; Sprules 1975; Yan 1975; Kwiatkowski and Roff 1976; Zimmerman and Harvey 1979).

In 1979, A1 and A2 were titrated to the selected pH over the two week period, June 21 to July 5. Approximately every third day, additions of acid were required to maintain the desired level of acidity. In 1980, the tubes were initially titrated during the one week period, May 15 to 22. However, evacuations from forest fires necessitated suspension of the acid additions required to maintain the depressed pH during two extended periods; the first from May 23 to June 2, and the second from June 19 to 25.

The acidification regime imposed in 1979 is similar, both in magnitude and rate, to the spring pH depressions in lakes in Sweden, Norway, and the Sudbury area of Ontario which are caused by the rapid melt of an accumulated snowpack of low pH (reviewed by Jeffries et al. 1979). The periodic

additions of acid roughly correspond to the additions of acid which accompany summer precipitation events in acid-affected regions.

Electrolyte grade sulfuric acid was used for the acidification. Heavy metal contamination of the acid was negligible with levels (in mg L^{-1} of acid) of iron (<20 mg L^{-1}), lead (<1 mg L^{-1}), and arsenic (<0.2 mg L^{-1}) all below the respective limits of detection (Schindler et al. 1980b).

Water sampling and analysis

In both 1979 and 1980, all water samples for chemical analysis were taken from the centre of each enclosure and from a standard station in the surrounding lake (Fig. 2a). All samples from within the tubes were taken over the side of a 3.7m aluminum canoe. Water samples were collected from 0.5m depth using a 3 L PVC Van Dorn bottle.

Samples for pH determinations were taken at least three times each week from the acidified tubes and at least weekly from the control tubes and lake, except during the two forest fire evacuations in 1980. During the 1979 experimental period, water samples for chlorophyll a (chl a) analyses were collected at weekly intervals, beginning on June 20. To provide a rough estimate of changes in the quality of food available to grazers, the samples collected between July 4 and August 14 were fractionated by filtering through Nitex screening to determine the concentration of chl a in the <10, 10-24, 25-50, and >50 um size-classes. No chl a measurements

were made in 1980. Water samples for analysis of cations (Na, K, Ca, Mn, Mg) were taken in September of 1979 and at monthly intervals in 1980. Oxygen, total dissolved nitrogen and phosphorus, and dissolved inorganic and organic carbon were monitored monthly in 1980.

All chemical analyses, except for pH determinations, were performed by the Analytical Unit of the Freshwater Institute as described by Stainton et al. (1977). pH measurements were made within one hour of sample collection with a Radiometer model 29 pH meter and combination electrode, calibrated at pH 4.0, 5.0, 6.0,and 7.0 with Fisher buffers.

Fish removal

Given that planktivorous fish can substantially alter the composition and structure of zooplankton communities (Brooks and Dodson 1965; Hrbáček 1962), the possibility that different numbers of fish were captured in each tube during filling, and that the resulting different levels of predation pressure could affect the zooplankton communities as greatly as the treatments, had to be eliminated. Therefore, the fish communities in the tubes were cropped using baited minnow traps. Galvanized wire mesh traps, approx. 45x15 cm with a 2.5 cm mouth opening, were set in the control tubes and polyethylene traps were used in the acidified tubes. Five traps were set in each tube for the first three weeks of enclosure and from July 28 to the end of sampling in 1979 for

a total of 445 trap-days tube^{-1}. Trapping was employed during the entire study period in 1980 for a total of 315 trap-days tube^{-1}. The traps were emptied at approximately 3 day intervals, with the fish released to the lake after enumeration. These traps only captured fish longer than 3.5-4.0 cm.

Zooplankton sampling

No standard method has yet been developed for sampling zooplankton in tubes. Samples have been taken only near the edge of the enclosure in some studies (Lawrence 1980; Marshall and Mellinger 1980), while in others only the centre of the enclosure has been sampled (Smyly 1976; Takahashi et al. 1975; Beers et al. 1977). In marine enclosures, Takahashi et al. (1975) have recorded horizontal and vertical patchiness of particulate matter and Grice et al. (1977) have observed similar patchiness of zooplankton. Consequently, a sampling scheme was designed to include both a horizontal and a vertical integration of sampling effort to minimize the influence of intratube patchiness on intertube comparisons of plankton abundance.

Samples were taken along transect lines stretched across each tube (Fig. 4a and b). Five samples per transect were collected from sampling points which were distributed in an areally-weighted manner. The surface of a tube (96.6 m^2) was divided into three regions; central, intermediate and outer, with areas of 19.6 m^2, 37.1 m^2, and 39.9 m^2, respectively

Figure 4. a. Distribution of zooplankton sampling points within a tube along transect A (●), used in 1979 and 1980, and along transect B (O), used in 1980 only.
b. One of the tubes with transect A installed.

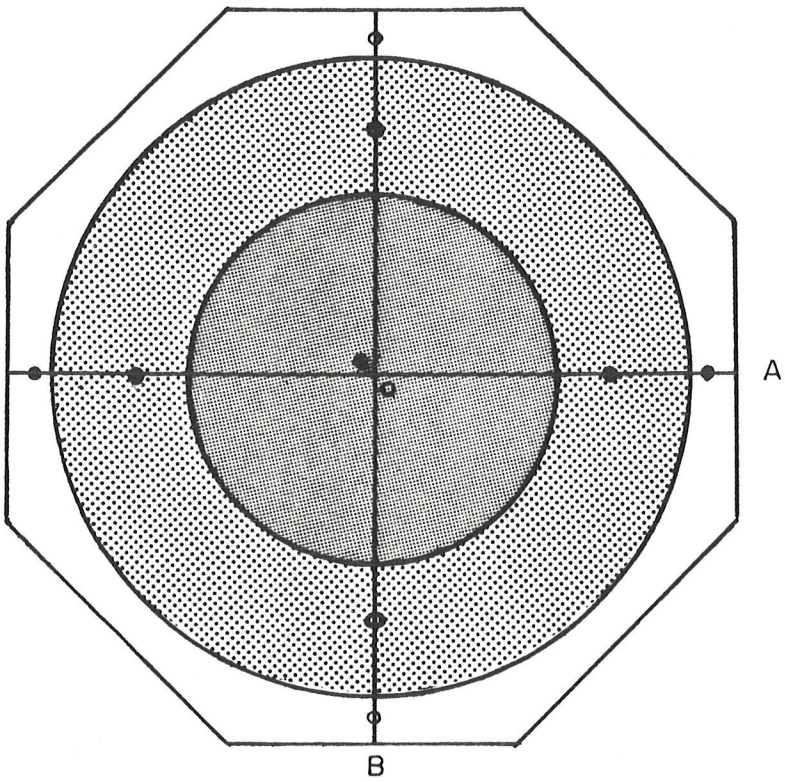
NOTICE/AVIS

PAGE(S) Figure 4 IS/~~ARE~~ EST/~~SONT~~ colour photo

PLEASE WRITE TO THE AUTHOR FOR INFORMATION, OR CONSULT THE ARCHIVAL COPY HELD IN THE DEPARTMENT OF ARCHIVES AND SPECIAL COLLECTIONS, ELIZABETH DAFOE LIBRARY, UNIVERSITY OF MANITOBA, WINNIPEG, MANITOBA, CANADA, R3T 2N2.

VEUILLEZ ECRIRE A L'AUTEUR POUR LES RENSEIGNEMENTS OU VEUILLEZ CONSULTER L'EXEMPLAIRE DONT POSSEDE LE DEPARTEMENT DES ARCHIVES ET DES COLLECTIONS SPECIALES, BIBLIOTHEQUE ELIZABETH DAFOE, UNIVERSITE DU MANITOBA, WINNIPEG, MANITOBA, CANADA, R3T 2N2.

a.



b.

(Fig. 4a). The sampling points were assigned to these regions in the ratio of 1:2:2 (Fig. 4a). Because a measurement of the horizontal distribution was not of primary interest in this study, the five samples collected along a transect were pooled to reduce sample analysis time.

The individual zooplankton samples were collected with a calibrated clear plexiglass tube (Fig. 5a), 2.5m long with a 7 cm (ID) mouth opening, to provide a vertical integration of any plankton patchiness. A sample was taken by lowering the tube vertically until it touched lake bottom, sealing the upper end with a No.13 rubber stopper, and raising the sampler until the tube mouth was just below the water surface. The lower end of the sampler was sealed with a stopper before removal from the lake. The captured animals were filtered from the contained water through a 50 um mesh-size net suspended from the side of the canoe (Fig. 5b). The coefficient of variation of replicate volume measurements made with the sampler was approximately $\pm$ 1%. Sampling was started on June 5, 1979, 7 (Ctrl 2, A1, and A2) and 8 (Ctrl 1) days after tube installation, and continued at approximately weekly intervals until October 20. Sampling was resumed on May 12, 1980 and continued, again at approximately weekly intervals other than during the two forest fires, until July 17.

The precision with which this sampling scheme estimated zooplankton abundance was examined by replicating the composite samples. In 1979, samples were replicated on

Figure 5. a. The plexiglass tube used for collecting zooplankton samples.
b. The 50 u mesh-size nets used to filter zooplankton samples.

NOTICE/AVIS

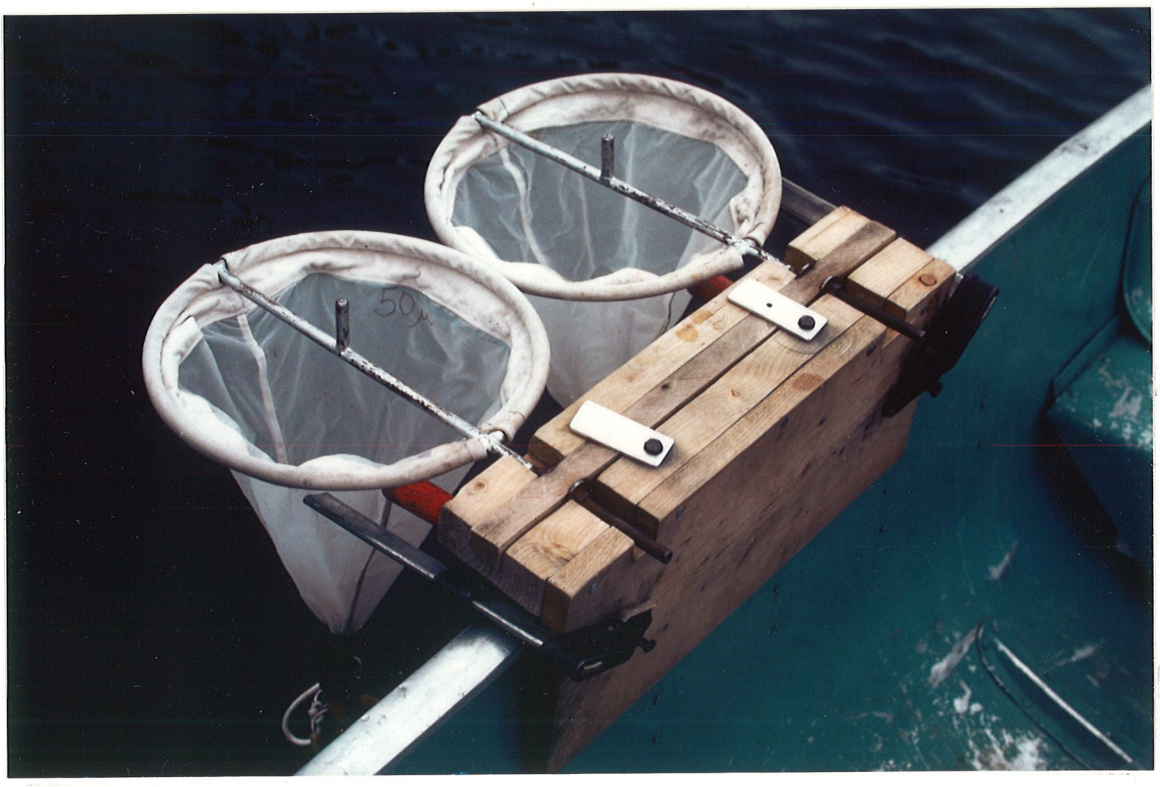
PAGE(S) Figure 5 IS/~~ARE~~ EST/~~SONT~~ colour photo

PLEASE WRITE TO THE AUTHOR FOR INFORMATION, OR CONSULT THE ARCHIVAL COPY HELD IN THE DEPARTMENT OF ARCHIVES AND SPECIAL COLLECTIONS, ELIZABETH DAFOE LIBRARY, UNIVERSITY OF MANITOBA, WINNIPEG, MANITOBA, CANADA, R3T 2N2.

VEUILLEZ ECRIRE A L'AUTEUR POUR LES RENSEIGNEMENTS OU VEUILLEZ CONSULTER L'EXEMPLAIRE DONT POSSEDE LE DEPARTEMENT DES ARCHIVES ET DES COLLECTIONS SPECIALES, BIBLIOTHEQUE ELIZABETH DAFOE, UNIVERSITE DU MANITOBA, WINNIPEG, MANITOBA, CANADA, R3T 2N2.

a.

b.



approximately half the sampling dates with the replicates taken along the same transect (Fig. 4a). Replicate samples were collected on all 1980 sampling dates with one composite sample taken along each of two transects arranged at right angles (Fig. 4a) to provide better horizontal distribution of the sampling effort. Discussion of the sampling precision achieved is contained in Appendix A.

For comparison of the zooplankton communities in the control tubes with that in the lake, five stations were established in the lake near the four enclosures (Fig. 2a) and these were sampled by the same method and with the same frequency as the tubes. The individual station samples were pooled on each sampling date and the lake composite sample replicated whenever replicate samples were collected from the enclosures.

On two occasions, August 20, 1979 and May 12, 1980, the individual samples collected at the lake stations and along transect A in the tubes were preserved separately for examination of the horizontal distribution of plankton in the tubes and surrounding waters. These data are discussed in Appendix B.

Collected samples were narcotized with 70% ETOH before preservation in 5% formalin solution (final concentration) to reduce egg loss (Gannon and Gannon 1975). After collection, the samples were allowed to settle overnight and then were reduced to a volume of 40 ml by drawing off excess preservative through a vacuum line covered with 50 um

mesh-size Nitex. The reduced samples were transferred to 45 ml glass vials to facilitate subsampling and storage.

Zooplankton sample analysis

For enumeration of copepod developmental stages, Bosmina longirostris, Chydorus sphaericus, Alona sp., and adult Tropocyclops prasinus mexicanus , a calibrated wide-mouthed glass pipette, 4mm ID x 15mm long, was used to take one ml subsamples by mixing the sample in all directions and then withdrawing the volume from the middle of the sample. The subsample was placed in a Sedgewick-Rafter cell and all contained organisms in the open cell enumerated under a compound microscope. Subsampling and enumeration continued until at least 200 individuals or the entire sample, whichever was the lesser, were counted. This procedure gave estimates of the total number of small crustaceans in each sample with a subsampling error of less than 7.5% (ie: coefficient of variation = $200^{-0.5}x100$ Cassie 1971). When possible, at least 40 individuals in each of the above groups were counted. For all other cladocerans and adult copepods, the entire sample was dispensed into a 2x2x18 cm trough made of 6mm thick clear plexiglass and counted under a stereo microscope, thereby eliminating subsampling error in estimates of the abundance of larger organisms. With the very low abundances which eventually resulted from the acidification, all crustaceans in the samples from A1 and A2 were counted for all sampling dates after August 20, 1979.

Therefore, subsampling error for these estimates is eliminated as well. Count data are expressed as individuals per litre.

Mature calanoid and cyclopoid copepods were identified to species using the keys of Wilson (1959) and Yeatman (1959) and were classified as male, female, or female with eggs. Cladocerans were identified to species using the key of Brooks (1957) and were classified as mature or immature female, female with eggs, or male. Copepodid instars of all calanoid species and of T. p. mexicanus, Cyclops bicuspidatus thomasi, and Mesocyclops edax were identified to species using size and morphological discriminators and were enumerated in two classes; copepodids 1-3 (C1-3) and 4-5 (C4-5). Nauplii were identified as calanoid or cyclopoid and counted in the classes nauplii 1-3 (N1-3) and 4-6 (N4-6).

Crustacean plankton biomass (mg wet weight L^{-1}) was calculated for each sampling date using the estimates of total number, the size distribution, and the length-weight relationship for each species (Edmondson 1971). Animals were measured under a compound microscope using a calibrated ocular micrometer; copepods from the anterior tip of the cephalothorax to the base of the caudal setae and cladocerans from the base of the shell spine to the anterior tip of the head.

The size distributions of the numerically important copepod adults, Diaptomus minutus and T. p. mexicanus, in each of the five communities were determined by measuring

10-20 individuals of each sex for each species from three dates in 1979 (June 20, July 20, and September 3) and two dates in 1980 (June 5 and June 30). There were no significant differences in the mean lengths of males or females of either species among the communities or sampling dates (2-way ANOVA $p>0.10$) so the data were pooled and the means of the pooled data used for biomass calculations. Adults of the less common copepod species were measured when encountered during sample analysis and mean lengths calculated from all measurements of each species. The adult mean lengths were used to estimate the mean lengths of the other copepodid categories using the relationships:

$$\bar{L} \text{ copepodids C4-5} = 0.764 \text{ M.A.L.}$$

$$\bar{L} \text{ copepodids C1-3} = 0.487 \text{ M.A.L.}$$

where $\bar{L}$=mean length in mm; and M.A.L.= mean adult length, an abundance-weighted average of male and female lengths. These proportions were derived using the moulting ratio of 1.2 (Brooks in Tessier 1960; Gurney 1929), in the equations:

$$\bar{L}\ C4\text{-}5 = \frac{\frac{M.A.L.}{1.2} + \frac{M.A.L.}{1.2^2}}{2} = 0.764 \text{ M.A.L.}$$

$$\bar{L}\ C1\text{-}3 = \frac{\frac{M.A.L.}{1.2^3} + \frac{M.A.L.}{1.2^4} + \frac{M.A.L.}{1.2^5}}{3} = 0.487 \text{ M.A.L.}$$

The applicability of this moulting ratio was checked by measuring individual copepodid instars of *D. minutus* and *T. p. mexicanus* from one sampling date, with the ratios

averaging 1.20 and 1.18, respectively. Biomass of nauplii was determined from volumes approximated from mean length, width, and depth measurements and an assumed specific weight of 1.0 (Edmondson 1971).

The size distributions of the numerically important cladocerans , Bosmina, Holopedium, and Diaphanosoma, were determined by measuring 40 individuals or all animals present, whichever was the lesser, of each species on each sampling date during their respective periods of occurrence. Because the size structure of the cladoceran populations changed with time, mean lengths on a given sample day were used to calculate biomass for that day only. Rare species were measured when encountered during enumeration and the mean of all measurements on a given day used for biomass calculation.

For all species other than Holopedium gibberum, biomass was calculated from published length-weight relationships (Table 1). The biomass of Holopedium was determined by fitting the volume of the organism, less gelatinous sheath, to a geometric shape, V=2/3LWH, and assuming a specific weight of 1.0.

To supplement the qualitative diagnosis of the effects of enclosure and acidification on community composition and structure, two quantitative indices were employed. The coefficient of community (CC), first used by Jaccard (1932), was calculated for all community pairs on each sampling date

Table 1. Relationships between body length, L in mm, and the wet weight, W in mg, of crustacean taxa used for biomass calculation.

Taxon	Formula	Source
Copepods	$W = 0.055\ L^{2.730}$	Klekowski and Shushkina (1966)
Bosmina	$W = 0.124\ L^{2.181}$	Pechen (1965)
Diaphanosoma	$W = 0.092\ L^{2.449}$	
Daphnia	$W = 0.052\ L^{3.012}$	
Ophryoxus	$W = 0.140\ L^{2.723}$	Winberg (1979)
Alona	$W = 0.091\ L^{2.646}$	
Chydorus, *Ilyocryptus*	$W = 0.203\ L^{2.771}$	
Sida, *Latona*	$W = 0.074\ L^{2.727}$	
Eurycercus	$W = 0.127\ L^{3.076}$	
Macrothrix	$W = 0.083\ L^{2.331}$	
Leptodora	$W = 0.006\ L^{2.850}$	

according to the formula:

$$CC = \frac{100 \cdot c}{a+b-c}$$

where a=the number of species in the first community; b=the number of species in the second community; and c=the number of species common to both communities. Thus it is a measure of the percentage similarity of community composition (Whittaker and Fairbanks 1958). The percentage similarity of community (PSC) index (Raabe 1952) was also calculated for all community pairs on each sampling date as follows:

$$PSC = 100-0.5 \sum |(a-b)|$$

where a and b are, for a given species, the proportional abundances in samples A and B respectively. Therefore, PSC is a measure of the similarity of community structure.

Zooplankton species diversity was measured as the total number of species sample^{-1}. This measure was selected because it is usually the only measure of diversity considered in studies of acidic lakes (Sprules 1975; Hendrey et al. 1976; Almer et al. 1978; Confer et al. 1983). Sprules (1975b) has also demonstrated that variation of species diversity with pH is due to differences in the number of species and not to the equitability of their abundances.

The significance of changes in CC, PSC, diversity, and in community and species abundance were assessed using Fisher's sign test (Hollander and Wolfe 1973). The application of this test is discussed in Appendix C.

Results

Physical and Chemical Measurements

A. Temperature

The thermal characteristics of the four enclosures were almost identical over the course of the study. The maximum intertube range of mean water column temperature, 0.5°C, occurred on May 12, 1980 and the temperature range averaged less than 0.2°C in the two seasons (Fig. 6). In 1979, temperatures in the lake and in the enclosures were identical from the beginning of sampling through the period of maximum heat content at the end of July (Fig. 6). At the onset of fall cooling in early August, the tube and lake temperatures began to diverge slightly, with the enclosures losing heat faster than the lake. On September 22, the mean water column temperature of the lake was 0.6°C warmer than in the tubes and this difference increased to 0.9°C by September 29. The maximum differential, 1.4°C, was recorded on October 13. Warm weather the following week increased the water temperature in the tubes by 1.4°C but had little effect on the lake temperature, causing a minor 0.2°C increase. This resulted in similar enclosure and lake temperatures on the final sampling date of 1979 (Fig. 6). In 1980, temperature differences between the lake and enclosures were of comparable magnitude but were not consistently higher or lower in the lake (Fig. 6). Ice-out was approximately three weeks earlier than in 1979. As a result, water temperatures on May 21 were already as warm as on June 5 in 1979 (Fig. 6). Although warming

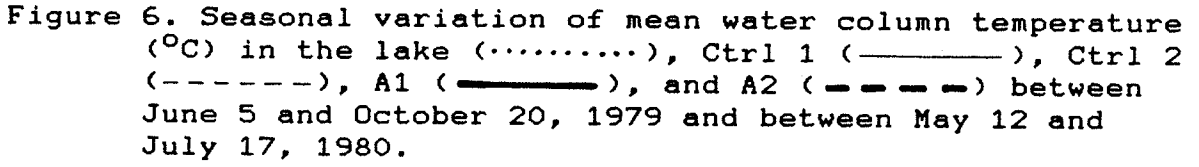
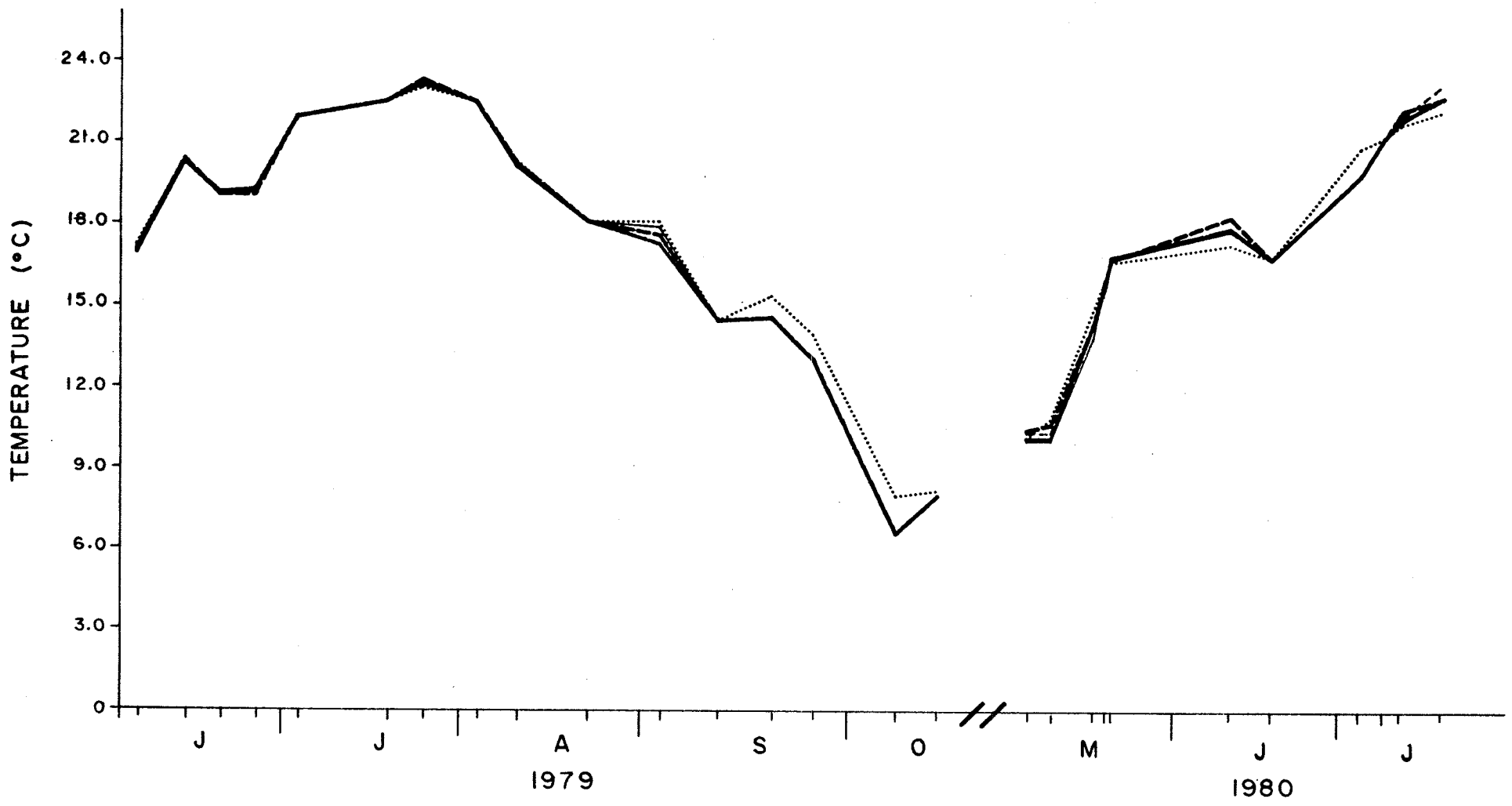


Figure 6. Seasonal variation of mean water column temperature (°C) in the lake (·····), Ctrl 1 (————), Ctrl 2 (- - - - - -), A1 (▬▬▬▬), and A2 (▬ ▬ ▬ ▬) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.


TEMPERATURE (°C)
24.0
21.0
18.0
15.0
12.0
9.0
6.0
3.0
0
J
J
A
S
O
1979
M
J
J
1980

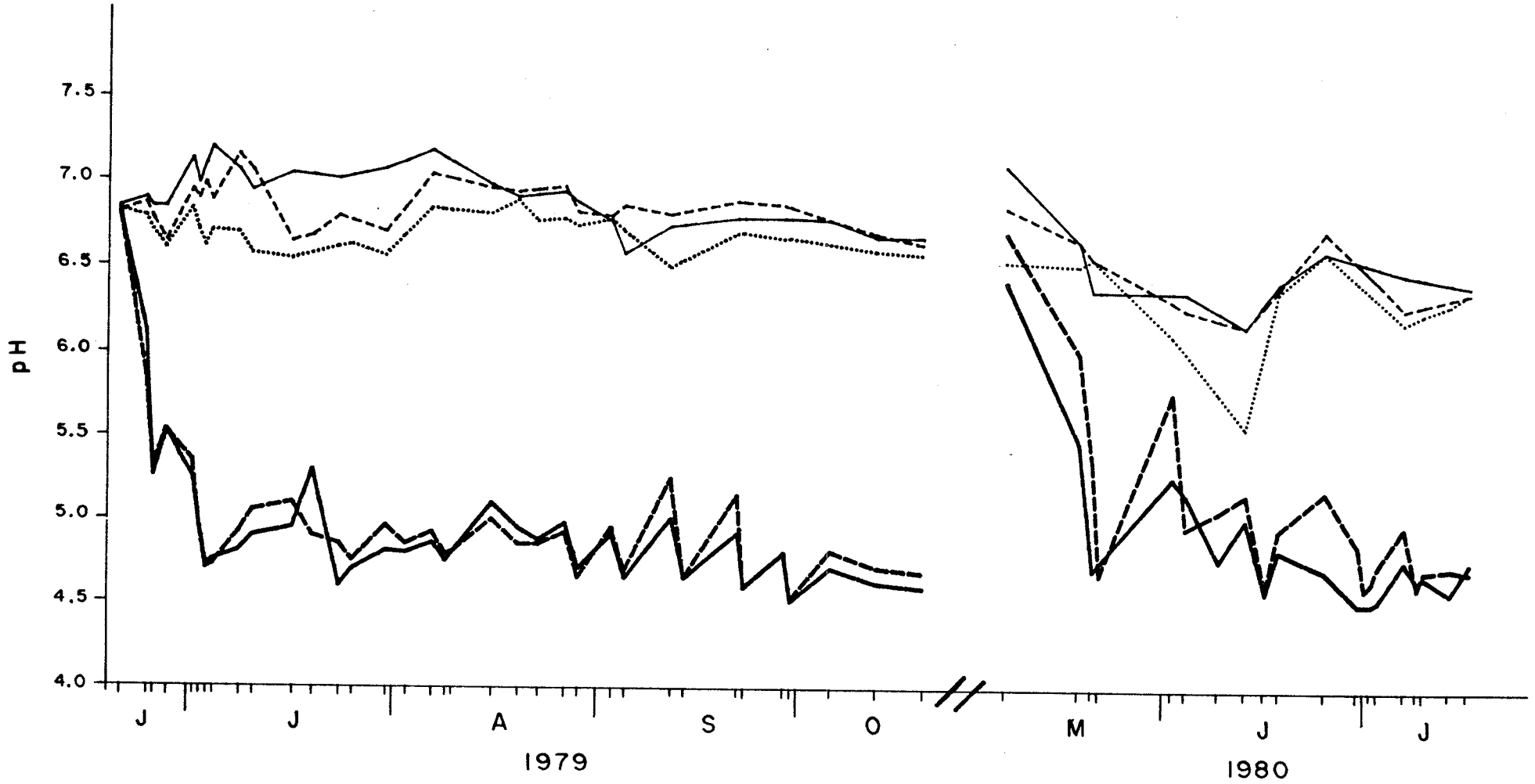
quickly in May, water temperatures in June of 1980 were cooler than in 1979 (Fig. 6).

B.pH

The lake and all four enclosures were of similar pH prior to beginning the acidification in 1979, with values of 6.83, 6.85, 6.82, 6.80, and 6.81 recorded in the lake, Ctrl 1 and Ctrl 2, and A1 and A2 ,respectively, on June 20. Addition of 12.1 ueq H^+ L^{-1} to A1 and 10.1 ueq H^+ L^{-1} to A2, in six installments between June 21 and July 4, reduced their respective pH levels to 4.72 and 4.70 (Fig. 7). The mean pH levels (time-weighted) of A1 and A2 were maintained at 4.80 and 4.84 for the remainder of the 1979 study period (July 4 - October 20), in contrast to mean pH levels of 6.92 and 6.87 in Ctrl 1 and Ctrl 2 for the same period (Fig. 7). While less acid was initially required to reduce the pH of A2, more was needed to maintain the increased acidity. Additions of acid to A2 averaged 14.8 ueq H^+ L^{-1} per week compared with the average addition of 13.2 ueq H^+ L^{-1} per week to A1. Lake pH was the same as or slightly lower than the pH in either control tube on all but one sampling date in 1979, September 5, with a mean level of 6.69 calculated for the period, July 4 to October 20 (Fig. 7).

The trial and error process of determining the quantity and frequency of acid additions necessary to maintain relatively constant levels of pH in the tubes resulted in slight increases above pH 5.0 in both treated tubes in

Figure 7. Seasonal variation of pH in the lake (·····), Ctrl 1 (————), Ctrl 2 (– – – – –), A1 (▬▬▬▬), and A2 (▬ ▬ ▬ ▬) between June 20 and October 20, 1979 and between May 8 and July 17, 1980.


pH
7.5
7.0
6.5
6.0
5.5
5.0
4.5
4.0
J
J
A
S
O
1979
M
J
J
1980

mid-July of 1979, with more constant acidity levels achieved for the remainder of July and August (Fig. 7). Maintenance of tube pH was restricted to weekends in September and October of 1979 which resulted in the broadly fluctuating pH levels during this period (Fig. 7). In mid-September, the pH in A2 increased more quickly after an acid addition than did the pH in A1 (Fig. 7).

By spring of 1980, the pH levels in the treated tubes had almost returned to control values, with the pH in A1 and A2 at 6.46 and 6.75, compared to values of 7.15 and 6.90 in Ctrl 1 and Ctrl 2 on May 8 (Fig. 7). Acidification was resumed on May 15 with a total of 5.8 ueq H^+ L^{-1} required to lower the pH of A1 to 4.75 by May 21 and with 7.1 ueq H^+ L^{-1} needed to depress the pH of A2 to 4.72 by May 22 (Fig. 7).

On two occasions in 1980, forest fires near the ELA camp forced suspension of tube sampling and acidification. During the first evacuation, from May 23 to June 2, the pH of the acidified tubes increased considerably, with values of 5.3 and 5.8 recorded in A1 and A2, respectively, when field studies resumed (Fig. 7). Pre-evacuation pH levels in the acidified tubes had just been re-established when the experiment was interrupted by the second fire on June 19. pH levels in the acid tubes again increased during the second evacuation, although not as greatly as during the first fire. This reflects the shorter duration of the second evacuation, with the pH rising from 4.53 to 4.75 in A1 and from 4.65 to 5.22 in A2 by June 25 (Fig.7). As in September of 1979, the

pH in A2 increased faster than in A1 after an acid addition. Upon resumption of field work following the second fire, pH levels in the acid tubes were quickly reduced to the target value, achieving mean pH levels of 4.67 and 4.80 in A1 and A2 respectively for the remainder of the study period (Fig. 7). Special note should be made of the different pH levels maintained in the acid tubes in June of 1980. Between June 5 and July 1, the pH in A1 exceeded 5.0 on just one date, June 13. Conversely, the pH in A2 was lower than 5.0 on just two dates, June 16 and July 1 (Fig. 7).

Control tube pH replicated well during the 1980 experimental period with synchronous temporal changes and similar mean levels of 6.55 and 6.51 in Ctrl 1 and Ctrl 2 between May 8 and July 17 (Fig. 7). Again, lake pH was lower than or equal to that in the control tubes, with a mean value of 6.34, and exhibited similar temporal dynamics (Fig. 7). Of note are the large pH declines which occurred in both control tubes and in the lake between the beginning of sampling and June 13, during which the pH of Ctrl 1, Ctrl 2, and the lake dropped 0.95, 0.70, and 0.98 units, respectively (Fig. 7).

C.Chlorophyll a

Chlorophyll a concentrations in the tubes and lake were quite different at the beginning of the experiment in 1979, with 1.75, 1.10, 1.55, 1.10, and 2.05 ug L^{-1} in Ctrl 1, Ctrl 2, A1, A2, and the lake, respectively, on June 20. However, neither enclosure nor acidification had a detectable effect

on the quantity of chl a on average, with mean concentrations during the 1979 study period (June 20 to October 21) of 2.38 and 2.80 ug L^{-1} in Ctrl 1 and Ctrl 2, 2.01 and 2.86 ug L^{-1} in A1 and A2, and 2.90 ug L^{-1} in the lake.

The only major difference between the control and the acidified tubes was the large peak (5.92 and 5.27 ug L^{-1} in A1 and A2) which developed in both acid tubes but not in either of the control tubes (3.1 and 2.67 ug L^{-1} in Ctrl 1 and Ctrl 2) on August 14 (Fig. 8). Otherwise, differences in the seasonal occurrence of chl a crossed treatment boundaries. In Ctrl 2, A2 and the lake, concentrations gradually increased over the course of the study while, in Ctrl 1 and A1, chl a levels reached their maxima in mid to late August with consistently low levels present in the autumn (Fig. 8).

While acidification had no effect on the quantity of phytoplankton, as measured by the chl a concentration, it did effect changes in the size distribution. Considerably more phytoplankton, on average, occurred in the >50 um size-class in the acid tubes than in the controls during the July 4 to August 14 period when fractionation was done (Table 2). Moreover, these higher concentrations of large-size algae did not develop in the acid tubes until early August and were primarily responsible for the peaks of total chl a at this time (Fig. 9). The size distributions of the phytoplankton communities in the control tubes were comparatively more constant, with 60 to 80% of total chl a in the <10 um

Figure 8. Seasonal variation of chlorophyll a concentrations (ug L^{-1}) in the lake (·····), Ctrl 1 (————), Ctrl 2 (– – – – – –), A1 (▬▬▬▬), and A2 (▬ ▬ ▬ ▬) between June 20 and October 21, 1979.

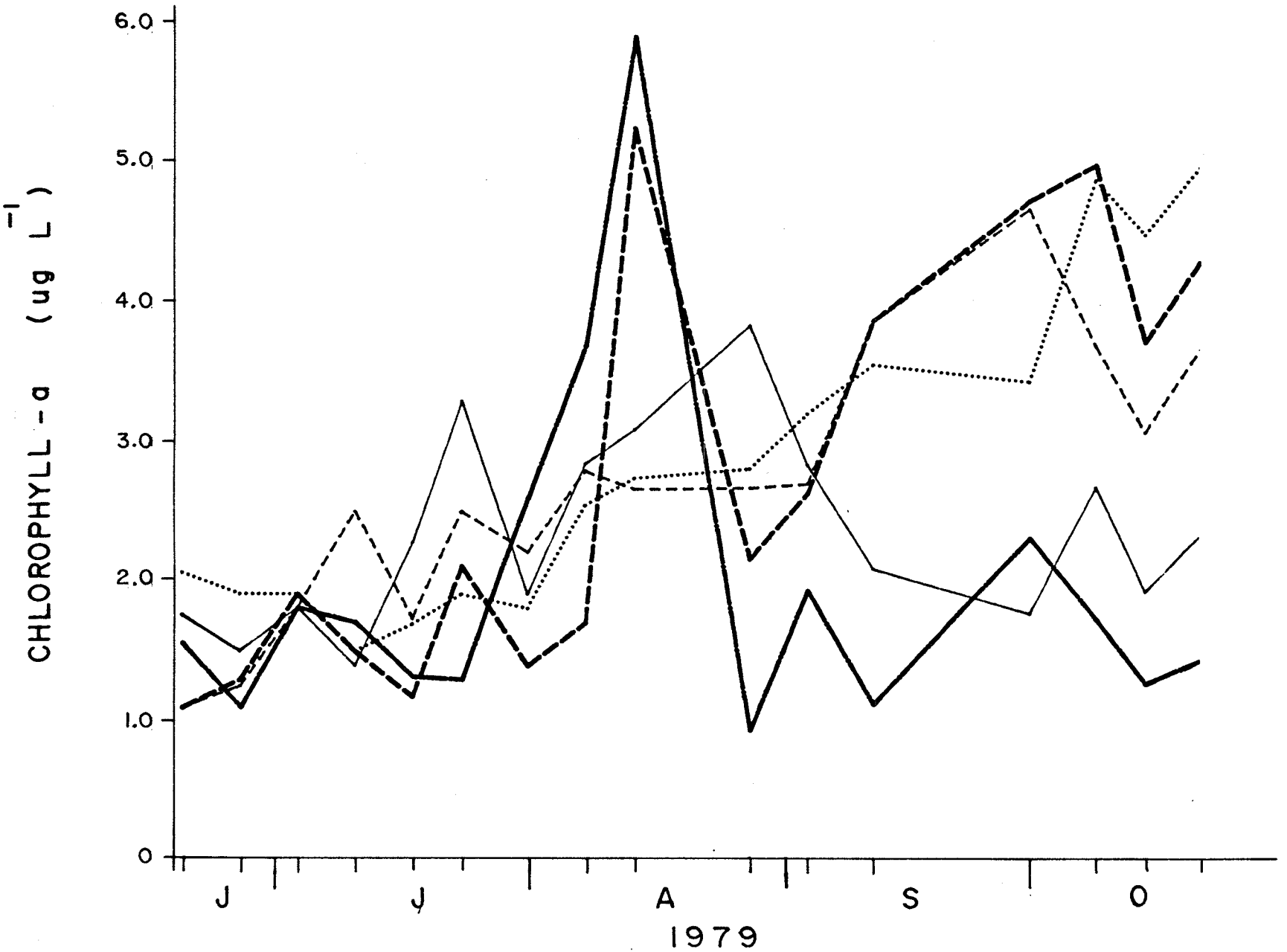
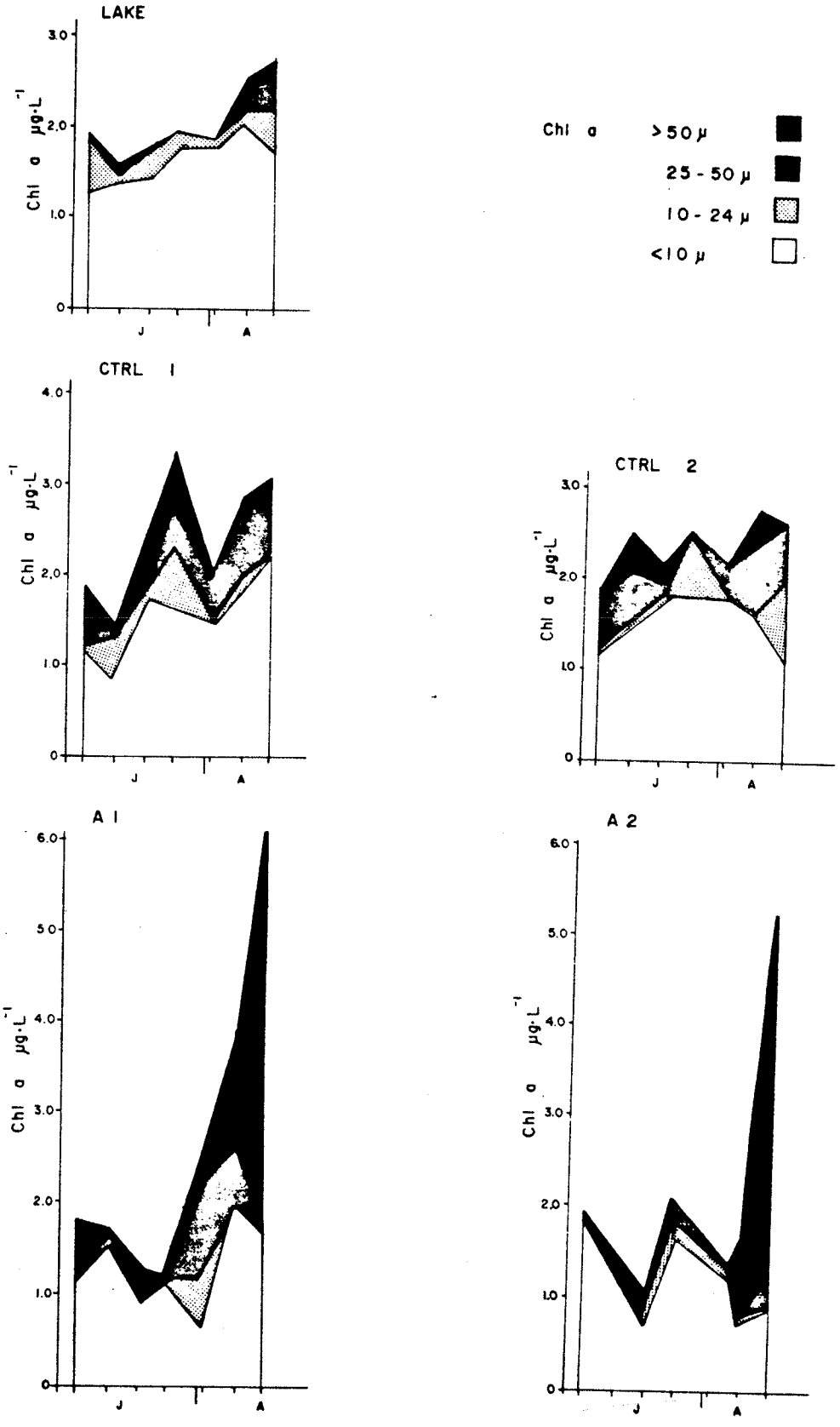

CHLOROPHYLL-a (ug L^{-1})
6.0
5.0
4.0
3.0
2.0
1.0
0
J
J
A
S
O
1979

Table 2. Mean concentration of total chlorophyll a (ug L^{-1}) and mean concentration in the >50, 25-50, 10-24, and <10 um size-classes in the lake, control tubes (Ctrl 1 and Ctrl 2) and acidified tubes (A1 and A2) between July 4 and August 14, 1979. Figures in () are the percentage of total chlorophyll a in that size-class.

	Total	>50 um	25-50 um	10-24 um	<10 um
Lake	2.02	0.02 (1.0)	0.14 (6.9)	0.20 (9.9)	1.66 (82.2)
Ctrl 1	2.37	0.22 (9.3)	0.38 (16.0)	0.17 (7.2)	1.60 (67.5)
Ctrl 2	2.36	0.12 (5.1)	0.47 (19.9)	0.23 (9.7)	1.54 (65.3)
A1	2.61	0.88 (33.7)	0.27 (10.3)	0.11 (4.2)	1.35 (51.7)
A2	2.15	0.75 (34.8)	0.10 (4.7)	0	1.30 (60.5)

Figure 9. Variation in the size distribution of chlorophyll a in the lake, control tubes (Ctrl 1 and Ctrl 2), and acidified tubes (A1 and A2) between July 4 and August 14, 1979.


LAKE
Chl a µg·L⁻¹
3.0
2.0
1.0
0
J
A
Chl a >50 µ
25 - 50 µ
10 - 24 µ
<10 µ
CTRL 1
4.0
3.0
2.0
1.0
0
CTRL 2
A 1
6.0
5.0
4.0
3.0
2.0
1.0
A 2

size-class throughout the period of examination (Fig. 9).

Enclosure also had some effect on the size distribution of the phytoplankton, but it was less extreme than in the acidified tubes. There was a greater proportion of total chl a <25 um in size in the lake (92.1%), on average, than in the control tubes (74.7 and 75.0% in Ctrl 1 and Ctrl 2) (Table 2, Fig. 9).

D.Chemistry

For all chemical parameters measured, concentrations in the control tubes and in the lake were usually very similar and values in the control tubes generally differed by no more than 10% of their mean (Table 3). When control tube values did differ slightly, the Ctrl 1 value was usually the higher. The acidified tubes exhibited a similar degree of replicability of all measurements and only three parameters, DIC, conductivity, and Mn^{++} were consistently different from control values. DIC concentrations in the acidified tubes averaged just 27% of control values in 1980 (Table 3). Conductivities in the acidified tubes averaged 42% higher than in the controls in 1980 (Table 3). Mn^{++} concentrations in the acidified tubes were about a factor of 10 higher than in the controls in both years (Table 3). Ca^{++} concentrations in the acid tubes were notably higher than in the control tubes on September 5, 1979 but were only marginally higher in 1980 (Table 3).

Table 3. Concentrations of cations (Na, K, Ca, Mg, Fe, Mn), total dissolved nitrogen (TDN), total dissolved phosphorus (TDP), dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), specific conductivity (Cond.), and oxygen in L302S, the control tubes (Ctrl 1 and Ctrl 2) and the acidified tubes (A1 and A2). Values for 1980 are means of measurements made on May 19, June 18, and July 16.

	5 September, 1979					1980				
	Lake	Ctrl 1	Ctrl 2	A1	A2	Lake	Ctrl 1	Ctrl 2	A1	A2
Na mg L^{-1}	1.00	1.03	1.07	1.05	1.09	0.73	0.76	0.76	0.75	0.83
K	0.35	0.40	0.38	0.38	0.40	0.38	0.39	0.37	0.38	0.35
Ca	1.75	1.84	1.58	2.41	2.19	1.72	1.74	1.60	1.78	1.79
Mg	0.60	0.82	0.58	0.70	0.70	0.57	0.61	0.55	0.59	0.59
Fe	0.03	(0.03	0.03	(0.03	(0.03	(0.04	(0.03	(0.03	(0.03	(0.03
Mn	0.01	0.03	0.03	0.37	0.33	(0.01	(0.01	(0.01	0.16	0.11
TDN ug L^{-1}						269	290	262	265	279
TDP ug L^{-1}						3	4	3	4	4
DIC umole L^{-1}						73	71	65	20	17
DOC umole L^{-1}						375	388	364	375	375
Cond. uS cm^{-1}						22.0	22.3	20.0	30.9	29.2
Oxygen mg L^{-1}						9.58	9.60	9.65	9.64	9.67

E.Fish

Considering the large fishing effort applied, rather few fish were removed from any of the enclosures over the course of the study (Table 4). In 1979, fathead minnows (Pimephales promelas Rafinesque), pearl dace (Semotilus margarita Cope), and fine scale dace (Chrosomus neogaeus Cope) were encountered in all four enclosures with fathead minnows and pearl dace the most abundant (Table 4). A few northern red belly dace (Chrosomus eos Cope) were captured from all but A1 (Table 4). Significant numbers of fish were captured from Ctrl 2 only in 1980 (Table 4). In total, fewer fish were caught in the acidified tubes than in the controls in 1979 (Table 4). This was the product of reduced (A2) or no (A1) fish captures after August 10. Previous to this date, 5 fish had been removed from each of Ctrl 1 and Ctrl 2 with 4 removed from A1 and 13 fish trapped in A2.

Zooplankton

1. Zooplankton communities in the enclosures and lake before the experiment

A total of 15 crustacean species were identified in the June 5 and 20, 1979 samples with 8 species common to the communities of the lake and all enclosures (Table 5). All of the remaining seven species were cladocerans with none comprising more than 0.3% of any community (Table 5). Mean zooplankton abundance in the five communities ranged from 95.54 ind L^{-1} in the lake to 184.01 ind L^{-1} in Ctrl 2, with

Table 4. Number and species composition of fish removed from the enclosures by minnow-trapping during 445 trap-days tube^{-1} in 1979 and 315 trap-days tube^{-1} in 1980.

	Enclosure							
	Ctrl 1		Ctrl 2		A1		A2	
Species	1979	1980	1979	1980	1979	1980	1979	1980
Pimephales promelas	10	--	14	4	2	1	6	--
Semotilus margarita	6	--	10	4	1	--	3	--
Chrosomus eos	4	--	4	--	--	--	4	--
Chrosomus neogaeus	2	--	4	1	1	--	1	--
Total catch	22	--	33	9	4	1	14	--

Table 5. Mean abundance (ind. L^{-1}) and percentage composition, in (), of planktonic crustacean species in the lake, control tubes (Ctrl 1 and Ctrl 2), and acidified tubes (A1 and A2) at the start of the experiment; June 5 and 20, 1979. For calculation of percentage composition, nauplii were apportioned among the species of their respective suborders according to copepodid abundance.

Species	Lake	Ctrl 1	Ctrl 2	A1	A2
Diaptomus minutus	7.67 (36.3)	47.41 (57.0)	27.82 (25.4)	20.06 (33.9)	17.75 (32.1)
Epischura lacustris	0.74 (3.5)	4.43 (5.5)	3.32 (3.0)	4.21 (7.1)	2.38 (4.3)
Calanoid nauplii	30.01	39.69	20.11	17.65	21.72
Tropocyclops prasinus mexicanus	1.48 (8.1)	2.07 (6.5)	1.60 (3.5)	0.78 (2.3)	3.95 (11.3)
Mesocyclops edax	4.43 (24.3)	2.87 (9.0)	2.10 (4.6)	0.91 (2.7)	2.18 (6.2)
Cyclops bicuspidatus thomasi	2.64 (14.5)	2.58 (8.1)	3.77 (8.2)	5.84 (17.4)	3.43 (9.8)
Cyclopoid nauplii	36.78	27.24	22.58	15.39	21.73
Bosmina longirostris	12.53 (13.0)	17.89 (12.2)	102.15 (55.5)	36.65 (35.8)	41.56 (36.2)
Holopedium gibberum	0.16 (0.2)	2.04 (1.4)	0.22 (0.1)	0.21 (0.2)	0.10 (0.1)
Diaphanosoma brachyurum	0.07 (0.1)	0.45 (0.3)	0.15 (0.1)	0.41 (0.4)	0.05 ((0.1)
Ophryoxus gracilis	--	--	0.02 ((0.1)	--	--
Chydorus sphaericus	--	--	0.02 ((0.1)	0.02 ((0.1)	--
Sida crystallina	--	0.05 ((0.1)	--	--	--
Eurycercus longirostris	--	--	0.08 ((0.1)	0.22 (0.2)	0.02 ((0.1)
Alona intermedia	--	--	0.02 ((0.1)	--	--
Daphnia retrocurva	--	0.04 ((0.1)	0.05 ((0.1)	--	--
Leptodora kindtii	0.03 ((0.1)	--	--	--	--
Total crustaceans	96.54	146.76	184.01	102.35	114.87

larger communities in the control enclosures than in the tubes to be acidified (Table 5). As measured by the coefficient of community (CC), the species compositions of the five communities were very similar at the end of the first week of enclosure, ranging from 77.8 to 88.9% (Table 6). The similarity of composition declined somewhat during the following two weeks for all community pairs except those involving A2 (Table 6). These declines were the result of the appearance of rare cladocerans in some of the communities (Table 5).

Of the major taxonomic groups, the abundance of cyclopoids varied least while cladoceran numbers varied most among the five communities, with respective coefficients of variation of 11.1 and 36.8% of the among tube means (Table 5). Intertube variation of calanoid copepod abundance was intermediate to these groups, with a coefficient of variation of 18.6%, mostly due to the very high abundance in Ctrl 1 (Table 5). High numbers of cladocerans in Ctrl 2 coupled with low abundance in Ctrl 1 and in the lake account for the large intertube variation in abundance of this group (Table 5).

Diaptomus minutus was the most important calanoid copepod in all five communities, contributing 83 to 92% of total calanoid abundance (Table 5). Similarly, B. longirostris accounted for the majority, 87.4 to 99.6%, of cladoceran abundance (Table 5). Consequently, the observed differences in community abundance were principally due to differences in the abundance of these species (Table 5). No

Table 6. Coefficient of community (Jaccard 1932) between all community pairs prior to acidification; June 5 and 20, 1979.

5 June

	A1	A2	Ctrl 1	Ctrl 2
A2	87.5	----	----	----
Ctrl1	88.9	77.8	----	----
Ctrl2	88.9	77.8	80.0	----
Lake	88.9	77.8	80.0	80.0

20 June

	A1	A2	Ctrl 1	Ctrl 2
A2	90.0	----	----	----
Ctrl1	66.7	72.7	----	----
Ctrl2	83.3	69.2	64.3	----
Lake	66.7	72.7	66.7	53.3

single species consistently predominated the cyclopoid component of the communities, with C. b. thomasi most numerous in A1 and Ctrl 2, M. edax in Ctrl 1 and the lake, and T. p. mexicanus in A2 (Table 5).

Bosmina longirostris and D. minutus were the only dominant species (i.e.: accounting for at least 10% of mean community abundance; after Patalas 1971) common to the five communities. B. longirostris was the most abundant organism, followed by D. minutus, in Ctrl 2, A1, and A2. Their positions were the reverse in the lake and Ctrl 1 (Table 5). Other dominant species were C. b. thomasi in A1 and the lake, T. p. mexicanus in A2 only, and M. edax in the lake only (Table 5).

While community composition was unaffected by the first three weeks of enclosure, the structure of the enclosed communitites, as measured by the percentage similarity of community index (PSC), had started to diverge from that in the lake just one week after the tubes were filled (Table 7). This divergence continued in Ctrl 2, A1, and A2 during the following two weeks, with slight decreases in similarity of structure occurring among the three communities as well (Table 7). Community structure in Ctrl 1 became more similar to that in the lake, and consequently less similar to the other enclosures, in the second and third weeks of enclosure (Table 7). This was the product of the reversed dominance positions of D. minutus and B. longirostris mentioned above which may have been the result of filling Ctrl 1 a day before

Table 7. Percent similarity of community index (Raabe 1952) between all community pairs prior to acidification; June 5 and 20, 1979.

5 June

	A1	A2	Ctrl 1	Ctrl 2
A2	82.5	----	----	----
Ctrl1	77.0	90.5	----	----
Ctrl2	90.5	84.0	79.5	----
Lake	66.5	58.0	56.5	59.0

20 June

	A1	A2	Ctrl 1	Ctrl 2
A2	79.5	----	----	----
Ctrl1	58.5	53.0	----	----
Ctrl2	73.5	81.0	41.0	----
Lake	51.0	46.5	76.5	41.5

the other tubes.

2.Responses of zooplankton to acidification and enclosure

A.Community composition and diversity

Enclosure effected a minor reduction in the similarity of species composition, as measured by the CC, in 1979. This reduction occurred in mid-July, after about 6 weeks of enclosure, and persisted at about the same level until the end of September (Fig. 10). On average the CC between the lake and Ctrl 1 was 63.9%, compared with 71.9% between Ctrl 1 and Ctrl 2, but this reduction was not consistent enough to be statistically significant (sign test, n=18, p=0.167). The average CC between the lake and Ctrl 2 was 62.1%, and represents a marginally significant reduction in the similarity of composition (sign test, n=18, p=0.052). During the first 6 weeks of enclosure in 1979, the communities in the control enclosures were no more similar to each other than to that in the lake and this was again the case through the first six sampling dates in 1980 (Fig. 10).

In total, 23 crustacean species were identified in the lake, Ctrl 1, and Ctrl 2 in the two study seasons (Table 8). Of these, 20 (2 calanoids, 6 cyclopoids, and 12 cladocerans) were common to the three communitites (Table 8). Leptodora kindtii and I. sordidus were absent from Ctrl 2 in both 1979 and 1980 and D. catawba , present in only one 1980 sample, was the only lake species never to be captured in the enclosures. Therefore, the reduced similarity of composition

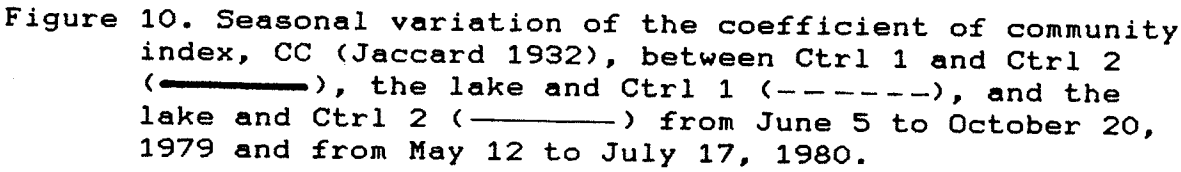


Figure 10. Seasonal variation of the coefficient of community index, CC (Jaccard 1932), between Ctrl 1 and Ctrl 2 (▬▬▬▬), the lake and Ctrl 1 (- - - - - -), and the lake and Ctrl 2 (——————) from June 5 to October 20, 1979 and from May 12 to July 17, 1980.

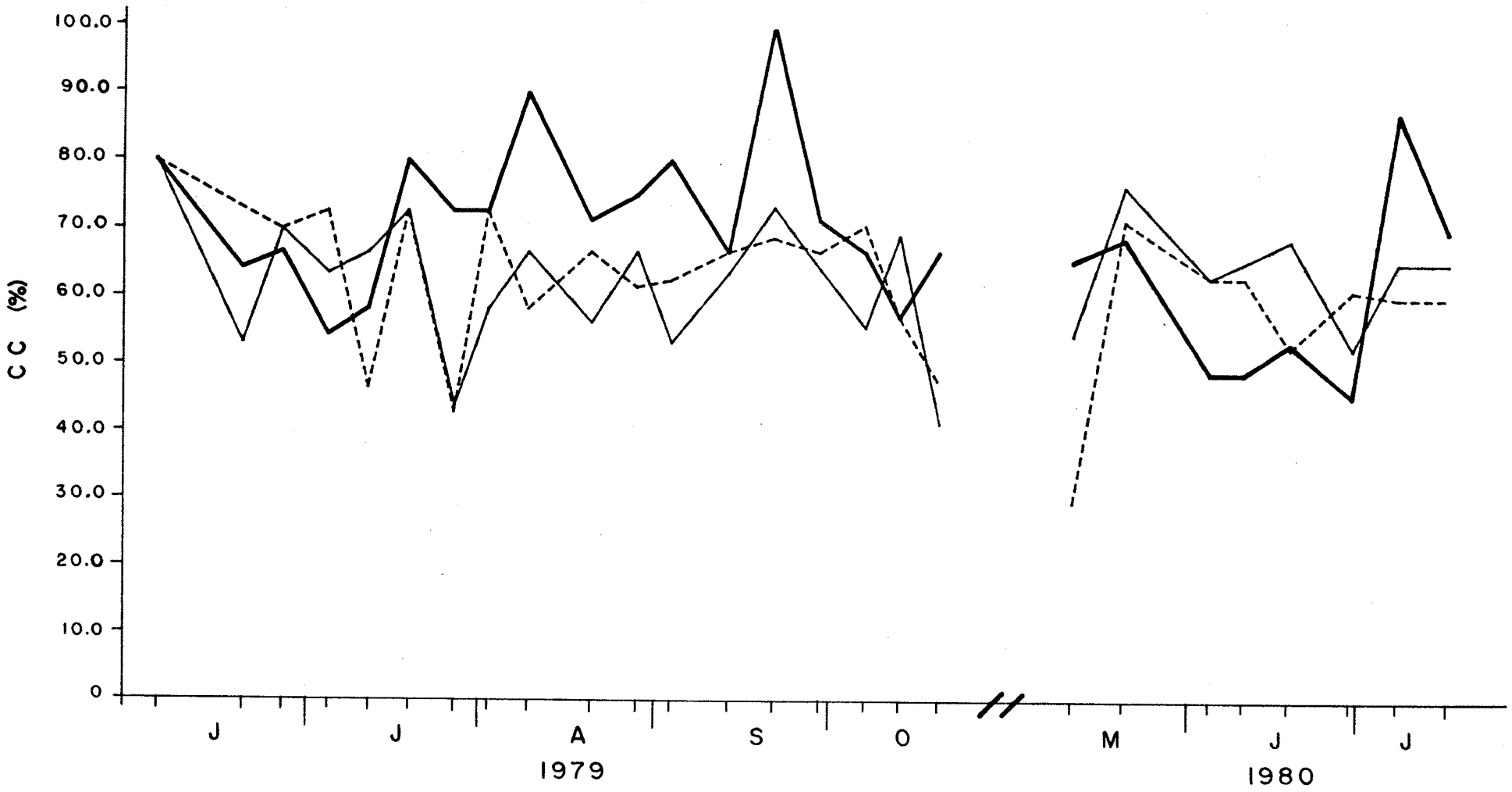

100.0
90.0
80.0
70.0
60.0
50.0
40.0
30.0
20.0
10.0
0
CC (%)
J
J
A
S
O
M
J
J
1979
1980

Table 8. Species compositions of the crustacean plankton communities in the lake, control enclosures (Ctrl 1 and Ctrl 2), and acidified enclosures (A1 and A2) in 1979 (June 5-October 20) and 1980 (May 12-July 17). ++ denotes species present in both years; +−, species present in 1979 only; −+, species present in 1980 only; −−, species absent in both years.

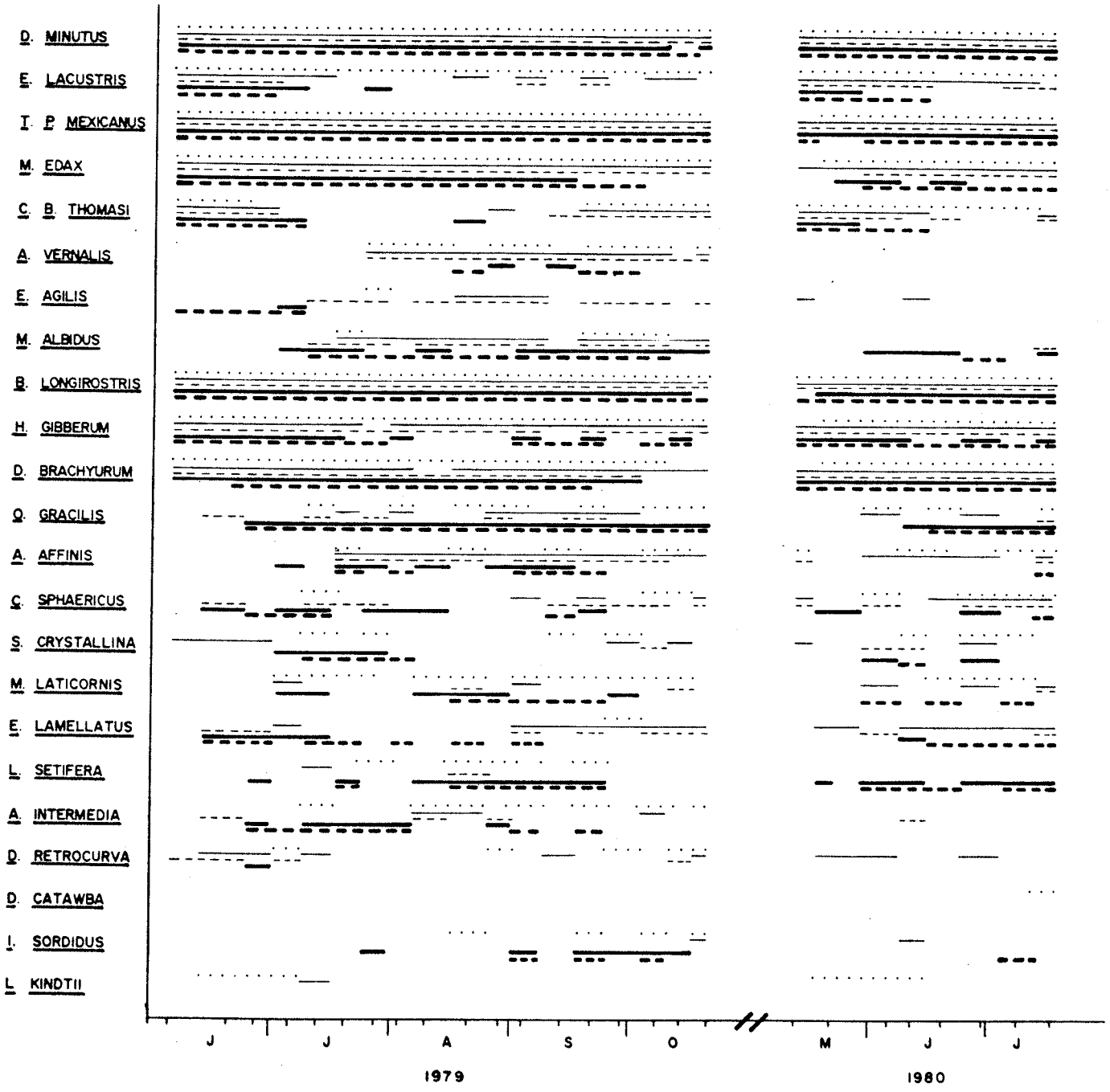
Species		Lake	Ctrl 1	Ctrl 2	A1	A2
Copepoda						
Diaptomus minutus	Lilljeborg	++	++	++	++	++
Epischura lacustris	Forbes	++	++	++	++	++
Tropocyclops prasinus mexicanus	Kiefer	++	++	++	++	++
Mesocyclops edax	(Forbes)	++	++	++	++	++
Cyclops bicuspidatus thomasi	Forbes	++	++	++	++	++
Acanthocyclops vernalis	Fischer	++	+−	+−	+−	+−
Eucyclops agilis	(Koch)	+−	++	++	+−	+−
Macrocyclops albidus	(Jurine)	+−	++	++	++	++
Cladocera						
Bosmina longirostris	(O.F.Muller)	++	++	++	++	++
Holopedium gibberum	Zaddach	++	++	++	++	++
Diaphanosoma brachyurum	(Lieven)	++	++	++	++	++
Ophryoxus gracilis	Sars	++	++	++	++	++
Alona affinis	(Liedig)	++	++	++	+−	++
Alona intermedia	Sars	+−	+−	++	+−	+−
Chydorus sphaericus	(O.F.Muller)	++	++	++	++	++
Sida crystallina	(O.F.Muller)	++	++	++	++	++
Macrothrix laticornis	(Jurine)	++	++	++	+−	++
Eurycercus longirostris	Hann	+−	++	++	++	++
Latona setifera	(O.F.Muller)	+−	+−	+−	++	++
Ilyocryptus sordidus	(Lieven)	+−	++	−−	+−	++
Daphnia retrocurva	Forbes	+−	++	+−	+−	−−
Daphnia catawba	Coker	−+	−−	−−	−−	−−
Leptodora kindtii	(Focke)	++	+−	−−	−−	−−

was not the result of the appearance or disappearance of species. Rather, the reduced CC values between the tubes and lake in 1979 were the product of the altered frequencies of occurrence of several minor species. Respectively, A. affinis and M. albidus occurred 2.5 and 2.9 times more frequently in the tubes than in the lake while the frequencies of occurrence of M. laticornis, L. setifera, and A. intermedia were reduced by 83, 80, and 58% (Fig. 11). These species made their first appearance in the plankton of all three communities in early to mid-July in 1979 (Fig. 11).

Acidification also produced significant changes in the zooplankton community composition. In 1979, the CC values between the acidified and control tubes decreased progressively with increasing duration of acidification and, on average, were significantly lower than the CC values between A1 and A2 (sign test, n=16, p=0 to 0.009 for the four pairings; Fig. 12). At the beginning of the experiment (June 20), the CC values between the control and acidified tubes ranged from 66.7 to 83.3% but, by October 20, the CC values were just 23.1 to 36.4%. With the hiatus of acidification over winter, the composition of the communities in the acid tubes had returned to that in the controls by the start of sampling in 1980 (Fig. 12). Following the resumption of acidification, community composition generally diverged from that in the controls, as in 1979 (Fig. 12).

The lower pH maintained in A1 in 1980 effected greater changes in community composition than were observed in A2.

Figure 11. Seasonal occurrence of crustacean plankton species in the lake (·····), Ctrl 1 (————), Ctrl 2 (- - - - - -), A1 (▬▬▬▬), and A2 (▬ ▬ ▬ ▬) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.


D. MINUTUS
E. LACUSTRIS
T. P. MEXICANUS
M. EDAX
C. B. THOMASI
A. VERNALIS
E. AGILIS
M. ALBIDUS
B. LONGIROSTRIS
H. GIBBERUM
D. BRACHYURUM
Q. GRACILIS
A. AFFINIS
C. SPHAERICUS
S. CRYSTALLINA
M. LATICORNIS
E. LAMELLATUS
L. SETIFERA
A. INTERMEDIA
D. RETROCURVA
D. CATAWBA
I. SORDIDUS
L. KINDTII
J
J
A
S
O
M
J
J
1979
1980

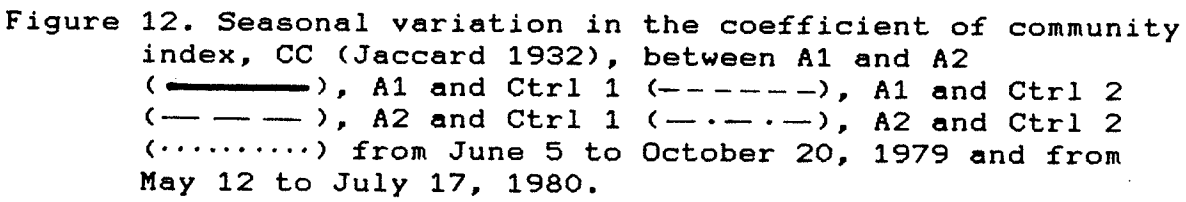
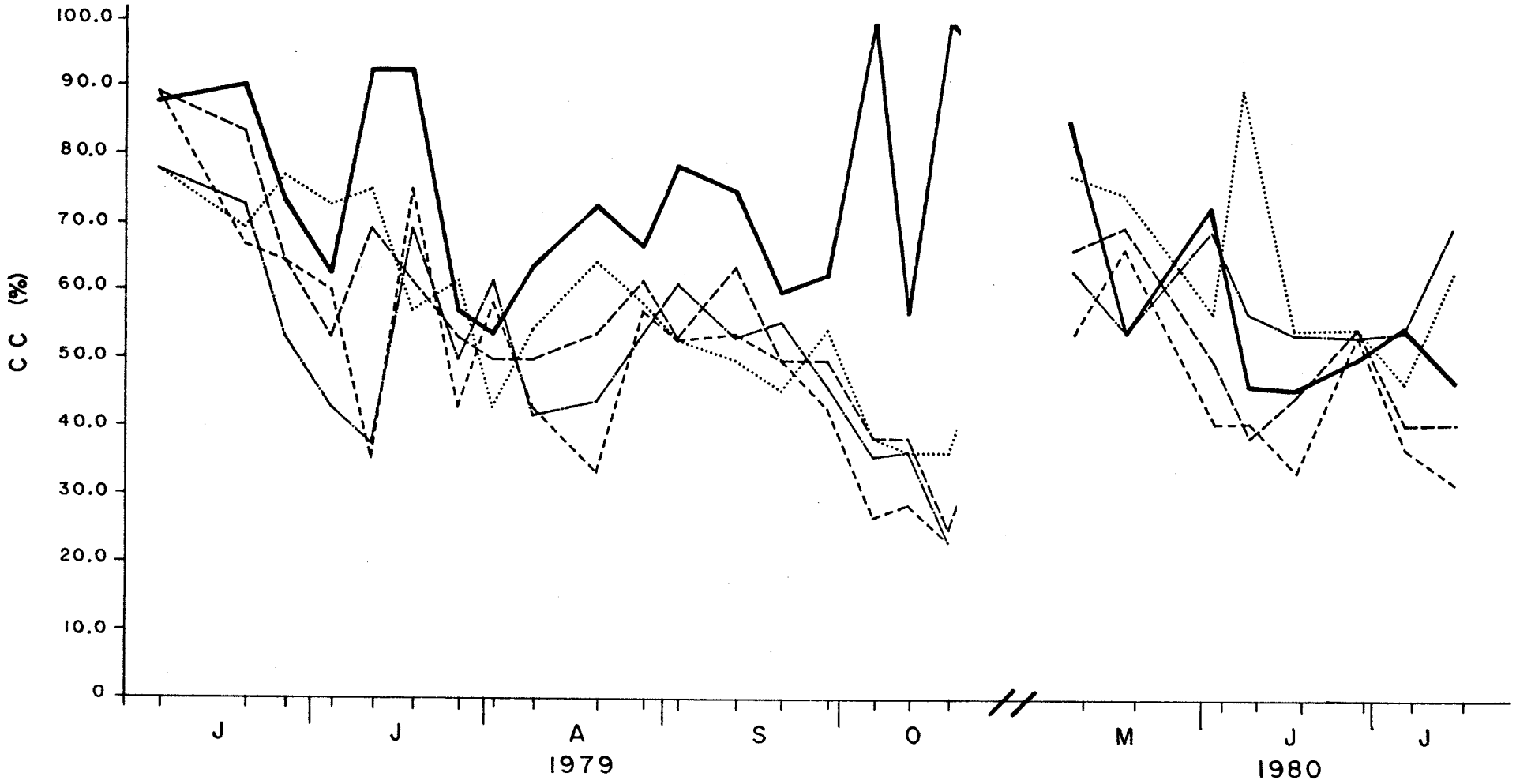


Figure 12. Seasonal variation in the coefficient of community index, CC (Jaccard 1932), between A1 and A2 (——————), A1 and Ctrl 1 (— — — — —), A1 and Ctrl 2 (— — — — —), A2 and Ctrl 1 (— · — · —), A2 and Ctrl 2 (·····) from June 5 to October 20, 1979 and from May 12 to July 17, 1980.


CC (%)
100.0
90.0
80.0
70.0
60.0
50.0
40.0
30.0
20.0
10.0
0
J
J
A
S
O
1979
M
J
J
1980

The CC values between Ctrl 2 and A1 were significantly lower than between Ctrl 2 and A2 (sign test, n=8, p=0.031) and the CC values between Ctrl 1 and A1 were also lower than between Ctrl 1 and A2, but not significantly so (sign test, n=8, p=0.109; Fig. 12). The composition of the communities in A1 and A2 diverged so greatly that the CC values between the control and acidified tubes weren't significantly lower than between A1 and A2 (sign test, n=8, p=0.109 to 0.273 for all community pairs; Fig. 12).

As in the control tubes, the alteration of community composition in the acidified tubes was not the result of the appearance or disappearance of species. Of the 22 species identified in the four enclosures in 1979, 19 were common to all communities (Table 8). Similarly, 15 of the 21 species identified in 1980 were common to the four enclosures (Table 8). No species was exclusive to the control enclosures in either year nor was any species unique to the acid tubes in 1979 (Table 8). Latona setifera was found only in the control tubes in 1980, but it was found in all tubes in 1979 (Table 8). This occurred because the shorter study period in 1980 did not include the period in which L. setifera occurred in the control tubes in 1979 (Fig. 11).

Three distinct classes of response by the constituent species to acidification acted to alter community composition in 1979. First, the period of occurrence of some species was truncated. E. lacustris and E. agilis were absent after July; C. b. thomasi was absent after August; and A. affinis, C.

sphaericus, S. crystallina, E. longirostris, and M. edax were absent in October (Fig. 11). These do not properly represent disappearances however, as the species either reappeared in the acid tubes in 1980 or there was insufficient replication in the control communities to conclude the species were excluded (Fig. 11). Secondly, the frequencies of occurrence of C. vernalis and H. gibberum were reduced by 78 and 35%, respectively (Fig. 11). And, finally, the frequencies of occurrence of I. sordidus, L. setifera, and O. gracilis were increased by factors of 4.5, 7.0, and 2.5, respectively, on average (Fig. 11). In 1980, the truncated occurrence of E. longirostris and C. b. thomasi, the reduced frequency of T. p. mexicanus, and the increased frequency of L. setifera contributed to the alteration of community composition in the acid tubes (Fig. 11). This response by T. p. mexicanus was not observed in 1979 (Fig. 11).

The reduced similarity of composition between the acidified communities was largely the result of the reduced frequency of occurrence of M. edax, H. gibberum, and E. lamellatus in A1 only and by the absence of A. affinis and M. laticornis from A1 (Fig. 11). With the exception of M. laticornis, those species differentially responding to the lower pH in A1 were also affected in both tubes in 1979, with prolonged reduction of pH below 5.0 the factor common to the response in both tubes in 1979 but in A1 only in 1980.

Community diversity, as measured by the number of species per sample, was unaffected by enclosure (Fig. 13). On

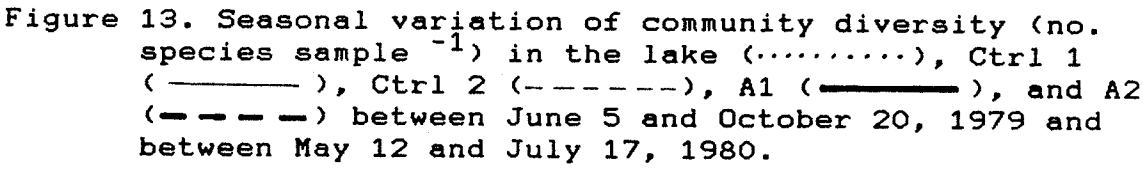
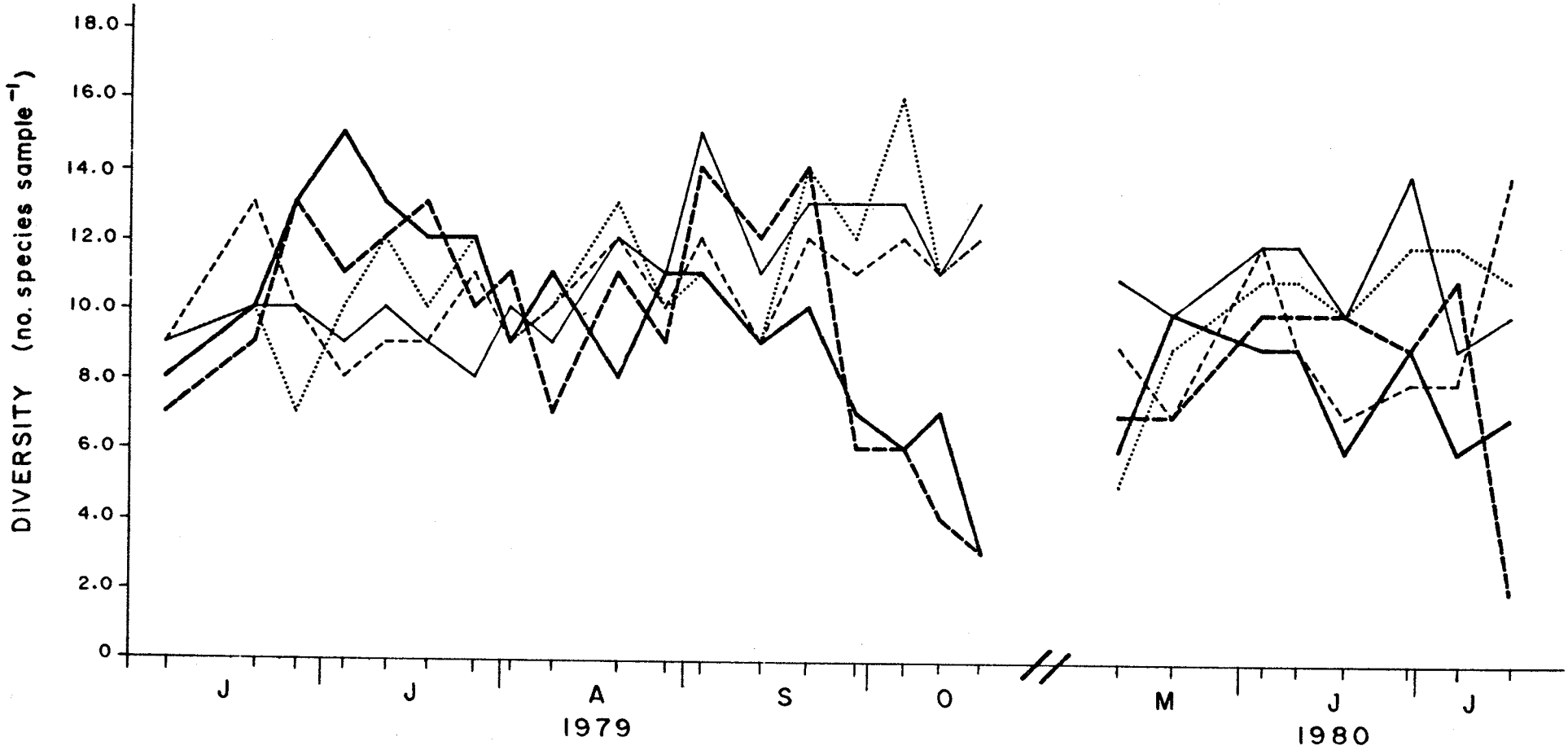


Figure 13. Seasonal variation of community diversity (no. species sample $^{-1}$) in the lake (·····), Ctrl 1 (————), Ctrl 2 (– – – – – –), A1 (▬▬▬▬), and A2 (▬ ▬ ▬ ▬) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.


DIVERSITY (no. species sample^{-1})
18.0
16.0
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0
J
J
A
S
O
1979
M
J
J
1980

average, there were 11.1 species per sample in the lake and Ctrl 1 and 10.4 species per sample in Ctrl 2 in 1979. The lower diversity in Ctrl 2 was due to the collection of fewer species in September and October (Fig. 13) but does not represent a significant reduction when the entire study season is considered (sign test, n=18, p=0.121). In 1980, the samples from the lake and Ctrl 1 averaged 10.9 and 11.0, respectively. Again, fewer species per sample were captured on average from Ctrl 2, at 9.3 (Fig. 13). However, as in 1979, this lower figure does not represent a significant reduction (sign test, n=8, p=0.109).

On average, community diversity was also unaffected by acidification (Fig. 13). In 1979, 9.8 species per sample were observed on average in both A1 and A2, fewer than in any of the other three communities but not a significant reduction (sign test, n=16, p=0.172). These lower mean diversities were the result of substantially fewer species appearing in the final three samples (Fig. 13).During the initial period of pH reduction in 1979, species richness in the acidified tubes increased relative to that in the control communities and remained at least 2 species per sample higher until the final week of July (Fig.13). Diversities in the four enclosures were similar through August to the end of September, when species richness in the acid tubes dropped sharply. The differential increased to the end of sampling, when only 3 species were captured from each of the acidic tubes while 12

species were captured in Ctrl 2 and the lake and 13 were collected from Ctrl 1 (Fig. 13). This dramatic decline of diversity was the cumulative result of the progressive truncations of the periods of species occurrence described above.

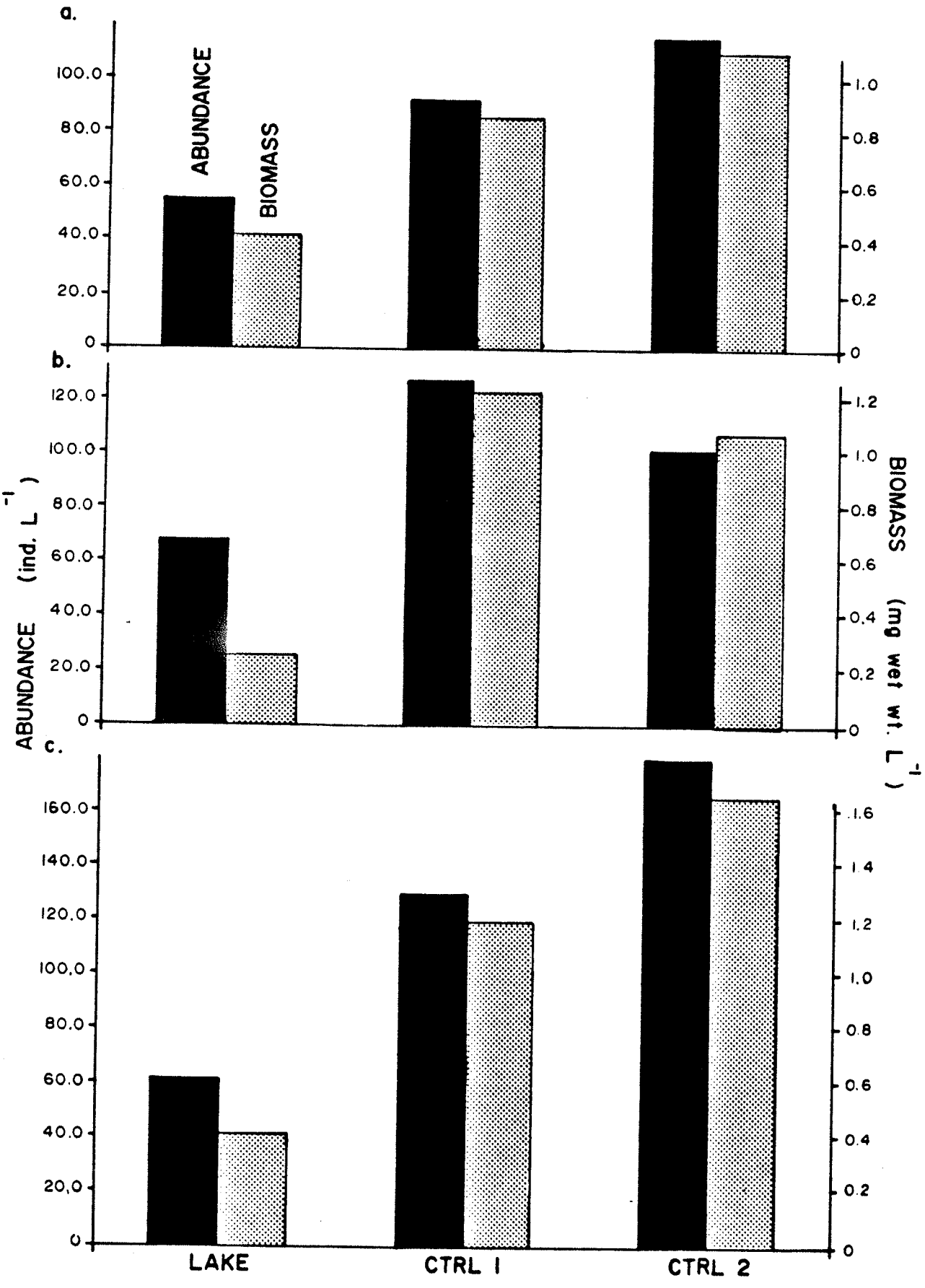
There was no increase in the number of species per sample in A1 and A2 after acidification was resumed in 1980, but diversities were generally within the range of those in the controls, as in August and September of 1979 (Fig. 13). At 8.0 species per sample, A1 had the lowest mean diversity although again not significantly so (sign test, n=8, p=0.219). The mean diversity in A2, at 9.9 species per sample, was within the range of control values. Consequently any pH effect is indistinguishable from natural variation.

B.Community abundance and seasonal dynamics

i. Enclosure

Total zooplankton community abundance and biomass were each significantly increased over those in the surrounding lake in both Ctrl 1 (sign test: 1979, n=18; abundance, p=0.001; biomass, p=0.012) and Ctrl 2 (sign test, n=18; abundance, p=0.012; biomass, p=0.012) in 1979 (Fig. 14a). This enhancement was again evident with continued enclosure in 1980 (Fig. 14b; sign test, n=8; Ctrl 1 abundance, p=0.031, biomass, p=0.004; Ctrl 2 abundance, p=0.0.031, biomass, p=0.031). There was no significant difference in abundance or biomass between the control tubes in either 1979 (sign test,

Figure 14. Mean crustacean plankton community abundance (ind. L^{-1}) and biomass (mg. wet wt. L^{-1}) in the lake, Ctrl 1, and Ctrl 2 between: a, June 5 and October 20, 1979; b, May 12 and July 17, 1980; and c, June 5 and August 2, 1979, the period in 1979 comparable to the 1980 sampling series.


a.
ABUNDANCE
BIOMASS
100.0
80.0
60.0
40.0
20.0
0
1.0
0.8
0.6
0.4
0.2
0
b.
120.0
100.0
80.0
60.0
40.0
20.0
0
1.2
1.0
0.8
0.6
0.4
0.2
0
ABUNDANCE (ind. L-1)
BIOMASS (mg wet wt. L-1)
c.
160.0
140.0
120.0
100.0
80.0
60.0
40.0
20.0
0
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
LAKE
CTRL 1
CTRL 2

n=18; abundance, p=0.196; biomass, p=0.167; Fig. 14a) or 1980 (sign test, n=8; abundance, p=0.219; biomass, p=0.273; Fig. 14b).

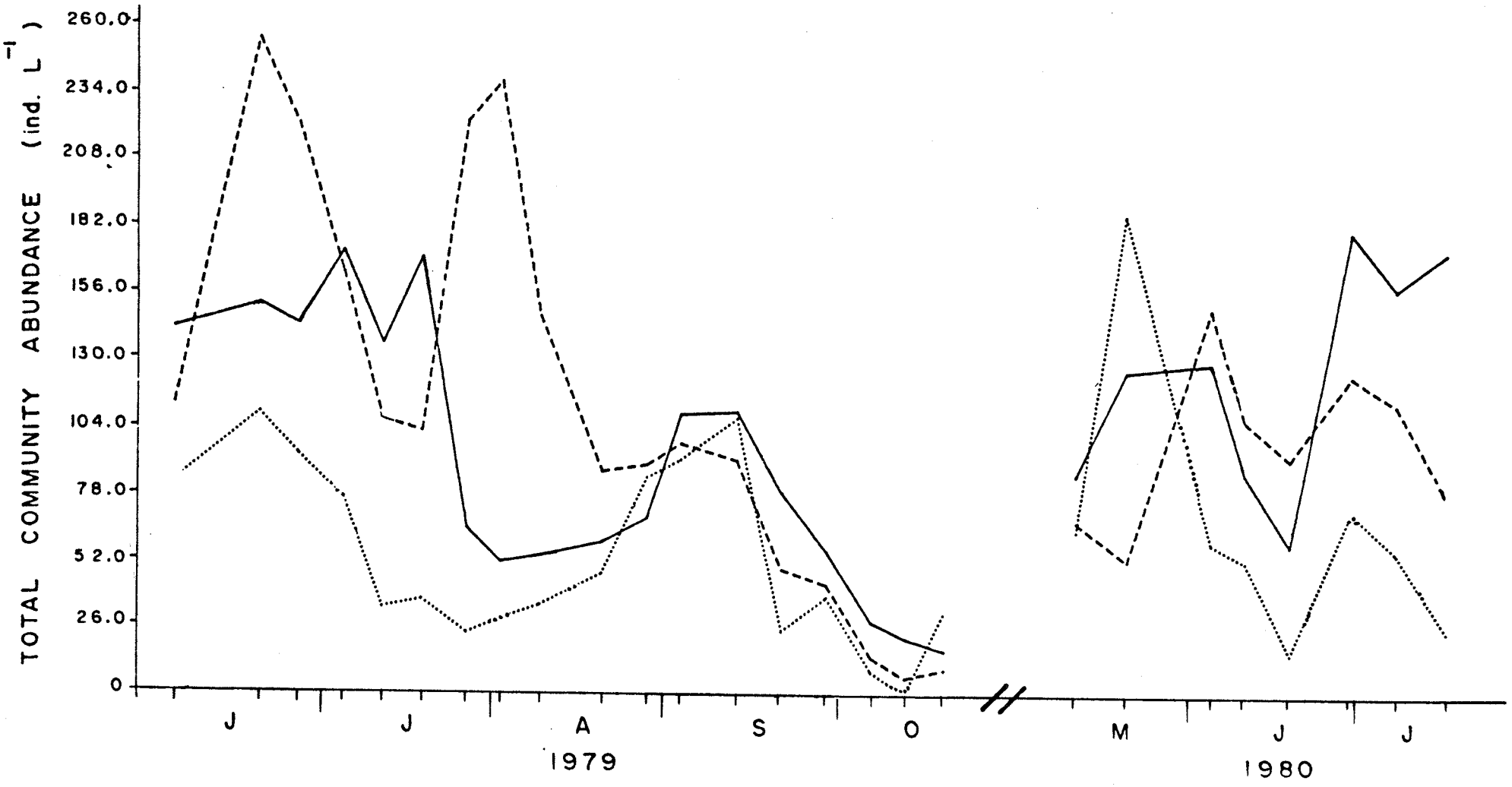
Because of the shorter sampling period and the three week earlier start of sampling in 1980, the effects of continued enclosure on community abundance cannot be directly compared with those observed in 1979. However, ice-out was also three weeks earlier in 1980. Consequently, the 1980 sampling series approximately corresponds with the first 8 sampling dates of 1979 (June 5 to August 2) with respect to the periods of community development being considered.

Comparing these periods, there was a smaller increase of abundance but a comparable increase of biomass due to enclosurein the second year. Abundance in the control enclosures averaged 2.5 times abundance in the lake in 1979 but was just 1.7 times greater in 1980 (Fig. 14b and 14c). Biomass in the control enclosures averaged 3.5 times that in the lake in 1979 and was 3.8 times higher in 1980 (Fig. 14b and 14c).

The reaction of the zooplankton communities in the control tubes to enclosure was almost immediate in 1979, with the increased abundance restricted to the spring and summer periods (Fig. 15). The seasonal dynamics of community abundance were also altered by enclosure in 1979, but only in Ctrl 2 (Fig. 15).

In the lake, community abundance followed a bimodal pattern of seasonal fluctuation (Fig. 15). The initial pulse

Figure 15. Seasonal variation of crustacean plankton community abundance (ind. L^{-1}) in the lake (.....), Ctrl 1 (————), and Ctrl 2 (– – – – –) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.


TOTAL COMMUNITY ABUNDANCE (ind. L⁻¹)
260.0
234.0
208.0
182.0
156.0
130.0
104.0
78.0
52.0
26.0
0
J
J
A
S
O
1979
M
J
J
1980

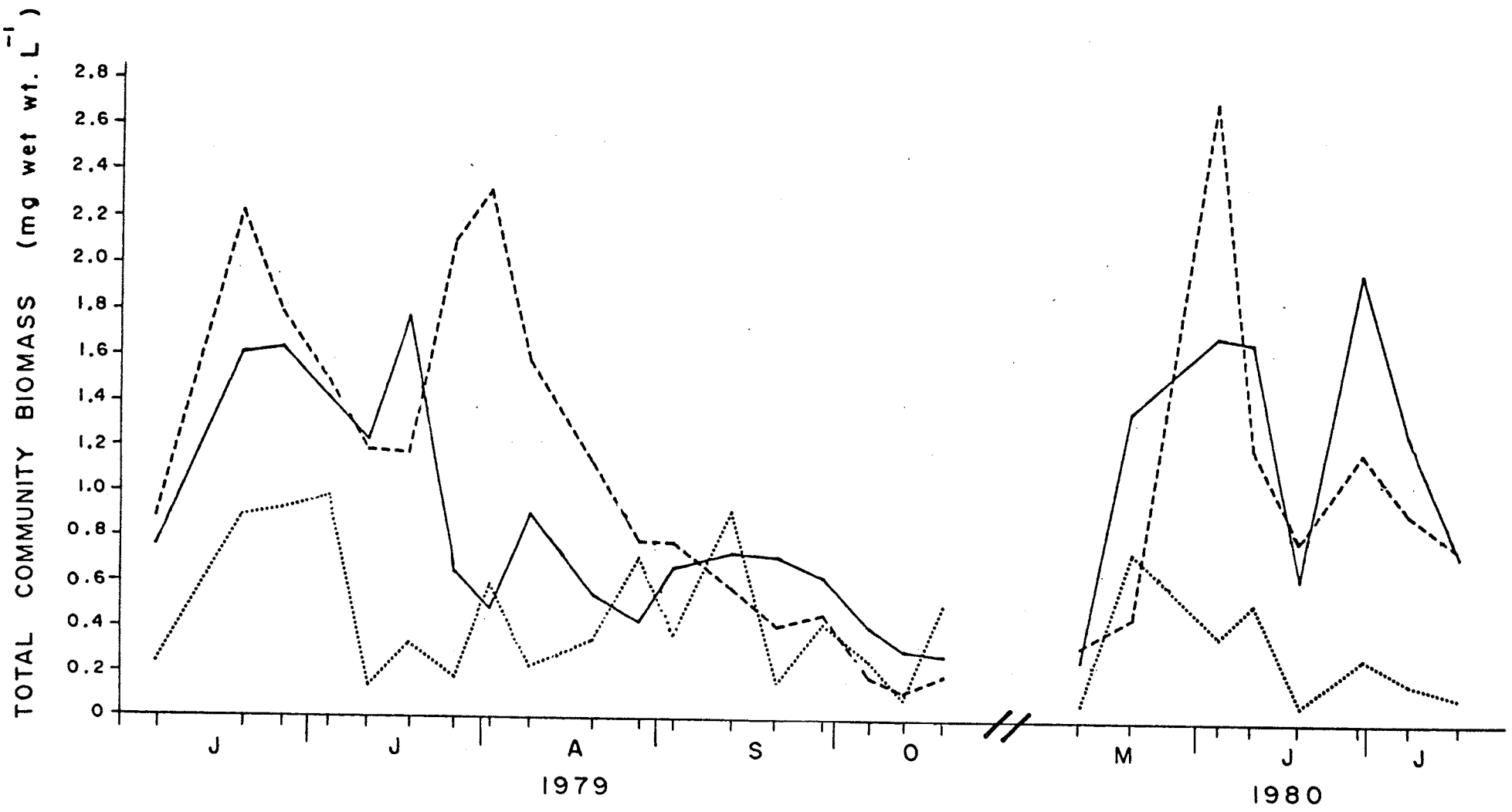
had already started to develop before sampling began in June and peaked at 110 ind L^{-1} in mid-month. Abundance declined in early July with the summer minimum of about 30 ind L^{-1} lasting for 2-3 weeks. The second pulse began to develop in early August, with the peak in mid-September of identical magnitude to the peak in the spring. Abundance declined more quickly than after the spring peak and fluctuated about the level of the summer minimum for the last month of sampling.

Although sampling began more than three weeks earlier in 1980, community development was at about the same stage as at the beginning of sampling in 1979 (Fig. 15). This corresponds with ice-out also occurring about three weeks earlier in 1980. The initial peak, at 188 ind L^{-1} in the third week of May, was much larger than the first peak in 1979. Also unlike 1979, this initial pulse was followed by an early summer pulse which peaked at 72 ind L^{-1} at the end of June (Fig. 15).

Community biomass in the lake followed a pattern of seasonal occurrence similar to that of abundance although the autumn peak in 1979 and the early summer peak in 1980 were much less pronounced (Fig. 16).

In 1979, community abundance in Ctrl 1 followed a bimodal curve similar to that in the lake with the major difference an enhancement and prolongation of the initial pulse (Fig. 15). Abundance was 70% higher than in the lake on the first sampling date and the peak of 150 ind L^{-1} persisted from mid-June to mid-July. Abundance declined quickly in the

Figure 16. Seasonal variation of crustacean plankton community biomass (mg. wet wt. L^{-1}) in the lake (·····), Ctrl 1 (————), and Ctrl 2 (– – – – –) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.


TOTAL COMMUNITY BIOMASS (mg wet wt. L⁻¹)
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
J
J
A
S
O
1979
M
J
J
1980

latter half of the month with the decline closely followed by the development of the second pulse which was identical to the second pulse in the lake (Fig. 15).

Unlike in either the lake or Ctrl 1, community abundance in Ctrl 2 followed a trimodal pattern of fluctuation in 1979 (Fig. 15). The initial pulse developed at the same time as in the lake but the peak of abundance was about 2.3 times higher (Fig. 15). Also as in the lake, abundance declined immediately following the peak. The additional pulse developed in mid-summer, peaking in early August at about the same level as the first pulse. The initial development of the third pulse in late-summer was obscured by the decline from the second, but the magnitude of the peak attained was identical to those in the lake and Ctrl 1 as was the subsequent decline (Fig. 15).

The fluctuations of community biomass in the control enclosures during the 1979 study season were synchronous with those of numbers. Again, the peak of biomass in Ctrl 2 at the beginning of August was the major difference between Ctrl 1 and Ctrl 2 (Fig. 16). As with numbers, biomass in the enclosures exceeded lake values only until mid-August (Fig. 16).

The spring and early-summer dynamics of community abundance in the control tubes replicated much better in 1980 and did not diverge from the dynamics of the lake community (Fig. 15). There was, however, a major difference in the development of the enclosed communities after a year of

enclosure which amounted to a relative delay in the enhancement of abundance. In 1979, abundance was already increased over that in the lake within 7 days of tube installation and was markedly higher by the peak of the first pulse. In 1980, the initial pulses in the tubes were slightly smaller than in the lake, although they occurred at about the same time as the first pulse in the lake (Fig. 15). Abundance finally began to exceed that in the lake in early June as a result of smaller declines following the first peak; on about the same date as in 1979 but 2-3 weeks later in community development. The much larger early summer pulses which subsequently developed in the tubes were more in character with the response to enclosure observed in 1979. These occurred at the same time as in the lake but the peaks were 1.7 to 2.5 times larger. This delay explains the smaller average increase of abundance in the first 8 weeks of 1980 than in 1979. Clearly, the prolonged enclosure had no additional effects on community abundance nor on community dynamics in the spring and early summer period when the major influence of enclosure was manifested in 1979.

The dynamics of community biomass in the control tubes were synchronized with those of numbers in 1980 as well (Fig. 16). Although the numbers of crustaceans in Ctrl 1 and Ctrl 2 weren't any greater than in the lake during the first peak, the biomass of these animals was, at 2.3 and 3.6 times that in the lake. This differential persisted in the control tubes for all subsequent 1980 sampling dates (Fig. 16).

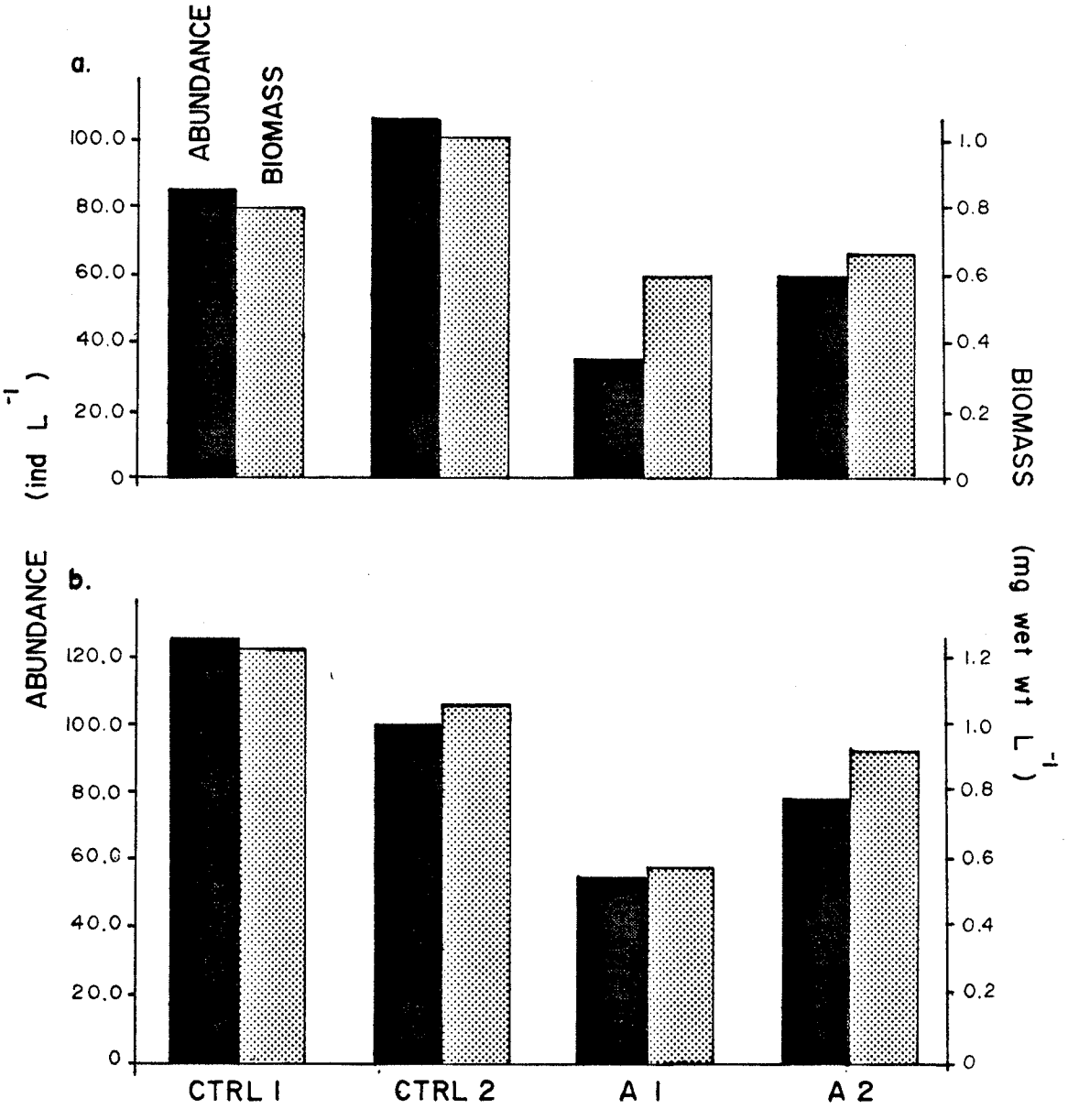
i. Acidification

Community abundance and biomass were reduced in both acidified tubes in 1979, although neither parameter replicated as well as in the controls (Fig. 17a). These reductions were highly significant in A1, with seasonal mean abundance at 36% (sign test, n=16, p=0.002) and biomass at 61% (sign test, n=16, p=0.009) of the control values. The reductions were just marginally significant in A2, with mean abundance at 65% (sign test, n=16, p=0.067) and biomass at 72% (sign test, n=16, p=0.067) of the control values .The greater reductions of both parameters in A1 than in A2 also represent a marginally significant difference (sign test, n=16, p=0.067 for both abundance and biomass).

Abundance and biomass were again lower in the acidified tubes than in the controls in 1980 (Fig. 17b). In A1, seasonal mean community abundance and biomass at 41% (sign test, n=8, p=0.004) and 50% (sign test, n=8, p=0.031) of the respective control means were again significantly reduced. Community abundance and biomass in A2 were 70% (sign test, n=8, p=0.273) and 80% (sign test, n=8, p=0.109) of the control means but neither reduction was significant. The reductions of abundance and biomass were significantly greater in A1 than in A2 (sign test, n=8; abundance, p=0.004; biomass, p=0.031).

The seasonal dynamics of zooplankton community abundance in the acidified tubes were distinguished from those in the

Figure 17. Seasonal mean crustacean plankton community abundance (ind. L^{-1}) and biomass (mg. wet wt. L^{-1}) in Ctrl 1, Ctrl 2, A1, and A2 between: a, June 21 and October 20, 1979; b, May 12 and July 17, 1980.

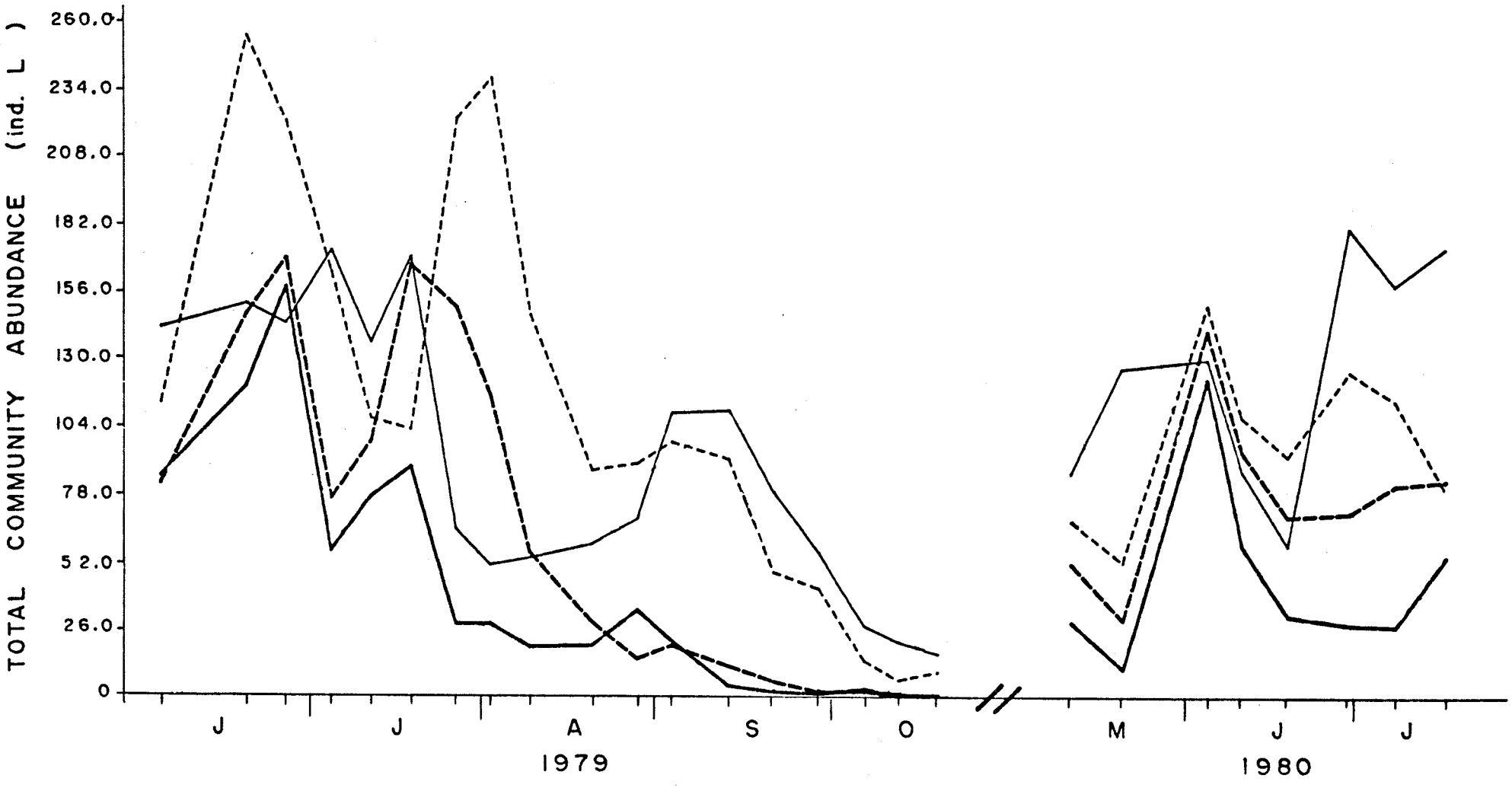

a.
ABUNDANCE
BIOMASS
100.0
80.0
60.0
40.0
20.0
0
(ind L -1)
1.0
0.8
0.6
0.4
0.2
0
BIOMASS
b.
ABUNDANCE
120.0
100.0
80.0
60.0
40.0
20.0
0
1.2
1.0
0.8
0.6
0.4
0.2
0
(mg wet wt L -1)
CTRL 1
CTRL 2
A 1
A 2

controls by better replication in the two seasons of study and the major effect of acidification was the elimination of the autumn pulse in 1979 (Fig. 18). The dynamics during the spring and summer of 1979 otherwise resembled those in Ctrl 2 (Fig. 18).

Although 60-80% lower than in the control tubes at the start of sampling in 1979, abundance in the acid tubes equalled that in Ctrl 1 at the peaks of the initial pulses 3 weeks later (Fig. 18). This period included the first week of pH reduction, June 21-27, which had no discernable effect on the rates of increase nor on the timing of the first pulse. Abundance in both acid tubes declined sharply in the week following the initial peak. This was coincident with the decline in Ctrl 2 but also with the second week of pH reduction. The summer pulses followed the first pulse more closely in the acid tubes than in Ctrl 2, peaking in mid-July rather than in early August. As in Ctrl 2, this second peak was of identical magnitude to the initial peak in A2, but abundance in A1 peaked at just 70% of the first peak and the greater abundance in A2 during this pulse was most responsible for the greater seasonal mean abundance than in A1 (Fig. 18). Abundance in both acid tubes declined more or less continuously from the second peaks, with no significant late-summer pulses appearing (Fig. 18). The failure to produce these later pulses was not the result of any additional change in the pH regimes of the acidified tubes.

Although the pH of the acidified enclosures returned to

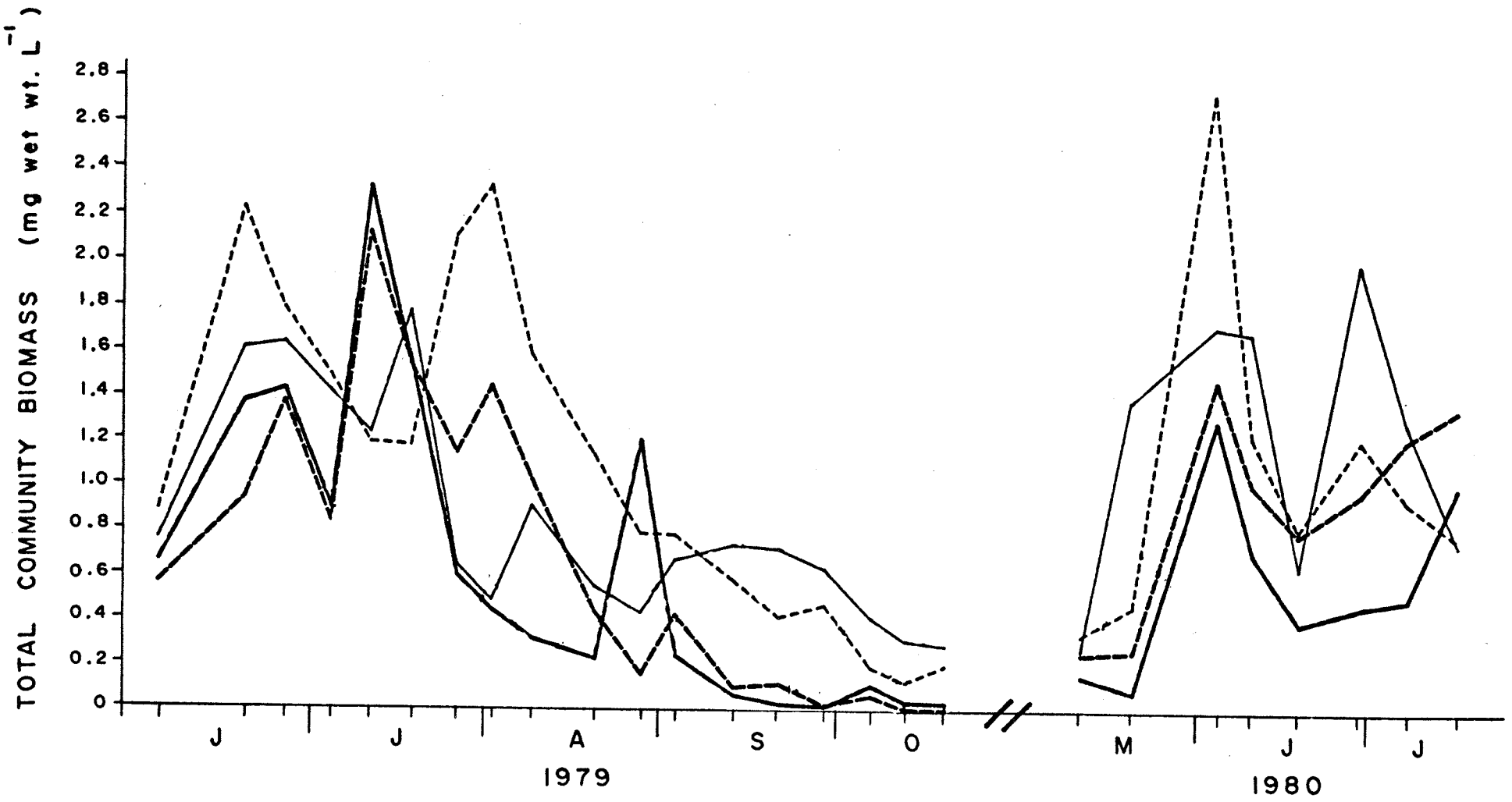
Figure 18. Seasonal variation of crustacean plankton community abundance (ind. L^{-1}) in Ctrl 1 (————), Ctrl 2 (– – – – – –), A1(▬▬▬▬), and A2 (▬ ▬ ▬ ▬) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.


TOTAL COMMUNITY ABUNDANCE (ind. L⁻¹)
260.0
234.0
208.0
182.0
156.0
130.0
104.0
78.0
52.0
26.0
0
J
J
A
S
O
M
J
J
1979
1980

control levels over the following winter, community abundance did not; ranging from 35-80% of control abundance at the resumption of sampling in 1980 (Fig. 18). Because the initial pulses coincided with the first forest fire in 1980, they were exposed to a relatively minor reduction of pH. However, neither this nor the lower abundance at the start of the 1980 season affected either the timing or the magnitude of the first pulses in the acid tubes (Fig. 18). Abundance in both acid tubes declined immediately following the peaks, as in the controls, but to a much greater degree in A1 than in A2, Ctrl 1, or Ctrl 2 (Fig. 18). This correlates with the larger reduction of pH in A1 than in A2 during the same period (Fig. 7). Subsequently, with the pH in both tubes maintained below 5.5, the early-summer pulses were delayed by 2-3 weeks. Also, the pH in A1 was generally below 5.0 during this period and abundance was consistently lower than in A2 (Fig. 18).

As in the control tubes, biomass in the acidified tubes generally followed the changes in numbers although the relative size of some peaks differed (Figs. 18 and 19). While the spring peaks of community numbers in 1979 were as large (A2) or larger (A1) than the mid-summer peaks, the mid-summer peaks of biomass were substantially larger than those in the spring. This is in contrast to Ctrl 2 where the midsummer peak of biomass was of the same magnitude as the first peak (Fig. 19). The small peak of abundance in A1 in late August becomes much more important when biomass is considered, and an early-August peak of biomass is evident in A2 is although

Figure 19. Seasonal variation of crustacean plankton community biomass (mg. wet wt. L^{-1}) in Ctrl 1 (————), Ctrl 2 (– – – – – –), A1 (▬▬▬▬), and A2 (▬ ▬ ▬ ▬) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.


TOTAL COMMUNITY BIOMASS (mg wet wt. L^{-1})
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
J
J
A
S
O
1979
M
J
J
1980

no pulse of numbers occurred at this time. Most important, however, is that biomass in the acid tubes was substantially lower than in the control tubes through September and October as were community numbers (Figs. 18 and 19). The 1980 patterns of biomass change were very similar to those of abundance (Fig. 19).

C. Species abundance and community structure

i. Enclosure

The increases of total community abundance in the control enclosures were the result of increases in the abundance of most numerically important species (Tables 9, 10, 11, and 13). In 1979, the increases which reproduced best between enclosures were those of D. minutus, T. p. mexicanus, D. brachyurum, and the cyclopoid nauplii; all in the 2-3.5 fold range (Table 9). For these four groups, the seasonal mean abundance in each tube was within 2-8% of the between tube mean and, for all but D. brachyurum, the increases were highly significant (sign test, $n=18$, $p<0.01$; Table 9). The increased abundance of D. minutus copepodids is even more dramatic in view of the very significant (sign test, $n=18$, $p<0.01$) 30-50% decreases of calanoid nauplius abundance in the control enclosures during the same period (Table 9). Though not identified to species, a large proportion of these were most certainly D. minutus, given that this species accounted for about 96% of total calanoid copepodid abundance in the two enclosures (Table 9).

Table 9. Mean abundance (ind. L^{-1}) and percentage composition, in (), of planktonic crustacean species in the lake and control enclosures from June 5 to October 20, 1979. For calculation of percentage composition, nauplii were apportioned among the species of their respective suborders according to copepodid abundance. *'s indicate results of Fisher's sign test of difference in seasonal mean abundance. *=0.10)p)0.05 , **=0.05)p)0.01 , ***=0.01)p.

Species	Lake	Ctrl 1	Ctrl 2
Diaptomus minutus	5.27 (37.3)	18.61 (32.0) ***	15.81 (20.5) **
Epischura lacustris	0.42 (3.0)	0.73 (1.3)	0.41 (0.5)
Calanoid nauplii	16.11	11.07 ***	7.71 ***
Tropocyclops prasinus mexicanus	1.65 (11.0)	2.91 (18.3) ***	3.05 (10.5) **
Mesocyclops edax	1.88 (12.5)	2.01 (12.6) *	4.08 (14.1) ***
Cyclops bicuspidatus thomasi	0.83 (5.5)	0.64 (4.0)	0.76 (2.6)
Other cyclopoids	1.19	1.03	1.77
Cyclopoid nauplii	14.50	31.23 ***	28.27 ***
Bosmina longirostris	11.62 (21.4)	18.84 (20.6)	50.77 (44.6)
Holopedium gibberum	0.27 (0.5)	3.45 (3.8) *	0.39 (0.3)
Diaphanosoma brachyurum	0.21 (0.4)	0.66 (0.7)	0.68 (0.6) *
Ophryoxus gracilis	0.05 (0.1)	0.02 ((0.1)	0.01 ((0.1)
Alona affinis	0.02 ((0.1)	0.07 ((0.1)	0.03 ((0.1)
Alona intermedia	0.06 (0.1)	0.01 ((0.1)	0.01 ((0.1)
Chydorus sphaericus	0.01 ((0.1)	(0.01 ((0.1)	0.01 ((0.1)
Sida crystallina	0.01 ((0.1)	0.01 ((0.1)	(0.01 ((0.1)
Macrothrix laticornis	0.04 (0.1)	(0.01 ((0.1)	0.01 ((0.1)
Eurycercus longirostris	(0.01 ((0.1)	0.03 ((0.1)	0.02 ((0.1)
Latona setifera	0.01 ((0.1)	(0.01 ((0.1)	(0.01 ((0.1)
Ilyocryptus sordidus	0.01 ((0.1)	(0.01 ((0.1)	—
Daphnia retrocurva	0.02 ((0.1)	0.02 ((0.1)	0.01 ((0.1)
Leptodora kindtii	0.01 ((0.1)	(0.01 ((0.1)	—
Total crustaceans	54.18	91.34 ***	113.80 **

Three species responded to different degrees in the two enclosures. H. gibberum was almost 13 times more abundant in Ctrl 1 than in the lake while abundance in Ctrl 2 increased by a factor of just 1.4 (Table 9). Conversely, M. edax abundance increased just marginally in Ctrl 1 yet it was 2.2 times more numerous in Ctrl 2 than in the lake (Table 9). Similarly, B. longirostris increased by a factor of 1.6 in Ctrl 1 but by a factor of 4.4 in Ctrl 2 (Table 9).

A similar picture emerges when biomass is considered, although the magnitude of the increases differs between the parameters for two species (Tables 9 and 10). The increases of D. minutus biomass were 20-35% smaller than the increases of numbers while the increases of H. gibberum biomass were about twice those of numbers.

Again, because of the shorter sampling period and the three week earlier start of sampling in 1980, the effects of continued enclosure on species abundance cannot be directly compared with those observed in 1979. However, ice-out was also three weeks earlier in 1980. Consequently, the period of study approximately corresponds with the first 8 sampling dates in 1979 (June 5 to August 2) with respect to the periods of species development being considered.

Comparing these periods, it is apparent that continued enclosure had little additional effect on the abundance of species which responded in 1979 and that no additional species were affected (Tables 11 and 12). The only major exception to this was T. p. mexicanus which increased about

Table 10. Mean biomass (mg. wet wt. L^{-1}) and percentage composition, in (), of planktonic crustacean species in the lake and control enclosures from June 5 to October 20, 1979. For calculation of percentage composition, nauplii were apportioned among the species of their respective suborders according to copepodid abundance. + denotes species present with mean biomass (0.001 mg L^{-1}. *'s indicate results of Fisher's sign test of difference in seasonal mean biomass. *=0.10)p)0.05 , **=0.05)p)0.01 , ***=0.01)p.

Species	Lake	Ctrl 1	Ctrl 2
Diaptomus minutus	0.179 (45.6)	0.414 (49.3) ***	0.434 (40.1) ***
Epischura lacustris	0.030 (7.7)	0.064 (7.6)	0.033 (3.1)
Calanoid nauplii	0.011	0.009 **	0.005 ***
Tropocyclops prasinus mexicanus	0.009 (2.4)	0.012 (1.7) *	0.019 (2.0) *
Mesocyclops edax	0.034 (9.2)	0.039 (5.5) *	0.090 (9.3) ***
Cyclops bicuspidatus thomasi	0.009 (2.4)	0.009 (1.3)	0.009 (0.9)
Other cyclopoids	0.017	0.020	0.032
Cyclopoid nauplii	0.008	0.017 ***	0.020 ***
Bosmina longirostris	0.095 (23.0)	0.154 (18.0)	0.414 (37.8)
Holopedium gibberum	0.003 (0.7)	0.069 (8.1) *	0.010 (0.9)
Diaphanosoma brachyurum	0.008 (1.9)	0.024 (2.8)	0.025 (2.3) *
Ophryoxus gracilis	0.004 (1.0)	0.002 (0.3)	0.001 (0.1)
Alona affinis	+	0.003 (0.2)	0.001 (0.1)
Alona intermedia	0.001 (0.2)	+	+
Chydorus sphaericus	+	+	+
Sida crystallina	0.002 (0.5)	0.004 (0.5)	+
Macrothrix laticornis	0.001 (0.2)	+	+
Eurycercus longirostris	+	0.001 (0.1)	0.001 (0.1)
Latona setifera	0.001 (0.2)	+	+
Ilyocryptus sordidus	+	+	—
Daphnia retrocurva	0.001 (0.2)	0.001 (0.1)	+
Leptodora kindtii	+	+	—
Total crustaceans	0.413	0.856 **	1.095 **

50% more than in the comparable period of the previous year (Tables 11 and 12). More species responded equally in the two enclosures in 1980. For each of M. edax and H. gibberum, abundance in both tubes increased as much as in the enclosure with the higher abundance in 1979 (Tables 11 and 12). However, some species responded to lesser degrees in 1980. D. brachyurum abundance increased by 53 and 17% of the margins recorded in Ctrl 1 and Ctrl 2, respectively, in 1979 (Tables 11 and 12). Similarly, the increases of B. longirostris abundance were 68 and 10% of those seen in the previous year (Tables 11 and 12). It was the much smaller increase of Bosmina numbers in Ctrl 2 which accounted for total crustacean abundance in this tube increasing by just 44% of the margin during the comparable period of 1979 (Tables 11 and 12).

As in 1979, the picture remains similar in most respects when biomass changes are considered (Tables 12 and 13). The most important deviation, and quite in contrast to the first year of enclosure, is that D. minutus biomass increased substantially more in the tubes in 1980 than during the corresponding period in 1979 (Tables 12 and 13). This was sufficient to make the increase of total community biomass in Ctrl 1 about 1.7 times greater than in 1979 (Tables 12 and 13). In Ctrl 2, this increase compensated for the much smaller increase of B. longirostris abundance in the second year (Tables 12 and 13). Other minor differences from the enclosure-related increases in numbers include the appearance

Table 11. Mean abundance (ind. L^{-1}) and percentage composition, in (), of planktonic crustacean species in the lake and in the control and acidified enclosures from May 12 to July 17, 1980. For calculation of percentage composition, nauplii were apportioned among the species of their respective suborders according to copepodid abundance. *'s indicate results of Fisher's sign test of difference in seasonal mean abundance between the lake and control enclosures and between the control and acidified enclosures. *=0.10)p)0.05 , **=0.05)p)0.01 , ***=0.01)p.

Species	Lake	Ctrl 1	Ctrl 2	A1	A2
Diaptomus minutus	5.37 (42.7)	25.23 (30.3) ***	26.34 (37.2) ***	0.47 (2.3) ***	3.31 (8.7) ***
Epischura lacustris	0.80 (6.4)	2.86 (3.4)	1.07 (1.5)	0.04 ((0.1)	0.30 (0.8)
Calanoid nauplii	26.68	14.21 **	11.33	0.71 ***	3.78 ***
Tropocyclops prasinus mexicanus	1.29 (8.5)	4.02 (14.8) **	3.65 (15.7) **	0.28 (1.1) ***	1.49 (3.9)
Mesocyclops edax	1.22 (8.1)	1.98 (7.3) **	2.57 (11.0) *	0.01 ((0.1) **	0.14 (0.4) **
Cyclops bicuspidatus thomasi	3.06 (20.2)	3.63 (13.4)	3.65 (15.7)	2.49 (9.4)	4.06 (10.5)
Other cyclopoids	0.25	2.09	0.53	0.03 **	0.03 **
Cyclopoid nauplii	19.91	42.55 **	34.26	2.03 ***	5.88 ***
Bosmina longirostris	7.95 (11.9)	25.55 (20.4) **	12.31 (12.3)	24.03 (52.9)	30.82 (39.5)
Holopedium gibberum	0.19 (0.3)	2.61 (2.1) ***	2.78 (2.8) ***	4.49 (9.9)	17.05 (21.8)
Diaphanosoma brachyurum	0.24 (0.4)	0.71 (0.6) **	0.22 (0.2)	10.35 (22.8) **	11.21 (14.4)
Ophryoxus gracilis	0.01 ((0.1)	(0.01 ((0.1)	(0.01 ((0.1)	0.38 (0.8) *	0.31 (0.4)
Alona affinis	0.02 ((0.1)	0.02 ((0.1)	0.01 ((0.1)	—	(0.01 ((0.1)
Alona intermedia	—	—	(0.01 ((0.1)	—	—
Chydorus sphaericus	0.01 ((0.1)	0.03 ((0.1)	0.03 ((0.1)	(0.01 ((0.1)	(0.01 ((0.1)
Sida crystallina	0.01 ((0.1)	0.01 ((0.1)	0.01 ((0.1)	(0.01 ((0.1)	(0.01 ((0.1)
Macrothrix laticornis	0.01 ((0.1)	0.01 ((0.1)	(0.01 ((0.1)	—	0.01 ((0.1)
Eurycercus longirostris	—	0.02 ((0.1)	0.01 ((0.1)	(0.01 ((0.1)	0.03 ((0.1)
Latona setifera	—	—	—	0.03 (0.1)	0.03 ((0.1)
Ilyocryptus sordidus	—	(0.01 ((0.1)	—	—	(0.01 ((0.1)
Daphnia retrocurva	—	0.01 ((0.1)	—	—	—
Daphnia catawba	(0.01 ((0.1)	—	—	—	—
Leptodora kindtii	0.01 ((0.1)	—	—	—	—
Total crustaceans	67.04	125.55 **	100.01 **	45.39 ***	78.08

Table 12. Ratios of abundance (ind. L^{-1}) and biomass (mg. wet wt. L^{-1}), in (), in the control enclosures to abundance and biomass in the lake during three periods: June 5 to October 20, 1979; June 5 to August 2, 1979; May 12 to July 17, 1980.

	June 5 - October 20, 1979		June 5 - August 2, 1979		May 12 - July 17, 1980	
Species	Ctrl 1	Ctrl 2	Ctrl 1	Ctrl 2	Ctrl 1	Ctrl 2
Diaptomus minutus	3.5 (2.3)	3.0 (2.4)	4.6 (2.4)	3.9 (2.3)	4.7 (7.6)	4.9 (9.9)
Calanoid nauplii	0.7 (0.8)	0.5 (0.5)	0.6 (0.9)	0.4 (0.5)	0.5 (0.7)	0.4 (0.4)
Tropocyclops prasinus mexicanus	1.8 (1.3)	1.9 (2.1)	2.0 (1.6)	2.0 (2.9)	3.1 (3.0)	2.8 (2.7)
Mesocyclops edax	1.1 (1.2)	2.2 (2.7)	0.9 (1.1)	1.8 (2.2)	1.6 (2.2)	2.1 (2.4)
Cyclopoid nauplii	2.0 (2.1)	2.0 (2.5)	2.1 (2.2)	1.5 (2.5)	2.1 (2.0)	1.7 (1.9)
Bosmina longirostris	1.6 (1.6)	4.4 (4.4)	4.7 (5.3)	15.5 (17.6)	3.2 (3.2)	1.6 (1.6)
Holopedium gibberum	12.8 (23.0)	1.4 (3.3)	11.7 (33.0)	3.4 (9.5)	13.7 (28.0)	14.6 (20.0)
Diaphanosoma brachyurum	3.1 (3.0)	3.2 (3.1)	5.7 (7.4)	5.4 (7.1)	3.0 (11.0)	0.9 (3.3)
Total crustaceans	1.7 (2.1)	2.1 (2.7)	2.1 (2.9)	3.4 (4.0)	1.9 (4.9)	1.5 (4.3)

of the 50% greater increase of T. p. mexicanus abundance as biomass in Ctrl 1 but not in Ctrl 2 (Table 12 and 13). Also, the influence of the smaller increase of D. brachyurum numbers did not extend to biomass in Ctrl 1 and was of lesser importance in Ctrl 2 when biomass is considered (Tables 12 and 13).

Enclosure affected zooplankton community structure to varying degrees in the two seasons of study. The magnitude of this effect was primarily dependent upon the degree to which B. longirostris abundance in the enclosures exceeded that in the lake.

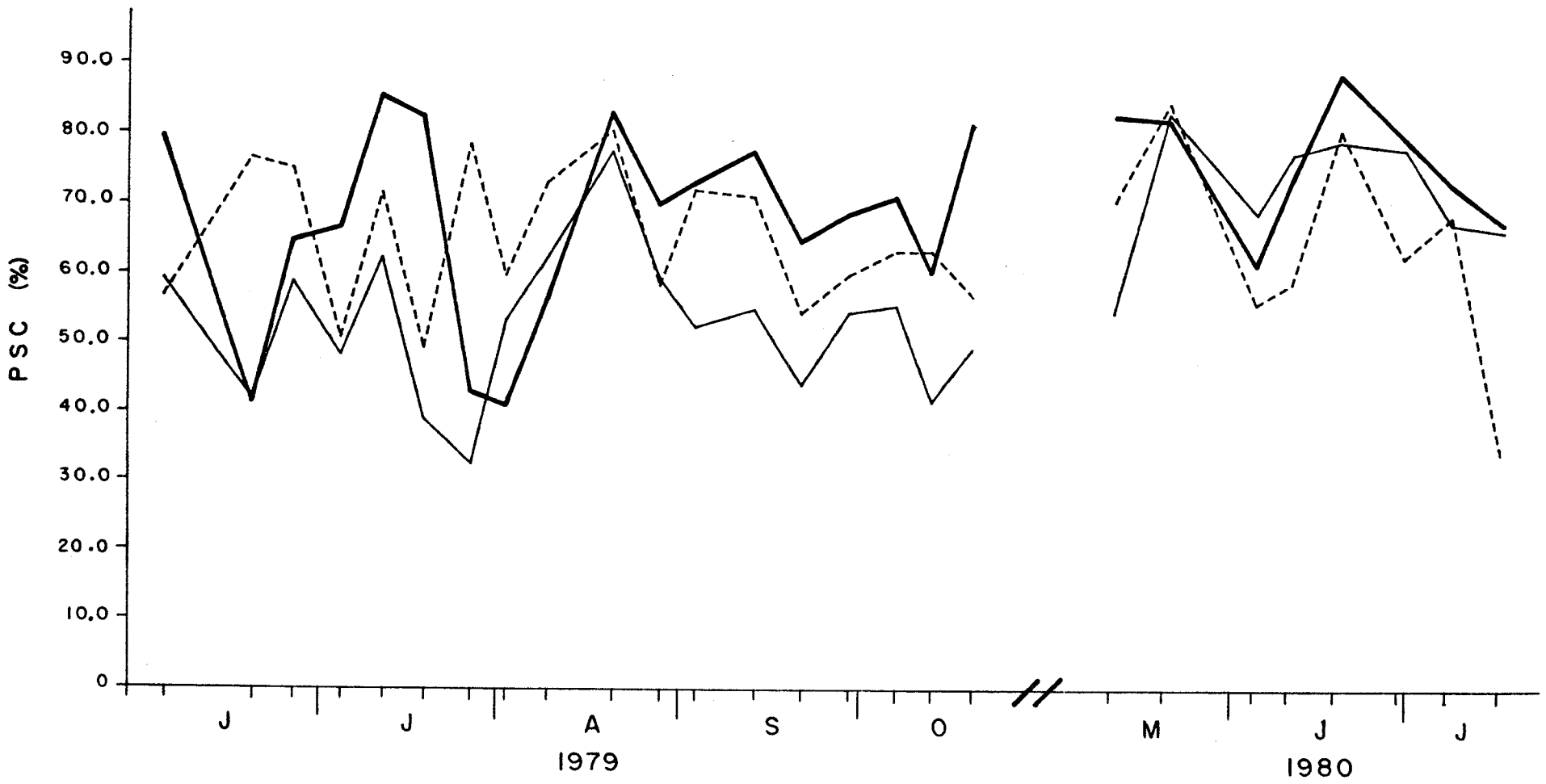
In 1979, the zooplankton communities in the lake and control enclosures were all at the same level of complexity with each dominated, on average, by the same four species (Table 9). D. minutus predominated the lake community, followed by B. longirostris, M. edax, and T. p. mexicanus. D. minutus also predominated Ctrl 1, with B. longirostris also in second place. With the two-fold increase of T. p. mexicanus abundance and no accompanying increase of M. edax, the dominance positions of these species were reversed in Ctrl 1. These relatively minor changes in the community hierarchy of Ctrl 1 effected a marginally significant reduction in the similarity of community structure, as measured by the PSC index (sign test, n=18, p=0.071). The PSC between Ctrl 1 and Ctrl 2 averaged 67.1% compared with 64.9% between the lake and Ctrl 1 (Fig. 20).

With the much greater increase of B. longirostris

Table 13. Mean biomass (mg. wet wt. L^{-1}) and percentage composition, in (), of planktonic crustacean species in the lake and in the control and acidified enclosures from May 12 to July 17, 1980. For calculation of percentage composition, nauplii were apportioned among the species of their respective suborders according to copepodid abundance. + denotes species present with mean biomass (0.001 mg. L^{-1}. *'s indicate results of Fisher's sign test of difference in seasonal mean biomass between the lake and control enclosures and between the control and acidified enclosures. *=0.10)p)0.05 , **=0.05)p)0.01 , ***=0.01)p.

Species	Lake		Ctrl 1			Ctrl 2			A1			A2		
Diaptomus minutus	0.073	(35.6)	0.553	(46.2)	***	0.721	(68.3)	***	0.007	(1.4)	***	0.072	(8.1)	***
Epischura lacustris	0.029	(14.2)	0.242	(20.2)		0.077	(7.3)		0.002	(0.4)		0.017	(1.9)	
Calanoid nauplii	0.021		0.014			0.009			0.001		***	0.003		**
Tropocyclops prasinus mexicanus	0.007	(3.4)	0.021	(2.0)	**	0.019	(1.9)	*	0.001	(0.1)	**	0.009	(1.1)	
Mesocyclops edax	0.018	(8.7)	0.039	(3.8)	**	0.044	(4.4)	*	0.001	(0.1)	*	0.002	(0.2)	*
Cyclops bicuspidatus thomasi	0.017	(8.3)	0.024	(2.3)		0.027	(2.7)		0.017	(3.1)		0.028	(3.3)	
Other cyclopoids	0.003		0.019			0.006			0.002			0.001		**
Cyclopoid nauplii	0.009		0.018			0.017			0.001		***	0.003		**
Bosmina longirostris	0.060	(24.3)	0.193	(15.9)		0.093	(8.7)	**	0.228	(39.6)		0.293	(32.0)	
Holopedium gibberum	0.002	(0.8)	0.056	(4.6)	**	0.040	(3.8)	**	0.063	(10.9)		0.226	(24.7)	
Diaphanosoma brachyurum	0.003	(1.2)	0.033	(2.7)	***	0.010	(0.9)	***	0.213	(37.0)	***	0.230	(25.1)	
Ophryoxus gracilis	+		+			+			0.034	(5.9)	*	0.027	(2.9)	
Alona affinis	0.001	(0.4)	0.001	(0.1)		+			—			+		
Alona intermedia	—		—			+			—			—		
Chydorus sphaericus	+		+			+			+			+		
Sida crystallina	0.002	(0.8)	0.004	(0.3)		0.002	(0.2)		0.001	(0.2)		0.001	(0.1)	
Macrothrix laticornis	+		+			+			—			+		
Eurycercus longirostris	—		0.001	(0.1)		+			+			0.001	(0.1)	
Latona setifera	—		—			—			0.004	(0.7)		0.004	(0.4)	
Ilyocryptus sordidus	—		+			—			—			+		
Daphnia retrocurva	+		+			—			—			—		
Daphnia catawba	+		—			—			—			—		
Leptodora kindtii	+		—			—			—			—		
Total crustaceans	0.247		1.217		***	1.067		**	0.576		***	0.917		

Figure 20. Seasonal variation of the percentage similarity of community index, PSC (Raabe 1952), between Ctrl 1 and Ctrl 2 (━━━━━), the lake and Ctrl 1 (- - - - - -), and the lake and Ctrl 2 (——————) from June 5 to October 20, 1979 and from May 12 to July 17, 1980.


PSC (%)
90.0
80.0
70.0
60.0
50.0
40.0
30.0
20.0
10.0
0
J
J
A
S
O
M
J
J
1979
1980

abundance in Ctrl 2 (Table 9), community structure was much more substantially altered than in Ctrl 1. The PSC between the lake and Ctrl 2 was very significantly reduced (sign test, n=18, p=0.003) and averaged just 52.2% (Fig. 20). Here, B. longirostris predominated, with D. minutus relegated to second place despite its presence in the same abundance as in Ctrl 1 (Table 9). Because of the similar increases of both M. edax and T. p. mexicanus numbers in Ctrl 2, the dominance positions of these species were the same as in the lake (Table 9). In Ctrl 2, the reduction of the PSC index was the product of consistently lower values over the season (Fig. 20).

In the 1980 study period, the communities in the enclosures were distinguished by a greater complexity of organization, with 4 and 5 dominants in Ctrl 1 and Ctrl , respectively, compared with 3 in the lake (Table 11). D. minutus predominated the lake, followed by C. b. thomasi, and B. longirostris. In Ctrl 2, the increased abundances of both T. p. mexicanus and M. edax accounted for the greater number of dominants. However, the community hierarchy remained very similar to that in the lake because the relative importance of D. minutus, C. b. thomasi, and B. longirostris went largely unchanged (Table 11). This similarity is reiterated in the PSC index which averaged 75.8% between the control tubes and which, at 71.6% between the lake and Ctrl 2, was not significantly lower (Fig. 20; sign test, n=8, p=0.219). This was not the case in Ctrl 1, however. The additional

dominant was also due to the increased abundance of T. p. mexicanus but, again, the much greater relative and absolute abundance of B. longirostris than in the lake (Table 11) effected a significant reduction in the similarity of community structure, with the PSC between the lake and Ctrl 2 averaging 64.2% (Fig. 20; sign test, n=8, p=0.03). Here D. minutus also predominated, but B. longirostris moved into second place followed by T. p. mexicanus and C. b. thomasi (Table 11).

Comparing the years, enclosure had an equal or lesser effect on community structure in 1980 than during the first 8 sampling dates of 1979. The PSC values between the lake and Ctrl 1 and between the lake and Ctrl 2 averaged 0.4% lower and 22.5% higher, respectively, in 1980 (Fig. 20). The structures of the communities in the control tubes were also more similar in 1980, with the PSC averaging 13% higher than in 1979 (Fig. 20). These increases in the similarity of structure can be traced to the lesser response of B. longirostris to enclosure in the second season, particularly in Ctrl 2 (Table 11).

ii. Acidification

The reductions of total community abundance effected by acidification represent the difference between decreases in the abundance of almost all copepod species and increases of several cladoceran species which were otherwise of minor numerical importance in the controls. Most seriously affected

in 1979 were D. minutus, the calanoid nauplii, and C. b. thomasi, with well replicated reductions of 80-90% (Table 14). M. edax abundance was also significantly reduced in both acidified tubes (Table 14). At a glance, the effect appears to have been greater in A1 but the ratio of abundance in A1 to that in A2 after a season of acidification was the same as on the two pre-acidification sampling dates (Table 5). Therefore, acidification effected the same proportional reduction in the two enclosures. In a similar manner, T. p. mexicanus appeared to suffer a very significant 50% decrease in abundance in A1, yet abundance in A2 averaged about 50% higher than in either of the controls (Table 14). This again could be an effect of different initial levels of abundance in the acidified tubes. Before the start of the experiment, abundance in A1 was about 50% of control levels while abundance in A2 was 50% higher than in either control (Table 5). In conclusion, T. p. mexicanus abundance was not detectably affected by acidification in 1979. E. lacustris was also unaffected by acidification in 1979 (Table 14) but the majority of population development had occurred before the target pH was reached (Fig. 11).

Among the group of species classed as "other cyclopoids", abundance was significantly reduced as well (Table 15). This was the product of much reduced numbers of A. vernalis and E. agilis and of a greater than 95% reduction of C1-5 abundance.

Table 14. Mean abundance (ind. L^{-1}) and percentage composition, in (), of planktonic crustacean species in the control and acidified enclosures from June 21 to October 20, 1979. For calculation of percentage composition, nauplii were apportioned among the species of their respective suborders according to copepodid abundance. *'s indicate results of Fisher's sign test of difference in seasonal mean abundance. *=0.10)p)0.05 , **=0.05)p)0.01 , ***=0.01)p.

Species	Ctrl 1	Ctrl 2	A1	A2
Diaptomus minutus	15.01 (26.5)	15.44 (20.3)	2.07 (9.4) ***	3.10 (7.0) ***
Epischura lacustris	0.24 (0.4)	0.05 ((0.1)	0.02 (0.1)	0.10 (0.2)
Calanoid nauplii	7.50	6.16	1.14 ***	1.01 ***
Tropocyclops prasinus mexicanus	3.01 (21.2)	3.23 (11.9)	1.52 (17.3) ***	4.55 (39.0)
Mesocyclops edax	1.87 (13.1)	4.34 (16.0)	0.34 (3.9) ***	0.84 (7.2) **
Cyclops bicuspidatus thomasi	0.40 (2.8)	0.40 (1.5)	0.05 (0.6)	0.03 (0.3)
Other cyclopoids	1.16	1.99	0.13 **	0.12 **
Cyclopoid nauplii	31.76	28.98	5.86 ***	22.29 **
Bosmina longirostris	18.96 (22.5)	44.34 (41.8)	12.82 (37.6)	15.76 (26.9)
Holopedium gibberum	3.62 (4.3)	0.42 (0.4)	1.54 (4.5)	1.46 (2.5)
Diaphanosoma brachyurum	0.69 (0.8)	0.74 (0.7)	7.31 (21.4) ***	8.23 (14.0) **
Ophryoxus gracilis	0.02 ((0.1)	0.01 ((0.1)	0.82 (2.4) ***	0.93 (1.6) ***
Alona affinis	0.08 ((0.1)	0.03 ((0.1)	0.03 ((0.1)	0.02 ((0.1)
Alona intermedia	0.01 ((0.1)	0.01 ((0.1)	0.17 (0.5)	0.02 ((0.1)
Chydorus sphaericus	(0.01 ((0.1)	0.01 ((0.1)	0.01 ((0.1)	0.01 ((0.1)
Sida crystallina	0.01 ((0.1)	(0.01 ((0.1)	0.01 ((0.1)	0.02 ((0.1)
Macrothrix laticornis	(0.01 ((0.1)	0.01 ((0.1)	0.02 ((0.1)	0.01 ((0.1)
Eurycercus longirostris	0.03 ((0.1)	0.02 ((0.1)	0.06 (0.2)	0.03 ((0.1)
Latona setifera	(0.01 ((0.1)	(0.01 ((0.1)	0.12 (0.4)	0.04 ((0.1)
Ilyocryptus sordidus	(0.01 ((0.1)	—	0.02 ((0.1)	(0.01 ((0.1)
Daphnia retrocurva	0.01 ((0.1)	(0.01 ((0.1)	(0.01 ((0.1)	—
Leptodora kindtii	(0.01 ((0.1)	—	—	—
Total crustaceans	84.39	106.18	34.06 ***	58.56 *

Table 15. Mean abundance (ind L^{-1}) of adult stages of species classed as "other cyclopoids" and of the associated cyclopoid C1-5 stages in the control and acidified tubes during the period; June 21 to October 20, 1979.

	Ctrl1	Ctrl2	A1	A2
A. vernalis	0.06	0.11	0.02	0.003
E. agilis	0.01	0.01	0.002	0.001
M. albidus	0.06	0.08	0.01	0.09
C1-5	1.03	1.79	0.03	0.03

Cyclopoid nauplius abundance was also significantly reduced in both acidified tubes (Table 14). It is difficult to attribute these reductions solely to acidification ,however, in the absence of data at the species level which would permit the presumably different contributions by the different levels of *T. p. mexicanus* abundance in the two enclosures to be factored out. Nevertheless, it was the greater abundance of nauplii in A2 which was largely responsible for total community abundance in A2 exceeding that in A1 (Table 14).

At least with respect to abundance, no cladoceran was detrimentally affected by acidification in 1979. *B. longirostris* abundances in A1 and A2 were somewhat lower than in the controls but not so low as to be distinguishable from the apparently broad degree of natural variation (Table 14). *H. gibberum* abundances replicated well in the acidic tubes and were intermediate to the control levels (Table 14). *D.*

brachyurum abundance was substantially elevated in the acid tubes, averaging 10 and 11.5 times the mean control level in A1 and A2 respectively (Table 14). Similarly, O. gracilis abundance increased to an extraordinary degree, although it remained a minor community component, averaging 60 times the mean control level (Table 14). All other cladoceran species occurred at levels at, or above (A. intermedia in A1 and L. setifera in both A1 and A2), those in the control enclosures (Table 14).

The pattern of acidification effects remains similar when biomass is considered (Table 16). However because of their comparatively large body sizes, the contributions of D. brachyurum and O. gracilis to community biomass were substantially greater than was the case for numerical abundance (Tables 14 and 16).

With continued acidification in 1980, T. p. mexicanus abundance in both A1 and A2 was lower than in either control tube but this reduction was significant in A1 only (Table 11). The acidification was also resumed early enough to expose the main period of E. lacustris population development to the increased acidity and reduced abundance was the result (Table 11). Among the other copepods, only C. b. thomasi did not respond as in 1979 (Table 11).

As in 1979, the abundances of the major copepod species (excluding C. b. thomasi) in A1 were lower than in A2 in 1980 (Tables 11 and 14). Again, because of the shorter period of study and the three week earlier start of sampling in 1980,

Table 16. Mean biomass (mg. wet wt. L^{-1}) and percentage composition, in (), of planktonic crustacean species in the control and acidified enclosures from June 21 to October 20, 1979. For calculation of percentage composition, nauplii were apportioned among the species of their respective suborders according to copepodid abundance. + denotes species present with mean biomass (0.001 mg. L^{-1}. *'s indicate results of Fisher's sign test of difference in seasonal mean biomass. *=0.10)p)0.05 , **=0.05)p)0.01 , ***=0.01)p.

Species	Ctrl 1	Ctrl 2	A1	A2
Diaptomus minutus	0.397 (50.2)	0.447 (44.1)	0.042 (7.3) ***	0.048 (7.3) ***
Epischura lacustris	0.037 (4.7)	0.003 (0.3)	0.003 (0.5)	0.011 (1.7)
Calanoid nauplii	0.005	0.003	0.001	0.001
Tropocyclops prasinus mexicanus	0.013 (2.0)	0.013 (1.4)	0.008 (1.5)	0.025 (4.4)
Mesocyclops edax	0.040 (6.2)	0.096 (10.4)	0.013 (2.4) ***	0.030 (5.3)
Cyclops bicuspidatus thomasi	0.006 (0.9)	0.005 (0.5)	0.001 (0.1)	+
Other cyclopoids	0.014	0.037	0.008	0.010
Cyclopoid nauplii	0.017	0.015	0.003 ***	0.010 **
Bosmina longirostris	0.154 (19.3)	0.361 (35.4)	0.104 (17.7)	0.128 (19.4)
Holopedium gibberum	0.073 (9.1)	0.010 (1.0)	0.042 (7.1)	0.032 (4.9)
Diaphanosoma brachyurum	0.025 (3.1)	0.027 (2.6)	0.267 (45.3) ***	0.271 (41.1) **
Ophryoxus gracilis	0.002 (0.3)	0.001 (0.1)	0.072 (12.2) ***	0.082 (12.4) ***
Alona affinis	0.002 (0.3)	0.001 (0.1)	0.001 (0.1)	+
Alona intermedia	+	+	0.001 (0.1)	+
Chydorus sphaericus	+	+	+	+
Sida crystallina	0.003 (0.5)	+	0.004 (0.7)	0.005 (0.8)
Macrothrix laticornis	+	+	+	+
Eurycercus longirostris	0.001 (0.1)	0.001 (0.1)	0.003 (0.5)	0.002 (0.2)
Latona setifera	+	+	0.017 (2.9)	0.005 (0.8)
Ilyocryptus sordidus	+	—	+	+
Daphnia retrocurva	0.001 (0.1)	+	+	—
Leptodora kindtii	+	—	—	—
Total crustaceans	0.800	1.020	0.589 ***	0.659 *

the magnitude of these differences cannot be compared directly with those in 1979. Selection of a period from 1979 to normalize for these differences in sampling schedule was made difficult by the much earlier start of acid additions in 1980; May 15 compared with June 21 in 1979. As it turns out, the ratio of abundance in A2 to abundance in A1 was independent of the period of 1979 selected for comparison with 1980 (Table 17). Comparing the years it is clear that there was a much greater difference in the abundance of *D. minutus*, *T. p. mexicanus*, *M. edax*, and the calanoid nauplii between A1 and A2 in 1980 than in 1979 (Table 17).

While the lower levels of *M. edax* and *T. p. mexicanus* abundance in A1 could be traced to lower levels at the start of the experiment in 1979, this did not seem to be the case in 1980 (Table 18). Even if the differentials present in 1979 continued through 1980, they would only partially account for the lower abundance in A1 (Table 17).

Table 18. Comparison of the abundance of several taxa in the acidified tubes on May 12, 1980.

Taxon	A1	A2
D.minutus	0.88	7.51
calanoid nauplii	3.92	8.44
T.p.mexicanus	0.08	0.03
M.edax	--	--

There were, however, different levels of both *D. minutus*

Table 17. Ratio of abundance in A2 to abundance in A1 in the 1979 and 1980 acidified periods and in four shorter periods of 1979 selected to normalize for the different periods of study in the two years.

Species	1980 May 12- July 17	1979 June 21- October 20	1979 June 5- August 2	1979 June 20- August 9	1979 June 27- August 20	1979 July 5- August 27
Diaptomus minutus	7.0	1.5	1.2	1.2	1.5	1.2
Calanoid nauplii	5.3	0.9	1.1	0.8	0.9	1.6
Tropocyclops prasinus mexicanus	5.3	3.0	3.1	2.8	2.6	2.7
Mesocyclops edax	14.0	2.5	2.6	3.2	2.7	2.1
Cyclopoid nauplii	2.9	3.8	3.3	3.6	3.6	4.6

and calanoid nauplius abundance in A1 and A2 at the start of sampling in 1980 (Table 18). D. minutus abundance in A2 was about 8 times that in A1 on May 12 and this is similar to the differential for the entire 1980 study period (Table 17). Calanoid nauplius abundance in A2 was about twice that in A1 at the start of sampling (Table 18), but this accounts for less than half of the difference between A1 and A2 over the full period (Table 17).

In summary, there were greater reductions in the abundance of T. p. mexicanus, M. edax, and calanoid nauplii in A1 than in A2 in 1980. These cannot be explained solely by the presence of lower abundance in A1 at the start of sampling in 1980.

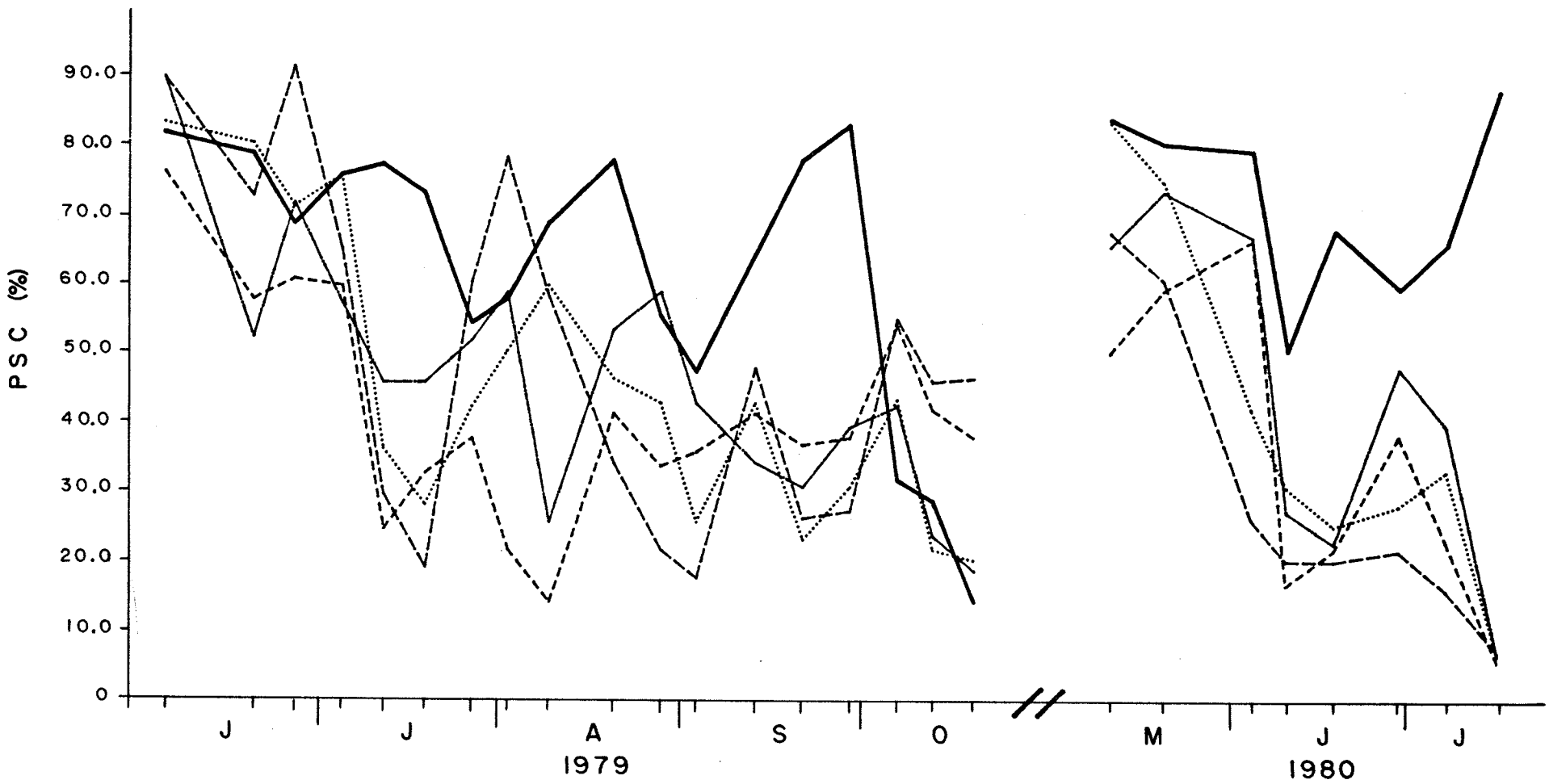
The responses of the cladocerans to acidification in 1980 generally followed the pattern set in 1979. B. longirostris abundance was as high (A1) or higher (A2) than in the controls (Table 11). Well replicated increases of D. brachyurum and O. gracilis abundance of the magnitude observed in 1979 were recorded again in 1980 (Table 11). Unlike 1979, H. gibberum abundance in both acid tubes was greater than in either control (Table 11). This increase was greater in A2, also unlike 1979 when abundances in the acid tubes were identical. No other cladoceran was affected by acidification in 1980 (Table 11).

With acidification differentially affecting the copepods community structure was simplified by acidification in 1979, with 3 rather than four dominants in each of A1 and A2 (Table

14). In A1 B. longirostris was most abundant, followed by D. brachyurum and T. p. mexicanus. In A2 T. mexicanus was most abundant, followed by B. longirostris and D. brachyurum (Table 14). These different orders of dominance are also reflected in a fairly low PSC between A1 and A2, which averaged 60.5% (Fig. 21). The structures of the acidified communities were, nevertheless, more similar to each other than to those in the controls, with seasonal mean PSC values ranging from 14.5 (Ctrl 2-A1) to 21.5% (Ctrl 1-A1) lower (Fig. 21). These reductions were significant (sign test, $n=16$, $p<0.07$) for all pairings except Ctrl 2-A1, which shared the same community dominant; B. longirostris. This divergence of community structure in the acid tubes occurred as a sharp drop between July 5 and 12, immediately following the reduction of pH to the target level (Fig. 21).

In 1980 the effects of acidification on community structure are best described by comparing the four most abundant species (Table 11). In both A1 and A2 these were B. longirostris, D. brachyurum, H. gibberum, and C. b. thomasi. In Ctrl 1 and Ctrl 2, these were D. minutus, T. p. mexicanus, B. longirostris, and C. b. thomasi. With only two of the six species in this category common to the four enclosures, community structure was significantly altered. At least partly due to the more similar stuctures of the control communities, the reductions in the similarity of community structure effected by acidification were greater and more distinct than in 1979 (Fig. 21). The PSC between A1 and A2

Figure 21. Seasonal variation of the percentage similarity of community index, PSC (Raabe 1952), between A1 and A2 (━━━━━), A1 and Ctrl 1 (– – – – – –), A1 and Ctrl 2 (— — —), A2 and Ctrl 1 (— · — · —), A2 and Ctrl 2 (· · · · · · · · · ·) from June 5 to October 20, 1979 and from May 12 to July 17, 1980.


PSC (%)
90.0
80.0
70.0
60.0
50.0
40.0
30.0
20.0
10.0
0
J
J
A
S
O
1979
M
J
J
1980

averaged 70.2% over the season compared with PSC values between the control and acidic communities which averaged 30.2 (Ctrl 2-A1), 35.3 (Ctrl 1-A1), 40.8 (Ctrl 2-A2), and 43.9% (Ctrl 1-A2) and all represent significant reductions (sign test, $n=8$, $p<0.004$). Again consistent with the trend of greater effects in A1, community structure also diverged more from the controls in A1 than in A2.

D. Seasonal dynamics of the dominant species

Detailed examination of the effects of enclosure and acidification on zooplankton seasonal dynamics will be limited to the seven species which attained the status of numerical dominants in at least one of the five communities studied.

i. Effects of enclosure

Although both E. lacustris and D. minutus were present in the communities, the latter was by far the more abundant on average (Tables 9 and 11; Fig. 22 and 23). In both years, the majority of E. lacustris population abundance was concentrated in a single cohort which developed in late spring (Fig. 22). Few individuals were seen following this cohort in the tubes in 1979, but a small pulse of C1-3 appeared in the lake in September (Fig. 22). Generally, the specimens identified as calanoid nauplii were considered as belonging to D. minutus.

D. minutus population development was already well under way by the time sampling was started in 1979, as indicated by

Figure 22. Seasonal variation of the abundance of Epischura lacustris life stages in the lake (·····), Ctrl 1 (————), and Ctrl 2 (– – – – –) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.

EPISCHURA LACUSTRIS

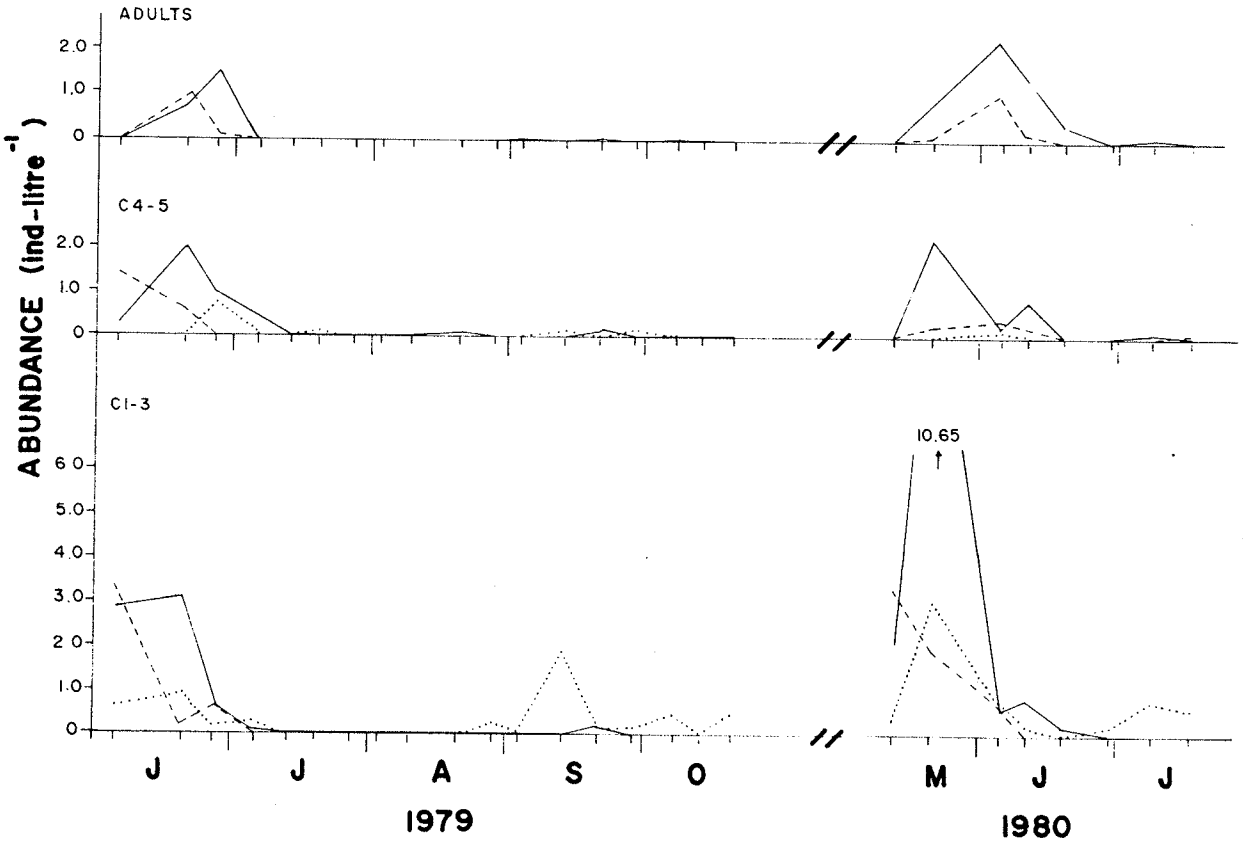
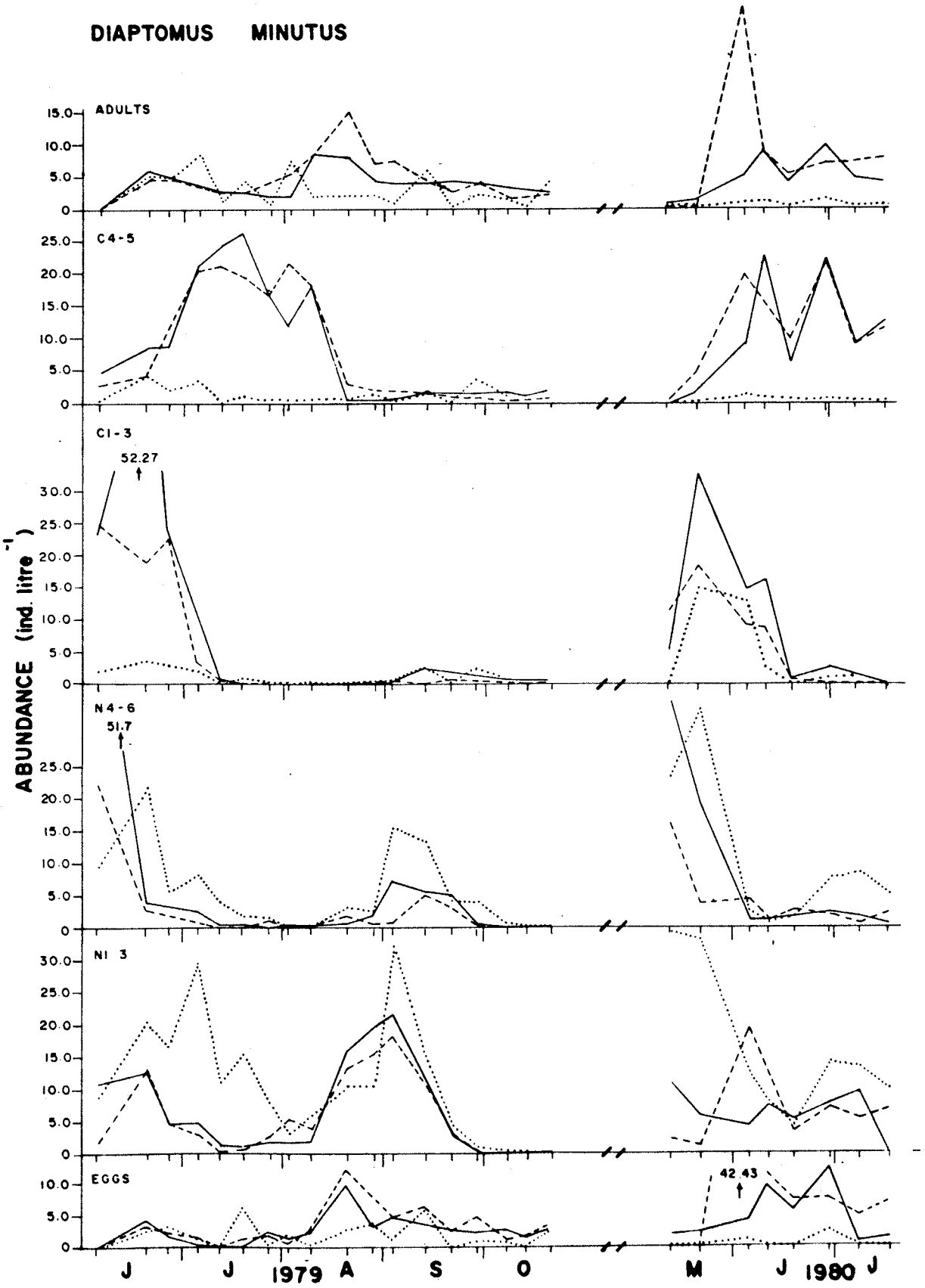


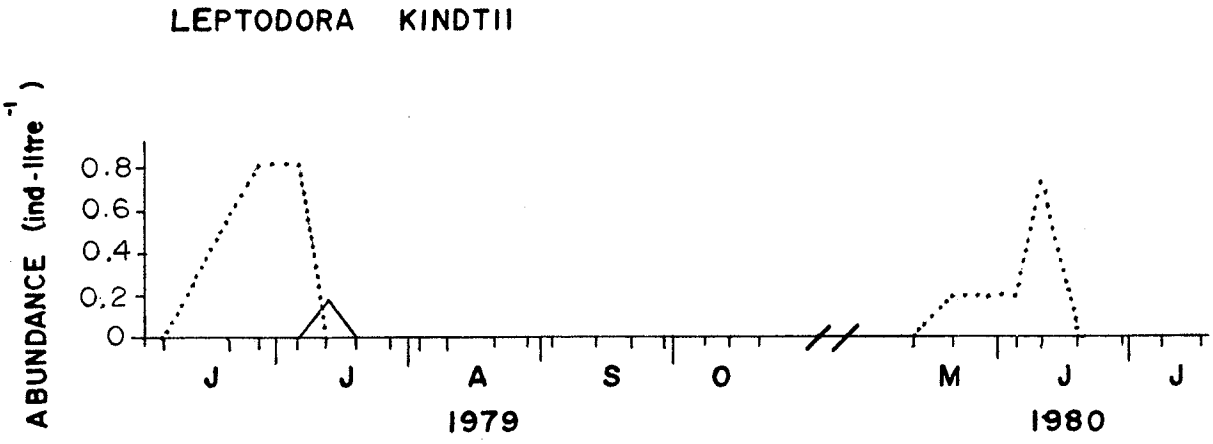
Figure 23. Seasonal variation of the abundance of Diaptomus minutus life stages and of the calanoid nauplii in the lake (·····), Ctrl 1 (————), and Ctrl 2 (– – – – –) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.


DIAPTOMUS MINUTUS
ADULTS
C4-5
C1-3
52.27
N4-6
51.7
N1 3
EGGS
42.43
ABUNDANCE (ind. litre -1)
J
J
1979
A
S
O
M
J
1980
J

the large numbers of late stage nauplii and early stage copepodids present on June 5 (Fig. 23). Moreover, the principle response of the populations to enclosure had also occurred in the one week interval between tube installation and the start of sampling. The greater abundance of D. minutus in the control tubes than in the lake in 1979 was solely the product of this first week of enclosure (Fig. 23). On June 5, 7 (Ctrl 2) and 8 (Ctrl 1) days after tube installation, C1-3 abundance in the tubes was 2.4 times higher than in the lake. The magnitude of this response is more evident in the pulses of C1-3 which peaked in mid-June (Fig. 23). Continued development of these animals subsequently produced large pulses of C4-5 and adults in both tubes at approximately monthly intervals (Fig. 23). This greater success of the populations in the enclosures also appeared at about the same time as a pulse of L. kindtii developed in the lake but which was much reduced (Ctrl 1) or absent (Ctrl 2) in the tubes (Fig. 24).

Following this initial response to tube installation, subsequent population development was little affected by enclosure in 1979. Gravid females and nauplii were present in almost all samples but only two cohorts are distinguishable in the period of examination in 1979 (Fig. 23). The first arose from a pulse of eggs which peaked in mid to late June. Substantially fewer N1-3 developed from these eggs in the control tubes, with N1-3 abundance peaking at less than half the level attained in the lake (Fig. 23). Pulses of N4-6,

Figure 24. Seasonal variation of the abundance of Leptodora kindtii in the lake (.....) and Ctrl 1 (————) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.


LEPTODORA KINDTII
ABUNDANCE (ind-litre⁻¹)
0.8
0.6
0.4
0.2
0
J
J
A
S
O
M
J
J
1979
1980

C1-3, and C4-5 closely followed this initial pulse in the lake but the continued development of this cohort in the tubes cannot be distinguished from the mass of animals in the previous cohort (Fig. 23).

The second cohort developed from a spate of egg production in mid to late August (Fig. 23). With the greater abundance of adults in the tubes at this time, the pulses of eggs produced were also much larger. However, the resulting N1-3 pulses were of very similar size and duration in the three populations and the subsequent N4-6 pulses were smaller in the tubes than in the lake (Fig. 23). This apparently lower success in the tubes may rather be accounted for by the pulse of E. lacustris which appeared in the lake but not in either of the enclosures in September (Fig. 22). The second cohort made but a minor contribution to population abundance beyond the C1-3 level in all three populations (Fig. 23). Egg production continued to the end of sampling in the three populations but no nauplii resulted, suggesting these were resting rather than subitaneous eggs (Fig. 23).

The effects of enclosure observed in 1979 were also recorded in 1980, with the additional effect of an advancement of population development in the tubes. D. minutus copepodid abundance was again increased in the early-season (Fig. 23). Despite starting sampling more than three weeks earlier in 1980, population development was only slightly less advanced than at the start of sampling in 1979 (Fig. 23). A pulse of nauplii had been produced by all three

populations prior to the start of sampling, as indicated by the large C1-3 pulses which developed in mid-May (Fig. 23). Although the relative sizes of the preceding naupliar pulses are unknown, they were produced earlier in the tubes than in the lake. N4-6 abundance peaked in the lake a week after sampling started, but was already at or declining from the peak in both tubes at the start of sampling. Similarly, N1-3 abundance was at or just past the peak in the lake on May 12 while the corresponding pulses in the tubes had largely diminished. This advancement of development in the tubes had largely disappeared by the time the cohort reached the C1-3 stage-class (Fig. 23).

Although potentially the product of different reproductive efforts or of the actions of differential mortality, these cohorts were of similar magnitude in the three populations at the C1-3 stage-class (Fig. 23). However, the cohort in the lake effectively disappeared between the C1-3 and C4-5 stage-classes (Fig. 23). In a manner similar to 1979, this was solely responsible for the greater abundance of D. minutus C4-5 and adults which subsequently appeared in the control tubes.

The increased abundance of adults in the tubes appeared earlier in the season in 1980 largely because the number of adults was the sole product of occurrences within the tubes rather than being a composite of the number of adults captured when the tubes were filled and of adults developing within the enclosures (Fig. 23). Population development was

also faster in 1980, with peak adult abundance appearing one month after the C1-3 peak rather than taking the two months required in 1979 (Fig. 23). Together, these features account for the greater increase of D. minutus copepodid biomass in 1980 than during the first 8 sampling dates of 1979 (Table 12).

As in 1979, egg abundance was proportional to the abundance of adults (Fig. 23). A large pulse of adults in Ctrl 2 in early June produced a large but short-lived spike of egg abundance. The resulting pulse of N1-3 was substantial but made no contribution to population abundance beyond the N1-3 level. All three populations produced pulses of nauplii in late June (Fig. 23). With the greater abundance of adults in the tubes, the abundance of eggs was correspondingly larger than in the lake. But, just as in 1979, fewer N1-3 developed from these eggs than in the lake. No pulse of N4-6 resulted in either tube but these N1-3 successfully developed into the N4-6 stage-class in the lake before the termination of sampling (Fig. 23).

Development of the T. p. mexicanus, M. edax, and C. b. thomasi populations was also well under way when sampling began in 1979 (Fig. 25, 27,and 28). Documentation of the effects of enclosure on these species, however, is less detailed than for D. minutus because the nauplii were not identified to species and the co-occurrence of up to 6 cyclopoid species precluded assignation of nauplii based on time of species occurrence.

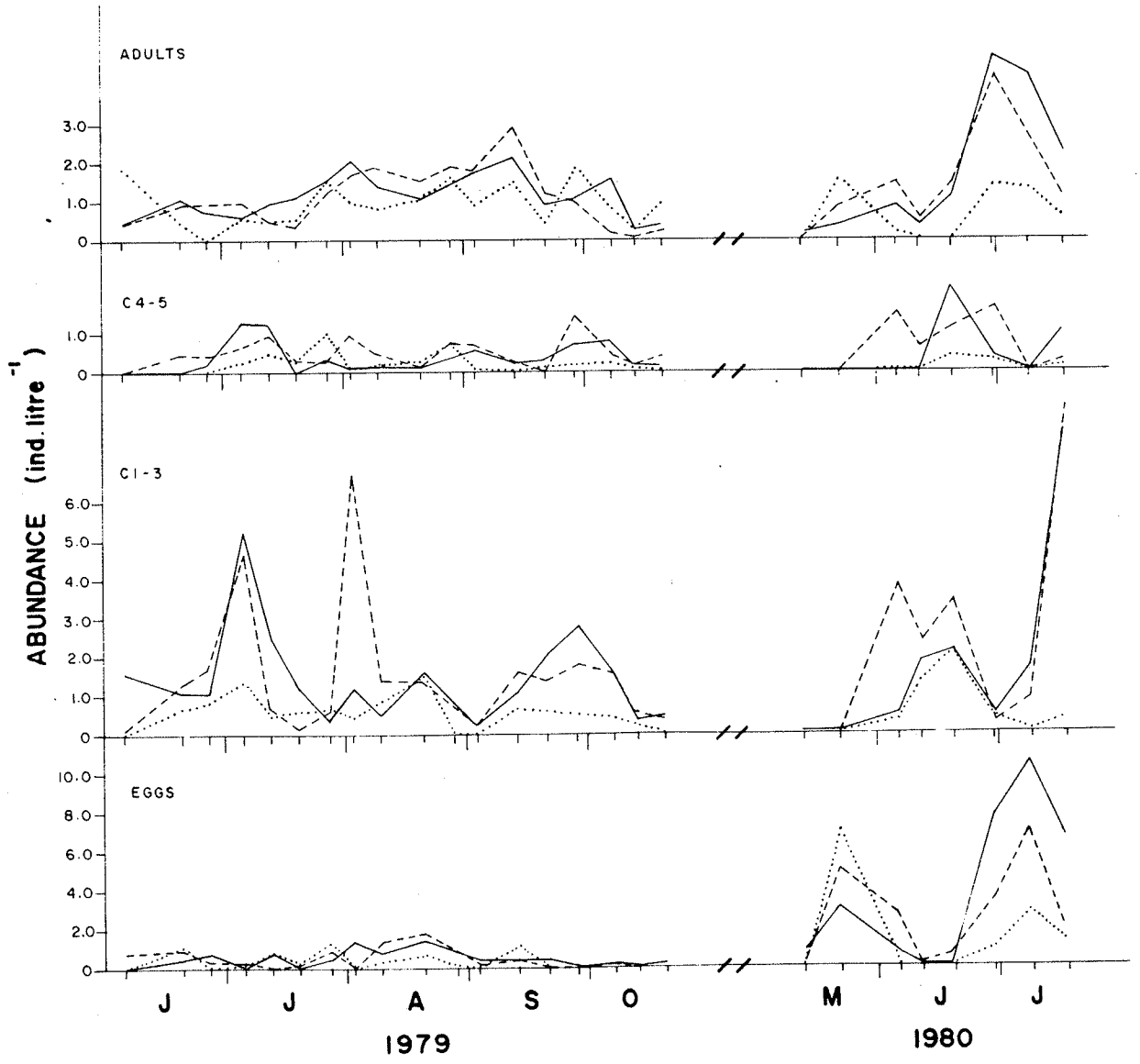
T. p. mexicanus population dynamics were unaffected by enclosure (Fig. 25). The same number of cohorts were produced by the three populations during the periods of examination and each cohort usually developed simultaneously in the lake and enclosures. In general, the greater seasonal mean abundance in the tubes was the product of increased abundance of C1-3 and C4-5 in the early summer and autumn (Fig. 25).

Though reproduction was continuous, four cohorts can be discriminated in 1979, with these produced at approximately monthly intervals (Fig. 25). The first cohort was the product of a pulse of eggs in mid to late June and was first evident as an outburst of C1-3 which peaked in early July (Fig. 25). While coming from similar numbers of eggs, these pulses were substantially larger in the tubes than in the lake. There also were greater numbers of cyclopoid nauplii in the tubes during this period (Fig. 26). A C4-5 pulse closely followed, peaking the following week, with these animals maturing in mid-late July (Fig. 25). The greater abundance of this cohort in the tubes continued through to the adult stage (Fig. 25).

The second cohort was less distinct than the others and was not produced simultaneously by the three populations (Fig. 25). In the lake it was the product of a month-long pulse of egg production in July, while short pulses of eggs in mid (Ctrl 1) and late (Ctrl 2) July were responsible in the tubes (Fig. 25). This cohort was next evident at the C4-5 stage-class, with abundance peaking in late July in the lake and Ctrl 1 and in early August in Ctrl 2 (Fig. 25). As they

Figure 25. Seasonal variation of the abundance of Tropocyclops prasinus mexicanus life stages in the lake (·····), Ctrl 1 (————), and Ctrl 2 (– – – – –) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.

TROPOCYCLOPS PRASINUS MEXICANUS



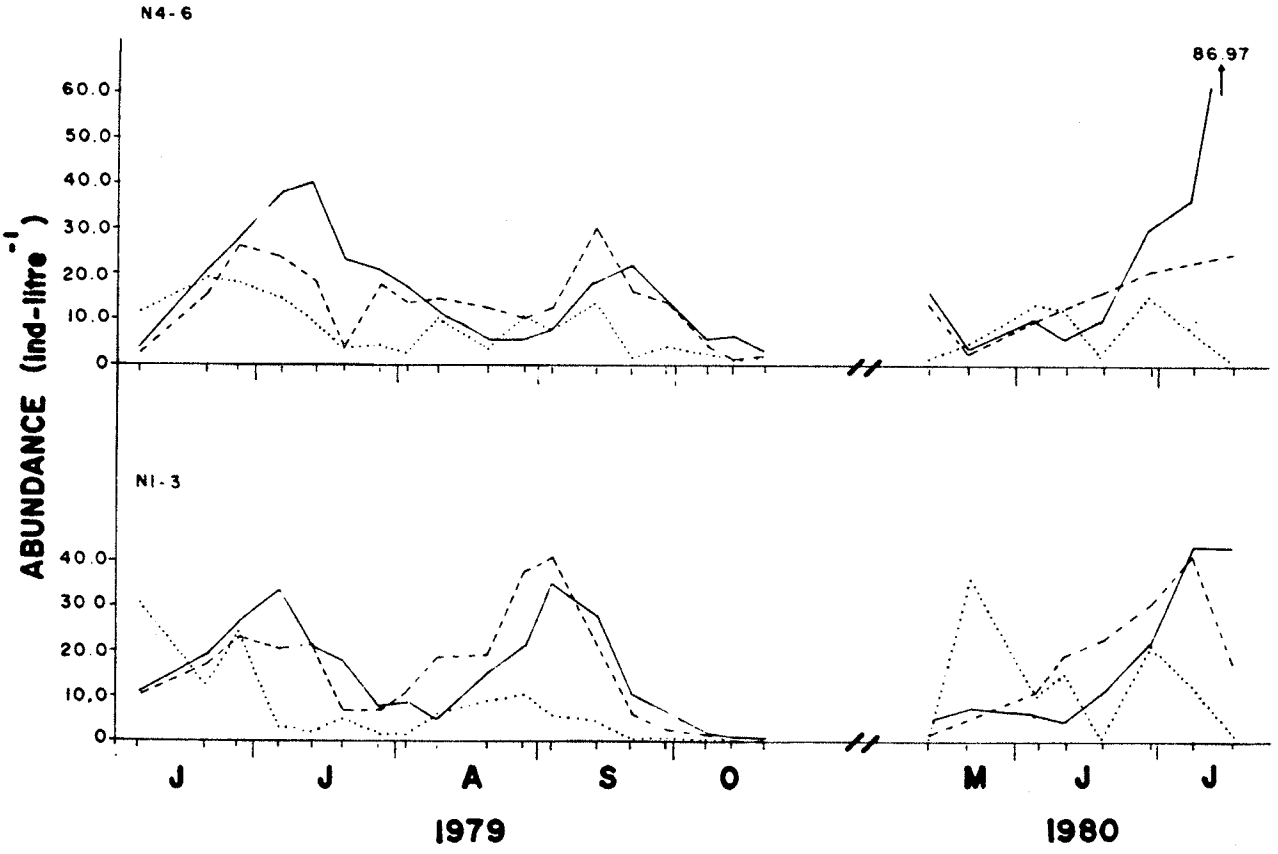
matured, these animals accumulated with the adults from the first cohort, producing peaks of adults in the lake in late July and in the enclosures in early August (Fig. 25). Unlike the preceding cohort, similar numbers of eggs produced similar numbers of C1-3 in the three populations (Fig. 25).

The third cohort was the product of a pulse of eggs which appeared at about the time the second cohort matured and which peaked around mid-August (Fig. 25). For some reason, this cohort was less successful in the tubes than in the lake. As a result of the greater abundance of adults in the tubes in early August, the egg pulses produced were about twice the size of that in the lake yet the C1-3 pulses which followed in the third week of August were of comparable size in the three populations (Fig. 25). Pulses of C4-5 and adults subsequently developed in all three communities at approximately weekly intervals (Fig. 25).

Continuing the pattern, the fourth cohort was the product of a spate of egg production by the maturing third cohort in early to mid-September (Fig. 25). The resulting C1-3 pulses peaked in mid to late September with the subsequent C4-5 flushes peaking within the following week (Fig. 25). Just as in the first cohort, development from eggs to C1-3 appeared more successful in the enclosures. Egg counts in the tubes were no higher than in the lake but C1-3 abundance peaked at more than twice the lake value (Fig. 25). Greater numbers of cyclopoid nauplii were again recorded in the enclosures at this time (Fig. 26).

Figure 26. Seasonal variation of the abundance of cyclopoid nauplii in the lake (.....), Ctrl 1 (————), and Ctrl 2 (– – – – –) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.

CYCLOPOID NAUPLII



Two distinct cohorts were produced during the period of study in 1980 (Fig. 25). The first arose from a spate of egg production in mid to late May; the product of a pulse of adults which peaked during the same period (Fig. 25). These adults probably came from diapause, as no C4-5 were present at or previous to this time. The first cohort was next evident as a pulse of C1-3 which peaked in early to mid June (Fig. 25). As in 1979, development from the egg to C1-3 stage-class appeared to be more successful in the enclosures early in the season. Approximately twice as many C1-3 developed from a given number of eggs in the control tubes as in the lake (Fig. 25). This was also evident between the C1-3 and adult stage-classes. Peak adult abundance in the lake was just 40% of that in Ctrl 1 while abundance of this cohort at the C1-3 stage-class was identical in the two populations (Fig. 25).

This apparently greater success of the T. p. mexicanus populations in the enclosures coincided with the greater success of the D. minutus populations in the tubes. In turn, both were coincident with a pulse of L. kindtii which appeared in the lake but not in the enclosures (Fig. 24).

Following the pattern evident in 1979, the second cohort arose from a pulse of eggs produced in early July by the maturing first cohort (Fig. 25). The standing crop of eggs produced in each population was roughly in proportion to the abundance of adults, so considerably more C1-3 appeared in the resulting pulse in the tubes than in the lake (Fig. 25).

Sampling was terminated before this pulse was completed.

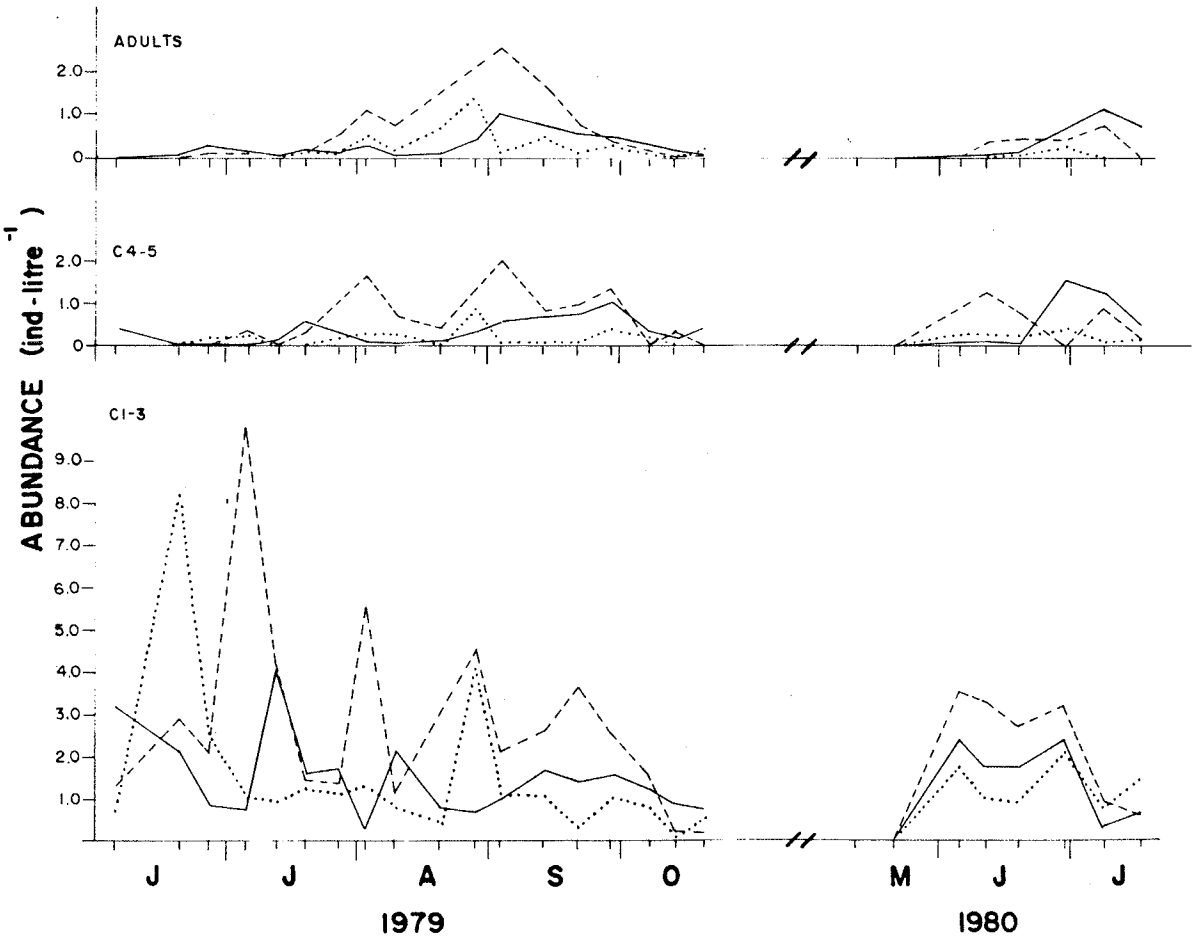
The seasonal dynamics of M. edax were also little affected by enclosure. Four cohorts were produced in the lake and each of the control tubes in 1979 (Fig. 27), with each cohort occurring as almost simultaneous pulses in the three copepodid classes. The pulses weren't equally distinctive in the three classes but, when the classes are considered jointly, the consequent picture emerges. In all three populations this pattern of cohort production is most evident at the C4-5 stage-class. The cohorts occurred more or less synchronously in the three populations despite the greater abundance in Ctrl 2 (Fig. 27).

The adult pulse of the first cohort appeared in the enclosures in late June with these animals developing from the large pulses of C1-3 which appeared in mid-month (Fig. 27). Mortality between the C1-3 and C4-5 stage classes appeared to be considerable in all three populations (Fig. 27).

The differential increase of M. edax abundance in Ctrl 2 developed between the first and second cohorts, with all stage-classes more abundant than in either the lake or Ctrl 1 in both the second and third cohorts (Fig. 27). The C4-5 pulses of the second cohorts in the lake and both enclosures appeared in late July with the corresponding peaks of adults occurring in early August (Fig. 27). This cohort made a lesser contribution to adult abundance in Ctrl 1 than did the second cohort in the lake (Fig. 27).

Figure 27. Seasonal variation of the abundance of Mesocyclops edax life stages in the lake (·····), Ctrl 1 (————), and Ctrl 2 (– – – – –) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.

MESOCYCLOPS EDAX



The C4-5 pulses of the third cohort developed in late August (Fig. 27). As in the preceding cohorts the consequent pulses of adults peaked simultaneously with the C4-5. These developed from the C1-3 flushes which appeared in early (Ctrl 1) to mid (Ctrl 2 and lake) August (Fig. 27).

The C4-5 pulses of the fourth and final cohort of the 1979 study season developed in late September in the three populations (Fig. 27). These pulses were quite distinct in the lake and Ctrl 2, but the fourth pulse in Ctrl 1 was merged with the preceding flush. No distinct fourth pulse of adults appeared in any of the populations (Fig. 27).

The four pulse pattern of seasonal dynamics was not evident in the pattern of egg production in any of the populations in 1979 (Table 19). Small numbers of eggs were produced in both the lake and Ctrl 1 in late June by the maturing adults in the first cohort. Eggs were again present in the lake during the third adult pulse in late August, and in Ctrl 1 during the second adult pulse in early August. The females in Ctrl 2 were only seen to carry eggs between early August and early September, during the large accumulation of adults from the second and third cohorts. This helps to explain how the population in Ctrl 2 maintained the higher abundance once it appeared but provides no clue as to how it originated. It may also explain the greater abundance of nauplii in Ctrl 2 than in Ctrl 1 or the lake during this period (Fig. 26).

The failure of the pattern of cohort production to

Table 19. Comparison of *Mesocyclops edax* egg counts (no. eggs L^{-1}) in the lake, control tubes (Ctrl 1 and Ctrl 2), and acidified tubes (A1 and A2) in the 1979 (June 5–October 20) and 1980 (May 12–July 17) study seasons.

	1979																				1980					
	June			July				August				September				October			May		June				July	
	5	20	27	5	12	19	27	2	9	20	28	3	13	21	29	7	13	20	12	21	5	11	19	30	8	17
Lake	—	—	0.04	—	—	—	—	—	—	—	0.49	1.82	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ctrl 1	—	0.28	0.03	—	—	—	—	0.52	0.19	—	—	—	—	—	—	—	—	—	—	—	0.15	—	—	—	0.60	0.05
Ctrl 2	—	—	—	—	—	—	—	0.64	1.01	1.16	0.19	0.21	—	—	—	—	—	—	—	—	—	—	—	0.42	0.18	—
A1	—	—	—	—	0.12	0.06	—	—	—	—	—	—	—	—	—	—	—	—	—	0.33	—	—	—	—	—	—
A2	—	—	—	—	—	0.09	—	—	—	—	—	0.06	—	—	—	—	—	—	—	—	—	—	—	—	—	—

appear in the egg counts may indicate the sampling program was inadequate for the quantitative collection of gravid females. M. edax adults, and particularly females, can assume a benthic mode of existence (Cole 1955) and would, therefore, be unavailable to capture. In contrast to the other copepod species, in which the ratio of males to females was generally below 1.0 and almost never above 2.0, the M. edax sex ratio was frequently greater than 1.0 and occasionally exceeded 3.0 in the three populations (Table 20). This indicates that a good proportion of the females in the populations could have been dwelling on the lake bottom.

Two cohorts were produced by each of the populations in the 1980 study period. The first appeared as a pulse of C1-3 in late May which peaked in early June in the lake and both enclosures (Fig. 27). A significant C4-5 pulse subsequently developed in Ctrl 2, peaking in mid-June, but not in either of the lake or Ctrl 1 and this largely accounts for the greater abundance in Ctrl 2 than in the lake in 1980 (Fig. 27). A minor increase of adult abundance followed in Ctrl 2.

The second cohort was first evident in late June with C1-3 abundance peaking in all three populations at the end of the month (Fig. 27). The resulting C4-5 pulses peaked simultaneously in the lake and Ctrl 1, but a week later in Ctrl 2. Despite the greater abundance in Ctrl 1 than in Ctrl 2 at the C4-5 stage-class, similar pulses of adults subsequently developed (Fig. 27). It was this apparently

Table 20. Comparison of male/female sex ratios of the Mesocyclops edax, Tropocyclops prasinus mexicanus, and Diaptomus minutus populations in the lake and contol tubes (Ctrl 1 and Ctrl 2) in the 1979 (June 5-October 20) and 1980 (May 12-July 17) study seasons. *'s denote dates when only males were present. Values of 1.5 or greater are underlined.

	1979																		1980							
	June			July				August				September				October			May		June				July	
	5	20	27	5	12	19	27	2	9	20	28	3	13	21	29	7	13	20	12	21	5	11	19	30	8	17
M. edax																										
Lake	—	—	1.0	1.3	1.5	*	3.3	1.0	1.8	3.0	1.1	1.0	0	0.2	1.3	1.0	—	1.9	—	*	*	*	0.4	0.9	*	—
Ctrl 1	—	0	0.3	0.1	1.0	*	1.0	0.8	1.5	3.3	2.6	1.2	1.4	1.4	2.9	1.5	2.0	0.4	*	*	2.0	1.3	4.3	43.3	4.9	6.3
Ctrl 2	*	—	1.0	1.3	*	2.0	1.6	2.0	1.2	1.7	1.0	1.4	0.8	0.7	0.5	0.1	0	0	—	—	0.7	1.6	9.7	2.2	16.2	*
T. p. mexicanus																										
Lake	0	0.2	—	0.3	1.4	0.6	1.1	1.0	1.6	1.3	0.9	3.3	1.3	1.1	0.8	1.2	0.7	0.4	—	0	0.6	0	*	1.6	0.6	0.7
Ctrl 1	0	0	0.4	0.7	0.7	0.3	0.7	0.5	0.6	1.2	0.3	0.7	1.2	1.0	0.5	0.9	1.4	0.3	0	0	0	0.2	4.0	1.5	0.9	0.5
Ctrl 2	1.0	0	0.1	1.9	0.8	0.7	1.0	0.1	0.5	1.2	0.7	1.2	1.4	0.9	0.9	0.4	*	0.8	0	0	0.2	0.7	2.8	1.7	0.6	0.8
D. minutus																										
Lake	0.5	0.5	0.4	0.6	0.8	0.5	0.4	0.5	1.1	0.4	0.3	0.2	0.4	0.5	0.5	0.9	0.4	0.9	5.7	0.6	0.2	0.2	0.5	0.2	0.4	0.7
Ctrl 1	1.0	1.0	0.9	0.7	0.9	0.8	0.5	0.3	1.0	0.7	0.8	0.6	0.7	0.8	0.5	0.5	1.0	0.5	1.8	1.6	0.8	1.0	0.9	0.8	1.1	0.8
Ctrl 2	1.0	0.9	0.7	0.7	1.2	1.1	0.9	0.9	1.1	1.3	0.7	0.8	0.5	0.6	0.5	0.5	0.5	0.5	1.0	5.7	0.9	0.9	0.8	0.8	1.0	0.8

greater survival of the second cohort between the C1-3 and C4-5 stage-classes in Ctrl 1 which accounted for the higher abundance in Ctrl 1 than in the lake in 1980 (Fig. 27).

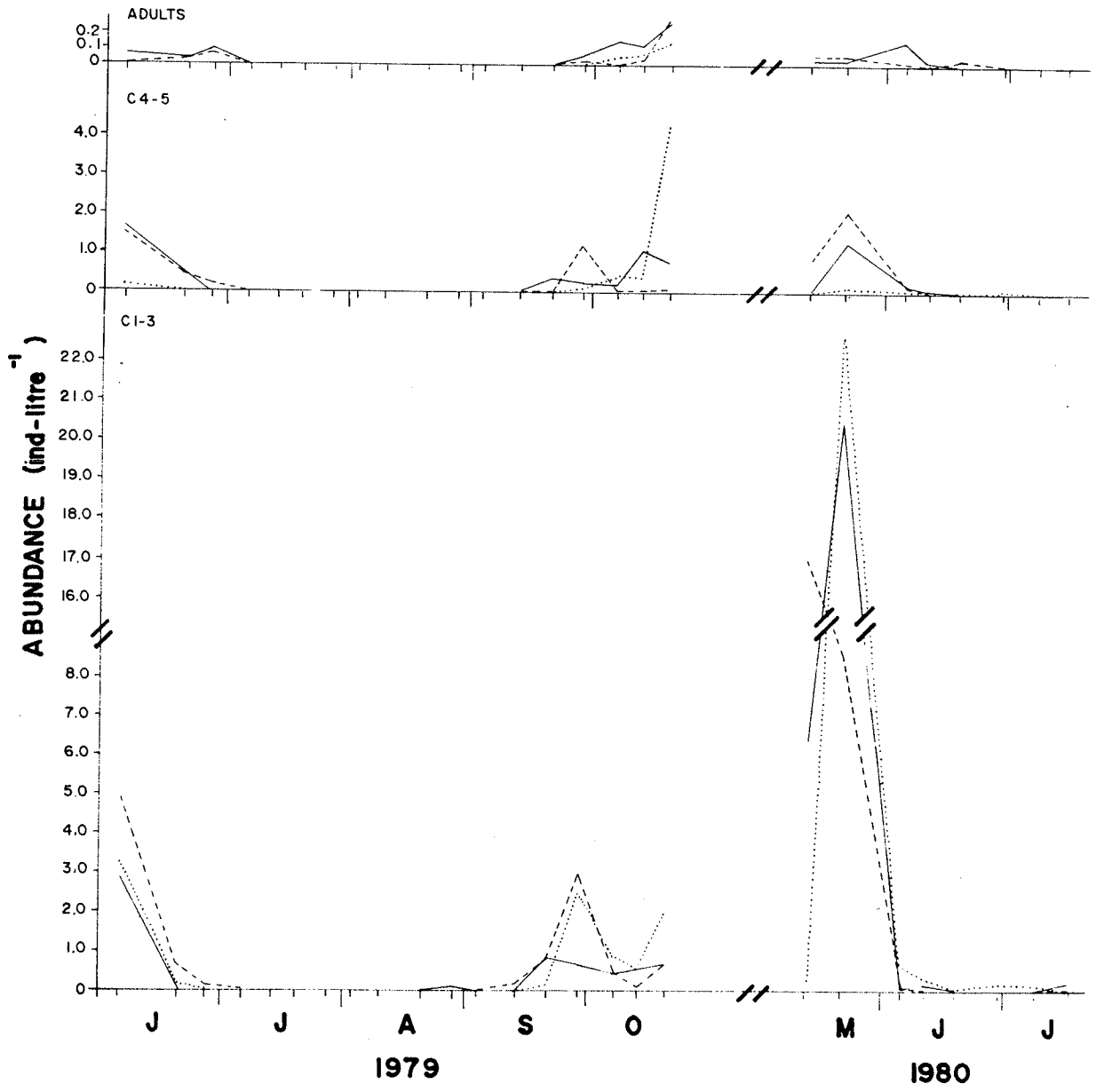
As in 1979, the pattern of pulse production was not evident in the egg counts (Table 19). No M. edax eggs were seen in the lake. A few eggs were seen in Ctrl 1 on June 5 and then again during the adult pulse in July and eggs were observed in Ctrl 2 only during the pulse of adults in July. Again, the sex ratios for M. edax were much higher than for the other species (Table 20).

The life history of C. b. thomasi differed greatly from that of T. p. mexicanus or M. edax, with the three populations entering a diapause phase in July and August during which no copepodids were observed (Fig. 28). The only effect of enclosure on this species was to slightly delay the entry of the populations into diapause.

All three populations were well into the declining phase of a spring pulse when sampling started in 1979 (Fig. 28). C1-3 abundance in the lake was intermediate to that in the control tubes on June 5 and remained there until the C1-3 disappeared from the water column around the end of the month. In contrast, C4-5 abundances were substantially higher in the tubes than in the lake on June 5 and remained higher until they, too, disappeared at the end of the month. Perhaps as a result of the higher C4-5 abundance, adults were present in both tubes from the start of sampling until the beginning of July, while none was seen in the lake (Fig. 28).

Figure 28. Seasonal variation of the abundance of Cyclops bicuspidatus thomasi life stages in the lake (.....), Ctrl 1 (————), and Ctrl 2 (– – – – —) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.

CYCLOPS BICUSPIDATUS THOMASI



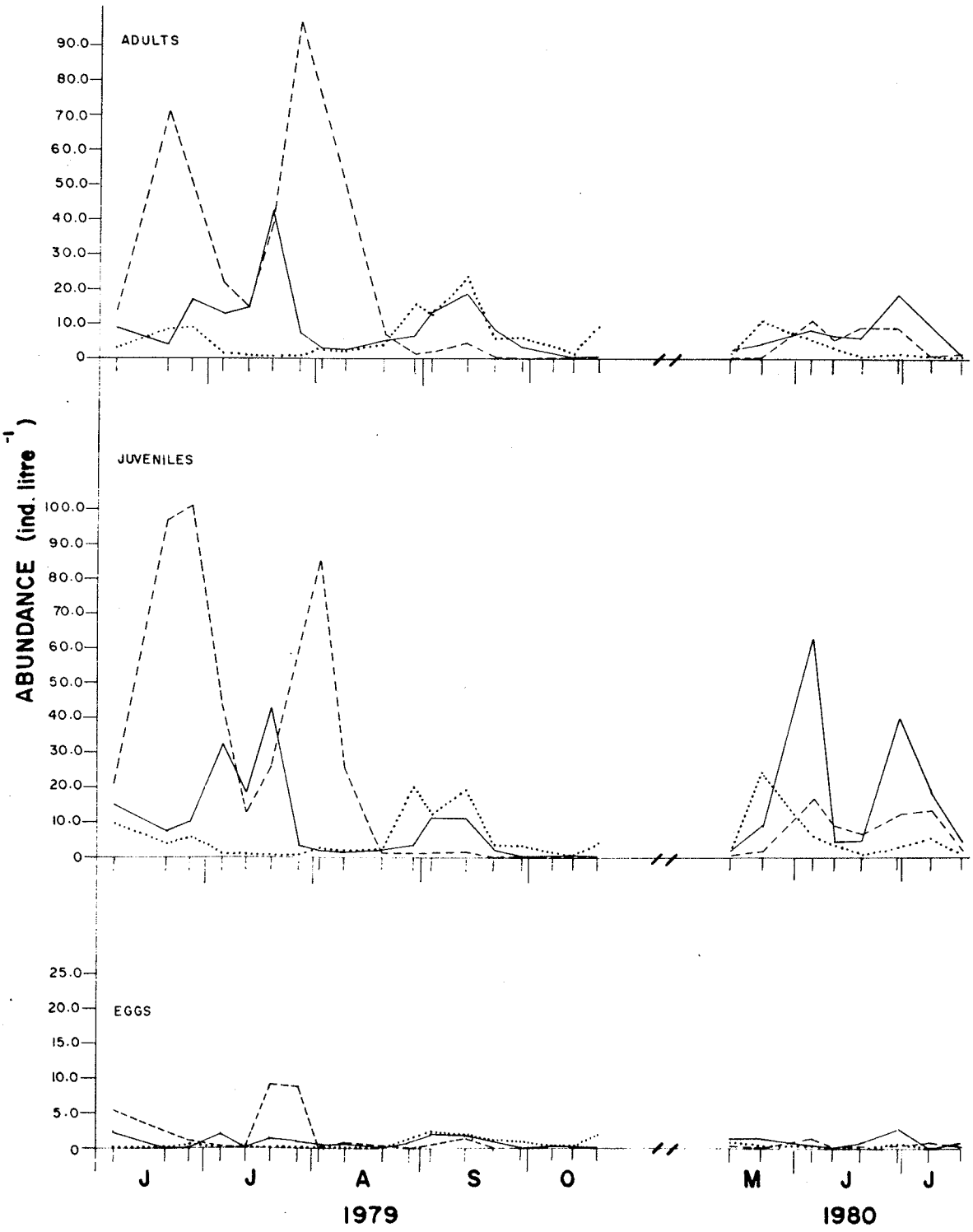
Although some C1-3 were encountered in Ctrl 1 at the end of August, the major reappearance occurred in mid-September in all three populations; with pulses developing at the end of the month (Fig. 28). The C4-5 reappeared in the tubes during the third week of September, one week earlier than in the lake. Adults reappeared around the beginning of October in all three populations (Fig. 28).

Spring population development was only slightly better documented in 1980 even with the earlier start of sampling. The response of C. b. thomasi to continued enclosure was the same as the initial response observed in 1979, at least as far as the pattern of spring population development is concerned (Fig. 28). Similarly-sized pulses of C1-3 developed in the populations in May, with abundance peaking in Ctrl 2 about a week before the lake or Ctrl 1 (Fig. 28). Despite the similar abundance of C1-3 in the three populations, significant pulses of C4-5 developed in the tubes only, as in 1979. Also as in 1979, adults appeared in the tubes but not in the lake. The spring pulses were largely finished by the first week of June, although most life history stages occurred sporadically to the end of sampling (Fig. 28).

The effects of enclosure on B. longirostris extended to its life history as well in 1979. Although not entirely synchronous in the two enclosures, each population produced three pulses while only two appeared in the lake (Fig. 29). In both tubes, the increased abundance was restricted to the spring and summer period.

Figure 29. Seasonal variation of the abundance of Bosmina longirostris life stages in the lake (·····), Ctrl 1 (————), and Ctrl 2 (– – – – –) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.

BOSMINA LONGIROSTRIS



The first pulse in the lake was produced before the start of sampling and matured in mid-late June (Fig. 29). Abundance was low through July with no gravid females observed (Fig. 29). Egg production began again in early August with the flush responsible for the second pulse developing at the end of the month and peaking in early September (Fig. 29). Juvenile and adult abundance subsequently peaked in mid-month (Fig. 29). Bosmina abundance declined from this peak through to mid-October, with slight increases of egg, juvenile, and adult abundance on the last sampling day (Fig. 29).

The initial response of B. longirostris to enclosure in 1979 differed considerably between the control tubes. The response was immediate in Ctrl 2. Within 7 days of enclosure, abundance was almost three times that in the lake and the egg count was greatly higher, at 5.5 eggs L^{-1}, compared with none in the lake (Fig. 29). These eggs translated into a much larger first pulse in Ctrl 2, which peaked at the same time as in the lake but at 8 times the level (Fig. 29). The egg counts in Ctrl 2 declined continually to early July and abundance dropped sharply following the peak (Fig. 29). The extra pulse developed in the second half of July from a massive pulse of eggs produced by the adults remaining from the first pulse (Fig. 29). Egg abundance peaked at greater than 9 eggs L^{-1} between July 19 and 27 and the resulting pulses of juveniles and adults peaked in early August at levels comparable to those in the first pulse (Fig. 29).

Again, abundance declined quickly following this peak, returning to the level in the lake by mid-late August (Fig. 29).

In comparison, the response of Bosmina to enclosure in Ctrl 1 was out of phase and appeared to be delayed. At the start of sampling, abundance in Ctrl 1 was about twice that in the lake and the egg count was greatly higher, although just half that in Ctrl 2 (Fig. 29). With alower egg stock, it could be expected that abundance would subsequently be lower than in Ctrl 2 but no pulse was produced in mid-month. Instead, abundance declined to the level in the lake over the following two weeks (Fig. 29). While not attributable to a pulse of eggs, abundance finally started to grow in the fourth week of June, producing the first, smaller, pulse at the end of the month (Fig. 29). The second, larger, pulse developed in mid-July at about the same time as the second pulse in Ctrl 2 (Fig. 29). The product of 90% fewer eggs, peak abundance was about half that in Ctrl 2 and the pulse was much shorter-lived, with abundance returning to the level in the lake by early August (Fig. 29).

The late-summer pulses occurred synchronously in the lake and both control enclosures (Fig. 29). Abundance in Ctrl 1 was comparable to that in the lake through this pulse; the products of similar numbers of eggs (Fig. 29). Egg counts in Ctrl 2 were markedly lower and abundance through this pulse was about 25% of that in the lake or Ctrl 1 (Fig. 29).

Clearly, the different initial responses of the Bosmina

populations in Ctrl 1 and Ctrl 2 primarily account for the different patterns of community dynamics in the spring and summer (Fig. 15) and for the differing community structure at the start of the experiment.

The population in the lake produced two pulses during the period of study in 1980. The first developed shortly after the resumption of sampling and peaked around May 21 (Fig. 29). The second developed just before the termination of sampling. Juvenile abundance peaked in the first week of July with no pulse of adults appearing before the end of the study on July 17 (Fig. 29).

Unlike in the previous year, the dynamics of the populations in the enclosures were similar and followed the pattern in the lake, at least until mid-summer. Also unlike 1979, abundance was higher in Ctrl 1 than in Ctrl 2.

The first pulses developed slightly later in the tubes, peaking in early June (Fig. 29). At the peak, abundance in Ctrl 2 was comparable to that in the lake. Abundance in Ctrl 1 was about twice that in either the lake or Ctrl 2, only due to the greater abundance of juveniles (Fig. 29). In the absence of samples from the previous two weeks because of the first forest fire, the cause of this greater abundance is not evident. The second pulses developed in late June at about the same time as in the lake and abundance peaked at the end of the month, slightly earlier than in the lake (Fig. 29). Peak abundance was 10 and 5 times greater in Ctrl 1 and Ctrl 2, respectively, with significant numbers reaching adulthood

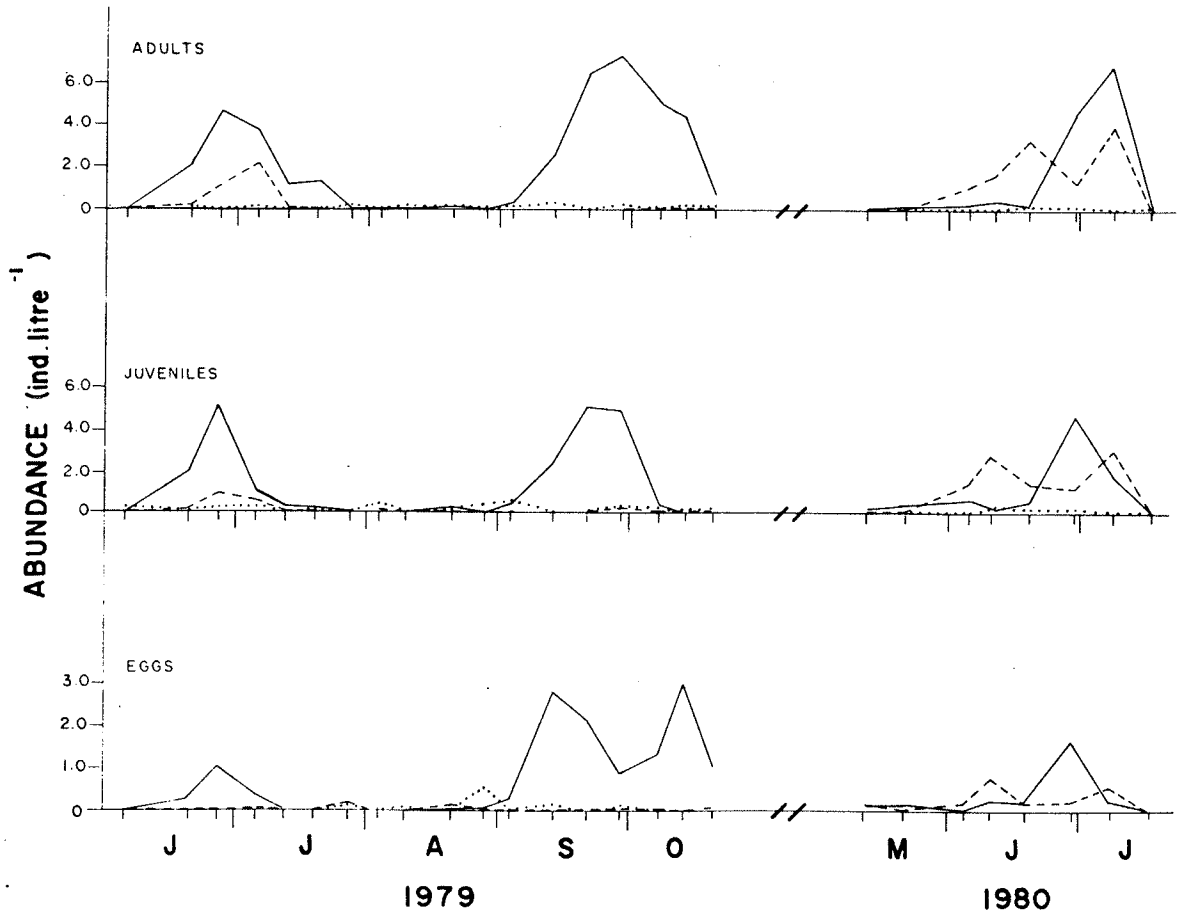
(Fig. 29).

Though present in most samples, H. gibberum was never an important contributor to the lake community. Total population abundance never exceeded 0.7 ind L^{-1} and was generally below 0.3 ind L^{-1} (Fig. 30). The degree of response by ~~Holopedium~~ to enclosure in 1979 differed as much between the tubes as did the response of Bosmina, but with the greater increase of abundance in Ctrl 1 rather than in Ctrl 2 (Fig. 30). Early-summer pulses were common to the populations in the enclosures and this pulse was solely responsible for the greater abundance in Ctrl 2 than in the lake (Fig. 30). In Ctrl 1, abundance began to increase shortly after tube installation (Fig. 30). The response in Ctrl 2 was somewhat delayed, with abundance not beginning to increase until after June 20 (Fig. 30). These first pulses peaked in both tubes around the end of the month, with abundance in Ctrl 1 at 3.5 times the level in Ctrl 2 (Fig. 30). The greater abundance in Ctrl 1 at this time appeared to be the product of greater fertility, with a disproportionately higher egg stock in Ctrl 1 than in Ctrl 2 (Fig. 30).

By the end of July, Holopedium abundance in the tubes had returned to the level in the lake and was uniformly low in the three populations through August (Fig. 30). These low levels continued in the lake and Ctrl 2 through to the end of sampling and only the population in Ctrl 1 produced an autumn pulse (Fig. 30). This developed from increased egg production in early September, with eggs, juveniles, and adults peaking

Figure 30. Seasonal variation of the abundance of Holopedium gibberum life stages in the lake (·····), Ctrl 1 (————), and Ctrl 2 (– – – – – –) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.

HOLOPEDIUM GIBBERUM



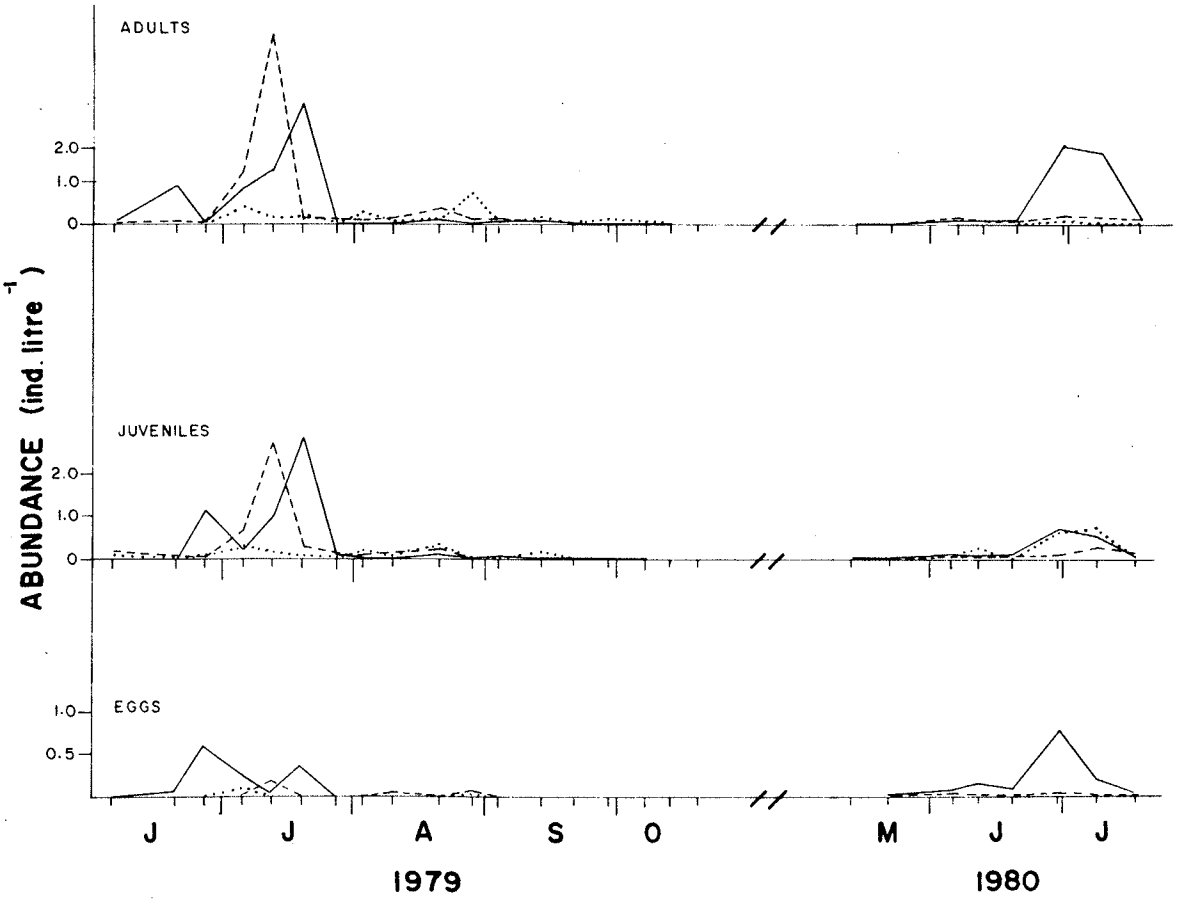
in turn at weekly intervals through the second half of the month (Fig. 30). The adults switched over to the production of resting eggs in October (Fig. 30).

The early-summer pulses were produced by the populations in the enclosures again in 1980, but, unlike 1979, the pulses were of comparable magnitude (Fig. 30). Holopedium abundance began to increase earlier in Ctrl 2 this year (Fig. 30). Much as in Ctrl 1 in 1979, this earlier increase in Ctrl 2 was the product of an earlier increase of egg production (Fig. 30). Abundance in both tubes returned to the level in the lake by the termination of sampling (Fig. 30).

D. brachyurum was also a minor contributor to the lake community, with total population abundance never exceeding 0.3 ind. L^{-1} (Fig. 31). The increased abundance of Diaphanosoma in the control enclosures in 1979 was the product of sharply defined early summer pulses (Fig. 31). In the same way as Holopedium responded in Ctrl 1, D. brachyurum numbers began to increase much earlier following enclosure in Ctrl 1 than in Ctrl 2 (Fig. 31). A pulse was produced shortly after enclosure with adult numbers peaking on June 20 (Fig. 31). Initiated by eggs produced by this pulse, the major second pulse began to develop at the end of June and reached peak abundance in mid-July (Fig. 31). In Ctrl 2, Diaphanosoma abundance did not begin to increase until the end of June. The resulting pulse was slightly larger and peaked one week earlier than in Ctrl 1 (Fig. 31). In both tubes, abundance returned to the level in the lake by the end of the month and

Figure 31. Seasonal variation of the abundance of Diaphanosoma brachyurum life stages in the lake (.....), Ctrl 1 (————), and Ctrl 2 (------) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.

DIAPHANOSOMA BRACHYURUM



remained there until the termination of sampling (Fig. 31).

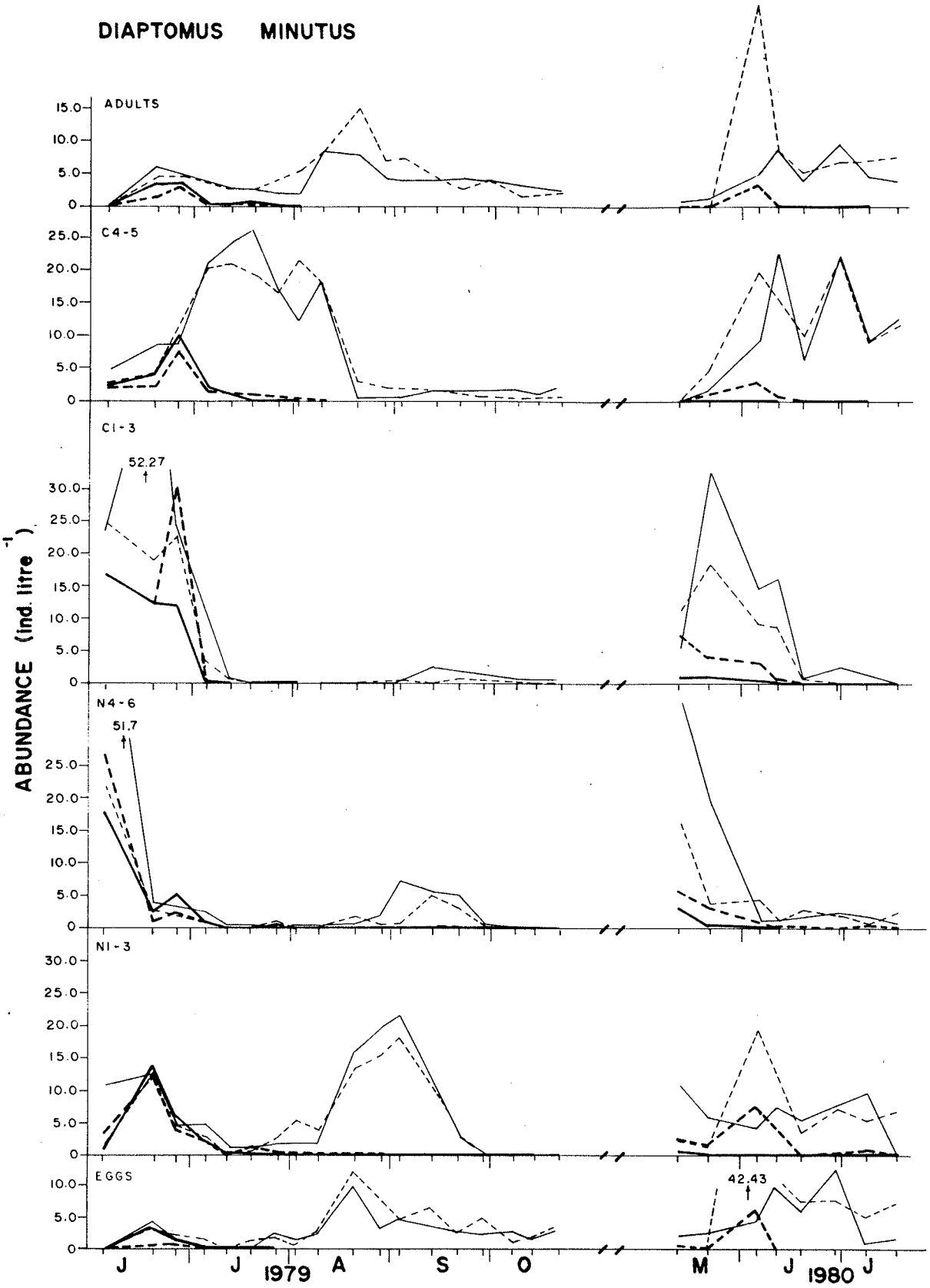
Diaphanosoma abundance only increased in Ctrl 1 in 1980, again as the product of an early-summer pulse. Abundance in both control tubes was the same as in the lake from the start of sampling to June 19 (Fig. 31). Identical pulses of juveniles developed in both the lake and Ctrl 1 at this time, but significant numbers of adults developed in Ctrl 1 only, peaking at the end of the month (Fig. 31). The reason for the absence of a corresponding pulse in Ctrl 2 isn't apparent. Egg counts were much lower than in Ctrl 1, but the pulse of juveniles in the lake appeared in the absence of eggs (Fig. 31).

ii. Effects of acidification

D. minutus was quickly affected by acidification once the pH was lowered below about 5.5. Population development in A1 and A2 paralleled that in the control tubes through the first three weeks of enclosure (May 29-June 20) and the first week of pH reduction (June 21-June 27), during which the pH was lowered to 5.5 in A1 and 5.6 in A2 (Fig. 32). Copepodid abundance was generally lower in A1 and A2 during this initial period but nauplius abundance was approximately the same in the four populations (Fig. 32). Egg abundance was also generally lower in A1 and A2, reflecting the fewer adults in these enclosures (Fig. 32).

The major reductions of D. minutus copepodid abundance occurred in the acidified enclosures during the second week

Figure 32. Seasonal variation of the abundance of Diaptomus minutus life stages and of calanoid nauplii in Ctrl 1 (————), Ctrl 2 (– – – – – –), A1 (▬▬▬▬), and A2 (▬ ▬ ▬ ▬) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.


DIAPTOMUS MINUTUS
ADULTS
C4-5
C1-3
52,27
N4-6
51.7
N1-3
EGGS
42,43
ABUNDANCE (ind. litre -1)
J
J
1979
A
S
O
M
J
1980
J

of pH reduction (June 28-July 5), when the pH was lowered to 4.7 in both A1 and A2. By July 5, the abundance of all copepodid stages was just 10% of that in the controls (Fig. 32). The major reductions of the percentage similarity of community index between the control and acid tubes closely followed these reductions (Fig. 21). No effect of this further pH reduction was evident on the calanoid nauplii, as it was applied when abundance was already well into a declining phase in all four enclosures (Fig. 32). No D. minutus eggs were found in the July 5 samples from either acid tube while 0.4 and 1.5 eggs L^{-1} were recorded in Ctrl 1 and Ctrl 2 (Fig. 32). The abundance of all D. minutus developmental stages continued to decline after July 5 and remained at very low levels until the end of sampling, although none was eliminated for more than two consecutive sampling periods (Fig. 32). As might be expected, egg abundance was very low during July, never exceeding 0.8 eggs L^{-1}, and no eggs were seen between July 27 and the termination of sampling in 1979 although adult females were occasionally observed (Fig. 32).

At the resumption of sampling in 1980, the abundances of most classes of D. minutus developmental stage were near those in the controls in A2 but were substantially lower in A1 (Fig. 32). With acidification of A1 to 4.75 between May 15 and 21, the abundance of all stages remained low or declined further (Fig. 32). The abundance of no class of developmental stages exceeded 1.0 ind L^{-1} in A1 on May 21 (Fig. 32). A2 was

only acidified to pH 5.4 during this period, with the abundance of C1-3 increasing slightly and the abundance of N1-3 and N4-6 decreasing somewhat, as in the controls (Fig. 32).Unlike in the control populations, C1-3 abundance in A2 decreased about 40% by May 21 (Fig. 32).

The pH of A2 was reduced to 4.75 by May 22 but no sampling could be done between this date and June 2, due to the first forest fire evacuation. During this period the pH levels in A1 and A2 rose to 5.3 and 5.8, respectively. Substantial increases in the abundance of eggs, N1-3, C4-5, and adults were recorded in A2 at the end of this period (Fig. 32). A ten-fold increase of adult abundance occurred in A1 during this period as well but this brought abundance to just 0.13 ind L^{-1} by June 5 compared with 3.5 ind L^{-1} in A2. The abundance of all other D. minutus stages in A1 decreased by approximately 50% between May 21 and June 5 (Fig. 32). Clearly, the main reason for the different population responses to the less severe pH regime was the greater number of C1-3 in A2 on May 21 (Fig. 32). These could be expected to develop into many more adults than would result from the few C1-3 in A1. With so few adults present, no egg pulse was produced in A1 and, therefore, no N1-3 pulse developed (Fig. 32). Independent of all subsequent pH fluctuations, low numbers (<0.3 ind L^{-1}) of all life stages were recorded in A1 on all sampling dates after June 5 (Fig. 32).

The pH of A2 was reduced to 5.0 between June 2 and 4 and, with the pH not exceeding 5.2 in the following ten

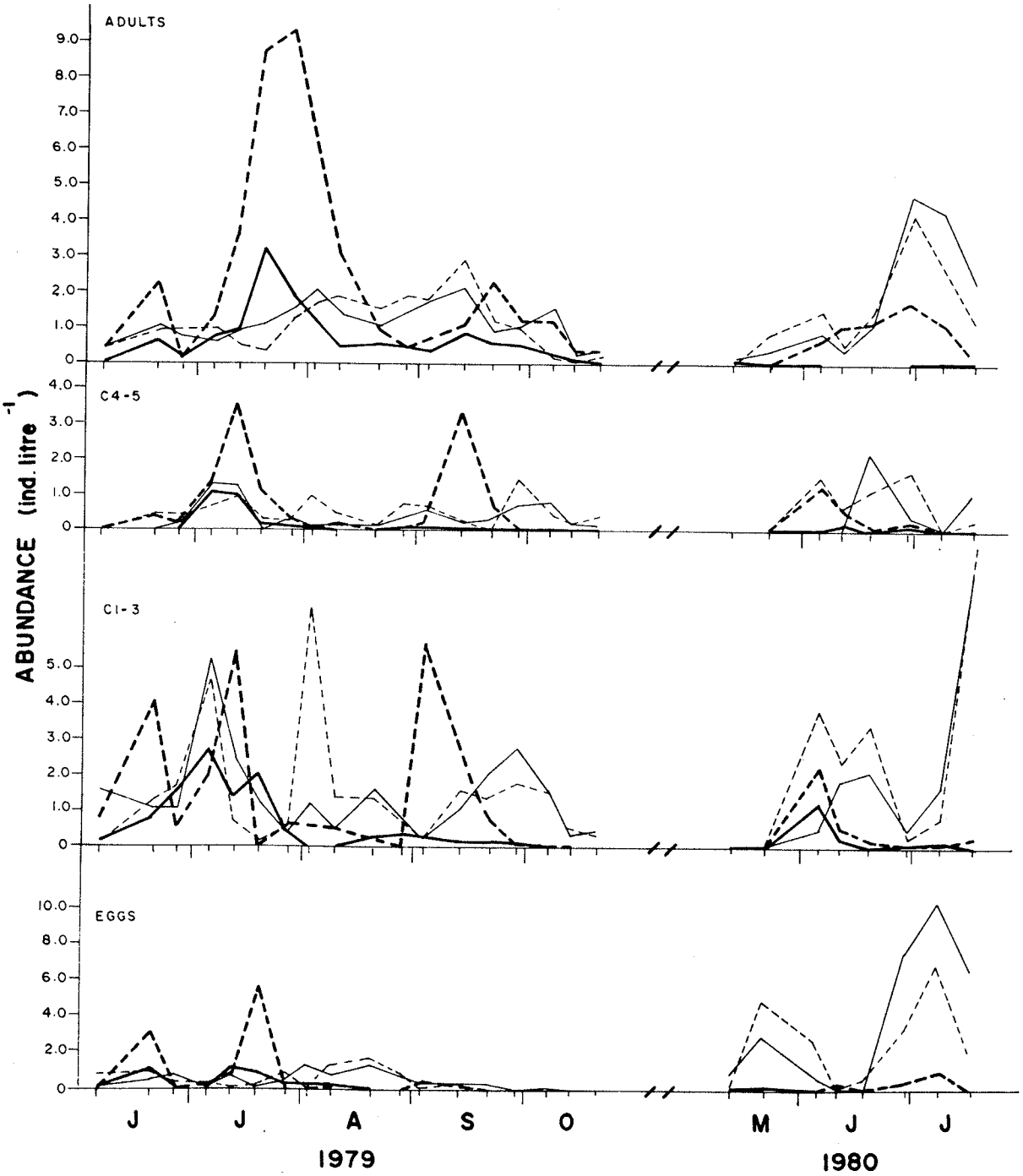
days, the abundance of all D. minutus life stages declined (Fig. 32). The pH was reduced to 4.75 on June 14 and no class of developmental stage exceeded 0.9 ind L^{-1} after June 19 (Fig. 32). Although the pH of A2 rose to 5.2 during the second fire evacuation (June 19-25), no significant population increases resulted, reflecting the few copepodids present on June 19 (Fig. 32).

The response of T. p. mexicanus to acidification was more gradual than the response of D. minutus. Abundance was unaffected, on average, in the first season but the fluctuations of abundance were considerably more dynamic than in the controls (Fig. 33). This appeared to be the product of transient variations of survival in the populations which were unrelated to the fluctuations of pH about the target value. These variations of survival occurred asynchronously in the two populations, quite in contrast to the stable and synchronous pattern of population dynamics in the control tubes. This destabilization of population development was followed by recruitment failure in the autumn.

Prior to acidification, population development in A1 paralleled that in the control tubes, although abundance averaged just 50% of control values (Fig. 33). Initial population development in A2 was slightly different than in the other three enclosures. A pulse of C1-3 appeared in June, peaking in mid-month, and this pulse may have been responsible for adult abundance increasing by three times the increment in the controls during the same period (Fig. 33).

Figure 33. Seasonal variation of the abundance of Tropocyclops prasinus mexicanus life stages in Ctrl 1 (————), Ctrl 2 (– – – – – –), A1 (▬▬▬▬), and A2 (▬ ▬ ▬ ▬) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.

TROPOCYCLOPS PRASINUS MEXICANUS



In the absence of previous samples the genesis of this pulse is unknown, but this increase accounted for total abundance in A2 averaging twice that in the controls in the pre-acidification period. All subsequent population development in A2 was about one week out of phase with that in the other three enclosures (Fig. 33).

Just as in the controls, pulses of eggs were produced in both A1 and A2 in June, with these peaking in mid-month and with the size of these pulses proportional to adult abundance (Fig. 33). The pulses of animals which developed from these eggs belong to what was termed the first cohort in the controls. Acidification had no negative effect on the progression of this cohort, with better survival to the adult stage than in the controls and with development progressing synchronously in the four populations (Fig. 33). In the C1-3 stage-class, abundance in A2 peaked at about the same level as in the controls while abundance in A1 peaked at about half this level. However, by the C4-5 stage-class, abundance in A1 was the same as in the controls and abundance in A2 was three times higher. This trend continued through to the adult stage with abundance in A1 peaking at about twice that in the controls while abundance in A2 peaked at 5 times the control level. As a result of this greater abundance, the first cohort was considerably more distinct at the adult stage in the acidified tubes than in the controls (Fig. 33).

Following the pattern set in the controls, the second cohort developed from a pulse of eggs produced by the

maturing first cohort (Fig. 33). With the greater abundance of adults in the acidified tubes at this time, the resulting pulses of eggs were also larger than in the controls (Fig. 33). This second cohort was next evident as pulses of C1-3 which peaked in the third week of July in A1 and in the fourth week in A2 (Fig. 33). In contrast to the development of the first cohort, survival to the C1-3 stage-class was much lower in A2 than in A1 (Fig. 33). Peak egg abundance in A2 was more than five times that in A1, yet the resulting peak of C1-3 was less than half that attained in A1. Lower survival of the second cohort was apparent in both acidified tubes at the C4-5 stage-class (Fig. 33). No pulses of adults appeared in either A1 or A2 (Fig. 33).

Despite the low survival of the second cohort, a third cohort was produced in both acid tubes. These animals originated from eggs produced in early August by adults of the second cohort (Fig. 33). The third cohort appeared as C1-3 in August with abundance peaking in A1 at the end of the month and in A2 in early September. Though starting from similar egg numbers, survival to the C1-3 stage-class was considerably lower in A1 and the greater abundance in A2 continued through to the adult stage, peaking at about twice that in A1 in mid-September (Fig. 33).

No significant fourth cohort was produced in either acidified tube. A few eggs were produced in A2 in early September by the maturing third cohort but these failed to develop into a notable pulse of C1-3 (Fig. 33). No eggs were

produced by the maturing third cohort in A1 (Fig. 33).

T. p. mexicanus eggs were also affected by acidification. Frequently in 1979, the adult females in the acid tubes carried eggs in a state which were termed "not countable"; that is, the females were carrying full egg sacs but the normally distinct spheres could not be differentiated (Fig. 34; Table 21). The viability of these eggs was not determined. The eggs were unique to the acidified tubes, occurring asynchronously in the two populations and independently of the fluctuations of pH between 4.6 and 5.2 (Table 21; Fig. 7). The occurrence of this condition also did not coincide with the variations of cohort success in the two populations.

In contrast to 1979, the effects of acidification on T. p. mexicanus were evident immediately following the resumption of acid additions in 1980 (Fig. 33). These effects were also more severe than in 1979, as indicated by the significant reductions of abundance. Further unlike 1979, the differences in abundance between the acidified populations were coincident with differences in the pH regimes (Fig. 33).

There was no marked difference in T. p. mexicanus abundance between A1 and A2 at the start of sampling in 1980, unlike 1979 (Fig. 33). Acidification was resumed on May 15 and abundances in both A1 and A2 were less than 10% of those in the controls by May 21 (Fig.33). With few adults and no gravid females present, no significant pulses of eggs were produced in either acid tube before the first fire

Figure 34. Comparison of eggs carried by Tropocyclops prasinus mexicanus females in the control tubes with those carried in the acidified tubes and classed as not countable: a, gravid female from Ctrl 1, August 2, 1979; b, gravid female from A2, July 19, 1979.

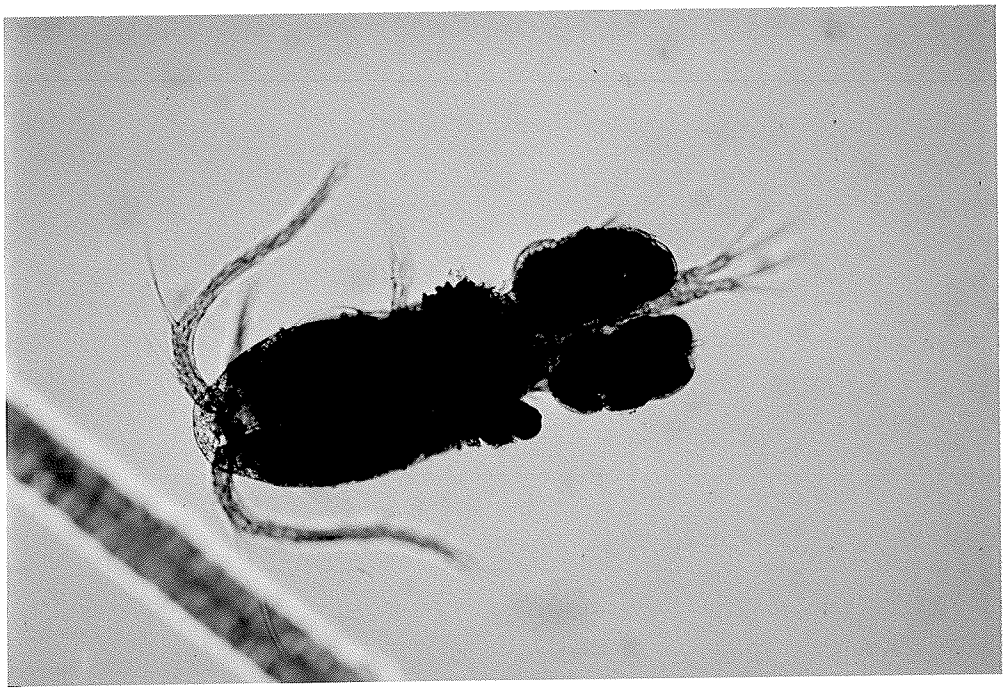
NOTICE/AVIS

PAGE(S) Figure 34 IS/~~ARE~~ EST/~~SONT~~ colour photo

PLEASE WRITE TO THE AUTHOR FOR INFORMATION, OR CONSULT THE ARCHIVAL COPY HELD IN THE DEPARTMENT OF ARCHIVES AND SPECIAL COLLECTIONS, ELIZABETH DAFOE LIBRARY, UNIVERSITY OF MANITOBA, WINNIPEG, MANITOBA, CANADA, R3T 2N2.

VEUILLEZ ECRIRE A L'AUTEUR POUR LES RENSEIGNEMENTS OU VEUILLEZ CONSULTER L'EXEMPLAIRE DONT POSSEDE LE DEPARTEMENT DES ARCHIVES ET DES COLLECTIONS SPECIALES, BIBLIOTHEQUE ELIZABETH DAFOE, UNIVERSITE DU MANITOBA, WINNIPEG, MANITOBA, CANADA, R3T 2N2.

a.



b.

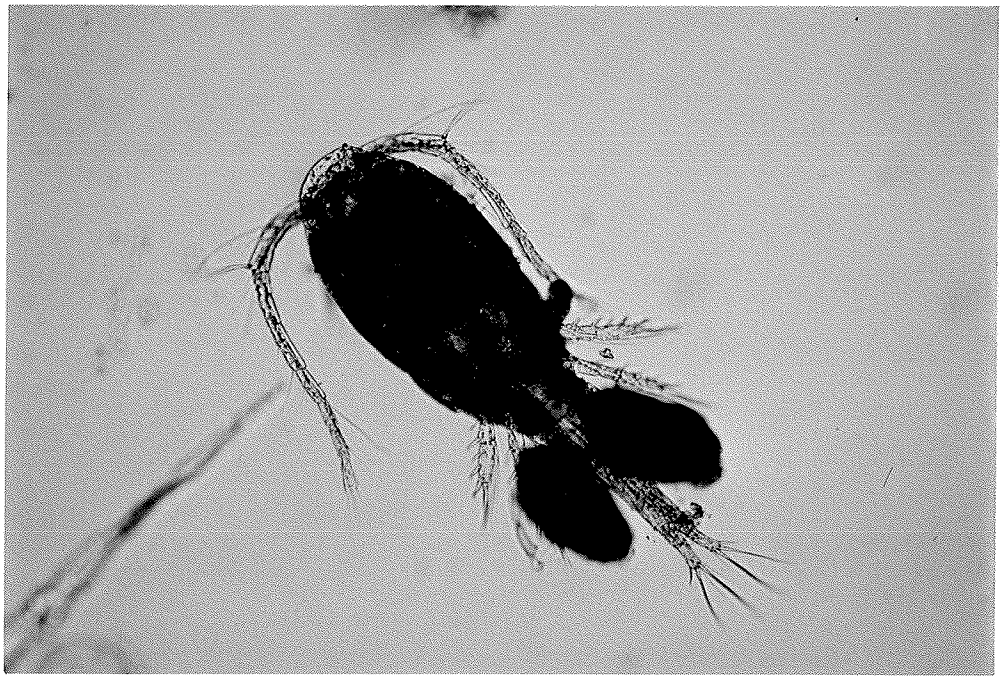


Table 21. Comparison of the proportion of gravid Tropocyclops prasinus mexicanus females with countable eggs in the control (Ctrl 1 and Ctrl 2) and acidified (A1 and A2) enclosures in the 1979 (June 5–October 20) and 1980 (May 12–July 17) study seasons. Values below 1.0 are underlined.

	1979																	1980							
	June			July				August				September			October			May		June				July	
	5	20	27	5	12	19	27	2	9	20	28	3	13	21	29	7	13	20	12	21	5	11	19	30	8	17
Ctrl 1	—	1.0	1.0	—	1.0	—	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	—	1.0	—	1.0	1.0	1.0	1.0	—	—	1.0	1.0	1.0
Ctrl 2	1.0	1.0	1.0	1.0	—	1.0	1.0	—	1.0	1.0	1.0	1.0	1.0	—	—	1.0	—	—	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
A1	—	1.0	—	0	1.0	0.3	1.0	1.0	1.0	0	—	0	—	—	—	—	—	—	—	1.0	—	—	—	—	—	—
A2	—	1.0	0	0.5	1.0	0.3	0	0	0.4	0	0	1.0	1.0	1.0	—	—	—	—	—	—	—	1.0	0	0.2	0.7	0

evacuation, unlike in the controls (Fig. 33).

Both populations responded to the suspension of acidification over the following twelve days with spates of egg production, as evidenced by the pulses of C1-3 present in early June (Fig. 33). A1 was acidified after sampling on June 5 with a pH of 4.8 recorded on June 9. By June 11, the pulse of animals produced during the first fire had suffered almost complete mortality (Fig. 33). No subsequent pulse of adults appeared and no adults were seen after June 5 (Fig. 33).

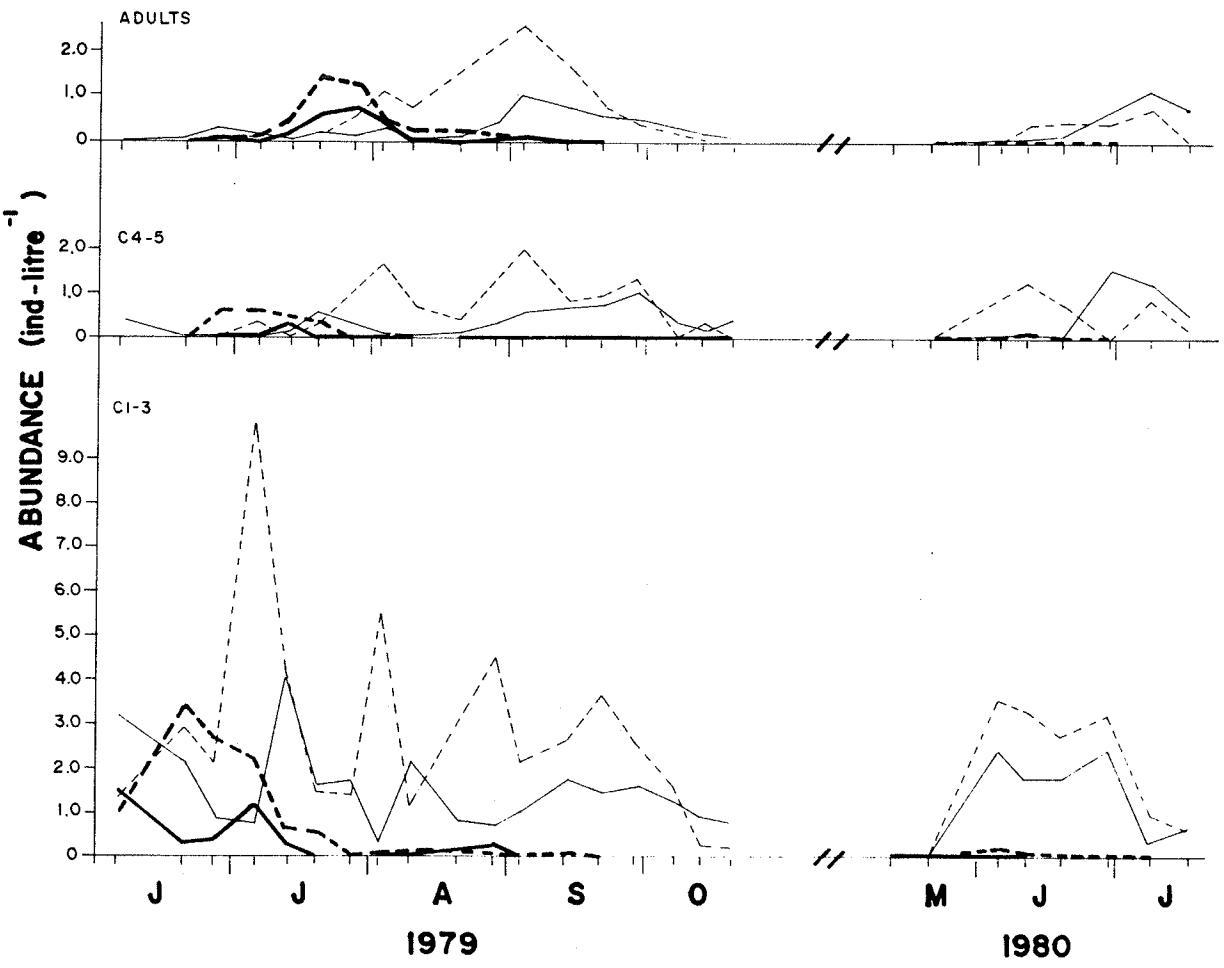
The pH of A2 remained at or above 5.0 until June 13 and the pulse successfully reached maturity (Fig. 33). Once in the adult stage, reduction of the pH below 5.0 had no apparent effect on abundance. There was no significant recruitment in A2 with the pH maintained below 5.2 after June 2 (Fig. 33). Eggs were frequently observed but the counts were low, due both to a low proportion of gravid females in the population and to the high frequency of uncountable eggs (Table 21). As a result adult numbers finally declined in July (Fig. 33).

The reductions of M. edax abundance in the acidified tubes in 1979 were not the product of mortality on all stages, as in D. minutus, but were due to recruitment failures.

Prior to the addition of acid, population development in A1 was in phase with that in Ctrl 1 and development in A2 was following the pattern in Ctrl 2 (Fig. 35). The C1-3 pulse of the first cohort in A1 peaked at or before the start of

Figure 35. Seasonal variation of the abundance of Mesocyclops edax life stages in Ctrl 1 (————), Ctrl 2 (– – – – – –), A1 (▬▬▬▬), and A2 (▬ ▬ ▬ ▬) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.

MESOCYCLOPS EDAX



sampling with a small increase of adult abundance occurring at the end of June. The second cohort was produced before acidification but development continued through the period of pH reduction, with the resulting C1-3 pulse developing in early July (Fig. 35). The C1-3 pulse of the first cohort in A2 peaked in mid-June with development also continuing through the period of pH reduction.

Acidification had no detectable effect on the development of these cohorts produced before acid was added (Fig. 35). As was the case for T. p. mexicanus, the resulting pulses of adults were larger than the corresponding cohort in the control tubes (Fig. 35). However, there was little evidence of subsequent cohort production, particularly at the C4-5 stage-class (Fig. 35). Very small C1-3 pulses appeared in both tubes in mid-August, with none seen after the end of the month in A1 or after mid-September in A2. There were sporadic occurrences of C4-5 in both tubes to the end of August and adults were present in low numbers to mid-September in A1 and to the end of August in A2 (Fig. 35).

No significant M. edax populations developed in the acidified tubes in 1980, with a failure of recruitment again the probable cause (Fig. 35).

In the absence of reliable egg counts and without counts of nauplii at the species level, the mechanism of the recruitment failure cannot be certainly determined. There is, however, some evidence to suggest that it occurred at the egg

or early nauplius level. In the controls, cyclopoid nauplius abundance did not track the fluctuations of either M. edax or T. p. mexicanus (Fig. 36). In the acid tubes, nauplius abundance followed the fluctuations of T. p. mexicanus abundance very closely after the addition of acid (Fig. 36).

Because of the experimental design, the spring population development of C. b. thomasi was not exposed to lower pH in 1979 (Fig. 7 and 37). Development in both A1 and A2 paralleled that in the control tubes through to the entry into diapause in early July (Fig. 37). The period of the autumn emergence from diapause was exposed to the acidification and the populations responded with an almost complete failure to emerge, which accounts for the reduced population abundance (Fig. 37). A few C1-3 appeared in A1 on August 20 and again from September 29 to the end of sampling, but abundance never exceeded 0.1 ind L^{-1}. Similarly, a few C4-5 appeared in A1 in October with the maximum abundance of 0.07 ind L^{-1} recorded on October 13 (Fig. 37). No C1-3 or C4-5 were observed in A2 after July 5 or June 27, respectively. No adults appeared after July 12 in either acidified tube in 1979 (Fig. 37).

No further information regarding the response of C. b. thomasi to acidification was obtained in 1980 because the majority of spring development had occurred before the pH was lowered and no important deviations from the dynamics in the control populations were observed (Fig. 37).

As was the case for abundance in 1979, B. longirostris

Figure 36. Seasonal variation of the abundance of cyclopoid nauplii in Ctrl 1 (————), Ctrl 2 (- - - - - -), A1 (▬▬▬▬), and A2 (▬ ▬ ▬ ▬) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.

CYCLOPOID NAUPLII

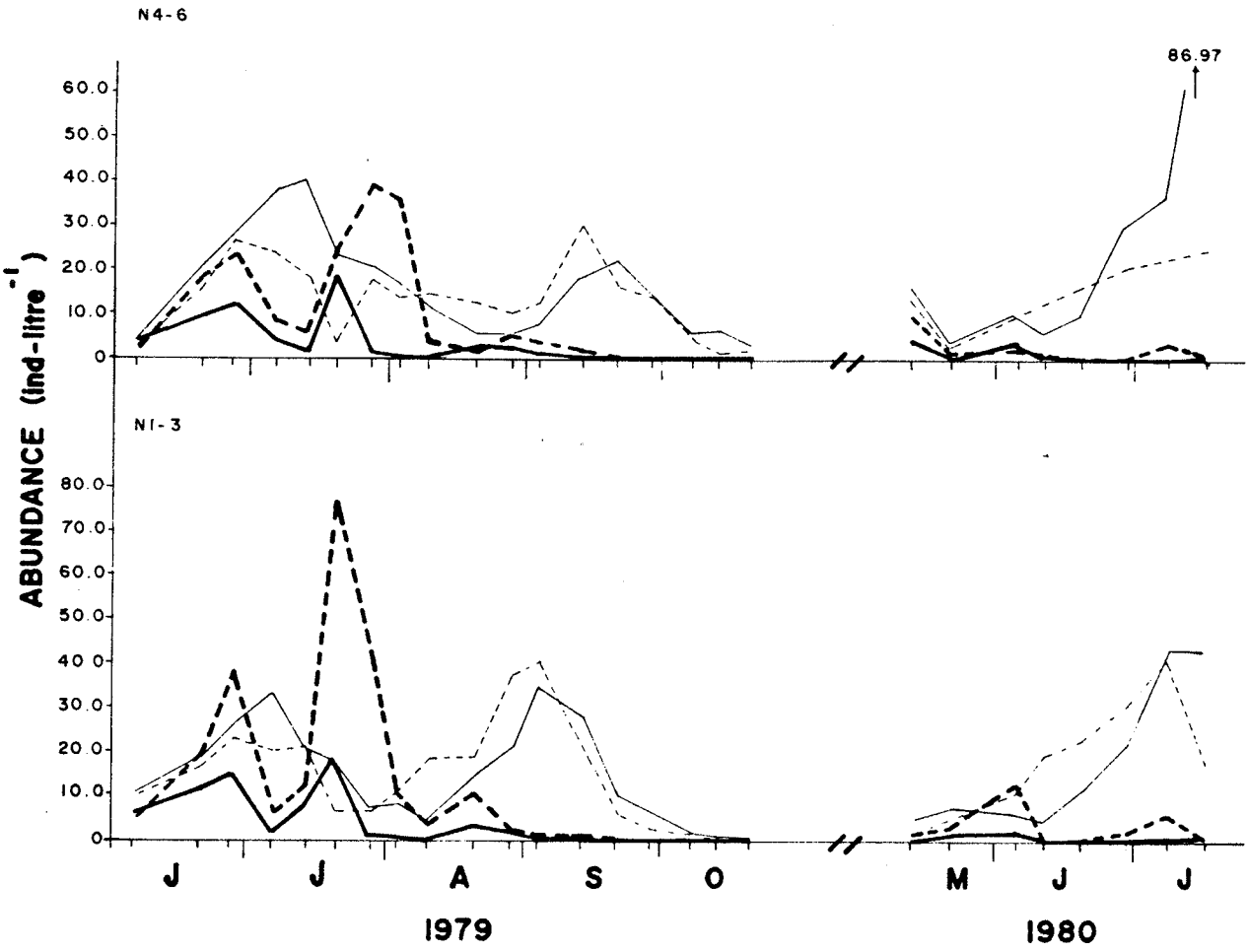
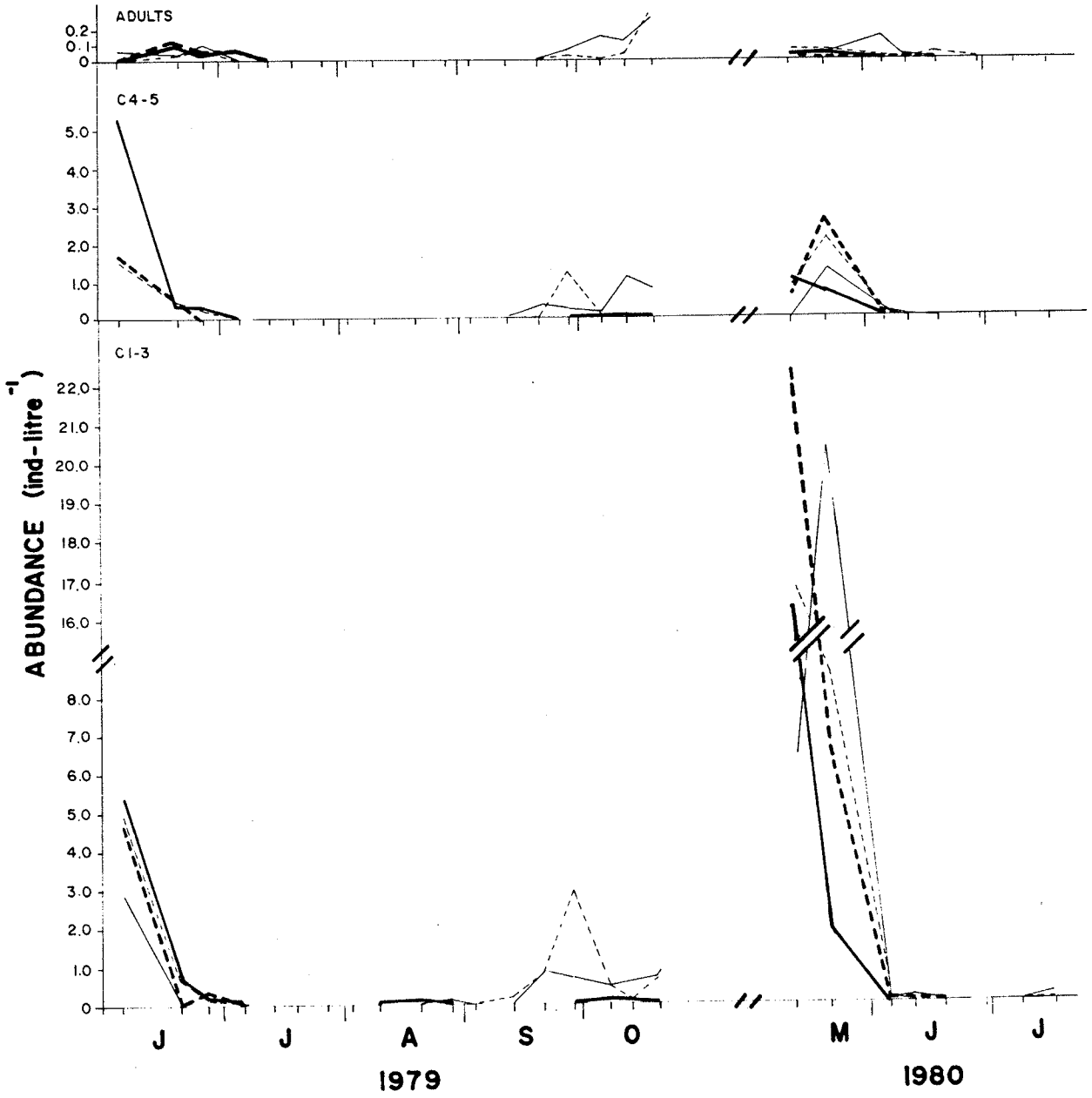


Figure 37. Seasonal variation of the abundance of Cyclops bicuspidatus thomasi life stages in Ctrl 1 (————), Ctrl 2 (– – – – –), A1 (▬▬▬▬), and A2 (▬ ▬ ▬ ▬) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.

CYCLOPS BICUSPIDATUS THOMASI



population dynamics weren't affected by acidification to a degree that could be distinguished from the variability between the control populations (Fig. 38). The populations in both acid tubes followed the dynamics of the population in Ctrl 2, with the three pulses occurring synchronously in the three enclosures at approximately monthly intervals (Fig. 38).

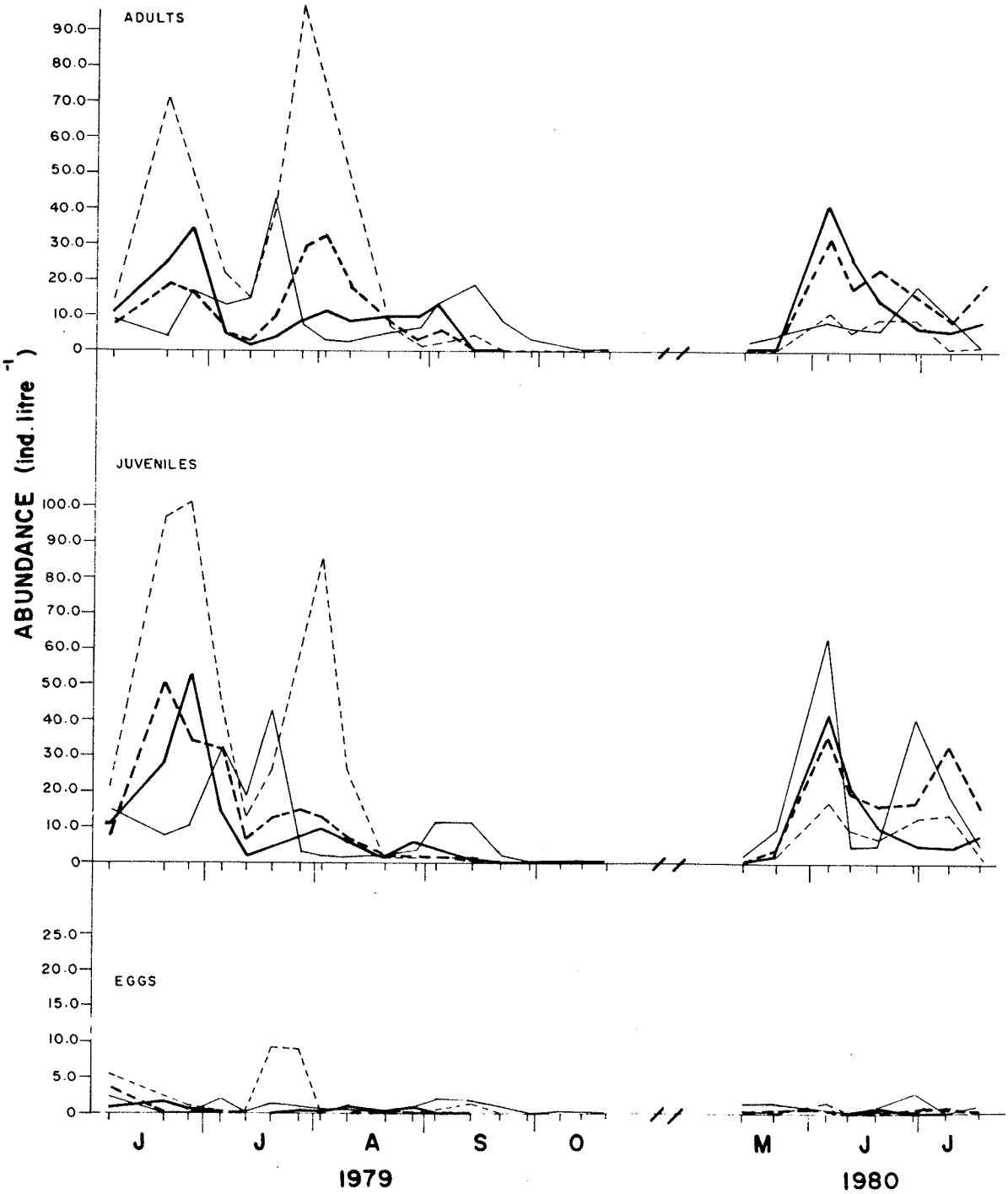
Unrelated to the acidification, the initial pulses in A1 and A2 were smaller than in Ctrl 2. Egg counts averaged 30-40% of those in Ctrl 2 through to July 12 (Fig. 38). Bosmina abundance in A1 and A2 averaged a comparable 40% of abundance in Ctrl 2 during the same period (Fig. 38).

The second pulses developed in the acid tubes despite the virtual absence of eggs in July (Fig. 38). They were much smaller in relation to the initial pulse than was the second pulse in Ctrl 2. At the peak of the second pulse, abundances in A1 and A2 were respectively 23 and 64% of peak abundance in the first pulse (Fig. 38). Peak abundances were identical in the first and second pulses in Ctrl 2 (Fig. 38). In the absence of adequate replication in the control populations, and based on the subsequent performance of the populations in the acid tubes in this season, this difference between Ctrl 2 and the acid tubes can be attributed to nothing more than natural variation. By August, egg numbers in the three tubes were comparable and through the third pulse abundances were as high or higher in A1 and A2 than in Ctrl 2 (Fig. 38).

In 1980, the bimodal dynamics of the control populations

Figure 38. Seasonal variation of the abundance of Bosmina longirostris life stages in Ctrl 1 (————), Ctrl 2 (– – – – – –), A1 (▬▬▬▬), and A2 (▬ ▬ ▬ ▬) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.

BOSMINA LONGIROSTRIS



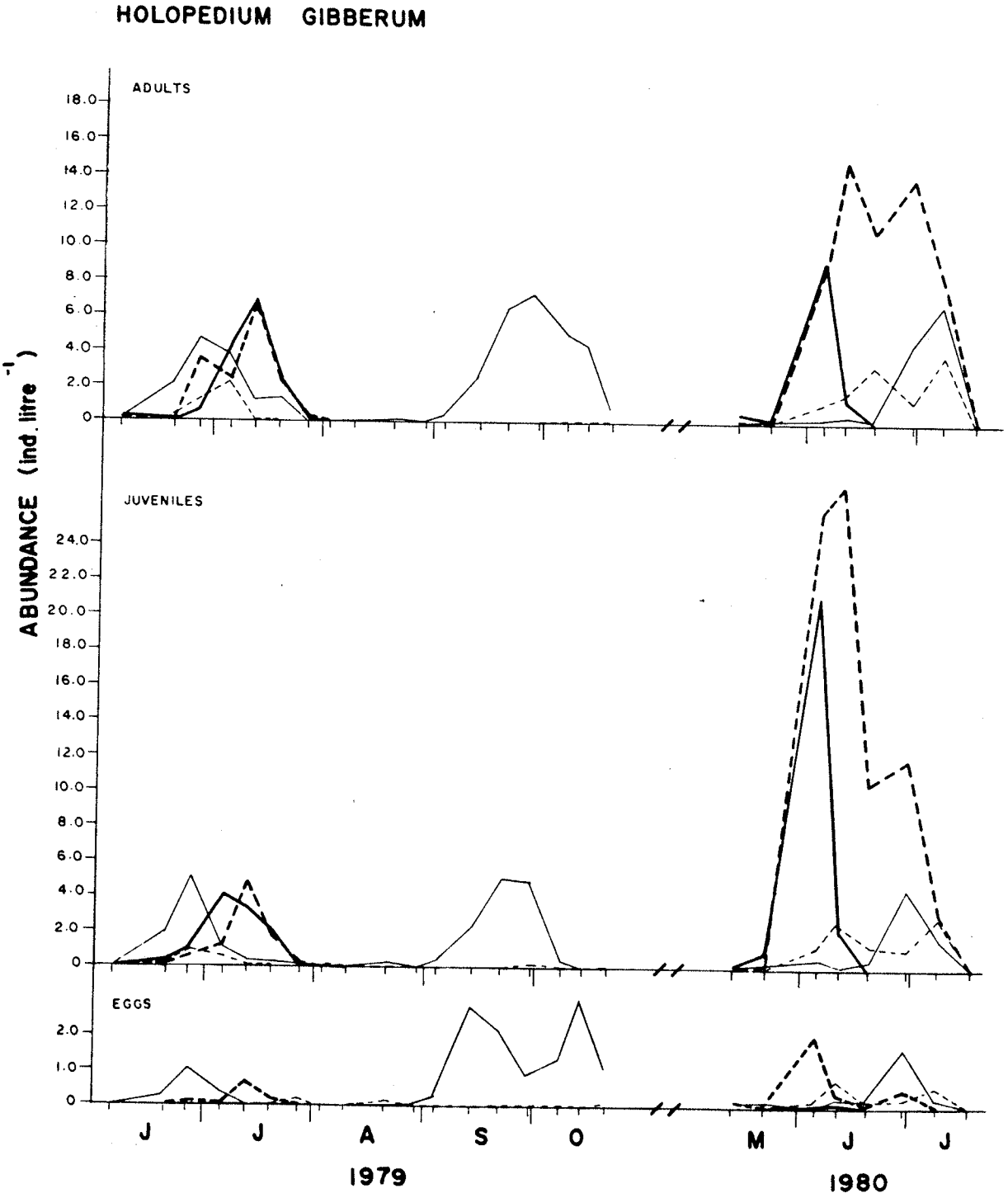
were reiterated in the acidified tubes (Fig. 38). With the better replication of the control populations in this year, some direct but minor responses of B. longirostris to fluctuations of pH became apparent.

Egg counts for the four populations were comparable through the period of study (Fig. 38). The first pulses peaked at the same time in the acid tubes as in the controls and, at the peak, juvenile abundances were intermediate to those in the controls (Fig. 38). Survival to the adult stage appeared to be much higher in the acid tubes, however, with adult abundance in both A1 and A2 peaking at more than twice the control value (Fig. 38). This greater survival coincided with the first forest fire and the associated suspension of acidification.

Unlike other species, the different pH regimes maintained in A1 and A2 during June did not effect marked differences in abundance, with numbers in both tubes gradually decreasing through the month (Fig. 38). The second pulses developed in the first half of July, somewhat later than in the controls and earlier in A2 than in A1 (Fig. 38). This earlier appearance in A2 coincided with the second fire and the associated excursion of pH above 5.0 while the pH in A1 remained below 5.0. Sampling was terminated before these pulses were completed.

Just as was the case for H. gibberum abundance, the population dynamics of this species weren't altered by acidification in 1979 (Fig. 39). The populations in A1 and A2

Figure 39. Seasonal variation of the abundance of Holopedium gibberum life stages in Ctrl 1 (————), Ctrl 2 (– – – – – –), A1 (▬▬▬▬), and A2 (▬ ▬ ▬ ▬) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.


HOLOPEDIUM GIBBERUM
ADULTS
JUVENILES
EGGS
ABUNDANCE (ind. litre -1)
18.0
16.0
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0
24.0
22.0
20.0
18.0
16.0
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0
2.0
1.0
0
J
J
A
S
O
M
J
J
1979
1980

replicated well and supported early summer pulses which occurred at the same time as in Ctrl 2 but which were comparable in size to that in Ctrl 1 (Fig. 39). Also as in Ctrl 2, no autumn pulse was produced in either of the acidified tubes and the populations persisted at very low levels from the end of July through to the termination of sampling (Fig. 39). There was however, some evidence of reproductive impairment. No gravid females and no loose eggs were ever observed in samples from A1 and none was seen in samples from A2 after July 19 (Fig. 39). Although counts were low, eggs were frequently observed in the samples from Ctrl 2 through to the end of sampling (Fig. 39). The period of July in which the small pulse of eggs appeared in A2 (Fig. 39) was also the period in which the pH in A2 was above 5.0 while the pH in A1 was below 5.0 (Fig. 7).

The increases of H. gibberum abundance recorded in the acidified tubes in 1980 developed during the fire evacuations when acidifcation was suspended (Fig. 39). On June 5, immediately following the first fire, juvenile abundances in A1 and A2 were 15-20 times higher and adult abundances were about 9 times higher than in the controls (Fig. 39). The mechanism of these increases again cannot be described in the absence of documentation during the preceding two weeks. These reponses do, however, demonstrate that the species was under some stress at depressed pH. Up to June 5, there was no difference in abundance between A1 and A2, although egg counts were substantially higher in A2, as in 1979 (Fig. 39).

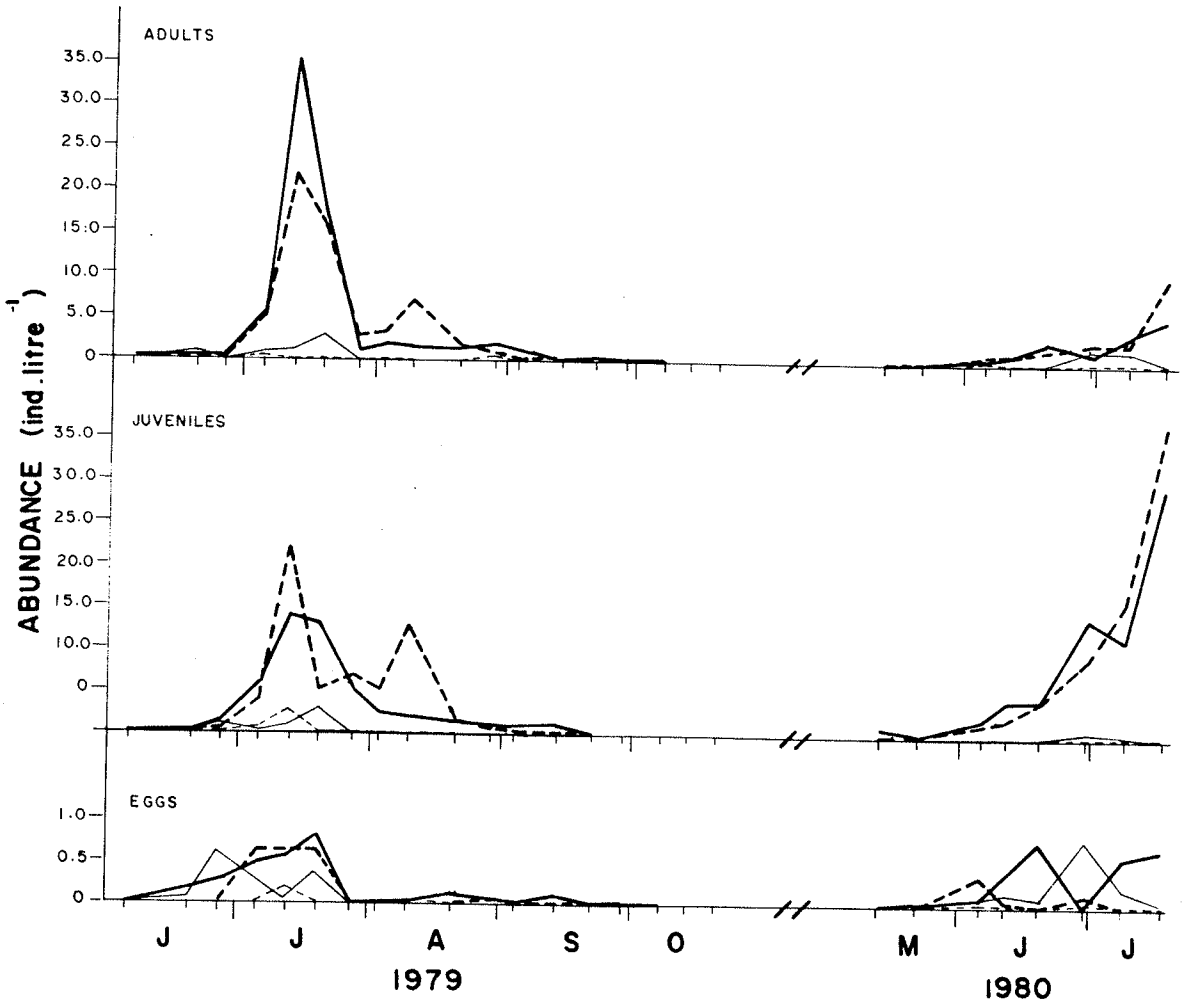
The different levels of H. gibberum abundance in A1 and A2 developed in the period between the fires; when the pH in A1 was generally below 5.0 and the pH in A2 was generally above 5.0. With the reduction of pH in A1 to 4.8 between June 5 and 11, abundance returned to control levels (Fig. 39).The pH was reduced to 4.6 between June 11 and 19 and the population had disappeared by the end of this period (Fig. 39). With the pH in A2 above 5.0 between June 5 and 11, juvenile abundance remained high and adult numbers continued to increase (Fig. 39).

Subsequent fluctuations of Holopedium abundance in A2 appeared to coincide with the excursions of pH above and below 5.0 (Fig. 7 and 39). However, these were also coincident with the second pulses in the control tubes (Fig. 39). Consequently, any pH effect is indistinguishable from normal population development.

The dramatic and well replicated increases of D. brachyurum abundance in the acidified tubes developed without great alterations to the species' seasonal dynamics (Fig. 40). In 1979, abundance began to increase at the same time as in Ctrl 2 and reached peak numbers at the same time, July 12 (Fig. 40). Abundance first exceeded that in the controls in the second week of pH reduction, and was 6-8 times the control level at the peak (Fig. 40). This increase appears to have initially been the product of increased survival since egg numbers weren't greatly larger than in Ctrl 1 until the peak was attained (Fig. 40). Recruitment fell off immediately

Figure 40. Seasonal variation of the abundance of Diaphanosoma brachyurum life stages in Ctrl 1 (————), Ctrl 2 (– – – – – –), A1 (▬▬▬▬), and A2 (▬ ▬ ▬ ▬) between June 5 and October 20, 1979 and between May 12 and July 17, 1980.

DIAPHANOSOMA BRACHYURUM



after the peak and abundance fell sharply through the second half of the month. Through August, abundance in A1 remained at or near the peak levels attained in the controls (Fig. 40). A small second pulse developed in A2 in early August, with similar levels of abundance in both acid tubes during the second half of the month (Fig. 40). Diaphanosoma abundance finally returned to control levels in mid-September, with no juveniles observed and with adults numbering fewer than 0.4 ind L^{-1} after September 13 (Fig. 40).

In 1980, there were no differences between the populations in the acid tubes related to the differing pH regimes. Abundance increased continually from May 21 to the end of sampling (Fig. 40). By July 17, juvenile abundance was over 40 times the peak control abundance and adults were 5-10 times more numerous and clearly not yet at the peak (Fig. 40). Again greater survival is implicated since egg counts didn't exceed those in Ctrl 1 for most of the period (Fig. 40).

Discussion

Effects of enclosure

The major effect of enclosure on crustacean plankton appears to be quantitative. Total community abundance in the enclosures was significantly increased in both seasons of study (Fig. 14) and averaged twice that in the lake from June

through October in 1979 (Fig. 15). This was the product of increases in the abundance of most of the numerically important species (Tables 9 and 11). No species was less abundant in the enclosures than in the lake. Because all species did not increase by the same proportion, there were minor alterations of community structure as well. This was indicated by slightly lower percentage similarity of community (PSC) values in both years (Fig. 20). In general, the control enclosures and the lake shared the same community dominants but with different relative abundances (Tables 9 and 11). The effect of enclosure was also relatively constant. For almost all of the major species, the increases of abundance in the second season were about the same as or slightly smaller than in the comparable period of the first year (Table 12). Similarly, the effect of enclosure on community structure in 1980 was no greater than in 1979 (Fig. 20).

Crustacean plankton community quality was generally not affected by enclosure. Community diversity in the enclosures, as measured by the number of species per sample, was not significantly different from that in the lake (Fig. 13). Community composition, as measured by the coefficient of community, was marginally affected by enclosure in the first season of study (Fig. 12). This was not due to the appearance or elimination of species but was the result of alterations in the frequencies of occurrence of several species of minor numerical importance (Fig. 11). Smyly (1976, 1978) and

Sprules (1980) also found that the effects of enclosure were primarily quantitative in a long-term examination of enclosure effects conducted in the large Lund tubes (Lund 1972; Lack and Lund 1974).

The influence of enclosure crossed taxonomic lines. D. minutus, T. p. mexicanus, B. longirostris, and H. gibberum responded most consistently with abundance elevated in both enclosures in both seasons of study (Tables 9 and 11). M. edax and D. brachyurum abundance also increased in the enclosures, but less consistently.

Among the copepods, the greater abundance in the tubes was the product of the more successful development of one (D. minutus) or more (T. p. mexicanus and M. edax) cohorts with no effect on the species' seasonal dynamics (Fig. 23, 25, and 27). For D. minutus, the greater abundance in the enclosures was the result of an almost instantaneous reduction in the lake population at the transition between the naupliar and copepodid stages (Fig. 23). The increased abundance of both T. p. mexicanus and M. edax copepodids could be traced to higher numbers of cyclopoid nauplii (Fig. 26). There was no increase in the standing stock of Tropocyclops eggs to account for the increases (Fig. 25) which implicates higher nauplius survival as the cause.

Among the cladocerans, the increased abundance was as much a product of alterations in the species' life histories as it was the greater success of a particular population pulse. B. longirostris was tricyclic in the enclosures but

dicyclic in the lake with much of the increased abundance occurring in the extra population pulse (Fig. 29). D. brachyurum was acyclic in the lake but distinctly monocyclic in the enclosures and all of the increase of abundance was accounted for in the pulse (Fig. 31). Also acyclic in the lake, Holopedium was dicyclic in Ctrl 1 and monocyclic in Ctrl 2 (Fig. 30). Just as for the copepods, these changes were not related to increased reproduction. The standing stocks of eggs were often higher in the tubes but were still generally in proportion to the abundance of adults. This again implicates some increase in survival as the cause. The increases of crustacean abundance in the Lund tubes reported by Smyly (1976, 1978) also were not due to increases in the egg stocks.

There are several possible mechanisms by which enclosure could have effected the increases recorded in this study. It is well known that, in the installation of enclosures, important vertebrate and invertebrate predators may be selectively included (Sprules 1980; Salki et al. 1984) or excluded (Smyly 1976, 1978; Sprules 1980; Kerfoot and DeMott 1980) either by chance or by design. Fish were intentionally removed from the enclosures but few were captured for the large fishing effort employed (Table 4). This would in turn suggest that fish were excluded from the enclosures during installation. However, based on the size and species of crustaceans which increased in the enclosures, the removal and/or exclusion of fish had at most a minor effect. The

selectivity of piscine planktivores for larger species of Daphnia and calanoid copepods is well documented (Hrbáček 1962; Brooks and Dodson 1965; Galbraith 1967; Hall et al. 1970), yet the species which displayed the strongest responses to enclosure (Diaptomus, Tropocyclops and Bosmina) are small and not particularly vulnerable to predation by fish (Taylor 1980, Drenner and McComas 1980). As larger species, the increased abundance of Holopedium and Diaphanosoma may have been the result of fish exclusion. Langford (1938) found ciscoes selected Holopedium over all other species in Lake Nipissing. Both species were actively selected at times by yellow perch in enclosure experiments conducted at Southern Indian Lake (D.Ramsey, unpublished data).

The increased abundance of small species in the enclosures is more indicative of an exclusion of predatory invertebrates (Dodson 1974). The major increases in abundance of several species developed in a narrow span of time. In 1979, D. minutus, T. p. mexicanus, B. longirostris and the cyclopoid nauplii were all more abundant than in the lake within 1 to 5 weeks of enclosure (Fig. 23, 25, 26, and 29). The elevated numbers of D. minutus, B. longirostris, and T. p. mexicanus all appeared between the end of May and mid-June in 1980. In all cases, the increases developed in the tubes at about the same time as substantial pulses of Leptodora kindtii appeared in the lake but not in either of the control enclosures (Fig. 24). L. kindtii can be an important predator

on other planktonic crustaceans and has been implicated in the control of a variety of species (Cummins et al. 1969; Wright 1965; Hall 1964). Salki et al. (1984) found that B. longirostris was never abundant (< 1.0 ind L^{-1}) when Leptodora exceeded 0.1 ind L^{-1}. The magnitude of the reductions effected were also comparable to the increases of Bosmina which developed in the absence of Leptodora in this study. There also was evidence that Leptodora had an effect on Tropocyclops (Salki et al. 1984).

The exclusion of Leptodora does not provide a complete explanation of the increased crustacean abundance in the enclosures, however. The pulse appeared too late in 1979 to be fully responsible for the higher D. minutus counts (Fig. 23). The pulse of Leptodora also did not persist long enough to be responsible for the greater success of the fourth T. p. mexicanus cohort in that year (Fig. 25).

Another predatory invertebrate, Chaoborus spp., may have been excluded from the enclosures as well. This organism is known to occur in the lake (Hamilton 1971) and occasionally appeared in the lake samples from early August on, in 1979. These occurrences generally amounted to about 1 individual in a sample of 30-40 litres. This is most probabaly a considerable underestimate of abundance, given the location at which the samples were collected in the lake (Fig. 2a), the very small mouth area of the sampler (38 cm^2), that the samples were collected during the day, and that the species is considered to prefer the benthos or deeper hypolimnetic

waters by day (Berg 1937; Roth 1968; Stahl 1966; Carter and Kwik 1977). With this behaviour, Chaoborus spp. could quite easily have not been included in the tubes when filled. The ability of this organism to affect zooplankton abundance is well known (Dodson 1974; Anderson and Raasveldt 1974).

Finally, the greater abundance of zooplankton in the enclosures may not have been a result of disruptions of biotic interactions at all. With the enclosures located in the littoral zone, the lake samples were collected from a region of comparable depth (Fig. 2a). For these samples to be indicative of enclosure effects, it must be assumed that there is little or no net immigration or emigration of the various species into or from the littoral zone. This is a rather difficult assumption to investigate and its validity was not examined in this study.

One phenomenon which may invalidate this assumption is "Uferflucht"; avoidance of shore (Hutchinson 1967; Siebeck 1980). This is an active avoidance of the shore zone, the mechanism of which is described by Siebeck (1980). Evidence for the occurrence of this phenomenon is rather weak. Burckhardt (1910) found planktonic Cladocera were virtually absent from the littoral region of Lago Lugano and that there were fewer copepods there as well. Lindstrom (1952) found fewer adult Arctodiaptomus laticeps inshore but the effect was not statistically significant. On occasion, all stages of Cyclops scutifer were less abundant in shallow water but at other times abundance was much greater than in the limnetic

zone. No avoidance of shore by Cladocera was recorded. In neither of these studies were other causes of these distributions (eg. predation) considered. Pennak (in Hutchinson 1967) has found no cases of shore avoidance. Salki (1981) found that there may be more or less plankton inshore than offshore depending on the abudance of macrophytes, the intensity of fish predation, and the development of hypolimnetic anoxia.

Shore avoidance was probably not important in the increases of most of the species in this study. B. longirostris and D. brachyurum, if not littoral species, are both commonly found in the littoral of lakes (Hutchinson 1967) which would indicate that they don't actively avoid shore. For both M. edax and T. p. mexicanus there was some evidence of greater cohort success at the nauplius level (Fig. 26) and this was sufficient to account for the higher numbers in the enclosures. Shore avoidance requires the ability of active movement, of which nauplii are probably less, if at all, capable (Hutchinson 1967).

"Uferflucht" could explain the greater abundance of D. minutus in the enclosures which developed between the N4-6 and C1-3 stage-classes in 1979 and between the C1-3 and C4-5 stage-classes in 1980 (Fig. 23). The C1-3 class is probably the first in which the behaviour could occur in this species, with the higher numbers in the tubes perhaps the result of their restriction from emigration. This provides a reasonable explaination for the almost instantaneous disappearance of

the species in the lake in both years. However, it is unclear why the behaviour should be manifested in different stage-classes in two successive years.

Shore avoidance also cannot be eliminated as a cause of the increased H. gibberum abundance in the tubes (Fig. 30).

Although this study was neither designed nor intended to determine the mechanism of the "enclosure effect", the results indicate that the disruption of biotic interactions, and specifically the exclusion of invertebrate predation, was important in effecting the increased zooplankton abundance in the enclosures. This is much the same conclusion as reached by Smyly (1976, 1978), Sprules (1980), and Salki et al. (1984). This result also reinforces the conclusion of Zaret (1980), that predation is one of the most important regulatory forces in aquatic ecosystems.

Another factor, restriction of dispersion by enclosure, also seemed to be important in causing apparent increases in the abundance of some species in the tubes. The use of enclosures may also permit examination of behaviours such as "Uferflucht" for which documentary support to date is weak.

Replicability

One of the major advantages of using enclosures is the possibility of replicating control and experimental units. This both permits statistical testing and reduces the effects of random variation to increase the precision of whatever is being estimated. However, replicates are seldom used in

practice (for a review see Hurlbert 1984). If employed, the results are generally used to justify their elimination from subsequent trials (Takahashi et al. 1975; Menzel 1977). Consequently, the degree of variation to be expected among experimental units and, therefore, the number of replicates required to detect an effect at the desired level of significance, is unknown. The degree to which enclosures may reduce temporal or geographic variability also has not been established.

In this study, the variability of seasonal mean community abundance between the control enclosures was fairly low, with a coefficient of variation of about 11% in the two seasons (Tables 9 and 11). Among the individual species, the intertube variability of D. minutus, T. p. mexicanus, and C. b. thomasi was consistently low, with seasonal mean abundance in each tube within 1-9% of the between tube mean in both years (Tables 9 and 11). In contrast, the intertube variability of B. longirostris was consistently high, ranging from 35-46% of the between tube mean (Tables 9 and 11). The intertube variation of H. gibberum, D. brachyurum, and M. edax abundance differed considerably between the years (Tables 9 and 11). For example, D. brachyurum abundance in each tube ranged from as little as 2% (1979) to as much as 53% (1980) of the between tube mean (Tables 9 and 11).

While some of these coefficients of variation may seem high, they must be viewed in perspective to what can be expected among lakes or within a lake from year to year.

Smyly (1972) found that mean annual abundance of the major species in Esthwaite Water commonly differed by a factor of 2 to 30 from year to year. Yan and Strus (1980) found that mean ice-free season biomass differed by as much as a factor of 2.5, with a coefficient of variation of 30%, among seven Muskoka-Haliburton lakes. In the same study, the coefficient of variation of mean community abundance in Clearwater Lake over 6 years was 48%. The coefficient of variation of mean annual community abundance in four man-made lakes in southern Manitoba was even higher, at 70% (Loadman 1980).

Although these are rough comparisons it is clear that the degree of variation between enclosures is much lower than both the geographic variation among closely located lakes and the temporal variation in year to year comparisons in a given lake. For total community abundance, variation is reduced by a factor of 2-7, while, for paricular species, the reduction may be a factor of 2-30. If more replicate enclosures were used in this study, this difference would probably be much higher. It is also apparent that the number of replicates required in an experiment will very much depend on the species to be considered. With little variation between tubes or years, very precise estimates of treatment effects may be attained for community abundance, D. minutus, T. p. mexicanus, or C. b. thomasi with just two-fold replication. For cladocerans, this level of replication would only permit the detection of catastrophic changes. The degree to which the variability of cladocerans can be reduced by increasing

the number of replicate experimental units remains to be determined.

A high similarity of community composition among the experimental units, as measured by the coefficient of community (CC), is attainable with the use of enclosures. In this study, the CC averaged 71.9% between Ctrl 1 and Ctrl 2 in 1979 (Fig. 10). Patalas (1971) compared the communities in 45 lakes in northwestern Ontario using the same measure. Among the 968 lake-pairs considered, only 17 (1.8%) had CC values of 70% or greater. This measure can also be used to scale the effects of enclosure observed in this study. The CC averaged 63.9% between the lake and Ctrl 1 and 62.1% between the lake and Ctrl 2 in 1979 (Fig. 10). Only 38 (3.9%) of the lake-pairs compared by Patalas (1971) had CC values of 60% or greater.

Enlcosures clearly provide a means of substantially reducing the variability of experimental units in limnological field studies. While previously considered suitable only for the examination of catastrophic effects (Steele 1979), the advantages of replication, if consistently applied, should make enclosures useful for the study of more subtle responses as well.

Acidification effects

Responses of the species

Acidification differentially affected the copepods in this experiment. There were substantial reductions in

abundance and/or alterations in the seasonal dynamics of Diaptomus minutus, Epischura lacustris, Tropocyclops prasinus mexicanus, Mesocyclops edax, Cyclops bicuspidatus thomasi, Acanthocyclops vernalis, and Eucyclops agilis when exposed to reduced pH (Tables 11 and 13 to 16; Fig. 33 to 37). The only copepod not affected was Macrocyclops albidus (Table 15).

With just a single level of acidification in this experiment, averaging about 4.8 in 1979, and the rapid depression of the pH to that level (Fig. 7), it is not possible to precisely identify the pH at which these effects occurred for most species. However, the fluctuations of pH which resulted from the two suspensions of the acidification schedule by forest fires in 1980 (Fig. 7) permitted a determination of the critical pH for D. minutus and T. p. mexicanus. For D. minutus, the abundance of all copepodid stages dropped sharply when the pH was reduced below 5.0, but the population could increase in size at or above pH 5.2 (Fig. 33). Similarly, there was serious mortality of all but the adult stage-class of T. p. mexicanus below pH 5.0 in the second study season (Fig. 34).

Superficially, all cladocerans appeared to be unaffected by the pH reductions imposed (Tables 11 and 13 to 16; Fig. 38 to 40). Substantial increases in the abundance of Diaphanosoma brachyurum, Holopedium gibberum, and Ophryoxus gracilis were recorded in one or both seasons of study. No cladoceran was significantly less abundant in the acid tubes than in the controls.

This general tolerance of the Cladocera was expected. None of the species included in the enclosed communities has a demonstrated sensitivity to the level of acidification applied (Sprules 1975; Roff and Kwiatkowski 1977; Confer et al. 1980). All of the species attaining dominant status (B. longirostris, H. gibberum, D. brachyurum), or their congeners, are common community constituents in culturally acidified lakes both in Scandinavia (Almer et al. 1974; Hendrey and Wright 1976) and North America (Sprules 1975; Roff and Kwiatkowski 1977; Confer et al. 1983; Crisman et al. 1980). This tolerance of acidification does not apply to all cladoceran species, however. Many daphnids are quite sensitive to depressions of pH below 6.0, as is Leptodora kindtii (Almer et al. 1974; Sprules 1975). Both taxa were effectively excluded from the enclosed communities in this experiment (Tables 11 and 13).

With one exception, the declines of the major copepod species in the acidified enclosures also occurred as would be predicted on the basis of their patterns of distribution with pH in acid-affected regions. Cyclopoid copepods are universally sensitive to acidification with much reduced relative abundance at pH below 5.0 both in Scandinavia (Hendrey and Wright 1976; Raddum et al. 1980) and in North America (Sprules 1975; Roff and Kwiatkowski 1977; Confer et al. 1983). Neither M. edax nor C. b. thomasi seems to be eliminated by acidification but the abundance and frequency of occurrence of each is greatly reduced below pH 5.0

(Sprules 1975; Roff and Kwiatkowski 1977; Confer et al. 1983) much as in this study.

T. p. mexicanus is considered to be the most acid-sensitive of the cyclopoid species which commonly occur in northeastern North America. This species is absent from lakes at or below pH 5.2 in the La Cloche and Adirondack regions (Sprules 1975; Roff and Kwiatkowski 1977; Confer et al. 1983) and is absent from Georgian Bay ponds below pH 6.0 (Carter 1971). Tropocyclops was certainly affected by pH below 5.0 in this study and the experiment was probably just of too short duration for elimination (Fig. 33).

E. lacustris is also considered to be quite sensitive to reduced pH. The species is absent below pH 5.5-6.0 in the La Cloche lakes (Sprules 1975; Roff and Kwiatkowki 1977), below 5.6 in the Georgian Bay ponds (Carter 1971), below 5.3 in the Adirondack region (Confer et al. 1983), and disappeared from L223 in ELA when the pH dropped below 6.08 (Malley et al. 1982). Epischura disappeared prematurely when exposed to reduced pH in this study (Fig. 7 and 11).

The response which was not in accord with the results of previous regional surveys was the decline of D. minutus. This species is generally considered to be the most acid-tolerant crustacean zooplankter in northeastern North America (Sprules 1975; Roff and Kwiatkowski 1977; Confer et al. 1983). That Lawrence (1980) also found greatly reduced D. minutus abundance at pH 4.0 and 5.0 in an enclosure experiment conducted in lake 223 (L223) at ELA immediately suggests that

the apparently acquired sensitivity to acidification could be an artefact of the utilization of enclosures. However, that Carter (1971) found D. minutus to be intolerant of pH below 6.0 in a series of dystrophic ponds on the shore of Georgian Bay prompted closer scrutiny.

Comparing all studies concerning D. minutus and reduced pH, the acid-tolerance of this species appears to be dependent on lake basin geology and/or on maximum lake depth, with the presence or absence of thermal stratification in summer the most likely functional correlate of basin depth. Of the 32 Georgian Bay ponds examined by Carter (1971), 24 had a maximum depth of less than 2.5m, the maximum depth of the enclosures used here and by Lawrence (1980). None of the ponds stratified in summer, neither did the L223 enclosures, nor did the enclosures in this study. All of the Georgian Bay ponds are in granite basins as are both L223 and L302. Conversely, only 2 of the LaCloche lakes studied by Sprules (1975) have maximum depths of less than 6.0m and the bedrock of all but two of the lake basins is quartzite. One of these lakes, Little Sheguindah, with a granite basin, maximum depth of 2.7m, and pH 5.0, has D. reighardi replacing D. minutus just as in the Georgian Bay ponds (Carter 1971). In the other shallow LaCloche lake, Freeland, with maximum depth of 1.8m, pH 4.2, and a quartzite basin, D. minutus accounted for just 4% of zooplankton abundance. This is comparable to the relative abundance of D. minutus maintained at pH 4.8 in the present study (Table 14). Among the other 24 LaCloche lakes

studied by Sprules (1975), all at or below pH 5.0, all in quartzite basins, and all with maximum depth of at least 8.0m, D. minutus was the predominant and often the only crustacean zooplankter collected. All 6 of the LaCloche lakes studied by Roff and Kwiatkowski (1977) also have maximum depths of at least 11.0m, with the deepest lakes also the most acidic; all are in quartzite basins; all thermally stratify in summer; and D. minutus dominated the acidic lakes. Similarly, all 20 of the lakes in the White Mountains of New Hampshire and the Adirondack Mountains of New York surveyed by Confer et al. (1983) were stratified in summer, although some of the lakes were between 3.0 and 6.0m deep, and the acid lakes were dominated by D. minutus. No description of watershed geology was provided by Confer et al. (1983).

Consequently, the response of D. minutus to acidification in this experiment can be considered as consistent with the behaviour of this species in lakes. While the relative importance of basin geology and thermal stratification to the acid-tolerance of D. minutus cannot be determined from the studies completed to date, neither can be eliminated on theoretical grounds. The occurrence of stratification may permit the development of some sort of higher pH refugium. Under anoxic conditions, which can develop in the hypolimnion of a stratified lake, reduction processes such as denitrification (NRCC 1981) or sulfate

reduction (Nriagu and Hem 1978) can produce alkalinity which in turn can raise the pH of the hypolimnion. Alternatively, the pH tolerance of D. minutus may be temperature dependent, although the relationship has yet to be examined for any crustacean.

Watershed geology determines the ionic content of lakewater through its composition and, therefore, its ease of weathering (NRCC 1981). Given that failure of ionic regulation is a potential cause of pH toxicity (Potts and Fryer 1979), a greater supply of essential ions could be important to D. minutus survival under acidic conditions. Ca^{++} concentrations in the LaCloche lakes are about 25% higher than in ELA lakes (NRCC 1981). No studies on the effect of increased ion supply on pH toxicity have been conducted.

It may be possible to eliminate one of these factors in a series of enclosure experiments. The importance of stratification could be determined by using deep and shallow enclosures. The influence of geology could be examined by repeating the experiment in the La Cloche region.

The major difference between the acidified enclosures studied in this experiment and culturally acidified lakes in general is the time scale of the pH reductions to which each is exposed. It may take 15-30+ years for the pH of a lake to be reduced to 4.8 by atmospheric deposition (NRCC 1981). This level was reached in the enclosures within two weeks (Fig. 7). As such, there was the potential for some species to

respond differently in the enclosures than has been observed in acid-affected lakes. However, after examination of the effects, it appears that the acidification regime applied did not induce any unusual responses.

Effects on community abundance

A number of previous investigations have implicated acidification in the reduction of zooplankton standing stocks. However, there is little agreement among these studies regarding the extent of this effect. Much of this disagreement may be the result of using invalid controls. Roff and Kwiatkowski (1977) found lower maximum community abundance in two La Cloche lakes below pH 5.0. This finding was based on samples collected during June and August of one year and during May and July of the subsequent year, with reduced numbers of cladocerans and cyclopoids responsible. Zooplankton abundance was strongly correlated with chlorophyll a concentration in these lakes which also decreased with pH. However, the lower chlorophyll a concentrations may not have been due to acidification. Therefore the lower standing stocks of zooplankton also may not be acid related.

Depending on the investigator and/or the year of study, community biomass in Cheat Lake, Virginia either has not been affected (DeCosta and Janicki 1978) or has been significantly reduced by acidification (Bible 1972). In these studies, abundance in the more acid main body of the reservoir was

compared with that in a shallow less-acid backwater on the assumption of previously similar abundance. Yan and Strus (1981) found that mean ice-free season community biomass in acid and metal contaminated Clearwater Lake, Ontario, was less than half the mean biomass in six non-acidic lakes in the Muskoka-Haliburton region of Ontario. Here, six years of data from Clearwater Lake were compared with one year of data from the control lakes. Carter (1971) found no relationship between pH to 4.7 and zooplankton standing crop in the Georgian Bay ponds. In an enclosure experiment conducted in L223 at ELA, Lawrence (1980) found no marked reduction of zooplankton community biomass with acidification to pH 4.0 nor with acidification to pH 4.0 of an enclosure to which 30 ug Cd L^{-1} was added in the previous year. Acidification of one enclosure to pH 5.0 produced a 60% reduction of community biomass but no reduction was observed when an enclosure to which 30 ug Cd L^{-1} was added in the previous year was acidified to pH 5.0 (S.Lawrence, Freshwater Institute, pers. comm.).

Given the substantial reductions of D. minutus, M. edax, and C. b. thomasi recorded in 1979, it is not surprising that total zooplankton community abundance and biomass were both significantly reduced with acidification below pH 5.0 in this experiment (Fig. 17). The reduction appeared greater in A1 than in A2, but this difference can largely be attributed to different initial levels of T. p. mexicanus abundance (Table 5) which were probably unrelated to acidification. In this

year, total community abundance and biomass were an average of 50 and 69%, respectively, of control values. The reduction of abundance was greater than for biomass because D. brachyurum abundance increased in the acid tubes (Fig. 40). The large body size of this species more than compensated for the reduced abundance of calanoid and cyclopoid nauplii in the biomass figures. Only A1 was acidified below pH 5.0 for an extended period in 1980, with abundance and biomass also significantly reduced in that tube only.

The results of this study would appear to contradict those of Lawrence (1980). The reason for this discrepancy may lie in the longer duration of the present study. The reductions of community abundance did not become apparent in this experiment until early to mid August, 4 (A1) to 6 (A2) weeks after the target pH had been reached (Fig. 18). Lawrence did not commence work until mid-July and the target pH levels were not attained until the end of July (pH 4.0) or early August (pH 5.0). Sampling was terminated in early October. Based on the present study, an effect could not have been expected until early to mid-September and, with samples collected at bimonthly intervals, only two samples were taken between this time and the end of the study. As a result, an acidification related reduction could have gone undetected.

The magnitude of the reductions recorded in this study should be considered as minima for extrapolation to acidic lakes in which D. minutus is affected. This is largely because the reductions of the various species were not

immediate, taking from two weeks to the full season to occur. By treating these reductions as if they occurred immediately, as they would be observed in a lake which has been acidic for some time, 50-60% reductions of abundance and 40-50% reductions of biomass, comparable to those reported by Yan and Strus (1980), could be expected at a pH of about 4.8.

Effects on seasonal dynamics of tolerant species

The seasonal succession of zooplankton in acidic lakes has been little studied. Moreover, those lakes in which life histories have been examined, metal contaminated Clearwater Lake, Ontario, and acid mine drainage Cheat Lake, Virginia, are not at all representative of the majority of acidified lakes. B. longirostris dominates the communities of both lakes and is usually monocyclic (Yan and Strus 1980; DeCosta and Janicki 1978). In contrast, the species is usually dicyclic in non-acidic Ontario lakes (Schindler and Noven 1971; Haney 1973). In both cases, cyclopoid copepod predation, by M. edax in Cheat Lake and by C. vernalis in Clearwater Lake, appeared to control the occurrence of Bosmina. In this study, B. longirostris dynamics were unaffected by acidification and followed a similar three pulse pattern of occurrence in all four enclosures in 1979 (Fig. 38). Variability of pulse size and timing between the acid and control populations was indistinguishable from variation between the controls. There also was no effect of the much reduced abundance of M. edax (Fig. 35) in 1980 on

the timing of Bosmina pulses.

Similarly, the dynamics of D. brachyurum were unaffected by acidification (Fig. 40). Despite the much greater abundance in the acid tubes, the species was primarily monocyclic with peak abundance in mid-July in all four enclosures. This pattern of seasonal occurrence appears to be typical for the species (Schindler and Noven 1971; Hutchinson 1967).

Causes of the reductions of abundance

From the results of field surveys and laboratory experiments, several mechanisms have been proposed to explain the reduction or elimination of species accompanying acidification. However, in the absence of documentation on the mode of decline of any species in the field, an assessment of the relative importance of these mechanisms has not been possible to date. In this experiment, the compressed time-scale of the acidification enabled description of the declines of several species. As a result, these suggested mechanisms can be evaluated.

For herbivorous species, reduced food availability has been implicated, given that reductions of primary productivity, chlorophyll a concentrations (Kwiatkowski and Roff 1977), and community diversity (Kwiatkowski and Roff 1976, Johnson et al. 1970, Almer et al. 1978, etc.) have been recorded in some acidic lakes. Such a trophic mechanism is an unlikely cause of the reductions of D. minutus, T. p.

mexicanus, or the herbivorous immature stages of M. edax and E. lacustris recorded in this study. Total chlorophyll a concentrations were unaffected by acidification to pH 4.8 although the concentration in the <50 u size-range was marginally reduced (Fig. 8 and 9; Table 2). The responses were also too rapid to be trophically mediated, with the reductions of D. minutus and M. edax and the initial response of T. p. mexicanus occurring before any change of the chlorophyll a size-distribution was evident in 1979.

The lack of an effect of acidification on phytoplankton standing crop in this experiment directly contradicts the results of Kwiatkowski and Roff (1976). It is, however, consistent with the results of more recent studies which indicate that phytoplankton standing crop and productivity are unaffected by reduced pH (Schindler 1980; Almer et al. 1978; Yan et al. 1979). This indicates that the situation Kwiatkowski and Roff have described may be the exception for acidified lakes. As suggested by Schindler (1980), the particular acidic lakes they considered may have always had lower biomass and rates of productivity. This is a possibility which must always be considered in after the fact comparisons but one which is rather difficult to address given the lack of pre-acidification data.

There was also no serious reduction of the food supply available to the predacious life-stages of E. lacustris or M. edax. Although preferring small or immature copedods, both species can survive quite well on small cladocerans (Confer

1971). The levels of Bosmina, Holopedium, and Diaphanosoma abundance in the acid tubes were at or above those in one or both of the control tubes (Fig. 38, 39, and 40) and the reductions of M. edax (Fig. 35) in 1979 and of E. lacustris in 1980 occurred when all of these species were most abundant. Vertebrate and invertebrate predation can also be eliminated as causes of any of the reductions. Fish catches were no higher than in the control tubes and were quite low overall (Table 4). No Leptodora appeared in any of the samples from the acid tubes (Tables 11 and 14).

Avoidance of acidic conditions is a factor which is not generally considered in assessments of the cause of reduced abundance. The reduction of C. b. thomasi abundance in 1979 was the result of an almost complete failure to emerge from diapause in late summer (Fig. 37). Whether this was the result of mortality to the diapaused population or to an attempt to avoid the reduced pH was not determined directly. However, the large numbers of copepodids present in the acid tubes when sampling resumed the following spring may indirectly indicate that their absence the previous year was not a result of mortality.

Some form of physiological stress is an obvious consideration and, by elimination, was the probable cause of the majority of reductions in abundance observed. Laboratory toxicity studies using daphnids as the test organisms have demonstrated that pH toxicity may directly reduce population abundance by reducing survivorship, or indirectly by

inhibiting reproduction (Davis and Ozburn 1969; Parent and Cheetham 1980; Walton et al. 1982). There is some disagreement regarding the relative importance of the two factors. Davis and Ozburn (1969) feel reproductive impairment is the more important while Walton et al. (1982) found reduced survivorship to be the principal variable affected.

The results of this experiment indicate that the level of action is species-specific, at least in the copepods. D. minutus suffered almost complete mortality in all copepodid stage-classes within one week of the pH being reduced below 5.0 (Fig. 32). The immediacy of the response to reduction of the pH below the critical level suggests that the pH toxicity acted in a threshold manner. Walton et al. (1982) found that such a threshold response occurred only when the acute lethal limit of a species was exceeded.

Recruitment failure distinguished the response of M. edax and appeared to be the sole cause of the reduced abundance (Fig. 35). With inadequate sampling of gravid females, it could not be determined if the failure was at the egg level or was the product of early nauplius mortality. Again, the immediate response to pH reduction is indicative of a threshold effect but it could not be precisely determined at what pH the effect occurred.

The stress acted at both levels in T. p. mexicanus although the effects were less immediately evident. There were periodic increases of mortality in both A1 and A2 with the pH maintained below 5.0 in 1979 (Fig. 33). These acted to

upset the population dynamics but, on average, did not effect a significant reduction of abundance relative to that in the controls (Table 14). A recruitment failure occurred in late summer. Egg development was also disrupted, with the uncountable eggs (Fig. 34; Table 22) perhaps indicating a failure to complete egg dormation. This could not be identified as the cause of the disruptions of seasonal dynamics or of the recruitment failure, howeber, because development times weren't measured which precluded an absolute estimation of recruitment.

In the second study season, survival of juvenile copepodids in A1 was impaired below pH 5.0 and this caused the failure of the population in A1 (Fig. 33). The adults in A2 seemed unaffected to about pH 4.7 (Fig. 33). Despite the persistence of adults, egg stocks in A2 were low at pH below 5.2 as a result of fewer gravid females in the population and a high number of uncountable eggs. This, coupled with the sensitivity of juveniles, resulted in the decline of the population in A2 (Fig. 33).

There has been little study of the relative sensitivity of different age-classes of crustaceans but Parent and Cheetham (1980) found greater survival of 7 day-old (d) D. magna than of 4d individuals at pH 5.0. The lack of an immediate response by Tropocyclops to the initial reduction of pH in 1979 indicates that the subsequent responses were the product of chronic exposure to a sublethal level of acidity (Walton et al. 1982).

The mechanism of the effect of low pH is not well known. Failure of ionic regulation is a possibility, given that pH below 5.0 inhibits sodium uptake and increases sodium loss by Daphnia magna (Potts and Fryer 1979). Similarly, sodium uptake by the crayfish Astacus pallipes is reduced below pH 6.0 (Shaw 1960). Fish death in acid water may also be due to a failure of ionic regulation (Leivestad and Muniz 1976; McWilliams and Potts 1978). The degree to which sodium balance is affected by reduced pH appears to be species-specific, with a much greater effect on D. magna than on Acantholeberis curvirostris (Potts and Fryer 1979). This may explain the quite different levels of tolerance displayed by various species. Because of its occurrence in fish (Neville 1979), acid-base imbalance has been suggested as an alternative source of physiological stress in crustaceans (Malley 1980).

Clearly, field experiments designed to examine the life-histories of affected species more closely are required to better identify the most sensitive stages of the various species. These should be followed with laboratory studies to determine the physiological basis of these effects.

Effects on community diversity

The most documented effect of acidification on zooplankton is a reduction of community diversity, as measured by the number of species per sample, below pH 5.0 (Almer et al. 1974; Sprules 1975; Crisman et al. 1980; Raddum

et al. 1980; Confer et al. 1983). In contrast, community diversity was not a particularly sensitive indicator of acidification effects in this study. Unaffected on average in both seasons, the only suggestion of a reduction was in late September and October of 1979 (Fig. 13). Technically, no species were eliminated in this experiment but the truncated periods of species occurrence which were recorded nevertheless functioned as eliminations in the index. These occurred as early as July but did not immediately appear as a reduction of diversity (Fig. 11). This was the result of the more frequent occurrence of O. gracilis, L. setifera, and I. sordidus and the altered periods of A. intermedia and S. crystallina occurrence which effected the increase of community diversity immediately following pH reduction and masked the species truncations until late September. Whether such an increase in diversity actually occurs in acidified lakes is unknown. However, it may be an effect of the compressed time-scale of the acidification, with several species responding at the single pH in this study while each may normally respond at a different level.

Effects on tolerant species

Although the cladocerans as a whole were quite tolerant of acidification to the level applied in this experiment, it does not mean that they were unaffected. B. longirostris abundance and population dynamics were not detectably altered by acidification in the first season of this experiment

(Tables 14 and 16; Fig. 38). If there was no effect on the species at all, then there should not have been a response to the elevations of pH during the second season, but this was not the case. In 1980, the first Bosmina pulses developed during the period of the first suspension of acidification in all four enclosures. The pH in both acid tubes rose above 5.0 (Fig. 7), and adult abundance in the tubes was substantially higher than in the controls when sampling resumed. This appeared to be the result of greater survival in A1 and A2 than in the controls. The second pulses developed in the control tubes at the same time as the second suspension of acidification. During this period, the pH in A1 remained below 5.0 while the pH in A2 rose above 5.0. The second pulse developed in A2 at about the same time as in the controls and much earlier than in A1.

In retrospect, the absence of a response by Bosmina in the first year of study was also indicative of an acidification effect. There were substantial reductions in the abundance of herbivorous copepods, particularly D. minutus (Fig. 32), and more of the food resource should have become available to Bosmina. Had Bosmina not responded to the increases of pH in 1980, then the absence of a response in 1979 would rather have indicated that food was not limiting the species. That Bosmina did respond to the fluctuations of pH in 1980 in the absence of the herbivorous copepods is at least an indirect suggestion of a pH effect. Alternatively, the greater abundance of adults in 1980 could have been a

result of the much reduced abundance of the predatory M. edax (Fig. 35). However, the development of very large numbers of Bosmina in Ctrl 2 (Fig. 38) in the presence of M. edax numbers which were as high or higher than in the acid tubes (Fig. 35) makes this possibility less attractive. Nevertheless, the presence of a second pulse in A2 where the pH was above 5.0 and its considerable delay, if not absence, below pH 5.0 in A1 is still indicative of a pH effect.

Similarly, H. gibberum was tolerant of acidification but did not go unaffected, and this effect was much greater than on Bosmina. Abundance and dynamics weren't notably altered in the first year of study but eggs were generally absent below pH 5.0 (Fig. 39). In 1980, abundances in A1 and A2 were 11 and 31 times that in the controls following the first suspension of acidification. There was no direct evidence of reduced pH affecting the survival of Holopedium adults or juveniles with the two pulse pattern of the control populations maintained in A2. No second pulse was produced in A1 with the pH maintained below 5.0. The absence of a second pulse in A1 would appear to be related to the sensitivity of reproduction that was demonstrated in the first season of the study.

The greater abundance of Holopedium in both A1 and A2 than in the controls following the first hiatus of acidification may again be indicative of an increase in availability of the food resource which in turn could indicate an effect on survival in the first year of the

experiment, as for Bosmina. However, the greater abundance may also have been a result of lower predation pressure due to the decline of M. edax. Neither possibility can be ruled out.

This is not the first report of Holopedium being affected by reduced pH. Roff and Kwiatkowski (1977) found that body weight was significantly reduced at pH 4.4 to 5.0 although no effect on egg production was found. There was also some suggestion of a reduction of body weight in this study. The increases of biomass in the acid tubes in 1980 averaged 80% of the increases of numbers (Table 13) but this is not as large as the 33% reduction found by Roff and Kwiatkowski (1977).

That pH below 5.0 eliminated the Holopedium egg stock in this experiment would appear contradictory to the findings of Roff and Kwiatkowski (1977). If reproduction is sensitive to pH below 5.0, its failure to appear in the LaCloche lakes may be a reflection of the broad range of pH fluctuation which has been recorded in these lakes. Roff and Kwiatkowski (1977) found that modal pH in Ruth and Roy lake was 4.38 but ranged from 4.05 to 4.6. Similarly, modal pH values in Johnie and Carlyle lakes were 4.68 and 5.00 but the ranges were 4.45-4.98 and 4.55-5.65, respectively. Also, less acidic refugia may exist in these lakes as discussed previously. Alternatively, the sampling procedures used in this study may have been inadequate for the retention of Holopedium eggs. However, the samples were narcotized with alcohol before

preservation with formalin to reduce egg expulsion (Gannon and Gannon 1975). Also, the 50 um mesh-size net used to concentrate the samples should have retained at least some eggs if expelled, as it did in the control samples.

Of the three abundant cladocerans in the acidified tubes, D. brachyurum was the only species for which no detrimental effects were detected. Abundance increased in the first year and the increases in the second year were unaltered by the fluctuation of pH and were the same in the two acid tubes despite the different pH regimes.

The increase of D. brachyurum abundance (Fig. 40) following the reduction of D. minutus (Fig. 32) in this study, and the occurrence of its congener D. leuchtenbergianum as a dominant only in the absence of D. minutus in other acidic lakes (Sprules 1975; Confer et al. 1983) provides some evidence of competitive interaction between the species. The mechanism of this interaction may be rooted in the size-ranges of food upon which the two species can feed. Diaphanosoma selects a very narrow range of particle sizes, <10-15 um, while diaptomids are capable of feeding on a broad range (Gliwicz 1977). As a result, Diaphanosoma is much more dependent on food concentration (Weglenska 1971). Consequently, the elimination of D. minutus as the dominant herbivore ammounted to an increase in food concentration thereby enabling increased growth and reproduction.

Importance of metals

Increased concentrations of some metals have been observed to accompany acidification as a result of atmospheric deposition (McFarlane et al. 1979; Franzin et al. 1979; Allen and Steimes 1980), leaching from the watershed (Dickson 1978; Cronan and Schofield 1979), and mobilization from lake sediments (Beamish and Van Loon 1977; Schindler et al. 1980a, 1980b). In general, atmospheric deposition is responsible for elevated concentrations of Cu, Ni, and Cd in lakes proximal to the source, such as near the base metal smelters in Sudbury, Ontario, and Flin Flon, Manitoba (Franzin et al. 1979; Beamish et al. 1975). Watershed leaching is the principle source of aluminum in acidified lakes (Cronan and Schofield 1979) while zinc concentrations are elevated both by direct deposition and watershed leaching (Franzin et al. 1979; Beamish and Van Loon 1977). Lake sediments are the primary source of manganese (Beamish and Van Loon 1977, Schindler et al. 1980?). All of these metals are toxic to zooplankton and the degree of succeptability varies greatly among the species (Baudouin and Scoppa 1974). Yan and Strus (1980) feel the elevated Cu and Ni levels in Clearwater Lake, Ontario, are responsible for the scarcity of D. minutus but these metals had no effect above that of acidification on zooplankton community biomass.

Because only the water and lake sediments were acidified in this study, only manganese levels should have been

elevated. Manganese concentrations in the acidified tubes were approximately 30 times the control concentrations after 10 weeks of acidification to pH 4.8 in 1979 (Table 3). Manganese concentrations were elevated more than 100 fold at pH 5.0 in a previous enclosure acidification experiment in L223 at ELA (Schindler et al. 1980). However, these concentrations are still 1.5 to 2 orders of magnitude below the chronic LC_{50} for Daphnia magna (Biesinger and Christensen 1972). Consequently, metal toxicity was not a factor in this study.

Conclusions

This experiment was conducted in order to provide answers to several questions regarding the effect of acidification on planktonic crustaceans which cannot be addressed by the study of affected lakes due to the lack of pre-acidification data. In order for such studies to have predictive value, however, it must be demonstrated that the experimental method provides an adequate simulation of the problem. In this case, the community structure which evolved in the enclosures following reduction of the pH below 5.0 was the same as that observed in culturally acidified lakes of comparable pH despite the compressed time scale of the experimental acidification. This provides at least partial confirmation of the ability of an enclosure experiment to simulate field conditions. This does not mean that enclosure had no effect on the contained zooplankton communities, only

that the enclosure effect did not interact with the treatment. Given that the major effect of enclosure appears to increased abundance due to exclusion of invertebrate predators, the independence of enclosure and treatment effects in this experiment is perhaps not too surprising. Such independence may not be universal and enclosure effects should always be examined, particularly when there is the potential for disruption of predator-prey interactions.

A very close degree of simulation was acheived in this experiment, as evidenced by the sensitivity of D. minutus and the increase of D. brachyurum to dominant status; responses which appear to be unique to relatively shallow, unstratified lakes in granitic watersheds. As such, the results of the study may only be directly applicable to this type of lake. A more general concept of the way acidification affects planktonic crustaceans could be developed by repeating the experiment using enclosures of sufficient depth for stratification to be maintained and by using both shallow and deep enclosures in different geologic areas. These experiments should be conducted in any event to investigate the dichotomous sensitivity of D. minutus.

On the basis of this experiment, it may be predicted that lakes of the type modeled here will suffer at least a 50% reduction of community abundance following depression of the pH to 4.5-5.0 as a result of the differential effect on the Copepoda. The lakes will probably be dominated by Bosmina and Diaphanosoma. Holopedium may also be important, provided

there are sufficient fluctuations of pH above 5.0 to permit reproduction. Although possibly different from those in other lakes, the seasonal dynamics of the tolerant species will be largely the same as before acidification.

Previous studies have not been able to determine the relative importance of physiological stress or the disruption of trophic interactions to the changes in community structure which accompany acidification. This study indicates that the former was the primary factor in the declines of the major copepod species which, in turn, effected the alteration of structure. There is a clear need for investigation of the mechanism of this pH toxicity, particularly considering that all laboratory studies to date have used cladocerans as the test organisms and that the mode of action appears to be species-specific.

Literature cited

Allan, R.O., and E. Steines. 1980. Contributions from long range transport to heavy metal pollution of surface soil. p.102-103. In D. Drablos and A. Tollan (eds.) Ecological Impact of Acid Precipitation. S.N.S.F. Project, Oslo.

Almer, B., W. Dickson, C. Ekstrom, and E. Hornstrom. 1978. Sulfur pollution and the aquatic ecosystem. p.271-311. In J.O. Nriagu (ed.) Sulfur in the environment: Part II. Ecological Impacts. John Wiley and Sons, New York, N.Y. 482pp.

Almer, B., W. Dickson, C. Ekstrom, E. Hornstrom, and U. Miller. 1974. Effects of acidification on Swedish lakes. Ambio. 3:30-36.

Anderson, R.S., and L.G. Raasveldt. 1974. Gammarus predation and the posible effects of Gammarus and Chaoborus feeding on the zooplankton composition in some small lakes and ponds in Western Canada. Occ. Pap. Can. Wildf. Serv. No. 18:1-24.

Baudoin, M.F., and P. Scoppa. 1974. Acute toxicity of various metals to freshwater zooplankton. Bull. Environ. Contam. Toxicol. 12:745-751.

Beamish, R.J., and H.H. Harvey. 1972. Acidification of the La Cloche Mountain Lakes, Ontario and resulting fish mortalities. J. Fish. Res. Bd. Can. 29:1131-1143.

Beamish, R.J., G.A. McFarlane, J.C. VanLoon, and J. Lichwa. 1975. An examination of the possible effects of Sudbury nickel mining and smelting operations on fishes and the water chemistry of lakes within the Whitefish Lake Indian Reserve. Environment Canada, Fish. Mar. Serv. Tech. Rep. 579:52p.

Beamish, R.J., and J.C. VanLoon. 1977. Precipitation loading of acid and heavy metals to a small acid lake near Sudbury, Ontario. J. Fish. Res. Bd. Can. 34:649-658.

Beers, J.R., M.R. Reeve, and G.D. Grice. 1977. Controlled ecosystem pollution experiment. Effects of mercury on enclosed water columns. IV. Zooplankton population dynamics and production. Mar. Sci. Comm. 3:355-394.

Berg, K. 1937. Contributions to the biology of Corethra Meigen (Chaoborus. Lichtenstein). Biol. Medd. K. Dan. Vidensk. Selsk. 13:1-101.

Bible, J.L. 1972. An analysis of the zooplankton community in an acid polluted reservoir. Proc. W. Va. Acad. Sci. 44:32-39.

Biesinger, K.E., and G.M. Christensen. 1972. Effects of various metals on survival, growth, reproduction and metabolism of Daphnia magna. J. Fish. Res. Bd. Can. 29:1691-1700.

Brooks, J.L. 1959. Cladocera, p.587-656. In W.T. Edmondson (ed.) Freshwater Biology, 2nd ed. John Wiley and Sons, New York, N.Y.

Brooks, J.L., and S.I. Dodson. 1965. Predation, body size, and the composition of plankton. Science. 150:28-35.

Brunskill, G.J., and D.W. Schindler. 1971. Geography and bathymetry of selected lake basins, Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Bd. Can. 28:139-155.

Burckhardt, G. 1910. Hypothesen und Beobachtungen uber die Bedeutung der vertikalen Planktonwanderung. Int. Rev. des. Hydrobiol. Hydrograph. 3:156-172.

Cassie, R.M. 1971. Sampling and statistics, p.174-209. In W.T. Edmondson and G.G. Winberg (eds.). A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters, IBP Handbook No. 17. Blackwell Scientific Publications, Oxford and Edinburgh. 358pp.

Carter, J.C.H. 1971. Distribution and abundance of planktonic crustacea in ponds near Georgian Bay (Ontario, Canada). in relation to hydrography and water chemistry. Arch. Hydrobiol. 68:204-231.

Carter, J.C.H., and J.K. Kwik. 1977. Instar succession, vertical distribution, and interspecific competition among four species of Chaoborus. J. Fish. Res. Bd. Can. 34:113-118.

Cole, G.A. 1955. An ecological study of the macrobenthic fauna of two Minnesota lakes. Am. Midl. Nat. 53:213-230.

Confer, J.L.1971. Intrazooplankton predation by Mesocyclops edax at natural prey densities. Limnol. Oceanogr. 16:663-666.

Confer, J.L., T.Kaaret, and G.E. Likens. 1983. Zooplankton diversity and biomass in recently acidified lakes. Can. J. Fish. Aqat. Sci. 40:36-42.

Conover, W.J. 1971. Practical Nonparametric Statistics. John Wiley and Sons, Toronto.

Conroy, N., K. Hawley, W. Keller, and C. Lafrance. 1975. Influences of the atmosphere on lakes in the Sudbury area. J. Great Lakes Res. Volume 2, Suppl. 1:146-165.

Crisman, T.L., R.L. Schulze, P.L. Brezonik, and S.A. Bloom. 1980. Acid precipitation: the biotic response in Florida lakes. p.296-297. In D. Drablos and A. Tollan (eds.) Ecological Impact of Acdi Precipitation. S.N.S.F. Project, Oslo.

Cronan, C.S., and C.L. Schofield. 1979. Aluminum leaching response to acid precipitation: effects on high-elevation watersheds in the northeast. Science. 204:304-306.

Cruikshank, D.R., J. Penny, and S. Levine. 1983. Construction of large enclosures for experimental studies in lakes. Can. Tech. Rep. Fish. Aquat. Sci. 1210:9p.

Cummins, K.W., R.R. Costa, R.E. Rowe, G.A. Moshiri, R.M. Scanlon, and R.K.Zajdel. 1969. Ecological energetics of a natural population of the predaceous zooplankter Leptodora kindtii Focke (Cladocera). Oikos. 20:189-223.

Davis, P., and G.W. Ozburn. 1969. The pH tolerance of Daphnia pulex (Leydig, emend., Richard). Can. J. Zool. 47:1173-1175.

DeCosta, J. 1975. The crustacean plankton of an acid reservoir. Verh. Internat. Verein. Limnol. 19:1805-1813.

DeCosta, J., and A. Janicki. 1979. Population dynamics and age structure of Bosmina longirostris in an acid water impoundment. Verh. Int. Verein. Limnol. 20:2479-2483.

Dickson, W. 1978. Some effects of the acidification of Swedish lakes. Verh. Int. Verein. Limnol. 20:851-856.

Dodson, S.I. 1970. Complimentary feeding niches sustained by size selective predation. Limnol. Oceanogr. 15:131-137.

Dodson, S.I. 1974. Zooplankton competition and predation: an experimental test of the size-efficiency hypothesis. Ecology. 55:605-613.

Drenner, R.W., and S.R. McComas. 1980. The roles of zooplankter escape ability and fish size selectivity in the selective feeding and impact of planktivorous fish. pp.587-593. In W.C. Kerfoot (ed.) Evolution and Ecology of Zooplankton Communities. Special Symposium Volume 3. American Society of Limnology and Oceanography. University Press of New England, Hanover, New Hampshire. 793 pp.

Edmondson, W.T. 1971. Properties of organisms, p.140-145. In W.T. Edmondson and G.G. Winberg (eds.) A Manual on Methodds for the Assessment of Secondary Productivity in Fresh Waters, IBP Handbook No. 17. Blackwell Scientific Publications, Oxford and Edinburgh. 358pp.

Franzin, W.G., G. A. McFarlane, and A. Lutz. 1979. Atmospheric fallout in the vicinity of a base metal smelter at Flin Flon, Manitoba, Canada. Environ. Sci. Technol. 13:1513-1522.

Galbraith, M.G. 1967. Size selective predation on Daphnia by rainbow trout and yellow perch. Trans. Amer. Fish. Soc. 96:1-10.

Gannon, J.E., and S.A. Gannon. 1975. Observations on the narcotization of crustacean zooplankton. Crustaceana. 28:220-224.

Gliwicz, Z.M. 1977. Food size selection and seasonal succession of filter feeding zooplankton in an eutrophic lake. Ekol. pol. 25:179-225.

Grice, G.D., M.R. Reeve, P. Koeller, and D.W. Menzel. 1977. The use of large volume, transparent, enclosed sea-surface water columns in the study of stress on plankton ecosystems. Helgolander wiss. Meersunters. 30:118-133.

Gurney, N.L. 1929. Dimorphism and the rate of growth in Copepoda. Int. Rev. Ges. Hydrobiol. Hydrogr. 21:189-207.

Hall, D.J. 1964. An experimental approach to the dynamics of a natural population of Daphnia galeata mendotae. Ecology. 45:94-112.

Hall, D.J., W.E. Cooper, and E.E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnol. Ocean. 15:839-928.

Hamilton, A.L. 1971. Zoobenthos of fifteen lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Bd. Can. 28:257-263.

Haney, J.F. 1973. An *in situ* examination of the grazing activities of natural zooplankton communities. Arch. Hydrobiol. 72:87-132.

Hendrey, G., K. Baalsruud, T.S. Traaen, M. Laake, and G. Raddum. 1976. Acid precipitation: some hydrobiological changes. Ambio. 5:224-227.

Hendrey, G., and R.F. Wright. 1976. Acid precipitation in Norway: effects on aquatic fauna. J. Great Lakes Res. 2(Suppl. 1): 192-207.

Hollander, M., and D.A. Wolfe. 1973. NonParametric Statistical Methods. John Wiley and Sons, Toronto. 503pp.

Hrbáček, J. 1962. Species composition and the amount of zooplankton in relation to fish stocks. Rozpr. Cesk. Akad. Ved. 72:1-116.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs. 54:187-211.

Hutchinson, G.E. 1967. A Treatise on Limnology. Volume II. Introduction to lake biology and the limnoplankton. John Wiley and Sons, New York, N.Y. 1115pp.

Jaccard, P. 1932. Die statistisch floristische Methode als Grundlage der Pflanzensoziologie. Handb. Biol. Arbeitsmeth. Aberhalden. 11:165-202.

Jackson, T.A., G. Kipphut, R.H. Hesslein, and D.W. Schindler. 1980. Trace metal chemistry in soft-water lakes of different pH levels. Can. J. Fish. Aquat. Sci. 37:387-402.

Janicki, A., and J. DeCosta. 1979. A multivariate analysis of the crustacean plankton of an acid reservoir. Arch. Hydrobiol. 85:465-481.

Jeffries, D.S., C.M. Cox, and P.J. Dillon. 1979. The depression of pH in lakes and streams in central Ontario during snowmelt. J. Fish. Res. Bd. Can. 36:640-646.

Johnson, M.G., M.F.P. Michalskie, and A.E. Christie. 1970. Effects of acid mine wastes on the phytoplankton communities of two northern Ontario lakes. J. Fish. Res. Bd. Can. 27:425-444.

Kerfoot, W.C., and W.R. DeMott. 1980. Foundations for evaluating community interactions:the use of enclosures to investigate coexistance of Daphnia and Bosmina. pp725-741. In W.C. Kerfoot (ed.) Evolution and Ecology of Zooplankton Communities. Special Symposium Volume 3, American Society of Limnology and Oceanography. University Press of New England, Hanover, New Hampshire. 793pp.

Kuiper, J. 1977. An experimental approach in studying the influence of mercury on a North Sea coastal plankton community. Helgolander wiss. Meersunters. 30:652-665.

Kwiatkowski, R.E., and J.C. Roff. 1976. Effects of acidity on the phytoplankton and primary productivity of selected northern Ontario lakes. Can. J. Bot. 54:2546-2561.

Lack, T.J., and J.W.G. Lund. 1974. Observationa and experiments on the phytoplankton of Blelham Tarn, English Lake District. Freshwater Biol. 4:399-415.

Langford, R.R. 1938. Diurnal and seasonal changes in the distribution of the limnetic crustacea of Lake Nipissing, Ontario. Ont. Fish. Res. Lab. Publ. No. 38. The University of Toronto Press, Toronto.

Lawrence, S.G. 1980. The effects of acid and cadmium on impounded zooplankton in a Canadian Shield lake. Can. Tech. Rep. Fish. Aquat. Sci. 975:81-90.

Leivstad, H., G. Hendrey, I.P. Muniz, and E. Snekvik. 1976. Effects of acid precipitation on freshwater organisms, p.87-111. In F.H. Braekke (ed.) Impact of acid precipitation on forest and freshwater ecosystems in Norway. S.N.S.F. Res. Report 6/76: 111p.

Leivestad, H., and I.P. Muniz. 1976. Fish kill at low pH in a Norwegian river. Nature (London). 259:391-392.

Likens, G.E., and F.H. Bormann. 1974. Acid rain: a serious regional environmental problem. Science. 184:1176-1179.

Lindstrom, T. 1952. Sur l'ecologie du zooplankton crustace. Rep. Inst. Frehwat. Res. Drottningholm. 38:131-153.

Loadman, N.L. 1980. A comparison of the crustacean zooplankton populations of four man-made lakes in southern Manitoba. MSc. Thesis. University of Manitoba, Winnipeg, Manitoba. 105pp.

Lund, J.W.G. 1972. Preliminary observations on the use of large experimental tubes in lakes. Verh. Internat. Verein. Limnol. 18:71-77.

Malley, D.F. 1980. Decreased survival and calcium uptake by the crayfish Orconectes virilis at low pH. Can. J. Fish. Aquat. Sci. 37:364-372.

Malley, D.F., D.L.Findlay, and P.S.S. Chang. 1982. Ecological effects of acid precipitation on zooplankton. In F.M. D'Itri (ed.). Acid Precipitation: Effects on Ecological Systems. Ann Arbour Science.

Marshall, J.S., and D.L. Mellinger. 1980. Dynamics of cadmium stressed plankton communities. Can. J. Fish. Aquat. Sci. 37: 403-414.

McFarlane, G.A., W.G. Franzin, and A. Lutz. 1979. Chemical analysis of Flin Flon area lake waters and precipitation: 1973-1977. Environment Canada, Fish. Mar. Serv. MS Rep. 1486:42p.

McLaren, I.A. 1969. Population and production ecology of zooplankton in Ogac Lake, a landlocked fjord on Baffin Island. J. Fish. Res. Bd. Can. 26:1485-1559.

McWilliams, P.G., and W.T.W. Potts. 1978. The effects of pH and calcium concentrations on gill potentials in brown trout Salmo tutta. J. Comp. Physiol. 126:277-286.

Menzel, D.W., and J. Case. 1977. Concept and design: controlled ecosystem pollution experiment. Bull. Mar. Sci. 27:1-7.

Müller, P. 1980. Effects of artificial acidification on growth of periphyton. Can. J. Fish. Aquat. Sci. 37:355-363.

Nero, R.W. 1981. The decline of Mysis relicta Loven in response to experimental acidification of a whole lake. MSc. Thesis. University of Manitoba, Winnipeg, Manitoba.

Neville, C.M. 1979. Sublethal effects of environmental acidification on rainbow trout (Salmo gairdneri). J. Fish. Res. Bd. Can. 36:84-87.

NRCC. 1981. Acidification in the Canadian Environment: Scientific Criteria for Assessing the Effects of Acidic Deposition on Aquatic Ecosystems. National Research Council of Canada. NRCC No. 18475. 369pp.

Nriagu, J.O., and J.D. Hem. 1978. Chemistry of pollutant sulfur in natural waters. p.211-270. In J.O. Nriagu (ed.) Sulfur in the Environment. Part III. Ecological Impacts. John Wiley and Sons, New York, N.Y.

Parent, K.G., and R.D. Cheetham. 1980. Effects of acid precipitation on Daphnia magna. Bull. Environ. Contam. Toxicol. 25:298-304.

Patalas, K. 1971. Crustacean plankton communities in 45 lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Bd. Can. 28:231-244.

Pielou, E.C. 1982. Choosing the right statistical analysis for environmental monitoring. Unpublished manuscript.

Potts, W.T.W., and G. Fryer. 1979. The effect of pH and salt content on sodium balance in Daphnia magna and Acantholeberis curvirostris (Crustacea: Cladocera). J. Comp. Phsiol. 129B: 289-294.

Raabe, E.W. 1952. Uber den Affinitatsswert in der Pflanzenziologie. Vegetatio, Haag. 4:53-68.

Raddum, G.G., A. Hobaek, E.R. Lomsland, and T. Johnson. 1980. Phytoplankton and zooplankton in acidified lakes in south Norway. p.332-333. In D. Drablos and A. Tollan (eds.) Ecological Impact of Acid Precipitation. S.N.S.F. Project, Oslo.

Roff, J.C., and R.E. Kwiatkowski. 1977. Zooplankton and zoobenthos communities of selected northern Ontario lakes of different acidities. Can. J. Zool. 55:899-911.

Roth, J.C. 1968. Benthic and limnetic distribution of three Chaoborus species in a south Michigan lake (Diptera. Chaoboridae). Limnol. Oceanogr. 13:242-249.

Salki, A.G. 1981. The crustacean zooplankton communities of three prairie lakes subject to varying degrees of anoxia. MSc. Thesis. University of Manitoba, Winnipeg, Manitoba.

Salki, A.G., M. Turner, K. Patalas, J.Rudd, and D. Findlay. 1984. The influencs of fish-zooplankton-phytoplankton interactions on the results of selenium toxicity experiments within large enclosures. Can. J. Fish. Aquat. Sci. in press.

Schindler, D.W. 1980. Experimental acidification of a whole lake. A test of the oligotrophication hypothesis. p.370-374. In D. Drablos and A. Tollan (eds.) Ecological Impact of Acid Precipitation. S.N.S.F. Project, Oslo.

Schindler, D.W., R.H. Hesslein, R. Wagemann, and W.S. Broecker. 1980a. Effects of acidification on mobilization of heavy metals and radionuclides from the sediments of a freshwater lake. Can. J. Fish. Aquat. Sci. 37:373-377.

Schindler, D.W., and B. Noven. 1971. Vertical distribution and seasonal abundance of zooplankton in two shallow lakes of the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Bd. Can. 28:245-256.

Schindler, D.W., R. Wagemann, R.B. Cook, T. Ruszczynski, and J. Prokopowich. 1980b. Experimental acidification of Lake 223, Experimental Lakes Area: background data and first three years of acidification. Can. J. Fish. Aquat. Sci. 37:342-354.

Schindler, D.W., T. Ruszczynski, and E.J. Fee. 1980c. Hypolimnion injection of nutrient effluents as a method for reducing eutrophication. Can. J. Fish. Aquat. Sci. 37:320-327.

Shaw, J. 1960. The absorption of sodium ions by the crayfish Astacus pallipes Lereboullet III. The effect of other cations in the external solution. J. Exp. Biol. 37:548-556.

Siebeck, H.O. 1980. Optical orientation of pelagic crustaceans and its consequence in the pelagic and littoral zones. pp.28-38. In W.C. Kerfoot (ed.) Evolution and Ecology of Zooplankton Communities. Special Symposium Volume 3, American Society of Limnology and Oceanography. University of New England Press, Hanover, New Hampshire. 793pp.

Smyly, W.J.P. 1972. The crustacean plankton, past and present, in Esthwaite Water. Verh. Internat. Verein. Limnol. 18:320-326.

Smyly, W.J.P. 1976. Some effects of enclosure on the zooplankton in a small lake. Freshwater Biol. 6:241-251.

Smyly, W.J.P. 1978. Further observations on limnetic zooplankton in a small lake and two enclosure containing fish. Freshwater Biol. 8:491-495.

Sprules, W.G. 1975. Midsummer crustacean zooplankton communities in acid-stressed lakes. J. Fish. Res. Bd. Can. 32:389-395.

Sprules, W.G. 1980. Nonmetric multidimensional scaling analysis of temporal variation in the structure of limnetic zooplankton communities. Hydrobiologia. 69:139-146.

Stahl, J.B. 1966. The ecology of Chaoborus in Myers Lake, Indiana. Limnol. Oceanogr. 11:177-183.

Stainton, M.P., M.J. Capel, and F.A.J. Armstrong. 1977. The chemical analysis of fresh water. 2nd ed. Fish. Mar. Serv. Misc. Spec. Publ. 25:166p.

Steele, J.H. 1979. The uses of experimental ecosystems. Phil. Trans. R. Soc. Lond. B. 286:583-595.

Takahashi, M., W.H. Thomas, D.L.R. Seibert, J. Beers, P. Koeller, and T.R. Parsons. 1975. The replication of biological events in enclosed water columns. Arch. Hydrobiol. 76:5-23.

Taylor, B.E. 1980. Size selective predation on zooplankton. pp.377-387. In W.C. Kerfoot (ed.) Evolution and Ecology of Zooplankton Communities. Special Symposium Volume 3, American Society of Limnology and Oceanography. University Press of New England, Hanover, New Hampshire. 793pp.

Tessier, G. 1960. Relative growth. In T.H. Waterman (ed.) The Physiology of Crustacea, Vol. 1. Metabolism and Growth. Academic Press, London. 670pp.

Watt, W.D., D. Scott, and S. Ray. 1979. Acidification and other chemical changes in Halifax County lakes after 21 years. Limnol. and Oceanogr. 24:1154-1161.

Walton, W.E., S. Compton, J.D. Allan, and R.E. Daniels. 1982. The effect of acid stress on survivorship and reproduction of Daphnia pulex (Crustacea: Cladocera). Can. J. Zool. 60:573-579.

Weglenska, T. 1971. The influence of various concentrations of natural food on the development, fecundity, and production of planktonic crustacean filtrators. Ekol. pol. 19:427-473.

Whittaker, R.H., and C.W. Fairbanks. 1958. A study of plankton copepod communities in the Columbia basin, southeastern Washington. Ecology. 39:46-65.

Wilson, M.S. 1959. Calanoida, p.738-794. In W.T. Edmondson (ed.) Freshwater Biology, 2nd ed. John Wiley and Sons, New York, N.Y.

Wright, J.C. 1965. The population dynamics and production of Daphnia in Canyon Ferry Reservoir, Montana. Limnol. Oceanogr. 10:583-590.

Wright, R.F., and E.T. Gjessing. 1976. Changes in lakewater chemistry due to acid precipitation. Ambio. 5:219-223.

Yan, N.D. 1975. Acid precipitation and its effects onphytoplankton communities of Carlyle Lake, Ontario. MSc. Thesis. University of Toronto, Toronto, Ontario.

Yan, N.D., R.E. Girard, and C.J. Lafrance. 1979. Survival of rainbow trout, Salmo gairdneri, in submerged enclosures in lakes treated with neutralizing agents near Sudbury, Ontario. Tech Rept. LTS 79-2. Ontario Ministry of the Environment.

Yan, N.D., and P. Stokes. 1978. Phytoplankton of an acidic lake, and its response to experimental alteration of pH. Environ. Conserv. 5:93-100.

Yan, N.D., and R. Strus. 1980. Crustacean zooplankton communities of acidic metal-contaminated lakes near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 37:2282-2293.

Yeatman, H.C. 1959. Cyclopoida, p.795-815. In W.T. Edmondson (ed.) Freshwater Biology, 2nd ed. John Wiley and Sons, New York, N.Y.

Zaret, T.M. 1980. Predation and freshwater communities. Yale University Press. New Haven, Connecticut. 187pp.

Zimmerman, A.P., and H.H. Harvey. 1979. Sensitivity to acidification of waters of Ontario and neighbouring states. Final report to Ontario Hydro, University of Toronto, Toronto, Ontario. 118pp.

Appendix A

The precision with which the composite sampling program estimated crustacean plankton community abundance was examined by collecting replicate composite samples on several occasions. The coefficient of variation between these replicate estimates was used as the measure of precision (Table A1).

Sampling precision varied considerably from date to date in all five communities, with coefficients of variation occasionally exceeding 20%. However, the sampling scheme provided a much more precise estimate of mean abundance over time. The differences between the replicate samples were somewhat compensatory, with coefficients of variation of 7.3 to 11.9% in the lake and control tubes in the two years. Variation between replicate samples in A1 was consistently high, yielding a coefficient of variation of 18.6 to 28.0% for mean abundance over time in the two years. This could have been a result of the patchy spatial distributions of several taxa recorded in A1. Variation in A2 was also very high in both years but differences between replicates were almost compensatory over time in 1979. These lower precisions in the acid tubes may also have been due to the lower abundances occurring there, particularly in the second half of 1979.

Table A1. The precision of estimates of total community abundance in the enclosures and the lake for selected dates in 1979 and 1980. The values listed are the coefficients of variation (%) for paired replicate composite samples. CV of $\bar{x}$ is the coefficient of variation of the mean of the replicates over time.

	1979										
	5/7	12/7	9/8	20/8	3/9	21/9	29/9	7/10	13/10	20/10	CV of $\bar{x}$
Lake	24.7	18.7	6.6	6.1	---	28.0	9.8	26.4	63.2	25.2	7.3
Ctrl 1	19.8	7.7	24.4	5.7	5.9	11.6	3.1	7.8	17.8	6.3	10.0
Ctrl 2	29.2	5.8	4.3	8.1	2.7	23.2	15.7	---	56.7	---	10.4
A1	19.5	24.8	62.1	21.3	2.0	---	22.0	42.2	75.5	33.3	18.6
A2	23.9	7.9	40.7	15.9	11.7	21.4	53.4	23.2	60.0	3.2	1.5

	1980								
	12/5	21/5	5/6	11/6	19/6	30/6	8/7	17/7	
Lake	14.0	12.5	13.4	1.4	4.7	13.9	3.5	15.7	8.7
Ctrl 1	8.7	5.9	48.2	10.0	7.0	16.3	9.0	8.2	11.9
Ctrl 2	26.5	---	21.1	7.7	2.3	---	7.2	2.6	11.5
A1	18.8	0.1	42.4	13.3	---	15.8	36.2	23.9	28.0
A2	28.6	---	9.7	25.7	16.7	30.9	48.7	9.6	22.6

Appendix B

The pattern of spatial distribution of crustaceans within ths enclosures and among the sampling stations in the lake was examined on two occasions; August 20, 1979, and May 12, 1980. The individual samples collected on these dates were preserved separately and all organisms in each sample were enumerated. The second occasion proved to be inappropriate for this purpose because of the very low abundance of most taxonomic groups at that time. Consequently, only the August 20 data will be considered here.

Following the suggestion of Elliott (1977), the presence of a random spatial distribution was the first to be considered. Agreement with a Poisson series was used as the criterion of randomness and the χ^2 test was used to test for equality of the variance to mean ratio in the test statistic:

$$\chi^2 = \frac{(n-1)\ s^2}{\bar{x}}$$

Where: n is the number of samples (5); s^2 is the sample variance; and, $\bar{x}$ is the mean abundance in the five samples.

Almost every taxon was randomly distributed in each of the five communities (table A1). The only exceptions to this pattern were; the cyclopoid C1-3 in the lake (uniform), the cyclopoid C1-3 in A1 (uniform), Bosmina longirostris in A1 (aggregated), and Holopedium gibberum in A1 (uniform).

Table B1. χ^2 statistic (Elliott 1977) indicating the spatial distribution of crustacean taxa within the enclosures and among the sampling stations in the lake. The distribution is significantly ($p<0.05$) different from random (denoted by a *) if $\chi^2>14.86$ (aggregated) or $\chi^2<0.21$ (uniform).

Taxon	Lake	Ctrl 1	Ctrl 2	A1	A2
Diaptomus minutus	0.46	2.50	14.00	0.65	1.76
Calanoid C1-3	0.74	0.48	0.90	--	--
C4-5	0.55	1.24	2.21	--	--
N1-3	1.05	3.24	0.43	0.64	1.58
N4-6	0.71	1.35	1.86	0.65	1.31
Tropocyclops prasinus mexicanus	1.14	0.86	1.17	0.34	0.87
Mesocyclops edax	4.81	--	0.71	--	0.38
Cyclopoid C1-3	3.06	2.71	1.50	0.10*	0.90
C4-5	2.19	0.21	0.34	0.65	0.78
N1-3	0.19*	5.15	3.49	2.31	1.63
N4-6	0.51	1.73	1.42	0.29	4.01
Bosmina longirostris	0.43	4.63	8.23	30.17*	10.12
Holopedium gibberum	0.30	1.60	0.68	0.10*	--
Diaphanosoma brachyurum	0.28	0.55	1.54	3.51	1.32
Alona intermedia	2.39	--	--	--	--

Appendix C

The non-parametric Fisher's sign test (Hollander and Wolfe 1973) was selected for analysis of the significance of differences in this study at the suggestion of Pielou (1982), when none of the differences in a string of comparisons (eg: Diaptomus minutus abundance in the acid and control enclosures; Fig. 23) using one-way ANOVA or t-tests turned out to be significant but all showed the same trend. The test basically measures the consistency of a difference and treats the outcome of n paired comparisons as n tosses of a coin on the null hypothesis that the coin is fair. For any single comparison, the probability of abundance in one tube being higher or lower than in another is 0.5. However, the probability of abundance in one tube being higher than in another on 10 successive occasions is $(0.5)^{10}$=0.10%. One advantage of this test is that it is independent of the assumption of normality of the population and therefore can be used on ratio data such as percentage similarity of community or coefficient of community values while parametric tests cannot.

The major disadvantage of this test is its lack of power. That is, it has a higher probability of a type II error (a higher probability of accepting H_o when H_o is false) than its parametric counterpart the t-test. This makes it a rather conservative statistical test. The reason for this lower power is that it does not consider the magnitude of a

difference but only the sign. This proved troublesome in the analysis of differences between cladoceran populations. For example, Bosmina longirostris abundance in Ctrl 2 averaged 4.4 times higher than in the lake in 1979 (Table 9) yet the sign test did not detect a significant difference (n=18, p=0.167). The reason for this was that the greater abundance was concentrated in the first 10 sampling dates and abundance in Ctrl 2 was lower than in the lake on the following 8 dates (Fig. 29). In this circumstance the results of the test were ignored and similarly for Holopedium gibberum (Fig. 30) and Diaphanosoma brachyurum (Fig. 31) in which the populations were concentrated in short-lived pulses.

Another potential problem can be the assumption of independence of observations on which the validity of the test is based. In this study, the validity of the assumption of independence was examined using the runs test (Conover 1971) and no violations were detected.

In summary, Fisher's sign test is a rather inefficient means of assessing the significance of differences. However, it is also unlikely to indicate a difference is significant when not.