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ECOLOGY OF PLANKTONIC ROTIFERA IN A SHALLOW EUTROPHIC LAKE OF WESTERN CANADA

by

ROBERT LAWRENCE BAKER

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA
FALL, 1977

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Ecology of Planktonic Rotifera in a Shallow Eutrophic Lake of Western Canada submitted by Robert Lawrence Baker in partial fulfillment of the requirements for the degree of Master of Science.

Donald N. Gallup
Supervisor

Fred C. Zwickel

Hugh F. Clifford

Date August 5, 1977

ABSTRACT

The population dynamics of the planktonic rotifers of Hastings Lake, Alberta were studied from May 1975 to July 1976. The major emphasis was on the environmental control of the distribution and abundance of the different species and on the adaptive significance and mechanism of cyclomorphosis in the genus *Keratella*. Environmental factors studied included temperature, food, oxygen, and predation. Duration of egg development was ascertained for some species.

Hastings Lake is highly eutrophic with dense concentrations of Chlorophyta and Cryptophyta occurring in the spring and fall and massive blooms of Cyanophyta occurring in the summer. Oxygen depletion occurs during warm, calm weather and under the ice. The three dominant rotifers, *Keratella quadrata*, *K. cochlearis*, and *K. earlinae*, were perennial, existing through widely varying environmental conditions. The birth rates of these and other rotifers were significantly affected by temperature. The birth rates of *Keratella* were also affected by the concentration of "edible" phytoplankton. Other rotifers, such as *Brachionus angularis* and *Filinia longiseta*, only occurred during the summer months. They appeared during times of high water temperatures, high oxygen concentrations, and dense Cyanophycean blooms. The importance of filamentous Cyanophyta as a food source for *Brachionus angularis* is discussed. Species such as *Notholca squamula* and *Conochilus natans* appeared restricted to colder water with high concentrations of "edible" cells.

Results are discussed in relation to hypotheses of population regulation. Environmental factors were important in controlling the population growth. No evidence for an intrinsic control was found, although the data do not lend themselves to a thorough analysis.

My results concerning the cyclomorphosis of *Keratella* are in contrast to much of the published literature on this subject. Spine length of *K. cochlearis* and *K. earlinae* showed a positive relationship with temperature and the longest spines were found at temperatures of approximately 20°C. Spine length of *K. quadrata* showed a negative relationship with temperature. The importance of cyclomorphosis is discussed in terms of predator avoidance. Some of the lorica and spine lengths were significantly correlated with predator density; however, the importance of predation in causing cyclomorphosis remains obscure. The importance of understanding the natural history of each species to explain cyclomorphosis is indicated.

ACKNOWLEDGEMENTS

Financial support came from graduate teaching assistantships and research grants to Dr. D.N. Gallup from the Canada Dept. of the Environment and the National Research Council.

I would like to thank Dr. D.N. Gallup for his support and supervision during the study. Thanks also to my committee; Dr. H.F. Clifford, Dr. M. Hickman, and Dr. F.C. Zwickel for their encouragement and critical review of the manuscript. Dr. H.F. Clifford read and made many helpful corrections on the first draft. Special thanks to Dr. D.S. Potter for his help in many aspects of the project and for his review of the manuscript.

Guy Girtel and Jason Poon provided able and willing field assistance. Jim Fuller also helped in the field and with other aspects of the project. Pat Mitchell and Neil Chymko helped with the crustacean identification and Gary Jenkerson helped with the phytoplankton as well as in the field. Mrs. G. Hutchinson analysed all the water samples, helped in the construction of the plankton trap and performed a host of various tasks. My fellow graduate students in limnology proved helpful, encouraging, and tolerant. Dr. K. Roy kindly allowed me to use his Model B Coulter Counter. Mr. F. Rourke kindly allowed me to store equipment on his property and added hospitality to my visits to the lake.

For their friendship, advice, and help in many ways I would like to thank H. Amerongen, R. Burke, D. Christiansen, D. Krause, B. Naylor, N. Panter, J. Rasmussen, W. Roberts, and J. Weisgerber.

Special thanks to my parents for their support and encouragement

throughout the study. Special thanks also to Maureen Lamont for her assistance throughout the project and for her patience and optimism.

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INTRODUCTION

The study of rotifers is a poorly developed field in North America. There is a paucity of information despite the ease of collection, world wide distribution, and interesting biology of rotifers.

In North America, Gilbert (1967, 1973) studied the predator-prey relationship between Asplanchna and Brachionus with emphasis on the adaptive significance of cyclomorphosis. King (1967, 1972) concentrated on laboratory and field populations of Euchlanis dilatata with special interests in the effects of rotifer age on population growth and the adaptations for seasonal environments. Edmondson (1960), one of the leading researchers in rotifer ecology, has studied population dynamics of rotifers in Bare Lake, Alaska, using the egg ratio method for determining instantaneous birth and death rates. George and Fernando (1969, 1970) studied seasonal distribution of rotifers, particularly Keratella, and the vertical migrations of rotifers in small lakes in southern Ontario.

In contrast to limited data from North America, European workers have contributed the vast majority of information on rotifers. The works of Pejler (1957a,b,c; 1961) deserve special attention. He studied the seasonal and geographical distributions of rotifers from Sweden and Lapland and compiled extensive notes on each species' relationships with environmental factors. Pejler (1962) also studied the cyclomorphosis of Keratella cochlearis. Ruttner-Kolisko (1974) contributed to the study of rotifers with her work concerning the taxonomy and general biology of the planktonic rotifers. Amren (1964a,b,c), working on Spitzbergen Island, utilized Edmondson's methods for determining instantaneous birth rates and developed interesting theories on the intrinsic control of population density and cyclomorphosis based on the theories of Wesenburg-Lund (1930).

Because of this general lack of field data on planktonic rotifers in North America, particularly western North America, one purpose of my study was to describe the seasonal distribution and population growth of planktonic rotifers from Hastings Lake and compare it to the published reports from other areas.

Population regulation has been a major area of study in ecology since the time of Malthus; it has been the focal point of much discussion and has led to literally thousands of ecological studies. In literature dealing with rotifers, discussion of population regulation has been based on two main viewpoints. Edmondson (1965) described the effects of temperature and food on birth rates of rotifers and suggested that populations are controlled by changing conditions in the environment. Amren (1964a,c), using the same methods as Edmondson and measuring the same environmental factors, reported no correlation between population dynamics and the environment. He suggested an intrinsic control of population growth. Therefore, a second purpose of my project was to study the population dynamics of planktonic rotifers in light of these two views.

A third purpose of my study was to examine the cyclomorphosis of the genus Keratella. This is a particularly difficult field when one considers the vast amounts of conflicting data concerning

cyclomorphosis. The idea was to study cyclomorphosis from the view of adaptive significance. Thus, the problem is not so much how rotifers change shape, but why; ie what are the selective pressures that determine the advantage of cyclomorphosis?
I believed that such an understanding could only come from a detailed field study, encompassing as many environmental factors as possible.

DESCRIPTION OF STUDY AREA

Hastings Lake is a small lake in central Alberta, situated approximately 40 km E-SE of Edmonton. It is a eutrophic, non-stratifying lake, subject to pronounced blue-green algal blooms during the summer and severe oxygen depletion under the ice. Ice cover usually lasts from early November to late April. Figure 1 presents a map and the geographic location of the lake. Table 1 presents morphometric parameters.

Bedrock in the area is termed the Edmonton Formation, which is a brackish water formation composed of bentonitic sandstones, clays, and coal seams (Bowser et al, 1962). During Wisconsin time, glaciers deposited a till varying from 7.5 to 30 m thick (Bowser et al, 1962). Hastings Lake lies in this glacial till and was probably formed as a kettle lake (Schwartz and Gallup, in press).

Most of the lake is surrounded by podzolic soils termed Cooking Lake Loam. The area to the northwest of the lake consists of solentzic soils termed Ministik Silty Clay Loam (Bowser et al, 1962).

Hastings Lake lies in the North Saskatchewan River drainage basin. In times of high water, Hastings Creek flows from the eastern end of the lake to BeaverHill Lake. During the study there was no perceptible flow in the creek.

Climate of the area is continental with warm summers and cold winters. Air temperature maxima, usually in July, rarely exceed 32°C and winter temperatures rarely drop below -40°C. Annual precipitation averages 40-45 cm, 70 per cent of this falling as rain and the remainder as snow. Most of the rain falls during June, July, and

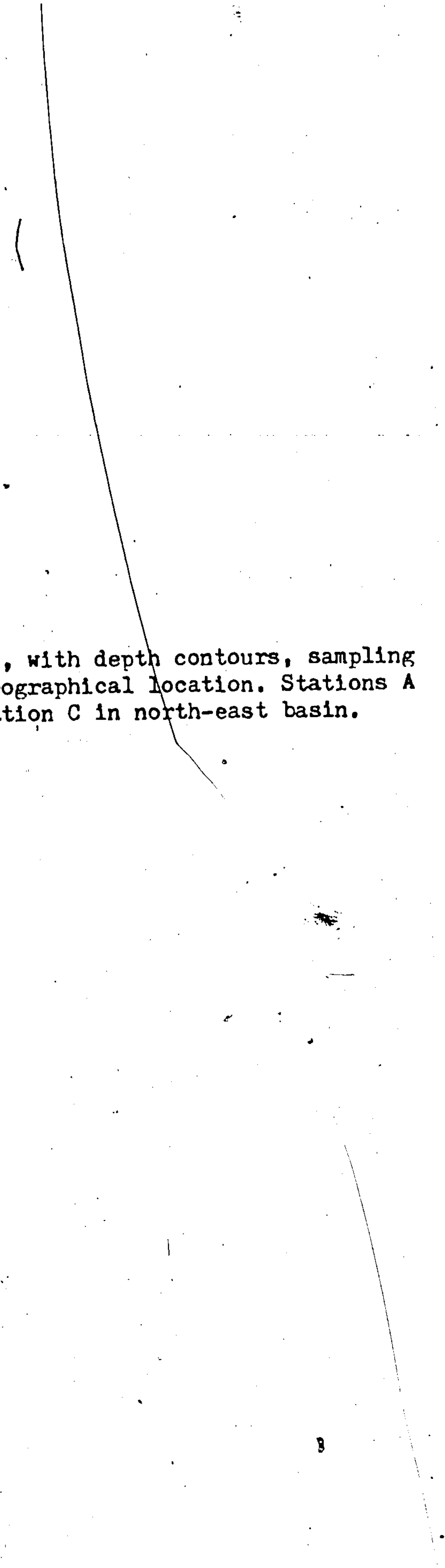


Figure 1. Outline of Hastings Lake, with depth contours, sampling stations (A,B,C), and geographical location. Stations A and B in main basin. Station C in north-east basin.

Hastings Lake

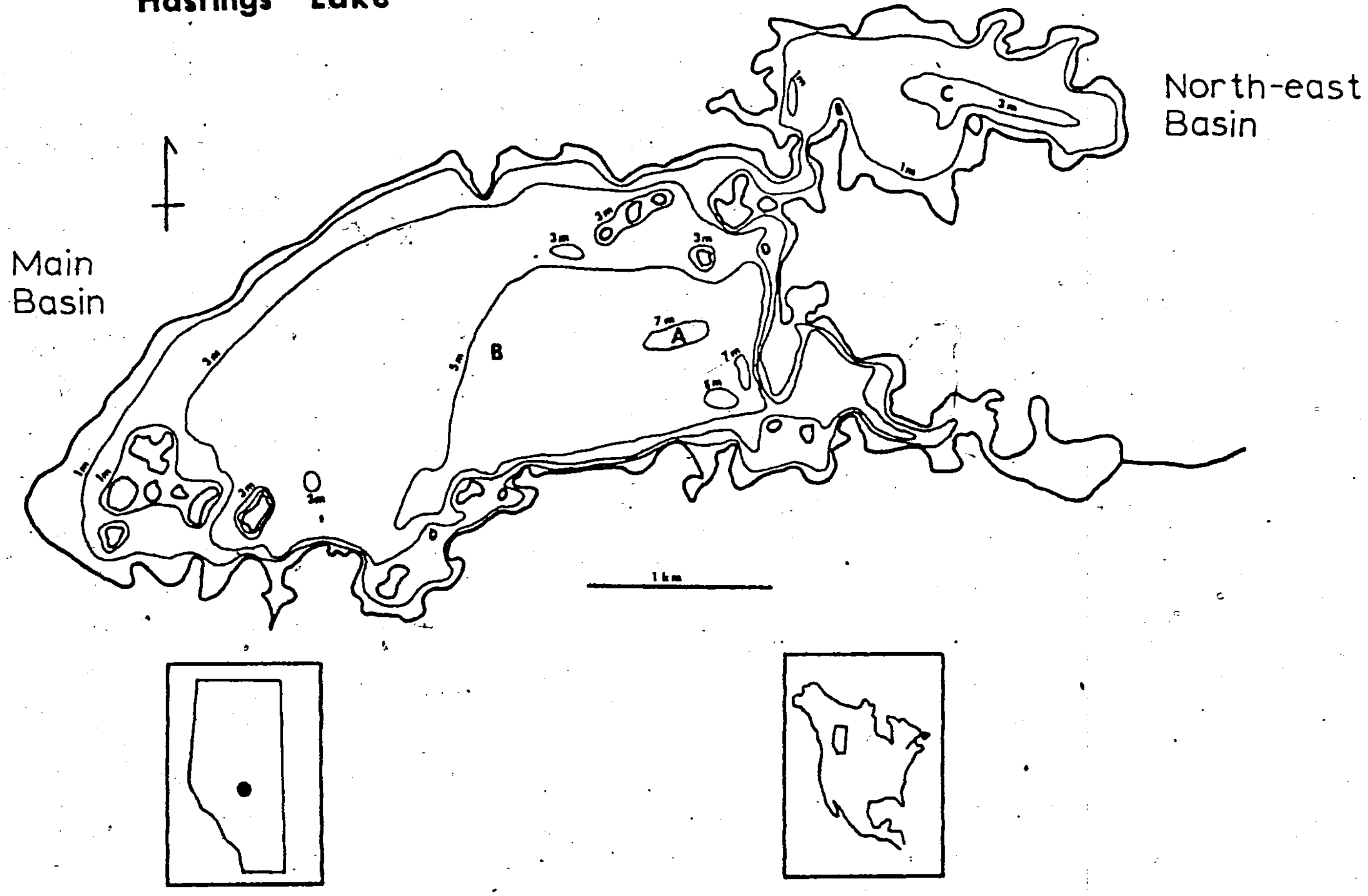


TABLE 1

Morphometry of Hastings Lake

	Main Basin		North-east Basin	
Area	7.3	km^2	1.4	km^2
Volume	ca. 0.20	km^3	ca. 0.02	km^3
Maximum Length	5105.0	m	2134.0	m
Effective Length	4953.0	m	2134.0	m
Maximum Width	1859.0	m	991.0	m
Effective Width	1859.0	m	991.0	m
Maximum Depth	8.1	m	3.0	m
Mean Depth	2.7	m	1.5	m
Shoreline Length	20.5 (without islands)	km	7.9 (without islands)	km
Shoreline Development	2.14		1.86	
Volume Development	1.01		1.52	
Elevation	735.0	m		

August. During the ice-free months the wind normally approaches the lake from the north-west with an average speed of 15 km/h.

Much of the natural vegetation around the lake has been cleared for agricultural purposes, particularly cattle pastures. The remaining natural vegetation is dominated by Populus tremuloides and and Populus balsamifera with scattered patches of Picea glauca.

A few houses and cottages are located around the lake, particularly on the south shore of the main basin. Because of blue-green algal blooms, the lake is used sparingly for summer recreation, but it does attract waterfowl hunters in the fall. According to local residents the lake supported populations of Perca flavescens and Esox lucius until 1970. During my study no evidence of fish was found.

MATERIALS and METHODS

Because of the field nature of this project, most of the methods discussed below describe the collection, enumeration and measurement of zooplankton, the calculation of birth rates for certain rotifer species, and the monitoring of selected environmental factors. Laboratory experiments, to determine the duration of eggs at specific temperatures, will be described after the field methods.

GENERAL

The map of Hastings Lake (Fig. 1) shows the location of sampling stations A, B, and C with depths of 8, 6, and 3 metres respectively. Routine sampling began on May 23, 1975 and was terminated on July 2, 1976. Station B was not sampled after November 2, 1975. During the ice-free period, sampling was carried out from a 14 foot boat equipped with a 15 horsepower motor. In winter, a snowmobile was used for transportation. Holes in the ice were made with a power auger.

ZOOPLANKTON

Zooplankton samples were taken twice a week during spring and summer 1975. In autumn 1975, sampling frequency was reduced to about one sampling period every five days. In winter 1975-1976, samples were taken biweekly with the exception of December 1975 when only one sampling period was performed due to ice conditions. After ice break-up on April 27, 1976 the original semiweekly sampling was resumed.

Samples were taken from each station at 1 metre intervals throughout the water column. During winter, the ice surface was considered the surface of the water. A Schindler-modified Patalas plankton trap of 9 liters (Schindler, 1969), constructed of transparent plexiglass and fitted with a #25 (64μ), "Nitex", plankton net, was used to collect zooplankton. Samples were placed in four ounce glass bottles and preserved in the field with 5% formalin. In the laboratory each sample was diluted to 75 ml in a flask, mixed by shaking, and subsampled with a 2 ml Henson-Stempel pipet. The subsample was poured into a counting chamber and allowed to settle. All rotifers and cladocerans were identified to species and the copepods were identified to genus. However copepod nauplii stages were not identified as cyclopoid or calanoid. Samples were counted on a Wild M40 inverted microscope at 40X. For each zooplankton species the population density at each station was computed by averaging numbers recorded at each depth. Station egg ratios, for egg carrying rotifer species, were computed by dividing the station total number of eggs by the station total number of females.

The ratio of eggs per female was used to determine instaneous birth rates according to equation (1) from Paloheimo (1974),

$$b = \frac{\ln\left(\frac{Ct}{Nt} + 1\right)}{D}$$

where b = instantaneous rate of birth
Ct = number/liter of eggs at time t
Nt = number/liter of amictic females at time t
D = duration of development of eggs

Since some illoricate rotifers were difficult to identify to species when preserved, living rotifers were collected with a #25 Wisconsin-type plankton net and returned to laboratory. Live specimens were mounted in a drop of lake water and observed through a Wild M20 microscope. For certain species it was necessary to remove the mastax from the rotifer's body to ensure proper identification. This was done by mounting a rotifer in a dilute solution of Chlorox, which dissolved the soft tissues but left the mastax intact (Edmondson, 1959). Rotifers were identified using keys from Edmondson (1959), Chengalath et al. (1971), and Ruttner-Kolisko (1974). Crustaceans were identified using keys from Brooks (1959), Wilson and Yeatman (1959), Pennak (1963), and Brandlova et al. (1972).

To investigate temporal variation of certain species, measurements were made of body and spine lengths. Measurements were made on samples from stations A and C, which were collected biweekly during the ice-free periods and monthly during the winter. Animals were mounted in glycerin and measured at 400X on a Wild M20 equipped with a calibrated ocular micrometer. Two measurements were made on specimens of Keratella cochlearis and K. earlinae, ie lorica length (from base of median anterior spines to base of posterior spine) and posterior spine length. Keratella quadrata was measured for lorica length (from base of median anterior spines to median posterior edge of lorica) and length of left and right posterior spines. The lengths of the two spines were subsequently averaged.

PHYTOPLANKTON

Phytoplankton samples were collected biweekly during ice-free periods and monthly during winter. Samples were taken from station A at the surface and at 2, 4, and 6 metres and from station C at the surface and at 2 metres. A 1200 ml brass Kemmerer water bottle was used to collect the samples which were preserved in the field with Lugol's solution and stored in 25 ml vials.

Samples were identified to genus according to Prescott (1970) and counted on a Wild M40 inverted microscope according to the method described in Lund et al (1958). Only those cells that I considered edible by the rotifers were counted but relative abundances of Cyanophyta were noted.

BACTERIA

Sampling the planktonic bacteria populations began on May 28, 1975. On this date and on June 23, 1975 samples were taken from station A at the surface and at depths of 3 and 7 metres. From July 7, 1975 until completion of the project samples were taken at the same times and locations as the phytoplankton samples. Samples were collected with a 1200 ml brass Kemmerer water bottle, placed in sterilized glass bottles, and returned within twenty-four hours to the Provincial Laboratory of Public Health for analysis. Bacteria cells were enumerated by the standard plate count method at 35°C. Samples were diluted when the counts were in excess of

3,000 cells per ml.

PARTICLE ENUMERATION AND SIZE ANALYSIS

During ice-free periods water samples for particle size analysis were taken biweekly from station A at the surface and at depths of 2, 4, and 6 metres and from station C at the surface and at 2 metres. During winter, samples were collected monthly from the same sites. Samples were collected with a 1200 ml brass Kemmerer water bottle, placed in clean 4 oz glass jars, and fixed in the field with 2%, 0.45 µ filtered, buffered formalin. Until December 1975 samples were analyzed with a Model B Coulter Counter (Coulter Electronics, Inc., Hialeah, Florida). Samples collected from December 1975 until completion of the project were analyzed with a Model TA II Coulter Counter. Samples were prepared for analysis by mixing 22.5 ml lake water with 2.5 ml 0.45 µ filtered 5.0% NaCl and 75 ml 0.45 µ filtered 0.5% NaCl. Both counters determine the number and volume of particles within discrete diameter ranges.

WATER CHEMISTRY

Water samples for chemical analysis were collected from stations A and C at 1 metre intervals. Samples were collected biweekly during 1975, then monthly at station A and bimonthly at station C in 1976. Samples were taken with a two liter polyethylene Van Dorn water sampler, placed in screw-top polyethylene bottles, returned to the laboratory, filtered and frozen until analysis. Water was analyzed for pH, conductivity, chlorine, total and calcium hardness, total and phenolphthalein alkalinity, total phosphate and orthophoshate, total Kjeldahl nitrogen, organic nitrogen, and nitrate nitrogen. Samples were analyzed by Mrs. G. Hutchinson in the Department of Zoology water laboratory according to A.P.H.A.'s Standard Methods (1971).

TEMPERATURE

Temperature recordings were taken with a Model 54 Dissolved Oxygen Metre (Y.S.I. Co., Yellow Springs, Ohio) until December 1975. During 1976 a Dissolved Oxygen Metre TDO-2 (Hydrolab Corp. Austin, Texas) was used. Temperature readings were taken on all sampling dates from each station at 1 metre intervals.

DISSOLVED OXYGEN

Dissolved oxygen readings were taken with the same instruments and at the same stations and depths as were the temperature readings from June 23, 1975 until completion of the sampling period. The readings in ppm were converted to percent saturation using Mortimer's nomogram (1956).

EGG DURATIONS

Laboratory experiments were neccessary to determine duration of development of eggs, D in equation (1). Rotifers were collected from Hastings Lake with a Wisconsin Plankton net and returned live to the laboratory. Non-ovigerous females were isolated from samples and placed in small chambers suspended in large bowls of lake water as in Amren (1964). The water was maintained at a known, constant temperature (± 0.5 C°). The chambers were plastic vials with holes cut in the sides; 64μ netting secured over the holes kept the rotifers in the chambers but allowed water and food to flow through. Animals were checked hourly and when an ovigerous animal was found it was isolated in another chamber. By checking individual ovigerous animals at hourly intervals it was possible to determine when eggs were hatched. Approximate laying and hatching times gave an estimate of duration of development at experimental temperatures. A least squares regression line was fitted to the data points for each species and values used in equation (1) were read from this line.

THE PHYSICAL-CHEMICAL ENVIRONMENT

WEATHER DURING STUDY

Precipitation and air temperature data from Environment Canada, Atmospheric Environment, recorded at the Edmonton International Airport, 45 km W-SW of Hastings Lake, are presented in Figure 2. During June and July 1975 monthly mean temperatures were close to normal for the area. August however, was a few degrees cooler and September a few degrees warmer than average. From November 1975 to May 1976 each monthly mean was higher than the average temperature, especially in January and February, when temperatures were a full 4 C° higher than usual. April was also a warm month, with maximum temperatures over 20°C during the first and second week. June 1976, in contrast to the mild winter and spring was slightly cooler than average. The precipitation graph followed the usual pattern with yearly maxima in June, July, and August. Snowfall was close to average during winter months with the exception of April 1976 when only 4.8 cm fell compared to the usual 13.7 cm.

TEMPERATURE

Because of its shallow depth and susceptibility to wind, Hastings Lake did not form a true hypolimnion. Thus isotherms recorded during ice-free periods can be explained as a result of air temperatures and strength and duration of wind. Under the ice the lake exhibited inverse thermal stratification. Heating of the lower depths during winter was probably a combination of heat transfer from sediments and influx of dense, warm water from the solar

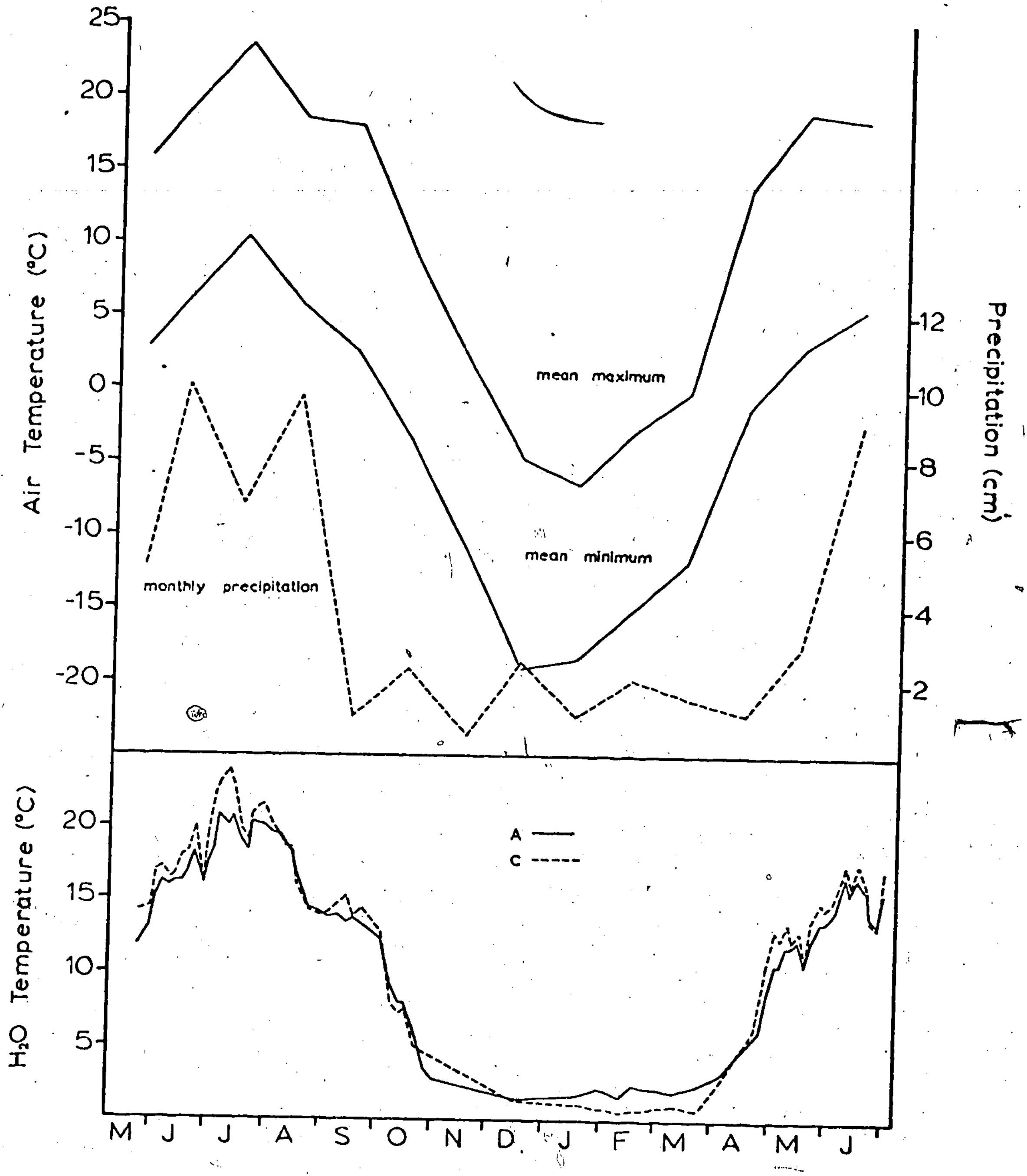


Figure 2. Maximum and minimum air temperatures, and total monthly precipitation; Edmonton International Airport. Mean water temperature at stations A and C. 1975-1976.

heated littoral zone (Wetzel, 1975).

Main Basin

According to local residents, spring break-up of 1975 occurred in early May. Water temperatures rose rapidly in late May, early June, and were equal to the air temperatures in late June (Fig. 3). The lake was homoiothermal during spring 1975. During early July the main basin exhibited a thermal gradient with the greatest temperature difference being 6 C° between the surface and lake bottom. On July 18 a rainstorm accompanied by high winds destroyed the gradient and left the lake homoiothermal at 19°C. The lake remained at 18-20°C for two weeks after the storm but never regained the thermal gradient.

The fall cooling trend began in early August and continued slowly until freeze-up on November 6. The lake was homoiothermal with the exception of a few days in mid September when the weather was calm and warm. Under the ice, water temperatures were inversely stratified; approximately 1°C near the ice and 3°C at the lake bottom. This temperature regime was stable for most of the ice-covered period. Warming of the water during spring 1976 began under the ice. Ice break-up in the main basin occurred on April 26; approximately two weeks earlier than usual according to local residents. Immediatly after ice break-up the water warmed rapidly; during May temperatures continued to increase but at a slower rate. Water temperatures in June 1976 were slightly colder than those of June 1975.

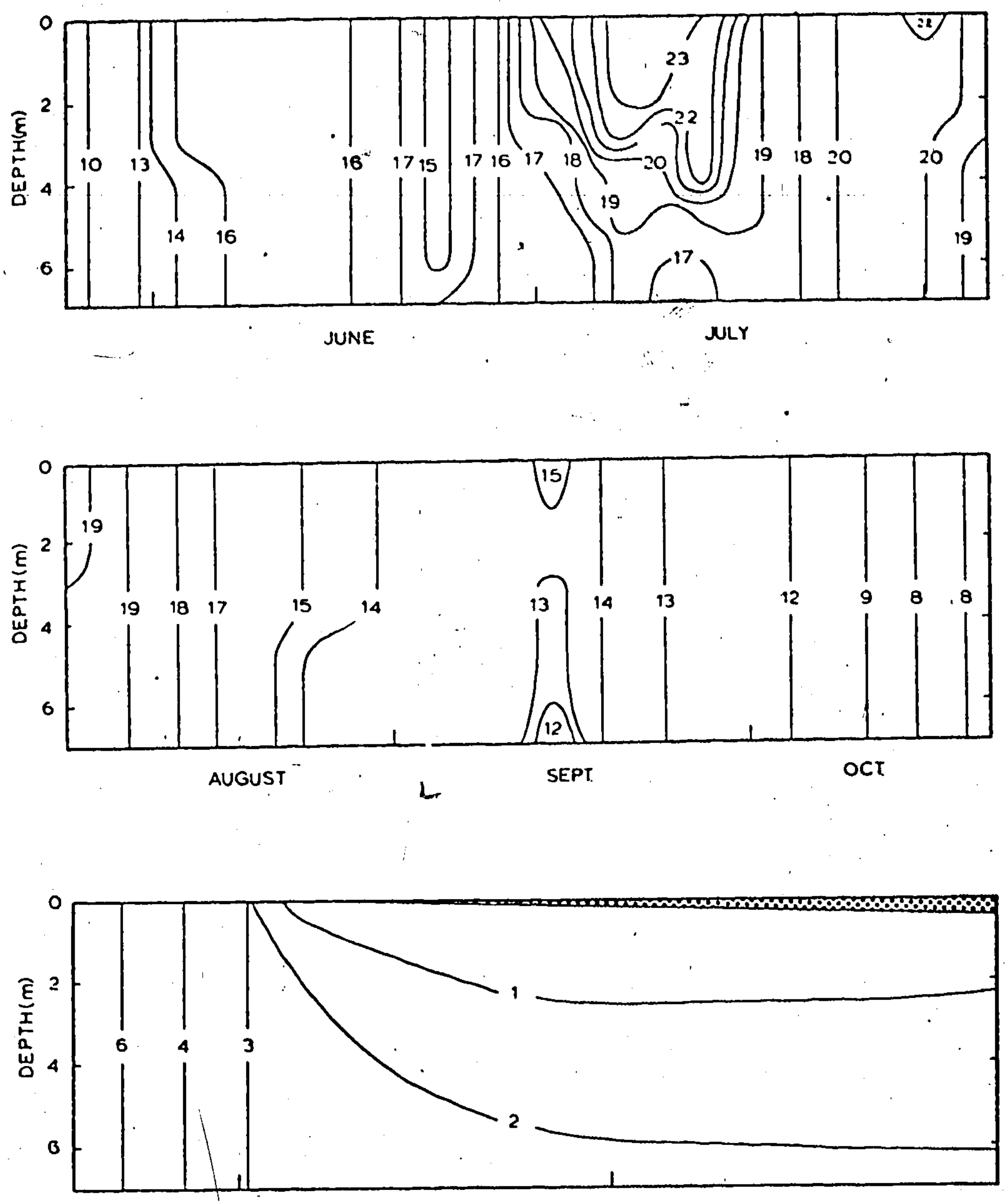


Figure 3. Isotherms (^{o}C) at station A, 1975-1976. Stippled areas represent ice drawn to scale. Continued.

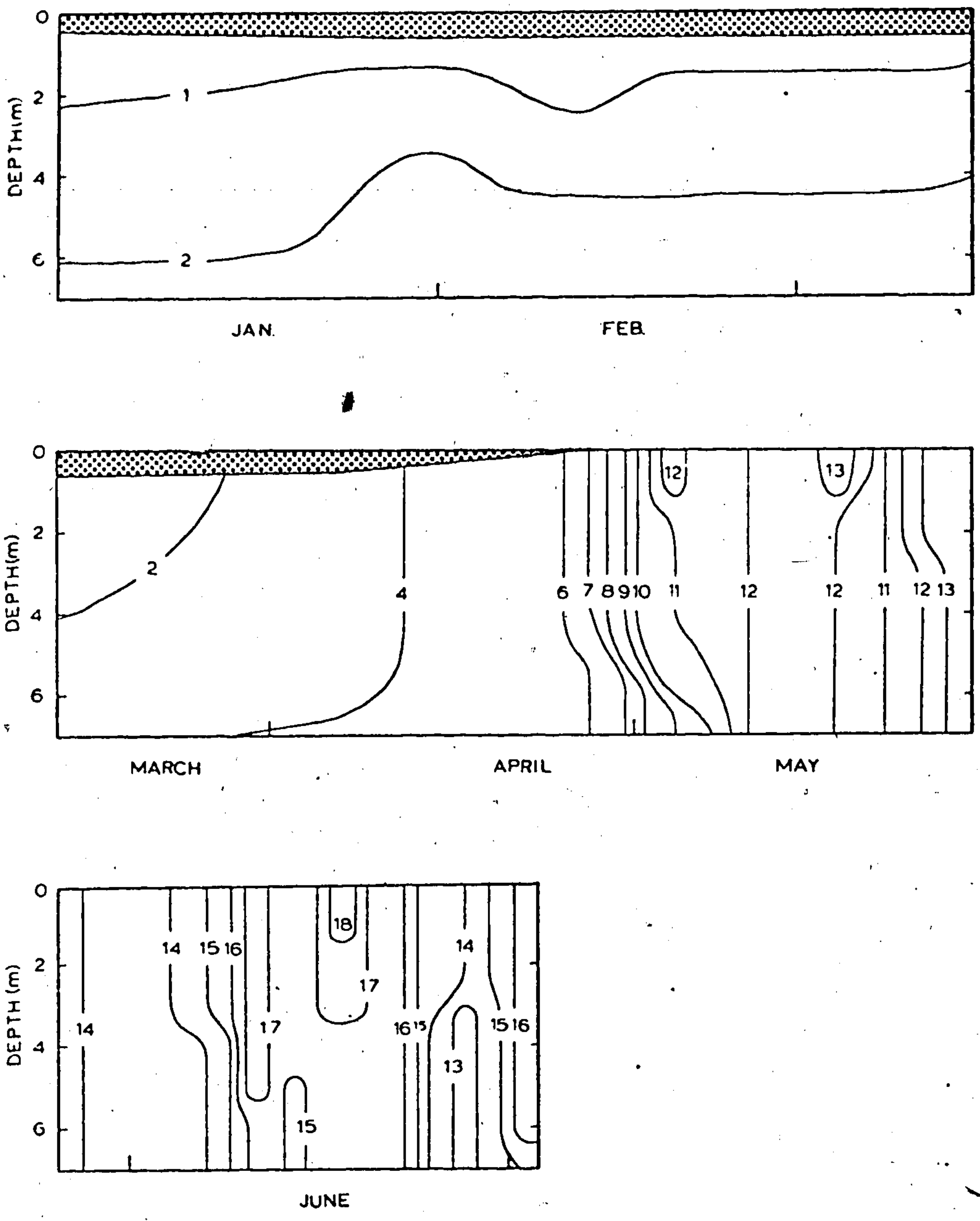


Figure 3. Continued.

North-east Basin

Because of the relative shallowness of station C, the thermal regime differed from that at station A in three ways: average temperatures were more extreme at station C, ie warmer in summer and colder in winter; changes in temperature occurred faster at station C; and the summer thermal gradient at station C was transitory and poorly developed. The 1975 spring and early summer isotherms at station C (Fig. 4) show the same homoiothermal pattern as station A but at a higher average temperature, with greater day to day fluctuations (Fig. 2). The water temperatures in early July showed a slight gradient. Water temperature dropped following the storm of July 18 but rose to over 20°C between July 25 and August 4. After August 4 the average temperature dropped slowly until freeze-up around November 4, 1975. Under the ice, temperatures averaged 1°C and showed an inverse stratification. After ice break-up, approximately April 21, 1976, the lake warmed rapidly to 13°C on May 4. During May and June the lake was homoiothermal and temperatures varied according to air temperature fluctuations.

DISSOLVED OXYGEN

Main Basin

Oxygen isopleths for late June showed high, uniform oxygen saturations (Fig. 5). Distinct oxygen stratification occurred during early July with 170% saturation at metre 2 and 10% saturation at metre 7. The high oxygen concentrations near the surface were indicative of rapid phytoplankton production.

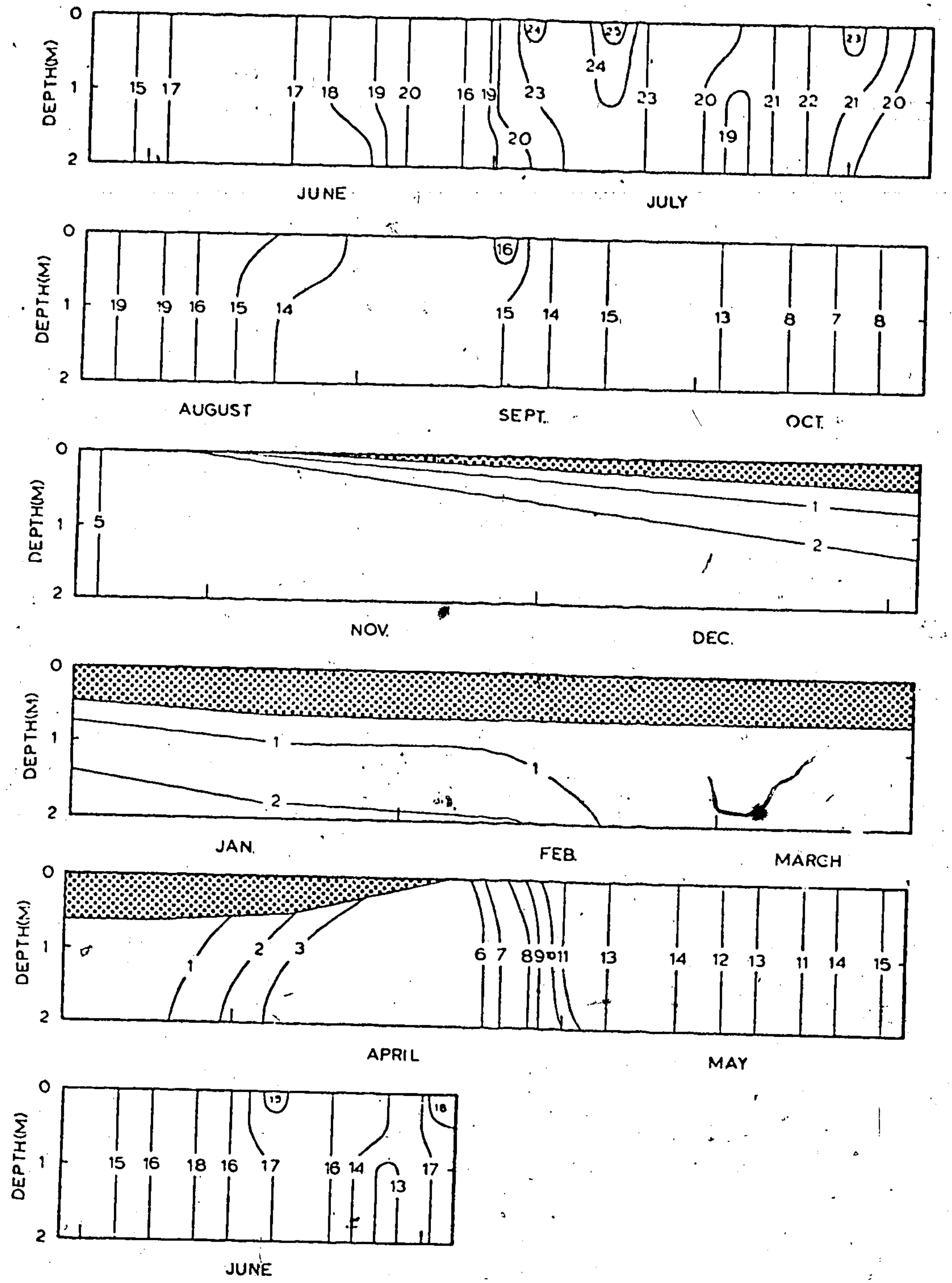


Figure 4. Isotherms (°C) at station C, 1975-1976. Stippled areas represent ice drawn to scale.

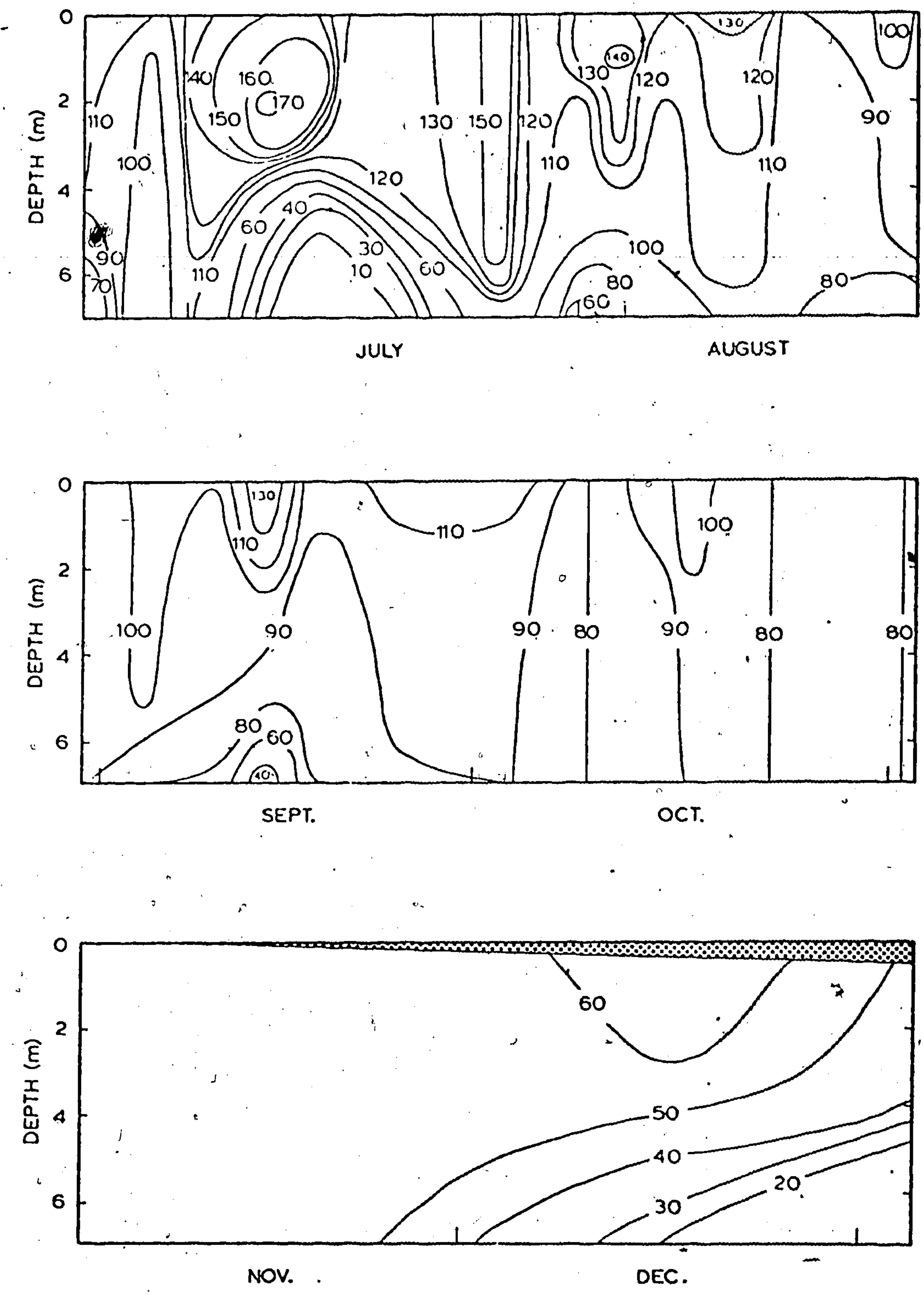


Figure 5. Isopleths of percentage oxygen saturation at station A, 1975-1976. Stippled areas represent ice drawn to scale. Continued.

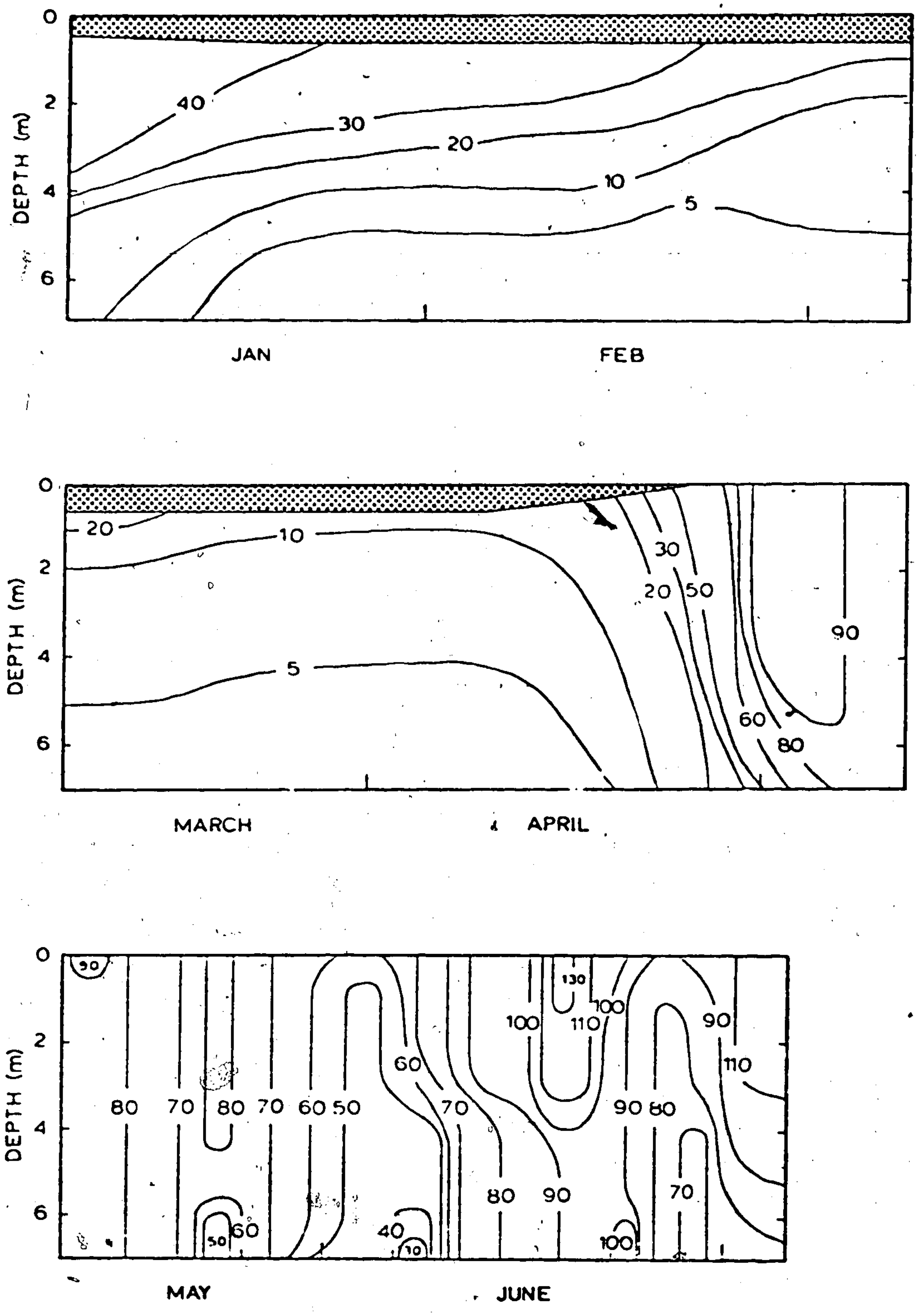


Figure 5. Continued.

After the storm of July 18, the stratification disappeared but the saturation remained above 100% until mid-August. The oxygen stratification period lasted longer after the storm than did the thermal stratification.

From mid-August until freeze-up, oxygen concentrations remained stable, fluctuating between 80 and 100% saturation. One brief exception to this occurred in mid-September when calm, warm weather prevailed; the surface oxygen concentration rose to 130% saturation while the bottom declined to 40% saturation.

By mid-December 1975 oxygen concentrations had dropped to 60% saturation at the ice and 20% saturation at the sediments. Oxygen saturation continued to drop until a mimimum was reached on April 6, 1976, with 10% saturation near the ice and less than 5% below the 5 metre depth. Phytoplankton production under the ice probably caused the increased saturation levels in late April.

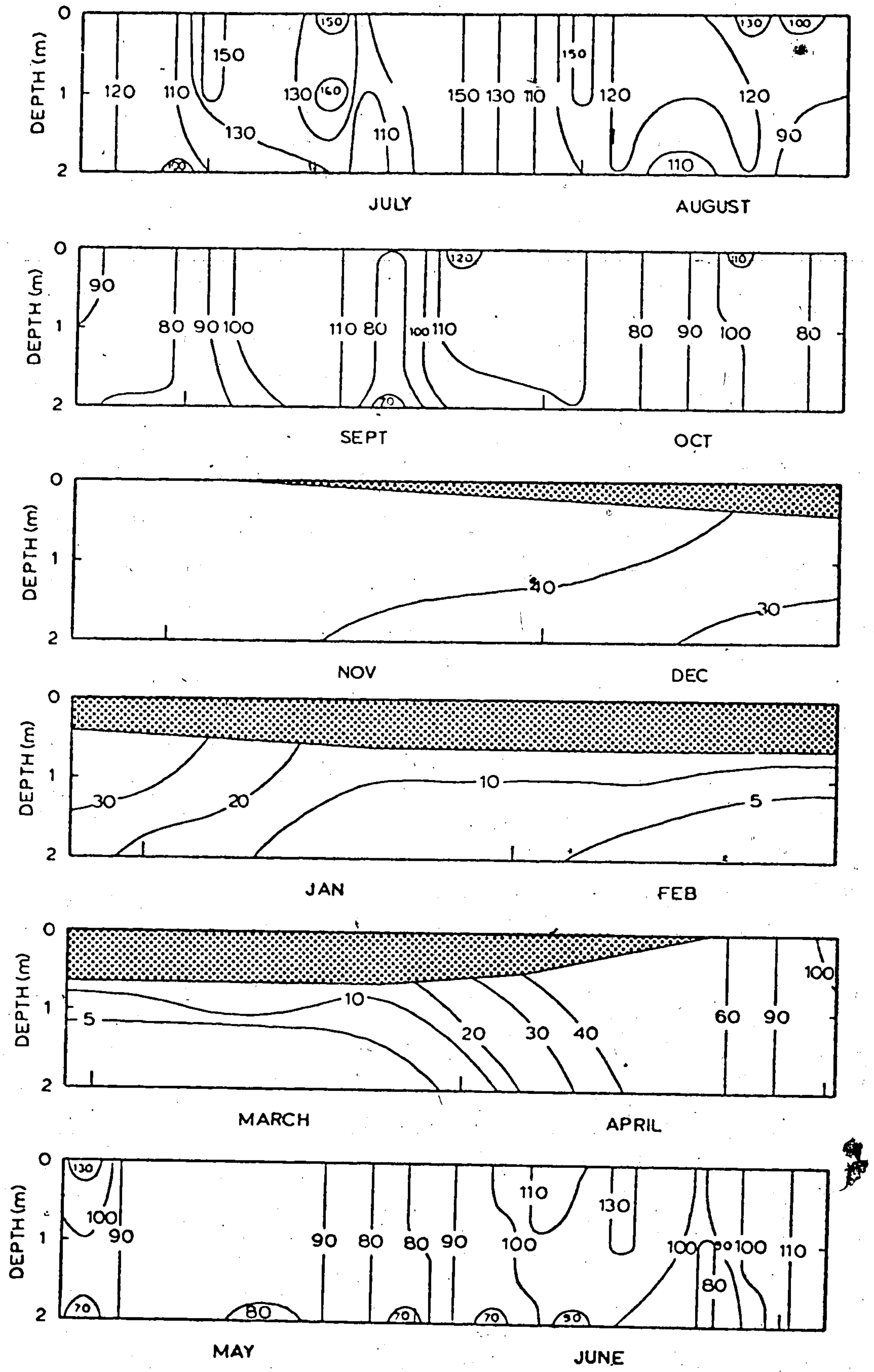
Oxygen saturation increased rapidly after break-up and was approximately 90% on May 7, 1976. The remainder of May was stable with oxygen saturations averaging 70%.

During overcast weather in early June, the oxygen saturation declined with water at most depths less than 50% saturated. By mid June the weather had cleared and the oxygen saturation increased to 80%.

North-east Basin

Oxygen saturations were high at station C during June 1975 (Fig. 6). During early July, the saturation rose to 160% but no oxygen depletion near the sediments was noted as in the main basin.

Figure 6. Isopleths of percentage oxygen saturation at station C, 1975-1976. Stippled areas represent ice drawn to scale.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MARCH
APRIL
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MAY
JUNE

Late July and August also showed high oxygen saturation, an indication of high primary productivity. During October the saturation dropped slightly but was stable at 80%.

Under the ice the oxygen saturation dropped more quickly at station C than at station A. By mid December the oxygen saturation was 40% and by late January the saturation had dropped to 10%. Low levels of oxygen were maintained until early April when increasing phytoplankton productivity raised the saturation to 30%. The spring increase in oxygen began earlier at station C than did the corresponding increase in the main basin.

After spring break-up the saturation rose rapidly and was approximately 100% by early May. During the rest of May and the first half of June, the saturation was stable, fluctuating between 80% and 90%. With the advent of clear weather in mid-June, the oxygen saturation rose to over 100% and, with the exception of 80% values in late June, remained over 100% until July 2. The 80% values in late June were associated with cold rainy weather.

WATER CHEMISTRY

Results of the water chemistry analyses are shown in Tables 2 and 3. The pH in Hastings Lake was always alkaline, the lowe[illegible] value being 7.8 recorded from station A in February 1976. No obvious seasonal trend was noted and values at stations A and C were similar. Conductivity values varied considerably but a distinct increase was noted during the winter. Values at stations A and C often differed considerably on any particular day but neither station showed a continuously higher reading. Total hardness values show

TABLE 2

Chemical parameters at station A.
All units are in mg/l except pH and conductivity (µmhos/cm).

		Hardness CaCO$_3$					Alkal. as CaCO$_3$	
	pH	Calc.	Total	Cond.	Cl$^-$	SO$_4$	Phenol.	Total
21/05/75	8.5	98	279	724	7.6	263	8	197
06/06/75	9.2	42	189	586	7.7	157	20	134
19/06/75	8.8	105	294	885	11.4	281	12	198
03/07/75	9.2	100	286	818	10.3	296	30	203
18/07/75	9.1	50	208	615	7.3	214	16	142
07/08/75	9.1	44	215	584	9.2	215	19	151
20/08/75	8.8	45	235	705	11.2	232	12	165
06/09/75	9.2	49	214	632	9.3	193	24	157
20/09/75	9.0	46	215	574	8.6	192	22	150
04/10/75	9.2	90	285	820	14.9	233	32	201
25/10/75	8.9	100	295	691	12.0	234	24	217
03/12/75	8.5	100	320	917	10.9	288	8	222
13/01/76	9.0	88	302	765	10.6	184	26	213
19/02/76	7.9	77	290	1075	12.7	279	--	--
16/03/76	8.6	123	344	983	11.3	204	17	272
06/04/76	8.8	73	346	1087	8.8	284	--	--
26/04/76	8.0	76	291	945	7.2	300	--	253
27/05/76	8.4	86	303	947	7.2	244	--	--
23/06/76	8.3	88	287	999	7.0	240	--	--

TABLE 2 (continued)

All Phosphate readings expressed as PO_4.

	Ttl PO_4	Ortho PO_4	Orgn PO_4	Ttl Kjl N	Orgn N	NO_3-N
21/05/75	0.31	0.06	0.14	2.15	2.13	0.07
06/06/75	0.28	0.08	0.12	1.75	1.57	0.05
19/06/75	0.49	0.34	0.10	2.49	2.43	0.07
03/07/75	0.43	0.29	0.11	2.19	2.07	0.06
18/07/75	0.50	0.25	0.10	1.92	1.91	0.03
07/08/75	0.36	0.11	0.19	2.28	2.17	0.09
20/08/75	0.39	0.08	0.14	2.38	2.10	0.05
06/09/75	0.26	0.04	0.14	2.22	2.14	0.07
20/09/75	0.29	0.08	0.10	2.16	2.09	0.04
04/10/75	0.32	0.06	0.13	2.31	2.22	0.06
25/10/75	0.38	0.04	0.16	2.25	2.19	0.06
03/12/75	0.25	0.05	0.12	2.63	2.44	0.13
13/01/76	0.87	0.55	0.14	3.30	2.96	0.09
19/02/76	0.97	0.76	0.12	--	--	--
16/03/76	1.13	0.72	0.20	3.36	2.96	0.16
06/04/76	0.86	0.56	0.18	2.62	2.23	0.13
26/04/76	0.73	0.40	0.25	--	--	--
27/05/76	0.64	0.37	0.13	--	--	--
23/06/76	0.69	0.48	0.09	--	--	--

TABLE 3

Chemical parameters at station C.
All units are in mg/l except pH and conductivity (μmhos/cm).

		Hardness $CaCO_3$					Alkal. as $CaCO_3$	
	pH	Calc.	Total	Cond.	Cl^-	SO_4	Phenol.	Total
03/06/75	9.2	91	271	726	9.0	267	28	177
19/06/75	8.8	75	252	743	7.9	162	14	163
02/07/75	9.1	45	223	597	9.4	191	18	140
17/07/75	9.1	46	198	578	7.6	172	18	138
07/08/75	9.1	40	218	673	10.6	205	24	149
20/08/75	9.0	44	216	737	10.4	202	17	152
06/09/75	8.8	55	201	745	8.2	181	17	159
20/09/75	9.2	56	228	671	10.2	233	25	164
25/10/75	8.7	106	283	898	10.0	229	18	212
11/06/76	8.5	111	300	714	9.3	186	8	226
02/07/76	8.8	113	288	698	12.4	177	22	226

TABLE 3 (continued)

All Phosphate readings expressed as PO_4.

	Ttl PO_4	Ortho PO_4	Orgn PO_4	Ttl Kjl N	Orgn N	NO_3-N
05/06/75	0.42	0.19	0.12	2.04	1.96	0.04
19/06/75	0.65	0.37	0.16	2.38	2.15	0.07
02/07/75	0.43	0.21	0.13	2.39	1.87	0.04
17/07/75	0.86	0.32	0.33	2.26	2.24	0.04
07/08/75	0.36	0.12	0.10	2.51	2.38	0.07
20/08/75	0.37	0.05	0.10	2.51	2.40	0.07
06/09/75	0.33	0.04	0.11	2.06	1.89	0.05
20/09/75	0.23	0.02	0.12	2.29	2.20	0.04
04/10/75	0.33	0.07	0.20	2.07	2.00	0.05
25/10/75	0.40	0.04	0.22	3.05	2.99	0.13
06/04/76	0.44	0.18	0.16	3.20	--	0.04
11/06/76	0.56	0.25	0.17	2.52	2.52	0.05
02/07/76	0.53	0.22	0.18	2.55	2.55	0.08

Hastings Lake to be a hardwater lake. Both calcium and total hardness were lowest during summer and early fall. Low values were also recorded in early June 1975 at station A. At both stations A and C, total alkalinity was high in the winter months but phenolphthalein alkalinity showed no obvious trends. Chloride readings show the lowest values during spring and early summer at station A. Lack of sufficient data makes it impossible to determine whether the same pattern held at station C.

Both total phosphate and orthophosphate showed high concentrations in late winter at station A. Readings from spring and early summer 1976 were higher than corresponding readings in 1975. Total and orthophosphate values for station C were usually higher than those at station A. A distinct pulse in both values was noted during July and August 1975.

Total Kjeldahl nitrogen readings were similar at both stations. No seasonal trend was noticed, but the spring and early summer 1975 values appeared low compared to the rest of the sampling period. Organic nitrogen generally followed the pattern of Kjeldahl nitrogen and made up the major portion of each total Kjeldahl reading. Nitrate readings were very low; maxima were found in late fall and through the winter. The high phosphate readings indicate the obvious eutrophic nature of Hastings Lake but, according to Vollenweider (1968), low nitrate levels are indicative of low trophic status. Ruttner (1963), however, has noted that "markedly eutrophic" lakes often show low concentrations of nitrate due to rapid uptake by phytoplankton.

FOOD

Data on food can be broken down into three areas: bacteria populations, phytoplankton populations, and particle size classification and enumeration. In some respects information on particles overlaps the other two areas.

BACTERIA

Because of the inefficiency of plate counts in determining the absolute number of bacteria cells in a water sample (Collins and Kipling, 1957), it is only possible to use the bacteria data in a comparative way. Edmondson (1965) used a factor of 200 to convert plate counts to actual numbers of cells present but admitted the ratio between direct counts and plate counts varied considerably. Since the counts in my study were not converted to biomass as Edmondson's were, the original plate counts were used.

Bacteria population dynamics at stations A and C are illustrated in Figure 7. The population at station A increased steadily during spring and early summer to a maximum in late July and early August. Numbers declined quickly after early August, were very low by October 3, and remained low through fall and into winter with some minor increases. A sudden increase in density was recorded in early April but the population appeared to die out by spring break-up three weeks later. The concentration remained low during May but a strong increase was seen during June, approximately the same time as the 1975 increase. The population at station C showed the same general trends as that at station A but the maxima were higher than

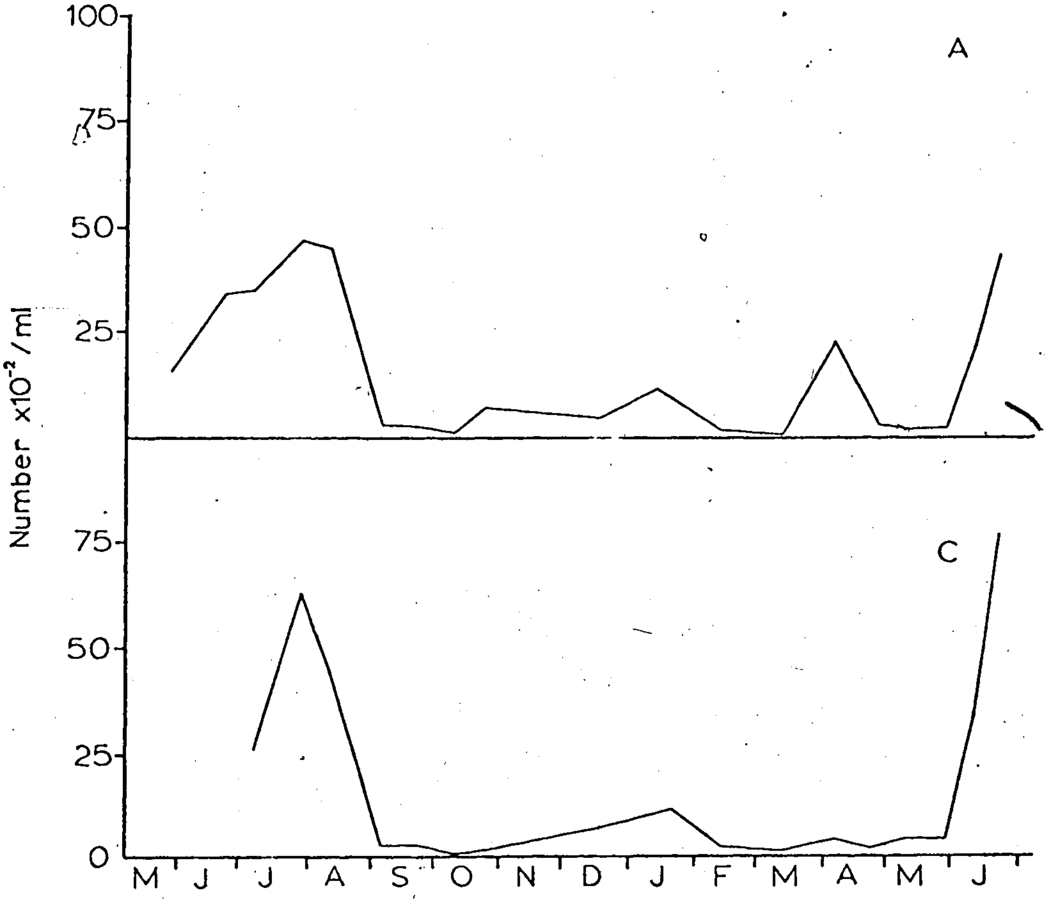


Figure 7. Bacteria cell numbers at stations A and C, 1975-1976.

those at station A.

For most of the year the vertical distribution pattern was uniform at both stations A and C. During times of high density, however, bacteria were more numerous at the surface at station A but more numerous near the bottom at station C. Under the ice bacteria concentrated near the water surface.

PHYTOPLANKTON

Quantitative data on phytoplankton exist only for those cells that I considered edible by rotifers. The decision concerning edibility of cells was based on Pourriot's (1957) work on food habits of rotifers and on results of Edmondson (1960, 1965). Only small cells were considered edible, ie cells with both length and width greater than 15µ were considered inedible. With the exception of Ankistrodesmus all cells considered edible were essentially spherical or elliptical in shape. Cells with long spines or processes were considered inedible. Cells considered edible were free of thick gelatinous sheaths. Only individual cells were considered edible, large colonies of otherwise edible cells were considered inedible. Of the eight cell types selected for counting, four were among those considered edible by Edmondson (1965). Edmondson did not count Kirchneriella as he considered it to be colonial. In my study the cells usually appeared as individuals and were counted. Relative abundances were recorded for three types of blue-green algae, since an observation, which will be discussed later, showed they may have some food value.

Cryptomonas

Cryptomonas, the largest cell included in counts, measured 15-20 µ by 5-10 µ. It may be too large for most rotifer species to ingest but it has been suggested (Edmondson, 1965) that it may be important for rotifers such as Polyarthra that possess a virgate mastax.

Cryptomonas reached maximum numbers in spring and fall (Fig. 8) and were rare or absent during July and August. At stations A and C the density of Cryptomonas dropped sharply during late May and early June 1975, then began a period of slower decline, reaching a minimum in August. In fall, numbers at both stations increased slowly with numbers at station C being approximately four times higher than those at station A; the winter population at station C was ofter an order of magnitude larger than that at station A. In February, a distinct increase, which continued until ice break-up, was observed at both stations. Numbers declined sharply after break-up, then rose and declined again during June 1976.

During the year Cryptomonas showed a uniform vertical distribution with the exception of winter months when cells were concentrated near the ice.

Rhodomonas

Rhodomonas appeared to be a highly "edible" cell. Cell size averaged 4 µ by 9 µ during summer and slightly longer in winter. Like Cryptomonas, Rhodomonas appeared in largest numbers during spring and fall with minima in summer and mid-winter (Fig. 9). During spring and summer 1975, numbers of Rhodomonas at stations

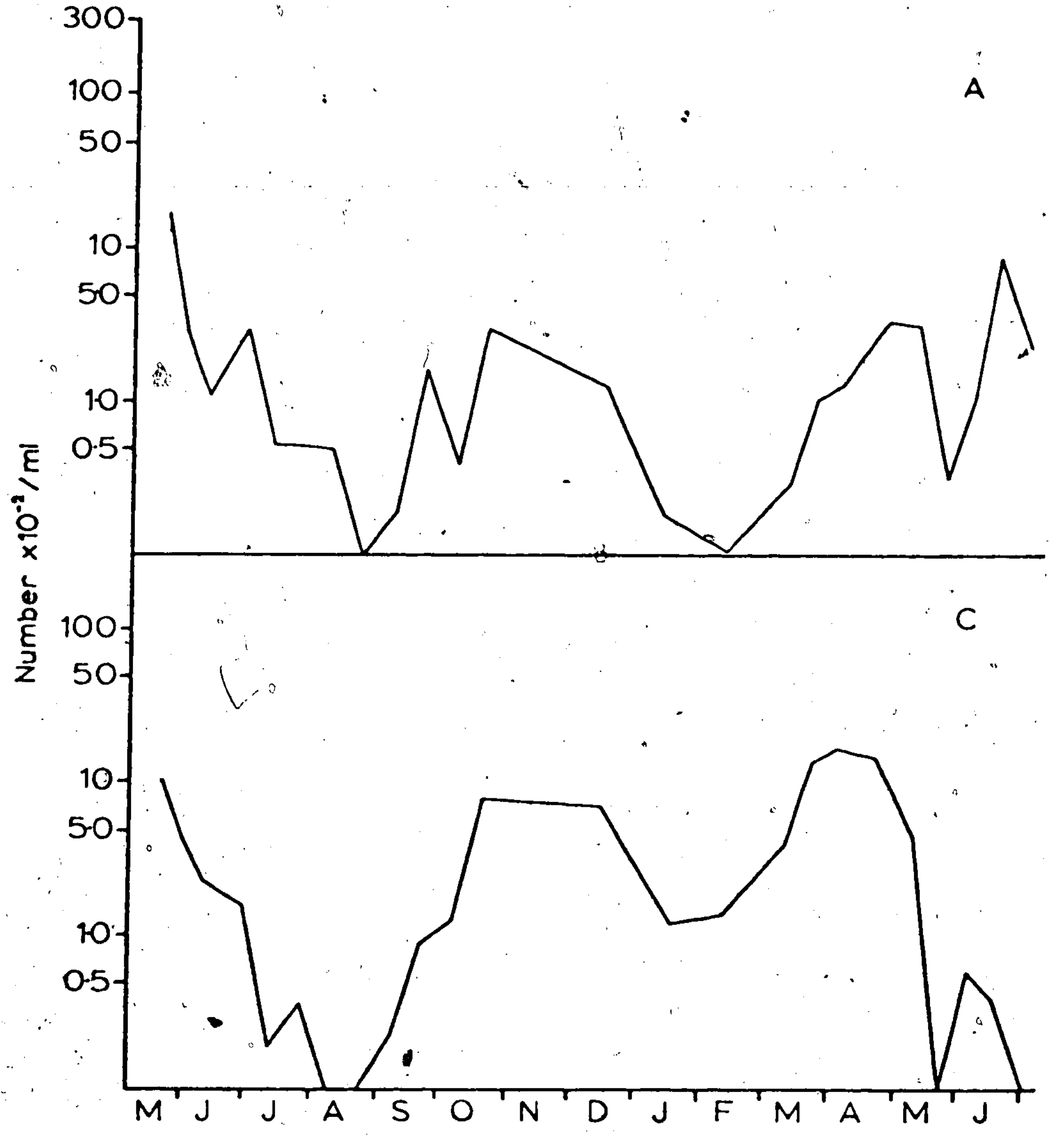


Figure 8. Cryptomonas cell numbers at stations A and C, 1975-1976.

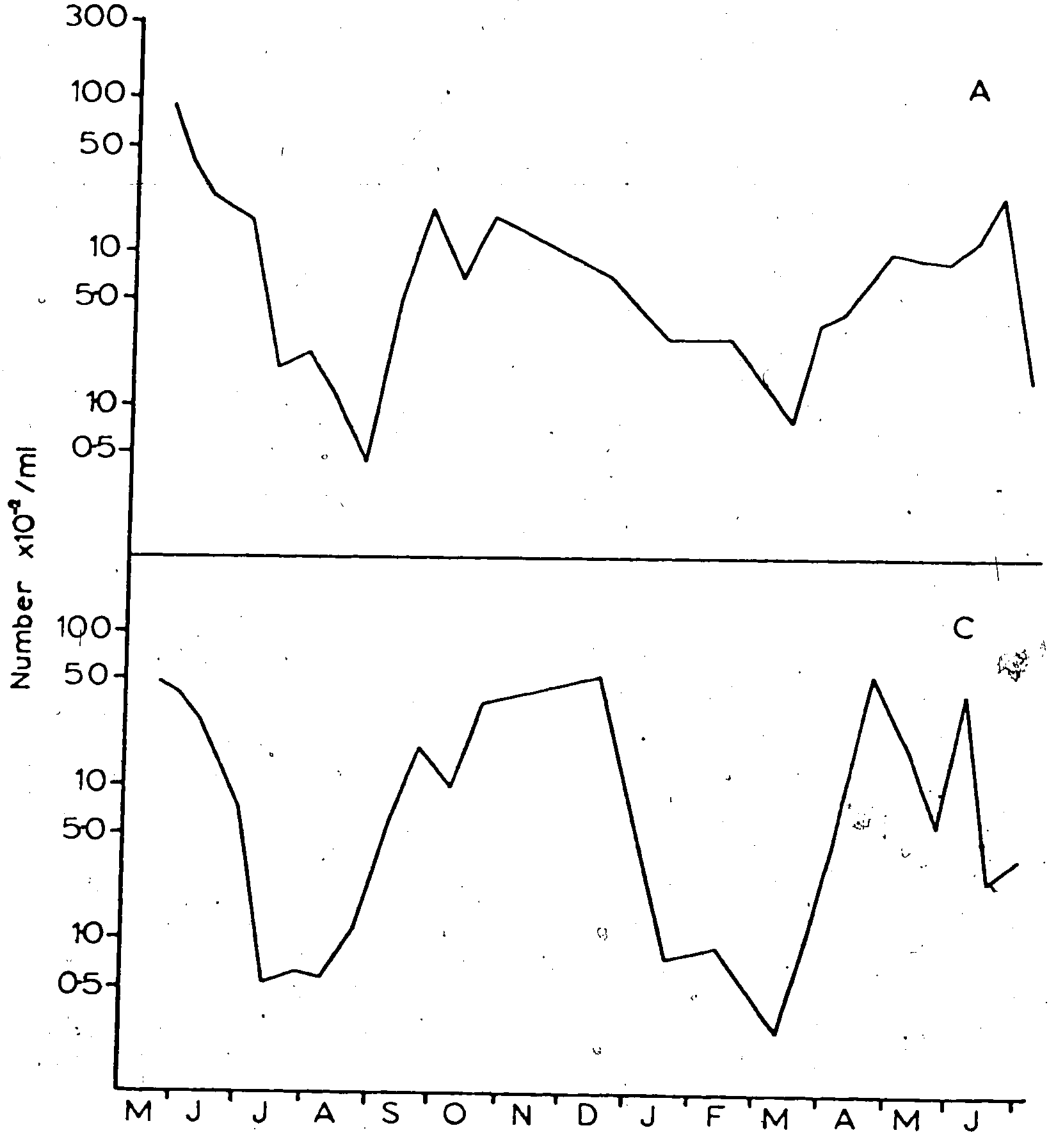


Figure 9. Rhodomonas cell numbers at stations A and C, 1975-1976.

A and C were similar. Densities at both stations declined steadily from late May to August. The fall increase ended with station C being more densely populated in December than station A. The remainder of winter was a period of dramatic decline in numbers at station C and more gradual decline at station A. Numbers at station A increased gradually during spring 1976 while the density at station C increased more rapidly but with a major drop in late May. Both populations appeared to be declining during early summer. While the 1975 and 1976 spring populations were similar at station C, the 1976 spring population at station A was much lower than that of 1975.

Rhodomonas often showed a preference for surface waters (Fig. 10). A strong surface concentration was observed during warm, calm weather in mid-July 1975. Surface concentrations were also noted during winter 1976, probably indicating a preference for higher light levels near the ice. During early spring 1976, vertical distribution was uniform but a preference for the surface was seen again during late May and June. Despite average winds during this time, Hastings Lake showed a gradient in oxygen concentration (Fig. 5), indicating a certain degree of stratification.

Chlamydomonas

A number of species of Chlamydomonas were probably present in Hastings Lake during the study period, ranging from 5µ to 15µ in diameter.

Like Cryptomonas, Chlamydomonas showed a rapid decline in density during early spring 1975, numbers of cells were approximately equal at stations A and C during this time (Fig. 11). Unlike Cryptomonas and

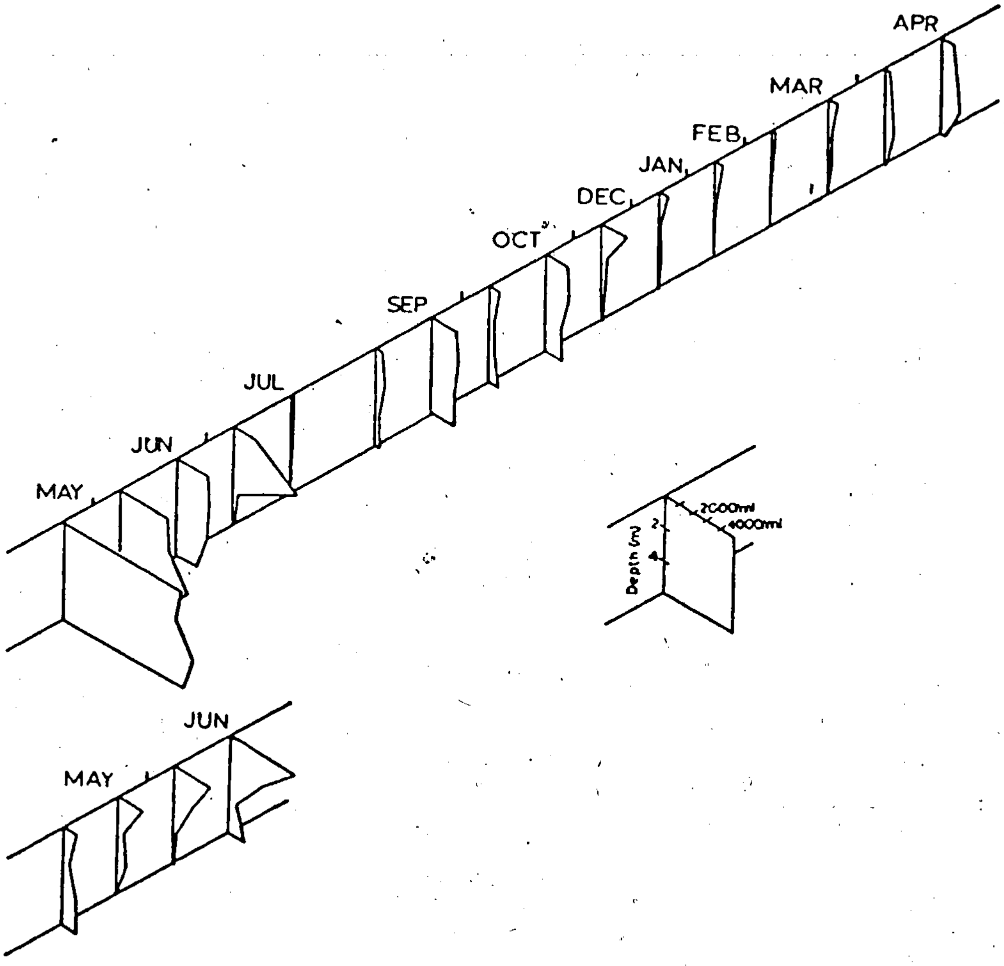


Figure 10. Vertical distribution of Rhodomonas at station A. May 23-July 14, 1975; September 10, 1975-June 18, 1976.

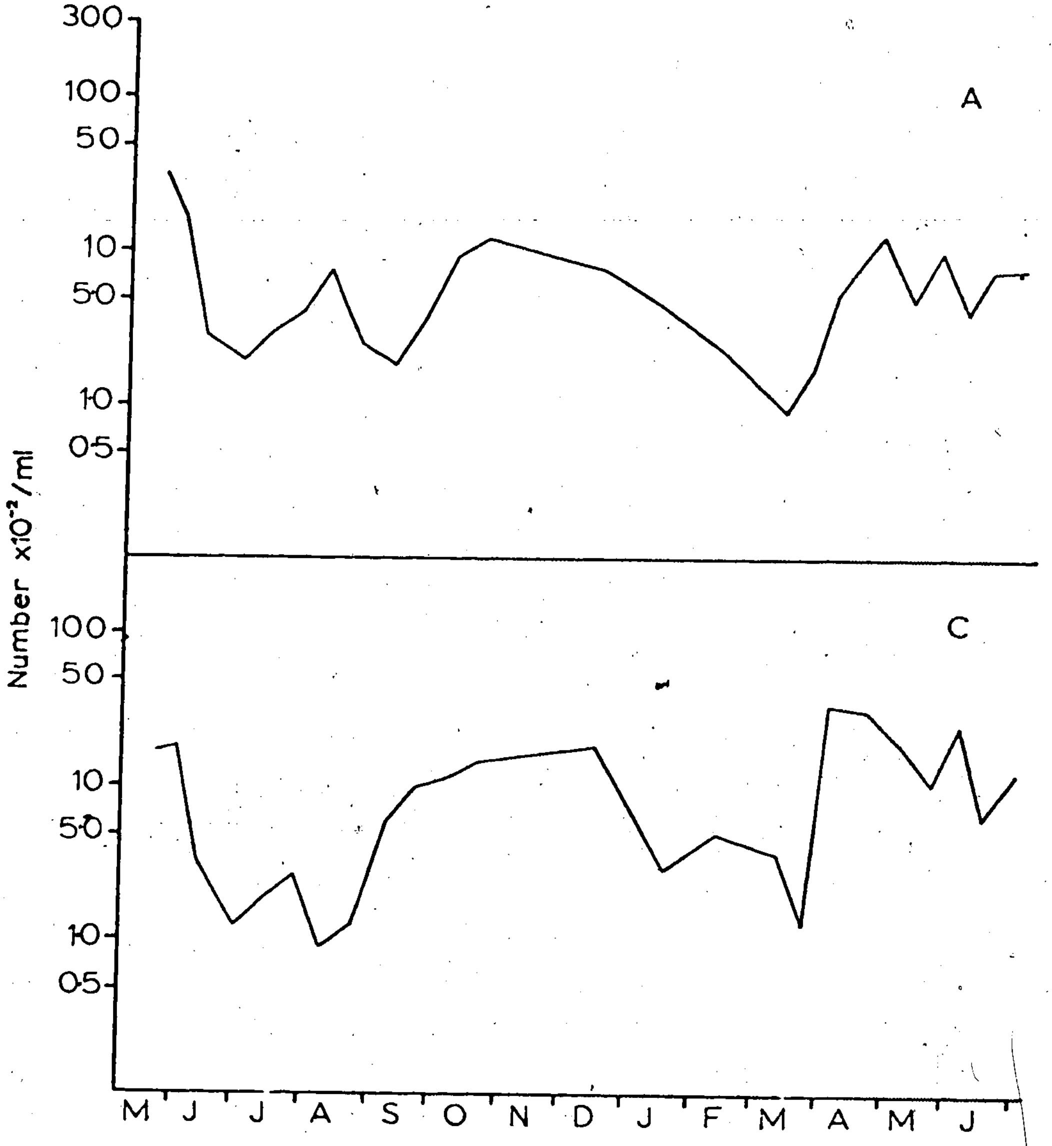


Figure 11. Chlamydomonas cell numbers at stations A and C, 1975-1976.

Rhodomonas, *Chlamydomonas* showed a distinct increase in numbers at stations A and C during July and August. It is possible that this increase indicated the presence of a species different from the spring population. Following the summer peak, the numbers declined in August but the population increased again during autumn. During winter, numbers at both stations declined to a minimum in March 1976. A sharp increase in numbers occurred in April with higher densities recorded at station C. Both populations appeared to stabilize during May and June. For most of the year, *Chlamydomonas* showed a uniform vertical distribution (Fig. 12). Surface concentrations were noted during winter and late spring 1976, a situation similar to that of *Rhodomonas*.

Kirchneriella

As mentioned earlier, *Kirchneriella* cells are often grouped into colonies and covered by mucilage. The individual cells are crescent-shaped and 5 to 7μ across the apices.

Populations of *Kirchneriella* at stations A and C declined sharply during early June, 1975 (Fig. 13). Numbers at the two stations were similar at this time. During the summer months *Kirchneriella* were rare or absent at both stations. A strong fall pulse occurred in September, 1975 with numbers increasing rapidly but levelling off during October. At station A, *Kirchneriella* remained at high numbers until March, 1976, while the station C population declined sharply during early winter. In late March and early April 1976 densities were equal at the two stations. In spring 1976 numbers at station A decreased but increased at station C.

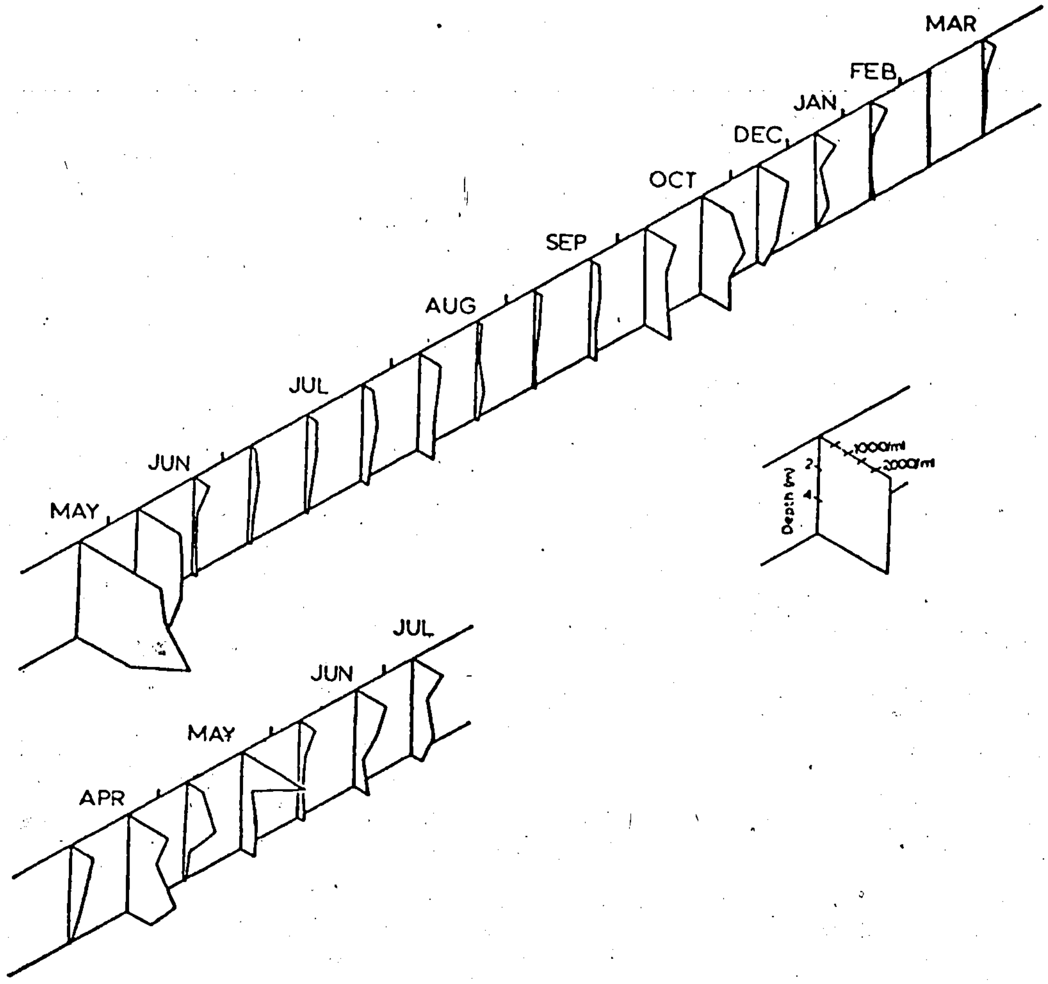


Figure 12. Vertical distribution of Chlamydomonas at station A. May 23, 1975-July 2, 1976.

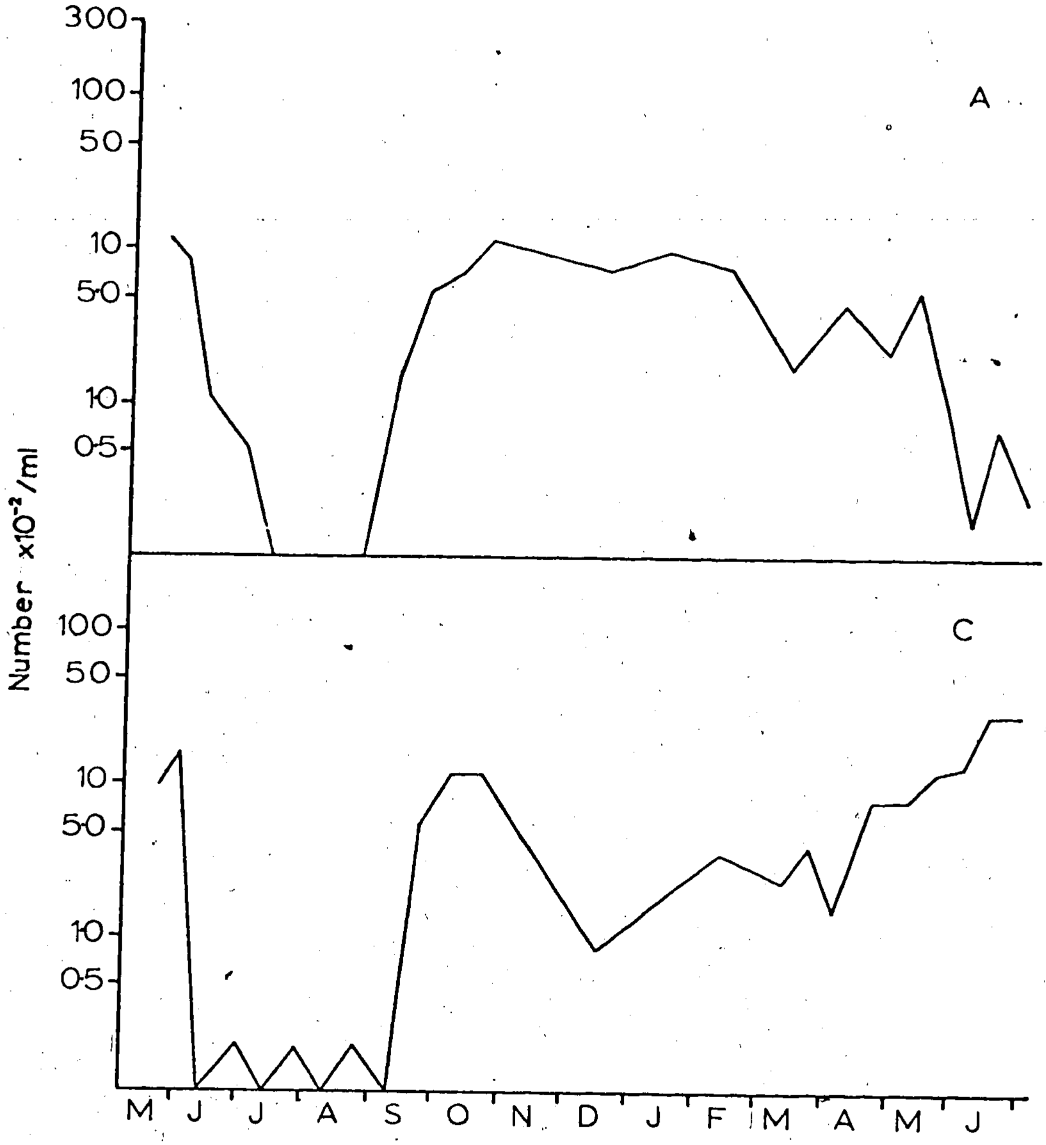


Figure 13. Kirchneriella cell numbers at stations A and C, 1975-1976.

Kirchneriella showed an interesting vertical distribution during the winter months (Fig. 14), concentrating closer to the lake bottom while most of the other cells concentrated near the ice. During ice-free periods distribution was uniform.

Ankistrodesmus

Ankistrodesmus was probably represented by several species during the year. The cells are long, often greater than 20μ , but narrow. Cells were usually single but were occasionaly seen in clusters.

Numbers of Ankistrodesmus dropped rapidly during late May and and early June 1975 (Fig. 15). During the remainder of June and throughout July, the numbers, approximately equal at stations A and C, declined slowly to a minimum in August, then increased to a maximum in late October. Numbers declined sharply after freeze-up and remained at low levels for the rest of the winter. Both stations showed increases during April and May 1976 but station C exhibited much higher numbers. The population density at station C appeared to be levelling off during June 1976 while the numbers at station A appeared to be increasing. Ankistrodesmus cells at station C were approximately an order of magnitude more dense than at station A during this time. For most of the year, Ankistrodesmus showed a uniform vertical distribution with the exception of late April and May 1976 when concentrations at the surface were observed.

Rhabdomonas

Rhabdomonas appeared to be a highly edible cell, approximately

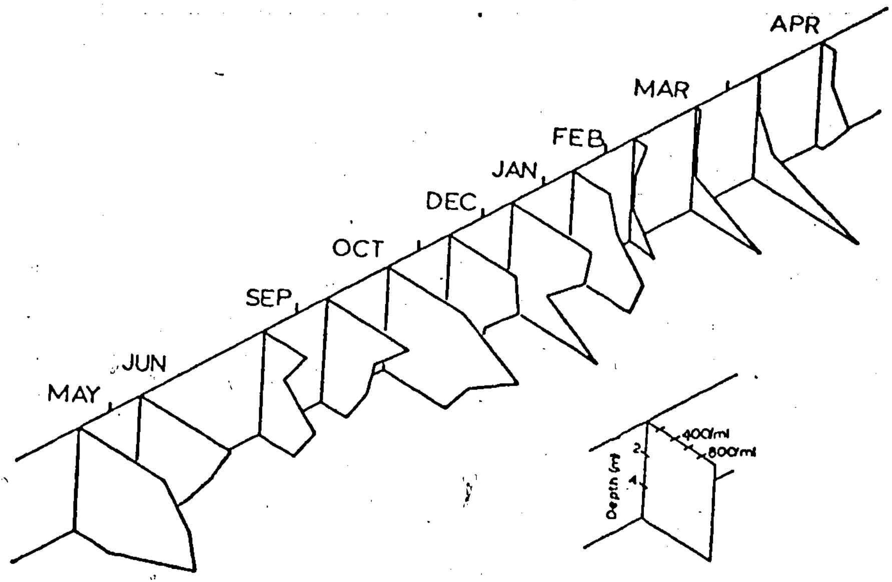


Figure 14. Vertical distribution of Kirchneriella at station A. May 23-June 6, 1975; September 23, 1975-April 27,1976.

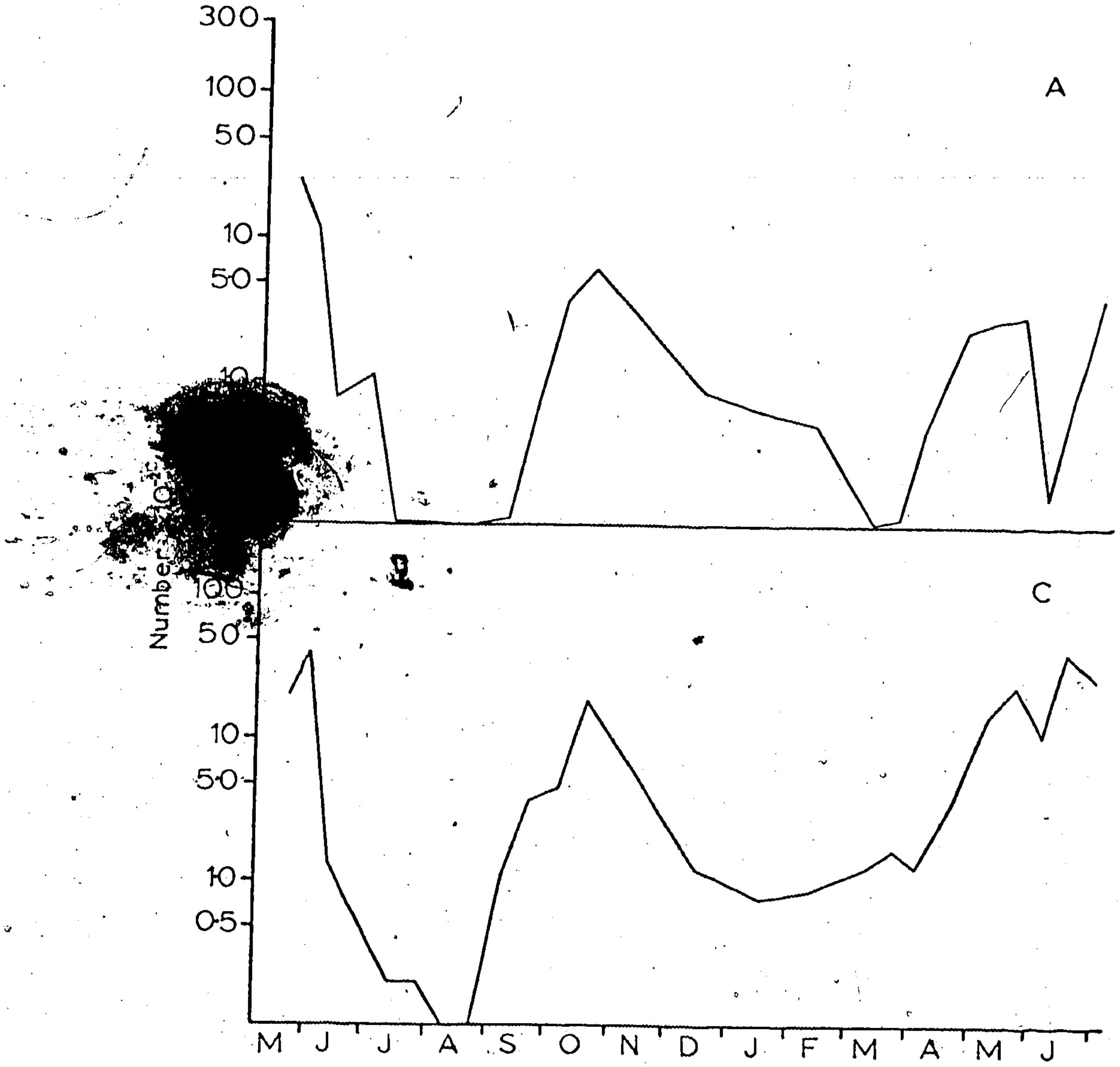


Figure 15. <u>Ankistrodesmus</u> cell numbers at stations A and C, 1975-1976.

4 μ by 1 μ and existed as individual, flagellated cells. It appeared in high numbers during spring only. When sampling began in late May 1975, the population at station A was over 1600 cells per ml but disappeared completely by mid-June, as did the small population at station C (Fig. 16). Until late winter 1976, populations remained at zero with the exception of a few cells seen during late August and early September 1975 and February 1976. The 1976 spring pulse began in late March at station A and continued until May when the numbers declined again. The population density in 1976 was never as high as in 1975 but, like spring 1975, no cells were seen after June. A short-lived pulse was seen at station C during April and May 1976 but again, the population density was less than that at station A. The vertical distribution was uniform with slight concentrations near the surface during April 1976.

Small Flagellates

Because of their size, 3 μ by 1 μ, the small flagellates proved difficult to identify but were counted because of their apparent edibility and large numbers. The cells counted do not represent a heterogeneous group of unidentified cells; rather, the size and form were regular throughout the year, indicating perhaps that the cells were of a single species.

Numbers of cells at station A declined rapidly during late May 1975 and a small population was maintained until August (Fig. 17). In contrast, no small flagellates were found at station C during spring and summer. Small flagellates were present at both stations

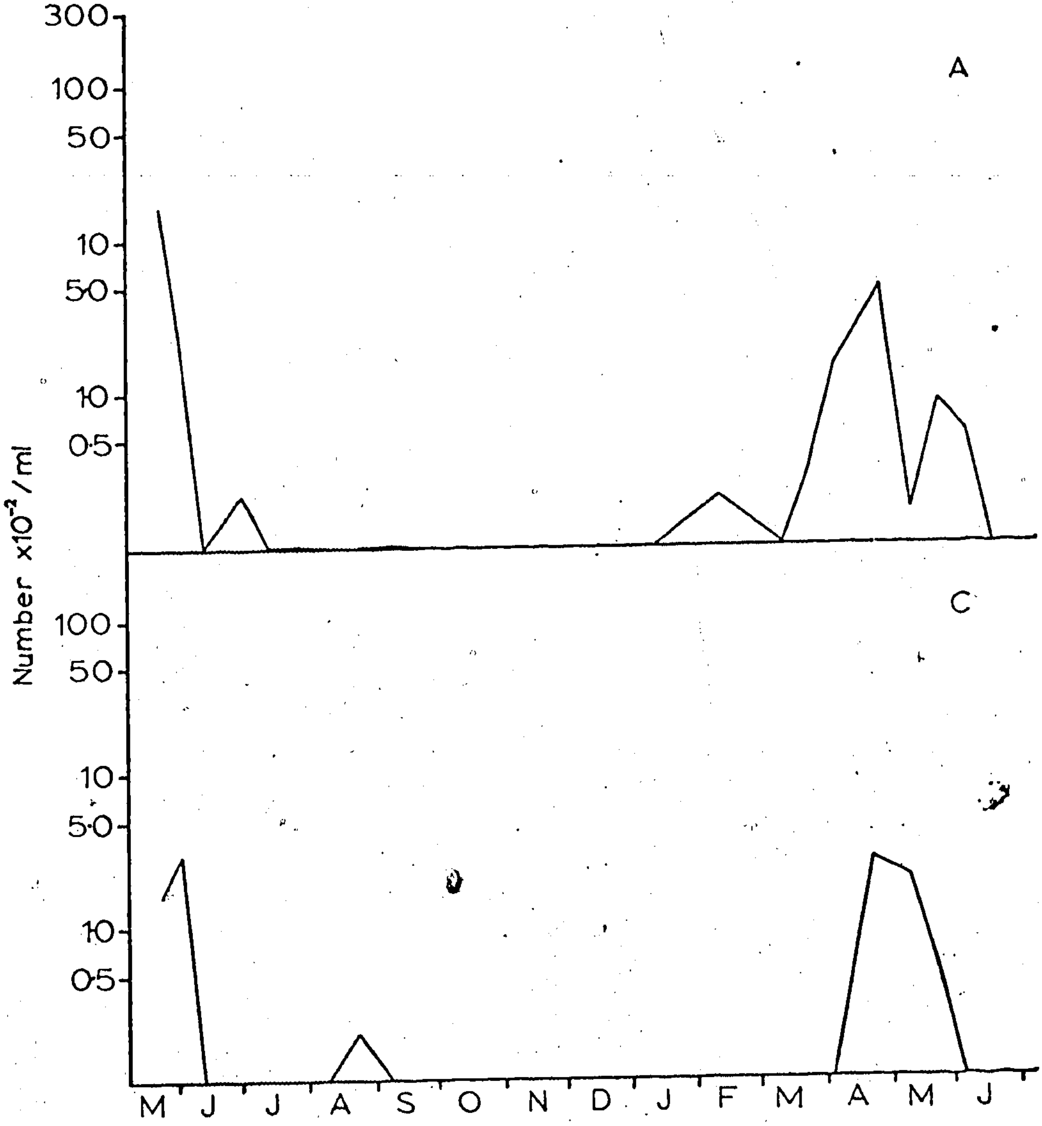


Figure 16. Rhabdomonas cell numbers at stations A and C, 1975-1976.

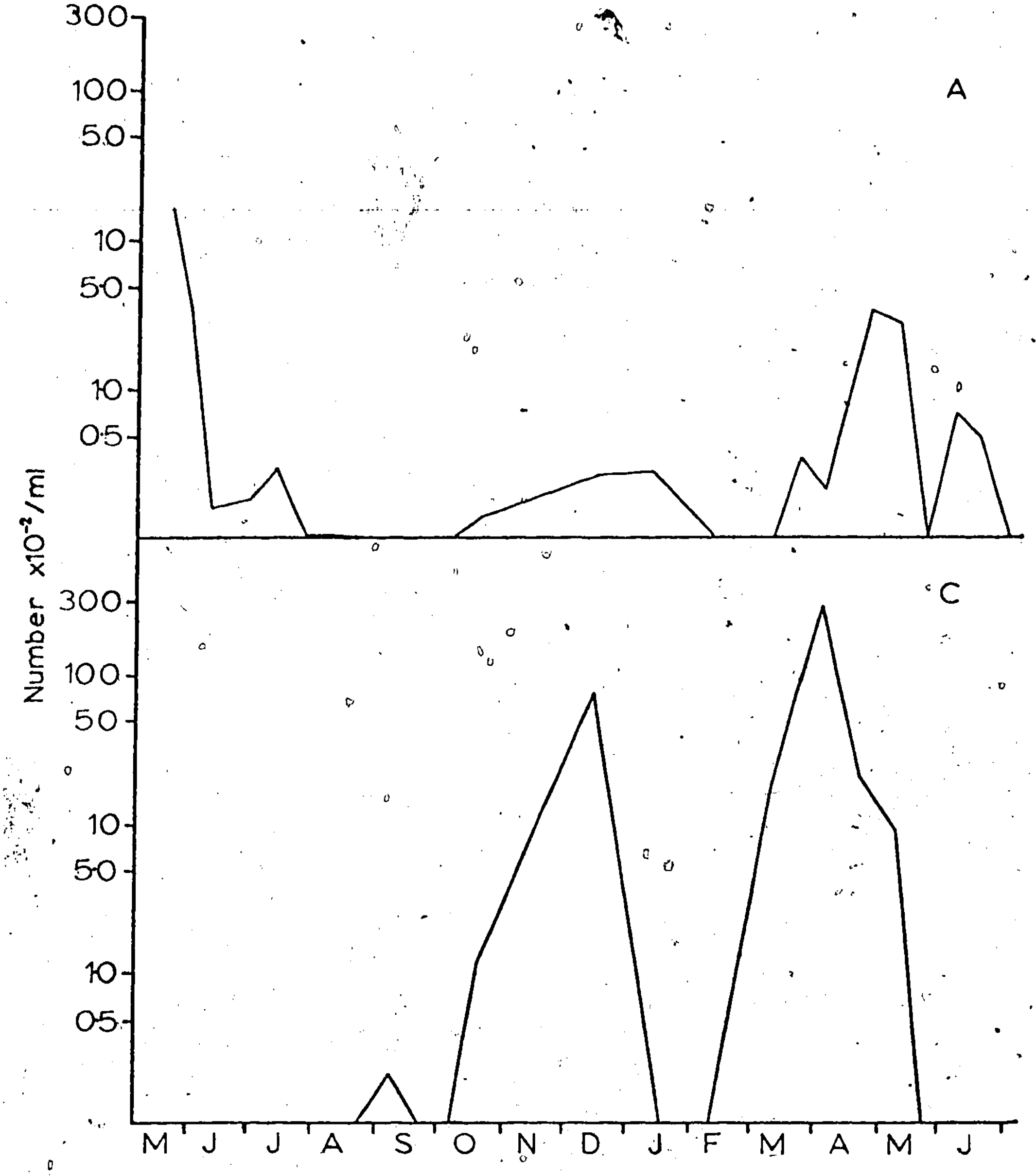


Figure 17. Small flagellates cell numbers at stations A and C, 1975-1976.

during fall and early winter, with station C supporting a much higher population. A second increase at station C, beginning in early March 1976, reached close to 30,000 cells per ml in early April. This population subsided quickly and no cells were found after early May. A second increase occurred at station A about this time, but the numbers were fewer and the population disappeared during late June 1976. The vertical distribution was uniform with the exception of late April and mid-May 1976 when cells were more concentrated near the surface.

Ochromonas

Ochromonas is 2 µ by 6 µ and elliptical in shape. During the study period Ochromonas appeared at station A during late March and early April 1976, rising in numbers from zero in mid-March to a maximum of 600 cells per ml in early April; no cells were found in late April. Most of the cells were found near the surface. Ochromonas was never found at station C.

Total Edible Cells

In an effort to summarize data on phytoplankton cells, population densities of each species were summed and expressed as Total Edible Cells (Fig. 18). An obvious decrease in numbers at both stations was seen during spring and early summer 1975. Population densities at the two stations were similar. Low numbers were recorded in July and August but the populations rose quickly in autumn with station C exhibiting consistently higher population densities. The population at station C increased slowly in early winter but a sudden decrease

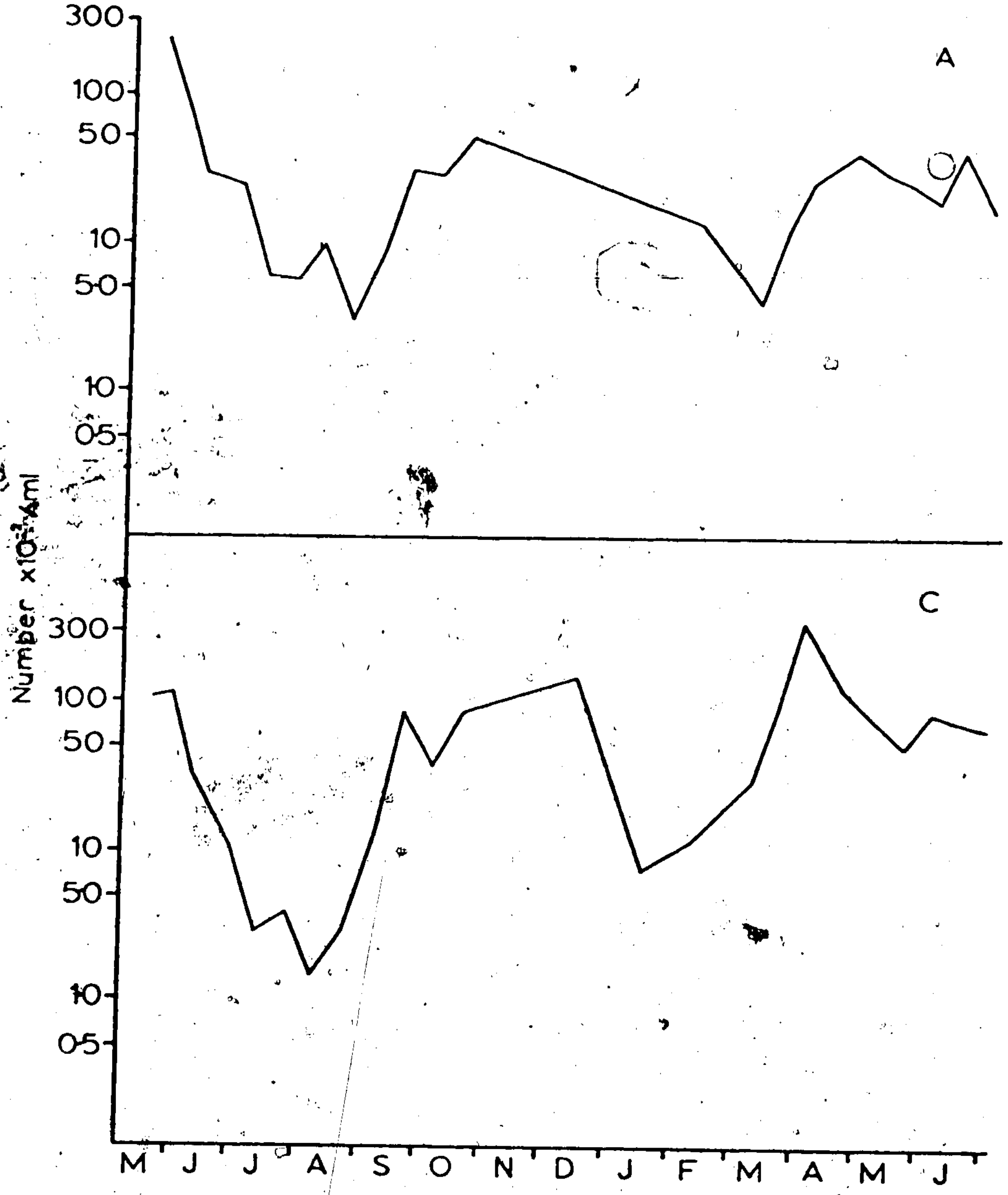


Figure 18. Total Edible Cells, cell numbers at stations A and C, 1975-1976.

was noted in January. Numbers increased again in February and reached a maximum of approximately 32,000 cells per ml in early April. The population density decreased after reaching the maximum but remained high for the remainder of spring and early summer. At station A the numbers decreased steadily during winter to a minimum of 400 cells per ml in March. The population density increased again during late winter and early spring and appeared to stabilize for the remainder of the study period. The population density at station C was consistently greater than that at station A during spring and early summer 1976.

Cyanophyta

Relative abundances of certain blue-green algae were recorded. Edmondson (1965) did not consider Cyanophyta important in his study but they are included here because of their dominance during summer months and the possiblilty, to be discussed later, of them acting as a food source. Three major cell types were quantified; <u>Anabaena</u>, a filamentous blue-green with round cells; <u>Microcystis</u>, a colonial algae with small cells tightly packed in mucilage; and <u>Aphanizomenon-Oscillatoria</u>, a combination of two filamentous genera with rectangular cells. Results are given in Table 4.

<u>Anabaena</u>

<u>Anabaena</u> first appeared in mid-June 1975. The population developed slowly at station A and was never rated more than "common". It had disappeared by early September. In 1976, <u>Anabaena</u> appeared at approximately the same time as it had in 1975. The station C

TABLE 4

Comparative abundances of Cyanophyta at stations A and C.
1 present; 2 fairly common; 3 common; 4 abundant; 5 very abundant.

Date		Anabaena	Aphanizomenon-Oscillatoria	Microcystis
23/05/75	A	---	---	---
	C	---	---	---
02/06/75	A	---	---	---
	C	---	---	---
13/06/75	A	1	---	---
	C	1	---	1
01/07/75	A	2	---	---
	C	1	1	1
14/07/75	A	3	3	3
	C	4	3	4
28/07/75	A	3	3	4
	C	5	5	5
11/08/75	A	3	4	4
	C	3	5	5
25/08/75	A	2	2	4
	C	3	3	3
10/09/75	A	2	2	3
09/09/75	C	2	5	2
24/09/75	A	1	2	2
	C	2	4	2
09/10/75	A	---	2	---
	C	1	4	2
23/10/75	A	---	2	---
	C	---	2	1
Winter 1975-76		---	---	---
07/06/76	A	---	---	---
	C	1	---	---
18/06/76	A	2	---	1
	C	2	---	---
02/07/76	A	2	---	---
	C	---	1	3

population of Anabaena, like that at station A, first appeared in mid-July 1975. However, the population at station C reached a higher density than that at A; it was rated "very abundant" in late July. The population persisted until early October. Populations were similar in 1975 and 1976.

Microcystis

Microcystis first appeared in mid-July 1975 at station C. Numbers rose quickly and cells were very abundant during late July and early August. The population declined through fall but remnants of colonies were still present in late October. Microcystis was first seen in early July in 1976 and was rated "common", indicating a rapid growth during late June. The 1975 population at station A was relatively short-lived and less dense than that at station C. It was first seen in mid-July and never rose above the "abundant" rating. No cells were found after late September. In 1976, a few cells were found in mid-June but none were found in early July.

Aphanizomenon - Oscillatoria

Filaments of Aphanizomenon and Oscillatoria did not appear until early July 1975 when they were found at station C. The population at station C reached "very abundant" levels during late July and early August, decreased during late August, but rose again in early September. The population was still "fairly common" in late October. In 1976, filaments were first found in early July. In 1975, population growth at station A was similar to that at station C but never reached the same high densities. No cells were found at station A during 1976.

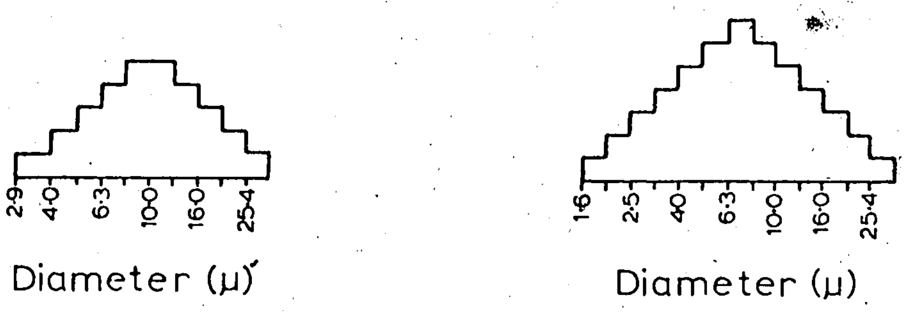
Although blue-green algae were found throughout the water column, all three groups concentrated in the surface layers. During calm weather the cells formed a thick "scum" on the surface.

PARTICLE SIZE ANALYSIS

In addition to bacteria and phytoplankton counts, data on particle size and abundance were collected in order to further define and measure food resources available to rotifers. A Coulter Counter was used in an effort to determine amounts of planktonic detritus in the lake. Results are difficult to interpret for two reasons. First, there is no information available on the use of particles as food; the organic content and degree of digestibility are unknown since particles may include phytoplankton cells, large bacteria, parts of decaying zooplankton (particularly shed exoskeletons), Protozoa, disturbed sediments from the bottom, etc. The second problem arises from the limitations of the machine. In computing the diameter of a particle, the machine determines the volume of the particle and then assumes a sphaerical shape and computes the diameter accordingly. It is clear that if a long, slender particle is counted the calculated diameter will be unrealistic. It should also be noted that variation in volume is more pronounced in larger size classes than in smaller since a large diameter particle constitutes a proportionately larger volume than a small diameter particle. It was impossible in this study to determine the importance of these errors.

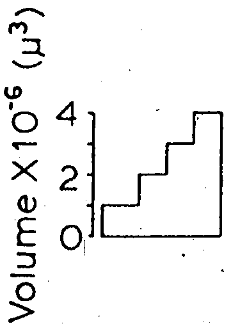
Results of the analyses are shown in Figure 19. One striking result was the similarity of the histograms from different depths.

Figure 19. Particle size analysis histograms from stations A and C at depths (m) indicated. Each histogram indicates total volume of particles in discrete size ranges.

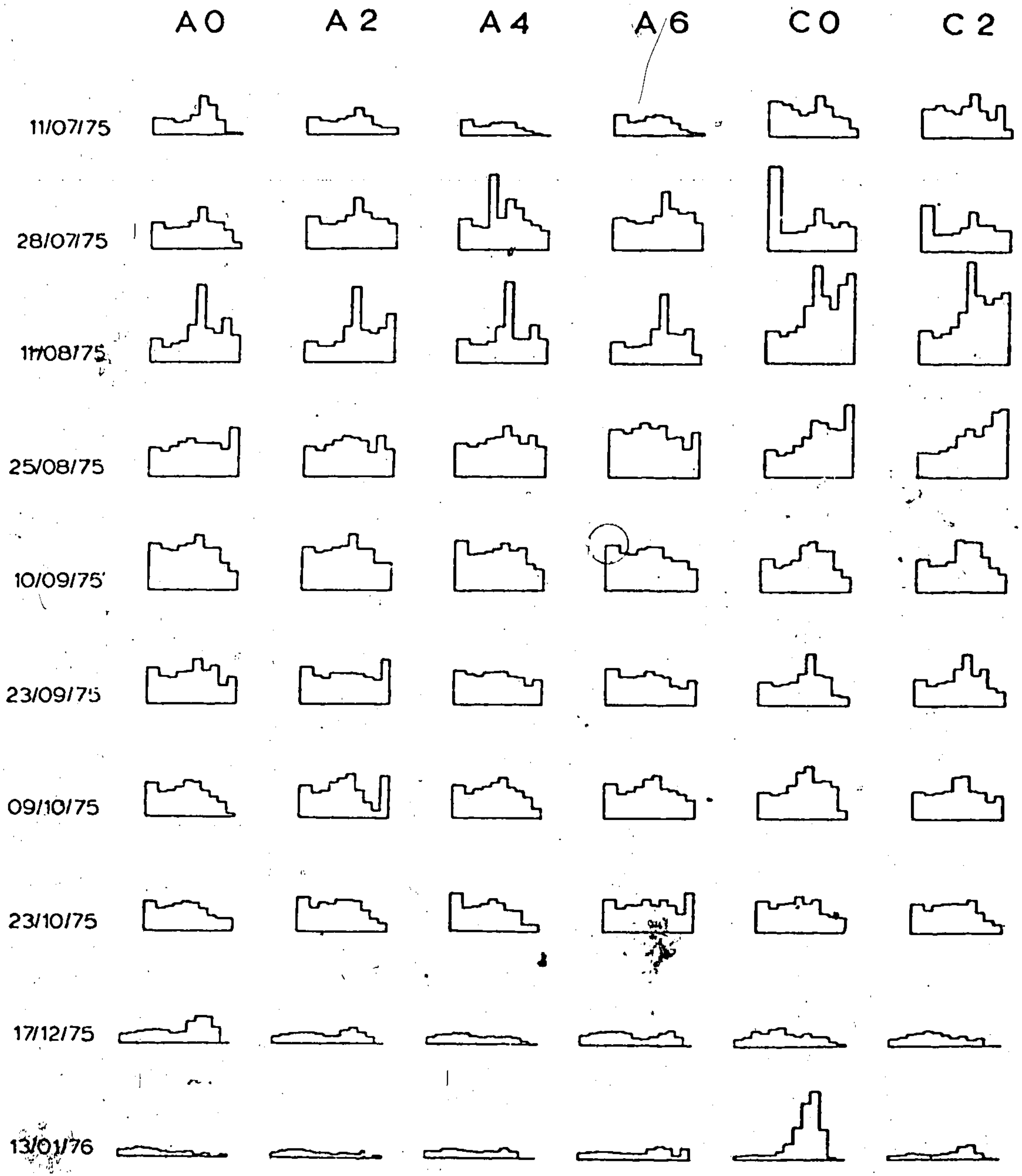


Size ranges used on Model B, used from 11/07/75-23/10/75. Approximately 2.6X.

Size ranges used on Model TA II, used from 17/12/75-02/07/76. Approximately 2.6X.



Volume scale drawn to scale.


A0
A2
A4
A6
C0
C2
11/07/75
28/07/75
11/08/75
25/08/75
10/09/75
23/09/75
09/10/75
23/10/75
17/12/75
13/01/76

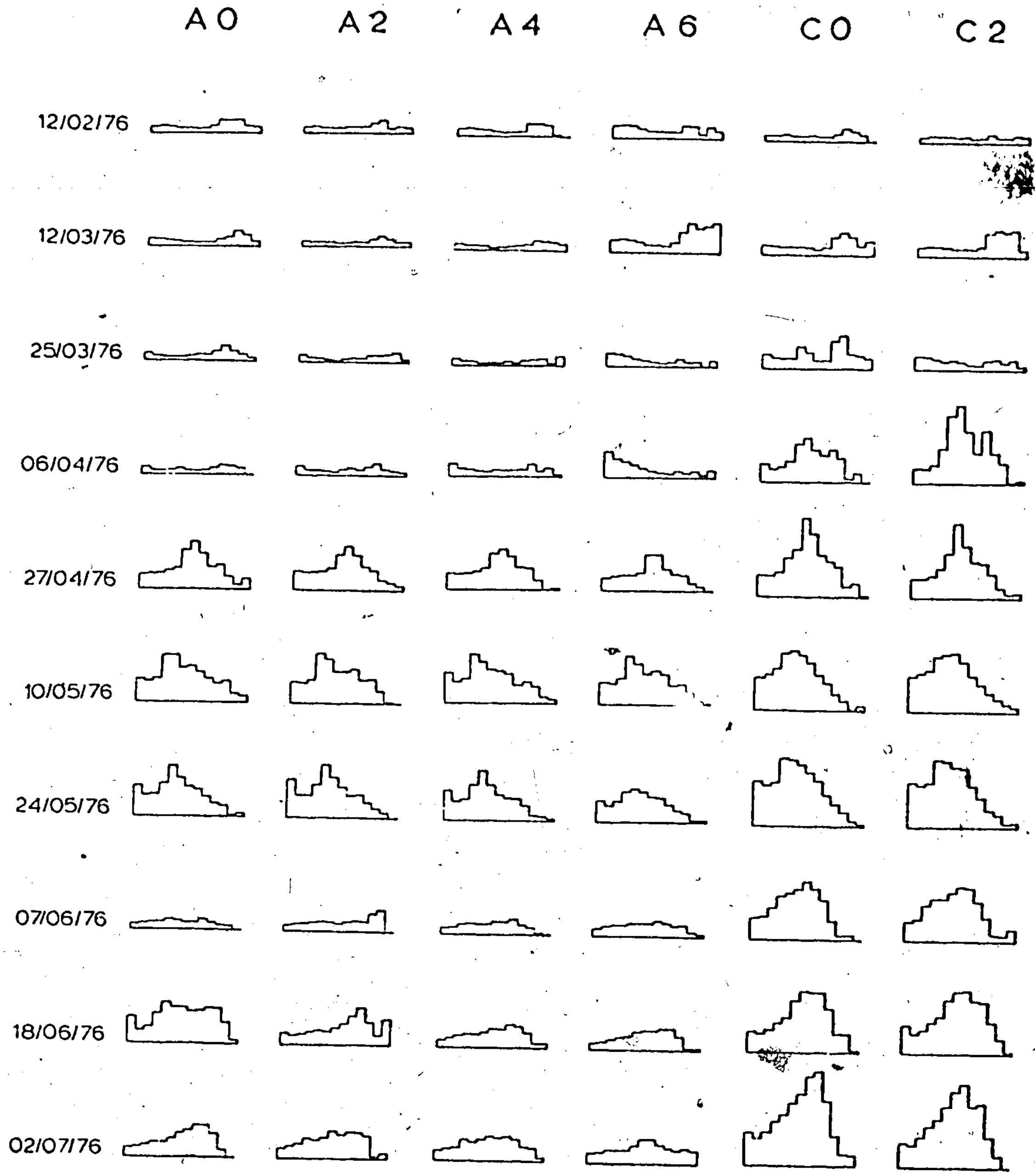


Figure 19. Continued.

Exceptions were noted at station C in mid-January when a larger volume in the 10 to 16 µ range was noted in the surface sample. Larger total volumes were also noted in March and early April 1976 at A6. In early March there was an increase in large particles while the next two dates showed a larger volume of small particles.

In mid-July, station A histograms showed low volumes with relatively even distribution across the channels. Throughout summer, volumes generally increased in all size classes. On August 11 a distinct peak was seen in the 10 to 12.6 µ size class. Total volumes stabilized again and remained high during late August and early September. A decrease was noted in late September that continued until late October with the larger size classes showing the greatest reduction.

Station C exhibited a different pattern during summer and fall 1975. A distinct peak in the 2.8 to 3.9 µ size class occurred in late July. The August 11 histograms show the same peak in the 10 to 12.6 µ size class as station A but also show a large proportion of the volume in larger size classes. Decline in total volume began in late August and, with a slight increase in early October, continued until freeze-up.

During the ice-free period total volumes at the two stations were approximately equal with the exception of August 11 when station C showed higher values.

After freeze-up, the Model TA-II was used to analyze samples. This machine included the same classes as the Model B but also extended the range down to particles 1.5 µ in diameter.

After freeze-up, total volumes dropped considerably at both stations. January [illegible] February readings were very low with the largest size channel (25 to 32 μ) often showing no volume. As mentioned earlier, a relatively large volume was recorded at CO in mid-January. This peak did not coincide with a peak in phytoplankton cells and remains unexplained. Histograms for station A during March and early April show the same low profile as the January and February data. Station C, however, showed slightly larger values during March and an obvious increase on April 6. This coincides with the observed phytoplankton increase at station C.

After break-up, volume at station A increased considerably with maximum volumes in the 5.0 to 6.3 μ and 6.3 to 8.0 μ ranges. This pattern persisted until early June. Station C maintained higher volumes than station A during this time but the maximum volumes were recorded in the same size ranges. Total volume dropped sharply at station A during early June. The volume increased again during late June and early July but maximum values were recorded in the 8.0 to 16.0 μ size range. Station C did not show a decrease in volume during early June but did show the same shift from maximum values in the 5.0 to 6.3 μ and 6.3 to 8.0 μ size classes to maximum values in the 8.0 to 16.0 μ range. During June and July 1976, station C showed high total volumes.

In general, changes in total volume were associated with changes in phytoplankton densities. High volumes in smaller size ranges during spring and fall were accompanied by peaks in the small phytoplankton cells and high volumes in the larger channels during summer and early fall were accompanied by Cyanophyta blooms. No obvious correlation with bacteria populations was noted.

CRUSTACEAN ZOOPLANKTON

Eight species of planktonic crustaceans were identified from Hastings Lake. The cladocerans were represented by *Daphnia pulicaria* Forbes, *Diaphanosoma leuchtenbergianum* Fischer, *Bosmina longirostris* O. F. Muller, and *Chydorus sphaericus* O. F. Muller. The copepod fauna consisted of two calanoid species, *Diaptomus oregonensis* Lilljeborg and *Diaptomus siciloides* Lilljeborg, and two cyclopoid species, *Cyclops vernalis* Fischer and *Cyclops bicuspidatus thomasi* Forbes. The following section describes distribution and abundance of these crustaceans in Hastings Lake during the study period.

Chydorus sphaericus

Chydorus sphaericus appeared during late summer in Hastings Lake (Fig. 20). A few individuals were found during May and June 1975 and May 1976 but were numerically insignificant compared to July and August populations. *Chydorus* was never found under the ice. The major pulse began in late July and increased rapidly to a maximum in August at all stations. Populations at stations A and B were similar in their development, reaching approximately the same numbers and declining at the same rate during September and October. The population at station C also developed during July and August 1975 but never reached the numbers observed at stations A and B. The station C population declined during late August but, in contrast to the main basin population, rose again during September to a maximum in mid-October.

Chydorus did not show any depth preferences during summer although

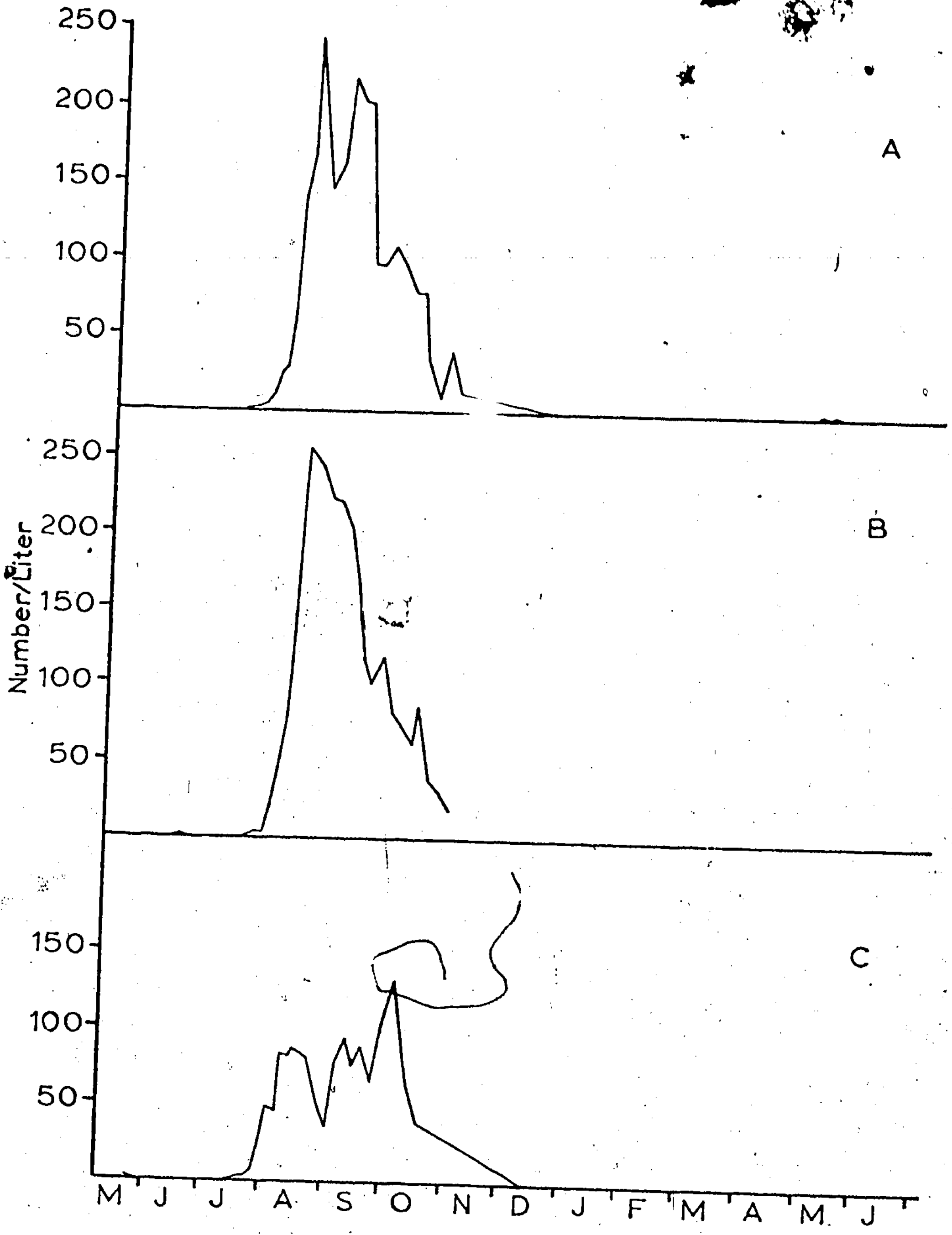


Figure 20. Population density of Chydorus sphaericus at stations A, B, and C. 1975-1976.

a slight concentration in deep water was observed on September 14, 1975 (Fig. 21). On this day the water column showed both temperature and oxygen concentration gradients. The surface water was 3 C° warmer than the bottom and was 130% saturated with oxygen, while the bottom metre was only 40% saturated.

Diaphanosoma leuchtenbergianum

During 1975, *D. leuchtenbergianum* was a mid summer species. It first appeared in early July samples and reached a maximum during August (Fig. 22). Populations at stations A and B were similar with respect to time of appearance, rate of growth, and density. The station C population reached a greater density than did the main basin populations; it appeared to increase faster than those at stations A and B and reached maximum numbers approximately two weeks earlier. All populations showed rapid decline after reaching maximum density and had disappeared by November 1975. During 1976, *Diaphanosoma* was only found at station C, first appearing in mid-June, approximately two weeks earlier than in 1975. Depth distribution was uniform (Fig. 23).

Daphnia pulicaria

Population curves for *Daphnia pulicaria* from stations A, B and C are shown in Figure 24. *Daphnia* was present at all stations when sampling began in late May, 1975. During early June, stations A and B experienced a rapid increase in numbers with maxima in mid-June. Numbers declined quickly after the maxima but peaked again during July. The station C population reached a maximum a few days earlier than

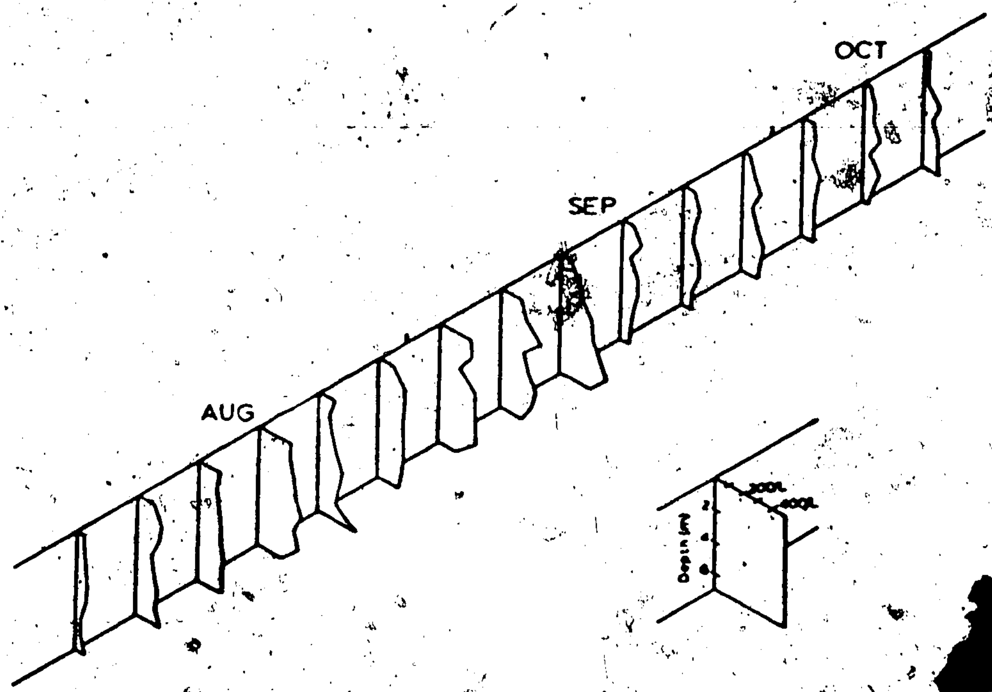


Figure 21. Vertical distribution of *Chydorus sphaericus* at station A. August 8-September 13, 1975.

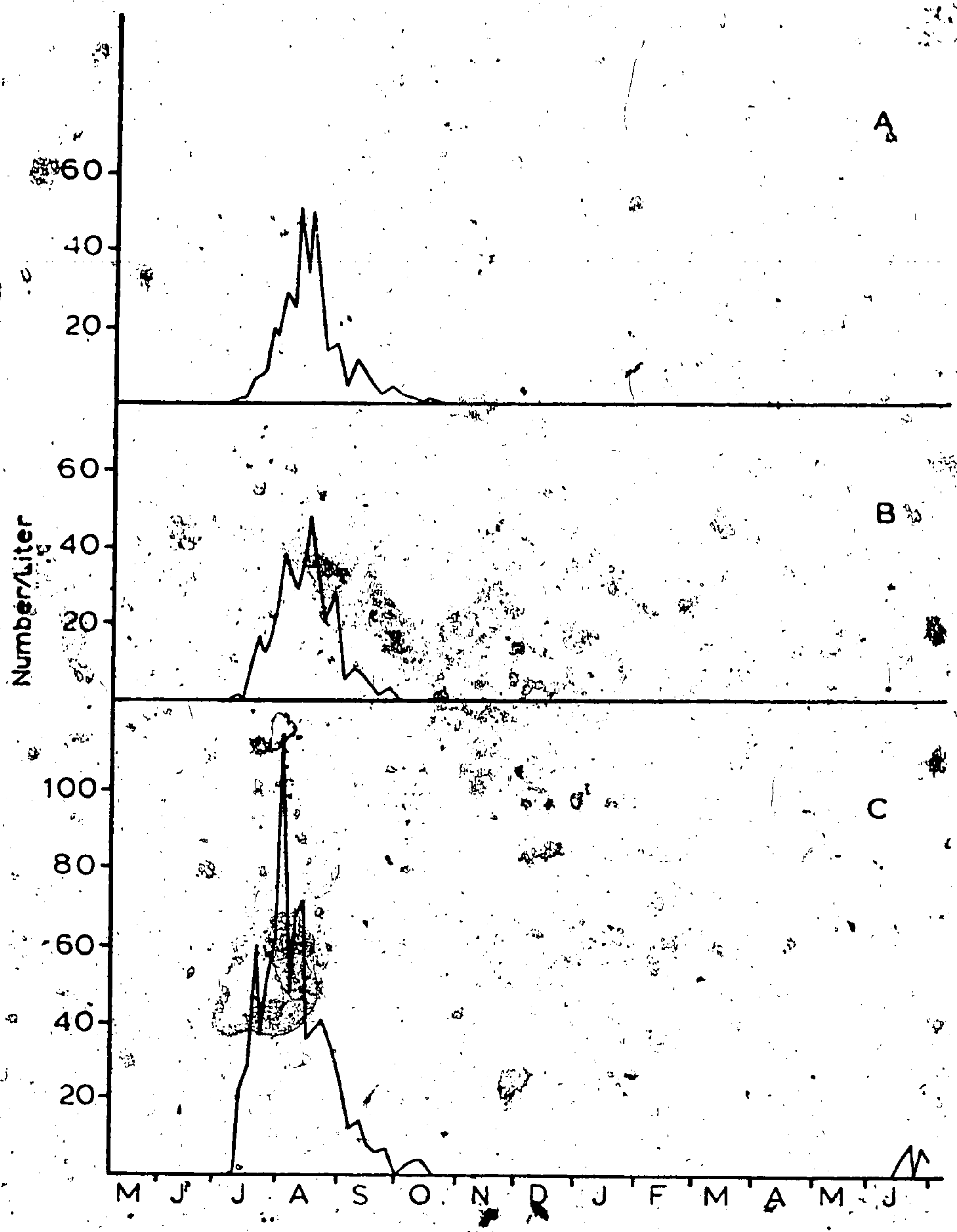


Figure 22. Population density of Diaphanosoma leuchtenbergianum at stations A, B, and C, 1975-1976.

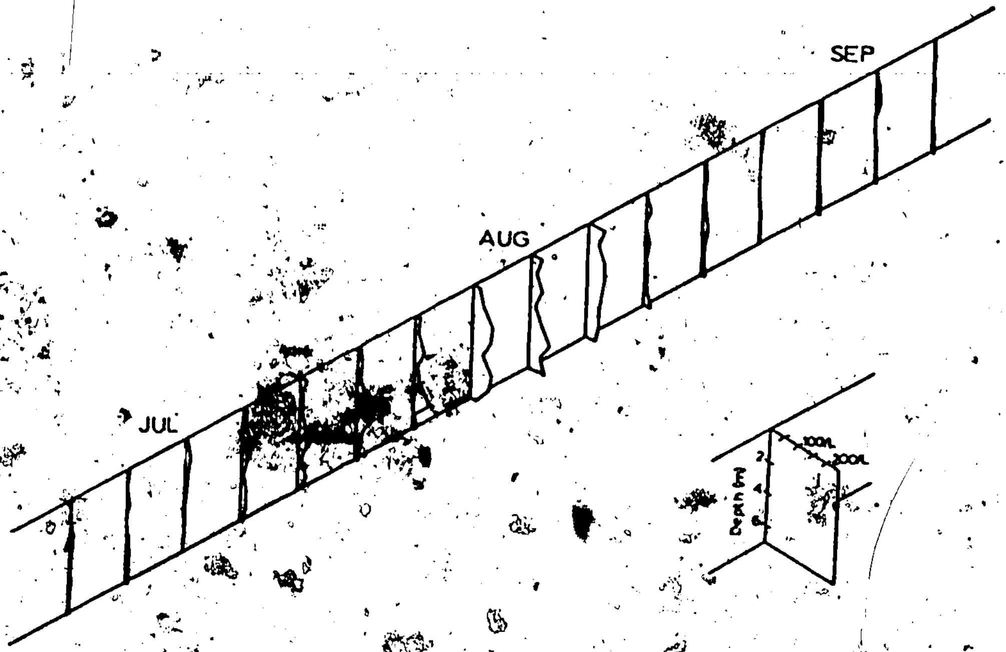


Figure 23. Vertical distribution of *Diaphanosoma leuchtenbergianum* at station A, July 19-September 18, 1975.

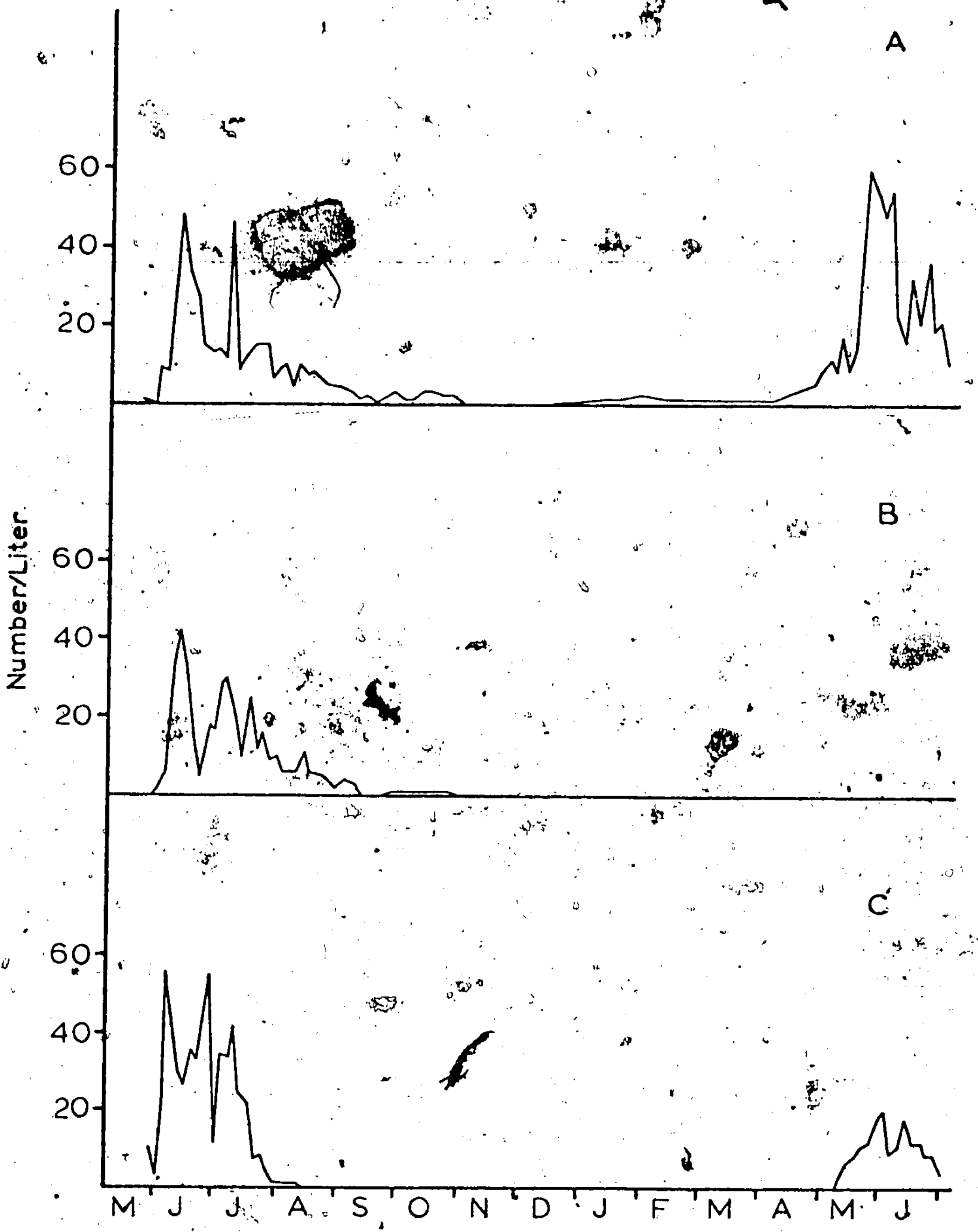


Figure 24. Population density of *Daphnia pulicaria* at stations A, B, and C. 1975-1976.

the main basin populations and the secondary peaks were stronger at station C than at either of stations A or B. The population disappeared in mid-August at station C while low numbers were found almost the entire year at station A.

The 1976 spring population increase began under the ice at station A. The population grew slowly for several weeks, but a rapid increase in numbers around the 20th of May resulted in a maximum on May 24. This maximum occurred twenty days earlier than in spring 1975, but the maximum levels were approximately equal. As in spring 1975, the population declined sharply after the maximum but peaked again ten days later. The 1976 spring pulse at station C appeared several days later than the pulse at station A, but never reached comparable numbers. At station C the 1976 maximum was less than the 1975 maximum.

Daphnia showed a slight preference for surface waters during the calm period in early July; during the rest of the year the vertical distribution was uniform (Fig. 25).

Bosmina longirostris.

Bosmina longirostris was present at all stations during June 1975, but the major increase in numbers began in mid-July at station C and late July at stations A and B (Fig. 26). The population at station A dropped sharply after reaching a maximum in mid-August and then stabilized until a second major decline occurred in October. The population appeared stable during December and January but dropped quickly during February. The station B population also declined after peaking in mid-August but rose again to a maximum in early September. The fall decline began slightly earlier at station B than

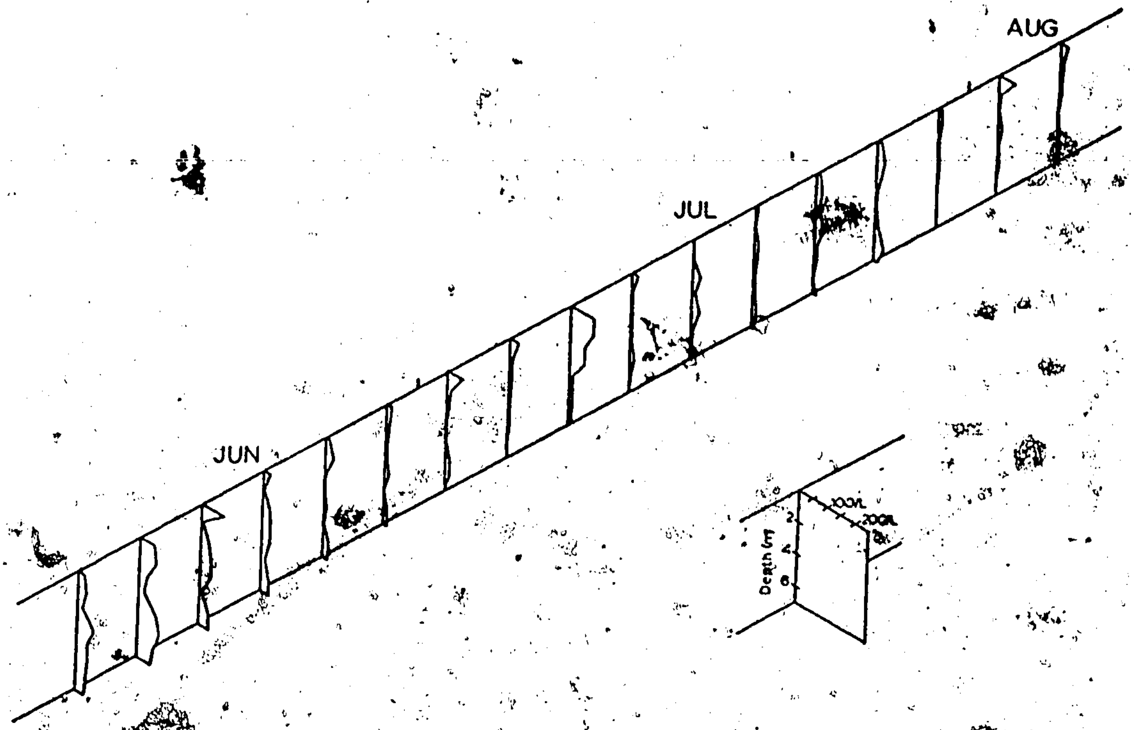


Figure 25. Vertical distribution of *Daphnia pulicaria* at station A. June 6-August 4, 1975.

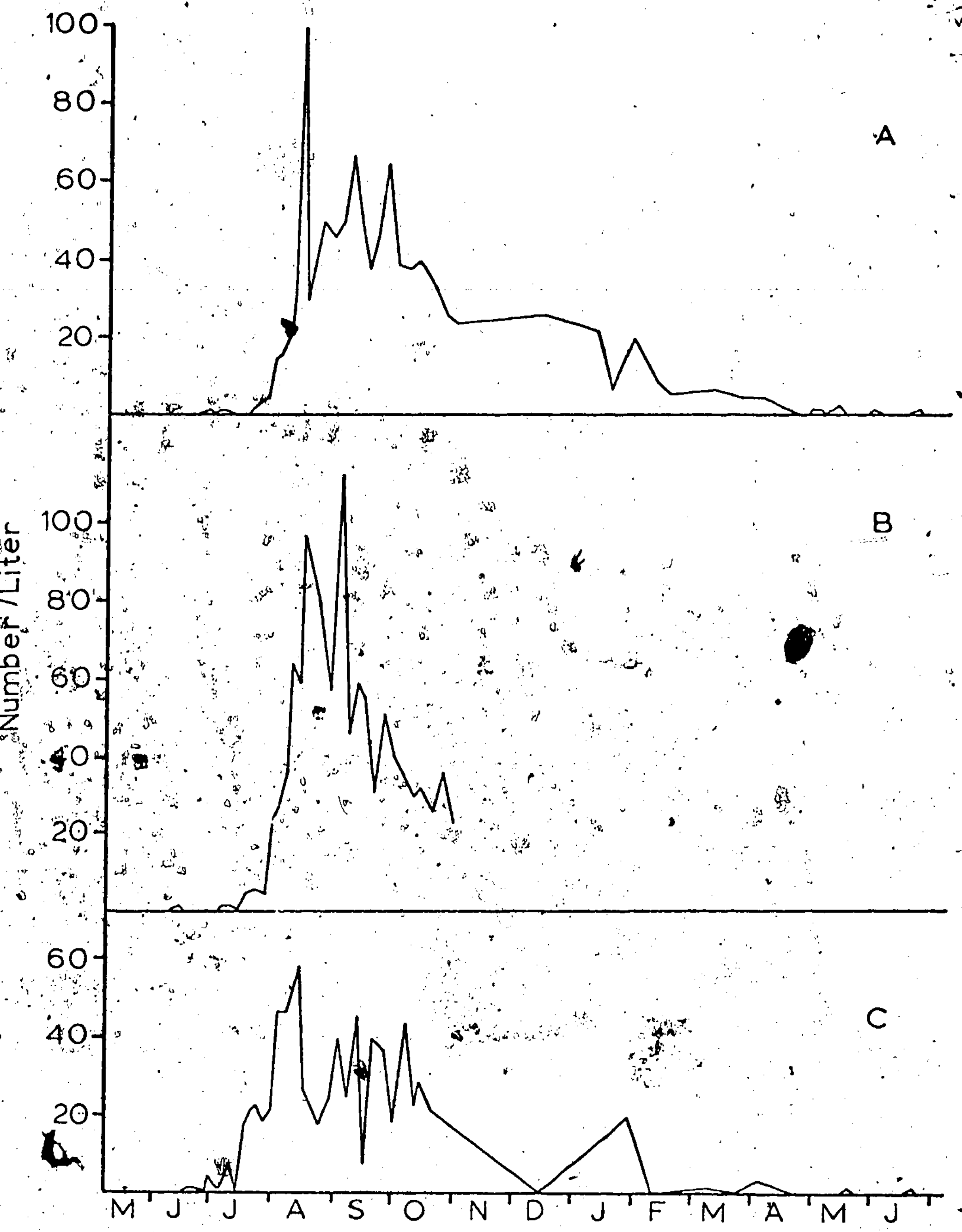


Figure 26. Population density of Bosmina longirostris at stations A, B, and C. 1975-1976.

at station A.

The population at station C appeared similar to that at station A although the density was higher at A. The maximum during early August was followed by a decline and subsequently a stable period during September and October. Numbers dropped rapidly during November and no specimens were found in December. Except for the seemingly spurious peak in January, the winter population was low. Bosmina was not numerically important at any station during spring and early summer 1976.

During the ice-free period, Bosmina did not show a preference for any particular depth (Fig. 27). However, on December 17 under the ice, Bosmina avoided the surface of the lake and concentrated in the deeper water. In January, when the deep water was depleted of oxygen (less than 10% saturation), Bosmina concentrated at the middle depths.

Diaptomus

Two species of Diaptomus, D. oregonensis and D. siciloides, were found in Hastings Lake. The three stations showed similar population densities during the year (Fig. 28). A small pulse in early June preceded the major pulse in late June and early July. The populations fluctuated widely but maintained high densities until early September when a definite decline occurred. The populations remained low during winter and disappeared during March and April. The spring population increase in 1976 began approximately two weeks earlier than did the increase in 1975.

When the lake was well-mixed the vertical distribution was uniform

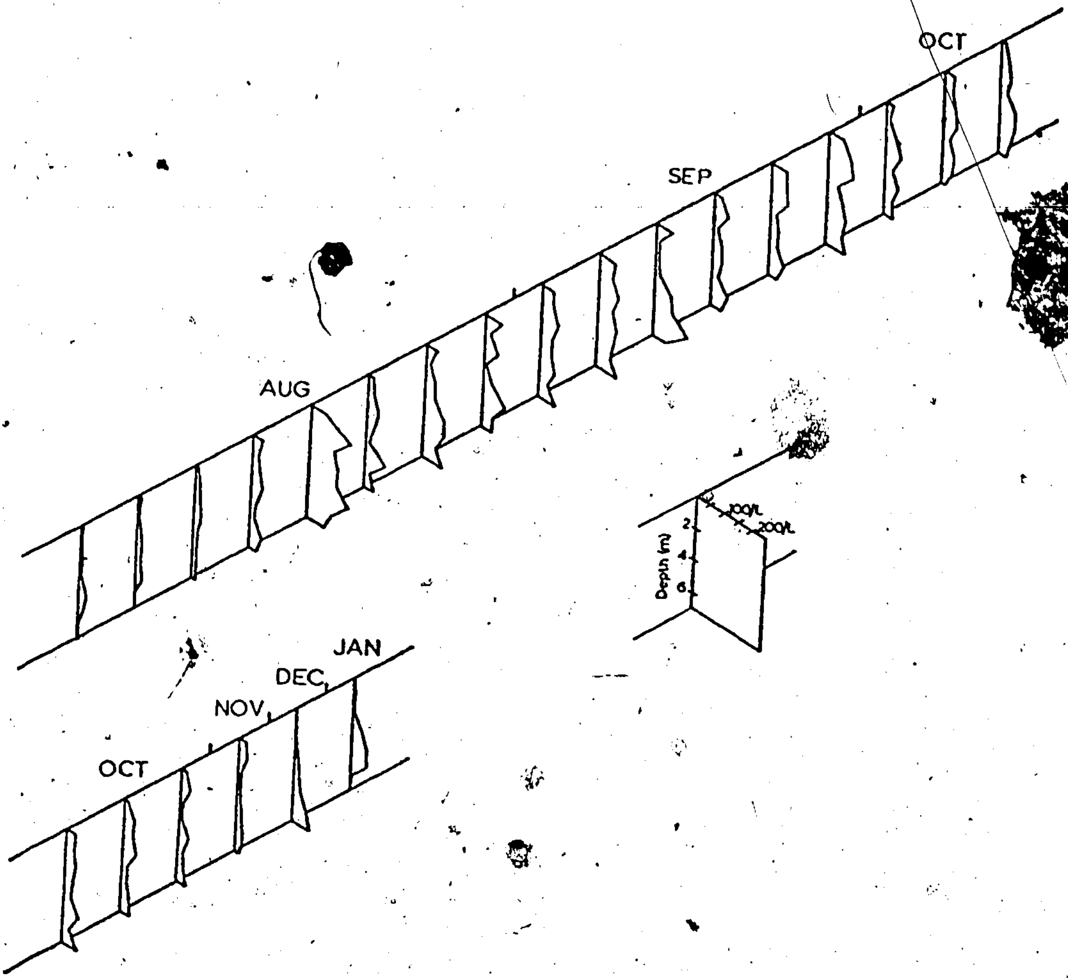


Figure 27. Vertical distribution of Bosmina longirostris at station A, August 1, 1975–January 13, 1976.

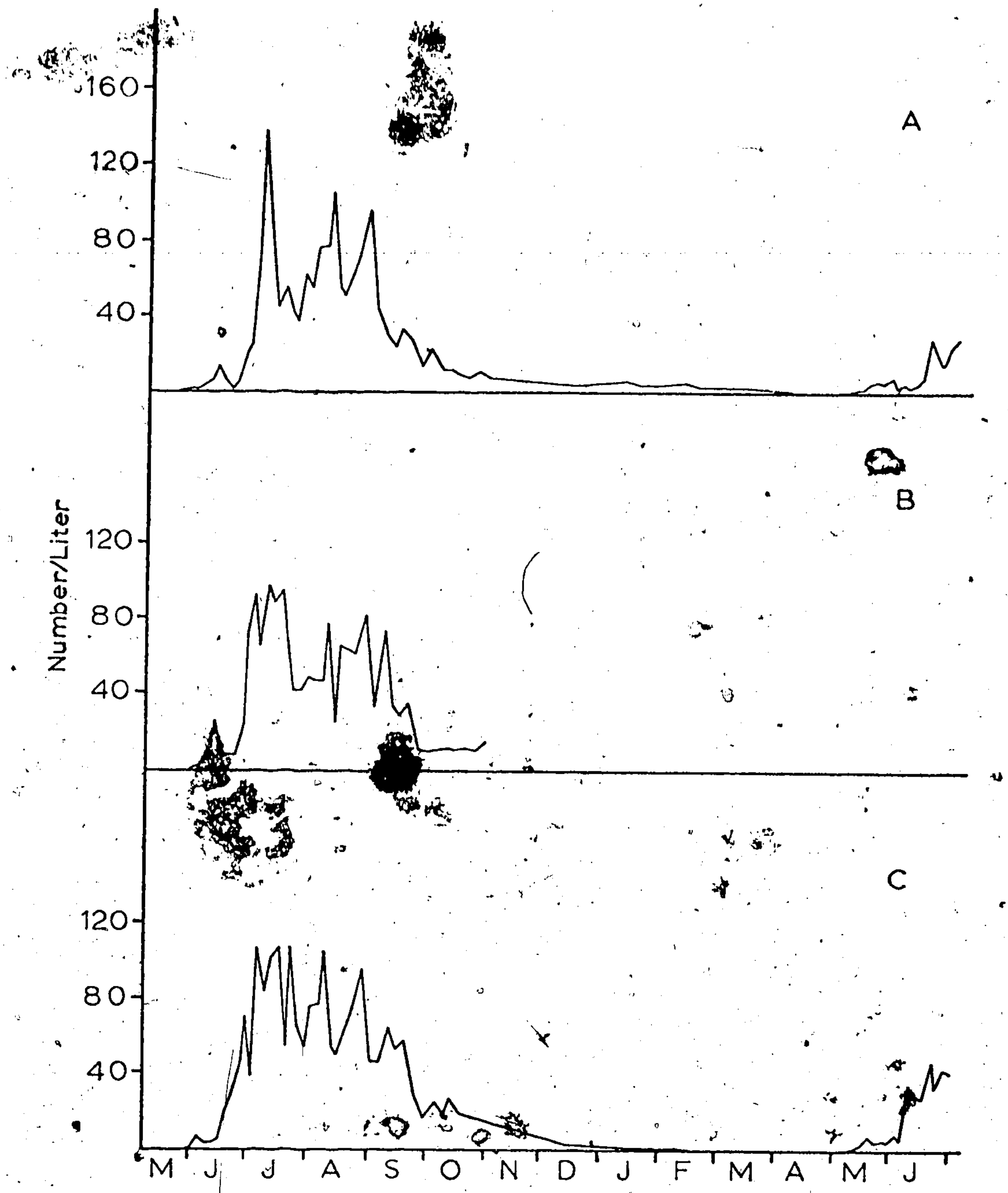


Figure 28. Population density of Diaptomus at stations A, B, and C. 1975-1976.

(Fig. 29). However, when the lake was calm for extended periods, ie during early July and mid September 1975, Diaptomus concentrated in the surface water.

Cyclops

The two species of cyclopoid copepods in Hasting Lake, Cyclops bicuspidatus thomasi and Cyclops vernalis were counted together and identified as Cyclops (Fig. 30).

Populations of Cyclops at stations A and B were similar. During late May and early June, densities rose rapidly to a maximum in the second week of June. Following the June maximum numbers decreased steadily, with only a small pulse at station B, until a second increase began in early August. Numbers peaked quickly in mid-August and declined again to a minimum in late September. Numbers rose again during October but declined slowly during winter. The spring increase at station A began suddenly during late April. The population grew to a maximum density in mid-May, three weeks earlier and 50% more dense than the 1975 spring maximum. Numbers dropped sharply after reaching the maximum but [illegible] contrast to the decline in 1975, began to rise again during late June.

Population growth at station C was slightly different from that seen in the main basin. The 1975 spring maximum had already been reached by the time sampling started in late May. Numbers declined during June and remained low in July, but in contrast to stations A and B, there was no peak during late August and early September. The late fall increase (during October in the main) began during September at station C. Population density declined steadily during

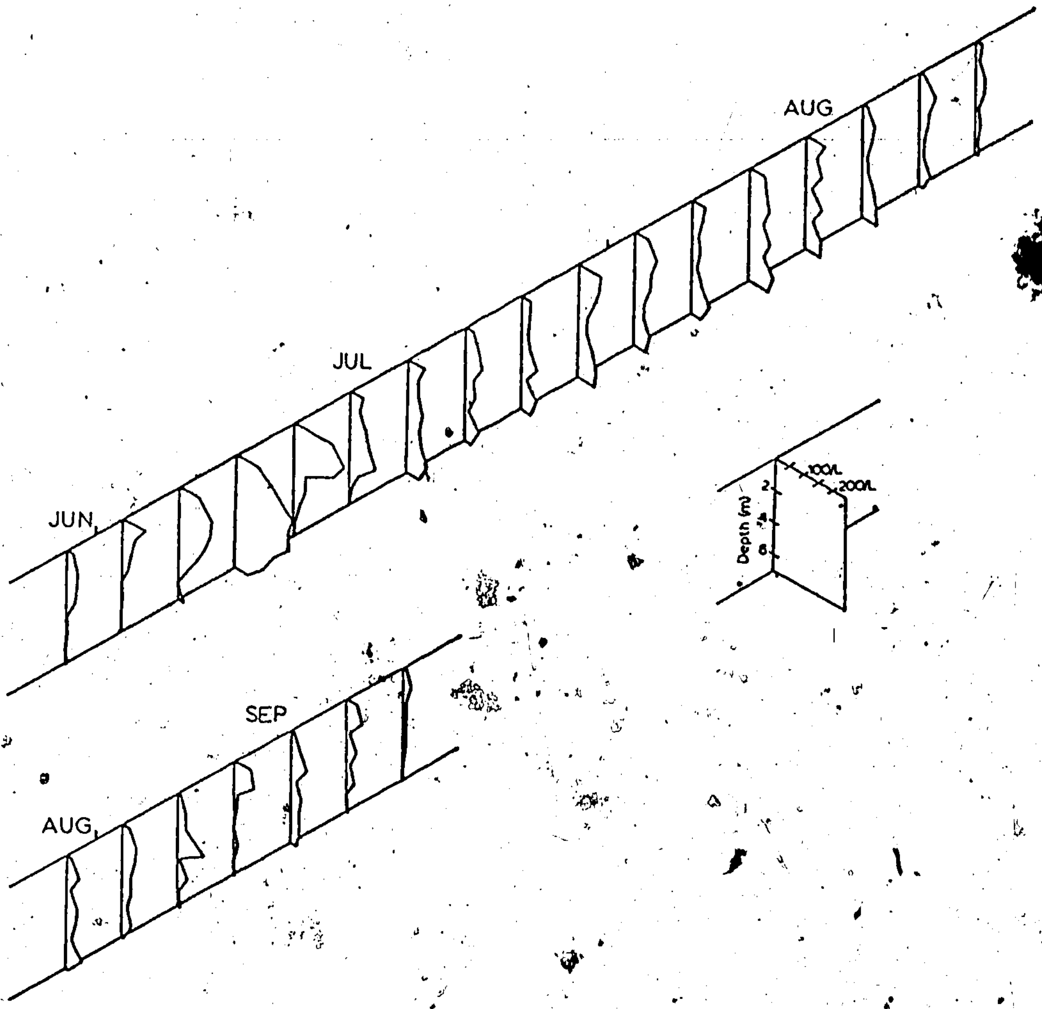


Figure 29. Vertical distribution of *Diaptomus* at station A. June 28-September 28, 1975.

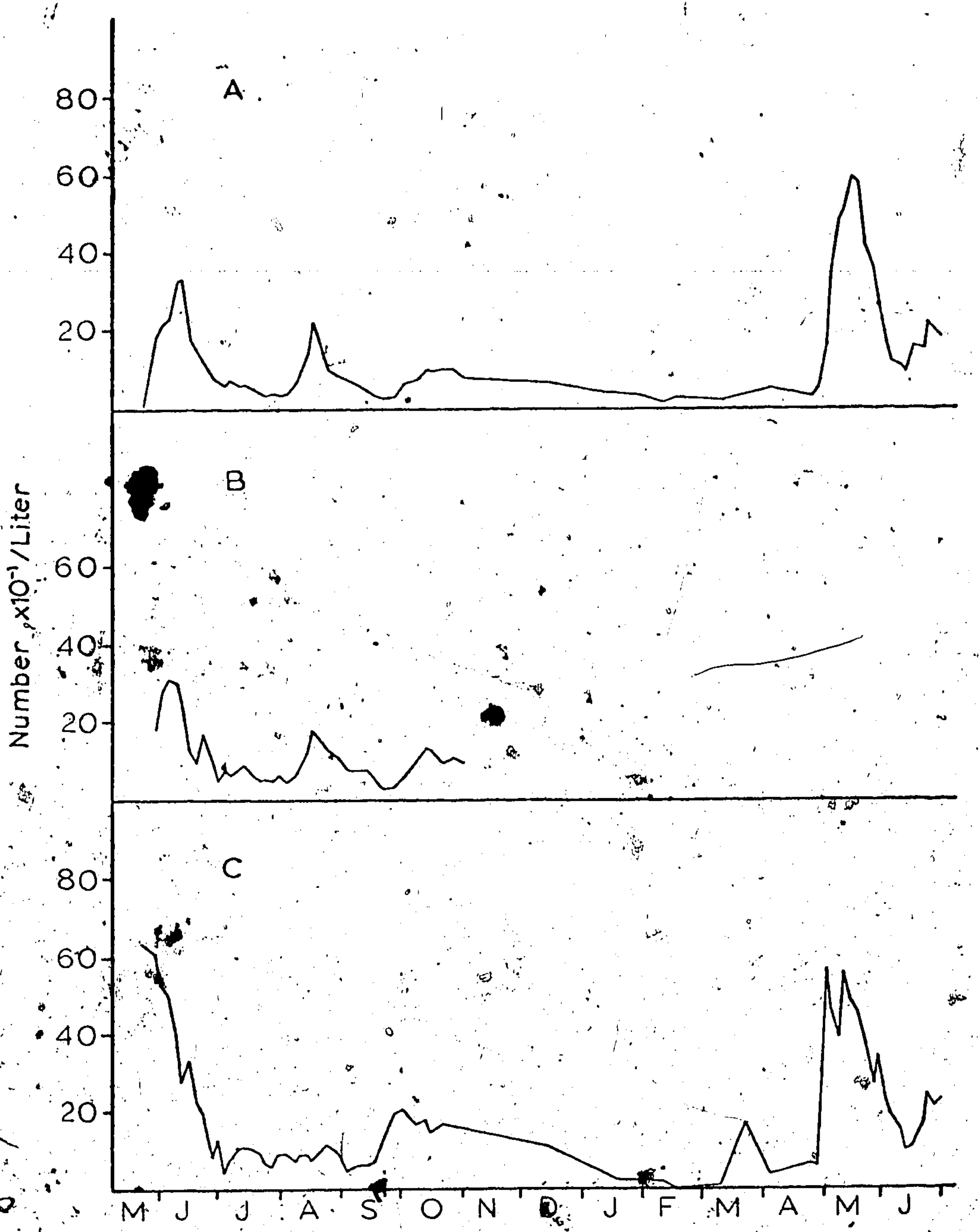


Figure 30. Population density of Cyclops at stations A, B and C. 1975-1976.

winter to a low in February. A pulse occurred during March but was short-lived. As in 1975, the spring pulse of 1976 began earlier at station C than at station A. After a decline during May and June, the population at station C, like that at station A, began to increase again.

Cyclops did not show a preference for any depth during the ice-free period. In December Cyclops concentrated at a depth of five metres at station A, but as the oxygen concentration dropped in the lower depths, the majority moved into surface waters.

Additional information concerning cyclopoid populations in Hastings Lake was obtained from data acquired during a detailed study of seven prairie parkland lakes (D. N. Gallup, unpublished data). Quantitative samples from station A were collected approximately monthly throughout the sampling period. It was impossible to identify the first three copepodite instars at the specific level so the counts were lumped into copepodites I-III. The IV, V, and adult instars were identified as Cyclops bicuspidatus thomasi or Cyclops vernalis. Figure 31 A shows the populations of the three groups. During 1975, copepodites I-III were most numerous in spring with peaks in mid-summer and autumn. Numbers declined through winter but increased rapidly in spring, 1976. Cyclops vernalis was most abundant during summer and early autumn, 1975, with low population densities during winter and spring 1976. The population density of C. bicuspidatus thomasi fluctuated during spring and summer 1975 and a small increase was seen during winter. A very strong increase was recorded during spring 1976.

It is generally assumed (McQueen, 1969; Anderson, 1970) that

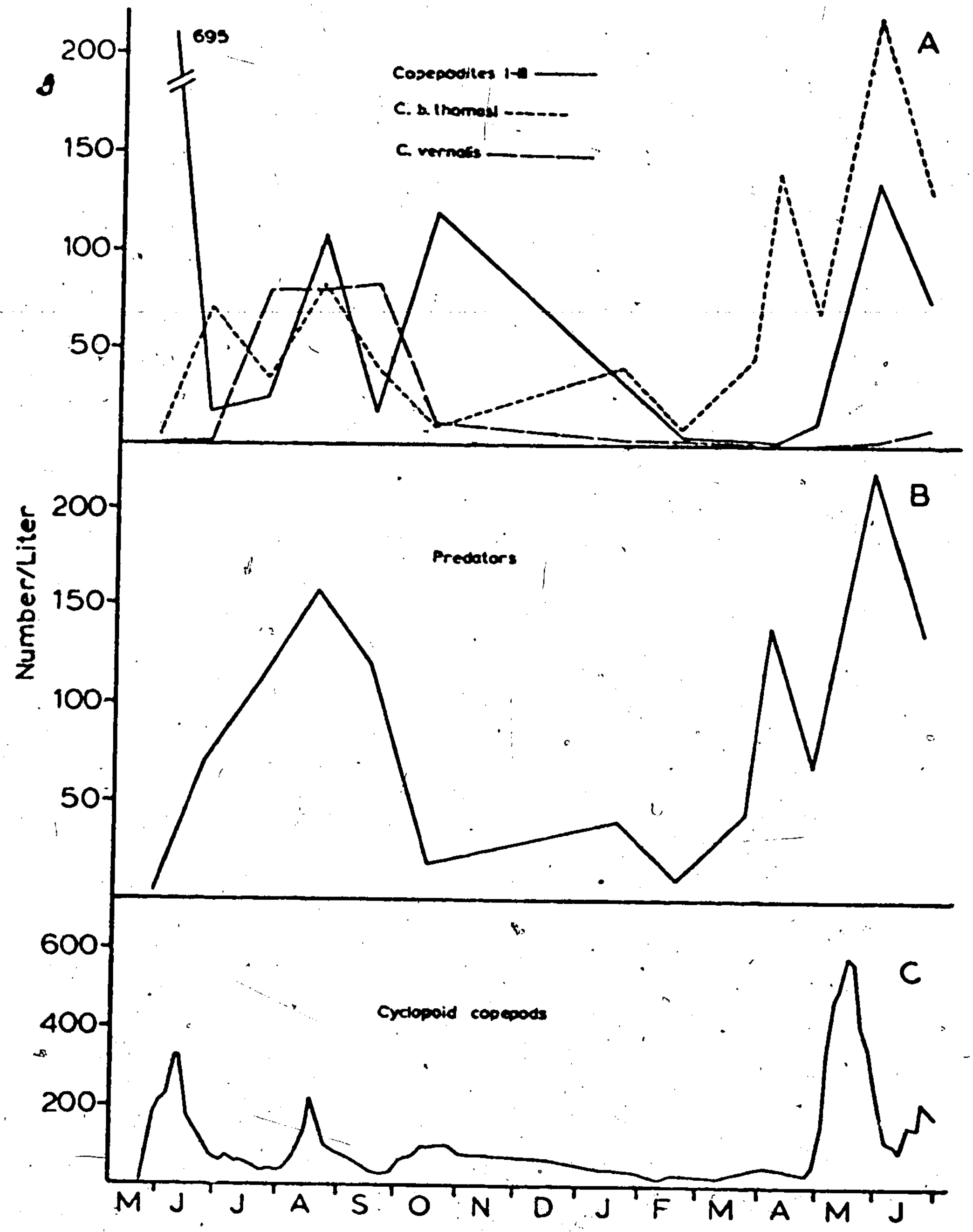


Figure 31. A. Numbers of cyclopoid copepodites I-III, *C. bicuspidatus thomasi*, and *C. vernalis*. B. Numbers of predators. C. Numbers of all cyclopoid copepods. All at station A. A and B from Gallup (unpublished data).

late copepodite and adult stages are the predaceous forms of cyclopoid copepods. Therefore, densities of the last two copepodite instars and adults of C. bicuspidatus thomasi and C. vernalis were summed to give an estimation of the density of predators (Fig. 31 B). Figure 31 C shows the density of Cyclops for comparison. The validity of this assumed predatory behaviour and composition of the predatory community will be discussed in predation sections of the chapters entitled "Population Dynamics" and "Cyclomorphosis".

Density of predaters was low in May but increased steadily through June and July to a maximum in August. Numbers dropped slightly in September and a major decline was noted in October. During winter numbers remained relatively low. Densities of predators in spring and summer 1976 were approximately equal to densities of C. bicuspidatus thomasi since C. vernalis was rare at this time. Thus, predatory density was high from early April through June.

Nauplii

Copepod nauplii showed the same pattern of occurrence at all three stations (Fig. 32). During late May 1975, populations, consisting almost exclusively of cyclopoid nauplii, were declining rapidly. This correlated with a simultaneous increase in numbers of cyclopoid copepods. After minima in mid-June, populations increased slowly through late June and July, showing considerable fluctuations in density. A large number of calanoid nauplii were present at this time. Populations started to decline in August and continued this trend through autumn. Numbers remained very low under the ice.

In April 1976 nauplii increased greatly in numbers. A maximum

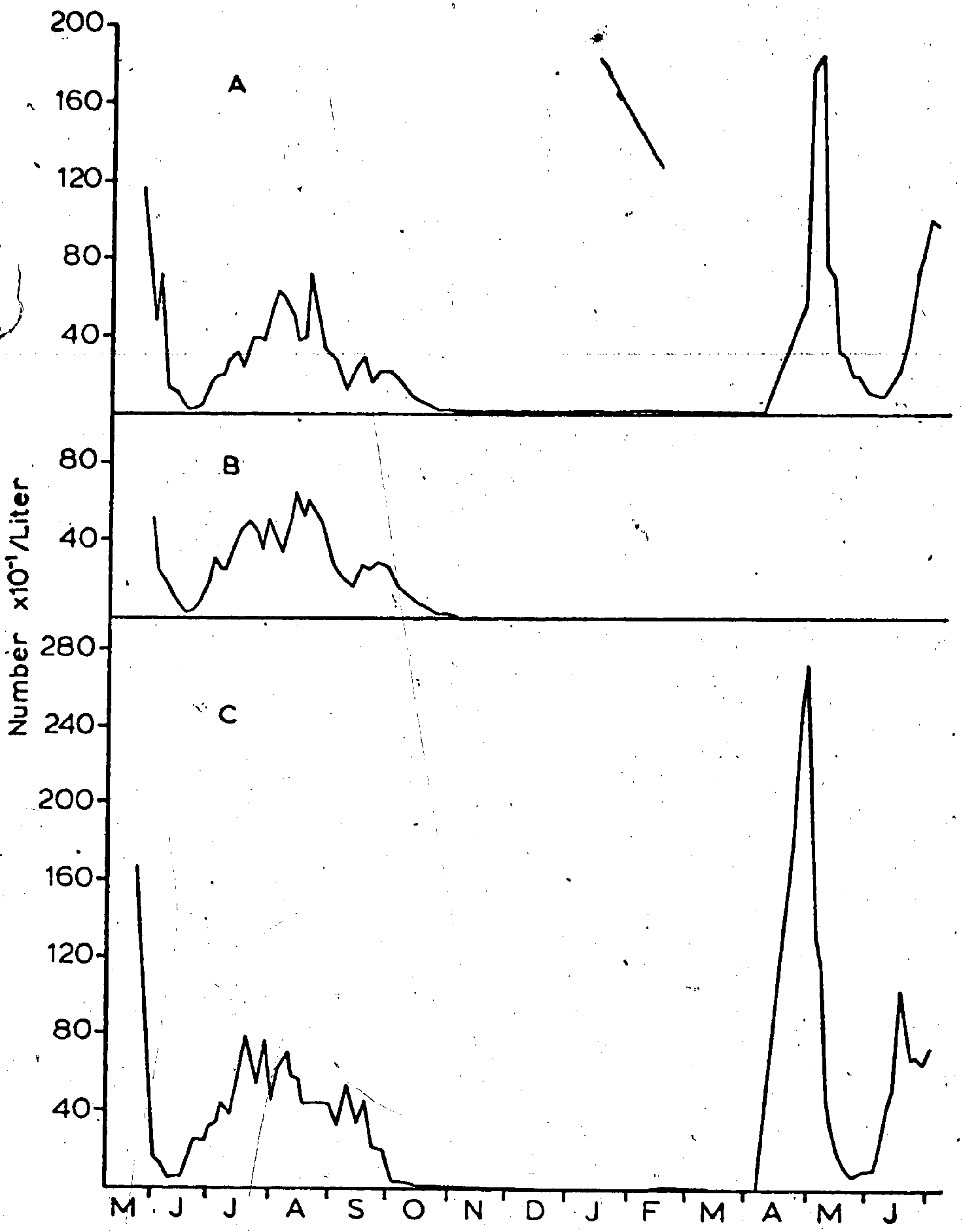


Figure 32. Population density of nauplii at stations A, B, and C. 1975-1976.

was reached on May 4 at both stations A and C with station C having the highest population density. After the maximum was reached, numbers declined as quickly as they rose. As in spring 1975, the population during the initial pulse was composed almost exclusively of cyclopoid nauplii. The second pulse of 1976 (including many calanoid nauplii) began on June 11, approximately two weeks earlier than the second pulse of 1975.

During mid-July 1975 and immediately after ice break-up 1976, nauplii were rare in deep, oxygen-depleted waters (Fig. 33). However, in late July and early August 1975 nauplii were concentrated in deeper water that was unsaturated with oxygen.

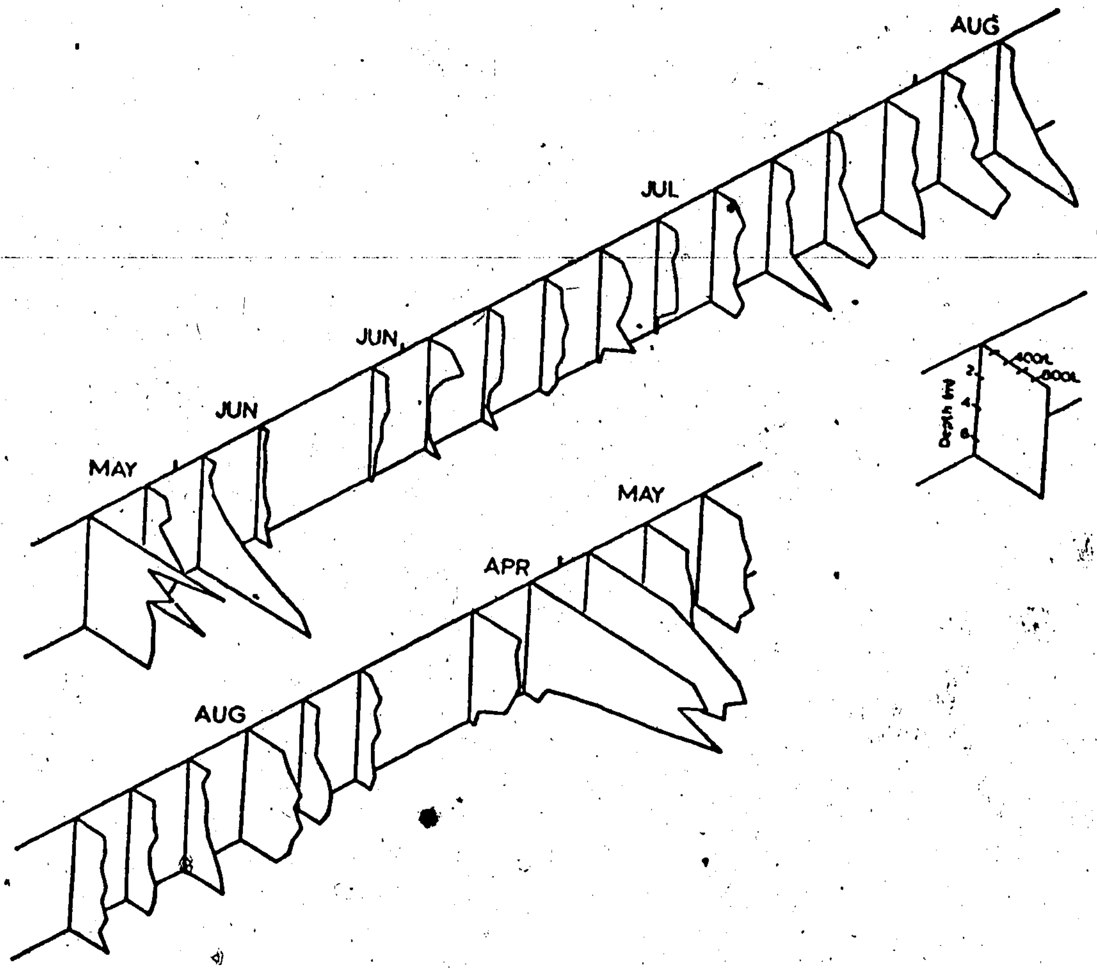


Figure 33. Vertical distribution of nauplii at station A. May 23-June 6, 1975; June 28-August 31, 1975; April 27-May 10, 1976.

EGG DURATIONS

This section will present data on the duration of development of rotifer eggs obtained in this study and discuss the use of data from Amren (1964a). Least squares regression lines used in equation (1) are shown in Figure 34. Information on the rate of development of Keratella cochlearis, Brachionus angularis, and Pompholyx sulcata was obtained in this study. Raw data are presented in Appendix I.

Keratella cochlearis was the easiest animal to culture; a total of 11 durations were recorded at temperatures of 10°C, 11°C, 20°C, and 20.5°C. Data for K. cochlearis were also used for K. earlinae due to the lack of data on K. earlinae and to the close relationship of these two species (Ruttner-Kolisko, 1974).

Seven durations were recorded for Brachionus angularis, 3 at 15°C and 4 at 19°C. This species was difficult to work with as eggs were often attacked by fungus.

Four durations were recorded for Pompholyx sulcata, 2 at 19°C and 2 at 22°C. This species also proved difficult to work with. Over forty animals were observed to lay eggs but only four lived long enough for the egg to hatch. This same problem was reported by Edmondson (1960) who was unable to record a single duration despite observing 15 eggs.

Experiments were also performed with Polyarthra dolichoptera and Filinia longiseta but produced confusing results. While duration of development for the other species tested was precise, results for F. longiseta and P. dolichoptera showed a wide range of values for

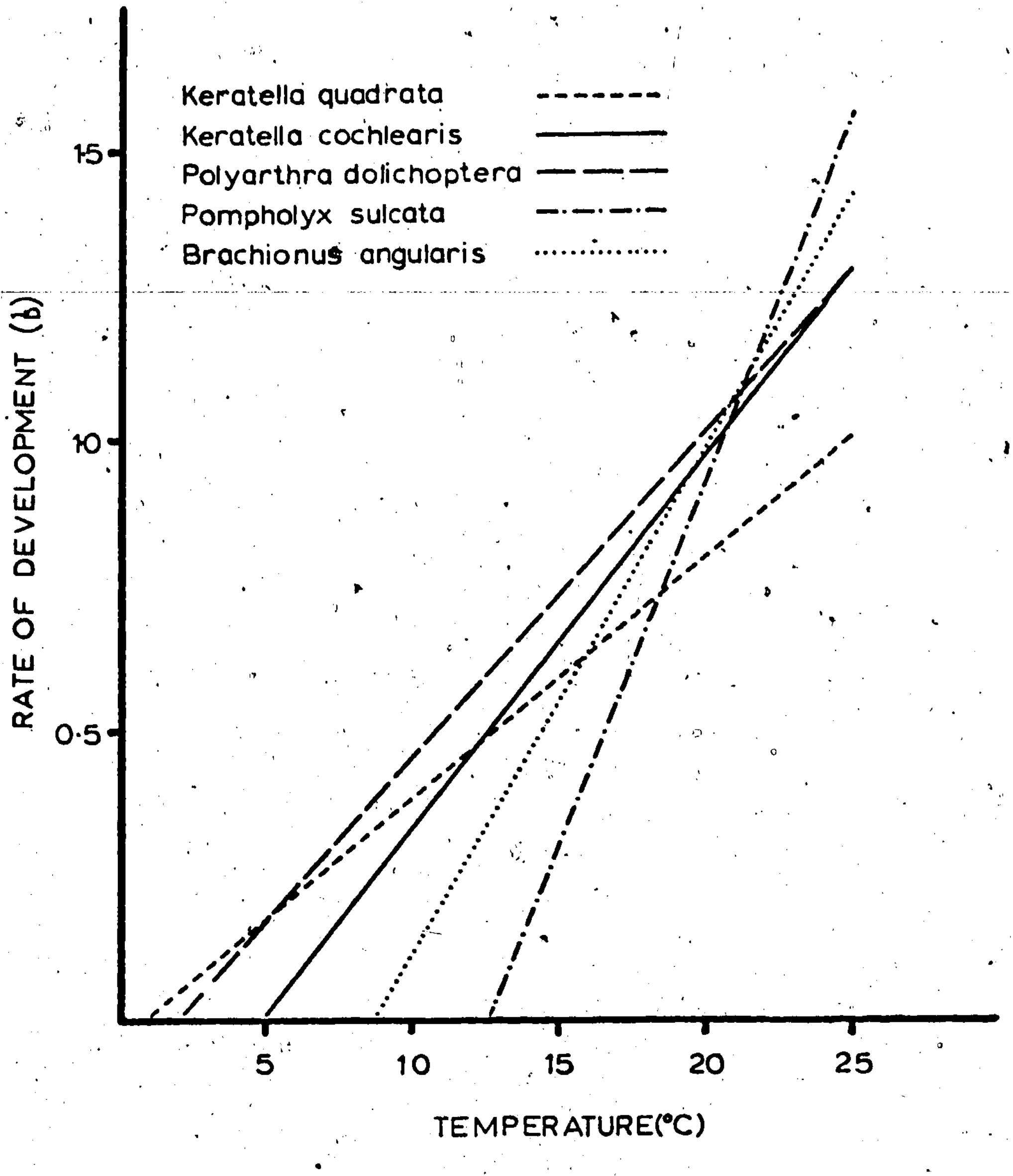


Figure 34. Least squares regression line for rate of development of eggs of *Keratella cochlearis*, *Keratella quadrata*, *Brachionus angularis*, *Pompholyx sulcata*, and *Polyarthra dolichoptera*. Data for *K. quadrata* and *P. dolichoptera* from Amren (1964a).

any particular temperature. When eggs of these species were first laid a considerable amount of structure was often visible within the egg; the developing mastax was particularly noticeable. It was also noted that the degree of development was different in freshly laid eggs; some showed no development while others appeared ready to hatch. It appears, therefore, that a variable amount of development takes place in the female before the egg is laid, thereby causing the wide spread of observed values. Because of this problem results were not used.

Data from Amren (1964a) were used in equation (1) for Keratella quadrata and Polyarthra dolichoptera. Amren's data were obtained from animals collected from Spitzbergen Island; therefore, the use of his data in my study assumes no difference in egg durations between the widely separated populations.

ROTIFERS

A total of seventeen species of planktonic rotifers were found in Hastings Lake. A few species of unidentified bdelloid rotifers and a few *Lecane* were found but were not considered euplanktonic and so were ignored. This section describes distribution and abundance of individual species and includes notes on their relationships with selected environmental factors. Birth rates are described for those species that carry eggs and cyclomorphosis patterns are described for the three dominant species of *Keratella*.

Conochilus unicornus Rousselet

Conochilus unicornus was the only colonial rotifer found in Hastings Lake. Ruttner-Kolisko (1974) describes the colonies as containing five to twelve individuals, but colonies of up to twenty individuals were occasionally seen. Horkan (1971) also noticed colonies of greater than twelve individuals. High numbers of individuals in a colony may be indicative of a rapid rate of reproduction (Ruttner-Kolisko, 1974). The trophi of *C. unicornus* is malleoramate with many small teeth on the unci. Pejler (1957a) suggests that *C. unicornus* eats particles with diameters less than 10 μ and Naumann (1923 in Pejler, 1957a) noted *C. unicornus* ingests particles smaller than those used by species of *Keratella*, *Filinia* and *Kellicottia*.

Conochilus unicornus was first collected from the main basin in early June 1975 (Fig. 35). Numbers at both stations A and B remained low for several days but a sudden increase was noted in mid-June.

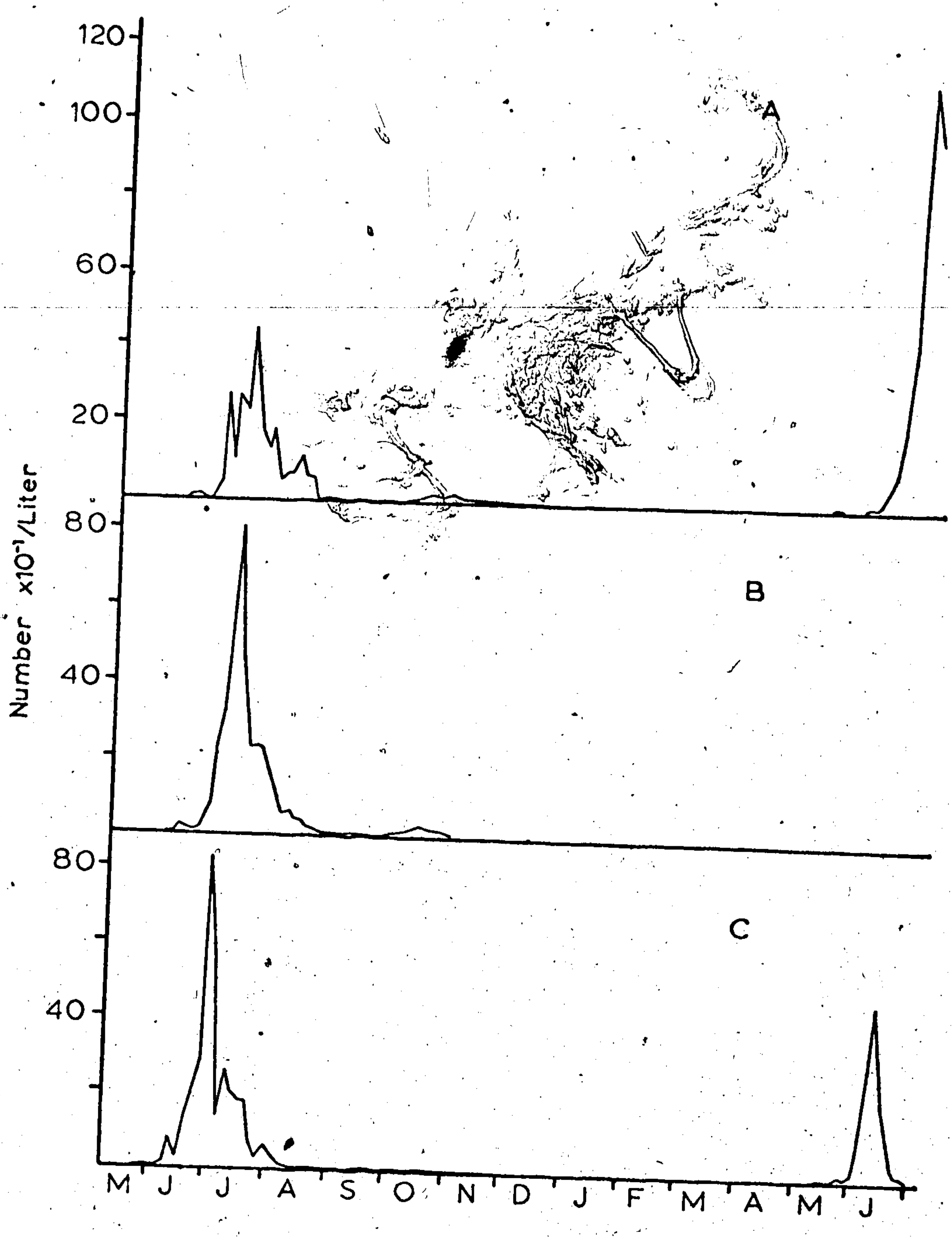


Figure 35. Population density of *Conochilus unicornis* at stations A, B, and C. 1975-1976.

The pulse at station B continued to a maximum in mid-July while the population at station A experienced a few setbacks during early July, reaching a maximum several days after the maximum at station B. During July numbers at station B were higher than numbers at station A. The vertical distribution graph of C. unicornus (Fig. 36) shows that this organism has a distinct preference for surface waters. It is possible that observed differences in population density at the two stations were a function of depth of water. A sign test (Sokal and Rolf, 1969) showed no significant difference in densities of C. unicornus in surface waters of the two stations, but the density at station A as a whole was low with respect to station B because the additional two metres of sparsely-populated water at station A reduced the average density. A sharp decline occurred at both stations immediately after maxima were reached in July. The decline continued through August but populations persisted in low numbers until October when small increases in density were noted. No specimens were found under the ice.

In 1976 C. unicornus was first seen in mid-May at station A. The population remained small during late May and early June but a rapid increase, starting the second week of June, led to a maximum in late June. The increase at station A in 1976 was two to three weeks earlier than the corresponding increase in 1975 and the 1976 maximum was twice as high as that of 1975.

Conochilus unicornus was present at station C when sampling began in late May. The population increased in mid-June and a maximum was reached on July 1, approximately two weeks earlier than in the main basin. The maximum was higher than the station A maximum but roughly equal to the station B maximum. Numbers dropped quickly immediately after the maximum was reached; the fall population persisted until freeze-up with no further increases.

In 1976 C. unicornus appeared at station C at approximately the same time as at station A. However, the increase at station C during early June continued to a maximum in mid-June, approximately two weeks earlier than the station A maximum. The population density dropped quickly after the maximum and was very low by early July. The 1976 maximum at station C was considerably lower than the 1976 station A maximum and lower than the 1975 station C maximum.

As mentioned earlier, the vertical distribution pattern (Fig. 36) showed that C. unicornus avoided deep water during the calm period in July when the lake had strong gradients in both temperature and oxygen concentration. In late June 1976, when the isotherms and isopleths showed slight gradients, C. unicornus had no depth preferences.

It appears that C. unicornus is a warm water species. It was found in water at 2°C during autumn but the population was obviously declining. No numerical increases were found at temperatures below 12°C and the maximum during 1975 was found at temperatures above 20°C while the maximum in 1976 occurred at temperatures above 16°C. Campbell (1941) found C. unicornus abundant in waters over 12°C and noted maxima in water of 18 to 20°C. He also found the major increases to occur from May through July. Chandler (1940) found maxima between temperatures of 22 and 24°C and Davis (1954) found abundant populations in a range of 15 to 22°C. In small lakes in southern Ontario, George and Fernando (1969) found C. unicornus

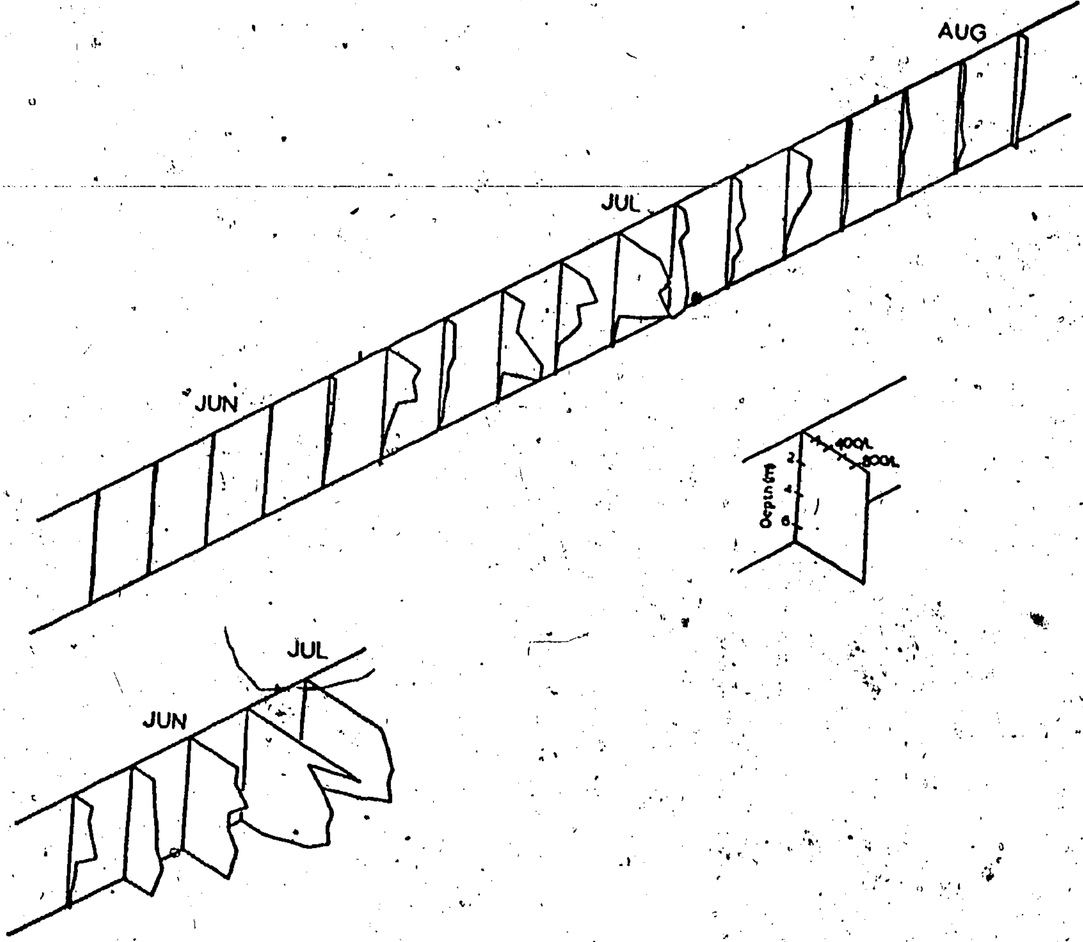


Figure 36. Vertical distribution of Conochilus unicornis at station A. June 13-August 8, 1975; June 18-July 2, 1976.

from May until September with maxima in mid-June, a situation similar to that in Hastings Lake.

Population growth did not coincide with the edible cell concentrations. Major peaks in 1975 occurred during Cyanophyta blooms. Population growth did coincide with increasing bacteria populations and it is possible, considering the ability of C. unicornus to ingest small particles, that bacteria cells could be used as a food source. However, populations of C. unicornus dropped despite high bacteria populations. Chandler (1940) and Davis (1954) also found C. unicornus in association with blue-green algae. Both authors also reported green algae being present but did not enumerate the small cells.

Conochilus unicornus usually occurred at times and in areas of high oxygen saturation. In early July 1975, C. unicornus appeared to avoid the oxygen-depleted water near the bottom. No ill effects to the population were noted, however, when the oxygen saturation dropped to 60% in June 1976.

Conochilus unicornus was present when the Keratella species dominated, but also when crustaceans such as Daphnia, Diaptomus, and copepod nauplii were numerous.

Density of C. unicornus increased during June and July 1975 while the predator populations were also increasing. However, the populations of C. unicornus dropped during late July as predators continued to increase and were very small in August when the predators reached a maximum. The small increase in the C. unicornus population during October occurred after predator populations had declined to low levels. In 1976 the populations of C. unicornus grew slowly while predator populations were high. Rapid growth of the C. unicornus populations occurred in late June when predators were still numerous but declining.

Conochilus natans (Selego)

Unlike C. unicornus, C. natans exist as single individuals. The mastax is malleoramate.

Conochilus natans was never common during the study period and was only found during early spring. A few individuals were seen during late May 1975 in the main basin but the population had disappeared by June 20. At station C the population had disappeared by early June. At station A in spring 1976, animals were first seen immediately after ice break-up. The population persisted in low numbers (2 to 3/liter) until mid-May. A similar pattern occurred in the north-east basin.

Conochilus natans was never found in water above 17°C and the highest densities were found in much colder water, although not under the ice. Pejler (1957a) describes C. natans as a rare "cold stenotherm" and cites 14.5°C as a maximum temperature. Pejler (1957b) also found it in eutrophic lakes during the winter and noticed it produced resting eggs in late April. In my study, C. natans occurred when the phytoplankton was dominated by edible cells.

Conochilus natans was never found in water with oxygen saturations less than 60%.

Conochilus natans was often found with large numbers of cyclopoid nauplii and Polyarthra dolichoptera. Keratella species were increasing as C. natans disappeared. During spring 1975, C. natans was present while predator populations were low, but in spring 1976, C. natans was associated with large numbers of predators.

Filinia longiseta Ehrenberg

Considerable confusion exists in the literature on the identification of Filinia longiseta and Filinia terminalis. Pejler (1957c), however, has shown the two species to be distinct. The small mastax of F. longiseta is malleoramate and Edmondson (1959) suggested the "long, thin gullet" restricts the size of particles ingested. Naumann (1923 in Pejler, 1957a) supported this idea by reporting that F. longiseta feeds on "ultraseston".

During my study F. longiseta was rare at stations A and B (Fig. 37). Specimens were found from mid-June to late October. A short-lived pulse occurred during late July and early August 1975. No specimens were found in the main basin during 1976. Owing to small sample sizes no birth rates were computed for main basin populations.

Since no information exists on the duration of development of F. longiseta eggs, the egg ratio was used as a rough approximation of the birth rate at station C. Filinia longiseta was present at station C when sampling began in late May 1975. The population remained at a low density until July when a distinct increase was noted. The egg ratio was high during early July but fluctuated considerably. A decrease in population density in early August was correlated with a drop in the egg ratio. A major population pulse started in early August and reached a peak a few days later. Numbers declined in mid-August but rose again in late August and early September. The egg ratio was high at the outset of the major peak but declined as the population reached the maximum and declined. The late August,

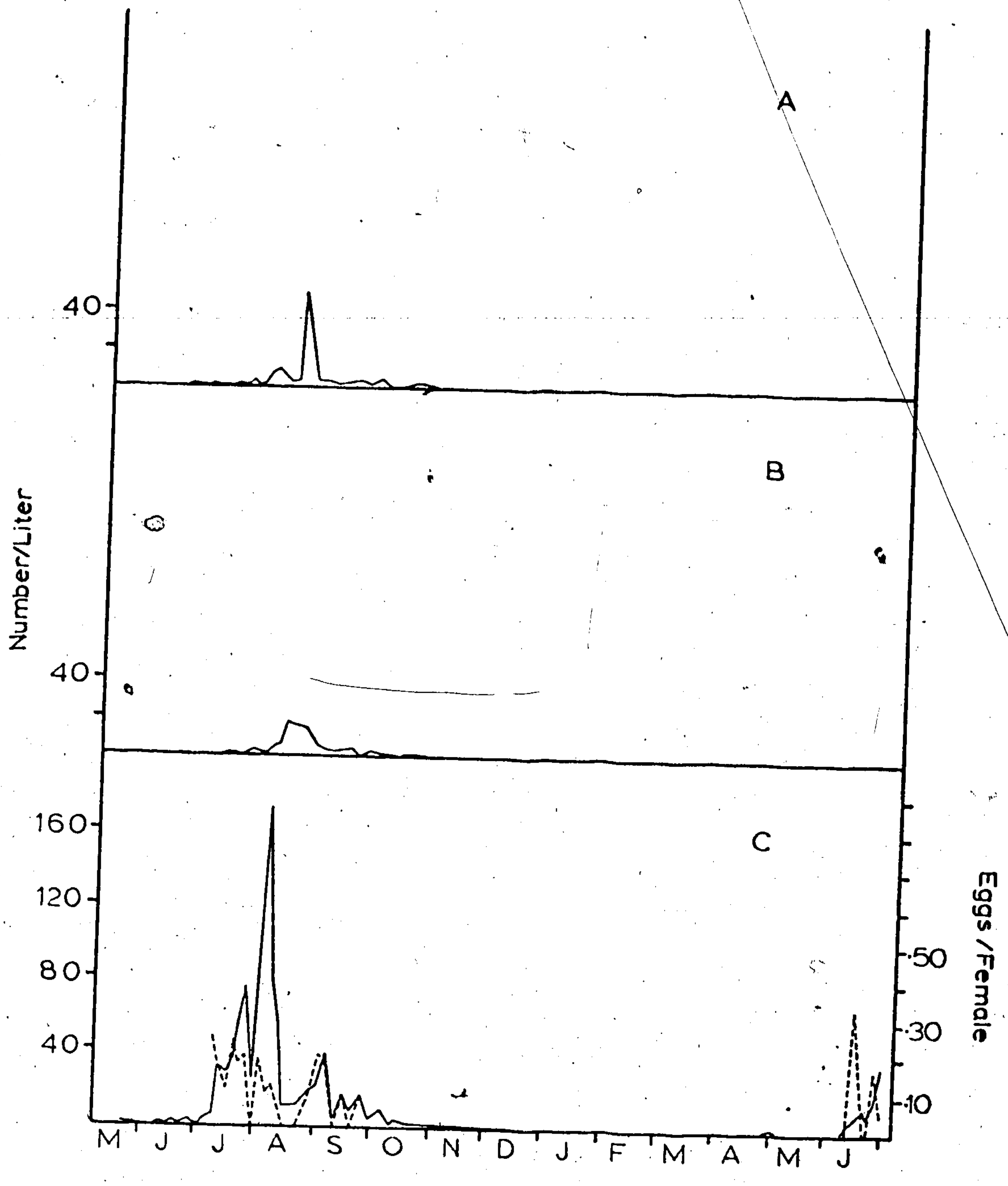


Figure 37. Population density and eggs per female of Filinia longiseta at stations A, B, and C. 1975-1976.

——density

------eggs per female

early September peak in population density was immediately preceded by a pulse in the egg ratio. Both the numbers and egg ratio declined during mid-September and the population persisted in low numbers until freeze-up. In 1976 F. longiseta was seen as early as late April but the population did not show any strong increases until June. The early growth stage was associated with a high egg ratio that appeared to drop very suddenly in mid-June. During the year, F. longiseta showed no particular depth preference (Fig. 38).

Although F. longiseta was found in water at 2°C, it appears to be a warm water species in Hastings Lake. No strong population growth occurred below 15°C and maxima occurred at temperatures over 20°C. This result concurs with Ruttner-Kolisko's (1974) comment that F. longiseta is a thermophile found in lakes above 15°C, usually above 20°C. Arora (1966) found F. longiseta at temperatures above 21°C. Other authors give conflicting reports on the temperature range of F. longiseta. Allen (1920) reports it present from January to July and Campbell (1941) found it in February. Chandler (1940) found this species in water from 5°C to 24°C but did not mention when maxima occurred. It may be that these authors were confusing F. terminalis, described by Ruttner-Kolisko (1974) as a cold stenotherm found at temperatures below 15°C, with F. longiseta.

Filinia longiseta was most abundant during blue-green algae blooms. It was also present while bacteria populations were high and, considering the small size of the mastax, it may be possible that F. longiseta utilized bacteria as a food source. Population increases seen at all stations correlated well with increases in bacteria populations. Numbers of F. longiseta at station C declined sharply

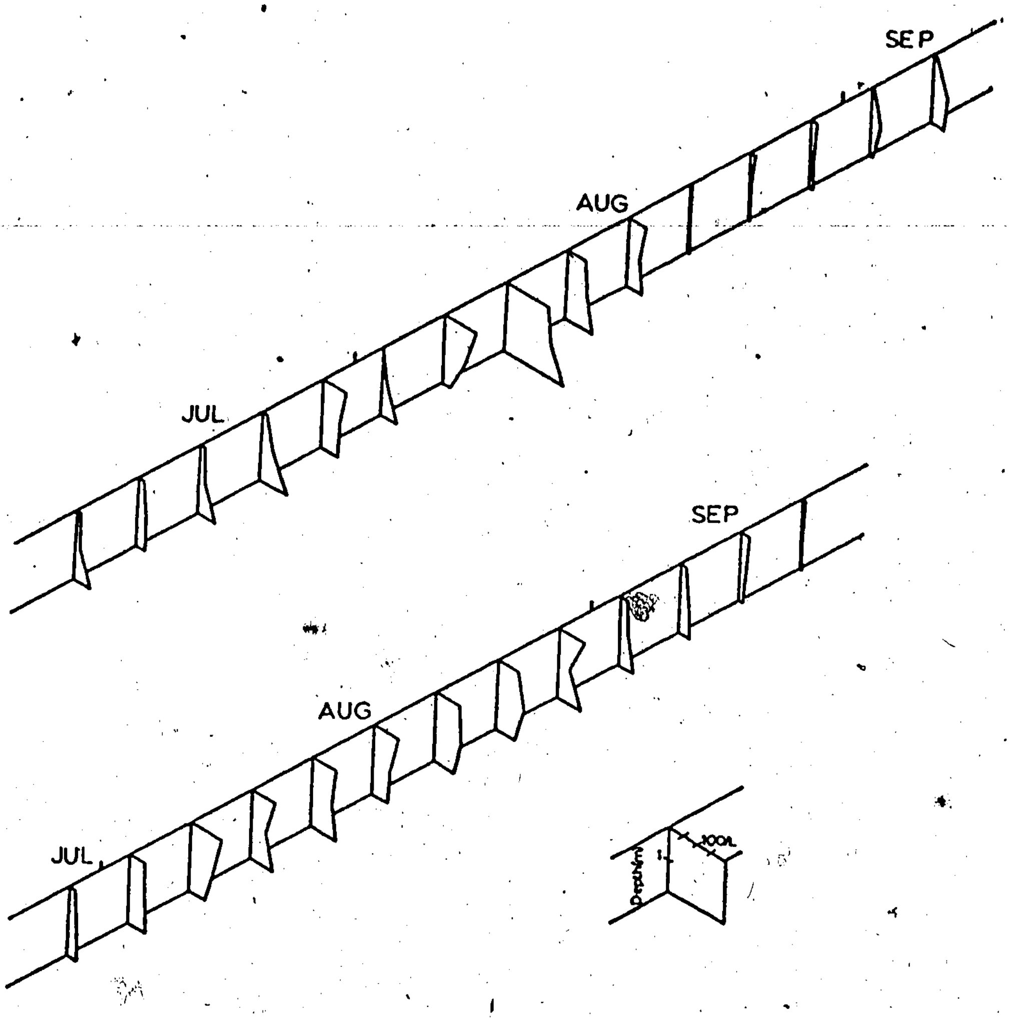


Figure 38. Vertical distribution of Filinia longiseta at station C. July 14-September 9, 1975. Upper figure. Vertical distribution of Brachionus angularis at station C. July 28-September 18, 1975. Lower figure.

during mid-August when the bacteria population dropped. Pejler (1957b) reports F. longiseta from eutrophic waters and Arora (1966) reports it in mixotrophic ponds.

Filinia longiseta was found in waters that were oxygen-rich; the lowest reading was approximately 80% saturation.

Filinia longiseta was common during mid-summer when the zooplankton fauna was dominated by crustaceans such as Diaptomus, Diaphanosoma, and copepod nauplii (mostly Diaptomus). Filinia longiseta was most abundant at station A during July and August when the predator population was at a maximum.

Pompholyx sulcata Hudson

Pompholyx sulcata possesses a malleoramate mastax with many teeth on the unci. No literature exists on its feeding habits but the size and type of mastax would indicate it grinds small phytoplankton cells and detritus.

A small population of P. sulcata was present in the main basin during late May 1975 (Fig. 39). The population density remained low until late June when it rose quickly. When the population first began to increase the birth rate was high; however, as the numbers continued to increase, the birth rate declined. The populations at stations A and B peaked during July. The maxima at station B were considerably higher than those at station A. The populations at both stations declined during late July and early August. The birth rate fluctuated considerably during this time. During late August and through September the populations appeared to stabilize somewhat. The birth rate declined during late August and remained low through September. A second

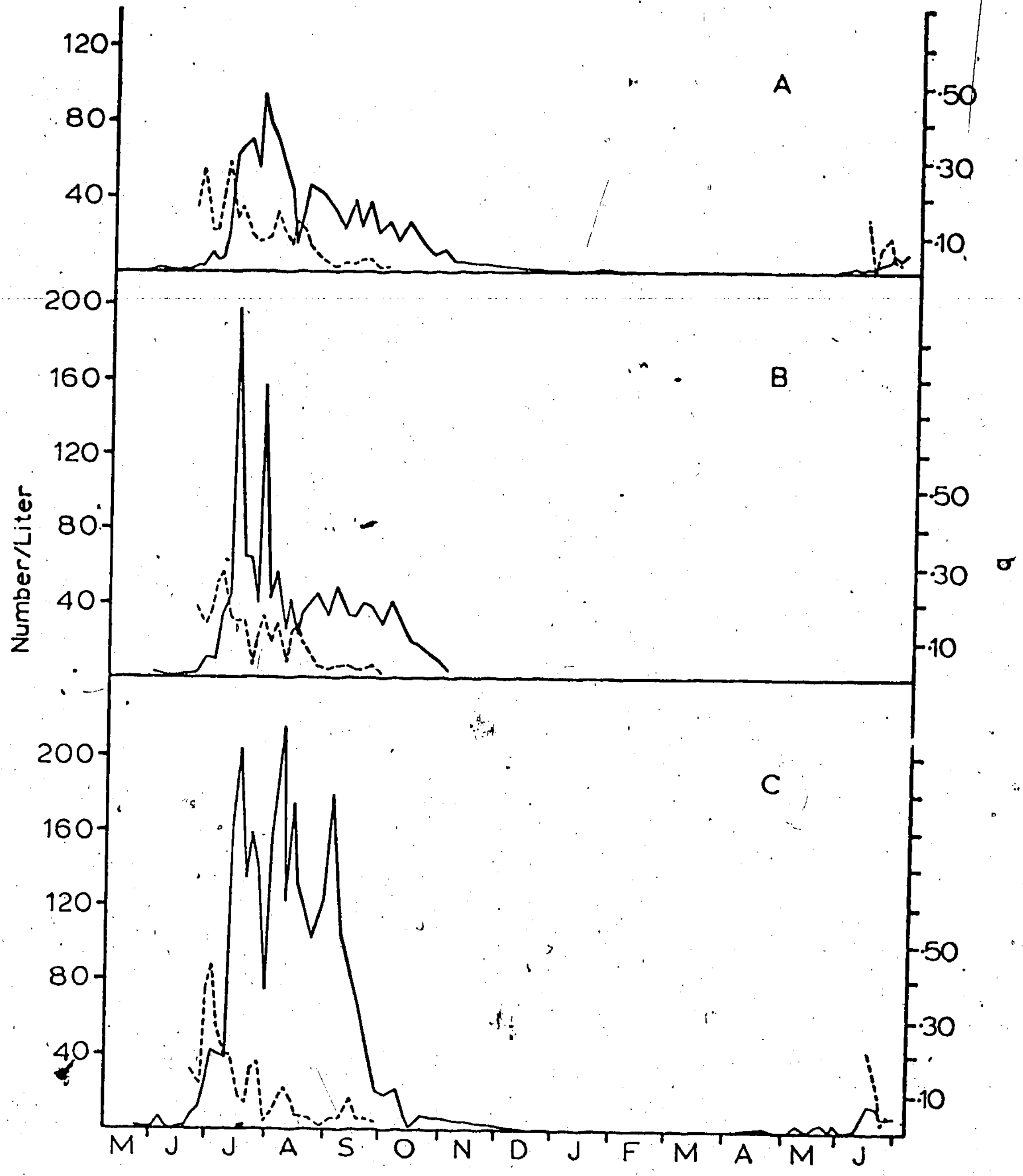


Figure 39. Population density and birth rate of *Pompholyx sulcata* at stations A, B, and C. 1975-1976.

——density

------birth rate

major population decline was seen at stations A and B during early October. Numbers were quite low at freeze-up but the population persisted at station A until January. Pompholyx sulcata reappeared in mid-May 1976 and persisted in low numbers until early June when a slight increase was seen. Birth rates were relatively low but fluctuated widely.

The population at station C developed similarly to populations in the main basin. A major increase was noted during late June and early July that was accompanied by a steadily decreasing birth rate. From mid-July through mid-September the population showed three major peaks. Each period of decline was accompanied by an increase in the birth rate. The final decline occurred in late September and the population disappeared in November. The population at station C during May and June 1976 was similar to that at station A.

Vertical distribution of P. sulcata was uniform when the lake was well-mixed (Fig. 40). During warm, calm days of July and August, however, P. sulcata occasionally preferred deeper water. In early July when the deep water was largely depleted of oxygen, the population concentrated immediately above the point of severe depletion, in areas of 50 to 60% saturation. In late July and in August, the population concentrated in the deepest water where the oxygen was above 60% saturation.

Pompholyx sulcata was present over a range of temperatures from $0^{o}C$ to $24.5^{o}C$. Due to a very long duration of development below $12^{o}C$ numbers decreased when the temperature was $12^{o}C$ or lower. Rapid population growth did not occur until the temperature was near $20^{o}C$. These results compare favourably with those of Pejler (1957b)

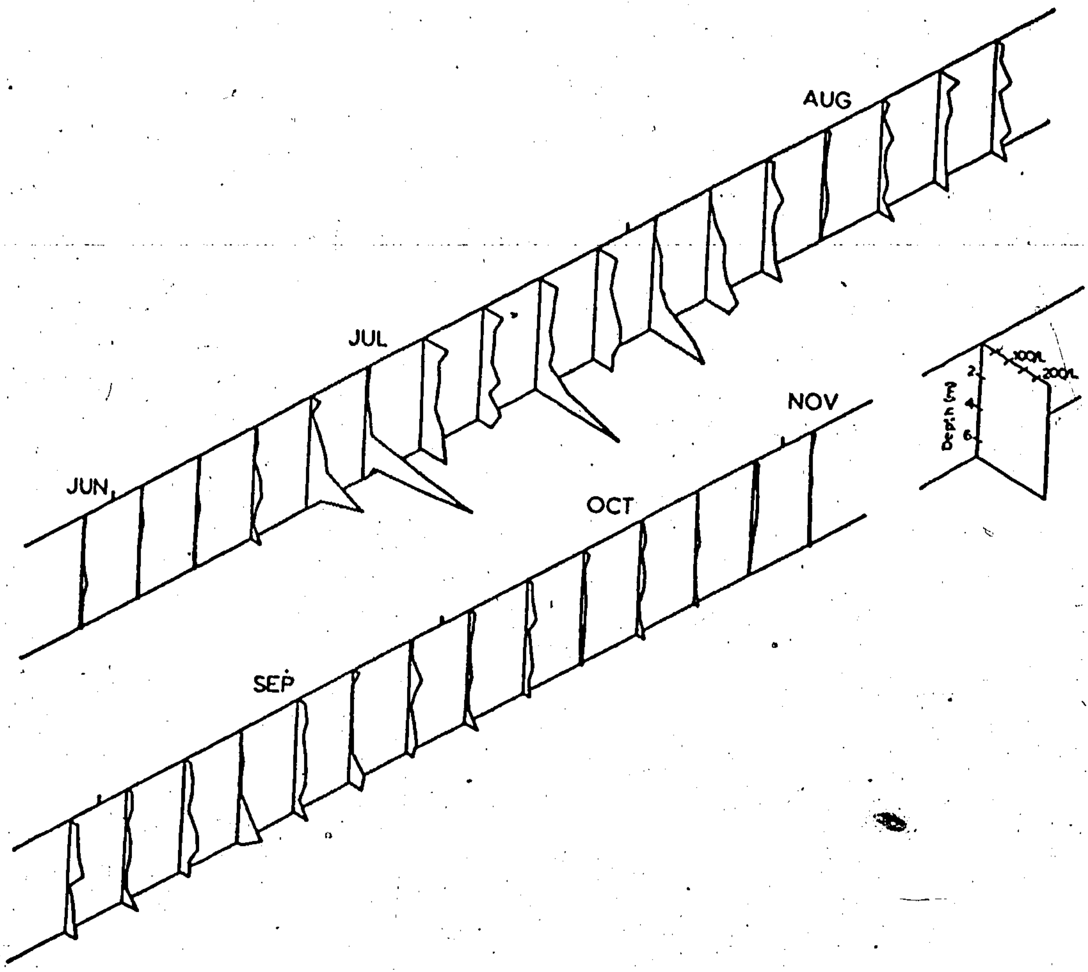


Figure 40. Vertical distribution of Pompholyx sulcata at station A. June 28-November 2, 1975.

who found maxima of P. sulcata in summer and small populations in November. George and Fernando (1969) found P. sulcata during May and September in a small lake in southern Ontario.

Numbers of P. sulcata in Hastings Lake showed rapid increase and maxima during the blue-green algal blooms and were low when the edible cells were most dominant.

Figure 41 shows the relationship between temperature and birth rate. Points are widely scattered; however a "border" of points, indicated by a dashed line, can be seen extending from the low birth rates at 12°C to the highest birth rate at 20°C. Edmondson (1965), in describing a similar graph, has attributed this border to the maximum birth rate possible under the temperatures indicated. Points lying below and to the right of the border represent birth rates that are lower due to some factor other than temperature. The border of points appears linear for most of the temperature range, indicating there is no inhibition of birth rate by temperatures as high as those encountered in the lake. The correlation coeffecient between birth rate and temperature is 0.62 ($P < 0.01$). As expected, the correlation coeffecient between birth rate and the total edible cells was low, -0.06, and not significant (N.S.).

Pompholyx sulcata tolerated a wide range of oxygen concentrations. During July 1975 it was found in water approximately 50% saturated with oxygen. In winter it was rare but present in water that was as little as 20% saturated.

Pompholyx sulcata was most abundant during warm months when crustaceans were also dominant. It was often found with Diaptomus, Diaphanosoma, Chydorus, Bosmina, and Diaptomus nauplii. Pompholyx

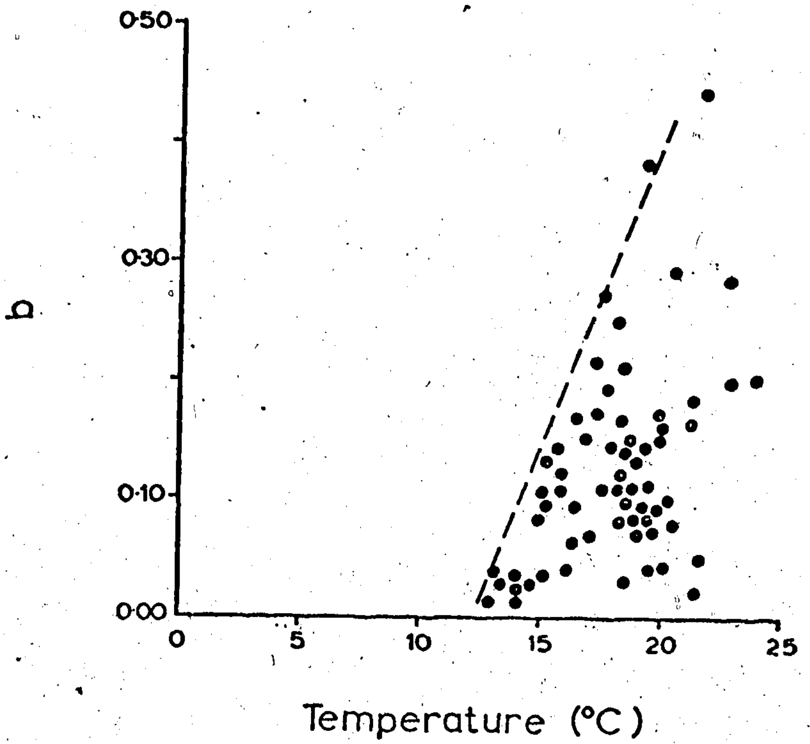


Figure 41. Relationship between temperature and the birth rate of <u>Pompholyx</u> <u>sulcata</u>. See text for details.

sulcata showed rapid population growth during July 1975 when the predator population was increasing; however, low numbers of P. sulcata in August were associated with a maximum of predators.

Testudinella patina (Herrmann)

Testudinella patina was very rare in Hastings Lake. A few specimens were found in the main basin during early July 1975 and a single specimen was found in mid-June 1976. Specimens were never found at station C. Ruttner-Kolisko (1974) notes T. patina occurs "mostly at low temperatures", but all specimens were found in warm, well-oxygenated water.

Collotheca mutabalis (Hudson)

Collotheca mutabalis is an elongate animal, partly enclosed in a gelatinous case. Edmondson (1959) suggests the small, uncinate mastax is adapted for trapping and tearing apart food items; however I know of no feeding studies.

Collotheca mutabalis was rare in Hastings Lake. Specimens were first collected in late June from the main basin. The population grew to a maximum in mid-July and disappeared in August. A second pulse was noted during late September and October. No specimens were found under the ice. In 1976 a few individuals were seen in late May and late June. The population at station C was similar to that in the main basin but the pulse in September 1975 was more short-lived than the pulse in the main basin. Because of small sample sizes the number of eggs per female is only a rough estimate of birth rate. A distinct increase in the egg ratio was noted immediately before the population maxima in both July and October 1975.

Collotheca mutabalis was present over a range of temperatures, from 2°C to 22°C, but populations declined at temperatures below 10°C. Campbell (1941) describes C. mutabalis as a rare species with maxima at temperatures from 18°C to 21°C. Chandler (1940) found it between 15°C and 26°C and Pejler (1957a) describes C. mutabalis as a "warm stenotherm", occasionaly found below 10°C. Collotheca mutabalis was found during blue-green algal blooms in mid-summer and peaks of edible cells in late fall. Pejler (1957b) notes it is found in eutrophic situations and Chandler (1940) found it in association with both blue-green algae and Chlorophyceae. Collotheca mutabalis was only found in water with high oxygen concentrations. It was seen during dominance of the Keratella species in the fall. During June and July 1975, C. mutabalis was associated with high numbers of predators but the fall pulse was associated with low predator population densities.

Collotheca pelagica (Rousselet)

Collotheca pelagica was similar in appearance to C. mutabalis but differed in lacking eye spots and possessing a tapering foot. Like C. mutabalis, C. pelagica possesses a small uncinate mastax and was rare during the study period.

Collotheca pelagica was not found at station A until late September 1975. A maximum was reached in early November. Thus the fall population of C. pelagica was similar to the fall population of C. mutabalis. In 1976, a few specimens were found in late June. During 1975 C. pelagica was very rare at station C, although a few individuals were collected in October. In 1976 a few specimens were collected in late May. Numbers rose rapidly during early June to a maximum in the second week of June. The population disappeared by late June. As with C. mutabalis it is difficult to interpret the egg ratio owing to the small sample sizes. However, in early June 1976 a distinct increase in the egg ratio preceded population growth at station C. As the population grew the egg ratio declined.

Although C. pelagica was found in water below 5°C, population growth did not occur in water below 10°C. Pejler (1957b) found this species during August and September. In Hastings Lake, C. pelagica was only found at times of high edible cell concentrations, when oxygen saturation was greater than 80%, and when Keratella species dominated the zooplankton community.

Synchaeta oblonga Ehrenberg

Synchaeta oblonga possesses a delicate, virgate mastax which functions to pierce and suck juices from prey items. Little is known about its choice of food but some species of Synchaeta can be cultured with Cryptomonas and small diatoms (Pourriot, 1965 in Ruttner-Kolisko, 1974).

Synchaeta oblonga was present in late May at stations A and B, but the populations disappeared by early June (Fig. 42). It was absent throughout the summer of 1975 but reappeared in mid-September. Numbers rose rapidly until a maximum was reached in late October, and by early November numbers had begun to decline until no specimens were found under the ice in December 1975. The population at station C appeared at the same time as populations in the main basin, but the maxima at stations A and B during September were much higher than the

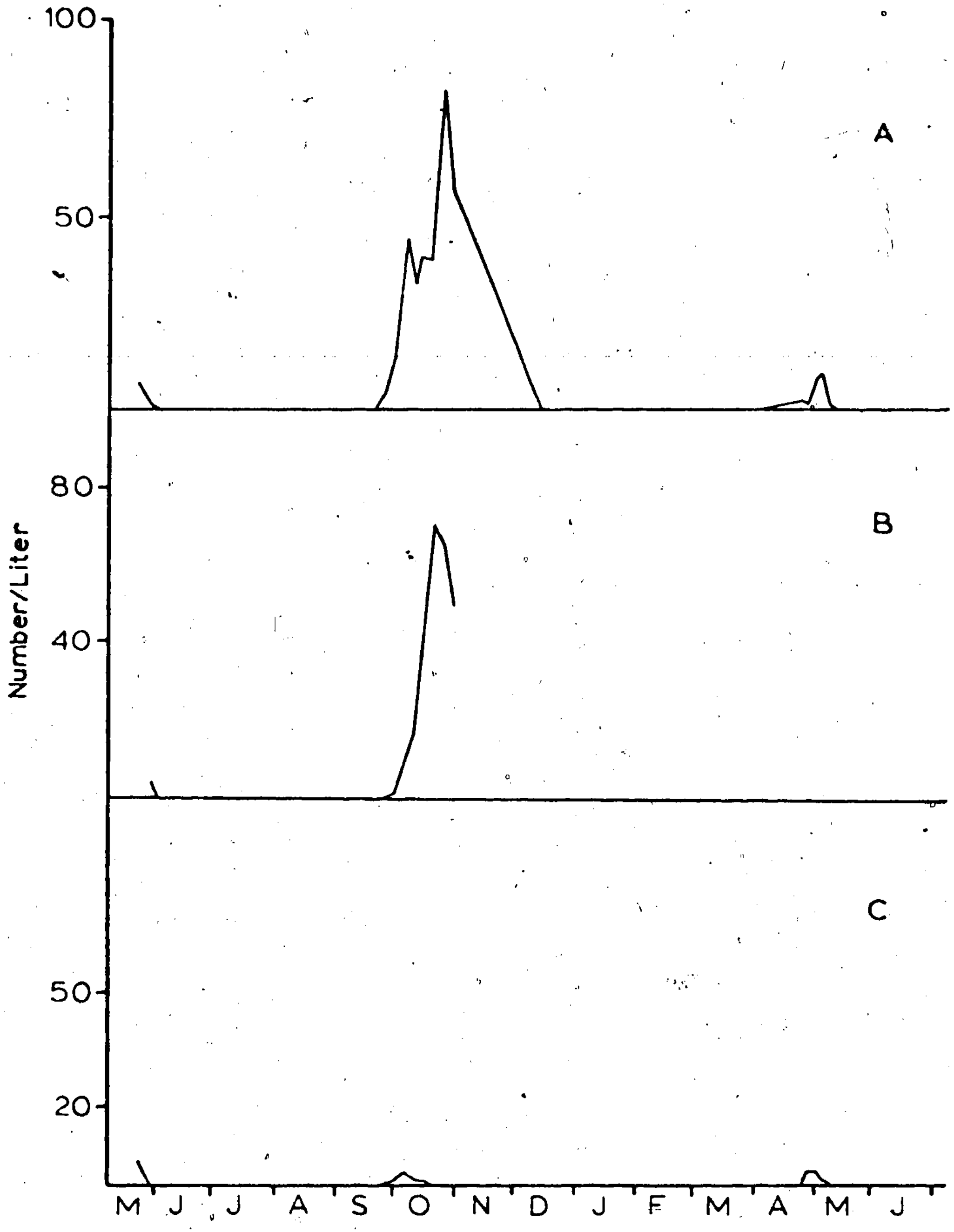


Figure 42. Population density of Synchaeta oblonga at stations A, B, and C. 1975-1976.

maximum recorded at station C. In 1976, small pulses were noted in late April and early May at both stations A and C. Vertical distribution was uniform.

Synchaeta oblonga was usually found in water below 12°C. Ruttner-Kolisko (1974) stated it is usually found in the 12°C to 15°C range, but noted that some specimens from Iceland were found in colder water. Pejler (1957b) found it during winter and spring.

In my study S. oblonga was found while concentrations of edible phytoplankton were high. However, the importance of these cells as a limiting factor is questionable as the maxima in the main basin during September and October were much larger than the maximum at station C, despite higher concentrations of edible cells at station C. Cryptomonas was also higher at station C than at station A during September and October.

Synchaeta oblonga appeared able to tolerate moderately low oxygen concentrations. The population at station A during April 1976 was found in water that was 50% saturated. During the rapid population growth in September 1975, oxygen saturation was 80 to 100%.

Autumn populations of S. oblonga were associated with large populations of Keratella species. Small populations in spring were associated with high numbers of copepod nauplii and Polyarthra dolichoptera. Rapid increase in numbers of S. oblonga during fall 1975 occurred when the predator population was very low.

Polyarthra dolichoptera Idelson

Polyarthra dolichoptera has a very large virgate mastax.

De Beauchamp (1938 in Pejler, 1957a) found that, unlike many other rotifers, *Polyarthra* would not accept *Chlorella* as food. Dieffenbach and Sachse (1911 in Pejler, 1957a) found that *Polyarthra euryptera* fed on *Cryptomonas ovata* but refused other cells of the same size. Pejler (1957a) found *Polyarthra vulgaris* in seasons and locations where *Cryptomonas* was present. In his statistical study, Edmondson (1965) found that all cells smaller than *Cryptomonas* were insignificant in affecting the birth rate of *P. vulgaris*. He noted that the birth rate was high when *Cryptomonas* was abundant and that the birth rate varied when *Cryptomonas* was rare, indicating that *P. vulgaris* is not totally dependent on *Cryptomonas*. He did find, however, that variation in birth rates were more strongly correlated with abundance of *Cryptomonas* than with water temperature.

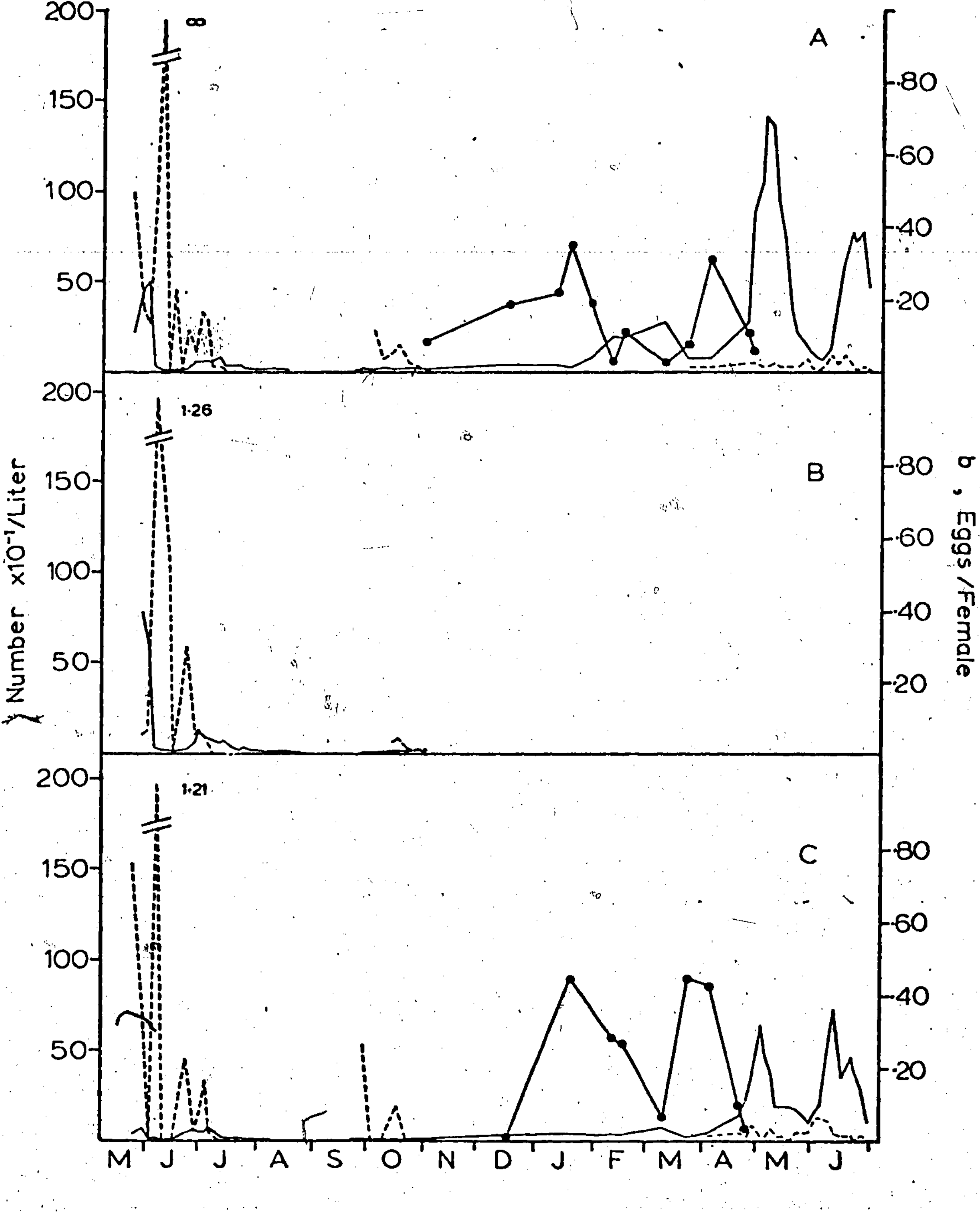
Population densities at stations A and B were dropping rapidly during late May 1975 and numbers were very low in early June (Fig. 43). Population density at station C was already low when sampling began. A small increase in numbers began in late June at all stations and continued to a peak in density in early July. Numbers declined sharply in late July, but the populations persisted until mid-August. The populations reappeared in late September at all stations, but remained at low densities until late January. Numbers increased in January and February with a higher maximum at station A than at station C. Both populations declined in late March and early April. Very rapid growth occurred at both stations immediately after ice break-up. A maximum of 1400/liter at station A and 630/liter at station C was reached in early May. Populations declined sharply after the maxima and were low by late May at station C and by early

Figure 43. Population density, birth rate, and eggs per female of *Polyarthra dolichoptera* at stations A, B, and C. 1975-1976.

——density

------birth rate

•——•eggs per female (winter only)


200
150
100
50
A
80
60
40
20
B
1·26
C
1·21
Number x10⁻¹/Liter
b, Eggs /Female
M
J
J
A
S
O
N
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June at station A. Another period of rapid growth was seen in June. Numbers at station C reached a maximum of 700/liter in mid-June and the population at station A reached a maximum of 760/liter in the third week of June. Population densities declined immediately after the maxima and the numbers at station C were very low in late June while the population at station A was still declining.

During early June 1975 birth rates appeared very high, probably an artifact of small sample sizes. At all stations, a distinct pulse in birth rate was noted before the small population pulse in July and a pulse in birth rate was noted in October. During winter, increases in numbers were also preceded by increases in egg ratio. According to Amren's (1964a) data on egg duration, the birth rate would be very low at temperatures of approximately 1°C, but many of the eggs must have developed to produce the pulse in population density. The egg ratio dropped during the increase in density but rose again immediately after the pulse. The major increase in numbers, immediately after break-up, appears to be the result of this pulse in eggs. As with the winter population, the calculated birth rates appear to be erroneous as the increased egg ratio apparently caused the pulse in density. Increase in numbers during June was preceded by a very small increase in birth rate; birth rates in this case were low due to a low egg ratio and not due to low temperatures.

Amictic eggs were found in late May 1975 at stations A and C. No more amictic eggs were found until late April 1976 when they were again recorded at both stations. Numbers of amictic eggs rose to a maximum of 73/liter on May 7, 1976 at station A and 21/liter at station C on May 4, 1976. None were found at either station after May 14, 1976.

Vertical distribution of P. dolichoptera was uniform for much of the year. In July 1975 they avoided deep water that was less than 10% saturated with oxygen. A similar avoidance of low oxygen concentration was seen under the ice (Fig. 44). During the two pulses in spring and early summer 1976, the vertical distribution was uniform.

Polyarthra dolichoptera was found in temperatures from 0°C to to 24.5°C. The large maxima were found in cool water but the July pulse occurred in water temperatures averaging 20°C. Amren (1964a) found highest numbers at temperatures of 10°C and noted high birth rates at temperatures of 5°C. Pejler (1957b) reports finding it during winter in eutrophic lakes and also in the hypolimnion of deep lakes during summer months. He notes in another publication (Pejler, 1961), however, that he has found it in water as warm as 19°C and at depths of only 3 to 4 metres.

Polyarthra dolichoptera was present when the edible cell concentration was high. The small pulse in July 1975 declined as the concentration of edible cells dropped in mid-July. It would be premature, however, to single out concentration of edible cells as a limiting factor since, in spring 1976, numbers of P. dolichoptera were higher at station A than at station C despite more edible cells at station C. Decline in numbers during spring 1975 was accompanied by a drop in the concentration of Cryptomonas. The small pulse in July 1975 was accompanied by a very small pulse of Cryptomonas. However, increases of P. dolichoptera during winter were associated with low concentrations of Cryptomonas. Concentrations of Cryptomonas

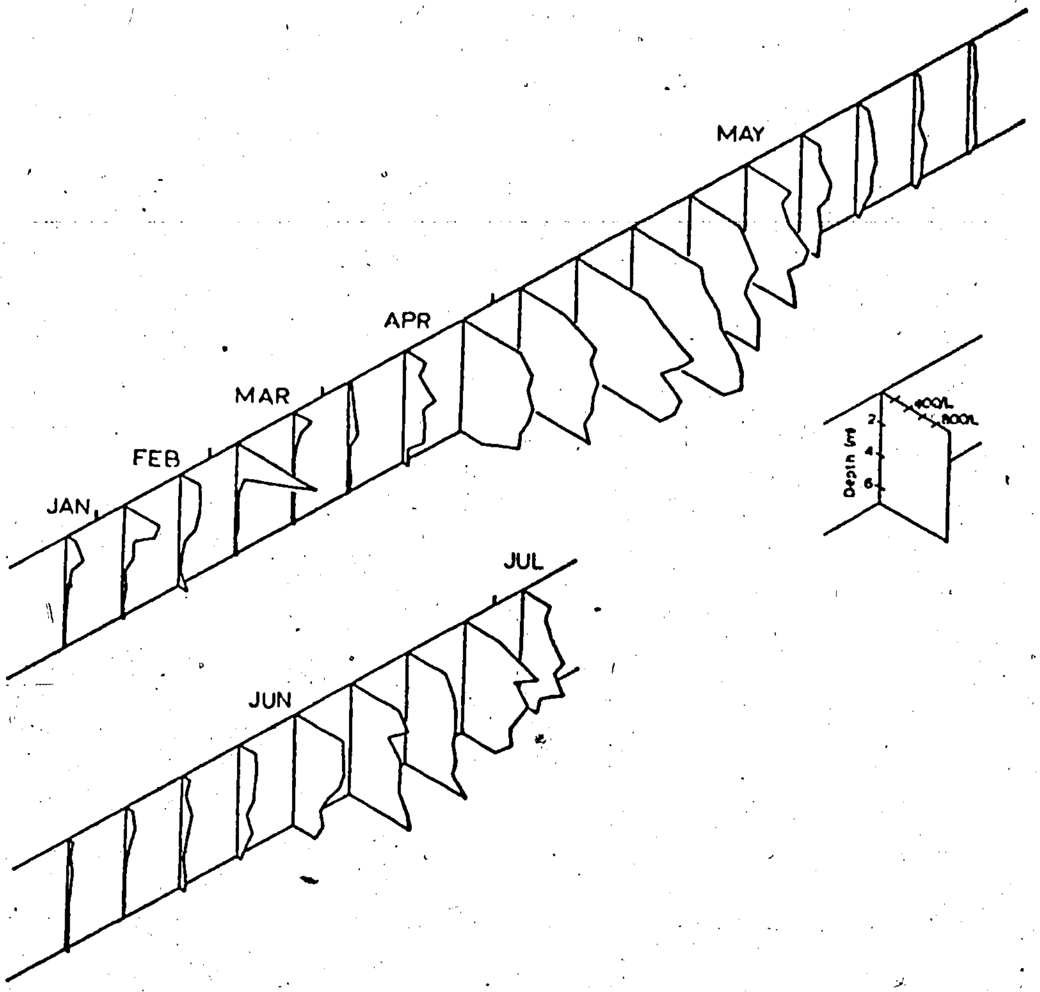


Figure 44. Vertical distribution of Polyarthra dolichoptera at station A. January 13-July 2, 1976.

were high during the early spring, 1976 pulse of *P. dolichoptera* at station C, but the spring pulse at station A occurred despite low concentrations of *Cryptomonas*. Thus in my study, the relationship between *P. dolichoptera* and *Cryptomonas* does not seem as clear as in studies with other species described earlier.

Polyarthra dolichoptera avoided areas of low oxygen concentration, but appeared to do well during winter despite saturation levels of only 20 to 40%.

When numbers of *P. dolichoptera* increased in early spring there were few animals present other than cyclopoid nauplii. Increases in July 1975 and June 1976 were associated with high densities of *Keratella*.

The pulse of *P. dolichoptera* at both stations during March 1976 occurred when predator populations were relatively low, but the late April and May pulse occurred while predators were common. Predator populations were still high but declining during the June 1976 pulse of this rotifer.

Trichocerca multicrinis Kellicott

Judging from the lack of information concerning *T. multicrinis* in the literature, it appears that this species is rare or absent in many parts of the world or, more likely, it is not considered truly planktonic. It is defined as planktonic, however, by Chengalath, Fernando, and George (1971).

Trichocerca multicrinis possesses a virgate mastax. Pourriot (1970 in Ruttner-Kolisko, 1974) reports that many species of *Trichocerca* pierce and suck the contents of algal cells and rotifer eggs.

Trichocerca multicrinis is a summer species in Hasting Lake. Specimens were first collected from stations A and B in mid-June (Fig. 45). Numbers increased during July to peak in late July and early August, then declined sharply and rose again during mid-August. Although the average population densities were comparable at stations A and B, the peaks were more pronounced at station A. Numbers declined slowly from late August through October. A few males were found in late September at station A. No specimens were found under the ice. In late May and June 1976 a few specimens were found at station A.

Trichocerca multicrinis appeared later at station C than it did in the main basin. The population density increased slowly through July until a maximum was reached in the second week of August. This peak coincided with the second major peak seen in the main basin, but the density at station C was lower. Numbers declined slowly and a few animals were still present in late October but none were found under the ice. In 1976 T. multicrinis was found during late May and June.

Vertical distribution was uniform throughout the year except in early July when T. multicrinis avoided deep water which was low in oxygen.

Although T. multicrinis was found in water as cold as 2°C, it appeared to be most successful in warm water in Hastings Lake. Major increases in population growth occurred in water above 20°C, while the population declined at temperatures below 18°C. However, the 1976 spring population started growing in water at 13°C. This small pulse probably represented the hatching of resting eggs.

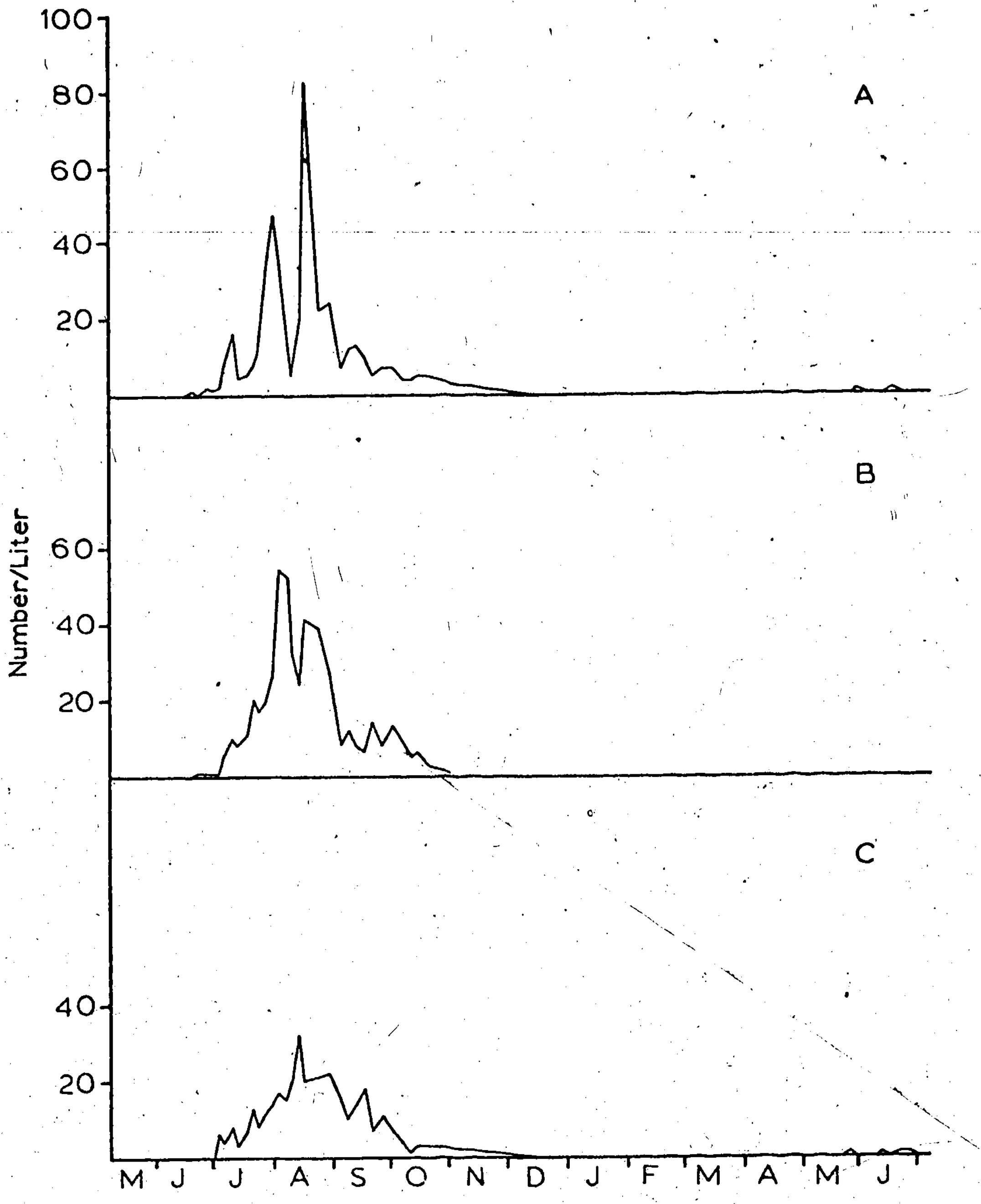


Figure 45. Population density of Trichocerca multicrinis at stations A, B, and C. 1975-1976.

Trichocerca multicrinis usually occurred when the water was well-oxygenated. As mentioned earlier, individuals appeared to avoid areas of low oxygen concentration during July 1975. This species was common during the crustacean dominance of the zooplankton community. Predator populations were relatively high during summer 1975 when T. multicrinis was most common.

Trichocerca stylata (Gosse)

Like T. multicrinis, T. stylata has a virgate mastax. It is small compared to T. multicrinis, being only 70 to 110 μ in length (Ruttner-Kolisko, 1974).

During my study, T. stylata was always rare. In the main basin a few specimens were found during July and one specimen was found in early October but none were found under the ice nor during spring and early summer 1976. At station C, a small population appeared in late July that developed to a maximum of 10/liter in early August. By mid-August, the population had disappeared. In 1976, specimens were found in late June and it appeared that the population was increasing when the study ended in early July.

Trichocerca stylata showed no preference for any particular depth during the study. It was usually found in water with temperatures over 15°C but an exception occurred in October when the temperature was approximately 10°C. Trichocerca stylata appeared in greatest numbers during the summer months when the phytoplankton was dominated by blue-green algae and the zooplankton was dominated by crustaceans. Oxygen concentrations were usually high when and where T. stylata was found. The population at station A during July 1975 was associated with relatively high numbers of predators.

Brachionus angularis Gosse

Brachionus angularis possesses a large malleate mastax with five large, stout teeth on the uncus. The species is not known to be a selective feeder, apparently feeding on algae and detritus of suitable size (Ruttner-Kolisko, 1974). An important fact concerning feeding of B. angularis was discovered during my study. During observations of living B. angularis I noted that a few individuals had filaments of Oscillatoria protruding from the mouth. The mastax was observed to be pounding rapidly on the end of the filament. These were not accidental occurrences as the animals were observed "searching" for the end of the filament. When an individual struck a filament it immediately stopped its normal spiralling motion, then moved slowly along the edge of the filament until the end was reached and maneuvered into the mouth. On most encounters the rotifer failed to reach the end of the filament either because currents moved the filaments away or else the rotifer apparently "gave up". However, several successful attempts were noted and when the filament was secure in the mouth the rotifer resumed its normal spiralling action. It is apparent, therefore, that B. angularis, and possibly other rotifers, can use some blue-green algae and perhaps some other filamentous algae as food sources.

Brachionus angularis was rare in the main basin of Hastings Lake. Specimens were first found in early June (Fig. 46). Numbers remained low until early August when a small but distinct increase

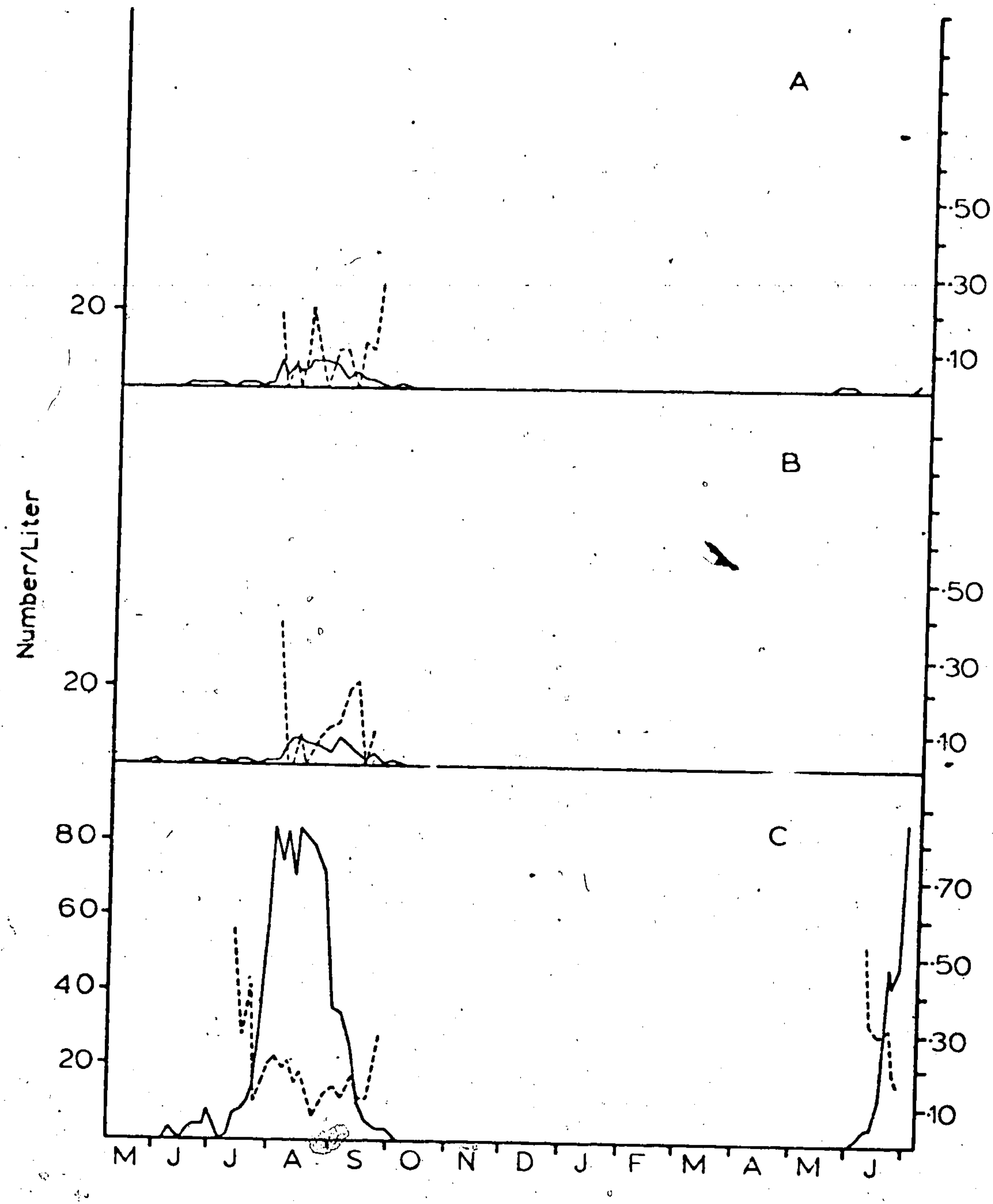


Figure 46. Population density and birth rate of Brachionus angularis at stations A, B, and C. 1975-1976.

—— density

----- birth rate

was noted. Population density remained stable during August but a definite decline occurred in September until by mid-October the population had disappeared. A few animals were collected in early May, 1976, but the population disappeared and no more specimens were found until early July. During the small pulses at stations A and B, birth rates varied considerably. It is difficult to determine whether this reflects the actual birth rate or is the consequence of small sample sizes

Brachionus angularis occurred at station C at approximately the same time as it occurred at stations A and B, but the population density at station C was much greater than in the main basin. The population at station C remained small during June and early July, but a rapid increase was recorded in Mid-July. As numbers rose in July, birth rates dropped sharply from 0.56 eggs/female/day to a minimum of 0.10 eggs/female/day. In August, the population density levelled off and remained high for approximately four weeks. As soon as the density levelled off the birth rate rose to approximately 0.20 eggs/female/day and remained at 0.15 eggs/female/day until August 25 when it declined to 0.06 eggs/female/day. This drop in birth rate preceded a rapid drop in numbers through September until mid-October when no individuals were found. It appeared that the birth rate rose during the decline in numbers but again, sample sizes were small. In 1976 specimens were first found in early June at station C. Numbers increased suddenly and were still increasing on July 2. During this increase the birth rate dropped, in a manner almost identical to the 1975 population. An interesting situation arose during 1975 and 1976 when the populations were increasing. During mid-July 1975 a slight reduction in rate of population growth was accompanied by an increase in birth rate. In late June 1976, a slight decline in density was accompanied by a small but distinct increase in birth rate.

Brachionus angularis showed no preference for any particular stratum of water (Fig. 38). It was found in water between 12 and 24°C. In 1975 the population at station C remained low until the water temperature was nearly 20°C, while in 1976 the population increased rapidly in water at 14 to 16°C. Ruttner-Kolisko (1974) calls *B. angularis* a "eurythermous" species, but the absence of this animal at temperatures below 10°C and the long duration time of eggs below 10°C suggests it is restricted to warm water in Hastings Lake. Allan (1920) found *B. angularis* to prefer temperatures around 20°C and Chandler (1940) found it between 21 and 26°C while Arora (1966) found it between 21 and 35°C. The correlation coefficient between temperature and birth rate was 0.46 ($P < 0.05$).

Brachionus angularis appeared during the blue-green algal blooms. Allan (1920) found that it preferred "organically enriched areas" and Arora (1966) found maximum population densities in sewage ponds. Chandler (1940) also found *B. angularis* in association with blue-green algae and Pejler (1957b) describes it as a "eutrophic" species. These findings, coupled with my observations of *B. angularis* feeding on *Oscillatoria*, indicate the importance of blue-green algae to this species. I noted that rapid increase in numbers of *B. angularis* began while the *Aphanizomenon*-*Oscillatoria* group rose from "present" to "common". However, the population of *B. angularis* at station C declined in September, well before the major decline in *Aphanizomenon*-*Oscillatoria*.

Brachionus angularis was found in waters well-supplied with oxygen. The few specimens found during early July 1975 at station A were near the surface in well-oxygenated waters.

Brachionus angularis was common while the zooplankton community was dominated by crustaceans such as Diaptomus nauplii and copepodites, Bosmina, and Chydorus. At station A it was most common when predators were numerous.

Notholca squamula (Muller)

Notholca squamula possesses a small malleate mastax. Beauchamp (1938 in Pejler, 1957a) reported that it eats the small cells of Chlorella, but he could not maintain population growth on this diet.

Notholca squamula was always rare in Hastings Lake with small populations in spring and early winter. In late May 1975 a few animals were collected from station C while none were found in the main basin. In mid-December 1975, 1/liter were found at station A while 10/liter were found at station C. The population at station C had disappeared by mid-January 1976, but the population at station A persisted until late January. The 1976 spring population at station A first appeared in mid-May. Population density remained at 1/liter until early June when the population apparently disappeared, but two animals were found on July 2.

The 1976 spring population at station C appeared at roughly the same time as the station A population. Numbers remained low until an increase was noted in late May from 1/liter on May 28 to 13/liter on June 7. Immediately after this maximum the population declined and no specimens were found after June 11.

Notholca squamula appears to be a cold water species; it was found in water from 1°C to 15°C, while population increases were seen in temperatures as low as 2°C. These results concur with information published on temperature ranges and geographic locations of N. squamula. Amren (1964c) found N. squamula in arctic ponds and Pejler (1957a) noted its presence during summer in ponds above the tree line. Pejler (1957b) also found it in summer in lakes below the tree line but noted it was only present in the hypolimnion.

With the exception of the early July 1976 recording, N. squamula was present during times of high concentrations of the edible cells. It was normally found in well-oxygenated water but appeared able to withstand low oxygen concentrations since it was found during January 1976 when the oxygen concentration was 30 to 40%.

Notholca squamula was present with cyclopoid copepodites and nauplii. It appeared with Polyarthra dolichoptera and was present while the Keratella species were increasing during spring. The 1976 spring and early summer populations of N. squamula were associated with numerous predators.

Keratella hiemalis Carlin

A single specimen of Keratella hiemalis was found on March 12, 1976 in water at 1°C and with an oxygen concentration of 5 to 10%.

Keratella quadrata Muller

Keratella quadrata was one of the most common rotifers in Hastings Lake during the study period. It is a very conspicuous animal in the plankton, attaining lengths over 150 µ and possessing two caudal spines. Nothing is known of its feeding habits, but its malleate mastax probably equips it to grind small phytoplankton cells and detritus.

Keratella quadrata was most abundant during spring and fall and it showed the same basic pattern of occurrence at all three stations (Fig. 47). Numbers in the main basin population were increasing when sampling began in late May. Population densities rose to a maximum in the second week of June. Birth rates were high during late May and early June, but dropped as the population increased. After the maxima, numbers at both stations dropped rapidly but rose again during late June and stabilized somewhat until mid-July. Birth rates rose during and immediately after the major decrease in density. While populations were stable in early July the birth rate was stable at station A, but appeared to rise at station B. After mid-July, the numbers declined at both stations and continued dropping until August when a slight peak was noted. During the decline in July and early August, the birth rate peaked twice, once when the population declined sharply in the third week of July and once in early August, immediately before the small peak in population density. The density remained low during August and through the first half of September. Birth rates were relatively high during this period but fluctuated at station B. Numbers began to increase in mid-September and continued increasing, reaching a maximum in late October. Birth rates remained relatively high during the early fall increase in numbers, but started to decline during October and were low by late October when population growth had stopped.

Despite low birth rates in late fall the population density

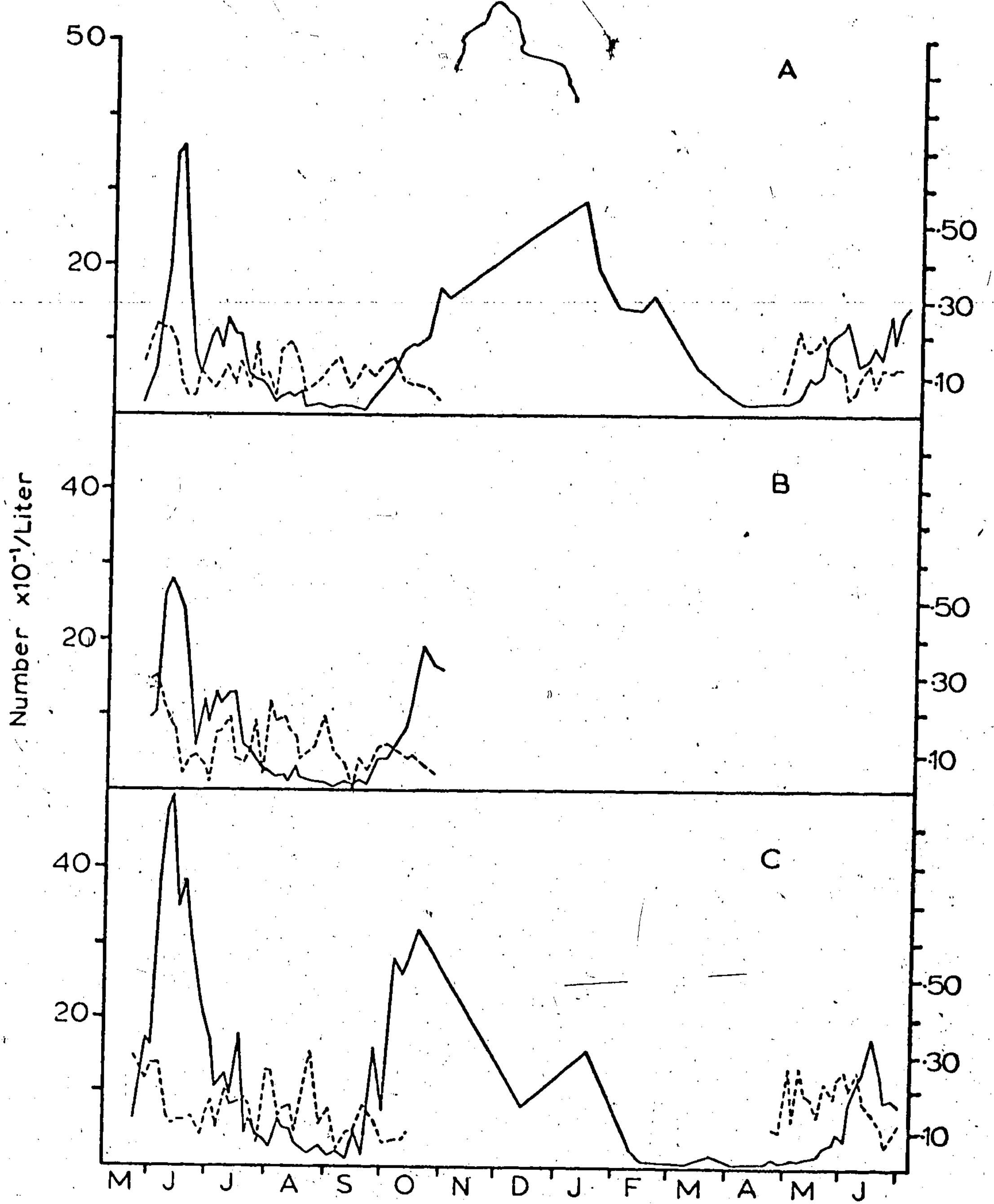


Figure 47. Population density and birth rate of Keratella quadrata at stations A, B, and C. 1975-1976.

——density

------birth rate

of K. quadrata at station A increased during December and January. In December, 27% of the animals carried an egg, but egg duration data (Fig. 34) indicated that duration times were extremely long, thus resulting in low birth rates. In mid-January, the density declined but appeared to stabilize in mid-February. After February the density dropped again and numbers were very low in April. Population density rose slowly to a maximum in late May 1976, but was much lower than the 1975 maximum. Birth rates were very high during late April and early May, but dropped as the population increased. In early June a drop in density was associated with a pulse in the birth rate, followed by an irregularly increasing density during the remainder of June.

Population growth at station C was similar to the growth in the main basin. The initial increase in numbers during late May and early June was accompanied by a decrease in birth rate, while a slight decrease in numbers on June 2, 1975 was accompanied by a pulse in birth rate. The population density reached a maximum in the third week of June while the birth rate was low. Numbers at station C at this time were higher than those at stations A and B, but dropped during the remainder of June and early July. This period of decline lasted longer than the corresponding decline in the main basin. Like the main basin, a secondary pulse occurred in the north-east basin during July, followed by a decline during late July and early August. The minimum in early August was accompanied by a peak in birth rates. A slight peak in density occurred during mid-August, followed by a gradual decline to a minimum in mid-September. Birth rates appeared similar to those in the main basin with a peak in late August and then a decline to a minimum in early September. Numbers increased in an irregular fashion during late September and October and stabilized somewhat during mid-October. Birth rates climbed during the second and third week of September, but declined in late September and early October. During early winter, numbers dropped quickly at station C. An increase was noted during January but by mid-February numbers were very low and remained low until May 1976. Population density of K. quadrata increased very slowly during late May; major increases were not seen until June. During this period the birth rate fluctuated but remained high. The first major drop occurred in June when the population showed a major increase to a peak in mid-June, followed by a decline during late June and early July. The 1976 peak at station C was similar in timing but much smaller than the peak in 1975. Also, the 1976 peak at station C was similar in size to that at station A but occurred almost a month later.

Keratella quadrata showed a uniform depth distribution for most of the year (Fig. 48). During July 1975, it appeared to prefer the warm surface waters that were supersaturated with oxygen. In mid-December the population concentrated in deeper water but as winter progressed and oxygen was depleted at lower depths the population moved to surface waters.

Keratella quadrata was found throughout the year in temperatures of 0°C to 24.5°C. Populations increased in both warm water (above 20°C) and cold (below 5°C) although the birth rate was always low below 5°C. High population densities were maintained during the winter despite temperatures of 0 to 2°C. Allan (1920) found

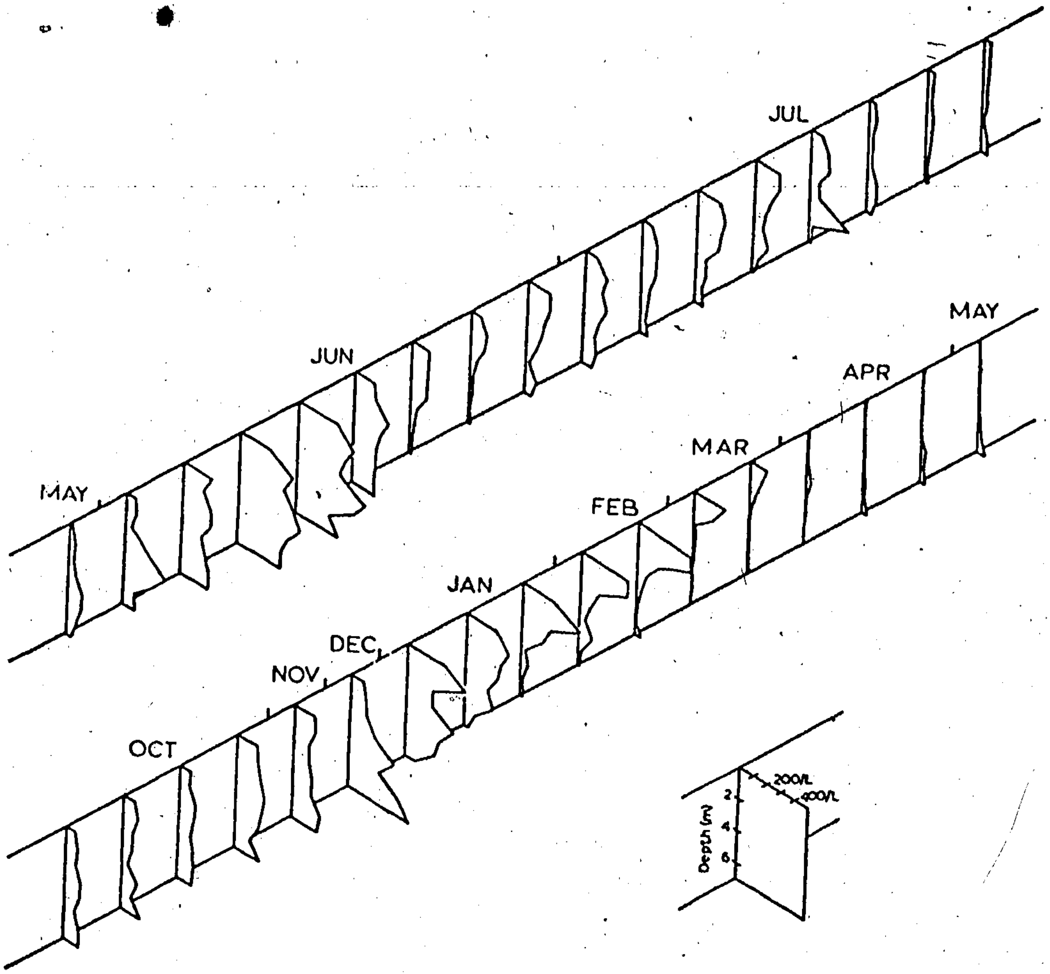


Figure 48. Vertical distribution of Keratella quadrata at station A, May 30-July 25, 1975; October 13, 1975-May 4, 1976.

K. quadrata common up to 23°C and noted increases during January and June. Amren (1964a) found that his Spitzbergen populations increased rapidly above 5°C and Davis (1954) found this species most common betwwen 4°C and 10°C. Ahlstrom (1943) found specimens in the hypolimnion of Lake Michigan during the warm months. George and Fernando (1969) found that numbers of K. quadrata increased during the winter at all depths, while during summer it was only found in the hypolimnion.

Keratella quadrata populations usually increased when the phytoplankton community was rich in edible cells, but small increases were noted during July when blue-green algae were dominant. Allan (1920) found K. quadrata more common near sewage outlets and Chandler (1940) found it most common when members of the Chlorophyceae were present. Amren (1964a) found marked reductions in birth rate of K. quadrata that did not coincide with changes in the "small monad" populations. He suggested that changes in age structure of the population and changes in fecundity of generations could be responsible for changes in birth rate.

Figure 49 shows the relationship between birth rate and temperature. The border, delineating the left side of the graph from the right side, probably represents maximum possible birth rate under the temperature conditions. The correlation coefficient between birth rate and temperature is 0.56 ($P < 0.01$). The fact that the highest birth rate was recorded when the water temperature was 14°C and that the border on the graph slopes downward at temperatures above 15°C may indicate a temperature inhibition of birth rate above 15°C. It is also possible, however, that the decline in

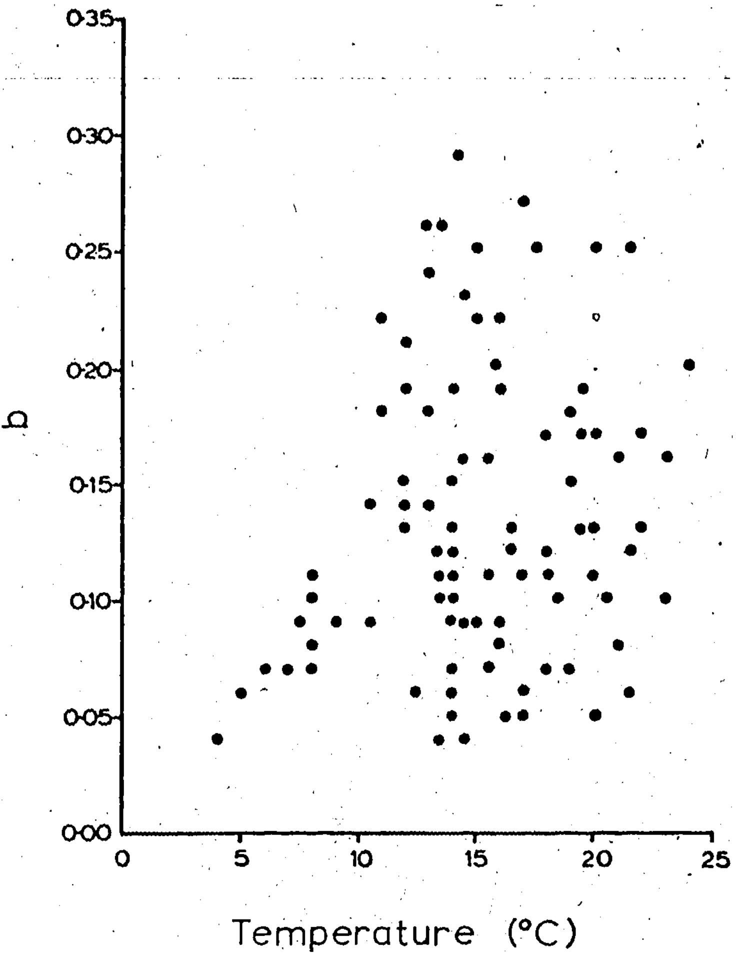


Figure 49. Relationship between temperature and birth rate of *Keratella quadrata*.

birth rate above 15°C was partly due to reduction in concentration of the total edible cells during summer.

The relationship between birth rate and concentration of edible cells is more obscure than that between birth rate and temperature. The correlation coefficient between birth rate and concentrarion of edible cells is 0.10 (N.S.) when data for the entire year are used. If points from the ice-free period only are used, the correlation coefficient is 0.48 ($P < 0.01$). This discrepancy is a result of winter water temperatures. Amren (1964a) showed that at 1°C, typical of the ice-covered period, the development time of K. quadrata eggs would be extremely long; thus the birth rates would be low despite high edible cell counts.

Despite these positive relationships between temperature and birth rate and between birth rate and edible cell concentrations, interpretation of Figure 50 still poses a few problems. As expected the border is lined with points of high edible cell concentrations, but a number of points of high edible cell concentrations are found well below and to the right of the border. In other words a high concentration of edible cells and a suitable temperature are not always associated with a relatively high birth rate.

Keratella quadrata was found in a wide range of oxygen saturations. During calm weather in July 1975 and during winter, the majority of the population moved from poorly-oxygenated waters near the bottom to surface waters. Despite this apparent preference for well-oxygenated waters, K. quadrata survived during the winter when oxygen saturation was low. For example, during March 1976 animals were found in water less than 10% saturated with oxygen.

Figure 50. Relationship between temperature, total edible cells, and birth rate of *Keratella quadrata*.

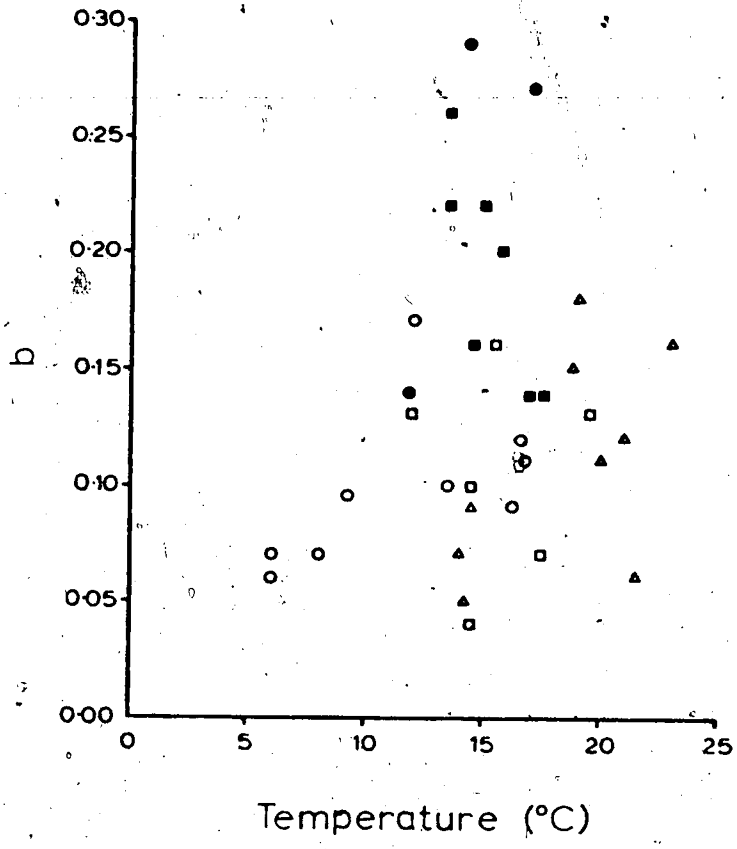
● >10,000 cells/ml

■ 5,000-10,000 cells/ml

○ 2,500-5,000 cells/ml

□ 1,000-2,500 cells/ml

△ <1,000 cells/ml


b
0·30
0·25
0·20
0·15
0·10
0·05
0·00
0
5
10
15
20
25
Temperature (°C)

Keratella quadrata was common in Hastings Lake when the zooplankton community was dominated by the congeneric species *K. cochlearis* and and *K. earlinae*. In 1975, the first major peak of *K. quadrata* preceded that of the other two *Keratella* species, while the secondary peaks of *K. quadrata* coincided with the first peaks of *K. cochlearis* and *K. earlinae*. During fall 1975, *K. quadrata* increased at the same time as *K. cochlearis* while *K. earlinae* started increasing more than a week earlier. In spring 1976, *K. quadrata* increased at the same time as *K. cochlearis*. Copepod nauplii were often abundant immediately before and after *K. quadrata* peaks; *Daphnia pulicaria* persisted at high population densities while populations of *K. quadrata* declined in early summer.

Keratella quadrata showed rapid population growth in late May and early June 1975 while predator density was low. The population declined in June as predators increased and the density was low during July and August when predators were common. The fall increase in numbers of *K. quadrata* occurred as the predator population declined. During May and June 1976, the population growth rate of *K. quadrata* was low when *Cyclops bicuspidatus thomasi* was abundant. The correlation coeffecient between density of *K. quadrata* and density of predators was -0.22 (N.S.) (Table 5).

Average lorica and spine lengths of *K. quadrata* are shown in Figure 51. During late May and June 1975, when the water was warming rapidly and the population was growing, lorica length at both stations was decreasing while spine length was increasing. In July spine length decreased suddenly and lorica length continued to decrease.

TABLE 5

Correlation coefficients between rotifer density, spine length and lorica length, and cyclopoid copepods. "Predators" represents the summation of the density of *Cyclops bicuspidatus thomasi* IV - VI and *Cyclops vernalis* IV - VI.

		Copepodites I - III	*Cyclops bicuspidatus thomasi* IV - VI	*Cyclops vernalis* IV - VI	Predators
Keratella quadrata	Spine Length	-0.20 (N.S.)	-0.35 (N.S.)	-0.50 (N.S.)	-0.68 $(P<0.05)$
	Lorica Length	0.260 (N.S.)	-0.09 (N.S.)	-0.84 $(P<0.01)$	-0.55 (N.S.)
	Density	0.008 (N.S.)	-0.01 (N.S.)	-0.44 (N.S.)	-0.22 (N.S.)
Keratella earlinae	Spine Length	0.001 (N.S.)	0.54 (N.S.)	0.30 (N.S.)	0.63 $(P<0.05)$
	Lorica Length	0.01 (N.S.)	-0.55 (N.S.)	-0.40 (N.S.)	-0.74 $(P<0.01)$
	Density	0.14 (N.S.)	-0.68 $(P<0.01)$	-0.02 (N.S.)	-0.65 $(P<0.05)$
Keratella cochlearis	Spine Length	0.03 (N.S.)	0.74 $(P<0.01)$	0.17 (N.S.)	0.46 (N.S.)
	Lorica Length	0.36 (N.S.)	-0.05 (N.S.)	-0.75 $(P<0.01)$	0.22 (N.S.)
	Density	-0.06 (N.S.)	0.27 (N.S.)	-0.06 (N.S.)	0.24 (N.S.)

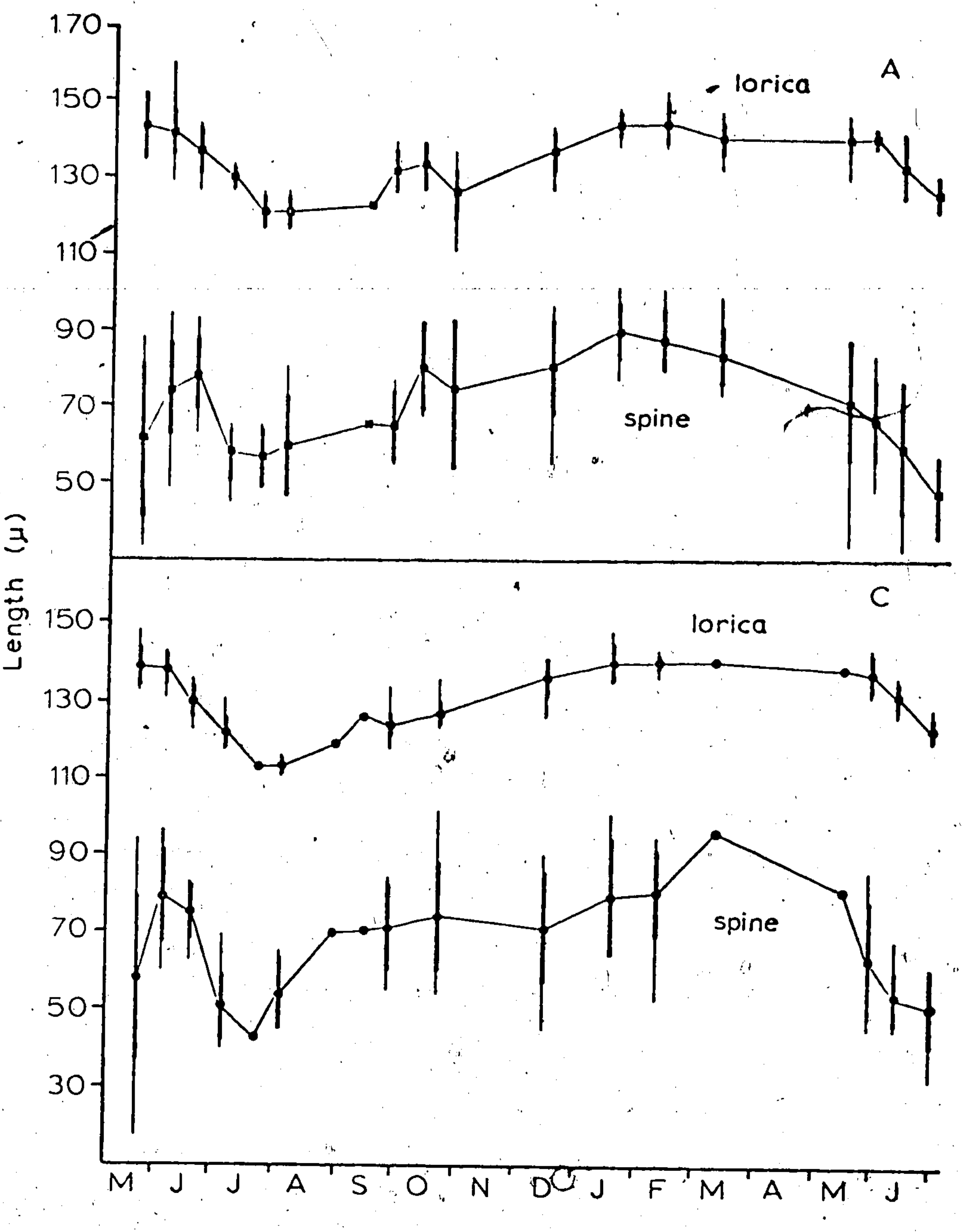


Figure 51. Average lorica and spine lengths of Keratella quadrata at stations A and C., 1975-1976. Thick bars indicate one standard deviation, thin bars indicate the range.

The sudden decrease in spine length occurred during the warmest time of the year and immediately after the maximum population density. During late July and August, while water temperatures were dropping and the population was low, both spine and lorica lengths increased with animals at station C showing larger increases than those at station A. During fall, lorica and spine lengths continued to increase. The graph for station A shows a sudden increase in both spine and lorica lengths during September, but both lengths appeared to decline again in late October. These increases in length occurred while the water temperature was dropping quickly and the population was growing. The population was stable when the lengths declined in October. During early winter both of these measurements increased slowly. The population at station C was declining during this period while the population at station A showed some increases. After February, the spine lengths at both stations declined while the lorica lengths remained constant. This decline in spine length continued through the spring and early summer of 1976. The lorica length remained constant through early spring but dropped during June. The water temperatures were increasing during May and early June but dropped in late June. The population showed slow growth during the period of declining spine and lorica lengths in spring 1976. The correlation coeffecient between temperature and spine length was -0.73 ($P < .01$), and the coeffecient between temperature and lorica length was -0.57 ($P < .01$).

Figure 52 shows the relationship between spine length and lorica length. The correlation coeffecient between the two lengths was 0.56 ($P < .01$) at station A and 0.48 ($P < .01$) at station C.

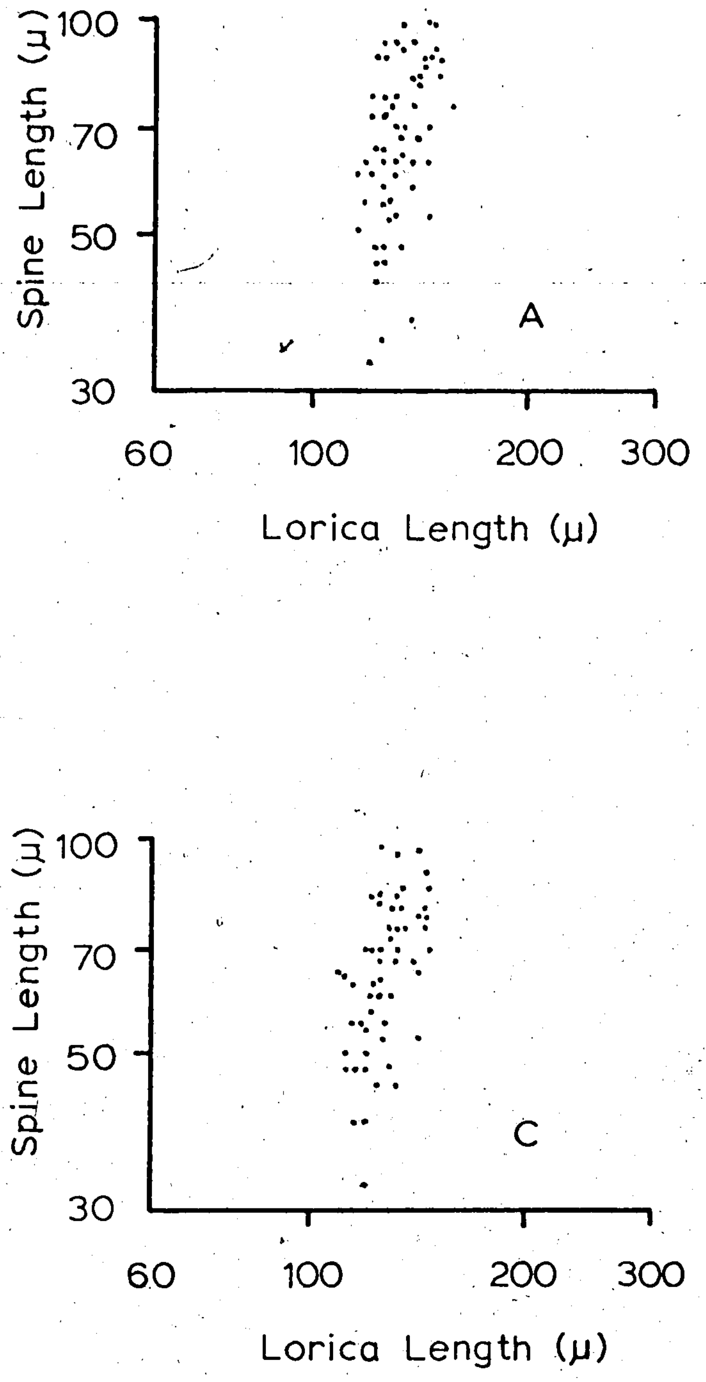
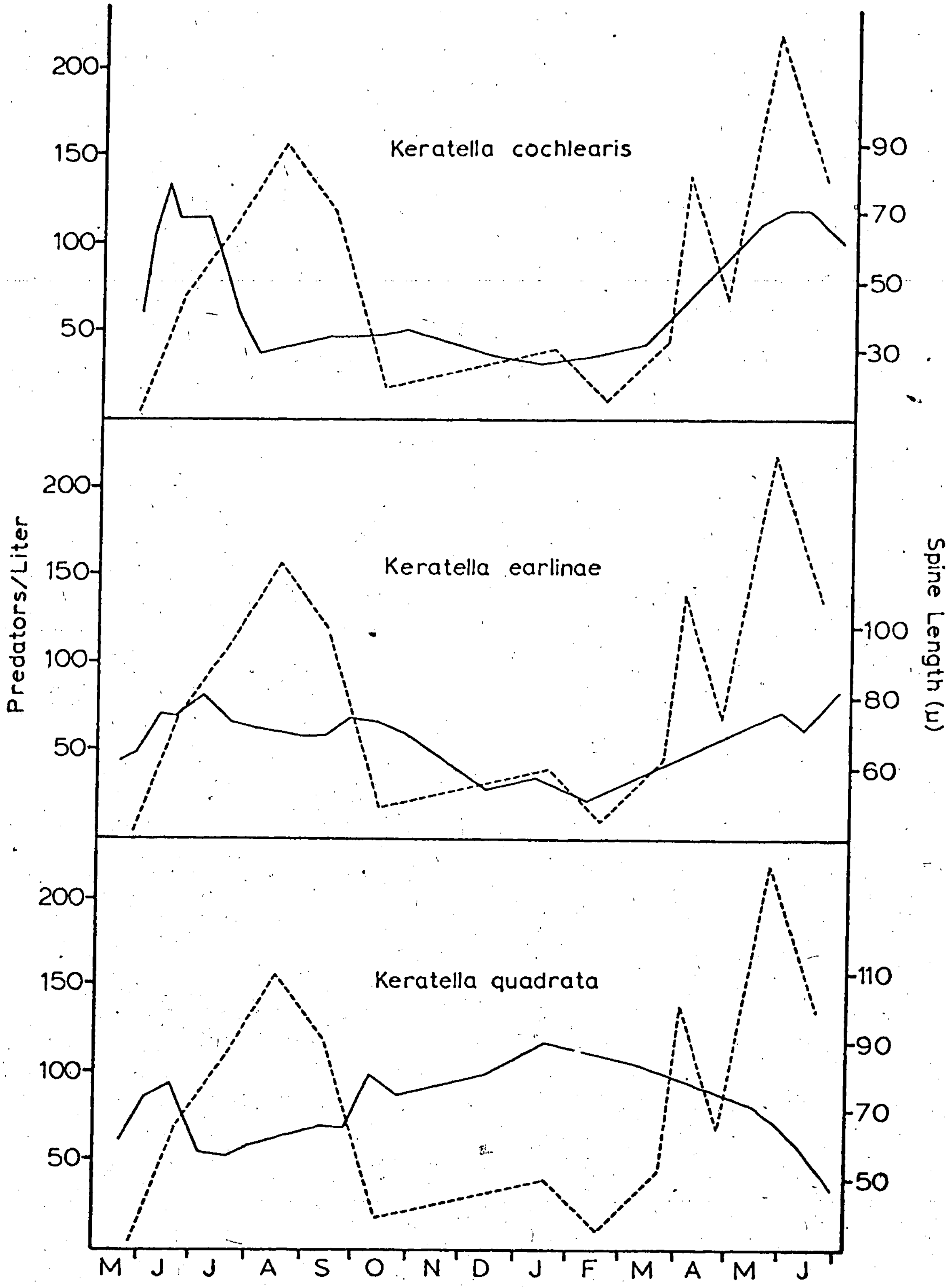


Figure 52. Relationship between lorica length and spine length of *Keratella quadrata* at stations A and C.

Figure 53. Spine length of _Keratella_ _quadrata_, _K._ _cochlearis_, and _K._ _earlinae_ with density of predators. 1975-1976.

——spine length

------predator density

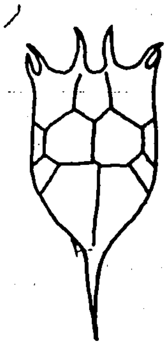

Keratella cochlearis
Keratella earlinae
Keratella quadrata
Predators/Liter
Spine Length (µ)
200
150
100
50
90
70
50
30
100
80
60
110
90
70
50
M J J A S O N D J F M A M J

Despite general increases in spine length with increases in lorica length, there is a large range of spine lengths for any particular lorica length. A sign test (Sokal and Rohlf, 1969) was used to determine any difference in both spine and lorica length between stations A and C. Average lorica and spine lengths were computed from each measured sample from station A and compared to the corresponding sample from station C. No signifigant difference between stations was found in either spine or lorica length.

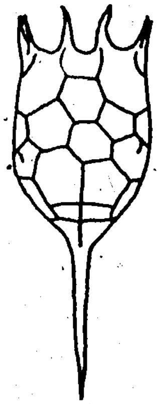
During early summer 1975, spine lengths increased and lorica lengths decreased as the predator population grew (Fig. 53). However, both lengths dropped in July when the predator population was still growing. A sudden increase was noted in both lengths as numbers of predators declined in October 1975. Both spine and lorica lengths were long in winter while predator populations were low. In spring 1976 spine lengths decreased as predator populations grew and lorica lengths dropped in June when predators were still numerous but declining. The correlation coeffecient between spine length and predator density was -0.68 ($P < .05$) and the coeffecient between lorica length and predator density was -0.55 (N.S.), (Table 5). Neither spine nor lorica lengths were correlated with numbers of *Cyclops bicuspidatus thomasi*, but a signifigant ($P < .01$) negative relationship occurred between the density of *Cyclops vernalis* and lorica length (Table 5).

Taxonomy of *Keratella cochlearis* and *Keratella earlinae*

Taxonomy of the "cochlearis group" (Ruttner-Kolisko, 1974), genus *Keratella*, is a difficult area of study. Ahlstrom (1943) determined several species and numerous varieties in this group. Ruttner-Kolisko (1974) prefers to call the entire group *Keratella cochlearis* and describes three major series, noting that morphological varieties seen in each series are often associated with environmental factors. Two easily distinguished forms were found in Hastings Lake, one corresponding to Ruttner-Kolisko's tecta series, (Ahlstrom's *K. cochlearis*) and one to Ruttner-Kolisko's irregularis series (Ahlstrom's *K. earlinae*). In my study Ahlstrom's original classification is used for the following reasons. The two forms showed an obvious and consistent difference in dorsal sculpturing of the lorica (Fig. 54), a characteristic considered to be of great taxonomic importance (Ahlstrom, 1943). *Keratella cochlearis* possesses a mid-dorsal keel while *K. earlinae* possesses irregular facets. *Keratella earlinae* was consistently bigger than *K. cochlearis* and showed a less exhuberant form of cyclomorphosis, although timing of major cyclomorphic events were similar. Birth rates of *K. cochlearis* were almost always higher than those of *K. earlinae*. When specimens were observed swimming, the rate of spiralling was clearly faster in *K. cochlearis* than in *K. earlinae*. The two forms also showed differences in vertical distribution during the calm period in July 1975. *Keratella cochlearis* concentrated in surface waters while *K. earlinae* preferred deeper water. Although criteria such as these may not warrant separating two forms into species, the forms seemed distinctive enough to warrant separate consideration of their populations.



Keratella cochlearis



Keratella earlinae

Figure 54. Dorsal views of *Keratella cochlearis* and *K. earlinae* to show sculpturing. (After Ahlstrom, 1943.)

Keratella cochlearis (Gosse)

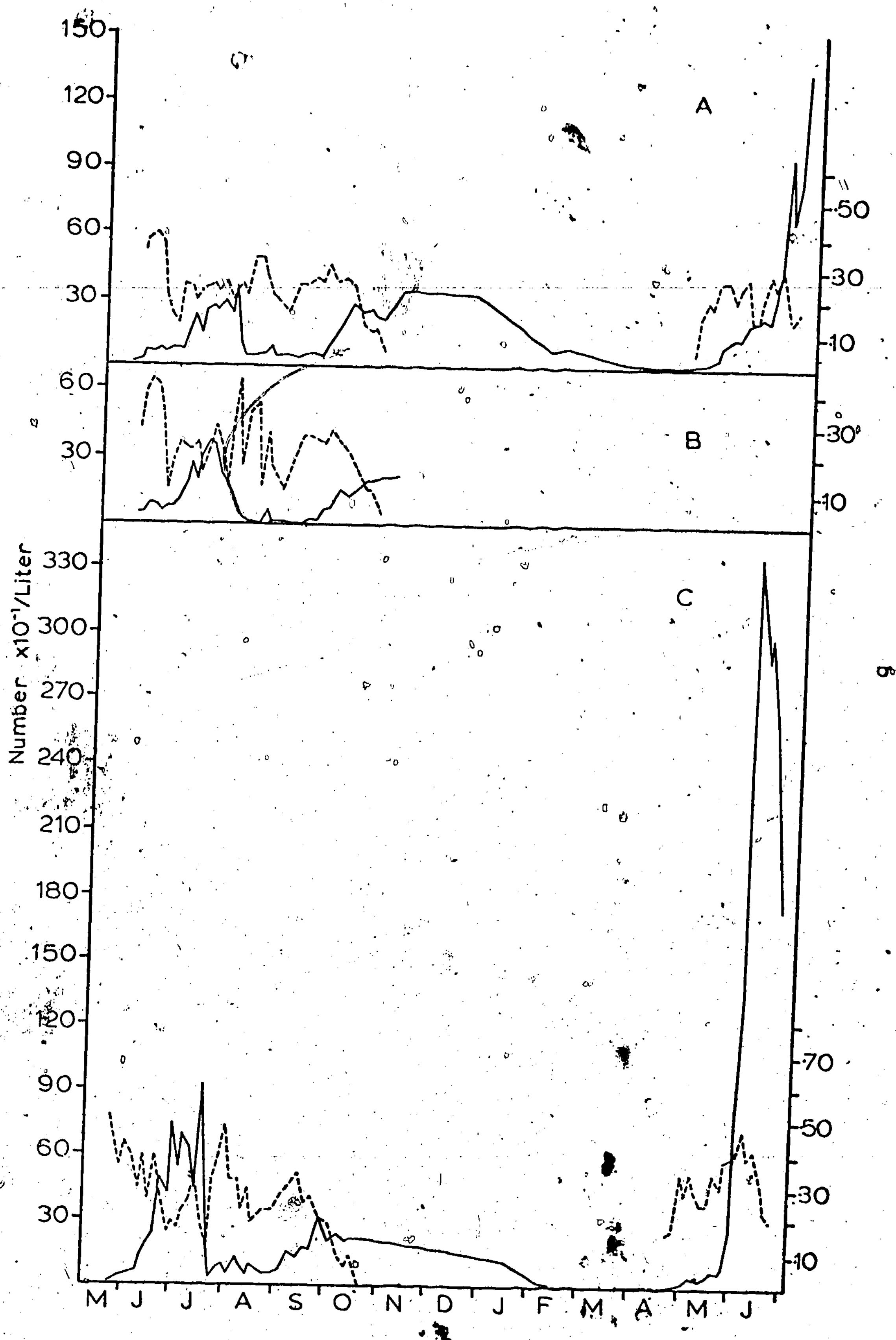
Keratella cochlearis has a relatively large malleate mastax. Naumann (1923 in Pejler, 1957a) noted that it shows little preference in selecting food particles. His experiments showed that specimens would fill their guts with carmine particles. Luntz (1926 in Pejler, 1957a) maintained a population of K. cochlearis on the flagellate Polytoma, and de Beauchamp (1938 in Pejler, 1957a) showed that K. cochlearis could eat Chlorella, but his populations died after one generation. Pejler (1957a) noted that K. cochlearis eats particles below 10-12 µ in diameter.

Like K. quadrata, K. cochlearis was most common during early summer and fall (Fig. 55). Populations at stations A and B were very low in late May 1975 and remained low with minor increases until late June when they increased rapidly. Birth rates were high in early June, but dropped rapidly in mid-June. A few days before the rapid increase in density the birth rates rose again. After increasing, the population appeared to level off and remained high for most of July with stable birth rates for most of this period. In late July, at both stations, a major decrease in density occurred, leaving very low numbers in early August. Numbers remained low until mid-August when a minor pulse was seen at both stations. Birth rates increased as the population dropped, and remained high during early August. A drop in birth rate occurred during the short pulse in density. Population density dropped again after the August pulse and remained low until mid-September and appeared to stabilize during October. Birth rates climbed during late August and remained

Figure 55. Population density and birth rate of Keratella cochlearis at stations A, B, and C. 1975-1976.

——density

------birth rate


150
120
90
60
30
A
50
30
10
60
30
B
30
10
Number x10'/Liter
330
300
270
240
210
180
150
120
90
60
30
C
70
50
30
10
M
J
J
A
S
O
N
D
J
F
M
A
M
J

high until early October when an obvious decline was observed. The egg ratio was high during October, but cold water temperatures caused low birth rates.

Winter was a period of slow decline in numbers. Numbers remained high during December but declined during January, February, and March to low densities in early April. Numbers increased slowly through May and early June, followed by a rapid increase in numbers during the second week in June. Numbers dropped during late June, but rose again immediately afterward and were still increasing in early July. Birth rates rose rapidly in late April and remained high for most of May, then dropped in early June, but rose again immediately before the period of rapid population increase. Birth rates dropped again when the population was increasing rapidly. Rate of population growth appeared much faster in 1976 than in 1975 and maximum population size was higher in 1976 than in 1975.

Seasonal occurrence of K. cochlearis at station C was similar to that in the main basin. The population showed a rapid increase that started in mid-June and rose to a maximum in early July. This increase occurred approximately two weeks earlier than increases at stations A and B. Birth rates dropped while the population was increasing, but the rate of decline was not as rapid as the decrease in birth rate seen in the main basin. Both numbers and birth rates levelled off for most of July although a drop in numbers during mid-July was accompanied by a pulse in birth rate and a subsequent pulse in density. The population dropped rapidly in late July and remained low, with minor peaks during August. Birth rates rose immediately after the decline in density and were very high in early August, but dropped again during the next two weeks. Population density increased slowly during September and reached a maximum in late September. Numbers dropped slightly immediately after the maximum but appeared stable for the rest of October. Birth rates rose in mid-August when numbers were low. They continued to rise with the population in the first two weeks of September, but dropped during late September and was very low in late O tober. The winter population at station C was similar to that at station A. Numbers dropped rapidly in January and February and remained very low during March and April. Population density increased slowly during May while birth rates were high. A very rapid increase in density was noted during early June, reaching a maximum on June 18. Numbers decreased immediately after the maximum and were still decreasing in early July. Birth rates remained high, even increasing slightly during the phase of rapid growth in early June, and did not drop until the population maximum was reached. The 1976 spring population increase at station C occurred earlier than the 1975 increase and earlier than the 1976 spring increase at station A.

Vertical distribution of K. cochlearis is shown in Figure 56. During spring and early summer, distribution was uniform, but in early July a preference for the surface was observed before the oxygen saturation declined in the deep water. As the calm period in July continued and oxygen was depleted near the bottom, the population moved away from the bottom layers. In December, concentrations were found near the surface and near the bottom. As the oxygen was depleted in

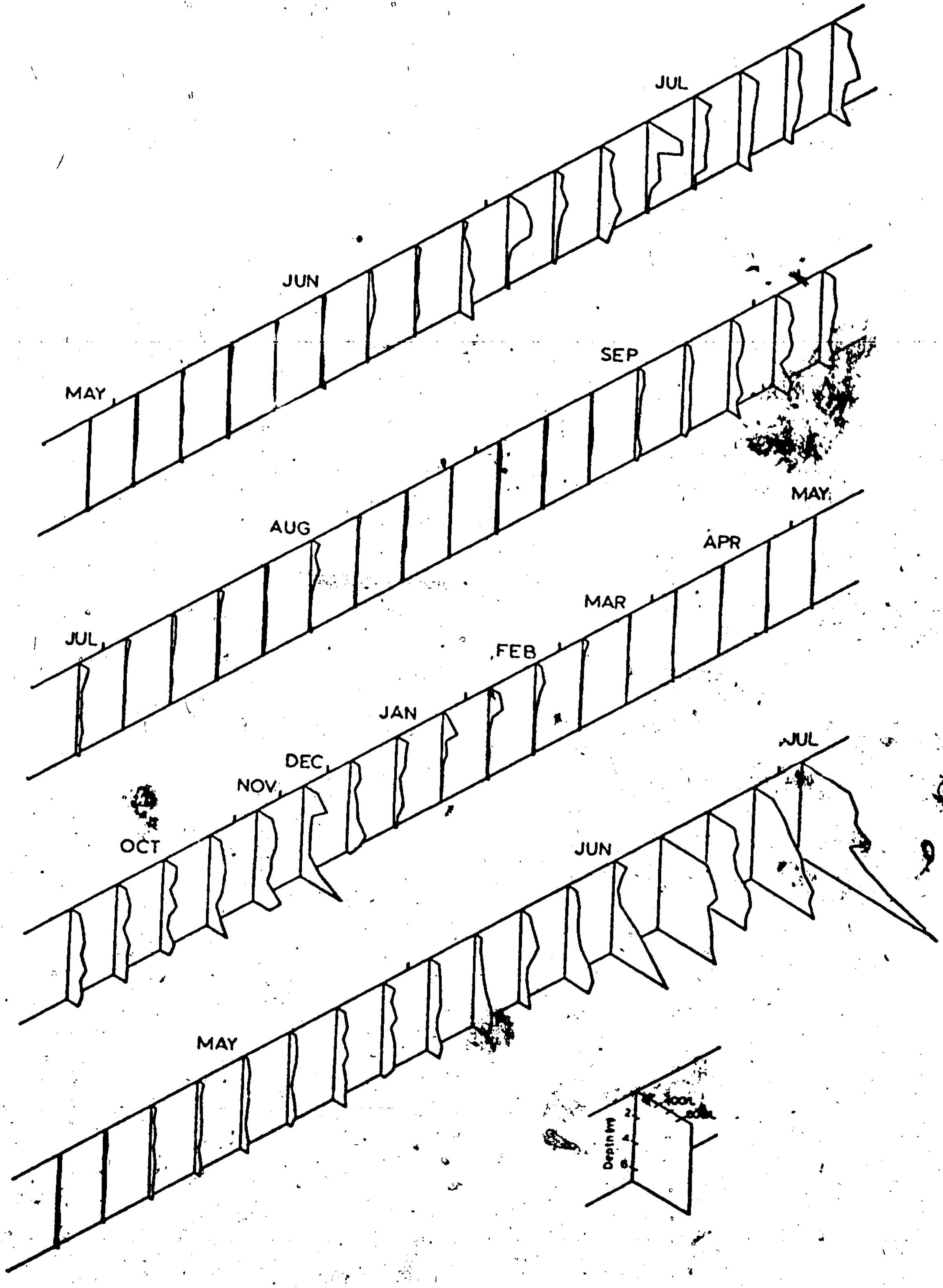


Figure 56. Vertical distribution of Keratella cochlearis at station A. May 30, 1975-July 2, 1976.

lower depths the population concentrated in the top metre. The spring 1976 population showed a uniform distribution pattern but during late June and early July the majority of the animals concentrated near the bottom, quite unlike the pattern seen in early July 1975.

Keratella cochlearis was found in a wide range of temperatures from 0°C to 24.5°C. It was noted, however, that major increases in density did not occur below 12°C and that birth rates were low below 10°C, an obvious result of long egg duration at temperatures below 10°C. Numerous references exist in the literature concerning the relationship between *K. cochlearis* and temperature. Many authors report that maximum population densities occur in spring or early summer and fall (Allen, 1920; Beach, 1960; Campbell, 1941; Chandler, 1940). Ahlstrom (1943) found maxima in summer in the hypolimnion of Lake Michigan. Campbell (1941) and Chandler (1940) both noted that spring maxima occurred in cooler water than fall maxima. Davis (1954) found population maxima over 13°C and noted that *K. cochlearis* was rare under 5°C. George and Fernando (1969) found *K. cochlearis* to be a "cold stenotherm" in Sunfish Lake, Ontario with maxima in January, but in nearby Paradise Lake they found maxima in June with small populations during winter. Edmondson (1965) showed a strong relationship between birth rate and temperature. The upper temperature limit of *K. cochlearis* appears unknown. Edmondson's data show high birth rates at 20°C and Arora (1966) found specimens at temperatures over 21°C. Horkan (1971) found *K. cochlearis* eggs at temperatures as high as 26.6°C.

Major increases in population density of *K. cochlearis* occurred while the edible cells were in relatively high concentrations. However, concentration of edible cells often dropped as numbers of *K. cochlearis* rose and maximum densities of *K. cochlearis* were often found with relatively low cell populations. The early summer population of *K. cochlearis* was stable during the dominance of the Cyanophyta. At station A, changes in the birth rate of *K. cochlearis* closely followed changes in the concentration of edible cells during spring and fall of 1975. However, high birth rates were noted in summer when the concentration of edible cells was low.

It is difficult to interpret literature concerning food resources and *K. cochlearis* as many early researchers collected phytoplankton samples with a net, thereby losing the small cells now realized to be important to rotifers.. Allen (1920) found *K. cochlearis* was more plentiful in areas of high concentrations of organic matter. Both Chandler (1940) and Davis (1954) found *K. cochlearis* in association with spring diatom blooms and Chandler found numerous *K. cochlearis* during fall when blue-green algae were common. Davis found fall populations associated with green algae, but did not collect the small cells. Edmondson (1965) associated certain phytoplankton species with high birth rates. He found *Chrysochromulina*, *Stichococcus* and miscellaneous flagellates to be significantly correlated with birth rate. He reported that *Rhodomonas* was of minor importance while *Cryptomonas*, *Chlamydomonas*, and colourless flagellates did not signifigantly affect the birth rate. In another work (Edmondson, 1960) he found an increase in birth rates after fertilizing the lake. Increased birth rates were correlated with a large concentration of *Ankistrodesmus*.

Figure 57 shows the relationship between birth rate and temperature. As with the similar graphs for Pompholyx sulcata and Keratella quadrata, the border probably represents the maximum birth rate possible under the temperatures indicated. It is important to note that the border extends farther to the upper right side of the graph than it does on the graph of K. quadrata. The second highest birth rate occurred at a temperature of 22°C. It seems, therefore, that the effect of temperature on the birth rate is linear within the range found in Hastings Lake and that the birth rate was not adversely affected by high temperatures. The correlation coefficient of temperature and birth rate was 0.73 ($P < .01$).

Figure 58 shows the relationship between birth rate, temperature and phytoplankton. The correlation between birth rate and the concentration of phytoplankton cells measured during the ice-free periods was 0.42 ($P < .05$). As expected, the border consists largely of points of high edible cell concentrations and the right side of the graph consists of points of low edible cell concentrations. Several exceptions to this generalization are apparent, however. For example it is noted that a dark square, indicating edible cell concentrations of 5000/ml to 10,000/ml, is positioned well below the border, as are two open squares representing phytoplankton concentrations of 1000/ml to 2500/ml. Thus, as with K. quadrata, a high concentration of cells is not always associated with a relatively high birth rate.

Since K. cochlearis was present during the entire sampling period, it withstood a wide range of oxygen concentrations. During the calm period in July 1975, animals avoided the depths that were less than 10% saturated. During early winter, many animals were found near

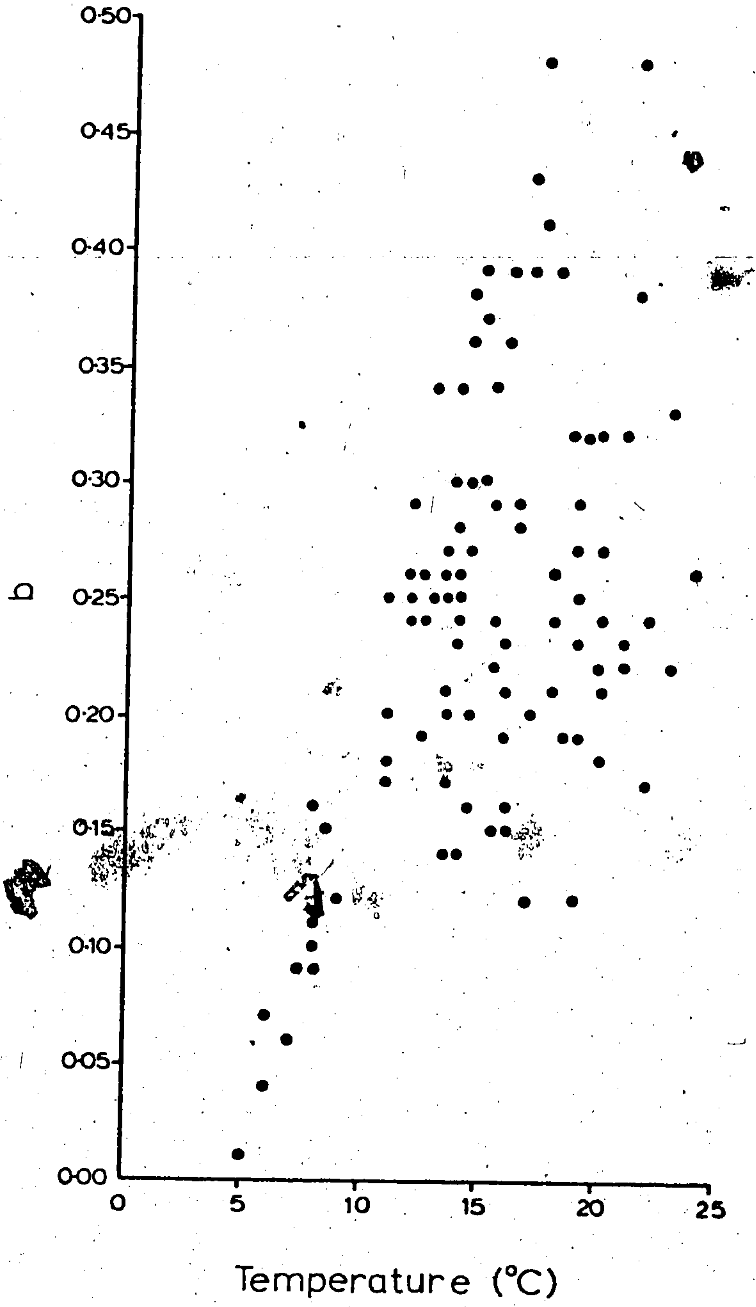


Figure 57. Relationship between temperature and birth rate of <u>Keratella</u> <u>cochlearis</u>.

Figure 58. Relationship between temperature, total edible cells, and the birth rate of Keratella cochlearis.

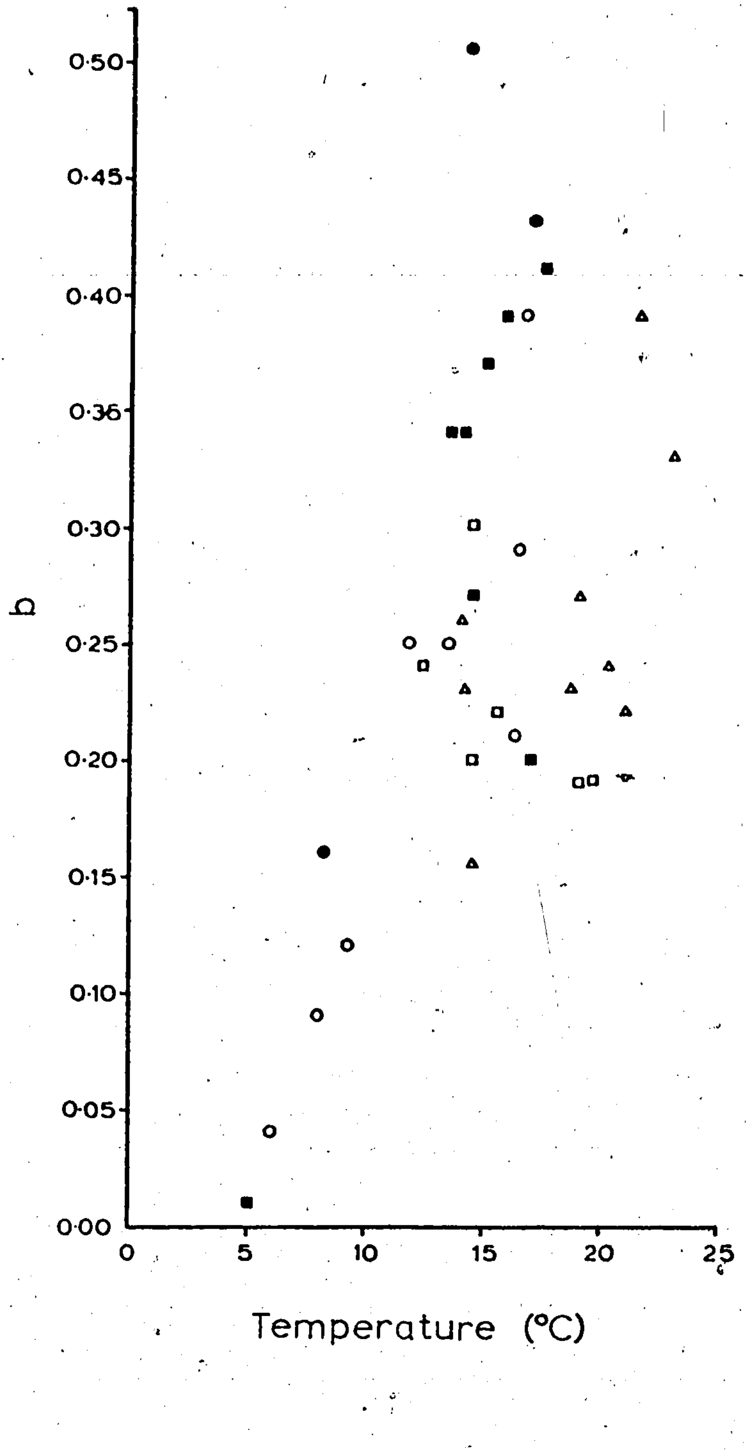
● > 10,000 cells/ml

■ 5,000-10,000 cells/ml

○ 2,500-5,000 cells/ml

□ 1,000-2,500 cells/ml

△ <1,000 cells/ml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15
20
25
Temperature (°C)

the bottom although the water was less than 20% saturated. As in July, however, the population avoided areas less than 10% saturated. Oxygen saturations at station C were below 10% for most of February and March 1976, and although *K. cochlearis* was present at this time, the population was much smaller than the main basin population where oxygen depletion was less severe.

Keratella cochlearis was dominant in early summer and fall along with *K. quadrata* and *K. earlinae*. It was noted, however, that *K. quadrata* sometimes peaked earlier than *K. cochlearis*. It was also noted that when *K. earlinae* was dominant in early summer 1975, *K. cochlearis* was relatively rare, while in summer 1976 when *K. cochlearis* was very abundant, *K. earlinae* was rare. *Daphnia pulicaria* populations were often dense when *K. cochlearis* was abundant but most of the other crustacean species were rare at these times. Elgmork (1964) found maximum *K. cochlearis* populations when cladoceran populations were low and suggested a competitive relationship between the two.

The major increase in density at station A during late June 1975 occurred while the density of predators was increasing. Predator population density was still increasing in July while numbers of *K. cochlearis* were stable, and low densities of *K. cochlearis* in August were correlated with a peak in predator density. The fall increase in *K. cochlearis* occurred as predators declined to low densities in October. *Keratella cochlearis* showed slow population growth, despite high birth rates, in May 1976 when numbers of *Cyclops bicuspidatus thomasi* were high. Rapid growth of the *K. cochlearis* population was seen in June when predators were still numerous but declining. The correlation coefficient between the density of *K.*

cochlearis and the density of predators was 0.24 (N.S.). The correlation coefficients between the density of K. cochlearis and the densities of the two predatory copepods, C. bicuspidatus thomasi and C. vernalis, were 0.27 (N.S.) and -0.06 (N.S.), respectively (Table 5).

Lorica and spine lengths of K. cochlearis are shown in Figure 59. During June 1975, when water temperatures were rising and numbers increasing slowly, average lorica lengths remained constant. Spine lengths, however, showed major increases in June. During late June and July, both spine and lorica lengths decreased. These decreases occurred during the warm spell in July when numbers were relatively high and stable. Both lengths remained small during August and September with some minor increases. During late September and early October, both lengths increased while the temperature dropped and the population increased slowly. A slight decline in lorica and spine lengths occurred at station C in late October. During early winter, spine lengths decreased again while lorica lengths increased. Starting in January, spine lengths increased again while lorica lengths remained stable. During early spring 1976, spine lengths increased at both stations but the increase at station C was much less than the increase at station A. Spine lengths declined during May and June while water temperatures increased. The populations showed rapid growth at both stations with station C reaching maximum numbers in mid-June. The correlation coefficient between temperature and lorica length was -0.14 (N.S.) and the coefficient between temperature and spine length was 0.49 ($P < .01$).

Figure 60 shows the relationship between the log of spine length and the log of lorica length. The correlation coefficient between

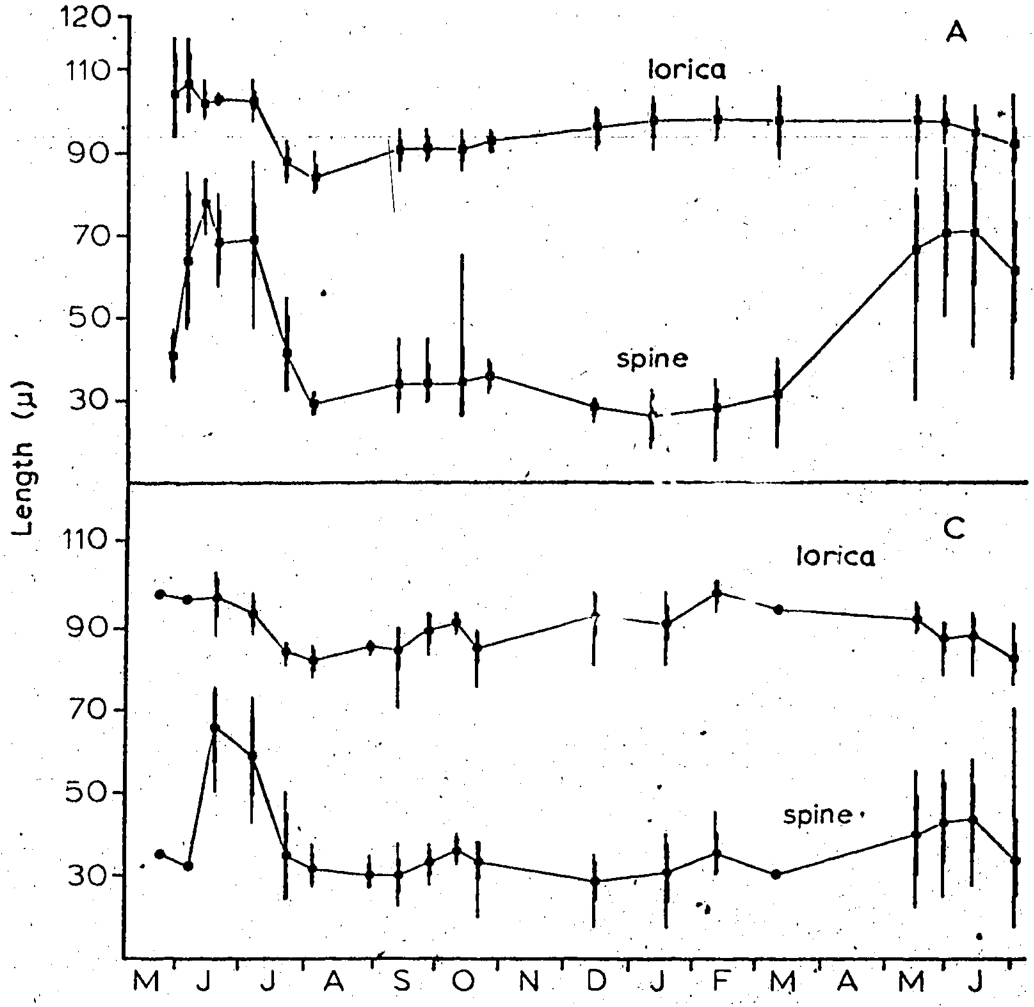


Figure 59. Average lorica and spine lengths of Keratella cochlearis at stations A and C. 1975-1976. Thick bars indicate one standard deviation, thin bars indicate the range.

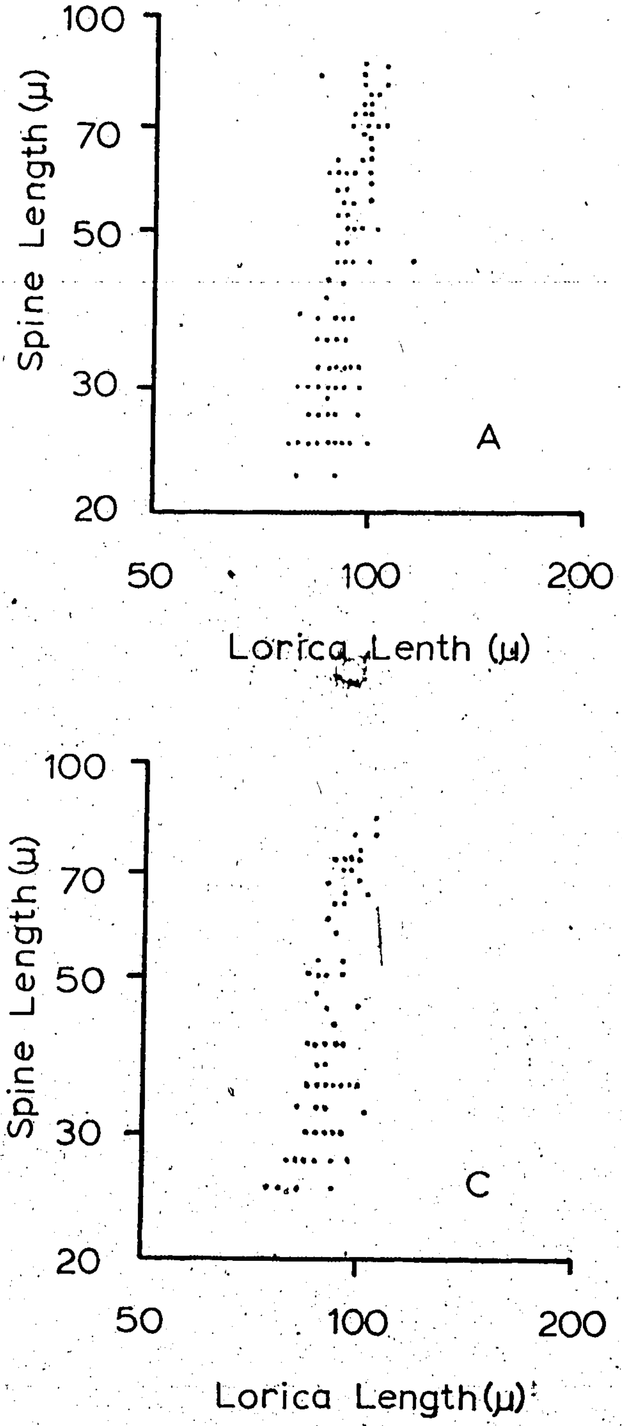


Figure 60. Relationship between lorica length and spine length of *Keratella cochlearis* at stations A and C,

spine length and lorica length was 0.42 ($P < .01$) at station A and 0.46 ($P < .01$) at station C. As with the similar graph for K. quadrata, Figure 60 shows a general increase in spine length with lorica length, but there is a wide range of spine lengths for any particular lorica length. A sign test showed no significant difference between average spine lengths at stations A and C, but did show that average lorica lengths at station A were larger ($P < .05$) than those at station C.

Average spine lengths of K. cochlearis increased (Fig. 54) and and average lorica lengths decreased during June 1975 as the predator population grew. However, peak spine length was reached in early July while predators were still increasing and short spine and lorica lengths were associated with high predator density in August. Small increases in both spine and lorica lengths were found in fall when the predator population declined. Spine lengths dropped in winter when predators were rare, but increased in spring when predators were abundant. Lorica lengths increased slightly during winter and remained high through spring when predators were numerous. The correlation coefficient between spine length and predator density was 0.46 (N.S.) and the coefficient between lorica length and predator density was -0.47 (N.S.). Despite insignificant correlations with density of total predators, spine lengths did increase ($P < .01$) with an increase in density of Cyclops bicuspidatus thomasi, and lorica lengths decreased ($P < .01$) with an increase in density of Cyclops vernalis (Table 5).

Keratella earlinae Ahlstrom

The structure of K. earlinae is similar to K. cochlearis. Little ecological data on this species exist in the literature, but its feeding habits are probably similar to those of K. cochlearis.

Like K. cochlearis, K. earlinae was most common in early summer and fall. The three populations at stations A, B, and C will be treated separately since the population graphs (Fig. 61) show some interesting differences. A rapid growth in numbers was seen at station A in late May 1975. Numbers rose to a peak in mid-June, dropped during late June, but rose again in July to a maximum on July 11. Birth rates rose in early June, but dropped as numbers increased. Decline in numbers during mid-June was associated with a distinct peak in birth rate which dropped again in early July as the numbers rose. Population density declined drastically in mid-July, but rose again in late July and stabilized somewhat until early August when it dropped again. Birth rates were low when the population declined in mid-July, but rose slowly through July and were quite high when numbers decreased in August. A small peak in numbers was seen in mid-August, but the density decreased again during late August. The fall increase started in early September and continued to a maximum in early October after which the numbers stabilized. The birth rate dropped during the mid-August peak, but started to increase in late August. Birth rates climbed with density in early September, but dropped quickly after the maximum density was reached in early October. Population density remained high during December and January. The population increase in January is somewhat surprising considering the very low birth rate. A steady decline in numbers

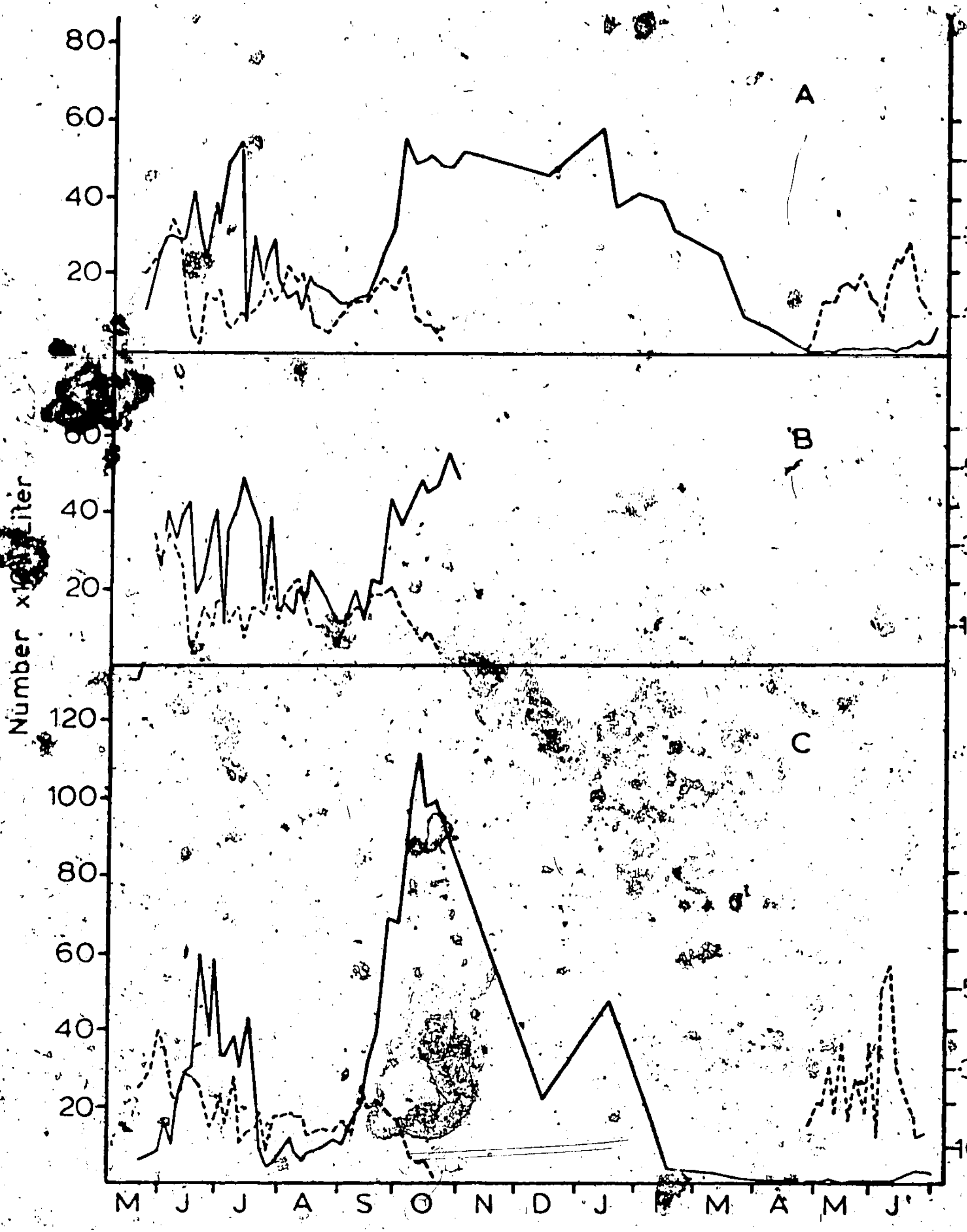


Figure 61. Population density and birth rate of _Keratella earlinae_ at stations A, B, and C. 1975-1976.

—— density

----- birth rate

began in late January and continued until late April. During May and June 1976, numbers remained low. A small increase was seen in late June and early July. Birth rates were high during most of May, but declined in early June. They rose again and were high in mid-June but declined in late June while the population increased slightly.

Rapid population growth was not seen at station B in early spring 1975, but sampling did not start at this station until a few days after the initial sampling at station A. Until early July, population growth and birth rates at station B were similar to growth and birth rates at station A. The station B population declined quickly during early July while numbers at station A were still increasing. Birth rates at station B were high compared with birth rates at station A at this time. The population increased again during the second week of July to maximum on July 14. Numbers dropped after the maximum to a low on July 25. Birth rates declined as the maximum was reached, but increased again when the numbers dropped. After July, population growth and birth rates at stations A and B were similar.

The spring 1975 increase in numbers at station C appeared later than the increase at station A. Numbers increased rapidly during June, reaching a maximum on June [illegible]. Numbers remained high during late June and early July. Birth rates were high in early June, but declined as the numbers increased. Population growth slowed around June 20 while birth rates increased slightly. Population density decreased in early July, but then stabilized until July 19 when a second decline was observed. Birth rates rose after the early July decline in numbers, but dropped immediately before the mid-July decline. A slight pulse in birth rate occurred as numbers declined. Both numbers and birth rates rose during late July and early August, but decreased again in mid-August. Fall population growth began slowly in mid-August; rapid growth was seen during late September and early August with numbers reaching a maximum in mid-October. Birth rates were stable during late August and early September although a small increase was noted in mid-September. In late September birth rates declined and were very low [illegible]id-October. During early winter numbers dropped at station C. A surprising increase was seen in January but numbers dropped after this peak and population density was very low during late winter, remaining low during May and early June. Birth rates were relatively high during this time but fluctuated considerably. A very high birth rate in early June preceded a slight increase in numbers in late June. Birth rates dropped as numbers increased. The 1976 spring population at station C was similar to the population at station A but much smaller than the 1975 spring population.

When the lake water was well-mixed K. earlinae showed a uniform depth distribution (Fig. 62). In late June and early July 1975, the population concentrated in deep water which was 4 C° colder than the surface water. On July 7 the majority of the population was near the bottom despite an oxygen saturation of only 11%. On July 11, oxygen concentration was less than 10% near the bottom and the population concentrated in waters directly above the area of oxygen depletion. In mid-September, the population concentrated near the bottom where the water was 40% saturated with oxygen and the temperature was 3 C° less than the surface water. In December, the population concentrated near the bottom where the water was 25%

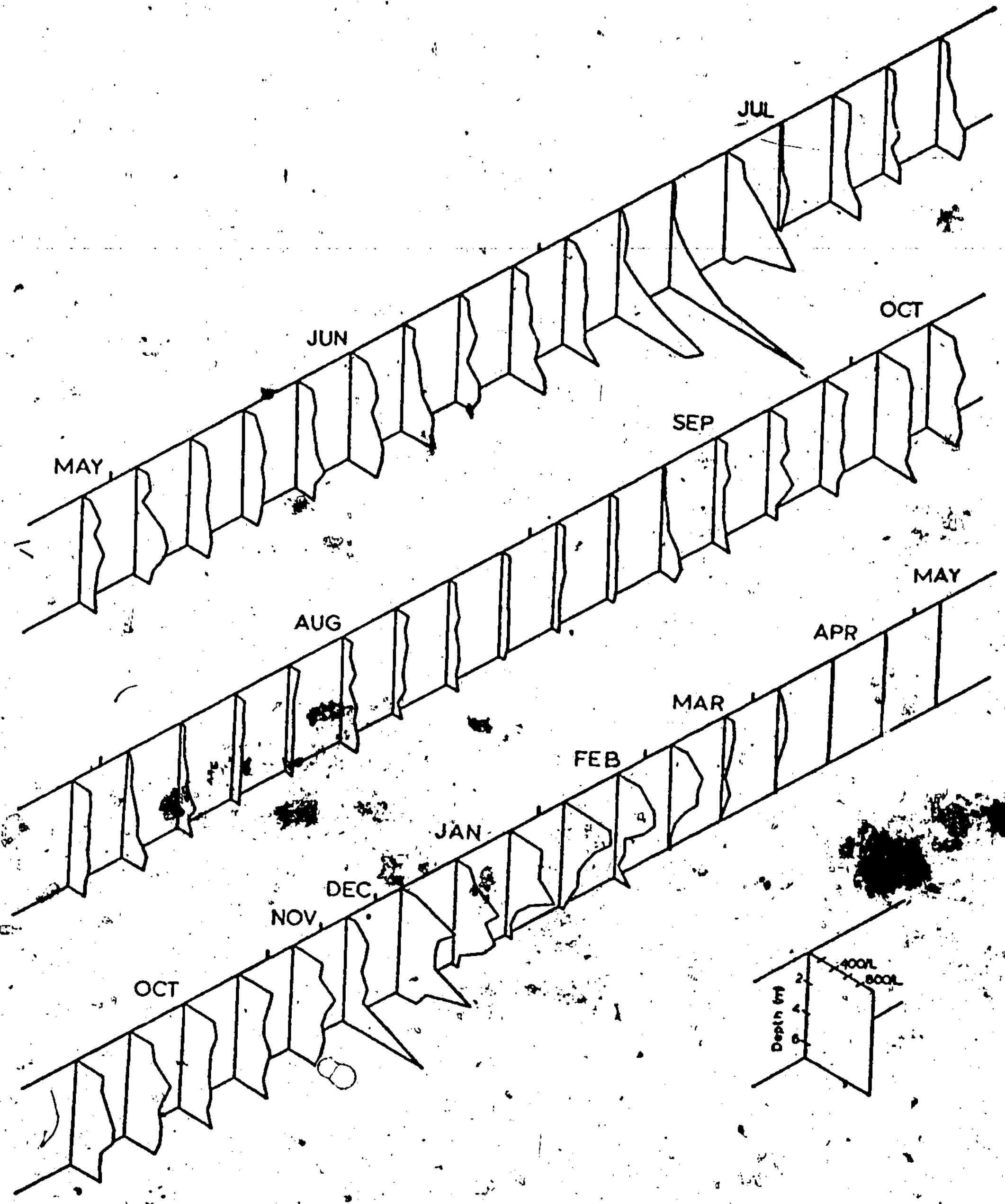


Figure 62. Vertical distribution of Keratella earlinae at station A. May 23, 1975–May 4, 1976.

saturated with oxygen. In January, the bottom three metres were less than 5% saturated and the population concentrated above the limit of 10% oxygen saturation. After ice break-up, the population was small, but appeared uniform in distribution.

Keratella earlinae was present in temperatures form 0°C to 24.5°C. Dense populations were found during the warm, calm period in July and under the ice in December. High birth rates were common in the spring, but pulses were seen in mid-summer. Birth rates were low below 10°C because of long egg duration. The vertical distribution graph (Fig. 62) indicates that *K. earlinae* may avoid warm temperatures when given the oppurtunity. For example, this species avoided the warm surface waters during calm periods. Ahlstrom (1943) notes that *K. earlinae* has been collected in North America from April to September. Horkan (1971) found specimens from 0°C to 26.6°C and noted eggs between 9.8°C and 26.6°C.

Keratella earlinae was present over a wide range of concentrations of edible cells. Population growth was seen in spring and fall 1975 when the concentration of cells was high. High birth rates occurred at times of high cell concentrations during spring and fall. However, high birth rates were also noted in summer when cell concentrations were low. The spring 1976 population showed high birth rates, but poor population growth, despite relatively high concentration of edible cells. It was also noted that the winter population at station C was lower than that at station A despite the higher edible cell concentration at station C.

The graph of birth rate and temperature (Fig. 63) shows a

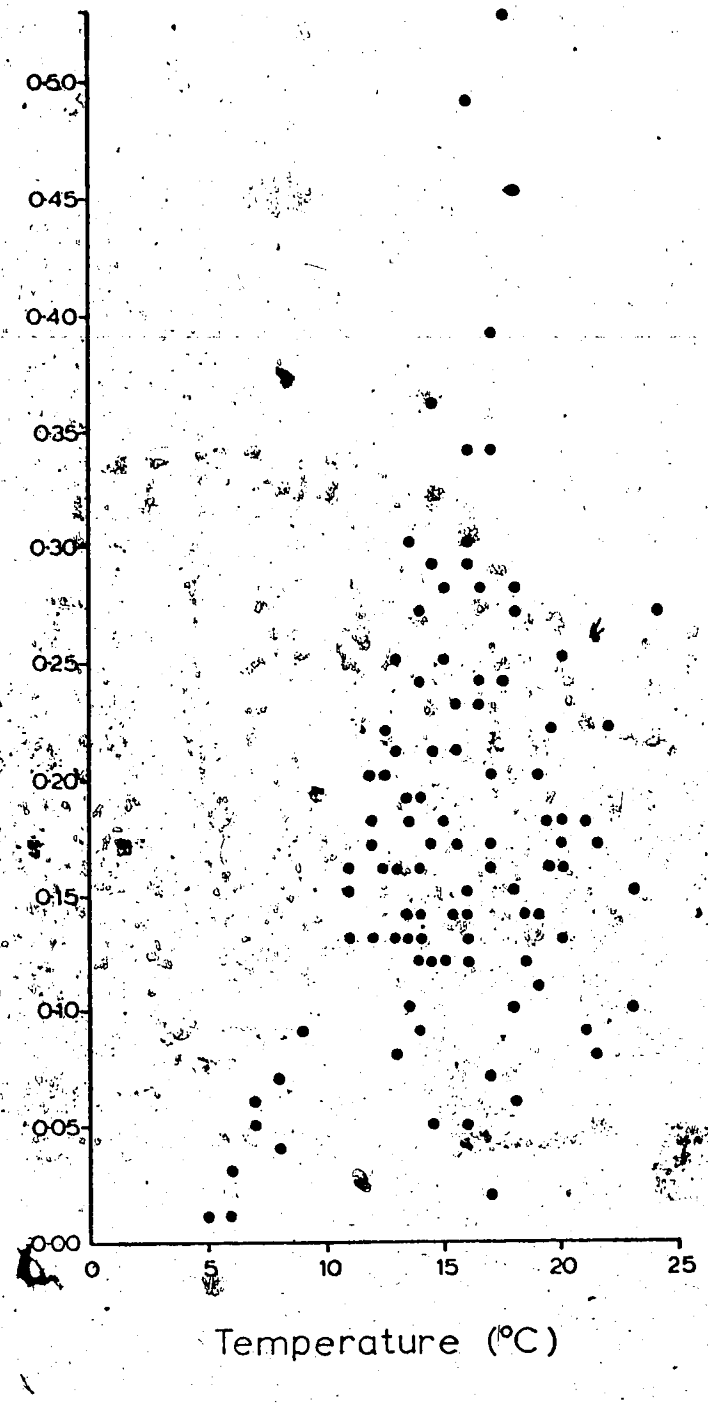


Figure 63. Relationship between temperature and birth rate of *Keratella earlinae*.

situation almost identical to that of K. cochlearis. It is noted, however, that the border appears further left in K. cochlearis than in K. earlinae. This may indicate that K. cochlearis sustains a higher birth rate at any particular temperature than K. earlinae. The correlation coefficient between birth rate and temperature is 0.57 ($P < .01$). The relationship between temperature, edible cell concentration and birth rate is shown in Figure 64. As expected, the border is lined with points of relatively high edible cell concentrations. Low cell concentrations are found near the bottom right hand corner of the graph. The correlation coefficient between the edible cell concentration and birth rate during the ice-free period was 0.46 ($P < .01$). As with the corresponding graph for K. cochlearis, some unexpected results are found. For example, at approximately 17°C a number of points of high edible cell concentrations are well below the border. The graph also shows differences from the graph for K. cochlearis. On the K. earlinae graph the black squares, indicating an edible cell concentration of 5,000-10,000/ml, are concentrated between birth rates of 0.20 to 0.25 eggs/female/day. The same points on the K. cochlearis graph are concentrated between birth rates of 0.35 to 0.40 eggs/female/day, possibly indicating that K. cochlearis can maintain a higher birth rate than K. earlinae at particular edible cell concentrations.

Keratella earlinae was found over a wide range of oxygen concentrations from 5% saturation to supersaturation. The vertical distribution graph shows K. earlinae moved away from areas below 10% oxygen saturation but remained in areas of only 20% saturation. In July 1975, the population concentrated in areas of 20% saturation even

Figure 64. Relationship between temperature, total edible cells, and the birth rate of *Keratella earlinae*.

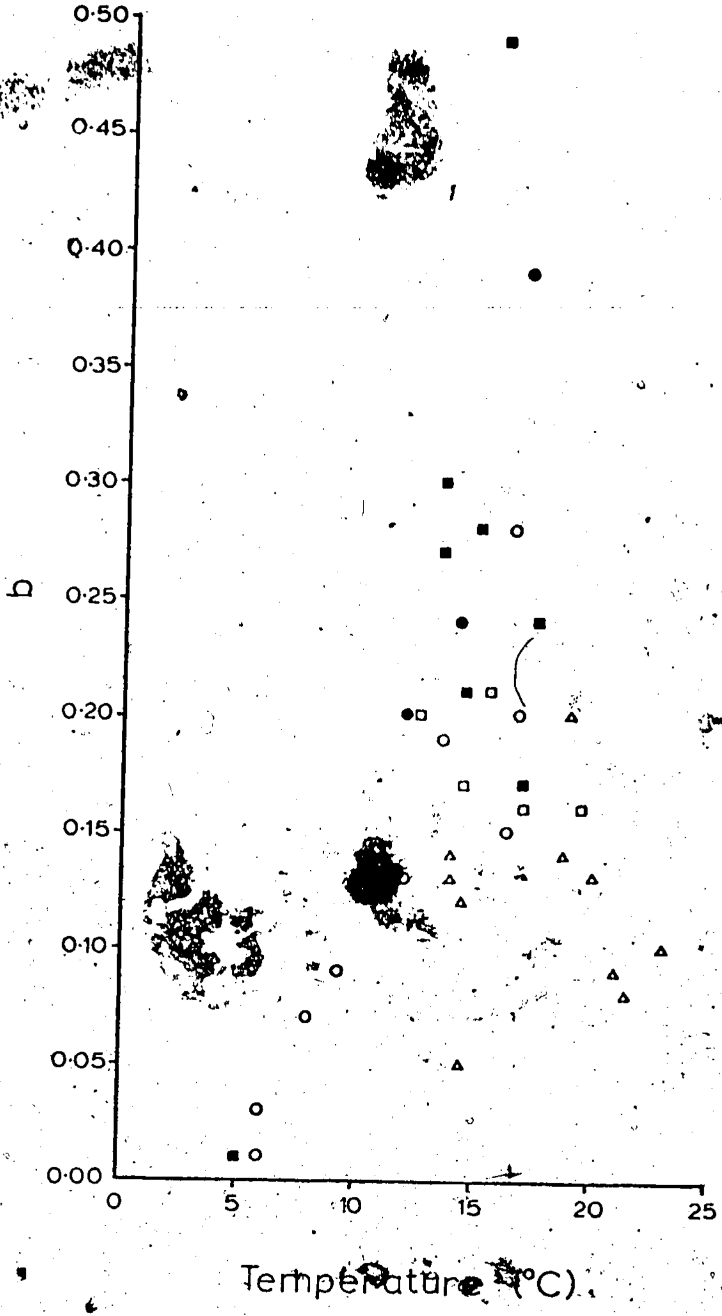
● > 10,000 cells/ml

■ 5,000-10,000 cells/ml

○ 2,500-5,000 cells/ml

□ 1,000-2,500 cells/ml

▲ < 1,000 cells/ml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15
20
25
Temperature (°C)

though much higher oxygen concentrations were available a few metres higher in the water column. *Keratella earlinae* was present at station C during late winter when oxygen saturation was less than 10%. Population density at station C, however, was less than the density at station A where oxygen depletion was less severe.

Keratella earlinae was often present with *K. quadrata* and *K. cochlearis*. However, the maximum density of *K. quadrata* occurred earlier in spring 1975 than the *K. earlinae* maximum and the maximum of *K. cochlearis* occurred after the maximum of *K. earlinae*. *Daphnia pulicaria* populations were high during early summer 1975 when *K. earlinae* was dominant. The low summer populations of *K. earlinae* were associated with many of the other crustacean species. Small populations in early summer 1976 were associated with high densities of *K. cochlearis*.

Like *K. quadrata*, *K. earlinae* showed rapid population growth in late May 1975 when predators were rare. Population growth slowed in June as the predator population increased. The low densities of *K. earlinae* in July and August were associated with peak densities of predators. The fall increase of *K. earlinae* occurred as the predator population dropped. Population density of *K. earlinae* remained very low during May and June 1976 when *Cyclops bicuspidatus thomasi* were numerous. The correlation coefficient between population density of *K. earlinae* and density of predators was -0.65 ($P < .05$). The correlation coefficient between densities of *K. earlinae* and and *C. bicuspidatus* thomasi was -0.68 ($P < .01$) but the same relationship with *C. vernalis* was -0.02 (N.S.).

Average lorica and spine lengths of *K. earlinae* are shown in Figure 65. The cyclomorphic pattern exhibited by *K. earlinae* was almost the same, with respect to timing, as that of *K. cochlearis*. During May and June 1975, spine lengths were increasing while lorica lengths remained fairly constant. Water temperatures were rising at this time and the population was growing. Decreases in both lorica lengths and spine lengths were noted during July. These decreases coincided with the warmest time of year, and with the ma[illegible] population crash seen during July at station A. However, decrease in size came before the major decrease in numbers at station C. During August, when the water was cooling, lorica lengths appeared to be increasing while spine lengths continued to decrease. Both lengths increased during September while the water temperature was dropping and numbers were increasing. During October, spine lengths at both stations decreased while lorica lengths at station A increased and lorica lengths at station C appeared to decrease. During early winter, spine lengths continued to decrease while the lorica lengths were stable. After February, spine lengths increased slowly at both stations while lorica lengths remained stable at station A but increased slightly at station C. In spring 1976, spine lengths increased rapidly at both stations. Spine lengths continued to increase at station A during June while they decreased at station C. Lorica lengths decreased at both stations during May and June. Water temperature was increasing during May and June 1976, but the population was very low with a small numerical increase in late June. The correlation coefficient between temperature and spine length was

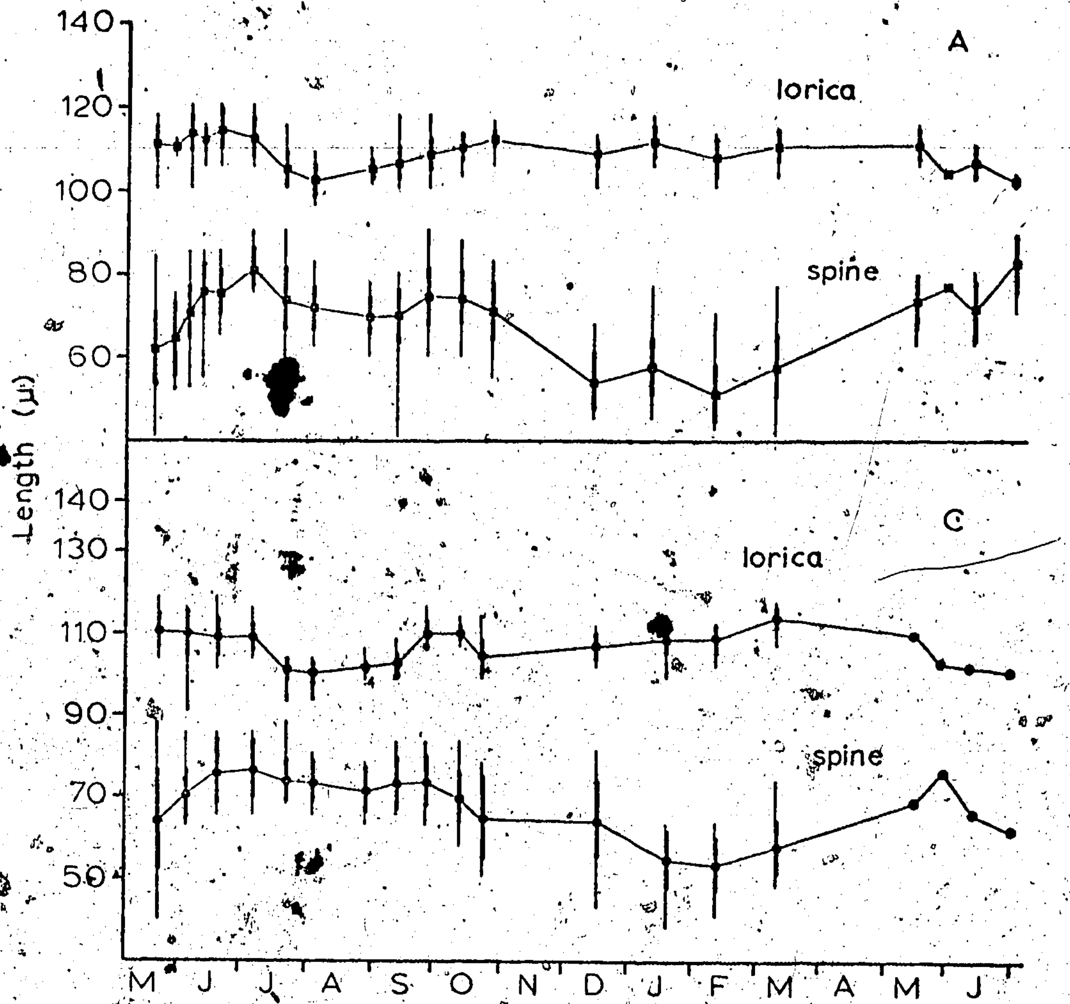


Figure 65. Average lorica and spine lengths of Keratella earlinae at stations A and C. 1975-1976. Thick bars indicate one standard deviation, thin bars indicate the range.

0.77 ($P < .01$) and the coefficient between temperature and lorica length was -0.29 (N.S.).

Figure 66 shows the relationship between spine length and lorica length for *K. earlinae*. The correlation coefficient was not significant at either station (0.002 at station A and -0.04 at station C). A sign test showed no significant difference between average spine lengths at station A and C, but average lorica lengths at station A were larger ($P < .01$) than average lorica lengths at station C.

During early summer 1975, lorica lengths of *K. earlinae* were stable, but average spine lengths increased with increasing numbers of predators (Fig. 54). Both lengths dropped in July when predators were still increasing and were quite short during the peak of the predator population in August. During fall 1975, spine and lorica lengths increased as predators declined. During winter, when predators were rare, spine lengths declined and lorica lengths were stable. As in 1975, spine lengths increased with increasing predator densities during spring 1976; however lorica lengths appeared to decrease. The correlation coefficient between spine length and predator density was 0.63 ($P < .05$) while the coefficient between lorica length and predator density was -0.74 ($P < .01$). Despite significant correlations between spine and lorica lengths and the density of total predators, no significant correlations were found for either length with either of the two separate predator species (Table 5).

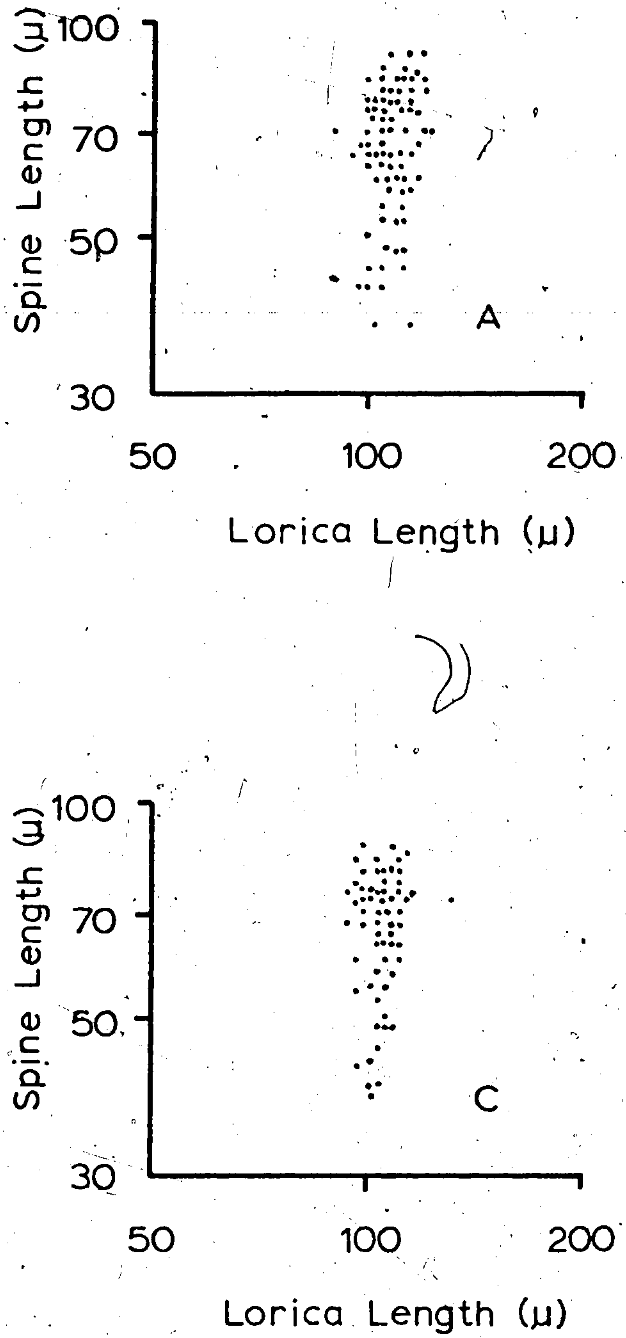


Figure 66. Relationship between lorica length and spine length of Keratella earlinae at stations A and C.

POPULATION DYNAMICS

Two basic theories can be defined concerning population regulation (Krebs, 1972). One school maintains that factors external to populations are responsible for control, ie limiting factors, whether they be density independent or density dependent, are the agents of control. The other school maintains that control is mediated through qualitative changes within a population, ie controlling factors are evolved mechanisms which are separate from the external limiting factors. These two points of view can be applied in connection with studies of planktonic rotifer populations.

EXTERNAL CONTROL

Concerning the first or "external control" theory, factors such as temperature, food, predation, oxygen, and parasitism have been viewed as important in controlling distribution and abundance of rotifers (Edmondson, 1965; Pejler, 1957a,b; Ruttner-Kolisko, 1974).

Temperature

Temperature can directly affect population growth in two ways: by acting as a limiting factor, and by altering the rate of change of density through its effect on birth rate, death rate and length of life. Indirectly, temperature can affect population growth by affecting food availability, competition coefficients, degree of parasitism, predator life history, etc. In considering temperature as a limiting factor, Pejler (1957a) has deemed it possible to roughly classify rotifer species according to their observed temperature ranges. Using data from northern Swedish Lapland he defines *Polyarthra dolichoptera*, *Keratella hiemalis* and *Nothalca squamula* as "exclusively cold water" species, *Keratella cochlearis* as eurythermal, and *Collotheca mutabalis* as a warm water species. Ruttner-Kolisko (1974) also classified many planktonic rotifers according to their temperature limits. Results of my study often concur with such classifications but some exceptions are noted. *Polyarthra dolichoptera* increased in warm water despite its cold water classification and *Testudinella patina* was only found in warm water, despite Ruttner-Kolisko's comment, "maximum at low temperatures if at all". In my study, seasonal distribution of certain species suggests the importance of temperature as a limiting factor. Data on egg duration (Fig. 34) predict no population growth below 9°C for *Brachionus angularis* and below 13°C for *Pompholyx sulcata*. These predictions are born out since neither rotifer population increased below 12°C. Amren's (1964a) egg duration data for *K. quadrata* predicts no population growth below 1.5°C, yet increases were seen during January at 0-1°C. It is possible that the increase was due to a movement of animals into the deeper part of the lake. It is also possible, however, that the lower end of the line showing egg duration for *K. quadrata* in Figure 34 is not linear as shown but approaches the X axis asymptotically. If such a situation exists then the large number of eggs in November and December could have developed and caused the numerical peak in January. Decreases in birth rates of *K. quadrata* at temperatures above 15°C suggest high temperatures are limiting and may explain low numbers of *K. quadrata* in summer.

Edmondson (1965) showed the effect of temperature on the birth rates of Keratella cochlearis, Polyarthra vulgaris, and Kellicottia longispina. He found significant correlations between temperature and birth rate for all three species, with birth rates of K. cochlearis showing the strongest relationship with temperature and Kellicottia longispina the weakest relationship of the three species. Unfortunately, Edmondson could not include data on population size in his study so, although the effect of temperature on birth rate is indicated, effects on population size can only be inferred. In my study, birth rates of K. cochlearis, K. earlinae, K. quadrata, Pompholyx sulcata, and Brachionus angularis were significantly related to temperature. However effects of birth rate on density remain unclear. High birth rates often failed to increase population density and strong population growth occurred despite relatively low birth rates.

A point that should be discussed here is effect of population age structure on birth rate. Pulses in population density of rotifers were often associated with sudden drops in birth rates. Also sudden declines in density were often associated with pulses in birth rates. When a population increases rapidly the age structure tends towards juvenile animals (Krebs, 1972). Thus when a particular rotifer population increases rapidly, the population is flooded with non-ovigerous, juvenile animals and the per capita birth rate will decrease. It is important to note that such a decrease in birth rate will occur despite stable environmental conditions; that is, a sudden drop in birth rate is not necessarily indicative of declining environmental conditions. Pulses of birth rate occurring immediately after a rapid decline in population density may indicate death of a large number of senile, non-ovigerous animals and again, do not necessarily indicate improving environmental conditions. This effect of age structure on birth rate may explain some of the unexpected data points shown in Figures 42, 51, 58, and 64. If a system could be devised whereby non-ovigerous adults could be discerned from juvenile animals, birth rates could be expressed in terms of eggs/adult/day and would alleviate this problem.

Food

Several authors have suggested that food is important in controlling rotifer populations (Edmondson, 1965; Pejler, 1957a; King, 1967). However, analyses of rotifer populations pertaining to food availability are rare due to difficulties in determining food habits. Type and size of the mastax gives general clues as to diet, but some reports indicate that distinct preferences are shown by some rotifers, preferences that cannot be predicted from the feeding apparatus. For example, Dieffenbach and Sachse (1911 in Pejler, 1957a) showed that Polyarthra euryptera will eat Cryptomonas ovata but refuses other cells of the same size. Edmondson (1965) showed that for three species of rotifers, certain phytoplankton species were more important than others in affecting birth rates. Of the phytoplankton species studied, Chrysochromulina was the most important in affecting birth rates of Keratella cochlearis and Kellicottia longispina. He notes a "striking relationship between the rate of reproduction in Polyarthra and the abundance of Cryptomonas". Edmondson's observations on the importance of food in controlling birth rates were supported in my study. Significant correlations between birth rates and concentration of total edible cells were found for Keratella quadrata, K. cochlearis, and K. earlinae. It must be remembered that phytoplankton counts are at best a rough estimate of food availability. Desirability of cells to zooplankton changes according to the growth phase of cell populations (Rigler, 1971), and production of cells cannot be determined from counts. These problems may be compounded by seasonally changing nutritional requirements of rotifers. A certain concentration of phytoplankton may be sufficient to sustain rotifer populations at 5°C but identical concentrations may be insufficient at 20°C.

By studying a laboratory population of Euchlanis dilatata, King (1967) showed that rate of population growth was "related to both food species and food concentration" but "ultimate density of the population depends only on food concentration". He showed that a diet of Chlamydomonas reinhardti maintained the highest rate of population growth, Euglena gracilis an intermediate rate of growth, and Euglena geniculata the lowest rate of growth. His results on birth rate agree with Edmondson's beliefs that different food species determine different birth rates. He found that Chlamydomonas reinhardti maintained the highest birth rates and Euglena geniculata the lowest birth rates, thus, control of density during the growth phase was mediated through birth rate. King (1967) also noted that rate of population growth was directly related to food concentration up to a certain level, above which the population did not increase any faster with further increases in food level. Thus, birth rate increases with food concentration until some other factor becomes limiting.

Parasitism

Ruttner-Kolisko (1974) notes that planktonic rotifers are "not infrequently" infested with parasites and that parasites may reduce "even dense populations near to extinction". Edmondson (1965) found that parasitic infestations did not affect birth rates of *Keratella cochlearis*, but did appear to lower birth rates of *Kellicottia longispina*. He noted that the importance of parasitism in *K. cochlearis* may have been underestimated owing to long periods between sampling dates. Unidentified parasites were seen in specimens collected from Hastings Lake, but owing to the manner of counting, it was impossible to quantify the degree of infestation. The *Keratella* species and *Brachionus angularis* were the species most often infected. Specimens of *K. quadrata* appeared to be particularly troubled by parasites. One live specimen of *K. quadrata* was so filled with a black, apparently fungal material that the mastax was pushed to one side of the body.

Predation

Few reports exist on the importance of predation on planktonic rotifer populations. Edmondson (1965) found no significant correlation between presence of the predatory rotifer *Asplanchna* and birth rates of *K. cochlearis*. This is to be expected unless *Asplanchna* preferentially takes either ovigerous or non-ovigerous females. He also notes that the presence of *Trichocerca capucina*, which is known to attack eggs of other planktonic rotifers, made no apparent change in birth rates.

McQueen (1969), in a study on feeding rates of *Cyclops bicuspidatus thomasi* from Marion Lake, B.C., showed that the IV, V, and VI copepodite instars readily ate *Keratella cochlearis* when the rotifers were the sole prey offered. Rate of feeding increased with prey concentrations, and at a prey concentration of 700 per liter, each copepod ate approximately five rotifers per day. However, when rotifers were present along with other prey such as *Diaptomus oregonensis*, *D. hesperus*, and *Cyclops* nauplii, the rotifers were virtually untouched, suggesting that although rotifers can be taken, they are not preferred prey. It is difficult to fully interpret McQueen's results since no data were given concerning ratios of prey species used in mixed prey experiments, although he mentions ratios were similar to those found in the lake. Marion Lake is a small "very oligotrophic" lake (Dickman and Efford, 1972). During periods of high rainfall the lake flushes in less than 2.5 days and thus is better described as a stream than a lake (Dickman, 1969). It appears, therefore, that Marion Lake is not a typical habitat of *K. cochlearis* and it may be assumed that the rotifers are rare relative to other zooplankton. P. Pearlstone (personal communication) also noted low numbers of rotifers in Marion Lake. Thus low feeding rates of *C. bicuspidatus thomasi* on *K. cochlearis* in McQueen's mixed cultures may reflect this assumed paucity of rotifers. If rotifers in Marion Lake were dominant, as they were in Hastings Lake, the feeding rate may have been much higher.

Concerning the predatory behaviour of *Cyclops vernalis*, Fryer (1957) stated that it was "markedly carnivorous", consuming oligochaetes, copepods, chydorids, and rotifers.

Cyclops bicuspidatus thomasi and *C. vernalis* were the only predators studied from Hastings Lake. No predatory rotifers were found although the feeding habits of *Trichocerca multicrinis* may include some predation on rotifer eggs. *Chaoborus* were found in the lake and McGowan (1974) showed that young instars of *Chaoborus anomalus* and *Chaoborus ceratopogones* feed on rotifers in Lake George, Uganda. Unfortunately, effects of *Chaoborus* predation on rotifer populations could not be analyzed in my study as the plankton trap seemed ineffective in catching the agile larvae.

Table 5 shows correlation coefficients between densities of the three *Keratella* species and densities of the cyclopoid copepods. *Keratella earlinae* was the only species that appeared affected by presence of cyclopoids. The most obvious relationship is with *Cyclops bicuspidatus thomasi* where a strong negative correlation is found. The fact that copepodites I to III did not significantly affect density of *K. earlinae* supports McQueen's (1969) assumption that the older copepodite instars are the predators.

Despite insignificant correlations between predator density and density of *K. quadrata* and *K. cochlearis*, predation may still be affecting the populations. For example, in spring 1976 birth rates of both *K. quadrata* and *K. cochlearis* were high, but the population densities remained low, suggesting conditions were adequate for reproduction but some factor was reducing the number of animals.

The predator population, particularly *C. bicuspidatus thomasi*, was very dense at this time and could have maintained the rotifer populations at low densities without affecting the birth rates.

Oxygen

In any discussion of the freshwater habitat, oxygen concentration must be included as an important environmental factor. It is difficult, however, to determine the exact effect of various oxygen concentrations on planktonic rotifers as the concentrations are related to other factors, particularly temperature.

Pejler (1957a) noted that of the several species inhabiting the hypolimnion of deep lakes in northern Swedish Lapland, only two species, *Keratella hiemalis* and *Filinia terminalis*, could withstand low oxygen concentrations. He also noted that *Polyarthra dolichoptera* and *Conochilus natans* were collected from "tarns" with a "deficiency of oxygen" in late winter when the water temperature was low. In my study, inferences on effects of oxygen concentration are obtained mainly from the vertical distribution data. During the calm period in July 1975, all rotifer species avoided areas below 10% saturation; however, several species such as *K. earlinae* and *Pompolyx sulcata* often appeared most numerous in waters only slightly above 10% saturation. It is doubtful that rotifers were selecting areas of low oxygen concentration but rather were moving to these areas to avoid some other factor, perhaps high temperature. Thus their position in the water column can be viewed as a balance between poor oxygen concentrations below and high temperatures above. Concentrations of *K. quadrata* and

K. cochlearis near the surface during July 1975 may indicate a greater tolerance for high temperature, although the relationship between birth rates of K. quadrata and temperature (Fig. 50) may indicate an inhibitive effect above 15°C. The three Keratella species and Polyarthra dolichoptera were the only major species to exist under the ice and P. dolichoptera was the only species to show rapid population growth during periods of low oxygen concentration. The Keratella species generally declined in numbers through the winter as the oxygen concentration dropped; decline in numbers was quicker at station C where oxygen depletion was more severe.

It is clear that external factors such as those discussed above affect rotifer populations. However, the importance, if any, of each factor in controlling populations remains obscure. In discussing control, Edmondson (1965) noted that much of the literature concerning population growth assumes a rather static reproductive schedule and only discusses mortality as a factor in controlling populations. It is obvious that changes in birth rate can also be a mechanism of control. Given a set mortality rate, a population will grow or decline depending on the difference between birth rate and death rate. Edmondson argues, therefore, that factors such as temperature and food availability can control population growth through their effect on birth rate. He suggests that food availability may be a density dependent control, noting that large populations of zooplankton can reduce food levels, thereby lowering the birth rate.

External Control and Seasonal Abundance

In an effort to summarize effects of extrinsic factors, it is helpful to utilize the graphical models concerning aspects of control in seasonal environments proposed by Fretwell (1972). Fretwell describes a simple model in which the carrying capacity of the environment is allowed to rise and fall in a seasonal pattern and rates of population growth and decline are density independent, ie the rate of population change is positive and constant when $N < K$, negative and constant when $N > K$, and zero when $N = K$ (Fig. 67A). Despite density independent growth, perturbations in N will return to equilibrium (Fig. 67B). Fretwell complicates his model by assuming density dependence (Fig. 67C) but notes the similarity to the situation in Figure 67A.

It is apparent from Fretwell's graphs that, although the population is ultimately controlled by the carrying capacity, the density recorded at any particular time may be largely independent of it. In other words, when $K - N$ is large, N is a function of the rate of increase and the duration of that increase. As K is approached (in a density dependent system) or reached (in a density independent system) the value of N depends on the value of K.

Figures 68 and 69 are population graphs of K. cochlearis, K. earlinae, K. quadrata, Pompholyx sulcata and Brachionus angularis plotted with total edible cells, on semi-log paper, to allow comparison of the data with Fretwell's models. The graphs show obvious seasonal trends, ie K. cochlearis, K. earlinae and K. quadrata show rapid growth and large populations in spring and fall and low populations

Figure 67. Theoretical population growth in a seasonal environment. See text for details. (Redrawn from Fretwell, 1972).

– – – – density (N)

·········· perturbed density

———— carrying capacity (K)

A. density independent growth

B. return of perturbation to equilibrium

C. density dependent growth

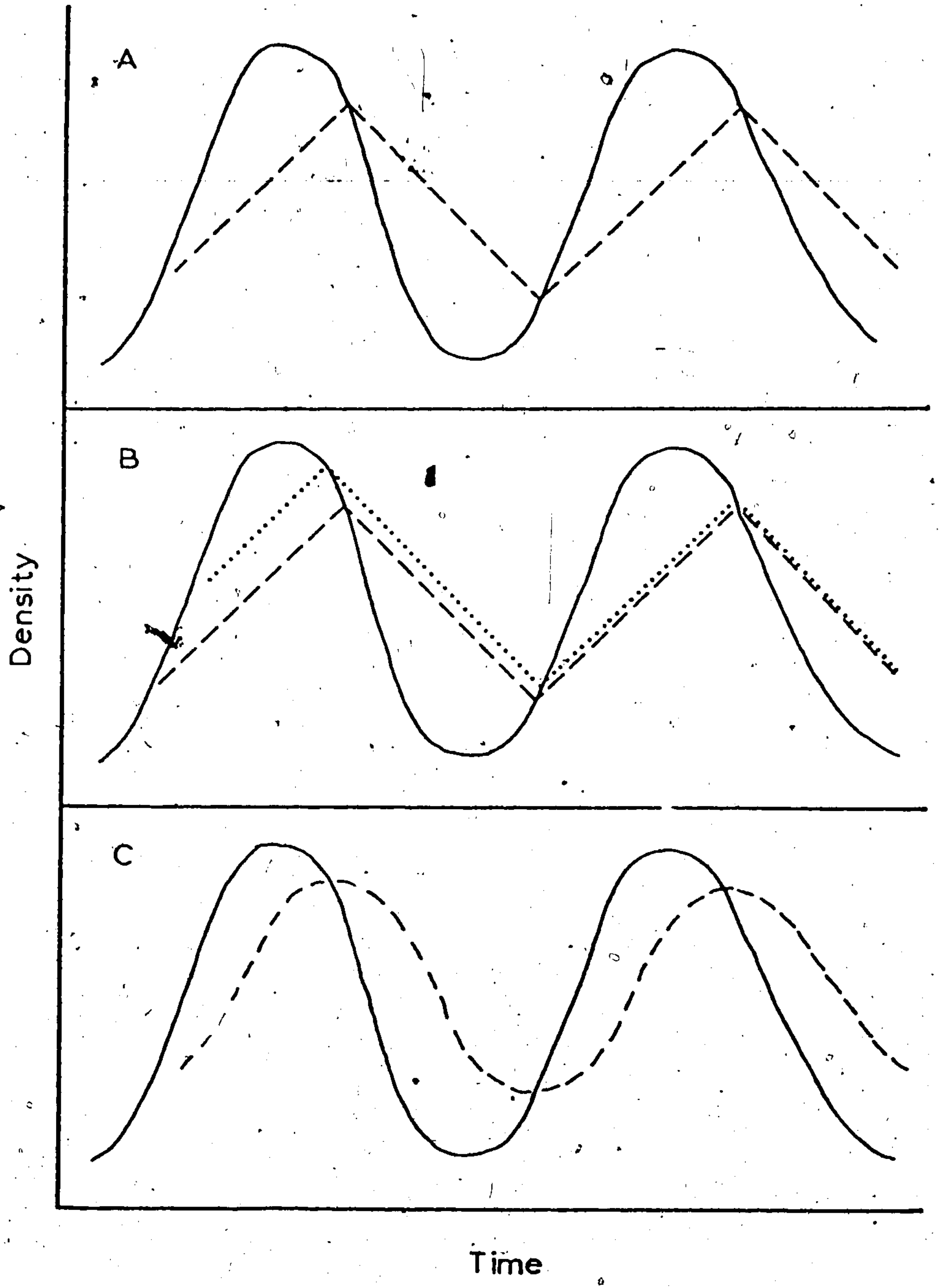
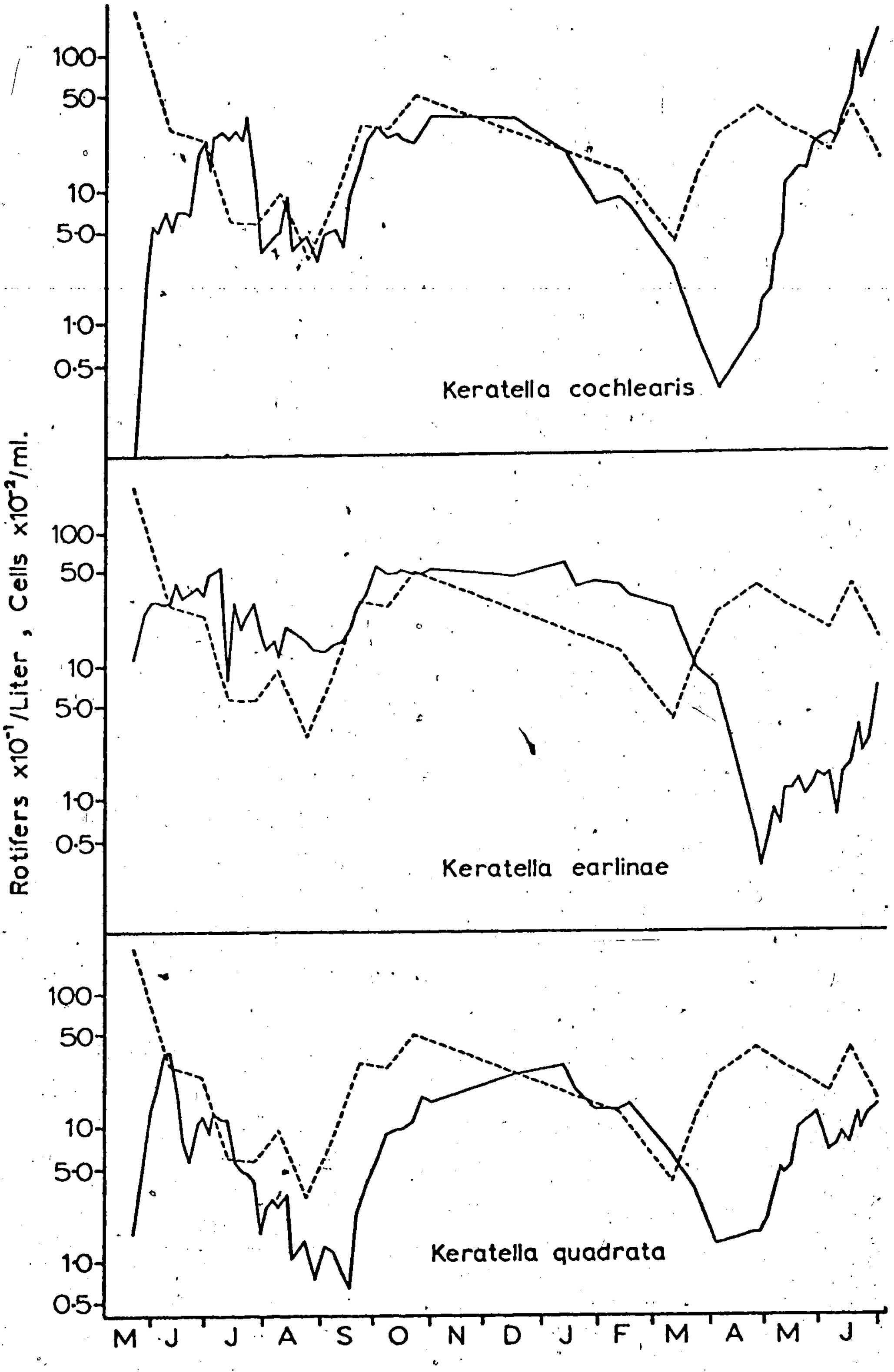

A
B
C
Density
Time

Figure 68. Logarithmic plots of the densities of Keratella quadrata, K. cochlearis, and K. earlinae with logarithmic plots of the total edible cells at station A. 1975-1976.

density of rotifers ————

concentration of cells ------------


Rotifers x10⁻¹/Liter , Cells x10⁻²/ml.
100
50
10
5·0
1·0
0·5
Keratella cochlearis
100
50
10
5·0
1·0
0·5
Keratella earlinae
100
50
10
5·0
1·0
0·5
Keratella quadrata
M
J
J
A
S
O
N
D
J
F
M
A
M
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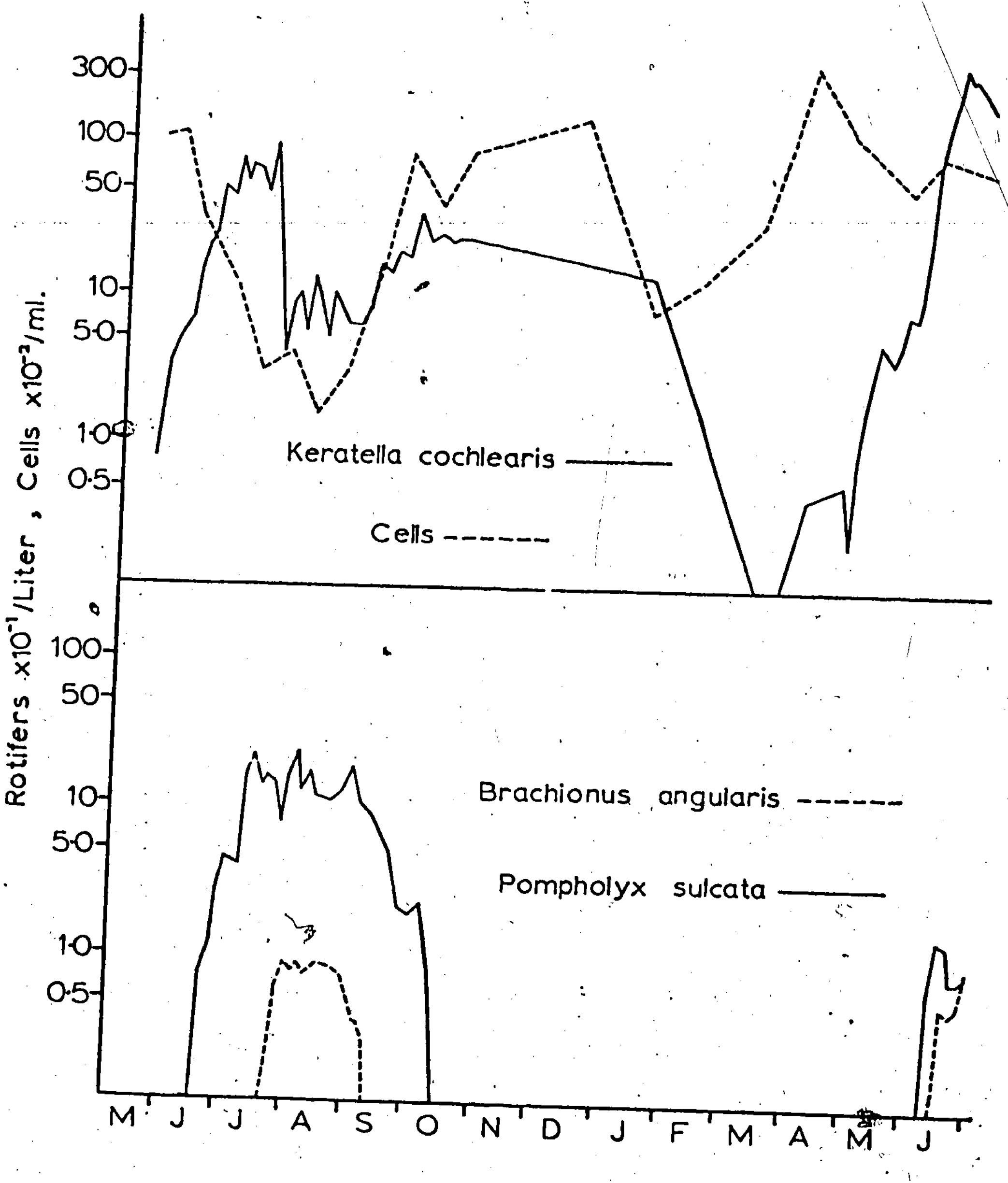

Figure 69. Logarithmic plots of the densities of Keratella cochlearis, with total edible cells, and logarithmic plots of Pompholyx sulcata and Brachionus angularis at station C. 1975-1976.

during summer, *Pompholyx sulcata* and *Brachionus angularis* show the reverse pattern with high population densities in summer. There are also some striking similarities between some populations, particularly *K. quadrata* and *K. cochlearis*, and concentrations of total edible cells.

With Fretwell's concepts in mind, and considering the environmental factors discussed earlier, it is possible to sketch some aspects of population growth of a perennial rotifer species in Hasting Lake. Immediately after break-up in spring, the concentration of edible cells is usually high but rotifer birth rates are low owing to low water temperatures. As water temperatures rise, birth rates increase and the population grows rapidly if there are few predators or parasites. Such a situation was seen in spring 1975. If the predator population is large in the spring, such as in 1976, rotifer birth rates will be high owing to large food supplies and increasing temperatures but population density will be low due to predation. As spring progresses, the concentration of edible cells will decrease owing to changes in nutrient concentrations, light levels, etc, and perhaps zooplankton grazing. When the rotifer population reaches the maximum density that can be maintained by the food levels it will level off or drop. If the population levels off, it may indicate that the carrying capacity is stable. If the population drops quickly after reaching a maximum, it could suggest that the carrying capacity has been reached while it is declining. This could possibly explain the spring 1975 population of *K. quadrata* at station A. The levelling off and subsequent decline in the population density could also be caused by increased predation. Small summer populations may be limited by low concentrations of edible cells and high densities of predators. High Keratella birth rates in summer 1975 may indicate that food resources were sufficient for reproduction and suggest that predators were important in maintaining low population densities. In autumn, the concentration of edible cells will increase again and birth rates will increase with it. If predators are rare, the population will grow, although less quickly than the spring population owing to colder water. Population density may level off in late fall and early winter; possibly because it approaches the carrying capacity but more probably because the cold water slows the reproductive rate. During early winter, population densities will remain high as long as food supplies remain stable. Population density will decrease during late winter because of decreases in the food level, declining oxygen concentrations, and the increasing senility of the population. Population curves for the Keratella species during winter suggest that rotifers live far longer than previously expected (Ruttner-Kolisko, 1974). I believe no reproduction took place after January yet animals were still present in April. Numbers of animals remaining in spring are important in determining when the spring maximum will be reached and may possibly affect the the density at the maximum. If early spring population density is high, the spring carrying capacity may be reached very quickly, whereas if the early spring population is small it will take longer to reach the carrying capacity; perhaps the rotifer populations will not reach the carrying capacity until it starts declining. Similar results can be expected if the early spring population is hatched from resting eggs laid the previous fall. In this case, the number of resting eggs produced and not the winter survival rate is important in affecting the spring maximum.

INTERNAL CONTROL

Evidence for an "internal control" of rotifer populations comes from work of Amren (1964a, c) and Wesenburg-Lund (1930). In his pioneering work on life cycles of rotifers, Wesenburg-Lund classified habitats and life histories of rotifers into several groups, paying particular attention to the seasons and environmental conditions under which sexual phases occurred. He studied a spectrum of habitats from small ephemeral woodland ponds to permanent lakes. In the ponds, he noted that the rotifer <u>Hydatina</u> hatched from resting eggs in spring, reproduced asexually for a certain number of generations and disappeared after a single sexual generation, even if the pond remained filled for some time. He also noted that populations of <u>Hydatina</u> in permanent waters also entered a resting stage after an apparently set number of generations. He recorded that some species of <u>Conochiloides</u> and <u>Brachionus</u> also appeared to have a set number of generations, but noted that in certain localities some amictic females remained after sexual periods and continued to give rise to more amictic females. He describes the <u>Keratella</u>-type of life history as maintaining amictic production all year round but capable of producing sexual stages in any season. From such studies Wesenburg -Lund concluded that timing of sexual periods, including those of <u>Keratella</u>, is an innate mechanism that protects rotifers from "exceptional conditions, which ... would expose then to the greatest specific dangers". In other words the set time of sexual reproduction apparently evolved as an adaptation to ensure that the population enters a resting stage before it is decimated by rapid development of poor conditions.

Amren (1964a,c) studied populations of K. quadrata and Polyarthra dolichoptera in a pond on Spitzbergen Island. He found that birth rates of both species were not correlated with water temperature nor with concentrations of "small monads", considered to be the food source. Resting eggs of K. quadrata appeared in late July despite warm temperatures and a large population of monads. By measuring lorica and spine lengths of K. quadrata Amren was able to identify animals from the first four generations. His results show that egg ratios on any particular date were highest in the first generation, second highest in the second generation, etc. Using these data, Amren argues that decreases in birth rates seen during the study were not a result of changing environmental conditions but rather a result of differences in each generation's "internal reproductive ability". Therefore, the decrease in birth rate was due to the first generation dying out and being replaced with less productive individuals. Amren's claim that declining fertility was the major cause of lowered birth rates is debatable on a number of points. For example, his raw data indicate that certain changes in birth rates are related to temperatures. However, his recording of the decline in fertility of sequential generations seems sound and could certainly affect birth rates as he suggests, thereby acting as the mechanism in the processes recorded by Wesenburg-Lund. In general Amren concurs with Wesenburg-Lund's ideas concerning the adaptive significance of limiting periods of amictic reproduction, noting that it "may be interpreted as a sign of the rotifers having adapted their life cycles to the most extreme conditions, ie to the years when the drying out or ice-covering takes place unusually early". He further states "In this way the populations avoid the risk of drastic decimation ... and marked annual fluctuations in the frequency are less liable to happen".

Although much is unknown concerning the importance of certain environmental factors to rotifer populations, many of the changes in population density in Hastings Lake can be discussed from the view of external control. In contrast, data from this study do not support the internal control point of view. Considering that Amren studied small arctic ponds and that I studied a temperate lake, the contrast in results is not surprising. If internal controls do operate on rotifer populations as suggested by Amren, they would most likely have evolved in distinctly ephemeral habitats. In Hastings Lake where the seasonal changes are not as severe, a mechanism of internal control may not be necessary. However, it can and should be argued that an internal control could be operating in Hastings Lake, but was not discovered due to a deficiency in methodology for measuring such a phenomenon. Specifically, the major perennial species were not observed to reproduce sexually, so the timing of this period could not be compared to the favourableness of the environment as Wesenburg-Lund could. No method for determining generations was discovered; therefore, reproductive rates of each generation could not be calculated as Amren could. The point remains, however, that while the measured environmental factors do not completely explain my results, they do indicate some control of the rotifer populations and it would appear most profitable to pursue this particular investigation by concentrating on aspects of external control.

CYCLOMORPHOSIS

Cyclomorphosis in the genus Keratella is a poorly understood phenomenon. There are many contradictory results (Hutchinson, 1967) that apparently stem from the inherent complexity of the material. Lack of experimental data, and limited and often poorly designed field studies add to the confusion. Compounding these problems are the taxonomic difficulties with the genus Keratella. It is essential, but often difficult, to determine whether different forms collected over time are genetically linked and thus are exhibiting true cyclomorphosis, or whether the forms represent different species appearing at different times (Gallagher, 1957).

Despite such problems, a few authors have attempted to summarize the existing data and present theories on the mechanism and adaptive value of cyclomorphosis. Wesenburg-Lund (1900 in Pejler, 1962) proposed that the cyclomorphic pattern displayed by planktonic rotifers is an adaptation to maintain bouyancy. He suggested that changes in the water's specifec gravity, caused by changes in temperature, would be sufficient to warrant a change in the bouyancy-enhancing structures of rotifers. Ostwald (1902 in Pejler, 1962) disputed the importance of specific gravity and suggested that temperature-induced viscosity changes were the controlling factors. Pejler (1962) criticized both of these ideas by noting that several authors have found the longest spines of K. cochlearis in winter when the specific gravity and viscosity are the greatest. He suggested that the cyclomorphosis of rotifer spines as in K. cochlearis, is an example of allometric growth, ie larger rotifers develop disproportionately longer spines than do smaller forms. He suggested that low temperatures, by slowing the developmental rate, cause large forms to develop; these are forms requiring larger spines for bouyancy. Lindström and Pejler (1975) showed experimentally that spine lengths of K. cochlearis increase when the rotifer is cultured at low temperatures. Therefore, Pejler viewed the bouyancy of large forms as the adaptive significance of the spine variation and allometric growth as its mechanism. This begs the question; namely, what is the significance of the change in body length with temperature? Pejler (1962) referred to Margaleff (1955) on this point, Margaleff suggesting that larger animals are more efficient than smaller animals in terms of oxygen consumption at low temperatures.

In contrast to Pejler's observations of longer spines in winter, Gallagher (1957) found the spines of K. cochlearis to increase with increases in temperature during spring, and the longest spines were found at maximum water temperature, approximately 24°C. Gallagher also suggested temperature as the controlling factor in cyclomorphosis. He suggested "if the rate of growth decreases in winter and the determination of the final goal of tissues proceeds on an independent time scale, the amount of tissue for determination will be less and the structure might be smaller. In summer the reverse will be true." Gallagher did not attempt to explain the adaptive signigicance of cyclomorphosis.

Amren (1964b) studied the cyclomorphosis of K. quadrata in connection with his studies on population dynamics of rotifers from ponds on Spitzbergen. His results show an increase in average spine lengths during spring and summer. He provides evidence that temporal variation is controlled by intrinsic factors, but acknowledges that environmental factors may have a modifying effect. Similar to Gallagher, Amren did not attempt an explanation of cyclomorphosis' adaptive significance.

Data from my study do not support Pejler's (1962) theories. The posterior spines of K. cochlearis and K. earlinae were short during winter, longest spines being found at temperatures of 16°C to 20°C. The correlation coefficient between spine length and temperature was 0.49 ($P < .01$) for K. cochlearis and 0.77 ($P < .01$) for K. earlinae; the correlation coefficients between lorica length and temperature were -0.14 (N.S.) and -0.29 (N.S.) respectively. Pejler's theory would have predicted a negative correlation coefficient between temperature and spine length. I found negative correlation coefficients for K. quadrata between temperature and spine length and temperature and lorica length (-0.73 $P < .01$, and -0.57 $P < .01$ respectively). This would support Pejler's theory; however, average spine length did increase in the spring of 1976 and data for K. quadrata, contrasting with data for K. cochlearis and K. earlinae, would indicate that the theory cannot be applied generally. The relationship between spine length and lorica length is also difficult to explain by Pejler's theory. Graphs of spine length versus lorica length for K. quadrata and K. cochlearis show a very wide range of spine lengths for any particular lorica length, although the general relationship is significantly positive. If Pejler's bouyancy theory is correct, a more precise relationship between the two lengths would have been expected. The data for K. earlinae indicate no relationship at all between spine and lorica length.

My data resemble Gallagher's (1957) observations; ie increasing spine lengths in spring with maximum spine lengths in early summer and short spine lengths in winter. Keratella quadrata, however, possessed long spines in the winter. Pejler (1962) doubted the importance of Gallagher's work for a number of reasons that do not relate to my study. For example, Gallagher studied a small pond and Pejler suggested "In such small water bodies the seasonal variation can sometimes be the reverse of that occurring in real lakes." However Hastings Lake is a "real" lake, and yet the pattern of cyclomorphosis was similar to that found by Gallagher. Pejler also noted that Gallagher's population disappeared in the winter and appeared to be "degenerate forms that sometimes appear in small populations." The populations of rotifers in Hastings Lake were perennial as were those described by Pejler; but the cyclomorphic pattern that I found was similar to the pattern shown by Gallagher's temporal population.

Despite the similarity between the results of my study and those of Gallagher's, it seems unlikely that Gallagher's ideas on the mechanism of cyclomorphosis are correct. Although Pejler's results do not compare favourably with my study or Gallagher's, Pejler's observations of longer spines in winter is a well-documented phenomenon, a phenomenon that Gallagher's hypothesis cannot explain. These two workers have recorded radically different cyclomorphic patterns, yet both have regarded temperature as the controlling factor. Neither Pejler's nor Gallagher's hypothesis can explain one another's data nor the data from my study, despite Pejler's (1962) claim "It seems, after all, as though we have detected a common denominator to all seasonal variation of zooplankters" and despite Gallagher's (1957) claim "This work ... brings cyclomorphosis in the Rotifera into line with that in Cladocera and Protozoa. Therefore it now seems proper to discuss the possible underlying mechanisms of cyclomorphosis as if it were common to all three groups."

As with data on population dynamics, it is difficult to fit my results in with Amren's hypothesis of intrinsic control of cyclomorphosis. An intrinsic mechanism could operate but go unnoticed because of undeveloped methodology needed for measuring such a phenomenon. However, in contrast to Amren's work, my data definitely indicate that temperature is related to the cyclomorphosis of Keratella. All three Keratella species showed significant correlation coefficients between spine length and temperature, although K. cochlearis and K. earlinae showed a positive relationship and K. quadrata showed a negative relationship. The correlation coefficient between temperature and lorica length was not significant for both K. cochlearis and K. earlinae, but it was negative and significant ($P < .01$) for K. quadrata. Also, the timing of the major cyclomorphic changes in K. cochlearis and K. earlinae was similar and apparently independent of population density, suggesting they were both responding to the same environmental cues and were not the result of changing age structure as suggested by Amren (1964b).

One possible factor in the cyclomorphism of Keratella, not discussed by any of the aforementioned authors, is predation.

Several researchers working with cyclomorphic cladocerans have suggested predation as being the ultimate cause of cyclomorphosis (Brooks, 1965, 1968; Jacobs, 1965; Green, 1967; Zaret, 1972). Brooks (1965) noted that predation by fish is highly size selective, (ie preferential selection of large prey), and he suggested that the reduction in body size, observed in many planktonic cladocerans during the summer months, is an adaptation to avoid such predation. He noted that the large helmets produced during the period of body size reduction are hyaline and suggested that they maintain a "critical" biomass necessary for reproduction but are invisible to the fish, thereby maintaining the appearance of an undesirably small food item. However, Jacobs (1967 in Dodson, 1974) pointed out that helmets increase the volume by only 1.1%. Dodson (1974) suggested that the long helmets are "a response to size selective invertebrate predation", ie the lengthening of the linear measurements is viewed as an effort to extend body size beyond the invertebrate predators' capabilities. Dodson's ideas and the results of my study appear contradictory. Spine length of K. earlinae increased ($P < .05$) with an increase in the numbers of total predators; however, lorica length decreased ($P < .01$) and no significant relationships were found with either of the two predator species taken separately (Table 5). Spine length of K. cochlearis increased ($P < .01$) with the density of Cyclops bicuspidatus thomasi, while lorica length did not change significantly; but lorica length decreased ($P < .01$) with an increase in the Cyclops vernalis density, while the spine length did not change significantly. Average spine length of K. quadrata did not change significantly with either of the two predator species, but decreased ($P < .05$) with an increase in the total numbers of predators. Lorica length also decreased ($P < .01$) with an increase in the density of C. vernalis. If changes in body size and shape are due to predation, the fact that no significant relationships were found between rotifer measurements and the number of copepodites stages I-III supports McQueen's (1969) assumption that the young copepodite instars are not predacious.

Despite the poor fit of Dodson's hypothesis to my results, predation may still act as a factor in affecting cyclomorphosis. Strickler and Twombly (1975) argued that the wake left behind a moving zooplankter is more important in determining the behaviour of potential predators than the actual size of the zooplankter. They described the "prey-following" behaviour of two predaceous copepods, Epischura nordenskioldi and Cyclops scutifer. Epischura nordenskioldi glided smoothly through water until encountering the wake of a potential prey. The predator then followed the direction of the wake, being positioned slightly above it. When the predator reached the prey, the predator dropped on it from above. Cyclops scutifer also followed the wake of potential prey, but followed directly down the wake and approached and captured the prey through a series of rapid "jumps." Strickler (1975) found that C. scutifer does not follow all the wakes it encounters. He presented photographs showing copepods actively avoiding one another's wakes and a single copepod avoiding a pulse of water pressure from a pipet. Copepods must, therefore, determine whether a wake is to be followed, avoided, or ignored. Possibly cyclomorphosis of Keratella is an adaptation to alter the wake. Spines may function to disperse or in some way mask the normal wake, and hence reduce the probability of a predator following the wake. Unfortunately, nothing is known of zooplankton wakes, and studies on the hydrodynamics of such animals are necessary before such a hypothesis of predator avoidance can be proposed.

Another possible function of cyclomorphosis in the presence of predators is the change in the cyclomorphic animal's swimming path. Short-spined individuals of K. cochlearis rotated in a tight helix; however, long-spined K. cochlearis moved in a large open helix (Fig. 70). If the predator followed directly down the wake of a rotifer the forms with long spines may be more difficult to catch, because they would be further from the line of direction. When a rotifer was touched by a copepod (or a pipet), it immediately stopped swimming and sank passively for several seconds before resuming normal swimming behaviour. If the prey's wake is important as suggested by Strickler and Twombly (1975), this method of sinking on contact may be advantageous. For example, the rotifer would escape the area of the predator by leaving as small a wake as possible.

Gerritsen and Strickler (1977) have shown mathematically that one of the best strategies for a planktonic prey species to avoid invertebrate predation is to slow the swimming rate. This reduction in speed lowers the probability of an encounter with a predator. I found that, because of the wide spiral swimming path, long-spined K. cochlearis swam slower than the short-spined forms. Hence, if spine elongation is a reaction to predation, it may function through slowing the swimming rate.

If cyclomorphosis of Keratella is a reaction to predation,

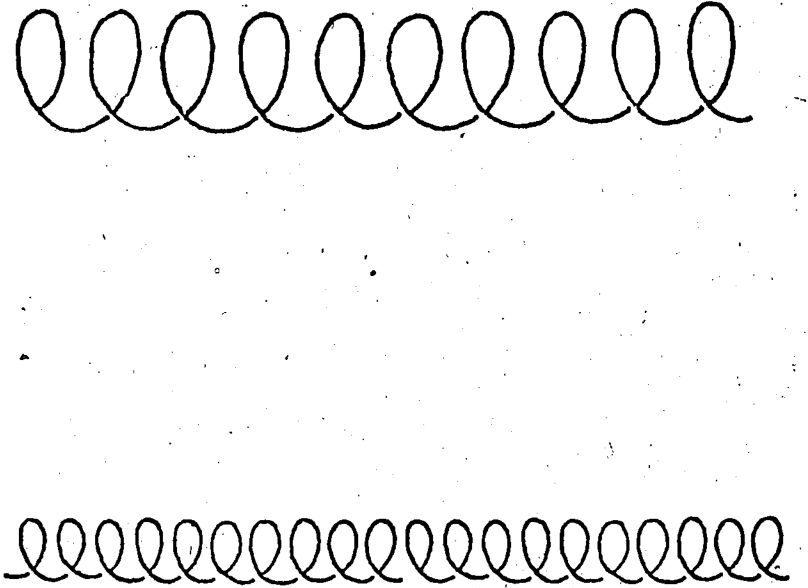

Figure 70. Stylized swimming paths of long-spined *Keratella cochlearis* (upper figure), and short-spined *Keratella cochlearis* (lower figure).

there must be some mechanism whereby the rotifer can determine or at least "predict" with a certain degree of accuracy, the presence of copepods. And in this respect, temperature may be important in affecting cyclomorphosis. If predators' life cycles are controlled in part by temperature, as is documented for Cyclops strenuus abyssorum (Smyly, 1973) and other Cyclops, the rotifers may react to the predators' presence through a common temperature cue. Hence, the relationship between temperature and cyclomorphosis may be stronger, as in my study, than the relationship between predator density and cyclomorphosis. If the prey responded directly to the presence of the predator, a more sophisticated control is possible. Such a control has been found in the relationship between the predatory rotifer Asplanchna brightwelli and the prey rotifer Brachionus calyciflorus (Gilbert and Waage, 1967). Asplanchna releases a substance into the water that stimulates the precleavage eggs of Brachionus to develop large lateral spines (Gilbert, 1967). These spines make it difficult for Asplanchna to swallow Brachionus, and this therefore reduces predation pressure. Perhaps cyclomorphosis in Keratella is in some way related to chemicals released from crustacean predators.

If Keratella species do not respond to predation pressure through cyclomorphosis, then the observed patterns of lorica and spine lengths and predation (Fig. 54, Table 5) may reflect a size selective pattern of predation. For example, in Figure 54 the peaks of predator density in summer of 1975 and spring and summer of 1976 were accompanied by a decrease in K. quadrata's spine length.

When predator density dropped in fall 1975, spine length rose abruptly. This may indicate that predators are selecting the largest forms, and removal of these large forms causes the average spine length to drop. However, the lower range of K. quadrata's spine lengths (Fig. 51) in July and August, 1975 is much lower than the lower range a month previously. This also holds for late spring, 1976. Although size-selective feeding may lower average spine length by reducing the upper range of values as described, it cannot extend the lower range of spine lengths. It would appear, therefore, that the decrease in spine length of K. quadrata is at least partly due to cyclomorphosis. The ranges in spine length of K. earlinae present a problem. Keratella earlinae's spine length increased ($P < .05$) with an increase in the density of total predators. However, the average spine lengths and the lower range of spine lengths were lower during the peak of predator density in summer, 1975 than they were in late June when predators were less abundant (Fig. 53, 65). Thus although the general trend is for the spines of K. earlinae to increase in length with total predator density, there was a distinct decrease in spine lengths during the peak of predator density of 1975. The same conflicting pattern is seen with spine lengths of K. cochlearis. The spine length was very short during peak population density of Cyclops bicuspidatus thomasi in the summer of 1975 despite the generally positive relationship ($P < .01$) between spine length and density of Cyclops.

It is obvious that controlled experiments are necessary to elucidate effects of predation on cyclomorphosis. Statistical methods are useful in analyzing field data and indicating what type of experiment would be most profitable, but are insufficient to determine cause and effect relationships.

Cyclomorphosis of freshwater animals is a fascinating subject, yet it is a difficult field, filled with numerous conflicting hypotheses. Many researchers apparently do not understand the difference between the ultimate reason for a structure and the environmental cue that triggers the development of a structure. Clearly, temperature is important in controlling cyclomorphosis, but it is now becoming apparent that temperature functions as a cue or mechanism for cyclomorphosis and is not the actual cause of cyclomorphosis. Another problem is that several researchers attempt to explain all cases of cyclomorphosis with one basic hypothesis. There is no <u>a priori</u> reason to assume that protozoans, rotifers, and crustaceans should change shape in the same manner. There is also no reason to assume that all species of rotifers should change shape in the same manner; indeed, there is no reason to assume that populations of the same species, living under different selective regimes, should change shape according to some species-specific format. Only by understanding the selective pressures imposed by a given environment will the causes of cyclomorphosis be discovered.

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APPENDIX I

Duration of development (hrs) of rotifer eggs at specific temperatures. Values expressed are minimum and maximum times of each duration.

Keratella cochlearis

Temperature			
10.0°C	11.0°C	20.0°C	20.5°C
71.0-77.0	56.0-60.0	21.0-28.0	21.0-23.0
70.0-74.0		21.0-28.0	24.0-26.0
		21.0-28.0	
		24.0-27.0	
		26.0-28.0	
		22.5-24.0	

Brachionus angularis

Temperature	
15.0°C	19.0°C
42.0-45.5	25.0-27.0
43.0-46.0	26.0-28.5
43.0-46.0	23.5-26.5
	28.0-30.0

Pompholyx sulcata

Temperature	
19.0°C	22.0°C
27.0-29.5	20.0-22.5
31.0-34.5	18.5-21.5