

THE UNIVERSITY OF MANITOBA

A COMPARISON OF THE CRUSTACEAN ZOOPLANKTON
POPULATIONS OF FOUR MAN-MADE LAKES
IN SOUTHERN MANITOBA

by

NANCY LOUISE LOADMAN

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IN MEMORY OF

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ABSTRACT

Seasonal variations in the abundance of eight species of crustacean zooplankton in four small man-made lakes in southern Manitoba were studied from samples taken in a one year period from June of 1977 to June of 1978. Three stations on each lake were sampled at weekly intervals in summer, 1977 and the spring of 1978 and at approximately biweekly intervals in autumn. Winter samples were taken at one station per lake biweekly. Crustacean species shared by the four lakes were: Diaptomus siciloides, Cyclops bicuspidatus thomasi, Cyclops vernalis, Mesocyclops edax, Daphnia galeata mendotae, Daphnia parvula, Ceriodaphnia lacustris, and Bosmina longirostris. Lake I had the highest total numbers of animals per liter in all seasons as well as the greatest relative abundance of cyclopoids and cladocerans.

In each lake, the number of dominant species ranged from one to five on various sampling dates. Lake IV generally had the least complex community in that in 21 of a total 32 sampling dates, no cladoceran was dominant. In the other lakes, combinations of one diaptomid, one to two cyclopoids and one or more cladocerans dominated more often than in Lake IV. A comparison of relative abundance and dominance in June of 1977 and June of 1978 showed a large shift in community composition in each of the four lakes

in favour of cyclopoid copepods which comprised over 60 percent of the total abundance of crustacean zooplankton by the spring of 1978.

The percent similarity of community index calculated for all possible lake pairs showed that the degree of similarity between the lakes changed in different seasons. Lake pairs I and IV and II and IV were least similar in autumn, 1977 (PSC = 46.0 and 40.6 respectively) and most similar in spring, 1978 (96.1 and 96.5 percent). Discriminant function analysis was performed on species abundance data from summer and fall, 1977. The analysis achieved good separation among Lakes I, II, and IV and poor discrimination between Lakes III and IV. Possible effects of differing environmental conditions on the abundance and timing of the seasonal maxima of some of the crustacean species were discussed.

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INTRODUCTION

A number of studies have been undertaken to compare zooplankton populations of lakes with different limnological conditions in attempts to characterize lakes on the basis of their plankton communities. These studies have often led to the formation of community types according to the dominant species of zooplankton and the accompanying limnological characteristics of the group of lakes (Whittaker and Fairbanks 1958; Anderson 1974; Patalas 1971). In recent years this relationship between community and environment has been investigated using principle components and discriminant function analyses to demonstrate the use of zooplankton as indicators of limnological conditions (Sprules 1977; Green and Vascotto 1978; Janicki and DeCosta 1979). These studies point out that more regional information is needed and that species considered indicators of certain conditions in one area may be abundant under quite different conditions in other regions.

Relationships between certain environmental conditions and the total abundance of zooplankton have also been investigated. Patalas (1971) found that the total numbers of plankton per unit area increased with maximum depth. Patalas (1972, 1973) also observed an increase in crustacean abundance with increased heat and chlorophyll content of the St. Lawrence Great Lakes and the lakes of the Okanagan Valley.

Others have observed relationships between the amount of zooplankton and total dissolved solids (Rawson 1942; Northcote and Larkin 1956), hypolimnetic oxygen deficits, (Rawson 1942) and epilimnetic temperature (Patalas 1975). An increasing proportion of cyclopoids and cladocerans and a reduction in calanoids has been observed with increasing productivity and eutrophy (Gannon 1972; Patalas 1972).

The primary objective of the present study was to provide an initial survey of the zooplankton populations of four small man-made lakes at Fort Whyte, Manitoba as part of an ongoing investigation into the limnology of these lakes. The zooplankton species present in these four lakes are common components of some of the large regional study areas previously mentioned and thus a description of the seasonal cycles and abundances of these species and the environmental conditions in which they are found adds to the information on regional differences. The four lakes are superficially very similar because of their origin and close physical proximity and, theoretically, their plankton communities should be very similar. Thus certain aspects of the abundance of the four zooplankton populations were compared and contrasted to observe their degree of similarity and an attempt was made to relate, in a qualitative way, the structure of the zooplankton communities with the limnological conditions prevailing in each of the lakes.

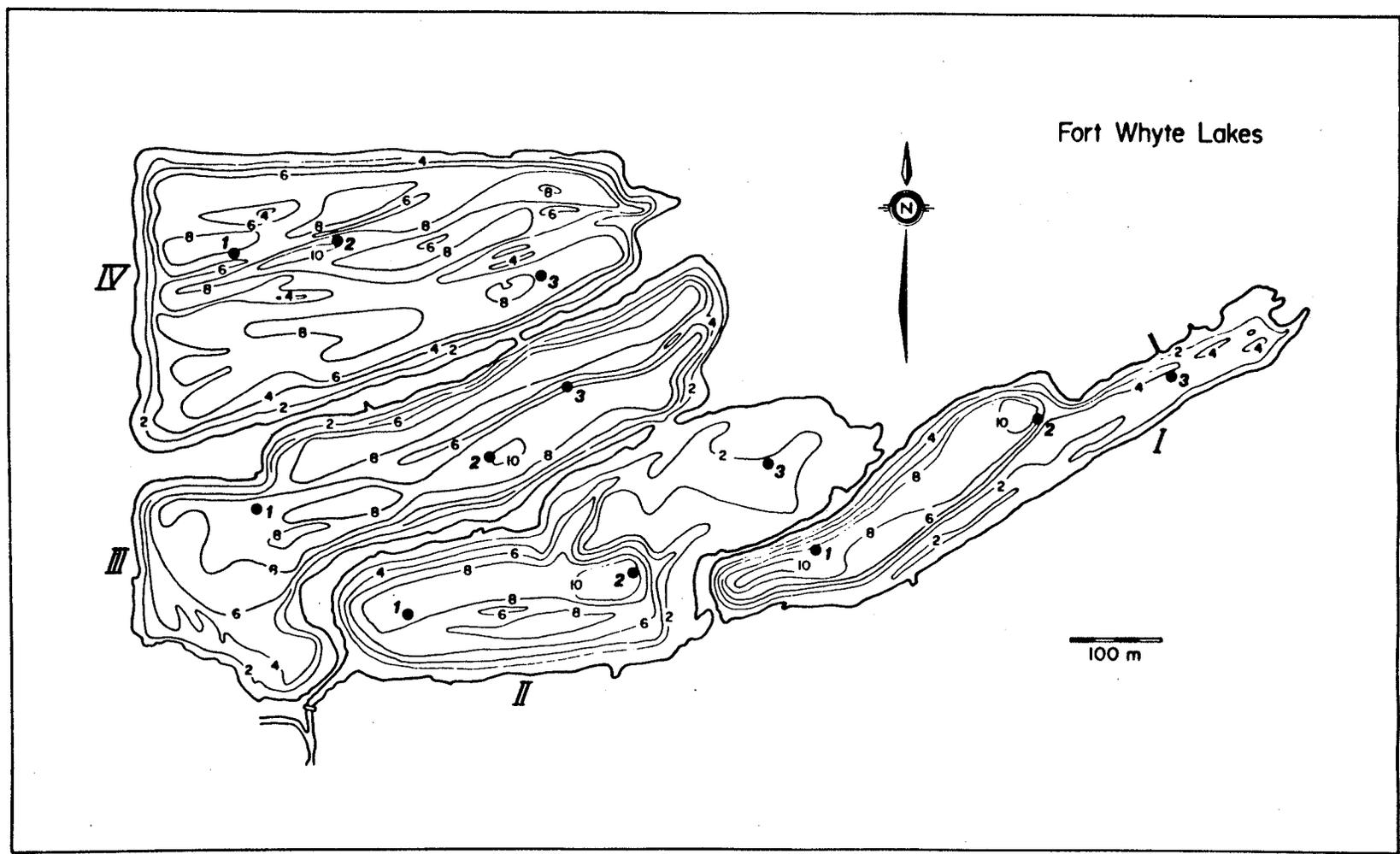
MATERIALS AND METHODS

Water samples for chemical analysis were taken at the deepest (centre) station on each lake (Fig. 1) on the same date on which zooplankton samples were taken. Water temperature was also measured at the centre station with a thermistor thermometer at one meter intervals. Samples for oxygen, alkalinity, pH, and water chemistry were taken at each meter interval with a 1 liter van Dorn bottle. Oxygen samples were titrated according to the modified Winkler method and alkalinity was determined using the methyl orange indicator method (A.P.H.A. 1965). Water chemistry analysis was performed at the Freshwater Institute, Environment Canada, Winnipeg according to the standard procedures outlined in Stainton et al (1974). An initial description of the results of the water chemistry analysis is contained in Ward et al (unpublished).

From June to August, 1977, zooplankton samples were taken weekly at three stations on each of the four lakes (Fig. 1). One series of samples was taken in September and two were taken in October, 1977. Under ice cover, samples were taken at biweekly intervals at the deepest station on each lake except in January and April, 1978 when the lakes were visited once per month. In May and June, 1978, samples were taken weekly at all three stations on each lake.

Figure 1. Contour map of the four Fort Whyte lakes showing the location of the zooplankton sampling stations.

Fort Whyte Lakes



The crustacean zooplankton were collected using an integrated tube sampler modified from Pennak (1962). The difference between the actual volume of sample contained within the sampling tube and the predicted volume calculated by multiplying the area of the tube by the depth to which it was lowered was less than 9% of the total volume in three trials. The contents of the sampler were filtered through a 64 μ screen mesh and the zooplankton preserved in 5% formalin. Samples were reduced to a volume of 25 ml by drawing off excess liquid with a syringe fitted with a 25 μ screen mesh. The contents of the sample vials were mixed vigorously in all directions and two one-half ml subsamples were withdrawn using a glass tube. The vial was mixed again before withdrawing the second subsample. Both subsamples were placed in a Sedgwick-Rafter cell and the entire crustacean zooplankton contents of the cell enumerated. To assess the adequacy of the subsampling technique, a variance-to-mean ratio test was performed on six subsamples from one sample and results are contained in Appendix A. The variance and mean were not significantly different for the dominant and largest species such as Daphnia galeata Sars mendotae Birge indicating that the subsampling method provided a representative random sample and that larger species were not selectively excluded from the glass tube.

Species of cladocerans were identified (Brooks 1957, 1959) and classified as immature, females, females with eggs, females with ephippia, or males. For Bosmina longirostris (O.F. Müller), only females with eggs were classified separately. Size measurements of at least fifty individuals of the three most abundant cladoceran species were taken as a further aid in classifying individuals as mature or immature (Appendix B). Measurements were made from the anterior margin of the head to the base of the caudal spine with the aid of an ocular micrometer. Cyclopoid copepods were identified using Yeatman (1959) and adults were classified as females, females with eggs, or males. The copepodid stages of the various species were combined into two categories: copepodids I through III (CI-III) and copepodids IV and V (CIV-V). Nauplii were classified as either calanoid or cyclopoid. Cyclopoid nauplii were apportioned according to the copepodid ratio of the three cyclopoid copepods and were included in the calculations of total numbers and relative abundance of Cyclops bicuspidatus thomasi Forbes, Cyclops vernalis Fischer, and Mesocyclops edax Forbes. In samples where C. vernalis and M. edax were rare, cyclopoid nauplii were regarded as C. b. thomasi. The only diaptomid was identified according to Wilson (1959) and Comita and Tommerdahl (1960) and individuals were placed into the same life history categories as the cyclopoids.

Count data from three stations on each lake were combined to produce a weighted mean for each lake on each sampling date, with weights corresponding to the depth of the stations. For each lake on a particular sampling date during the ice free period, at least 200 individuals were counted. At least 64 individuals of each dominant cyclopoid, calanoid, and cladoceran were enumerated. Counting at least 64 individuals set the 95% confidence limits at a maximum of $\pm 25\%$ (Elliot 1971), assuming a Poisson distribution where the variance approximates the mean. Edmondson (1971) suggested that counting at least 40 animals of the major species would adequately represent the population. In this study, a 1 ml subsample from each station was usually sufficient to achieve this minimum number. After calculating the total number of each species in the whole sample, the number of individuals per liter was found by dividing by the volume of water in the integrated sampler. The number of animals per liter thus represented an average for the entire water column.

The percent similarity of community index was calculated for each season according to the formula

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

where a and b are, for a given species, the percentages of the total animals of samples A and B which that species represents (Whittaker and Fairbanks 1958).

Discriminant function analysis (DFA) was performed on log-abundance of the eight zooplankton species as well as cyclopoid nauplii in an attempt to distinguish between the lakes (groups) on the basis of their planktonic communities. Abundance data from the centre station of each lake for sixteen sampling dates representing summer and autumn, 1977 were used in the analysis. Discriminant analysis weights and linearly combines the discriminating variables so that the groups are as statistically distinct as possible, using the equation:

$$D_i = d_{i1}Z_1 + d_{i2}Z_2 + \dots d_{ip}Z_p$$

where D_i is the score on the discriminant function, d_{ij} are the weighted coefficients, and the Z 's are the standardized values of the p discriminating variables (Nie et al 1975). Once the discriminant functions were derived and each sampling date was given a score on each function, the population data were entered into the classification phase. The classification of the data from each sampling date originally used to derive the functions and the comparison of the predicted and actual group membership resulted in a measure of the success of discrimination. A graph of the discriminant scores for each sampling date and the group means was constructed to aid in visualizing the separation of the four lakes achieved through the analysis. A packaged computer programme (SPSS-DISCRIMINANT) was used to perform the analysis (Nie et al 1975).

THE LAKES

The four small study lakes are located in the southwestern section of the City of Winnipeg adjacent to the Canada Cement LaFarge Company (Fig. 1). The lakes were formed by dredging in order to extract the mud and clay used in the cement product.

Historical records from the cement plant indicate that excavation began at the shallow east ends of Lakes I and II in the early part of the second decade of this century using a horse-drawn shovel. A steam driven dragline was used to complete excavation of the western portion of Lakes I and II. By 1920 most of the first basin had been dug, thus making Lake I the oldest of the four lakes. Lake II was completed in the late 1940's. Lake III was first dug in 1951 and completed in 1962. Excavation of Lake IV began in the latter part of 1962 and this lake is currently being dredged with a diesel-powered dragline. Thus, in age, the lakes form a sequence: Lake I is over 50 years old, and Lake IV, the youngest lake, is less than twenty years old and has yet to be completed.

Lakes II, III, and IV are now connected by shallow trenches (Fig. 1). The formation of the channel between Lakes II and III, whether by intent or simple erosion, occurred between 1957 and 1967. The channel connecting

Lakes III and IV appeared between 1967 and 1977. Although no direct connection exists between Lakes I and II, surface water is pumped from Lake II to the west end of Lake I to raise the level in that lake. Water is pumped from and returns to the east end of Lake I via the cement plant where it is used in the manufacturing process.

The draw-down from Lake I has been estimated at $946 \text{ m}^3 \text{ day}^{-1}$. The rate of return is not known but is considerably less than the draw-down. In the summer of 1977 the water levels in the lakes affected by pumping varied as much as 1 meter. The lakes are essentially a closed system; though they are connected, there is no outflow.

Water levels in all four lakes were unusually low in the spring of 1977 because of reduced precipitation during the preceding winter and a warm, dry spring. By August of 1977, the channel between Lakes III and IV was dry. Lake II received nutrient rich water in spring, 1977 from the ditch at the west end which drained farmland from the north and west. Lake I received an effluent from an impoundment of ducks and geese on the south shore of the lake.

None of the lakes have any true littoral zone. For their size, the lakes are relatively deep and the basin slopes are steep, dropping quickly to two meters just offshore (Fig. 1). As a result of excavation, the lakes

share a similar basin morphometry although maximum width, area, and volume are all greater in the younger lakes (Table 1). The lakes all have a maximum depth of 10 m but the mean depth of Lakes I and II are somewhat lower as a result of their shallow eastern ends.

Lake I was already thermally stratified by May, 1977 (Fig. 2). The temperature of the epilimnion was about 20C to a depth of 3 m. The metalimnion extended from 3 to 7 m and the temperature dropped from 20 to 7C at the lower limit (Ward et al unpublished). The hypolimnion extended below 7 m. Thermal stratification became more complete in July. The epilimnion dropped to 4 m and the surface temperature was 24C. By the end of August the epilimnion had begun to cool and by October the entire water column was 9C, at which time mixing could have occurred. Ice formed in November and reached a maximum thickness of one meter by March.

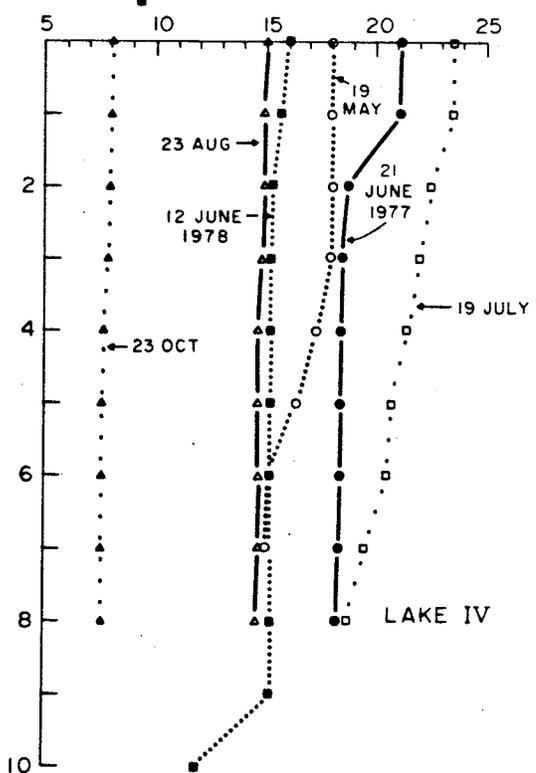
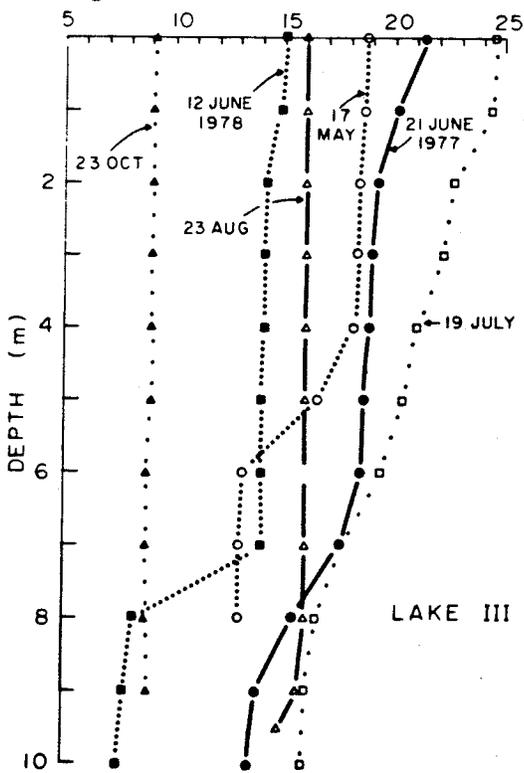
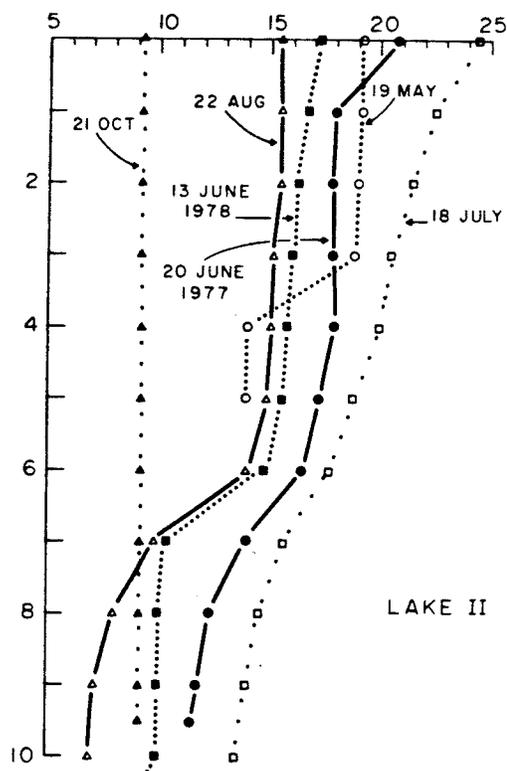
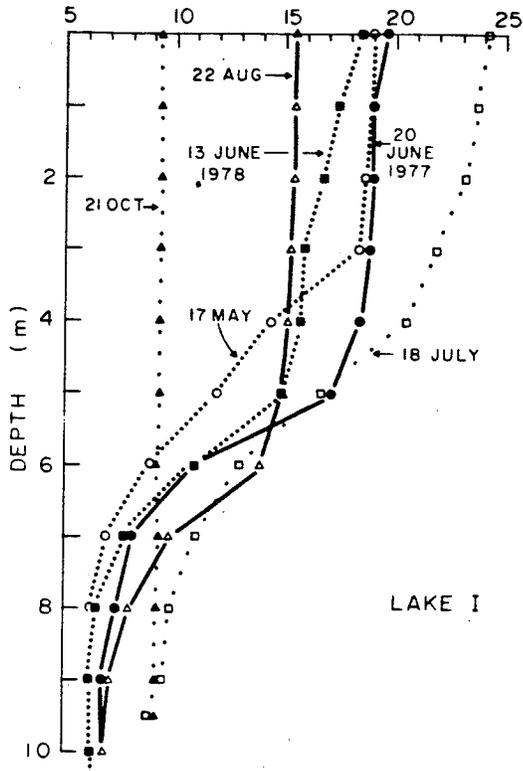
Thermal stratification was not as intense in Lake II. In July, the boundary of the epilimnion and metalimnion was obscure, thus indicating that the hypolimnion was not as isolated from the overlying waters as in Lake I (Fig. 2). Stratification occurred only briefly in Lake III in May, 1977 (Fig. 2) and mixing probably occurred near the bottom in summer because the temperature of the hypolimnion always exceeded 12C. Lake IV showed the least evidence for

Table 1. Morphometry of the Fort Whyte Lakes (1977-1978).

	L a k e			
	I	II	III	IV
Maximum length (km)	.72	.64	.75	.65
Maximum width (km)	.14	.22	.28	.32
Maximum depth (m)	10	10	10	10
Area (ha)	6.43	9.26	11.27	13.35
Mean depth (m)	4.31	4.12	6.07	6.07
Volume (m ³)	276,000	383,000	686,000	807,000

Figure 2. Temperature profiles of the Fort Whyte lakes, 1977-1978. All profiles are from 1977 except where indicated.

TEMPERATURE (C)



stratification and there was little difference between surface and bottom temperatures (Fig. 2). Aided by wind action and the constant dredging operation, this lake was mixed throughout the summer.

The oxygen regimes of the four lakes reflected the degree and duration of thermal stratification as described above. Lake I showed summer and winter oxygen deficits in the hypolimnion (Fig. 3). Lakes II and III had reduced hypolimnial oxygen concentrations in summer but deficits were less severe than those in Lake I (Fig. 3). Except for a brief period in May, 1977, the constant mixing in Lake IV ensured high oxygen levels at all depths. In Lakes I and II in particular, mixing appeared to be incomplete in the spring of 1978 and the lakes were not fully recharged with oxygen.

The annual mean concentration of total dissolved phosphorus in 1977-1978 in Lake I was twice that of Lake II and more than seven times the mean level in Lake IV (Table 2). Particulate phosphorus levels in Lakes I and II were similar and higher than those in Lakes III and IV.

Particulate carbon values were highest in Lake I but the concentration in all the lakes exceeded 1000 mg m^{-3} . On an annual basis, Lakes I, III, and IV had similar values of chlorophyll-a (Table 2) but the level in Lake II was

Figure 3. Monthly mean epilimnion and hypolimnion values for oxygen in the Fort Whyte lakes, 1977-1978.

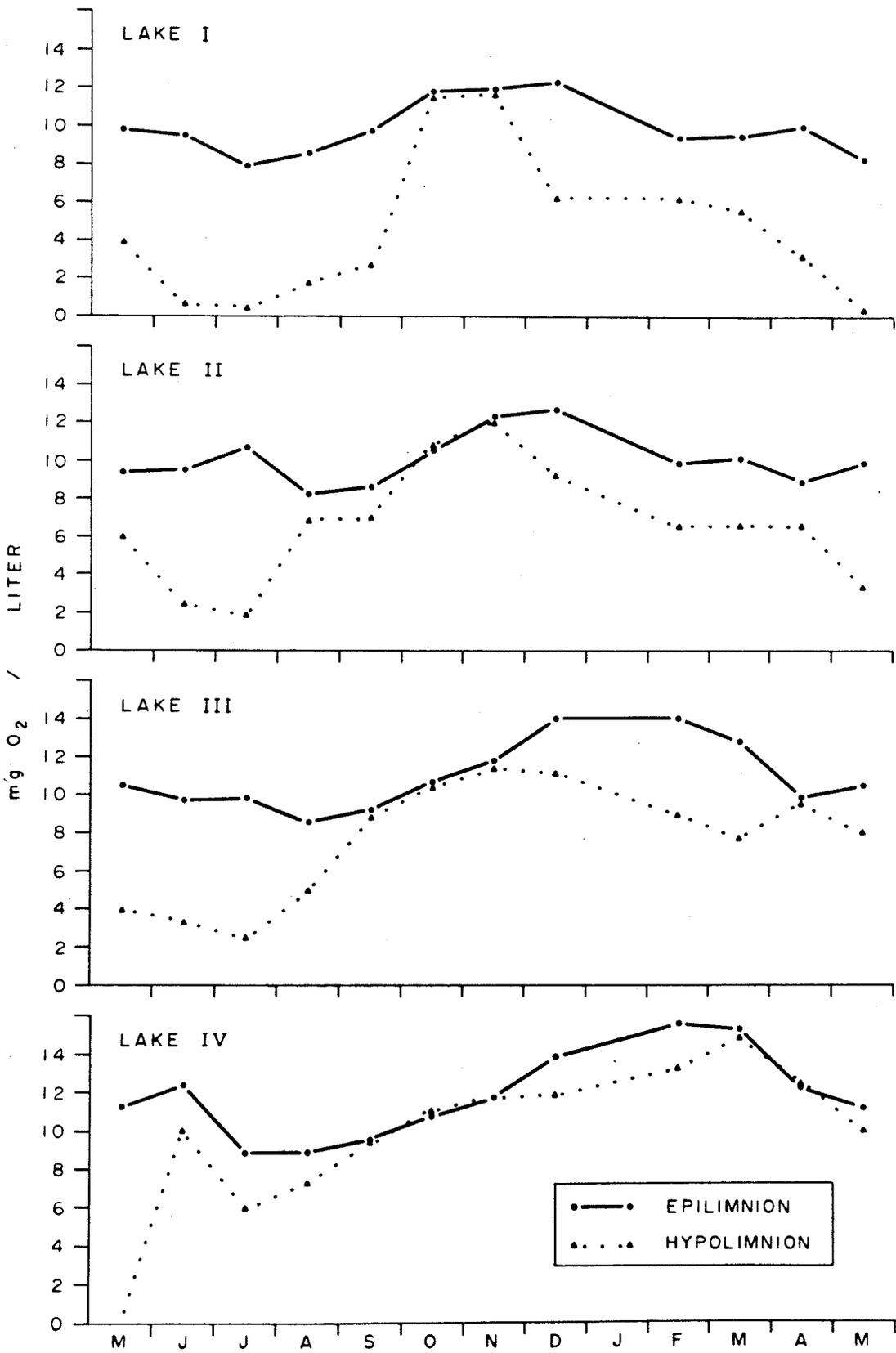


Table 2. Annual mean values for chemical parameters in the Fort Whyte Lakes, May 1977 to May 1978.

Parameter	Units	L a k e			
		I	II	III	IV
Oxygen	g/m ³	7.1	7.9	8.9	10.7
pH		8.1	8.1	8.2	8.4
Alkalinity	g/m ³	202	172	171	180
Ammonia	mg/m ³	813	293	162	45
Nitrate	mg/m ³	84	200	124	33
Particulate Nitrogen	mg/m ³	154	170	141	128
Total Dissolved Phosphorus	mg/m ³	95	44	17	12
Particulate Phosphorus	mg/m ³	23	22	17	17
Particulate Carbon	mg/m ³	1218	1096	1129	1087
Chlorophyll	mg/m ³	5.1	8.2	5.7	5.1
Total Dissolved Solids	g/m ³	674	335	390	473
Conductivity	x10 mS/m	11.0	5.4	6.2	7.2
Temperature	°C	10.6	11.3	12.8	13.4

somewhat higher (8.2 mg m^{-3}). In Lake II in July, 1977, chlorophyll-a values reached 22 mg m^{-3} likely caused by a bloom of blue-green algae. This bloom also affected Lake III to a lesser extent (Ward et al unpublished).

Nitrate levels were considerably higher in Lake II, possibly because of the addition of fertilizer enriched runoff. High particulate nitrogen levels in this lake may have been associated with the blue-green algal bloom. The very high levels of ammonia in Lake I as compared to the other lakes were, in part, caused by the isolation of the anoxic hypolimnion in summer but the major source of this ammonia is thought to be the effluent from the wildfowl impoundment (Ward et al unpublished). High ammonia levels also occurred in winter in this lake when oxygen concentrations near the bottom were low.

Alkalinity values were quite high in all the lakes but were highest in Lake I (202 mg l^{-1}). pH values also indicate that all the lakes were slightly alkaline (Table 2).

Total dissolved solids and conductivity were highest in Lake I and second highest in Lake IV (Table 2). The retention of elements in the sediments with some return to the overlying waters, as well as the continuous effluent from the waterfowl enclosures may have contributed to the high T.D.S. values in Lake I. Constant dredging, resulting in high levels of suspended inorganic matter may have elevated T.D.S. values in Lake IV above those found in Lakes II and III (Ward et al unpublished).

In summary, the four man-made lakes, though superficially similar, showed differences in age, morphometry, thermal stratification, oxygen deficits, and nutrient levels. Lake I, the smallest and oldest lake, had the highest levels of most dissolved substances, the greatest degree of thermal stratification, and the largest and most prolonged hypolimnial oxygen deficit. These characteristics indicate that this lake is the most eutrophic. Lake II had relatively high nutrient levels and the highest chlorophyll-a values also indicating a certain degree of eutrophy. Lakes III and IV, the youngest lakes, lacked the direct nutrient input known for Lake I, have had less time to accumulate nutrients in the sediments, and circulated more frequently. Lake IV seemed the least productive of the four lakes, and was shown to have the lowest levels of phosphorus, nitrogen, and chlorophyll-a.

RESULTS

The four lakes shared eight species of crustacean zooplankton: Diaptomus siciloides Lilljeborg, Cyclops bicuspidatus thomasi Forbes, Cyclops vernalis Fischer, Mesocyclops edax Forbes, Daphnia galeata Sars mendotae Birge, Daphnia parvula Fordyce, Ceriodaphnia lacustris Birge, and Bosmina longirostris (O. F. Müller). Scapholeberis sp. was found on only one occasion in June, 1978 in Lake I.

The average annual total number of crustacean zooplankton per liter (June 1977-June 1978) decreased substantially from Lake I to Lake IV, the latter having an annual average of slightly more than half that in Lake I (Table 3). This same pattern of decreasing abundance from Lake I to Lake IV was evident for the mean values in summer (June 1977-August 1977) and autumn (September and October 1977). The winter populations (November 1977-April 1978) of the lakes were quite low with Lake I having the highest total numbers per liter and Lakes II, III, and IV having lower and similar total numbers. All four lakes showed a large increase in average total numbers in spring (May-June 1978), but the same relationship from Lake I to Lake IV was evident.

Table 3. Annual and seasonal mean total abundance of crustacean zooplankton in the Fort Whyte lakes, 1977-1978. (animals liter⁻¹).

	Lake I	Lake II	Lake III	Lake IV
Annual mean	151.4	123.6	95.6	80.5
Summer (June-August)	136.3	113.1	78.8	57.8
Autumn (September-October)	117.8	77.8	50.1	26.7
Winter (November-April)	58.3	25.8	27.2	30.5
Spring (May-June)	356.0	332.6	269.5	239.8

Separating total abundance into the three major taxonomic groups in different seasons demonstrates some of the basic differences and similarities in the composition of the crustacean communities of the four lakes. The lakes contained approximately the same numbers of the calanoid copepod, Diaptomus siciloides, throughout the year and in each lake the number of individuals per liter declined in winter and increased again in spring (Table 4). Lake I had the highest mean numbers of cyclopoid copepods in all seasons. A large increase in the number of cyclopoids per liter occurred in all the lakes in the spring of 1978. The absolute abundance of cladocerans was always lowest in Lake IV (Table 4). Lakes I and II generally had the highest mean numbers of cladocerans except in spring, 1978 when the mean from Lake III was highest.

The weighted monthly means of the number of calanoids per liter in all the lakes showed the same general pattern of abundance throughout the year. In Lake I, numbers declined after August and increased slightly in November. Numbers of calanoids per liter were highest in Lake II in summer, 1977 (Fig. 4). The abundance of calanoids was quite similar in Lakes III and IV with numbers reaching a maximum in July of 1977 (Fig. 4).

Cyclopoids were most abundant in Lake I in summer and autumn, 1977, and began to increase in March of 1978 several weeks in advance of the other lakes (Fig. 5).

Table 4. Annual and seasonal mean abundance of the major taxonomic groups in the Fort Whyte Lakes, 1977-1978. (animals liter⁻¹).

Lake	Calanoids				Cyclopoids				Cladocera			
	I	II	III	IV	I	II	III	IV	I	II	III	IV
Annual mean	26.2	33.4	27.6	21.7	85.7	57.2	46.2	50.1	39.5	33.0	21.8	8.7
Summer	45.6	55.2	43.8	31.2	38.1	13.5	19.0	18.2	52.6	44.4	15.9	8.5
Autumn	15.2	16.8	17.8	10.7	47.5	16.6	12.9	9.4	55.1	44.4	19.5	6.6
Winter	8.1	9.9	7.2	9.1	31.8	5.9	10.8	20.5	18.4	10.1	9.2	0.9
Spring	20.0	34.0	31.4	27.3	297.8	257.4	180.8	189.0	38.2	41.2	57.3	23.5

Figure 4. Monthly mean abundance of calanoids in
Fort Whyte lakes, 1977-1978.

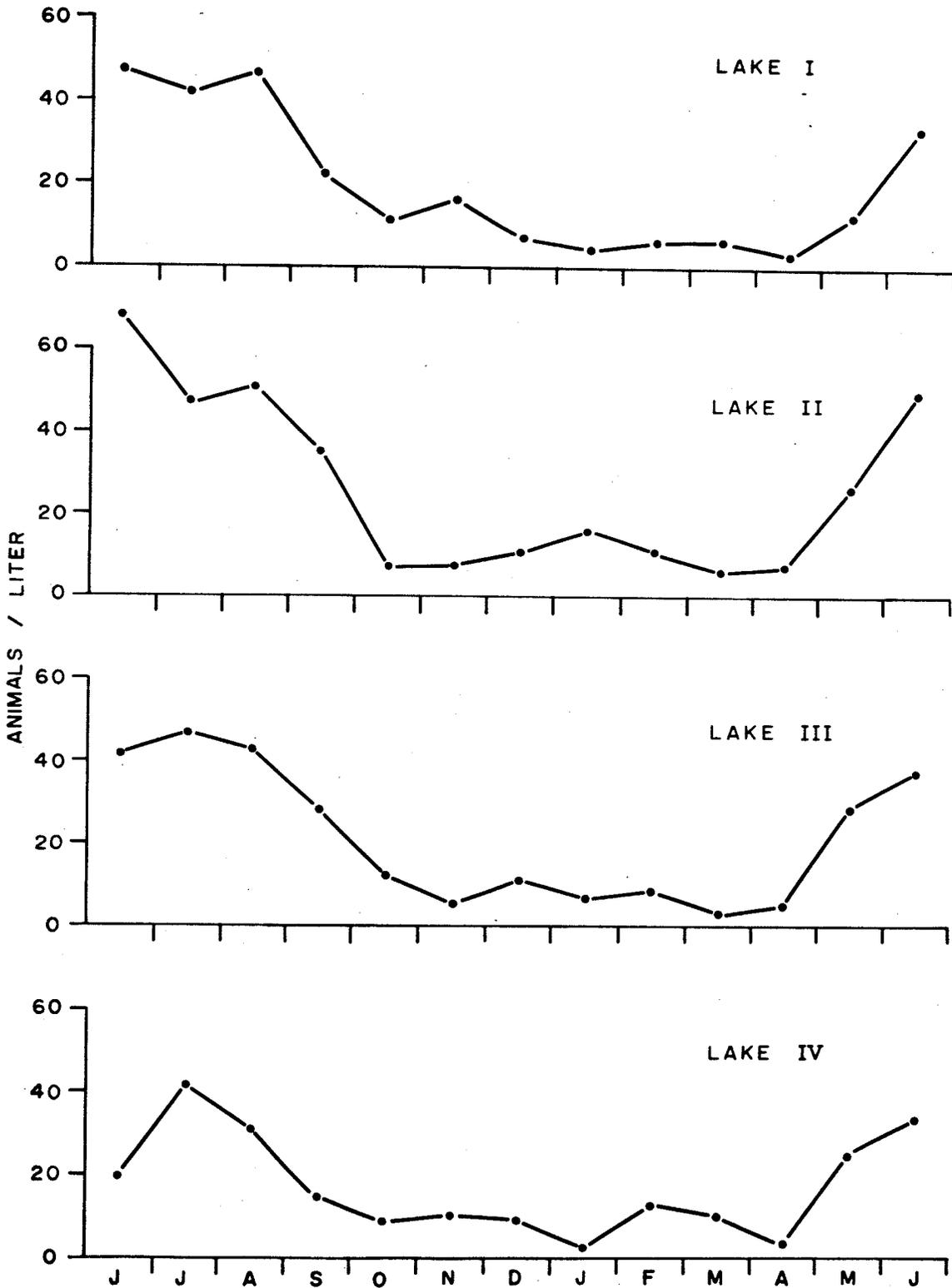
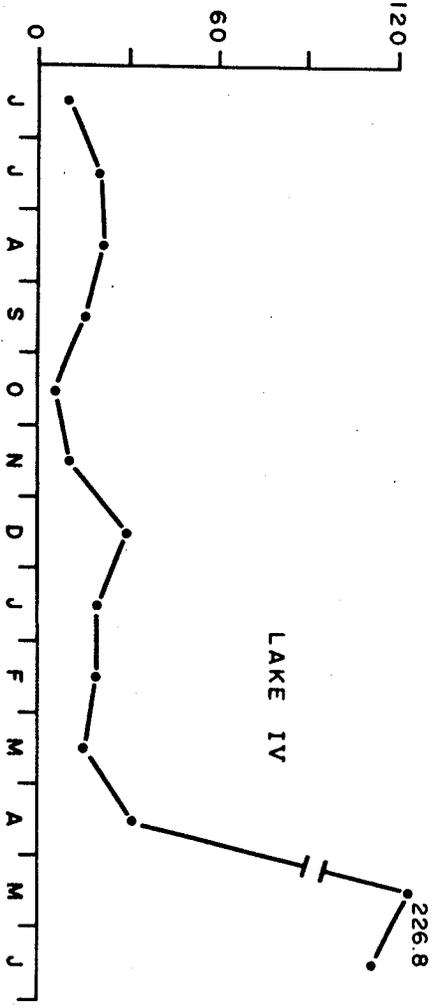
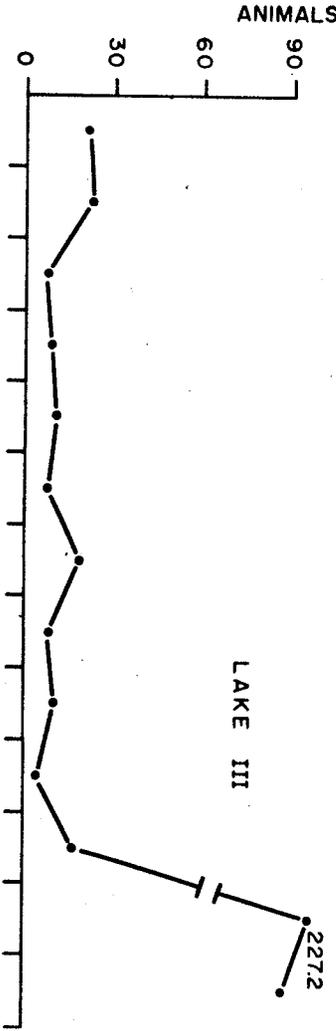
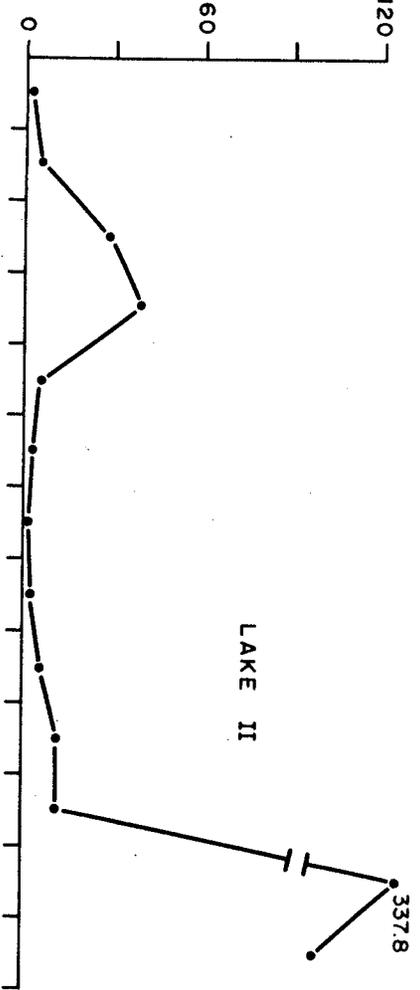
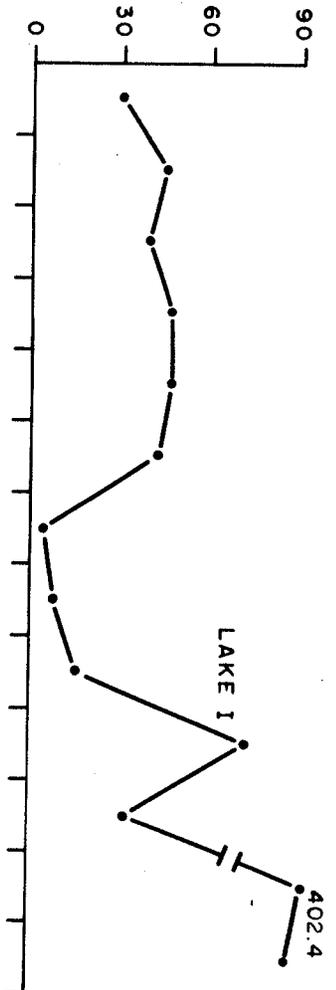


Figure 5. Monthly mean abundance of cyclopoids in the Fort Whyte lakes, 1977-1978.



Lake II had the lowest abundance of cyclopoids in June and July 1977 and in winter samples (Fig. 5). The number of cyclopoids did not fluctuate greatly in Lake III in summer, 1977 (Fig. 5). This group seemed to overwinter most successfully in Lake IV (Fig. 5). The samples from May of 1978 show large increases in cyclopoid copepods and by June all the lakes had similar numbers in this group.

The annual pattern of monthly means of the Cladocera highlight an important difference between the lakes. The two peaks in cladoceran abundance in Lake I occurred in June and July and in October and November (Fig. 6). In Lake II the maxima were in June and in August-September (Fig. 6). Peaks in cladoceran abundance in Lake III appeared at the same time as in Lake I but the number of animals was much less. Lake IV contained the lowest numbers of cladocerans in all 1977 samples (Fig. 6). A spring bloom of cladocerans in 1978 occurred in each lake, their numbers reaching a maximum earlier in Lakes II and III.

The seasonal pattern of the total number of D. siciloides per liter determined from each sampling date was quite similar in all the lakes and the number of animals per unit volume was not greatly different in any season (Fig. 7). There were no large peaks in abundance of this species during the summer of 1977 except in Lake II on June 13 where the total number of all life history stages of this species reached

Figure 6. Monthly mean abundance of cladocerans in the Fort Whyte lakes, 1977-1978.

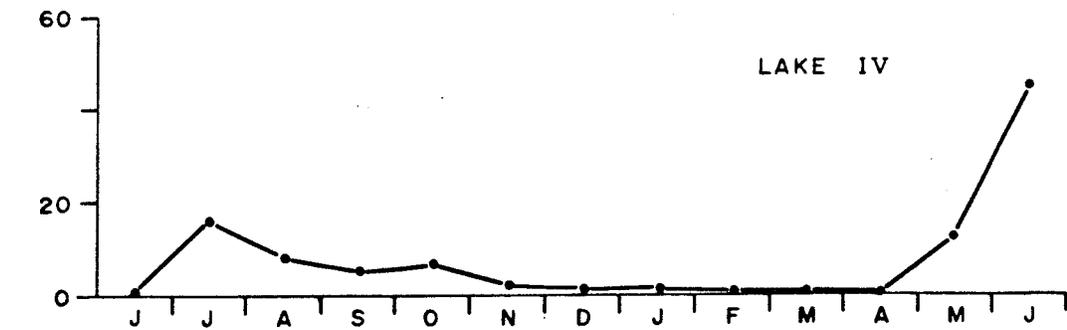
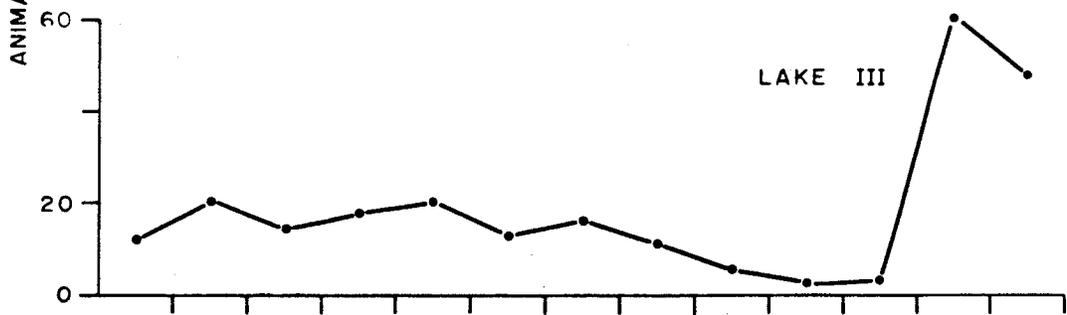
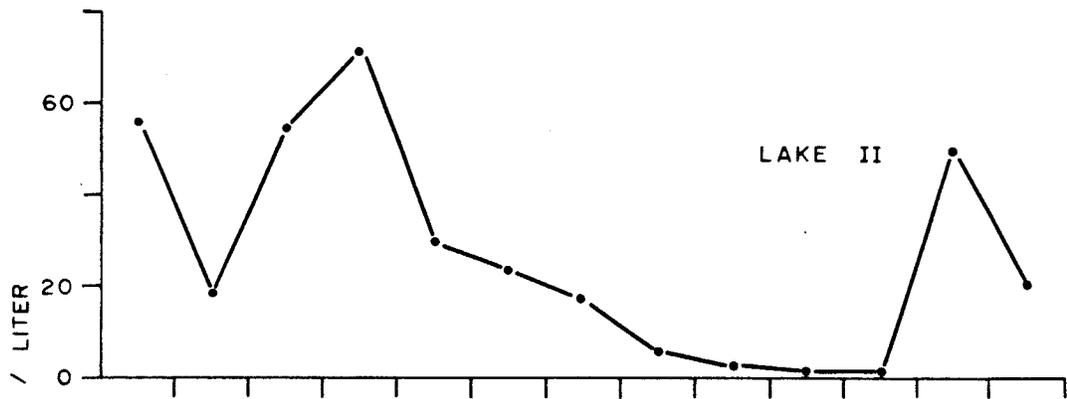
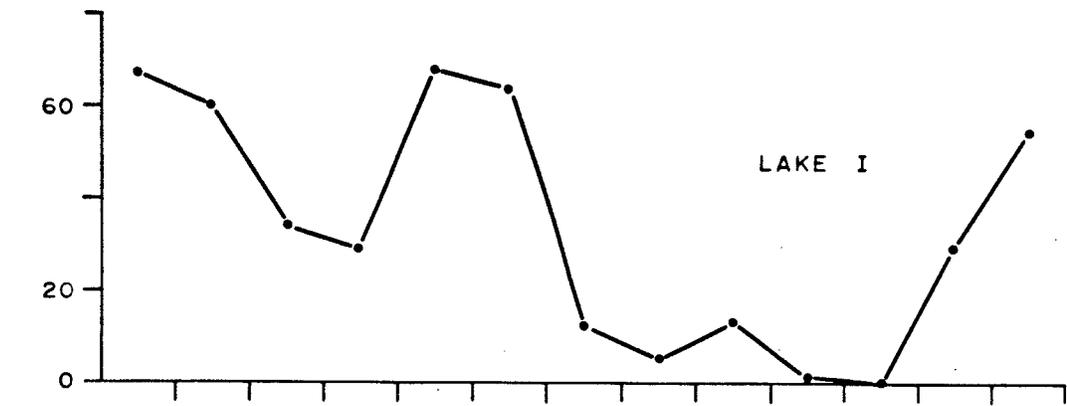
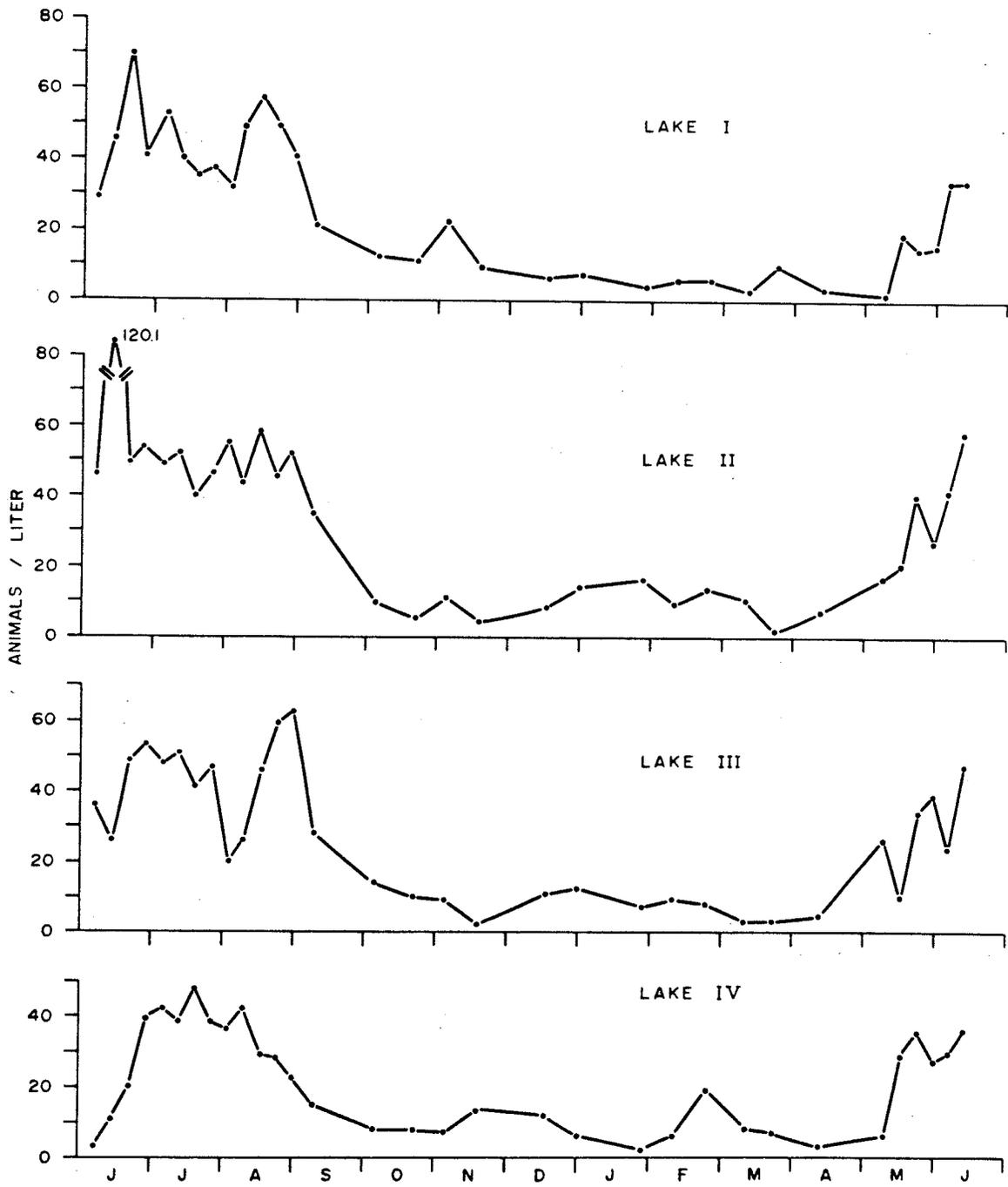


Figure 7. Seasonal changes in the estimated total number of Diaptomus siciloides in the Fort Whyte lakes, 1977-1978. Nauplii are included.

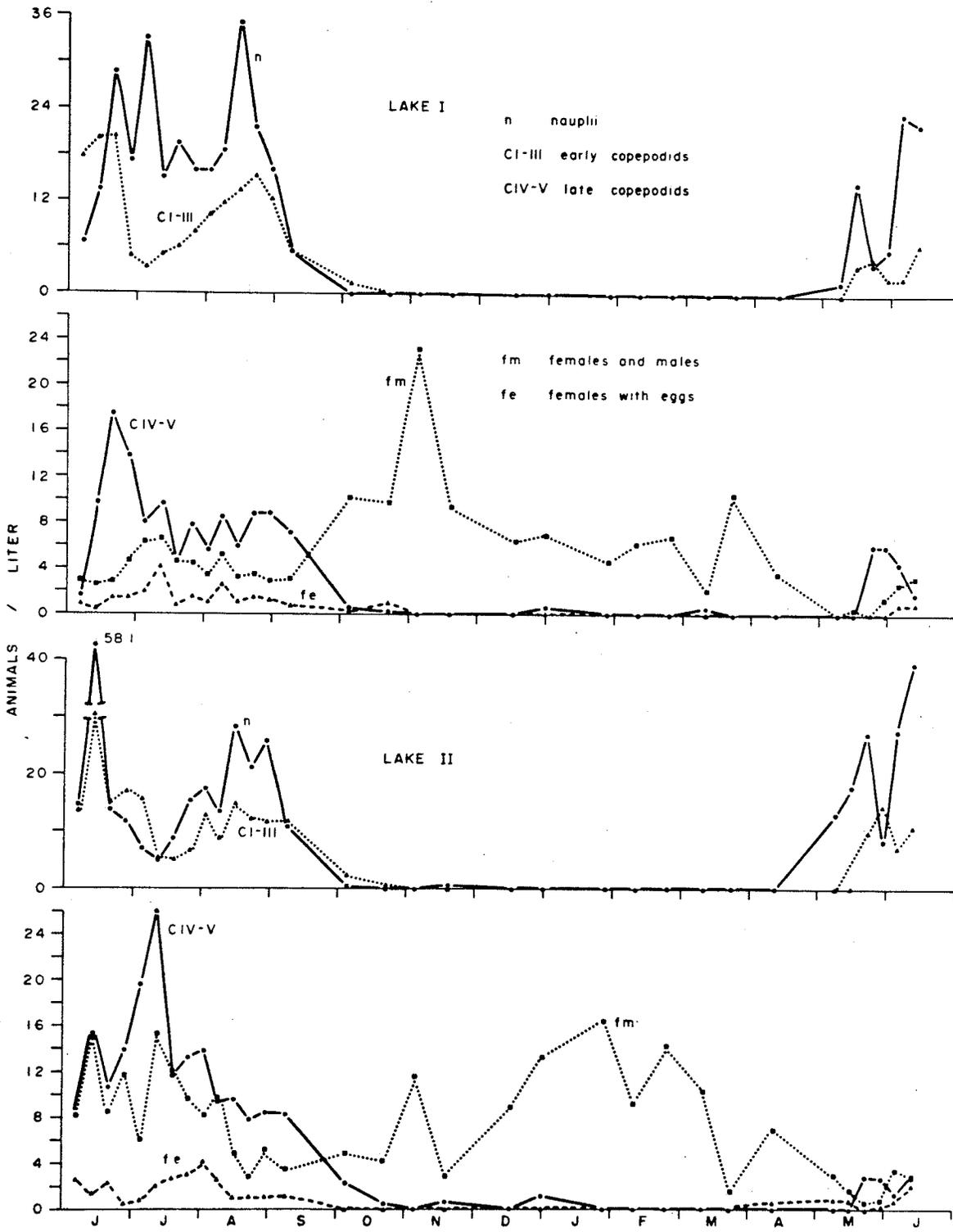


120 animals per liter (Fig. 7). The population of D. siciloides was slower to reach its summer maximum in Lake IV but by early July its numbers were comparable to the other lakes (Fig. 7). The abundance of this species was at a minimum during December, January, and February in Lake I and its numbers remained relatively lower in the following spring samples (Fig. 7).

By the time sampling had begun in 1977 in Lake I, the first naupliar pulse of D. siciloides had probably already occurred since the first samples in June contained early stage copepodids (Fig. 8). Three main pulses of nauplii were apparent in June, July, and August, though nauplii and females with eggs were found continually throughout the summer. The second copepodid peak occurred in August and by the last sampling date before freeze-up most of the survivors had become adults which overwintered with numbers at a maximum in November. These adults presumably produced the spring generation. Females were found again in May of 1978, though the presence of dislodged calanoid egg sacs in samples from April, 1978, indicated that reproduction probably began earlier under ice cover. The large mid-June copepodid maximum of 1977 was not repeated in 1978 (Fig. 8).

The life cycle of this diaptomid in the other three lakes varied only slightly from the one described in Lake I. In Lakes II, III, and IV, copepodid stages I-III were present

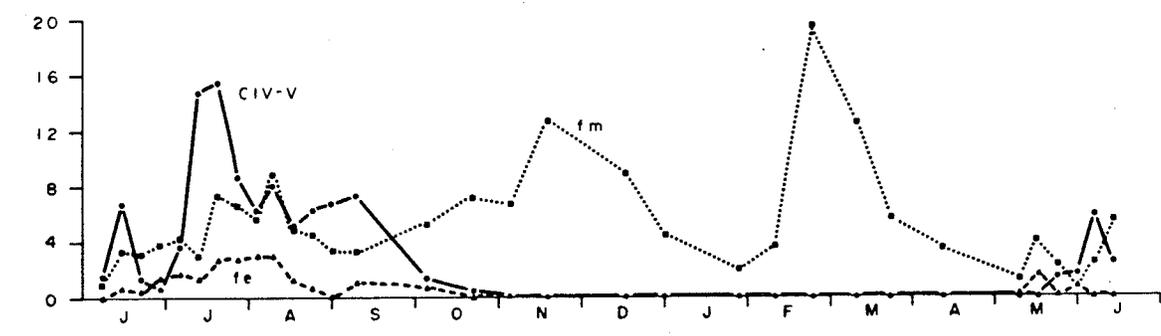
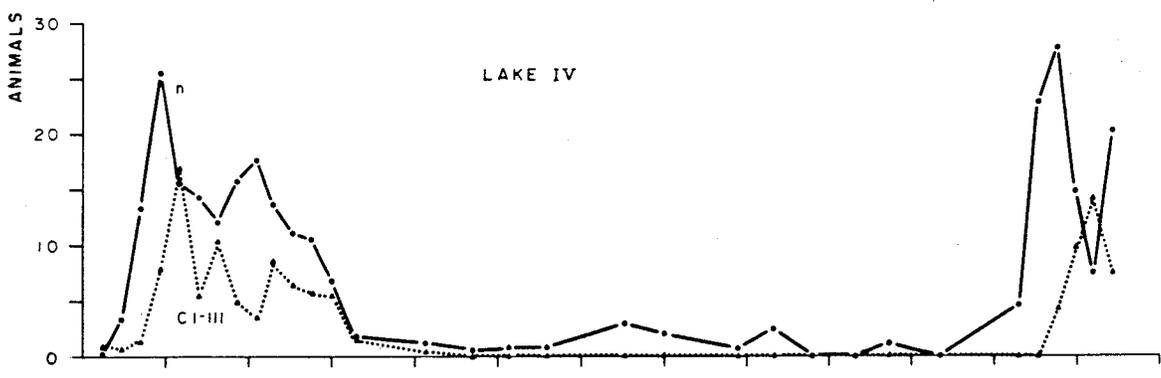
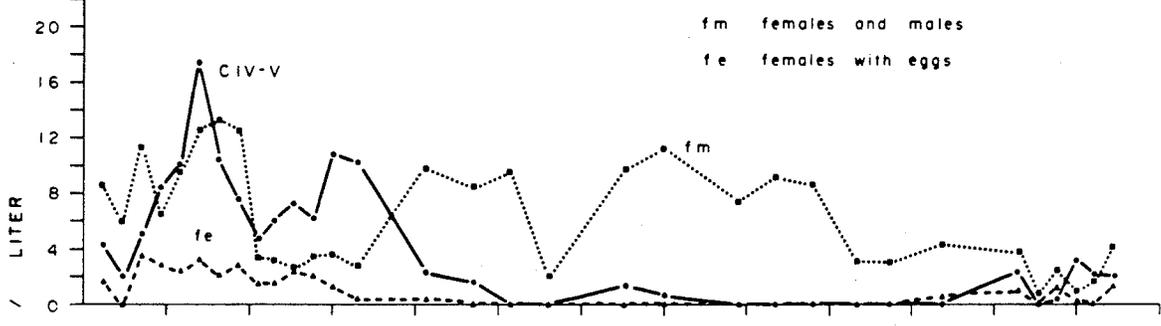
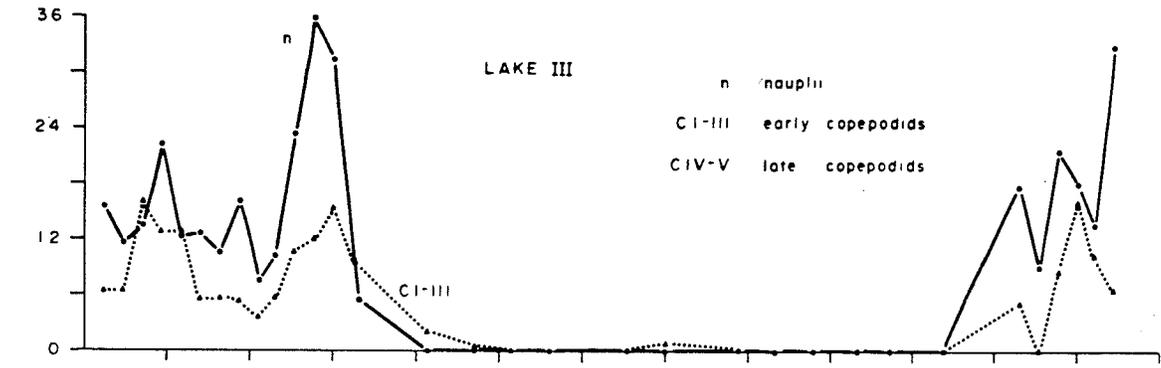
Figure 8. Seasonal changes in the abundance of life history stages of Diaptomus siciloides in Lakes I and II, 1977-1978.



in the first June samples so that, as in Lake I, at least two generations were produced during the summer. Two fairly distinct naupliar peaks occurred in June and August in Lake II and females with eggs were found in all summer samples (Fig. 8). Copepodid peaks were apparent in June and July, the first composed mainly of CI-III and the latter, by the second week of July, mainly CIV-V. The majority of copepodids found in August samples were CI-III stages and survivors of late-hatched animals overwintered as adults. The occasional CIV or V instar was found until January 1978. The highest number of adult females was found in January and February. Females bearing attached spermatophores were found in March 1978 but females with eggs were not found until April. Naupliar abundance peaked in May and again in June 1978 and by late May copepodid stages had reached a small peak.

Two small peaks in naupliar abundance in late June and early July of 1977 in Lake III preceded a third and larger peak in August (Fig. 9). The largest proportion of CI-III copepodids occurred in June and August and, in July and late August-September, CIV-V stages were more abundant. As in the other lakes, females with eggs were found regularly in summer thus suggesting overlapping generations. Adults overwintered and in April, 1978, females with eggs were present. By the first week in May early copepodid stages had begun to appear.

Figure 9. Seasonal changes in the abundance of life history stages of Diaptomus siciloides in Lakes III and IV, 1977-1978.



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In Lake IV, the largest concentration of nauplii occurred in late June and a less distinct peak in August (Fig. 9). Copepodids reached a maximum in July and early and late stages were equally abundant at this time. Unlike the other lakes, calanoid nauplii were sampled intermittently under ice cover in Lake IV. None of these nauplii appeared to reach the copepodid stage although copepodids were found in low numbers in Lakes I, II, and III. Unattached calanoid egg sacs were found in samples during March and April but females with eggs were not found until May of 1978. Nauplii reached a peak in May and young copepodids followed in early June.

The total numbers of Cyclops bicuspidatus thomasi (including nauplii apportioned according to the copepodid ratio) were generally greatest in Lake I in summer, 1977, with a maximum reaching 63.4 animals per liter by late autumn and early winter (Table 5). In Lake II this species was most abundant in late August and September, but was scarce during the earlier summer months. Numbers of C. b. thomasi in Lake III declined rapidly after June of 1977 and began to increase in autumn and winter samples (Table 5). In Lake IV, this species reached a maximum of 22.5 animals per liter on July 19 and a second maximum was reached in December (Table 5). This copepod increased in numbers dramatically in spring, 1978, the earliest and largest increase shown in Lake I.

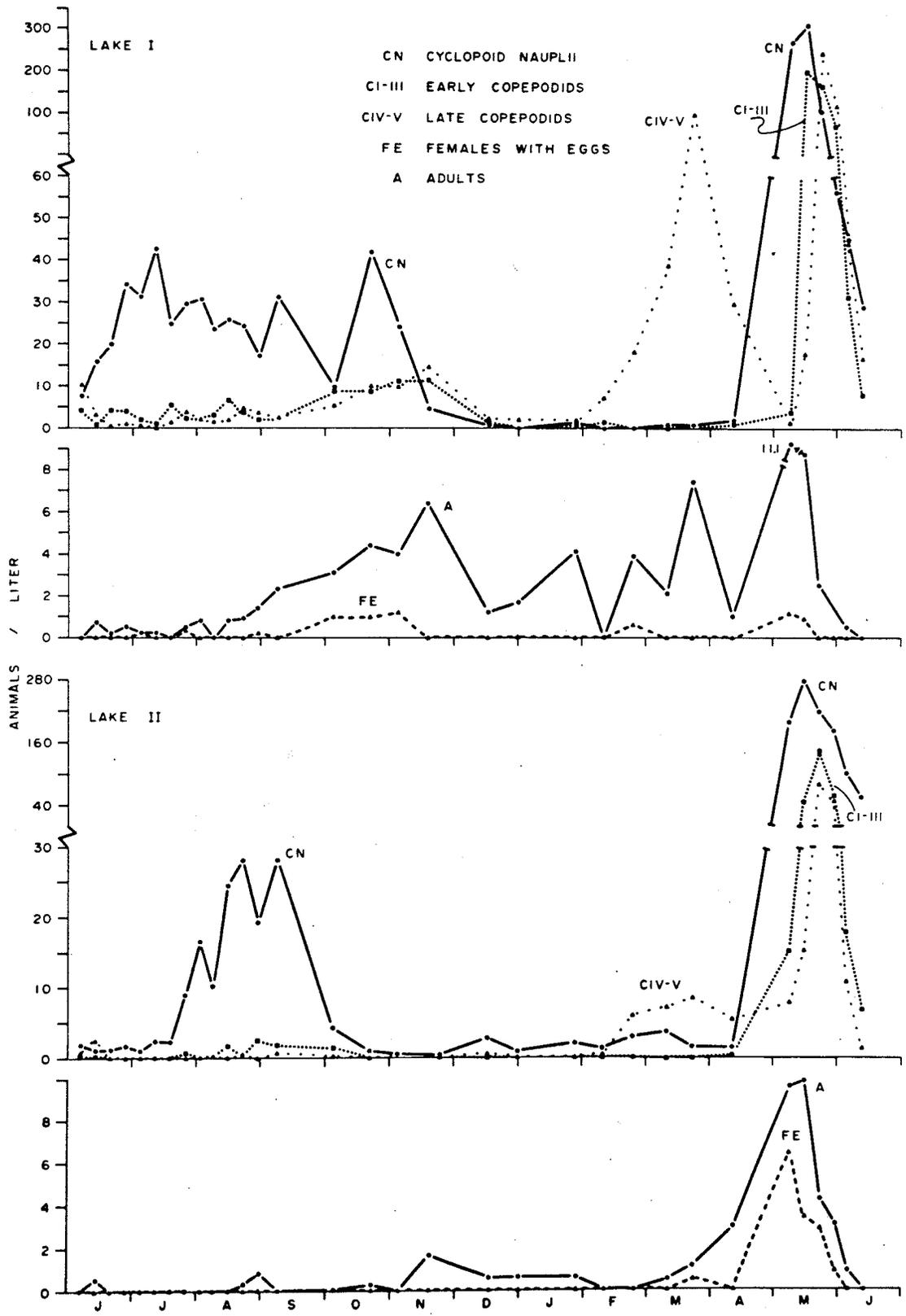
Table 5. Estimated total abundance of cyclopoid copepods in the Fort Whyte lakes, including nauplii (animals liter⁻¹). Cyclopoid nauplii were apportioned according to the copepodid ratio.

Date	Lake I			Lake II			Date	Lake III			Lake IV		
	C. b. thomasi	C. vernalis	M. edax	C. b. thomasi	C. vernalis	M. edax		C. b. thomasi	C. vernalis	M. edax	C. b. thomasi	C. vernalis	M. edax
June 6	21.7	0.3	0	2.8	0	0	June 7	18.3	12.1	0.3	9.2	4.9	1.4
13	14.6	6.7	0.7	4.4	0.4	0	14	4.2	3.8	4.0	4.9	0.8	0.5
20	15.0	13.4	0.2	1.4	0	0	21	5.8	4.7	6.8	3.5	3.5	2.2
27	18.4	25.2	3.8	1.7	0	0	28	11.8	2.9	10.4	2.0	0.6	4.7
July 4	10.0	23.0	3.3	0	1.4	0.3	July 5	4.5	5.7	8.7	2.1	0	6.6
11	2.3	52.8	3.1	0.6	1.9	1.6	12	2.9	12.4	13.1	8.0	5.3	4.8
18	16.3	23.6	2.0	0.9	0.8	2.6	19	0.5	9.4	10.0	22.5	6.1	5.6
25	20.8	21.8	1.3	3.7	3.7	3.6	26	1.2	14.2	11.0	10.8	5.6	5.4
Aug. 2	18.6	17.8	5.7	3.1	13.0	3.6	Aug. 3	0.5	10.3	9.5	7.2	8.1	13.3
8	13.0	13.8	8.7	2.5	4.7	8.8	9	1.2	1.7	4.8	7.2	6.5	10.1
15	20.5	19.2	5.6	5.3	11.9	18.8	16	2.4	6.5	4.9	10.9	5.4	9.2
22	21.4	15.8	4.5	2.9	21.5	11.8	23	3.7	3.0	6.5	10.6	2.1	6.2
29	16.5	10.2	4.0	6.7	18.9	10.7	30	2.5	2.0	9.2	5.4	3.3	6.7
Sept. 8	26.8	14.9	5.3	9.1	19.3	11.0	Sept. 9	9.0	3.0	3.1	6.6	3.7	6.0
Oct. 4	26.4	1.3	0.7	4.5	2.8	1.2	Oct. 4	7.1	3.0	2.1	3.0	1.6	1.0
21	63.4	3.7	0	0.6	1.7	0	21	6.8	4.1	0.4	2.8	3.2	0.3
Nov. 4	50.6	0.6	0	1.7	0	0	Nov. 4	4.8	7.1	0	4.8	1.9	0
18	37.7	0	0	2.9	0.6	0	18	3.9	0	0	13.5	0	0
Dec. 16	4.7	0	0	3.9	0	0	Dec. 16	24.4	0	0	33.1	8.1	0
30	5.2	0	0	1.7	0	0	30	13.3	0	0	14.9	3.8	0
Jan. 27	7.6	0	0	2.8	0	0	Jan. 27	8.0	0	0	17.5	3.4	0
Feb. 10	8.4	0	0	2.0	0	0	Feb. 10	14.2	0	0	20.6	0.9	0
24	22.6	0	0	9.2	0	0	24	6.2	0	0	19.0	0	0
Mar. 10	41.4	0	0	11.5	0	0	Mar. 10	5.1	0	0	19.7	0	0
22	106.0	0	0	11.8	0	0	22	4.3	0	0	12.1	0	0
Apr. 11	33.5	0	0	10.5	0	0	Apr. 11	16.6	0	0	31.4	0	0
May 8	288.8	0.3	0	237.8	1.0	0.5	May 9	167.7	0	0.4	91.1	5.4	0.2
15	543.8	0.5	0.5	353.6	0	0	16	176.2	0.2	0	253.5	0.5	0.5
22	524.8	1.0	0	456.6	0	0.2	23	337.5	1.2	0.4	321.8	0.9	0
20	249.5	0.5	0	297.6	0	0.5	30	224.0	0.8	0.4	231.1	1.9	0.2
June 5	121.7	0	0.5	131.2	0	0.5	June 6	120.4	0	0.4	158.3	0.2	0
12	53.7	0	0.5	64.5	0	0	13	54.9	0	0	67.9	0	0

In Lake I, cyclopoid nauplii were found in all summer samples, the largest peaks occurring in July and autumn samples (Fig. 10). The majority of C. b. thomasi copepodids after the first June sample until mid-August were CI-III stages. In August more CIV-V stages were found and by late fall both young and old copepodids reached maximum abundance. The maximum number of adults were found in late November. This species was rare in December and January at which time oxygen was depleted in this lake. In subsequent winter samples there was a dramatic rise in the number of CIV-V copepodids which reached a maximum of 97.9 animals per liter in late March. Since previous samples did not contain large numbers of females with eggs, nauplii, or even early copepodid stages, it is possible that these copepodids had emerged from diapause or that they overwintered in or near the bottom waters and thus avoided capture. Whatever the method of overwintering, these copepodids returned to the water column while the lake was still ice-covered and developed into adults to produce the large spring bloom of nauplii and the subsequent CI-III copepodid maximum (Fig. 10).

In June and July of 1977 in Lake II, C. b. thomasi copepodids and adult females were present in low numbers. Cyclopoid nauplii did not reach a maximum until August and September (Fig. 10). Low numbers of C. b. thomasi adults

Figure 10. Seasonal changes in the abundance of life history stages of Cyclops bicuspidatus thomasi in Lakes I and II, 1977-1978. Nauplii of Cyclops vernalis and Mesocyclops edax are included.



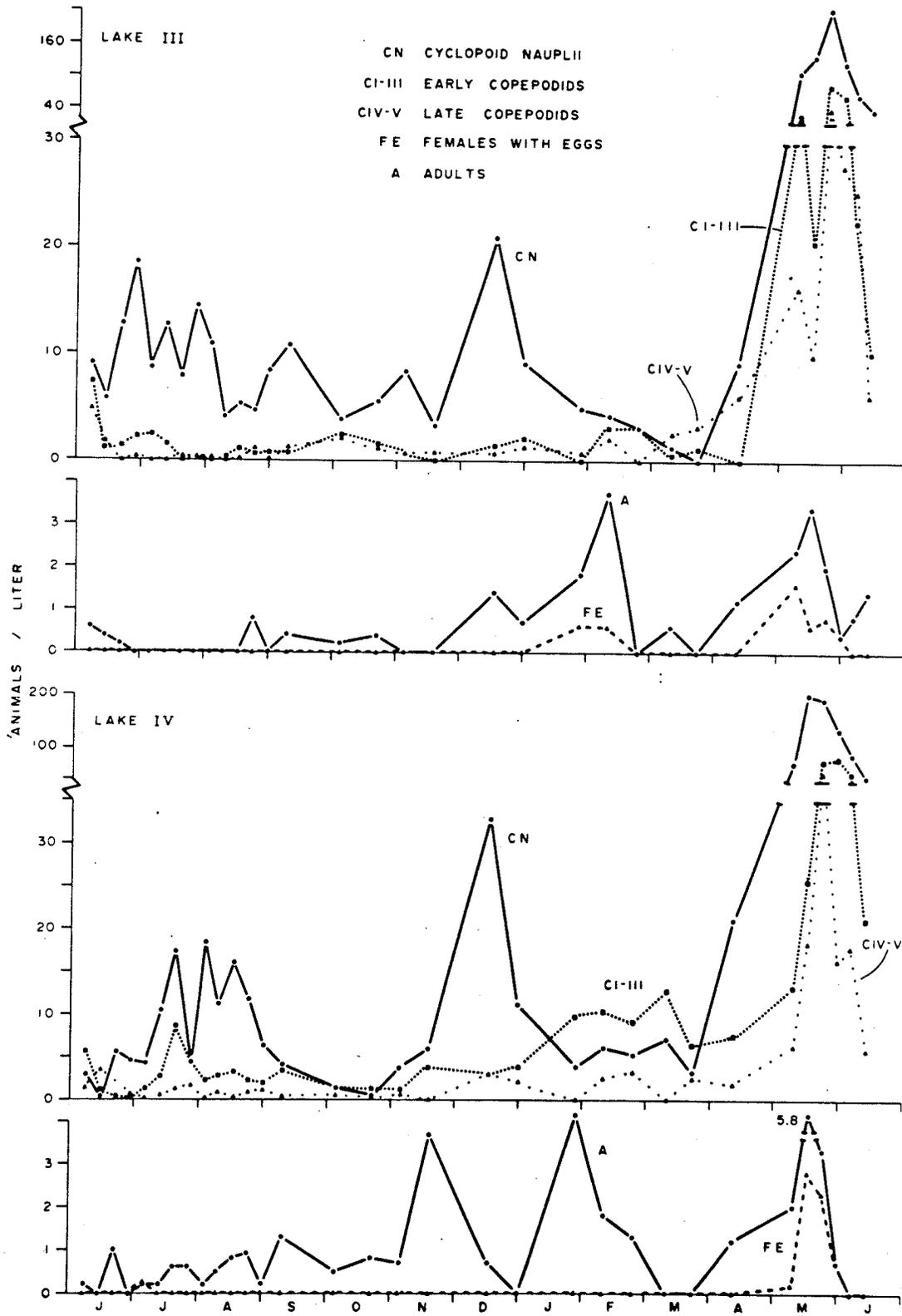
and copepodids as well as cyclopoid nauplii were found under ice cover. In February, March, and April, CIV-V copepodids appeared, though in fewer numbers than in Lake I. These presumably moulted to adults and produced the spring pulse of nauplii.

Cyclopoid nauplii were produced throughout the summer in Lake III. Adults of C. b. thomasi were most abundant in autumn and winter and females with eggs were found under ice cover (Fig. 11). The largest peak of nauplii occurred in December followed by an increase in copepodid numbers. Females with eggs and males were found in January and February and it seems most likely that these adults produced the spring naupliar peak.

Cyclopoid naupliar abundance was high in July and August in Lake IV and declined to a minimum in October of 1977 (Fig. 11). Copepodids of C. b. thomasi were more abundant in Lake IV than in Lakes II and III in summer, 1977, and reached a maximum on July 19. Adults of C. b. thomasi increased in numbers in late summer and autumn and probably produced the nauplii sampled in December. Nauplii had reached the copepodid stages by February and March in Lake IV and these copepodids developed into adults to produce the spring generation.

The total abundance of Cyclops vernalis (including cyclopoid nauplii apportioned according to the copepodid ratio)

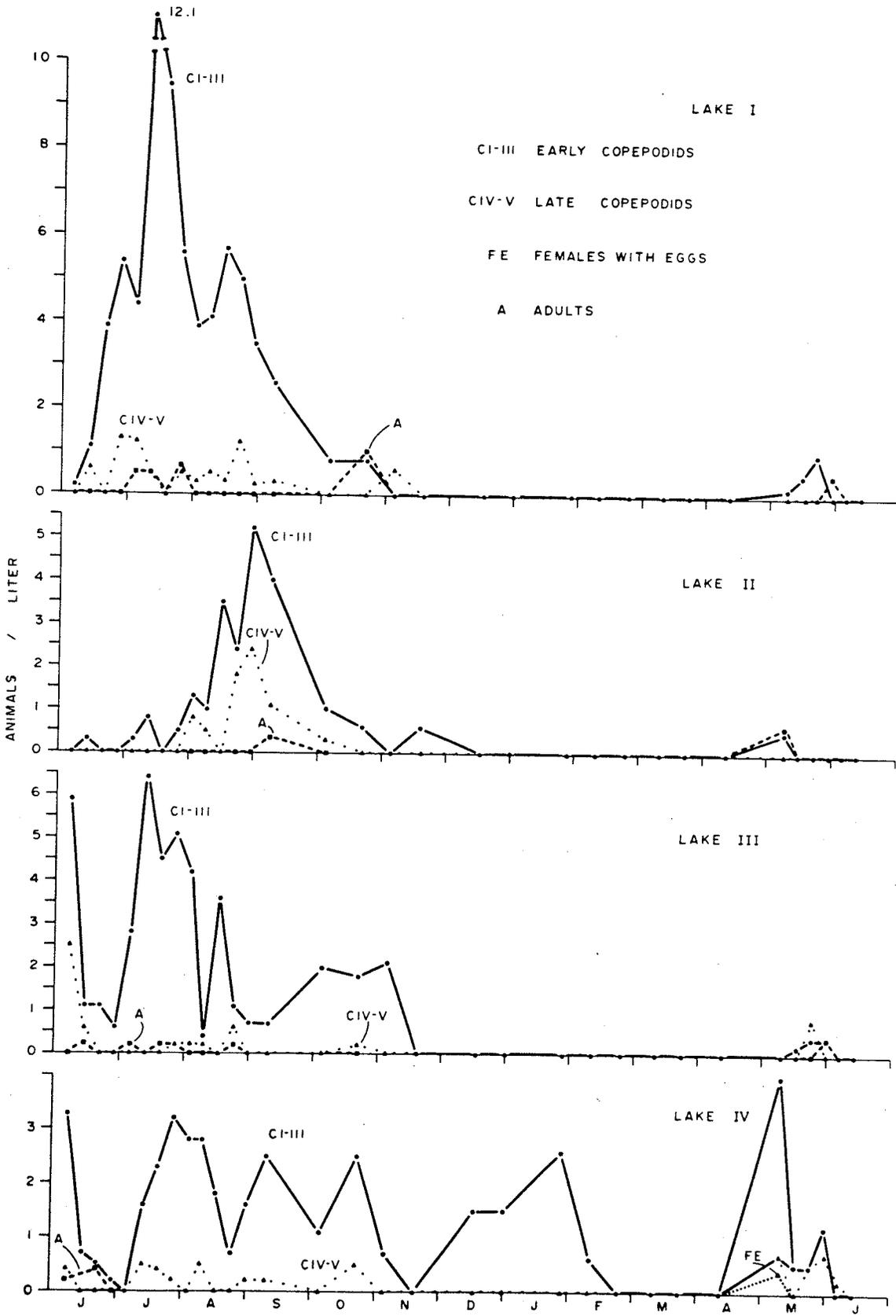
Figure 11. Seasonal changes in the abundance of life history stages of Cyclops bicuspidatus thomasi in Lakes III and IV, 1977-1978. Nauplii of Cyclops vernalis and Mesocyclops edax are included.



reached a maximum of 52.8 animals per liter in July of 1977 in Lake I and declined thereafter (Table 5). The maximum concentration of this species in Lake II (21.5 animals liter⁻¹) was sampled six weeks after the maximum in Lake I (Table 5). C. vernalis was not found in winter in Lakes I and II. The summer maximum of C. vernalis in Lake III occurred in July as in Lake I, but numbers reached only 14.2 animals per liter. This copepod remained below 10 animals per unit volume at all times in Lake IV but it was relatively more abundant in winter samples than in the other lakes (Table 5).

Copepodids of C. vernalis were most abundant in Lake I in July and August. Few of these survived to adulthood as shown by the small numbers of adults in July and in October and November (Fig. 12). Small numbers of copepodids and adults appeared the following spring. Copepodids reached a maximum in late August in Lake II but the only adult was found in March samples under the ice (Fig. 12). Peaks in the number of copepodids were found in June and July in Lake III and adults of C. vernalis were found periodically throughout the summer months in 1977 and on May 30, 1978 (Fig. 12). Copepodids of this species were found in low numbers in Lake IV on the majority of sampling dates and were more common in 1978 samples than in the other lakes (Fig. 12). Small numbers of adults in this lake were sampled in June of 1977 and May, 1978.

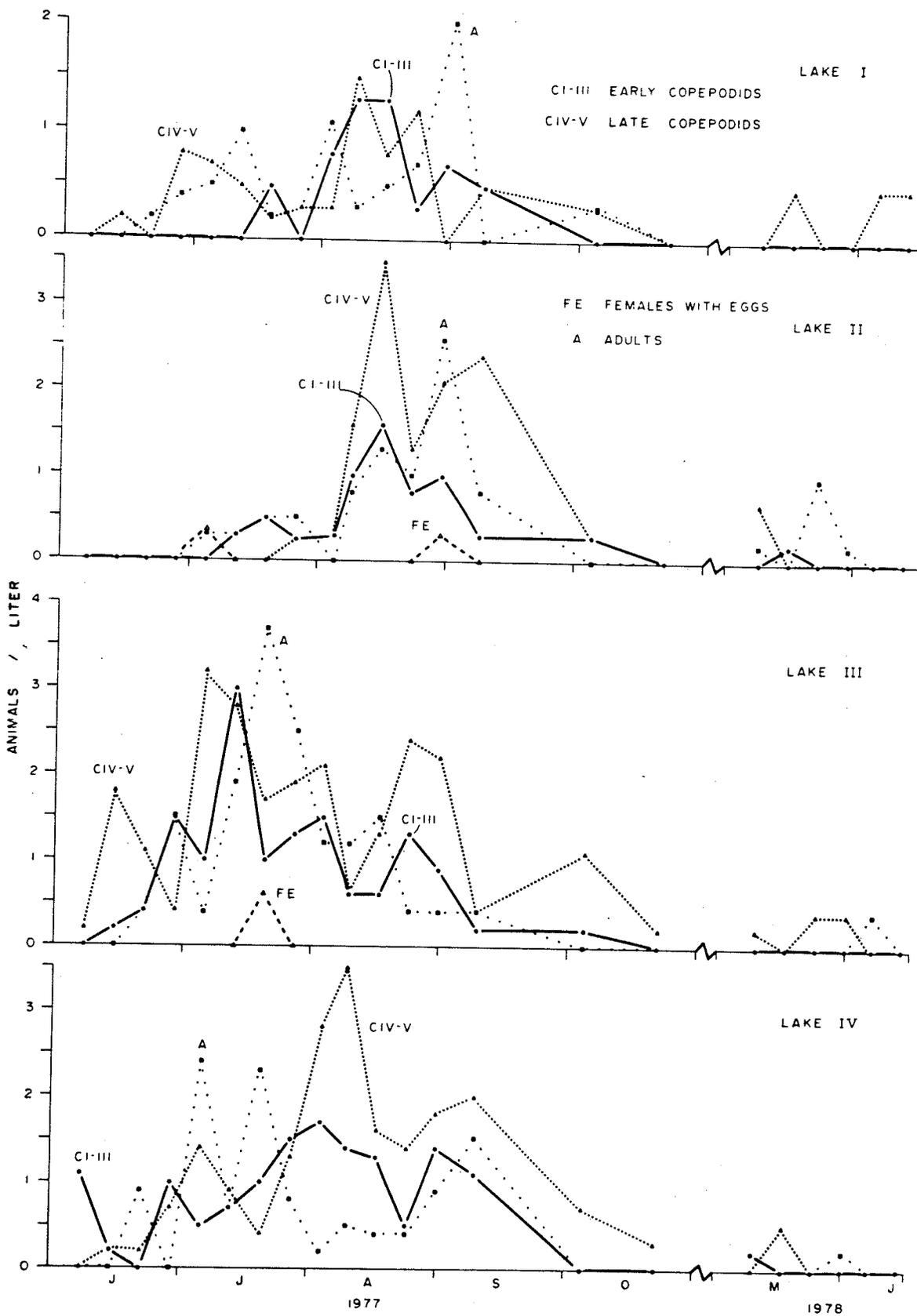
Figure 12. Seasonal changes in the abundance of life history stages of Cyclops vernalis in the Fort Whyte lakes, 1977-1978.



The total numbers of Mesocyclops edax per liter (including apportioned nauplii) were lowest in Lake I with a maximum of 8.7 animals per liter on August 8 (Table 5). Maximum numbers of this species also occurred in August in Lake II and Lake IV. M. edax was most prevalent in July in Lake III, the maximum abundance of 13.1 animals per liter preceded that in the other lakes by at least three weeks (Table 5).

The seasonal cycle of M. edax was similar in Lakes I and II. By the time sampling had begun in June of 1977, adult females and males and late stage copepodids were present in Lake I (Fig. 13). By late August the number of adults had reached a maximum. This cyclopoid was not sampled during winter but copepodids appeared again in May of 1978. The same basic cycle occurred in Lake II except that the first copepodids did not appear until July (Fig. 13). Adults were most prevalent in August. Copepodids and adult males were found the following spring. The maximum abundance of copepodids occurred earlier in Lake III, in July (Fig. 13). Adults reached a maximum in late July and females with eggs were found at this time. Adults were most abundant in July in Lake IV, and copepodids reached a maximum in August (Fig. 13). This species was sampled more frequently throughout the summer in Lakes III and IV.

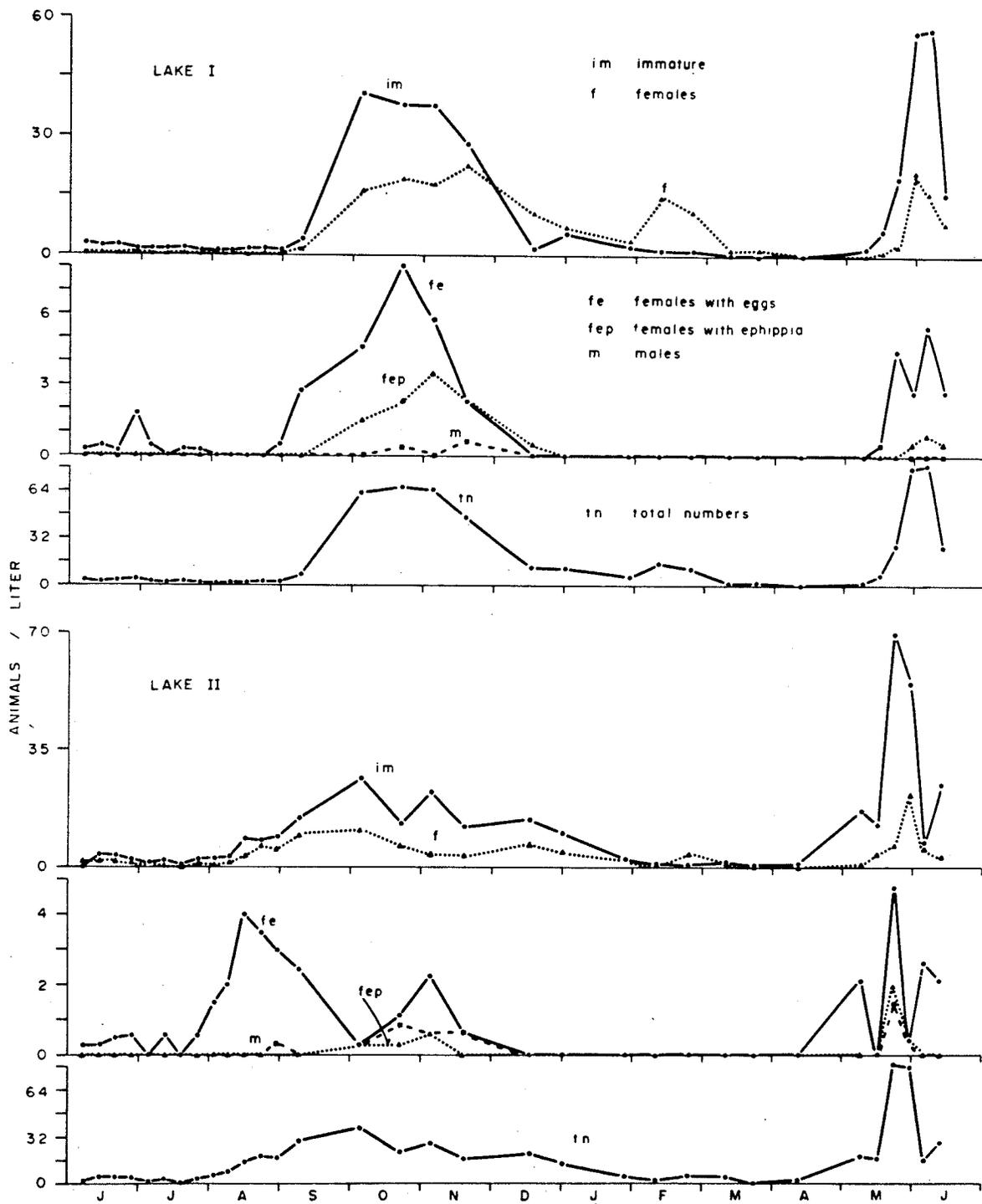
Figure 13. Seasonal changes in the abundance of life history stages of Mesocyclops edax in the Fort Whyte lakes, 1977-1978.



Daphnia galeata mendotae was rare in early summer samples in all the lakes in 1977 but was relatively more abundant in Lakes I and II. Two peaks in autumn, 1977, and the spring of 1978 in the estimated abundance of D. g. mendotae were recorded in Lake I (Fig. 14), the first of which greatly exceeded the maximum abundance in any of the other lakes. The large increase in the number of immature individuals in October and November in Lake I resulted either from a hatch of resting eggs or from the few females with eggs found in samples from August to mid December (Fig. 14) or from both sources. Concurrent with this population increase, females with ephippia and males were produced. The population declined in December and by February most of the animals had become adults. Another maximum of immature individuals occurred in the spring and females with ephippia and males were produced in late May and early June. After the ice broke in 1978, the shorelines of the lakes were littered with ephippia and it is not known whether the spring peak in numbers of this cladoceran was a result of hatching of these eggs or the product of the overwintering females. The autumn maximum in estimated total numbers of D. g. mendotae in Lake II (Fig. 14) followed a progressive increase in numbers throughout the August samples, a pattern unlike the other lakes. The maximum number of females with eggs occurred



Figure 14. Seasonal changes in the abundance of Daphnia
galeata mendotae in Lakes I and II, 1977-1978.

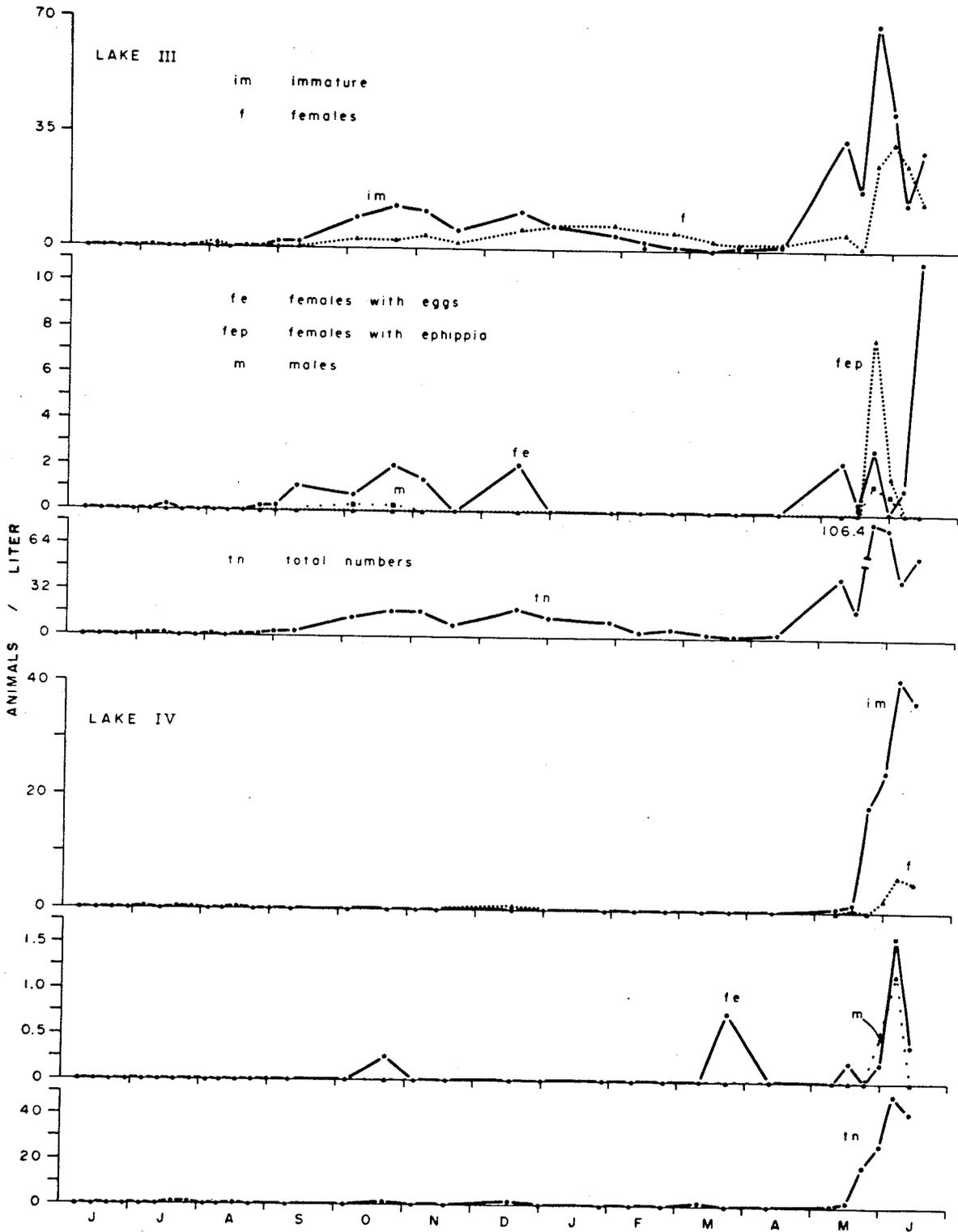


in mid-August and males were found in late August. Females with ephippia and males were sampled in October and November during which time immature individuals were most abundant. More females with eggs were found in Lake II than in Lake I prior to the maximum number of immature animals, thus the fall generation in this lake was most likely a product of subitaneous eggs rather than ephippia. After a decline in numbers in the early part of 1978, immature individuals began to increase in early May and reached a maximum of 70.0 animals per liter by the end of that month (Fig. 14). Males and ephippial females were found in late May.

The autumn maximum of this species in Lake III was composed of far fewer individuals, yet the maximum total numbers of D. g. mendotae in this lake in spring (106.4 animals per liter) exceeded that found in both Lakes I and II (Fig. 15). Males were produced in October though no ephippial females were found during the autumn maximum. Females overwintered and in early May immature individuals increased in numbers. Ephippial females and males were most prevalent in late May, 1978.

This cladoceran was rare in all samples taken in Lake IV (Fig. 15) until the spring of 1978 where its estimated total numbers increased rapidly during the first week of June, as in Lake I. This spring maximum occurred two weeks earlier in Lakes II and III. Unlike the other lakes,

Figure 15. Seasonal changes in the abundance of Daphnia galeata mendotae in Lakes III and IV, 1977-1978.



females with eggs were found under ice cover in March in Lake IV, prior to the spring bloom (Fig. 15). By early June immature individuals reached approximately 40 animals per liter. Ehippial females were not sampled in spring but males appeared in late May and early June.

Daphnia parvula was restricted to summer and fall samples in each of the lakes. The population in Lake I appeared to be dicyclic with peaks in abundance in early and late summer, but females with eggs were found continuously during the summer months (Fig. 16). Males were recorded in autumn during which time the species disappeared from the lake and very few individuals were found the following spring.

The population in Lake II also showed a large June maximum but a second autumnal increase in numbers was not evident (Fig. 16). The number of immature and female animals declined rapidly in early July and remained relatively constant in late July and August. Unlike the other lakes, an ehippial female was found in June and a lone male in July in Lake II. By autumn this species was scarce and males were not recorded in September and October.

D. parvula was much less abundant in Lakes III and IV; the major peak in total numbers occurred in July and a smaller one in autumn samples (Fig. 17). The maximum number of immature stages, females, and females with eggs were recorded in June and July in Lake III after which the population declined (Fig. 17). Males appeared in October

Figure 16. Seasonal changes in the abundance of Daphnia parvula in Lakes I and II, 1977.

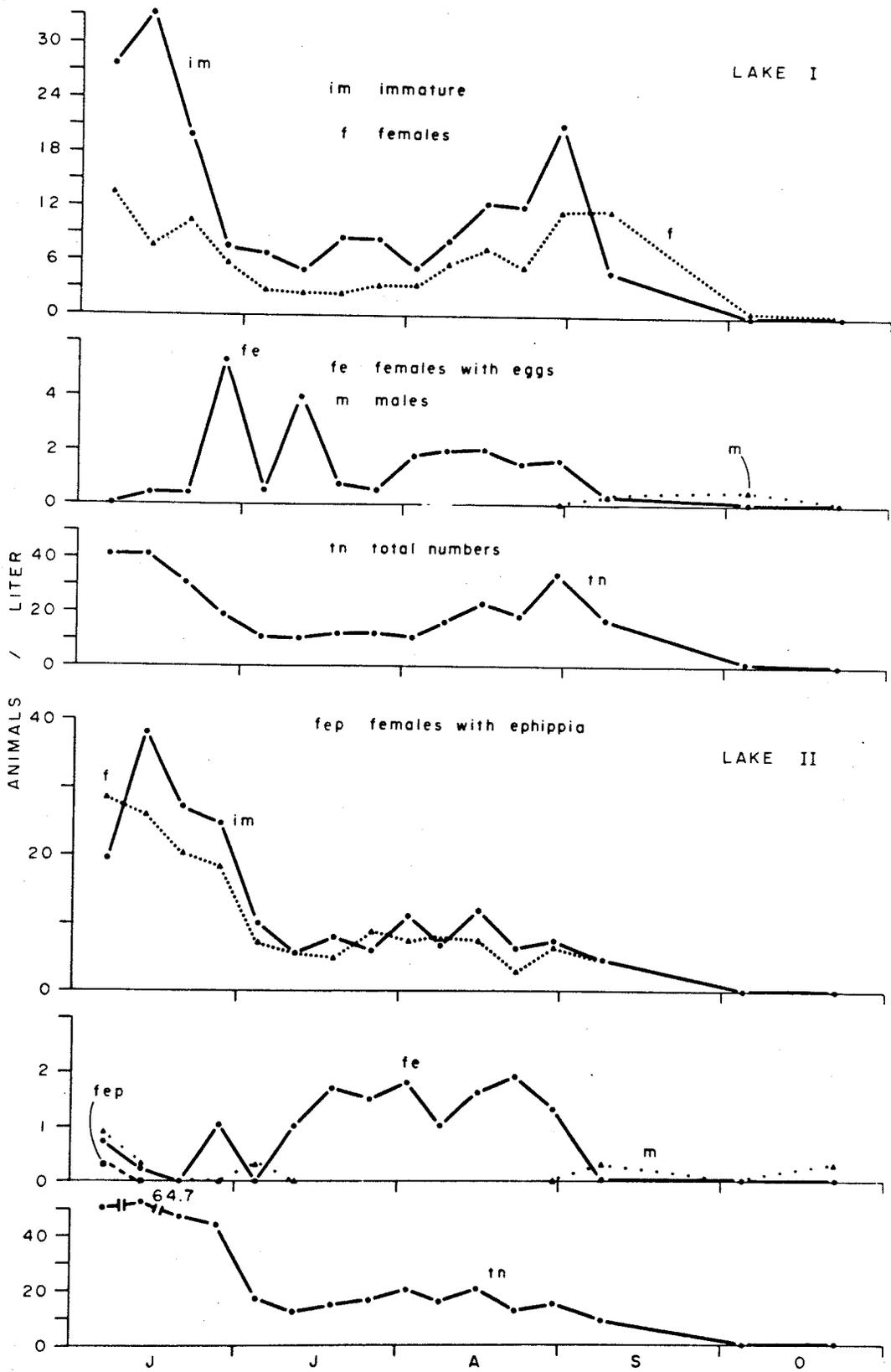


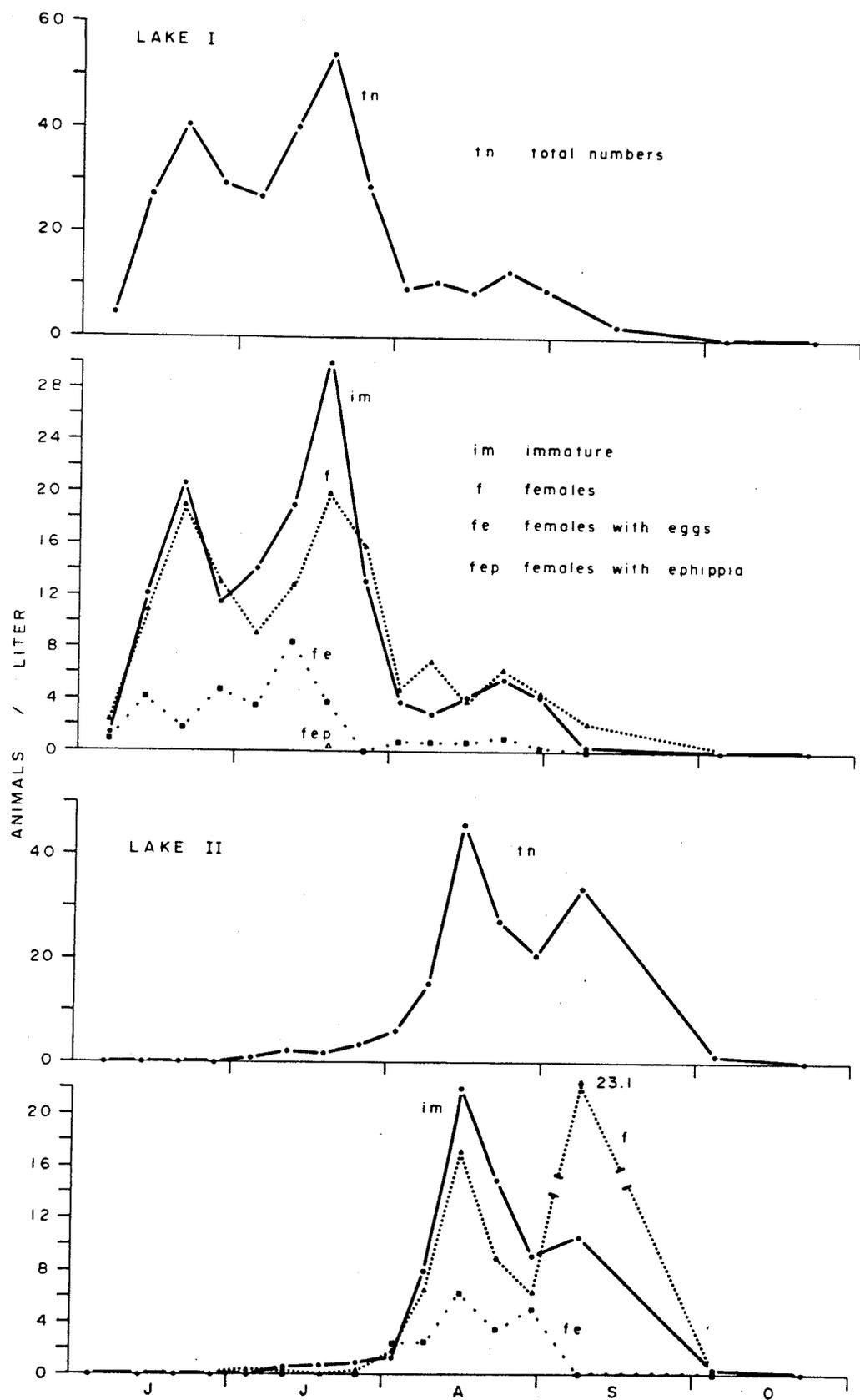
Figure 17. Seasonal changes in the abundance of Daphnia parvula in Lakes III and IV, 1977.

but no ehippial females were recorded. This cladoceran was absent from 1978 samples in this lake. D. parvula appeared to be monocyclic in Lake IV with a single maximum of immature animals in late July about five weeks later in the season than in Lakes I and II (Fig. 17). Females and females with eggs were most abundant at this time. Both males and ehippial females were found in October and November. The population declined slowly; individuals were found as late as December and January. Few of these animals survived the winter since this species was extremely rare in spring samples from Lake IV.

The abundance and timing of the seasonal cycle of Ceriodaphnia lacustris differed considerably among the four lakes except for the fact that in each lake it was found only during the ice free period of 1977. Lake I supported the largest population of this species, with the maximum number of immature stages and females in late June and late July (Fig. 18).

The first appearance of this species in Lake II were females in July but the maximum number of immature individuals was not reached until mid-August, two months after the first maximum in Lake I (Fig. 18). Females were most abundant in September, and by late October none remained.

Figure 18. Seasonal changes in the abundance of Ceriodaphnia lacustris in Lakes I and II, 1977.



The population maximum of C. lacustris in Lake III also occurred in August but the estimated number of animals per liter was comparatively much lower (Fig. 19). Females with eggs were first found in late July in Lake III, and immature individuals were most abundant in August (Fig. 19), as in Lake II. Few of these animals seemed to reach maturity and by late August this species was rare. The only male was found in Lake III in October.

C. lacustris existed in very low numbers in Lake IV, the total number of animals never exceeded five per unit volume (Fig. 19). Immature individuals were first recorded on July 12 and females were most prevalent in August samples.

Bosmina longirostris demonstrated two midsummer peaks in abundance in June and July in Lake I and the estimated total number of animals exceeded that found in the other lakes (Fig. 20). Females with eggs were most prevalent at that time. Numbers per liter declined after July and remained low until this species disappeared from samples in late November. In Lakes II and III, immature and female individuals were most common in August and September. In Lake II, egg bearing females were found in July and August (Fig. 20). In Lake III, females with eggs were found sporadically throughout the summer and autumn samples and reappeared along with immature individuals in early May of 1978 (Fig. 20). B. longirostris was found

Figure 19. Seasonal changes in the abundance of Ceriodaphnia lacustris in Lakes III and IV, 1977.

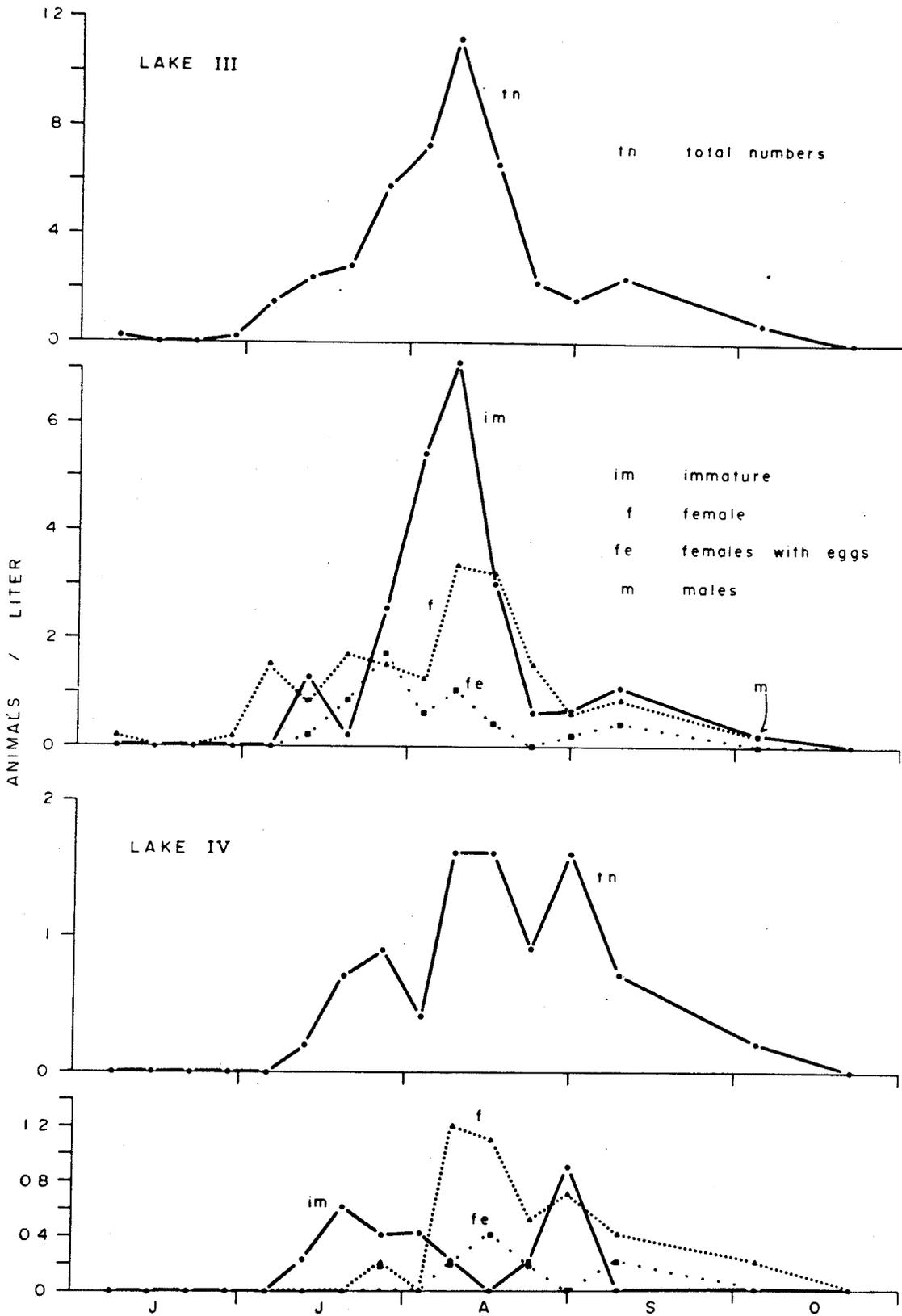
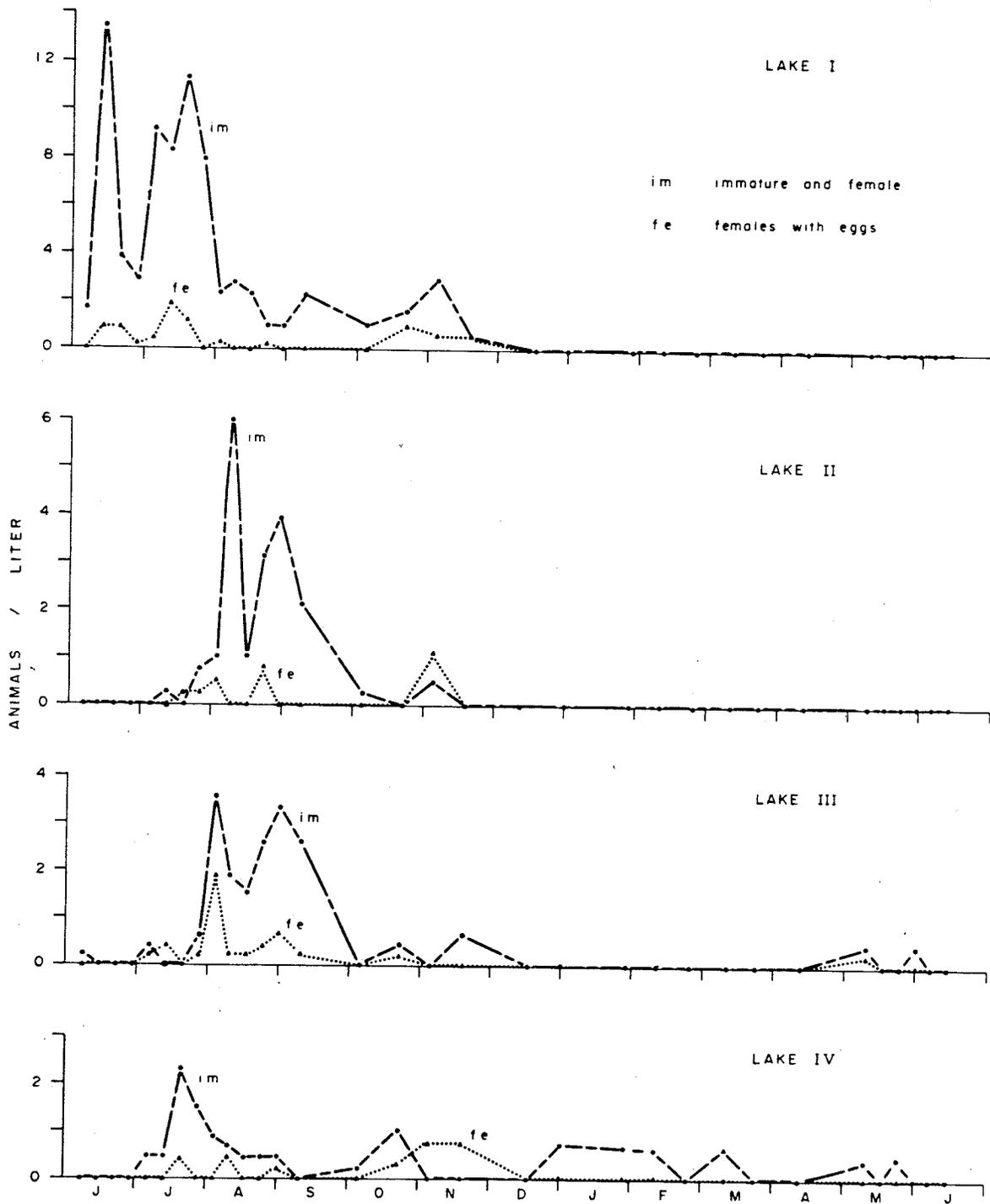


Figure 20. Seasonal changes in the abundance of Bosmina
longirostris in the Fort Whyte lakes, 1977-1978.



year round in Lake IV, always at low numbers (Fig. 20). Immature individuals were most abundant in July and egg bearing females were also found at that time. Females with eggs were sampled again in November and small numbers of immature bosminids were found only in this lake in December, January, and February. Females with eggs occurred again in March and immatures were sampled in May, 1978. Males and ehippial females of this species were never recorded in any of the lakes.

The relative abundance or proportion of the total plankton population represented by a particular taxonomic group varied from lake to lake in different seasons (Table 6). On an annual basis and throughout the seasons, Lake I had the lowest percentage of calanoids (as represented by D. siciloides) while the other lakes had a higher and generally similar relative abundance of this group. From the summer of 1977 through to the following spring, the percentage of cyclopoids in each community increased to the point where they represented over three-quarters of the entire plankton assemblage in Lakes I and IV by the spring of 1978. Lake II generally had the lowest percentage of this taxonomic group, while Lakes I and IV had the highest relative abundance. The greatest percentage of cladocerans occurred in Lakes I and II (Table 6) in summer and autumn samples. Cladocerans never represented a large proportion of the plankton in Lake IV.

Table 6. Annual and seasonal mean relative abundance (percent) of the major taxonomic groups in the Fort Whyte lakes, 1977-1978.

Lakes	Calanoids				Cyclopoids				Cladocera			
	I	II	III	IV	I	II	III	IV	I	II	III	IV
Annual	22.0	37.8	36.5	37.9	45.4	28.3	36.9	51.7	32.2	33.7	26.7	10.4
Summer	33.7	51.4	55.2	54.9	28.4	10.8	24.1	33.7	37.8	37.8	20.7	11.4
Autumn	13.8	19.5	33.9	39.8	39.8	16.5	25.8	33.2	46.3	64.0	40.3	27.1
Winter	17.0	39.8	27.6	30.7	50.9	28.1	39.0	65.5	32.1	32.1	33.3	3.9
Spring	9.2	14.1	13.4	12.1	76.1	73.6	65.0	77.0	14.7	12.3	21.6	10.9

The number and kind of dominant species in the Fort Whyte lakes which comprised more than ten percent of the total population (Patalas 1964) varied between one and five on various sampling dates. On an annual basis, a trio of dominants, one diaptomid, one cyclopoid, and one cladoceran was the most common assemblage in Lakes I and III. In Lake II a combination of one calanoid and one cladoceran dominated equally as often as one calanoid, one cyclopoid, and one or more cladocerans. In Lake IV, on the majority of sampling dates, one calanoid and one to two cyclopoids were dominant.

D. siciloides was dominant in all the lakes throughout most of the sampling year, but the percent composition of this species in Lakes II, III, and IV was similar and considerably higher than in Lake I (Fig. 21). Except for a small peak in relative abundance in winter samples, there was a general decreasing trend in percent abundance of this species and by May, 1978 it had dipped below the dominance level in Lakes I, II, and IV (Fig. 21).

C. b. thomasi was the most frequently dominant cyclopoid in Lake I and only during four sampling dates in June and July of 1977 did it represent less than ten percent of the total population (Fig. 22). In Lake II, this copepod was not dominant in summer, 1977 and was less well represented in winter samples than in the other lakes (Fig. 22). C. b. thomasi was dominant on two sampling dates in June of

Figure 21. Relative abundance (percent) of Diaptomus siciloides in the Fort Whyte lakes, 1977-1978.

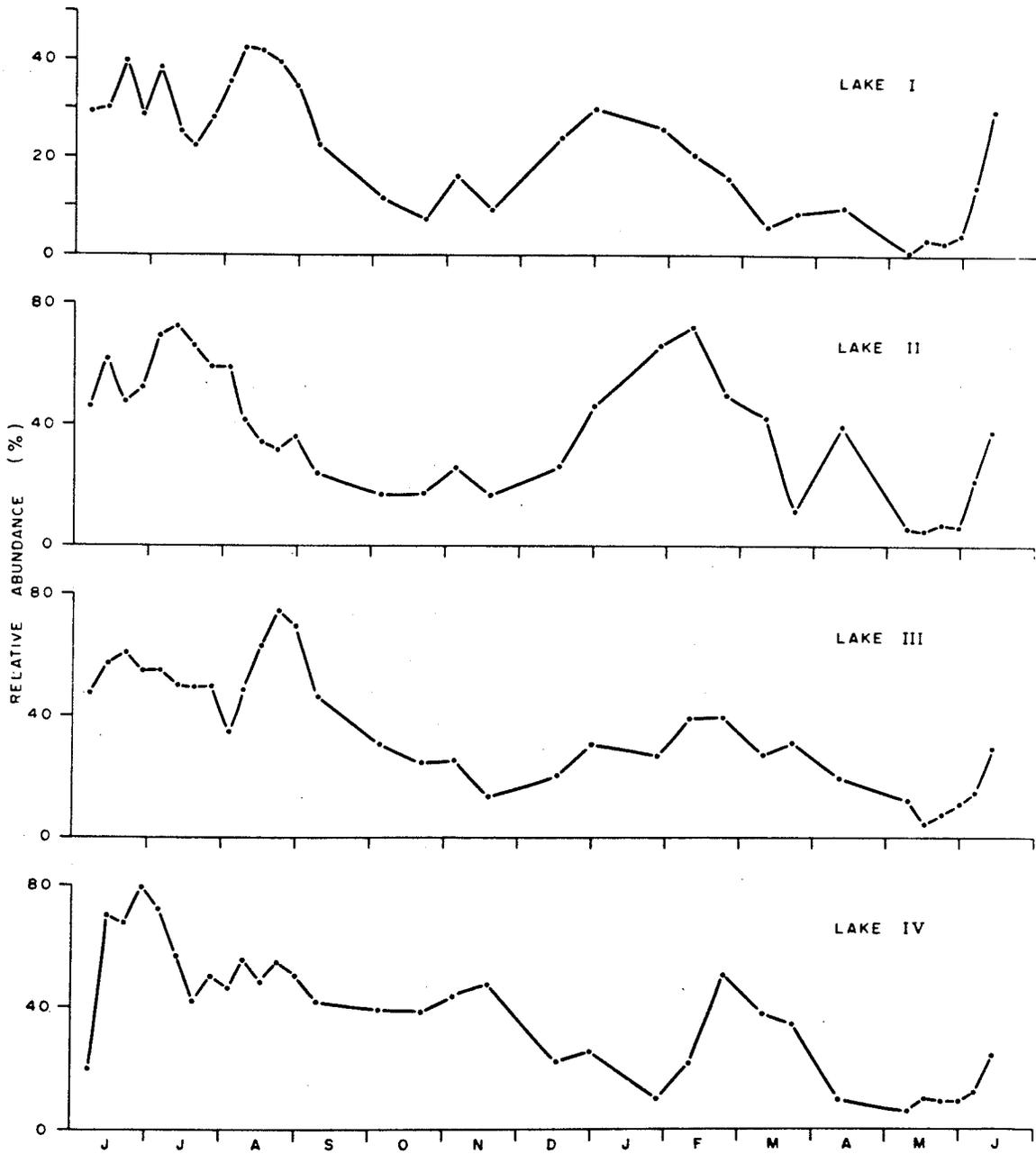


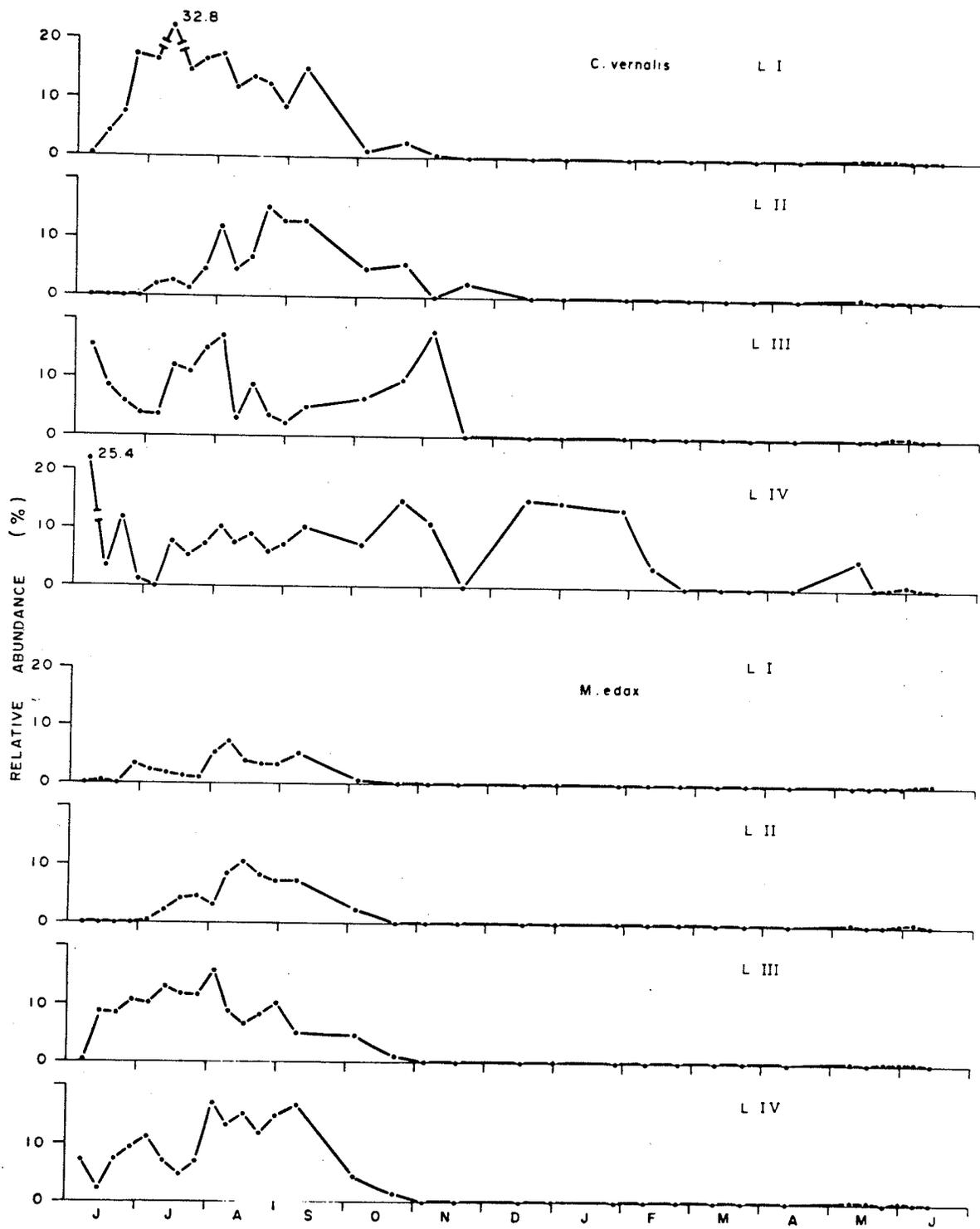
Figure 22. Relative abundance (percent) of Cyclops
bicuspidatus thomasi in the Fort Whyte lakes,
1977-1978. Apportioned nauplii are included.

1977 in Lake III and on each date after August (Fig. 22). This species was dominant on all but five sampling dates in Lake IV and represented over 50 percent of the total plankton population in most of the winter samples (Fig. 22). In spring, 1978, C. b. thomasi comprised well over 50 percent of the total population in all four lakes with Lake I having the highest proportion (over 90 percent) in March, April, and most of May.

C. vernalis was a consistent dominant in Lake I in July and August of 1977 (Fig. 23) and codominant with C. b. thomasi on nine occasions in summer and autumn. This copepod was dominant on only four sampling dates in August and September, 1977 in Lake II (Fig. 23) and on six dates in summer and autumn in Lake III. C. vernalis was dominant on only three sampling dates in June and August in Lake IV (Fig. 23) but was a frequent codominant with C. b. thomasi from September, 1977, to January of 1978, unlike the other lakes where the latter species was the common cyclopoid winter dominant.

M. edax never represented more than ten percent of the total population in Lake I and was dominant on only one occasion in August in Lake II (Fig. 23). This species was mainly dominant in Lake III from June 28 to August 3, and on July 5 and throughout August and September in Lake IV (Fig. 23).

Figure 23. Relative abundance (percent) of Cyclops vernalis and Mesocyclops edax in the Fort Whyte lakes, 1977-1978. Apportioned nauplii are included.



The seasonal succession of dominant cladocerans was different in each of the lakes. In Lake I, the dominant cladoceran species varied monthly during the summer season. In three June samples from this lake both D. parvula and C. lacustris were dominant, in July only C. lacustris was dominant and in August and September D. parvula was the only dominant cladoceran (Fig. 24). By October, D. g. mendotae had replaced these two summer species and its relative abundance frequently exceeded 35 percent of the total until March of 1978. In Lake II (Fig. 25), only D. parvula was dominant in June and July of 1977. By August, both C. lacustris and D. g. mendotae had increased to the dominance level (Fig. 25) and on the last sampling date in that month all three cladocerans exceeded the ten percent level, making a total of five dominant species on that date. Daphnia parvula was a dominant cladoceran in Lake III (Fig. 26) in June and July, 1977, and on two sampling dates in August C. lacustris was also dominant. As in Lake I, D. g. mendotae began to replace the other two species in October and remained as the sole dominant daphnid throughout the winter and following spring (Fig. 26).

Cladocerans did not form a large portion of the crustacean community in Lake IV, and in the brief periods in which they represented more than ten percent of the population, only one species was dominant at one time. Daphnia parvula

Figure 24. Relative abundance (percent) of the four cladoceran species in Lake I, 1977-1978.

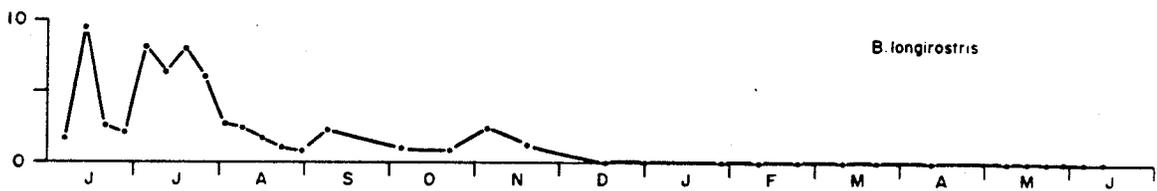
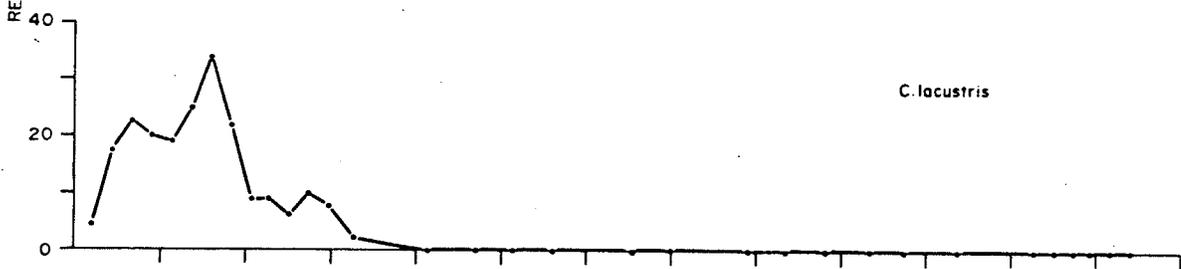
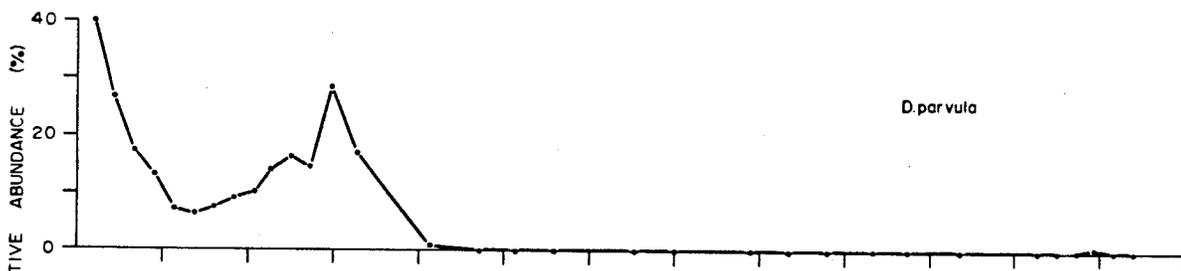
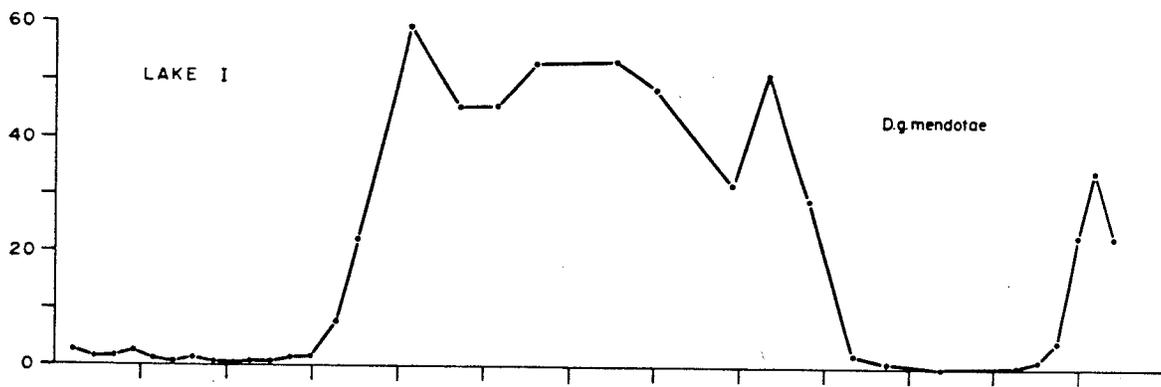


Figure 25. Relative abundance (percent) of the four cladoceran species in Lake II, 1977-1978.

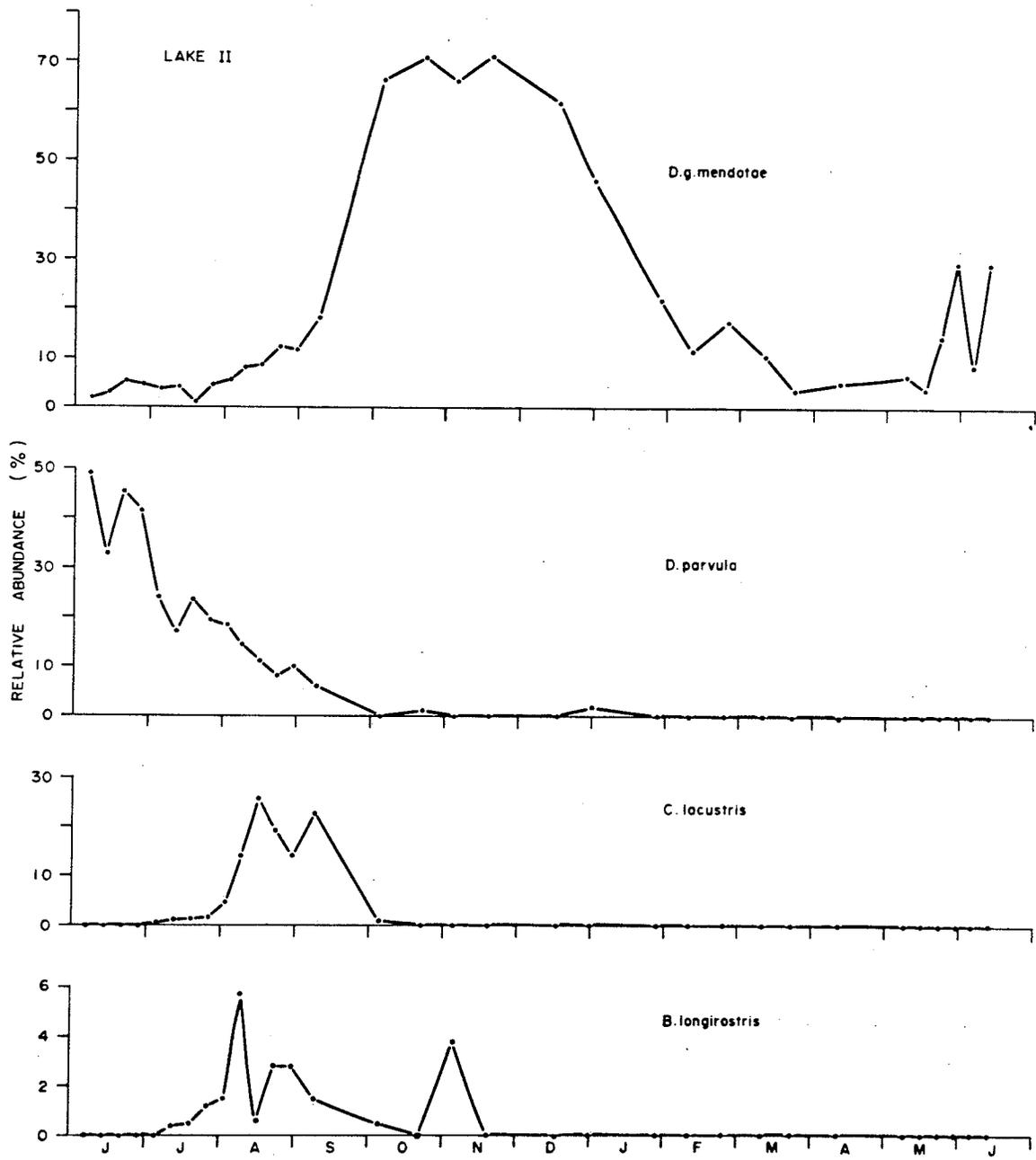
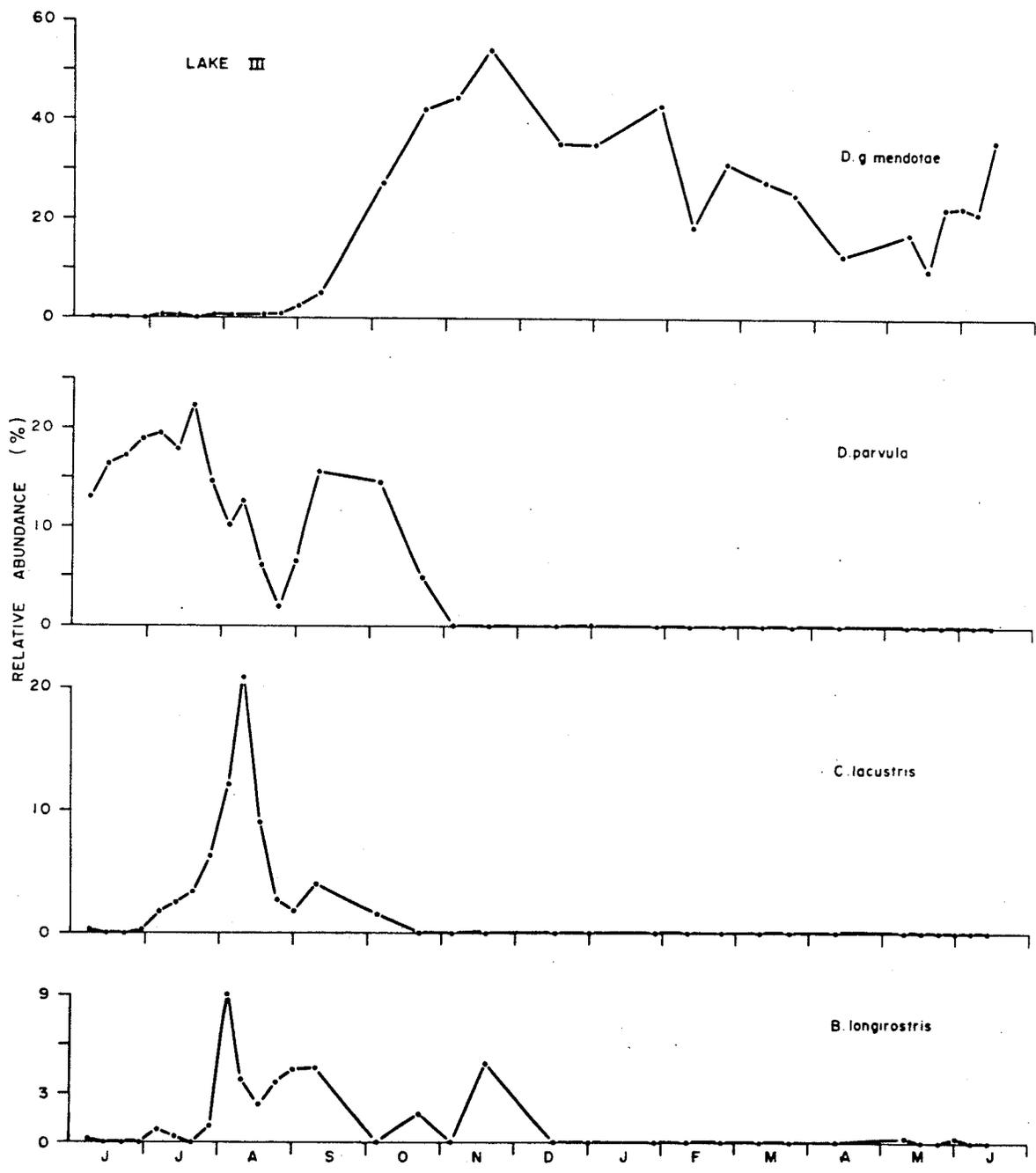


Figure 26. Relative abundance (percent) of the four cladoceran species in Lake III, 1977-1978.

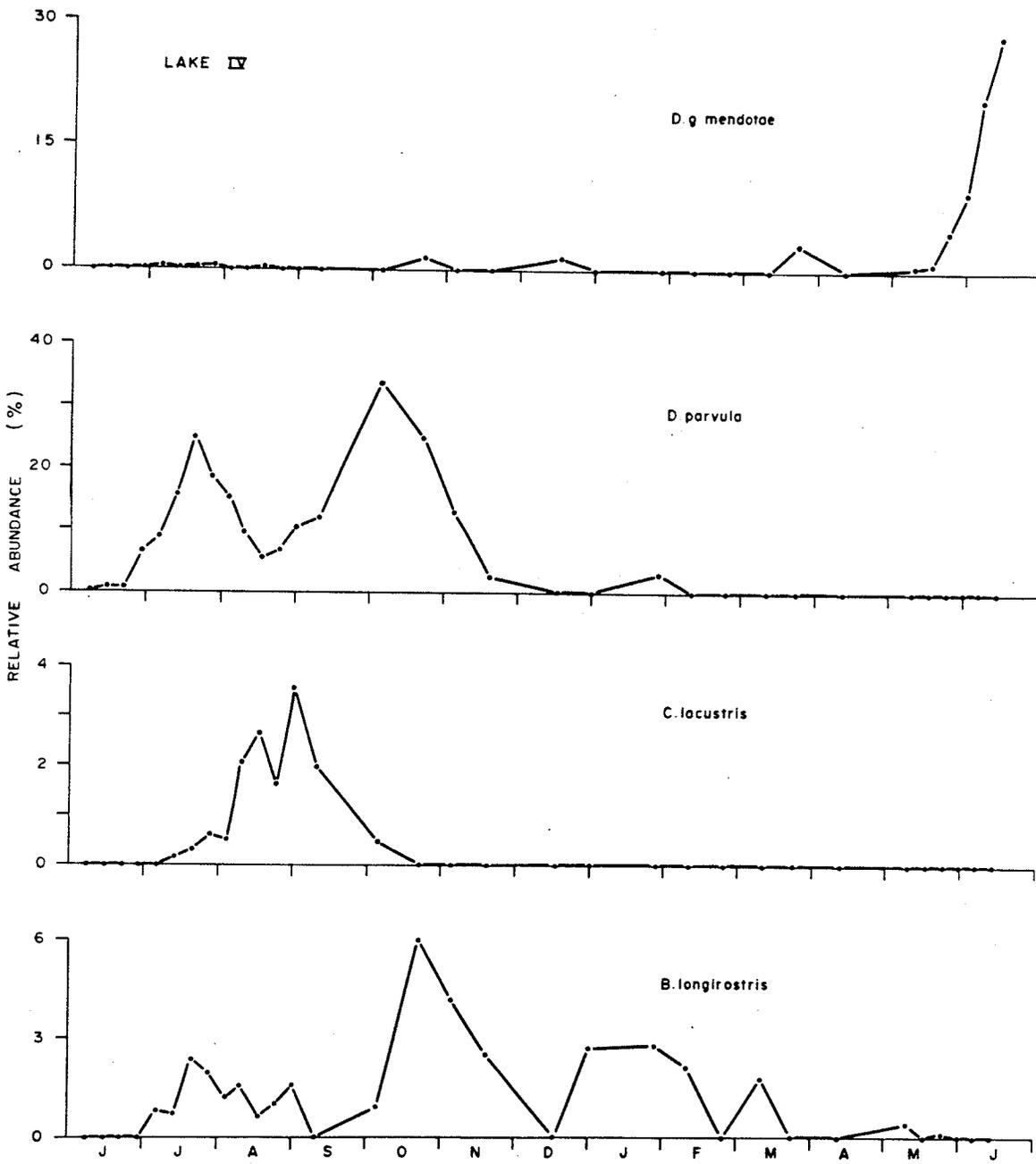


was the only dominant cladoceran in summer and autumn samples in 1977, and C. lacustris remained well below the ten percent level at all times (Fig. 27). D. g. mendotae did not become a dominant in autumn samples from Lake IV and, unlike the other lakes, the winter community was dominated only by copepods.

Bosmina longirostris was not a dominant cladoceran in any of the lakes. It represented a greater portion of the total community in Lakes I and III in summer 1977, yet it was found more frequently in winter samples from Lake IV.

Thus, although the same species were found in each lake, the complexity of the four communities was variable. In summer, 1977, Lake I was the most complex in that in this lake the crustacean community was most often dominated by one calanoid, one to two cyclopoids, and one to two cladocerans. The community composition in Lakes I, II, and III was more stable in winter with one calanoid, one cyclopoid and one cladoceran most often dominant. Lake IV, however, was less diverse in winter with only the copepods dominant. A comparison of the relative abundance of each species in the lakes between samples from June of 1977 and June, 1978, shows a large shift in the pattern of dominance: M. edax and C. vernalis were replaced by C. b. thomasi and D. g. mendotae took the place of the other cladoceran species.

Figure 27. Relative abundance (percent) of the four cladoceran species in Lake IV, 1977-1978.



The percent similarity of community index, calculated for all possible lake pair combinations using the average percent composition of the eight zooplankton species, shows that the degree of similarity between lakes changed in different seasons (Table 7). The largest change occurred between lake pairs I and IV and II and IV between autumn and spring samples where the PSC index increased from approximately 40 to over 90 percent. The low values for autumn samples were mainly caused by the lack of D. g. mendotae in Lake IV. In summer, the greatest similarity occurred between Lakes III and IV (89.5%). The least similar lakes were Lakes I and IV (67.9%) probably because of the overriding predominance of copepods in the latter lake. Lakes I and II had the second lowest similarity value in summer likely because of the low percentage of cyclopoids and high percentage of calanoids in Lake II relative to Lake I. The lowest similarity values in winter occurred in those lake pairs involving Lake IV again because of the very low relative abundance of cladocerans in this lake. The PSC values for spring, 1978 were all very high, reflecting the large percentage of C. b. thomasi in each of the four lakes.

The results of the discriminant analysis summarized some of the differences and similarities in the plankton communities of the four lakes in summer and autumn of 1977. The first two discriminant functions accounted for 58.9 and 39.8 percent, respectively, of the among group (lake)

Table 7. Percent similarity of community for all lake pairs in different seasons, 1977-1978.

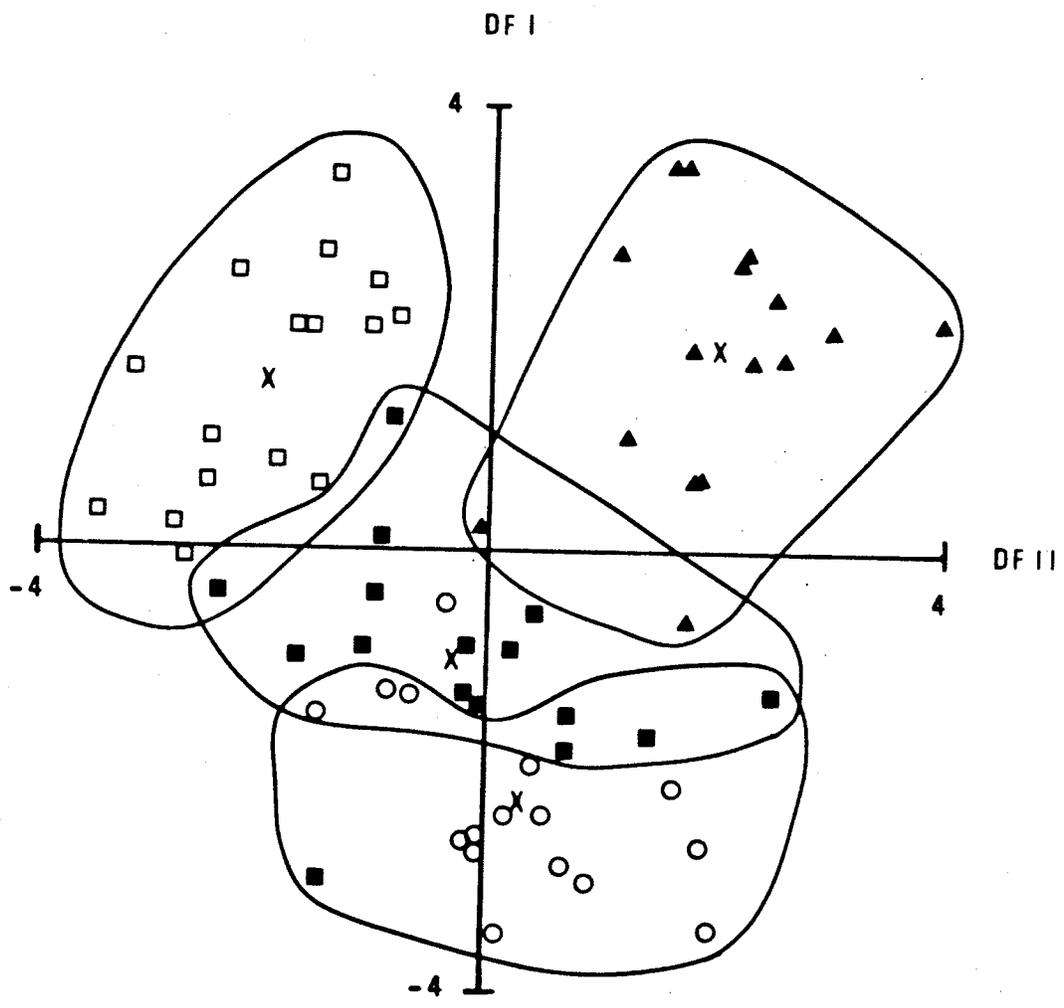
Season	L a k e s					
	I-II	I-III	I-IV	II-III	II-IV	III-IV
Summer	68.5	71.6	67.9	82.1	73.5	89.5
Autumn	69.4	70.7	46.0	64.9	40.6	74.4
Winter	76.8	86.4	68.6	87.0	59.8	66.9
Spring	95.1	88.9	96.1	90.7	96.5	88.1

variance (Table 8). This percentage of the variance is a measure of the relative importance of the associated function, thus function I was the most important. Function III could be ignored since the percent variance associated with this function was very small compared to the first two. The absolute value of the standardized discriminant function coefficients (Table 8) represent the relative contribution of each variable to a particular function. The three most important variables which made the greatest contribution to function I were M. edax, D. g. mendotae, and C. lacustris. C. b. thomasi made the largest contribution to function II. The first function primarily served to separate Lakes III and IV from Lakes I and II (Fig. 28). The scores of the group means of Lakes I and II on function I were very similar (Fig. 28), a fact that is not surprising considering the reduced abundance of M. edax and the greater abundance of D. g. mendotae and C. lacustris in these lakes in summer and autumn relative to Lakes III and IV. The second function separated Lakes I and II primarily on the basis of the relative contribution of C. b. thomasi which was most abundant in Lake I and least abundant in Lake II in summer and autumn, 1977. The group means of Lakes III and IV fell in an intermediate position on this second function (Fig. 28). The plot of the scores for each case on each function, as well as the classification results, indicate that Lakes III and IV were the most similar and

Table 8. Discriminant functions and standardized coefficients derived from analysis of zooplankton abundance data for the Fort Whyte lakes.

	Function	I	II	III
Percent of variation		58.9	39.8	1.3
Cumulative percent		58.9	98.7	100.0
Variables (log-abundance)	Standardized discriminant function coefficients			
<u>D. siciloides</u>		0.58	-0.18	
<u>C. b. thomasi</u>		-0.11	0.89	
<u>D. g. mendotae</u>		0.82	-0.66	
<u>C. lacustris</u>		0.79	0.41	
<u>B. longirostris</u>		-0.35	0.08	
<u>C. vernalis</u>		-0.17	0.22	
<u>M. edax</u>		-0.88	-0.34	
<u>Cyclopoid nauplii</u>		0.07	0.54	
<u>D. parvula</u>		0.38	-0.27	

Figure 28. The separation of the four Fort Whyte lakes on the first two discriminant functions of the nine crustacean zooplankton abundance variables. Group means shown by an X.



- ▲ LAKE I
- LAKE II
- LAKE III
- LAKE IV

the analysis was less successful in discriminating between these lakes. The most frequent misclassifications occurred between Lakes III and IV with only 56.3 and 75.0 percent, respectively, of the cases correctly classified (Table 9). Lake III was most often "mistaken" for Lake IV and vice versa. The clusters of sampling dates from Lakes I and II were however, considerably more distinct and showed little overlap with the other lakes (Fig. 28). This was substantiated by the classification results in which 87.5 percent of the cases were correctly classified in Lake I and a full 100.0 percent in Lake II (Table 9) indicating a high degree of success in discrimination. The similarity between Lakes III and IV was also demonstrated by the PSC index (Table 7) which showed that these lakes had the highest degree of similarity in percent composition of the eight species in summer and autumn. The separation of Lakes I and II from Lake IV on the first discriminant function, to which the two cladoceran species D. g. mendotae and C. lacustris are major contributors, was also evident in the low PSC values in autumn between lake pairs I and IV and II and IV (Table 7) primarily because of the very low abundance of C. lacustris and the lack of autumnal maximum of D. g. mendotae in Lake IV. As previously shown, M. edax was primarily dominant and more abundant in Lakes III and IV and also served to distinguish these lakes from Lakes I and II on

the first discriminant function. Thus the DFA provides some statistical confirmation of the similarities and differences in the zooplankton communities of the lakes in summer and autumn shown by the seasonal abundance count data and the PSC index.

Table 9. Results of classification procedure following discriminant function analysis.

Actual Group	No. of Cases	Predicted Group Membership			
		I	II	III	IV
Lake I	16	14 (87.5%)	0 (0.0%)	2 (12.5)	0 (0.0%)
Lake II	16	0 (0.0%)	16 (100.0%)	0 (0.0%)	0 (0.0%)
Lake III	16	0 (0.0%)	2 (12.5%)	9 (56.3%)	5 (31.3%)
Lake IV	16	0 (0.0%)	0 (0.0%)	4 (25.0%)	12 (75.0%)

Percent of "grouped" cases correctly classified = 79.7%

DISCUSSION

All of the crustacean zooplankton species found in the small Fort Whyte lakes are also found in the Laurentian Great Lakes (Watson 1974) and in many other North American lakes so that any generalizations concerning the environment in which these species are found can only be made for a restricted geographical area. It is interesting to note however, some of the different conditions under which these species have been found.

In Lake Michigan, Torke (1974) found that D. siciloides usually occurred in eutrophic situations in harbors and river mouths. According to Patalas (1964), Cyclops bicuspidatus thomasi was common in alpine Colorado lakes not deeper than 5 m, yet was characteristic of much deeper lakes in ELA (Patalas 1971) and was the most abundant cyclopoid in all Great Lakes (Watson 1974). Whittaker and Fairbanks (1958) found C. vernalis abundant in some lakes with high T.D.S. as did Carter (1969) who suggests that this species may prefer a more eutrophic environment. In 32 central Ontario ponds, Acanthocyclops vernalis was more common in small shallow lakes and Diacyclops bicuspidatus thomasi in cold, deep, and transparent lakes (Carter 1971). Patalas (1971) found M. edax in all lake types in ELA but in greater abundance in smaller lakes of shallow to medium depth and highly coloured waters. Apart from colour, which was not measured, this description fits the Fort Whyte lakes.

Patalas (1971) found D. g. mendotae more frequently in larger, deeper, more transparent waters in ELA but it was present in all types of lakes. Brooks (1957) considers D. parvula typical of small lakes and larger ponds. Its presence in the Fort Whyte lakes gives some confirmation to Brooks' observations that this species extends further northward in the prairie region. Sprules (1977), using principle components analysis, concluded that lakes in the Haliburton district with M. edax and C. lacustris would be predicted to be small and productive. Patalas (1971) found C. lacustris in small and shallow lakes in ELA. Bosmina longirostris is a common plankter in a wide variety of lake types (Brandlova et al 1972; Carter 1971) and is a frequent constituent of the planktonic community in the Great Lakes (Davis 1969; Patalas 1969).

These species, which are present in the Fort Whyte lakes, are thus common components of lakes in southern Canada and cannot be considered as indicators of limnological conditions over a broad geographic region. The differences in total numbers, relative abundance, and timing of the seasonal cycles may however be a reflection of the different physical and chemical conditions present in the lakes and a description of these four zooplankton communities is therefore of fundamental value.

Lake I, which is long and relatively narrow and most protected by surrounding vegetation, had the greatest degree

of thermal stratification (Fig. 2). The oxygen regimes reflect the degree of stratification; the longest and most severe hypolimnial oxygen deficit occurred in Lake I in both summer and winter. Lakes III and IV were more subject to wind produced mixing and mixing was enhanced in Lake IV by the dredging operation. Lake I had the highest mean annual levels of dissolved substances, in particular, phosphorus and nitrogen (Table 2), the source of which is thought to be the wildfowl enclosure (Ward et al unpublished) and, being the oldest lake, there has probably been a greater accumulation of these nutrients in the sediments. This combination of age, morphometry, and nutrient conditions has resulted in Lake I being the most eutrophic and productive of the four lakes. Lake IV, which is the most recently formed lake and the most frequently mixed, had the lowest nutrient levels and thus seemed to be the least eutrophic lake.

The total number of zooplankton per unit volume in the ice free period from June, 1977 to June, 1978 was consistently highest in Lake I, second highest in Lake II, and lowest in Lake IV (Table 3). Patalas (1971) found that the abundance of plankton per unit area increased with increasing maximum depth in ELA lakes and that crustacean abundance increased with increased heat and chlorophyll content of the Great Lakes and the lakes of the Okanagan Valley (Patalas 1972; Patalas and Salki 1973). The magnitude of the difference in total numbers observed in these investigation is greater than

those in the present study. The maximum depth is the same for the Fort Whyte lakes so that maximum depth alone cannot be responsible for differences in total abundance. The greater degree of thermal stratification and the oxygen deficit in the hypolimnion may have confined the plankton in Lake I to the warmer strata to a greater degree than in the other lakes in summer. Patalas (1975) found a high correlation between epilimnion water temperature and plankton abundance in fourteen North American great lakes and that temperature affected abundance directly by controlling growth and indirectly by controlling nutrient input and turnover rate (Patalas 1972). Nutrient levels in Lakes I and II and mean chlorophyll in Lake II were higher than in the other lakes, and these measures, which are related to lake productivity, may also be important factors determining the greater total abundance of zooplankton in these two lakes.

The numerical abundance of cladocerans (Fig. 6) and, in particular, cyclopoids (Fig. 5) in Lake I frequently exceeded that found in the other lakes. The number of calanoids, however, was approximately the same in each of the lakes. The relative abundance of cyclopoids plus cladocerans was always highest in Lake I, while calanoids made up a smaller portion of this community than in Lakes II,

III, and IV (Table 6). Gannon (1972) suggested that the proportion of calanoids to cyclopoids and cladocerans was an indication of trophic status. Patalas (1972) noted an increasing proportion of cyclopoids and cladocerans and a reduction in calanoids in going from oligotrophic to eutrophic conditions. The reduced relative abundance of calanoids in Lake I may thus indicate further advancement toward eutrophy. Watson (1974) points out that, in the Great Lakes, increasing eutrophication allows the development of larger summer populations of cyclopoids and cladocerans and that calanoid populations remain the same or decrease slightly. This relationship does not hold true in Lake II, which also seemed more eutrophic than Lakes III and IV in terms of nutrient and chlorophyll-a levels, where calanoids represented a larger portion of the population than cyclopoids and cladocerans in summer, 1977 (Table 6). The reduced abundance of cyclopoids in this lake in 1977, at present, cannot be satisfactorily explained. Suitable conditions allowing the development of large cyclopoid populations must have been present in spring, 1978, when the number of cyclopoids per liter in Lake II was comparable to that in Lake I and exceeded that found in Lakes III and IV (Table 4). The large increase in the abundance of cyclopoids in the spring of 1978 in all the lakes was an example of the variability of the relative proportions of the three taxonomic groups exhibited by the four lakes.

More data, gathered over a number of years, are needed to determine the nature of the relationship between the abundance of calanoids and the trophic status of the Fort Whyte lakes.

In each of the four lakes in this study, D. siciloides had at least two generations in the summer of 1977 and females with eggs were found continually. In Severson Lake, Minnesota, D. siciloides was shown to have five annual generations (Comita 1972). Comita assumed that the final generation of adults produced overwintering eggs in October because first instar nauplii were not found after egg production. In Lakes I, II (Fig. 8) and III (Fig. 9) D. siciloides nauplii were not produced after the middle of October even though females with eggs were found both during and after that time. This may indicate that, here too, resting eggs were produced in the autumn and yet the presence of females with spermatophores under ice cover as well as females with eggs found in April and May, 1978, indicate that it was the overwintering adults that produced the spring generation. The large copepodid peak of D. siciloides in June of 1977 was not repeated in June of 1978 in Lake I (Fig. 8) either because development was delayed as a result of lower spring water temperatures in 1978 or because of predatory pressure from C. b. thomasi. This lake had the greatest concentration of C. b. thomasi which comprised over 90 percent of the crustacean community in spring, 1978, and this large increase in the number of carnivorous copepods could have exerted a considerable effect on the calanoid, D. siciloides.

Copepodid stages IV and V and the adults of C. b. thomasi were shown by McQueen (1969) to prey extensively on diaptomid nauplii. In Lake I, the peak of CIV or V of C. b. thomasi coincided with a trough in the calanoid nauplius curve on May 29 (Fig. 8 and Fig. 10).

It is not clear whether or when C. b. thomasi entered a resting stage in Lake I. Carter (1974) presumed that CIV C. b. thomasi copepodids emerged from diapause after the ice departed in Black Pond. These animals were shown to produce the spring generation which did not advance beyond CIV but emerged the following spring. In Lake I, the large increase in late stage copepodids in March of 1978 indicated that they returned from the sediments or bottom waters and produced the spring generation, yet there was no evident time in 1977 when the species totally disappeared from the lake, an event often noted in other studies of cyclopoid species which undergo diapause. The first samples of 1977 contained mostly late stage copepodids but these declined in numbers and none were found on July 11 (Fig. 10). This may indicate a period where the copepodids left the water column, but the species did not disappear and in fact, C. b. thomasi females with eggs and adults were found periodically after July 11

and cyclopoid nauplii were sampled throughout the summer. Late stage copepodids reached another maximum in November after which time their numbers declined markedly (Fig. 10). It may be that at this time development was arrested and the copepodids migrated to deep waters and were not caught. This situation is unlike that found in Lake Mendota by Birge and Juday (1908) who were first to discover that Diacyclops bicuspidatus thomasi encysted in the mud from June to September. Watson and Smallman (1971) determined experimentally that photoperiod and temperature are critical factors controlling diapause. Elgmork et al (1978) found that, in only one of five closely situated lakes in southern Norway, C. scutifer was dominant mainly in the copepodid IV stage in the deepest part of the lake from July to April but, because the lakes were in the same area, temperature and photoperiod would not have been the likely cause of diapause in only one of the five lakes. In Lake I, the decline in late stage copepodids of C. b. thomasi in the water column may have been related to the considerable reduction in hypolimnial oxygen levels between November and December 1977 (Fig. 3) but, as Hutchinson (1967) pointed out, there is no clear evidence that oxygen is a regulatory factor in diapause of copepodids. The fact that males and females were present throughout winter in Lake I indicates that at least some portion of the population overwintered in the water column and these adults may have reproduced in spring and contributed to the spring generation.

Late stage copepodids also appeared in Lake II in March, though to a much lesser extent than in Lake I (Fig. 10). No females with eggs were found previous to this increase but small numbers of nauplii were sampled, perhaps indicating reproduction under the ice. The large pulses of nauplii in December in Lakes III and IV and the presence of females with eggs in January in Lake III indicate that reproduction did occur in these lakes under ice cover.

In Lake I the time between the two CIV-V peaks in March and May of 1978 was about 60 days. Armitage and Tash (1967) suggested that a complete life cycle in spring required about 35 days. Carter (1974) estimated that C. b. thomasi underwent a complete cycle from CIV to CIV in approximately three to four weeks in Black Pond near Georgian Bay. McQueen (1969) estimated a time of 45 days from egg to CIV, but his figures of the standing stock of C. b. thomasi in Marion Lake indicate the time between the maximum numbers of CIV copepodids was about 77 days, at spring temperatures slightly higher than in the Fort Whyte lakes.

C. vernalis was most prevalent in summer, 1977 samples in Lakes I, II, and III (Fig. 12) but became scarce in winter and spring, 1978, when populations of C. b. thomasi were increasing. In Lake IV, small numbers of copepodids were found until February. Few of these copepodids seemed to survive to adulthood and the origin of the spring generation is obscure. In the Great Lakes and some of the Okanagan

lakes, C. vernalis was abundant only when C. b. thomasi was not (Patalas 1972; Patalas and Salki 1973). Anderson (1970c, 1972) showed that C. vernalis declined in the presence of abundant C. b. thomasi. The large populations of the latter species in the spring of 1978 also may have had a similar depressing effect on the populations of C. vernalis in the Fort Whyte lakes.

Carter (1974) found the overwintering generation of M. edax to enter diapause at CIV in late autumn in Black Pond. In this study, the autumn samples from Lakes I, III, and IV contained mostly late stage copepodids (Fig. 13), but no animals were found in winter, perhaps indicating that these copepodids left the water column to overwinter in or near the sediments. In Lakes I, II, and IV the first samples in spring, 1978, contained no early copepodid stages thus the late stage copepodids may have returned to the water column after the ice left the lakes and developed directly into adults. Few M. edax females with eggs were counted in any of the lakes. Cole (1955) suggested that adult females are mainly benthic for extended periods and were thus perhaps inadequately sampled.

Daphnia galeata mendotae was found to have both autumn and spring maxima in Lakes I, II, and III and a single spring maximum in 1978 in Lake IV (Figs. 14 and 15). Birge (in Hutchinson 1967) found D. galeata to be a perennial species with two population maxima in spring and autumn in Lake Mendota.

McNaught and Hasler (1964) found D. g. mendotae during the fall, with D. shoedleri dominating from May to August. Brooks (1946) reported a spring maximum in May for D. galeata, with very low numbers in July and August. Hall (1964) observed two population peaks in June and December in Baseline, Michigan also with much lower numbers in July and August. The abundance of this species in summer in 1977 was low in each of the four lakes. Wells (1960) found no evidence of a spring maximum in Lake Michigan, but in the Fort Whyte lakes, the spring population maximum may have already occurred before sampling had begun in 1977. Spring came earlier in 1977 and temperatures of the epilimnia of the four lakes were higher in June of 1977 than in June of 1978 (Fig. 2). Wright (1965) found that D. g. mendotae had higher birth rates when lower water temperatures prevailed. Perhaps the earlier onset of spring conditions encouraged earlier development of the maximum numbers of this species so that the population had already reached a minimum by June, 1977. At present, I can find no satisfactory explanation for the absence of the autumnal maximum of this species in Lake IV. The temperatures of the four lakes were very similar and approximately isothermal during the maximum numbers of D. g. mendotae in October in Lakes I, II, and III, thus some factor other than temperature must have been involved.

According to Hutchinson (1967) the most well known cause of male production in cladocerans is crowding, within certain limits of food levels and temperature. Crowding may have been a factor in the case of D. g. mendotae because the production of males in Lakes I, II, and III occurred during the maximum population density of this species in autumn, 1977 and spring, 1978 (Fig. 14 and Fig. 15). Hutchinson (1967) also relates that the stimulus for ehippial production may be a rapid decrease in available food but that photoperiod may also be a controlling factor in the production of both males and ehippia because in some cases they appear well after the peak numbers of animals. There was no evidence of a rapid depletion of food resources in the four lakes, but the synchrony of the production of ehippial females of D. g. mendotae in Lakes I and II in the autumn of 1977 and in Lakes I, II, and III in spring, 1978, may suggest the role of photoperiod as a controlling factor.

Daphnia parvula occurred predominantly in summer and autumn samples in all the lakes. In Lakes I, (Fig. 16), III, and IV (Fig. 17) this species showed two peaks in abundance in early summer and late summer or autumn. Comita (1972) found D. parvula from early June until freeze-up in early November in Severson Lake, Minnesota, with the greatest numbers of animals present in June. Janicki et al (1979) found D. parvula to be a consistent dominant in summer among four eutrophic impoundments in West Virginia. Males were sampled

in all the lakes in September and October after the main pulse of the population had passed so that overcrowding would not seem to be the cause of male production in this species. Despite the production of resting eggs (sampled in Lakes II and IV), this species had not reappeared by June of 1978 except very rarely. Conditions for hatching of the resting eggs may have been unsuitable in spring, 1978, but it is equally possible that this species may have become abundant after sampling had been discontinued in 1978 and after the spring bloom of D. g. mendotae had ended. The lower June 1978 temperatures may also have delayed the increase in numbers of this summer species.

Ceriodaphnia lacustris was restricted to summer and autumn samples in all the lakes and conforms to Hutchinson's (1967) description of aestival species which usually have a single summer maximum. Similar to the seasonal cycle of C. lacustris in the Fort Whyte lakes, Kwik and Carter (1975) found that C. quadrangula had a single midsummer maximum and that the species had disappeared by October. The only ehippial female was found in Lake I on July 18 and the only male was found in Lake III, well after the population had reached a peak, indicating that factors other than crowding influenced the production of males.

B. longirostris demonstrated two population pulses in June and July in Lake I and in August in Lakes II and III but did not show any clear peak in abundance in Lake IV (Fig. 20). Kwik and Carter (1975) found

B. longirostris to be triacmic in Hangdog Pond in which it was the most abundant cladoceran. This species appeared to overwinter in the water column only in Lake IV in low numbers (Fig. 20). Schindler and Noven (1971) found that B. longirostris possibly overwintered in ELA. Ehippial females and males were never recorded in any of the lakes suggesting that overwintering may have occurred in Lakes I, II, and III as well but that the animals migrated to the bottom sediments. Kwik and Carter (1975) suggested that B. longirostris may periodically abandon the limnoplankton for a benthic existence thus avoiding capture.

Throughout the sampling year, the number of dominant zooplankton species ranged from one to five in each of the lakes depending on the sampling date. On the majority of sampling dates, one cladoceran, one cyclopoid and one calanoid species was dominant in Lakes I and III. The complexity of the community in Lake II was more variable with a combination of one calanoid and one cladoceran dominating equally as often as one calanoid, one cyclopoid, and one or more cladocerans. In 21 of the total 32 sampling dates in Lake IV no cladoceran dominated (Fig. 27). According to Patalas' (1971) findings at ELA, cladocerans were dominant only in the more complex communities. Thus, considered in these terms, Lake IV generally had the least complex community of which the copepods were the most important component.

Some of the variation in the number and kind of dominant cladocerans could be explained by simple seasonal succession within a lake but the variation between lakes may have been caused by a variety of interrelated factors such as the prevailing environmental conditions, habitat complexity,

competition, or the age and corresponding maturity of the community. During most seasons, Lakes I and II generally had the highest concentrations of cladocerans and they represented a greater portion of the total community (Table 6). Absolute and relative abundance of cladocerans was always lower in Lake IV. Only one species of this group was dominant in one time in this lake (Fig. 27) and the duration of dominance was shorter than in the other lakes. There is little if any evidence that food limitations existed for the cladocerans in Lake IV. Mean chlorophyll-a levels, which rather crudely indicate phytoplankton standing stock, are not significantly lower in this lake (Table 2) and the lack of information on algal diversity and the ability of the species involved to utilize alternate food sources such as bacteria and dissolved organic matter precludes any conclusions regarding the availability of food for the cladocerans in Lake IV.

Lakes I, II, and III were capable of supporting at least one dominant cladoceran during most of midsummer so that conditions in these lakes were seemingly more favourable to their development. In these lakes, particularly Lake I, the greater nutrient additions and ecological niches provided by shallow areas and greater macrophyte growth may allow greater diversity as shown by the presence of Scapholeberis sp. in Lake I and the development of larger populations of the rarer cladoceran species such as C. lacustris and B. longirostris.

Anderson (1967) found that in mountain lakes, the number of species per community increased with the complexity of the aquatic habitat presumably because of the greater number of ecological niches available.

According to Margalef (1963) the maturity and complexity of a community increases with age in an undisturbed environment. In this context, Lake IV might be predicted to have a less complex community because it occupies the most recently formed basin and the aquatic environment is constantly being disturbed as a result of the dredging operation. Maturity can only be a partial explanation for the variation between the lakes because even the older, supposedly more "mature" lakes exhibit differences with regard to complexity and the seasonal succession of the dominant cladocerans, particularly in the case of C. lacustris. In Lake I in June, July, and August, D. parvula and C. lacustris alternated as the dominant cladoceran with a brief period of overlap between the two populations (Fig. 24). In Lake II, the succession of cladocerans was much less discrete. D. parvula was the only dominant in June and July but by August different combinations of three cladocerans were dominant, with C. lacustris having the greatest relative abundance (Fig. 25). The maximum abundance of C. lacustris in Lake I was coincident with the occurrence of an intense bloom of blue-green algae in Lake II. The presence of the blue-green bloom may have delayed the summer maximum of C. lacustris in Lake II if these algae were an unsuitable food source for

this small cladoceran. The maximum abundance of C. lacustris also occurred in Lake III after the less extensive blue-green bloom in this lake had subsided. Roff and Kwiatkowski (1977) found that reduced zooplankton diversity in acidic Ontario lakes may have been related to the presence of blue-green algae. Arnold (1971) found ingestion, assimilation, survivorship, and reproduction rates of Daphnia that were fed blue-green algae were lower than those fed green algae, but as Schindler (1971) points out, differences occur between species of zooplankton and their ability to assimilate different algal species so that blue-greens as a whole cannot be regarded as a poor food source for all cladocerans. The relationship between phytoplankton and zooplankton feeding needs further investigation but the reduced diversity of food resources may have increased competition and prevented dominance by C. lacustris in Lakes II and III until after the blue-green bloom had ended.

The presence of a second peak in abundance of D. parvula in August and September of 1977 (Fig. 16) may have delayed the increase in numbers of D. g. mendotae in Lake I. This second maximum of D. parvula was not evident in Lake II and D. g. mendotae (Fig. 14) increased in abundance much earlier than in Lake I. A second small peak of D. parvula in September in Lake III may have had a similar effect on the population of D. g. mendotae. Similar situations occurred in Azicoos Lake

where Daphnia catawba exhibited a late summer maximum and coexisted with D. g. mendotae which was relatively less common in summer (Tappa 1965) and in Base Line Lake with D. retrocurva and D. g. mendotae in summer (Hall 1964). Competition with D. catawba and with D. retrocurva may have been a cause of delaying the autumnal maximum of D. g. medotae in both of these lakes (see discussion in Hutchinson 1967 and Wetzel 1975).

The cladoceran component of the communities in winter was less diverse with a single dominant, D. g. mendotae in Lakes I, II, and III and no dominant cladoceran in Lake IV. In the absence of D. g. mendotae in Lake IV, D. parvula existed as a dominant for a slightly longer time with a small second peak in October when D. g. mendotae was very abundant in the other lakes. The combination of a lack of competition from D. g. mendotae and the presence of higher oxygen levels in Lake IV may have allowed the small population of B. longirostris to survive in the water column (Fig. 20) with greater success than in the other lakes. Obviously, conditions suitable for the maximum development of cladoceran populations occurred at different times in the lakes.

Patalas (1971) found that midsummer zooplankton community patterns in ELA were relatively stable and that a series of samples taken at a comparable time would be representative of community structure. In the Fort Whyte lakes, the change in dominance pattern shown by a comparison of the first two samples in June of 1977 and June of 1978 indicates a considerable shift in

community structure. In Lake II in June 1977, only one calanoid and one cladoceran dominated, in the following year, the cyclopoid C. b. thomasi was the overwhelmingly dominant species. The observed changes in percent composition of the crustacean zooplankton species in these small lakes at a comparable time in different years may have been a response to changes in the aquatic environment. Spring conditions in 1977 and 1978 were quite different; lake levels were higher in 1978, the center station of the lakes increased by one meter of depth, and the lakes did not warm as rapidly. Further sampling in 1978 may have shown a return of community composition to that found in 1977, hence the apparent shift in dominance in spring 1978 may have been simply a result of a delay in development of the summer planktonic community.

The percent similarity index leads to groupings of communities on the basis of dominant species without consideration of species composition (Whittaker and Fairbanks 1958). The four lakes shared the same species thus the numerical comparison provided by this index was the most appropriate. The PSC index has usually been used to compare the summer plankton communities of a large number of lakes and/or lakes with very different limnological conditions such as pH (e.g. Roff and Kwiatkowski 1977). In this study, it was useful in showing temporal changes in the similarity of lake pairs during the sampling year. Lake

pairs I and IV and II and IV showed the greatest variation, the difference between autumn and spring values exceeding 50 percent (Table 7). It is not unreasonable to expect that the relative abundance of the species in a community would change in different seasons but the large shifts in the similarity index between lake pairs indicate that the communities did not change in the same way. The exception to this are the spring 1978 samples where the similarity index was very high for all lake pairs during the rapid increase in the numbers of Cyclops bicuspidatus thomasi.

Discriminant function analysis proved a useful tool in demonstrating differences in the abundance of the zooplankton species of the four lakes. The degree of similarity between the lakes demonstrated by the multivariate analysis was basically similar to that shown by the PSC index with the added advantages of comparing all the lakes at once and identifying the species most important in achieving separation. A further extension of this analysis would be to define the zooplankton communities in terms of the physical and chemical conditions present in the lakes in order to provide environmental "explanations" for observed differences in biota (e.g. Green 1978).

In summary, the four small Fort Whyte lakes contained the same crustacean zooplankton species and these species are common components of the plankton of North American lakes of widely differing physical and chemical characteristics. Despite

the superficial similarity and physical connection between the lakes, there were definite differences in their limnological conditions and zooplankton communities. Lake I differed from the other lakes because of its greater age, morphometry, intense thermal stratification and oxygen deficits, and greater nutrient supply. These combined characteristics indicate that this lake was the most eutrophic and productive. The greater total abundance of crustacean zooplankton and the larger proportion of cyclopoids and cladocerans in this lake are consistent with a trend toward increasing eutrophication found in this and other studies. The seasonal cycles of the eight species were not radically different from those found in other studies but the timing of the seasonal maxima and dominance of the cladocerans were found to differ between the lakes and may have been related to competition as well as the presence of blue-green algae. The youngest lake, Lake IV, generally had the least complex community in terms of the numerical dominance of cladocerans and this may be an indication of reduced habitat diversity and/or that the community is still in the early stages of its development. The physical and chemical characteristics of the four lakes may be sufficiently different to cause the apparent variation in the four communities and future research may show the Fort White lakes to be a useful practical laboratory in further defining the relationship between community and environment.

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APPENDIX A

The variance-to-mean ratio was compared with the χ^2 distribution. With 5 degrees of freedom at the 5% ($p=.05$) level of significance $\chi^2 = 11.07$.

Here, χ^2 approximates $\frac{s^2}{\bar{x}} (n-1)$, the variance-to-mean ratio (from Cassie 1971).

Results for 6 replicate subsamples:

Species		$\frac{s^2}{\bar{x}} (n-1)$	Critical value
<u>D. siciloides</u>	nauplii	3.08 (p > .5)	11.07 (p=.05)
	copepodids	5.81 (p > .25)	11.07
	adults	7.26 (p > .10)	11.07
<u>C. b. thomasi</u>	copepodids I-III	7.01 (p > .1)	11.07
	copepodids IV-V	10.66 (p > .05)	11.07
<u>D. g. mendotae</u>	immatures	4.82 (p > .25)	11.07
	females	3.16 (p > .5)	11.07

For each of these species, the difference between the mean and variance was non-significant. Thus the subsampling technique was considered adequately random.

APPENDIX B

Mean Minimum Size of Egg Bearing Females

<u>Species</u>	<u>Size (mm)</u>
<u>Daphnia galeata mendotae</u>	1.21
<u>Daphnia parvula</u>	0.82
<u>Ceriodaphnia lacustris</u>	0.45

Cladocerans were measured from the anterior margin of the head to the base of the caudal spine. Measurements were taken from various samples in different lakes at different times of the year.