

THE UNIVERSITY OF MANITOBA

Relative Abundance and Biomass,
Age, and Growth of Yellow Perch,
Perca flavescens (Mitchill),
in Four Adjacent Man-Made Lakes
in Southern Manitoba

by

Raymond A. Ratynski

A Dissertation

Submitted to the Faculty of Graduate Studies
in Partial Fulfillment of the Requirements for the Degree
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ABSTRACT

Characteristics of populations of yellow perch, Perca flavescens (Mitchill), in four adjacent man-made lakes in southern Manitoba were examined during the open water periods of 1978 and 1979. Studies of the physical and chemical regimes of the Fort Whyte lakes during 1977-1978 indicated greatest eutrophy in Lakes I and II and lowest in Lakes III and IV. Relative perch abundance and biomass values in 1979 were highest in Lake I but were similar for Lakes II, III, and IV. Dissimilarity of recruitment of the 1977 and 1978 year classes between Lake I and the other three lakes is attributed to intraspecific predation of young perch by numerous adult perch in Lake I. Older perch dominated the catch in Lake I while the newly recruited one-year-olds formed 9% of the population in 1978 and 3% in 1979. In the other lakes there were fewer old perch. In 1978, age 1 perch made up 33%, 44% and 26% of the population in Lakes II, III, and IV respectively. In 1979, they represented 65% of the population in Lake II, 64% in Lake III, and 69% in Lake IV. Among Lakes II, III, and IV, mean length of perch at time of annulus formation in 1978 was highest in Lake II and lowest in Lake IV for all ages.

In comparison to the other lakes, yellow perch in Lake I had the highest mean length for ages less than 3 but the lowest mean length for ages greater than 3. These differences were not great in magnitude. At the time of annulus formation in 1979, there were no significant differences in mean lengths at each age. In comparison to other North American waters, growth of perch at Fort Whyte was slow. The major response of the perch population in Lake I to greater eutrophy was to increase its biomass but this was by increasing population size rather than by increasing growth. The perch population of Lake II failed to respond similarly perhaps because nutrient input to the lake is sporadic and sustained loading is required for increased productivity. A greater magnitude of difference in perch biomass than in perch abundance between Lake I and Lakes II, III, and IV is attributed to higher incidence of older, larger fish in Lake I.

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INTRODUCTION

Analyses of the characteristics of populations of yellow perch, Perca flavescens (Mitchill), are common but comparisons between populations are less frequent. Grimaldi and Leduc (1973) investigated growth of perch in six areas of Quebec and attempted to relate growth differences to environmental dissimilarities of the habitats. Nakashima and Leggett (1975) related differences in perch biomass of the north and south basins of Lake Memphremagog, Quebec-Vermont, to differences in basin productivity. Recently, Hopky (1982) compared perch population characteristics between two saline-eutrophic lakes in southwestern Manitoba.

The Fort Whyte lakes, located in southwestern Winnipeg, Manitoba, are small man-made lakes resulting from dredging activities extending over a seventy year period. Although adjacent to one another, the four lakes differ in their physical and chemical regimes (Ward and Loadman MS 1981). Loadman (1980) found that zooplankton abundance and timing of seasonal maxima of zooplankton varied among lakes. For instance, the total numbers of zooplankton per unit volume from June 1977 to June 1978 were always highest in Lake I, second highest in Lake II, and lowest in Lake IV (Loadman 1980).

The perch populations at Fort Whyte were investigated to determine if they had distinct characteristics associated with each lake. The main objectives of this research were to determine relative abundance and biomass of perch in each lake, to define the age and length structures of the populations, and to estimate the growth characteristics of the four perch populations. Comparisons of the above parameters were made among the lakes. The results of this investigation will be related to lake characteristics and to the characteristics of the zooplankton populations. Sampling was performed during the ice-free periods of 1978 and 1979.

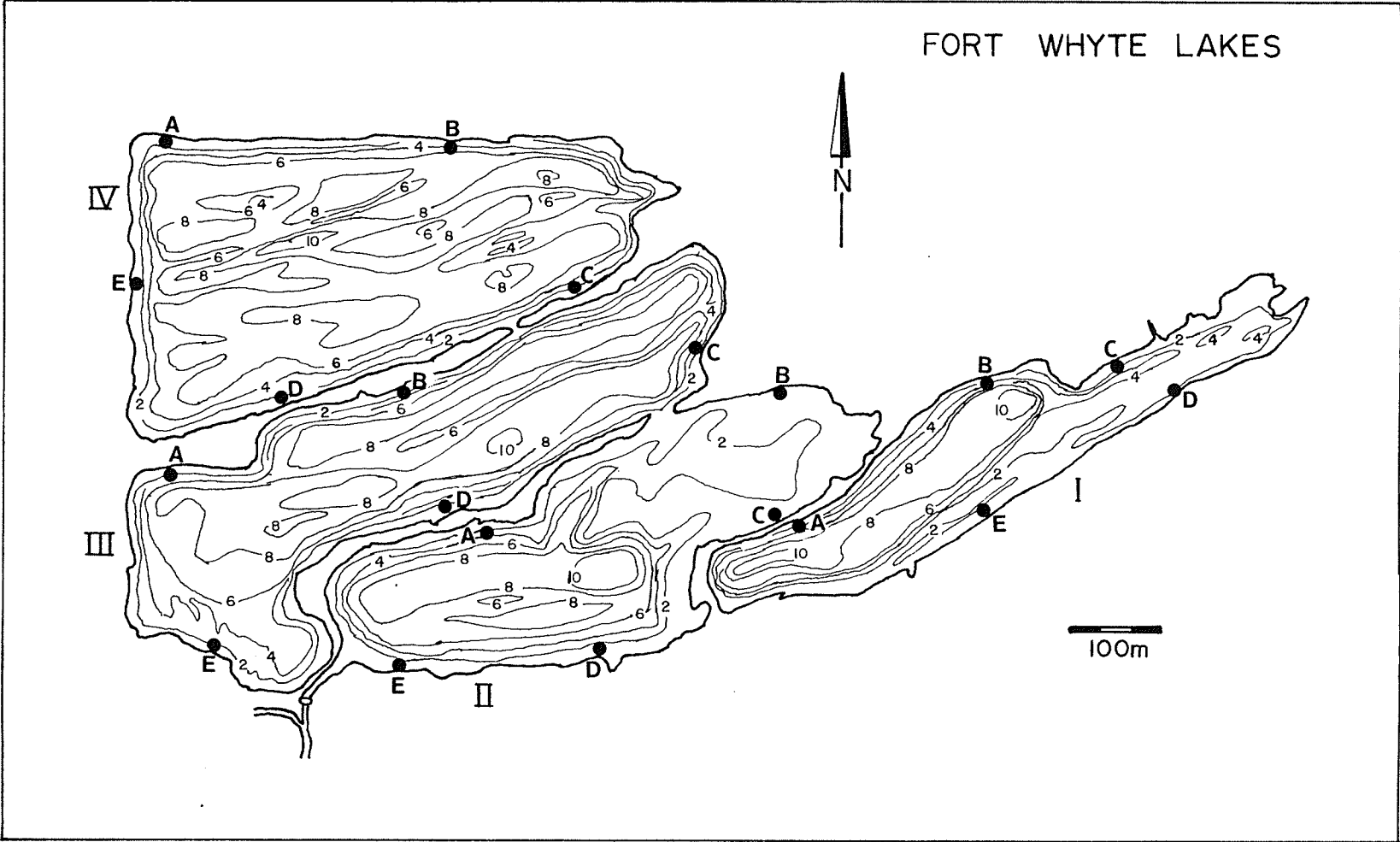
LAKE DESCRIPTIONS

Fort Whyte is located at the southwestern extremity of Winnipeg, Manitoba. The four lakes investigated are located on land owned by the Canada Cement Lafarge, Ltd. and were originally excavated for clay used in cement making. Recorded history of the system is sparse and incomplete. Lake I was completed by 1920. Lake II was completed in the late 1940's. Excavation of Lake III began in 1951 and ended in 1962. Work on Lake IV began in the latter part of 1962 and dredging of its north shore currently continues. The two oldest lakes were partly dug by horse-drawn draglines, which accounts for their shallow east ends (Fig. 1). The deeper western portions of their basins and Lakes III and IV were formed entirely by mechanical draglines.

Lakes II, III, and IV are sometimes joined by shallow channels (Fig. 1). These developed between II and III during the period of 1957-1967 and between III and IV during 1967-1977. A drainage ditch empties into the southwest end of Lake II in spring in years when lake levels are low. When lake levels are high, water may flow out through the ditch. As well, all four lakes are joined when high spring water levels overflow the lake basins, as occurred in the spring of 1979. Lake I receives runoff from waterfowl ponds located on its south shore.

Figure 1. Contour map of the Fort Whyte lakes
indicating the main sampling stations.
Depths are in m.

FORT WHYTE LAKES



Lake I is maintained as a reservoir for water utilized as a coolant in the nearby cement plant. Water is pumped from and then returns slightly warmed to the east part of the lake. Some is lost in the process and water is pumped from Lake II into the extreme west end of Lake I to replenish supplies. However, since pumping does not begin until the water level in Lake I drops by 1 m or more, fluctuations in level occur.

Except for the short periods as mentioned above, the Fort Whyte lakes are isolated entities with little exchange of water between them and with little flow from the surrounding area.

The lakes differ in most morphometric measurements, although maximum depth is the same (Table 1). Area and volume increase from Lake I to Lake IV. Mean depth is lowest in Lakes I and II and highest in Lakes III and IV. Where excavation by a mechanically operated dragline occurred, the lake basins are steep sided. As a result, the littoral zone of Lakes III and IV and of the west ends of Lakes I and II are not large in extent. For their surface areas, the lakes are very deep.

Ice usually leaves the Fort Whyte lakes between late April and mid May with the east part of Lake I the first area to clear (possibly the flow of water returning from the cement plant accelerates ice breakup). Lake I is completely open one or two weeks before Lake II and two or three weeks

Table 1. Morphometry of the Fort Whyte Lakes (1977-78).

	LAKE			
	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

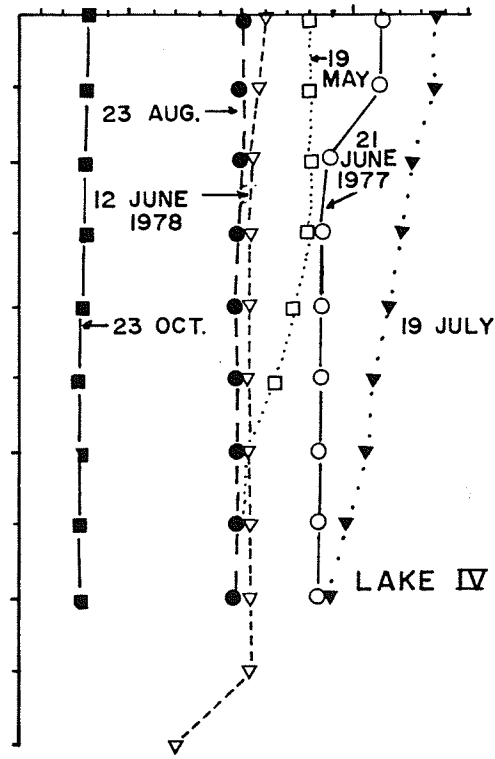
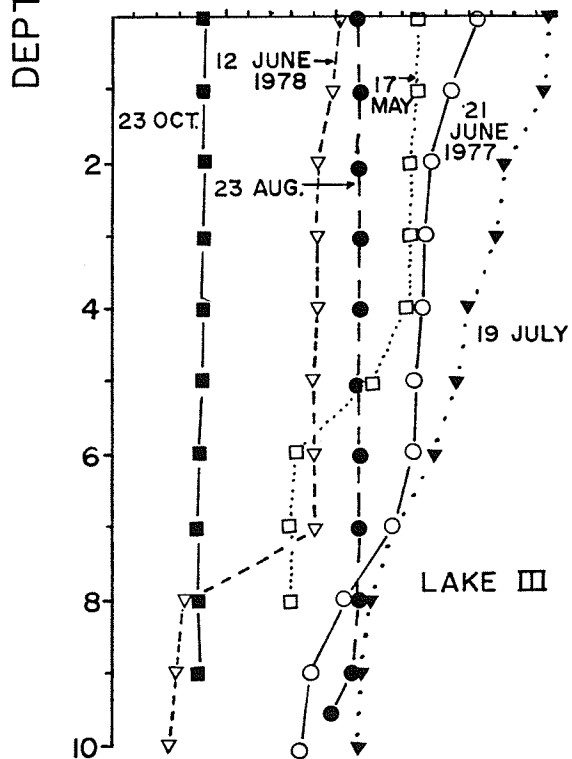
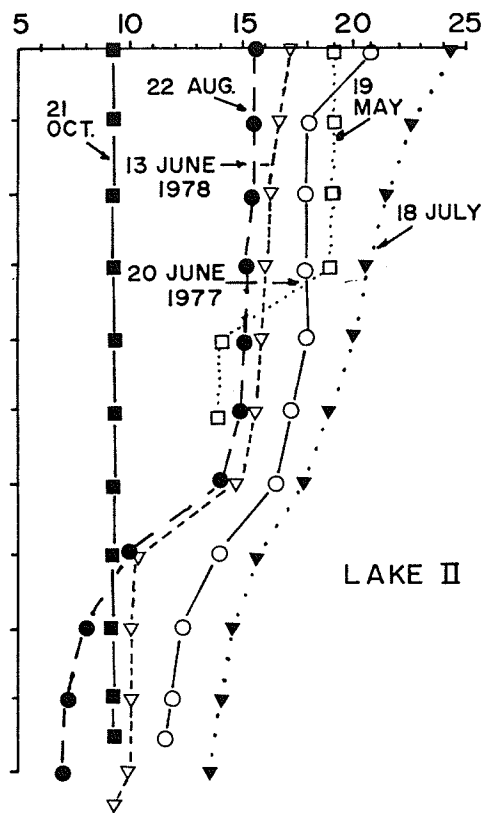
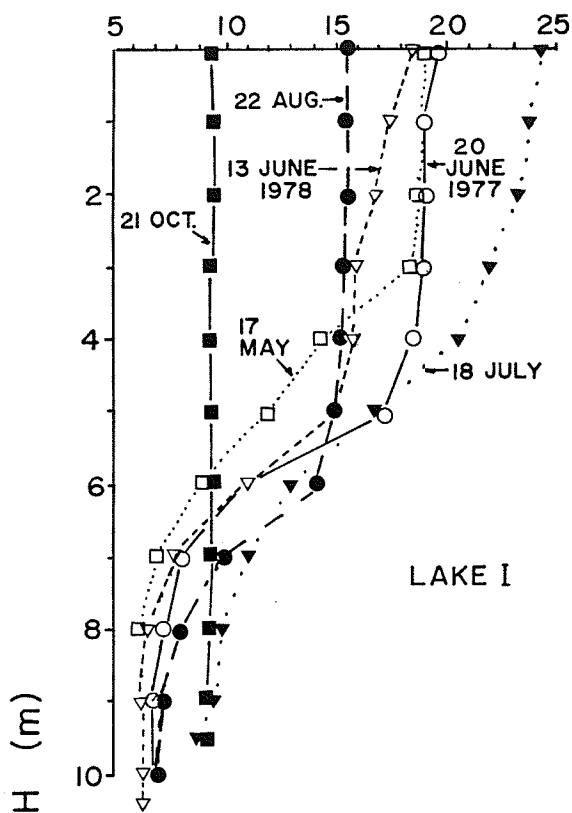
before Lakes III and IV. In 1977, thermal stratification in Lake I was well established by mid May (Fig. 2). Epilimnion temperature was about 20°C to a depth of 3 m. Temperature of the metalimnion, which extended from 3 m to 7 m, dropped from 20°C to 7°C at the lower limit (Ward et al., unpublished). The hypolimnion extended below 7 m. Thermal stratification continued to develop during the summer. In mid July the epilimnion extended to 4 m and the surface temperature was 24°C. By the end of August the epilimnion began to cool, and by October 21 the entire water column was presumably mixing at a constant 9°C.

In Lake II the temperature regime was similar, although thermal stratification was not so pronounced. In July, the boundary of the epilimnion and metalimnion was obscure, indicating that mixing was occurring at greater depths than in Lake I (Fig. 2). Lake III stratified only briefly during calm periods. The hypolimnion temperature, always above 12°C in spring and summer, indicates some mixing was occurring. Lake IV showed the least evidence for thermal stratification. Constant mixing, as indicated by the relatively uniform temperature of the water column, occurred throughout the ice-free season (Fig. 2).

After vernal and autumnal circulation, oxygen levels below 4 m (4 m was the depth of the epilimnion in Lake I during stratification and is used as a basis for making comparisons with the other lakes which failed to stratify

Figure 2. Temperature profiles of the Fort Whyte lakes during the ice-free period of 1977 and in June, 1978.

TEMPERATURE (C)



strongly) declined rapidly in Lake I but with decreasing rapidity in Lakes II, III, and IV (Fig. 3), indicating that the highest levels of biochemical oxidation were in Lake I and the lowest in Lake IV. These temperature and oxygen data indicate that fish in Lake I may be restricted to the epilimnion for much of the year while in Lake IV they may be able to utilize the entire lake for a longer period.

Major differences among the lakes also existed in the mean values of other chemical parameters during 1977-1978. Ammonia levels were highest in Lake I, second highest in Lake II, and lowest in Lake IV at both 0-4 m and 4 m-bottom (Table 2). The high ammonia concentration below 4 m in Lake I is partly the result of well developed thermal stratification and hypolimnial anoxia (Ward and Loadman MS 1981). Lake IV had the least highly developed thermal stratification.

High levels of total dissolved phosphorus in Lake I were probably caused by nutrient enriched wastewater entering from the waterfowl enclosures. The mean total dissolved phosphorus value at 4 m-bottom in Lake I was more than twice that of Lake II and more than eleven times the level in Lake IV at the same depth range (Table 2). However, these concentrations were generally unavailable to the phytoplankton. Above 4 m, total dissolved phosphorus was highest in Lake II, second highest in Lake I, and lowest in Lake IV (Table 2).

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

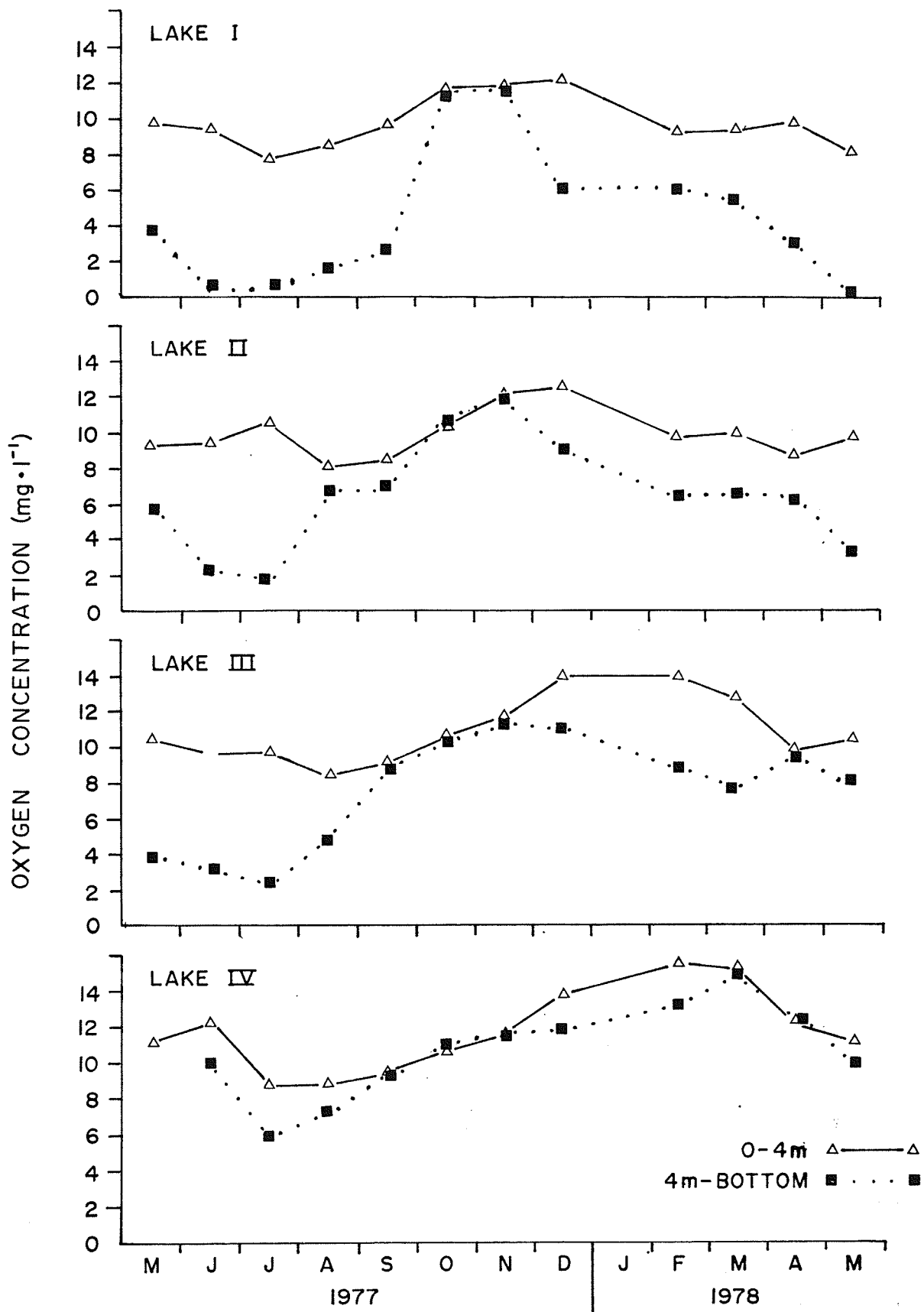


Table 2. Annual mean values of chemical parameters in the Fort Whyte lakes (June 1977 - October 1978)^a.

Parameter	LAKE							
	I		II		III		IV	
	0-4m	4m-bottom	0-4m	4m-bottom	0-4m	4m-bottom	0-4m	4m-bottom
Ammonia (mg. m ⁻³)	127	1124	113	350	94	204	35	57
Total dissolved phosphorus (mg. m ⁻³)	20	124	27	49	17	13	12	11
Chlorophyll (mg. m ⁻³)	7.6	4.8	14.1	4.2	6.9	3.6	5.2	4.2
Total dissolved solids (mg. m ⁻³)	576	692	330	360	379	392	456	467
pH	8.5	7.9	8.4	8.0	8.5	8.1	8.5	8.4

^a Data taken from Ward and Loadman MS (1981).

The surface waters of Lake II had the highest mean value of chlorophyll (Table 2). This was the result of a bloom of blue-green algae which occurred in 1977 (Ward and Loadman MS 1981). A less intense bloom also occurred in Lake III. In the spring of 1977 there was an influx of fertilizer-enriched water from the farm field drainage ditch into Lake II with some spillover into Lake III. No algal blooms or influx of nutrient-enriched waters occurred in 1978 or 1979. Lake I had the second highest levels of chlorophyll, probably the result of nutrient-rich water entering the lake from the waterfowl ponds. Lake IV had the lowest chlorophyll levels (Table 2).

Mean total dissolved solids were highest in Lake I at both depth ranges (Table 2). A higher value in Lake IV than in Lakes II and III probably results from more frequent wind caused mixing and also from high levels of suspended organic matter caused by dredging activity (Ward and Loadman MS 1981). pH was high in all lakes (Table 2).

A more detailed description of the limnology of the Fort Whyte lakes can be found in Ward and Loadman (MS 1981).

In summary, the lakes showed differences in age, morphometry, thermal stratification, oxygen deficits, and nutrient levels. Lake I, the smallest and oldest lake, had a lower mean depth, a well developed thermal stratification, high hypolimnial biochemical oxygen demand, and high nutrient levels resulting from a year round flow of

nutrient-enriched water from a waterfowl enclosure. Lake II also had high nutrient levels because of an occasional influx of nutrient-rich water from a drainage ditch. Some spills over into Lake III. Lake IV, the largest and youngest lake, had a higher mean depth, poorly developed thermal stratification, and higher hypolimnial oxygen levels. Nutrient levels were low because there was no direct input of fertilized water as there was to the other lakes.

Eight species of fish are known to occur in the Fort Whyte lakes (Table 3). All species were present in Lake I, six in Lake II, five in Lake III, and only four in Lake IV. The yellow perch was the most abundant species with northern pike, carp, and largemouth bass also numerous. The remaining species were rarely encountered. It is unknown how or when the various species first entered the lakes. Some may have entered naturally via the drainage ditch which ultimately joins the Red River. Others, like the bass, were introduced by man. It is known, however, that fish have been present in Lake I for many years. A largemouth bass in the Fish Museum, Dept. of Zoology, University of Manitoba, was reported captured from Lake I in 1946. The populations in the new lakes, III and IV, are obviously the result of more recent plantings or movements.

Table 3. Fish species occurring (x) in the Fort Whyte lakes^a.

Scientific Name	Common Name	Lake			
		I	II	III	IV
<u>Esox lucius</u> Linnaeus	northern pike	x	x	x	x
<u>Cyprinus carpio</u> Linnaeus	common carp	x	x	x	x
<u>Pimephales promelas</u> Rafinesque	fathead minnow	x	x	x	
<u>Catostomus commersoni</u> (Lacépède)	white sucker	x			
<u>Ictalurus nebulosus</u> (Lesueur)	brown bullhead	x			
<u>Culaea inconstans</u> (Kirtland)	brook stickleback	x	x		
<u>Micropterus salmoides</u> (Lacépède)	largemouth bass	x	x	x	x
<u>Perca flavescens</u> (Mitchill)	yellow perch	x	x	x	x

^a Scientific and common names of fishes taken from Robins et al. (1980).

MATERIALS AND METHODS

In 1978, hoop nets and seines were used to sample yellow perch, all with 6.4 mm mesh size (stretched-mesh measure). In 1979, a fine mesh (12 meshes per cm) trap net (Beamish 1972; 1973) modified with 10 m wings was used almost exclusively. All hoop and trap nets were fished parallel to shore usually in 2-4 m of water, with one wing tied onshore and the other anchored offshore, with no leader. They were checked daily. A standard seine haul consisted of setting the seine at 90° to the shore and making a sweep in an arc to shore.

Fork length was measured on all specimens to the nearest millimetre. Weight was measured to 0.1 g. Sex was ascertained by gross examination of the gonads. All measurements were performed with fresh fish. Young-of-the-year perch were not examined.

Relative abundance and biomass of perch in the Fort Whyte lakes was estimated, in 1979, from weekly catch-per-unit-effort (CPUE) data expressed as numbers and as weight(g) of perch caught per hour. Weights were calculated from fork lengths and the weight-length relation pooled by sex for fish in the particular lake. Standardized trap nets were utilized to obtain data. Nets were set in 2-4 m water

(above the thermocline) and checked daily. With only three nets available, it was impossible to fish all four lakes in the same 24 hour period. In each week four fishing periods were defined. Each lake was fished for three of these approximately 24 hour periods each week with a different combination of three lakes fished during each period. Lakes I, II, and III were fished during the first period; I, II, and IV in the second; I, III, and IV in the third; and II, III, and IV in the fourth. This sequence was repeated for ten weeks from late June to late August. Each lake was fished at the same location for the entire week. Five equidistant locations along the shoreline of every lake were previously determined (Stations A to E) (Fig. 1). Beginning with a northwest location (Station A) trap nets were moved weekly to the next location in a clockwise rotation. Thus, each location was fished for two three-day periods over the ten-week sampling program. Under the above conditions CPUE values reflect population abundance (Moyle 1948). Changes in perch distribution, possibly caused by high surface water temperatures, required that the weekly rotation of locations be abandoned in Lake I. Only Stations A and B were fished in Lake I for the last five weeks of the experiment. Comparisons of CPUE were made among lakes by analysis of variance (Steel and Torrie 1980). A randomized complete block design was utilized for comparing numbers of perch and a completely randomized design for comparing weight of perch caught per hour.

Perch were aged from scales removed from the left side of the fish, below the lateral line, near the tip of the pectoral fin (laid flat against the body). Scale impressions were made on acetate slides with a roller press (Smith 1954). Usually at least three scales were pressed per fish. Slides were viewed with a Bausch and Lomb projector at a magnification of 45X. Scales were examined twice without reference to fish size or sex and assigned an age. An annulus was assumed to be present on the edge of scales obtained in spring before growth had begun (Jobes 1952; el-Zarka 1959; Berg and Grimaldi 1967). Validity of the scale method of ageing was described for yellow perch by Jobes (1952) and Joeris (1957).

Length and age compositions of the Fort Whyte yellow perch populations were examined. Percent length frequency distributions (5 mm length intervals were used) were constructed from samples collected over a short period of time in each lake in both 1978 and 1979. From subsamples, length frequency distributions separated by age and sex were constructed and the percentage of the total sample represented by each year class calculated. It was assumed that the number of individuals in any age class found in a particular length interval in the subsample was proportional to the number of individuals of that age class and length in the sample (Ketchen 1950). In 1978 subsamples were randomly selected except that there was a tendency to include more of

the larger fish. In 1979 a stratified random selection technique was employed (Ketchen 1950) with up to 15-16 perch subsampled from every 5 mm size interval.

Bi-weekly percent length frequency distributions were also constructed to examine size distributions over the entire 1979 sampling season.

Weight-length relationships, using samples collected in June and early July 1979, were determined for each lake by the least squares method and the equation $\log_{10} W = \log_{10} a + b \log_{10} L$ where W is the weight (g), a is a constant, b is the regression coefficient, and L is the fork length (mm). The relationship was compared between sexes within lakes and then compared among lakes by analysis of covariance tests (Snedecor and Cochran 1967). Relative condition of perch in each lake was compared using adjusted mean weights (Le Cren 1951).

A body length-scale radius relationship was determined, utilizing data from aged subsamples from both years, for each lake from the equation $L = a + bS$ and the least squares method where L is the fork length (mm), a is a constant, b is the regression coefficient, and S is the total scale radius (X45 mm). Back calculations of perch length at each annulus were made with a modification of the above direct proportion formula: $L_n - a = S_n(L - a) / S$ (Fraser 1916; Lee 1920) where L_n is the fork length at the n'th annulus (mm) and S_n is the total scale radius at the n'th annulus (X45 mm). The

value of \underline{a} was obtained from the body-scale relationship. \underline{S} was measured to the nearest millimetre (X45) from the nucleus to the middle of the front margin of each scale. \underline{S}_n was similarly measured. Mean lengths at each annulus were calculated separately for males and females and intra-lake comparisons between sexes and inter-lake comparisons within each sex were made. Inter-lake comparisons were performed by two-way analysis of variance, with lake-age interaction where necessary (Steel and Torrie 1980), using the SAS general linear model procedure for unbalanced designs (Helwig and Council 1979). Only lengths at the last completed year of growth for each year class were utilized in inter-lake comparisons. Data for the years 1978 and 1979 were examined separately.

RESULTS

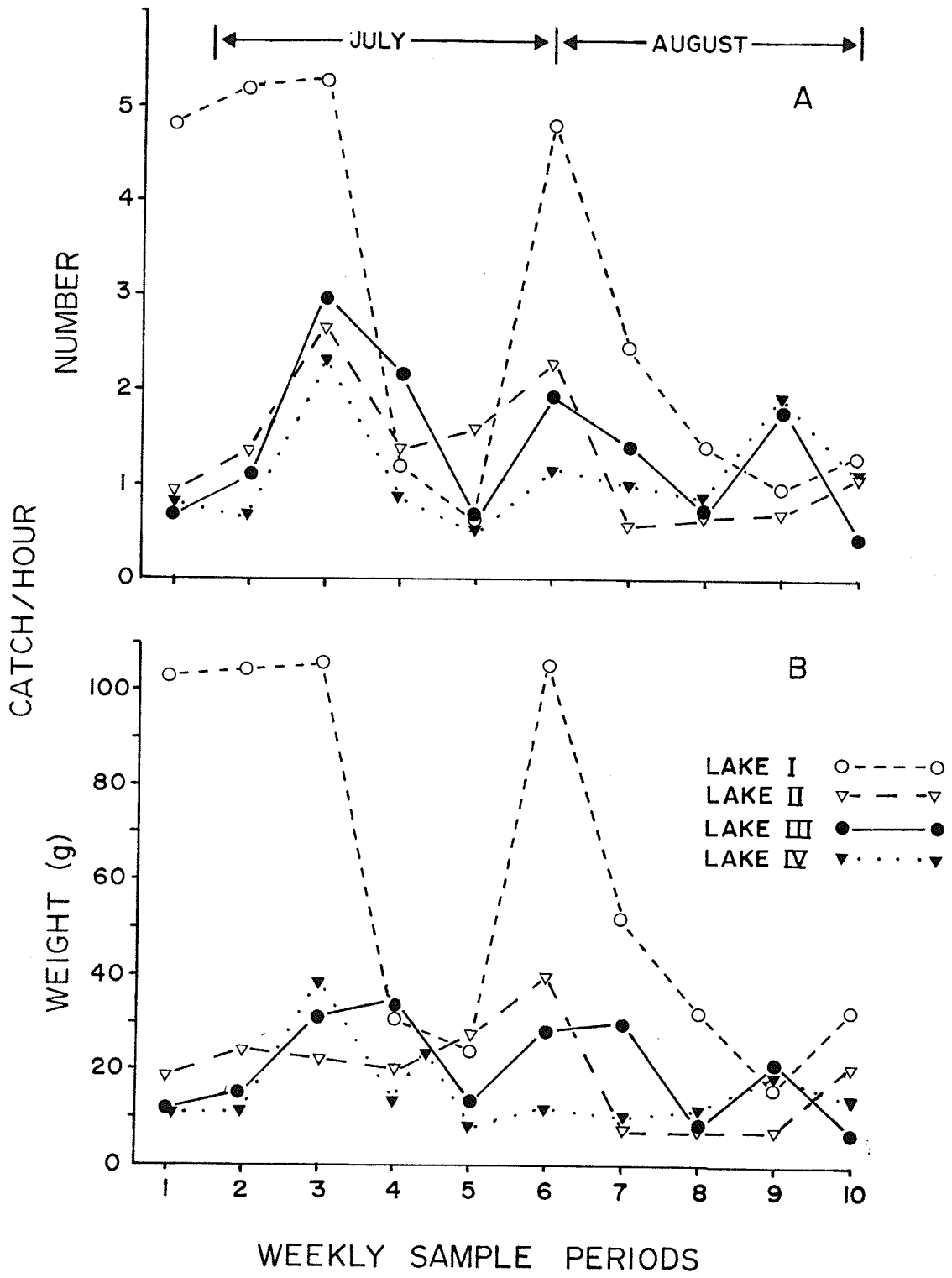
Relative Abundance and Biomass

Catch-per-unit-effort values varied considerably from week to week but were usually highest in Lake I (Fig. 4). Lake I exhibited the greatest variability as values declined greatly for Weeks 4 and 5 (Stations D and E, Fig. 1). They increased again for Week 6 (Station A) but again declined even though fishing was limited to Stations A and B for the last five weeks of the experiment (Fig. 4).

Comparisons of CPUE among lakes were performed by analysis of variance. To meet the assumptions of the analyses it was necessary to transform data to the square root of the number of perch caught per hour and to \log_{10} weight(g) of perch caught per hour. These transformations were based on Taylor's power law (Green 1979).

Bartlett's test (Snedecor and Cochran 1967) indicated homogeneity of variances for both the transformed number of perch ($P=0.043$) and weight of perch ($P=0.930$) caught per hour. There was a significant difference among lakes ($P=0.004$) in the transformed number of perch caught per hour. Overall mean transformed number of perch caught per hour over the 10 week sampling period was 1.569 for Lake I, 1.108 for Lake II, 1.137 for Lake III, and 1.028 for

Figure 4. Weekly CPUE values during June 26 - August 31, 1979. A. Number of perch caught per hour. B. Weight (g) of perch caught per hour.



Lake IV. Pairwise comparisons of all means were made by least significant difference (LSD) (Steel and Torrie 1980). The Critical Region (CR) was $\geq t_{0.025, (a-1)(b-1)}$ $(2 \text{ MSE}/b)^{1/2} = 0.230$. The mean for Lake I was significantly higher than for the other lakes (Table 4). There was no significant difference among Lakes II, III and IV (Table 4).

Results of analysis of variance indicated a significant difference in the transformed weight(g) of perch caught per hour each week among all lakes ($P < 0.001$). Overall mean transformed weight(g) of perch caught per hour over the 10 week sampling period was 1.691 for Lake I, 1.242 for Lake II, 1.234 for Lake III, and 1.070 for Lake IV. With a CR $\geq t_{0.025, a(n-1)}$ $(2 \text{ MSE}/n)^{1/2} = 0.300$, LSD pairwise comparisons indicated no significant differences in the means among Lakes II, III, and IV but that it was significantly higher for Lake I (Table 4).

These results indicate that Lake I had a significantly higher relative perch abundance and perch biomass. The overall arithmetic mean number of perch caught per hour was 2.8 for Lake I, 1.3 for Lake II, 1.4 for Lake III, and 1.1 for Lake IV. The overall arithmetic mean weight(g) of perch caught per hour was 60.6 for Lake I, 19.9 for Lake II, 20.0 for Lake III, and 15.0 for Lake IV. Thus, relative perch abundance in Lake I was 2.2 times higher than in Lake II, 2.0 times higher than in Lake III, and 2.5 times higher than in Lake IV, while relative perch biomass in Lake I was 3.0

Table 4. Least significant difference comparison of overall mean transformed number of perch caught per hour and of overall mean transformed weight (g) of perch caught per hour.

Difference in mean number of perch caught per hour between lakes				Difference in mean weight of perch caught per hour between lakes			
Lake	IV	III	II	Lake	IV	III	II
I	0.541*	0.432*	0.461*	I	0.621*	0.457*	0.449*
II	0.080	0.029		II	0.172	0.008	
III	0.109			III	0.164		

* significant

times that in Lakes II and III, and 4.0 times higher than in Lake IV. These data indicate that the average size of perch captured in Lake I was greater than in the other lakes.

Age and Length

In 1978, perch of a wide range in length and in age were numerous in Lake I but there were few one-year-olds (Fig. 5). The 1977 year class (age 1) formed only 9% of the total catch. Perch of the 1976, 1975, and 1974 year classes were numerous making up 47%, 17%, and 24% of the catch respectively. There were only a few (2%) five-year-old fish (the 1973 year class).

In Lakes II (Fig. 6), III (Fig. 7), and IV (Fig. 8) a narrower length range of perch was captured with the majority of the fish in the 1977 and 1976 year classes. The 1976 year class dominated the catches, forming 59% of the sample in Lake II, 50% in Lake III, and 65% in Lake IV. The 1977 year class made up 33% of the catch in Lake II, 44% in Lake III, and 26% in Lake IV. There were few older perch: the 1975 year class represented 5%, 5%, and 7%, the 1974 year class 2%, 1%, and 1%, and the 1973 year class less than 0.5%, 0%, and 1% of the sample in Lakes II, III, and IV respectively.

Length frequency distributions from June and early July 1979 indicated the same pattern as in 1978. In Lake I

Figure 5. Length distributions of Lake I perch captured during August 20-25, 1978.

A. Percent length frequency distribution of entire sample. B through F are length frequency distributions constructed from a subsample of 208 perch separated by age and sex. B. 1977 year class. C. 1976 year class. D. 1975 year class. E. 1974 year class. F. 1973 year class. * indicates < 0.5%. M and F refers to males and females respectively.

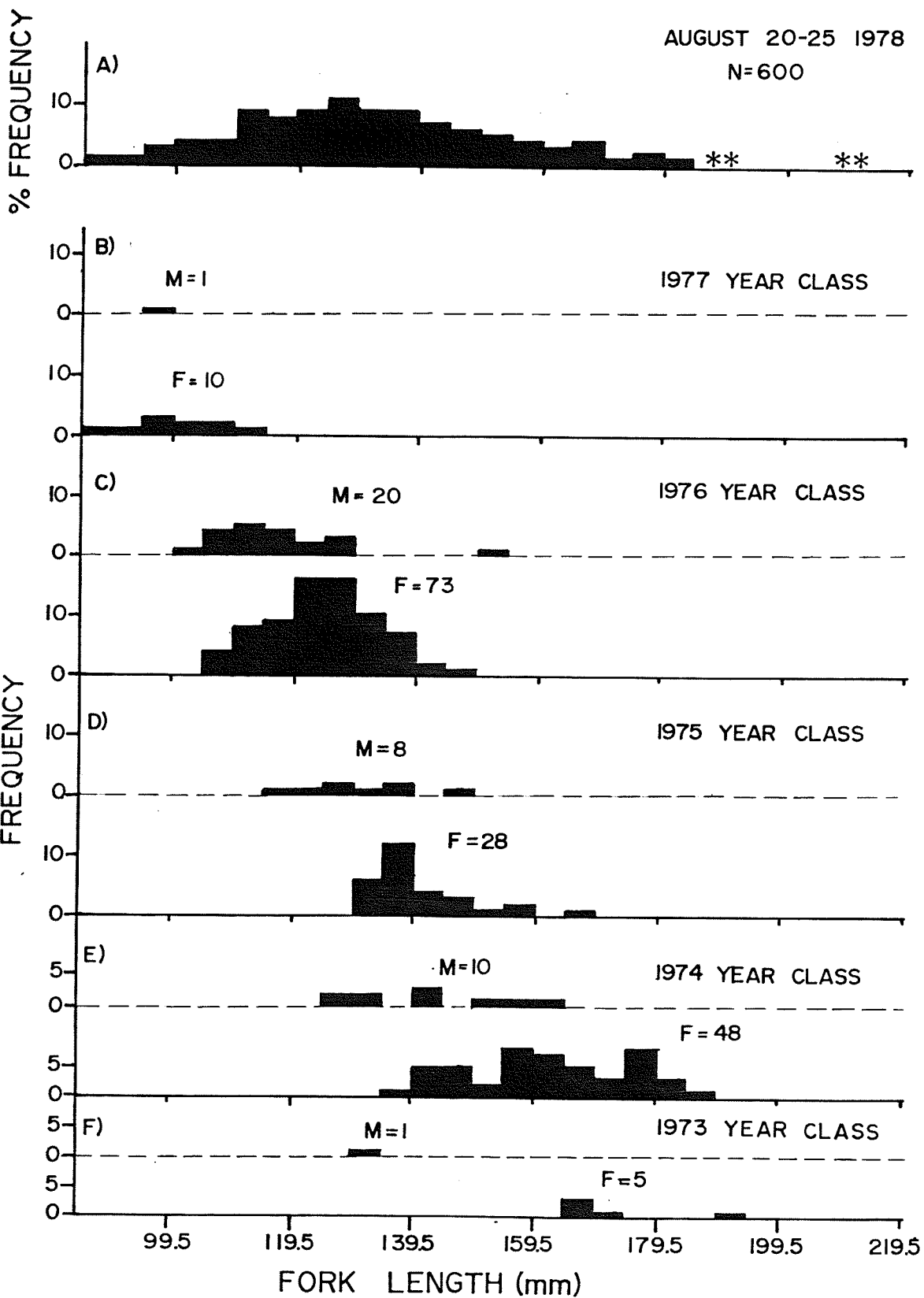


Figure 6. Length distributions of Lake II perch captured during July 21-31, 1978. A. percent length frequency distribution of entire sample. B through F are length frequency distributions constructed from a subsample of 155 perch separated by age and sex. B. 1977 year class. C. 1976 year class. D. 1975 year class. E. 1974 year class. F. 1973 year class. * indicates < 0.5%. M and F refers to males and females respectively.

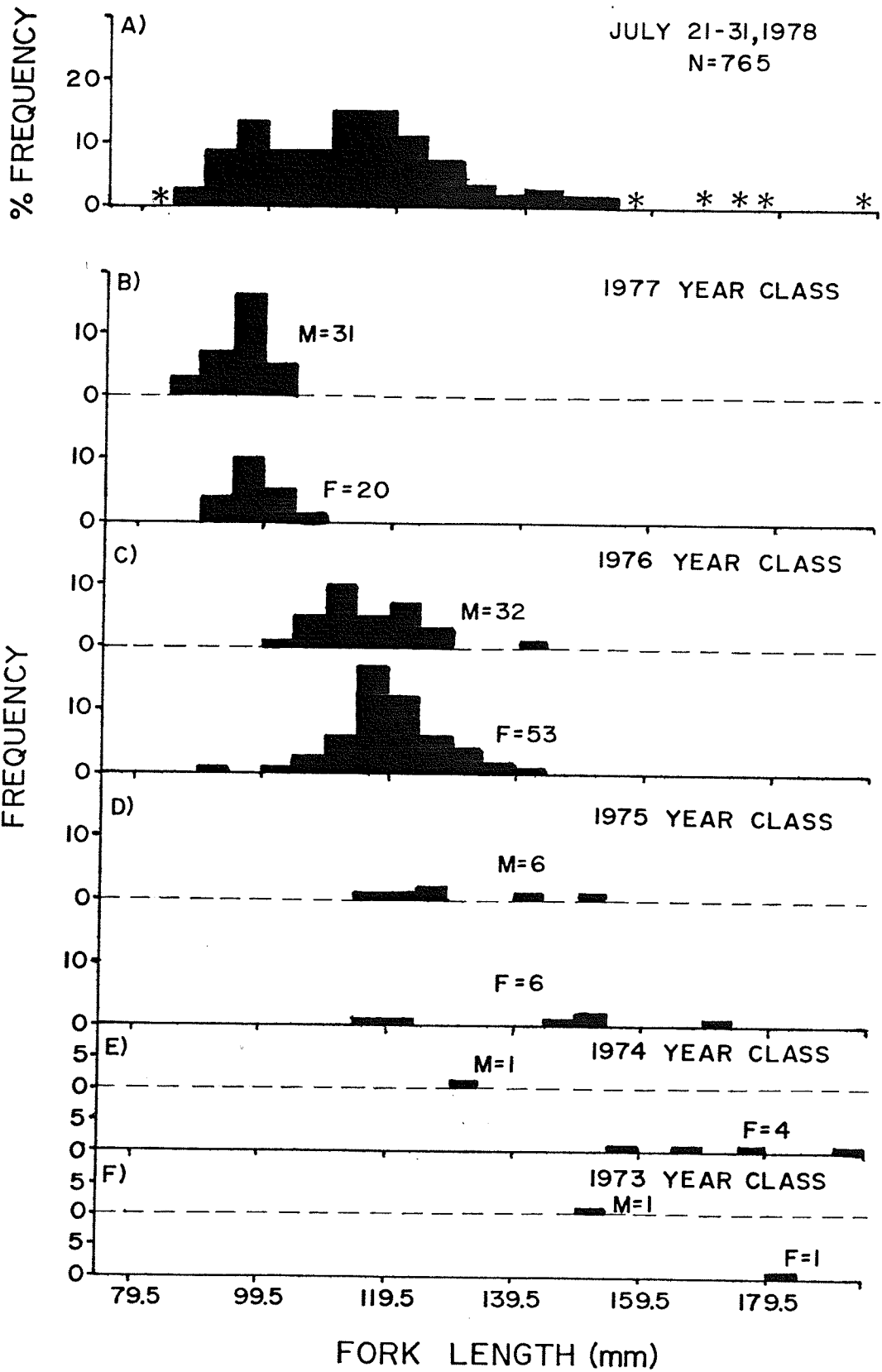


Figure 7. Length distributions of Lake III perch captured during July 27 - August 10, 1978.

A. percent length frequency distribution of entire sample. B through F are length frequency distributions constructed from a subsample of 148 perch separated by age and sex. B. 1977 year class. C. 1976 year class. D. 1975 year class. E. 1974 year class. F. 1973 year class. M and F refers to males and females respectively.

JULY 27-AUGUST 10, 1978

N=149

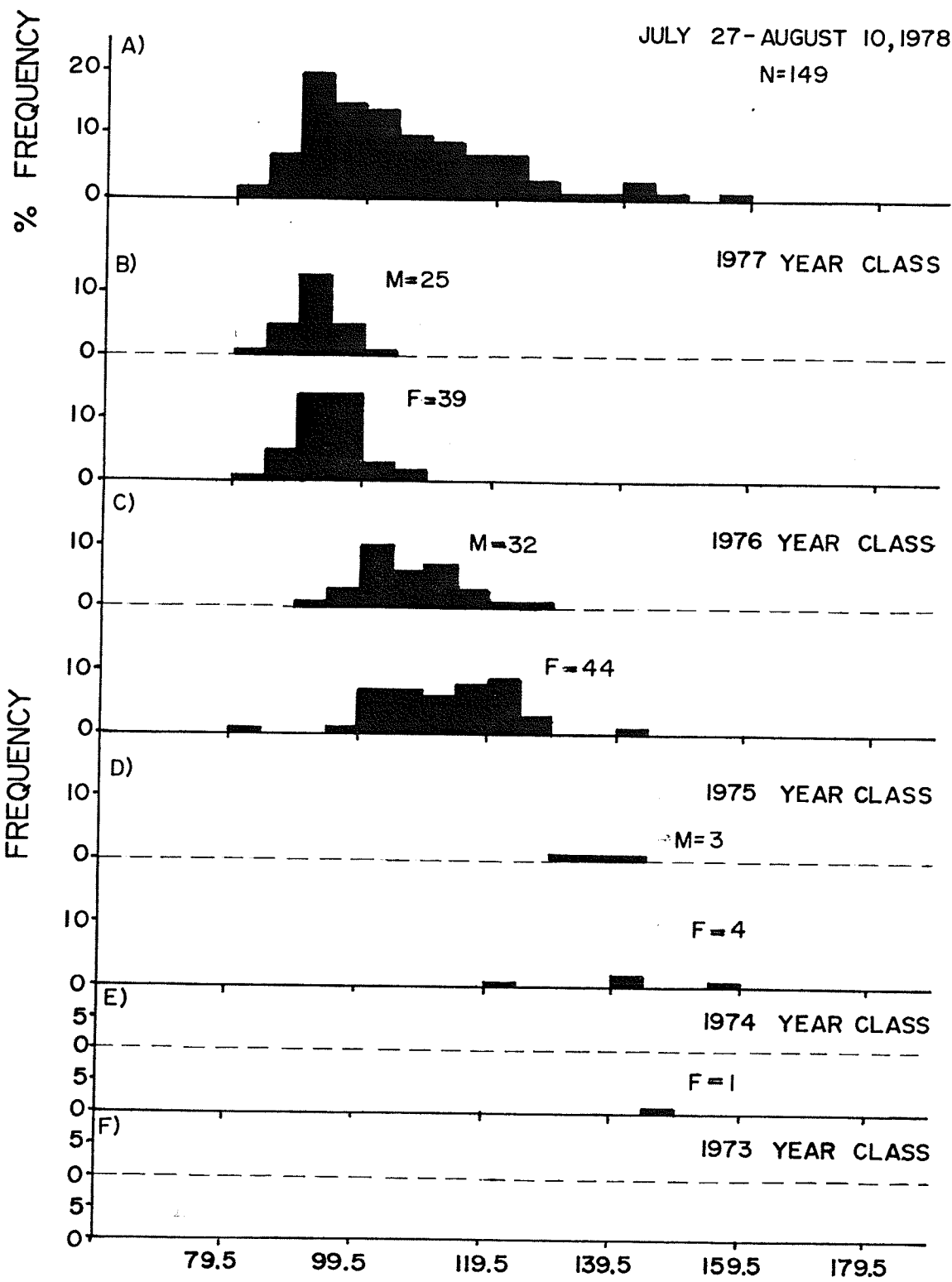


Figure 8. Length distributions of Lake IV perch captured during August 1-15, 1978.

A. percent length frequency distribution of entire sample. B through F are length distributions constructed from a subsample of 101 perch separated by age and sex.

B. 1977 year class. C. 1976 year class.
D. 1975 year class. E. 1974 year class.
F. 1973 year class. M and F refers to males and females respectively.

larger, older perch made up the largest percentage of the population (Fig. 9). The newly recruited 1978 year class formed only 3% of the total catch, indicating a second year of poor recruitment. The 1976 year class again dominated the sample (72% of catch). The 1977 year class represented 10%, the 1975 year class 12%, and the 1974 year class 3% of the total catch. There were only two perch older than age five.

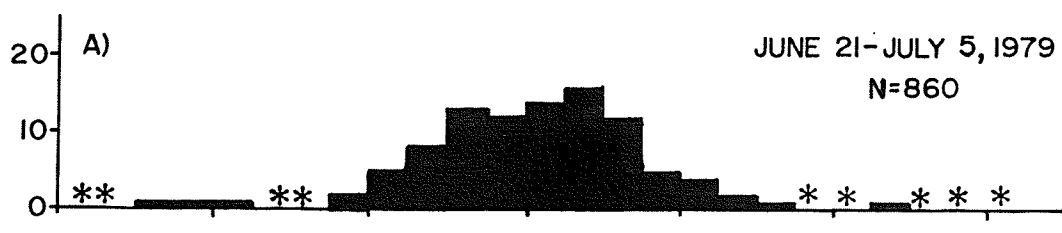
In contrast, the 1978 year class was very strong in Lakes II (Fig. 10), III (Fig. 11), and IV (Fig. 12) and formed 65%, 64%, and 69% of their populations respectively. Perch of the 1977 and 1976 year classes remained numerous but their percentage of the sample declined to 18% and 13% respectively in Lake II, 8% and 24% respectively in Lake III, and 11% and 16% respectively in Lake IV. Older fish were not abundant. The 1975 year class made up 2%, 3%, and 3%, and the 1974 year class 1%, less than 0.5%, and 1% of the sample in Lakes II, III, and IV respectively.

In addition to the inter-lake differences indicated above, there were also intra-lake differences in length frequency distributions between years that were common to perch populations in all the Fort Whyte lakes. In 1978, there was considerable overlap of the various age groups and the length distributions of the entire sample were basically unimodal in each lake (Figs. 5, 6, 7, and 8). In 1979, the distributions were bimodal with the 1978 year class forming

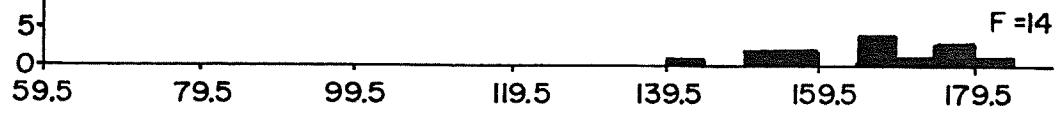
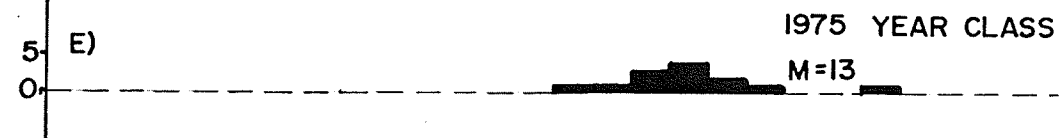
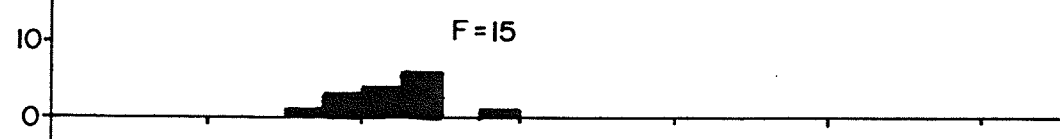
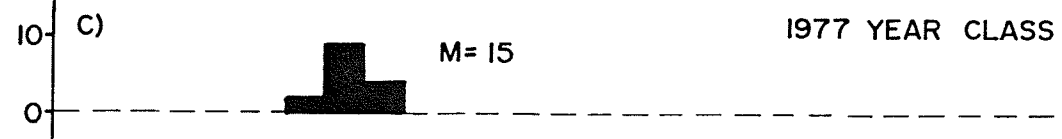
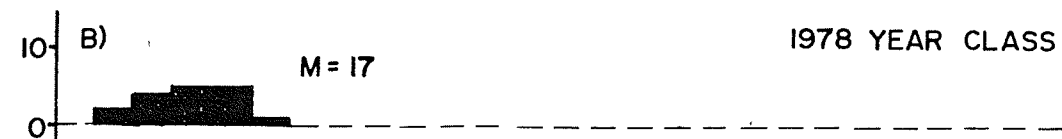
Figure 9. Length distributions of Lake I perch captured during June 21 - July 5, 1979.

A. percent length frequency distribution of entire sample. B through F are length frequency distributions constructed from a subsample of 204 perch separated by age and sex. B. 1978 year class. C. 1977 year class. D. 1976 year class. E. 1975 year class. F. 1974 year class. * indicates < 0.5%. M and F refers to males and females respectively.

% FREQUENCY



FREQUENCY



FORK LENGTH (mm)

Figure 10. Length distributions of Lake II perch captured during June 14-20, 1979.

A. percent length frequency distribution of entire sample. B through F are length frequency distributions constructed from a subsample of 174 perch separated by age and sex. B. 1978 year class. C. 1977 year class. D. 1976 year class. E. 1975 year class. F. 1974 year class. * indicates < 0.5%. M and F refers to males and females respectively.

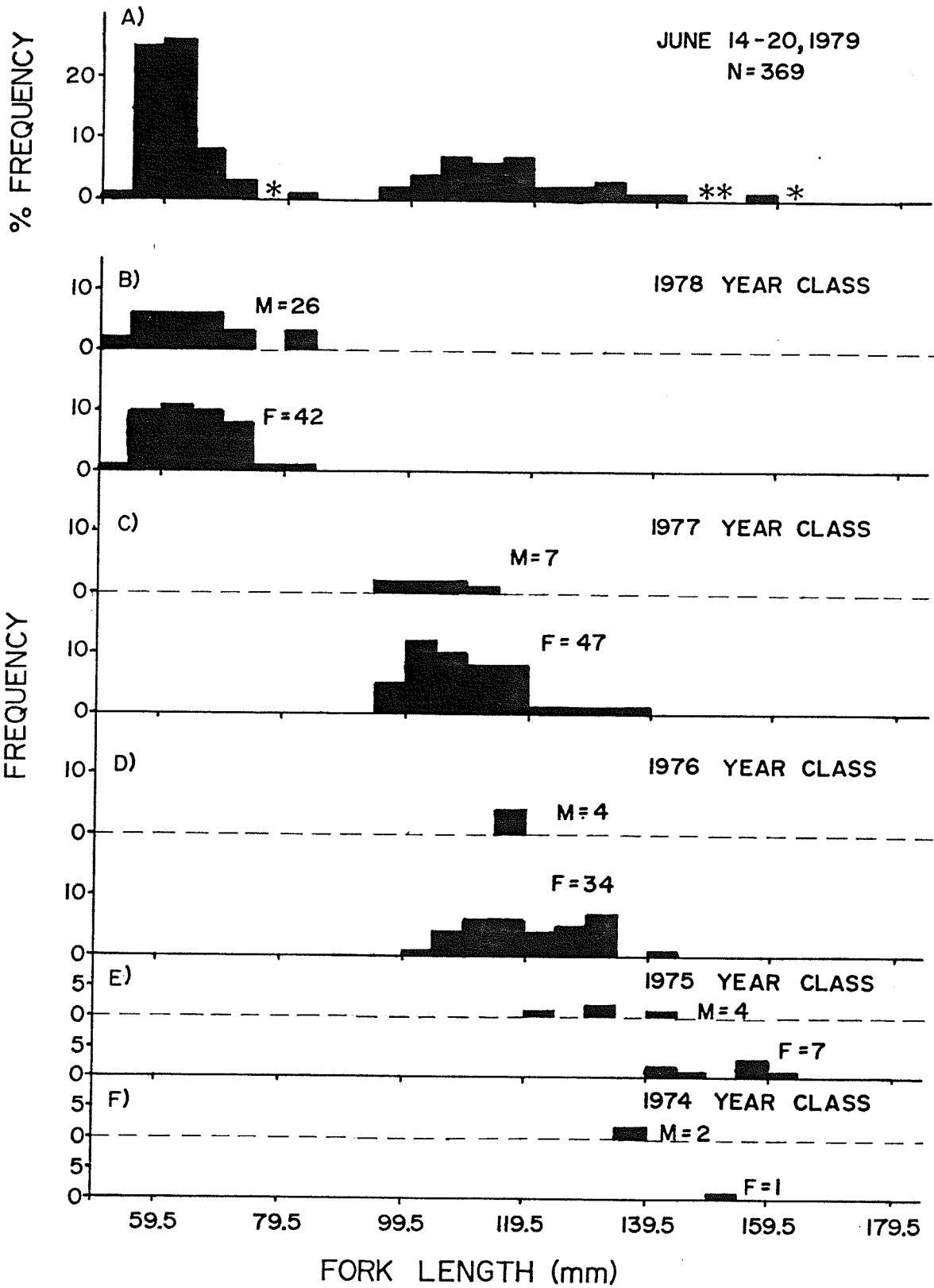


Figure 11. Length distributions of Lake III perch captured during June 12-13, 1979.

A. percent length frequency distribution of entire sample. B through F are length frequency distributions constructed from a subsample of 205 perch separated by age and sex. B. 1978 year class. C. 1977 year class. D. 1976 year class. E. 1975 year class. F. 1974 year class. * indicates < 0.5%. M and F refers to males and females respectively.

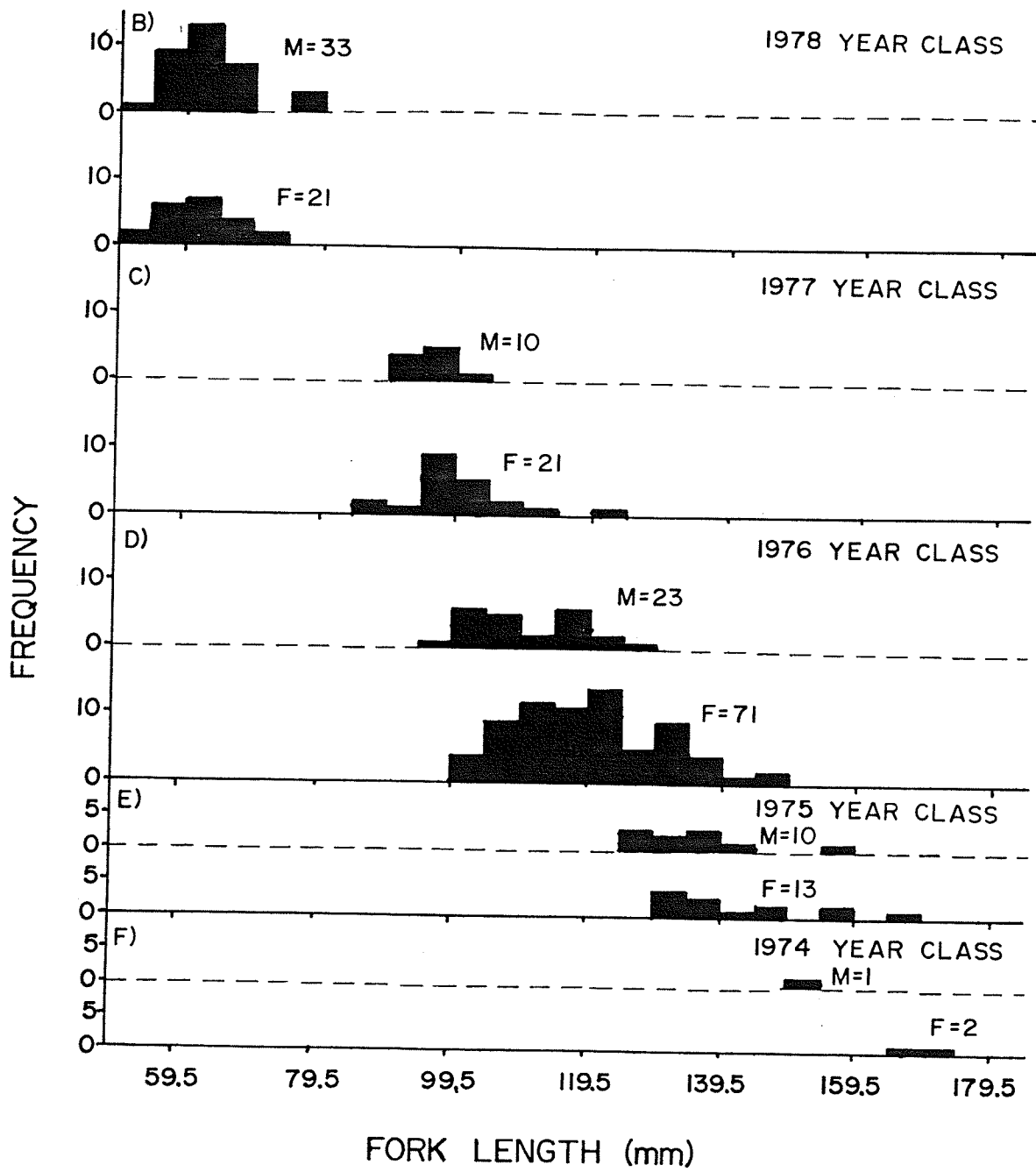
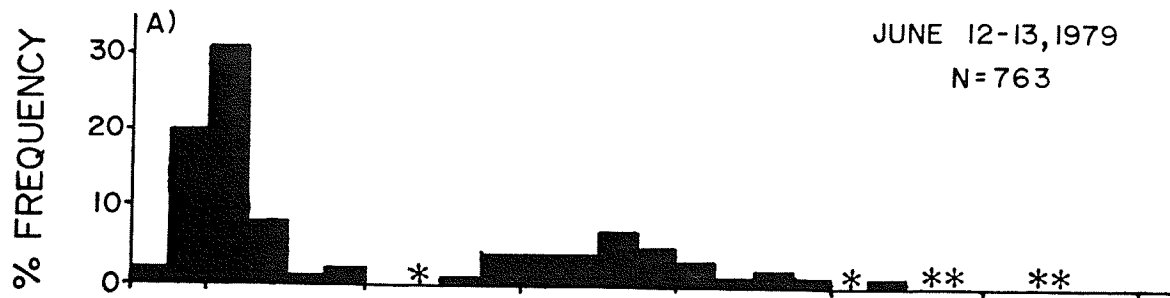


Figure 12. Length distributions of Lake IV perch captured during June 5-8, 1979.

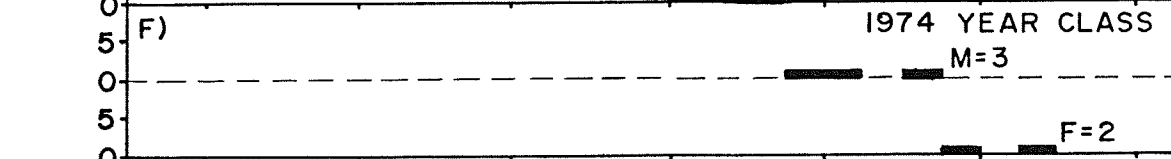
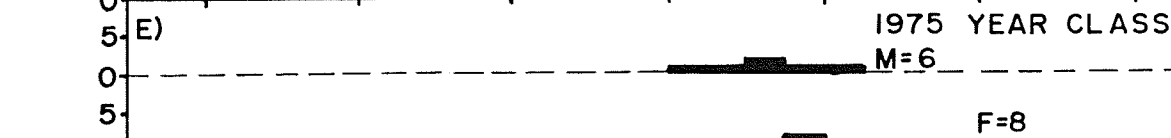
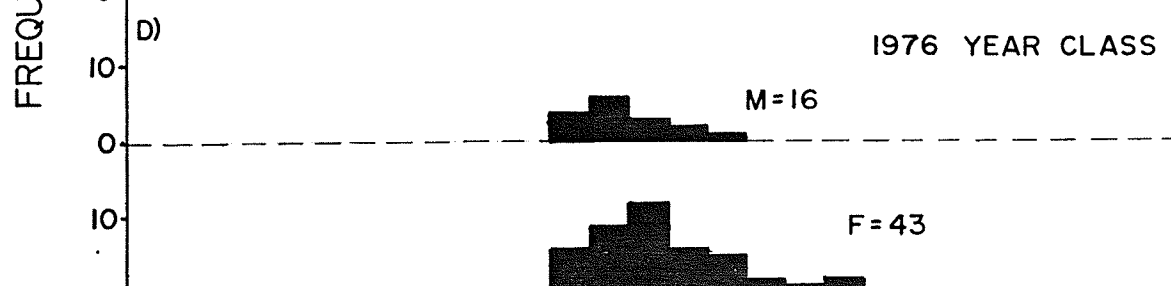
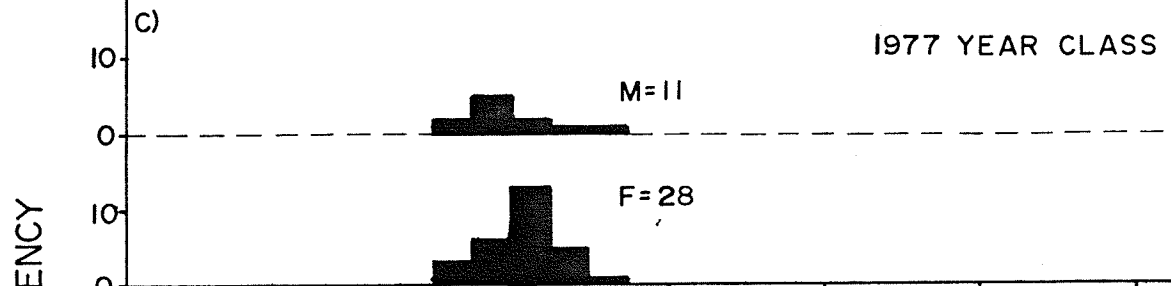
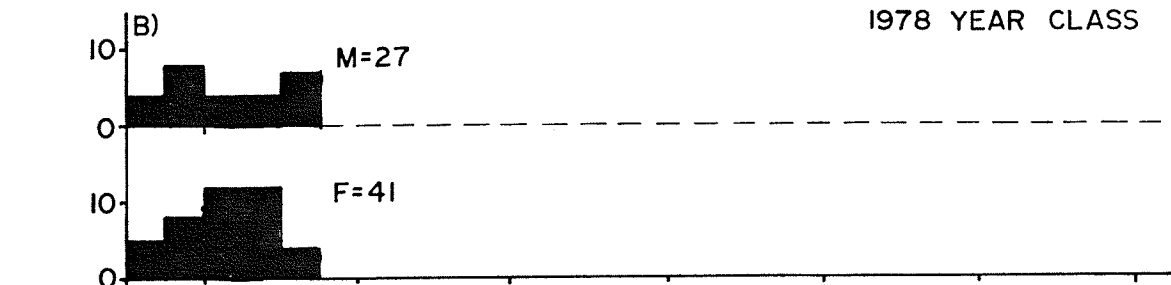
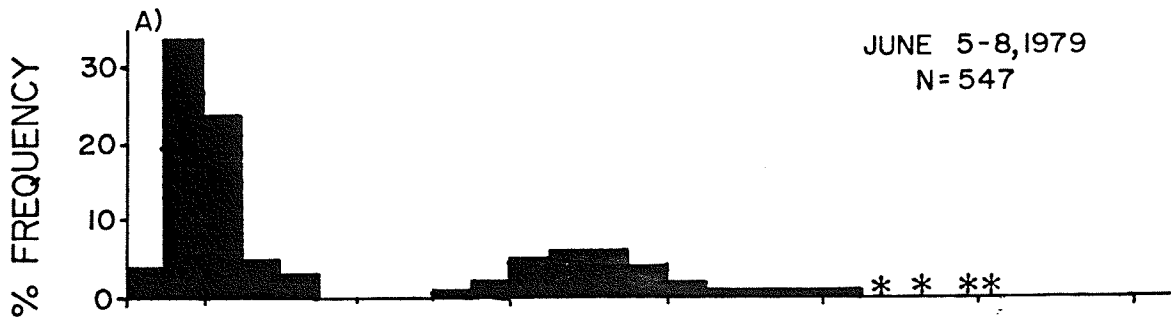
A. percent length frequency distribution of entire sample. B through F are length distributions constructed from a subsample of 185 perch separated by age and sex.

B. 1978 year class. C. 1977 year class.

D. 1976 year class. E. 1975 year class.

F. 1974 year class. * indicates <0.5%.

M and F refers to males and females respectively.



FORK LENGTH (mm)

a distinct mode (Figs. 9, 10, 11, and 12). This mode remained distinct in all lakes for the entire 1979 sampling season (Figs. 13, 14, 15, and 16 for Lakes I, II, III, and IV respectively) and indicated changes in perch growth had occurred between years sampled. As summer progressed, larger sized perch made up a smaller percentage of the total catch in each lake in 1979.

Growth

Bartlett's test indicated homogeneity of variances about the regressions for all comparisons of weight-length relationships. For comparisons between sexes within lakes, $P=0.202$, $P=0.870$, $P=0.730$, and $P=0.156$ for Lakes I to IV respectively. For comparison among all lakes, with sexes pooled, $P=0.071$ and for comparison among lakes excluding Lake I, with sexes pooled, $P=0.032$. There were no significant differences in the weight-length relationships between sexes within lakes (Table 5), therefore data for males and females were pooled for further analyses. There were significant differences in the weight-length relationships, pooled by sex, among all lakes (Table 5). When Lake I was removed from the analysis, there was no longer a significant difference in the regression coefficients among lakes although there remained a significant difference in the y-intercepts (Table 5). It was concluded that \underline{b} was significantly lower for Lake I and that the increase in

Figure 13. Percent length frequency distributions of Lake I perch during the 1979 sampling season. * indicates < 0.5%.

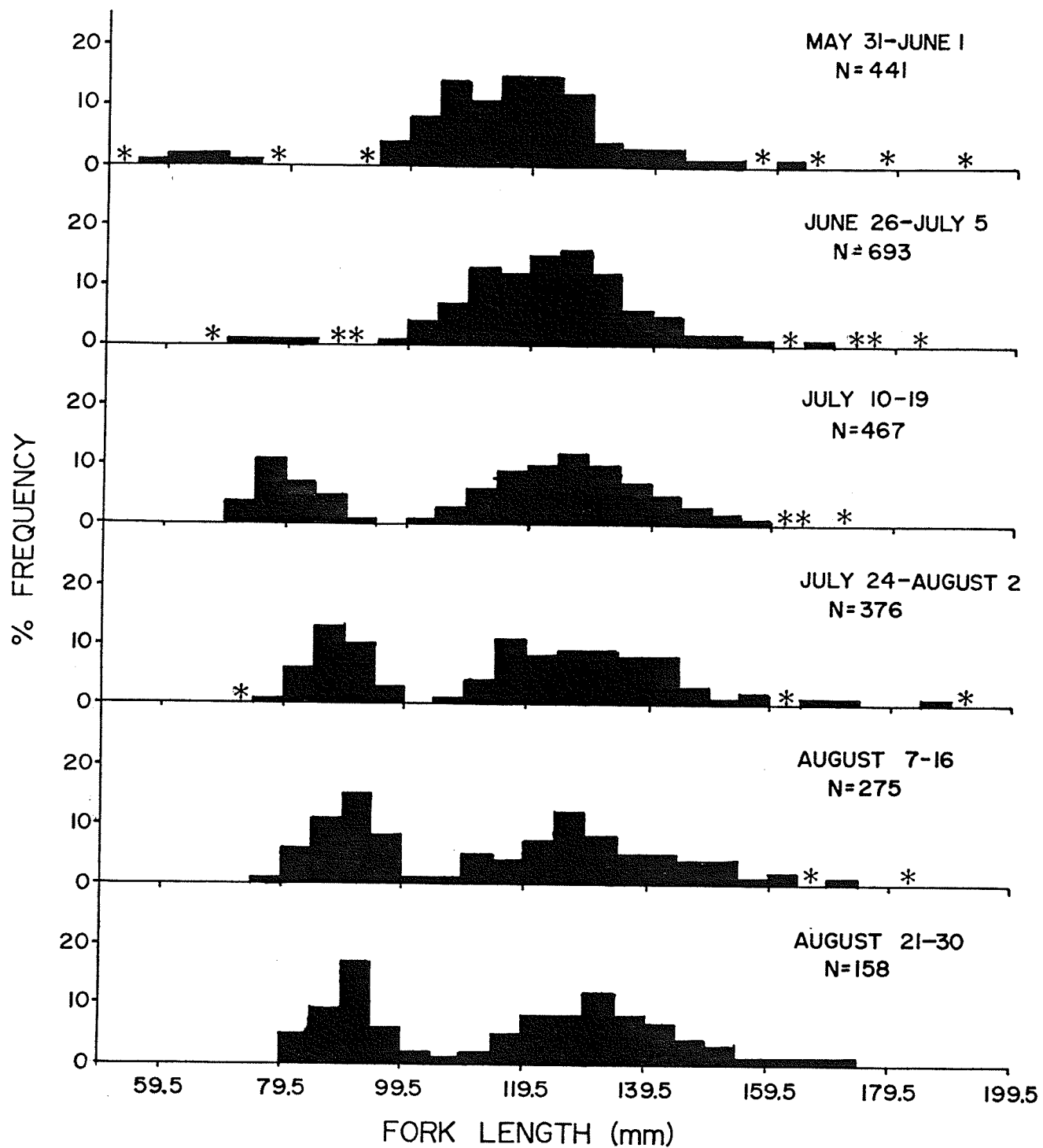


Figure 14. Percent length frequency distributions of Lake II perch during the 1979 sampling season. * indicates < 0.5%.

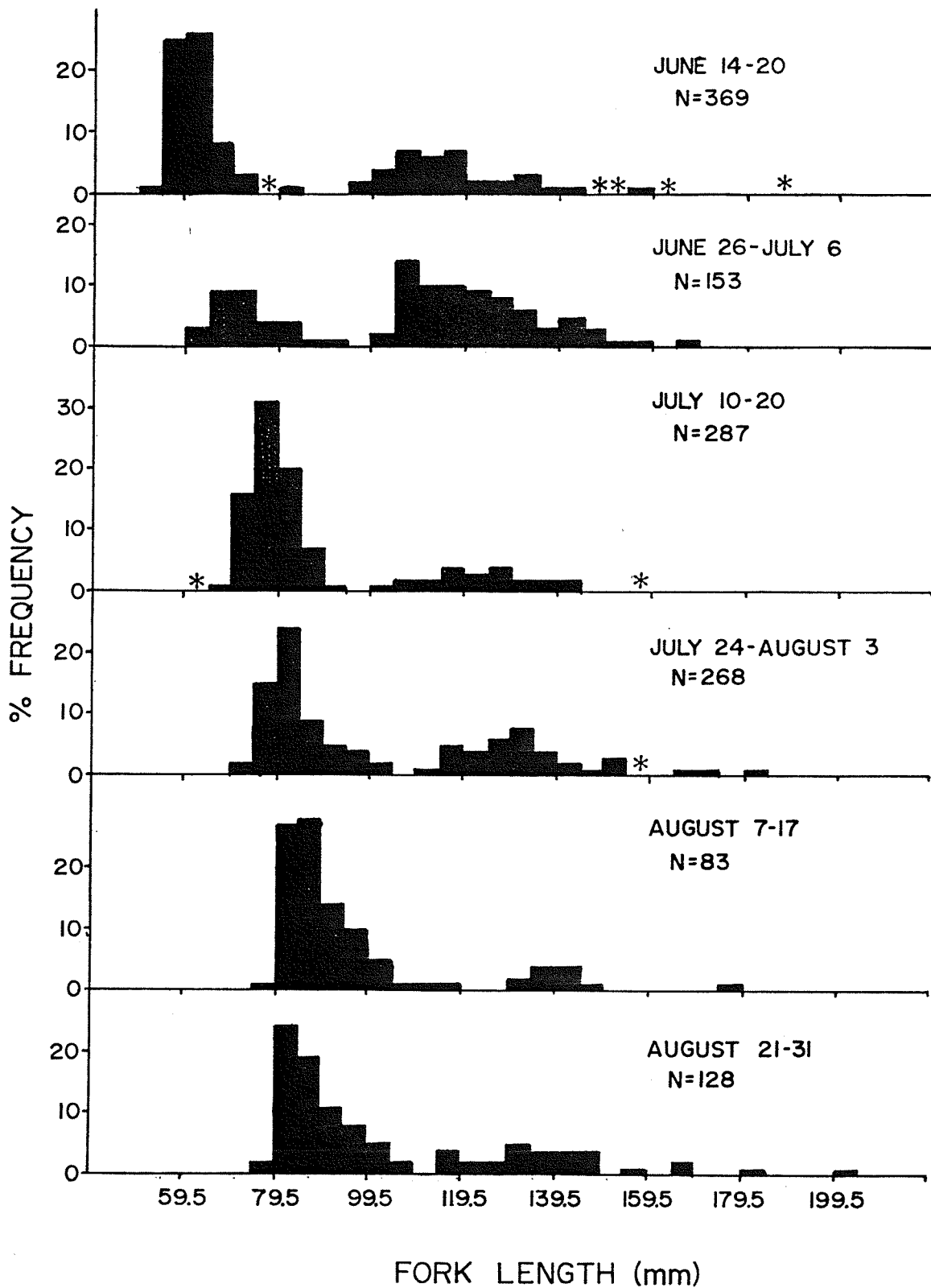


Figure 15. Percent length frequency distributions of Lake III perch during the 1979 sampling season. * indicates <0.5%.

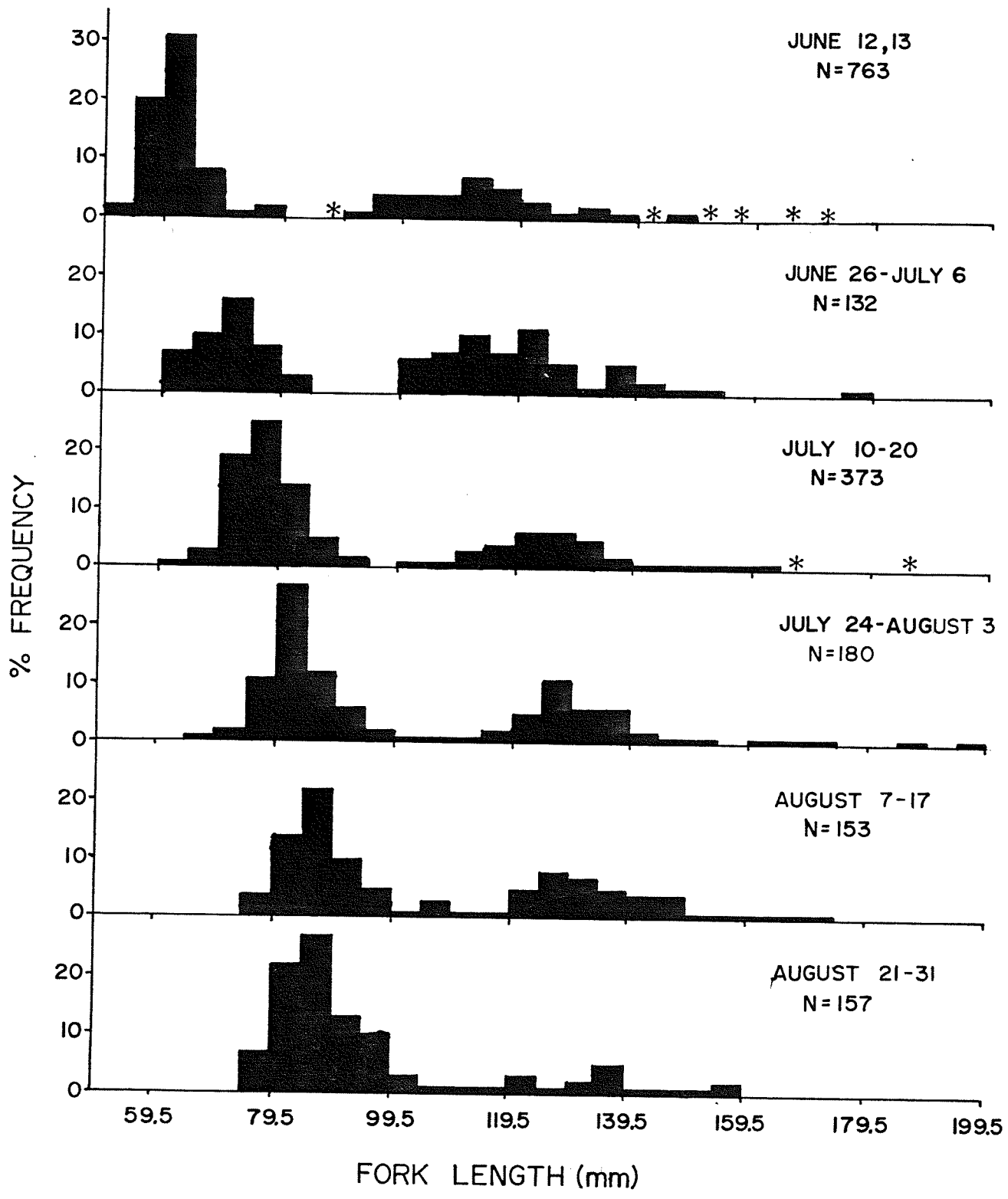


Figure 16. Percent length frequency distributions of Lake IV perch during the 1979 sampling season. * indicates < 0.5%.

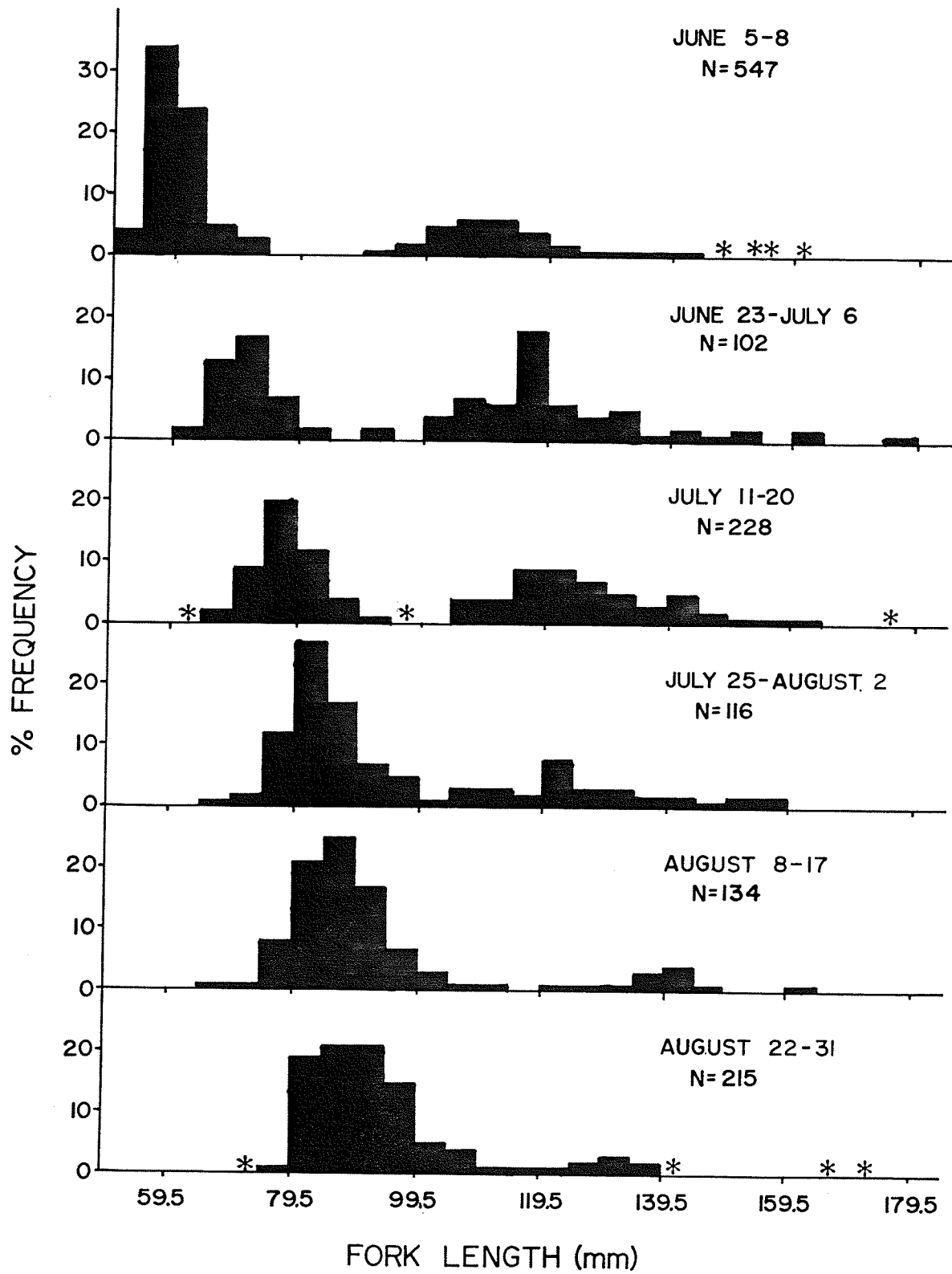


Table 5. Weight-length relationships and comparison by analysis of covariance.

Comparisons	N	r ²	b	Standard error b	Comparison of regression coefficients			log ₁₀ a	Comparison of y-intercepts		
					d.f.	F	P		d.f.	F	P
Lake I Males	120	0.989	3.167	0.030				-5.238			
Females	229	0.988	3.104	0.023	1;345	2.573	0.105	-5.118	1;346	4.374	0.035
Lake II Males	71	0.994	3.228	0.032				-5.355			
Females	216	0.992	3.256	0.019	1;283	0.542	0.469	-5.409	1;284	0.007	0.892
Lake III Males	108	0.993	3.265	0.027				-5.442			
Females	198	0.992	3.223	0.020	1;302	1.530	0.215	-5.362	1;303	0.340	0.568
Lake IV Males	95	0.990	3.250	0.034				-5.434			
Females	193	0.992	3.271	0.021	1;284	0.302	0.590	-5.471	1;285	0.918	0.341
Lakes I	349	0.989	3.112	0.017				-5.132			
II (pooled by sex)	287	0.993	3.248	0.016				-5.394			
III (pooled by sex)	306	0.993	3.235	0.015	3;1222	16.983	<0.001	-5.387	3;1225	32.940	<0.001
IV (pooled by sex)	288	0.992	3.266	0.018				-5.463			
Lakes II (pooled by sex)	287	0.993	3.248	0.016				-5.394			
III (pooled by sex)	306	0.993	3.235	0.015	2;875	0.894	0.412	-5.387	2;877	50.120	<0.001
IV (pooled by sex)	288	0.992	3.266	0.018				-5.463			

\log_{10} weight per unit increase in \log_{10} length was less than for Lakes II, III, and IV.

Adjusted mean weights were 1.150 for Lake II perch, 1.132 for Lake III, and 1.117 for Lake IV. Pairwise comparisons of all adjusted mean weights were made by LSD. The CR was $\geq t_{0.025, (n-x)} S_{\bar{D}} = 0.006$. All adjusted mean weights were significantly different from one another. The difference between Lakes II and III was 0.018, between Lakes II and IV 0.033, and between Lakes III and IV 0.014.

Differences in these adjusted mean weights indicate differences in relative condition of perch in the Fort Whyte lakes (Le Cren 1951). Lake II perch had the highest adjusted mean weight and thus were in the "best" condition (i.e. were the heaviest for their length) while Lake IV perch were in the "poorest" condition (i.e. were the lightest for their length). Because the slope for the Lake I weight-length relationship was different, no conclusion concerning the condition of Lake I perch relative to those of Lakes II, III, and IV can be inferred.

It was necessary to calculate a separate body-scale relationship for two length groups within each lake. Perch less than approximately 90 mm in fork length (roughly up to two years of age) had a different body-scale relationship than perch longer than 90 mm (roughly older than age two). Jobes (1952) and el-Zarka (1959) found similar results in Lake Erie and in Saginaw Bay, Lake Huron respectively. The

smaller regression coefficients of the body-scale relationships of perch less than 90 mm in length reflect a phase of growth where the scales are expanding at a faster rate than body length. The body-scale relationships for perch less than 90 mm were used in back calculating mean lengths for ages 1 and 2. The body-scale relationships of perch longer than 90 mm were utilized in calculation of length beyond the second annulus.

Initially, growth of male and female perch was similar but by age 3 the females were noticeably larger than males (Tables 6, 7, 8 and 9).

Mean lengths obtained from samples of the same year class collected in different years sometimes differed. In Lake I, mean length at a given age was usually less for the 1979 sample than for the 1978 sample of the same year class (Table 6). This discrepancy could be caused by a higher mortality of the faster growing perch in a year class between years (Lee's Phenomenon) (Ricker 1975). In Lakes III (Table 8), and IV (Table 9) mean length at a given age was usually greater for the 1979 sample than for the 1978 sample of the same year class. This suggests a higher mortality of the slower growing perch occurred between years (Negative Lee's Phenomenon) (Ricker 1975). The change from random age sampling to stratified random age sampling may also have somehow contributed to these small differences in back calculated lengths.

Table 6. Calculated mean lengths (mm) of Lake I perch at the end of each year of growth.

Year Class	Year Sampled	Age											
		Males						Females					
		N	1	2	3	4	5	N	1	2	3	4	5
1973	1978	1	68	86	93	108	116	5	72	93	105	124	141
1974	1978	10	72	92	102	118		48	71	95	110	128	
	1979	7	69	88	100	115	141	16	69	93	106	127	158
1975	1978	8	72	94	110			28	73	96	112		
	1979	16	70	93	110	137		24	71	95	113	142	
1976	1978	20	72	95				73	73	97			
	1979	39	66	85	111			50	70	92	121		
1977	1978	1	66					10	71				
	1979	15	65	92				15	66	97			
1978	1979	24	63					28	62				

Table 7. Calculated mean lengths (mm) of Lake II perch at the end of each year of growth.

Year Class	Year Sampled	Age											
		Males						Females					
		N	1	2	3	4	5	N	1	2	3	4	5
1973	1978	1	67	79	100	112	121	0	-	-	-	-	-
1974	1978	0	-	-	-	-	-	4	65	94	125	147	
	1979	4	70	87	109	123	147	3	67	90	112	127	152
1975	1978	6	61	92	109			6	61	92	114		
	1979	6	65	89	105	133		12	65	93	113	147	
1976	1978	32	59	85				51	60	86			
	1979	8	63	89	118			34	60	83	116		
1977	1978	31	66					20	67				
	1979	8	66	101				47	68	104			
1978	1979	43	62					51	63				

Table 8. Calculated mean lengths (mm) of Lake III perch at the end of each year of growth.

Year Class	Year Sampled	Age											
		Males						Females					
		N	1	2	3	4	5	N	1	2	3	4	5
1974	1978	0	-	-	-	-	-	1	63	91	105	139	
	1979	1	66	91	102	123	151	3	68	93	110	127	159
1975	1978	3	64	95	106			3	63	91	111		
	1979	14	68	93	110	137		18	66	95	110	143	
1976	1978	32	60	81				43	61	81			
	1979	23	63	83	110			71	61	83	119		
1977	1978	24	65					39	66				
	1979	10	65	95				21	67	99			
1978	1979	49	62					31	62				

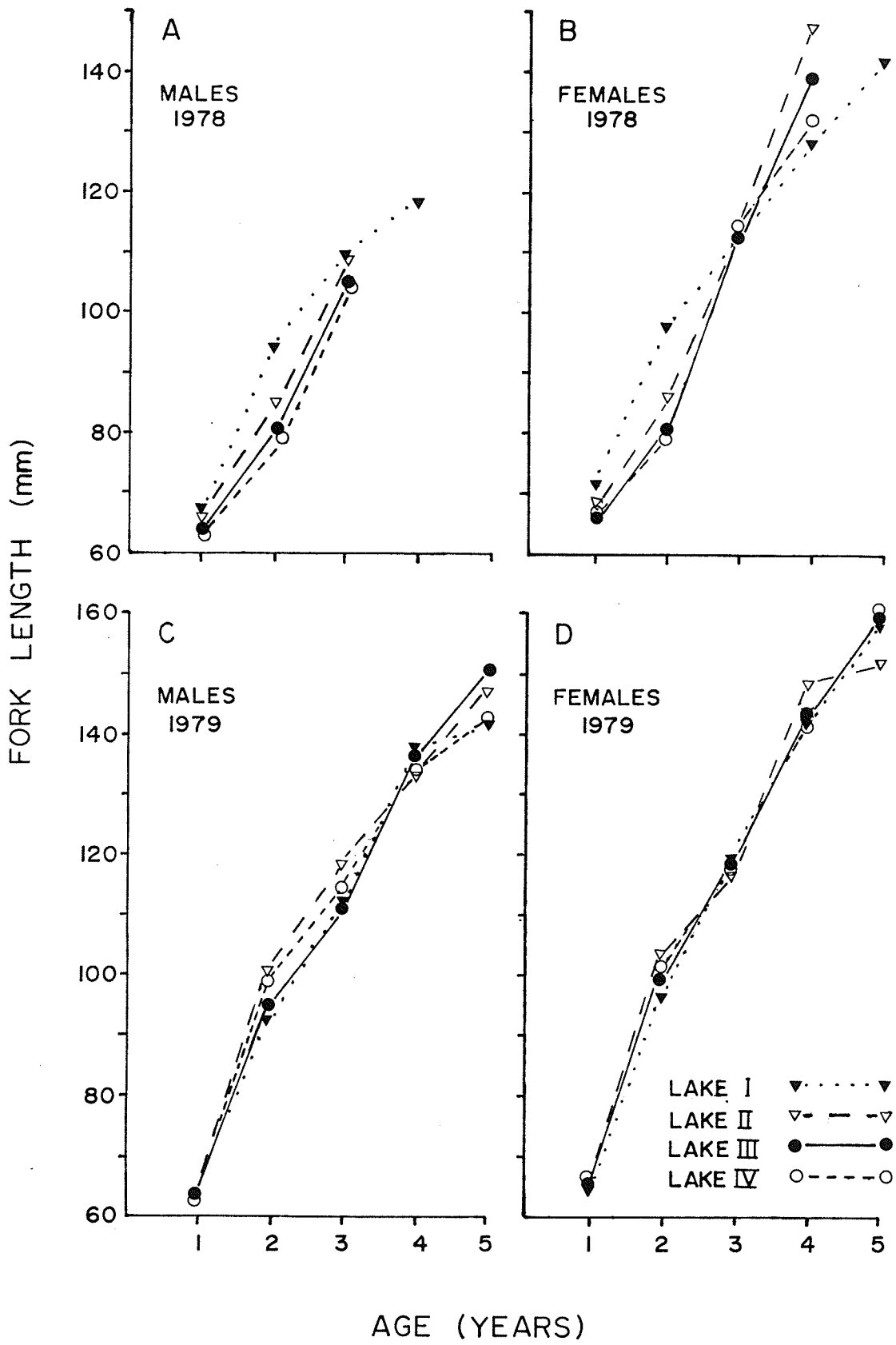
Table 9. Calculated mean lengths (mm) of Lake IV perch at the end of each year of growth.

Year Class	Year Sampled	Age											
		Males					Females						
		N	1	2	3	4	5	N	1	2	3	4	5
1974	1978	0	-	-	-	-	-	4	70	97	121	132	
	1979	4	70	91	109	120	142	5	67	92	117	135	160
1975	1978	2	64	90	105			9	67	94	115		
	1979	12	72	95	112	134		16	68	93	114	140	
1976	1978	22	60	78				38	60	79			
	1979	19	65	87	115			42	62	84	118		
1977	1978	14	64					13	65				
	1979	11	65	99				28	67	101			
1978	1979	41	63					57	62				

Inter-lake comparisons of growth by two-way analysis of variance were performed on transformed data. The reciprocal square root of 1978 length data and the \log_{10} of 1979 length data were analyzed. These transformations were based on Taylor's power law (Green 1979). Bartlett's test was performed to test for homogeneity of variances with the variances of all cells being compared.

Transformed lengths of males, calculated from 1978 data (ages 1-3) at the end of the last completed year of life, were compared among all lakes. Variances were homogeneous ($P = 0.060$). There was a significant lake effect ($P = 0.009$) but also a significant lake-age interaction ($P = 0.015$). When Lake I was removed from the analysis, there was a significant lake effect ($P < 0.001$) and interaction was no longer required in the model. Variances were again homogeneous ($P = 0.045$). Plots of the arithmetic mean lengths at age also indicate these results (Fig. 17). There were differences in the lengths of males at each age among Lakes II, III, and IV with Lake II having the highest and Lake IV the lowest mean length for all ages. Interaction was a result of the growth pattern of Lake I perch. At age 1, mean lengths in Lakes I and II were equal and only slightly higher than in Lakes III and IV (Fig. 17). At age 2, the mean length in Lake I was significantly higher. By age 3, the difference between Lake I and the other lakes is considerably reduced. Beyond age 3, the data suggest Lakes

Figure 17. Growth curves based on mean length at the end of the last completed year of growth. A. Males sampled in 1978. B. Females sampled in 1978. C. Males sampled in 1979. D. Females sampled in 1979.



II, and III, and IV will surpass Lake I in mean length (Fig. 17).

Analysis of female growth among lakes, employing transformed 1978 data (ages 1-4), displayed a pattern similar to that of males. There was a significant lake effect ($P < 0.001$) and a significant lake-age interaction ($P < 0.001$) among all lakes. Variances were heterogeneous, however ($P < 0.001$). With Lake I removed from the analysis, interaction was not required in the analysis of variance model. There was homogeneity of variances ($P = 0.035$) and a significant lake effect ($P < 0.001$). Arithmetic mean lengths were highest in Lake II and lowest in Lake IV (excepting age 3) for all ages (Fig. 17). Interaction was due to the pattern of growth in Lake I. Below age 3, Lake I females have the highest mean length while beyond age 3 they have the lowest mean length (Fig. 17).

In 1979, data were available for comparing growth up to age 5. Among males from all lakes there was no significant lake effect ($P = 0.476$) but variances were not homogeneous ($P < 0.001$). There was also no significant lake effect ($P = 0.617$) among females in 1979 but there was homogeneity of variances ($P = 0.208$). Lake-age interaction was not required in the analysis of variance model for 1979 data. The lack of growth differences among lakes in 1979 data is evident in the untransformed growth curves (Fig. 17).

In all the above comparisons age effects were significant. This indicates that significant differences existed in mean lengths of fish of different age groups.

The difference in results between annual samples may have been caused by changes in perch growth within the lakes. Excepting age 1, mean lengths for a given age were usually greater in 1979 than in 1978. This is illustrated by growth curves of male perch (Fig. 18). Females showed a similar pattern. This increase in length varied by lake and by age and resulted in elimination of significant statistical differences in 1979 growth curves among lakes as found in 1978 data.

Over the long term, growth among lakes was probably not very different. Growth curves for each lake, derived from past growth histories of all year classes, were similar (Fig. 19).

Figure 18. Comparison of growth curves of male perch, based on mean length at the end of the last completed year of growth for each year class, between 1978 and 1979 samples.

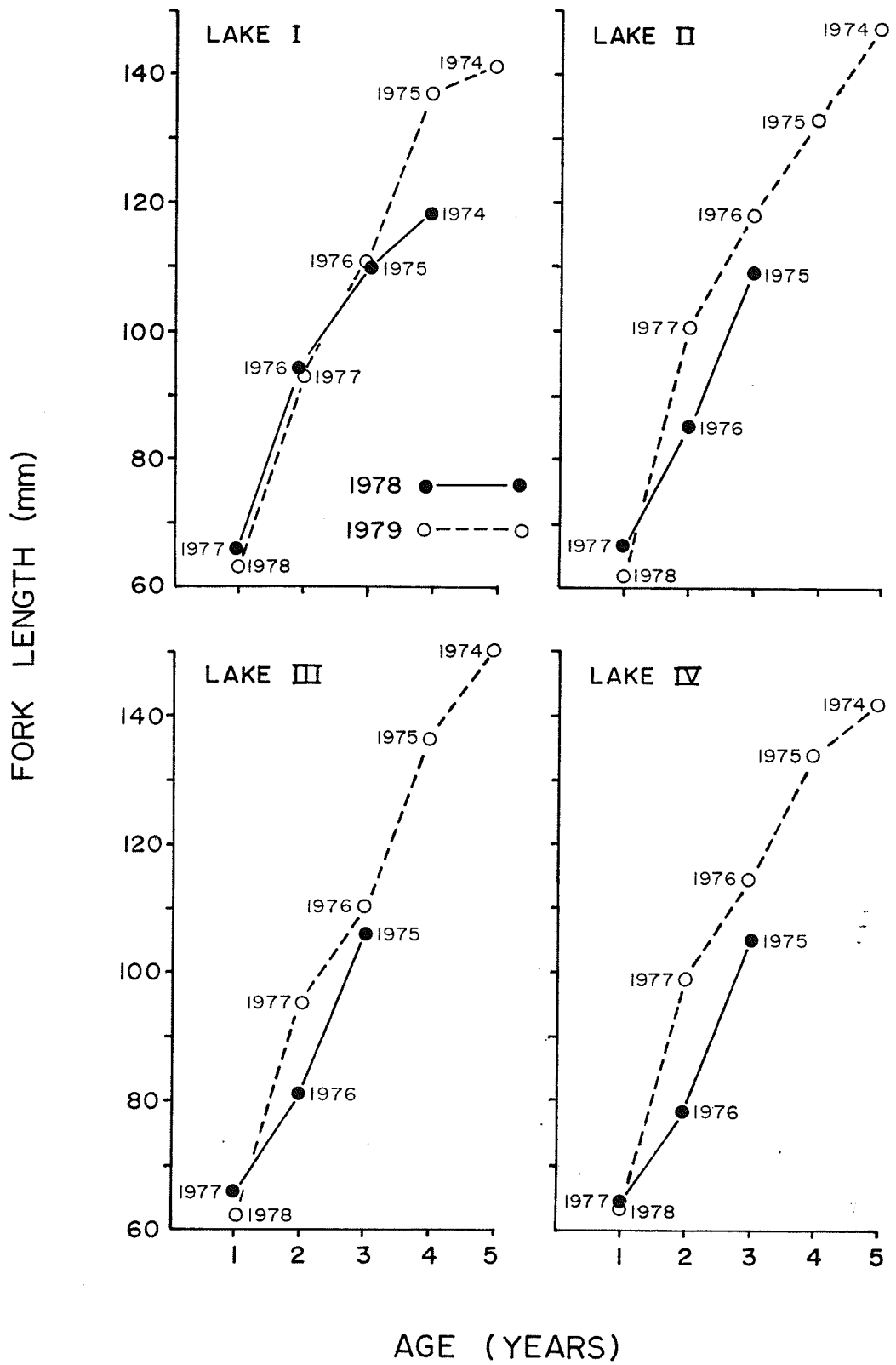
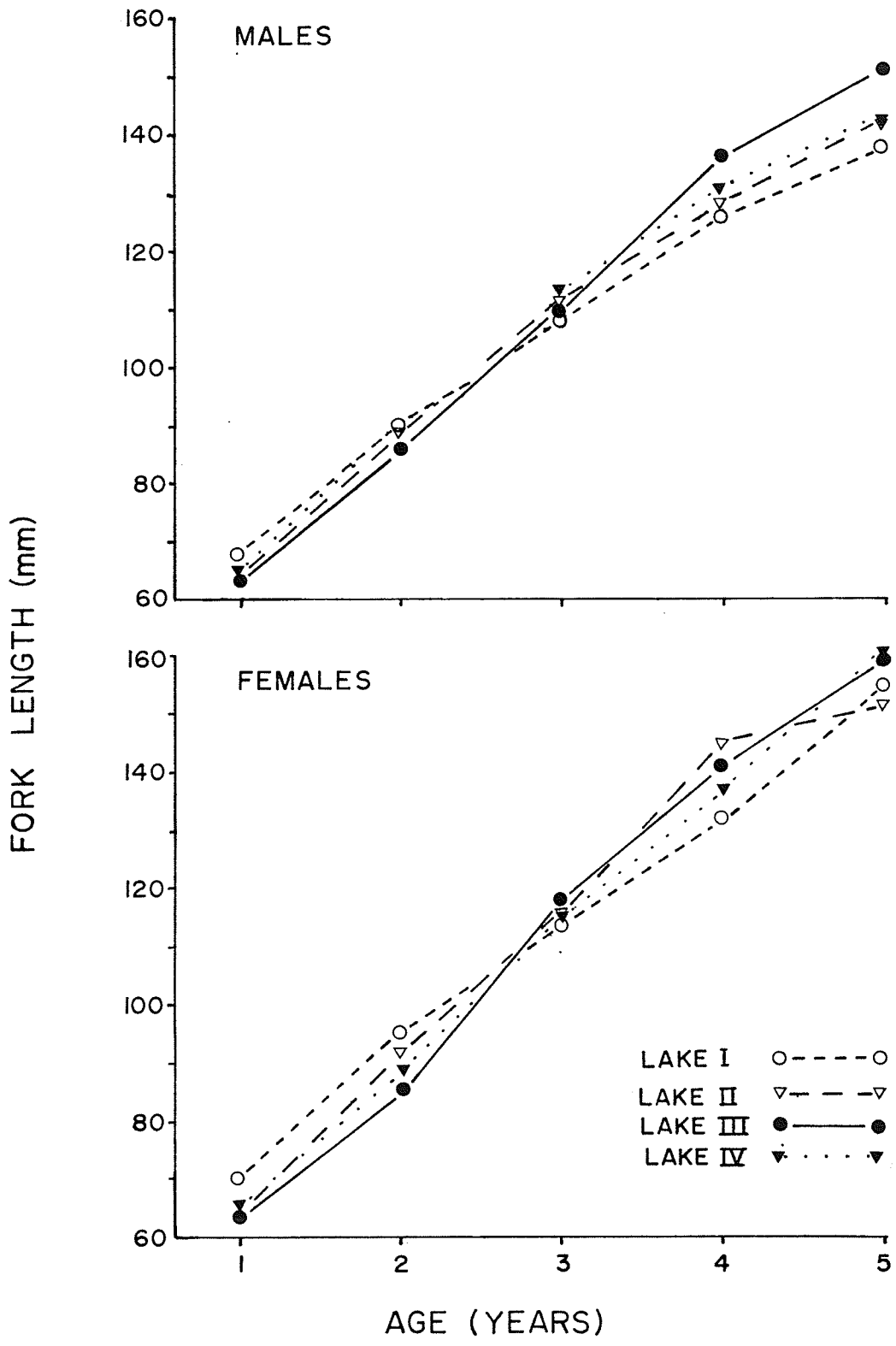


Figure 19. Growth curves based on mean lengths derived from back calculated lengths for all ages and year classes and both sample years.



DISCUSSION

Examination of morphometric and water chemistry data from the Fort Whyte lakes led to the prediction that perch abundance and biomass would be highest in Lakes I and II and lowest in Lakes III and IV. For example, abundance and biomass of perch in Lake Memphremagog, Quebec-Vermont, was greater in the south basin, where phytoplankton and benthic biomass was higher, than in the north basin (Nakashima and Leggett 1975). Hopky (1982) found higher perch abundance and biomass in St. Dalmas Lake than in South Thomas Lake, Manitoba. Values of total dissolved solids, chlorophyll-a, and zooplankton biomass were also higher in St. Dalmas Lake. However, at Fort Whyte perch abundance and biomass differences were not entirely consistent with lake trophy differences. Although abundance and biomass values were high in Lake I, values for Lake II were similar to those of Lakes III and IV. Perch abundance in Lake I was 2.2, 2.0, and 2.5 times higher than in Lakes II, III, and IV respectively. Biomass was 3.0 times higher than in Lakes II and III, and 4.0 times higher than in Lake IV. The greater magnitude of difference in relative biomass than in relative abundance indicates perch were larger in Lake I. The prevalence of large perch in Lake I was apparent while collecting samples.

The above values probably underestimated the differences in relative abundance and biomass of perch which existed between Lake I and Lakes II, III, and IV during the spring of 1979 when the CPUE experiment was initiated. This was caused by an avoidance by perch of some areas sampled and also to a mortality of perch in Lake I. These two factors resulted in a reduction in the number of perch and weight(g) of perch caught per hour in Lake I.

The first major decline in CPUE in Lake I occurred when the warmed, shallow eastern and southern areas of Lake I were sampled during Weeks 4 and 5 (Fig. 4). Surface water temperatures had earlier reached the summer maximum. Previous catches from June through early July, 1978 indicated large numbers of perch frequented the eastern part of the lake. Perhaps perch had moved to areas with better access to deeper and cooler water. The weekly rotation among the five sampling stations was abandoned in Lake I because of this change in perch distribution. Further sampling was limited to two stations (A and B) where the gradient was steep. Relative abundance and biomass values increased initially to previous levels but then continued to decline through the summer (Fig. 4). In comparison, a small hoop net captured 6.47 perch per hour at Station A and 8.26 perch per hour at Station B during a similar period in 1978. This second drop in CPUE was an indication that the perch population of Lake I had been reduced greatly since spring.

Unstandardized trap and hoop nets set as checks in the eastern part of Lake I during this time also failed to make significant catches.

Dead perch were in evidence in Lake I soon after the surface water temperature reached the summer maximum of 27°C. Upper lethal temperatures for yellow perch ranged from 26.5°C to 29.2°C, depending on acclimation temperature, in British Columbia (Black 1953). A similar but less severe mortality occurred in 1978. Dead perch had red fins and lesions, liquified caudal regions, no fat, no food in their stomachs, and were infected by Aeromonas hydrophila (Souter, personal communication, Freshwater Institute). A. hydrophila is usually associated with haemorrhagic septicaemia of fishes which are under stress for some other reason (Richards and Roberts 1978). Waters with a high organic load, such as Lake I, are normally considered to be its natural habitat (Richards and Roberts 1978).

Although not a direct cause of death, high water temperatures were a source of stress on the perch population of Lake I. Anoxic conditions below 4 m prevented escape to more suitable temperatures. Lakes II, III, and IV had cooler surface temperatures (summer maximum of 26°C, 26°C, and 25°C respectively) and anoxic conditions only below 6 m. Thus, perch in these lakes could avoid unfavourable temperatures to a greater extent. No mortality of perch was apparent in Lakes II, III, and IV in 1978 or 1979.

The age distributions of the perch population of Lake I were different from those of Lakes II, III, and IV. Members of the younger age groups (1977 and 1978 year classes) were not numerous in Lake I but they were very numerous in Lakes II, III, and IV. Conversely, older age groups of perch (1974 and 1975 year classes) were more numerous in Lake I than in the other lakes. Members of the 1976 year class were abundant in all lakes.

Samples collected in each lake during short periods in both years were assumed to represent population age and length distributions. As indicated by the length frequency distributions for the entire 1979 sampling season, there was variability among sampling periods (Figs. 13, 14, 15, and 16). However, length and age samples from both years indicated similar trends--thus, the similarities among Lakes II, III, and IV and the dissimilarity of Lake I in length and age distributions are accurately represented by the data.

Wide fluctuations in year class strength are common to yellow perch (Hile and Jobes 1941; Jobes 1952; el-Zarka 1959; Heyerdahl and Smith 1971; Eshenroder 1977; Koonce et al. 1977), and to the Eurasian perch, P. fluviatilis (L.) (Alm 1952; Le Cren 1955; Kipling 1976; Willemsen 1977). Many factors can influence year class strength including temperature (Clady 1976; Kipling 1976; Eshenroder 1977; Le Cren et al. 1977), wind (Clady and Hutchinson 1975; Clady

1976), food density during the pelagic larval stage (Hokanson 1977), interspecific competition (Johnson 1977), interspecific predation (Forney 1971; Nielson 1980), and water fluctuations and amount of newly inundated terrestrial vegetation in reservoirs in spring (Nelson and Walburg 1977).

None of these factors explains the development of weak 1977 and 1978 year classes in Lake I while strong ones developed in Lakes II, III, and IV. Climatic factors would have affected the adjacent lakes equally. Wind can cause mortality of perch eggs through dispersal and physical destruction (Clady and Hutchinson 1975; Clady 1976). However, wind would not have a great effect on small bodies of water and moreover would have more impact on Lake IV with its greater exposed surface area than on Lake I. Food density would not appear to be a problem for young perch in Lake I because zooplankton abundance was higher in all seasons during June 1977-June 1978 than in the other lakes (Loadman 1980). Zooplankton is the major food item of small perch (Tharratt 1959; Schneider 1972; Wong 1972; Henderson 1977; Keast 1977). Interspecific competition and predation would not be factors because the dominant fish species are thought to be the same in all four lakes. Spring water levels are similar and draw-down of Lake I occurs over a long time period.

The preponderance of older, larger perch in Lake I and their scarcity in Lakes II, III, and IV suggest that differences in age compositions of the populations may be causing variable recruitment. Cannibalism can have an effect on recruitment especially when the density of adult perch is high (Eschmeyer 1937; Alm 1946; Alm 1952; Sumari 1971; Kipling 1976; Holčík 1977; Goldspink and Goodwin 1979). In some instances a single very abundant year class dominates and prevents the formation of strong new year classes until its density drops to low levels (Eschmeyer 1937; Alm 1952; Sumari 1971). Alm (1952) reported that a strong year class of Eurasian perch dominated and suppressed formation of new year classes for 15 years. In South Twin Lake, Michigan, Eschmeyer (1937) postulated a much shorter cycle for yellow perch during which one year class was dominant for three years before succumbing to starvation (because of a shortage of intermediate sized prey). A new dominant year class then developed.

At Fort Whyte, barring catastrophic events or climatic factors, a similar cycle of dominant and suppressed year classes may be occurring under the control of intraspecific predation. A series of strong year classes is followed by a succession of weak ones. In Lake I, a perch population dominated by numerous larger, older individuals suppressed recruitment of the 1977 and 1978 year classes. In Lakes II, III, and IV there were few old perch and recruitment of the

1977 and 1978 year classes was high. No direct evidence for cannibalism is available because a detailed analysis of yellow perch diet at Fort Whyte was not undertaken. However, McCormack (1970) found young-of-the-year Eurasian perch were first cannibalized by those of 115-139 mm total length (approximately 110-134 mm fork length). At Fort Whyte perch failed to reach 110 mm until age 3. In 1978, a large percentage of perch in Lake I were age 3 or older (43%). In Lakes II, III and IV only a small percentage of perch were age 3 or older (7%, 6%, and 9% in Lakes II, III, and IV respectively). Perhaps the 1974 year class in Lake I developed when members of older age groups were not abundant. The 1975 and 1976 year classes were also strong because few perch were large enough to cannibalize them or required to because of a sufficient supply of other suitably sized food. Similarly, in Lakes II, III, and IV a strong 1976 year class developed in the absence of many adult perch and recruitment of the 1977 and 1978 year classes was also strong. Eventually the age and length structures of Lake I and those of Lakes II, and III, and IV may be reversed as the cycle of dominant and suppressed year classes progresses. Detailed analyses of perch diet and perch fry abundances as well as monitoring of the age and length structures of the Fort Whyte perch populations over several years would be required to substantiate the hypothesis clearly.

The weight-length relationship was similar between sexes within lakes. The relation pooled by sex varied among lakes (Table 5). The regression coefficient, \underline{b} , was significantly lower for Lake I than for Lakes II, III, and IV, which had similar slopes. Thus, the increase in \log_{10} weight per unit increase in \log_{10} length was lowest in Lake I. Different slopes indicate different populations (Le Cren 1951; Bagenal and Tesch 1978). However, no major biological significance should be inferred from the small actual variation in \underline{b} (3.112 for Lake I compared to 3.248, 3.225, and 3.226 for Lakes II, III, and IV respectively).

A pooled regression can be calculated when \underline{b} is not significantly different and the y-intercept values adjusted for the common slope. Adjusted y-intercepts, as reflected by the adjusted mean weights, are measures of condition (Le Cren 1951). The adjusted mean weights indicated Lake II perch were heaviest for their length (i.e. in "best" condition), Lake IV perch lightest for their weight (i.e. in "poorest" condition), and Lake III perch in between. The value of \underline{a} can vary with time of day, with season, and between habitats (Bagenal and Tesch 1978). Collection time during the day was similar in all lakes. Differences in lake trophy could have caused variation. However, samples utilized for comparison of weight-length relationships differed in their state of growth with Lake II perch the most advanced. For example, when samples were collected,

scales of one-year-old perch from Lake II had distinct first annuli plus some additional growth while those from Lake III had first annuli which had just formed. The first annulus had not yet developed in one-year-old perch when samples were taken from Lake IV. Hence, a difference in growth state may have been the main cause of significant statistical differences in the adjusted mean weights.

Female perch at Fort Whyte grew more rapidly than males after two years. Sexual dimorphism in growth, as found at Fort Whyte, has been widely reported by many others including Schneberger (1935), Eschmeyer (1937; 1938), Hile and Jobes (1942), Muncy (1962), Fortin and Magnin (1972), and Smith (1977).

Differences in growth curves were found among lakes from fish samples collected in 1978. Amongst Lakes II, III, and IV, mean length at each age was highest in Lake II and lowest in Lake IV (Fig. 17). These dissimilarities are consistent with differences in lake trophy as indicated by morphometric and water chemistry data of the Fort Whyte lakes and also with differences in zooplankton abundance as found by Loadman (1980).

Between Lakes I and the others, mean lengths were higher in Lake I for ages 1 and 2 and lower for ages 4 and 5. This growth pattern was probably caused by a combination of factors including differences in lake trophy and the effects of perch density. The greater mean length of the 1977 year

class in Lake I compared with Lakes III and IV at the time of annulus formation in 1978 was not unexpected given the difference in lake trophy. The dissimilarity between Lakes I and II cannot be explained on the basis of morphometric and chemical differences between the lakes. However, total numbers of zooplankton per litre were higher in Lake I in all seasons (Loadman 1980) and zooplankton are the major food of small perch (Tharratt 1959; Schneider 1972; Wong 1972; Henderson 1977; Keast 1977). This greater food supply in Lake I could account for these growth differences. Intraspecific competition for food during the 1977 growing season was also reduced in Lake I because of the lowered density of the 1977 year class compared to that in Lake II. Ryan and Harvey (1980) have suggested that a reduction in population density of perch in acid-stressed lakes resulted in a decrease in intraspecific competition and an increase in growth of younger perch. It is generally accepted, though, that no relation exists between young-of-the-year perch density and growth (Alm 1946; Pycha and Smith 1955; Le Cren 1958; Forney 1971; Ney and Smith 1975; Willemsen 1977). Selective predation of smaller members of the 1977 year class by adults in Lake I could also account for the greater back calculated mean length. Only faster growing individuals of the 1977 year class would have survived to be sampled in 1978. However, back calculated mean lengths (Table 6) indicated the opposite.

Two-year-old perch (the very strong 1976 year class) were also larger in Lake I than in the other lakes. According to Keast (1977), perch up to 96 mm total length (approximately 91 mm fork length) in Lake Opinicon are mainly zooplankton feeders. Because perch fail to reach this length until their third summer at Fort Whyte, zooplankton would probably remain the major food of perch through their second year of growth. Therefore, growth would remain density independent. Alm (1946) and Le Cren (1958) found population density had little effect on second year growth.

Beyond age 3, mean length of perch in Lake I was lower than in the other lakes. This may have been the result of intraspecific competition among older perch for suitably sized food. Growth of older perch is usually inversely related to density (Alm 1946; Bardach 1951; Alm 1952; Le Cren 1958; Eshenroder 1977). Higher numbers of older perch in Lake I probably resulted in depletion of the supply of mid- and large-sized food items, such as larger crustaceans and fish, which they prey upon (Tharratt 1959; Schneider 1972; Clady 1974; Keast 1977). There is little competition for food between perch of different sizes (Buck and Thoits 1970; Schneider 1972; Keast 1977). The few large perch in Lakes II, III, and IV probably had a more plentiful supply of suitably sized food. Evidence for more abundant food in Lakes II, III, and IV was the large incidental catch of crayfish in the sampling gear. Fewer crayfish were captured

in Lake I. Buck and Thoits (1970) found an inverse relation between standing crop of perch and standing crop of crayfish in experimental ponds. Scarcity of suitable food organisms for intermediate sized perch was blamed for slow growth of the extremely dense perch population of oligotrophic South Twin Lake, Michigan, reported by Eschmeyer (1937). Grimaldi and Leduc (1973) attributed slow growth in eutrophic Lake Hertel, Quebec, to an inadequate food supply caused by over population of fish.

No growth differences among lakes were evident from 1979 data. This difference between years could have been the result of changes in growth. Evidence for growth rate differences includes the unimodal length frequency distributions of 1978 (Figs. 5, 6, 7, 8) and the bimodal length frequency distributions, with the 1978 year class forming a distinct mode, in 1979 (Figs. 9, 10, 11, 12). This shift from unimodal to bimodal length frequency distributions was caused by a small reduction in mean length attained by one-year-old perch and an increase in mean length reached by older perch at each age in 1979 than in 1978 (Fig. 18).

In comparison with the dissimilarities in abundance and biomass between Lake I and the other lakes, growth differences apparent in 1978 data were small. The growth differences among Lakes II, III, and IV were also not large. In 1979 any growth differences caused by density effects were negated by other factors. Over the long term, growth is probably similar in all lakes (Fig. 19).

Growth of perch at Fort Whyte was amongst the poorest reported in Manitoba. It was much slower than in Lake Manitoba (Kennedy 1949), somewhat less than in Heming Lake and similar to that found in Wapun Lake (Lawler 1953) (Table 10). First year perch growth at Fort Whyte was greater than reported for St. Dalmas and South Thomas Lakes by Hopky (1982). Thereafter, mean length at each age was greater in St. Dalmas and less in South Thomas. In comparison to other North American waters, Fort Whyte perch also grew slowly. Growth in the Lake of the Woods (Carlander 1950), Lake Erie (Jobes 1952), la Grande-Anse, Québec (Grimaldi and Leduc 1973), and in the Red Lakes, Minnesota (Smith 1977) was more rapid. In Lake Hertel, Quebec (Grimaldi and Leduc 1973) and in Lake Opinicon, Ontario (Keast 1977) growth was similar to that at Fort Whyte. Although growth was slow at Fort Whyte, no year class stopped growth completely as occurred in South Twin Lake, Michigan (Eschmeyer 1937). Initial growth in most of the above lakes is similar; i.e., there is a sufficient supply of zooplankton. Once perch begin to shift to larger food items good growth continues in some bodies of water but not in others, suggesting that the latter have an inadequate supply of larger food items.

The perch population of Lake I responded to greater eutrophy by increasing its biomass. Lake I thus has a higher relative carrying capacity for perch -- i.e. a higher relative biomass which can be supported. Biomass growth is

Table 10. Mean lengths (mm) of perch at each age from various locations.

Locality	Age								
	1	2	3	4	5	6	7	8	9
Lake Erie ^a	94	170	216	241	264	279	-	-	-
Lake Manitoba ^b	-	127	160	201	224	254	274	-	-
Lake of the Woods ^b	94	131	172	197	222	244	255	-	-
Red Lakes, Minnesota ^a	74	132	176	210	231	244	252	256	257
La Grande-Anse, Quebec ^a	80	125	160	191	216	236	-	-	-
South Twin Lake, Michigan ^a	102	103	145	152	-	-	-	-	-
Heming Lake, Manitoba ^{bc}	71	86	124	142	170	213	231	259	302
Lake Opinicon, Ontario ^a	65	96	119	136	151	167	186	280	-
Lake Hertel, Quebec ^a	69	95	115	127	140	153	164	-	-
Wapun Lake, Manitoba ^{bc}	66	84	117	130	-	-	-	-	-
St. Dalmas, Manitoba ^b	55	90	118	148	176	189	198	213	224
South Thomas, Manitoba ^b	46	73	99	125	147	168	183	197	211
Fort Whyte lakes, Manitoba ^b	65	89	113	134	150	-	-	-	-

^a Total length.

^b Fork length.

^c Average length during growing period, not back calculated.

by recruitment and/or by growth of individuals (Carlander 1966). In Lake I the increase in biomass has been through an increase in abundance rather than in growth rate. The usual reported response to higher nutrient levels is an increase in growth rate (Nakashima and Leggett 1975). An increase in size of sockeye salmon occurred after fertilization of Bare Lake, Alaska (Nelson 1959). However, Nakashima and Leggett (1975) have also attributed the higher biomass of perch in the more productive south basin of Lake Memphremagog to greater perch abundance rather than growth. Obviously, survival of young perch must somehow be increased. At Fort Whyte, stronger year classes develop in Lake I than in the other lakes when intraspecific cannibalism is not a significant factor. Perch of older age groups, exposed to more years of mortality, dominate the catch in Lake I yet abundance is higher than in the other lakes where younger age groups dominate the population. The greater magnitude of difference in relative biomass than in relative abundance between Lake I and the other lakes is simply the result of the dissimilarity in age structures of the populations.

Relative abundance and biomass of perch among Lakes II, III, and IV was similar even though Lake II was more eutrophic. This could be the result of two factors. The carrying capacity for a fish species is dependent on the biomass of the other fish species present (Carlander 1966).

Total fish biomass may differ among the three lakes as a result of differences in biomass of other species even though perch biomass does not. Insufficient data are available for comparison. Another possible explanation is that the higher nutrient content of Lake II apparent in 1977-78 data is the result of a single pulse of nutrient-enriched water from the field drainage ditch in 1977. No influx of nutrient occurred in 1978 or 1979. Phosphorus is usually the first limiting nutrient in most systems and steady phosphorus loading is required for sustaining increased productivity (Wetzel 1975). Fish production in ponds that had been fertilized for 15 years was approximately the same as in ponds never fertilized three years after phosphate fertilization ended (Swingle et al. 1965). The similarity of trophic state of Lakes II, III, and IV is indicated by the components of their zooplankton populations. The proportion of calanoids to cladocerans and cyclopoids may be an indication of trophic status (Gannon 1972). A decrease in proportion of calanoids and an increase in cyclopoids and cladocerans was found by Patalas (1972) to indicate a progression from oligotrophic to eutrophic conditions. Annual mean percent relative abundance of cladocerans and cyclopoids combined was similar in Lakes II, III, and IV and highest in Lake I (Loadman 1980). Conversely, calanoids in Lakes II, III, and IV comprised a larger percentage of the population than in Lake I.

When it is considered that only the top 3-4 m of water could be utilized by fish in Lake I for most of the year compared to about 5-6 m in the other lakes, the productive capacity of the utilizable portion of Lake I in terms of perch is apparent. Unfortunately, the increased organic loading of Lake I was beginning to have a detrimental effect. Perch in Lake I were unable to escape high water temperatures in summer because of the low oxygen levels below 3-4 m. This was compounded by the fact that water pumped from the lake for use in the cement plant was taken from the epilimnion, further restricting area available for fish. The infections by A. hydrophila and summer mortality of perch in 1978 and 1979 in Lake I were indications the population was under stress.

Further investigations at Fort Whyte are required to understand more fully the responses of the yellow perch populations to their environment. Detailed long term analyses of abundances of perch during their first year of life in conjunction with an examination of the diet of adult perch should be undertaken. This would confirm whether a cycle of dominant and suppressed year classes was occurring under the control of intraspecific predation. Analyses of the age and length characteristics of the perch populations over several years would also be required. The response of perch in Lake I to reduced population size would also provide another area of study. Recently, the flow into Lake

I of nutrient-enriched water from waterfowl ponds has been curtailed. I expect that perch abundance and biomass in this lake will decrease and eventually be maintained at lower levels than found in the spring of 1979. Future researchers should endeavour to substantiate this.

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Appendix A. Two-way analysis of variance (randomized complete block design) table for the comparison of transformed weekly number of perch caught per hour ($Z = \text{number}^{\frac{1}{2}}$) among the Fort Whyte lakes.

Source of Variation	Sum of Squares	d.f.	F	P
Treatments (Lakes)	1.779	3	$F_{(3,22)} = 5.559$	0.004
Blocks (Weeks)	2.926	9	$F_{(9,27)} = 3.047$	0.012
Error	2.880	27		
Total	7.585	39		

Appendix B. One-way analysis of variance (completely randomized design) table for the comparison of transformed weekly weight (g) of perch caught per hour ($Z = \log_{10}$ weight) among the Fort Whyte lakes.

Source of Variation	Sum of Square	d.f.	F	P
Treatments (Lakes)	2.127	3	$F_{(3,36)} = 9.433$	<0.001
Error	2.706	36		
Total	4.833	39		

Appendix C. Percent agreement of age, between two independent readings, of perch used in age frequency distributions.

Lake	Sample year	
	1978	1979
I	94.3	96.6
II	96.8	97.7
III	99.3	99.5
IV	97.0	98.9

Appendix D. Bartlett's Chi-square statistic for equality of variance of weight-length relationships between sexes within lakes and also among lakes pooled by sex.

Comparisons		N	Length Range (mm)	d.f.	χ^2	P
Lake I	Males	120	53-173	1	1.850	0.202
	Females	229	59-228			
Lake II	Males	71	53-181	1	0.028	0.870
	Females	216	52-201			
Lake III	Males	108	54-158	1	0.126	0.730
	Females	198	52-195			
Lake IV	Males	95	52-170	1	2.372	0.156
	Females	193	52-178			
Sexes Pooled	I	349	53-228			
	II	287	52-201	3	7.022	0.071
	III	306	52-195			
	IV	288	52-178			
Sexes Pooled	II	287	52-201			
	III	306	52-195	2	6.867	0.032
	IV	288	52-178			

Appendix E. Body-scale relations calculated by the least squares method and the equation $L=a+bS$ where L is the fork length (mm), a is a constant, b is the regression coefficient, and S is the total scale radius (X45 mm).

Length	Lake	N	r^2	a	b	Standard Error b
< 90 mm	I	52	0.826	40.232	0.684	0.044
	II	94	0.942	38.236	0.726	0.019
	III	80	0.928	39.366	0.711	0.022
	IV	98	0.918	38.555	0.761	0.023
> 90 mm	I	386	0.795	32.609	1.007	0.026
	II	273	0.864	43.793	0.801	0.019
	III	306	0.868	36.423	0.906	0.020
	IV	239	0.874	44.114	0.834	0.021

Appendix F. Two-way analysis of variance (with lake-age interaction) table for comparison of transformed length ($Z = \text{length}^{-1/2}$) at the last completed year of growth for males collected in 1978. All lakes were compared, ages 1-3.

Source of Variation	Type IV Sum of Squares	d.f.	F	P
Lake	15.903×10^{-5}	3	$F_{(3,183)} = 3.986$	0.009
Age	516.645×10^{-5}	2	$F_{(2,183)} = 194.272$	<0.001
Lake-Age Interaction	21.783×10^{-5}	6	$F_{(6,183)} = 2.729$	0.015
Error	243.334×10^{-5}	183		
Corrected Total	1843.268×10^{-5}	194		

Appendix G. Two-way analysis of variance table for comparison of transformed length ($Z = \text{length}^{-\frac{1}{2}}$) at the last completed year of growth for males collected in 1978. Lakes II, III, and IV were compared, ages 1-3.

Source of Variation	Type IV Sum of Squares	d.f.	F	P
Lake	31.394×10^{-5}	2	$F_{(2,161)} = 11.531$	< 0.001
Age	1041.709×10^{-5}	2	$F_{(2,161)} = 382.614$	< 0.001
Error	219.170×10^{-5}	161		
Corrected Total	1283.937×10^{-5}	165		

Appendix H. Two-way analysis of variance (with lake-age interaction) table for comparison of transformed length ($Z = \text{length}^{-\frac{1}{2}}$) at the last completed year of growth for females collected in 1978. All lakes were compared, ages 1-4.

Source of Variation	Type IV Sum of Squares	d.f.	F	P
Lake	36.841×10^{-5}	3	$F(3, 374) = 7.371$	<0.001
Age	2199.094×10^{-5}	3	$F(3, 374) = 440.118$	<0.001
Lake-Age Interaction	183.347×10^{-5}	9	$F(9, 374) = 12.231$	<0.001
Error	622.910×10^{-5}	374		
Corrected Total	5958.599×10^{-5}	389		

Appendix I. Two-way analysis of variance table for comparison of transformed length ($Z = \text{length}^{-1/2}$) at the last completed year of growth for females collected in 1978. Lakes II, III, and IV were compared, ages 1-4.

Source of Variation	Type IV Sum of Squares	d.f.	F	P
Lake	46.629×10^{-5}	2	$F_{(2,225)} = 11.231$	<0.001
Age	2038.182×10^{-5}	3	$F_{(3,225)} = 327.263$	<0.001
Error	467.097×10^{-5}	225		
Corrected Total	2704.663×10^{-5}	230		

Appendix J. Two-way analysis of variance table for comparison of transformed length ($Z = \log_{10} \text{length}$) at the last completed year of growth for males collected in 1979. All lakes were compared, ages 1-5.

Source of Variation	Type IV Sum of Squares	d.f.	F	P
Lake	287.385×10^{-5}	3	$F_{(3,346)} = 0.839$	0.476
Age	$647195.414 \times 10^{-5}$	4	$F_{(4,346)} = 1417.584$	<0.001
Error	39491.413×10^{-5}	346		
Corrected Total	$731593.759 \times 10^{-5}$	353		

Appendix K. Two-way analysis of variance table for comparison of transformed length ($Z = \log_{10}$ length) at the last completed year of growth for females collected in 1979. All lakes were compared, ages 1-5.

Source of Variation	Type IV Sum of Squares	d.f.	F	P
Lake	216.336×10^{-5}	3	$F_{(3,564)} = 0.604$	0.617
Age	$1042261.094 \times 10^{-5}$	4	$F_{(4,564)} = 2182.895$	<0.001
Error	67322.897×10^{-5}	564		
Corrected Total	$1163036.949 \times 10^{-5}$	571		

Appendix L. Fork length-total length conversions of perch at Fort Whyte calculated by the least squares method and the equation $TL = a + b FL$. TL is the total length (mm), a is a constant, b is a regression coefficient, and FL is the fork length (mm).

Lake	N	r^2	a	b	standard error b
I	131	0.999	1.417	1.035	0.002
II	103	0.999	1.051	1.038	0.002
III	111	0.999	0.892	1.040	0.002
IV	103	0.999	0.606	1.042	0.003