ANNUAL PRODUCTION AND POPULATION DYNAMICS
OF A RELATIVELY UNEXPLOITED WALLEYE,
Stizostedion vitreum vitreum (Mitchill 1818),
POPULATION IN SAVANNE LAKE, ONTARIO

by

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ABSTRACT

Most studies of the walleye have been conducted on highly exploited populations. Savanne Lake in northwestern Ontario, and having an area of 364.29 ha, was exploited until 1969, whereupon it was designated a fish sanctuary. Study was conducted during the spring months of 1973, 1974 and 1976. Walleyes were marked and recaptured in trapnets. Marking was accomplished by attaching a Floy tag FTF69 under the second dorsal fin with monofilament line. The 6th, 12th and second dorsal spines were clipped in the springs of 1973, 1974 and 1976, respectively, for Schumacher-Eschmeyer estimates. Schumacher-Eschmeyer spring population estimates of 5211, 5184 and 5463 for the three study years represent the spawning population most vulnerable to the gear.

The annual mortality rates were a high 8 to 85% for the component of the population sampled and characteristically increased with age over the three years of study.

Growth retardation was observed among tagged walleyes; some of the walleyes neither grew in length nor laid down a new annulus in each year of their life. These observations were attributed to limited food supply and extensive handling, tagging and fin-clipping of the fish over the study period.

No relationship was noted between year-class strength and year-class growth. Walleyes showed similar annual percentage increments in their growth during the three sampling years. Relative growth of walleyes increased substantially by the end of the first year, decreased sharply the second year and continued to decrease at a lesser rate until, on the average, the fifth or sixth year. After this, growth was very slow.

Annual biomass of 6.58 $kg.ha^{-1}$ for 1973-74, 6.06 $kg.ha^{-1}$ for 1974-75 and 2.64 $kg.ha^{-1}$ for 1975-76 for age groups 7 and older was low. Production estimates of 1.0 $kg.ha^{-1}.yr^{-1}$ for 1973-74, 1.31 $kg.ha^{-1}.yr^{-1}$ for 1974-75 and 0.52 $kg.ha^{-1}.yr^{-1}$ for 1975-76 for age groups 7 and older are likely values for a theoretical yield of 1.9 $kg.ha^{-1}.yr^{-1}$ based on the morphoedaphic index (Ryder 1965) and support the 30 percent rule. The brood stock production estimate of 1.85 $kg.ha^{-1}.yr^{-1}$ for fish of age 5.5 (weighted mean age to first maturity) and older, and representing about 20% of the total walleye production in the lake, relates closely to the theoretical yield of 1.9 $kg.ha^{-1}.yr^{-1}$ based on the 30 percent rule.

The slow growth of the walleyes was attributable to chemical characteristics typical of lakes in this region of the Canadian Shield, as well as to their high density relative to the available food.

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INTRODUCTION

Most studies of walleyes, *Stizostedion vitreum vitreum* (Mitchill), have been conducted on highly exploited populations. Savanne Lake in northwestern Ontario was exploited until 1969, whereupon it was designated a fish sanctuary. The purpose of this study is to provide a basic understanding of walleye population structure, production and population dynamics in a relatively unperturbed environment. This information can be used as a base line for comparative purposes between exploited and unexploited populations. It also provides a basis in determination of an exploitation strategy for better management of walleye stocks, while contributing to estimates of percid production within boreal lakes.

Description of lake

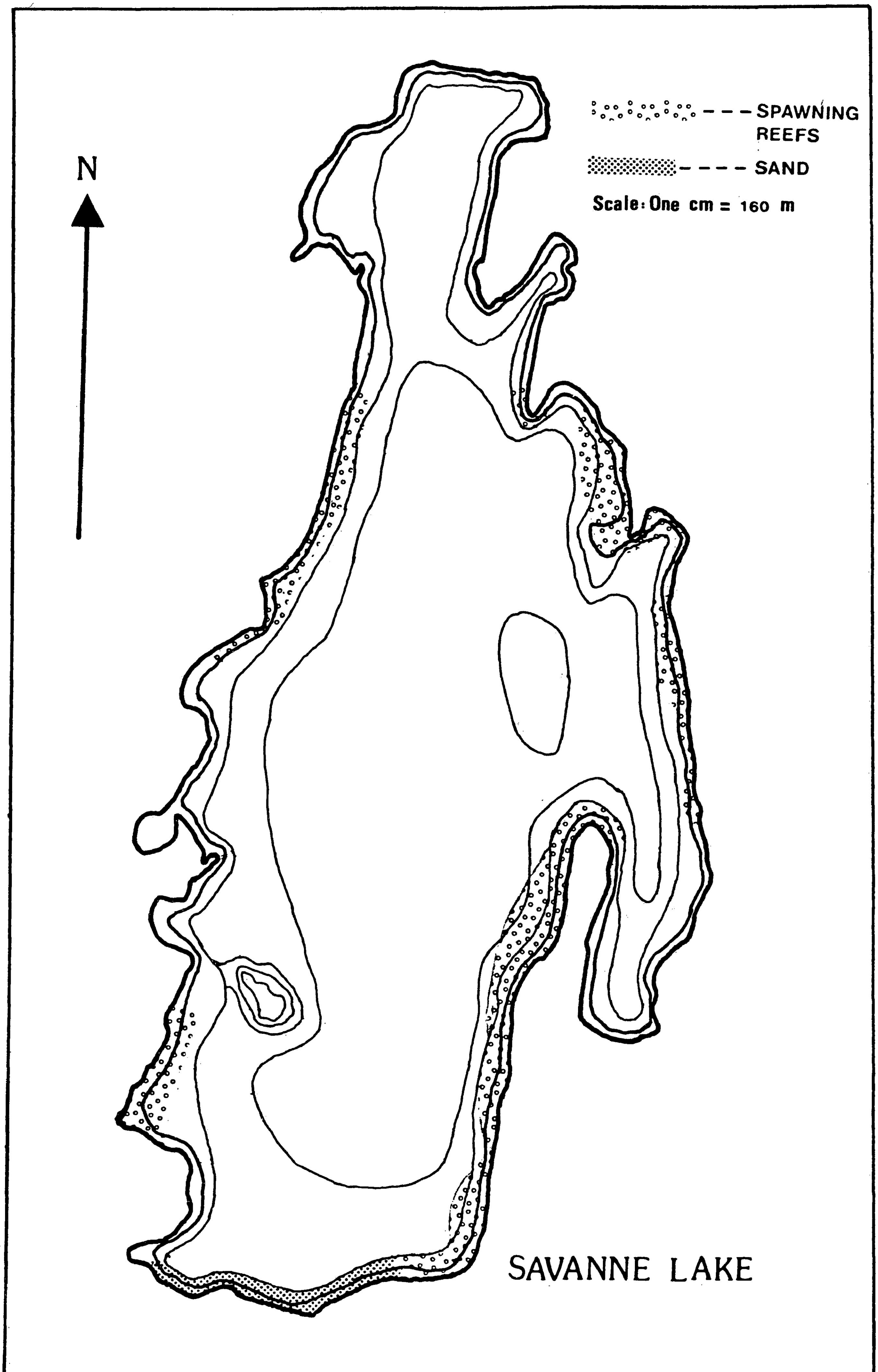
Savanne Lake is of intermediate size (364.29 ha) and is located approximately 128 km northwest of Thunder Bay, Ontario (Lat. 48^{o} 49'30", Long. 90^{o} 06'00"). It receives a heat input of 2268.6 degree days above $0^{o}C$ and 1350.2 degree days above $5^{o}C$ calculated at the nearby Upsala, Ontario weather station (Aston 1977). It is part of a group of several lakes in a study area controlled by the Ministry of Natural Resources, walleye research unit, involved in a long term study of walleye exploitation.

Savanne Lake is 3.2 km long and 1.2 km wide, and is quite shallow with respective maximum and mean depths of 4.27 m and 2.57 m (Table 1). It lies approximately in a north-south alignment (Fig. 1), and its 14.8 km perimeter is encircled by black spruce, balsam, poplar and white birch. The extreme north end of the lake is marsh and the bottom sediments are primarily silt. Several rocky reefs extend out into the lake (Fig. 1), and much of the bottom sediments consist of organic detritus, sand, gravel and rock. The water is soft and dark (Table 2). These are common characteristics of many walleye lakes in the region. Total dissolved solids vary from 31 to 80 $mg.l^{-1}$ with a mean of 55.46. The highest measure of total dissolved solids recorded in June-July was 65 $mg.l^{-1}$. This was used for calculating the morphoedaphic index and potential yield estimates.

Several types of aquatic plants and zooplankton were found in Savanne Lake (Appendix 1). Invertebrates in order of greatest abundance in Savanne Lake were Amphipoda, Diptera, Plesipora, Ephemeroptera and Tricoptera (Table 3).

Fish species present in the lake are: walleye; northern pike, *Esox lucius*; yellow perch, *Perca flavescens*; shallow water cisco, *Coregonus artedii*; white sucker, *Catastomus commersonii*; burbot, *Lota lota*; trout perch, *Percopsis omiscomaycus*; mimic shiner, *Notropsis volucellus*; black nose shiner, *Notropsis heterolepis*; johnny darter, *Etheostoma nigrum*; Iowa darter, *Etheostoma exile*.

Fig. 1. Map of Savanne Lake showing depth contours (in metres) and spawning reefs.



N
SPAWNING REEFS
SAND
Scale: One cm = 160 m
SAVANNE LAKE

Table 1. Physical features of Savanne Lake: T D S = Total dissolved solids; M E I = Morphoedaphic Index (Ryder 1965); P Y E = Potential yield estimate.

Area (hectares)	Volume (cu. metres)	Mean depth ($\bar{D}$) (metres)	Maximum depth (metres)	T D S	M E I a/ (metric)	P Y E b/ ($kg.ha^{-1}.yr^{-1}$)
364.29	9.37	2.57	4.27	65	25.29	6.22

a/ $M\,E\,I = \frac{T\,D\,S}{\bar{D}} = \frac{65}{2.57} = 25.29$

b/ $P\,Y\,E = 1.237\sqrt{M\,E\,I}$

$= 1.237\sqrt{25.29}$

$= 6.22\ kg.\ ha^{-1}.yr^{-1}$

Table 2. Chemical analysis[a] (mg/l) of water samples taken from Savanne Lake on 14 May 1973.

Item	May 14/73	April 15/75	March 31/77
Dissolved solids	31 - 80		range 55.46
Hardness as $CaCO_3$	16	28	---
Total alkalinity [b]	15	23	---
Turbidity (F.T.U.)[c]	1.7	1.8	---
Conductivity (in Micromhos)	36	47	---
Iron as Fe	0.45	.50	---
Magnesium	1	3	---
Manganese as Mn[d]	0.019	0.10	---
Calcium as Ca	4	6	---
Potassium as K	1	0.65	---
Sodium as Na	1	1.2	---
Silica as SiO_2	8.2	2.8	---
Chloride as Cl	< 1	<1	---
Sulphate as SO_4	9	5	---
Nitrogen as N			
Free ammonia	0.01	.03	---
Total Kjeldahl	0.51	.54	---
Nitrite	0.005	.006	---
Nitrate	0.01	.01	---
Phosphorus as P[e]			
Total	0.027	.023	---
Soluble	0.003	.014	---
		field analysis[f]	
pH[d]	7.1	S 6.4	S 7.5
		M 6.5	M 7.2
		B 6.5	B 6.4
O_2 (mg/l)	---	S 12.3	S 12.0
		M 7.8	M 12.0
		B 5.3	B 2.2
Temp. (°C)[d]	8.3°C	S 0°C	S 1.1°C
		M 2.2°C	M 3.3°C
		B 3.8°C	B 4.4°C

[a] Analysis by the Ontario Ministry of the Environment

[b] Total alkalinity = bicarbonate alkalinity

[c] F.T.U. = Formazin Turbidity Units

[d] Test performed on preserved sample

[e] Low values are reliable to 0.002 mg/l

[f] S = Surface; M = Middle; B = Bottom

Table 3. Predominant benthic animals collected in Savanne Lake, and listed in descending order of abundance.

Animals	Depth in metres
1. *Hyalella azteca*	1.0
2. Chironomids (*Chironomus* sp.)	3.0 to 4.0
3. *Hexagenia* sp.	2.0
4. Plesiopora (aquatic earthworms)	0 to 1.0
5. *Ephemera* sp. (may flies)	2.0
6. Trichoptera (caddis flies)	2.0
A *Oecetus* sp.	
B *Caenis* sp.	
C *Neureclipsis* sp.	
7. Chaoborinae (phantom midge)	3.0 to 4.0
8. *Pisidium* sp. (clams)	0 to 1.0

MATERIALS AND METHODS

The study was conducted over a period of three years --1973, 1974 and 1976. The lake was divided into red, green, yellow and blue areas (Figs. 2 to 4) based on spawning and habitat preference of mature walleyes. In the sampling year of 1973, 1492 walleyes were tagged (Table 4) and 378 walleyes were recaptured using 27 trap net locations (Fig. 2). In the sampling years of 1974 and 1976, 1389 and 1399 walleyes were tagged (Table 4) and 238 and 262 walleyes were recaptured using 12 and 14 trap net locations respectively (Figs. 3 and 4).

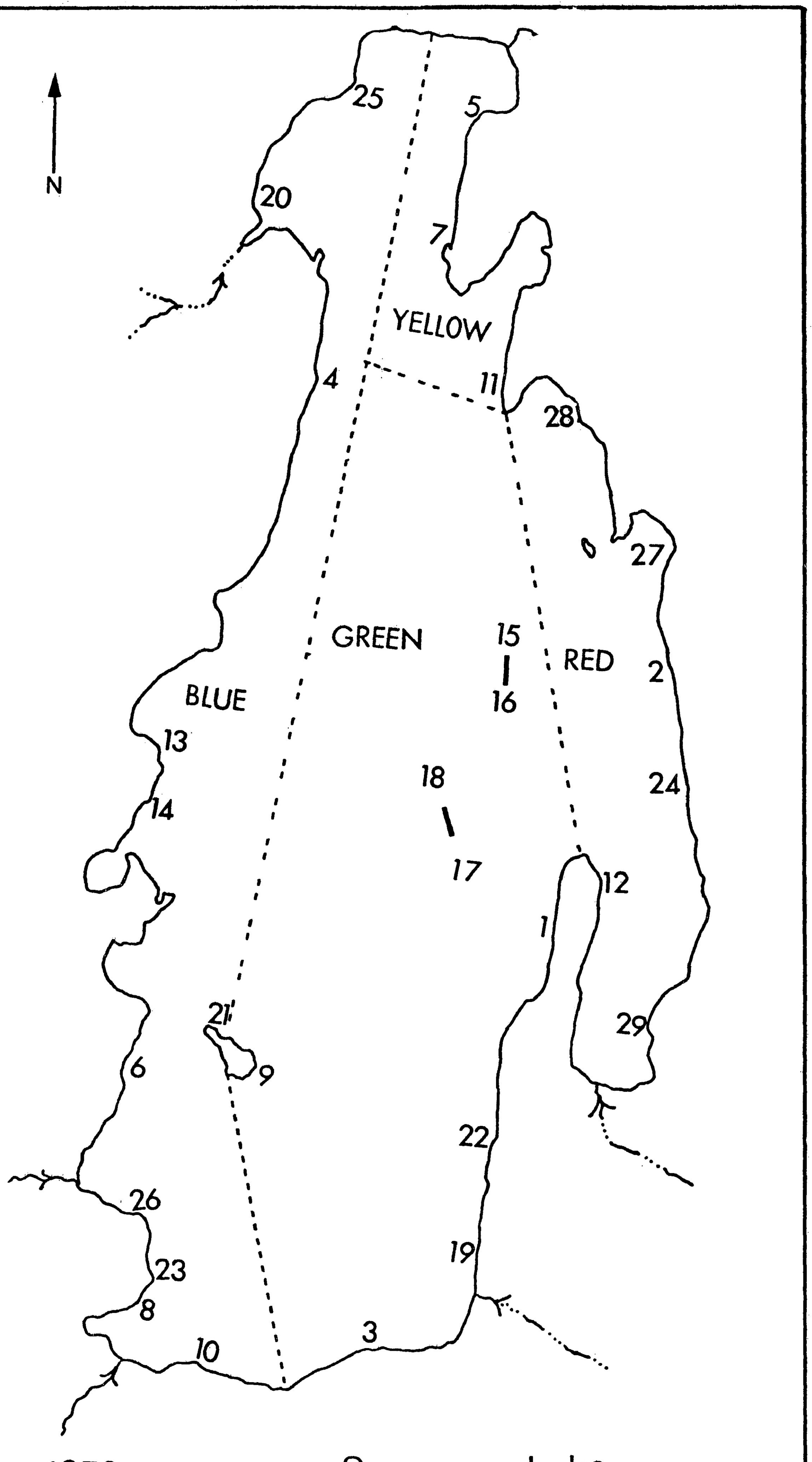
Trap netting

Four 1.22 metre, six 1.83 metre and eight 2.44 metre trap nets were used for sampling fish. A standard trap consists of crib, house, heart, wings and lead (Fig. 5). The specific dimensions of the trap nets are given in Table 5. Trap netting began immediately following ice-out, on May 3, 1973, May 15, 1974 and May 5 in 1976, and continued until the middle of June, when the water temperatures ranged from 16.7 to 20.5^{o}C. The net locations (Figs. 2, 3 and 4) were selected for areas of known concentrations and to insure that all habitats were sampled. Nets were frequently moved when the marked to unmarked ratio exceeded twenty percent, or the total catch became low. This insured a more representative population sampling. Trap nets were checked each morning. An anaesthetic, MS222 (Tricaine methane-sulphonate) was used in the spring of 1976 to allow measurement of the weight of live fish for the purpose of calculating a length-weight relationship. The total length of each walleye was measured to the nearest mm and 10 to 15 scales were taken from the "key scale" area. This area is located fifteen scale rows posteriorly from the gill opening and then two scale rows below the lateral line (Smith 1949).

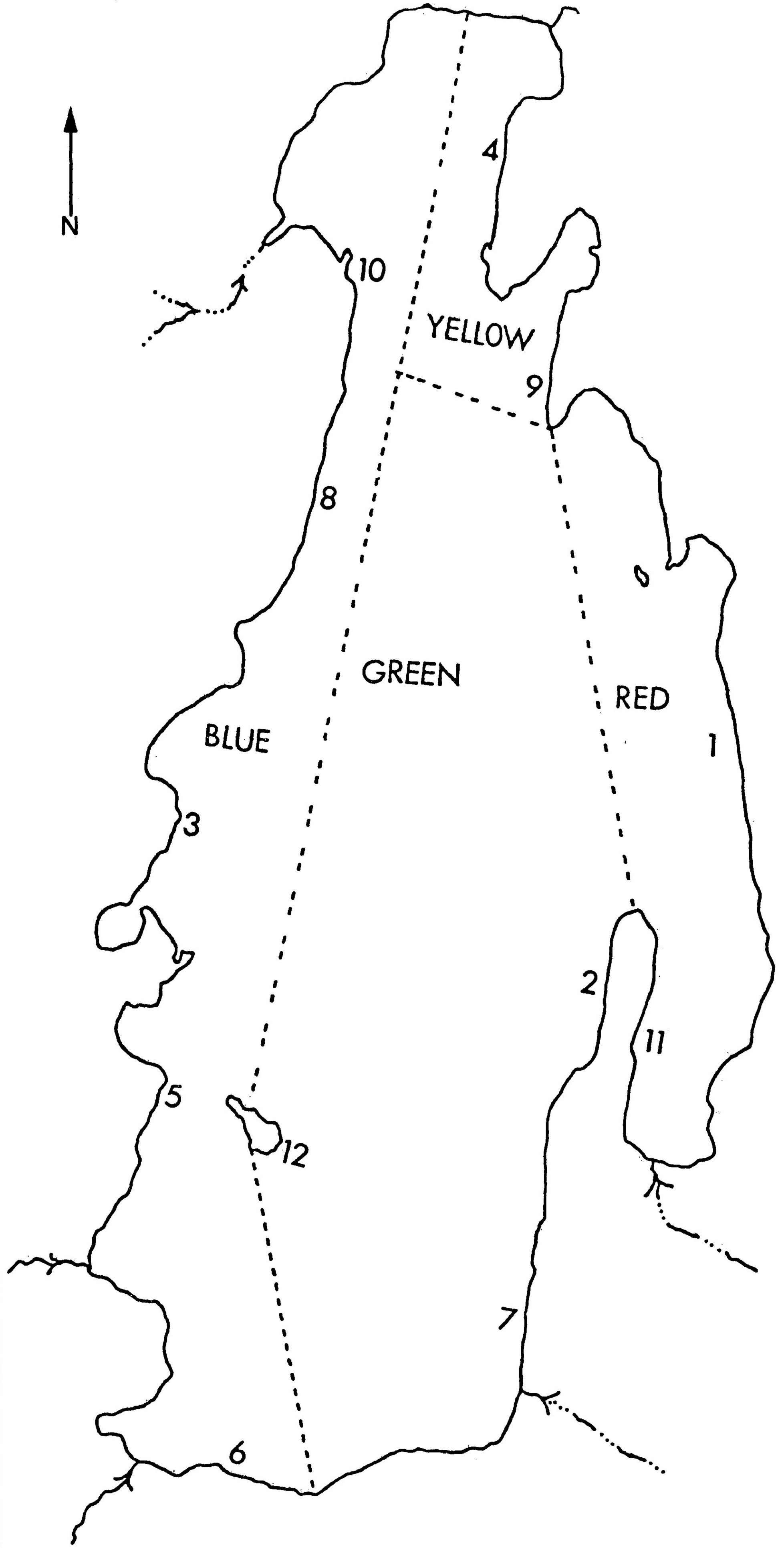
Table 4. Walleyes tagged and recaptured over a period of three years of sampling in Savanne Lake.

Year	Total number of walleyes handled	Number of walleyes marked	Number of walleyes not released	Number of unmarked walleyes released alive	Marked Recaptures
1973	2491	1492	115	506	378
1974	1828	1389	32	169	238
1976	1939	1399	42	236	262

Fig. 2, 3 and 4. Maps of Savanne Lake showing trap net locations for 1973, 1974 and 1976.

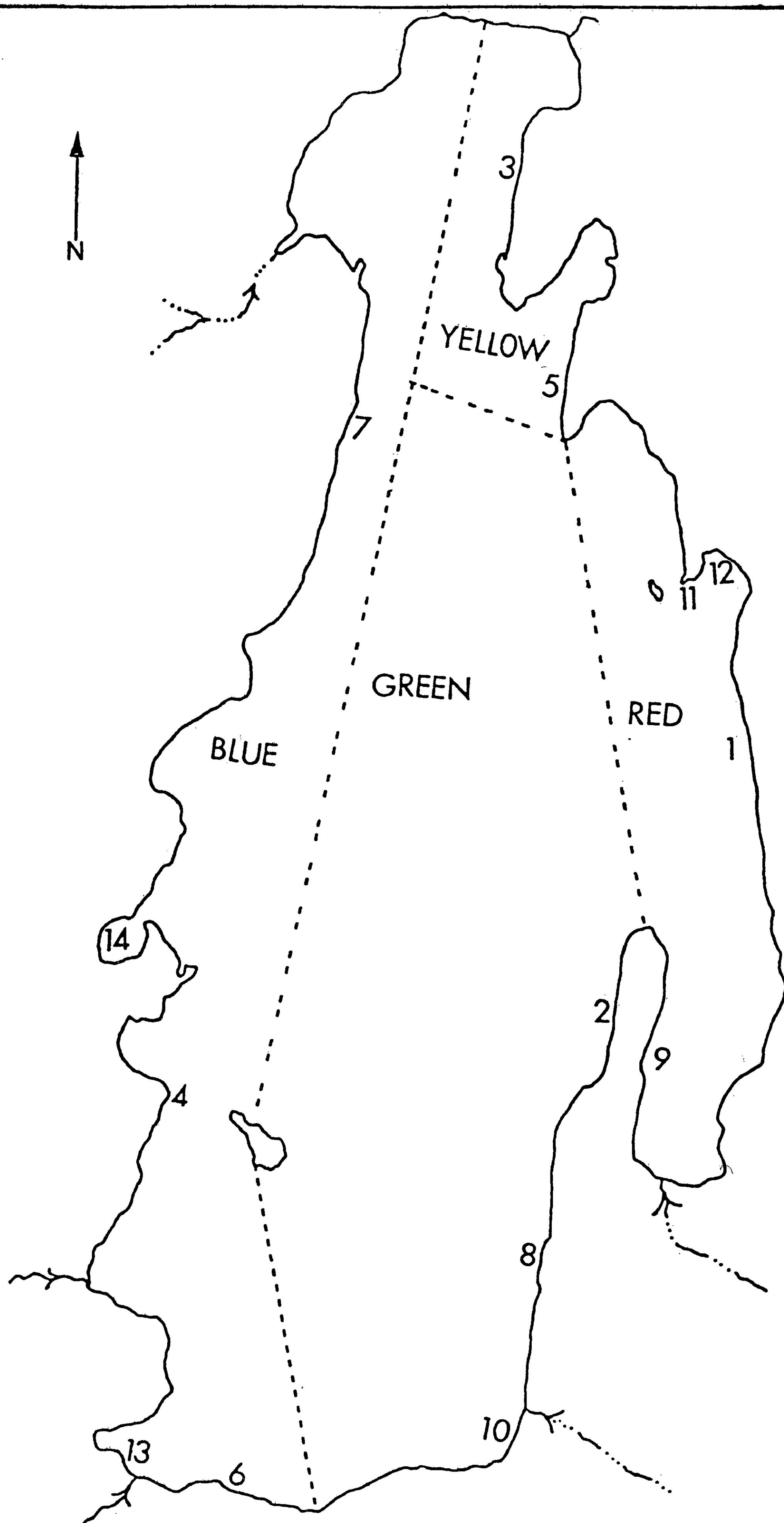


Savanne Lake
Scale :1Cm= 160 m



1974

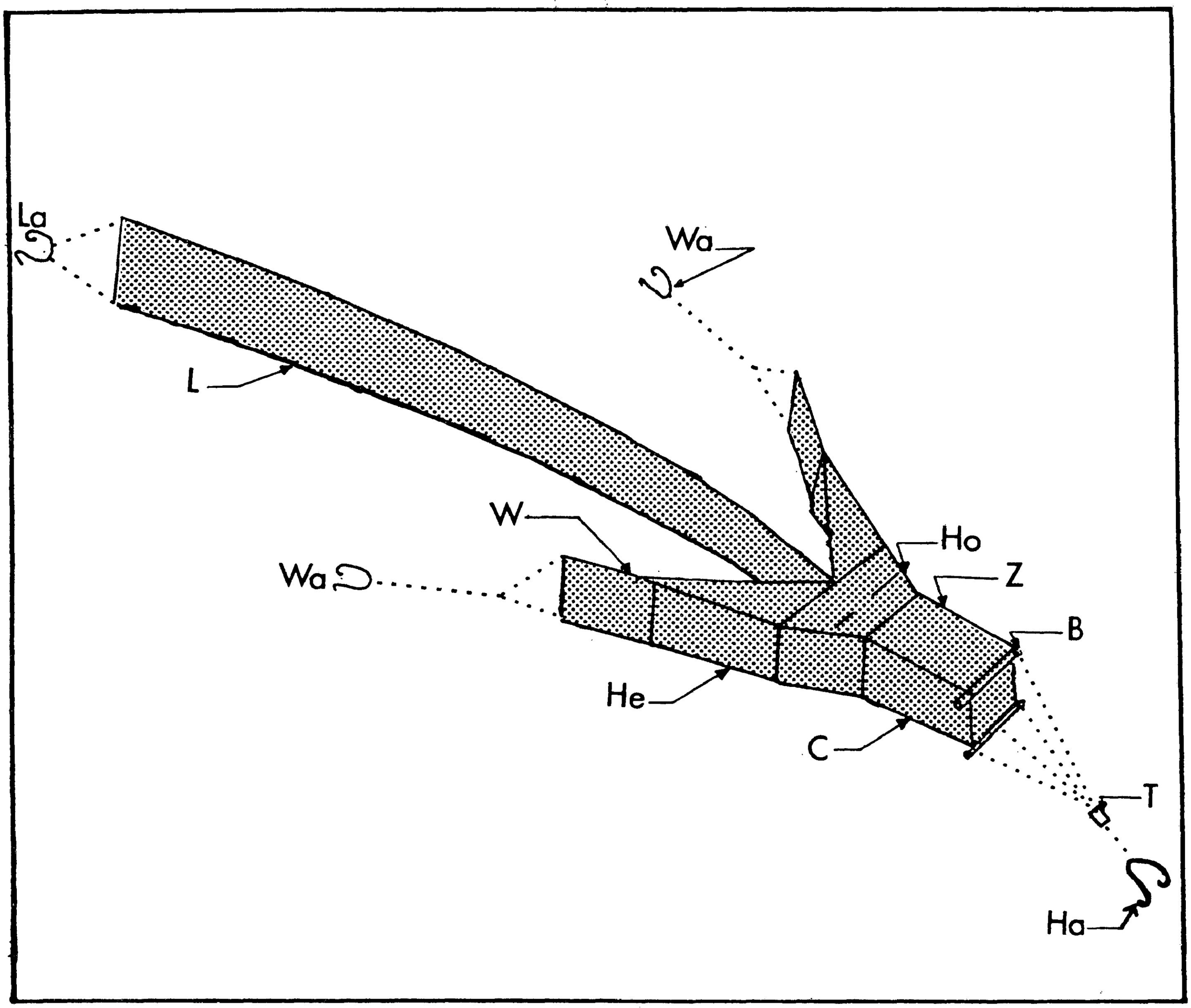
Savanne Lake
Scale : 1Cm = 160 m



1976

Savanne Lake
Scale :1Cm= 160 m

Fig. 5. Fully set trap net showing various parts: B = Brales; C = Crib; Ha = Head anchor; He = Heart; Ho = House; L = Lead; La = Lead anchor; T = Toggle; W = Wing; Wa = Wing anchor; Z = Zipper.



FULLY SET TRAP NET

Table 5. Dimensions stretched mesh and number of trap nets used in parenthesis at Savanne Lake for sampling of walleyes from 1973 to 1976.

	1973	1974	1976
Net size	(2) 1.22 metres (four ft)		(2) 1.22 metres (four ft)
	(1) 1.83 metres (six ft)	(3) 1.83 metres (six ft)	(3) 1.83 metres (six ft)
	(2) 2.44 metres		
Total Number of Sets	95	51	77
Net type	1.22 metres (four ft)	1.83 metres (six ft)	2.44 metres (eight ft)
length of lead	18.3 m	36.6 m	45.7 m
depth of lead	1.22 m	1.83 m	2.44 m
mesh size of lead	1.27 cm	5.08 cm	5.08 cm
length of pot	2.44 m	3.96 m	5.49 m
width of pot	1.22 m	1.83 m	2.44 m
depth of pot	1.22 m	1.83 m	2.44 m
mesh size of pot	1.27 cm	5.08 cm	5.08 cm
width of house	1.83 m	2.74 m	3.66 m
mesh size top of house	1.27 cm	7.62 cm	7.62 cm
length of wings	1.83 m	3.66 m	5.49 m
mesh size top of heart	1.27 cm	5.08 cm	7.62 cm

Body-scale relationship

Savanne Lake walleyes were sub-sampled to determine body-scale relationships. Stratified sub-samples of 15% of the walleyes were taken from a total catch of 1492, 1389 and 1399 in three study years of 1973, 1974 and 1976. These provided a sufficiently representative sample of a stock or population for age-growth studies (Ketchen 1949). To avoid excessive scale development, walleyes were trap netted at spawning time, immediately following the ice out. However, walleyes 1+ and 2+ had to be obtained by seining during the summer.

Scales from each fish were measured using a small strip of paper running from the focus to the last completed annulus and to the scale edge along the anterior most radius. These tabs were later used in back calculations of the fish's length for each year of growth. Scales were read twice to increase the accuracy in aging. January 1 was considered as the commencement of each new year and each complete year of life is designated by arabic numerals.

The linear relationship between fish length in centimetres (x) and magnified anterior scale radius in centimetres (y) was determined using least squares regression for the combined data of three years of study:

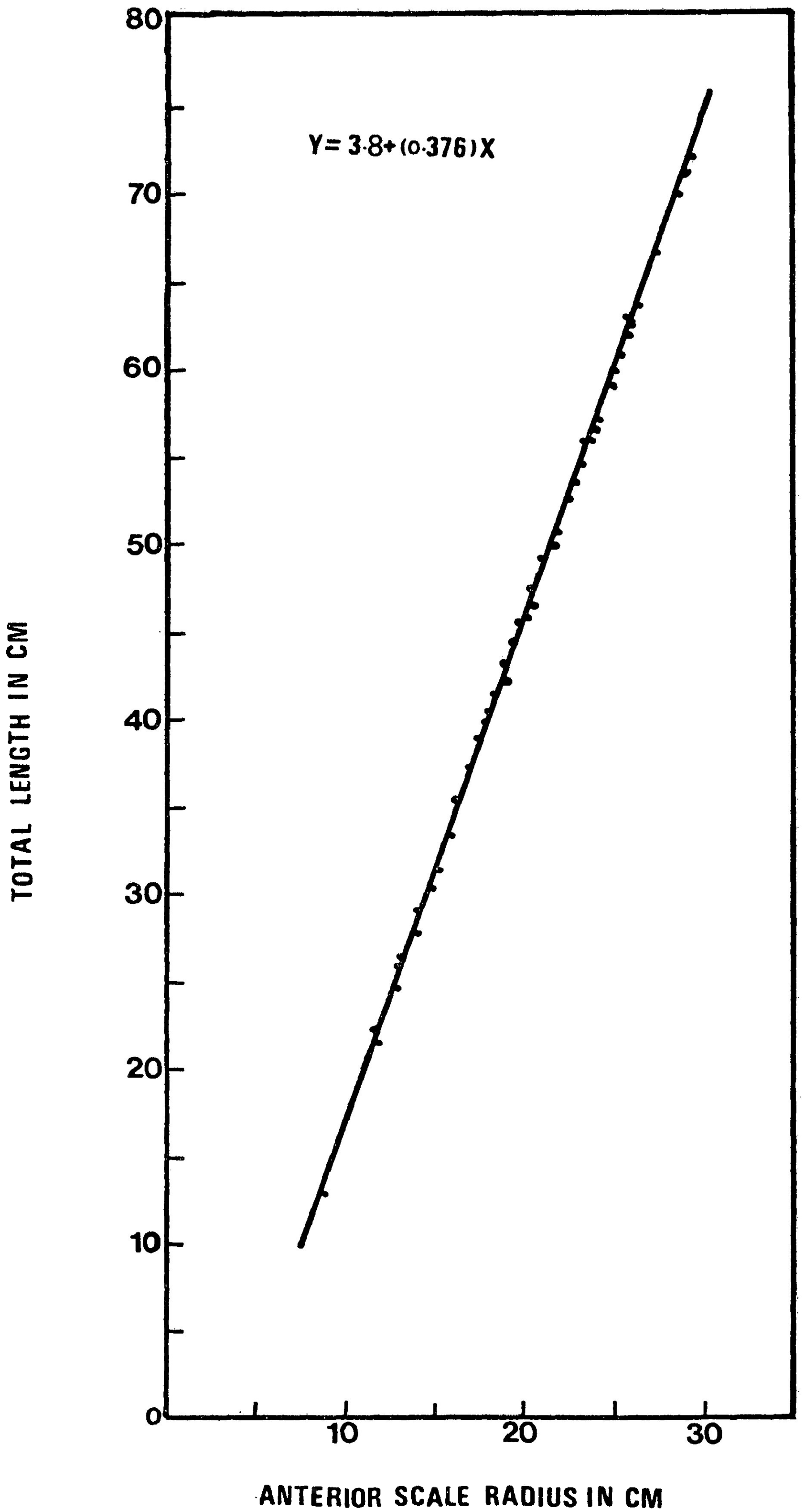
$$\log y = 3.8 + (0.367)(x)$$

x = total length in cm

y = scale radius in cm

The line was extrapolated to the ordinate to obtain the value of 3.8 cm (Frazer's correction). After determining Frazer's correction, a nomograph was constructed (Carlander and Smith 1944) for the back calculations of length at each annulus.

Fig. 6. Linear relationship between body length and anterior scale radius of Savanne Lake walleyes for the combined data of 1973-1976.



Y= 3·8+(0·376)X
TOTAL LENGTH IN CM
ANTERIOR SCALE RADIUS IN CM
0
10
20
30
40
50
60
70
80
10
20
30

The intercept of 3.8 cm gave a good fit (Fig. 6), the correlation coefficient of 0.864 being significant ($P < .05$). For Savanne Lake walleyes, the cubic equation:

$$Y = 8.390 - 0.0548X + 0.0012\,X^2 + 0.000X^3$$

where: X = total length in cm

Y = scale radius in cm

gave the best fit with correlation coefficient of 0.873 being highly significant ($P < .01$).

Hile (1970) criticizes the use of polynomials to describe body-scale relationships. The S-shaped curves have been used occasionally in walleye studies (Carlander 1945, 1950; Eschmeyer 1950; Wolfert 1972). Most studies, however, (Deason 1936; Cleary 1949; Schloemer and Lorch 1942; Forney 1965; Mraz 1968) have used a linear relationship. In some of these studies, the limited sample size and the absence of younger fish in the samples may have obscured any indication of curvilinearity (Wolfert 1972). Carlander (1950) observed that body-scale relationship varies from species to species and often with different populations within the same species. A difference in the location from which key scales are removed from the fish's body may result in differences in the body-scale relationship between populations (Regier 1962; Wolfert 1972).

Moenig (1975) also calculated a large intercept value of 10.638 cm for Dexter Lake walleyes. Forney (1965) calculated an intercept of 5.79 cm using a linear body-scale relationship. Carlander (1945), when using a cubic relationship with an intercept of 1.89 cm for Lake of the Woods walleyes, found calculated lengths at first year of life to be 30 percent higher than observed lengths. In four different lakes, Carlander (1950) used an arbitrary intercept of 1.5 cm when an empirical starting point could not be determined due to the lack of small specimens. Carlander and Whitney (1961) calculated an intercept of 8.1 cm using straight-line relationship for walleyes in Clear Lake, Iowa. Priegel (1964b) found that scale development begins at total length of about 24 mm, but is not completed until about 45 mm.

Tagging

Marking was done by attaching numbered Floy tags FTF69, which were affixed under the second dorsal fin with monofilament line of 2.7 kg test using 5.08 cm sewing needle. The 6th, 12th and second dorsal spines were respectively clipped in the spring of 1973, 1974 and 1976 for Schumacher-Eschmeyer (1943) estimates. Tags coloured red, green, yellow and blue were intended for the calculation of Jolly estimates. These four colours indentified the area in which the walleyes were tagged. Subsequent recaptures and recording of clipped dorsal spines made the fish easily recognizable. If the fish already possessed a tag from a previous year, the tag was removed and its number recorded, length measured, scale samples taken and fish retagged. Recapture of fish made in the same year required no further scale sampling, only the tag number was recorded in such cases. All walleyes were released at the site of the trap. All other species captured in the trap nets were recorded, and measurements and scale samples taken. A total number of 1492, 1389 and 1399 walleyes were marked respectively in the springs of 1973, 1974 and 1976.

Age determination

Ages of captured walleyes were determined by counting the annuli visible on scale impressions made on cellulose acetate slides (Smith 1954; Casselman 1967). The scales were mounted on plastic acetate slides and pressed by a hand roller to obtain scale impressions, a procedure used by Nesbit (1934), Lea and Kent (1936) and Hile (1941). The acetate slide impressions were read on an Eberbach scale projector similar in design to one described by Van Oosten et al. (1934), using a 32 mm lens at 40 x magnification. The criteria to define the annulus were derived from Lagler (1956) and Calhoun (1966). They were:

> a wide space between series of circuli and discontinuous ridges between two continuous ones;
> cutting over of circuli on lateral margins of scale was considered the best method of recognition of the annulus; and
> a close approximation of circuli which are often closer together just before the line which marks the annulus.

Sometimes the annulus is a clear, narrow streak encircling the focus, but more often it is not so easily identified.

RESULTS & DISCUSSIONS

Spawning

Spawning of Savanne Lake walleyes begins at the time of ice break up, at water temperatures of 4^{o}C to 5.8^{o}C. Scott and Crossman (1973) indicate that spawning begins at water temperatures of 6.7 to 8.9^{o}C, but it has been known to take place over a range of 5.6 to 11.1^{o}C. The ratio of spawning habitat area to surface area for Savanne Lake walleyes is 0.15. In Texas, a stocking evaluation study on 17 reservoirs suggested a spawning habitat ratio of spawning habitat area to surface area of 0.001 as a minimum requirement for maintaining a natural reproducing population (Prentice 1977). In Savanne Lake, males dominate over females during the entire spawning period (Tables 6 and 7) and the ratio of males to females varies from 4:1 to 29:1. As commonly reported, males dominate over females on the spawning grounds (Adams and Hankinson 1928; Schneberger 1938, 1940; Rawson 1957; Ryder 1957; Derback 1947; Eddy and Surber 1947; and Eschmeyer 1950). In Savanne Lake, the maximum proportion of females on the spawning grounds reached 19.7 percent on May 13, 1975 and 20 percent on May 11, 1976 (Tables 6 and 7). Eschmeyer (1950) found females constituted 58 and 72 percent of the spawning run in 1947 and 1948 respectively in the Muskegon River, Michigan. In Lake Gogebic, females composed 28 percent of the spawning population (Eschmeyer 1950). Ryder (1957) and Eschmeyer (1950) believe that trapnets bias the sampling in favour of males, since dipnet samples often reveal higher proportions of the more sedentary females. Ryder (1957) suggests a figure between those obtained from trapnets and dipnets might be more realistic.

Table 6. Total number of spawning walleyes examined in the catch, percentage identified by sex and male/female ratio for Savanne Lake walleyes in the spring of 1975.

Date	Total catch	Males	Females	% of females in the catch	% sexed	Male/female ratio
May 13/75	86	53	13	19.7	77%	4:1
May 14/75	66	56	4	6.6	91%	14:1
May 15/75	59	51	4	7.2	93%	13:1
May 16/75	81	67	3	4.2	86%	22:1
May 21/75	27	14	1	6.6	55%	14:1

Table 7. Total number of spawning walleyes examined in the catch, percentage identified by sex and male/female ratio for Savanne Lake walleyes in the spring of 1976.

Date	Total catch	Males	Females	% of females in the catch	% sexed	Male/female ratio
May 5/76	134	108	19	14.9	94%	8:1
May 6/76	132	113	16	12.4	98%	7:1
May 7/76	111	95	13	12.0	97%	7:1
May 11/76	47	24	6	20.0	64%	4:1
May 12/76	122	58	2	3.3	49%	29:1
May 13/76	49	10	1	10.3	22%	10:1
May 14/76	69	1	0	0	1.3%	0

The sex of a walleye was determined on the spawning grounds by exertion of gentle pressure on the fish's abdomen and identification of the resulting gonadal product. The fish were difficult to identify by this method after the spawning run peaked.

Movements

Walleye movements have been described by Stoudt and Eddy (1939), Rawson (1957), Payne (1964), Eschmeyer (1950), Ferguson and Derksen (1971) and Ryder (1968). Frequently, the distance from the point of marking and subsequent recapture is over 16 km (Ryder 1968), with fish occasionally moving further than 160 km (Eschmeyer 1950). In Savanne Lake, the maximum distance covered from the point of marking to recapture was only 4.3 km. This was simply due to the small size of the lake and the fact that it is a closed system with no possible emigration and immigration through tributaries.

Over a period of three years of study in Savanne Lake, a total of 1092 walleyes were tagged in the red area, 1416 in the green area, 741 in the yellow area and 313 in the blue area. Of the red-tagged fish 83% were recaptured in the red and green areas, 84% of green-tagged fish were recaptured in the red and green areas, 67% of yellow-tagged fish were recaptured in the red and green areas, and, similarly, 76% of blue-tagged fish were recaptured in the red and green areas of the lake (Table 8). More fish were recaptured in the red and green areas of the lake than in the yellow and blue areas which are shallower and considered less preferred habitat for older fish.

Table 8. Number of fish tagged, percentage recapture, and number of trap net sets by area, for 1973, 1974 and 1976 combined.

Number of fish tagged by area	Number of sets[a]	Total recaptures	% recapture by area Red	Green	Yellow	Blue
Red 1090	48	114	51	32	12	5
Green 1416	56	221	38	46	11	4
Yellow 741	57	241	33	34	24	9
Blue 313	62	68	29	47	15	9

a/ Trap net sets fished approximately twenty-four hours. The number of sets per location (Fig. 2, 3 and 4) varied with season and between years, depending on fishing success.

Population estimates

Schumacher-Eschmeyer (1943) spring population estimates were made during all three years of the study. The marking-recapture intervals were May 3 to June 28 in 1973, May 15 to June 27 in 1974 and May 6 to June 23 in 1976. We assume that mortality of marked and unmarked fish were similar and that mortality of adult fish was minimal during each period. The Schumacher-Eschmeyer method of population estimate is more convenient than the Jolly method and provides daily estimates. The Jolly method, on the other hand, cannot be calculated until the final fishing interval is entered and requires larger daily catches.

The following assumptions were considered for Schumacher-Eschmeyer population estimates:

1. The marked fish suffer the same natural mortality as the unmarked fish.
2. The marked and unmarked fish are equally vulnerable to fishing gear.
3. The tagged fish do not lose their tags. All fish tagged were also marked by clipping of 6th, 12th and 2nd dorsal spine in the spring of 1973, 1974 and 1976.
4. The marked fish become randomly mixed with the unmarked fish. Or the distribution of fishing efforts is proportional to the number of fish present in different locations in the lake.
5. It is assumed that the population is closed (no immigration and emigration) and constant during the experiment.

The information available for estimating the population size (Appendix 2, Table 2A, 2B and 2C) using the Schumacher-Eschmeyer formula is:

$$\hat{N} = \frac{\Sigma Mi^2(ni)}{\Sigma(Mimi)} \text{ or } \frac{\Sigma n^2(m+u)}{\Sigma nm}$$

where: Mi = total number of marked fish on i th day,

ΣMi = total number of marked fish in the population,

$\hat{N}$ = estimated population size,

ni = total sample taken on the i th day,

Σmi = total recapture in the population,

S.E. = standard error,

C.L. = confidence limits

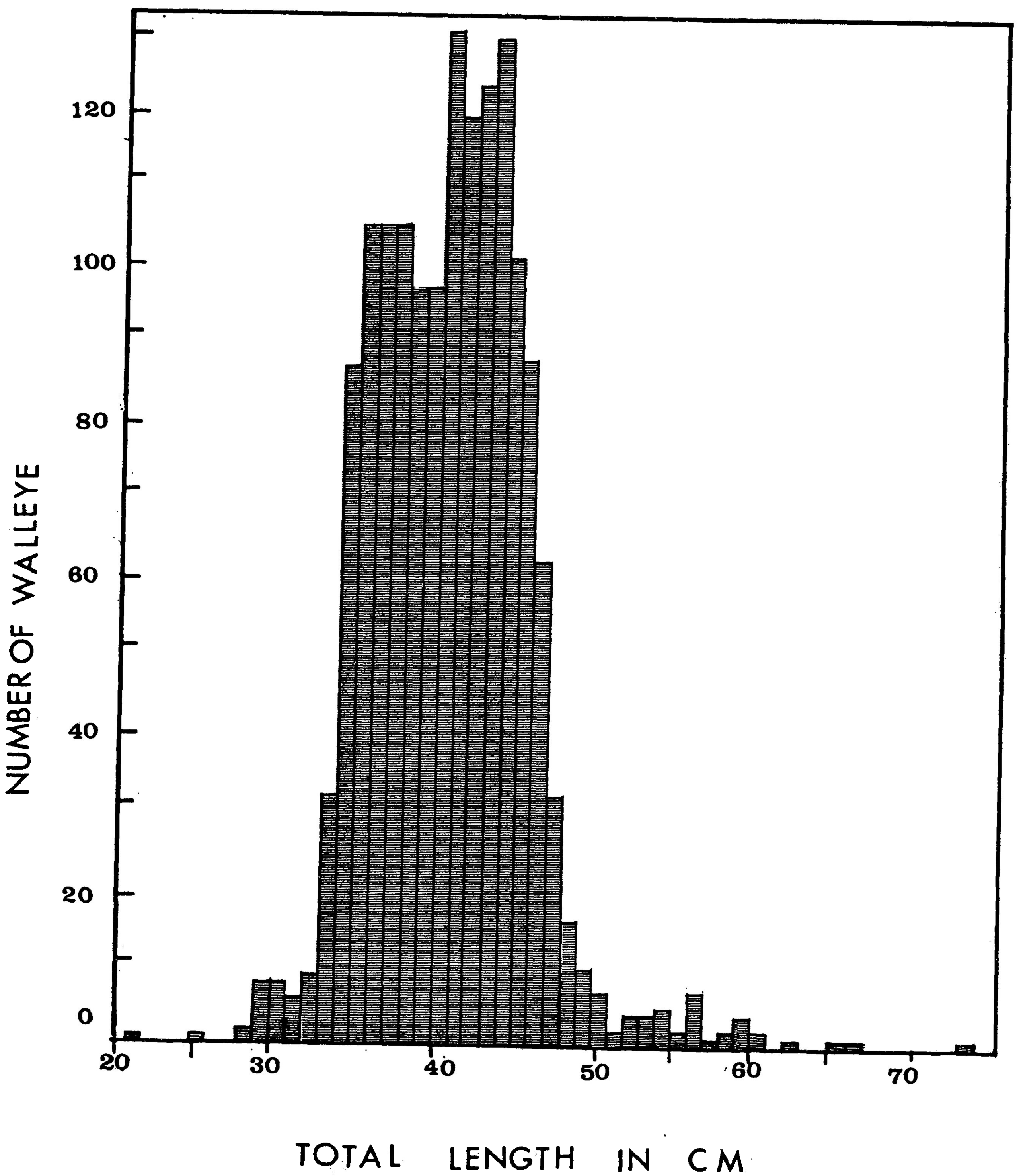
A total of 1489, 1395 and 1449 walleyes were caught during the spring trap net operations. Their length frequency distributions (Fig. 7, 8 and 9) show that the majority of walleyes caught were of 35-48 cm size range. From these figures, it is clear that trap nets are selective for walleyes larger than 30 cm.

The spring population estimates of 5211, 5184 and 5463 (Table 9) for 1973, 1974 and 1976, respectively, represent the spawning population most vulnerable to our gear. The fall population estimate of 1973 was calculated but not included in the present study. The fall estimate of 3569 was 40% lower than the spring estimate of 5211. Similarly, in a small reclaimed lake in northern Minnesota, the fall mark and recapture estimates were about 50% lower than those the following spring (Johnson and Osborn 1977). These authors believed that the low estimates indicated non-ramdom distribution of marked fish, making a substantial portion of walleye population unavailable to the sampling gear used in the fall. Differences between the fall and spring estimates reflect possible changes in seasonal behavioural characteristics of the walleye population.

Table 9. Spring population estimates (Schumacher-Eschmeyer), standard error of the estimates and confidence limits for Savanne Lake walleyes captured with trap nets, 1973-74 and 1976.

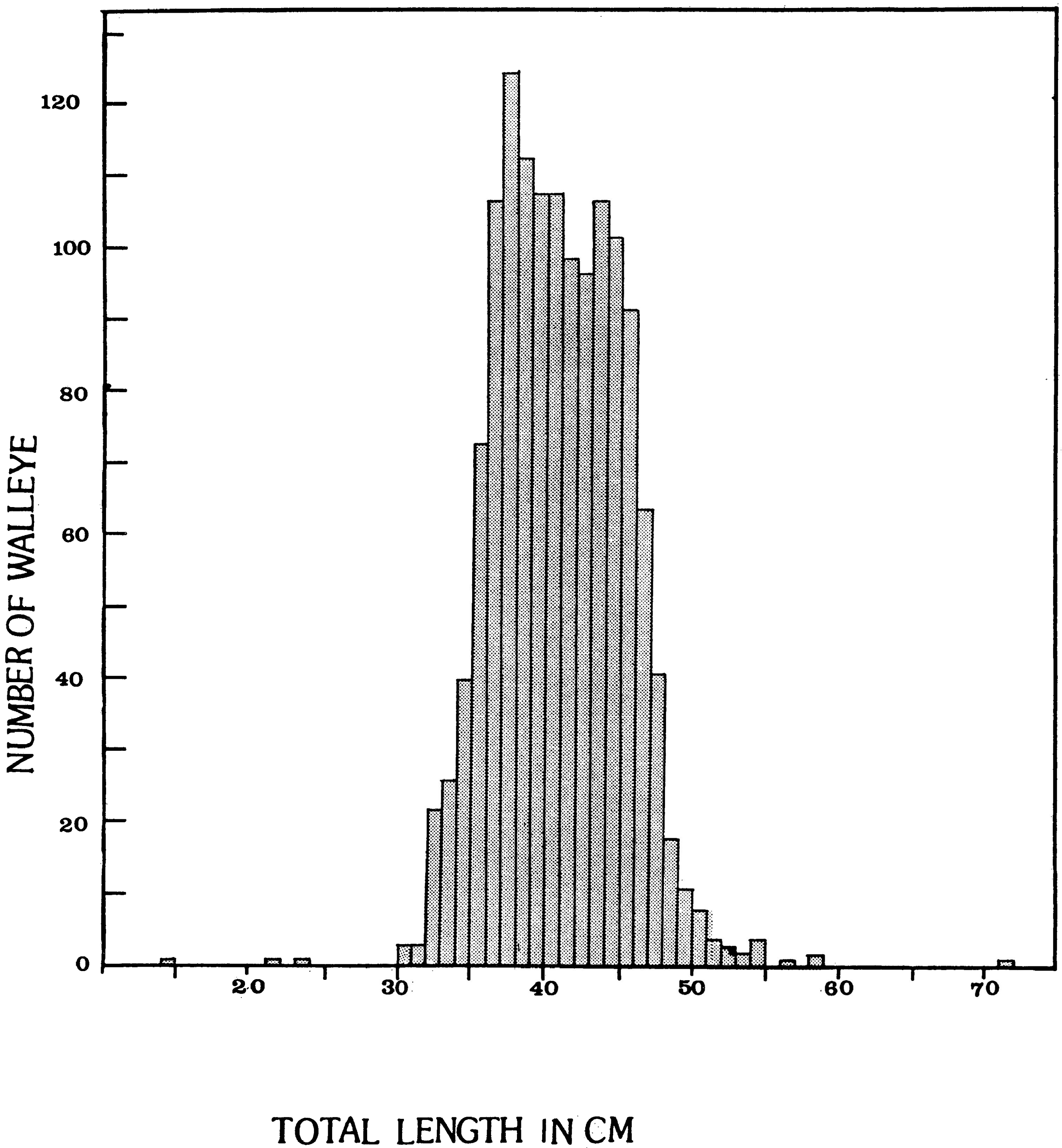
Year	Population estimates	Standard error	95% confidence limits
1973	5211	326	±662
1974	5184	316	±652
1976	5463	264	±540

Fig. 7. Length-frequency distribution of walleyes in Savanne Lake vulnerable to the trap nets in the spring of 1973.



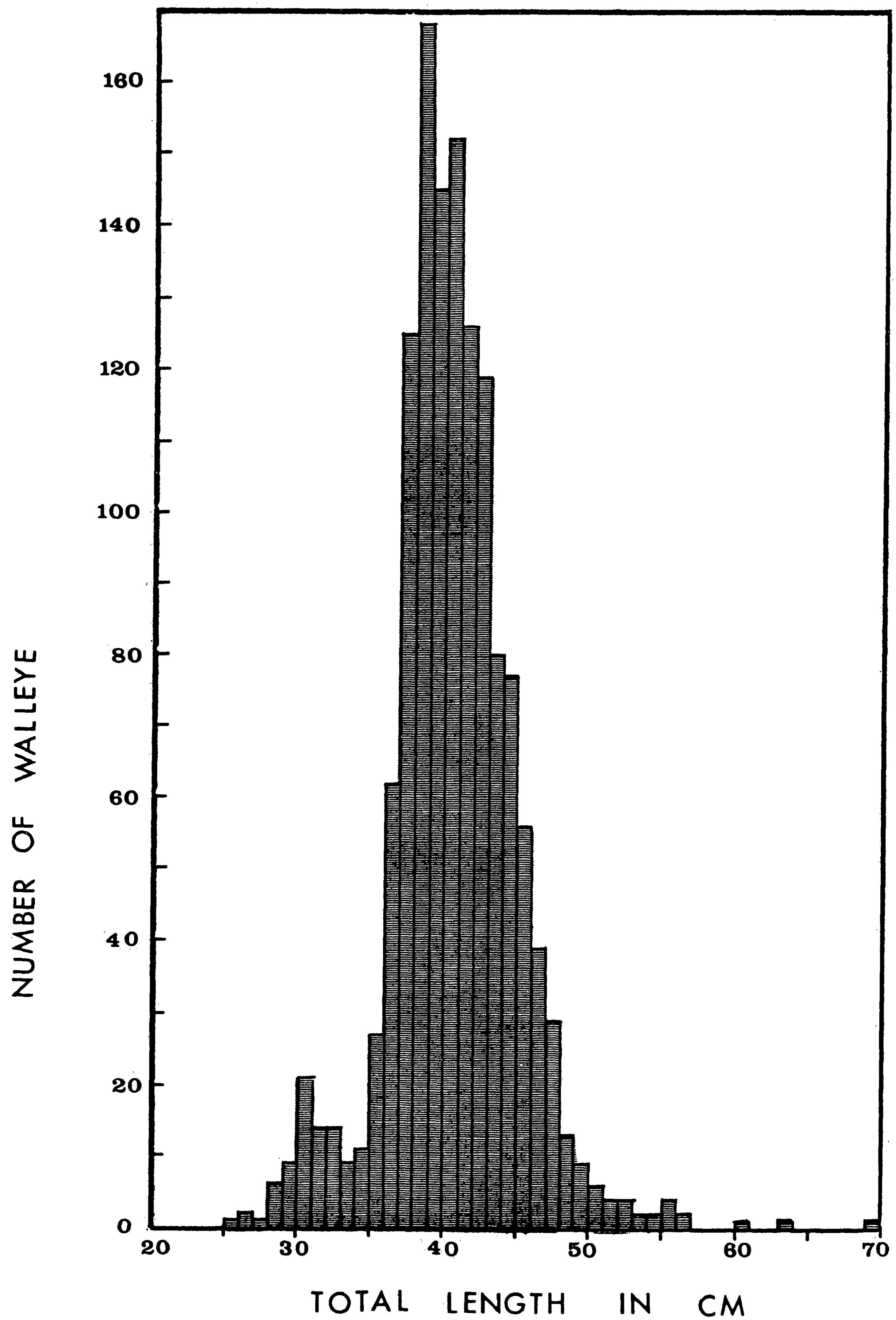
NUMBER OF WALLEYE
120
100
80
60
40
20
0
20
30
40
50
60
70
TOTAL LENGTH IN CM

Fig. 8. Length-frequency distribution of walleyes in Savanne Lake vulnerable to the trap nets in the spring of 1974.



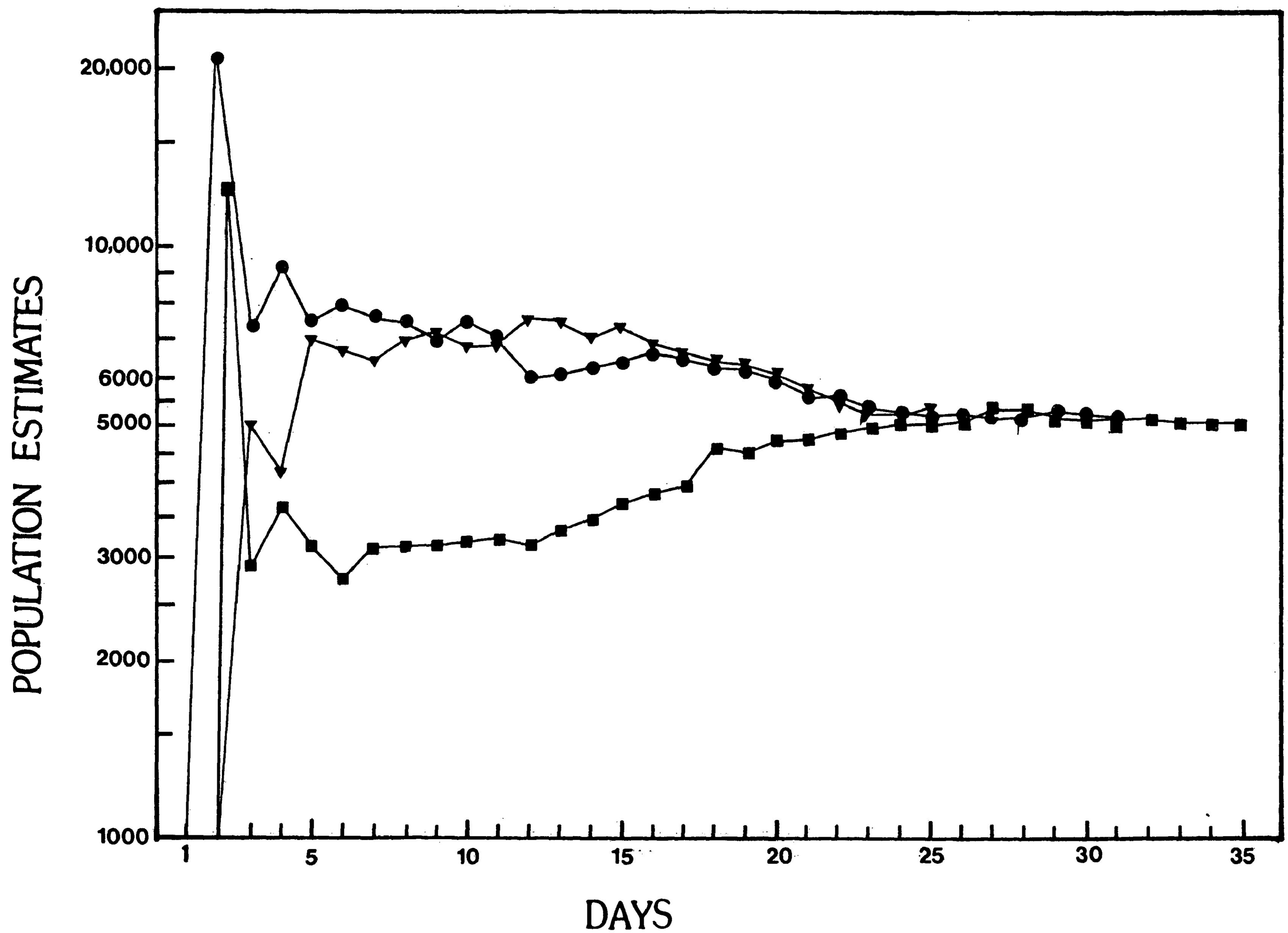
NUMBER OF WALLEYE
TOTAL LENGTH IN CM
0
20
40
60
80
100
120
20
30
40
50
60
70

Fig. 9. Length-frequency distribution of walleyes in Savanne Lake vulnerable to the trap nets in the spring of 1976.



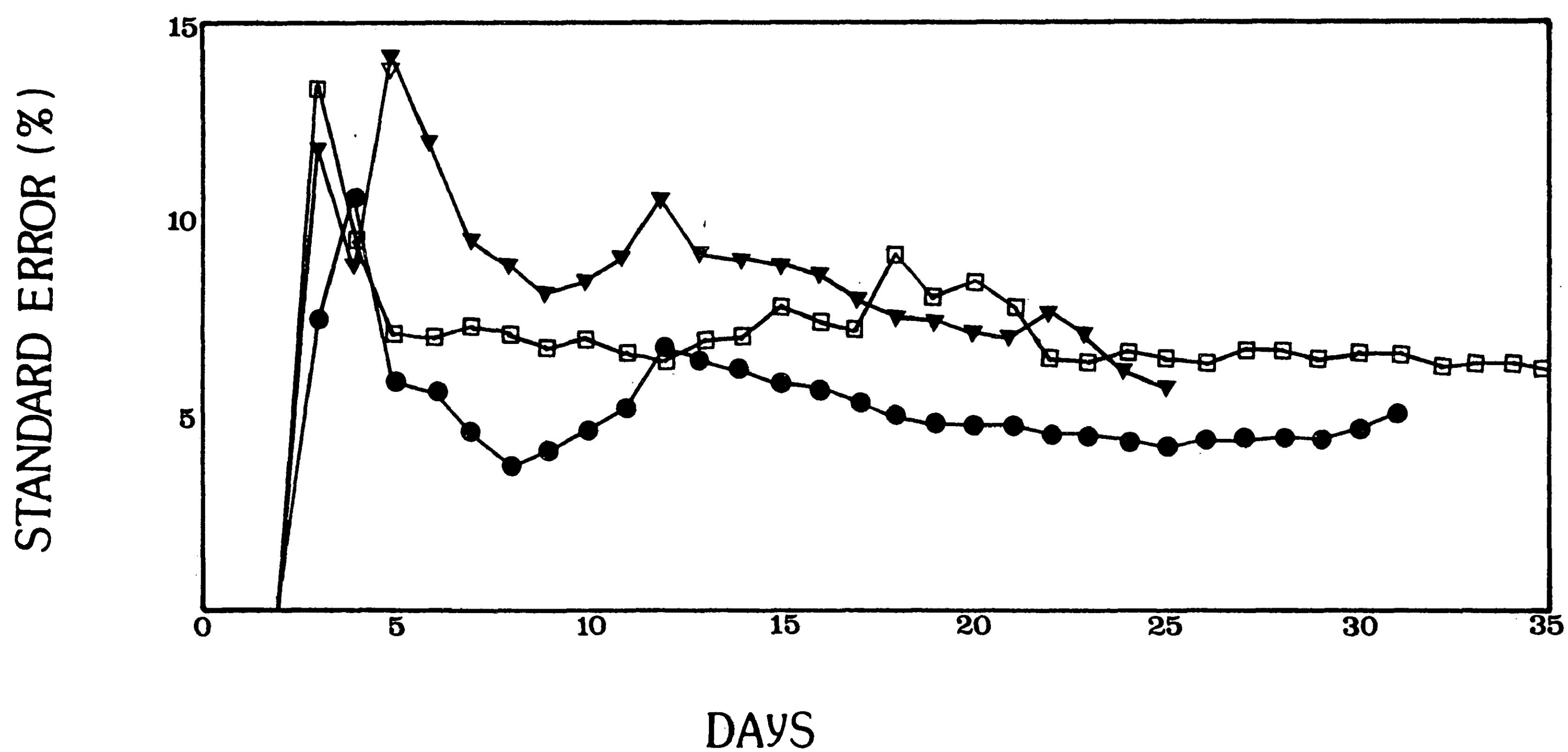
NUMBER OF WALLEYE
0
20
40
60
80
100
120
140
160
20
30
40
50
60
70
TOTAL LENGTH IN CM

Fig. 10. Schumacher-Eschmeyer population estimates during three study years 1973 (squares), 1974 (triangles) and 1976 (circles) for Savanne Lake walleyes.



POPULATION ESTIMATES
20,000
10,000
6000
5000
3000
2000
1000
1
5
10
15
20
25
30
35
DAYS

Fig. 11. The percent standard error for Schumacher-Eschmeyer estimates during the three study years 1973 (squares), 1974 (triangles) and 1976 (circles).


STANDARD ERROR (%)
15
10
5
0
5
10
15
20
25
30
35
DAYS

The spring estimates appeared most reliable.

The daily population estimate curves (Fig. 10) level off by the 25th day of sampling, with a standard error of 6.5% (Fig. 11) for three years of study. Hence, our population estimates closely approximate the true numbers of fish vulnerable to the gear. Population estimates with standard errors of 10-15% are considered reliable.

An analysis of age structure of the catch, mean lengths and percent composition by age in the catch (Tables 10, 11 and 12) indicate that 46% of walleyes sampled in 1973 were of age 7 ; 40% of those sampled in 1974 were of age 8 ; and 40% of the fish taken in 1976 were of age 6 . The catches also indicate the ages at which walleyes were fully vulnerable to the gear. The mean weighted ages of 6.82, 6.95 and 6.90 years, along with their mean weighted lengths of 41.5 cm, 41.6 cm and 41.9 cm respectively for 1973, 1974 and 1976, indicate a stable recruitment of walleye population in Savanne Lake over the three years of the study. Usually, a decrease in mean age results from an increase in recruitment, an increase in growth rate and a reduction in age of first maturity. All these factors are indications of an externally stressed population (Nikolskii 1969).

Table 10. Age structure and respective mean lengths, and weighted mean age and length of walleyes sampled for the 1973 population estimate.

Age	Number	% of catch	Mean length (cm)
3	98	1.9	30.4
4	664	12.8	34.0
5	591	11.4	37.8
6	311	6.0	37.6
7	2375	46.0	43.0
8	238	4.6	42.5
9	416	8.0	45.2
10	321	6.2	46.3
11	79	1.5	51.8
12	50	1.0	55.9
13	19	0.4	53.5
14	4	0.07	58.1
15	15	0.28	60.0
16	0	0	0
17	7	0.14	64.2
mean age	6.82	mean length	41.5

Table 11. Age structure and respective mean lengths, and weighted mean age and length of walleyes sampled for the 1974 population estimate.

Age	Number	% of catch	Mean length (cm)
4	251	4.6	33.0
5	1207	22.1	36.7
6	803	14.7	38.4
7	546	10.0	42.6
8	2185	40.0	44.6
9	126	2.3	46.0
10	186	3.4	49.3
11	76	1.4	51.5
12	33	0.6	55.8
13	43	0.8	51.8
14	0	0	0
15	0	0	0
16	4	0.07	72.0
mean age	6.95	mean length	41.6

Table 12. Age structure and respective mean lengths, and weighted mean age and length of walleyes sampled for the 1976 population estimate.

Age	Number	% of catch	Mean length (cm)
3	47	0.9	28.4
4	203	3.9	31.2
5	133	2.6	38.1
6	2100	40.3	38.3
7	922	17.7	42.8
8	1360	26.1	46.1
9	271	5.2	49.9
10	83	1.6	51.5
11	52	1.0	51.5
12	16	0.3	54.2
13	16	0.3	56.4
14	4	0.07	60.4
15	4	0.07	69.2
mean age	6.90	mean length	41.9

Length-weight relationship

The length-weight relationship of Savanne Lake walleyes was based on measurements of 4280 fish caught in the sampling years of 1973, 1974 and 1976 and is represented by the relationship:

$$W = aL^b$$

where: W = weight in gm,

L = length in mm

and a and b are constants.

The length and weight measurements taken during the three study years were converted to logarithms, from which the following regression equation was calculated by the least squares method (Table 13):

$$\text{Log } W - -4.8332286 + 2.915278 \, (\text{Log } L)$$

Using co-variance analysis, no significant differences were found in the slopes for the years 1973-74, 1974-76 and 1973-76 (Appendix 3). However, there was significant difference of intercepts at ($P < .05$) for the years 1973-74, 1974-76 and 1973-76, indicating a characteristic annual difference in the length-weight relationship over the three year study period. Good agreement is evident between the observed data and the calculated length-weight relationships (Fig. 12).

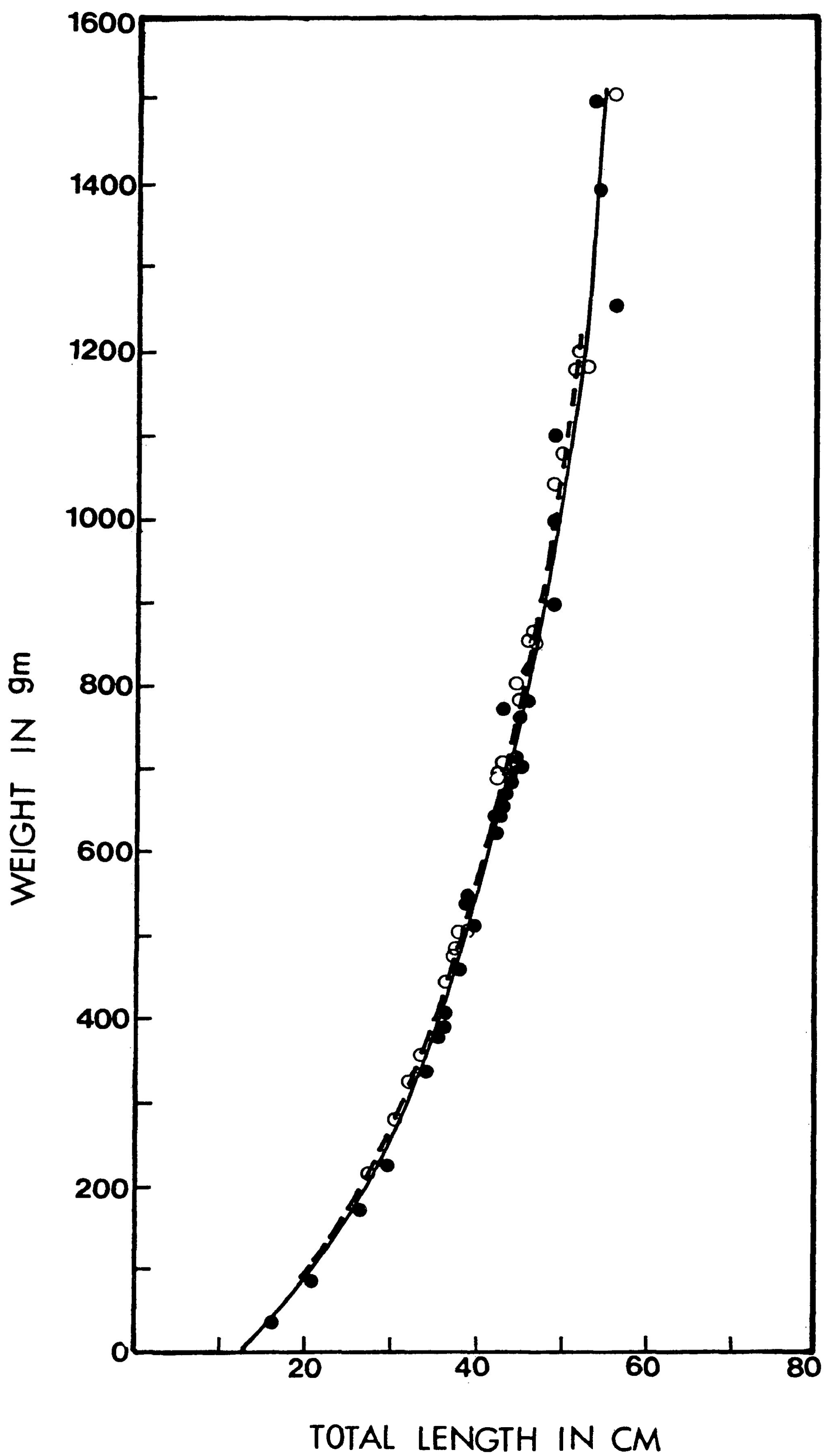
No significant difference was found between the length-weight relationships of males and females (Table 13). This is consistent with most other waters studied (Van Oosten and Deason 1957; Priegel 1969a; Lewis 1970), except (Table 14) for the Mississippi River in Iowa (Vasey 1967) and Center Hill Reservoir, Tennessee (Muench 1966). There was evidence of poor condition when length-weight relationships from different bodies of water were compared

(Table 14). Both intercept (a) and slope (b) were lower for Savanne Lake walleyes than for those in other waters, indicating that Savanne Lake walleyes were gaining more length per unit weight.

Table 13. Length-weight relationship for Savanne Lake walleyes over a three year study period.

Year	Equation
1973	Log W = -5.529692 + 3.058860 (Log L)
1974	Log W = -4.417897 + 2.752685 (Log L)
1976	Log W = -4.820142 + 2.900615 (Log L)
	Combined for 1973 to 1976
Total	Log W = -4.8332286 + 2.915278 (Log L)
Males	Log W = -4.7888809 + 2.739450 (Log L)
Females	Log W = -4.7242513 + 2.877599 (Log L)

Fig. 12. Length-weight relationship for Savanne Lake walleyes for the three study years combined, using calculated data (open circles) and observed data (closed circles).



1600
1400
1200
1000
800
600
400
200
0
20
40
60
80
WEIGHT IN gm
TOTAL LENGTH IN CM

Table 14. Length-weight relationships for walleyes from various waters.

Formula	Location	Reference
Units: wt = gm; TL = mm		
Log W = -4.83322 + 2.91527 Log L (Sexes Comb.)	Savanne Lake, Ontario	Present Study
Log W = -5.39540 + 3.18672 Log L "	Dexter Lake, Ontario	Moenig (1975)
Log W = -5.80964 + 3.20447 Log L	Lake Sakakawea, N. Dak.	Wahtola et al. (1972)
Log W = -5.099 + 3.040 Log L (♀)	Lake Meredith, Tex.	Kraai and Prentice (1974)
Log W = -4.584 + 2.845 Log L (♂)	Lake Meredith, Tex.	Kraai and Prentice (1974)
Log W = -0.02770 + 3.03 Log L (♂)	Center Hill Res., Tenn.	Muench (1966)
Log W = -0.03119 + 2.99 Log L (♀)	Center Hill Res., Tenn.	Muench (1966)
Log W = -0.01719 + 3.16 Log L (Sexes Comb.)	Center Hill Res., Tenn.	Muench (1966)
Log W = -5.4403 + 3.15399 Log L	Pike Lake, Wis.	Mraz (1968)
Log W = -4.7817 + 2.8930 Log L	Makoop Lake, Ontario	Armstrong (1965)
Log W = -5.3806 + 3.140 Log L	Des Moines River, Iowa	Schmulback (1959)

Table 14 (Cont'd).

Formula	Location	Reference
$\log W = -4.9216 + 2.9721 \log L$	Canton Reservoir, Okla.	Lewis (1970)
$\log W = -5.0131 + 3.3959 \log L$	(♀) Mississippi River, Iowa	Vasey (1967)
$\log W = -4.6770 + 3.2618 \log L$	(♂) Mississippi River, Iowa	Vasey (1967)
$\log W = -5.1824 + 3.04957 \log L$	Red Lakes, Minn.	Smith and Pycha (1961)
$\log W = -4.8055 + 2.9141 \log L$	North Caribou Lake, Ont.	Lewis et al. (1964)
$\log W = -5.0758 + 3.1103 \log L$	Deer Lake, Ontario	Lewis et al. (1964)
$\log W = -5.0263 + 2.9932 \log L$	Sandy Lake, Ontario	Lewis et al. (1964)
$\log W = -5.1732 + 3.0513 \log L$	Wunnummin Lake, Ontario	Lewis et al. (1964)
$\log W = -3.9028 + 2.5658 \log L$	Lake St. Joseph, Ontario	Lewis et al. (1964)
$\log W = -4.3507 + 2.7499 \log L$	Attawapiskat Lake, Ont.	Lewis et al. (1964)

Condition factor or coefficient of condition (K)

The condition factor reflects changes in plumpness or relative well-being of fish. As fish grow older, they tend to gain proportionately more in weight than in length, so that the value of (K) will increase with age. The condition factor (K) assumes weight is related to length by the cube law. The formula is:

$$K = \frac{W \times 10^5}{L^3}$$

where: W = weight in gm and

L = length in mm.

The K values for Savanne Lake walleyes over three years of study decreased with respect to both length and age (Table 18). Hence, these fish gained proportionately less in weight than in length as they grew older, which was indicative of their poor condition.

The average condition factor (K) for adult walleyes ranged from 1.26 (Mud Lake, Iowa) to 1.855 (Utah Lake, Utah). Some authors found no significant differences in conditions with increasing length (Schloemer and Lorch 1942; Cleary 1949; Rawson 1951; Hile 1954; Smith and Pycha 1961; Lewis 1970), whereas others noticed a slight tendency for the coefficient to increase with increasing length (Stroud 1949a; Slastenenko 1956; Van Oosten and Deason 1957; Schmulback 1959; Seward 1967). In Lake Winnebago, Wisconsin, condition factors of walleyes increased markedly with age (Priegel, 1969a). Food availability appears to be the main factor governing the condition of adults. Condition factors tend to be low in areas where forage is scarce (Stroud 1949b; Slastenenko 1956) and high in areas where forage is abundant (Rose 1951; Arnold 1960).

The condition factor of 0.88 for Savanne Lake walleyes was comparable to 0.89 for Red Lakes, Minnesota (Smith and Pycha 1961) and 0.81 for Lake Winnebago, Wisconsin (Priegel 1969a). However, condition factor was much lower than 1.01 for nearby Dexter Lake (Moenig 1975). As compared with other waters (Table 16), Savanne Lake produces walleyes with the lowest condition factor (K) yet recorded. This means that they are in very poor condition. It may be due to limited food availability, which in older walleyes is used mostly for maintenance rather than growth. This may be typical for walleyes from smaller unexploited and closed systems, like Savanne Lake.

Relative condition factor (kn)

The relative condition factor (kn) compares actual weight of fish to the calculated weight ($\hat{W}$) of a fish of the same length as determined from length-weight regression. The calculated weight (W) from the length-weight regression (Log W = 4.8332286 + 2.9152728 (Log L) and mean observed weight (W) were calculated for age class. The values were used to calculate the relative condition factor using the following formula:

$$kn = \frac{W}{\hat{W}} \text{ or } \text{Log } kn = \text{Log } W - \text{Log } \hat{W}$$

There was no significant difference in the mean kn values among age groups (Table 17, Mann-Whitney test (P .05)). Thus, the fish of all sizes seem to be in relatively similar condition.

Table 15. Condition factor (K) for Savanne Lake walleyes over a period of three years of study.

Age	1973	1974	1976
3	.9040	-	.9080
4	.8955	.8987	.9021
5	.8868	.8901	.8859
6	.8879	.8865	.8864
7	.8779	.8782	.8787
8	.8792	.8746	.8726
9	.8738	.8732	.8667
10	.8725	.8679	.8646
11	.8640	.8646	.8646
12	.8587	.8587	.8610
13	.8620	.8640	.8578
14	.8555	-	.8531
15	.8537	-	.8431
16	-	.8404	-
17	.8487	-	-

Table 16. Condition factor $\frac{W \times 10^5}{L^3}$ for walleyes from various waters.

Location	Condition factor (sexes combined)	Source
Units: wt = gm; TL = mm		
Savanne Lake, Ontario	0.88 (1973-76)	Present Study
Dexter Lake, Ontario	1.01 (1968)	Moenig (1975)
Red Lakes, Minn.	0.89	Smith and Pycha (1961)
Lake Winnebago, Wis.	0.81	Priegel (1969a)
Canton Res., Okla.	1.03	Lewis (1970)
Units: wt = gm; SL = mm		
Utah Lake, Utah	1.85	Arnold (1960)
Lake of the Woods, Minn.	1.47	Carlander (1948)
West Okoboji Lake, Iowa	1.37	Carlander (1948)
Spirit Lake, Iowa	1.71	Carlander (1948)
Spirit Lake, Iowa	1.63	Rose (1951)
Diamond Lake, Iowa	1.84	Carlander (1948)
Mud Lake, Iowa	1.26	Carlander (1948)
Clear Lake, Iowa	1.49	Cleary (1949)
Lake Gogebic, Mich.	1.66	Eschmeyer and Crowe (1955)
Great Slave Lake, N.W.T.	1.44	Rawson (1951)
Three Mile Lake, Ontario	1.38	Slastenenko (1956)
Lake Huron (Saginaw Bay)	1.28	Hile (1954)
Red Lakes, Minn.	1.48	Van Oosten and Deason (1957)

Table 17. Relative condition factors (kn) for Savanne Lake walleyes over a period of three years of study.

Age	1973	1974	1976
3	0.9792	0.9460	0.9910
4	0.9927	1.0464	0.9154
5	1.0962	1.0434	0.9431
6	0.9787	1.0481	0.9860
7	1.0523	0.9730	0.9878
8	1.0269	0.9566	0.9538
9	1.0392	0.9699	1.0072
10	1.0955	0.8912	1.0217
11	0.8846	1.0326	-
12	0.9908	-	

Natural mortality

Most estimates of natural mortality of walleye populations have been obtained from exploited populations (Regier, Applegate and Ryder 1969). These range from 5% (Olson 1958) and 6% (Forney 1967) to 10% (Mraz 1968). A moderately exploited population studied by Payne (1966) was estimated to have an annual mortality rate of about 33%. Ryder (1968) estimated the annual mortality rate of lightly exploited Nipigon River walleye population to be 50%. Annual mortality prior to exploitation in Dexter Lake was estimated to be about 48% for walleyes age 4 and above. Annual mortality rates varied for different age groups ranging from 17% to 70% for 1968-69 season with highest mortality in the youngest and oldest year-classes having a mean value of 40.1% (Moenig 1975). In lightly exploited West Blue Lake, annual natural mortality of walleyes greater than 25 cm was 80% (Kelso and Ward 1972). The annual natural mortality rate of walleyes in Savanne Lake for 1973-74 varied from 8% to 73% with a mean value of 47% for ages 7 to 16 walleyes (Table 18).

In 1974-75 the annual mortality rate for each year-class averaged 40%. But in 1975-76 annual mortality rate continuously increased with age from 17% to 85%. However, the mean value was 52% for walleyes age 8 to 14 (Table 18). These values are thus in general agreement with those calculated for other lightly exploited or unexploited populations.

Certain environmental parameters may affect mortality rates. Winter-kill from oxygen depletion has been observed to cause large mortality among adults in Red Deer Lake, Manitoba (Dickson 1963) and Lake Koshknong, Wisconsin (Threinen 1952). Work by Ryder (1968), Kempinger and Churchill (1972) and Moenig (1975) suggests that with

Table 18. Estimates of annual mortality rate (A), survival rate (S) and instantaneous rate of mortality (Z), calculations using the method of Ricker (1948).

Age	1973-74			1974-75			1975-76		
	A	S	Z	A	S	Z	A[a]	S	Z
7- 8	0.08	0.92	0.083	0.400	0.600	0.509	-	-	-
8- 9	0.47	0.53	0.640	0.400	0.600	0.510	0.170	0.830	0.19
9-10	0.55	0.45	0.805	0.397	0.603	0.505	0.037	0.063	2.75
10-11	0.76	0.24	1.436	0.398	0.602	0.507	0.320	0.680	0.38
11-12	0.58	0.42	0.875	0.395	0.605	0.502	0.860	0.140	1.94
12-13	0.14	0.86	0.164	0.394	0.606	0.500	0.650	0.350	1.05
13-14	-	-	-	0.396	0.604	0.503	0.800	0.200	1.60
14-15	-	-	-	-	-	-	0.850	0.150	1.87
15-16	0.73	0.27	1.339	-	-	-	-	-	-

a/ The age groups for the year 1975 were reconstructed following Pivnicka and Svatora (1977) using a survival and mortality rate of 0.60 and 0.40 respectively.

increased fishing mortality, the natural mortality rate tends to decrease.

In Savanne Lake, the pattern and magnitude of natural mortality of walleyes were similar to nearby Dexter Lake. Also, the higher natural mortality rates of unexploited populations could be due to density dependent factors, like a limited food supply, slow growth and/or an increase in age of first maturity and spawning, or underestimating the ages of older fish.

Effects of tagging on Savanne Lake walleyes

Tagging mortality appeared to be low. Estimates of tagging mortality were usually restricted to observations of dead fish in or around the tagging area shortly after tagging (Zimmerman 1966a; 1966b; Rose 1955; Ryder 1968). McDonald (1969) found an 11.1% mortality among walleyes after a dart-tagging application was followed by a 24 hour holding period. Retardation in walleye growth following use of jaw tags has been observed by Rose (1949), Eschmeyer and Crowe (1955), Mraz (1968) and others. Occasionally, Lake Gogebic walleyes showed a loss in total length soon after handling and tagging, due to loss of the distal portion of the caudal fins (Eschmeyer and Crowe 1955). In Savanne Lake, few fish were affected by frayed caudal fins. Mraz (1968) observed growth retardation for both sexes of Pike Lake walleyes. The smaller fish suffered the least effects because of faster growth rate. Very large females showed no growth at all. A 50% retardation occurred for two-year tagged fish with no growth evident for older fish. Clipped walleye in Pike Lake, however, gave no such evidence of growth retardation. Walleyes in Savanne Lake were tagged and fins clipped right after ice melt until mid-June.

Savanne Lake walleyes are under stress and exhibit poor growth due to a limited food supply and/or because of tagging, fin clipping and handling over the several years of study. Tagging continued from 1972 to 1976, excepting 1975. Observations were made on 100 walleyes that had been tagged and fin clipped and at large for two years. Walleyes were tagged in the spring of 1974 and recaptured for aging in the spring of 1976. Scale samples were read and the results showed that 37 walleyes had laid down two annuli, 44 added only one annulus and 19 walleyes added no annuli (Table 19). In addition, the growth history of 37 tagged and fin clipped walleyes was followed for three consecutive years. Walleyes tagged and aged in the fall of 1973 had fully completed annuli. The same fish captured in the spring of 1974 had formed no additional annuli. When the same fish were recaptured two years later, in the spring of 1976, 6 walleyes of age groups 5 and 6 had laid down two annuli, 12 walleyes of age groups 7, 8 and 9 had formed no annuli (Table 20), and 19 walleyes of age groups 5, 7, 8 and 10 had formed only one annulus in the two year period.(Table 21).

Since some of the walleyes neither grew in length nor laid down a new annulus in two years, it appears that there is a possibility of underestimating the ages of walleyes from unexploited populations. This would explain the unusually high values of instantaneous growth rate (G) of 0.531 for age groups 15-16 in 1973-74, 0.453 for age groups 13-14 in 1974-75 and 0.390 for age groups 14-15 in 1975-76 (Table 23). These observations were based on a single specimen of a larger fish which was much older than most of the other fish examined. This resulted in very high estimates of production for the oldest fish. The ages of these fish may be greatly underestimated using the scale reading technique, and therefore the observations on production estimates represent a summation of G values over several years. These observations can be attributed either to the effects of tagging and fin clipping on feeding behaviour and metabolism, to slow growth due to limited food supply, or to both. Normally, fish do form annuli and grow in length each year.

Table 19. Age, total length and number of walleyes tagged in 1974, recaptured in 1976, and grouped according to whether two, one or no annuli were formed.

Known age at tagging	Number of fish examined within groups	Total number of tagged fish recaptured	$\overline{X}$ length (mm) at tagging	Age at recapture	$\overline{X}$ length (mm) at recapture
		Two annuli			
4	3	3	343	6	377
5	16	21	374	7	390
6	16	18	391	8	407
7	1	8	373	9	391
8	1	42	404	10	416
Total	37				
		One annulus			
5	5	-	375	6	389
6	2	-	384	7	393
7	5	-	430	8	435
8	28	-	430	9	439
9	-	3	-	10	-
10	4	4	437	11	435
Total	44				
		Zero annuli			
7	2	-	432	7	432
8	13	-	434	8	439
9	3	-	421	9	420
10	-	-	-	-	-
11	1	1	462	11	457
Total	19				

Table 20. Length of fall tagged (1973) walleyes, recaptured in the spring of 1974. Age groups 5 and 6 formed two annuli. None was formed in the two-year period after age 6.

	Tagged in fall of 1973		Recaptured and tagged in spring of 1974		Recaptured in spring of 1976	
Sample size	Age	$\overline{X}$ length (mm)	Age	$\overline{X}$ length (mm)	Age	$\overline{X}$ length (mm)
2	5	372	5	378	7	396
4	6	402	6	397	8	422
2	7	430	7	432	7	432
8	8	443	8	436	8	443
2	9	402	9	426	9	427

Table 21. Length of fall tagged (1973) walleyes, recaptured in the spring of 1974 and forming only one annulus in the two-year period for age groups 5, 7, 8 and 10.

	Tagged in fall of 1973		Recaptured and tagged in spring of 1974		Recaptured in spring of 1976	
Sample size	Age	$\bar{X}$ length (mm)	Age	$\bar{X}$ length (mm)	Age	$\bar{X}$ length (mm)
2	5	394	5	395	6	412
3	7	433	7	434	8	442
12	8	442	8	437	9	447
2	10	450	10	450	11	451

Growth expressed as Walford line

Von Bertalanffy growth curves (Walford 1946) were fitted to 1973, 1974 and 1976 age-length data (Ricker 1958). Length at age L(t) was plotted against length at age L(t+1) and resultant points were plotted against a straight line crossing the 45^0 line at $L(\infty)$ (Appendix 4, Fig. 4A, 4B and 4C). The point of union of two lines is the calculated ultimate attainable size of walleyes in Savanne Lake. The general formula is:

$$L(t+1) = L(\infty)\ (1-k) + kL(t)$$

where: $L(t)$ = total length in cm at age t,

$L(\infty)$ = ultimate growth in cm, and

k = the slope of Walford line.

The asymptotic size of fish was calculated from the resultant equation. The asymptotic lengths of Savanne Lake walleyes calculated for the years 1973, 1974 and 1976 were 82, 78 and 80 cm, respectively (Table 22). The largest walleye caught in 1973 was 77 cm.

A mean growth curve was obtained from the combined age-length data of three sampling years, 1973, 1974 and 1976. The resultant growth equation $Lt + 1 = 9.04 + .88Lt$, gave the asymptotic size as $L\infty$ 80.0. It was based on fish from 1 to 17 years old and 10.5 cm to 64.2 cm in length (Appendix 4, Table 4A).

A plot of resultant points of $\log_e (L\infty - Lt + 1)$ against t (Appendix 4, Table 4A) showed that the points did not fall on a straight line (Fig. 13). Adjustments to these points were made by assuming new values for $L\infty$ (Ricker 1958). Several trial points with different asymptotic length ($L\infty$) showed that at $L\infty = 82.0$ cm (App. 4, Table 4B) the points fell much closer to a straight line (Fig. 13) than they did for the original estimate of $L\infty = 80.0$ cm. Thus, using the new asymptotic size ($L\infty = 82.0$), the equation for best describing growth attained by walleyes in Savanne Lake is:

$$Lt + 1 = 82.0\,(1 - .890) + .890\,Lt$$

$$Lt + 1 = 9.02 + .890\,Lt$$

Instantaneous rates of growth (G) were determined indirectly from length measurements. All length measurements for three years of study were converted to weights using the relationship:

$$\text{Log } W = -4.8332286 + 2.915278\,(\text{Log } L)$$

where: W = weight in gm,

L = total length in mm

The catches of walleyes were sub-divided into age-classes obtained from scale reading using age frequency data plotted at 1 cm intervals. The mean weight for each age-class in each catch was then calculated into the instantaneous rate of growth (G) by the expression:

$$\log_e \frac{Wt}{Wo} = G$$

where: G = instantaneous rate of growth,

Wt = the final weight at time t, the end of period for which growth is being determined,

Wo = initial weight at time o, beginning of the period, and

$\log_e$ = logarithm to the base e of the ratio

The instantaneous rate of growth ranged from 0.15 to 0.531 for 1973-74, 0.243 - 0.453 for 1974-75 and 0.21 - 0.390 for 1975-76 (Table 23). The instantaneous rate of growth was higher in 1973-74 than in 1974-75 and 1975-76.

Table 22. Equation and asymptotic lengths of Savanne Lake walleyes for three sampling years.

Year	Age	Length range (cm)	Equation	Asymptotic length (cm)
1973	3-17	30.4 - 64.2	Lt + 1 = 9.2 + 0.89 Lt	82.0
1974	4-16	33.0 - 72.0	Lt + 1 = 8.9 + 0.88 Lt	78.0
1976	3-15	28.4 - 69.2	Lt + 1 = 9.04 + 0.89 Lt	80.0

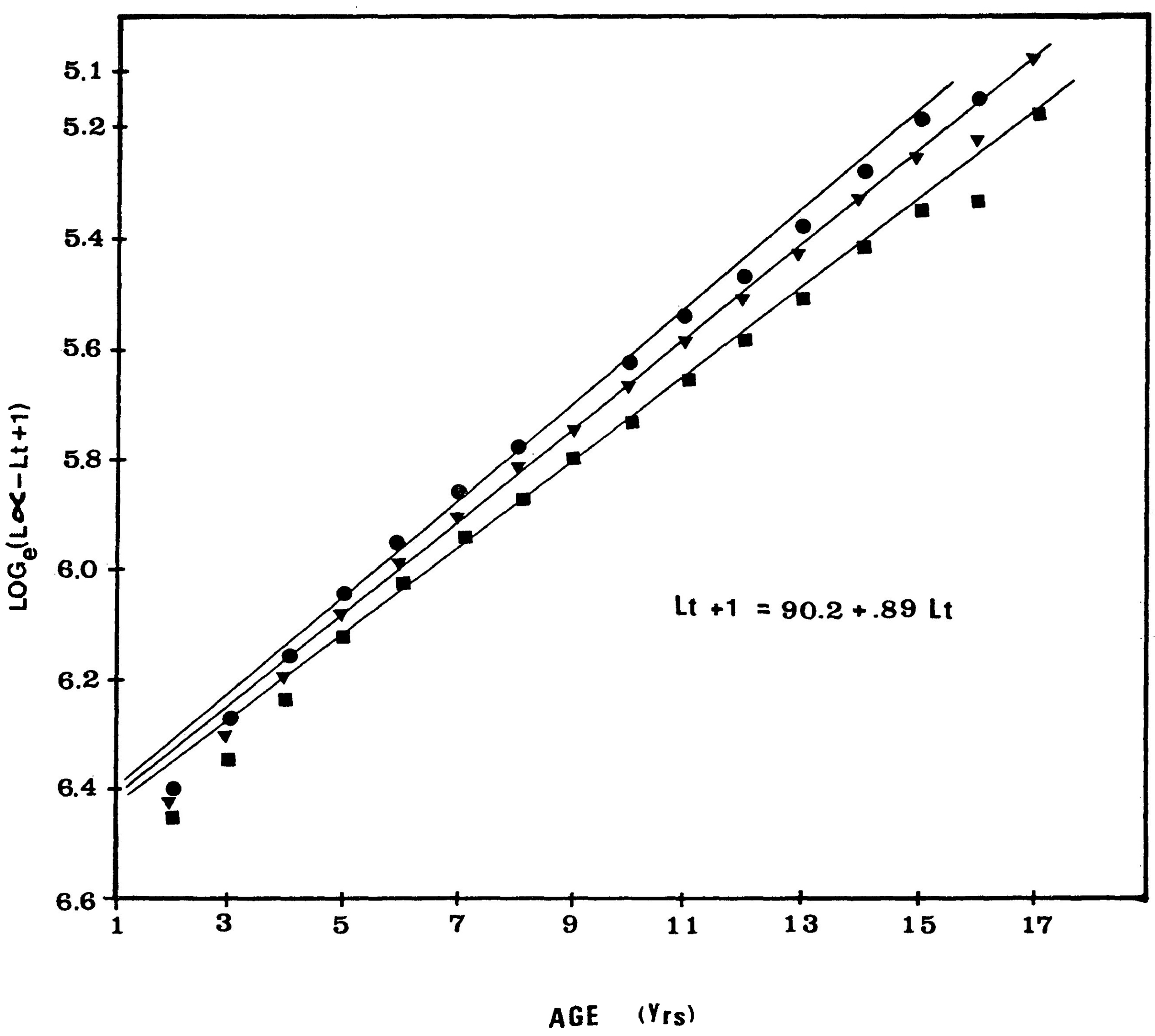
Table 23. Instantaneous rate of growth (G) of Savanne Lake walleyes from 1973-76. Wo = initial weight of stock; Wt = average weight of stock.

Age	1973-74			1974-75			1975-76		
	Wo	Wt	G	Wo	Wt	G	Wo	Wt	G
7	698	776	0.105	679	866	0.243	-	-	-
8	675	850	0.230	776	968	0.221	866	1077	0.218
9	807	1040	0.253	850	1010	0.172	968	1181	0.198
10	866	1181	0.310	1040	1202	0.144	1010	1181	0.156
11	1201	1492	0.216	1181	1357	0.138	1202	1371	0.131
12	1500	1201	0.222	1492	1679	0.118	1357	1539	0.126
13	1320	-	-	1201	1890	0.453	1679	1880	0.113
14	1678	-	-	-	-	-	1890	2794	0.390
15	1844	3137	0.531	-	-	-	-	-	-

Since Savanne Lake is unexploited, the age-length relationship curve resulting from the 1973 sample typifies the growth of fish in the population. However, age-length curves from samples of walleyes collected in 1973, 1974 and 1976 (Fig. 14) show that walleyes do not always increase in length at given ages in successive sample years.

The mean calculated lengths of walleyes for 1973, 1974 and 1976 along with their growth increments, percentage of growth and number examined in the samples are given in Appendix 5, Table 5A, 5B and 5C. In all three sampling years, walleyes increase in length up to age 6; then there is a gradual decrease in length increments. Ages 14 and 15 of the sampling year 1976 are exceptions, but these length increments are based on a single older fish in the sample. The various mean growth increments of each age group for each year of life for 1973, 1974 and 1976 (Appendix 5, Table 5D 5E and 5F) show variations from the back calculated lengths because increments are determined by age group and not from the individual year-class. There is no difference between the back calculated mean length and observed mean length along with their growth increments, hence growth is constant in all sampling years (Table 24). Moreover, calculated length of walleyes up to age five is less than the observed length in all sampling years. After age 5, observed lengths exceed the calculated lengths.

Fig. 13. Walford graph for length of Savanne Lake walleyes using combined data of three years of study. $\log_e (L_\infty - L_t)$ against age plotted for original combined estimate of L = 80.0 cm (triangles), for trial values of L = 79.0 cm (circles) and L = 82.0 cm (squares).



LOG$_e$(L∝−Lt+1)
5.1
5.2
5.4
5.6
5.8
6.0
6.2
6.4
6.6
1
3
5
7
9
11
13
15
17
Lt +1 = 90.2 + .89 Lt
AGE (Yrs)

Fig. 14. Age-length relationship of 1 to 17-year age groups of walleyes in Savanne Lake, with total calculated length in cm during the three study years 1973 (squares), 1974 (triangles) and 1976 (circles).

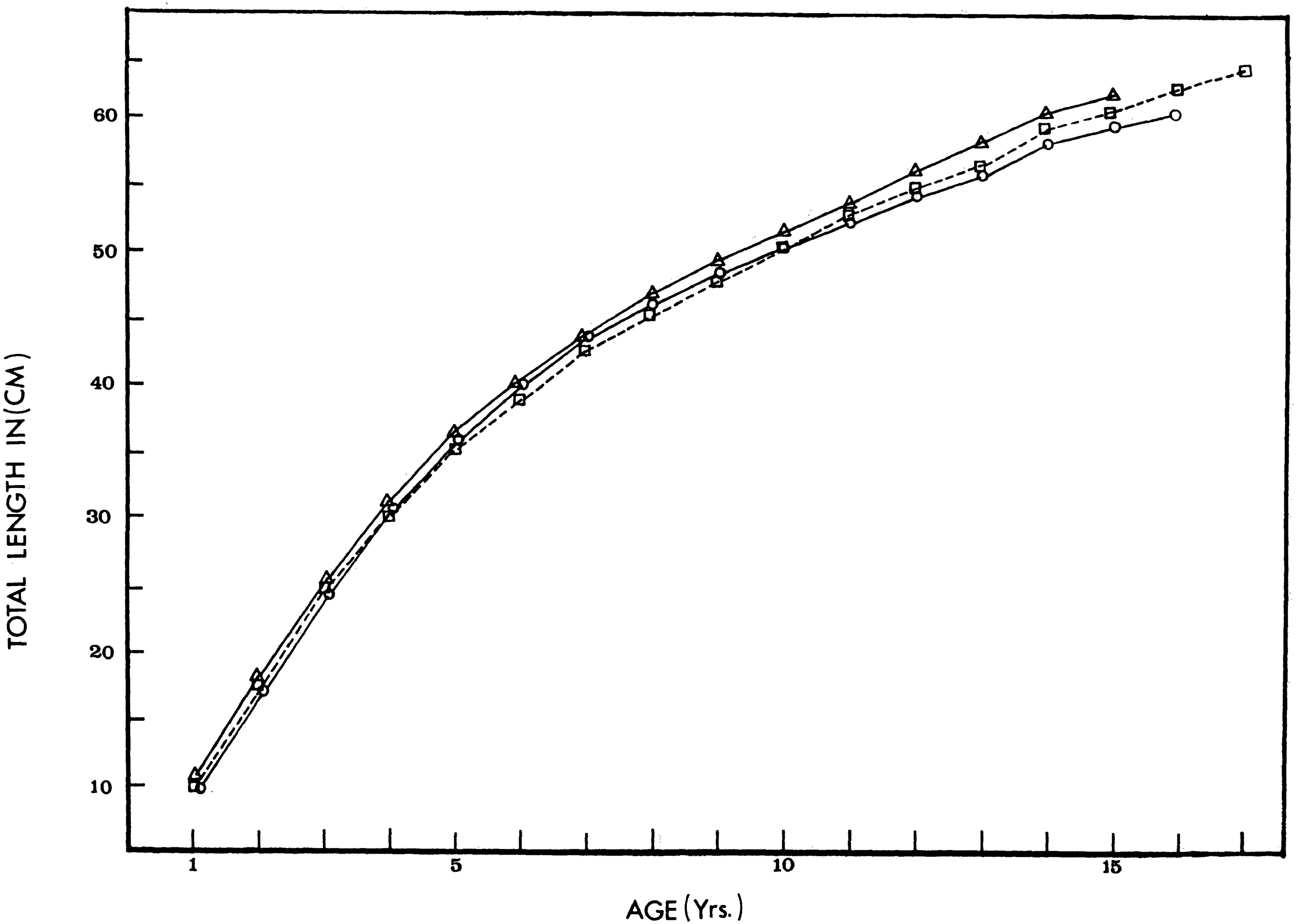

TOTAL LENGTH IN(CM)
10
20
30
40
50
60
1
5
10
15
AGE (Yrs.)

Table 24. Comparison of mean calculated length and observed mean length of walleyes and their growth increments in cm for 1973-74 and 1976.

	Ages in years																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
mean calculated length (1973)	10.3	18.3	25.3	30.8	35.7	39.7	43.2	45.8	48.1	50.6	53.0	54.9	56.7	59.3	60.9	62.4	64.2
mean observed length	-	-	30.4	34.0	37.8	37.6	43.0	42.5	45.2	46.3	51.8	55.9	53.5	58.1	60.0	-	64.2
growth increment	10.3	8.0	7.0	5.5	4.9	4.0	3.5	2.6	2.3	2.5	2.4	1.9	1.8	2.6	1.6	1.5	1.8
mean calculated length (1974)	10.3	18.1	25.1	31.2	36.1	40.4	44.0	46.7	49.2	51.9	54.6	57.4	59.6	69.8	71.1	72.0	-
mean observed length	-	-	-	33.0	36.7	38.4	42.6	44.6	46.0	49.3	51.5	55.8	51.8	-	-	72.0	-
growth increment	10.3	7.8	7.0	6.1	4.9	4.3	3.6	2.7	2.5	2.7	2.7	2.8	2.2	10.2	1.3	9.0	-
mean calculated length (1976)	10.9	18.7	25.6	31.2	36.3	40.3	44.0	47.0	49.6	51.8	54.2	56.9	60.0	64.1	69.2	-	
mean observed length	19.5[a]	25.6[a]	28.4	31.2	38.1	38.3	42.8	46.1	49.9	51.5	51.5	54.2	56.4	60.4	69.2	-	
growth increment	10.9	7.8	6.9	5.6	5.1	4.0	3.7	3.0	2.6	2.2	2.4	2.7	3.1	4.1	5.1	-	

a/ determined from the mean of 1+ and 2+ taken from the trawls in the month of August, 1976.

Seasonal growth

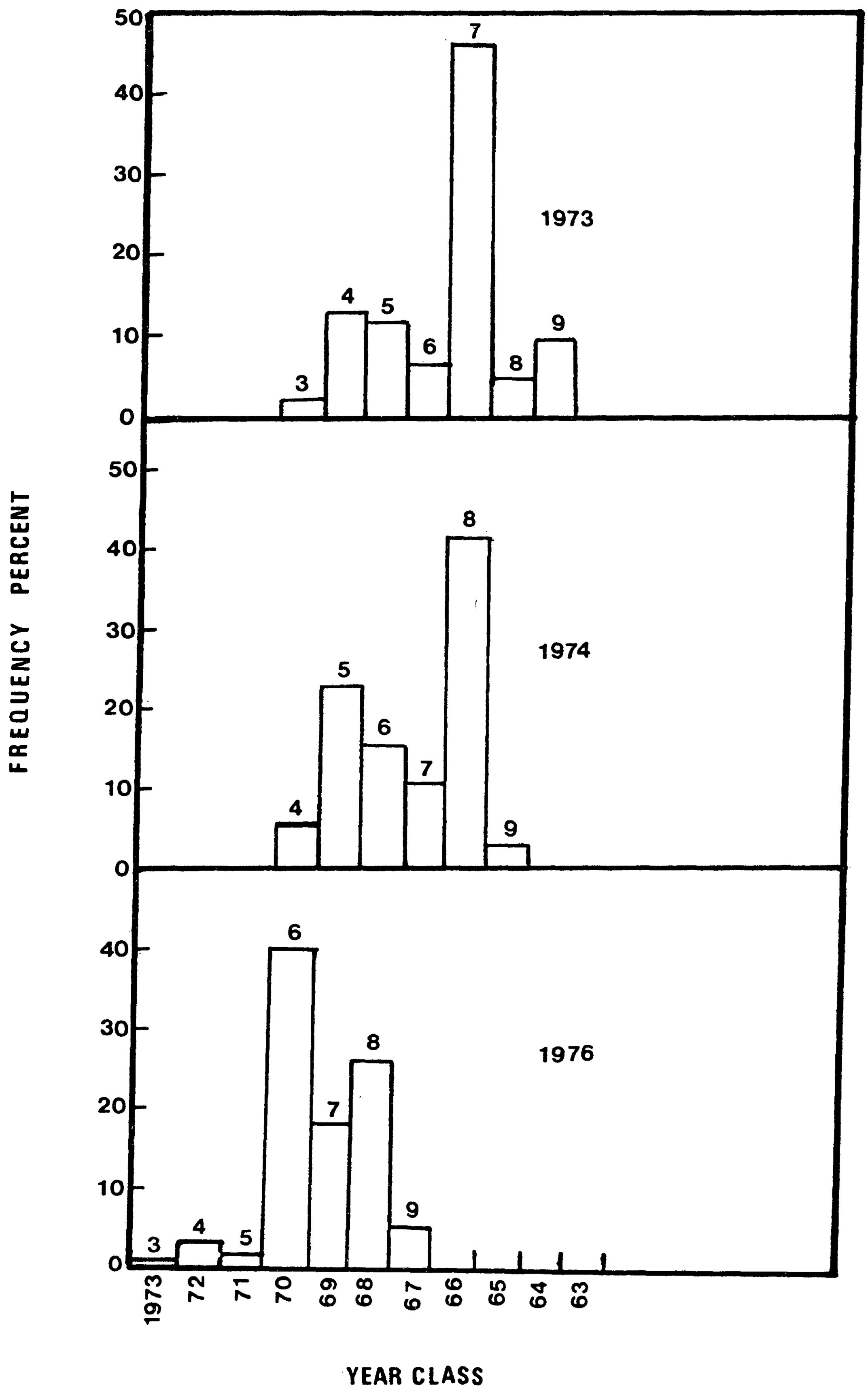
In order to obtain the least variation in estimating growth rates, the scales were collected in the shortest time possible, during a period when circuli were not added to the scales. Fish did not add any circuli in the month of May, but growth started by mid-June. Walleyes collected by the end of June had formed few circuli beyond the last annulus. Hile (1941) determined that little if any growth occurred in walleyes during May and June. Kelso and Ward (1972) estimated that 90% of walleye growth occurs from July to October in West Blue Lake, Manitoba. Forney (1966) found that growth increments were highest in August and September. Moenig (1975) observed very little growth of walleyes in Dexter Lake, Ontario, between May and mid-July. In Norris Reservoir, Tennessee, early spring growth was rapid for all age groups (Stroud 1949a), then slowed during early and mid-summer, increased again during late summer and finally tapered off during the fall. He suggested that although forage species are abundant in the reservoir, they may not be readily available at all times in the strata of water occupied by walleyes. Little or no growth appeared to occur during the winter (Stroud 1949a). The absence of winter growth appeared to be due to low temperature, and not to lack of food in Norris Reservoir, where forage fish suitable for walleyes were abundant during the winter (Stroud 1949a). In Norris Reservoir Tennessee, only 16 percent of seasonal growth occurred between late July and early October, when water temperatures were highest (Eschmeyer and Jones 1941).

The growth rate of adult walleyes seems to be affected by two factors, temperature and forage abundance. The temperature fluctuations cause year to year variation in growth. In heterothermal systems, temperature selection by percids significantly affects growth. Walleyes on fixed rations show up to twofold increments in annual growth, which may be entirely due to differences in summer temperatures. Variations in food quality have a lesser effect (Kitchell et al. 1977). Excellent forage abundance is a chief reason for good growth in a number of lakes (Stroud 1949a; 1949b; Rose 1951; Forney 1965; Miller 1967; Hofmann 1972). This factor not only influences adult growth but directly effects recruitment.

Growth and abundance of year-classes

Length at all ages was estimated by back calculations using scale samples (Appendix 5, Table 5A, 5B, 5C). No relationship was found between year-class abundance and year-class growth. The age composition analysis revealed only one abundant year-class present during 1973 and 1974. This was the 1966 year-class (Fig. 15). It contributed 46% of the 1973 catch at age 7 and 40% of the 1974 catch at age 8 . In the sampling year of 1976, there were two dominant age groups designated as the 1968 (8) and 1970 (6) broods. They contributed 26% and 40% of the 1976 catch (Fig. 15). In West Blue Lake, Manitoba, two abundant year-classes resulted from the 1967 and 1972 broods (Schweight, Ward and Clayton 1977). Glen (1969) also found 1963 and 1964 (3+) year-classes predominated in the 1966-67 catch in West Blue Lake, Manitoba. Kelso and Ward (1972) found the 1964 (2+) and 1967 (7+) year-classes to be abundant in West Blue Lake, Manitoba. Moenig (1975) reported that 1963 (5+) and 1966 (4+) year-classes were abundant in Dexter Lake, Ontario. Strong year-classes were formed in 1963 and 1966 in Red Lakes, Minnesota (Smith 1977) and Lake of the Woods,

Fig. 15. Relative year-class abundance of Savanne Lake walleyes during three years of sampling in 1973, 1974 and 1976. Values above bars are ages.



FREQUENCY PERCENT
YEAR CLASS
1973
1974
1976
0
10
20
30
40
50
3
4
5
6
7
8
9
1973
72
71
70
69
68
67
66
65
64
63

Minnesota (Schupp and Macins 1977). Elsey and Thomson (1977) have also reported that strong year-classes were also formed in 1963 and 1966 in Lac des Mille Lacs, Ontario. Strong year-classes from various waters are indicated in Table 25.

Moenig (1975), Heyerdahl and Smith (1971), Regier, Applegate and Ryder (1969), Forney (1965; 1966), Maloney and Johnson (1957) and Pycha and Smith (1955) have suggested that walleye growth and abundance are related to yellow perch abundance.

Forney (1977) has observed the production of strong perch year-classes to be concurrent with rapid growth of older walleyes. Moenig (1975) observed perch fry as a dominating factor in initiating the abundance of a year-class in Dexter Lake, Ontario. Growth rates of young-of-the-year walleyes are also closely related to water temperature. Low spring temperatures result in later than normal reproduction and hatching, whereas high spring temperatures have the opposite effect (Smith and Pycha 1960; P. J. Colby, Unpub.). Colby (Unpub.) found that in Savanne Lake, Ontario, in a year with late spring, growth was slow initially. However, it increased sharply during the first two weeks of August when water temperatures were 2 to 3^{o}C higher than normal during the last two weeks of July.

Table 25. Years between 1960 and 1975 in which strong year-classes of walleyes were observed for various bodies of water.

Lakes	Reference	1960	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
Savanne Lake, Ont.	Present Study							X									
Dexter Lake, Ont.	Moenig (1975)				X			X									
West Blue Lake, Man.	Glen (1969)				X	X											
West Blue Lake, Man.	Kelso and Ward (1972)					X			X								
West Blue Lake, Man.	Schweight, Ward and Clayton (1977)								X					X			
Red Lakes, Minn.	Smith (1977)				X			X									
Lake of the Woods, Minn.	Schupp and Macins (1977)				X			X									
Lac des Mille Lacs, Ont.	Elsey and Thomson (1977)				X			X									

<u>Growth in various calendar years and growth of Savanne Lake walleyes compared to other waters</u>

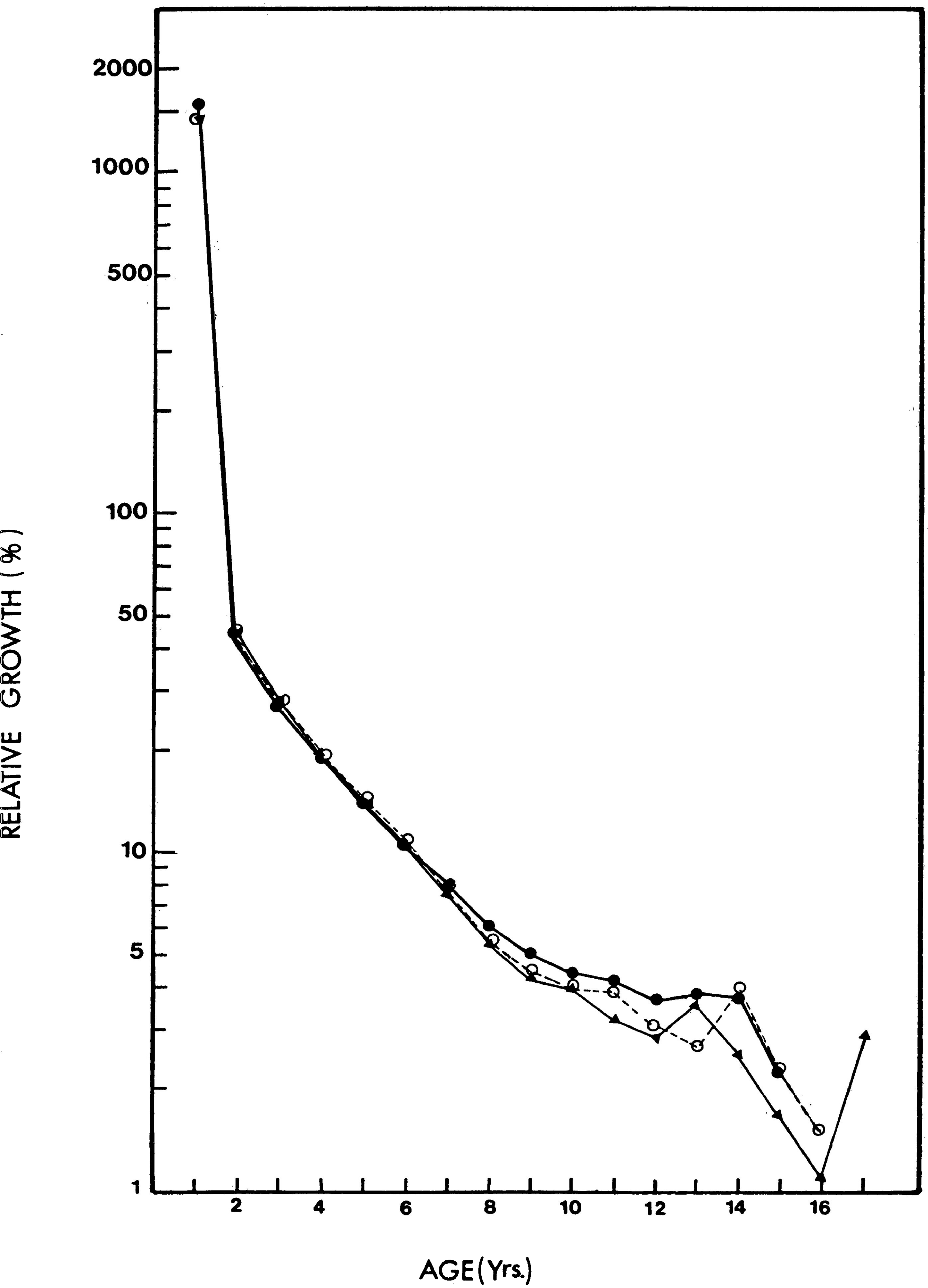
Walleyes in Savanne Lake showed similar annual percentage increments in their growth during the three different years of study (Fig. 16). Relative growth of walleyes was very great by the end of the first year, ranging from 1471 to 1557 percent in Savanne Lake for 1973-74 and 1976. Growth decreased sharply the second year and continually decreased at a lesser rate until, on average, the fifth or sixth year. After this, growth was irregular and very slow (Fig. 16). Relative growth of walleyes by the end of the first year ranged from 6471 percent in Belton Reservoir, Texas (sexes combined) to 814 percent in Killens Reservoir, Montana, using 7 mm as the standard hatching length for calculations (Colby et al., In press).

In some lakes, however, relative growth decreases each year up to the last observed age class (Carlander 1942; Eschmeyer 1950), whereas in other populations the growth pattern is irregular after only the second year (Slastenenko 1956; Armstrong 1961).

In Savanne Lake, more than half of the growth is completed when walleyes are four years old. Walleyes reach up to 43.8 cm in length at age seven; afterwards, growth is very slow. During the First three years, Savanne Lake walleyes grew slower than those in nearby Dexter Lake (Table 26). Afterwards, Savanne Lake walleyes grew faster than Dexter Lake walleyes.

In the present study, maximum size is attained at ages 16 and 17, rather than ages 7 and 10, as in most other lakes (Table 26). Average calculated lengths at age one attained by Savanne Lake walleyes are comparable to those of Dexter Lake walleyes (Moenig 1975), Clear Lake, Iowa (Schloemer and Lorch 1942) and Lake Gogebic in

Fig. 16. The percent relative growth at each annulus for Savanne Lake walleyes during the years 1973 (triangles), 1974 (open circles) and 1976 (closed circles).



2000
1000
500
100
50
10
5
1
RELATIVE GROWTH (%)
2
4
6
8
10
12
14
16
AGE(Yrs.)

northern Michigan (Eschmeyer 1950). Lengths are somewhat less, however, than those observed in Iowa lakes (Carlander 1948), Lake of the Woods (Carlander 1945), Oneida Lake (Forney 1965) and Wisconsin lakes (Schloemer and Lorch 1942). Comparison of calculated lengths of Savanne Lake walleyes for age one and older suggest that growth rates are similar to those for Dexter Lake walleyes (Moenig 1975) and showed evidence of asymptotic growth. In most other lakes (Table 26), walleyes were larger than Savanne Lake walleyes at earlier ages and showed no evidence of asymptotic growth.

The slow growth of Savanne Lake walleyes is due to the chemical characteristics of lakes in this region of the Canadian Shield (R. A. Ryder, pers. comm.), as well as to their high density relative to the available food. Walleye growth in Northern Ontario is therefore slow (Regier, Applegate and Ryder 1969).

Table 26. Growth of walleyes in Savanne Lake and various other bodies of water.

Area	Number of fish examined	Reference		Average total length in cm in each age, sexes combined																
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Savanne Lake, Ont.	652	Present Study		10.5	18.3	25.3	31.1	36.2	40.3	43.8	46.5	48.8	51.1	53.3	55.2	57.1	59.5	60.9	61.4	64.2
Dexter Lake, Ont.	1212	Moenig (1975)		11.4	20.1	26.1	31.1	35.1	38.3	40.8	42.6	44.6	46.8	49.0	51.3	55.0	60.0	58.9	60.3	62.4
Iowa Lakes, Iowa	216	Carlander (1948)		12.7	23.4	31.5	38.1	43.4	47.2	50.5	54.6	58.9	62.7	65.8	67.6					
Lake Gogebic, Mich.		Eschmeyer (1950)		11.7	23.9	30.7	35.1	40.1	43.7	45.7	47.8	49.5	50.8							
Clear Lake, Iowa	77	Schloemer and Lorch (1942)a/		10.2	20.3	27.2	32.0	35.6	39.9											
Lake of the Woods, Minn.	2898	Carlander (1945)b/		16.5	23.4	29.2	34.3	37.6	42.2	46.0	50.3	54.6	57.4							
Lake Erie, Mich.	1430	Deason (1933)		10.7	21.3	28.7	36.6	45.7	52.8											
Wisconsin Lakes, Wis.	1132	Schloemer and Lorch (1942)		13.7	24.8	33.5	40.4	45.2	49.5	55.4	59.2	63.0	66.3							
Trout Lake, Wis.	429	Schloemer and Lorch (1942)		13.5	24.6	34.8	42.2	48.3	52.6	55.1	56.6	58.7	59.2							
Minnesota Lakes, Minn.	6599	Eddy and Carlander (1939)c/		12.4	23.1	32.3	40.1	48.5	54.9	61.5	67.6	71.6								
Bay of Quinte, Lake Ontario (Lower Bay)	3526	Payne (1964)		22.6	34.2	42.5	49.3	54.9	58.9	61.9	65.1	67.3	68.9	70.8	71.3	72.7	74.8			
Oneida Lake, N. Y.		Forney (1965)d/	M	15.5	23.4	29.5	34.0	36.6	38.9	40.4										
			F	16.0	24.1	30.7	35.8	39.4	42.4	44.7										
Scriba Creek, N. Y.		Forney (1965)d/	M			32.5	35.3	36.8	38.4	40.1	41.9	43.4	43.9	45.7	48.5	46.2	48.8			
			F				38.4	40.6	42.9	45.5	47.2	49.2	52.6	55.4	57.2	58.2	54.4			

a/standard length converted to total length using coefficients given by Schloemer and Lorch (1941)

b/standard length converted to total length using coefficients given by Carlander and Smith (1954)

c/fork length converted to total length using 0.944 as conversion coefficient (Carlander and Smith 1945)

d/calculated mean lengths for Scriba Creek and Oneida Lake are of the same population but given separately for each sex M, Males; F, Females.

Biomass and production

Biomass and production are, in part, measures of a population's response to its environment; they are calculated from data on age structure, mortality, growth and population estimates. The instantaneous rate of mortality (Z) is equal to the natural logarithm, with the sign changed, of the complement of annual survival rate (Table 18). Thus, $Z = \log_e (1 - S)$. The instantaneous rate of growth (G) is the logarithm to the base $_e$ of the ratio of the average weight of the population at the beginning and end of the period during which growth is being determined (Table 23). The initial biomass (Wo) is determined by multiplying the number of fish in each age group by the average weight of fish in that age group. The weight change factor (K) is the difference between the instantaneous rate of growth (G) and instantaneous rate of mortality (Z). Thus, $K = (G - Z)$. It can be negative when mortality losses exceed the weight gain represented by instantaneous rate of growth (Tables 27, 28 and 29). Production (P) is equal to the instantaneous rate of growth times the mean biomass ($\overline{W}$) summed for each age group (Tables 27, 28 and 29). The mean biomass is estimated by $\overline{W} = Wo(\frac{e^k-1}{K})$. The age groups for the year 1975 were reconstructed following Pivnicka and Svatora (1977) using a 0.60 survival rate to calculate biomass and production for that year. The mean biomass and production (Tables 27, 28 and 29) over three years of study decrease with age. In a small unexploited system like Savanne Lake older fish are likely using the limited food supply primarily for maintenance and maturation, rather than growth. The total mean biomass of the mature population of 6.58 $kg{\cdot}ha^{-1}$ and 6.06 $kg{\cdot}ha^{-1}$ for 1973-74 and 1974-75, respectively, were much higher than that of 2.64 $kg{\cdot}ha^{-1}$ for 1975-76 (Table 30). Also, the production of the mature population of 1.0 $kg{\cdot}ha^{-1}{\cdot}yr^{-1}$ for 1973-74 and 1.31

$kg \cdot ha^{-1} \cdot yr^{-1}$ for 1974-75 was higher than the estimated 0.52 $kg \cdot ha^{-1} \cdot yr^{-1}$ for 1975-76.

There were several reasons for lower biomass and production in 1975-76. The instantaneous rate of mortality for all age groups was higher ranging from 0.19 to 2.75 in 1975-76, with a mean of 1.39, ranging from 0.08 to 1.43, with a mean of 0.76 for 1973-74 and ranging from 0.50 to 0.51, with a mean value of 0.50 for 1974-75. The instantaneous rate of mortality in 1975-76 far exceeded the growth in 1975-76, thus lowering biomass and production (Table 29). The strong 1966 year-class contributed most of the biomass between 1973-74 and 1974-75, but then declined in importance and did not contribute significantly to the estimates for the period between 1975-76. The age groups 6 and 7 were not included in the 1975-76 estimates, hence biomass was further reduced from 6.06 $kg \cdot ha^{-1}$ for 1974-75 to 2.64 $kg \cdot ha^{-1}$ for 1975-76; similarly, production declined from 1.31 $kg \cdot ha^{-1} \cdot yr^{-1}$ for 1974-75 to 0.52 $kg \cdot ha^{-1} \cdot yr^{-1}$ in 1975-76.

The unusually high values of instantaneous rate of growth (G) values of 0.531 between age 15 and 16 in 1973-74, 0.453 between age 13 and 14 in 1974-75 and 0.390 between age 14 and 15 in 1975-76 are based on a few specimens of larger fish which was much older than most of the other fish examined. The older walleyes contributed high values of production to the tail end of the production estimates for those years. These fish may even be older than the age derived from scale samples, and may therefore represent several years of production and a summation of G values over several years. The annual biomass of 6.06 $kg \cdot ha^{-1}$ for 1974-75 is comparable to the 7.20 kg·ha^{-1} in nearby Dexter Lake (Moenig 1975); 5.7 kg·ha^{-1} age 3 and older in Clear Lake, Iowa (Carlander and Payne 1977); and 6.1 kg·ha^{-1} in West Blue Lake, Manitoba (Kelso and Ward 1972; 1977). Some of the higher biomass values were: 20.50 kg·ha^{-1} in Oneida Lake (Hofmann 1972); 13.57 kg·ha^{-1} in Hoover Reservoir, Ohio (Momot et al. 1977); and 9.1 kg·ha^{-1} in some Minnesota game fish lakes (Moyle et al. 1950). The lower biomass values encountered in the Vistula River, Poland (Backiel 1971), were: 1.1-1.4 kg·ha^{-1} for pike perch, *Stizostedion lucioperca*; 1.8-2.4 kg·ha^{-1} for northern pike (*Esox lucius*); and 0.095 kg·ha^{-1} for the Eurasian perch, *Perca fluviatilis*. The mean biomass of Savanne Lake walleyes is close to the North American mean of 6.73 kg·ha^{-1} (Carlander 1955).

The annual production of 1.31 kg·ha^{-1}·yr^{-1} was very close to the 1.21 kg·ha^{-1}·yr^{-1} for Clear Lake, Iowa (Carlander and Payne 1977), and the 1.78 kg·ha^{-1}·yr^{-1} (ages 3-13) in Dexter Lake (Moenig 1975), but slightly lower than the 2.10 kg·ha^{-1}·yr^{-1} in West Blue Lake, Manitoba (Kelso and Ward 1977). The following low production values were found in the Vistula River, Poland (Backiel 1971): 0.79-1.03 kg·ha^{-1}·yr^{-1} for pike perch; 0.04 kg·ha^{-1}·yr^{-1} for Eurasian perch; and 1.5 kg·ha^{-1}·yr^{-1} for northern pike. Northern pike in one Czechoslovakian reservoir had a low production value of 0.75 kg·ha^{-1}·yr^{-1} (Holcik 1972). The northern pike of Lake Windemere, England, presented the highest value for a coolwater species at 14.2 kg·ha^{-1}·yr^{-1} (Kipling and Frost 1970).

Most of the other production estimates involve younger age groups (3-6+) than those used in this study; these groups were not included in calculating the Savanne Lake estimates, due to incomplete recruitment of fish less than age 6+. Hence, Savanne Lake biomass and production estimates were considerably lower than those for other bodies of water (Table 30).

Table 27. Annual biomass and production of walleyes in Savanne Lake, 1973-74. Z = instantaneous rate of mortality; G = instantaneous rate of growth; K = weight change factor; Wo = initial biomass; $\overline{W}$ = mean biomass of stock; P = annual production; P/$\overline{B}$ = annual turnover ratio. Values for Wo, $\overline{W}$ and P are in kg, unless otherwise specified.

Age	Z	G	K = (G - Z)	Wo	$\overline{W}$	P = G$\overline{W}$	P/$\overline{B}$
7-8	0.083	0.105	+0.022	1658.0	1676.7	176.0	.10
8-9	0.640	0.230	-0.410	160.9	132.0	30.3	.23
9-10	0.805	0.253	-0.552	335.5	257.8	65.2	.25
10-11	1.436	0.310	-1.126	278.3	167.0	51.8	.31
11-12	0.875	0.216	-0.659	94.5	69.2	14.9	.21
12-13	0.164	0.222	-0.058	75.3	77.5	17.2	.22
13-14							
14-15	-	-	-	-	-	-	-
15-16	1.339	0.531	-0.808	26.7	18.3	9.7	.53
Total	5.342	1.867	-3.591	2629.2	2398.6	365.2	
Mean	0.76	0.27		Totals in $kg \cdot ha^{-1}$	6.58	1.00	0.15

Table 28. Annual biomass and production of walleyes in Savanne Lake, 1974-75. Z = instantaneous rate of mortality; G = instantaneous rate of growth; K = weight change factor; Wo = initial biomass; $\overline{W}$ = mean biomass of stock; P = annual production; $P/\overline{B}$ = annual turnover ratio. Values for Wo, $\overline{W}$ and P are in kg, unless otherwise specified.

Age	Z	G	$K = (G - Z)$	Wo	$\overline{W}$	$P = G\overline{W}$	$P/\overline{B}$
7-8	0.509	0.243	-0.266	370.9	325.6	79.1	.24
8-9	0.510	0.221	-0.289	1695.7	1472.6	325.4	.22
9-10	0.505	0.172	-0.333	106.7	90.7	15.6	.17
10-11	0.507	0.144	-0.363	185.7	155.7	22.4	.14
11-12	0.502	0.138	-0.364	90.2	75.6	10.4	.14
12-13	0.500	0.118	-0.382	48.9	40.6	4.8	.12
13-14	0.503	0.453	-0.050	51.1	49.8	22.5	.45
Total	3.536	0.489	-2.047	2549.2	2210.6	480.2	
Mean	0.50	0.21		Totals in $kg \cdot ha^{-1}$	6.06	1.31	0.22

Table 29. Annual biomass and production of walleyes in Savanne Lake, 1975-76. Z = instantaneous rate of mortality; G = instantaneous rate of growth; K = weight change factor; Wo = initial biomass; $\overline{W}$ = mean biomass of stock; P = annual production; P/$\overline{B}$ = annual turnover ratio. Values for Wo, $\overline{W}$ and P are in kg, unless otherwise specified.

Age	Z	G	K = (G - Z)	Wo	$\overline{W}$	P = G$\overline{W}$	P/$\overline{B}$
8-9	0.19	0.218	+0.028	284.0	288.0	62.8	.22
9-10	2.75	0.198	-2.552	1269.0	458.5	90.8	.20
10-11	0.38	0.156	-0.224	77.0	69.0	10.8	.16
11-12	1.94	0.131	-1.809	135.0	62.4	8.2	.13
12-13	1.05	0.126	-0.924	62.0	40.4	5.1	.13
13-14	1.60	0.113	-1.487	34.0	17.7	2.0	.11
14-15	1.87	0.390	-1.480	49.0	26.6	9.9	.37
Total	9.78	1.332	-8.448	1910.0	962.6	189.6	
Mean	1.39	0.19		Totals in $kg \cdot ha^{-1}$	2.64	0.52	0.20

Table 30. Biomass ($\overline{B}$) and production (P) in $kg \cdot ha^{-1}$, and annual turnover ratios ($P/\overline{B}$) over the three years of study.

Year	Age	B	P	$P/\overline{B}$
1973-74	7-16	6.58	1.00	0.15
1974-75	7-14	6.06	1.31	0.22
1975-76	8-15	2.64	0.52	0.20

The $P/\overline{B}$ ratio

The $P/\overline{B}$ ratio (turnover ratio) of biomass, annual production (P) divided by mean annual biomass ($\overline{B}$), varied from 0.10 to 0.53 for 1973-74, 0.12 to 0.45 for 1974-75 and 0.11 to 0.37 for 1975-76, and decreased with increased age (Table 31), with the exception of age groups 15-16, 13-14 and 14-15 for 1973-74, 1974-75 and 1975-76. These higher values of 0.53, 0.45 and 0.37 are based on a single larger fish in the sample and not from a dominant year-class. There were no substantial differences in annual $P/\overline{B}$ ratios between 1973 and 1976. This would indicate little fluctuation in biomass replacement occurred over the three years of study.

The total annual turnover ratios of 0.15, 0.22 and 0.20 from 1973-76 are slightly lower than the ratios of 0.25, 0.30 and 0.23 for 1967, 1968 and 1969 in nearby Dexter Lake (Moenig 1975). The $P/\overline{B}$ ratios of 2.24-0.11 for age groups 1-5+ in Clear Lake, Iowa (Carlander and Payne 1977), although higher than those for Savanne Lake walleyes, show a similar decrease with increasing age.

In warm-water lakes, rivers and reservoirs, the $P/\overline{B}$ ratios are generally less than one, while $P/\overline{B}$ ratios in cold-water streams and lakes are greater than one. The $P/\overline{B}$ ratio of percids varies from 0.10 to 0.72 in warm-water mesotrophic lakes, rivers and reservoirs (Table 32). Higher values of 1.5 to 2.4 were found in salmonids in oligotrophic cold-water lakes and streams (Table 33). The The dissimilarity in $P/\overline{B}$ ratios results either from inherent differences between the warm- and cold-water species, or from inherent differences between the two types of ecosystems. Since salmonid communities predominate in low nutrient lakes and streams, most likely the higher $P/\overline{B}$ ratios involve inherent differences in the community structure between mesotrophic and oligotrophic ecosystems. The community structure is generally more complex in mesotrophic waters than in oligotrophic environments, resulting in a greater number of side chains and dead ends. In a structurally complex community such as a mesotrophic lake, this could result in less energy flow to terminal predators (W. T. Momot, unpublished manuscript).

Where production estimates include the youngest fry, the $P/\overline{B}$ ratios are much higher (Mathews 1971). Where estimates of $P/\overline{B}$ in salmonid populations consist almost entirely of juveniles, with their higher growth rates, the $P/\overline{B}$ ratios reach up to 5.0, e.g.: the brown trout nursery streams in New Zealand (Hopkins 1971); juvenile migrating rainbows in Bothwell's Creek, Ontario (Alexander and MacCrimmon 1974); and juvenile coho salmon in Oregon streams (Chapman 1965). On the other hand, low values were apparently due to extremely slow growth, especially within populations having higher proportions of older fish (Crisp et al. 1975).

In contrast to most invertebrates, fishes generally have lower $P/\overline{B}$ ratios, because of their longer life spans of up to 10 years or more. The $P/\overline{B}$ ratios in invertebrates are higher; that of the crayfish ranges between 0.7 and 2.00 (Momot 1978). For a variety of benthic invertebrates, the $P/\overline{B}$ ratio varies from 2 to 15 (Waters 1969). The annual $P/\overline{B}$ ratios for single-species populations of zooplankton are even higher than those for benthos, because of the shorter life span and many more generations per year (Waters 1969).

Table 31. The annual turnover ratios ($P/\overline{B}$) of Savanne Lake walleyes over three years of study.

Age group	1973-74	1974-75	1975-76
7-8	0.10	0.24	-
8-9	0.23	0.22	0.22
9-10	0.25	0.17	0.20
10-11	0.31	0.14	0.16
11-12	0.21	0.14	0.13
12-13	0.22	0.12	0.13
13-14		0.45	0.11
14-15	-		0.37
15-16	0.53		
Overall[a/] $P/\overline{B}$	0.15	0.22	0.20

a/ = total annual production divided by annual biomass

Table 32. Estimated biomass ($\bar{B}$) in $kg \cdot ha^{-1}$, production (P) in $kg \cdot ha^{-1} \cdot yr^{-1}$ and annual turnover ratios ($P/\bar{B}$) of percids and northern pike from various waters.

Lake	Author	Year	Age	Species	$\bar{B}$	P	$P/\bar{B}$
Savanne Lake, Ont.	Present Study	1973-74	7-16	walleye	6.58	1.00	0.15
		1974-75	7-14	walleye	6.06	1.31	0.22
		1975-76	8-15	walleye	2.64	0.52	0.20
Dexter Lake, Ont.	Moenig (1975)	1967	3-13	walleye	7.20	1.78	0.25
West Blue Lake, Man.	Kelso and Ward (1977)	1969-70	1-4	walleye	6.1	2.10	0.34
Clear Lake, Iowa	Carlander and Payne (1977)	1948-73	3+a/	walleye	5.7	1.21	0.21
		1947-73	1+a/	walleye	7.2	3.08	0.42
Hoover Reservoir, Ohio	Momot et al. (1977)	1967-73	2+a/	walleye	13.57	2.16	0.16
Oneida Lake, N. Y.	Hofmann (1972)	1967	3-8+	walleye	20.50	3.39	0.16
		1968	3-8+	walleye	20.29	7.56	0.37
Minnesota game fish lakes, Minn.	Moyle et al. (1950)	-	-	walleye	9.1	-	-
Vistula River, POLAND	Backiel (1971)			pikeperch, *S. lucioperca*	1.1-1.4	0.79-1.03	0.72
Vistula River, POLAND	Backiel (1971)			European perch	0.095	0.04	0.41
Lake Balaton, HUNGARY	Biro (1975)			pikeperch, *S. lucioperca*		5.5	0.57
Vistula River, POLAND	Backiel (1971)			northern pike	2.1	1.5	0.7
Reservoir, CZECHOSLOVAKIA	Holcik (1972)			northern pike		0.75	0.32
Lake Windemere, ENGLAND	Kipling and Frost (1970)			northern pike		14.2	0.65-0.71

a/ + = fish of specified age and all older fish in the population.

Table 33. Estimated production (P) in $kg \cdot ha^{-1} \cdot yr^{-1}$ and annual turnover ratios ($P/\overline{B}$) of salmonids from various waters.

Lake or stream	Author	Species	P	$P/\overline{B}$
Four New York lakes	Hatch and Webster (1961)	brook trout	6.7	1.0-1.5
Cultus Lake, B. C.	Ricker and Foerster (1948)	sockeye salmon	66	2.0
Valley Creek, Minn.	Hanson and Waters (1974)	brook trout	145	1.4
Larry's Creek, Penn.	Cooper and Scherer (1967)	brook trout	58	1.34
Lawrence Creek, Wis.	Hunt (1974)	brook trout	116	1.6
Bothwell's Creek, Ont.	Alexander and MacCrimmon (1974)	rainbow trout (juvenile only)	132	2.4
Oregon streams	Chapman (1965)	coho salmon	86	2.4
Hinau Mainwater (nursery streams) NEW ZEALAND	Hopkins (1971)	brown trout	89	5.0

MANAGEMENT IMPLICATIONS

Walleye populations have been observed to fluctuate widely in waters which are heavily exploited, e.g.: Lake Erie (Regier et al. 1969); Rainy Lake, Ontario-Minnesota (Chevalier 1977); and Red Lakes, Minnesota (Smith and Pycha 1961). Under heavy exploitation, density-dependent factors lessen in importance, and year-class success becomes increasingly dependent on abiotic factors. If long-term sustained commercial yields (all species) do not exceed theoretical yields (based on the MEI; Ryder 1965) in northern Ontario lakes, the community structure appears to remain relatively stable. Even under varying degrees of fishing intensity, percids (mainly walleyes) consistently comprised approximately 30 percent of the catch (by weight) among certain northern Ontario lakes where theoretical yields were not exceeded. This may exist as an emergent property of predominantly percid fish communities in boreal shield lakes (Adams and Olver 1977). However, among over-exploited lakes where actual commercial yields exceeded theoretical yields for several years, and walleye yields exceeded 30 percent of total theoretical yields, the walleye populations have or are beginning to collapse (Adams and Olver 1977).

Bonar (1977) noted a similar relationship in Polish pikeperch lakes where percentage yield of predators attained a maximum at 25-30% of the total catch. The functional relation of percid yield to the MEI suggests that an MEI range of 6-11 is optimum for walleye yields in boreal percid lakes. The lakes with this range of MEI are considered mesotrophic to slightly eutrophic (Adams and Olver 1977).

In Savanne Lake, the annual production estimates of 1.0 $kg \cdot ha^{-1} \cdot yr^{-1}$ (ages 7-16) for 1973-74, 1.31 $kg \cdot ha^{-1} \cdot yr^{-1}$ (ages 7-14) for 1974-75, and 0.52 $kg \cdot ha^{-1} \cdot yr^{-1}$ (ages 8-15) for 1975-76 (Table 30) are closely similar to the theoretical yield estimate of 1.9 $kg \cdot ha^{-1} \cdot yr^{-1}$, based on the MEI (Ryder 1965) and applying the 30 percent rule. The mean annual production of 0.94 $kg \cdot ha^{-1} \cdot yr^{-1}$ for Savanne Lake was close to the 1.0 $kg \cdot ha^{-1} \cdot yr^{-1}$ for walleyes of similar ages in nearby Dexter Lake (Moenig 1975) and 1.2 $kg \cdot ha^{-1} \cdot yr^{-1}$ for Clear Lake, Iowa (Carlander and Payne 1977). Production estimates of 2.1 $kg \cdot ha^{-1} \cdot yr^{-1}$ for West Blue Lake, Manitoba (Kelso and Ward 1977) and 2.2 $kg \cdot ha^{-1} \cdot yr^{-1}$ for Hoover Reservoir, Ohio (Momot et al. 1977) were slightly higher (Table 34). Data based on growth of walleyes, tabulated by Colby et al. (in press), indicate that growth rates increase from north to south. Increased yields to the south are to be expected because the growing seasons are longer, and yield is more a function of production than of biomass (Carlander 1977).

The younger age groups (3-6) which contribute much of the production were not included in the estimates due to incomplete recruitment. This permitted only partial annual estimates of production which were not subject to total mortality. The youngest fully recruited age-class of walleyes in the trap nets was 7 years old. The rate of mortality of younger age-classes was then estimated from the ratio of the number of fish of completely recruited age-class 6 to the numbers of 7 year old fish caught in experimental gill nets. This ratio of 1.346, used for the combined catches over the three years of study, was extrapolated back to attain estimates of 1724, 2321, 3124, 4205, 5660, 7618 and 10,254 for ages 6, 5, 4, 3, 2, 1 and 0 (Table 35) respectively. Thus, the calculated young-of-the-year estimate of 10,254 agrees approximately with the summer seine and trawl YOY mid-range estimate of 9397, with range values of 2241 to 16,553 (Table 36).

Another approach at approximating the number of YOY fish in the lake by late summer is to make some reasonable assumptions concerning fecundity, sex ratio and early life history mortalities using the literature, and thus calculate the number of YOY walleyes which could be produced from the mature female population in the lake. Assuming a 50:50 sex ratio among 5286 adult fish, we have 2643 mature females. Thus, multiplying the number of females with the average weight of fish of 0.85 kg will give 2260 kg. Using a mean fecundity of 50,000 eggs/kg of fish--a reasonable mean value for mesotrophic waters (Table 37; Colby et al. in press)--we can estimate that 113 million eggs were produced. Accepting Forney's (1976) estimate that mortality consistently exceeded 0.995 between spawning and the time cohorts attain a mean length of 9-10 mm, and using a mortality factor of 0.999, we have 113,000 fry of size 9-10 mm in Savanne Lake. Forney and Houde (1964) reported first year mortalities to range from 67-75 percent in Oneida Lake, New York. However, Noble (1972) estimated the mortality to be 95 percent over a two week period (approximately 1-15 June) for a localized fry population in the lake. Thus, if we assume a 90% mortality for a small and closed ecosystem such as Savanne Lake, we would have about 11,300 YOY in the lake by late summer or fall, when they are becoming less vulnerable to predation. Hence, our three independent YOY estimates from fecundity data, summer YOY estimates and using survival ratios agree fairly well with each other.

Annual production (including the younger groups) was obtained by multiplying the mean $P/\overline{B}$ ratio (annual turnover ratio) with mean weight and population estimates in each age group (Table 35). The $P/\overline{B}$ ratios of age groups 1 to 6 were used as calculated by Carlander and Payne (1977). Thus, brood stock production of 1.85 $kg \cdot ha^{-1} \cdot yr^{-1}$ at mean age 5.5 to first maturity (Appendix 6) is very similar to the theoretical yield of 1.9 $kg \cdot ha^{-1} \cdot yr^{-1}$, which is based on the 30 percent rule and is about 20% of total walleye production in the lake (Table 38).

Although percids may be capable of forming up to one-third of the total yield, there is obviously an upper limit to sustainable yield. Few northern Ontario lakes appear capable of sustaining commercial yields greater than 1.50 $kg \cdot ha^{-1} \cdot yr^{-1}$; a sustainable commercial yield of percids of 1.0-1.25 $kg \cdot ha^{-1} \cdot yr^{-1}$ is probably a reasonable expectation without significantly changing the structure of the fish community, for many moderately to intensively fished lakes in this region (Adams and Olver 1977). I believe that the close agreement between theoretical yield of 1.9 $kg \cdot ha^{-1} \cdot yr^{-1}$ and production estimate of 1.85 $kg \cdot ha^{-1} \cdot yr^{-1}$ found in this lake supports the conclusion of Adams and Olver (1977). In Savanne Lake, a yield of 1.9 $kg \cdot ha^{-1} \cdot yr^{-1}$ would be equivalent to recovering the surplus adult production--most likely without significantly changing the community structure.

Table 34. **Similarity between theoretical walleye yields (TYE x .3)**, based on the total theoretical yield calculated from the morphoedaphic index and the 30 percent rule, and mean production estimates in $kg \cdot ha^{-1} \cdot yr^{-1}$ for various bodies of water.

Lake	Surface Area (ha)	Ages included	TYE	TYE x .3	Production Mean	Production Range	Reference
Savanne Lake, Ont.	364	7-16	6.3	1.9	0.94	0.52-1.31	Present Study
Dexter Lake, Ont.	368	4-16	6.3	1.9	1.0	0.4-1.8	Moenig (1975)
West Blue Lake, Man.	162	1-4	5.0	1.5	2.1		Kelso and Ward (1977)
Clear Lake, Iowa	1474	3+[a]	10.1	3.0	1.2	0.4-3.1	Carlander and Payne (1977)
		1+[a]	-	-	3.1	0.9-7.0	
Hoover Reservoir, Ohio	1143	2+[a]	7.0	2.1	2.2	1.3-4.1	Momot et al. (1977)

[a] + = fish of specified age and all older fish in the population.

Table 35. Mean production estimates in kg·ha^{-1}·yr^{-1} over three study years for walleyes in Savanne Lake, Ontario.

Ages	Number	$\bar{X}$ weight (gm)	P/$\bar{B}$	Estimated production (kg)	Production (kg·ha^{-1}·yr^{-1})	Cumulative production
0	*10,254*	-	-	-	-	-
1	*7618*	70	2.24[c/]	1194.5	3.28	9.57
2	*5660*	154	1.00	871.6	2.39	6.29
3	*4205*	231	0.43	417.7	1.14	3.90
4	*3124*	316	0.24	236.9	0.65	2.74
5	*2321*	470	0.16	174.5	0.48	2.09[b/]
6	*1724*	491	0.11	93.1	0.26	1.61[b/]
7	1281	689	0.17	150.0	0.41	1.35
8	1261	769	0.22	213.3	0.59	0.94
9	271	912	0.21	51.9	0.12	0.35
10	197	1029	0.20	40.5	0.11	0.23
11	69	1188	0.16	13.1	0.04	0.12
12	33	1454	0.16	7.7	0.02	0.08
13	26	1353	0.28	9.8	0.03	0.06
14	3	1779	0.37	2.0	0.01	0.03
15	6	2319	0.53	7.4	0.02	0.02
16	1	3137	-	-	-	
17	2	2246	-	-	-	

a/ Numbers in italics were back-calculated using a value of 1.346, which is the ratio of 6 to 7 year old fish in Savanne Lake fully recruited to experimental gill nets. Therefore, an annual percentage survival and mortality of 74.3 and 25.7, respectively, for ages 1-7 is assumed.

b/ Brood stock production of 1.85 kg·ha^{-1}·yr^{-1} at mean age to first maturity (5.5) (Appendix 6) represents mid-range between production estimates of 2.09 and 1.61.

c/ The P/$\bar{B}$ ratios of age groups 1 to 6 were used as calculated by Carlander and Payne (1977).

Table 36. Comparison of population estimates and CUE (catch-per-unit-effort) for YOY (young-of-the-year) walleyes in Savanne Lake. Estimates were calculated from seine and trawl data.

Year	CUE	Population estimates	Mid-range of estimates
1972[b]	156.6	-	
1973[b]	45.3	16,553	
1974[b]	22.0	2,241	9,397
1975[c]	16.2	298[a]	
1976[c]	57.1	2,459	
1977[c]	36.6	-	

a/ This figure was not used to calculate mid-range because YOY fish were believed to be too scarce for a reliable estimate.

b/ Only seines were used for YOY population estimates.

c/ Both seines and trawls were used for YOY population estimates.

Table 37. Fecundity of walleyes from some North American waters (From Colby et al. in press).

Location and reference	No. eggs/kg of fish Range	Average
Lake of the Woods, Minn. (Carlander 1945)		50,000
Wisconsin Waters (Niemuth et al. 1966)	28,600 - 99,000	
L. Winnebago, Wis. (Priegel 1970)	63,441 - 96,116	
L. Gogebic, Mich. (Eschmeyer 1950)	57,922 - 67,797	61,846
Little Cutfoot Sioux L., Minn (Johnson 1971b)	48,840 - 73,700	65,239
Muskegon R., Mich (Eschmeyer 1950)	65,778 - 95,955	
L. Erie (western basin) (Wolfert 1969)	56,314 - 123,249	82,700
L. Erie (eastern basin) (Wolfert 1969)	41,191 - 96,914	61,149
Utah L., Utah (Arnold 1960)	27,900 - 52,562	47,410
Mississippi R. (Nord 1967)	50,600 - 110,100	
Center Hill Res., Tenn (Muench 1966)	37,954 - 143,827	64,715
Norris Res., Tenn (Smith 1941)	28,415 - 32,727	29,700
Lake Meredith, Tex. (Kraai and Prentice 1974)	36,500 - 72,200	52,000

Table 38. Weighted mean age to first maturity: number of mature fish (sexes combined) in sample (N); accumulated number of newly matured fish within each age group, or accumulated numerical increments (I); percentage of total accumulated increments (P) expressed as P/100; and contribution of each age group (A), their sum being equal to the weighted mean age to first maturity.

Ages	N	I	P/100		A
2+	1	1	0.01		0.02
3+	3	2	0.03		0.09
4+	15	12	0.17		0.68
5+	15	0	0		0
6+	71	56	0.79		4.74
Total	105	71	1.00	Sum	5.53[a]

[a] Weighted mean age to first maturity.

SUMMARY

1. Savanne Lake is approximately 128 km northwest of Thunder Bay. It is 3.2 km long, 1.2 km wide, and is quite shallow, with mean and maximum depths of 2.67 and 4.27 metres, respectively. Fish species present in the lake are: walleye, northern pike, yellow perch, shallow water cisco, white sucker, burbot, trout perch, mimic shiner, black nose shiner, johnny darter and Iowa darter.
2. Savanne Lake belongs to a group of several lakes in that area, controlled by the Ontario Ministry of Natural Resources, Walleye Research Unit, which is undertaking a long term study of walleye exploitation.
3. Savanne Lake was exploited until 1969, whereupon it was designated a fish sanctuary.
4. A three year study (1973, 1974 and 1976) was conducted during the spring months. Walleyes were marked and recaptured in trap nets.
5. In the spring months of 1973, 1974 and 1976, the numbers of walleyes marked were 1492, 1389 and 1399.
6. Marking was accomplished by attaching a Floy tag FTF69 under the second dorsal fin with monofilament line.
7. The 6th, 12th and second dorsal spines were respectively clipped in the springs of 1973, 1974 and 1976 for Schumacher-Eschmeyer estimates.
8. Walleyes spawned along the rocky shoreline right after the ice break-up, at water temperatures of $4^{o}C$ to $5.8^{o}C$
9. Males arrived first on the spawning grounds, succeeded by females and other males. As commonly reported in the

literature, males dominated over females on the spawning grounds; the maximum proportion of females reached was 9.3% for 1975 and 12.2% for 1976.

10. Schumacher-Eschmeyer spring population estimates of 5211, 5184 and 5463 were made for 1973, 1974 and 1976, and represent the spawning population most vulnerable to the gear.

11. The fall population estimates were 40% lower than the spring estimates and were not included in the present study.

12. The majority of walleyes caught were of 35-48 cm size range, and trap nets were selective for walleyes larger than 30 cm.

13. The mean weighted ages of 6.82, 6.95 and 6.90 for 1973, 1974 and 1976, respectively, indicate a stable population in Savanne Lake. A decrease in mean weighted age with time signifies a stressed population (Nikolskii 1969).

14. Length and weight measurements were transformed to logarithms, and length-weight relationship for 4280 Savanne Lake walleyes over the three study years, using the least squares method, was represented by the following equation:

$$\text{Log } W = -4.8332286 + 2.915278 (\text{Log } L)$$

where: W = weight in gm, and

L = total length in cm.

15. No significant difference was found between the length-weight relationships of males and females.

16. The condition factor (K) values for Savanne Lake walleyes, over three years of study, decreased with respect to both length and age. Hence, these fish gained proportionately less in weight than in length as they grew older, an indication that the walleye population is in poor condition.

17. The annual natural mortality rates were high, varying from

8% to 73% for walleyes of age 7 and over in 1973-74. In 1974-75, the annual mortality rate averaged at 40%. Annual mortality rates continuously increased with age from 17% to 85% for 1975-76. However, unexploited populations have higher natural mortality rates than exploited populations.

18. Tagging mortality appeared to be low. Growth retardation was observed among tagged walleyes. Some of the walleyes neither grew in length, nor laid down a new annulus in each year of their life. These observations were attributed to limited food supply and extensive tagging and fin clipping of the fish over the study period.

19. No increase in year-class growth rates was observed through any of the three sampling periods.

20. The asymptotic total length of walleyes in 1973, 1974 and 1976 was found to be 82, 78 and 80 cm, respectively, and the mean growth curve for the combined data of the three sampling periods gave the following equation, with an asymptotic length of 80.0 cm, which is very close to the larger walleyes (77 cm) taken during the study period.

$$Lt + 1 = 9.04 + 0.887\ Lt$$

where: Lt = total length in cm

21. No relationship was found between year-class abundance and year-class growth. Age composition analysis revealed only one strong year-class (1966) which contributed 46% of the 1973 catch at age 7, and 40% of the 1974 catch at age 8. In the sampling period of 1976, two dominant age groups were observed, being the 1968 (8) and 1970 (6) broods, which contributed 26% and 40% of the 1976 catch.

22. Walleyes in Savanne Lake showed similar annual percentage

increments in their growth during the three sampling periods. Relative growth of walleyes increased substantially by the end of the first year, ranging from 1471 to 1557 percent. Growth decreased sharply in the second year, and continually decreased at a lesser rate until, on the average, the fifth or sixth year. Thereafter the growth rate was irregular and very slow.

23. The rate of growth of Savanne Lake walleyes was much slower than those in other bodies of water, reflecting the chemical characteristics of the lake, as well as to the high density of walleyes relative to the available food.

24. The annual biomass of 6.58 $kg \cdot ha^{-1}$ for 1973-74, 6.06 $kg \cdot ha^{-1}$ for 1974-75 and 2.64 $kg \cdot ha^{-1}$ for 1975-76 for age groups 7 and older was low. The annual production of 1.0 $kg \cdot ha^{-1} \cdot yr^{-1}$ (ages 7-16) for 1973-74, 1.31 $kg \cdot ha^{-1} \cdot yr^{-1}$ (ages 7-14) for 1974-75 and 0.52 $kg \cdot ha^{-1} \cdot yr^{-1}$ for 1975-76 compared closely to estimates for nearby Dexter Lake (Moenig 1975) for similar ages. Production of older fish in these lakes were lower than those of younger fish recorded by Kelso and Ward (1977) for West Blue Lake, Manitoba.

25. Mean biomass and production decreased with age over the three years of study. This was probably due to limited food supply which was used mostly for maintenance, rather than growth, in older fish.

26. The brood stock production of 1.85 $kg \cdot ha^{-1} \cdot yr^{-1}$ for fish of age 5.5 (weighted mean age to first maturity) and older, representing about 20 percent of the total walleye production in the lake, is closely similar to the theoretical yield of 1.9 $kg \cdot ha^{-1} \cdot yr^{-1}$, based on yield estimates using the MEI (Ryder 1965) and the 30 percent rule (Adams and Olver 1977).

27. The $P/\overline{B}$ ratio (turnover ratio) varied from 0.10 to 0.53 for 1973-74, from 0.24 to 0.45 for 1974-75 and from 0.22 to 0.37 for 1975-76, and decreased with increased age. There was no change in annual $P/\overline{B}$ ratios from 1973 to 1976, indicating that there was no change in biomass throughout the three years of study.

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APPENDICES

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Appendix 1. The various species of aquatic plants, zooplankton and benthos found in Savanne Lake.

Several types of aquatic plants are to be found at various locations, affixed in clay and sand, detritus and sand, silt and muck. They range in depth from 0 to 1.5 metres and consist of the following species: *Eleocharis palustris*; *Equisetum fluviatile*; *Sparganium fluctuans*; *S. angustifolium*; *Potamogeton praelongus*; *P. richardsonii*; *Isoetes macrospora*; *Myrica gale*; *Chamaedaphne calyculata*; *Nuphar rubrodiscum*; *N. microphyllum*; *Fontinalis hypnoides*; *Chlorophyceae* (green algae); *Phragmites communis*; and *Sagittaria latifolia*.

Seasonal distribution of zooplankton differed between years. In 1974, the greatest abundance occurred in June, while numbers were low in July and August. In 1975, moderate numbers were found in June and a sharp increase was noted in late July and August. *Copepods* predominated in 1974, and various species of *Daphnia* in 1975. The Savanne Lake zooplankton are listed below in the descending order of relative abundance:

> *Cyclops b. thomasi*; *Diaptomus oregonensis*; *Daphnia schoedleri*; *Daphnia g. mendotae*; *Daphnia retrocurva*; *Daphnia catawba*; *Bosmina longirostris*; *Holopedium gibberum*; *Epischura lacustris*; *Diaphanosoma leuchtenbergianum*.

A qualitative sample of benthos made at depths of 0 to 4 metres from various stations gave the following results: Annelids found were leeches of the families: Glossiphoniidae; Erpobdellidae; aquatic earthworms of the orders Plesiopora and Prosopora; and flatworms of the class Turbellaria. Molluscs included Gastropod snails of the families: Physidae (*Physa*); Planorbidae (*Helisoma*);

Amnicolidae (*Amnicola*); and freshwater mussels of the family Sphaeriidae (*Pisidium*). Crustaceans found were Amphipods of the families: Talitridae (*Hyalella*); Gammaridae (*Gammarus*) water fleas; Polyphemidae (*Polyphemus*); and the Decapods (*Orconectes virilis*). Insects include the may flies, Ephemeropterans of the families: Ephemeridae (*Hexagenia*), (*Ephemera*); Heptageniidae (*Stenonema*); and Baetidae (*Caenis*). Trichopterans found included the genera: *Neureclipsis*; *Oecetis*; *Platycentropus*; *Molanna*; *Psychomyia*; *Polycentropus*; and Helicopsychidae (*Helicopsyche*). Dipterans included the families: Chironominae; Tabanidae; Chaoborinae; Ceratopogonidae; and Simuliidae. The true bugs, Hemipterans, were of the families: Notonectidae; Pleidae; and Nepidae. Odonatans were represented by the family Libellulidae (*Macromia*). Coleopterans were found, belonging to the families: Dytiscidae (*Coptotomus*); Haliplidae (*Haliplus*); Chrysomelidae (*Donacia*). Elmidae, Gyrinidae (*Dineutus*) and Megalopterans sampled were of the family Sialidae (*Sialis*). Invertebrates in Savanne Lake, in order of greatest abundance, were Amphipoda, Diptera, Plesiopora, Ephemeroptera and Trichoptera (Table 3).

Appendix 2

Table 2A Schumacher-Eschmeyer population estimates of adult walleyes vulnerable to trap nets in Savanne Lake, Ontario, spring 1973

Date	ΣMi (n)	mi (m)	ni (m + u)	$\hat{N}$
May 3	0	0	376	0
4	189	3	198	12474
7	378	11	47	2918
8	413	17	172	3671
9	512	24	121	3114
10	570	19	65	2752
11	602	17	128	3156
14	672	2	10	3162
15	677	8	39	3177
16	694	3	16	3197
17	699	7	38	3247
18	716	10	35	3166
21	741	11	73	3359
22	777	6	43	3490
23	814	10	75	3734
24	878	19	101	3885
25	960	12	64	4008
28	1011	12	132	4686
30	1116	29	104	4548
May 31	1187	7	53	4767
June 1	1232	18	70	4770
4	1282	30	135	4938
6	1370	6	28	4988
8	1390	12	62	5133
11	1417	6	20	5120
13	1430	6	28	5169
15	1452	12	68	5354
18	1492	4	12	5336
19	1492	5	11	5285
20	1492	10	23	5198
22	1492	8	34	5239
25	1492	16	55	5232
26	1492	10	23	5159
27	1492	5	22	5187
June 28	1492	3	10	5184

$$\hat{N} = \frac{\Sigma Mi^2 ni}{\Sigma (Mimi)} \quad \text{or} \quad \Sigma n^2 \frac{(m+u)}{\Sigma nm}$$

Computations for Schumacher-Eschmeyer confidence limits for walleyes in the spring of 1973:

$$\hat{N} = \frac{\leqslant(Mi^2\ (ni)}{(Mi\ mi)} = \frac{1964859484}{379007} = 5184$$

$$S^2 = \frac{\leqslant\frac{Mi^2}{ni} - \frac{\leqslant(\leqslant Mi\ mi)^2}{\leqslant(Mi^2\ (ni))}}{m-1} = \frac{82.66 - \frac{(379007)^2}{1964859484}}{35-1}$$

$$S^2 = \frac{82.66-73.10}{34} = 2.81$$

$$S = .530$$

and standard error of $\frac{1}{\hat{N}}$ is

$$S.E.\ (\frac{1}{\hat{N}}) = \frac{S}{\sqrt{\leqslant(\leqslant Mi^2 ni)}} = \frac{.530}{\sqrt{1964859484}} = .0000119$$

The 95% confidence range for $\frac{1}{\hat{N}}$ is computed (Schumacher and Eschmeyer, 1946) when t with m-1 = 34 degrees of freedom = 2.031.

Confidence intervals are:

$$C.L. = \frac{1}{\hat{N}} \pm t\ (S.E.)$$

$$= .00019 \pm 2.031 \times .0000119$$

$$= .00019 \pm .000214$$

$$C.L_1(\frac{1}{\hat{N}}) = \frac{1}{.0001658} \qquad \hat{N} = 6031$$

$$C.L_2(\frac{1}{\hat{N}}) = \frac{1}{.000214} \qquad \underline{N} = 4672$$

Population Estimates = 5184 $\pm$ 680

Table 2B Schumacher-Eschmeyer population estimates of adult walleyes vulnerable to trap nets in Savanne Lake, Ontario, spring 1974

Date		ΣM_i (n)	M_i (m)	n_i (m + u)	$\hat{N}$
May	15	0	0	178	0
	16	151	0	120	0
	17	271	8	110	4988
	18	370	6	55	4181
	23	414	6	175	7034
	24	564	6	66	6760
	28	621	7	68	6544
	29	682	6	75	6977
	30	751	6	64	7178
	31	804	4	21	6818
June	4	820	0	7	6996
	5	827	1	33	7612
	6	859	11	92	7502
	7	934	8	39	7003
	11	965	8	79	7379
	12	1031	10	44	6908
	13	1064	9	48	6743
	14	1099	17	70	6285
	18	1150	3	13	6237
	19	1159	10	40	6061
	20	1189	13	47	5836
	21	1222	13	34	5530
	25	1243	21	78	5381
	26	1299	39	155	5329
	27	1389	26	117	5463

Computation for Schumacher-Eschmeyer confidence limits for walleyes in the spring of 1974.

$$\hat{N} = \frac{\Sigma(Mi^2\ (ni))}{\Sigma(Mi\ mi)} = \frac{1364450401}{249778} = 5463$$

$$S^2 = \frac{\Sigma\frac{Mi^2}{ni} - \frac{\Sigma(\Sigma Mi\ mi)^2}{\Sigma(Mi^2(ni))}}{m-1} = \frac{49.40 - \frac{(249778)^2}{1364450401}}{25-1}$$

$$S^2 = \frac{49.40 - 45.72}{24} = .1533$$

$$S = 0.390$$

and standard error of $\frac{1}{\hat{N}}$ is

$$S.E\left(\frac{1}{\hat{N}}\right) = \frac{S}{\sqrt{\Sigma(\Sigma\ Mi^2 ni)}} = \frac{.391}{\sqrt{1364450401}} = .0000106$$

The 95% confidence range for $\frac{1}{\hat{N}}$ is computed (Schumacher-Eschmeyer, 1946) when t with m-1 = 24 degrees of freedom = 2.064. Confidence intervals are

$$C.L = \frac{1}{\hat{N}} \pm t\ (S.E)$$

$$= .000183 \pm 2.064X\ .0000106$$

$$= .000183 \pm .0000218$$

$$C.L_1\left(\frac{1}{\hat{N}}\right) = \frac{1}{.000161} = \hat{N} = 6211$$

$$C.L_2\left(\frac{1}{\hat{N}}\right. = \frac{1}{.000204} = \underline{N} = 4902$$

Population estimates = 5463 $\pm$ 654

Table 2C Schumacher-Eschmeyer population estimates of adult walleyes vulnerable to trap nets in Savanne Lake, Ontario, spring 1976

Date	ΣM_i (n)	mi (m)	ni (m + u)	$\hat{N}$
May 5	0	0	192	0
6	131	1	162	21222
7	252	5	116	7340
11	359	1	48	9369
12	406	8	130	7568
13	517	3	53	7938
14	566	6	75	7643
15	635	7	79	7496
18	707	7	54	6973
19	753	5	69	7530
20	816	7	42	7008
21	851	13	56	6081
24	892	6	45	6153
25	930	8	64	6334
26	985	7	50	6416
27	1028	8	65	6650
May 28	1085	11	60	6541
June 2	1131	13	59	6322
3	1173	9	51	6354
4	1210	21	81	6025
5	1269	28	96	5667
8	1334	15	53	5564
9	1370	17	51	5402
10	[a]1402	22	75	5322
11	1401	26	79	5182
15	1399	0	5	5217
16	1399	2	9	5228
17	1399	0	1	5235
18	1399	1	8	5265
22	1399	0	2	5278
June 23	1399	5	9	5211

[a]Note: one recap. was retained, as a result ΣM_i becomes one less for next day dated June 10/76

Computations for Schumacher-Eschmeyer confidence limits for walleyes in the spring of 1976.

$$\hat{N} = \frac{\Sigma(Mi^2\ (ni))}{\Sigma(Mi\ mi)} = \frac{1499398090}{287689} = 5211$$

$$S^2 = \frac{\frac{\Sigma mi^2}{ni} - \frac{\Sigma(\Sigma Mi\ mi)^2}{\Sigma(Mi^2 ni)}}{m-1} = \frac{59.46 - \frac{(287689)^2}{1499398090}}{31-1}$$

$$S^2 = \frac{59.46 - 55.19}{30} = 0.142$$

$$S = 0.378$$

and standard error of $\frac{1}{N}$ is

$$S.E(\frac{1}{\hat{N}}) = \frac{S}{\sqrt{\Sigma(\Sigma Mi^2 ni)}} = \frac{0.378}{\sqrt{1499398090}} = .0000097$$

The 95% confidence range for $\frac{1}{\hat{N}}$ is computed (Schumacher-Eschmeyer, 1946) when t with m-1 = 30 degrees of freedom = 2.042. Confidence intervals are:

$$C.L = \frac{1}{\hat{N}} \pm t\ (S.E)$$

$$= .000191 \pm 2.042 \times .0000097$$

$$= .000191 \pm .0000198$$

$$C.L_1(\frac{1}{\hat{N}}) = \frac{1}{.000171} = \hat{N} = 5847$$

$$C.L_2(\frac{1}{\hat{N}}) = \frac{1}{.000211} = \underline{N} = 4741$$

Population estimates = 5211 $\pm$ 553

Table 3A. Analysis of covariance on the 1973 and 1974 length-weight relationships (using $\log_{10}$ transformations)

						Residuals		
Line	df	SS_x	SS_{xy}	SS_y	Slope	df	SS	MS
1973	90	.78	2.38	7.661	3.0512	89	.399	.00448
1974	82	.430	1.191	3.94	2.7520	81	.640	.00792
					Pooled Residuals	170	1.039	.00611
Common Slope	172	1.210	3.571	11.601		171	1.062	.0062
						1	.023	.024
Single Regression	173	1.535	3.51	11.708		172	2.498	
						1	1.435	

F_{Slope} = .023/.00611 = 3.76 with (1,170) degree of freedom, not significant at f=.05

$F_{\text{Intercept}}$ = 1.435/.0062 = 231.45 with (1,171) degrees of freedom significant at f=.01

Table 3B. Analysis of covariance on the 1974 and 1976 length - weight relationships (using $\log_{10}$ transformations)

Year	df	SS_x	SS_{xy}	SS_y	Slope	Residuals df	Residuals SS	Residuals MS
1974	82	.430	1.191	3.94	2.750	81	.640	.0079
1976	244	1.765	5.114	15.723	2,897	243	.906	.0037
				Pooled residuals		324	1.546	.0047
Common Slope	326	2.195	6.305	19.663		325	1.553	.0047
						1	.007	.007
Single Regression	327	2.195	6.309	19.692		326	1.599	
						1	.046	

F_{Slope} = .007/.0047 = 1.27 with (1,324) degrees of freedom; not significant at F = .01

$F_{\text{Intercept}}$ = .046/.0067 = 9.78 with (1,325) degrees of freedom; significant at F = .05

Table 3C. Analysis of covariance on the 1973 and 1976 length - weight relationships (using $\log_{10}$ transformations)

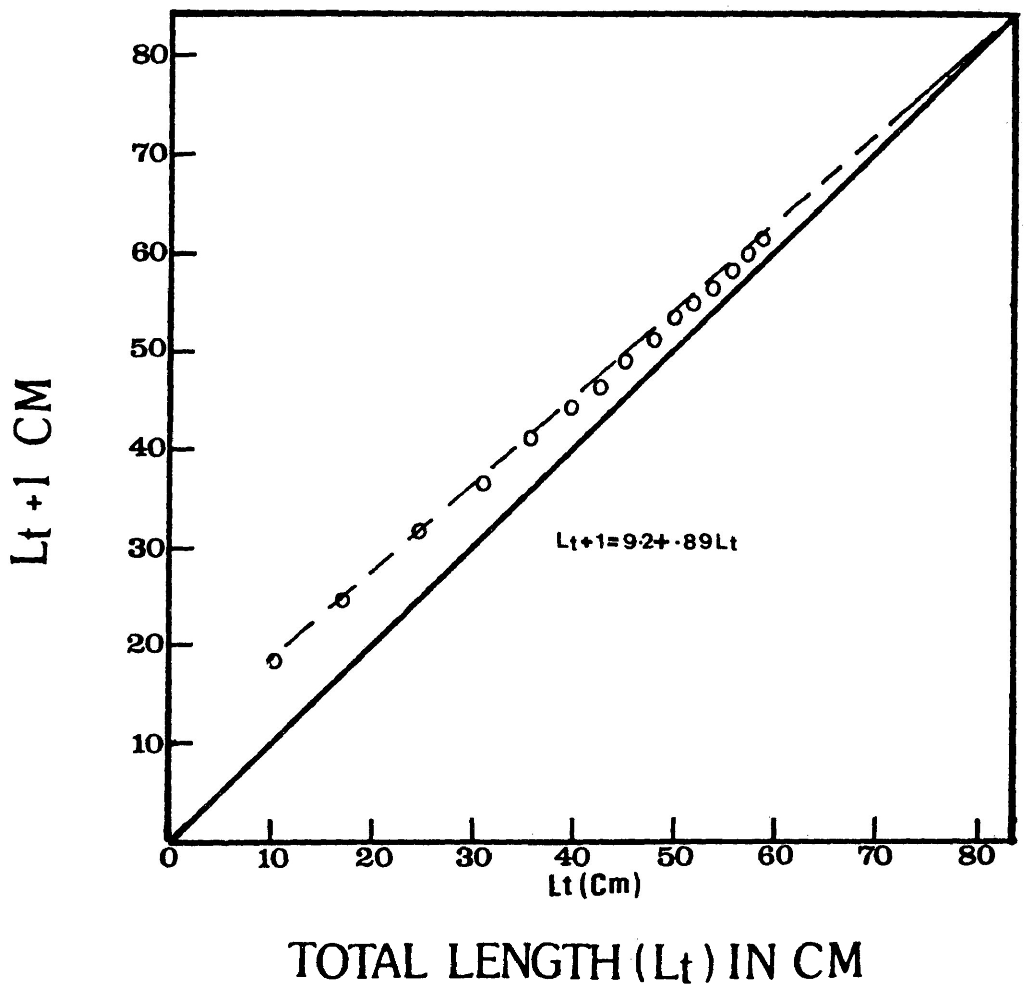
Year	df	SS_x	SS_{xy}	SS_y	Slope	Residuals df	Residuals SS	Residuals MS
1973	90	.78	2.38	7.661	3.0512	89	.399	.00448
1976	244	1.765	5.114	15.723	2.897	243	.906	.00372
				Pooled residuals		332	1.305	.0039
Common Slope	334	2.545	7.494	23.384		333	1.318	.0039
						1	.013	.013
Single Regression	335	2.876	7.681	23.513		334	2.9992	
						1	1.6812	

F_{Slope} = .013/.0039 = 3.33 with (1,332) degrees of freedom; not significant at F = .01

$F_{\text{Intercept}}$ = 1.6812/.0039 = 431.07 (1,333) degrees of freedom; significant at F = .01

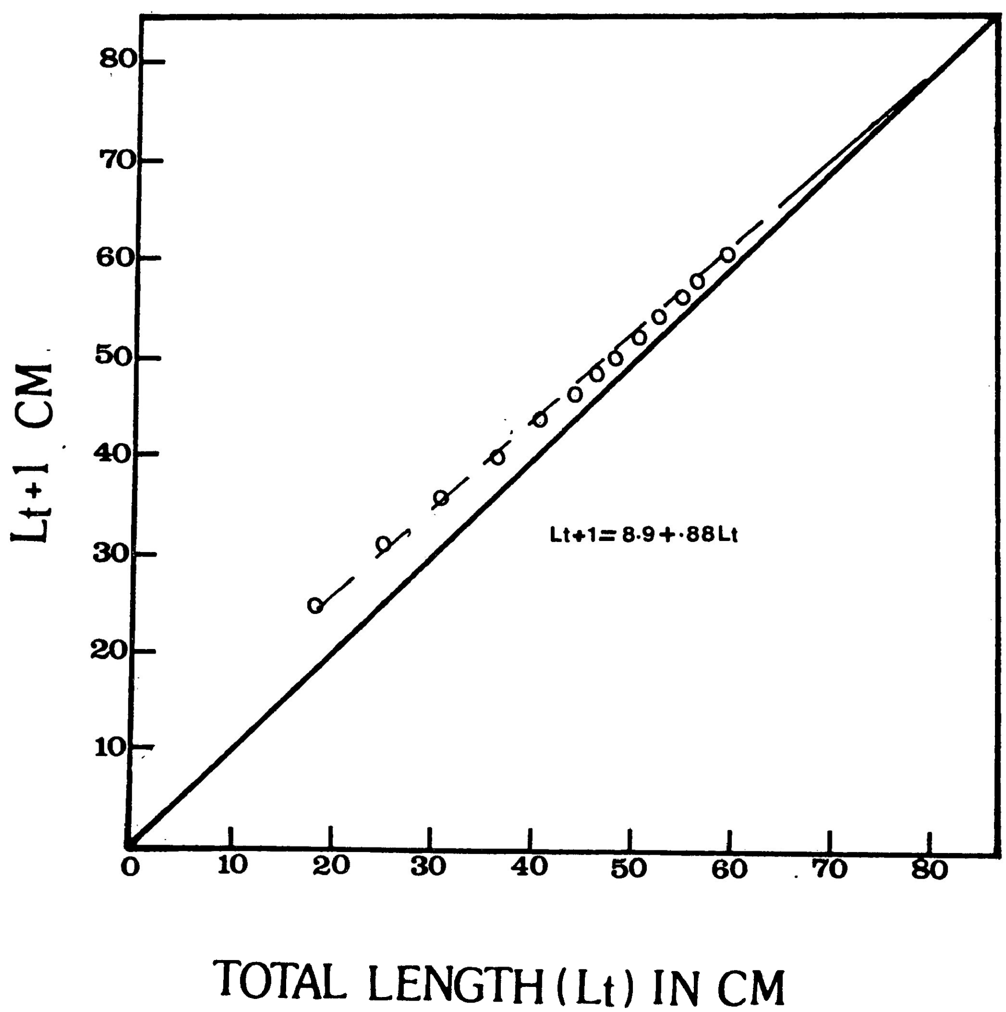
Appendix 4

Fig. 4A. Walford line; length at age Lt plotted against length-at-age Lt + 1. The resultant points were plotted against a straight line crossing the 45^{0} line. Union of two lines was the ultimate attainable size (82.0 cm) for Savanne Lake walleyes in 1973.



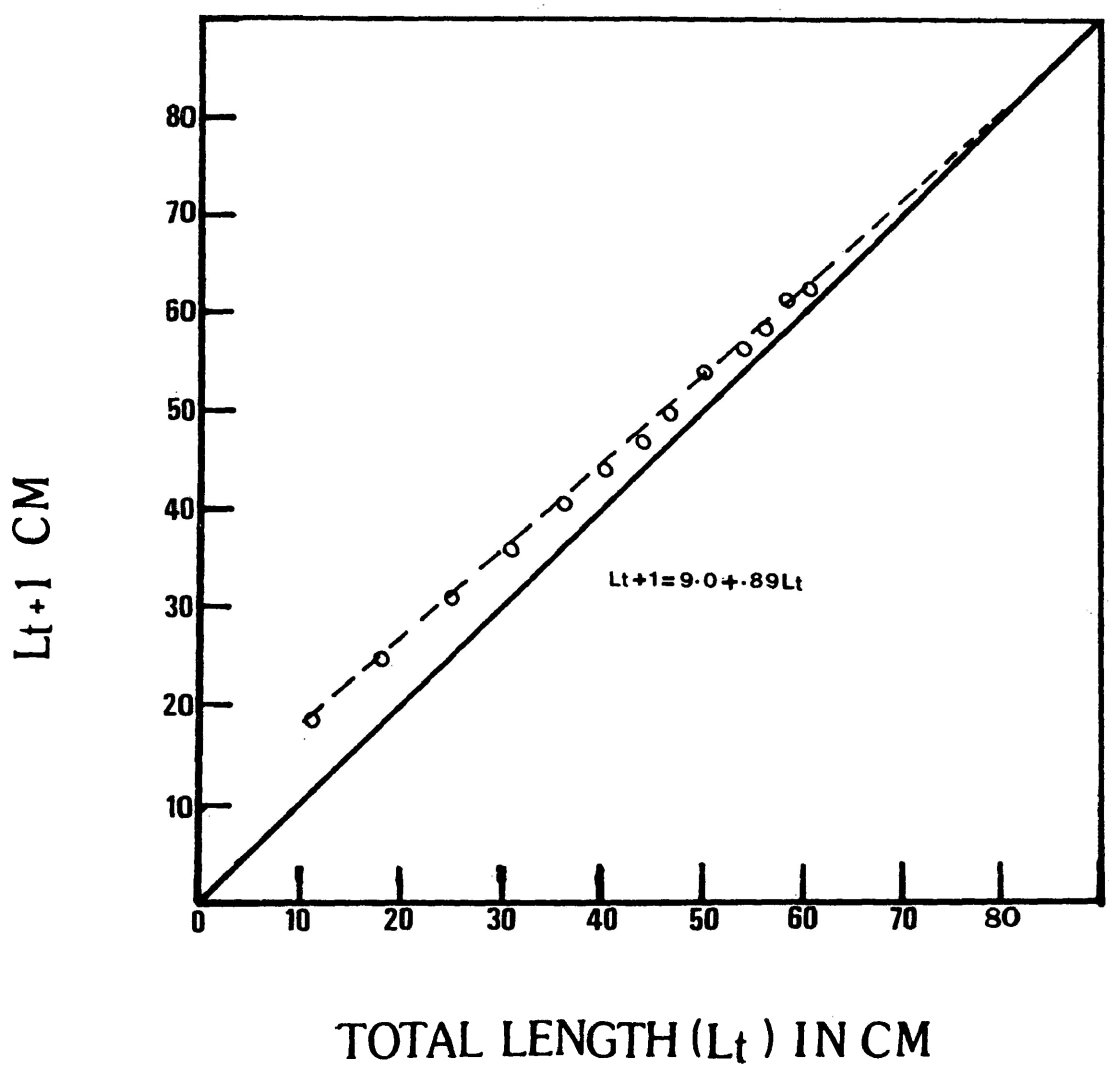
Lt +1 CM
80
70
60
50
40
30
20
10
0
10
20
30
40
50
60
70
80
Lt(Cm)
Lt+1=9·2+·89Lt
TOTAL LENGTH (Lt) IN CM

Fig. 4B. Walford line; length at age Lt plotted against lenght-at-age Lt + 1. The resultant points were plotted against a straight line crossing the 45^{0} line. Union of two lines was the ultimate attainable size (78.0 cm) for Savanne Lake walleyes in 1974.



Lt+1 CM
80
70
60
50
40
30
20
10
0
10
20
30
40
50
60
70
80
Lt+1= 8·9+·88Lt
TOTAL LENGTH (Lt) IN CM

Fig. 4C. Walford line;length at age Lt plotted against length-at-age Lt + 1. The resultant points were plotted against a straight line crossing the 45^{o} line. Union of two lines was the ultimate attainable size (80.0 cm) for Savanne Lake walleyes in 1976.



Lt+1 CM
80
70
60
50
40
30
20
10
0
10
20
30
40
50
60
70
80
Lt+1=9.0+.89Lt
TOTAL LENGTH (Lt) IN CM

Appendix 4

Table 4A. Mean length of age classes of combined samples of walleyes from Savanne Lake for fitting a Walford line to length using mean value of $L\infty$ = 80.0 cm.

Age (yr)	$L\infty$ (cm)	Lt + 1 (cm)	$L\infty$- (lt + 1) (cm)	$\log_e$ ($L\infty$-Lt + 1)
1	80.0	10.5	69.5	6.5439
2	80.0	18.3	61.7	6.4248
3	80.0	25.3	54.7	6.3044
4	80.0	31.1	48.9	6.1923
5	80.0	36.2	43.8	6.0822
6	80.0	40.3	39.7	5.9839
7	80.0	43.8	36.2	5.8916
8	80.0	46.5	33.5	5.8141
9	80.0	48.8	31.2	5.7430
10	80.0	51.1	28.9	5.6664
11	80.0	53.3	26.7	5.5872
12	80.0	55.2	24.8	5.5134
13	80.0	57.1	22.9	5.4337
14	80.0	59.5	20.5	5.3230
15	80.0	60.9	19.1	5.2522
16	80.0	61.4	18.6	5.2257
17	80.0	64.2	15.8	5.0625

Table 4B. Mean length of age classes of combined samples of walleyes from Savanne Lake for fitting a Walford line to length using a trial value of $L\infty$ = 82.0 cm.

Ages (yrs)	$L\infty$ (cm)	Lt + 1 (cm)	$L\infty$ - (Lt + 1) (cm)	$\log_e(L\infty$ - (Lt+1)
1	82.0	10.5	71.5	6.5722
2	82.0	18.3	63.7	6.4567
3	82.0	25.3	56.7	6.3403
4	82.0	31.1	50.9	6.2324
5	82.0	36.2	45.8	6.1268
6	82.0	40.3	41.7	6.0330
7	82.0	43.8	38.2	5.9454
8	82.0	46.5	35.5	5.8721
9	82.0	48.8	33.2	5.8051
10	82.0	51.1	30.9	5.7334
11	82.0	53.3	28.7	5.6594
12	82.0	55.2	26.8	5.5909
13	82.0	57.1	24.9	5.5174
14	82.0	59.5	22.5	5.4161
15	82.0	60.9	21.1	5.3518
16	82.0	61.4	20.6	5.3278
17	82.0	64.2	17.8	5.1817

Appendix 5

Table 5A. Back-calculated mean length in cm. at given age, growth increments and number of fish examined in each age group in the sampling year of 1973.

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
	11.7	20.0	25.9	32.5	36.6	42.1	47.1	50.4	52.8	54.8	56.1	57.2	59.4	60.7	61.8	62.4	64.2
	8.0	15.1	24.0	29.1	34.5	40.0	43.8	46.3	48.1	50.7	53.1	55.1	57.4	59.0	60.0		
	11.5	22.3	28.5	34.3	38.5	41.3	44.9	47.1	48.8	51.0	52.6	54.6	56.6	58.1			
	9.9	17.0	24.6	30.9	36.8	40.0	42.4	45.3	47.0	48.7	50.2	51.8	53.5				
	10.5	19.0	25.5	32.5	38.2	42.2	45.6	48.3	50.6	52.5	54.4	55.9					
	10.6	18.6	26.3	32.0	36.2	40.3	43.5	46.0	48.0	50.1	51.8						
	9.3	18.2	24.4	29.6	34.2	38.2	40.7	42.7	44.6	46.3							
	10.2	18.6	25.2	30.2	34.6	38.2	41.0	43.7	45.2								
	8.6	15.9	22.3	28.0	33.0	37.7	40.4	42.5									
	10.8	17.7	24.0	28.6	34.2	39.5	43.0										
	10.4	16.4	22.0	27.8	33.4	37.6											
	9.4	15.6	24.0	31.6	37.8												
	10.6	20.0	37.6	34.0													
	13.1	21.5	30.4														
Mean calculated length	10.3	18.3	25.3	30.8	35.7	39.7	43.2	45.8	48.1	50.6	53.0	54.9	56.7	59.3	60.9	62.4	64.2
Growth increments	10.3	8.0	7.0	5.5	4.9	4.0	3.5	2.6	2.3	2.5	2.4	1.9	1.8	2.6	1.6	1.5	1.8
Number of fish examined	0	0	27	33	20	9	76	6	15	14	11	8	3	1	1	0	2

able 5B. Back-calculated mean length in cm. at given age, growth increments and number of fish examined in each age group in the sampling year of 1974.

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	10.5	21.0	28.3	34.3	39.5	46.1	52.6	56.8	59.3	61.5	63.8	65.8	67.5	69.8	71.1	72.0
	10.4	16.1	24.1	31.0	36.3	40.4	42.6	44.7	46.1	47.5	49.1	50.6	51.8			
	10.4	19.5	26.2	32.8	38.2	41.7	44.4	46.5	49.0	51.4	54.1	55.8				
	10.7	18.1	25.0	31.5	36.4	39.7	42.7	45.0	47.3	49.8	51.5					
	9.4	17.9	24.3	29.6	35.0	39.4	42.7	45.4	47.8	49.3						
	9.6	16.7	23.7	29.9	35.1	38.9	41.8	43.9	46.0							
	10.4	17.5	23.5	28.4	33.8	39.0	42.7	44.6								
	11.0	17.7	24.3	29.7	35.0	39.8	42.6									
	9.1	15.1	23.0	29.9	35.4	38.4										
	10.0	19.1	26.6	32.8	36.7											
	12.2	19.9	27.6	33.0												
Mean calculated length	10.3	18.1	25.1	31.2	36.1	40.4	44.0	46.7	49.2	51.9	54.6	57.4	59.6	69.8	71.1	72.0
Growth increments	10.3	7.8	7.0	6.1	4.9	4.3	3.6	2.7	2.5	2.7	2.7	2.8	2.2	10.2	1.3	0.9
Number of fish examined	0	0	0	25	32	21	14	76	5	16	9	8	2	0	0	

able 5C. Back-calculated mean length in cm. at given age, growth increments and number of fish examined in each age group in the sampling year of 1976.

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
	12.1	22.6	29.8	36.8	43.6	47.5	50.0	53.5	56.6	59.9	62.2	63.8	65.9	67.8	69.2
	7.7	15.0	23.5	27.9	32.6	37.7	41.9	45.4	48.4	50.1	52.7	55.3	57.8	60.4	
	10.3	17.0	24.2	29.9	35.2	38.9	42.5	45.4	47.6	49.9	52.3	54.2	56.4		
	10.4	16.7	23.1	30.0	34.9	39.0	42.0	44.5	47.1	49.7	52.1	54.2			
	10.0	18.2	24.8	29.5	34.3	38.9	42.7	45.3	47.7	49.7	51.5				
	11.9	18.9	25.1	30.4	36.0	40.6	44.7	47.7	49.7	51.5					
	10.8	18.4	24.8	30.1	36.8	41.1	45.2	48.0	49.9						
	11.2	18.5	24.6	29.8	34.2	40.2	44.1	46.1							
	10.7	18.8	26.3	32.6	37.5	40.8	42.8								
	10.8	19.1	26.3	32.3	35.8	38.3									
	10.8	20.5	27.5	33.5	38.1										
	12.1	17.4	24.6	31.2											
	13.5	22.5	28.4												
Mean calculated length	10.9	18.7	25.6	31.2	36.3	40.3	44.0	47.0	49.6	51.8	54.2	56.9	60.0	64.1	69.2
Growth increments	10.9	7.8	6.9	5.6	5.1	4.0	3.7	3.0	2.6	2.2	2.4	2.7	3.1	4.1	5.1
Number of fish examined	0	0	11	33	11	47	22	43	23	12	5	4	4	1	1

Table 5D.. Calculated mean annual increments from each age group, length at age Lt + 1, total length in cm and percentage increments for age 1 to 17 for walleyes in the sampling year of 1973.

Age															Mean increments	Lt + 1	Percentage increments
17														1.8	1.8	60.8	2.9
16														0.6	0.6	59.0	1.0
15													1.0	1.1	1.0	58.4	1.7
14												1.5	1.6	1.3	1.5	57.4	2.6
13											1.7	2.0	2.3	2.2	2.0	55.9	3.6
12										1.5	1.6	2.0	2.0	1.1	1.6	53.9	2.9
11									1.7	1.9	1.5	1.6	2.4	1.3	1.7	52.3	3.2
10								1.7	2.1	1.9	1.7	2.2	2.6	2.0	2.0	50.6	3.9
9							1.5	1.9	2.0	2.3	1.7	2.2	2.8	2.4	2.1	48.6	4.3
8						2.1	2.7	2.0	2.5	2.7	2.9	2.2	2.5	3.3	2.5	46.5	5.4
7					3.5	2.7	2.8	2.5	3.2	3.4	2.4	3.6	3.8	5.0	3.3	44.0	7.5
6				4.2	5.3	4.7	3.6	4.0	4.1	4.0	3.2	2.8	5.5	5.5	4.3	40.7	10.5
5			6.2	5.6	5.6	5.0	4.4	4.6	4.2	5.7	5.9	4.2	5.4	4.1	5.1	36.4	14.0
4		6.4	7.6	5.8	4.6	5.7	5.0	5.2	5.7	7.0	6.3	5.8	5.1	6.6	5.9	31.3	18.8
3	8.9	7.6	8.4	5.6	6.3	6.4	6.6	6.2	7.7	6.5	7.6	6.2	8.9	5.9	7.1	25.4	28.0
2	8.4	9.4	6.2	6.0	6.9	7.3	8.4	8.9	8.0	8.5	7.1	10.8	7.1	8.3	8.0	18.3	43.7
1	13.1	10.6	9.4	10.4	10.8	8.6	10.2	9.3	10.6	10.5	9.9	11.5	8.0	11.7	10.3	10.3	1471

Table 5E. Calculated mean annual increments from each age group, length at age Lt + 1, total length in cm and percentage increments for age 1 to 16 for walleyes in the sampling year of 1974.

Age												Mean increments	Lt + 1	Percentage increments
16											0.9	0.9	60.5	1.5
15											1.3	1.3	59.6	2.2
14											2.3	2.3	58.3	3.9
13										1.2	1.7	1.5	56.0	2.7
12									1.7	1.5	2.0	1.7	54.5	3.1
11								1.7	2.7	1.6	2.3	2.1	52.8	4.0
10							1.5	2.5	2.4	1.4	2.2	2.0	50.7	3.9
9						2.1	2.4	2.3	2.5	1.4	2.5	2.2	48.7	4.5
8					1.9	2.1	2.7	2.3	2.1	2.1	4.2	2.5	46.5	5.4
7				2.8	3.7	2.9	3.3	4.0	2.7	2.2	6.5	3.4	44.0	7.7
6			3.0	4.8	5.2	3.8	4.4	3.3	3.5	4.1	6.6	4.3	40.6	10.6
5		3.9	5.5	5.3	5.4	5.2	5.4	4.9	5.4	5.3	5.2	5.2	36.3	14.3
4	5.4	6.2	6.9	5.4	4.9	6.2	5.3	6.5	6.6	6.9	6.0	6.0	31.1	19.3
3	7.7	7.5	7.9	6.6	6.0	7.0	6.4	6.9	6.7	8.0	7.3	7.1	25.1	28.3
2	7.7	9.1	6.0	6.7	7.1	7.1	8.5	7.4	9.1	5.7	10.5	7.7	18.0	42.8
1	12.2	10.0	9.1	11.0	10.4	9.6	9.4	10.7	10.4	10.4	10.5	10.3	10.3	1471

Table 5F. Calculated mean annual increments from each age group, length at age Lt + 1, total length in cm and percentage increments for age 1 to 15 for walleyes in the sampling year of 1976.

Age														Mean increments	Lt + 1	Percentage increments
15														1.4	62.3	2.2
14												2.6	1.9	2.3	60.9	3.8
13											2.2	2.5	2.1	2.3	58.6	3.9
12										2.1	1.9	2.6	1.6	2.1	56.3	3.7
11									1.8	2.4	2.4	2.6	2.3	2.3	54.2	4.2
10								1.8	2.0	2.6	2.3	1.7	3.3	2.3	51.9	4.4
9							1.9	2.0	2.4	2.6	2.2	3.0	3.1	2.5	49.6	5.0
8						2.0	2.8	3.0	2.6	2.5	2.9	3.5	3.5	2.9	47.1	6.1
7					2.0	3.9	4.1	4.1	3.8	3.0	3.6	4.2	2.5	3.5	44.2	7.9
6				2.5	3.3	6.0	4.3	4.6	4.6	4.1	3.7	5.1	3.9	4.2	40.7	10.3
5			4.6	3.5	4.9	4.4	6.7	5.6	4.8	4.9	5.3	4.7	6.8	5.1	36.5	14.0
4		6.6	6.0	6.0	6.3	5.2	5.3	5.3	4.7	6.9	5.7	4.4	7.0	5.8	31.4	18.5
3	5.9	7.2	7.0	7.2	7.5	6.1	6.4	6.2	6.6	6.4	7.2	8.5	7.2	6.9	25.6	26.9
2	9.0	5.3	9.7	8.3	8.1	7.3	7.6	7.0	8.2	6.3	6.7	7.3	10.5	7.8	18.7	41.7
1	13.5	12.1	10.8	10.8	10.7	11.2	10.8	11.9	10.0	10.4	10.3	7.7	12.1	10.9	10.9	1557

Appendix 6

Procedure for calculations of weighted mean age.

To calculate the mean age to first maturity, experimental gill net data (consisting of 15.24 m of each 2.5, 3.8, 5.1, 6.4, 7.6, 8.9, 10.2 and 11.4 cm stretched mesh) from June 1976 was used for age composition analysis. The total number of fish sampled for determination of age at maturity was 105 (sexes combined). The walleyes in this sample were checked for maturity until the 100% maturity level was found. This was age 6+. The mature fish identified at ages 2+, 3+, 4+, 5+ and 6+ were 1, 3, 15, 15 and 71, respectively. The total increments of newly mature fish entering each age group were 1, 2, 12, 0 and 56 (Table 38). The percentage of the increments of the mature fish in each age group was calculated and multiplied by its age class. The sum of all ages was 5.5 (weighted mean age to first maturity).