THE ECOLOGY OF NORTHERN PIKE, *Esox lucius* Linnaeus,

IN SAVANNE LAKE, ONTARIO

by

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A thesis submitted to the Department of Biology in partial fulfillment of the requirements for the Degree of Master of Science

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ABSTRACT

Important aspects of the life history and population dynamics of the northern pike, Esox lucius, in Savanne Lake, Ontario were studied during 1977 and 1978. Feeding relationships involving northern pike and walleyes, Stizostedion vitreum vitreum, and the initial impact of an open water sport fishery on these unexploited populations were also examined.

Schumacher-Eschmeyer spring population estimates of 2,621 and 2,508 for 1977 and 1978, respectively, represented the mature northern pike population (ages 4-14 and greater than 45 cm in length) most vulnerable to the sampling gear. Adult northern pike did not appear to establish home ranges but moved throughout the lake during the year. A sex ratio of 1.19 females to every male was observed. Females were heavier than males at a given length and grew more rapidly at most ages. Fecundity estimates of 9,675 eggs per unit body-weight (kg) and an average of 20,081 eggs per mature pike were low for this species. Growth rates of Savanne Lake northern pike were slightly below average growth rates in Ontario and Minnesota waters and probably reflect the chemical characteristics of this lake, as well as the high density of piscivores relative to available food. Total mean biomass and annual production for age-groups 4-12 were estimated at 8.69 $kg \cdot ha^{-1}$ and 2.76 $kg \cdot ha^{-1} \cdot yr^{-1}$, respectively, for the 1977-78 period. Low annual production was attributed to slow growth, low annual mortality, and the dominance of older age-groups in this unexploited population.

Relative abundance and seasonal availability determined the incidence of prey consumed by adult northern pike and walleyes. Yellow perch (Perca flavescens), especially juveniles (60-110 mm in length), and shallow water ciscos (Coregonus artedii) predominated in observed annual diets of both species. Invertebrates,

notably mayfly nymphs (Ephemeridae) and crayfish (Orconectes virilis), were of seasonal importance. Prey size was not a critical factor in determining predation, since the majority of examined northern pike and walleyes were capable of consuming far larger prey than were actually found in their stomachs.

Northern pike appeared more vulnerable to angling than walleyes and comprised the greater portion of total angling yield for the open water study period. Catch per unit efforts of 0.88 fish per man-hour and 1.12 kg per man-hour for northern pike and 0.66 fish per man-hour and 0.48 kg per man-hour for walleye resulted from minimal angling pressure (1.24 hours per ha). Angling catches consisted primarily of northern pike, 50–70 cm in length and 5–7 years old, and walleyes, 40–50 cm in length and 6–10 years old, representing dominant age and size classes in the mature populations.

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INTRODUCTION

Most studies of northern pike, <u>Esox lucius</u> (Linnaeus), concern populations subjected to intensive recreational or commercial fishing in addition to pressures resulting from a variety of other human activities. Very little information exists concerning unperturbed populations and their response to exploitation. This study defines the role of northern pike as a major predator in the relatively unexploited fish community of Savanne Lake, Ontario, with regards to its life history, population dynamics, production, and seasonal food habits. A previous study of walleye production and population dynamics in Savanne Lake (Sandhu 1979) combined with the present analysis of the food habits of pike and walleyes, has allowed a comparison of the community and trophic status of these species. The initial impact of a sport fishery on both populations is also assessed in order to provide insights for the management of northern pike and walleye stocks in boreal lakes.

Lake Description

Savanne Lake is located approximately 128 km northwest of Thunder Bay, Ontario (Lat. 48^{o} 49' 30", Long. 90^{o} 06' 00"). Game fish populations were exploited by a sport fishery until 1969, whereupon the lake was designated a provincial fish sanctuary by the Ontario Ministry of Natural Resources for the purpose of a long term study of controlled walleye exploitation and percid community dynamics.

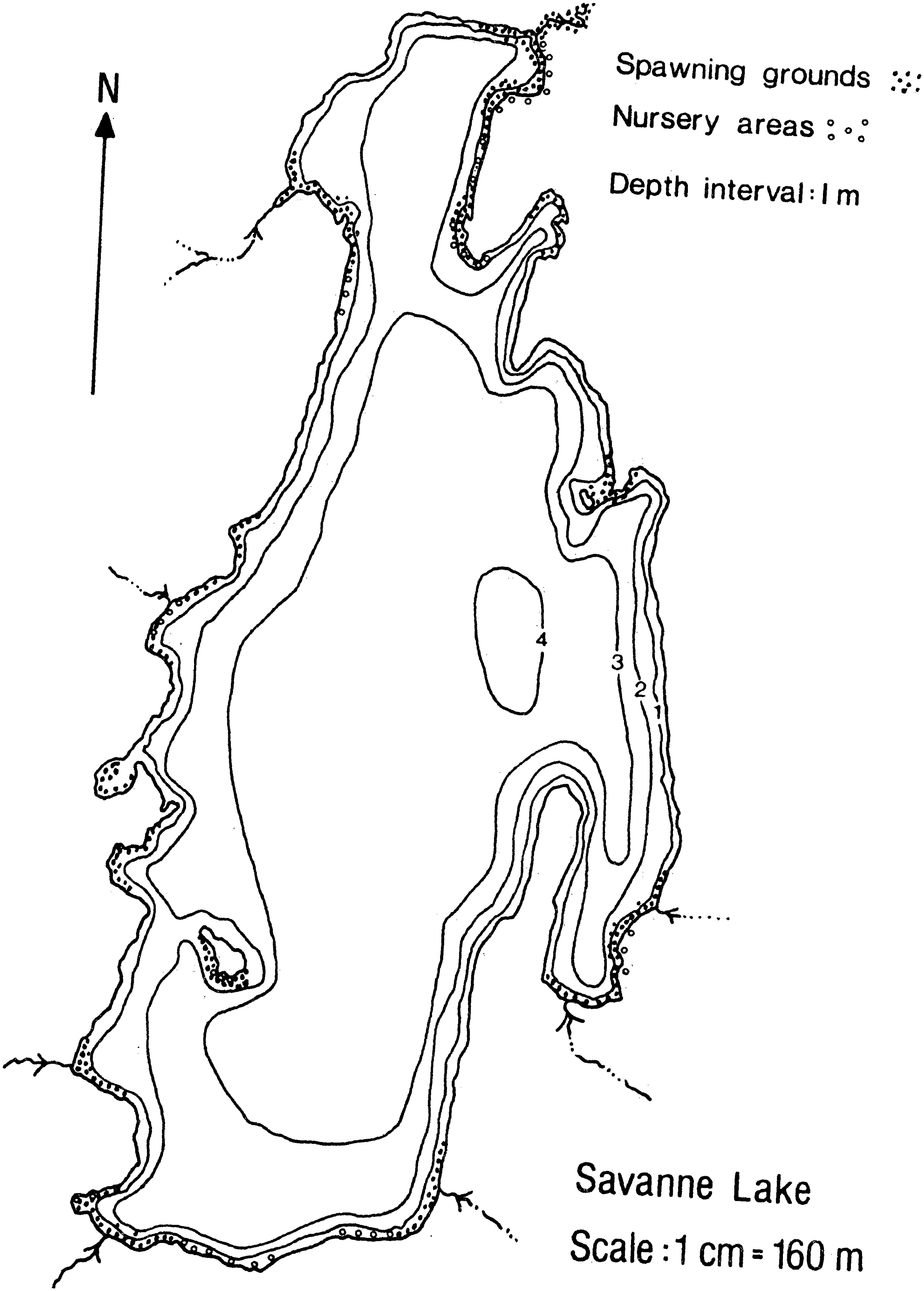
Savanne, a relatively shallow lake (2.5 m mean depth and 4.27 m maximum depth), is of intermediate size, 364.29 ha (Fig. 1). Its important physical (Table 1) and chemical (Table 2) characteristics were previously described by Sandhu (1979). Adequate oxygen levels are found throughout the water column in late winter and midsummer (Table 2).

This homothermous lake is characterized by very low water temperatures during the early winter following ice cover formation in late November (Appendix 1, Table 1). At this time, temperatures of $3.0^{o}C$ were recorded at maximum lake depths (4.25m). Water temperatures had increased to $4.0^{o}C$ in these locations by early March 1978. Similar warming of deeper waters over winter in Finnish boreal lakes (Nissinen 1972) has been attributed to the gradual transfer of stored heat from bottom sediments to water layers above. The warming of sediments in shallow areas due to the increased incidence and penetration of solar radiation during late winter may also result in the horizontal movement of warm, denser water from the shallows into deeper lake basins.

A variety of aquatic plants, zooplankton, and invertebrates have been found in Savanne Lake (Appendix 2, Table 1).

The fish fauna consists of the following species: walleye, Stizostedion vitreum vitreum (Mitchill); northern pike, Esox lucius Linnaeus; yellow perch Perca flavescens (Mitchill); shallow water cisco, Coregonus artedii Lesueur; white sucker, Catostomus commersoni (Lacépède); burbot, Lota lota (Linnaeus); trout-perch, Percopsis omiscomaycus (Walbaum); mimic shiner, Notropis volucellus (Cope); blacknose shiner, Notropis heterolepis Eigenmann and Eigenmann; johnny darter, Etheostoma nigrum Rafinesque; and Iowa dater, Etheostoma exile (Girard).

Figure 1. Map of Savanne Lake showing depth contours (depth interval = 1 m), northern pike spawning grounds, and areas favoured for young-of-the year northern pike development.



N
Spawning grounds
Nursery areas
Depth interval: I m
4
3
2
1
Savanne Lake
Scale: 1 cm = 160 m

Table 1. Physical features of Savanne Lake (Sandhu 1979): T D S = Total dissolved solids; M E I = Morpho-edaphic 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 ($mg \cdot l^{-1}$)	M E I a/ (metric)	P Y E b/ ($kg \cdot ha^{-1} \cdot yr^{-1}$)
364.29	9.37×10^{6}	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/ $P Y E = 1.237 \sqrt{M E I}$

$= 1.237 \sqrt{25.29}$

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

Table 2 . Selected chemical characteristics of water samples taken from Savanne Lake, Ontario at various times (Sandhu 1979).

Item	May 14/73	April 15/75	March 31/77
pH[a]	7.1[d]	S 6.4	S 7.5
		M 6.5	M 7.2
		B 6.5	B 6.4
O_2 (Mg/l)[b]	-	S 12.3	S 12.0
		M 7.8	M 12.0
		B 5.3	B 2.2
Temp. (°C)[b]	8.3[d]	S 0.0	S 1.1
		M 2.2	M 3.3
		B 3.8	B 4.4

[a] Test performed on preserved sample.

[b] Tests performed in the field.

[c] S = Surface (0.0 m); M = Middle (2.0 m); B = Bottom (4.0 m).

[d] Mean of values recorded at surface, middle and bottom depths.

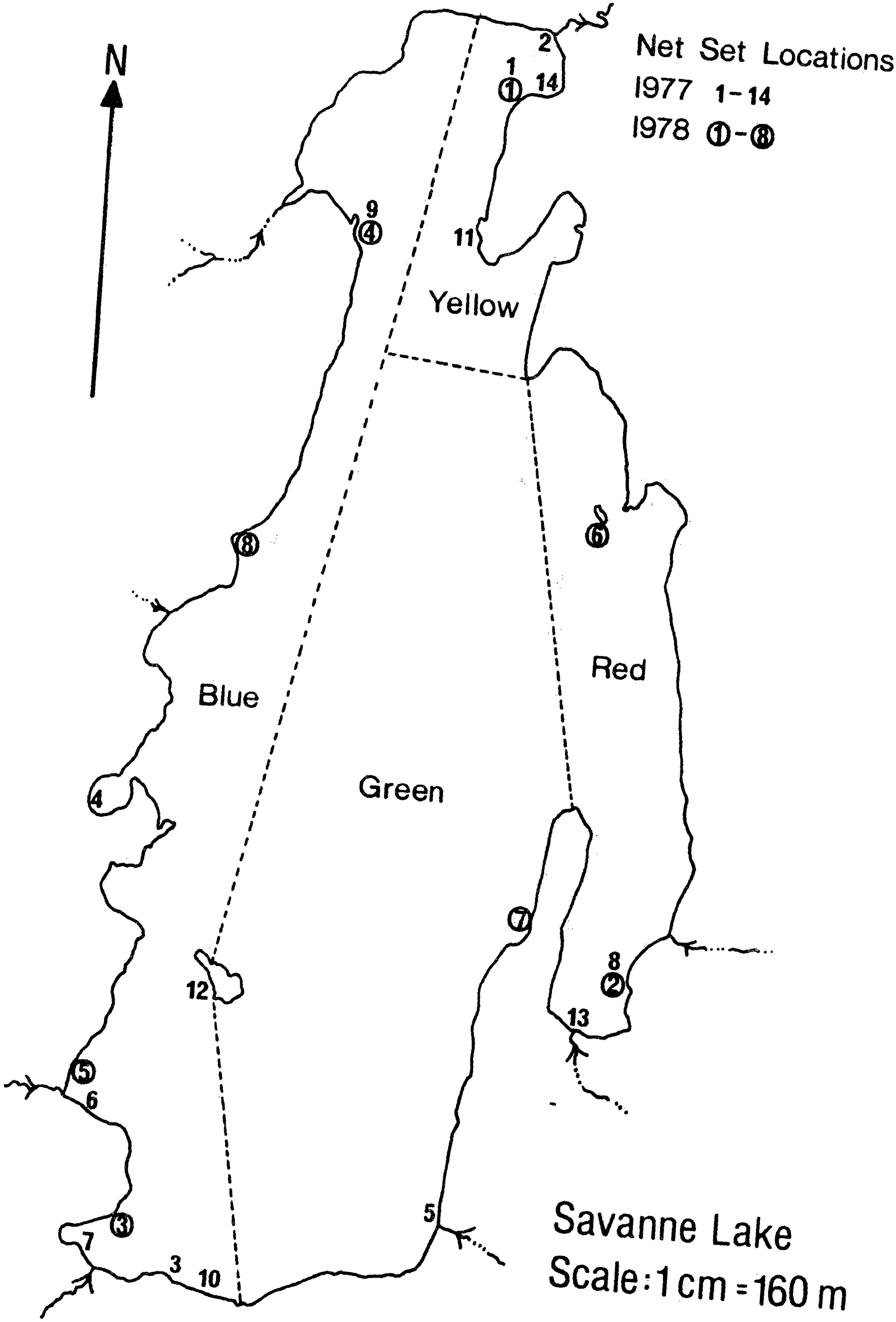
METHODS AND MATERIALS

Population Assessment

Mark and recapture population estimates (Schumacher and Eschmeyer 1943) of mature northern pike in Savanne Lake were carried out in the spring of 1977 and 1978. Both 1.22 metre (four foot) and 1.83 metre (six foot) trap nets of the standard Lake Erie design (Sandhu 1979) were used for sampling fish. Leads of 15.2 metres (fifty feet), 30.5 metres (one hundred feet), and 60.9 metres (two hundred feet) were employed with both sizes of trap net, as dictated by the water depth at net set locations. In 1977 and 1978, 49 and 32 net sets were made in 14 and 8 locations, respectively (Fig. 2).

A variety of habitats in addition to known spawning areas were sampled. Nets were moved frequently when catches decreased or when the ratio of marked to unmarked fish in the catch exceeded twenty percent. Trap netting began two days after ice-out, on April 26, 1977 and on the day of ice-out May 7, 1978. Population estimates were completed by May 31 in both years. Trap nets were checked each morning after having fished a minimum of twenty hours. Northern pike were anaesthetized in a solution of MS-222 (Tricaine methane-sulfonate) and Quinaldine sulfate (60:20 mg./litre) to facilitate handling and to reduce injury to the fish. For each northern pike, total length was measured to the nearest millimeter and weight was recorded to the nearest 5 grams using a Chantillon tube-type spring scale. Total length refers to the measured distance from the tip of a fish's snout to the end of the its longest caudal rays when squeezed to an extreme position (Ricker 1975). Sex was

Figure 2. Map of Savanne Lake showing lake sectors and spring trap net locations in 1977 and 1978.


N
Net Set Locations
1977 1-14
1978 ①-⑧
Yellow
Blue
Green
Red
1
①
2
14
9
④
11
⑧
⑥
4
⑦
8
②
12
13
⑤
6
③
7
3
10
5
Savanne Lake
Scale: 1 cm = 160 m

determined both on the basis of extruded gonadal products and externally by the urogenital method (Casselman 1974a). Fish were examined for previous fin clips and tags. Several scales were removed from the key scale sample area on the left side of the body for age determination. This area, which includes the rows of scales immediately above, below, and on the lateral line, is located on the midlateral region directly above the anterior insertion of the pelvic fin (Casselman 1978). Different marks were used to identify captured northern pike in both years. The posterior upper portion of the caudal fin was clipped in 1977 and the posterior lower portion of the caudal fin was clipped in 1978. In addition, fish captured in 1977 were tagged with numbered disc-type tags (Floy tag FTF 69). These were affixed under the anteriormost part of the pterigiophore, underlying the dorsal fin with monofilament line of 2.7 kg test using a 6.0 cm suturing needle. In 1978, tubular "spaghetti" tags (Floy tag FT-4) were affixed in the same anterior position under the dorsal fin with 10 kg test polypropylene line (White and Beamish 1972). The two types of tags were coloured yellow, green, red and blue, identifying the area in which the northern pike were tagged (Fig. 2). Although tag loss was noted, clipped caudal fins made these fish easily recognizable. If the fish already possessed a tag from a previous year, the tag was removed and its number recorded. The fish was retagged after its length was measured and scale samples were taken. Only the tag number was recorded for fish recaptured in the same year. All northern pike were released at the site of the trap. A total of 825 and 785 pike were marked, and a total of 166 and 146 fish were recaptured respectively, in the spring of 1977 and 1978.

Sampling to determine the overall age and size structure of the northern pike population in Savanne Lake was conducted several times between 1976 and 1978. Test gill nets of various lengths and mesh compositions (Appendix 3, Table 1) sampled a full range of habitats during the open water season. All captured northern pike were retained and examined. Stomach contents were collected. Sex was determined by internal examination and scales and cleithra taken.

Age and Growth Determination

Northern pike from Savanne Lake were sub-sampled to determine age composition, growth, annual production, and the body-cleithrum relationship. A ten percent stratified subsample of the northern pike were aged (Ketchen 1949). Scales and cleithra were collected from May 1977 to May 1978, in conjunction with the feeding study. Additional small fish were sampled by trap netting, gill netting, and beach seining during this period.

Scales from each fish were mounted on plastic acetate slides and pressed by a hand roller to obtain scale impressions (Nesbit 1934). These slide impressions were read on an Eberbach scale projector using a 32 mm lens at 40X magnification. Northern pike were aged by counting the annuli visible on the slide impression according to criteria described by several authors (Williams 1955; Frost and Kipling 1959; Wainio 1966; Casselman 1967). Distances (in mm) from the focus to each completed annulus and to the scale edge along the anteriormost radius (Fig. 3) were used to determine the relationship between total body length and the total anterior scale radius.

The left cleithrum, a flat bone from the pectoral girdle, was also removed from each fish (Casselman 1974). Cleithra were cleaned with hot water and a fine brush. They were examined with the aid of a dissecting microscope at 4X magnification against a dark background in reflected light. Ages of northern pike were determined by interpreting the zonation of translucent and opaque bands on the inner side of the cleithrum blade (Fig. 4). Translucent areas are inversely

Figure 3. Diagram of a northern pike scale, showing terminology used to identify salient features and regions.

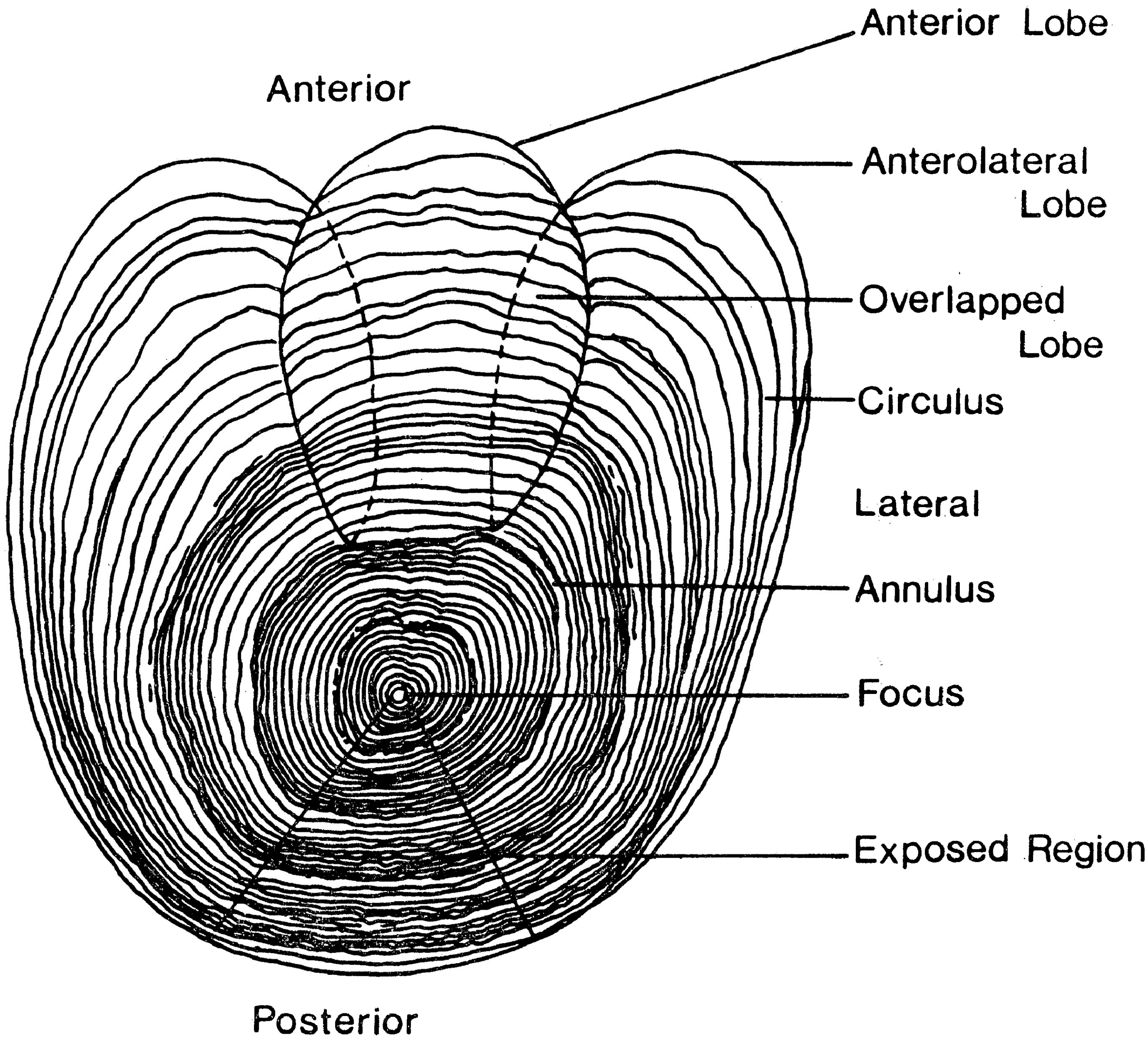
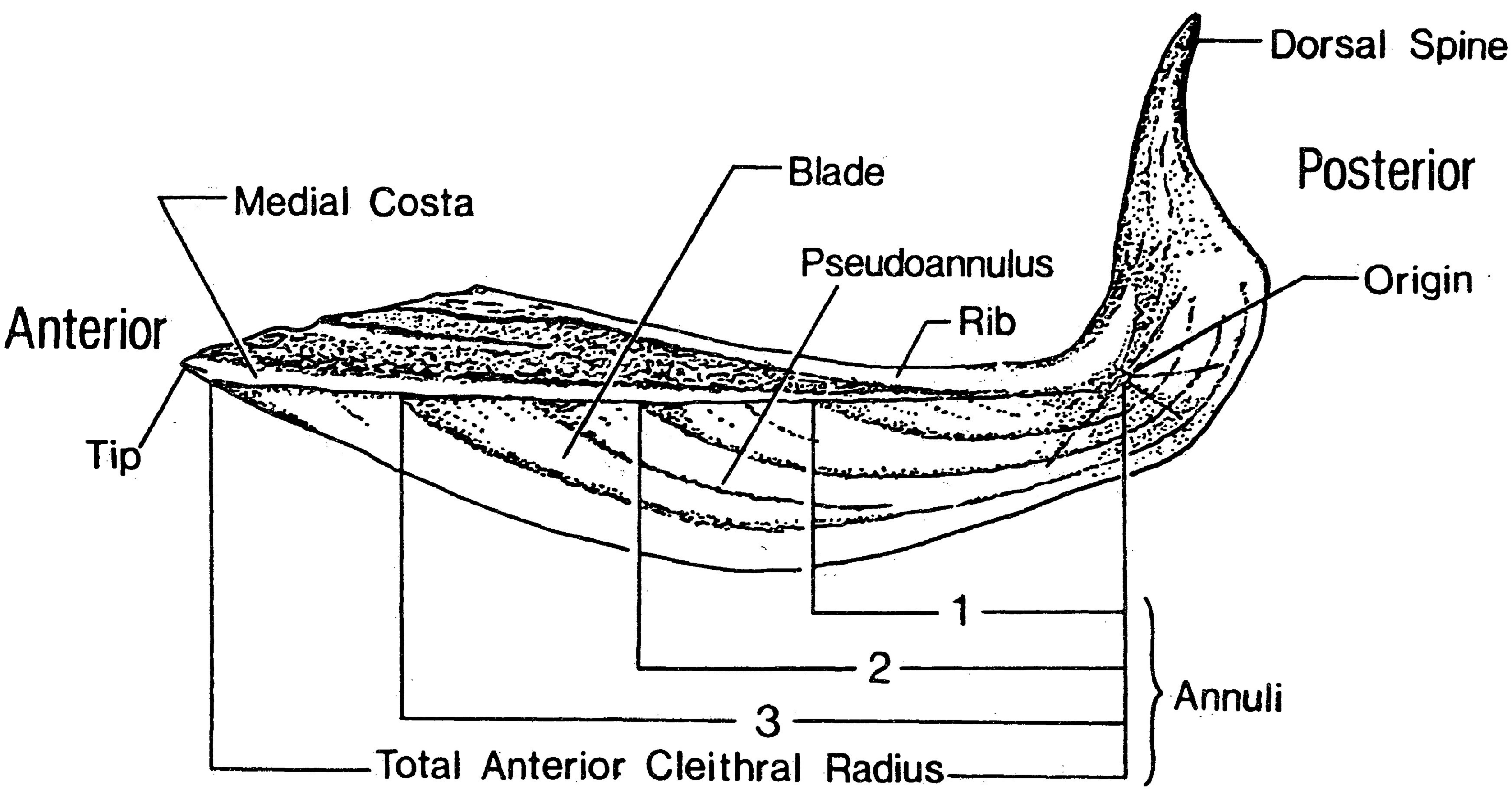

Anterior Lobe
Anterior
Anterolateral Lobe
Overlapped Lobe
Circulus
Lateral
Annulus
Focus
Exposed Region
Posterior

Figure 4. Diagram of the medial surface of a northern pike cleithrum showing various regions and terminology used to describe basic features. In addition, various cleithral measurements are depicted.


Anterior
Tip
Medial Costa
Blade
Pseudoannulus
Rib
Dorsal Spine
Posterior
Origin
1
2
3
Annuli
Total Anterior Cleithral Radius

related to the rate of calcified tissue growth (Casselman 1974b) and therefore, act as definitive checks in the overall growth pattern. Annuli or year marks are associated with the most prominent translucent zones which can be traced around the blade, from the anterior to the most posterior regions. Pseudoannuli or false year marks are less distinct in comparison and do not usually circumscribe the entire blade, especially into the posterior areas. They are found just inside the true annuli with which they converge towards the middle regions of the surface. Growth, following the appearance of a pseudoannulus, is disproportionately greater in the anterior than in the posterior regions of the blade. Annulus formation is complete when both the cleithrum and body resume growth in the spring at water temperatures exceeding 7.5°C (Casselman 1978).

Measurements (to the nearest 0.1 mm) of the anterior cleithral radii (the linear distance from the origin to the points where the translucent annuli intersect the medial costa of the blade) were made using a needle-tipped dial caliper (Fig. 4). This facilitated the assessment of back-calculated growth. The total anterior cleithral radius (the linear distance from the origin to the point where the anteriormost tip of the blade intersects the medial costa) was used to calculate a body length-cleithrum relationship (Casselmen 1978). The location of the origin on the cleithrum can be determined on the basis of translucent streaks and various striae which radiate out from this point (Fig. 4).

Data for calculation of yearly growth increments, body length-cleithrum relationship, back-calculated lengths, and the length-weight relationship were obtained from 125 female and 110 male northern pike. In addition, lengths were back-calculated from scale measurements of 40 fish in this sample, collected in late April and May. Calculations were performed on an IBM 360 computer using a program entitled FISHMAP (Teleki and Martin 1977) which assumes an isometric growth pattern in fish and a resulting linear relationship between total fish length and scale diameter. Casselman (1978) demonstrated that both scales and cleithra of northern pike grow at different rates when compared to body growth. In order to substitute scale with cleithral measurements in the present FISHMAP calculations, a direct linear relation was used, pending refinement of a more accurate model that would better reflect cleithrum and body growth rates (J. M. Casselman, pers. comm.).

The age structure of mature pike was based on age assessment of the stratified subsample, divided into ten centimeter length intervals over the entire length range. The number of fish belonging to a specific age group within a sample interval was expressed as a percentage of the total number sampled in that interval (Ketchen 1949). These percentages, applied to length-frequency distributions of northern pike vulnerable to trap netting during the 1977 and 1978 spring estimates (Fig.6), gave the age structure of the population.

Fecundity

Materials for a fecundity study were obtained during the spring seasons in 1978 and 1979 from 1.22 metre and 1.83 metre nets set on known spawning grounds. Mature fish were sampled in 10 cm size intervals over a range of 40 to 100 cm total length. Fish were judged ripe if the ventral abdominal region was fully distended and if eggs had not yet begun to "run" upon the external application of pressure. Eggs, removed from the opened body cavity, were pooled with materials collected from fish of similar size and preserved in a buffered ten percent formalin solution. Total length, weight, and previous tag history were recorded for each fish. Both scales and cleithra were also retained. Samples were washed in distilled water and sieved through fine mesh cheese cloth to separate eggs from extraneous materials. A subsample of 5 percent of each sample's total egg volume was measured by water displacement, and eggs were counted. Total egg numbers were calculated from a volumetric determination (Medford and MacKay 1978). Fecundity was expressed as the mean egg count per unit body-weight (the total number of eggs from all sampled fish divided by the total weight of all fish sampled) and the mean egg count per mature female (the total number of eggs from all fish sampled divided by the total number of fish in the sample).

Early Development

Young-of-the year northern pike were collected weekly from June 1 to August 31 in 1977 and 1978. Fish were caught using fine mesh hand dip nets, an 18.3 m (sixty foot) long bag seine, and plexi-glass larval fish traps (Casselman and Harvey 1973). The total length of each fish was measured to the nearest millimeter and its weight was recorded to the nearest 0.5 grams. Stomach contents were analysed using a dissecting microscope and appropriate taxonomic keys.

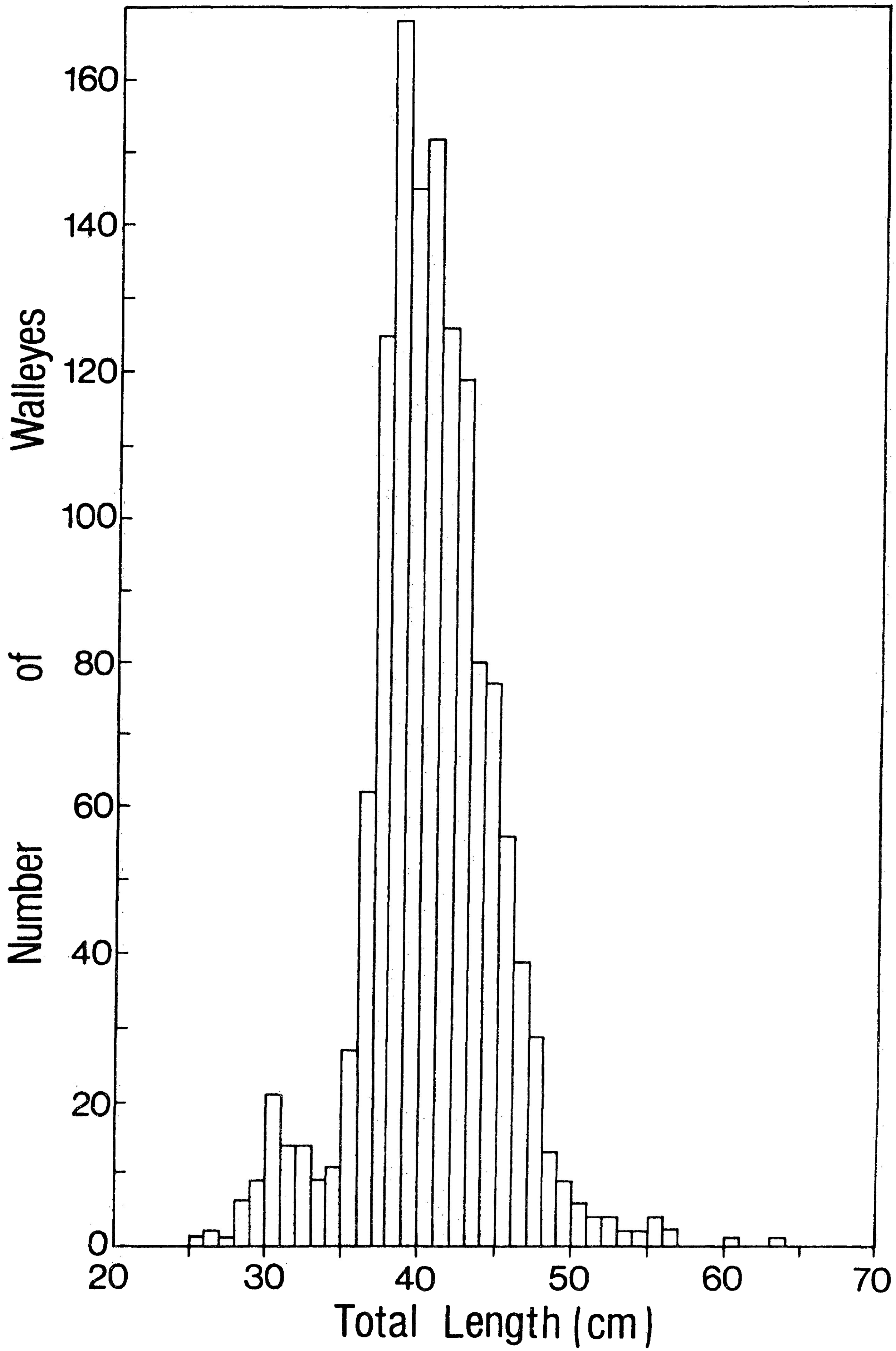
During these intervals, shoreline and backwater areas of Savanne Lake were examined for habitats favouring early northern pike development. This assessment was highly subjective in nature since unusually high lake levels, thick shoreline vegetation and the inherent sedentary behaviour of these larval fish made quantitative sampling difficult. Visual counts of young-of-the year northern pike were made within measured shoreline distances. The physical character of each sampling area was described, noting shoreline structure, type of substrate and macrophyte growth present. Both inshore water temperatures and prevailing atmospheric conditions (e.g. light conditions) were also recorded.

Feeding Study

Specimens of northern pike (208) and walleyes (254) were examined for food habits. This sample represents less than ten percent of each population and so minimizes the exploitive effect on the fish community. Both species were sampled during a one to two week period at the end of each month from June 1977 to May 1978 and again in December 1978. Each month's sample reflected the length frequency distributions of both walleye (Sandhu 1979) and northern pike populations (Figs. 5 and 6). All small pike (less than 40 cm) and walleyes (less than 30 cm) were retained for aging and feeding studies.

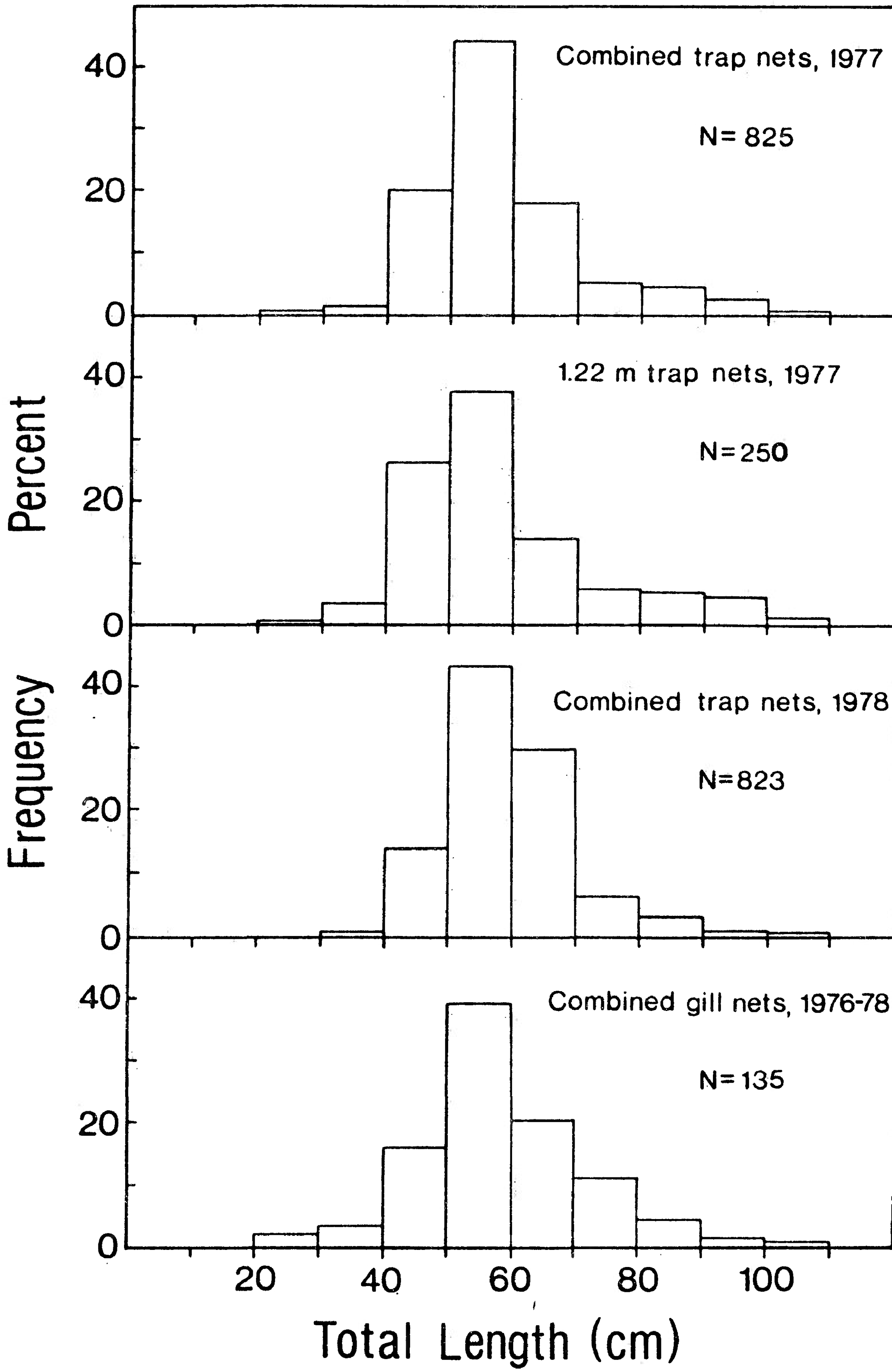
Fish were caught from May to October by angling (See Exploitation, Methods and Materials). Poor angling success during the

Figure 5. The length-frequency distribution of walleyes in Savanne Lake, Ont. vulnerable to trap nets in the spring of 1976 (Sandhu 1979).



Number of Walleyes
0
20
40
60
80
100
120
140
160
20
30
40
50
60
70
Total Length (cm)

Figure 6. Length-frequency distributions of northern pike in Savanne Lake vulnerable to 1.22 and 1.83 m trap nets in the springs of 1977 and 1978, 1.22 m trap nets in the spring of 1977, and gill nets in 1976 and 1978.



Combined trap nets, 1977
N= 825
1.22 m trap nets, 1977
N=250
Combined trap nets, 1978
N=823
Combined gill nets, 1976-78
N=135
Percent Frequency
40
20
0
20
40
60
80
100
Total Length (cm)

iced-over period (late November to April) resulted in the collection of monthly samples by gill netting. Graduated monofilament gill nets, 45.7 m in length and composed of five panels (9.15 m by 1.83 m) of various mesh sizes (25, 36, 67 and 114 mm stretched), were set beneath the ice with the aid of a creeping ice jigger (Appendix 4, Fig. 1). Nets set at mid-day were lifted the following morning after having fished for a minimum of twenty hours. The full range of lake habitats and depths were sampled during each month.

Captured fish which fulfilled sample length requirements, were weighed, examined for previous tags and marks, and sexed. Scales were taken from walleyes and both scales and cleithra were retained from northern pike. The entire digestive tract of each fish was removed, wrapped in cheese cloth, labelled, and preserved in a buffered ten percent formalin solution (Lagler 1956).

The intestinal tract was examined separately for the presence of undigested food. Intestinal contents of northern pike longer than 20 cm were usually too digested to be identifiable. Total stomach contents were determined volumetrically (Ball 1948). While invertebrates were counted and identified only to the generic level, fishes were determined to species. Because of digestion, some food items could only be identified as fish or invertebrate remains. Positive identification based on the presence of distinctive morphological structures (e.g. type of scales, skeletal structure, shape and number of gastric caeca) was aided by comparison with preserved specimens and taxonomic keys. Volumes of larger food items were determined separately, while very small organisms were measured collectively. Maximum body lengths and maximum body depths of each item were measured to the nearest mm. These measurements were approximated in cases of advanced digestion by comparison with similar items found in a less digested state.

The stomach contents were recorded as the percentage of northern pike and walleyes containing each food item [frequency of occurrence, (Frost 1954)] and as the percentage of total volume occupied by each food item (Wolfert and Miller 1978). All percentages were based only on fish containing food in their stomachs (L. D. Johnson 1969).

No allowance was made for possible regurgitation of stomach contents. Both Frost (1954) and Lawler (1965) noted that pike did not appear to regurgitate their stomach contents as readily as other species (e.g. walleye) when enmeshed in gill nets. Since the number of gill netted walleyes represented a small percentage of total fish sampled, regurgitation of stomach contents was not considered significant. All retained fish were immediately dispatched by cervical dislocation.

Exploitation

Both northern pike and walleyes were angled to provide samples for the feeding study and to assess the initial impact of exploitation on the community. Angling occurred from June 1977 to May 1978 during the last two weeks of each month. A variety of lures, plugs, and worm baited spinners were used in the open water season (May to

October). Hand lines baited with live minnows and jigs were fished through holes in the ice during winter (November to April). The shallow, homothermous nature of Savanne Lake insured that both species were equally vulnerable at any one instance to the gear employed. During each month, a full range of lake habitats and lake depths were fished. Angling throughout the open water season was restricted to daylight hours between dawn and dusk, but during winter, lines were fished for twenty-four hours. Detailed creel census forms recorded the number of anglers in each party, the time of day, the total number of hours angled, methods employed, and geographic locations fished in the lake (e.g. off the southwest corner of Red Island). Each fish in the catch was identified and its total length was measured to the nearest millimeter. Also noted were water depths and temperatures (surface and bottom) in the locations fished, and prevailing atmospheric conditions at the time of angling. The majority of fish caught were subsequently released at the capture site but a number were retained for stomach analysis. Scales and/or cleithra were obtained from these fish. All fish caught were either weighed or weights were estimated from the length-weight relationships for walleye (Sandhu 1979) and northern pike (present study).

LIFE HISTORY

Spawning

Northern pike spawning was observed at ice-out on April 24, 1977 and on May 7, 1978 at water temperatures of 4.5 to 6.0°C. Spawning activity peaked at beach temperatures of 8.4°C in 1977 and 6.8°C in 1978 (Appendix 1, Table 2). The temperature range for spawning of this species is 4.0 to 14.4°C (Toner and Lawler 1969).

The major spawning area was located along the shore and outlet at the northeast end of the lake. Less extensive areas along the east and southwest shores were also utilized (Fig. 1). As commonly reported (Toner and Lawler 1969), spawning occurred on flooded, marshy, shoreline areas over submerged aquatic and terrestrial vegetation, in less than 0.5 m of water. Greatest activity was noted on sunny days between 1200 and 1700 hours EST.

Males dominated the spawning population. The overall ratio of males to females varied from 1.4:1 to 1.5:1 in 1977 and 1978, respectively. Males predominated during the early and late stages of the spawning run (Table 3). During peak periods of spawning activity, equal numbers of males and females were identified on spawning areas. The maximum proportion of females on the spawning grounds peaked at 58 percent on April 27, 1977 and 57 percent on May 13, 1978. Rawson (1932) reported males and females to be about equal in numbers during spawning, but Clark (1950) stated that while males predominated in the early portion of the run, females became more numerous with time.

Table 3 . Numbers of spawning northern pike in the daily trap net catch, percentage identified to sex and male/female ratios in Savanne Lake, Ontario in the springs of 1977 and 1978.

Date			Total catch	Males	Females	% Female	% Sexed	Male to female ratio
1977	April	27	101	37	52	58.4	88.0	0.7:1
		28	71	41	26	38.8	94.0	1.6:1
		29	86	39	39	50.0	91.0	1:1
		30	52	24	23	48.9	90.0	1.1:1
	May	1	54	29	17	40.0	85.0	1.7:1
		2	53	30	12	28.6	79.0	2.5:1
		3	33	22	5	18.5	82.0	4.4:1
		4	30	22	1	4.3	77.0	22.0:1
		5	23	7	1	12.5	35.0	7.0:1
1978	May	8	90	60	24	28.6	93.0	2.5:1
		9	67	40	25	38.5	97.0	1.6:1
		10	136	82	53	39.3	99.0	1.6:1
		11	128	63	63	50.0	98.0	1:1
		12	58	26	26	50.0	90.0	1:1
		13	15	6	8	57.0	93.0	0.8:1
		14	68	35	8	18.6	63.0	4.4:1
		15	58	25	10	28.5	60.0	2.5:1
		16	74	32	7	17.9	53.0	4.6:1
		17	57	15	2	11.8	30.0	7.5:1

Fecundity

The average number of eggs per unit body-weight (kg) for the sampled northern pike population was estimated at 9,675 per kg, with a range of 7,500 to 10,540 per kg (Table 4). Mature females produced an average of 20,081 eggs. The number of ova per unit body-weight did not increase significantly ($p > 0.05$, t-test) with age and weight of fish examined, as previously noted by Healey (1956) and Frost and Kipling (1967). However, the largest females sampled were the most fecund.

Although considerable variation exists in the number of eggs produced by this species within local populations and throughout their distributional range (Berg 1962), fecundity estimates for Savanne Lake northern pike are low when compared to reported values. Carbine (1944) observed mean egg counts for northern pike in Houghton Lake, Michigan, of 7,691 to 97,273 per mature fish. Scott and Crossman (1973) cite egg counts of 19,800 per kg body-weight and 32,000 per mature female as average for this species. Walleyes also exhibit a very low fecundity in Savanne Lake (P. J. Colby unpublished data).

Early Development

The temporal sequence of early northern pike development in Savanne Lake closely parallels that described by several authors (Carbine 1942; Wurtz 1945; Frost and Kipling 1967). Free-swimming fry, 20-23 mm long, were first observed along shoreline areas on May 26, 1977 and on June 8, 1978 approximately four weeks after spring break-up and after commencement of northern pike spawning. Toner and Lawler (1969) report that development from fertilized egg

Table 4 . Fecundity estimate for northern pike in Savanne Lake, Ont. presented as the calculated mean egg number ($\bar{x}$) per unit body-weight (kg) $\pm$ standard deviation (S.D.). Number of fish sampled for each size interval is designated as (N).

Size interval (cm)	N	Mean age (yr)	Weight: Average (g)	Weight: Total (g)	Total number of eggs	$\bar{x} \pm$ S.D.
40 - 49.9	8	4.4	680.0	5,440.0	40,800	7,500 ± 3,245
50 - 59.9	10	5.6	926.0	9,260.0	90,000	9,720 ± 1,304
60 - 69.9	7	7.0	1,548.0	10,835.0	93,000	8,583 ± 2,100
70 - 79.9	7	8.3	2,387.0	16,710.0	152,061	9,100 ± 1,603
80 - 89.9	5	9.2	3,493.0	17,465.0	178,140	10,200 ± 3,200
90 - 99.9	5	10.2	5,492.0	27,460.0	289,428	10,540 ± 4,102
Totals	42			87,170.0	843,429	

to the free-swimming stage takes three to four weeks. Upon resorption of the yolk sac, fry may remain in spawning areas for one to two weeks before moving into the main bodies of lakes (Hunt and Carbine 1951; Franklin and Smith 1963).

During late spring and summer seasons in 1977 and 1978, young-of-the year northern pike were found along shallow sand and rocky beach areas of Savanne Lake, protected by overhanging shoreline vegetation and offshore beds of emergent macrophytes such as *Phragmites communis* and *Equisetum fluviatile* (Fig. 1). Very few fry were observed in the marshy, soft-bottomed areas favoured by spawning adults, although they were found along hard-bottomed shorelines adjacent to such areas. In the early season, young-of-the year were observed alone, hovering within a few centimetres of the water surface, or beneath shoreline vegetation and debris. Their presence and general activity was more pronounced on sunny, calm days than under cloudy, agitated conditions. As the summer progressed, their behaviour became more secretive and they were found in slightly deeper water and among offshore macrophyte beds within these nursery areas.

Rapid growth of young-of-the year northern pike followed from the early free-swimming stage (20 mm) in late May and early June until late August (Table 5). The average length of fry increased at a rate of 1.3 mm per day in 1977 and 1.7 mm per day in 1978. Although the 1978 spawning season was delayed two weeks over the previous year, fish achieved the same approximate size (130-140 mm) by the end of each summer. A similar growth rate was observed for young-of-the

Table 5 . Seasonal stomach contents of age-0 northern pike in relation to their growth in Savanne Lake during 1977 and 1978.

Date		Sample size	Average length (mm)	Average weight (g)	Stomach contents
1977					
May	26	4	23.0	0.08	Copepods (Cyclops sp.); cladocera (Daphnia sp.)
	31	6	40.0	0.25	YOY white suckers, walleye, n. pike; Chironominae
June	2	4	45.0	0.40	YOY white suckers, walleye; Chironominae
	10	3	56.0	1.00	YOY white suckers and yellow perch
	17	4	65.0	1.40	YOY white suckers and yellow perch
	29	3	82.0	2.20	YOY yellow perch; Ephemeridae nymph
July	6	2	90.0	4.50	YOY white suckers and yellow perch
	8	1	106.0	6.40	stomach empty
	15	2	100.0	7.50	YOY yellow perch
	30	1	110.0	13.00	YOY yellow perch; adult darter
August	18	2	130.0	16.00	YOY yellow perch
1978					
June	4	3	20.0	0.05	Copepods; cladocerans
	8	6	26.0	0.09	Copepods; Chironominae; Simuliidae
	16	3	36.0	0.23	YOY white suckers and walleye; Chironominae
	23	4	51.0	0.70	YOY white suckers and walleye
	29	2	75.0	1.60	YOY white suckers and adult darters
July	14	2	80.0	2.50	YOY yellow perch; Ephemeridae nymph
	21	2	85.0	3.85	YOY yellow perch; Notonectidae
August	4	2	110.0	6.50	YOY yellow perch
	13	1	140.0	18.00	YOY yellow perch

year northern pike in Houghton Lake, Michigan (Carbine 1942).

Entomostraca, primarily copepods (e.g. Cyclops biscuspidatus thomasi) and cladocera (e.g. Daphnia sp.) formed the greatest portion of stomach contents from northern pike fry, 20 to 30 mm long. Larval fish (Perca flavescens and Catostomus commersoni) were the most common items in both beach seines and in examined stomachs of larval pike over 30 mm (Table 5). Walleye fry, adult darters (Etheostoma nigrum and Etheostoma exile), larval insects (Chironominae, Tabanidae, Simuliidae, Notonectidae, Ephemeridae), and northern pike fry were also found. Insect larvae occurred in sampled fry over 25 mm but they were never of dietary importance. Hunt and Carbine (1951) stressed the prevalence of insect larvae, especially Chironominae, in the diet of northern pike (25-50 mm) in Houghton Lake, Michigan. The observed pattern of feeding in Savanne Lake was similar to that described for young-of-the year pike in Lake Windermere (Frost 1954). There, Entomostraca formed the major portion of the diet until fish attained a length of 35 mm, when perch fry (Perca fluviatilis) became important.

Toner and Lawler (1969) listed a number of important predators of young pike. Of these, yellow perch, dragonfly and damselfly nymphs, dytiscid beetles, and loons were sighted at some time along shoreline nursery areas. Cannibalism among young-of-the year northern pike was reported by Hunt and Carbine (1951) and does occur in Savanne Lake (Table 5). Cannibalism involving yearling and older pike is probably significant since these fish actively feed in littoral areas favoured by fry. Young-of-the year were found in stomachs of several adult northern pike and walleyes.

Movements

Adult northern pike moved throughout Savanne Lake during the year with the greatest movements occurring in the spring during spawning. In the spring of 1977, a total of 388 fish were tagged in the yellow sector, 242 in the blue sector, 123 in the red sector, and 72 in the green sector of the lake (Fig. 2). These fish were recaptured in the following spring with 1.22 m and 1.83m trap nets set in the same locations where spawning fish had been previously tagged. Of recaptured fish, 79 percent of the yellow tagged and 50 percent of the blue tagged fish were caught in the yellow sector, while 67 percent of the red tagged and 52 percent of the green tagged recaptures were caught in the red sector (Table 6). The importance of the north end marshes and outlet, and to a lesser extent the shallow southeast bay as major spawning grounds was evidenced by the seasonal concentration and yearly movement of adult fish into these areas. After spawning, fish dispersed throughout the lake. Several northern pike, previously tagged in the yellow sector at the far northeast end, were recaptured within 24 hours at the extreme southwest corner of Savanne Lake, a distance of 4.0 km. Similarly, fish tagged in the red sector, were recaptured

Table 6 . Number of northern pike tagged in the various sectors of Savanne Lake, spring 1977 and the percentage recaptured by sector in the spring, 1978 with trap nets.

Sector	Number tagged	Number of tagged fish recaptured	Site of recapture (%)			
			Red	Green	Yellow	Blue
Red	123	39	66.6	2.6	25.6	5.2
Green	72	27	52.0	0.0	26.0	22.0
Yellow	388	72	11.0	0.0	79.0	10.0
Blue	242	20	25.0	0.0	50.0	25.0
Totals	825	158				

in yellow and green sectors within a few days of release.

Apart from widespread movements in the spring to preferred spawning grounds (Rawson 1932; Carbine 1942), adult northern pike are reported to be fairly sedentary and almost territorial, establishing themselves in areas that provide adequate cover and food (Wistrom et al. 1957; Buss 1961; Scott and Crossman 1973). Both Malinin (1969, 1970) and Makowecki (1973) state that northern pike have an established home range and restrict their movements to an area several hundred metres at maximum. Diana et al. (1977) monitored the movements of northern pike in a shallow moderate sized lake in central Alberta using ultrasonic transmitters, which were implanted in the fishes' stomachs. They found that pike did not establish well-defined home ranges, and most daily movements were less than 1000 m. Similar movement patterns are suspected for northern pike in Savanne Lake. In the course of monthly sampling during 1977 and 1978, previously tagged northern pike were recaptured at consecutive intervals from different parts of this lake (Table 7). These recapture locations were sufficiently distant to indicate that these pike did not restrict their movements to a defined home range but moved throughout the lake during the year.

Table 7. Consecutive recaptures of tagged adult northern pike, caught by angling in Savanne Lake, Ont., June 1977–May 1978.

	Tagged		Recapture			
Tag number	Date	Location[a]	Date	Location	Date	Location
Yellow 441	26/04/77	Yellow #1	23/09/77	Green shore	11/05/78	Red shore
Yellow 443	26/04/77	Yellow #1	23/09/77	Red-green pt.	22/10/77	Red island
Yellow 839	10/05/77	Yellow #11	25/08/77	Red-green pt.	21/10/77	Red island
Yellow 435	26/04/77	Yellow #1	28/09/77	Red island	17/05/78	Blue #5[b]
Yellow 465	27/04/77	Yellow #2	23/06/77	Blue island	23/09/77	Red-green pt.
Yellow 931	17/05/77	Yellow #11	21/07/77	Yellow pt.	21/10/77	Yellow pt.
Red 081	10/05/77	Red #8	23/09/77	Red-green pt.	11/05/78	Yellow #1[b]
Red 988	05/05/77	Red #8	23/10/77	Green shore	11/05/78	Yellow #1
Green 460	14/05/77	Green #5	23/09/77	Red-green pt.	18/05/78	Yellow shore
Green 483	12/05/77	Green #5	30/10/77	Red-green pt.	12/05/78	Blue #3[b]
Blue 208	10/05/77	Blue #7	21/07/77	Yellow pt.	21/10/77	Red island
Blue 027	16/05/77	Blue #12	22/07/77	Green shore	22/12/77	Blue island

a/ Trap net locations (1977) designated in Figure 2.

b/ Trap net locations (1978) designated in Figure 2.

DYNAMICS OF THE POPULATION

Population Structure

Population estimates —— Schumacher-Eschmeyer (1943) population estimates (Appendix 5, Tables 1 and 2) were made in the springs of 1977 and 1978. The estimated populations of 2,621 and 2,508 (Table 8) represent mature fish most vulnerable to the 1.83 m and 1.22 m trap nets employed. In both years, estimates leveled off by the 14th day of sampling, with a standard error of 11.0 percent for 1977 and 7.7 percent for 1978. Population estimates with maximum standard errors of 10-15 percent are considered reliable (Schumacher and Eschmeyer 1943). The 1977 spring estimate was terminated on May 12 (Appendix 5, Table 1). Rates of recaptures (greater than 20 percent) in succeeding days, led to an underestimation of population size, according to the criteria for this method of population estimate (Schumacher and Eschmeyer 1943).

Analysis of length-frequency data on fish trap netted in the spring of 1977, revealed that northern pike, 40-49.9 cm total length, were more fully represented in catches from 1.22 m trap nets than from 1.83 m nets. Fish of this size comprised 26.8 percent of total catch from 1.22 m trap nets (Fig. 6) as compared to 20.5 percent of catch from 1.83 m nets and 22.2 percent of total combined catch from both types of nets (Fig. 6). This 4.6 percent increase was applied to the estimated population size for 1977 and thus, increased the estimate by 121 individuals to 2,742 total.

Size composition —— Northern pike, 50-59.9 cm long, predominated in

Table 8 . Spring population estimates (Schumacher - Eschmeyer), standard error of the estimates, and confidence limits for Savanne Lake northern pike captured with trap nets, 1977 and 1978.

Year	Population estimates	Standard error	95% confidence limits
1977	2621 2742[a]	289	± 659
1978	2508	194	± 403

[a] Total is adjusted to 1.22 m trap net catch ratio.

the total catch. This size class comprised 44 percent of spring trap net catches (Fig. 6), 40 percent of angling catches in 1977 and 1978 (Fig. 22), and 37.8 percent of the combined gill net catches from 1976 to 1978 (Fig. 6). Fish greater than 60 cm total length made up 36, 40 and 37 percent of the spring trap net, angling,and gill net catches respectively. Fish less than 50 cm total length, comprised only 20-27 percent of the total catch for each of the sampling methods.

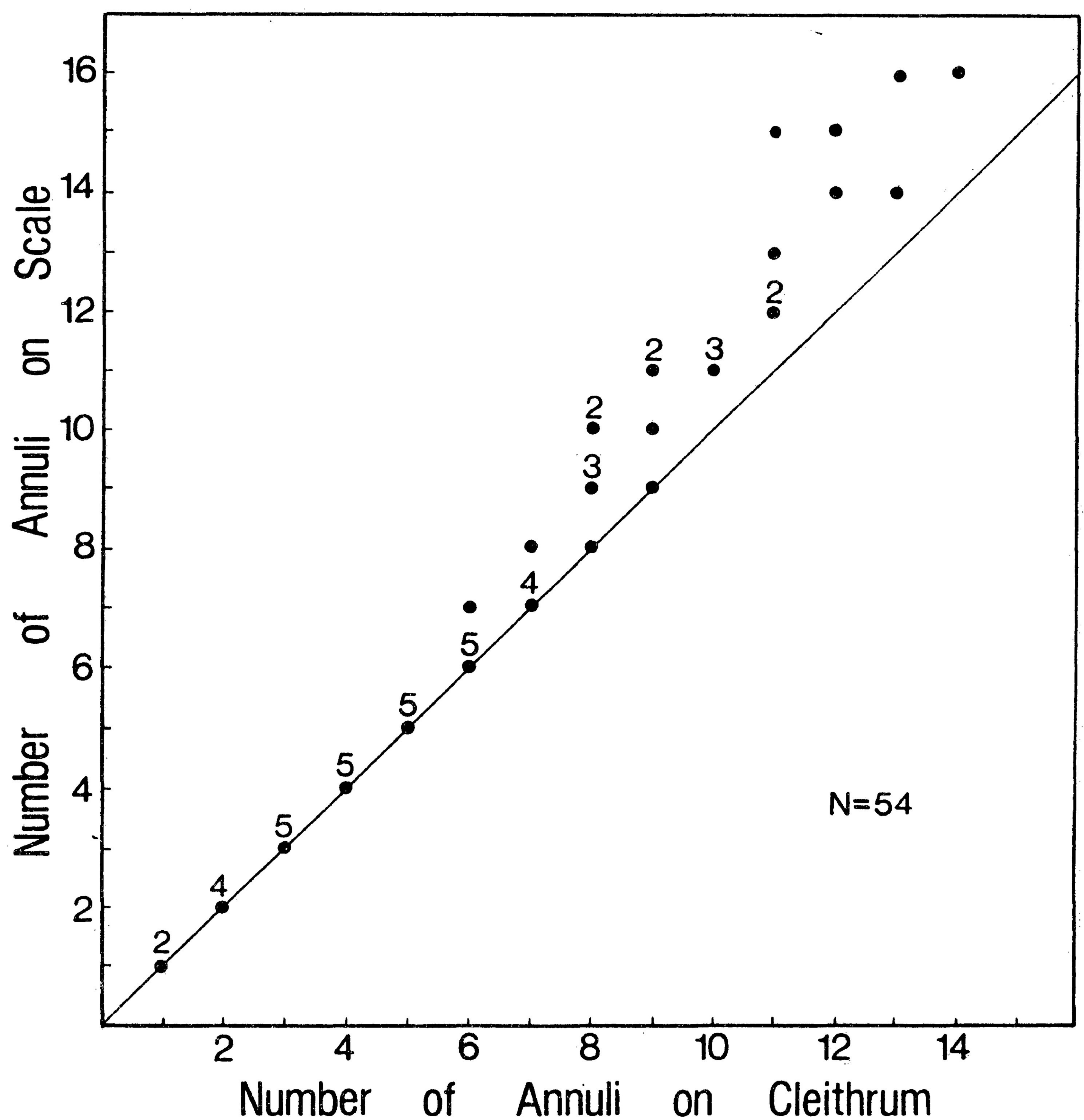
Yearly spawning success, resulting in the formation of dominant age and size classes, is reflected in population data. Length-frequency distributions, based on spring trap net catches for 1977 and 1978 (Fig. 6), represent that portion of the spawning population (greater than 45 cm total length) most vulnerable to 1.22 m and 1.83 m trap nets. Sandhu (1979) found similar trap net selectivity for walleyes larger than 30 cm in Savanne Lake. Several attempts were made to assess the actual population structure. Gill nets of various lengths and constructions (Appendix 3, Table 1) were used to sample all the important lake habitats in June 1976, June 1978, and again in September 1978. The length-frequency distribution of gill netted pike (Fig. 6) was similar to those for spring trap netted (Fig. 6) and angler-caught fish for the 1977-78 seasons (Fig. 22). Only fish greater than 45-50 cm total length were well represented. Strong recruitment of size classes greater than 50 cm to the sampling gear continued throughout the study. Apparently, smaller fish were not fully vulnerable to this gear.

Age composition — Age composition was determined by subsampling

235 fish from the total caught in 1977 and 1978. The resulting age class structure, weighted mean lengths and mean ages reflect only the mature population vulnerable to sampling in each study year (Tables 9 and 10). Individual fish in the subsample were aged by examination of both scales and cleithra. Cleithra provided a more reliable structure for estimating ages of all sizes of pike especially older fish, since true annulus formation on cleithra could be more accurately determined than on scales. Age determination, based on scale samples, agreed closely with those from cleithra up to age 8. The presence of false checks in the formation of annuli on scales from fish of age 8 and older may have resulted in an overestimation of true age (Fig. 7). Casselman (1975a) reported that scales from muskellunge (Esox masquinongy) older than age 10 in the upper St. Lawrence River had fewer annuli present than in cleithra, and their use underestimated ages of older fish.

In Savanne Lake, age composition of the northern pike population showed stable recruitment, the presence of strong year classes, and the dominance of older age-groups (Tables 9 and 10). Ages 4, 5, 6 and 7, predominated in catches and comprised 82.4 percent and 77.6 percent of estimated populations in 1977 and 1978, respectively. Age 4 fish probably were not fully represented in the total catch for the 1978 spring estimate. In that year, mostly large (1.83 m) trap nets were used in sampling which restricted the catch to fish greater than 45 cm long. The difference in weighted mean lengths and mean ages in 1977 and 1978 (Tables 9 and 10), demonstrate the

Figure 7. The relationship between the number of points interpreted as annuli on scales and on cleithra of 54 northern pike collected in Savanne Lake, Ont., 1977-78. Numbers indicate points representing more than one individual.



Number of Annuli on Scale
Number of Annuli on Cleithrum
N=54

Table 9 . Age structure and respective mean lengths, and weighted mean age and length of the estimated northern pike population vulnerable to sampling gear in Savanne Lake, 1977.

Age	Number	% of estimated population	Mean length (cm)
2	15	0.55	28.1
3	77	2.83	36.4
4	546	19.93	45.4
5	802	29.24	51.1
6	542	19.80	57.1
7	368	13.46	63.7
8	185	6.77	73.2
9	95	3.46	80.7
10	66	2.43	88.6
11	44	1.62	92.6
12	2	0.07	96.0
Mean age 5.75		Mean length 56.4	

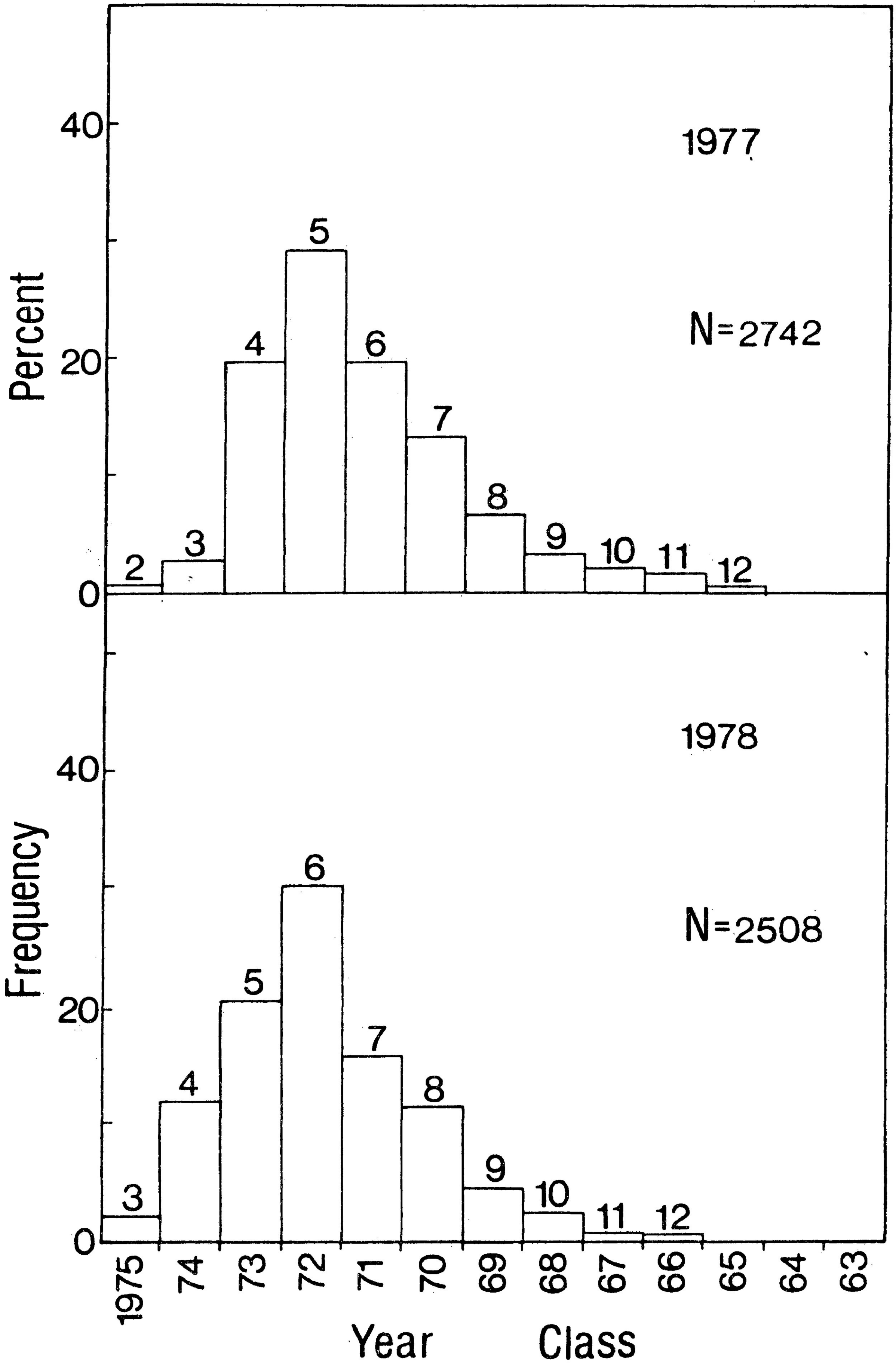
Table 10 . Age structure and respective mean length, and weighted mean age and length of the estimated northern pike population vulnerable to sampling gear in Savanne Lake, 1978.

Age	Number	% of estimated population	Mean length (cm)
2	5	0.02	26.8
3	55	2.20	36.3
4	293	11.67	44.6
5	510	20.37	51.6
6	753	30.04	57.7
7	390	15.59	63.3
8	286	11.43	70.5
9	114	4.57	78.9
10	62	2.49	87.2
11	22	0.89	92.9
12	18	0.73	96.5
Mean age 6.2		Mean length 58.6	

selectivity for larger, older fish in 1978. The dominant age-group in the two years of study was the 1972 year class. It contributed 29 percent to the 1977 catch at age 5 and 30 percent to the 1978 catch at age 6 (Fig. 8). As commonly reported (Scott and Crossman 1973), females predominated in older age-groups. The oldest male sampled was age 10 and 89 cm in length. The oldest fish aged was a 14 year old female, 102 cm in length. Northern pike attain a maximum age of 10 years in Lake Erie (Clark and Steinbach 1959) and Lake Ontario (Wolfert and Miller 1978), 15 years in the lower Saskatchewan River (Rawson 1932), 17 years in northern Wisconsin (Bennett 1962), and 24 to 26 years in arctic lakes of northern Canada (Miller and Kennedy 1948). However, these fish were aged by the scale method and their reported ages may be overestimates.

Sex ratio — A ratio of 1.19 females for every male was determined from a subsample of 235 northern pike captured by angling and gill nets from May 1977 to May 1978. Of 226 fish sexed, 45.6 percent were males, and 54.4 percent were females (Table 11). Toner and Lawler (1969) reported a similar composition (46.2 percent males and 53.8 percent females) for 5,320 fish from Irish lakes. Casselman (1975b) estimated sex ratios of 1.11 to 1.15 females for every male in Ontario populations. In Savanne Lake, males predominated among smaller fish, representing 64.4 percent of fish less than 50 cm total length. Females predominated among larger fish, comprising 77.8 percent of fish over 60 cm and 100 percent of those over 90 cm. Females live longer and achieve a greater maximum size than males

Figure 8. The relative year-class abundance of Savanne Lake northern pike during 1977 and 1978, based on spring population estimates. Values above bars are ages.



1977
N=2742
1978
N=2508
Percent
Frequency
40
20
0
2
3
4
5
6
7
8
9
10
11
12
1975
74
73
72
71
70
69
68
67
66
65
64
63
Year Class

Table 11 . Relative size and number of northern pike identified to sex of a 235 fish subsample caught by angling and gill nets from May 1977 - May 1978 in Savanne Lake, Ontario.

Size interval (cm)	Sample size	Males	Females	Unidentified
0 - 29.9	5	0	0	5
30 - 39.9	30	20	6	4
40 - 49.9	45	27	18	0
50 - 59.9	83	40	43	0
60 - 69.9	40	12	28	0
70 - 79.9	15	2	13	0
80 - 89.9	10	2	8	0
> 90	7	0	7	0
Totals	235	103	123	9

over the whole northern pike range (Scott and Crossman 1973).

Sex ratios of 1.4 and 1.5 males for every female were observed on spawning grounds in 1977 and 1978, respectively. These fail to reflect the true composition of the population since males matured earlier and were present in greater numbers at this time (Table 12). Annual fluctuations in sex ratio do occur (Toner and Lawler 1969) and can result from variations in the growth and strength of different year classes, affecting their differential recruitment to the sampling gear (Kipling and Frost 1970). In several other Ontario populations, ratio estimates were strongly biased by sampling methods used and by the season of capture (Casselman 1975b). The sexes had biannual peaks of availability related to their activity, males being more active and available to capture during the spring and autumn, while females predominated in summer and winter.

Age at maturity — Most males were mature at age 3 and an average total length of 36.3 cm. Most females were mature at age 4 and an average total length of 44.3 cm. The smallest spawning male observed was 31.4 cm long and age 3, while the smallest spawning female was 39.0 cm in length and age 3.

Age and size at maturity of northern pike varies with latitude. This corresponds to a general decrease in growth rate and an increase in longevity for populations as one proceeds northwards (Scott and Crossman 1973). Frost and Kipling (1967) found that length rather than age determined when pike first spawned. Miller and Kennedy (1948) reported 5 to 6 years at first maturity for slow growing populations in Great Bear Lake. In southern Canada and the northern

Table 12. Sex ratios, relative size, and numbers of northern pike identified to sex which were vulnerable to trap nets during spring runs in 1977 and 1978 in Savanne Lake.

Size interval (cm)	1977 Sample size	1977 Male	1977 Female	1978 Sample size	1978 Male	1978 Female
0 - 29.9	0	0	0	0	0	0
30 - 39.9	6	6	0	5	4	1
40 - 49.9	121	82	39	85	72	13
50 - 59.9	210	130	80	250	165	85
60 - 69.9	62	21	41	164	79	85
70 - 79.9	14	5	9	32	7	25
80 - 89.9	12	5	7	20	7	13
> 90	3	0	3	5	0	5
Totals	428	249	179	561	334	227

Male/female ratio = 1.4 : 1

Male/female ratio = 1.5 : 1

United States, females mature at 2 to 4 years and males at 2 to 3 years of age (Buss 1961).

Length-Weight Relationship

The length-weight relationship (sexes combined) of Savanne Lake northern pike, based on measurements of 235 fish sampled in 1977 and 1978, is as follows:

(1) $\text{Log } W = -5.1321 + 2.9611 \ (\text{Log } L)$

where: W = weight in gm,

L = total length in mm,

$r = 0.985$.

Length-weight relationships for females (2) and males (3) respectively are:

(2) $\text{Log } W = -5.477 + 3.0739 \ (\text{Log } L)$

where: $r = 0.986$.

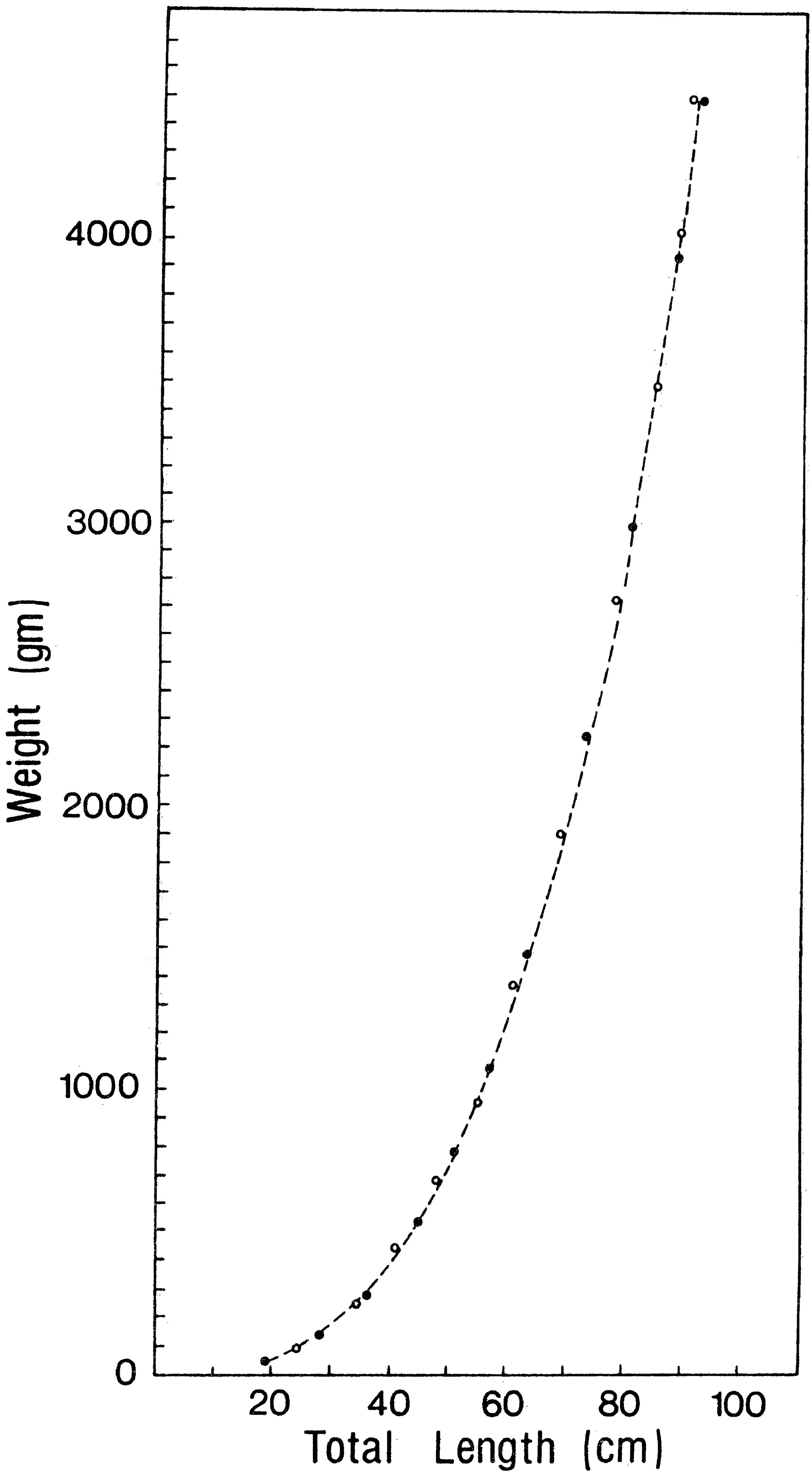
(3) $\text{Log } W = 5.0487 + 2.9313 \ (\text{Log } L)$

where: $r = 0.988$.

Significant differences were found between intercepts of the length-weight relations of males and females (Covariance, $P < .05$). Hence, females were heavier than males at a given length. Similar differences were noted for northern pike in Lake Erie (Brown and Clark 1965) and Lake Windermere (Johnson 1966).

Good agreement exists between the observed data and the calculated length-weight relationship (Fig. 9). The length-weight relationship for Savanne Lake northern pike is similar to values from other waters (Table 13).

Figure 9. The length-weight relationship for Savanne Lake northern pike, 1977-1978, using calculated data (open circles) and observed data (closed circles).



Weight (gm)
4000
3000
2000
1000
0
20
40
60
80
100
Total Length (cm)

Table 13. Length-weight relationships for northern pike from various waters.

Location	Reference	Formula
		Units: wt(W) = g ; TL = total length (mm) ; FL = fork length (mm) ; SL = standard length (mm)
Savanne Lake, Ontario	Present study	Log W = -5.132 + 2.961 Log TL (Sexes combined) Log W = -5.447 + 3.074 Log TL (Females) Log W = -5.048 + 2.931 Log TL (Males)
Lake Erie, Ohio	Brown and Clark (1965)	Log W = -4.826 + 2.902 Log TL (Females) Log W = -4.579 + 2.779 Log TL (Males)
Lake Ontario, New York	Wolfert and Miller (1978)	Log W = -5.285 + 3.035 Log TL (Sexes combined)
Lac Waswanipi, Quebec	Magnin (1964)	Log W = -4.951 + 2.926 Log FL (Sexes combined)
Lake of the Woods, Minnesota	Carlander (1942)	Log W = -6.208 + 3.066 Log SL (Sexes combined)
Lake Windermere, England	Johnson (1966)	Log W = -5.866 + 3.271 Log FL (Females) Log W = -5.615 + 3.176 Log FL (Males)
Lake Choin, Scotland	Munro (1957)	Log W = -5.406 + 3.077 Log TL (Sexes combined)

Calculated Growth

The largest growth increments in length were attained by both sexes of northern pike during their first year of life (Table 14). Growth continued rapidly until age 4 by which time, both sexes were mature. Although yearly length increments declined overall with increasing age, weight increased with age following sexual maturity (Table 15). Females at all ages were larger than males and grew more rapidly, except at ages 2 and 10, when mean length increments were similar (Tables 14 and 16). The more rapid growth of female northern pike in various waters, especially in northern areas of their distribution, has been established (Scott and Crossman 1973). Exceptions to this pattern were noted by Miller and Kennedy (1948), Balon (1965) and Mann (1976), who found no difference in growth rates between sexes. Healey (1956) reported that growth rates were similar in young fish but females grew more rapidly than males as age increased.

Overall, northern pike in Savanne Lake are slightly below the growth average for Ontario (Devitt 1958) and Minnesota (Kuehn 1949) waters (Table 17) but grow considerably faster than northern pike in Waskesiu Lake, Saskatchewan (Rawson 1932). Average calculated lengths at age one are comparable to those for northern pike in Lake Ontario (Wolfert and Miller 1978), Wisconsin (Van Engel 1940) and Ontario inland lakes (Devitt 1958). Considerable latitudinal variation in growth occurs over the entire range of northern pike distribution in North America and results from differences in the length of growing seasons, water temperatures and food availability

Table 14 . Comparison of mean calculated lengths, observed mean lengths, and mean growth increments in cm for male, female, and combined samples of northern pike from Savanne Lake in 1977-78. Sample size appears in parenthesi

	Ages in years													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
A. Combined males and females (235)														
Mean cleithral calculated length[a]	24.4	35.1	42.2	48.9	55.1	62.0	69.3	78.2	85.1	89.6	92.6			
Mean scale calculated lengths[a/b]	18.1	35.5	45.4	53.7	60.6	66.7	73.9	78.5	84.0	89.1	93.5			
Mean observed length	19.8	28.1	36.4	45.4	51.0	57.1	63.7	73.2	80.7	88.6	92.6	96.3	101.6	102.
Mean growth increment[a]	24.4	10.7	6.7	5.5	4.9	4.9	4.2	4.5	3.5	2.3	1.7			
B. Females (125)														
Mean cleithral calculated length[a]	25.6	36.4	43.7	50.3	56.1	63.2	70.2	78.9	86.5	90.1	92.6			
Mean observed length	22.4	28.9	36.4	45.5	51.4	57.3	64.6	73.4	82.9	89.4	92.6	96.3	101.6	102.
Mean growth increment[a]	25.6	10.7	7.0	5.7	5.1	5.0	4.4	4.6	3.6	2.3	1.6			
C. Males (110)														
Mean cleithral calculated length[a]	22.7	33.5	40.5	47.1	52.9	58.9	65.2	74.2	78.0	83.9				
Mean observed length	19.1	27.6	36.3	45.3	50.7	56.7	60.7	71.5	76.3	83.9				
Mean growth increment[a]	22.7	10.8	6.5	5.2	4.4	4.3	2.9	3.4	2.9	2.4				

a/ Represents weighted means.

b/ Number of fish = 40.

Table 15. Mean observed weights (grams) of 200 male, 250 female, and combined sample of northern pike at various ages from Savanne Lake in 1977-78. Mean weight increments are given for the combined sample.

	Ages in years											
	1	2	3	4	5	6	7	8	9	10	11	12
Mean observed weight of females	59	137	266	529	786	1074	1548	2291	3346	4207	4486	5230
Mean observed weight of males	43	127	285	546	757	1053	1286	2080	2512	3317		
Mean observed weight combined	46	131	282	544	771	1071	1485	2235	2992	3938	4486	5230
Mean weight increment	46	85	151	262	227	300	414	750	757	946	548	744

Table 16 . Calculated total lengths (cm) at the end of each year of life based on cleithral measurements of male (M) and female (F) northern pike of various age-groups from Savanne Lake in 1977-78.

			Year of life										
Age-group	Sex	Number of fish	1	2	3	4	5	6	7	8	9	10	11
1	M	1[a]	19.1										
	F	0	-										
2	M	8[a]	20.0	27.6									
	F	4[a]	22.4	28.9									
3	M	25	22.2	30.5	36.3								
	F	13[a]	23.5	31.1	36.4								
4	M	30	23.2	34.3	40.1	45.3							
	F	15	26.7	35.3	40.4	45.5							
5	M	18	23.3	35.9	42.5	46.9	50.6						
	F	28	25.7	37.1	43.3	47.7	51.4						
6	M	14	23.4	35.9	43.8	49.5	53.4	56.7					
	F	20	25.5	37.9	44.7	49.7	53.7	57.3					
7	M	5	25.2	37.3	44.2	50.1	54.3	58.8	60.7				
	F	19	26.3	37.6	46.7	53.5	58.2	61.6	64.6				
8	M	4	19.5	31.1	39.2	47.4	54.8	63.2	67.2	71.5			
	F	11	27.5	40.2	47.8	54.9	61.1	66.6	69.9	73.4			
9	M	3	20.1	34.2	44.6	51.4	60.5	67.5	71.6	74.0	76.3		
	F	4	25.6	38.4	47.4	54.3	62.6	70.1	76.4	80.2	82.9		
10	M	2	20.6	34.4	44.5	51.7	61.8	68.5	72.8	77.1	81.5	83.9	
	F	6	24.2	35.1	44.4	52.0	61.2	71.2	78.0	84.6	87.5	89.4	
11	M	0	-	-	-	-	-	-	-	-	-	-	
	F	5	25.5	36.9	46.1	54.2	62.8	70.7	77.8	83.2	88.1	90.9	92.6
Weighted means	M	110	22.7	33.5	40.5	47.1	52.9	58.9	65.1	74.2	78.0	83.9	-
	F	125	25.6	36.4	43.7	50.3	56.1	63.2	70.2	78.9	86.5	90.1	92.6

[a] Represents immature fish.

Table 17. Mean total lengths (cm) of northern pike from various locations.

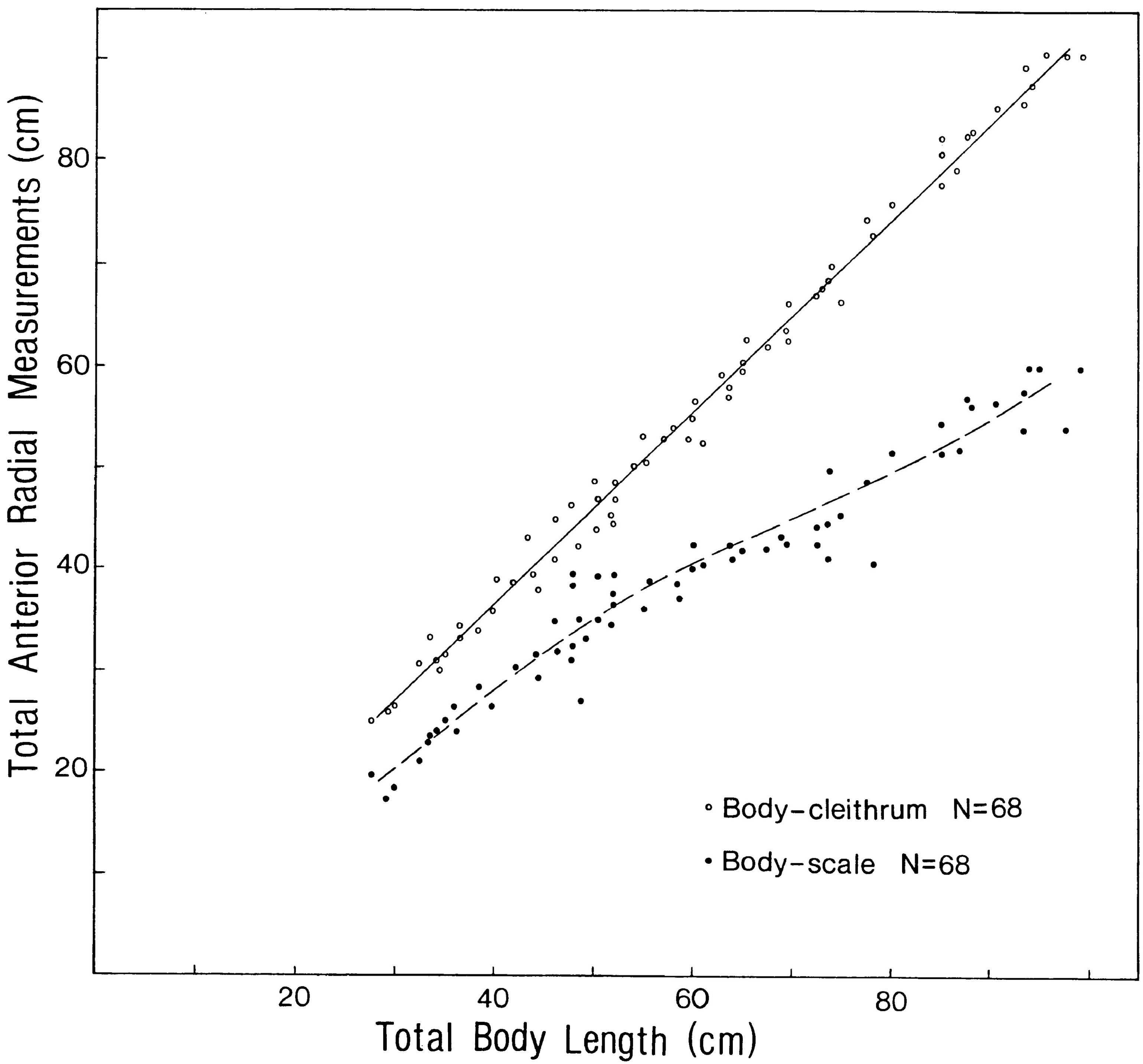
Location and reference	Years of growth completed											
	1	2	3	4	5	6	7	8	9	10	11	12
Lake Ontario (Wolfert and Miller 1978)	24.3	50.6	65.2	71.8	75.4	77.7	78.8	80.7				
Lake Erie (Clark and Steinbach 1959)	29.0	44.7	53.9	60.0	64.8	67.1	72.7	76.5	79.2	83.3		
Wisconsin lakes (Van Engel 1940)	25.4	45.7	58.4	68.6	76.5	83.8	91.4	96.5	101.6	111.8		
Minnesota lakes (Kuehn 1949)	19.8	33.6	45.0	53.6	61.5	68.1	73.7	79.0	84.1	89.2		
Ontario lakes (Devitt 1958)	23.4	36.0	43.9	52.8	58.7	65.8	72.9	80.3	86.4	89.4	90.9	97.0
Georgian Bay, Ont. (Wainio 1966)	39.5	52.7	62.2	68.7	73.1	84.5	87.0	89.5	-	103.5		
Waskesiu Lake, Sask. (Rawson 1932)	16.0	24.8	36.0	43.2	49.5	50.3	55.0	61.0	66.5	71.5	75.5	79.0
Great Bear Lake, N.W.T. (Miller and Kennedy 1948)	9.5	14.6	21.5	28.3	35.6	40.5	46.6	54.5	61.0	67.0	70.0	72.7
Savanne Lake, Ont. (Present study)	24.3	35.1	42.2	49.0	55.1	62.0	69.3	78.2	85.1	89.6	92.6	

(Scott and Crossman 1973). Sandhu (1979) attributed the slow growth of walleyes in Savanne Lake to chemical characteristics of lakes in this region of the Canadian Shield (R.A. Ryder, pers. comm.) and to the high density of walleyes relative to available food. Similar factors may also limit growth of northern pike in this lake.

Both scales and cleithra from sampled northern pike were examined but cleithra were more suited to calculation of the body-calcified tissue relationship. A comparison of cleithrum and scale measurements with length of fish (Fig. 10) shows that the body-cleithrum relationship is linear over the entire size range of fish examined, while the body-scale relationship is curvilinear. This indicates an increasing allometry in growth patterns of scales when compared to the body length of larger individuals. A curvilinear body-scale relationship was also found in several other studies of northern pike (Miller and Kennedy 1948; Oliva 1956; Frost and Kipling 1959; Casselman 1978; Harrison 1978). The determination of a linear body-cleithrum relationship in the present study agrees with similar findings for northern pike (Casselman 1974b and 1978) although slight curvilinearity in this relation has also been noted (Casselman and Harvey 1975). While growth of the cleithra and scales relative to that of the body follow similar seasonal patterns, growth rates of cleithra more closely parallel linear body growth throughout the entire annual cycle (Casselman 1978).

Ideally, the body-cleithrum relationship should be constructed from samples collected at the cessation of growth when the annulus

Figure 10. Scatter diagram of total fish length (cm) plotted against total anterior cleithral radius (cm) and total anterior scale radius (cm) for northern pike in Savanne Lake, Ont., May 1977-May 1978. Total anterior cleithral radial measurements are given at 10X magnification while total anterior scale radial measurements appear at 40X magnification.


Total Anterior Radial Measurements (cm)
20
40
60
80
Total Body Length (cm)
20
40
60
80
◦ Body-cleithrum N=68
• Body-scale N=68

forms. Sampling time in the seasonal growth cycle is known to greatly affect the body-calcified tissue relationship (Casselman 1978). The greatest discrepancies between growth as estimated from cleithra and actual body growth occur in samples taken during the rapid growth period, especially in younger, more rapidly growing members of the population. In an extensive study of the seasonal dynamics of calcified tissue growth and its relation to body growth in two Ontario northern pike populations, Casselman (1978) observed that both scales and cleithra grew significantly faster than the body during the season of most rapid growth (midspring to midsummer). These calcified tissues grew slower than the body during decreasing and slow body growth in late summer and autumn. Linear growth of the body, scales and cleithra virtually ceased from winter until midspring. To balance the seasonal effects of positive and negative allometric growth in cleithra sampled during the present study, a body-cleithrum relationship was determined from equal numbers of cleithra collected monthly. In addition, cleithra sampled prior to and during spawning in May 1977 and 1978 were emphasized in the calculations.

A linear regression of total body length (TL) against anterior cleithral radial length (CL) for 235 northern pike produced an overall body-cleithrum relationship as follows:

$$TL = 10.33\ CL + 32.92;\ r = 0.992$$

where body length and cleithrum length are in millimeters. Similar regressions, based on data from 110 male and 125 female pike in the sample, produced body-cleithrum relationships of

$$TL = 10.70\ CL + 15.71 \text{ where } r = 0.992 \text{ for males,}$$

$$TL = 10.15\ CL + 43.77 \text{ where } r = 0.991 \text{ for females}$$

The total body length at each annulus (TL_i) was back-calculated from the proportional relationship (Whitney and Carlander 1956)

$$TL_i = (TL-y)\ (\frac{CL_i}{CL}) + y$$

where CL_i = anterior cleithral radial length (mm) from the origin to annulus "i" and y=intercept of the regression line on the y-axis. Total body lengths at each annulus were also back-calculated from scale measurements of 40 fish in the sample using this same relationship.

Correlation coefficients (r) for each of the calculated body-cleithrum relations are significant ($P<0.05$) and indicate a high degree of linearity in these relationships. Positive intercept values (e.g. 32.92 mm) in the calculated expressions are higher than the range of similar values (9.5 - 20.6 mm) reported by Casselman (1975c) for northern pike. These may have resulted from minor handling damage to the anterior tip of examined cleithra but more likely reflect the lack of small fish in the sample, especially females.

The mean lengths at various ages calculated from scale measurements are significantly larger ($P<0.05$) than those from cleithral measurements (Table 14). This difference is atributed to a greater allometry in growth between scales and body length than between cleithra and body length, even though scale measurements were obtained during the period of minimal growth, just prior to annulus formation in the spring.

The mean calculated lengths from both scales and cleithra are greater than mean observed length at most ages (Table 14). Evidently, an increase in calculated lengths of younger fish from successively older age groups exists (Tables 16 and 18). This "reversed" Lee's phenomenon (Lee 1912) accounts for higher mean values of calculated length than those of observed length. It most likely results from the paucity of small specimens and the dominance of older, larger fish, especially faster-growing and longer-lived females, in the sample from which lengths were back-calculated (Ricker 1975). This difference may also reflect a change in growing conditions incurred in the return of an exploited population to an unexploited state in which growth is slower. Lee's phenomenon is reported in growth studies on exploited northern pike populations based on examination of opercular bones (Frost and Kipling 1959) and scales (Van Engel 1940; Wolfert and Miller 1978). Frost and Kipling (1959) attributed this condition to gill net selection of slower-growing age-groups in the population.

Annual Production and Biomass

Total mean biomass of the mature northern pike population, ages 4 to 12 years, was estimated at 8.69 kg $\cdot$ ha^{-1} for 1977-78. Annual production for the same period was 2.76 kg $\cdot$ ha^{-1} $\cdot$yr^{-1}. The P/$\bar{B}$ ratio (turnover ratio of biomass) was calculated at 0.276.

Figure 11. The age-length relationship for Savanne Lake northern pike, 1977- 1978, using total cleithral calculated length (solid line) and total observed length (broken line) in cm.

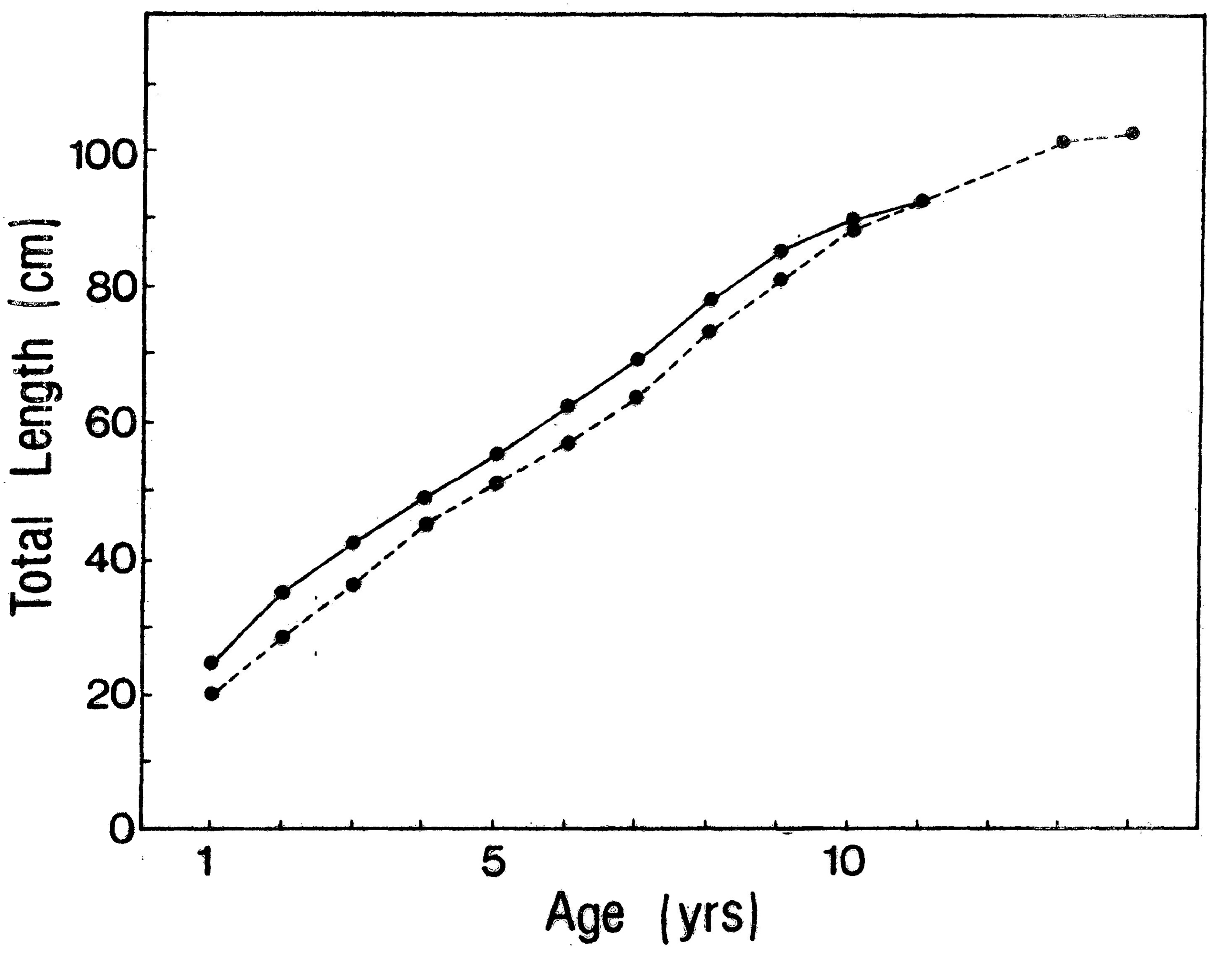

Total Length (cm)
0
20
40
60
80
100
Age (yrs)
1
5
10

Table 18 . Calculated total lengths (cm) at the end of each year of life based on scale measurements of both male and female northern pike of various age-groups from Savanne Lake in May 1977 and 1978.

Age-group	Number of fish	Year of life										
		1	2	3	4	5	6	7	8	9	10	11
1	0											
2	3	18.8	28.0									
3	6	13.2	29.9	35.2								
4	5	20.9	31.8	38.5	44.1							
5	6	18.2	32.6	42.5	47.5	51.7						
6	7	18.2	35.4	48.1	54.2	56.8	59.5					
7	3	22.4	44.4	56.9	60.5	66.7	68.5	70.9				
8	5	20.1	42.8	51.6	58.7	65.2	69.0	71.5	74.6			
9	2	16.6	40.4	53.3	62.9	68.8	74.9	78.6	81.8	82.6		
10	2	16.1	33.8	48.4	60.6	67.2	71.8	76.4	81.0	83.9	86.0	
11	1	12.6	41.0	52.2	60.8	69.4	74.5	81.5	86.1	87.1	91.0	93.5
Weighted means	40	18.1	35.5	45.4	53.7	60.6	66.7	73.9	78.5	84.0	89.1	93.5

Dominant age and size classes, represented by age-groups 5, 6 and 7, contributed 66 percent of annual production and 50 percent of the estimated biomass (Table 19). The greatest contribution to annual production was made by the 1970 year class (ages 7-8), which also had the highest instantaneous growth rate (0.409) for the period. With this exception, mean biomass, production and respective $P/\bar{B}$ ratios decreased with increasing age (Table 19). Sandhu (1979) stated that in a small unexploited system like Savanne Lake, older fish are likely to utilize limited food resources for maintenance and maturation, rather than somatic growth.

The estimated northern pike population (ages 4-12) is characterized by slow growth, low annual mortality and the dominance of older age classes which account for low observed production, biomass and $P/\bar{B}$ ratios. Both annual production (2.76 $kg \cdot ha^{-1} \cdot yr^{-1}$) and estimated total mean biomass (8.69 $kg \cdot ha^{-1}$) are low but within the range of similar values from exploited populations (Table 20). Carlander (1955) reported an average standing crop of 9.55 $kg \cdot ha^{-1}$ for northern pike in fifty-nine North American lakes. Production values for this species range from 0.75 $kg \cdot ha^{-1} \cdot yr^{-1}$ for a Czechoslovakian reservoir (Holcik 1972) to 14.2 $kg \cdot ha^{-1} \cdot yr^{-1}$ for Lake Windermere, England (Kipling and Frost 1970). Although the overall $P/\bar{B}$ ratio (0.276) for Savanne Lake northern pike is within the expected range for fish species from mesotrophic lakes, it is lower than turnover ratios calculated for exploited northern

Table 19 . Annual production and biomass of northern pike in Savanne Lake, 1977-78. Survival rate (S); total mortality rate (A); instantaneous rate of mortality (Z); instantaneous rate of growth (6); weight change factor (K); initial biomass (Wo); mean biomass of stock ($\bar{W}$); annual production (P); annual turnover ratio ($P/\bar{B}$). Values for Wo, $\bar{W}$, P are in kg, unless otherwise specified.

Age-group	S	A = (1-S)	Z=-lnS	G	K = (G-Z)	Wo	$\bar{W}$	$P = G\bar{W}$	$P/\bar{B}$
4 - 5	0.934	0.066	0.068	0.349	+ 0.281	297.02	342.95	119.69	0.347
5 - 6	0.939	0.061	0.063	0.329	+ 0.266	618.34	708.38	233.06	0.327
6 - 7	0.719	0.281	0.329	0.327	- 0.002	580.48	579.90	189.63	0.327
7 - 8	0.777	0.223	0.252	0.409	+ 0.157	546.48	591.71	242.01	0.408
8 - 9	0.616	0.384	0.485	0.292	- 0.199	413.46	374.92	109.48	0.290
9 - 10	0.652	0.348	0.428	0.275	- 0.153	284.24	263.56	72.48	0.274
10 - 11	0.333	0.667	1.099	0.130	- 0.969	259.91	166.44	21.64	0.121
11 - 12	0.409	0.591	0.894	0.128	0.766	197.40	137.90	17.65	0.118
Totals							3165.76	1005.64	
				Totals in $kg \cdot ha^{-1}$			8.69	2.76	

Table 20. 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 northern pike from various waters.

Location	Reference	Age	$\bar{B}$	P	$P/\bar{B}$
Savanne L., Ont.	Present Study	4-12	8.69	2.76	0.276
Minnesota game fish lakes, Minn.	Moyle et al. (1948)	3+[a]	9.0	-	-
Minnesota coarse fish lakes, Minn.	Moyle et al. (1948)	3+[a]	6.1	-	-
North American game fish lakes	Carlander (1955)	-	9.55	-	-
Escanaba L., Wisc.	Kempinger and Carline (1978)	2+[b]	1.9-9.9	-	-
		4+[c]	4.7-10.1	-	-
Murphy Flowage, Wisc.	Snow (1978)	2+[a]	17.5	-	-
Reservoir, Iowa	Carlander (1955)	0+[a]	22.4	-	-
Vistula River, Poland	Backiel (1971)	1-9	1.8-2.4	1.5	0.7
Reservoir, Czechoslovakia	Holcik (1972)	-	-	0.75	0.32
Lake Windermere, England	Kipling and Frost (1970)	2+[a]	6.2[d]	14.2	0.65-0.71
Lake Choin, Scotland	Munro (1957)	0+	5.4	-	-
Pilica River, Poland	Penczak et al. (1976)	0-5	9.2	10.6	1.18

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

b/ = fish of specified age and older during the period 1959-1964.

c/ = fish of specified age and older during the period 1965-1972.

d/ Represents the mean value.

pike from similar environments (Table 20). Turnover ratios for northern pike from other waters range from 0.32 in a Czechoslovakian reservoir (Holcik 1972) to 1.18 in the Pilica River, Poland (Penczak 1976). Crisp et al. (1975) stated that low $P/\bar{B}$ ratios were apparently due to slow growth, especially within populations having higher proportions of older fish, as is the case in unexploited Savanne Lake.

Annual production and biomass were calculated from age, mortality and growth data based on the sequential spring population estimates of 1977 and 1978, using the Ricker (1975) method similarly employed by Sandhu (1979) in estimating annual production and biomass for walleye in Savanne Lake. Initial biomass (Wo) and instantaneous rate of growth (G) were calculated from mean weights of fish (ages 4-12) as observed in the 1977 spring trap net catch.

FEEDING RELATIONSHIPS

A total of 208 northern pike and 254 walleye stomachs, sampled monthly from June 1977 to May 1978, were examined. Winter samples were taken at bimonthly intervals (e.g. January-February; February-March; March-April) due to unfavourable ice conditions in late November and April . In addition, the November-December sample represents the first week of December 1978 since the catch from the same period of the previous year was negligible.

Equal numbers of fish were not caught throughout the calendar year. While open water monthly samples (May to October) reflect observed population numbers and size structures, winter samples are based on much smaller catches of fish, especially walleyes. Poor catches of both species during ice-cover likely resulted from reduced movement and feeding activity of fish at low water temperatures. Data represent the food habits of mature northern pike and walleyes, greater than 35 cm in length. Although angling and gill nets selected against smaller fish of both species, no seasonal differences were seen in the sex and size composition of the catch during spring, summer and fall months, irrespective of method of capture. However, larger female northern pike dominated winter gill net samples. Casselman (1975b) also reported more female than male pike in angling and gill net catches during summer and winter months.

The use of stomach samples probably underestimates the presence of annelids, fish and amphibians, and overestimates crustaceans and most insects (Alexander and Gowing 1976). Oligochaetes are evacuated much faster than fish in trout stomachs (Alexander and Gowing 1976) while the evacuation rates of insects and crustaceans are slower due to the presence of indigestible chitin in their exoskeletons. Small chitinous items (e.g. insect larvae) are gastrically removed at the same rate as digestible organic materials (Kionka and Windell 1972). Differences in evacuation rates had little observable impact on stomach samples from Savanne Lake fish, since invertebrates, except for mayfly nymphs, do not form a major component of the overall diet of both species (Tables 21 and 22). Differences in evacuation rates may account for the general absence of annelids (e.g. leeches) in examined stomachs and the high incidence of ephemeropteran larvae during certain periods.

A quantitative assessment of food habits of northern pike and walleyes could not be made due to a lack of knowledge concerning digestive rates for these species. Information on these rates would have permitted the estimation of daily food rations and allowed for a more accurate interpretation of observed food volumes. Digestive rates and daily rations are reported for both the walleye (Swenson and Smith 1973) and northern pike (Johnson 1966; Seaborg and Moyle 1964; Diana 1979). However, these studies lack an accurate, valid method of estimating fish consumption rates in the field. The present study provides at least, a qualitative assessment of seasonal food habits of northern pike and walleyes.

General Food Habits

Fish predominated in the observed diet of both species, occurring in 80.5 percent of feeding northern pike and 76.6 percent of feeding walleyes (Tables 21 and 22). Identified and unidentified fish contributed 94.5 percent and 90.6 percent of the total food volumes consumed by northern pike and walleyes, respectively (Tables 23 and 24). Apparently, northern pike fed more heavily on fish ($P < 0.5$) and on a greater diversity of identifiable fish prey than did walleyes. Yellow perch (*Perca flavescens*) were the principal prey of both species, followed by unidentified fish remains (larval and otherwise), and shallow water ciscos (*Coregonus artedii*). All three items were more prevalent in walleyes than in northern pike. Burbot (*Lota lota*), northern pike, white suckers (*Catostomus commersoni*), and trout-perch (*Percopsis omiscomaycus*) were found in examined stomachs of both species but appeared to be more important in the diet of northern pike than of walleyes. The contributions of burbot and walleyes, expressed as percentages of the total food volume consumed by northern pike (Table 23), are exaggerated since they represent volumes occupied by single large fish. Both walleyes and darters (*Etheostoma nigrum* and *E. exile*) were identified only in northern pike stomachs.

Invertebrates occurred in 19.5 percent of northern pike and 23.4 percent of walleyes examined (Tables 21 and 22). Invertebrates comprised a slightly greater portion of the total food volume of walleyes (9.4%) than in northern pike stomachs [5.5% (Tables 23 and

Table 21. Percentage frequency occurrence of specific food items consumed monthly by northern pike, caught by angling and gill nets in Savanne Lake, Ont. from June 1977 to May 1978 and including November-December 1978. All percentages are based on fish containing food. Numbers appear in parenthesis.

	June	July	August	Sept.	Oct.	Nov.-Dec.	Jan.-Feb.	Feb.-March	March-April	May	Average % occurrence
Sample Size	20	26	31	27	22	11	11	10	17	33	
% of fish with food	65.0	57.7	41.9	29.6	36.3	36.3	72.7	100.0	64.7	57.6	
Yellow perch	69.2(9)	73.3(11)	46.2(6)	25.0(2)	12.5(1)	50.0(2)	25.0(2)	20.0(2)	18.2(2)	31.6(6)	39.4
Ciscos	0	0	7.7(1)	37.5(3)	37.5(3)	25.0(1)	12.5(1)	10.0(1)	9.0(1)	5.3(1)	11.0
Burbot	0	6.6(1)	0	0	25.0(2)	25.0(1)	12.5(1)	0	0	5.3(1)	5.5
Walleyes	7.7(1)	13.3(2)	7.7(1)	0	12.5(1)	0	0	0	0	10.5(2)	6.4
White suckers	0	6.6(1)	0	0	0	0	12.5(1)	0	0	0	1.8
Northern pike	0	0	7.7(1)	0	12.5(1)	0	0	10.0(1)	0	0	2.8
Trout-perch	0	0	0	0	12.5(1)	0	0	20.0(2)	0	47.4(9)	11.0
Darters	0	0	0	0	0	0	0	20.0(2)	0	0	1.8
Unidentified fish remains	15.4(2)	0	15.4(2)	25.0(2)	0	0	25.0(2)	10.0(1)	9.0(1)	10.5(2)	11.0
Unidentified larval fish	15.4(2)	13.3(2)	0	25.0(2)	0	0	0	0	0	0	5.5
Mayfly nymphs	0	0	15.4(2)	0	12.5(1)	0	12.5(1)	60.0(6)	81.8(9)	0	17.4
Mayfly adults	0	0	0	0	0	0	0	0	0	0	0.0
Crayfish	7.7(1)	6.6(1)	7.7(1)	12.5(1)	0	0	0	10.0(1)	0	0	4.6
Invertebrate remains	7.7(1)	0	7.7(1)	0	0	0	0	0	0	0	1.8

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Table 22. Percentage frequency occurrence of specific food items consumed monthly by walleyes, caught by angling and gill nets in Savanne Lake, Ont. from June 1977 to May 1978 and including November-December 1978. All percentages are based on fish containing food. Numbers appear in parenthesis.

	June	July	August	Sept.	Oct.	Nov.-Dec.	Jan.-Feb.	Feb.-March	March-April	May	Average % occurrence
Sample size	40	54	36	30	30	5	1	2	9	47	
% of fish with food	57.5	50.0	52.7	53.3	56.7	60.0	0	100.0	55.6	42.6	
Yellow perch	30.4(7)	51.9(14)	42.1(8)	62.5(10)	76.5(13)	33.3(1)	0	50.0(1)	40.0(2)	45.0(9)	49.2
Ciscos	4.3(1)	0	21.1(4)	31.2(5)	11.8(2)	33.3(1)	0	50.0(1)	40.0(2)	10.0(2)	13.6
Burbot	0	0	0	6.3(1)	5.9(1)	0	0	0	0	10.0(2)	3.0
Walleyes	0	0	0	0	0	0	0	0	0	0	0.0
White suckers	0	0	0	6.3(1)	0	0	0	0	0	0	0.8
Northern pike	0	3.7(1)	5.3(1)	0	0	0	0	0	0	0	1.5
Trout-perch	0	0	0	0	0	0	0	0	0	5.0(1)	0.8
Darters	0	0	0	0	0	0	0	0	0	0	0.0
Unidentified fish remains	30.4(7)	30.0(8)	21.1(4)	12.5(2)	11.8(2)	0	0	0	0	10.0(2)	18.9
Unidentified larval fish	13.0(3)	18.5(5)	15.8(3)	0	0	0	0	0	0	0	8.3
Mayfly nymphs	4.3(1)	14.8(4)	0	0	0	33.3(1)	0	0	20.0(1)	50.0(10)	12.9
Mayfly adults	17.4(4)	0	0	0	0	0	0	0	0	0	3.0
Crayfish	0	7.4(2)	0	12.5(2)	0	0	0	0	0	5.0(1)	3.8
Invertebrate remains	26.0(6)	11.1(3)	0	6.3(1)	0	0	0	0	0	15.0(3)	9.8

Table 23. Percentage of total monthly food volumes for specific food items consumed by northern pike, caught by angling and gill nets in Savanne Lake, Ont. from June 1977 to May 1978 and including November-December 1978. Individual volumes (ml) are expressed in parenthesis.

	June	July	August	Sept.	Oct.	Nov.-Dec.	Jan.-Feb.	Feb.-March	March-April	May	Average % of total food volume
No. of fish with food	13	15	13	8	8	4	8	10	11	19	
Total food volume (ml)	92.5	74.0	107.2	26.9	351.1	544.0	155.1	81.7	88.4	451.5	
Yellow perch	58.9(55)	70.0(52)	41.5(45)	34.5(9)	3.1(11)	1.2(7)	5.9(9)	23.8(19)	17.8(16)	24.3(110)	16.8
Ciscos	0	0	20.3(22)	29.0(8)	38.3(135)	0.5(3)	1.3(2)	13.4(11)	1.1(1)	11.7(53)	11.9
Burbot	0	1.4(1)	0	0	17.1(60)	98.4(535)	59.9(93)	0	0	6.2(30)	36.4
Walleyes	16.2(15)	16.0(12)	8.4(9)	0	35.8(126)	0	0	0	0	31.5(142)	15.3
White suckers	0	5.4(4)	0	0	0	0	30.4(47)	0	0	0	2.6
Northern pike	0	0	8.4(9)	0	2.3(8)	0	0	17.4(14)	0	0	1.6
Trout-perch	0	0	0	0	3.1(11)	0	0	15.9(13)	0	24.7(112)	6.7
Darters	0	0	0	0	0	0	0	3.7(3)	0	0	0.2
Unidentified fish remains	15.8(15)	0	15.9(17)	9.7(3)	0	0	1.9(3)	1.2(1)	5.1(5)	1.2(5)	2.4
Unidentified larval fish	2.7(3)	5.8(4)	0	7.3(2)	0	0	0	0	0	0	0.8
Mayfly nymphs	0	0	1.9(2)	0	0.3(1)	0	0.6(1)	20.4(17)	76.0(67)	0	4.5
Mayfly adults	0	0	0	0	0	0	0	0	0	0	0.0
Crayfish	5.4(5)	1.4(1)	3.4(4)	19.5(5)	0	0	0	3.1(3)	0	0	0.9
Invertebrate remains	1.0(1)	0	0.2(1)	0	0	0	0	1.0(1)	0	0	0.1

Table 24. Percentage of total monthly food volumes for specific food items consumed by walleyes, caught by angling and gill nets in Savanne Lake, Ont. from June 1977 to May 1978 and including November-December 1978. Individual volumes are expressed in parenthesis.

	June	July	August	Sept.	Oct.	Nov.-Dec.	Jan.-Feb.	Feb.-March	March-April	May	Average % of total food volume
No. of fish with food	23	27	19	16	17	3	0	2	5	20	
Total food volume (ml)	133.2	143.3	180.3	220.3	208.8	42.8	0	4.5	23.8	279.6	
Yellow perch	28.2(38)	59.7(86)	48.9(88)	48.7(107)	78.8(165)	42.9(18)	0	77.8(4)	71.0(17)	58.1(162)	55.3
Ciscos	27.0(36)	0	29.4(53)	31.8(70)	9.4(20)	50.7(22)	0	22.2(1)	16.8(4)	17.3(48)	20.5
Burbot	0	0	0	4.8(11)	5.1(11)	0	0	0	0	10.0(28)	3.9
Walleyes	0	0	0	0	0	0	0	0	0	0	0.0
White suckers	0	0	0	1.8(4)	0	0	0	0	0	0	0.3
Northern pike	0	1.5(2)	8.9(16)	0	0	0	0	0	0	0	1.5
Trout-perch	0	0	0	0	0	0	0	0	0	2.7(8)	0.6
Darters	0	0	0	0	0	0	0	0	0	0	0.0
Unidentified fish remains	7.5(10)	18.1(26)	10.5(19)	7.0(15)	6.8(19)	0	0	0	0	1.1(3)	7.5
Unidentified larval fish	5.3(6)	3.2(5)	2.3(4)	0	0	0	0	0	0	0	1.2
Mayfly nymphs	0.8(1)	6.3(9)	0	0	0	6.4(3)	0	0	12.2(3)	9.2(26)	3.3
Mayfly adults	10.6(14)	0	0	0	0	0	0	0	0	0	1.1
Crayfish	0	2.1(3)	0	5.0(11)	0	0	0	0	0	0.7(2)	1.3
Invertebrate remains	21.6(28)	9.1(13)	0	0.9(2)	0	0	0	0	0	0.8(2)	3.7

24)]. Walleyes also fed on a greater diversity of invertebrates than northern pike. Mayfly nymphs of the families Ephemeridae (*Hexagenia sp.* and *Ephemera sp.*), Heptageniidae (*Stenonema sp.*) and Baetidae (*Caenis sp.*) commonly occurred in the stomachs of both fish. Mayfly nymphs (especially Ephemeridae and Baetidae), observed in greater numbers, represented a slightly larger portion of the total food volume of northern pike than of walleyes. Crayfish (*Orconectes virilis*), both young-of-the year and adults, appeared to be more important in the walleye diet. Leeches (Glossiphoniidae and Erpobdellidae) and back swimmers (Notonectidae), though present, were insignificant to the total observed diet of both species. A variety of other invertebrates including adult and sub-imago mayflies, dragonfly nymphs (Odonata) and pupal midges (Chironomidae) were found only in walleye stomachs.

Adult northern pike are generally described as carnivorous. Although fish comprise over 90 percent of the seasonal diet (Scott and Crossman 1973; Toner and Lawler 1969), adults do feed on a variety of available vertebrates including frogs, salamanders, mice muskrats, and ducklings. The importance of invertebrate foods, especially micro-crustaceans and insect larvae, in the early diet of young-of-the year northern pike is well documented (Hunt and Carbine 1951; Frost 1954) but invertebrates sometimes contribute significantly to the adult diet (Mongeau 1955; Munro 1957). Carlander (1955) reported some cannibalism among adults, but predation by adults on young-of-the year and subadult northern pike is probably more common (Hunt and Carbine 1951; Franklin and Smith 1963).

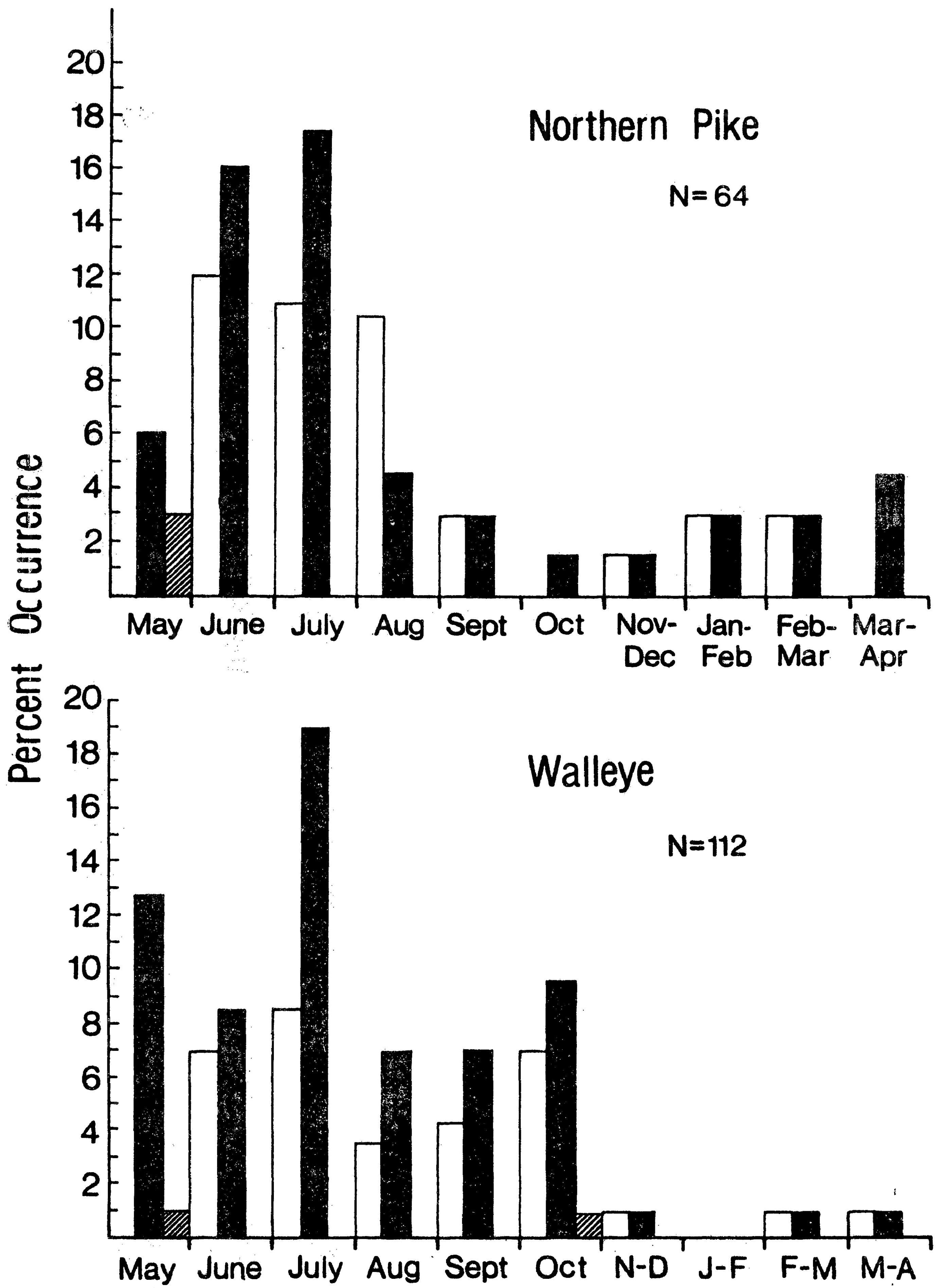
Adult and juvenile walleyes are largely piscivorous, feeding on various prey fishes (Colby et al. 1979) and utilizing any readily available species (Scott and Crossman 1973). Invertebrates, especially mayfly nymphs and amphipods, are important in the diets of young-of-the year, juveniles, and adults during the late spring and early summer in many lakes. Where prey fishes are scarce or absent, adult walleyes may rely entirely on invertebrates (Colby et al. 1979). Other items such as crayfish, frogs, snails, salamanders, and small mammals have also been found in walleye stomachs (Scott and Crossman 1973). Cannibalism is reported to be extreme amoung young-of-the year in hatcheries (Titcomb 1921) and in nature (Scott and Crossman 1973), if prey of suitable size are not available. Adults are known to feed occasionally on juveniles (Ryder 1977). Chevalier (1973) and Forney (1976) found that cannibalism by adults on young-of-the year in Oneida Lake, New York was a decisive factor in the determination of walleye year class strength in years when larval yellow perch, the major walleye prey, were scarce.

Seasonal Food Habits

Definite seasonal changes occured in the diets of both northern pike and walleyes, although annual variation in the intensity of feeding was not clearly evident (Tables 21 and 22).

Both predators fed predominantly on yellow perch, especially juveniles [60-110mm in length (Fig. 12)]. Though found in fish sampled from all months, juvenile perch were most numerous in spring and summer samples. Their reduced occurrence in stomachs during winter reflects the smaller number of predators sampled at this time (Fig. 12). Juveniles formed the principal food of walleyes caught during post-spawning feeding activity in late May and during the period from late July to October. They predominated in the observed pike diet in late June and July, but were also important during late May. The high spring and summer incidence of juvenile perch in both northern pike and walleyes corresponds to their reported presence at this time in the shallows (Falk 1971). Both juvenile and adult perch are known to school in open water during the day while at dusk, schools disperse and fish move inshore, becoming inactive and demersal (Hasler and Villemonte 1953; Falk 1971; Engel and Magnuson 1976). They are vulnerable to northern pike predation during daylight hours when both species are active in shallow areas. Yellow perch, because of their diurnal activity pattern, are probably protected from daytime predation by walleyes, which are normally crepuscular or nocturnal feeders (Scott and Crossman 1973). Ali et al. (1977) proposed that the classic predator-prey relationship of walleye and yellow perch is based on the photoreceptor and visual pigment differences between the two species. Walleyes make feeding movements onto shallow, rocky shoals and littoral areas at night

Figure 12. The percentage frequency occurrence of young-of-the year (unshaded), juvenile (shaded), and adult yellow perch (striped) observed in adult northern pike and walleye stomachs, sampled by angling and gill nets from Savanne Lake, Ont., 1977-78.


Percent Occurrence
Northern Pike
N=64
20
18
16
14
12
10
8
6
4
2
May
June
July
Aug
Sept
Oct
Nov-
Dec
Jan-
Feb
Feb-
Mar
Mar-
Apr
Walleye
N=112
20
18
16
14
12
10
8
6
4
2
May
June
July
Aug
Sept
Oct
N-D
J-F
F-M
M-A

(Carlander and Cleary 1949). These movements are inversely proportional to ambient subsurface illuminations (Ali et al. 1977). Adult and sub-adult walleyes are negatively phototactic because they possess a tapetum lucidum in the retina of the eye (Moore 1944; Scherer 1976). Since yellow perch lack such morphological adaptations to low intensity light, they are restricted primarily to daylight conditions, although they are reported to exhibit a bimodal feeding pattern which peaks during twilight hours of dawn and dusk (Hasler and Villemonte 1953; Ali et al. 1977). The presence of both species on rocky shoals and shallows during twilight, places yellow perch at a visual disadvantage and leaves them more vulnerable to walleye predation (Ali et al. 1977; Ryder 1977). Juvenile perch are also vulnerable at this time to predation by northern pike, which are active in littoral areas during twilight hours (Lawler 1969; Malinin 1969; J. M. Casselman, unpublished data). Since pike are visual feeders but lack retinal adaptations to lower light intensities, they are probably not as efficient predators as walleyes during early morning and late evening periods. Both walleyes (Forney 1966; F. H. Johnson 1969) and yellow perch (Ferguson 1958; Brazo 1973), move into deeper, warmer waters in the fall and winter, as do northern pike. The occurrence of juvenile perch in the fall and winter diets of Savanne Lake northern pike and walleyes confirms their continued association at this time (Fig. 12).

Young-of-the year yellow perch (less than 60 mm long), despite their importance in the northern pike and walleye diet during summer, fall and winter seasons, occurred less frequently than juveniles in most months (Fig. 12). Possibly the smaller sized young-of-the year perch are more readily digested than larger juveniles and the full magnitude of their contribution may be somewhat underestimated. During most fall and winter samples, young-of-the year and juveniles occurred in similar numbers in stomachs of both northern pike and walleyes (Fig. 12). Colby et al. (1979) reported that young-of-the year, when available, are the primary prey of adult and subadult walleyes in north and central regions of their North American distribution. Young-of-the year perch are also a principal food of adult northern pike during summer and fall in North American (Lawler 1965; Seaborg and Moyle 1964; L.D. Johnson 1969; Diana 1979) and European waters (Allen 1939; Frost 1954). Perch fry, approximatly 25 mm in length, were first observed in northern pike and walleyes from Savanne Lake in late June. Swenson (1977) and Kelso and Ward (1977) found that young-of-the year were especially vulnerable to walleye predation at this time, since they were active at night near the surface of open water. Young-of-the year perch move into littoral areas in midsummer (mid-July to early August), corresponding to their development of a typical "barred" colour pattern of adults (Echo 1954; Kelso and Ward 1977). Inshore movements of perch fry probably account for their high incidence in Savanne Lake northern pike in late August (Fig. 12). Perch fry were the major food of walleyes in West Blue Lake, Manitoba (Kelso and Ward 1977) and Lake of the Woods, Minnesota (Swenson 1977) during August and September, although they were less abundant in open waters at night and appeared to be in closer association with the substrate and submerged macrophyte beds.

Adult yellow perch (larger than 110 mm in length) were a minor component in the observed diet of both northern pike and walleyes (Fig. 12). Sampling with various fishing gear throughout this study indicated the presence of few adults in the overall yellow perch population. Both northern pike and walleyes fed upon adult perch during late May. Spawning perch were captured in the shallows with trap nets at this time. The incidence of adult perch in walleye stomachs in late October suggests the association of both species in deeper waters during the fall.

The seasonal incidence of shallow water ciscos in northern pike and walleyes (Tables 21 and 22) coincides with their presence throughout Savanne Lake during fall, winter and spring seasons, as evidenced in experimental gill net catches. Ciscos were most important in the diet of both species during late summer and fall, although they also occurred in stomachs examined during the winter and spring. Shallow water ciscos are known to seek the cooler, well oxygenated waters of lakes in summer, moving into deeper offshore areas as late spring inshore temperatures increase (Scott and Crossman 1973). Such movement may account for the absence of ciscos in the diet of northern pike in late June and July, and in walleyes during July (Tables 21 and 22). As littoral waters cool in late August and September, they return to shallower areas (Fry 1937). Walleyes in Savanne Lake do not appear to utilize ciscos as they do in deeper lakes during summer. Rawson (1957) found that walleyes in Lac la Ronge, Saskatchewan, followed ciscos, their principal food, into deeper waters with the onset of warmer inshore temperatures.

Ciscos remain a primary food of walleyes during summer months in Shebandowan Lake (Ryder and Kerr 1978) and Lac des Mille Lacs, Ont. (R. Hamilton, pers. comm.).

Burbot, which form a minor component of the fish community in Savanne Lake, were of seasonal importance, primarily as juveniles and adults, in the diet of both northern pike and walleyes (Tables 21 and 22). They were fed upon by northern pike from October to February and also in May. They occurred in walleyes in late September, October and May. Like ciscos, adult burbot prefer cool water (less than 18.3°C) and are usually found in the hypolimnion of lakes during summer (Scott and Crossman 1973). Cooler inshore temperatures in fall, winter and early spring allow burbot greater range of movement in Savanne Lake and increase their chance of contact with both northern pike and walleyes. Young-of-the year burbot are known to be abundant and nocturnally active in the shallows (0.5-4 m) during summer months (Ryder and Varmo 1978). Although they were generally absent in northern pike and walleye from Savanne Lake at this time, burbot fry occurred frequently in northern pike sampled during July and August from nearby Henderson and Dexter Lakes (P.J. Colby, unpublished data).

Trout-perch formed a major source of food for post-spawning northern pike in late May, although they also contributed to the northern pike diet in October and March (Table 21). During late May and early June, spawning concentrations of trout-perch were observed at night in shallow waters (less than 1.0 m) at the mouths of small tributaries, the northeast outlet, and along sandy beach areas of

Savanne Lake. Trout-perch, which likely possess a retinal _tapetum lucidum_ (Ryder and Kerr 1978), move into deeper waters (Scott and Crossman 1973) or to shelter in the shallows as daylight increases at dawn (Ryder and Kerr 1978). They become most vulnerable to northern pike predation during these twilight movements. Lawler (1965) found trout-perch to be the primary food of northern pike in Heming Lake, Manitoba, especially during May and June. They are a principal food of walleyes in Lake Winnebago, Wisconsin (Priegel 1969) and the Red Lakes, Minnesota (Magnuson and Smith 1963) but are of minor importance in most other waters (Colby et al. 1979). The only incidence of trout-perch in the Savanne Lake walleye diet was in late May when two specimens were identified in walleye stomachs.

White suckers, despite their abundance as adults and young-of-the year, were not important contributors to the diet of northern pike and walleyes. Young-of-the year suckers schooled in littoral areas during early summer and probably constituted an unknown portion of the unidentified larval fish observed in predator stomachs at this time (Tables 21 and 22). Most studies have indicated that adult white suckers are not an important prey of northern pike and walleyes.

Adult northern pike fed upon young-of-the year and subadult pike in late August, October and February to March. Lawler (1965) noted an increase in the occurrence of northern pike in stomachs of adult fish during the period from October to midwinter. Cannibalism during fall and winter reflects the greater vulnerability of young pike to adult predation following their movement from protected, weedy areas of summer habitation to deeper warmer waters in the fall. L.D. Johnson (1969) found a higher incidence of young pike in stomachs of adults during summer months in Murphy Flowage, Wisconsin. Cannibalism in Lake Windermere, England was found to be minimal with little seasonal variation in its intensity (Frost 1954). Young pike were only identified in walleyestomachs during summer months when they were relatively abundant in littoral areas frequented by feeding walleyes.

Walleyes and darters (Etheostoma nigrum and E. exile) occurred in northern pike stomachs only. Walleyes contributed to the northern pike diet most frequently during spring and summer months but were absent during winter (Table 21). Young-of-the year walleyes were fed upon in late June, July and August, when they actively schooled in shallow waters during daylight. Both adult and subadult walleyes were vulnerable to pike predation in spring months during feeding and post-spawning movements. Darters were identified in pike stomachs in the February-March sample only.

Mayfly nymphs and crayfish were the dominant invertebrates fed upon by northern pike (Table 21). Mayfly nymphs, while absent in late June and July samples, were present in pike during late August, October and January to February. They were most prevalent during late winter samples in February-March, and March-April, occurring in 60 percent and 81.8 percent of pike stomachs examined and comprising, 20.4 percent and 76 percent of total food volumes, respectively (Table 23). This high incidence of Ephemeropteran nymphs, primarily burrowing mayflies (Hexagenia sp. and Ephemera sp.), in the adult northern pike diet at this time is unusual and unique. A review of available literature failed to show a similar occurrence for other studied localities. The greatest occurrence was noted from medium-sized and large northern pike captured in deeper waters (3.0-4.25 m) by gill nets. Ciscos, walleyes, white suckers and yellow perch were also caught in these same areas and were of suitable size to be considered as food items for pike. Northern pike sampled during late June and July in nearby Henderson Lake, and during August in Argon Lake, Ontario, contained substantial numbers of mayfly nymphs (P.J. Colby unpublished data). Both Lawler (1965) and Frost (1954) reported that mayfly nymphs were minor contributors in observed diets of adult northern pike. Lawler (1965) found them in approximately equal frequencies in fish from summer and winter months, while Frost (1954) observed the highest incidence of Ephemeropteran nymphs in pike stomachs in May. Crayfish were observed in the Savanne Lake northern pike diet during late June to late September and again in the February-March sample. Their incidence in pike stomachs during summer and early fall corresponds to yearly peaks in their abundance in littoral areas frequented by feeding pike.

Invertebrates were important in the observed walleye diet during late May, June and July, occurring in 70, 47.7 and 33.3 percent of all stomachs containing food, respectively. Invertebrates appeared to decrease in importance as the summer progressed, signalling a seasonal shift in walleye feeding from invertebrates to more abundantly available fishes (e.g. yellow perch), Mayfly sub-imagoes, primarily

Hexagenia sp., were a major diet component in late May. Their observed emergence as adults in late June, coincides with the incidence of adult and emergent forms in walleye stomachs at this time. Adult mayflies were absent in walleyes during the remainder of the study period. Mayfly nymphs also occurred in walleyes caught in November-December, and March-April samples. Eschmeyer (1950) and Priegel (1965) noted that invertebrate foods became important in the winter diet of walleyes when the availability of prey fish was limited. Young-of-the year crayfish were identified in Savanne Lake walleyes during late July and September. Adult crayfish were found in stomachs in May when walleyes fed heavily on the benthos.

Predator - Prey Relationships

Type of food -- Although dominant food items were present in most or all sizes of feeding northern pike and walleyes examined, important differences in the frequency of their occurrence were noted (Tables 25 and 26).

Yellow perch were found most frequently in small and medium-sized northern pike (25-60 cm long) but were much less evident in larger fish (Table 25). Yellow perch constituted the only food item observed in small pike less than 30 cm in length. Trout-perch, ciscos, burbot, and walleyes occurred in all sizes of northern pike longer than 30 cm. Ciscos, burbot, and walleyes increased in occurrence as the size of pike increased, reaching their highest incidence in fish exceeding 60 cm. Trout-perch were consumed by pike greater than 30 cm. Northern pike were found only in stomachs of adults greater than 45 cm in length.

Table 25. Percentage frequency occurrence of specific food items in relation to relative size of 109 northern pike, caught by angling and gill nets in Savanne Lake, Ontario, 1977 to 1978. Fish with empty stomachs excluded.

	Length Interval (cm)			
Food Species	0-29.9	30-44.9	45-59.9	60 and Over
Yellow perch	100.0	53.3	57.1	28.6
Ciscos	0	6.6	5.4	25.8
Burbot	0	6.6	5.4	8.6
Walleyes	0	6.6	5.4	8.6
White suckers	0	0	3.6	0
Northern Pike	0	0	3.6	2.9
Darters	0	6.6	0	2.9
Trout-perch	0	13.3	10.7	14.3
Unidentified fish remains	0	26.7	12.5	14.3
Unidentified larval fish	0	13.3	7.2	8.6
Mayfly nymphs	0	13.3	21.4	25.8
Crayfish	0	0	3.6	8.6
Invertebrate remains	0	6.6	3.6	0
Sample Size	3	15	56	35

Table 26. Percentage frequency occurrence of specific food items in relation to relative size of 132 walleyes, caught by angling and gill nets in Savanne Lake, Ontario, 1977 to 1978. Fish with empty stomachs excluded.

Food Species	Length interval (cm)						
	0 - 24.9	25 - 29.9	30 - 34.9	35 - 39.9	40 - 44.9	45 - 49.9	50 and Over
Yellow perch	33.3	33.3	60.0	68.0	55.5	58.3	50.0
Ciscos	0	0	0	0	15.5	20.8	50.0
Burbot	0	0	0	0	6.7	4.2	0
White suckers	0	0	0	0	2.2	0	0
Northern Pike	0	0	0	0	2.2	4.2	0
Trout-perch	0	0	0	4.0	0	0	0
Unidentified fish remains	0	20.0	40.0	8.0	17.8	20.8	16.7
Unidentified larval fish	16.7	20.0	40.0	20.0	13.3	8.3	16.7
Mayfly nymphs	33.3	0	0	8.0	17.8	20.8	0
Mayfly adults	0	0	0	4.0	2.2	8.3	0
Crayfish	16.7	0	0	0	8.9	0	0
Invertebrate remains	0	33.3	20.0	4.0	11.1	12.5	16.7
Sample Size	6	10	10	25	45	24	12

Unidentified fish remains (both larval and otherwise) occurred most frequently in stomachs of pike, within a size range of 30-45 cm, and decreased in incidence with increasing fish size. Mayfly nymphs, while absent in pike smaller than 30 cm, increased in occurrence with increasing predator size, reaching their greatest incidence in fish longer than 60 cm. Contrary to these results, both Frost (1954) and Lawler (1965) found the highest incidence of mayfly nymphs in stomachs of small and medium-sized pike. Nymphs were generally absent in fish larger than 60 cm. Crayfish were observed in Savanne Lake northern pike greater than 45 cm in length and appeared more frequently in larger fish. Invertebrate remains (unspecified) were represented in stomachs of pike, 30-60 cm, but were absent in smaller and larger specimens.

Yellow perch occurred in all size groups of walleyes examined but were most prevalent in fish longer than 30 cm (Table 26). Ciscos were found only in walleyes greater than 40 cm in length. Their occurrence increased with increasing fish size, especially in walleyes 50 cm and longer. Burbot, white suckers, and northern pike were also found in stomachs of medium and larger-sized fish (40-50 cm long). Unidentified fish were present in all sizes of walleyes, but were most prevalent in those 30-35 cm in length. Mayfly nymphs occurred in stomachs of the smallest size group and in the 35-50 cm size group. Their incidence increased in fish up to 50 cm. Walleyes, 35-50 cm also fed on both adult and emergent mayflies. Crayfish occurred in fish smaller than 25 cm and of moderate size (40-45 cm). Invertebrates remains were found in all sizes of walleyes longer than 25 cm, especially in smaller fish (25-35 cm).

The occurrence of prominent food items in stomachs of 109 northern pike (greater than 23 cm in length) and 132 walleyes (larger than 15 cm) was expressed as a percentage frequency based on the total number of feeding fish in a given size group (Tables 25 and 26).

Size of food items --- Although large food items were usually found in large fish of both species, most northern pike and walleyes were capable of consuming far larger prey than were normally found in their stomachs (Tables 27 and 28, Fig. 13). Small prey, less than 35 mm long, accounted for over half of the observed totals (Fig. 13). Despite the similar size distribution of prey items in both predators, important differences were found in the length of prey consumed by each species ($P<0.05$, t-test). Though smaller prey (20-35 mm in length) predominated in both northern pike and walleye stomachs, they were more important in the pike diet. These small items, corresponding to observed lengths of larval fishes and mayfly nymphs, were especially prevalent in northern pike larger than 45 cm and in walleyes larger than 40 cm in length (Tables 27 and 28). Walleyes consumed a significantly greater number of prey under 20 mm than did northern pike (Fig. 13). A significantly greater number of medium-sized prey (50-110 mm in length) were also found in walleye stomachs. These were identified as juvenile or subadult fishes, primarily yellow perch and ciscos. Prey items larger than 170 mm and identified as adult

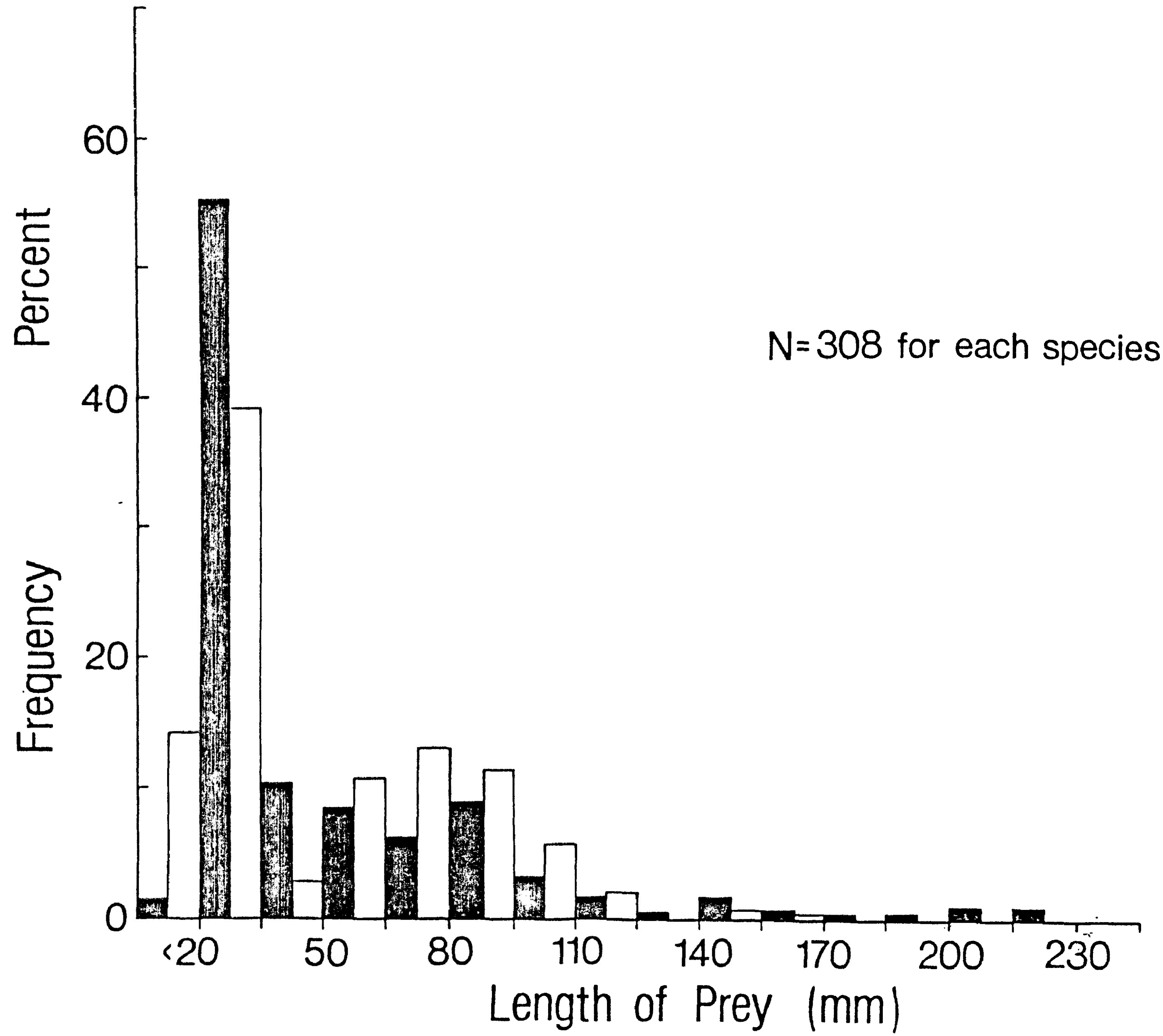
Table 27. The relationship between total length of 109 northern pike and length of prey items found in their stomachs. Pike were sampled by angling and gill nets from Savanne Lake, Ont., 1977-78. Occurrence of prey is expressed as a percentage while numbers appear in parenthesis.

Total length of northern pike (cm)	Length of prey (mm) 0-19.9	20-34.9	35-49.9	50-64.9	65-79.9	80-94.9	95-109.9	110-124.9	125-139.9	140-154.9	155-169.9	170-184.9	185-199.9	200-214.9	over 215	No. of prey
0 - 29.9	0	50.0 (1)	50.0 (1)	0	0	0	0	0	0	0	0	0	0	0	0	2
30 - 44.9	13.6 (3)	13.6 (3)	13.6 (3)	18.2 (4)	9.1 (2)	18.2 (4)	13.6 (3)	0	0	0	0	0	0	0	0	22
45 - 59.9	1.1 (2)	60.2 (112)	6.9 (13)	7.5 (14)	6.5 (12)	10.8 (20)	3.2 (6)	1.6 (3)	0	0.5 (1)	0.5 (1)	0.5 (1)	0.5 (1)	0	0	186
60 and over	0	55.1 (54)	15.3 (15)	8.2 (8)	5.1 (5)	3.1 (3)	1.0 (1)	2.0 (2)	1.0 (1)	4.1 (4)	1.0 (1)	0	0	2.0 (2)	2.0 (2)	98
Totals	5	170	32	26	19	27	10	5	1	5	2	1	1	2	2	308
Mean percent occurrence	1.6	55.2	10.4	8.4	6.2	8.8	3.2	1.6	0.3	1.6	0.7	0.3	0.3	0.7	0.7	

Table 28. The relationship between total length of 132 walleyes and length of prey items found in their stomachs. Walleyes were sampled by angling and gill nets from Savanne Lake, Ont., 1977-78. Occurrence of prey is expressed as a percentage while numbers appear in parenthesis.

Total length of walleyes (cm)	Length of prey (mm) 0-19.9	20-34.9	35-49.9	50-64.9	65-79.9	80-94.9	95-109.9	110-124.9	125-139.9	140-154.9	155-169.9	170-184.9	185-199.9	200-214.9	over 215	No. of prey
0 - 24.9	31.5 (5)	50.0 (8)	12.5 (2)	6.3 (1)	0	0	0	0	0	0	0	0	0	0	0	16
25 - 29.9	44.0 (4)	0	0	12.0 (1)	44.0 (4)	0	0	0	0	0	0	0	0	0	0	9
30 - 34.9	0	0	0	28.6 (2)	57.1 (4)	14.3 (1)	0	0	0	0	0	0	0	0	0	
35 - 39.9	5.7 (2)	22.9 (8)	0	31.4 (11)	22.9 (8)	17.1 (6)	0	0	0	0	0	0	0	0	0	35
40 - 44.9	19.8 (32)	47.5 (77)	3.9 (5)	6.8 (11)	6.8 (11)	8.6 (14)	4.9 (8)	1.2 (2)	0	0.6 (1)	0.6 (1)	0	0	0	0	162
45 - 49.9	1.5 (1)	39.7 (27)	2.9 (2)	10.3 (7)	13.2 (9)	14.7 (10)	13.2 (9)	2.9 (2)	0	1.5 (1)	0	0	0	0	0	68
50 and over	0	9.2 (1)	0	0	36.3 (4)	36.3 (4)	0	18.2 (2)	0	0	0	0	0	0	0	11
Totals	44	121	9	33	40	35	17	6	0	2	1	0	0	0	0	308
Mean percent occurrence	14.3	39.3	2.9	10.7	13.0	11.4	5.6	1.9	0	0.6	0.3	0	0	0	0	

Figure 13. The length-frequency distribution of prey items (mm) observed in 109 northern pike (shaded) and 132 walleye (unshaded) stomachs, sampled by angling and gill nets from Savanne Lake, 1977-78.


Percent
Frequency
60
40
20
0
N=308 for each species
‹20
50
80
110
140
170
200
230
Length of Prey (mm)

and subadult ciscos, walleyes and burbot, were observed only in northern pike stomachs (Fig. 13).

The overall distribution of prey sizes based on body depth or the maximum lateral body width (Tables 29 and 30), closely paralleled the distribution relating body lengths of prey to observed size groups of northern pike and walleyes (Tables 27 and 28). Both species relied to much the same extent on prey having body depths of from 10 to 25 mm (38.1% occurrence in northern pike and 41.6 % occurrence in walleyes). Walleyes consumed a higher percentage of smaller prey items, less than 5 mm in depth, than northern pike. Greater numbers of prey, 5 to 10 mm in depth, were found in northern pike than walleye stomachs. The contribution of prey items with body depths greater than 25 mm in diets of both species was minimal, although northern pike appeared capable of consuming prey of greater overall depth than walleyes (Tables 29 and 30). L. D. Johnson (1969) found that body depth rather than body length of prey critically influenced pike predation in Murphy Flowage, Wisconsin. The maximum body depth of prey that could be swallowed was largely determined by the jaw width of northern pike. L.D. Johnson (1969) observed considerable variation in the closed jaw width of northern pike within the same size group, especially among members of larger size groups.

The average size of consumed prey increased with a corresponding increase in predator size. A similar relationship has been reported in other studies of northern pike (Frost 1954; Nikolsky 1963; Lawler 1965; Diana 1979) and of walleyes (Parsons 1971; Colby et al. 1979).

Table 29. The relationship between total length of 109 northern pike and body depth of prey found in their stomachs. Pike were sampled by angling and gill nets from Savanne Lake, Ont., 1977-78. Occurrence of prey is expressed as a percentage while numbers appear in parenthesis.

Total length of northern pike (cm)	Body depth of prey (mm) 0-4.9	5-9.9	10-14.9	15-19.9	20-24.9	25-29.9	30-34.9	35-39.9	40-44.9	45-49.9	over 50	No. of prey
0 - 29.9	50.0 (1)	50.0 (1)	0	0	0	0	0	0	0	0	0	2
30 - 44.9	12.5 (3)	20.8 (5)	33.3 (8)	29.2 (7)	4.2 (1)	0	0	0	0	0	0	24
45 - 59.9	32.6 (60)	38.5 (72)	11.4 (21)	13.0 (24)	2.7 (5)	0	0.5 (1)	0	0.5 (1)	0	0	184
60 and over	31.6 (31)	37.8 (37)	16.3 (16)	7.1 (7)	2.0 (2)	2.0 (2)	1.0 (1)	2.0 (2)	4.1 (4)	1.0 (1)	1.0 (1)	98
Totals	95	115	39	38	8	2	2	2	5	1	1	308
Mean percent occurrence	30.8	37.3	12.7	22.8	2.6	0.6	0.6	0.6	1.6	0.3	0.3	

Table 30. The relationship between total length of 132 walleyes and body depth of prey found in their stomachs. Walleyes were sampled by angling and gill nets from Savanne Lake, Ont., 1977-78. Occurrence of prey is expressed as a percentage while numbers appear in parenthesis.

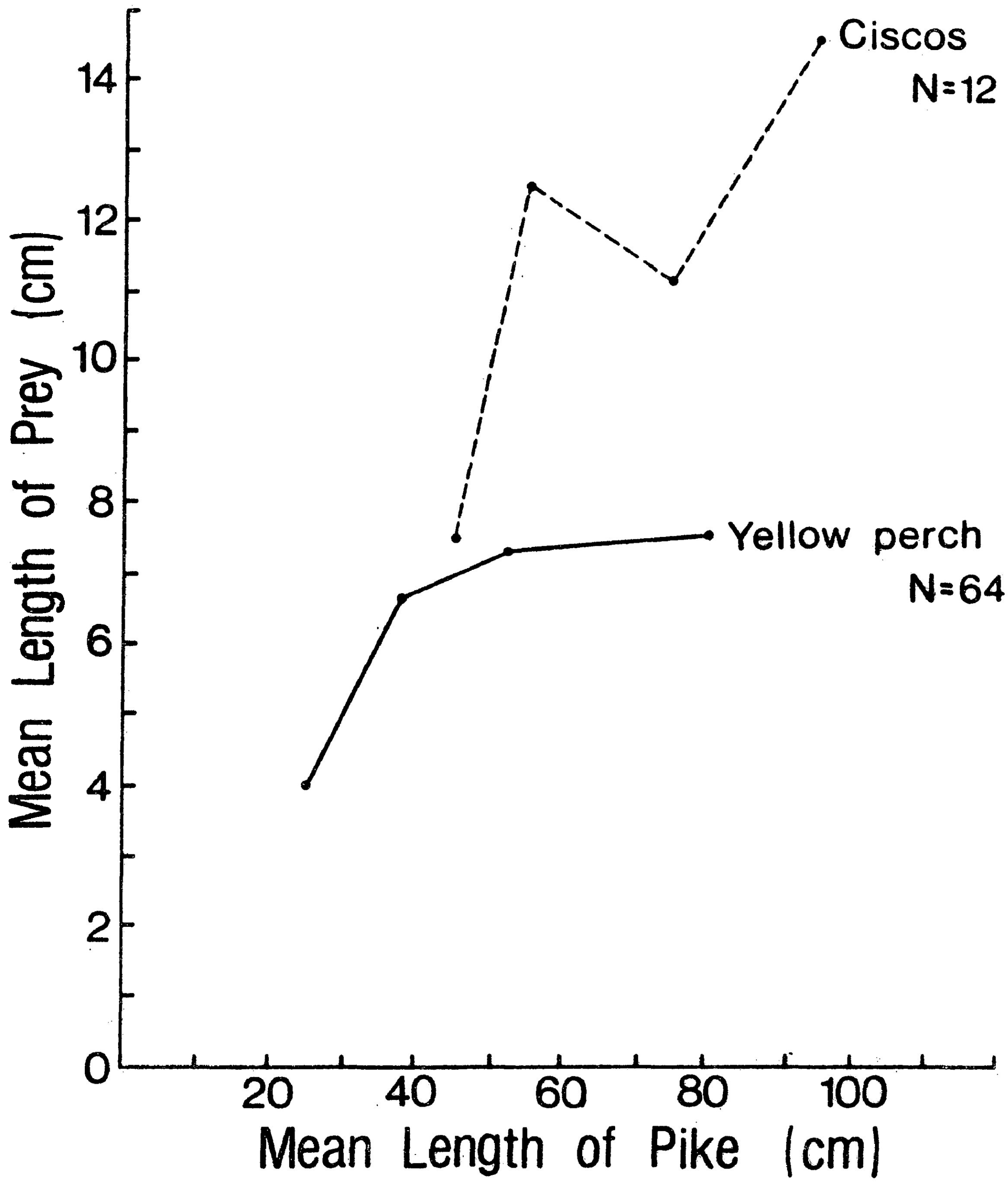
Total length of walleyes (cm)	Body depth of prey (mm)											No. of prey
	0-4.9	5-9.9	10-14.9	15-19.9	20-24.9	25-29.9	30-34.9	35-39.9	40-44.9	45-49.9	over 50	
0 - 24.9	62.5 (10)	25.0 (4)	6.3 (1)	6.3 (1)	0	0	0	0	0	0	0	16
25 - 29.9	33.3 (3)	22.2 (2)	11.1 (1)	33.3 (3)	0	0	0	0	0	0	0	9
30 - 34.9	0	0	57.0 (4)	43.0 (3)	0	0	0	0	0	0	0	
35 - 39.9	20.0 (7)	8.6 (3)	37.0 (13)	28.6 (10)	5.7 (2)	0	0	0	0	0	0	35
40 - 44.9	57.4 (93)	11.7 (19)	11.1 (18)	10.5 (17)	7.4 (12)	1.9 (3)	0	0	0	0	0	162
45 - 49.9	41.2 (28)	1.5 (1)	17.6 (12)	20.6 (14)	13.2 (9)	4.4 (3)	0	1.5 (1)	0	0	0	68
50 and over	0	9.1 (1)	18.2 (2)	27.3 (3)	27.3 (3)	9.1 (1)	9.1 (1)	0	0	0	0	11
Totals	141	30	51	51	26	7	1	1	0	0	0	308
Mean percent occurrence	45.8	9.7	16.6	16.6	8.4	2.3	0.3	0.3	0	0	0	

Larger fish of both species fed on larger prey items in Savanne Lake, notably yellow perch and ciscos, which are available over a greater size range as young-of-the year, juveniles and adults than are other common prey. The mean length of ciscos from examined stomachs increased with the length of both northern pike and walleyes [$P<0.05$, t-test(Figs. 14 and 15)]. The relationship involving consumed yellow perch was less well defined. Although an increase in the mean length of yellow perch in northern pike up to a length of 55 cm was noted, the average length of perch (about 75 mm) for larger fish remained relatively constant (Fig. 14). Lawler (1965) found a positive direct relationship between average length of yellow perch and average length of northern pike examined. In walleyes (Fig. 15), the average length of perch increased from 40 mm in 20 cm walleyes to a peak of 94 mm in fish averaging 42.5 cm. Mean lengths of yellow perch declined to 80 mm in walleyes larger than 50 cm in length.

Owing largely to their greater overall size, northern pike were capable of feeding on a wider range of available prey sizes than walleyes (Fig. 13). Northern pike consumed a greater size range of yellow perch than did walleyes, even though length frequency distributions of perch from both species (Fig. 16) were similar ($P>0.01$, $t = 1.37$). Northern pike fed upon ciscos over a greater range in size (Fig. 17) and at significantly larger average length than did walleyes ($P<0.01$, $t = 9.1$). Ciscos averaged 112.0 mm in length in northern pike and 103.3 mm in walleyes.

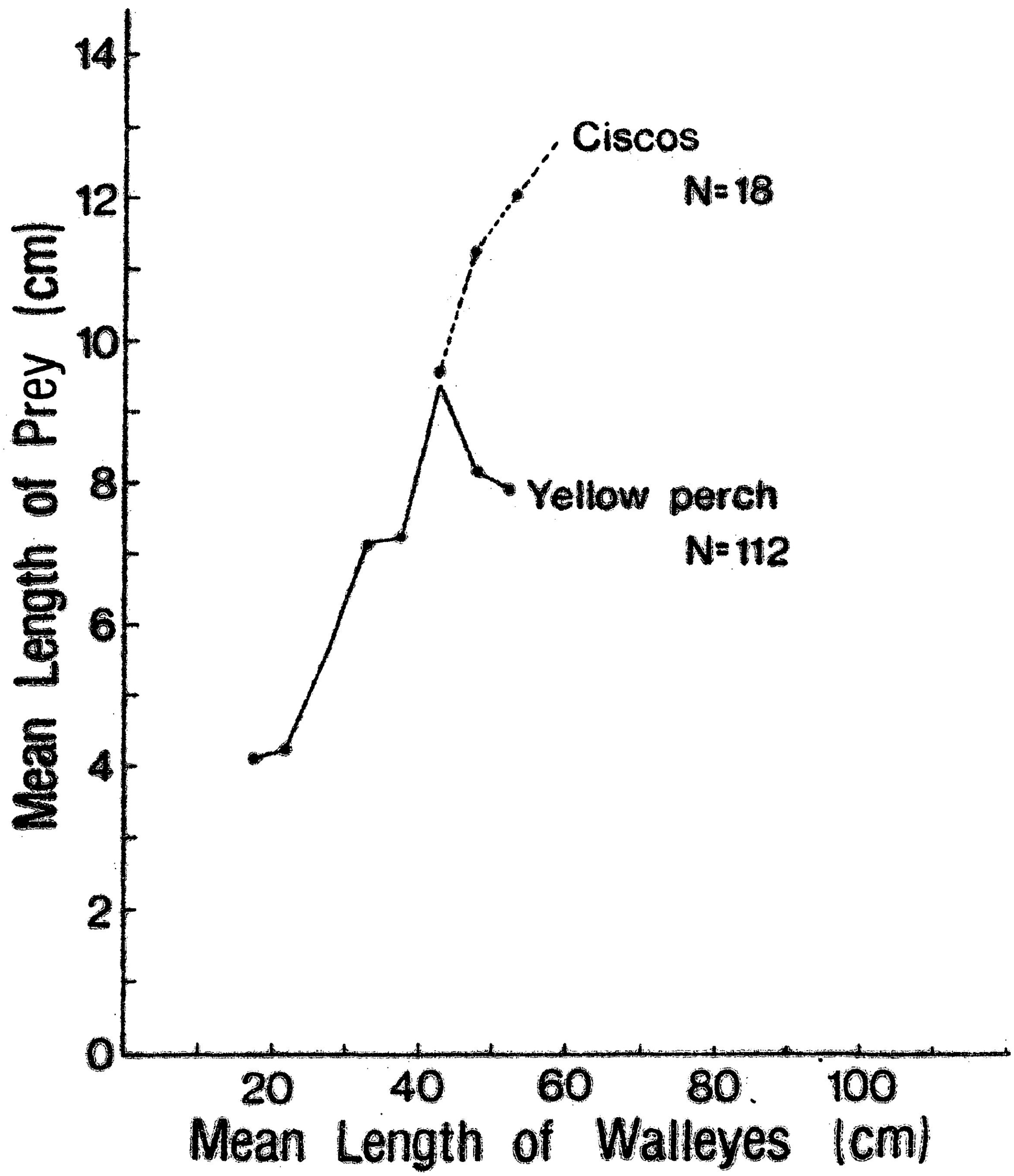
The relationships between predator length and lengths (Tables 27

Figure 14. The relationship between mean lengths of northern pike (cm) and mean lengths of yellow perch and ciscos (mm) found in pike stomachs from Savanne L., Ont., 1977-78.



Ciscos
N=12
Yellow perch
N=64
Mean Length of Prey (cm)
0
2
4
6
8
10
12
14
20
40
60
80
100
Mean Length of Pike (cm)

Figure 15. The relationship between mean lengths of walleyes (cm) and mean lengths of yellow perch and ciscos (mm) found in walleye stomachs from Savanne Lake, Ont., 1977-78.



Ciscos
N=18
Yellow perch
N=112
0
2
4
6
8
10
12
14
Mean Length of Prey (cm)
20
40
60
80
100
Mean Length of Walleyes (cm)

Figure 16. The length-frequency distribution of yellow perch (mm) observed in 43 northern pike (striped) and 65 walleye (shaded) stomachs, sampled by angling and gill nets from Savanne Lake, Ont., 1977-78. Northern pike were 23-95 cm in length while walleyes were 15-54 cm long.

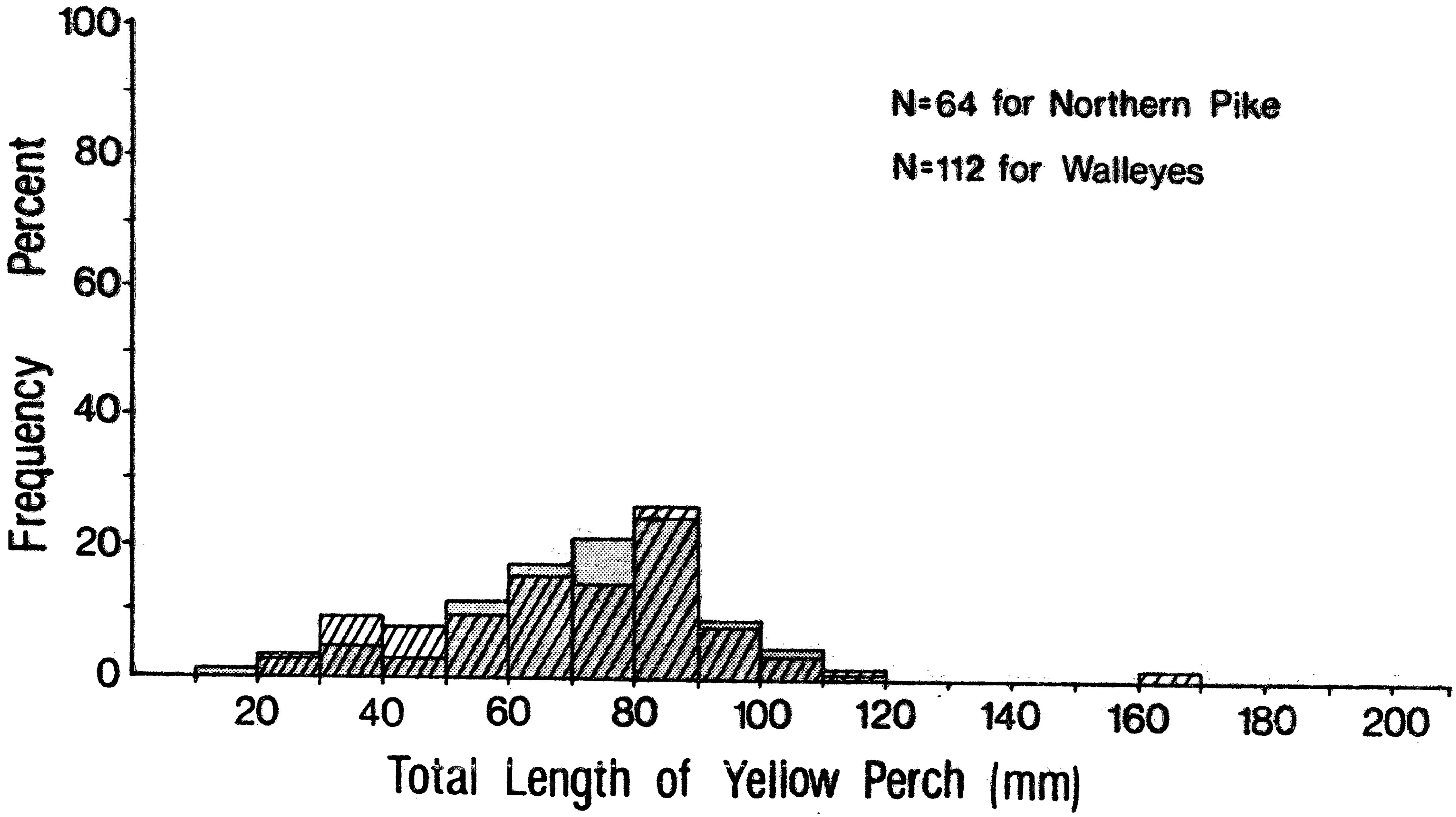
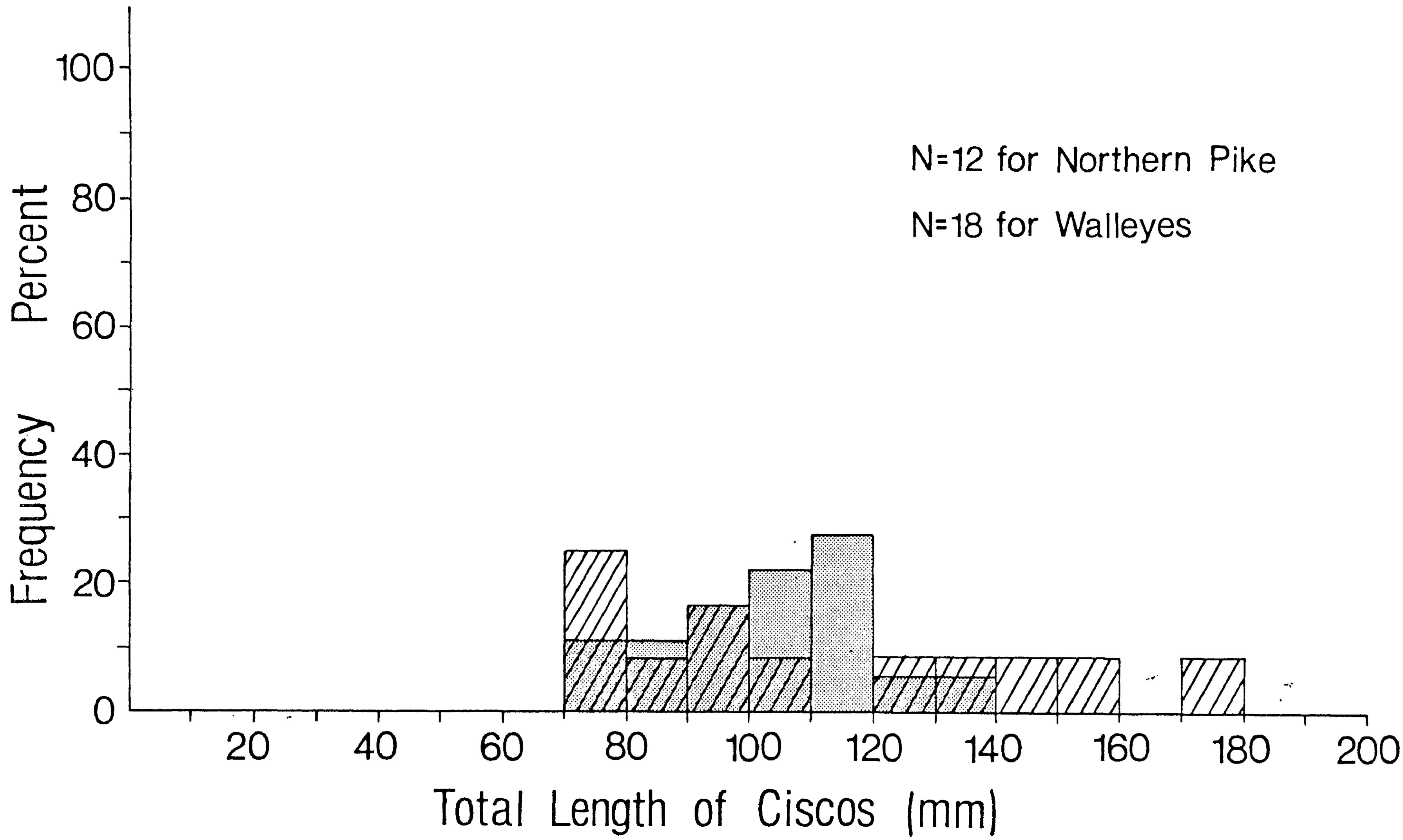

N=64 for Northern Pike
N=112 for Walleyes
Frequency Percent
0
20
40
60
80
100
20
40
60
80
100
120
140
160
180
200
Total Length of Yellow Perch (mm)

Figure 17. The length-frequency distribution of ciscos (mm) observed in 12 northern pike (striped) and 18 walleye (shaded) stomachs, sampled by angling and gill nets from Savanne Lake, Ont., 1977-78. Northern pike were 30-95 cm in length while walleyes were 40-54 cm long.



N=12 for Northern Pike
N=18 for Walleyes
Frequency Percent
0
20
40
60
80
100
20
40
60
80
100
120
140
160
180
200
Total Length of Ciscos (mm)

and 28) and body depths (Tables 29 and 30) of consumed prey resulted from samples of 109 northern pike, 23-95 cm long, and 132 walleyes, 15-54 cm long. Fish from each sample contained 308 prey items, whose maximum body length and body depth could be accurately measured or approximated in cases of partial digestion. The occurrence of given sized prey was expressed both as a percentage of the total number of prey found in fish within a certain size interval and as a mean percent occurrence based on the total number of prey found in all size groups of fish sampled. Size intervals were assigned arbitrarily and reflected differences in the size distribution of predator and prey species. The relationship between lengths of northern pike and walleyes, and mean lengths of consumed yellow perch and ciscos (Fig. 16 and 17) were determined from a total of 64 yellow perch and 12 ciscos identified in northern pike and 112 yellow perch and 18 ciscos found in walleyes. Data reflect average lengths of these prey items observed in various size groups of both predators.

Number of food items --- Prey size was not a critical factor in determining predation since most prey items identified in Savanne Lake northern pike and walleyes were less than 95 mm in length (Fig. 13). The relationship between predator size and the average number of organisms consumed by both species was compared to assess the impact of predation on these smaller items, notably yellow perch, ciscos and mayfly nymphs.

Overall, the average number of mayflies ingested increased with increasing predator size. Walleyes, 37.5 cm and longer, consumed anywhere from 9 to a maximum of 13.5 nymphs (Fig. 19). The number of nymphs found in northern pike greater than 55 cm in length varied from 9 to 30 per fish (Fig. 18). Even though the mean number of mayflies eaten by northern pike (45-65 cm) and walleyes larger than 30 cm were about equal, larger pike consumed the greatest number of nymphs.

No relationship between predator size and the average number of ingested perch (less than 95 mm long) was apparent (Figs. 18 and 19). The number of small perch observed in northern pike, 23 to 85 cm in length, varied from 1 to 2 per fish. Walleyes contained greater numbers of yellow perch on the average, than did northern pike. An average of 1.3 to 2.3 perch were consumed by walleyes in the 15 to 54 cm length range.

The quantity of ciscos consumed by both species did not increase with corresponding increase in predator length (Figs. 18 and 19) but remained constant at 1 per fish for all sizes. The largest ciscos were eaten by the larger individuals of both species.

The relative role of small prey items was determined from actual counts of ingested food items. The average number of each was plotted against the average length of predator (Figs. 18 and 19). Data from individual fish were combined to reflect all feeding fish sampled within a given size interval.

Figure 18. The average number of yellow perch, ciscos, and mayfly nymphs (less than 95 mm long) observed in northern pike (23-95 cm long) from Savanne Lake, Ont., 1977-78.

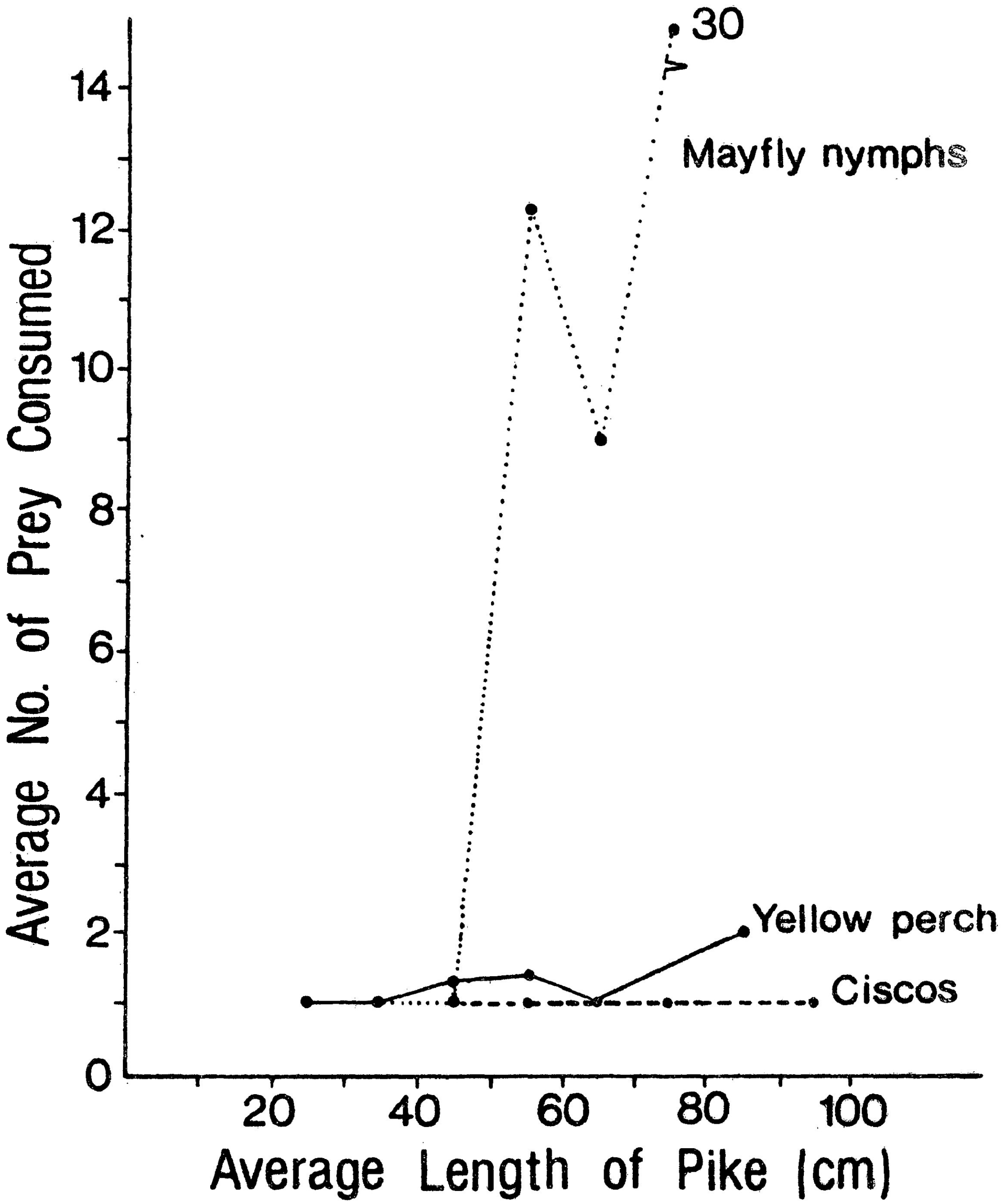
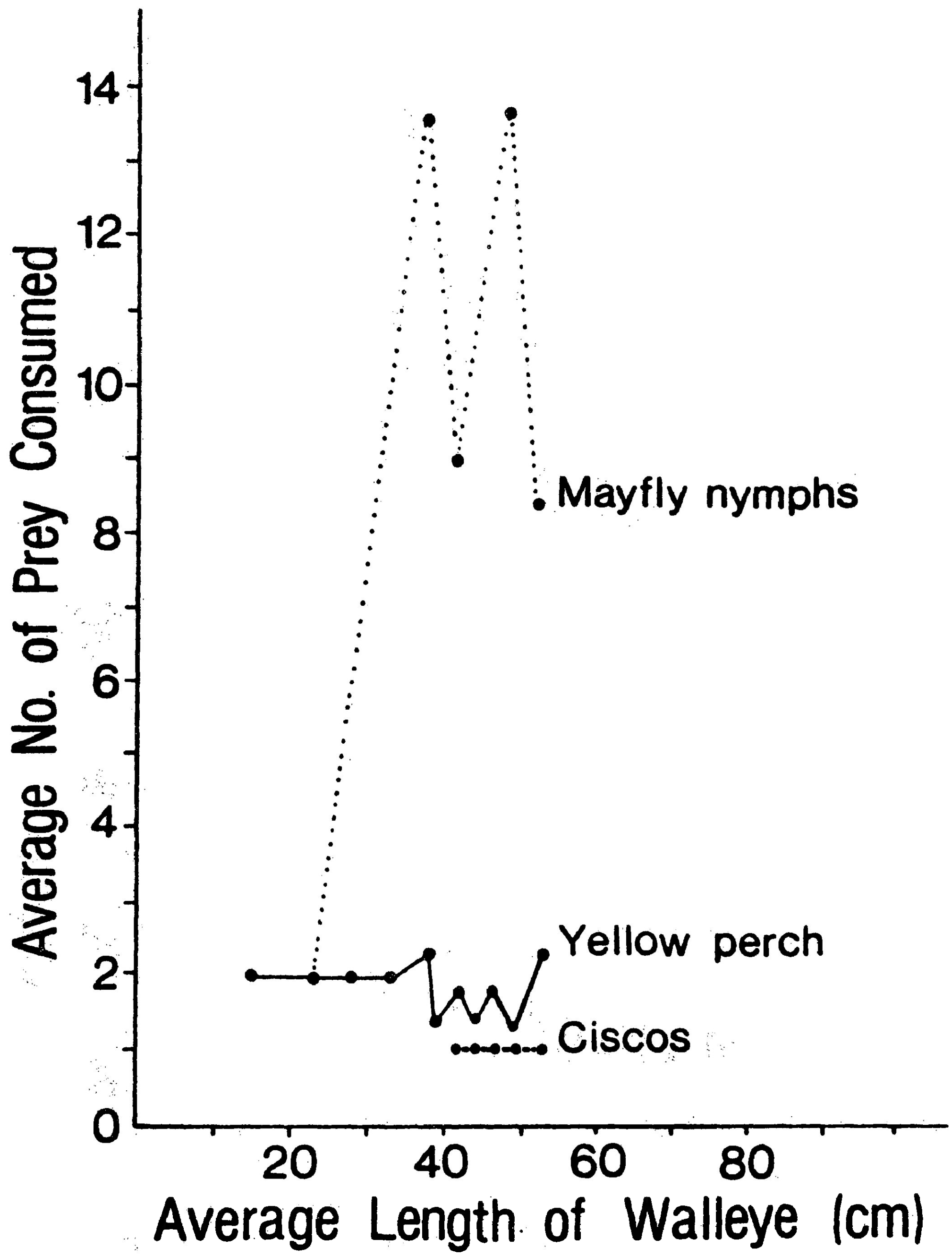

30
14
12
10
8
6
4
2
0
Mayfly nymphs
Yellow perch
Ciscos
20
40
60
80
100
Average No. of Prey Consumed
Average Length of Pike (cm)

Figure 19. The average number of yellow perch, ciscos, and mayfly nymphs (less than 95 mm long) observed in walleyes (15-54 cm long) from Savanne Lake, Ont., 1977-78.



Average No. of Prey Consumed
14
12
10
8
6
4
2
0
20
40
60
80
Average Length of Walleye (cm)
Mayfly nymphs
Yellow perch
Ciscos

EXPLOITATION

Sampling for feeding study materials allowed an assessment of the initial impact of sport angling on these relatively unexploited populations of northern pike and walleyes. A total of 452.8 man-hours of angling yielded 399 northern pike, weighing 508.6 kg., and 298 walleyes, weighing 216.8 kg. Angling encompassed the open water season (late June to late October in 1977) and a period in late May, 1978. Poor angling success for both species was experienced throughout the winter (late November to late April) and these data were not included.

It was assumed both species were equally vulnerable to angling which was restricted to daylight hours between dawn and dusk. Although both northern pike and walleyes are known to actively feed during daytime in littoral areas following spring spawning (MacKay 1963; Ryder 1977), walleyes are reported to become more crepuscular or nocturnal in their feeding habits during summer and autumn months. Casselman (unpublished data) observed that northern pike were more active and fed more intensively on cloudy, overcast days than on bright, sunny days during open water. When daytime light intensities were high, pike fed more actively during evening and morning periods. Northern pike and walleyes were caught in similar areas of Savanne Lake during daytime for most of the study interval. Both the shallow nature of this lake and the darkly stained character of its waters accounted for the daylight feeding activity of both species. Ryder (1977) observed that walleyes are more inclined to feed intermittantly throughout daylight in waters of low transparency than in clear lakes. Swenson and Smith (1973) noted that walleye feeding during periods of low food consumption was uniformly distributed between night and day.

Yield

An average angling effort of 1.24 hours per ha during the open water period (late May to late October) yielded 1.4 kg·ha for northern pike and 0.6 kg·ha for walleye. Even though angler pressure was low, yields for both species in Savanne Lake were comparable to those from more intensively fished waters (Table 31). Presumably, yields would rise as angling pressure increased. The walleye yield was within the range (0.3-4 kg·ha) observed for other nearby northwestern Ontario lakes [e.g. Northern Light Lake (Martin 1973); Lac des Mille Lacs (Elsey and Thomson 1977)].

Catch Per Unit Effort

Northern pike were more vulnerable to angling than walleyes and comprised the greater portion of total angling yield for the overall period. Catch per unit efforts for northern pike averaged 0.88 fish per man-hour and 1.12 kg per man-hour (Table 32). Catch per unit efforts for walleyes averaged 0.66 fish and 0.48 kg per man-hour fished. Angling success for both northern pike and walleyes in Savanne Lake, expressed as numbers of fish caught per man-hour, exceeded similar values for both species from exploited waters, including lakes in close

Table 31. Angling yield and effort estimates for northern pike and walleye from various waters.

Species	Location and source	Year and Season	Estimated yield (kg•ha)	Estimated effort (hr•ha)
Northern pike	Savanne L., Ont. (Present study)	1977 (spring, summer and fall)	1.4	1.24
	Escanaba L., Wisc. (Kempinger and Carline 1978)	1959 - 1972 (all year)	1.0 - 3.6	83.4 - 222.3
	Murphy Flowage, Wisc. (Snow 1978)	1955 - 1970 (all year)	6.7	181.7
Walleye	Savanne L., Ont. (Present study)	1977 (spring, summer and fall)	0.6	1.24
	White L., Ont. (Price 1972)	1972 (summer)	1.6	6.2
	Northern Light L., Ont. (Martin 1973)	1973 (summer)	0.3	1.2
	Lac des Mille Lacs, Ont. (Elsey and Thompson 1977)	1975 (summer)	4.4	14.4[a]
	Seagull L., Minnesota (Micklus 1961)	1957 (summer)	0.5	1.9
	Escanaba L., Wisc. (Kempinger and Carline 1977)	1948 - 1975 (all year)	9.0	158.0

[a] Estimated effort for all species.

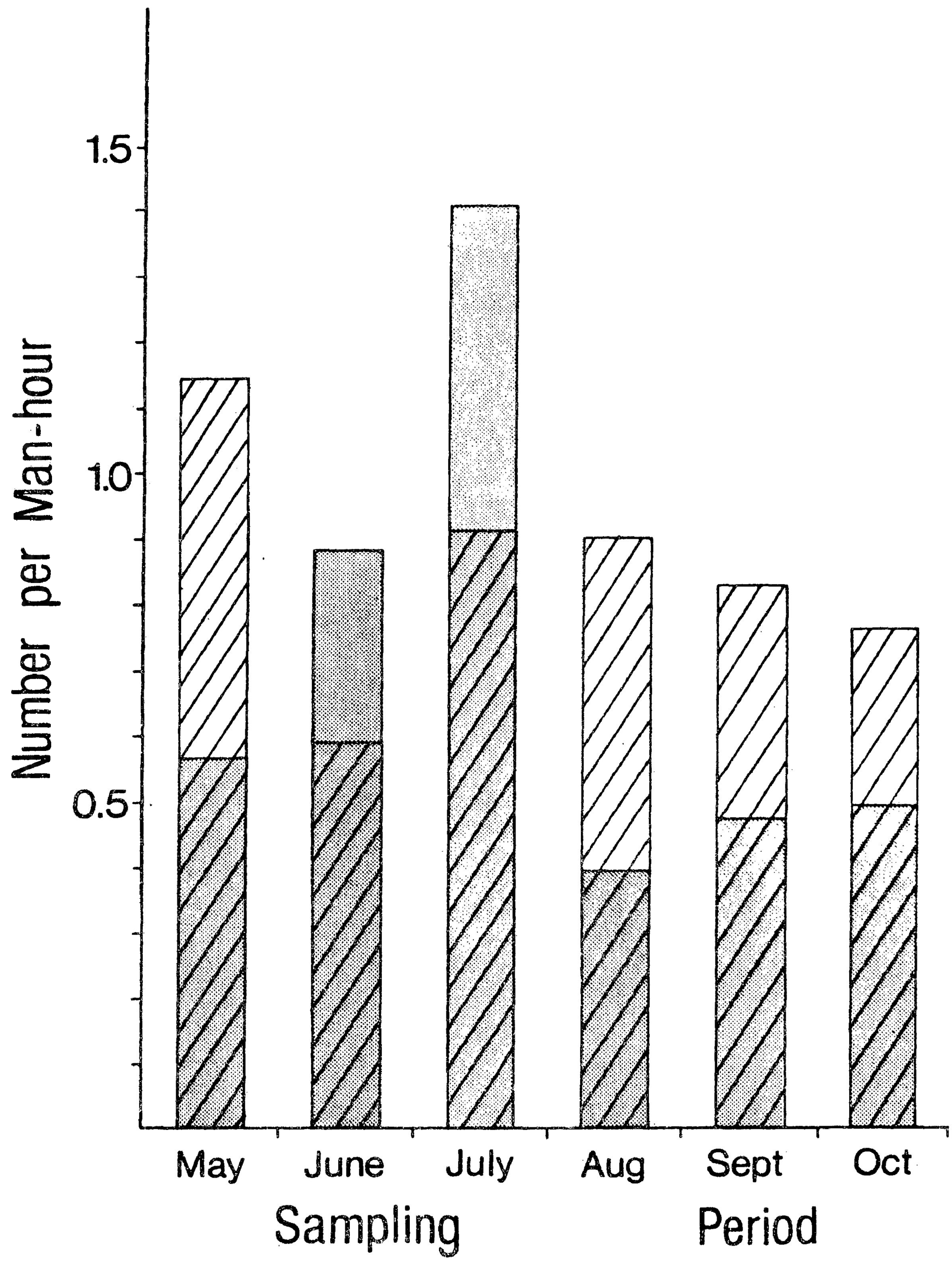
Table 32. Angling catch per unit effort (C.U.E.), expressed as the number of fish caught per man-hr. fished, for northern pike and walleye from various waters.

Species	Location and source	Year and season	Angling C.U.E. (no. caught/hr. fished)
Northern pike	Savanne L., Ont. (Present study)	1977 (spring, summer and fall)	0.88
	Escanaba L., Wisc. (Kempinger and Carline 1978)	1958 - 1963 (all year)	0.007 - 0.04
	Murphy Flowage, Wisc. (Snow 1978)	1955 - 1969 (spring, summer and fall)	<0.05
Walleye	Savanne L., Ont. (Present study)	1977 (spring, summer and fall)	0.66
	Polly L., Ont. (Ryder 1968)	1960 (summer)	0.33
	Lac des Mille Lacs, Ont. (Drysdale 1973)	1958 - 1973 (summer)	0.4 - 1.6
	Whitefish L., Ont. (Drysdale 1974)	1974 (summer)	0.34
	Escanaba L., Wisc. (Churchill 1956, 1959)	1946 - 1956 (summer)	<0.01 - 0.43
	Caribou L., Minn. (Johnson 1957)	1956 - 1958 (summer)	0.18 - 0.32

proximity (Table 32). Scott and Crossman (1973) reported that good angling success for northern pike is usually rated at 1.8 to 2.2 fish per hour while good walleye fisheries are characterized by catch per unit efforts of 0.3 fish per hour (Colby et al. 1979).

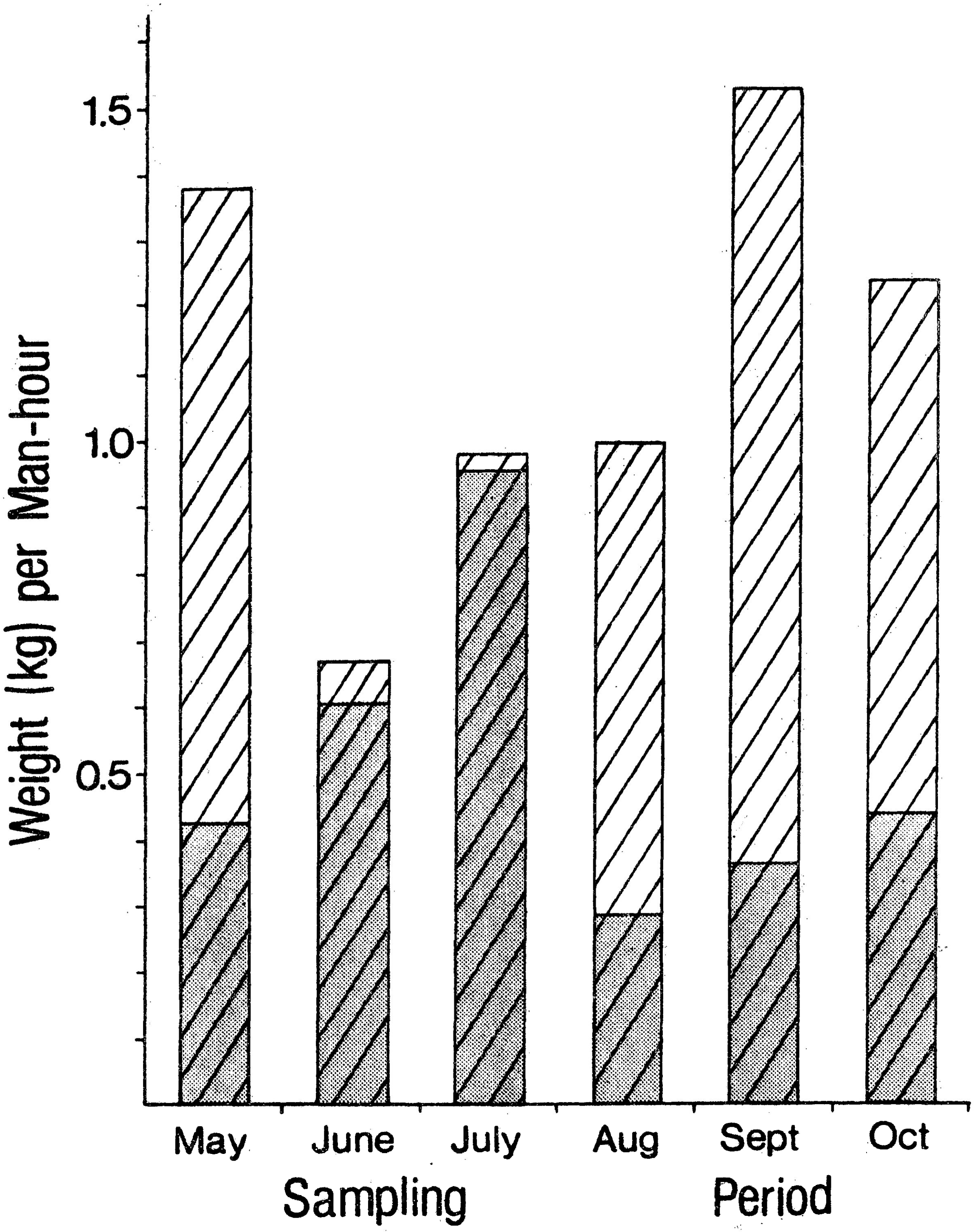
Northern pike were more vulnerable to angling than walleyes during most months, excepting June and July (Fig. 20). Northern pike were most vulnerable to angling during late May while least vulnerable in late June. Vulnerability remained constant throughout the summer, decreasing slightly in the autumn. Di Constanzo and Ridenhour (1957) and Snow (1978) found that angling success for northern pike was better during spring months than in midsummer. In contrast, walleyes were most vulnerable to angling in Savanne Lake during late June and July (Fig. 20). Lowest catch per unit efforts occurred from late August to late October, although angling for walleyes improved slightly in the autumn. Colby et al. (1979) reported that angling success for walleyes is generally better during spring and fall months but tapers off in the summer. MacKay (1963) cited an increase in walleye catches during autumn months. Northern pike gave greater yields than walleyes in all study months, including June and July (Fig. 21). Hence, the average weight of angler caught pike exceeded that of walleyes during all months. Even though angling success for northern pike decreased in the autumn (Fig. 20), monthly catch per unit efforts (expressed as the weight of pike per man-hour) increased, especially in late September. Increased angling success for larger fish accounted for this trend.

Figure 20. Catch per unit effort, expressed as the number of fish per man-hour, for northern pike (striped) and walleyes (shaded) caught by angling in Savanne Lake, Ont., June-October, 1977 and May 1978.



Number per Man-hour
1.5
1.0
0.5
May
June
July
Aug
Sept
Oct
Sampling Period

Figure 21. Catch per unit effort, expressed as the weight (kg) of fish per man-hour, for northern pike (striped) and walleyes (shaded) caught by angling in Savanne Lake, Ont., June-October, 1977 and May 1978.



Weight (kg) per Man-hour
1.5
1.0
0.5
May
June
July
Aug
Sept
Oct
Sampling Period

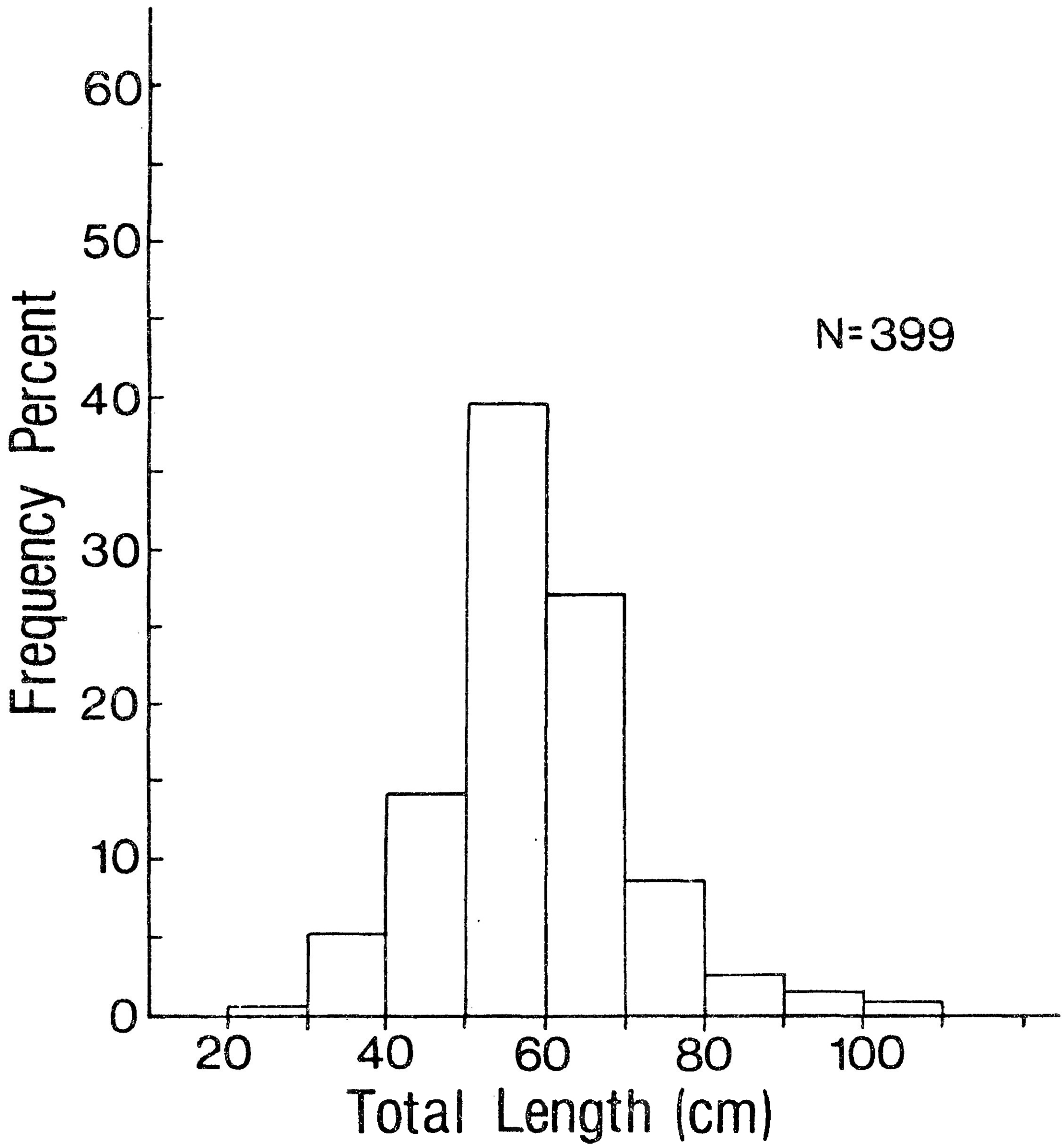
Composition of Catch

The size composition of angler caught northern pike (Fig. 22) closely paralleled length-frequency distributions of trap netted and gill netted pike (Fig. 6). Fish larger than 50 cm total length were the most vulnerable to experimental angling methods. Most of the catch consisted of 5 to 7 year olds, 50-70 cm in length, which represented dominant age and size classes. Small northern pike, (less than 40 cm), comprised only 25% of the total catch.

Fish 40-50 cm long and older than 6 years of age dominated the overall length-frequency distribution of walleyes in the angling catch (Fig. 23). These were also the major age and size classes present in spring trap net estimates (Sandhu 1979). Fish smaller than 40 cm comprised only 24% of the total angling catch.

Seasonal differences in the size composition of monthly catches existed. Northern pike, less than 50 cm in length, appeared least vulnerable to angling during the autumn months of September and October (Table 33). In contrast, northern pike greater than 60 cm, were most vulnerable to angling in late September and October, representing 73.8% and 57.4% of the catch, respectively. Walleyes larger than 45 cm, also formed a greater portion of the catch during the autumn and spring (Table 34) although this trend was more pronounced for northern pike. Large fish, especially northern pike, account for the observed increase in catch per unit efforts (expressed as weight of fish per man-hour) during autumn months.

Figure 22. The length-frequency distribution of northern pike caught by angling in Savanne Lake, Ont., June-October, 1977 and May 1978.



Frequency Percent
60
50
40
30
20
10
0
N=399
20
40
60
80
100
Total Length (cm)

Figure 23. The length-frequency distribution of walleyes caught by angling in Savanne Lake, Ont., June-October, 1977 and May 1978.

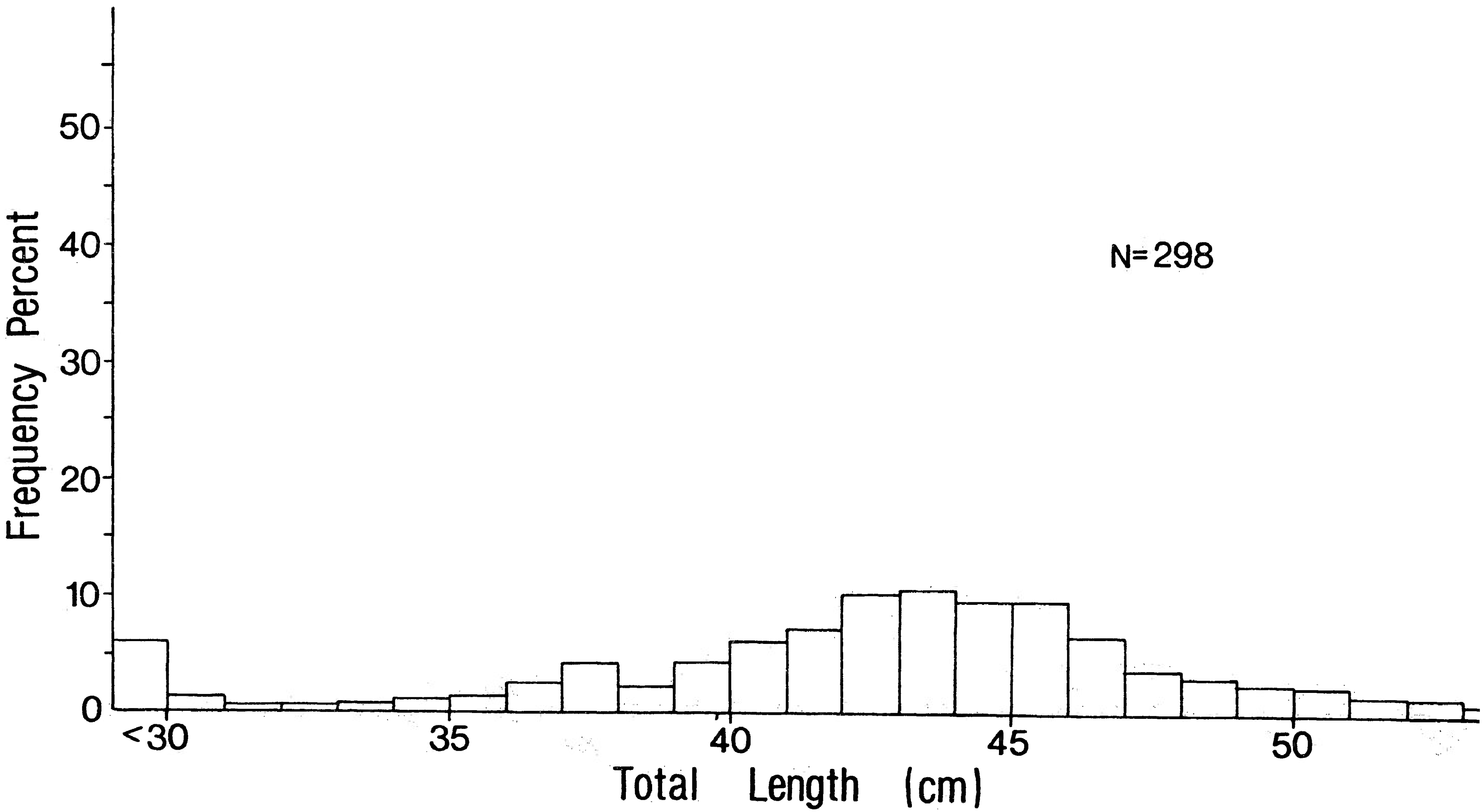

Frequency Percent
0
10
20
30
40
50
N=298
<30
35
40
45
50
Total Length (cm)

Table 33. The length-frequency distribution of northern pike in the total angling catch and in the monthly angling catch from June-October 1977 and May 1978 in Savanne L., Ont. Frequencies are expressed as both percentages and as numbers of fish (in parenthesis).

Angling period	No. of fish caught	Total length (cm) 0-29.9	30-39.9	40-49.9	50-59.9	60-69.9	70-79.9	80-89.9	90-99.9	over 100
May 1978	99	0 (0)	5.1 (5)	16.2 (16)	40.4 (40)	27.3 (27)	9.1 (9)	1.0 (1)	1.0 (1)	0 (0)
June 1977	36	2.8 (1)	2.8 (1)	13.9 (5)	44.4 (16)	25.0 (9)	8.3 (3)	2.8 (1)	0 (0)	0 (0)
July	56	0 (0)	7.1 (4)	16.1 (9)	48.2 (27)	19.6 (11)	5.4 (3)	3.6 (2)	0 (0)	0 (0)
August	112	0.9 (1)	8.0 (9)	17.9 (20)	44.6 (50)	19.6 (22)	5.4 (6)	1.8 (2)	0.9 (1)	0.9 (1)
September	42	0 (0)	4.8 (2)	9.5 (4)	11.9 (5)	42.9 (18)	16.7 (7)	7.1 (3)	4.8 (2)	2.4 (1)
October	54	0 (0)	0 (0)	5.6 (3)	37.0 (20)	38.9 (21)	11.1 (6)	1.9 (1)	3.7 (2)	1.9 (1)
Totals	399	2	21	57	158	108	34	10	6	3
Mean percent frequency		0.5	5.3	14.3	39.6	27.1	8.5	2.5	1.5	0.8

Table 34. The length-frequency distribution of walleyes in the total angling catch and in the monthly angling catch from June–October 1977 and May 1978 in Savanne L., Ont. Frequencies are expressed as both percentages and as numbers of fish (in parenthesis).

Angling period	No. of fish caught	Total length (cm) 0–19.9	20–24.9	25–29.9	30–34.9	35–36.9	37–37.9	38–38.9	39–39.9	40–40.9	41–41.9	42–42.9	43–43.9	44–44.9	45–45.9	46–46.9	47–47.9	48–48.9	49–49.9	over 50
May 78	49	0 (0)	0 (0)	4.1 (2)	0 (0)	0 (0)	6.1 (3)	0 (0)	2.0 (1)	2.0 (1)	12.2 (6)	8.2 (4)	14.3 (7)	8.2 (4)	20.4 (10)	6.1 (3)	4.1 (2)	4.1 (2)	2.0 (1)	6.1 (3)
June 77	54	0 (0)	0 (0)	3.7 (2)	3.7 (2)	3.7 (2)	3.7 (2)	7.4 (4)	11.1 (6)	1.9 (1)	7.4 (4)	14.8 (8)	12.9 (7)	9.3 (5)	9.3 (5)	1.9 (1)	1.9 (1)	1.9 (1)	1.9 (1)	3.7 (2)
July	87	2.3 (2)	2.3 (2)	5.8 (5)	5.8 (5)	3.5 (3)	4.6 (4)	3.5 (3)	3.5 (3)	9.2 (8)	5.8 (5)	9.2 (8)	8.1 (7)	11.5 (10)	9.2 (8)	3.5 (3)	3.5 (3)	1.2 (1)	2.3 (2)	5.8 (5)
August	49	4.8 (2)	0 (0)	2.0 (1)	6.1 (3)	12.2 (6)	4.1 (2)	0 (0)	0 (0)	4.1 (2)	6.1 (3)	14.3 (7)	12.2 (6)	8.2 (4)	4.1 (2)	10.2 (5)	2.0 (1)	6.1 (3)	4.1 (2)	0 (0)
Sept.	24	0 (0)	4.2 (1)	4.2 (1)	8.3 (2)	0 (0)	4.2 (1)	0 (0)	0 (0)	16.7 (4)	8.3 (2)	0 (0)	0 (0)	4.2 (1)	4.2 (1)	16.7 (4)	8.3 (2)	4.2 (1)	4.2 (1)	12.5 (3)
October	35	0 (0)	0 (0)	0 (0)	0 (0)	2.9 (1)	0 (0)	0 (0)	5.7 (2)	5.7 (2)	5.7 (2)	8.6 (3)	14.3 (5)	14.3 (5)	8.6 (3)	11.4 (4)	5.7 (2)	5.7 (2)	2.9 (1)	8.5 (3)
Totals	298	4	3	11	12	12	12	7	12	18	22	30	32	29	29	20	11	10	8	16
Mean per cent frequency		1.3	1.0	3.7	4.0	4.0	4.0	2.4	4.0	6.0	7.4	10.1	10.7	9.7	9.7	6.7	3.7	3.4	2.7	5.4

MANAGEMENT IMPLICATIONS

The formulation of any harvest strategy depends on the distribution of biomass and production in target populations (Healey 1978; Snow 1978; Serns 1978). These parameters are primarily influenced by inherent rates of growth, reproduction, and mortality, defining fish community structure within the limits of the productive capacity of an environment. A management strategy for northern pike and walleye populations in Savanne Lake, Ontario is examined within this context.

Northern pike (the present study) and walleyes (Sandhu 1979) in Savanne Lake are characterized by a conservancy of biomass, low annual production, stable recruitment, and slow growth, representing a mature fish community in the absence of exploitation. While annual mortality rates were lower for northern pike, they were in contrast higher than those found for walleyes in exploited populations. Northern pike matured at an earlier age but were neither as numerous nor as long-lived as walleyes. Although they exhibited rates of annual production similar to walleyes, northern pike dominated the carnivore biomass, which was vulnerable to sampling gear.

Northern pike and walleye occupied the same trophic level as terminal predators in Savanne Lake. Both species depended heavily on the same type and sizes of prey throughout the year. Relative abundance and seasonal availability determined the incidence of prey consumed by both. Perhaps only differences in diel activity patterns between these species serve to partition food resources in this community (Ryder and Kerr 1978).

Although angling pressure during this study was considered minimal (1.24 hr./ha), observed patterns resulting from experimental exploitation reflect the initial stage of a more intensive fishery on resident northern pike and walleye populations. Catch per unit effort and total angling yields for the overall period were dominated by the more vulnerable northern pike. Angling success (C.U.E.) for both species throughout the open water season, exceeded similar values from exploited waters in close proximity (Table 32). Catches consisted primarily of northern pike, 50-70 cm in length and 5-7 years old, and walleyes, 40-50 cm in length and 6-10 years old, representing dominant age and size classes.

If Savanne Lake were opened to public fishing within existing provincial regulations, the initial result would be a productive, intensive fishery, directed towards walleyes and large pike. The relatively high yields for both species would reflect the dominance of larger size and older age-groups in the populations. Angling, by selectively removing these larger mature individuals, would eventually reduce stock densities and biomass. When Mill Lake, Michigan, was opened to angling following a five-year closed season, large initial decreases in stock resulted from relatively little fishing pressure (Schneider 1973). Resident fish stocks were saved from serious depletion only because of their reduced catchability. Exploitation is known to elicit compensatory responses (e.g. increases in growth rate, earlier maturity, and increases in relative fecundity) in both freshwater and marine populations (Healey 1978; Spangler et al. 1977). It is very unlikely that increased growth and recruitment of Savanne Lake walleyes and northern pike would immediately replace the mature individuals removed by angling. In the short-term, sustained pressure would result in decreased angling quality. While smaller walleyes, esteemed for their eating rather than their sporting qualities, might prove acceptable, smaller pike are normally viewed as a poor substitute for larger, "trophy" fish by local anglers.

A more important consideration in view of the predicted decrease in adult densities, is the serious loss of spawning stock, resulting in a reduced reproductive potential for both populations. Although compensatory responses to exploitation (e.g. decreases in the age of maturity and increases in relative fecundities) might offset such losses, knowledge concerning the temporal duration of any response is lacking. Reproduction of northern pike and walleyes in Savanne Lake does not appear limiting even though relative fecundities for both species are below reported averages (the present study; P.J. Colby, unpublished data). Recruitment is stable and good habitat for spawning and larval development exists. Significant reductions in adult densities might not lead to an immediate collapse in these populations but protection of brood stocks should remain an important concern since stock-recruitment relationships for both species are unknown.

Predacious fish are known to have a direct influence on community structure (Popova 1978). They supposedly stabilize communities by consuming the most abundant species, thus balancing all levels within a food chain. In Polish lakes, a high percentage of predators was associated with low densities of non-predatory and undesirable fish (Bonar 1977). Excessive exploitation of dominant piscivores may interfere with existing predator-prey relationships. Over exploitation has usually shifted the species composition within fish communities where larger species (generally piscivorous) are reduced in abundance in favour of smaller species (pelagic and/or planktivorous) that increase in numbers, often occupying trophic roles previously held by larger components (Regier and Henderson 1973; Spangler et al. 1977; Bonar 1977; Popova and Syntina 1977). Reductions in the density of adult northern pike and walleyes in Savanne Lake, would probably affect the structure and abundance of major prey populations. Yellow perch, especially juvenile forms, were the principal food of both predators throughout the year. While young-of-the year and juvenile perch were abundant, few adults were present. Predation by northern pike and walleyes is likely responsible for high juvenile mortality. Kempinger and Carline (1978) found that northern pike predation on juvenile centrarchids and perch in Escanaba Lake, Wisconsin had a direct influence on the numbers of these prey surviving to adulthood. The ultimate year class strength of yellow perch in Oneida Lake, New York was largely determined by mortality of juveniles resulting from walleye predation (Nielsen 1980). Lawler (1965) noted increases in the number of yellow perch, especially adults, following intensive removal of northern pike from Heming Lake, Manitoba. Initial declines in predator densities through angling, might also increase the survival of juveniles and result in greater numbers of adult perch in Savanne Lake.

The implementation of minimum size limits for the management of walleye and northern pike populations in coolwater communities is of current interest. Major strategy objectives are to maximize yields, increase catch rate of large fish, and to protect potential spawners (Serns 1978; Schneider 1978). The Ricker equilibrium yield model for recruitment (Ricker 1975) has been used to determine size limits and to assess their impact on existing populations (Kempinger and Carline 1977 & 1978; Schneider 1978). This model was employed in the present study to examine the effects of age of entry (hence fish size) and fishing rate on both potential yield and stock characteristics of the mature northern pike population, ages 5-11, in Savanne Lake. It provides a simple technique for establishing yields under steady-state conditions, given instantaneous rates of natural mortality, growth, and fishing mortality. Calculations were executed by a computer program (Paulik and Bayliff 1967) using values represented in Table 35. Rates of instantaneous growth and total annual mortality for various age classes were those observed. Estimates of fishing and natural mortality were calculated from exploitation rates, based on fish removed by experimental angling during the open water period in 1977. Exploitation was light, averaging 4%, while fishing effort averaged 0.2 man-hours per hectare. Beginning with a cohort of 802

Table 35. Values employed in the calculation of the equilibrium yield model (Ricker 1975), expressing rates of exploitation (E), survival (S), total instantaneous mortality (Z), natural mortality (M), fishing mortality (F), instantaneous growth (G), and initial biomass (W_0) for northern pike, age-groups 5-11, in Savanne L., Ont., 1977-78.

Age-group	N_0	N_t	Number removed by angling	E	$S = \frac{N_t}{N_0}$	$Z = -\ln S$	M	$F = Z - M$	G	W_0 (kg)
5	802	753	30	0.037	0.939	0.063	0.027	0.036		618.34
									0.329	
6	542	390	18	0.033	0.719	0.329	0.290	0.039		580.48
									0.327	
7	368	286	14	0.032	0.777	0.252	0.209	0.043		546.48
									0.409	
8	185	114	5	0.027	0.616	0.485	0.452	0.034		413.46
									0.292	
9	95	62	4	0.042	0.652	0.428	0.376	0.052		284.24
									0.275	
10	66	22	3	0.045	0.333	1.099	1.024	0.075		259.91
									0.130	
11	44	18	3	0.068	0.409	0.894	0.791	0.103		194.70
Totals	2102	1645	77							

fish (average weight of 771 gm) recruited to the fishery at age 5 and continuing to age 10, equilibrium yields (kg) were computed for various ages of entry and at fishing rates of one-half to sixty times that observed (fishing rate multipliers, Table 36). Predicted yields (Table 36) suggest that the northern pike population in Savanne Lake could be best managed as a "trophy" fishery. By restricting age of entry to fish 8 years and older, maximum yields are achieved and the highest fishing rate is accommodated. Although predicted yields peak at lower fishing rates when age of entry is 5 years, removal at this age limits recruitment to older age-groups. Implementation of a 75 cm minimum size limit, corresponding to average fish size at age 8, would maximize yield since greatest growth potential is realized during the eighth year of life (Table 35). By restricting age of entry to fish older than 8 years, substantial losses through decreased growth and increased mortality are predicted.

The major disadvantage of the equilibrium yield model stems from inherent assumptions that rates of recruitment, growth, natural mortality do not change as the density of the population is altered. A number of studies on exploited populations prove that such assumptions are invalid and that minimum size regulations, based on this model's predictions, may be detrimental to fish populations involved. The imposition of minimum size limits have led to decreases in growth rates and increases in natural mortality in northern pike populations (Kempinger and Carline 1978; Snow and Beard 1972) and similar decreases in growth rates and condition in walleye populations (Serns 1978).

Table 36. Predicted total maximum yields (kg) per 802 recruits (at age 5) at various ages of entry and fishing rates for northern pike in Savanne L., Ont., 1977-78.

Age at entry	Predicted maximum yields (kg)																			
10	19.9	39.2	93.6	173.5	241.9	300.7	351.2	394.8	432.4	465.1	493.6	518.5	540.3	559.4	576.3	591.3	604.7	616.6	653.0	678.4
9	41.4	80.7	186.8	330.5	441.7	528.2	595.8	648.9	691.0	724.4	751.3	772.9	790.4	804.8	816.5	826.4	834.5	841.4	860.0	870.4
8	57.3	110.8	251.6	432.7	563.9	659.9	731.0	784.0	824.2	855.0	879.0	897.8	912.9	925.2	935.4	943.8	951.0	957.2	975.3	987.4
7	76.4	146.5	323.6	533.9	671.6	762.4	822.7	862.9	889.9	908.0	920.0	928.0	933.1	936.3	938.0	938.8	938.9	938.5	934.2	928.4
6	91.7	173.4	372.5	590.0	717.0	790.9	833.4	857.3	870.2	876.5	878.9	879.0	877.9	876.0	873.8	871.5	869.2	866.9	859.4	854.1
5	102.5	192.6	402.2	611.0	717.0	768.2	790.3	797.1	796.0	791.0	784.2	776.8	769.3	762.1	755.3	749.0	743.1	737.7	719.5	705.7
	0.5	1.0[a]	2.5	5.0	7.5	10.0	12.5	15.0	17.5	20.0	22.5	25.0	27.5	30.0	32.5	35.0	37.5	40.0	50.0	60.0
	Fishing rate multipliers																			

[a] Represents the current fishing rate.

These compensatory responses have been attributed to the increased recruitment of sub-legal fish and resulting high densities relative to available food (Kempinger and Carline 1978). In all cases, minimum size limits reduced the number of legal-sized fish available to anglers and yields declined drastically.

Minimum size limits have been judged to have an adverse effect on coolwater communities such as Savanne Lake where dominant predators, like pike, exhibit high densities as mature fish, high rates of reproduction, and slow growth (Anderson and Weithman 1978). The implementation of similar size regulations in an effort to maximize yields and establish a "trophy" fishery for northern pike and walleyes in Savanne would probably result in an accumulation of fish below the size limit as evidenced in the foregoing studies. Greater densities of sub-legal fish would increase pressure on existing prey fish populations, especially yellow perch which already suffer high mortalities as juveniles from northern pike and walleye predation. Increased recruitment of northern pike in Escanaba Lake, Wisconsin, following the initiation of minimum size limits (Kempinger and Carline 1978) led to a collapse in the harvest of panfish (yellow perch and centrarchids). Reduced growth and increased mortality of sub-legal fish resulting from high densities relative to available food would eventually reduce the recruitment of legal-sized fish and result in stunted populations (Serns 1978).

Johnson and Anderson (1974) have advanced the concept of a "slot" length limit that protects fish in the medium size ranges in an effort to increase the quality of a sport fishery. A size limit of this type directs angling pressure towards smaller and larger fish and is best suited to waters where good natural reproduction exists. It's effectiveness appears to depend on the presence of favourable growth in protected size classes. Since medium size ranges predominate in Savanne Lake, it seems unlikely that slot size management could improve growth rate and structure by protecting most of the fish in these slow growing populations. Instead, a management strategy aimed at concentrating angling pressure on these size groups would be a more logical approach. At present, a recreational fishery with no size regulations would likely have the same initial impact on northern pike and walleye populations in this lake since dominant intermediate size classes appear the most vulnerable to angling.

Regulation of angler harvest by limiting access rather than by protecting segments of populations might prove the most effective means of maintaining angling "quality". A controlled sport fishery with no size limits would allow the harvest of fish at a size which is satisfactory to the angler while restricting overall angling pressure to levels which are compatible with the low productive capacity of this environment.

SUMMARY

1. Savanne Lake, located approximately 128 km northwest of Thunder Bay, was exploited by a sport fishery until 1969 whereupon it was designated a provincial fish sanctuary by the Ontario Ministry of Natural Resources, for the purpose of a long term study of controlled walleye exploitation and percid community dynamics.
2. Savanne Lake is of intermediate size, 364.29 ha, and is relatively shallow (2.5 m mean depth and 4.27 m maximum depth). Fish species present in the lake are: walleye, northern pike, yellow perch, shallow water cisco, white sucker, burbot, trout-perch, mimic shiner, blacknose shiner, johnny darter and Iowa darter.
3. This homothermous lake is characterized by very low water temperatures during the early winter following ice cover formation in late November. Warming of temperatures throughout the water column over winter is similar to that described for Finnish boreal lakes (Nissinen 1972).
4. A two year study was conducted during 1977 and 1978. Important aspects of the life history and population dynamics of northern pike were examined. The feeding relationships of northern pike and walleyes and the initial impact of an open water sport fishery on the unexploited populations of both species were also studied.
5. Northern pike spawning was observed on the day of ice break-up in the springs of 1977 and 1978, at water temperatures of 4.5 to 6.0°C.

6. Northern pike spawned during daytime in shallow water (less than 0.5 m), over submerged aquatic and terrestrial vegetation, along flooded marshy shorelines. The major spawning area is located along the shore and outlet at the northeast end of the lake.
7. While males dominated the overall spawning population and were present in greater numbers during the early and later stages of the spawning run, equal numbers of males and females were identified on spawning areas during peak periods of spawning activity.
8. Fecundity estimates of 9,675 eggs per unit body-weight (kg) and an average of 20,081 eggs per mature female pike were low in comparison to reported values.
9. Young-of-the year northern pike favoured shallow, hard-bottomed, sand and rocky beaches adjacent to the marshy soft-bottomed spawning areas during their first summer of development.
10. Growth of young-of-the year northern pike during their first summer was rapid. The average length of free-swimming fry increased at a rate of 1.3 mm per day in 1977 and 1.7 mm per day in 1978. Although adult spawning commenced two weeks later in 1978, young-of-the year achieved approximately the same size (130-140 mm) by the end of each summer.
11. Entomostraca, primarily copepods and cladocera, formed the principal food of northern pike fry 20-30 mm in length. Young-of-the year greater than 30 mm long fed primarily on larval fish, especially yellow perch (<u>Perca flavescens</u>) in both study years.
12. Adult northern pike moved throughout Savanne Lake during the year

with the greatest movements occurring in the spring to preferred spawning grounds. After spawning, fish dispersed about the lake and did not appear to establish home ranges, as commonly reported.

13. Schumacher-Eschmeyer spring population estimates of 2,621 and 2,508 were made in 1977 and 1978, respectively and represent the mature population most vulnerable to the 1.22 m and 1.83 m trap nets employed.

14. The majority of northern pike caught were 50-70 cm long, with the 50-59.9 cm size class predominating. Similar length-frequency distributions were obtained from trap nets, gill nets and angling during the study. Northern pike smaller than 45 cm in length were not fully vulnerable to sampling methods since stable recruitment of size classes greater than 50 cm was apparent.

15. Although northern pike were aged by examination of both scales and cleithra, cleithra proved a more reliable structure for estimating ages of all sizes of pike. The presence of false checks in the formation of annuli on scales from fish, age 8 and older, led to an overestimation of true age.

16. Age-groups 4-7 predominated in catches and comprised 82.4 percent and 77.6 percent of estimated populations in 1977 and 1978, respectively.

17. The dominant age-group was the 1972 year class, which contributed 29 percent of the 1977 estimate at age 5 and 30 percent of the 1978 estimate at age 6.

18. The overall mature population sampled by angling was dominated by females in the ratio of 1.19 females for every male. While males predominated among smaller size classes, females comprised the majority of fish larger than 60 cm (77.8%).

19. Most males were mature at age 3 and an average total length of 36.3 cm while most females were mature at age 4 and an average total length of 44.3 cm.

20. The length-weight relationship of Savanne Lake northern pike, based on measurements of 235 fish sampled in 1977 and 1978, was represented by the following equation:

$$\text{Log } W = -5.1321 + 2.9611 \text{ (Log } L)$$

where: W = weight in gm, and
L = total length in mm.

21. Significant differences were found between intercepts of the length-weight relations of males and females sampled throughout the year. Hence, females were heavier than males at a given length.

22. The largest growth increments in length were attained by both sexes during their first year of life. Growth continued rapidly until age 4 when both sexes were fully mature. Weight increased with age following sexual maturity.

23. Females at all ages were larger than males and grew more rapidly. As commonly reported, females lived longer and achieved a greater maximum size than males.

24. Northern pike in Savanne Lake were slightly below the reported growth average for Ontario and Minnesota waters. Slow growth

of Savanne Lake northern pike may reflect the chemical characteristics of this lake, as well as the high density of piscivores relative to available food.

25. Although lengths of northern pike (ages 1-11) were back-calculated from both cleithral and scale measurements, cleithral calculated lengths were in closer agreement with observed lengths at most ages. In addition, the body-cleithrum relationship was found to be linear while the body-scale relationship was curvilinear and indicated an increasing allometry in growth patterns of scales and body length of larger individuals. This supports a previous study on northern pike (Casselman 1978) which found that growth rates of cleithra more closely paralleled body growth throughout the entire annual cycle.

26. Mean calculated lengths from both scales and cleithra were considerably higher than mean observed lengths at various ages. This "reversed" Lee's phenomenon, an increase in calculated lengths of younger fish from successively older age-groups, probably resulted from the dominance of larger, faster-growing individuals in the sample from which back-calculations were made. It may also reflect a decrease in growth rates within the population, following a return to an unexploited state.

27. Total mean biomass of the mature northern pike population, ages 4-12 years, was estimated at 8.69 $kg \cdot ha^{-1}$ for the 1977-78 period. Annual production (ages 4-12) for the same period was 2.76 $kg \cdot ha^{-1} \cdot yr^{-1}$. The annual $P/\bar{B}$ ratio (turnover ratio of biomass) was

calculated at 0.276. Slow growth, low annual mortality, and the dominance of older age-groups in the observed northern pike population account for lower production, biomass, and $P/\bar{B}$ values than those reported for exploited pike populations.

28. Dominant age and size classes, represented by age-groups 5, 6 and 7, contributed 66 percent of annual production and 59 percent of the estimated biomass.

29. Mean biomass, production and respective $P/\bar{B}$ ratios for various age-groups decreased with increasing age, with the exception of the 1970 year class (age-group 7-8) which made the largest contribution to annual production and had the highest instantaneous growth rate (0.409) for the period.

30. Fish predominated in observed annual diets, occurring in 80.5 percent of feeding northern pike and 76.6 percent of feeding walleyes. Yellow perch (*Perca flavescens*), especially juveniles, formed the major component in the diet of both species, followed by unidentified fish remains (larval and otherwise), and shallow water ciscos (*Coregonus artedii*).

31. Invertebrates, primarily mayfly nymphs (Ephemeridae) and crayfish (*Orconectes virilis*), were of seasonal importance, occurring in 19.5 percent of feeding northern pike and 23.4 percent of walleyes. Walleyes fed upon a greater diversity of invertebrate items than did northern pike.

32. Relative abundance and seasonal availability determined the incidence

of prey consumed by northern pike and walleyes. Although definite seasonal changes occurred in the diet of both species, annual variation in the intensity of feeding was not apparent.

33. Juvenile yellow perch (60-110 mm in length) were the principal prey of both northern pike and walleyes during late spring and summer. They remained the primary food of walleyes during fall and winter months.

34. Shallow water ciscos occurred most frequently in the diet of both species during late summer and fall but were also present in winter and spring samples. Ciscos were absent in diets during midsummer when they were restricted to open water areas by warm inshore temperatures.

35. Although spawning trout-perch formed a major source of food for northern pike in late May, they were of minor importance in the annual diet of both species.

36. Mayfly nymphs, notably burrowing mayflies (Hexagenia sp. and Ephemera sp.), were an important food of adult northern pike during late winter (February-March and March-April), occurring in 60 percent and 81.8 percent of pike stomachs and comprising 21.4 percent and 76 percent of total food volumes, respectively. The high incidence of mayfly nymphs in medium-sized and large pike at this time is unusual and unique. Walleyes fed upon mayflies, especially sub-imago and emergent forms, during May, June and July.

37. Prey size was not a critical factor in determining predation,

since the majority of prey items (larval fishes and insects) identified in both species were less than 35 mm in length. Most adult northern pike and walleyes were capable of consuming far larger prey than were usually found in their stomachs.

38. Walleyes consumed a significantly greater number of small prey less than 20 mm long (insect larvae) and medium-sized prey, 50-110 mm (juvenile fish, especially yellow perch), than northern pike.

39. Owing to their greater overall size, adult pike were able to feed on a wider range of available prey sizes than were walleyes, particularly prey items larger than 170 mm, identified as adult and subadult ciscos, walleyes, and burbot. Northern pike fed upon ciscos at a significantly greater average length than did walleyes.

40. The average number of mayfly nymphs consumed increased with increasing size of both predators. No relationship between predator size and the quantity of ciscos and yellow perch ingested was apparent.

41. Northern pike and walleyes were caught in similar areas of Savanne Lake during daytime for most of the open water angling season. Both the shallow nature of this lake and the darkly stained character of its waters accounted for the daylight feeding activity of both species.

42. Although angling pressure was considered low (1.24 hours per ha), angling success for both species during open water expressed as

numbers of fish caught per man-hour, exceeded similar values from exploited waters, including lakes in close proximity. Catch per unit efforts for northern pike averaged 0.88 fish per man-hour and 1.12 kg per man-hour while walleye C.U.E. averaged 0.66 fish per man-hour and 0.48 kg per man-hour fished.

43. Northern pike were more vulnerable to angling than walleyes during most months. The average weight of angler caught pike exceeded that of walleyes and they comprised the greater portion of total angling yield for the overall period.

44. Northern pike were most vulnerable to angling in late May whereas walleyes were most vulnerable during late June and July. Poor angling success for both species, especially walleyes, during the period of winter ice-cover was attributed to their reduced movement and feeding activity at low water temperatures.

45. Angling catches consisted primarily of northern pike, 50-70 cm in length and 5-7 years old, and walleyes 40-50 cm and 6-10 years old, representing dominant age and size classes in the mature populations. Larger fish, especially northern pike, appeared most vulnerable to angling during autumn.

46. In the short-term, sustained angling pressure on northern pike and walleyes in Savanne Lake would reduce angling quality since it is unlikely that compensatory growth and recruitment would immediately replace mature individuals selectively removed by angling.

47. The implementation of minimum size regulations in an effort to maximize yields and improve angling quality might prove detrimental. The increased recruitment of sub-legal fish would likely result in reduced growth and increased mortality within these populations because of high densities relative to available food.

48. Regulation of angling pressure by controlling access exists as an alternative management strategy that would allow the harvest of fish at sizes satisfactory to the angler and at levels compatible with the low productive capacities of boreal lakes such as Savanne.

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APPENDICES

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Appendix 1 , Table 1 . Mid-lake water temperatures (^{o}C) during ice-cover, Savanne Lake Ont., 1978.

Date	Bottom (4.25 m)	Mid-depth (2.0 m)	Surface (0.0 m)
January 4, 1978	3.0	1.0	0.25
February 5, 1978	3.4	1.5	0.25
March 5, 1978	4.0	1.9	0.25
April 9, 1978	4.0	2.7	0.25
December 4, 1978	3.0	1.6	0.25

Appendix 1 , Table 2 . Mean daily beach temperatures (^{o}C) recorded on northern pike spawning grounds (yellow beach), Savanne Lake, Ont., 1977-78.

Date	Temp. 1977	Temp. 1978	Date	Temp. 1977	Temp. 1978	Date	Temp. 1977	Temp. 1978
April 18	4.1	No record	May 8	10.6	4.7	May 28	23.1	20.1
19	4.1	"	9	11.4	4.2	29	21.0	18.5
20	4.1	"	10	12.8	4.7	30	19.9	15.8
21	4.4	"	11	13.5	6.8	31	19.1	14.7
22	4.4	"	12	15.7	8.6	June 1	17.4	13.6
23	*4.8	"	13	16.7	8.4	2	17.6	13.0
24	5.4	"	14	16.2	8.7	3	17.6	13.3
25	5.2	"	15	16.3	10.5	4	18.2	13.7
26	5.4	"	16	17.4	13.2	5	17.2	14.5
27	6.3	"	17	No record	17.1	6	17.5	15.6
28	6.3	"	18	"	18.8	7	15.9	15.1
29	8.4	"	19	"	18.6	8	15.7	14.1
30	9.8	"	20	"	14.7	9	16.6	14.4
May 1	10.1	"	21	"	10.1	10	16.8	14.7
2	10.0	"	22	"	11.9	11	16.3	15.3
3	10.8	"	23	"	13.7	12	17.4	16.4
4	10.7	4.9	24	15.3	14.5	13	17.9	15.9
5	10.8	4.9	25	20.6	16.5	14	17.0	14.8
6	9.7	4.8	26	21.1	17.4	15	16.2	15.3
7	10.0	*5.1	27	22.1	18.0	16	16.4	15.6

* Ice-out.

Appendix 2. The various species of aquatic plants, zooplankton, and benthos found in Savanne Lake (Sandhu 1979).

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 algea); *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*.

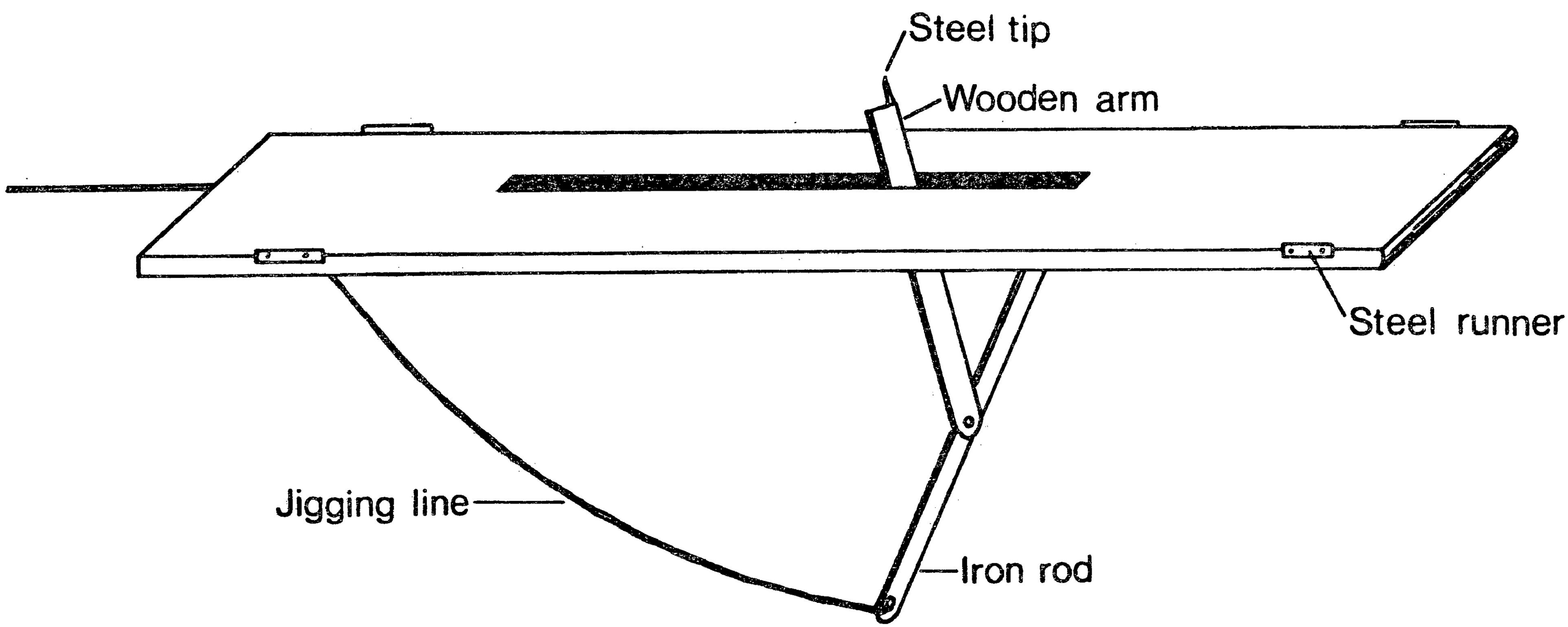
A qualitative sample of benthos made at depths of 0 to 4 metres from various stations gave the following results: Annelids found were leeches of the families: Glossiphoniidae; Erpobdellidae; aquatic earthworms of the orders Plesiopora and Prosopora; and flatworms of the class Turbellaria. Molluscs included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

Appendix 3, Table 1. Description of gill nets and number of net sets used in the assessment of the northern pike population structure in Savanne L., Ont., 1976 and 1978.

Date	Number of sets	Total length of net (m)	Depth of net (m)	Number of panels	Mesh construction	Mesh size (mm)
June 22-29, 1976	10	122.03	1.83	8	white, cotton multifilament	25, 38, 51, 64, 76, 89, 102 and 114 (stretched)
June 1-8 , 1978	11	1. 30.0	1.83		Swedish-type green multifilament	19 (square)
		2. 30.0	1.83		Swedish-type green multifilament	25 (square)
September 29-30, 1978	5	1. 45.8	1.83	5	white, monofilament	25, 38, 64, 89, 114 (stretched)
		2. 30.0	1.83		Swedish-type green multifilament	19 (square)
		3. 30.0	1.83		Swedish-type green multifilament	45 (square)

Appendix 4, Figure 1. Diagram of a creeping ice jigger.

Ice Jigger



Appendix 5, Table 1. Schumacher-Eschmeyer population estimates of adult northern pike vulnerable to trap nets in Savanne Lake, Ont., spring 1977. Values represented are the total number of fish marked in the population ($\sum Mi$), the number of fish recaptured on the i^{th} day (mi), the total sample taken on the i^{th} day (ni), and the estimated population size ($\hat{N}$).

Date		$\sum Mi$ (n)	mi (m)	ni (m + u)	$\hat{N}$
April	27	0	0	128	0
	28	101	0	71	0
	29	172	4	90	4923
	30	258	10	60	2258
May	1	308	4	58	2863
	2	362	6	59	3090
	3	415	8	41	2770
	4	448	7	37	2674
	5	478	8	31	2489
	6	501	4	19	2477
	9	516	4	35	2677
	10	547	8	17	2416
	11	556	13	78	2620
	12[a]	620	13	55	2621
	13	662	10	45	2671
	17	695	24	70	2503
	18	740	7	29	2545
	19	762	12	27	2448
	20	777	13	30	2373
	25	794	8	22	2361
	26	806	1	11	2415
	27	816	1	6	2436
	30	820	1	12	2499

[a] End of estimate.

$$N = \frac{\sum[(\sum Mi)^2 ni]}{\sum[(\sum Mi) mi]}$$

Computations for Schumacher-Eschmeyer confidence limits for northern pike in the spring of 1977:

$$\hat{N} = \frac{\sum[(\sum Mi)^2 ni]}{\sum[(\sum Mi) mi]} = \frac{106613796}{40684} = 2621$$

$$S^2 = \frac{\sum\frac{(mi^2)}{(ni)} - \frac{\sum[(\sum Mi)\ mi)^2]}{\sum[(\sum Mi)^2 ni]}}{m - 1}$$

$$= \frac{17.985 - \frac{(40684)^2}{106613796}}{14 - 1}$$

$$S^2 = \frac{17.985 - 15.525}{13} = 0.18923$$

$$S = 0.435$$

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

$$S.E.\ \frac{1}{\hat{N}} = \frac{S}{\sqrt{\sum[(\sum Mi)^2 ni]}} = \frac{0.435}{\sqrt{106613796}} = 0.0000421$$

The 95% confidence range for $\frac{1}{\hat{N}}$ is computed (Schumacher and Eschmeyer, 1943) when t with $m - 1 = 13$ degrees of freedom $= 2.16$

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

$$= 0.000382 \pm 2.16 \times 0.0000421$$

$$= 0.000382 \pm 0.0000909$$

$$C.L._1 \quad \frac{1}{\hat{N}} = \frac{1}{0.000291} \qquad \hat{N} = 3436$$

$$C.L._2 \quad \frac{1}{\hat{N}} = \frac{1}{0.000473} \qquad \hat{N} = 2119$$

Population Estimates = 2621 ± 659

Appendix 5 , Table 2 . Schumacher-Eschmeyer population estimates of adult northern pike vulnerable to trap nets in Savanne Lake, Ont., spring 1978.

Date	$\sum$ Mi (n)	mi (m)	ni (m + u)	$\hat{N}$
May 8	0	0	90	0
9	90	5	73	1314
10	157	3	140	4389
11	287	22	151	2278
12	393	21	80	1862
13	450	3	18	1929
14	465	15	83	2118
15	532	11	69	2358
16	590	14	88	2652
17	663	24	82	2537
18	717	2	8	2547
19	723	13	42	2516
23	751	4	15	2529
24[a/]	762	5	14	2508
25	771	4	10	2405
26	777	0	7	

[a/] End of estimate

Computations for Schumacher-Eschmeyer confidence limits for northern pike in the spring of 1978:

$$\hat{N} = \frac{\sum[(\sum Mi)^2 ni]}{\sum[(\sum Mi) mi]} = \frac{179289949}{71484} = 2508$$

$$s^2 = \frac{\sum\frac{(mi^2)}{(ni)} - \frac{\sum[(\sum Mi)\ mi)^2]}{\sum[(\sum Mi)^2 ni]}}{m - 1}$$

$$= \frac{30.717 - \frac{(71484)^2}{179289949}}{14 - 1}$$

$$s^2 = \frac{30.717 - 28.501}{13} = 0.1705$$

$$S = 0.4129$$

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

$$S.E.\ \frac{1}{\hat{N}} = \frac{S}{\sqrt{\sum[(\sum Mi)^2 ni]}} = \frac{0.4129}{\sqrt{179289949}} = .0000308$$

The 95% confidence range for $\frac{1}{\hat{N}}$ is computed (Schumacher and Eschmeyer, 1943) when t with m - 1 = 13 degrees of freedom = 2.16.

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

$$= .0003987 \pm 2.16 \times .0000308$$

$$= .0003987 \pm .0000665$$

$$C.L._1\ \frac{1}{\hat{N}} = \frac{1}{.0004652} \qquad \hat{N} = 2150$$

$$C.L._2\ \frac{1}{\hat{N}} = \frac{1}{.0003322} \qquad \hat{N} = 3010$$

Population Estimates = 2508 $\pm$ 430