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Initial effects of the exploitation of walleye, Stizostedion vitreum vitreum (Mitchill) on the boreal percid community of Henderson Lake, Northwestern Ontario

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Initial Effects of the Exploitation of Walleye *Stizostedion vitreum vitreum* (Mitchill) on the Boreal Percid Community of Henderson Lake, Northwestern Ontario

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

by

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DECLARATION

The research presented in this thesis was carried out by the author, and has not been previously submitted for credit toward any degree or diploma. The work of others, where included, has been appropriately cited.

ABSTRACT

The effect of large scale exploitation of walleye *Stizostedion vitreum vitreum* on the boreal percid community of Henderson Lake, northwestern Ontario, was studied from 1979 to 1981. Investigations centered on the two major predators in the community, the walleye and the northern pike *Esox lucius*. Population estimates were done in 1979, 1980 and 1981, and the accuracy of Schnabel, Schumacher Eschmeyer and Peterson estimates were compared. Previous to exploitation (1979-1980) both walleye and northern pike exhibited the lowest production and $P/\overline{B}$ ratios yet recorded for either species (walleye 4-14 yrs, P=1.01 $kg ha^{-1} yr^{-1}$, $P/\overline{B}$ =0.137; northern pike 7-14 yrs, P=0.716 $kg ha^{-1} yr^{-1}$, $P/\overline{B}$ =0.086). Low production in both species was partially attributed to competition for major prey species, and the small size of available prey items. Sticklebacks *Pungitius pungitius*, yellow perch *Perca flavescens*, and mayfly subimagoes Ephemoptera sp. were the most important prey items in the lake. Long-term patterns of prey utilization by both predators showed considerable annual variation. Abundant white sucker and cyprinid species were not important in the diet of either walleye or northern pike, and may represent a net energy loss to the production of these two species.

In summer 1980, a total of 1332 walleye (5.43 $kg \cdot ha^{-1}$) were removed by trap and gill netting, exceeding the calculated potential yield (PYI) of 4.93 $kg \cdot ha^{-1} yr^{-1}$. In the 1980-1981 season production of walleye decreased 35% (4-14 yrs, P=0.651 $kg \cdot ha^{-1} yr^{-1}$) and the $P/\overline{B}$ ratio dropped to 0.118. The size of the catchable population of walleye was maintained by increased recruitment of 2,3 and 4 year old fish. These age groups showed significantly increased growth, and earlier maturity compared to fish of similar ages in 1980. These changes may reflect compensatory growth responses due to exploitation. No similar changes were seen in the northern pike population or in walleye older than 4 years. Yellow perch increased in the diet of both predators, but this could not be solely attributed to the removal of adult walleye. The use of a mean age of the population index to indicate exploitive stress in fish populations is discussed, and possible results of continued exploitation are considered.

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1. INTRODUCTION

The harmonic percid community (Ryder and Kerr 1978) consists of four co-occurring basic components; walleye, Stizostedion vitreum vitreum, northern pike, Esox lucius, white sucker, Catostomus commersoni and yellow perch, Perca flavescens. Each contribute to the persistence and continuing integrity of the community through regular and definite patterns of competitive interactions (Ryder and Kerr 1978). Community structure is thus not static but a balance of the four species, and varies along climatic and trophic clines (Adams and Olver 1977, Kerr 1977, Ryder and Kerr 1978). Prey size (Kerr and Ryder 1977), light intensity (Ali et al. 1977, Kerr and Ryder 1977, Ryder 1977) and species temperature preferences (Hokanson 1977, MacLean and Magnuson 1977) are considered important to the maintenance of this community structure.

Boreal percid communities of northern Ontario have been characterized as having a low net production, high community stability and conservation of biomass (Adams and Olver 1977, Kelso and Bagenal 1977). The complex species interrelationships necessary to maintain community structure in the face of inherent low productivity make such boreal percid communities extremely susceptible to exploitive stress. Ostensibly commercial fishery exploitation destabilizes such communities by disrupting their structural complexity and the self-regulation thought to be inherent in percid community organization (Adams and Olver 1977, Spangler et al. 1977a).

In this study therefore, I characterized the unexploited percid community of Henderson Lake in terms of growth, production and biomass of its two major community components, the walleye and the northern pike, and studied the inter- and intraspecific relationships within the community through studies of patterns of prey utilization by walleye and northern pike. I assessed the relative importance of walleye and northern pike in shaping and maintaining the structural complexity of the community, and attempted to determine if either could be considered a keystone predator; whose abundance and activities within the community were most responsible for the integrity and persistance of the community structure (Paine 1969). Most importantly I measured the initial effects of large scale removal of walleye on the growth and production of walleye, and on the community as a whole.

2. MATERIALS AND METHODS

2.1 Study area

Henderson Lake, one of five restricted lakes in the Savanne Lake Research Area is located approximately 135 km northwest of Thunder Bay (Figure 1). Henderson Lake is a small (150.9 ha), relatively shallow lake (mean depth 2.5 m, maximum depth 5.25 m). It is 3.0 km long with a maximum width of 1.0 km. Its major axis lies in a northeast southwest alignment. A small chain of islands and shallows divides the lake into two major portions. The large southern basin has a steeply sloping littoral zone and a broad flat floor. The littoral area is composed of sand, gravel and cobble, while the floor is very flocculent (Figure 2). The shallower northern basin contains numerous mud banks and rubble reefs (Figure 2). The prevailing wind is from the west to southwest. The physical and chemical characteristics of Henderson Lake are summarized in Table 1. The lower morphoedaphic index (M.E.I.) (Ryder 1965), and potential yield index (P.Y.I.)(Colby 1982) suggest that Henderson Lake is less fertile than nearby Savanne Lake (Mosindy 1980, Sandhu 1978).

Since 1969, this lake has been a provincial fish sanctuary, closed to sport fishing. Previous to 1969, poor accessibility kept fishing pressure low.

Fish species found in the lake include walleye, Stizostedion vitreum vitreum; northern pike, Esox lucius; yellow perch, Perca flavescens; white sucker, Catastomus commersonii; burbot, Lota lota; mimic shiner, Notropis volucellus; black nosed shiner, Notropis heterolepis; Iowa darter, Ethestoma exile; and ninespine stickleback, Pungitius pungitius.

Figure 1. Map showing the location of Henderson Lake.

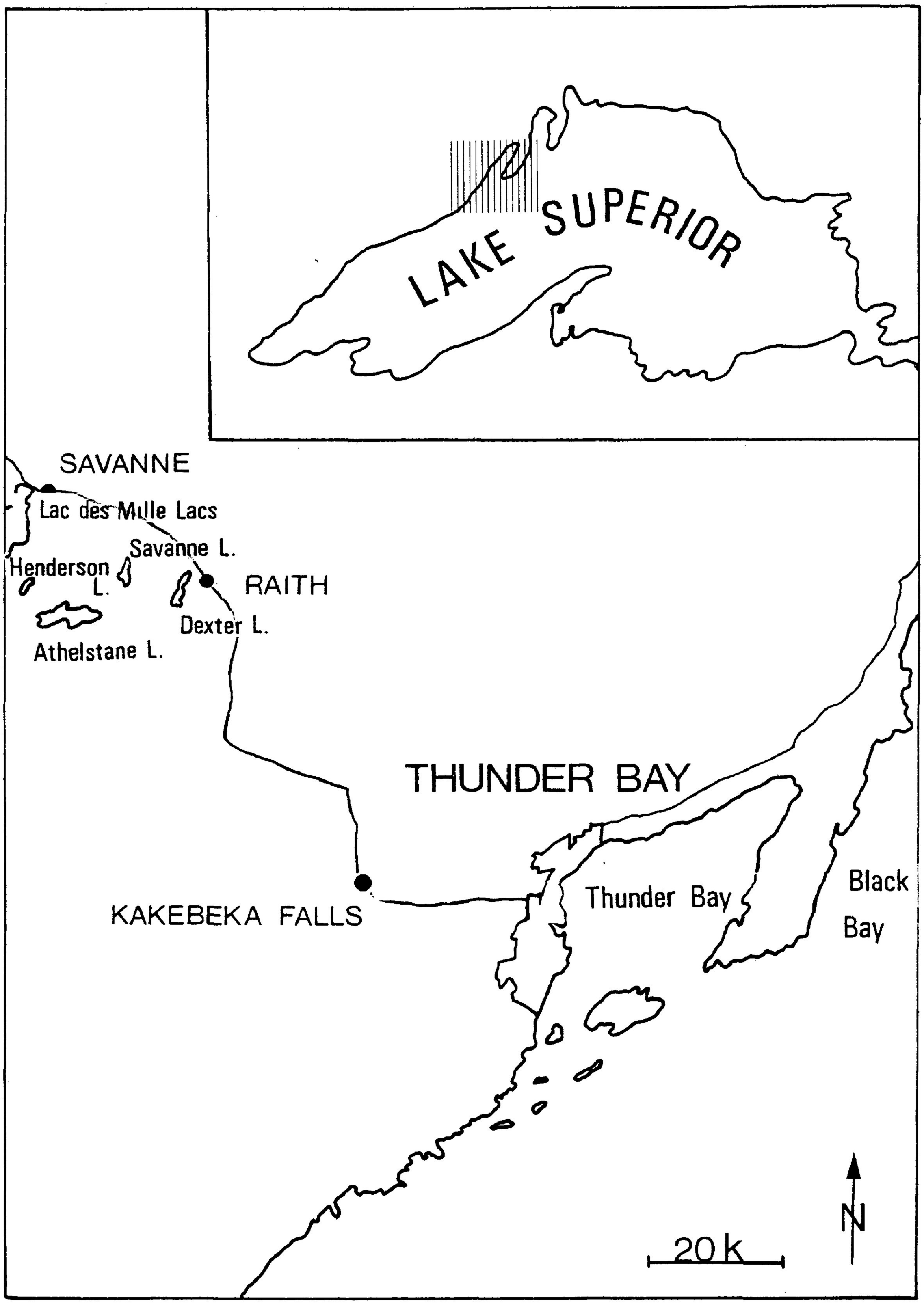
LAKE SUPERIOR
SAVANNE
Lac des Mille Lacs
Savanne L.
Henderson L.
RAITH
Dexter L.
Athelstane L.
THUNDER BAY
KAKEBEKA FALLS
Thunder Bay
Black Bay
N
20 k

Figure 2. A. Depth contour map of Henderson Lake. Depth contours are given in meters.

B. Bottom type map of Henderson Lake. Categories are : ooze ; mud ; sand ; gravel ; and cobble .

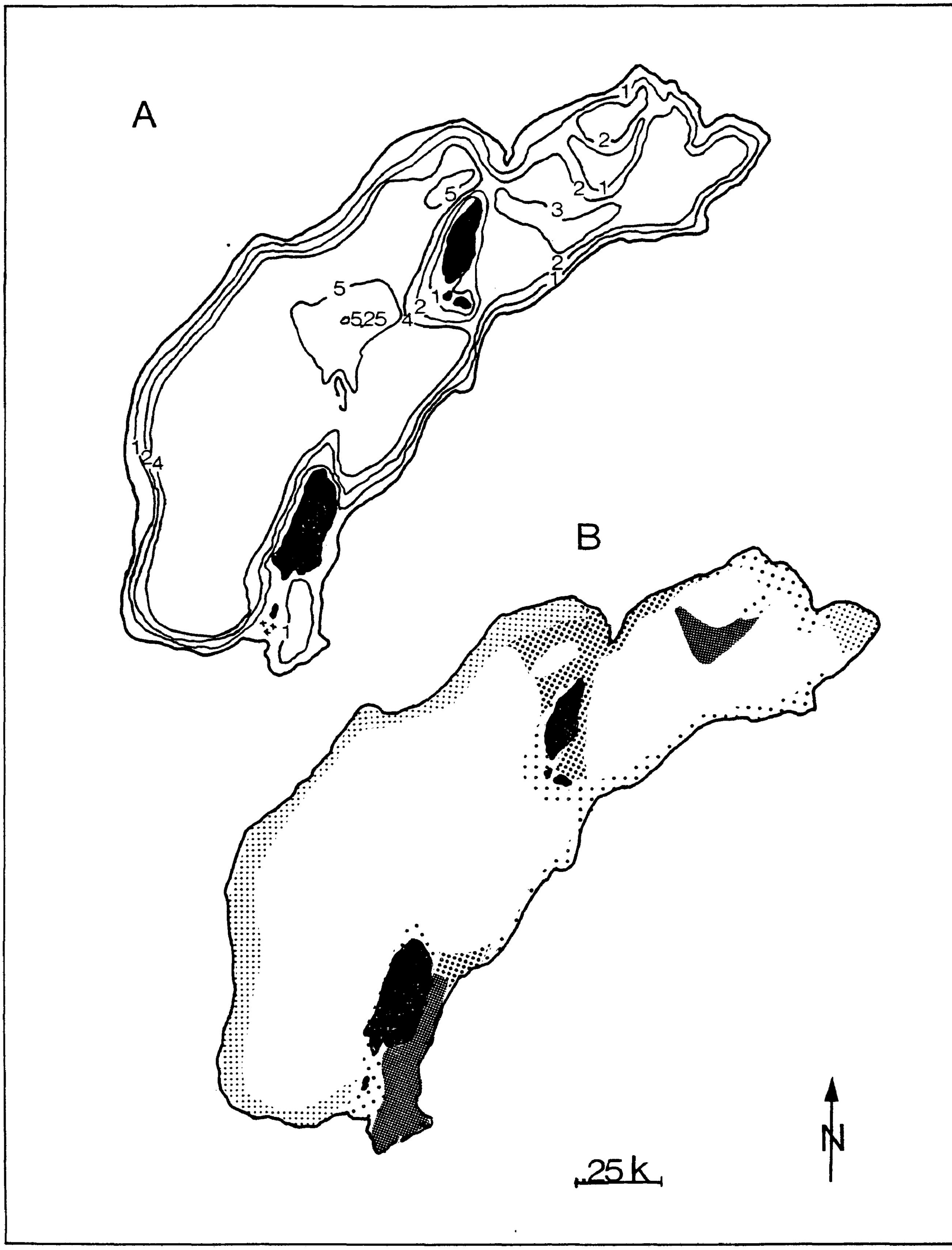
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Table 1. Major physical and chemical characteristics of Henderson Lake.

Date recorded	14 May 1973	14 July 1980
Conductivity (mh)[1]	38.0	49.0
Total dissolved solids (T.D.S.)	40.0	41.0
Hardness $CaCO_3$ (mg/l)	14.0	20.0
Turbidity (F.T.U.)[2]	2.0	0.75
pH[3]	7.2	7.5
Volume (m^3)	3.63×10^6	
Morphoedaphic index (M.E.I.)[4]	16.4	
Potential yield index (P.Y.I.) (kg ha^{-1} yr^{-1})[5]	4.9	

[1] mh = μmhos/cm^2

[2] F.T.U. = Formazine turbidity units

[3] preserved sample

[4] (M.E.I.) = (T.D.S. / mean depth)

[5] (P.Y.I.) = $1.4(\text{M.E.I.})^{0.45}$

2.2 Population estimates

In 1979, 1980 and 1981, mark and recapture estimates were made of walleye and northern pike populations. In 1979 Schumacher Eschmeyer population estimates (Ricker 1975) were begun 24 May and ended 30 June. All areas of the lake were sampled by 1.82 m (6 ft) and 1.22 m (4 ft) standard Lake Erie design trapnets (Mosindy 1980). A variety of lead lengths, 18.3 m (50 ft), 36.6 m (100 ft) and 73.2 m (200 ft) were employed to allow the best set according to water depth at each location. In 1980, Schumacher Eschmeyer estimates were begun 1 May and continued until 25 May. An additional third trap net size of 2.44 m (8 ft) was used. In 1981, a modified Schumacher Eschmeyer or Schnabel (Ricker 1975) population estimate was used, in which recaptured fish, identified by a second clip, were not considered recaptures upon subsequent recapture. The population estimate began 21 May and ended 28 June. Trapnets of all sizes; 1.22 m, 1.82 m, and 2.44 m were used.

All areas of the lake were sampled each year (Figure 3). Nets were frequently moved either when catches diminished, or if the number of recaptures in the net began to increase.

In 1981, a Peterson estimate was carried out during the walleye removal to check the results of the Schnabel population estimate. Walleye being removed from the lake were checked for appropriate 1981 clips (Figure 4). Recaptured pike, clipped in 1981, were again clipped by notching the dorsal fin (Figure 4), released, and were not counted upon subsequent recapture.

In all three years a similar sampling and marking procedure was followed. Trapnets were checked daily. Total length of each new fish was measured to the nearest mm, and weight was determined to the nearest 10 g using a Chattilion tube type scale. Sex was determined on the basis of extruded

Figure 3. Locations of trapnet sets during population estimates, 1979-1981, Henderson Lake. Numbers indicate trapnet locations referred to in Sections 2.8 and 3.7.

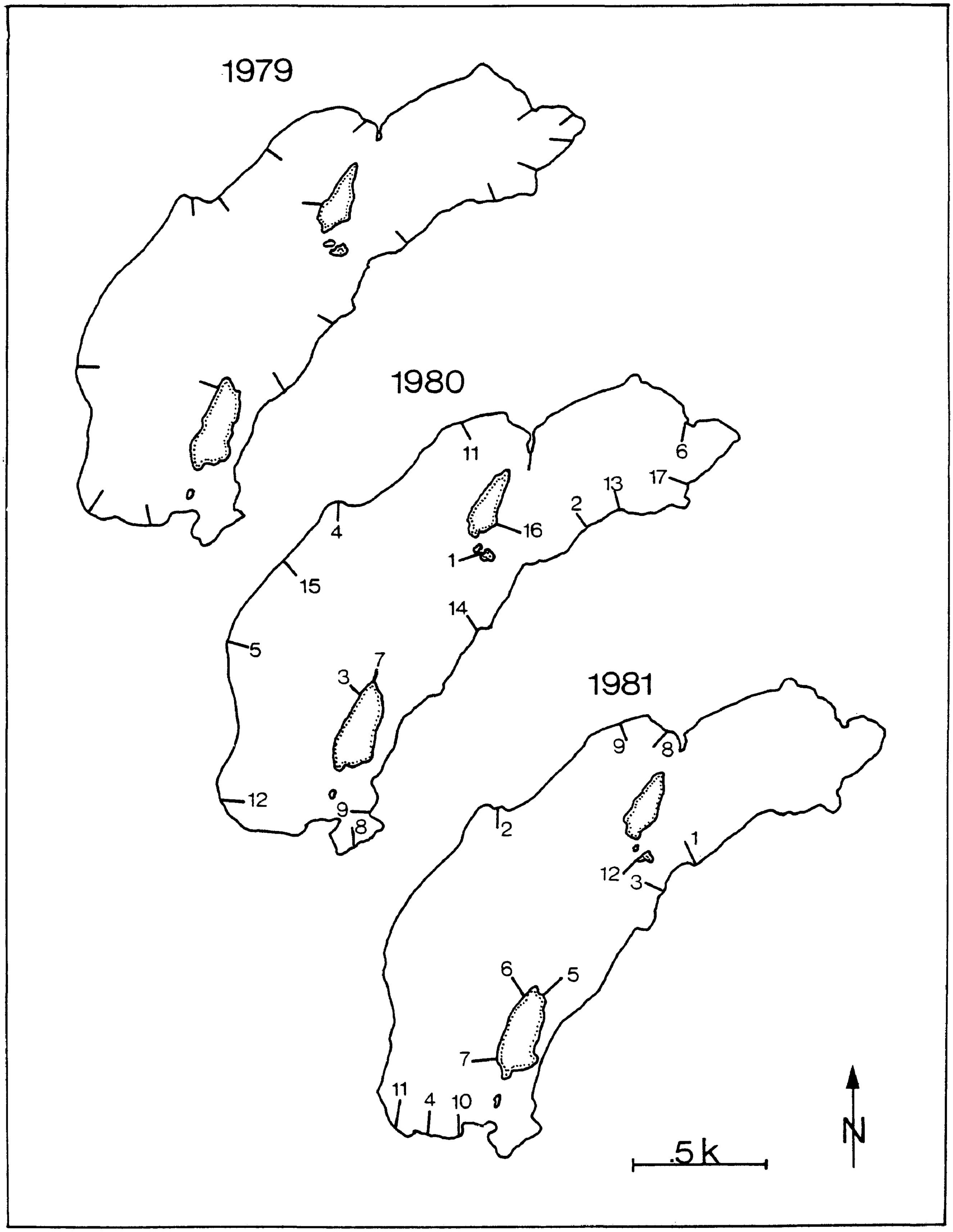
1979
1980
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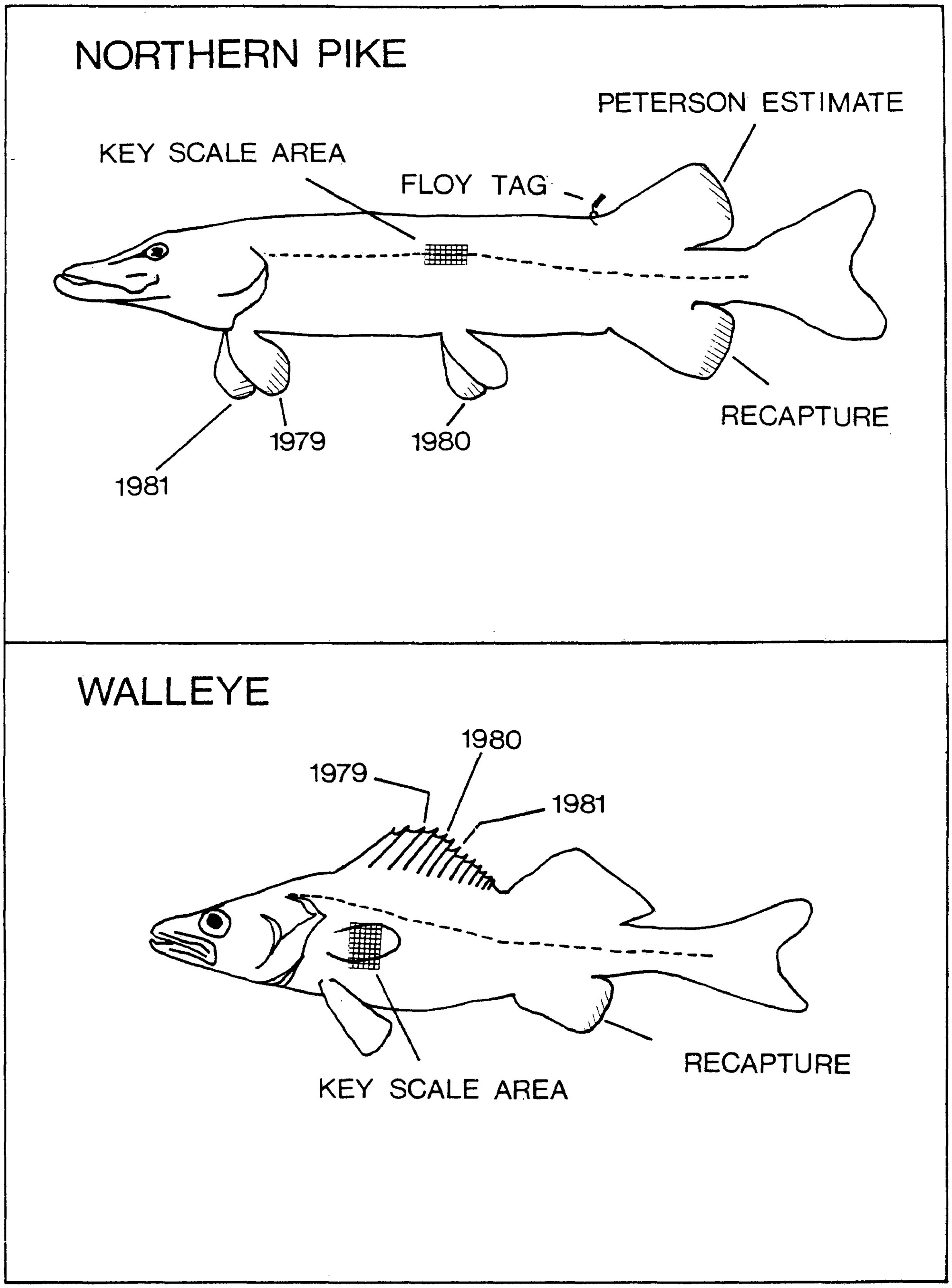
Figure 4. Illustration of key scale areas, location of floy ribbon tags, and the spines and fins clipped to mark walleye *Stizostedion vitreum vitreum*, and northern pike *Esox lucius*, Henderson Lake. Years refer to the year the fin or spine was clipped. Recapture indicates the second fin clipped during Schnabel estimates, done in 1981.


NORTHERN PIKE
PETERSON ESTIMATE
KEY SCALE AREA
FLOY TAG
RECAPTURE
1979
1980
1981
WALLEYE
1980
1979
1981
KEY SCALE AREA
RECAPTURE

gonadal products whenever possible. In 1981, the sexes of captured northern pike were determined using the external urogenital method (Casselman 1974a). Fish were checked for previous marks (in 1980 and 1981) and were appropriately clipped (Figure 4). Spines clipped from walleye were retained for aging purposes. Several scales were removed from the key scale area of each fish (Figure 4) and stored in scale envelopes for aging. The fish were then released.

Processing of recaptured fish varied each year. In 1979, the recapture was noted, and the fish released. In 1980, length and weight were measured, sex and previous clips were noted before releasing the fish. In 1981, length was measured, previous clips were noted, and the fish was then reclipped (Figure 4) before release.

All fish were immersed in a solution of malachite green previous to release to reduce potential infection due to handling. Fish were released in the immediate area of the net in which they were captured. Total numbers of marked and recaptured fish are given in Appendix 1.

2.3 Age and growth

Northern pike and walleye were subsampled to determine age composition, growth rates and sex ratios. The majority of fish used in age and growth studies were collected within two weeks of the completion of population estimates. Fish from feeding and removal samples were used to supplement length intervals with small sample sizes.

Fish were captured using trapnets and standard test gill nets (Appendix 2). Length-weight measurements were taken following the procedure described during population estimates. Sex and the stage of maturity of each fish were determined by internal examination. A number of scales were removed from the key scale area of each fish (Figure 4) to be used for aging. The same spine in the dorsal series clipped to mark walleye during the population estimate was removed and stored. In addition bony structures were removed from a subsample of fish for use in aging. Walleye opercles, a wide flat bone of the opercular series and northern pike cliethra, a long flat bone of the pectoral girdle were retained. These bones, cleaned of muscle and connective tissue, were stored with the scale samples.

Scales from each fish were mounted on a plastic acetate slide and pressed by a hand roller to obtain scale impressions (Bagenal and Tesch 1978). They were enlarged using an Eberbach scale reader, using a 32 mm lens at 30X magnification. Attempts to read the scale impressions according to the criteria of various authors (Frost and Kipling 1959, Casselman 1967, Bagenal and Tesch 1978, Campbell and Babaluck 1979) proved inconclusive. Annuli on the scales of both species were illdefined. I therefore decided not to use scales to determine age of Henderson Lake fish.

Opercles and cliethra were prepared for reading by cleaning and drying. In 1980, bones were cleaned by soaking in hot but not boiling water and then rubbing with a fine brush (Campbell and Babaluck 1979). This was found to cause numerous surface scratches and clouding of the bone, making the annuli indistinct. In 1981, bony structures were soaked in cold water for not less than two weeks. After soaking, the flesh rotted off and could easily be removed by rubbing with a soft cloth. Since little or no damage resulted, this method was adopted.

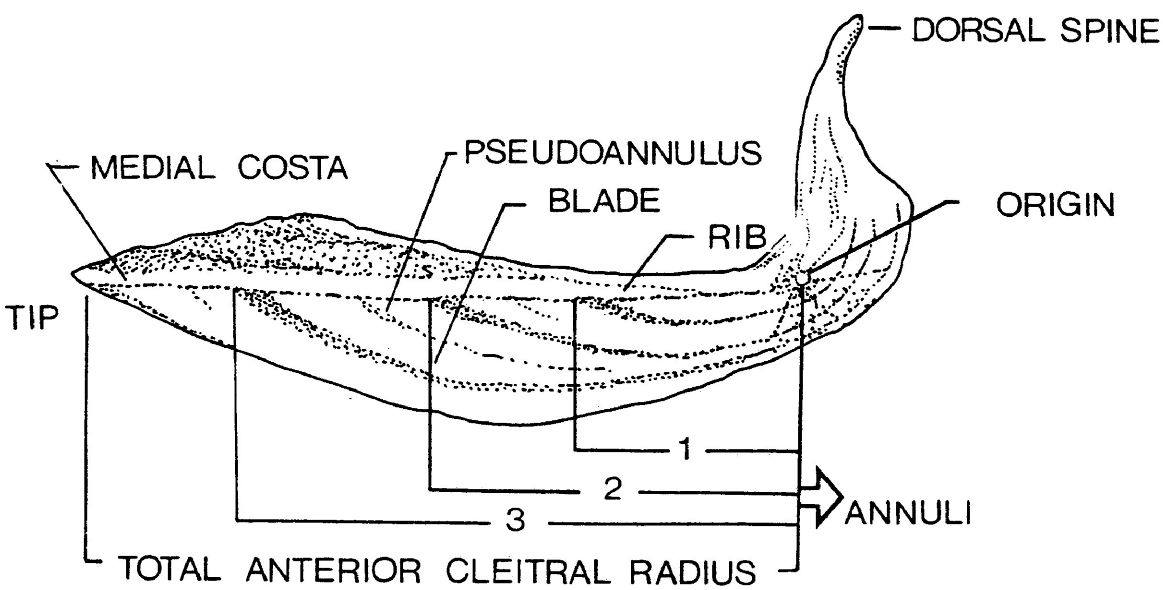
Once cleaned, opercles and cliethra were examined under a low power dissecting microscope against a black background (Casselman 1974b) under reflected light (Campbell and Babaluck 1979). The age of each fish could be determined by examining the patterns of translucent and opaque bands on the bony structure. Translucent bands represent winter periods, and the broader opaque bands represent the faster summer growth (Le Cren 1947, Casselman 1974 b, Bagenal and Tesch 1978). A 10% alcohol solution was applied to the surface of the bony structures to reduce the confusing effect of surface scratches. The bands representing the first several years of growth were more apparent after application of alcohol (Bagenal and Tesch 1978). The end of a translucent band and beginning of an opaque band was considered a true year mark (Le Cren 1947, Casselman 1978). True annuli showed a distinct margin between the two bands, which extend completely from anterior to posterior portions of the cliethra, or completely across the blade of the opercle. Pseudoannuli, or false year marks were common on both opercles and cliethra. False annuli were less distinct and often did not extent the entire length or width of the bone. False annuli often appeared within a summer growth band and were distinguished by their abrupt change from an opaque zone to a thin transparent zone followed by an opaque zone (Le Cren 1947).

Opercles and cliethra were measured to the nearest 0.01 mm using needle tipped calipers. Cliethra were measured from the origin to where each true annuli intersected the medial costa of the blade (Figure 5). Opercles were measured from the origin (Le Cren 1947) to the point where each true annuli intersected the edge of the blade (Figure 5).

Mean length at age was determined for both sexes. Data for back calculations of growth were obtained from all fish aged. Calculations of bony structure - body growth relationships were determined by the method of Le Cren (1947). The following formula was used to determine corrected back calculated growth:

$$F(x) = F(y) \frac{B(x)^a}{B(y)^a}$$

Figure 5. Diagram of a cliethra and an opercle, indicating the appearance and location of the origin, true and pseudoannuli, and the measurements used in aging northern pike *Esox lucius* and walleye *Stizostedion vitreum vitreum*, respectively.


DORSAL SPINE
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1
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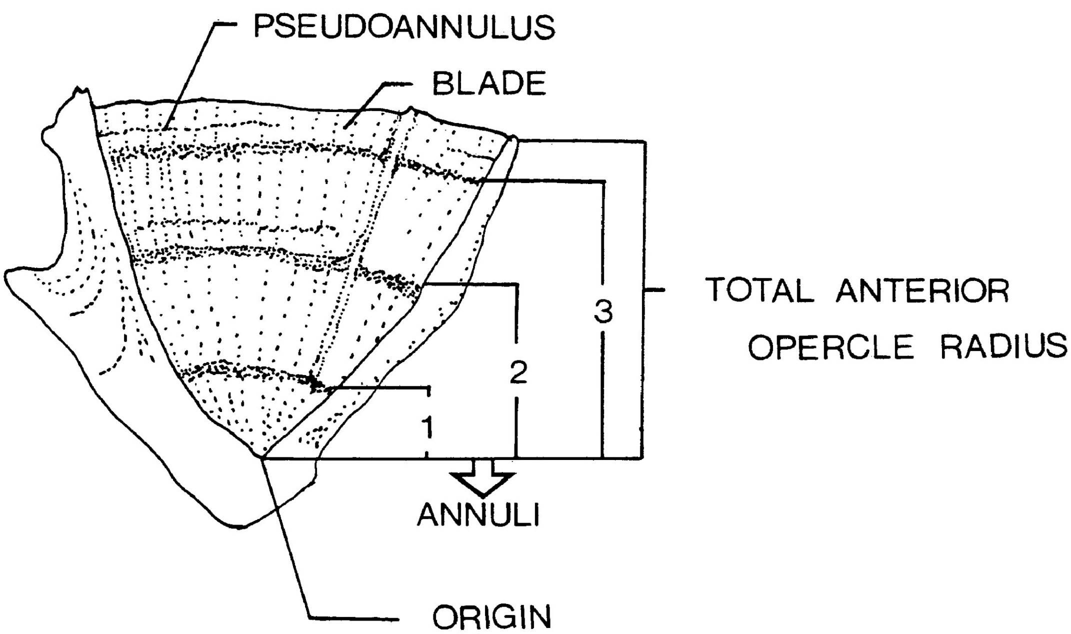
ANNULI
TOTAL ANTERIOR CLEITRAL RADIUS


PSEUDOANNULUS
BLADE
3
TOTAL ANTERIOR
OPERCLE RADIUS
2
1
ANNULI
ORIGIN

where B(x) = length of aging structure at a particular age, F(x) = the corresponding length of fish, B(y) = final length of aging structure, F(y) = final length of fish and a = the correction between assumed allometric growth and the actual pattern of growth. Corrected back calculated lengths were used to determine patterns of yearly growth. Absolute growth increments (Ricker 1975) were calculated for both males and females. Back calculated ages were used to determine length at age (and age frequencies) for both species in 1979. The 1979 length frequencies were not subdivided by sex because of insufficient sex ratio data.

Spines of walleye captured in 1980 were used to check ages based on opercles. Spines of fish aged by opercles were mounted in acetate, sectioned (Campbell and Babaluk 1979) and mounted on glass slides. They were examined under a medium power microscope under transmitted light, and the growth rings were counted. Ages obtained were compared to those determined using opercles.

Total numbers of each age group were calculated according to Ketchen (1949). The aged subsample was divided into 5 cm intervals, with the numbers of each age group within an interval expressed as a percentage. This percentage was applied to the number of fish within that interval, estimated during the population estimates.

Mean lengths for combined sexes and males of ages not represented in the aging sample were estimated from mean growth increments and back calculated lengths. Sex ratios were determined from fish killed for age and growth studies. Sex of killed fish was determined by internal examination. The sex ratio obtained from the aged subsample was applied to the total population.

2.4 Length-weight relationships

Length-weight relationships were determined for each species in 1979, 1980 and 1981. In 1980 and 1981, length-weight relationships were also calculated for males and females separately.

Regression lines were determined using the formula :

$$\log \text{weight} = \log a + b \log \text{length}$$

where log a represents the y intercept and b the regression coefficient (Ricker 1975).

2.5 Condition and effects of marking

During the 1981 removal, walleye and northern pike were examined to determine the effects of marking and handling during the population estimates in the two previous years. Fulton's condition index (Ricker 1975, Colby et al. 1979) was used to compare fish which had been marked once, twice, or which were unmarked.

Fish not previously marked, and assumed not to have been handled were compared to fish which had been marked in either 1979 or 1980, and fish that were marked both in 1979 and 1980.

2.6 Maturity

Male and female walleye removed from the lake during August of 1980 and 1981, and October 1981 were used to determine the mean age at maturity. During the removal fish were examined and the condition of the gonads recorded. Ovaries were classed as mature if they showed well developed eggs, and the fish appeared capable of spawning the next year. Maturing virgins (Kestevan 1960) were noted as having large reddish ovaries, but few, if any , visible eggs. Male testes were classed as mature if they showed obvious development. Fish with undeveloped gonads were classed as immature.

The weighted mean percentage of maturity was calculated for each group of each sex in both years. The mean age of maturity was calculated by the regression method, and a corrected version of Abrosov's formula (Lysack 1980), and the rate of maturity was determined.

Numbers of northern pike sampled were insufficient to determine a mean age of maturity, or rate of maturity. The lengths of both mature and immature females captured in spring 1980, and fall 1981 were compared to length at age to estimate an age of maturity.

2.7 Fecundity

Walleye and northern pike were sampled at various times form 1979 to 1981 to determine total egg production and the relationship between body length, weight and total fecundity. Fish were sampled using gillnets (Appendix 2) during October 1979, March and April 1980, March 1981 and October 1981, specifically for fecundity samples. In addition ovaries of mature females caught in August 1980 were also kept. All fish captured were examined for sex, gonadal condition and length and weight were measured. Ovaries were removed from obviously mature females in springtime, or in an advanced state of development in the fall, wrapped in cheese-cloth and individually stored in 5% formalin.

Once the eggs had hardened in formalin, total number of eggs per female was determined by the gravimetric method (Wolfert 1969, Bagenal and Braum 1978). Excess surface moisture was removed and each ovary was weighed individually. Three subsamples were taken from each left ovary at the anterior, mid and posterior regions. Each subsample was weighed and the number of eggs in each was counted. Egg counts from all three subsamples were combined to determine the mean number of eggs per gram. This figure was multiplied by the total ovary weight to determine the total number of eggs per female.

2.8 Movements

Movements of fish in the lake were determined from recaptures of marked and tagged fish. In June 1980, 16 walleye caught in the north end of the lake (Location 2, Figure 3) were marked by clipping the dorsal tip of the caudal fin, and 39 walleye caught in the south basin (Location 3, Figure 3) were marked by clipping the ventral tip of the caudal fin. Subsequent recaptures of these fish were noted as to date and location within the lake.

In August 1980, 162 northern pike were tagged with Floy ribbon tags. Fish were anesthetized in a solution of tricaine methane sulphonate (MS-222) and quinaldine sulphate (60:20 mg/litre). Length, weight and marks were recorded as described in Section 2.2. Each numbered ribbon tag was affixed by passing a black polypropylene thread around the pterigiophore under the dorsal fin (Figure 4) and tying the tag to this line. The end of the line was then fused to the tag by heating to avoid tag loss. The fish were dipped in malachite green and released.

All recaptured previously tagged pike were measured for length and weight, and tag number, date and the location of capture were recorded before fish were released.

2.9 Removal

Fish sampled for aging and growth, fish caught during fecundity studies, and fish captured for feeding analysis, as well as fish taken from the lake during controlled harvest efforts were included in the removal totals. In

1980, controlled harvest began 1 August and ended 26 August. Trapnets and trapnet locations were similar to those employed during the 1980 population estimate (Figure 3). Northern pike and white sucker captured were released alive. All walleye captured were killed by cervical dislocation. I measured length and weight, and recorded all marks from previous population estimates. Sex of each walleye was determined by internal examination of the gonads.

In 1981, removal began immediately after the completion of the population estimates (28 June) and continued until 20 August. During the first two weeks, all fish caught were sampled for age and growth studies (Section 2.3). Once a 10% stratified random subsample (Ketchen 1949) was achieved, white suckers and northern pike were measured for length and weight, marks and/or tags were noted and the fish was released. All walleye caught were killed and sampled as they had been in 1980.

2.10 Biomass and production

Annual production and biomass were calculated for both walleye and northern pike for the 1979-1980 and 1980-1981 season (Ricker 1975). Estimates for the 1979-1980 season were calculated using back calculated lengths to determine the 1979 age groups. Because of a lack of sex ratios for the 1979 data I was not able to calculate a separate production estimate both for males and females. Separate production and biomass estimates were done for each sex in 1980-1981. Whenever possible observed weights were used in the calculations, but if necessary, missing weights were calculated from length-weight equations (Section 2.3).

2.11 Feeding analysis

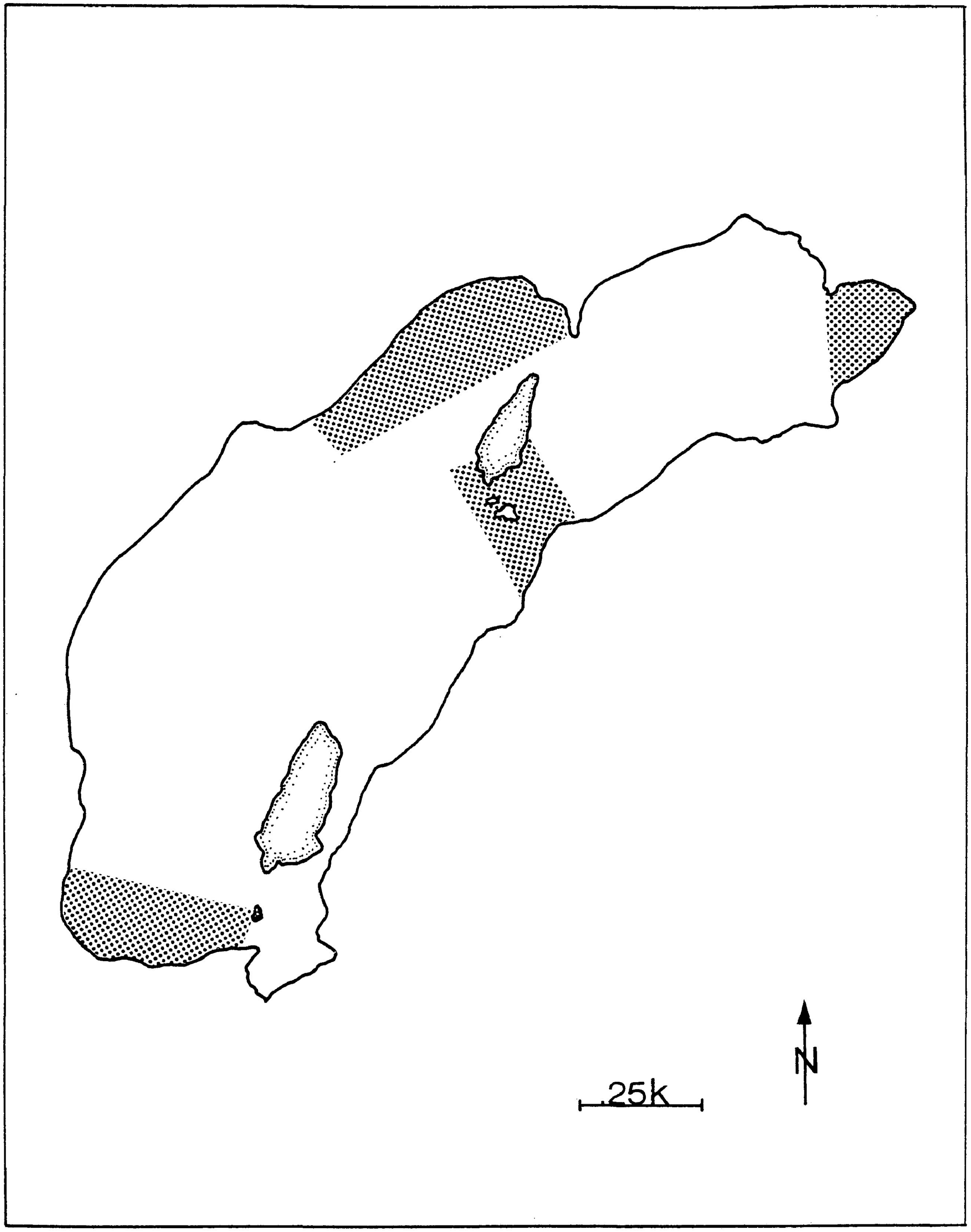
Feeding studies were carried out from fall 1979 to fall 1981. Stomach samples from the summers of 1980 and 1981 were supplemented with samples from October 1979, March and April 1980, March 1981 and October 1981. A total of 557 northern pike and 752 walleye stomachs were examined. Only stomachs containing food were included in the calculations.

In 1980 sampling began 4 June. Four areas of the lake were chosen as sampling sites (Figure 6). Each area was widely separated and had both different bottom types and orientation with respect to the prevailing wind. Standard test mesh gill nets were set randomly within each area, during three times of day; dawn, 0400-0800, midday, 1200-1700, and dusk, 2000-2400. Nets were lifted after a maximum of four hours. Walleye and northern pike were taken from the net, and immediately killed by cervical dislocation. Each fish not immediately sampled had a 10% formalin solution introduced to the stomach via a syringe and stomach tube to halt digestion. Fish were examined for marks, length and weight were measured, and sex was determined by internal examination of the gonads. The stomach was cut at the entrance of the esophagus to the stomach, and at the pyloric valve, and preserved in a 10% formalin solution in an individual whirl-pak. Any regurgitated food items found in the throat and mouth were added to the sample.

In 1981, sampling began 29 June and ended 15 August. Methods were similar to those described for 1980. Stomachs were also taken from fish caught for fecundity samples in spring and fall 1979 to 1981. During these periods nets were left in overnight to offset low catches.

Stomachs were opened and contents blotted to remove excess moisture. When possible food items were identified to species or genus . Unrecognizable items were grouped as fish or invertebrate remains. Counts of recognizable

Figure 6. Location of sampling areas used during feeding studies, 1980-1981, Henderson Lake.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food items were made. Total length of intact food items were measured. The total volume of each food category in the stomach was determined volumetrically (Hyslop 1980).

Frequency of occurrence and percentage of total volume (Hyslop 1980) were calculated for each food item found in walleye and northern pike stomachs. Comparisons were made with incidental feeding data gathered in 1969, 1977 and 1978 by the Fisheries Research Branch of the Ontario Ministry of Natural Resources. Length frequencies of walleye and northern pike sampled for stomach contents in 1980 and 1981 were divided into five and ten cm length intervals, and frequency of occurrence of food items within each length interval was determined.

3. RESULTS

3.1 Population estimates

Walleye and northern pike populations were higher in 1980 than in 1981 (Table 2). Schnabel population estimates done in 1981 indicated that the Schumacher Eschmeyer estimate was affected by the number of multiple recaptures (Table 3). Schnabel estimates for walleye and northern pike were 22% (264/1179) and 25% (262/1048) higher than the corresponding Schumacher Eschmeyer estimates. Peterson population estimates for walleye were 17% (159/1179) higher than the Schumacher Eschmeyer estimates, while Peterson estimates of northern pike were 12% higher (127/1048). Estimated numbers of walleye in 1979 were increased by 1.25 x to correct for sampling variability due to seasonal variation in catchability of the fish.

Length frequencies of walleye in 1979, 1980 and 1981 (Figure 7) all exhibited a bimodal structure. Length frequencies of northern pike in all three years (Figure 8) had a single pronounced peak. The truncated peak in 1979 was due to limited sampling of northern pike 49-61 cm long.

3.2 Age and growth

Average length at age of walleye and northern pike are shown in Tables 4 and 5. Wilcoxon rank sum tests analyzed for significant differences between sexes within each year and within each sex between years of walleye aged 2 to 8 years in 1980, and 2 to 9 years in 1981. Female walleye of ages 2,3,4 and 7 years were significantly ($p < 0.05$) larger than males of the same age in 1980. In 1981, 4 and 6 year old females were significantly ($p < 0.05$) larger than similar aged males. Female walleye aged 2,3 and 4 years

Table 2. Mean population estimates of walleye, *Stizostedion vitreum vitreum* and northern pike, *Esox lucius*, in Henderson Lake, 1979, 1980 and 1981.

Species	Date	$\bar{x}$	95% Confidence Limits
walleye	1979 24 May - 30 June	1252[1]	188
	1980 1 May - 25 May	1461[1]	292
	1981 21 May - 28 June	1179[1]	201
	1981 21 May - 28 June	1443[2]	267
	1981 28 June - 23 July	1338[3]	94
northern pike	1979 24 May - 30 June	1863[1]	224
	1980 1 May - 25 May	2229[1]	312
	1981 21 May - 28 June	1048[1]	291
	1981 21 May - 28 June	1310[2]	262
	1981 29 June - 12 Aug.	1175[3]	188

[1] Schumacher Eschmeyer estimate

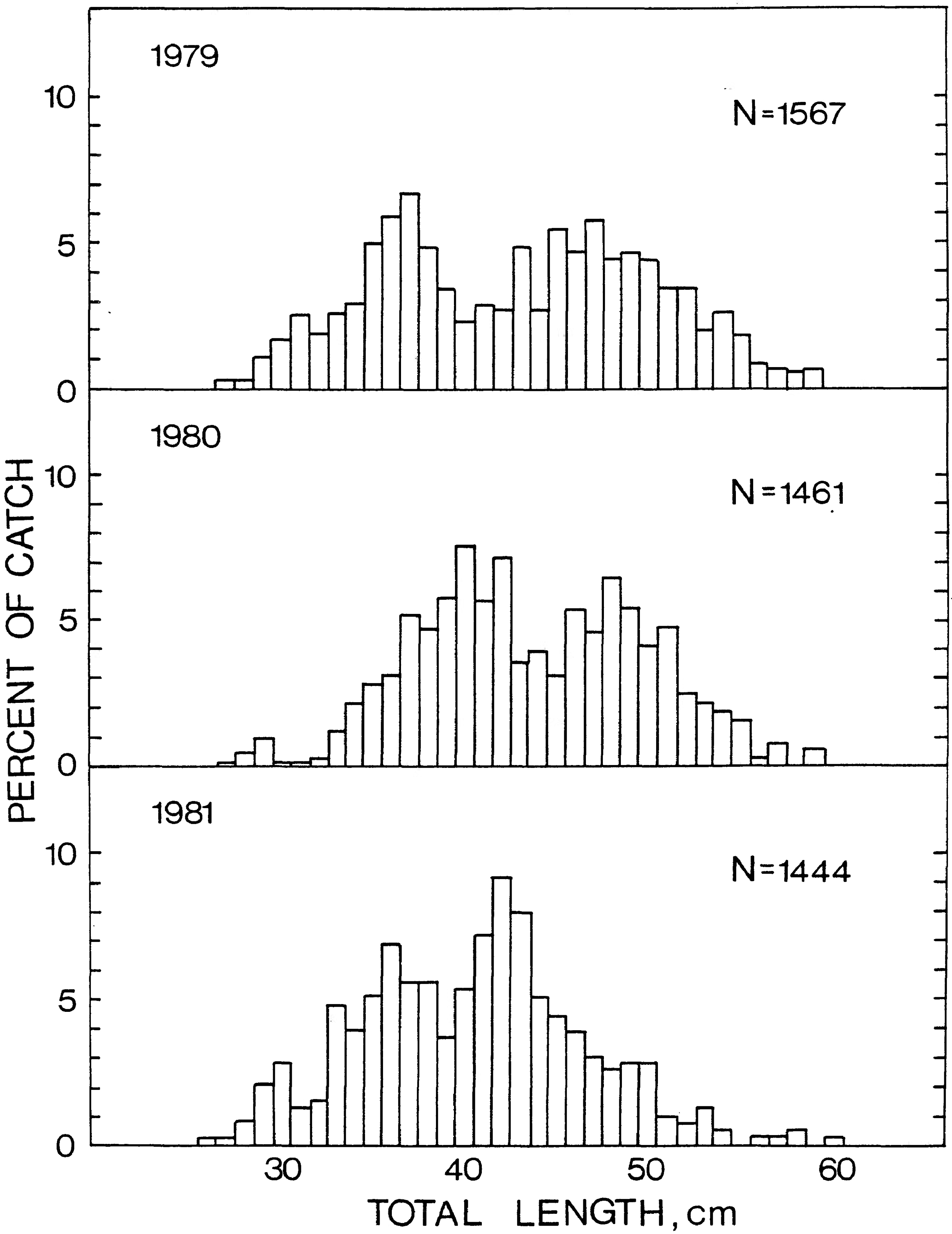
[2] Schnabel estimate

[3] Peterson estimate

Table 3. Multiple recaptures of walleye, *Stizostedion vitreum vitreum*, and northern pike, *Esox lucius*, expressed as a percentage of marked and recaptured fish in 1981 population estimates.

Species	Number of fish marked	Number of fish recaptured	Number of multiple recaptures	% of total number marked	% of total number recaptured
Walleye	427	108	26	6.1	24.1
Northern pike	294	43	8	2.7	18.6

Figure 7. Length frequency histograms of estimated walleye *Stizostedion vitreum vitreum* populations, expressed as a percentage of the total catch, 1979-1981, Henderson Lake.



1979
N=1567
1980
N=1461
1981
N=1444
PERCENT OF CATCH
0
5
10
30
40
50
60
TOTAL LENGTH, cm

Figure 8. Length frequency histograms of estimated northern pike *Esox lucius* populations, expressed as a percentage of the total catch, 1979-1981, Henderson Lake.

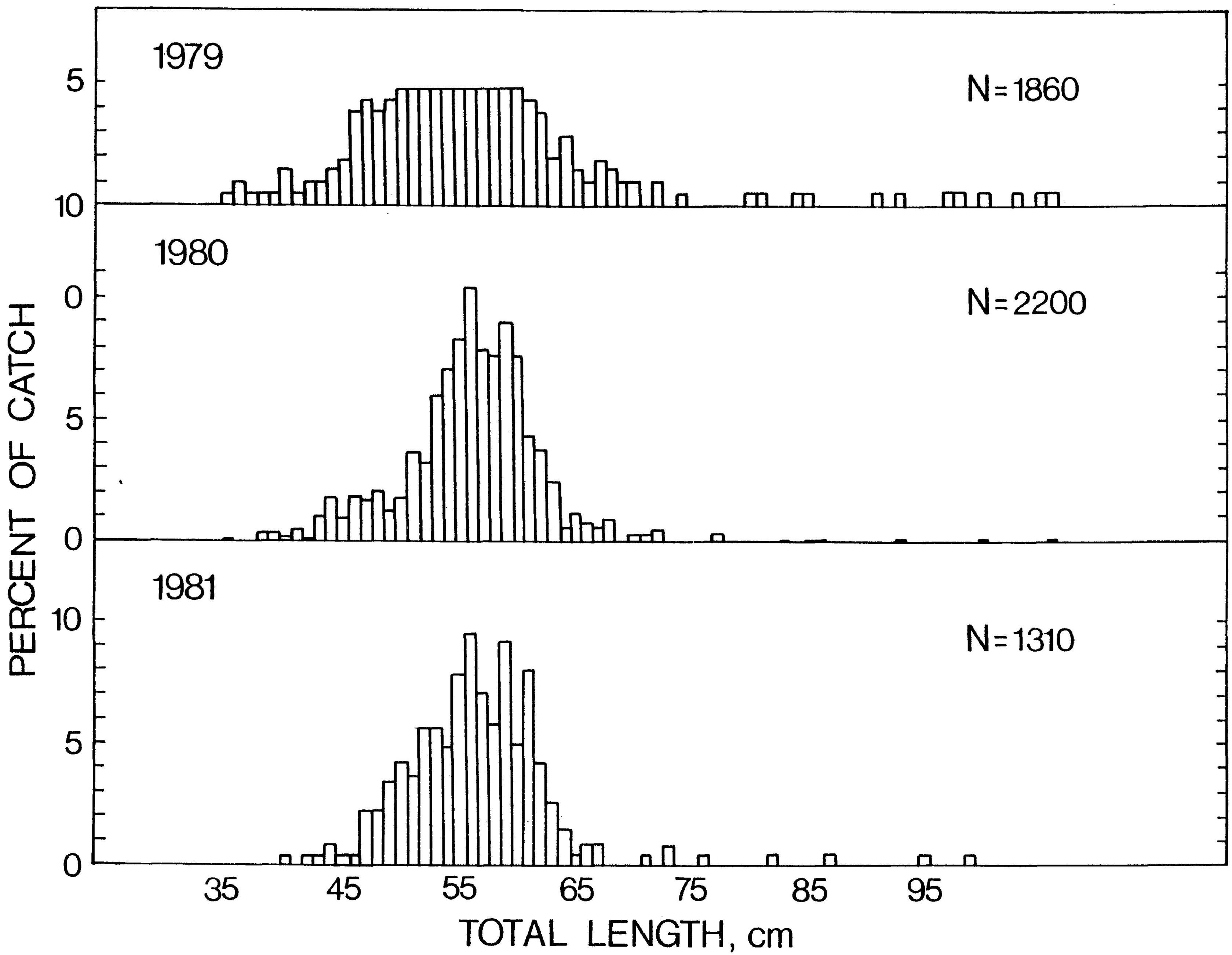

1979
N=1860
1980
N=2200
1981
N=1310
PERCENT OF CATCH
0
5
10
0
5
0
10
5
35
45
55
65
75
85
95
TOTAL LENGTH, cm

Table 4. Mean length (cm) at age (yr) of male, female and combined sexes of walleye, Stizostedion vitreum vitreum, 1979-1981, Henderson Lake. 1979 lengths are back-calculated from 1980 data.

1979	Length (cm)		
Age	Male	Female	Combined
2			21.9 ± 1.8 (18)[a]
3			28.0 ± 2.4 (22)
4			36.2 ± 4.8 (33)
5			40.1 ± 2.8 (14)
6			46.0 ± 3.1 (12)
7			49.2 ± 2.4 (7)
8			47.9 ± 2.3 (3)
9			50.0 ± 2.8 (4)
10			51.0 ± 3.4 (4)
11			52.0 ± 2.7 (6)
12			51.0 ± 4.6 (4)
13			54.7 (1)[b]
14			---
15			49.9 ± 2.3 (2)
16			---
17			49.7 (1)[c]

[a] Mean ± S.D. (sample size)

[b] back-calculated from female only

[c] back-calculated from male only

Table 4. Continued

1980	Length (cm)		
Age	Male	Female	Combined
2	22.2 ± 0.8 (5)	22.4 ± 3.1 (8)	22.3 ± 2.2 (13)
3	29.4 ± 1.1 (8)	30.2 ± 1.4 (10)	29.8 ± 1.3 (18)
4	34.2 ± 2.4 (11)	35.5 ± 2.1 (11)	34.9 ± 2.2 (22)
5	40.8 ± 5.8 (6)	39.5 ± 3.2 (27)	39.7 ± 3.7 (33)
6	43.4 ± 1.9 (5)	44.0 ± 1.4 (9)	43.8 ± 1.6 (14)
7	45.2 ± 1.7 (6)	47.3 ± 1.5 (6)	46.3 ± 1.2 (12)
8	51.0 ± 4.2 (2)	50.4 ± 0.5 (5)	50.5 ± 3.1 (7)
9	47.5 ± 0.8 (2)	51.0 (1)	51.0 ± 2.8 (3)
10	48.0 (1)	54.0 ± 1.0 (3)	52.5 ± 3.6 (4)
11	49.5 ± 0.8 (2)	54.5 ± 0.7 (2)	52.0 ± 3.4 (4)
12	51.0 (1)	55.6 ± 2.1 (5)	54.8 ± 3.2 (6)
13	48.5 ± 0.8 (2)	54.0 ± 2.8 (2)	51.3 ± 3.7 (4)
14	---	56.0 (1)	---
15	---	---	---
16	50.0 (1)	49.0 (1)	49.5 ± 0.7 (2)
17	---	---	---
18	50.0 (1)		

Table 4. Continued

1981	Length (cm)		
Age	Male	Female	Combined
2	26.4 ± 2.4 (6)	27.9 ± 2.2 (4)	26.4 ± 2.1 (14)[d]
3	31.9 ± 2.3 (11)	31.5 ± 2.0 (27)	31.6 ± 2.1 (38)
4	35.0 ± 2.2 (14)	35.3 ± 1.1 (24)	35.3 ± 1.9 (40)
5	39.0 ± 6.6 (14)	38.1 ± 3.1 (7)	38.7 ± 4.9 (21)
6	41.6 ± 1.7 (23)	43.0 ± 3.3 (29)	42.4 ± 2.8 (52)
7	44.9 ± 5.1 (3)	45.2 ± 4.4 (11)	45.1 ± 4.5 (14)
8	47.0 ± 2.2 (7)	48.5 ± 2.7 (6)	47.7 ± 2.5 (13)
9	49.7 ± 0.7 (4)	---	---
10	---	50.8 ± 2.3 (3)	---
11	49.2 ± 4.7 (2)	54.0 (1)	51.6 ± 5.3 (3)
12	49.0 (1)	50.5 (1)	49.8 ± 1.1 (2)
13	48.5 (1)	54.5 (1)	51.5 ± 4.2 (2)
14	50.2 (1)	54.5 (1)	52.4 ± 3.0 (2)
15	50.5 (1)	---	---
16	---	---	---
17	---	---	---

[d] Fish of unknown or immature sex included in calculations.

Table 5. Mean length (cm) at age (yr) of male, female and combined sexes of northern pike, *Esox lucius*, 1979-1981, Henderson Lake.

1979	Length (cm)		
Age	Male	Female	Combined
2			27.1 ± 9.4 (9)[a]
3			38.0 ± 4.0 (10)
4			47.3 ± 2.8 (14)
5			52.4 ± 2.8 (14)
6			54.4 ± 1.8 (20)
7			57.2 ± 1.6 (15)
8			58.9 ± 2.8 (10)
9			60.7 ± 1.2 (4)
10			61.2 ± 2.6 (7)[b]
11			61.9 ± 0.8 (6)[b]
12			67.1 (1)[b]
13			76.1 (1)[b]
14			66.0 (1)[c]
15			---
16			---
17			81.0 (1)[b]

[a] Mean ± S.D. (sample size)

[b] back-calculated from females only

[c] back-calculated from males only

Table 5. Continued

1980	Length (cm)					
Age	Male		Female		Combined	
2	---		24.9	(1)	---	
3	38.3 ± 3.3	(5)	39.3 ± 4.3	(4)	38.7 ± 4.4	(9)
4	47.0 ± 3.6	(6)	45.6 ± 6.4	(4)	46.4 ± 4.1	(10)
5	49.8 ± 2.7	(9)	51.2 ± 1.3	(5)	50.3 ± 2.3	(14)
6	54.5 ± 1.7	(11)	53.9 ± 3.5	(3)	54.1 ± 2.9	(14)
7	55.8 ± 1.4	(12)	57.1 ± 2.1	(8)	56.3 ± 2.1	(20)
8	58.2 ± 1.3	(7)	59.2 ± 1.6	(8)	58.7 ± 1.7	(15)
9	59.6 ± 2.7	(8)	63.2 ± 0.5	(2)	60.3 ± 2.7	(10)
10	60.8 ± 0.3	(2)	62.7 ± 0.7	(2)	61.4 ± 2.1	(4)
11	---		62.5 ± 3.0	(7)	---	
12	---		63.7 ± 1.8	(6)	---	
13	---		67.5	(1)	---	
14	---		78.9	(1)	---	
15	70.3	(1)	---		---	
16	---		---		---	
17	---		---		---	
18	---		82.7	(1)	---	
19	---		---		---	
20	---		---		---	
21	---		---		---	
22	---		100.0	(1)	---	

Table 5. Continued

1981	Length (cm)		
Age	Male	Female	Combined
2	---	---	---
3	---	38.3 (1)	---
4	50.4 ± 1.9 (3)	46.9 ± 3.1 (5)	47.8 ± 3.3 (8)
5	52.3 ± 5.0 (9)	52.5 ± 3.2 (4)	52.4 ± 4.5 (13)
6	56.9 ± 3.6 (12)	57.4 ± 4.6 (7)	57.1 ± 3.8 (19)
7	57.7 ± 3.5 (7)	58.4 ± 4.2 (8)	58.1 ± 3.7 (15)
8	57.2 ± 2.7 (4)	58.8 ± 6.1 (4)	57.9 ± 4.5 (8)
9	58.6 ± 4.1 (6)	62.6 ± 6.9 (2)	59.5 ± 4.7 (8)
10	58.5 ± 3.6 (2)	62.7 ± 1.6 (4)	61.3 ± 3.2 (6)
11	59.4 (1)	63.9 ± 0.9 (3)	62.7 ± 2.4 (4)
12	58.3 ± 1.0 (2)	64.3 ± 0.1 (2)	61.3 ± 3.5 (2)
13	---	67.4 (1)	---
14	---	---	---
15	---	---	---
16	---	---	---
17	---	---	---
18	---	82.7 (1)	---

and 3 and 4 year old males were significantly ($p < 0.05$) larger in 1981 than in 1980. Male walleye of 5 years of age were significantly ($p < 0.05$) smaller in 1981 than 1980. Female walleye aged 6 to 8 years and 7 and 8 year old male walleye were smaller, but not significantly smaller than fish of similar age in 1980 ($p > 0.05$).

Female and male northern pike did not differ significantly in 1980 ($p > 0.05$). In 1981 only 4 year old female northern pike were significantly larger than males of similar age. Northern pike aged 4 to 7 years were longer in 1981 than in 1980, but only 5 and 6 year old females were significantly ($p < 0.05$) longer. Male and female northern pike of 8 years of age, and females 9 years old in 1981 were smaller, but not significantly smaller ($p > 0.05$) in 1981 than in 1980.

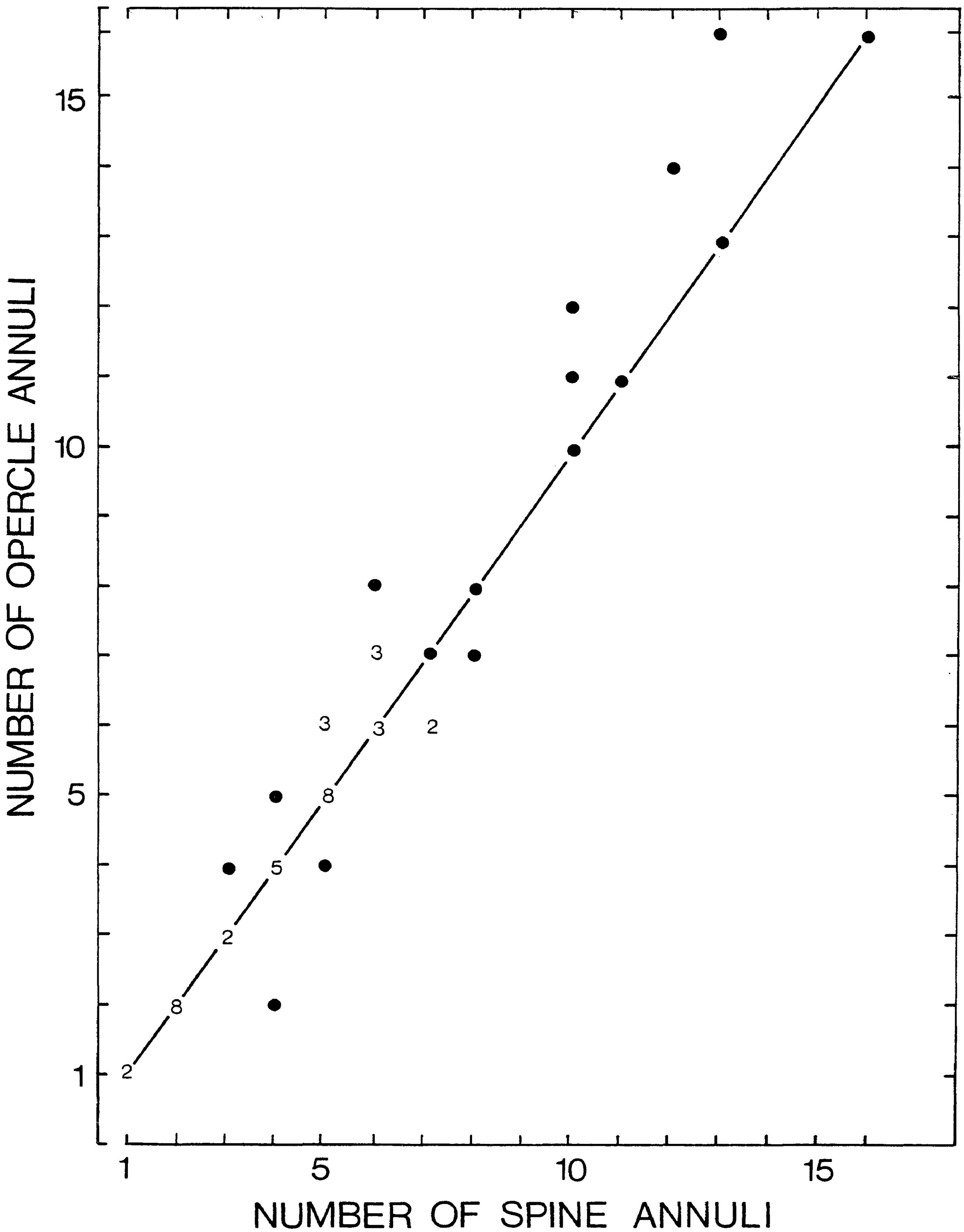
In 1980 the opercle-body growth relationship indicated that the opercles grew faster than the body ($a=0.85$, $r=0.976$). In 1981 both grew at the same rate ($a=1.0$, $r=0.944$). Northern pike cliethra grew slower than the body in both 1980 and 1981 (1980; $a=1.07$, $r=0.701$: 1981; $a=1.19$, $r=0.743$). Thus uncorrected back calculated lengths would have overestimated walleye lengths using 1980 data while underestimating lengths of pike back calculated from 1980 and 1981 data.

Relative growth increments for both species are shown in Table 6. No definite trends between sexes could be determined.

Ages determined for 1980 walleye by spines and opercles showed significant agreement ($r=0.974$, $p < 0.05$). The mean age of the sample aged by opercles and spines was respectively 5.74 years and 5.36 years (Figure 9).

The 1975 year class dominated the walleye population. It comprised 30% of the total population in 1979, 32% in 1980 and 31% in 1981 (Figure 10). The

Figure 9. Regression of the number of spine annuli against the number of opercle annuli of walleye *Stizostedion vitreum vitreum*, 1981, Henderson Lake. Numerals indicate the number of concurrent points.



NUMBER OF OPERCLE ANNULI
NUMBER OF SPINE ANNULI
1
5
10
15
2
8
2
5
8
3
3
3
2

Figure 10. Age frequency distribution of walleye *Stizostedion vitreum vitreum*, expressed as a percentage of the total catch, 1979-1981, Henderson Lake. Numbers above bars are the estimated number of fish in each age group.

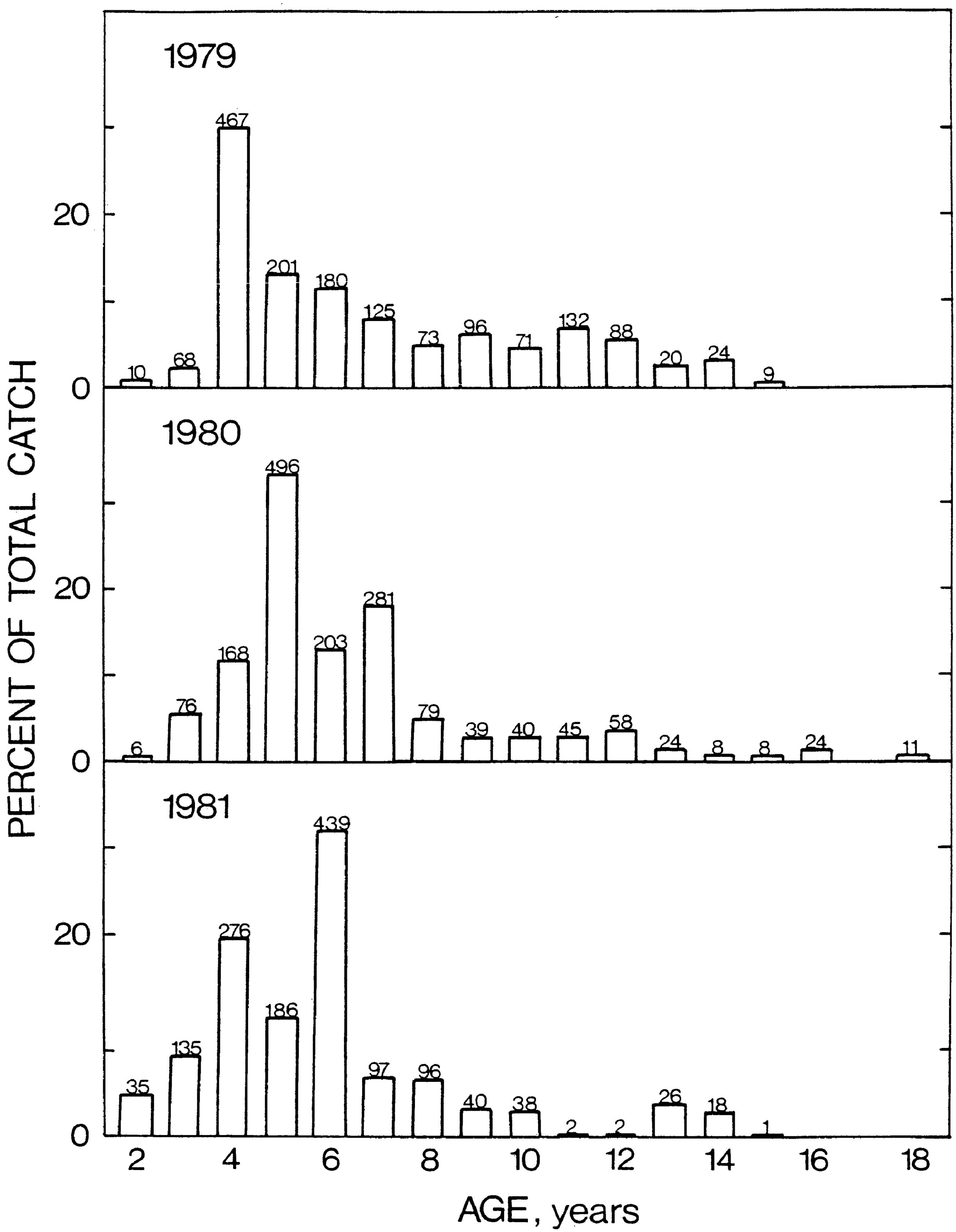

1979
1980
1981
PERCENT OF TOTAL CATCH
AGE, years
0
20
2
4
6
8
10
12
14
16
18
10
68
467
201
180
125
73
96
71
132
88
20
24
9
6
76
168
496
203
281
79
39
40
45
58
24
8
8
24
11
35
135
276
186
439
97
96
40
38
2
2
26
18
1

Table 6. Relative growth increments of male, female and combined sexes of walleye, *Stizostedion vitreum vitreum*, and northern pike, *Esox lucius*, 1981, Henderson Lake.

Age Interval	Walleye			Northern pike		
	Male	Female	Combined	Male	Female	Combined
0-1			0.95[1]			0.96[1]
1-2	0.63	0.66	0.64	0.78	0.77	0.78
2-3	0.40	0.38	0.40	0.31	0.40	0.36
3-4	0.21	0.27	0.25	0.13	0.18	0.14
4-5	0.11	0.14	0.13	0.07	0.06	0.07
5-6	0.06	0.09	0.07	0.05	0.03	0.04
6-7	0.04	0.05	0.05	0.03	0.04	0.04
7-8	0.03	0.03	0.03	0.03	0.02	0.04
8-9	0.02	0.04	0.03	0.02	0.02	0.02
9-10	0.02	0.03	0.02	0.02	0.02	0.02
10-11	0.03	0.02	0.02	0.03	0.02	0.02
11-12	0.02	0.03	0.02	0.02	0.01	0.01
12-13	0.01	0.02	0.02	0.01	0.01	0.01
13-14	0.01	0.02	0.03			
14-15		0.02				
15-16		0.03				
16-17		0.01				

[1] based on hatch sizes from Carlander (1969)

1973 year class constituted 27% of the northern pike population in 1979, and 19% in 1980 (Figure 11). It was replaced in 1981 by the 1975 year class which subsequently made up 23% of the population (Figure 11). Mean weighted age of the walleye population was 6.6 years in 1979 and 1980, decreasing to 5.8 years in 1981. Mean weighted age of the northern pike population increased from 6.4 in 1979, to 6.7 in 1980 and 7.1 in 1981.

Numbers of male and female walleye in 1980 were nearly equal, while females were more abundant in 1981 (Table 7). Though males dominated the northern pike population each year, the percentage of males in the population did increase from 1980 to 1981 (Table 8).

3.3 Length-weight relationships

Walleye showed significant increases in weight at length, and in rate of increase in weight with length from 1978 to 1980 (Table 9). Length-weight relationships determined for 1981 walleye did not differ significantly from those in 1980. Males were significantly heavier at length and increased with weight faster than females in 1980, but no differences were found between sexes in 1981 (Appendix 3).

Length-weight relationships of northern pike in 1979 were significantly higher than length-weight relationships in 1978, 1980 and 1981 (Table 10). Males in 1981 were significantly heavier at length and increased weight faster with length than males in 1980, and females in 1980 and 1981. No significant differences were found between sexes in 1980 (Appendix 3).

3.4 Effects of marking

Analysis of covariance indicated no significant difference ($p > 0.05$) be-

Figure 11. Age frequency distribution of northern pike *Esox lucius*, expressed as a percentage of the total catch, 1979-1981, Henderson Lake. Numbers above the bars are the estimated number of fish in each age group.

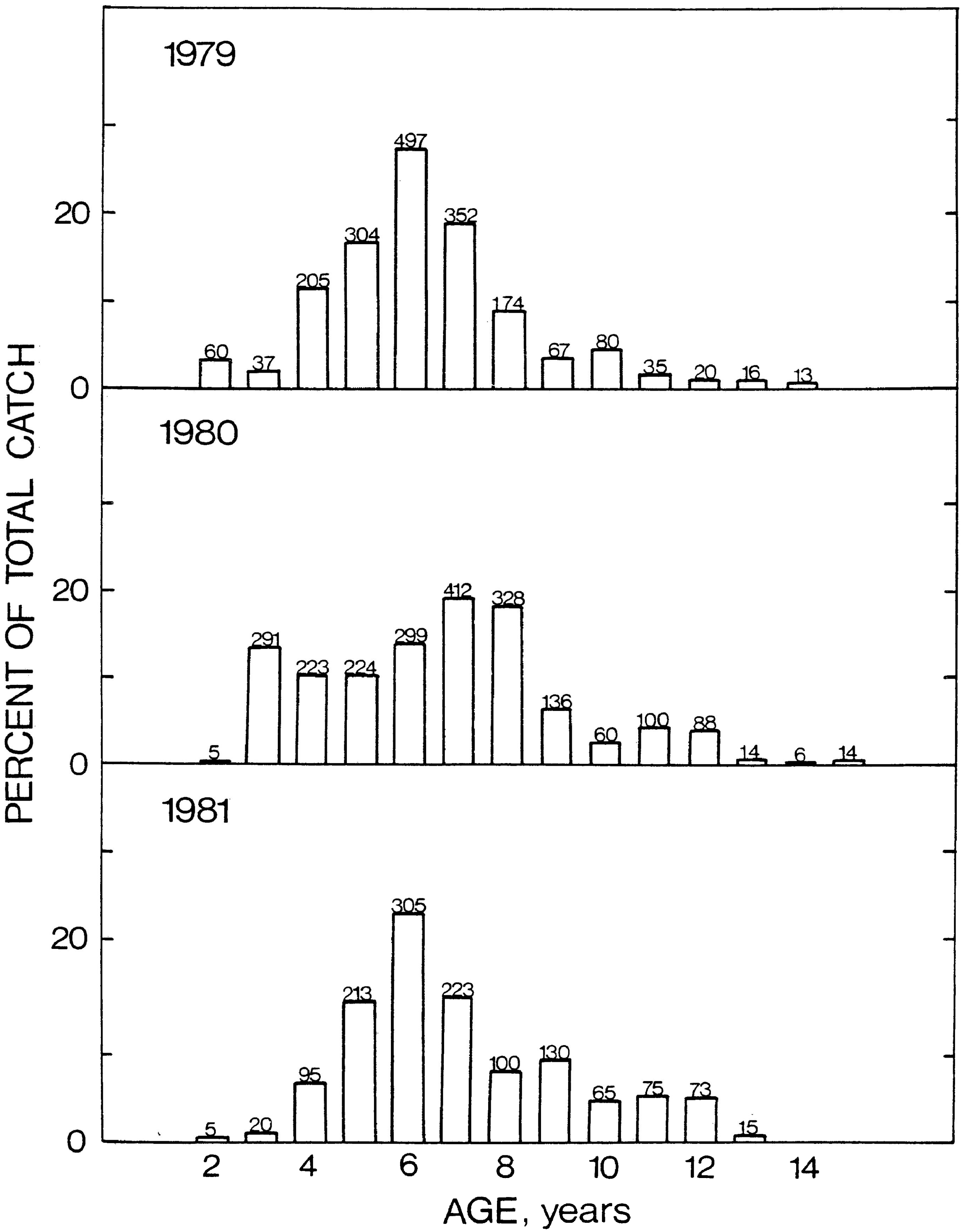

1979
497
352
304
205
174
60
37
67
80
35
20
16
13
1980
412
328
291
223
224
299
136
5
60
100
88
14
6
14
1981
305
213
223
95
100
130
65
75
73
5
20
15
20
0
PERCENT OF TOTAL CATCH
2
4
6
8
10
12
14
AGE, years

Table 7. Sex ratios of walleye, Stizostedion vitreum vitreum aged 2 - 18 years, 1980–1981, Henderson Lake.

	1980			1981		
Age	Total Number	% Male	% Female	Total Number	% Male	% Female
2	6	67	33	35	31	69
3	76	59	41	135	39	61
4	168	60	40	276	42	58
5	496	52	48	186	47	53
6	203	46	54	439	47	53
7	281	48	52	97	39	61
8	79	57	43	96	33	67
9	39	54	46	40	40	60
10	40	55	45	38	34	66
11	45	47	53	2	50	50
12	58	38	62	2	0	100
13	24	54	46	26	38	62
14	8	13	87	18	33	67
15	8	13	87	1	0	100
16	24	54	46			
17	--					
18	11	55	45			
weighted mean		51.2	48.8		42.3	57.7

Table 8. Sex ratios of northern pike, *Esox lucius*, aged 2 - 15 years, 1980-1981, Henderson Lake.

	1980			1981		
Age	Total Number	% Male	% Female	Total Number	% Male	% Female
2	5	60	40	5	100	0
3	291	70	30	20	45	55
4	223	73	27	94	48	52
5	224	80	20	211	74	26
6	299	84	16	304	67	33
7	412	86	14	224	67	33
8	328	75	25	107	60	40
9	136	62	38	131	56	44
10	60	47	53	66	50	50
11	100	60	40	75	55	45
12	88	42	58	73	40	60
13	14	21	79	14	0	100
14	6	17	83			
15	14	29	71			
weighted mean		73.5	26.5		61.2	38.8

Table 9. Length-weight relationship equations of male, female and combined sexes of walleye, *Stizostedion vitreum vitreum*, 1978-1981, Henderson Lake. Length (cm), weight (gm), $y = \log_{10}$ weight, $x = \log_{10}$ length.

Year	Sex	Equation	Correlation Coefficient	Sample Size
1978	combined	$y = 2.471x - 1.178$	0.891	158
1979	combined	$y = 2.974x - 2.019$	0.992	159
1980	combined	$y = 3.159x - 2.284$	0.975	246
	male	$y = 3.322x - 2.545$	0.980	95
	female	$y = 3.047x - 2.104$	0.963	151
1981	combined	$y = 3.189x - 2.184$	0.963	337
	male	$y = 3.199x - 2.239$	0.942	148
	female	$y = 3.137x - 2.129$	0.980	189

Table 10. Length-weight relationship equations of male, female and combined sexes of northern pike, *Esox lucius*, 1978-1981, Henderson Lake. Length (cm), weight (gm), $y = \log_{10}$ weight, $x = \log_{10}$ length.

Year	Sex	Equation	Correlation Coefficient	Sample Size
1978	combined	$y = 1.735x - 0.728^{-1}$	0.700	184
1979	combined	$y = 3.086x - 2.385$	0.970	120
1980	combined	$y = 2.633x - 1.577$	0.945	178
	male	$y = 2.611x - 1.530$	0.963	104
	female	$y = 2.759x - 1.812$	0.950	74
1981	combined	$y = 2.335x - 1.014$	0.918	127
	male	$y = 2.915x - 2.017$	0.923	71
	female	$y = 2.197x - 0.780$	0.917	56

tween groups of differently marked fish in either walleye or northern pike (Table 11). No significant change in condition with length ($p > 0.05$) occurred in either species.

3.5 Maturity

Both male and female walleye matured at younger ages in 1981 than in 1980. Females were fully mature by 8 years of age in both 1980 and 1981 (Table 12). All males were mature at 8 years of age in 1980 and at 7 years of age in 1981 (Table 13). The mean age of the catchable population decreased from 6.6 to 5.8 years during the same period (Table 14).

The mean age of maturity of both male and female walleye varied depending upon the method of analysis used. Regression analysis produced values much higher than the corrected Abrosov's formula (Table 14). It appeared that small sample sizes in younger age groups seriously affected the regression method. Both methods indicated a decrease in the mean age of both sexes of walleye from 1980 to 1981 while the female rate of maturity (slope of the regression line) was not significantly different ($p > 0.05$) between 1980 and 1981, males matured significantly faster ($p < 0.05$) in 1980.

Seventy-five percent of male northern pike 5 to 6 years old (50-55 cm) captured in January to April 1980 were mature. Few females smaller than 55 cm were captured. Those larger than 55 cm (6 years old) were all mature.

3.6 Fecundity

Total numbers of walleye eggs correlated significantly with both total length ($r=0.85$) and weight ($r=0.57$). Similar results were found for northern pike using both length ($r=0.74$) and weight ($r=0.77$).

Table 11. Average condition factor of walleye, *Stizostedion vitreum vitreum*, and northern pike, *Esox lucius*, 1981, Henderson Lake. Condition factor (k) = $(W/L^3) \times 10^{-5}$

Species	Years marked	Condition ($\bar{x}$ ± S.D.)	Number of fish examined
Walleye	unmarked	0.956 ± 0.131	239
	1979	0.961 ± 0.081	20
	1980	0.968 ± 0.131	30
	1979 and 1980	0.957 ± 0.126	19
Northern pike	unmarked	0.629 ± 0.235	112
	1979	0.607 ± 0.069	23
	1980	0.601 ± 0.051	30
	1979 and 1980	0.595 ± 0.047	17

Table 12. Percentage maturity at age of female walleye, Stizostedion vitreum vitreum, aged 2 - 10 years, 1980-1981, Henderson Lake.

	% Mature	
Age	1980	1981
2	0	19.0
3	0	20.8
4	35.6	66.9
5	49.8	64.4
6	96.1	95.9
7	99.6	98.1
8	100.0	100.0
9	100.0	100.0
10	100.0	100.0
Number examined	253	362

Table 13. Percentage maturity at age of male walleye, *Stizostedion vitreum vitreum*, aged 2 - 10 years, 1980-1981, Henderson Lake.

	% Mature	
Age	1980	1981
2	0	0
3	0	10.5
4	11.9	36.9
5	70.6	77.7
6	99.0	96.4
7	99.2	100.0
8	100.0	100.0
9	100.0	100.0
10	100.0	--
Number examined	342	330

Table 14. Mean age at maturity, mean age of the population, and rate of maturity of male, female and combined sexes of walleye, *Stizostedion vitreum vitreum*, 1980-1981, Henderson Lake.

			Mean age at maturity (yrs)		
Year	Sex	Mean age of the population	Regression method	Modified Abrosov	Rate of maturity
1980	male	6.6	7.0	5.2	0.200
	female	6.7	6.7	5.2	0.163
	combined	6.6	6.8	5.2	---
1981	male	5.7	6.3	4.8	0.238
	female	5.8	6.4	4.4	0.158
	combined	5.8	6.4	4.6	---

The rate of increase in fecundity, indicated by the slope of the log-length/ log-total egg regression, was not significantly higher in 1981 than in 1980 ($p > 0.05$, $t=-4.127^{-2}$). The intercepts were not significantly different ($p > 0.05$, $t=0.02$). Both the rate of increase of fecundity, and fecundity at initial maturity (intercept) were not significantly different for northern pike between the two years (slope $t=0.808$, intercept $t=-0.502$, $p > 0.05$). Total numbers of eggs and length of walleye and northern pike are shown in Figures 12 and 13.

3.7 Movements

In 1981, 63 (39%) of the 162 northern pike tagged in 1980 were recaptured at least once. Sixty-two percent ($^{39}/63$) of all fish recaptured were taken in the same end (north or south end) of the lake in which originally tagged in 1980. The majority ($^{17}/21$, 81%) of fish caught more than once came from or near the same net throughout the season. Four fish initially tagged in the north end of the lake moved to the south (Table 15).

In 1980, 56% ($^{28}/55$) of caudally clipped walleye tagged in June were recaptured during July and August 1980. Walleye clipped in the north end of the lake tended to move to the south ($^{7}/9$, 88%), while walleye originally caught in the south end tended to remain there ($^{12}/19$, 63%).

3.8 Removal

Walleye yield in 1980 was 5.43 $kg\text{-}ha^{-1}$. A total of 1332 walleye weighing an average of 0.614 kg were removed from Henderson Lake in 1980 (Figure 14). Northern pike yield in 1980 was 1.67 $kg\text{-}ha^{-1}$, and consisted of 226 fish averaging 1.116 kg each (Figure 15).

Figure 12. Scattergram of total numbers of eggs against total length of walleye *Stizostedion vitreum vitreum*, Henderson Lake; ■ , 1979; ●, 1980; ▲ , 1981.

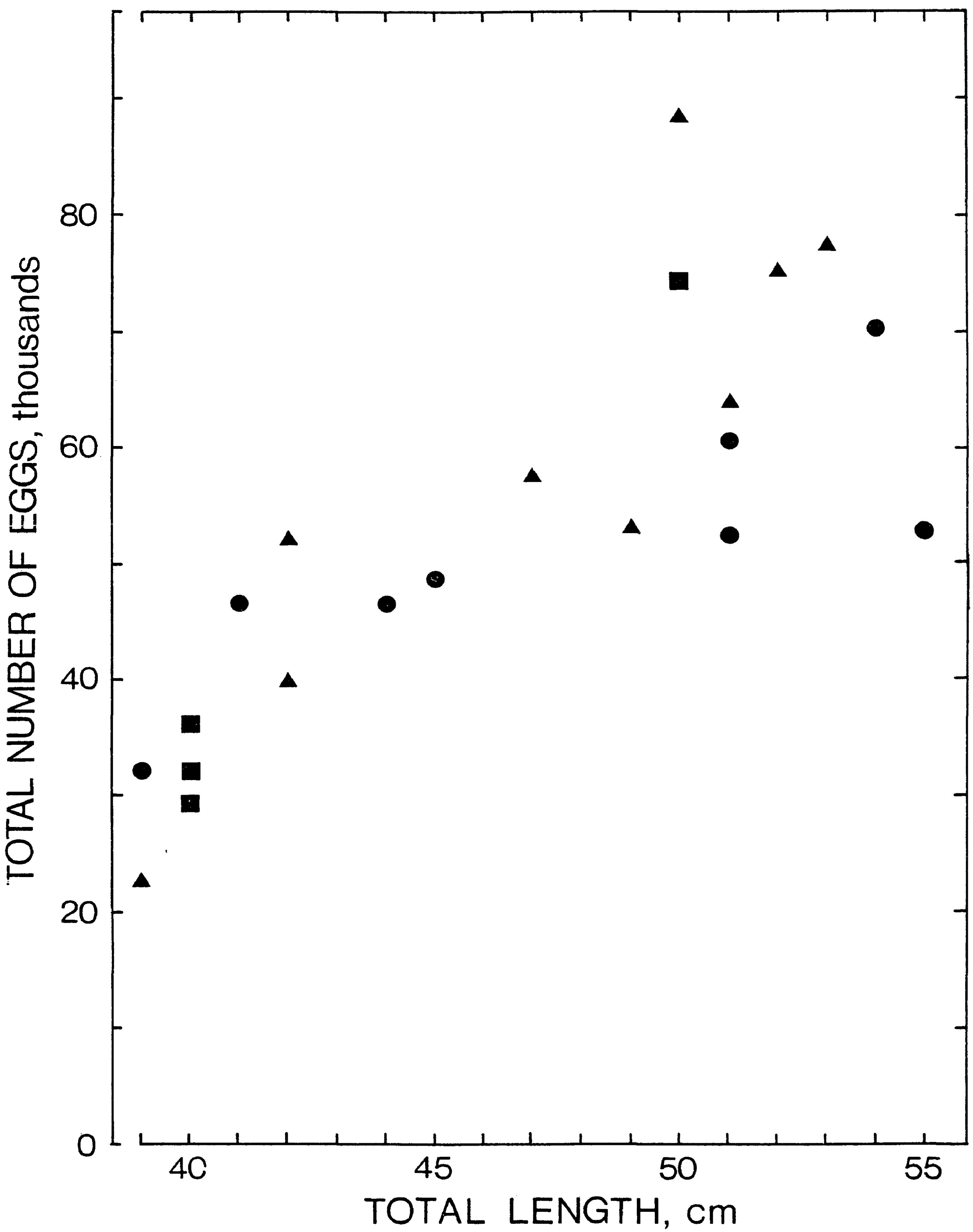

TOTAL NUMBER OF EGGS, thousands
0
20
40
60
80
40
45
50
55
TOTAL LENGTH, cm

Figure 13. Scattergram of total numbers of eggs against total length of northern pike Esox lucius, Henderson Lake; ● , 1980; ▲ , 1981.

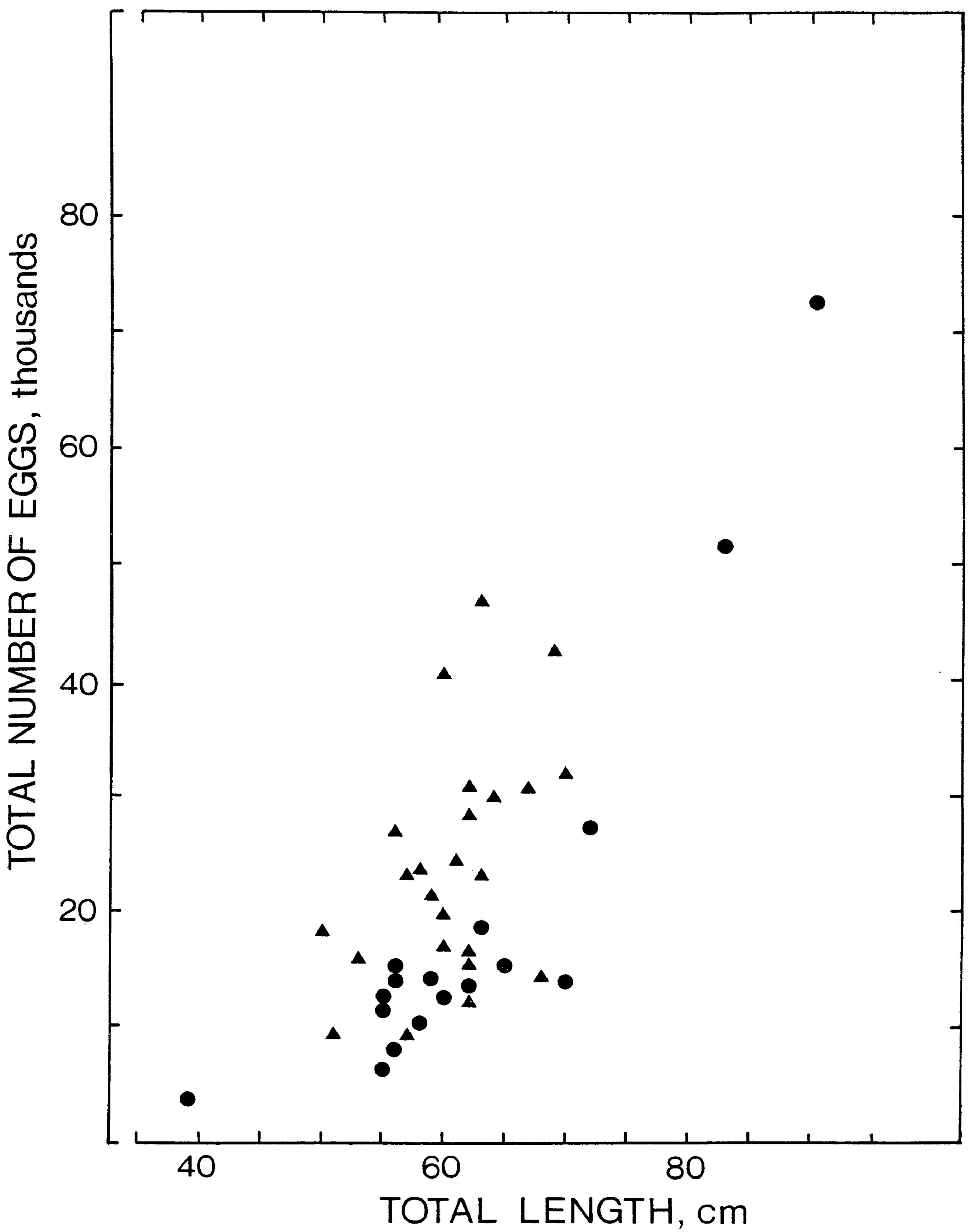
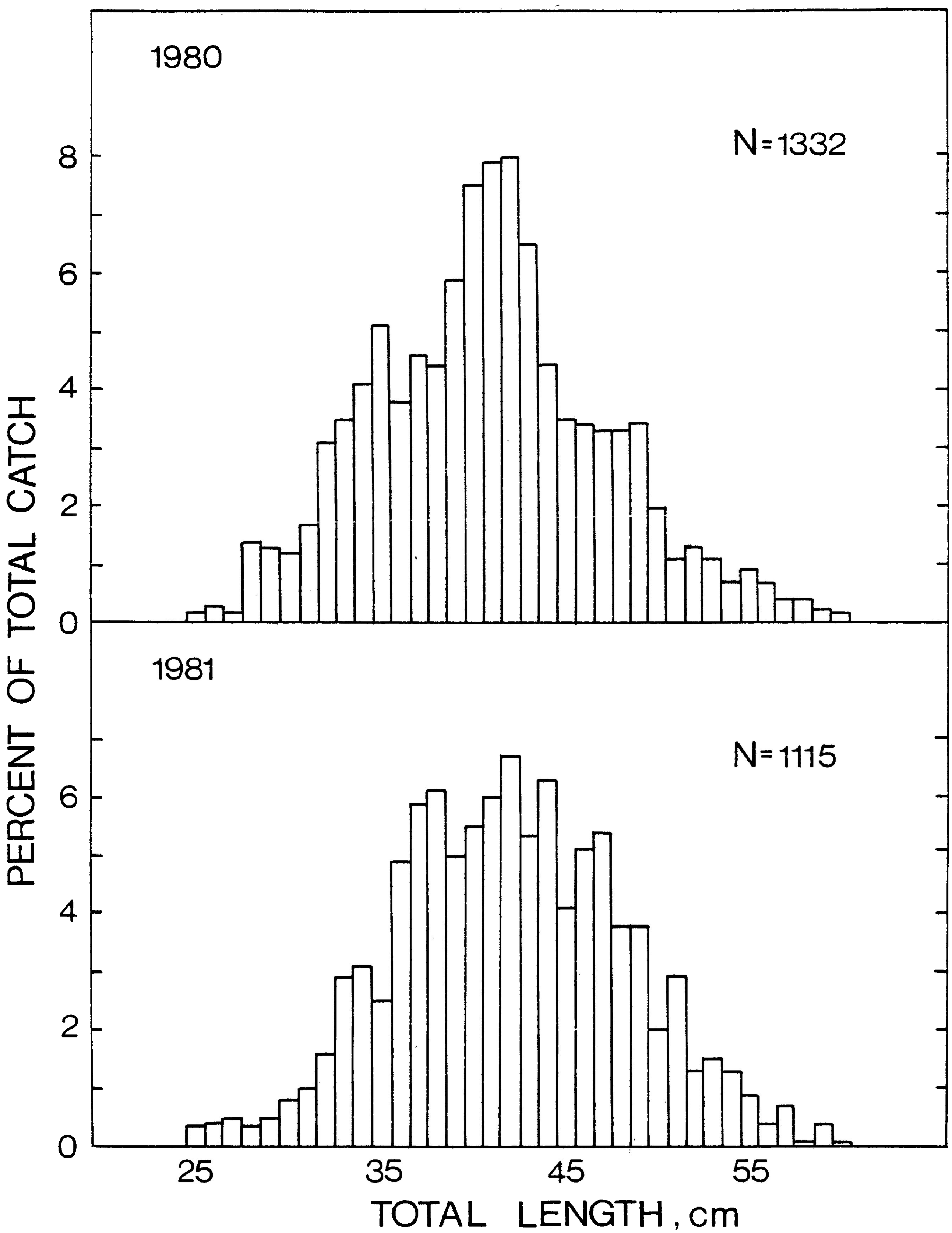

80
60
40
20
TOTAL NUMBER OF EGGS, thousands
40
60
80
TOTAL LENGTH, cm

Table 15. Number and location of recaptures, and number of days between recaptures of tagged northern pike, *Esox lucius*, 1981, Henderson Lake. Net locations, refer to Figure 3.

Number of times recaptured	Net location	Number of fish recaptured	Number of days between recaptures: Minimum	Mean	Maximum
		Fish recaptured in the same location			
2	1 5-6[1]	2 5	11	23	35
3	1 6	1 1	18	26	42
4	1 5-6[1]	2 1	4	20	41
> 4	1 5	3 2	5	16	46
		Fish recaptured in different locations			
2	1-12 1-6 5-7	1 1 1	- - -	11 101 54	- - -
3	1,6,11	1	5	16	27

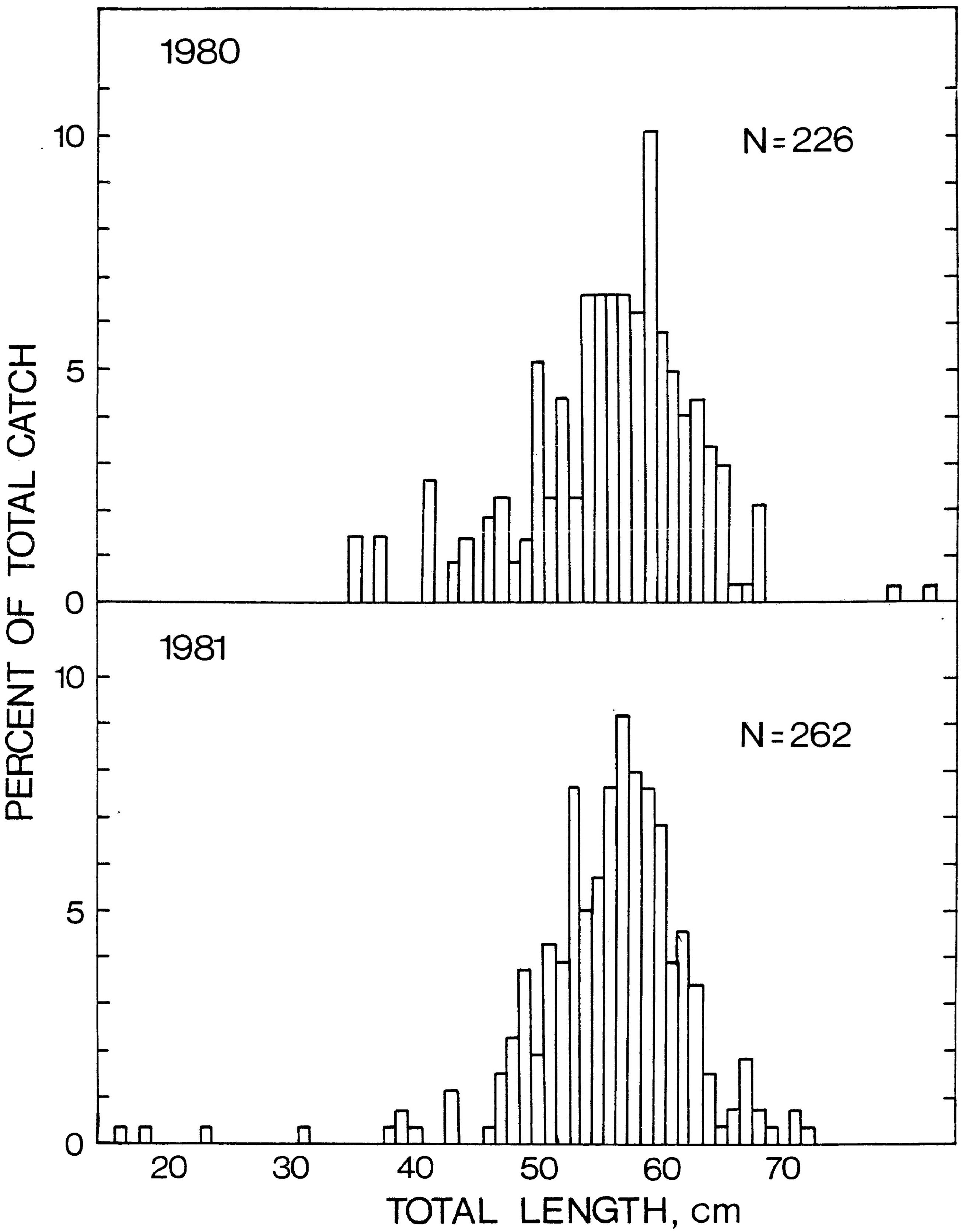
[1] because of proximity considered one location

Figure 14. Length frequency distribution of walleye *Stizostedion vitreum vitreum*, removed from Henderson Lake, 1980 and 1981, expressed as a percentage of the total catch.



1980
N=1332
1981
N=1115
PERCENT OF TOTAL CATCH
0
2
4
6
8
25
35
45
55
TOTAL LENGTH, cm

Figure 15. Length frequency distribution of northern pike *Esox lucius*. removed from Henderson Lake, 1980 and 1981, expressed as a percentage of total catch.


1980
N=226
1981
N=262
10
5
0
10
5
0
PERCENT OF TOTAL CATCH
20
30
40
50
60
70
TOTAL LENGTH, cm

Total walleye yield in 1981 was 5.7 $kg\text{-}ha^{-1}$. A total of 1115 walleye, averaging 0.77 kg each were removed. Northern pike yield was 2.17 $kg\text{-}ha^{-1}$, and was composed of 262 fish averaging 1.22 kg each.

3.9 Annual production and biomass

Total annual production of walleye aged 4-14 in Henderson Lake was 1.01 $kg\text{-}ha^{-1}$ in 1979-1980 (Table 6) and 0.651 $kg\text{-}ha^{-1}$ in 1980-1981. In 1980-1981 males and females produced 0.197 $kg\text{-}ha^{-1}$ (30%)(Table 17) and 0.455 $kg\text{-}ha^{-1}$ (70%)(Table 18) respectively. Total mean biomass of walleye was 1109.9 (7.37 $kg\text{-}ha^{-1}$) in 1979-1980 and 832.7 (5.53 $kg\text{-}ha^{-1}$) in 1980-1981. Males accounted for 408.4 kg (49%) while females formed 424.3 kg (51%) of the total biomass in 1980-1981.

Instantaneous mortality rates (Z) of the walleye population increased from an average of 0.312 in 1979-1980 to 0.520 in 1980-1981, an increase of 67%; Z-values being highest in the 6 to 9 year age groups, particularily in 1980-1981. Instantaneous growth rates (G) of walleye were highest in the abundant 6 to 8 year olds, while low or negative in older fish. Average growth rates did not vary between years,being 0.094 in 1979-1980 and 0.091 in 1980-1981.

$P/\bar{B}$ ratios of the walleye population decreased from 0.137 in 1979-1980 to 0.118 in 1980-1981. Males in 1980-1981 had a lower $P/\bar{B}$ ratio than females. $P/\bar{B}$ ratios were highest in younger age groups, and showed an irregular decrease with age.

Northern pike aged 6-14 had an annual production of 0.716 $kg\text{-}ha^{-1}$ in 1979-1980 (Table 19). Northern pike aged 6-13 years had an annual production of 1.004 $kg\text{-}ha^{-1}$ in 1980-1981; 0.482 $kg\text{-}ha^{-1}$ (48%) produced by males (Table 20),

Table 16. Annual production and biomass of walleye, *Stizostedion vitreum vitreum*, aged 4 - 14 years in 1979-1980. S = survival, Z = instantaneous mortality, A = total mortality, G = instantaneous growth rate, k = weight gain factor, W_o = initial biomass, $\bar{W}$ = mean biomass, P = annual production, $P/\bar{B}$ = annual turnover rate.

Age group	S	A	Z	G	k=(G-Z)	W_o (kg)	$\bar{W}$ (kg)	$P=G\bar{W}$ (kg)	$P/\bar{B}$
4-5	1.06	0	0	0.331	0.331	191.5	227.0	75.14	0.33
5-6	1.00	0	0	0.231	0.231	122.0	137.0	31.7	0.23
6-7	1.56	0	0	0.061	0.445	161.1	202.9	12.4	0.61
7-8	0.632	0.368	0.459	0.043	-0.416	135.5	109.2	4.7	0.04
8-9	0.672	0.328	0.397	-0.055	-0.452	75.0	60.3	-3.3	-0.05
9-10	0.579	0.421	0.546	0.152	-0.394	106.8	88.3	13.4	0.15
10-11	0.833	0.167	0.183	0.074	-0.109	83.6	79.2	5.9	0.07
11-12	0.586	0.414	0.534	0.101	-0.433	153.8	124.8	12.6	0.10
12-13	0.338	0.662	0.08	-0.006	-1.086	103.7	63.3	-0.4	-0.01
13-14	0.40	0.60	0.916	0.012	-0.904	26.9	17.7	0.2	0.01
						Total	1109.9	152.3	0.137
						=	7.36 kg ha^{-1}	1.01 kg ha^{-1} hr^{-1}	

Table 17. Annual production and biomass of male walleye, Stizostedion vitreum vitreum, aged 4 - 14 years in 1980-81. S = survival, A = total mortality, Z = instantaneous mortality, G = instantaneous growth rate, k = weight gain factor, W_o = initial biomass, $\bar{W}$ = mean biomass, P = annual production, $P/\bar{B}$ = annual turnover rate.

Age group	S	A	Z	G	k=(G-Z)	W_o (kg)	$\bar{W}$ (kg)	$P=G\bar{W}$ (kg)	$P/\bar{B}$
4-5	0.880	0.22	0.130	0.41	0.28	35.6	41.1	11.5	0.28
5-6	0.810	0.190	0.212	0.12	-0.09	144.1	137.8	16.5	0.12
6-7	0.404	0.596	0.906	0.04	-0.087	72.9	48.7	1.95	0.04
7-8	0.237	0.763	1.44	0.0	-1.44	122.6	65.0	0	0
8-9	0.356	0.644	1.03	0.07	-0.96	48.8	31.4	2.2	0.07
9-10	0.619	0.381	0.479	0.19	-0.29	20.4	17.7	3.4	0.19
10-11	0.590	0.410	0.528	-0.11	-0.63	28.3	21.0	-2.31	-0.11
11-12	0.429	0.571	0.846	-0.06	-0.91	25.9	17.0	-1.02	-0.06
12-13	0.455	0.545	0.787	-0.15	-0.94	28.3	18.4	-2.8	-0.15
13-14	0.444	0.556	0.812	-0.02	-0.79	14.9	10.3	0.21	0.02
						Total	408.4	29.13	0.073
						=	2.71 kg ha^{-1}	0.197 kg ha^{-1} yr^{-1}	

Table 18. Annual production and biomass of female walleye, *Stizostedion vitreum vitreum*, aged 4 - 14 years in 1980-81. S = survival, A = total mortality, Z = instantaneous mortality, G = instantaneous growth rate, k = weight gain factor, W_o = initial biomass, $\bar{W}$ = mean biomass, P = annual production, $P/\bar{B}$ = annual turnover rate.

Age group	S	A	Z	G	k=(G-Z)	W_o (kg)	$\bar{W}$ (kg)	$P=G\bar{W}$ (kg)	$P/\bar{B}$
4-5	1.44	0	0	0.15	0.15	26.8	28.9	4.3	0.15
5-6	0.967	0.033	0.034	0.21	0.18	139.8	153.2	32.2	0.21
6-7	0.541	0.459	0.614	0.22	-0.41	77.9	63.9	14.1	0.22
7-8	0.438	0.562	0.826	-0.01	-0.836	15.4	10.4	-0.10	-0.01
8-9	0.706	0.294	0.348	0.05	0.398	39.9	49.0	2.5	0.05
9-10	1.39	0	0	0.11	0.11	19.5	20.6	2.3	0.11
10-11	0.944	0.59	0.059	0.14	0.082	23.4	24.4	3.4	0.14
11-12	0.667	0.333	0.405	0.04	-0.365	28.0	23.5	0.94	0.04
12-13	0.444	0.545	0.787	0.14	-0.647	48.6	35.8	5.01	0.14
13-14	1.09	0	0	0.26	0.26	12.8	14.6	3.8	0.26
						Total	424.3	68.45	0.161
							= 2.82 kg ha^{-1}	0.455 kg ha^{-1} yr^{-1}	

Table 19. Annual production and biomass of northern pike, *Esox lucius*, aged 6 - 14 years, in 1979-80. S = survival, A = total mortality, Z = instantaneous mortality, G = instantaneous growth rate, k = weight gain factor, W_o = initial biomass, $\bar{W}$ = mean biomass, P = annual production, $P/\bar{B}$ = annual turnover rate.

Age group	S	A	Z	G	k=(G-Z)	W_o (kg)	$\bar{W}$ (kg)	$P=G\bar{W}$ (kg)	$P/\bar{B}$
6-7	0.829	0.171	0.188	0.103	-0.085	455.9	437.1	45.0	0.10
7-8	0.932	0.068	0.071	0.051	-0.02	364.3	360.7	18.4	0.05
8-9	0.782	0.218	0.246	0.083	-0.163	196.6	181.4	15.1	0.08
9-10	0.896	0.104	0.40	-0.011	-0.411	84.8	69.5	-0.77	-0.01
10-11	1.25	0	0	0.071	0.07	101.6	105.2	7.45	0.07
11-12	2.15	0	0	0.212	0.212	46.6	51.9	11.0	0.21
12-13	0.70	0.30	0.357	0.219	-0.138	30.9	28.9	6.3	0.22
13-14	0.375	0.625	0.981	0.282	-0.699	26.4	19.0	5.4	0.28
						Total	1253.7	107.88	0.086
							= 8.32 kg ha^{-1}	0.72 kg ha^{-1} yr^{-1}	

Table 20. Annual production and biomass of male northern pike, *Esox lucius*, aged 6 - 13 years, in 1980-81. S = survival, A = total mortality, Z = instantaneous mortality, G = instantaneous growth rate, k = weight gain factor, W_o = initial biomass, $\bar{W}$ = mean biomass, P = annual production, $P/\bar{B}$ = annual turnover rate.

Age group	S	A	Z	G	k=(G-Z)	W_o (kg)	$\bar{W}$ (kg)	$P=G\bar{W}$ (kg)	$P/\bar{B}$
6-7	0.817	0.183	0.202	0.198	-0.004	232.7	232.2	45.9	0.20
7-8	0.428	0.572	0.849	0.178	-0.671	333.9	243.2	43.3	0.18
8-9	0.261	0.739	1.74	0.067	-1.273	270.7	153.1	10.3	0.07
9-10	0.881	0.119	0.127	0.008	-0.119	98.5	92.9	0.74	0.01
10-11	1.178	0	0	-0.019	-0.049	35.3	34.4	-1.69	-0.05
11-12	0.683	0.317	0.381	-0.217	-0.598	88.1	66.3	-14.4	-0.22
12-13	0.649	0.351	0.432	-0.131	-0.563	55.9	42.7	-5.6	-0.13
						Total	864.8	78.55	0.09
							= 5.742 kg ha^{-1}	0.522 kg ha^{-1} yr^{-1}	

and 0.522 kg-ha^{-1} by females (52%)(Table 21). Total mean biomass of northern pike was 1237.0 kg (8.21 kg-ha^{-1}) in 1979-1980, and 1298.8 kg (8.62 kg-ha^{-1}) in 1980-1981 of which 434.0 kg (34%) was formed of males and 864.8 kg (66%) by females.

Instantaneous mortality of northern pike was extremely variable with age, both within each production estimate, and between the production estimates in 1979-1980 and 1980-1981. No definite increase or decrease with age could be determined. Instantaneous growth rates were highest among the youngest age group in each year. These values decreased with age in all production estimates. However G values in the 1979-1980 and female 1980-1981 production estimates decreased only until the 10-11 year age-group, and then increased.

$P/\bar{B}$ ratios of the northern pike population increased from 0.086 in 1979-1980 to 0.116 in 1980-1981. Male $p/\bar{B}$ ratios were higher than those of females. Variation of the $P/\bar{B}$ ratios with age was similar to the variation in growth with age.

3.10 Feeding analysis

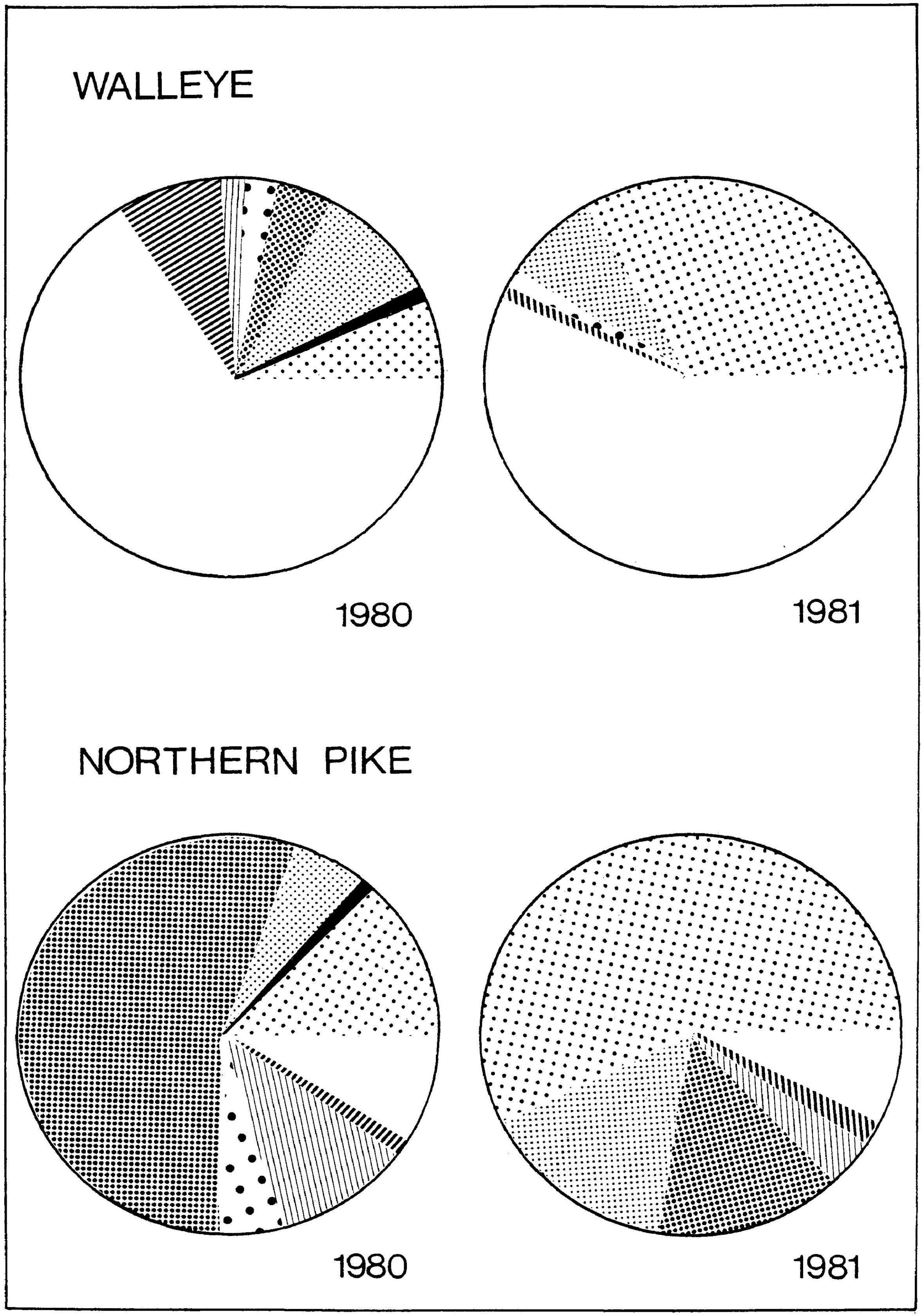
The walleye diet in 1980 and 1981 (Figure 16) was dominated by sticklebacks in both years. They made up 50% of the total stomach volume and constituted the most important identif able food item during all months of the two year feeding study (Appendix 4). Mayfly sub-imagoes were an important component of the diet in 1980, particularilly in April, May and June, but were insignificant in the total volume of the 1981 diet. Yellow perch made up more than 10% of the total volume in July, August and October of 1981.

Northern pike diets were more varied than those of walleye. Yellow perch, sticklebacks, white sucker and walleye each composed greater than 10% of total food volume in 1980 (Figure 16). Yellow perch and sticklebacks were

Table 21. Annual production and biomass of female northern pike, *Esox lucius*, aged 6 - 13 years, in 1980-81. S = survival, A = total mortality, Z = instantaneous mortality, G = instantaneous growth rate, k = weight gain factor, W_o = initial biomass, $\bar{W}$ = mean biomass, P = annual production, $P/\bar{B}$ = annual turnover rate.

Age group	S	A	Z	G	k=(G-Z)	W_o (kg)	$\bar{W}$ (kg)	$P=G\bar{W}$ (kg)	$P/\bar{B}$
6-7	1.56	0	0	0.445	0.445	48.1	60.5	26.9	0.45
7-8	0.729	0.271	0.316	0.269	-0.047	49.0	57.6	15.5	0.27
8-9	0.905	0.095	0.099	0.166	0.067	74.5	77.1	12.8	0.17
9-10	0.635	0.365	0.454	-0.004	0.45	65.2	92.6	-0.37	-0.004
10-11	1.063	0	0	0.004	0.004	44.0	44.0	0.176	0.004
11-12	1.225	0	0	0.143	0.143	55.0	59.1	8.5	0.14
12-13	0.276	0.724	1.29	0.194	1.096	70.9	43.1	8.4	0.20
						Total	434.0	71.9	0.17
						=	2.88 kg ha^{-1}	0.477 kg ha^{-1} yr^{-1}	

Figure 16. Percentage of total food volume of major food catagories from the stomachs of walleye *Stizostedion vitreum vitreum* (1980, N=297; 1981, N=256), and northern pike *Esox lucius* (1980, N=241; 1981, N=164). Categories for food types are: *Perca flavescens*; *Pungitius pungitius*; Ephemeroptera subimagoes; *Orconectes virilis*; other invertebrates; large fish species; small fish species; fish remains; insect remains.


WALLEYE
1980
1981
NORTHERN PIKE
1980
1981

found in northern pike stomachs in all months of the 1980 feeding study (Appendix 4). Mayfly sub-imagoes made up small portions of the diet in all months of the study. Crayfish were the most important invertebrate food item in 1980, and were present in June, July and August samples. In 1981 yellow perch dominated the diet and constituted 64% of the total volume. Yellow perch were present in northern pike stomachs in all months of the 1981 feeding study (Appendix 4). Sticklebacks accounted for 8% of the total food volume, followed closely by white sucker (7%), and walleye (7%). Crayfish were the most important invertebrate food item (4% total volume) and occurred in June, July and August, similar to 1980 (Figure 16).

Frequency of occurrence of food items from 1969 to 1981 (Figure 17) indicate that the primary prey of walleye were sticklebacks, yellow perch and mayfly sub-imagoes. Hirudinea occurred in small numbers in all years. The overall ratio of fish to invertebrate prey items was 2.85:1 (74%/26%), but this ratio varied from year to year. The most frequent prey items in northern pike stomachs were sticklebacks, yellow perch and crayfish (Figure 17). Mayfly sub-imagoes, Hirudinea and dragonfly nymphs occurred in moderate numbers in 1978 and 1980. Large fish such as walleye, white sucker, burbot, and northern pike were infrequent prey items. The overall ratio of fish to invertebrate prey items was 1.78:1 (68%/32%), but as for the walleye this ratio varied from year to year. The ratio of fish to invertebrate prey was similar in northern pike and walleye stomachs within each year of the study. Fish prey items were more important to walleye than to northern pike in each year (Table 22).

Type of prey selected did not vary with total length of walleye. In 1980 and 1981 yellow perch, sticklebacks, and mayfly subimageos were the most frequent food items in all length intervals of walleye (Figure 18).

Figure 17. Percentage frequency of occurrence of major food catagories in the diet of walleye *Stizostedion vitreum vitreum* (1969, N=12; 1977, N=32; 1978, N=47; 1980, N=297; 1981, N=265) and northern pike *Esox lucius* (1977, N=18; 1978, N=35; 1980, N=241; 1981, N=164). Categories for food types are: *Perca flavescens*; *Pungitius pungitius*; Ephemeroptera subimagoes *Orconectes virilis*; other invertebrates; large fish species; small fish species; fish remains; insect remains.

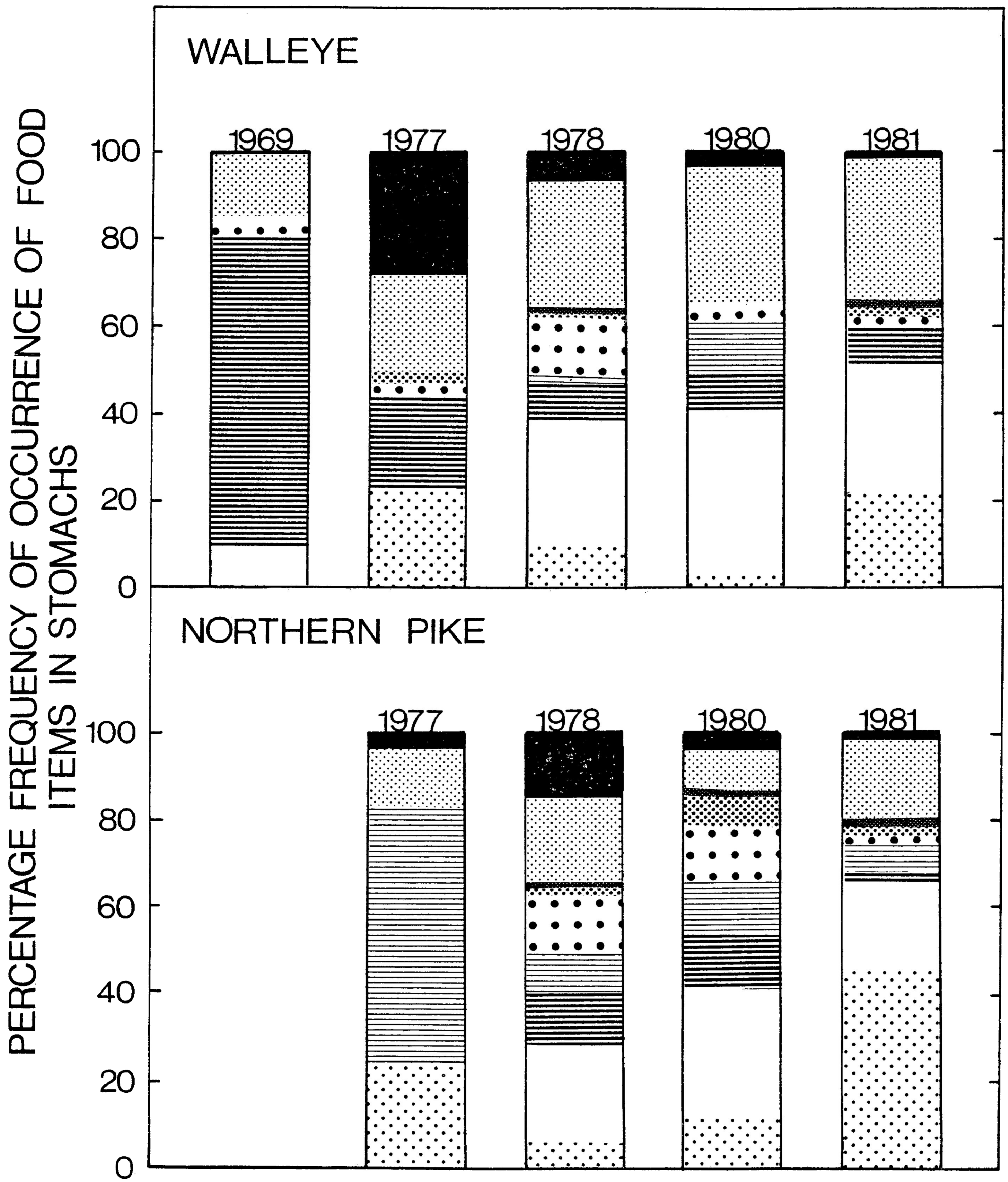
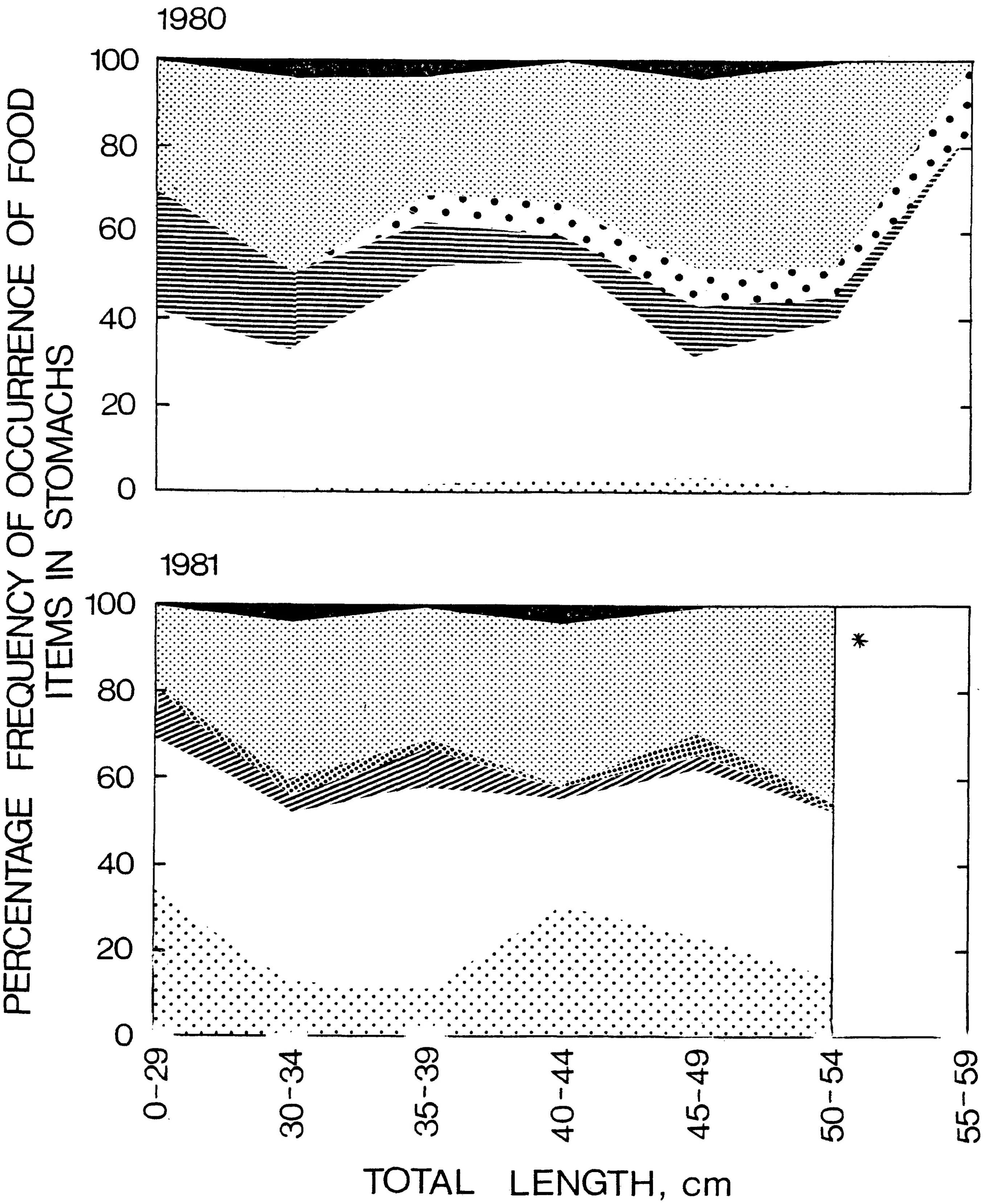

WALLEYE
NORTHERN PIKE
PERCENTAGE FREQUENCY OF OCCURRENCE OF FOOD
ITEMS IN STOMACHS
1969
1977
1978
1980
1981
1977
1978
1980
1981
100
80
60
40
20
0
100
80
60
40
20
0

Table 22. Ratio of frequency of occurrence of fish to invertebrate prey items in walleye, *Stizostedion vitreum vitreum*, and northern pike, *Esox lucius* stomachs, 1977-1981, Henderson Lake.

Year	Species	% Frequency of Occurrence fish	invertebrates	Ratio
1977	walleye	46	54	1 : 1.17
	northern pike	37	63	1 : 1.7
1978	walleye	67	33	2.03 : 1
	northern pike	61	39	1.56 : 1
1980	walleye	75	25	3 : 1
	northern pike	58	42	1.3 : 1
1981	walleye	93	7	13.3 : 1
	northern pike	91	9	10.1 : 1

Figure 18. Percentage frequency of occurrence of major food catagories in the diet of walleye *Stizostedion vitreum vitreum* of given lengths (1980, N=290; 1981, N=260), Henderson Lake. Categories of food types are: *Perca flavescens*; *Pungitius pungitius*; Ephemeroptera subimagoes; large fish species; fish remains; insect remains; other invertebrates. * indicates no samples in length interval.


1980
1981
PERCENTAGE FREQUENCY OF OCCURRENCE OF FOOD ITEMS IN STOMACHS
100
80
60
40
20
0
*
0-29
30-34
35-39
40-44
45-49
50-54
55-59
TOTAL LENGTH, cm

In 1980 and 1981 northern pike diets did vary with total length (Figure 19). Smaller fish (0-49 cm) ate sticklebacks and yellow perch most frequently. Iowa darters were present only in northern pike less than 45 cm in length. Larger individuals (greater than 50 cm) ate large prey items such as walleye, northern pike, white sucker and burbot. Crayfish occurred only in the stomachs of northern pike greater than 50 cm.

No significant relationship was found between mean length of prey items and total length of predator for either walleye ($R=0.015$, $p > 0.05$) or northern pike ($R=0.06$, $p > 0.05$). Prey length was relatively constant for walleye of all lengths (Figure 20). In walleye stomachs 91% (58/64) of all measured prey items had a mean length of less than 5 cm. Maximum prey length in northern pike stomachs somewhat increased with predator length (Figure 20). The mean length of 75% (65/86) of all measured prey items was less than 5 cm and only 3 food items were longer than 15 cm.

Figure 19. Percentage frequency of occurrence of major food catagories in the diet of northern pike _Esox lucius_ of given lengths (1980, N=164; 1981, N=240), Henderson Lake. Categories of food types are: ⁘ _Perca flavescens_; ◯ _Pungitius pungitius_; ▥ Ephemeroptera subimagoes; ▦ large fish species; ░ fish remains; ● insect remains ; ‖‖ _Orconectes virilis_; • • other invertebrates.

*indicates no samples in length interval.

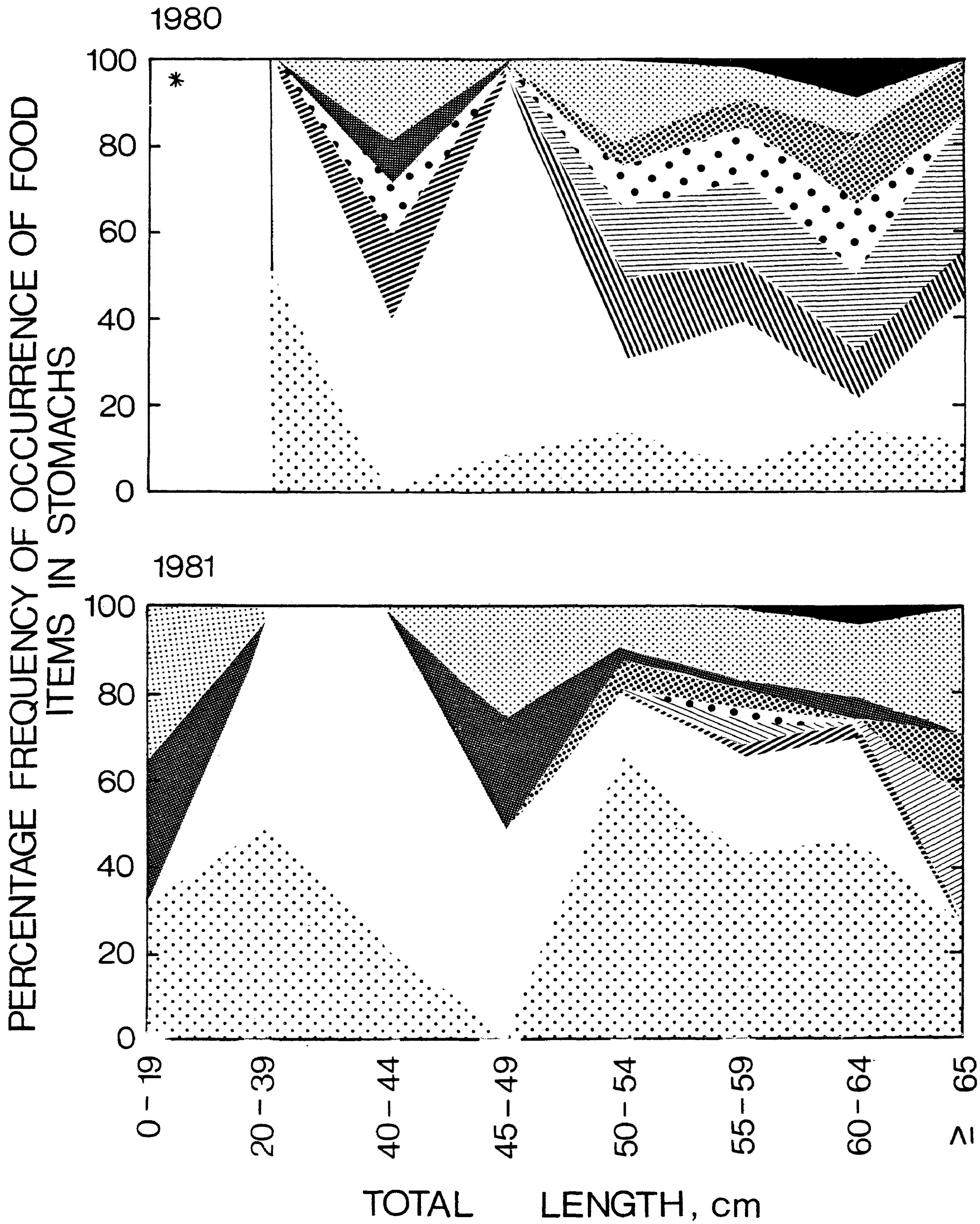
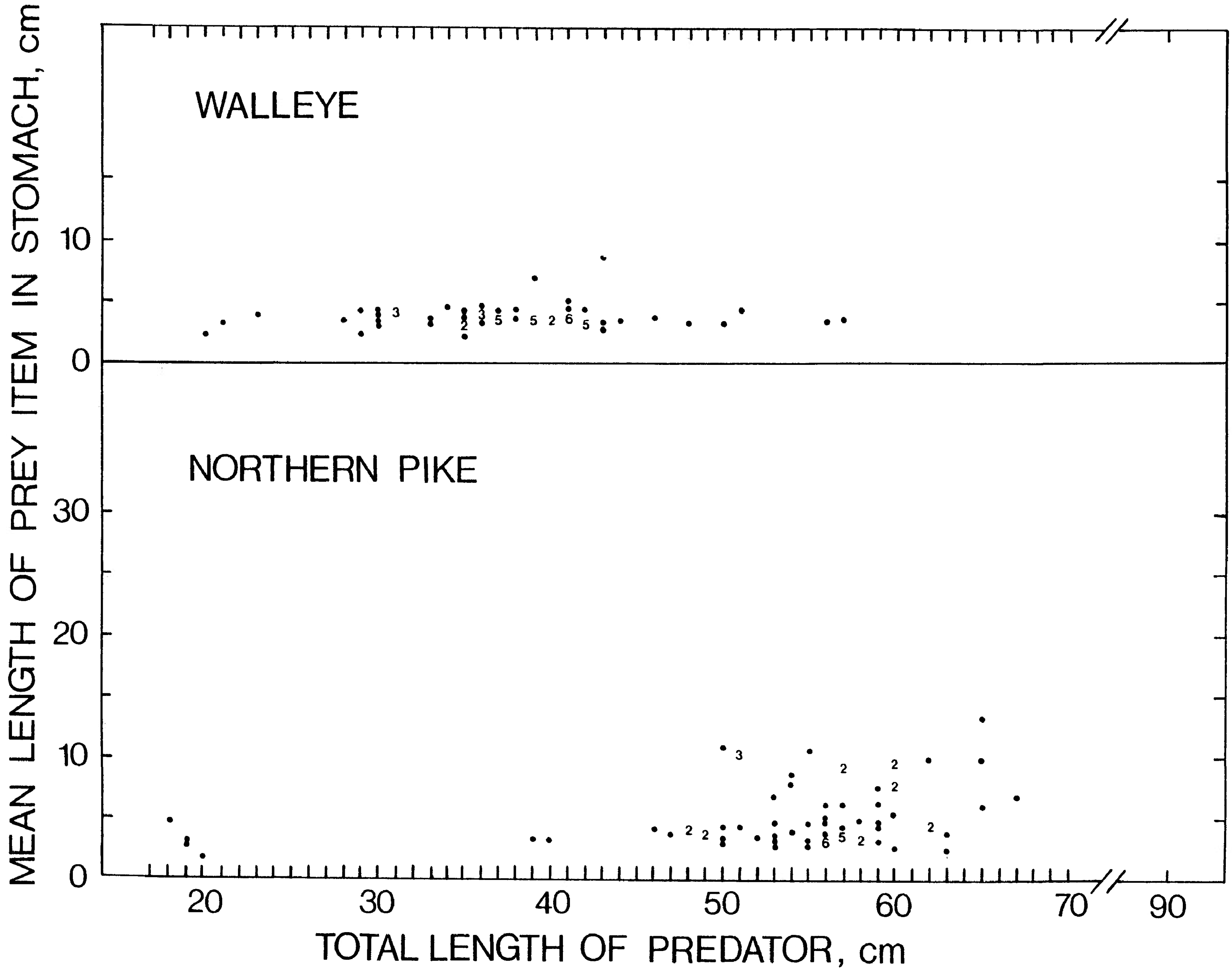

1980
1981
100
80
60
40
20
0
*
PERCENTAGE FREQUENCY OF OCCURRENCE OF FOOD ITEMS IN STOMACHS
0 - 19
20 - 39
40 - 44
45 - 49
50 - 54
55 - 59
60 - 64
≥ 65
TOTAL LENGTH, cm

Figure 20. Mean length of prey items in stomachs of walleye *Stizostedion vitreum vitreum* (N=64) and northern pike *Esox lucius* (N=86) of given lengths, 1980 and 1981 samples combined, Henderson Lake.


WALLEYE
NORTHERN PIKE
MEAN LENGTH OF PREY ITEM IN STOMACH, cm
TOTAL LENGTH OF PREDATOR, cm
0
10
20
30
40
50
60
70
90

4. DISCUSSION

4.1 Population estimates

Several differences were noted between estimated populations of walleye and northern pike during the three years. These were due to seasonal variation in the behavior of each fish, the type of population estimate carried out and effects of large scale removal of walleye. The 1980 population estimates were determined during spawning, while 1979 and 1981 estimates were carried out on post-spawning populations. Ricker (1975) warned of variation in the catchability of a fish stock due to physiological and behavioral differences at different times of the season. Spawning behavior increases the localized density of walleye (Colby et al. 1979), increasing the numbers of individuals vulnerable to sampling gear. The same is true for northern pike (Casselman 1978).

In unexploited percid populations mortality, though variable, is generally low (Kelso and Bagenal 1977). Annual mortality between the adjusted 1979 and the 1980 populations in Henderson Lake was 30%, well within the range of mortality of other unexploited percid populations (Kelso and Bagenal 1977, Colby et al. 1979).

Schnabel population estimates indicated that the 1981 Schumacher Eshmeyer estimates under estimated the populations of walleye and northern pike, due to some fish being recaptured more than once. Multiple recaptures appear to be a serious problem in estimating fish populations in small lakes, particularily when concerned with more sedentary species such as northern pike. The 1979 and 1980 Schumacher Eschmeyer estimates of walleye and northern pike populations may have been similarily biased.

Construction of length frequency histograms of walleye and northern pike reflect trap selectivity as well as size of vulnerable fish. While the left sides of the length frequency histograms (Figures 7 and 8) reflect the selectivity of the trap net, which in turn influences the minimum size of fish captured, right sides of the histograms reflect the length frequencies of the populations (Nikolskii 1965). Length frequency histograms of walleye in all 3 years of the study showed a peak in numbers of larger fish in the population (Figure 7). This peak resulted from both irregular recruitment and dominance of older age groups common to walleye populations in northern habitats (Kelso and Bagenal 1977).

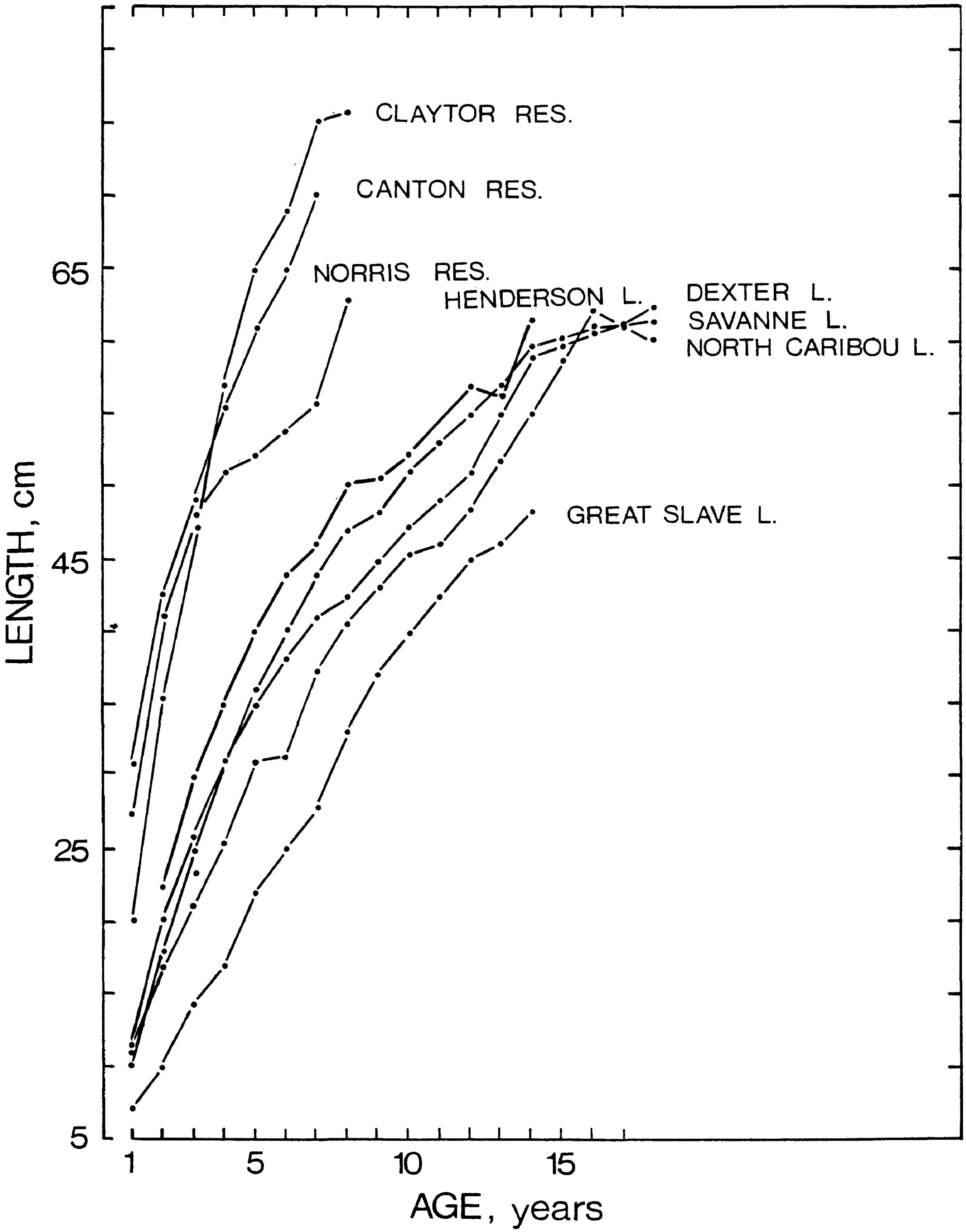
Exploitation of walleye noticably affected the length frequency of the population. The peak in numbers evident at 47 cm and 49 cm in 1979 and 1980 disappeared in 1981. Numbers of larger fish were reduced initially due to selective removal of larger fish (Regier and Loftus 1972, Spangler et al. 1977a). The total number of walleye was then maintained through recruitment of smaller fish into the catchable size range (Figure 7).

4.2 Age and growth

4.2.1 Length at age

Henderson Lake walleye were slightly longer than those of nearby Savanne (Sandhu1979) and Dexter (Moenig 1975) Lakes. All 3 populations exhibited long life spans and decreased growth rate (Figure 21). The slow growth rates of walleye in Savanne and Dexter Lakes are attributed to the relative infertility of these lakes, resulting in a high predator to prey ratio retarding growth (Sandhu1979). Growth rate of walleye has been related to food availability (Colby et al. 1979). Growth, being strongly temperature dependent shows a clinial trend with latitude (Hokanson 1977, Colby et al. 1979)

Figure 21. Total length at age of walleye *Stizostedion vitreum vitreum*, from various waters: Canton Reservoir, Oklahoma (Lewis 1970); Claytor Reservoir, Virginia (Rosebury 1951); Dexter Lake, Ontario (Moenig 1975); Great Slave Lake, Northwest Territories (redrawn from Rawson 1951); Henderson Lake, Ontario (present study); Norris Reservoir, Texas (Stroud 1949); Savanne Lake, Ontario (Sandhu 1979); (modified from Colby et al. 1979).


CLAYTOR RES.
CANTON RES.
NORRIS RES.
HENDERSON L.
DEXTER L.
SAVANNE L.
NORTH CARIBOU L.
GREAT SLAVE L.
LENGTH, cm
65
45
25
5
1
5
10
15
AGE, years

(Figure 21). The similarity in low growth rates between Henderson, Dexter and Savanne Lakes may be considered characteristic of northern Ontario lakes.

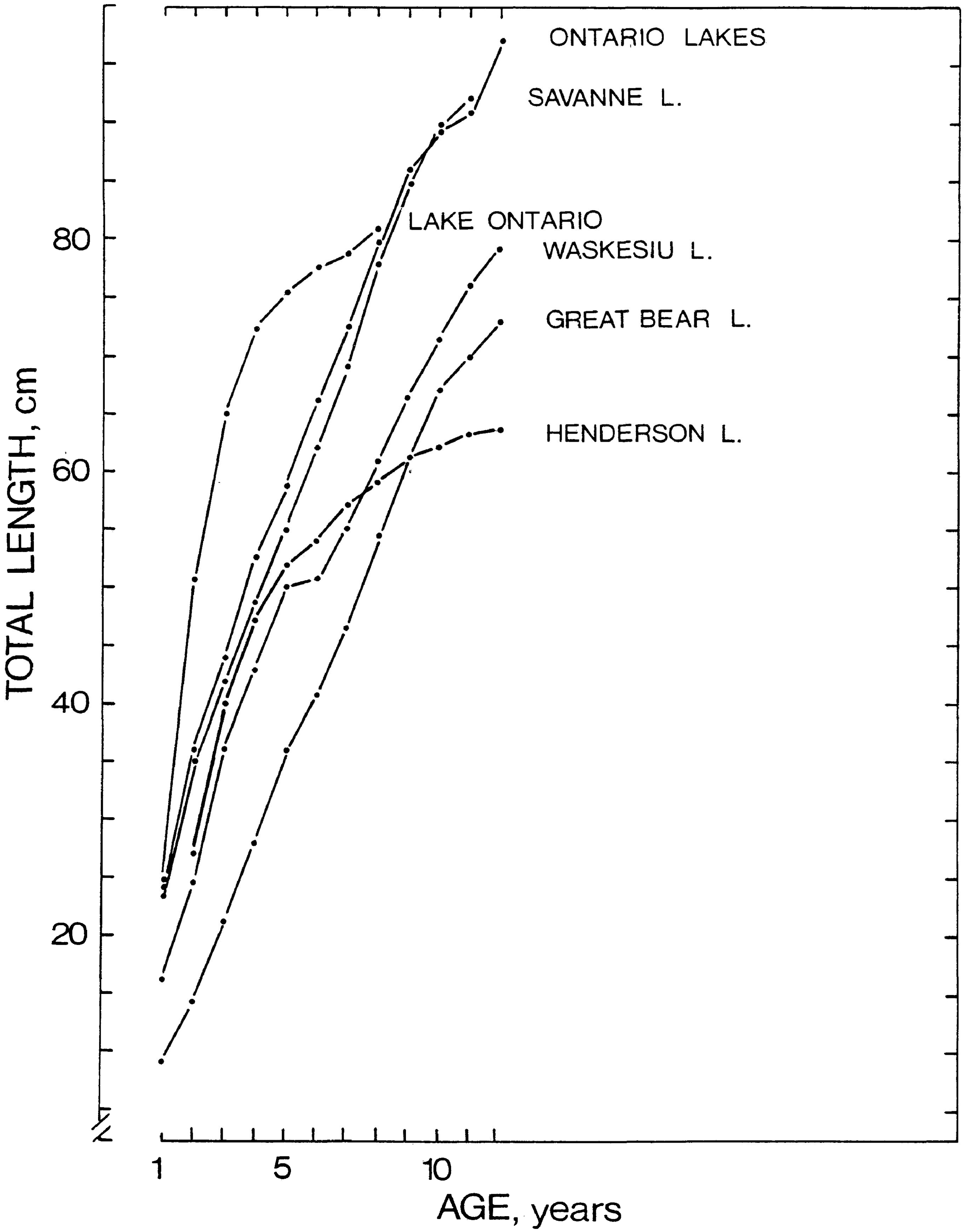
Female walleye are generally larger than males of the same age, particularly in older age groups (Colby et al. 1979). Female walleye in Henderson Lake were significantly larger than males in several age groups and never significantly smaller than males of similar age. In some age groups the weighted mean length of females was shorter than that of males. Relative growth increments indicated that the greatest growth of both male and female walleye of Henderson Lake occurred in the first year of life. This is common to all walleye populations (Colby et al. 1979).

Northern pike display a variable growth rate with latitude (Scott and Crossman 1973). Mosindy (1980) found growth rates of northern pike in Savanne Lake to be slightly below the averages for Ontario and Minnesota waters. At ages 1 to 5 years, growth rates of northern pike in Henderson Lake were similar to those of Savanne Lake, indicating comparable conditions for growth. After age 5 years growth of Henderson Lake fish dramatically decreased (Figure 22). Unavailability of large prey items (Section 3.10) may have contributed to the rapid decrease in growth rate. Large prey items have been determined vital to growth of northern pike, particularily for larger fish (Banks, cited in Mann 1976, Diana 1979). Relative growth increments of northern pike in Henderson Lake were highest in the first years of life, similar to northern pike in other waters (Scott and Crossman 1973, Mosindy 1980).

4.2.2 Bony structure-body growth relationships

The body-cliethra growth relationship for northern pike in Henderson Lake approached linearity (1980 a=1.07, 1981 a=1.17). Cliethra taken from fish during early to late June 1980-1981 grew slightly faster than the body. This

Figure 22. Total length at age of northern pike *Esox lucius*, from various waters; Great Bear Lake, Northwest Territories (Miller and Kennedy 1948); Henderson Lake, Ontario (present study); Lake Ontario, Ontario (Wolfert and Miller 1979); Ontario Lakes, average (Devitt 1958), Savanne Lake, Ontario (Mosindy 1980); Waskesiu Lake, Saskatchewan (Rawson 1932).


ONTARIO LAKES
SAVANNE L.
LAKE ONTARIO
WASKESIU L.
GREAT BEAR L.
HENDERSON L.
TOTAL LENGTH, cm
80
60
40
20
1
5
10
AGE, years

agreed with Casselman's (1978) finding that cliethra and scales grew faster than the body during the peak growth period of mid-spring to mid-summer. Diana (1979) found that maximum growth in northern pike in Lac Ste Anne, Alberta, occurred in June and July.

No similar study of walleye opercle versus body growth has been done, but this relationship likely resembles the body cliethra relationship of northern pike. Faster body growth in Henderson Lake fish sampled in early June 1980 may indicate an early somatic response to increased nutrition. Growth of bone caught up to, and eventually surpassed body growth as the walleye entered the peak growth period. The increased opercle growth of walleye in late June 1981 in Henderson Lake indicated that the peak growth period began in late summer similar to other populations (Kelso and Bagenal 1977, Moenig 1975, Colby et al. 1979).

4.2.3 Population structure

The decrease in the mean age of the population of walleye in Henderson Lake vulnerable to the sampling gear is a result of the decrease in numbers of older fish in the population, and an increasing importance of younger age groups due to an increase in recruitment. Fish older than the dominant 1975 year-class decreased in importance from 68% in 1979, to 33% in 1980, to 25% in 1981. Fish younger than the 1975 year-class increased from 5% in 1979, to 16% in 1980 and 43% in 1981. In particular, 2 and 3 year old fish increased from 13% to 30% of the catchable population.

Compared to walleye, the northern pike population structure appeared relatively constant in all 3 years. The dominant age groups were either the 6 or 7 year olds. While it appeared that good recruitment occurred in 1980, this was not the case in 1981, as indicated by the increase in mean age of the population from 1979 to 1981. Mosindy (1980) found stable recruitment with several strong year-classes produced in Savanne Lake. Unstable recruitment of northern pike in Henderson Lake may have been caused by a series of dry years in the mid 1970's (P. Colby pers. comm). Such droughts are known to influence recruitment of northern pike by causing high mortality of eggs on the spawning beds (Scott and Crossman 1973).

4.3 Length-weight relationships

Length-weight regressions indicated that the rate of weight gain in Henderson Lake walleye was similar to that of Savanne (Sandhu 1979) and Dexter (Moenig 1975) Lake walleye. Weight at length of walleye in Henderson and Dexter Lakes was also comparable. However Henderson Lake walleye were heavier at length than those from Savanne Lake. Length-weight regressions of the walleye population of Henderson Lake are comparable to populations in various waters throughout the species range (Table 23).

Most populations do not show significant differences between male and female length-weight regressions, although in some waters females are heavier than males of comparable length (Colby et al. 1979). The significantly larger males found in Henderson Lake in 1980 are unusual. The females length-weight regression may have been influenced by including data from a number of larger females which were disproportionately lighter than fish of shorter lengths. The significant increase in both weight at length and rate of weight gain from 1978 to 1980 may have been due to improved growing conditions over the 3 study years. Increased prey availability and favorable temperature regimes during peak growth periods are known to increase walleye growth (Colby et al. 1979). Northern pike length-weight relationships in Henderson Lake were similar to those of Savanne Lake (Mosindy 1980) and comparable to other populations

Table 23. Length-weight relationship equations of walleye, *Stizostedion vitreum vitreum* from various waters (modified from Sandu, 1979).

Location	Reference	Formula
Units: wt = gm; TL = mm		
Savanne Lake, Ontario	Sandhu (1979)	Log W = -4.83322 + 2.91527 Log L (Sexes combined)
Dexter Lake, Ontario	Moenig (1975)	Log W = -5.39540 + 3.18672 Log L (Sexes combined)
Lake Sakakawea, N. Dakota	Wahtola et al. (1972)	Log W = -5.80964 + 3.20447 Log L
Lake Meredith, Texas	Kraai and Prentice (1974)	Log W = -5.099 + 3.040 Log L (Females)
Lake Meredith, Texas	Kraai and Prentice (1974)	Log W = -4.584 + 2.845 Log L (Males)
Centre Hill Res., Tenn.	Muench (1966)	Log W = -0.01719 + 3.16 Log L (Sexes combined)

(Table 24). Significant differences between female regressions from 1980 and 1981, and male and female regressions in 1981 are due to the small slope and intercept of 1981 females. This may be due to use of data from longer, disproportionately lighter females in the calculations.

4.4 Condition and effects of marking

Similarity in condition factors of marked and unmarked walleye and northern pike demonstrate that they were not affected by handling and fin-clipping during the population estimates of 1979 and 1980. In previous studies, the clipping of one or two pectoral fins from walleye did not affect their growth (Colby et al. 1979). However clipping of caudal fins resulted in a decrease in walleye growth rate (Eschmeyer and Crowe 1955). Sandhu (1979) found that frayed caudal fins did not adversely affect the growth rate of walleye, however he attributed poor growth of walleye in Savanne Lake to be partially due to repeated handling.

The condition factor of walleye in Henderson Lake was midway between that for Dexter Lake walleye (1.01, Moenig 1975) and Savanne Lake walleye (0.89, Sandhu 1979). Condition factors vary widely across the range of walleye habitats, from 1.85 in Utah Lake, Utah, to 0.81 in Winnebago Lake, Wisconsin, primarily due to differences in food availability (Colby et al. 1979). Condition factors of 0.89 to 0.97 are considered average for adult walleye (Colby et al. 1979). Condition factors of northern pike in Henderson Lake were among the lowest yet recorded. Condition factors of northern pike vary from a low average of 0.60 for populations in Illinois to a high of 0.97 for northern pike in Iowa (Carlander 1969). Condition factors did not increase with length in either walleye or northern pike. This indicated that weight

Table 24. Length-weight relationship equations of northern pike, Esox lucius, from various waters (modified from Mosindy 1980).

Location	Reference	Formula	
Units: wt (W) = g; TL = total length (mm); FL = fork length (mm); SL = standard length (mm)			
Savanne Lake, Ontario	Mosindy (1980)	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, Ontario	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, Minn.	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)

did not increase after growth in length ceased at maturity. Increases of weight after maturity are associated with provision of proper growing conditions for adult growth in both walleye (Colby et al. 1979) and northern pike (Mosindy 1980).

4.5 Maturity

Walleye in Henderson Lake matured at ages between those of walleye in populations in Savanne Lake (Sandhu 1979) and Dexter Lake (Moenig 1975). Mean age of maturity for these lakes (Table 25) are similar to other northern populations with low growth rates and long life spans (Colby et al. 1979).

Maturity of walleye is strongly related to growth rate (Forney 1965, Colby et al. 1979) since walleye, like most fish species, achieve maturity at a particular size rather than a particular age (Nikolskii 1965). Climatic factors and food availability affect growth, they also affect the age of maturity (Colby et al. 1979).

The decrease in mean age at maturity of male and female walleye was due to the increase in maturity of younger age groups (Tables 12 and 13). This may have been due to a disproportional capture of mature versus immature individuals in age groups not fully recruited to the gear since mature walleye tend to be larger than immature fish from the same year-class (Forney 1965). A decrease in the mean age of maturity is often related to exploitation due to an increase in growth rate. Nikolskii (1965) gave several examples of decreases in the mean age of maturity of north Atlantic fish populations after decades of exploitation. In comparing estimates taken at 35 year intervals Wolfert (1969) found a one year decrease in the age at which 99% of Lake Erie walleye matured. A large increase in growth rate was also seen. Wolfert (1969) attributed the increased growth rate and decreased mean age of maturity to

Table 25. Mean age at maturity of walleye, *Stizostedion vitreum vitreum* populations from lakes in the Savanne Lake Research Area.

Lake	Observed life span	Mean age at maturity (yrs)	
		Males	Females
Dexter Lake (Moenig 1975)	16+	4.0	5.0
Savanne Lake (Sandhu 1979)	16+	5.5	5.5
Henderson Lake			
1980	17+	5.2	5.2
1981	15+	4.4	4.8

reduced inter- and intraspecific competition due to reduction of walleye and extinction of blue pike (S. vitreum glaucum) and sauger (S. canadense). Similar decreases in mean age of maturity were found in the walleye population of Dexter Lake, Ontario, after several years of exploitation (Moenig 1975).

Numbers of northern pike sampled (sex determined by internal examination) from Henderson Lake were insufficient to determine mean age at maturity. Male northern pike were still 25% immature at ages 5-6, while in Savanne Lake, male northern pike were mature at age 3 (36.3 cm). Females were mature at 6+ years in Henderson Lake, as compared to Savanne Lake where female northern pike were mature at 4 years of age (44.3 cm). This suggested that northern pike in Henderson Lake matured at older ages than in Savanne Lake, due to the slower growth rate in Henderson Lake.

4.6 Fecundity

Total fecundity values of both walleye and northern pike in Henderson Lake are among the lowest recorded (Tables 26 and 27). Although exploitation is known to cause an increase in fecundity (Le Cren 1958, Nikolskii 1965, Kipling and Frost 1969, Borosov 1978) walleye fecundity was not significantly different between 1980 and 1981. Any increase due to exploitation may have been masked by the effects of low food supply (Scott 1962, Bagenal 1969) and short growing season (Frost and Kipling 1967, Hokansen 1977). Large individual variatition in fecundity has also been found in northern pike (Kipling and Frost 1969) and in walleye (this study).

Weight has been determined to be the most accurate predictor of total fecundity of walleye (Wolfert 1969) and northern pike (Frost and Kipling 1967). In Henderson Lake, total length was an equally accurate predictor. This may be due to the poor growth in weight of older mature fish in Henderson Lake.

Table 26. Mean number of eggs per kilogram of walleye, *Stizostedion vitreum vitreum*, from various locations (modified from Colby et al. 1979).

Location	Mean number of eggs/kg	Range eggs/kg	Reference
Norris Reservoir	29,700	28,415 - 32,727	Smith (1941)
Henderson Lake, Ontario	42,947	17,809 - 64,713	Present study
Utah Lake, Utah	47,410	27,900 - 52.562	Arnold (1960)
Lake of the Woods, Minnesota	50,000		Carlander (1969)
Lake Meredith, Texas	52,000	36,500 - 72,200	Kraai and Prentice (1974)
Lake Erie, eastern basin	61,149	41,491 - 96,914	Wolfert (1969)
Lake Gogebic, Minnesota	61,846	57,922 - 67,797	Eschmeyer (1950)
Centre Hill Reservoir, Tennessee	64,715	37,954 - 143,827	Muench (1966)
Little Cutfoot Sioux Lake, Minn.	65,239	48,840 - 73,700	Johnson (1971b)
Lake Erie, western basin	82,700	56,314 - 123,249	Wolfert (1969)

Table 27. Mean number of eggs per kilogram of northern pike, *Esox lucius*, from various locations

Location	Mean number of eggs/kg	Range eggs/kg	Reference
Savanne Lake, Ontario	9,675	7,500 - 10,540	Mosindy (1980)
Siljön, Sweden	13,200		Lindroth (1962)[1]
Henderson Lake, Ontario	14,589	6,934 - 30,609	Present study
average for species range	19,800		Casselman (1967)
Minnesota lakes average	23,000		Carlander (1969)
Aral Sea, Russia	25,000		Berg (1962)[1]
Windemere Lake, England	27,000		Frost and Kipling (1967)
Volga River, Russia	30,000		Berg (1962)[1]
Houghton Lake, Michigan		7,691 - 97,273	Carbine (1942)

[1] in Kipling and Frost (1969)

4.7 Movements

Northern pike are reported to be relatively sedentary fish (Ivanova 1969, Nursall 1973, Scott and Crossman 1973, Diana 1979). Diana et al. (1977) found northern pike to be active only during the day, and movements were usually less than 1000 m. Large scale movements of northern pike are restricted to times of spawning activity (Rawson 1932, Carbine 1942, Miller 1948). Evidence supporting (Makowecki 1973, Malinin cited in Diana et al. 1977) and challenging (Diana et al. 1977, Diana 1979, Mosindy 1980) the idea that northern pike have home ranges has been presented in the literature.

Northern pike in Henderson Lake tended to remain in the same area of the lake. Most recaptured northern pike were continually recaught at the same net location. Similar data has been used as evidence of home ranges (Malinin, cited in Diana et al. 1977). The large variation in the number of days between recaptures of individual fish suggested that the fish moved in and out of the area around the net location. Generally northern pike stayed in either the north or the south basin. Few tagged fish ever moved between the two areas. This distribution most likely resulted from the influence of basin morphometry on availability of food and cover. However, these areas appeared too diffuse to be termed home ranges.

Localized movements of walleye during all seasons have been documented by Colby et al. (1979). Movements to and from the spawning beds are common to all walleye populations (Forney 1963, Spanger et al. 1977b, Bodaly 1980). Late summer movements of walleye from the north to the south basin of Henderson Lake indicated a migration of walleye into the deeper water of the south basin. Similar movements have been noted for other populations (Colby et al. 1979). They may have been due to walleye actively seeking a preferred prey, prey density (Rawson 1957) or temperature (Johnson 1969).

4.8 Removal

Combined yield of walleye and northern pike in 1980 and 1981 exceeded the potential yield index (Colby 1982) of 4.93 kg-ha^{-1} calculated for Henderson Lake. Percids are generally said to compose 30% of total fish yield by weight from northern communities. A percid yield of 1.00 to 1.25 kg-ha^{-1} is considered a reasonable level of exploitation for lakes in northern Ontario (Adams and Oliver 1977) yet intense exploitation of walleye in Henderson Lake increased the percid component of the total yield to approximatly 75% and exceeded the generally suggested percid yield by a factor of 4.5.

4.9 Annual production and biomass

Comparisons of annual production and biomass estimates in different fish populations are difficult to make. Variation in the number of fish in each population, and the number and relative strengths of year-classes included in each estimate can greatly affect estimated production and biomass. Walleye and northern pike in Henderson Lake showed great variation in length at age, particularilу in older age groups. Production and biomass estimates, and instantaneous growth and mortality rates of older age groups were based on only a few fish. The variation in length and weight in these fish is reflected in the variation in growth, survival and production and biomass of older age groups.

Estimated annual production of walleye in Henderson Lake was the lowest yet recorded (Table 28). The abundant, faster growing and younger age groups dominated production. The 1975 year-class (4 year olds in 1979) produced 49% and 50% of total walleye production in Henderson Lake in 1979-1980 and 1980-1981. Similarily in Savanne Lake, the 1966 year-class (7 year olds) contributed on average, 55% of total production from 1973 to 1976 (Sandhu 1979), and in

Table 28. Estimated annual production, biomass and P/$\bar{B}$ ratios and lake area, population numbers, and density of walleye, Stizostedion vitreum vitreum, from various waters.

Location	Area (ha)	Population (# of individuals)	Density (#/ha)	Age	Biomass (kg ha^{-1})	Production (kg ha^{-1} yr^{-1})	P/$\bar{B}$
Henderson Lake	150.6						
unexploited		1,461[a]	9.7	4-14	7.37	1.01	0.137
exploited		1,463[b]	9.6	4-14	5.53	0.651	0.118
Savanne Lake (Sandhu 1979)	364.3	5,184	14.23	7-14	6.06	1.31	0.22
Dexter Lake (Moenig 1975)	368.0	3,979	10.8	4+	7.2	1.78	0.25
West Blue Lake (Kelso and Ward 1977)	160.0	3,656[c]	22.85	1-4	6.1	2.1	0.33
Hoover Reservoir (Momot et al. 1977)	1143.3	20,660	18.1	1-9[d]	13.6[d]	2.16[d]	0.16
Clear Lake Carlander and Payne 1977)	1747.0	34,578[e]	19.79	1+	7.23	3.08	0.53

[a] Schumacher Eschmeyer estimate

[b] Schnabel estimate

[c] based on May 1969 population estimate

[d] mean values from seven estimates

[e] based on average of 1948 to 1974 estimates

West Blue, Manitoba the 1967 year-class (2 year olds) produced 53% of total annual walleye production (Kelso and Ward 1977).

Decreased production of walleye in the 1980-1981 season in Henderson Lake was due to the reduction in size of older age groups; a result of exploitation. Although total estimated numbers of walleye were similar in 1980 and 1981, the number of fish involved in the production estimate decreased from 1370 in 1980 (94% of the total population) to 1010 in 1981 (69% of the total population). Population numbers in 1981 were maintained by an increase in 2,3 and 4 year old walleye vulnerable to the gear (Figure 10).

Exploitation in 1980 increased the instantaneous mortality of the walleye population and decreased annual production, particularily in the 6 to 9 year olds. These ages appeared most susceptible to the gear, and contributed most biomass to the fishery. The decrease in production was also due to the drop in production of the 1975 and 1976 year-classes (4 and 5 year olds in 1979), which together produced 70% of annual production (0.71 $kg\text{-}ha^{-1}\ yr^{-1}$) in 1979-1980, but only 34% (0.43 $kg^{-1}ha^{-1}yr^{-1}$) in 1980-1981. This appeared to be due to an increase in mortality of these age groups, due to the removal of walleye in 1980. The lack of estimated mortality in the 4 to 6 year olds in 1979-1980 may have been due to their not being fully recruited to the gear in 1979, and possibly caused an overestimation of their production and biomass in the 1979-1980 season.

No growth response to the removal of walleye was seen in any of the age groups included in the production estimates (Section 4.2.1). Overall growth rates of walleye did not vary between 1979-1980 and 1980-1981, resulting in lower production in the smaller post-exploitation walleye population.

The $P/\bar{B}$ ratio of the walleye population was the lowest yet recorded. This was due to the concentration of biomass in the older, less productive age group (Crisp et al. 1975). The decrease in the $P/\bar{B}$ ratio from 1979-1980 to 1980-1981 was primarily due to the decrease in productivity of the dominant 1975 and 1976 year-classes and the lack of an increase in growth necessary to offset the increased mortality in the population.

Northern pike in Henderson Lake exhibited the lowest known production and $P/\bar{B}$ values thus far reported for the species (Table 29). This was due to the almost complete lack of growth in adult fish (Section 3.2) and the dominance of older age groups in the population. A similar but less extreme situation exists in Savanne Lake, where low production was atributed to the large number of older, less productive fish (Mosindy 1980).

4.10 Feeding analyses

Competitive feeding interactions between percids and other major predators in percid communities are considered important in maintaining the coherence of community structure (Kerr and Ryder 1977, Ryder and Kerr 1978). Walleye and northern pike are both considered opportunistic feeders (Scott and Crossman 1973, Ryder and Kerr 1978, Colby et al. 1979) which minimize interspecific competition by partitioning food resources by temporal feeding patterns; enforced by the physiological and morphological characteristics of each species.

Walleye are primarily visual predators, although other senses (hearing, taste and smell) are considered important in locating prey (Regier et al. 1969). Walleye possess a well developed *tapetum lucidum*, an adaptation of the eye allowing vision at low light levels (Ali and Anctil 1977, Ali et al. 1977). Feeding is restricted to periods of low light, from dusk to dawn in clear water lakes, and during the day in turbid or ice covered lakes where subsurface illumination is reduced (Ryder 1977). Northern pike, also a visual

Table 29. Estimated annual production, biomass, $P/\bar{B}$ ratios, lake area, population numbers, and density of northern pike, *Esox lucius*, from various waters.

Location	Area (ha)	Population (# of individuals)	Density (#/ha)	Age	Biomass (kg ha^{-1})	Production (kg ha^{-1} yr^{-1})	$P/\bar{B}$
Henderson Lake	150.6						
unexploited		2,229[a]	14.8	6-14	8.2	0.716	0.086
exploited		1,310[b]	8.7	6-13	8.6	1.004	0.116
Visula River (Backiel 1971)	22,606.0	—	—	1-9	1.8-2.4	1.5	0.714
Savanne Lake (Mosindy 1980)	364.3	2,742	7.5	4-12	8.69	2.76	0.318
Lake Windemere (Kipling and Frost 1970)	550.0[c]	18,468[d]	33.6	> 2	5.49[d]	3.77[d]	0.687

[a] Schumacher Eschmeyer estimate

[b] Schnabel estimate

[c] area of lake < 10 m depth, considered suitable northern pike habitat

[d] average estimated from data 1944 to 1963

predator, do not possess adaptations to lesser illumination resulting in a diurnal feeding pattern (Scott and Crossman 1973).

The single most important prey item of walleye, both in frequency of occurrence, and total volume was the ninespine stickleback. It occurred in all months of the feeding study and was eaten by walleye of all sizes. Sticklebacks are walleye food items in numerous lakes, although their importance varies considerably (Rawson 1957, Scott and Crossman 1973, Kerr and Ryder 1978). Observations at Henderson Lake indicated that sticklebacks migrated to the surface and toward shore at dusk, although small numbers could be found lying on the bottom in shallow water, particularily on overcast days. This made them vulnerable to predation by walleye which showed similar movement patterns at dusk. Ninespine sticklebacks rely on active evasion rather than their spines to avoid predation (Hoogland et al. 1957, Wootton 1976), although they appear less wary at night when walleye are feeding (Ryder and Kerr 1978).

Sticklebacks occurred in 25% of northern pike stomachs, but composed less than 10% of the total stomach volume. Thus although eaten often, they made up only a small portion of the ration of northern pike. Various species of sticklebacks are common prey of Esocid species in Europe and North America (Frost 1954, Scott and Crossman 1973, Wootton 1976, Reist 1980). Although the frequency of occurrence of sticklebacks in the diets of northern pike and walleye decreased only slightly from 1980 to 1981, few sticklebacks were seen in the lake in 1981, as compared to the previous year when sightings were common. This may indicate selective predation on sticklebacks by both walleye and northern pike.

Yellow perch were of secondary importance as a walleye food item in 1980 and 1981, and of primary importance to northern pike diets in 1981. The life history and behavior of yellow perch makes them particularily vulnerable to both predatory species in Henderson Lake. Ali et al. (1977) proposed that walleye and juvenile and adult yellow perch are involved in a classic predator-prey relationship. Yellow perch, lacking the well developed tapetum lucidum of the walleye are restricted to diurnal activity patterns, with peaks of activity at dawn and dusk. During these times they are vulnerable to predation by dark adapted walleye that move onto the reefs and into the shallows to feed (Colby et al. 1979), and to those northern pike that are still actively feeding (Lawler 1969). During daylight hours yellow perch fall prey to day-active northern pike.

Henderson Lake walleye ate yellow perch from June to August 1980, and July, August and October 1981. These summer months correspond to the period of growth of young of the year perch and their subsequent movements inshore (Scott and Crossman 1973, Kelso and Bagenal 1977). Young of the year yellow perch are considered the single most important walleye prey item when available in sufficient number (Colby et al. 1979). Their activity at night in surface waters exposes them to intensive walleye predation (Kelso and Ward 1977, Swenson 1977). Mosindy (1980) found that young of the year and juvenile yellow perch were the predominant prey of walleye and northern pike in Savanne Lake; young of the year being most important in the summer months.

Yellow perch were found in pike stomachs in all months of 1980 and 1981 sampled. Young of the year, juvenile and adult yellow perch are often a major prey item of northern pike in Europe and North America (Frost 1954, Seaborg and Moyle 1964, Lawler 1965, Johnson 1969, Mann 1976, Diana 1979). In Savanne Lake Mosindy (1980) found that young of the year and juvenile yellow perch were the most important prey item of northern pike, while adult yellow perch were seldom eaten.

Various invertebrates were eaten by walleye and northern pike in 1980 and 1981. Mayfly subimagoes, considered the most common invertebrate prey of walleye (Colby et al. 1979), increased in importance in walleye diets in Henderson Lake from Junuary 1980 to their emergence in mid June, but were of little importance in July and August. They were however unimportant in 1981 walleye diets. This was because mayfly species in the Savanne Lake Research Area have a two year life cycle, with one strong and one weak year-class (Riklik and Momot, 1982). The peak mayfly year was in 1980, as seen by their importance in walleye diets of that year. Walleye in Savanne Lake ate mayfly subimagoes in the months previous to emergence (Mosindy 1980), similar to the pattern of utilization found in this study.

Mayfly subimagoes made up small percentages of total food volumes in northern pike stomachs from January to August 1980, and a significant volume of January 1981 samples. Mayfly subimagoes are known to be important food items of northern pike in various waters (Frost 1954, Lawler 1965). Mosindy (1980) found that they were a major food item in northern pike stomachs from February to April in Savanne Lake. This importance of mayflies to winter diets of northern pike may be common to lakes in northern Ontario.

Crayfish were found in walleye stomachs only in August 1980 and 1981. They constituted over 50% of the total food volume of August 1980, but only occurred in 3 stomachs. Ryder and Kerr (1978) described crayfish as a relatively unimportant prey item for walleye, possibly because of resource partitioning with bottom feeding specialists such as burbot and small-mouth bass. Walleye in Savanne Lake (Mosindy 1980) ate crayfish, particularily in May.

Crayfish were the most important invertebrate food items in northern pike diets in Henderson Lake. They occurred in pike stomachs in June, July and August 1980 and 1981. Mosindy (1980) found them to occur in Savanne Lake northern pike diets primarily in the summer months. This seasonal importance may be due to the increased summer activity of yearling and male crayfish in shallow water and subsequent exposure to predation (Momot and Gowing 1972).

Incidental invertebrates found in the diets of both walleye snd northern pike included leeches, dragonfly larva, caddisfly larva and freshwater clams. Leeches are known to be eaten by walleye (Colby et al. 1979) although some species may be distasteful to fish (Ryder and Kerr 1978). All other incidental invertebrates are substrate dwellers with various behavioural patterns and specialist strategies (eg. caddisfly cases) which make them unlikely candidates for predation by walleye and northern pike.

Large fish species were not important in walleye diets. In two years only two northern pike and one walleye were found in walleye stomachs. Northern pike have been previously reported to be uncommon walleye food items (Ryder and Kerr 1978), possibly due to their largely diurnal activity patterns. Cannabalism is common to walleye populations, particularly when usual prey items are scarse (Forney 1974). The tendency of walleye to school with young yellow perch, and the habit of various sizes of walleye to school together may increase the possibility of cannabalism (Ryder and Kerr 1978, Colby et al. 1979). White sucker was abundant in Henderson Lake, but did not occur in walleye diets, possibly due to a well developed predator "early warning system" (Ryder and Kerr 1978).

Large prey species were infrequent but important in northern pike diets. White sucker, walleye, northern pike and burbot occurred in 1% to 3% of pike stomachs, but contributed 7% to 23% of the total volume of 1980 samples. They were not as important in 1981, when only white sucker and walleye (both 2% occurrence, 7% volume) were eaten, possible due to the increase in availability of yellow perch aand its buffering effect on other prey species (Forney 1974). Walleye, burbot, northern pike and white sucker have all been reported to be food items of northern pike from various waters (Frost 1954, Johnson 1969, Scott and Crossman 1973, Mosindy 1980).

It is common practice to consider large prey items to be exaggerated in importance to the overall diet when using volumetric analysis (Mosindy 1980). However, single, large prey items may be the most important factor in growth of northern pike. Banks (cited in Mann 1976) determined that most of the nutrition of large pike resulted from ingestion of large, infrequent prey items, regardless of the number of smaller prey items eaten. Diana (1979) pointed out that northern pike that fed only infrequently on large prey items, would still consume a larger ration than those feeding on smaller prey. The value of a single large prey item (ie. a full stomach) to a sedentary predator such as a northern pike is obvious. Relieved of the necessity to expend energy to chase and catch food, more energy could be diverted into growth. The lack of large prey in the diets of northern pike in Henderson Lake was most likely detrimental to their growth rate.

Small fish species in Henderson Lake, Iowa darters and mimic and black-nosed shiners were almost nonexistent in walleye and northern pike diets, despite their great abundance in Henderson Lake, and their importance to the diets of predatory fish in other waters (Black 1945, Scott and Crossman 1973, Eddy and Underhill 1974).

Long term patterns of prey selection by walleye and northern pike were remarkably similar. The diet of both species showed an absence of sticklebacks in 1977, a dramatic rise in importance of sticklebacks in 1980 and 1981, an increase in yellow perch utiliztion and a decrease in the importance of mayfly subimagoes in 1981. Together with the similar ratios of fish versus invertebrate prey items between species each year (Table 22), this appears to indicate that diet was more a result of availability of particular prey items, mediated by predator selection, rather than a species preference for specific prey items alone. These finding correspond to descriptions by Scott and Crossman (1973) and Kerr and Ryder (1977) of walleye and northern pike as opportunistic feeders. This also indicates that patterns of prey utilization, even in unperturbed situations are not static but vary considerably with time, and are not easily descernable with only a few years of data.

The diet of walleye in Henderson Lake was unrelated to total length of the fish. Common prey species in each year dominated the diets of all lengths of walleye. There was a tendancy by smaller fish (less than 30 cm) to eat more invertebrates and larger fish (greater than 50 cm) to eat more fish. This agreed with Kerr and Ryder (1977) who inferred that the diet of smaller walleye (in Lake Erie) would consist of invertebrates and small fish, while the adults would become fully piscivorous.

Although the maximum prey size eaten by northern pike in Henderson Lake increased with total length, the average prey size remained relatively constant, due to the number of small prey items such as sticklebacks and perch in the diet. Northern pike in both Henderson Lake and Savanne Lake (Mosindy 1980) ate prey much smaller than the one third to one half total body length considered optimal (Scott and Crossman 1973).

Other studies have shown that optimal prey size increased with the length of walleye (Parsons 1971, Colby et al. 1979). The small prey size of walleye and northern pike in Savanne and Henderson Lakes may indicate that larger prey species are unavailable to these predators due to a shortage of these items or because of temporal or behavioral segregation. The small prey size in the diet of the dominant predators most likely reflects the predominant particle size in boreal fish communities.

4.11 The pre-exploitive percid community in Henderson Lake

The two major species studied in Henderson Lake, the walleye and northern pike exhibited high biomass, low production, and low $P/\bar{B}$ ratios which all characterize climax communities (Odum 1969). This was primarily due to the lack of growth by adult fish. Environmental and abiotic factors are important determinants of growth of both northern pike (Casselman 1978) and walleye (Hokanson 1977, Kelso and Bagenal 1977, Colby et al. 1979, Colby and Nepzy 1982). The similarities in growth, length at age and length-weight relationships of walleye in Savanne (Sandhu 1979), Dexter (Moenig 1975) and Henderson Lakes, the similarities in biomass of 4+ walleye in Henderson and Dexter Lakes, and the similarities in growth of young northern pike in Henderson and Savanne Lake (Mosindy 1980) indicate that, as expected, environmental and abiotic factors are similar in these three adjacent lakes. The extremely poor growth of adult northern pike, and the lack of increase in weight after maturity in both walleye and northern pike in Henderson indicate that prey size and/or prey abundance may not be suitable for optimal growth of either species.

The difference between the optimal prey size and the average prey size actually eaten was much greater for northern pike than for walleye in Henderson Lake, and may partially explain the much poorer growth of northern pike compared to walleye. The average prey size of walleye and northern pike in Henderson Lake were similar to those found for populations in Savanne Lake (Mosindy 1980). However, the absence of shallow water cisco Coregonus artedii, an important prey item of walleye and northern pike in Savanne Lake, and the lack of trout perch Percopsis omiscomaycus a prey species of seasonal importance to northern pike in Savanne Lake (Mosindy 1980) may account for some of the differences in adult growth between the two lakes. The irregularities in length and weight at age in older fish from Henderson Lake may indicate that a few fish, by utilizing large prey items realize their growth potential (Diana 1979).

A large percentage of the potential yield and net community biomass of Henderson Lake appeared to be made up of species which were not involved in the production of the two major predators. Large populations of 2 species of shiners and white sucker exist in Henderson Lake, but did not substantially contribute to the diet of either walleye or northern pike. Reported diets of mimic and blacknosed shiners (Siefert 1972, Eddy and Underhill 1974) and white sucker (Scott and Crossman 1973, Johnson 1977) resemble those of juvenile walleye (Colby et al. 1979) and yellow perch (Scott and Crossman 1973, Clady and Hutchinson 1976, Keast 1977) indicating that a dietary overlap may exist. These species may represent a net energy loss to the production of walleye and northern pike in Henderson Lake. Similarily Mosindy (1980) concluded that white sucker represented an energy sink in Savanne Lake. Johnson (1977) showed that the removal of white sucker improved the growth of yellow perch and walleye, possibly by reducing competition for invertebrate food items. Removal of the cyprinid species (as in bait fish industries) also may benefit walleye populations in boreal percid communities. A better understanding of the interactions of small fish species within the percid community would be necessary to accurately predict the results of such removals.

Competition is important in maintaining community structure in boreal percid communities, by enforcing patterns of resource partitioning (MacLean and Magnuson 1977, Ryder and Kerr 1978). However the dietary overlaps of walleye and northern pike (Figure 17) suggest that competition for some food items may exist. Johnson (1977) determined that if the frequency of occurrence of a food item exceeded 25% in the diet of two or more species, competition may be occurring. The frequency of occurrence of yellow perch in 1977 and 1981 and sticklebacks in 1978, 1980 and 1981 approached or exceeded 25% in the diets of walleye and northern pike. This indicates that the two species may have been competing for major prey items. Walleye and northern pike are thought to minimize competition by temporal segregation, although in turbid waters such as Henderson Lake, walleye may feed during the day, and possibly out-compete northern pike (Ryder 1977). Competition for major prey species (yellow perch and sticklebacks) between walleye and northern pike may be partially responsible for the poor growth of adult northern pike.

Although walleye are generally considered to have a greater effect on the percid community through predation than northern pike (MacLean and Magnuson 1977) this does not appear to be the case in Henderson Lake. Northern pike ate a larger size range and a greater variety of prey species, and the larger northern pike population likely consumed more biomass than did the walleye. However this does not qualify the northern pike for the role of 'keystone predator'. Keystone predators are not necessarily generalists (or specialists) in feeding strategy, nor are they necessarily the prime net energy converter in the community (Paine 1969). It is impossible to assign either species the role of 'keystone predator' on the basis of feeding patterns alone. Only by examination of the long term effects of the exploitation of walleye in Henderson Lake, and similar experiments on northern pike will it be possible to determine each species effects on the stability and persistance of the boreal percid community.

4.12 Responses of the boreal percid community to exploitation

Compensatory responses of fish populations undergoing exploitation are a result of density dependent mechanisms within the population itself (McFadden 1978). The decrease in the number of conspecifics due to exploitation reduces intraspecific competition for food, resulting in better nutrition and increased growth (Nikolskii 1965, Spangler et al.1977a, McFadden 1978). Increased growth rates result in a decrease in the mean age of maturity, a possible increase in individual fecundity and increased recruitment of younger fish into the catchable population. Historical studies of major walleye fisheries in North American lakes, indicated that compensatory responses have accompanied large scale exploitation (Rainy Lake, Chevalier 1977; Lake Nippissing, Anthony and Jorgenson 1977; Lake Erie, Wolfert 1969, Spangler et al. 1977b; Shoal Lake, Schupp and Macins 1977).

The increased growth of 2, 3 and 4 year old female walleye, and 3 and 4 year old male walleye in 1981 appeared to be in response to the exploitation of the walleye population in 1980. The decreased number of larger fish may have reduced intraspecific competition for prey items to the benefit of the growth of younger fish. The rapidity of this response of young fish in Henderson Lake may have been due to the diet similarity of all lengths of walleye.

Variation in recruitment resulting in strong and weak year-class strength is common in both perturbed and unperturbed walleye populations (Kelso and Bagenal 1977). The increased number of 2, 3 and 4 year old walleye in the catchable population in 1981 as compared to 1979 or 1980, could have been due to strong year-classes entering the fishery. However, as these groups also showed increased growth rates in 1981, their increased recruitment was likely due at least in part to compensatory growth response to the exploitation. Increased growth rate resulted in these fish attaining a size vulnerable to the trapnets at a younger age.

Healey (1978, 1980) found remarkably similar initial responses in exploited whitefish Coregonus clupeaformis populations. Intensive exploitation of whitefish in several lakes in the Northwest Territories resulting in increased recruitment and growth of younger age groups after one year. Such increases were proportional to the intensity of exploitation applied to each lake. Healey (1980) suggested that the increased recruitment and growth of younger fish may have been a response to decreased competitive exclusion by adults which allowed juveniles to move into the prime feeding (and fishing) areas. The effect of social interactions in walleye populations is unknown. Walleye of all sizes have beeen reported to school together (Colby et al. 1979) which would suggest that competitive exclusion by larger fish does not occur in walleye populations. In Henderson Lake, where all sizes of walleye ate similar prey items, it would appear that competition between fish was for food items, rather than feeding areas.

The increased growth rate also resulted in increased maturity of younger age groups, and a decrease in the mean age of maturity of the population. Decreases in the mean age of maturity are a common response to exploitation of fish populations, and act to offset the reproductive potential lost by the removal of older, more fecund adults (Nikolskii 1965). However, as the mean age of maturity approaches the minimum age at which the species can mature, compensatory responses become less effective in countering the effect of continued exploitation. As the mean age of the catchable population approaches the mean age of maturity, the ability of the population to respond to exploiteve stress declines. The difference between these two population parameters is a good indicator of the condition of the population.

After one year of intensive exploitation of walleye in Henderson Lake, the difference between the mean age of maturity and the mean age of the catchable walleye population decreased from 1.4 to 1.2 years. This indicated that the compensatory response had not completely kept up with the changes in age stucture caused by the removal of older walleye. The significance of a 0.2 year change in the reproductive lifetime of the fish is not known. The difference of 1.2 years still falls within the range of 1.0-2.5 years that Abrosov (1969) considered necessary to ensure continued reproductive success of exploited pikeperch populations. In 1981 female walleye in Henderson Lake were maturing at age 2, the youngest age at which female walleye are known to mature (Colby et al. 1979). This indicated that compensatory changes in maturity may be approaching their lower limit. Continued exploitation may result in erosion of the ability of the walleye population to maintain recruitment.

No significant growth response to the exploitation occurred in walleye involved in the 1980-1981 annual production estimate (those greater than 4 years of age). As a result, annual production decreased 36% and biomass decreased 25%, as compared to the previous season, due to a drop in the number of walleye involved in the estimate. The more rapid decrease in production than biomass, and the resulting decrease in $P/\bar{B}$ ratios, may be the result of the fishery selecting for faster growing, more productive fish (Willemsen 1977).

Walleye yields in the first two years of exploitation in Henderson Lake were based on standing crop rather than production, which is common in the initial stages of exploitation in high biomass-low production boreal percid communities (Adams and Olver 1977). Production to yield ratios ($P/_Y$ ratios) indicated that the contribution of annual production to the walleye yield decreased from 19% in 1980 ($P/_Y$=0.19) to 11% in 1981 ($P/_Y$=0.11). As compensatory responses to the exploitation begin to influence production, $P/_Y$ ratios should increase, reflecting the shift toward a production based, or turnover fishery (Adams and Olver 1977).

Spangler et al. (1977a) suggested that alteration of the genotypic character of a walleye population may result from exploitation, particularily in larger lakes where discrete spawning stocks exist. Willemsen (1977) stated that in Holland, exploitation of pikeperch previous to their first spawning resulted in the removal of faster growing fish, and selection for slow growing, smaller fish. There is little evidence however that growth rate, age of maturity and fecundity are genetically determined in percids (Colby and Nepszy 1982). In the small, heavily exploited population in Henderson Lake, where only one major spawning site is known, genetic selection appears to be a very remote possibility.

The intensive exploitation of walleye in Henderson Lake in 1980 and 1981 exceeded the 1.00 to 1.25 $kg\text{-}ha^{-1}yr^{-1}$ walleye yield, considered sustainable yield for lakes in northwestern Ontario (Adams and Olver 1977). Such a high level of exploitation could not be maintained without destabilization of the community structure, and changes in species interrelationships, particularily because exploitation was almost exclusively directed toward the walleye. No hard evidence for changes in species interactions in Henderson Lake were found after the first year of exploitation. Undoubtably such changes are occurring, due to the shift of the reduced walleye population toward dominance by younger, smaller fish. It is tempting to attribute the increased utilization of yellow perch by both northern pike and the remaining walleye in 1981, to be due to an increased survivorship (of yellow perch) due to decreased predation pressure from the exploited walleye population. However, patterns of prey utilization by walleye and northern pike varied considerably from year to year in the unexploited situation and it may be possible that the shift in dietary importance of yellow perch was totally unrelated to the exploitation of the walleye.

The future effects of exploitation of the walleye in Henderson Lake remains to be seen. It is likely that the boreal percid community in Henderson Lake will re-establish itself at a new equilibrium, within the confines of environmental restrictions of the growth and production of the major species. Possible situations that may result are as follows: 1) a return of the walleye population to its former abundance, due to continued compensatory response 2) increased abundance, growth and production of northern pike due to decreased competition from a reduced walleye population 3) increased abundance of yellow perch due to reduction of walleye, its major predator and competitor and 4) changes in abundance of coarse fish.

Only continued monitoring of the boreal percid community of Henderson Lake will allow an understanding of the process set into motion by this study.

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Appendix 1.1 Schumacher Eschmeyer population estimates of walleye, *Stizostedion vitreum vitreum*, 1980, Henderson Lake.

Date	Number of fish marked (cumulative)	Number of fish recaptured (Daily)	Estimated population $\bar{x}$	95% confidence interval
May 1	0	0	---	---
2	43	0	---	---
3	73	8	596.9	132.5%
4	120	7	618.9	52.4%
5	147	6	672.6	35.1%
6	171	15	648.5	20.9%
7	208	1	996.9	72.3%
8	251	3	1051.8	62.9%
9	265	0	1111.9	62.1%
10	269	1	1276.3	65.1%
11	286	2	1375.4	61.8%
12	299	2	1483.9	59.2%
13	315	2	1541.6	55.3%
14	327	10	1357.9	43.9%
15	344	14	1155.9	37.2%
16	358	12	1182.7	32.2%
21	389	32	1375.5	27.9%
22	492	6	1370.4	25.7%
23	502	12	1365.7	23.0%
24	520	4	1368.9	21.8%
25	526	14	1461.1	21.5%

Appendix 1.2 Schumacher Eschmeyer population estimates of northern pike, *Esox lucius*, 1980, Henderson Lake.

Date	Number of fish marked (cumulative)	Number of fish recaptured (Daily)	Estimated population $\bar{x}$	95% confidence interval
May 1	0	0	---	---
2	34	3	3037.0	141.6%
3	294	8	3402.2	9.5%
4	373	3	4360.5	55.8%
5	420	9	3534.6	41.6%
6	467	22	2550.6	41.9%
7	527	35	2208.9	28.2%
8	610	8	2218.4	23.8%
9	632	5	2213.3	20.9%
10	642	2	2286.9	21.8%
11	655	5	2326.8	20.2%
12	671	5	2298.1	18.6%
13	680	11	2188.0	19.0%
14	692	4	2206.1	17.9%
15	703	10	2174.8	16.3%
16	718	5	2152.6	15.5%
21	725	9	2247.1	15.9%
22	754	2	2268.3	15.5%
23	759	3	2261.7	14.8%
24	762	0	2268.6	14.6%
25	763	9	2229.0	13.8%

Appendix 1.3 Schnabel population estimates of northern pike, *Esox lucius*, 1981, Henderson Lake.

Date	Number of fish marked (cumulative)	Number of fish recaptured (Daily)	Estimated population $\bar{x}$	95% confidence interval
May 21	0	0		
22	22	0		
23	49	1		
24	67	0		
25	86	3		
26	108	0		
27	126	1	1738.4	95.3%
June 3	138	1	1551.5	73.7%
4	144	1	1463.1	60.6%
5	149	0		
6	170	1	2020.7	71.2%
7	179	2	1953.8	55.8%
8	196	2	1790.2	45.6%
9	207	1	1884.0	43.3%
10	215	4	1573.5	36.9%
11	228	3	1516.4	31.4%
17	241	5	1320.2	29.1%
18	252	0		
25	254	3	1421.8	24.8%
26	268	0		
27	277	4	1332.1	22.1%
28	286	3	1310.0	20.7%

Appendix 1.4 Schnabel population estimates of walleye, _Stizostedion vitreum vitreum_, 1981, Henderson Lake.

Date	Number of fish marked (cumulative)	Number of fish recaptured (daily)	Estimated population $\bar{x}$	95% confidence interval
May 21	0	0		
22	5	0		
23	37	2		
24	63	4		
25	86	3		
26	128	1		
27	154	5	1518.9	67.5%
June 3	198	4	1334.7	49.3%
4	214	4	1350.1	38.6%
5	236	1	1520.2	41.9%
6	250	2	1533.8	36.8%
7	260	5	1344.1	34.3%
8	270	1	1384.6	32.9%
9	275	1	1675.4	41.4%
10	294	4	1527.4	37.9%
11	301	6	1418.5	32.7%
17	315	16	1331.5	24.7%
18	352	4	1289.5	23.2%
25	356	6	1423.5	23.5%
26	385	7	1446.6	21.5%
27	403	8	1434.6	19.9%
28	418	7	1443.1	18.5%

Appendix 2. Statistics of trap and gill nets used on Henderson Lake, 1979-1981.

<u>Trap nets</u>

Net type	1.22 meters (four ft)	1.83 meters (six ft)	2.44 meters (eight ft)
Standard length of lead	18.3 m	36.6 m	45.7 m
Depth of lead	1.22 m	1.83 m	2.44 m
Mesh size of lead	1.27 cm	5.08 cm	5.08 cm
Length of pot	2.44 m	3.96 m	5.49 m
Width of pot	1.22 m	1.83 m	2.44 m
Depth of pot	1.22 m	1.83 m	2.44 m
Mesh size of pot	1.27 cm	5.08 cm	5.08 cm
Width of house	1.83 m	2.74 m	3.66 m
Mesh size top of house	1.27 cm	7.62 cm	7.62 cm
Length of wings	1.83 m	3.66 m	5.49 m
Mesh size top of heart	1.27 cm	5.08 cm	7.62 cm

<u>Gill nets</u>

Standard test mesh gill nets were composed of 8 - 50 ft panels of variable size mesh arranged as:

25 mm, 38 mm, 51 mm, 64 mm, 76 mm, 89 mm, 102 mm, 114 mm

Appendix 3. Z values and significance of comparisons of length-weight relationships of walleye, Stizostedion vitreum vitreum, and northern pike, Esox lucius, 1978-1981, Henderson Lake.

		Z values			
Species	Equations compared	Intercept	Sig.	Slope	Sig.
walleye	1978-1979 combined sex	3.27	$P < 0.05$	4.47	$P < 0.05$
	1979-1980 combined sex	2.57	$P < 0.05$	3.46	$P < 0.05$
	1980-1981 combined sex	0.45	$P > 0.05$	0.159	$P > 0.05$
	1980 between sexes	3.14	$P < 0.05$	3.21	$P < 0.05$
	1981 between sexes	0.652	$P > 0.05$	0.585	$P > 0.05$
northern pike	1978-1979 combined sex	6.30	$P < 0.05$	8.9	$P < 0.05$
	1979-1980 combined sex	3.70	$P < 0.05$	4.5	$P < 0.05$
	1979-1981 combined sex	6.30	$P < 0.05$	6.1	$P < 0.05$
	1980 between sexes	0.841	$P > 0.05$	1.14	$P > 0.05$
	1981 between sexes	7.60	$P < 0.05$	3.14	$P < 0.05$
	1980-1981 males	1.53	$P > 0.05$	1.65	$P > 0.05$
	1980-1981 females	2.8	$P < 0.05$	3.80	$P < 0.05$

Appendix 4.1. Actual volume (ml) and percent of total volume of food items in walleye, Stizostedion vitreum vitreum stomachs, January - August 1980, Henderson Lake.

Food Item	Month						Total
	January	April	May	June	July	August	
Perca flavescens				42.7 (14%)	9.6 (1%)	3.5 (11%)	55.8 (6%)
Pungitius pungitius	8.0 (70%)		18.5 (95%)	142.3 (48%)	392.6 (77%)	12.1 (39%)	573.4 (66%)
Catostomus commersoni							
Stizostedion v. vitreum							
Esox lucius					37.1 (7%)		37.1 (4%)
Hiruninea	0.2 (2%)			3.0 (1%)	8.0 (2%)		11.2 (1%)
Sialis larva							
Odonata				11.8 (4%)	7.8 (2%)		19.6 (2%)
Ephemeroptera sp.				46.6 (16%)			46.6 (5%)
Hexagenia	0.2 (2%)	1.0 (13%)	0.9 (5%)	1.4 (<1%)	9.7 (2%)		12.4 (1%)
Pentagenia				5.9 (2%)		0.2 (<1%)	6.1 (1%)
Orconectes virilis						14.5 (48%)	14.5 (2%)
Etheostoma exile							
Notropsis heterolepis							
Mollusca							
Lota lota							
Tricoptera							
Fish remains	3.0 (26%)	6.7 (87%)		34.2 (11%)	42.1 (8%)	0.4 (1%)	86.4 (10%)
Insect remains				11.4 (4%)	0.1 (1%)		11.5 (1%)
No. of stomachs	3	11	4	156	106	17	297

Appendix 4.2. Actual volume (ml) and percent of total volume of food items in walleye, Stizostedion vitreum vitreum stomachs, January - October 1981, Henderson Lake.

Food Item	Month						Total
	January	May	June	July	August	October	
Perca flavescens				114.5 (22%)	121.8 (31%)	42.4 (26%)	334.9 (30%)
Pungitius pungitius		19.7 (100%)	5.5 (58%)	357.8 (69%)	207.2 (52%)	98.6 (61%)	632.6 (57%)
Catostomus commersoni							
Stizostedion v. vitreum					5.0 (1%)		5.0 (4%)
Esox lucius							
H iruninea				1.7 (<1%)	1.1 (<1%)		2.8 (<1%)
Sialis larva							
O donata							
Ephemeroptera sp.				5.2 (1%)	6.8 (2%)		12.0 (1%)
Hexagenia					17.2 (4%)		17.2 (2%)
Pentagenia							
Orconectes virilis					2.6 (<1%)		2.6 (<1%)
Etheostoma exile					0.2 (<1%)		0.2 (<1%)
Notropsis heterolepis							
M ollusca							
Lota lota							
Tricoptera							
Fish remains	0.9 (100%)		4.0 (42%)	40.9 (7%)	35.8 (9%)	21.4 (13%)	104.2 (9%)
Insect remains				0.7 (<1%)			0.7 (<1%)
No. of stomachs	2	4	3	106	126	24	256

Appendix 4.3. Actual volume (ml) and percent of total volume of food items in northern pike, Esox lucius, stomachs, January - August 1980, Henderson Lake.

Food item	Month					Total
	January	April	June	July	August	
Perca flavescens	1.0 (1%)	78.4 (26%)	69.5 (16%)	33.2 (6%)	3.5 (11%)	185.6 (13%)
Pungitius pungitius	21.1 (25%)	14.5 (5%)	53.4 (13%)	47.7 (8%)	12.1 (39%)	148.8 (10%)
Catostomus commersoni	62.0 (74%)	35.5 (11%)	102.0 (24%)	32.0 (5%)		231.0 (16%)
Stizostedion v. vitreum		130.0 (42%)		201.0 (33%)		331.0 (23%)
Esox lucius			84.0 (20%)	47.0 (8%)		131.0 (8%)
Hirudinea			46.1 (28%)	2.5 (<1%)		48.6 (3%)
Sialis larva				2.5 (<1%)		2.5 (<1%)
Odonata			9.0 (2%)			9.0 (1%)
Ephemeroptera sp.		0.9 (<1%)	2.7 (<1%)	0.2 (<1%)		3.8 (<1%)
Hexagenia	0.3 (<1%)	1.1 (<1%)	7.5 (2%)	0.2 (<1%)	0.2 (<1%)	9.1 (1%)
Pentagenia			1.1 (<1%)			1.3 (<1%)
Orconectes virilus			19.9 (5%)	115.4 (19%)	14.5 (47%)	149.8 (10%)
Etheostoma exile			2.0 (<1%)	0.4 (<1%)		2.4 (<1%)
Notropsis heterolepis						
Mollusca			0.1 (<1%)			0.1 (<1%)
Lota lota				120.0 (20%)		120.0 (7%)
Tricoptera			1.2 (<1%)			1.2 (<1%)
Fish remains		47.4 (15%)	18.2 (4%)	7.1 (1%)	0.4 (1%)	73.1 (5%)
Insect remains			9.9 (2%)			9.9 (1%)
No. of stomachs	12	42	132	47	8	241

Appendix 4.4 Actual volume (ml) and percent of total volume of food items in northern pike, Esox lucius stomachs, January - October 1981, Henderson Lake.

Food Item	Month						
	January	May	June	July	August	October	Total
Perca flavescens	33.5 (22%)	32.7 (45%)	10.0 (17%)	18.7 (22%)	39.0 (55%)	607.6 (73%)	909.8 (64%)
Pungitius pungitius	20.6 (14%)	30.4 (42%)	38.5 (66%)	16.9 (20%)	4.2 (6%)		110.6 (8%)
Catostomus commersoni	12.0 (8%)			23.5 (28%)		70.0 (9%)	105.5 (7%)
Stizostedion v. vitreum	25.0 (17%)					79.0 (10%)	104.0 (7%)
Esox lucius							
Hirudinea						1.0 (<1%)	1.0 (<1%)
Sialis larva							
Odonata			0.1 (<1%)				0.1 (<1%)
Ephemeroptera sp.	14.0 (9%)		0.4 (<1%)				14.4 (1%)
Hexagenia	10.5 (7%)			0.2 (<1%)			10.7 (<1%)
Pentagenia							
Orconectes virilis			8.9 (15%)	5.7 (7%)	21.0 (29%)		57.6 (4%)
Etheostoma exile	0.6 (<1%)			0.7 (<1%)			1.3 (<1%)
Notropsis heterolepis						5.9 (<1%)	5.9 (<1%)
Mollusca							
Lota lota							
Tricoptera							
Fish remains	6.8 (5%)	10.2 (13%)	0.6 (1%)	19.0 (22%)	7.4 (10%)	60.2 (7%)	104.3 (7%)
Insect remains	5.0 (3%)						5.0 (<1%)
No. of stomachs	21	13	12	46	28	44	164