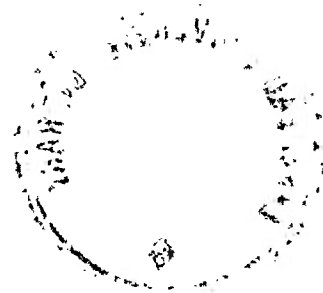COMMUNITY DYNAMICS RESULTING FROM AN

EXPERIMENTAL PULSE FISHERY ON THE WALLEYE

(STIZOSTEDION VITREUM VITREUM MITCHILL)

IN HENDERSON LAKE, ONTARIO

BY

BRIAN D. WISENDEN©

A thesis submitted to the Department of Biology in

partial fulfillment of the requirements for the

Degree of Master of Science

Lakehead University

Thunder Bay, Ontario

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Abstract

Henderson Lake is a small 151 ha boreal percid lake approximately 128km northwest of Thunder Bay. A pulse fishery conducted from 1980 to 1982 inclusively, removed 3226 walleye reducing the stock to very low levels (Reid, 1985).

The current study had four objectives: first, to continue monitoring the population density, age structure, production and biomass of walleye, northern pike and white suckers; second, to collect comparative walleye age and growth data from a nearby control lake; thirdly, to investigate the feeding ecology of young of the year walleye as well as to discern any potential competitive interactions with the superabundant yellow perch population; and fourth, to review the community dynamics of Henderson Lake for signs of shifts in species abundance and growth in response to the walleye exploitation. These data provided interesting insights into the feasibility of a pulse fishery as an alternative walleye management strategy.

Since 1980, the walleye decreased in mean age to maturity and increased in fecundity and growth (Reid, 1985) but unexpectedly, had five consecutive years of recruitment failure between 1980 and 1984. Normal walleye recruitment in the nearby Lanigon Lake suggests that the year class failures in Henderson Lake were not due to climatic factors. Possible causes include recruitment overfishing (Cushing, 1977) exacerbated by variable spring water thermal regimes.

The stunted yellow perch population, the principal forage

species, both increased in abundance and became further stunted in response to reduced walleye predation. Four years after removal stopped, northern pike aged four and older increased both in growth as well as fecundity. As recruitment increased growth of young pike stabilized. Pike production, biomass and turnover rates dramatically increased from 1982 to 1986. These changes were probably a delayed response to improved forage opportunities and decreased walleye abundance. No changes were observed in the sucker population in response to the walleye removal.

The first evidence for walleye population recovery came with production of strong year classes in 1985 and 1986. Young of the year (YOY) walleye in Henderson Lake grew faster than any others reported in the literature with the exception of Lake Erie fish in 1959 (Parsons, 1972). YOY walleye made regular crepuscular feeding forays into shallow water with peaks of activity at 21:20hr at a mean ambient light intensity of $2.76W/m^2$. Stomach contents revealed a diet of fish (94.68-99.79% by weight) most of which were YOY yellow perch. Dietary overlap indices between YOY walleye and adult yellow perch in the length ranges of 91-131mm and 131-200mm (total length) indicated that perch were potential competitors with 10-41% and 10-33% dietary overlap, respectively.

The recovery period for walleye must be reasonably brief if pulse fishing is to be a viable method of walleye management. Both the increase in perch abundance, and consequentially pike production, may delay reestablishment of walleye densities sufficient to support another pulse fishery. The variable spring

thermal regime and short growing season imposed by the north-temperate climate of Henderson Lake delayed the responses in the percid community. Pulse fishing as an alternative management strategy must consider the possibility of recruitment failure, time lags in the community dynamics and interspecific suppression of the recovery process and even complete collapse.

Acknowledgements

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Introduction

Of the 3601 known walleye lakes in Ontario approximately eighty nine percent are located in northwestern Ontario (AFS, 1984). Since this region has over 3200 walleye lakes and since walleye are the most sought after species by anglers the tourism potential of this resource in this region is enormous.

As user demand increases, effective management of the walleye resource becomes of paramount importance to the development and maintenance of tourism in this region.

Adams and Olver (1977) outlined three approaches to walleye harvest management. The first is to maximize production. This has been employed on both the east coast and the Great Lakes. This strategy often exceeds the adaptive capabilities of the fish population, increasing the amplitude of both population and species fluctuations (ie. less stability) while eroding economic confidence in the resource. The second option aims for high community stability similar to that found in unperturbed populations. Such a strategy precludes anything other than a very low level of exploitation. Their third and recommended stategy is to develop a pulse fishery. This represents a compromise between maximum preservation and total economic exploitation. A pulse fishery management scheme alternates a short period (1 - 3 years) of intense exploitation followed by by a moratorium on fishing. Upon fishery closure, stock density should recover to pre-exploitation levels. A group of lakes could then be managed on a rotational basis, i.e. while one is being fished the others

recover.

Determining which indices to select for both assessment of fishery closure and estimation of the duration of the recovery period is crucial to the successful implementation of such a scheme.

The advantages of pulse fishing are numerous. Anglers realise a high biomass yield and the community dynamics are kept intact (Adams and Olver, 1977). As a result the fish community should be better able to cope with external perturbations. Monitoring the stock and enforcing regulations on one lake from amongst a larger number requires fewer staff (field biologists, conservation officers, etc), and so makes more efficient use of present resources. A pulse fishery of high intensity can be described by models (Sluczanowski, 1984) that is more useful to managers than one based on precise measurement of fishing mortality (F), the widely used index of exploitation rate. In such cases the recovery period serves as a measure of exploitation since it varies with the severity of exploitation and the resiliency of the stock. Through fishery closure, the recovery period is both easier to estimate as well as easier to control through fishery closure relative to the precise measurement of the F statistic (Sluczanowski, 1984).

Exploitation of fish populations can result in several classic responses: increased growth, increased fecundity, decreased mean age to maturity and decreased mean age of the population (Nikolskii, 1969; Healey, 1975; Spangler et.al., 1977). Such responses must be understood in order to develop

responsible fisheries management policies.

An experimental pulse fishery was started on Henderson Lake walleye in 1980 (Nunan, 1982). In three years, 3226 walleye were removed reducing the stock to very low levels (Reid, 1985). By 1984 the following were observed: a growth response in young walleye, a fecundity increase and a decrease in the mean age to maturity (Reid, 1985). Good predictors of imminent stock collapse were the observed changes in annual production, Petersen population estimates, growth of young walleye and Abrosov's index of mean age to maturity (Reid and Momot, 1985).

This investigation had four objectives: first, to continue measurement of walleye, northern pike and white sucker abundance, age structure, production and biomass during the post harvest period; second, to investigate the feeding ecology of the young of the year walleye and assess potential competitive interactions with other species that might hinder their recruitment; third, to review the community dynamics of Henderson Lake for signs of shifts in species abundance and growth in response to walleye exploitation and finally, to estimate the time required for recovery (restoration of walleye abundance), with regards to the possible role of interspecific interactions in suppressing recovery.

Materials and Methods

Study Area

Henderson Lake is mesotrophic, 150.9 hectares in area and located approximately 128 kilometers northwest of Thunder Bay, Ontario (Fig..1). Henderson Lake is one of the five Savanne Lake area provincial fish sanctuaries designated in 1969, made available by the Ontario Ministry of Natural Resources for this study in 1979 (Nunan,1982; Reid,1985).

The lake is formed from two basins (Fig..2). The northern smaller, shallower basin contains a central mud shelf from which emergent vegetation grows in mid to late summer. A gravel reef and a large island separate the southern basin from the northern basin. The mean depth is 2.5 metres and the maximum depth of 5.44 metres occurs in the southern basin. Thermal stratification is usually precluded by summer wind and wave action. The chemical and physical characteristics of Henderson Lake are listed in Table 1.

Historically, the ichthyofauna of Henderson Lake comprised nine species: walleye (Stizostedion vitreum vitreum); northern pike (Esox lucius); common white sucker (Catostomus commersoni); yellow perch (Perca flavescens); Iowa darter (Etheostoma exile); burbot (Lota lota); blacknose shiner (Notropis heterolepis); mimic shiner (Notropis volucellus) and the nine-spined

Figure 1. Location of Henderson Lake with respect to Thunder Bay, Ontario.
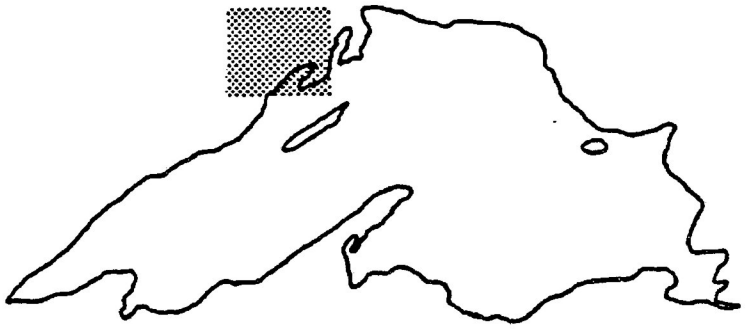
LAKE SUPERIOR
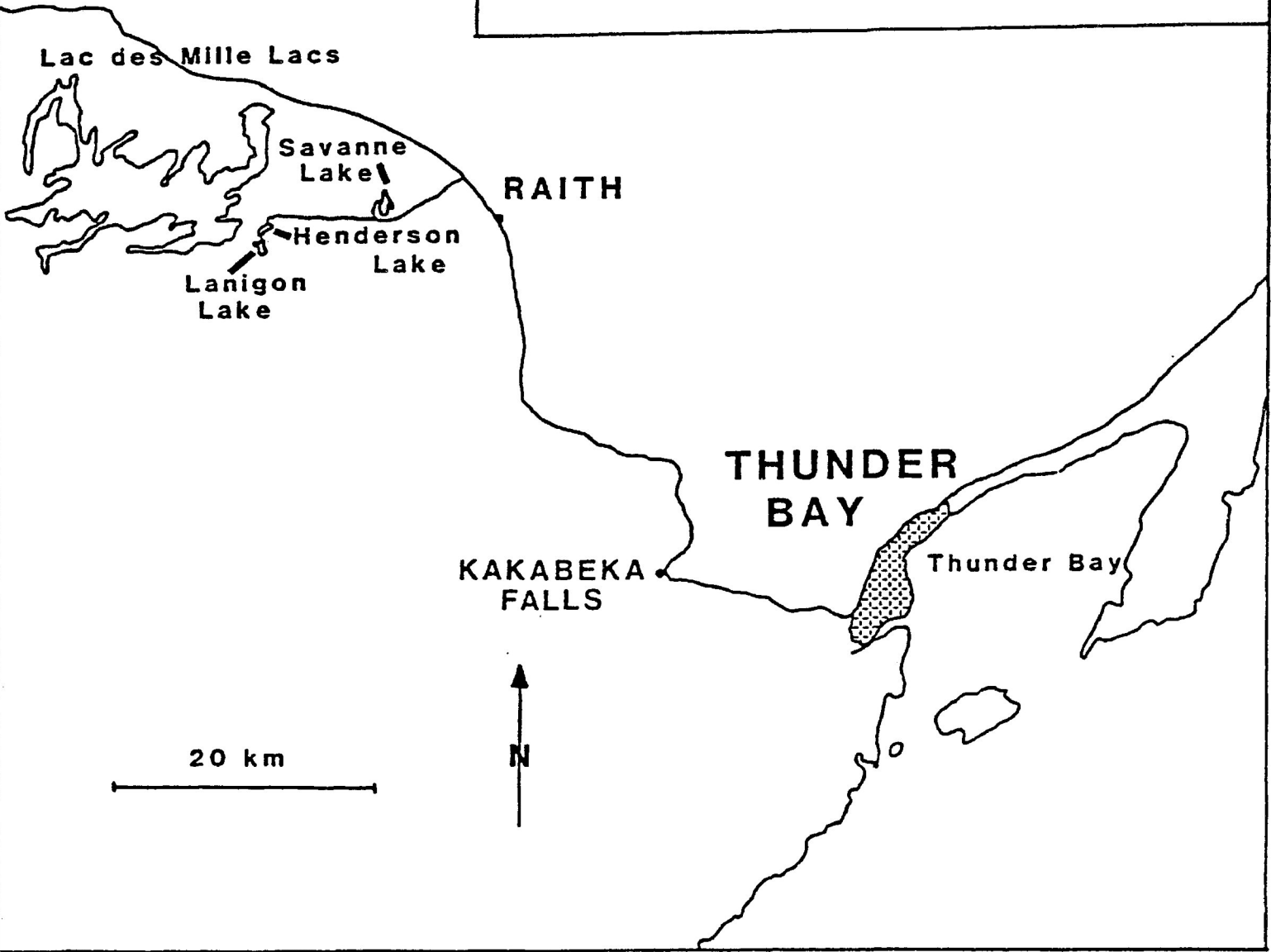
Lac des Mille Lacs

Savanne
Lake

RAITH

Henderson
Lake

Lanigon
Lake

THUNDER
BAY

KAKABEKA
FALLS

Thunder Bay

20 km

N

Figure 2. Bathymetric map of Henderson Lake, Ontario. Depth contours are in metres.

HENDERSON LAKE

1
2
2
1
3
2
1
5
2
1
5
4 2 1
1 2 4
1

N

To
Lanigon
Lake

.50km
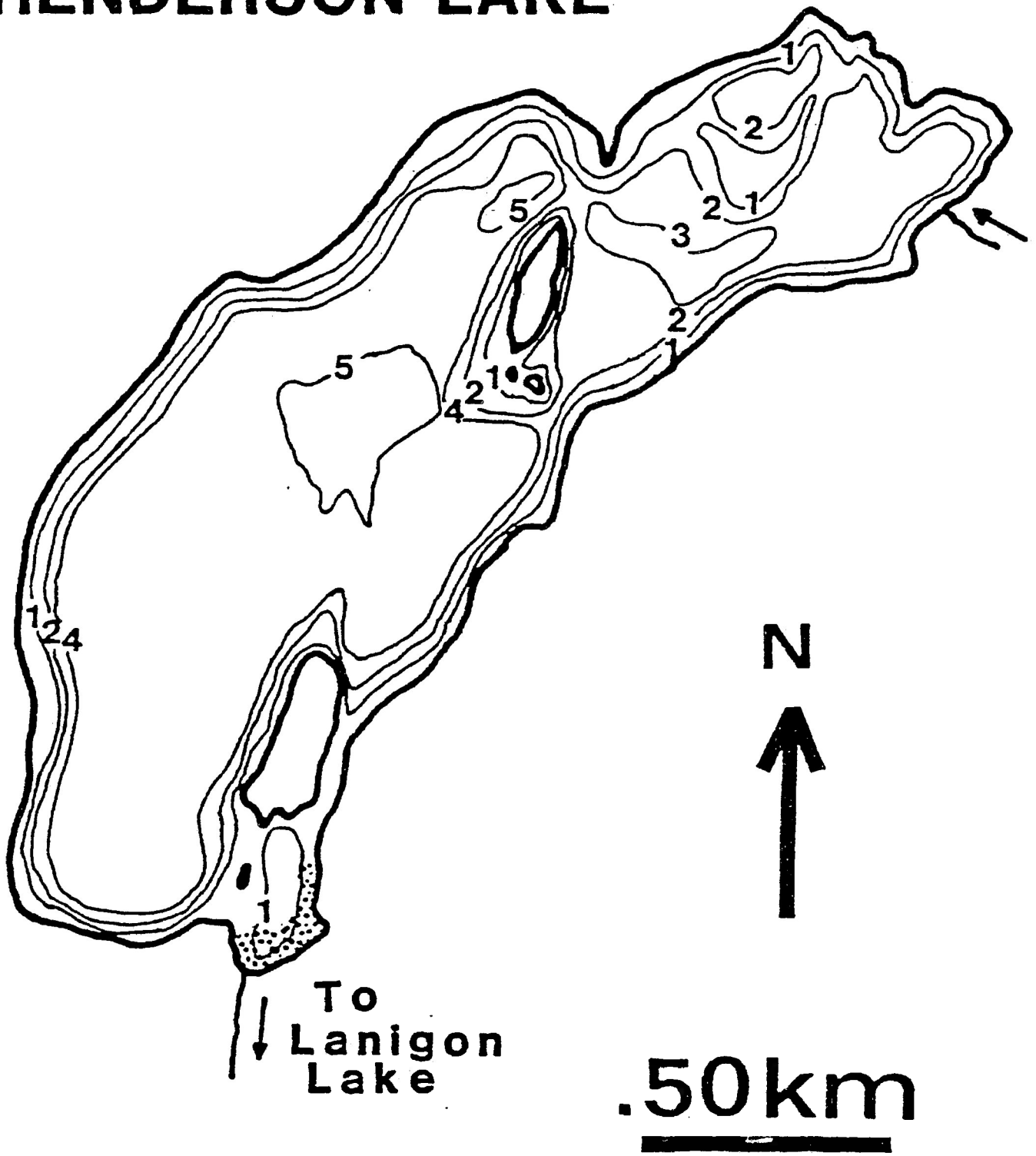
Table 1. Physical and chemical characteristics of Henderson Lake, Ontario.

Surface area	150.9 ha	Colour	14 hazen
Mean depth	2.5 m	Turbidity	1.2 formazin
Maximum depth	5.25 m	Total N	0.39 mg/l
pH	7.5	Ammonia	0.01 mg/l
Total solids	40 mg/l	Nitrite	0.001 mg/l
Calcium hardness	17.5 mg/l	Nitrate	0.025 mg/l
Calcium	4.4 mg/l	Total P	0.015 mg/l
Magnesium	1.6 mg/l	Dissolved P	0.002 mg/l
Total dissolved solids	43 mg/l	Conductivity	42 umhos/cm

----

stickleback (<u>Pungitius pungitius</u>). The stickleback population unexpectedly collapsed in 1982 and this species has not been collected since 1984 (Reid,1985).

Population Estimates

In addition to previous estimates by Nunan (1982) and Reid (1985), Schumacher-Eschmeyer (1943) mark and recapture population estimates were conducted in early spring of 1985 and 1986 on the walleye, northern pike and common white sucker populations. Fish were sampled daily from standard 1.83m (6') and 2.44m (8') trap nets. Weight to the nearest 25 grams, total and fork length in millimetres were noted. Sex was determined by extrusion of gonadal products when possible and all previous marks were recorded for each walleye, pike, and sucker. All fish were released on the side of the net opposite the entrance. Trap net locations for the 1985 and 1986 population estimates are shown in Fig. 3 and Fig. 4 respectively.

Walleye were marked by removing the eighth dorsal spine in 1985 and the tenth dorsal spine in 1986. Northern pike were marked with a right ventral fin clip in 1985 and a dorsal fin clip in 1986. In addition, scales were taken posteriolaterally to the dorsal fin above the lateral line. Suckers were marked with an anal fin clip in 1985 and a left pectoral fin clip in 1986. Walleye dorsal spines, pike scales and sucker fin ray sections were used for determining age. Pike and sucker scales were used

Figure 3. Trap net locations of 1985 population estimates of walleye, northern pike and white suckers, in Henderson Lake, Ontario.

T = Trap net location

(6) = six foot trap net

(8) = eight foot trap net

.

N

4(6)

5(6)

15(6)

2(8)

9(6)

8(6)
7(6)

14(6) 10(6)

1(6)

6(6)

12(6)
13(6)

11(6)

3(6)
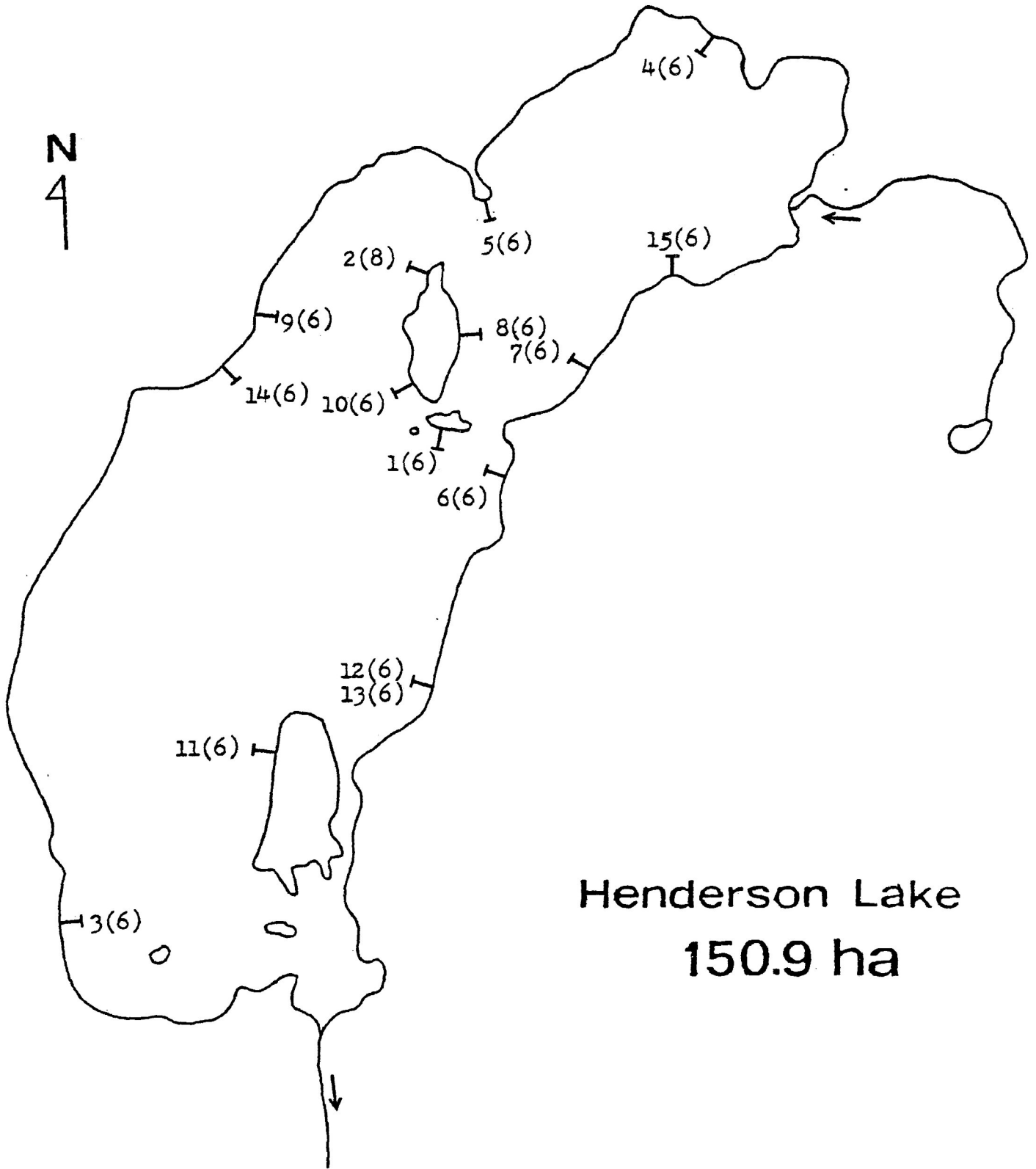
Henderson Lake

150.9 ha

Figure 4. Trap net locations of 1986 population estimates of walleye, northern pike and white suckers, in Henderson Lake, Ontario.

G = Small mesh gill net location

T = Trap net location

(6) = six foot trap net

(8) = eight foot trap net

N

3(8)
18(8)
26(8)

G2

2(6),9(6)
23(6)

6(6)
21(6)

22(6)
17(6)

19(8),13(6)
24(6)

10(6)

25(6)

27(8)

G3

1(6),7(6)

5(6)
8(8)
20(6)

12(6)

14(6)   15(6)

11(6)

4(8)
16(6)

G1
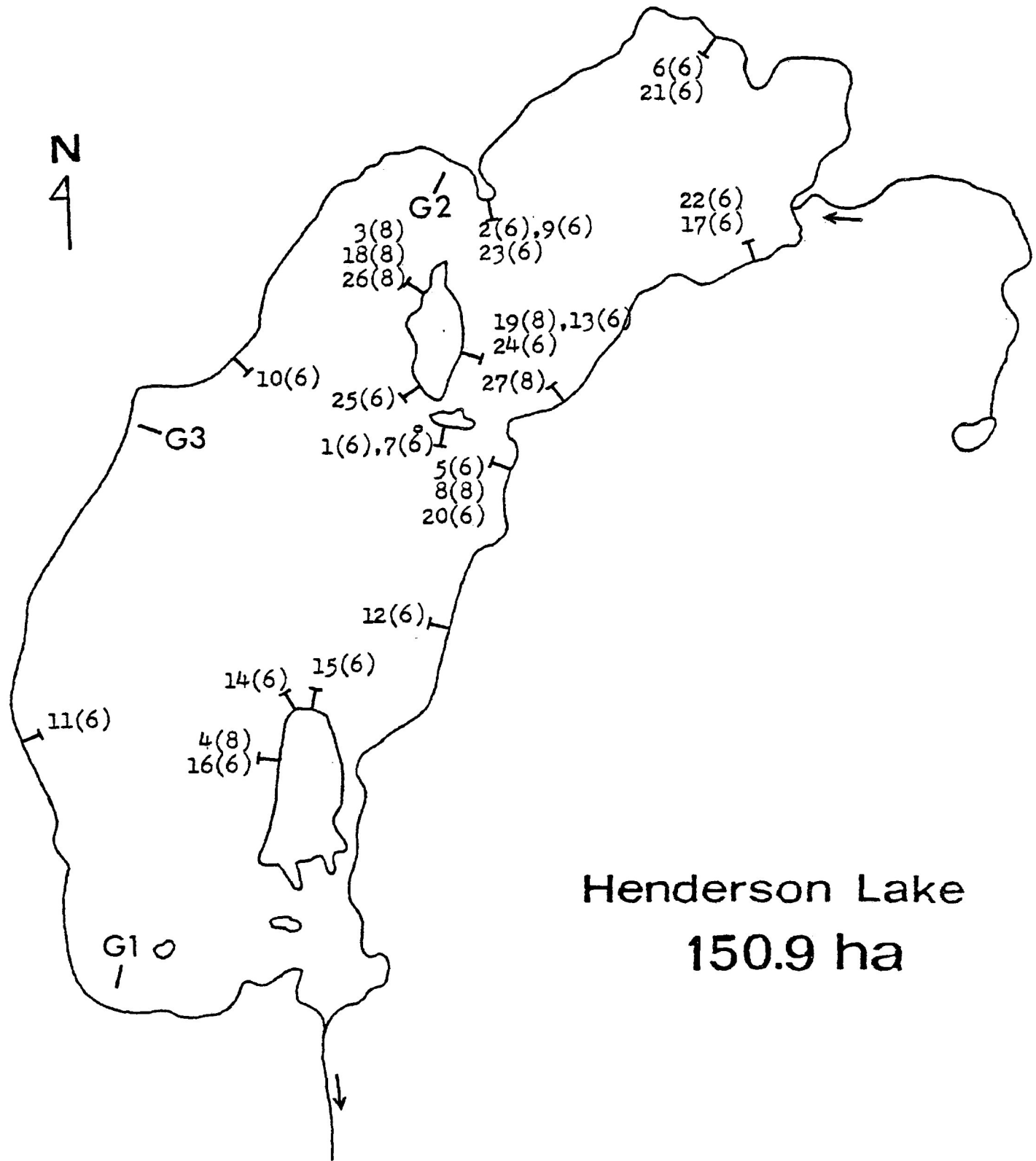
Henderson Lake
150.9 ha

for backcalculating growth. Younger age classes of suckers were obtained during 1986. Clips used for marking each species from 1979 to 1986 are listed in appendix E.

Age Determination

All tissues used for ageing were allowed to air dry. Walleye dorsal spines and sucker fin rays were embedded in five minute epoxy, and sectioned using an Isomet 11-1180 Buehler Ltd. low speed saw (Campbell and Babaluk, 1979). Two to five sections were taken from each fish as close to the base of the spine as possible. The sections were 1.2mm and 1.5mm thick for walleye and suckers respectively. All sections were permanently mounted on glass slides with Diatex mounting medium and examined under a microscope to observe the annuli.

A scale roller (Arnold,1951; Smith,1954) was used to make impressions of northern pike scales on acetate slides. The impressions were projected on a microfiche projector at 26X magnification. Fish ages and backcalculation slips were obtained from these projections. Backcalculations of northern pike and suckers were conducted using an Apple software program.

Assigned ages were verified by comparing results with those obtained by persons experienced in aging tissues of these species. Age distributions for pike and suckers were calculated after stratified subsampling (Ketchen, 1950; FAO, 1981).

Lanigon Lake

Lanigon Lake (63.5 ha) is connected to Henderson Lake by a small creek (Fig. 5). Though not a sanctuary lake, Lanigon is very lightly exploited due to its inaccessibilty. Its fish population thus served as a control for this experiment. In 1986, the Lanigon Lake walleye were sampled (total length, weight, tenth dorsal spine collected for ageing) using two 1.83m trapnets and by angling. These fish were compared to Henderson Lake walleye.

Young of the Year Walleye Investigation

For the first time since the onset of this project in 1979, young of the year (YOY) walleye were captured in seines in 1985. In 1986, a preliminary study was conducted to provide some information on food habits and growth of YOY walleye. Most of the YOY walleye were collected using 19.1mm (0.75 inch) and 25.4mm (1.00 inch) stretch mesh monofilament gill net gangs consisting of four panels sequentially connected as follows 0.75-1.00-0.75-1.00, at depths from 0.5m to 5.44m in locations illustrated in Fig. 4. Nets were fished for durations of approximately twenty minutes from July 18 to August 31 from 12:00 (noon) to 01:00, with maximum concentration at dusk. Total length in millimetres and weight to 0.1 gram of each fish were measured. In addition dorsal spines and opercles were taken from all walleye. YOY

Figure 5. Location of trap nets (T) in Lanigon Lake, Ontario, 1986.

Henderson
Lake

N
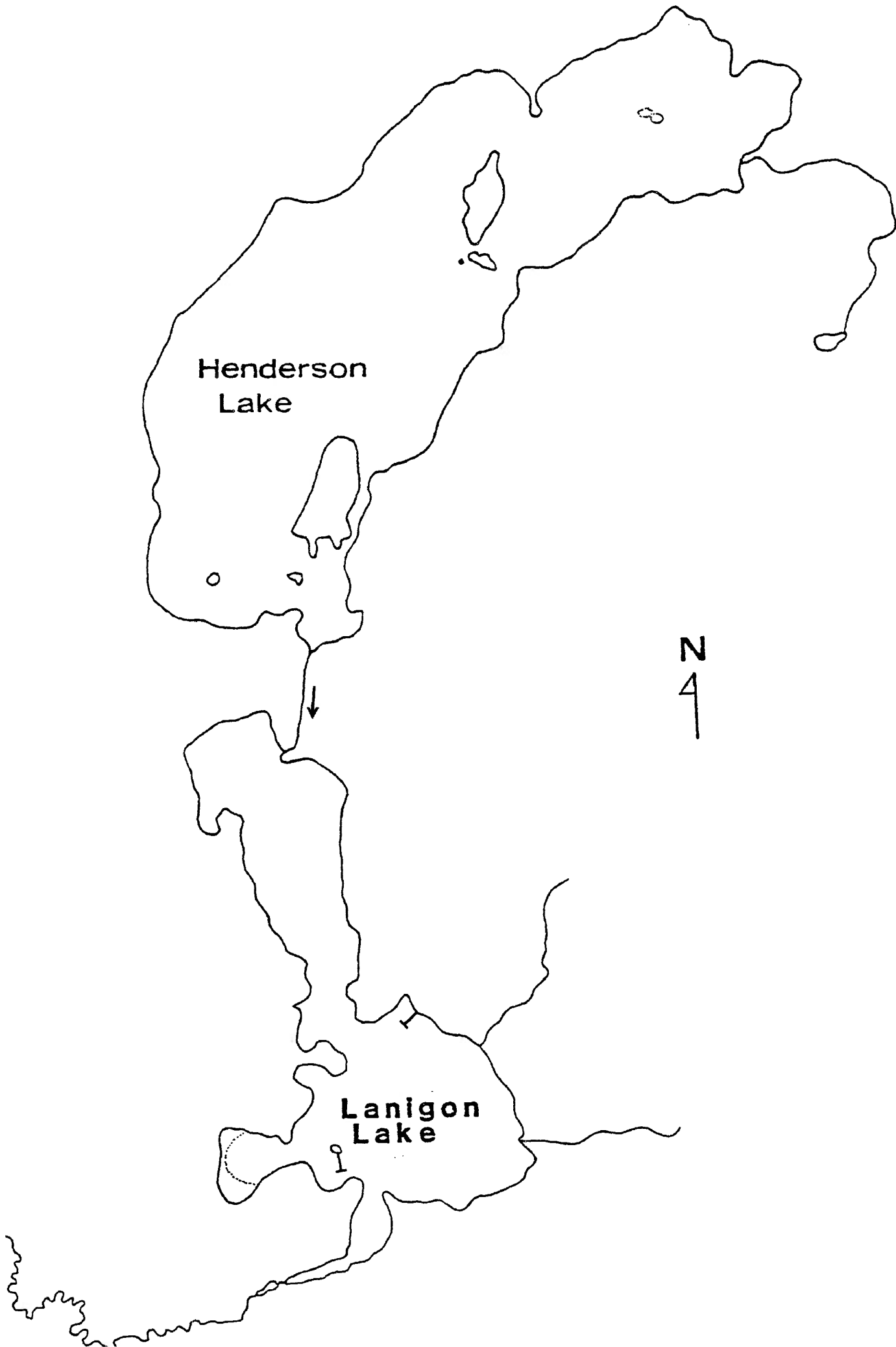
Lanigon
Lake

walleye were opened and preserved in 10% formalin and placed in labelled Whirlpacs. Panel depth, determined by the mean of the depths of each end of each panel as well as surface light intensity in watts per square metre at lift time were recorded for each walleye sampled. In the Lakehead University laboratory facilities, the walleye were transferred to 70% ethanol. Stomachs were dissected and contents identified to genus and species when possible. Total length of intact prey items was measured. All individual prey items and total stomach contents from each fish were placed on bibulous paper to remove excess water. Wet weight was determined to the nearest 0.001 gram on a Mettler electronic weigh scale. Diet analyses were carried out by methods outlined in Hyslop (1980) and Wallace (1981).

Statistical Analyses

All t-tests and some linear regressions were computed using a Sharp EL5103 pocket calculator. More complex analyses were conducted on the Lakehead University VAX180 mainframe computer using the Statistical Package for the Social Sciences-X (SPSSX) (Nie at.al.1985). Unless otherwise stated, significance levels of tests are p = 0.05.

Results

Population Estimates

Since there was little recruitment the walleye population steadily dwindled from 152 fish in 1984, to 129 in 1985 and further to 101 in 1986 (Table 2) due to natural mortality. Pike abundance declined from approximately 2200 in 1980 to 817 in 1983. In 1986 the population of 1310 approximated (p=0.05) the eight year mean population estimated at 1354 (Table 2). Sucker abundance also abruptly declined from 1280 fish in 1981 to 750 fish in 1982. However, the 1986 estimate of 1244 did not differ significantly (p=0.05) from the eight year mean of 1155 (Table 2).

Length Distributions

The shape of the Henderson Lake walleye length distribution changed from bimodal to unimodal from 1979 to 1984 (Reid, 1985) but remained consistent between 1984 and 1986. However, the modal length shifted to the right by about 25mm per year since 1984 (Fig. 6).

The Lanigon Lake walleye length distribution differs (Fig. 7). The Lanigon Lake curve is much broader based (34cm to 57cm) than Henderson Lake (43cm to 58cm) and the modal length is about 9 centimetres lower.

Table 2. Shumacher-Eschmeyer SE(N) and Petersen P(N) population
estimates for walleye, northern pike and white sucker
from 1979 to 1986 in Henderson Lake, Ontario.
95% confidence limits in parentheses. Data from 1979 to
1981 from Nunan (1982) and data from 1982 to 1984 from
Reid (1985).

Walleye

Year	SE(N)	95%C.L.	P(N)	95%C.L.
1979	1336	1122 - 1652	- -	
1980	1588	1310 - 2016	2707	2504 - 2910
1981	1183	1008 - 1431	2163	1982 - 2344
1982	945	750 - 1276	1194	1087 - 1310
1983	375	334 - 428	312	275 - 349
1984	152	133 - 177	169	141 - 197
1985	129	91 - 167	- -	
1986	101	73 - 128	- -	

Northern pike

Year	SE(N)	95%C.L.
1979	1963	1705 - 2313
1980	2285	2020 - 2631
1981	1104	938 - 1342
1982	1064	938 - 1383
1983	817	768 - 872
1984	1171	1073 - 1289
1985	1120	941 - 1299
1986	1310	1143 - 1477
Mean	1354	

White suckers

Year	SE(N)	95%C.L.
1979	1454	1172 - 1914
1980	1058	683 - 2356
1981	1281	902 - 2208
1982	748	497 - 1517
1983	976	840 - 1165
1984	1146	1027 - 1296
1985	1336	360 - 2311
1986	1244	1020 - 1467
Mean	1155	

Figure 6. Length distributions of walleye in Henderson Lake,

Ontario, 1979 - 1986.

% = Percent of total catch

1979 - 1981 data from Nunan, 1982

1982 - 1984 data from Reid, 1985
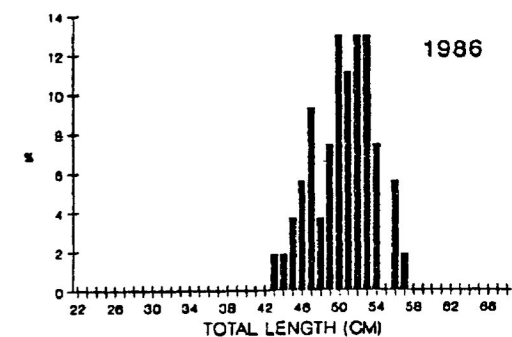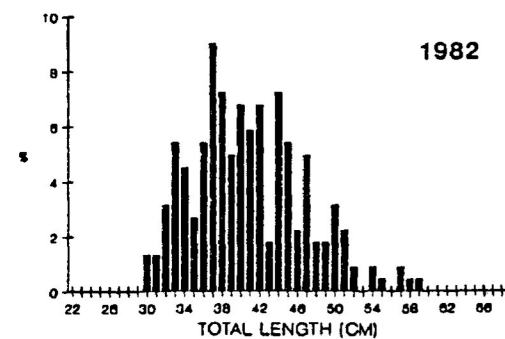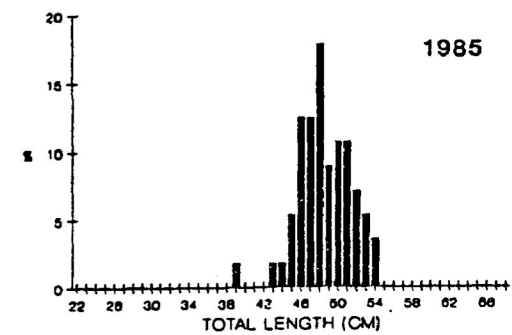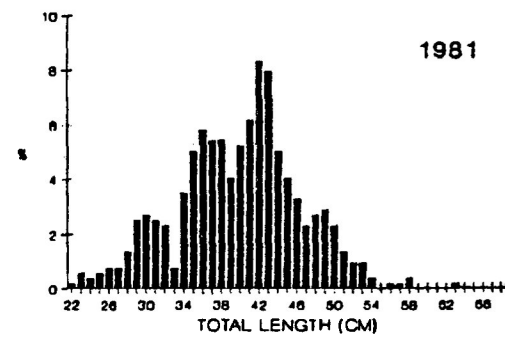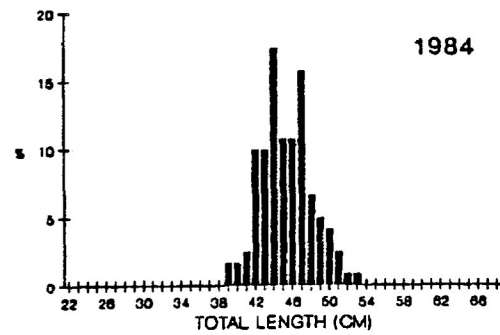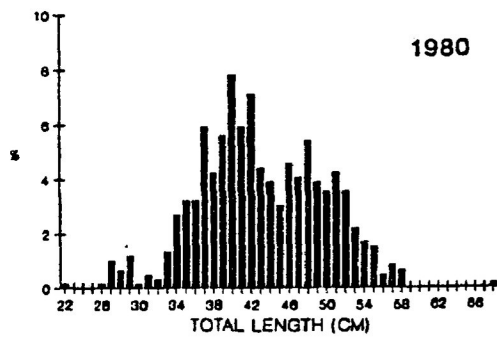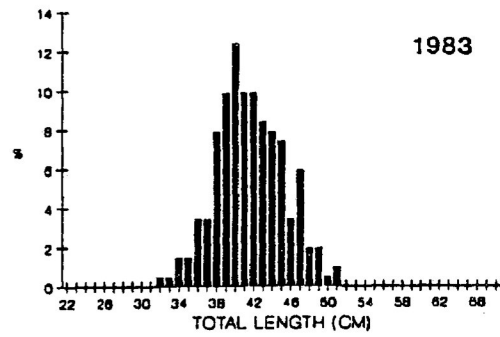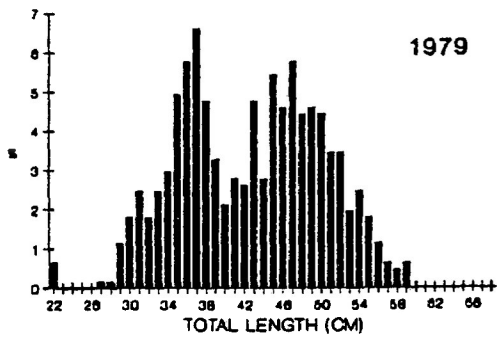
Figure 7. Length distribution of walleye in Lanigon Lake,

Ontario, 1986, compared with the 1986 Henderson Lake

walleye length distribution.

% = Percent of total catch
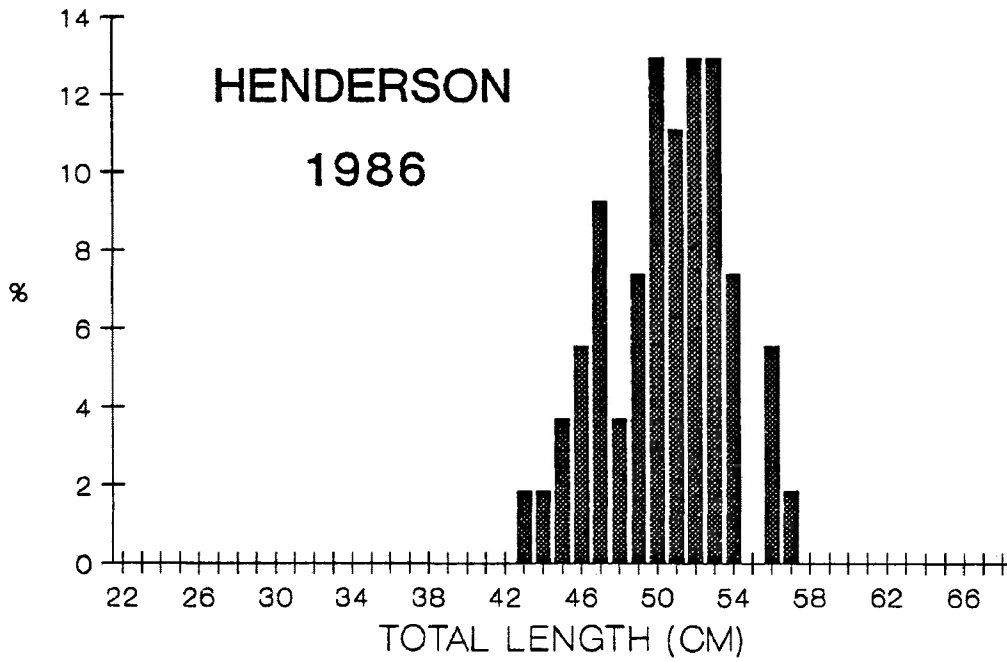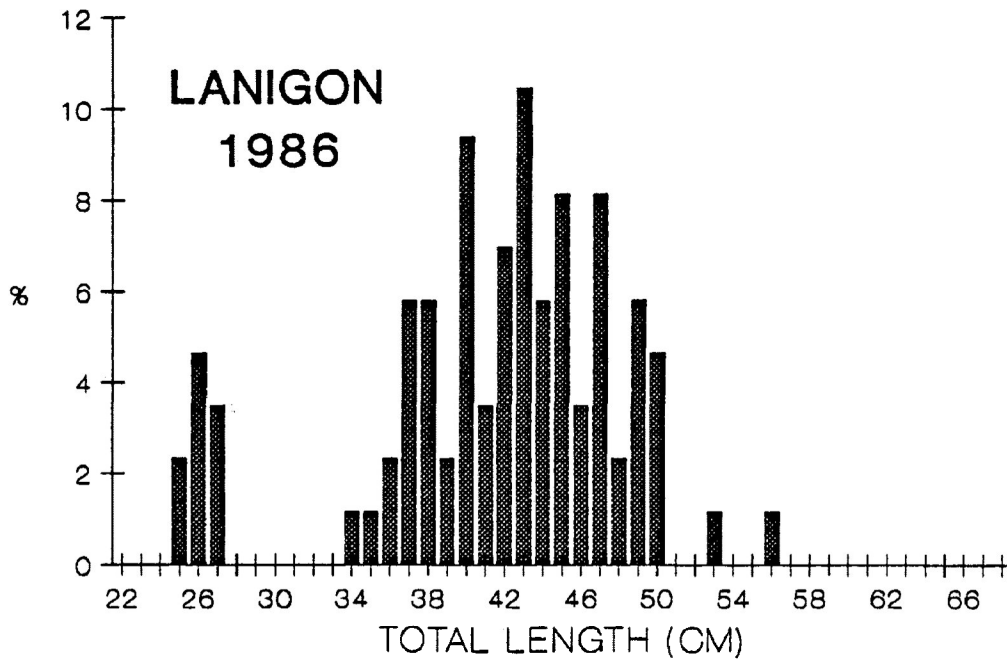
Figure 8. Length distributions of northern pike in Henderson
Lake, Ontario, 1979 - 1986.

% = Percent of total catch

1979 - 1981 data from Nunan, 1982

1982 - 1984 data from Reid, 1985
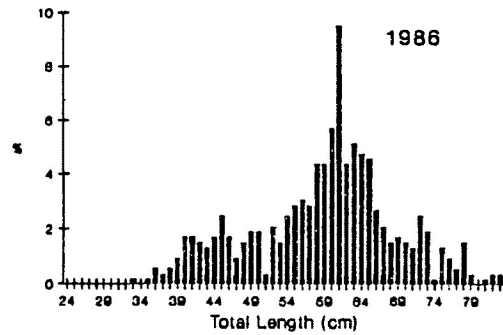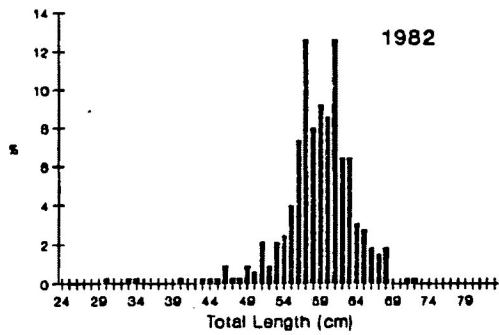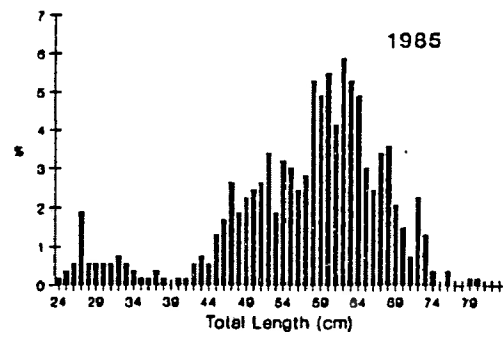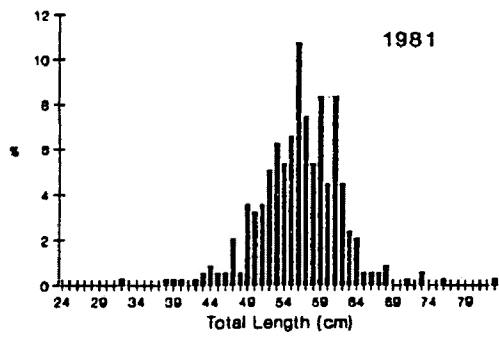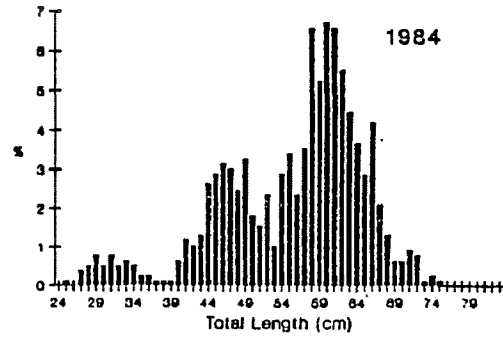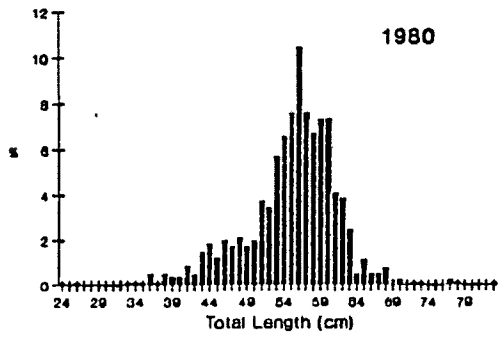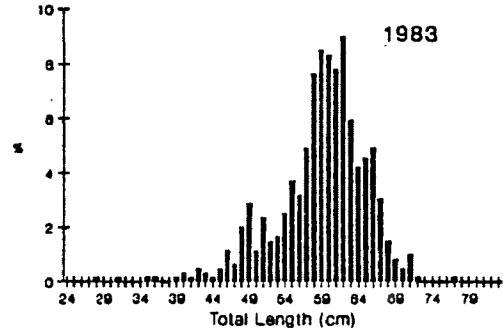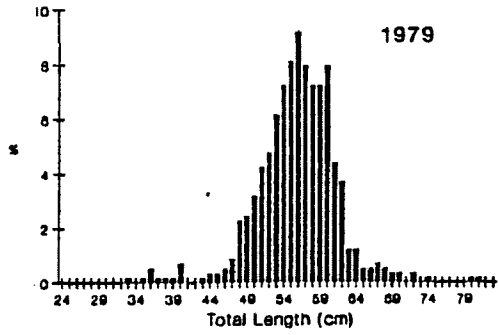
Figure 9. Length distributions of white suckers in Henderson
Lake, Ontario, 1979 - 1986.

% = Percent of total catch

1979 - 1981 data from Nunan, 1982

1982 - 1984 data from Reid, 1985
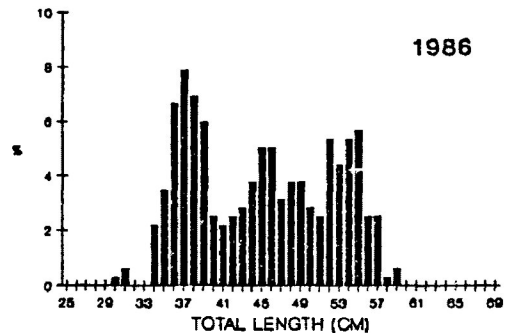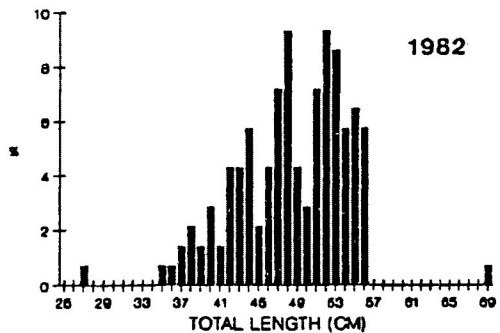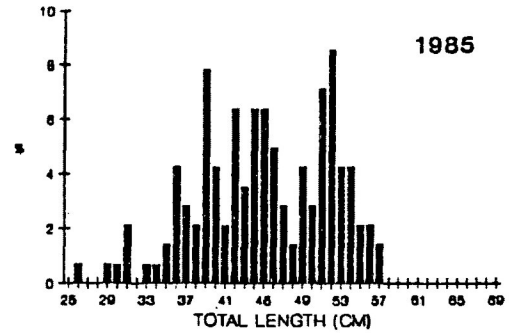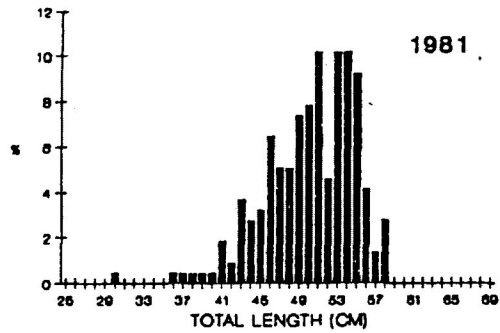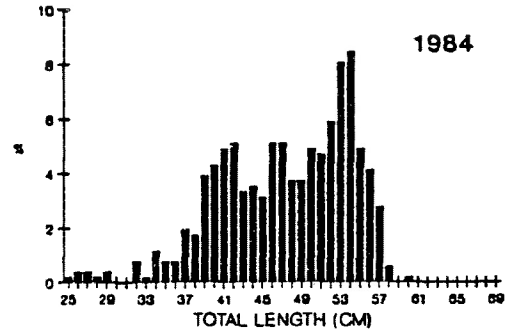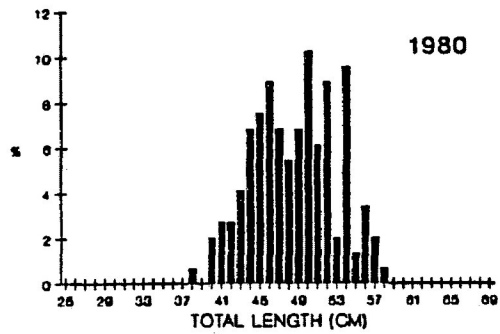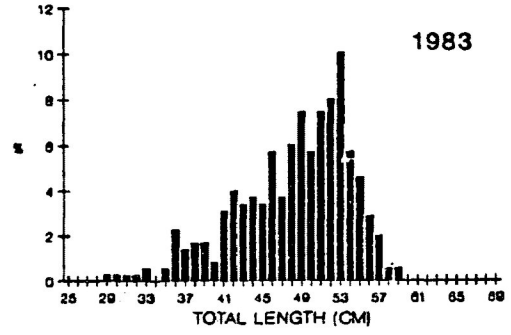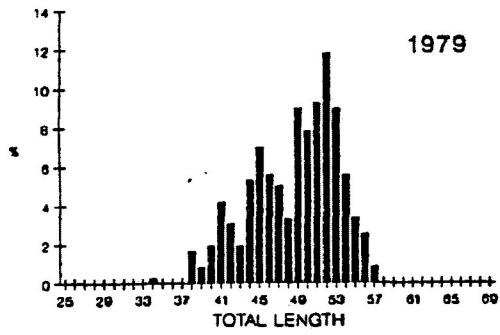
Table 3. Length weight regressions[1] of walleye, northern pike and
white suckers in Henderson Lake, Ontario, 1985 and 1986.
M = Male, F = Female, C = Combined sexes.
W = Weight (g), TL = Total length (mm), Log = Log_{10}

	1985	1986

Walleye - Population estimate data

Sex		
M	W = 6.279TL - 1971.977 r=0.93 n=10	W = 7.382TL - 2376.684 r=0.92 n=25
M	LogW = 2.867LogTL - 4.672 r=0.93 n=10	LogW = 2.958LogTL - 4.868 r=0.92 n=25
F	W = 5.97oTL - 1626.119 r=0.98 n=3	W = 6.007TL - 1605.491 r=0.92 n=21
F	LogW = 2.133LogTL - 2.624 r=0.98 n=3	LogW = 3.170LogTL - 5.445 r=0.98 n=21
C	W = 6.127TL - 1821.328 r=0.87 n=56	W = 6.526TL - 1933.590 r=0.92 n=54
C	LogW = 2.576LogTL - 3.862 r=0.88 n=56	LogW = 2.768LogTL - 4.357 r=0.92 n=53

Walleye - gillnet and population estimate data combined

Sex		
M		W = 4.666TL - 1035.227 r=0.94 n=26
M		LogW = 3.412LogTL - 6.091 r=0.99 n=26
F		W = 5.621TL - 1411.705 r=0.96 n=25
F		LogW = 3.343LogTL - 5.919 r=0.99 n=25
C		W = 3.486TL - 472.626 r=0.96 n=278
C		LogW = 3.188LogTL - 5.531 r=0.998 n=278

Northern pike

Sex		
M	W = 4.711TL - 1543.463 r=0.91 n=208	W = 5.337TL - 1864.200 r=0.94 n=334
M	LogW = 2.749LogTL - 4.535 r=0.96 n=208	LogW = 2.848LogTL - 4.802 r=0.97 n=334
F	W = 7.134TL - 2866.158 r=0.93 n=49	W = 6.395TL - 2377.488 r=0.89 n=148
F	LogW = 2.991LogTL - 5.190 r=0.96 n=49	LogW = 2.526LogTL - 3.889 r=0.89 n=149
C	W = 4.776TL - 1518.796 r=0.93 n=432	W = 5.468TL - 1876.697 r=0.91 n=651
C	LogW = 2.905LogTL - 4.969 r=0.99 n=432	LogW = 2.922LogTL - 5.010 r=0.96 n=654

Table 3. continued

	1985[2]	1986

- -

White suckers

Sex
M	W = 3.914TL - 792.614 r=0.95	W = 3.848TL - 797.224 r=0.93 n=110
M	LogW = 2.978LogTL - 4.896 r=0.98	LogW = 2.982LogTL - 4.905 r=0.98 n==110
F	W = 5.368TL - 1218.287 r=0.95	W = 7.013TL - 1870.863 r=0.95 n=230
F	LogW = 2.930LogTL - 4.734 r=0.99	LogW = 3.166LogTL - 5.348 r=0.98 n=230
C	W = 5.060TL - 1115.167 r=0.95	W = 6.056TL - 1488.910 r=0.92 n=382
C	LogW = 2.986LogTL - 4.889 r=0.99	LogW = 3.152LogTL - 5.326 r=0.99 n=382

- -

1 All log - log transformations are to the base ten
2 1985 sucker age data from McIver 1985

Condition Factors

The mean condition factors for walleye, pike and suckers are shown in Fig. 10 and appendix F. Condition factors were computed using the following formula: $K = (W/L^3) \times 10,000$ (Bagenal and Tesch, 1978). Sample sizes were not always sufficient to permit testing of the length - weight relationship to see if the slopes were not significantly different from three. Therefore, three (ie. the exponent of L) was assumed to adequately represent the allometric growth of walleye, pike and suckers.

Linear regressions of the lines in Fig. 10 yielded the following equations:

Walleye: $K = 0.03083 \text{Year} - 1.61204$, $r = 0.934$

Pike: $K = 0.00019 \text{Year} + 0.58508$, $r = 0.012$

Suckers: $K = -0.02922 \text{Year} + 3.70584$, $r = 0.744$

A test of slopes (Steel and Torrie, 1980) revealed both walleye (t=4.59) and sucker condition factors to be significant regressions (p=0.05) while pike (t=0.05) indicated no change in condition factor from 1982 to 1986.

The slight increase in K for walleye from 1982 to 1986 may reflect improved forage conditions but also the older mean age and scarcity of young individuals in the Henderson Lake walleye population. Comparing the Lanigon Lake walleye mean condition to the combined data of the Henderson Lake population estimate and young walleye age classes illustrates this point (appendix F).

The pike have fluctuated from a high value in 1982 of 0.62

Figure 10. Annual fluctuations in mean condition factors (K) of
walleye, northern pike and white suckers from
Henderson Lake, Ontario.

$K = ((Weight /(Total Length)^3) X 10^5$

1980 - 1981 data from Nunan, 1982

1982 - 1984 data from Reid, 1985
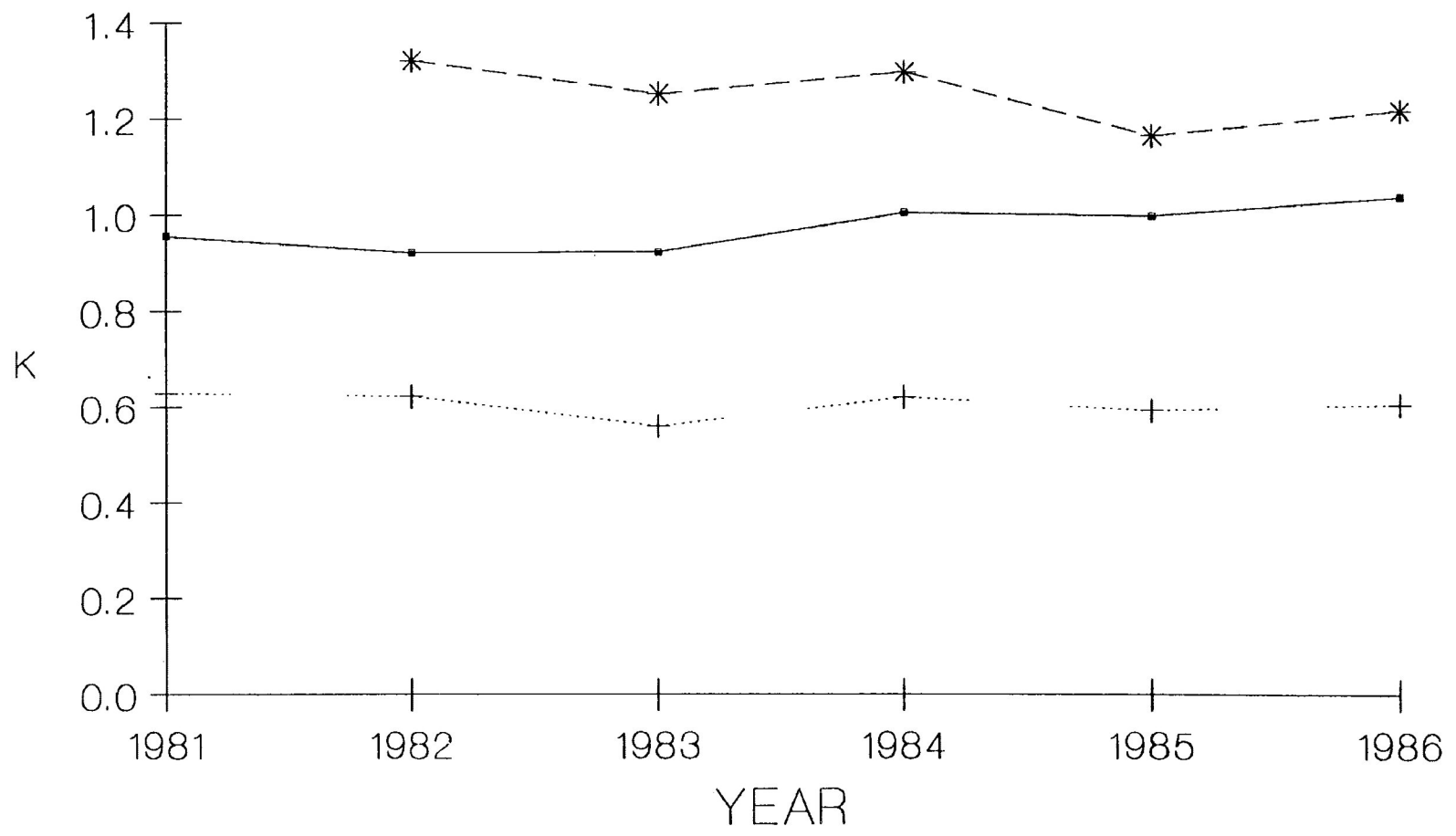
to a low value in 1983 of 0.56 and 0.61 in 1986.

Sucker condition values were stable until 1985 when they abruptly dipped from 1.30 in 1984 to values of 1.17 in 1985 and 1.22 in 1986.

Age Distributions

The age distribution of 1985 and 1986 Henderson Lake walleye population is clearly indicative of an aging population with virtually no recruitment (Fig. 11). In 1984 most of the population was more than five years old. This increased to a minimum mean age of six in 1985 further increased to age seven by 1986. Reproductive failure occurred in Henderson Lake for the past five consecutive years (1980 to 1984 inclusive). However, the 1985 and 1986 year classes were highly successful and should be vulnerable to the trap net gear by 1987. An additional five years are needed before younger age classes (2 to 6) can restore the earlier age structure noted in 1979 and 1980 (Fig. 11). In contrast, Lanigon Lake walleye display successful recruitment in every year except 1980 (Fig. 12).

Age two and three fish dominated pike age distributions of 1985 and 1986 (Fig. 13). The marked bimodality observed in 1984 is slowly disappearing through consistent recruitment in 1985 and 1986. Although age one fish are only partially amenable to the trap net gear in spring population estimates, the 1986 year class appears less numerous than in the past. There was an abrupt disappearance of age eight and older fish in 1982. This side of

Figure 11. Age distributions of walleye in Henderson Lake,

Ontario, 1979 - 1986

% = Percent of total catch

1979 - 1981 data from Nunan, 1982

1982 - 1984 data from Reid, 1985
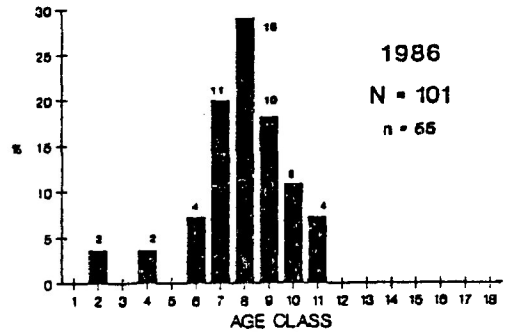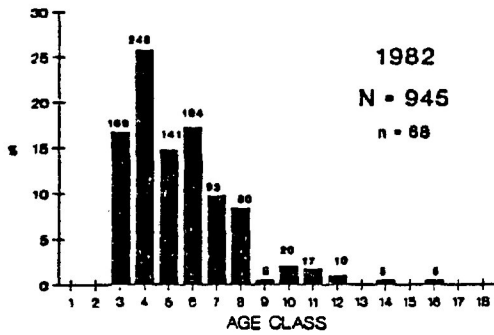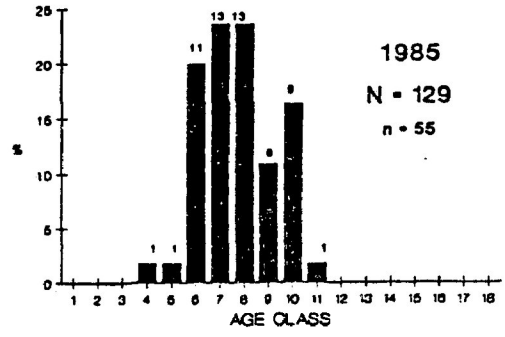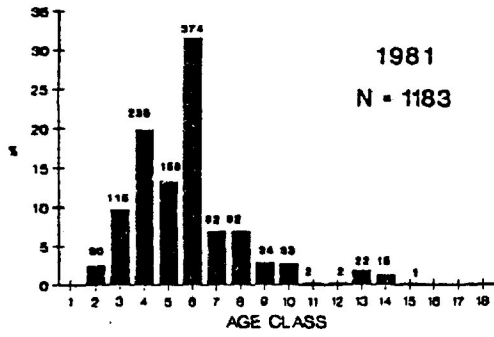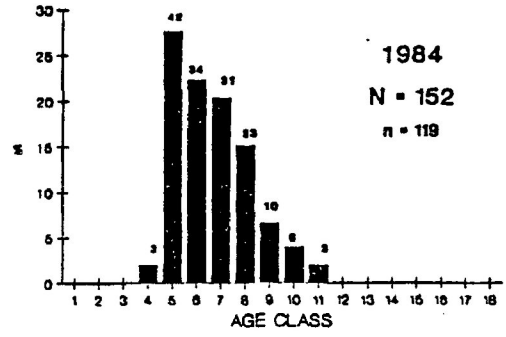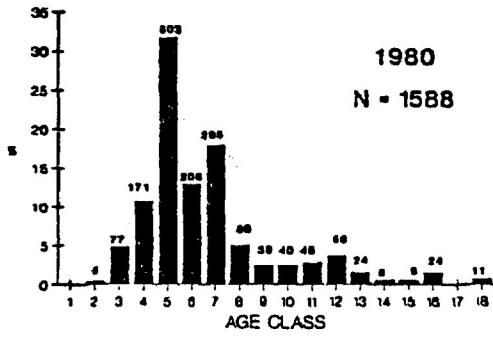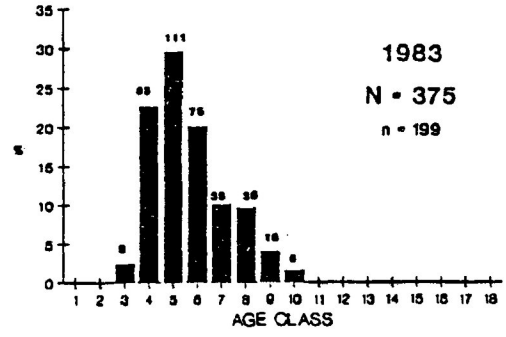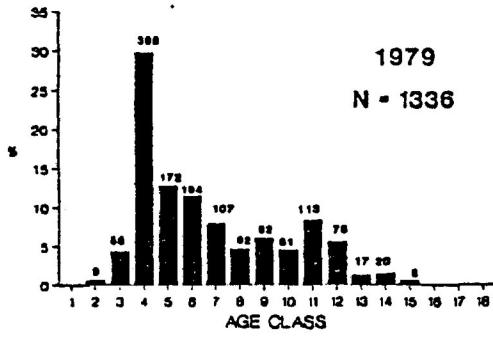
the age distrbution was partially restored by 1986.

Data on sucker age distributions are limited to 1985 and 1986. Age five fish dominated in both years. The older age classes were abundant with the 1975 and 1976 year classes still comprising about twenty five percent of the catchable adult population in 1986 (Fig. 14).

Mean Ages

The mean age of walleye initially declined in 1981. Recruitment failure since 1983 resulted in a steady increase in mean age (Table 4). The mean age of Lanigon Lake walleye in 1986 at 6.3 years was similar to that of pre-exploitation Henderson Lake walleye.

Pike mean age has decreased since 1981 (Table 4) both as a result of older fish disappearing from the population and the increased recruitment since 1984 of younger age classes dominating the age distribution (Fig. 13).

Suckers did not recruit to trap net gear until age 5 (~35cm) and had a mean age of 7.3 in 1986 (Fig. 14). Insufficient data precludes the analysis of long term trends in age distribution.

Length and Weight at Age

Older age classes (6+) of walleye showed a decrease in

Figure 12. Comparison of the age distribution of walleye in

Lanigon Lake and in Henderson Lake, Ontario, 1986.

Henderson Lake data from 1986 population estimate

Lanigon Lake data from six foot trap nets

% = Percent of total catch

HENDERSON

1986

n = 55

LANIGON

1986

n = 86
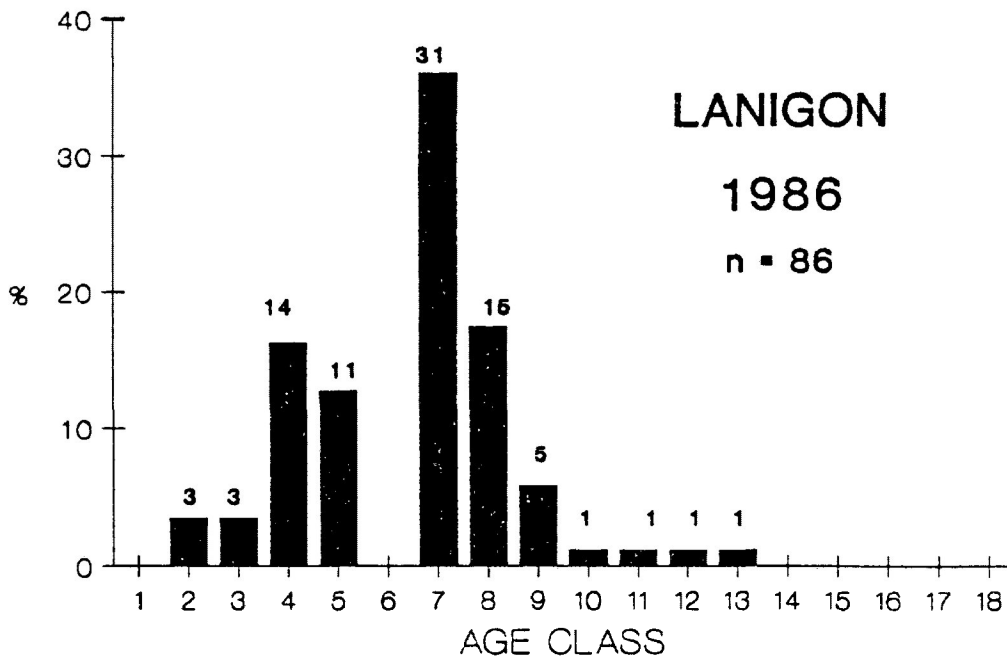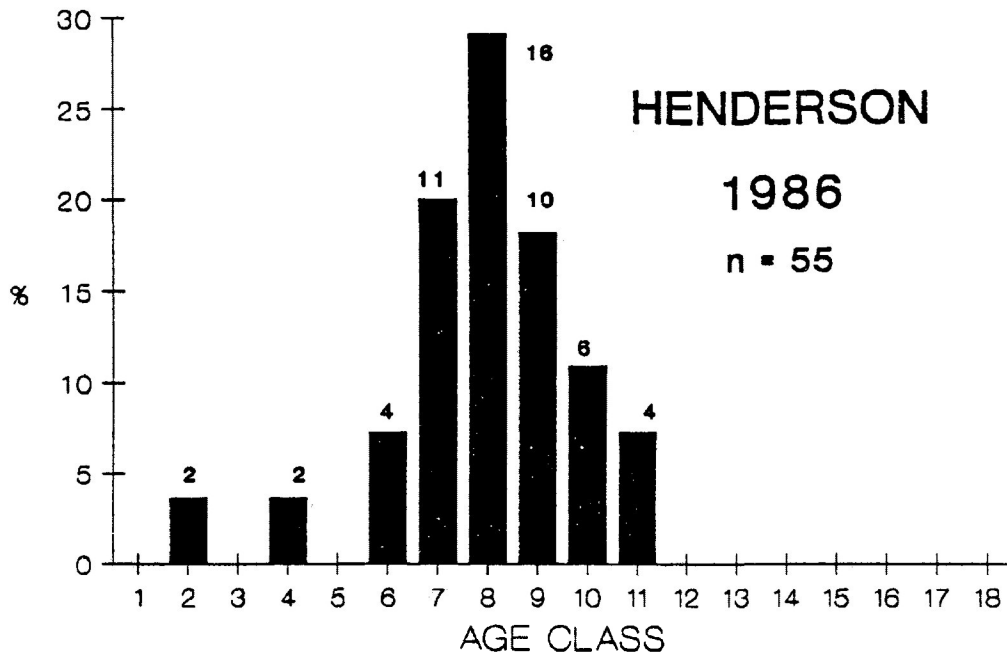
Figure 13. Age distributions of northern pike in Henderson Lake,

Ontario, 1979 - 1986.

% = Percent of total catch

1979 - 1981 data from Nunan, 1982

1982 - 1984 data from Reid, 1985

30
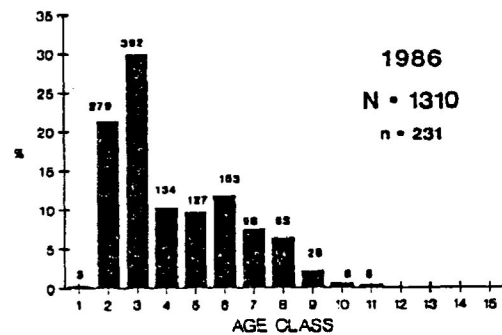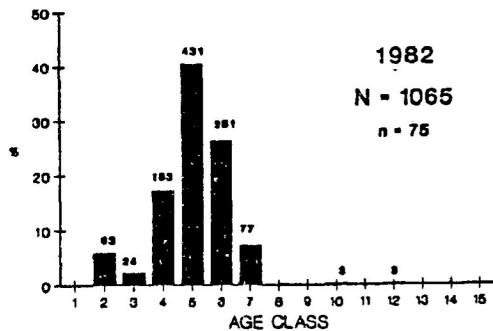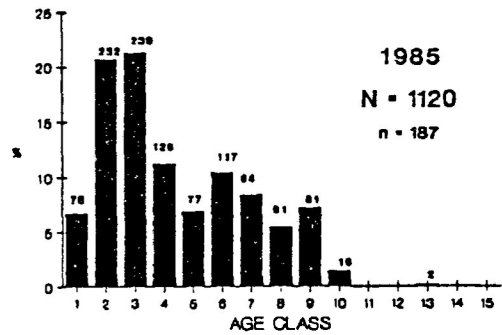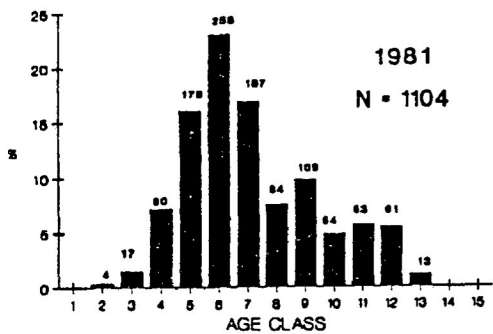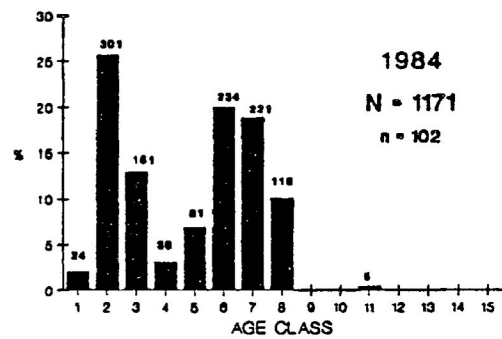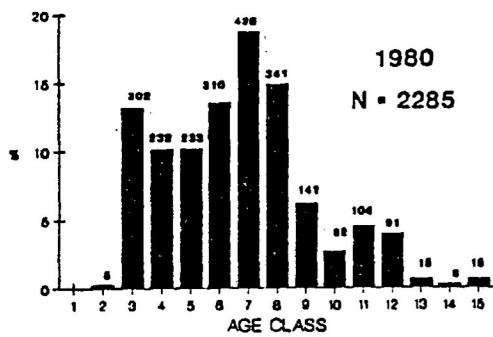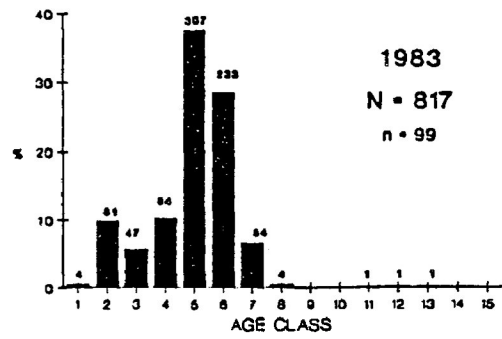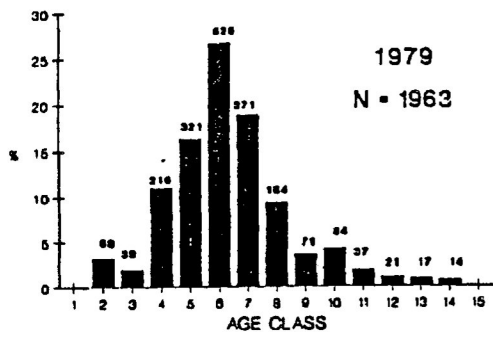
Figure 14. Age distributions of white suckers in Henderson Lake,

Ontario, 1985 - 1986.

% = Percent of total catch

1985 data from McIver, 1986

1985

N = 1336

n = 143

282

174

141

109 112

98

28

14

AGE CLASS

1986

N = 1244

n = 319

380

206

170

156

134

89

23 23

36

8

AGE CLASS
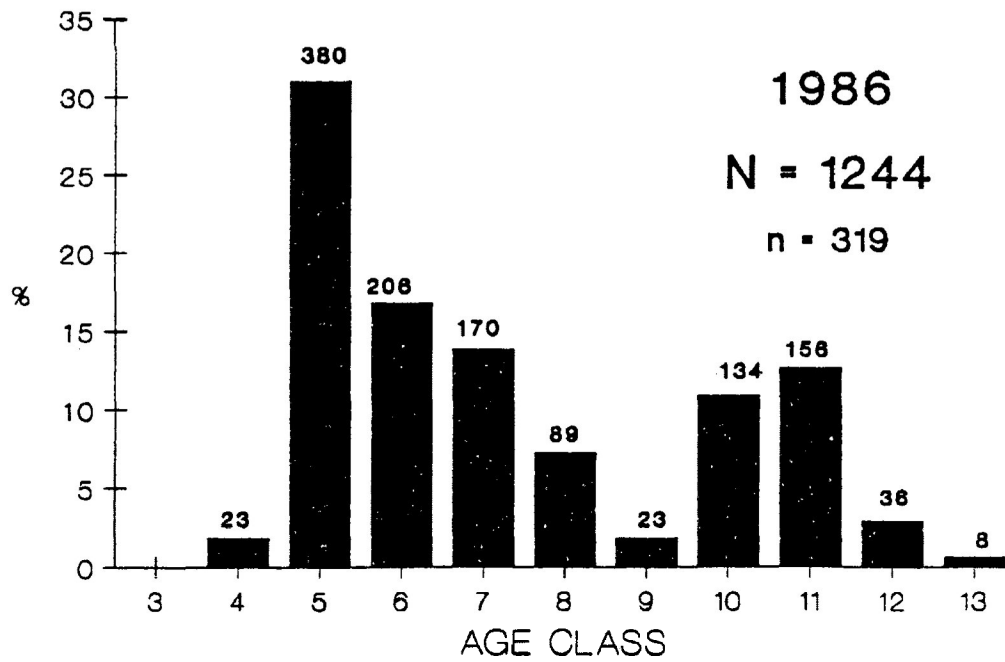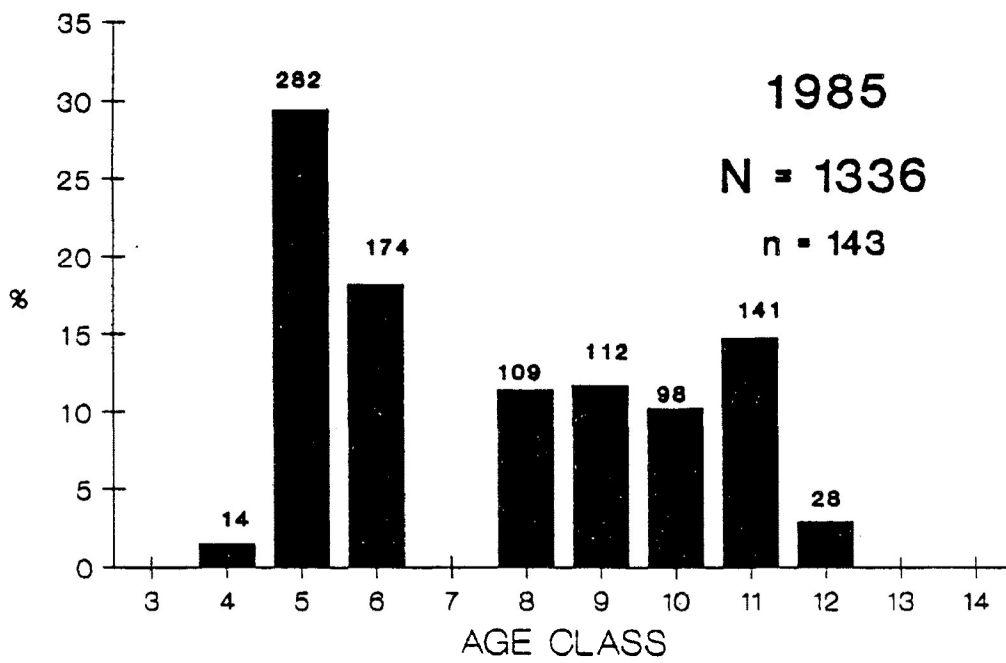
Table 4. Mean ages ($\pm$ S.D.) for walleye, northern pike and white suckers in Henderson Lake, Ontario from 1979 to 1986. Sexes combined.

Year	Walleye $\overline{X} \pm$ S.D.		Pike $\overline{X} \pm$ S.D.		Suckers $\overline{X} \pm$ S.D.	
1979	6.7	3.0	6.4	2.1		
1980	6.6	2.8	6.7	2.6		
1981	5.7	2.3	7.1	2.3		
1982	5.9	2.7	5.0	1.2		
1983	5.7	1.6	4.9	1.4		
1984	6.6	1.6	4.8	2.3		
1985	7.7	1.5	4.4	2.5	7.6	2.4
1986	7.9	1.9	4.3	2.1	7.3	2.4

size from 1979 to 1983, 1982 being the final year of walleye harvest. However from 1982 to 1986 length at age of Henderson Lake walleye increased for ages IV through VIII to approximate pre-exploitation sizes (Fig. 15). Weight, which is a cubic function of length, dramatically increased from age IV through X (Table 5). Younger age classes displayed the most pronounced growth response. In comparison, Lanigon Lake had lower mean length and weight at ages except for age IX weights and age IX and X lengths at age in 1986 (p=0.05) (Fig. 16; Table 6).

Northern pike also displayed a growth response in length and weight to the walleye removal (Fig. 17). While age one pike increased slightly in 1986, age two and three fish exhibited depressed growth. However pike four to nine years of age markedly increased in size particularly so in 1985 and 1986. Age data from Nunan (1982) had to be omitted due to suspected aging disparities.

There was no change in sucker length at age data backcalculated from 1985 and 1986 scales (McIver, 1986) (Fig. 18).

<u>Growth</u>

A comparison of total length at age of walleye from Henderson Lake with walleye from Lanigon Lake illustrates a faster growth rate of walleye in Henderson Lake (Appendix G).

Older northern pike (ages 4 to 7) increased in length at age from 1985 to 1986 (Fig. 17). Generally females were larger in

33

Figure 15. Mean length at age of walleye in Henderson Lake,
Ontario, 1979 - 1986.

TL = Total length in millimetres

1979 - 1981 data from Nunan, 1982

1982 - 1984 data from Reid, 1985
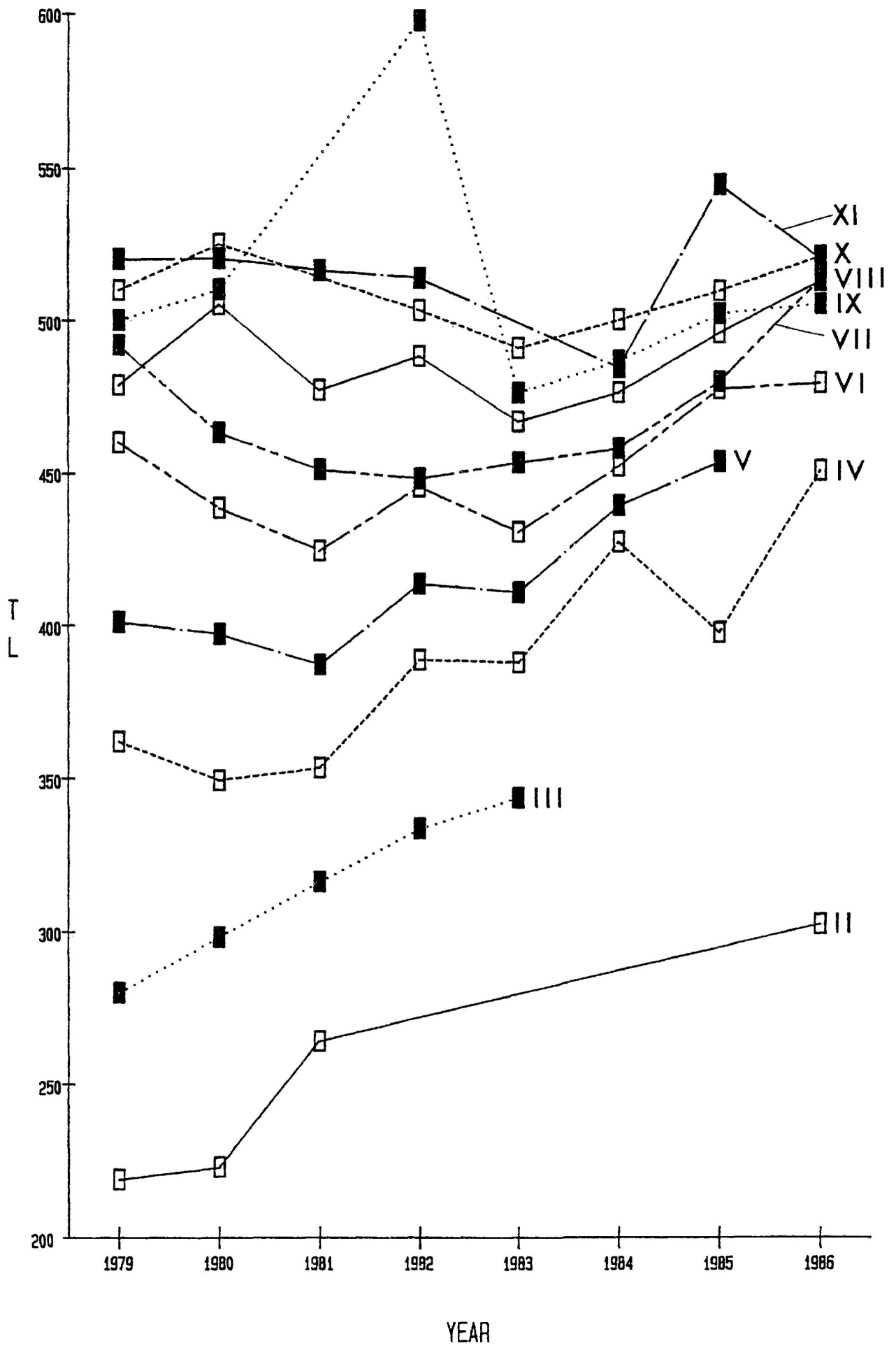
Table 5. Mean empirical weight (g) and length (mm) at age for walleye, sexes combined, in Henderson Lake, Ontario, 1985 and 1986.

Age	Year		Mean	S.D.	Min	Max	n
2	1985	W					
		L					
	1986	W	250.0	--	--	--	1
		L	302.0	--	--	--	1
3	1985	W					
		L					
	1986	W					
		L					
4	1985	W	675.0	--	--	--	1
		L	397.0	--	--	--	1
	1986	W	887.5	53.0	850	925	2
		L	450.0	5.6	446	454	2
5	1985	W	1000.0	--	--	--	1
		L	453.0	--	--	--	1
	1986	W					
		L					
6	1985	W	1120.4	181.3	875	1400	11
		L	476.6	22.2	435	512	11
	1986	W	1143.8	136.0	1000	1325	4
		L	478.8	25.2	453	511	4
7	1985	W	1126.9	155.9	850	1450	13
		L	497.1	19.5	446	515	13
	1986	W	1430.6	240.0	1100	1800	9
		L	512.6	27.3	463	541	9
8	1985	W	1188.5	191.7	900	1500	13
		L	495.0	22.1	464	535	13
	1986	W	1385.9	305.6	975	2050	16
		L	511.9	37.1	430	566	16
9	1985	W	1245.8	199.0	1000	1550	6
		L	501.3	19.2	473	533	6
	1986	W	1387.5	242.4	1075	1900	10
		L	504.3	22.2	468	542	10
10	1985	W	1269.4	181.0	1000	1550	9
		L	508.9	29.1	456	548	9
	1986	W	1450.0	169.6	1250	1650	5
		L	520.0	35.5	490	574	5

Table 5. Continued

11	1985	W	1675.0	--	--	--	1
		L	543.0	--	--	--	1
	1986	W	1468.8	114.3	1350	1600	4
		L	519.0	12.8	503	532	4

Figure 16. Comparison of Henderson Lake and Lanigon Lake, Ontario walleye mean length at age, 1986.

TL = Total length in millimetres

600 —

500 —

400 —

T
L 300 —

200 —

100 —

0 —

2   3   4   5   6   7   8   9   10   11   12   13

AGE CLASS
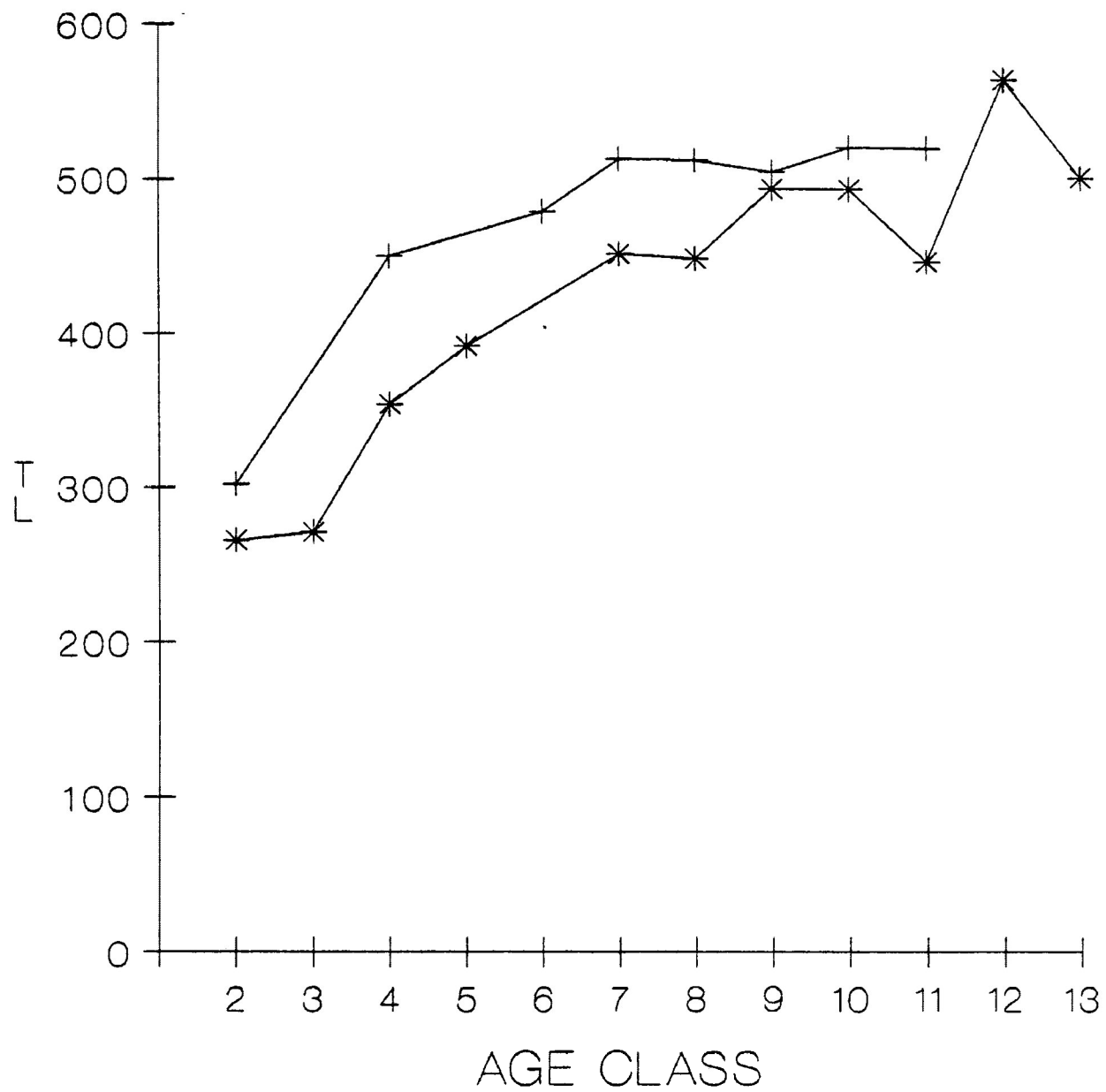
—+— HENDERSON 1986   —*— LANIGON 1986

Table 6. Mean empirical length (mm) and weight (g) (± standard deviation) at age of walleye in Lanigon Lake, Ontario in 1986.

Length at age

Age	Males X̄	± S.D.	n	Females X̄	± S.D.	n	Sexes Combined X	± S.D.	n
2				265.7	1.5	3	*265.7	1.5	3
3				271.0	2.0	3	271.0	2.0	3
4	348.0		1	297.0	77.1	3	*353.8	52.7	14
5				396.5	14.8	2	391.5	22.1	11
6									
7	433.0	11.1	6	481.8	24.9	4	*451.5	29.3	31
8	451.0	15.1	3	457.0	--	1	*448.4	25.0	15
9				484.7	24.2	3	493.6	30.4	5
10				493.0	--	1	493.0	--	1
11							*446.0	--	1
12							563.0	--	1
13							500.0	--	1

Weight at age

Age	Males X̄	± S.D.	n	Females X̄	± S.D.	n	Sexes Combined X	± S.D.	n
2				165.0	8.7	3	*165.0	8.7	3
3				175.0	25.0	3	175.0	25.0	3
4				270.0	199.2	3	*415.4	156.4	12
5				512.5	53.0	2	541.8	92.9	11
6									
7	722.5	28.1	6	975.0	162.0	4	*835.2	172.1	31
8	745.0	39.7	3	850.0	--	1	*822.3	158.3	15
9				950.0	173.2	3	1030.0	205.7	5
10				1200.0	--	1	*1200.0	--	1
11							*800.0	--	1
12							1300.0	--	1
13							1175.0	--	1

----

* significantly smaller than corresponding 1986 Henderson Lake walleye by students t-tests (p=0.05)

Figure 17. Mean length at age of northern pike in Henderson Lake,
Ontario, 1982 - 1986.

TL = Total length in millimetres

1982 - 1984 data from Reid, 1985
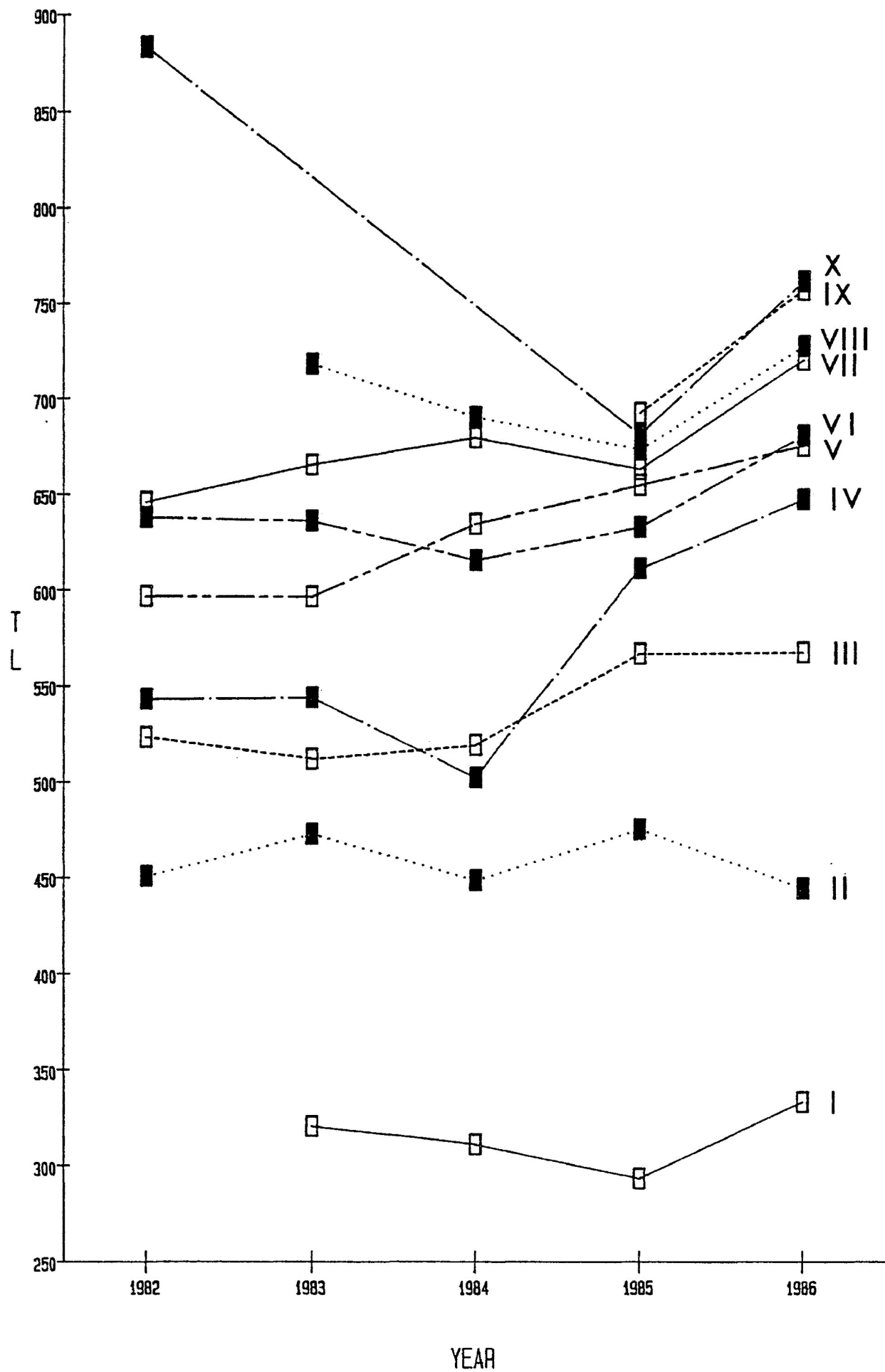
both length and weight (Table 7) (Appendix K,L,M,N).

Suckers also exhibit sexual dimorphism with mature females being larger than males (Table 8) (Appendix P,Q,R). Suckers showed no growth response to the walleye removal (Fig. 18).

Biomass and Production Estimates

Annual mean biomass and production were calculated using Ricker's (1975) method from 1979 to 1986 for walleye (Table 9), 1982 to 1986 for northern pike (Table 10) and 1985 to 1986 for white suckers (Table 11). In some instances the instantaneous rate of mortality (Z) was negative. When this occurred, the Z value for that particular age group was assumed to be zero ie. S = 1.000.

Historically, walleye production has been highly variable in Henderson Lake dropping from a maximum of 495.4kg in 1980-1981 to a low of -4.5kg in 1981 1982. Consequently, the turnover rate (P/B) also varied (Fig. 19b).

Walleye production fell in 1985 and 1986 as a consequence of the increase in mean age and absence of significant recruitment (Fig. 19b). The instantaneous rate of growth (G) was less for 1984 85 across all age classes except age 10 - 11. Instantaneous rate of growth (G) increased slightly into 1986 but not enough to recover the high rate of growth seen between 1983-84. The annual-age group mortalities were generally very low with several year classes showing negative mortalities as a result of inconsistent vulnerability of individual age groups to

Figure 18. Mean length at age of white suckers in Henderson Lake, Ontario, 1976 - 1986, backcalculated from scales, 1985 and 1986.

TL = Total length in millimetres

1985 data from McIver, 1986
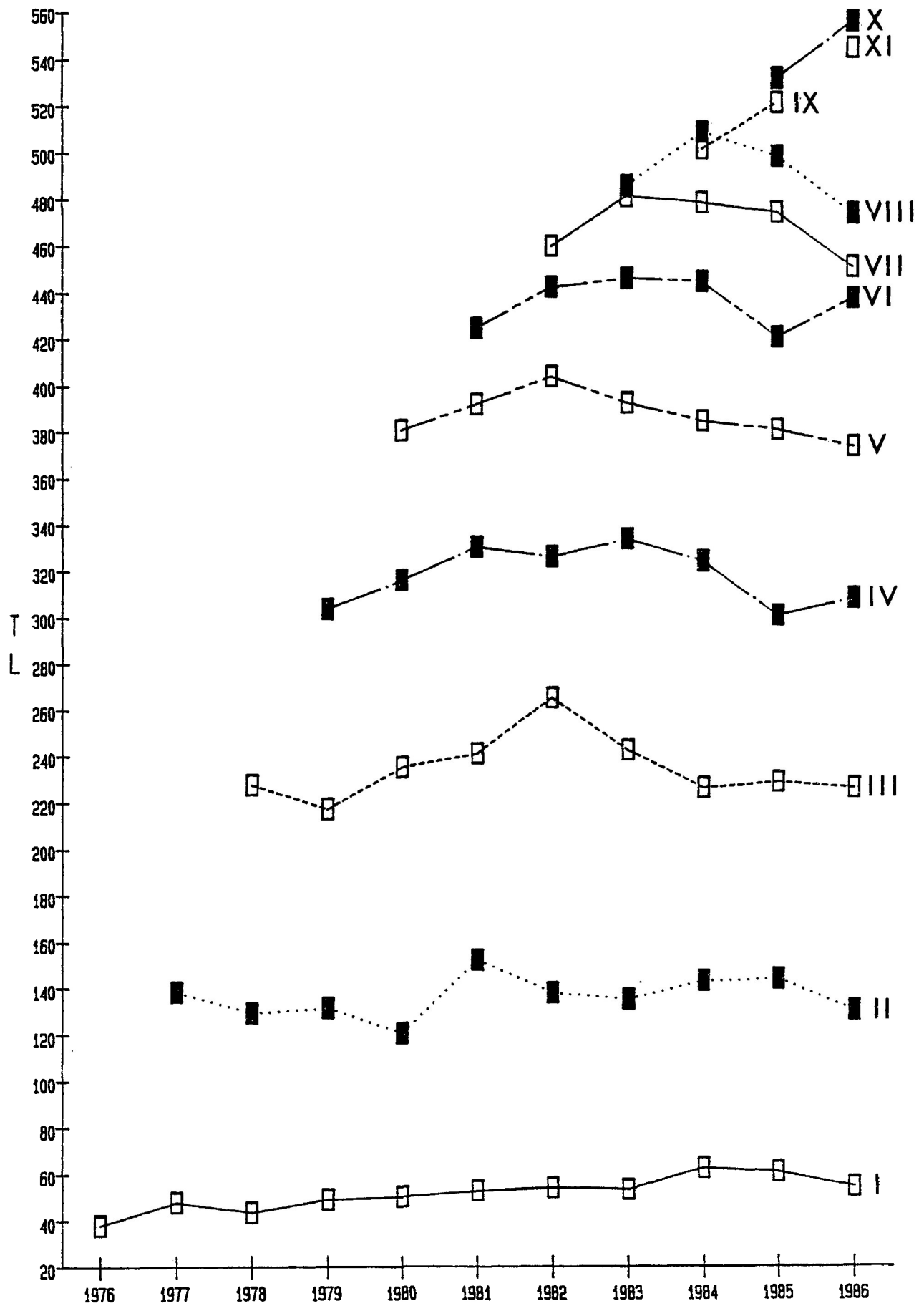
Table 7. Mean empirical weight (g) and total length (mm) (±
        standard deviation) at age for northern pike, sexes
        combined, in Henderson Lake, Ontario, 1985 and 1986.

Age	Year		Mean	± S.D.	Min	Max	n
1	1985	W	167.0	50.3	90	250	16
		L	293.2	28.9	244	339	16
	1986	W	325.0	- -	- -	- -	1
		L	333.0	- -	- -	- -	1
2	1985	W	695.7	259.2	250	1800	46
		L	474.3	47.3	358	596	46
	1986	W	569.6	230.3	250	1550	67
		L	443.7	53.5	362	650	67
3	1985	W	1097.8	260.0	600	1800	35
		L	566.0	37.5	502	625	36
	1986	W	1160.7	283.3	450	1700	49
		L	566.4	49.7	427	647	49
4	1985	W	1350.0	300.0	1000	2200	17
		L	610.9	40.2	558	696	17
	1986	W	1690.8	389.6	1125	2500	19
		L	646.4	52.4	575	743	19
5	1985	W	1600.0	361.2	1100	2150	12
		L	654.3	44.4	581	710	12
	1986	W	1863.8	548.1	1175	2950	20
		L	674.0	63.6	572	770	20
6	1985	W	1520.0	320.0	950	2100	15
		L	632.3	42.6	527	692	15
	1986	W	1884.1	593.1	1100	3000	22
		L	680.0	60.5	590	781	22
7	1985	W	1770.6	589.8	750	2800	17
		L	663.0	68.1	545	765	17
	1986	W	2319.4	857.2	1425	4050	18
		L	719.6	60.3	611	820	19
8	1985	W	1758.2	398.9	1250	2700	11
		L	672.8	47.5	608	766	11
	1986	W	2492.2	947.2	1550	4250	16
		L	726.4	76.8	612	831	16
9	1985	W	1885.7	588.8	1150	3400	14
		L	692.0	53.4	598	801	14
	1986	W	2717.9	947.2	1550	4250	7
		L	756.0	58.6	658	836	7

Table 7. Continued

10	1985	W	1833.3	475.2	1350	2300	3
		L	680.3	74.1	595	728	3
	1986	W	3250.0	1909.2	1900	4600	2
		L	760.0	127.3	670	850	2

11	1985	W					
		L					
	1986	W	1550.0	- -	- -	- -	1
		L	665.0	- -	- -	- -	1

12	1985	W					
		L					
	1986	W					
		L					

13	1985	W	3400.0	- -	- -	- -	1
		L	796.0	- -	- -	- -	1
	1986	W					
		L					

Table 8. Mean empirical weight(g) and length(mm) at age for
white suckers, sexes combined, in Henderson Lake,
Ontario, 1985[a] and 1986.

Age	Year		Mean	± S.D.		n
1	1985	W	14.4			
		L	106			23
	1986	W	19.0	- -		1
		L	131.0	- -		1
2	1985	W	72.3			
		L	182			16
	1986	W	92.6	27.5		11
		L	203.8	18.9		11
3	1985	W	217.0			
		L	263			17
	1986	W	225.8	111.2		8
		L	264.6	32.8		8
4	1985	W	431.2			
		L	331			22
	1986	W	400.0	80.8		6
		L	325.7	16.7		6
5	1985	W	656.3			
		L	381			9
	1986	W	709.2	225.8		30
		L	378.7	26.4		30
6	1985	W	948.4			
		L	431			6
	1986	W	1025.0	284.8		21
		L	437.9	30.2		21
7	1985	W	1460.0			
		L	498			2
	1986	W	1147.1	331.1		17
		L	456.7	39.9		17
8	1985	W	1251.9			
		L	473			2
	1986	W	1543.8	347.6		8
		L	493.4	42.9		8
9	1985	W	1576.8			
		L	511			3
	1986	W	1565.0	480.8		2
		L	490.5	14.9		2

Table 8. continued.

Age	Year		Mean	±	S.D.		n
10	1985	W	1670.8				
		L	521				7
	1986	W	2065.0		384.5		10
		L	543.4		28.7		10
11	1985	W	1702.1				
		L	524.3				4
	1986	W	2023.1		442.2		13
		L	544.9		29.9		13
12	1985	W	1900.8				
		L	544.0				1
	1986	W	2075.0		459.6		2
		L	538.0		22.6		2
13	1986	W	1875.0		--		1
		L	560.0		--		1

----

a = Data from 1985 from McIver, 1986.

Table 9.   Annual production, biomass and turnover of Henderson Lake walleye, 1979 to 1986[b].
S = survival rate, Z = instantaneous mortality rate, G = instantaneous growth rate,
K = weight change factor (G-Z). Wo= initial cohort biomass, W = mean cohort biomass,
P = annual production (kg/yr), B = mean biomass (kg), P/B = turnover.

1979 - 1980

Age Class	S	Z	G	K	Wo	W	P	B	P/B
4 - 5	1.261	0	0.344	0.344	165.19	196.89	67.73	229.47	0.30
5 - 6	1.198	0	0.351	0.351	96.49	115.59	40.57	130.34	0.31
6 - 7	1.851	0	0.119	0.119	129.82	137.86	16.41	200.48	0.08
7 - 8	0.748	0.291	0.193	-0.098	110.21	104.98	20.26	105.06	0.19
8 - 9	0.629	0.464	0.304	-0.160	58.96	54.49	16.56	54.62	0.30
9 - 10	0.488	0.718	0.267	-0.451	88.64	71.35	19.05	72.56	0.26
10 - 11	0.738	0.304	0.179	-0.125	69.91	65.72	11.76	65.78	0.18
11 - 12	0.522	0.650	0.287	-0.363	137.18	115.04	33.02	116.29	0.28
12 - 13	0.320	1.139	0.136	-1.003	85.95	54.26	7.38	58.73	0.13
13 - 14	0.471	0.754	0.204	-0.550	24.00	18.46	3.77	----	----
						Total	236.51	1033.13	0.23
						Total per hectare	1.57	6.84	

Table 9. Continued

1980 - 1981

Age Class	S	Z	G	K	Wo	W	P	B	P/B
4 - 5	0.924	0.079	0.666	0.587	66.52	90.50	60.27	93.06	0.65
5 - 6	0.744	0.296	0.551	0.255	293.75	334.60	184.36	336.60	0.55
6 - 7	0.398	0.921	0.437	-0.484	164.18	130.15	56.88	132.68	0.43
7 - 8	0.288	1.246	0.440	-0.806	270.75	273.28	120.24	195.84	0.61
8 - 9	0.425	0.856	0.297	-0.559	99.92	76.54	22.73	78.54	0.29
9 - 10	0.846	0.167	0.336	0.169	50.27	54.77	18.40	54.88	0.34
10 - 11	0.050	2.996	0.294	-2.702	56.48	19.50	5.73	----	----
11 - 12	0.044	3.124	0.211	-2.913	61.65	20.01	4.22	----	----
12 - 13	0.373	0.986	0.152	-0.834	95.40	64.71	9.84	----	----
13 - 14	0.625	0.470	0.416	-0.054	31.51	30.67	12.76	----	----
						Total	495.43	891.30	0.52
					Total per hectare		3.28	5.90	

Table 9. Continued

1981 - 1982

Age Class	S	Z	G	K	Wo	W	P	B	P/B
4 - 5	0.600	0.511	0.137	-0.374	132.78	110.78	15.18	112.08	0.14
5 - 6	1.038	0	0.075	0.075	119.61		----	126.72	----
6 - 7	0.249	1.392	-0.203	-1.595	378.86	189.33	-38.43	227.88	----
7 - 8	0.976	0.025	-0.135	-0.160	101.19	93.51	-12.62	93.72	----
8 - 9	0.061	2.797	0.316	-2.481	120.95	44.67	14.12		
9 - 10	0.588	0.531	-0.344	-0.875	57.15	38.09	-13.10		
10 - 11	0.515	0.663	-0.247	-0.910	59.50	39.07	-9.75		
						Total	-4.45	560.40	----
						Total per hectare	----	3.71	

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Table 9. Continued

1982 - 1983

Age Class	S	Z	G	K	Wo	W	P	B	P/B
4 - 5	0.453	0.792	0.173	-0.619	130.83	97.54	16.88	100.66	0.17
5 - 6	0.532	0.631	0.110	-0.521	91.37	71.21	7.83	72.80	0.11
6 - 7	0.232	1.461	0.029	-1.432	133.82	71.13	2.06	82.87	0.02
7 - 8	0.387	0.949	0.103	-0.846	76.91	51.90	5.35	54.96	0.10
8 - 9	0.188	1.671	-0.107	1.778	86.24	40.31	-4.31	50.39	----
						Total	27.81	361.68	0.08
					Total per hectare		0.18	2.40	

Table 9. Continued

1983 - 1984

Age Class	S	Z	G	K	Wo	W	P	B	P/B
4 - 5	0.494	0.705	0.436	-0.269	45.73	40.10	17.48	40.34	0.43
5 - 6	0.306	1.184	0.365	-0.819	70.48	48.12	17.56	50.80	0.35
6 - 7	0.413	0.884	0.279	-0.605	54.22	40.68	11.35	41.93	0.27
7 - 8	0.605	0.503	0.255	-0.248	31.92	28.27	7.21	28.42	0.25
8 - 9	0.278	1.280	0.242	-1.038	33.01	20.54	4.97	22.34	0.21
9 - 10	0.400	0.916	0.280	-0.636	14.54	10.76	3.01	11.12	0.28
10 - 11	0.500	0.693	0.085	-0.608	6.35	4.76	0.40	4.90	0.08
						Total	61.98	199.85	0.31
						Total per hectare	0.41	1.32	

Table 9. Continued

1984 - 1985

Cohort	S	Z	G	K	Wo	W	P	B	P/B
4 - 5	0.667	0.406	0.305	-0.101	2.21	2.10	0.64	2.10	0.30
5 - 6	0.619	0.480	0.323	-0.157	34.08	31.54	10.18	31.60	0.32
6 - 7	0.912	0.092	0.172	0.079	32.27	33.58	5.77	33.60	0.17
7 - 8	1.000	0.000	0.168	0.168	31.16	33.92	5.68	34.00	0.17
8 - 9	0.609	0.496	0.118	-0.378	25.46	21.20	2.51	21.45	0.12
9 - 10	2.100	0	0.067	0.067	11.88	12.28	0.82	19.27	0.04
10 - 11	0.333	1.099	0.273	-0.826	7.65	5.21	1.42	5.50	0.26
						Total	27.02	147.53	0.18
						Total per hectare	0.18	0.98	

Table 9. Continued

1985 - 1986

Cohort	S	Z	G	K	Wo	W	P	B	P/B
4 - 5	----	----	----	----	----	----	----	----	----
5 - 6	4.000	0	0.134	0.134	2.00	2.14	0.29	5.58	0.05
6 - 7	0.692	0.368	0.244	-0.123	29.13	27.41	6.70	27.44	0.24
7 - 8	1.032	0	0.207	0.207	34.93	38.81	8.03	39.64	0.20
8 - 9	0.645	0.438	0.155	-0.284	36.84	32.08	4.97	32.30	0.15
9 - 10	0.714	0.337	0.152	-0.185	17.44	15.93	2.42	15.97	0.15
10 - 11	0.381	0.965	0.146	-0.819	26.66	18.20	2.65	19.20	0.14
						Total	25.05	140.13	0.18
						Total per hectare	0.17	0.93	

a   Z values less than zero are assumed to be equal to zero.

b   Calculations from 1979 to 1984 from Reid 1985

Table 10. Annual production, biomass and turnover of Henderson Lake pike, 1982 to 1986[a].
S = survival rate, Z = instantaneous mortality rate[b], G = instantaneous growth rate,
K = weight change factor (G-Z), Wo= initial cohort biomass, W = mean cohort biomass,
P = annual production (kg/yr), B = mean biomass (kg), P/B = turnover.

1982 - 1983

Age Class	S	Z	G	K	Wo	W	P	B	P/B
2 - 3	0.746	0.293	0.463	0.170	38.68	42.15	19.51	42.25	0.46
3 - 4	3.500	0	-0.129	-0.129	24.22	22.72	-2.93	49.37	----
4 - 5	1.678	0	0.181	0.181	179.08	196.31	35.53	269.56	0.13
5 - 6	0.541	0.615	0.101	-0.515	568.51	444.40	44.66	454.17	0.10
6 - 7	0.192	1.649	0.016	-1.633	451.15	222.31	3.65	269.64	0.01
7 - 8	0.052	2.958	0.251	-2.707	128.59	44.34	11.12	63.59	0.16
8 - 9	0.050	0.693	0.324	-0.370	41.10	34.36	11.12	34.75	0.32
						Total	122.66	1188.33	0.10
						Total per hectare	0.81	7.87	

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Table 10. Continued

1983 - 1984

Age Class	S	Z	G	K	Wo	W	P	B	P/B
2 - 3	1.864	0	0.340	0.340	50.82	60.52	20.56	91.95	0.22
3 - 4	0.766	0.267	-0.198	-0.465	45.83	36.66	-7.26	37.32	----
4 - 5	0.964	0.036	0.558	0.522	74.52	97.83	54.60	100.03	0.55
5 - 6	0.762	0.272	0.074	-0.198	360.04	326.67	24.08	327.73	0.07
6 - 7	0.949	0.053	0.249	0.196	339.83	675.34	93.27	376.55	0.25
7 - 8	2.185	0	0.228	0.228	88.13	98.98	22.57	165.01	0.14
8 - 9	1.250	0	0.002	0.002	8.58	8.59	0.02	9.67	----
						Total	207.84	1108.26	0.19
						Total per hectare	1.38	7.34	

Table 10. Continued

1984 - 1985

Age Class	S	Z	G	K	Wo	W	P	B	P/B
2 - 3	0.794	0.231	0.588	0.358	183.50	220.60	129.78	222.94	0.58
3 - 4	0.834	0.181	0.427	0.246	133.07	150.83	64.33	151.58	0.42
4 - 5	2.139	0	0.693	0.693	28.60	41.26	28.60	76.00	0.38
5 - 6	1.444	0	0.020	0.020	125.55	126.78	2.47	151.70	0.02
6 - 7	0.402	0.912	0.338	-0.574	295.43	224.80	76.03	230.93	0.33
7 - 8	0.276	1.287	0.056	-0.231	413.27	237.66	13.36	260.56	0.05
8 - 9	0.686	0.376	-0.084	-0.460	241.90	193.92	-16.19	197.32	----
9 - 10	3.600	0	-1.281	-0.069	10.75	10.39	-0.71	23.44	----
						Total	297.65	1314.52	0.23
						Total per hectare	1.97	8.71	

Table 10. Continued

1985 - 1986

Age Class	S	Z	G	K	Wo	W	P	B	P/B
2 - 3	1.697	0	0.512	0.512	161.39	210.75	107.88	308.20	0.35
3 - 4	0.561	0.579	0.432	-0.147	262.39	244.04	105.38	244.48	0.43
4 - 5	1.008	0	0.323	0.323	170.10	200.73	64.74	203.40	0.32
5 - 6	1.987	0	0.163	0.163	123.20	133.84	21.87	205.73	0.11
6 - 7	0.838	0.177	0.423	0.245	177.84	201.56	85.18	202.57	0.42
7 - 8	0.883	0.125	0.342	0.217	166.44	185.90	63.54	186.53	0.34
8 - 9	0.459	0.779	0.430	-0.349	107.86	91.06	39.15	91.98	0.43
9 - 10	0.099	2.315	0.544	-1.771	152.74	71.58	38.96	89.37	0.44
10 - 11	0.313	1.163	-0.168	-1.331	29.33	16.22	-2.72	18.54	----
						Total	523.97	1550.80	0.34
						Total per hectare	3.47	10.27	

a = 1982 - 1984 data from Reid 1985

b = Z values less than zero were assumed to equal zero

Table 11. Annual production, biomass and turnover of Henderson Lake suckers, 1985[a] to 1986.
S = survival rate, Z = instantaneous mortality rate[b], G = instantaneous growth rate,
K = weight change factor (G-Z), Wo= initial cohort biomass, W = mean cohort biomass,
P = annual production (kg/yr), B = mean biomass (kg), P/B = turnover.

1985 - 1986

Age Class	S	Z	G	K	Wo	W	P	B	P/B
5 - 6	0.731	0.314	0.446	0.132	185.07	197.83	88.21	198.11	0.45
6 - 7	0.977	0.023	0.190	0.167	165.02	176.61	34.16	180.01	0.19
7 - 8	1.000	0	0.056	0.056	129.94	133.64	7.46	133.67	0.06
8 - 9	0.211	1.556	0.223	-1.333	136.46	75.39	16.83	86.23	0.20
9 - 10	1.196	0	0.270	0.270	176.60	202.71	54.67	226.66	0.24
10 - 11	1.592	0	0.191	0.191	163.73	180.44	34.52	239.67	0.14
11 - 12	0.255	1.365	0.198	-1.167	239.99	141.63	28.06	157.35	0.18
12 - 13	0.286	1.253	-0.014	-1.267	53.22	30.18	-0.41	34.10	----
						Total	262.47	125.79	0.21
						Total per hectare	1.74	8.32	

a = 1985 data from McIver 1985

b = Z values less than zero were assumed to equal zero

Figure 19. Production (P), biomass (B) and turnover ratio (P/B) trends of northern pike (a) and walleye (b) in Henderson Lake, Ontario, 1982 (b) and 1979 (a) to 1986. Units are explained under the graph.

1979 - 1981 data from Nunan, 1982

1982 - 1984 data from Reid, 1985

PIKE

WALLEYE

YEAR

■ P (KG/HA/YR)   ▨ B (KG/HA)   ⊞ TURNOVER (P/B)X10
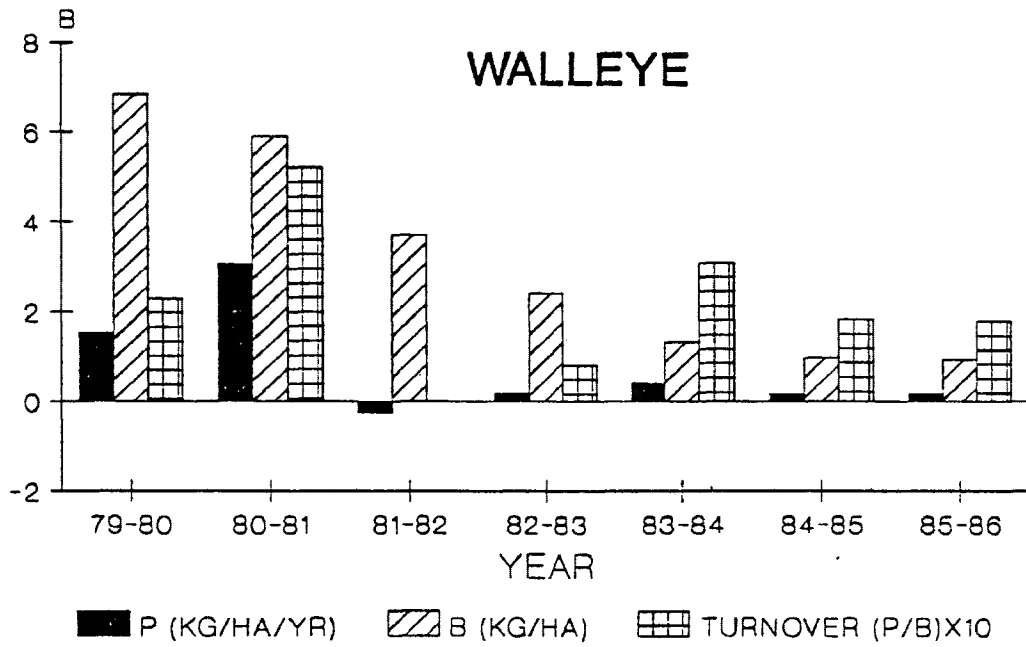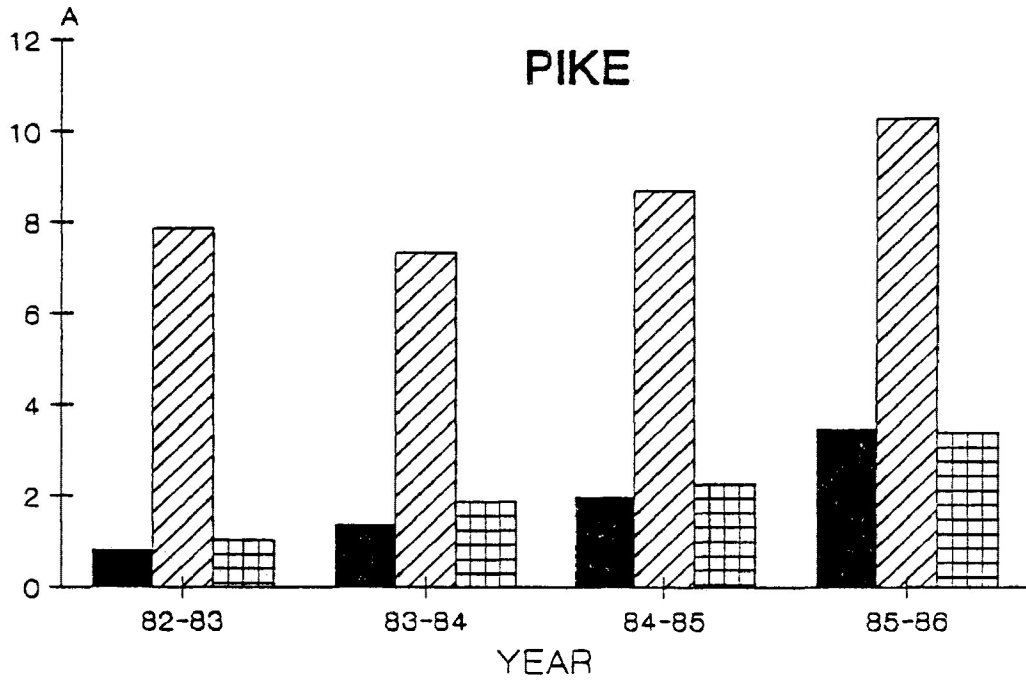
the gear in subsequent years. The decline in walleye production in 1985 and 1986 can be attributed almost entirely to declining mean biomass.

Pike production data are only available from 1982 - 1983 to 1985 - 1986 due to suspected aging disparities between Nunan (1982) and Reid (1985). Reid (1985) reported that pike were not fully recruited to trap net gear until age six and thus ignored all production by younger age classes. For the present study pike production from 1982 to 1984 has been recalculated to include the younger age classes even though age two and perhaps age three pike were not fully recruited until 1985 and 1986. Including most of the production of young age classes provides a better approximation of the status of the pike population than by omitting these data.

Revised production estimates from Reid (1985) and the present study show an unequivocal increase in pike production from 0.81kg ha^{-1} yr^{-1} in 1982 - 1983 to 3.47kg ha^{-1} yr^{-1} in 1985 - 1986 (Fig. 19a; Table 10). Turnover ratios (P/B) increased from 0.10 to 0.34 even though biomass increased from 7.87kg ha^{-1} to 10.27kg ha^{-1} in the same time period. Thus there is a major response by pike to both a smaller walleye population as well as an increased yellow perch abundance.

Sucker production from 1985 - 86 was 1.77kg ha^{-1} yr^{-1} with a mean biomass of 9.23kg ha^{-1} of age five and older fish (Table 11).

Catch per Unit Effort

Generally, six foot trap nets catch per unit effort (CUE) data reflected relative walleye abundance. The data for eight foot trap nets remained inconclusive (Reid and Momot, 1985).

However, six foot trap net data for pike and sucker CUE's were inconsistent with Schumacher-Eschmeyer population estimates (Table 12) resulting in low regression coefficients of 0.645 and 0.508 for pike and sucker respectively.

Walleye CUE continued to decline in 1985 and 1986 as population abundance declined (Fig. 20). Walleye six foot trap net CUE data were contrasted using Kruskal-Wallis non parametric one-way ANOVAS (Table 13). All years were significantly different except for 1979, 1980 and 1981; and 1983 and 1984.

Walleye six foot trap net data were regressed against Shumacher-Eschmeyer population estimates from 1979 to 1986 and against Petersen population estimates from 1980 to 1984 (high population density) with Schumacher-Eschmeyer population estimates from 1985 and 1986 (low population density) (Fig. 20). Schumacher-Eschmeyer population estimates seriously underestimate fish abundance at high population densities (Momot and Reid, 1985). Petersen population estimates gave a much better fit (r=0.969; Table 12).

Lanigon Lake walleye CUE was calculated to be 0.121 fish per six foot trap net hour. Assuming a similar relationship to hold for Lanigon Lake walleye, this value was substituted into the six foot trap net regression equation derived from Henderson

Table 12. Regressions of 1979 to 1986 catch per unit (CUE) effort
          data from six and eight foot trap nets with Schumacher
          Eschmeyer (SE), Petersen (P) population estimates
          and Petersen and Schumacher-Eschmeyer population
          estimates combined (P+SE) for walleye, northern pike
          and white suckers in Henderson Lake, Ontario.
          r = correlation coefficient; df = degrees of freedom
          P = significance of r; NSIG = not significant at p=0.05

Six foot trap net data

			r	df	P
Walleye:	SE(N)	= 3364.468(CUE) + 144.955	0.93	6	0.01
	P(N)	= 6780.389(CUE) + 19.221	0.96	3	0.05
	P+SE(N)	= 6823.443(CUE) + 5.216	0.97	5	0.01
Pike:	SE(N)	= 3255.453(CUE) + 468.889	0.65	6	NSIG
Suckers:	SE(N)	= 1318.604(CUE) + 1010.708	0.51	6	NSIG
All species:	SE(N)	= 3055.173(CUE) + 1547.853	0.80	6	0.05

Eight foot trap net data

			r	df	P
Walleye:	SE(N)	= 1241.551(CUE) + 495.491	0.55	6	NSIG
Pike:	SE(N)	= 271.393(CUE) + 1292.793	0.07	6	NSIG
Suckers:	SE(N)	= 723.326(CUE) + 1113.133	0.14	6	NSIG
All species:	SE(N)	= 1680.306(CUE) + 2583.247	0.48	6	NSIG

Figure 20. Catch per unit effort (CUE), in fish per trap hours, of walleye from six foot trap nets plotted against Petersen , P(N), and Schumacher-Eschmeyer, SE(N), population estimates in Henderson Lake, Ontario.

N = Estimated walleye abundance

CUE = Catch per Unit Effort

1979 - 1981 data from Nunan, 1982

1982 - 1984 data from Reid, 1985

P(N)

SE(N)

N

SIX FOOT TRAP NET CUE

Table 13. A comparison of 1979 to 1986 walleye six foot trap net
catch per unit effort from Henderson Lake, Ontario
using Kruskal - Wallis non parametric one way ANOVAS
S = significantly different (p=0.05)

	1979	1980	1981	1982	1983	1984	1985
1980	NS						
1981	NS	NS					
1982	S	S	S				
1983	S	S	S	S			
1984	S	S	S	S	NS		
1985	S	S	S	S	S	S	
1986	S	S	S	S	S	S	S
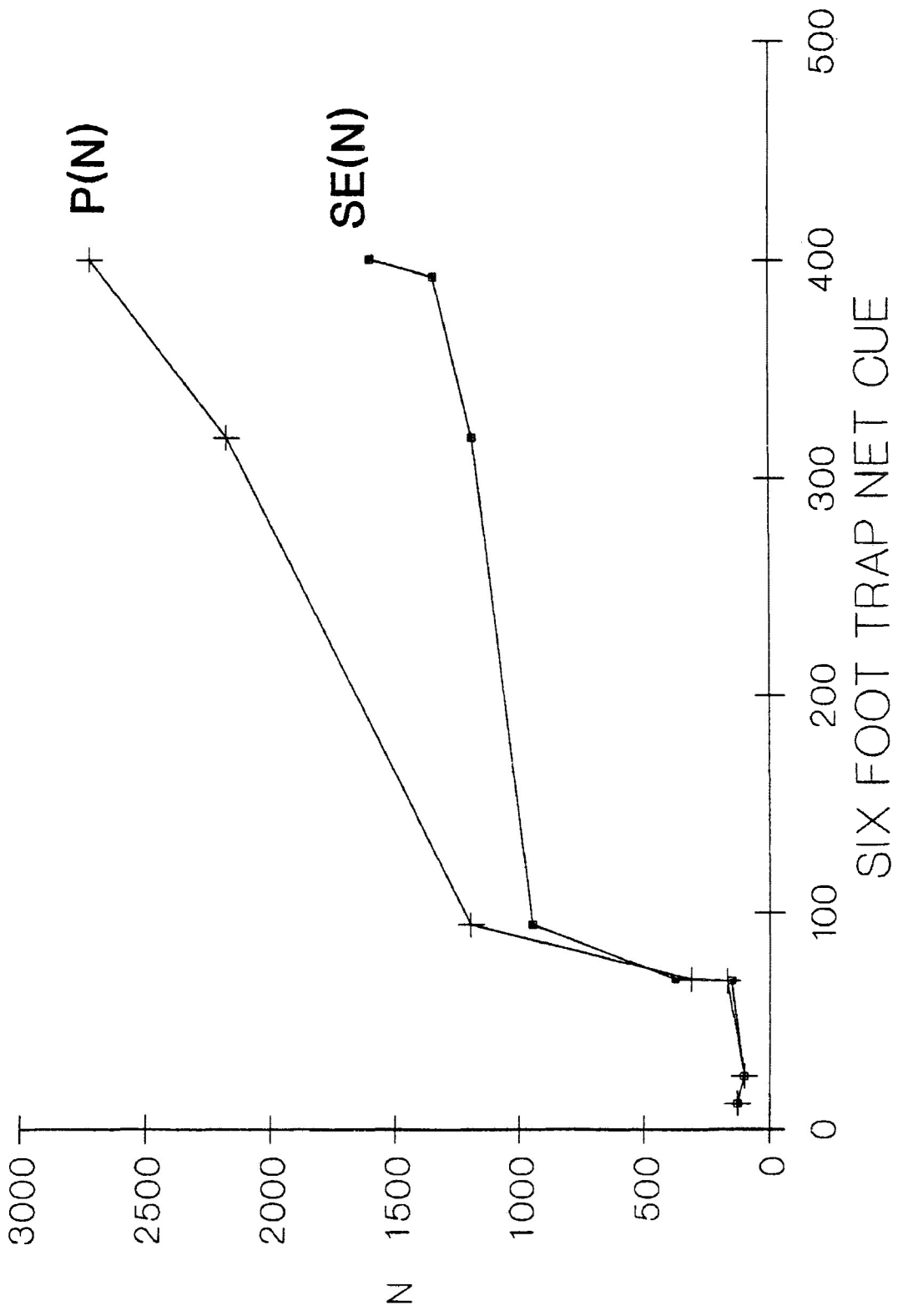
Lake Schumacher-Eschmeyer data provided an estimated population size of 552 walleye for Lanigon Lake. Substituting Lanigon Lake CUE into the Henderson Lake Petersen population estimate regression generated a value of 830 fish. Expressed in number of fish per hectare, both of these values are consistent with pre-exploitation densities in Henderson Lake. From the Schumacher-Eschmeyer data the Henderson walleye density in 1980 was estimated at 10.52 while in Lanigon in 1986 density was 8.69 fish per hectare. Using Petersen data the 1980 estimate for Henderson was 17.93 and 13.07 fish per hectare in Lanigon. Lower densities in Lanigon may be a result of sampling in only one of two basins (Fig. 5).

YOY Investigation

Growth

The growth data of Henderson Lake young of the year (YOY) walleye is given in Fig. 21. The length-weight regression for YOY walleye is linear with very little improvement of fit (r) with data transformation to log-log (Fig. 22). The rapid growth rate is graphically illustrated by comparing the length frequencies of YOY walleye sampled at the end of July 1986, with those sampled at the end of August 1986 (Fig. 23). The mean length increased

Figure 21. Growth of young of the year (YOY) walleye during July and August 1986 in Henderson Lake, Ontario.

TL = Total length in millimetres

TL ▪ 0.916 DATE ‒ 89.786   r▪0.947
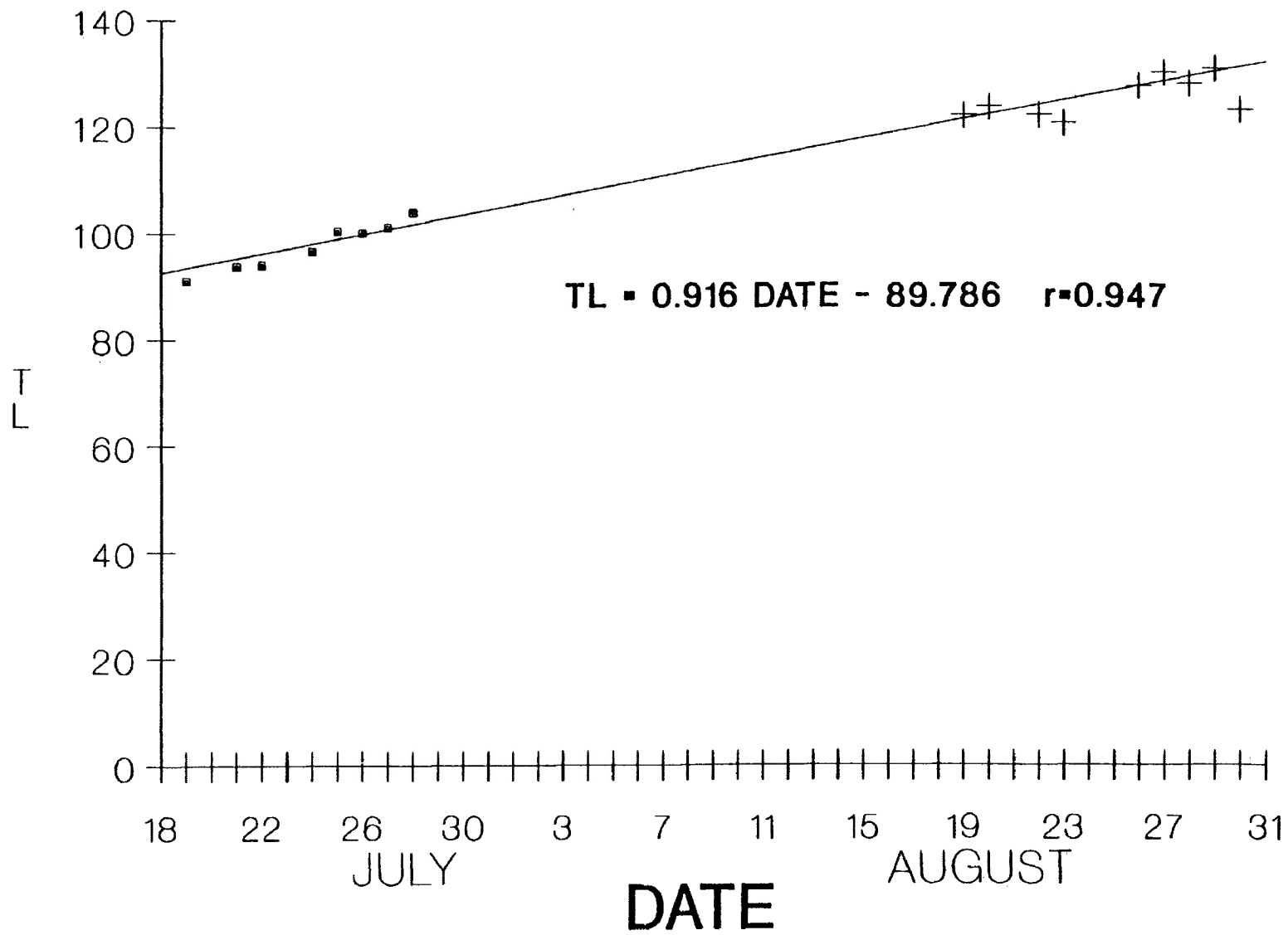
Figure 22. A) Plot of total length with weight and

B) Plot of Log_{10} total length with Log_{10} weight of

young of the year (YOY) walleye during July and August

1986 in Henderson Lake, Ontario.

A

WT = 0.296TL − 22.254   r=0.982

B

LOG$_{10}$WT = 3.009 LOG$_{10}$TL − 5.512

R = 0.986

66
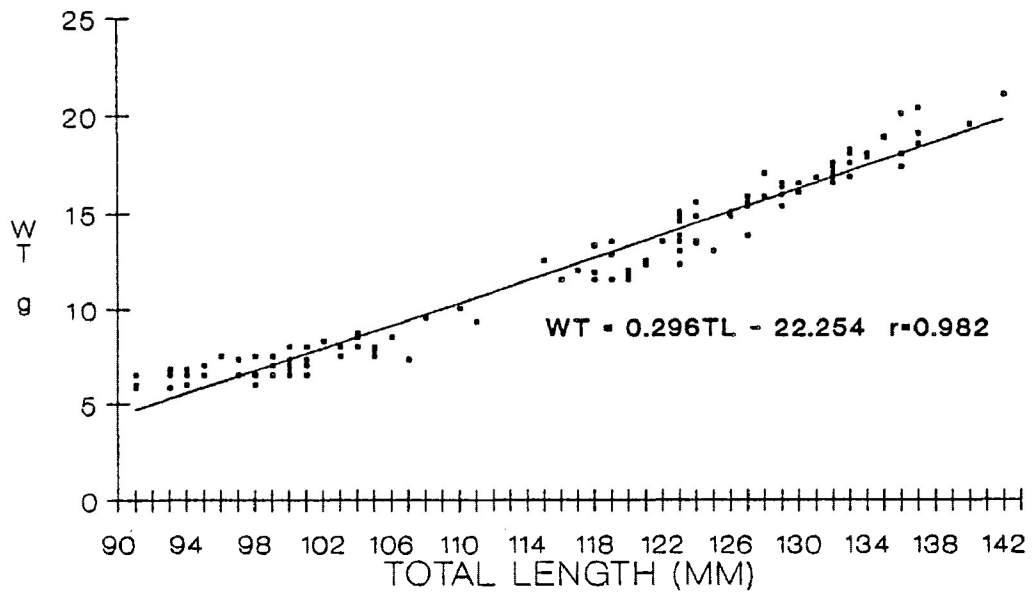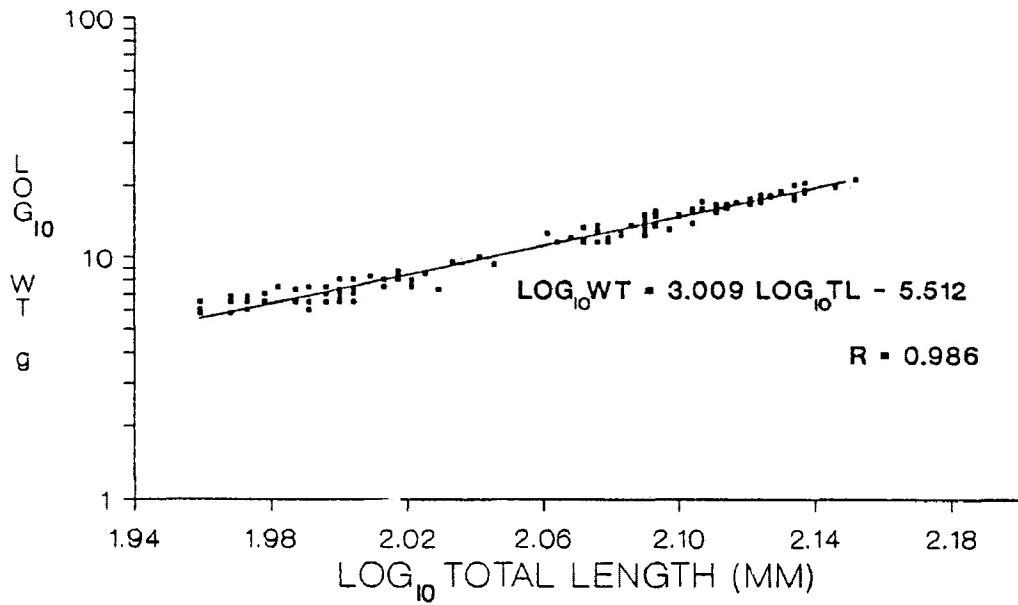
Figure 23. Length distributions of young of the year (YOY)
        walleye in Henderson Lake, Ontario, 1985 and 1986.

        1985 data from two seine hauls, time of day specified
        under figure
        1986 data from short duration small mesh gill nets set
        in evenings
        F = Percent frequency of total catch

1985

F

TOTAL LENGTH (MM)

■ JULY 29 14:50   ▨ AUGUST 2 20:00

1986

F

TOTAL LENGTH (MM)
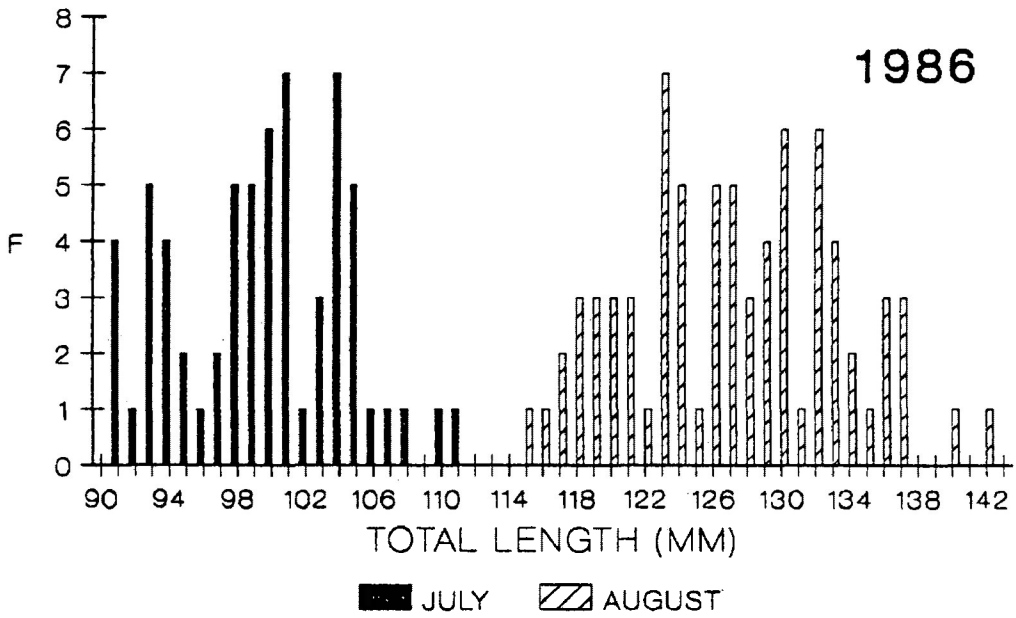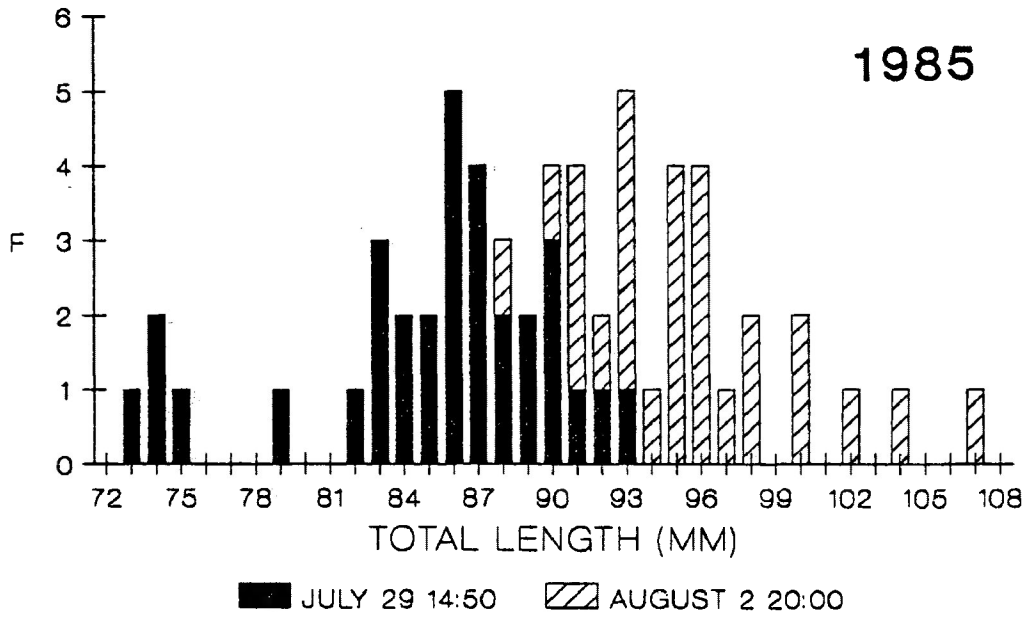
■ JULY   ▨ AUGUST

from 99.6mm to 127.2 from July to August and mean weight increased from 7.3g to 15.4g over the same period.

YOY Feeding Habits

All feeding data were collected from fish sampled in July and August, 1986. YOY walleye diets were classified into nine prey type categories: YOY yellow perch; shiner species (Notropis spp.); unidentified fish remains; burrowing ephemeroptera nymphs (Hexagenia sp. and Ephemera sp.); chironomid larvae; terrestrial (aerial) insects; Gyrinus sp. larvae; miscellaneous items and detritus. Fish prey items, the vast majority of which were YOY perch, dominated the diets of YOY walleye in both the July and August. There was an unmistakable shift towards insects in August. This trend is borne out in four analyses of diet composition (Fig. 24; Table 14). Also, the presence of shiners in the YOY walleye diets in August is of note as this food source was thought to be under utilized by walleye in Henderson Lake (Reid, 1985).

Both percent occurrence (the percentage of all stomachs containing food in which each prey item occurred) and the percent by number of all prey items of all fish exaggerate the importance of small prey items (Wallace, 1981). When expressed in terms of weight, the insect component and the subsequent bioenergetic value is reduced to a more realistic value (Fig. 24).

The mean total length of intact perch eaten by YOY walleye

Figure 24. Percent occurrence, percent by number, percent by
         weight and percent weight per stomach of diet items in
         young of the year (YOY) walleye in Henderson Lake,
         Ontario in 1986.

FR = Unidentified fish remains;

YOYP = young of the year perch;

SHI = Shiners (Notropis spp.);

EPH = Burrowing ephemeropterans;

DIP = Diptera larvae;

AER = Aerial (terrestrial) insects;

GYR = Whirligig beetle larvae (Gyrinus spp.);

DET = Detritus;

MIS = Miscellaneous food items;

FISH = All fish prey categories combined (FR + YOYP + SHI);

INS = All insect prey categories combined (EPH + DIP + AER + GYR)

PERCENT OCCURENCE

PERCENT BY NUMBER

PERCENT BY WEIGHT

MEAN PERCENT PER STOMACH

Prey types: FR YOYP SHI EPH DIP AER GYR DET MIS FISH INS

JULY   AUGUST   POOLED
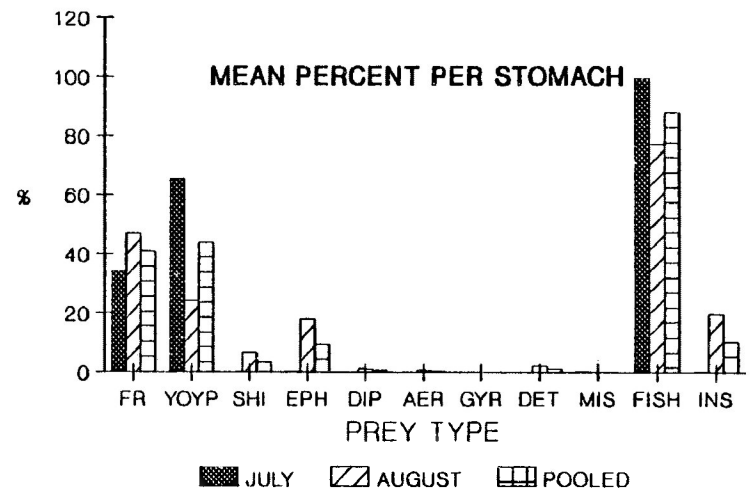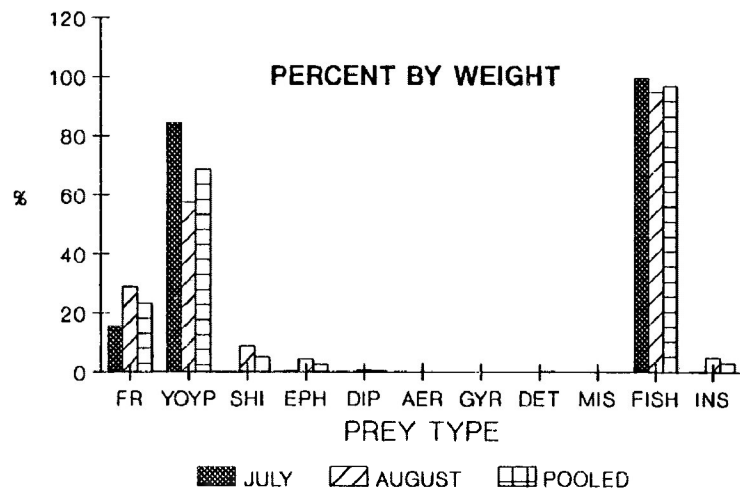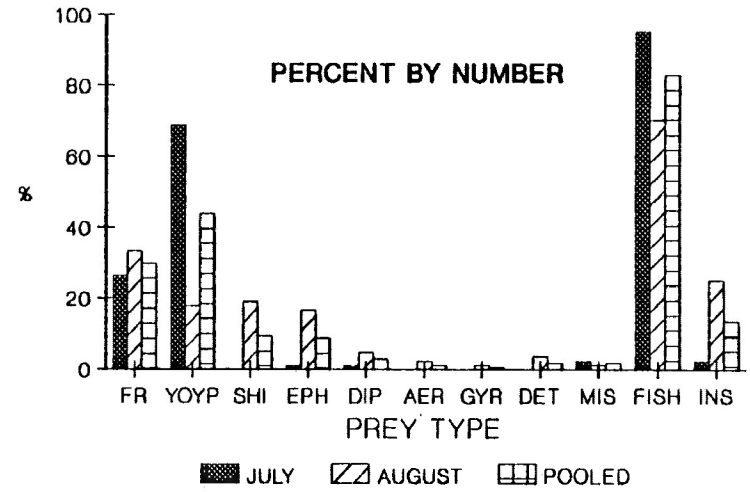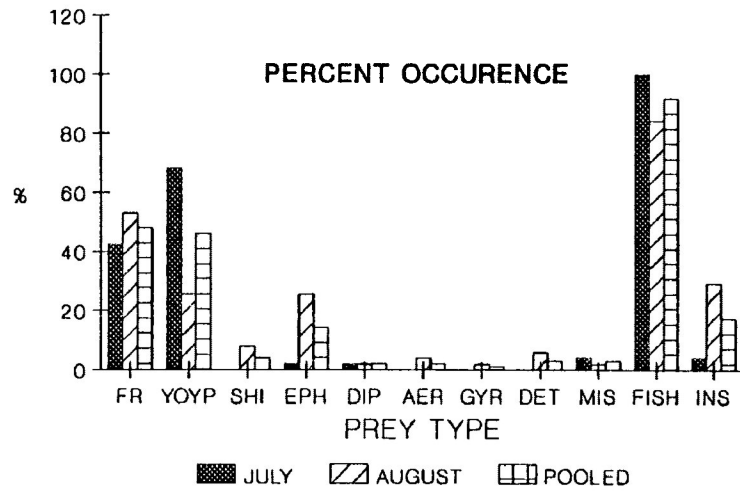
Table 14. Mean total length and weight of young of the year walleye consuming each prey item in Henderson Lake, Ontario, 1986.

Total length (mm)

Prey item	July $\overline{X}$	$\pm$ S.D.	n	August $\overline{X}$	$\pm$ S.D.	n
Fish remains	99.7	5.1	20	127.2	6.4	27
YOY perch	98.2	4.8	32	127.3	5.4	13
Shiner spp.				128.8	3.8	4
Burrowing mayfly	103.0	--	1	126.8	5.2	13
Aerial insects				128.0	1.4	2
Gyrinus sp.				129.0	--	1
Diptera larvae	100.0	--	1	123.0	--	1
Miscellaneous	100.5	2.1	2	124.0	--	1
Detritus				128.7	8.0	3
Empty	102.1	4.2	14	124.9	7.0	16
Fish combined	98.8	4.9	52	127.4	5.8	44
Insects combined	101.5	2.1	2	126.8	4.6	17
All full stomachs	98.9	4.8	56			
All prey items	99.6	4.8	70	126.8	5.9	81

Weight (g)

Prey item	July $\overline{X}$	$\pm$ S.D.	n	August $\overline{X}$	$\pm$ S.D.	n
Fish remains	7.37	1.08	20	15.61	2.44	27
YOY perch	7.22	0.94	30	15.62	2.37	13
Shiner spp.				15.81	1.46	4
Burrowing mayfly	8.00		1	15.09	1.96	13
Aerial insect				15.25	--	1
Gyrinus sp.				15.25	--	1
Diptera larvae	7.00	--	1	14.75	--	1
Miscellaneous	7.65	0.92	2	15.50	--	1
Detritus				16.53	4.02	3
Empty	7.31	0.69	14	14.41	2.30	16
Fish combined	7.28	0.99	50	15.64	2.31	44
Insect combined	7.50	0.71	2	15.10	1.70	17
All prey items	7.30	0.91	68	15.31	2.26	81

----

was 25.64 ± 3.68mm (n=58) in late July, and 44.29 ± 4.39mm (n=7) in late August. The mean total length of perch consumed by age one walleye sampled in July was 24.00mm ± 4.02 (n=10). There were no intact perch from age one walleye stomachs in the August sample. In 1984, YOY perch grew from 30mm total length in early July to 45mm total length by late August (Trimble, 1988). Assuming the perch were in the same size range in 1986 as they were in 1984, all perch consumed were YOY. These data, along with data presented in Table 17 suggest that YOY walleye may be selecting the smallest individuals available.

The mean weight of July YOY walleye was 7.28 ± 0.99g for those consuming fish, 7.50 ± 0.71g for those consuming insects and 7.30 ± 0.91g overall (Table 14). The mean weight of August YOY walleye was 15.31 ± 2.26g overall and 15.64 ± 2.31g and 15.10 ± 1.70g for piscivorous and insectivorous walleye respectively. Student's t-tests between category means of combined fish prey items, combined insect prey items and grand total of all items showed no significant differences (p=0.05) for either sampling period.

The mean total length of July YOY walleye was 99.56 ± 4.81mm overall, 98.77 ± 4.90mm for YOY walleye eating fish and 101.50 ± 2.12mm for insectivorous walleye (Table 14). In August these values increased to an overall mean total length of 126.78 ± 5.86mm with individual means of 129.39 ± 5.82mm and 126.82 ± 4.63 for fish and insect consumers. Student's t-tests showed no significant differences (p=0.05) between 1) length of fish eaters and lengths of insect eaters; 2) length of fish eaters and grand

mean length or 3) length of insect eaters and grand mean length for the August sample. Mean lengths of piscivores to insectivores and piscivores to the grand mean length were both significantly different (p=0.05) for the July sample. Whether these differences are real is debatable. The grand mean includes all YOY walleye sampled, including those with empty stomachs. For reasons unknown, YOY with empty stomachs were captured predominantly in the latter part of the July sampling period. The fish mean length, particularly the YOY perch category, was biased towards walleye sampled during the first half of the two week sampling period. Within the sampling periods themselves growth was rapid. The lengths and weights were increasing daily as the sampling program continued. Thus the significant differences between length of fish eaters and the grand mean length is an artifact of growth between sampling dates of fish eating walleye and walleye with empty stomachs. When the walleye with empty stomachs are removed from the grand mean length, the new mean is reduced to 98.93 $\pm$ 4.77mm. A t-test comparison between the fish mean and this new mean resulted in no significant differences (p=0.05).

The mean length comparison of fish eaters to mean length of insect eaters is dubious as the insect sample for July was comprised of only two fish. These two fish were caught on the fifth and fourth last day of July and their larger size is likely a function of their advanced growth.

The sample sizes of prey from age one walleye stomachs were very small as these fish were not targeted and were only sampled as an incidental catch. The gill net mesh sizes used

Table 15. Mean weight (mg) of items in each prey category consumed by young of the year walleye in Henderson Lake, Ontario, 1986.

Prey type	July $\bar{X}$ $\pm$ S.D.		n	August $\bar{X}$ $\pm$ S.D.		n
Fish remains	74.04	65.62	23	158.43	152.43	28
YOY perch	154.53	68.30	60	588.53	333.35	15
Shiner spp.				83.25	115.46	16
Burrowing mayfly	13.00	-	1	16.14	40.43	14
Aerial insect				4.00	4.24	2
Gyrinus sp.				13.00	- -	1
Diptera larvae	2.00		1	25.25	15.06	4
Miscellaneous	4.00	-	1	3.00	- -	1
Detritus				16.33	2.52	3
All prey types	126.41	79.16	87	183.52	160.11	84

(0.75 - 1.00 inch stretch) selectively caught only the smaller age one walleye. Comparing age one walleye weight and total length to prey types consumed is not very meaningful.

No evidence of size assortative predation by YOY walleye was found in the more comprehensive 1986 YOY walleye diet data. The transition from a fish dominated diet to a mixture of fish and insects is a function of altered prey availability rather than increased walleye size.

The mean weights of individual prey in each prey category consumed by YOY walleye are listed in Table 15. The largest increase was that of YOY perch of 154.5mg to 588.5mg from July to August. Despite increased growth of the chief prey item (perch), the mean weight of prey items consumed increased only 57.1mg from July to August. This was because of the influx of the much smaller insect prey. Perch were therefore growing out of the preferred size range consumed by YOY walleye.

Potential Interactions with other Species

Food items consumed by YOY walleye from both months were pooled and compared to the diets of both shiners and YOY perch from Henderson Lake, 1984 (Trimble, 1988) using Schoener's (1970) index of dietary overlap. YOY walleye had a percent dietary overlap of only 0.04% and 3.30% respectively with shiners and YOY perch which fed mainly on zooplankton and insects. It is more meaningful to compare YOY walleye with adult perch. Diets (percent by number) of adult perch of three different size

Table 16. Percent dietary overlap of young of the year walleye
with three size classes of adult perch[a] in Henderson
Lake, Ontario.

	July		August	
Perch size class	1981	1982	1981	1982
<91mm TL	4.59	32.84	15.48	27.86
91 - 131mm TL	10.72	41.42	25.22	31.61
131 - 200mm TL	9.60	32.66	26.83	25.95

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a = Ritchie, 1984

classes from July and August 1981 and 1982 (Ritchie, 1984) were contrasted with 1986 YOY walleye diet (percent by number) using Schoener's index of dietary overlap (Table 16). The results show up to a 41.4% overlap. However month to month and year to year trends were inconsistent. Generally, 1982 perch of all sizes overlap more so than 1981 perch, particularly in July. This is because of cannibalism of 1982 perch. The dramatic increase in overlap in August between 1981 perch and 1986 walleye reflects higher utilization of invertebrates by walleye in that month.

Peak Feeding Period

Walleye are crepuscular feeders in clear lakes (Ryder, 1977) with the peak feeding activity occurring at dawn and dusk. Feeding periodicity was examined only at dusk. A sharp peak occurs at 21:22hr for the pooled summer data (Fig. 25). Individual peaks for July and August were 21:20 and 21:01 respectively. The earlier peak in August results from the shortening photoperiod. Light intensities (Watts per square metre) correlate YOY feeding activity to ambient light levels. Unfortunately the light meter batteries had expired early in the August sampling period and so only the light readings for July are available. Light intensity versus time (Fig. 26) shows the decline of light levels at dusk. A plot of base ten logarithm against time transformed this relationship yielding the linear regression line:

Figure 25. Peak feeding activity of young of the year (YOY) walleye during July and August, 1986, in Henderson Lake, Ontario.

F = Percent frequency of total catch
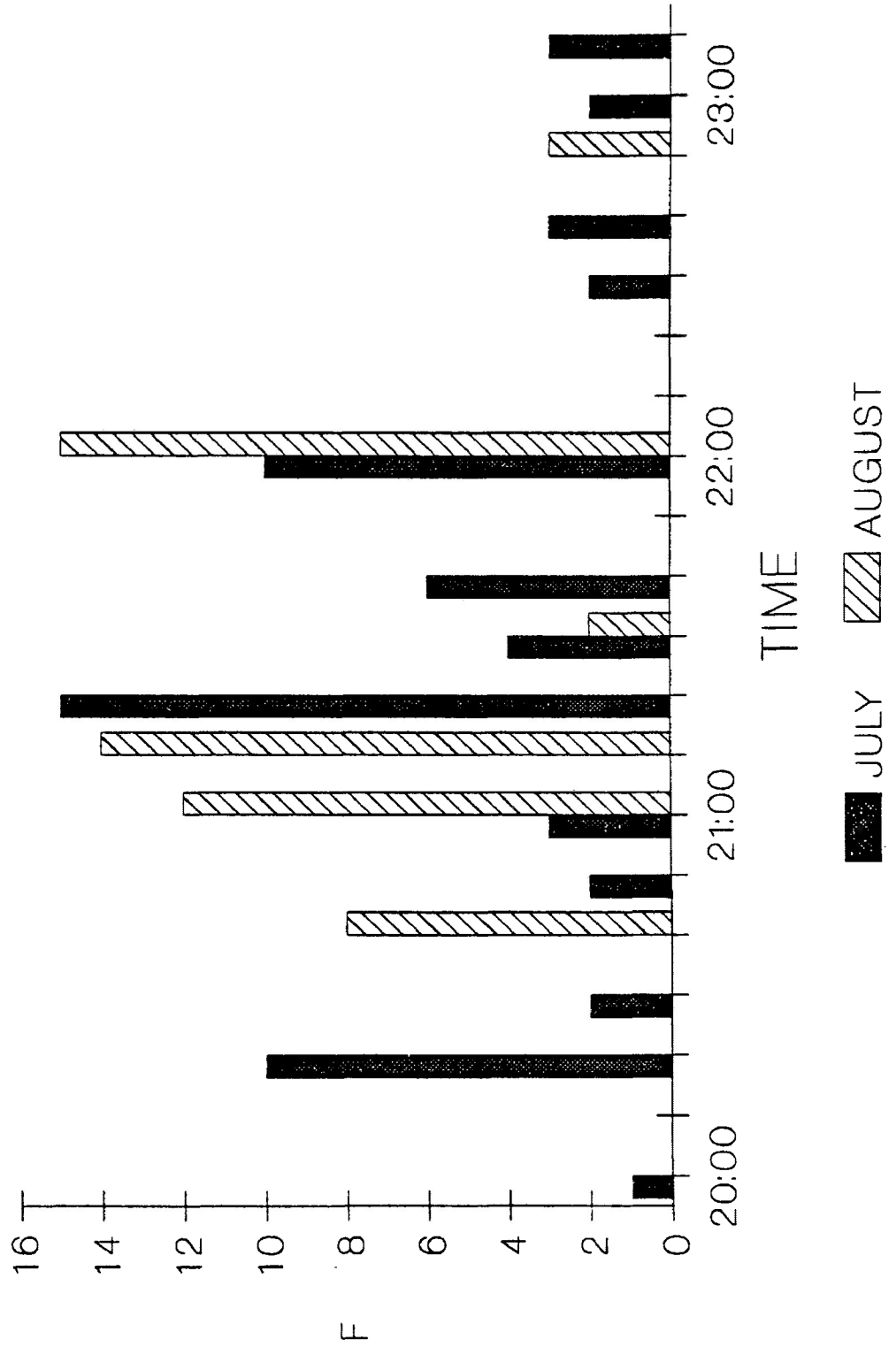
Figure 26. Evening attenuation of ambient surface illumination (W/m^2) during July, 1986, in Henderson Lake, Ontario.
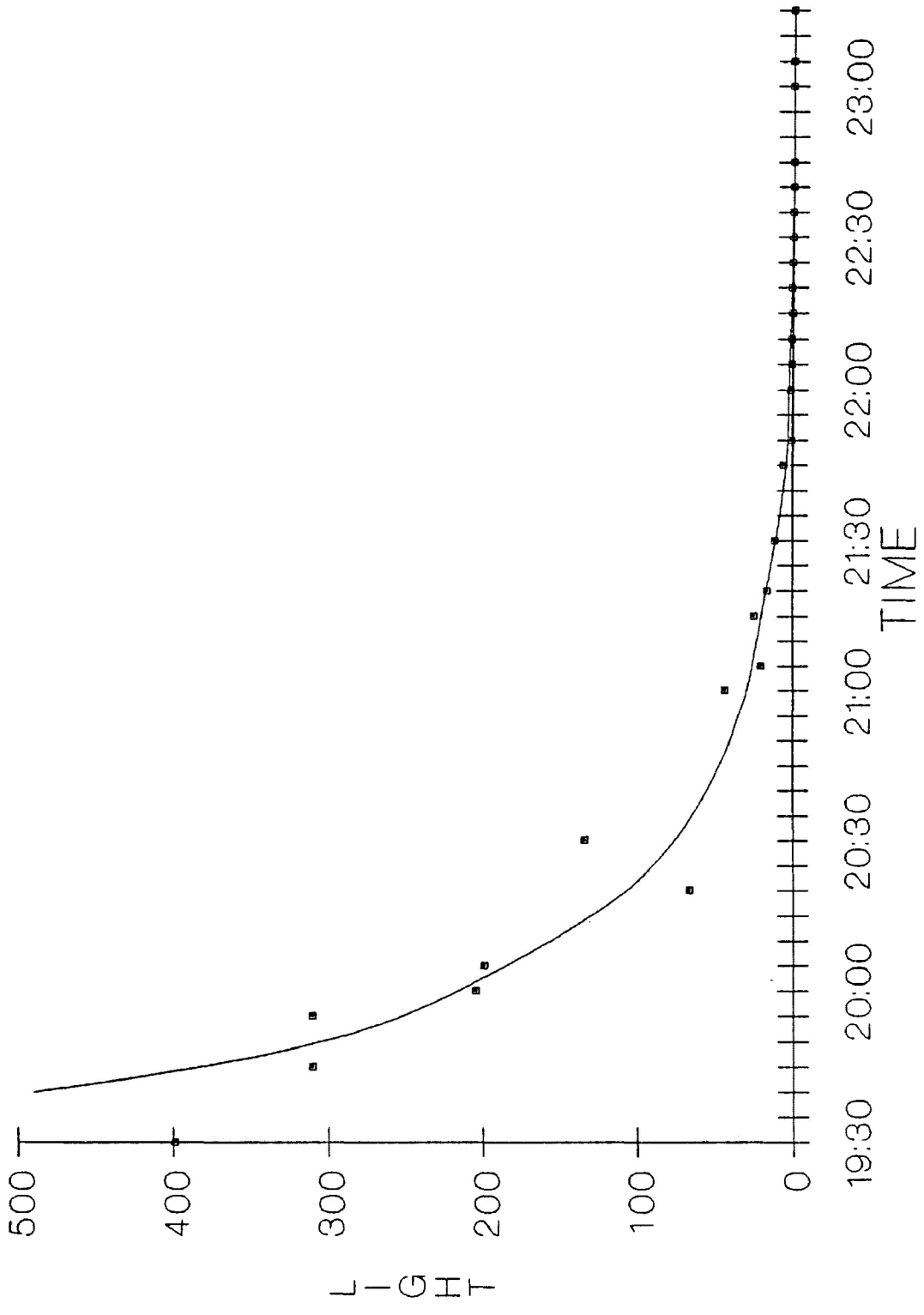
Table 17. Evening atennuation of ambient surface
illumination on Henderson Lake, Ontario, in July, 1986.

Time	Light intensity (W/m^2)	Percent change per minute
19:30	399.000	
19:45	310.000	1.49
20:00	204.250	2.27
20:05	199.000	0.51
20:30	133.750	1.31
20:35	130.000	0.56
21:00	43.540	2.66
21:15	24.700	2.88
21:20	16.000	7.04 <- Peak feeding
21:30	10.824	3.24 time
21:45	5.530	3.26
22:00	1.426	4.95
22:05	0.479	13.28
22:15	0.173	6.39
22:20	0.085	10.17
22:25	0.036	11.53
22:30	0.013	12.78
22.35	0.009	6.15
22:40	0.005	8.89
22:45	0.000	

$$LOG_{10}Light\ Intensity = 35.01382 - 0.02701\ (Time),\ r=-0.917$$

where time is 24 hour time expressed in minutes. Substituting the peak feeding time of 21:20hr (=1280 minutes) for July yields a peak feeding light intensity of 2.76 W/m^{-2}. Ryder (1977) described how adult walleye feeding activity was more highly correlated with the rate of change of light intensity. An attempt to duplicate Ryder's work was inconclusive. The major problem was that as light approached very low levels the percentage of decrease increased (Table 17). Rate of decrease was calculated by the formula :

$$\%\ Decrease = (1 - (LI_{t+1}\ \ LI_t)\ X\ 100$$

where LI_{t+1} and LI_t are light intensities from two consecutive readings. However, rate of change of individual light readings at irregular intervals showed an abrupt increase at 21:20hr but became inconsistent after 22:00hr (Table 17). This increase at 21:20hr concurs exactly with the empirically derived peak feeding activity.

Effect of Depth and Time

Length frequencies of YOY walleye captured in 1985 suggested that larger, more precocious individuals within the cohort with advanced development of the _tapetum lucidum_ had

adopted the crepuscular feeding habits of adult walleye (Fig. 23). Smaller individuals were still feeding during the day having not yet made this transition. Fish captured at 14:00 July 29 had a mean total length of 85mm (n=32) and those on August 2 at 20:00 were 95mm mean total length (n=27).

The effect of depth and time on YOY walleye feeding activity was measured by plotting LOG_{10} weight with date. This generated a growth rate regression. Individual fish residuals (the difference between observed weight and weight predicted from the weight versus date regression) were then plotted with respect to depth and time of capture (Fig. 27). No patterns or trends were revealed. The apparent shift of YOY walleye into deeper water from July to August is confounded by nonstandardized fishing effort in deep water.

Figure 27. Individual weight residuals calculated from the
regression of young of the year (YOY) walleye growth
(Fig 21) plotted against depth and time of capture
in Henderson Lake, Ontario.

+ = Observed weight of captured YOY walleye greater
than expected weight for that date from Fig 21

- = Observed weight of captured YOY walleye smaller
than expected weight for that date from Fig 21

Depth (m)	20:00	20:15	20:30	20:45	21:00	21:15	21:30	21:45	22:00	22:15	22:30	22:45	23:00	23:15	23:30
1.00	-	--	-+	++			+ -		++-+		++		++	++	
1.25		+							+--						
1.50															
1.75															
2.00					++	++									
					--	-+--+		+-+							
2.25					+-	+--									
2.50															
2.75						-+			++-						
3.00					+										
3.25					++				-+						
3.25					++				-						
3.50															
3.75		-+				++--									
		++-			-+-	----		-+-							
4.00						-+-+									
4.25				-+-					-+-++						

4.50															
4.75				-+++		++-									
5.00						+									

DISCUSSION

Population Estimates

Petersen population estimates were not employed in 1985 and 1986 since any additional adult fish removal might have collapsed the stock. Reid (1985) concluded that Schumacher-Eschmeyer (SE) mark-recapture population estimates accurately measure walleye abundance at low population densties, but underestimate fish abundance at high densities. Thus, SE population estimates were presumed to accurately reflect walleye population size but likely to underestimate pike and sucker densities. However, for consistency, population sizes of pike and suckers in this study are compared with abundances derived from SE population estimates of Reid (1985) and Nunan (1982).

Walleye density dwindled to 101 fish in 1986 but should rebound sharply when the 1985 and 1986 year classes become vulnerable to trap net gear. Whether the population will reach preexploitation densties requires further investigation.

Both pike and sucker showed declining densties from 1979 to 1983 (Table 2). The cause of these declines are not known.

Catch per Unit Effort

Catch per unit effort (CUE) has been used as an indicator of population abundance (Hamley, 1975). A relationship between

CUE and adult walleye density assumes the population estimates accurately describe walleye abundance. While this may be true at low densities, Schumacher-Eschmeyer population estimates misrepresent walleye numbers at high densities (Fig. 20). Petersen population estimates provide a more accurate account of walleye density and thus generated a better correlation with CUE data (r=0.96)(Table 12).

For correlations between 1979 to 1986 six foot trap net data and SE population estimates only walleye showed a good relationship (r=0.87). Pike and suckers generated poor correlations of r=0.65 and r=0.51 respectively (Table 12). The stronger relationship for walleye was only apparent because the walleye population was measured at extreme levels at a considerable expenditure of effort. Kipling and Frost (1970) found high effort levels were required in order for CUE data to serve as a reliable measure of fish abundance. Roff (1983) doubts CUE is reliable and cautions that CUE data be limited to measuring only widely fluctuating fish densities such as occurred in Henderson Lake walleye. Reid and Momot (1985) showed that both CUE and Schumacher-Eschmeyer population estimates poorly predicted imminent stock collapse during the exploitation phase of this pulse fishing project.

Catch per unit effort data are influenced by many other variables including spawning activity, food availability, temperature, weather conditions, fish condition as well as fish density (Hamley, 1975). Minor changes in population density by pike and suckers could easily be masked by variations in these

other factors. Schumacher-Eschmeyer population estimates of high density pike and sucker populations are not sensitive to minor fluctuations since a sizable proportion of each population is probably not measured.

Condition Factors

An increase in fish size results in a disproportional increase in fish weight over fish length since weight is a cubic function of length. Therefore the increase in mean condition factor ($K = $ Weight/(Length)^3 X 10^5) of Henderson Lake walleye (Fig. 10) does not necessarily reflect improved foraging opportunities but simply the increase in mean age (Table 4) and the scarcity of small individuals in the population (Fig. 6).

Growth Response

Large fish are more vulnerable to trap net gear (Laarman and Ryckman, 1982; Latta, 1959). Intensive exploitation culls fast growing fish (Borisov, 1978). The result is a decrease in the mean length at age of walleye from 1979 (preexploitation) to 1983 (post exploitation). Younger age classes (3 to 5yr), which became newly vulnerable to fishing gear at the time fishing ceased, were not subjected to selective mortality of larger individuals within the year class. These age groups exhibited a growth response from 1980 to 1986 (Fig. 15). When the selective harvest ended in 1983 the older age classes rebounded to attain

lengths observed prior to exploitation. By 1986 age six fish surpassed the size attained by fish of this age in 1979. This was expected since this was the first cohort subjected to reduced intraspecific competition through every stage of its development.

Whether the walleye are at their maximum growth potential can not be absolutely determined, however the very low densities and large forage base available suggest that the maximum is being approached. Following sexual maturity, as early as age 3.3 for males and 4.4 for females in this population (Reid, 1985), gonadal product synthesis displaces somatic growth (Purdom, 1979; Bagenal, 1973). Glenn (1969) reported the growing season in Manitoba spans from June 28 to August 7. Smith and Pycha (1961) stated the duration of growth in Minnesota is usually less that four months and sometimes as short as two months. Given the thermal limits imposed by the north-temperate climate of Henderson Lake there is a physiological ceiling to growth attainable by walleye feeding on given food items.

A population can respond to increased forage opportunities in two ways: increased growth and/or increased abundance (Regier, 1977; Nikolskii, 1969). Yellow perch which were stunted before exploitation, further increased their numbers with no appreciable increase in growth (Trimble, 1988). Walleye have thus far responded only by increasing in growth.

Henderson Lake northern pike indicate both an increase in growth and recruitment. Fish aged four years and older increased in mean length at age between 1982 to 1986. However pike age one to three have remained stable (Fig. 17). Pike age distributions

indicate substantial recruitment of age two and three fish since 1984 (Fig. 13). Increased intraspecific competition was probably responsible for these constant growth rates within these age classes.

Statistical comparisons of walleye and pike length and weight at age are presented in Appendix C.

Production

Since 1979 walleye production has declined due to negligible recruitment and increasing mean age. In 1985 and 1986, production and biomass were well below those of other lakes (Table 18). This situation should change as younger age classes enter the portion of the population that can be sampled.

From 1982 to 1986, the only years for which comparable age data were available, pike production, biomass and turnover ratios increased by 327%, 31%, and 227% respectively (Table 10). These increases reflected increased growth rates of older pike as well as increased relative abundance of younger pike. Pike production expanded following increased yellow perch abundance in concert with reduced consumption of this increased food supply by walleye. There were major time lags between stimulus (1980 to 1982 walleye exploitation) and response (1983 recruitment, 1986 growth) within the fish community. This eloquently illustrates the value of long term, systematically collected data in measuring changes in population dynamics of long lived fish species of boreal lakes. Short term, sporadically collected data

Table 18. Walleye production (kg/ha/yr), biomass (kg/ha) and P/B ratios from other waters (after Reid, 1985).

Lake	Reference	Year	Age	P	B	P/B
Henderson L	Present study	1979-80	4-14	1.57	6.84	0.23
Ontario		1980-81	4-14	3.28	5.90	0.52
		1981-82	4-11	--	3.71	--
		1982-83	4-9	0.18	2.40	0.08
		1983-84	4-11	0.41	1.32	0.31
		1984-85	4-11	0.18	0.98	0.18
		1985-86	5-11	0.17	0.93	0.18
Savanne L.	Sandu, 1979	1973-74	7-16	1.00	6.58	0.15
Ontario		1974-75	7-14	1.31	6.06	0.22
		1975-76	8-15	0.52	2.64	0.20
West Blue L Manitoba	Kelso and Ward, 1972	1969-70	1-4	2.10	6.10	0.34
Oneida L.	Hofman, 1972	1967	3-8	3.39	20.50	0.16
New York		1968	3-8	7.56	20.59	0.37
Dexter L. Ontario	Moenig, 1975	1967	3-13	1.78	7.20	0.25
Hoover Reservoir Ohio	Momot et.al., 1977	1967-73	2+	2.16	13.57	0.16
Clear L.	Carlander and	1948-73	3+	1.21	5.70	0.21
Iowa	Payne, 1977	1947-73	1+	3.08	7.20	0.42

are nearly worthless in this regard. Pike were not responding so much to walleye absence but rather to increased presence of perch. Approximately 68% of known pike diet is perch (Nursall, 1973). Pike cohort strength is dependent on growth achieved during the first year (Craig and Kipling, 1983). Response by pike was conditional on a perch response, hence the time lag. Smith and Krefting (1954) found northern pike fluctuations showed no consistent relationship with either perch or walleye abundance, while perch and walleye showed a classic predator-prey interdependence. Perhaps the strong interactions between perch and walleye supercede the influence of pike. Only upon near extirpation of adult walleye further accompanied by five consecutive years of walleye year class failures could the predatory potential (carrying capacity) of pike be fully realised and measured.

Increased walleye abundance should stabilize or lower pike production allowing walleye to return to previous levels. Pike production from nearby Squeers Lake (oligotrophic lake trout lake) in 1984 - 85 was 0.35kg/ha (ages 3 - 9) (A. Laine pers. comm.) and 2.76kg/ha in nearby Savanne Lake (mesotrophic walleye lake) in 1977 - 78 (Mosindy, 1980). Pike production in Henderson Lake increased from 0.81kg/ha in 1982 - 83 to 3.47kg/ha in 1985-86 (Table 10).

Recruitment

Extreme variation in walleye hatching success can still result in large year classes (Clady, 1976; Busch, Scholl and Hartman, 1975; Clady and Hutchison, 1975; Smith and Koenst, 1975; Wolfert, Busch and Baker, 1975; Allbaugh and Manz, 1964; Derback, 1947). Year class strength is also influenced by abundance and synchrony of prey (YOY yellow perch) availability (Knight, Margraf and Carline, 1984; Forney, 1974; Chevalier, 1973; Parsons, 1971; Smith and Pycha, 1961), predation (Lyons, 1984) and cannibalism (Valiant, 1984; Chevalier, 1973; Carlander 1942).

Temperature regulates hormone production, enzyme activity, feeding, growth, survival, reproduction and dispersion of percids (Craig, 1987). Temperature also controls timing and abundance of suitably sized prey, crucial for successful establishment of a walleye year class (Momot, Erickson and Stevenson, 1977).

Spring water temperatures were slightly warmer in 1985 and 1986 than in 1979, and from 1981 to 1984 during the month of May (Fig. 28). The sharp rise in water temperature in early May 1980, followed by an abrupt decline of 7°C may have caused the recruitment failure evident in both Henderson and Lanigon Lakes in 1980 (Fig. 11; Fig. 12). Smith and Krefting (1954) found no significant relationship between walleye year class strength and mean temperature or mean minimum temperature during the 30 day period after spawning. A significant correlation has been documented between the coefficient of variation (standard deviation/mean) of May water temperature and fall YOY walleye

Figure 28. Spring water temperatures during May and June in
          Henderson Lake, Ontario from 1979 - 1986.

          1979 - 1981 data (in part) from Nunan and Romani,
                      unpublished
          1981 - 1982 data (in part) from Ritchie, 1984
          1982 - 1984 data (in part) from Reid, 1985
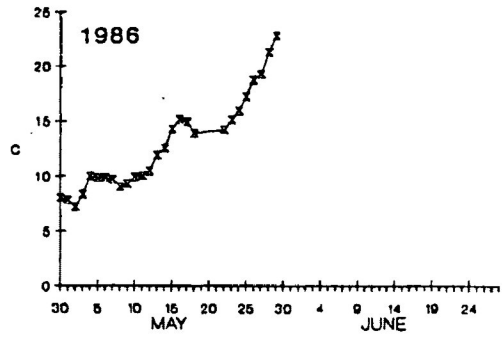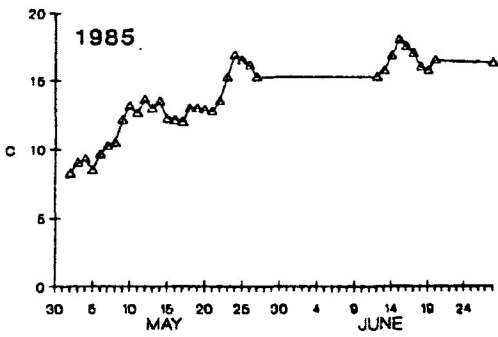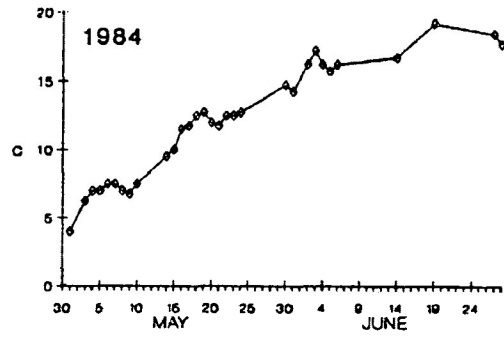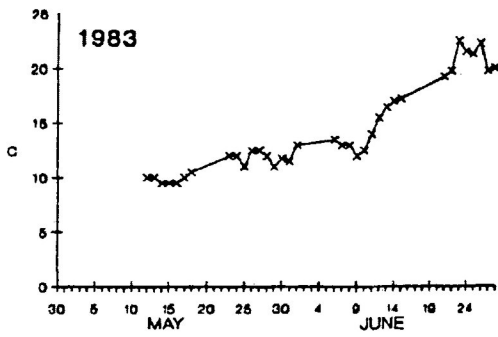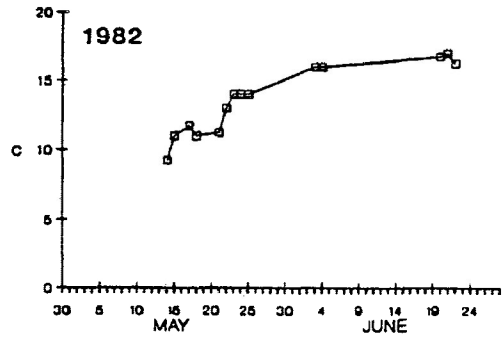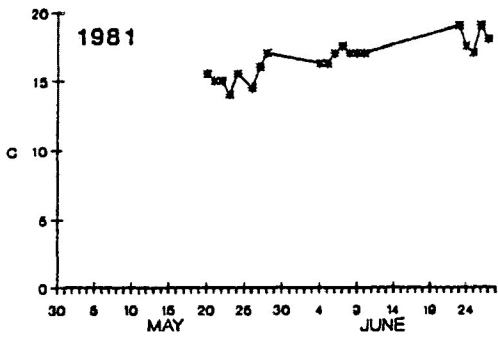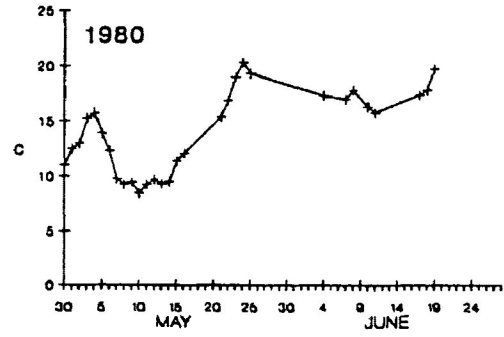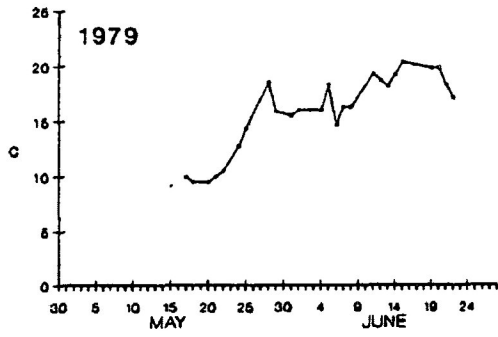
densities in Escanaba Lake, Wisconsis (Serns, 1982). Coefficients of variation (CV's) less than 0.096 were correlated with good year classes while CV's greater than 0.100 were correlated with poor year classes. CV's generated from Henderson Lake temperature data indicate 1981 to be the only "good" year and 1986 to be the absolute worst based on the aforementioned criteria (Table 19). These predictions are not congruent with observed YOY walleye densities in Henderson Lake since 1979. The CV of 0.329 in 1986 (n=26) calls into question the reliability of this method as a predictor of walleye year class strength from spring water temperature data.

However Busch, Scholl and Hartman (1975) found a positive effect of the rate of warming on egg density and resulting year class strengths in Lake Erie. They reported warming rates between April 1 and May 15 greater than 0.28°C/day resulted in good year classes while rates less than 0.18°C/day resulted in poor year classes. Due to differences in latitude spring is delayed relative to Lake Erie by about three weeks to a month in the Thunder Bay area and generally walleye spawning does not occur in Henderson Lake until the last week of April. Temperature data from May 1 to June 15 were compared to the Lake Erie data. Using the criteria described by Busch, Scholl and Hartman (1975), 1986, 1984, 1982 and 1979 should have produced strong year classes while 1985, 1983, 1981 and 1980 could have been expected to produce marginal to poor year classes (Table 20). A more elaborate model (Koonce et. al., 1977) based on the same data set met with only partial success in predicting year class success.

Table 19. Coefficients of variation (standard deviation/mean) of
May water temperatures (°C) in Henderson Lake, Ontario,
from 1979 to 1986. Predicted walleye year class
strength (Yr CL Str) from Serns (1982) criteria.
Coeficient of variation ≤ 0.096 indicates good fall
age-0 walleye density, less than 0.100 indicates a low
fall age-0 walleye density.

Year	Mean	Standard Deviation	No. of cases	Coefficient of Variation	Predicted Yr Cl Str
1979	12.66	3.24	10	0.256	Poor
1980	12.94	3.72	21	0.287	Poor
1981	15.31	0.92	8	0.060	Good
1982	12.61	1.68	9	0.138	Poor
1983	10.96	1.11	16	0.101	Poor
1984	9.97	3.04	22	0.305	Poor
1985	12.50	2.40	26	0.192	Poor
1986	13.01	4.28	26	0.329	Poor

Table 20. Henderson Lake spring water temperature warming rates
(°C/day) from May 1 to June 15.

Year	Regression			Rate(°C/day)
1979	°C = 0.329 Date + 4.645	r=0.88	n=21	0.329
1980	°C = 0.178 Date + 8.382	r=0.67	n=29	0.178
1981	°C = 0.183 Date + 9.940	r=0.95	n=6	0.183
1982	°C = 0.297 Date + 6.156	r=0.94	n=11	0.297
1983	°C = 0.178 Date + 7.074	r=0.88	n=27	0.178
1984	°C = 0.302 Date + 5.492	r=0.96	n=28	0.302
1985	°C = 0.180 Date + 9.722	r=0.85	n=30	0.180
1986	°C = 0.458 Date + 6.348	r=0.95	n=26	0.458

Data compiled from: Nunan and Romani (unpublished) 1979 - 1981

                     Ritchie (1984) 1981 - 1982

                     Reid (1985) 1982 - 1984

Despite extensive small mesh gillnetting and beach seining (Trimble, 1988; Ritchie, 1984) in Henderson Lake from 1980 to 1986, not a single YOY walleye was ever caught until 1985 (a cold year) and 1986 (a warm year). Therefore, although warm temperatures can be an important determinant of YOY walleye success many other biotic factors such as food supply, year class strength and predator abundance determine the size of a year class during a cold spring or conversely, negate the benefits of a warm one.

A remarkable even year biannual pulse in production is evidenced by increased YOY walleye abundance in nearby Savanne Lake and increased walleye fecundity the following spring in Henderson Lake walleye (Ritchie and Colby, 1988). These increases were attributed by Ritchie and Colby (1988) to large biannual hatches of the burrowing mayfly Hexagenia limbata. However the even year cyclic nature of spring warming rates (Table 20) may be primarily responsible for this production since food conversion is a function of temperature (Seaburg and Moyle, 1964). Also, both Preigel (1969) and Forney (1966) noted invertebrate prey produced poorer growth in YOY walleye than fish prey items.

The Henderson Lake walleye age distribution is indicative of an aging population in the absence of any measurable recruitment (Fig. 11). In contrast, in Lanigon Lake walleye have a normally distributed age structure with exception of the 1980 year class (Fig. 12). The two lakes are connected by a small creek less than a kilometre in length flowing from Henderson into Lanigon (Fig. 5). Considering their juxtaposition, one would

expect similar climatic conditions in each lake during the critical larval period and produce similar densities and availabilities of suitable prey items. The effect of weather on spawning success and fry survival has been noted to be frequently state-wide (Moyle, 1949; Koonce et. al. 1977). No climatic factors can account for the disparity of recruitment success between the two populations.

One of the great enigmas of fisheries science has been to predict recruitment from brood stock size. Many attempts have been made to fit one year old recruits against egg production with either an asymptotic (Beverton and Holt, 1957) or dome shaped (Ricker, 1954) curve. Few such attempts have provided a functional relationship between recruitment and the number of eggs spawned (Garrod and Knights, 1979). However, Shuter and Koonce (1977) reported walleye recruitment increased with stock size, thus forming the left side of a Ricker (1954) stock-recruitment curve. Examination of the discordant recruitment between Lanigon Lake and Henderson Lake (presence versus absence) reveals the obvious difference in brood stock size to be the most likely explanation for this disparity.

Recruitment overfishing occurs when adult stocks are reduced to a point where year class strength suffers as a result of declining recruitment (Cushing, 1977). Ultimately, adult density could be reduced to such a low level that recruitment becomes negligible.

When walleye spawn, males occupy the spawning shoal in advance of females (Colby, McNicol and Ryder, 1979; Scott and

Crossman; 1973). As individual females ripen they move from deep water, spawn and immediately return to deep water. Males however, remain until all the females have spawned. Duration of egg deposition depends on temperature (Eschmeyer, 1950), size of spawning population (Johnson, 1971) and number and size of quality spawning sites (Preigel, 1970). Often spawning activity lasts for only one or two nights (Ryder, 1977).

A smaller population deposits fewer eggs over a shorter duration. Concentrating reproductive effort over a narrow time span makes the year class more vulnerable or sensitive to unfavourable environmental conditions. If the spawning run were extended over many days more heterogeneity in the developmental status of eggs and larvae might occur. Should temporary conditions lethal to a certain life stage be produced, mortality to the year class would be only partial. By extending its spawning season, a population enhances reproductive success. Developing walleye embryos and larvae are buffered to some degree against the variable spring conditions typical of north-temperate boreal lakes (Fig. 28) by spanning a broader range of momentary requirements. Therefore, when a walleye population is substantially reduced, the chances of reproductive failure increase.

Henderson Lake adult walleye were reduced to very low densities (less than one per hectare for 1985 and 1986). With only 130 and 100 older adult walleye in 1985 and 1986, the spawning population consisted of about 65 and 50 females. Why were the two years having the lowest adult densties the only

years in which a large numbers of YOY walleye were produced? Rawson (1957), Eschmeyer(1950), Carlander (1945) and Deason (1933) reported some older females may be sterile or fail to spawn annually. However, Kennedy (1947) in agreement with observations on Henderson noted that a very small walleye population produced "normal" recruitment in Tathlina Lake, N.W.T. in 1942.

Stock size is therefore only one of a myriad of influences determining recruitment success. Physical condition of adults, success of fertilization, the distribution of spawning in time and space in relation to physical characteristics of the environment, and relative abundance of prey or predator organisms appropriate to each phase of fish development all contribute to annual variability in recruitment (Garrod and Knights, 1979). Therefore faltering walleye recruitment from a critically reduced brood stock is hypothesized to be synergistically exacerbated by variable environmental and biotic factors influencing recruitment success.

Adams and Olver (1977) issued a prescient warning on the implementation of a walleye pulse fishery. Namely that a "rapid change in the density of any species population can alter interspecific balance and subsequent net reproductive success". Perhaps this has occured in Henderson Lake.

Most likely, recruitment overfishing combined with variable environmental conditions produced the contrasting 1986 walleye age distributions of Henderson and Lanigon Lakes. Extensive beach seining and small mesh gillnetting during other

studies on Henderson Lake (Trimble, 1988; Ritchie, 1984) indicate that the walleye reproductive effort since 1980 had failed very early in the developmental sequence. Perhaps some kind of social stimulus that synchronizes spawning was disrupted by the exploitation program.

Regardless of etiology, the implications of five consecutive years of year class failures on conclusions drawn from this study can not be ignored. Stock recovery begins only with reproductive success of the remaining adults. Even though exploitation ceased in 1982, true recovery of the Henderson Lake walleye population was delayed by three years and did not begin until 1985. The time period required for reestablishment of walleye densities sufficient to support another pulse fishery was delayed by the five years of recruitment failure.

Young of the Year Walleye Growth

Growth of YOY walleye varies seasonally due to fluctuations in temperature (Knight, Margraf and Carline, 1984; Serns, 1982; Koenst and Smith, 1976; Busch, Scholl and Hartman, 1975; Forney, 1966; Maloney and Johnson, 1965; Allbaugh and Manz, 1964; Raney and Lachner, 1942), length of growing season (Kelso and Ward, 1972; Smith and Pycha, 1961), prey abundance (Knight, Margraf and Carline, 1984; Lyons, 1984; Wolfert, 1977; Forney, 1976; Swenson and Smith, 1976; Wahtola, Miller and Owen, 1972; Maloney and Johnson, 1965; Arnold, 1960), prey synchrony (Paxton,

Day and Stevenson, 1981; Garrod and Knights, 1979; Momot, Erickson and Stevenson, 1977; Parsons, 1971) and year class strength (Carlander and Payne, 1977; Kempinger and Carline, 1977).

When a weak year class of forage fish species is produced (Knight, Margraf and Carline, 1984; Forney, 1976; Maloney and Johnson, 1965) or if the forage rapidly grows out of the size range consumed by YOY walleye (Parsons, 1971; Johnson, 1969), YOY growth declines due to lower metabolic conversion efficiency of ingested non-fish dietary items (Forney, 1966).

Ultimate year class strength of walleye is often determined by length attained by the end of the first growing season (Forney, 1966). Smaller fish accrue higher mortality to predation and often lack sufficient energy reserves to survive until spring (Newburg and Schupp, 1986; Adams, McLean and Huffman, 1982). Forney (1976) showed that an apparent increase in mean size of young walleye was attributable to differential mortality of the smallest individuals.

Forage abundance may become limiting before the end of the growing season (Knight, Margraf and Carline, 1984; Forney, 1966; Maloney and Johnson, 1965). Populations facing a food shortage often consume a greater variety of food items than do populations with unlimited food supplies (Werner and Hall, 1974; Nikolskii, 1962; Ivlev, 1961). The number of non-fish prey items in the diet of YOY walleye increased from 2.36% in July to 25.00% in August (Fig. 24). Whether this event impacted growth is doubtful since the fish component of walleye diets decreased by a mere 5.1% from

99.8% in July to 94.7% fish in August.

Henderson Lake supports vast cyprinid populations. Seine hauls of 10,000 fish were not uncommon. Crepuscular feeding habits of adult walleye may preclude minnows serving as prey. Northern pike and walleye in Minnesota fed mostly on yellow perch even when minnows and small centrarchids were common (Seaburg and Moyle, 1964). Blacknose shiner behaviour and distribution were attributed to an avoidance of predation by bass and pike (Black, 1945). YOY walleye in Lake Erie have been noted to eat shiners in spring (Knight, Margraf and Carline, 1984). Parsons (1972) reported YOY walleye consumption of YOY yellow perch was far greater than that of shiners in Lake Erie. Hofman (1972) and Forney (1974) showed yellow perch to be the dominant prey item over all other fish species present.

Yet in Henderson Lake YOY walleye diets in August contained 8.64% shiners and 4.98% insects by weight (Fig. 24). These increases may be a result of limited availability of YOY perch or superabundance of shiners and insects. Maloney and Johnson (1965) noted an increase in invertebrate content in August YOY walleye diets in Lake Winnibigoshish, Minn., attributing it to perch growing out of the size range of preferentially consumed by walleye. Mean total length of perch recovered from Henderson Lake YOY walleye stomachs was 25.64 ± 3.68mm in July and 44.29 ± 4.39mm in August, 1986. YOY perch in 1984 were 30mm in early July and 45mm in mid August (Trimble, 1988). These data make it doubtful that YOY perch availability was limiting growth. The enormous densities of shiners and the

even year pulse of mayfly abundance (Ritchie and Colby, 1988) can easily account for these shifts in prey selection by YOY walleye.

Walleye of the size range sampled in this study, preferred fish. The same is true of a major portion of YOY walleye diets in other waters: 94.7-99.8% fish in this study; 82.6% in Lake Winnebago, Wisc. (Preigel, 1970); 88% in Lake Gobebic, Mich. (Eschmeyer, 1950); 98.9% in Lake des Mille Lacs, Minn. and $\geq$99% in Lake Winnibigoshish, Minn. (Maloney and Johnson, 1965); 70.2% in Lake Vermillion, Minn, (Dobie, 1966); 92.9% (Raney and Lachner, 1942) and 86.3% (Hofmann, 1972) in Oneida Lake, N.Y.; 99% (Price, 1963 after Parsons, 1971) and 100% (Knight, Margraf and Carline, 1984) in Lake Erie, Ont.; 97% in Lac La Ronge, Sask. (Rawson, 1957) and 99% in Lake of the Woods, Minn. (Swenson and Smith, 1976).

Growth of Henderson Lake YOY walleye in late July and late August was greater than for any other locality reported in the literature with the exception of Lake Erie (Parsons, 1972) in 1959 (Table 21). Rapid growth was probably due to warm spring temperatures in 1986 (Fig. 28), but good growth was also shown by YOY walleye from the cool spring of 1985 indicating fast growth may be a result of reduced competition, reduced threat of cannibalism from older age classes and an abundance of forage. Walleye growth rate increases in Lake Erie during the 1950's were attributed to 1) extirpation of a major competitor, the blue pike (Stizostedion viteum glaucum), 2) reduction of walleye (less intraspecific competition) and 3) superabundance of forage

Table 21. Young of the year walleye growth from Henderson Lake and other waters.
All values represent total length (mm)

Water	Study	Date	June		July		August		September	
Henderson Lake	Present study,1988	1986				99.6	127.2			
Ontario		1985				85.1	95.5		139.6	
Savanne Lake	Colby, pers.comm.	1986				87.6	117.8			
Ontario		1985				48.5	80.8	106.0		
		1984			54.0	75.8	80.9			
		1983			60.8	76.0			117.9	
		1982		23.9	35.8	65.5	99.4	111.7		
		1981		33.3	50.4	86.5	87.2	101.7		
		1980			54.9	90.0	107.2	103.9		
		1979			40.5	62.5	78.8	95.8		
		1977			69.1	79.3	107.7	112.4		
		1976			68.8	91.6	115.1	116.5		
		1975			58.2	86.4	108.0	116.0		
		1974			39.5	64.0	100.6	120.3	102.3	
		1973			40.0	57.5	79.3	110.0		90
		1972			70.3	94.9	112.5	117.4		
Peterkin Lake	Colby, pers.comm.	1973			39.8	61.0	73.8	86.2		
Ontario										
Oneida Lake	Forney, 1966	1964			50		90		125	
New York		1963			46		84		118	

Table 21. Continued.

Water	Study	Date	June		July		August		September	
Oneida Lake New York	Forney, 1966	1962			64		108		135	
		1961			40		87		124	
		1960			48		95		131	
		1959			58		102		143	
		1958			36		73		103	
		1957			55		101		138	
		1956			42		76		112	
Oneida Lake New York	Raney and Lachner, 1942	1940			48	56	82	99	117	127
Winnibogoshish Minnesota	Johnson,	1969			49	67	102		.123	
Winnibigoshish Minnesota	Maloney and	1954			67	84-92	102-105	113-118		
L. Mille Lacs Minnesota	Johnson, 1965	1954			61	69-92	102-115	113-136		
Lake Erie Ontario	Parsons, 1972	1959	64		108		154			215
Lac LaRonge Sasketchewan	Rawson, 1957	1950-56	24.2		59		94			
Lake Gogebic Michigan	Eschmeyer, 1950	1941	38		65		103			
		1947			31	59	85	99		116
Clear Lake Iowa	Carlander, English and Erickson, 1950 (after Preigel, 1969)		. 41		58		104			124

Table 21. Continued.

Water	Study	Date	June		July		August		September	
Lake Winnebago	Preigel, 1970	1967					74		92	
Wisconsin		1966					104		116	
		1965					81		113	
		1964					88		108	
		1962					100		115	
		1961					79		108	
		1960					66		83	
		1959					91		148	
		Mean		37.4	51.5	75.5	92.8	111.7	118.6	130.3
		n		6	28	25	38	22	21	6

(Wolfert, 1977). The stunted Henderson Lake perch were vulnerable to YOY walleye for a longer period (Ritchie, 1984; Wahtola, Miller and Owen, 1972). Perch abundance would also play a role in reducing predation by both older walleye (Chevalier, 1973) and pike (Lyons, 1984) on younger walleye (Forney, 1974; Johnson, 1969).

Feeding Behaviour

Adult walleye make crepuscular feeding forays into shallow water in inverse proportion to ambient subsurface illumination (Ali, Ryder and Anctil, 1977). The reflective epithelial lining of the eye, the tapetum lucidum, is well developed in the walleye (Zyznar and Ali, 1975). This allows walleye to exploit low light levels for feeding activity (Craig, 1987).

Walleye larvae are photopositive during the pelagic planktivorous stage of development (Houde and Forney, 1970). Phototaxis of young walleye changes from positive to negative which is acquired before the second year of life (Ryder, 1977). This coincides with a dietary shift from plankton to fish, at the post-larval stage (≥ 3cm). These fish then move from shallow to deep water (Raney and Lachner, 1942). Johnson (1969) suggested this movement may be a result of decreased tolerance to warm surface waters.

Henderson Lake YOY walleye feeding activity was inversely proportional to surface illumination by late July (Fig. 25). Walleye greater than 10mm were found at depths of 1.8m to 3.7m in

Clear Lake (Noble,1972). Johnson (1969) stated that fingerling walleye were found at a depth of 0.61m to 0.92m during mid July (33 to 49mm TL), 1.23m to 1.84m in late July and early August (~67mm TL) and 1.23m to 4.3m in mid August (102mm TL). Higher catches in deeper water in August in Henderson (Fig. 27) support Johnson's findings but may have been an artifact of non-standardized effort.

YOY walleye seined in 1985 suggested that smaller YOY are less photonegative and so feed in full daylight (Fig. 23). There is also a possibility that some sort of social hierarchy might be operating. However comprehensive sampling in 1986 did not support these data (Fig. 27) and these hypotheses were rejected. Johnson (1969) also found no segregation of sizes related to depths.

Community Dynamics

Although walleye production is increased at reduced abundance, a minimum walleye stock may be required to keep prey (yellow perch) abundance in check (Forney, 1980). Failure to ensure this safeguard coupled with rapid expansion of prey density may cause "shifts in species abundance which would be difficult to reverse".

Perhaps Henderson Lake has provided the scenario to test this hypothesis. Walleye year class recruitment failed from 1980 to 1984, while the adult population waned. Perch recruitment, phenomenal in 1981, was low in 1982 and 1983, improving in 1984

and becoming significant (25% of 1981) in 1985 (Trimble, 1988). With this scenario, the potential for dietary competition between YOY walleye and adult perch developed. This is indicated by Schoener (1970) indices of dietary overlap comparing adult perch from 1981 (good perch year) and 1982 (poor perch year). Two species sharing greater than 25% (frequency of occurrence) of their dietary components are assumed to be potential competitors (Johnson, 1977).

Bulkley, Spykermann and Inmon (1976) found very little overlap between pelagic larvae of walleye, yellow perch and spottail shiners. Each fish species concentrated on different plankters reducing competition. Knight, Margraf and Carline (1984) used Schoener's index to compare Lake Erie YOY walleye with yellow perch from 150-199mm TL and 200-290mm TL size classes. Stunted perch in Henderson Lake however never attain 200mm. Lake Erie perch of 150-199mm TL compared with Lake Erie YOY walleye were found to have 27% overlap. Values from Henderson Lake ranged from 9.60% to 32.66% over this size range (Table 16). These values vary if perch become more cannibalistic (piscivorous) or if walleye begin to rely heavily on invertebrates.

Could increases in perch abundance threaten walleye recruitment and hence inhibit reestablishment of the walleye population as a dominant piscivore in Henderson Lake? The production of successful walleye year classes in 1985 and 1986, particularly in light of the impressive growth rate of 1986 YOY walleye (Table 21), seems to refute Forney's hypothesis. When

walleye abundance increases, increased predation on perch will reduce perch density. How far the walleye-perch predator prey pendulum will swing before establishing a stable mean, and to what extent pike will play a role remains open to speculation. If undisturbed after a period of experimental removal species compositions eventually reestablish themselves to original proportions (Moyle, 1949; Johnson 1948).

Johnson (1977) suggests that an increase in perch abundance might increase competition with suckers for invertebrate prey items. However, no change in Henderson Lake suckers growth has been observed (Fig. 18).

The Henderson Lake fish community may require a more lengthly recovery period than originally conceived in order to reestablish proportions and densities of fish stocks present before exploitation. If the objective of a pulse fishery management scheme is to reharvest walleye again before preexploitation conditions are reestablished (ie. in order to maintain maximum intrinsic rate of population growth) then this time would be shortened.

Younger, subordinate walleye are not as amenable to the trap net gear at high population densities. Because of walleye behaviour, the Schumacher-Eschmeyer population estimates misrepresented the actual population density. During the early phases of walleye removal a sizable portion of the walleye population was therefore not measured by the Schumacher-Eschmeyer population estimates. This lead to an underestimate of population density. Removal of a large percentage of the estimated walleye

present did not result in a large change in the subsequent Schumacher-Eschmeyer population estimate since the reserve of walleye previously missed by the population estimate replaced the removed fish. Successive removals eventually exhausted this reserve causing the population density to appear to abruptly collapse. By underestimating population size, the Schumacher-Eschmeyer population estimates misled researchers into increasing fishing mortality to remove the apparent surplus. This led to a gross overharvest (90% of adults) of the walleye stock (Nunan, 1982; Reid, 1985).

In the current study trap nets and gill nets were used for walleye removal. A pulse fishery based on angling would not impact the population to this extent. Had the stock collapse been forestalled walleye may have had normal recruitment. The presence of young walleye would have kept the perch numbers in check and perhaps the pike response may have never occurred. Any hindrance of walleye stock recovery caused by the pike expansion would also have been mitigated.

There is also a distinct possibility that the increase in pike production may be, at least in part, a natural cycle unrelated to the walleye removal. The concurrent declines of both sucker and pike abundance from 1979 to 1983 indicate other population density control mechanisms were operating. The sudden disappearance of over one half of the pike population from 1980 to 1981 and all pike age eight and over by 1982 is baffling. The pike population may be simply rebounding to previous densities and not responding to manipulations of the walleye population and

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the subsequent enhanced forage availability. This could easily account for the increased recruitment and increased growth of older pike. If this is the case then it is very unlikely that the observed increase in pike production will hinder the rate nor the end point of the walleye recovery.

Management Implications

Since it reduces management costs in several key areas, pulse fishing may be economical to implement. Since rotational lake closures are part of the pulse fishing scheme, manpower requirements are reduced since it is necessary to measure exploitation rates on only one lake at a time for an immediate management decision. Furthermore only the currently exploited population requires close scrutiny to ascertain stock resilience and thus any necessity of a decision for fishery closure. Lakes closed to allow for stock recovery do not require sampling for at least the minimum recovery time (eg five years) and then only periodically thereafter.

Assessing the feasibility of pulse fishing as an alternative management strategy requires (1) accurate stock assessment and (2) determination of the closure period for the fishery with establishment of a minimum or mean recovery period for each species or lake type.

Predicting imminent stock collapse proved to be more complex than first imagined due to faulty population assessment

with the Schumacher-Eshmeyer method. Reid and Momot (1985) concluded annual production, Petersen population estimates, growth of young fish (when present) and Abrosov's index of mean age to maturity provided the best criteria. Poor indices of stock abundance include catch per unit effort data, Schumacher-Eschmeyer population estimates, condition factors and fecundity increases.

Establishment of a minimum recovery period has also been fraught with unforseen complications. Recruitment failure postponed any hope of walleye recovery for five years. Whether increases in pike and perch abundance is a response to the long vacated walleye niche requires further study. Because of faulty Schumacher-Eschmeyer estimates walleye were reduced to extremely low densities far below what would normally occur in a pulse fishery. Thus the main difficulty lay in the initial assessment of stock size rather than with the idea of "fallow" period following harvest. Had the walleye continued to recruit normally the status of the pike and perch may have been much different.

Interspecific interactions exhibited considerable and unpredictable time lags in the community dynamics of Henderson Lake. Brevity of growing season and interdependence of perch and walleye, and perch and pike may have contributed to these delays.

Still unresolved is the abrupt disappearance of the stickleback population. Its cause, and any effect of their absence on the Henderson Lake fish community may never be known. Fish communities in unfished lakes are certainly not as stable as theorists presuppose.

Another important matter is whether pulse fishing necessarily improves biomass yield over time. Economic benefits may justify slight losses in yield. However the scope of this question is too broad to be dealt with here.

Potential problems can arise with a pulse fishing scheme. The applicability of pulse fishing as a viable alternative management strategem will have to consider the possibility of complete stock collapse, recruitment failures, time lags in the community dynamics and possible interspecific suppression of recovery. It is not the intention of this study to either endorse or abrogate pulse fishing as a feasible management tool. That is a decision for fishery managers. Hopefully, results accrued from this investigation will help formulate an informed management policy.

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Appendices

Appendix A.   Table 1. Backcalculated lengths at annulus formation from scales for Henderson Lake northern pike 1985, 1986.

Northern pike 1985

Age	1	2	3	4	5	6	7	8	9	10	11	12	13
1	295.15												
2	287.12	474.21											
3	285.22	470.38	565.90										
4	302.82	449.17	554.74	610.78									
5	246.58	389.46	523.11	600.95	654.29								
6	262.15	399.65	505.56	564.47	608.37	632.18							
7	273.01	414.53	525.82	588.11	625.62	648.50	662.58						
8	261.21	383.92	485.42	552.03	591.83	627.22	654.96	672.62					
9	253.19	407.94	526.96	578.68	614.45	633.81	657.81	682.21	694.87				
10	245.51	374.37	496.65	546.13	587.37	619.40	643.10	655.07	672.45	680.32			
11	---	---	---	---	---	---	---	---	---	---	---		
12	---	---	---	---	---	---	---	---	---	---	---	---	
13	299.49	469.30	593.39	622.94	944.34	659.81	678.65	698.07	724.24	736.92	767.16	786.00	796.00

Age	1	2	3	4	5	6	7	8	9	10	11	12	13
Mean	278.71	439.50	534.88	583.22	618.19	636.00	658.36	676.51	692.88	694.47	767.16	786.00	796.00
n	190	173	127	91	74	62	47	30	19	4	1	1	1

Northern pike 1986

Age	1	2	3	4	5	6	7	8	9	10	11
1	332.81										
2	262.49	435.48									
3	285.11	473.41	565.39								
4	305.08	495.15	598.15	645.26							
5	295.05	471.56	581.59	643.09	680.77						
6	286.12	455.60	555.94	612.66	651.44	677.30					
7	295.27	446.44	569.22	630.1	668.00	690.54	721.65				
8	285.21	434.26	550.04	621.34	658.70	683.44	711.41	726.77			
9	267.88	430.59	555.84	606.70	650.60	682.94	713.92	738.43	755.88		
10	286.39	384.98	479.85	531.04	601.19	654.51	699.88	719.23	741.73	759.52	
11	328.45	411.73	487.45	553.79	585.50	605.66	621.65	634.90	641.06	653.45	664.43

Age	1	2	3	4	5	6	7	8	9	10	11
Mean	281.13	453.59	566.85	626.09	661.20	683.66	713.74	725.83	741.57	724.16	664.43
n	239	238	161	111	92	71	47	27	10	3	1

Appendix A.   Table 2. Backcalculated lengths at annulus formation from scales for Henderson Lake suckers 1985, 1986.

Suckers 1985

Age	1	2	3	4	5	6	7	8	9	10
1	60.95									
2	54.05	145.47								
3	52.46	145.47	235.10							
4	52.46	138.38	230.44	298.87						
5	46.99	130.32	232.76	311.06	365.04					
6	50.40	152.93	267.74	333.62	379.93	415.72				
7	44.26	120.30	265.07	347.23	407.48	464.05	492.75			
8	43.38	131.63	235.10	330.30	403.43	445.86	478.19	497.70		
9	47.47	141.17	223.63	323.76	387.61	419.89	459.44	487.85	502.70	
10	32.46	165.67	254.68	314.19	387.61	424.11	454.86	482.99	512.86	533.79

Age	1	2	3	4	5	6	7	8	9	10
Mean	52.46	141.17	235.10	428.38	473.43	487.85	507.76	489.10	506.09	533.79
n	85	74	59	43	20	11	6	4	3	1

Suckers 1986

Age	1	2	3	4	5	6	7	8	9	10	11	12	13
1	54.60												
2	60.95	130.32											
3	70.81	142.59	225.88										
4	54.05	131.63	221.41	307.97									
5	55.70	131.63	221.41	301.87	372.41								
6	58.56	145.47	252.14	336.97	395.44	437.03							
7	49.90	151.41	262.43	333.62	387.61	424.11	450.34						
8	54.05	121.51	217.02	304.90	376.15	424.11	454.86	473.43					
9	---	---	---	---	---	---	---	---	---				
10	47.94	117.92	210.61	307.97	395.44	464.05	502.70	528.48	539.15	555.57			
11	43.38	111.05	200.34	292.95	372.41	424.11	464.05	487.85	507.76	528.48	544.57		
12	---	---	---	---	---	---	---	---	---	---	---	---	
13	88.23	142.59	204.38	278.66	333.62	391.51	437.03	478.19	502.70	518.01	528.48	544.57	555.57

Age	1	2	3	4	5	6	7	8	9	10	11	12	13
Mean	56.83	137.00	232.76	317.35	383.75	432.68	454.86	487.85	518.01	533.79	539.15	544.57	555.57
n	86	84	75	67	60	36	21	9	5	5	3	1	1

Appendix B. Henderson Lake spring water temperatures

Date		1979	1980	1981	1982	1983	1984	1985	1986
April	20		4.2						
	23								5.2
	24								6.8
	25								6.3
	26								7.2
	27								7.0
	28								7.3
	29								7.3
	30		11.0						8.0
May	1		12.5				4.0		7.8
	2		13.0					8.2	7.2
	3		15.3				6.3	9.0	8.3
	4		15.7				7.0	9.3	10.0
	5		13.9				7.0	8.5	9.8
	6		12.3				7.5	9.6	9.8
	7		9.8				7.5	10.3	9.7
	8		9.2				7.0	10.5	9.0
	9		9.4				6.8	12.1	9.3
	10		8.5				7.5	13.1	9.9
	11		9.2					12.6	10.0
	12		9.7			10.0		13.6	10.4
	13		9.3			10.0		13.0	11.9
	14		9.5		9.3	9.5	9.5	13.5	12.5
	15		11.4		11.0	9.5	10.0	12.3	14.3
	16		12.1			9.5	11.5	12.1	15.1
	17	10.0			11.8	10.0	11.8	12.0	14.9
	18	9.5			11.0	10.5	12.5	13.0	13.9
	19						12.8	13.0	
	20	9.5		15.5			12.0	12.9	
	21	10.0	15.4	15.0	11.3		11.8	12.8	
	22	10.5	16.9	15.0	13.0		12.5	13.5	14.2
	23		19.0	14.0	14.0	12.0	12.5	15.3	15.1
	24	12.8	20.3	15.5	14.0	12.0	12.8	16.9	15.9
	25	14.4	19.3		14.0	11.0		16.5	17.2
	26			14.5		12.5		16.1	18.7
	27			16.0		12.5		15.3	19.2
	28	18.5		17.0		12.0			21.3
	29	15.9				11.0			22.8
	30					11.8	14.8		
	31	15.5				11.5	14.3		
June	1	16.0				13.0			
	2						16.3		
	3				16.0		17.3		
	4	16.0	17.3	16.3	16.0		15.3		
	5	18.3		16.3			15.8		
	6	14.7		17.0		13.5	16.3		
	7	16.3	17.0	17.5		13.0			
	8	16.3	17.8	17.0		13.0			

Appendix B. Continued

Date		1979	1980	1981	1982	1983	1984	1985	1986
June	9			17.0		12.0			
	10		16.3	17.0		12.5			
	11	19.3	15.8			14.0			
	12	18.7				15.5		15.3	
	13	18.2				16.5		15.8	
	14	19.2				17.0	16.8	16.8	
	15	20.3				17.3		18.0	
	16							17.5	
	17		17.4					17.0	
	18		17.9					16.0	
	19	19.8	19.8				19.3	15.8	
	20	19.8			16.8			16.5	
	21	18.3			17.0	19.3			
	22	17.1			16.3	19.8			
	23			19.0		22.5			
	24			17.5		21.5			
	25			17.0		21.3			
	26			19.0		22.3			
	27			18.0		19.8	18.5		
	28					20.0	17.8	16.3	
	29					20.5	20.0		
	30		19.9			20.0	19.2	17.2	
July	1		19.0			20.0	21.5	18.5	

Data compiled from: Nunan and Romani (unpublished) 1979 - 1981

Ritchie (1984) 1981 - 1982

Reid (1985) 1982 - 1984

Appendix D. Summary of 1986 Henderson Lake YOY walleye diet analyses.

Prey category	Percent Occurence			Percent by number			Percent by weight			Mean % weight / stomach		
	July	August	Pooled	July	August	Pooled	July	August	Pooled	July	August	Pooled
Fish remains	42.55	52.94	47.96	26.44	33.33	29.82	15.48	28.78	23.24	34.25	47.05	40.91
YOY perch	68.09	25.49	45.92	68.97	17.86	43.86	84.31	57.27	68.52	65.45	24.28	44.03
Shiner	--	7.84	4.08	--	19.05	9.36	--	8.64	5.04	--	6.50	3.38
Burr mayfly	2.13	25.49	14.29	1.15	16.67	8.77	0.12	4.19	2.49	0.19	17.98	9.45
Diptera larvae	2.13	1.96	2.04	1.15	4.76	2.92	0.02	0.66	0.39	0.01	1.19	0.62
Aerial insect	--	3.92	2.04	--	2.38	1.17	--	0.05	0.03	--	0.63	0.33
Gyrinus sp.	--	1.96	1.02	--	1.19	0.58	--	0.08	0.05	--	0.05	0.03
Detritus	--	5.88	3.06	--	3.57	1.75	--	0.32	0.19	--	2.10	1.09
Miscellaneous	4.26	1.96	3.06	2.30	1.19	1.75	0.07	0.02	0.04	0.10	0.04	0.07
Fish total	100.00	84.31	91.84	95.40	70.20	83.00	99.79	94.68	96.81	99.70	77.41	88.10
Insect total	4.26	29.41	17.35	2.30	25.00	13.50	0.14	4.98	2.96	0.20	19.84	10.42

Appendix E. Fin clips used to mark walleye, northern pike,
             and white suckers during population estimates
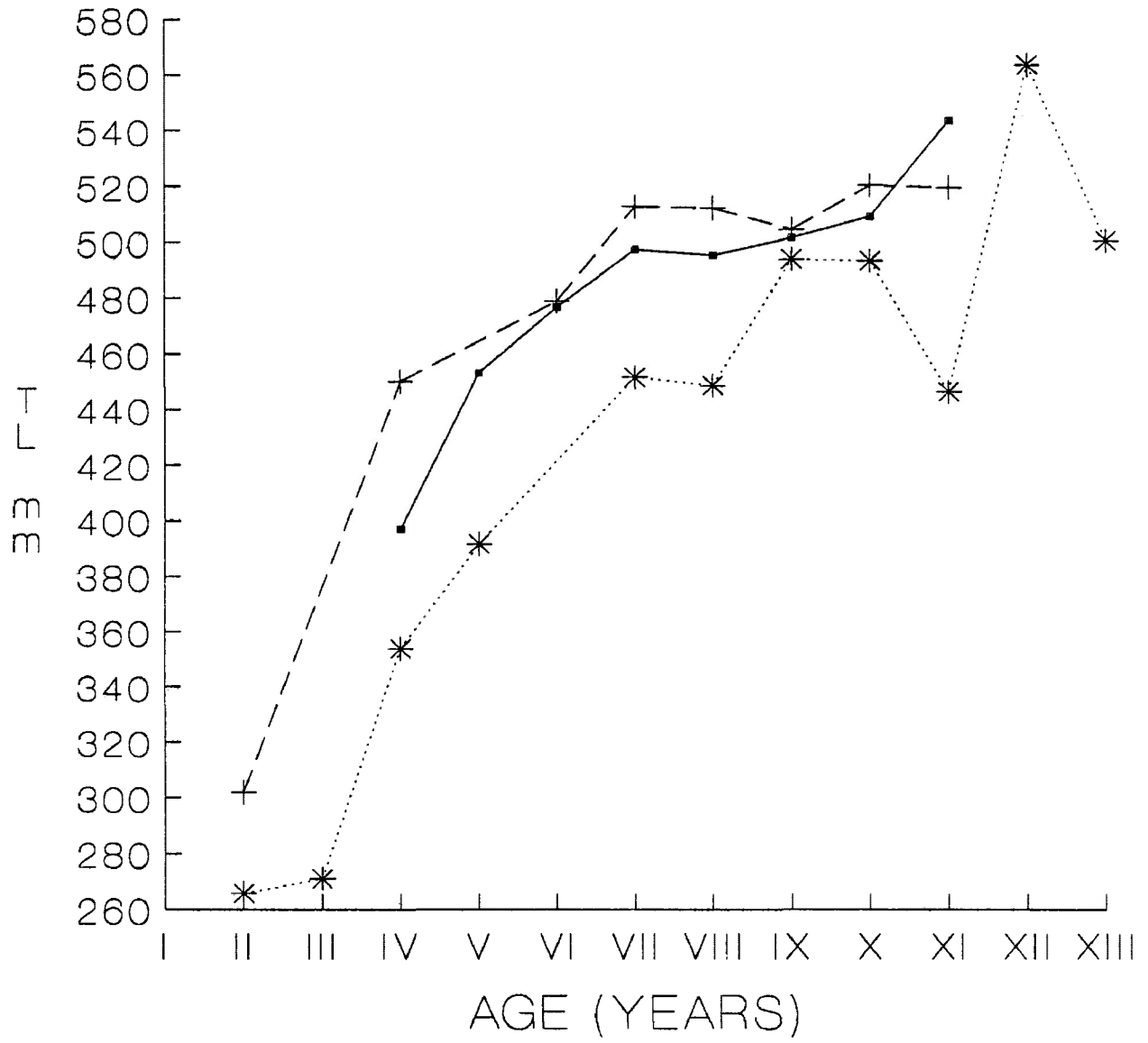   from 1979 to 1986 IN Henderson Lake, Ontario.

Species	Year	First clip	Second clip
Walleye	1979	3rd dorsal spine	
	1980	5th dorsal spine	
	1981	6th dorsal spine	7th dorsal spine
	1982	9th dorsal spine	anal fin
	1983	2nd dorsal spine	left pectoral fin
	1984	4th dorsal spine	
	1985	8th dorsal spine	
	1986	10th dorsal spine	
Pike	1979	left pectoral fin	
	1980	right ventral fin	
	1981	right pectoral fin	anal fin
	1982	left ventral fin	right pectoral fin
	1983	left pectoral fin	lower caudal
	1984	right ventral fin	
	1985	anal fin	
	1986	dorsal fin	
Suckers	1979	left pectoral fin	
	1980	right ventral fin	
	1981	right pectoral fin	
	1982	left ventral fin	anal fin
	1983	right ventral fin	left pectoral
	1984	right pectoral fin	
	1985	anal fin	
	1986	right pectoral	

Appendix F. Mean condition factors ($K = W/TL^3 \times 10^5$) for walleye, northern pike and white suckers in Henderson Lake, Ontario and walleye from Lanigon Lake, Ontario. M = Males, F = Females, C = combined sexes

| Species	Sex	1985 $\overline{X}$	$\pm$ S.D.	n	1986 $\overline{X}$	$\pm$ S.D.	n
Henderson Lake		Northern pike					
	C	0.594	0.077	432	0.607	0.064	523
	M	0.597	0.079	211	0.608	0.061	301
	F	0.616	0.083	52	0.597	0.066	100
		White suckers					
	C	1.166	0.135	139	1.219	0.171	315
	M	1.092	0.091	27	1.130	0.139	92
	F	1.208	0.133	73	1.267	0.161	210
		Walleye from population estimate data					
	C	0.999	0.086	56	1.039	0.083	54
	M	0.938	0.050	10	1.047	0.063	25
	F	1.070	0.026	3	1.044	0.096	21
Walleye from population estimate and gill net data combined							
	C				0.799	0.137	265
	M				1.035	0.091	26
	F				1.015	0.120	24
Lanigon Lake		Walleye					
	C				0.894	0.065	84
	M				0.865	0.060	9
	F				0.878	0.071	20

Appendix G. Mean length at age for walleye in Henderson
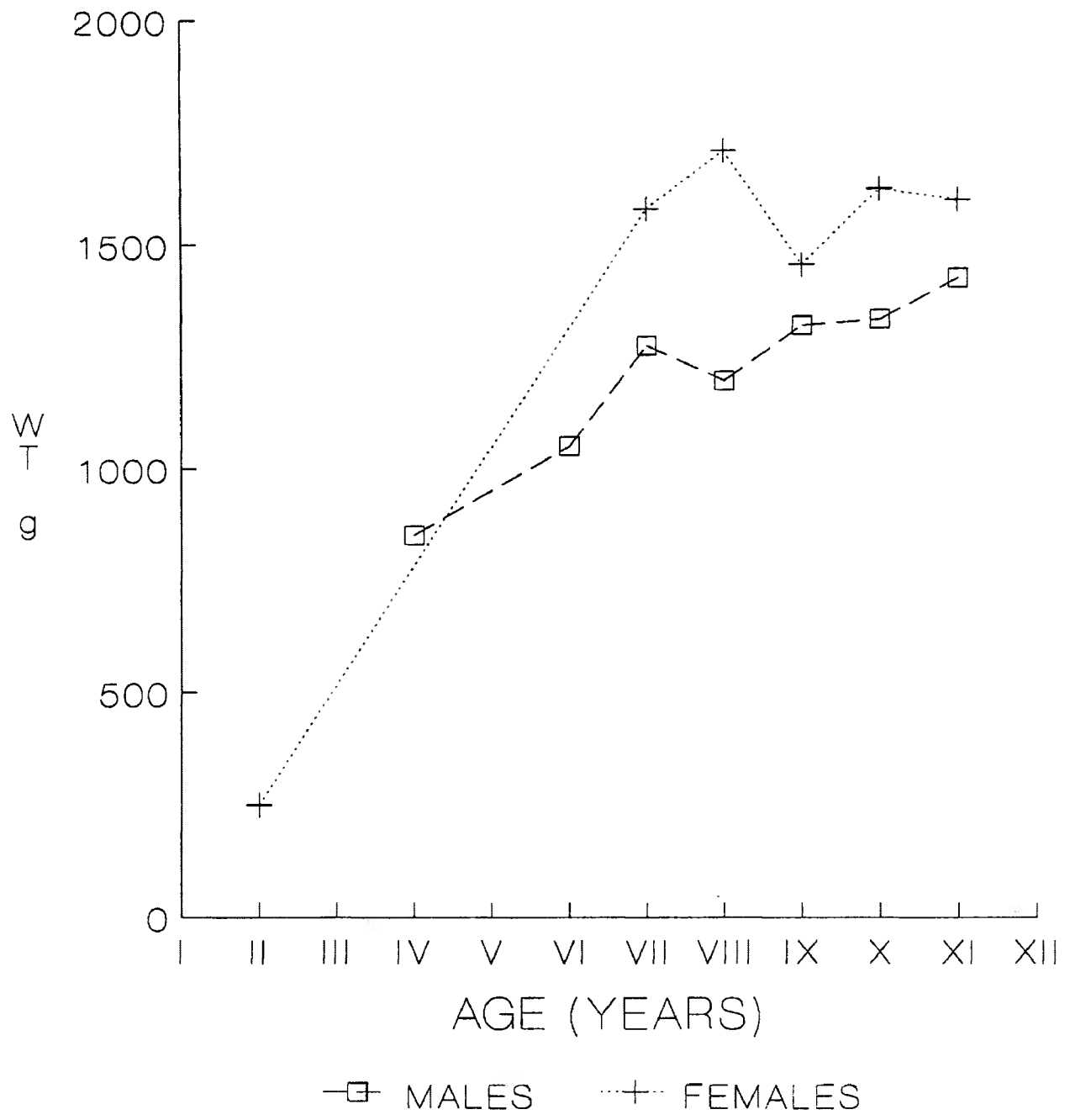   Lake, Ontario, in 1985 and 1986, and Lanigon
          Lake, Ontario in 1986.

HENDERSON 1985   HENDERSON 1986
LANIGON 1986

Appendix H. Mean length at age for male and female walleye
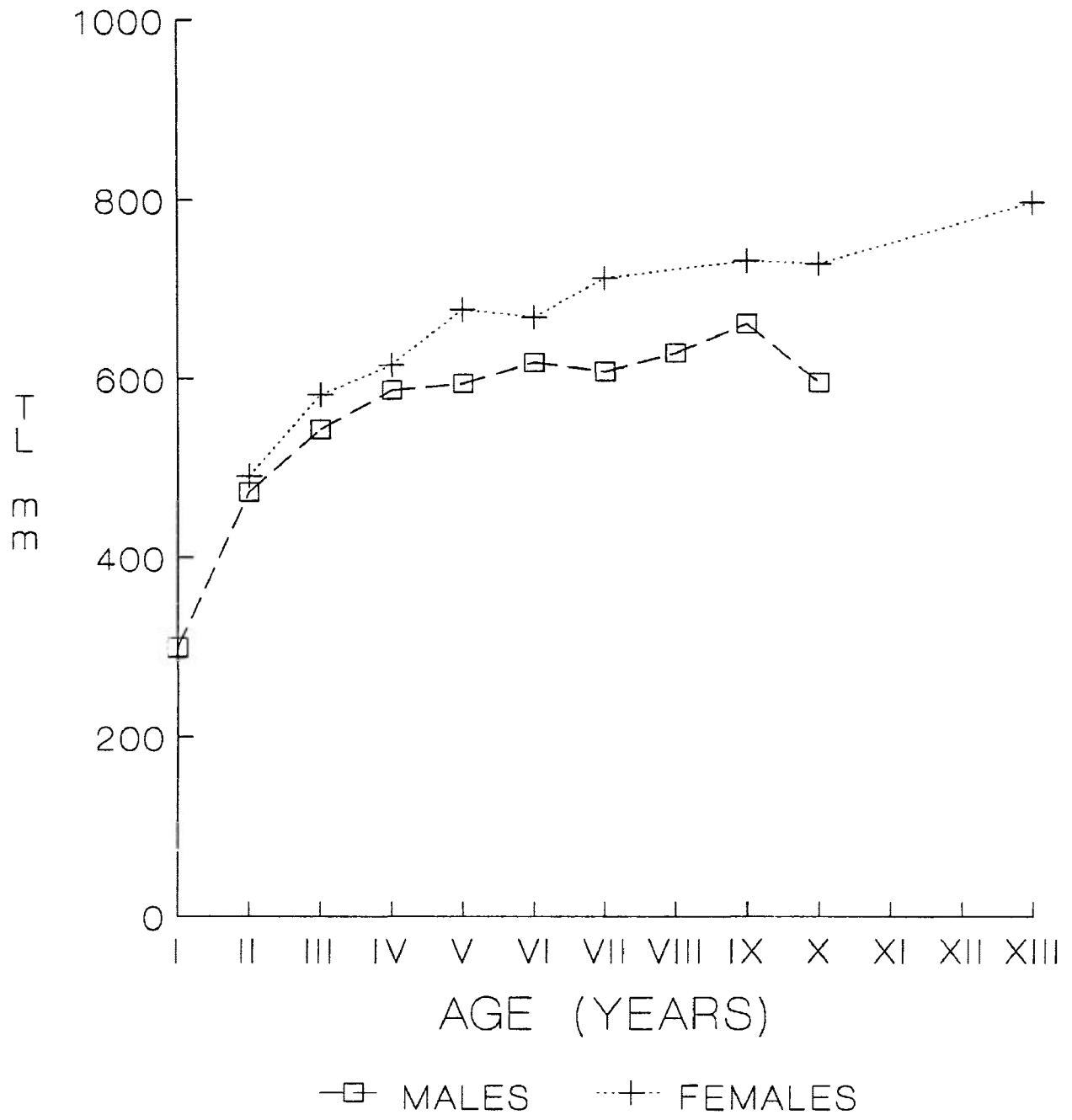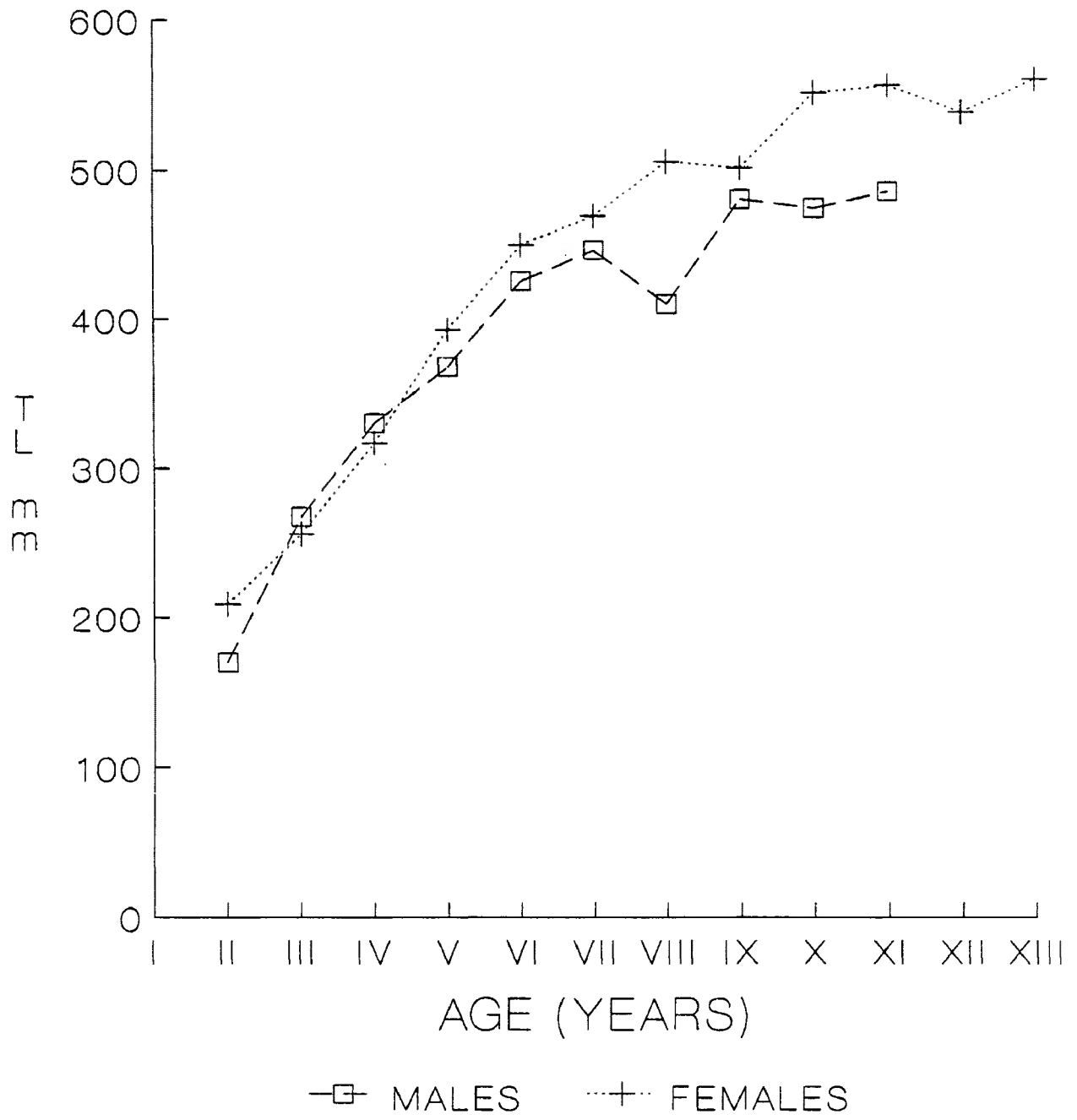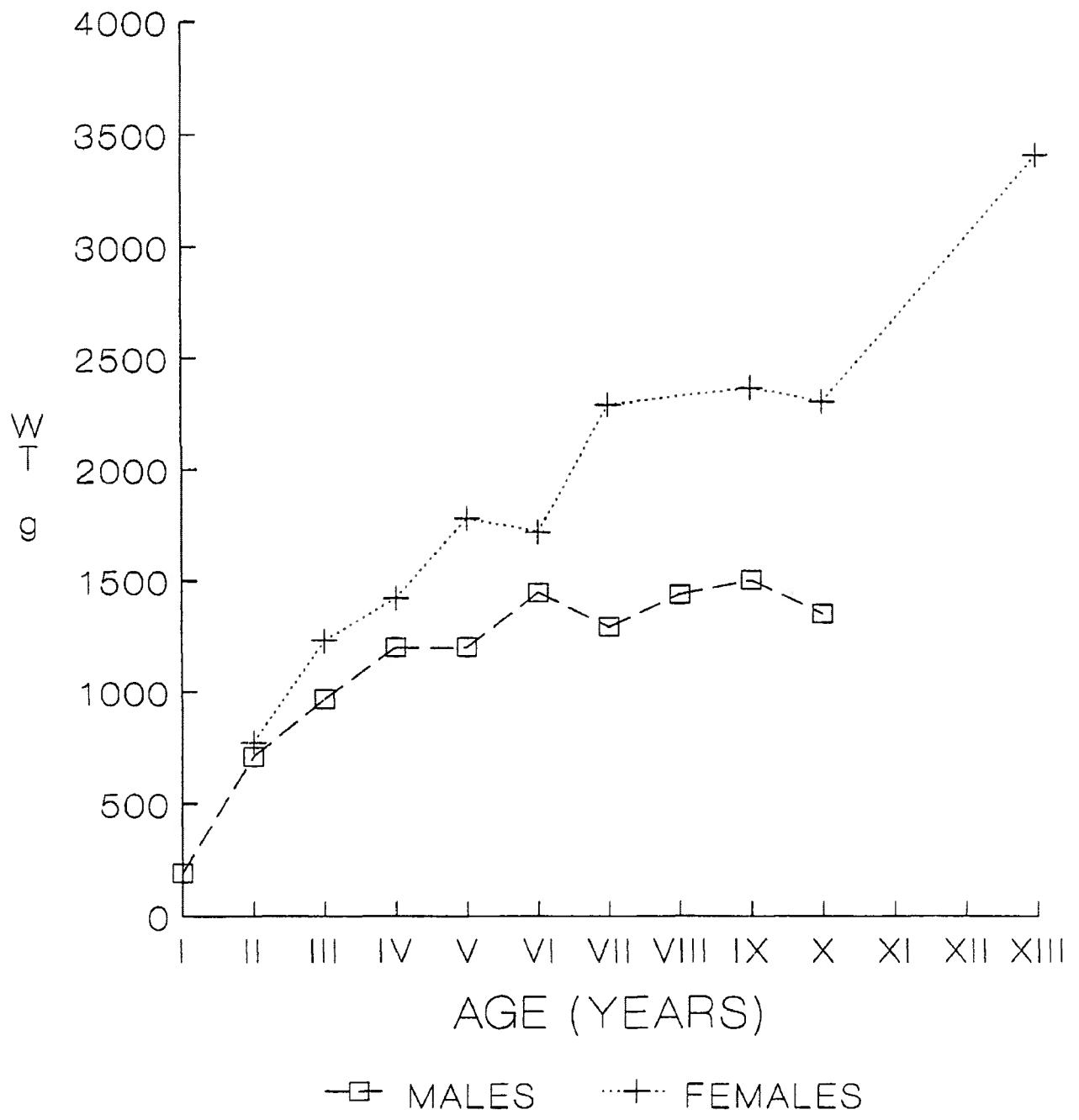in Henderson Lake, Ontario, in 1986.
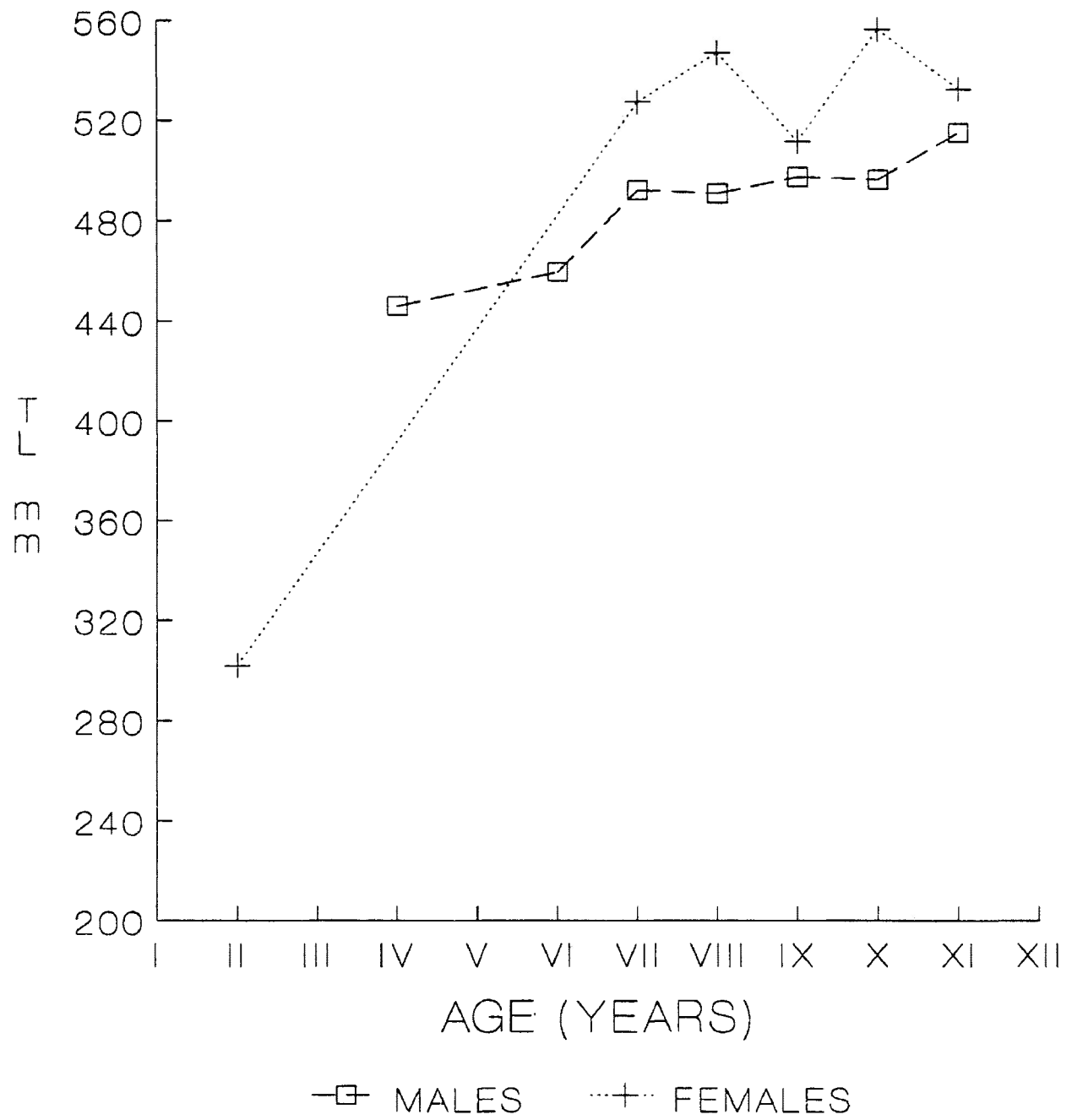
Appendix J. Mean weight at age for male and female walleye in Henderson Lake, Ontario, in 1986.

140

Appendix K. Mean length at age for male and female pike
in Henderson Lake, Ontario, in 1985.

Appendix L. Mean length at age for male and female pike

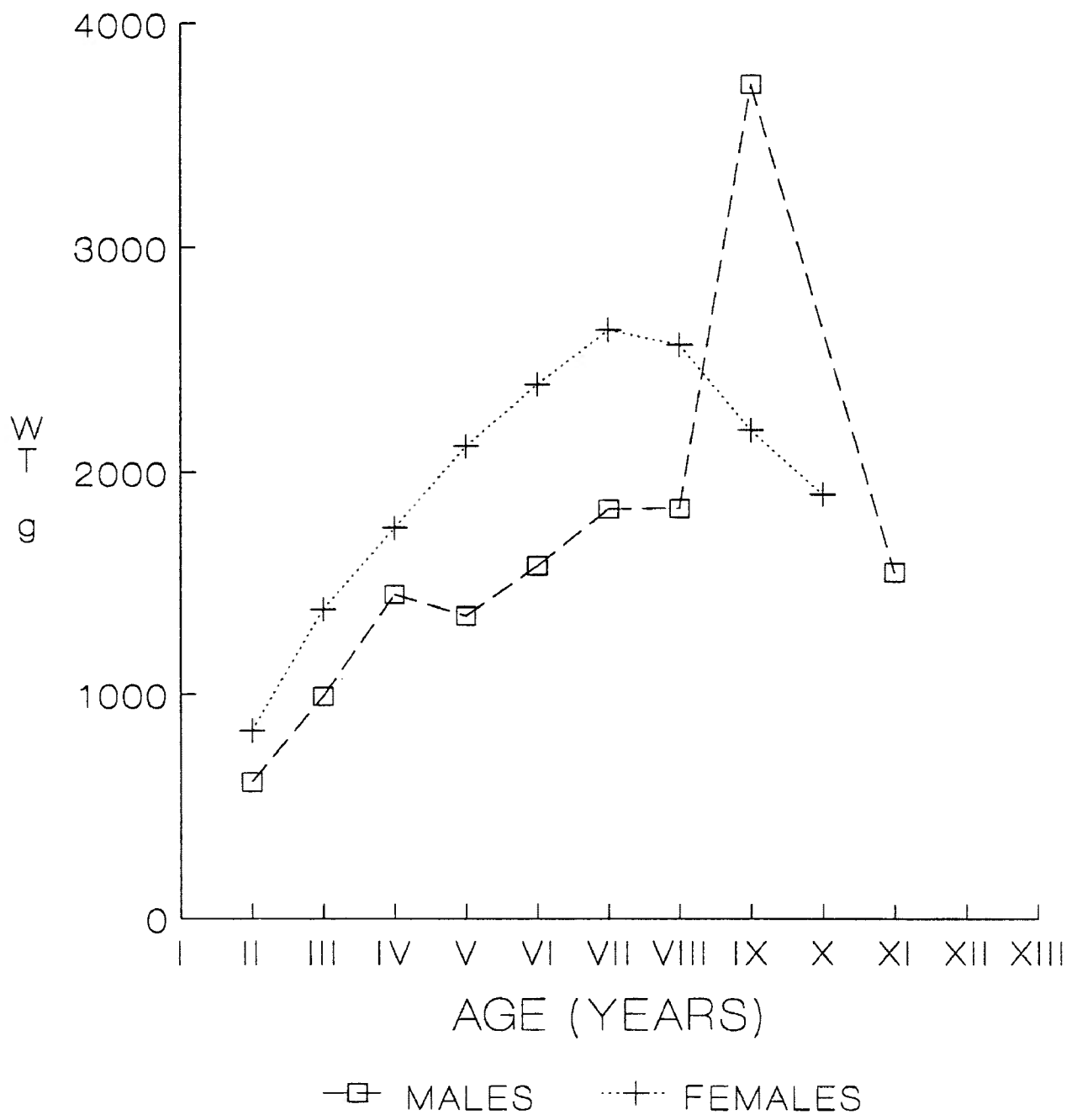in Henderson Lake, Ontario, in 1986.

Appendix M. Mean weight at age for male and female pike
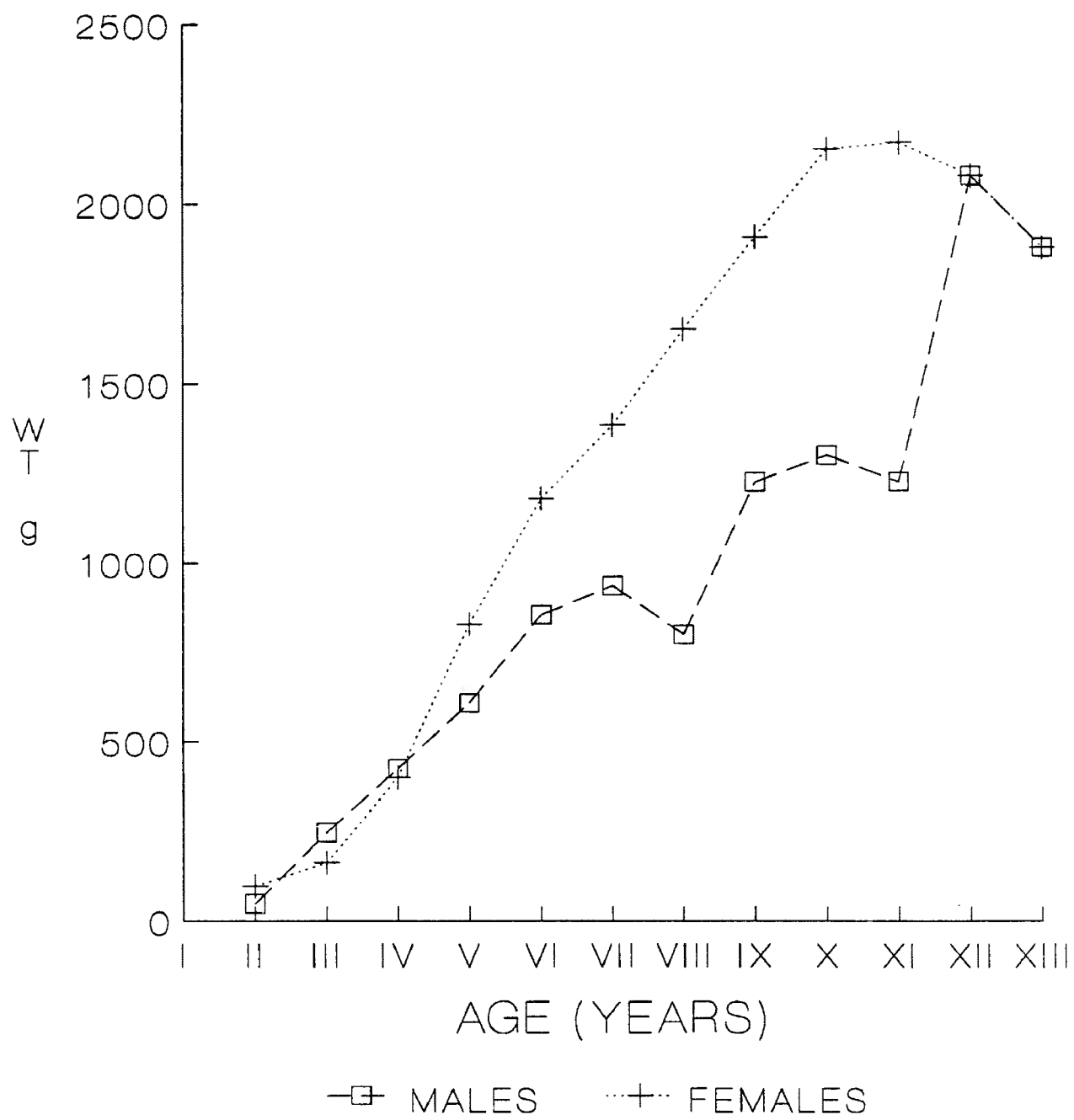in Henderson Lake, Ontario, in 1985.

WT g

4000

3500

3000

2500

2000

1500

1000

500

0

I II III IV V VI VII VIII IX X XI XII XIII
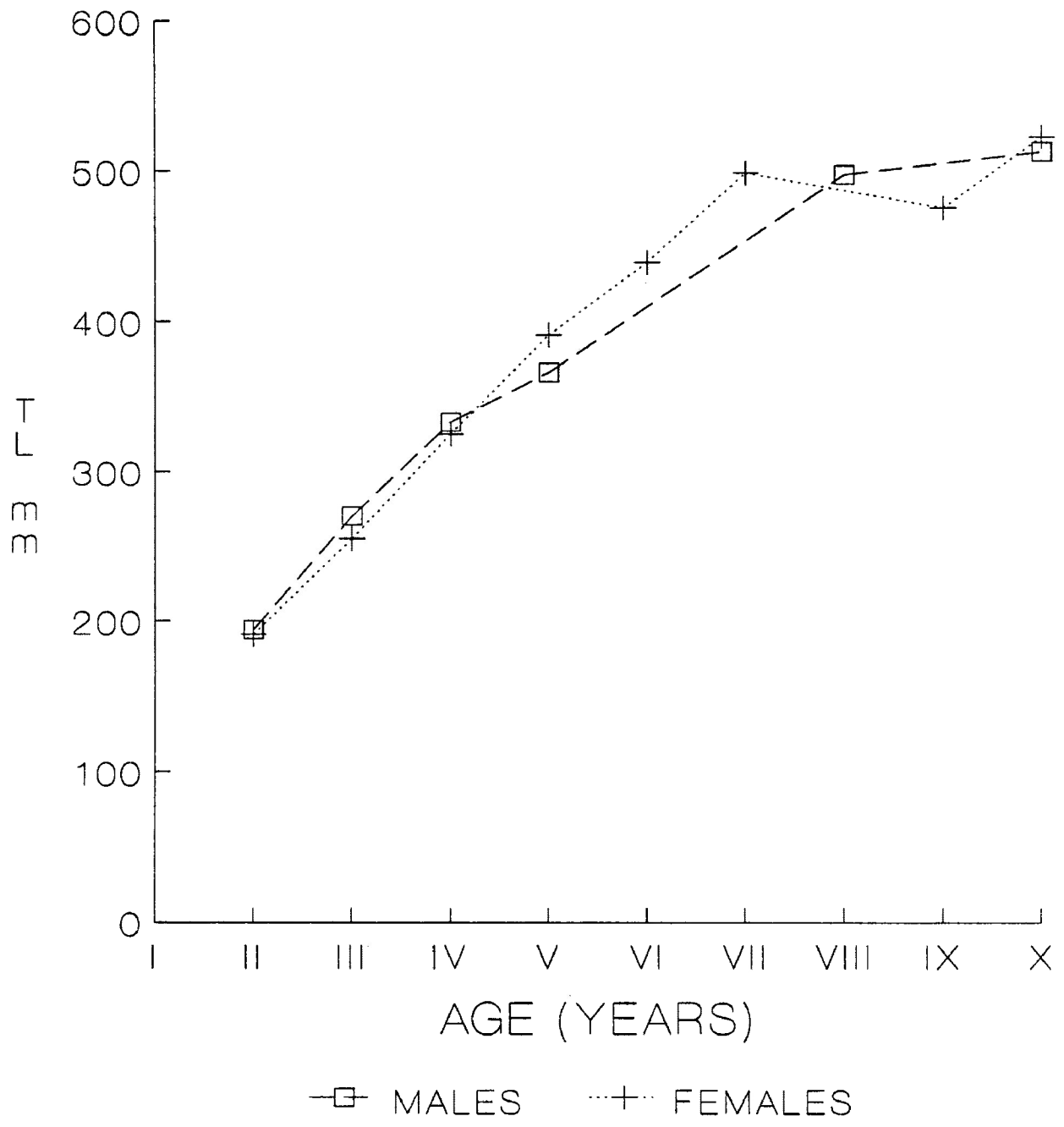
AGE (YEARS)

—□— MALES   ⋯+⋯ FEMALES

Appendix N. Mean weight at age for male and female pike
in Henderson Lake, Ontario, in 1986.

Appendix P. Mean weight at age for male and female suckers in Henderson Lake, Ontario, in 1986.

Appendix Q. Mean length at age for male and female suckers in Henderson Lake, Ontario, in 1985.

Appendix R. Mean length at age for male and female suckers in Henderson Lake, Ontario, in 1986.