


ECOLOGY OF A NORTHERN PIKE (Esox lucius)
POPULATION IN A SMALL, OLIGOTROPHIC LAKE,
WITH COMPARISONS TO OTHER NORTHWESTERN
ONTARIO POPULATIONS

BY
ARNOLD LAINE 

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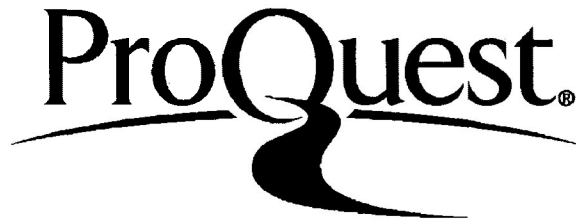
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ABSTRACT

The life history and population dynamics of the northern pike (Esox lucius) within Squeers Lake, Ontario were studied in order to provide information on pike found within oligotrophic lakes. Results clearly demonstrate the Squeers Lake northern pike population is relatively stable but small in size, has a very low production rate, exhibits rapid growth, an early age of maturity and an intermediate life span. The low availability of spawning (and to a lesser extent nursery) habitat apparently regulates population size. The rapid growth may be the result of abundant food, lack of serious competition for food resources and presence of favourable environmental conditions. Epilimnetic summer temperatures (16-21°C) within the main lake basin were very near optimal for "adult" pike (ie 18-20°C, Casselman, 1978), whereas summer temperatures within the Western Arm (which formed the main spawning and nursery area within the lake) were near optimum for young-of-the-year and yearling pike (ie 26°C, Hokansen et al 1973).

To assess accuracy in age and growth assessment for the Squeers Lake northern pike population, the validity of using scales and cleithra was examined. The high percent frequency of agreement, low index of average error (Beamish and Fournier 1981) and index of precision (Chang 1982) indicate both scales and cleithra are equally suitable tissues for assigning age structure to Squeers Lake northern pike provided that marks interpreted as annuli are in fact annually formed. An examination of the accuracy of age estimates through the use of partly known aged fish (via

tetracycline labelling and mark-recapture methods) confirmed that the checks identified on both aging tissues were in fact annuli. Cleithra, were, however, more accurate for northern pike \geq age 10. Therefore, when age estimates are required without killing the fish, the use of scales can be recommended provided that the population is relatively fast growing and precision levels between the two tissues do not exceed 5%.

In order to further determine what factors may influence northern pike growth and population size, the influences of lake morphometry and chemistry on 14 northwestern Ontario populations (including Squeers Lake) were investigated. Northern pike populations found within deep-oligotrophic lakes exhibited low population densities, a superior growth rate, piscivory and were spawning and nursery habitat limited. Northern pike populations from meso-eutrophic lakes had much greater population densities, exhibited much poorer growth rates, were generally opportunistic predators and appeared to be food limited. Northern pike from mesotrophic and shallow-oligotrophic lakes exhibited intermediate population size and growth rates with the maximal individual size of fish from these populations approaching that of northern pike from deep-oligotrophic lakes. With the increased acceptance of individual lake management, a number of management alternatives are proposed.

ACKNOWLEDGEMENTS

I would like to give sincere thanks to my principal academic advisors Dr. Walter Momot and Mr. Phil Ryan for their advise, encouragement, patience and constructive criticism for this project. I am also grateful to Drs. Murray Lankester, George Osborne and E.J. Crossman for being on my academic committee and reviewing my thesis. This research project could not have been completed without the funding and support facilities received from the Quetico-Mille Lacs Fisheries Assessment Unit of the Ontario Ministry of Natural Resources, Lakehead University, and from the NSERC operating grant (A0217) awarded to Dr. W. Momot.

It was through the valued assistance and support by Jon George of the QMLFAU, and my partner in crime on Squeers Lake, Helen Ball, that made this project possible. Also crucial to the completion of this thesis, whether it was in the field, in the lab, at "The Study", angling for pike at night, or some other corner where I forced you to listen to some of my idle speculation was the valued assistance that I received from George Morgan, Bev Ritchie, Kevin and Sue Trimble, Alan Dextrase, Mike Freutel and the many field staff at QMLFAU (1984-1987).

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TABLE OF CONTENTS

Title Page.....	i
Abstract.....	ii
Acknowledgements.....	iv
Table of Contents.....	v
List of Tables.....	vii
List of Figures.....	x
List of Appendices.....	xii
GENERAL INTRODUCTION.....	1
CHAPTER ONE: BIOLOGY OF A NORTHERN PIKE POPULATION WITHIN A SMALL NORTHWESTERN ONTARIO OLIGOTROPHIC LAKE	
INTRODUCTION.....	4
STUDY AREA.....	5
METHODS.....	8
Spring Population Estimates.....	8
Monthly Index Netting Program.....	10
Young-of-the-year Collections.....	13
Data Analysis.....	13
RESULTS.....	17
Population Estimates.....	17
Production Estimates.....	19
Population Characteristics.....	20
Diet Analysis.....	26
a) Diet Composition.....	30
b) Diet in Relation to Size.....	30
Seasonal Movements and Depth Distribution.....	35
Young-of-the-Year	40
a) Distribution of Y-O-Y During the Open-water Season...	40
b) Y-O-Y Growth and Dietary Changes.....	48
Abundance and Distribution of the White Sucker and Lake Trout Populations.....	50
a) White Sucker.....	50
b) Lake Trout.....	52
DISCUSSION.....	54
Population Estimate Variability.....	54
Population Dynamics.....	56
a) Life Cycle and Possible Mechanisms Regulating Population Size.....	56
b) Growth and Production.....	62
c) Feeding Behaviour and Conspecific Interaction.....	68
Species Interactions.....	74
CHAPTER TWO: THE VALIDITY OF USING SCALES AND CLEITHRA TO AGE A NORTHERN PIKE (<u>Esox lucius</u>) POPULATION FROM A SMALL, OLIGOTROPHIC	

LAKE

INTRODUCTION..... 81

MATERIALS AND METHODS..... 82

RESULTS..... 85

 Comparison of Scale and Cleithra Ages..... 85

 Comparisons of Ages Assigned to Scales and Cleithra by Two
 Ages..... 86

 Time of Annulus Formation..... 88

 Validation by Mark-Recapture..... 91

 Validation Through the Use of Oxytetracycline Established
 Marks..... 91

DISCUSSION..... 93

CHAPTER THREE: THE POTENTIAL ROLE OF LAKE MORPHOMETRY AND WATER
CHEMISTRY ON THE REGULATION OF POPULATION SIZE AND GROWTH OF
NORTHERN PIKE FROM 14 NORTHWESTERN ONTARIO LAKES

INTRODUCTION..... 98

STUDY AREA..... 99

METHODS..... 104

RESULTS..... 109

 Relative Abundance and Population Estimates..... 109

 Size Structure..... 111

 Age and Growth..... 111

 Mean Age at Maturity..... 121

 Total Annual Mortality..... 125

 Diet..... 125

DISCUSSION..... 127

 MANAGEMENT CONSIDERATIONS..... 136

LITERATURE CITED..... 141

APPENDICES..... 159

LIST OF TABLES

Table

- | | | |
|-----|---|----|
| 1.1 | Spring population estimates (N) as determined by the Schumacher-Eschmeyer (S-E) and modified Peterson estimates (Ricker 1975), and catch summaries depicting the number of pike which were marked (M), caught (C) and recaptured (R) during each of the 1982, 1984 and 1985 spring, summer and fall sampling intervals on Squeers Lake, Ontario. | 18 |
| 1.2 | Length-weight relationships calculated for the male (M), female (F) and overall (C) population of pike sampled from Squeers Lake, Ontario during 1982, 1984 and 1985. | 23 |
| 1.3 | Relationship between fecundity (F) and i) fork length (FL), total weight (W) and iii) age (A) of a subsample (n=16) of northern pike collected from Squeers Lake, Ontario in 1982, 1984 and 1985. | 27 |
| 1.4 | Mean fork length at age (mm) for the male, female and overall components of the northern pike population from Squeers Lake, Ontario sampled during spring 1982, 1984 and 1985. | 28 |
| 1.5 | A comparison of the Index of Relative Importance (IRI) food values of various prey items encountered within the stomachs of pike sampled from Squeers Lake, Ontario during the unstratified, stratified and overall open-water periods of 1982, 1984 and 1985. | 31 |
| 1.6 | A comparison of the Index of Relative Importance (IRI) food values of various prey items encountered within the stomachs of pike A) 300-499 mm, B) 500-699 mm and C) \geq 700 mm long (fork length) sampled within Squeers Lake, Ontario during the unstratified, stratified and overall open-water seasons of 1982, 1984 and 1985. | 34 |
| 1.7 | Catch per unit effort (expressed as the number of fish/24 hours/100 m of net) and amount of effort (E, expressed as the number of hours/15.24 m of net fished/month) for northern pike (NP), lake trout (LT) and white sucker (WS) caught within gillnets set within Squeers Lake, Ontario at depths < 10 metres during the 1985 open-water season. | 39 |
| 1.8 | Variation in the catch-per-unit-effort (CUE), expressed as the number of northern pike (NP), lake trout (LT) and white sucker (WS) during four daily time periods over monthly sampling carried out on Squeers Lake, Ontario during the 1985 open-water season. | 42 |

- 1.9 Average number of pike young-of-the-year (YOY) and other 44
members of the associated small fish community caught
within morning (M) and evening (E) lifts of Casselman
traps (Casselman and Harvey 1973) set within the Western
Arm of Squeers Lake, Ontario during the 1985 open-water
season.
- 1.10 Summary of the number of fish caught by species at 46
various seine locations within the western arm of Squeers
Lake, Ontario during monthly 1985 summer netting
activities.
- 1.11 Average number of pike young-of-the-year and other 47
members of the associated small fish community caught
within morning (M) and evening (E) lifts of Casselman
traps set within the channel area separating the two lake
basins of Squeers Lake, Ontario during the 1985 open-water
season.
- 1.12 Monthly length distributions (by 100 mm length 53
increments) of white sucker caught in index gillnets
set within Squeers Lake, Ontario during the 1985 field
season.
- 1.13 Comparison of fecundity estimates (expressed as the 58
number of eggs per gram overall body weight) for various
populations of northern pike.
- 1.14 Production estimates for various populations of northern 67
pike cited in the literature.
- 2.1 Percent frequencies of agreement, mean index of average 87
error (APE), coefficient of variation (CV) and index of
precision (D) for northern pike ages from samples
collected from Squeers Lake, Ontario, as determined from
scales and cleithra by two readers.
- 2.2 Time of annulus formation as determined by the presence 89
of new growth following the outermost annulus on scales
collected from northern pike sampled from Squeers Lake,
Ontario during 1982, 1984 and 1985.
- 2.3 Time of annulus formation as determined by the presence 90
of new growth following the outermost annuli evident on
cleithra collected from northern pike sampled from Squeers
Lake, Ontario during 1982, 1984 and 1985.
- 2.4 Comparison of the expected and actual number of annuli 92
formed on scales collected from recaptured northern pike
in Squeers Lake, Ontario during 1982, 1984 and 1985.
- 2.5 Comparison of the expected and actual number of newly 94

formed annuli following the oxytetracycline label on cleithra from northern pike recovered from Squeers Lake, Ontario one month to three years after initial capture and the intraperitoneal injection of 0.5 cc/kilogram oxytetracycline.

- 3.1 Selected physical and chemical characteristics of 14 northwestern Ontario lakes from which northern pike were collected. 100
- 3.2 Criteria summarized from the literature to determine study lake trophic status. 102
- 3.3 Fish species documented to occur within Greenwater (1), Little Gull (2), Pettit (3), Pickerel (4), Squeers (5), Bernadine (6), Crooked Pine (7), Lac des Mille Lacs (8), Niobe (9), Henderson (10), Ice (11), Muskeg (12), Savanne (13) and Whitefish (14) Lakes, northwestern Ontario. 103
- 3.4 Estimated fishing effort (expressed as rod-hours per hectare), harvest, potential yield and the Relative Yield Index (RYI: Ont. Min. Nat. Res. 1983) for 14 northwestern Ontario pike populations. 105
- 3.5 Catch-per-unit-effort (CUE), expressed as the number of fish caught per 100m of gillnet per 24 hour period by depth strata, and population estimates (N) expressed on a number per hectare basis for 14 northwestern Ontario northern pike populations. 110
- 3.6 Mean fork length, the Proportional Stock Density (PSD), Relative Stock Density (RSD) of fish >750 mm, mean age and size of the onset of maturity (as calculated by the modified Abrosov's (1969) method (Lysack 1980)) for the combined (C), male (M) and female (F) portions, and annual mortality (A) rate values for 14 northern pike populations sampled in northwestern Ontario. 115

LIST OF FIGURES

1.1	Map showing the location and bathymetry of Squeers Lake, Ontario (48°31' W, 90°33' N).	7
1.2	Length frequency distributions for northern pike from Squeers Lake, Ontario during spring sampling carried out in A) 1982, B) 1984 and C) 1985.	21
1.3	Age frequency distributions for northern pike from Squeers Lake, Ontario during spring sampling carried out in A) 1982, B) 1984 and C) 1985.	24
1.4	Growth curves depicting the mean length at age (cm) for the male, female and overall components of the northern pike population from Squeers Lake, Ontario sampled during spring 1985.	29
1.5	The relationship between the length of northern pike (mm) and the length of prey items (mm) encountered within pike stomachs sampled from Squeers Lake, Ontario during 1982, 1984 and 1985.	32
1.6	Seasonal and spatial distribution of northern pike caught in index gillnets set within Squeers Lake, Ontario during the 1982, 1984 and 1985 open-water seasons.	38
1.7	Diel activity of northern pike caught by index gillnets set within Squeers Lake, Ontario over four daily periods during the 1982, 1984 and 1985 open-water field seasons.	41
1.8	Mean monthly increases in the fork length (cm) and weight (g) of young-of-the-year northern pike sampled from Squeers Lake, Ontario during the 1985 field season.	49
1.9	Monthly dietary changes exhibited by young-of-the-year northern pike sampled from Squeers Lake, Ontario during the 1985 field season.	51
1.10	Comparisons in the mean length at age of northern pike from various populations found throughout its North American range.	63
1.11	Comparisons in the mean length at age of five northwestern Ontario northern pike populations.	65
3.1a	Fork length frequency distributions of northern pike from 5 oligotrophic northwestern Ontario lakes.	112
3.1b	Fork length frequency distributions of northern pike from 4 mesotrophic northwestern Ontario lakes.	113

3.1c	Fork length frequency distributions of northern pike from 3 meso-eutrophic northwestern Ontario lakes.	114
3.2a	Age distributions of northern pike from 5 oligotrophic northwestern Ontario lakes.	117
3.2b.	Age distributions of northern pike from 4 mesotrophic northwestern Ontario lakes.	118
3.2c	Age distributions of northern pike from 3 meso-eutrophic northwestern Ontario lakes.	119
3.3	Comparison of the mean growth rates for northern pike populations from northwestern Ontario oligotrophic, mesotrophic and meso-eutrophic lakes.	120
3.4a	Comparison of the empirical mean fork length at age for northern pike from 5 oligotrophic northwestern Ontario lakes.	122
3.4b	Comparison of the empirical mean fork length at age for northern pike from 4 mesotrophic northwestern Ontario lakes	123
3.4c	Comparison of the empirical mean fork length at age for northern pike from 5 meso-eutrophic northwestern Ontario lakes	124
3.5	Percent frequency of occurrence of food items identified in stomachs of northern pike from A) oligotrophic, B) mesotrophic, C) meso-eutrophic and D) overall samples by lake type from 9 populations examined within northwestern Ontario.	126

LIST OF APPENDICES

Appendix

A) Physical and Chemical Characteristics of Squeers Lake

INTRODUCTION.....	159
Description of the Lake and Watershed Area.....	159
MATERIALS AND METHODS.....	160
RESULTS AND DISCUSSION.....	161
Lake Morphometry.....	161
Temperature.....	162
Oxygen.....	163
Water Chemistry and Trophic Status.....	164
REFERENCES.....	167

B) Squeers Lake Study

Table B.1. Annual production and biomass for northern pike (<u>Esox lucius</u>) ages 3-9, collected from Squeers Lake, Ontario, 1984-1985.....	176
--	-----

Table B.2. Results of covariance analysis of the length-weight relationships between sexes, sample years and seasons of pike sampled from Squeers Lake, Ontario during the 1982, 1984 and 1985 open-water seasons.....	177
--	-----

Table B.3. Diet comparisons of small (300-499 mm), medium (500-699 mm) and large sized (≥ 700 mm) northern pike, excluding young-of-the-year sampled during the unstratified (April 29-June 15, September 15-November 6) and stratified (June 15-September 15) portions of the 1982, 1984 and 1985 open-water seasons on Squeers Lake, Ontario.....	178
---	-----

C) Age Validation Study

Table C.1. Level of disagreement (expressed in years) between ages assigned to northern pike from Squeers Lake, Ontario during 1982, 1984 and 1985 by scales and cleithra as determined by two readers.....	179
---	-----

Table C.2. Level of disagreement (expressed in years) between two readers for ages assigned to northern pike collected from Squeers Lake, Ontario during 1982, 1984 and 1985 as determined from A) scales and B) cleithra.....	180
--	-----

Table C.3. A comparison of the estimated and actual number of years at liberty for each age group of northern pike tagged in Squeers Lake, Ontario during 1982, 1984 and 1985 as determined by	
--	--

the number of newly formed annuli on the scales of fish
recaptured one month to three years after intial tagging.....181

D) Comparative Study

Table D.1. The percent frequency of mature male (M) and female
(F) northern pike by a) age and b) 5 cm length classes from 14
northwestern Ontario lakes.....182

GENERAL INTRODUCTION

Northern pike (*Esox lucius*) exhibit a holarctic distribution. Their natural habitat range varies from ultra-oligotrophic to brackish water (Inskip 1982). Typically northern pike are found within shallow mesotrophic to meso-eutrophic lakes and quiet rivers (Scott and Crossman 1973). This species, extensively sought after by both commercial and sport fishermen throughout its natural range, has been extensively studied. This is made readily apparent by the number of studies listed within the recent northern pike bibliography by Crossman and Casselman (1987). General information on the dynamics of northwestern Ontario northern pike populations is lacking, however, especially on populations found within the oligotrophic lakes in this region. There are only 2 northwestern Ontario lake studies which provide information on northern pike population dynamics and production (Savanne Lake: Mosindy 1980; and Henderson Lake: Nunan 1982, Reid 1985, Wisenden 1988). In addition, there are a number of unpublished Ontario Ministry of Natural Resources (OMNR) District creel and netting program reports which provide additional information on growth and population size (eg Donetz 1982, Pelligrini 1984, Laine 1986).

In addition to northern pike, other fish species which commonly occur within oligotrophic lakes include lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), lake herring (*Coregonus artedii*), white sucker (*Catostomus commersoni*), longnose sucker (*Catostomus catostomus*), and to a

lesser extent walleye (Stizostedion vitreum) and smallmouth bass (Micropterus dolomieu). However, little is known of northern pike biology within such systems. Studies to date have been limited to Lake Huron (Wainio 1966), far north Canadian and Alaskan lakes (Miller and Kennedy 1948, Falk and Dahlke 1974, Falk and Gillman 1975, Chihuly 1980), Lake Windermere (Kipling 1983) and most recently an oligotrophic lake in Norway (Vollestad et al 1986). Except for work by Chihuly (1980), however, these studies concentrate primarily on the growth rates (as determined by mean length at ages) of these populations. They provide little or no information on stock size, food habits or spatial resource partitioning with other species present within these water bodies.

Squeers Lake, Ontario (48°31'W, 90°33'N) is a small (384.4 ha), oligotrophic lake which contains lake trout, white sucker and northern pike. This type of fish association is found in 10% of all surveyed lakes in northwestern Ontario (Johnson et al 1977). Such lakes, therefore, form an important component of the area's fishery resource. The lake itself became subject to heavy fishing pressures in 1978 when a forestry access road was put into the area. In one weekend in February 1979, 100% of the lake's total potential harvest of lake trout, as predicted by the morphoedaphic index (Ryder 1965, OMNR 1983) was harvested. Therefore, the lake was declared a sanctuary lake (Ryan and Ball 1985). Presently, the lake is the focus of an experimental lottery winter lake trout sport fishery. Ball (1988) presented a detailed examination of the lake trout population within the lake, estimated its capacity for

fish production, and reported the results of the first 2 years of the experimental fishery carried out on the lake between 1985-1986.

The present study examined the northern pike population present within Squeers Lake. It described the demography of the population and determined the level of interaction between northern pike and lake trout. The thesis itself has been written as three discrete chapters. Although all the material presented is interrelated, each Chapter deals with a specific topic warranting separate analysis. Chapter 1, the principal component of the thesis, provides a detailed examination of the basic ecology of a northern pike population found within a small, oligotrophic, northwestern Ontario lake. Chapter 2 delves into detail on the processes carried out in order to verify and validate the ages assigned to northern pike sampled from Squeers Lake. Finally, Chapter 3 examines the population characteristics of northern pike from 14 northwestern Ontario lakes so as to determine the influence of lake morphometry and/or water chemistry on northern pike population size and growth. Some sections within each of the chapters may provide greater descriptive detail than may have been required, particularly within the methods sections. This approach was taken however, in an attempt to meet the mandate requested by the OMNR for the present project.

CHAPTER ONE

BIOLOGY OF A NORTHERN PIKE POPULATION WITHIN A SMALL NORTHWESTERN ONTARIO OLIGOTROPHIC LAKE

INTRODUCTION

The northern pike (Esox lucius) ranks as an important game and commercial fish species throughout its holarctic distribution. Therefore, a considerable number of studies have examined its life history, population dynamics and management. Many of these studies are summarized within the synopses by Toner and Lawler (1969), Machniak (1975), Hess and Heartwell (1978) and Raat (1988).

Except for the extensive studies on northern pike from Lake Windermere, England (Kipling 1983, LeCren 1987), there is little information available on the dynamics of indigenous populations within oligotrophic lakes, particularly within the boreal portions of the northern pike's range where most of the well established fisheries for this species exist. When northern pike occur within glacial oligotrophic lakes, they have been noted to prefer the littoral zone and shallow bays where this species is the main predator (Ryder 1972, Toivonen 1972). Some data are available for Ontario (ie Lake Huron:Wainio 1966), however, most studies have focussed on northern pike populations from subarctic and arctic Canadian (Miller and Kennedy 1947, Falk and Dahlke 1974, Falk and Gillman 1975), Alaskan (Chihuly 1980) and more recently Norwegian (Vollestad et al 1986) oligotrophic lakes. This general lack of data reflects earlier research emphasis on mesotrophic-eutrophic

habitat areas considered more conducive to supporting optimal northern pike fisheries.

The unknown importance of northern pike within oligotrophic lakes increases the need for information on their life history and population dynamics. Piscivores structure aquatic ecosystems, both directly through predation upon prey populations and indirectly through modifying energy flow and nutrient cycling at lower trophic levels (Carpenter et al 1985). It has been demonstrated that northern pike, a top level predator within mesotrophic and eutrophic lakes (Lawler 1965, Mann 1982, Diana 1979, Bregazzi and Kennedy 1980, Mosindy 1980, Nunan 1982), are apparently important in structuring fish assemblages at least within small, boreal lakes (Robinson and Tonn 1989). Northern pike act as both competitor and predator to native European salmonids (Larsen 1966, Fitzmaurice 1983, Kipling 1983, Mann 1985, Larsson 1985). However, the interaction of northern pike with lake trout in the oligotrophic lakes of North America remains relatively unknown. This study therefore, provides information on the population dynamics, production and utilization of habitat and food resources by an unexploited northern pike population found in a small, northwestern Ontario oligotrophic lake. It also provides initial information on the level of interaction between a piscivorous northern pike and a polyphagous lake trout population.

STUDY AREA

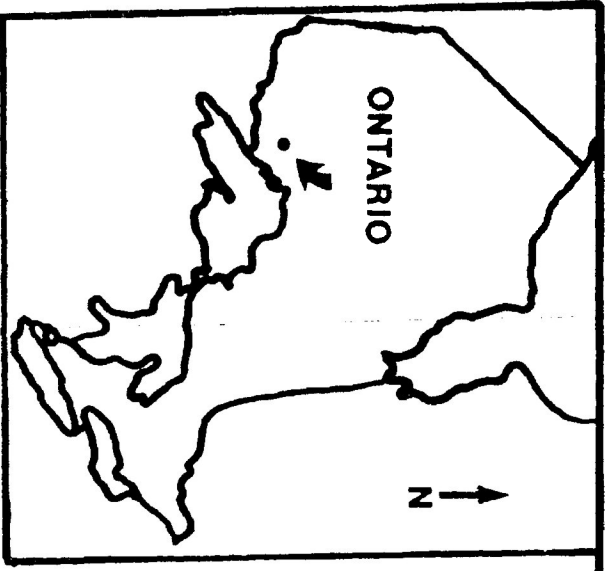
Squeers Lake, Ontario (48°31'W, 90°33'N) is a 384.4 hectare lake located approximately 100 kilometres west-north-west of

Thunder Bay, Ontario (Figure 1.1). The lake is composed of a central basin and an elongated western arm (Figure 1.1). The western arm is nearly physically separated. However, there is a continuous interchange of littoral zone fish species between these two water bodies, therefore they are considered as one lake. The main basin with a mean and maximum depth of 11.5 and 33 metres respectively, is oligotrophic and develops a strong thermocline by mid-June. The eutrophic western arm, however, remains isothermal during the open-water period with water temperatures generally reflecting average daily air temperatures. A more detailed description of the lake's morphometric and chemical characteristics are presented in Appendix A.

Most of the littoral zone's bottom (ie area with depths <6.2m, making up approximately 28% of the main lake basin) is covered by sand, cobble or large rock. Aquatic vegetation is restricted to a few isolated pockets of submergent vegetation located within sheltered bays of the main basin. The substrate within the western arm of the lake, however, consists of mud and decaying vegetative matter, and supports areas of abundant emergent and submergent macrophytes.

The large fish species present within Squeers Lake include the lake trout (Salvelinus namaycush), white sucker (Catostomus commersoni) and northern pike. Other fish species present within the lake include yellow perch (Perca flavescens), burbot (Lota lota), Iowa darter (Etheostoma exile), blacknose shiner (Notropis heterolepis), longnose dace (Rhinichthys cataractae), ninespine stickleback (Pungitius pungitius), northern redbelly dace

Figure 1.1. Map showing the location and bathymetry of Squeers Lake, Ontario (48°31' W, 90°33' N). Depth contours are in meters.



(Chrosomus eos), lake chub (Couesius plumbeus), slimy sculpin (Cottus cognatus) and deepwater sculpin (Myoxocephalus quadricornis).

This lake trout sanctuary lake was the subject of a joint study between the Quetico-Mille Lacs Fisheries Assessment Unit (QMLFAU) of the Ontario Ministry of Natural Resources (OMNR) and Lakehead University. Prior to this study, Squeers Lake has been subject to both an intensive fish community study under the auspices of the QMLFAU (Laine 1984, Ryan and Ball 1985) and a detailed examination of its lake trout population (Ball 1988).

METHODS

The primary open-water sampling program was carried out in 1985. It was divided into three separate activities: i) a spring mark and recapture program to estimate the population of mature, spawning individuals, ii) a monthly index netting program in order to characterize the seasonal changes in diet and distribution and iii) a monthly sampling of the young-of-the-year (YOY) northern pike population present within Squeers Lake. Additional information on the northern pike population within Squeers Lake was also available from initial netting and tagging programs carried out by the OMNR in 1982 (QMLFAU unpublished data) and by the author in 1984.

Spring Population Estimates

Schumacher-Eschmeyer (S-E) mark and recapture estimates (Ricker 1975) of northern pike and white sucker populations were obtained the spring of 1982, 1984 and 1985. Netting began at ice-

out during 1985. In 1982 and 1984, however, netting did not begin until May 16 and May 13 respectively. In all 3 years, population estimates were completed by mid-June.

Trapnets of 1.22m and 1.83m in size (with 30.5m leads) were set in areas of potential northern pike movement throughout the lake. These nets were checked daily, and moved if low catches occurred for two consecutive days, or if current recaptures within a given catch reached 20%. Additional fish captured within index gillnets (described below) and by angling (when time allowed) provided a valuable supplement to catches during these periods, and were included within the spring population estimates.

Results in 1982 and 1984 indicated spawning took place only within the western arm. Therefore, in 1985 prior to ice-out, a 38mm monofilament gillnet panel was periodically placed within the channel separating the two lake basins (ie March 23 and 30, April 18, 19 and 24) in order to monitor early movements. A 1.22m trapnet was also set in a weir-like fashion (ie with its lead removed and wings fastened directly to shore) within the channel immediately after ice-out. This trapnet documented the spawning migrations of both northern pike and white sucker populations into the western arm. The narrowness, depth and short length of the channel connecting the two lake basins precluded the use of two oppositely set traps to determine fish movement between basins. Therefore, only unidirectional movement was monitored. The net was set within the channel such that fish moving from the main lake basin were trapped prior to entering the western arm. This trapnet did not impede the return of spawned out fish. This is evidenced by

subsequent recapture in the main basin of fish released within the western arm while the net was still in place. Except for the May 10-12 period, this net was checked daily from May 2-21.

During population estimates, captured northern pike were anaesthetized with tricaine methane sulfonate (MS 222), tagged with a serially numbered disc tag, administered an accessory clip (ie 1982:severed left pectoral; 1984:caudal fin punch; 1985:severed upper caudal lobe), sampled, and allowed to recover within a holding trap prior to release. White suckers were given a fin clip only (similar to those administered to northern pike) during the population estimates. For each fish, fork and total length (in mm), weight (in g), sex (as determined by external examination if possible), a scale sample for age determination and previous capture information (as determined by the presence of tags and/or clips) were taken. In 1982 and 1984, a subsample of northern pike caught were also given an intraperitoneal injection of 0.5 cc Oxytetracycline per kilogram body weight (Weber and Ridgeway 1962) for age validation purposes (see Chapter 2).

Monthly Index Netting Program

During the 1985 open-water season a monthly index netting program was carried out. This permitted: i) calculation of independent seasonal population estimates using the modified Petersen mark-recapture method (Ricker 1975) in order to verify the spring S-E population estimates, ii) determination of seasonal depth distributions through comparisons of seasonal catch-per-unit-effort (CUE, expressed as the number of fish/ 100m of net/ 24 hour period) data by depth of gear, iii) determination of movement

within the lake on the basis of tag recaptures, iv) procurement of stomach samples for feeding analysis, v) procurement of scale and cleithral samples for age verification and validation and vi) acquisition of maturity data and fecundity information. No winter netting activity was attempted due to the disjunct distribution of northern pike within the lake and to prevent a high incidental catch of lake trout.

Preliminary gillnet surveys in late June, 1982 and 1984 provided initial information on the depth distribution and overall age and size structure of the various fish populations within Squeers Lake following thermocline formation in mid-summer. Multifilament or monofilament nets consisting of 3-9 panels (with mesh sizes varying from 12.5-125 mm) separated by 3m spacing lines in order to prevent net leading were set overnight in randomly chosen locations throughout all depths of the lake. In order to obtain initial seasonal distribution and feeding information, additional netting (using trap and gill-net locations previously identified in the spring) also took place in late August and September, 1984.

The 1985 monthly index netting program (utilizing both trap and gill nets) was modified on the basis of the 1982 and 1984 results. Thus in 1985, netting effort was concentrated at depths ≤ 10 meters over the full range of habitats present within the littoral zone of the lake. Very small numbers of northern pike were caught at depths greater than 10 meters. Therefore this depth limit was chosen to reduce any potential mortality resulting from sudden pressure changes, particularly for any incidentally netted

fish species. The actual type, amount and location of effort varied, depending on physical conditions and sizes of fish catches. Unlike 1982 and 1984, gillnets in 1985 were set perpendicular to the shore in order to determine depths occupied by northern pike.

Due to the generally narrow width of the lake's littoral areas, both the 3m spacing lines as well as 3 panels were removed from the gillnets used. The 10.2, 11.4 and 12.7mm panels were omitted due to the relative ineffectiveness in sampling northern pike.

The actual number of index sites were reduced over the course of the 1985 field season due to a lack of time and manpower. Sites which were continually fished were those locations resulting in the highest yield of northern pike. These locations were not randomly chosen.

In 1985 netting mortalities were minimized by checking each gill-net location at least 4 times daily (with lift intervals of 4 hours or less), and releasing all live fish encountered. A monthly subsample of 10-15 fish (including any net mortalities, with approximately 2-3 fish per 10 cm interval) were examined. Due to this small sample size, the data was examined on a seasonal rather than monthly basis. The open-water period was divided into three seasons corresponding to the presence of summer thermal stratification: ie spring (April 29-June 14, summer (June 15-September 15) and fall (September 15-November 6). All gillnetted northern pike caught in 1982 and 1984 were killed.

In addition to length and weight measurements and scale samples, killed fish also provided cleithra, stomach samples, and sex information. Ovaries were collected from all females sampled

in September to November, as well as fish harvested during a concurrent controlled experimental winter lake trout fishery. Stomachs and ovaries preserved in 10% and 5% formalin respectively, were stored in whirlpacs for later analysis.

Young-of-the-year Collections

Young-of-the-year northern pike were collected during the first week of each month from June 3 to November 6, 1985. Fish were caught at index netting sites using a variety of gear. Plexiglass larval fish traps (Casselman and Harvey 1975), small mesh (25-38mm stretched mesh) gillnet attached to the monthly index gillnets and seining provided most of the samples. Plexiglass traps were set at all potential northern pike spawning locations. Up to 5 locations representative of habitat types present within the western arm were sampled with a small-mesh (6mm stretched mesh) 18.3m X 1.8m bag seine (used in an encircling manner and encompassing an area of 26 m²). Additional gear used included 1.22m fyke nets, and a fine mesh dipnet.

Additional information on density of aquatic vegetation and fish distribution within the Western Arm were obtained by underwater transects. Underwater observations were made on 3 occasions over the spring and early summer period using a wet suit, mask and snorkel. The diver moved slowly along predetermined transects which included the entire shoreline perimeter. When fish were encountered, the species, approximate number, and habitat association were noted.

Data Analysis

Due to the small number of fish actually killed for the

present study, scales were the primary tissue used to age fish for the purposes of any age-related analysis. The use of scales for aging the northern pike population within Squeers Lake was validated by the multiple recapture of the same fish over successive time periods and the recapture of fish which had previously been marked with oxytetracycline in 1982 and 1984. There was close agreement between ages assigned from scales and cleithra (ie 92% total agreement) when the two tissues were compared. Where disagreement occurred, the cleithral age was considered to be the correct measurement of chronological age (further details on the aging and validation techniques used within this study can be found within Chapter 2).

The 1984 and 1985 spring samples provided length frequency distributions, age composition and growth information (as assessed by plotting empirical mean length and mean weight at age) for that proportion of the population vulnerable to the gear. The information was also used to calculate the annual production for age groups 3-7 (Ricker 1975).

Sex ratios and state of maturity were determined from the gross examination of gonads. Lysack's (1980) modification of the Abrosov (1969) equation was used to determine the mean weighted age and length at the onset of first maturation for both males and females in the population. Fecundity of female northern pike caught in the fall of 1982, 1984 and 1985 was determined by the gravimetric method (Kipling and Frost 1969). Excess moisture was removed from both ovaries via towel drying. The eggs were then scraped from the connective membrane and weighed to a precision of

.001g. Three subsamples from the anterior, mid-section and posterior regions of each ovary representing at least 5% of the overall ovary weight were counted to determine the mean number of eggs/gram. From this value, the total number of eggs per female was determined. Fecundity was regressed on fork length, weight and age using the least squares method (Sokal and Rohlf 1981). Due to the small sample sizes between years, the samples were combined. This may create an inherent bias should fecundity have been affected by differing environmental factors between the 3 years from which the samples were collected. However, the sample sizes collected from each year were too small (due to the small size of the mature population) to warrant separate analysis.

Stomach contents from 81 y-o-y and 180 \geq age one northern pike were examined. This included a subsample of 15 fish for which gastric lavage was attempted in September, 1984 and May, 1985 using the system developed by Crossman and Hamilton (1978). This method was discontinued as fish taken from gillnets did not revive well after gillnetting and gastric lavage (particularly when increasing water temperatures were encountered). Trapnetted fish were not used in any of the diet analyses since netted northern pike often ingest other fish entrapped in such gear. Stomachs containing food items from all collections were examined in the laboratory. Items were identified to "lowest" possible taxon, counted, measured, weighed and expressed as a percentage of occurrence and volumetric displacement (Hyslop 1980) on a seasonal and size specific (ie every 100 mm interval $>200\text{mm}$) basis. Partially digested fish were identified from anatomical features, meristic characteristics and

scale shape. However, any doubtful fish were listed as unknown fish remains. The index of relative importance (IRI) (Pinkas et al 1971) was used to determine the contribution of prey items to the diet of fish. This reduced at least some of the biases caused by infrequently caught large items or more frequently caught, small items which contributed little to the overall diet (Wallace 1981, Wallace and Ramsey 1983). The index was calculated as: $IRI = (N+V) \times FO$

where: N= the numerical percentage of a given food type

V= the volumetric percentage of a given food type

and FO= the percentage frequency of occurrence of a food type within stomachs containing food items.

Diet indices were used to compare diet overlap between the different size categories of northern pike and lake trout collected by Ball (1988). No single measure of diet is adequate for the actual representation of prey item importance (Wallace 1981). However, in the absence of resource-availability data, the Schoener index provides the most appropriate measure of diet overlap (Hulbert 1978, Wallace 1981, Wallace and Ramsey 1983). The Schoener (1970) index was calculated as:

$$S = 1 - 0.5 \left(\sum_n^i |P_{xi} - P_{yi}| \right), \text{ where}$$

n= the number of food items

P_{xi} = the proportion of a prey item in species x

and P_{yi} = the proportion of a prey item in species y.

Data sets were tested for normality by using the Wilk-Shapiro test for sample sizes ≤ 50 , or the Kolmogorov-Smirnov test for sample sizes > 50 . The parametric student's t-test with unpooled

variances or the nonparametric Mann-Whitney U test were used for comparative purposes. All other statistical tests used are mentioned directly within the text.

RESULTS

Population Estimates

The spring population estimates as calculated in 1982, 1984 and 1985 indicate that the population of northern pike \geq age 3 is small but stable. It ranged from a low of 206 fish in 1982 to a high of 270 fish in 1984 (Table 1.1). All population estimates calculated within the present study apply only to fish \geq 3 years of age at the time of initial marking. Although 1 and 2 year old fish were caught each year, the low number of subsequent recaptures indicated these age classes were not very vulnerable to the gear. The 1 and 2 year old northern pike collected during monthly sampling further decreased the number of marked fish from these two age groups.

In general, the spring S-E population estimates agreed with seasonal Petersen estimates calculated from subsequently netted fish (Table 1.1). However, in 1982 Petersen estimates calculated exceeded the S-E estimate by more than 150%. Population size deviated by less than 5% between the 1984 estimates and 17% between the 1985 estimates. The calculated 1985 Petersen population estimates were also within 10% of the virtual population size (ie 168 fish \geq age 3) as determined by the number of fish handled at least once during 1985.

The above population estimates were calculated assuming no

Table 1.1. Spring population estimates (N) as determined by the Schumacher-Eschmeyer (S-E) and modified Petersen estimates (Ricker 1975), and catch summaries depicting the number of pike which were marked (M), caught (C) and recaptured (R) during each of the 1982, 1984 and 1985 spring, summer and fall sampling intervals on Squeers Lake, Ontario.

	M	C	R	N	95% C.L.
<u>1982 Population Estimate</u>					
S-E (1982 Spring, ≥ 3 yr)	75	82	8	206	143-384
Petersen (1984 Spring, ≥ 5 yr)		86	13	472	297-958
Petersen (1985 Spring, ≥ 6 yr)		118	17	502	333-913
<u>1984 Population Estimate</u>					
S-E (1984 Spring, ≥ 3 yr)	105	135	27	270	208-385
Petersen (1985 Spring, ≥ 4 yr)		168	69	256	205-329
Petersen (1985 Summer, ≥ 4 yr)		24	9	265	155-662
Petersen (1985 Fall, ≥ 4 yr)		34	15	232	150-442
<u>1985 Population Estimates</u>					
S-E (1985 Spring, ≥ 3 yr)	156	257	101	220	193-257
Petersen (1985 Summer, ≥ 3 yr)		42	36	183	136-269
Petersen (1985 Fall, ≥ 3 yr)		38	32	186	136-281

emigration or immigration within the Squeers Lake. Mortality due to the stress of handling was also discounted. If gillnets are used as the capture gear, mortality of marked fish can be a problem. However, the high recapture ratio of individual fish following three years of multiple handling lent confidence that handling did not introduce additional mortality. Short-term holding experiments in which visibly stressed northern pike were held for 4-24 hours within pens also indicated that netting and tagging negligibly effected fish survival. All 7 of the dead fish found within the western arm during or soon after tagging (of which 4 had been tagged within this time period) were spent fish, whereas fish at the time of tagging were generally ripe or running. Reproductive effort was likely the crucial factor influencing the mortality of these individuals (although additional tagging stress may compound this problem).

By using only the appropriate age groups for each population estimate, the effect of recruitment as a potential bias was removed. Similarly, tag losses were minimal (ie 2.0% within the same year, 3.1% after one year), and any fish suffering tag loss could be identified by its accessory clip. Therefore, this factor was not taken into account in any of the population estimates.

Production Estimates

The total mean northern pike biomass was 656.8 kg, or 1.71 kg/ha, whereas the total annual production of northern pike aged 3-9 within Squeers Lake was 104.2 kg or 0.27 kg/ha in 1984-1985 (Appendix Table B.1). The overall P/B ratio (the turnover ratio of biomass) of 0.16, generally decreased with fish age from 0.33

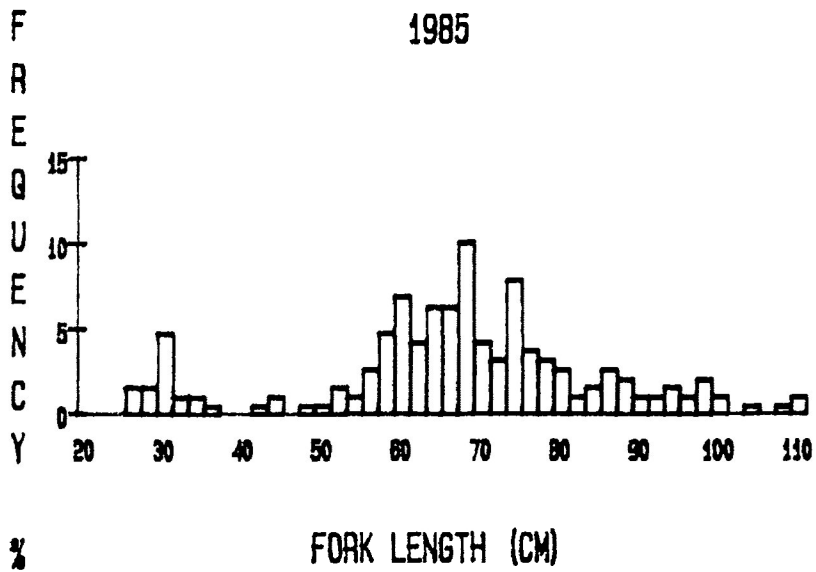
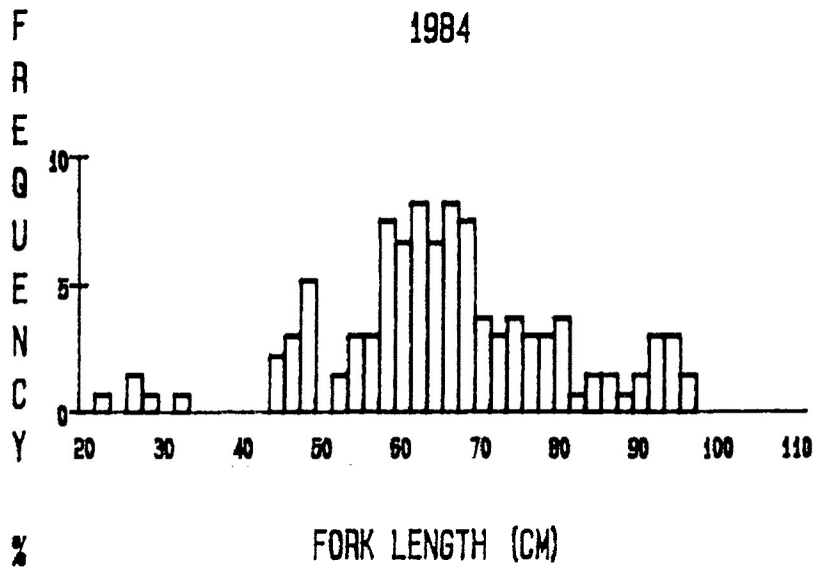
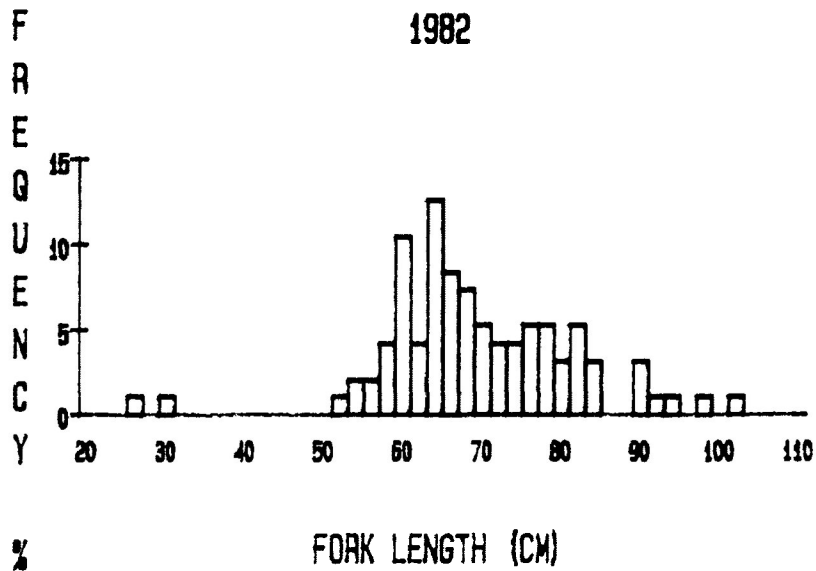
for age 3 fish to 0.08 for age 7 fish, and was negative for age 8 and 9 fish. Older age groups (ie ages 8-9 and 9-10) included within the production estimate exhibited negative instantaneous growth rate values. This indicates a net loss in weight within a given year class. Since the sex of a large number of fish could not be determined accurately, no effort was made to estimate separate male or female production levels.

Sampling obviously affected the annual production estimate for the Squeers Lake northern pike population. The average annual mortality rate (A) for age groups 3 to 9 was calculated to be 0.39 between 1984 and 1985. Approximately 37% of the total mortality could be accounted for by sampling. Sampling mortality for the age 6 and 7 year classes represented 100% of the reduction in the estimated numbers of these two age groups between 1984 and 1985. This would create an adverse effect on the production estimate for these two year classes. Sampling mortality also explained 16-26% of the mortality between years for the age 3-5 age groups within the production estimate, but did not account for any of the mortality for age 8 and 9 fish.

Population Characteristics

Squeers Lake northern pike exhibited a unimodal length frequency distribution (Figure 1.2). Lengths varied from 260-1110 mm FL, and the majority of fish ranged from 550-750 mm FL. There were no significant differences in the mean lengths of fish (ie 700.2 ± 120.4 mm FL, 664.2 ± 147.7 mm FL, and 678.7 ± 178.0 mm FL in 1982, 1984 and 1985 respectively) caught during the spring sampling programs between 1982 and 1985 nor 1984 and 1985. However, the

Figure 1.2. Length frequency distributions for northern pike from Squeers Lake, Ontario during spring sampling carried out in A) 1982, B) 1984 and C) 1985.



mean size of the fish sampled were significantly larger in 1982 than 1984 ($p < .05$, student-t test). The mean length of females sampled were significantly greater than the males in all 3 sample years ($p < .05$, student-t test).

Length-weight relationships were calculated by least square linear regression methods (Sokal and Rohlf 1981) for the 1982, 1984 and 1985 spring caught northern pike within Squeers Lake (Table 1.2). Natural logarithmic transformation of the data gave the best linear fit. Although there were no significant differences in the slopes of the regression lines, there were significant differences between elevations (Appendix Table B.2). Females were significantly heavier than males at a given length and no males greater than 860 mm were sampled from the population. There were also significant differences between years. However, there was no trend with respect to increases or decreases in weight at a constant length between years (analysis of covariance $P < .001$, Appendix Table B.2). Seasonal comparisons of samples collected during 1985 also demonstrated that heavier fish were caught in the fall (analysis of covariance, $P < .001$). No attempt was made to distinguish between the male or female components during these sampling intervals due to the live release of the majority of sampled fish.

Although population size was relatively stable, there were some variations in year class strength (eg the weak 1980 and 1983 year classes, ie ages 1 and 4 in 1984, ages 2 and 5 in 1985, Figure 1.3). Age 3-8 fish dominated in 1984 and 1985 respectively, with no clearly dominant age class. The mean age in 1985, however, was

Table 1.2. Length-weight relationships calculated for the male (M), female (F) and overall (C) population of pike sampled from Squeers Lake, Ontario during 1982, 1984 and 1985.

YEAR	SEASON	SEX	N	SLOPE	Y-INTERCEPT	R ²	F-VALUE	SIGNIF.
Untransformed								
1982	Spring	M	28	11.949	-548.734	0.941	411.004	0.0001
		F	45	13.947	-6613.279	0.892	355.459	0.0001
		C	94	12.876	-5934.078	0.882	685.571	0.0001
1984	Spring	M	47	9.480	-3957.100	0.890	363.929	0.0001
		F	41	11.478	-4890.336	0.857	234.200	0.0001
		C	127	11.060	-4781.113	0.862	780.343	0.0001
1985	Spring	M	84	8.225	-3023.678	0.810	350.071	0.0001
		F	54	12.250	-5300.687	0.852	298.801	0.0001
		C	187	10.519	-4275.856	0.839	961.712	0.0001
1985	Fall	C	43	10.713	-4573.223	0.912	426.783	0.0001
Transformed (natural log)								
1982	Spring	M	28	3.138	-12.627	0.954	538.340	0.0001
		F	45	3.104	-12.391	0.979	2033.618	0.0001
		C	94	3.116	-12.778	0.982	5194.246	0.0001
1984	Spring	M	47	2.873	-10.973	0.926	559.005	0.0001
		F	41	2.801	-10.455	0.975	1545.767	0.0001
		C	127	2.887	-11.052	0.968	3787.989	0.0001
1985	Spring	M	84	2.796	-10.454	0.917	906.833	0.0001
		F	54	3.133	-12.673	0.980	2539.730	0.0001
		C	187	3.013	-11.871	0.985	12550.201	0.0001
1985	Fall	C	43	3.113	-12.482	0.976	1689.882	0.0001

Figure 1.3. Age frequency distributions for northern pike from Squeers Lake, Ontario during spring sampling carried out in A) 1982, B) 1984 and C) 1985.

F
R
E
Q
U
E
N
C
Y

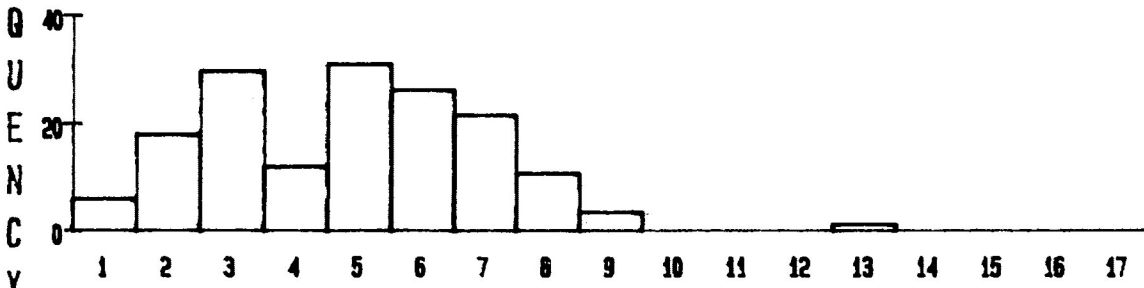
1982 AGE FREQUENCY



AGE (YEARS)

%
F
R
E
Q
U
E
N
C
Y

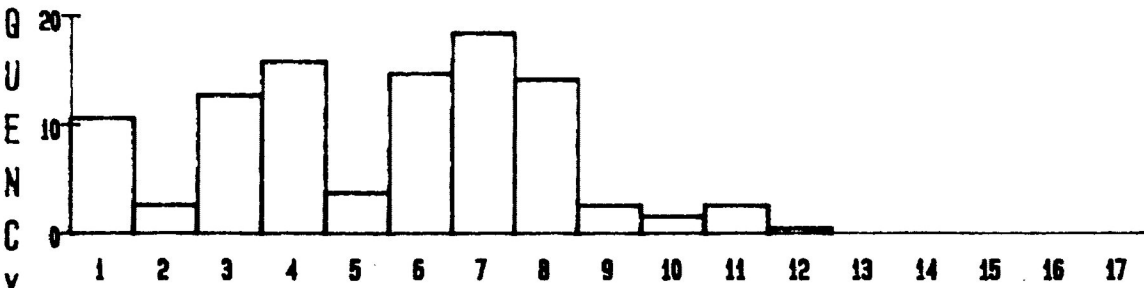
1984 AGE FREQUENCY



AGE (YEARS)

%
F
R
E
Q
U
E
N
C
Y

1985 AGE FREQUENCY



AGE (YEARS)

%

significantly greater (ie 5.4 ± 2.6 yrs) than in 1984 (ie 4.7 ± 2.2 yrs; $p < .05$, Mann-Whitney U test) despite the considerably greater number of age 1 fish caught in 1985. In 1982, the fish caught exhibited a unimodal age distribution with a dominant age 4 year class, and mean age at 5.1 ± 2.1 years. No significant differences occurred between the mean age of males or females within all 3 years ($P < .05$, Mann-Whitney U test).

Squeers Lake northern pike exhibit early maturity. Males exhibit a mean age of onset of maturity at 2.4 years whereas females exhibit a mean age of onset of maturity of 3.1. All males and females had matured by age 3 and age 5 respectively. Insufficient numbers of fish were sampled to determine mean size at maturity. Observations of live-released and sacrificed fish disclosed the first males were mature by 450 mm FL with all being mature by 500 mm FL, whereas females first mature by 480 mm FL with all being mature by 550 mm FL. This maturation pattern precluded the use of regression techniques (Lysack 1980) and the Probit Method (Ritchie 1984).

The ratio of males:females increased slightly between 1984 and 1985. The sex ratios were 1.16:1 and 1.33:1 for males:females during the 1984 spring population estimate and summer gillnetting, respectively. In 1985, however, these ratios increased to 1.53:1 and 1.89:1 respectively. Sex ratios were not determined for spring 1982 since the majority of the fish handled were already spent.

The average fecundity was estimated to be 19422 (± 5080 , 1 S.D.) eggs per kg body weight for the females sampled during the three year period. Absolute fecundity estimates varied from 37486

eggs for an age 6, 668 mm FL female to 164113 eggs for an age 8, 931 mm FL female. Fecundity was linearly related to total weight and fork length of the female (Table 1.3) but only marginally correlated to age ($r^2=0.449$, Table 1.3). Natural logarithmic transformations did not appreciably improve the correlation.

The average length at age of northern pike caught in 1982, 1984 and 1985, and between sexes as demonstrated by fish caught in 1985 are shown in Table 1.4 and Figure 1.4, respectively. The growth rate was rapid. Fish reached a mean length of 600 mm FL by age 3 and 800 mm FL by age 8. Except for the mean length for age 5 fish between 1982 and 1985, there were no significant differences in mean length by age class between years (Mann-Whitney U test, $p<0.05$). However, after age 2 (with the onset of maturity) males grow significantly slower than females of the same age (Mann-Whitney U test, $P<.05$).

Diet Analysis

A total of 63% of the 180 stomachs examined from fish \geq age 1 contained food items. Due to small sample sizes, the overall diet composition was examined within 4 seasonal periods: spring (April 29 - May 31), early summer (June 1 - July 31), late summer (August 1 - September 15) and fall (September 16 - November 8). To allow for a sufficient sample size while detecting size and seasonal differences, northern pike were grouped into 3 size categories: small (300-499 mm FL), medium (500-699 mm FL) and large (\geq 700 mm FL), and divided into 2 time periods: the stratified (June 15-September 15) and unstratified (ice-out-June 14, and September 16-ice formation) portions of the open-water season.

Table 1.3. Relationship between fecundity (F) and i) fork length (FL), ii) total weight (W) and iii) age (A) of a subsample (n=16) of northern pike collected from Squeers Lake, Ontario in 1982, 1984 and 1985.

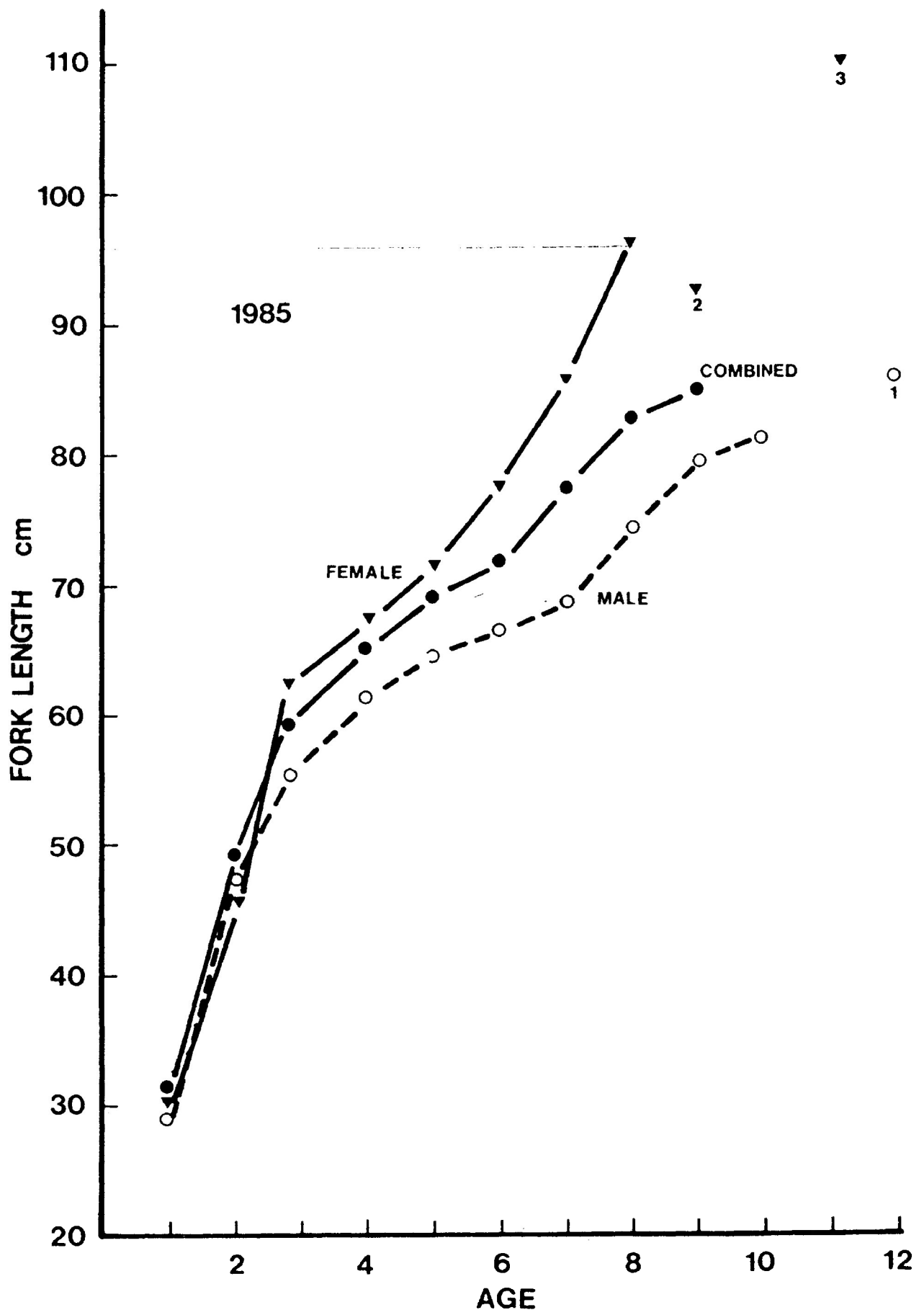
Parameter	Intercept	Slope	R ²	Test F Ratio	Signif. Level
Fork Length	-126525.66	260.30	0.635	24.424	0.001
log Fork length	-4.87	2.41	0.665	27.799	0.001
Weight	1386.95	18.31	0.787	47.954	0.001
Log Weight	4.81	0.77	0.729	34.906	0.001
Age	-6208.89	13200.85	0.449	11.400	0.005

Table 1.4. Mean fork length at age (mm) for the male, female and overall components of the northern pike population from Squeers Lake, Ontario sampled during spring 1982, 1984 and 1985. Sample sizes appear within parentheses.

Age	1982			1984			1985		
	M	F	C	M	F	C	M	F	C
1	-	315 (1)	293 (2)	-	283 (3)	276 (5)	282 (4)	308 (5)	310 (20)
2	-	-	-	476 (7)	495 (4)	491 (15)	472 (2)	456 (1)	485 (5)
3	559 (1)	590 (3)	592 (10)	569 (7)	620 (9)	597 (25)	559 (10)	624 (8)	589 (24)
4	620 (8)	669 (16)	658 (33)	601 (3)	661 (4)	633 (10)	614 (9)	683 (10)	657 (30)
5	645 (10)	778 (12)	717 (23)	643 (12)	708 (4)	667 (26)	653 (3)	731 (2)	694 (7)
6	718 (2)	834 (5)	783 (8)	668 (11)	777 (7)	709 (22)	660 (16)	753 (6)	697 (28)
7	688 (2)	803 (4)	785 (7)	750 (6)	863 (8)	822 (18)	686 (16)	823 (11)	770 (34)
8	780 (3)	-	793 (4)	767 (2)	950 (4)	878 (9)	741 (14)	970 (9)	847 (27)
9	752 (1)	932 (3)	869 (5)	787 (1)	-	899 (3)	796 (4)	-	832 (5)
10	-	986 (1)	986 (1)	-	-	-	821 (3)	-	821 (3)
11	-	-	-	-	-	-	807 (2)	1103 (3)	985 (5)



Figure 1.4. Growth curves depicting the mean length at age (cm) for the male, female and overall components of the northern pike population from Squeers Lake, Ontario sampled during spring, 1985.



Although the size groups were chosen arbitrarily, they generally correspond to the sub-adult, mature adult and large adult components of the northern pike population.

a) Diet Composition

Northern pike \geq age 1 within Squeers Lake are piscivorous. While aquatic macroinvertebrates (ie mayfly and dragonfly nymphs, crayfish and leeches) occurred within 14% of the stomachs, they account for only 0.6% of the total prey volume. Due to their infrequent occurrence, all invertebrates were combined into one prey category for ease of analysis and graphic presentation. Similarly, small fish (ie blacknose shiner, Iowa darter, nine-spine stickleback, slimy sculpin and lake chub) were rarely encountered. Therefore, they were grouped into a small fish category despite differences in their behavioural activity and habitat requirements.

Although most fish species were present, yellow perch and white sucker accounted for more than 50% of the encountered prey items (Table 1.5). However, there were seasonal differences. Yellow perch were important (as determined by the IRI) during spring and early summer. In contrast, white sucker were most important during late summer and fall (Table 1.5). Small fishes formed an important secondary component during spring, whereas burbot and lake trout were utilized during fall. Only 3 (1 y-o-y and 2 age 1) northern pike were encountered within the stomachs examined suggesting cannibalism is probably minimal.

b) Diet in Relation to Size

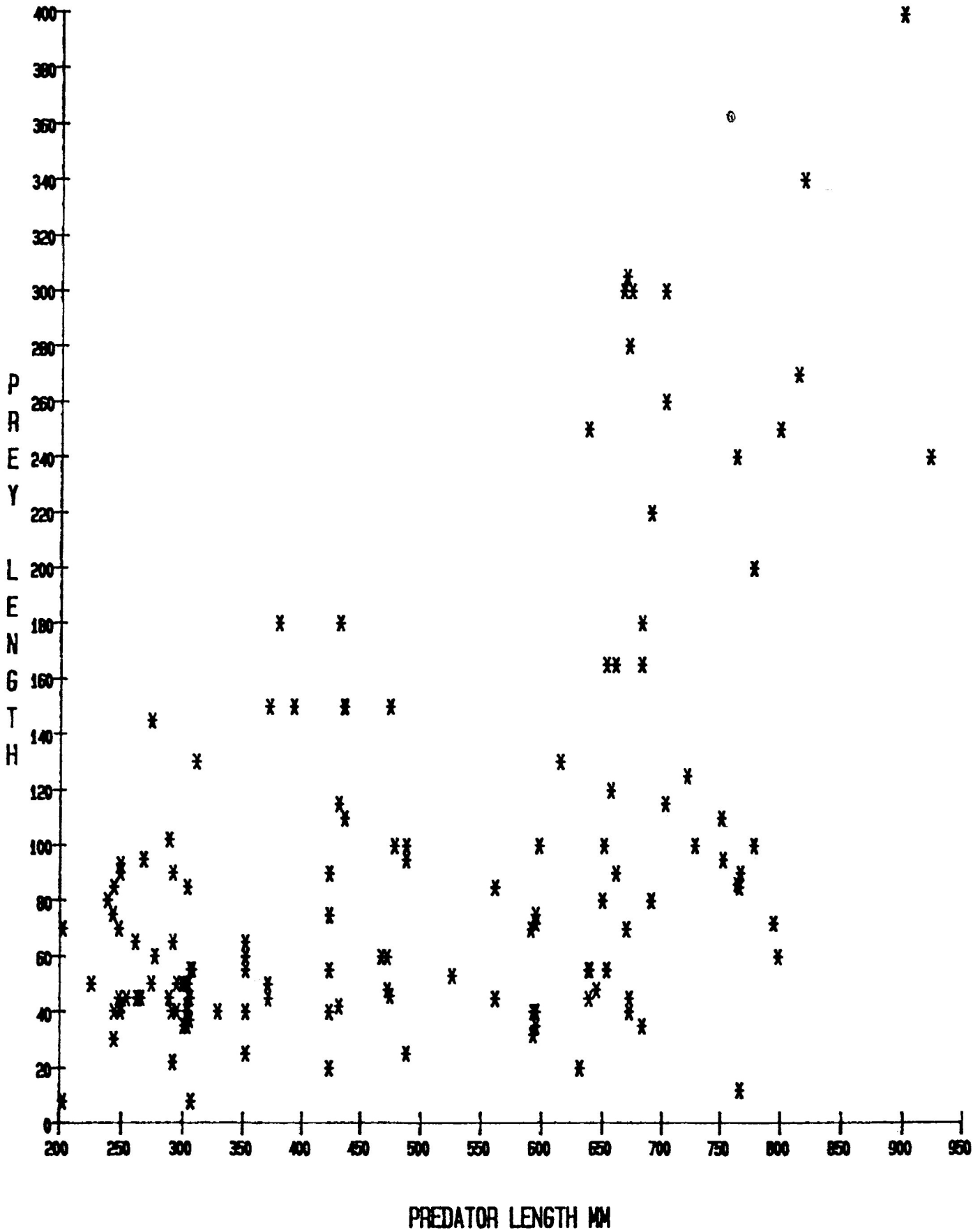
Generally, the range of sizes of prey consumed increased proportionately with predator size (Figure 1.5). Although the

Table 1.5. A comparison of the Index of Relative Importance (IRI) food values of various prey items encountered within the stomachs of pike sampled from Squeers Lake, Ontario during the unstratified, stratified and overall open-water periods of 1982, 1984 and 1985.

Food Item	Open-water Season		Overall
	Unstratified	Stratified	
Yellow Perch	800	2288	1892
White Sucker	1376	2496	2345
Lake Trout	768	30	205
Burbot	456	225	327
Small Fish	728	456	586
Invertebrates	60	192	134
Pike	-	77	20

Figure 1.5. The relationship between the length of northern pike (mm) and the length of prey items (mm) encountered within pike stomachs sampled from Squeers Lake, Ontario during 1982, 1984 and 1985.

PREDATOR/PREY SIZE COMPARISON



linear relationship between prey:predator length was statistically significant (ie $Y=0.195X-4.133$, $P<.0001$), the level of variation between prey:predator size makes this relationship questionable given the very weak coefficient of determination ($R^2=.252$). The prey:predator length ratio for the overall population was $0.189 \pm .116$ (S.D.) with minimum and maximum values of 0.016 and 0.529 . Thus Squeers Lake northern pike selected a broad variety of prey sizes.

Yellow perch < 100 mm FL and white sucker <150 mm FL were heavily preyed upon by 300-499 mm FL northern pike (Appendix Table B.3). Small fish species and burbot <150 mm TL were also seasonally important during the unstratified open-water season (Table 1.6).

Yellow perch between 50-150 mm FL were clearly the dominant prey item for northern pike between 500-699 mm FL, regardless of season (Table 1.6, Appendix Table B.3). The small fish group formed the next most important prey group during the stratified open-water season whereas burbot were the next most important prey item during the unstratified open-water season. White sucker, lake trout and aquatic macroinvertebrates made minor contributions to the diet of this size group.

White sucker between 150-400 mm FL were most frequently encountered in the stomachs of northern pike ≥ 700 mm FL (Table 1.6, Appendix Table B.3). Yellow perch and lake trout were the next most important prey items for these northern pike. Yellow perch >50 mm FL was the second most important prey item during the stratified open-water period. At this time, lake trout and prey

Table 1.6. A comparison of the Index of Relative Importance (IRI) food values of various prey items encountered within the stomachs of pike A) 300-499 mm, B) 500-699 mm and \geq 700 mm long (fork length) sampled within Squeers Lake, Ontario during the unstratified (ie), stratified (ie) and overall open-water seasons of 1982, 1984 and 1985.

Food Item	Open-Water Season		
	Unstratified	Stratified	Overall
A) Pike 300-499 mm			
Yellow Perch	540	4392	2500
White Sucker	1020	3850	2760
Lake Trout	-	-	-
Burbot	1480	434	663
Small Fish	3250	609	875
Invertebrates	-	139	54
Pike	-	-	-
B) Pike 500-699 mm			
Yellow Perch	3397	2166	2418
White Sucker	109	323	238
Lake Trout	420	336	392
Burbot	2100	442	1066
Small Fish	140	1188	774
Invertebrates	-	360	175
Pike	-	125	52
C) Pike \geq 700mm			
Yellow Perch	168	1440	788
White Sucker	4300	5220	4982
Lake Trout	3268	-	472
Burbot	-	73	26
Small Fish	-	-	-
Invertebrates	312	154	235
Pike	-	153	57

items from the small fish community were totally absent from the diet. During the unstratified open-water season, lake trout formed the second most important prey item. Yellow perch and aquatic macroinvertebrates made up the rest of the diet at this time (Table 1.6).

Seasonal Movements and Depth Distribution

Adult movement during the open-water season was greatest during spring spawning. In all 3 years northern pike spawned only in the western arm. The importance of the western arm is reflected by the fact that i) 69% of the fish initially tagged in the spring of 1985 were caught in the trapnet set in the channel separating the 2 lake basins, and ii) a further 17% of the initially tagged fish were caught within the western basin itself despite netting effort throughout the lake.

The monitoring of fish movement into the western arm was initiated on an intermittent basis on March 23, 1985 and began in earnest on April 29 (the day of ice-out on the main lake basin). The gillnet initially set within the channel indicated that individual males begin to enter the western arm by mid-April, before ice-out. The main spawning run occurred between May 2-8, when 79% of the mature fish actually entered the western arm for the first time in 1985 (note: 48 mature pike, representing 22% of the estimated mature population within Squeers Lake were captured within the channel net location on May 2). The movement of northern pike into the western arm was primarily at night, with very few fish observed within the channel trapnet prior to dusk. Spawning was observed within the shallow areas supporting emergent

vegetation (primarily Equisetum spp and Carex spp) as early as May 1. Water temperatures had warmed rapidly within the western arm, and mid-day readings as high as 15 C were recorded by May 1 within the sheltered shallow areas directly beside the shore. Water temperatures within the main basin itself were only 5 C at this time. Spawning habitat was extremely limited, even within the western arm where <500 m of the shoreline actually supported emergent vegetation. Courtship activity was observed within this intermittent fringe of vegetation and on detrital matter immediately bordering this area.

Netting suggested that males generally stayed within the spawning area longer than females. Although the ratio of females:males captured within the gear remained relatively constant with the onset of the main spawning run, few females were recaptured on a regular basis. A number of males, however, were recaptured up to 3 times within the western arm over the two week spawning period.

Following spawning, northern pike rapidly disperse throughout the lake from the western arm. Visual observations revealed that by May 10 northern pike had re-entered the main lake from the western arm (primarily during the evening). By May 8, gillnet catches within the main lake basin caught increased numbers of fish initially tagged within the western arm. Snorkel transects carried out within the western arm on May 20 revealed only 4 "adult" northern pike along the basin's perimeter. By June 13 when the transects were repeated, only y-o-y were observed. These observations were further supported by the netting results within

the western arm of the lake. Combined trapnet and gillnet catches from this area decreased to between 1-15 individuals (including y-o-y's) for the remainder of the sampling year. Hence this portion of the lake is primarily a spawning area for mature northern pike, and serves only as a transitory feeding area.

Despite attempts at netting all habitat types about the lake's perimeter, no specific concentration areas of mature northern pike were found. Most of the young-of-the-year and yearling northern pike captured within gillnets set within the main basin were caught within the small, protected bays along the southernmost shoreline at depths < 3 m, often associated with the small areas supporting submerged vegetation. Areas such as the large rock shelf within the southeast end of the lake, the area adjacent to the inflow from the western arm and the lake trout spawning shoals all exhibited seasonal importance with respect to larger numbers caught at one location (ie >5). However, solitary fish comprised the majority of the catches.

Tagged fish were rarely caught at the same location upon subsequent recapture suggesting that the majority of northern pike within Squeers Lake did not establish a home range. Of 103 subsequent recaptures which occurred after May 15 (the date established for the present study as near or at the end of spawning), 75% were at different locations indicating individual northern pike were not confined to any defined area. However, two of the 20 fish recaptured twice, and 2 of the 6 fish recaptured 3 times within the same year were caught at the tagging site. Therefore, a number of individuals may have an affinity to a given

Figure 1.6. Seasonal vertical distribution of northern pike caught within index gillnets set within Squeers Lake, Ontario during the 1982, 1984 and 1985 open-water seasons. (Note: on the basis of 1982 and 1984 results, 1985 netting efforts were limited to depths ≤ 10 m)

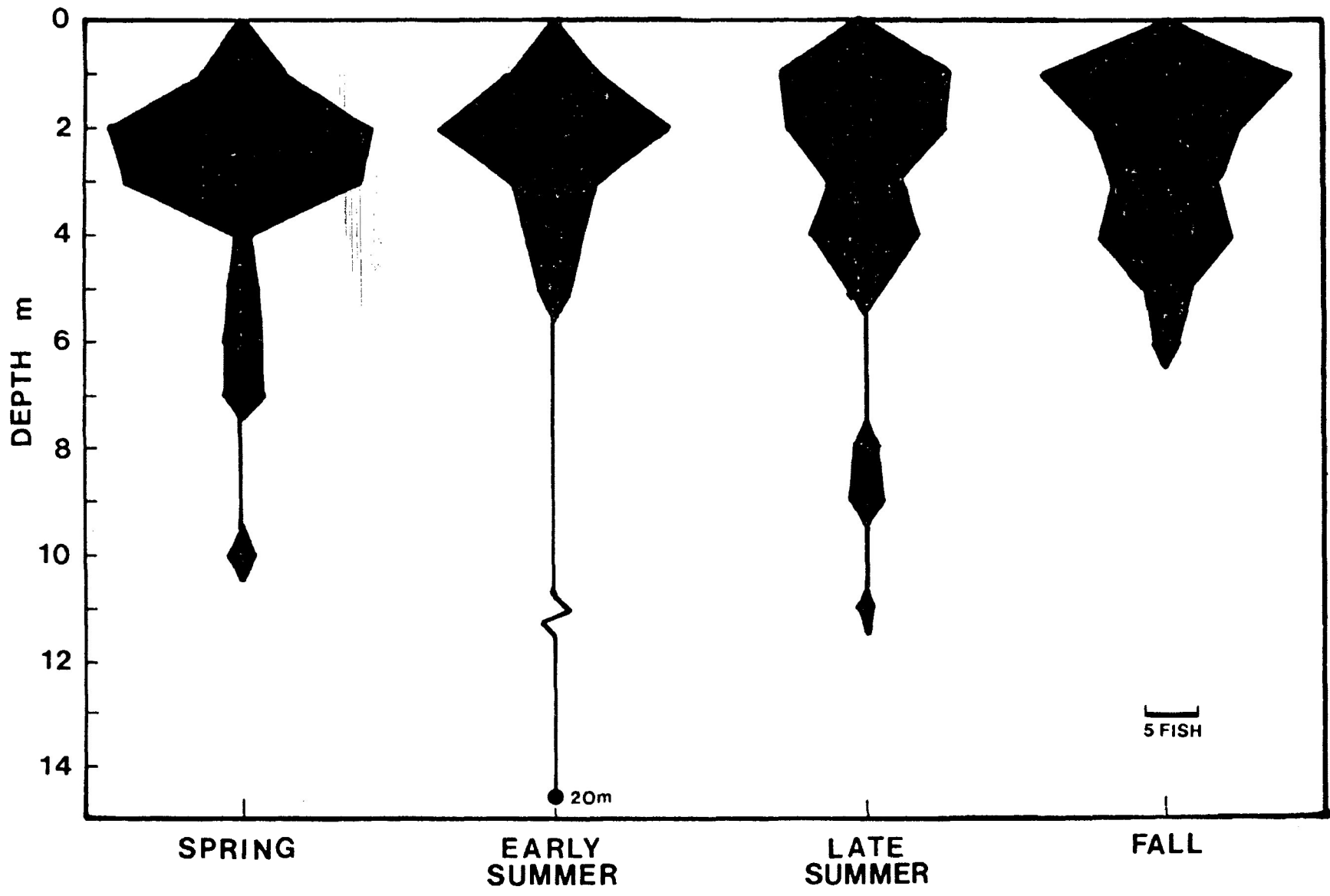


Table 1.7. Catch per unit effort (expressed as the number of fish/24 hours/100m of net) and amount of effort (E, expressed as the number of hours/15.24m of net fished/month) for northern pike (NP), lake trout (LT) and white sucker (WS) caught within gillnets set within Squeers Lake, Ontario at depths < 10 metres during the 1985 open-water season.

Depth (M)	May				June			
	E	LT	WS	NP	E	LT	WS	NP
0.0-0.9	154.0	2.1	59.7	8.3	183.0	2.6	13.8	3.4
1.0-1.9	178.3	21.2	27.6	9.6	183.0	8.6	28.9	6.9
2.0-2.9	201.3	13.2	44.5	6.3	136.0	4.9	35.7	5.4
3.0-3.9	133.0	18.4	27.2	2.4	114.3	6.9	87.5	2.7
4.0-4.9	86.5	49.5	22.2	-	67.5	2.3	54.8	1.2
5.0-5.9	42.8	1.8	1.8	-	22.8	-	34.6	-
6.0-6.9	42.8	-	-	-	22.8	6.9	13.8	6.9
7.0-7.9	22.0	-	-	-	-	-	-	-
8.0-8.9	22.0	-	-	-	-	-	-	-
9.0-9.9	22.0	14.3	14.3	-	-	-	-	-
	July				August			
	E	LT	WS	NP	E	LT	WS	NP
0.0-0.9	158.5	-	78.9	5.0	134.0	-	21.1	2.4
1.0-1.9	158.5	-	106.9	20.0	134.0	-	35.4	0.8
2.0-2.9	136.3	-	90.6	-	111.8	-	9.6	1.0
3.0-3.9	89.5	-	59.3	1.2	88.0	-	12.5	1.8
4.0-4.9	89.5	-	39.6	-	68.8	-	-	5.7
5.0-5.9	43.0	-	69.6	-	45.0	-	7.0	-
6.0-6.9	43.0	3.7	54.9	-	45.0	-	21.0	-
7.0-7.9	43.0	-	62.3	-	45.0	-	31.5	-
8.0-8.9	19.8	-	39.9	-	-	-	-	-
9.0-9.9	19.8	15.9	47.8	-	-	-	-	-
	September				October			
	E	LT	WS	NP	E	LT	WS	NP
0.0-0.9	109.5	-	8.2	2.9	121.5	18.7	-	13.0
1.0-1.9	109.5	-	21.6	8.2	121.5	21.4	1.7	2.6
2.0-2.9	88.5	0.9	6.2	1.4	97.0	25.8	5.2	6.5
3.0-3.9	65.0	-	3.6	4.8	90.5	17.9	2.3	4.0
4.0-4.9	43.5	-	-	-	70.8	20.0	4.5	1.1
5.0-5.9	43.5	-	-	-	45.0	49.0	7.0	-
6.0-6.9	43.5	-	3.6	-	46.3	20.4	-	3.4
7.0-7.9	59.8	2.6	10.5	-	46.3	57.9	-	3.4
8.0-8.9	59.8	4.0	13.2	13.2	-	-	-	-
9.0-9.9	77.5	3.0	16.3	4.1	-	-	-	-
	November							
	E	LT	WS	NP				
0.0-0.9	70.5	8.9	4.5	4.5				
1.0-1.9	70.5	13.4	11.8	2.9				
2.0-2.9	50.0	12.0	1.6	5.7				
3.0-3.9	30.0	3.7	-	1.6				
4.0-4.9	27.0	1.7	-	9.9				

area.

Netting suggests that northern pike generally moved alongshore. Northern pike were rarely caught at distances > 30 meters from shore (unless associated with one of the outlying reefs or rock shelves located within the lake) or at depths > 7m (Figure 1.6, Table 1.7). The majority of northern pike captured within gillnets were caught at depths between 2-6m (often at the point of the net located at a sharp drop off). The seasonal distribution of northern pike within the water column remained the same. Numbers do increase within the first meter during the late summer and fall periods (Figure 1.6). However, this generally reflected the increased susceptibility of y-o-y to gillnets at this time of year.

Activity of adult northern pike within Squeers Lake was crepuscular. Gillnet catches increased sharply with the onset of dusk, decreased slightly overnight and at dawn and noticeably decreased during daylight. Only 21% of the northern pike caught within gillnets set during 1984 and 1985 were captured between 08:00-18:00 hours (Figure 1.7, Table 1.8).

Young-of-the-Year

a) Distribution of Y-O-Y During the Open-water Season

Monitoring of young-of-the-year was initiated June 3, 1985, approximately 20-30 days post-spawning, and continued until November 6, 1985. Despite the use of a variety of gear (including .6m and 1.2m fyke nets, seines, plexiglass traps and fine mesh gillnets) throughout the lake's littoral area, y-o-y northern pike were not caught within the main basin until early to mid-August in

Figure 1.7. Diel activity of northern pike caught by index gillnets set within Squeers Lake, Ontario over four daily periods during the 1982, 1984 and 1985 open-water field seasons. (Note: the numbers above each bar depict actual sample size).

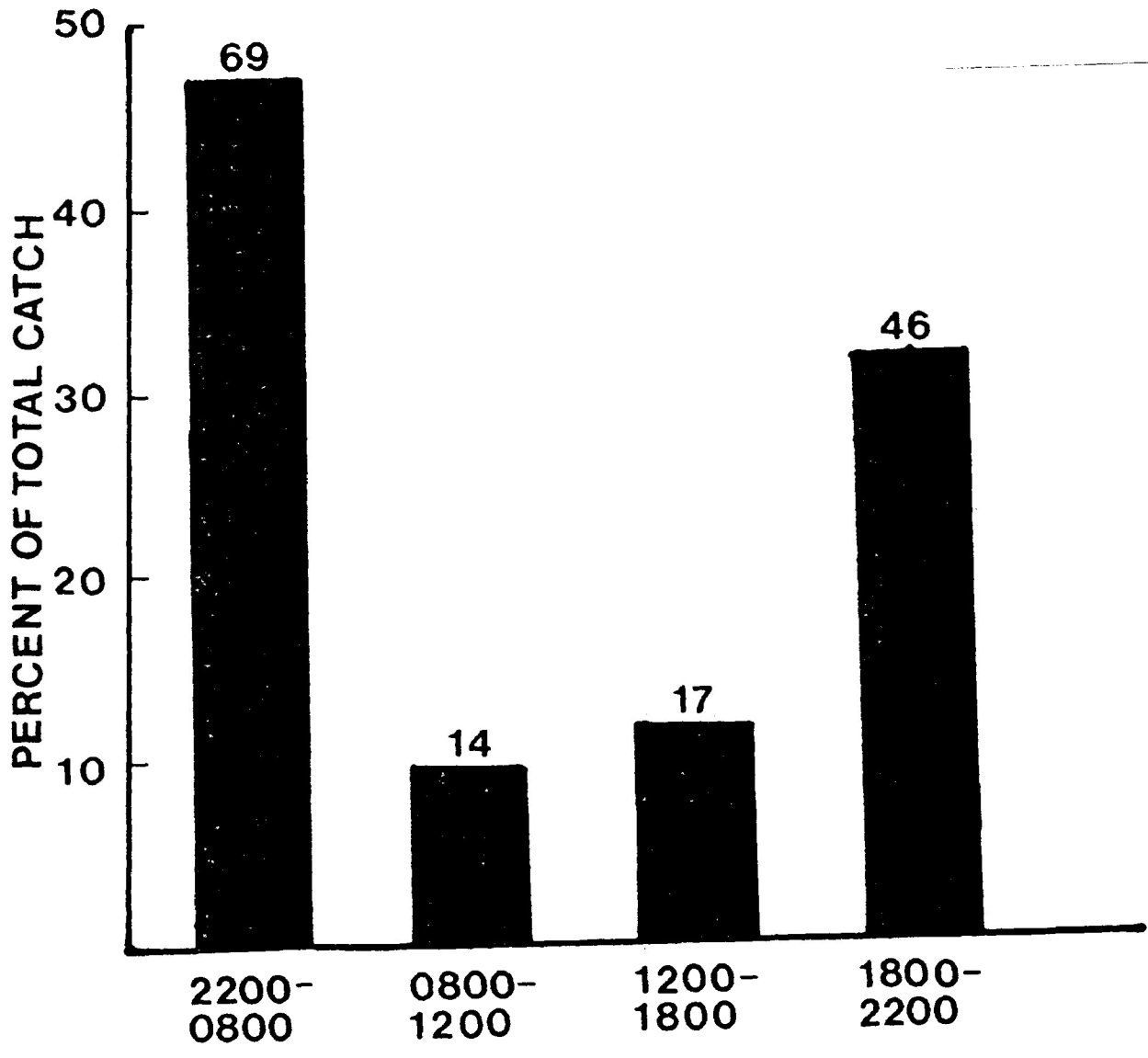


Table 1.8. Variation in the catch-per-unit-effort (expressed as the number of northern pike (NP), lake trout (LT), and white sucker (WS) during four daily periods over monthly sampling carried out on Squeers Lake, Ontario during the 1985 open-water season.

Month	TIME											
	08:00-12:00			12:00-18:00			18:00-22:00			22:00-08:00		
	LT	WS	NP	LT	WS	NP	LT	WS	NP	LT	WS	NP
May	0.44	0.04	0.17	0.07	0.08	0.08	1.19	2.41	0.38	1.04	1.73	0.11
June	0.16	0.22	0.14	0.18	0.40	0.04	0.20	2.46	0.64	0.18	2.66	0.27
July	0.00	0.22	0.18	0.00	0.46	0.18	0.05	2.36	0.06	0.05	6.23	0.21
August	0.00	0.40	0.00	0.00	0.04	0.04	0.00	3.25	0.40	0.00	1.15	0.10
September	0.04	0.04	0.17	0.04	0.08	0.00	0.00	2.51	0.68	0.22	1.36	0.50
October	0.00	0.00	0.15	0.05	0.00	0.16	2.63	0.63	0.59	1.07	0.17	0.42
November	0.00	0.00	0.23	1.18	0.21	0.63	0.83	0.12	0.45	0.05	0.00	0.20

both 1984 and 1985. This further suggests that the western arm provides the only major spawning and nursery area within Squeers Lake.

Shoreline and underwater transects disclosed y-o-y northern pike were associated with the narrow, intermittent fringe of emergent vegetation, or areas protected by overhanging shoreline vegetation (primarily leatherleaf, Chaemaedaphne calyculata) found along the shoreline of the western arm during the late spring - early summer period (ie June 3 - July 10). Submergent vegetation was sparse to non-existent during these sample intervals. The aquatic macrophytes present (primarily Potamogeton spp.) had a height of approximately 10-15 cm by mid-June and .25-.5m in early July. Y-O-Y northern pike at this time could only be collected by using dipnets or plexiglass traps set approximately 2m from shore (Table 1.9). Seine catches within the central basin area of the western arm were low consisting primarily of yellow perch <50 mm or pelagic white sucker larvae (Table 1.10).

The annual dispersal of young-of-the-year northern pike toward the main lake basin begins by mid-June. Age 0+ pike were captured within plexiglass traps set within the channel area separating the two lake basins as early as June 13. Observed fry movement was greatest during daylight, with twice as many being caught during the afternoon vs morning lifts in June and July (Table 1.11).

Submergent macrophytes were abundant by early August, and were found throughout approximately 30% of the basin. Thick beds of Utricularia spp. found within the shallow (<.5m) westernmost portion of the basin apparently provided poor fish habitat. Seine

Table 1.9. Average number of pike young-of-the-year (YOY) and other associated small fish species caught within morning (M) and evening (E) lifts of Casselman traps (Casselman and Harvey 1973) set within the Western Arm of Squeers Lake, Ontario during the 1985 open-water season.

Species	Sample Month									
	June		July		August		Sept		Oct	
	M	E	M	E	M	E	M	E	M	E
Pike y-o-y	11	13	5	8	1	1	-	-	-	-
Blacknose Shiner										
<40 mm	20	20	7	2	117	6	62	346	-	1
40-60 mm	408	58	181	7	-	-	-	-	-	-
>60 mm	2	2	-	-	-	-	-	-	-	-
Yellow Perch										
<50 mm	6	5	28	3	65	35	3	180	-	-
50-100 mm	2	-	1	-	15	29	1	7	-	-
>100 mm	2	-	-	-	-	-	-	-	-	-
White Sucker										
<150 mm	-	-	-	-	4	-	-	-	-	-
≥150 mm	-	-	-	-	2	2	1	-	-	-
Longnose Dace	27	7	7	-	1	-	4	-	-	-
Burbot y-o-y	1	-	-	-	6	-	-	2	1	-
Iowa Darter	-	4	1	-	-	-	1	-	-	-
Nine-spine Stickleback	1	-	-	-	-	-	-	-	-	-
Number of Trap Locations:		10		6		6		4		5

catches from these areas (ie sites 1 and 2) were considerably lower than the other areas sampled within the basin (Table 1.10). Beds of Potamogeton spp. were located throughout the central portions of the western arm.

Age 0 and 1 northern pike fully utilize the Western basin. Every seine sweep made during August within this basin contained at least one individual per haul. However, numbers of fry captured with the plexiglass traps drastically fell by August suggesting that y-o-y northern pike were no longer as closely associated with the immediate shoreline and/or were as vulnerable to capture by this gear.

Young-of-the-year northern pike were vulnerable to the 25mm and 38mm index net meshes by early August. Young-of-the-year pike were caught along the entire length of the net set across the width of the Western Arm, indicating that they utilize all depths available within this basin. Gillnets set in the main basin also caught the first y-o-y at this time. The y-o-y captured within the main basin remained within shallower water areas (ie <3m), usually at distances <25m from shore.

By early September, the submergent vegetation had began to die. A decreased catch of y-o-y occurred within the Western Arm at this time. No y-o-y were captured within the plexiglass traps, and seine catches of northern pike fry had dropped sharply. However, large numbers of y-o-y yellow perch and blacknose shiner were captured within both gears at this time (Tables 1.9 and 1.10). Young-of-the-year northern pike continued to be captured within both lake basins throughout the remaining open-water sampling

Table 1.10. Summary of the number of fish caught by species at various seine locations within the Western Arm of Squeers Lake, Ontario during monthly 1985 summer netting activities.

Sample Site: Species	June			July			August					September					
	1	2	3	1	2	3	1	2	3	4	5	1	2	3	4	5	6
Northern Pike																	
y-o-y	-	-	-	-	-	-	1	-	2	3	1	1	-	-	-	-	-
_ 1 yr.	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-
Blacknose Shiner																	
4 cm	-	-	-	-	-	54	215	2	350	200	100	14	4	67	34	208	-
4-6 cm	-	2	-	6	34	6	-	-	-	40	-	-	-	-	-	1	-
6 cm	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Yellow Perch																	
5 cm	13	2	7	9	55	-	28	32	10	-	3	153	14	149	217	374	68
5-10 cm	-	-	-	3	28	-	8	16	10	15	13	11	7	27	33	-	34
10 cm	-	-	-	1	22	-	-	-	-	-	-	1	4	13	-	-	6
White Sucker																	
y-o-y	-	-	72	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15 cm	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-
Iowa Darter	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Burbot	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Longnose Dace	-	-	-	-	-	-	-	-	-	-	-	-	-	5	2	4	7

period (ie September - November), primarily within the sheltered bays along the southern shore of the lake.

b) Y-O-Y Growth and Dietary Changes

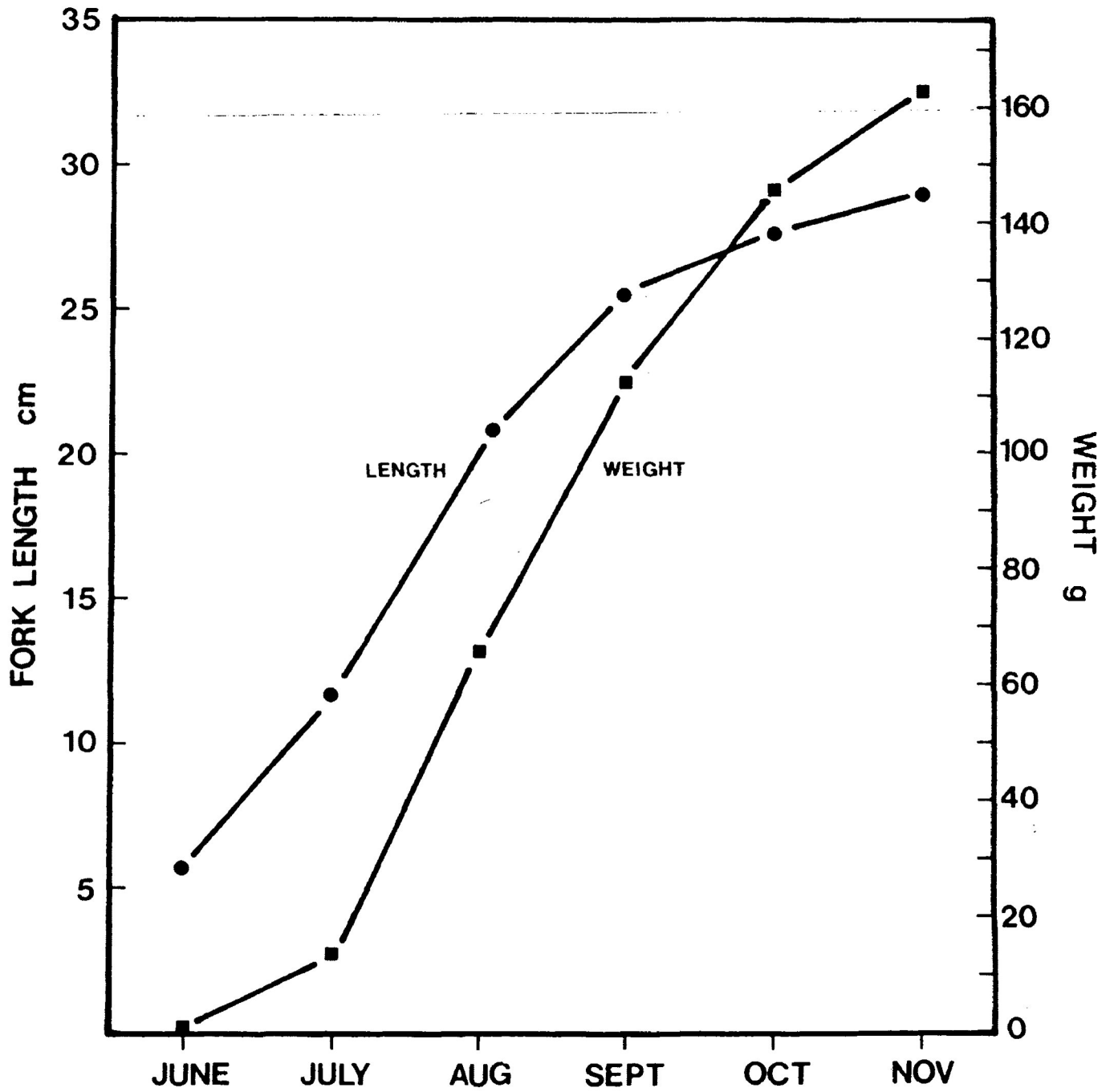
Y-O-Y northern pike grow rapidly within Squeers Lake (Figure 1.8). Y-O-Y exhibited an average rate of increase of 2.5mm/day between early June to early September. This rapid growth is accompanied by a rapid change in diet such that y-o-y are essentially piscivorous by early July, approximately 50 days post-spawning (Figure 1.9).

Age 0 northern pike collected approximately 20-30 days post-spawning, exhibit a mean fork length (\pm S.D.) and weight (\pm S.D.) of 56.4 ± 8.2 mm and 0.91 ± 0.21 grams. At this time, the principal prey item were cladocerans (consisting primarily of Polyphemus pediculus) which comprised 89% of the food items encountered. However, amphipods (Hyallolella azteca) and larval fish fry (primarily white sucker, Iowa darter and blacknose shiner) were already present, although in low numbers within the diet of larger individuals (ie within 59% and 24% of the stomachs sampled respectively).

By early July, y-o-y northern pike exhibited a mean fork length and weight of 117.8 ± 8.9 mm and 13.3 ± 2.8 g respectively. Although epibenthic invertebrates present within the diet in June were still present, fish (strictly y-o-y blacknose shiner) were found in most of the stomachs (ie 82%) containing food items.

Mean fork lengths and weights were 207.7 ± 2.7 mm 65.8 ± 22.0 g respectively by early August. By this time y-o-y northern pike were essentially piscivorous, feeding on the various components of

Figure 1.8. Mean monthly changes in the fork length (cm) and weight (g) of young-of-the-year northern pike sampled from Squeers Lake, Ontario during the 1985 field season.



the small fish community present within the western basin. Only rarely is there an inclusion of invertebrate prey items (primarily Hyallolella azteca). The size of the prey consumed increased such that items up to 100 mm FL were being utilized by late-August.

By early September, y-o-y northern pike have nearly reached their maximum length (Figure 1.8). However, y-o-y continue to increase in weight during fall. This is clearly shown by a 30% increase in mean weight between early September and early November (ie from 112.6 ± 18.0 g to 166.0 ± 35.3 g) despite a mean increase of only 30.2 mm in fork length during this same time.

Abundance and Distribution of the White Sucker and Lake Trout Populations

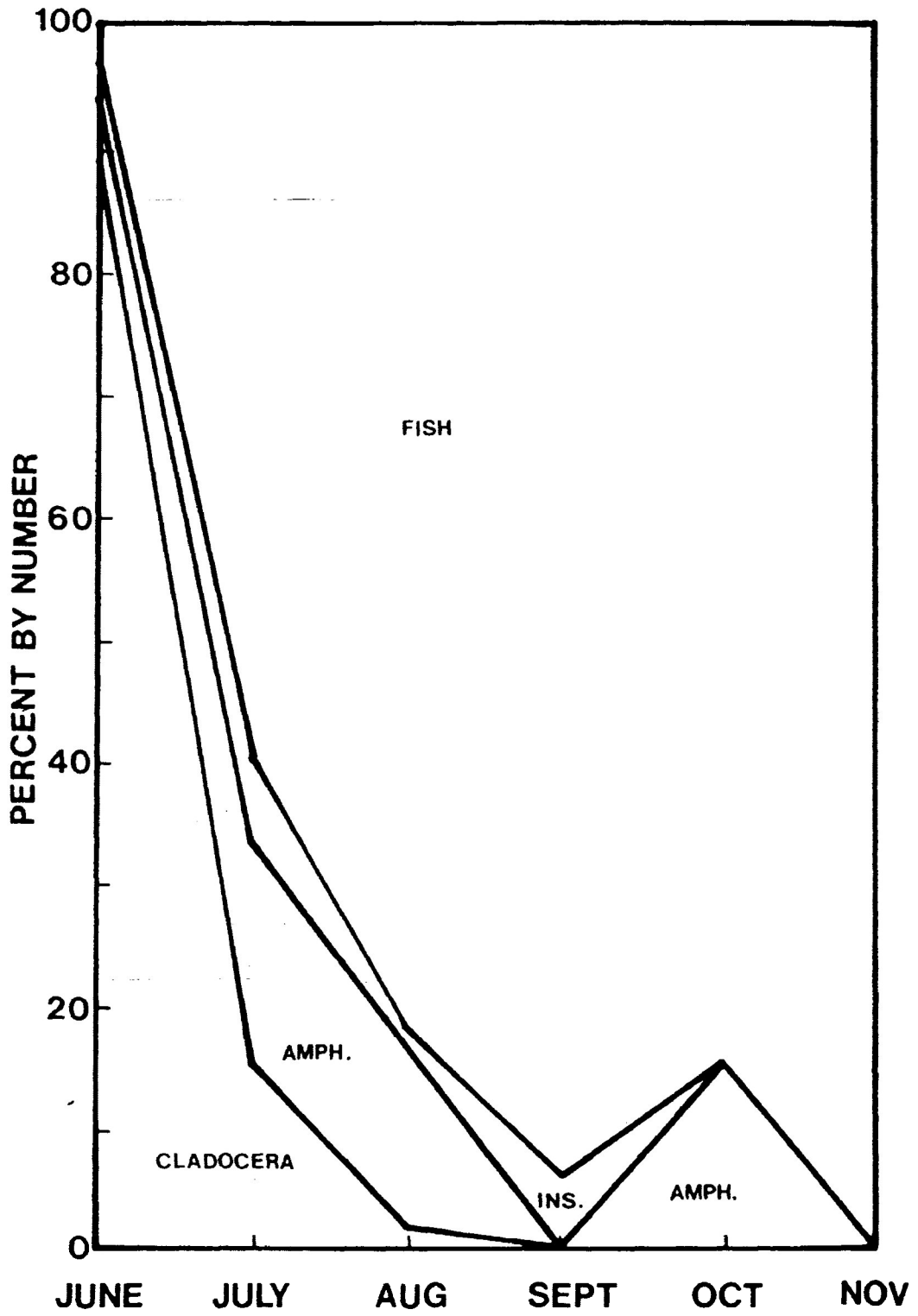
Population estimates and gillnet CUE results show white sucker and lake trout to be the most dominant species within Squeers Lake in terms of both numbers and biomass.

a) White Sucker

The spring, 1985 white sucker S-E population estimate was calculated to be 1457 fish >300 mm FL (95% C.L.=1220-1786). Gillnet results over the 1985 open-water period indicate that there were even greater numbers of suckers <300 mm FL. However, this size range could not be included within the population estimates due to their low vulnerability to this gear.

The potential for the mixing of fish populations between Squeers and Watershed Lake (the next lake downstream) was noted in late May, 1985. Despite the presence of an old beaver dam, spawning suckers from Watershed Lake utilize the Squeers Lake outflow stream and actually enter and congregate within the outflow

Figure 1.9. Monthly dietary changes exhibited by young-of-the-year northern pike sampled from Squeers Lake, Ontario during the 1985 field season.



bay of Squeers Lake. The possibility of the movement of other fish species between the two lakes was not examined, but should be considered, particularly if the beaver dam was removed.

White suckers, which were caught in nearly equal numbers at all depths $\leq 10\text{m}$ (Table 1.7), exhibited crepuscular and nocturnal activity patterns during sampling (Table 1.8). Very few suckers $>300\text{mm}$, however, were caught within the gillnets set at depths $\leq 10\text{m}$ during the 1985 summer stratified season (Table 1.12). This absence of larger suckers within these nets suggest the "adult" component of the population apparently inhabit the profundal area of the lake avoiding the shallow littoral areas during summer.

b) Lake Trout

The seasonal and vertical distribution of lake trout within the first 10 m of the Squeers Lake water column related directly to temperature. No fish were ever found in water temperatures exceeding 18 C. CUE data indicate that trout were found to occupy the shallow water strata only during the spring and fall sampling periods (Table 1.8). During this time, trout were captured at all depths and at all locations excepting the western arm. Netting shows that of the three major species, lake trout is the most active during daylight (Table 1.9).

There were approximately 7010 lake trout $> 360\text{mm}$ (C.L.=5733-7746) in 1985 within Squeers Lake (Ball 1988). Lake trout found at depths $\leq 10\text{m}$ during the spring prior to thermal stratification in 1982 and 1984 are larger than trout occupying depths $>10\text{m}$. However, even these exhibited a mean fork length of only 358mm (range=100-550mm), characteristic of a stunted population (Ball

Table 1.12. Monthly length distributions (by 100 mm length increments) of white sucker caught within index gillnets set within Squeers Lake, Ontario during the 1985 field season. Note: all netting effort was limited to depths ≤ 10 m.

Month	Length Intervals				
	100-199	200-299	300-399	400-499	≥ 500
May	46	23	16	58	3
June	90	69	26	22	-
July	168	138	14	28	-
August	21	37	15	3	-
September	6	14	10	8	-
October / November	1	1	2	16	-

1988).

DISCUSSION

Population Estimate Variability

Although population estimates approximate actual population size, choosing the most accurate estimate is difficult. There are a number of problems inherent in the use of any population estimates (Cormack 1968, Ricker 1975, Seber 1982). In a comparison of 4 population estimate techniques for a small brook trout (Salvelinus fontinalis) population, Havey et al (1981) found population estimates derived by different methods difficult to compare when the confidence intervals include the point estimate of each estimate employed (Table 1.1). In the present study, the 1984 and 1985 S-E and point Petersen population estimate series reflect the Squeers northern pike population size. However, the 1982 S-E estimate is likely too low whereas the 1982 Petersen estimate series is likely too high.

The situation within the present study closely parallel problems encountered by Havey et al (1981) in that the errors between population estimates are exacerbated by the field techniques used within the studies rather than any fault inherent within the methods used. Petersen estimates theoretically should be more accurate provided that there is no recruitment, emigration, immigration or excess mortality of tagged fish since they allow a greater time interval for mixing of marked vs unmarked fish and reduce the potential of "trap-happy" fish. However, there is an inherent problem with this type of estimate if there is an active

segregation of the fish population between sampling intervals, or before initial tagging actually begins. Northern pike have a quite disparate distribution within Squeers Lake. Individual northern pike were found throughout the lake at depths <10 meters (Figure 1.6). A true representation of the size of at least the mature portion of the population therefore would require a tagging series during the main spawning run. A majority of the northern pike tagging was carried out in one specific area of the lake in all 3 years of sampling (ie within the western arm which is the only area utilized for spawning by the mature population). Provided that this area was the only spawning area available, random dispersal throughout the lake would follow. However, in 1982 initial sampling occurred after the main portion of the mature population had spawned and left the area. Such a small population could not be accurately sampled once it had dispersed throughout the lake's littoral zone. The steep-sided nature of the lake's basin further compounded the problem by limiting the use of trapnets to the southern and eastern shores after northern pike had dispersed from the spawning area. Despite a similar amount of netting effort between 1982 and 1984, the numbers of fish actually marked and recaptured in 1982 was very low. This alone would lead to an underestimate by the S-E method simply because of the low numbers of fish actually handled in 1982, especially if any recaptured fish were "trap-happy" or exhibited a home range distribution as suggested for northern pike by Malinin (1969, cited in Diana et al 1977). The overestimate of the 1982 population estimates by the Petersen method would occur due to the capture of

a greater proportion of the mature fish within the population on or near the spawning areas where they were more vulnerable to capture in 1984 and 1985.

Therefore, although netting partly explains the imbalance between the estimates of population size, the disparate distribution of mature northern pike within deep, oligotrophic lakes obstructs attempts to determine population size, despite intensive netting effort. Either method would estimate the mature portions of such small populations provided that the initial mark-recapture period precedes the principal spawning period. If economics and logistics permit only one sampling period, then minimally the S-E estimate should be carried out. A second year's population estimate should be initiated however, in order i) to obtain a Petersen estimate as an independent check of the previous spring's S-E estimate and ii) to produce a second year's S-E estimate which would provide the minimum information required for an initial calculation of an annual production estimate of a given population.

Population Dynamics

a) Life Cycle and Possible Mechanisms Regulating Population Size

The mean age at the onset of maturity for the Squeers Lake population is similar to the mean age at maturity reported for other northwestern Ontario populations and appears "typical" for northern pike populations (Mosindy 1980, Donetz 1982, Reid 1985 and references cited therein). Northern pike mature as early as age 1 within southern extremes, and conversely, as late as age 5 within the northernmost part of its range.

Fecundity estimates for Squeers Lake northern pike are higher than previously reported for northwestern Ontario populations, but are apparently slightly below average when compared to that of other populations throughout its range. Table 1.13 expresses eggs/gram total body weight for a number of populations. Changes in northern pike fecundity appear to be a density dependent, stress-mediated physiological response (Kipling and Frost 1969, Bagenal 1973, Craig and Kipling 1983). This may account for differences between the northwestern Ontario populations. However, reasons for the low fecundity rates in northwestern Ontario compared to other area populations could not be appraised.

The spawning pattern of Squeers Lake northern pike is typical of other populations. Many populations undergo a migration out of the main lake into alternate spawning areas with or following ice-out (Carbine 1942; Carbine and Applegate 1948; Franklin and Smith 1963; Priegel and Krohn 1975; Koshinsky 1979; Gravel and Dube 1979). Present results agree with previous studies which report that males are first to enter spawning areas. The sex ratios of 1 female to 1.16 males in 1984 and 1.56 males in 1985 appear "typical" for northern pike populations, and fit well within the reported extreme ranges of 1.2:1 (Casselman 1975) and 1:3 (Carbine 1942). Water temperatures encountered during the present study (Appendix Table A.3) were well within the range of 5-17 C considered critical for spawning (Clark 1950; Fabricius and Gustaffson 1958; Franklin and Smith 1963; Priegel and Krohn 1975; Dumont et al 1979; Sukhanova 1979).

Before northern pike can successfully spawn, vegetation,

Table 1.13. Comparison of fecundity estimates (expressed as the number of eggs per gram overall body weight) for various populations of northern pike.

Lake	eggs/gram	Reference
Squeers L., Ontario	19.42	present study
Henderson L., Ontario	14.59	Nunan (1982)
Savanne L., Ontario	9.68	Mosindy (1980)
Lac la Ronge, Saskatchewan	25.29	Koshinsky (1979)
Houghton Lake, Michigan	23.50	Carbine (1944)
Lake George, Minnesota (1963)	28.83	Franklin and Smith
Minnesota Average	23.00	Carlander (1969)
Windermere, England	27.3-31.9	Frost and Kipling (1969)
Siljon, Sweden	13.2	Lindroth (1946, cited in Frost and Kipling 1969)

preferably flooded terrestrial grasses or emergent aquatic vegetation are required to support their phytophilous eggs (Carbine 1941; Fabricius and Gustaffson 1958; Forney 1968; Il'ina and Gordeyev 1970; McCarraher and Thomas 1972; Priegel and Krohn 1975; Dumont et al 1979). The paucity of emergent vegetation and total lack of submergent vegetation at the time of spawning, however, limits the actual area and type of habitat which can be utilized by the Squeers Lake spawning population. The potential area of spawning substrate within the western arm (including areas of overhanging leatherleaf which may be partially submerged at times of high water) varies between 700 and 1400 square meters depending on water levels. Since northern pike are a broadcast spawner (Fabricius and Gustaffson 1958), there may be insufficient vegetation for all the adhesive eggs produced. Eggs deposited on the vegetal remains from the previous year or soft silt may remain viable and hatch (Clark 1950; Frost and Kipling 1967). However, the present study did not investigate egg viability or hatching success.

The northern pike population is small but relatively stable (with annual estimates varying between 0.53-0.70 fish/ha). Forage is apparently adequate as indicated by a high growth rate for all length and age groups. The reproductive potential is also high with respect to the size of the mature population (with a population fecundity of approximately 5,647,257 eggs per annum, based on the 1985 spawning population). The size of the Squeers Lake population is therefore affected by a low recruitment into the mature portion of the population. This high mortality rate

between egg deposition and recruitment is likely due to the lack of spawning habitat and to a lesser extent nursery habitat. A very strong link has been established between the presence of vegetation and juvenile northern pike survival (Grimm 1981a,1983; Holland and Huston 1984,1985).

High egg deposition within a limited spawning area could result in an initial level of severe competition between newly hatched fry for both attachment locations and food resources. This would result in a high mortality and low growth rate (Fabricius and Gustaffson 1958). Density-dependent mortality of northern pike fry due to cannibalism may also potentially regulate numbers at high fry densities (Kipling and Frost 1970, Craig and Kipling 1983, Giles et al 1986, Wright and Giles 1987). Mortality rates from egg deposition to the fry emigration stage (approximately 30 days post-hatching) has been reported to be as high as 85-99.93% due to variations in habitat and climatic conditions (Carbine 1941, Franklin and Smith 1963, Forney 1968). Age 0 northernpike sampled within 20 days postspawning had grown rapidly, had full stomachs and exhibited no indication of cannibalism. This suggests that the key factors limiting pike numbers may occur prior to exogenous feeding.

Hassler (1970) demonstrated egg mortality rates approaching 100% if water temperatures either suddenly drop below 10 C or are prolonged at temperatures near 5 C. This could explain low egg survival in a water body such as the Western Arm of Squeers Lake which exhibits variable water temperatures which are directly proportional to changing air temperatures (Appendix A). Cold

spring water temperatures may also inhibit macrophyte growth thereby further reducing attachment sites and increasing crowding. Hassler (1970) demonstrated that siltation of eggs also resulted in high egg mortality (ie up to 97%), although once fry had hatched it was no longer important. Monten (1948, cited in Kipling and Frost 1970) gave mortality rates of 99.4% between the total number of eggs laid to fry (15-21mm), 99.1% between eggs laid to fry 9-13mm long (corresponding to the alevin stage which is still dependent on endogenous food sources), 78.1% between eggs hatched to fry 9-13mm long and 28.6% between fry 9-13mm to 15-21mm long. If the probability of survival to age 2 (ie 0.00002) observed in Windermere Lake from 1944 to 1980 (Craig and Kipling 1983) is applied to the 1985 Squeers Lake egg potential estimate, the resulting number of 113 age 2 fish is reasonably close to the actual number observed within this population.

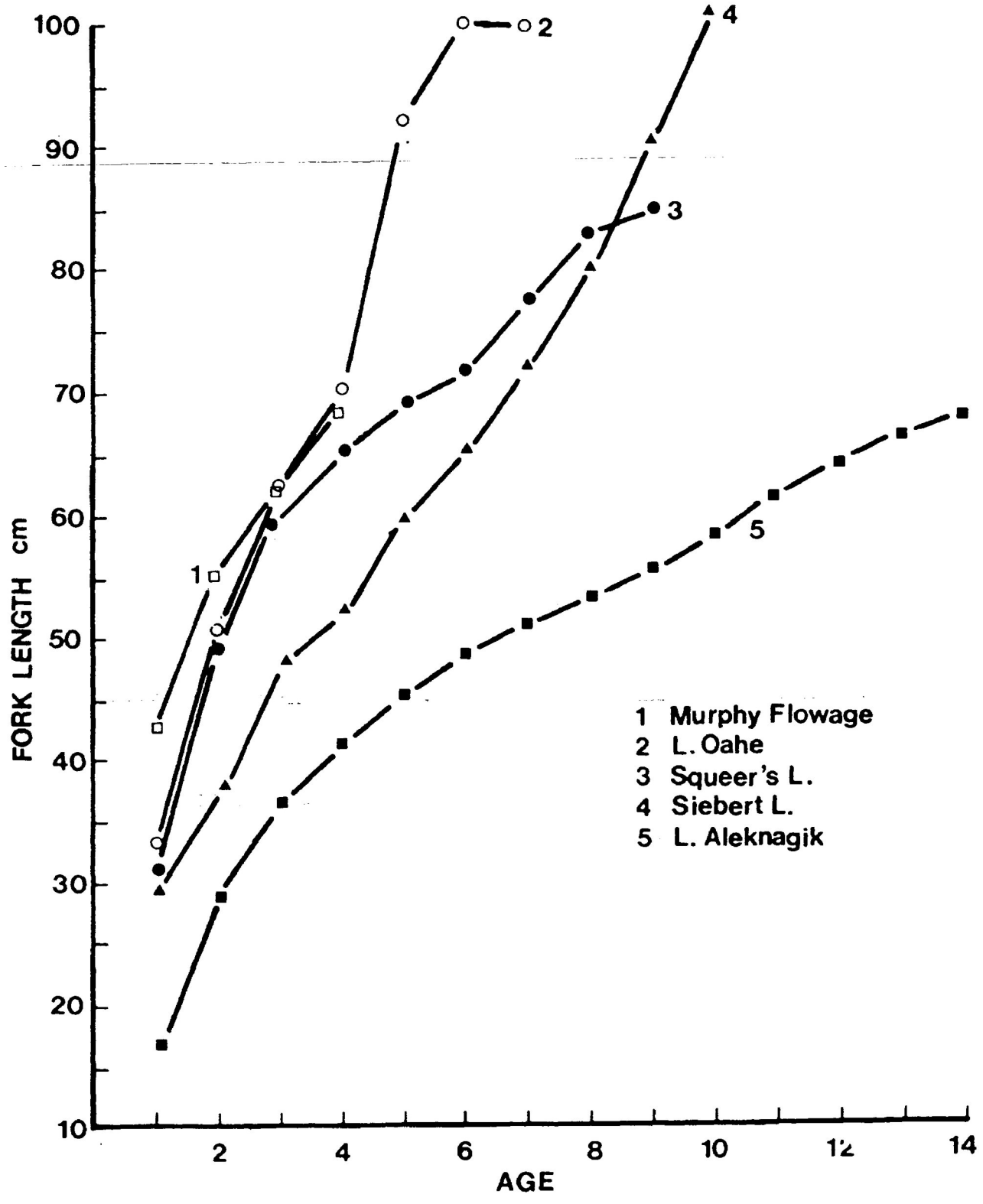
Fluctuating environmental conditions may be responsible for the annual variation in recruitment, although these factors were not examined. For a number of northern pike populations, fluctuating water levels or temperatures, particularly those caused by sudden cold snaps, heavy winds and rains, or the lack of inundated vegetation have delayed or totally inhibited spawning activities for a given year (Clark 1950; Fabricius and Gustaffson 1958; June 1970, 1974, 1977; Koshinsky 1979). Low water levels within Squeers Lake could also conceivably separate the two lake basins. Water levels never exceeded 40 cm within the shallowest portion of the channel connecting the two basins at the time of spring melt, and a depth of only 5 cm was recorded during late

August-November, 1985 despite "normal" precipitation levels for 1985. If the basins separated, this could either i) isolate the only spawning area within the lake during a spring drought or ii) if flow stopped after spawning, this would isolate age 0 and 1 fish within the western arm. In addition to increased conspecific competition for potentially limited resources (both habitat and food), y-o-y would not be able to migrate into the main basin. Hence, northern pike trapped within the western arm may also be faced with a winterkill situation. Oxygen levels within this basin (Appendix A) have reached potential winterkill conditions (Patriarche and Merna 1970, Casselman and Harvey 1975). All of these factors could adversely affect recruitment in low water years.

b) Growth and Production

Normally, northern pike growth should decrease with increasing latitude due to the strong relationship between temperature and growth (Miller and Kennedy 1948, Scott and Crossman 1973). However, the growth rate of Squeers Lake northern pike, a mid-range population, compares quite favourably with the more southerly populations such as those sampled from Murphy Flowage, Wisconsin or Lake Oahe, South and North Dakota (Figure 1.10). Because of exceptional growth during the first 3 years, the average calculated lengths at age attained by this population compares favourably with other North American populations, and greatly exceeds growth reported for sub-arctic (Miller and Kennedy 1948) and arctic oligotrophic lake populations (eg Lake Aleknagik, Alaska: Figure 1.10).

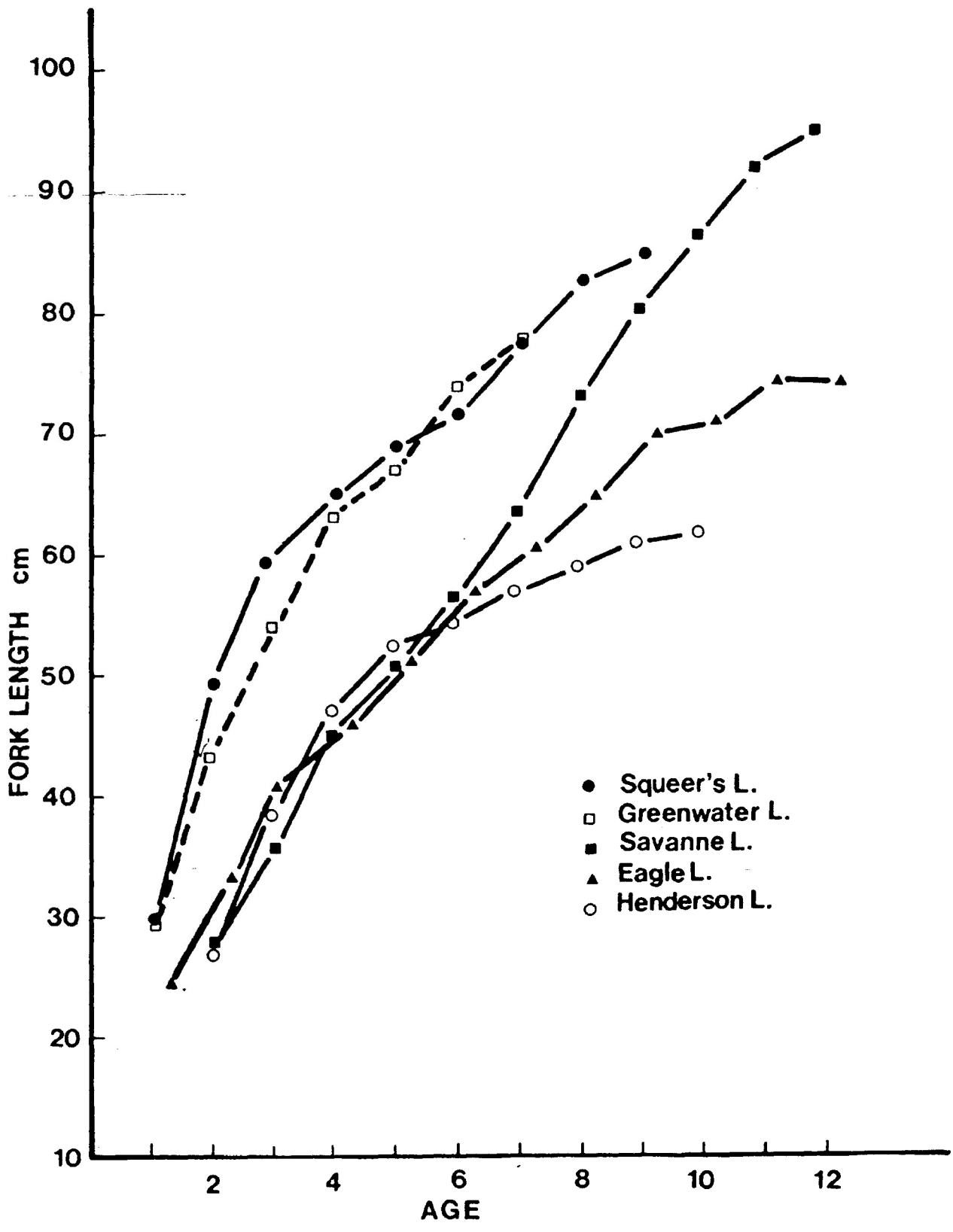
Figure 1.10. Comparisons in the mean length at age of northern pike from various populations found throughout its North American range.



Squeers Lake pike grow rapidly compared to the average reported for Ontario lakes (OMNR 1983), particularly in northwestern Ontario. Figure 1.11 displays the growth curves for 5 northwestern Ontario pike populations. These comparisons reveal some intriguing differences between the growth of populations from lakes of varying trophic level. The populations from low productivity lakes (Squeers and Greenwater Lakes), grew more rapidly than northern pike from mesotrophic (Eagle Lake: Chevalier 1975) and meso-eutrophic lakes (Henderson Lake: Nunan 1982; Savanne Lake: Mosindy 1980).

The length at age of fish from Greenwater Lake (a 3060.2 ha oligotrophic lake), was nearly identical to that exhibited by Squeers Lake fish (Figure 1.11). Furthermore, up to age 8, both of these populations grew more rapidly than populations from northwestern Ontario mesotrophic and meso-eutrophic water bodies. These observed differences in growth rates between lakes of varying trophic levels likely reflect the more abundant food source of an appropriate size found in oligotrophic lakes. This would promote good growth provided the population is of limited size. Mosindy (1980), Nunan (1982) and Reid (1985) all showed that no size-selective predation occurred within the more abundant northern pike populations found within meso-eutrophic Savanne (7.2 fish/ha) and Henderson (12.3 fish/ha) Lakes. These northern pike prey mainly on small food items, particularly yellow perch and aquatic macroinvertebrates. Few prey items >100 mm are consumed. In Squeers and Greenwater Lake small prey items are consumed when encountered (Chapter 3), but the most important food items within

Figure 1.11. Comparisons in the mean length at various ages of five northwestern Ontario northern pike populations.



the diet of northern pike >650 mm FL consists of larger prey items, (primarily white sucker and lake trout seasonally within Squeers Lake, white sucker and coregonids within Greenwater Lake). Since these northern pike utilize larger prey items and live within optimal summer temperatures (see below), they are able to grow faster in oligotrophic lakes.

Fish production estimates reflect both growth and biomass (Chapman 1978). The biomass, production and P/B ratios calculated for Squeers Lake pike are very low (Table 1.14). Only the Henderson Lake northern pike population prior to an experimental walleye pulse fishery (initiated in 1980) had a slightly lower P/B ratio. Fish in this lake exhibited very slow growth and the population was dominated by old fish (Nunan 1982). These production estimates, however, do not take into consideration the potential production of younger age classes. Clearly, age 0+ and 1+ fish within Squeers Lake were the most abundant year classes as made evident by the virtual number removed over the course of the 1985 open-water season. However, there was no accurate means of actually quantifying the numbers of these two age-classes. Similarly, the effects of sampling undoubtedly affected our production estimates, particularly in the older age groups. The level of sampling in 1984 would clearly put in place a potential bias on the production and population structure of a small "unexploited" population, despite later attempts to minimize sampling mortality.

The high growth rates achieved by the older age groups in Squeers Lake (particularly for the female component of the

Table 1.14. Production estimates for various populations of northern pike cited within the literature. Data Sources: Squeers Lake-present study; Henderson Lake-Nunan 1982; Savanne Lake-Mosindy 1980; Lake Windermere-Kipling and Frost 1970; River Stour and River Frome-Mann 1980; Alinen Mustajarvi-Rask and Arvola 1985; Lake Warniak-Ciepielewski 1973.

Lake	Age Classes	Number/ hectare	Biomass (kg)	Production (kg)	P/B
Squeers L., Ont.	3-7	0.6	1.33	0.23	0.084
Henderson L., Ont.	6-14	14.8	8.20	0.72	0.086
Savanne L., Ont.	4-12	7.5	8.69	2.76	0.318
Windermere, England	>2	33.6	5.49	3.77	0.687
River Stour, England	1-10	61.0	45.80	26.10	0.570
River Frome, England	0-10	159.0	68.60	51.50	0.750
Alinen Mustajarvi, Finland	-	20.0	6.90	2.60	0.400
Lake Warniak, Poland	2-9	33.0	22.30	13.80	0.620

population) resulted in a relatively constant level of mean biomass and production for ages 3-7, with some fluctuation on the basis of year-class strength. This continued increase in somatic growth rates of the population even after reaching reproductive maturation suggests that feeding conditions are optimal. They must be high in order to meet the metabolic demands and the diversion of energy toward the development of reproductive products in this population.

The high rate of mortality exhibited by northern pike > age 8 (independent of known sampling influences) suggest that these fish rarely live for more than 10 years within Squeers Lake. This population therefore exhibits an intermediate life span when compared to the reported range for other populations.

c) Feeding Behaviour and Conspecific Interaction

Northern pike are characterized as opportunistic predators feeding on whatever invertebrate or vertebrate prey item is most available (Scott and Crossman 1973). Within Squeers Lake, northern pike are piscivorous by the end of their first year (Figure 1.9), with the size and type of prey taken varying with the age and size of the fish (Table 1.6). However, all size groups consumed a wide size variety of prey sizes (Figure 1.5, Table 1.6).

Northern pike have been generally characterized as a sedentary fish (Ivanova 1969, Nursall 1973, Diana 1980). Radiotelemetry work (Diana et al 1977, Diana 1980, Chapman and Mackay 1984) demonstrated northern pike move < 1000 m, primarily during daylight. However, the development of home ranges apparently depends on the population being examined. Malinin (1969, cited in Diana et al 1977), Makowecki (1973) and Nunan (1982) suggest home

range development within their populations whereas Moen and Henegar (1971), Diana et al (1977), Diana (1980), Mosindy (1980), Chapman and Mackay (1984) and the present study failed to demonstrate any such pattern. The pattern of northern pike movement as determined by netting effort and tag recaptures within Squeers Lake strongly supports the telemetry work by Diana et al (1977) and Chapman and Mackay (1984). They demonstrated northern pike moved randomly at depths of 2-6m, usually around the edge of the lake. Furthermore, Diana et al (1977) demonstrated northern pike may revisit some areas several times. This could account within the present study for those few fish showing little displacement as determined by net recapture.

Although northern pike do not possess visual adaptations to low light conditions such as the tapetum lucidum in walleye (Ali et al 1977), northern pike in Squeers Lake are generally crepuscular (Figure 1.7). CUE results demonstrated that northern pike locomotor activity increased to a maximal level at dusk but decreased considerably by daylight the following day. Similar behavioural patterns have been exhibited by northern pike populations studied by Lawler (1969), Casselman (1978), Mackay and Craig (1983) and Trimble (1988). Net avoidance may cause some of the observed differences in the diel catches during periods of high light intensity (Diana 1980). However, this increased crepuscular activity within Squeers Lake may also correspond with an increase in feeding activity.

Due to the small population size, the diel feeding pattern of northern pike within Squeers Lake could not be quantified.

However, the crepuscular activity exhibited by this population corresponds with a period of peak movement (and therefore vulnerability to predation) of white sucker and yellow perch (Emery 1973, Engel and Magnuson 1976, Ritchie 1984, Trimble 1988). Additional information supporting this twilight feeding hypothesis is the seasonal presence of burbot within the northern pike's diet, which has been demonstrated to be strictly nocturnal with respect to its movement activities (Hackney 1973, Scott and Crossman 1973). The development of such a behavioural pattern would capitalize on the increased chance of encountering preferred prey items when most vulnerable.

Presently there are two foraging models in use to predict selection or predator preference. Hodgson and Kitchell (1987) succinctly summarized them as follows:

i) Functional Response Hypothesis: Prey appear in the diets of a predator in proportion to their encounter. Diet breadth remains unchanged or increases slightly as relative prey availability increases, and

ii) Optimal Foraging Hypothesis: The abundance of low-ranked prey in the diet is inversely proportional to that of more highly ranked prey. Diet breadth decreases with increases in relative prey availability because the presence of low ranked prey in the diet depends on the relative abundance of more highly ranked prey. Diet breadth decreases as relative prey availability increases.

In Squeers Lake, northern pike alter their diet to fully exploit the entire available food base. Despite previous studies suggesting that northern pike consume prey items $1/4$ - $1/3$ of their

overall size (Nursall 1973), the present study strongly supports Banks' (1970) contention that the overall size of the northern pike only sets an upper limit on the prey size consumed. The wide range in prey items and sizes utilized even though "optimal-sized" prey are abundant nullifies the underlying concepts of the optimal foraging hypothesis supported by Werner and Hall (1974), Werner and Gilliam (1984) and Hart and Connellan (1984). O'Brien et al (1986) while working on the zooplanktivorous white crappie (Pomoxis annularis), pointed out that since search time had already been expended to locate a prey item, the predator would have to expend further energy to reposition itself after the initial run should it fail to pursue the prey. This seems energetically advantageous not only for the planktivorous fish species worked on by O'Brien et al (1986), but for all ambush-type predators to always pursue and attack a located prey item. Hart and Hamrin (1988) demonstrated northern pike actually chose prey from the smaller size categories when multiple sized prey items are offered. The reason for this is that northern pike can easily accelerate to catch smaller prey items more readily than larger prey, given that both prey items are being pursued under similar conditions. Hart and Hamrin (1988) state the expected number caught is thus a function of the rate at which prey are encountered and the probability of capture. The large variability in size and type of prey items consumed by northern pike within Squeers Lake (Figure 1.5, Table 1.6) reflects substantial opportunism and strongly support these view points. The northern pike within Squeers Lake also take multiple prey items. This further enforces the

suggestion that it is more advantageous for individuals to consume any and all prey items encountered.

The above arguments do not discount the importance of large prey items within the diet. The occurrence of infrequent large prey items within the diet apparently provide a greater net benefit to an individual (Diana 1979, 1987). Nunan (1982) believed it was the absence of large prey items that limited northern pike growth within nearby Henderson Lake. Furthermore, adult northern pike changed their behavioural pattern such that they became crepuscular, thus coinciding their primary movements with the period of most active movement by their principal prey items (white sucker and yellow perch). This suggests that selective adjustment can occur. These results strongly support Hodgson and Kitchell's (1987) conclusion for largemouth bass another ambush-type predator, that "the rules for prey choice are more complex than those based on encounter frequency, yet not so rigorous as those based on prey switching and strict optimization". Therefore, northern pike within Squeers Lake may have modified their behaviour to correspond with the movement of their "preferred" food item, but will still feed on any prey item encountered.

Heterogeneous temperature regimes produced habitat segregation between age and size classes in the the Squeers Lake population. This may be an adaptation or response to limit competition for food or cannibalism (Schoener 1974, Keast 1978, Brandt 1980, Hamrin 1986). Due to the small populations size, the sub-adult and adult portions of the northern pike population can spatially segregate within Squeers Lake. The present study supported previously

demonstrated ontogenetic changes in temperature preferences. Larger fish generally occupy greater depths (and therefore cooler temperatures) than smaller fish (Ferguson 1958; Hokansen et al 1973; Casselman 1978; McCauley and Huggins 1979). Northern pike y-o-y have a distinctly higher thermal optimum for growth (ie 26 C, Hokanson et al 1972) than do adults (ie 18-20 C: Casselman 1978). The greatest numbers of y-o-y captured throughout the season remained within the western arm where water temperatures as high as 25.5 C were recorded. Adult northern pike, however, were rarely present within the western arm of the lake after spawning. These fish were most frequently caught at depths of 2-6m within the main lake basin, where water temperatures varied from 16-21 C during the summer period. Therefore, by staying within the main basin and deeper water, adult northern pike within Squeers Lake avoid any thermal stress conditions and actually occupy areas of optimal temperatures for metabolic activity throughout the summer months. Similarly, the utilization of the western arm by age 0 and 1 northern pike ensures these age classes remain within an environment which i) is near thermal optima, ii) contains apparently large prey populations of near optimal size, and iii) reduces the impact of potential conspecific competition and predation by being spatially separated from the adult component of the population.

Once y-o-y northern pike enter the main lake basin, their survival becomes extremely dependent on their foraging capacity. Initial studies have indicated that small fishes (including yellow perch) are abundant but concentrated within the small embayment and

sandy areas of the lake (Laine 1984; present study). This distributional pattern could reflect gear selectivity. However, if the gear accurately depicts the true distribution, y-o-y are forced to prey on rarely encountered forage until they find areas of concentrated food items. Northern pike are able to survive long periods of starvation (Ince and Thorpe 1975). Therefore, locating these forage areas is within the physiological capacity of y-o-y northern pike. Since the sheltered embayments are concentrated along the southeastern shoreline, this in part may explain why y-o-y were not caught in the sampling gear until August.

Species Interactions

The Squeers Lake lake trout - white sucker - northern pike fish assemblage is considered "typical" of 10% of all surveyed lakes in northwestern Ontario (Johnson et al 1977). On the basis of depth distribution (as determined by gillnet CUE expressed by depth of capture), there is a strong overlap in the habitat occupied by these three species during the fall and mid-spring period (Table 1.8). This study shows that northern pike concentrate at depths between 2-6m, lake trout frequent these areas but only when the lake is not thermally stratified, and white sucker are equally distributed on the bottom throughout the lake. All 3 species are most active during dusk and night.

Lake trout were caught in depths of less than 0.5m at all sampling locations besides the western arm during the spring and fall (Table 1.8). This suggests lake trout and northern pike in Squeers Lake undergo considerable spatial overlap within the littoral zone, at least when the lake is unstratified.

Lake trout and northern pike also do compete at some level for the same food supply. However, differences in food preference and areal distribution of the two species likely minimize direct competition. Lake trout inhabiting shallow areas (ie <10m) fed primarily on fishes, concentrating on yellow perch and the other small fish species (Ball 1988). A comparison of Schoener's (1970) dietary indices for both species, however, indicates low diet overlap between lake trout occupying the uppermost 10m of the water column and the 3 size categories of northern pike examined. Values varied between 0-0.12 when all dietary items were considered, and increased to only 0.07-0.43 when comparisons were limited to the piscivorous component of this polyphagous trout population. The largest overlap occurred between the 300-499 mm FL northern pike and piscivorous trout component of the 2 populations due primarily to the importance of the "small fish" component to the diet of both these fishes.

An ambush predator like the northern pike (Moody et al 1983) is capable of utilizing prey items up to 50% of its own size that it encounters because of its larger size (reflecting its rapid growth rate) and its large mouth-gape size (Keast 1978). Depending on the size of the fish, this would make all but the largest component of the white sucker and lake trout populations available as prey items.

Lake trout, on the basis of its much smaller overall size and more limited mouth-gape, should be considered to be a cruising predator which is thermally isolated from the lake's littoral zone during its most productive period. The very large population size

of this species within Squeers Lake has generally forced lake trout to forage on small prey of less than optimal size (Ball 1988). Previous studies have clearly shown that fish require food of increasingly larger size in order to continue their indeterminate growth (Kerr 1971). The high level of intraspecific competition demonstrated by this species, particularly during summer, as well as absence of a suitable pelagic forage fish species has resulted in a high consumption of microinvertebrates, which are apparently an energetically inferior food source at least to lake trout (Kerr and Martin 1970, Konkle and Sprules 1986, Ball 1988). The low growth rate in Squeers Lake fish suggests the lake trout's net energy intake was insufficient to meet its increased foraging demands and maintenance requirements, therefore limiting its overall mean size.

Therefore, although these two species do share the same microhabitat areas during this time period and to a lesser extent the same food resources, the differences in foraging behaviour, mouth-gape size, and overall size of the fish reduces competitive pressure between these two species. Furthermore, although there is a dietary overlap, the diet breadth is wide for both species and does not usually include the same fish prey species. This suggests there is little or no competition between these two piscine predators. However, the extremely slow growth of the Squeers Lake trout population may actually increase its potential as a prey item for northern pike.

Despite examining 588 stomachs, Ball (1988) found no evidence of lake trout predation on northern pike. Lake trout, however,

apparently form an important seasonal component of the diet of northern pike >700 mm FL such that it accounted for 38% and 53% of the total number and volume of food items encountered within stomachs during the unstratified portion of the year. If 38% of the diet of northern pike during the unstratified period is truly made up of lake trout at this time, and northern pike have a 1.7%-3% daily requirement during the winter months for maintenance as reported by Bevelheimer et al (1985) and Johnson (1966) respectively, the northern pike population within Squeers Lake could consume between 461.7-814.8 kg or 923-1630 lake trout as determined using the mean size of lake trout identified from stomachs containing these food items (Note: these daily requirement values represent the lowest and highest maintenance values found within the available literature for winter conditions). Although these levels may be construed to be a large amount of lake trout biomass removal, it still represents less than 14-23% of the estimated population size of lake trout >360mm FL present within the lake. Furthermore, the largest lake trout observed within a northern pike's stomach was only 350mm FL, indicating that the northern pike's predation pressure is acting only on the portion of the trout population which was not yet vulnerable to the gear in use for assessing lake trout population size. Similarly, although an estimated 753.3-1072.2 kg or 2283-3216 white sucker were estimated to have been consumed over the fall-spring period, few fish greater than 300mm FL were eaten. This proportion of the population which was fed upon was not included within the population estimate. This suggests that due to large population

sizes, northern pike predation pressure had minimal effects on the lake trout and white sucker populations.

Studies of co-habiting populations of lake trout and northern pike examined to date (Great Slave Lake: Rawson 1951; Keller Lake: Johnson 1972; Cold Lake: Roberts 1975; Lac la Ronge: Koshinsky 1979) have demonstrated that there was some dietary overlap. However, the northern pike's limited depth distribution around these lakes' periphery minimized the interaction between the two fish species. There was also no evidence of northern pike predation on the lake trout populations themselves within these lakes. However, this was readily explained by the relatively large mean size of lake trout found within the shallower portions of these lakes, and the distribution of smaller lake trout in the deeper offshore areas. Similar results were also found for northern pike populations which were found to co-habit with lake trout in northwestern Ontario lakes which also contained cisco and whitefish (Chapter 3, Laine 1986; QMLFAU, unpubl. data). The above results suggest that within lakes which contain cisco and/or whitefish, the predatory effort of northern pike on lake trout is limited due to the abundance of these slower, more suitably sized prey items. Due to their co-utilization of these pelagic fish species, lake trout also reach a larger maximal size, thus further reducing their potential as a prey item. Polyphagous lake trout populations are subject to seasonal predation by pike, however. This viewpoint is supported by Paterson (1968) who documented that polyphagous lake trout in Swan Lake, Alberta were eaten by northern pike, although the actual level of predation was not recorded. It

would appear however, the sizes of such lake trout populations are large enough to counter-balance any predatory effects exerted by northern pike.

The role and interaction between northern pike and the other fish species present in Squeers Lake is less clearly understood. The importance (at least on a seasonal basis) of white sucker, yellow perch and burbot are clearly indicated by the presence of these species within the northern pike's diet. However, the actual level of interaction between these species were not measured within the present study. Since it is primarily a benthivorous predator, there is little evidence large white sucker directly competes with northern pike. Similarly, although yellow perch and burbot are the only other potentially piscivorous species present within Squeers Lake, their lake distributional pattern and relatively small size (ie yellow perch are < 200 mm and burbot are < 400 mm) restrict the type and size of prey they consume. Therefore, no direct competition is suspected to occur between these species and northern pike >500 mm FL.

The interactions between y-o-y northern pike, age 0 and 1 burbot and all size classes of yellow perch which coinhabit the same microhabitat areas within the western arm, however, are unclear. Potential diet overlap among coinhabiting, age 0 zooplanktivorous fish species are probably influenced by a multiplicity of factors including the temporal similarity of mouth gapes, feeding modes, shifts to non-zooplanktivorous foods among fish species and the characteristics of the zooplankton community itself (Michaletz et al 1987). Zooplankton and aquatic macro-

invertebrates are the primary dietary component of similar sized yellow perch (Ritchie 1985, Trimble 1988) and burbot (Ryder and Kerr 1978) populations within nearby lakes. They are also the most important dietary component of age 0 northern pike from the point of first exogenous feeding until they switch to a piscivorous diet in early to mid-July. However, the apparent "full" nature and rapid growth rate exhibited by the y-o-y northern pike examined within the present study suggests that there are minimal competitive interactions between these species of the fish community.

CHAPTER TWO

THE VALIDITY OF USING SCALES AND CLEITHRA TO AGE A NORTHERN PIKE (Esox lucius) POPULATION FROM A SMALL, OLIGOTROPHIC LAKE

INTRODUCTION

Scales have traditionally been used to age northern pike (Williams 1955, Wainio 1966). However, a number of problems are inherent in the use of scales as the principal aging tissue. Evidence presented by Frost and Kipling (1959), Casselman (1974, 1978), Harrison and Hadley (1979) and Chihuly (1980) using other bony tissues suggested that scale ages often underestimated the age composition of northern pike following post-maturational decreases in growth, and may therefore affect estimates of growth, population structure, age at maturity and mortality. Since bony tissues preserve calcium which is often resorbed from scales, they provide a more valid aging tissue (Simkiss 1974). Casselman (1978, 1979) showed cleithra are much more accurate than scales for aging esocids. However, their use necessitates killing the fish.

Assessment of the demography of northern pike within Squeers Lake entails the accurate determination of the population's age composition. The small size of this population necessitated that few fish be killed. Therefore most age data were obtained from scales collected from live fish. Initially, scale and cleithrum ages from all sampled fish were compared in order to determine whether the same number of annuli were formed on both aging tissues. Such a comparison does not validate an age assessment, but simply provides a measure of agreement. It does however, provide some indication of the confidence to be placed in the

interpretations (Beamish and McFarlane 1983,1987; Casselman 1983). Beamish and McFarlane (1983) encouraged that assigned ages be validated so as to prove accuracy. They emphasized the importance of accurate age assessment in understanding life-history traits. Validation is considered successful only when the growth zones considered to be annuli are demonstrated to form annually for all age groups in a population either through the use of mark-recapture studies, or through the capture of known-age fish from the population (Beamish and McFarlane 1983, 1987). To ensure that zones identified as annuli on both aging tissues actually formed once a year, this study examined partially known aged fish from: i) a mark-recapture program and ii) a subsample of northern pike injected with oxytetracycline (OTC) during initial tagging in order to establish a "time" mark. OTC binds with proteins in the blood and is incorporated only in newly forming and mineralizing bone and cartilage (Frost et al 1961, cited in McFarlane and Beamish 1987). The use of such mark-recapture techniques and the placing of a spatial and temporal orientation mark in calcified tissue (such as through the use of OTC) not only provides the scientific basis required for age and growth assessment, but also reference material for improving subsequent interpretations (Casselman, 1983).

MATERIALS AND METHODS

Northern pike were sampled on Squeers Lake during 1982 by a Ministry of Natural Resources field crew and in 1984 and 1985 by the author. The majority of samples were taken from northern pike

captured during spring population estimates over the three years of sampling. At that time, fish were anesthetized with MS 222, sampled, tagged with an individually numbered oval Floy tag, given an accessory clip, and released. Sampling included the determination of sex by external means if possible, a fork length, total length and weight measurement, and a scale sample from above the lateral line, just anterior to the dorsal fin, on the left side of the fish. Scale samples were taken from the right side of the fish upon subsequent recapture. A portion of the fish captured in 1982 (n=44) and 1984 (n=75) were also given an intraperitoneal injection of 0.5 cc oxytetracycline (brand name Liquimycin) per kilogram of body weight in order to produce a "time" mark on bony tissues (Weber and Ridgeway 1962, Kobayashi et al 1964).

Additionally, cleithra and previous tagging history was recorded from all northern pike sacrificed during subsequent monthly index gillnetting (a more detailed description of the netting activities carried out for this study is available in Chapter 1). Sacrificed fish were representative of all size classes (and hopefully all age groups) within the population. The index netting program also included a sample of 77 young-of-the-year and 52 yearling northern pike which were used to identify and locate the first annulus. Of the 125 northern pike over age two which were fully sampled, a total of 44 (35%) had been injected with OTC.

Ages for all northern pike sampled were determined by counting the number of annuli visible on scale impressions made on cellulose acetate slides by a hand operated roller. Annuli were

assigned following the criteria outlined by Williams (1955), Frost and Kipling (1959), Wainio (1966) and Casselman (1967). The scale impressions were read on a microfiche reader at 24-33X magnification. The locations of each year increment were marked on a paper slip, and the time of year that annulus formation (as determined by the presence of "plus" growth following the outermost annulus) occurred was noted. From the scale samples of all recaptured northern pike examined, the number of interpreted annuli at the time of release and at recapture for each fish were compared in order to determine if only one of the interpreted annuli was formed annually.

The cleithra from all northern pike sacrificed for the present study were viewed under a magnifying lamp (at a magnification of 4X) against a black background. Annuli were assigned following the criteria outlined by Casselman (1979). All cleithra collected during the present study were also examined under a dissecting microscope at 6X using an ultraviolet light source for the presence of OTC marks. The location of the OTC label on the "marked" cleithrum with respect to the outside edge was noted, and the number of apparent annuli outside the mark was recorded. To ensure unbiased reading and that the mark identified as an OTC label was not due to natural fluorescence, all cleithra were examined under ultraviolet light in order of collection. Any doubtful marks present on any of the cleithra were not considered to be an OTC label.

Precision of interpretation between tissues from the same individual fish and two readers was calculated initially by

determining the percentage level of disagreement. However, percent agreement assesses only whether ages assessed by one method equals that of the other method. It does not quantify the magnitude of differences (Mills and Beamish 1980), nor account for the number of age classes within the population (Beamish and Fournier 1981). Therefore two alternative indices were also calculated to determine the reproducibility of the ages assigned between tissues and agers. Beamish and Fournier (1981) and Chang (1982) alternatively proposed the use of the average percent error (APE) and of the coefficient of variation (CV) and an index of precision (D) respectively, ie.

$$\text{APE} = 1/R \sum |X_{ij} - X_j| / j * 100$$

$$\text{CV} = 1/R \sum \text{Standard Deviation} / X_j * 100$$

$$D = \text{CV} / \sqrt{R}$$

where R = the number of times the sample was aged

X_{ij} = the i th age determination of the j th fish

and X_j = the average age calculated for the j th fish.

These measurements are not age independent and provide a statistical basis to evaluate the reproducibility of age estimates between tissues and/or agers.

RESULTS

Comparison of Scale and Cleithra Ages

Generally, both scales and cleithra from Squeers Lake northern pike exhibited a readily identifiable pattern of growth zones. Only a low level of disagreement occurred between the ages assigned to scales and cleithra from the same individual by the principal ager for this study. There was 92% total agreement and 99%

agreement within +1 year between the ages assigned to the two tissues (Table 2.1). Disagreements between the two tissues occurred as early as age 4 (Appendix Table C.1). However there was a very high level of precision between the two aging structures as demonstrated by the very low values of the mean average percentage error, coefficient of variation and index of precision (Table 2.1). Whenever disagreements occurred, cleithral ages were generally older than scale ages.

A definite difference was evident with respect to aging fish of different sexes. There was 100% agreement between the scale and cleithral ages in females. However, some aging difficulties were encountered with the scales and to a lesser extent with cleithra collected from males, particularly those over 8 years of age. Annuli of male fish became more crowded at the edge and had a much greater incidence of pseudo-annuli, particularly on the cleithra.

Ages assigned to a subsample of 60 fish by a second reader produced an overall lower percentage agreement (72%) between the two tissues. However, the mean APE, V or D values did not exceed 3%, which reflects that the precision level was still high (Table 2.1).

Comparisons of Ages Assigned to Scales and Cleithra by Two Readers

Comparing the ages assigned by two readers to the same structure, cleithra gave the best results with 88% total agreement. However, both scale and cleithral ages had 93% and 97-98% agreement within \pm one year and \pm two years respectively, and the mean values for APE, V and D were all $< 3\%$ (indicating a high level of

Table 2.1. Percent frequencies of agreement, mean index of average error (APE), coefficient of variation (V) and index of precision (D) for northern pike ages from samples collected from Squeers Lake, Ontario, as determined from scales (Sc) and cleithra (Cl) by two readers.

Reader	Structure	N	% Agreement				APE (%)	V (%)	D (%)
			100	+1yr	+2yr	+3yr			
1	Sc:Cl	155	92	99	100	-	0.56	0.80	0.57
2	Sc:Cl	57	72	89	97	100	2.51	3.86	2.73
1 and 2	Sc	113	78	93	97	100	1.78	2.51	1.73
1 and 2	Cl	61	88	93	98	100	1.15	1.20	0.85

agreement between the two readers for either aging tissue)(Table 2.1). Overall, the principal ager (Reader 1) assigned older ages to the same tissue relative to the second reader (Appendix Table C.2). The major discrepancy came in determining whether plus growth had yet begun within a given growing season. However, no problem occurred with respect to the location of the first annulus.

Time of Annulus Formation

The major aging problems in this study dealt with the presence or absence of plus growth on the outside edge of the scale from samples collected during May to July (Note: for purposes of the present paper, plus growth was defined to occur when a minimum of 1-3 circuli were present after the outermost annulus). Therefore, the time of annulus formation for Squeers Lake northern pike was determined by examining scales and cleithra collected during April to September. This information was supplemented by the multiple recapture of tagged fish over the course of the same year.

The time of annulus formation varied with both age and the type of aging tissue used. No new growth was evident at the outer edge of either tissue until mid-May to early June, when fish formed the first to third annuli (Tables 2.2-2.3). Older age groups, however, did not begin to display annulus formation until mid- to late June, and annulus formation was not fully complete on either aging tissue until mid- to late July. At this time, some difficulty occurred in interpreting the edge of the aging structure, particularly with older, slower growing males. In several instances it could not be determined if the narrow band of translucent material on the outside edge had been formed previously

Table 2.2. Time of annulus formation as determined by the presence of new growth following the outermost annuli on scales collected from northern pike sampled from Squeers Lake, Ontario during 1982, 1984 and 1985. The numerator represents the number of fish sampled during a given time period showing plus growth whereas the denominator represents the actual number of a given age group sampled.

Scale Age(years)	May			June			July	August
	1-10	11-20	21-31	1-10	11-20	21-30	1-10	1-10
1	0/5	3/4	4/4	8/8	3/3	2/2	5/5	6/6
2	-	0/4	1/3	4/5	9/10	-	1/1	-
3	0/18	2/23	0/5	3/9	5/12	2/3	7/9	3/3
4	0/23	3/30	0/3	1/4	3/6	1/9	4/5	-
5	0/7	4/29	0/1	2/8	4/12	6/10	0/2	-
6	0/20	0/25	0/3	0/7	1/9	0/1	1/5	-
7	0/34	0/17	0/2	0/4	0/5	0/3	0/1	0/1
8	0/24	0/11	0/1	0/3	0/1	-	0/1	1/1
9	0/5	0/4	0/2	0/1	-	0/1	-	1/1
10	0/2	0/2	-	-	0/1	0/1	-	-
11	0/5	-	-	-	0/1	-	-	-
12	0/1	-	-	-	0/1	-	-	-

Table 2.3. Time of annulus formation as determined by the presence of new growth following the outermost annuli evident on cleithra collected from northern pike sampled from Squeers Lake, Ontario during 1982, 1984 and 1985. The numerator represents the number of fish sampled during a given time period showing plus growth whereas the denominator represents the actual number of a given age group sampled.

Cleithra Age (years)	May 1- May 20	May 20- June 10	June 10-20	July 1-10	August 1-10
1	0/5	7/8	4/4	5/5	3/3
2	0/1	1/2	1/2	0/1	-
3	0/1	0/3	1/3	4/4	3/3
4	0/1	0/2	2/5	1/2	-
5	-	0/2	4/9	0/1	-
6	0/1	0/1	1/4	-	1/1
7	0/1	0/6	0/4	0/2	-
8	0/3	0/3	-	-	-
9	-	-	0/1	0/1	-
10	-	-	0/1	-	0/1

or within a given calendar year. In all cases, annulus formation on scales preceded such development on cleithra.

Validation by Mark-Recapture

Comparing age at release with age at recapture of tagged fish indicated that either scales or cleithra are valid for aging Squeers Lake northern pike to at least age 12 (Table 2.4, Appendix Table C.3). Scale annuli agreed with the known-age of the fish 90.5% of the time. Of those misaged, 84% (16) were underaged by one year. There was 100% agreement between assigned cleithra age and expected age. When growth between the time of initial spring tagging and time of recapture was compared, 16 fish (8 males, 2 females and 6 of unknown sex) showed fewer annuli than expected, 8 exhibited less than 1 cm of growth while 13 exhibited less than 2 cm of growth over a period varying from 4 months to 2 years.

Validation Through the Use of Oxytetracycline Established Marks

Of the 44 and 75 fish tagged and injected with OTC in 1982 and 1984 respectively, a total of 44 (37%) (including 2-1982 and 1-1984 tag losses) were recaptured over the 1982, 1984 and 1985 sampling periods. This ratio is similar to that used in previous studies which have utilized OTC labels on bony tissues (Beamish et al 1983, McFarlane and Beamish 1987). It suggests that the procedure used did not increase the mortality rate of oxytetracycline injected fish, a concern raised by McFarlane and Beamish (1987). Seventy-five percent of this sample exhibited an OTC mark on the cleithra. The mark was clearly visible on the majority of the samples as a bright yellow band under ultraviolet light, particularly on the anterior third portion of the cleithra.

Table 2.4. Comparison of the expected and actual number of annuli formed on scales collected from recaptured northern pike initially tagged in Squeers Lake, Ontario during 1982, 1984 and 1985. (Note: the underlined values are the number of northern pike which formed the expected number of annuli over the given time of release before recapture)

Number of Annuli formed	Number of years after tagging			
	0	1	2	3
-1	8	-	-	-
0	<u>87</u>	4	-	-
1	-	<u>67</u>	2	2*
2	1	1	<u>10</u>	2
3	-	-	-	<u>7</u>

*sample number represents the same fish which was caught twice during the 1985 tagging season.

Some fish exhibited a very wide tetracycline mark. This overfluorescence was caused by bone growth being more than just unidimensional (Brothers 1983).

The cleithral age from fish recaptured one to three years after initial release had correspondingly increased by one to three years at recapture (Table 2.5). Scale ages for 30 of the 33 samples also agreed with cleithral ages assigned. The fork lengths of two mature males showed fewer annuli than expected on scales. These fish had increased by less than 1 cm over one and three years respectively. The third sample being an apparent tag loss had no initial fork length information available.

DISCUSSION

The high percent frequency of agreement and low index of average error and index of precision between aging tissues and between agers (Table 2.1) indicates both scales and cleithra seem equally suitable tissues for assigning age structure to Squeers Lake northern pike provided that marks interpreted as annuli are in fact annually formed. Some disagreement occurred in assigned ages given by the two readers for both aging tissues. However 35% and 66% of the ± 1 year disagreement between scales and cleithra respectively was accounted for by the presence/absence of plus growth. This type of disagreement underlines the importance of using a coding system such as the one developed by Casselman (1983) which describes both the number of annuli present, and the condition of the outside edge of the scale following the last

Table 2.5. Comparison of the expected and actual number of newly formed annuli following the oxytetracycline label on cleithra from northern pike recovered from Squeers Lake, Ontario one month to three years following initial capture and the intraperitoneal injection of 0.5 cc/kilogram oxytetracycline.

Number of annuli formed	<u>Number of annuli expected</u>				Age groups represented
	0	1	2	3	
0	7	-	-	-	3-7
1	-	20	-	-	3-8
2	-	-	1	-	6
3	-	-	-	5	7-11

annulus and of documenting the time of annulus formation for all age groups within a given population. The results follow a general trend for most fish species such that when differences between aging tissues occurs, scale ages are generally lower than corresponding ages determined from an alternate bony tissue.

The present study strongly supports previous findings that the time of annulus formation depends on age and occurs earlier in young, sexually immature fish (Casselman, 1967, 1978). Casselman (1967) believed that for immature northern pike, temperature was the most important factor controlling linear growth and annulus formation. However, in mature northern pike, Casselman (1967) believed that annulus formation represented a combination of: a cessation in growth related to decreasing water temperature; the accumulation of reproductive products; and an interruption in the resumption of growth in the spring due to spawning.

The problems associated with not validating age determinations have been discussed by Beamish and McFarlane (1983, 1987), Brothers (1983) and Casselman (1983). However, despite the number of studies examining the age and growth of northern pike, only two have actually validated their aging techniques either through the use of mark-recapture or OTC marking methods (Frost and Kipling 1959, Casselman 1978). The results from the present mark-recapture and OTC marking experiments confirm that the checks identified on both aging tissues within the present study were in fact annuli. Upon recovery of these fish and examination of the scales and/or cleithrum, i) the number of expected zones had formed beyond the previously identified age or ii) the number of zones following the

OTC mark equalled the number of years at liberty in most cases. Particularly interesting were fish which showed fewer annuli than expected on scales and exhibited little or no growth over the period of time of initial tagging and subsequent recapture. The scope of the present study did not permit us to determine whether this lack of growth was due to continuous handling (some of these fish were handled up to four times within the time frame of the study) or the nearly complete cessation of growth by these individuals. The majority of these fish were older mature males (ie. 11 of 13).

In the future, any study assessing ages of northern pike populations in northern Ontario should include a combination of both scales and cleithra for age assignment. The present study has demonstrated the validity of using either scales or cleithra to assign ages to northern pike, at least within Squeers Lake. The results also suggest that, provided the precision level between the two tissues in estimating ages are high, scales will provide a much quicker method of age assessment while also allowing for the live release of the sampled fish. Ricker (1975) and Powers (1983) both feel a 10% precision level is acceptable. However, they were dealing with marine fisheries having species with 20 or more age classes. When examining populations of shorter lived species such as northern pike, which rarely have more than 10 major age classes, a 5% precision level should be used. A maximum mean APE, CV, or D level of 5% would ensure a 95% chance that an individual fish could be assigned the same age, regardless of tissues used or agers involved. This would ensure a method that is both consistently

repeatable and practical (Prince et al 1985). A mark-recapture or OTC labelling program should be considered if the precision level exceeds 5%. This would ensure that the age structure for the sampled portion of the population is validated. The ease of analysis of this additional data collected from any ongoing mark-recapture program would quickly validate the population's age structure.

Therefore if there is a high precision level between validated scales and cleithra, scales can be used as the principle aging tissue for northern pike (although any study using a combination of the two tissues would be superior to studies using only scales). This would permit live release thereby lowering the impact on the examined population while still ensuring a high degree of accuracy in age determination.

CHAPTER THREE
THE POTENTIAL ROLE OF LAKE MORPHOMETRY AND WATER CHEMISTRY ON THE
REGULATION OF POPULATION SIZE AND GROWTH OF NORTHERN PIKE FROM 14
NORTHWESTERN ONTARIO LAKES

INTRODUCTION

Northern pike (Esox lucius) have been extensively studied throughout its holarctic distribution. Tolerant of a wide range of environmental conditions, northern pike achieve maximum abundance in large, shallow mesotrophic lakes (Scott and Crossman 1974, Inskip 1982). Northern pike are solitary (Scott and Crossman 1973, Diana et al 1977, Diana 1980, Chapman and Mackay 1984) and opportunistic in their feeding habits (Lawler 1965, Scott and Crossman 1973, Mann 1982).

Despite the large number of northern pike populations and their importance as the second most frequently caught and kept game fish in northwestern Ontario (Dentry et al 1980, Bedi and Clifford 1980), this species has not received much attention from researchers. Exceptions are studies by: i) Mosindy on the northern pike population present within Savanne Lake (1980) ii) Donetz (1982) who synthesized the information on populations from Lake of the Woods prior to 1982, iii) Nunan (1982), Reid (1986) and Wisenden (1988) who examined the northern pike population within Henderson Lake as part of the community response to walleye (Stizostedion vitreum) removal via a pulse fishery and iv) the author, who examined northern pike within Squeers Lake (Chapter 1, this study). Initial comparisons made of growth rates between pike populations from 5 northwestern Ontario lakes of varying physico-chemical properties suggested northern pike grew more rapidly in

oligotrophic rather than in the more "typical" mesotrophic lakes (Chapter 1). However, as stated within Chapter 1, there is little information available on northern pike populations from oligotrophic lakes.

An understanding of the factors which influence northern pike growth and population size have practical management applications. Therefore the objectives of this study were i) to determine the population characteristics (ie abundance, age and size structure, growth, age at maturity and survival) for populations from 6 northwestern Ontario oligotrophic lakes, ii) to compare these to 8 populations found within mesotrophic and meso-eutrophic lakes and iii) offer suggestions for managing the northwestern Ontario northern pike sport fishery.

STUDY AREA

Fourteen northwestern Ontario lakes located within the Precambrian Shield area, were chosen for study. In order to decrease latitudinal or longitudinal differences, the lakes were chosen with regard to the existence of northern pike with the lake, and their relatively close proximity to one another (Table 3.1). Ontario Ministry of Natural Resources' (OMNR) Quetico-Mille Lacs Fisheries Assessment Unit (QMLFAU) and Walleye Research Unit (WRU) provided information on the northern pike populations, lake morphometry and water chemistry for each lake. The lakes chosen include: three lakes which have been the subject of research for MSc. theses at Lakehead University (ie Mosindy 1980, Nunan 1982, Chapter 1 of the present study); three lakes subjected to internal OMNR reports (Mosindy 1982, Laine 1984, 1986, 1987, Ritchie 1987)

Table 3.1. Selected physical and chemical characteristics of 14 northwestern Ontario lakes from which northern pike were collected.

CLASSIFICATION/ LAKE NAME	LAT	LONG	SURFACE AREA (HA)	VOLUME (M ³ x 10 ⁶)	DEPTH (M)		PERCENT LITTORAL	TOTAL PHOSPHOROUS (ug/l)	CHLOROPHYLL <u>a</u> (ug/l)	SECCHI (M)	MEI
					MAX	MEAN					
Oligotrophic											
Greenwater	48°34'	90°26'	3060.2	538.6	59.1	17.6	29	7	2.2	5.4	2.5
Little Gull	49°05'	91°36'	325.4	36.8	36.3	11.3	30	6	2.2	5.8	2.4
Pettit	48°57'	92°16'	1197.1	126.9	25.0	10.6	27	12	3.3	2.8	2.8
Wickerel	48°37'	91°19'	6058.8	1072.4	80.4	17.7	32	4	1.3	4.0	1.2
Queers	48°31'	90°33'	384.4	44.0	36.1	11.5	32	5	1.1	7.0	2.4
Mesotrophic											
Bernadine	49°06'	92°18'	383.7	34.5	19.0	9.0	42	10	2.5	3.3	2.4
Brooked Pine	48°47'	91°04'	1604.0	98.3	17.4	6.1	49	10	2.5	4.4	5.7
Lac des Mille Lacs	48°50'	90°26'	24101.0	1638.9	24.4	6.8	58	23	4.1	1.8	4.8
Loke	48°43'	91°20'	317.0	7.8	19.5	6.4	60	10	2.5	3.6	3.7
Meso-eutrophic											
Anderson	48°48'	90°17'	158.0	3.6	5.3	2.4	100	15	6.1	2.5	16.6
Bece	48°51'	90°05'	111.9	1.8	3.0	1.6	100	29	11.3	1.0	43.8
Buskeg	49°00'	90°02'	3473.3	163.2	12.0	4.7	66	15	4.7	2.6	9.1
Chavanne	48°49'	90°06'	364.3	9.4	4.3	2.6	100	50	8.1	1.5	25.3
Whitefish	48°13'	90°00'	3015.0	60.3	6.4	2.0	99	27	3.6	1.5	33.0

and eight lakes for which the collected data has received only cursory examination (P.A. Ryan, QMLFAU unpublished data, Dr. P.J. Colby, WRU unpublished data).

Since the terms oligotrophic, mesotrophic and eutrophic do not have a definite or universally acceptable scale of reference, this has resulted in some confusion in their use (Vollenweider et al 1974, Forsberg and Ryding 1980). Table 3.2 therefore lists the parameters and ranges used in establishing lake trophic status for purposes of the present study. On the basis of the mean seasonal physical and chemical parameters listed in Table 3.1, the lakes were divided into three categories: i) deep oligotrophic, ii) shallow oligotrophic or mesotrophic and iii) meso-eutrophic.

The presence/absence of a thermocline may also be used to separate lakes. The five deep, oligotrophic lakes exhibit a well developed thermocline between 9-12 m during the mid- to late summer. In the remaining nine lakes however, a thermocline was either non-existent or difficult to discern. Summer winds periodically mix these lakes and prevent any long-term chemical or thermal stratification. This therefore allows a continual recirculation of nutrients within an apparently oligotrophic lake such as Bernadine Lake. This allows it to support large areas of aquatic vegetation and contain a "typical" boreal coolwater percid rather than a coldwater salmonid community.

A partial listing of the fish fauna present within the study lakes is presented in Table 3.3. Other fish species may also be present since the small fish communities have not yet been completely examined within several of the lakes.

Table 3.2. Criteria summarized from the literature to determine study lake trophic status.

CRITERIA	TROPIC CLASS			REFERENCE
	OLIGO- TROPIC	MESO- TROPIC	EUTROPHIC	
Total-P (ug/l)	<15	15-25	>25	Forsberg and Ryding 1980
	<10	10-18.5	>18.5	Dillon and Rigler 1975
	<12	12-24	>24	Carlson 1977
	<10	10-20	>20	Wetzel 1975
Chlorophyll <u>a</u> (ug/l)	<3	3-7	>7	Forsberg and Ryding 1980
	<2	2-5	>5	Dillon and Rigler 1975
	<2.5	2.5-6.5	>6.5	Carlson 1977
	<4.3	4.3-8.8	>8.8	Dobson <u>et al</u> 1974
Secchi Depth (m)	>4	2.5-4	<2.5	Forsberg and Ryding 1980
	>5	3-5	<3	Dillon and Rigler 1975
	>4	2-4	<2	Carlson 1977
Morphoedaphic Index	0.8-5.9	6.0-7.3	7.4-50	Adams and Olver 1977

Table 3.3. Fish species documented to occur within Greenwater (1), Little Gull (2), Pettit (3), Pickerel (4), Squeers (5), Bernadine (6), Crooked Pine (7), Lac des Mille Lacs (8), Niobe (9), Henderson (10), Ice (11), Muskeg (12), Savanne (13) and Whitefish (14) Lakes, northwestern Ontario.

Fish Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Northern Pike	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Lake Trout	+	+	+	+	+	-	-	-	+	-	-	-	-	-
Lake Whitefish	+	+	+	+	-	-	+	+	+	-	-	+	-	+
Cisco	+	+	+	+	-	+	+	+	+	-	-	+	+	-
Walleye	-	+	+	+	-	+	+	+	+	+	+	-	+	+
Smallmouth Bass	-	+	-	+	-	-	+	-	+	-	-	-	-	-
Yellow Perch	+	+	+	+	+	+	+	+	+	+	+	+	+	+
White Sucker	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Longnose Sucker	-	-	-	-	-	-	-	+	-	-	-	-	-	-
Shorthead Redhorse Sucker	-	-	+	+	-	-	-	-	-	-	-	-	-	-
Burbot	+	+	+	+	+	+	+	+	-	+	-	-	+	-
Iowa Darter	+	+	+	+	+	+	+	+	+	+		+	+	
Johnny Darter	-	+	+	-	-	+	+	-	+	-		-	+	
Log Perch	-	-	+	+	-	+	-	+	-	-		-	-	
Trout-Perch	+	-	+	+	-	+	+	+	+	-		+	+	
Lake Chub	+	+	-	-	+	-	-	-	-	-		+	-	
Pearl Dace	-	-	-	+	-	-	+	-	-	-		+	-	
Fathead Minnow	-	-	-	-	-	-	+	-	+	-		-	-	
Bluntnose Minnow	-	-	-	+	-	-	+	+	+	-		-	-	
Mimic Shiner	+	+	+	-	-	+	+	-	+	+		-	-	
Spottail Shiner	+	-	+	+	-	+	+	+	+	-		+	-	
Common Shiner	+	+	-	+	-	-	+	-	+	-		-	-	
Blacknose Shiner	+	+	+	+	+	+	+	+	+	+		-	-	
Emerald Shiner	-	-	-	-	-	+	-	-	-	-		-	-	
Golden Shiner	-	-	-	-	-	+	-	-	-	-		-	-	
Blacknose Dace	+	-	-	-	-	-	-	-	-	-		-	-	
Longnose Dace	+	-	-	+	+	-	+	-	+	-		-	-	
Finescale Dace	+	-	-	-	-	-	+	-	-	-		-	-	
Northern Redbelly Dace	+	-	-	-	+	-	-	-	+	-		-	-	
Sculpin (<i>Cottus</i> sp)	+	+	+	+	+	+	+	+	+	-		-	-	
Deepwater Sculpin	+	+	-	-	+	-	-	-	-	-		-	-	
Nine-spine Stickleback	+	+	+	+	+	-	+	+	-	+		+	+	
Pumpkinseed	-	+	+	+	-	+	+	-	+	-		-	-	
Green Sunfish	-	-	-	-	-	-	-	-	+	-		-	-	
Central Mudminnow	-	-	-	-	-	-	-	-	+	-		-	-	
Smelt	-	-	-	+	-	-	-	-	-	-		-	-	

Fishing pressure on these northern pike populations varies from unexploited to highly exploited. Four lakes receive sufficient pressure to have yields which are near or exceed their theoretical potential as calculated through the use of the morphoedaphic index (Ryder 1965, Ont. Min. Nat. Res. 1983). Table 3.4 lists estimated fishing effort levels and harvest as available. Although varying levels of fishing pressure introduces an unaccountable variable, its inclusion does reflect the potential growth response to exploitation by these populations. Therefore, these lakes provide at least some indication of the maximal ranges in the growth potential which may be possible for populations within the 3 different lake types.

METHODS

Spring Schumacher-Eschmeyer (S-E) population estimates (Ricker 1975) were calculated for seven fish populations employing primarily 1.2m, 1.8m and 2.4m trapnets. The low number of recaptures prevented the calculation of an S-E population estimate on two additional lakes which had tagging programs. Therefore, population estimates were determined through the use of the modified Petersen estimate (Ricker 1975) for northern pike caught during the subsequent year subsequent netting activities or by anglers as reported within creel data. The population estimates were computed only for fish ≥ 400 mm FL in order to reduce any gear selective bias.

Northern pike data were also obtained from mid-summer gillnet surveys carried out on 11 of the study lakes. Nets used included both white multifilament and green monofilament nets consisting of

Table 3.4. Estimated fishing effort (expressed as rod-hours per hectare), harvest, potential yield and the relative yield index (RYI:Ont. Min. Nat. Res. 1983) for 14 northwestern Ontario pike populations.

Lake	Estimated Effort (R-H/ha)	Estimated Harvest (kg/ha)	Potential Yield (kg/ha)	RYI (%)	Source of Est'd Effort and Harvest
Greenwater	a	-	-	-	OMNR 1988
Little Gull	0.9	0.36	0.4	90	Laine 1987
Pettit	3.0	0.25	0.55	46	OMNR 1988
Pickerel	a	-	-	-	OMNR 1988
Squeers	b	-	-	-	
Bernadine	3.4	0.31	0.53	58	Ritchie 1987
Crooked Pine	10.0	0.9	0.75	120	OMNR 1988
Henderson	b	-	-	-	
Ice	b	-	-	-	
Lac des Mille Lacs	14.9	0.9	0.50	180	OMNR 1988
Niobe	2.3	0.12	1.24	10	OMNR 1988
Savanne	b	-	-	-	
Muskeg	a	-	-	-	OMNR 1988
Whitefish	?	1.40	1.64	85	OMNR 1988

a: no available data, fishing effort believed low

b: unexploited (sanctuary lake)

3-10 15.2m panels (2.5,3.8,5.1,6.4,7.6,8.9,10.1,11.4 and 12.7mm stretched mesh). These were separated by 3m spacing lines in order to prevent the leading of fish from one panel to another.

These studies provided northern pike catch per unit effort (CUE, expressed as the number of fish/100m of net/24 hr period) data.

Live released northern pike were anesthetized with tricaine-methane sulfonate (MS-222), measured, weighed, tagged with an individually numbered disc tag, and sexed externally if possible. A scale sample was also taken prior to release. In addition to the aforementioned information, cleithra were collected as a supporting aging tissue and state of sexual maturity data were recorded from northern pike collected within gillnets. Diet information was also available from stomachs collected from a number of the lakes examined.

Trapnet CUE data were not used because of seasonal differences in the vulnerability of northern pike to this gear type. Trapnetting success increases during spring when spawning northern pike concentrate within shallow areas compared to the remaining months when fish scatter throughout the lake. The selective nature of this gear for mature northern pike > 400mm FL also limits the value of CUE information.

Comparisons between populations were complicated by i) sample sizes, ii) sex-ratio differences, iii) presence of sexually dimorphic growth rates, iv) accuracy of aging (particularly for populations not aged with a bony tissue), v) seasonal distribution of sampling effort and vi) varying levels of exploitation between the various populations. Attempts to rectify these problems were

made to ensure consistency within the data comparisons.

Twelve of the fourteen northern pike populations were aged by the scale method as these fish underwent live release after sampling. The scale method was validated for the Squeers Lake northern pike \leq age 10 by using oxytetracycline and mark-recapture methods (Chapter 2). Scale ages were verified with cleithral ages whenever this tissue was available. Cleithral ages are more accurate than scale ages (Casselman 1978, Chapter 2). Therefore assigned cleithral ages were used to resolve any discrepancies between the two tissues. The Savanne Lake and Henderson Lake populations were aged by cleithra (Mosindy 1980, Nunan 1982).

Problems were encountered in aging the slow growing populations. There was evidence of non-formation of annuli and/or scale resorption (as determined by irregular scale edges and the merging of scale annuli on the scale edges) once fish reached near asymptotic size. There were also some problems in discerning the first annulus on both aging tissues for these populations.

Length frequency histograms were used to describe the length frequency of the portion of the populations which were vulnerable to the gear in use. Proportional Stock Density (PSD) and the Relative Stock Density of northern pike \geq 750 mm FL (RSD-75) values, as described by Anderson and Weithman (1978) and Gabelhouse (1984) were used to describe the percentage of quality-sized fish within each of the populations sampled. Minimum stock, quality, preferred, memorable and trophy lengths that have been assigned to northern pike in the literature are 350, 530, 710, 860 and 1120mm TL respectively (Gabelhouse 1984). It must be noted that the RSD-

X value assigned for the present study is slightly less than the 860 mm TL assigned by Gabelhouse (1984) as the "memorable" size caught.

As a result of seasonal variation in samples from the various lakes, the mean length at age data for each population were calculated from lengths back-calculated (using the package developed by Frie 1982) to the time of last annulus. On the basis of arguments presented by Carlander (1983), a standard intercept value of rectilinear body-scale regressions using the Fraser-Lee method for calculating growth from scales was determined for the examined northwestern Ontario northern pike populations. The standard a value (121 mm) was calculated from the eight northern pike populations which demonstrated a coefficient of variation (r^2) value ≥ 0.75 for their rectilinear body-scale regressions.

Fitting age and growth data for each lake to a von Bertalanffy growth curve produced good fits for only seven lakes. Therefore, empirical age and growth data were used to construct growth curves for each population. For general comparisons, mean length at age curves were truncated to include only those age groups which had ≥ 5 samples per calendar year in order to decrease the possibility of an aberrant growth curve. Due to the relatively small sample sizes for most age groups, comparisons were not made between sexes.

Lysack's (1980) modification of Abrosov's (1969) formula was used to determine the mean weighted age and size at maturity for each population. The reproductive life span of the average northern pike was determined by subtracting the mean weighted age at the onset of maturity from the mean age of the catch. To ensure

the time of sampling caused no bias with respect to the first age at maturity, an additional calendar year was added to the age of all fish sampled between June and December. Survival estimates were estimated by catch curve analysis (Robson and Chapman 1961) using the age frequency distribution of each population.

In addition to the detailed examination of the feeding habits of northern pike populations from Savanne Lake (Mosindy 1980), Henderson Lake (Nunan 1982, Reid 1985, Trimble 1988) and Squeers Lake (Chapter 1), field identification of stomach contents for pike sampled from seven of the remaining eleven lakes were also available. These data (which when expressed as the frequency of occurrence of prey items present) allowed a preliminary examination of the differences and similarities in diets between lakes and lake type.

RESULTS

Relative Abundance and Population Estimates

The relative abundance of northern pike was clearly highest in meso-eutrophic lakes and lowest within the oligotrophic lakes (Table 3.5). The majority of northern pike sampled were caught within the littoral zones, particularly within the oligotrophic lakes. The numbers caught within the summer-set gillnets increased substantially at all depths with increasing lake trophic level to a point such that CUE was nearly constant at all depths within the meso-eutrophic lakes.

The greatest density of northern pike occurred within meso-eutrophic lakes. Population levels of northern pike ≥ 400 mm FL

Table 3.5. Catch-per-unit-effort (CUE), expressed as the number of fish caught per 100m of gillnet per 24 hour period by depth strata, and population estimates (N) expressed on a number per hectare basis for 14 northwestern Ontario northern pike populations. N/A depicts the absence of information with respect to either gillnet CUE or population estimate data.

LAKE	CUE				POPULATION ESTIMATE		Data Source
	0-6.5m	6.5-13.0m	13m	overall	N	95% C.L.	
Oligotrophic							
Greenwater	1.07	0.24	0.02	0.36	N/A	-	QMLFAU, unpublished
Little Gull	1.14	2.08	0.19	1.20	0.87	0.43-1.90	Laine, 1986
Pettit	1.66	0.49	0.00	0.70	0.64	0.24-1.61	OMNR, 1988
Pickereel	2.11	0.39	0.00	0.53	N/A	-	QMLFAU, unpublished
Squeers	3.02	0.33	0.14	1.01	0.57	0.50-0.67	present study
Average:	1.80	0.71	0.07	0.76	0.69		
Mesotrophic							
Bernadine	5.50	5.26	4.72	5.31	4.30	2.87-6.76	Ritchie, 1987
Crooked Pine	4.22	2.60	1.50	1.50	0.80	0.40-2.91	OMNR, 1988
Lac des Mille Lacs	3.73	1.91	0.00	2.94	N/A	-	QMLFAU, unpublished
Niobe	2.96	0.62	0.00	1.76	3.30	1.78-10.57	OMNR, 1988
Average:	4.10	2.60	1.56	3.41	2.80		
Meso-eutrophic							
Henderson	N/A	N/A	N/A	N/A	7.41	6.79-8.15	Nunan, 1982
Ice	N/A	N/A	N/A	N/A	9.00	7.69-10.85	Colby, unpublished
Savanne	N/A	N/A	N/A	N/A	6.88	5.78-7.99	Mosindy, 1980
Muskeg	16.33	13.43	-	15.03	N/A	-	QMLFAU, unpublished
Whitefish	11.15	5.52	-	8.97	N/A	-	QMLFAU, unpublished
Average:	13.74	9.48	-	12.00	7.76		

for the nine lakes this information was available (expressed on a per-unit area basis) increased substantially between each lake type, such that numbers increased from an average of 0.7/ha in oligotrophic lakes to 2.8/ha in mesotrophic lakes, and 7.8/ha within the meso-eutrophic lakes sampled (Table 3.5). The population estimates for Crooked Pine and Niobe Lakes were of low precision as the size of the catch and/or the number of subsequent recaptures were low upon resampling.

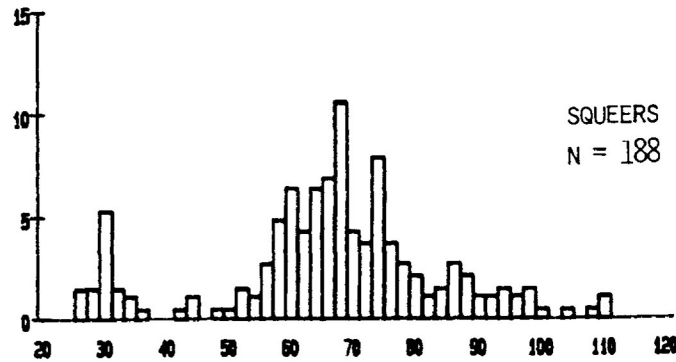
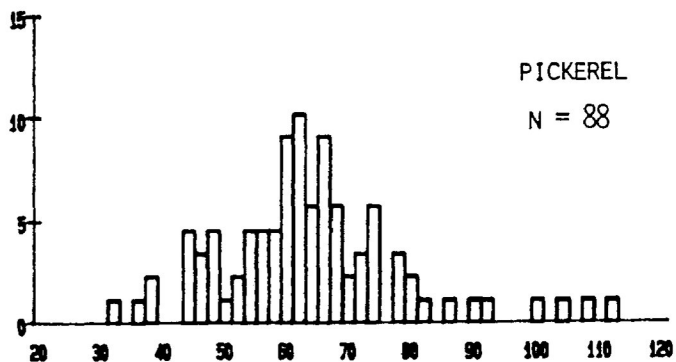
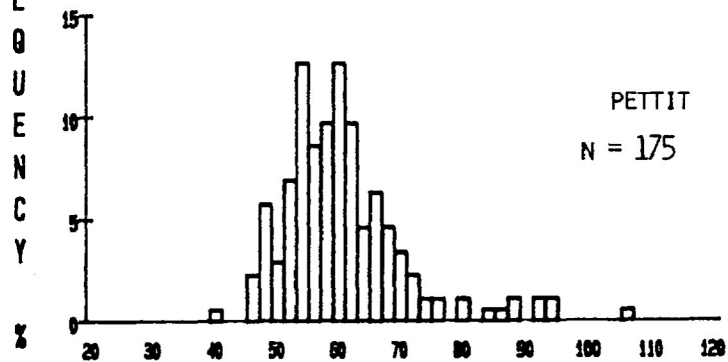
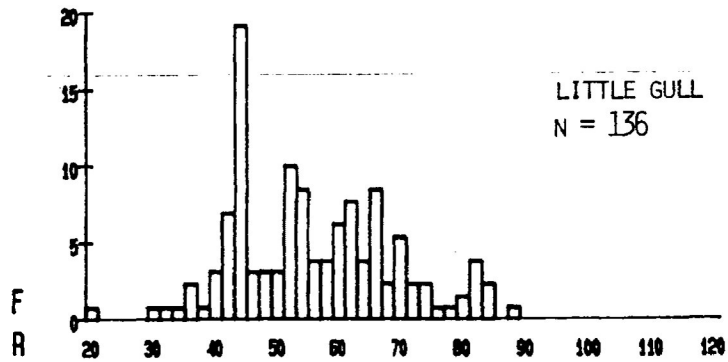
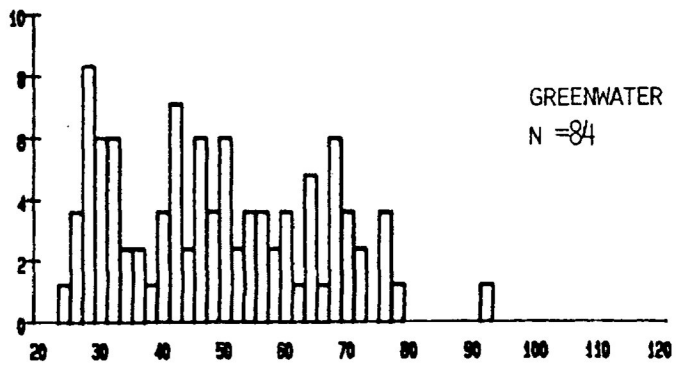
Size Structure

The size structure of the populations determined by the length frequency histograms, PSD and RSD-75 varied markedly within the 14 study lakes (Figure 3.1a-c, Table 3.6). The overall population length frequency distributions were generally unimodal. Although all populations examined had a mean length between 480-656 mm FL (Table 3.6), few fish greater than 600 mm FL were present within the meso-eutrophic and small mesotrophic lakes. Populations from the oligotrophic and large, mesotrophic lakes clearly contained the greatest proportion of large sized individuals (Figure 3.1, Table 3.6). Similarly, although PSD values varied from 0.364-0.914 within the lake data set, RSD-75 values for the oligotrophic and large mesotrophic lakes averaged 11.6% (with the lowest value of 6.7% occurring in oligotrophic Pettit Lake). In the small mesotrophic and meso-eutrophic lakes this value averaged 2.9% (range:0-10), with only the Savanne Lake population exceeding an RSD-75 value of >5% (Table 3.6).

Age and Growth

All 14 northern pike populations exhibited similar unimodal

Figure 3.1a. Fork length frequency distributions of northern pike from 5 oligotrophic northwestern Ontario lakes.



FORK LENGTH (CM)

Figure 3.1b. Fork length frequency distributions of northern pike from 4 mesotrophic northwestern Ontario lakes.

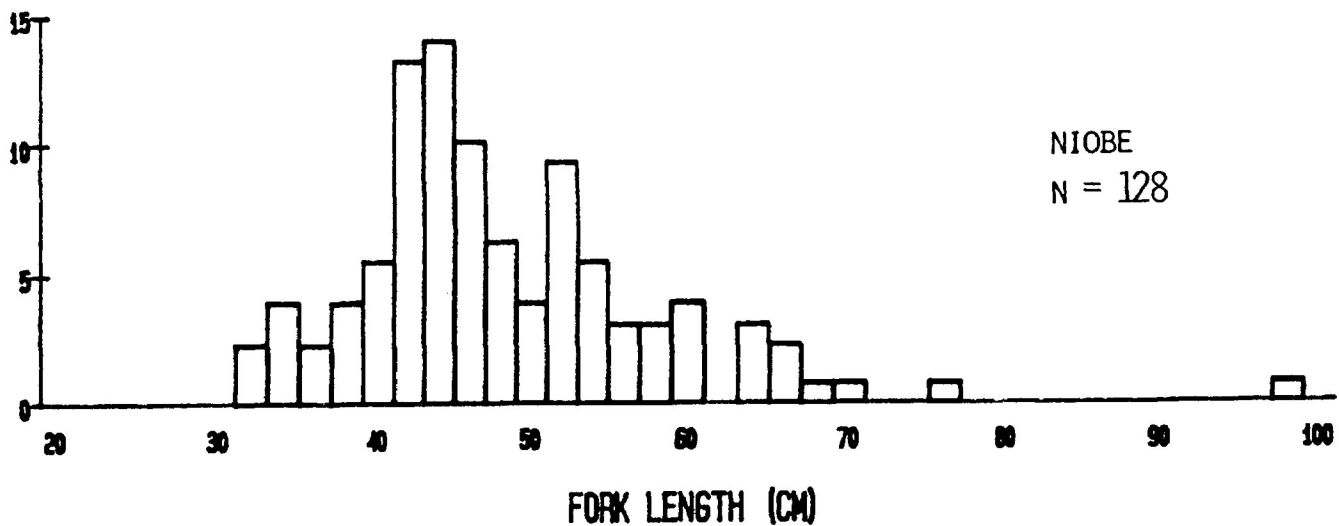
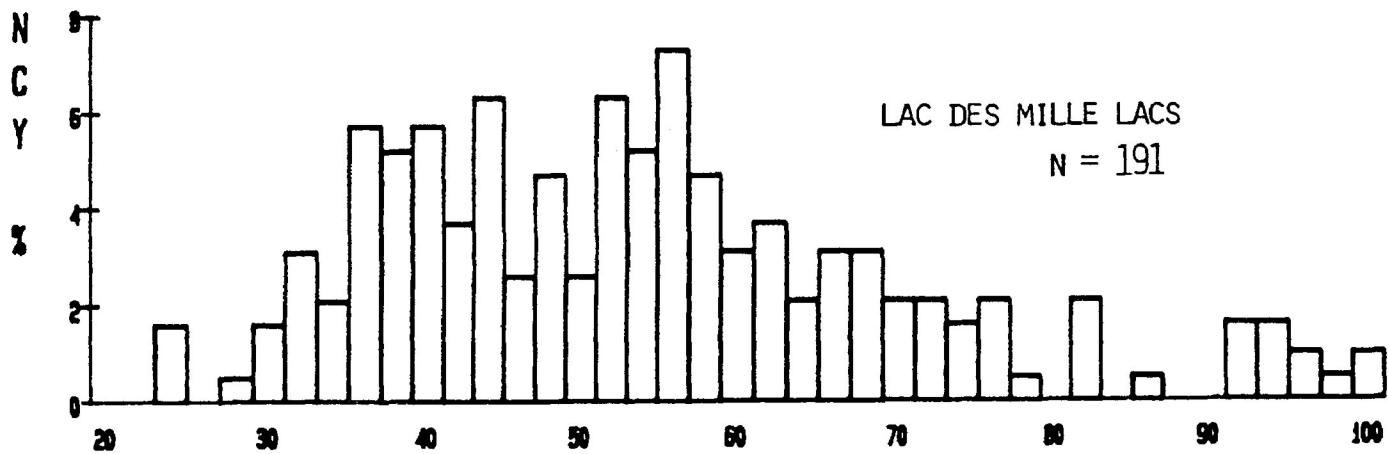
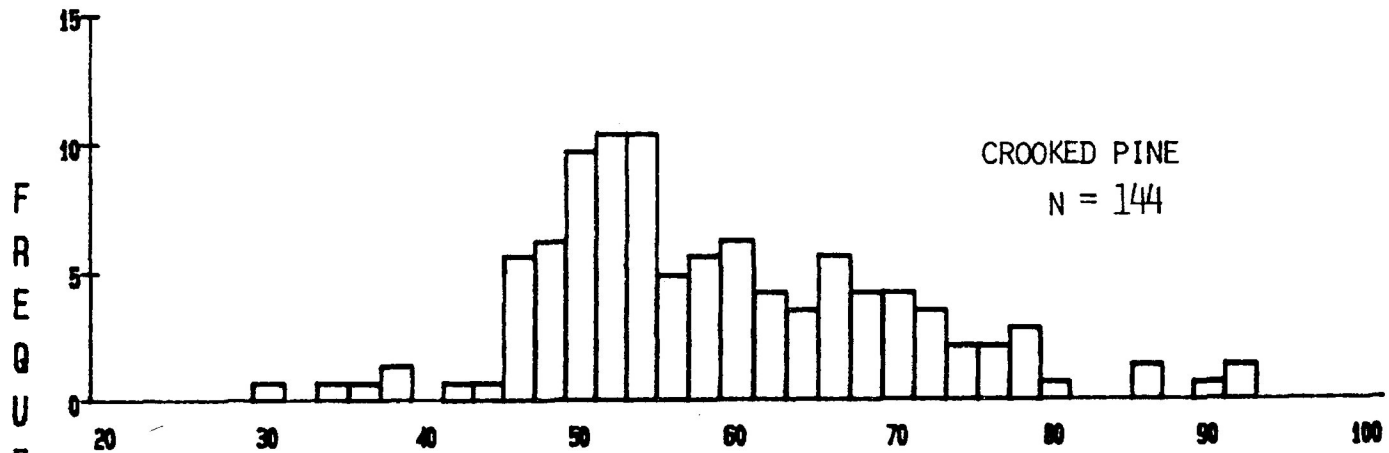
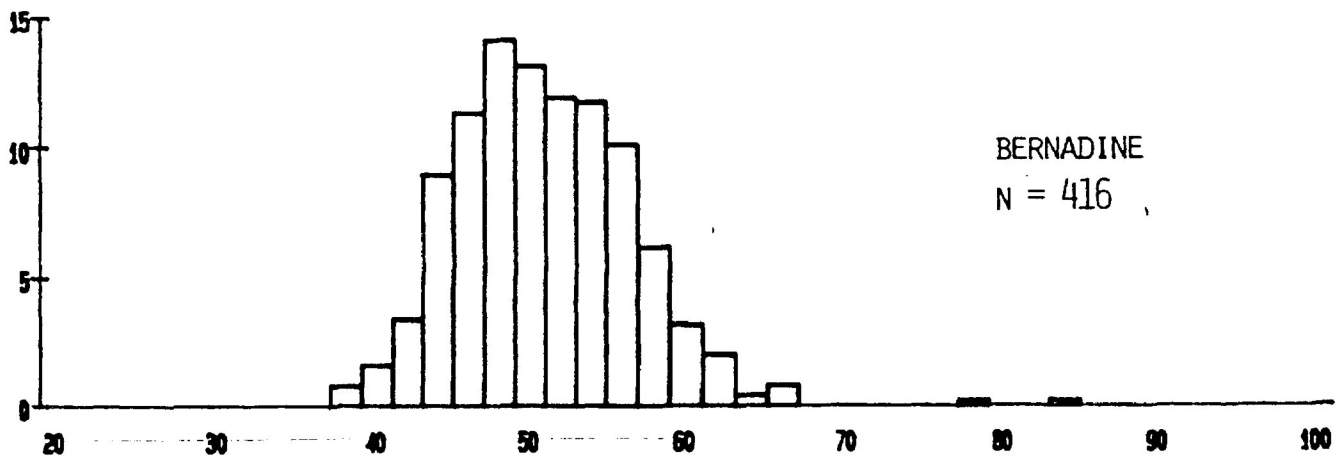


Figure 3.1c. Fork length frequency distributions of northern pike from 3 meso-eutrophic northwestern Ontario lakes.

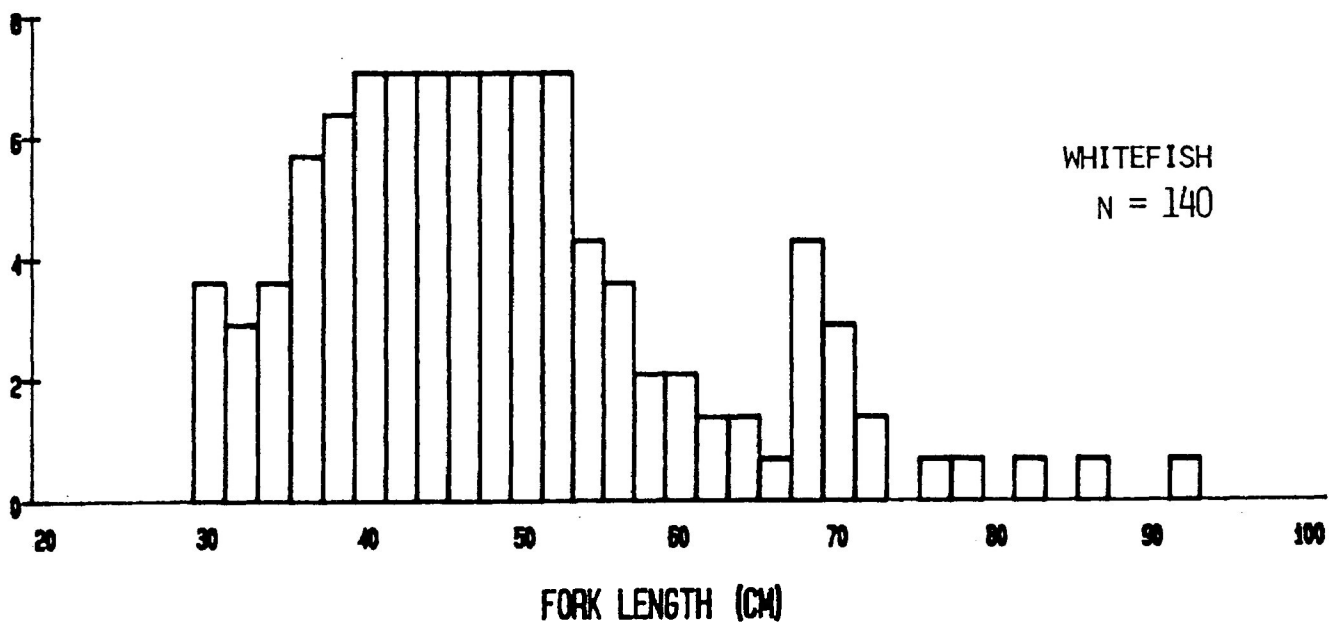
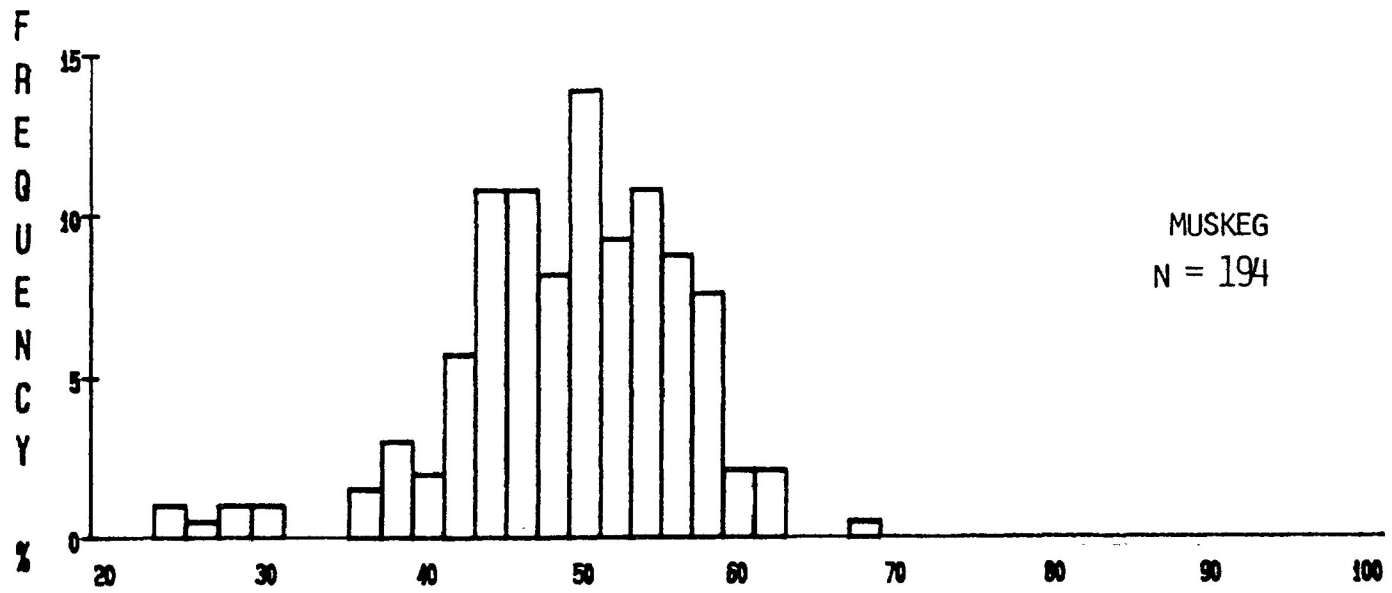
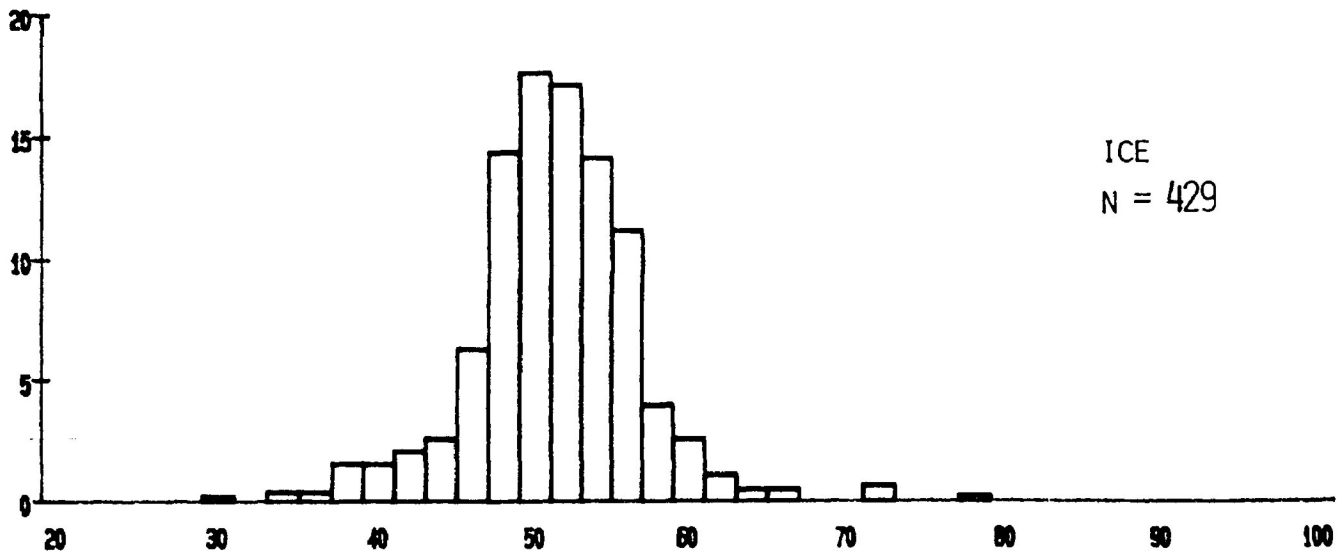


Table 3.6. Mean fork length, the Proportional Stock Density (PSD), Relative Stock Density of fish >750 mm, mean age and size of the onset of maturity (as calculated by the modified Abrasov's (1969) method (Lysack 1980)) for the combined (C), male (M) and female (F) portions, and annual mortality rate (A) values for 14 northern pike populations sampled in northwestern Ontario. N/A indicates that no calculations were possible because of insufficient data available.

Lake	Population Parameter										
	Mean length (mm)	PSD (%)	RSD -75 (%)	Mean Age (yr)	Mean Age at Mat (yr)			Mean Size at Mat (mm)		A (%)	Age Grps
					C	M	F	M	F		
Oligotrophic											
Greenwater	495	62	13	3.2	3.1	2.6	3.3	429	562	31	2-10
Little Gull	592	57	10	4.1	3.4	2.7	3.7	N/A	523	36	3-10
Pettit	605	91	7	4.0	N/A	N/A	N/A	N/A	N/A	43	5-8
Pickereel	623	83	10	6.3	N/A	N/A	N/A	N/A	N/A	41	6-11
Squeers	656	78	22	5.5	2.8	2.4	3.1	425	529	44	5-9
Mesotrophic											
Bernadine	518	60	0.5	5.2	N/A	N/A	3.5	N/A	420	55	5-9
Crooked Pine	597	83	9	6.2	3.3	2.5	3.7	350	468	36	5-11
LDML ^a	549	53	10	4.3	3.3	3.1	3.6	403	440	33	2-11
Niobe	480	37	2	4.3	N/A	3.1	4.2	385	458	39	3-9
Meso-eutrophic											
Henderson	499	22	0	4.3	3.8	3.9	3.8	N/A	N/A	37	5-10
Ice	501	70	0.2	5.0	N/A	N/A	N/A	N/A	N/A	51	5-9
Muskeg	494	53	0	6.2	4.1	4.6	3.9	469	473	25	3-12
Savanne	586	80	10	5.9	N/A	N/A	N/A	363	443	44	5-10
Whitefish	491	36	3	3.6	2.9	2.6	3.2	358	453	47	4-10

^aLac des Mille Lacs

age distributions, with the majority of each population comprised primarily of fish between the ages of 2-8. Mean ages of the populations varied from 3.2 to 6.27 years, with little or no apparent influence due to lake type. All of the populations were dominated by younger fish (Figure 3.2a-c), however fish up to age 14 were caught. The general absence of age 1 and 2 fish reflects gear selectivity towards larger, mature fish.

Growth differences were apparent in these 14 populations. Apparently growth progressively increases for populations from the meso-eutrophic to mesotrophic to oligotrophic lakes, although there were several exceptions. The slower growth of northern pike in meso-eutrophic and to a lesser extent in mesotrophic lakes was accompanied by a greater variation in the size of individuals.

The average length at age for the 5 populations from deep, stratified oligotrophic lakes was significantly greater than for the populations from meso-eutrophic and mesotrophic lakes (Mann-Whitney U test, $p < 0.05$, Figure 3.3). However, a considerable variation in mean length at age was exhibited even within the oligotrophic lake set. Generally, each of these populations grew rapidly up to age 4 (Figure 3.4a). Following this age (which roughly corresponds to the age at which 100% of the individuals reach sexual maturity), the growth rate decreases but there is a continuous addition of somatic tissue as evidenced by increases in length. The Pickerel Lake population provided the exception in that initial growth rates were significantly less than those of the other northern pike populations up to age 4 (Mann-Whitney U test, $p < 0.05$). Following this point however, mean length at age

Figure 3.2a. Age distributions of northern pike from 5 oligotrophic northwestern Ontario lakes.

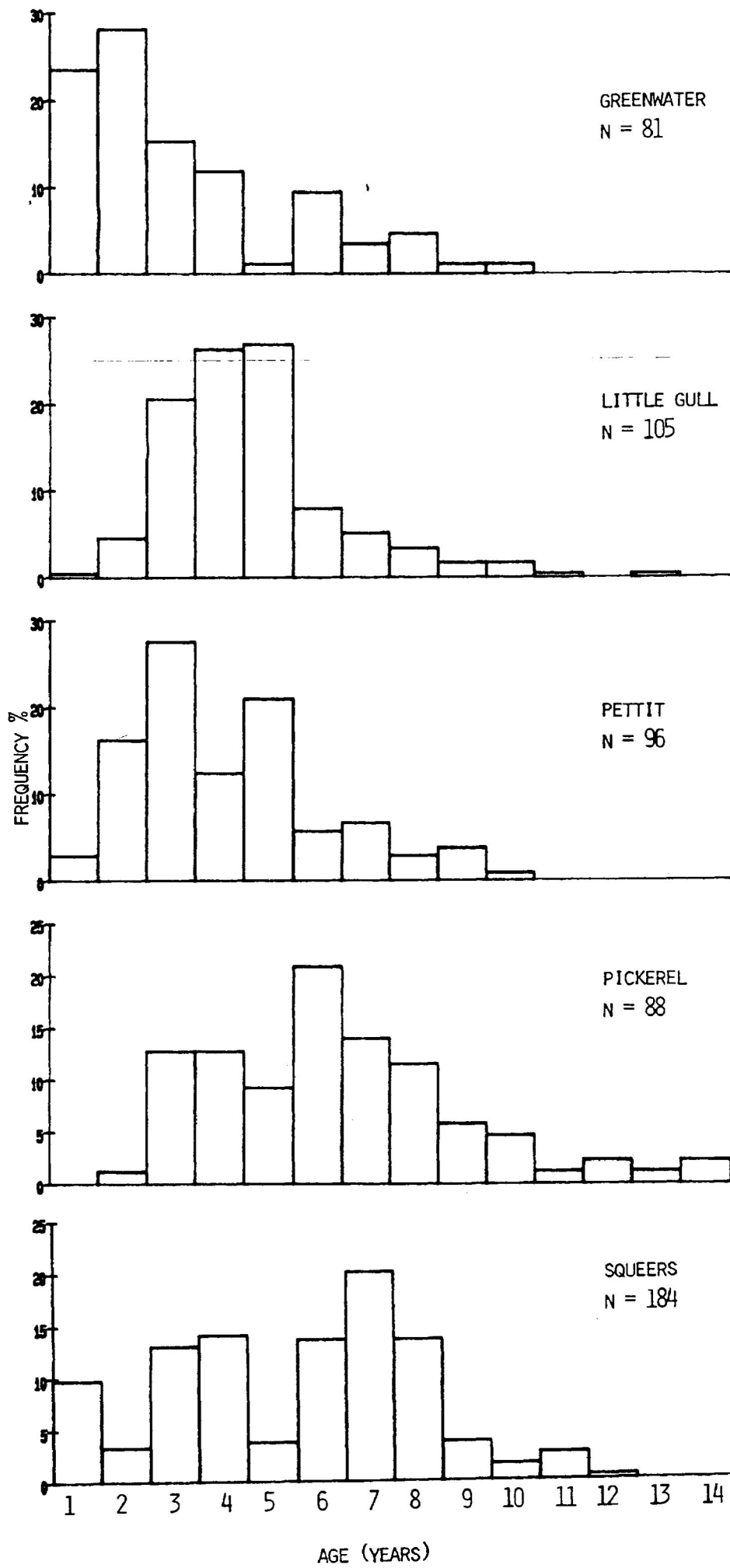


Figure 3.2b. Age distributions of northern pike from 4 mesotrophic northwestern Ontario lakes.

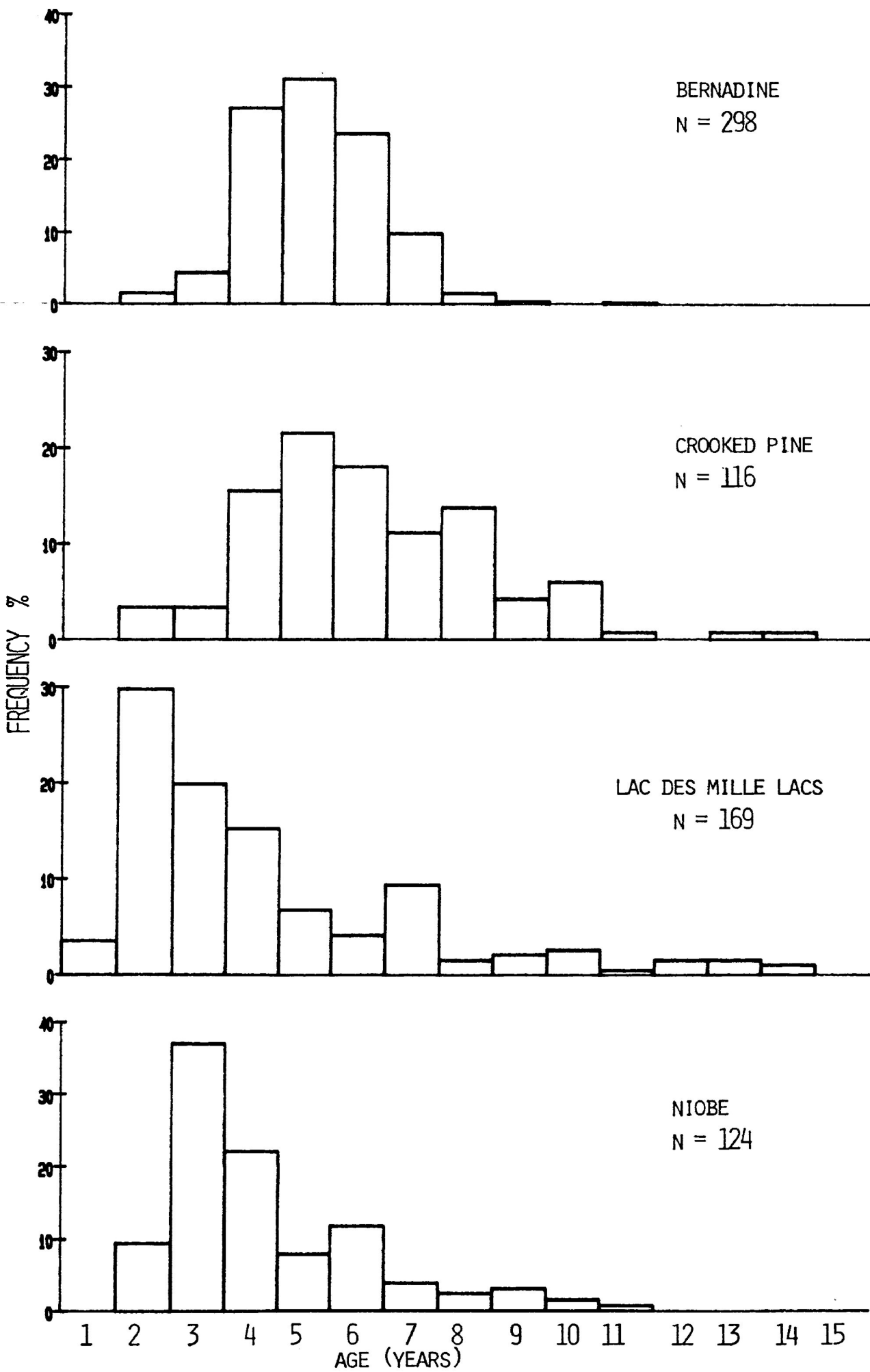


Figure 3.2c. Age distributions of northern pike from 3 meso-eutrophic northwestern Ontario lakes.

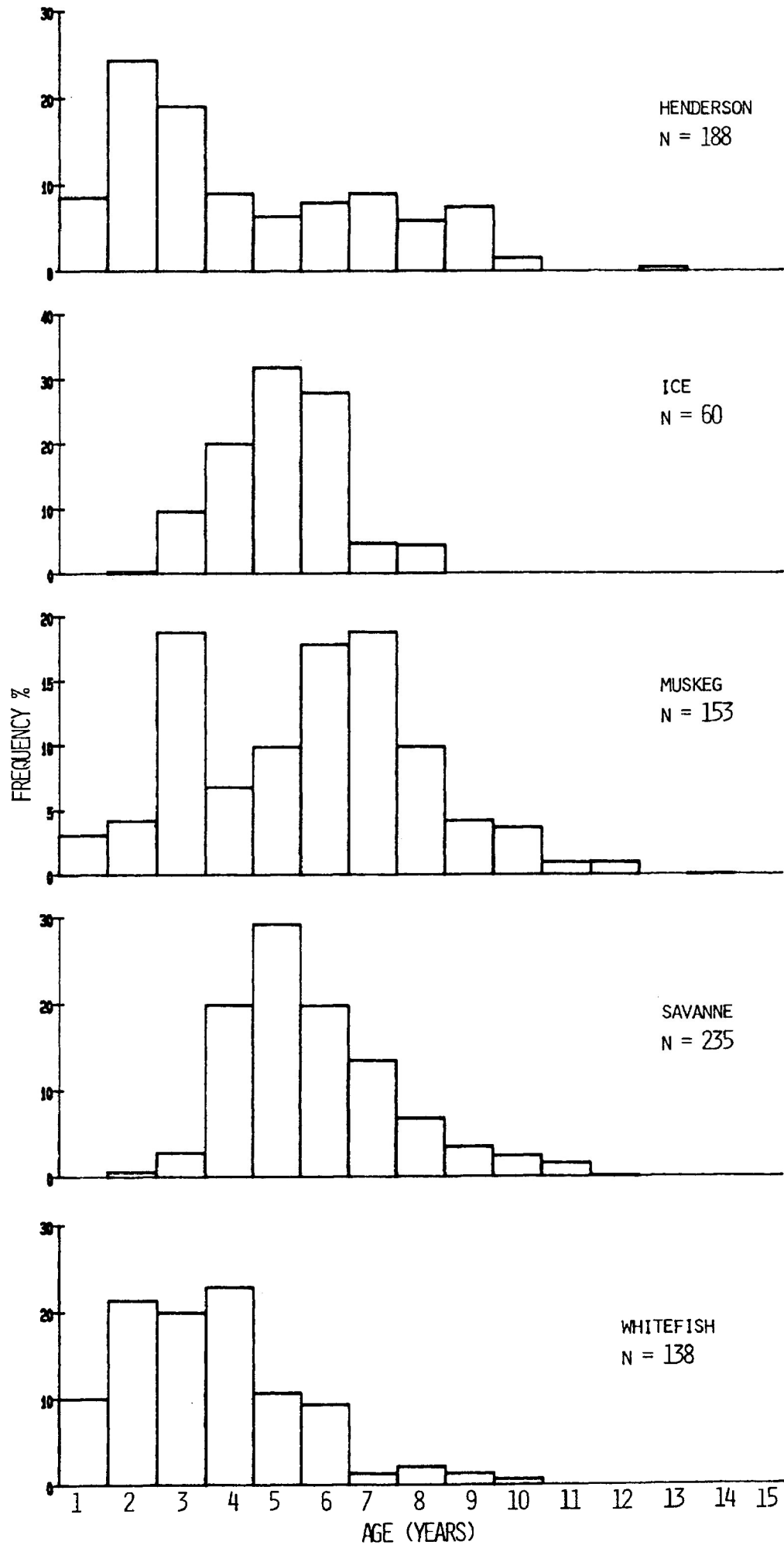
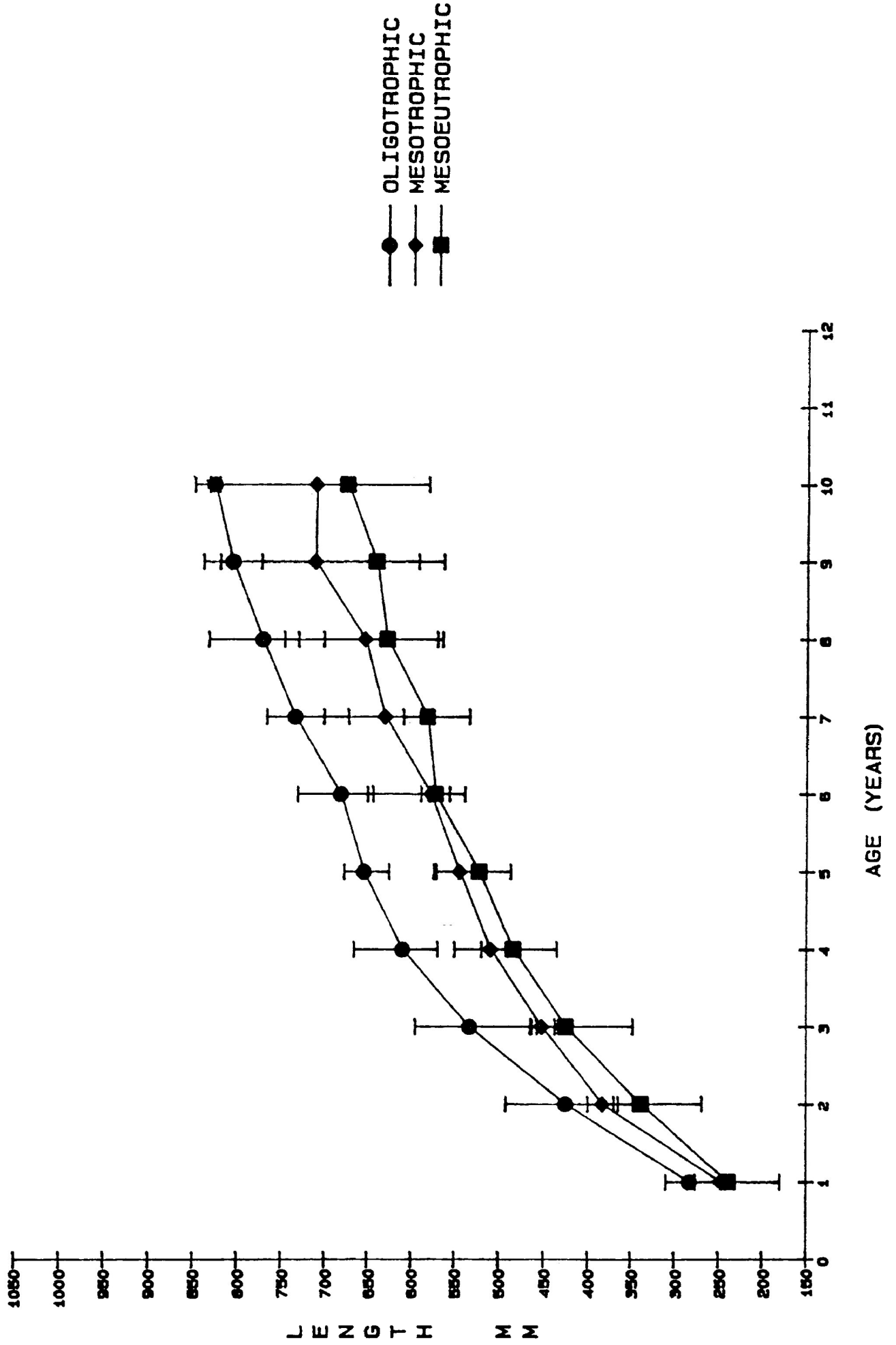


Figure 3.3. Comparison of the mean growth rates for northern pike populations from northwestern Ontario oligotrophic, mesotrophic and meso-eutrophic lakes. Error bars depict \pm one standard deviation.

MEAN FORK LENGTH AT AGE BY LAKE TYPE



generally equalled that of the other oligotrophic populations.

Although the populations from mesotrophic lakes appear larger in size at specific ages than meso-eutrophic populations, there was no significant differences (Mann-Whitney U test, $p < 0.05$) in the mean size at age between these two lake types (Figure 3.3). Two patterns of growth appears to occur within northwestern Ontario mesotrophic lakes (Figure 3.4b). Fish from the two larger lakes (ie > 1000 ha) continued to increase in size after age six. Their mean length by age eight nearly approaches lengths recorded for populations sampled from oligotrophic lakes. Fish from small, mesotrophic and meso-eutrophic lakes (Figure 3.4c), however, approach an asymptotic mean size at or near 600 mm FL. These latter populations consist primarily of small northern pike from many age groups with only a few individual fish larger than 600 mm FL present. The Savanne Lake population sampled by Mosindy (1980) was the apparent exception. This population exhibited a slow, constant growth rate throughout all age groups sampled, with no evidence of a growth decrease (Figure 3.4c).

Mean Age at Maturity

Small sample sizes for the younger age groups seriously affected the estimates of mean age and size at onset of maturity for a number of the populations (Appendix D.1). Typically, males matured at a younger age and smaller size than females (Table 3.6). The earliest observed age at first maturity for both male and female components was age two (Appendix D.1). The oldest maturing population was from an unexploited meso-eutrophic water body (ie Muskeg Lake), where neither males nor females reach 100% maturity

Figure 3.4a. Comparison of the empirical mean fork length at age for northern pike from 5 oligotrophic northwestern Ontario lakes.

MEAN FORK LENGTH AT AGE COMPARISONS
FOR OLIGOTROPHIC LAKES

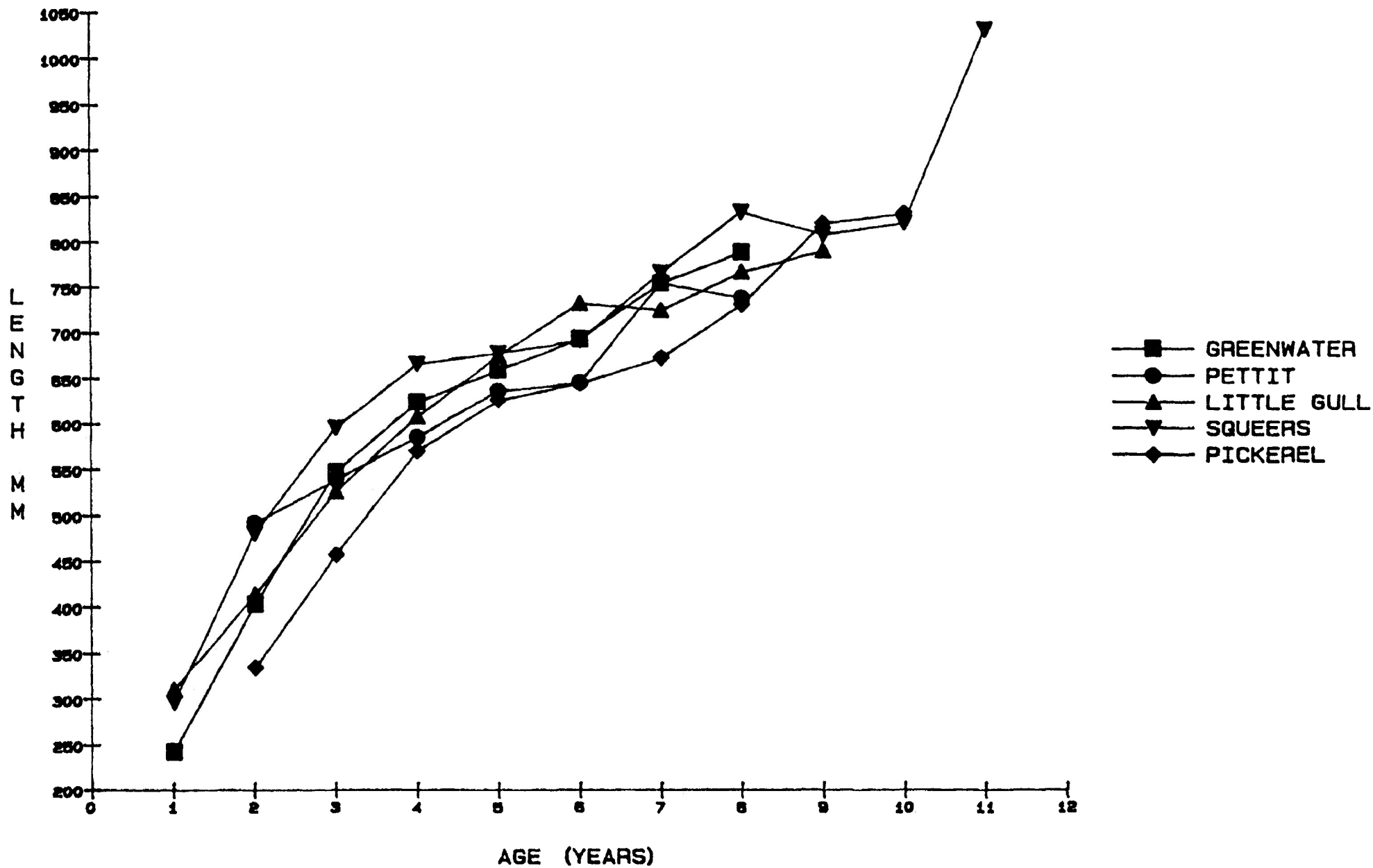


Figure 3.4b. Comparison of the empirical mean fork length at age for northern pike from 4 mesotrophic northwestern Ontario lakes.

MEAN FORK LENGTH AT AGE COMPARISONS
FOR MESOTROPHIC LAKES

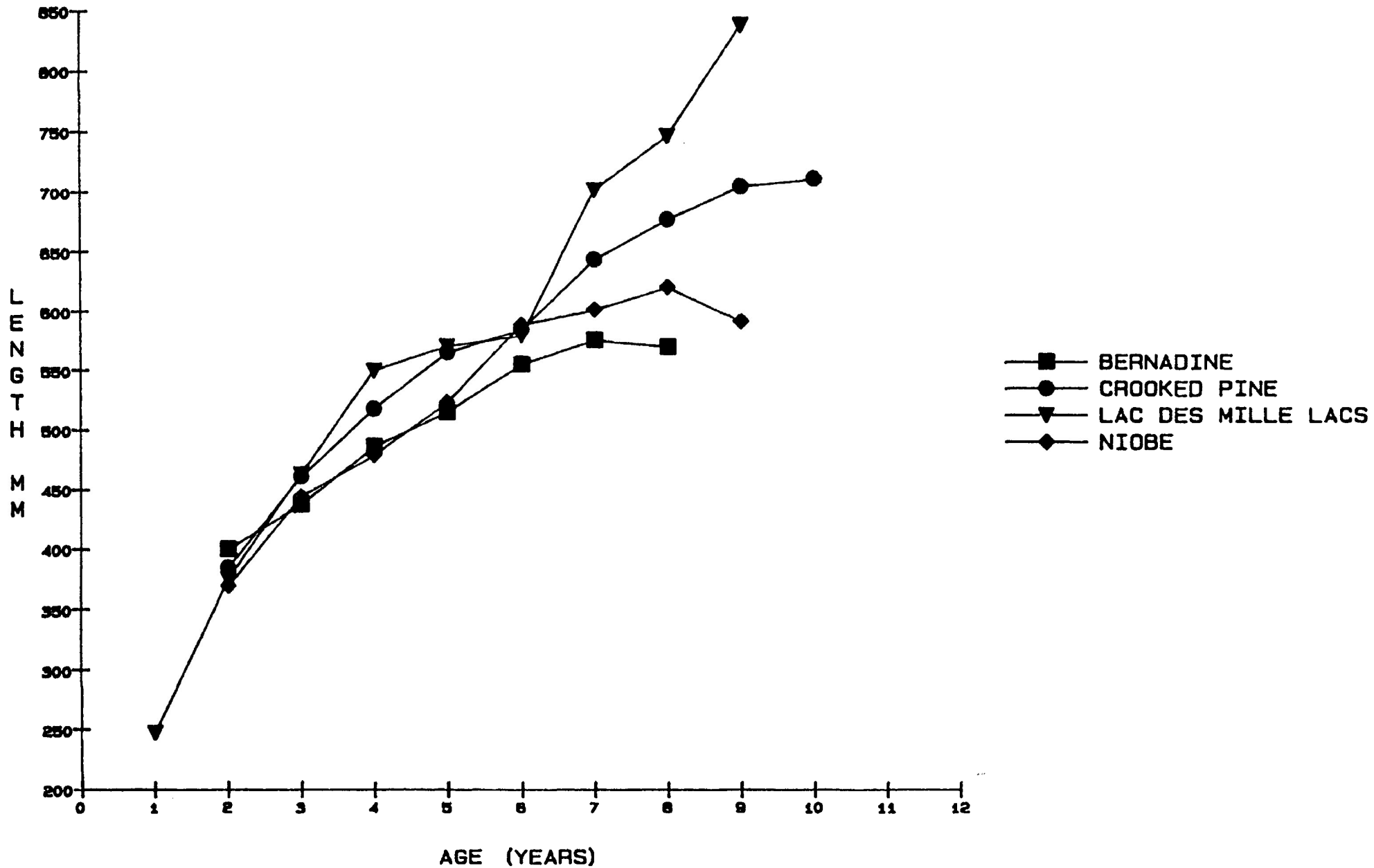
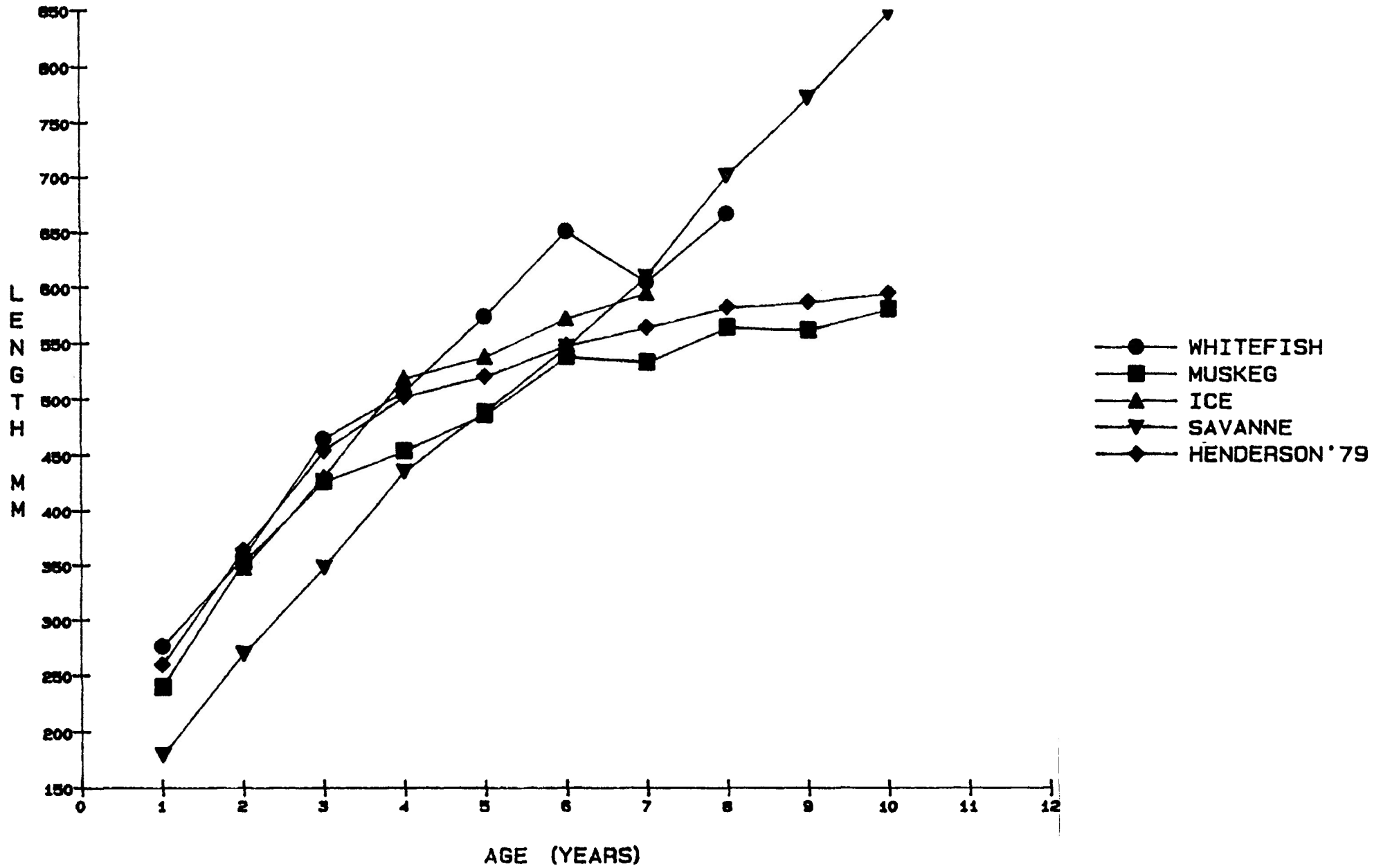


Figure 3.4c. Comparison of the empirical mean fork length at age for northern pike from 5 meso-eutrophic northwestern Ontario lakes.

MEAN FORK LENGTH AT AGE COMPARISONS
FOR MESO-EUTROPHIC LAKES



until age 8.

Populations from meso-eutrophic lakes (and to a lesser extent from mesotrophic lakes) mature at a slightly smaller size but generally older age than northern pike from oligotrophic lakes (Table 3.6). Hence, even though growth rates were much slower in the mesotrophic and meso-eutrophic lakes, the age at maturity was similar.

Total Annual Mortality

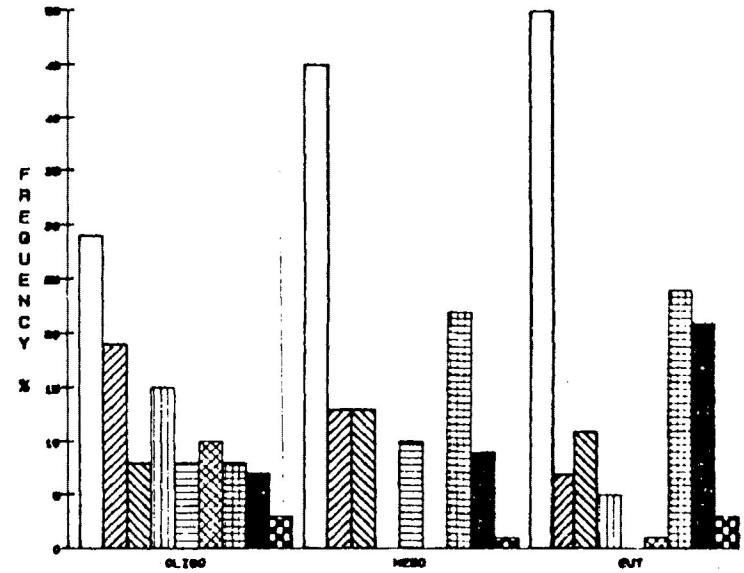
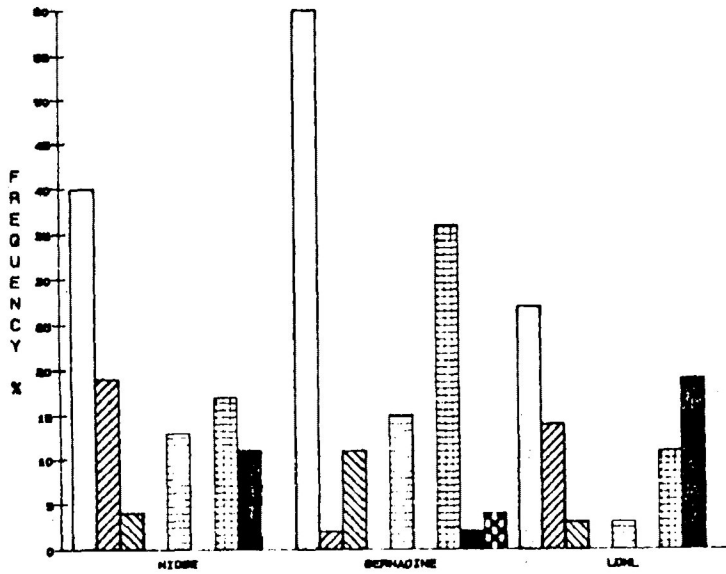
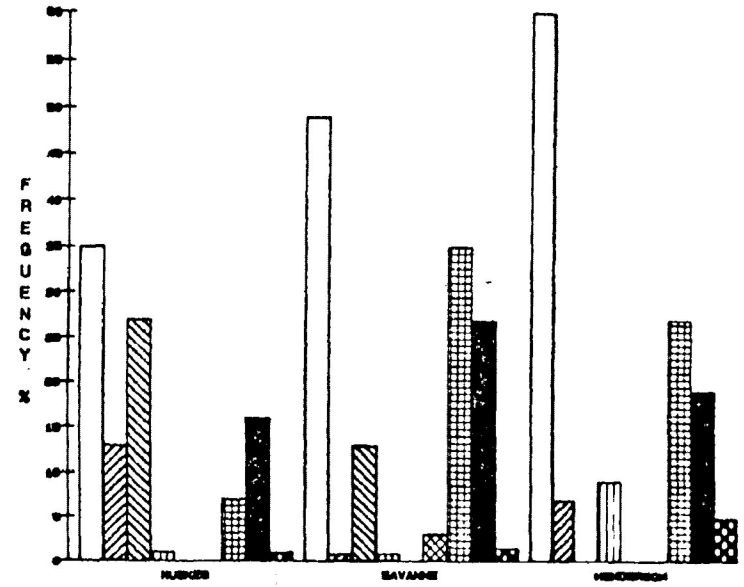
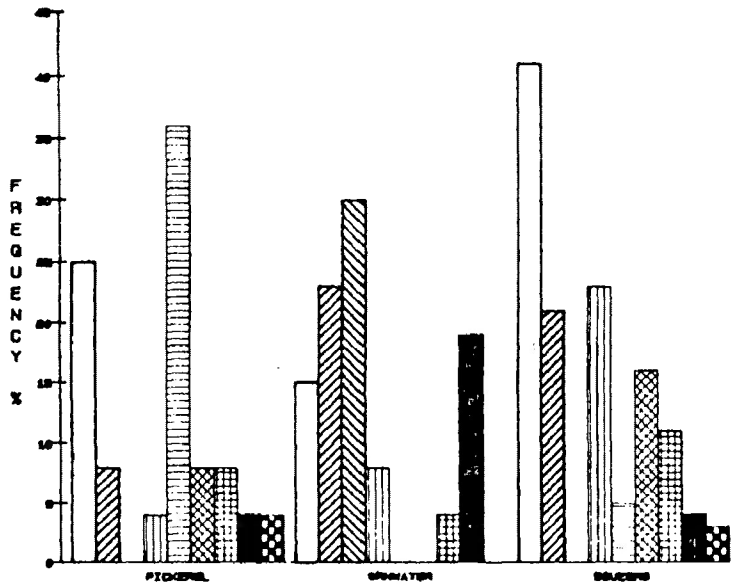
For most of the northern pike populations, total annual mortality (A) equalled or exceeded 35% (Table 3.6). Total annual mortality ranged from 25% for ages 3-12 in Muskeg Lake to 55% for ages 5-9 in Bernadine Lake. Although fish up to age 14 were encountered within a number of the populations, a high rate of natural mortality apparently occurs after age 7 (Figure 3.2a-c).

Diet

Northern pike in oligotrophic lakes are primarily piscivorous, but very opportunistic with respect to prey fish species selected (Figure 3.5). Within the three lakes examined, the fish prey species consumed generally reflected the species diversity present within each of the water bodies. Northern pike from Squeers Lake, a headwater lake with a relatively simple fish community, consumed primarily yellow perch and white sucker. Greenwater Lake northern pike concentrated on the two coregonine species present, whereas the diet of Pickerel Lake's northern pike consisted primarily of yellow perch and other game fish (ie walleye and smallmouth bass) found inhabiting the littoral zone.

Mesotrophic and meso-eutrophic populations generally fed on

Figure 3.5. Percent frequency of occurrence of food items identified in stomachs of northern pike from A) oligotrophic, B) mesotrophic, C) meso-eutrophic and D) overall samples by lake type from 9 populations examined within northwestern Ontario. Data Sources: Savanne Lake: Mosindy (1980); Henderson Lake: Nunan (1982); Squeers Lake: Chapter 1; Pickerel, Greenwater, Lac des Mille Lacs, Niobe, Bernadine and Muskeg Lakes: QMLFAU (unpubl. data).



similar food items (Figure 3.5). Yellow perch was the predominant food item (Figure 3.5). However, aquatic macroinvertebrates (primarily mayfly, stonefly and dragonfly larvae) were second in importance. Cisco were of major importance (particularly for northern pike >500 mm FL) in all lakes where found (Mosindy 1980, QMLFAU, unpubl. data).

DISCUSSION

The productivity of a lake is based largely on climate and its nutrient supply. However, the manner in which nutrients enter the food web depends upon many other factors including solar radiation, exposure to wind, and shape and size of the lake basin (Beeton and Edmondson 1972). The littoral zone with its associated vegetation is the most important area of fish production within most north temperate lakes. These areas are particularly important to northern pike. Other factors being equal, fish production within shallow lakes with large littoral zones is much higher than in deep lakes with small littoral areas (Hanson and Legget 1982, 1986). However, a greater level of production is not always reflected by an increase in growth. Previous studies have shown that poor growth rates occur within eutrophic lakes where northern pike are the primary or only predator present (Holcik 1968, Snow and Beard 1972, Bregazzi and Kennedy 1980). It is also clearly illustrated by comparing the mean size at age of northern pike populations from mesotrophic and meso-eutrophic lakes when compared to populations from oligotrophic lakes. The data suggest that both the pattern of resource use and thermal conditions directly affect

the age-specific growth rate of these different populations.

Deep oligotrophic lakes provide much better summer thermal conditions than non-thermally stratified lakes, especially in hot summers where water temperatures exceed 25 C. Northern pike grew rapidly in the stratified oligotrophic lakes which have both optimal epilimnial temperatures (ie between 18-21 C, Casselman 1978) throughout the summer (eg Appendix Figure A2), and abundant forage fish species present.

northern pike growth within three unstratified Michigan lakes may have been inhibited by sub-optimal thermal conditions during the summer months (Diana 1983). This view was supported further by Headrick's (1985, cited in Diana 1987) work in Ohio reservoirs and Diana's (1987) computer simulations with respect to growth within stratified vs unstratified lakes. Headrick (1985, cited in Diana 1987) demonstrated that populations in the southernmost areas of the northern pike's range took refuge from warm temperatures in the metalimnion of well-oxygenated lakes.

Lakes too shallow to stratify or lacking oxygen in the metalimnion force northern pike to remain at temperatures well above optimum (Headrick 1985). This leads to reduced ingestion, increased metabolic costs and reduced or even negative growth. Lawler (1965) reported activity of northern pike in Heming Lake became reduced and feeding nearly stopped when maximum water temperatures occurred in July. Therefore, a shorter life span and poorer growth in northern pike could be the result of higher maintenance costs brought about by high temperatures (Bregazzi and Kennedy 1980). Northern pike (especially older age groups) found

within such lakes are thus subjected to an additional stress affecting growth during their supposedly "prime" growing season. Therefore, upon reaching a certain maximum size (which generally coincides with the mean size of onset of maturity), the energy required for routine metabolism and the production of reproductive products probably equal or exceed what can be procured and converted into available nutrients. Thus no surplus energy is available for growth (Webb 1978).

Northern pike density apparently affects the population's growth rate. The majority (ie 78%) of the 14 populations grew rapidly up to and including age 2 (Figure 3.4). However, by age 4, while oligotrophic lake populations continue to grow rapidly, meso-eutrophic and to a lesser extent, mesotrophic lake populations enter a period of near growth cessation. As fish grow, the upper size range of prey consumed normally also increases. If larger prey are not available, or not utilized, the growth rate normally decreases. Slower growth of older northern pike age groups (ie \geq age 2) rarely resulted in increased cannibalism. However, a high level of intraspecific competition for food items within a given habitat could lead to decreased or even a cessation of growth. Dietary intake in such cases meet only maintenance and reproductive energy requirements. These problems are further compounded when a number of year-classes of similar size overlap. Within the shallower non-stratified lakes this could result in heavy conspecific competition due to the much higher northern pike densities.

Results presented in Chapter 1 supported by shoreline

inspection of the other deep oligotrophic lakes suggest lack of spawning habitat and to a lesser extent nursery habitat influences abundance levels within oligotrophic lakes. The shoreline and littoral zone of the 5 oligotrophic lakes consist primarily of bedrock, boulder, rubble or sand. Generally less than 1% of these shorelines support aquatic vegetation, particularly during the critical spawning period. Therefore, for northern pike within oligotrophic lakes it is the presence of vegetation which is required for both reproduction as well as for cover and attachment sites by those newly hatched y-o-y which survive to the point of exogenous feeding.

Mesotrophic and meso-eutrophic lakes however, are shallower, warmer and have a preponderantly mud-silt bottom, which supports large areas (up to 70% in lakes such as Whitefish Lake) of emergent and/or submergent vegetation. This greater abundance of vegetation provides sufficient suitable spawning substrate and cover. This ensures the survival of high densities of y-o-y northern pike regardless of adult densities. This has been demonstrated for northern pike fry, particularly within heavily vegetated stocking ponds. Grimm (1981a, 1981b, 1983) demonstrated that the abundance of vegetation and not the number of northern pike >50 cm was the limiting factor controlling the biomass of age 0+ northern pike. This has also been shown for largemouth bass (Micropterus salmoides), another ambush-type predator noted to inhabit vegetated areas. Young-of-the-year largemouth bass survival was best at levels of 20-36% aquatic macrophyte cover (Reynolds and Babb 1978, Durocher et al 1984, Wiley et al 1984).

The presence of excessive vegetation within a water body, however, may create a major problem to be faced by a foraging fish. Increased structural complexity due to increased macrophyte abundance may provide at least partial protection for prey species from predation and increase energy expenditure required by the predator to capture a given prey item (Cooper and Crowder 1979, Heck and Thoman 1981, Savino and Stein 1982, Crowder and Cooper 1982, and references cited therein). The numbers and types of prey items used by northern pike from oligotrophic lakes suggested no quantitative or qualitative restriction on their diet. However, mesotrophic and meso-eutrophic lake populations are apparently strongly influenced by availability of larger prey which are necessary for continued growth. Diana (1981, 1987) demonstrated the importance to northern pike of the rare inclusion of large sized prey. Therefore the very low contribution of fish to the diets of northern pike in meso-eutrophic and mesotrophic lakes, particularly those < 500 mm indicate these populations to be food limited. The dogma of optimal foraging suggests larger sized food items would be advantageous for northern pike > 300 mm. However, as Mosindy (1980), Nunan (1982), Reid (1985) and Trimble (1988) have demonstrated for the populations within Savanne and Henderson Lakes, the diets of these fish are nearly devoid of larger-sized prey items despite the presence of suitably-sized fish (ie 100-300 mm) within these lakes.

Evidence suggests a potential "bottleneck" constraining growth occurs since these northern pike, according to optimal foraging, are inefficiently feeding on smaller prey items such as aquatic

macroinvertebrates and small yellow perch rather than the larger prey present within these lakes. The low growth rates of northern pike which feed on small mean prey size are due to the high cost of capturing each gram of food eaten (Hart and Connellan 1984). Therefore, the evidence obtained thus far supports the concept that northern pike are truly opportunistic predators. Although northern pike will prey on larger items when they are encountered (which therefore results in greater net benefit to the individual), it is the consumption of the small prey items which are more often encountered that ensures the survival of this fish.

Such a bottleneck does not necessarily constrain year-class strength. Being the top level predator within a majority of the systems examined, these northern pike populations are subject only to conspecific predation effects. However, the field data suggests only a low level of cannibalism occurs. Thus decreased foraging success for larger food items and increased conspecific competition apparently act concurrently so as to depress growth to such a point that upon reaching maturation, northern pike meet only their energy requirements for basic maintenance and reproduction.

Lake size and other community components cannot be discounted and also appear to influence growth rates, particularly for younger fish where competition might be greatest. Northern pike within Pickerel Lake, an oligotrophic lake with a diverse fish fauna sharing the epilimnetic portions of the lake, showed slower initial growth rates up to age 5 (mean length 626 mm FL). However, after age 5, growth rates increased substantially and equalled those of northern pike from oligotrophic lakes with simple fish communities

(Figure 3.4). Overall lake size is another factor which may affect growth within Pickerel Lake. Although only 32% of the lake is littoral zone, embayment and riverine fluvial areas existing within the lake form large localized mesotrophic conditions within the lake. These growth rates could be therefore more reflective of mesotrophic rather than strictly oligotrophic habitats.

Another factor influencing growth differences within several of these lakes may be the constant cropping of a fish stock. Angling generally removes the larger, faster growing individuals, which generally leads to the selection for females (Clady et al 1975, Barisov 1978, Otto 1979, Goedde and Coble 1981). As a result, there would be decreased growth and possibly lower mortality rates. The constant cropping of the larger individuals in each age group would allow in overlap in size at age and could account for the length and age frequency distributions exhibited by the populations in Whitefish and Bernadine Lakes. Although all mesotrophic study lakes have moderate to heavy fishing pressure which could remove larger individuals in the smaller lakes (Table 3.4), the larger size of Lac des Mille Lacs and Crooked Pine Lake make at least some of their larger fish less vulnerable to anglers. This is reflected by the presence of larger fish as depicted by their length frequency distributions (Figure 3.1b) and RSD-75 values which equal those of the oligotrophic lakes examined (Table 3.6).

In Bernadine Lake another factor is the apparent heavy exploitation of walleye (Ritchie 1985). A decrease in competition from another top predator such as the walleye could result in

either increased growth, or increased density which could result in a stunting response (Alm 1946, Regier 1977, Nikolskii 1969). The Bernadine Lake population resembles that of experimentally harvested Henderson Lake (Nunan 1982, Reid and Momot 1985, Wisenden 1988). In Henderson Lake, northern pike increased in numbers in response to decreased competition with walleye (Wisenden 1988). Northern pike growth within Bernadine Lake may also be reduced due to a high level of handling. Creel data indicate 80% of the catchable sized northern pike were caught and released at least once over one open-water season.

Some problems can result from comparisons made between generally unexploited oligotrophic and highly exploited mesotrophic and meso-eutrophic populations. For example, growth differences between fish in meso-eutrophic Whitefish and Muskeg Lake suggest that there is strong growth compensation due to exploitation within Whitefish Lake. While not providing a clearcut demonstration of the behaviour of this species under exploitation, the data nevertheless suggest that growth rates increase when the fish community is perturbed by exploitation or removal of a competing predator (Wisenden 1988). This response as well as a high fecundity rate allow exploited northern pike populations to compensate for increased fishing mortality. Furthermore, the minimum age of maturity appears to decrease to age 2 in both males and females. These effective compensatory mechanisms are somewhat offset however by the greater vulnerability of larger fish to capture.

There are still several elements of the hypotheses presented

which require further testing. Two of the most paramount questions that have remained unanswered at least within the present study include i) the foraging behaviour of northern pike within meso-eutrophic lakes and how it is affected by the increased heterogeneity of the surrounding environment within this type of lake, and ii) the mortality factor regulating the actual number of young-of-the-year produced within oligotrophic lakes. However, the present study does not reflect the variability of northern pike growth within northwestern Ontario. Fish characteristically display a considerable intraspecific range of growth rates manifested according to different conditions of food, space, population size, competition or environmental conditions (Weatherly and Rogers 1978). Northern pike growth rates are apparently greater within deep, oligotrophic lakes largely due to i) reduced density resulting in decreased intraspecific competition and consequently increased food availability and ii) more optimal environmental conditions conducive to northern pike growth. It is the shallower, meso-eutrophic lakes, however, which yield the greater amount in terms of actual population density and yearly production.

The use of the scale method (such as within the present study) has been shown to result in non-random ageing errors biased toward more younger ages particularly for slow growing populations (Beamish and Harvey 1969, Power 1978, Mills and Beamish 1980, Beamish and Fournier 1983). This would actually lead to an underestimate of the differences in the growth rates between populations. Therefore once validated ages become available for each population, actual growth differences will likely be greater

than presently reported for populations from the different lake types.

Management Considerations

Although the pike is often less highly regarded by local northwestern Ontario residents than other sport fish species such as walleye, lake trout or smallmouth bass, due to their importance to non-resident anglers, they are the second most harvested sport fish in Ontario (OMNR 1980). The sport fish yield (0.12-1.4 kg/ha) for the seven study lakes for which there was fishing pressure information clearly demonstrates the highest yield coming from meso-eutrophic Whitefish Lake (Table 3.3).

Angling harvest technologies have greatly improved. Techniques now employ trolling motors, depth sounders, downriggers, and temperature/oxygen meters. Furthermore, increased knowledge of the biology of the sport fish sought by the fisherman make fish far more vulnerable. Management agencies have attempted to counter this by increasing the control over exploitation through regulations such as maximum, minimum or slot size management, shortening seasons, decreasing limits, catch and release fishing and alternative angling techniques such as lighter tackle, barbless hooks and flies only (Colby 1984, Novinger 1984, Brousseau and Armstrong 1987, Larkin 1988). In order to protect the northwestern Ontario northern pike fishing resource, recommendations are necessary if we are to prevent major problems. For example, according to the calculated relative yield based on the morphoedaphic index (OMNR, 1983), a number of the study populations are presently overharvested (Table 3.4).

Local knowledge has led to specific lakes being considered for "trophy" lake status. However, such an assessment has generally lacked any biological background for such a designation. The suitability of these choices are dependent on the ability of individual fish within these populations to reach a large overall size. Data from the present study should help to determine which lake types may be best suited for development as a trophy northern pike fishery.

The development of a trophy fishery requires the presence of sufficient numbers of large sized northern pike. Populations found within oligotrophic lakes often have a large proportion of their population consisting of large sized individuals (Table 3.6). However, the relatively low overall population sizes present within such oligotrophic lakes requires that harvest levels of large fish be kept low. In addition the amount of fishing pressure that can be sustained while retaining such lakes as a trophy fishery is unknown. The majority of the oligotrophic lakes examined in this study are essentially unexploited (Table 3.4). Therefore, trophy fishing within oligotrophic lakes may realistically have to be restricted to fly-in lakes where fishing effort is already constrained by accessibility.

The two large mesotrophic lakes examined on the other hand can still produce a good number of "trophy" sized northern pike (Table 3.6) despite heavy fishing pressure (Table 3.4) by northwestern Ontario standards. Therefore it would appear the best candidate northwestern Ontario lakes that can be effectively managed for a trophy fishery are the large (ie >1000 ha)

oligotrophic and mesotrophic lakes.

It is important not to impose a minimal size limit since this may adversely affect the population. The arbitrary imposition of minimum size limits may cause unfavourable changes in population density and age structure. Research has shown that angling can quickly alter northern pike growth and mortality rates, adversely effect the angling pressure and thereby reduce the utilization of the resource (Snow and Beard 1972, Kempinger and Carline 1978, Dunning et al 1982). Such management regulations actually result in a questionable conservation practice if full utilization of the available resource is being sought (Snow and Beard 1972). Any potential resulting benefits therefore must be weighed to determine if a proposed angling regulation invoked to preserve a fish stock may actually be self-defeating.

If the potential to develop a trophy fishery exists, the present study suggests a trophy size category of 800 mm TL (750 mm FL) be established (Note: The differences between fork length and total length within this discussion have been rounded off to the nearest 5 cm interval. Although this is not totally accurate, it was done for greater ease in i) presenting management implications and ii) future enforcement). Furthermore, daily possession should be limited one fish >800 mm TL/day. To protect such a fishery, the elimination of the spring angling season should also be considered. This would protect spawners that are extremely vulnerable to angling at this time. For example, in Squeers Lake a total angling effort of 23.8-28 rod-hrs/spring (ie 0.06-0.07 rod-hrs/ha) captured 15% of the population and 15-18% of the entire biomass of mature

northern pike in the lake. This high angler vulnerability of northwestern Ontario northern pike populations was also clearly shown by Mosindy et al (1987) who demonstrated that with only 1.24 rod-hrs/ha over the entire year, they effectively removed 50% of the total annual production of 2.76 kg/ha.

Within oligotrophic lakes (as demonstrated by the Squeers Lake population in Chapter 1), northern pike clearly exhibit sexually dimorphic growth rates favouring females. As a result any trophy-type fishery would be selective toward females. Therefore implementation of a protective slot limit of 700-800 mm TL (650-750 mm FL) should seriously be considered in order to protect the main portion of the mature female component of the population. This would allow each female 2-3 spawning opportunities while ensuring the fisherman that a trophy situation will be maintained through continued recruitment of larger fish. Alternatively, if this is considered impractical by putting in place too many restrictions and regulations, it is suggested a limit of one fish >700 mm TL such as is presently pending for the Northwest Region should be implemented.

Finally, the present limit of six fish/day in all likelihood could be maintained for fish <700 mm TL. Fish of this size are believed to be more resilient to angling. It has generally only been the larger component of the population which faces the greatest possibility of being adversely affected by angling (Otto 1979). By harvesting the more abundant younger year-classes the negative effect of minimum size limits on the quality size of fish (Snow and Beard 1972, Kempinger and Carline 1978) could be avoided.

The adoption of the above recommendations would minimally effect the majority of the existing northern pike fisheries, particularly those within the small mesotrophic and meso-eutrophic lakes where the fish caught are generally <650mm FL (Figure 3.4), and where the most active northern pike fisheries presently occur (Table 3.4). These recommendations would also allow the development of additional management and marketing strategies to help realize the full potential of this sport fish in northwestern Ontario.

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APPENDIX A: Physical and Chemical Characteristics for Squeers Lake**INTRODUCTION**

Squeers Lake, Ontario (48°31'N, 90°33'W) is a 384.4 hectare lake located approximately 100 kilometres west-northwest of Thunder Bay, Ontario (Figure A.1). Declared a lake trout sanctuary lake in February, 1979, it has since become the subject of intensive fisheries research by the Quetico-Mille Lacs Fisheries Assessment Unit (QMLFAU) of the Ontario Ministry of Natural Resources and Lakehead University. In an attempt to provide initial background information on Squeers Lake, the following section was prepared in order to present a general description of the study area, and a brief summary of the physico-chemical characteristics of the lake itself.

Description of the Lake and Watershed Area

The Squeers Lake watershed, consists of a total drainage area (including lake surface area) of 1281.2 hectares, and is primarily underlain by poorly soluble granitic and syenitic rock (mainly hornblende granite and hornblende syenite). There are also bands of basic metavolcanic rock (consisting mainly of tuff, basic metasedimentary rock, and some gabbro) along the northwest and southeast shoreline (Ont. Dept. Mines, 1963). The topography of the drainage basin is generally low and gently rolling, with an overburden composed of a thin, discontinuous, sandy glacial till (Zoltai, 1965).

The climate of the region is continental, with a mean annual temperature of 1.1°C (Environment Canada, Atikokan, Ontario). Mean

monthly temperatures vary from -18.4oC in January to 17.2oC in July. Prevailing winds for this region are from the west or northwest, although the wind strength and frequency from these directions do not greatly exceed that from other directions. Precipitation has a yearly mean of 724 mm, of which approximately 30% falls as snow. Ice-cover in northwestern Ontario usually lasts from early November to early May. The maximum ice thickness recorded for Squeers Lake to date has been 57 cm.

The immediate area surrounding Squeers Lake is uninhabited, and is dominated by vegetation typical of the boreal subclimax forests found within the Quetico section of the Great Lakes/ St. Lawrence forest region. Intermixed stands of poplar (Populus tremuloides and P. balsamifera), black spruce (Picea mariana), and balsam fir (Abies balsamae) are predominant in this area (Forest Resource Inventory Map No.485903). Other tree species identified to occur within the watershed in order of abundance include white birch (Betula papyrifera), jackpine (Pinus banksiana), white spruce (Picea glauca), eastern white cedar (Thuja occidentalis), white pine (Pinus strobus), black ash (Fraxinus nigra), and sugar maple (Acer saccharum).

MATERIALS AND METHODS

Squeers Lake was initially surveyed by a M.N.R. Aquatic Habitat Survey crew in 1974 and a bathymetric chart was prepared according to the criteria outlined within the Aquatic Habitat Survey manual (Dodge et al,1984) at that time. Aquatic macrophyte and littoral substrate type was determined by shoreline cruises of

the lake's perimeter.

Frequent limnological measurements were taken from open-water stations at the deepest part of the main basin and the western arm of the lake during 1984 and 1985. Water transparency was measured using a 20 cm secchi disc, and temperature/oxygen profiles were measured using a YSI Model 57 temperature-oxygen meter. In 1984, water samples for chemical analyses were also collected on a monthly basis from May to August according to the criteria set by the QMLFAU, outlined in Laine (1983). All chemical analysis was performed by the Ontario Ministry of Environment according to the methods presented in "Outlines of Analytical Methods (1981).

RESULTS AND DISCUSSION

Lake Morphometry

Squeers Lake is comprised of a central U-shaped basin and a westerly arm separated by a small, shallow channel (Figure A.1). The surface areas of the two lake basins are 384.4 and 7.0 hectares, and the maximum depths are 33.6 and 1.75m respectively. Further morphometric characteristics of the two basins are shown in Table A.1. The narrow, littoral zone of the main basin slopes rapidly to deepwater. The shoreline substrate which consists primarily of rubble and boulder material (there are several sandy areas in the southern and western ends of the lake), providing an inadequate substrate for aquatic vegetative growth. Macrophytes were sparse within the main basin. There were no areas of emergent vegetation with submergent vegetation limited to the few small, sheltered bay areas of the lake (Figure A.1). The shallow western

arm, however, which has a substrate consisting primarily of mud and detritus, supports abundant macrophytes during the summer months.

Temperature

When sampling began in 1985, Squeers Lake was covered with 0.57m of ice. At that time, water temperatures within both basins exhibited a zone of inverse stratification (Figure A2, Table A.2). The temperature turnover (ie. at 4oC) occurred immediately with ice-out. This occurred during the last week of April within the western arm, and during the first week of May within the main basin. Water temperatures gradually increased, until a marked stratification (ie. a 6oC difference from surface to bottom) had developed by late May within the main basin (Figure A.2). The summer thermocline remained well established between 10-14m until early September. During this time, epilimnetic water temperatures continued to increase, reaching a recorded maximum of 20.6oC in 1985, and 23.0oC in 1984. Hypolimnetic waters, however, varied only by a 2.5oC difference, and bottom temperatures never exceeded 6.0oC.

The heating and cooling of the water column within the western arm during the open water period was considerably more erratic than that recorded for the lake's main basin. Water temperatures within the western arm warmed gradually after ice-out and became isothermal throughout the water column (Table A.2). However, temperature changes fluctuated on a day to day basis, reflecting changes in daily air temperatures. This was most evident for the temperatures recorded in early July, where water temperatures had dropped to 11.5oC, but reached 22.0oC two days later. Cool fall

air temperatures caused a rapidly cooled the western arm in September, with water temperatures at 5.0oC just prior to freezeup.

The limited temperature data available for the 1984 field season (which is presented in Figure A.3 and Table A.2) strongly support the observations of temperature changes exhibited in 1985. The slightly warmer summer water temperatures within the western arm of the lake and within the epilimnion of the main basin may be accounted for by the more cooler, rainy conditions encountered during the 1985 field season.

Oxygen

The seasonal and vertical changes in dissolved oxygen concentrations for the main basin of Squeers Lake for the 1984 and 1985 field seasons are presented in Figures A.2 and A.3. Oxygen concentrations within the main basin underwent a slow gradual decrease corresponding with the gradual increase in water temperatures. The high oxygen values within the basin for most of the year is indicative of the lake's oligotrophic nature. Hypolimnetic oxygen levels did decrease to levels <5 mg/l for a short period just prior to spring and fall turnover. However, oxygen concentrations never reached below 0.5 mg/l, the level at which redox-labile nutrients begin to be released from sediments (Mortimer, 1942). Low oxygen levels (which were of short duration) occurred at a time when water temperatures did not restrict coldwater species to the hypolimnion, and therefore probably did not affect the fish community nor its distribution to any great extent. Similar decreases in hypolimnetic oxygen concentrations were noted within other oligotrophic lakes monitored by the QMLFAU

(Little Gull Lake (Laine, 1986), and Pettit Lake (QMLFAU, 1986 field data)), and within the Experimental Lakes Area (Schindler, 1971), suggesting that this hypolimnetic depletion may be "typical" for oligotrophic lakes within this region. Schindler (1971) has suggested these oxygen conditions may be due to either incomplete vernal or autumnal mixing or due to the influx of allochthonous material from the surrounding watershed, whereas Cornett and Rigler (1979) have suggested that it may be due to lake morphometry.

The western arm of Squeers Lake appeared to undergo little or no stratification of oxygen levels during the 1984-1985 sampling periods. Oxygen levels never approached anoxic levels within the western arm, and remained near 100% saturation levels during the open water season. It would appear that the continual mixing of the water column during the open water period ensures oxygen levels remain high. The potential for winterkill situations does appear to exist for the western arm as oxygen levels of as low as 27% saturation levels were recorded in late March, 1985. Such low oxygen levels are near those reported to create winterkill situations for the species to inhabit the western arm (Patriarche and Merna, 1970; Casselman and Harvey, 1975) and may have been due to abnormally high snow and ice levels present over the 1984-1985 winter period. Snow and ice levels similar to those present in March, 1985 have been reported to be sufficient to inhibit photosynthesis beneath the ice and create winterkill situations (Patriarche and Merna, 1970).

Water Chemistry and Trophic Status

The results of selected water chemistry samples examined from

Squeers Lake are shown in Tables A.3 and A.4. Little seasonal or interbasin difference occurred with respect to the majority of the water quality parameters examined within the present study. The pH, alkalinity and colour values were slightly higher within the western arm. However, this simply reflects the lower water volume and the greater importance of allochthonous material entering the western basin of the lake from the surrounding watershed.

Lakes within the Quetico/Atikokan area are extremely dilute with respect to major ion levels and poorly buffered (with CaCO_3 as the major buffering system for these lakes) due to the underlying acid igneous bedrock (Kramer, 1979; Maki et al, 1980). The pH and alkalinity values for Squeers Lake (which indicate neutral to slightly alkaline conditions exist within the lake) are slightly higher than most of the lakes within the region. Metasedimentary and metavolcanic rock underlies much of the watershed, and these rock types have been demonstrated to contain a higher fraction of calcareous material than watersheds underlain strictly by igneous material (Coker and Shilts, 1979). This therefore increases the inherent buffering capacity within this lake.

The main basin is oligotrophic with low nutrient levels, generally good oxygen conditions, and high secchi values. The lake's western arm which also had low nutrient levels (Table A.4), supports abundant aquatic macrophytic growth throughout most of the basin. Chlorophyll a levels reached levels are indicative of meso-eutrophy (Ontario Ministry of the Environment, 1981b). The lack of temperature or oxygen stratification within the western arm

greatly enhanced the productivity of the basin. This is due to the fact temperature and oxygen are dominant regulators of nearly all physico-chemical cycling and consequently of all lake metabolism (Welch, 1974). Due to the shallow, polymictic nature of this basin, there is a continuous mixing of nutrients present and this allows them to remain available despite their low levels. It is therefore on this basis that the western arm of the lake may be classified as meso-eutrophic.

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Appendix Table A.1. Selected morphometric characteristics for Squeers Lake, Ontario.

	West Arm	Squeers Lake ^a
Elevation (m)		488
Lake Surface Area (ha)	7.02	384.4
Lake Volume	39×10^3	44×10^6
Maximum Depth (m)	1.75	33.6
Mean Depth (m)	0.83	11.5
Perimeter (km)	1.64	11.3
Fetch (km)	0.67	2.65
Percent Littoral Zone	100	32
Total Drainage Area	258.8	1143.9
Flushing Rate (years) ^b	0.06	9.26

^a Including the western arm

^b Calculated by the format outlined by Brunskill and Schindler (1971). Note: Evaporation and evapotranspiration maps from the Hydrological Atlas of Canada (1978) were used in the calculation of the lake flushing rate. Schindler *et al* (1976) have demonstrated that the use of such regional data to a local area can lead to inaccuracies within the calculations. However, with the absence of accurate outflow and local evaporation and evapotranspiration rates, this data source was used in the present study.

Appendix Table A.2. Seasonal temperature (T in °C) and dissolved oxygen (D.O., in mg/l) readings from the Western Arm of Squeers Lake, Ontario during the 1984 and 1985 sampling seasons.

Date	Depth								
	0.5M		1.0M		1.5M		snow	ice	
	T	D.O.	T	D.O.	T	D.O.			cm
1984									
May	15	7.2	10.9	7.1	10.9	7.0	10.8		
	17	8.6	10.2	8.6	10.2	8.6	10.2		
	20	7.0	11.4	7.0	11.4				
	21	7.0	11.4	7.0	11.4				
June	2	19.5	8.5	19.5	8.5	19.5	8.5		
	7	17.8	8.1	17.8	8.0				
	15	17.2	9.0	17.2	9.0	17.2	9.0		
	18	20.0	8.8	20.0	8.8	20.0	8.8		
	21	23.8	8.2	23.2	8.2	23.2	8.1		
July	20	21.7	7.8	21.5	7.5				
	24	23.8	7.2	23.2	7.2	23.2	7.1		
Aug	28	25.5	8.0	24.8	8.2				
1985									
March	13	0.8	3.8	1.2	4.6			24	55
	23	1.8	7.2	2.8	5.2	3.3	5.5	0-3	57
April	17	4.2	10.4	4.2	9.4	4.2	9.4	0	43
	23	3.8	11.0	3.8	11.0				6
May	1	12.2	10.6	12.2	10.6	12.2	10.6		
	3	11.5	10.4	11.5	10.4	11.5	10.4		
	6	12.5	11.0	12.2	11.2	12.0	11.4		
	8	13.0	11.4	13.0	11.0	13.0	10.8		
	9	15.0	9.1	14.5	9.8	15.0	9.8		
	13	15.1	9.2	14.5	9.2	14.3	9.4		
	15	12.5	9.1	12.5	9.1	12.5	9.1		
	20	13.5	9.0	13.5	8.9	13.0	7.0		
June	5	15.0	8.9	14.9	8.8	14.5	8.8		
	10	15.1	8.4	15.0	8.0	15.0	8.6		
	13	15.2	9.0	15.0	9.0				
July	3	11.1	5.9	11.1	5.9				
	5	22.5	8.3	22.2	8.4	22.0	8.6		
	7	22.0	8.2	21.0	8.2	21.3	8.0		
	8	20.0	7.8	20.0	7.8				
Aug	7	23.2	8.2	23.2	8.0	23.2	8.0		
	10	21.0	8.4	21.0	8.4				
Sept	6	16.3	9.3	16.2	9.3	16.1	9.3		
Oct	2	5.9	11.1	5.9	11.1				
	31	5.0	11.2	4.9	11.0				

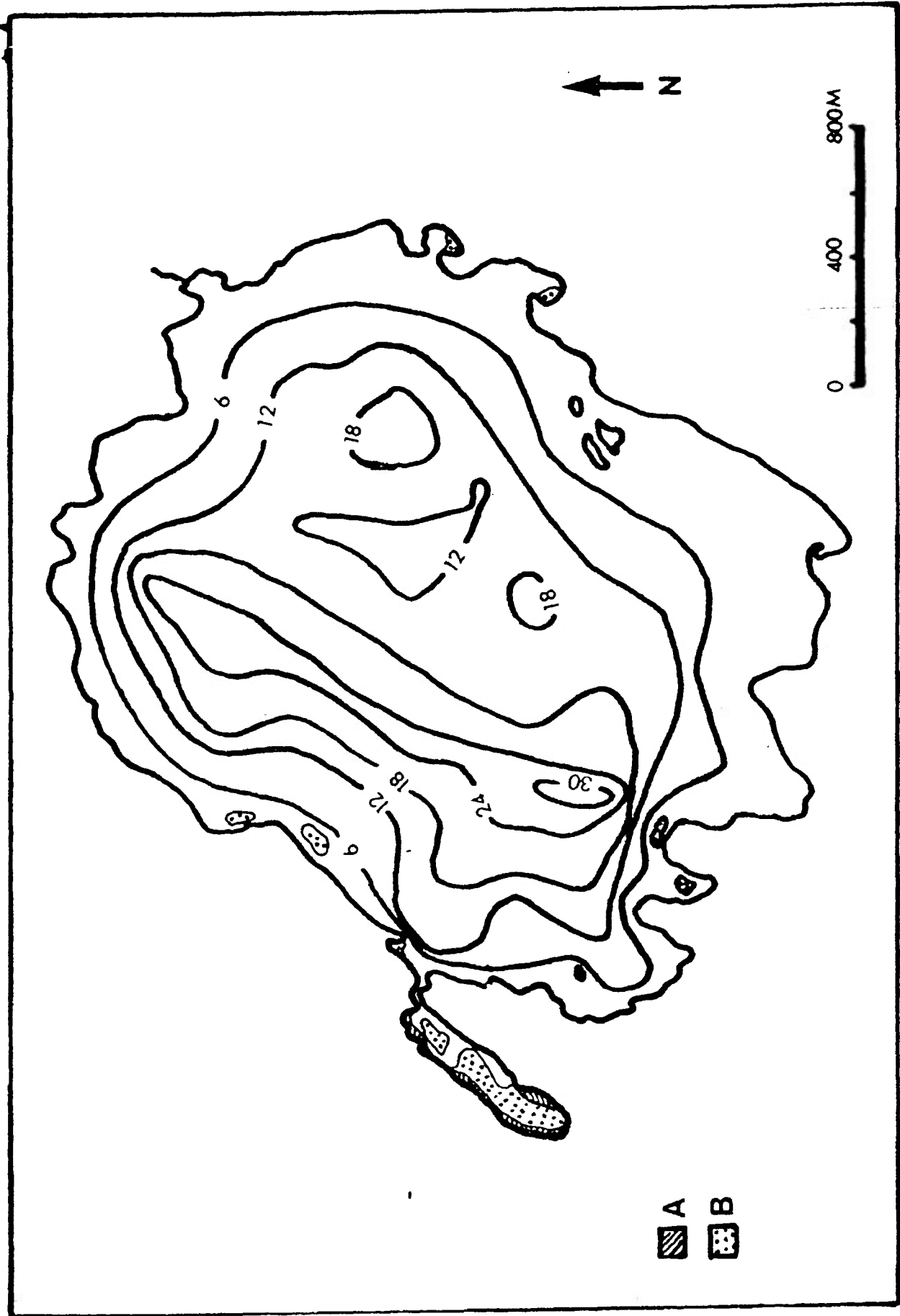
Appendix Table A.3. Water chemistry for the main basin of Squeers Lake, Ontario during the 1984 sampling season (Note: all measurements are recorded as mg/l unless noted otherwise).

	Date				
	May 23	June 4	June 18	July 25	Aug 29
Secchi (m)	5.2	5.0	6.0	6.0	6.8
Chlorophyll <u>a</u> (ug/l)	*	1.0	1.6	0.6	*
Turbidity (Formazin Units)	0.8	1.2	0.6	0.5	1.0
Colour (Hazen Units)	12	14	8	11	13
pH	*	7.3	7.2	7.4	7.3
Alkalinity-TFE	*	14.6	14.2	13.9	14.1
-TIP	*	12.6	12.3	12.0	12.2
Conductivity	*	41	40	40	44
Total Phosphorus	0.01	0.02	0.02	0.02	0.02

Appendix Table A.4. Water chemistry for the Western Arm of Squeers Lake, Ontario during the 1984 sampling season (Note: all measurements are recorded as mg/l unless noted otherwise).

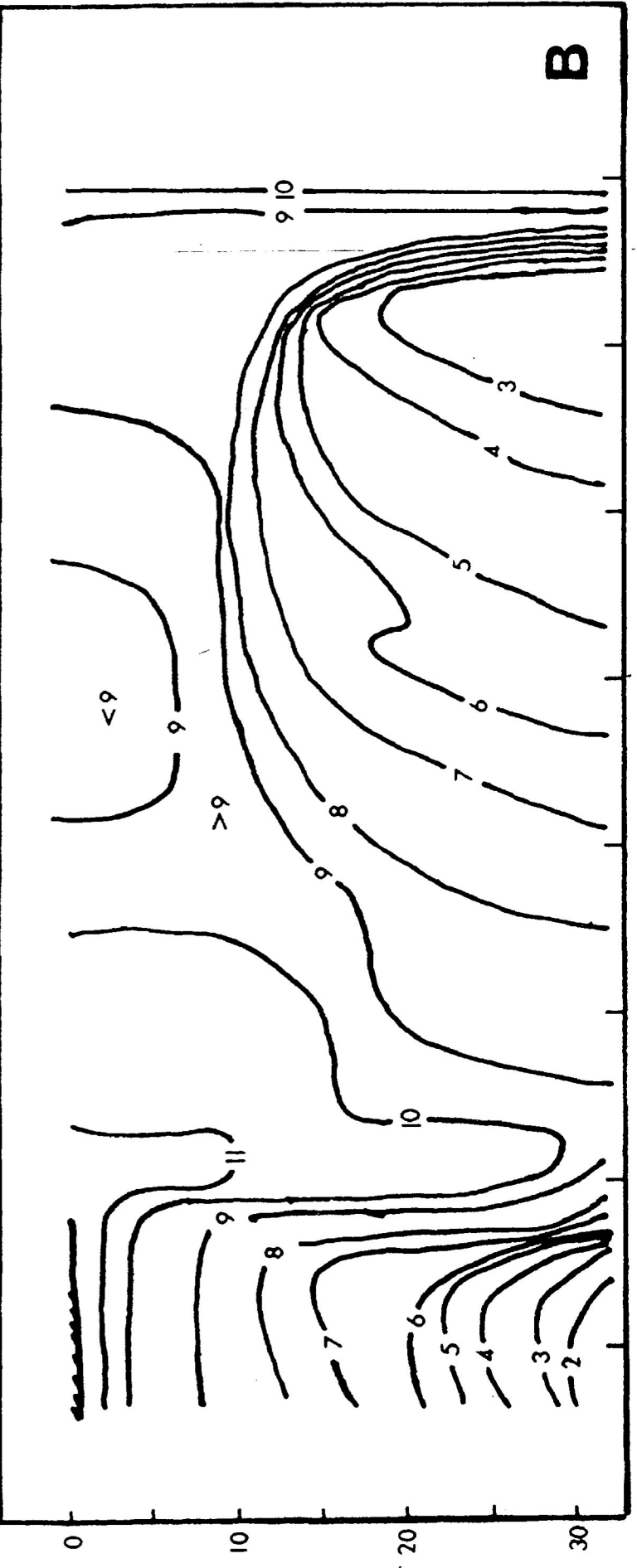
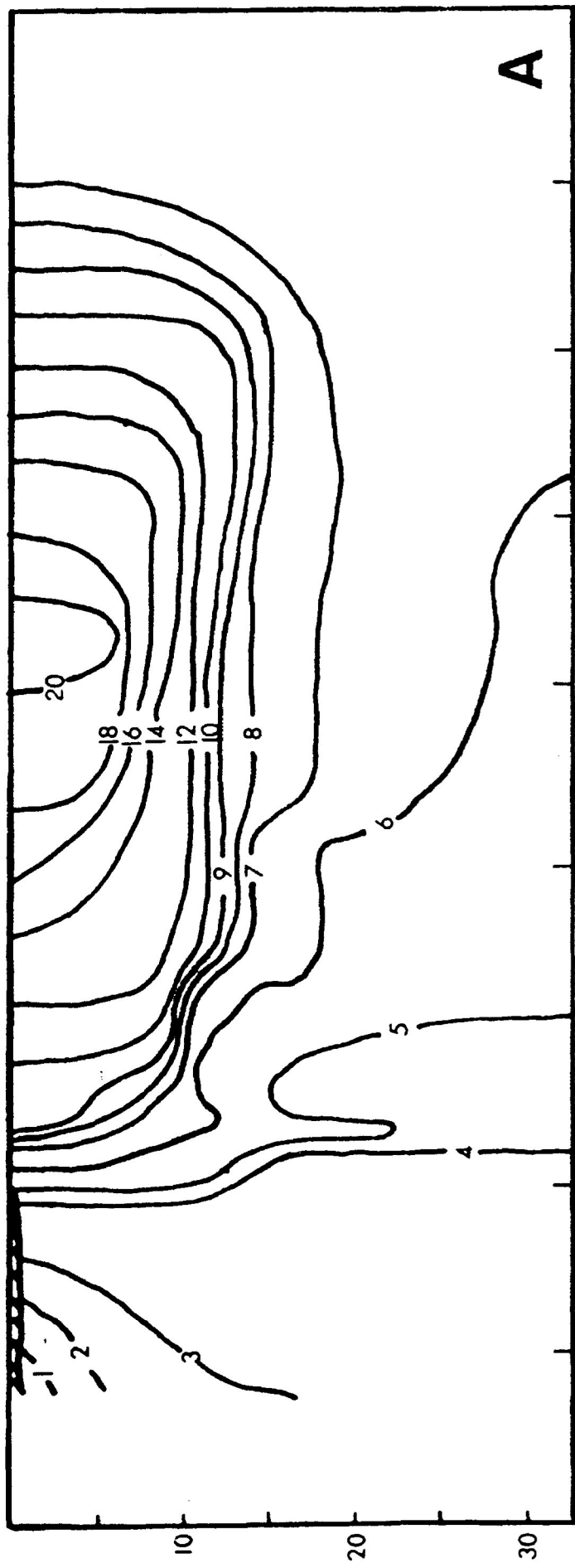
	Date				
	May 23	June 4	June 18	July 25	Aug 29
Chlorophyll <u>a</u> (ug/l)	*	3.1	4.1	1.2	*
Turbidity (Formazin Units)	0.8	0.7	0.7	0.7	0.7
Colour (Hazen Units)	31	29	32	11	21
pH	*	7.4	7.7	7.5	7.4
Alkalinity-TFE	*	19.6	20.1	21.1	21.0
-TIP	*	17.6	18.1	19.0	19.1
Conductivity	*	54	54	54	54
Total Phosphorus	0.02	0.02	0.02	0.01	0.01

Appendix Figure A.1. Bathymetric map and distribution of aquatic vegetation within Squeers Lake, Ontario. A represents areas where emergent species predominate; B represents areas where submergent and floating leaved species predominate.



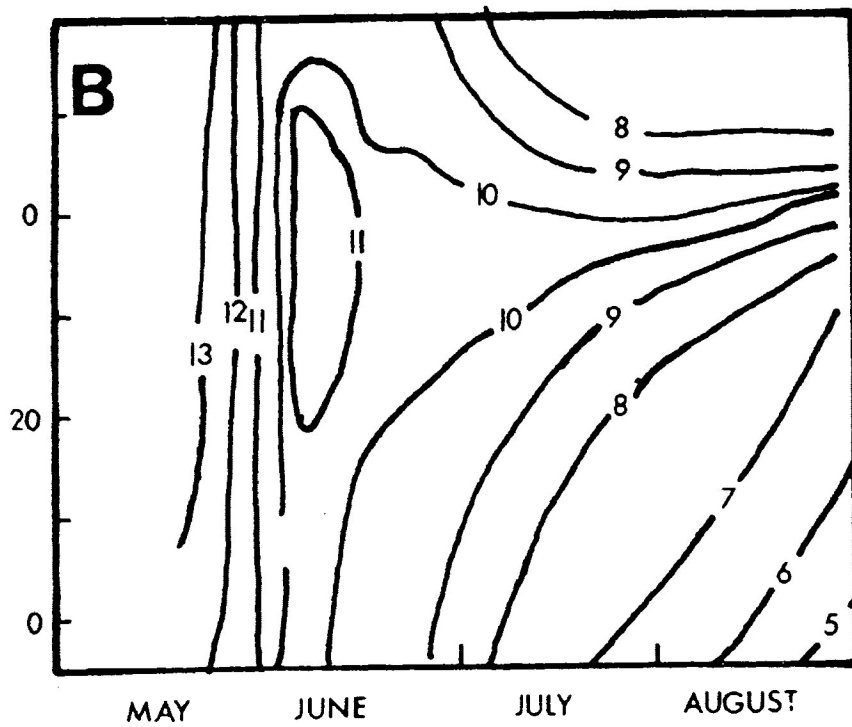
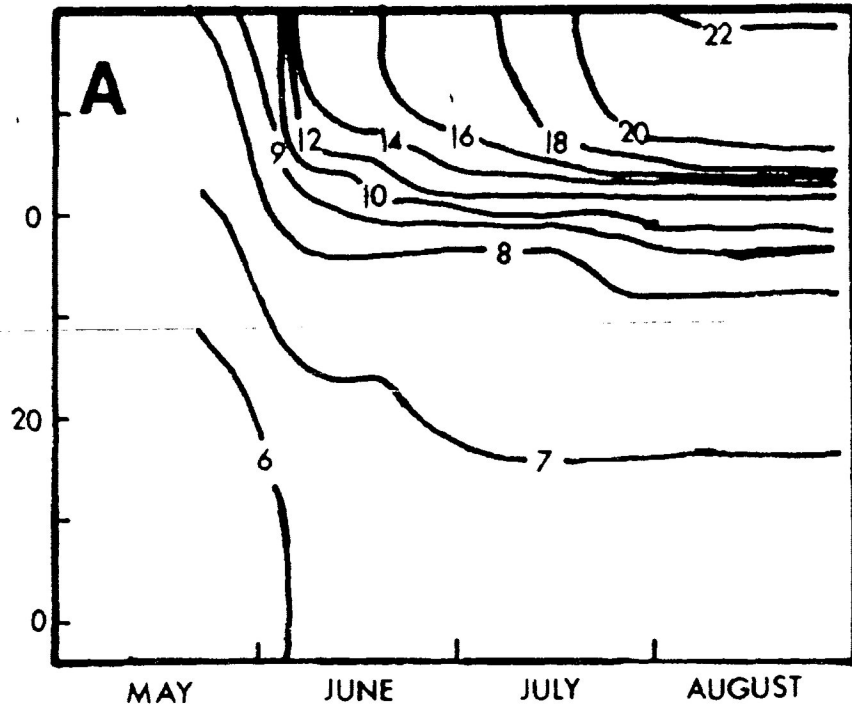
A
B

Appendix Figure A.2. Seasonal and vertical changes in A) temperature (in °C) and B) dissolved oxygen (in mg/l) within the main basin of Squeers Lake, Ontario during the 1985 sampling season.



MARCH APRIL MAY JUNE JULY AUG SEPT OCT NOV

Appendix Figure A.3. Seasonal and vertical changes in A) temperature (in C) and B) dissolved oxygen (in mg/l) within the main basin of Squeers Lake, Ontario during the 1984 sampling season.



Appendix Table B.1. Annual production and biomass for northern pike (*Esox lucius*) ages 3-9, collected from Squeers Lake, Ontario, 1984-1985. N=sample size, \bar{S} =survival, A=annual mortality, Z=instantaneous mortality, G=instantaneous growth rate, K=weight gain factor, W_0 =initial biomass, \bar{W} =mean biomass, P=annual production, \bar{B} =average biomass, P/\bar{B} =turnover ratio of biomass.

1984		1985		S	A	Z	G	K	W_0	\bar{W}	P	\bar{B}	P/\bar{B}
Age	N	Age	N										
3	59	4	40	0.68	0.32	0.39	0.325	-0.065	96.64	93.56	30.41	93.66	0.325
4	24	5	9	0.38	0.62	0.97	0.294	-0.676	45.24	32.88	9.67	34.00	0.284
5	62	6	38	0.61	0.39	0.49	0.160	-0.330	138.38	117.85	18.86	118.93	0.159
6	52	7	46	0.89	0.11	0.12	0.342	0.222	133.07	148.98	50.95	149.43	0.341
7	43	8	36	0.84	0.16	0.17	0.080	-0.090	191.82	183.42	14.67	182.83	0.080
8	21	9	7	0.33	0.67	1.11	-0.209	-1.319	122.72	68.16	-14.25	77.95	-0.183
9	7	10	4	0.57	0.43	0.56	-0.222	-0.782	39.90	27.68	-5.46	29.08	-0.211
											104.17	656.80	0.159
											=0.27	=1.71	
											kg/ha	kg/ha	

Appendix Table B.2. Results of covariance analysis of the length-weight relationships between sexes, sample years and seasons of pike sampled from Squeers Lake, Ontario during the 1982, 1984 and 1985 open-water season. All significance values are based on $P < .001$.

Comparison	Slope		Elevation	
	F-value	Signif. level	F-value	Signif. level
1982:1984	0.609	0.436	0.576	0.4489
1982:1985	0.006	0.939	283.622	0.0001
1984:1985	0.333	0.564	112.021	0.0001
1985 Male:1985 Female	0.060	0.807	54.062	0.0001
1985 Spring:1985 Fall	0.005	0.944	218.72	0.0001

Appendix Table B.3. Diet comparisons of small (300-499 mm), medium (500-699 mm) and large sized (≥ 700 mm) northern pike, excluding young-of-the-year sampled during the unstratified (April 29-June 15, September 15-November 6) and stratified (June 15-September 15) portions of the 1982, 1984 and 1985 open-water seasons on Squeers Lake, Ontario.

Prey Item	Unstratified			Stratified		
	300- 499	500- 699	≥ 700	300- 499	500- 699	≥ 700
<u>Hexagenia limbata</u>	-	-	1	2	2	-
Odonata	-	-	-	-	1	-
<u>Orconectes virilis</u>	-	-	1	-	1	-
Leech	-	-	-	-	-	1
Ninespine Stickleback	3	-	-	-	2	-
Slimy Sculpin	1	-	-	-	1	-
Iowa Darter	2	-	-	-	2	-
Lake Chub	-	-	-	-	1	-
Blacknose Shiner	-	1	-	4	1	-
Yellow Perch <50mm	1	-	-	6	-	-
50-99mm	1	3	-	4	4	2
≥ 100 mm	-	-	1	-	2	2
Burbot <150mm	2	1	-	1	2	1
>150mm	-	-	1	1	2	1
Northern Pike	-	-	-	-	2	1
White Sucker ≤ 150 mm	3	1	3	5	1	1
>150mm	-	-	1	2	2	4
Lake Trout	-	1	3	-	1	-
Number of stomachs containing prey items:	10	7	8	14	16	11
Number of empty stomachs:	1	12	17	10	12	18

Appendix Table C.1. Level of disagreement (expressed in years) between ages assigned to northern pike from Squeers Lake, Ontario during 1982, 1984 and 1985 by scales and cleithra as determined by two readers.

Reader	Level of Disagreement (years)	Scale Age											
		1	2	3	4	5	6	7	8	9	10	11	12
1	-1	-	-	-	1	-	-	-	-	-	-	-	-
	0	41	10	16	17	13	12	18	11	2	1	2	-
	+1	-	-	-	-	2	2	1	-	1	2	1	1
	+2	-	-	-	-	-	-	-	-	1	-	-	-
2	-1	-	-	-	1	-	1	1	-	-	1	-	-
	0	6	5	5	7	3	5	6	1	2	-	-	-
	+1	-	-	-	1	1	1	1	1	1	-	1	-
	+2	-	-	-	-	-	1	-	2	-	1	-	-
	+3	-	-	-	-	-	1	-	-	-	1	-	-

Appendix D.1. The percent frequency of mature male (M) and female (F) northern pike by a) age and b) 5 cm length classes from 14 northwestern Ontario lakes.

	Greenwater		Little Gull		Pettit		Pickerel		Squeers	
	M	F	M	F	M	F	M	F	M	F
Age Class										
1	0	0	0	0	N/A		N/A		0	0
2	46	17	33	0					57	10
3	100	50	100	73					100	90
4	100	100	100	71					100	90
5	100	100	100	91					100	100
6	100	100	100	100					100	100
7	100	100	100	100					100	100
≥8	100	100	100	-					100	100
Size Class										
25-29	0	0	N/A	0	N/A		N/A		0	0
30-34	17	0		0					0	0
35-39	25	0		0					0	17
40-44	50	10		0					33	25
45-49	100	30		20					67	50
50-54	100	50		100					100	0
55-59	100	50		100					100	100
60-64	100	86		85					100	100
65-69	100	100		100					100	100
≥ 70	-	100		100					-	-
N	54	65	19	45					54	68

Table D.1. (continued)

	Bernadine		C. Pine ^a		LDML ^b		Niobe		Henderson ^c	
	M	F	M	F	M	F	M	F	M	F
Age Class	N/A									
1		0	0	0	0	0	0	0	25	16
2		50	50	0	33	0	100	0	58	59
3		100	100	77	82	50	86	43	-	77
4		55	100	83	87	92	100	88	80	71
5		71	100	75	91	100	100	50	91	100
6		75	100	100	100	100	100	100	90	92
7		100	100	100	100	100	100	100	100	100
≥8		-	100	100	100	100	-	-	-	100
Size Class	N/A									
25-29		0	0	0	0	0	0	0	N/A	
30-34		0	50	0	0	0	100	0	N/A	
35-39		50	100	0	69	25	80	33	N/A	
40-44		100	100	67	92	62	100	25	N/A	
45-49		83	100	80	100	100	100	100	N/A	
50-54		89	100	67	91	88	100	75	N/A	
55-59		88	100	100	92	100	100	100	N/A	
60-64		100	100	100	100	100	-	100	N/A	
65-69		100	-	100	100	100	-	100	N/A	
≥70		-	100	100	100	100	-	-	N/A	
N		27	37	61	58	78	45	27	65	79

^a Crooked Pine

^b Lac des Mille Lacs

^c data for 1983 taken from Reid (1985)

Table D.1. (continued)

	Ice		Muskeg		Savanne		Whitefish	
	M	F	M	F	M	F	M	F
Age Class	N/A				N/A			
1			0	0			0	0
2			0	0			83	14
3			33	60			64	64
4			50	88			100	100
5			70	67			89	100
6			92	100			100	100
7			92	93			100	-
≥8			100	100			100	-
Size Class	N/A				N/A			
25-29			0	0			-	0
30-34			0	0			-	0
35-39			0	0			83	0
40-44			36	44			58	57
45-49			82	78			92	88
50-54			95	85			100	100
55-59			100	96			100	100
60-64			-	100			100	100
65-69			-	100			100	-
≥70			-	-			100	-
N			93	92			50	43