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THE UNIVERSITY OF ALBERTA

ANNUAL CYCLE IN CONDITION AND NUTRIENT COMPOSITION OF NORTHERN PIKE (*ESOX LUCIUS* L.)

by

BRIAN A. MEDFORD ©

A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Annual Cycle in Condition and Nutrient Composition of Northern Pike (*Esox lucius* L.)" submitted by Brian A. Medford, in partial fulfilment of the requirements for the degree of Master of Science.

W. C. Mackay
Supervisor

D. Clandinin

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Date June 7, 1976

ABSTRACT

Northern pike (*Esox lucius*) were sampled at regular intervals from Lac Ste. Anne, Alberta, between May, 1973 and July, 1974. Condition and the protein and lipid content (on a percentage basis) of liver, gonad and muscle were measured. Somatic body weight (condition) and the total protein and total lipid content of liver and gonad were calculated for a pike of 50 cm fork length to elucidate seasonal changes in these parameters.

In general, somatic body weight was high from late summer (August) to late winter (March) except for males which showed a transient decrease in body weight in September. After March, body weight dropped approximately 12.6% in females to a minimum in April (prior to spawning) and 14.9% in males to a minimum in June (after spawning). Liver weight for 50 cm males and females increased from about 8.6 g in May to 23.5 g in March, or from about 1% to 2.4% of gross body weight. The temporal differences between the sexes in the rate of loss of body weight and of liver weight prior to and after spawning were probably related to energy demands for final ovary maturation in females and greater spawning activity in males.

Total liver protein increased to a greater extent in females than in males through fall and winter and in March it exceeded that of males by 1.21 g (165%). From March to July, total protein in female liver dropped 1.96 g (62%) compared to 0.79 g (41%) in males.

Total liver lipid in both sexes was highest in August (1.29 g and 0.97 g for males and females, respectively) and lowest (0.55 g, 0.20 g) immediately after spawning (May) but was significantly higher in males

than in females throughout the year. Liver lipid declined approximately 0.34 g in each sex between March and June, or by 35% in males and 47% in females.

Gonad growth began in midsummer (July) when ovaries and testes were 0.43% and 0.15% of gross body weight, respectively. Maturation of ovaries proceeded continuously through fall and winter and reached 15% of gross body weight in April. There was no loss in body condition of females prior to March. Testes reached a maximum weight in September (2.1% of gross body weight) when a marked drop in liver weight and somatic body weight of males occurred. Females deposited 14.5 times more protein (33.30 g) and almost 10.5 times more lipid (7.95 g) than males into gonads.

Muscle protein, lipid and water (% wet weight) all fluctuated significantly through the year but were not significantly different between sexes at any time. The combined ranges of sample means for males and females were as follows: protein, 18.4%-20.2%; lipid, 0.59%-0.80%; water, 77.3%-80.1%.

Since the northern pike examined did not have any large fat storage depots, it appears that the changes in somatic body weight observed were due to the catabolism of whole muscle tissue.

ACKNOWLEDGMENTS

I wish to express my sincere gratitude to my supervisor, Dr. W. C. Mackay, for his support and guidance throughout the duration of this study. Special thanks also go to my supervisor and to Dr. D. D. Beatty for their critical review of the manuscript.

G. Cormie, A. [illegible] and K. Kivett aided in the collection of animals.

G. Cormie, B. Diana and B. Donovan helped in the preparation of the manuscript.

T. Fenton, Department of Animal Science, provided invaluable technical assistance with the nitrogen analyser.

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INTRODUCTION

Seasonal changes in condition and chemical composition have been described for many fishes (see reviews by Love, 1970; Kizevetter, 1973; Shul'man, 1974) and provide evidence for annual cycles of energy storage and depletion. Each year fish require a considerable amount of energy for the growth of gonads which are rich in fat and protein, for spawning, and perhaps for spawning migration. These reproductive energy requirements are superimposed on seasonal changes in energy demands for body growth, maintenance and general activity. Love (1970) has suggested that the death of older fish of some species at least may be attributed to the large amount of energy required for gonad maturation and spawning.

Many fish reduce or stop feeding at times of the year which may coincide with any or all of the events associated with reproduction and, consequently, the nutrient reserves of these fish can be severely depleted. The utilization of stored energy by salmon during gonad maturation and homing migration has been well documented (Greene, 1926; Idler and Tsuyuki, 1958; Idler and Bitners, 1958, 1960; Idler and Clemens, 1959 and others). Liver and body condition and liver lipid (% wet weight) of cod (*Gadus morhua*) are low during the spawning period (March-May) but show recovery in June when heavy feeding is resumed (Jangaard *et al.*, 1967a). For Atlantic herring (*Clupea harengus*) which spawn in winter, food availability is poor following spawning and therefore nutrient (fat) continues to be depleted until spring (Wood, 1958). American plaice (*Hippoglossoides platessoides*) feed neither over winter nor at spawning but have adopted a strategy of feeding and energy storage during summer when food is most abundant. This may allow for more efficient use of energy during the annual cycle than would continuous feeding (MacKinnon, 1972). The patterns of energy storage and depletion in fishes are extremely diverse, varying both interspecifically and intraspecifically according to mode of life and ecological conditions (Shul'man, 1974).

Many fish deposit substantial reserves of fat in the muscle, liver or viscera which are used as an energy source later during the annual cycle when exogenous energy intake is insufficient to meet the requirements for normal vital activity. Shul'man (1974) has reviewed investigations on the dynamics of fat in the life cycles of fish and discussed the significance of fat as a major form of energy storage in fishes. Pike are "lean" fish and therefore differ from fatty fish which use the body musculature as a primary depot for fat. Seasonal maximums of 10-30% muscle fat (on a wet weight basis) are characteristic of several fatty fishes (Clark and Almy, 1918; Marshall *et al.*, 1939; Hardy and Keay, 1972; Shimizu *et al.*, 1973). The flesh of a deep water subspecies of lake trout, *Salvelinus namaycush siscowet*, may contain 10-67% fat (Thurston, 1962; Eschmeyer and Philips, 1965). The criterion of lean vs fatty fish is arbitrary, and Shul'man (1974) states that the overall fat content of lean fish is no more than 2-5% of the body mass. According to Kluytmans and Zandee (1973), the total lipid content of the somatic body of pike is about 2%.

Most of the research on energy storage and depletion has been concentrated on economically important marine species and little attention has been directed toward temperate-zone freshwater fishes. The chemical composition of various freshwater species has been determined (Thurston et al., 1959; Ananichev, 1961; Makhmudov, 1972; Mangold, 1973) but usually from samples taken at one time of year. The purpose of such studies has been to determine the relative content of the various nutrient components for comparative purposes. The paucity of information on seasonal variation can probably be attributed to the effort required and difficulty involved in winter sampling. However, a few annual studies have been conducted on freshwater fishes in which annual energy cycles were either implied (LeCren, 1951; Ball and Jones, 1960; Gritsenko, 1970; Kashem, 1970; Gorbach, 1971; Moroz, 1971; Mackay, 1975) or directly shown by caloric measurement (Sandercock, 1969). Temperature affects the metabolism, activity and feeding rates of fishes and its influence on seasonal energetics is probably greater in temperate freshwater fishes which experience large seasonal temperature changes than in marine species which live in a more thermally stable environment.

Northern pike, *Esox lucius*, were chosen for the present study because they are active and readily caught throughout the year. The pike is a typical predator in the freshwaters of the northern hemisphere and its distribution is circumpolar. In Canada it is important both as a commercial and as a sport fish. Studies on the feeding ecology of pike (Frost, 1954; Lawler, 1965) indicate that they feed most of the year. However, Frost (1954) found a low rate of feeding in April, suggestive of a spawning fast, and thus it is conceivable that nutrient reserves would be depleted at this time. Depot fat is known to be a major form of nutrient reserve in fishes (Shul'man, 1974) and in *E. lucius* the viscera may be the only area of notable fat storage as in

Esox reicherti (Kizevetter, 1973). Hence the aim of the present study was to determine whether seasonal changes occur in condition and in tissue protein and lipid content of individuals from a population of northern pike.

MATERIALS AND METHODS

Description of Study Area

Lac Ste. Anne is a shallow eutrophic lake located approximately 74 km west-northwest of Edmonton, Alberta. The geographic location of the lake is approximately 114° 24'W longitude and 53° 43'N latitude. The lake is about 57 km^2 in area with a maximum depth of 10 m and an average depth of 4.8 m (Department of Water Resources Hydrographic Survey of Lac Ste. Anne, June, 1965). Water depth in the sample area was 3-4 m. In addition to northern pike, other teleost species present in Lac Ste. Anne are: Walleye (*Stizostedion vitreum*), Perch (*Perca flavescens*), Burbot (*Lota lota*), Lake Whitefish (*Coregonus clupeaformis*), White Sucker (*Catostomus commersoni*), Spottail Shiners (*Notropis hudsonius*), Brook Stickleback (*Culaea inconstans*) and Iowa Darter (*Ethiostoma exile*).

Sampling Procedure

Northern pike (*Esox lucius*) were collected on nine occasions between May, 1973, and July, 1974. Specimens were obtained by gill net except in late April when prespawning pike were caught by dip net from a tributary of Lac Ste. Anne. An attempt was made to obtain 14 fish of each sex during each collection period (Appendix Table 1). In order to reduce size-dependent variability, only individuals from 45-55 cm fork length were sampled. Work by Lane (1971) indicates that pike in this size range are more abundant in terms of numbers of individuals captured by gill net than any other size range. Some pike captured in the present study were aged from annuli on scales and were found to represent

4+ and 5+ age classes. All fish were adult and had spawned at least once or were about to spawn for the first time.

Measurements were made and samples were taken from fish within 18 hours but more often in less than 6 hours after removal from the nets. During this time interval, specimens were packed in ice or kept in a cold room (4 C). An exception was the May 1973 sample which was immediately frozen (-25 C) and partially thawed 4 weeks later for measurement and sampling. For each fish, the stomach was emptied and gross body weight determined to 1.0 g. Gonads and liver were blotted dry and weighed to the nearest 0.01 g. Fork length was measured to 0.1 cm. A portion (10-25 g) of the white dorsolateral epaxial muscle was removed, starting about 2 cm behind the head and proceeding posteriorly. Care was taken to exclude bone, skin and red muscle tissue from the white muscle sample. Whole liver, whole gonad and muscle tissue samples were placed in separate vials, weighed to 0.01 g and stored at -25 C. These were later freeze-dried to constant weight and water content was determined by subtracting final from initial weight. After drying, samples were ground to a fine powder with a mortar and pestle and returned to cold storage (-25 C) in vials sealed with parafilm. Later, samples were analysed in a random sequence for nitrogen and lipid content. Gonads of fish taken in May 1973, June 1973, June 1974 and July 1974 were rudimentary and gonads were therefore pooled with respect to sex and time of capture prior to analysis.

Fat bodies were observed along the gut wall in pike taken throughout the year. In order to assess the role of visceral fat as an energy storage depot, fat bodies were removed from the stomach and intestine of prespawning (March 1974) and postspawning (June 1974) pike, blotted dry and weighed to 0.01 g.

Procedures for Protein and Lipid Analysis

Total nitrogen was measured with a Heraeus Micro-Rapid N gas analyser (W. C. Heraeus Company, Hanau, Germany) set at maximum combustion time (approximately 2 minutes) and equipped with an additional combustion furnace which was found necessary for the analysis of materials containing significant quantities of fat (T. Fenton, personal communication). Aluminum or tin Heraeus combustion boats were used to contain the 16-20 mg freeze-dried samples. Duplicate analyses of tris (hydroxymethyl) aminomethane (Fisher certified primary standard) were done initially and every 10 samples thereafter to monitor the accuracy of the technique. When necessary, a correction based on the theoretical N content of the standard was applied. Reproducibility by this method was high as determined from duplicate determinations of the nitrogen content of muscle tissue samples from 50 fish in which variability was never greater than ± 1.0% of the mean for the duplicates. Consequently, the remainder of samples were each analysed once only. Protein was calculated as total N x 6.25 (Kleiber, 1975).

Total lipid was determined by refluxing portions of the dried sample in a Soxhlet apparatus for 5 hours with chloroform/methanol (2:1). The chloroform/methanol extract was then washed once with a 0.05% aqueous $CaCl_2$ solution according to the procedure of Folch et al. (1957). The washed chloroform phase was collected in pre-weighed beakers, evaporated to dryness and the quantity of lipid residue determined gravimetrically. Before weighing, beakers were dried at low heat (70-80 C) for no more than 5 minutes and then cooled to room temperature in a desiccator. The quantity of freeze-dried liver, gonad and muscle used for lipid determination was 0.25, 0.20, and 0.50 g, respectively. Duplicate blanks were run each day to correct for error due to non-volatile contaminants of the chloroform/methanol mixture. Variability of the extracting technique was determined for each type of tissue from six replicates of a "standard" homogenate. The lipid content as a percentage of the dry tissue weight (mean ± 1 SD) was 12.00 ± 0.78, 16.84 ± 0.69, and 3.64 ± 0.18 for liver, gonad and muscle tissue, respectively.

Statistical Analysis

The mean lengths of male pike sampled during each collection period did not differ significantly (Duncan's multiple range test, $p<0.01$) from one another. However, the mean length of females sampled in July 1973 was significantly less than in August 1973 and September 1973. Body, liver and gonad weights as well as protein and lipid content of liver and gonad were calculated for fish of 50 cm fork length. The calculations assumed a linear relationship between fork length and the parameters measured within the 10 cm size range of fish studied. The body weight reported is the somatic body weight (gross body weight minus liver and gonad weights). Data for individuals from sampling dates which approximately overlapped the annual cycle were grouped with respect to sex and time of year as follows:

1) May 1973 ♂ and June 1974 ♂
2) May 1973 ♀ and June 1974 ♀
3) July 1973 ♂ and July 1974 ♂
4) July 1973 ♀ and July 1974 ♀

These data were used to test the assumption of linearity between somatic body weight and fork length. Using arithmetic (raw) values, tests for curvilinearity were non-significant but were highly significant for linearity (Appendix Table 2). A similar linear relationship is assumed between gonad weight and fork length as well as between liver weight and length of fish. The weight/fork length ratio of each weight parameter measured for each individual was multiplied by 50 to obtain a value for a 50 cm fork length pike.

Seasonal variations in the parameters studied were determined by analysis of variance and Duncan's multiple range test. Unless otherwise stated in the text, differences were not considered to be significant if $p>0.01$. Significant differences ($p<0.01$) between sexes in each sample category were determined using Student's t-test for unpaired samples.

RESULTS

Somatic Body Weight

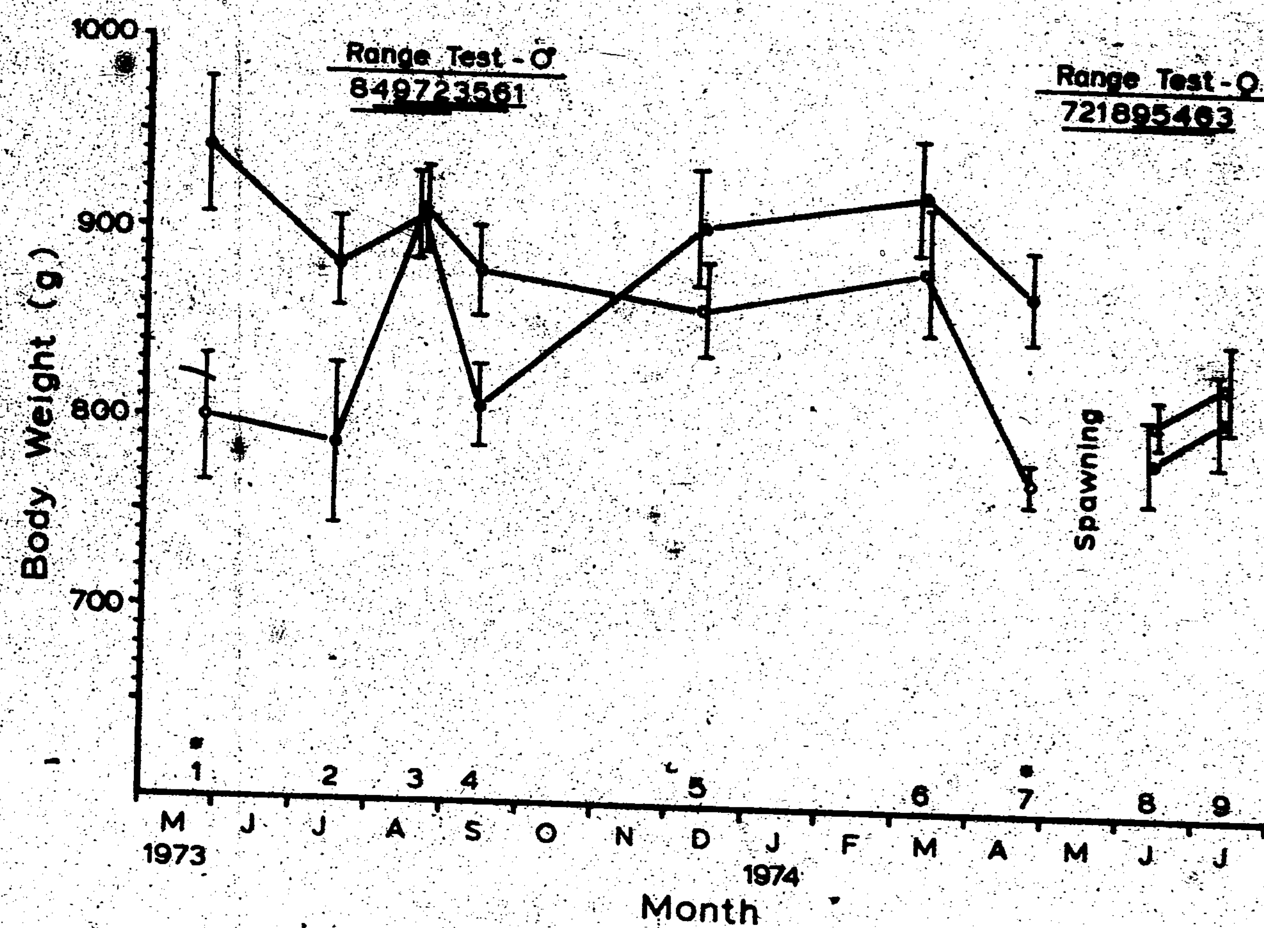
In order to determine whether seasonal changes occurred in condition of northern pike, the somatic body weight (gross body weight minus liver and gonad weights) of individuals in each sample was calculated for a standard fish of 50 cm fork length (Fig. 1). Liver and gonad weights were subtracted from the gross body weight so that real changes in the weight of the remaining somatic portion of the body were not affected by alterations in liver size or gonad size. The mean somatic body weight of 50 cm females varied from 773.0 to 912.0 g and the weight of 50 cm males from 786.0 to 943.0 g during the year.

In general, somatic body weight or condition (Fig. 1) was highest from late summer through winter and lowest in late spring after spawning. Female somatic body weight increased mainly in summer and remained relatively steady over winter until March, then decreased by about 111.0 g (12.[illegible]%) during the period prior to spawning (March-April). The seasonal fluctuation in somatic body weight was not as regular in males. Male somatic body weight was higher for postspawned males in 1975 than in 1974. It dropped significantly ($p<0.05$) from August to September coinciding with a final increase in testes weight, then increased until December when a weight ([illegible] g) similar to females was reached. Males lost about 50.8 g (5.5%) somatic body weight before spawning and an additional 87.8 g (9.4% of the somatic body weight in March) during spawning (April-June). Raw data for somatic body weight as well as gross body weight calculated for 50 cm pike are reported in Appendix Table 3.

FIGURE 1. Seasonal variation in somatic body weight (gross body weight minus liver and gonad weights) calculated for a 50 cm fork length northern pike. Mean ± 1 SE. Closed circles—male, open circles—female. Significant differences ($p<0.01$) between sexes at any one sampling period are indicated by an asterisk above that sampling period on the abscissa of the graph. Ea[illegible] period is numbered above the abscissa [illegible] to one another by Duncan's multiple [illegible] shown [illegible] the [illegible] Sampling periods [illegible] the same level are not significantly diff[illegible] Significance levels for analysis of [illegible]

Analysis [illegible] (s[illegible]s): [illegible].05

Analysis of va[illegible] [illegible]0.05


Range Test - ♂
849723561
Range Test - ♀
721895463
Body Weight (g)
1000
900
800
700
1 2 3 4 5 6 7 8 9
M J J A S O N D J F M A M J J
1973
1974
Month
Spawning

Liver Weight

Total liver weights were calculated for a 50 cm fish rather than expressing them as a percentage of the gross body weight to eliminate the possibility of apparent changes in liver weight which were the result of fluctuations in somatic body weight.

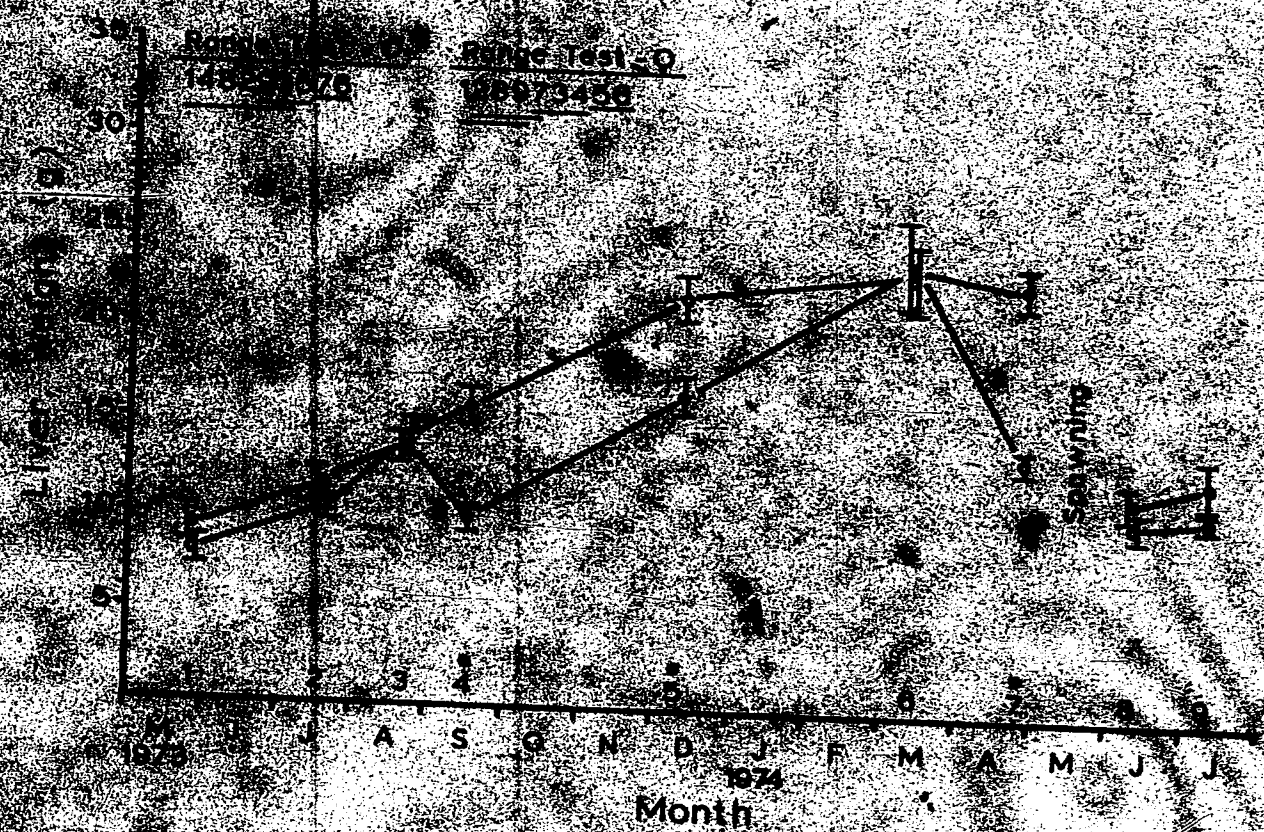
Liver weight for each sex was lowest (approximately 8.6 g) after spawning (May 1973) and increased almost 3-fold to about 23.5 g the following March, or from 1.0% to 2.4% of gross body weight (Fig. 2 and Appendix Table 4). The increase was steady in females but male liver weight increased over the summer, then dropped markedly (but not significantly, $p>0.05$) in September to its original postspawning value and it was approximately 6 g lower than that of females at this time as well as in December (significant difference, $p<0.01$). In the spring of 1974 almost 89% of the decrease in female liver weight occurred before spawning whereas liver weight of males did not decrease significantly until spawning.

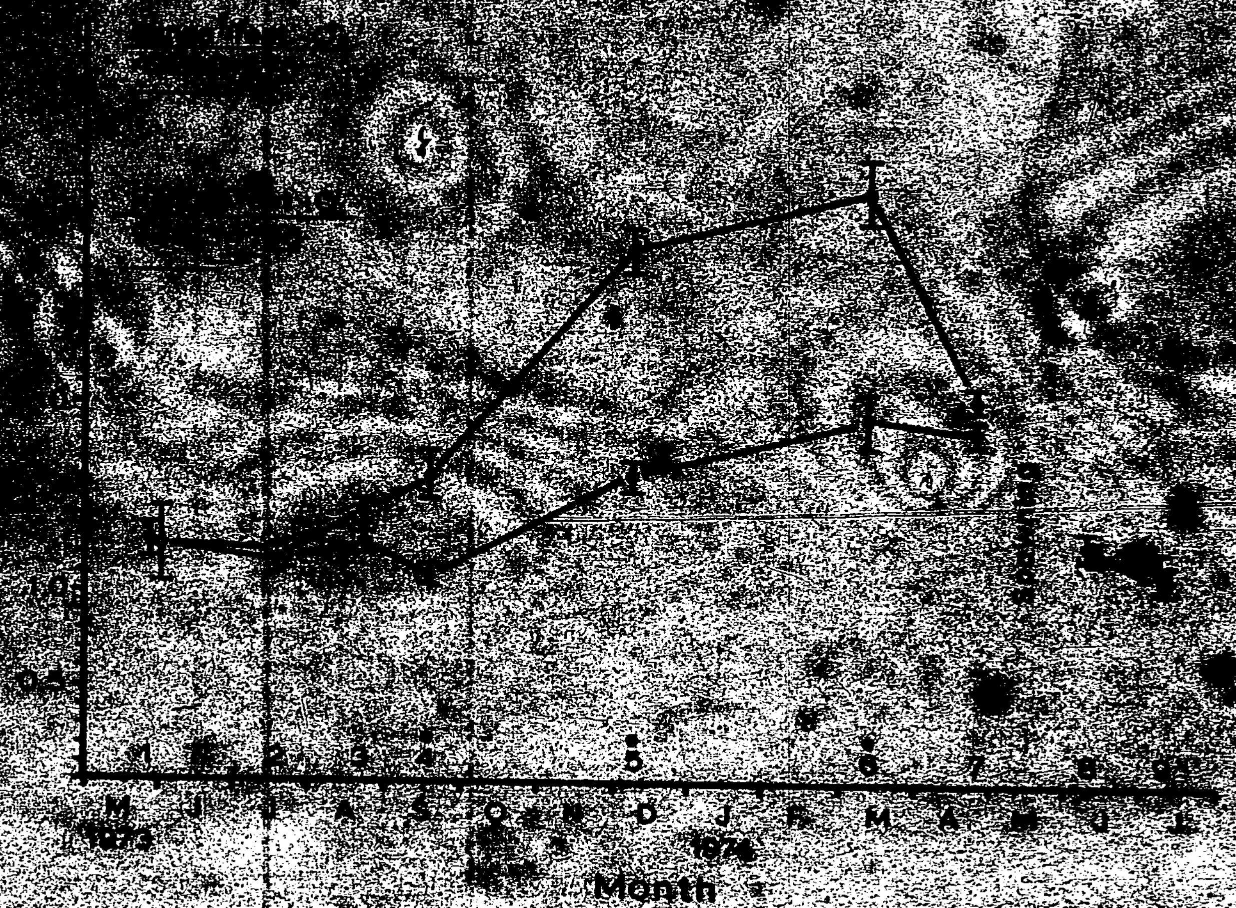
Liver-Chemical Data

Liver protein averaged 1.26 g for both sexes in May 1973 and remained relatively stable over summer (Fig. 3 and Appendix Table 4). Protein content of male liver declined slightly to 1.10 g in September at a time when it was increasing in females. Total liver protein increased over winter in both sexes but by a greater amount in females and by March it had reached 3.14 g in females compared to 1.93 g in males. During the period before spawning (March-April), female liver protein fell 1.11 g to very nearly the level found in male fish. No change was seen in male liver protein over the same time interval.

FIGURE 2. Seasonal variation in liver weight calculated for a 50 cm fork length northern pike. Mean ± 1 SE. Closed circles—male; open circles—female. Statistical representation as in Figure 1.

Analysis of variance (males): $p<0.01$
Analysis of variance (females): $p<0.01$


Month
1973
1974
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
Spawning
30
5



M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
1973
1974
Month

Protein declined by a slightly greater amount in females (0.85 g) than in males (0.72 g) from April to July.

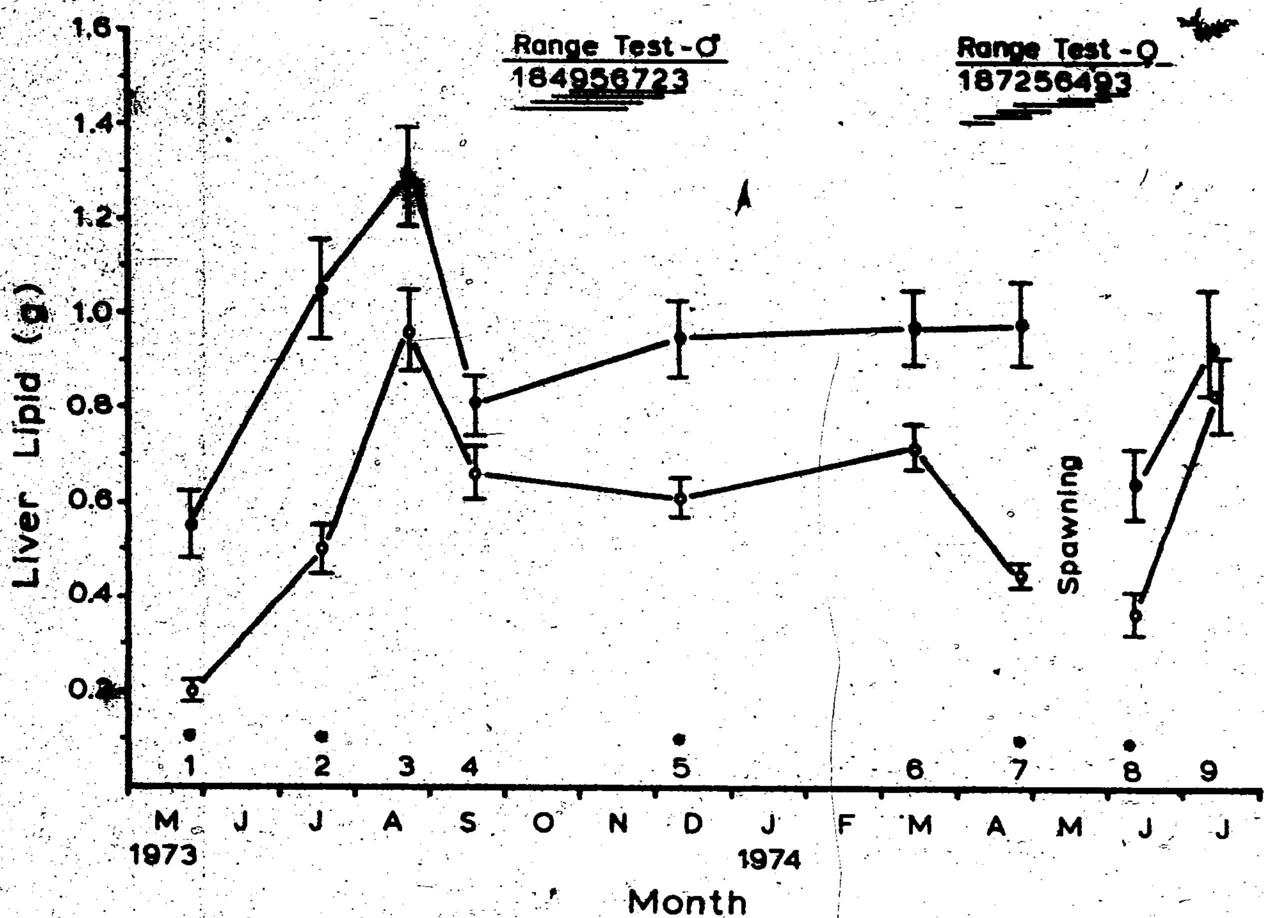
The patterns of seasonal change in the quantity of liver lipid (Fig. 4 and Appendix Table 4) were similar between sexes but lipid content was significantly greater for males during most of the year. Lipid content increased to a maximum in August (M:1.29 g; F:0.97 g), dropped significantly in both sexes in September and remained relatively constant through the winter. In the spring, male and female liver lipid declined 0.33 g and 0.35 g, respectively, but almost all of the decrease in female liver lipid occurred prior to spawning (Fig. 4). In June 1974 (after spawning) male liver contained 0.64 g lipid compared to 0.38 g lipid in females.

Liver water, protein and lipid as a percent of the wet weight are shown in Appendix Table 5. Water content was greater in females throughout the year and, for both sexes, it was generally highest in May (M:75.5%; F:79.5%) and lowest in August (M:67.6%; F:71.8%). Seasonal variations in percent protein and percent lipid did not parallel seasonal fluctuations in the quantities of these nutrients (Figs. 3 and 4) due to the marked cycle of liver weight. Percent liver protein in both sexes was similar in May (M:12.6%; F:13.6%), then dropped over summer to lows in August (M:9.4%; F:10.4%) and increased in September. While the percentage of protein in male liver further declined over fall and winter, it rose in females to a maximum of 14.9% in April, which was notably higher than that of males (8.2%) at this time. Percent liver lipid was higher in males than in females throughout the year and both sexes showed a maximum in August (M:9.7%; F:6.9%). Liver lipid levels decreased

FIGURE 4. Seasonal variation in total liver lipid calculated for a 50 cm fork length northern pike. Mean ± 1 SE. Closed circles—male; open circles—female. Statistical representation as in Figure 1.

Analysis of variance (males): $p<0.01$

Analysis of variance (females): $p<0.01$


Range Test - ♂
184956723
Range Test - ♀
187256493
Liver Lipid (g)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
Spawning
1
2
3
4
5
6
7
8
9
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
1973
1974
Month

during the fall, then remained stable until the following summer.

Gonad Weight

Gonad growth commenced after mid-July when ovaries and testes weighed approximately 3.6 g and 1.4 g (0.43% and 0.15% of gross body weight), respectively, for a 50 cm pike (Fig. 5 and Appendix Table 6). Ovary weight increased continuously throughout the fall and winter to a maximum of 138.6 g (15% of gross body weight) in April. Approximately 12% of this increase took place in summer (July 16—September 18), 60% in fall and winter (September 18—March 14) and 28% in early spring (March 14-- April 25) prior to spawning. The rate of gonad growth for males and females was approximately the same from July to September. Testes reached a weight (17.1 g) in September which did not differ significantly from the annual maximum of 18.3 g (2% of gross body weight) for a 50 cm pike in April. Of the total increment in testes weight, 53% occurred in July/August and 40% in August/September. The significant drop in weight of testes which occurred from September to December was determined from dry weight data to be almost entirely (94.8%) the result of a decrease in water content. Spawning probably occurred in early or mid-May. Regression of spent gonads was observed for each sex until July.

Gonad-Chemical Data

Large differences were seen between sexes in the amount of nutrient deposited into gonads when comparing fish of similar size. Temporal changes in the quantity of protein and lipid present in the gonad are shown in Figure 6 and Figure 7, respectively and in Appendix Table 6.

FIGURE 5. Seasonal variation in gonad weight calculated for a 50 cm fork length northern pike. Mean ± 1 SE. Closed circles—male; open circles—female. Statistical representation as in Figure 1.

Analysis of variance (males): $p<0.01$
Analysis of variance (females): $p<0.01$

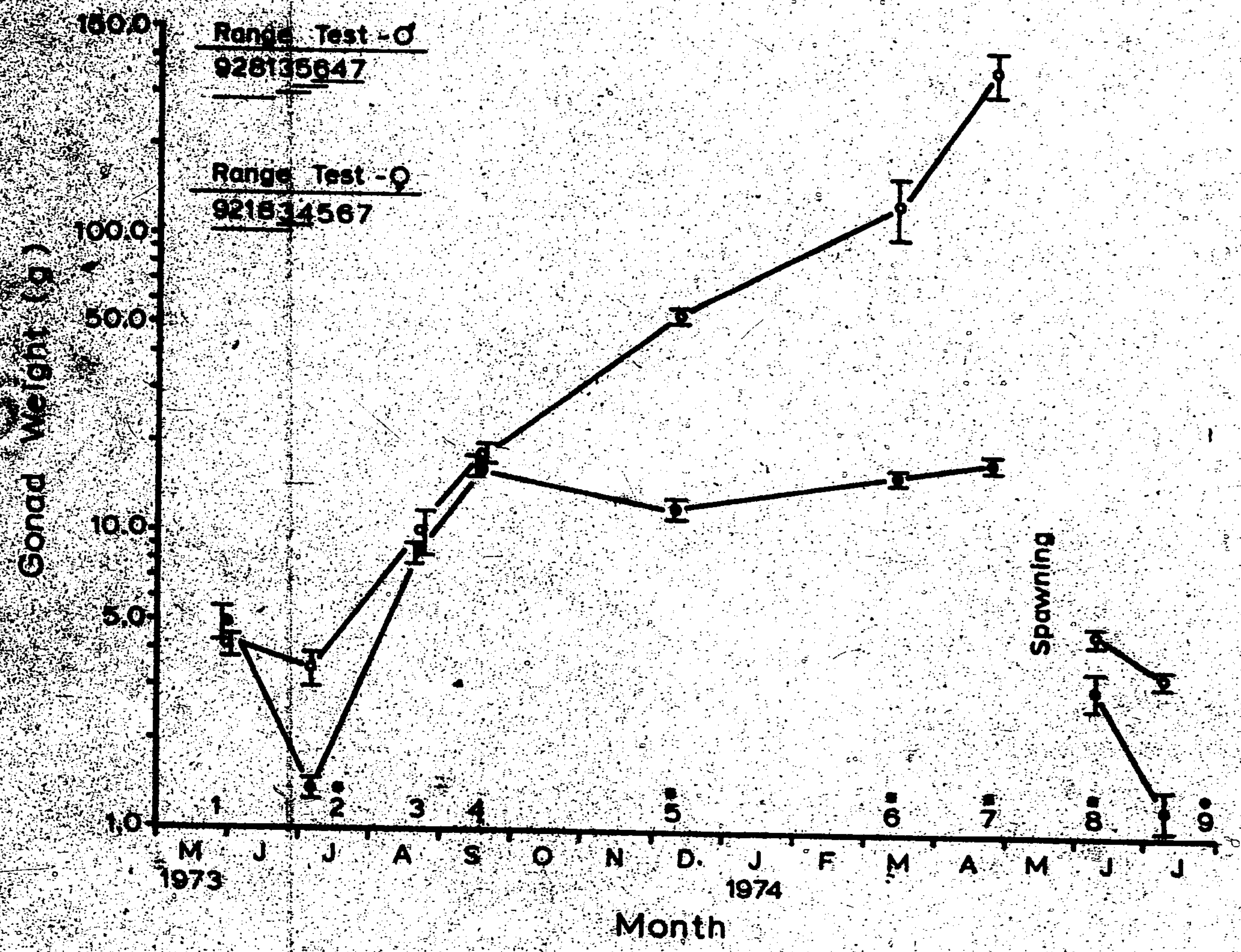

Range Test - ♂
928135647
Range Test - ♀
921834567
Gonad Weight (g)
160.0
100.0
50.0
10.0
5.0
1.0
1 2 3 4 5 6 7 8 9
M J J A S O N D. J F M A M J J
1973
1974
Month
Spawning

FIGURE 6. Seasonal variation in total gonad protein calculated for a 50 cm fork length northern pike. Mean ± 1 SE. Closed circles—male; open circles—female. Statistical representation as in Figure 1.

Analysis of variance (males): $p<0.01$

Analysis of variance (females): $p<0.01$

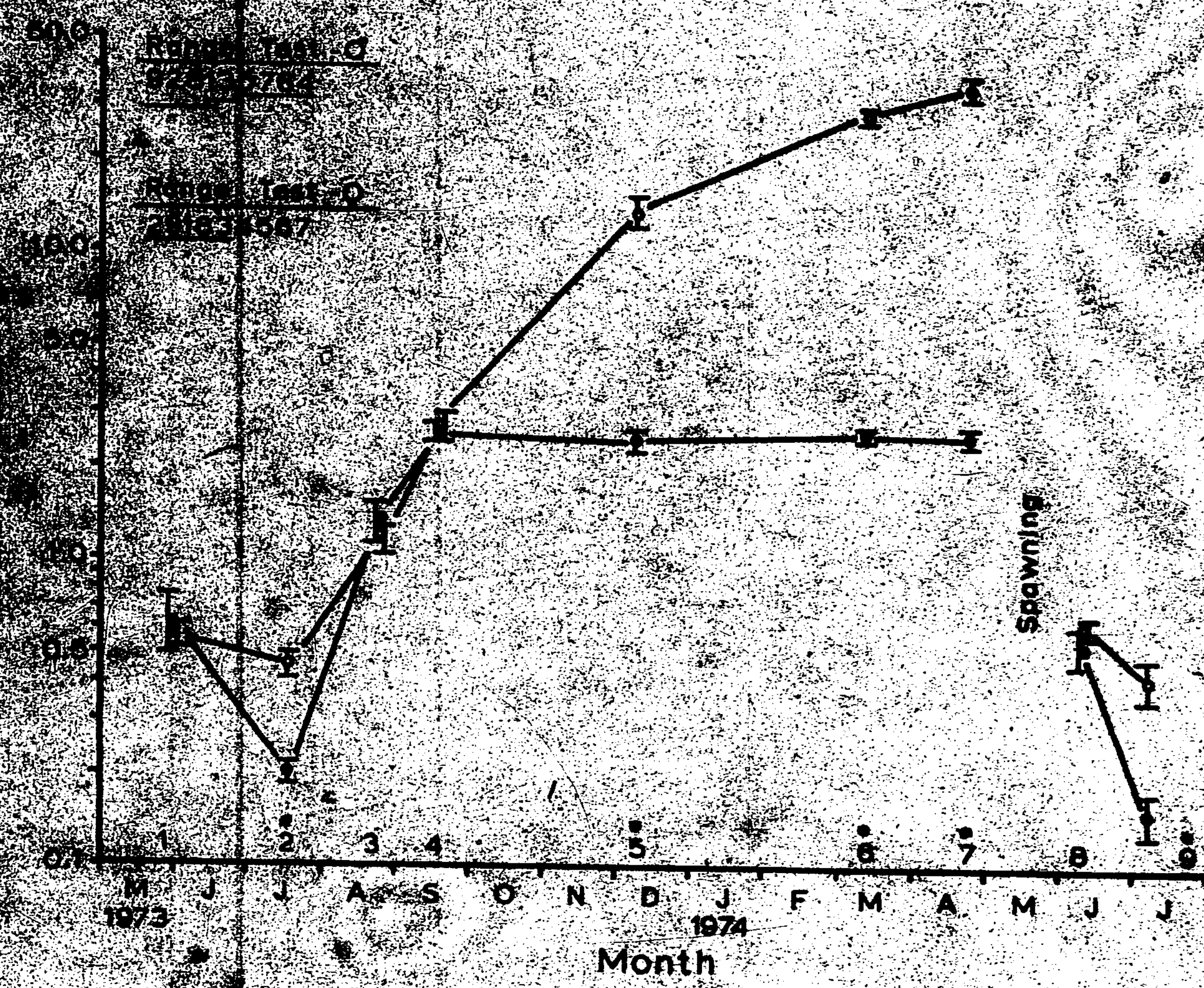
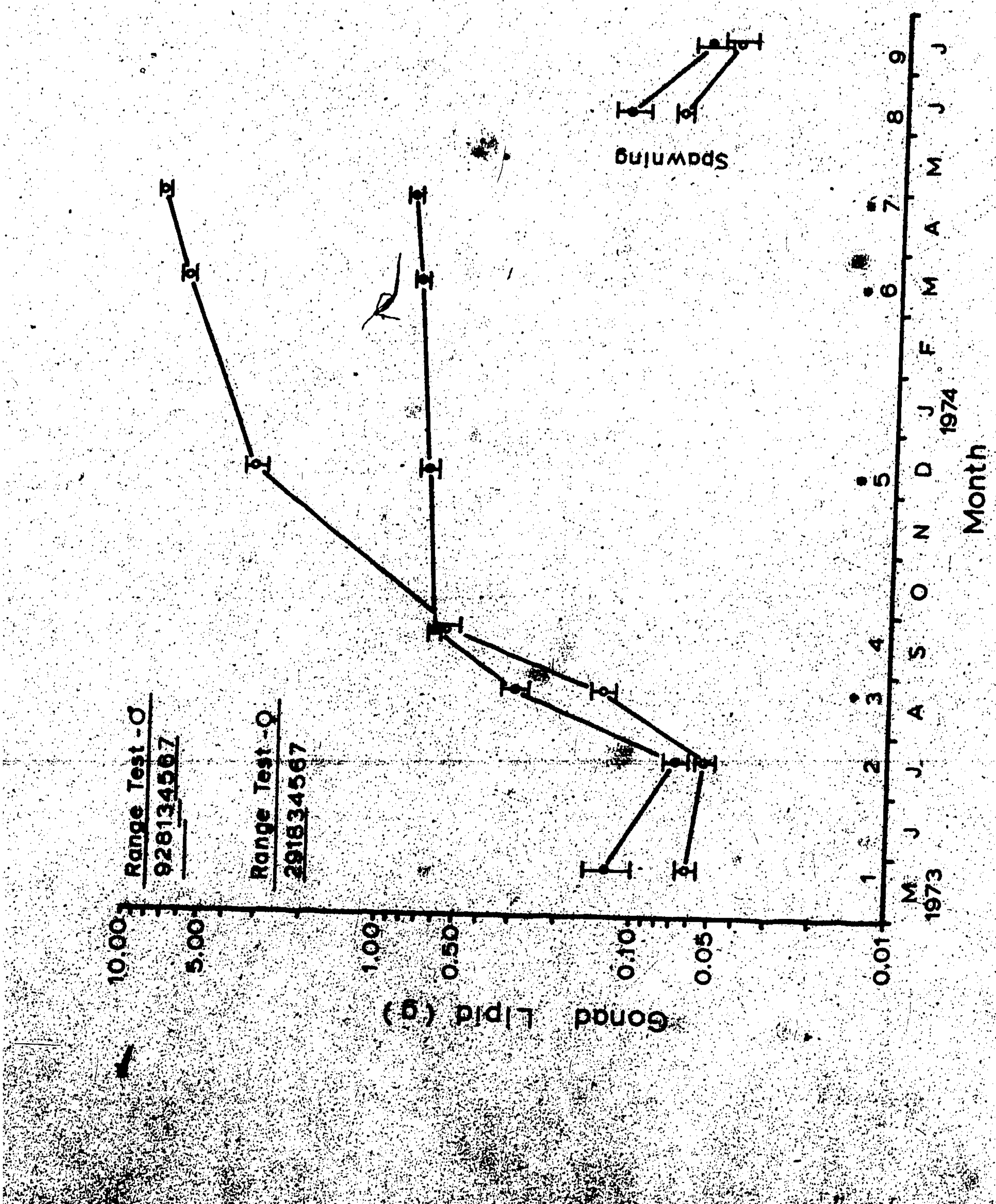

Spawning
1 2 3 4 5 6 7 8 9
M J J A S O N D J F M A M J J
1973
1974
Month

FIGURE 7. Seasonal variation in total gonad lipid calculated for a 50 cm fork length northern pike. Mean ± 1 SE. Closed circles—male; open circles—female. Statistical representation as in Figure 1.

Analysis of variance (males): $p<0.01$

Analysis of variance (females): $p<0.01$


Gonad Lipid (g)
10.00
5.00
1.00
0.50
0.10
0.05
0.01
Range Test -♂
9281345667
Range Test -♀
2918134567
Spawning
M
1973
J J A S O N D J F M A M J J
1974
1 2 3 4 5 6 7 8 9
Month

The rate of deposition of fat and protein into gonad was approximately the same in both sexes between July and September but major differences were seen between sexes in the deposition of nutrient over winter. Females deposited 14.5 times more protein (33.[illegible]0 g) and almost 10.5 times more lipid (7.95 g) into gonads than did males. This represented a 76-fold increase in protein and a 151-fold increase in lipid content of ovaries from July to April. Protein content of testes rose by only 2.36 g (12-fold) from July to September and remained at an almost constant level until spawning. The increment in lipid content of testes was 0.76 g (11-fold) by April but 72% of this increase had occurred by September.

Gonads of a 50 cm pike underwent considerable chemical change in the course of their development (Appendix Table 7). Percent water was about 83-84% in spent ovaries and it decreased with increasing ovary weight to 64.1% in March. As water content declined from July to December, protein (% wet weight) increased from about 13% to 26% and lipid rose from 1.5% to 6.1%. The percentage water, protein and lipid remained relatively constant from December to March while ovaries continued to grow. Water in male gonad remained near 80% for most of the year but fell to 75.9% in December. This loss of water in testes was primarily responsible for the high percentages of protein (18.6%) and lipid (5.4%) observed in December, as determined from dry weight data. Percent protein in testes decreased from about 16.6% in March to 12.2-14.2% in July. Testes lipid (% wet weight) was 4.9% in July as well as in March, although it had dropped to 3.1% in August. An augmentation in water from 64.1% to 67.1% in female gonad and from

79% to 82% in male gonad was observed immediately prior to spawning (March-April). In April, the protein level in mature ovaries (24.4%) was two times greater than that found in mature testes (13.6%) and the lipid level was about 25% higher (4.6% and 5.8% in testes and ovaries, respectively).

Muscle-Chemical Data

Muscle protein and muscle lipid were expressed as percent wet weight and are shown with water content in Table 4. All three components fluctuated significantly during the year. Percent water in both sexes was lowest in August (M:77.3%; F:77.6%) coincident with a higher protein content at this time (M:20.1%; F:20.0%). Muscle protein was lower in both males and females in March (M:18.4%; F:18.5%). Percent muscle lipid in males was lowest after spawning in 1973 (0.65%) and highest in April (0.80%) and a similar trend was seen for females (0.59% in May 1973; 0.76% in April). Muscle protein (% wet weight) was significantly higher ($P<0.05$) in males than females in December and male muscle lipid was significantly higher than female muscle lipid ($p<0.05$) in June.

Visceral Fat

Visceral fat along the stomach and intestine was expressed as a percent of the somatic body weight. Visceral fat content of males was 0.23% ± 0.04 (mean ± 1 SE, N=[illegible]) in [illegible] and 0.22% ± 0.03 (N=12) in June. In March, visceral fat in [illegible] 0.17% ± 0.02 (N=9) of the somatic body weight and [illegible] 0.02 [illegible]. Males tended [illegible] generally [illegible] in each month but these [illegible] and lipid (% wet weight) of male and female northern pike captured at various times during an annual cycle.

	1973 [illegible]	July 16	Aug. 21	Sept. 18	Dec. 9	1974 March 14	April 25	June 10	July 11	RANGE TEST*	Analysis of Variance
	1	2	3	4	5	6	7	8	9		
[illegible]	[illegible] ± 0.3	78.8 ± 0.3	77.3 ± 0.2	78.7 ± 0.3	79.1 ± 0.6	79.1 ± 0.4	77.7 ± 0.7	79.6 ± 0.2	79.7 ± 0.8	[illegible]	p<0.05
[illegible]	[illegible] ± 0.4	78.5 ± 0.3	77.6 ± 0.3	78.7 ± 0.4	78.5 ± 0.2	79.4 ± 0.3	78.8 ± 0.5	80.1 ± 0.2	79.8 ± 0.4	[illegible]	p<0.05
[illegible]	18.7 ± 0.3	[illegible]	20.1 ± 0.1	19.5 ± 0.3	[illegible] ± 0.4	18.4 ± 0.3	20.2 ± 0.6	18.9 ± 0.2	19.0 ± 0.7	[illegible]	p<0.05
Females	19.7 ± 0.2	19.7 ± 0.1	20.0 ± 0.2	19.0 ± 0.4	19.3 ± 0.1	19.5 ± 0.2	19.7 ± 0.4	18.7 ± [illegible]	[illegible] ± 0.2	[illegible]	p<0.05
Lipid											
Males	0.65 ± 0.03	0.6[illegible] ± 0.02	0.72 ± 0.03	0.67 ± 0.03	0.75 ± 0.04	0.73 ± 0.06	0.80 ± 0.03	0.68 ± 0.02	0.66 ± 0.04	2 1 9 4 8 3 6 5 7	p<0.01
Females	0.59 ± 0.02	0.59 ± 0.02	0.69 ± 0.03	0.63 ± 0.03	0.75 ± 0.03	0.66 ± 0.02	0.76 ± 0.02	0.62 ± 0.02	[illegible] ± 0.02	1 2 8 4 9 6 3 5 7	p<0.01

*Each number represents a sampling date (see code). Numbers underlined at the same level are not significantly different (p>0.01).

differences were not significant, probably because of individual variability and the small number of fish examined. Hence, the quantity of visceral fat was extremely small and was not significantly different between prespawning and postspawning fish.

DISCUSSION

This study provides direct evidence for an annual cycle in nutrient (protein and lipid) content of liver and gonads and indirect evidence for an annual cycle in energy (nutrient) content of the somatic portion of the body. In general, pike appear to be in best condition from late summer through winter and are in poorest condition in spring immediately following spawning. There was a depletion of energy from the somatic portion of the body and from the liver during the final stages of ovary maturation and, in male fish, during spawning as evidenced by a decrease in somatic body weight (Fig. 1), liver weight (Fig. 2) and liver protein and lipid (Figs. 3 and 4). Males exhibit an additional period of depletion in September coinciding with final increase in testes weight.

The approach used in the present study of determining the absolute amounts of lipid and protein in the liver and gonads of 50 cm pike provides the most meaningful assessment of the fluctuations of these nutrients during the annual cycle. Seasonal fluctuations (or variations with stage of maturity of the germinal tissue) in some aspects of the chemical composition of the liver and/or gonads of fish have been shown by some workers (Swift, 1955; Jangaard *et al.*, 1967a, 1967b; Golovanenko *et al.*, 1970; Hardy and Keay, 1972; Kus'mina and Zhilina, 1973; Lizenko *et al.*, 1973; Valtonin, 1974 and others). In these studies the seasonal changes in the relative content (expressed as mg/g tissue or as a percentage of the wet weight) were described but are difficult to interpret since changes in one nutrient may simply reflect conjugate changes in the percentage composition of other constituents. However, a few observations have been made on the dynamics of the absolute (total) content of nutrients in liver and gonads (Idler and Bitners, 1959; Maslennikova, 1970; Rimsh, 1970; Shatunovskiy, 1971; Shchepkin, 1971; Shul'man, 1974; Mackay, 1975).

A severe drain on body energy reserves takes place during spring, hence this is a critical time of year for pike. A detailed analysis of the extent to which pike feed at various times during the year was not possible in this study owing to the small sample sizes. Although an analysis of feeding intensity based on the frequency of empty stomachs may be misinterpreted (Roberts, 1975), observations made in the present study (Appendix Table 8) support those of Frost (1954) which suggest that feeding is much reduced or stopped at spawning. Hence, pike must convert to endogenous nutrition at a time when there is a considerable energy demand for spawning activity and, in the case of females, final ovary maturation. Movement of pike from one spawning area to another was observed by Miller (1948). Therefore, some stored energy may be expended during spawning associated with movement and activity. Pike sampled in April prior to spawning may therefore have travelled a considerable distance within the lake before finally entering the tributary from which they were taken. As well, maintenance requirements were likely increased in the spring as a result of fluctuating, but progressively increasing water temperature. Cold acclimated fish are known to have a higher metabolism at warmer temperatures than at colder temperatures (Dean, 1969). Temperature profiles for Lac Ste. Anne obtained in this study (Appendix Fig. 1) and in studies from other years (Mackay and Beatty, 1968; Roth, 1969; Langer, 1974) generally indicate a rapid rise in temperature between April and June. However, Johnson

(1966) found that a doubling of the maintenance requirement of Lake Windermere pike in late spring was only partially dependent on temperature.

Temporal differences between males and females in the rate at which condition falls at spawning (Fig. 1) are related to the reproductive demands of each sex. The greater loss of somatic body weight by females prior to spawning is probably due to the utilization of endogenous nutrients for gonad growth. It is impossible to ascertain when feeding is interrupted after March; however, much of the increase in nutrient content of the ovaries from March to April probably occurs at the expense of the somatic portion of the body. A transfer of substrate from somatic to germinal tissue was demonstrated from energy data on *Hippoglossoides platessoides*, which have coinciding periods of gonad maturation and non-feeding (MacKinnon, 1972). Winters (1970) suggested that the decline in fat content and round body weight of capelin, *Mallotus villosus*, during the prespawning period was associated with gonad maturation, even though feeding intensity was high at this time. It should be noted that the loss in somatic body weight of female pike during the prespawning period cannot be attributed entirely to gonad maturation since a decreasing trend in gross body weight is also observed at this time (Appendix Table 3). From the drop in somatic body weight observed for male pike over spawning (April-June), one may infer a more active mobilization of body energy in males than in females for muscular activity associated with the rigors of spawning. Furthermore, several investigators have observed that male pike arrive on the spawning grounds first (Clark, 1950; Fabricius and Gustafson, 1958; Frost and Kipling, 1967). Frost and Kipling found that male pike spend more time on the spawning ground than do females. The pattern of change in liver weight of northern pike at spawning coincides, in general, with the pattern of variation in somatic body weight at this time. Evidence which suggests a greater expenditure of liver lipid by males than females for spawning activity has been noted in the present study. A similar observation was made in Baltic cod (*Gadus morhua callarius*) by Shatunovskiy (1971) and in scorpionfish (*Scorpaena porcus*) by Shchepkin (1971).

The dichotomy between sexes in liver nutrient content is difficult to interpret since a particular liver constituent may be primarily of structural importance, it may represent mostly energy storage or it may reflect metabolic processes which are occurring. For example, female liver contains 1.21 g more protein than male liver by the end of winter (March) although liver weights are similar between sexes. This, in fact, may be indicative of a higher concentration of enzymes associated with metabolic processes which are required for the synthesis of the constituents of germinal tissue. If this is so, then the decline in liver protein of female pike immediately prior to spawning reflects a decrease in the quantity of enzymes required for this type of metabolic activity. Although he did not measure protein content, an increase in the liver weight of female perch (*Perca fluviatilis*) with ovary maturation over winter followed by a greater loss in liver weight by females than males during the prespawning period was explained similarly by Makarova (1973). An alternative explanation is that the protein in female liver represents a storage depot and this nutrient reserve is depleted with ovary development during the prespawning fast. With the data available, it is impossible to state that liver nutrients are transferred into ovary tissue. In any case, since total protein and total lipid in female gonad increases 6.4 g and 1.77 g, respectively, from March to April, most of these nutrients must be derived from the body (or via de novo synthesis from somatic tissue) if feeding is reduced or stopped.

Although direct determination of carbohydrate content in liver was not made, estimated values (Appendix Table 5) indicated that much less was deposited in the liver of females than in males. In March, estimated relative content of carbohydrate was 17.8% of the wet liver weight (4.28 g) in males compared to 5.8% (1.34 g) in females. Quantitative differences between sexes may in part be attributed to an increase in the carbohydrate content of the maturing ovary, resulting in lower liver glycogen in females at this time. Both glucose and glycogen have been reported to accumulate in the ovary during maturation (Greene, 1926; Fontaine and Hatey, 1953; Chang and Idler, 1960; Yanni, 1961). Lewander *et al.* (1974) suggested that this might explain the lower liver glycogen observed in silver eels than in yellow eels (*Anguilla anguilla*). The apparent high carbohydrate content of the liver in male pike and the depletion of an estimated 3.33 g of glycogen during spawning compared to only 0.33 g lipid suggests that this nutrient is the primary liver storage product that is mobilized by males for spawning activity. Other studies (Bogoyavlenskaya and Veltishcheva, 1972; Plisetskaya and Kus'mina, 1972; Kus'mina and Zhilina, 1973; Valtonen, 1974) indicate that the dynamics of changes in glycogen reserves are extremely variable in fish.

Muscle lipid in Lac Ste. Anne pike is comparable to or lower than that reported for other non-fatty fishes (Swift, 1955; Thurston *et al.*, 1959; Mangold, 1973; Fraser *et al.*, 1961). The percent lipid in the muscle of Lac Ste. Anne pike (0.6—0.8%) falls within the lower half of the range of values reported elsewhere for pike of various sizes (0.7—1.7% — Thurston *et al.*, 1959; 0.45—2.0% — Mangold, 1973; 1.22% — Ince and Thorpe, 1976). However, a direct correlation between the weight of pike and the fat content of their flesh was observed for *Esox reicherti* (Kizevetter, 1973). The relative fat content of *E. lucius* in Lac Ste. Anne is within the range (0.6—0.9%) reported for *E. reicherti* of similar weight.

Fishes which do not have appreciable amounts of fat in muscle may concentrate lipid reserves in the liver. The highest relative fat content in pike liver was 9.7% of the wet liver weight recorded for males in September. A similar quantity (9%) was reported for pike from Alaska taken in summer (Wilbur, 1954). In March, the liver of pike is only 2.4% of the gross body weight and the lipid content approximately 3—4%. Studies on cod (*Gadus morhua*), a lean fish which uses the liver to store lipid, show that the liver may contain 15—65% lipid and represents 2—11% of the body weight depending on age, stage of maturity of the gonads and time of year (Jangaard *et al.*, 1967a; Maslennikova, 1970; Bogoyavlenskaya and Veltishcheva, 1972; Krivobok and Tokareva, 1972). Thus liver lipid is not substantial in pike when compared to species such as cod which use the liver as a major storage depot for fat.

Many fish store large quantities of fat in the abdominal cavity and visual inspection of the visceral cavity of pike revealed some accumulation of lipid along the gut. However, visceral fat of Lac Ste. pike was only 0.2% (average for males and females) of the somatic body weight in March and did not differ in June after spawning. Visceral fat in goldeye (*Hiodon alosoides*) may account for up to 1.5% of the total body weight (P. Aster, personal communication). In Atlantic herring (*Clupea harengus*), visceral fat may increase to at least 1.3% of the total body weight during fattening (Gakichko and Dubrovskaya, 1970) and Lovern and Wood (1937) considered it to be a significant fat depot though less important than other body fat.

The amount of visceral fat in Lac Ste. Anne pike is low when compared to the range of values reported for *E. reicherti* (0.6—1.3% of the total body weight — Kizevetter, 1973). The total loss of visceral fat, calculated from the percent visceral fat and the drop in somatic body weight from March to June, was 0.39 g and 0.29 g in males and females, respectively. This loss is similar to that of liver lipid (Fig. 4). Therefore, it appears that fat along the stomach and intestine does not constitute a substantial fat depot in Lac Ste. Anne pike and, in view of the large loss of somatic body weight at spawning, it is probably not important to the energetics of the whole fish.

The absence of large quantities of fat in the body of pike implies that the significant decreases which occur in somatic body weight during the annual cycle are mainly the result of the catabolism of whole muscle tissue. A breakdown in body tissue is suggested by the data of Templeman and Andrews (1956) on naturally starved plaice (*Hippoglossoides platessoides*) and by Johnston and Goldspink (1973) on experimentally starved plaice (*Pleuronectes platessa*). Wilkins (1967) found a reduction in structural lipid (phospholipid) and proteins in the muscle of experimentally starved herring (*Clupea harengus*). The utilization of body protein as an energy source has also been shown in salmon (C. H. Greene, 1919; C. W. Greene, 1919, 1926; Idler and Bitners, 1958; Idler and Clemens, 1959 and others). Because of the low concentration of fat in pike muscle, Kangur (1971) did not consider muscle fat to be metabolically important. Endogenous protein must therefore participate to a large extent as an energy substrate in the metabolism of northern pike. The mobilization of protein in non-fatty fish is generally accompanied by an increase in water content (Love, 1970) and this trend was observed in postspawning male and female pike.

The suggestion, here, that whole muscle tissue of pike is broken down is contrary to that of Ince and Thorpe (1976) who suggested that body protein was conserved while lipid and glycogen reserves were preferentially utilized. Their interpretation was based on an experiment in which pike were starved in the laboratory for 3 months. They observed that the concentrations of liver and muscle glycogen and liver lipid decreased with increasing starvation time while the percent muscle protein did not change. However, they made no attempt to quantify these losses with respect to a 12.5% loss of total body weight after 3 months. Furthermore, their results indicated a greater storage (% wet weight) of lipid in the muscle and liver of their pike than I observed in Lac Ste. Anne pike, and they reported a considerable reduction in visceral fat with starvation, which was also not quantified. It is conceivable that whole muscle tissue was still being catabolized in the pike Ince and Thorpe studied even though muscle water and protein (% wet weight) did not change significantly. This response may be more pronounced in Lac Ste. Anne pike in view of their extremely low fat content.

The seasonal cycle in gonad weight is similar to that described for other temperate spring-spawning freshwater species (LeCren, 1951; Roth, 1969): testes grow mainly from midsummer through early fall with little subsequent change in size while ovaries, which also start to grow in midsummer, continue to develop throughout winter. A similar pattern of change was reported for the gonado-somatic index of Lac Ste. Anne pike by Huang (1967) and for the ovary index of Lake Oahe pike by June (1971). Using heat equivalents for fat and protein (Kleiber, 1975), the increase in ovary energy during maturation was 235.4 kcal whereas the total rise in energy content of testes was less than 8% (18.2 kcal) of the value for ovaries. Females build up ovaries without any loss of somatic body weight or liver weight prior to March. Growth of male gonads from mid-July to September parallels that of female gonads at this time. However, there is apparently a large demand on male energy reserves from August to September, as indicated by the drops in somatic body weight (100.5 g) and liver weight (3.71 g).

Lofts and Marshall (1957) found that the testicular weight of Lake Windermere pike was highest in the fall (September-December) and that spermatogenesis was complete by December. Testes were inactive during the coldest period of the year (December-April). In perch (*Perca fluviatilis*) the most intensive period of spermatogenesis occurs from August to October (Kulayev, 1927, cited by Makarova, 1973) and Makarova (1973) suggested from his data on perch that spermatogenesis proceeds at the expense of endogenous nutrients (in this case, depot lipid) whereas mainly food energy allows for ovary growth over winter. A similar strategy of gonad growth is suggested here for pike. However, the depletion of male energy reserves from August to September cannot be attributed solely to the processes of gametogenesis and testes growth, as evidenced by 1) the magnitude of the losses in somatic body weight and liver weight and 2) a loss of 0.42 g liver lipid compared to a deposition of 0.32 g lipid into testes. Some other factor(s) must therefore be responsible for the depletion which is seen only in males at this time of the year. Perhaps males are less well adapted than females for growing gonads or feeding conditions were poorer for males. Furthermore, since dietary nutrients are apparently sufficient to meet energy demands for ovary growth in pike during winter, it follows that females must consume more food than males, at least in late winter when somatic body weight is similar between sexes. This feature of pike biology is worthy of future study.

The increase (3%) in the relative water content of female gonads in April is an indication that the maturation of ovaries is progressing to the "ripe" stage. The incorporation of water into the ovary immediately prior to spawning has been observed in other species (Braekkan and Boge, 1962, cited by Love, 1970; MacKinnon, 1972; Saeger, 1973) and may be considered a general feature of the ripening process. A similar increase (3%) in the water content of pike testes was also observed in April. This observation provides evidence that the April sample was taken very close to the beginning of the spawning period and that there was little further gonad growth after this date.

Mean somatic body weight of postspawned males was significantly different between 1973 and 1974 suggesting that caution must be taken in the interpretation of seasonal variation based on observations of only one annual cycle. Females showed a more cyclic annual pattern of somatic body weight change than did males. Males may have been in better condition before spawning in 1973. Possibly, environmental conditions were more favourable for males in spring, 1973. Ivanova (1969), for example, found that the availability of food for pike varied in spring with water level conditions and that the feeding conditions of each sex differed. Lac Ste. Anne is subject to considerable year to year differences in hydrological conditions at springtime (personal observation). In spring, 1973, the lake water level was low following a mild winter season. Spring, 1974, followed a long winter with heavy snowfall and there was extensive flooding of the lake and its tributaries.

In general, condition was recovered over summer when temperature and feeding conditions were optimal and annual growth in length as well as weight was probably occurring. Johnson (1966) showed experimentally that growth of 0+ and 1+ Lake Windermere pike occurred from March to December, with a maximum in May-June. The recovery of somatic body weight of 50 cm fork length pike was achieved by growth in weight proceeding at a faster rate than growth in length and was not the result of an accumulation of lipid reserves. That changes in condition may in part or in whole be attributed to alterations in rate of growth in weight vs growth in length has been suggested by others (LeCren, 1951; Ball and Jones, 1960) and alternating periods of growth in weight and growth in length were shown with the use of condition factors for *Salmo trutta* held at constant temperature (Brown, 1946). Johnson (1966) also showed that maintenance requirements of Lake Windermere pike were lower over fall and winter than during the rest of the year. Growth of ovaries in adult pike are therefore probably best achieved from fall through winter when energy demands for body growth and maintenance are low. Unfortunately, the annual growth cycle of Lac Ste. Anne pike is not known, but it is likely of shorter duration than in Lake Windermere because of the longer period of colder water in Lac Ste. Anne.

In summary, northern pike appear to catabolize primarily whole muscle tissue as an energy source during the prespawning and spawning periods and therefore are generally in poor condition after spawning. From the higher somatic body weight of spent males in 1973 compared to 1974, I suggest that the extent to which body energy reserves are depleted over spawning, and/or the rate of recovery after spawning, may vary from year to year for either sex according to feeding conditions. It is hoped that the present study will stimulate future research on the pike population of Lac Ste. Anne, particularly with a view to defining the annual growth cycle, i.e. the annual increment in body length and body mass and the period during the year when this occurs. The energetics of production could then be determined for the population.

LITERATURE CITED

Ananichev, A. V. 1961. Comparative biochemical data for some freshwater invertebrates and fish. Biochemistry, N.Y. 26: 16-26.

Ball, J. N., and J. W. Jones. 1960. On the growth of the brown trout of Llyn Tegid. Proc. Zool. Soc. Lond. 134: 1-41.

Bogoyavlenskaya, M. P., and I. F. Veltishcheva. 1972. Some data on age changes in the fat and carbohydrate metabolism in Baltic cod. Tr. Vses. Naucho-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. (VNIRO) 85: 56-62. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2730, 1973).

Braekkan, O. R., and G. Boge. 1962. A comparative study of amino acids in the muscle of different species of fish. FiskDir. Skr. Serie Teknologiske undersokelser 4(3), 19p. Cited in Love, R. M. 1970. The chemical biology of fishes. Academic Press, Inc., London. 547p.

Brown, M. E. 1946. The growth of brown trout (*Salmo trutta* Linn.). II. The growth of two-year-old trout at a constant temperature of 11.5 C. J. Exp. Biol. 21: 130-142.

Chang, V. M., and D. R. Idler. 1960. Biochemical studies on sockeye salmon during spawning migration. XII. Liver glycogen. Can. J. Biochem. Physiol. 38: 553-558.

Clark, C. F. 1950. Observations on the spawning habits of the northern pike, *Esox lucius* L., in north western Ohio. Copeia (4): 285-288.

Clark, E. D., and L. H. Almy. 1918. A chemical study of food fishes. The analysis of twenty common food fishes with especial reference to a seasonal variation in composition. J. Biol. Chem. 33: 483-498.

Dean, J. M. 1969. The metabolism of tissues of thermally acclimated [illegible]t (*Salmo gairdneri*). Comp. Biochem. Physiol. 29: 185-196.

Eschmeyer, P. H., and A. M. Philips. 1965. Fat content of the flesh of siscowets and lake trout from Lake Superior. Trans. Am. Fish. Soc. 94: 62-73.

Fabricius, E., and K-J. Gustafson. 1958. Some new observations on the spawning behaviour of the pike, *Esox lucius* L. Rep. Inst. Freshwat. Res. Drottningholm 39: 23-54.

Folch, J., M. Lees, and G. H. Sloane Stanley. 1957. A simple method for the isolation and purification of total lipides from animal tissues. J. Biol. Chem. 226: 497-509.

Fontaine, M., and J. Hatey. 1953. Contribution to the study of glucose metabolism in the salmon (*Salmo salar*) at different stages of its development and of its migrations (in French). Physiologia comp. Oecol. 3: 37-52.

Fraser, D. I., A. Mannan and W. J. Dyer. 1961. Proximate composition of Canadian Atlantic fish. III. Sectional differences in the flesh of a species of Chondrostei, one of Chimaerae, and of some miscellaneous teleosts. J. Fish. Res. Bd. Canada 18: 893-905.

Frost, W. E. 1954. The food of pike, *Esox lucius* L., in Windermere. J. Anim. Ecol. 23: 339-360.

Frost, W. E., and C. Kipling. 1967. A study of the reproduction, early life, weight-length relationship and growth of pike, *Esox lucius* L., in Windermere. J. Amer. Ecol. 36: 651-693.

Gakichko, S. I., and T. A. Dubrovskaya. 1970. Studies on the relationship between the fat content of Atlantic herring, physiological condition of their gonads and ability to mature. Tr. Vses. Naucho-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. (VNIRO) 73: 87-101. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 1732, 1971)

Greene, C. H. 1919. Changes in nitrogenous extractives in the muscular tissue of the king salmon during the fast of spawning migration. J. Biol. Chem. 39: 457-477.

Greene, C. W. 1919. Biochemical changes in the muscle tissue of king salmon during the fast of spawning migration. J. Biol. Chem. 39: 435-456.

Greene, C. W. 1926. The physiology of the spawning salmon. Physiol. Rev. 6: 201-241.

Golovanenko, L. F., T. F. Shuvatova, Ye. P. Putina, L. S. Fedorova and A. L. Arakelove. 1970. A physiological and biochemical description of Don pike-perch females at different stages of the sexual cycle. J. Ichthyol. 10: 260-267.

Gorbach, E. I. 1971. Condition and fatness of the grass carp (*Ctenopharyngodon idella* Val.) in the Amur basin. J. Ichthyol. 11: 880-890.

Gritsenko, O. F. 1970. Fatness and condition of the Arctic char (*Salvelinus alpinus* L.) from northern Sakhalin. J. Ichthyol. 10: 95-101.

Hardy, R., and J. N. Keay. 1972. Seasonal variations in the chemical composition of Cornish mackerel, *Scomber scombrus* (L.), with detailed reference to the lipids. J. Fd. Technol. 7: 125-137.

Huang, Chau-Ting. 1967. A study of the binding of inorganic iodide to the plasma proteins of some freshwater teleost fishes. M.Sc. Thesis. Univ. of Alberta, Edmonton, Alberta. 69p.

Idler, D. R., and I. Bitners. 1958. Biochemical studies on sockeye salmon during spawning migration. II. Cholesterol, fat, protein and water in the flesh of standard fish. Can. J. Biochem. Physiol. 36: 793-798.

Idler, D. R., and I. Bitners. 1959. Biochemical studies on sockeye salmon during spawning migration. V. Cholesterol, fat, protein and water in the body of the standard fish. J. Fish. Res. Bd. Canada 16: 235-241.

Idler, D. R., and I. Bitners. 1960. Biochemical studies on sockeye salmon during spawning migration. IX. Fat, protein and water in the major internal organs and cholesterol in the liver and gonads of the standard fish. J. Fish. Res. Bd. Canada 17: 113-122.

Idler, D. R., and W. A. Clemens. 1959. The energy expenditures of Fraser River sockeye salmon during the spawning migration to Chilko and Stuart Lakes. Inter. Pacif. Salmon Fish Commiss. Progress Report, 80p.

Idler, D. R., and H. Tsuyuki. 1958. Biochemical studies on sockeye salmon during spawning migration. I. Physical measurements, plasma cholesterol and electrolyte levels. Can. J. Biochem. Physiol. 36: 783-791.

Ince, B. W., and A. Thorpe. 1976. The effects of starvation and force-feeding on the metabolism of the northern pike, *Esox lucius* L. J. Fish. Biol. 8: 79-88.

Ivanova, M. N. 1969. The behavior of predatory fish during feeding. J. Ichthyol. 9: 574-577.

Jangaard, P. M., H. Brockerhoff, R. D. Burgher and R. J. Hoyle. 1967a. Seasonal changes in general condition and lipid content of cod from inshore waters. J. Fish. Res. Bd. Canada 24: 607-612.

Jangaard, P. M., R. G. Ackman and J. C. Sipos. 1967b. Seasonal changes in fatty acid composition of cod liver, flesh, roe, and milt lipids. J. Fish. Res. Bd. Canada 24: 613-627.

Johnson, L. 1966. Experimental determination and food consumption of pike, *Esox lucius*, for growth and maintenance. J. Fish. Res. Bd. Canada 23: 1493-1505.

Johnston, I. A., and G. Goldspink. 1973. Some effects of prolonged starvation on the metabolism of the red and white myotomal muscles of the plaice *Pleuronectes platessa*. Marine Biology 19: 348-353.

June, F. C. 1971. The reproductive biology of northern pike, *Esox lucius*, in Lake Oahe, an upper Missouri River storage reservoir.

In Reservoir fisheries and limnology. G. E. Hall, Ed. 1971. Special publication No. 8. Am. Fish. Soc., Washington, D.C. p.53-71.

Kangur, A. 1971. The content and dynamics of some nitrogen fractions in the muscles of fishes. I. General nitrogen and protein (in Russian). Eesti. Nsv. Tead. Akad. Toim. Biol. 20: 23-33.

Khashem, M. T. 1970. Condition and fatness of the blue bream (*Abramis ballerus* L.) in Rybinsk Reservoir. J. Ichthyol. 10: 320-327.

Kizevetter, I. V. 1973. Chemistry and technology of Pacific fish. Keter Press. Jerusalem. 304p. (Transl. from Russian).

Kleiber, M. 1975. The fire of life. Robert E. Krieger Publishing Co., Inc. New York. 453p.

Kluytmans, J.H. F.M., and D. I. Zandee. 1973. Lipid metabolism in the northern pike (*Esox lucius* L.). II. The composition of the total lipids and of the fatty acids isolated from lipid classes and some tissues of the northern pike. Comp. Biochem. Physiol. 44B: 459-466.

Krivobok, M. N., and G. I. Tokareva. 1972. Dynamics of weight variations of the body and individual organs of Baltic cod during the maturation of gonads. Tr. Vses. Naucho-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. (VNIRO) 85: 45-55. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2722, 1973).

Kulayev, S. I. 1927. Observations on changes in the testes of the perch (*Perca fluviatilis* L.) in the course of the life cycle (in Russian). Russk. zool. zhurn, 7, No. 3. Cited in Makarova, N. P. 1973. Seasonal changes in some of the physiological characteristics of the perch (*Perca fluviatilis* L.) of Ivan'kovo Reservoir. J. Ichthyol. 13: 742-752.

Kuz'mina, V. V., and L. P. Zhilina. 1973. The ratio of glycogen concentrations in the liver and muscles of some freshwater teleost fishes. J. Ichthyol. 13: 623-627.

Lane, C. B. 1971. A survey of the fishery resources of Isle, Lac Ste. Anne and Matchayaw or Devils lakes, 1969. Survey Report No. 14. Alberta Fish and Wildlife Division, Department of Lands and Forests, Edmonton, Alberta. 96p.

Langer, O. E. 1974. Seasonal variations in food, mouth anatomy, and distribution of adult yellow perch (*Perca fluviatilis flavescens*) and yellow walleye (*Stizostedion vitreum vitreum*) in Lac Ste. Anne. M.Sc. Thesis. Univ. of Alberta, Edmonton, Alberta. 119p.

Lawler, G. H. 1965. The food of pike, *Esox lucius* L., in Heming Lake, Manitoba. J. Fish. Res. Bd. Canada 22: 1357-1377.

LeCren, E. D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). J. Anim. Ecol. 20: 201-219.

Lizenko, Ye.I., U. S. Sidorov and O. I. Potapova. 1973. Lipid content in the gonads of the cisco (*Coregonus albula* L.) of Urosozero (Lake Uros). J. Ichthyol. 13: 253-261.

Lewander, K., G. Dave, M-J. Johansson, A. Larson and U. Lidman. 1974. Metabolic and hematological studies on the yellow and silver phases of the European eel, *Anguilla anguilla* L. I. Carbohydrate, lipid, protein and inorganic ion metabolism. Comp. Biochem. Physiol. 47B: 571-581.

Lofts, B., and A. J. Marshall. 1957. Cyclical changes in the distribution of the testis lipids of a teleost fish, *Esox lucius*. Q. Jl. Microsc. Sci. 98: 79-89.

Love, R. M. 1970. The chemical biology of fishes. Academic Press, Inc., London. 547p.

Lovern, J. A., and H. Wood. 1937. Variations in the chemical composition of herring. J. Mar. Biol. Ass. U.K. 22: 281-293.

Mackay, W. C., and D. D. Beatty. 1968. Plasma glucose levels of the white sucker, *Catostomus commersonii*, and the northern pike, *Esox lucius*. Can. J. Zool. 46: 797-803.

Mackay, W. C. 1975. Annual changes in the nutrient and energy content of native fish. Unpublished report to the Alberta Environmental Research Trust, Edmonton, Alberta, Canada. 32p.

MacKinnon, J. C. 1972. Summer storage of energy and its use for winter metabolism and gonad maturation in American plaice (*Hippoglossoides platessoides*). J. Fish. Res. Bd. Canada 29: 1749-1759.

Makarova, N. P. 1973. Seasonal changes in some of the physiological characteristics of the perch (*Perca fluviatilis* L.) of Ivan'kovo Reservoir. J. Ichthyol. 13: 742-752.

Makhmudov, A. M. 1972. The biochemical composition of meat of commercial fish in the lakes of the Sary-Su system. Pishch. Promysl. 7: 43-45. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. [illegible]81, 1974)

Marshall, S. M., A. G. Nicholls and A. P. Orr. 1939. On the growth and feeding of young herring in the Clyde. J. Mar. Biol. Ass. U.K. 23: 427-456.

Mangold, H. K. 1973. Invisible fats and other lipids in freshwater fish. Wiss. Veroeff. Dtsch. Ges. Ernaehr. 24: 32-38. (Transl. from German by Fish. Mar. Serv. Transl. Ser. No. 3223, 1974).

Maslennikova, N. V. 1970. Seasonal changes in the nutritional value of Baltic cod. Tr. Vses. Naucho-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. (VNIRO) 73: 73-86. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 1731, 1971).

Miller, R. B. 1948. A note on the movement of the pike, *Esox lucius*. Copeia (1): 32.

Moroz, I. Ye. 1971. Dynamics of metabolism in the carp (*Cyprinus carpio* L.) during overwintering. J. Ichthyol. 11: 592-595.

Plisetskaya, E. M., and V. V. Kuz'mina. 1972. Glycogen content in organs of Agnatha (Cyclostomata) and fish (Pisces). J. Ichthyol. 12: 297-306.

Rimsh, E. Ya. 1970. Some peculiarities of protein and lipid metabolism in grass carp. Tr. Vses. Naucho-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. (VNIRO) 74: 222-243. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 1770, 1971).

Roberts, W. E. 1975. Food and space utilization by the piscivorous fishes of Cold Lake with emphasis on introduced coho salmon. M.Sc. Thesis. Univ. of Alberta, Edmonton, Alberta. 145p.

Roth, R. R. 1969. Some aspects of steroid metabolism and excretion in *Catostomus commersonii*. Ph.D. Thesis. Univ. of Alberta, Edmonton, Alberta. 156p.

Saeger, H.-M. 1973. Condition factor and water content in cod, plaice, and flounder (*Gadus morhua* L., *Pleuronectes platessa* L., *Platichthys flesus* L.) of the Baltic Sea. Ber. Dtsch. Wiss. Komm. Meeresforsch. 23: 33-46. (Transl. from German by Fish. Mar. Serv. Transl. Ser. No. 3238, 1974).

Sandercock. F. K. 1969. Bioenergetics of the rainbow trout (*Salmo gairdneri*) and the kokanee (*Oncorhynchus nerka*) populations of Marion Lake, British Columbia. Ph.D. Thesis. Univ. British Columbia, Vancouver, B.C. 92p.

Shatunovskiy, M. I. 1971. Alterations in the qualitative composition of lipids in the organs and tissues of the Baltic cod (*Gadus morhua callarias* L.) as the gonads mature. J. Ichthyol. 11: 790-798.

Schchepkin, V. Ya. 1971. Dynamics of lipid composition of the scorpion-fish (*Scorpaena porcus* L.) in connection with maturation and spawning. J. Ichthyol. 11: 262-267.

Shimuzu, Y., M. Tada, and K. Endo. 1973. Seasonal variations in chemical constituents of yellow-tail muscle. I. Water, lipid and crude protein. Nihon Suisan Gakkaishi 39: 993-999. (Transl. from Japanese by Fish. Res. Board Can. Transl. Ser. No. 3000, 1974)

Shul'man, G. E. 1974. Life cycles of fish. John Wiley and Sons, New York and Toronto. 258p. (Transl. from Russian by N. Kaner)

Swift, D. R. 1955. Seasonal variations in the growth rate, thyroid gland activity and food reserves of brown trout (*Salmo trutta* Linn.) J. Exp. Biol. 32: 751-764.

Templeman, W., and G. L. Andrews. 1956. Jellied condition in the American plaice *Hippoglossoides platessoides* (Fabricius). J. Fish. Res. Bd. Canada 13: 147-182.

Thurston, C. E. 1962. Physical characteristics and chemical composition of two sub-species of lake trout. J. Fish. Res. Bd. Canada 19: 39-44.

Thurston, C. E., M. E. Stansby, N. L. Karrick, D. T. Miyauchi, and W. C. Clegg. 1959. Composition of certain species of freshwater fish. II. Comparative data for 21 species of lake and river fish. F[illegible]s. 24: 493-502.

Valtonin, T. 1974. Seasonal and sex-bound variation in the carbohydrate metabolism of the liver of the whitefish. Comp. Biochem. Physiol. 47A: 713-727.

Wilber, C. G. 1954. Lipids in the northern pike. Trans. Am. Fish. Soc. 84: 150-154.

Wilkins, N. P. 1967. Starvation of the herring, *Clupea harengus* L.: Survival and some gross biochemical changes. Comp. Biochem. Physiol. 23: 503-518.

Winters, G. H. 1970. Biological changes in coastal capelin from the over-wintering to the spawning condition. J. Fish. Res. Bd. Canada 27: 2215-2224.

Wood, R. J. 1958. Fat cycles of North Sea herring. J. Cons. 23: 390-398.

Yanni, M. 1961. Studies on carbohydrate content of the tissues of *Clarias lazera*. Z. vergl. Physiol. 45: 56-60.

APPENDIX

APPENDIX TABLE 1. Fishing dates and numbers of 45—55 cm fork length northern pike in each sample category.

Fishing Date	N-Males	N-Females
May 30, 1973	12	10
July 10, 18, 19	14	10
August 20, 21	13	13
September 18	14	14
December 7-10	13	13
March 11, 16, 1974	8	9
April 24, 25	14	14
June 6, 10, 11, 12	14	14
July 10, 11	7	13

APPENDIX TABLE 2. F values and degrees of freedom for tests of curvilinearity on length-weight data for groups combined as shown. F values required for significance are also indicated.

	May 1973 + June 1974		July 1973 + July 1974	
	♂	♀	♂	♀
F for total regression	157.34	81.68	25.64	82.54
Degrees of freedom	2 and 23	2 and 21	2 and 18	2 and 20
F at p = 0.01	5.66	5.78	6.01	5.85
F for X^2 component	0.05	0.13	0.97	0.0046
Degrees of freedom	1 and 23	1 and 21	1 and 18	1 and 20
F at p = 0.05	4.28	4.32	4.41	4.35

weight minus liver and gonad weights) and in gross body weight
an ± 1 SE.

18	Dec. 9	1974 March 14	April 25	June 10	July 11
	905±30	923±29	873±24	786±22	810±24
	863±24	884±33	773±11	807±13	828±23
	935±33	960±33	913±26	804±23	825±28
	940±28	1007±39	924±15	821±13	843±25

APPENDIX TABLE 4. Seasonal variation in liver weight, liver protein and liver lipid calculated for a 50 cm fork length northern pike. Mean ± 1 SE.

	1973 May 30	July 16	Aug. 21	Sept. 18	Dec. 9	1974 March 14	April 25	June 10	July 11
LIVER WEIGHT (g)									
males	9.33±0.86	11.74±0.85	13.72±0.85	10.01±0.61	16.63±1.02	23.93±2.43	22.90±1.02	11.76±0.78	12.78±1.28
females	8.03±0.61	10.41±0.55	14.39±0.99	15.97±0.94	21.89±1.17	23.17±1.75	13.69±0.45	10.56±0.64	10.85±0.51
LIVER PROTEIN (g)									
males	1.26±0.07	1.18±0.06	1.26±0.05	1.10±0.04	1.62±0.07	1.93±0.14	1.86±0.06	1.28±0.06	1.14±0.09
females	1.26±0.20	1.19±0.06	1.44±0.06	1.66±0.15	2.81±0.11	3.14±0.16	2.03±0.05	1.25±0.05	1.18±0.04
LIVER LIPID (g)									
males	0.55±0.07	1.06±0.11	1.29±0.10	0.81±0.07	0.95±0.09	0.97±0.08	0.98±0.09	0.64±0.07	0.93±0.13
females	0.20±0.02	0.50±0.05	0.97±0.09	0.67±0.06	0.61±0.04	0.73±0.04	0.45±0.02	0.38±0.05	0.83±0.08

APPENDIX TABLE 5. Liver water, protein, lipid and estimated carbohydrate (% wet weight) of male and female northern pike captured at various times during an annual cycle. Mean ± 1 SE.

	1973 May 30	July 16	Aug. 21	Sept. 18	Dec. 9	1974 March 14	April 25	June 10	July 11
WATER									
males	75.5±0.6	71.9±0.8	67.6±1.6	71.9±0.7	71.6±0.8	69.5±0.7	68.9±0.4	74.3±0.4	72.6±1.7
females	79.5±0.4	76.7±0.8	71.8±0.8	75.9±0.6	76.3±0.6	76.7±0.4	75.6±0.2	78.1±0.7	73.6±0.6
PROTEIN									
males	12.6±0.4	10.3±0.3	9.4±0.6	11.3±0.4	9.9±0.3	7.6±0.3	8.2±0.2	11.2±0.4	9.8±1.0
females	13.6±0.3	11.5±0.4	10.4±0.3	11.8±0.8	13.0±0.4	13.4±0.6	14.9±0.2	12.1±0.5	11.0±0.3
LIPID									
males	5.5±0.5	8.9±0.7	9.7±0.9	8.7±0.7	5.8±0.7	4.0±0.2	4.4±0.5	5.5±0.6	9.0±0.9
females	2.6±0.2	4.8±0.4	6.9±0.6	4.6±0.3	2.8±0.1	3.1±0.1	3.3±0.1	3.5±0.3	7.7±0.7
CARBOHYDRATE[a]									
males	5.4	7.9	12.3	7.1	11.7	17.9	17.5	8.0	7.6
females	3.3	6.0	9.3	3.1	6.9	5.8	5.2	5.3	6.7

[a]Estimated by difference from mean values for water, protein and lipid. Also assumes 1.0% ash.

APPENDIX TABLE 6. Seasonal variation in gonad weight, gonad protein and gonad lipid calculated for a 50 cm fork length northern pike. Mean ± 1 SE.

	1973 May 30	July 16	Aug. 21	Sept. 18	Dec. 9	1974 March 14	April 25	June 10	July 11
GONAD WEIGHT (g)									
males	4.92±0.65	1.40±0.10	10.29±1.59	17.09±1.27	12.70±0.94	16.20±0.88	18.34±1.08	[illegible]	1.25±0.19
females	4.16±0.36	3.55±0.36	8.66±0.53	18.85±1.31	56.06±3.35	106.47±5.94	138.58±[illegible]	[illegible]	[illegible].44±0.18
GONAD PROTEIN (g)									
males	0.61±0.13	0.20±0.02	1.31±0.20	2.56±0.15	2.37±0.19	2.53±0.10	2.50±0.18	[illegible]	0.15±0.02
females	0.56±0.04	0.45±0.04	1.17±0.07	2.68±0.28	14.41±1.35	27.36±1.32	33.75±1.54	0.62±0.04	0.43±0.06
GONAD LIPID (g)									
males	0.13±0.03	0.07±0.01	0.29±0.04	0.62±0.03	30.68±0.05	0.76±0.03	0.83±0.05	0.12±0.02	0.06±0.01
females	0.06±0.01	0.05±0.01	0.13±0.01	0.55±0.07	3.32±0.34	6.24±0.34	8.00±0.41	0.08±0.01	0.05±0.01

APPENDIX TABLE 7. Gonad water, protein and lipid (% wet weight) of male and female northern pike captured at various times during an annual cycle. Mean ± 1 SE.

	1973 May 30	July 16	Aug. 21	Sept. 18	Dec. 9	1974 March 14	April 25	June 10	July 11
WATER									
males	79.9±0.6	78.8±2.0	80.2±1.9	80.4±0.5	75.9±1.2	79.0±0.3	82.0±0.2	80.2±0.6	81.3±0.5
females	82.8±0.6	83.5±0.4	81.6±0.3	76.9±0.7	64.7±0.6	64.1±0.4	67.1±0.6	84.3±0.2	83.5±1.0
PROTEIN									
males	16.2[a]	14.2[a]	14.9±1.4	15.4±0.4	18.6±1.0	16.1±0.3	13.6±0.2	15.7[a]	12.2[a]
females	13.6[a]	12.7[a]	13.4±0.1	16.5±0.6	26.0±0.3	26.4±0.3	24.4±0.4	12.7[a]	13.4[a]
LIPID									
males	3.4[a]	4.9[a]	3.1±0.3	3.7±0.1	5.4±0.3	4.9±0.1	4.6±0.1	3.6[a]	4.8[a]
females	1.5[a]	1.5[a]	1.7±0.1	3.2±0.2	6.1±0.2	6.2±0.2	5.8±0.1	1.5[a]	1.5[a]

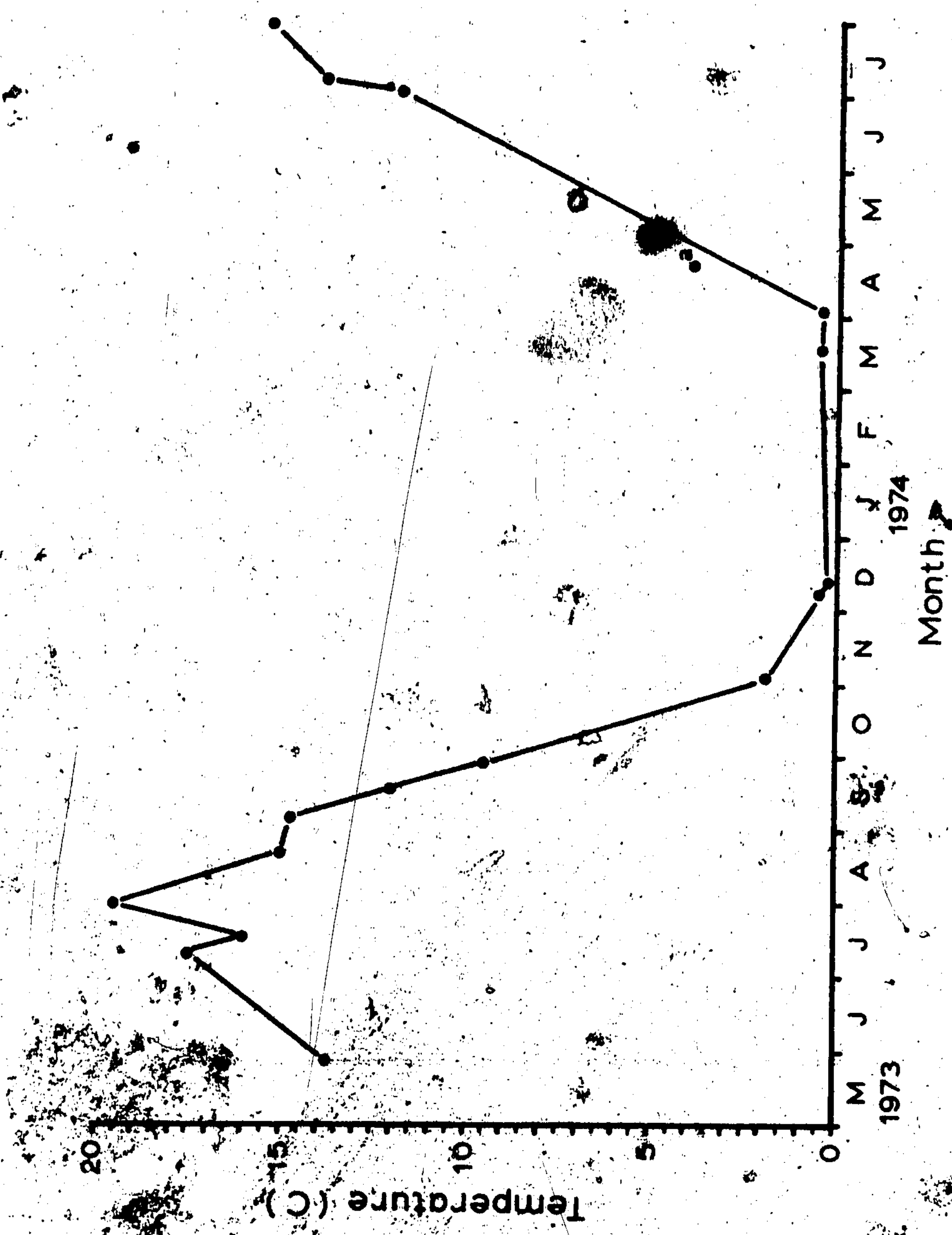
[a] Mean value for pooled sample.

APPENDIX TABLE 8. Number of pike feeding (based on stomachs containing food) as percentage of total number of fish examined for each month. Data for Lake Windermere pike are taken from Frost (1954) to allow comparison.

Month	Lake Windermere	Lac Ste. Anne
January	45	—
February	40	—
March	43	43
April (before spawning)	15	7
May (after spawning)	83	84
June	71	39
July	62	45
August	53	46
September	65	71
October	54	—
November	66	—
December	55	26
Total number of fish examined in study	2,783	219

APPENDIX FIGURE 1. Temperature regime for Lac Ste. Anne during 1973-74. Temperatures were recorded at approximately 2 m depth.

[a]Surface temperature in a tributary from which prespawning fish were taken.


Temperature (°C)
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1973
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