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CANADIAN THESES ON MICROFICHE

THÈSES CANADIENNES SUR MICROFICHE

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TITLE OF THESIS/*TITRE DE LA THÈSE* An energy budget for northern pike (Esox lucius) in Lac Ste Anne, Alberta.

UNIVERSITY/*UNIVERSITÉ* University of Alberta

DEGREE FOR WHICH THESIS WAS PRESENTED/ *GRADE POUR LEQUEL CETTE THÈSE FUT PRÉSENTÉE* Ph. D

YEAR THIS DEGREE CONFERRED/*ANNÉE D'OBTENTION DE CE GRADE* 1979

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THE UNIVERSITY OF ALBERTA

AN ENERGY BUDGET FOR NORTHERN PIKE (*ESOX LUCIUS*) IN LAC STE. ANNE, ALBERTA.

by

© JAMES S. DIANA

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

DEPARTMENT OF ZOOLOGY
EDMONTON, ALBERTA
FALL, 1979

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 "An energy budget for northern pike (Esox lucius) in Lac Ste. Anne, Alberta" submitted by James S. Diana, in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

W. C. Mackay
Supervisor

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Mark V.H. Wilson

DATE. May 30 1979

ABSTRACT

An annual energy budget for northern pike (Esox lucius) in Lac Ste. Anne, Alberta, was estimated by a combination of field and lab experiments. Lac Ste. Anne is characterized by a fairly constant temperature regime, with summer temperatures (from May to October) near 16 C (range 14-20 C) and winter temperatures (from November to April) near 1 C. The energy budget of three-year-old pike (which were sexually mature) was examined during various portions of the year to elucidate seasonal and sex-related changes in energy accumulation and use. In addition, annual budgets were examined for each age class (0-3) that was adequately represented in the samples, to assess age-related changes in energy partitioning.

Northern pike were sampled from Lac Ste. Anne at regular intervals between March 1976 and September 1978. The caloric content of the liver, gonads, and body of each age class (0-4) of fish were measured at 5 intervals over the year. Three-year-old males grew 335 kcal in body energy annually, 35% of which was in the winter. Body growth in females was approximately the same amount as in males, but all of it occurred during summer. Three-year-old male pike completed all of their testicular growth in August (17 kcal), while ovarian growth in females (totaling 436 kcal) continued over winter. Both sexes significantly depleted somatic energy reserves during spawning. The same annual growth pattern was observed for all age classes of pike, except young-of-year fish which did not mature.

Maintenance requirements were estimated by controlled experiments. Routine metabolic rate (cal/day) was described by the equation:

$R_{met} = 1.6\ W^{0.97}$ at 1 C, and $R_{met} = 27.5\ W^{0.82}$ at 14 C, where W = somatic weight (in g). During spawning, metabolic rate in males was higher than in females.

Diel and seasonal activity patterns were determined by ultrasonic telemetry. Pike were inactive over 80% of the time during both seasons. The fish were completely inactive at night, and sporadically active throughout the day. Because of the low level of activity found in the fish population, active metabolic rate in nature was assumed to equal the level of routine metabolism.

Daily ration was estimated from the stomach contents of pike captured regularly over the three years. Gastric evacuation (determined by controlled experiments) was 12 days at 2 C and 48 hours at 14 C. Daily ration was always higher in females than in males. Maximum rations were ingested in June, rations were high from May to August, and were very low over winter. The fish fasted during the spawning interval (late April to early May).

The annual allocation of energy to growth, maintenance, and reproduction was estimated by combining all of these data. Three-year-old males allotted 67% of their assimilated energy (1689 kcal) to maintenance, 26% (651 kcal) to growth, and 7% (177 kcal) to reproduction. Three-year-old females allotted 47% of their assimilated energy (1705 kcal) to maintenance, 25% (923 kcal) to growth, and 28% (1023 kcal) to reproduction. The energy allocations of other age classes of mature pike were similar to three year olds. Immature pike (age 0) allotted 72% (1077 kcal) of their assimilated energy to growth, and 28% (427 kcal) to maintenance. Ration predicted by energy budget and observed ration were usually in good agreement.

ACKNOWLEDGMENTS

I would like to express my sincere appreciation to everyone who aided me in various ways throughout this study, and especially to the persons listed below. W. C. Mackay (my supervisor) was foremost in support and guidance, and has been of great aid throughout my tenure at the University of Alberta. The members of my supervisory committee, J. F. Addicott, J. S. Nelson, and J. R. Nursall, helped guide this study to completion. E. J. Crossman expended much time and effort to serve as the external examiner on my thesis defense.

The field and lab work for this study was completed at the Lac Ste. Anne Fish Research Laboratory, supported by the Department of Zoology, University of Alberta. My field work was completed with the assistance of many persons; including B. Boog, D. Glass, D. Goulet, C. Hawryshin, B. Medford, T. Miller, D. Pehowich, D. Porter, P. Praegert, R. Tanasichuk, C. Thoresen, and M. Wiegand.

Financial assistance was provided by an NSERC grant (A6387) to W. C. Mackay, as well as a Graduate Teaching Assistantship, Graduate Research Assistantship, and a Dissertation Fellowship from the University of Alberta.

Special thanks are extended to R. Tanasichuk and B. Medford, for their extra help throughout this study, and to B. Diana, who aided both morally and physically in all portions of this work.

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GENERAL INTRODUCTION

For any animal, the energy accumulated by feeding is used for maintenance, activity, growth, and reproduction. The energy available from feeding has a physical limit, due to stomach capacity, limited food resources, endogenous regulation of food intake, or exogenous factors. This energy must then be partitioned for use in the functions of maintenance, activity, growth, or reproduction. The allocation of energy to each component is termed an energy budget. Diel and seasonal changes in temperature, food availability, and day length may influence either intake or utilization of energy, and because of this, energy budgets of animals should show considerable adaptation to local variations in these conditions. In poikilothermic animals, the dependence of energy allocation on temperature cycles is very significant, since temperature may drastically affect most physiological functions.

An overall energy budget can be estimated in two ways. The first is to measure food intake, remove from this the energy lost in assimilation, active metabolism, and growth efficiency, and the excess energy should be accumulated in body or gonad growth. The second method is to measure growth, back calculate for growth efficiency, active metabolism, and assimilation, then predict the total ration. Because of inaccuracies encountered in the measurement of each component, it is doubtful that the energy budget determined for any population in nature would balance precisely between these two methods. However, the relative fit for the budget could be assessed by comparing these values. This is the only reliable method to assess the accuracy of an energy budget, and the only reasonable way to do this is to independently evaluate each component of the budget.

Energy budgets of fish have been calculated from controlled laboratory experiments (see reviews of Fry 1957; 1971; Brett 1970) as well as from field experiments (Mann 1969, Healey 1972). Most components can be measured by either technique, but the accuracy of the final budget depends on the reality of the assumptions involved. In the following sections, I will evaluate methods to measure each parameter for a fish population, and define the best methods to use in an energy budget study based mainly on field analyses.

Growth

Data on the growth of a natural fish population are the first prerequisite for determination of an energy budget. Body and gonad growth of natural populations can be determined from field samples of each age class of fish captured at intervals throughout the year. To estimate total production for individual fish, the absolute quantity of energy in the body and gonads of many fish must be determined during several different periods of the year. The growth of fish in weight has often been examined over some periods of time (Weatherley 1972, 1976), but these studies do not necessarily determine changes in total energy, since lipid, protein, and water contents of fish bodies often vary throughout the year (Love 1970, Shul'man 1974).

The energy dynamics of fish were first examined by Idler and Bitners (1958, 1960) for migratory sockeye salmon (Oncorhynchus nerka). They collected data on the length, body weight, gonad weight, and tissue constituents for salmon during various times in their freshwater migration. They then used appropriate regressions to convert all of the data to values expected for a 50 cm fish. This allowed them to utilize all fish as a single sample, regardless of their size or age. The conversion assumed that none of the fish grew in length during the study, since concomitant growth in length and weight would be neglected by conversion to a standard fish length. This assumption was reasonable since there was no evidence that salmon grew during the freshwater phase of their spawning migration. However, the "standard fish" technique has since been used by some authors (MacKinnon 1972, Craig 1977, Medford and Mackay 1978) to analyze seasonal production in individual fish. This type of analysis cannot estimate total production, since the only variations measured are changes in "plumpness" of the fish, i.e. changes in weight per unit length. Some authors (Healey 1972, Foltz and Norden 1977) have examined energy production of fish, taking growth in length into account. This approach truly measures production, since total energy changes in the fish are assessed, rather than changes in energy per unit length.

The timing of body growth, gonad growth, and spawning in fish is very precise from year to year (Love 1970, Shul'man 1974). There may be large differences between sexes in the amount of energy required for gonad growth and maturation (Love 1970, Shul'man 1974), since ovarian tissue usually contains much more energy than testicular tissue. There may also be differences in the timing of gonad growth between each sex of the same fish species (Shul'man 1974). These differences in the magnitude and timing of gonad growth between sexes of fish must have considerable influence on the pattern of energy use. In addition, the proportional allocation of energy to body and gonad growth may vary with age of the fish.

Feeding

The daily ration of fish can be estimated by several types of controlled experiments. One type would be to measure the components of an energy budget, then predict the ration by back calculation (Mann 1965, Mel'nichuk 1973, Lasker 1970). However, this type of ration estimate would be of little use in verifying an energy budget, since it is based on the budget parameters. The second type of controlled experiment would be to feed fish varying amounts of food, then measure the growth rate. The growth could then be compared to the actual growth rate of the population, and the ration predicted (Davis and Warren 1968, Gerking 1972, Carline and Hall 1973). This type of experiment assumes that activity and feeding behavior are similar for the experimental fish and for fish in nature. It is doubtful if this assumption is true in many cases (Nakashima and Leggett 1978). However, ration data of this sort could be used to verify an energy budget, since they are based on an independent analysis.

Daily ration can also be evaluated from the stomach contents of samples of field-caught fish. These contents can be used to directly calculate ration (Thorpe 1977, Nakashima and Leggett 1978), or can be combined with estimates of digestive rate to measure daily ration (Darnell and Meierotto 1962, Swenson and Smith 1973). The best method to use depends on the feeding duration, meal frequency, and gastric evacuation rate of the fish in question. This type of feeding analysis is determined independently from the other components of the budget, and does not depend heavily on assumptions from laboratory experiments. Because of this, field analyses of rations are best suited to verify the energy budget for a natural fish population.

Metabolism

At present, the only feasible technique to determine metabolic parameters for fish is by controlled experiment, although biotelemetric equipment may be available soon to monitor these parameters in the field. The energy required for maintenance by a fish can be measured by determining the standard metabolic rate (by oxygen consumption), the level of feeding necessary to preserve a steady energy state (no weight loss or gain), or the loss of energy during starvation. Different results are often obtained for the same fish species using these various methods (Brown 1957, Fry 1957, Niimi and Beamish 1974, Brett 1976). This lack of agreement is due mainly to the different histories of the fish used in each type of experiment. Oxygen consumption is usually measured on post absorptive fish, and is either measured at rest (Dolinin 1973) or extrapolated to the zero activity level (Brett 1964). Maintenance ration experiments include fish activity due to feeding, as well as increased metabolic rate during digestion due to specific dynamic action (Brett 1976). Starvation experiments involve inactive fish, which usually show a decrease in metabolic rate during starvation (Niimi and Beamish 1974). Because of difficulties in measuring food consumption and in maintaining fish at a steady energy state, oxygen consumption experiments are most commonly used to estimate maintenance requirements.

The metabolism of poikilotherms is directly dependent on temperature. In measuring physiological data for extrapolation to a natural population, the temperature regime must be taken into account. Not only are seasonal changes in temperature important, but diel changes can also influence fish physiology. To accurately estimate fish metabolism in the field, controlled experiments must be closely tied to the temperature conditions of the habitat.

To predict an energy budget, one also needs to measure active metabolic rate and the efficiency of energy flow from ingestion to growth. The active metabolic rate of fish, which includes maintenance and activity costs, depends on swimming speed and duration in nature, and is described in the next section. Once food is ingested, most is absorbed, while the remainder is lost as feces. The efficiency of food absorption is termed assimilation efficiency. The absorbed energy is available to be used for maintenance or growth. The conversion of absorbed energy to new tissue is termed the growth efficiency (Kelso 1972). Several growth efficiencies are commonly measured. Gross efficiency (K_1) is defined as kcal grown per kcal eaten, net efficiency (K_2) is kcal grown per kcal assimilated, and yield efficiency (K_3) is kcal grown per kcal remaining after maintenance costs are removed. All of the above efficiencies can be determined from controlled feeding experiments.

Activity

The active metabolic rate of fish is dependent on swimming speed and duration (Brett 1964). However, few people have measured the swimming speed of fish under natural conditions. For energy budget analyses, Winberg (1956) examined existing data, and predicted that the active metabolic rate of a fish is approximately twice standard metabolism. Mann (1965) examined other data, and confirmed Winberg's conclusions. Since that time, few people have measured active metabolic rate for fish species, but rather they have assumed that it is twice the standard rate. The validity of this assumption is questionable, especially when applying it to all fish species (Brett 1964).

Activity of fish could be measured by direct observation or by biotelemetry. Using telemetric techniques, one can measure fish activity directly using a swimming velocity device attached to the fish (Sciarrotta and Nelson 1977), or indirectly by measuring distances displaced over short time intervals (Sciarrotta and Nelson 1977, Poddubnyi et al. 1970). If a sufficient number of observations are conducted over various day and night periods, one can eventually determine average swimming velocity, the duration of swimming bouts, and the length of rest periods during the day. One could then measure oxygen consumption at various swimming speeds and durations, and couple this with field swimming measurements to quantitatively evaluate active metabolic rate. To my knowledge, this has not been done previously.

Energy budgets

Now that each component has been considered in general terms, it is possible to evaluate previously published energy budgets to determine the best strategy for assessing an accurate budget for fish. Idler and Clemens (1959) estimated energy losses for sockeye salmon during their freshwater migration. Since the fish they studied did not feed during migration, their energy losses were used to estimate a budget. Gerking (1952, 1955, 1972) did considerable work on bluegill

(*Lepomis macrochirus*) energetics, but his calculation of an energy budget still relied on the assumption that active metabolic rate was twice the standard level. Gerking's budget did not balance between predicted ration (from controlled feeding experiments) and observed growth, but his studies were a first attempt to extrapolate energetic data to a natural fish population. Similarly, Mann (1964, 1965) used mainly lab data to predict energy budgets for many fish species in the River Thames.

The first predominantly field-oriented energy budget for fish was estimated by Healey (1972). Healey also determined ration from field collections, and the budget did not balance between predicted and actual rations. His budget was based on several assumptions, which may not have been valid. He also attempted to calculate budgets for several fish species by combining data from literature sources and making assumptions where necessary. None of these budgets balanced, which indicates that the same species may respond differently in energetic terms because of adaptations to local temperature cycles, day lengths, or other habitat characteristics. The errors in these budgets may also be due to assumptions used in the calculations. The best method to calculate an energy budget is to measure as many terms as possible and avoid any unnecessary assumptions. The measurements should all be made on fish taken from the population in question, and experimental conditions should be kept as close to nature as possible.

In estimating an energy budget, it must be emphasized that most bioenergetic conversions occur at an efficiency much less than 100% (Lehninger 1965). In most previous energy budget studies in fish, body and gonad growth were measured, and maintenance requirements were estimated from lab experiments. These values were then used to estimate energy allocation to growth, reproduction, and respiration. Energy requirements for growth are much greater than the actual growth, because conversion from food energy to tissue is inefficient. In addition to this factor, one must also include the costs of reproductive activity in estimates of energy allotted to reproduction. I have not encountered a fish energy budget study that took all of these factors into account. Another factor often ignored in other studies is the effect of age on energy allocation, even though the tissue growth of fish is often allometric and varies considerably with age.

The present study

One of the main problems encountered in assessing the energy budget of any animal is extrapolation of laboratory data to the animal in nature. In many aquatic habitats, water temperature may vary with time of day, month, or depth. Since temperature directly affects physiological processes of poikilotherms, one must be able to accurately predict the temperature of the animals at all times to extrapolate lab data to the field. Since fish may vary their location or depth at will, this is very difficult to do in a thermally non-homogeneous habitat. For this reason, Lac Ste. Anne presents an excellent environment for energy budget studies. The lake is isothermal, and water temperatures are fairly constant through summer (14-18 C from May to October) and winter (2 C from November to April) (Appendix Figure 1). This constant, predictable temperature regime allows extrapolation of lab experiments to field conditions with little loss in accuracy.

The measurement of growth and ration from field samples requires that a large number of animals be collected throughout the year. In collecting these animals, one must not deplete the population, for this could alter food availability, growth, or social interactions. Northern pike (*Esox lucius*) are an abundant fish in Lac Ste. Anne, supporting a large commercial and sports fishery. It is possible to catch large numbers of them for experiments year round, without further depleting the population. Pike are top carnivores, feeding on few large items. This should allow daily rations to be quantified more easily than for fish which utilize many small prey items. In addition to this, pike are large, which allows much easier implantation of transmitters for telemetric observations. All of the above considerations indicate that pike are good experimental animals for energetic analysis.

The present work began as a study of the foraging and growth of northern pike from Lac Ste. Anne, Alberta. However, as time progressed it became evident that the population of pike in Lac Ste. Anne was excellent for prediction of an energy budget, and the emphasis shifted to measure all of the necessary components of the budget. The presentation in this text will follow two main trends to analyze energetics of pike. Total trends will be evaluated for each sex and age class that was adequately sampled, so age-related changes in the energy budget can be assessed. Secondly, seasonal changes in each component will be evaluated for 3-year-old pike of both sexes. Three-year-olds were chosen for this analysis because they had all undergone at least one spawning cycle, so their annual maturation process was more distinct than that of younger fish.

Chapter 1. THE DEPOSITION AND DEPLETION OF ENERGY IN THE LIVER, BODY, AND GONADS OF NORTHERN PIKE FROM LAC STE. ANNE

INTRODUCTION

In energy budget studies, the component of growth has always been measured for natural populations. Growth of fish is so dependent on environmental conditions that it cannot be accurately predicted from lab data, yet growth is easily determined by collections of samples from the field. Net annual production can be assessed by comparing the various age classes of fish captured at one time. However, gross production requires collection of a series of samples of each age class throughout the year, since depletion of body reserves may occur at some time and since gonad production requires considerable energy, yet most gonad energy is released from the body during spawning. Certain organs have been shown to function as energy stores, and these should also be examined to determine their role in body and gonad production. Possible energy storage depots in fish include the carcass, visceral fat bodies, and the liver (Shul'man 1974).

Northern pike commonly spawn in early spring. Testicular growth occurs mainly in August, while ovary growth continues during winter (Huang and Hickman 1968). Ovary tissue also contains much more energy than testicular tissue of similar size mature pike (Medford and Mackay 1978). Pike energy storage depots include the body and liver, while the remainder of the viscera do not store significant amounts of energy (Medford and Mackay 1978).

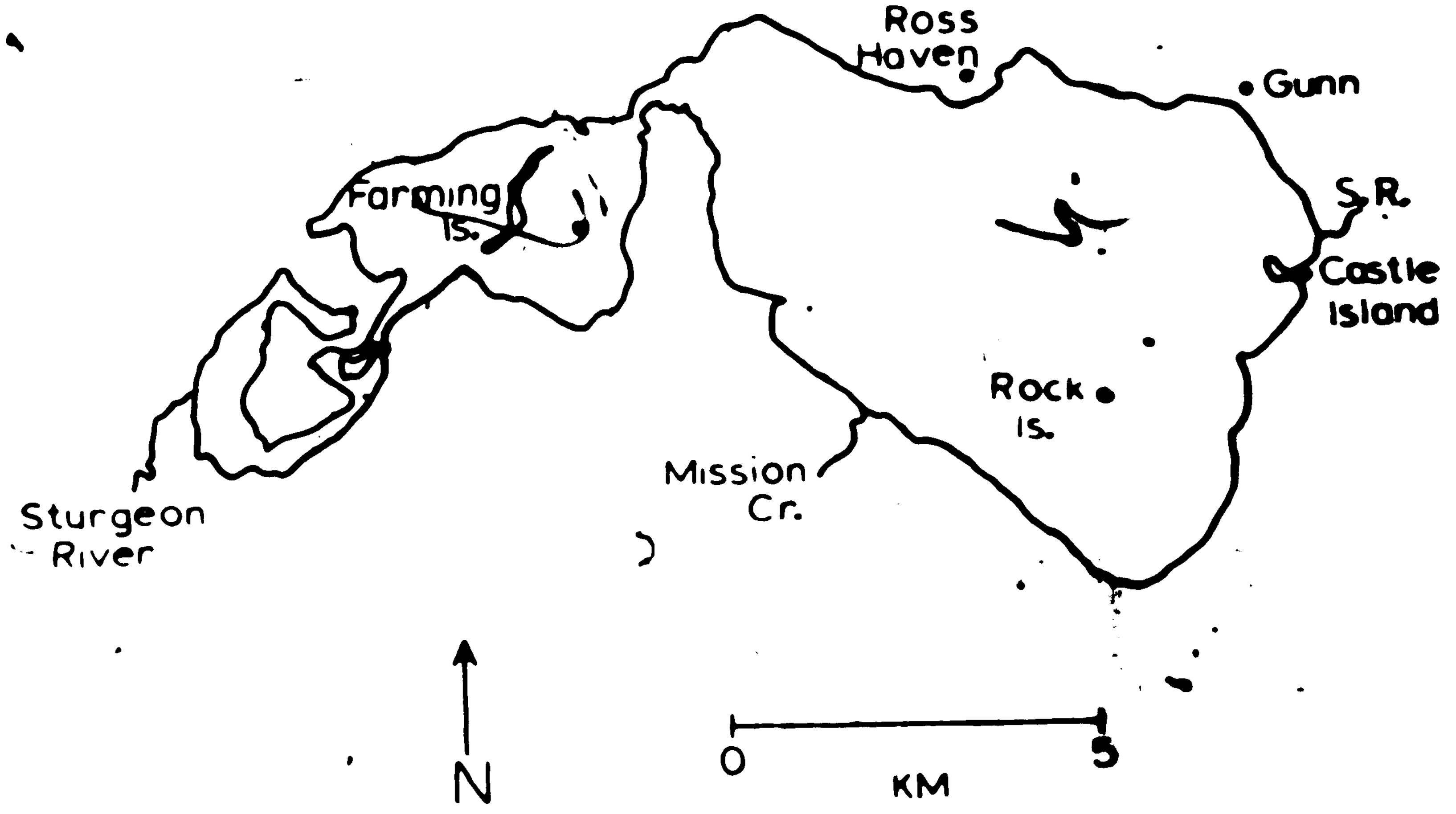
The purpose of this study was to determine the timing and magnitude of energy deposition and depletion in the body, liver, and gonads of northern pike during the year. A sufficient number of fish were sampled to allow growth in length and in total calories to be determined for several age classes. The effects of age, season, [illegible] sex on growth were examined to allow a better understanding of the production process in individual fish.

DESCRIPTION OF THE STUDY AREA

Lac Ste. Anne (114°24'W, 53°43'N) is a moderate size (57 km^2), shallow (average depth 4.8 m) eutrophic lake located approximately 74 km northwest of Edmonton. The lake is divided into three basins (Figure 1), and the Lac Ste. Anne Fish Research Laboratory is located on the northeast shore of the large eastern basin. The majority of the fish collected for this study were taken from the area near the lab.

The water in Lac Ste. Anne is usually isothermal, with a temperature regime as shown in Appendix Figure 1. The lake is characterized by fairly constant temperatures during the summer (14 to 18 C from May to October) and winter (1 to 2 C from November to April). Only during brief periods in October and April do water temperatures differ much from one of these two regimes. The lake is usually covered by ice (which reaches a thickness of 0.8 to 1 m) from early November to late April. It is uncertain whether the temperature regime or fish populations differ between the basins. Most measurements for this study were made in the eastern basin, and the energy budget that is described may not apply to fish in the other areas.

Figure 1. Map of Lac Ste. Anne, indicating the locations of various landmarks cited in the text. The Lac Ste. Anne Fish Research Lab is located in Gunn. The Sturgeon River enters the lake in the western basin, and exits at the northeast extremity (S. R.).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S.R.
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MATERIALS AND METHODS

Northern pike were collected by various size gillnets from Lac Ste. Anne on 26 occasions between March 1976 and September 1978 (Appendix Table 1), except for April 1977 when they were collected by seine from a tributary stream. The fish were sealed in plastic bags, frozen at -25 C, and thawed for later analysis. The gross body weight was measured to 0.1 g, and the standard length to 0.5 cm. Four pike from each sex and age class (when possible) were selected from samples collected on six occasions between March 1976 and May 1977 and were used for caloric analysis. The body (fish without liver, gonads, or digestive tract), liver, and gonads of each fish were dried to constant weight at 80 C, ground to powder in a coffee mill, then stored in vials at -25 C until later analysis. Body samples were passed through a meat grinder (with ports 0.8 cm in diameter) prior to drying.

Calorific equivalents (kcal per gram dry weight) were determined using a Parr adiabatic calorimeter following standard methods (Paine 1971, see Appendix A). A value of 5.0 ± 0.02 kcal per gram (mean ± 2 SD) was obtained from six replicates of one somatic sample. Because of this precision, only one determination was done per sample.

Pike were aged by counting the number of annuli on scales taken from the left side of each fish, dorsal to the lateral line and just anterior to the dorsal fin (Frost and Kipling 1959). Approximately 5% of the fish could not be aged by scales, and were classed with similar sized fish from the same sample that had been aged.

Seasonal and age-related changes in energetic parameters were determined by analysis of variance and the Student-Newman-Keuls test.

Differences were considered significant if $P < 0.05$. Analysis was done on the University of Alberta computer using programs from the SPSS package (Nie et al. 1975).

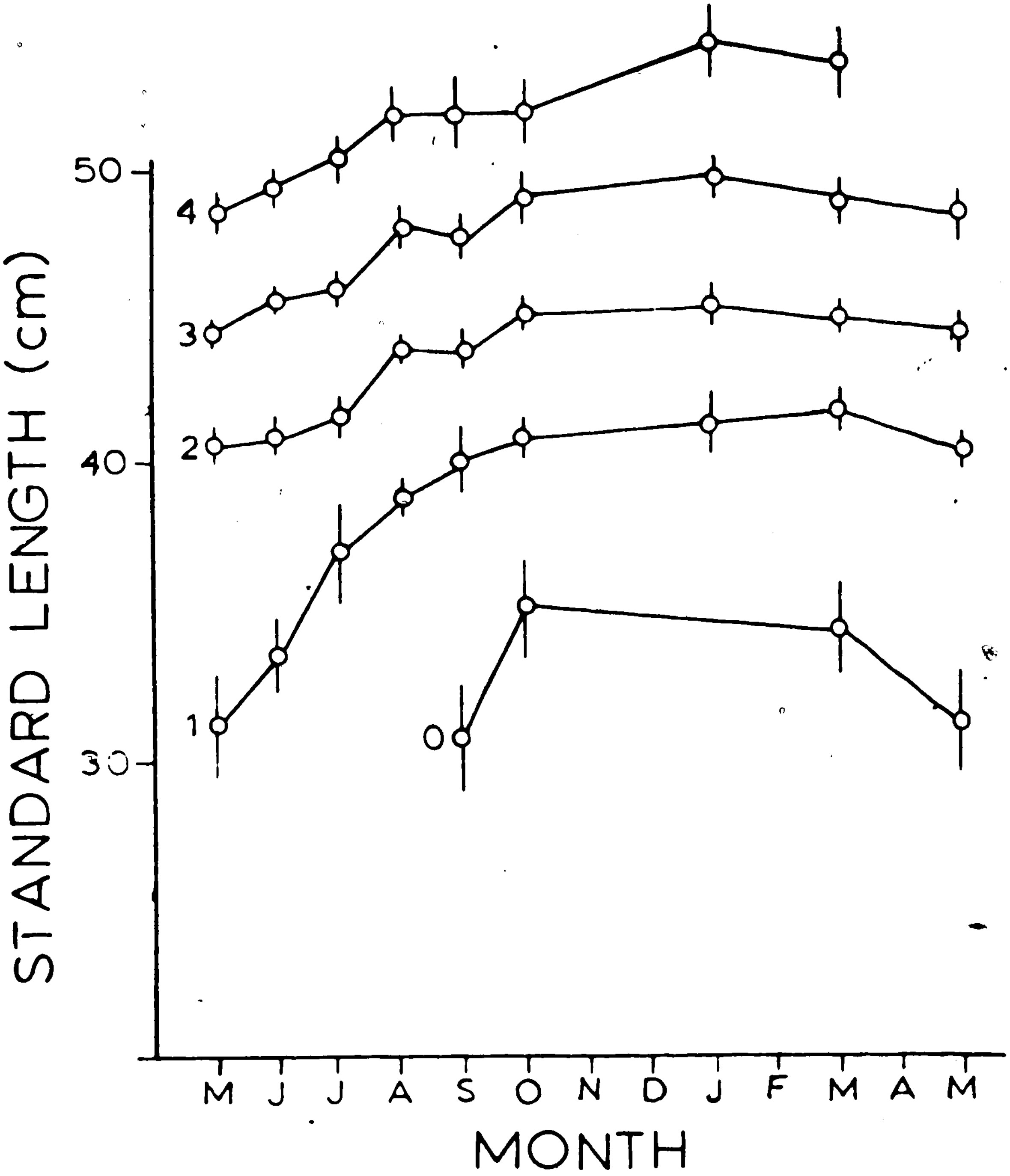
RESULTS

Body growth

Significant growth in length by adult northern pike from Lac Ste. Anne occurred only from May to September (Figure 2). The mean standard lengths of respective age classes during any particular month were similar for both sexes. There were no significant differences between monthly values from 1976, 1977, or 1978 (Appendix Table 2); so all data from the 3 years were pooled to give a single monthly growth curve. Annuli were completed between May and June by all age classes. The largest increments in length occurred in June or July, except young-of-year fish which increased dramatically in length from August to November.

There were no significant differences in body calorific equivalents (kcal per gram dry weight) or percent water between any monthly samples (Table 1), nor were there any differences between age classes or sexes. Values for each of these parameters were fairly precise, and the coefficients of variation were from 1.6 to 3.4%. Contrarily, the body weights for individuals of any sex and age class were much more variable than the calorific values, and the coefficients of variation for each sex and age class (pooled by month) averaged 15%. It did not appear that more determinations would greatly increase the precision of calorific equivalent or percent water values. Since the between animal variance associated with percent water and calorific equivalent was insignificant compared to between animal variances in body weight, the total body calories for animals collected in March, May, August,

Figure 2. The standard length of each age class of northern pike collected monthly in Lac Ste. Anne from 1976 to 1978. $\bar{x} \pm 2$ SE. The age is indicated by the number before each group. The values are based on a total of 1365 pike, with n for each group listed in Appendix Table 2.


STANDARD LENGTH (cm)
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MONTH

Table 1. The percent water (%W) and calorific equivalents (kcal per dry gram) for body, liver, and gonad tissue of pike collected at Lac Ste. Anne from March 1976 to May 1977. $\bar{x} \pm 95\%$ CL. N for each group is listed in parentheses.

Group	Body %W	Body calorific equivalent	Liver %W	Liver calorific equivalent	Gonad %W	Gonad calorific equivalent
			MALES			
March	75.2 ± 0.6 (14)	4.7 ± 0.1 (21)	72.1 ±15.2 (6)	5.4 ± 0.2 (4)	73.8 ± 2.0 (5)	5.4 ± 0.1 (4)
May	75.4 ± 0.6 (9)	4.7 ± 0.1 (13)	74.9 ± 1.5 (34)	5.1 ± 0.8 (3)	77.8 ± 4.1 (12)	5.1 ± 0.1 (3)
August	75.7 ± 0.4 (6)	4.7 ± 0.1 (8)	66.9 ± 1.2 (37)	5.9 ± 0.2 (8)	76.2 ± 4.4 (37)	5.1 ± 0.1 (8)
January 1977	75.1 ± 0.6 (11)	4.6 ± 0.1 (15)	71.3 ± 1.0 (27)	5.3 ± 0.1 (4)	79.0 ± 0.8 (27)	5.4 ± 0.1 (5)
March	75.7 ± 0.6 (14)	4.8 ± 0.1 (14)	69.7 ± 1.1 (24)	5.0 ± 0.2 (5)	77.6 ± 1.9 (24)	5.5 ± 0.2 (5)
May	75.8 ± 0.5 (11)	4.9 ± 0.1 (11)	77.2 ± 1.8 (29)	5.6 ± 0.3 (5)	83.0 ± 1.9 (14)	5.3 ± 0.1 (5)
			FEMALES			
March	76.1 ± 0.9 (11)	4.9 ± 0.1 (12)	78.4 ± 2.0 (5)	5.7 ± 0.1 (5)	63.3 ± 1.9 (5)	5.7 ± 0.2 (5)
May	74.5 ± 0.9 (8)	4.5 ± 0.1 (9)	77.8 ± 1.2 (14)	5.1 ± 0.2 (5)	78.7 ± 6.0 (13)	5.1 ± 0.1 (6)
August	76.0 ± 0.7 (13)	4.8 ± 0.1 (18)	68.9 ± 2.6 (30)	6.4 ± 0.3 (12)	82.7 ± 1.4 (30)	4.8 ± 0.1 (10)
January 1977	75.8 ± 0.6 (13)	4.6 ± 0.1 (13)	79.4 ± 0.8 (33)	5.2 ± 0.1 (5)	65.5 ± 0.7 (33)	5.8 ± 0.1 (5)
March	76.5 ± 0.7 (14)	4.6 ± 0.1 (14)	78.0 ± 0.6 (43)	5.0 ± 0.1 (5)	65.2 ± 0.5 (43)	5.9 ± 0.1 (5)
May	76.3 ± 0.7 (9)	4.7 ± 0.1 (9)	81.9 ± 1.4 (16)	5.3 ± 0.2 (5)	85.3 ± 2.7 (10)	5.1 ± 0.1 (5)
			MEAN			
Male	75.5 ± 0.3 (77)	4.7 ± 0.2 (93)	71.9 ± 0.9(169)	5.7 ± 0.2 (29)	78.5 ± 1.4(131)	5.3 ± 0.1 (30)
Female	75.9 ± 0.3 (68)	4.7 ± 0.1 (75)	76.8 ± 0.9(141)	5.6 ± 0.2 (37)	71.9 ± 1.6(134)	5.3 ± 0.2 (36)

and January of all years were calculated by multiplying individual body weights by the overall mean calorific equivalent and percent dry matter.

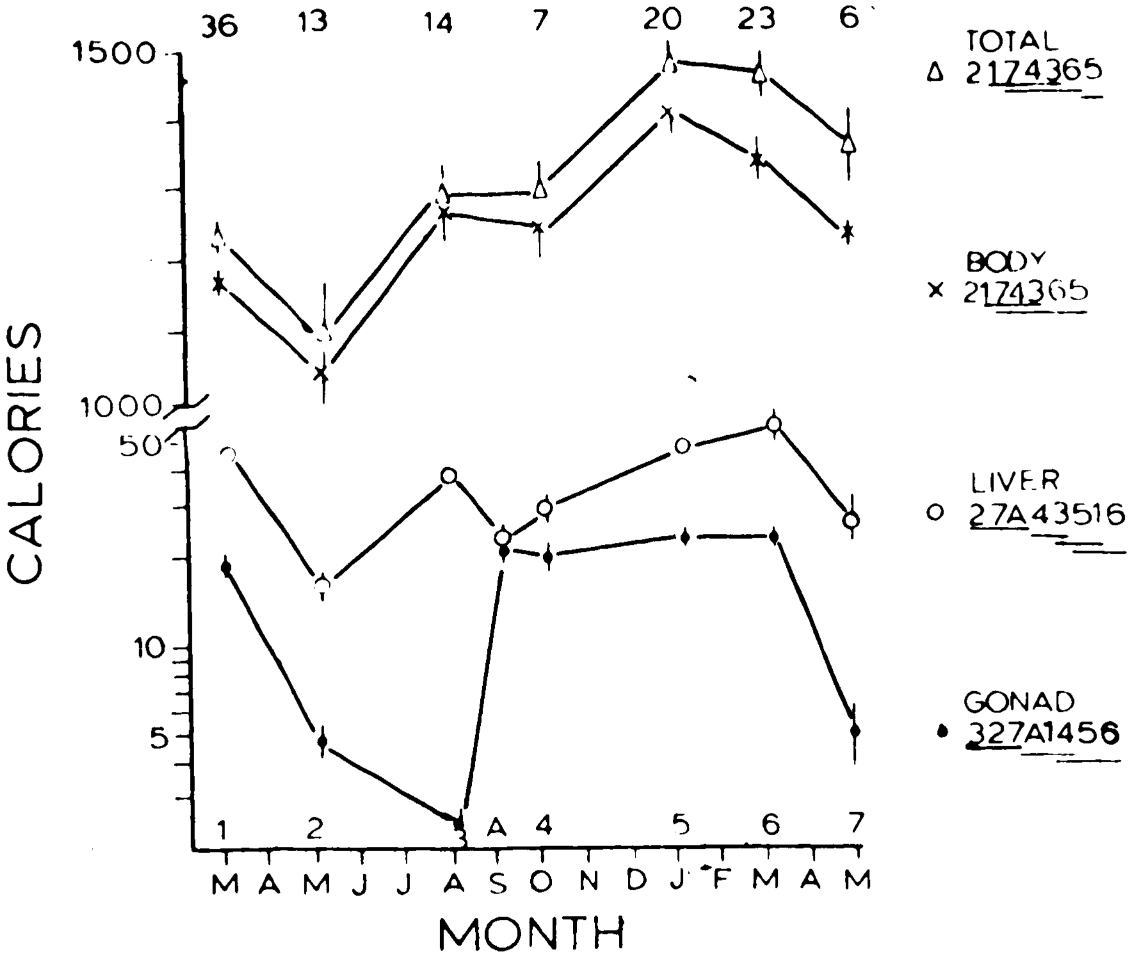
Depletion of body reserves occurred in both sexes during spawning (March to May, Figure 3). Body energy increased from June to January in three-year-old males, while females increased in body energy only over the summer (June to October).

Gonad growth

The water contents and calorific equivalents of the liver and gonads of each sex of pike varied significantly in different months (Table 1), but did not vary between age classes during any month. The monthly calorific equivalents and percent water values were fairly precise for both sexes (Table 2). Absolute gonad and liver weights differed significantly between months, sexes, and age classes; and the mean monthly values for each age-sex class showed considerable variation (Table 2). Since the greatest between animal variation was again attributable to weights of each organ, the total liver and gonad calories were computed for each animal collected in March, May, August, and January by multiplying individual organ weights by the monthly mean calorific equivalents and proportion of dry matter.

Little change in the gonad energy content occurred from May to August (Figure 3). Spawning occurred in late April or early May: only young-of-year fish did not mature. Testicular growth occurred entirely in August of each year. Ovary caloric growth began in August, and nearly all ovarian growth occurred during the winter (October to March).

Figure 3. The caloric content of the liver (open circles), gonad (closed circles), body (crosses), and total (triangles) tissues of three-year-old male (next page) and female (following page) pike captured at various times from 1976 to 1978. $\bar{x}$ ± SE. Each sampling period is numbered above the abscissa. The values of each parameter (indicated at right by their symbols) were analyzed over the months by a Student-Newman-Keuls test. Sample dates underlined at the same level were not significantly different ($P > 0.05$). The number of animals included in each group are listed across the top of the graph.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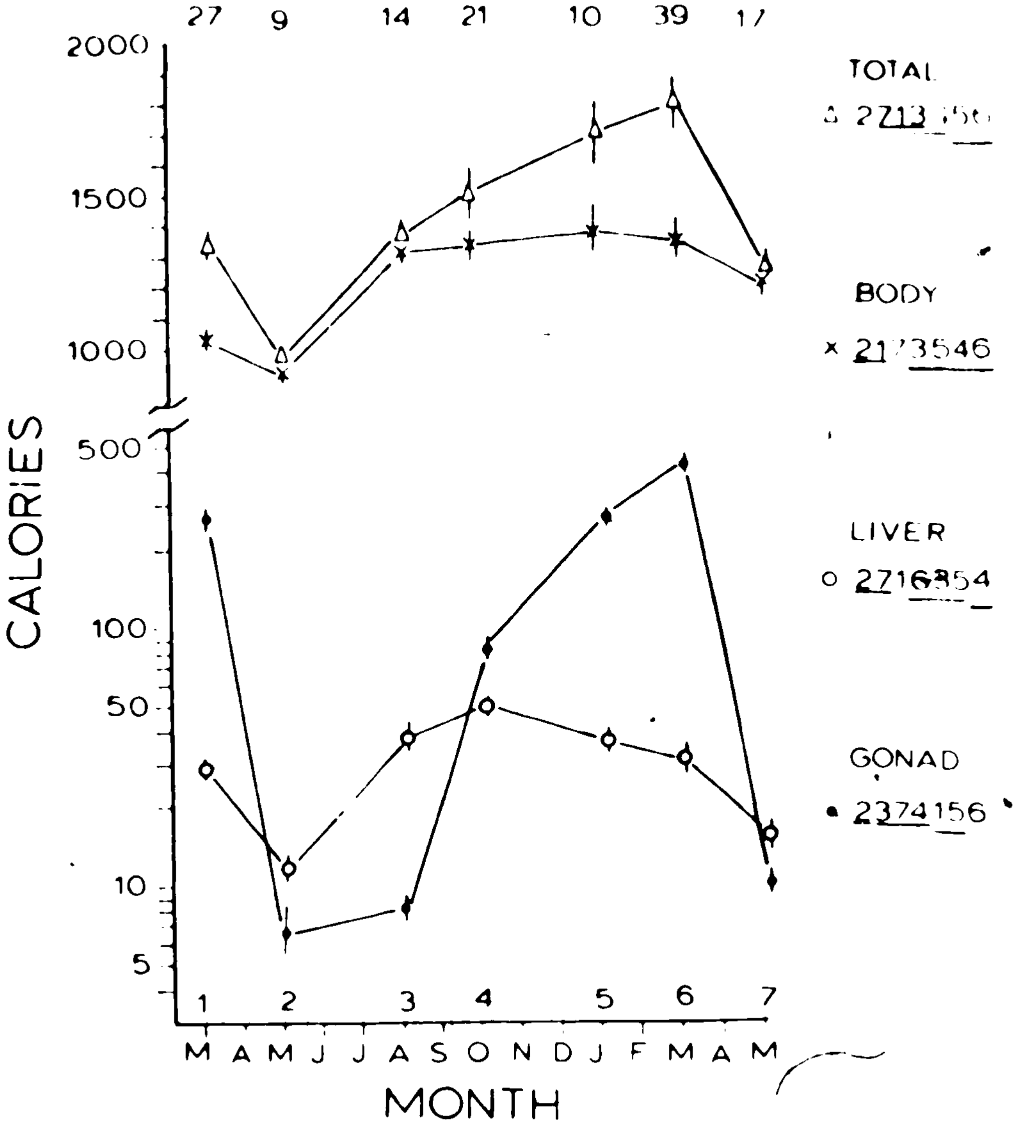
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BODY
× 2173546
LIVER
○ 2716354
GONAD
● 2374156

Table 2. Average coefficients of variation for monthly data on percent water and calorific equivalents of liver and gonads from northern pike, as well as the overall average CV for the wet weight of each organ for each sex-age class (pooled by month).

Parameter	Coefficient of Variation	
	Males	Females
Liver percent water	3.5%	5.4%
Liver calorific equivalent	3.3%	4.1%
Liver wet weight	28.1%	27.1%
Gonad percent water	4.3%	6.7%
Gonad calorific equivalent	1.7%	2.1%
Gonad wet weight	40.7%	35.6%

Gonad energy content of mature fish was positively correlated with body weight for both sexes. However, there was no significant change in the relative gonad energy (gonad kcal per body kcal) with age or weight for either sex.

Liver growth

Total liver energy of three year old pike (Figure 3) decreased during the spring each year, then increased through the summer. The loss of energy from the male liver in August (15.6 kcal) approximately equaled the amount of testis growth (16.8 kcal) during that time. Fifty-three percent of the total liver growth occurred from May to October in males, while all of the female liver growth occurred during that time.

Liver energy content in both sexes was positively correlated with age and body weight. There was no change in the relative liver energy (liver kcal per body kcal) of either sex with age or weight.

The spawning depletion

The causes of depletion were assessed by measuring energy content of tissues from pike captured during the spawning time. During late April, males were readily captured by gillnet, while relatively few females were taken. The results for females are therefore based on a small April sample (5 fish). Total liver energy decreased significantly in two-year-old males during both the prespawning (March to late April) and spawning (late April to May) periods (Table 3). A significant decrease in body energy occurred only in the prespawning phase. There was no change in testis energy content from March to late April.

Table 3. The caloric content (in kcal) of tissues from 2-year-old northern pike collected in early March, late April, and early May 1977 and 1978 from Lac Ste. Anne. The symbols listed under range test indicate each sample, and symbols underlined at the same level were not significantly different (P > 0.05, Student-Newman-Keuls test).

		March	late April	May	Range Test
Male	N	36	27	13	
	Body	1165 ± 22	999 ± 21	1037 ± 43	Mr Ap My
	Liver	45.3 ± 1.9	34.1 ± 1.9	15.2 ± 1.6	Mr Ap My
	Gonad	17.9 ± 0.9	17.3 ± 1.0	5.5 ± 0.6	Mr Ap My
	Somatic	1210 ± 23	1033 ± 22	1052 ± 44	Mr Ap My
Female	N	22	5	9	
	Body	1043 ± 25	959 ± 41	956 ± 23	Mr Ap My
	Liver	28.4 ± 1.2	17.8 ± 2.2	12.7 ± 1.6	Mr Ap My
	Gonad	268 ± 18.0	320 ± 17.1	6.4 ± 0.7	Mr Ap My
	Somatic	1071 ± 25	976 ± 43	969 ± 22	Mr Ap My

Two-year-old females experienced a significant decrease in total liver energy only in the prespawning period. Somatic energy showed a significant decreasing trend from March to May. Ovary energy content did not change significantly from March to late April.

As much as 68% of the total liver energy was used during spawning depletion in pike, which indicates that the liver is an energy depot. Somatic energy was only depleted by 13%, but this depletion contributed 4.6 times more energy than the liver losses, indicating that the body is the most important energy store in pike.

Total production

Gross annual production for individual northern pike from Lac Ste. Anne (Table 4) was calculated as the difference in energy content (either total or somatic) between May and the following March for each age class. This period did not include the April depletion time. Three-year-old males increased 352 kcal in total energy over this time. Thirty-four percent of this increase occurred in the winter when the water temperature was less than 2 C (Figure 3).

Three-year-old females accumulated 905 kcal of new tissue from May ~~to~~ March (2.6 times the male increase). Growth during the winter accounted for 35% of the total increase. Caloric growth in both seasons was more than twice as high in females as in males. A significant increase in somatic energy only occurred during the summer in females, while ovary growth occurred only in the winter. There was no concomitant depletion of somatic energy during ovary growth (October to March).

Somatic production (Table 4) was high during the first year of

Table 4. The total and somatic energy content (in kcal) for each age class of pike collected from Lac Ste. Anne in March and May. Production (Prod) = March mean − May mean, production efficiency (Eff) = production / initial energy content of fish. $\bar{x}$ ± 95% CL (N).

Age	Group	May (A)	March (B)	Prod (B-A)	Eff (B-A)/A
			MALES		
0	Somatic	0	554 ± 60 (22)	554	--
	Total	0	558 ± 63 (22)	558	--
1	Somatic	677 ± 81 (3)	926 ± 45 (18)	249	37%
	Total	681 ± 76 (3)	945 ± 47 (18)	264	39%
2	Somatic	814 ± 61 (22)	1210 ± 47 (36)	396	49%
	Total	818 ± 62 (22)	1228 ± 48 (36)	410	50%
3	Somatic	1052 ± 95 (13)	1387 ± 65 (23)	335	32%
	Total	1057 ± 96 (13)	1409 ± 67 (23)	352	33%
4	Somatic	1244 ± 42 (6)	1928 ±180 (5)	684	55%
	Total	1252 ± 43 (6)	1962 ±182 (5)	711	57%
			FEMALES		
0	Somatic	0	554 ± 61 (22)	554	--
	Total	0	558 ± 63 (22)	558	--
1	Somatic	677 ± 81 (3)	930 ± 83 (9)	253	37%
	Total	681 ± 76 (3)	1107 ±102 (9)	426	63%
2	Somatic	779 ± 70 (10)	1071 ± 52 (22)	292	37%
	Total	784 ± 71 (10)	1339 ± 80 (22)	555	71%
3	Somatic	969 ± 52 (9)	1444 ± 70 (31)	475	49%
	Total	975 ± 52 (9)	1880 ±106 (31)	905	93%
4	Somatic	1256 ± 53 (17)	1722 ± 94 (26)	466	37%
	Total	1267 ± 53 (17)	2176 ±121 (26)	909	72%

life, when virtually no energy was used in gonad growth. Total production was lowest in the second year, then increased for both sexes. Total annual production by females was 1.6 to 2.6 times the male level from ages 1 to 3 respectively. Male production was maximum at age 4, female at age 3 and 4. Total production and production efficiencies were always higher in females than males, whereas somatic production was similar in both sexes.

DISCUSSION

Significant total energy accumulation occurred in both sexes during winter and summer. In this study, about 35% of pike growth occurred in the winter at a temperature of approximately 1 C. While other studies have demonstrated energy accumulation over the summer, fish have generally been found to utilize energy stores for metabolism and gonad maturation during winter (Healey 1972, MacKinnon 1972, Craig 1977, Foltz and Norden 1977). Pike continue to feed during winter (Lawler 1965, Keast 1968), although their ration is only 5% of the summer level (see Chapter 3). The winter growth observed in this study is in contrast with the conclusions of Johnson (1966), who found that immature pike from Lake Windermere would not grow in captivity at winter temperatures. Yellow perch (*Perca flavescens*) in Lac Ste. Anne also grow over winter (Tanasichuk 1978). In northern areas like Lac Ste. Anne, where fish may spend half of their lives at winter temperatures near 1 C, adaptations to the seasonal cycle may have occurred to allow growth at this temperature.

The timing of growth in length for Lac Ste. Anne pike was similar to pike from two English rivers (Mann 1976). The mean lengths of age classes at the beginning of the growth year were intermediate when compared to a large number of pike populations (Toner and Lawler 1969). Since pike from Lac Ste. Anne show similar timing and magnitude of growth as other populat[illegible], their energy dynamics should also be similar. Therefore, one might expect that in other populations of pike significant male somatic and female gonad growth would occur in winter. To properly evaluate winter production, one must sample individuals in late winter before the spawning depletion.

Significant depletions of somatic energy stores occurred in both sexes during spawning. Pike fasted from mid-April to the termination of spawning activity (Frost 1954, see Chapter 3) which resulted in this depletion. Motor activity by pike may have also been higher at this time than during other periods of the year (Miller 1948, see Chapter 4). No gonad growth took place in either sex from March to May, yet significant depletion of somatic energy occurred. Therefore, this depletion was mainly due to spawning-related activities and fast, rather than to gonad growth.

Depletion of body energy occurred without any change in body calorific equivalents (kcal per gram). Since protein and fat have different calorific equivalents (Phillips 1972), depletion of body energy appears to occur by catabolism of whole tissue rather than catabolism of specific constituents which would alter the calorific equivalents. The liver showed significant changes in calorific equivalents during the year, which indicates that specific constituents are preferentially stored or utilized dur[illegible] various seasons. Similar results to these were found by Medford and Mackay (1978) in pike from Lac Ste. Anne, as well as in the controlled experiments described in this text (Chapter 2). However, Ince and Thorpe (1976) found that English pike preferentially utilized muscle fat and glycogen during 3 months of forced starvation. The inability of Ince and Thorpe to use entire fish for their composition analysis, the effect of 3 months starvation (much longer than in the present study), or a difference between the pike examined could explain the discrepancy between my results and theirs.

Gonad growth commenced in August for both sexes, and testicular growth was complete by September. Energy for testis growth may have come from endogenous stores in the liver, since both organs showed nearly the same magnitude of caloric changes during that time. These results are further strengthened by the work of Glass et al. (1977) who found that a specific fatty acid was produced by the liver of male pike during summer, and this fatty acid was depleted from the liver and accumulated in the testis of ripe fish. Ovarian growth continued until March, and the energy required for this must have resulted from food intake, since no depletion of somatic energy occurred during this time.

During their first year, pike produced tissue at an extremely rapid rate. With the onset of sexual maturation, somatic production reached a minimum in both sexes. However, older fish had high production efficiencies, and total production was still high at age 4. Only fish through age 4 were captured frequently enough to estimate production, which did not allow an age comparison over many years. However, my data show no decrease in somatic production with age, indicating that the pike were not becoming overwhelmed by reproductive requirements as they grew older.

Chapter 2. AN EXPERIMENTAL ANALYSIS OF THE METABOLIC RATE AND FOOD UTILIZATION OF NORTHERN PIKE

INTRODUCTION

Energy ingested by feeding is available for the production processes. However, not all ingested energy is used for growth. The energy required for assimilation, maintenance, activity, and specific dynamic action (SDA) must be removed first, then energy remaining from ingestion can be converted into body or gonad tissue. While growth and feeding can be determined from field analyses, maintenance must be estimated by controlled experiments, and active metabolism requires both lab and field evaluations to be accurately assessed.

The present study was undertaken to predict the maintenance requirements, assimilation efficiency, SDA, and conversion efficiency for northern pike from Lac Ste. Anne. Attempts were made to use a large size range of fish whenever possible. Experiments were conducted at 1 and 14 C, which are near the average temperatures for Lac Ste. Anne during winter and summer. The experiments were designed to give the best practical data for an overall energy budget estimated mainly from field analyses. Even limited results for some metabolic parameters should be better predictors than assumptions based on previous literature.

MATERIALS AND METHODS

Young-of-year (YOY) pike used in metabolic experiments were collected by seine. In 1976, the fish were collected from Sturgeon River, a tributary to Lac Ste. Anne (Figure 1). In 1977, high water levels prevented collection of pike from this area, so the fish were taken from Moose Lake, Alberta. Adult pike used in these experiments were collected by angling, gillnet, and seine from Lac Ste. Anne.

Metabolic experiments were of two types: measurements of oxygen consumption or ration. Both types of experiments were conducted at the Lac Ste. Anne Fish Research Laboratory. The fish were held in aquaria which were filled with lake water and kept under ambient light conditions and water temperatures during summer and winter. The tanks were flushed at least once a week, and aeration was provided to aid in ammonia removal from the water.

Conversion efficiency, maintenance ration (R_{maint}), and assimilation efficiency were determined by ration experiments with YOY pike (Table 5). In these experiments, the fish were kept individually in 16 L aquaria. Preweighed amounts of live perch, river shiners (<u>Notropis blennius</u>), or rainbow trout (<u>Salmo gairdneri</u>) were introduced into each aquarium at the appropriate feeding regime, and the aquaria were checked daily to determine when feeding occurred. For ad libitum feeding, three prey items were kept in each aquarium whenever possible. During the summer, any remaining prey items were removed at weekly intervals. The fish were then starved for 24 h, weighed, and new prey items were introduced into each aquarium. In winter, remaining prey items were changed weekly, but the fish were

Table 5. Physical description of ration experiments done in 1976 and 1977, including season conducted, temperature ($\bar{x} \pm SD$), number of fish used, feeding regime, and experimental duration.

Year	Season	Temperature	Number of fish	Experiment done	Experimental duration
1976	Summer	14.7 ± 0.02	6	Ad libitum ration	16 days
		14.7 ± 0.02	6	Maintenance ration	43 days
	Winter	3.1 ± 0.4	6	Maintenance ration	45 days
1977	Summer	14.2 ± 4.0	4	Ad libitum ration	30 days
		14.2 ± 4.0	4	Maintenance ration	30 days
		13.1 ± 1.6	3[a]	Starvation	30 days
	Winter	2.3 ± 0.7	3	Ad libitum ration	37 days
		2.3 ± 0.7	3	Maintenance ration	37 days
		2.0 ± 0.04	4[a]	Starvation	37 days

[a] Adult pike were used for these experiments, since YOY fish would not survive starvation for the required period.

only weighed at the beginning and end of each experiment. Feces were collected by siphon from the aquaria of fish at R_{maint} to determine assimilation efficiency.

All pike were killed on termination of each experiment. The pike, as well as samples of prey items and feces, were dried at 80 C and ground to powder in a coffee mill. The calorific equivalent of each item was determined with a Parr adiabatic calorimeter (see Appendix A). Mean equivalents were used to calculate total caloric growth (or loss) for each experimental animal, as well as the number of calories consumed and excreted. R_{maint} was calculated as kcal eaten per day, while the other parameters were computed as defined previously.

Metabolic rates were measured for YOY and adult pike by oxygen consumption experiments (Table 6), using closed vessel respirometry (see Appendix D). The oxygen consumption over a time interval was measured in mg oxygen consumed per day. This was then converted to calories per day using the factor of 3.20 cal per mg oxygen consumed (Brafield and Solomon 1972).

In 1977, YOY pike were used to analyze the type of product (fat or protein) deposited during growth and utilized during depletion. Three groups of fish were held under the following feeding regimes each season: 1) ad libitum, 2) R_{maint}, and 3) starvation. Control fish were killed and frozen immediately, while the experimental groups were kept under the appropriate conditions for one month, then killed. All fish were dried at 80 C, ground to powder, and used for chemical analysis.

The samples were analyzed for lipid levels using the method of

Table 6. Physical description of oxygen consumption experiments conducted from 1976 to 1978, including season, temperature ($\bar{x} \pm$ SD), age of fish, number of fish, and total number of measurements.

Year	Season	Experimental temperature	Type of fish	Number of fish	Number of Measurements
1976	Winter	0.8 ± 0.5	Adult	3	11
1977	Summer	14.2 ± 4.0	YOY	4	11
	Winter	2.3 ± 0.7	YOY	3	7
1978	Summer	17.5 ± 1.7	Adult	3	9
	Winter	1.5 ± 0.0	Adult	3	11
	Spawning	7.7 ± 0.7	Adult	4	12

Folch et al. (1957, [illegible] Appendix B), protein level by micro-kjeldahl (Steyermark 1961, s[illegible] Appendix C), and calories. Percent lipid, water, protein, and calorific equivalents for control fish were used to calculate the initial value for each parameter in the experimental fish, and the final values for each parameter were calculated directly.

RESULTS

The ration experiments were used to estimate R_{maint}, conversion efficiency, energy loss during starvation, and assimilation efficiency (Table 7). R_{maint} increased with an increase in pike weight, and data from experiments during each season were fitted to power curves. The slopes for both curves were significant ($P < 0.01$), and had similar weight exponents ($P > 0.05$). For a 50 g fish, summer R_{maint} would be 0.6 kcal/day, and the winter level would be 0.4 kcal/day (56% less).

Gross conversion efficiencies were similar at summer and winter temperatures. During winter, yield efficiency (K_3) was greater than 100% when corrected for R_{maint}. This indicates that winter R_{maint} estimates may be too large. An R_{maint} of about 2.6 cal/g/day would be required for equal yield conversion efficiencies summer and winter. Routine metabolic rate (R_{met}) was calculated for each fish (using the equation in Table 8) in winter conversion experiments, and was substituted for R_{maint} in calculation of yield efficiency in winter.

Daily weight loss during starvation was also higher in summer than winter. In winter, metabolic requirements during starvation were considerably lower than R_{maint}, again indicating that the winter R_{maint} values were too high. In summer, the metabolic requirements from starvation (8.20 kcal/kg/day) were similar to the values for R_{maint} of fish in the same size range (7.14 to 5.78 kcal/kg/day).

The assimilation efficiencies were similar for both seasons and for three different species of prey items.

Ration experiments were also analyzed to determine the composition

Table 7. Values for maintenance ration, gross conversion ($\bar{x} \pm SD$), net conversion, yield conversion, starvation energetics, and assimilation efficiency of northern pike determined by ration experiments during the summer and winter, as outlined in Table 5. W = somatic weight.

Parameter	Summer value	Winter value
Maintenance ration	$R_{maint} = 55.3\ W^{0.62}$	$R_{maint} = 16.2\ W^{0.82}$
(cal/day)	($r^2 = 0.9$, n = 11)	($r^2 = 0.9$, n = 6)
Gross conversion	0.277 ± 0.056	0.246
	(n = 5)	(n = 2)
Net conversion	0.319 ± 0.064	0.283
Yield conversion	0.513 ± 0.101	0.353
Starvation losses	8.20 ± 2.7	2.29 ± 1.43
(cal/g/day)	(n=3, W=217-380)	(n=4, W=563-1465)
Assimilation	0.872 ± 0.060	0.869 ± 0.052
	(n = 9)	(n = 11)

of energy stores used during starvation and accumulated during growth (Figure 6). There was no significant change in total body fat, protein, or calories at R_{maint} in summer or winter. At ad libitum, both total protein and calories increased significantly in both seasons. During starvation, both protein and calories decreased significantly. Total lipid did not show consistent trends, and significant changes in lipid content did not occur in any season or experiment.

Oxygen consumption experiments were used to estimate R_{met} as well as specific dynamic action (Table 8). In these experiments, YOY and adult pike were used. There were no significant differences between R_{met} for male and [illegible]ale pike at any time except during the spawning period (describ[illegible]r). R_{met} and body weight were fitted to power curves for data [illegible] fish during each season. The weight exponents for both seasons were not significantly different ($P > 0.05$). Estimating R_{met} and R_{maint} for similar size fish (50 g), the summer values (13.60 kcal/kg/day R_{met}, 12.51 kcal/kg/day R_{maint}, 9% difference) were similar. R_{met} and starvation losses for similar size fish (330 g) were also similar (9.85 and 8.20 kcal/kg/day respectively).

Winter estimates of maintenance requirements for similar size fish (50 g) were considerably different (8.01 kcal/kg/day R_{maint}, 1.37 kcal/kg/day R_{met}, 485% difference). This again indicates the excessively high value for winter R_{maint}. However, R_{met} data compared well with the value predicted for similar summer and winter yield efficiencies (2.60 kcal/kg/day), as well as with the starvation losses in winter (2.29 kcal/kg/day).

The metabolic rate of pike during spawning differed significantly

Figure 4. Changes in the body composition of pike kept under experimental regimes of maintenance (M, scale x 0.1), ad libitum (AL, scale x 1) and starvation (S, scale x 10) during summer and winter. Lipid (clear bars) and protein (stippled bars) were measured in g, calories (striped bars) in kcal. The data were analyzed by a paired T test for changes between initial and final levels, * = $P < 0.05$, ** = $P < 0.01$.

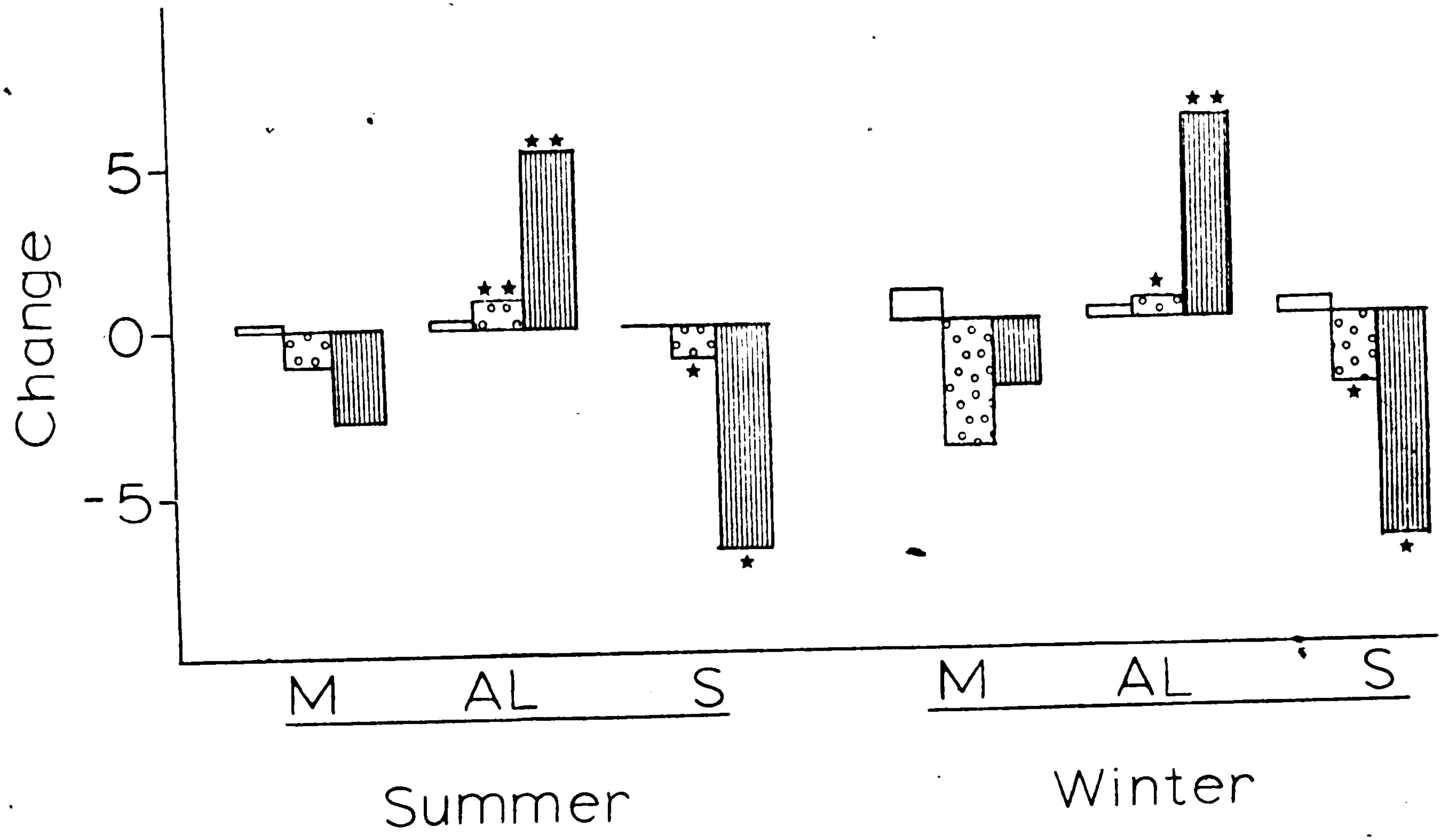
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Table 8. Values for R_{met} and SDA measured during oxygen consumption experiments on northern pike during summer and winter. Metabolic rates = $\bar{x} \pm$ SD, elevation of rate = SDA - R_{met}, metabolic rate during spawning = rate at 8 C in late April 1978, W = somatic weight.

Parameter	Summer value	Winter value
R_{met} (cal/day)	$R_{met} = 27.5\ W^{0.82}$ ($n=17$, $r^2=0.99$, $W=5\text{-}1200$ g)	$R_{met} = 1.6\ W^{0.97}$ ($n=21$, $r^2=0.96$, $W=29\text{-}1901$)
Spawning rate		
female	2.07 ± 0.58 ($n = 5$, $W = 1170\text{-}1606$)	
male	3.70 ± 1.19 ($n = 6$, $W = 870\text{-}1050$)	
SDA		
met. rate during digestion	26.76 ± 3.03	4.03 ± 0.79
(cal/g/day)	($n=28$, $W=5\text{-}11$ g)	($n=26$, $W=29\text{-}35$ g)
duration	42 hours	9 days
elevation of met. rate (cal/g/day)	6.63 (33%)	2.25 (126%)

between sex of fish ($P < 0.05$). The female level (2.07 kcal/kg/day) was lower than the level predicted by Q_{10} calculations for 8 C (3.36 kcal/kg/day), while the male level was higher than predicted (3.70 kcal/kg/day).

DISCUSSION

Maintenance requirements were estimated by ration and oxygen consumption experiments. Studies on fish metabolism (Fry 1957, Niimi and Beamish 1974) usually indicate significant differences for maintenance values estimated by R_{met}, R_{maint}, and starvation. For pike, R_{maint} was the most difficult to measure, because more variables were added to the experiment (SDA, feeding activity, weighing the fish and prey, proper adjustment of the feeding regime) and because only small pike would feed in the lab. Under most conditions, starvation losses underestimate maintenance requirements (Brown 1957, Niimi and Beamish 1974) because starved fish are able to reduce their activity and metabolic rate. Starvation losses and R_{met} were similar for pike in this study. Starving pike did not appear to reduce their metabolic rate, indicating that routine activity during R_{met} experiments was minimal. Ince and Thorpe (1976) found that starving pike did not decrease their rate of weight loss during 1 or 3 months starvation, also indicating that the fish were unable to reduce their metabolic rate in response to starvation.

The relationship between R_{met} and body weight during summer and winter was mathematically described by a power curve, and the weight exponents for both seasons were similar, which has also been found in previous investigations (Fry 1957, Wallace 1973). The exponents agree well with the literature on fish metabolism and weight (Fry 1957), since most fish studied have shown exponents from 0.8 to 1.0. Because of this agreement, as well as the large size range of pike used in R_{met} determinations, the maintenance requirements estimated by R_{met}

will be used in future calculations of energy budgets in this text.

In estimating standard metabolic rate (which is generally used to calculate maintenance requirements), fish activity must be taken into account (Fry 1957, Brett 1964), while R_{met} values normally include a low and immeasurable level of spontaneous activity. Pike are extremely inactive under experimental conditions, so R_{met} and S_{met} are probably similar. Minimal levels of routine activity were also indicated in the comparison between starvation losses and R_{met}. Dolinin (1973) measured S_{met} in adult pike whose movement was restricted, and his values (5.4 kcal/kg/day at 15 C, 1.5 kcal/kg/day at 5 C) are fairly similar to my results. It is difficult to directly compare our results, since he did not indicate the size of fish used. However, my data for pike from 1 to 2 kg would indicate an R_{met} of 7.9 to 7.0 kcal/kg/day at 15 C, 1.3 kcal/kg/day at 2 C, both of which are similar to Dolinin's results.

Many fish show diurnal changes in oxygen consumption (Dolinin 1973, Pierce and Wissing 1974, Brett and Zala 1975). It took me 5 to 24 hours to complete an oxygen consumption experiment, so diurnal changes in R_{met} could not be assessed and my values are assumed to be average daily rates. Conversion of metabolic rate from mg oxygen consumed to calories used assumes that pike utilized protein in respiration (Brafield and Solomon 1972). Since depletion of pike tissue resulted from protein catabolism, this assumption was probably not violated.

Summer R_{maint} values agreed well with the results from R_{met} experiments, but winter values did not. SDA caused an increase of 33 to 126% in metabolic rate after feeding during summer and winter respectively. Assimilation efficiency also increased R_{maint} estimates over R_{met} values, but the effect was small (13%) and similar for both seasons. The SDA effects were especially pronounced in winter, and must have caused at least part of the large R_{maint} discrepancy. The effects of SDA on metabolic rate have been examined by Pierce and Wissing (1974), Schalles and Wissing (1976), Tyler and Dunn (1976), and Weatherley (1976); and their results are comparable to mine. If I correct winter R_{maint} of a 50 g fish for SDA and assimilation effects, the resultant value (5.23 kcal/kg/day) still varies considerably from R_{met} (1.37 kcal/kg/day), indicating that other errors must also be present. Johnson (1966) measured R_{maint} for YOY pike at various temperatures, and found little change in R_{maint} between late summer at 16 C and winter at 2 C. His values for R_{maint} varied with time of year rather than temperature, and his summer (4.9 g/kg/day) and winter (3.1 g/kg/day) values varied considerably from my results for the same size fish (64 g fish, summer = 11.4, winter = 7.7 kcal/kg/day). This lack of agreement again indicates the amount of error inherent in ration experiments with pike.

SDA was shown to have a considerable influence on the metabolic rate of pike, and this factor should be included in an energy budget. SDA would affect maintenance ration experiments, but is not included in R_{met} values which will be used to estimate maintenance requirements for the overall budget. SDA could therefore be included as a part of growth efficiency, or considered separately. Since no growth efficiency calculations remove SDA effects, it is usually included as a part of the overall efficiency. I will attempt to evaluate SDA effects on the energy budget in Chapter 5.

Johnson (1966) found the net conversion efficiency (K_2, in grams) for pike was 0.437, while Gammon (1963) found that the gross conversion efficiency (K_1, in grams) for muskellunge (Esox masquinongy) was 0.37. These results are similar to mine. Since few winter measurements of conversion efficiency were successful, my summer values will be used in all calculations.

During the spawning period, male pike had a higher R_{met} than did females. Increases in sporadic activity were not observed during the experiments, but may have occurred. Also, hormone levels may have affected the metabolic rate differently for the two sexes. Moore and Potter (1976) found that male lampreys (Lampetra fluviatilis and L. planeri) also had higher metabolic rates than females during spawning. Since the female metabolic rate was lower and possibly unaltered by spawning, that value will be used for R_{met} in October for the calculation of the overall budget. The measured levels for each sex will be used as R_{met} during spawning (April, see Chapter 5).

In the ration experiments, pike growth occurred by significant protein accumulation, and depletion utilized protein for the energy source. Similar results were predicted from population growth (see Chapter 1). Accumulation and depletion of lipid may have also occurred, but the lipid levels were small (less than 10% dry weight) and slight errors in measurement could obscure any changes. These results conflict with Ince and Thorpe (1976), and this conflict is dealt with in Chapter 1. Dave et al. (1975) considered that eel (Anguilla anguilla) depletion was due to whole muscle catabolism, but Larsson and Lewander (1973) considered that liver fat was also an important energy source in starving eels. The great importance of the body as an energy store in pike (see Chapter 1), combined with the present data, indicate that energy requirements during starvation come mainly from catabolism of whole muscle tissue or muscle protein, and the liver plays but a minor role in the starvation energetics.

Chapter 3. THE FEEDING PATTERN AND DAILY RATION OF NORTHERN PIKE IN LAC STE. ANNE

INTRODUCTION

Studies on the feeding of natural fish populations have followed three main lines: 1) analysis of the frequency of prey species found in the stomachs of a sample of fish, 2) determination of the weight or volume of food found in the stomach samples, and 3) calculation of a daily ration, based on weight of food in the stomach and on rate of digestion. The latter analysis is most useful in understanding growth cycles, while the former two aid in the study of predation and food chains.

Several studies have attempted to quantify the daily ration of fish (Bajkov 1935, Darnell and Meierotto 1962, Popova 1966, Keast and Welsh 1968, Swenson and Smith 1973, Thorpe 1977, Doble and Eggers 1978, Nakashima and Leggett 1978). However, the techniques used often assume that the fish feed over long time periods relative to digestion. While this assumption may be approximated by many fish populations, it is not valid for most top carnivores, which often eat a meal consisting of one item, and the feeding interval is very short relative to total digestion time.

The purpose of this study was to determine the daily ration of pike from Lac Ste. Anne and to assess seasonal changes in feeding. Since the assumptions of published feeding models were not valid for pike, the data collected in this study were used to develop a model of top carnivore feeding. The contribution of various prey items to the pike diet was analyzed to allow a better understanding of the feeding process.

MATERIALS AND METHODS

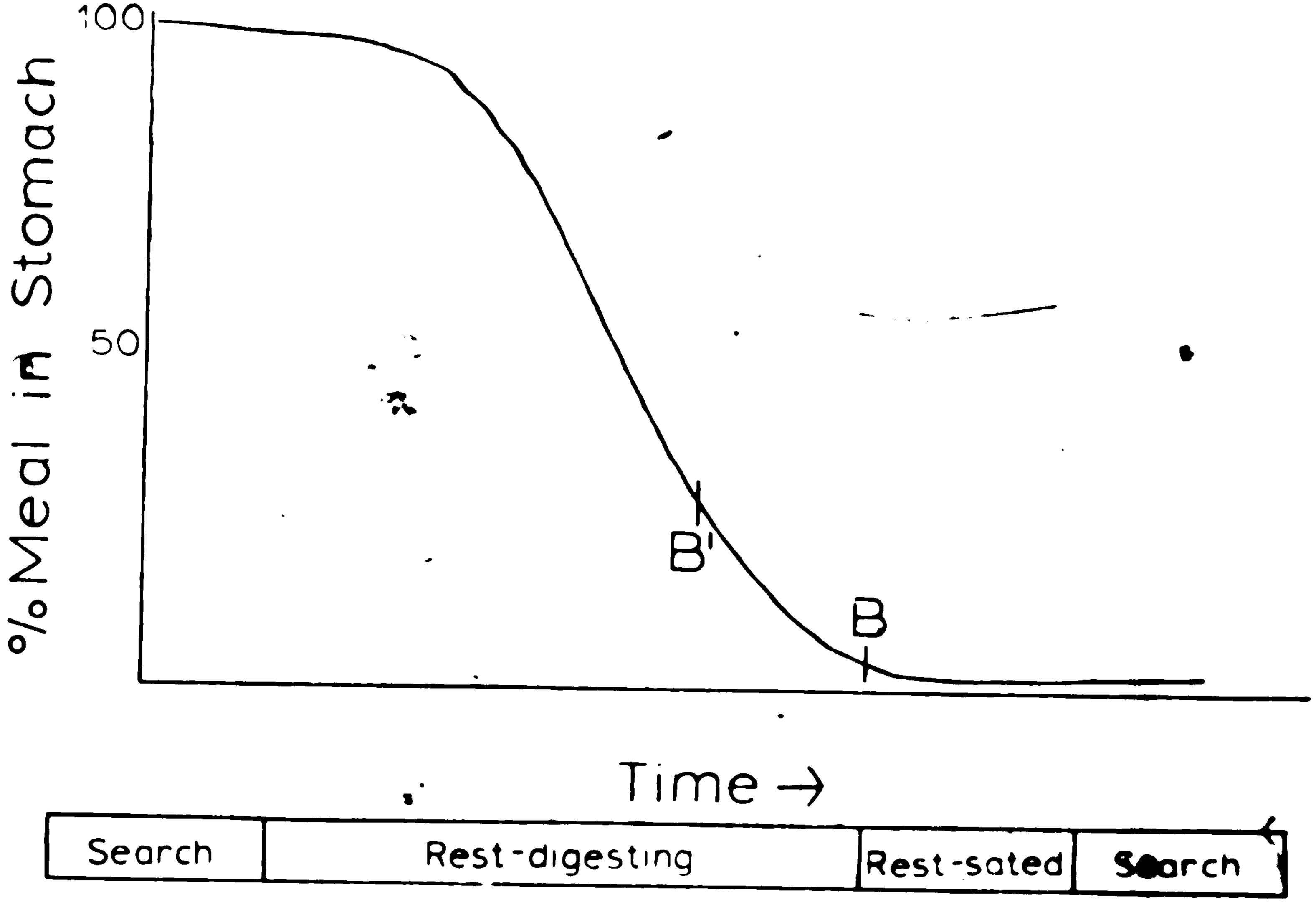
Theoretical considerations

There are two main variables which must be measured to calculate ration; meal frequency and meal size. One can visualize animals occupying two extremes for these parameters, one animal which feeds continually and digests while feeding (Type 1), the other which eats a meal quickly then digests the food before feeding again (Type 2). Herbivores, detritivores, and other animals from lower trophic levels would approximate Type 1, while one would expect top carnivores to be more similar to Type 2.

The feeding sequence of an individual top carnivore is graphically depicted in Figure 5. The behavioral events underlying feeding are not easily measured, while the expression of their stomach contents can be quantified. A meal is ingested over a short time period, digestion and rest occur over a prolonged time relative to feeding and then the next meal is ingested. Variations in the time interval between successive meals are dependent on both appetite and prey availability, which affect search and rest times. If a population has a synchronous feeding pattern (for example, every animal feeds each evening), then in a single sample tne stomach contents of all animals would be at a similar point on Figure 5. However, if the feeding pattern is asynchronous (animals feed at any time), then any sample of predators would have some animals representing each portion of Figure 5 (including some with empty stomachs).

For piscivores, the ingested weight (or calories) of prey items

Figure 5. A model of top carnivore feeding. The lower axis represents the behavioral events associated with feeding, while the upper graph represents the observed stomach contents at various portions of the feeding period. The actual feeding time would be 1 or more points in the search portion. B and B' = gastric evacuation times.



Feeding Behavior

removed from the stomach can be back calculated by measuring the length of each item, then fitting it into a length-weight ratio for that species. If the item had undergone considerable digestion before being removed from the stomach, the length could not be measured but the age could (by scales or by size). The ingested weight could then be estimated from the mean size of the age classes of the prey species at that time of year. Finally, digestion would occur to a point where the age could not be determined either (B' in Figure 5), and the ingested weight of that item could not be estimated.

Gastric evacuation rates can be determined by lab experiments (Windell 1966, Swenson and Smith 1973) or by field analyses (Darnell and Meierotto 1962, Keast and Welsh 1968, Steigenberger and Larkin 1974), and these can be used to establish the time scale for Figure 5. For proper analysis, one should not only measure the gastric evacuation time (B on Figure 5), but also the time until the ingested weight of prey items can no longer be determined (B'). With a knowledge of meal size and digestion times, one can then calculate the daily ration for the animal in question.

A sample of pike collected at any time (total number = N) consists of a number of fish with food in their stomachs (S) and a number with empty stomachs (N-S), indicating that the feeding is asynchronous and that time between meals is longer than digestion time. Average meal size ($\overline{M}$, in g or kcal/kg) can be calculated for a sample of pike from the estimated weight of prey ingested by each pike with food in the stomach. Meal frequency (F) can be estimated from the proportion of empty stomachs in the sample and the gastric evacuation time. For this analysis, the time B' should be used for gastric evacuation, and fish with stomach contents digested beyond recognition should be considered to have empty stomachs, since the ingested weight can not be determined. For this analysis, the ratio S/B' equals N/F, and F can be calculated as

$$F = \frac{B \text{[illegible]} x\ N}{S/ \text{[illegible]} S}$$

Daily ration equals meal size / meal frequency, or

$$R = \frac{\overline{M}}{(B' \times N)/S} = \frac{\overline{M} \times S}{B' \times N}$$

Data collection

Northern pike were collected by gillnet from Lac Ste. Anne on 26 occasions between March 1976 and September 1978. From March to September 1976, monofilament gillnets were used with five 15 x 1.8 m sections of 1.9, 2.5, 3.8, 5.1, and 6.4 cm stretched mesh. During the remainder of the study, 91 x 1.8 m multifilament nets were used with 6.4 cm stretched mesh. Gillnets were lifted after 3 hours in summer and usually after 1 day in winter. Collected fish were processed as described in Chapter 1. The digestive tract (esophagus to rectum) was removed from the fish. Stomach contents were identified to species, and each item was measured in length (when possible) or estimated in age (when significant digestion had occurred). Stomach and intestine contents were then put into preweighed containers, dried to constant weight at 80 C, and weighed to 0.1 g.

Prey items were collected by seine, gillnet, and trawl during the study. Length-weight ratios (Table 9) and monthly values for mean weight of the age classes for each species (Appendix Table 3) were determined. Whole fish samples for each species were dried at

Table 9. The standard length (SL)-weight (W, in g) relationship, proportion of dry matter in the body, and body calorific equivalent (kcal/g dry weight) for various species of fish collected from 1976 to 1978 in Lac Ste. Anne.

Prey species	Length-weight	Dry matter content	Calorific equivalent
Perch	$W = 0.00000837\ SL^{3.15}$[a]	0.237	4.5
Spottail shiner	$W = 0.0000569\ SL^{2.67}$[a]	0.303	5.1
Burbot	$W = 0.0643\ SL^{3.12}$[b]	0.199	4.9
Sucker	$W = 0.00000346\ SL^{3.34}$[a]	0.268	4.7
Walleye	$W = 0.0336\ SL^{2.74}$[b]	0.251	4.7
Whitefish	not determined	0.223	4.7

[a] Standard length in mm.

[b] Standard length in cm.

80 C and ground in a coffee mill. Calorific equivalents (kcal per dry gram) were determined for these samples with a Parr adiabatic calorimeter.

Preliminary experiments were done to estimate gastric evacuation time of pike at 2 and 16 C. After this, adult pike were starved to allow gastric clearance (2 days at 16 C, 2 weeks at 2 C), then force-fed 2 year old perch. Six fish were used at each temperature, sacrificed at intervals of 1/6 the estimated digestion time, and the weight loss of the stomach contents was determined. The digested perch were preserved for use as stage of digestion standards (Darnell and Meierotto 1962) to estimate the time of consumption for various prey items taken from the stomachs of field caught pike.

In the summer of 1976 and winter of 1977, the stomach contents of captured pike containing 2 to 5 items were compared to the perch stage of digestion standards to estimate the time since each item had been ingested. Each item in a stomach was assigned a stage of digestion value from 1 to 6. The duration of feeding activity for each pike was assessed by comparing the difference between stage of digestion values for the first and last ingested item in each stomach. The values for all analyzed pike were pooled by season to calculate the average duration of feeding activity during consumption of multiple item meals.

RESULTS

The numerical importance of prey items to pike diets (Table 10) varied with month and season. Data from all years were similar, and were pooled by month to give overall values. Yellow perch were the most common item eaten throughout the year, followed by spottail shiners (<u>Notropis</u> <u>hudsonius</u>), burbot (<u>Lota</u> <u>lota</u>), white suckers (<u>Catostomus</u> <u>commersoni</u>), whitefish (<u>Coregonus</u> <u>clupeaformis</u>), and walleye (<u>Stizostedion</u> <u>vitreum</u>). Invertebrates and pike were rarely eaten. Empty stomachs were very common, occurring in 29 to 62% of the fish sampled each month. The mean number of items in the stomachs of pike (excluding fish with empty stomachs) was approximately 2 during every month except October, when pike consumed large numbers of young-of-year perch.

When the caloric contributions of prey species to pike diet were considered (Table 11), perch were still predominant, but their relative contribution was reduced to half the total intake. Suckers and burbot increased in importance, due to the relatively large size of individuals eaten, while the smaller shiners decreased in importance.

Digestive rates followed the curve outlined in Figure 5, and the gastric evacuation time (B) was 48 hours in summer, 12 days in winter. The value for B' was 8 days in winter, and 30 hours (1.25 days) in summer. The perch stage of digestion standards had been digested for consecutive intervals of 8 and 48 hours in summer and winter.

The relative duration of feeding can be evaluated by examining

Table 10. The number and percent of the total (in parentheses) of various prey items found in the stomachs of pike collected from 1976 to 1978 in Lac Ste. Anne. The number of fish sampled is listed below each month. The proportion of empty stomachs is based on all pike collected, and the number of prey per stomach is based only on pike with food in the stomach.

Prey species	May 178	June 249	July 124	August 214	Sept. 119	Oct. 127	Jan. 90	March 189	Total 1290
Perch	132(86)	121(33)	41(66)	99(85)	62(79)	369(87)	40(65)	106(77)	970(69)
Spot. shiner	15(10)	226(62)	3 (5)	9 (8)	4 (5)	44(10)	7(11)	14(10)	322(24)
Burbot	5 (3)	8 (2)	7(11)	4 (3)	9(12)	9 (2)	12(19)	17(12)	71 (5)
Sucker	1 (1)	10 (3)	8(13)	3 (2)	3 (4)	1 (1)	3 (5)	0	29 (2)
Whitefish	0	0	2 (3)	1 (1)	0	0	0	0	3 (0)
Walleye	0	1 (0)	1 (2)	0	0	0	0	0	2 (0)
Pike	0	0	0	1 (1)	0	0	0	0	1 (0)
Unident. fish	11	14	6	27	8	8	2	24	-
Invertebrates	0	13	0	2	0	0	0	0	-
Empty	87(49)	99(40)	72(58)	106(50)	65(55)	37(29)	56(62)	89(47)	611(47)
Fish/stomach	1.73	2.66	1.31	1.49	1.91	5.24	1.79	1.60	2.32

Table 11.—Estimated caloric content of each prey species at the time of ingestion by [illegible] collected from Lac Ste. Anne from 1976 to 1978. Total (in kcal) and percent of the monthl[illegible]tal (in parentheses).

Species	May	June	July	August	Sept.	Oct.	Jan.	March	Total
Pe[illegible]	1176(85)	1825(47)	585(31)	639(53)	397(44)	961(81)	300(54)	403(74)	6286(54)
Shiner	30 (2)	650(17)	8 (0)	0	16 (2)	62 (5)	23 (4)	40 (7)	829 (7)
Burbot	34 (2)	370(10)	325(17)	119(10)	199(22)	85 (7)	82(15)	99(18)	1313(11)
Sucker	149(11)	939(24)	670(35)	310(26)	293(32)	82 (7)	149(27)	0	2592(22)
Walleye	0	0	312(16)	54 (4)	0	0	0	0	366 (3)
Whitefish	0	70 (2)	0	70 (6)	0	0	0	0	140 (1)
Pike	0	0	0	23 (2)	0	0	0	0	23 (0)
Total	1389	3854	1900	1215	905	1190	554	542	11549

the frequency of sampled pike containing various numbers of prey items in their stoma[illegible] (Figure 6). The most common meal consisted of 1 item, and all pike with 1 item in their stomach must have consumed that meal in a very short time. In the summer of 1976, 28 pike were captured with 2 to 5 prey items in their stomachs. The maximum time difference between the first and last ingested item was 3 stage of digestion units, and the average difference was 0.9 ± 0.2 units ($\bar{x}$ ± SE). In the winter of 1977, 5 pike were captured with 2 to 5 items in their stomachs. The maximum difference between the first and last ingested item was 2 stage of digestion units, and the average difference was 0.5 units. Considering that there are 6 units in the total gastric evacuation time, the feeding duration for pike consuming 2 to 5 items was much less than the total digestion time in both seasons. It was not feasible to estimate the time of consumption for each item in meals containing 6 or more items. However, pike with meals of this size constituted less than 10% of all pike with food in their stomachs.

Since growth of pike in Lac Ste. Anne was similar from year to year (and ration should also be similar), data from each year were pooled by month and the daily ration (Table 12) was calculated for each sex. Pike captured in small mesh gillnets had considerably higher proportions of empty stomachs than ones captured in larger mesh nets, although their size range was similar. Small mesh nets also captured prey items, which may have attracted hungry pike (with empty stomachs) into the nets. All data from pike captured in small mesh nets were excluded from daily ration analysis.

Female pike had higher rations than males nearly every month, igure 6. The frequency of various numbers of prey items in the stomachs of pike collected from 1976 to 1978. The percentage of fish included in each category is listed at the top of each bar.

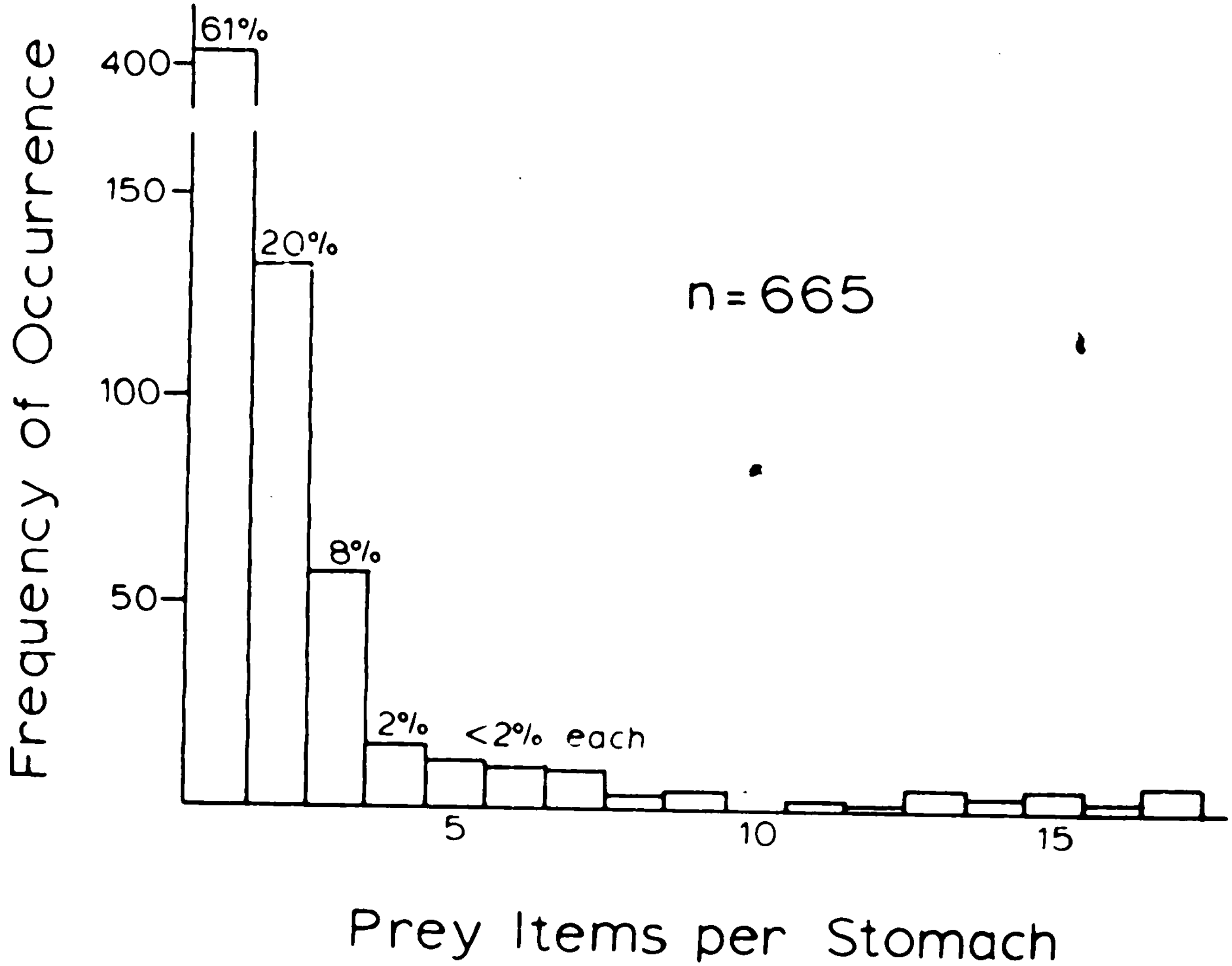

n=665
Frequency of Occurrence
400
150
100
50
61%
20%
8%
2%
<2% each
5
10
15
Prey Items per Stomach

Table 12. The daily ration of northern pike for various time periods sampled during 1976 to 1978 in Lac Ste. Anne. Meal size = kcal/kg, ration = kcal/kg/day, time = days.

Time period	Sex	Meal size	Time between meals	Daily ration
May	Male	30.4	3.1	9.6
	Female	32.4	2.3	14.0
June	Male	35.0	1.9	18.1
	Female	66.5	2.2	30.9
July	Male	36.5	2.1	11.5
	Female	54.1	2.8	19.2
August	Male	23.1	3.8	6.0
	Female	25.4	2.6	9.8
September	Male	22.5	3.5	6.4
	Female	31.4	4.2	7.5
October	Male	17.4	2.2	7.9
	Female	16.5	1.9	8.6
January	Male	9.8	34	0.3
	Female	22.0	23	1.0
March	Male	10.9	22	0.5
	Female	21.6	26	0.8
April	Male	14.9	59	0.3
	Female	14.8	59	0.3
Winter	Male	10.6	25	0.4
	Female	21.8	25	0.9
Summer	Male	30.8	2.8	11.4
	Female	47.0	2.7	17.4

and the mean female ration was 1.5 (summer) to 2.3 (winter) times the male ration. Higher female rations were due to larger meals, and average feeding frequencies for each sex were similar both seasons. Stomach contents (dry weight as a percent of body weight) of females were significantly greater than those of males (Mann-Whitney U Test, $P < 0.001$). While the number and length of prey eaten by females were also greater than the male values, these differences were not statistically significant. Maximum rations were ingested in June, high values were common from May to July, and rations were very low in winter. Rations of both sexes were approximately 0 from mid-April to May, indicating the presence of a spawning fast. Mean daily rations were approximately 20 times higher in summer than winter for both sexes.

The annual accumulation of energy was assessed for 3-year-old pike for one year beginning in May (Figure 7). Monthly ration was calculated by multiplying values for daily ration for each sex by the mean size of 3-year-old pike each month (Appendix Table 6) and by the total number of days in each month. About 65% of the total annual ration was ingested from May 1 to August 1. Total ingestion by females was also much higher than ingestion by males.

The daily ration values for 3-year-old pike during each summer month were compared to daily maintenance costs and observed growth rates to assess the relative agreement between ingestion and growth (Figure 8). Female rations were in excess of maintenance requirements and observed growth rates from May through August, but were lower than required in September and October. Male rations were equal to or in excess of maintenance and growth in all summer months

Figure 7. The total energy accumulated by 3-year-old male and female pike for one year beginning in May.

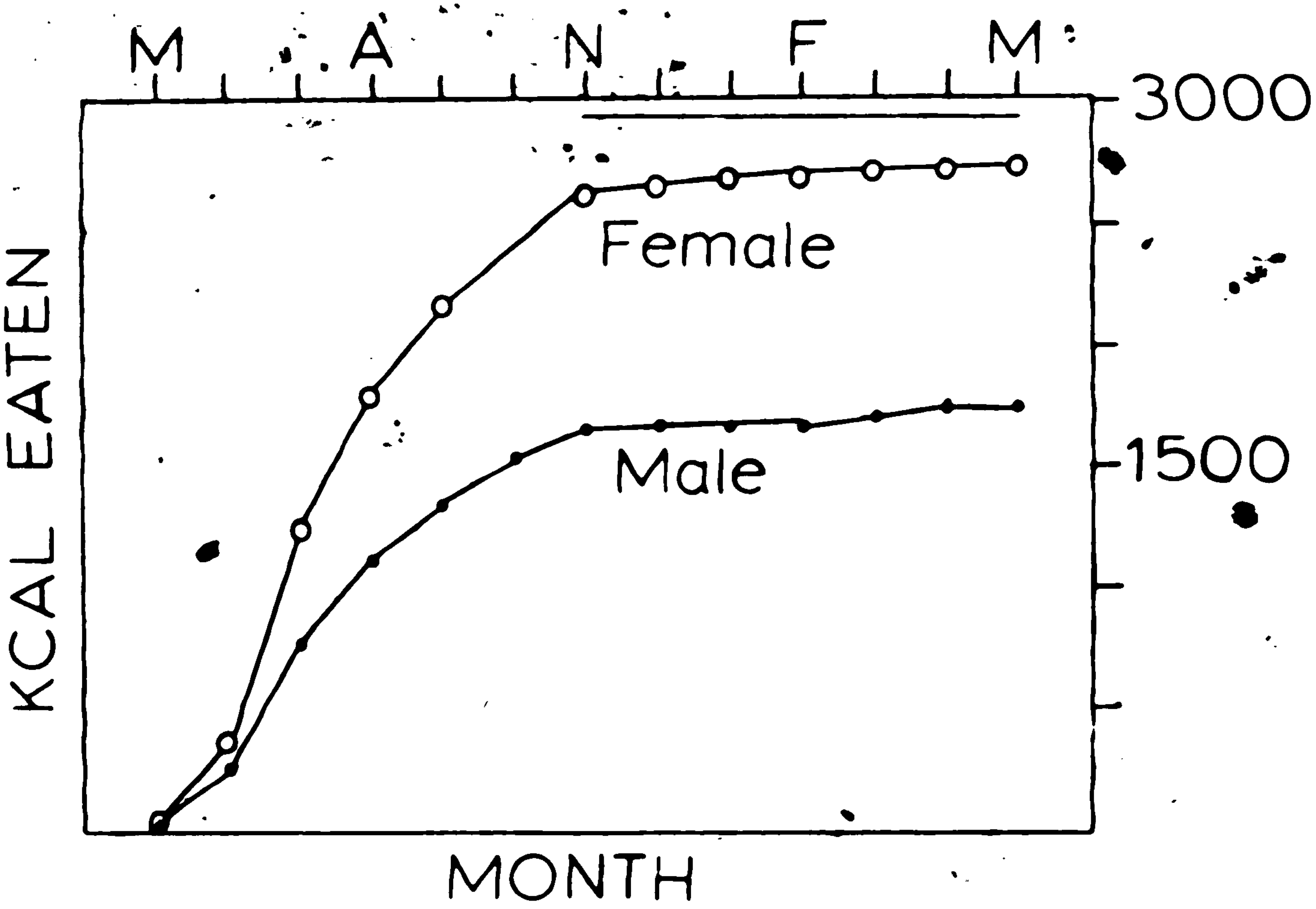
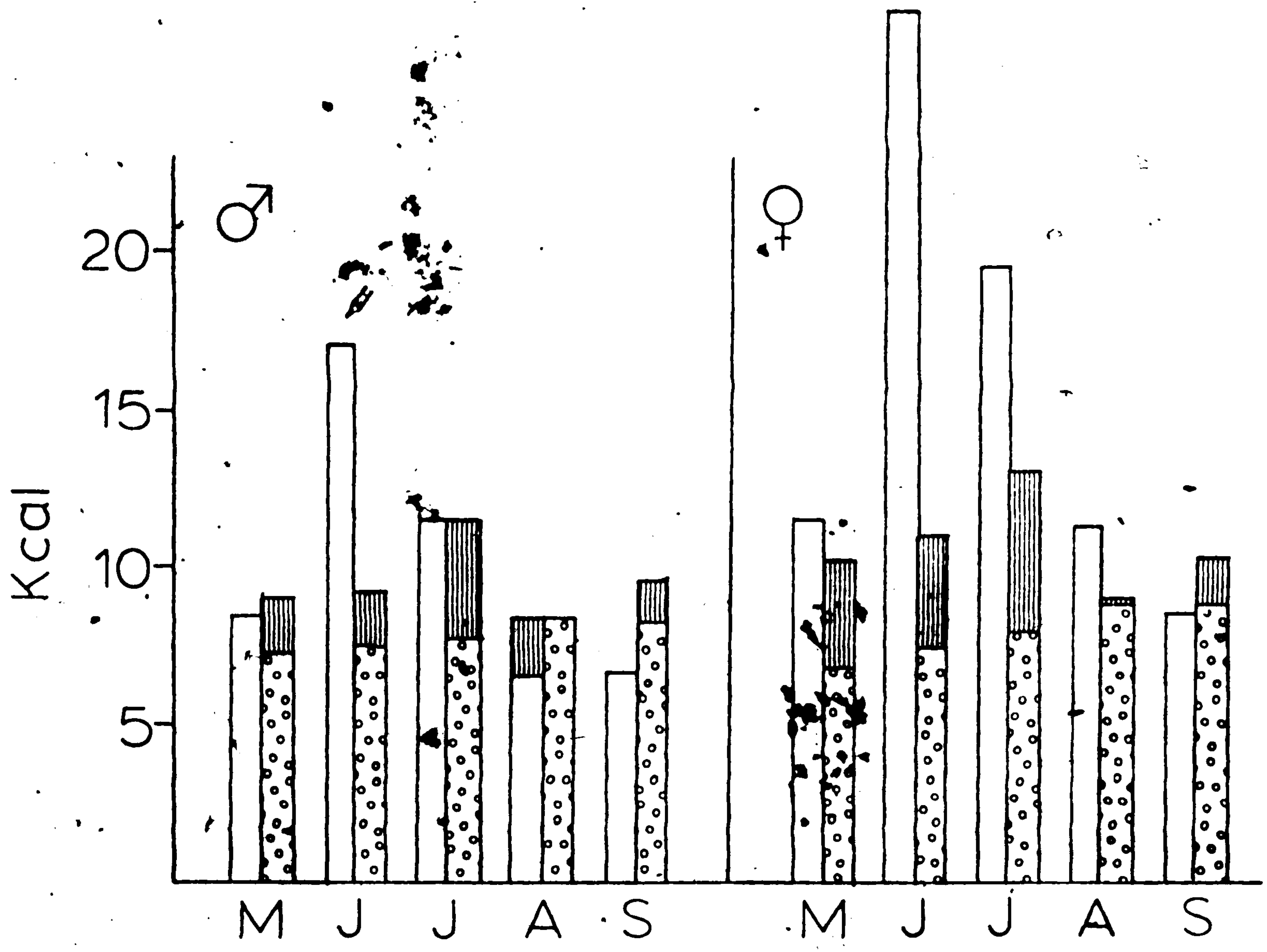

M
A
N
F
M
3000
1500
KCAL EATEN
Female
Male
MONTH

Figure 8. Comparison between observed ration (clear bars), maintenance requirements (stippled bars), and daily growth rate (striped bars) during the summer for male and female 3-year-old pike. When growth rate is coupled with ration, this indicates that weight loss occurred during that time, which contributed to maintenance needs.


♂
♀
Kcal
20
15
10
5
M
J
J
A
S
M
J
J
A
S

except October. Winter comparisons could not be made, due to the limited growth data in winter, which could only assess growth rates over long periods.

The accuracy of ration determinations was also assessed by measuring the ration for samples of fish captured on three consecutive days in June 1978. Male ration values were 9.6 and 8.4 kcal/kg/day (based on 10 and 19 animals), while the female values were 11.1, 12.0, and 12.7 kcal/kg/day (based on 12, 25, and 24 animals). Using the present method, ration calculations appear to be reproducible with little variance between similar samples, and are also sufficient to allow the summer observed growth to occur.

During the summer of 1976, attempts were made to analyze diurnal changes in pike feeding by sampling fish every four hours over one 24 hour period each month. There were no significant changes in weight of stomach contents during any portion of the day (Appendix Table 4).

There was a significant positive correlation ($P < 0.001$) between length of prey eaten and length or weight of pike. However, the predictive value of the correlation ($r^2 = 0.07$) was weak, indicating that the pike consumed a large size range of prey items. There was a significant correlation ($P < 0.01$) between dry weight of stomach and intestine contents and weight of pike, but there was none between these values as a percent of body weight and the weight of pike, indicating that rations should be calculated in kcal per kg body weight.

DISCUSSION

The daily ration for pike was maximum in June and high from May to August. About 65% of the annual energy accumulation occurred in early summer (May 1 to July 31). Other studies on pike feeding (Frost 1954, Seaburg and Moyle 1964, Ivanova 1969) have predicted these findings in various ways, but none have measured them directly. Pike from Lac Ste. Anne exhibited a spawning fast, which resulted in a depletion of body reserves (Chapter 1). The maximum rate of feeding occurred immediately after this depletion, and high rations continued through the major period of body growth (May to August). Winter rations were extremely low, and winter metabolism must be very low to allow growth to occur (as indicated in Chapter 1). Female rations were greater [illegible] male levels during summer and winter.

Perch were predominant in pike diet in the present study, and also in a number of other studies where the diversity of available prey species and habitats differed considerably from Lac Ste. Anne (Allen 1939, Frost 1954, Healy 1956, Seaburg and Moyle 1964, Lawler 1965). Empty stomachs were also common for pike in all of these studies.

The present model of feeding is similar to that described by Swenson and Smith (1973) for walleye. However, they did not include fish with empty stomachs in their consumption calculations, even though 10 to 30% of the fish sampled had empty stomachs (Swenson and Smith 1976). Except for this oversight, they presented an excellent analysis of feeding by walleye, and their techniques are especially applicable to animals that may eat more than 1 meal per day. In the present model, fish with empty stomachs are considered as part of the normal feeding population, and not as sampling errors. This is mainly due to the fact that empty stomachs were so common in all samples. Samples of many other top aquatic carnivores have also been shown to contain high proportions of fish with empty stomachs, including bass (Micropterus salmoides, by Seaburg and Moyle 1964), sauger (Stizostedion canadense, by Swenson and Smith 1976), squawfish (Ptychocheilus oregonensis, by Steigenberger and Larkin 1974), burbot (by Clemens 1950), muskellunge (by Gammon and Hasler 1965) and chain pickerel (Esox niger, by Warner 1973). The type of feeding exhibited by pike and other top carnivores appears similar, and the present model of feeding should also apply to them.

Published methods for quantifying daily ration depend on either digestive rate analysis (Darnell and Meierotto 1962, Po[illegible]va 1966, Swenson and Smith 19[illegible]) or diurnal changes in the weight of stomach contents (Keast and Welsh 1968, Thorpe 1977, Nakashima and Leggett 1978). The fish examined in these studies often have consistent meal sizes and feed over long time periods (similar to Type 1). It is difficult to extrapolate the digestive rate estimated for captive fish to the population, because water temperatures vary in most aquatic habitats with time of day, month, or depth, and the digestive rates of fish would also vary with changes in these factors. Since Lac Ste. Anne is isothermal and has relatively constant temperatures over summer (16 C) and winter (2 C), variations in digestive rates due to temperature are minimal.

The factors which contribute the greatest variance to pike ration analysis are the estimation of meal size and frequency. The present technique placed much emphasis on their determination. The techniques for quantifying ration listed above suffer from a lack of confidence limits, but repeat samples in this study indicate that values obtained from the present method are reproducible. There was good agreement between daily ration and daily needs for maintenance and growth for 3 year old pike in most summer months, also indicating the relative accuracy of ration determinations.

The present calculation of daily ration relies mainly on two untested assumptions. The most important of these is that gastric evacuation rate is similar for fish [illegible] in my lab experiments, and that this rate is [illegible] regardless of meal size or type. Previous studies have not [illegible] consistent trends between meal size [illegible] digestion time for fish (Windell 1966, Beamish 1972, Swenson [illegible] 1973, Steigenberger and Larkin 1974). I attempted to minimize any errors by using a common prey item of intermediate size which should give an average digestion time. Seaburg and Moyle (1964) determined pike digestion time in the summer (using force-feeding), and their value (50 h) was very similar to my results. Force-feeding may increase total digestion time (Swenson and Smith 1973, Steigenberger and Larkin 1974), but adult pike were unwilling to feed in captivity. Although the force-feeding technique may have caused slower digestion, this bias should be constant for all ration values.

A second assumption in ration analysis was that the stomach contents of captured fish were representative of the fish population in general. Meal sizes were underestimated somewhat, because some captured pike with 1 item (or even more) in the stomach might have continued feeding, but they were caught before doing so and their meal size was calculated for 1 item only. Relatively little digestion could have occurred while the pike were in the gillnets, since set times were only 1/12 to 1/16 of the gastric evacuation time. However, regurgitation of stomach contents could have occurred during this time. Healy (1956) considered regurgitation to be a significant problem for gillnetted pike. However, the amount of regurgitation during capture is uncertain, and its effects were considered negligible in the present study and also in Lawler (1965).

Pike growth has generally been considered variable, with fish of the same age differing considerably in length and weight (Kipling and Frost 1970, Mann 1976, see Chapter 1). The inclusion of large, rare prey items in pike diets may [illegible] a significant effect of growth. An individual that is able to feed regularly on suckers (due to learned behavior, its location in the lake, or some other variable) would have a much higher ration than one that fed on smaller perch. This would inevitably lead to a faster growth rate for the former individual. Since prey sizes and availability vary between many habitats in a lake, one would expect pike ration and growth to be equally variable.

Chapter 4. LOCOMOTOR BEHAVIOR AND ACTIVITY PATTERN OF NORTHERN PIKE IN LAC STE. ANNE

INTRODUCTION

Under any combination of environmental conditions, the maintenance costs for an animal should be fairly constant, while energy allocations to growth, activity, and reproduction may vary. Theoretical examinations of foraging strategies (Schoener 1969a, 1969b, 1971) predict that animals should trade off between active foraging (which requires considerable energy) and lurking predation (requiring much less energy) depending on the distribution, abundance, and behavior of prey items. This assumes that natural selection will favor foraging strategies which optimize net energy gain. In these theories, active metabolic requirements are not constant among all animals (even of the same species) but vary in response to foraging strategy. If one accepts this, then one must refute the assumption of Winberg (1956) that active metabolism for fish is equal to twice the standard metabolic rate. Active metabolism should be dependent on foraging strategy, and should be measured by determining the activity of the species in question (Lindsey 1978).

Mann (1965) demonstrated that many fish species used up to 75% of their assimilated energy in respiration (including maintenance and activity). Since respiration appears to be the predominant energy use in fish, any changes in active metabolism would make large changes in the overall budget. It is obvious that the arbitrary doubling of standard metabolism to account for activity can cause large errors in an energy budget study, and the determination of active metabolic rate should be a high priority.

To estimate active metabolic rate, one must first determine the durations of activity and the swimming speeds of fish under natural conditions. Although telemetry has been used primarily to determine long range movements of fish, some studies have focused on locomotor behavior such as swimming speed, turn frequency, and diel activity patterns (Poddubnyi et al. 1970; Malinin 1971; Young et al. 1972; Kelso 1976a, b; Sciarrotta and Nelson 1977). These studies have generally been of short duration, and the fish in question have been tracked for only a few days. The stress of capture and handling could affect the swimming behavior and activity of fish for several days after release (Summerfelt 1972, Diana et al. 1977 - see Appendix E). A preferable technique would be to examine swimming characteristics over long time periods. This would give more reliable results on diel and seasonal changes in behavior, since the patterns would be described from many observations during each time period.

The purpose of the present study was to measure the amount of time spent swimming and the swimming speeds of northern pike in Lac Ste. Anne. To do this, the locations of pike were determined from close range at five-minute intervals.

METHODS

Telemetric observations were conducted from March to July 1978 in Lac Ste. Anne. Ultrasonic transmitters (Smith-Root Electronics, model SR 69A) were surgically implanted in the body cavity following methods described in Crossman (1977). Six fish were successfully implanted (Table 13); one died 38 days after release, while the remainder survived the duration of telemetric contact.

The fish were routinely located by long-range triangulation (Diana et al. 1977, see Appendix E). Close-range tracking was conducted when possible from two observation stations which were established approximately 100 m apart and 100 m from the fish. These stations consisted of anchored boats during the summer (marker buoys were used to ascertain that no drifting occurred and to aid in later location of the stations) or holes through the ice during winter. The position of the fish was simultaneously monitored from both stations, and compass bearings of the fish's direction were recorded every five minutes for at least one hour. Stations were relocated if the fish's movement led to a poor geometric relationship for triangulation from the original stations. Observation intervals were varied so all major day and night periods were adequately sampled. After several hours of observation, the locations of tracked fish were pinpointed by triangulation from the stations, and the distances between successive locations were determined by tape measure (when less than 36 m) or by an optical rangefinder (Ranging Inc., Rochester, N.Y.).

Fish movements were generally detected by changes in bearings from both stations, and minimum detectable displacements were

Table 13. The size, sex, total tracking time, and hours of close range tracking for each of six pike observed in Lac Ste. Anne from March to July 1978.

Fish number	Standard length	Weight	Sex	Date released	Last located	Total time	Hours of close range tracking
1	59 cm	2215 g	F	14III78	3IV78	17 days	15
2	49 cm	1281 g	M	28III78	9IV78	12 days	12
3	46 cm	942 g	M	3IV78	11V78[a]	38 days	4
4	51 cm	1040 g	F	9V78	29VI78	51 days	31
5	55 cm	1910 g	F	28V78	2VI78	5 days	0
6	46 cm	947 g	M	18VI78	29VI78	11 days	23

[a] This fish died on 11V78.

approximately 2 m (winter) to 5 m (summer). No specific tests were conducted to determine the accuracy of this method, but the greater errors in summer siting were due to wave action, which affected both taking a bearing and triangulation. The accuracy obtained was sufficient for reliable measurements of net movement over five minute intervals. It was not feasible to use shorter time intervals, although several were tried. The fish were not continuously monitored, but close range tracking was conducted sporadically for the duration of telemetric contact.

RESULTS

Northern pike were generally inactive, and measurable displacements occurred during less than 20% of all [illegible] five-minute obs[illegible]tion intervals in summer and winter (Table 14). Data from all fi[illegible] combined, and the time intervals for grouping were arbitr[illegible]en from changes in fish behavior and solar insolation. Durin[illegible] periods of the day pike were most commonly inactive. Pike activit[illegible] sporadic, and often the fish would not move at all for up [illegible] 24 hours. Pike were almost completely inactive at night during both summer and winter. During both seasons, the only significant changes in activity were the decreases at night. There were no significant differences between the activity of pike in summer or winter (chi square = 2.71, P = 0.10).

Assuming that peak displacements during five minute observations occurred by bouts of continuous straight line swimming, the distances moved can be used to calculate swimming speeds (Table 15). Any displacements of less than 45 m in 5 minutes were assumed to be due to nonlinear or discontinued movements. Only four fish exhibited this type of movement, and 28 such displacements were measured during this study. Maximum swimming speeds for each fish varied from 17 to 42 cm/s. Swimming velocities were higher in summer than winter, both in absolute (cm/s, $T = 2.77$, $P < 0.02$) and relative (body lengths/s, $T = 3.61$, $P < 0.01$) terms.

Table 16. The number and percent occurrance (in parentheses) of pike active and inactive periods during five minute observation intervals at various times of day in summer and winter. Inactive = movement less than 5 cm (minimum movement that can be accurately detected). Sunrise period = 1/2 hour before to 1 hour after sunrise, day = sunrise period to sunset period, sunset period = 1 hour before to 1/2 hour after sunset, night = sunset period to sunrise period. Range test = 4 x 2 chi square test, if P > 0.05, the symbols are underlined at the same level.

Time interval	Active	Inactive
	SUMMER	
Sunrise	19 (22%)	68 (78%)
Day	71 (17%)	351 (83%)
Sunset	16 (21%)	62 (79%)
Night	1 (2%)	63 (98%)
Total	107 (16%)	544 (84%)
Range test	Sr Dy Ss Ni	
	WINTER	
Sunrise	9 (23%)	30 (77%)
Day	34 (19%)	142 (81%)
Sunset	26 (35%)	49 (65%)
Night	1 (2%)	43 (98%)
Total	70 (21%)	264 (79%)
Range test	Sr Dy Ss Ni	

Table 15. Calculated swimming velocities for four pike tracked during 1978 in Lac Ste. Anne. $\bar{x} \pm$ SD. The values are based on displacements of 45 m or more in five minutes. The number of these displacements is also given.

Fish number	Number of displacements	Total velocity (cm/s)		Relative velocity (BL/s)	
		Maximum	Mean	Maximum	**Mean**
1	7	29	18.9 ± 4.7	0.49	0.32 ± 0.08
2	2	18	17.2	0.37	0.36
4	13	38	25.5 ± 6.6	0.75	0.50 ± 0.13
6	6	42	25.9 ± 9.1	0.91	0.56 ± 0.20
Total	28	42	23.1 ± 2.6	0.91	0.45 ± 0.05

DISCUSSION

Northern pike have long been considered sedentary (Ivanova 1969, Malinin 1969, Nursall 1973) and the present study gives even more convincing evidence regarding this inactivity. Although some diel changes in locomotor behavior were apparent, pike generally remained inactive. Malinin (1969, 1971) and Poddubnyi et al. (1970) considered pike to be crepuscular in their activity, with few day movements and no nocturnal displacements. Their conclusions were based on telemetric data, but they did not indicate how much of an increase in activity occurred in morning or evening. Also, it is uncertain how long their telemetric contact was maintained. Lawler (1969) thought pike were most active at night, based on changes in gillnet catch. However, both the present data and gillnet results (Appendix Table 5) indicate that pike in Lac Ste. Anne are inactive at night and sporadically active throughout the day, with peak activity sometimes occurring in the afternoon and evening.

During five minute tracking intervals, pike activity could vary from no movement to a constant swim. Swimming speed could vary as well, but for this analysis I assume that speed was constant. Calculation of swimming speed also assumes that the fish swam in a straight line. During the winter, I determined turn frequency (indicated by changes in the signal strength) over five minute intervals; the average number during periods of movement was two turns, with a maximum of four. It appears that the pike rarely turned during five minutes and moved in approximately a straight line.

Several different swimming speeds were calculated from the data (Table 15). Jones et al. (1974) determined in the laboratory that the critical velocity (maximum sustainable velocity for 10 minutes) of pike from 12 to 62 cm in length was best described by the formula: $CV = 4.9\ FL^{0.55}$, where FL is the fork length of the fish. Using this formula, the critical velocity of pike similar in size to those examined in this study would be 44 cm/s (0.86 BL/s). They also determined that the highest maintained speed (for 100 min) for pike was approximately 60% of the critical velocity, or 26 cm/s for similar size fish. Both values are close to the maximum and mean swimming speeds observed for free swimming fish in the present study.

Poddubnyi et al. (1970) measured pike swimming velocity in a manner similar to mine, and found the mean speed to be 5.5 cm/s, with a maximum of 300 cm/s (over one minute). The low mean values they obtained indicate that they probably included inactive periods in calculation of mean speed. The high value was probably due to a burst movement which lasted a minute at most. It is doubtful that such a speed could be maintained over five minutes (Jones et al. 1974); no speeds of this magnitude were detected in the present study.

Calculated pike swimming velocities were slower in winter than summer. Winter habitat (no vegetation, ice cover, cold temperatures) may influence swimming speed. Jones et al. (1974) found that pike swam slower at low temperatures in the lab, and Beamish (1978) indicates that this is true for most fish species. However, the slower winter speeds I determined may also be due to less extensive data from winter tracks. Only 9 long distance movements were recorded in winter, compared to 19 summer values. Long movements by pike could not always be monitored to completion during the winter, due to the time involved in relocating stations.

The six northern pike tracked in this experiment showed sporadic movement patterns with no localized home ranges. These results are similar to a previous study (Diana at al. 1977, Appendix E), and indicate that pike showed similar movements when transmitters were implanted orally or surgically. Since neither type of stress resulted in appreciably different behavior, the observed locomotor patterns are probably similar to those of undisturbed fish.

The present study described pike movement during summer and winter. However, some authors (Miller 1948, Moen and Henegar 1971) suggest that pike may be more active in spring. I was unable to determine the extent of spring movements because of poor ice conditions during late April (when spawning occurred). Pike tracked just prior to the end of winter appeared more active and were often difficult to follow. However, the amount of activity during the spawning period remains unknown.

When I began this study, I hoped to delimit the time budget of various activity patterns for pike, then assess the metabolic rate of pike at various swimming speeds to evaluate active metabolism in nature. However, in summer and winter, movement by pike occurred during less than 20% of the five minute observation periods. Increases in metabolic rate during activity, while dependent on swimming speed, (Brett 1964), are generally considered to result in a doubling of the resting metabolic rate during activity (Winberg 1956, Mann 1965). Since pike are active so infrequently, the active metabolic rate (based on the 2 x standard assumption) would result in an average daily metabolic rate of less than 1.2 times the R_{met} ([24 h x 0.8 (proportion of time inactive) x R_{met}] + [24 h x 0.2 x $2R_{met}$] = 1.2 R_{met}). Because of the minimal alteration in metabolic rate due to activity, the costs of activity will be considered nil in future calculations of the energy budget.

Chapter 5. THE ANNUAL ENERGY BUDGET FOR NORTHERN PIKE FROM LAC STE. ANNE

INTRODUCTION

The purpose of this entire study was to measure the parameters necessary to compute an energy budget for northern pike from Lac Ste. Anne. In an effort to circumvent problems encountered in previous studies, the fish stocks, light levels, photoperiod, water quality, and water temperature were kept as close to Lac Ste. Anne conditions as possible during controlled experiments. As many portions of the budget were measured as possible, to allow an overall comparison and to avoid using unnecessary assumptions. Now that these parameters are available, I will fit them into a budget for 3-year-old fish. This budget will be divided by season and sex, so that the effects of these factors can be assessed. Finally, the proportional allocation of energy to maintenance, growth, and reproduction will be examined for all ages of pike.

METHODS

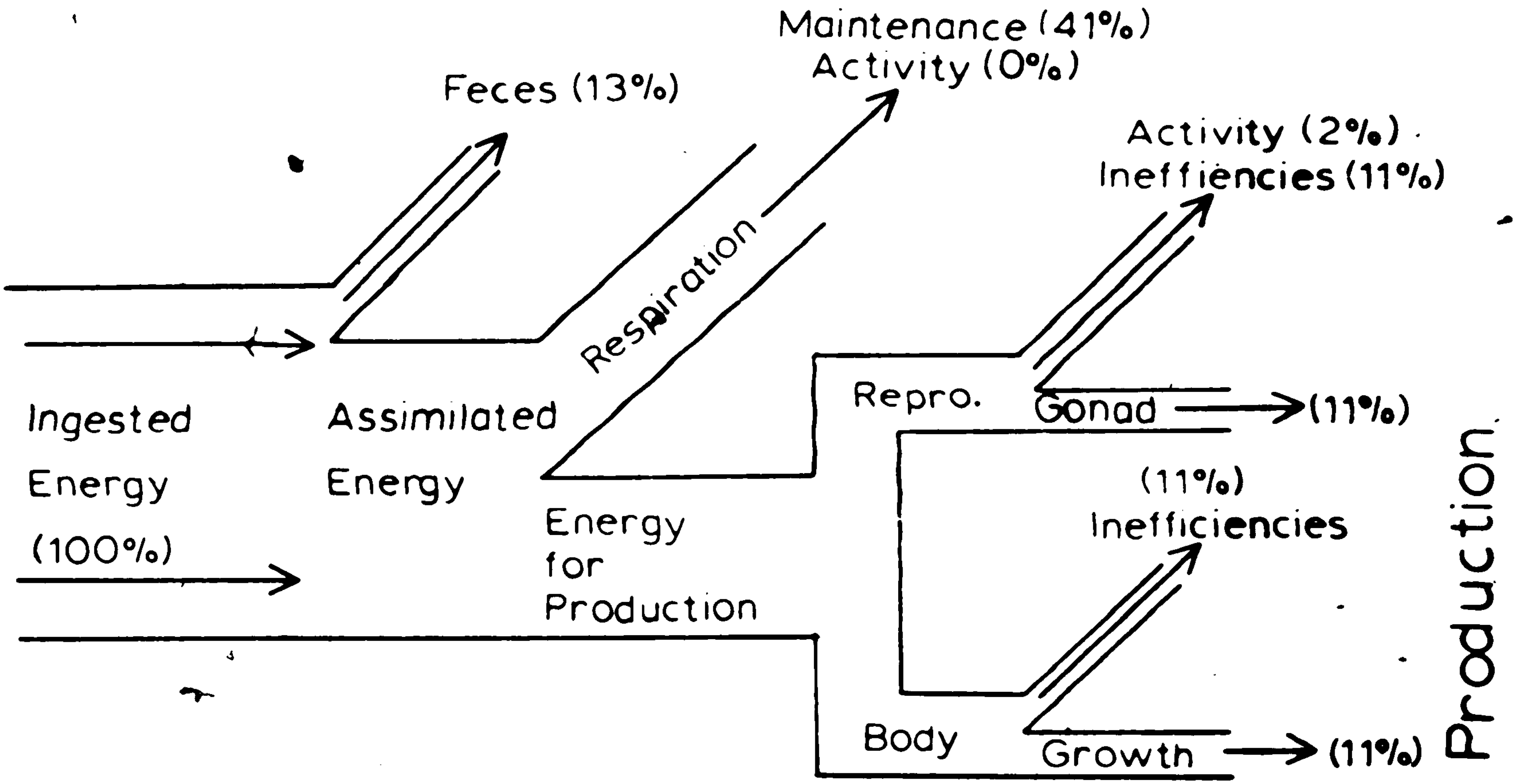
A flow diagram outlining the energy budget is given in Figure 9, based on pike data, and the calculations for each parameter are described below. The daily ration of 3 year old pike (Chapter 3) was converted to total energy intake by multiplying monthly ration values by the mean size for each sex at the start of each month, then converting for the number of days in the month (Appendix Table 6). In months when ration estimates were not measured, the closest estimate in time and season was used to approximate the ration for that month. During October, rations were assumed to continue at summer levels for 15 days, then decrease to winter values. During April, rations were assumed to remain at winter levels for 15 days, then decrease to zero during the spawning fast. Assimilated energy was then calculated by multiplying the total intake by the assimilation efficiency (0.87, see Chapter 2).

The metabolic requirements for each month were determined by inserting mean monthly body weights for each sex of 3 year old fish into the R_{met} equations for summer and winter (Table 8, Appendix Table 6). October requirements were estimated by assuming that for 15 days the R_{met} remained at the summer level, then for 16 days it was equal to the value for 8 C (female level, see Chapter 2). April metabolic requirements were estimated by assuming that for 15 days the metabolic rate was similar to winter, then for 15 days it was at the spawning level (8 C).

The differences between assimilated energy and metabolic requirements were used to predict growth. If there was excess energy after

Figure 9. Diagrammatic representation of the flow of energy through a 3-year-old female pike. The widths of various channels are proportional to the actual energy for each function for the entire year. % values = % energy into each channel, from the total ingested energy.

Energy Losses



this subtraction, it was multiplied by 0.51 (K_3) to calculate predicted growth. This included body and gonad growth, and it was assumed that both types of growth occurred with similar efficiencies. If the remaining energy after subtraction was negative, the predicted loss of energy stores was considered to equal the negative energy balance, since I assumed that catabolism occurred at 100% efficiency.

Predicted energy budgets were compared to observed growth of pike to verify the budget's accuracy. Observed growth over most time periods (groups of months, i.e. May to August) was determined from changes in total calories of the pike (somatic and gonad, see Chapter 1). However, the observed growth from March to May was estimated from somatic calories only, because no gonad growth and all gonadal excrudescence occurred during that time.

In estimating energy allocation of 3-year-old pike to various functions, metabolism values for each time period were taken from Table 16. Energy required for body and gonad growth was estimated by dividing the observed growth for each time period and sex (Table 4) by the conversion efficiency. Energy for reproductive activity was assumed to equal the loss in somatic energy from March to May (Table 4), since the only obvious reason for this loss was due to spawning fast and behavior (Chapter 1 and 3). The total energy allotted to reproduction was the sum of the energy costs of gonad growth and reproductive activity. The total assimilated energy for each period was considered the sum of metabolic, growth, and reproductive costs. Ration values were not used for this estimate only, because of a lack of agreement between measured food intake and observed growth during some periods of the year (see Results). Calculations of energy allocation for fish from age classes 0 to 2 were done in a manner similar to three-year-olds.

The cost of specific dynamic action was assessed for the energy budget of 3 year old pike during the summer. At that time, SDA was observed to cause an increase of 33% in metabolic rate for 42 hours (1.75 days) after feeding (Chapter 2). The number of meals consumed per month was calculated from data on feeding frequency (Table 12) and number of days in each month. SDA was calculated by multiplying R_{met} values for each month and sex (Appendix Table 6) by 0.33 (increase in R_{met} due to SDA). The total SDA energy cost for each sex and month was calculated by: number of meals x SDA increase in R_{met} x 1.75 days of SDA increase per meal (Appendix Table 7). This value was then pooled by sex for all summer months to calculate the total SDA cost over summer.

RESULTS

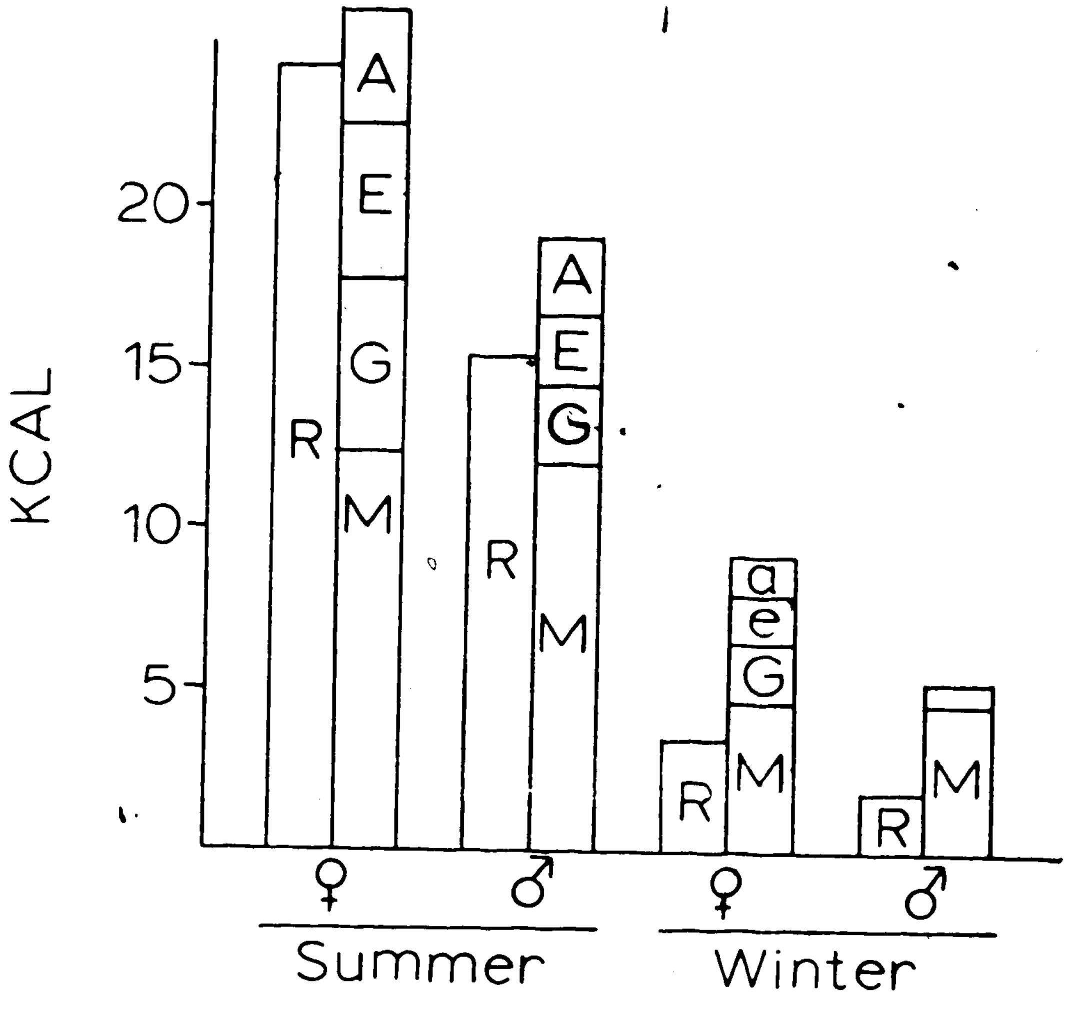
A summation of the energy budget calculations, including ingestion, assimilation, maintenance requirements, and growth efficiency can now be examined (Table 16). The budget was calculated for individual 3-year-old pike for one year beginning in May. Monthly data were pooled into groups of several months or into seasons, and the summer and winter groupings will be discussed further. The predicted (from energy budget data) and actual rations (from field analyses) were in good agreement in the summer (Figure 10). The actual rations predicted the proper magnitude of growth observed in the population (Table 16), and were probably well within the margins of error for a combination of all the measurements. Winter energy budgets failed to predict the proper magnitude of growth. The error in actual ration was considerable. This error could arise from several sources, and will be evaluated further.

Metabolism of pike could be predicted during all portions of the year, since it was directly dependent on temperature and fish size. Growth could also be evaluated over all periods, since samples were collected frequently enough to assess it over periods of 3 months or less. During the summer, ration values changed considerably each month. Winter rations could only be evaluated in late winter, and these values had to be extrapolated to the period from October to January. If the budget is broken down into these two periods of winter (October to January and January to May), one can evaluate the accuracy of this extrapolation (Figure 11). The majority of winter growth occurred from October to January, and from January to May

Table 16. Actual and predicted growth by 3-year-old pike for various periods of the year. -Data are calculated as described in text and in Appendix Table 6.

Time period	Sex	Kcal ingested	Kcal assimilated	Kcal for maintenance	Kcal predicted growth	Kcal actual growth
May 1 - July 31	M	1130	983	800	149	242
	F	1813	1577	681	457	304
Aug. 1 - Sept. 31	M	400	348	510	-162	-11
	F	608	529	543	-14	134
Oct. 1 - Dec. 31	M	154	137	250	-113	180
	F	244	212	276	-64	206
Jan. 1 - Feb. 28	M	26	23	94	-71	-62
	F	68	59	92	-33	96
March 1 - April 30	M	28	24	134	-110	-143
	F	41	36	108	-77	-138
Summer	M	1530	1331	1200	67	231
	F	2421	2106	1224	880	328
Winter	M	212	184	478	-294	-62
	F	353	307	476	-169	364

Figure 10. Comparison between actual ration (R) and ration predicted by maintenance (M), growth (G), growth efficiency (E), and assimilation efficiency (A) requirements for 3-year-old male and female pike in summer and winter.


KCAL
20
15
10
5
R
A
E
G
M
R
A
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G
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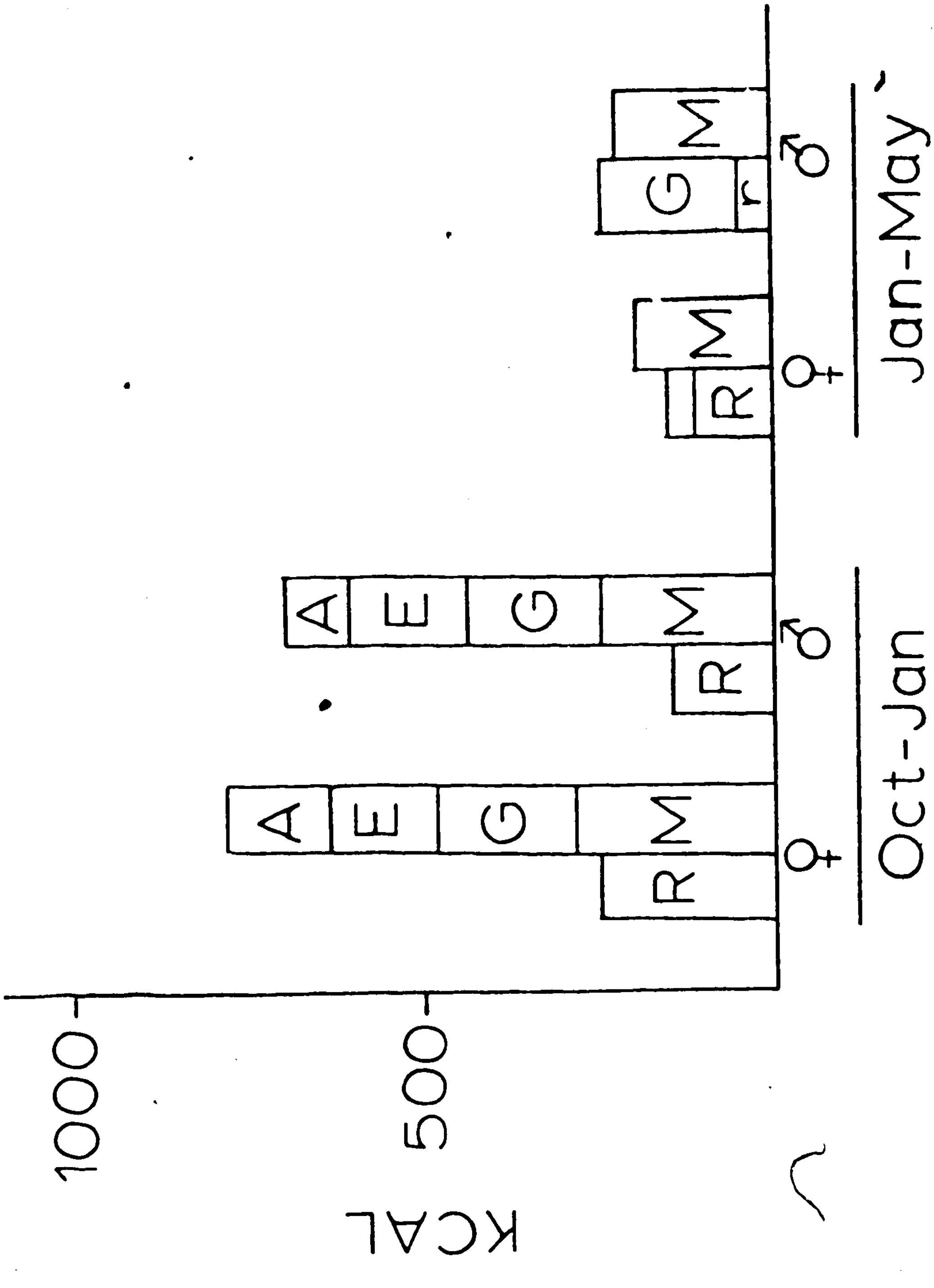
R
a
e
G
M
R
M
♀
♂
♀
♂
Summer
Winter

Figure 11. Comparison between actual and predicted rations in early and late winter for 3-year-old northern pike. Body losses in Jan.-May are coupled with observed rations, since these losses contributed to maintenance needs.


KCAL
1000
500
R
M
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A
♀
R
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G
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Oct-Jan
R
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r
G
M
♂
Jan-May

(when ration values were estimated)the fish actually lost weight. The winter budget balanced well over late winter, but was extremely inaccurate in early winter, apparently due to a lack of good ration data at that time. However, poor ice conditions made it dangerous to collect fish between November 1 and late December. The budget would balance over this period if rations of 7.4 (male) to 8.2 (female) kcal per day could be consumed.

During the spawning period (March to May), the predicted energy losses (Table 16) were less than actual losses for both sexes. This may indicate that activity was higher during this period of the year (also see Chapter 4).

Examining the energy budget in terms of my original expectations, the annual costs of metabolism, body growth, and reproduction can be assessed (Table 17). Activity costs were essentially nil, and will be ignored. Immature fish (age 0) were very efficient at body growth, allocating 72% of their assimilated energy to this process. There was a significant difference between the energy budget of males and females. From ages 1 to 3, the cost of maintenance was constant at about 50% (female) to 60% (male) of the assimilated energy. The relative allocations of energy to body growth and reproduction were constant and similar for all ages of females (about 25% of the budget to each), while males allotted 3 times more energy to body growth than to reproduction. Females had to accumulate 1.1 to 1.5 times more energy than males for their budget to balance. Total energy required for growth and maintenance was similar for both sexes, but females required 3.3 to 5.8 times more energy for reproduction than males. This excess energy was required entirely for ovarian growth.

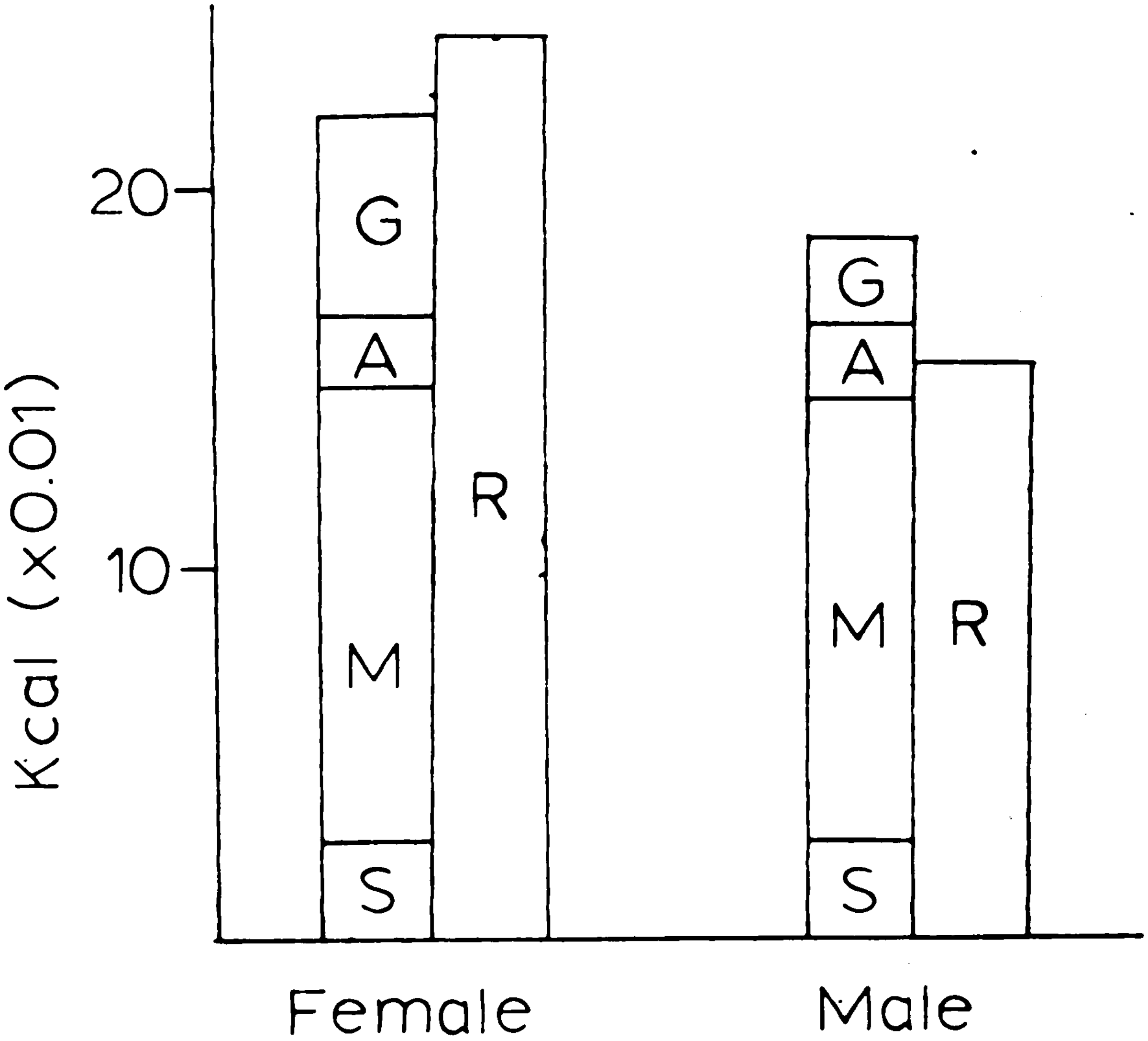
Table 17. Annual allocation of energy to each component of the energy budget by each sex and age class of northern pike.

Sex	Age	Growth	Reproduction	Maintenance	Total
Male	0	1077 (72%)	0 (0%)	427 (28%)	1504
	1	484 (28%)	141 (8%)	1089 (64%)	1714
	2	770 (33%)	185 (8%)	1385 (59%)	2340
	3	651 (26%)	177 (7%)	1689 (67%)	2517
Female	0	1077 (72%)	0 (0%)	427 (28%)	1504
	1	492 (24%)	487 (24%)	1083 (53%)	2062
	2	568 (22%)	614 (24%)	1375 (54%)	2557
	3	923 (25%)	1023 (28%)	1705 (47%)	3651

Three-year-old male pike accumulated 68% of their annual energy needs during the summer, when 77% of their growth was completed. Females achieved a larger portion of their growth during winter (39% of the total) than did males. Absolute female growth was almost twice the male level during both seasons.

The effect of SDA on the energy budget can be assessed for summer data, when the balance between predicted and actual rations was good. When calculated SDA costs were included seperately in the budget (Figure 12), the energy remaining for growth (40 kcal) was much less than the observed growth for males (231 kcal) over the same period. However, the energy remaining for females (861 kcal) was in excess of the observed growth (528 kcal). Extrapolation of SDA data altered the budget drastically for males, but not for females. Difficulties in extrapolating SDA to the energy budget are not unexpected, due to the limited size of fish used in SDA experiments, and the combination of many measured parameters into one value. The present evaluation suggests that the cost of SDA may vary by sex in mature fish. However, the observed SDA costs were from 10% (female) to 17% (male) of the energy assimilated during the summer.

Figure 12. Comparison between actual (R) ration and ration predicted from SDA (S), maintenance (M), assimilation (A), and growth (G) for 3-year-old pike in summer.


Kcal (x0.01)
20
10
G
A
M
S
R
G
A
M
S
R
Female
Male

DISCUSSION

The allocation of energy to maintenance, growth, and reproduction varied with age and sex of pike. Very few budget studies have analyzed the change in allocations with age and sex. Lasker (1970) did a similar analysis for sardines (*Sardinops caerulea*) and found that the relative cost of respiration increased with age, the cost of reproduction was constant, and the energy left for body growth declined with age. His budget did not include any ration data, so its validity is uncertain. Also, the costs of reproductive activities and growth efficiencies were not included. My data [illegible]t indic[illegible] continual decrease in growth with age, but rather a plateau after maturation. The same is indicated for reproductive costs. However, I was unable to provide valid data for fish older than 3 years, and the decreases defined by Lasker might occur in older pike.

Most fish energy budgets have either been done on immature fish or the budget has not been seperated by age. For a comparison with the literature, data for 3-year-old males will be used, since their allocations to reproduction were small. These fish used 69% of their budget for metabolism and 31% for growth. Energy budgets of other fish species have been divided in the following manner (% energy to metabolism: % to growth); sand gobies (*Gobius minutus*) 71:29 (Healey 1972), rainbow trout 65:35 (Brocksen et al. 1968), sticklebacks (*Pungitius pungitius*) 71:29 (Cameron et al. 1973), bluegill 73:27 (Gerking 1972), sockeye salmon 75:25 (Brett 1970), sardines 81-98:19-2 (Lasker 1970), roach (*Rutilus rutilus*), bleak (*Alburnus alburnus*), dace (*Leuciscus leuciscus*), perch (*Perca fluviatilis*), and gudgeon

(Gobio *gobio*) 74:26 (all by Mann 1965). All of these studies differ in assumptions and methods of determination, but the proportional energy allocation is similar for all of the fish except sardines.

The accuracy of any energy budget determination can only be verified by comparing independently measured ration values with rations predicted by the energy budget and growth observed. Of the studies listed above, only Healey (1972), Gerking (1972), and Cameron et al. (1973) included such analyses, and all of those budgets were grossly in error. It is difficult to assess whether the error was due to poor ration analysis, budget determination, or assumptions. The budget predicted in the present study balanced fairly well, especially considering the limitations in the ration data during early winter. During the summer, actual rations were only 7% (female) to 19% (male) lower than predicted rations. From January to May, observed rations were 19% (male) to 30% (female) lower than predicted. These margins of error are probably acceptable, considering that each parameter had considerable variation. Also, it was expected that the ration values would underestimate the actual ration of pike in nature (Chapter 3). Accounting for all of this, one must consider the present energy budget relatively accurate.

In most examinations of fish energy budgets, active metabolism was assumed to be twice the routine level (Mann 1965, Gerking 1972). Brett (1964) indicated that the relationship between active and routine metabolism depended on the swimming speed and duration in nature. To my knowledge, no previous fish energy budget study evaluated the amount of natural activity demonstrated by the fish, although energy budgets of other poikilothermic vertebrates have included this as a major portion of the study (Alexander and Whitford 1968, Fitzpatrick 1973). This factor could be one reason why predicted energy budgets have seldom balanced, and active metabolic rate is one of the most important parameters to assess in measuring an energy budget. The problems in dealing with assumptions for energy budget components are indicated by Gerking (1972), who recalculated energy budgets for bluegill several times using different assumptions, and still did not get a reasonable balance. In the present study I determined that pike are mainly inactive, and R_{met} should be an adequate measure of active metabolic rate in nature. Since the budget roughly balanced, this prediction appears to be true.

The contrasts between male and female energetics indicate that each sex may show a different adaptation to local conditions. Few studies have critically analyzed the differences between energetic parameters for male and female fish. Foltz and Norden (1977) determined that female smelt (<u>Osmerus</u> <u>mordax</u>) require more energy than males for gonad growth, and Healey (1972) came to the same conclusion for female gobies. Shul'man (1974) suggested that females of most fish species utilize more energy for maturation than do males. The area of sexual differences in energetic parameters for fish needs much further research before the proportional differences between sexes can be estimated for many species, and any general trends can be confirmed.

Seasonal differences in energetic costs make it possible for some fish to exploit each season to advantage. During the summer, digestion and food consumption were maximum for pike, and rapid growth (mainly somatic) occurred. However, low metabolic requirements in winter allowed growth to occur at low rations, and this slow growth was mainly used for ovary production. Several studies (Healey 1972, Krivobok and Tokareva 1972, MacKinnon 1972, Folts and Norden 1977) have indicated that ovary growth occurred over winter in fish, but this growth was due to catabolism of energy stores and therefore due to summer feeding. Tyler and Dunn (1976) found that winter ovary production in flounder (_Pseudopleuronectes americanus_) was less for fish on limited rations than for those on unrestricted rations. They then examined fish from a natural population and determined that ovary production in these fish was restricted by low winter food intake. Further studies are necessary to indicate whether growth in fish is limited by food availability, physiology, or both.

There are likely to be several strategies regarding seasonal accumulation of energy and its effect on the overall energy budget. One would expect energy intake and flow to be responsive to many environmental factors. At present, there is insufficient data available to assess the effects of these factors on an energy budget. However, one might expect top carnivores to show year round growth, since food density should remain fairly constant throughout the year. In contrast to this, planktivores would be expected to show more drastic seasonal changes in growth, since plankton changes significantly in density over the year. Food availability is obviously not the only factor to consider. Some animals are physiologically adapted to function more efficiently in cold temperatures than others. Because of all these factors, energy budgets should not be expected to remain similar for all fish, but rather should be adapted to local conditions. As more studies become available, it may be possible to directly assess the effects of various factors on fish populations by examining the energy budget relationships. As shown in the present study, even age and sex must be considered as variables which affect the pattern of energy accumulation and use.

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APPENDIX

Appendix A. CALORIE DETERMINATIONS

Calorific equivalents for dried tissue were determined using a Parr adiabatic calorimeter. Approximately 1 g of sample was put into a pre-weighed sample pan, and the exact weight was recorded (to 0.001 g). Gonad and liver samples were pelleted prior to weighing, but body samples were not pelleted due to their extremely dry condition. A fuse wire 10 cm in length was connected to the bomb head and touched against the sample in the pan. The assembled bomb was then filled with oxygen to 30 atmospheres pressure, then lowered into a distilled water container with 2 kg of water. A fuse wire was connected to the bomb, and the calorimeter was closed. The water temperature in the bomb container and in the calorimeter jacket were equalized by adding hot or cold water to the jacket.

The temperatures were allowed to balance for 5 minutes, then the bomb container temperature was recorded to 0.01 F. The bomb was detonated, and the temperature of the calorimeter jacket was kept approximately equal to the bomb container while the bomb temperature increased. When the temperature stabilized, the two temperatures were balanced for 5 minutes, then read to 0.01 F.

The bomb was opened, washed with distilled water and methyl orange, and the washings were collected. The washing was titrated with 0.0725 N Na_2CO_3, and the volume of titre equalled the extra energy added to the run by conversion of N to NO_3. The unburned portion of fuse wire was measured, and the factor of 2.3 cal/cm was used to determine the amount of energy added to the run by combustion of the fuse. The calorific equivalent of the sample was calculated as follows:

$$CE = (tw - c_1 - c_2)/m,$$

where t = temperature rise, W = cal per °F, c_1 = fuse correction, c_2 = N correction, and m = mass of sample. W (cal/°F) was determined by combustion of benzoic acid, which has a known caloric content of 6318 cal/g. The mean W value for all runs (1360 ± 10, X ± SD, n = 14) was used for the calculation of CE. Benzoic acid standards were burned before each series of calorimetric determinations to ascertain that no change in W occurred during the study.

Preliminary determinations of the sulphur content of 6 pike body samples indicated a mean of 0.83% S (range 0.71 to 0.98). These sulphur contents would increase calorific values 11.0 to 12.1 cal/g for each run. Because of the time involved in sulphur determinations, the low level of sulphur in pike tissue, and the slight changes in CE due to sulphur, corrections for the sulphur content of each sample were not made.

The accuracy of calorific determinations was evaluated by repeated runs of benzoic acid standards and by 6 repeats of 1 pike somatic sample (5.0 ± 0.02 kcal/g). Since both results were very repeatable and accurate, only 1 determination was done per sample.

Appendix B LIPID DETERMINATION

Vials of powdered samples were held in an oven at 70 C for one hour prior to analysis. Fifteen determinations were done at one time, including 2 blanks and 13 samples. Samples of approximately 0.5 g were accurately weighed on ash-free filter paper (to 0.0001 g), then the paper was folded and put into extraction thimbles. Blank papers were also folded and put into thimbles. All the samples were put in a Soxhlet apparatus, and fat was extracted in 2 chloroform: 1 methanol mixture for 5 hours. The solutions were collected in a flask, allowed to cool, then put into seperatory funnels. The flasks were rinsed twice, and the volume in each funnel was increased to 120 ml with chloroform methanol. These solutions were washed in 30 ml of 0.05% $CaCl_2$, then allowed to stand overnight. The lipid containing portion of the solutions were put into preweighed beakers, then evaporated on a steam bath. The beakers were dried at 80 C, then allowed to cool in a desicator. The difference between initial and final beaker weights was taken as the uncorrected weight of lipid, which was corrected by subtracting the blank value. The percent lipid was determined by dividing the corrected lipid weight by the initial sample weight.

Multiple determinations of the lipid content of a pike ovary sample (13.54 ± 2.14%, n = 8) had considerable variation (SD = 16% of mean). Therefore, duplicate lipid determinations were done for each sample.

C. PROTEIN DETERMINATIONS

Vials of samples were dried at 70°C for one hour prior to analysis. Approximately 100 mg of sample was weighed to 0.001 g on a cigarette paper. The paper was folded and inserted into a 30 ml digestion flask. Twelve analyses were done for each run: 1 blank, 1 THAM (tris(hydroxymethyl)aminomethane) as a standard, and 10 samples. To each flask, 0.5 g of potassium sulphate, 1 ml mercuric sulphate solution (10 g HgO + 2 ml conc. H_2SO_4 brought to 100 ml with distilled water), and 3.5 ml conc. sulphuric acid were added. The flasks were placed on burners and boiled until 30 minutes after the solutions had cleared. They were allowed to cool, and distilled water was added to dissolve all precipitated salts.

Each solution was put into a distillation apparatus with 5 ml of sodium thiosulphate solution (550 g caustic soda + 30.06 g $Na_2S_2O_3$ brought to 1000 ml with distilled water). The sample was distilled, and the distillate was collected in a flask containing 5 ml boric acid indicator (13.3 ml 0.2% alcoholic methyl red = 6.6 ml alcoholic methylene blue brought to 1000 ml with 4% boric acid). Approximately 40 ml of distillate was collected from each sample, and was titrated with 0.1 N HCl (acid standardized to 0.001 N using 0.1 N NaOH which had been standardized using 0.100 N potassium biphthalate). Percent nitrogen was calculated as follows:

$$\%N = ((ml_{sample\ titre} - ml_{blank\ titre}) \times 0.14 \times N_{acid})/wt\ sample.$$

Percent protein was considered to be 6.25 x %N (Kleiber 1975).

THAM has a known nitrogen content of 11.65%, and repeat determinations by kjeldahl gave values of 11.50 $\pm$ 0.30%. Duplicates of each sample were run for protein determination, even though the accuracy of the method appeared sufficient for one determination only to be necessary.

Appendix D. METABOLIC RATE DETERMINATIONS

The metabolic rate of pike was determined by closed vessel respirometry. Containers for these experiments (64 l aquaria for adult pike, 4 l jars for YOY) were submerged in larger holding tanks where the fish were normally kept. A sample of water was taken from the large tank, and this was considered to represent the initial oxygen content of the water in each experimental chanber. The fish were then gently guided into the chambers, without removing them from the water. The tanks were sealed (with lids for the 4 l jars, plywood tops for the 64 l aquaria), and the surface of the lid was kept below the surface of the water in the larger holding tanks. A stop watch was used to time the duration of each experiment. Winter experiments lasted 12-24 hours, summer ones from 3-12 hours. The lids were removed at the termination of each experiment and water samples were taken by siphon from each chamber.

Dissolved oxygen concentrations of water was measured using the azide modification of the Winkler method. The concentration (mg/l) of oxygen was converted to total oxygen content by multiplication for the volume of water in the experimental chamber (including a correction for the volume of the fish used, assuming 1 g of fish displaced 1 ml of water). Oxygen consumption (mg/day) was determined by subtracting final values from initial values, then extrapolating the observed experimental time to 24 hours. The values were converted to kcal/day using a conversion factor of 3.20 cal/mg O_2 consumed (Brafield and Solomon 1972).

Appendix E. MOVEMENTS AND HABITAT PREFERENCE OF NORTHERN PIKE (*ESOX LUCIUS* L.) IN LAC STE. ANNE, ALBERTA.

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Reprinted from Transactions of the American Fisheries Society, Volume 106, No. 6, November 1977. Pages 560-565.

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[1] This study was supported by a grant from the Alberta Environmental Research Trust and in part by a National Research Council of Canada grant (A6587) to W. C. M. This research was conducted at the Lac Ste. Anne Fish Research Laboratory, University of Alberta. David Porter aided in some of the track

ABSTRACT

Movements of northern pike (Esox lucius) in Lac Ste. Anne, Alberta were monitored for 5 to 47 days using ultrasonic transmitters which were implanted in the fishes' stomachs. None of the nine fish studied established well defined home ranges. The pike were usually found within 300 m of shore and in water less than 4 m deep. No major differences were found in the extent of movement or in habitat selection between summer and winter. Daily pike movements were from 0 to 4000 m, but most daily movements were less than 1000 m.

INTRODUCTION

Restricted home ranges have been demonstrated for a number of species of fish (Gerking 1959, Malinin 1969). The techniques used to demonstrate restricted home ranges in fish have been either direct observation of marked fish or the recapture of tagged individuals in the area from which they were first captured. In the latter case it is assumed that the fish has remained in the same area between successive captures. Such approaches have been particularly fruitful in studies of fish which live in streams, tidepools, and tropical reefs; all of these habitats are amenable to either direct observation or to relatively complete census. The development of small ultrasonic transmitters for fish has made it possible to locate tagged individuals as frequently as is desired when direct visual observation or complete censuses are impossible.

The primary use of ultrasonic transmitters in fish has been to examine orientation and swimming speed. In [illegible] of the earliest studies using ultrasonic transmitters Hasler *et al*. (1969) located white bass (*Roccus chrysops*) approximately every 30 min for up to 10 hrs in order to determine whether the fish were able to orient to directional cues in their environment. Similarly Kelso (1974, 1976) has used ultrasonic transmitters to determine the effects of thermal discharge on frequency and sharpness of turns in brown bullhead (*Ictalurus nebulosus*), yellow perch (*Perca flavescens*) and white suckers (*Catostomus commersoni*) for periods of about 7 hrs. Malinin (1970a, b; 1971a, b) and Poddubnyi *et al*. (1970) used ultrasonic transmitters to continuously monitor the movements of many north temperate species, including northern pike (Esox lucius), for 50 to 60 hrs. In the above cases the length of observation was too short to determine whether the species examined had home ranges.

Investigations of the extent of northern pike movement have largely been confined to mark and recapture techniques. In spring some individuals may migrate from lakes into tributary streams to spawn while those that remain in the lake move extensively during this time (Miller 1948). Makowecki (1973) found very little displacement of large northern pike which had been tagged in a shallow lake and recaptured one year later. Malinin (1969) cited evidence that pike were sedentary and lived in an area approximately 100 m in diameter for a long time. Using ultrasonic transmitters in the Rybinsk Reservoir, Russia, Malinin (1969) found that pike had some ranges 50 to 150 m in diameter in areas where the bottom was flat; but in areas of the old riverbed pike moved along the riverbed for up to 500 m. he did not state the length of time over which the observations were made. Malinin (1969) also reported that pike showed a marked diurnal activity pattern being most active in morning and evening and completely inactive at night.

The purpose of the present study was to determine whether northern pike maintain a restricted home range, and if they do to estimate its size during winter and summer. To do this we monitored the gross day to day movements of northern pike, which were tagged with ultrasonic transmitters, for up to 47 days.

METHODS

This study was conducted in Lac Ste. Anne, a moderate sized (57 km^2), shallow (average depth 4.8 m), eutrophic lake located approximately 74 km northwest of Edmonton, Alberta. The northern pike that were used weighed from 1.6 to 4.1 kg and were obtained by angling.

Tracking studies were conducted during the summers of 1974 and 1976 and winters of 1973-1974 and 1976-1977. During 1973-1974 the ultrasonic transmitters (Smith-Root Electronics, Vancouver, Washington, models SR-69, SR-69A) were placed in the fishes' stomach using the technique of Kendle and Morris (1965). Stomach implantation was decided upon over coelomic implantation because of the large size of the transmitter and the significant proportion of the battery life that would expire during holding of the fish after surgery. Henderson et al. (1966) found that white bass were recaptured more often and thus experienced lower mortality when sham transmitters were implanted in the stomach than when they were surgically implanted. The transmitter was lashed to one end of a 1/8 inch teflon rod with silk thread and a loop approximately 2.5 cm in diameter, perpendicular to the axis of the rod, was formed in the other end. Fish were anaesthetized with tricaine methane sulfonate until they could not right themselves when pushed onto their side. The transmitter was activated, coated with bees wax, lubricated with glycerol, and inserted into the stomach. The looped end of the teflon rod was placed around the glossohyal through 0.5 cm slits in the floor of the mouth and the loop tied with nylon thread. The distance between the transmitter and the loop was sufficient for the transmitter to be located in the anterior region of the stomach.

The time interval between capture and release of the "tagged" fish near the capture site was less than one and one-half hours.

During 1976-1977, transmitters were prepared for implantation by attaching them to teflon rods with vinyl tape. The rods were formed in a V with the loose ends extending away from the transmitter. The activated transmitter was then placed in the fishes' stomach and the teflon rods extended through the last gill arch. The fish used during this time were transported to lab facilities on the lake shore immediately after capture. They were "tagged" and kept in aquaria overnight to insure that they had recovered from the stress of capture and insertion of the transmitter. The fish were released at the point of capture the following morning.

Two fish were implanted with dummy transmitters using the method described above; they were held in aquaria and showed no visible damage when they were sacrificed and dissected after 30 days. One fish that was released in the field with an activated transmitter regurgitated it after 10 days, while 4 other fish kept their transmitters for the duration of observation.

During the winter fish were located by triangulation from two or more siting holes in the ice using a directional hydrophone (Smith-Root Inc., Model SR-70H). A hole was drilled in the ice at the fish's position, and the depth of water and other habitat characteristics were determined. The siting holes were located by triangulation on three or more shore landmarks with a bearing compass. The same siting holes were used when possible, and the hole locations were rechecked until the bearings on all landmarks crossed at a single point when plotted on a map. Maps of the shoreline and landmarks were prepared from enlargements of aerial photographs taken during 1973.

In order to determine the accuracy of locating tagged fish, sitings of single fish were done on 21 occasions from three holes. Usually the bearing lines formed a small triangle when plotted on a map. The intersection of the lines from the two holes nearest to the fish was considered to be the fish's position, while the distance from this point to the farthest angle of the triangle was used to estimate the accuracy. This distance averaged 68 m.

During the summer fish were tracked from a boat which was moved close enough to the fish that the signal strength from the transmitter was equal in all directions. The boat was anchored and the location of the boat was then determined by triangulation on shore landmarks; the depth of water and other habitat characteristics were recorded. Attempts were made to locate the tagged fish three times each day, in the morning, at mid-day, and in the early evening. In most instances we have only plotted the first position each day. Signal strength from the ultrasonic transmitter was reduced by aquatic vegetation which contained air cells, and signals that normally travelled up to a mile were only discernible within 50 m or less. During June, as growth of emergent vegetation progressed, increasing difficulty was encountered in finding the fish.

RESULTS

The nine northern pike that were followed showed considerable variation in the direction and magnitude of displacement from day to day. The gross daily movement (Table 1) was considered to be the linear distance between locations of the fish on successive mornings. Movements varied from 0 to 4000 m per day. The distances moved, when broken down into 200 m intervals, were not significantly different between fish tracked during the summer or winter when analyzed by a G test (Table 1).

None of the pike monitored for more than five days established well defined home ranges (Figs. 1 and 2), although several of them occupied a restricted area for up to nine days (Fig. 1b, d; Fig. 2f, g, h, i). These fish all moved to different areas after a period of time. When the fish moved within confined areas, these areas had a radius of approximately 0.5 km. However, the extent of their total displacements were in areas from one to five km in radius. Individual fish moved over large areas of the lake, but many of them revisited their earlier positions (Fig. 1a, d; Fig. 2a, c).

Characteristics of the habitat utilized by pike are given in Table 2. The pike select vegetated zones of Lac Ste. Anne when possible, mainly during the summer. They were seldom (only 5% of the time) found in water over 4 m deep in the summer, and 78% of their locations were within 300 m of shore. During the winter the submergent vegetation dies and the area of emergent vegetation is reduced by ice cover which reaches to a depth of 75 cm. Pike locations in the winter were significantly less frequent than in the summer within 100 m of

Table 1. The frequency and percent occurrence (in parentheses) of various distances of gross daily movements by northern pike in Lac Ste. Anne.

Distance moved	Winter	Summer
0-199 m	13 (30%)	5 (15%)
200-399 m	10 (23%)	8 (24%)
400-599 m	5 (11%)	8 (24%)
600-799 m	3 (7%)	6 (14%)
800-999 m	2 (5%)	3 (9%)
1000-1199 m	1 (2%)	2 (6%)
1200-1399 m	3 (7%)	0 (0%)
1400-1599 m	3 (7%)	0 (0%)
1600-1799 m	0 (0%)	1 (3%)
1800-1999 m	2 (5%)	0 (0%)
2000 m +	2 (5%)	1 (3%)

gure 1. The locations of 5 northern pike which were followed in the winter. Circles represent observed locations of the fish. Data shown in a and e were obtained in 1973-1974, while b, c, and d were obtained in 1977. Closed triangles represent the release site; open triangles indicate the last location of the fish before the ultrasonic transmitter stopped. The number of days between observations are represented by numbers on the lines between circles.

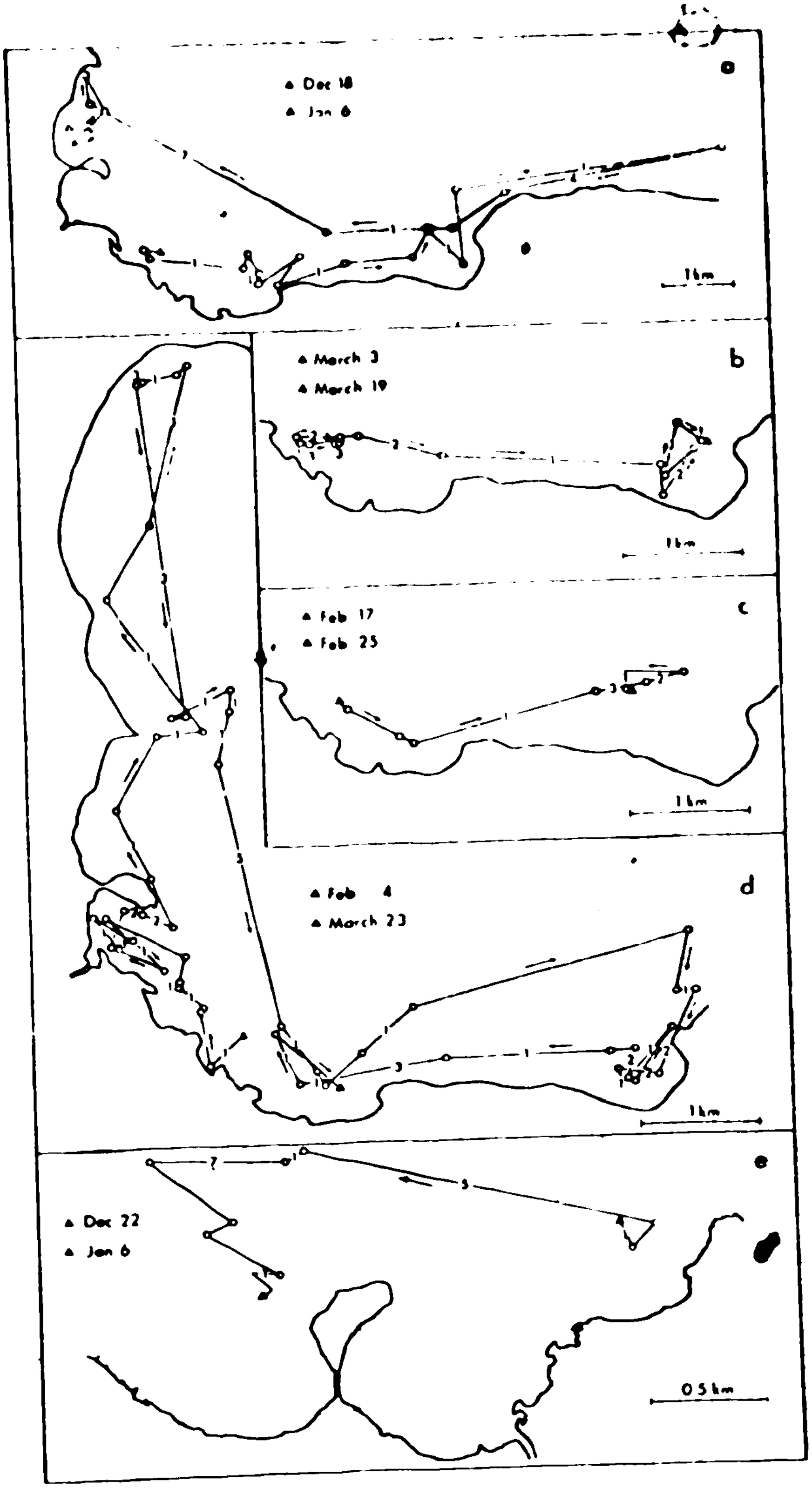

a
▲ Dec 18
▲ Jan 6
1 km
b
▲ March 3
▲ March 19
1 km
c
▲ Feb 17
▲ Feb 25
1 km
d
▲ Feb 4
▲ March 23
1 km
e
▲ Dec 22
▲ Jan 6
0.5 km

Figure 2. The locations of 4 northern pike which were tracked in the summer. Data shown in f, h, and i were obtained in 1974, while g was done in 1976. Symbols are the same as described in Fig. 1.

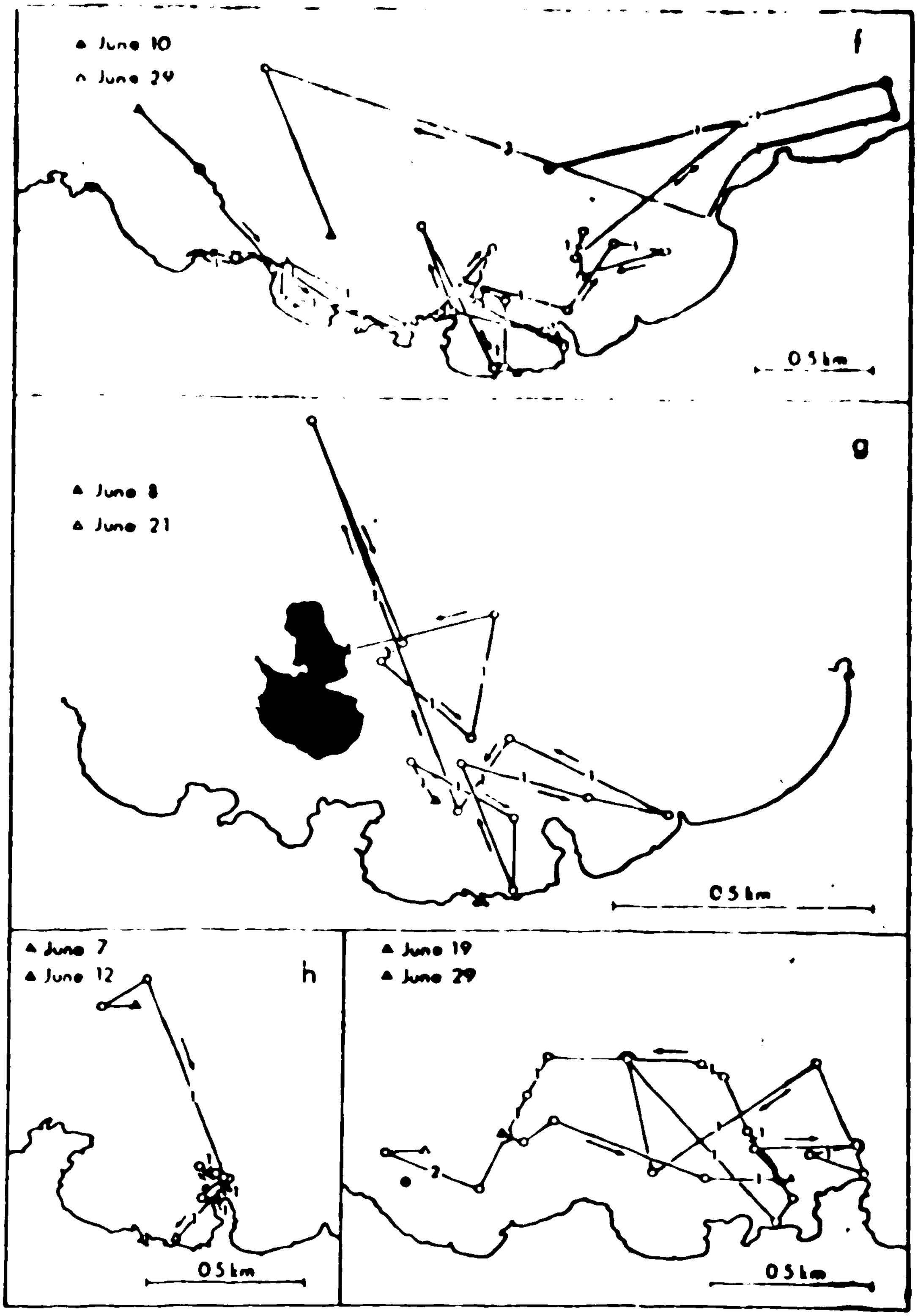
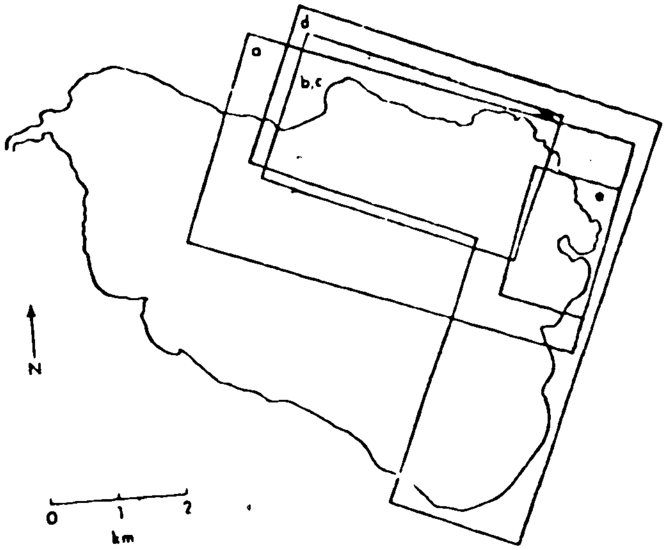
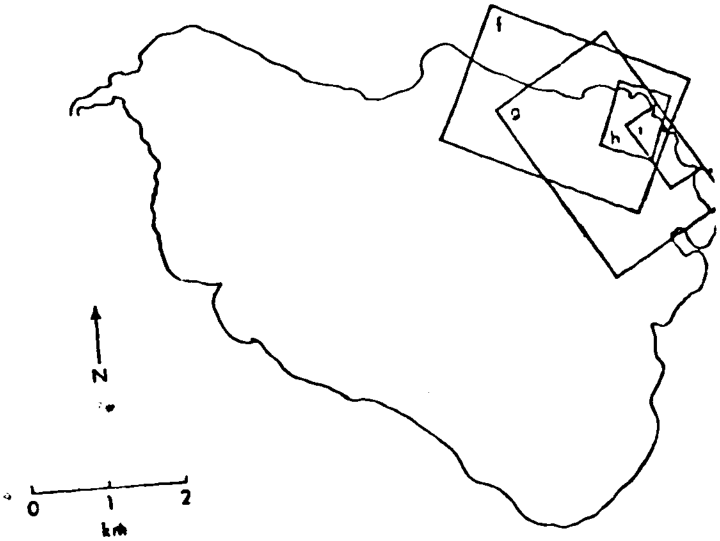

▲ June 10
○ June 29
f
0.5 km
▲ June 8
△ June 21
g
0.5 km
▲ June 7
▲ June 12
h
0.5 km
▲ June 19
▲ June 29
0.5 km

Figure 3. (a) Map of Lac Ste. Anne showing the location on the lake of each area from Fig. 1. (b) Map of Lac Ste. Anne showing the locations of each area from Fig. 2.



(a)



(b)

Table 2. The frequency and percent occurrence of various habitat characteristics selected by northern pike in Lac Ste. Anne. The characteristics followed by asterisks showed significant differences between summer and winter by a G test at the 0.05 probability level.

Characteristic		Summer	Winter
depth:	0-1.9 m	23 (52%)	4 (21%)
	2-3.9 m	19 (43%)	12 (63%)
	4 m +	2 (5%)	3 (16%)
vegetation:	emergent	31 (49%)	2 (12%)
	submergent*	29 (46%)	0 (0%)
	none*	3 (5%)	15 (88%)
distance from shore:	0-99 m*	27 (40%)	21 (21%)
	100-299 m	26 (38%)	54 (53%)
	300-599 m	13 (19%)	23 (23%)
	600 m +	2 (3%)	3 (3%)

shore (G = 5.02, $P < 0.05$), and the depths they utilized were somewhat greater. However, 74% of the sitings were within 300 m of shore and 84% were in depths less than 4 m. In Lac Ste. Anne, areas with depths less than 4 m comprise only 39% of the total surface area of the lake.

DISCUSSION

The northern pike we studied did not have a well defined home range but rather appeared to move at random throughout a relatively narrow zone around the edge of the lake. The distances moved were within the range of 160 to 1600 m per day found by Moen and Henegar (1971) in a tag and recapture study of pike in Lake Oahe, North and South Dakota for time intervals of 2 to 3 months. Our findings are in direct disagreement with the evidence cited by Malinin (1969, 1970b) that pike are relatively sedentary with a home range of 50 to 150 m in diameter where the bottom is flat. However the transmitters he used only lasted for 50 to 60 hrs (Malinin 1971b, 1970a) which is probably insufficient time to define a home range. Makowecki (1973) predicted, based on tag and recapture up to one year later, that northern pike have a restricted home range. Our observation that pike tend to revisit some areas several times could explain Makowecki's observation and lead to the conclusion that pike show little displacement.

Some authors (Stott _et al_. 1963, Funk 1957) have suggested that a population of fish may consist of two groups, one which occupies a restricted area and another group which moves more extensively. Jenkins (1969) reviewed the available data and hypothesized that fish populations in streams may have both transients and residents, and suggested that population density is the factor regulating the number of transients present. Chapman (1962) tested the same hypothesis and found that nomadic fish would occupy restricted areas when they were moved to uninhabited sections of stream. Jenkins (1969) also found that resident fish could only hold stations in areas without a large number of transients. All of the above studies were done in streams, where fish movement is well studied and also where such a division of the population seems more likely because suitable food and space resources are more limited than in a lake.

Our fish were captured by angling in areas fairly close to the shore and weed beds. Gillnet results from Lac Ste. Anne also demonstrate that these areas have the highest pike densities. If Jenkin's theory on transients applies to pike, then we would expect to find the highest proportion of nomadic pike in the shoreline areas, and our sampling for fish to track could have been biased towards using these transients. Either the selection of transients in the present study or the previously mentioned shortcomings of other pike movement studies could explain the discrepancies between our results and those of Malinin and Makowecki.

The areas frequented by northern pike in this study were shallow and near shore. Malinin (1971b) and Kipling and Frost (1970) also found that pike utilized this type of area in rivers and lakes that were quite different from Lac Ste. Anne. Pike locations during the summer could be explained by selection of depth, distance from shore, vegetation, or bottom type. In Lac Ste. Anne, all of these characteristics are closely linked in their occurrence; vegetation is found in shallow water, near shore, and on mud bottoms. No single characteristic from our data can be assigned most importance to pike habitat selection during the summer. In winter, pike appear to select their habitat on the basis of depth and distance from shore. This selection is not very different from summer, except that the vegetation zones are missing.

There were no significant differences between summer and winter in the distance that pike moved. However, during the winter fish moved longer distances (> 1000 m) more frequently than in the summer. Because of the poor transmission of ultrasonic signals in the summer we would more likely have lost fish which moved more than 1000 m.

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Appendix Table 1. The sampling dates, locations, and number of pike collected from Lac Ste. Anne during this study.

Date	Location	Fish caught
March 17-27, 1976	Rock Island	55
May 7-13	Farming Island	93
June 2-4	Gunn	80
July 6	Castle Island	35
August 3-4	Ross Haven	64
August 19	West Basin	61
September 9-13	Gunn	45
October 16-20	Gunn	67
January 16-20, 1977	Castle Island	60
March 2-5	Gunn	69
April 13, 17	Mission Creek	35
April 22	Gunn	38
May 5-7	Gunn	52
May 31-June 1	Gunn	38
June 7	Gunn	51
July 5-11	Gunn	54
August 2-7	Gunn	43
August 31-September 3	Gunn	42
October 5-7	Gunn	60
January 14-31, 1978	Gunn	30
March 27-April 4	Gunn	72
April 25	Gunn	32
May 8-9	Gunn	52
June 5-7	Gunn	81
July 4	Gunn	38
August 1-2	Gunn	37
September 1	Gunn	32
TOTAL (27 collections)	--	1416

Appendix Tab[illegible]. The standard lengths ($\bar{x} \pm$ SD (n)) of each age class of pike collected in 1976, 1977 and 1978 from Lac Ste. Anne.

Age	Year	May	June	July	August
0	76	30.5 ± 3.4 (26)	---	---	13.7 ± 0.6 (7)
	77	31.2 ±12.5 (7)	---	---	33.7 ± 2.6 (4)
	78	32.6 ± 2.4 (11)	---	---	32.3 ± 0.4 (2)
	$\bar{x}$	31.2 ± 5.5 (44)	---	---	22.7 ±10.3 (13)
1	76	40.0 ± 1.9 (27)	31.9 ± 4.0 (31)	---	38.2 ± 2.8 (59)
	77	40.9 ± 1.4 (14)	37.2 ± 6.0 (7)	36.8 ± 3.4 (4)	40.6 ± 1.4 (7)
	78	39.8 ± 1.9 (10)	35.4 ± 2.5 (13)	36.8 ± 2.9 (10)	38.9 ± 2.1 (16)
	$\bar{x}$	40.2 ± 1.8 (51)	33.5 ± 4.5 (51)	36.8 ± 2.9 (14)	39.6 ± 2.7 (82)
2	76	44.8 ± 1.1 (13)	39.7 ± 2.3 (17)	41.4 ± 2.0 (7)	43.6 ± 1.7 (40)
	77	44.3 ± 1.4 (17)	41.6 ± 1.7 (21)	41.2 ± 1.8 (23)	43.8 ± 0.9 (16)
	78	44.0 ± 1.1 (10)	41.4 ± 2.7 (22)	42.8 ± 1.1 (7)	44.8 ± 0.8 (8)
	$\bar{x}$	44.4 ± 1.2 (40)	41.0 ± 2.3 (60)	41.5 ± 1.8 (37)	43.8 ± 1.5 (64)
3	76	48.4 ± 1.2 (8)	44.9 ± 1.1 (17)	45.6 ± 1.2 (12)	47.6 ± 1.6 (17)
	77	48.1 ± 1.8 (13)	45.5 ± 1.0 (37)	45.7 ± 0.8 (9)	48.1 ± 0.9 (8)
	78	48.4 ± 2.1 (17)	45.6 ± 1.2 (18)	46.4 ± 1.3 (8)	48.2 ± 1.7 (6)
	$\bar{x}$	48.3 ± 1.8 (38)	45.3 ± 1.1 (72)	45.9 ± 1.1 (29)	47.9 ± 1.5 (31)
4	76	60 (1)	48.9 ± 1.6 (13)	50.2 ± 2.6 (15)	51.8 ± 1.5 (9)
	77	50.5 (1)	48.1 ± 3.1 (20)	49.7 ± 1.8 (13)	52.4 ± 1.1 (5)
	78	57 (1)	50.4 ± 1.9 (26)	52.4 ± 1.7 (8)	51.3 ± 2.6 (4)
	$\bar{x}$	55.8 ± 4.9 (3)	49.3 ± 2.5 (59)	50.5 ± 2.3 (36)	51.8 ± 1.7 (18)

Appendix Table 2. Continued.

Age	Year	September	October	January	March
0	76	---	32.4 ± 1.5 (4)	---	34.1 ± 4.2 (8)
	77	29.3 ± 1.5 (3)	35.8 ± 3.1 (11)	40 (1)	35.0 ± 3.5 (3)
	78	32.5 ± 0.7 (2)	---	33.8 ± 2.5 (2)	33.6 ± 2.7 (6)
	$\bar{x}$	30.6 ± 2.1 (5)	34.9 ± 3.1 (15)	35.8 ± 4.0 (3)	34.1 ± 3.1 (17)
1	76	39.1 ± 0.5 (4)	40.1 ± 1.5 (21)	---	41.2 ± 1.5 (6)
	77	41.2 ± 2.4 (6)	41.4 ± 1.1 (7)	41.5 ± 1.1 (8)	41.5 ± 1.3 (16)
	78	39.4 ± 2.9 (7)	---	40.5 ± 3.0 (3)	40.1 ± 1.2 (9)
	$\bar{x}$	40.0 ± 2.4 (17)	40.5 ± 1.5 (23)	41.2 ± 1.7 (11)	41.1 ± 1.5 (31)
2	76	42.8 ± 1.5 (16)	44.3 ± 1.5 (22)	---	45.5 ± 1.4 (19)
	77	44.7 ± 1.2 (9)	45.3 ± 1.6 (17)	45.2 ± 1.1 (19)	44.5 ± 0.9 (21)
	78	43.9 ± 0.9 (8)	---	45.1 ± 1.0 (9)	44.3 ± 1.4 (26)
	$\bar{x}$	43.6 ± 1.5 (33)	44.7 ± 1.6 (22)	45.1 ± 1.1 (28)	44.6 ± 1.5 (66)
3	76	45.6 ± 1.4 (14)	46.9 ± [illegible] (11)	---	50.4 ± 2.3 (15)
	77	49.2 ± 2.0 (19)	49.7 ± [illegible].7 (17)	49.2 ± 1.8 (25)	48.5 ± 1.6 (14)
	78	46.9 ± 1.0 (6)	---	50.0 ± 1.8 (11)	48.6 ± 1.6 (33)
	$\bar{x}$	47.6 ± 2.3 (39)	48.6 ± 2.1 (28)	49.4 ± 1.8 (36)	[illegible].7 ± 1.9 (62)
4	76	50.4 ± 2.2 (8)	50.7 ± 2.3 (7)	---	54.6 ± 3.2 (5)
	77	53.5 ± 2.4 (5)	52.1 ± 1.8 (8)	53.4 ± 2.4 ([illegible])	53.0 ± 2.2 (14)
	78	51.7 ± 2.1 (7)	---	54.3 ± 2.2 (5)	52.7 ± 1.9 (15)
	$\bar{x}$	51.7 ± 2.5 (20)	51.5 ± 2.1 (15)	53.8 ± 2.3 (12)	53.1 ± 2.2 (34)

Appendix Table 3. Mean standard length (in mm) of the age classes of prey from Lac Ste. Anne during various months of the year.

Species	Age	Jan.	March	May	June	July	Aug.	Sept.	Oct.
Perch	0	44	44	--	--	--	40	**44**	**44**
	1	76	82	45	50	63	64	**69**	70
	2	110	110	82	84	86	94	**99**	110
	3	--	--	110	110	113	114	115	120
	4	--	--	125	--	--	--	--	--
Shiner	0	30	30	--	--	--	--	**26**	**28**
	1	42	42	30	32	34	42	**42**	**42**
	Ad.	--	--	42	44	48	51	[illegible]	**60**
Burbot	0	--	--	--	--	--	90	--	--
	1	--	--	--	--	--	140	--	--
Sucker	2	--	--	--	--	170	--	--	--

Appendix Table 4. The stomach contents of pike, expressed as percent body weight, for fish captured at various times of day in the summer of 1976. $\bar{x} \pm SD$ (n).

Time	May	June	July	August
2200 to 0200	0.1 ± 0.1 (4)	0.2 ± 0.1 (7)	0.3 ± 0.5 (11)	0.1 ± 0.2 (16)
0200 to 0600	0.5 ± 0.2 (2)	0.2 ± 0.1 (5)	0.1 ± 0.0 (5)	0.1 ± 0.1 (7)
0600 to 1000	0.4 ± 0.2 (5)	0.2 ± 0.1 (7)	0.2 ± 0.2 (7)	0.2 ± 0.2 (13)
1000 to 1400	-- (0)	0.3 ± 0.2 (10)	0.1 ± 0.1 (2)	0.2 ± 0.2 (12)
1400 to 1800	0.4 ± 0.3 (8)	0.2 ± 0.1 (2)	0.3 ± 0.2 (10)	0.1 ± 0.2 (8)
1800 to 2200	-- (0)	0.4 ± 0.1 (2)	-- (0)	-- (0)

Appendix Table 5. Catch results (in number of pike) for one gillent set and pulled every four hours over one 24 hour period every month in the summer of 1976.

Time	May	June	July	August	Total
0200-0600	6	4	2	3	15
0600-1000	6	8	5	4	23
1000-1400	6	6	9	8	29
1400-1800	-	3	-	5	8
1800-2200	0	5	5	8	18
2200-0200	1	0	1	2	4

Appendix Table 6. Some values used for the calculation of an overall energy budget for 3-year-old northern pike from Lac Ste. Anne.

Value	Sex	May	June	July	August	September	October
No. of days		31	30	31	31	10	31
Body weight	M	893 ± 132	941 ± 111	987 ± 57	1085 ± 114	1034 ± 126	1069 ± 115
	F	831 ± 60	920 ± 57	1012 ± 131	1150 ± 88	1151 ± 122	1191 ± 171
R_{met}	M	7.2	7.6	7.8	8.5	8.2	8.4 (2.2)
(kcal/day)	F	6.8	7.4	8.0	8.9	8.9	[illegible] (2.5)
Daily ration	M	8.6	17.0	11.4	6.5	6.6	8.5 (0.4)
(kcal/day)	F	11.6	28.4	19.4	11.3	8.6	10.2 (1.1)
Body energy	M	1057 ± 159			1299 ± 137		1288 ± 135
	F	975 ± 68			1369 ± 103		1503 ± 225
Growth	M	242			-11		—
	F	394			134		—

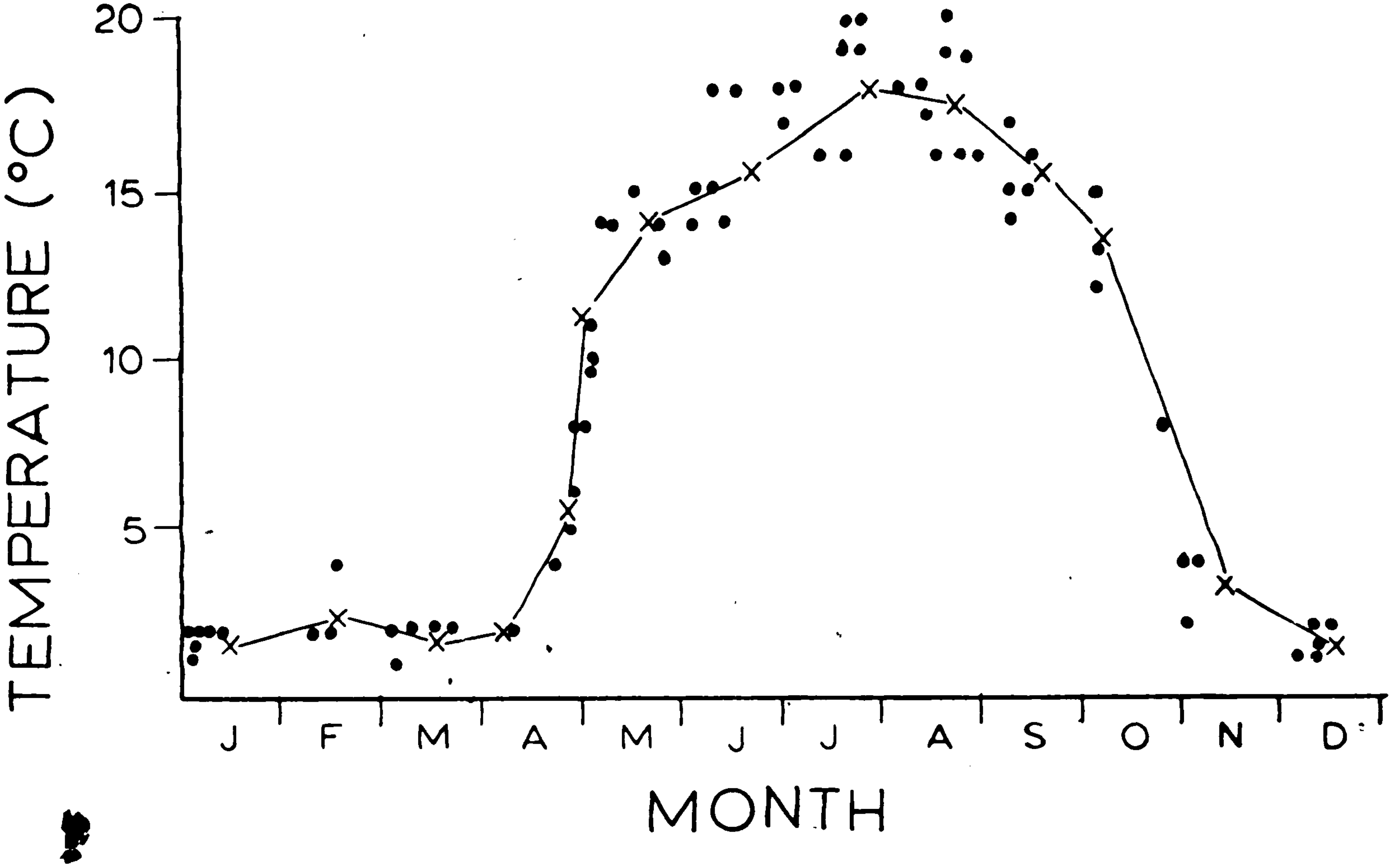
Appendix Table 6. Continued.

Value	Sex	November	December	January	February	March	April
No. of days		30	31	31	28	31	30
Body weight	M	1115	1160	1210 ± 134	1215	1225 ± 88	1119 ± 126
	F	1200	1205	1208 ± 121	1180	1111 ± 161	1193 ± 182
R_{met}	M	1.4	1.5	1.6	1.6	1.6	1.5 (4.1)
	F	1.6	1.6	1.6	1.5	1.5	1.5 (2.5)
Daily ration	M	0.4	0.4	0.4	0.5	0.6	0.6 (0.0)
	F	1.1	1.2	1.2	1.1	0.9	1.0 (0.0)
Body energy	M			1471 ± 164		1409 ± 155	
	F			1709 ± 179		1805 ± 311	
Growth	M	183		-62		-143	
	F	206		96		-138	

Appendix Table 7. Data used to calculate the SDA costs for 3-year-old pike in the summer.

	May	June	July	August	September	Total
		MALES				
Number of days	31	30	31	31	30	
Feeding frequency (days)	3.1	1.9	2.1	3.8	3.5	
Meals per month	10	16.8	14.8	8.2	8.6	
Days SDA per month	17.5	29.4	25.9	14.4	15.1	
SDA cost per day (kcal)	2.4	2.5	2.6	2.8	2.7	
Total SDA cost (kcal)	42	73	67	40	41	263
		FEMALES				
Feeding frequency	2.3	2.2	2.8	2.6	4.2	
Meals per month	13.5	13.6	11.1	11.9	7.1	
Days SDA per month	23.6	23.8	19.4	20.8	12.4	
SDA cost per day	2.2	2.4	2.6	2.9	2.9	
Total SDA cost	52	57	50	60	36	255

Appendix Figure 1. The temperatures at 3 m depth, taken during collecting trips from the Lac Ste. Anne Fish Research Lab in 1966, 1967, 1968, 1969, 1973, 1974, 1976, 1977, and 1978. The line drawn passes through the mean value for each month. These temperatures are not the seasonal averages, since they were taken only one day per month and there is probably a bias in scheduling summer collecting trips during warm weather (with warmer water temperatures).


TEMPERATURE (°C)
20
15
10
5
J
F
M
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MONTH