THE UNIVERSITY OF MANITOBA

POPULATION PARAMETERS AND BIOENERGETIC

DEMANDS OF WALLEYE,

Stizostedion vitreum vitreum (Mitchill),

IN RELATION TO THEIR TROPHIC DYNAMIC ECOLOGY,

WEST BLUE LAKE, MANITOBA

by

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

WINNIPEG, MANITOBA

FALL, 1971

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ACKNOWLEDGEMENTS

ABSTRACT

During 1969-70, 569 walleye age II and older were marked in West Blue Lake of which 56 were recaptured. No short term mortality was found in conjunction with mark and release periods. As well, distribution of marked fish was essentially random, and similar segments (by age) of the population were under examination at all times. Frequency distributions and x^2 tests indicate that net selection was not by age and unlikely to be by size. The May 1969 population, 1090 walleye, decreased to 819 individuals in May 1970, but was augmented by 2100 new recruits in September, 1969. Petersen estimates, the Jolly (1965) approach, and the triple-catch trellis provided similar descriptions of the population. Mortality on a per day basis was small, mean $i = 0.0045$, and was greatest during fall and winter. Growth, and consequently production, was greatest between June and September. Biomass, approximately 800 kg, was stable from year to year, and production, 340 kg, was primarily from younger fish.

Conversion, K_1 ($\frac{\Delta W}{R \Delta t}$) and K_2 ($\frac{\Delta W}{pR \Delta t}$), was affected by neither ration size nor temperature, but decreased with increasing fish size. K_3 conversion ($\frac{\Delta W}{pR-T_R \Delta t}$) was affected only by temperature. Walleye assimilation efficiency was dependent upon diet type (least efficient for invertebrates, and most efficient for fish), and fish size. Maintenance per unit walleye was independent of size but was affected

by temperature. Maintenance requirements, all converted to 20C for various age walleye approximates Winberg's (1956) $T = \alpha w^{\gamma}$ for routine metabolism.

A seasonal cycle in caloric content of whole walleye (less gonads) occurred and was also evident in perch. No such cycle was apparent in invertebrates examined.

Greatest energy contribution to the nutrition of West Blue Lake walleye was by perch and sticklebacks. Greatest numerical contribution was by amphipods and mayflies but both provided less energy.

Laboratory conversion and assimilation efficiency was applied to the natural diet of walleye for an estimation of population intake. The resident population required from 40 to 1860 K cal/kg/day for production, and the intake depended upon season and population structure.

INTRODUCTION

Investigations into quantitative relationships of fish and their food follow three general approaches: defining biomass of food and fish; determining turnover in inorganic materials, such as nitrogen; and establishing energy transformations. Allan (1951) and Johnson (1966) utilized maintenance requirements and gross conversion in the definition of population requirements. In addition, Gerking (1962) has described the turnover of nitrogen in the bluegill sunfish. Mann (1965) located the energy transformation in a river using procedures originally pointed out by Winberg (1956).

The objectives of this study were twofold: a) to determine characteristics of growth, number, survival and ultimately biomass and production of an unexploited population of walleye, Stizostedion v. vitreum (Mitchill), and b) to describe under controlled conditions the effect of temperature, ration, and walleye size on growth, maintenance, and assimilation. The latter aspect of this investigation was based on theoretical reviews of growth and metabolism (Paloheimo and Dickie, 1965, 1966a and b). The stated objectives were fundamental components in understanding production processes in natural systems and were consequently extended to describe seasonal differences in intake required to produce observed production in an unexploited population.

This study utilized the calorie to describe two

primary facets, production and laboratory studies, of the research. All parameters of this closed population were defined in 1969-70 to provide a basis for estimating seasonal energy requirements. Laboratory experiments and analysis of natural feeding were conducted after the population studies to eliminate external influences on the population.

The scope of an investigation into energy transformation in a population inherently results in difficulties both in field and laboratory analysis. Generalization to natural systems upon the basis of controlled experiments is difficult in spite of the conducted experiments which were designed to show the role of specific mechanisms known to influence growth. Nevertheless, the definition of population changes and energy input is worthwhile both in terms of the trophic dynamic ecology of the walleye in West Blue Lake and in terms of fishery management practices.

METHODS AND MATERIALS

West Blue Lake (latitude 51° 36', longitude 100° 55') is located centrally in the Duck Mountain Provincial Park of west-central Manitoba. The lake (160 ha.), described by Bell and Ward (1970), is essentially a closed system with no permanent inlet or outlet. The characteristics of stratification in oxygen and temperature (Bell and Ward, ibid) are relatively static from year to year and are subject to rather minor changes in magnitude.

Throughout the course of this investigation, provincial authorities prohibited all but experimental fishing in the lake; therefore, the population demonstrates primarily induced changes of natural causes.

VITAL STATISTICS OF THE POPULATION

Capture and Handling

Fish utilized throughout this study were captured in a standard gang composed of three sections each 30.5 m long and 1.8 m deep. Mesh sizes were 3.81, 6.35, and 8.89 cm, stretched measure.

As the mean depth of the lake is 11 m, and the basins have steeply sloping sides, the sites for capture are limited (Fig. 1). A standard gang was set at one of the possible sites approximately 30 minutes prior to sunset

4

Fig. 1.　West Blue Lake showing location of gill
netting sites.

5 15
25
30
15 5
N

I KILOMETER
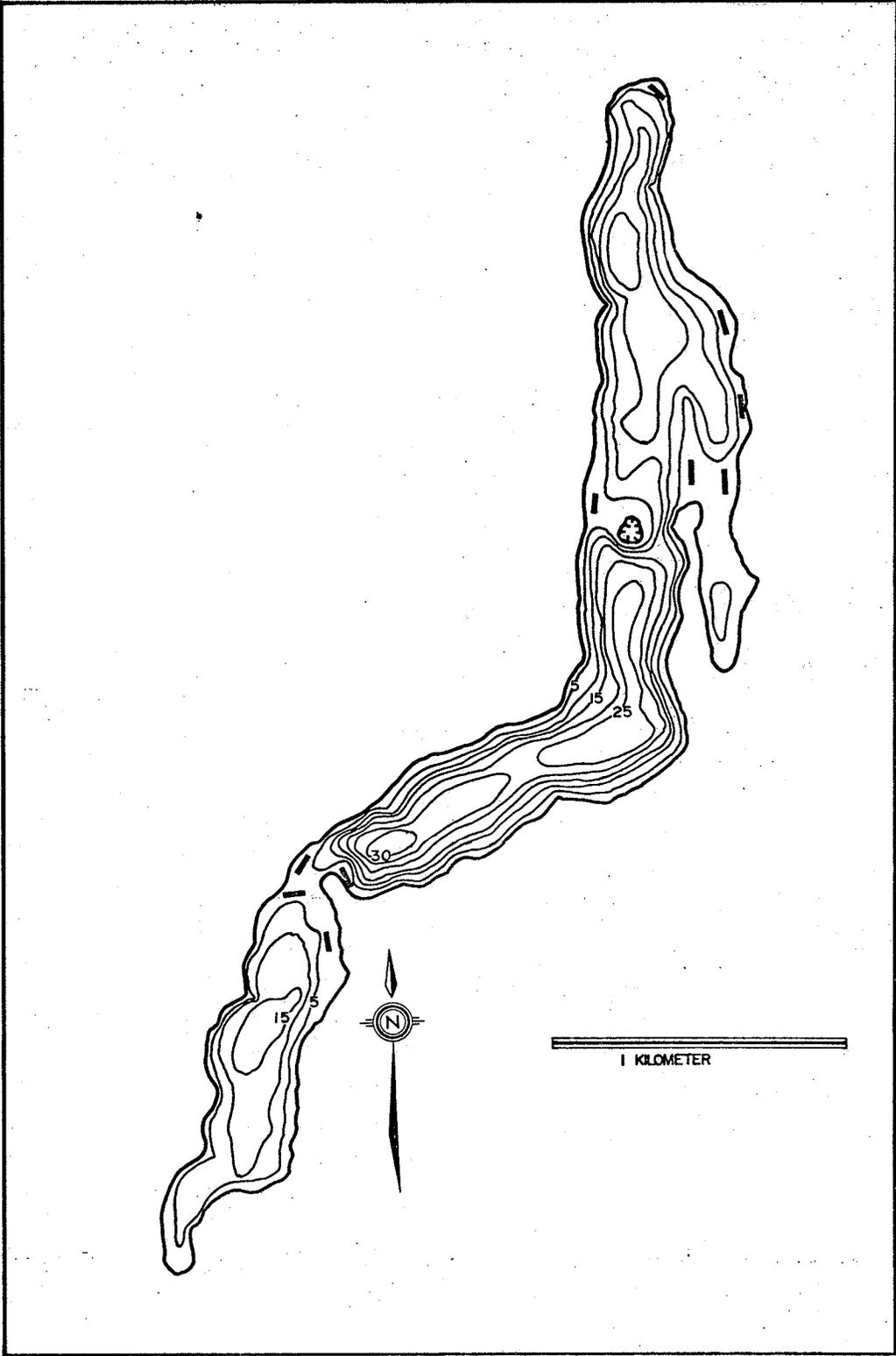
in 3-15 m of water. Nets had been installed in 3-25 m of
water on bottom and mid-water during all times of day;
however, all captures were limited to dark hours and occurred
in water less than 15 m in depth. Duration of nocturnal
fishing depended upon the catch and environmental conditions.
After installation, nets were continuously patrolled by boat
and captured fish were either placed immediately in a "live
box", or transported to it after storage for 3 to 5 minutes
in 250 l of water maintained at air saturation with oxygen.
No entangled fish remained in the net longer than 10 minutes.
Fishing time in each basin was approximately equal for any
marking and release period.

Captured fish were retained overnight in a live box
constructed from a plastic boat (length 2.55 m; width 1.22 m;
mean depth 0.38 m) drilled with holes so that it could be
almost filled with water. In June, this live box was sub-
divided to facilitate the separation of each night's catch
by mesh size. A maximum of 40 walleye were retained in the
live box from each night of sampling. The live box was
anchored approximately 30 m offshore to permit ventilation
by surface currents.

The following morning, after fish were examined
for ill-effects of handling, the total length (from tip of
the snout to the farthest projection of compressed lobes of
the caudal fin) and fork length (from tip of the snout to
angle between lobes of caudal fin) were obtained for each
fish. In addition, a scale sample was taken, using a forceps,
from the left side just above the lateral line on a diagonal
between the posterior insertion of the second dorsal and the

anterior insertion of the anal fin. Fish were then marked
with an injector type tagging gun (Dell, 1968).

Mortality Trials

In conjunction with each marking and release experi-
ment (except during May 1969) a mortality trial was conducted
on shore. Eight or twelve fish were held in two lots of equal
numbers of marked and unmarked individuals in 560 l fibreglass
tanks. Walleye utilized in holding trials were approximately
paired in terms of length. One member of each pair was
subjected to procedures identical to those applied to fish
involved in the regular periods of marking and release. The
other member of the pair was transferred to the holding tanks
with a minimum of handling. Water was supplied by pumps with
intakes installed 1.5 m below the surface of the lake and
provided a tank turnover time of 45 minutes. Experiment
duration was seven to twenty-seven days. No food was supplied
during holding. Temperatures in each tank were recorded daily
with Taylor maximum and minimum registering thermometers.
Dissolved Oxygen, determined using the Azide modification of
the Winkler method, was determined several times at irregular
intervals during the holding periods.

Estimation of Abundance

Six mark and recapture experiments were carried out
during 1969-70 (Table I). It was originally intended that
several techniques for the assessment of population character-
istics be employed; however, only a limited approach was feasible.

Population abundance at six times during 1969-70
was estimated by the Petersen technique (see Ricker, 1958).
Each estimate was originally intended to be based on samples
of 100 fish, captured during each of the six sampling periods.
In West Blue Lake, the new recruits appearing in the population
are readily recognizable by their size and were marked and
released as a separate cohort in September 1969 (Table I).
Any analysis of canimal populations involving mark and recapture
is affected by various assumptions (Ricker, 1958); therefore,
as many assumptions as possible were investigated. One
requirement of abundance estimates in that an equal (or
measurable) mortality occurs within marked and unmarked
populations. If this stipulation is valid, captures and
recaptures subsequent to initial marking can be summed.
Since short-term holding trials indicated no mortality, I
chose to base each estimate on adjacent capture periods, thus
eliminating the possibility of long-term mortality. Remaining
assumptions affecting population estimates, defined in terms
of applicability to this study, are presented later.

Because of the ease of separation of new recruits,
from the May 1969 population, the population can be monitored
in terms of total number (all fish, including new recruits)
and original number. Throughout this investigation the
population was generally considered as being those fish of
total length greater than 25 cm.

The observed population was stratified further
into age groups by locating proportions of each age group
in the catch and apportioning $\hat{N}$ accordingly. Marks and

recaptures for each age were too small to permit separate population estimates for each age.

Natural Mortality

Survival rates can be derived from comparison of recaptures to the marks released by the following procedure:

$$\hat{S}_{12} = \frac{M_2 \ (R_{13})}{M_1 \ (R_{23}+1)}$$ where $\hat{S}_{12}$ = survival rate between times 1 and 2

M_1 = marks released at time 1

M_2 = marks released at time 2

R_{13} = recaptures from M_1 at time 3

R_{23} = recaptures from M_2 at time 3

In this instance, mortality is a result of natural causes; therefore, since $s = (1 - a)$ where i = total instantaneous mortality for that period $i = -\log_e s$

Symbolism here is identical to that of Ricker (1958); however, estimation of $\hat{S}_{12}$ is an adaptation of Ricker's equation 5.2. In this case, the recaptures are in a point of time rather than occurring over an extended period. Statistical limits for all estimates are those described by Ricker (1958). Since recaptures for any age group were relatively small, survival - consequently mortality - applies to the whole population.

In addition to population estimates obtained using the Petersen procedure, I calculated estimates of N, s, and r (recruitment) by procedures outlined by Jolly (1965). As well, for periods of approximately constant recruitment and mortality, the triple-catch trellis (Ricker, 1958), was used to obtain estimates of walleye abundance.

Growth

Estimates of seasonal growth can be determined by either direct or indirect approaches. Since only lengths were obtained from any sample of walleye, length increments provided the only direct approach available.

To define growth by the indirect method, several scales from one fish were mounted on an acetate slide and impressions made using a roller press. Mounted scale impressions were then examined using a Bausch & Lomb projector (magnification of 43.5X, determined by a calibrated stage micrometer). For each fish, the anterior scale radius from the focus, and the distance of each annulus from the focus was recorded. Each slide was examined twice and disagreement resulted in further reading. A linear regression equation was found suitable for describing the relationship between scale radius and fork length.

Annulus formation in most West Blue Lake walleye occurs during the last week in June (Glenn, MS 1969); therefore the growing season was considered as being the period from the end of June 1969 to the end of June 1970. Fish captured during this period were utilized to assess seasonal growth. The increment from annulus to time of capture was determined as follows:

1) An estimated scale radius from focus to the scale periphery was determined for each fish by using its fork length in the scale radius-fork length linear equation.

2) This theoretical distance was then compared to the actual measured distance to provide a correction term for all measurements for that particular individual (Hile, 1941).

3) The distance ᐃL was determined by subtracting the distance of the focus to the periphery from the distance of the focus to the outside annulus.

4) The distance between each annuli was located using the above procedure.

5) Weight at time of capture and last annulus was found using $\log W = -5.463 + 3.163 \log L$ where W = weight and L = total length (Glenn, MS 1969).

6) The difference, ᐃG, was obtained by subtraction.

Relative growth rates were calculated using:

$$h = \frac{S_2 - S_1}{S_1}$$

where h is the relative growth rate, and S, in terms of length or weight, refers to size at times one and two. Relative rates were transformed to instantaneous rates (g) expressed on a daily basis $(g = \log_e (h+1))$.

Biomass and Production

Biomass changes in a stock are dependent upon the initial biomass (B_1) and instantaneous rates of growth (g) and mortality (i). Therefore, average biomass of the stock $(\bar{B})$, defined as all members of the population 25 cm or greater in total length, was determined by:

$$\bar{B} = \frac{B_1 (e^{g-i} - 1)}{g - i} \qquad (g > i)$$

$$\text{or } \bar{B} = \frac{B_1 (1 - e^{-(i-g)})}{-(i - g)} \qquad (g < i)$$

In addition to describing $\bar{B}$ by using instantaneous rates, the average biomass was found by using the

arithmetic mean of two adjacent estimates of biomass, i.e
$\frac{B_1 + B_2}{2}$ as estimates were made within a short interval
(Chapman, 1968). In this case, results obtained by both
techniques were only slightly different; therefore, the
latter, more straightforward approach was utilized in
describing the population energy demands.

As well, production (total proliferation of fish
flesh including those that do not survive to end of Δ t) was
calculated for each time period using $P = g \overline{B}$.

LABORATORY FOOD STUDIES

Capture and Transport

Thirty-three walleye, age II to VI, were captured
in a standard gang during the period between May 22 and 26,
1970, stored in the 560 l tanks on the lakeshore, and trans-
ported to the Department of Zoology, University of Manitoba
on May 26, 1970. Transportation took 4.5 hours from the
field station to the university. Anesthetized fish (MS222
at 75,000 ppm) were transported in two plastic tanks of 455
and 270 l capacity. Water was maintained between 6 and 8C
by ice, and oxygen was kept at air saturation using an aerator
operating on a 12V wet cell battery. Fish were upright and
mobile, but quiescent. On arrival, all fish were placed in
one 2730 l fibreglass tank and held at 8C.

Holding Conditions

The water system for the aquatic holding facilities utilizes the domestic supply of the city of Winnipeg. Incoming water is passed through activated charcoal filters to remove chlorine. Dechlorinated water is available from three lines at 3.3, 11.7 and 26.7C. All plumbing for the system is PVC (polyvinylchloride). Air saturation with oxygen is 100% (3.3 and 11.7C lines) and 85% (at 26.7C). Alkalinity of all three supply lines is 120 mg/l and pH varies from 8.5 to 8.9.

Temperature control in holding tanks and all feeding experiments was achieved using a Power Series 440 Fotoguard mixing valve. The mixing valve was modified so that all three temperatures could be united, yielding a wider temperature range and higher oxygen saturation. Temperature adjustments were made, if necessary, twice daily. All animals under experimental conditions were subjected to a diel cycle of 14 hours light and 10 hours dark. All tanks, except when stated, were 560 l fibreglass tanks covered by a translucent green fibreglass cover.

To minimize the incidence of infections, malachite green, at an initial concentration of 150 mg/l, was administered to walleye soon after their arrival at the Zoology facilities. Residence time of the fungicide was approximately 1.5 hours and rapid dilution occurred during this period.

Experimental Treatment

Food used in all experiments (excluding those to estimate assimilation) was a cyprinid, the emerald shiner,

Notropis atherinoides (Rafinesque), captured by seining
at Delta Marsh on Lake Manitoba on May 14 to 16, 1970.
Most of these minnows were frozen in sealed, sterile, plastic
Whirl-Pak bags. The remainder were maintained live as food
for fish age III[+] and older. Bimonthly samples of the frozen
food were analysed to define gross change in caloric content
during experimentation.

After holding for one week at 8C, food in approxi-
mately 100g units was placed in the tank once daily. Surplus
food was removed after one hour. This practice was continued
until most fish readily accepted the food. Fish were allotted
to the experimental tanks and acclimated to the new conditions.
Individuals in an experimental group were closely matched, each
group having a narrow range in weight. Those individuals not
under experimental conditions were kept at 12C and fed at 3%
of body weight per day.

Individuals used to assess growth and maintenance
requirements were acclimated from 8 to 12C to the new temp-
erature at the rate of 1 degree change per day. Each experi-
mental group was then subjected to experimental conditions of
food and temperature for two weeks before an experiment was
considered started. Frozen emerald shiners were the staple
food for all II[+] fish under conditions to determine growth
and maintenance. A suitable unit of food was partially thawed,
counted when amounts introduced were less than 20g, and weighed
using a top loading balance accurate to $\pm$ 0.01g. Walleye
aged III[+] and older refused to accept dead food; therefore,
size comparisons necessitated using live emerald shiners of

known energy content. Live weight was obtained by introducing the minnows into a tared 500 ml beaker containing aerated tank water. All walleye were fed six days per week at the rate of one food lot per day. Walleye were measured and weighed, using the top loading balance, on the seventh day after being anesthetized in a solution of 25,000 ppm MS222, and blotted dry. The amount of food administered to those on maintenance diet was adjusted daily until walleye attained a constant weight for a period of 3 to 4 weeks. Overflow of all tanks was screened by a double layer of nylon seine net to trap all excess food. Screens were removed and cleaned daily. Tanks were cleaned weekly as the turnover in the 560 l tanks, once per 25 minutes, was insufficient to remove all excreta.

To assess assimilation of major natural items of the diet, walleye were acclimated to 12 and 20C in 40 and 220 l glass aquaria. Large food items (perch, _Perca flavescens fluviatalis_; and crayfish, _Orconectis virilis_) were placed in the pharynx and were voluntarily swallowed by all walleye. Smaller organisms (_Gammarus lacustris_ and emerald shiners) were introduced into the stomach by a force-feeder consisting of a plunger in a smooth Tygon plastic tube. All foods except emerald shiners were obtained from West Blue Lake. Initial experiments defined the time between ingestion and egestion; therefore, individuals were continuously observed at the time of expected feces emission. Feces were collected within an hour of emission using a large pipette. This concentrate of water and feces was subsequently strained through a 53 micron copper sieve. Feces were in the form of solid streamers,

and when placed on the screen, remained suspended in a large bead of water. All collected feces were oven-dried at 105C until a constant weight was reached. Dry weights were the only feasible way of expressing the magnitude of emission since water uptake frequently occurred even during the short time before collection. To test for complete collection of feces, three tanks were cleared in the normal way and then filtered through a Whatman No. 1 filter. These filters were then compared to filters through which a similar volume of water, taken directly from the main water lines, has been passed.

NATURAL FEEDING

A standard net was installed at one of the sampling sites (Fig. 1) 1.5 to 2 hours after sunset. Five separate collections were made of walleye aged II[+] and older. Captured animals were immediately removed from the net, placed in plastic bags, and frozen at -25C for future determination of walleye caloric content, and species number and weight of ingested foods.

The stomach was removed while the walleye was still completely frozen. The excised gut was opened and all contents were removed as a solid block. The gastro-intestinal tract was then replaced and the fish and its empty digestive tract kept frozen until caloric analysis commenced. Material found in the gut was thawed at room temperature, then sorted into taxonomic groups and counted. Members of each taxa were

blotted using paper towels and subsequently weighed to $\pm$ 0.0001g (wet weight) using a single-beam Sartorius analytical balance.

Food items in walleye stomachs were not analysed calorically since energy removal may be immediate on ingestion and time of ingestion was unknown. A sample of 5 to 8 walleye was retained from each collection period for caloric analysis after gut contents and gonads were removed. The remaining fish from each collection were supplied to the Freshwater Institute, Fisheries Research Board of Canada for other investigations concerning Manitoba walleye.

In conjunction with walleye collections for gut analysis, live samples of the major food organisms were obtained directly from West Blue Lake. Gammarus lacustris were removed manually from samples of detritus and submerged aquatic vegetation. Dr. N.B. Snow, utilizing underwater diving apparatus, obtained samples of O. virilis and Haemopsis sp. Samples of age 0$^+$ perch were supplied by B. Wong and older members of this species by M.R. Falk. All samples were generally weighed live, then frozen for later caloric determination. Wherever possible, frozen samples were measured to aid interpretation of materials found in gut samples. Other bases for comparison of weight or individuals in the gut resulted from seasonal growth patterns of yellow perch in West Blue Lake described by B. Wong and M.R. Falk. Only live samples from the lake were combusted to provide caloric values of materials ingested by walleye.

CALORIMETRY

All samples used to determine caloric content were weighed live (wet weight) and then dried at 105C until a constant weight was attained (dry weight). Duration of drying was from 3 (for small organisms) to 8 days (for adult walleye). If storage after drying was necessary, samples were placed in desiccators with either silica gel or phosphorus pentoxide (P_2O_5) as desiccants.

All walleye were pulverized individually in a Waring 2-speed blender until the dried pulverate was homogeneous. Approximately 50g was then returned to the oven where it was re-dried. Each estimate for caloric value of walleye tissue was the mean of two determinations. If values for the two combustions differed by more than 125 cal/g, an additional sample was burned. From one walleye pulverized in the blender, 5 samples were taken and combusted to define the degree of homogeneity attained by this technique. Smaller organisms were ground to a fine powder manually in either a porcelain or agate mortar and pestle. All perch older than age 0 were processed in the manner described for walleye.

Organisms yielding 0.75g or more of dried material were combusted in a Gallenkamp automatic adiabatic bomb calorimeter. The instrument was regularly standardized using benzoic acid (6318 cals/g) as a standard fuel. Heat capacity of the bomb did not alter throughout analysis (2506.0 cal. per degree C rise in temperature of the water jacket), but was nevertheless determined weekly.

All organisms yielding less than 0.75g of dried

material were combusted in a Phillipson micro-bomb calorimeter. This instrument, described originally by Phillipson (1964), was supplied by Gentry and Wiegert Instruments, Inc. Temperature rise on combustion of a sample in 28 atmospheres (400 psi) of oxygen is measured by thermocouples in contact with the stainless steel bomb. The recording potentiometer used was a Honeywell Elektronic 19. Samples were between 8 and 40 mg, therefore only the 0.2 and 0.5 mv scales were required. A linear relation between mv deflection and caloric content (measured by the changing temperature of the thermocouples) occurs between the two scales. This instrument, as well, was standardized weekly using benzoic acid as a standard fuel. All biological samples for combustion in the Phillipson microbomb were dried and stored as previously described.

In order to obtain the percent ash content of samples, the dried material was placed in pre-combusted aluminum foil weighing dishes and heated at 500C for 24 hours. Caloric content was expressed as cal/g dry weight and values for ash content were included whenever determination was possible.

TERMINOLOGY AND STATISTICAL ANALYSIS

As a result of inconsistent usage and frequent ambiguity, the terms of importance to this study must be defined. Production and biomass have been defined symbolically earlier in this section; however, an additional term - biocontent - referring to the energy stored at any one time

by the designated population will be used in the calculation of energy demand.

The basic energy equation for an individual or a population may be written as $\frac{\Delta W}{\Delta t} = pR-T$ where the energy deposition in terms of growth during any time Δt is the resultant of the ration R (corrected to that which is available by pR) and the total metabolic expenditure T. It has been shown (Paloheimo and Dickie, 1965) that $T = \alpha W^{\gamma}$ and $\log T = \log \alpha + \gamma \log W$, where W is the weight, α is a constant defining the level of metabolic expenditure and γ defines the rate of metabolic expenditure with weight. These relationships, discussed in detail by Paloheimo and Dickie (ibid), are the basis for the description of energy transformation by the walleye. Throughout this study the coefficient for availability of the ration - p - is determined by the difference between ingested ration and the material egested as feces. Winberg (1956) states that disregarding excretion of soluble wastes results in an error of less than 3% of the energy consumed.

From the basic energy equation, efficiencies of growth (K) for a particular species may be determined. Two forms are possible $\left(K_1 = \frac{\Delta W}{R \Delta t} \text{ and } K_2 = \frac{\Delta W}{pR \Delta t} \right)$ and are termed growth coefficients of the first and second order respectively. The effect of fish and ration size on K values are defined in this investigation. In addition, for a particular ration size, the metabolic expenditure T can be obtained by $T = pR - \frac{\Delta W}{\Delta t}$. It is possible, from solution for T in the maintenance experiments, where $\frac{\Delta W}{\Delta t} = 0$ that

the parameters, α and γ, can be described from nutrition
studies for walleye. By applying the line of best fit to
maintenance requirements of various sizes of walleye and to
requirements corrected to a common temperature (20C), both
α and γ can be obtained from the log-log plot. As well,
K_3 ($K_3 = \frac{\Delta W}{pRAt-T}$), where T is the standard metabolic require-
ment, represents the conversion of energy truly available to
walleye for growth.

RESULTS

VITAL STATISTICS OF THE POPULATION

Periods of marking, and consequently recapture, were relatively short varying between four and twelve days (Table 1). Two additional periods were scheduled for mark and release (early August 1969, and early April 1970). In April, nets were placed beneath the ice in normal sampling locations and monitored throughout the day, but only four walleye were captured. During August, captured fish seemed particularly susceptible to handling and mortality was high. Consequently, data from the August sample was utilized only in growth studies.

No fish was recaptured twice. During May and June 1969, only fish greater than 25cm were marked (age II^+ fish and older); however, from September onwards, the samples included new recruits (two years old in late June 1969).

Mortality Trials

Short term mortality trials indicated no mortality of marked and unmarked fish in 7 to 28 days (Table II). Mortality occurred during the July 19 to 27 holding experiment. One unmarked and two marked fish died, all from different pairs (Table II). Temperature altered during most trials (Table II), and a slight diel change occurred. Dissolved oxygen was between 9.7 and 12.2 mg/1 during experimentation. Although mortality was higher among marked

Table I. Numbers of walleye captured, released, marked and recaptured from May 1969 to June 1970 in West Blue Lake

Marking period	Number captured		Number released	Number marked	Recaptures from marking period				
					1	2	3	4	5
May 14–20, 1969	111		111	111	—	—	—	—	—
June 16–22	107		107	97	10	—	—	—	—
Sept. 3–12	95(	III+)a	95	81	8	6	—	—	—
	133(	II+)b	133	119					
Oct. 5–12	86		86	79	2	3	2	—	—
May 18–26, 1970	117		97	83	3	4	4	3	—
June 15–19	97		82	—	2	1	3	2	3

a excludes recruitment

b includes recruited individuals released as a cohort.

than unmarked fish, a marking and release experiment was not conducted concurrently (Table I). The differential mortality indicated did not necessarily apply to any enumeration experiments conducted. In fact, other trials (Table I) provided no evidence that marking and handling resulted in mortality to fish used in estimating abundance.

This lack of mortality demonstrated in holding trials was supported by observations made during periods of marking and release. Walleye were extremely hardy and when handled with reasonable care showed no ill effects from normal handling procedures. No carcasses were seen during regular shoreline patrols following marking periods, even though the bottom was usually observable up to depths of 5 of 6 m, again indicating an absence of mortality from handling and marking.

Background to Mark and Release Experiments

Although samples of recaptured fish were too small to permit analysis for randomness of distribution, recapture data did allow comparisons among numbers recaptured in the three basins. Assuming random distribution, the probability of recapture would be the same in each basin and independent of release site.

These data, although scanty, do indicate considerable movement of fish between basins. However, the assumption of random distribution was not apparently true for all basins. The effect of small recapture samples is indicated in recapture data for basin 1. Data does not readily support the hypothesis of

Table II. Effects of handling and marking on walleye survival.

Duration of experiment	No. marked and unmarked	No. per tank	Tank temperatures (C)	Mortality marked	Mortality unmarked
June 24–July 21, 1969	8	4	12.2 increased to 16.6	0	0
July 19–27	12	6	14.4 increased to 17.7	2	1
Sept. 7–14	8	4	12.2 decreased to 10.9	0	0
Oct. 6–13	8	4	7.4 decreased to 7.0	0	0
May 20–28, 1970	8	4	6.0	0	0

random distribution, but does indicate the absence of discrete subpopulations in West Blue Lake.

Comparison between sites of release (numbers released are in parenthesis) and point of recapture for walleye in each basin of West Blue Lake, 1969-70.

Point of Release	Point of Recapture	Number Recaptured	Probability of Recapture
B_1 (147)	B_1	4	0.03
	B_2	2	0.02
	B_3	2	0.01
B_2 (110)	B_1	4	0.03
	B_2	2	0.02
	B_3	5	0.02
B_3 (216)	B_1	13	0.08
	B_2	12	0.10
	B_3	12	0.06

No. Recaptured at Release Point = 18

Rates of recapture of walleye age II to VI were assumed to be constant between adjacent mark and release periods as well as the whole experimental period. The validity of this hypothesis was tested (Table III) using a 2x5 chi-square analysis. Comparison of recapture to those not recaptured (Table III) indicated that no significant difference existed in rates of recapture between adjacent periods and during the entire experiment.

Incomplete reporting of marks did not occur in

Table III. Results of chi-square tests of the hypothesis that rates of recapture for fish age II to VI were similar between adjacent capture periods and for the entire 1969-70 period.

Marking date	Recapture date	Total no. obs'ns	x^2
May 14-20, 1969	June 16-22, 1969	96	1.99 ns
June 16-22,1969	Sept. 3-12, 1969	96	1.90 ns
Sept. 3-12, 1969	Oct. 5-12, 1969	115	1.29 ns
Oct. 5-12, 1969	May 18-26, 1970	79	1.27 ns
all fish, 1969-70		386	5.089 ns

this study as individuals were each given a numbered tag.
Two fish caught in June 1970 had lost their mark; however,
the tag anchor was still imbedded in the flesh. Both
individuals were probably tagged in May of June, 1969.
Tag losses only affected estimates using the Jolly (1965)
procedure.

Throughout this investigation, a total of 792
walleye were captured by gill net for various aspects of the
research program. No fish were taken during the day even
though, on rare occasions, walleye were observed in 3 to 7
m of water. An apparent onshore migration takes place
coincident with the onset of darkness, followed by an
emigration to deeper areas just before dawn.

A total of 390 walleye, age II to VIII years, were
identified by the mesh size used to capture them. During
1969-70, there were few age III^+ fish, probably the most
vulnerable to the 6.35cm net. Therefore, the incidence of
this age group is overshadowed by the capture of more abundant
ages. The 3.81cm was highly effective in capturing walleye
230 to 280mm in fork length (Fig. 2), and only few older
fish (approximately 4-6%) became entangled. The 8.89cm net
proved most effective in capturing fish of lengths 400 to
480mm (Fig. 2), but the descending limb of the frequency
distribution was extended by the influence of a few larger
fish in the sample of 72 walleye. Both the 3.81 and 8.89cm
gill nets exhibited typical frequency distributions although
showing the effect of entanglement of a few larger fish.

Fig. 2.   Length frequency distributions of walleyes captured
by 3.81, 6.35 and 8.89cm gill nets in West Blue Lake, 1969-70.
N represents number captured in each mesh.
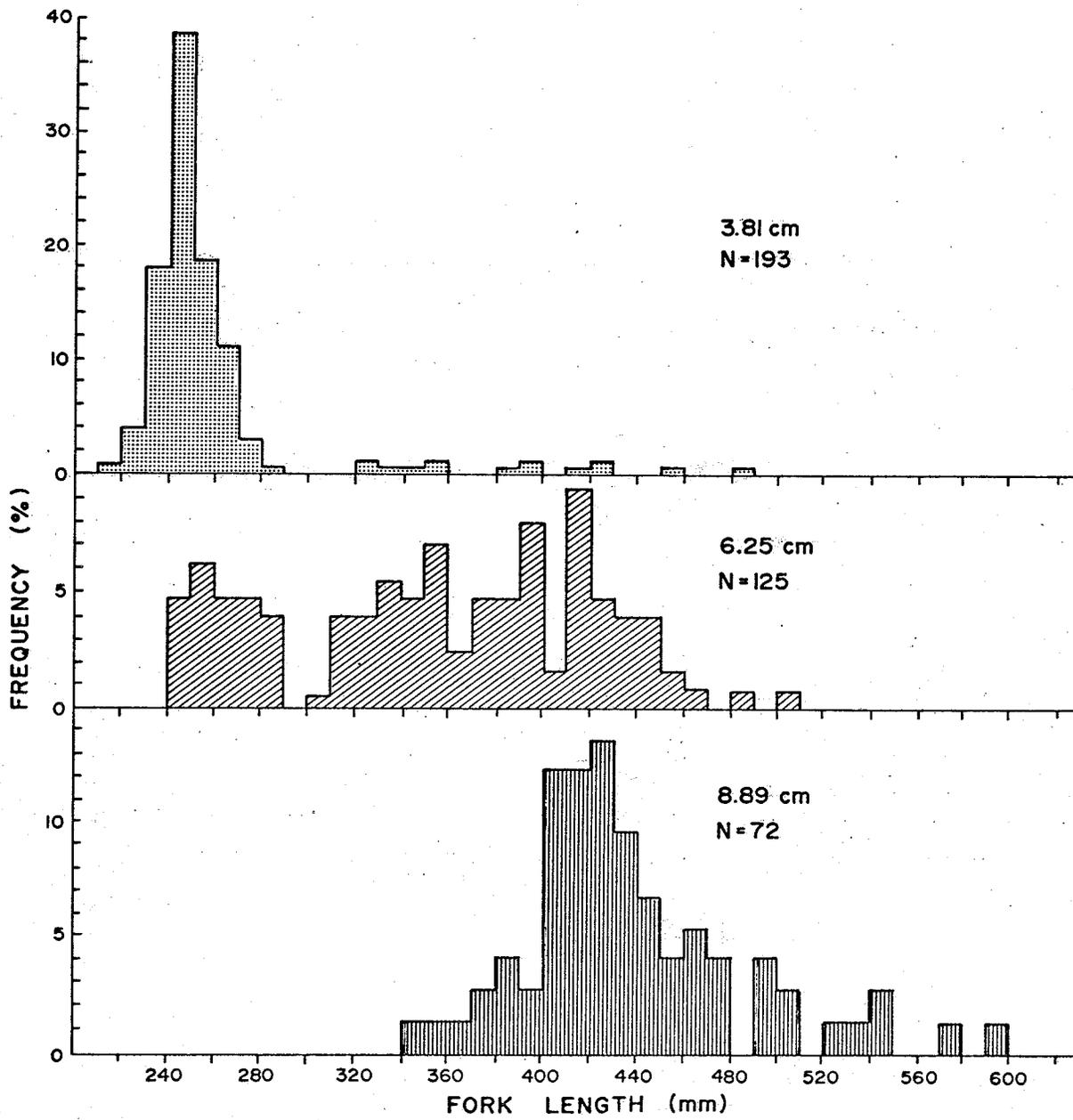
Abundance Estimates

New recruits, determined by age and length analysis, could be excluded or included in population estimates. The population originally described in May 1969 (Table IV) declined in estimated number. Limits located for $\hat{N}_1$ overlap, but, after one year, the population was only slightly less abundant than the May 1969 population. New individuals entering the catchable population in September more than doubled the number originally estimated by the Petersen procedure in May 1969. The maximum number within the stipulated size range occurred in the fall (Table IV). The number estimated for May 1969 was not appreciably altered, but new recruits greatly augmented the initial population. The population including recruits ($\hat{N}_2$) suffered overwinter losses and decreased to a level only slightly higher to that of the previous spring (Table IV).

In estimates of N using the standard Petersen procedure, the bias is approximated by $100e^{-MC/N}$ and becomes negligible when the product of the two sample sizes (MxC) exceeds $\hat{N}$ by a factor of 3 or 4 (Robson and Regier, 1964). In only one instance, May 1970, was the ratio of MC/N small enough (1.97) to introduce a significant bias into the estimate of N_1. The bias applying to other estimates was negligible, and consequently, the average estimates of N can be considered as $0.95\ N$, demonstrating only a slight negative bias.

The technique of multiple mark and recapture analysis outlined by Jolly (1965) considered both immigration

Table IV. Estimates of West Blue Lake walleye abundance excluding ($\hat{N}_1$) and including recruitment ($\hat{N}_2$), standard deviations indicated in parenthesis.

Period	$\hat{N}_1$	$\hat{N}_2$
May 14-20, 1969	1090(298)	1090(298)
June 16-22	1330(450)	1330(450)
Sept. 3-12	1350(654)	3451(1690)
Oct. 5-12	931(526)	2331(836)
May 18-26, 1970	819(461)	2037(890)

and emigration in the form of survival and recruitment (Table V). Estimates of N_2, the total population, were essentially similar to those described above (Table IV). The June population, 1334 (1330 using Petersen formula), increased to 3678 in October 1969. A comparison of the recruited population, 3678 by the Jolly method and 3451 using the Petersen procedure, indicated a comparable increase. Recruitment, 2296 (standard deviation $\pm$ 1278) (Table V), was similar to the difference, 2121 new walleyes, between the September and June estimates of the recruited population (Table IV). Survival rates obtained using Jolly's procedure (Table V), when not affected by the influx of new individuals (September 1969), were similar to those calculated from tag recapture data from two adjacent capture periods (Table VI). The effects of recruitment using Jolly's procedure were delayed until October 1969. An application of the observed survival rate ($\phi_1 = 1.123$) for the May 1969 release period (Table V) resulted in an initial population estimate similar to that obtained using the Petersen approach. The pattern of change and population size estimated by these two techniques are virtually identical.

Since the triple-catch trellis method was applicable only to periods of uniform recruitment and mortality (Ricker, 1958), the six periods of estimates were subdivided into two periods on the basis of presence or absence of recruitment (Table VII). The May to September 1969 populations (Table VII) were virtually identical to the $\hat{N}_1$

Table V. Estimates of West Blue Lake walleye population characteristics using Jolly's (1965) procedure. Symbols in parenthesis at column heads are those used throughout this study. Figures in parenthesis are standard deviations.

Period	$\hat{N}_i(\hat{N}_2)$	$\phi_i(\hat{S})$	$B_i(r)$
May 14-20, 1969		1.123	
June 16-22	1334 (574)	0.778 (0.329)	142.2 (409.9)
Sept. 3-12	1169 (499)	1.182 (0.406)	2296.1 (1278.3)
Oct. 5-12	3678 (2205)	0.720 (0.644)	-369.6 (1177.8)
May 18-22, 1970	2278 (1537)		

Table VI. Survival and instantaneous mortality rates of walleye in West Blue Lake.

Period	Survival rate (s)	Instantaneous mortality (i) per day
May 14-20, 1969		
	$s_{12} = 0.999 \ (\pm 0.465)$	$i_{12} = 0.00003$
June 16-22		
	$s_{23} = 0.835 \ (\pm 0.546)$	$i_{23} = 0.00223$
Sept. 3-12		
	$s_{34} = 0.664 \ (\pm 0.421)$	$i_{34} = 0.01356$
Oct. 5-12		
	$s_{45} = 0.525 \ (\pm 0.407)$	$i_{45} = 0.00280$
May 18-22, 1970		

mean $i = 0.00446$

estimates obtained using Petersen and Jolly procedures
(Tables IV and V). As well, recruitment during this time
is essentially 1 (0.987), indicating no recruitment. Two
estimates for September 3 to 12, 1969 (Table VII) result
from the stratification of population estimates by recruit-
ment. The triple-catch trellis placed recruitment in
September 1969 and its magnitude, approximately 2000 fish,
compared favorably with that determined by the two previous
techniques. Considering the initial May to September 1969
estimates, the population increased slightly (0.000076 on
an instantaneous daily basis); conversely, the latter portion
of the estimates, September 1969 to May 1970, describe a
decreasing population (0.00153 on an instantaneous daily
basis).

Natural Mortality

In addition to abundance estimates for the mark
and release periods, survival rates were calculated for
intervals between marking (Table VI). Rates between two
periods, $\hat{s}_{ij}$, are presented, even though the time span of
these periods differed.

Stock depletion, based on survival rates, was
greatest during late fall and throughout the winter. On
the other hand, instantaneous mortality rates per day
(Table VI) indicated that mortality was generally low
throughout the year, but was greatest between September
and October. Mean instantaneous mortality per day was

Table VII. Population characteristics of West Blue Lake walleye
derived from a triple-catch-trellis analysis procedure during periods
of constant recruitment (May to September, 1969, and September 1969
to May, 1970). Figures in parenthesis are standard deviations.

Period	$\hat{N}_2$	$\hat{s}_{ij}$	$\hat{r}_{ij}$
May 14-20, 1969	1087		
		0.999 (0.465)	
June 16-22	1088 (587)		
			0.987 (0.421)
Sept. 3-12	1092		
Sept. 3-12, 1969	3203		
		0.885 (0.585)	
Oct. 5-12	3055 (2309)		
			0.545 (0.825)
May 18-26, 1970	2165		

0.00446 (Table VI) and for the whole year was 1.6275 based
on mean daily mortality calculated for each day.

Growth

Since measures of length were taken of all captured
fish the separation of new recruits from the initial stock
was readily achieved (Fig. 3). As well, in spite of growth,
length frequency distributions, determined for all catches,
were similar in form (Fig. 3). The smallest length cohort
formed a large portion of any particular catch. In addition,
the length distribution of older fish was dominated by those
of 380 to 440mm in fork length. Extremely few individuals
greater than 480mm were captured. The frequency distribu-
tions of May and June 1969 demonstrate many similarities.
No growth in length was apparent between these periods and
the population structure by size remained similar (Fig. 3).
The population described in September also showed marked
similarities to the earlier ones and graphically indicates
the size increase caused by summer growth. Length distri-
butions in October 1969 and May 1970 were similar and clearly
show the dominance of the smaller cohort.

Recruits were readily identified as a distinct
group of small fish. Age II fish, nearing age III, also
formed a distinct group in terms of length (Fig. 3) during
May and June 1969; however, no further groups were readily
identifiable. Presumably, slow and variable growth caused
length overlap among the older members of the population
precluding their separation by length.

Fig. 3. Length frequency distributions of walleye in West Blue
Lake captured during mark and release periods.

FREQUENCY OF OCCURRENCE

.15
.10
.05

MAY   14-20   1969

.10
.05

JUNE   16-22   1969

.10
.05

SEPTEMBER   3-12   1969

.10

.132   .250   .181

.05

OCTOBER   5-12   1969

.10

.05

MAY   18-26   1970

200   250   300   350   400   450   500   550   600
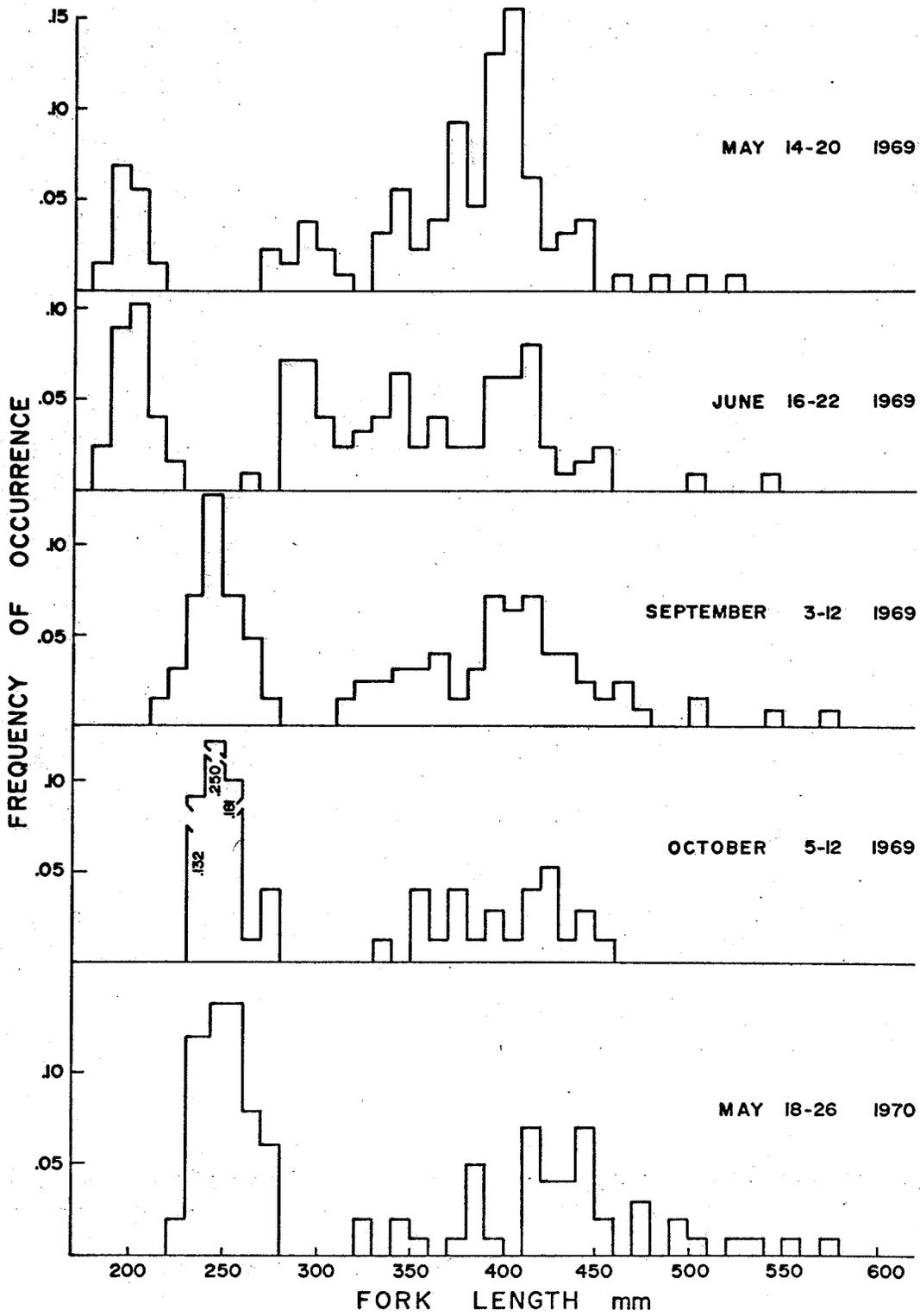
FORK   LENGTH   mm

To describe growth of walleye a relationship between anterior scale radius and fork length was calculated. All fish aged during this study, 702, were grouped in 5mm length classes on the basis of anterior scale radius, the independent variable. Classes with less than 5 observations were not included in the calculation. Fork lengths for a particular scale radius were quite variable; but variances were homogeneous according to Bartlett's test (x^2 = 37.16, d.f. = 33). The linear regression describing fork length and scale radius was $Y = 85.858 + 1.613X$ where Y was fork length, and X the scale radius in mm. For these data, the coefficient of determination ($r^2 = 0.986$) indicates that 98.6% of the variability in fork length could be attributed to changes in scale radius.

Growth increments determined by direct and indirect techniques were quite different (Fig. 4). Results obtained using the direct approach were affected by within sample variability. During 1969 few individuals III^+ were captured after annulus formation - the last week in June. Since sample sizes were small and a large range of lengths existed for this age group, as well as for age V, growth increments estimated by the direct method were rather variable. On the other hand, seasonal increments were much more homogeneous when based on the examination of scales, i.e. the indirect method (Fig. 4); therefore, only the indirect approach will be utilized.

Length increases during the growth period in this climatic zone formed a general trend followed by all age

Fig. 4.   Length increments (ΔL) of West Blue Lake walleye
during the growth year (from last week of June to one year
later).
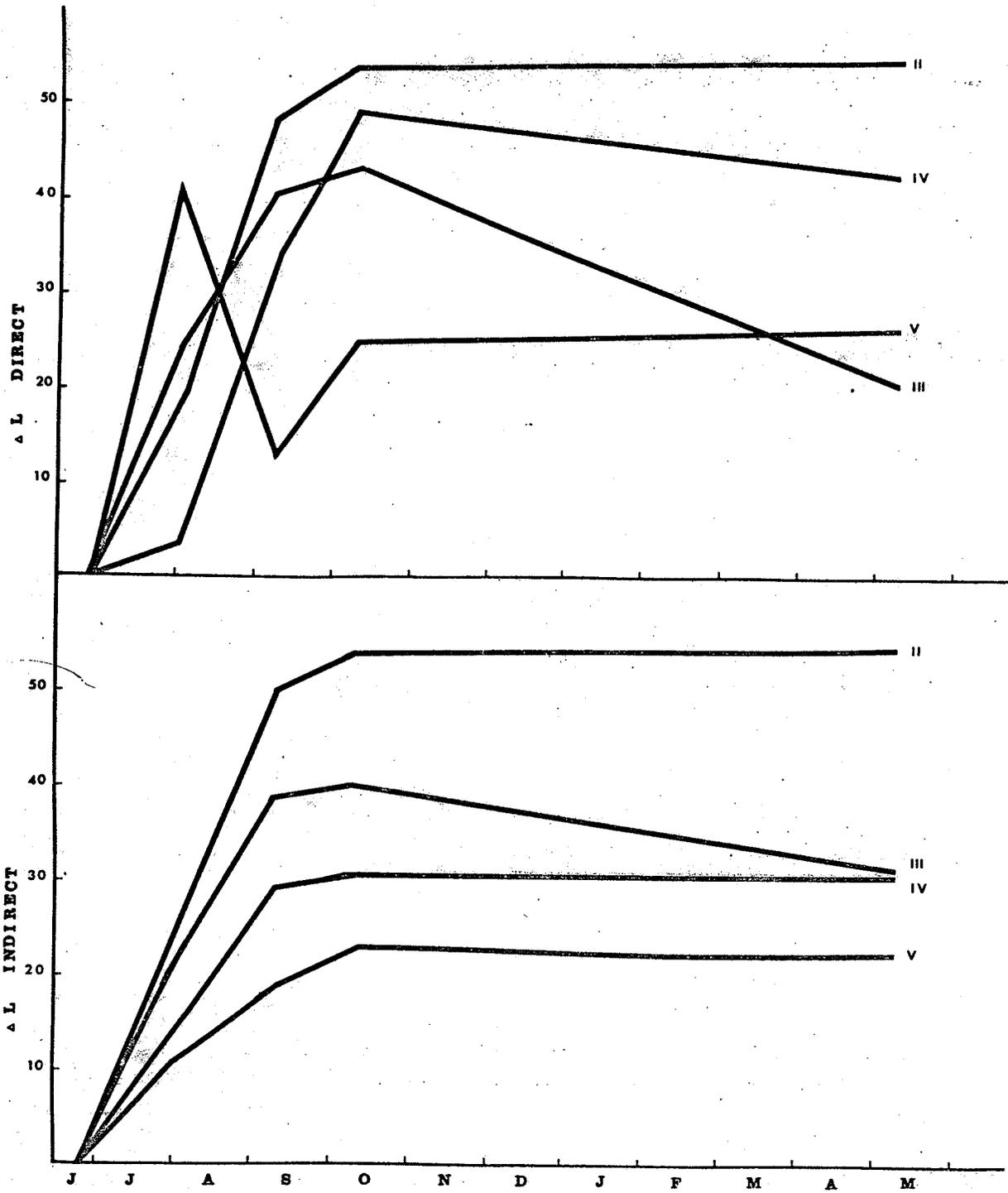
groups (Fig. 4). Growth, in terms of length increments was greatest among age II$^+$ fish followed by III, IV and V. Since individuals older than five years old were rarely captured, growth in the population was essentially limited to fish between ages II$^+$ and V$^+$. Most of the annual growth had occurred by September with only slight increases occurring during the fall.[1]

Paired "t" tests were performed on various measures of growth to determine if fish grew significantly between the time of ice break-up in May and annulus formation in late June, 1969 (Table VIII). In general, no differences were found between measured fork length (except for age IV$^+$ individuals) in samples of walleye collected in May 14 to 20 and June 16 to 22, 1969. A significant difference was found between fork lengths of age IV$^+$ walleye collected in May and June; however, when the growth from last annulus (ΔL) was compared for the two collections, no difference was found. Therefore it was highly probably that no growth occurred in walleye in the spring prior to formation of annulus.

To relate growth in length to growth in weight, the regression equation, determined for West Blue Lake walleye, log W = -5.463 + 3.163 log L (Glenn, MS 1969) was used (Fig. 5); however, conversion from fork lengths (used here) to total lengths was necessary. A conversion of lengths was obtained using the regression of total length (Y) on fork length (X),

---

[1] A more complete description of growth in length and weight is available (Appendix I) and limits for estimates are included.

Table VIII. Results of paired "t" tests applied to growth measures for the period between May and June 1969. NS means not significant.

Age	Test criterion	Degrees freedom	"t"
I[+]	Fork length	52	0.37 NS
II[+]	Fork length	42	1.24 NS
III[+]	Fork length	38	1.09 NS
IV[+]	Fork length	89	2.26(P<0.05)
	ΔL (direct)	87	0.42 NS
V[+]	Fork length	21	0.09 NS
	ΔL (direct)	21	0.33 NS

Fig. 5. The relation between weight (kg) and total length (mm) for West Blue Lake walleye (Glenn, MS 1969).

$$\log W = -5.463 + 3.163 \log L$$

TOTAL LENGTH   mm

WEIGHT   Kg
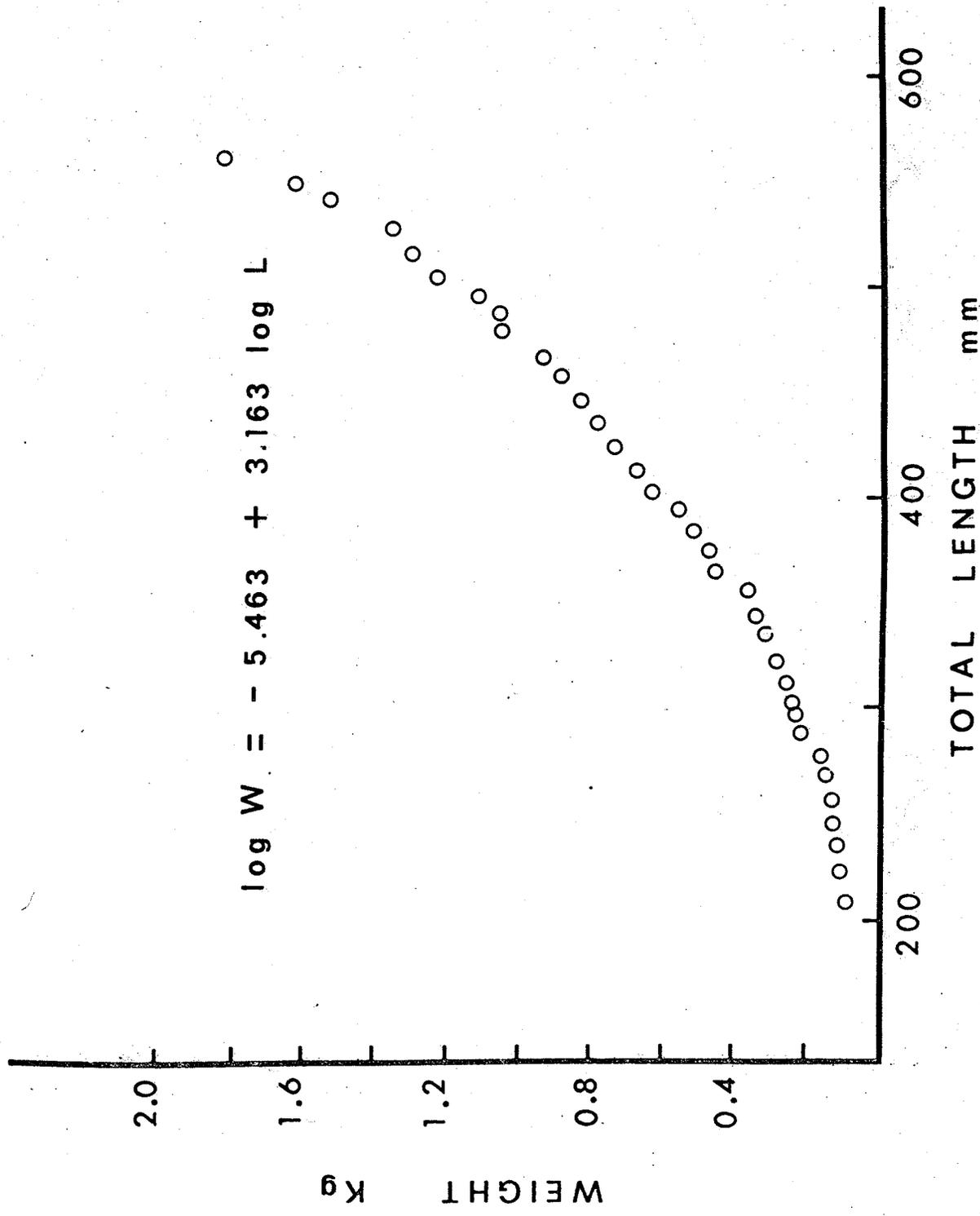
$Y = 4.089 + 1.050 X$. Variances were homogeneous and the regression coefficient differed significantly from zero (H_0: $\beta = 0$, $F = 13067.5$ $P < 0.01$). The coefficient of determination ($r^2 = 0.953$) indicated that over 95% of the variability in total length was attributable to changes in fork length.

Growth, expressed by length increments, was greatest for age II fish with age III, IV and V rates decreasing in order. On the other hand, weight increases had a different order (Fig. 6). Weight increments were approximately similar for fish aged III, IV and V, but lowest for age II walleye. Greatest increase in weight occurred in age IV fish despite their relatively slow growth in length.

Capture of walleye in West Blue Lake was dispersed primarily during the period June 1969 to June 1970; however, samples were also taken prior to annulus formation in 1969 and after annulus formation in 1970. Back calculation of lengths at annulus formation (Table IX) indicated that, regardless of time of capture, the previous growth history was similar. Only fork lengths at annuli were presented, but weights (required in computation of relative growth rates) can be readily obtained. Apparently, each sample described the same growth history. The fork length estimated for annulus I (slightly out of the range considered by the presented length-scale radius equation) varied only slightly for each brood year (Table IX); however, the difference between brood years was rather large, from 136.5 to 163.8 mm.

Fig. 6. Cumulative growth in walleye (ΔG) in grams wet weight during the growth year 1969-70, in West Blue Lake.
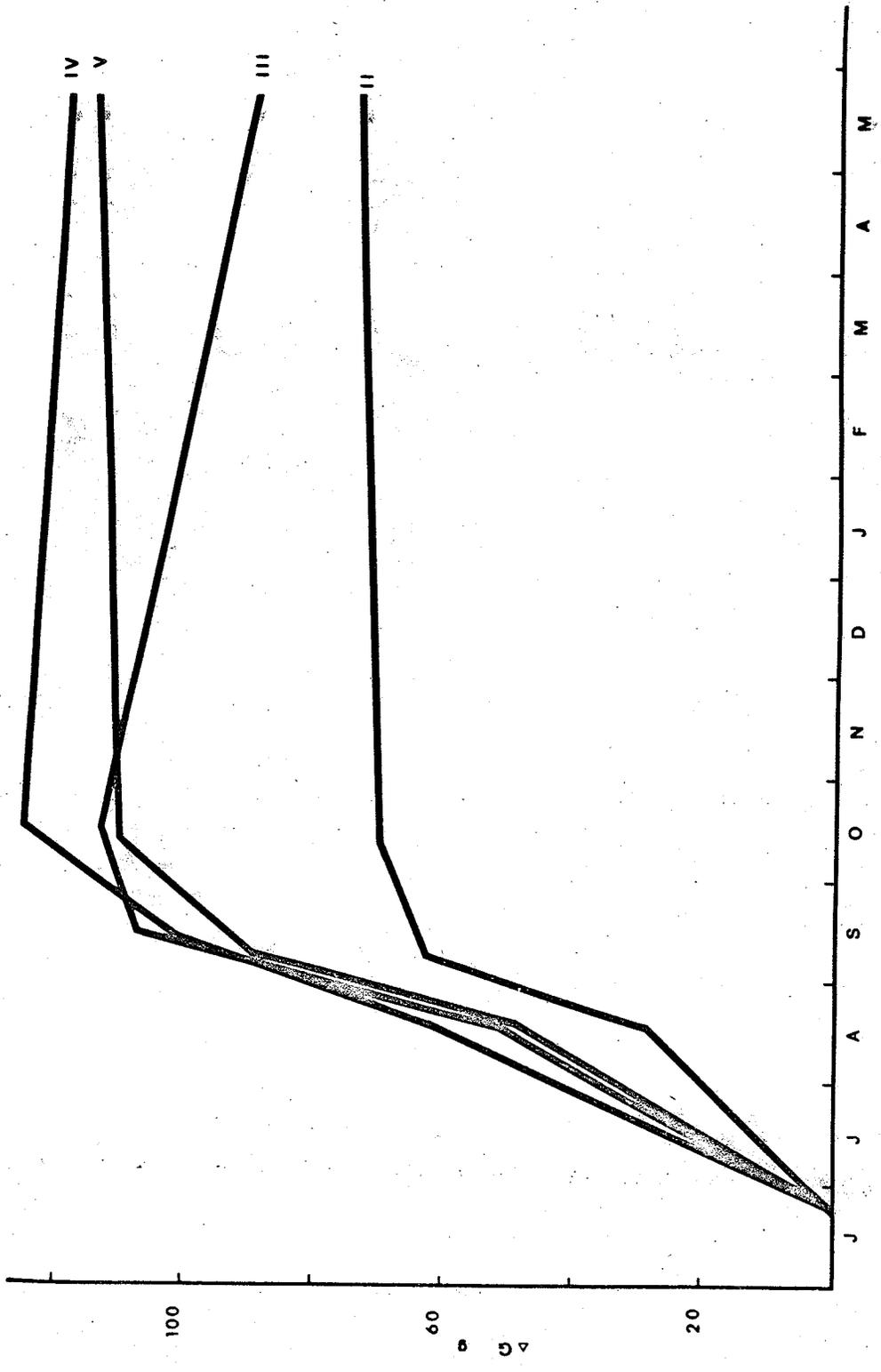
walleye in West Blue Lake, 1969-70.
N represents the number in each sample.

Brood year	N	AGE I	II	III	IV	V	Collection date
1967	48	140.9					May-June, 1969
	150	136.5	194.2				Aug,1969-May,1970
	37	137.8	199.9	259.9			October, 1970
1966	44	156.0	243.5				May-June, 1969
	32	155.8	242.7	297.5			Aug,1969-May,1970
	7	163.8	249.1	303.3	344.3		October, 1970
1965	40	154.8	237.9	311.3			May-June,1969
	20	153.6	240.6	313.3	351.4		Aug,1969-May,1970
	4	158.3	239.6	314.6	362.5	399.3	October, 1970
1964	89	150.4	240.8	314.8	378.8		May-June, 1969
	60	149.6	240.9	314.4	367.3	398.4	Aug,1969-May,1970

This tendency of brood year differences persisted in lengths calculated for other age groups.

Instantaneous growth in length and weight between May and June 1969 was negligible (Table X) and confirmed the results of the paired "t" tests (Table VIII). Magnitude of growth in relative and instantaneous terms was greatest between annulus formation and August. Growth was still rapid from August until September (Table X). Rates decreased until the period of October 5 to 12 and were essentially zero during winter. Relative and instantaneous growth was generally greatest in the youngest fish examined and decreased with age.

Growth occurring during portions of the year can be expressed as percentages of the annual total. Two approaches are available. Since growth was negligible between May and late June (the time of annulus formation), the size in May or June may be taken as the size when growth was completed for that particular year. On the other hand, the sample collected in October 1970 provided the total growth for the preceding growth year, i.e. June 1969 to June 1970. Calculated increments differed only slightly from those obtained using the first approach (Table XI). It is clear only that the majority of growth (70-90%) was completed by September, and this period composes the primary growing season. Virtually all growth (80-100%) was accomplished by October. Contrary to previous evidence, these data indicated that some growth did occur prior to annulus formation.

Table X. Relative growth in length and weight (h_L and h_G respectively) from previous annuli and instantaneous rates of growth in length and weight (g_L and g_G respectively) for walleye, 1969-70.

AGE		May 14-20,1969	June 16-22	Aug. 2-4	Sept. 3-12	Oct. 5-12	May 18-26,1970
	h_L	0.4092	0.3825	0.1222	0.2354	0.2638	0.2715
	h_G	1.7453	1.7118	0.3855	0.8832	0.9957	1.0179
I-II	g_L	-0.00065	0.00335	0.00131	0.00197	0.00020	
	g_G	-0.00039	0.00959	0.00843	0.00206	0.00005	
	h_L	0.2046	0.2014	0.0693	0.1189	0.1260	0.1044
	h_G	0.7623	0.7266	0.1884	0.3910	0.4072	0.4014
II-III	g_L	-0.00025	0.00199	0.00127	0.00029	-0.00096	
	g_G	-0.00052	0.00838	0.00123	0.00047	-0.00031	
	h_L	0.1182	0.1062	0.0392	0.0718	0.0832	0.0817
	h_G	0.3616	0.3281	0.1280	0.2182	0.2633	0.2615
III-IV	g_L	-0.00027	0.00115	0.00079	0.00031	0.00000	
	g_G	-0.00069	0.00359	0.00214	0.00107	0.00000	
	h_L	0.0734	0.0719	0.0331	0.0444	0.0531	0.0536
	h_G	0.2124	0.2119	0.0688	0.1263	0.1599	0.1604
IV-V	g_L	0.00004	0.00096	0.00032	0.00028	0.00000	
	g_G	0.00001	0.00022	0.00122	0.00098	0.00000	

Table XI.   Percentage of annual growth in walleye by comparison
to length of May 1970 samples, and to the increment obtained
from October back calculated length at annulus (in parenthesis).

Age	August, 1969	September	October	May, 1970
II	45.0 (42.0)	87.3 (81.6)	97.2 (90.8)	100 (93.4)
III	66.4 (53.4)	111.4 (91.6)	120.6 (97.1)	100 (81.4)
IV	48.0 (38.7)	87.8 (70.9)	100.6 (81.2)	100 (80.7)
V	59.9 (49.2)	83.0 (69.2)	99.2 (81.5)	100 (82.1)

Biomass and Production Estimates

Results presented in previous sections were
obtained to achieve a major objective of this research -
the definition of seasonal biomass changes and production
in an unexploited population of walleye. As indicated,
choices of techniques and approaches were possible. To
obtain estimates of biomass changes and production, methods
were selected on the basis of precision, scope, and simplicity.
For instance, Petersen estimates which can include or exclude
recruitment were used simply because they present the most
information regarding the resident population.

In the following descriptions of biomass and pro-
duction, estimates of N_1 and N_2 were apportioned on the
basis of the relative abundance of age groups in each sample.
This process leads to descriptions of the population energy
requirements by age group rather than in terms of an average
individual. Average biomass during 1969-70 was calculated
(Table XII) using the most straightforward approach, that of
using the arithmetic means of biomass occurring at two adjacent
periods partitioned according to age class abundance. Also,
descriptions of biomass based on total population (Appendix
II) and on instantaneous descriptions (Appendix III) were
included. Production defined by arithmetic and instantaneous
approaches were similar, a difference of about 20 kg. In
terms of biomass of the population (Table XII) the greatest
contributor was age group IV in May and June, becoming age V
in late June. Biomass and production estimates for the first
age group (Table XII) were obtained by applying mortality

(g). Estimates of N in parenthesis are recruited population. Estimates of N in ... each age group and instantaneous growth in weight

Date	N	Age	$\bar{w}$(g)	g	B kg		Age	$\bar{B}$ kg $\frac{B_1 + B_2}{2}$	P (g $\bar{B}$)kg
May 14–20, 1969	1090	I	(79.8)	-0.0128	(204.767)		I	(205.031)	-2.624
		II	267.6	-0.0172	36.394		II	76.068	-1.308
		III	470.1	-0.0223	82.268		III	108.223	-2.413
		IV	676.7	+0.00021	387.749		IV	360.233	+0.076
		V	861.5	+0.0004	143.871		V	107.343	+0.004
		VI	1354.4		52.822		VI	62.356	+0.003
June 16–22	1330	I	(80.1)	0.6313	(205.296)		I	(264.135)	166.748
		II	282.3	0.3293	115.743		II	119.111	39.223
		III	444.3	0.1989	134.179		III	123.165	24.498
		IV	712.4	0.1187	332.691		IV	414.626	49.216
		V	863.6	–	70.815		V	159.406	18.922
		VI	1041.9	–	71.891		VI	71.891	8.534
Sept. 3–12	1350 (3451)	II	154.2	0.0619	323.974		II	259.607	16.097
		III	411.0	0.0143	122.478		III	125.413	1.793
		IV	581.1	0.0322	112.152		IV	129.733	4.177
		V	785.7	0.0295	496.562		V	408.988	12.065
		VI	1092.5	–	247.998		VI	145.015	4.278
Oct. 5–12	931 (2331)	II	162.7	+0.00099	195.240		II	188.904	+0.187
		III	430.7	+0.00929	128.349		III	90.732	0.843
		IV	660.6	0	147.314		IV	108.355	0
		V	861.7	0	321.414		V	388.931	0
		VI	1136.0	0	42.032		VI	44.350	0
May 18–22, 1970	819 (2037)	II	163.3	–	182.569				
		III	354.1	–	53.115				
		IV	625.2	–	69.397				
		V	876.1	–	456.448				
		VI	1261.3	–	46.668				

$$\Sigma P = 340.319$$

rates calculated for the population (Table VI) to the
estimated number of new recruits (2101 individuals) in
September. Age I was not recruited during May and June
1969, and therefore was not under direct analysis (presented
in parenthesis in Table XII). This youngest age group in
the population, although not having the largest biomass,
contributed approximately half of the total production
(166.748 kg) as a result of its abundance and high rate of
growth ($g = 0.6313$).

General trends in the walleye population of West
Blue Lake are readily apparent (Table XII). There was a
general decrease in number of virtually all age groups in
the population. Age group V in September was the only
obvious descrepancy from this general trend. This segment
of the population may have been overestimated, but because
of slow growth, they contribute little to the production of
the system (12.065 kg). Mean weights presented for each age
group are the result of individual weights derived by using
observed lengths in the length-weight equation. As such,
the mean weights of certain age groups, III and VI, are
subject to variation because of scarcity in the samples
causing variability within the sample. However, production
by these ages is relatively small.

Biomass estimates using these techniques were
similar in May and June 1969 (703.104 and 725.319 kg,
respectively). Production between these periods was
negative (losses occurred in ages I, II and III). Since

most production in walleye occurred between June and September, accurate estimates of $\overline{B}$ between these periods are crucial. As stated earlier, the age V population in September was over-estimated. Nevertheless, the instantaneous approach (Appendix III) for determining $\overline{B}$ yielded results similar to the arithmetic approach (Table XII) even though the former utilized the June estimate of age V abundance which was undoubtedly an adequate description of that population.

Production of walleye flesh occurs from September to October (38.410 kg) and is essentially zero during the winter months (Table XII). Production in terms of wet walleye weight was 340.319 kg during the 1969-70 growth year. Negative or zero production occurred from May to June and from October to May. Proliferation of flesh was limited to the period from late June to early October.

LABORATORY STUDIES

No losses were incurred during transport of walleye, but after the first week of holding only fish age II$^+$ readily accepted food. Older walleye did not feed. Specimens aged III, IV, V and VI were segregated into 560 1 tanks and live emerald shiners were introduced daily. Even though the older fish began to feed, they persisted in feeding during dark hours and did not take amounts sufficient to produce signi-ficant growth.

All emerald shiners, frozen or alive, had energy

values of 4963.6 cal/g (standard deviation ± 67.6); 12.6%
of dry weight was ash, and 75.9% of the live wet weight was
removed on drying. The preceding diet qualifications were
the result of 28 determinations made during the course of
the investigation (5 months of storage). Because of the
narrow statistical limits, the energy content of the food
was considered constant in all studies of growth and main-
tenance for walleye.

Since all walleye used in nutrition experiments
were captured at the same time (May 22 to 26, 1970) as a
sample in West Blue Lake used to define calorific values
of resident animals, all fish used in growth and assimila-
tion studies were assumed to have 4580.2 (± 76.9) cal/g at
the start of all experiments. Investigations into growth
and maintenance began approximately 3 weeks after arrival
at the laboratory, thus caloric changes in walleye were
probably minor.

In all laboratory feeding trials where feeding
was voluntary, the weight of the experimental animals was
critical. The largest member of the group generally
completed feeding before the small fish would approach food.
This dominance was not evident if individual weights differed
by less than 25g live weight; length appeared to play no
role in governing this phenomenon. As well, in any experi-
ment where consumption was above the maintenance ration,
only age II[+] individuals could be utilized. Older fish
would consume a minimal amount of food, then cease feeding;
therefore, in spite of the obvious effect size may play in

conversion, walleye aged III, IV, V and VI could not be utilized in assessments of growth conversion. This tendency of low consumption in older groups persisted throughout the duration of feeding trials. In addition, two walleye aged V and VI did not feed and had obviously swollen abdomens. Dissection later showed that both were mature females and still carried eggs. The mature ovaries physically occluded gut openings and the stomach was shrunken and mucus filled. No evidence of feeding was found in either of the two females.

Effect of Ration Size on Conversion

Conversion experiments using age II+ walleye were initiated as soon as acclimation to food and temperature was considered complete. Since the selection of ration size was open to value judgement, the fish in the conversion series were fed at 4% of wet body weight. However, to establish the effect of ration size (R) on conversion efficiencies (K), groups of fish were fed for 2 weeks on a ration 2.50 to 8.36% of body weight. The range in conversion efficiencies (Table XIII) was relatively narrow, 0.109 to 0.149. There appeared to be a slight optimum at approximately 4% (Fig. 7). Since two separate determinations were made near a 4% ration, but the values were rather different, the relationship was slightly confused. The two rations differed by only 0.20% of body weight but conversion efficiencies differed by 0.013. The observed difference was almost certainly not the result of walleye weight differences (Table XIII). Nevertheless, it

Table XIII. Effect of ration size (% body weight) on conversion (K_1 and K_2) for walleye at 16C.

No. of animals	Intake (cals)	Growth (cals)	% B.W.	pR	Maintenance for week	K_1	K_2	Mean walleye size (g)
3	86,218	10,554	2.50	83,028	31,560.3	0.122	0.128	160.12
	87,578	10,594	2.48	84,318	32,104.3	0.121	0.126	162.88
3	142,902	18,778	3.32	137,615	39,377.4	0.131	0.137	200.09
	146,674	19,096	3.32	141,248	40,405.5	0.131	0.135	205.00
3	142,902	18,515	3.98	137,615	32,866.6	0.130	0.135	161.84
	144,292	18,629	3.96	138,376	39,062.2	0.129	0.135	166.75
3	153,276	21,827	4.16	147,605	28,831.8	0.142	0.148	136.94
	153,326	21,814	4.17	147,599	30,014.4	0.142	0.149	146.28
4	271,261	34,430	6.16	261,224	39,034.2	0.127	0.132	146.52
	261,185	34,188	5.69	251,521	40,741.8	0.131	0.136	153.27
4	393,415	42,371	8.53	378,859	43,473.9	0.108	0.113	162.39
	391,380	41,010	8.20	376,899	45,522.2	0.106	0.109	170.70

Fig. 7. Effect of ration size on conversion (K_1) at 16C for walleye
fed on emerald shiner.

Figure showing $K_1 = \dfrac{\Delta W}{R \Delta t}$ (vertical axis, 0.100 and 0.200 marked) versus RATION %BW / DAY (horizontal axis, marked 2, 4, 6, 8).
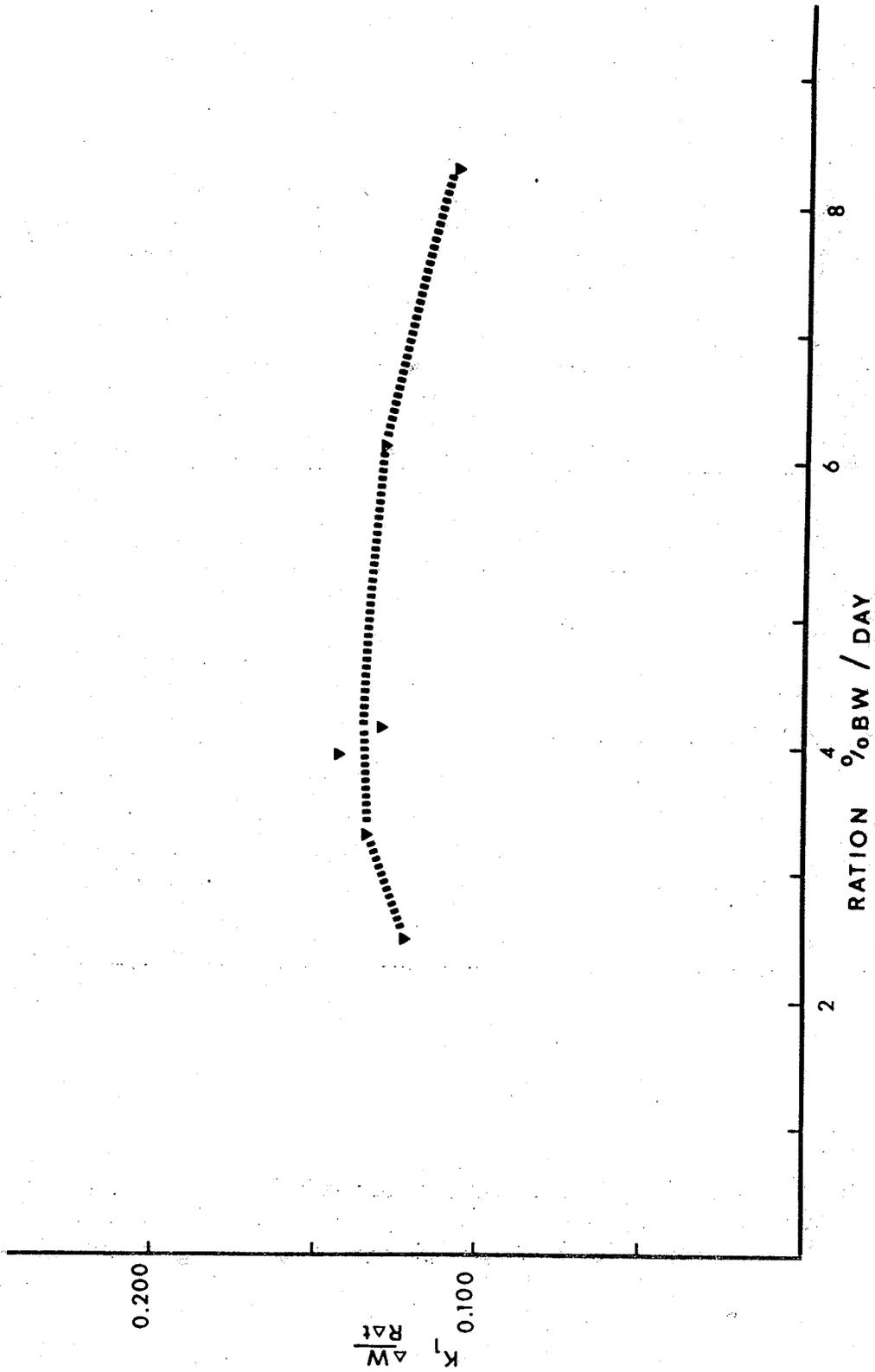
appeared that at higher levels of consumption, greater than 6% of body weight, gross conversion efficiency was reduced. At moderate ration sizes, 3.3 to 4.3%, conversion was within a relatively narrow range (0.129 to 0.142). Since only one small ration size was administered (2.49% of body weight), the effect of low rations on conversion was not fully defined but was apparently not much different from rations at 4% of body weight. It does seem that the optimum ration was approximately 4% and that conversion efficiency decreased for both extremely high and low rations (Fig. 7).

Conversion Efficiency

In the assessment of the conversion of ingested material to walleye caloric content, an "optimum" ration (4% live body weight) was administered to experimental groups of walleye held at stable temperatures in the range encountered by fish in West Blue Lake. Growth was apparent and relatively homogeneous throughout each experiment (4 to 13 weeks). Walleye weight changes (g) and consumption were treated as being cumulative for initial inspection. Gross inspection of walleye weight gain (Fig. 8) seemed greatest for animals held at 20C; however, initial weight, exact ration, caloric deposition, number of walleye in an experimental group, and changes in assimilation affect the interpretations of growth from an ingested ration. Fish used in all growth studies grew at similar rates, but the conversion of ration (cal.) to growth (cal.) was of most interest.[2]

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(2) Weekly analysis of food and growth histories in individual experiments appear in Appendix IV.

Fig. 8. Accumulation of weight (g) by walleye fed at 4% body
weight at 20, 16, and 16-8C.
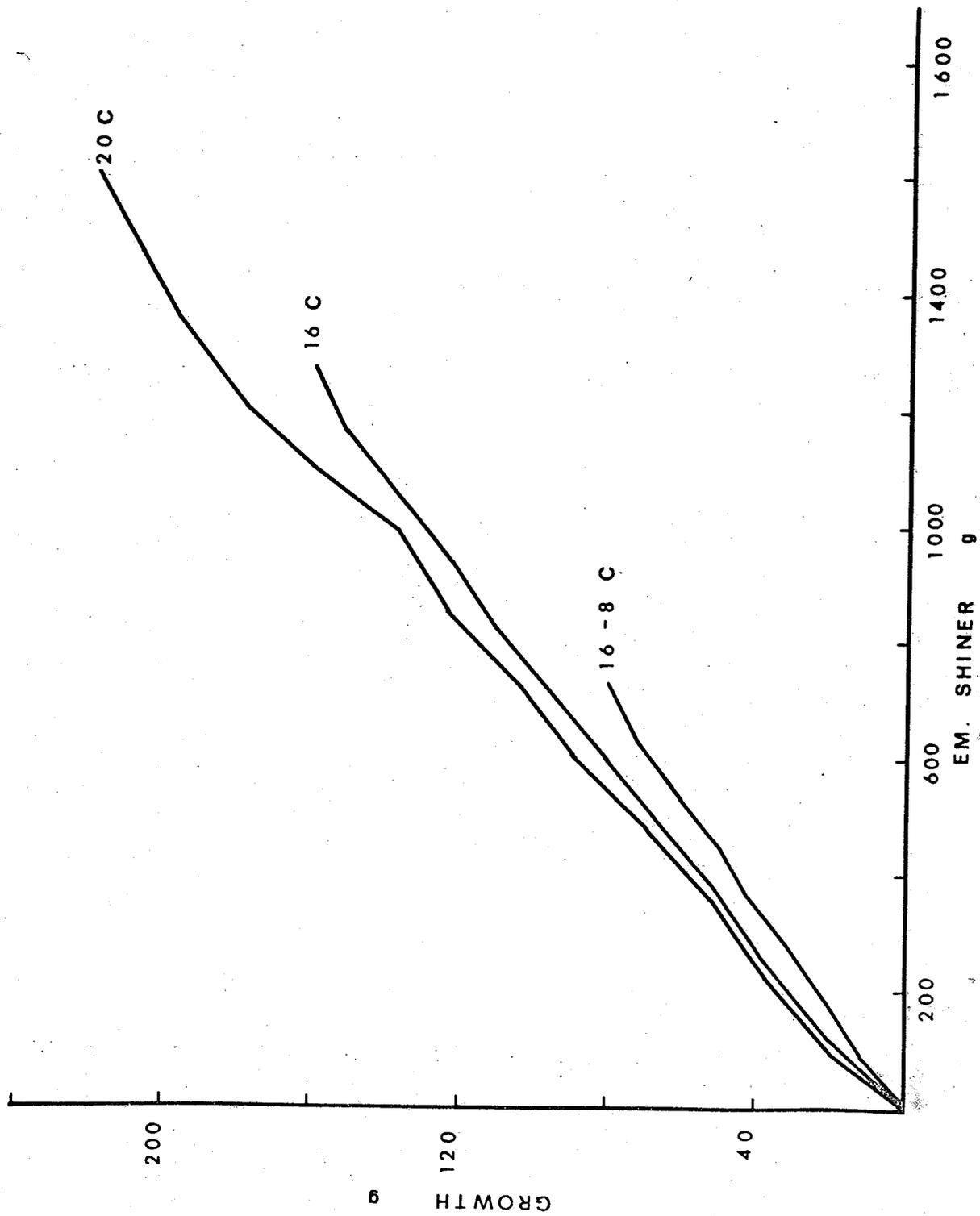
Although experiments began at approximately the same time, and the animals were, therefore, assumed to be all of one energy content (4580.2 ±76.9 cal/g), variation in the duration of experiments affected the terminal caloric values. However, weekly caloric gains were similar (Table XIV). Even though gross energy content varied with trial duration, the weekly gain (Table XIV) was relatively constant for each experiment. The terminal caloric values for the variable temperature (16-8C) and 12C series were not reliable estimates since the variability associated with the former experiment was great and the latter resulted from only one determination. Nevertheless, the relatively constant weekly calorific gain, indicated by "before" and "after" measurements (Table XIV), were supported by evidence from the field. Data on the natural population, to be presented, indicated that energy accumulated at a relatively constant rate from May to September in wild fish. Therefore, wet weight gains in laboratory experiments were converted into energetic terms on the basis of the average weekly caloric gain found for each appropriate experiment (Table XIV).

Weekly values of K_1 ($\frac{\Delta W}{R \Delta t}$) during experiments of 8 to 13 weeks were extremely variable (Fig. 9). Experiments at 20C indicated general decreased in growth efficiency. On the other hand, gross conversion was either variable (16C) or quite static (16-8C variable day cycle). Gross conversion in walleye can be stated as ranging generally from about 0.100 to 0.160 for rations of 4% body weight. Estimates of K_1 conversion for the entire duration of each feeding trial

Table XIV. Changes in energy content of whole age II$^+$ walleye before and after growth determinations (standard deviations are in parenthesis).

Experiment	Duration weeks	START Cal/g	No. analyzed at end	END Cal/g	% Moist	Weekly caloric gain
20C	13	4580.2(76.9)	2	5042.5(56.1)	74.72(.79)	35.6
16C	11		2	4936.8(29.9)	74.47(.20)	32.4
16-8C	8		2	4856.2(130.3)	74.63	34.5
12C	4		1	4676.4	74.54	35.4

61

Fig. 9. Effect of experiment duration on K_1 for walleye held at
20, 16, and 16-8C. All fish were fed at a ration of 4% body
weight.

20 C
16
16 – 8

DURATION wks

0.200

0.100

$K_1 \dfrac{\Delta W}{\Delta R_t}$
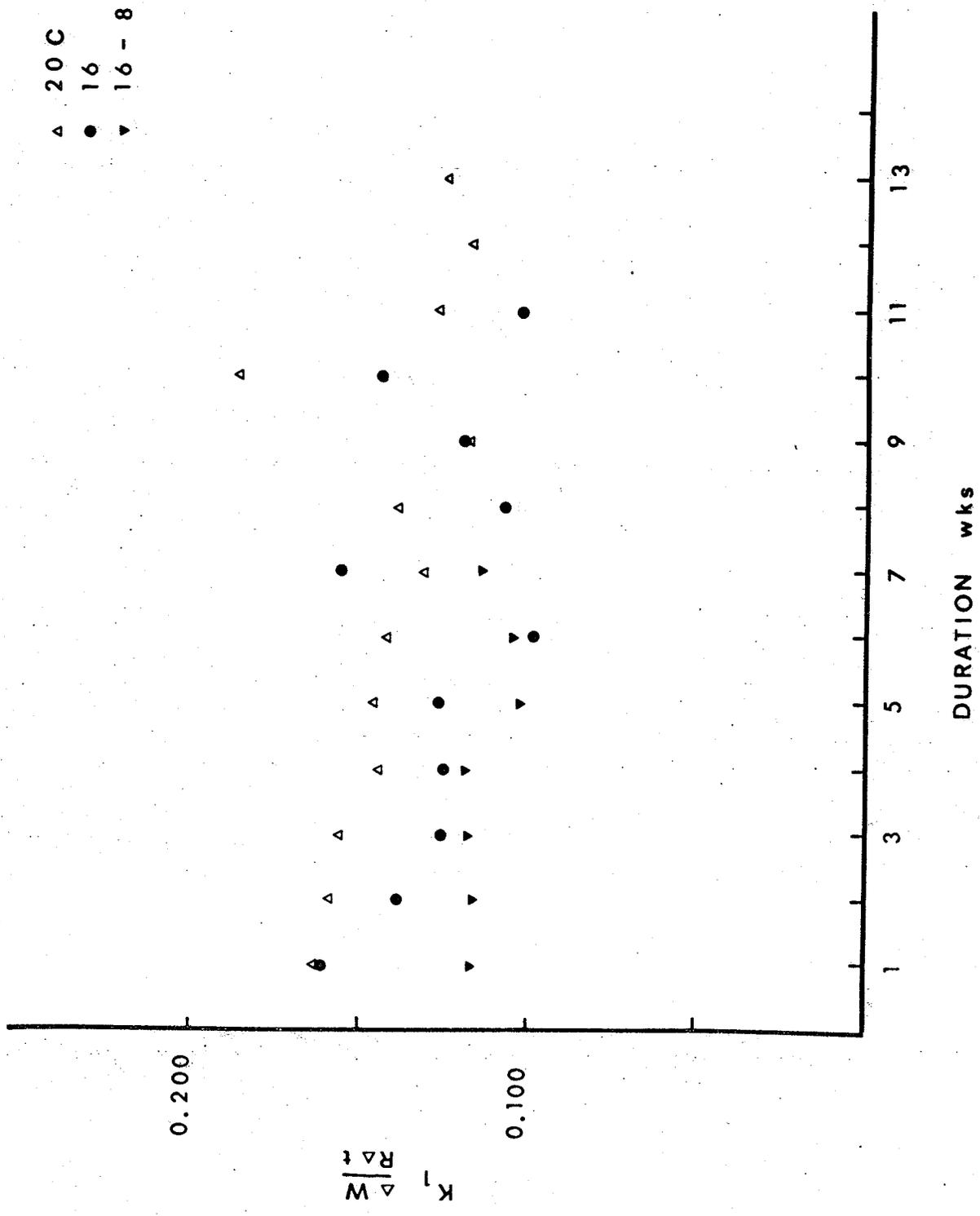
was 0.143 ±0.020 (20C), 0.127 ±0.021 (16C), and 0.139 ±0.018 (12C) (Table XV). The cycled temperature change series (16-8C) yielded a somewhat lower estimate for gross conversion (K_1) of 0.113 (±0.006) which had relatively narrow limits. Gross conversion (K_1) calculated for the three stable temperature experiments (Table XV) was not significantly different ($F = 2.036$ ns).

An extension of conversion efficiency to include the energy which is available to an individual (pR) must consider the effect of fish size on the assimilation coefficient (p) of a ration. Assimilation efficiencies for emerald shiner were derived (to be presented subsequently) for various sizes of walleye and applied to the ration ingested. K_2 ($\frac{\Delta w}{pR\Delta t}$) was only slightly higher than gross conversion (K_1) because of the remarkable efficiency of food utilization by walleye - maximum efficiency for emerald shiner of 97.87%. Since assimilation did decrease with increasing fish size (Fig. 10), estimates of net conversion (K_2) are increased slightly for the latter estimates made during each feeding trial.[3] Graphic descriptions of K_1 and K_2 for 20C (Fig. 10) indicate generally decreasing efficiencies with increasing mean walleye weights. Decreased assimilation efficiencies occurring in the latter parts of feeding trials did not affect K_2 to an appreciable extent. The variability in conversion in the 16C experiment was still evident. At 12C, weekly net conversion (K_2) followed the pattern of gross conversion (K_1).

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[3] see Appendix IV.

Table XV. Conversion efficiencies (standard deviations are in parenthesis) of age II^+ walleye for experiments at different temperatures.

Temperature C	K_1	K_2	K_3	Experiment duration in weeks
20	0.143 (0.020)	0.149 (0.021)	0.229 (0.031)	13
16	0.127 (0.021	0.132 (0.021)	0.173 (0.023)	11
16-8	0.113 (0.006)	0.117 (0.006)	0.134 (0.006)	8
12	0.139 (0.018)	0.145 (0.018)	0.169 (0.023)	4

Fig. 10. Conversion efficiencies in three orders (K_1, K_2, and K_3) as affected by size of experimental walleye.
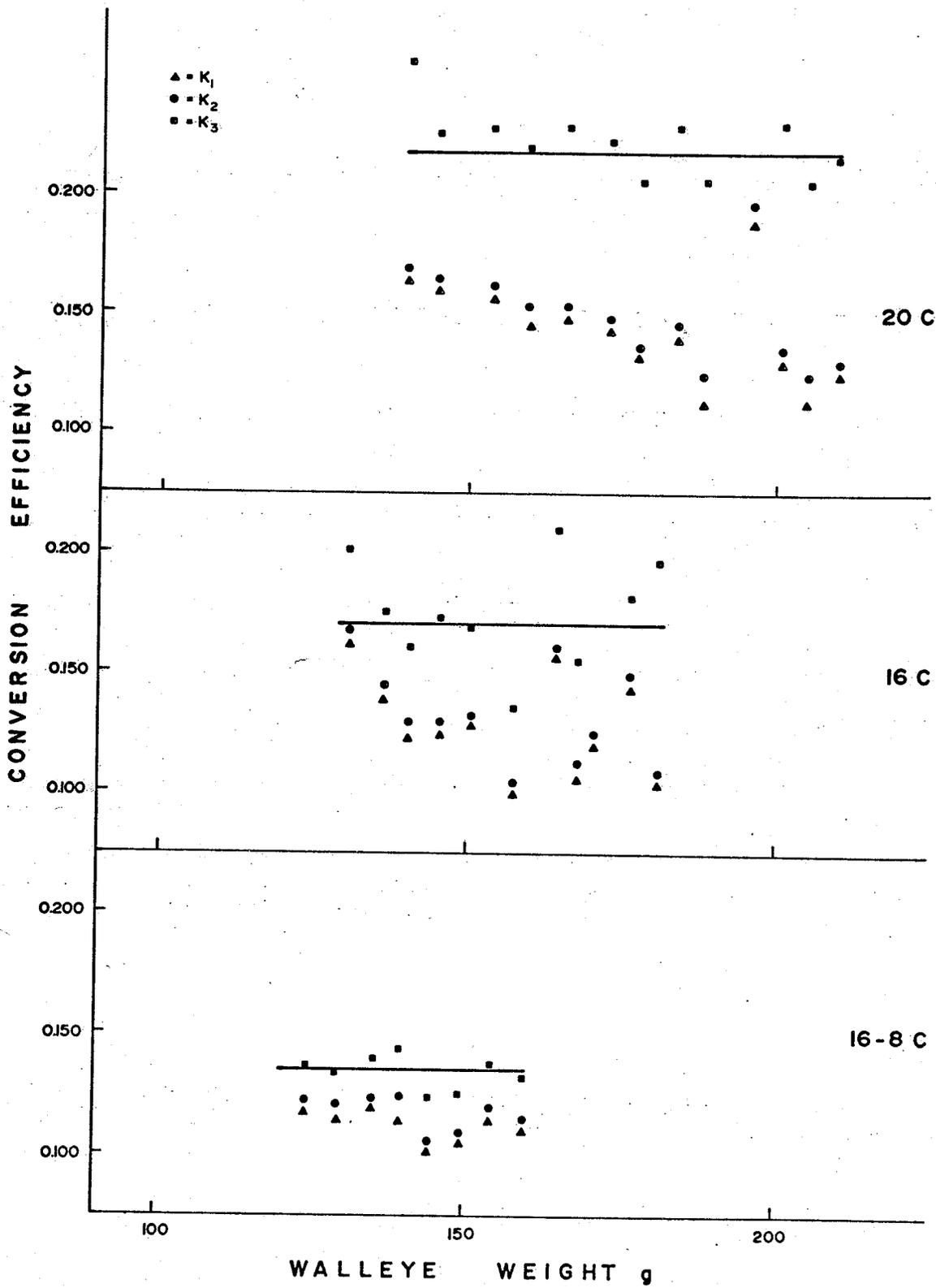
Differences between K_1 and K_2 at the three stable temperatures were minor (Table XV) and all estimates were within relatively narrow limits. Analysis of variances among K_2 descriptions at stable temperatures indicated no significant differences (F = 2.0238 ns). Once again mean net conversion at the variable temperature (Table XV) was considerably lower (0.117) than conversion at stable temperatures (0.132, 0.145, and 0.149).

The conversion coefficient of the third order, K_3 = $\frac{\Delta w}{pR-T_R \Delta t}$, is a measure of conversion for that portion of the ration which can be assimilated and is not required for basal body upkeep and routine activity. Since this routine expenditure (T_R) is temperature dependent and is approximated by $T_R = 0.3W^{0.8}$ (Winberg, 1956), the expenditure was corrected by applying Krogh's temperature correction to metabolism at 20C. Maintenance requirements for walleye of various sizes were found (presented later) and a log-log plot through these requirements, plus those of one size at several temperatures corrected to 20C, described the level of metabolism, α = 0.301 mg O_2/hr, and the weight exponent, γ = 0.841. Because of the similarity of these two estimators of routine expenditure, Winberg's generalized formula was corrected to experimental temperatures and used to define K_3.

At 20C, K_3 values were approximately linear throughout the experiment duration (Fig. 10) and were apparently not affected by weight changes. The linear regression for the relation of K_3 values on fish was not significant ($H_0: \beta = 0$,

$F = 0.03$). The lack of any relationship was also visually apparent (Fig. 10). Variability in the magnitude of this measure of conversion, K_3, still occurred at 16C (Fig. 10). In the variable temperature experiment, the homogeneity of conversion still persisted although lower than conversion estimates at stable temperatures (Table XV). Examination of the mean K_3 values from the three stable temperatures revealed a significant difference ($F=15.595$ $P < .05$). Tukey's w-procedure for locating means not significantly different (5% level)

20C	16C	12C
0.229	0.173	0.169

indicated that a similarity of conversion existed only at adjacent temperatures. As with K_1 and K_2 conversion coefficients, K_3 conversion for the 16-8C variable temperature experiment was less than at stable temperatures (Table XV).

Growth conversion estimates, determined at three stable temperatures, indicated that gross and net conversions (K_1 and K_2) were similar. Conversion ranged between 0.099 and 0.189 (K_1) and 0.104 and 0.196 (K_2). Conversion in the variable temperature regime was lower, 0.113 and 0.117 for K_1 and K_2. Conversion coefficients adjusted to consider the basal energy demand, K_3, differed among the stable temperature experiments, but showed no effect of fish size.

Maintenance Requirements

Maintenance requirements for walleye depend essentially on fish size and ambient temperatures. An examination

of the requirements for walleye of various sizes was con-
ducted at 12C using II, IV, V and VI year old fish (Table
XVI). Requirements expressed as a per gram requirement were
similar regardless of specimen size and varied within a
narrow range, 36.5 to 38.2 mg/g/wk. Maintenance requirements
per unit walleye were independent of fish size.

Since caloric loss or deposition may occur in walleye,
independent of weight changes, during maintenance feeding,
the age II individuals were analysed calorically after two
maintenance trials conducted at 8 and 20C. Once again, 4580.2
cals/g dry weight (standard deviation ±76.9) was the initial
caloric value. Calories/g remained unchanged throughout
these two series of experiments. At the end of two separate
trials, caloric content of two walleye (one from a maintenance
trial at 8C, the other at 20C) was 4608.2 and 4610.5 cals/g
respectively. Variation within all trials was not determined
since experimental animals were limited; however, it seems
reasonable that, for the 5 or 6 weeks duration of maintenance
experiments, no caloric depletion or deposition occurred.

Since the energy required per unit weight for main-
tenance of walleye was independent of size, three walleyes
at 4 and 8C and two individuals at 12, 16 and 20C were fed
maintenance diets to define temperature effects. Requirements
were converted from a gram/gram basis to cal/g and indicate
a rapidly increasing demand from 12 to 20C (Fig. 11). At
the three lowest temperatures (4, 8 and 12C) the maintenance
requirements were within narrow limits, 33.25 to 45.70 cals/
g/wk. No difference between regression equations of maintenance

Table XVI. Maintenance requirements expressed as mg/g/wk of II, IV, V and VI year old walleye at 12C.

Mean walleye size (g wet wt.)	Exp't duration weeks	Average weekly consumption	mg/g/wk requirement
169.56	4	12.72	38.2
476.77	3	33.83	36.5
682.72	3	49.36	36.7
889.05	3	66.21	37.3

Fig. 11.   Relationship between maintenance requirements
(caloric values in parenthesis) and temperature for walleye.

mg / g / wk   log M = 1.366 + 0.029 T
                r = 0.979

cal / g / wk   log M = 1.286 + 0.029 T
                r = 0.980
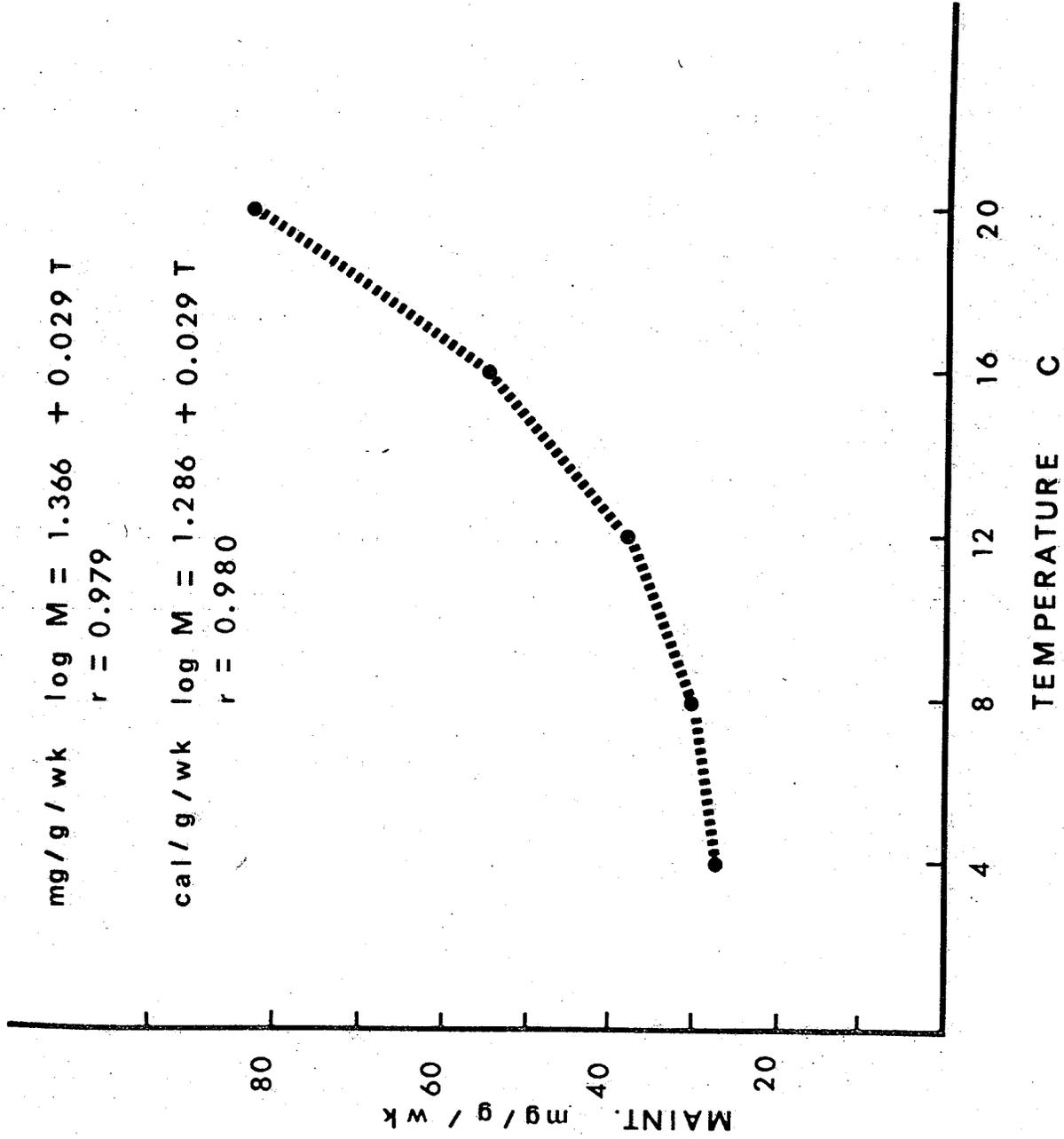
and temperature relations existed (Fig. 11) since wet weight has been converted to calories; however, for ease in comparison to previous investigations, wet weights are presented.

In maintenance trials, Δg is zero and the total metabolic expenditure (T_R) is the available ration (pR). Since maintenance was determined for various sizes of walleye and for age II fish at several temperatures, all measures were converted to 20C by Krogh's correction (Winberg, 1956). A log-log plot of $\log T_R = 252.3 + 0.841 \log W$ described adequately the relationship between walleye weight and routine metabolism. The level of metabolism, 252.3 cals., when converted to mg O_2/hr is 0.301. In this relationship, 87.2% of the variability (r^2 x 100) in the dependent variable could be attributed to the independent variable (weight).

Available Ration

Since the total energy available, i.e. the fraction of ingested food which is subsequently assimilated, limits the amount available for expenditure in growth and metabolism, it was necessary to obtain the effect of ration type (perch age 0, emerald shiner, amphipods and crayfish), ration amount, and fish weight on the amount of solid unused material.

Most foods were egested as a solid stream of waste; however, when fed crayfish, experimental animals retained the ingested material for approximately 10 to 16 hours and then regurgitated the carapace intact, but empty of soft tissue, along with partially emptied abdominal segments. Three trials

(for a total of 15 walleye) were conducted using crayfish and the observed phenomenon occurred in two trials. Only the latter trial was considered in analysis as it was not apparent whether regurgitation of crayfish is a natural phenomenon. Fecal material from animals that had regurgitated was undetectable. Egestion time depended essentially on meal type. The amphipod, Gammarus lacustris, had the shortest residence time in the gut, from 28 to 36 hours, and appeared in the feces with exoskeletons intact. Parts of the exoskeleton (legs and abdominal portions) were fragmented, but the fecal contents were readily recognized as amphipods. Egestion time for crayfish varied from 38 to 72 hours for those that had retained the entire ingested meal. Unidentified remains of both emerald shiners and age 0 perch were egested 48 to 56 hours after ingestion.

Filtration of the tank contents indicated that all material was removed by extraction with pipette. The two series of filters (experimental tank water after feces removal, and the water direct from supply lines) had the same calorific values (the overall variation of 75 cal. was within the expected experimental error).

Neither the energy content of feces nor the amount of ash utilized was known; therefore, both caloric values and ash content of egested food was assessed to determine the utilization of an ingested ration. Caloric content of fecal material was generally low, 1099 to 2979 cals/g dry weight. Ash content of fecal materials was high, but since only about 40% of ash ingested appeared in the feces, neither ingested

nor fecal calories were corrected to cals/ash free gram.
Only 11 comparisons of ash in food to that appearing in the
feces were available but do indicate considerable utilization
of the ash fraction. Only age 0 perch of the larger ration
sizes provided sufficient material for combustion and ash
determination.

Occurrence of ash in feces as a per cent of that
ingested by walleye in assimilation studies.
Numbers in parenthesis are standard deviations.

Size of walleye	No. of determinations	% ash in feces
II[+] 113.2 to 173.3g	7	42.7 ($\pm$ 7.3)
IV,V 360.4 to 476.8g	4	38.5 ($\pm$19.2)

Since efficiency of utilization may be affected by
the meal size ingested, rations of age 0 perch ranging from
7.80 to 44.91 cals/g - 0.7 to 5.2% body weight - were admin-
istered to walleye of various sizes (Fig. 12). Ration sizes
much larger than 5% of body weight could not be administered
because the increased handling, associated with force feeding
of small organisms to walleye, was detrimental to experimental
animals. For the range of ration sizes used assimilation
efficiency $\frac{\text{ingested ration (cals) - feces (cals)}}{\text{ingested ration (cals)}}$ X 100
was constant. Regressions applied through both assimilation
descriptions, II[+] fish and those of larger sizes, indicated
that the slope was zero (H_0: β = 0), F value for age II walleye
is 0.044 and for older fish is 3.33. Neither was significant
(5% level). The dispersion of efficiencies in the older fish
(Fig. 12) appeared to be related to fish size as fish of
approximately 360g were generally more efficient in assimila-

Fig. 12. Effect of ration size (in calories ingested) on the assimilation of age 0 perch by walleye II$^+$ (upper) and older (lower) at 16C.
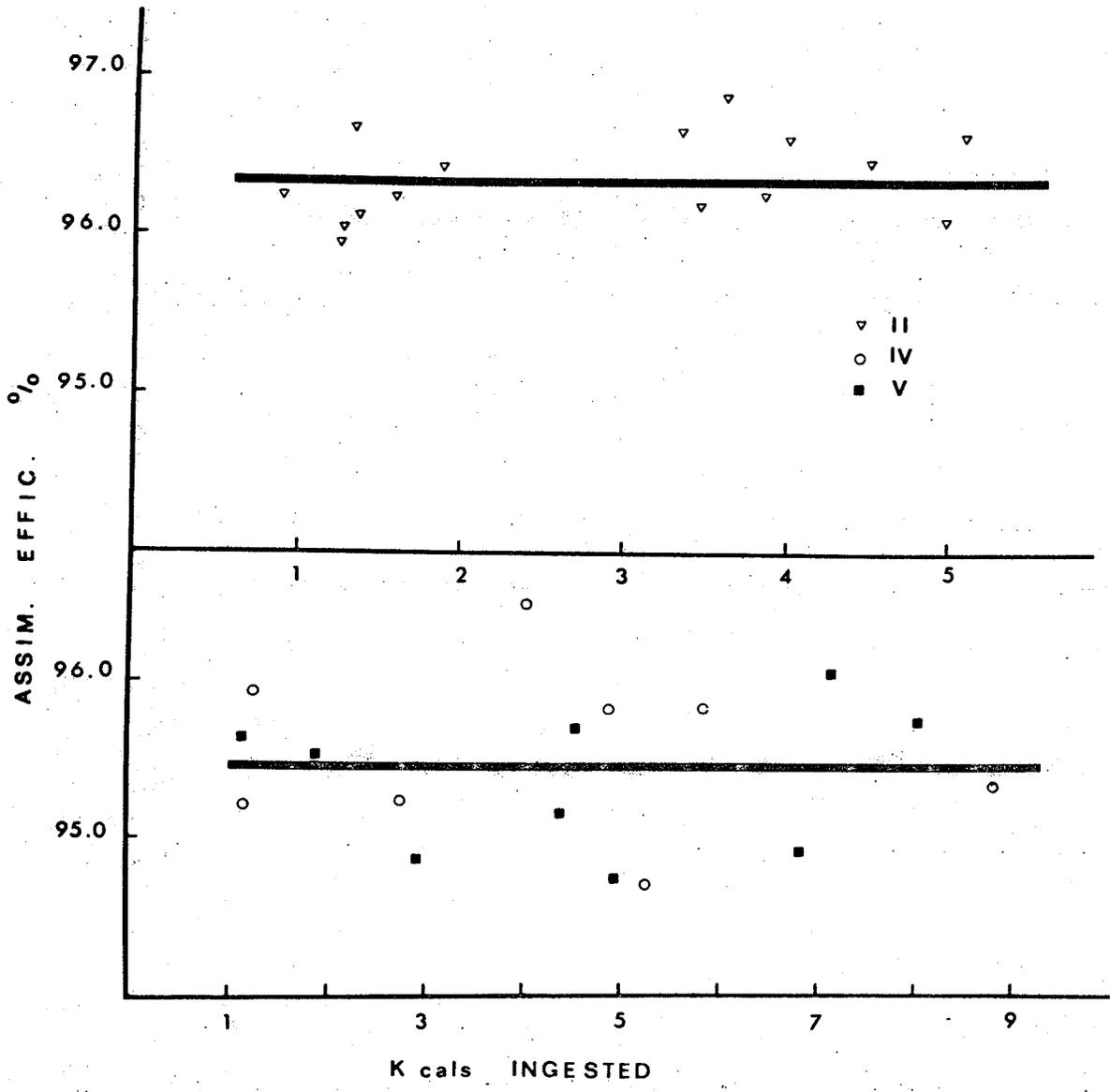
tion of age 0 perch than walleye of 500g.

To examine the effect of walleye size on assimilation efficiency, fish of various weights ranging from 113.2 to 502.0g were fed rations between 7.80 and 11.06 cals per gram (Fig. 13). Only meal sizes within this range were used in the regression analysis as the effect of larger meals (> 60 cal/g) on assimilation was not examined (Fig. 13). Assimilation efficiency decreased with increasing fish size, $E = 96.851 - 0.0045 W$ where E is the assimilation efficiency and W is fish weight. The regression coefficient was significant (Table XVII) and 82.4% of the variability in assimilation efficiency was attributable to weight changes. To determine if this relationship applied to other diet types, walleye of different sizes were fed amphipods at a rate of 8.21 to 11.17 cal/g. This relationship, $E = 82.103 - 0.0041 W$, was also highly significant and r^2 is 0.859. Regression coefficients from assimilation equations of both age 0 perch and amphipods were tested for homogeneity ($H_0 : \beta_1 = \beta_2$). The hypothesis was accepted ("t" = 0.418 ns) and slopes were assumed to be similar. The obvious difference in intercepts reflected the utilization of various food types. The effect of fish size on assimilation efficiency was not determined for all food types. The two regression lines (Table XVII) for crayfish and emerald shiners were derived by solution using a "b" value of 0.0045. The slope from the age 0 perch trials was utilized since more experimental animals were available in that assessment (14 walleyes). In solution for the intercepts (a) of Table XVII, 4 walleye of similar

Fig. 13. Effect of fish size (g wet weight) on assimilation
efficiencies for walleye fed at 16C.

Y = 96.85 — 0.0045 X

F = 55.97
r = 0.908

WET WEIGHT g

100   300   500

ASSIM. EFFIC. %

96.0   98.0
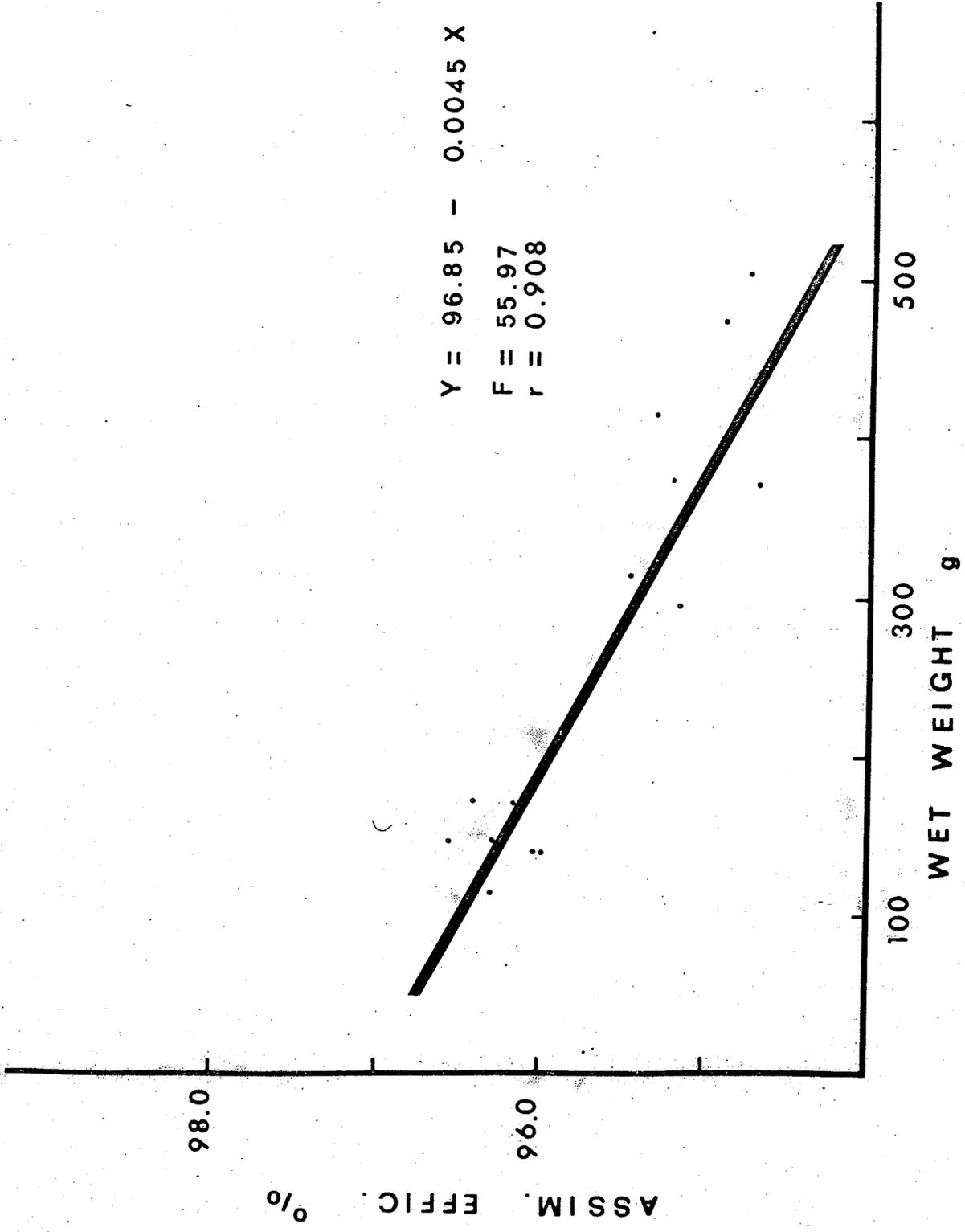
Table XVII. Experimental and derived (equations for crayfish and emerald shiners derived by procedures in the text) relations between assimilation efficiency (E) and walleye weight (W) for various natural food organisms.

Food organism	Regression expression	No. observations	F	r^2
age O perch	$E=96.851-.0045W$	14	55.97	0.824
amphipods	$E=82.103-0.0041W$	8	33.79	0.859
crayfish	$E=83.535-.0.0045W$	4		
emerald shiner	$E=97.871-0.0045W$	4		

size were fed known amounts of food and results were combined
to provide a better value for assimilation by a particular
fish size.

It was apparent (Table XVII) that assimilation was
highest for perch and emerald shiners, and lowest for the two
invertebrate foods. A comparison between assimilation effic-
iencies for amphipods and crayfish was not possible since the
natural utilization of O. virilis has not been defined (regur-
gitation may be a common phenomenon). Assimilation of
emerald shiners appears to be only slightly greater (1%)
than West Blue Lake perch.

Assimilation (determined in terms of solid egesta)
of ingested material in walleye was essentially independent
of ration size. However, increasing fish size decreased
assimilation (Fig. 13). Maximum utilization of a ration varied
according to the food species ingested (Table XVII) and is
between 82.10 (amphipods) and 97.87 (emerald shiners).

An Unaccounted for Energy Excess

In the laboratory nutrition section, measures of
available ration, routine metabolic expenditure and growth
have been described - including their major controlling
factors. The experiments provided a relatively complete
description of energy flow in walleye with an important
exception. All fish in experimental growth series were fed
similar ration sizes ($\approx 4\%$ of body weight), and had differing
K_3 conversions which were temperature related. Lower temp-
eratures produced lower K_3 conversions; thus, the energy

Table XVIII. Energy utilization by walleye for maintenance, routine metabolism (T_R) and the excess in energy (ΔT) above twice the routine level (T-2 (T_R). All measures are in calories and figures in parenthesis are standard deviations.

Temp.	$T=pR-\frac{\Delta W}{\Delta t}$	Maintenance	$2(T_R)$ (Winberg 1956)	$\Delta T=T-2(T_R)$
20C	121,206 (7,743)	45,141 (3,147)	94,581 (9,654)	27,318 (9,322)
16C	115,607 (12,180)	33,887 (3,207)	60,217 (5,194)	55,390 (14,090)
16-8C	93,631 (5,849)	13,261 (1,133)	25,311 (1,720)	68,320 (5,984)
12C	121,769 (11,271)	21,127 (1,024)	39,381 (1,534)	82,388 (10,599)

not considered by routine expenditure, growth, or available energy increased with decreasing temperature. A portion of the total metabolic expenditure (from $T = pR - \frac{\Delta w}{\Delta t}$) was utilized for routine metabolism ($T_R = 0.3W^{0.8}$). Differences between T and T_R cannot be stratified further from this study, but it is evident (Table XVIII) that, within the range of temperatures where significant growth occurs in West Blue Lake, the energy above the routine level increased with decreasing temperatures.

It was apparent (Table XVII) that the expenditure (ΔT) at 20C, 27,318 cals, was considerably less than at 16C, 55,390, and 12C, 82,388. In addition, the expenditure in the variable temperature regime was intermediate (Table XVII) to that of the two adjacent stable temperatures. If the active metabolic expenditure, taken as $2T_R$ (Winberg, 1956), was corrected from 20C and applied to the weights of fish at 16 and 12C, the excess above this requirement was still greater than at lower temperatures.

From this study, it appears that temperature plays no role in gross or net conversion (K_1 and K_2) but drastically affects that portion of the available ration (pR) which is utilized in metabolic functions.

NATURAL FEEDING

Caloric Content of Walleye and Their Food

Samples of living walleye food organisms were

Table XIX. Cals/g dry weight, moisture and ash content of crayfish, (O.virilis), collected in West Blue Lake, 1969-70. Standard deviations are in parenthesis.

Collection date 1970	No. analysed	Cals/g dry weight	% moisture	% ash
May 23	12	3035.8(480.7)	75.57(2.0)	36.99(5.28)
June 18	4	3093.3(259.0)	76.00(1.0)	36.3 (3.30)
July 22	3	2906.8(117.9)	74.93(3.4)	38.2 (3.54)
Aug. 20	3	3118.4(239.5)	76.50(2.2)	32.8 (3.25)
Oct. 15	3	3135.2(318.7)	74.96(1.9)	37.7 (6.73)
Grand Total	25	3051.4(364.9)	75.6 (1.98)	36.6 (4.65)

analysed for caloric content. In addition, ingested food
species and their relative amounts were determined from cap-
tured walleye. Furthermore, caloric values of walleye were
determined from these fish. Collections for this phase of
the study occurred during the ice-free period of 1970 only.

Calorific values of whole crayfish varied widely
within any one sample as indicated by the broad limits
(Table XIX). The results of a one-way analysis of variance
(F = 0.173 ns) indicated that mean values did not vary between
collections. As ash content varied considerably (27.3 to
43.6% of dry weight) a correction for endothermy (Paine, 1966)
was applied to the cal/g dry weight. Mean corrected cal/g
was 3128.1 standard deviation ±336.4 irrespective of collec-
tion date and a decreasing trend[4] of energy with increasing
ash content became evident. Adjustment for endothermy removed
little of the apparent ash effect. As well, the trend per-
sisted when values were examined as cal/ash free gram.

A slight increase in ash with increasing dry weight
indicated that the effect may be size influenced. There was
insufficient evidence for further analysis; therefore, the
mean value determined from all samples (3051.4 cals/g dry
weight) was used to estimate the contribution of crayfish to
the walleye diet.

Caloric determinations from meter net collections
of age 0 perch indicated a seasonal trend in relative energy
content (Table XX). Highest values occurred in late June
accompanied by low ash content, but values decreased there-

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(4)   see Appendix Fig. 1 for descriptions of caloric trends
in crayfish.

Table XX. Calories/gram, ash and moisture of age 0 perch
Perca flavescens (Mitchill), and older fish collected from
West Blue Lake, 1970. Figures in parenthesis are standard
deviations.

Collection date	Age	Cal/g dry weight	% ash	% moisture
June 18, 1970	0	5355.1		
June 20	older	4805.8(85.10)	16.27(3.68)	76.4(1.30)
July 22	0	5059.8(208.1)	10.6 (1.21)	76.6(1.08)
July 22	older	4807.6(162.1)	15.19(2.98)	76.4(1.00)
August 21	0	4994.9(78.1)	11.0 (1.48)	76.3(0.57)
August 23	older	4927.5(53.8)	18.20(2.18)	75.9(1.26)
October 14	0	4967.1(47.8)	14.1 (2.27)	75.3(0.90)
October 14	older	5052.7(103.1)	17.76(2.94)	75.9(1.90)

after until late summer (ash content increased slightly).
Because of the variability about mean estimates for July,
August and October this energy trend was not well defined.
In older perch (Table XX), a distinct increase in mean energy
content occurred from June (4805.8) to October (5052.7 cals/g
dry weight). Analysis of variance to determine apparent
changes indicated that a temporal difference did exist in the
mean energy content of adult perch ($F = 4.70$, $P < .05$). As
will be demonstrated, a distinctive seasonal trend in energy
content of walleye also exists; thus it is not unusual that
a similar change could occur in perch.

Seasonal analysis of the caloric content of an
amphipod, Gammarus lacustris, indicated a large within sample
variability (Table XXI). Since there was no change in mean
energy value when animals were grouped into 0.5mm length
classes ($F = 0.310$ ns, d.f. = 19) values (Table XXI) represent
natural variability occurring independent of size.

Additional collections of resident organisms,
(sticklebacks (Culaea inconstans), leeches (Haemopsis sp),
dragonfly nymphs (Tetragoneuria sp), mayfly larvae (Blasturus
sp) and caddisfly pupae (Phryganea)) indicated a wide variability
in energy content (Table XXI). These organisms were not
always available, or vulnerable, during all times of the
year; therefore, combustion was limited to available
organisms (Table XXI).

A seasonal trend in caloric content was obvious
for walleye in West Blue Lake (Fig. 14). Since samples of

Table XXI. Energy content (cals/g), percent moisture, and ash of common walleye diet items, West Blue Lake, 1970. Standard deviations are in parenthesis.

Organism	Collection date	Samples combusted	Cal./g	% moisture	% ash
Gammarus lacustris	May 23,1970	4	3770.4(302.9)	78.2(2.18)	
	June 23	4	3973.0(229.0)	77.2(2.04)	
	Aug. 22	4	3940.1(179.7)	76.7(3.61)	
	Oct. 5	4	3898.4(437.3)	78.7(1.23)	31.1(4.31)
	Grand mean	16	3895.3(268.1)	77.8(2.03)	
Culaea inconstans	May 23, 1970	4	5097.9(169.1)	76.0	
	July 21	3	4827.3(53.7)	75.5	16.8(2.91)
	Grand mean			75.68(1.20)	
Haemopsis	May 23,1970	3	5636.0(105.6)	80.70	
	July 22	3	5661.7(69.3)	82.1	
	Grand mean		5648.8(81.10)	81.4(1.05)	3.61(2.74)
Tetragoneuria	June 21, 1970	3	5744.5(104.8)	77.5(3.89)	
Blasturis	June 21, 1970	2	5453.1(106.0)	69.9	
Phyryganea	June 21,1970	2	5805.0(118.9)	77.1	

Fig. 14. Change in energy content of walleye during 1970 in West Blue Lake.
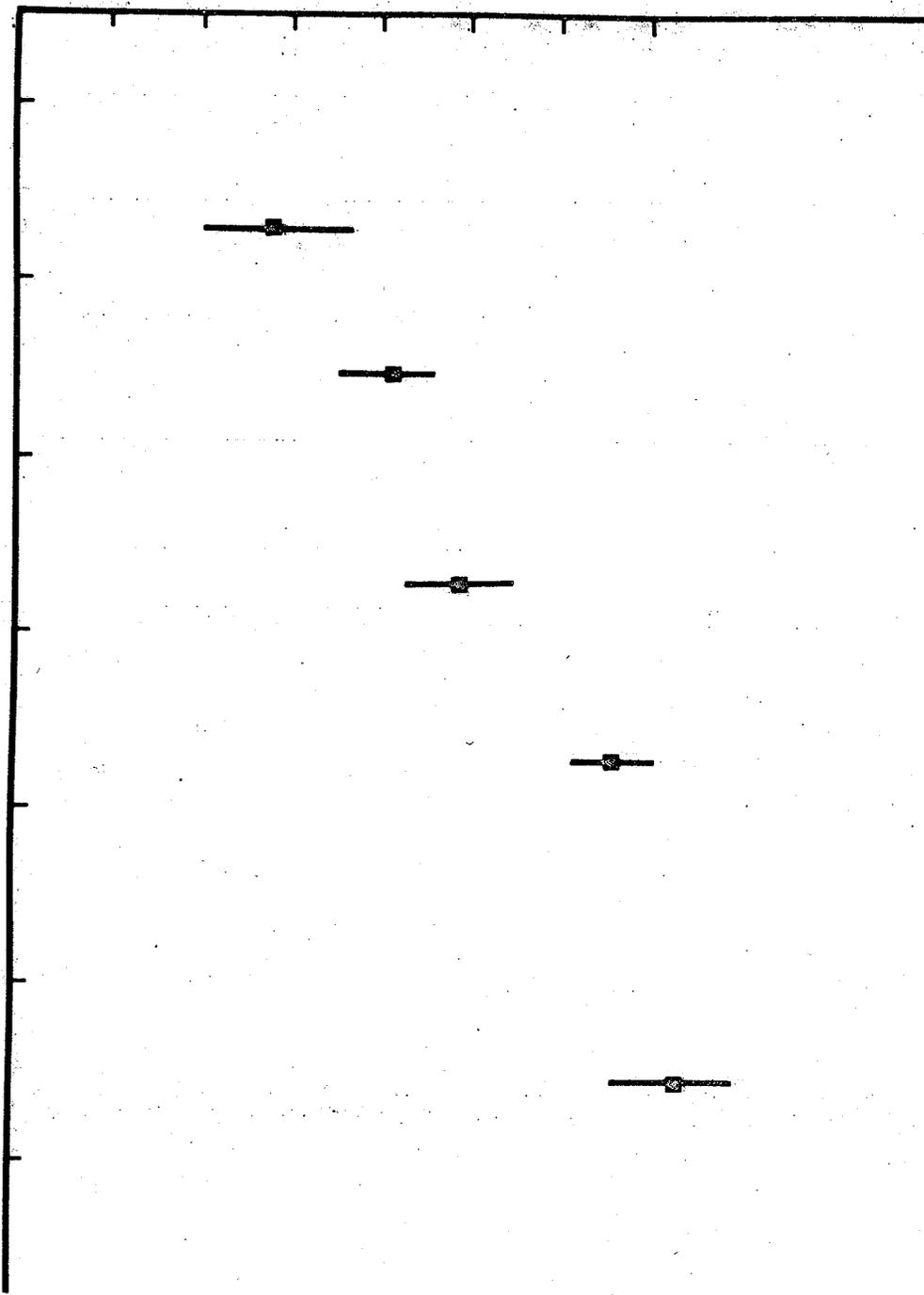
various ages (two to six years of age) were combusted, results of an analysis of variance between immature (II year old fish) and maturing or mature individuals (all older fish) indicated no significant difference (F = 0.237 ns) between means. As well, one walleye, age IV$^+$, was subsampled five times and a 1g sample combusted from each. From this replicate series, the mean energy of this fish was found to be 5004.7 cal/g dry weight (range 4974.8 to 5041.7 cal/g) with a standard deviation of 26.4. It was apparent then that the variability within a sample was very small and well within the stipulated precision of the Gallenkamp calorimeter.

Natural Walleye Feeding

The peak catch during any night of fishing was generally 1/2 to 3/4 hours after dusk; all walleye used for stomach examinations were captured 1.5 to 2 hours after the initial migration into the inshore waters.

Number of empty stomachs was greatest in October (Table XXII) but was also high in August. The presence of large, partially digested perch in several stomachs collected in May complicated interpretation of material in walleye stomachs. Several of the large perch (9.69, 43.60 and 45.30g in the stomachs) were not included in the computations and, although probably still over-estimating the ingested material for that night, are presented as an adjusted stomach weight (Table XXII).

Total stomach contents as a function of fish size (Fig. 15) was variable during 1970. To estimate uningested

Table XXII. Summary of walleye feeding in West Blue Lake during the ice-free period, 1970.

Collection date	No. empty stomach	No. with food present	Average stomach wt(g)	Avge g/g	Avge cals per stomach	Avge cal/g	
May 16, 1970	1	15	10.15 10.83	0.0136 0.0145	16,059.2 17,129.7	17.994 19.194	a b
Corrected for previous ingestion	1	13	4.10 4.44	0.0092 0.0099	4,689.1 5,080.5	9.350 10.129	
June 16	2	13	1.575 1.817	0.0076 0.0088	2,287.1 2,638.9	9,289 11,300	
July 21	3	13	1.742 2.144	0.0054 0.0067	2,734.5 3,365.5	7.780 9.580	
August 17–18	4	14	2.052 2.639	0.0094 0.0120	2,504.3 3,219.8	11.607 14.924	
October 14–15	6	10	1.298	0.0046 0.0069	2,567.8 4,108.5	9.556 14.390	

a all fish are included

b only those with food present

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Fig. 15. Contribution of all diet items in terms of weight (------)
and calories (——) in relation to body size of walleye in West
Blue Lake, during the ice free period, 1970.
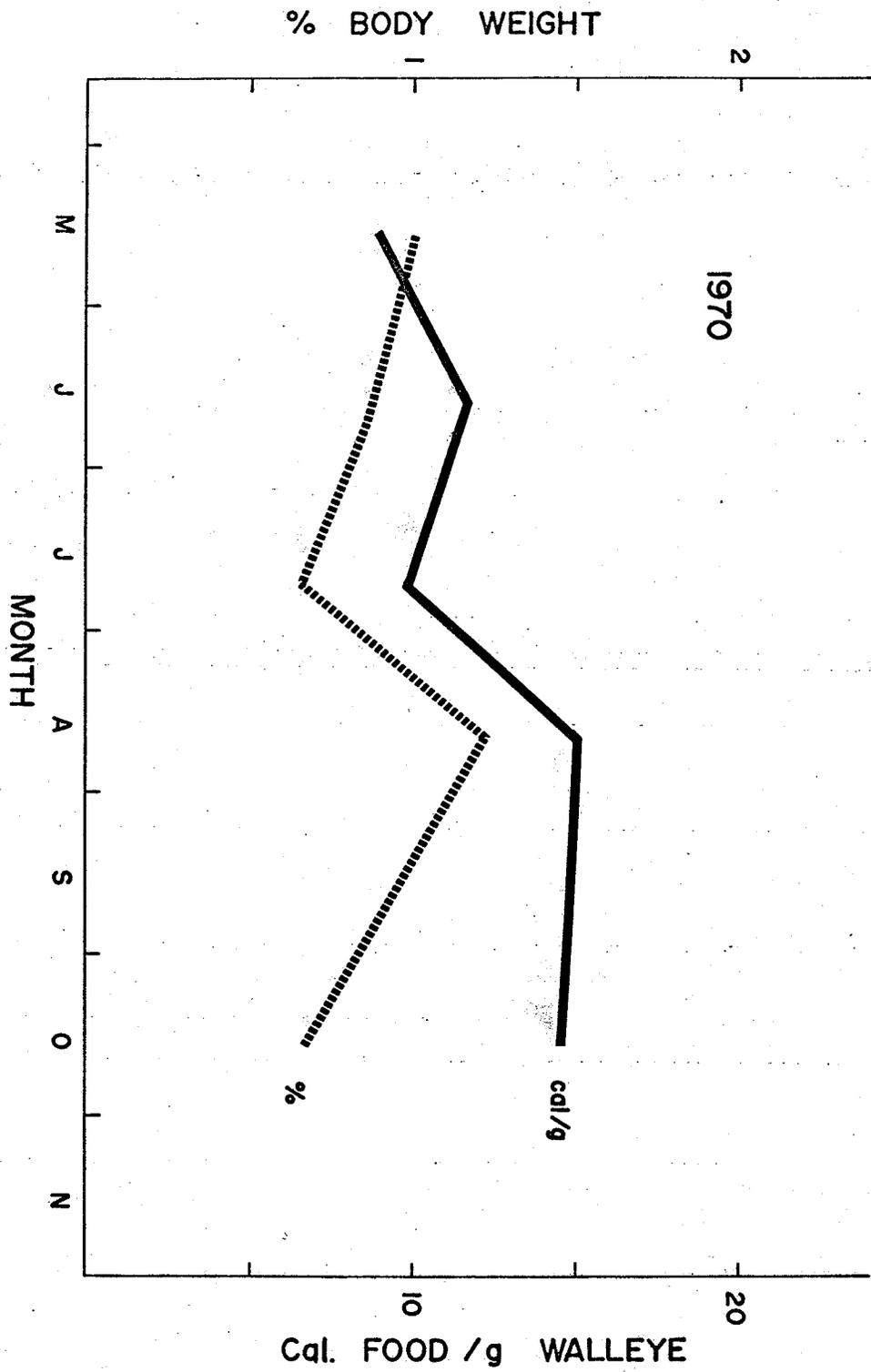
calorific values of food items, organisms were first adjusted
to live weight and then converted to energy units on the basis
of data in Tables XX and XXI. Both descriptions of stomach
contents (% body weight and cal/g) follow similar patterns
(Fig. 15). Inclusion of all fish (empty or containing food)
indicated that maximum ingestion occurred in mid-August
(Table XXII).

Few species were utilized as food (Fig. 16) and
the major caloric contribution was provided by fishes in
West Blue Lake (perch and stickleback). Results using four
methods of presenting data on natural feeding by walleye
(number, weight in the stomach, weight calculated from
uningested foods, and calories) differ greatly and emphasis
shifts from one taxon to another (Fig. 16).

Amphipods were always present, to a lesser or
greater extent, in the walleye diet (Fig. 16). Maximum
consumption was in May and August (166 and 888 individuals
respectively) and lowest in July and October (4 and 54 amphi-
pods). In several cases, the theoretical live weight (from
samples processed for calorimetry) was less than weights
determined from materials present in the stomachs (Fig. 16).
This difference, occurring only in amphipods, was generally
slight (1-2% less in "expected" weight) except in the June
16 sample when stomach weight (3.896 g) was twice the weight
of coincident live samples (1.712 g). Although Gammarus
lacustris was the dominant food organism in terms of numbers
present, their caloric contribution was less than that of
ingested fish flesh (Table XXIII).

90.

Fig. 16. Contribution, by taxon, of resident organisms to the diet of walleye in West Blue Lake, 1970.

NUMBER

WEIGHT IN STOMACH

EXPECTED WEIGHT

CALORIES/g DRY WEIGHT

WEIGHT IN STOMACH

EXPECTED WEIGHT

CALORIES /g DRY WEIGHT

MAY 16, 1970

JUNE 16

JULY 21

AUGUST 17-20

OCTOBER 14

1. Gammarus lacustris
2. Adult P. fluviatalis flavescens
3. Age 0, P. fluviatalis flavescens
4. Culaea inconstans
5. Haemopsis sp.
6. Blasturus sp.
7. Phryganea sp.
8. Orconectes virilis
9. Miscellaneous

NUMBER

EXPECTED WEIGHT

WEIGHT IN STOMACH

CALORIES/g DRY WEIGHT

Table XXIII. Contribution of the diet items found in walleye stomach to walleye nutrition, West Blue Lake, 1970.

Organism	Number	Stomach weight	Live weight	Calories
G. lacustris	1205	34.564	25.753	22,915.0
Adult perch	6	134.308	210.3	239,123.8
Larval perch	102	38.067	47.990	57,837.9
Sticklebacks	27	20.539	36.910	45,911.1
Haemopsis	5	13.464	13.464	15,932.4
O. virilis	4	12.954	19.589	14,584.7
Blasturus	626	10.920	11.560	18,974.4
Misc.		4.991	5.168	6,969.9

Mayflies, Blasturus sp, appeared in large numbers (626) in June and provided a similar caloric contribution (18,974.4 cals) to that of amphipods. In the June walleye sample (Fig. 16), mayflies were the dominant contributor to stomach contents regardless of the method of expression.

In spite of the relatively small number of larval (102) and adult perch (6 individuals) in stomach contents, their contribution in terms of weight and calories was large (Table XXIII). Older perch (excluding young-of-the-year) were the largest contributor in terms of weight (134.308 g and 239,123.8 calories), but were few in number, occurring primarily in the May collection. Larval perch were significant contributors in all respects to the stomach contents in July and October samples (Fig. 16).

Sticklebacks consistently appeared throughout the sampling period (Fig. 16), and provided a contribution similar (45,911.1 cals) to that of larval perch (Table XXIII).

The sporadic occurrence of the remaining items (leeches, crayfish, Trichoptera, and a small bird) provided minor additions (Table XXIII) to the diet of walleye during the 1970 sampling.

From analysis of the number of empty walleye stomachs after a period of ingestion, it becomes evident that ingestion was less frequent during latter part of the ice-free period (Table XXII). Examination of contents at a particular time only partially reflects the intensity of feeding since average contents (including empty stomachs) indicated only that the stomach contents were greatest in the August sample. From

Fig. 16, it was evident that consumption of amphipods during the sampling period was persistent. Amphipod contribution to the diet was not nearly as great as the calories of fish flesh ingested. Fish utilized by walleye (Table XXIII) were the main caloric contributors to the natural diet. Other foods ingested by walleye did not appear consistently during the sampling period and contribute only a minor portion of energy intake.

POPULATION CONSUMPTION

Biomass and production estimates were available (Table XII) in terms of wet weight. To define caloric intake (R), caloric deposition in walleye flesh (Fig. 14) must be considered in addition to observed production. Negative production (loss to the system) occurring in the spring of 1969 and the winter of 1969-70 was included as absolute losses from the particular size groups. Production in calories was the result of caloric accumulation (Fig. 14), growth in instantaneous terms, and biomass ($\bar{B}$) expressed as biocontent. Production in energetic terms (Table XXIV) generally reflected production measured by weight. The former considered the regular caloric increase of walleye flesh, and because of this uptake, increased energy production by older fish.

Since both K_1 and K_2 conversion estimates were temperature independent, and since K_2 considered that

conversion adapted to natural situation.

Period	Age	$\overline{B}$(Kg)	P(Kg)	Temp. C	Maint(Kcal/wk)	Natural eff. / lab. eff.	P(Kcalx10^3)	R(Kcalx10^3)	R(Kcal/Kg/day)
May 14-20 to June 16-22,1969	I	205.031	-2.624		7709.166	87.6/97.5	-12.018	-12.018	-1.953
	II	76.068	-1.308		2860.157	86.8/96.7	-6.000	-6.000 a	-2.628
	III	108.223	-2.413	8	4069.185	85.9/95.8	-11.038	-11.038	-3.042
	IV	360.233	0.076		13544.761	84.9/94.8	0.348	3.185	0.295
	V	107.343	0.004		4046.097	84.1/94.0	0.018	0.165	0.051
	VI	62.356	0.003		2444.586	81.9/91.8	0.014	0.131	0.071
June 16-22 to Sept. 3-12	I	264.135	66.748		10301.265	87.6/97.5	322.860	2840.640	1345.000
	II	119.111	39.223		4645.329	86.7/96.6	190.232	1776.855	1866.446
	III	123.165	24.498	16-8	4803.435	86.0/95.0	59.735	534.600	543.453
	IV	414.626	49.216		16170.414	84.8/94.6	238.698	2152.126	651.246
	V	159.406	18.922		6216.834	84.1/94.0	91.772	841.243	686.455
	VI	71.891	8.533		2832.749	83.3/93.1	41.385	382.550	664.149
Sept. 3-12 to Oct. 5-12	II	259.607	16.070		9761.216	87.3/97.2	80.832	717.058	816.873
	III	125.413	1.793	8	4715.529	86.2/96.0	9.019	80.711	190.000
	IV	129.733	4177		4857.961	85.4/95.3	21.000	188.442	426.337
	V	408.0988	12.065		15377.949	84.5/94.3	60.687	551.700	39.674
	VI	145.015	4.278		5452.564	83.1/93.0	21.518	214.200	43.447
Oct. 5-12,1969 to May 18-22,1970	II	188.904	0.187		6292.702	87.3/97.2	0.906	80.377 a	19.331
	III	90.732	-0.843		3021.376	86.1/95.9	-3.054	-3.054 a	-1.538
	IV	108.355	0	4	3608.222	85.0/94.9	0	0	0
	V	388.931	0		12851.402	84.1/94.0	0	0	0
	VI	44.350	0		1476.855	82.9/92.8	0	0	0

a negative production is presented as a direct loss from the population.

which was available, the latter was used in estimating in-
take. Net conversion $(K_2 = \frac{\Delta W}{pR\Delta t})$ considers assimilation
which was affected by fish size (Fig. 13) but not the magni-
tude of ration. Therefore, the weight of particular age
groups was required (Table XII) to determine intake.

The slope of the assimilation-fish size regression
remained constant (Table XVII) for the food organisms investi-
gated. A suitable intercept for describing assimilation for
natural diet items was also required prior to calculating
energy intake. To provide the intercept $(E = a + bW$ where
the intercept is maximum efficiency and B is the slope of
-0.0045) the caloric contribution of natural walleye foods
(Table XXIII) was multiplied by the assimilation determined
in the laboratory. The products were then reduced by a
common denominator and a weighted mean of all products was
found. Assimilation for the natural food spectrum of walleye
was $E = 88.01 - 0.0045 W$. The average weights $(\overline{w})$ for each
age group (Table XII) were inserted in the derived equation
to provide estimates of natural assimilation.

To determine intake (R) necessary to produce the
observed production a modified K_2 which considered the
efficiency altered by the natural diet was required. Natural
net efficiency was found by $\frac{\text{natural efficiency}}{\text{laboratory efficiency}} \times K_2$.
Intake, and daily ration, to produce the observed seasonal
production was calculated by dividing production by the
derived net conversion.

Natural assimilation (Table XXIV) was less (approx-

imately 10%) than laboratory conversion of emerald shiners.
During periods of peak production, June to October, intake to
support this proliferation was greatest (Table XXIV). Ration
on a daily per unit fish basis during this period varied from
0.3 to 18.7% body weight. Maximum intake was by the age II
fish of the June to September period. Minimum intake was by
the age III fish and appeared to be out of sequence with
intakes of other ages. This age class was not well represented
during the study and production was calculated from growth
rates based on small samples. The fast growing fishes (age
I and II) had greatest intakes, 1345.00 and 1866.446 K cal
(Table XXIV). Since assimilation and growth was less among
older fishes consumption was therefore less for any period
(Table XXIV). Periods of no growth or caloric loss (mini-
mized by weight measures, but intensified by caloric descrip-
tions i.e. biocontent) were reflected by caloric loss or
negligible intakes (Table XXIV).

Calculated rations per unit fish weight greatly
exceeded observed rations as found in stomachs (Table XXII
and Fig. 15). However, amounts present in walleye stomachs
did not reflect daily intakes, but only indicated seasonal
differences.

In this investigation, production in West Blue Lake
was determined in calories by applying seasonal changes (Fig.
14) in energy content to production (Table XII) observed
during 1969-70. The influence of ration, temperature, and
walleye size on growth, maintenance , and assimilation was
applied directly to the natural situation. Only ration

availability (p) of the parameters investigated was altered
by natural food and conditions. Since both energy production
and the processes whereby energy was utilized were known for
this system, the seasonal differences in requirement were
established (Table XXIV). For production, 10,334.873 K cals
were required. The major demand existed from June to September.
The greatest requirement was for age I to III walleye. Main-
tenance requirements (Table XXIV) were presented only to
indicate the extent of the expenditure for routine requirements.

DISCUSSION

VITAL STATISTICS OF THE POPULATION

Abundance Estimates

Information is scarce regarding population changes occurring in a small, and sometimes virtually closed system such as West Blue Lake. Information presented from this study gains little support from present literature. Data on seasonal stock changes within the year are also limited (Ricker and Foerster, 1948; Alexander and Shetter, 1961), but seasonal decreases in unrecruited populations have been indicated. Alexander and Shetter, op.cit., encountered the problem of overlapping limits as in the present study (Tables IV, V and VII), but used these seasonal estimates as being true assessments of abundance. Ricker and Foerster, op.cit., estimated mortality rates occurring within short periods and applied these to the initial population to assess biomass changes and production and has been one of the few to locate short term population changes and extend these to assessments of production. Results of the above investigations support the regular but small decrease in the unrecruited stock of West Blue Lake.

Walleye greater than 25cm in West Blue Lake more than doubled in abundance within a one year period (Tables IV, V and VII). Recruitment occurred after June 1969. The unrecruited stock (Table IV) decreased from May 1969 to May 1970.

Previous analyses of walleye populations have provided year-to-year differences (Pycha, 1961; Forney, 1967) or have dealt with discrete point estimates (Rose, 1947). Several of these studies utilized the spawning population, and may have marked an incomplete segment of the resident population. This study found that a lower population existed in May (when reproduction takes place) and detectable recruitment (Tables IV, V and VII) occurred until June 1969. This trend may have resulted from random sampling variation; however, the possibility exists that, even in this study, the random distribution and population structure was altered by spring spawning. Estimates conducted after spawning, June and September, indicated that abundance (Table IV) and composition (Fig. 3) was relatively static although abundance was slightly greater than in May. Distribution at time of reproduction may very well be localized in West Blue Lake and only a segment of the population was available for marking.

Other investigations concerning walleye populations have been directed towards commercial fishing enterprises (Pycha, 1961; Smith and Pycha, 1961; Ryder, 1968) or a sport fishing situation which required investigation (Rose, 1947; Forney, 1967). On the whole, information regarding unexploited fisheries is scarce; for walleye it is non-existent. Therefore, these data concerning the population and its changes are of interest and importance when information on an unexploited fishery resource is required.

Previous investigations regarding walleye populations infrequently examined inadequacies in procedure. However,

in this case, efforts were made to ensure that variation in parameters was real and not the effect of sampling deficiencies. Conditions applicable to mark-recapture experiments (Ricker, 1958) were examined to ensure maximum reliability in descriptions of population energy requirements.

The problem of gear selectivity is ominous in all investigations into fish populations (Moyle, 1950; Berst, 1961) and is indeed important to this study. Forney (1961) compared year-class distributions of walleye collected by five different gear types. From this, Forney stated that age structures of gill net captures were similar to the "real" population determined by trap net samples of successive spawning runs; however, he also states that specific incidences demand confirmation. x^2 tests (Table III) of successive gill net captures in West Blue Lake indicate that similar segments of the population, by age, were captured. Frequency distributions of the standard net (Fig. 2) indicate that an excellent degree of overlap exists among mesh sizes. As well, apparent normality of each frequency distribution (3.81 and 8.89 cm nets) is altered by the entanglement of only a few larger fish in each sample. Comparisons with other gears is impossible because of the morphometry of West Blue Lake. From Fig. 3, the reproducibility of captures from adjacent marking periods (particularly of the more abundant age groups, II, IV and V) supports non-selection by the standard net. Frequency distributions of captures made in May and June 1969 were virtually identical both in the size range of walleye captured, and the age composition of the sample. Variability in size about the

mean length, particularly of age II fish, was consistently similar for each collection during 1969-70 (Fig. 3). The apparent normality of the May through October samples of the new recruits further indicates that the gear provided a good representation of size in at least this age group. Although net selectivity by age does not occur, selection by size may be present. Excellent agreement with Glenn (MS 1969) exists in descriptions of seasonal growth, but selection by size may exist in both studies. The agreement with Glenn, op.cit., and the evidence presented by x^2 tests and frequency distributions negates net selection by age. If size selection does exist, it may only alter estimates of growth and consequently production.

In spite of attempts made to capture walleye at all depths and times of day in West Blue Lake, specimens were secured only after dusk and before dawn in 3 to 7m of water. Rawson (1957) found that in the course of netting 24 hours in the day, walleye were caught primarily during dark hours and agreed with Carlander and Cleary (1949) and Carlander (1953) that capture differences resulted from increased activity at night. Incidental sightings of walleye inshore during the day in West Blue Lake further confounded the picture. Their ability to see in poor light, due to a modified retinal epithelium (Moore, 1944) supported nocturnal activity – observed in 560 1 tanks in the course of the laboratory feeding trials – and increased the importance of the question of daytime activity. McCann and Carlander (1970) have captured walleye during the day by bottom trawl, but indicated that activity did increase

at night in the attempt to procure food.

In particular cases where investigations concerning walleye or other species involved a mutilation or tag application, loss caused by handling or tagging has not been intensively studies. The effect of marking has been examined (Ricker, 1949; Churchill, 1963; Muir, 1963; Shetler, 1967). Each investigation has shown that the mark in use - fin clip or metal tag - has in some way adversely affected growth, survival, or the ability to avoid capture. Marking by a mechanical applicator (Dell, 1968) has proved remarkably successful in this study. Problems of mark retention and incomplete reporting were eliminated by these procedures, and individuals were readily recognized as to time and place of previous examination. Onshore mortality trials (Table II) in conjunction with regular shoreline patrol found no short-term mortality associated with periods of mark and release. Since only short-term mortality was studied, summation of subsequent capture and recapture samples (to provide large capture sizes for Petersen estimates) was not done. Adjacent collections circumvented long-term mortality problems and ensured maximum reliability in the ratio C/R. As well, growth of marked fish was within the range accomplished by untagged individuals.

An original approach to this study called for a monthly (if feasible) assessment of abundance, recruitment and survival. Onshore mortality trials proved indispensable as significant mortality (Table II) was found in a mortality trial conducted prior to a proposed date of mark and release

(July 1969). The cause of mortality was unknown as both
marked and unmarked individuals died. Black (1958) and
Beamish (1966) suggested that increased activity at higher
temperatures, elaborated by the stress of capture in this
case, may cause lactic acid build-up sufficient to induce
mortality. Mortality may occur some time after activity as
death was not instantaneous.

Since each fish was readily identifiable by number,
the problem of interspersion of marks with unmarked fish was
approached. The tendency of walleye to return to specific
spawning sites in streams or lakes has been noted (Stoudt
and Eddy, 1939; Rawson, 1957; and Forney, 1963); however, it
has been assumed (Rose, 1947; Whitney, 1958) that marked fish
became randomly mixed in certain populations. Forney, op.cit.,
Rawson, op.cit., and Ryder (1968) were of the opinion that
movement in some bodies of water is not random. In this case
the three basins of West Blue Lake do not present physical
barriers to movement, but localized sub-populations may occur.
Comparison of release to recapture sites readily indicated
that in this small closed system, dispersion of marked indivi-
duals into the population can be considered random.

New recruits can be eliminated by length analysis
as in this study, and excluded mathematical procedures (Robson
and Flick, 1965; and Parker, 1955) used to eliminate the effects
of recruitment on population estimates. Recognition of recruits
also permitted subdividing abundance to either include or
exclude recruits. Since the triple-catch-trellis requires
experimentation during periods of constant mortality and

recruitment (Ricker, 1958), the examination during May 1969 to May 1970 was subdivided on the basis of completion of recruitment. This analysis provided estimators of numbers, survival and recruitment with broad limits for the latter half of the study (Table VII), but was directly comparable to analysis by the other analytical procedures.

The Jolly (1965) approach to sequential analysis of populations considers changes in mortality and recruitment in its design and is certainly the most readily applicable of the sophisticated designs of population analysis. Other multi-sample analyses (Darroch, 1959; Seber, 1965) consider death and immigration, but include situations i.e. removal on capture or no estimates of variances, which preclude obtaining maximum information regarding the population. Recruitment, therefore, is not detrimental to analytical results of the three procedures - Petersen formula, triple-catch trellis, and Jolly stochastic approach - used in this study.

Recruitment in this study was considered complete in September 1969 (Fig. 3), and consisted of individuals generally of 25cm and greater in total length. In addition, recruitment can adversely affect population estimates, yet stringent monitoring of size permitted assessment of the West Blue Lake walleye population. In the available literature inclusion of recruitment has been avoided because of the dilution of marks in the capture samples (McCann and Carlander, 1970). This analysis was designed to assess the contribution of young individuals (age II[+] in this case) to a vulnerable stock. The new recruits, from the 1967 spawning season,

numbered between 2100 and 2300, and significantly increased the May 1969 population (Tables IV, V and VII). In instances where recruitment was assessed (Gerking, 1962) it has been accomplished by marking the population segment under scrutiny. Descriptions of the production system, to follow, indicate the massive contribution of newly recruited individuals to biomass and caloric production.

The Petersen, Jolly (1965), and triple-catch-trellis techniques are not independent methods of estimating abundance or other characteristics of the population. Calculation of population parameters by each technique was based on the same mark and recapture sample (Table I). The three approaches were included to indicate the amount of information provided by each method and their general agreement. Petersen estimates and mortality estimated by marking was employed in calculations of production since these approaches provided more information for the period from May 1969 to May 1970.

It is apparent from examination of conditions inherent in mark and release experiments that no systematic bias is introduced into descriptions utilized herein. As well, an additional criterion regarding sample size (Robson and Regier, 1964) generally applies and adds further weight to results and techniques employed.

Natural Mortality

Information regarding losses in unexploited populations, regardless of species, is rare. Because of the current approach used in describing numerical changes of walleye,

seasonal measures of survival determined particular periods
of loss from the West Blue Lake population. Annual total
mortality in the relatively unexploited lake trout popula-
tion of Great Slave Lake (Kennedy, 1954) was between 37 and
65% for ages 13 to 24 - conversely 63 to 35% of a particular
age group survived to the end of one year. Mortality of
lake trout tended to increase with increasing age. Ricker
(1947) examined several unexploited species and estimated
annual mortality of a magnitude similar to that of lake trout.
Age dependent mortality also existed. In this study seasonal
mortality has been assessed and was small (Table VI). The
loss to the resident population, irrespective of age, was
calculated as survival could not be assessed for a particular
age group (tag releases for any one age was small, and unequal
year class strength prevented comparisons of subsequent ages
for any sample). In West Blue Lake, survival was highest
between May and June. Greatest loss occurred in the fall and
under ice cover (Table VI). Comparison on a per day basis of
instantaneous mortality - mortality was solely by natural
means since no losses from marking resulted - indicated that
mortality was generally small and relatively constant. However,
instantaneous per day mortality was slightly greater during
fall and winter. The high survival rate in the spring of the
year may result from inadequate sampling at spawning time,
mentioned earlier. Conversion of total annual mortality rate
to survival for all age groups (Table VI) indicated that 20
to 37% of the population survives to the end of the experi-

mental year (May to May). Even though losses between
samplings were small, this large loss far exceeded that
discussed by Regier et al. (1969) for walleye in Lake Erie
and Forney (1967) in Oneida Lake. Mortality for this unex-
ploited population of walleye are in general agreement with
estimates from other locations (Kennedy, op.cit.; Ricker,
op.cit.).

Causes of mortality in this system can only be
surmised. Disease and parasitism may well result in loss in
West Blue Lake; however, only incidental intestinal worms
and several incidents of a sporozoan (Ichthyophtherius sp)
have been observed. This population of walleye was short
lived, virtually all the population was 6 years old or less,
contrary to populations described by most other investigations
of walleye (Carlander, 1945; Eschmeyer, 1950; Forney, 1961
etc.). No real predators exist - pike (Esox lucius) are
present but rare - for walleye in this system, and the cause
of the observed losses remains as a perplexing, as well as
an intriguing, area of interest.

Growth

Growth rates in fishes are generally determined
from increments in length or weight during discrete time
periods. Although growth rates may be assessed from direct
measures, captured walleye were only measured as weighing
would increase stress from added handling. The only direct
measure of growth available to this investigation is the
progression of length during the growing season (Fig. 4).

Glenn (MS, 1969), as in this study, described direct growth in length terms and in both studies in West Blue Lake, progression in length is similar to that found by indirect means. Direct growth descriptions are infrequently used as sizes at commencement of growth - the last week in June (Glenn, op.cit.) - and subsequent samples make assessing length increments for any particular age group difficult.

For indirect analysis of growth, a regression describing the relation between anterior scale radius and fork length was developed. Carlander and Smith (1945) have indicated that fork length was the best measure for walleye and is supported by this study since the variability about a mean fork length was less than that for the total length of the same fish. Abrasion of caudal fin lobes occurred in walleye, further justifying the use of fork length. The intercept of the regression expression for fork length and scale radius - $Y = 85.858 + 1.613 X$ where Y is fork length - is frequently considered as the length at first scale formation. Priegel (1964) demonstrated that scalation of young walleye is complete at 45mm, indicating that some factor(s) influence the located intercept (85.858). Eschmeyer (1950), Carlander (1945), and Smith and Pycha (1961) located non-linear relationships between these two variables and stated that it resulted from the population and the particular segment under investigation. In this instance, it is apparent that a straight line relationship was the line of best fit.

Since length increments of real samples can be

computed from the length-scale dimension relationship, a
means of describing weight changes from length measures was
required. Glenn (MS, 1969), from 665 walleye between 195
and 650mm, found that log W = -5.463 + 3.163 log L, where
W is weight and L length, for walleye in West Blue Lake.
As well, Glenn (op.cit.) tried to assess the seasonal effect
on the length-weight relationship but was only partially
successful. No differences in growth of males and females
existed in West Blue Lake.

The question of whether growth occurs between
breakup and annulus formation cannot as yet be answered.
A comparison of two samples (May and June, 1969) indicated
no apparent growth (Table VIII). On the other hand, scale
measurements indicated (May to June, 1970) that 5.6 to 19.3%
of annual growth occurred during this time (Table XI). The
latter estimate of spring growth was no doubt an overestimate
(possibly a result of small sample size in October, 1970,
used to locate annulus position) as Gerking (1966) found 90%
of the total annual length increment in sunfish to be completed
by September in northern Indiana. As well, Forney (1966)
ascribed over 90% of the annual growth of young-of-the-year
walleye to the period before September. Hile (1941) supported
the no growth phase of May to June in walleye and indicated a
weight loss occurred during the winter ice-cover.

Growth in weight indicated that weight deposition
(Fig. 6) was similar in age IV, V and III walleye in 1969-70.
The apparent loss in weight of III[+] fish in latter portions
of the growth season certainly resulted from small samples.

The apparent weakness of this age class made adequate sampling impossible. Even though deposition appeared to be less in II^+ fish, relative and instantaneous rates indicated gradually decreasing growth in length and weight with progressing age (Table X). The magnitude and form of change in weight and length in West Blue Lake was supported by Glenn (MS, 1969) and followed general patterns of growth, found for other ecosystems in the range of walleye.

The apparent lack of age III walleye made estimation of growth, survival, and contribution to production difficult. Unequal year class strength detected in other cases (Carlander, 1944; Hile, 1954; Pycha, 1961; Smith and Pycha, 1961) can introduce a degree of instability into biomass and production of a system. West Blue Lake was also subject to fluctuations in year class strength since the 1966 brood year was virtually absent from samples taken between May 1969 and October 1970. Causes for this phenomenon are not yet understood. However, Derback (1947) has found that adverse weather conditions frequently disrupt spawning. Causes must be of natural origin since fishing pressures were slight previous to closure by provincial authorities and were under scrutiny since 1965 by members of the research station at West Blue Lake.

Biomass and Production

An extension of population number, growth characteristics, survival and recruitment yields a description of seasonal biomass and production for an unexploited closed

system (Table XII). Since several forms of expression for
population characteristics are available from this study,
but Petersen estimates (defining the original stock plus
new recruits) and mean weights of each capture were chosen to
define biomass and production.

Instantaneous expressions in computations of pro-
duction have been used (Patriarche, 1968; Ricker, 1948;
Gerking, 1962). However, the instantaneous approach (Appendix
III) results in such a small difference from the arithmetic
approach (Chapman, 1968) that the latter was utilized in
this study (Table XII).

The use of mean weights in determining production
by the arithmetic approach requires adequate sampling. I
have demonstrated that net selection is probably not serious,
at least with respect to age. Selection by size may still
occur. The standard nets in use could select particular
sizes of walleye thus providing inadequate samples for estab-
lishing mean weights and growth rates. Data concerning
selection by the gear in use tend to negate selection. The
magnitude and influence of size selection by gill nets on
production estimates cannot be established from this study,
but seem to be minimal.

Instantaneous expressions of growth (for $P = g \overline{B}$)
are bound by the limits of sampling size and procedure, but
are the best available criteria in spite of the possible
influence of net selection. If the instantaneous approach
to production is desired, age-dependent mortality should be
assessed as mortality differing with age has been shown to

exist for other species (Ricker, 1947; Kennedy, 1954), and
may exist in walleye. The selection of the arithmetic
approach for determining production was not entirely arbi-
trary but resulted from consideration of the applicability
of factors necessary for the computations.

Production (the proliferation of fish flesh whether
it survives or not) in the West Blue Lake walleye population
is limited to the months of June to October (Table XII).
During the remainder of the calendar year net production is
negative. When growth is maximized (Figs. 4 and 6), whether
by age, environmental conditions or food availability, pro-
duction generally follows suit. On the other hand, biomass
reflects the seasonal interplay of growth, mortality and
recruitment.

Virtually all investigations utilized the instan-
taneous approach to production. Ricker (1948) stated that
production was concentrated in the summer months and fell to
zero in the winter. In a description of food utilization by
bluegill sunfish, Gerking (1962) used year to year differences
to calculate production. Since Gerking determined seasonal
growth for the Wyland Lake population, a general statement
was made to the effect that production was an event of the
summer. Gerking (op.cit.) also found the greatest production
in the youngest age group that was successfully captured.
Few other assessments of production in the natural environ-
ment are available in the literature (Saila, 1956; Cooper,
Hider and Anderson, 1963). Patriarche (1968) utilized
Ricker's approach and also found greater production in

younger age groups. Even though production has been assessed for several isolated species, this investigation demonstrated the effect of naturally varying year-class strength on production (Table XII) and provided the first documentation of production for an unexploited population.

Several techniques for community analysis are available, but have rarely been applied to fish populations not influenced by man. Production was limited to summer months, and a loss occurred to the system during the winter, indicating that use of any fishery should occur primarily after most of the annual production has occurred. The population characteristics of the unexploited West Blue Lake walleye population were successfully documented in 1969-70. To provide an understanding of population requirements and utilization of natural food, nutrition studies were conducted under controlled conditions in 1970. Laboratory and natural studies on walleye feeding (to follow) provide measures to further understand the processes in the natural system.

LABORATORY STUDIES

Walleye are not the most ideal animals for laboratory study as initial acclimation to food and confinement is difficult and time consuming. Older walleye (III, IV, V and VI years of age) refused to consume energy sufficient to produce significant growth during the course of the laboratory studies. This investigation has already found that production

occurred during June to October of the calendar year. Therefore, since growth may well be under the influence of hormonal control (Swift, 1955; Swift and Pickford, 1965), laboratory studies were conducted coincident with the occurrence of natural growth. Moreover, factors dictating natural or laboratory growth of fishes are not completely known. Temperature and light are the most commonly accepted controls. This study, although incomplete in the sense that not all mechanisms controlling growth are examined, does present efficiencies and requirements of fishes under known conditions and provides a basis for understanding the West Blue Lake walleye production.

Obtaining sufficient quantities of food to support experimental walleye was challenging as West Blue Lake could not yield adequate bulk of a homogeneous food type. It has been found that emerald shiners, Notropis atherinoides (Rafinesque), were frequently consumed by walleye (Rainey and Lachner, 1942; Eschmeyer, 1950; Priegel, 1963; and others). Large inshore migrations of shiners occurred at Delta Marsh on Lake Manitoba during the spring and presented a large quantity of a similar food. Storage did not affect the energy content of the shiners, and walleye aged II[+] readily accepted food while showing no ill-effects during holding on this diet. Items used in assimilation studies were obtained from West Blue Lake and were major components of the natural diet of walleye in that ecosystem.

The unit of measure in the assessment of requirements, expenditures, growth, and efficiencies in fishes is controversial. Protein has been considered as the primary

measure of growth (Gerking, 1952; 1954; 1955) yet it is
understood that energy, for metabolism at least, is derived
from all nutritional sources. Protein, the main constituent
of protoplasm, is undoubtedly an excellent index of growth
alone, yet when the disposition of ingested material is
considered, nutritional analysis must be in a form that
considers all forms of available energy. Pandian (1967a, b,
and c; Menzel, 1960; Brett et al, 1969) have considered non-
protein sources of energy, but caloric flow, if assessed,
has been generally from measures of fat, protein and carbo-
hydrate determinations. Relative proportions of carbohydrate,
fat, and protein are in a labile and dynamic state - deaminated
proteins can be converted into fats and/or carbohydrates
(Baldwin, 1952) - thus the contribution in terms of energy
can be most readily expressed in caloric terms. This investi-
gation uses the calorie alone to assess growth - therefore
considers fat deposition which may be mobilized and utilized
for later expenditure - and conversion since the major food
forms can all be utilized to support growth and general well-
being of organisms.

Caloric content (or nutrient constituents) of
experimental fish have not usually been examined during feed-
ing studies - notable exceptions being Menzel (1960) and
Brett et al (1969) - but are of critical importance as can
be seen from this work. The assumption that caloric content
is homogeneous at the beginning of laboratory holding is
realistic since West Blue Lake walleye show consistent age
independent energy content when experimental animals were

captured (Fig. 14). Caloric uptake in fish flesh has been considered as occurring at a constant rate during the course of this study (Table XIV), but this phenomenon has apparently not been of great import to previous studies. Caloric uptake in flesh is of consequence to this investigation.

The exclusion of the caloric increase in walleye flesh results in an apparent decline in conversion if wet weight alone is used in the calculation (Fig. 8). As well, the energy increase in walleye flesh (not considered by weight measures) amounts to a considerable portion of the intake during experimentation. The assumption of linear uptake (Table XIV) was not fully substantiated by lab studies as size, distance of transport, food supply and holding facilities limits the number of experimental animals. Nevertheless, natural fish show an apparent linear uptake in calories (Fig. 14) for whole fish (excluding gonads) of a magnitude similar to that of laboratory held animals.

Behavioral investigations into feeding habits of walleye are not available; therefore, the dominance of larger fish in feeding regimes cannot be readily discussed. Investigations of behavior of other fishes indicate that a "peck order" may well exist (Greenberg, 1947; Onodera, 1967). The retention of reproductive products by female walleye in particular has not been noted in the literature. D. Gillespie (personal communication) has, on the other hand, found similar egg retention by female walleye from other sources in Manitoba and attributes this as being the only apparent cause of mortality for adult walleye in other holding trials conducted here in Winnipeg.

Temperature has been known to influence the amount of food consumed by laboratory fishes (Hathaway, 1927; Baldwin, 1956; Bridges, 1961; Rozin and Mayer, 1961, and others). Keast (1968) has shown that low winter temperatures greatly depressed intake of fresh-water fish and when temperatures increased, consumption resumed when temperatures reach 8-15C. Intake in walleye at temperatures less than 12C was insufficient to produce detectable growth. Below 12C intake was sufficient only for maintenance requirements. Growth in north temperate climates is limited to relatively short periods within the year (Hile, 1954; Gerking, 1966), and although not apparently controlled by temperature alone (Coble, 1966), did occur in West Blue Lake after thermal stratification (approximately 12 to 15C at surface) occurred. Experiments in this investigation were conducted between 12 and 20C (latter is the maximum normal surface temperature of West Blue Lake). In addition, feeding was conducted at controlled ration sizes less than ad libitum. Since seasonal differences in stomach contents of fishes occur (Raney and Lachner, 1942; Priegel, 1963; Lawler, 1965; Northcote and Lorz, 1966), but do not generally fulfill the capacity of the organism to feed, rations below maximum were used. Since natural consumption is less than maximum, and since feeding at extremes may alter conversion by depressing assimilation, moderate rations were considered a better approximation of natural processes. In addition, conversion was found to be constant for walleye within a narrow range at lower rations (Fig. 7).

Photoperiodic responses play a part in growth and conversion (Gross, Roelofs, and Fromm, 1965). Photoperiod was not cycled but maintained constant at 14 hours light since this approximates mean conditions in nature when growth occurred. Walleye undergo diel migrations, thus temperature of hypothetical locations (thermocline and inshore regions) were applied to photoperiodic changes to asses the interplay of conditions (Fig. 9). Effects of light and variable temperature were not exhaustively investigated as the scope of laboratory trials precluded intensive investigations into these areas. Data collected in varied conditions indicated a situation very dissimilar (Table XV) from stable conditions.

Conversion efficiencies are of great importance when energy disposition in the wild or laboratory are under scrutiny. Three forms of conversion are utilized in this study: $K_1 = \Delta w/R\Delta t$ or gross conversion; $K_2 = \Delta w/pR\Delta t$ or net conversion; $K_3 = \Delta w/pR-T_R\Delta t$ which considers the routine metabolic requirement reflected by maintenance consumption. In almost all other cases, only the first two forms of conversion are considered - Johnson (1966) has utilized the maintenance requirement in establishing conversion of pike, but has not determined the available ration; Brody (1945) and Brown (1945, 1957) also considered the maintenance fraction -. yet it will become evident that the K_3 descriptions of efficiency are extremely enlightening in descriptions of food utilization.

Brett et al (1969) has found an "optimum" ration for young sockeye which was affected primarily by temperature and

ration size. In this instance an optimum conversion was not
readily apparent (Fig. 7) and the observed relationship may
result from experimental variability alone. Walleye evidently
do not consistently consume large rations in nature (Table
XXI, Fig. 15); therefore the apparent decline in gross con-
version is not of great importance and only lower rations
need be considered. The differences in conversions at rations
of 2.4 to 6.0% body weight (at 16C) are slight (Fig. 7).
Further experimentation would be desirable; however, time
was limiting as feeding trials were to be conducted during
the primary natural growing season. Paloheimo and Dickie
(1966b) in their summary of available literature found that
increasing rations generally decrease growth efficiencies
(log K_1). Their descriptions of the relation were limited by
experimental procedures of the research they summarized and
the relationship may be a result of inadequate information.
Warren and Davis (1967) are also of the opinion that Paloheimo
and Dickie were not sufficiently restrictive in selecting data
and stipulating conditions. In this case the experiment dura-
tion was brief (maximum of 11 weeks), size played no role (all
members of a group were within 20g), caloric content was
examined in the walleye, and ration was homogeneous. On the
other hand, in spite of information presented in this study
and those of Brett (op.cit.) the relationships defined by
Paloheimo and Dickie (op.cit.) may be real and peculiar to a
species or a particular size.

Direct conversion of ingested material into fish
flesh is quite low in walleye, 0.10 to 0.16, and can be

considered independent of temperature at any one ration size
(Table XV). Net conversion is slightly higher, but the assim-
ilation of an ingested meal in walleye is so efficient (95%
or higher for emerald shiners) that gross values are only
slightly less than net conversion (Fig. 10). Menzel (1960)
found gross conversion of 0.16 to 0.25 for a reef fish, and
estimated that 89 to 98% of ingested material was available
to the fish. Both conversion and assimilation (Menzel, op.cit.)
were found to be temperature independent, and thus are in
general support of the results of this investigation. Other
investigations into conversion of food into fish flesh are
available (Moore, 1941; Pentelow, 1939; and others), yet
methods of determination in these studies and most associated
with protein efficiencies cannot be directly compared with
those used in this study.

Inspection of the relation of conversion (gross or
net) to body weight supports the finds of Paloheimo and Dickie
(1966b) in that conversion decreases with increasing fish
weight (Fig. 10). If only the conversion in terms of food
to fish weight (excluding caloric increases in the fish flesh)
were considered, the relation is identical to those described
by Paloheimo and Dickie (op.cit.) who summarized investiga-
tions available to that time. However, if net conversion is
considered, decreasing assimilation efficiency with increasing
size reduces somewhat the observed effect of weight on conver-
sion (Fig. 10). The inclusion of the regular caloric change
observed during feeding trials further reduces the effect of

increasing weight and results in obvious arithmetic linearity compared to log plots of Paloheimo and Dickie (op.cit.) for the relation of conversion to weight. However, since the maintenance requirements (thus routine metabolism) also increase with increasing size (Table XVI), there is, in essence, less of the ingested energy truly available for growth.

As discussed by Paloheimo and Dickie, the T-line (where $T = \alpha w^{\gamma}$ is expressed in logarithmic terms) provides an adequate description of the routine metabolic level of oxygen consumption studies. Generally, maintenance ration in feeding trials is considered to describe the energy required for activity, respiration, tissue replacement, restoration of mucous coats etc. A logarithmic description of the effect of weight on maintenance ($T = pR$ corrected to 20C by Krogh's correction) is in excellent agreement with Winberg's (1956) approximation of $T = 0.3w^{0.8}$ which has been supported by intensive respirometry of various species of fresh water fishes (Mann, 1965). It seems, then, that nutritional studies are in agreement with accepted expressions of routine metabolism by respirometry. Job (1960) has already indicated the agreement between growth and respirometry studies for caloric approximation in speckled trout. Laboratory studies of the type conducted herein are perhaps more realistic than respirometric investigations since time is extended in laboratory feeding (compared to several hours in an enclosed respirometry chamber).

Rates of gastric digestion have been shown to be temperature dependent, generally decreasing at lower tempera-

tures (Hunt, 1960; Molnar and Tolg, 1962; Seaburg and Moyle, 1964). However, temperature has no effect on the assimilation efficiency of walleye. Menzel (1960) and Pandian (1967) support the independency of assimilation. Rate of gastric clearance certainly plays a role in the frequency of feeding - walleye cease feeding above the maintenance level below 12C; also found for various other fresh water species by Keast (1968) - but clearance rate has no apparent effect on efficiency. The remarkable efficiency of fishes in assimilating food has been verified (Menzel, op.cit.; Pandian, op.cit; Gerking, 1955) and all studies are somewhat in excess of Winberg's hypothesized efficiency of 80%. Walleye appear to assimilate food in this range (Table XVII) - only solid egesta were considered; Winberg (1956) states that loss in soluble form is less than 3% of ingested ration - although efficiency is dependent upon food species consumed and size of walleye. Walleye appear able to utilize some of the ash fraction of ingested material (see text table). This seems not to have been detected in any other case but seems logical since material such as $CaCO_3$ is readily soluble in an acid media.

Ration size does not seem to affect assimilation in walleye (Fig. 12); however, increasing weight decreases efficiency (Fig. 13). Menzel (1960) found that neither temperature nor fish size played a significant role in assimilation of the red hing (89 to 98%). Gerking (1955) found efficiencies, in the range of 95.8 to 97.6% for protein, which were not affected by meal size, but did not examine the effect of fish size on assimilation. Davis (1963) found generally increasing conver-

sion with increasing ration for goldfish of similar size.
On the other hand, Pandian (1967a,b) found that neither temp-
erature nor fish weight play a part in assimilation efficiency.
The lower efficiency for absorption of invertebrates by walleye
(Table XVII) no doubt results from the exoskeleton which
contains large amounts of chitin, not considered digestible
by fish (Gerking, 1952). In walleye, assimilation efficiency
is high (80 to 98%) and is reduced in larger fish. Efficiency
is also governed by food type and is independent of tempera-
ture and ration size. The straight line relationship between
conversion and fish weight persists for two diverse food
types (age 0 perch and amphipods).

Stress has not been placed on the validity of the
feces collection method. Filtration of tank contents through
Whatman No.1 filter paper was similar to Menzel's (1960)
method. However, the pore size and effectiveness of the
filters is uncertain (D. Gillespie, personal communication),
indicating that in spite of the precautions taken, collections
may be only partially complete (the error certainly was
minute but must be considered).

In this study, theoretical reviews of growth,
metabolism, and food (Paloheimo and Dickie, 1965, 1966a and b)
have been applied to walleye in captivity. Maintenance require-
ments, parallel routine metabolism found by oxygen consumption
studies, and assessments of metabolic expenditure indicate
that no abnormal stresses were applied to experimental
animals. General support is provided to the relationships
established by Paloheimo and Dickie; however, it has been

shown that caloric examination of experimental animals,
particular relations of ration size and fish weight, assimila-
tion efficiencies, and food type are critical in assessments
of feeding and metabolic characteristics by laboratory
nutritional analysis.

However, as a result of this study, a peculiar point
has arisen. Variable temperature series used to approximate a
more "natural" condition for walleye, define generally lower
K_1, K_2 and K_3 efficiencies. Information on conversion under
natural conditions is available (Johnson, 1966 and others) but
do not define the effects of stable temperature regimes. Main-
tenance at the variable temperature is slightly higher than
the mean temperature of the series and tends to indicate that
when exposed to a naturally changing water temperature (coin-
cident with movement to and from inshore areas) energy is
required for a compensation of some sort. No information is
available to support this claim as respirometry has been per-
formed in stable temperatures with acclimated subjects.

These investigations on walleye have defined growth,
assimilation, and a maintenance requirement. Obviously an
excess of approximately 15 to 65% of the ingested ration
remains (Table XVII). Since all fish were on a 4% ration at
all temperatures, it is evident (Table XVIII) that the excess
energy (ΔT) increases at lower temperatures. This phenomenon
occurs, although is not stated as such, in other cases as K_1
and K_2 conversions have been shown to be temperature independent.
My results and others necessarily infer that some mechanism

(increased specific dynamic action at lower temperatures;
increased excretion in some form at lower temperatures; or,
improbably, an increased metabolism at lower temperatures) is
in action whereby this excess is put to use or removed. The
latter suggestion is impractical and contrary to all measures
of oxygen consumption, but the initial two possibilities are
feasible. No explanation can as yet be soundly based.

Warren and Davis (1967) have also found a metabolic
excess for fish fed similar amounts at stable temperatures.
In their work on Cichlasoma bimaculatum, in the range of 20
to 36C, the specific dynamic action expenditure (SDA) is greater
at the upper and lower temperature extremes. The SDA (Warren
and Davis, op.cit.) was found by taking the difference of O_2
consumption of fed and unfed fish. Energy consumed was similar
between 20 and 32C indicating a system similar to that established
by these nutritional studies on walleye. However, in both
cases, the SDA component includes soluble wastes. The true
form of utilization of the ΔT component (of this study) can
not be apportioned.

The application of K_3 conversion efficiencies to
nutritional studies on walleye clarifies, to some extent,
energy utilization in fishes. If weekly maintenance rations
(parallels Winberg's $0.3W^{0.8}$) are removed from the available
energy, conversion is constant at any one temperature (Fig.10).
K_3 conversion decreases at lower temperatures (Table XV) as
the maintenance fraction decreases at the lower temperatures.
This form of conversion is probably more realistic since

temperature affects metabolic expenditure (Beamish, 1964; Beamish and Mookherjii, 1964) and therefore decreases the available energy for growth. In addition, the observed effect of weight on gross and net conversion in essence is an effect of increased metabolism of the growing fishes, decreasing available energy, and not a decreased ability to grow per se.

Laboratory analysis of energy utilization by walleye has provided a basis for examining the natural utilization of food by fish. The total picture has not yet been obtained and many areas of future study must be completed before our understanding is adequate. Low conversion efficiencies for walleye may result from weekly handling which could alter either excretion rates or metabolic patterns. Conversely the walleye, at a terminal trophic level, may differ from species studied to date. Agreement of maintenance studies with metabolic studies tends to negate adverse effects from handling. However, the effect of variable conditions, causes of lower efficiencies, and the dispensation of the energy excess (ΔT) must be examined before we can achieve an adequate understanding of energy utilization. I have avoided many inadequacies of previous research and provided partial answers to the above problems. However, the application of laboratory studies to the natural situation must be considered tentative until further research is forthcoming.

NATURAL FEEDING

Caloric descriptions of food, growth, maintenance, assimilation, and the natural diet were required to assess energy requirements of walleye in West Blue Lake. Since only small sacrifices of wild fish were made in order to preserve the trophic system under study, the results presented for natural feeding can be only of general application to the natural consumption and habits of walleye.

Coincident collection of walleye for stomach analysis and uningested diet items yielded several interesting observations regarding change in prey as well as changing energy contribution of the prey. Seasonal variation in caloric content of plants and animals exists (Golley, 1961), but information on energy changes in natural populations is rare. Valuable assessments of caloric values of flora and fauna exist (Slobodkin and Richman, 1961; Comita and Schindler, 1963; Cummins, MS 1967; Wissing and Hasler, 1968; Platt, Brawn, and Irwin, 1969). However, caloric approximation of food materials from available literature eliminates individual, seasonal, age, and geographical differences of energy content. Factors governing energy differences are many; for example seasonal and spatial variability in food availability, change in consumption, storage prior to deprivation etc. Causes of energy differences have not been determined by this study. Energy changes in primary walleye diet items were found to establish the natural feeding history of walleye.

Walleye themselves underwent a pronounced seasonal change in energy content (Fig. 14). To date, seasonal changes

in condition of fishes have been found (Hile, 1954; Keast,
1968), but changes in neither nutrient composition nor gross
energy content have been reported. Superimposed on the
seasonal patterns of growth (Figs. 4 and 6) was a seasonal
change in calories/gram of whole fish (Fig. 14). A 500 cal/g
difference existed between May and September of 1970 in West
Blue Lake walleye. Reproducibility of results was shown to
be excellent. Since the observed caloric difference was real
and was age-independent, the phenomenon must result from
natural conditions. Walleye are not sexually mature until
at least 3 to 4 years of age (Eschmeyer, 1950; Glenn, MS 1969)
or older (Rawson, 1957), and if a difference existed resulting
from sex or maturity, only older fish would demonstrate the
observed caloric depletion. Sexually immature, age II[+]
walleye, underwent the same seasonal change in energy content,
suggesting that the cause is winter conditions which may decrease
food availability, ability to procure food, or in general
decrease consumption. The regular change in caloric content
is apparent in perch other than young-of-the-year (Table XX).
The increase in energy, probably either interstitial or abdom-
inal fat deposits, is not true growth in terms of protein
deposition. The observed depletion indicates a utilization
of some sort and is a significant contribution to the energy
demands of walleye.

Age 0 perch, an important diet item of walleye,
reflect early life history by their energy content (Table XX).
The true picture has not been clearly defined - small samples
of early life stanzas limited possible combustions - but

indicate a decreasing caloric content during early life and a plateau when latter stanzas of seasonal growth are attained. The high energy content in June (Table XX) probably results from the absorbed high energy portion of the ova (approximately 6,000 cal/g). Later depletion could result from the deposition of fat deposits into protein. Fat deposition from ingested protein has been detected (Menzel, 1960), and the observed situation in perch fry may well occur as a result of changes in fat and protein.

Analysis of other food items of walleye indicates a variable state in terms of seasonal energy change (Table XXI). The analysis presented here does not negate the existence of a seasonal trend, but does indicate that in critical stages of walleye production, energy content of food items (Table XXI) is variable. Caloric data presented for these organisms are in close agreement to those of single collections made by authors of the caloric reviews presented earlier.

It is known that chitin is not available to the nutrition of fishes (Gerking, 1955; Pandian, 1967a, b, c). It has been shown that the assimilation efficiency of amphipods and crayfish is least, about 80%, which includes utilization of some of the ash component (Table XVII). The expression of calories from animals of high ash content is difficult. Calories per gram dry weight seems to decrease in the crayfish, Orconectes virilis, and may be the result of endothermic reactions (Paine, 1966). Correction (Paine, op.cit.) does not modify the apparent decrease caused by higher ash content. However, since ash may increase with increasing size, the total calories of a

crayfish may be related to organism size. Amphipods, Gammarus lacustris, exhibited neither seasonal nor size-dependent energy variation and the grand mean was considered adequate for the period May to October (Table XXI).

Walleye undergo diel movements to and from inshore areas and generally feed during the night in the shallow regions of the lake. Since it has also been found that stomach contents increase to a maximum some 2 to 3 hours after the initial migration (Ward, unpublished), samples were collected at this time to obtain an indication of the amount and species diversity of the walleye diet. Collections made at this time provided an index of seasonal differences in intensity as well as diet item occurrences (Fig. 15).

The most comprehensive available study of the diet of walleye (Eschmeyer, 1950) indicated that fish comprise the major portion of the walleye diet in areas where forage fish are abundant. It was found that seasonal differences do occur when mayfly, midge larvae, crayfish and leeches become significant contributors to the diet of walleye. Rawson (1957), Priegel (1963) and Fedoruk (1966) all support Eschmeyer's conclusions and attribute the contribution of fish as being 58 to 97% of the diet.

This study utilized four approaches to gut analysis: 1) frequency of occurrence, 2) weight in the stomach, 3) expected weight determined from uningested diet items, and 4) calories present in the gut determined from uningested food materials (Fig. 16). Representations of feeding by the

four forms analyses were somewhat contradictory (Fig. 16).
Amphipods and mayflies were the dominant contributors in terms
of number for May to October; however, their weight and caloric
contribution were of lesser importance. The "expected" weight
presents a problem in amphipod analysis since stomach weight
was greater than expected weight. The expected weights (dry
weight) were determined from 100 to 200 individuals collected
for each bomb analysis and when applied to the number located
in stomachs of walleye, resulted in an expected weight less
than actual weights. Uptake of digestive secretions into
orifices of the carapace as well as incomplete blotting of
the irregular amphipod surfaces probably accounted for the
discrepancy. Amphipods were in stomachs of all collections,
but the mayflies (Blasturus sp) appeared only in June.

Adult perch were dominant in terms of weight and
caloric contribution (Fig. 16); however, only 7 adult perch
were responsible for the observed energy. Larval perch appeared
in the diet after June and provided significant numbers, weights
and calories to the diet of walleye. Sticklebacks as well
were prominent in the diet and appeared regularly in all
collections.

Seasonal comparisons of stomach contents per unit
walleye provided no real answers (Fig. 16). On the other hand,
the number of empty stomachs noticeably increased later in
the growing season indicating decreased feeding.

Investigations describing field procedures to des-
cribe natural consumption (Bajkov, 1935; Darnell and Meirotto,
1962) were not considered for use in this study as sacrifices

of walleye would be large. Since the range of food organisms
consumed has been determined, a theoretical maximum assimila-
tion efficiency (the intercept of efficiency regressions) was
developed by weighting the caloric contribution of diet items.

POPULATION CONSUMPTION

This investigation provides a basis for calculating
energy requirements of the unexploited, closed population of
walleye in West Blue Lake. Other studies (Allan, 1951; Gerking,
1962; Mann, 1965; Johnson, 1966; and others) have achieved
similar ends using different means. This study indicated
that difficulties in population assessments and in laboratory
nutritional determinations, although permitting the allocation
of seasonal requirements, require considerable experimentation
before reliable descriptions of trophic dynamics can be achieved.

Laboratory determinations of conversion, maintenance,
and assimilation were applied to field situations for the
estimation of intake. The independence of net conversion (K_2)
from temperature (Table XV) permitted direct application of
this criterion to the wild population. Since food type governs
assimilation efficiency (Table XVII), laboratory results were
modified to consider the natural diet (see Results for explana-
tion). Because older fish did not feed, intake for these
members, age III and older, was determined by correcting net
conversion by the appropriate assimilation efficiency. Deter-
minations of conversion, maintenance, and assimilation efficiency

under controlled conditions were readily obtained. Assimilation of natural diet items was considerably less, approximately 10%, than that of fish used in growth determinations. However, because only assimilation affected net conversion, the effect of diet and walleye size could be integrated into assessments of natural conversion. However the application of laboratory studies to a natural situation results in calculations of energy requirements that cannot be verified.

Since production (both in terms of weight and energy) was limited from June to October (Table XXIV), intake was greatest during this period. Negative production, during winter months, resulted in a calculated loss of up to 3.04 K cal/kg/day from walleye. The total requirement of walleye was not affected by temperature; however, to indicate the diversion of energy into routine requirements, maintenance requirements were calculated for "hypothetical" temperature regimes. These "hypothetical" temperatures were derived by locating mean water column temperatures (includes the thermocline and epilimnion) for the winter, spring, and fall, as this portion of the water column was probably encountered by walleye during diel migrations. As expected from field and laboratory growth studies, calculated intake was greatest, 1300 to 1900 K cal/kg/day, among younger fishes (Table XXIV). Decreased utilization of older fishes was reflected by higher intakes to produce a similar production (IV and VI year old fish during September and October). Peak production expressed in terms of weight does not reflect the extensive caloric

deposition in walleye flesh alone, but does indicate primary periods of proliferation during 1969-70.

This study gains only general support from past investigations into population requirements. Gerking (1962), Johnson (1966) and Mann (1965) used protein, wet weight and caloric approximations to describe annual population requirements of various freshwater fishes. My work uses the calorie alone and assesses seasonal requirements of an unexploited population. Although techniques differ, maximum production (consequently intake) seems always greater among younger fishes.

Although this investigation has overcome many inadequacies of previous studies, certain areas introduce error into calculations of this nature. In spite of all precautions taken by the author, estimates of biomass and production may be influenced by sample size, gear selectivity for size, differential mortality between marked and unmarked walleye, and behavior patterns, and each could affect estimates of number, growth, and mortality. Most factors that could alter estimates were examined and were shown to be of minor importance (Tables II, III, IX and Fig. 2). The extent of even a minor contribution by the detracting factors is as yet unknown. Laboratory studies indicated that extensive research must yet be done in determining effects of ration size, handling, variable conditions and the dispensation of the ΔT component. This description of walleye intake does present an excellent reflection of seasonal energy requirements for production using the best techniques available.

Establishing energy requirements of this population by integrating laboratory and field procedures is sound. The problem arises in assessing the validity of experimental design. Solving the deficiencies of laboratory studies can be readily achieved by further experimentation; however, the problem of gear selectivity must be resolved. Nevertheless, the apparent stability of biomass, and the well defined relations of conversion, maintenance, and assimilation will permit estimation of energy utilization in this situation. Valuable corrobarative evidence to the estimate of intake could be achieved by field techniques (Bajkov, 1935; Darnell and Meierotto, 1962) designed to estimate daily intake.

This study does indicate that the period after production is an opportune time to harvest walleye. Walleye also appear to maintain yearly stability in biomass resulting from relative age class structure. Greater production occurs among younger age groups, and intakes are lower than that required by older fish for a similar production. Because of this, younger walleye (and probably most other species) are more economical in utilizing the natural resource. Investigations under controlled experiments have described several controlling factors of conversion, but indicate the need of studies under more "natural" conditions.

West Blue Lake is an ideal situation for studies of this type, and if the indicated deficiencies are remedied, an excellent representation of energy flow within a population will be available.

SUMMARY

1.   A total of 569 walleye age II and older were marked during 1969-70 in West Blue Lake, of which 56 were recaptured.

2.   No short term mortality was found in conjunction with mark and release periods.

3.   Distribution of marked fish was essentially random, and similar segments of the population (by age) were captured at all times. Frequency distributions and x^2 tests indicated that net selectivity was not by age and probably not by size.

4.   The May 1969 population, 1090, decreased to 819 individuals in May 1970, but was augmented by new recruits, 2100, in September 1969. Petersen estimates, the Jolly (1965) approach, and the triple-catch trellis provided similar descriptions of the population.

5.   Mortality on a per day basis was small, mean i of 0.0045, and was least in May-June 1969. Largest loss occurred during the fall and winter.

6.   Growth, and consequently production, was greatest between June and September with significant growth occurring until early October.

7.   Biomass, approximately 800 kg, was stable from year to year.

8. Production, 340 kg, was coincident with growth and the major contribution was by younger fish.

9. Conversion, both K_1 and K_2, was affected by neither ration size nor temperature, but did decrease with increasing fish size. K_3 conversion was not affected by ration size or fish size but decreased with decreasing temperature.

10. Assimilation efficiency of walleye was dependent upon diet type - greatest for perch and other fish, and least for invertebrates - and walleye size.

11. Maintenance requirements per unit fish was independent of fish size, but was affected by temperature. Maintenance converted to 20C for various sized walleye approximated Winberg's (1956) $T = \alpha w^r$ for routine metabolism.

12. A seasonal cycle in cal/g of walleye flesh occurred in West Blue Lake. Energy content of whole fish (less gonads) was greatest in the fall. The cycle was also evident in perch.

13. Greatest energy contribution to walleye nutrition was by fish, perch of all ages and sticklebacks. Greatest numerical contribution was by amphipods and mayflies, but both provided lesser energy contributions.

14. Uptake in calories and growth in the laboratory was similar to natural growth.

15. Laboratory conversion and assimilation efficiency was applied to the natural diet of walleye for an estimation of population intake.

16. The resident population required from 40 to 1860 K cal/kg/day for production and was governed by fish size and magnitude of production.

17. Further experimentation in the field and in the laboratory is required before the best estimation of energy flow within a population can be obtained.

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A P P E N D I X

change in weight (ΔW) for samples (N) using walleye caught during mark and release periods (1969–70). Included in parenthesis are standard deviations.

		May, 1969	June	August	September	October	May, 1970
I–II	N	19	35	19	48	54	33
	L	200.9 (7.4)	200.5 (10.6)	216.1 (10.8)	244.9 (13.6)	248.8 (11.3)	249.2 (12.8)
	AL	61.3 (5.6)	57.3 (7.6)	25.2 (3.6)	48.4 (7.3)	54.4 (6.0)	56.0 (8.4)
	AG	45.7 (6.2)	44.8 (9.6)	27.8 (33.6)	63.7 (15.0)	71.6 (13.9)	73.4 (15.5)
II–III	N	14	30	5	17	8	3
	L	292.9 (11.2)	297.2 (15.2)	321.0 (5.3)	338.9 (15.1)	338.6 (36.7)	315.3 (40.2)
	AL	53.0 (7.2)	52.1 (5.6)	21.9 (7.2)	37.6 (7.8)	39.8 (10.8)	33.0 (9.0)
	AG	110.9 (22.8)	109.3 (16.5)	52.5 (11.6)	108.9 (28.2)	114.3 (45.0)	111.8 (17.4)
III–IV	N	18	22	2	11	6	4
	L	350.4 (13.3)	345.4 (14.8)	350.5 (7.8)	376.0 (11.9)	390.5 (13.4)	382.5 (6.1)
	AL	39.1 (5.0)	34.8 (6.1)	14.7 (4.2)	26.8 (6.4)	30.7 (6.2)	30.6 (4.8)
	AG	116.3 (21.4)	105.5 (18.6)	60.4 (5.0)	102.9 (22.5)	124.1 (26.0)	118.6 (19.7)
IV–V	N	59	32	2	36	10	15
	L	394.2 (14.4)	401.5 (14.7)	442.5 (43.3)	413.9 (15.8)	425.9 (11.1)	428.3 (13.0)
	AL	29.6 (5.8)	29.0 (4.1)		18.8 (4.5)	22.5 (3.4)	22.7 (5.3)
	AG	121.0 (24.8)	126.7 (21.0)	48.2 (11.2)	88.5 (22.9)	111.8 (18.9)	112.4 (24.3)
V–VI	N	17	6	–	9	–	–
	L	427.6 (17.8)	426.8 (16.5)		453.2 (29.8)		
	AL	19.2 (6.4)	18.2 (3.3)		11.7 (3.5)		
	AG	94.8 (26.0)	92.6 (22.6)		73.3 (18.4)		

Appendix Fig. 1. Relationship between cals/g and ash content (upper) and ash content and crayfish size (lower) West Blue Lake.
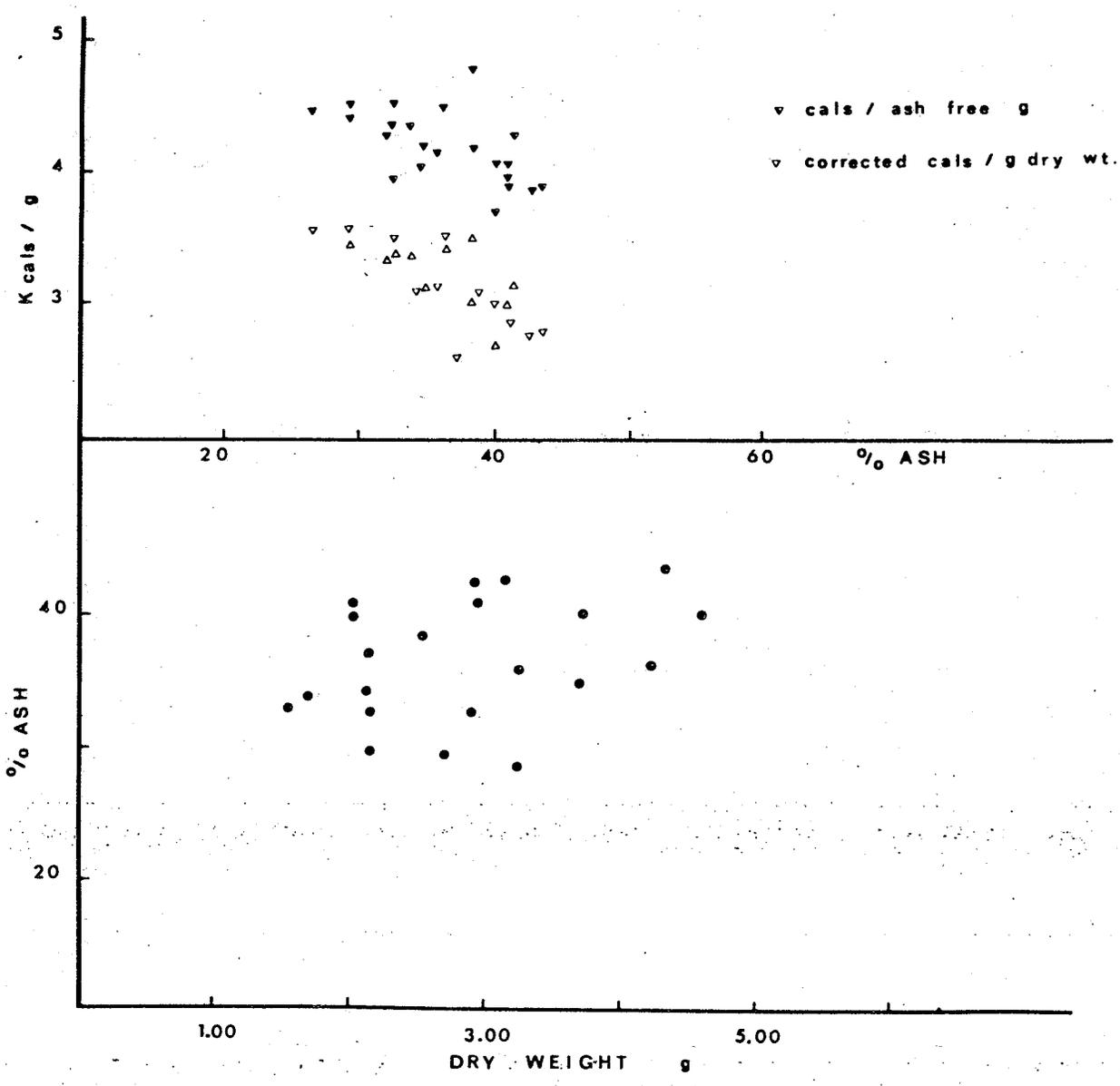
Appendix Table II. Descriptions of biomass (B) and production (P) from May 1969 to May 1970 for walleye in West Blue Lake using the unstratified population (N). Numbers in parenthesis refer to the recruited population.

	N	$\bar{w}$	B		$\bar{B}$	g_G	P
May 14–20, 1969	1090 (3656)	528.9 406.4	576.501 1485.7984	II all	641.099 1536.0979	−0.0073 −0.0099	−4.6800 −15.2074
June 16–22	1330 (3893)	530.6 407.5	705.698 1586.3975	all	825.281 1624.3721	.1768 .2496 .2526	145.9097 410.3164
Sept 3–12	1350 (3451)	699.9 481.7	944.865 1662.3467	all	1213.6239	.0335	40.6564
Oct 5–12	931 (2331)	328.1	764.8011	all	836.8552	−0.00166	−13.8918
May 18–26, 1970	819 (2037)	446.2	908.9094				

all $= \Sigma P$ 417.0005
older $= \Sigma P$

Appendix Table III. Estimates of biomass and production using the instantaneous approach. Symbols are explained in the test.

Date	$\hat{N}$	N age	$\bar{w}$ g	B ($\bar{w}$N)		$\bar{B}=\dfrac{B_1(e^{G-2}-1)}{G-2}$	$P(g_G\bar{B})$
May 14–20, 1969	1090	(2566)	(79.8)	(204.767)	I	(171.796)	−2.1989
		136	267.6	36.394	III	33.698	−0.5796
i=0.00100		175	470.1	82.268	III	76.475	−1.7054
		573	676.7	387.749	IV	387.749	+0.0814
		167	861.5	143.871	V	143.871	+0.0057
		39	1354.4	52.822	VI	52.822	+0.0021
June 16–22	133	(2563)	(80.1)	(205.296)	I	(258.691)	163.3116
		410	282.3	115.743	III	125.686	41.3884
i=0.1803		302	444.3	134.179	III	145.7212	28.9839
		467	712.4	332.691	IV	314.328	37.3107
		82	863.6	70.815	V	66.906	7.9417
		69	1041.9	71.891	VI	67.923	8.0625
Sept. 3–12	1350 (3451)	2101	154.2	323.974	III	215.479	13.3382
		298	411.0	122.478	III	101.224	1.4475
i=.4050		193	581.1	112.152	IV	93.450	3.0091
		632	785.7	496.562	V	418.012	12.3314
		227	1092.5	247.998	VI	208.762	6.1578
Oct. 5–12	931 (2331)	1200	162.7	195.240	III	143.746	0.1423
		298	430.7	128.349	III	134.284	−0.1248
i=.6444		223	660.6	147.314	IV	108.062	0
		373	861.7	321.414	V	235.774	0
		37	1136.0	42.032	VI	30.832	0
May 18–26, 1970	819 (2037)	1118	163.3	182.569			
		150	354.1	53.115			
		111	625.2	69.397			
		521	876.1	456.448			
		37	1261.3	46.668			

Σ P = 318.9056

Date	Intake	G	$\hat{p}$	pR	K_1	K_2	K_3	T	T_w	T	M=
June 15-22	119,525.3	19,534.1	96.23	115,019.2	.1634	.1698	.2579	95,485.1	78,724.8	16,760.3	39,281.9
22-29	159,728.7	25,433.9	96.21	153,675.0	.1592	.1655	.2254	128,241.1	81,194.4	47,046.7	40,849.8
June 29-July 6	154,268.7	24,006.8	96.17	148,360.2	.1556	.1618	.2276	124,353.4	84,873.6	39,479.8	42,875.7
6-13	150,397.1	21,728.7	96.14	144,591.8	.1445	.1503	.2187	122,863.1	87,393.6	35,469.5	44,773.2
13-20	147,617.5	21,687.9	96.11	141,875.2	.1469	.1529	.2273	120,187.3	90,014.4	30,172.9	46,477.8
20-27	153,275.9	21,826.6	96.09	147,282.8	.1424	.1482	.2202	125,456.2	93,038.4	32,417.8	48,166.5
July 27-Aug. 3	154,616.2	20,148.3	96.06	148,524.3	.1313	.1357	.2042	128,376.0	93,895.2	34,480.8	49,853.4
3-10	149,205.8	20,861.1	96.04	143,297.3	.1398	.1456	.2271	122,436.2	97,624.8	24,811.4	51,441.8
10-17	145,681.7	17,470.6	96.02	139,883.6	.1199	.1249	.2005	122,413.0	99,590.4	22,822.6	42,762.4
17-24	147,071.5	27,702.0	95.98	141,159.2	.1883	.1963	.3209	113,456.6	102,765.6	10,691.0	54,845.4
24-31	142,902.0	18,515.0	95.96	137,128.8	.1296	.1350	.2282	118,613.8	104,832.0	13,781.8	56,221.3
Aug.31-Sept.7	150,744.5	18,041.7	95.94	144,624.3	.1197	.1248	.2072	126,582.6	106,797.6	19,785.0	57,555.9
7-14	152,184.0	18,739.8	95.92	145,974.9	.1231	.1284	.2153	127,235.1	108,813.6	18,421.5	58,932.8
Mean.								121,205.6	94,581.4	27,318.3	45,140.9

V(a)

Date											
June 22-29	152,779.6	24,599.0	96.27	147,080.9	.1610	.1672	.2025	122,481.9	51,950.8	70,531.1	25,623.8
June 29 July 6	156,800.1	21,608.5	96.25	150,920.1	.1378	.1432	.1741	129,311.6	53,854.0	75,457.6	26,820.3
6-13	150,148.9	18,606.7	96.22	144,473.3	.1239	.1288	.1595	125,866.6	56,109.7	69,756.9	27,843.4
13-20	123,593.6	15,368.1	96.20	118,897.1	.1243	.1293	.1704	103,529.0	56,849.8	46,679.2	28,682.7
20-27	137,541.4	17,375.4	96.18	132,287.3	.1263	.1314	.1693	114,911.9	58,330.1	56,531.8	29,625.1
July27 Aug.3	141,462.6	14,066.0	96.15	136,016.3	.0994	.1035	.1340	121,950.3	60,585.0	61,365.3	31,039.6
3-10	151,191.3	23,737.0	96.12	145,325.1	.1569	.1633	.2100	121,588.1	62,524.2	59,063.9	32,309.6
10-17	122,420.4	12,984.1	96.11	117,641.0	.1061	.1104	.1534	104,656.9	63,546.3	41,110.6	32,976.2
17-24	110,837.2	13,173.6	96.10	106,514.6	.1189	.1236	.1808	93,341.9	64,603.6	28,737.4	33,671.6
24-31	148,213.1	21,146.9	96.07	142,388.3	.1427	.1485	.1965	121,241.4	66,330.6	54,910.8	34,786.7
31- Sept7	131,436.1	13,447.3	96.05	126,244.4	.1023	.1065	.1485	112,797.1	67,705.2	45,091.9	35,487.4

	I	G	p	p^R	K_1	K_2	K_3	T	T_w	T	M=
June24 July 6	112,524.8	13,193.4	96.30	108,361.4	.1173	.1228	.1363	95,168.0	22,720.9	72,448.0	11,586.0
6-13	115,900.0	13,422.2	96.27	111,576.9	.1158	.1203	.1350	98,154.7	23,636.0	74,518.7	12,116.9
13-20	113,318.9	13,306.4	96.25	109,069.4	.1174	.1220	.1380	95,763.0	24,368.0	71,395.0	12,639.4
20-27	99,321.6	11,899.3	96.23	95,577.2	.1198	.1245	.1442	83,677.9	25,008.0	58,669.9	13,065.7
July27 Aug.3	98,775.6	10,128.0	96.21	95,032.0	.1025	.1066	.1242	84,904.0	25,616.0	59,288.0	13,457.6
3 -10	113,318.9	11,877.0	96.19	109,001.5	.1048	.1090	.1249	97,124.5	26,304.0	70,820.5	13,913.8
10-17	115,056.3	13,197.0	96.16	110,638.1	.1147	.1193	.1372	97,441.1	27,056.0	70,385.1	14,417.2
17-24	113,467.9	12,456.2	96.14	109,269.6	.1098	.1142	.1320	96,813.4	27,776.0	69,037.4	14,888.8

Intake	Growth	p	p^R	K_1	K_2	K_3	T	T_w	T	Maint.
132,081.4	21,023.1	96.21	127,075.6	.1592	.1654	.1963	106,052.5	81,295.2 / 37,636.7	68,415.8	19,975.5
154,020.5	17,862.4	96.18	148,136.9	.1160	.1206	.1401	130,274.5	83,613.6 / 38,710.0	91,564.5	20,674.7
158,388.5	22,687.6	96.15	152,290.6	.1432	.1490	.1735	129,603.0	86,436.0 / 40,016.7	89,586.3	21,522.1
147,071.5	20,235.9	96.13	141,379.8	.1376	.1431	.1670	121,143.9	88,905.6 / 41,160.0	79,983.9	22,333.6

4580.2 at
35.4 cal./wk
74.54% moist.