## THE UNIVERSITY OF MANITOBA

# SEASONAL RATES OF GROWTH WITHIN A POPULATION OF WALLEYE, STIZOSTEDION VITREUM VITREUM (MITCHILL), IN WEST BLUE LAKE, MANITOBA, DURING 1966-1967 

A Thesis
Presented to the Faculty of Graduate Studies and Research in Partial Fulfillment of the Requirements for the Degree Master of Science
by
Clifford L. G1enn


November, 1969
c Clifford L. Glenn 1969

## TABLE OF CONTENTS

PAGE
INTRODUCTION ..... I
LITERATURE REVIEW ..... 3
DESCRIPTION OF AREA ..... 15
METHODS ..... 19
RESULTS ..... 34
DISCUSSION ..... 45
SUIIMARY ..... 51
LITERATURE CITED ..... 54
APPENDIX ..... 61

## LIST OF FIGURES

## FIGURE

1. Bathymetric map of West Blue Lake (contour intervals of 5 m ). Each sampling area denoted by a dot.16
2. Vertical distribution of water temperatures (C) and dissolved oxygen ( $\mathrm{mg} / \mathrm{I}$ ) for three sampling dates from Basin 2, West Blue Lake, during summer of 1966 .18
3. The relationship between various total length classes of walleye captured in 1966 from West Blue Lake and the average anterior scale radius of each class.................................................25
4. Length-weight relationship of walleye in West Blue Lake based on measurement of 665 fish.... 26
5. Mean increase in length (mm) between time of annulus formation (June 28) and succeeding sampling dates for vulnerable walleye captured during summer of 1966 and spring of 1967.......36
6. Mean increase in weight (g) between time of annulus formation (June 28) and succeeding sampling dates for vulnerable walleye captured during summer of 1966 and spring of 1967....... 37

## LIST OF TABLES

TABLE
I. Dimensions of gill net gangs employed in sampling walleye at West Blue Lake during 1966 and 1967.................................................19
II. Number of walleye assigned given ages for 83 randomly selected samples22
III. Slope of the logarithm of the length-weight curve for walleye between $301-400 \mathrm{~mm}$ in length for each of the sampling periods.28
IV. Annual length increments (mm) for year classes of walleye captured at June 24 and July 12 , 1967 and the grand mean increments for age groups netted during 196631

V. Relative growth rates of male and female
walleye collected from West Blue Lake ..... 33
VI. Number of walleye in each age group cap- tured after annulus formation (in 1966) during 1966 and 1967 ..... 34
VII. Mean sizes and rates of growth of vulnerable walleye captured at sampling dates during 1966-1967 ..... 35
VIII. Growth statistics calculated for walleye fromWest Blue Lake between time of annulusformation (4th week in June) to succeedingsampling periods, 1966-1967....................... 40-44

## LIST OF APPENDICES

TABLE
PAGE
A-I. Annual rates of growth from back calculated lengths for West Blue Lake walleye collected in 1966............................ 62

A-II. Mean total lengths back calculated for walleye collected in West Blue Lake during 1966 63

## ACKNOWLEDGEMENTS

The author wishes to thank Drs. F. J. Ward and J. H. Gee, Department of Zoology, University of Manitoba, and to Dr. L. Johnson, Freshwater Institute, Fisheries Research Board of Canada, Winnipeg, for guidance. Appreciation is expressed to those staff members and students of the University of Manitoba who have offered advice and suggestions. The author is also indebted to $\mathrm{R} . \mathrm{K}$. Bell for assistance in collection of data. My wife helped with data preparation for analyses.

Financial assistance was received from Department of Mines and Natural Resources, Province of Manitoba; National Research Council of Canada; Canadian National Sportsmen's Shows; and the Manitoba Wildlife Federation.


#### Abstract

Seasonal growth rates for walleye age II and over in West Blue Lake were calculated from changes in mean size of fish between sampling periods and from changes in size between annulus formation and time of capture. In 1966 the annulus was formed by the fourth week in June for most walleye under age $V$. Lengths at each annulus were back calculated using a straight line body-scale relationship with an intercept at 51 mm total length. Weights at corresponding lengths were estimated from a length-weight relationship $(\log W=-5.463+3.163 \log \mathrm{~L})$ obtained from logarithms of mean length and weight for length intervals of one cm .

Growth in length was greatest during the period from annulus formation to July 19 and then decreased progressively over the remainder of the growing season. The summer length increment was greatest in walleye age II and decreased with each older age group. Greatest summer weight increments were noted for walleye age III followed by IV, II, V, and VI and over respectively. There was no variation in growth rates between sexes.


## INTRODUCTION

Most studies concerning growth in walleye, Stizostedion vitreum vitreum (Mitchill), have investigated changes in annual growth rates of exploited populations (Carlander, 1948; Cleary, 1949; Kennedy, 1949; Eschmeyer, 1950; Rose, 1951; and Forney, 1965). Seasonal change in growth, particularly in unfished populations, has received less attention. The objective of the present study is to examine seasonal change in growth rate in walleye, age II and over, captured during 1966 and 1967 in West Blue Lake, Duck Mountain Provincial Park, Manitoba. During this time the stock, except for experimental catches, was virtually unexploited.

Estimates of growth in fishes, as Lagler (1956) and Rounsefell and Everhart (1953) point out, generally requires a use of: (1) scale criteria to age fish, (2) a method of estimating sizes at previous ages, and (3) a method of expressing changes in sizes between periods. In this study, seasonal growth rates for each vulnerable age group were examined by two methods. Estimates of growth were obtained from the difference between mean sizes of fish captured at each sampling date. Secondly, the growth rates of individual fish were determined from the difference between the back calculated length at annulus formation and the length at capture. A mean growth rate between annulus formation
and time of capture was then computed and from the difference between successive samples the growth rate for the various time periods was determined.

## LITERATURE REVIEW

The natural range of Stizostedion vitreum vitreum extends from the Mackenzie delta, east to Labrador, south to North Carolina, and west to Arkansas (La Monte, 1958). Within this area, the species is called: Pike-perch, yellow pike, dore, dory, yellow pickerel, pickerel, and walleye. According to Slastenenko (1958), Mitchill in 1818 applied Perca vitrea to walleye when first describing specimens from Cayuga Lake, New York. Later, in 1896, Jordan and Evermann proposed the present name, Stizostedion vitreum. A subspecific title S. vitreum vitreum is acknowledged to distinguish it from the blue pike, S. vitreum glaucum.

Walleye can be distinguished from other members of the perch family by the following features: opaque eyes, strong canine teeth, and three pyloric caeca (equal in length). Smooth, scaleless cheeks and a black blotch at base of last dorsal spine distinguish it from the closely related sauger (S. canadense). Walleye attain the largest size of the North American members of the Percidae. Slastenenko (1958) states that the walleye is larger at comparable ages than its Eurasian counterpart, the sander, Stizostedion 1ucioperca.

Within its range, walleye inhabit most deep lakes and large rivers. They are generally found near the lake bottom or
river bed (Niemuth et al, 1962) in depths up to 15 m (Deason, 1933; Rawson, 1957). On the basis of gill net catches, Carlander and Cleary (1949) conclude that walleye are more active between dusk and dawn. This is substantiated by their apparent ability to see in poor light which is due to a modified retinal epithelium, the tapetum lucidum, that reflects back through the retina a large proportion of the light and thus increases the stimulation of the visual cells (Moore, 1944).

In the evening, walleye leave deep water and migrate to the littoral zone to feed (Niemuth et al, 1962; Ward and Glenn, MIS). Houde (1967) noted that young walleye begin to feed even before the yolk is completely absorbed. Other studies, including those of Smith and Moyle (1945), Eschmeyer (1950), and Maloney and Johnson (1957) found that fingerlings up to approximately 25 mm in length first begin to feed on small crustaceans and insects before becoming piscivorous. Ciscoes (Rawson, 1957; 1959) and yellow perch (Eschmeyer, 1950; Rawson, 1960; Priegel, 1963; and Fedoruk, 1966) are the main prey of larger walleye.

From recaptures of released marked fish, Stoudt and Eddy (1939), Doan (1942), and Eschmeyer (1950) have shown that walleye move considerable distances (up to approximately 100 miles) within lakes. Smith et al (1952) have recorded adult marked walleye
travelling up to 120 miles from their spawning sites but most travel less than 20 miles.

Some movement is associated with spawning behaviour;
sexually mature fish generally return to their natal spawning sites (Eschmeyer and Crowe, 1955; Rawson, 1957; Crowe, 1962; Olson and Scidmore, 1962; Forney, 1963). Crowe et al (1963) have found that a population will break down into discrete subpopulations, each with its particular spawning site. Stoudt and Eddy (1939) have suggested that only $10 \%$ change spawning areas. After spawning, the subdivisions generally reunite to form a homogeneous population. Smith et al (1952) concluded on the basis of movements and rates of growth and condition, that the population in both Upper and Lower Red Lakes (combined area of 275,000 acres) was homogeneous.

Several accounts of size and age of sexually mature walleye have been published. Eschmeyer (1950) found in Lake Gogebic that male walleye in the spawning run ranged between 12-22 inches but females ranged between 15-28 inches. Smith and Pycha (1961) noted similar findings in Red Lakes, Minnesota, with males ranging between 11-22 inches and females between 13-26 inches. Age at maturity varies with the population studied. Cleary (1949) captured mature 2 year old males and 3 year old females in Clear Lake, Iowa. In Oneida Lake, New York, Forney (1965)
found that males became sexually mature at age IV and females at age V. Similar restilts were noted by Carlander (1945) in Lake of the Woods. However, Rawson (1957) found only $50 \%$ of both sexes mature at 7 years in Lac La Ronge.

Walleye spawn in spring before the end of May (Derback, 1947; Eschmeyer, 1950; and Forney, 1963), but Bajkov (1930) noted fish with ripe gonads until mid-June in Lake Manitoba. Eschmeyer (1950), Rawson (1957), Niemuth et al (1962), and Ellis and Giles (1965) have recorded spawning in waters ranging from 4 to $13^{\circ} \mathrm{C}$. Eggs, each having a diameter between 1.5 - 1.7 mm (Derback, 1947) are deposited in gravel beds (Derback, ibid; Eschmeyer, 1950; Johnson, 1961) in water approximately I m deep. Hinks (1943) quotes the fecundity of females as "approximately 45,000 eggs per pound of body weight." Eggs are fertilized by one or more accompanying males. Johnson (1961) found egg fertility high (from 96\%-100\%) and egg survival highest (up to $35 \%$ ) on gravel-rubble in Lake Winnibigoshish, Minnesota. Niemuth et al (1962) state that hatching occurs in 7 days at a mean temperature of $14^{\circ} \mathrm{C}$ but in 21 days when water temperatures are between $10-13^{\circ} \mathrm{C}$. However, they present no data.

Fry are approximately 1 cm long at hatching (Niemuth et al, (1962). Once hatched, they leave the spawning site and move
to open water (Eschmeyer, 1950). The larvae lead a pelagic existence for 4 to 6 weeks (Houde, 1967) or until they are 2 to 3 cm in length. They then return to the littoral zone and form schools, sometimes with perch.

Growth rates in fishes are generally determined from increments in length or weight during discrete time periods. Although growth rates may be estimated from direct measurements, growth history must be determined indirectly and requires knowledge of fish size at specific times or ages. Fish may be aged from direct observations but indirect procedures are more commonly available. Modes in length frequency distributions sometimes indicate ages but patterns of growth lines on bones or scales are generally used to interpret age and past growth of fishes.

When walleye are 24 mm in length, scales begin to develop in the caudal region (Priege1, 1964). Development continues anteriorly until the fish is completely covered. New scales are not developed as the fish grows, instead scales grow in size throughout life. Scale size, therefore, might be expected to be proportional to fish size. The bony layer of the scale and the ridges on the undersurface of the scale are formed by osteocytes (Neave, 1936). A new bony ridge or circulus is formed in walleye by the cells every 3 or 4 weeks throughout the year (Eddy and Carlander, 1939).

When growth conditions are good, the distance between circuli is much greater than when conditions for growth are poor. A zone of crowded circuli (called an annulus by Clutter and Whitsel, 1956) might be expected in winter when conditions are severe. Counting annuli or winter growth rings determines age. Buchholz and CarIander (1963), Sprugel (1954), and Regier (1962) noted that poor growing periods other than during the winter season may cause the formation of false annuli in yellow bass and bluegills. Forney (1962) noted false annuli in walleye. Other difficulties in using scales for age determination is lateral scale resorption (Buchholz and Carlander, 1963) or the failure of scales to form annuli (Forney, 1965). Nevertheless, most investigators, including Deason (1933), Schloemer and Lorch (1942), Carlander (1945, 1948), Cleary (1949), Eschmeyer (1950), Rose (1951), Rawson (1957), Carlander and Whitney (1961), Smith and Pycha (1961), and Forney (1965) have aged walleye by scale annuli.

As indicated, fish scales may also provide information concerning body lengths at previous ages and, consequently, growth rates. Back calculation is a procedure by which past body lengths are determined from measurements between successive scale annuli. The method requires the assumption that the ratio of total anterior scale radius to total body length is constant at all ages. Therefore, scale radius and size at capture can be used along with scale
radius measurements to particular annuli to compute estimated lengths at these annuli. Various methods of back calculating body sizes at annuli from the body-scale relationship are summarized by Lagler (1956). In walleye a curvilinear relationship exists between length of scale radius and body length (Carlander, 1945, 1950; Carlander and Whitney, 1961). However, in back calculating walleye lengths, Cleary (1949), Carlander (1956), Carlander and Whitney (1961), and Smith and Pycha (1961) have assumed a linear relationship. Rose (1951) used a straight-Iine direct proportion formula for his walleye studies but most investigators introduce a correction factor, such as the one used by Fraser (1920), into the formula to account for growth occurring prior to scale formation. To facilitate computations, nomographs can be used. The construction and operation of such apparatus for converting scale measurements into body lengths are described by Ery (1943), Carlander and Smith (1944), Hile (1948), and Schuck (1949).

Carlander (1945) noted Lee's phenomenon in back calculated lengths of walleye over age III from Lake of the Woods, Minnesota. The phenomenon is an apparent change in growth rate between young and older fish. In older fish, lengths determined by back calculation are generally less than fish sampled at that age. Carlander (ibid) attributed results to selective fishing.

The accuracy in back calculation of sizes from scale criteria assumes (1) scales are constant in number throughout life of fish, (2) growth of the scale is proportional to growth of the fish, (3) the annulus is formed at approximately the same time each year (Van Oosten, 1929). In walleye the time of annulus formation differs between years and among age groups (Smith and Pycha, 1961). Carlander (1945) and Cleary (1949) reported annulus formation in May but Smith and Pycha (1961) found most age groups of walleye had well developed annuli by the last week in June.

Growth is commonly expressed in absolute, relative, or instantaneous terms. Absolute growth is change in size at each age and is often plotted as a regression of size at age (Rounsefell and Everhart, 1953). Relative growth rate, expressed as:

$$
h=\frac{s_{2}-s_{I}}{s_{I}}
$$

where $h$ is relative rate, $S_{2}$ is size at time period 2 , and $S_{1}$ is size at time period 1 ; is the increase in size in each time interval expressed as a percentage of the size at the beginning of the time period (Ricker, 1958). Instantaneous growth, denoted by formula:

$$
g=\log _{e}(h+1)
$$

where $g$ is instantaneous growth, $h$ is relative growth, and $\log _{e}$ is base of natural logarithms; is an expression of the natural
logarithm of the ratio of final size to initial size for a unit of time (Ricker, ibid).

Variation in annual growth of walleye occurs between individuals, year classes, and populations. Carlander (1945, 1948), Cleary (1949), Rose (1951), Rawson and Atton (1953), and Carlander and Whitney (1961) found length increments greatest during first year of life but thereafter they decreased with age. However, Eschmeyer (1950) and Deason (1933) reported similar length increments occurred during the first two years of life followed by decreasing increments thereafter.

Seasonal growth has been investigated for young-of-theyear walleye by Smith and Pycha (1960) and Forney (1966). They found that approximately $90 \%$ of the annual length increase is completed by September. Apparently little work has been done with seasonal growth in older walleye.

It is often necessary to compute weights from lengths. The length-weight relationship follows approximately the cube law relationship expressed by the formula, $K=W / L^{3}$, in which $W$ is the symbol of weight and $L$ the symbol for length. However, fish are prone to change in body proportions or specific gravity during life so that the cube law seldom applies throughout the life of a fish. Therefore, as Rounsefell and Everhard (1953) point out, a
more satisfactory formula for expression of the relationship is:

$$
w=c L^{n}
$$

where W is weight, L is length, and c and n are constants. The values of the constants may be determined by fitting a straight line to the logarithms of $L$ and $W$. The value $c$ would be represented by the intercept of the line and n would be the slope. Ricker (1958) suggests, to reduce computations, that data may be grouped into short length-classes before establishing the logarithmic relationship of average length with average weight.

Weight increments generally increase with age in fish but Cleary (1949) reported that maximum weight increment for walleye in Clear Lake, Iowa, occurred during their fifth year.

Differences in growth rates between sexes have been noted by Eschmeyer (1950), Rawson (1957), Carlander and Whitney (1961), and Forney (1965). They found in adult walleye that mean lengths of females were generally greater than lengths of males of the same age. Differences in growth rate between sexes does not apply to all walleye populations because Carlander (1945), Kennedy (1949), and Derksen (MS) found little difference in growth between males and females.

Environmental factors such as population density, length of growing season, abundance of forage species, and productivity of
habitat might be responsible for variations in growth of walleye populations. Carlander (1948) attributed high growth rates of walleye in Diamond Lake, Iowa, to low population densities. However, Smith and Pycha (1960) and Forney (1965) found growth of year classes independent of year class strength. Temperature as an environmental factor affecting growth is also in debate. Carlander (1948) found growth rates greater in southern Iowa lakes and proposed that higher summer temperatures increased metabolic rate and hence growth but Smith and Pycha (1960) and Forney (1965) found little correlation between water temperatures and growth. Type of food seems the one factor very important to growth. Smith and Moyle (1945) found the introduction of fertilizers to ponds increased crustacean populations and also the biomass of walleye populations. Forney (1966) noted that growth of young-of-the-year to be more rapid when walleye fed on fish than when invertebrates were common in diet. Glenn and Ward (1968) and Ward and Glenn (MS) found the main item in the summer diet of walleye in West Blue Lake to be yellow perch. Forney (1965) noted growth increments in walleye closely correlated with abundance of young perch. Smith and Moyle (1945) found no evidence that pond size nor concentration of carbonates and sulphates had any effect on walleye production.

The ecological factors discussed may only be important to growth by providing physiological opportunity. Parker and Larkin (1959) present data which indicate that increases in growth rates of fishes are proportional to increases in metabolic rates. Therefore, growth is dependent on direct and indirect controls of metabolism. Paloheimo and Dickie (1966a, 1966b) discuss these controls such as temperature, oxygen consumption, food types, size of food particles, food intake in relation to growth efficiency, salinity of surrounding environment, and presence of metabolic wastes with respect to their effect on growth of fishes.

## DESCRIPTION OF AREA

West Blue Lake is centrally located in Manitoba's Duck Mountain Provincial Park. The Duck Mountains, containing the highest elevation in the province, Mt. Baldy, ( 894.6 m above sea level), represent part of the north-eastern edge of the Manitoba Escarpment (Davies et al, 1962). These highlands have resulted from shale moraines deposited by the Keewatin ice sheet on Upper Cretaceous bedrock (Wickenden, 1953). According to Weir (1960), the moraine is covered by "mixed woods." Forests of aspen, white spruce, and balsam fir occupy the well drained sites. In areas disturbed by fire or forestry produce stands of aspen, balsam poplar and jack pine. Black spruce and tamarack are located in poorly drained regions. Hazel and mountain maple are dominant shrubs.

Scattered throughout the park are many small lakes. West Blue Lake (Fig. 1) was formed by glacial action (personal communication from R. W. Klassen). It is a type of "kettle lake" known as a "channel lake." Apparently, active glacial ice re-occupied a former meltwater channel filling it with ice and drift. The present multibasin morphometery has resulted from the melting of buried ice. There are three distinct basins in the lake having a total surface area of 160 hectares and a volume of approx-


Figure 1. Bathymetric map of West Blue Lake (contour intervals of 5 m ). Each sampling area denoted by a dot.
imately $9.2 \times 10^{6} \mathrm{~m}^{3}$. The mean depth and maximum depths are respectively 11 and 31 m . There are only two small temporary influent streams and no surface outlets, therefore, water levels seem to be dependent on ground water and local runoff. The basins have steeply sloping sides limiting the littoral zone and the growth of rooted aquatic vegetation.

Ice usually forms by mid-November and covers the lake until mid-May (actual dates for 1966-1967 were November 5 and May 26). Small surface area relative to volume and the heavy forest which continues down to the shoreline limits wind produced mixing in spring and fall. As water temperature increases in spring the lake stratifies (Fig. 2). Associated with thermal stratification are variations in the vertical distribution of dissolved oxygen (Fig. 2). Secchi disk transparency ranges from 6-10 m.

Species of fish present are: walleye (Stizostedion vitreum), northern pike (Esox 1ucius), lake trout (Salvelinus namaycush), yellow perch (Perca fluviatilis), fathead minnow (Pimephales promelas), and the brook stickleback (Eucalia inconstans).



FIGURE 2. Vertical distribution of water temperatures $(C)$ and dissolved oxygen (mg/l) for three sampling dates from Basin 2, West Blue Lake, during summer of 1966.

## METHODS

White nylon gill nets were joined by sidelines to form gill net gangs. These gangs were placed as bottom sets, diagonal to the shoreline, in depths less than 5 m . As walleye were more vulnerable in the littoral zone after dark (Ward and Glenn, MS), nets were set, at dusk and lifted during the night or next morning.

In 1966 sets were made in each of the three basins
(Fig. 1) with net gangs of varying mesh sizes (Table I). Each basin was sampled at two week intervals from June to September. Walleye age II and older were vulnerable to the gear used. Only six net sets were made in Basin 3 between May 23-25 of 1967.

Table I. Dimensions of gill net gangs employed in sampling walleye at West Blue Lake during 1966 and 1967.

| Date | Gang measurements $(\mathrm{m})$ | Mesh sizes in mm <br> (stretched measure) |
| :--- | :--- | :--- |
| May 27-June 4/66 | $2.44 \times 45.72$ | 76.2 |
| June 20 | $2.44 \times 45.72$ | 76.2 |
| June 27 | $1.52 \times 121.92$ | $38.1,63.5,88.9,114.3$ |
| June 28-30 | $1.52 \times 121.92$ | $38.1,63.5,2(88.9)$ |
| July 17-21 | $1.52 \times 121.92$ | $38.1,63.5,2(88.9)$ |
| August 3-6 | $1.52 \times 121.92$ | $38.1,63.5,2(88.9)$ |
| August 13-15 | $1.52 \times 121.92$ | $38.1,63.5,2(88.9)$ |
| August 25.27 | $1.52 \times 121.92$ | $38.1,63.5,2(88.9)$ |
| September 12-14 | $1.52 \times 121.92$ | $38.1,63.5,2(88.9)$ |
|  |  |  |
| May 23-25/67 | $1.52 \times 121.92$ | $38.1,63.5,88.9$ |
| May 23-25 | $1.52 \times 121.92$ | $50.8,76.2,101.6$ |

The total length, to the nearest mm , of each walleye was
determined on a measuring board and then recorded. Fish were weighed (to the nearest ounce) using a Chatillon (model 1000) spring weighing scale. Subsequently, weights were converted to grams. As sex of walleye could not be determined from observation of gonads in summer, only the sex of fish captured in the spring when gonads were mature were recorded. During May 27 to June 4, 1966 and May 23-25, 1967, mature walleye were sexed by applying abdominal pressure to extrude eggs or milt. Relative growth rates between male and female fish captured during these periods were compared to note possibility of variation in growth rates between sexes.

Both direct and indirect approaches in calculation of seasonal growth rates in walleye were taken. In the direct approach, a mean length and weight was determined for fish of each vulnerable age group at each sampling period during the year. Mean seasonal growth rates were then estimated from changes in size. Data obtained by this method was used to support rates calculated using the following indirect approach.

The indirect method used scale criteria in calculation of growth rates. Basically, the procedure involved the following steps:
(1) Eish were aged using scale criteria so that age specific growth rates could be calculated.
(2) A relationship between scale length and body length was determined so that the length of individual fish at annulus formation could be estimated.
(3) A length-weight relationship was established to provide estimates of weight at any given length.
(4) Growth rates for individual fish were calculated from the change in estimated length and weight at time of annulus formation and observed length and weight at time of capture. The growth immediately after annulus formation represented growth at the beginning of the growing season.
(5) Growth rates of fish in each vulnerable year class were averaged to obtain a mean growth rate.
(6) Seasonal growth was estimated from the difference between mean growth rates of fish of known age captured at successive sampling dates.

To obtain indirect age and growth data, several scales were selected from the left side of each fish between the first and second dorsal fins immediately above the lateral line. Impressions of several scales from each walleye were made on a $0.040^{\prime \prime} \times 1^{\prime \prime} \times 3^{\prime \prime}$ acetate plastic sheet using a rollex press as described by Smith (1954). Images of scale impressions were then projected onto a screen using a Bausch and Lomb Tri-Simplex microprojector. The images were magnified 48 times. Annuli were counted and age determined without reference to the size of the fish. More than one impression was examined if images were not clear or annuli not distinct. A sample of scales was reread to test consistency in using scale characteristics as age indicators.

Winter growth rings were located by identifying crowding and "cutting over" of circuli. Scales of young walleye in West Blue Lake had well developed annuli; aging by counting impressions of annuli on plastic slides was not difficult for these young fish but difficulties did occur in fish older than age IV. Rereading 83 randomly selected scale impressions showed a $91 \%$ agreement with previously assigned ages (Table II).

Table II. Number of walleye assigned given ages for 83 randomly selected samples.

| Reading |  |  |  |  |  |  |  |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| period | I | Age |  |  |  |  | II | III |

First $\begin{array}{llllllllll}\text { reading } & 2 & 18 & 21 & 21 & 9 & 7 & 4 & 1\end{array}$

Second
$\begin{array}{lllllllll}\text { reading } & 2 & 18 & 21 & 21 & 12 & 4 & 3 & 2\end{array}$
A peripheral scale annulus was formed during the last week in June during 1966. One hundred and forty-seven scale samples collected between Miay 27 to June 20 showed no evidence of complete annulus formation. Of 95 walleye netted between June 27-30, 38 had scales with a complete annulus. These were observed only on scales of fish aged II, III, and IV at this time, suggesting that younger walleye, undergoing rapid growth, form annuli earlier than older, slower growing fish. Examination of scale impressions from walleye netted between July 17-20 showed
$94 \%$ of the fish with well developed annuli. The four scale impressions of the 64 scales examined in which the annuli could not be identified were from fish aged VI and older. In support of the 1966 results, all fish age II and $64 \%$ of walleye aged III captured on June 24, 1967 had a peripheral annulus. No peripheral annulus could be found on older fish at this time. However, all fish caught during the July 16, 1967 netting period had annuli with the exception of two fish aged VIII and IX. Since young fish in both years had annuli by the end of June and these younger age groups made up the majority of the fish in all samples, it was assumed that all age groups had the annuli developed by June 28. Consequently this date was considered to be the beginning of the growing season. The second step in determining seasonal growth rates by the indirect approach, required an estimate of fish length at time of formation of the last annulus. The distance between annulus and scale focus was measured to the nearest millimeter along the anterior scale radius. The total antexior radius of each scale was also measured. The anterior radius was selected to prevent errors which may have been caused by lateral scale development or resorption (Buchholz and Carlander, 1963). A nomograph (Schuck, 1949) was used to back calculate lengths at annulus using the formula:

$$
L_{I}=C+\frac{R_{1}}{R_{2}}(L-C)
$$

where $\mathrm{L}_{1}$ is body length when the outer annulus is formed, L is total body length, $R_{1}$ is length of scale radius to annulus, $R_{2}$ is total length of scale radius, and $C$ is a correction factor. The correction factor was determined by plotting scale measurements against body lengths and extrapolating the regression line obtained to the "y" intercept (Fig. 3). Mean body lengths (lengths were grouped into 1 cm intervals) were plotted against anterior scale radius of a sample of 891 walleye. The linear regression equation was $Y=51.45+2.023 X$. The $Y$ intercept of this line indicated that walleye in West Blue Lake were 51 mm in length before scales were developed and that body length increased at a rate of 2.02 times the basic scale measurement. Lengths obtained from the nomograph (designed to include the correction factor) and calculated lengths had a mean difference of only 0.14 mm for 25 samples ranging in total length from 238 to 523 mm . As a result the nomograph was used for all back calculation.

After back calculating the corresponding body length at the time of formation of the peripheral annulus for each fish, the weight for this length was determined from the computed length-weight relationship. In fish, weight is a function of length; this length-weight relationship (Fig. 4) can be described by equation:

$$
W=c L^{n}
$$



FIGURE 3. The relationship between various total length classes of walleye captured in 1966 from West Blue Lake and the average anterior scale radius of each class.


FIGURE 4. Length-weight relationship of walleye in West Blue Lake based on measurement of 665 fish.
where $W$ is weight, $L$ is length, and $c$ and $n$ are constants of proportionality (Rounsefell and Everhart, 1953). Six hundred and sixtyfive walleye ranging in length from $195-650 \mathrm{~mm}$ were weighed to the nearest ounce. Weights were then converted to grams. The relationship was computed by grouping lengths of walleye into one centimetex intervals and obtaining a mean weight for each length class $(\log W=-5.463+3.163 \log \mathrm{~L})$. This length-weight relationship was then used to determine the weight at last annulus from estimated back calculated lengths. Changes in weight, which resulted from growth in length, provided estimates of rates of growth in weight.

Changes within the length-weight relationship during the growing season were examined. The slope of the logarithm of the length-weight curve was determined for walleye between $301-400 \mathrm{~mm}$ in length for each of the summer sampling periods (Table III). Only this portion of the length-weight curve could be examined as only fish of this length were available at all sampling periods. Estimates of slope indicate there may be a trend for increasing weight with respect to length over the summer. However, as sufficient data was not available for the calculation of a lengthweight relationship for each of the sampling periods, the lengthweight curve determined from all samples collected in 1966 was
used for estimating weights for back calculated lengths.
Table III. Slope of the logarithm of the length-weight curve for walleye between $301-400 \mathrm{~mm}$ in length for each of the sampling periods. The corresponding slope calculated from all fish captured during 1966 was 3.16 .

## Sampling date

|  | June <br> $20-30$ | July <br> I7-21 | July 29 <br> -Aug. 6 | Aug. <br> $25-27$ | Sept. <br> $12-14$ | May <br> $23-25$ |
| :--- | :--- | :--- | :--- | ---: | :--- | :--- |
| Slope | 2.91 | 3.89 | 3.31 | 3.43 | 3.59 | 3.50 |

Growth can be expressed as increments or as relative or instantaneous growth rates. Although relative rates were calculated to obtain corresponding instantaneous rates, only growth increments and instantaneous rates are presented in this study. Changes in length and weight, expressed as millimeter or gram increments over previous sizes, were used to estimate percentage of annual growth completed at end of each sampling date. Instantaneous growth rates, (Ricker, 1958), were calculated to provide estimates in growth between sampling periods. Because an instantaneous growth rate calculated at a given unit of time is the sum of a series of instantaneous rates within the corresponding time unit (ie instantaneous rates are additive or $g_{t}=g_{1}+g_{2}+\ldots$. $\left.g_{t-2}+g_{t-1}\right)$, the difference between the final rate $\left(g_{t}\right)$ and the rate $\left(g_{t-2}\right)$ would provide an estimate of rate $\left(g_{t-1}\right)$. Using this procedure as will be shown, instantaneous growth rates of walleye
were determined for the periods between sampling dates. Also the use of instantaneous rates permitted calculation of growth per day, thus permitting comparison of growth in sampling periods of unequal length.

The individual differences in estimated length and weight between the time of annulus formation (beginning of growing season) and time of capture were determined and, as described, the mean increment for each age class was computed. This increment was compared to the annual increment to obtain the percentage of annual growth completed at each sampling date. To obtain the annual increment, the lengths at each annulus of 641 walleye captured in 1966 was estimated by back calculation. The mean length at each age for each year class was then determined. Finally, a grand mean length at each age was obtained by averaging means of each year class. The difference in length between ages was considered the annual increment. A corresponding weight for the grand mean length at each age was determined from the lengthweight relationship and the difference between ages represented annual weight increment.

Annual increments computed from back calculated lengths for age groups of walleye captured in 1966 did not refer specifically to annual growth completed between spring of 1966 and
spring of 1967 when the seasonal rates were investigated. For this reason, annual growth increments were determined for the period between time of annulus formation in 1966 and time of annulus formation in 1967. Lengths at annulus formation in 1966 were back calculated for the 65 walleye captured on June 24 and July 12, 1967. From the difference between length at capture and the back calculated length of these fish, an estimate of the annual growth for the growing year 1966-1967 was obtained. Data (Table IV) indicate that growth in length occurring between 1966 and 1967 was similar to the calculated grand mean increments for age groups of walleye netted during 1966. As shown, the mean length increments by any age group captured in 1967 had a maximum deviation from the grand mean increment of only 8 mm . This was noted in fish aged $\mathrm{V}+$ and was based on data from only two walleye. There were no trends in the variations of annual increments of 1967 data from the grand mean, that is, annual length increments of fish netted in 1967 to show annual growth between annulus formation in 1966 to annulus formation in 1967 were not consistently larger nor smaller than the grand mean calculated from samples collected in 1966. Because there were no apparent trends, it was concluded that seasonal growth increments could be compared to the grand mean because the greater
number of samples in each year class from all fish collected in 1966 provided a more reliable estimate than actual data recorded from 65 walleye captured on June 24 and July 12, 1967. However, it must be realized that the grand mean increments of each age group were a substitute for the mean annual increments which occurred during the year when seasonal growth rates were studied.

Table IV. Annual length increments (mm) for year classes of walleye captured at June 24 and July 12, 1967 and the grand mean increments for age groups netted during 1966. Number of fish examined in each age group is shown in parenthesis.

| Age |  |  |  |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Year | II-I | III-II | IV-III | V-IV | VI-V | VII-VI | VIII-VII | IX-VIII |
| Mean |  |  |  |  |  |  |  |  |
| from | (1) | $(40)$ | $(5)$ | $(13)$ | $(2)$ | $(2)$ | $(1)$ | (1) |
| I967 | 109 | 95 | 66 | 38 | 38 | 33 | 26 | 12 |
| catch |  |  |  |  |  |  |  |  |
| Mean |  |  |  |  |  |  |  |  |
| from | $(641)$ | $(633)$ | $(428)$ | $(266)$ | $(126)$ | $(16)$ | $(6)$ | (1) |
| 1966 <br> catch | 108 | 96 | 70 | 43 | 30 | 26 | 24 | 18 |

The magnitude of error which may be in olved using grand mean increments from 1966 data rather than actual growth increments calculated from walleye netted in 1967 would not be great. For example, when the seasonal length gain of 9 mm in walleye age $\mathrm{V}+$ captured July 17-21, 1966, was compared as a percentage of 30 and 38 mm (annual increments for this age group as presented in Table IV) a difference of only $7 \%$ was produced. When seasonal gains
of other age groups were compared to their respective annual length increments, smaller percentages were found to exist. Because the annual grand mean increments calculated from 1966 data and annual length increments of fish netted in 1967 were in close agreement, use of the 1966 data would not seriously affect the results of this investigation.

Seasonal instantaneous rates were derived by the following procedure: the increment between the 1966 summer annulus (from back calculation) and length at time of capture was expressed as a fraction of the back calculated length. Means of these relative growth rates for each age group were computed for fish collected at the various sampling dates. Mean relative growth rates were then converted to instantaneous rates by formula:

$$
g=\log _{e}(h+1)
$$

where $g$ is instantaneous growth rate, $h$ is relative growth rate, and $\log _{e}$ is base of natural logarithms. The seasonal growth rate between sampling dates was determined by calculation of the difference between instantaneous rates of consecutive sampling periods. This instantaneous rate was then divided by the number of days between periods to obtain a length increase per day. A similar procedure was used to obtain weight increase.

Age specific seasonal growth rates were estimated for
fish age II and older because only these age groups were vulnerable to gear employed. Fish age VI and over were grouped and treated as having a common growth rate since they constitute only a small percentage of the fish examined. The magnitude of any error introduced into this study by grouping these ages is insignificant because these older walleye made up only $5.3 \%$ of the catchable population.

Another aspect which must be considered in growth studies is growth rates of sexes. Carlander (1945, 1961), Eschmeyer (1950), and Stroudt (1949) have reported that mature male and female walleye have different rates of growth. Table V presents mean relative rates between sexes. A Wilcoxon sign-rank test showed no significant difference in rates of growth between sexes ( T value $=8$, critical $T$ value when n is $8=4$ or less at $P=0.95$ ). Because growth rates were similar in both sexes, it was not considered ne cessary to treat males and females individually in this study.

Table $V$. Relative growth rates of male and female walleye collected from West Blue Lake. Data based on 22 males and 20 females captured in 1966 and 1967.

| Sex | Relative growth in length between ages |  |  |  |  |  |  |  |  |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
|  | I | II |  | III | IV | V | VI | VII | VIII | IX |
| Female | 0.97 | 0.43 | 0.20 | 0.13 | 0.07 | 0.05 | 0.05 | 0.03 |  |  |
| Male | 1.02 | 0.42 | 0.20 | 0.10 | 0.09 | 0.07 | 0.04 | 0.03 |  |  |

Estimates of seasonal growth rates were determined from measurement of 643 walleye age II and older captured during the sampling dates of 1966-1967 (Table VI). As described, growth rates were estimated from both a direct and an indirect approach.

Table VI. Number of walleye in each age group captured after annulus formation (in 1966) during 1966 and 1967.

| Sampling | Age |  |  |  |  |  |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: |
| date | II | III | IV | V | VI and over | Total |
|  |  |  |  |  |  |  |
| June 20-30 | 21 | 44 | 34 | 23 | 14 | 136 |
| July 17-21 | 26 | 21 | 10 | 5 | 3 | 65 |
| July 29-Aug. 6 | 17 | 11 | 6 | 2 | - | 36 |
| August 25-27 | 94 | 52 | 29 | 14 | 14 | 203 |
| September 12-14 | 47 | 27 | 11 | 2 | 6 | 93 |
| May 23-25, 1967 | 80 | 15 | 4 | 7 | 4 | 110 |
| Total | 285 | 170 | 94 | 53 | 41 | 643 |

In the direct approach changes between mean lengths and weights for each vulnerable age group were used to calculate instantaneous rates of growth per day between sampling dates (Table VII). Results from the direct approach, in general, indicated greatest increase in length and weight during June 28 to mid-September. Little growth occurred in winter months (Fig. 5 and Fig. 6).

Estimated lengths at annulus formation in 1966 and lengths at capture provided data for calculation of instantaneous

Table VII. Mean sizes and rates of growth of vulnerable walleye captured at sampling dates during 1966-1967. ( $\mathbb{N}$ is number of walleye sampled, L is mean length (mm) at capture, $W$ is mean weight ( g ) at capture, $1 / \mathrm{d}$ is instantaneous growth in length per day, w/d is instantaneous growth in weight per day.)

| Age | Sampling date |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Growth data | $\begin{gathered} \text { June } \\ 20-30 \\ \hline \end{gathered}$ | $\begin{gathered} \text { July } \\ 17-21 \end{gathered}$ | July 29 <br> -Aug. 6 | $\begin{array}{r} \text { Aug. } \\ 25-27 \\ \hline \end{array}$ | Sept. $12-14$ | $\begin{array}{r} \text { May } \\ 23-25 \\ \hline \end{array}$ |
| II | N | 21 | 26 | 17 | 94 | 47 | 80 |
|  | L | 244 | 264 | 293 | 306 | 319 | 319 |
|  | W | 131 | 149 | 222 | 241 | 250 | 257 |
|  | 1/d | 0.00360 .0070 |  | $0.0019 \quad 0.0023$ |  | 30.0000 |  |
|  | w/d | 0.00620 .0266 |  | 0.00350 .0021 |  | 10.0001 |  |
| III | N | 44 | 21 | 11 | 52 | 27 | 15 |
|  | L | 338 | 357 | 362 | 387 | 387 | 394 |
|  | W | 345 | 410 | 431 | 511 | 509 | 541 |
|  | 1/d | 0.00270 .0006 |  | $0.0030 \quad 0.0000$ |  | 0.0001 |  |
|  | w/d | 0.00820 .0033 |  | $0.0074-0.0002$ |  | 2.0001 |  |
| IV | N | 34 | 10 | 6 | 29 | 11 | 4 |
|  | L | 411 | 421 | 431 | 441 | 438 | 458 |
|  | W | 641 | 680 | 791 | 794 | 765 | 985 |
|  | 1/d | 0.00110 .0016 |  | $0.0010-0.0004$ |  | $4 \quad 0.0002$ |  |
|  | w/d. | 0.00290 .0106 |  | $0.0002-0.0020$ |  | $0 \quad 0.0009$ |  |
| V | N | 23 | 5 | 2 | 14 | 2 | 6 |
|  | L | 461 | 457 | 503 | 492 | 506 | 496 |
|  | W | 950 | 890 | 1205 II | 11121 | 1205 | 1110 |
|  | 1/d | -0.0004 0.0064 |  | -0.0009 0.0015 |  | $5-0.0001$ |  |
|  | w/d | -0.0029 0.0202 |  | -0.0033 0.0046 |  | $6-0.0003$ |  |
|  | N | 14 | 3 | - | 14 | 6 | 4 |
| VI | L | 512 | 506 | - 5 | 526 | 535 | 549 |
| and | W | 1282 | 1257 | 13 | 1381 | 1479 | 1673 |
| over | 1/d | -0.0005 |  | 0.0010 | 0.0009 | 9.0001 |  |
|  | w/d | -0.0009 |  | 0.0025 | 0.0037 | 0.0005 |  |



FIGURE 5. Mean increase in length (mm) between time of annulus formation (June 28) and succeeding sampling dates for vulnerable walleye captured during summer of 1966 and spring of 1967.


EIGURE 6. Mean increase in weight (g) between time of annulus formation (June 28) and succeeding sampling dates for vulnerable walleye captured during summer of 1966 and spring of 1967.
growth rates and for determination of growth increments which occurred between sampling dates (Table VIII). As in the procedure outlined, mean length increments (Fig. 5) and mean weight increments (Fig. 6) at each sampling date were compared to annual increments between ages (Table A-I, Appendix) to obtain percentage of annual growth completed at each sampling date. The grand mean total length at each age (Table A-II, Appendix) is used to determine annual changes in length.

Results by the indirect method indicate the most rapid growth rates in length for catchable walleye occur between June 28 and mid-July. It then decreases progressively between following sampling dates (Table VIII). Growth in weight follows a similar pattern. Growth in length was greatest for walleye age II and decreased progressively with each older year class. However, weight increments obtained by the indirect method, in general, appear largest for walleye age III followed by ages IV, II, V, VI and over respectively.

When growth rates calculated by the direct and indirect methods were examined, it was noted that similar results were obtained in relation to length increments. However, estimates of seasonal weight increments were not in such close agreement. Seasonal weight gains by the direct method showed greater fluc-
tuations than by the indirect method. This is to be expected because weight increments from observed weight data would be independent of the length-weight proportion. In the indirect method, estimates of seasonal weight increments were calculated from the length-weight curve and this assumes that all walleye captured have the same length-weight proportion.
Table VIII．Growth statistics calculated for walleye from West Blue Lake between time of annulus formation （4th week in June）to succeeding sampling periods，1966－1967．

| $6000^{\circ} 0$ | I00 0 | $700^{\circ} 0$ | SIO 0 | IZO 0 | poṭxə ．outr <br>  <br>  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| \％ 28 | \％85 | $\% L S$ | \％67 | \％てて |  <br>  |
| 96 I | 6 6I | 9EI | LII | 2S |  <br>  |
| I000 0 | I00＊ 0 | $200^{\circ} 0$ | $900^{\circ} 0$ | $800^{\circ} 0$ |  <br>  <br>  |
| OIO ${ }^{\circ} \mp 96 \varepsilon^{\circ} 0$ | $\varepsilon 历 0^{\circ} \mp$ \％$\underbrace{\circ} 0$ | $670^{\circ} \mp 62 \varepsilon^{\circ} 0$ | $970^{\circ}+\square 9 z^{\circ} 0$ | SIO ${ }^{\circ} \mp 0 \angle I \cdot 0$ |  әұех чұмохถิ әлโาетәх นеәјл |
| \％I6 | \％28 | \％$¢$ | \％09 | \％88 |  <br>  |
| 6 | 8 | 焐 | $\varepsilon 乙$ | $8 \varepsilon$ | potixad siutidures snoṭィəxd <br>  |
| $z^{\circ} 8 \mp 76$ | $9^{\circ} \angle \mp \varepsilon 8$ | 6．879 6 | 6．6戸I9 | $L^{\circ} 9 \mp 8 \varepsilon$ | （•p•s Y 7 TTM）uuu <br>  |
| L9／GZ－EZ Kejut | \＃I－ZI ${ }^{\text {²das }}$ | $L Z-S Z \cdot S n\}$ |  | IZ－LI $\mathrm{KI}^{\text {nI }}$ | 5！7st7e7S 47MOX5 |

Table VIII. Growth statistics calculated for walleye from West Blue Lake between time of annulus formation
(Continued)
(4th week in June) to succeeding sampling periods, 1966-1967.

| Age IV |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Growth Statistic | July 17-21 | July 29-Aug. 6 | Aug. 25-27 | Sept. 12-14 | May 23-25/67 |
| Mean length increment in mm (with s.d.) | $15 \pm 6.5$ | $27 \pm 7.0$ | $31 \pm 5.9$ | $35 \pm 8.2$ | $49 \pm 12.3$ |
| Length increment over previous sampling period | 15 | 12 | 4 | 4 | 14 |
| Percentage of annual growth in length completed | 28\% | 50\% | 57\% | 65\% | 91\% |
| Mean relative grow th rate in length (with $t=.95$ ) | $0.037 \pm .013$ | $0.066 \pm .021$ | $0.077 \pm .006$ | $0.087 \pm .015$ | $0.118 \pm .052$ |
| Instantaneous growth rate in length per day from preceeding sampling period | 0.002 | 0.002 | 0.0004 | 0.0005 | 0.0001 |
| Mean weight increment (g) from annulus formation | 59 | 168 | 161 | 164 | 274 |
| Percentage of annual growth in weight completed | 19\% | 54\% | 51\% | 52\% | 87\% |
| Instantaneous growth rate in weight per day from preceeding sampling period | 0.005 | 0.013 | -0.002 | 0.001 | 0.0005 |

Table VIII. Growth statistics calculated for walleye from West Blue Lake between time of annulus formation (4th week in June) to succeeding sampling periods, 1966-1967. (Continued)


## DISCUSSION

Seasonal rates of growth in length and weight have been examined for vulnerable walleye by a direct method (using changes in mean lengths and weights of fish netted at sampling dates) and by an indirect method (using changes in mean lengths and weights between time of annulus formation and time of capture). Results by the direct and indirect methods showed similar growth patterns (Fig. 5, Fig. 6, and Tables VII and VIII). However, data from the indirect approach should be more reliable because the direct approach assumes that growth rates calculated from differences of mean sizes of samples is equal to the mean growth rates calculated from changes in size of individual fish. The direct method would be ideal if it were possible to obtain the change in size of all the same samples during the year or if the mean sizes of differing groups of samples were constant at any sampling date. In the West Blue Lake study, different specimens were examined at each sampling date and data (not presented in thesis) indicated that their mean sizes for the beginning of the growing season varied. The direct method also assumes that all sizes of fish are equally vulnerable to the gear used. It is not known if there was change in net selectivity due to growth within an age group during the year. The indirect data was not subject to changes in net
selectively because size at annulus formation and time of capture, hence size increments, were obtained from the same sample.

Results show, for this previously unexploited population, that rate of growth in length in all age groups is greatest in early summer but declines thereafter (Fig. 5). It has been shown that approximately $65-80 \%$ of annual length growth is completed between June and midSeptember for fish between ages II to $V$ inclusive (Table VIII). This percentage would seem a conservative estimate since Smith and Pycha (1960) record percentages over $90 \%$ by August for first-year walleye in Red Lakes, Minnesota and Gerking (1966) found $90 \%$ of total length increment completed in sunfish (Lepomis macrochirus) in northern Indiana lakes by September. Rawson (1957) also noted the majority of growth for walleye completed between July and September in Lac La Ronge. One reason for apparent slower growth rates in walleye over age $V$ may be caused by later annulus formation. If the annulus of older fish was not laid down until after the last week in June, growth estimates from the period between time of annulus formation and following sampling date would then be increased and subsequent rates would be less. The larger weight gain, which appears later in the growing season (Fig. 6), can be explained by the length-weight relationship. Since weight increases, approximately as the cube of length, the length
attained in the latter part of the growing season would produce a higher percentage of total weight increase.

It has been shown that the length-weight relationship may not remain constant throughout the growing season and that estimates of weights from back calculated lengths are based on a mean relationship (fish from all sampling dates were used.) Because a mean relationship was used, the two decreasing growth rates in weight for older fish (Table VIII) were probably caused by sampling error rather than by actual fluctuations in the growth rate. Data (Table VI) show that computations for decreasing rates were based on 6 walleye aged IV and 3 fish aged VI and over. Growth increments in length between June to September, in general, progressively decreased with each age group studied (Fig. 5). Similar results for annual growth in walleye have been recorded by many authors although Eschmeyer (1950) and Deason (1933) found equal growth between some age groups. However, weight increments generally were greatest for walleye aged III and IV followed by the younger and older fish (Fig. 6). Consideration of the length-weight relationship provides information. In the length-weight relationship of fish:

$$
\mathrm{w}=\mathrm{kL}^{\mathrm{w} / 1}
$$

(where $W$ is weight, $k$ is a constant, $L$ is length, $w$ is coefficient
of growth in length) change in weight results from changes in length and the corresponding change of the equilibrium constant (represented by $w / 1$ ). For example, when the range of lengths of age groups are considered within the length-weight curve (Fig. 4), fish aged II are found to have an equilibrium constant of 3.06 while fish aged III, IV, $V$, and VI and over have equilibrium constants of $3.21,3.23$, 3.24 , and 3.41 respectively. Therefore, the weight increase per unit increase in length of walleye aged $V$ and $V I$ and over is greater than younger fish but because these older fish do not have large length gains between sampling dates, increase in biomass of older walleye is restricted. Conversely, young walleye (age II) grow rapidly in length but their corresponding weight increase is restricted by a small equilibrium constant. The large weight increments for walleye age III and IV are the product both relatively large length gains and equilibrium constants.

Conditions responsible for this rapid growth in July and August are not known. Carlander (1948) and Smith and Pycha (1960) noted positive correlations between water temperature and walleye growth. Smith and Moyle (1945) and Gerking (1966) found no correlation between growth and water chemistry such as oxygen, carbonate, or sulphate content. Gross et al (1965) presents evidence that growth was related to light and food consumption. Forney (1965)
found changes in growth were closely related to abundance of young perch. Fish, predominately perch, are the major component of the summer diet of West Blue Lake walleye (Glenn and Ward, 1968). Furthermore, Ward and Glenn (MS) found that weight of stomach contents was highest in mid-July when growth rates were highest. Limnological data, as previously presented, were not adequate to establish possible relationships between seasonal growth rates and environmental conditions. Data (Fig. 2) indicate the occurance of variations in vertical distributions of water temperatures and percentage saturation of oxygen in West Blue Lake during the summer of 1966. Ward and Glenn (NS) found that walleye in West Blue Lake tended to migrate from the deeper water where they spent the daylight hours to the littoral zone in the evening. Because the walleye may be located at various water depths during a 24 hour period, it would be difficult to determine the effects of the different limnological regines on growth rates. Also, since the seasonal growth study was confined to one year, no possible correlation could be noted between growth rates and environmental factors between years. Further investigation would be needed to establish those factors which may control seasonal growth.

Provided the stock in West Blue Lake does not suffer a
high summer mortality nor a heavy winter recruitment rate, the results from this investigation would indicate that only walleye over age III should be harvested. Because walleye age II and III experience rapid growth rates, contributions to the biomass of the population by these age groups will be greater than older year classes. Cropping fish over age III should produce high yields because the major portion of population bulk would be available. Also harvesting only ader age groups should ensure sufficient numbers of sexually mature fish (males mature at age IV, females at age $V$ in West Blue Lake) for a successful brood stock. If conditions of mortality and recruitment exist as stated, fishing in autumn would produce the best yield. During summer months, growth rates are high so that annual population bulk would approach its maximum by September or October. Cropping at this time would remove fish before they were lost by a possible heavy winter mortality. In most sport and established commercial fisheries, intense fall exploitation is not practical. However, concentration of fishing effort at this time might produce the best long term yield.

During 1966-1967 a sample of 643 walleye netted in West Blue Lake provided data on seasonal growth rates of fish aged II and over. Length and weight increments as well as instantaneous growth rates in length and weight per day were calculated by both absolute changes of mean sizes of fish between sampling dates and by estimating change in size of fish between time of annulus formation and capture date. Scale criteria were used to age fish and to estimate back calculated sizes at annulus formation. Walleye in West Blue Lake had well developed annuli and ages of fish under age $V$ were easily determined. A body-scale relationship of:

$$
\text { length }=51.45+2.023(\mathrm{X} 48) \text { scale radius }
$$

was established from a least squares regression between body length and anterior scale radius. To account for body growth before scale formation, the correction factor of 51 mm was introduced into the nomograph before back calculating body lengths at annulus. Weights at each length were estimated from a lengthweight relationship of:

$$
\log W=-5.463+3.163 \log \mathrm{~L}
$$

Seasonal variations in growth occurred within the vulnerable age groups. Both the direct and indirect approach for
estimation of seasonal growth in length indicate rapid growth during the period between June 28 and August 27 and little growth during the remainder of growing season. Also both procedures indicate length increments between sampling dates were, in general, greatest in walleye age II and decreased progressively with each older age group.

Seasonal growth in weight by both methods was, in general, greatest between June 28 and August 27 but a greater percentage of weight increase occurred during the winter period for older fish. Summer growth rates in weight estimated by the indirect method were greatest for walleye age III followed by IV, II, V, and VI and over respectively. Results of weight increase by the direct method indicate larger gains by the older age groups. However, rates estimated by this procedure were subject to fluctuations caused by comparison of data between samples.

Seasonal growth data derived from the indirect approach should be more reliable than the direct approach because estimates by the indirect method were based on growth data within groups of samples rather than between groups of samples. Environmental conditions responsible for the rapid growth rates which occurred in early summer are not known and further investigations into possible relationships should be undertaken. Provided that walleye

## LITERATURE CITED

Bajkov, A. 1930. Fishing industry and fisheries investigations in the prairie provinces. Trans. Am. Fish. Soc., 60:215-237.

Buchholz, Marvin M., and Kenneth D. Carlander. 1963. Failure of yellow bass, Roccus mississippiensis, to form annuli. Trans. Am. Fish, Soc., 92(4):384-390.

Carlander, Kenneth D. 1945. Age growth, sexual maturity, and population fluctuations of the yellow pike-perch, Stizostedion vitreum vitreum (Mitchi11), with reference to the commercial fisheries of Lake of the Woods, Minnesota. Trans. Am. Fish. Soc., 73(1943):90-107.
1948. Growth of the yellow pikeperch, Stizostedion vitreum vitreum (Mitchill), in some Iowa lakes, with a summary of growth rates reported in other areas. Iowa State College Jour. Sci., 22(3):227-237.
1950. Some considerations in the use of fish growth data based on scale studies. Trans. Am. Fish. Soc., 79(1949):187-194.
1956. Appraisal of methods of fish population studyPart 1 - Fish growth rate studies: techniques and role in surveys and management. Trans. 2Ist N . Am. Wildife Conf., pp. 262-274.
1961. Variations on rereading walleye scales. Trans. Am. Fish. Soc., 90(2):230-231.

Carlander, Kenneth D., and Robert E. Cleary. 1949. The daily activity patterns of some freshwater fishes. American Midland Naturalist, 41(2):447-452.

Carlander, Kenneth D., and Lloyd L. Smith, Jr. 1944. Some uses of nomographs in fish growth studies. Copeia, 3:157-162.

Carlander, Kenneth D., and R. R. Whitney. 1961. Age and growth of walleyes in Clear Lake, Iowa, 1935-1957. Trans. Am. Fish. Soc., $90(2): 130-138$.

Clutter, R. I., and L. E. Whitesel. 1956. Collection and interpretation of sockeye salmon scales. Internat. Pacific Salmon Fish. Comm., Bull. IX, 159 pp.

Cleary, Robert E. 1949. Life history and management of the yellow pikeperch, Stizostedion vitreum vitreum (Mitchill), of Clear Lake, Iowa. Iowa State College Jour. Sci., 23(2):195-208.

Crowe, Walter R. 1962. Homing behaviour in walleye. Trans. Am. Fish. Soc., 91(4):350-354.

Crowe, Walter R., Ernest Karvelis, and Leonard S. Joeris. 1963. The movement, heterogeneity, and rate of exploitation of walleye in northern Green Bay, Lake Michigan, as determined by tagging. Int. Comm. Northwest At1. Fish., Spec. Publ. No. 4:38-41.

Davies, J. R., B. B. Bannatyne, G.S. Barry, and H. R. McCabe. 1962. Geology and mineral resources of Manitoba. Man. Mines Brch. Publ., 190 pp.

Deason, Hilary J. 1933. Preliminary report on the growth rate, dominance and maturity of the pike-perches (Stizostedion) of Lake Erie. Trans. Am. Fish. Soc., 63:348-360.

Derback, B. 1947. The adverse effect of cold weather upon the successful reproduction of pickerel, Stizostedion vitreum, at Heming Lake, Manitoba, in 1947. Can. Fish. Cult., 2(1):22-23.

Derksen, Arthur J. 1967. Variations in abundance of walleyes, Stizostedion vitreum vitreum (Mitchill), in Cedar and Moose Lakes, Manitoba. MSC. Thesis, University of Manitoba, 98 pp.

Doan, Kenneth H. 1942. Some meteorological and limnological considerations as factors in the abundance of certain fishes in Lake Erie. Ecol. Monogr., 12(3):293-314.

Eddy, Samuel, and Kenneth D. Carlander. 1939. The growth rate of wall-eyed pike Stizostedion vitreum (Mitchill) in various lakes of Minnesota. Proc. Minn. Acad. Sci., 7:44-48.

Ellis, D. V., and M. A. Giles. 1965. The spawning behaviour of the walleye, Stizostedion vitreum (Mitchill). Trans. Am. Fish. Soc., 94(4):358-361.

Eschmeyer, Paul. 1950. The life history of the walleye in Michigan. Mich. Dept. Cons., Inst. Fish. Res., Bull. No. 3, 99 pp.

Eschmeyer, Paul H., and W. R. Crowe. 1955. The movement and recovery of the tagged walleye in Michigan, 1929-1953. Mich. Dept. Cons., Publ. 8, 32 pp.

Fedoruk, Alex N. 1966. Feeding relationship of walleye and smallmouth bass. J. Fish. Res. Bd. Canada, 23(6):941-943.

Forney, John L. 1962. Marking of walleye and smallmouth bass; routine sampling of Oneida Lake fish populations. N.Y. Div. of Fish and Game, Job Completion Report, Federal Aid Proj. F-17-R-5 (Mimeo).
1963. Distribution and movement of marked walleyes in Oneida Lake, New York. Trans. Am. Fish. Soc., 92(1):47-52.
1965. Factors affecting growth and maturity in a walleye population. New York Fish and Game Jour., 12(2):217-232.
1966. Factors affecting first-year growth of walleye in Oneida Lake, New York. New York Fish and Game Jour., 13(2):146-167.

Fraser, C. M. 1920. Growth rate in the Pacific Salmon. Trans. Roy. Soc. Canada (V), III, 13:163-226.

Fry, F. E. 1943. A method for the calculation of the growth of fishes from scale measurements. Univ. of Toronto Studies, Biol. Ser. 51, Publ. Ont. Fish. Res. Lab., 61:5-18.

Gerking, Shelby D. 1966. Annual growth cycle, growth potential, and growth compensation in the bluegill sunfish in northern Indiana lakes. J. Fish. Res. Bd. Canada, 23(12):1923-1956.

Glenn, C. L., and F. J. Ward. 1968. Evaluation of "wet" weight as a field method for measuring the stomach contents of walleye, Stizostedion vitreum vitreum (Mitchill). J. Fish. Res. Bd. Canada, 25(7):1505-1507.

Gross, W. L., E.W. Roelof, and P. O. Fromm. 1965. Influence of photoperiod on growth of green sunfish, Lepomis cyanellus. J. Fish Res. Bd. Canada, 22(6):1379-1383.

Hile, Ralph. 1948. Standardization of methods of expressing length and weights of fish. Trans. Am. Fish. Soc., 75(1945):157-164.

Hinks, David. 1943. The fishes of Manitoba. Dept. Mines and Natur. Resources, Prov. Manitoba, 102 pp.

Houde, E. D. 1967. Food of pelagic young of the walleye, Stizostedion vitreum vitreum, in Oneida Lake, New York. Trans. Am. Fish. Soc., 96(1):17-24.

Johnson, Fritz H. 1961. Walleye egg survival during incubation on several types of bottom in Lake Winnibigoshish, Minnesota, and connecting waters. Trans. Am. Fish. Soc., 90(2):312-322.

Kennedy, William A. 1949. Relationship of length, weight and sexual maturity to age in three species of Lake Manitoba fish. Fish. Res. Bd. Canada, Bull. 81, 5 pp.

Lagler, Karl F. 1956. Freshwater fishery biology. Wm. C. Brown Co., Dubuque, Iowa, 421 pp.

La Monte, Francesca. 1958. North American game fishes. Doubleday and Co. Inc., New York, 206 pp.

Maloney, J. E., and F. H. Johnson. 1957. Life histories and interrelationships of walleye and yellow perch, especially during their first summer, in two Minnesota lakes. Trans. Am. Fish. Soc., 85(1955):191-202.

Moore, George A. 1944. The retinae of two North American teleosts with special reference to their tapeta lucida. Jour. Comp. Neur., 80(3):369-379.

Neave, Ferris. 1936. The development of the scales of Salmo. Trans. Roy. Soc. Can., Ser. 3, 30. Sect. 5:55-76.

Niemuth, Wallace., Warren Churchill, and Thomas Wirth. 1962. The walleye, its life history, ecology and management. Wisconsin Conserv. Dept. Pub1. 227, 14 pp.

Olson, Donald E., and Warren J. Scidmore. 1962. Homing behaviour of spawning walleyes. Trans. Am. Fish. Soc., 9I(4):355-361.

Paloheimo, J. E., and L. M. Dickie. 1966a. Food and growth of fishes. II. Effects of food and temperature on the relation between metabolism and body weight. J. Fish. Res. Bd. Canada, 23(6):869-908.

1966b. Food and growth of fishes. III. Relations among food, body size, and growth efficiency. J. Fish. Res. Bd. Canada, 23(8):1209-1248.

Parker, R. R., and P. A. Larkin. 1959. A concept of growth in fishes. J. Fish. Res. Bd. Canada, 16(5):721-745.

Priegel, G. R. 1963. Food of walleye and sauger in Lake Winnebago, Wisconsin. Trans. Am. Fish. Soc., 92(3):312-313.
1964. Early scale development in the walleye. Trans. Am. Fish. Soc., 93(2):199-200.

Rawson, D. S. 1957. The life history and ecology of the yellow walleye, Stizostedion vitreum, in Lac La Ronge, Saskatchewan. Trans. Am. Fish. Soc., 86(1956):15-37.
1959. Limnology and fisheries of Cree and Wollaston Lakes in northern Saskatchewan. Fisheries Rept. No. 4, Fisheries Branch, Dept. Nat. Res., Sask. 73 pp.
1960. Five lakes on the Churchill River near Stanley Saskatchewan. Fisheries Rept. No. 5, Fisheries Branch, Dept. Nat. Res., Sask. 38 pp.

Rawson, D. S., and F.M. Atton. 1953. Biological investigation and fisheries management at Lac La Ronge, Saskatchewan, Fisheries Rept. No. I, Fisheries Branch, Dept. Nat. Res., Sask. 40 pp.

Regier, Henry A. 1962. Validation of the scale method for estimating age and growth of bluegills. Trans. Am. Fish. Soc., 9I(4):362-374.

Ricker, W. E. 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Bd. Canada, No. 119, 300 pp.

Rose, Earl T. 1951. Notes of the age and growth of Spirit Lake Yellow pike-perch (Stizostedion vitreum). Proc. Iowa Acad. Sci., 58:517-526.

Rounsefell, G. A., and W. H. Everhart. 1953. Fishery science: Its methods and applications. John Wiley and Sons, New York, 444 pp .

Schloemer, Clarence L., and Ralph Lorch. 1942. The rate of growth of the walleye pike, Stizostedion vitreum (Mitchill), in Wisconsin's inland waters, with special reference to the growth characteristics of the Trout Lake population. Copeia, 4:201-211.

Schuck, H. A. 1949. Problems in calculating size of fish at various ages from proportional measurements of fish and scale size. J. Wildl. Mgmt., 13(3):298-303.

Slastenenko, E. P. 1958. The freshwater fishes of Canada. Kiev Printers, Toronto, 385 pp .

Smith, I. L., Jr., L. W. Krefting, and R. L. Butlex. 1952. Movements of marked walleyes, Stizostedion vitreum vitreum (Mitchill), in the fishery of the Red Lakes, Minnesota. Trans. Am. Fish. Soc., 81(1951):179-196.

Smith, Lloyd L., Jr., and John B. Moyle. 1945. Factors influencing production of the yellow pike-perch, Stizostedion vitreum vitreum, in Minnesota rearing ponds. Trans. Am. Fish. Soc., 73(1943):243-261.

Smith, Lloyd I., Jr., and Richard L. Pycha. 1960. First-year growth of the walleye, Stizostedion vitreum vitreum (Mitchil1), and associated factors in the Red Lakes, Minnesota. Limnol. and Oceanogr., 5(3):281-290.
1961. Factors related to commercial production of the walleye in Red Lakes, Minnesota. Trans. Am. Fish. Soc., 90(2):190-217.

Smith, Stanford H. 1954. Method of producing plastic impression of fish scales without using heat. Prog. Fish-CuIt., 16:75-78.

Sprugel, George, Jr. 1954. Growth of bluegills in a new lake, with particular reference to false annuli. Trans. Am. Fish. Soc., 83(1953):58-75.

Stoudt, J. H., and Samuel Eddy. 1939. Walleye pike tagging study, 1937-1938, Chippewa National Forest. Trans. 4th N. Am. Wild1. Conf., pp. 305-310.

Stroud, R. H. 1949. Growth of Norris Reservoir walleye during the first twelve years of impoundment. J. Wild. Mgmt., 13(2):157-177.

Van Oosten, John. 1929. Life history of the lake herring (Leucichthyes artedi LeSoeur) of Lake Huron as revealed by its scales, with a critique of the scale method. Bull. U.S. Bur. Fish., 44:265-428.

Ward, F. J., and C. L. Glenn. (MS). Nocturnal feeding by walleye (Stizostedion vitreum vitreum) in West Blue Lake, Manitoba, 11 pp.

Weir, Thomas R. 1960. Economic atlas of Manitoba. Man. Dept. of Industry and Commerce Publ., 81 pp.

Wickenden, R. T. D. 1953. Mesozoic stratigraphy of the eastern plains, Manitoba and Saskatchewan. Can. Dept. Mines and Resources, 87 pp.

APPENDIX A. Included in this section is data on back calculated lengths at annulus formation for the vulnerable walleye in West Blue Lake and the annual growth rates of these samples.
Table A-II. Mean total lengths back calculated for walleye collected in West Blue Lake during 1966.

| Age |  | Mean Total Length in Millimeters at Annulus |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Class | Fish | I | II | III | IV | V | VI | VII | VIII | IX |
| I | 8 | 147 |  |  |  |  |  |  |  |  |
| II | 205 | 120 | 233 |  |  |  |  |  |  |  |
| III | 162 | 141 | 233 | 332 |  |  |  |  |  |  |
| IV | 140 | 132 | 249 | 337 | 407 |  |  |  |  |  |
| V | 62 | 151 | 258 | 361 | 422 | 466 |  |  |  |  |
| VI | 49 | 141 | 258 | 358 | 435 | 475 | 503 |  |  |  |
| VII | 9 | 143 | 254 | 368 | 442 | 494 | 527 | 547 |  |  |
| VIII | 5 | 139 | 239 | 332 | 412 | 468 | 506 | 540 | 566 |  |
| IX | $\frac{1}{641}$ | 128 | 258 | 373 | 436 | 463 | 496 | 529 | 544 | 562 |
| Grand |  |  |  |  |  |  |  |  |  |  |
| Total |  | 133 | 241 | 342 | 417 | 471 | 506 | 544 | 562 | 562 |

