

# Vital Statistics, Biomass, and Seasonal Production of an Unexploited Walleye (*Stizostedion vitreum vitreum*) Population in West Blue Lake, Manitoba

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The population of walleye, *Stizostedion vitreum vitreum*, (25 cm and greater) in West Blue Lake, Man., in May 1969 decreased from 1090 to 819 in May 1970. During summer and fall, the initial population was supplemented by new recruits, age II<sup>+</sup>, reaching a maximum of 3451 in September 1969. The total population in May 1970 was 2037. Mean daily mortality for all ages was small for the year, 0.0045, but loss rate was greatest in fall and winter. Growth in length was greatest for age II<sup>+</sup> followed by older fish. Growth in weight was similar for ages III-V and lowest for age II<sup>+</sup>. Mean biomass, approximately 800 kg, was similar in May 1969 and May 1970. Production, 340 kg, coincided with the growing season (June to October) and was greatest from June to September. Greatest contribution to walleye production and biomass was made by age II<sup>+</sup> fish. During winter and spring, zero or negative production occurred.

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La population de dorés jaunes (*Stizostedion vitreum vitreum*) (de 25 cm de longueur et plus) du lac West Blue, Manitoba, a passé de 1090 en mai 1969 à 819 en mai 1970. En été et en automne, de nouvelles recrues d'âge II<sup>+</sup> sont venues grossir la population initiale, qui atteignait un maximum de 3451 en septembre 1969. En mai 1970, la population totale comptait 2037 individus. La mortalité quotidienne moyenne de tous les âges a été faible, 0.0045, durant toute l'année, mais le taux de perte atteignait un sommet en automne et en hiver. La croissance en longueur a été la plus forte chez les poissons d'âge II<sup>+</sup>, plus faible chez les poissons plus âgés. La croissance pondérale a été la même chez les poissons d'âges III à V; elle a été la plus faible chez les poissons d'âge II<sup>+</sup>. La biomasse moyenne, d'environ 800 kg, était la même en mai 1970 qu'en mai 1969. La production de 340 kg, coïncidant avec la saison de croissance (juin à octobre), atteignait un sommet de juin à septembre. Les poissons d'âge II<sup>+</sup> sont ceux qui ont contribué le plus à la production et à la biomasse des dorés jaunes. La production a été nulle ou négative en hiver et au printemps.

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THE purpose of this paper is to describe seasonal biomass changes and production in the unexploited walleye (*Stizostedion vitreum vitreum*) population of West Blue Lake, Man.

Effects of angling and commercial fisheries on walleye populations have frequently been evaluated (Pycha 1961; Smith and Pycha 1961; Ryder 1968; Rose 1947; Forney 1967) but mortality and biomass changes have seldom been described for unexploited

fish populations. Exceptions are the work of Ricker (1947) and Kennedy (1954).

Within-year changes in survival and biomass have seldom been evaluated. Ricker and Foerster (1948) and Alexander and Shetter (1961) have indicated seasonal decreases in unrecruited salmonid stocks. Ricker and Foerster (1948) determined mortality rates estimated for short periods of the year and used these rates, applied to an initial biomass estimate, to calculate biomass changes and production. We calculated a series of biomass estimates and used growth, recruitment, and survival data to estimate seasonal production. Basic data were provided by a series of mark-and-release experiments carried out

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during the period from May 1969 to May 1970. During this time, angling and commercial fishing were prohibited.

## Methods and Materials

### SAMPLING AND MORTALITY TRIALS

Fish were captured in a standard gang of three sections, each 30.5 m long and 1.8 m deep. Mesh sizes were 3.8, 6.4, and 8.9 cm, stretched measure.

The standard gang was set at one of the possible sites approximately  $\frac{1}{2}$  hr before sunset in 3–15 m of water. Previously, we failed to capture fish during daylight and at depths greater than 15 m. The net was continuously patrolled by boat and captured fish were transferred to a perforated "live box" divided into four equal compartments. Fishing sites were alternated so that all three basins received comparable fishing effort. Captured fish (to a maximum of 40), sorted according to the mesh size of the capturing net, were retained overnight in the live box (length  $2.55 \times 1.22 \times 0.38$  m deep), anchored approximately 30 m offshore.

The following morning, total length and fork length were obtained for each active fish. Scales were taken 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 released after marking with a numbered streamer tag inserted between the interspinous rays of the spiny dorsal fin (Dell 1968).

To estimate mortality from handling and marking, eight or 12 fish, paired by length, were held in 560-liter fiber glass tanks (4–6 fish per tank) located on shore. One from each pair was subjected to procedures identical to those applied to marked-and-released fish. The other was transferred to the holding tanks with minimum handling.

Water, supplied by pumps with intakes installed 1.5 m below the surface of the lake, was replaced in each tank at about 45-min intervals. Holding periods were: June 24–July 21, July 19–27, September 7–14, 1969, and May 20–28, 1970. No food was supplied during holding.

### POPULATION ANALYSES

Six mark-and-recapture experiments were carried out during the year (Table 1). Recaptured individuals were classified according to their previous history.

Population abundance estimates from these data were calculated by the Petersen technique (Ricker 1958). New recruits, appearing in the population in September 1969 (Table 1), were readily recognizable by their size and were released as a separate lot. The population considered was age II<sup>+</sup> fish and older (total length generally greater than 25 cm).

The population was stratified by age by determining proportions of each age-group in the catch and by apportioning the estimate of total number (N) accordingly. Marked-and-recaptured fish in each age were too few to permit separate estimates.

Survival rates were estimated by an adaptation of Ricker's (1958) equation 5.2. Recaptures were at a point in time rather than over an extended period. Because sample sizes were small, survival — and consequently mortality — applied to the whole population. Fishing was prohibited, therefore all mortality resulted from natural causes.

An indirect method based on scale analyses was used to estimate growth rates. Several scales from one fish were mounted on an acetate slide and impressions made which were then examined at  $43.5\times$ . For each fish, the anterior scale radius from the focus and the distance of each annulus from the focus were recorded. Each slide was examined twice. Disagreement resulted in further reading.

TABLE 1. Numbers of walleye captured, released, marked, and recaptured in West Blue Lake during 1969 and 1970.

| Marking period | No. captured and released            | No. marked | Recaptures from marking experiment: |    |   |   |   |
|----------------|--------------------------------------|------------|-------------------------------------|----|---|---|---|
|                |                                      |            | 1                                   | 2  | 3 | 4 | 5 |
| 1969           |                                      |            |                                     |    |   |   |   |
| May 14-20      | 111                                  | 111        | —                                   | —  | — | — | — |
| June 16-22     | 107                                  | 97         | 10                                  | —  | — | — | — |
| Sept. 3-12     | 95 (III <sup>+</sup> ) <sup>a</sup>  | 81         | 8                                   | 6  | — | — | — |
|                | 133 ( II <sup>+</sup> ) <sup>b</sup> | 119        |                                     |    |   |   |   |
| Oct. 5-12      | 86                                   | 79         | 2                                   | 3  | 2 | — | — |
| 1970           |                                      |            |                                     |    |   |   |   |
| May 18-26      | 117                                  | 83         | 3                                   | 4  | 4 | 3 | — |
| June 15-19     | 97                                   | —          | 2                                   | 1  | 3 | 2 | 3 |
| Totals         | 651 <sup>a</sup>                     | 489        | 25                                  | 14 | 9 | 5 | 3 |

<sup>a</sup>Excludes recruitment.

<sup>b</sup>Includes recruited individuals released as a cohort.

Fork lengths for a particular scale radius were variable, but variances were homogeneous ( $\chi^2 = 37.16$  ns,  $df = 33$ ). The linear regression was  $Y = 85.86 + 1.61X$ , where  $Y$  is fork length and  $X$  is scale radius in millimeters. Coefficient of determination ( $r^2 = 0.99$ ) indicated that 99% of the variability in fork length could be attributed to changes in scale radius.

Annulus formation in most West Blue Lake walleye occurs during the last week in June (Glenn MS 1969); therefore, the growth year was the period from the end of June 1969 to the end of June 1970. Length increments were 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  $\Delta L$  was determined by subtracting the distance from the focus to the periphery from the distance from the focus to the outside annulus; (4) The distance between each annulus was determined using the above procedure; (5) Weight at time of capture and last annulus was found using the equation  $\log W = -5.463 + 3.163 \log L$ , where  $W$  = weight in grams and  $L$  = total length (Glenn MS 1969); (6) The difference,  $\Delta G$ , was obtained by subtraction.

Average biomass ( $\bar{B}$ ) of the stock, defined as all members age II<sup>+</sup> and older, was determined using the arithmetic mean of two adjacent biomass estimates (Chapman 1968). This method requires that time intervals between the biomass estimates be short. Production was calculated using  $P = g\bar{B}$  where  $g$  is instantaneous growth in weight.

## Results

Periods of marking, and consequent recapture, were of relatively short duration, and varied from 4 to 12 days in length (Table 1). No fish was recaptured twice.

The only mortality during holding trials occurred during the July 19–27 experiment; one unmarked and two marked fish died, all from different pairs. This holding trial was not held concurrently with a marking and release experiment (Table 1); therefore, we conclude that handling and marking did not produce immediate mortalities among the marked fish used to estimate abundance. This absence of mortality was supported by the lack of carcasses observed during routine shoreline patrols.

Assuming random distribution, the probability of recapture would be independent of the basin of release. Utilizing all three basins of release and recapture, the null hypothesis was accepted ( $\chi^2 = 1.68$  ns,  $df = 4$ ,  $P < .05$ ). Although numbers of recaptures are low, they satisfy the minimum theoretical (expected) frequency of two for adequate chi-square approximation.

The data indicated considerable movement of walleye between basins. No evidence existed to indicate discrete subpopulations in West Blue Lake.

Rates of recapture of walleye aged II–IV were constant between adjacent mark and release periods as well as for the whole experimental period. Results of a  $2 \times 5$  chi-square analysis applied to those recaptured and to those not recaptured indicated that no significant difference existed ( $\chi^2$  between 1.27 and 5.09 for 79–386  $df$ ) either between adjacent periods or throughout the entire experiment.

A total of 390 walleye, age II–VIII years, were identified according to the mesh size used to capture them (Fig. 1). Few age III<sup>+</sup> fish, generally the most vulnerable to the 6.4-cm section, were captured. Consequently, the length frequency of fish captured by this mesh could not be adequately defined. Both the 3.8 and 8.9-cm gillnets captured a wide range of sizes but had relatively narrow ranges of lengths in which capture was most efficient, 230–280 and 400–480 mm, respectively. The 6.4-cm net captured a broad range in sizes and no size seemed particularly vulnerable. A large degree of overlap existed among the three sections of the standard net.

Separation of new recruits from the initial stock was possible from information provided by length frequency distributions, which were determined for all catches and were similar in form. Recruits were a distinct group of small fish on the right of all length

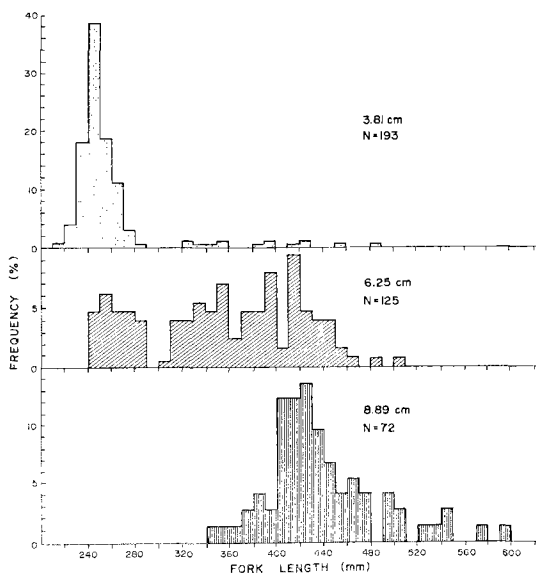


FIG. 1. Length-frequency distributions of walleye captured by 3.81-, 6.35-, and 8.89-cm gillnets in West Blue Lake, 1969 and 1970 (N represents number captured).

frequency curves. Age II<sup>+</sup> fish, nearing age III, also formed a distinct group in terms of length (Fig. 2), but no older groups were identified.

Original abundance, indicated by the May 1969 estimate (Table 2), declined markedly by May 1970 (new recruits excluded). New individuals entering the catchable population in September (N<sub>2</sub>) more than doubled the number originally estimated (N<sub>1</sub>) in May 1969. The maximum number within the stipulated size range occurred in the fall. The unre-cruited May 1969 population was not appreciably altered, but new recruits greatly augmented the initial population. The population including recruits (N<sub>2</sub>) suffered overwinter losses and decreased to a level somewhat greater than that of the previous spring (Table 2).

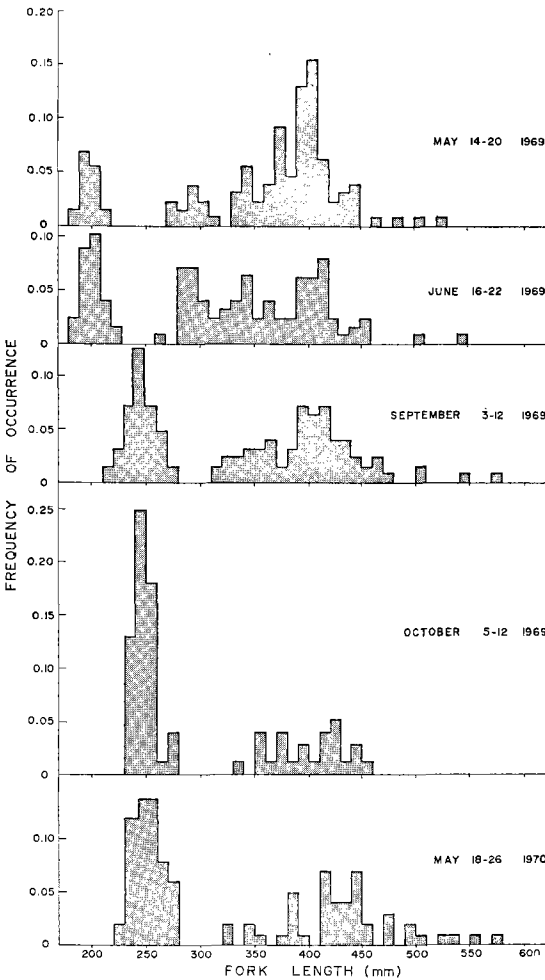


FIG. 2. Length-frequency distributions of walleye in West Blue Lake captured during mark-and-release experiments.

For abundance estimates, bias is approximated by the equation  $100_e MC/N$ . Bias becomes negligible when the product of the two sample sizes ( $M \times C$ ) exceeds the abundance estimate,  $N$ , by a factor of 3 or more (Robson and Regier 1964). In only one case, the May 1970 data, was the ratio of  $MC/N$  small enough (1.97) to introduce a significant bias into the estimate of  $N_1$ ; therefore average estimates can be considered as 0.95  $N$ , demonstrating negligible bias.

Instantaneous daily mortality rates (Table 3), calculated using tag recapture data from adjacent experiments, indicated that mortality was generally low throughout the year, but was greatest between September and October. Mean instantaneous daily mortality was 0.0045 and for the whole year was 1.6225.

Growth, in terms of length increments, was greatest among age II<sup>+</sup> fish followed by fish aged III, IV, and V (Fig. 3). Since individuals older than five years were rare, analysis of growth data was limited to fish

TABLE 2. Estimates of West Blue Lake walleye abundance excluding (N<sub>1</sub>) and including recruitment (N<sub>2</sub>). Standard deviations are in parentheses.

| Period     | N <sub>1</sub> | N <sub>2</sub> |
|------------|----------------|----------------|
| 1969       |                |                |
| May 14-20  | 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)      |
| 1970       |                |                |
| May 18-26  | 819(461)       | 2037(890)      |

TABLE 3. Survival and instantaneous mortality rates of walleye in West Blue Lake. Standard deviations are in parentheses.

| Period     | Survival rate (s)           | Instantaneous mortality (i) per day |
|------------|-----------------------------|-------------------------------------|
| 1969       |                             |                                     |
| May 14-20  | $s_{12} = 0.999(\pm 0.465)$ | $i_{12} = 0.00003$                  |
| June 16-22 | $s_{23} = 0.835(\pm 0.546)$ | $i_{23} = 0.0022$                   |
| Sept. 3-12 | $s_{34} = 0.664(\pm 0.421)$ | $i_{34} = 0.0136$                   |
| Oct. 5-12  | $s_{45} = 0.525(\pm 0.407)$ | $i_{45} = 0.0028$                   |
| 1970       |                             |                                     |
| May 18-22  |                             | mean $i = 0.0045$                   |

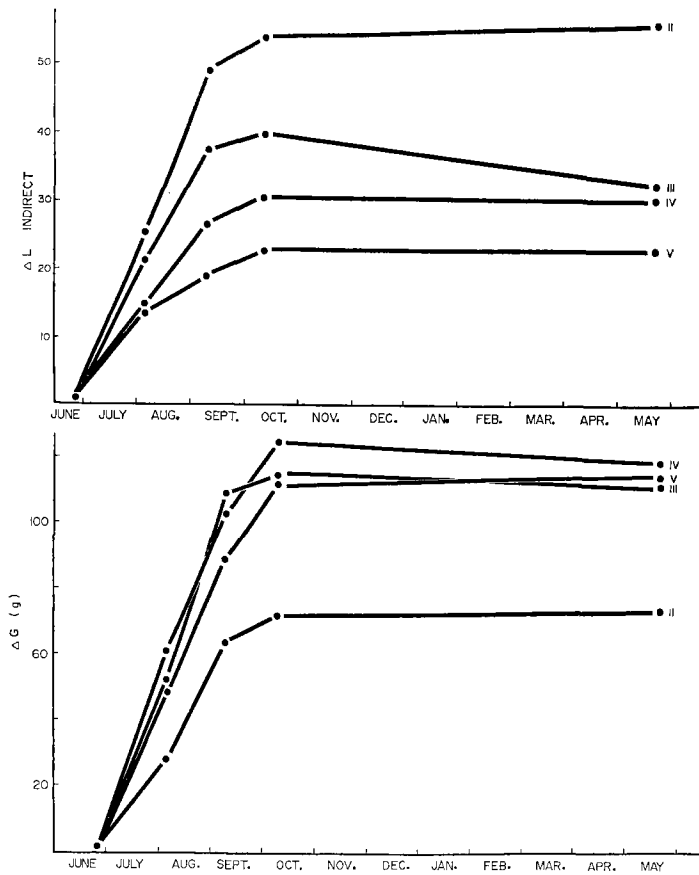


FIG. 3. (top) Length increments ( $\Delta L$ ) of West Blue Lake walleye (ages II, III, IV, and V) during the growth season (from last week in June to 1 year later).

FIG. 4. (bottom) Cumulative growth in walleye ( $\Delta g$ ) in grams wet weight during the growth year 1969–70, in West Blue Lake.

from age II<sup>+</sup>–V<sup>+</sup>. Apparently, most of the annual growth had occurred by September.

Paired “*t*” tests were performed on growth data to determine if fish grew significantly between ice break-up in May and annulus formation in late June 1969. Generally, no differences were found between fork length (except for age IV<sup>+</sup> individuals) in samples of walleye collected from May 14 to 20 and from June 16 to 22, 1969. A significant difference occurred between mean lengths of age IV<sup>+</sup> walleye collected in May and in June, ( $F = 2.26$ ,  $P = 0.05$ ,  $df = 89$ ) but when growth from the last annulus was compared for the two collections, no difference was found ( $F = 0.42$  ns,  $df = 87$ ).

Length increments were greatest among age II fish with respectively smaller values for age III, IV, and V fish. Weight increments were approximately simi-

lar for fish aged III, IV, and V, but lowest for age II walleye (Fig. 4). Greatest increase in weight occurred in age IV walleye.

Lengths at annulus formation, estimated from scale data, indicated that, regardless of time of capture, previous growth history was similar (Table 4). The fork length estimated for annulus I (slightly out of the range considered by the length–scale radius equation) varied only slightly for each brood year, but the difference between brood years was rather large, from 136.5 to 163.8 mm. Brood year length differences persisted in older age-groups.

Instantaneous rates of growth between May and June 1969 were negligible (Table 5), confirming the results of the paired “*t*” tests. Magnitude of growth in relative and instantaneous terms was greatest between annulus formation and August. Growth was

still rapid from August until September. Rates decreased until the period of October 5–12 and approached zero during winter. Relative and instantaneous growth was generally greatest in young fish but decreased with age. Although results indicated that

some spring growth occurred, most growth (70–90%) was completed by September and virtually all growth (80–100%) was accomplished by October.  
Population estimates ( $\hat{N}_1$  and  $\hat{N}_2$ ) were apportioned according to the relative abundance of age-

TABLE 4. Lengths of walleye at annulus formation in West Blue Lake, 1969–70 (N refers to number in each sample).

| Brood year | N   | AGE   |       |       |       |       | Collection date    |
|------------|-----|-------|-------|-------|-------|-------|--------------------|
|            |     | I     | II    | III   | IV    | V     |                    |
| 1967       | 48  | 140.9 |       |       |       |       | May–June 1969      |
|            | 150 | 136.5 | 194.2 |       |       |       | Aug. 1969–May 1970 |
|            | 37  | 137.8 | 199.9 | 259.9 |       |       | Oct. 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 |       | Oct. 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 | Oct. 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 |

TABLE 5. Relative growth in length and weight ( $H_L$  and  $H_G$ , respectively) from previous annuli and instantaneous daily rates of growth in length and weight ( $g_L$  and  $g_G$ , respectively) for walleye, 1969–70.

|            | May<br>14–20<br>1969 | June<br>16–22 | Aug.<br>2–4 | Sept.<br>3–12 | Oct.<br>5–12 | May<br>18–26<br>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               |
| Age I–II   |                      |               |             |               |              |                      |
| $g_L$      | –0.00065             | 0.00335       | 0.00131     | 0.00197       | 0.00020      |                      |
| $g_G$      | –0.00039             | 0.00959       | 0.00943     | 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               |
| Age 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               |
| Age 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               |
| Age 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      |                      |

groups in samples. Age-group IV in May and June, becoming age V in late June, formed the largest portion of the population biomass. Biomass and production estimates for the first age-group were obtained by applying mortality rates calculated for the population (Table 6) to the estimated number of new recruits (2101 individuals) in September. This age-group contributed approximately half of the total production (167 kg) as a result of its abundance and high rate of growth ( $g = 0.6313$ ).

There was a general seasonal decrease in age-group abundance (Table 6). Age-group V in Sep-

tember was the only obvious discrepancy, but because of slow growth they contributed little to production (12 kg). Variable production by age III<sup>+</sup> and VI<sup>+</sup> was caused by their scarcity in the population.

Biomass estimates (excluding estimated age I abundance) were similar in May and June 1969 (703 and 725 kg, respectively). Production between these periods was negative (losses occurred in ages I, II, and III).

Production of walleye flesh occurs from September to October (36 kg) and is essentially zero during the winter months (Table 6). Production in terms of net

TABLE 6. Estimates of biomass (B), mean biomass ( $\bar{B}$ ) and production (P) (kg) for West Blue Lake walleye (the average weight (g) for individuals in each age-group is W and  $g_G$  is the instantaneous growth rate in weight<sup>a</sup>).

|                   |                     | Total for age-groups |                   |        |         |          |           |          |            |
|-------------------|---------------------|----------------------|-------------------|--------|---------|----------|-----------|----------|------------|
|                   |                     |                      | Abundance         | W      | $g_G$   | B        | $\bar{B}$ |          | P          |
| May 14-20<br>1969 | 1090                | I                    | 2566 <sup>c</sup> | 79.8   | -0.0128 | 204.767  |           |          |            |
|                   |                     | II                   | 136               | 267.6  | -0.0172 | 36.394   |           |          |            |
|                   |                     | III                  | 175               | 470.1  | -0.0223 | 82.268   |           |          |            |
|                   |                     | IV                   | 573               | 676.7  | 0.0002  | 387.749  | I         | 205.031  | -2.6244    |
|                   |                     | V                    | 167               | 861.5  | 0.0004  | 143.871  | II        | 76.068   | -1.3084    |
|                   |                     | VI                   | 39                | 1354.4 |         | 52.822   | III       | 108.223  | -2.4132    |
| June 16-22        | 1330                |                      |                   |        |         | 907.871  | IV        | 360.233  | 0.0756     |
|                   |                     | I                    | 2563              | 80.1   | 0.6313  | 205.296  | V         | 107.343  | 0.0043     |
|                   |                     | II                   | 410               | 282.3  | 0.3293  | 115.743  | VI        | 62.356   | 0.0025     |
|                   |                     | III                  | 302               | 444.3  | 0.1989  | 134.179  |           | 919.254  |            |
|                   |                     | IV                   | 467               | 712.4  | 0.1187  | 332.691  |           |          |            |
|                   |                     | V                    | 82                | 863.6  | -       | 70.815   | I         | 264.135  | 166.7484   |
| Sept. 3-12        | (3451) <sup>b</sup> | VI                   | 69                | 1041.9 | -       | 71.891   | II        | 119.111  | 39.2233    |
|                   |                     |                      |                   |        |         | 930.615  | III       | 123.165  | 24.4975    |
|                   |                     | II                   | 2101              | 154.2  | 0.0619  | 323.974  | IV        | 414.626  | 49.2161    |
|                   |                     | III                  | 298               | 411.0  | 0.0143  | 122.478  | V         | 159.406  | 18.9215    |
|                   |                     | IV                   | 193               | 581.1  | 0.0322  | 112.153  | VI        | 71.891   | 8.5335     |
|                   |                     | V                    | 632               | 785.7  | 0.0295  | 496.562  |           | 1152.334 |            |
| Oct. 5-12         | (2331)              | VI                   | 227               | 1092.5 | -       | 247.998  | II        | 259.607  | 16.0970    |
|                   |                     |                      |                   |        |         | 1303.164 | III       | 125.413  | 1.7934     |
|                   |                     | II                   | 1200              | 162.7  | 0.0010  | 195.240  | IV        | 129.773  | 4.1774     |
|                   |                     | III                  | 298               | 430.7  | 0.0093  | 128.349  | V         | 408.988  | 12.0652    |
|                   |                     | IV                   | 223               | 660.6  | 0       | 147.314  | VI        | 145.015  | 4.2779     |
|                   |                     | V                    | 373               | 861.7  | 0       | 321.414  |           | 1068.796 |            |
| May 18-22<br>1970 | (2037)              | VI                   | 37                | 1136.0 | 0       | 42.032   | II        | 188.904  | 0.1870     |
|                   |                     |                      |                   |        |         | 834.349  | III       | 90.732   | 0.8429     |
|                   |                     | II                   | 1118              | 163.3  | -       | 182.569  | IV        | 108.355  | 0          |
|                   |                     | III                  | 150               | 354.1  | -       | 53.115   | V         | 388.931  | 0          |
|                   |                     | IV                   | 111               | 625.2  | -       | 69.397   | VI        | 44.350   | 0          |
|                   |                     | V                    | 521               | 876.1  | -       | 456.448  |           | 821.272  | P=340.3175 |
|                   |                     | VI                   | 37                | 1261.3 | -       | 46.668   |           |          |            |
|                   |                     |                      |                   |        |         | 808.197  |           |          |            |

<sup>a</sup>Instantaneous growth rates are daily rates (Table 5) multiplied by days between the midpoints of adjacent sampling periods.

<sup>b</sup>Estimates in parentheses include recruitment.

<sup>c</sup>Italicized estimates were calculated from survival rates applied to September data (see text).

walleye weight was 340 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.

### Discussion

Accuracy of biomass and production estimates depends on the precision of population, mortality, and growth estimates. Moyle (1950) and Berst (1961) have indicated that gear selectivity produced unrepresentative samples, but Forney (1961) demonstrated that the age structure in samples from gillnet catches was similar to the “real” population as indicated from trap catch data. Our catch data (Fig. 1) showed that total catches, made using the three mesh sizes, samples all fish longer than approximately 25 cm but each mesh size was selective. For instance, the 3.8-cm net sampled small fish more efficiently than either the 6.4- or 8.9-cm nets.

Catches made during the season (Fig. 2) provided some information regarding gear selectivity. The distinct group of small fish on the left of the size frequency distributions increased in average length during the year. The ability of catch data to demonstrate the change in mean length of this group indicated that, at least in this general size range, segments of the population were not unavailable.

Recaptured walleye, although too few for accurate estimates of growth, had grown at the rate calculated (Table 5) from seasonal gillnet catches. Although firm conclusions cannot be made, there is no evidence that gear selectivity was a major source of error. Similarly, the absence of mortality among fish held concurrently with the marking experiments indicated that an immediate differential mortality affecting only marked fish was not a source of error.

Small samples were probably not a serious source of error to population estimates because the estimates were generally demonstrated to be unbiased according to the criterion described by Robson and Regier (1964). Small samples did, however, contribute to wide limits in population abundance estimates (Table 3). Chapman (1968) indicated that the principal deficiency of any production estimate, namely large sampling error, can still inspire confidence when adequate precautions are taken and when production estimates are confined only to intervals between population estimates.

Because of the variety of errors affecting all parameters used to calculate biomass changes and production and because of possible interrelations, some errors may tend to cancel whereas others may be additive — actual biomass estimates and production

may be considerably in error. Nevertheless, it is unlikely that the seasonal changes to be described were not real.

Both Ricker and Foerster (1948) and Alexander and Shetter (1961) described decreases in an unrecruited population similar to the decreases found in West Blue Lake walleye, but our results show that new recruits, age II<sup>+</sup> from spawning in 1967, significantly increased the May 1969 population (Table 2). Their maximum contribution, between 2100 and 2300, was made in September 1969. Considering recruits, the walleye population increased from approximately 1100 in May 1969 to over 3400 in September. During the winter it decreased again to 2037, but the May 1970 population was considerably more abundant than the one present during the previous May. This seasonal cycle in the abundance of fish over 25 cm results from seasonal changes in both growth, as it affects recruitment, and mortality.

Daily mortality rates, applying to the population as a whole, were low. Natural mortality in the West Blue Lake walleye population was generally low and also relatively constant. On the other hand, conversion of the total annual mortality rate to total survival (all age-groups) indicated that from 20 to 37% of the initial population survived to the following May. This represented a large natural loss from the population, far exceeding losses described by Regier et al (MS 1969) for Lake Erie and Forney (1967) for Oneida Lake. Results, however, agree approximately with those presented by Kennedy (1954) for lake trout in Great Slave Lake and for several other unexploited species (Ricker 1947).

Causes for mortality in West Blue Lake are not apparent, but in comparison with other populations (Forney 1961; Carlander 1945) these walleye seem short lived, very few surviving beyond six years of age. No major predators are abundant. Pike, *Esox lucius*, are present but rare.

Glenn (MS 1969) showed that West Blue Lake walleye in 1967–68 gained most of their annual growth in both length and weight during a relatively brief period, between late June and early fall. Similar results were obtained in terms of fork length in this study. Growth increments in weight followed a pattern similar to the pattern described for West Blue Lake walleye by Glenn (MS 1969). Again, most growth in weight was put on during a relatively brief period in summer.

Some growth may occur in walleye in the spring prior to annulus formation. Accepting the apparent maximum amount of spring growth, the data still indicated that the major fraction occurred in summer. Forney (1966) also found that most growth (90%) in walleye fry and fingerlings occurred prior

to September. Hile (1941), too, found little or no growth in walleye in the May-June period. Furthermore, he concluded that weight loss occurred in winter.

Biomass and production data indicated that production was limited to the period between June and October 1969. During the remainder of the year net production was zero or negative. In general, production was maximal when growth was also high. In contrast, biomass changes reflect the seasonal interplay of growth mortality and recruitment.

Our results agree with the findings of Gerking (1962) who concluded that production in Wyland Lake bluegill sunfish occurred only in summer. He also found that production was greatest in the youngest vulnerable year-class, as we did.

The walleye population of West Blue Lake seems rather atypical because of the virtual absence of older fish, an unexpected situation in an unexploited population. This may mean that maximal production takes place in age-groups younger than in other lakes where older fish are relatively more abundant. It may also mean that the ratio of mean annual biomass to production (0.34) is somewhat higher in West Blue Lake than in populations with relatively more old fish, although this is speculative because similar data are lacking for other walleye stocks.

Annual production of walleye flesh in West Blue Lake in 1969-70 was 2.1 kg/ha compared with a mean catch of 2.8 kg/ha (2.5 lb/acre) for the Red Lakes stock in Minnesota during the period 1930-53 (Smith and Krefting 1954). Assuming that the Red Lakes were intensively fished and, therefore, catch approximated production, production in these two very different systems was similar.

Obviously the West Blue Lake population would be most efficiently exploited in late summer and early fall, during the period of rapid production. Conversely, a late spring and early summer fishery might remove fish before they had contributed significantly to new biomass. Other populations in north central North America may have similar production patterns.

We have presented evidence indicating year-to-year differences in abundance. The population of fish over 25 cm in May 1969 was about 1100, but in May 1970 the total was over 2000; seasonal variations were even more pronounced, increasing from 1100 to over 3400 and decreasing again to 2000 within a 12 month period. Biomass changes, although not independent of abundance changes, did not follow a similar pattern. Spring population estimates were different but biomass was similar. Evidently, in this unexploited population, natural regulation of numbers and biomass also occurs within a year and seems to follow a seasonal pattern.

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