

**INTERNATIONAL PACIFIC SALMON
FISHERIES COMMISSION**

PROGRESS REPORT

NO. 3

**SEASONAL AND ANNUAL CHANGES IN
AVAILABILITY OF THE ADULT CRUSTACEAN
PLANKTERS OF SHUSWAP LAKE**

BY

F. J. WARD

COMMISSIONERS

**SENATOR THOMAS REID
A. J. WHITMORE
F. D. MATHERS**

**ROBERT J. SCHOETTLER
ARNIE J. SUOMELA
EDWARD W. ALLEN**

**NEW WESTMINSTER, B.C.
CANADA
1957**

INTERNATIONAL PACIFIC SALMON
FISHERIES COMMISSION

Appointed under a Convention
Between Canada and the United States for the
Protection, Preservation and Extension of
the Sockeye Salmon Fisheries in
the Fraser River System

PROGRESS REPORT

SEASONAL AND ANNUAL CHANGES IN AVAILABILITY
OF THE ADULT CRUSTACEAN PLANKTERS OF
SHUSWAP LAKE

by

F.J. Ward

COMMISSIONERS

Senator Thomas Reid	Robert J. Schoettler
A. J. Whitmore	Arnie J. Suomela
F. D. Mathers	Edward W. Allen

DIRECTOR OF INVESTIGATIONS

Loyd A. Royal

New Westminster, B. C.

Canada
May, 1957

ABSTRACT

Samples of adult crustacean plankters were obtained from Shuswap Lake, B.C. during 1954, 1955 and 1956. The validity of quantitative plankton sampling techniques used during the investigation were examined. Data were analysed for evidence of seasonal and annual variations in availability of adult crustacean plankters.

Rapid, random changes in efficiency of Wisconsin large-type nets when used as vertical samplers did not obscure differences in availability of plankton at different stations. Comparison of catches of a new net to those made by a well-used net showed that the nets maintained constant and equal efficiency for periods of at least three months. The means of groups of hauls made at three different rates of haul did not vary significantly and it was concluded that variability in rate of haul was not a serious source of error. A series of thirty consecutive hauls was divided into five groups. The means of the groups were tested by analysis of variance and it was found that, although there were significant differences between the means, there was no evidence that a progressive decline in the efficiency of the net occurred. Increased accuracy in measurement of relative abundance of adult crustacean zooplankters was obtained by washing samples on a screen before centrifuging. By this process most of the phytoplankton and small zooplankters were removed.

Short-term changes in availability of the adult crustacean component of the plankton occurred on all stations during all three years; however, these rapid changes in availability did not hide seasonal trends or annual differences in availability.

Examination of average catches representative of the same time-interval in each year showed that availability of plankton in 1955 was lower than

either 1954 or 1956 for all stations. These data also showed that consistent differences in availability occurred at the various stations.

Conclusions regarding the effect of the dominant year-class of sockeye on availability of plankton cannot be reached at present, although it can be concluded that low plankton availability does not limit the abundance of sub-dominant and "off year" runs of sockeye.

Average annual differences in water temperatures apparently do not cause annual differences in plankton availability.

Differences in productivity of different parts of the lake were probably caused by differences in dissolved mineral content of the water, which in turn were probably caused by differences in geology of the watersheds of the parts of the lake.

ACKNOWLEDGEMENTS

The author wishes to express his thanks to Prof. Trevor Kincaid, University of Washington for his identification of the Copepoda and to Mr. Rufus W. Kiser, Centralia Junior College, who identified the Cladocera.

TABLE OF CONTENTS

	PAGE
INTRODUCTION	1
SHUSWAP LAKE	2
Watershed	2
Geology	2
Morphometry	2
Mineral Content	4
Pelagic Crustacean Plankters	4
Productivity	4
METHODS OF QUANTITATIVE PLANKTON SAMPLING	6
PROCEDURE IN SAMPLING	10
LABORATORY TREATMENT OF SAMPLES	13
The Efficiency of the Screening Technique	13
The Efficiency of the Centrifuge	15
Mathematical Treatment of the Centrifuged Volumes	15
EFFICIENCY OF GEAR AND METHOD	16
Rapid Changes in Net Efficiency	16
Gradual Changes in Net Efficiency	18
Changes in Rate of Haul	19
Effect of Clogging on Net Efficiency	21
SHORT TERM CHANGES IN AVAILABILITY AT THE SAME STATION	23

	PAGE
SEASONAL CHANGES IN AVAILABILITY	27
ANNUAL CHANGES IN AVAILABILITY	30
AVERAGE ANNUAL AVAILABILITY	33
STATION AVAILABILITY	39
DISCUSSION	43
Annual Differences	43
A. Nutrients	44
B. Water Temperatures	44
C. Predation by Sockeye Salmon	46
Differences in Station Availability	47
Canoe Station	49
Sicamous Station	49
Seymour Station	50
Sorrento Station	50
Narrows Station	50
General Relationships	51
SUMMARY AND CONCLUSIONS	51
LITERATURE CITED	54

SEASONAL AND ANNUAL CHANGES IN AVAILABILITY
OF THE ADULT CRUSTACEAN PLANKTERS OF
SHUSWAP LAKE

INTRODUCTION

Lake productivity has been intensively investigated by many workers both in North America and in Europe. Much of this work, especially in Europe, has had the object of establishing a suitable method for classifying lakes on the basis of their total biological productivity. In fewer instances, the object has been to relate productivity of waters to the population dynamics of a commercially important species of fish. Juday, Rich, Kemmerer and Mann (1932) investigated Karluk Lake on Kodiak Island with the object of evaluating its productivity in relation to sockeye salmon, Oncorhynchus nerka (Walbaum). Ricker (1938a) at Cultus Lake, studied the relationship of the plankton population to the vital statistics of the sockeye salmon population. Langford (1938) sampled plankton in Lake Nipissing and related variations in distribution of plankton to the movements of ciscoes, Leucichthys artedi (Le Sueur).

In the spring of 1954 the International Pacific Salmon Fisheries Commission initiated a plankton sampling program at Shuswap Lake. The purpose of this program was to investigate relationships which might exist between availability of adult crustacean plankters and the vital statistics of the Adams River sockeye population. Fish of this population spend the first year of their lives in Shuswap Lake. During their lacustrine life young sockeye feed almost exclusively on crustacean plankters (Ricker, 1937). The possibility exists, therefore, that availability of this source of food might have a great effect on growth rate and survival of young sockeye.

This paper is concerned with the validity of sampling procedures and with examining the data for evidences of seasonal and annual fluctuations in the availability of adult crustacean plankters. Possible causes of quantitative differences are examined.

SHUSWAP LAKE

Watershed

Shuswap Lake is part of the Thompson River watershed which drains the south-central portion of British Columbia. Shuswap Lake has a watershed area of 6,010 square miles. The streams which drain this area into Shuswap Lake range in size from small temporary creeks to relatively large rivers. These larger streams are of two main types, those which drain other lakes and those which arise in the hills and mountains surrounding the lake. The location of the major streams is shown in Figure 1.

Geology

The rock formations of the area surrounding Shuswap Lake are primarily Pre-Cambrian in origin (Daly, 1915). Granitic masses characteristic of the area at the extremity of Salmon Arm are geologically more recent and are believed to be of Jurassic origin. There is a large formation of limestone on the northwest shore of Salmon Arm. A few smaller formations are present at other widely separated localities. Granite formations make up most of the area surrounding Seymour and Anstey Arms. Most of the district surrounding the Main Arm is composed of greenstones which Daly (1915) suggests are basaltic.

Morphometry

Some physical characteristics of Shuswap Lake are as follows:-

- | | |
|-------------------------|---------------------------|
| (1) Surface Area | - 76,500 acres. |
| (2) Volume | - 15,508,000 acre-feet. |
| (3) Mean Depth | - 202 feet. |
| (4) Maximum Depth | - 530 feet. |
| (5) Mean Elevation | - 1,139 feet. |
| (6) Shore Line | - 194 miles. |
| (7) Shore Development | - 0.20. |
| (8) Secchi-disk Reading | - 33 feet (Aug. 7, 1943). |

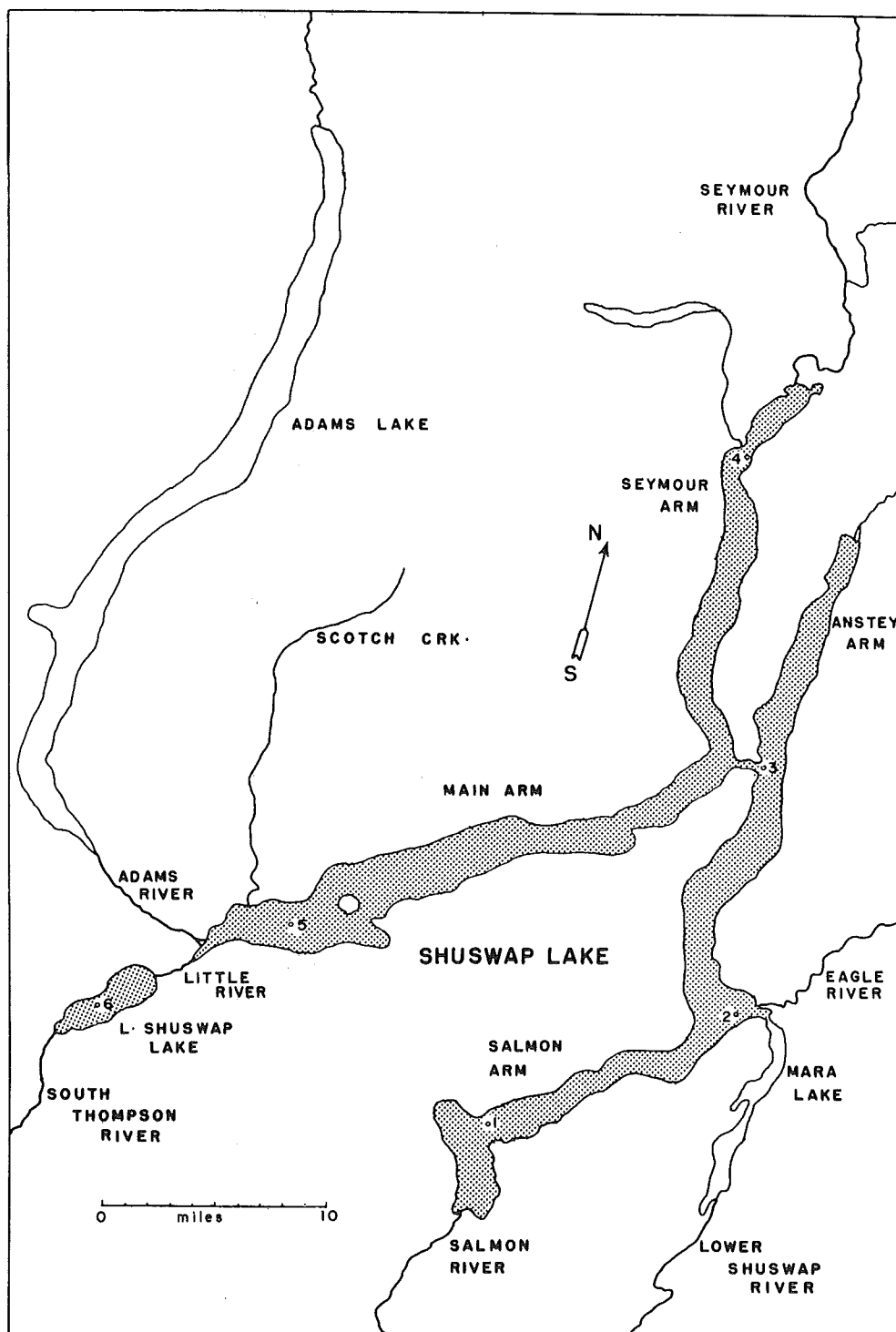


Figure 1. Shuswap Lake.

Mineral Content

Total dissolved solids were measured in samples collected from Shuswap Lake during 1956 by the electrical conductivity method described by Northcote and Larkin (1956). Values ranging from 61 p.p.m. to 112 p.p.m. were obtained.

Pelagic Crustacean Plankters

Clemens, Foerster, Carter and Rawson (1937) reported that relatively few species were represented in plankton catches made in the open waters of Shuswap Lake. This statement was found to be especially true of the crustacean component of the zooplankton of the pelagic region during the Salmon Commission investigation. Two major groups were represented in the catches, the Cladocera and the Copepoda. The following forms were identified by the authorities referred to in the acknowledgements:-

Copepoda: Diaptomus ashlandi Marsh 1893.

Cyclops bicuspidatus Claus 1857.

Epischura nevadensis Lilljeborg 1889.

Cladocera: Daphnia longispina subsp. hyalina mendotae
Birge 1918.

Daphnia longispina subsp. longiremis Sars 1861.

Bosmina longirostris (O. F. Muller) 1848.

Diaphanosoma brachyurum (Lieven) 1848.

Leptodora Kindtii (Focke) 1844.

Productivity

Biological productivity of a lake is controlled by its geographic location, by the waters which flow into it and by its morphometry (Naumann, 1932).

Northcote and Larkin (1956) have subdivided the province into areas where conditions which affect lake productivity are relatively homogeneous.

Shuswap Lake lies in the Columbia Mountain region of their classification. These authors state that lakes in this area exhibit a great range of characteristics. Compared with lakes of the Southern Interior Plateau region, the ten Columbia Mountain lakes which they studied were relatively poor in dissolved nutrients and plankton; however they appeared to be more productive than lakes of the coastal area of the province.

Total dissolved solids have been used by Northcote and Larkin (1956) as an index of lake productivity. They have pointed out that this measure was not always satisfactory when comparing lakes with similar values. In some cases, lakes with a high total dissolved solids content had less plankton than lakes with lower values; but when two lakes with greatly differing dissolved mineral content were compared the lake with the lowest value was the least productive of plankton.

The average total dissolved solids value of thirty-nine lakes of the Southern Interior Plateau region studied by Northcote and Larkin (1956) was 241 p.p.m., whereas the range of values obtained from the Shuswap samples was from 61 p.p.m. to 112 p.p.m. If it can be assumed that most of the Interior Plateau lakes were eutrophic, Shuswap Lake, on the basis of total dissolved solids, is relatively oligotrophic.

Northcote and Larkin (1956) state, "In lakes of relatively high mean depth, say above 150 feet, amounts of plankton are never as high as those which may be found in lakes of low mean depths." Since the mean depth of Shuswap Lake is 202 feet it may be typified as oligotrophic on this basis.

Lake typology may lead to erroneous conclusions concerning the economic importance of lakes. Most large lakes, in temperate climates,

are oligotrophic yet many of them support economically important fisheries.

In British Columbia many large, oligotrophic lakes serve as rearing areas for anadromous sockeye salmon. While biological productivity per unit of volume may be less than in smaller eutrophic lakes, the characteristic of their tributaries and the composition of the biota make these large lakes suitable for reproduction and growth of sockeye.

METHODS OF QUANTITATIVE PLANKTON SAMPLING

No practical method of quantitative plankton sampling proposed to date is entirely satisfactory. The unequal distribution of plankton within a lake and the changes in distribution which can occur within a short time make adequate sampling difficult. The investigator must be clearly aware of the objectives of the research program, the sources of error and the amount of time and effort that can be expended upon the investigation. With these factors in mind it is possible to select or design a sampling program which will give results which will be applicable to the objectives of the program.

Langford (1953), Rawson (1953), and Ricker (1933, 1938 b) have discussed the value of different types of quantitative plankton sampling gear. These writers have suggested that pumps and plankton traps are not as useful as tow-nets of various designs. Ricker (1938 b) has suggested that certain of the larger more active zooplankters are able to avoid plankton traps and pump intakes. Langford (1953) described a new type of pump sampler which has promise of being a valuable addition to the roster of limnological equipment. This gear, however, is not yet in common use. Both Ricker and Rawson are generally agreed that the most

practical quantitative sampling gear is a tow-net of the same or similar design as the large-type Wisconsin tow-net designed by Birge and Juday. Welsh (1948) gives a description of this net. The Clarke-Bumpus sampler (Clarke and Bumpus, 1950), another type of tow-net with an integral current meter, is also coming into use as a quantitative plankton sampler. The current meter measures the amount of water passing through the net and, therefore, allows the catch to be expressed as a quantity per unit volume of water. The Clarke-Bumpus sampler is particularly useful for programs requiring numerous horizontal tows. Several of these nets may be attached to a weighted tow-line at intervals. With this method, samples are collected simultaneously at different depths.

For programs concerned with sampling frequently from different locations on a large lake the Wisconsin net and the Clarke-Bumpus sampler are the most commonly used types of gear. The final choice between these two gears depends upon the type of sampling program that is selected. The standard Clarke-Bumpus sampler is too small to filter sufficient plankton to give readily measurable amounts when it is used as a vertical sampler in oligotrophic lakes. Similarly, the Wisconsin net is difficult to calibrate when used as a horizontal sampler and is therefore much less suitable than Clarke-Bumpus nets.

Ricker (1938 b) has shown conclusively that the mesh-size of the net has a very important bearing upon the efficiency of tow-nets. He found that nets made of No. 20 bolting silk varied greatly in efficiency over extended periods of use and even from haul to haul, while nets with straining areas of No. 10 bolting silk maintained relatively constant efficiency for periods up to a year and a half. Nets constructed with No. 10 bolting silk will not sample the phytoplankton as a whole, nor the

smaller zooplankters quantitatively, but will sample adult crustacean plankters in proportion to their abundance.

Errors characteristic of plankton sampling programs are of two types. The first and most fundamental type may be termed biological error - that produced by the irregular vertical and horizontal distribution of plankton. The second type of error is essentially mechanical and is associated with inadequacies of the sampling gear and the shortcomings of laboratory technique. Obviously, the way to overcome errors arising from irregularity of vertical and horizontal distribution of plankton is to sample at all depths over the whole lake. This is impractical and generally one of two compromises is chosen. One method makes the arbitrary assumption that distribution is relatively constant over fairly wide areas of the lake; if a series of vertical samples are obtained from a number of stations located at widely separated points on the lake, these samples may then be assumed to be representative of the general area from which they were obtained. Wisconsin large-type nets are generally used in such programs. The second method involves sampling horizontally at a number of different depths over a relatively wide area in each portion of the lake. This latter method is theoretically more desirable because samples are representative of a greater volume of water than are those collected from fixed stations. The recent introduction of Clarke-Bumpus samplers have made programs of this type practical.

The object of the study at Shuswap Lake was to determine quantitatively the seasonal and annual variations in the availability of adult crustacean zooplankters. The first requirement necessary to fulfill this objective was to use a sampling gear which would consistently capture adult

cladocerans and copepods in proportion to their abundance. The second requirement was to sample enough areas to insure that a usable measure or index of total availability could be obtained.

An index of abundance does not require that the actual size of the population be known. As long as it is possible to sample the population in proportion to its abundance, the index will serve as a measure of relative abundance and will reflect numerical changes in the population. It was, therefore, not necessary to measure the adult crustacean component of the plankton in terms of abundance per unit volume of water. As stated, Ricker (1938 b) showed that nets constructed of No. 10 bolting silk maintained constant efficiency over long periods of use. Stated in a different manner, nets constructed of this material sample adult crustaceans in proportion to their abundance and continue to do so even after long periods of use. For these reasons nets of No. 10 bolting silk were used throughout the Shuswap Lake plankton study. Wisconsin large-type nets were used to make vertical hauls from a number of different stations. The average catch, measured volumetrically, was used as an index of the availability of plankton at each station at the time of sampling.

The weakest part of the program was the assumption that samples obtained from a station were generally representative of a significant percentage of the total volume of the lake. The program required that seasonal and annual differences should be measured. It was assumed that the lake would respond as a whole to these long term changes and that any differences would be measurable.

PROCEDURE IN SAMPLING

Each net was used for a period of three months and was then replaced by a new net of identical construction. At the end of each sampling day the net was carefully washed in lukewarm water with a mild facial soap and then rinsed thoroughly with plankton-free water.

Sampling was conducted at a number of permanent stations located at representative points on the lake (Figure 1). All hauls were made vertically from a depth of one hundred feet. Rate of haul was approximately three feet per second. During 1954 twelve consecutive hauls were made on each station; however, it was found that the number of hauls per station could be reduced to six without appreciable loss of accuracy; therefore in 1955 and 1956 only six consecutive hauls were made on each station per sampling day.

In 1954 four stations were sampled, Canoe, Sicamous, Narrows and Sorrento, shown in Figure 1 as stations 1, 2, 3, and 5. In 1956, sampling was initiated on a station located at the upper end of Seymour Arm, shown as No. 4. A further sampling station was established on Little Shuswap Lake in the spring of 1956, and is shown as station 6.

One of the requirements of the program was that each station be sampled twice monthly, but weather conditions caused occasional interruptions and ice cover during the winter months prevented sampling. Whenever conditions were suitable samples were taken on all stations on or about the 10th of each month and again about the 25th of each month. Whenever possible all stations were sampled on the same day and between the hours of 8:00 a.m. and 4:00 p.m. During these twice monthly sampling periods no station was ever sampled in the early morning, evening or

during darkness. Table 1 shows the dates on which plankton sampling was conducted in 1954, 1955 and 1956.

In addition to twice-monthly samples, periods of five-day sampling were carried out to measure short term fluctuations in availability of adult crustacean plankters as follows:-

- (1) June 21-25, 1954 (Canoe and Sicamous stations).
- (2) April 21 - May 3, 1955 (five stations).
- (3) July 21-25, 1955 (five stations).
- (4) Jan. 20-24, 1956 (five stations).
- (5) April 30 - May 4, 1956 (six stations).
- (6) June 6-10, 1956 (six stations).
- (7) July 16-20, 1956 (six stations).
- (8) Sept. 17-22, 1956 (six stations).

Other experimental sampling was conducted as follows:-

- (1) Used nets and new nets were compared for possible changes in net efficiency.
- (2) The effect of different rates of haul was measured.
- (3) The effect of clogging of the net pores by phytoplankton was evaluated.

Throughout the whole study bathythermograph records of temperature to a depth of one hundred feet were obtained from each station during the twice monthly sampling tests.

Samples of surface water for total dissolved solids analysis were taken from each station twice monthly commencing on May 22, 1956.

TABLE 1

DATES ON WHICH PLANKTON SAMPLING WAS CONDUCTED AT
SHUSWAP LAKE IN 1954, 1955, 1956.

Month	1954	1955	1956
	Sampling Date (4 Stations)	Sampling Date (5 Stations)	Sampling Date (6 Stations)
Jan.		8 25	20
Feb.		15	
March	21-24		
April	14-16	21 29	30
May	6 27	10-11 24	4 22
June	22	9 24	6 26
July	17	15 22	10 20
Aug.	2 19	10 22	10 22
Sept.	6-8 25	8	10 22
Oct.	12-14 30	10 24	12 22
Nov.	15	24	14 26
Dec.	7-9 23	19	12 22

LABORATORY TREATMENT OF SAMPLES

All samples were washed through a No. 10 bolting silk screen to remove phytoplankton and small zooplankters. It was found that samples attained a constant volume after twenty minutes of centrifuging; therefore residues were centrifuged for this period and then measured in graduated centrifuge tubes.

The investigation was restricted to a study of the adult crustacean component of the zooplankton. Since the nets sampled these forms and only these forms quantitatively, the removal of phytoplankton and small zooplankters increased the accuracy of measurement of availability of the adult crustacean component. It was, therefore, necessary to test the efficiency of the screening technique.

The Efficiency of the Screening Technique

Six samples, taken from the Sorrento station on December 12, 1956, were each diluted to a volume of 50 ml. Each sample was thoroughly agitated and a one ml. subsample was removed. Each subsample was placed in a counting cell and all the zooplankters counted. Filamentous algae and diatoms were abundant so individuals of these forms were counted in only three squares of the twenty-four composing the cell. After all counts were made each sample was washed with a moderate jet of water for five minutes on a No. 10 bolting silk screen which was fixed within a funnel. The residue remaining on the screen was then washed into a graduate and brought to a volume of 50 ml. Each sample was thoroughly agitated and a one ml. subsample removed. Each subsample was placed in the cell and counts were made as described above. The results of this experiment are presented in Table 2.

TABLE 2

COUNTS OF PLANKTON BEFORE AND AFTER WASHING UPON A NUMBER TEN MESH SILK SCREEN.

Haul No.	No. Cyclops	No. Diaptomus	No. Epischura	No. Bosmina	No. Daphnia	No. Nauplii	No. Rotifers	No. Filaments of Algae	No. Diatoms
<u>Before Screening</u>									
1	25	110	0	11	0	37	23	14	191
2	25	92	1	4	1	34	19	17	141
3	35	100	2	6	6	35	17	15	108
4	30	111	2	12	1	26	27	14	141
5	23	113	4	14	2	29	17	9	142
6	21	81	2	13	0	27	13	11	123
\bar{x}	26.5	101.2	1.8	10.0	1.7	31.3	19.3	13.3	141
<u>After Screening</u>									
1	27	87	0	10	1	3	2	0	0
2	33	123	0	14	2	4	1	0	0
3	37	86	1	14	5	4	1	0	0
4	20	104	3	13	1	9	12	1	0
5	19	100	4	12	2	1	2	0	0
6	29	91	5	15	3	7	6	0	0
\bar{x}	27.5	98.5	2.2	13.0	2.3	4.7	4.0	0.17	0

A very small amount of phytoplankton was left in the residue after washing. Conversely, the counts suggest that no appreciable numbers of adult crustaceans passed through the screen during the procedure. Approximately eighty percent of small zooplankters (nauplii and rotifers) were removed from the sample by screening.

The Efficiency of the Centrifuge

Rawson (1953) has pointed out that under certain conditions centrifuged volumes of plankton give erroneous quantitative measures. For instance, gelatinous or spiny forms do not pack down during centrifuging. This source of error did not apply during the Shuswap Lake investigation. The spiny forms were rotifers and diatoms. Both groups were reduced in numbers by screening before centrifuging. No gelatinous crustaceans such as members of the genus Holopedium were found in any of the samples.

Mathematical Treatment of the Centrifuged Volumes

The sampling program was designed so that results could be treated suitably by analysis of variance (Snedecor, 1946). Availability of plankton was found to vary greatly from station to station on the same day and that station means and standard deviations were proportional. To make appropriate comparisons of means it was necessary to transform the data so that the proportionality between means and standard deviations was eliminated (Winsor and Clarke, 1940). This was accomplished by multiplying the centrifuged sample volume by one hundred and transforming to logarithms (base ten).

EFFICIENCY OF GEAR AND METHOD

Mechanical errors may result from changing net efficiencies and varying rates of haul. Gradual changes in net efficiency result in catches which are not comparable over long periods of time whereas rapid, random changes in efficiency, for example from haul to haul, produce catches which are not representative of the true availability of plankton at the time of sampling.

A rapid, progressive decline in net efficiency from haul to haul could also produce catches which would not be comparable to each other and when taken as a whole, would not be representative of plankton abundance.

If slight changes in the rate of haul effected the catches then fluctuations in hauling speed would be a serious source of error to this program. Catches might not be comparable either on a haul to haul basis or from season to season.

Several tests have been designed to investigate these sources of error.

Rapid Changes in Net Efficiency

If variations in catch from haul to haul were great it might be expected that differences in availability between stations would be obscured. Each "F" value presented in Table 3 represents a comparison between stations sampled during the same twice-monthly sampling period. The comparisons in all cases have been made by an analysis of variance. Only twice out of fifty-one tests were there no significant differences in the plankton catches between the stations. Test number 2 made on

TABLE 3

"F" VALUES AND THEIR SIGNIFICANCE OBTAINED BY ANALYSIS OF VARIANCE APPLIED TO REGULAR TWICE-MONTHLY PLANKTON SAMPLES FROM THE STATIONS.

Test No.	1954		1955		1956	
	F	P	F	P	F	P
Jan. 1			8.70	≤ 0.01		
2			0.20	≥ 0.05	20.00	≤ 0.01
Feb. 3						
4			21.25	≤ 0.01		
March 5						
6	120.88	≤ 0.01				
April 7						
8	77.80	≤ 0.01	0.83	≥ 0.05	55.30	≤ 0.01
May 9	9.55	≤ 0.01	71.25	≤ 0.01	74.24	≤ 0.01
10	210.00	≤ 0.01	4.81	≤ 0.01	250.00	≤ 0.01
June 11			33.50	≤ 0.01	12.79	≤ 0.01
12	575.00	≤ 0.01	8.69	≤ 0.01	23.20	≤ 0.01
July 13			29.00	≤ 0.01	104.00	≤ 0.01
14	166.50	≤ 0.01	21.43	≤ 0.01	34.00	≤ 0.01
Aug. 15	142.00	≤ 0.01	18.33	≤ 0.01	6.00	≤ 0.01
16	61.00	≤ 0.01	11.38	≤ 0.01	35.33	≤ 0.01
Sept. 17	138.25	≤ 0.01	22.73	≤ 0.01	126.67	≤ 0.01
18	158.00	≤ 0.01	8.31	≤ 0.01	30.00	≤ 0.01
Oct. 19	15.67	≤ 0.01	41.25	≤ 0.01	18.86	≤ 0.01
20	5.67	≤ 0.01	28.33	≤ 0.01	50.80	≤ 0.01
Nov. 21					20.00	≤ 0.01
22	8.50	≤ 0.01	66.00	≤ 0.01	23.20	≤ 0.01
Dec. 23	98.00	≤ 0.01			41.33	≤ 0.01
24	96.33	≤ 0.01	6.13	≤ 0.01	40.00	≤ 0.01

January 25, 1955 and test number 8 made on April 29, 1955 both indicated that differences between stations were too small to be detected by the sampling method and procedures of analysis used in this investigation. In all other tests variations in volumes of zooplankton obtained from haul to haul did not obscure station differences.

The results of these tests indicate that short term random changes, although they may be a source of some inaccuracy, do not obscure station differences in availability.

Gradual Changes in Net Efficiency

Ricker (1938 b) has stated that efficiency of nets fitted with straining cones of No. 10 bolting silk does not vary significantly over long periods of continuous use; however, since the Shuswap investigation required intensive sampling, it was decided to re-examine this question. During the spring of 1956, catches made with a net three months old were compared with those made with a new net. Before use, both nets were thoroughly washed and rinsed. Sampling was conducted on three stations on May 22 and 23. Both nets were hauled simultaneously six times on each station from a depth of one hundred feet. Collecting buckets were exchanged between each haul so that the nets alternated buckets. Both nets were hauled at the same rate during a simultaneous haul. Table 4 presents the results of an analysis of variance, multiple classification, (Snedecor, 1946).

TABLE 4

"F" VALUES AND THEIR SIGNIFICANCE OBTAINED FROM AN ANALYSIS OF VARIANCE - MULTIPLE CLASSIFICATION - APPLIED TO VOLUMETRIC SAMPLES TAKEN AT THREE STATIONS BY SIMULTANEOUSLY SAMPLING WITH A USED NET AND A NEW NET.

"F" nets	P nets	"F" stations	P	"F" int.	P int.
0.044	\triangleright <u>0.05</u>	177.61	\triangleleft 0.01	0.435	\triangleright <u>0.05</u>

These results show that there were no significant differences between volumes of zooplankton obtained by each net on the same station although there were highly significant differences in catches from station to station. The results of this test show that the efficiency of a well-used net is very similar to that of a new net. By sampling on three different stations it was possible to compare the efficiencies of the two nets at different levels of plankton availability. The mean \log_{10} of centrifuged, corrected volume of zooplankton on the Canoe station was 2.26 with the used net and 2.22 with the new net whereas on the Sorrento and Little Shuswap stations respectively the means were 1.30 - used, 1.36 - new and 1.18 - used, 1.12 - new. It is therefore valid to say that efficiencies of nets were not significantly different at either high or low levels of zooplankton availability.

Changes in Rate of Haul

It has been demonstrated previously that small mechanical sources of error do not obscure differences in the availability of zooplankton from station to station during a particular sampling day. However, the

possibility that the most obvious of these errors - variations in the rate of haul - might make comparisons between catches made days or months apart invalid must also be examined.

On the Sorrento station on May 25, 1956, six hauls were made at an average rate of 1.31 feet per sec. (0.40 m/sec.). Six more hauls were made immediately after the first six at an average rate of 3.03 feet per sec. (0.92 m/sec.), the standard rate of haul for the whole investigation. A third series of six hauls was made at an average rate of 4.76 feet per sec. (1.45 m/sec.). This rate of haul was much greater than any attained during normal sampling. All hauls were made vertically from a depth of one hundred feet and the whole test was completed within an hour.

Before the data were treated by analysis of variance, Bartlett's test for homogeneity of variance was applied (Snedecor, 1946). It was not necessary to correct the centrifuged volumes and transform them into logarithmic values because the variances and means were not correlated. The probability of the chi-square, obtained from the test for homogeneity of variance, was between 0.30 and 0.50; it was therefore concluded that the variances were sufficiently similar to allow use of analysis of variance to test the significance of differences in sample means.

The "F" value obtained from the analysis of variance was 2.50 with a $P > 0.05$. It was concluded that there were no significant differences between the three groups of centrifuged volumes of zooplankton. Wide variations in rate of haul of nets result in similar catches.

Effect of Clogging on Net Efficiency

Abundant phytoplankton will reduce straining efficiency of a plankton net by clogging pores of the net so that more and more water "boils" out of the net and less and less passes through the meshes. When fine-meshed nets are used to sample eutrophic lakes their value as quantitative samplers is restricted by this source of error. When relatively coarse-meshed nets are used in oligotrophic lakes, clogging by phytoplankton may never occur.

During the Shuswap Lake investigation No. 10 bolting silk nets were used. It has been demonstrated that efficiency of No. 10 nets does not vary significantly over long periods and that variations from haul to haul do not obscure station differences. This still does not eliminate the possibility that the net may be less efficient after a long series of hauls than it was at the beginning. An experiment was carried out at the Little Shuswap Lake station on October 31, 1956 to investigate the problem of declining net efficiency. Twenty-four consecutive hauls were made. The net was then thoroughly washed in plankton-free water, after which six more consecutive hauls were made. The whole series was then divided up into five groups of six consecutive hauls. Table 5 shows the mean centrifuged volumes of adult crustacean zooplankters of each group of catches and standard deviations of these means. Volumes were measured in millilitres.

TABLE 5

MEANS AND STANDARD DEVIATIONS OF FIVE GROUPS OF VOLUMETRIC
SAMPLES TAKEN FROM THE LITTLE SHUSWAP LAKE STATION.

	1st Group	2nd Group	3rd Group	4th Group	5th Group (Clean net)
n	6	6	6	6	6
\bar{x}	0.48 ml.	0.28 ml.	0.38 ml.	0.38 ml.	0.37 ml.
S.D.	0.044 ml.	0.077 ml.	0.044 ml.	0.063 ml.	0.089 ml.

Bartlett's test for homogeneity of variance (Snedecor, 1946) was applied to these groups of data. A chi-square value of 2.81 was obtained which corresponded to the 0.60 level of probability. This suggested that variances of the groups of samples were sufficiently homogeneous to allow an analysis of variance. The analysis of variance gave an "F" ratio of 5.75. This value had a probability of less than 0.01. It is concluded that there were significant differences in means. It will be noted that the mean of the second group of samples was considerably lower than the other means. This is contrary to what one would expect if the efficiency of the net was declining steadily as a result of clogging. It might be expected that the fourth group of hauls would have the smallest mean and that the fifth group, made with a clean net, would have a mean similar to that of the first six samples.

There are two logical explanations for the observed differences. They may have been caused by random variations in net efficiency or random changes in availability of plankton. Little Shuswap Lake has a high flushing rate and it is possible that "clouds" of plankton of different densities were moving past the anchored boat during the test. There is no

evidence to suggest that any progressive clogging of the net pores took place during the experiment.

SHORT TERM CHANGES IN AVAILABILITY AT THE SAME STATION

Short-term variations in the availability of plankton at the stations, if they occurred, could mask the presence of long-term changes. If great daily fluctuations occurred these fluctuations might obscure any general seasonal trends or any annual differences that might have existed. In a situation of this type sampling, even though quantitative, would measure only daily availability of adult crustacean plankters at each station.

To detect the presence of rapid, short-term fluctuations, series of daily samples were collected from a number of stations. Whenever conditions permitted, these daily samples were taken from all stations for five consecutive days. Catches on each station, each day, were treated by analysis of variance. During 1954 only two stations were sampled consecutively for five days. These two stations were the Canoe and Sicamous stations, which were sampled consecutively from June 21 to June 25 inclusive. From data collected on the Canoe station an "F" value of 378 was calculated. For this value, P was less than 0.01. From the Sicamous data "F" was 655 and P was less than 0.01. These results lead to the conclusion that significant differences in daily availability of adult crustacean zooplankton occurred.

Three periods of frequent sampling were conducted in 1955. From April 21 to May 3 five stations were sampled and from July 21 to July 25 inclusive the same five stations were again sampled. The January 20-24, 1956 period has also been included with the 1955 data. During the

April-May test it was not possible to sample each station each day for five days. The Canoe and Sicamous stations were sampled for five consecutive days beginning on April 29 and ending on May 3. The other three stations were each sampled five times during the period April 21 to April 29 inclusive. Data collected during the April-May, July and January, 1956 tests were treated by analysis of variance. The results of these analyses are presented in Table 6.

During the April-May test only the Sicamous station showed any significant variation in the volumes taken from day to day during the test. The catches from the other four stations did not vary significantly from day to day during the test. Similarly, during the July test only the Canoe station exhibited any significant daily fluctuations in availability. During the January, 1956, test two stations showed no significant daily variations in availability.

During 1956 the number of five-day tests was increased. The data were treated by the same method used for analysis of the 1954 and 1955 data. The results of these treatments are presented in Table 7.

These tests indicate that significant differences in the catches from day to day occur in all seasons, on all stations, and are not uncommon.

Weather conditions, and local edaphic factors probably cause these daily fluctuations in availability on different stations. When conditions for reproduction and growth are suitable "blooms" of plankton occur. Under these conditions the horizontal distribution of plankton density may be shifted by water movements produced by winds causing the availability of plankton to vary from day to day.

TABLE 6

"F" VALUES AND THEIR SIGNIFICANCE OBTAINED BY ANALYSIS OF VARIANCE APPLIED TO VOLUMETRIC SAMPLES TAKEN AT FIVE STATIONS DURING PERIODS OF FREQUENT SAMPLING IN 1955.

Sampling period	Canoe Station		Sicamous Station		Narrows Station		Seymour Station		Sorrento Station	
	"F" days	P	"F" days	P	"F" days	P	"F" days	P	"F" days	P
Apr. 21 - May 3	1.15	≥ 0.05	9.11	< 0.01	4.67	≥ 0.01	1.64	≥ 0.05	0.93	≥ 0.05
July 21 - July 25	9.67	< 0.01	2.69	≥ 0.05	3.75	≥ 0.01	3.33	≥ 0.01	3.56	≥ 0.01
Jan. 20 - Jan. 24 1956	0.23	≥ 0.05	2.50	≥ 0.05	8.75	< 0.01	8.20	< 0.01	7.88	< 0.01

TABLE 7

"F" VALUES AND THEIR SIGNIFICANCE OBTAINED BY ANALYSIS OF VARIANCE APPLIED TO VOLUMETRIC SAMPLES TAKEN AT SIX STATIONS DURING PERIODS OF FIVE-DAY CONSECUTIVE SAMPLING IN 1956.

Sampling Period	Canoe Station		Sicamous Station		Narrows Station		Seymour Station		Sorrento Station		Little Shuswap Station	
	"F" days	P	"F" days	P	"F" days	P	"F" days	P	"F" days	P	"F" days	P
Apr. 30 - May 4	22.50	<0.01	72.67	<0.01	12.81	<0.01	9.58	<0.01	3.05	<u>>0.01</u>	12.20	<0.01
June 6 - June 10	300.00	<0.01	2.93	<u>>0.01</u>	123.00	<0.01	35.00	<0.01	69.00	<0.01	12.50	<0.01
July 16 - July 20	6.25	<0.01	5.00	<0.01	14.60	<0.01	11.67	<0.01	12.50	<0.01	12.54	<0.01
Sept. 17 - Sept. 21	8.00	<0.01	0.02	<u>>0.05</u>	2.50	<u>>0.05</u>	60.00	<0.01	8.33	<0.01	18.00	<0.01

These fluctuations in daily availability were potentially an important source of error to this program and it was necessary to determine whether or not they masked seasonal and annual differences in plankton availability.

SEASONAL CHANGES IN AVAILABILITY

The hypothesis that short-term fluctuations in zooplankton availability might obscure any seasonal trends in availability was tested by analysis of variance, multiple classification. This test was applied to catches made during seasonal periods of five-day sampling conducted in 1955 and 1956. The results of the comparison for 1955 are presented in Table 8. Again the January 20-24, 1956 test has been included with the 1955 data.

On all stations F ratios for seasons were significant but for days, with the exception of the Narrows station, the F ratios indicated that there was no significant daily variation in plankton availability regardless of season.

Five-day consecutive test-periods made in 1956 were also compared using the same hypothesis. The pertinent results of the analysis of variance, multiple classification, are presented in Table 9.

The F ratios for seasons for all stations were significant as were the F ratios for days. Although daily variability in plankton availability was greater in 1956 than in 1954, seasonal differences in availability were not obscured.

Unfortunately, as stated previously, only one period of frequent sampling was conducted in 1954 and only on two stations; therefore it was not possible to determine if seasonal trends could have been hidden by

TABLE 8

THE SIGNIFICANCE OF "F SEASONS" AND "F DAYS" OBTAINED BY COMPARING VOLUMETRIC SAMPLES
TAKEN DURING THREE FIVE-DAY TESTS CONDUCTED AT DIFFERENT SEASONS IN 1955.

Source of Variation	Canoe		Sicamous		Narrows		Seymour		Sorrento	
	F	P	F	P	F	P	F	P	F	P
Seasons	258.84	<0.01	66.07	<0.01	21.67	<0.01	55.45	<0.01	81.82	<0.01
Days	0.62	>0.05	3.43	>0.01	10.33	<0.01	2.55	>0.01	1.82	>0.05

TABLE 9

THE SIGNIFICANCE OF "F" SEASONS " AND "F" DAYS " OBTAINED BY COMPARING VOLUMETRIC SAMPLES
TAKEN DURING FOUR FIVE-DAY TESTS CONDUCTED IN 1956.

Source of Variation	Canoe		Sicamous		Narrows		Seymour		Sorrento		L. Shuswap	
	F	P	F	P	F	P	F	P	F	P	F	P
Seasons	795.75	<0.01	608.00	<0.01	673.28	<0.01	878.60	<0.01	1177.57	<0.01	599.53	<0.01
Days	13.75	<0.01	52.60	<0.01	4.00	<0.01	13.60	<0.01	12.14	<0.01	12.33	<0.01

daily fluctuations. It is improbable, in view of the results obtained in 1955 and 1956, that this could have occurred.

It is concluded that although the availability of adult crustacean zooplankton does sometimes fluctuate significantly from day-to-day these fluctuations do not obscure seasonal trends in availability.

ANNUAL CHANGES IN AVAILABILITY

Annual differences in availability of zooplankton during comparable calendar periods in two or more years might be obscured by short-term fluctuations within the periods. This hypothesis has been tested by comparing equivalent periods of frequent sampling in different years by an analysis of variance - multiple classification. The results of the April - May tests, 1955 and 1956, are presented in Table 10. The Little Shuswap Lake station was not included because this station was not sampled in 1955.

The "F" values were all significant and suggest that plankton availability differed greatly during the two periods even though, in most cases, there were significant daily fluctuations in plankton availability at the stations.

Only one period representing sampling on only two stations was available for comparison in 1954. These data, collected on the Canoe and Sicamous stations from June 21-25, were compared to samples obtained at the Canoe and Sicamous stations from June 6-10, 1956. Results of analysis of variance are shown in Table 11.

The "F" values were again significant and indicate that availability was greatly different during the two sampling periods

TABLE 10

THE SIGNIFICANCE OF "F_{YEARS}" AND "F_{DAYS}" OBTAINED BY COMPARING VOLUMETRIC SAMPLES TAKEN DURING THE SAMPLING PERIODS APRIL 21 - MAY 3, 1955 AND APRIL 30 - MAY 4, 1956 AT FIVE STATIONS.

Source of Variation	Canoe		Sicamous		Narrows		Seymour		Sorrento	
	F	P	F	P	F	P	F	P	F	P
Years	22.50	<0.01	35.00	<0.01	158.13	<0.01	215.71	<0.01	461.87	<0.01
Days	0.67	> <u>0.05</u>	27.50	<0.01	14.88	<0.01	7.86	<0.01	1.39	> <u>0.05</u>

TABLE 11

THE SIGNIFICANCE OF " F_{YEARS} " AND " F_{DAYS} " OBTAINED BY COMPARING
 VOLUMETRIC SAMPLES TAKEN DURING THE SAMPLING PERIODS
 JUNE 21-25, 1954 AND JUNE 6-10, 1956 AT TWO STATIONS.

Source of Variation	Canoe		Sicamous	
	F	P	F	P
Years	335.00	< 0.01	534.00	< 0.01
Days	55.00	< 0.01	22.40	< 0.01

compared although significant daily fluctuations occurred.

Consecutive sampling was conducted on five stations from July 21-25 inclusive in 1955 and on six stations from July 16-20 inclusive in 1956. These periods were also compared and the results are presented in Table 12. The data collected from the Little Shuswap station has again been omitted.

With the exception of the Canoe station differences in availability between years on all stations were significant. Significant daily fluctuations occurred on some of the stations. In the case of the Canoe station availability of plankton was such that daily variability and variation from haul to haul obscured any annual differences in availability.

It was concluded that the method of sampling was sufficiently accurate to detect annual differences in availability.

AVERAGE ANNUAL AVAILABILITY OF ADULT CRUSTACEAN PLANKTERS

It has been demonstrated that short-term fluctuations did not in general obscure annual differences in the availability of adult crustaceans. This finding leads to the consideration of average availability on each station for the three years studied.

To obtain the data necessary to make this study, each month of the year was divided into two parts. Samples collected on or before the fifteenth of each month were included in the first division of the month: those taken after the fifteenth of each month were included in the second division of the month. This procedure assumes that samples collected on May 7, 1954, for example, were representative of the period May 1 to May 15 inclusive.

TABLE 12

THE SIGNIFICANCE OF "F_{YEARS}" AND "F_{DAYS}" OBTAINED BY COMPARING VOLUMETRIC SAMPLES TAKEN DURING THE SAMPLING PERIODS JULY 21-25, 1955 AND JULY 16-20, 1956 AT FIVE STATIONS.

Source of Variation	Canoe		Sicamous		Narrows		Seymour		Sorrento	
	F	P	F	P	F	P	F	P	F	P
Years	0	≥ 0.05	126.87	< 0.01	205.71	< 0.01	125.00	< 0.01	115.00	< 0.01
Days	12.60	< 0.01	1.25	≥ 0.05	11.43	< 0.01	5.00	< 0.01	2.50	≥ 0.05

Since sampling was not possible during certain portions of the year because of weather conditions, comparable annual averages could not be obtained. The inclusion of sample volumes taken during January and February of one year would reduce the mean annual value in comparison to a year in which no data were available for January and February. Comparisons were, therefore, made only for comparable periods during the three years. Ten of these comparable samples were available from each year on four stations. The Seymour station was not sampled during 1954 so data were available only for 1955 and 1956.

These comparable semi-monthly periods extend from May 1 to October 31. Samples were lacking during the June 1 to 15 period and July 16 to 31 period in 1954 so the data collected during these two periods in 1955 and 1956 have also been omitted.

The additional assumption has been made that samples collected during a semi-monthly period of one year are comparable with those collected during the same semi-monthly period in other years. If plankton availability is controlled by environmental conditions this assumption is unlikely to be true. Plankton availability under this assumption would be related to growing conditions and not to time; however, the time-interval under consideration includes the period of population increase after the winter minimum, the summer maximum, and the fall decline, for each of the three years. In this situation the three time-intervals are comparable and an average volume of plankton based on samples taken at periods throughout each time-interval is likely to be representative of average plankton availability for each time-interval.

Table 13 presents the mean centrifuged volume of adult crustacean zooplankters obtained during each annual time-interval on each station. Limits at the 0.05 level of probability have been placed on these means by a method described by Snedecor (1946, page 462). The variances for the means of each set of hauls which composed the semi-monthly plankton sampling period were calculated. A weighted variance for the time-interval was then obtained by averaging the period variances. The standard error was calculated from this variance in the usual manner and was used to place fiducial limits on the time-interval mean.

Table 13 and Figure 2 shows that availability of adult crustacean zooplankters on all stations in 1955 was considerably lower than availability in 1954 and 1956. With the exception of the Narrows station, availability was greater in 1954 than in 1956. An inversion in the relationship between 1954 and 1956 occurred at this station and the mean volume obtained in 1956 was considerably greater than that obtained in 1954. Although the Sorrento, 1954, value was greater than that obtained in 1956, the limits on the means overlap to such an extent that it is doubtful if the slight difference is significant. The values obtained on the Canoe and Sicamous stations were clearly greater in 1954 than in 1956. The inference drawn from the 1954 and 1956 data is that there is some indication that availability was greater in 1954 than in 1956 but not greatly so and that no definite conclusions can be made about differences in availability between these two years. No such reticence is required in discussing the 1955 means. It is concluded that overall plankton availability in 1955 was from one-half to two-thirds as great as in either 1954 or 1956.

TABLE 13

MEAN CENTRIFUGED VOLUMES OF ADULT CRUSTACEAN PLANKTERS
OBTAINED FROM THE STATIONS DURING A COMPARABLE PERIOD
IN EACH YEAR (FIDUCIAL LIMITS SHOWN).

Station	Mean centrifuged Volume of Zooplankton (ml)		
	1954	1955	1956
Canoe	1.43 ± 0.03	0.81 ± 0.06	1.19 ± 0.05
Sicamous	1.09 ± 0.02	0.53 ± 0.03	0.98 ± 0.06
Narrows	0.64 ± 0.03	0.37 ± 0.03	0.77 ± 0.04
Seymour		0.31 ± 0.02	0.64 ± 0.03
Sorrento	0.77 ± 0.02	0.33 ± 0.02	0.75 ± 0.04

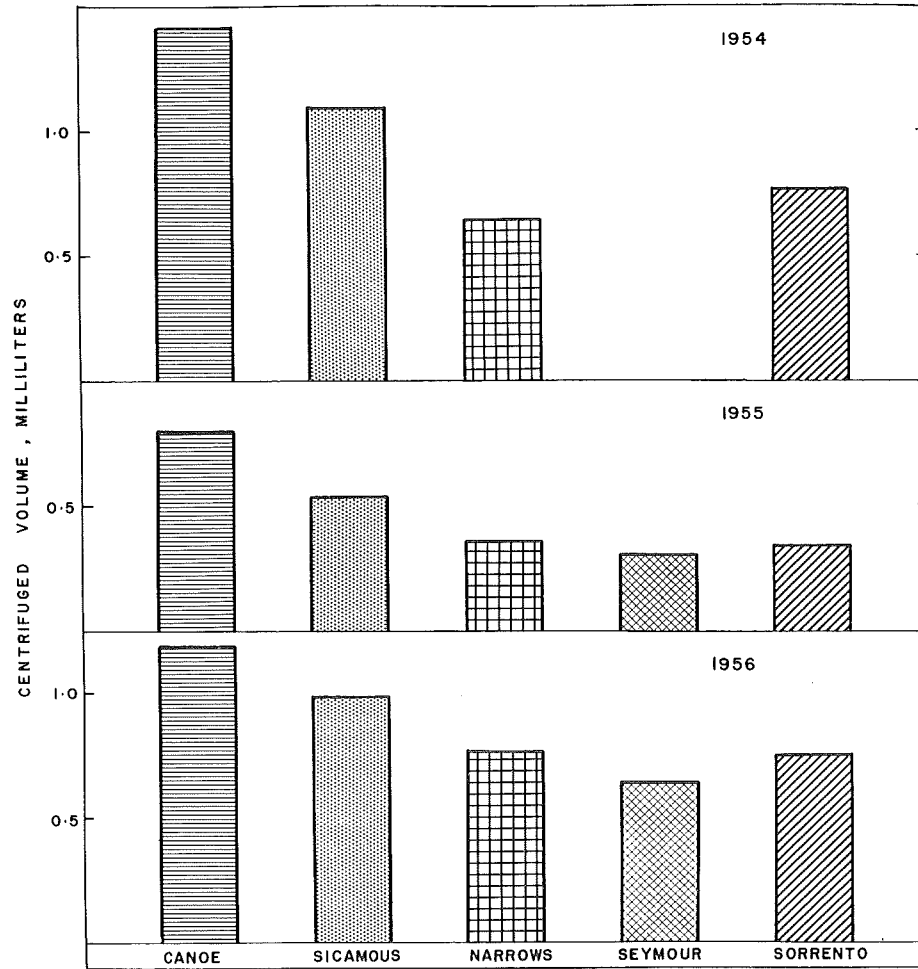


Figure 2. Average annual availability of adult crustacean plankters at the stations.

STATION AVAILABILITY

There were obvious differences in availability between stations (Table 13 and Figure 2). The consistency of the relationship between stations is particularly noteworthy. In 1954, the Canoe station yielded the greatest mean volume of centrifuged crustacean plankton, followed by the Sicamous, Sorrento and Narrows stations in that order. In 1955 the Canoe station had the greatest yield followed by the Sicamous station (as in 1954), but the Narrows station yielded slightly more plankton than the Sorrento station, thus reversing the 1954 order. The Seymour station was sampled consistently in 1955 and had the lowest mean volume of any of the stations. In 1956, the 1955 order was duplicated for all stations.

Not only were the relationships between the stations remarkably consistent in all years, they were consistent when great differences in annual availability occurred. For example, the mean volume obtained from the Sicamous station for the 1955 time-interval was 0.53 ml. as compared to the 1954 value of 1.09 ml., yet in both years this station ranked second in order of magnitude of mean catches.

These differences in availability between stations are caused either by a large number of consistent, localized populations or by area differences in productivity. If each locality has a characteristic population density, then these differences between stations are of no particular significance; however, if differences in station catches are indicative of differences in population density in major portions of the lake one is led to the conclusion that productivity is different

and furthermore consistently different in the major divisions of the lake. To examine these two possibilities more critically, it seems doubtful that closely associated localities would exhibit consistent differences in plankton availability. Wind produces water currents which shift water masses containing plankton from one locality to another (Mortimer, 1952). In this case sampling in one locality would not be on a fixed population but on a number of populations. If sampling were random and quantitative, catches would reveal whatever differences existed between these populations. If these localized populations were randomly distributed throughout the whole lake and no portion of the lake was more productive than another it is likely that water movements would bring about randomly distributed catches on all stations with similar mean catches on all stations. Unless water movements can be disregarded the hypothesis of a large number of localized populations of plankton does not seem tenable.

It seems much more reasonable to account for station differences by postulating that there are differences in productivity between major divisions of the lake. Figure 1 shows that Shuswap Lake is composed of two major divisions joined by a narrow body of water (Cinnemousun Narrows) which has a maximum depth of less than a hundred feet. Differences in morphometric characters in these two divisions of the lake could result in differences in productivity. The physical characteristics of the arms themselves could also result in differences in productivity. The chemical composition and temperature of the water flowing into the arms might also lead to differences in plankton

production which would be revealed by quantitative sampling.

When the data in Table 14 were treated by analysis of multiple regression (Snedecor, 1946) neither the regression of plankton (Y) on total dissolved solids (X_1) nor plankton on water temperature (X_2) were significant. The multiple correlation coefficient, $R = 0.956$, was not significant; however the correlation coefficient of plankton and total dissolved solids was 0.946, whereas the correlation coefficient of plankton and water temperature was 0.554. When the temperature variable was eliminated from the analysis and the data were treated as a single correlation of plankton and total dissolved solids, $r = 0.946$, which was significant beyond the 0.01 level of probability. Conversely, the correlation of plankton and water temperature, when treated similarly, was not significant.

Assuming that station differences were caused by differences in water temperatures and total dissolved solids it was evident that total dissolved solids was the major contributing factor to these station differences, although it is likely that extreme water temperatures effectively control the upper and lower limits of zooplankton abundance. Pratt (1943) showed that cultures of Daphnia magna reared in the laboratory attained different equilibrium populations when subjected to different temperatures.

No relationship was detected between plankton availability and morphometric differences such as mean depth.

TABLE 14

TOTAL DISSOLVED SOLIDS, MEAN VOLUMES OF CENTRIFUGED CRUSTACEAN PLANKTON AND MEAN WATER TEMPERATURES AT THE STATIONS DURING COMPARABLE PERIODS IN 1956.

Station	Total Dissolved Solids (p.p.m.)	Mean Volume of Zooplankton (ml.)	Mean Water Temperature (°F)
Canoe	96	1.14	63
Sicamous	88	0.89	62
Narrows	78	0.84	62
Seymour	70	0.69	61
Sorrento	74	0.81	58

DISCUSSION

Annual Differences

Annual fluctuations in the numbers of several species of both phytoplankters and zooplankters have been observed by limnologists. Southern and Gardiner (1926) found that numbers of Daphnia longispina, Bosmina longirostris, Bosmina coregoni, and Diaptomus gracilis occurring in Lough Derg fluctuated annually. Ricker (1938 a) showed that annual fluctuations in the abundance of several species of both phytoplankters and zooplankters occurred at Cultus Lake. Annual differences in the phytoplankton crop from western Lake Erie were demonstrated by Verduin (1951). Rawson (1956) observed that annual variations in numbers of net plankton organisms occurred in Great Slave Lake. He further demonstrated that availability of Entomostraca varied annually.

Although it has been shown that seasonal and annual differences in plankton availability do occur, causes of these fluctuations are not easily demonstrated.

As phytoplankton has been considered to be the base of the food-chain, factors which control and limit plant abundance have been thought to be of prime importance in determining biological productivity in aquatic environments. McCombie (1953) suggested that phytoplankton cycles were basically controlled by water temperatures which in turn were controlled by intensity of solar radiation. He also stated that effects of this control might be obscured by local weather and/or nutrient supply. Pearsall (1932) presented evidence which indicated that production of phytoplankton was differentially affected by different ions. Verduin (1951) believed that differences between the 1949 and 1950 phytoplankton crops in western Lake Erie could have been caused by cloudy

weather and more turbid water in 1950. Fleming (1939) on theoretical grounds decided that grazing by zooplankters might have an important effect on the abundance of marine diatoms.

Data which, after analysis, might expose the causes of annual fluctuations in abundance of adult crustacean zooplankters in Shuswap Lake were not sufficiently complete for definite conclusions to be reached; however, three possible factors acting independently or in concert might have caused the observed fluctuations.

A. Nutrients

A lack of nutrients during the 1955 season might have resulted in a failure of the phytoplankton crop which in turn limited the population of adult crustaceans. Borecky (1956) showed that abundance of Cladocera was related to concentration of nutrients. This possibility cannot be examined at Shuswap Lake because no measures of the phytoplankton crop were taken nor were samples of water analysed for dissolved nutrients in either 1954 or 1955.

B. Water Temperatures

Comprehensive water temperature data were collected each year. If water temperatures were consistently lower in 1955 than in 1954 or 1956 it might be argued that low water temperatures limited the ultimate size of the plankton population. Average water temperatures were calculated for the same time-interval as was used to obtain the mean plankton values presented in Table 13.

Temperatures tended to be uniformly low even in summer below a depth of fifty feet regardless of station or year; therefore the average

temperatures from the surface to thirty feet were used to compare stations and years. It was believed that by averaging temperatures to a depth of thirty feet, the effects of diurnal temperature changes would be eliminated. Table 15 shows the mean seasonal station temperatures obtained during comparable periods in all three years.

TABLE 15

AVERAGE WATER TEMPERATURES OBTAINED FROM THE STATIONS
DURING COMPARABLE PERIODS IN 1954, 1955 AND 1956.

Station	Temperature (°F)		
	1954	1955	1956
Canoe	56	58	62
Sicamous	56	58	62
Narrows	56	58	62
Sorrento	56	58	61
Seymour		58	59
Mean	56	58	61

Apparently mean temperature had little to do with the ultimate size of the zooplankton population. In 1954, when the average catch of Entomostraca was high, average water temperatures were lowest. In 1956, when the average catches were again high, the average temperatures were highest. Intermediate temperatures occurred in 1955 when availability of adult crustacean plankters was lowest. Unless differences between years were caused by critical temperatures during a particular limited period of the biological cycle, observed differences between years cannot be explained on the basis of differing average water temperatures.

C. Predation by Sockeye Salmon

As Fleming (1939) has pointed out, grazing by zooplankters is a possible explanation for variations in abundance of phytoplankton. Perhaps fluctuations in abundance of Entomostraca can be associated with varying rates of predation.

A large year-class of sockeye was present in the lake from May 1955 until June of 1956. These fish were the offspring of the 1954 escapement of two million adults. It is possible that this great population of plankton-feeders maintained the zooplankton population at a lower level than in 1954 or 1956 when there were few young sockeye in the lake.

Before a positive relationship between sockeye and plankton can be established two requirements must be met. First, the 1955 low point in plankton abundance will have to be duplicated in 1959 when the next dominant population of sockeye is resident in the lake and secondly, no other comparable low years of plankton must occur during the intervening period. If a low-year should occur the decline in zooplankton availability in 1955 cannot be definitely attributed to sockeye predation.

One conclusion can be reached regarding the strength of sockeye year-classes and abundance of plankton. When the sampling program was being planned the hypothesis was formulated that the dominant year-class of sockeye might reduce the plankton population to such an extent that it might take one or more years to recover and thus limit the size of subsequent year-classes of sockeye. On the basis of present evidence this hypothesis can be discarded. Assuming for the moment that the sockeye population was responsible for low availability of zooplankton

in 1955, it is evident from Figure 3 that the period of low availability did not extend into the 1956 growing season. It is therefore concluded that low zooplankton availability does not restrict the abundance of the subdominant and "off" year-classes of sockeye.

Differences in Station Availability

Rawson (1951) suggested that differences in basin morphometry and geology of surrounding land masses accounted for differences in productivity of major divisions of Great Slave Lake. He emphasized the value of measures of total dissolved solids as indicators of general productivity. Total dissolved mineral content of an area depends on materials carried into the basin from the surrounding territory (Naumann, 1932).

The geology of the terrain surrounding Shuswap Lake varies considerably as shown previously. These differences probably account for the observed differences in station availability of adult Entomostraca. Waters, poor in dissolved minerals, flowing into the lake probably limit the growth of the local plankton populations. Conversely, tributary waters, rich in dissolved minerals, probably produce larger plankton populations.

Descriptions of tributary streams adjacent to the various stations and descriptions of their watersheds offer at least a partial explanation for differences in station total dissolved solids values and, perhaps, station differences in productivity.

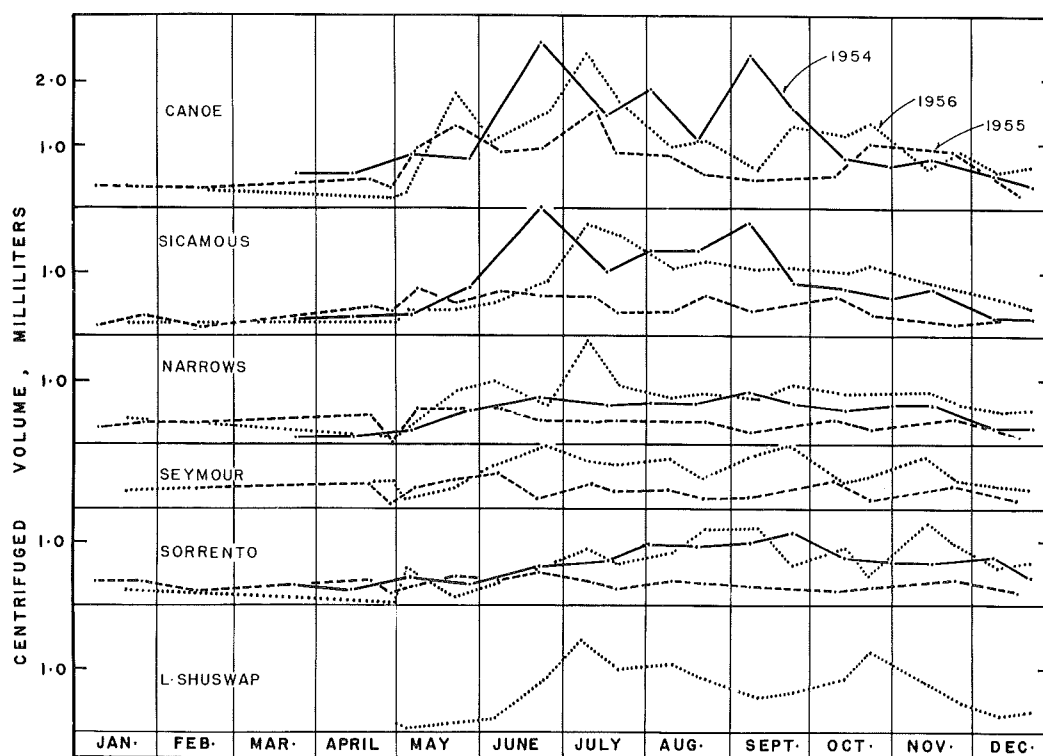


Figure 3. Availability of adult crustacean plankters at the stations during 1954, 1955 and 1956.

Canoe Station

Water samples from the Canoe station had the highest dissolved solids content and the greatest average volume of adult crustacean plankters (Table 14). This station (No. 1) is located near the southern end of Salmon Arm (Figure 1). The Salmon River, which is the chief source of water to this section of the lake, drains a long fertile valley. Waters draining the farmlands of the Salmon River valley are probably rich in phosphates which Riley (1940) showed were necessary for the development of phytoplankton pulses. The largest deposits of limestone near the lake shore are also located in the region of the Canoe station. The quantity of dissolved calcium carbonate might also contribute to increased plankton production in this area.

Sicamous Station

The Sicamous station had the next highest average total dissolved solids value and the next highest average yield of adult crustacean plankters. The largest streams which drain into this section of the lake also drain extensive, fertile valleys. The Eagle River drains a long valley which extends towards the north-east and the Lower Shuswap River drains a farming district located south-west of the lake.

The Watersheds of the Salmon River, Lower Shuswap and Eagle Rivers, are similar in character but different from the watersheds of other streams tributary to the lake. According to the classification used by Northcote and Larkin (1956) the watersheds of these three streams are similar to those found in the Southern Interior Plateau Region.

Seymour Station

Of all stations, the one located near the end of Seymour Arm was least productive of adult crustacean plankters and water samples from this station had the lowest average dissolved solids content (Table 14).

The Seymour River, arising in the high mountains to the north, supplies most of the water to Seymour Arm, and it carries, during part of the year, considerable amounts of glacial silt. Streams of this type have a low dissolved mineral content and lakes fed by streams of this type are usually poor producers of plankton. The terrain surrounding Seymour Arm is composed of Pre-Cambrian formations (Daly, 1915) which are insoluble and likely to contribute little nutrient material to the lake.

Sorrento Station

Intermediate values for both total dissolved solids and plankton were recorded from the Sorrento station. The portion of the lake represented by this station is diluted by water from Adams Lake carried by the Adams River. Adams Lake is a very deep, cold, oligotrophic lake with total dissolved solids values of the order of 60 p.p.m. Adams River is a short, swiftly-moving stream flowing over gravel bars and through rocky canyons. Water from this source is unlikely to contribute much to the productivity of Shuswap Lake.

Narrows Station

Samples taken from the Narrows station are probably from a mixture of waters representing several areas of the lake. The central location of the station might serve as an explanation for the median values obtained for both total dissolved solids and plankton.

General Relationships

The Salmon Arm area is the most productive portion of the lake. The character of the watershed of this area offers a reasonable explanation for productivity. Tributary streams drain farmland areas which are probably rich in plant nutrients. Seymour Arm is the least productive part of the lake. It is suggested that the productivity of this area is limited by surrounding rock formations. The Main Arm is intermediate in productivity. Waters from Adams Lake which enter the Main Arm through the Adams River are unlikely to contribute greatly to the productivity of Shuswap Lake.

SUMMARY AND CONCLUSIONS

1. Plankton samples were collected from Shuswap Lake during 1954, 1955 and 1956 in order to investigate possible relationships between the abundance of sockeye and the availability of adult crustacean plankters. This report is concerned with the validity of sampling techniques and with evidence pertaining to seasonal and annual variations in availability.
2. The productivity of Shuswap Lake is probably affected by geographic location, morphometry, and mineral content. These criteria suggest that the lake is relatively oligotrophic.
3. Few genera and species were present in catches of crustacean plankters from the pelagic region of Shuswap Lake.
4. Wisconsin-type nets as vertical samplers on a number of well-distributed stations were chosen.

5. Twice-monthly samples were taken at four stations in 1954, five in 1955 and six in 1956. To determine the magnitude of short-term fluctuations in plankton availability, stations were sampled for five days. Whenever possible, during these periods, all stations were sampled for five consecutive days.
6. Rapid, random changes in net efficiency did not obscure differences in availability between stations.
7. Nets were not subject to gradual changes in efficiency during the period they were used. A new net and a net used for three months caught similar amounts of adult crustacean plankters.
8. Catches were not significantly different over a wide range hauling rates. The rate at which the net was pulled was not a significant source of error.
9. No evidence was found to support the hypothesis that the efficiency of nets declined steadily during a long series of hauls.
10. Significant daily fluctuations in the availability of adult crustacean plankters did occur in all three years.
11. Short-term fluctuations in the availability did not obscure seasonal differences in availability.
12. Comparisons between periods of frequent sampling in different years showed that short-term fluctuations did not, in general, obscure annual differences in the availability of adult crustacean zooplankters.
13. Comparisons between representative average annual catches revealed that the availability of adult crustacean zooplankton on all

stations during the 1955 sampling season was significantly lower than in 1954 or 1956. The average availability in 1955, considering all stations, was only from one-half to two-thirds as great as in 1954 or 1956. Availability may have been slightly greater in 1954 as compared with 1956.

14. Consistent differences in station availability were observed between years. These differences probably reflected or partially reflected differences in area productivity. Differing concentrations of dissolved nutrients as measured by total dissolved solids determinations was offered as an explanation for these consistent differences.
15. Average water temperatures obtained during the three seasons were not correlated with plankton availability. Water temperatures in 1955 were intermediate to those obtained in 1954 and 1956, while plankton availability was lowest in that year.
16. No conclusions can be drawn at present regarding the effect of the dominant year-class of sockeye salmon which were in the lake during 1955 on the availability of adult crustacean plankters; however it is unlikely that the availability of adult crustacean plankters is a factor limiting the production of sockeye salmon of the subdominant and "off" year-classes.
17. Characteristic geological formations surrounding different parts of the lake probably cause the observed differences in dissolved minerals which in turn probably cause area differences in entomostracan production.

LITERATURE CITED

- Borecky, Gloria W.
1956. Population density of the limnetic Cladocera of Pymatuning Reservoir. *Ecol.* 37: 719-727.
- Daly, R.A.
1915. A geological reconnaissance between Golden and Kamloops, B.C. along the Canadian Pacific Railway. *Can. Geol. Surv. Mem.* 68.
- Clarke, G.L. and D.F. Bumpus.
1950. The plankton sampler - an instrument for quantitative plankton investigations. *Am. Soc. Limnology & Oceanogr. Special Pub.* 5.
- Clemens, W.A., R.E. Foerster, N.M. Carter, and D.S. Rawson.
1937. A contribution to the limnology of Shuswap Lake, British Columbia. *B.C. Dept. Fish. Rept.* 1937: T91-T97.
- Fleming, R.H.
1939. The control of diatom populations by grazing. *J. Cons. Int. Explor. Mer.* 14: 210-227.
- Juday, C., Willis H. Rich, G.I. Kemmerer and Albert Mann.
1932. Limnological studies of Karluk Lake, Alaska, 1926-1930. *Bull. U.S. Bur. Fish.* 47: 407-436.
- Langford, R.R.
1938. The food of the lake Nipissing cisco, Leucichthys artedi (Le Sueur), with special reference to the utilization of the limnetic crustacea. *Univ. Toronto Stud. Biol.* 45. *Pub. Ont. Fish. Res. Lab.* 57: 143-190.

1953. Methods of plankton collection and a description of a new sampler. *J. Fish. Res. Bd. Can.* 10: 238-252.
- McCombie, A.M.
1953. Factors influencing growth of phytoplankton. *J. Fish. Res. Bd. Can.* 10: 253-282.
- Mortimer, C.H.
1952. Water movements in lakes during summer stratification; evidence from the distribution of temperature in Windermere. *Phil. Trans. Roy. Soc. London. Ser. B.* 236: 355-404.
- Naumann, E.
1932. Principles of regional limnology. 122 pp. E. Schweizerbart (Erwin Nägele) Ltd., Stuttgart. (Trans. from German).

Northcote, T.G. and P.A. Larkin.

1956. Indices of productivity in British Columbia lakes. J. Fish. Res. Bd. Can. 13: 515-540.

Pearsall, W.H.

1932. Phytoplankton in the English lakes II. The composition of the phytoplankton in relation to dissolved substances. J. Ecol. 20: 241-262.

Pratt, D.M.

1943. Analysis of population development in *Daphnia* at different temperatures. Biol. Bull. 85: 116-140.

Rawson, D.S.

1951. The total mineral content of lake waters. Ecol. 32: 669-672.
1953. The standing crop of net plankton in lakes. J. Fish. Res. Bd. Can. 10: 224-237.
1956. The net plankton of Great Slave Lake. J. Fish. Res. Bd. Can. 13: 53-127.

Ricker, W.E.

1933. The utility of nets in fresh water plankton investigations. Trans. Am. Fish. Soc. 62: 292-303.
1937. The food and food supply of sockeye salmon (*Oncorhynchus nerka* Walbaum) in Cultus Lake, British Columbia. J. Fish. Res. Bd. Can. 3: 450-468.
- 1938a. An adequate sampling of the pelagic net plankton of a lake. J. Fish. Res. Bd. Can. 4: 19-32.
- 1938b. Seasonal and annual variations in quantity of pelagic net plankton, Cultus Lake, British Columbia. J. Fish. Res. Bd. Can. 4: 33-47.

Riley, G.A.

1940. Limnological studies in Connecticut. III. The plankton of Linsley Pond. Ecol. Monogr. 10: 279-306.

Snedecor, G.W.

1946. Statistical methods applied to experiments in agriculture and biology. 485 pp. 4th Ed. Collegiate Press, Ames, Iowa.

Southern, R. and A.C. Gardiner.

1926. The seasonal distribution of the Crustacea of the plankton in Lough Derg and the River Shannon. Fish. Ire. Sci. Investig. 1: 1-170.

Verduin, J.

1951. Comparison of spring diatom crops of western Lake Erie in 1949 and 1950. *Ecol.* 32: 662-668.

Welsh, P.S.

1948. *Limnological methods*. 381 pp. Blakiston Co., Philadelphia & Toronto.

Winsor, C.P. and G.L. Clarke.

1940. A statistical study of variations in the catch of plankton nets. *J. Mar. Res.* 3: 1-34.