INTERACTIVE SEGREGATION BETWEEN ADULT DOLLY VARDEN (*Salvelinus malma*) AND CUTTHROAT TROUT (*Salmo clarki clarki*) IN SMALL COASTAL BRITISH COLUMBIA LAKES

by

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ABSTRACT

The object of this field study was to examine Nilsson's hypothesis (Nilsson, 1965, 1967) of interactive segregation as it might apply to feeding and spatial distribution of Cutthroat trout (_Salmo clarki clarki_) and Dolly Varden (_Salvelinus malma_) in allopatric and sympatric populations of the two species in small lakes. _Salmo clarki clarki_ living alone changed their depth distribution throughout the summer season but no diel movement was recorded. The changes in food habits closely corresponded with seasonal change in distribution, and a wide variety of food organisms was eaten.

Salvelinus malma living alone underwent considerable diel changes in spatial distribution, with the majority caught at the surface during the evening. Their diet consisted primarily of zooplankton and surface-caught insects.

Sympatric _Salmo clarki clarki_ and _Salvelinus malma_ were spatially segregated throughout the summer. Cutthroat trout occurred mostly near the surface and in littoral areas and fed in these areas. In contrast, Dolly Varden were mostly benthic in distribution and fed primarily on bottom organisms. By comparing food habits and distribution in allopatric and sympatric situations it was inferred that food competition contributes to the segregation of the species in sympatry. Seasonal differences in food and spatial segregation occur suggesting interactive segregation is a temporary phenomenon. In general, the data support Nilsson's hypothesis of interactive segregation.

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INTRODUCTION

Dolly Varden and Cutthroat trout frequently occur together in many coastal lakes of British Columbia. These fish utilize similar habitats and are potential competitors. With the exception of the brief account by Godfrey (1955) there has been no detailed study on the ecology and feeding habits of lake residents of either form.

Nilsson (1955, 1960, 1961, 1963, 1965) has examined competitive interaction between the arctic char (Salvelinus alpinus) and the brown trout (Salmo trutta) and has developed the hypothesis of "interactive segregation." This term, originally used by Brian (1956) in his work on the ant Genus Myrmica, has since been adopted by Nilsson (1965, 1967).

According to Nilsson (1967) the term means "that the ecological differences between species (eg. in food or habitat selection) are often magnified through interaction, i. e. the species segregate into different niches through competition and/or predation." On the basis of nearly twenty years of data Nilsson (1965, 1967) hypothesizes that food segregation in fish is the result of one or more mechanisms such as food competition (exploitation and interference), territoriality, food fighting and predation. Clearly then, interactive segregation is not a description of these mechanisms involved in population interactions, but rather it describes the results of these mechanisms.

The hypothesis of interactive segregation has been supported to some extent by experimental and field observations of Hartman (1965) who observed spatial segregation between underyearling coho salmon and steelhead trout during the spring and summer in laboratory experiments as well as in some small coastal streams of British Columbia. Nilsson (1967) cites several other cases of interactive segregation including that of Gee and Northcote (1962) on food segregation between two closely related species of dace (Rhinichthys) in the Fraser River system.

The purpose of this study was therefore to investigate in the field the possibility of interaction between coastal Cutthroat trout and Dolly Varden and to examine the relationships between them in the light of Nilsson's hypothesis of interactive segregation. This was done by recording vertical distributions and feeding habits of populations of Dolly Varden and Cutthroat in two separate lakes and comparing them with the results from another lake where the two species occur together.

Obviously it is virtually impossible to find lakes with the appropriate species combination which are identical limnologically. The lakes used in this study were not similar hence limiting the effectiveness of testing Nilsson's hypothesis.

II. DESCRIPTION OF THE STUDY AREAS

1. Marion Lake

Marion Lake (49° 31' 30" N, 123° 10' 30" W) is situated approximately 40 kilometers north of Vancouver at an altitude of 533 meters (Fig. 1). The lake is shallow with a mean depth of 4.5 meters and a maximum depth of 12.1 meters. The inlet stream flows from Phyllis Lake with approximately 100 meters separating the two lakes. At the outlet of Marion Lake is an old wooden dam that allows water to pass through, over or around it, at all times. This dam affects the water level, and there is an estimated drop of 1.0 meter during the warm months of August and September.

The lake is divided into two distinct basins, the deeper near the inlet end (Fig. 1). The east shoreline has considerable littoral area in contrast to the steep-sided west shoreline. Bottom sediments are primarily of brown mud with extensive amounts of leaf litter in the littoral areas.

The lake contains large populations of Cutthroat trout and Dolly Varden of approximately equal size range. No other species of fish are present.

2. Placid Lake

Placid Lake (49° 19' 0" N, 122° 34' 49" W) is located in the U. B. C. Research Forest approximately 48 kilometers east of Vancouver at an altitude of 503 meters. The lake is shallow with a mean depth of 4.3 meters and a maximum depth of 6.7 meters (Fig. 2). There is no appreciable surface inflow or outflow with seepage important in regulation of the water level. To a large extent the shoreline is composed of *Sphagnum*

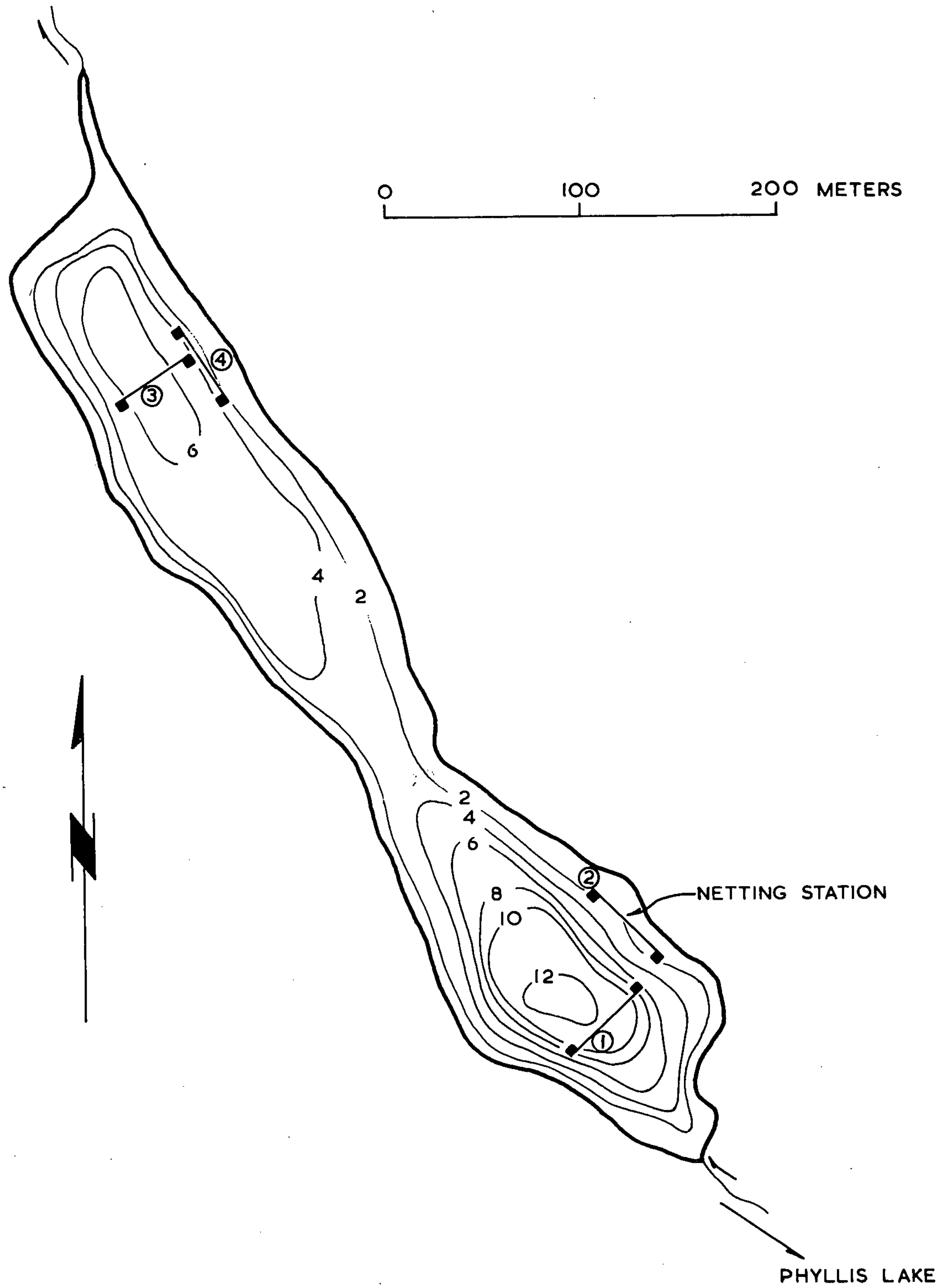

FIG. I Morphometric features of Marion Lake, B.C., with location of netting stations. Depths in meters.

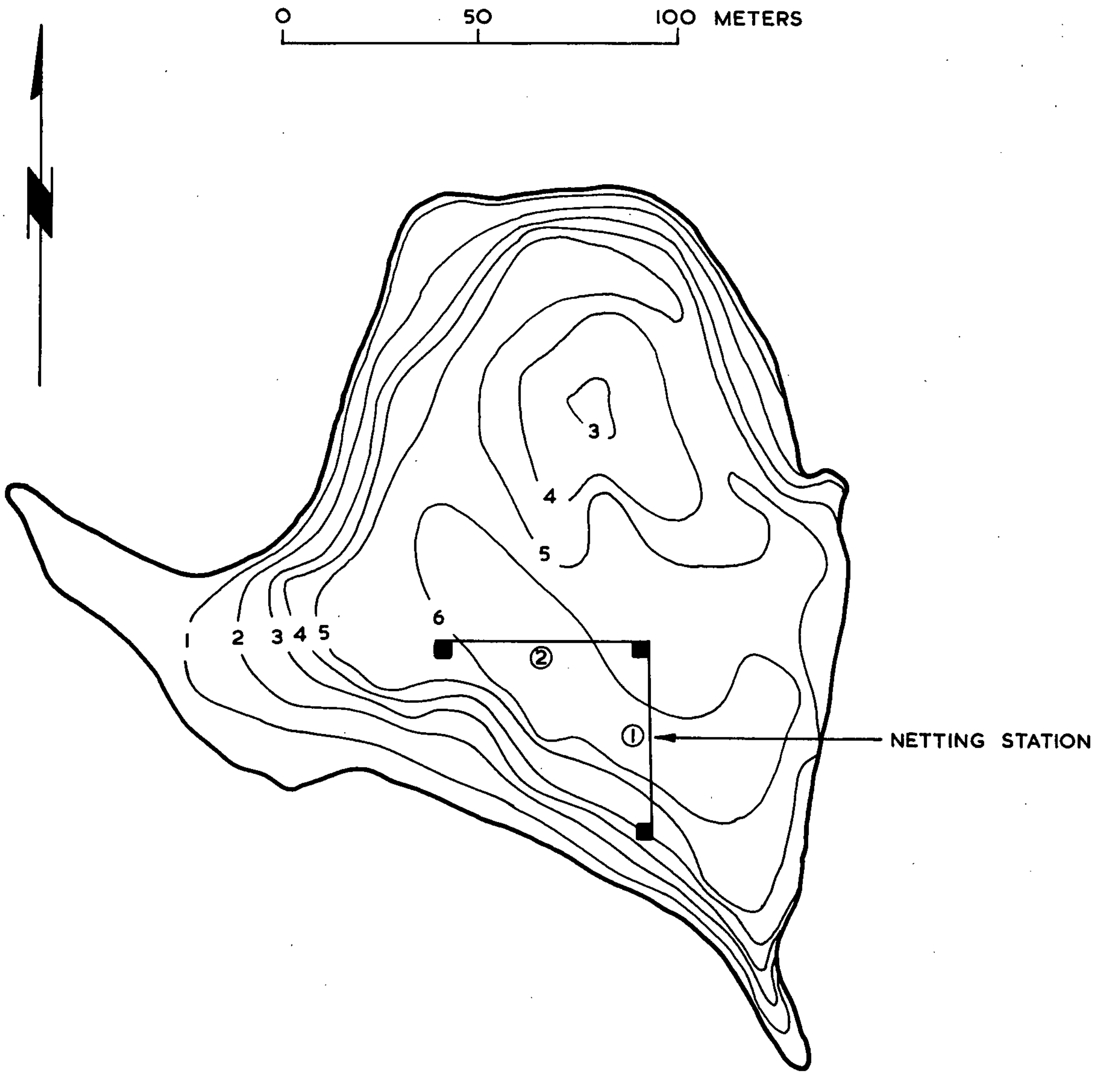

FIG. 2 Morphometric features of Placid Lake, B.C., with location of netting stations, 1 and 2. Depths in meters.

mats which, especially along the southwest shoreline, overhang considerably.

Bottom sediments consist primarily of soft brown ooze with small amounts of plant debris. Placid Lake contains a population of coastal Cutthroat trout, the only species of fish present.

3. Dickson Lake

Dickson Lake (49° 19'0'' N, 122° 05' 30'' W) is located approximately 110 kilometers northeast of Vancouver at an altitude of 671 meters. This lake is deep and steepsided with a mean depth of 35.6 meters and a maximum of 76 meters. The shoreline consists largely of stones and gravel with a very restricted littoral area. For comparison with Marion and Placid Lakes, a shallow bay at the outlet stream was used as the study area. This bay has a rocky shoreline and a bottom consisting of rocks, gravel and small areas of mud. Dickson Lake has a population of Dolly Varden, the only species of fish present.

III. MATERIALS AND METHODS

1. Physical-Chemical Limnology

Temperature was recorded with a rapid responding thermistor (Model 44TB - Y. S. I. Co. Inc.) and a F. B. A. model oxygen-temperature probe. The two probes were calibrated to $\pm .5^{\circ}C$.

Dissolved oxygen determinations were with the F. B. A. oxygen-temperature probe and also by the unmodified Winkler method (Standard

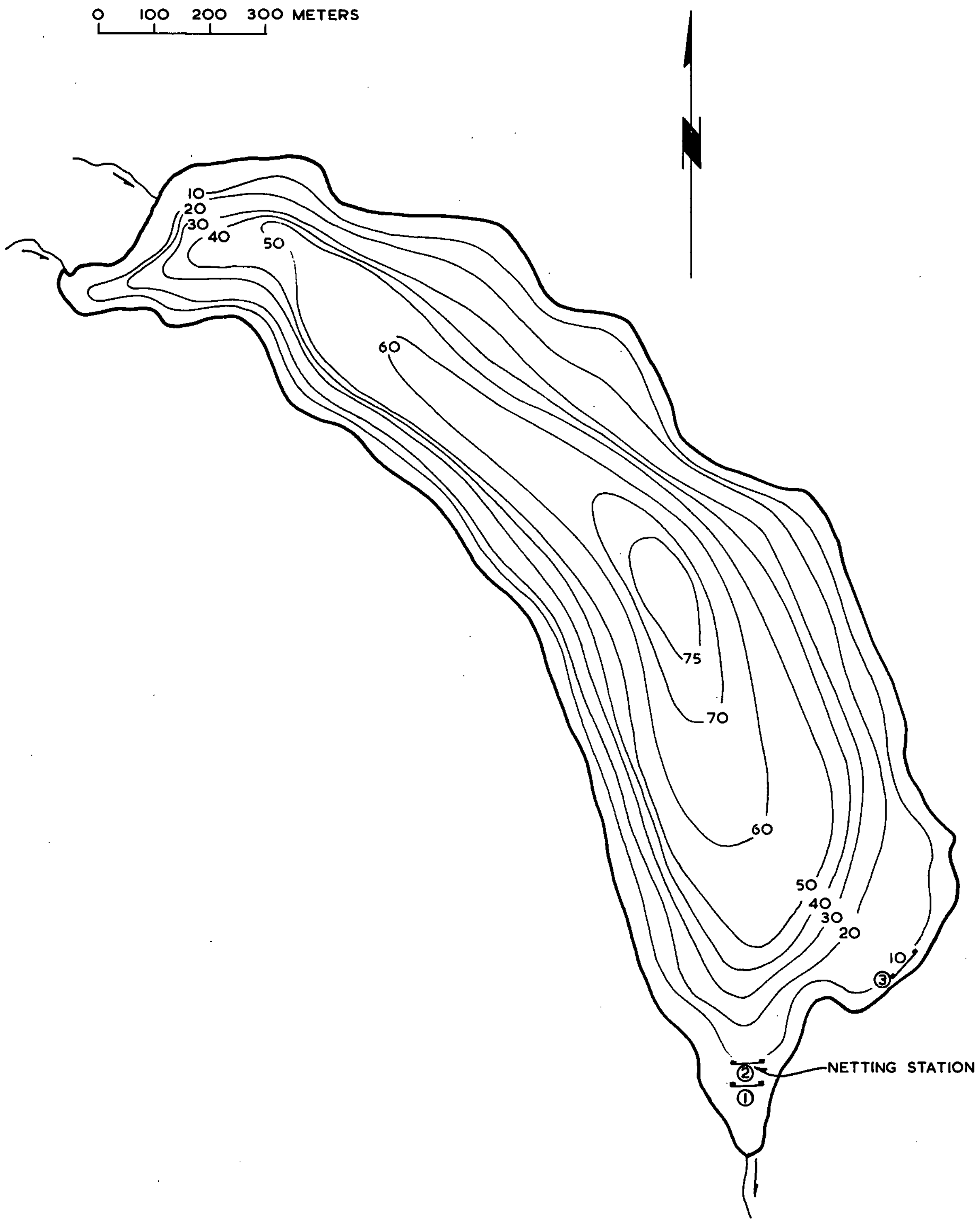

FIG. 3 Morphometric features of Dickson Lake, B.C., with netting stations at the outlet creek. Depths in meters.

Methods, 1960). Winkler samples were taken with a Kemmerer water bottle, transferred to 300 ml. B. O. D. bottles, fixed in the field, and thentitrated within 24 hours in the laboratory.

Transparency was measured with a standard 20. cm. diameter Secchi disk.

2. Bottom Fauna

Bottom fauna samples were collected with an Ekman dredge (225 cm^2) periodically throughout the summer from Marion Lake and from Dickson Lake in June. Samples were washed through a 0. 56 mm. size screened-bottom bucket. Usually the animals were separated alive and only a few samples were picked after preservation with 10% formalin. Almost all Marion Lake samples were taken from areas around, or within, the deeper end of the lake. Dickson Lake samples were taken from the bay near the outlet.

3. Zooplankton

All zooplankton samples were collected with a Clarke-Bumpus sampler fitted with a No. 10 (0. 13 mm.) nylon net and preserved in the field with approximately 5% formalin.

Once a month during the summer and in November, single samples were taken during the day from the deepest part of Marion Lake. Depth intervals used in collecting were: surface, 1-3 m, 4-6 m, and 7-9 meters. Samples were also taken from Placid and Dickson Lakes.

To calibrate the sampler, it was lowered with net attached to 2m and towed over a measured distance. Two values, 7.21 and 6.44 liters per revolution, were obtained for two different nets used during the study and these values were used to calculate the number of animals per liter for the various depths sampled.

Each zooplankton sample was diluted to a known volume. After stirring with a glass rod, a 1 ml. subsample was placed in a Sedgewick Rafter cell and the total number of each species counted using a stereo-binocular microscope (20-30X magnification). Five such 1 ml. subsamples were counted for each sample, values averaged and then multiplied by the dilution factor to determine the total number of animals of each species in the sample. This value was then multiplied by the appropriate calibration value to obtain numbers of animals per liter sampled.

4. Fish Distribution in Gill Net Sets

During the summer of 1967, netting series were made in Marion Lake at about weekly intervals to record vertical distributions of fish. Nets were also set at monthly intervals in Placid Lake and twice (June and July) in Dickson Lake. A single series was made in Phyllis Lake in mid-August.

In autumn, single series were made in Placid and Dickson Lake and two in Marion Lake during November.

In all cases, the nets were single knot, monofilament (0.2 mm) gill nets with stretched mesh sizes of 25. 4 mm. , 38. 1 mm. , and 50. 8 mm. The depths of the nets were either 3, 5, or 10 meters. In most cases, nets were set to fish the total depth from surface to the bottom.

Each net consisted of three, five meter sections with one mesh size per section. In all cases the nets were marked horizontally at one meter intervals for convenience in recording fish distribution. Normally, a gang of three nets was used for each series, so that the total length of nets usually fished per station was 45 meters. In the following presentation the abbreviations 3 M. F. , 5 M. F. and 10 M. F. refer to 3, 5 and 10 meter deep floating nets. Similarly, 5 M. S. refers to a 5 meter deep sinking net.

Fish were measured (fork length) to the nearest millimeter and weighed to the nearest gram. Sexes were determined where possible. Only the contents of the digestive tract from oesophagus to pyloric caeca were used for food analysis. Contents of each fish stomach was placed in an individual glass vial containing 70% alcohol and each vial was separately labelled as to time of capture, species and net type.

The most intensive fishing effort was carried out on Marion Lake where Cutthroat trout and Dolly Varden live together. Permanent netting stations were established on all three lakes as indicated in Figures 1-3. Additional information on distribution of Dolly Varden in Dickson Lake was obtained with a 50 Kc/s recording Furuno F-701 echo sounder.

Nets were fished in all three lakes from mid-afternoon to dusk

(13:00 - 19:00 hours). Minimum time that any net was fished was 1 1/2 hours and usually nets were set for 3 hours. Overnight sets (usually 12 hours) were made to obtain information on nocturnal distribution of fish.

5. Age Analysis of Fish

Age determination was attempted only on Marion Lake fish and was restricted to length-frequency and scale analysis methods. To assign ages to the modes of length-frequency plots representative scales of each model group for both species were mounted and ages determined with the aid of a Bausch-Lomb scale projector.

6. Statistical Tests

Numbers of fish for each species in Marion Lake were totalled for each 1 meter depth interval. Since the vertical distributions of each species were sufficiently consistent throughout the summer, data were pooled for all sets. Chi-square tests (Siegel, 1956) were applied to test the null hypothesis that there were no differences ($\alpha = .05$) in the proportions of Dolly Varden and Cutthroat trout caught in the 10 meter nets for the depth intervals of 0-3 meters and 4-10 meters. This same null hypothesis was tested for the intervals 0-2 and 3-5 meters of the 5 meter nets. An adjustment for continuity was used in all of the 2X2 tables.

A chi-square test was also applied to the catches in the 10 meter nets for the day versus night sets. The null hypothesis was that the proportions of Dolly Varden (and also Cutthroat) caught in the 0-3 meter and 4-10 meter depth intervals were the same ($\alpha = .05$) between day and night sets.

An analysis of variance was performed on data on the horizontal distribution of fish in the 10 meter nets set perpendicular to shore during the summer. The null hypothesis tested was that there were no differences (α =. 05) in numbers of fish caught in the onshore, middle and offshore nets.

The distribution within the net of both species for mesh sizes 25. 4 mm. and 38. 1 mm. was analyzed for randomness. For Dolly Varden, data were restricted to the 5 -10 meter depth intervals because of the vertical distribution differences (the numbers caught at each meter interval below five meters were almost equivalent and so could be compared, whereas those intervals less than 5 meters had significantly fewer fish and therefore could not be included in the analysis). The same criterion was applied to the Cutthroat where only the first 4 meter intervals were used.

Numbers of fish in each segment per mesh size (1 meter high by 5 meters in length) were counted and the frequency distribution compared to a Poisson distribution, using a chi-square goodness of fit criterion.

7. Stomach Analysis

During the summer months all Cutthroat were examined but only about half of the Dolly Varden caught were analyzed. To assess differences in diet between Dolly Varden and Cutthroat several methods of stomach analysis were employed. The following procedures were used in the present study:

a) Fullness Index

An arbitrary index of the fullness of the stomach was made for

Marion Lake fish using a range of values from 0 (empty) to 20 (completely full). This allows a rough demonstration of seasonal variation in food intake and partially overcomes the problem of different sizes of fish.

b) Percent Composition

Stomach contents were placed in a petri dish and divided into major components using disecting needles and a binocular disecting scope (10-30X magnification). Each portion was then alloted a percentage of the entire contents on the basis of bulk.

c) Volume Displacement

This method is similar to percent composition but more quantitative. Non-digestible materials such as stones, sticks and fir needles were excluded from the volume measurement. The total volume of food material in the stomach was first measured by displacement in water to the nearest . 05 ml. by dry-blotting the food on paper, placing it in a centrifuge tube (calibrated to 0. 1 ml.), and measuring the food volume by water displacement, using a graduated pipette (0. 5 ml.).

After total volume was recorded, volumes of major components were recorded separately by the same technique. Food volumes for each category were totalled for the month and expressed as a percentage of total consumed for that month. Average of individual volume percentages for each food category in each of the stomachs analyzed was also calculated (after Larimore 1957, pp. 11, 15).

Average of volume percentages has the advantage of not being influenced by size or fullness of the stomach. It is influenced by frequency of occurrence of a food type and so favors small food items that appear frequently in the stomachs. Percentage of total volume is not influenced by frequency of occurrence and favors the importance of large, bulky foods items. This method, as Windell (1968) suggests, may be misleading due to the occasional occurrence of a large volume of one organism which, on a percentage volume basis, tends to appear important to all fish for that sample. Furthermore, it tends to reflect the diet of the population as a whole rather than food habits of individuals of a population.

d) Percent Occurrence

Individual food items identified for each stomach from the percentage composition analysis were recorded as present or absent for every stomach and then expressed as a percentage of the total number of stomachs examined for each month. Only types of organisms consumed are expressed by this method and no account is made of either the numbers or volume.

e) Numbers

Counts of individual food items were attempted but due to advanced digestion in some cases plus the high occurrence of soft-bodied organisms (particularly zooplankton and dipteran adults) the method proved to be unreliable and further consideration was felt unjustified.

In the above methods, except the first, percentages were determined only on those stomachs which had food in them. Empty stomachs were noted but not included in calculations.

Despite weaknesses of each of the above-described techniques only small variations were evident between the results of each. These findings are in agreement with Nilsson (1966), Hynes (1950) and others who feel that simple techniques are valid for comparative food habit studies. In some cases there were notable differences between results of volume percentages and percentage of the total volume for reasons described previously. Where considerable differences occur between the two methods, both are presented, otherwise only results of the percentage of total volume are used.

f) Food Categories

Food items listed were grouped into appropriate faunistic categories. Consequently, the larger littoral larvae, pupae and nymphs of Trichoptera, Plecoptera and Odonata were separated from the smaller, less mobile benthic forms such as Pisidium, chironomid larvae, other dipteran larvae, gastropods and leeches.

Included in the category of winged terrestrial insects were a few aquatic adult insects. In Marion and Dickson Lakes the aquatic portion was less than 5% of the total insect volume. In Placid Lake the percentage of aquatics was estimated at about 25-35% of total insect volume.

Chironomid pupae (plus a few miscellaneous dipteran pupae) were kept separate as presumably they are available in all parts of the water column.

Chaoborus larvae from Placid Lake were treated separately because of their known occurrence in the mud during day and in the water column at night.

It would have been desirable to identify all organisms to species due to variations in life history and behavioral patterns. However, condition of organisms in the stomachs, inadequate keys for British Columbia insects plus amount of time involved made this task nearly impossible for all organisms. Caddis larvae were keyed out as far as possible because of their importance in the diet of Marion Lake fish.

IV. RESULTS

1) Physical -chemical limnology

a) Temperature

Marion Lake never developed a sharp thermocline during the summer of 1967. Maximum surface temperature recorded was 19.5°C on 16 August, 1967 (Fig. 4). The bottom layers of water never reached 10°C at any time.

Placid Lake was sharply stratified thermally by early summer (Fig. 5). A maximum surface temperature of 23°C was recorded on 17 June, 1967, and by late summer the entire water column was above

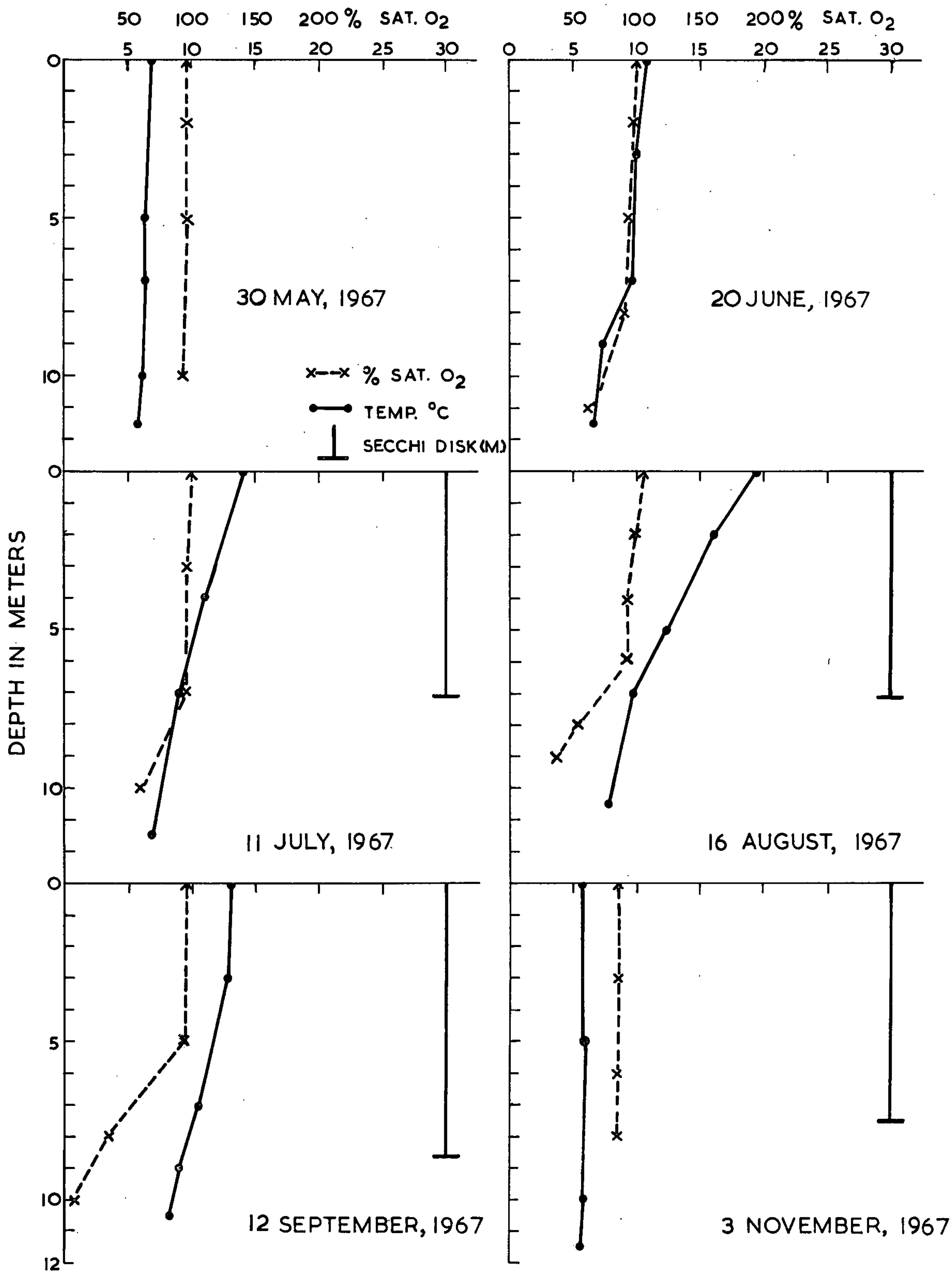

FIG. 4 TEMPERATURE (°C), % SATURATION OF OXYGEN AND SECCHI DISK READINGS FROM MARION LAKE, 1967.

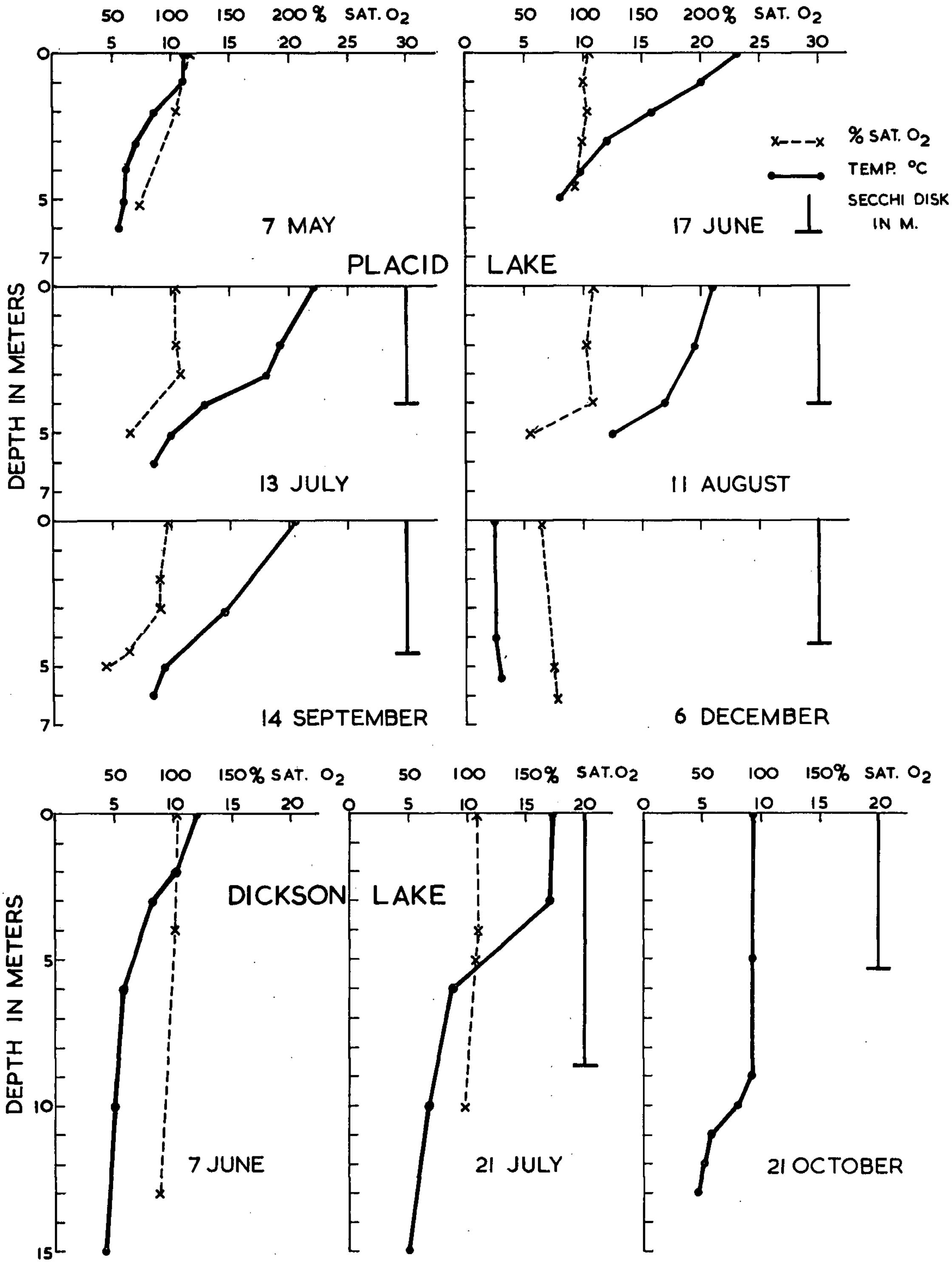

FIG. 5 TEMPERATURE (°C), % SATURATION OF OXYGEN AND SECCHI DISK READINGS FOR PLACID AND DICKSON LAKES, 1967.

10^{o}C with the thermocline close to the bottom.

In Dickson Lake a sharp thermocline developed by mid-July between 3-6 meters. Surface temperature on 21 July 1967 was 17. 3^{o}C. By October surface layers had cooled considerably although a thermocline was still present at 10-12 meters (Fig. 5).

b) Dissolved Oxygen

Maximum percentage saturation level recorded in Marion Lake was 105% at the surface on 30 August, 1967. Deeper layers of Marion Lake were depleted in oxygen during late summer. The decrease in dissolved oxygen starts as early as mid-June at depths greater than 8m. and attained a minimal value of 8% at 10 m. by mid-Septmeber (Fig. 4).

Placid Lake oxygen profiles have a similar pattern to those of Marion Lake. A maximum saturation of 120% was recorded at 3 meters on 28 June, 1967. Surface waters were almost always over 100% saturation but there was a decrease in saturation below 4 meters after mid-June. By mid-September there was a minimum saturation at 5. 5 meters of 9% (Fig. 5).

c) Light

Marion Lake was relatively transparent with an average Secchi disc reading of 7. 5 meters during late summer (Fig. 4). Placid Lake was less transparent (most readings about 4) whereas Dickson Lake had the highest reading of 8. 7 meters (Fig. 5).

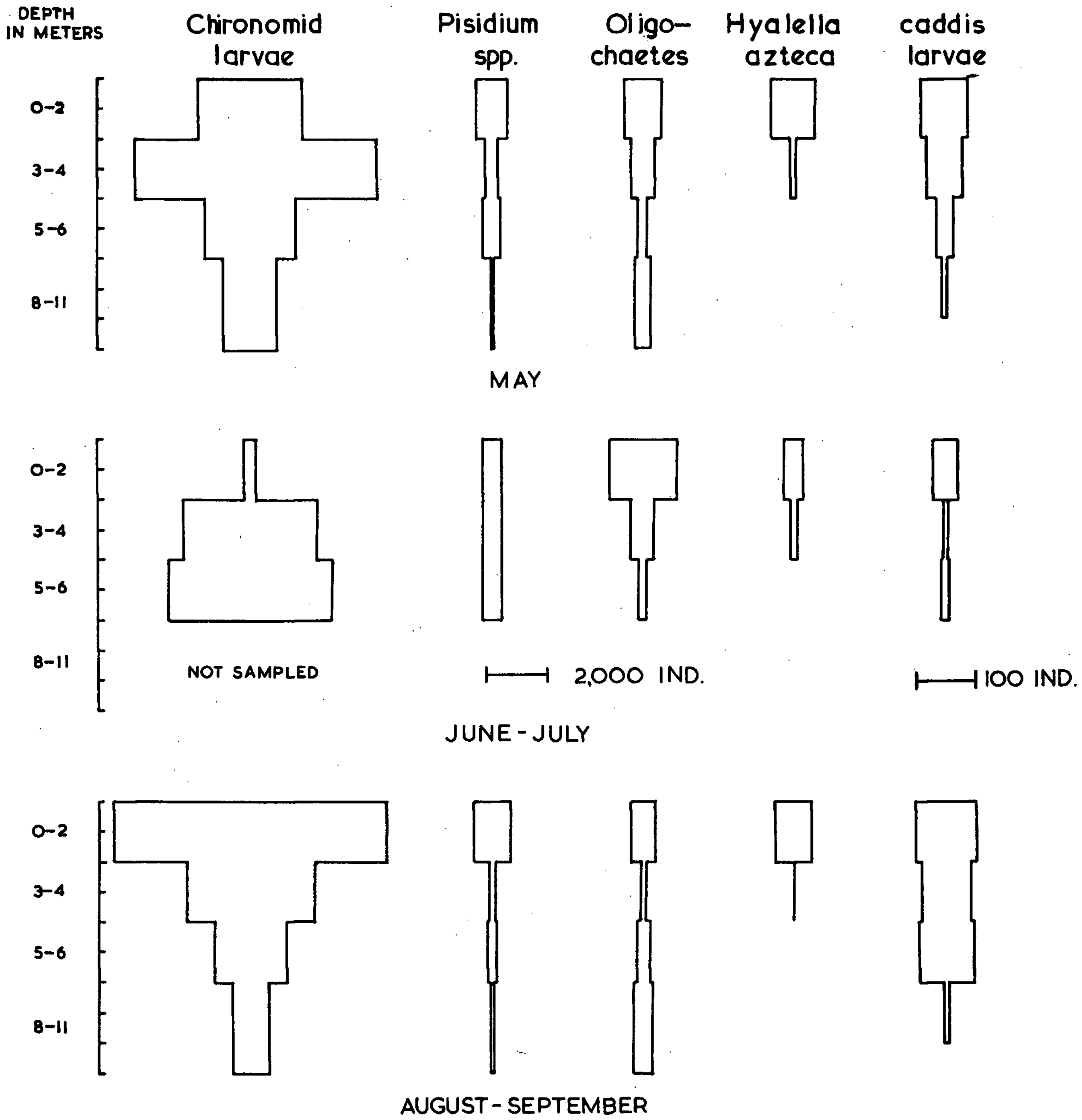

FIG. 6 BATHYMETRICAL DISTRIBUTION OF SOME BOTTOM ORGANISMS IN MARION LAKE, 1967. (NUMBERS PER SQUARE METER.)

2) Bottom Fauna

The results of the samples taken are shown in Appendix table I. In Marion Lake, chironomid larvae, oligochaetes and *Pisidium spp.* were numerically the most abundant benthic organisms. *Hyalella azteca* was restricted to the littoral zone and ceratopogonid and other dipteran larvae also were most abundant there. Figure 6 illustrates the distribution of some benthic organisms from Marion Lake.

Trichopteran larvae were found primarily in the littoral and sub-littoral areas as indicated in Figure 6. Only Leptoceridae and Limnephilidae were found in the bottom samples - the families Psychomyiidae and Phyryganeidae were identified from stomach contents. Larvae of *Mystacides alafimbriata* were most abundant in the Ekman samples - especially during early summer. These larvae were vertically distributed from 0-6 m. in equal numbers but were absent below 7 m. The family Limnephilidae was encountered mostly in September samples.

From the few samples taken in Dickson Lake it is apparent that the bottom fauna of this lake is relatively sparse (Appendix table I). Samples were taken from selected areas where the expectation was that bottom organisms would be most abundant, the remainder of the bottom area being chiefly rock and gravel.

3) Zooplankton

Figure 7 shows seasonal changes in vertical distribution of

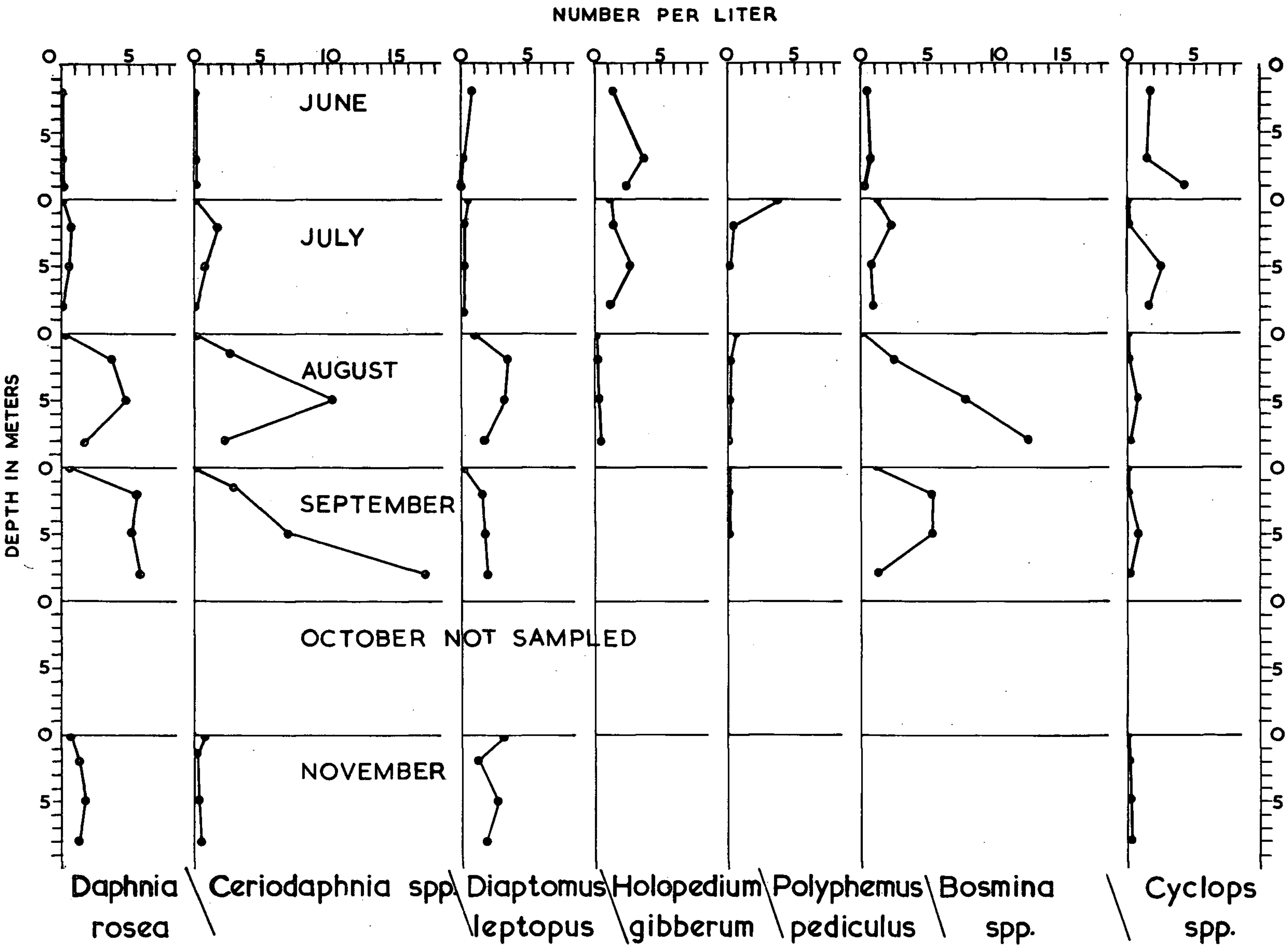

FIG. 7 DAYTIME DISTRIBUTION OF ZOOPLANKTON IN MARION LAKE IN NUMBERS PER LITER JUNE - NOVEMBER 1967

Marion Lake zooplankton. Holopedium gibberum was most abundant during the early summer but virtually absent by September. Daphnia rosea, Ceriodaphnia sp. and Bosmina sp. were most abundant during late August and early September with maximum numbers in the deeper levels. Diaptomus leptopus was also most numerous during September but more evenly distributed with depth.

Placid Lake zooplankton was similar to that of Marion Lake. Holopedium gibberum was abundant during early summer whereas Daphnia rosea and Diaphanosoma leuchtenbergianum were numerically abundant in August (Northcote, unpublished data). Diaptomus oregonensis were most numerous in June and again in December.

4) Fish Distribution

a) Placid Lake

Cutthroat were predominantly in surface waters during May and June (Fig. 8). As summer progresses the concentration of fish gradually moved to deeper water, particularly the 4 and 5 meter zones. Night sets during July and August showed no appreciable difference in distribution from the corresponding day sets (Fig. 8).

A single sample taken in December just prior to ice formation suggested that the fish were maintaining their deep position in the lake during fall and perhaps during winter conditions.

b) Dickson Lake

Day net sets took very few fish with most nets empty after 4-5

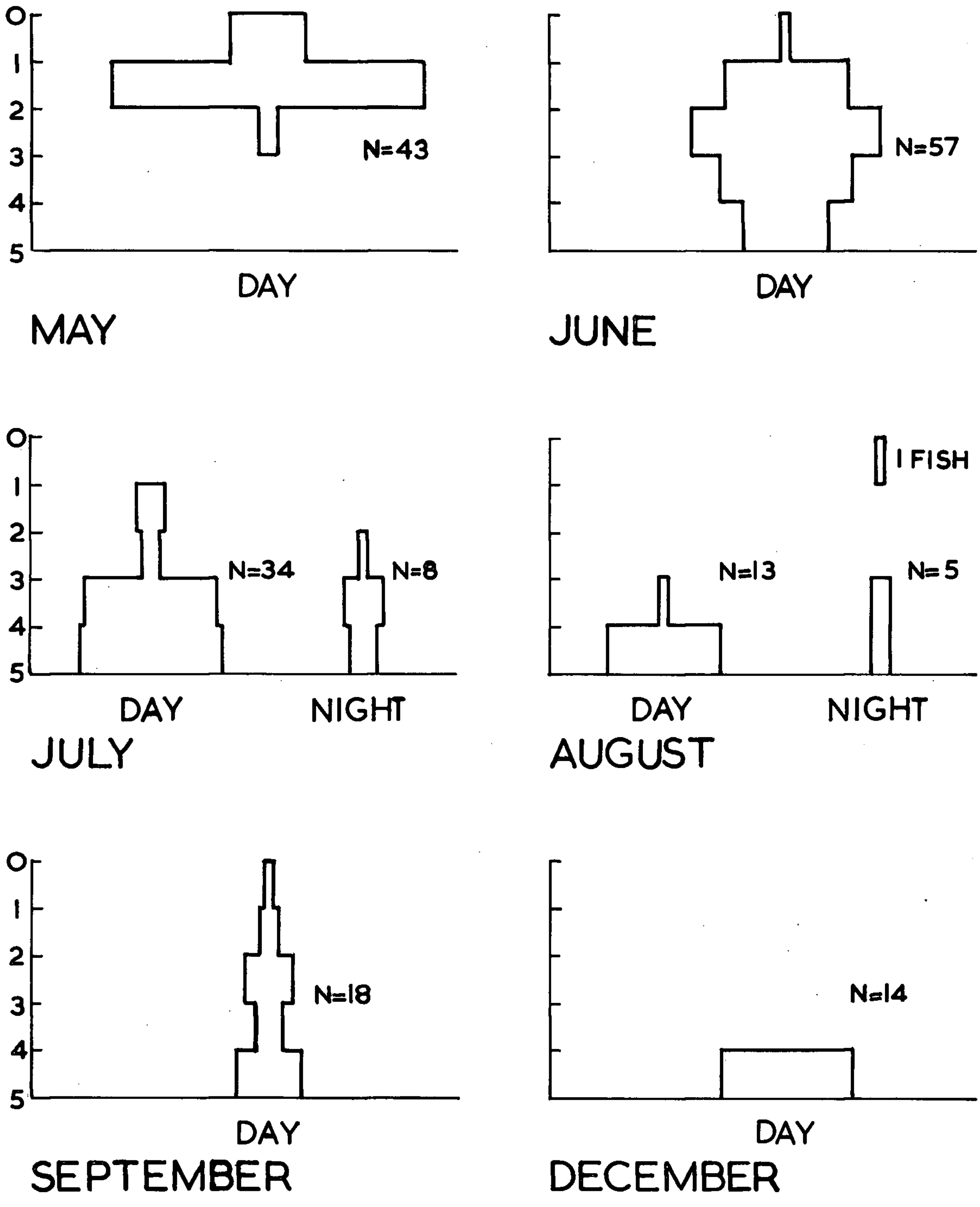

FIG. 8 VERTICAL DISTRIBUTION OF CUTTHROAT TROUT IN GILL NETS SET AT STATIONS 1 AND 2, PLACID LAKE, 1967.

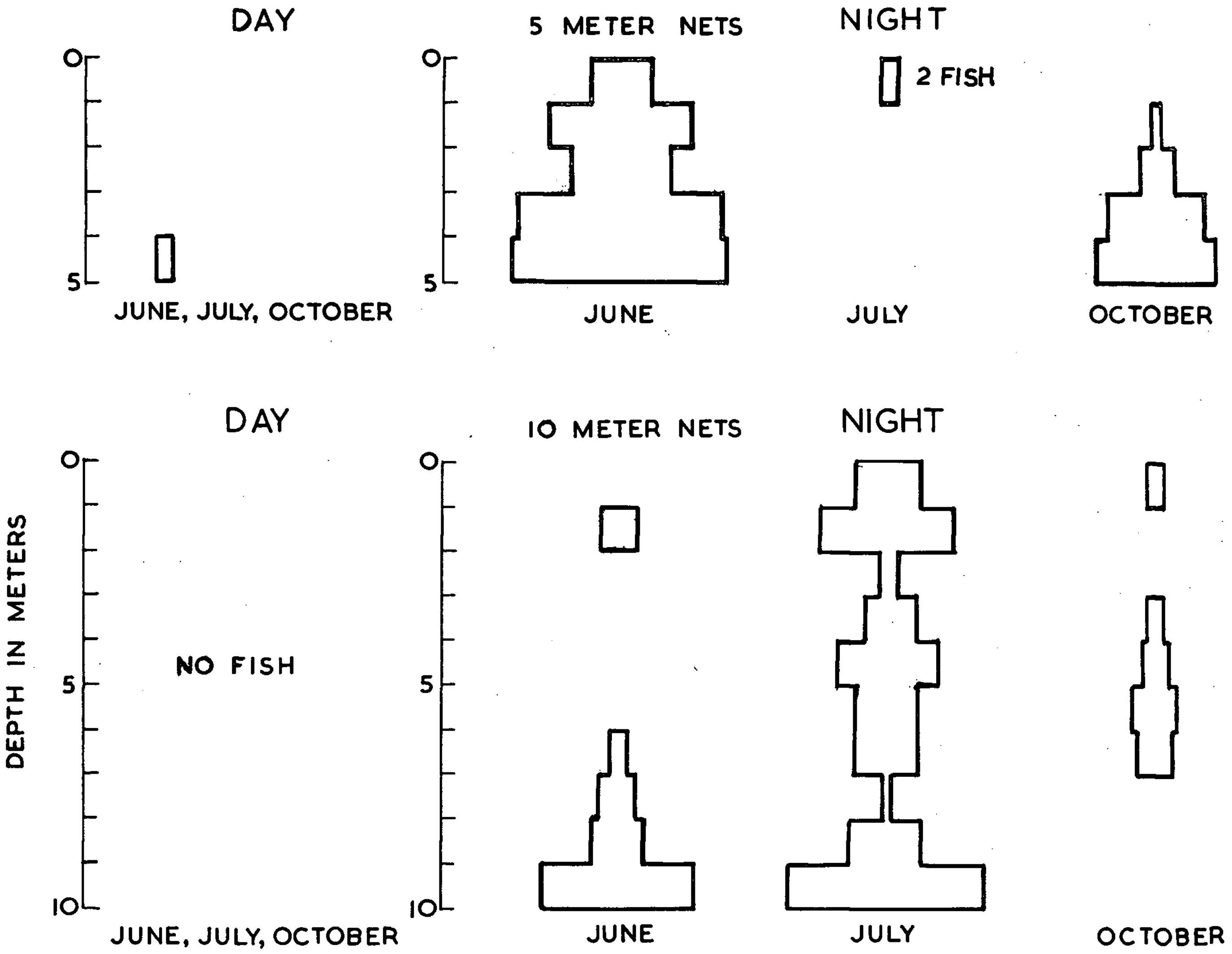

FIG. 9 VERTICAL DISTRIBUTION OF DOLLY VARDEN IN GILL NETS SET DURING DAY AND NIGHT AT DICKSON LAKE, 1967.

hours whereas at dusk and during the night large numbers of Dolly Varden were taken at all depths fished (Fig. 9). Echo soundings (not shown) and net sets strongly suggest that Dolly Varden in Dickson Lake undergo considerable diel movements. During day fish appeared scattered at relatively deep depths(about 25 meters on the echo sounder traces) whereas at night, large numbers of fish were recorded and netted in shallow depths. During June and July the Dolly Varden in Dickson Lake were widely distributed in the upper 10 m. at least during the night.

c) Marion Lake

i) Vertical Distribution

The first netting series in Marion Lake was made on the first day that the lake became ice free (13 May, 1967). Day sets yielded no fish but results of overnight sets are shown in Figure 10. The proportion of Cutthroat caught in the first two meters (0-2 m.) and bottom three meters (3-5m.) do not differ significantly ($\alpha = 5\%$) from the proportion of Dolly Varden caught in the same intervals. Evidently, this sample reflects a pre-summer condition with both species associated with the bottom.

Figures 10, 11a and 12 summarize data from the 3, 5 and 10 meter nets set throughout summer. The proportions of both species caught at night in shallow (0-3m.) and deep(4-10m.) intervals of the 10 m. nets did not differ significantly from those

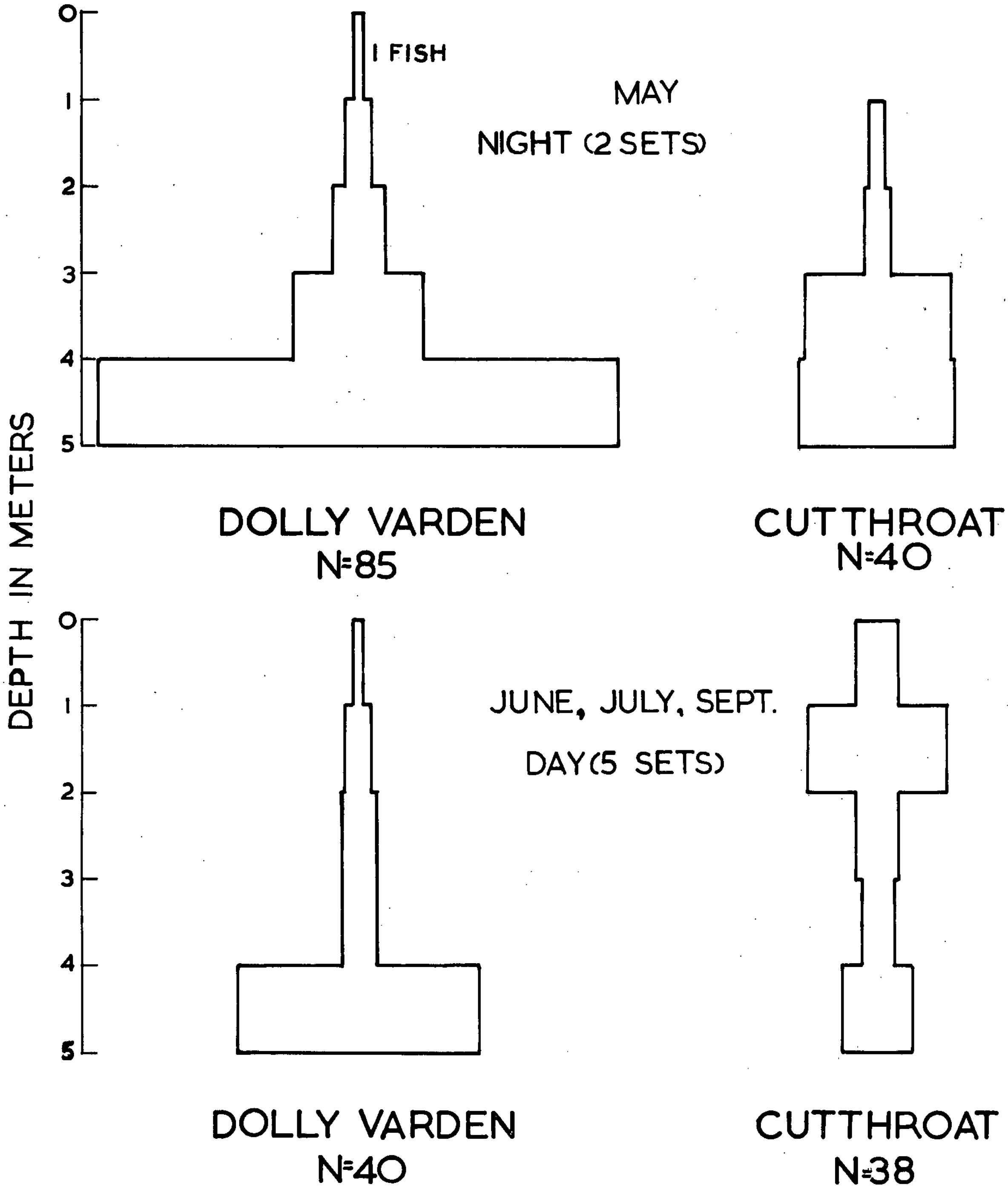

FIG. 10 VERTICAL DISTRIBUTION OF CUTTHROAT AND DOLLY VARDEN CAUGHT IN 5-METER NETS IN MARION LAKE, SPRING AND SUMMER, 1967.

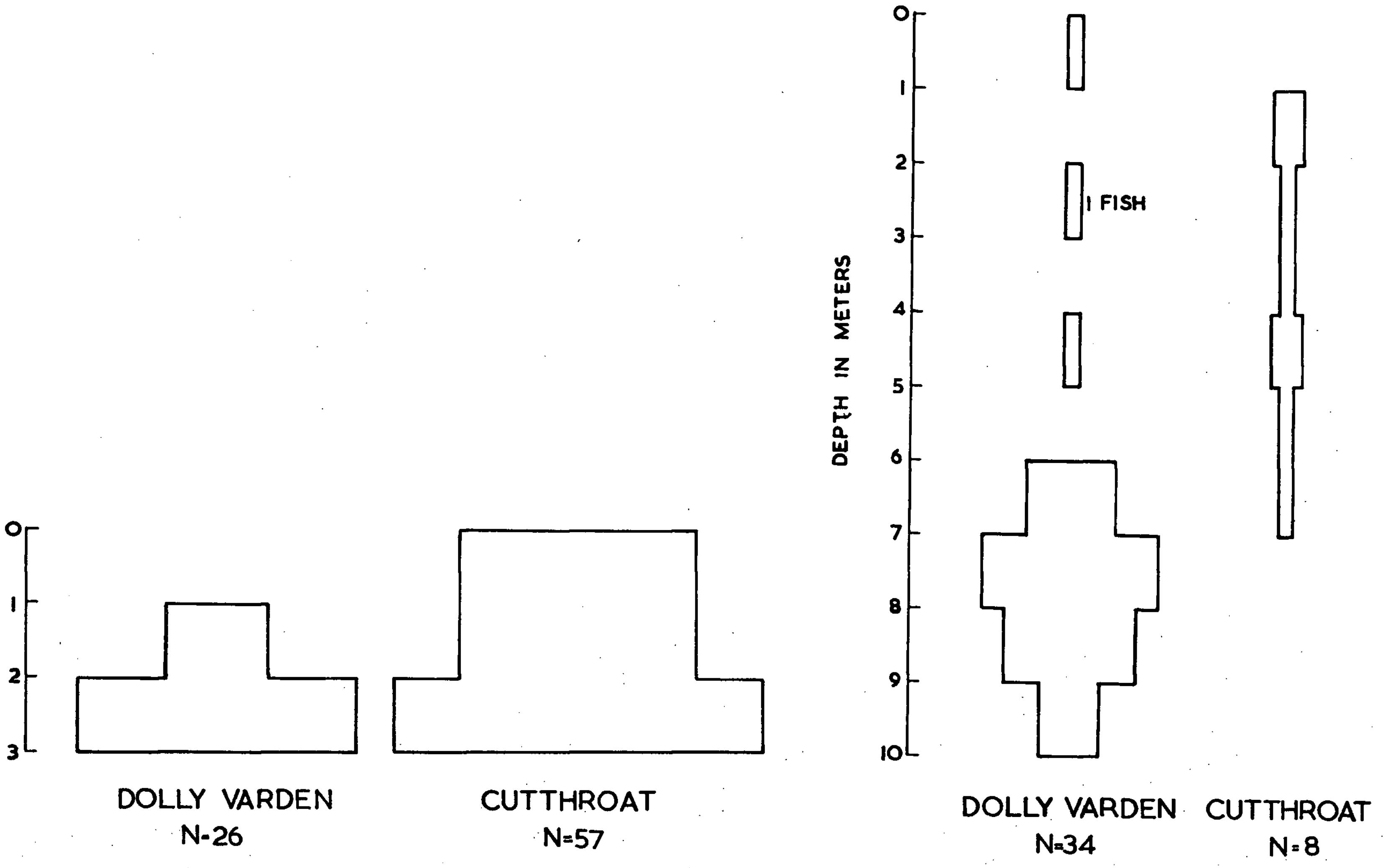

FIG. 11 VERTICAL DISTRIBUTION OF DOLLY VARDEN AND CUTTHROAT TROUT FROM:
A. 3-METER NETS SET PARALLEL TO SHORE IN THE LITTORAL ZONE OF MARION LAKE, JUNE-SEPTEMBER 1967.
B. 10-METER NETS SET IN PHYLLIS LAKE, 15 AUGUST 1967.

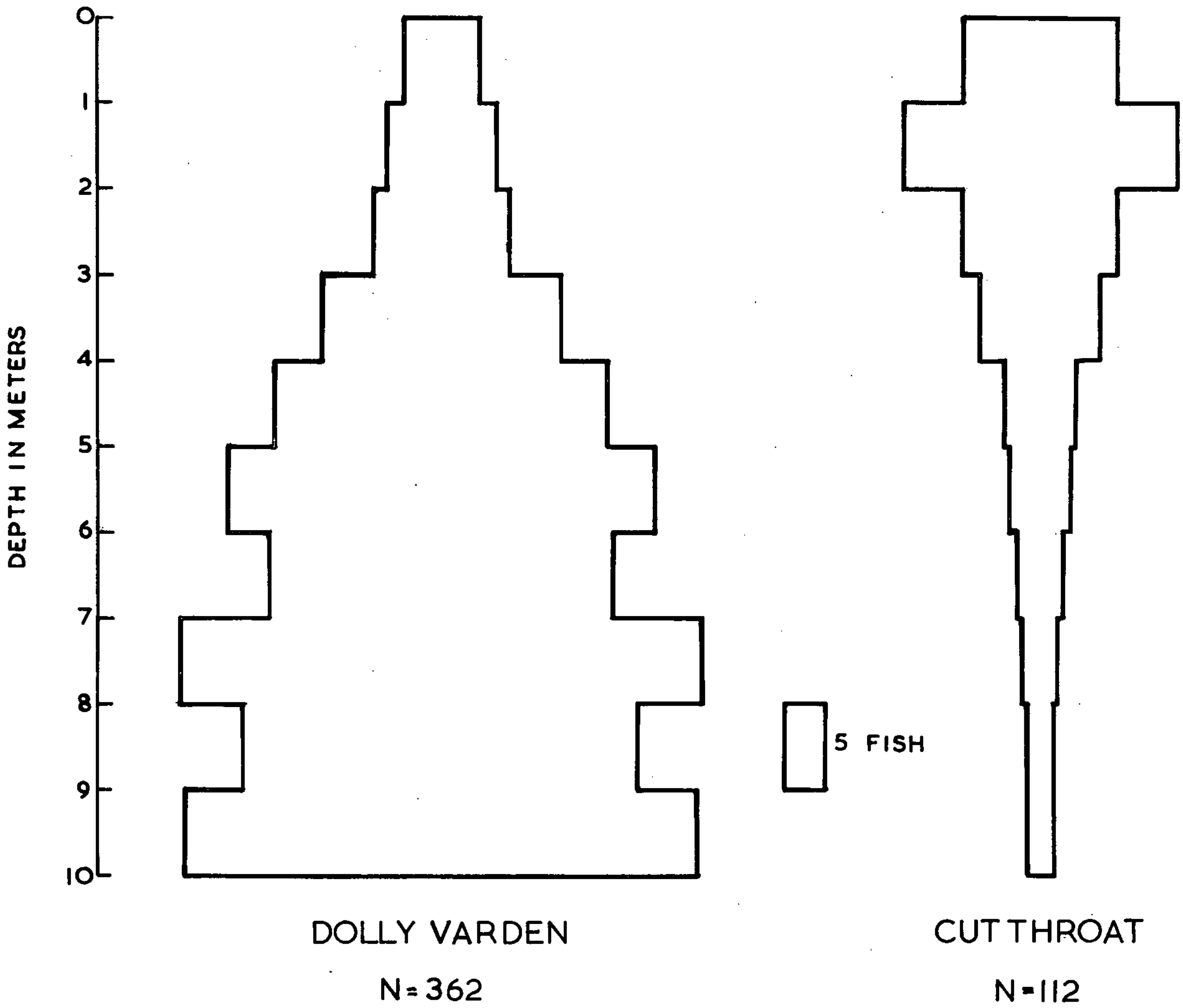

FIG. 12 VERTICAL DISTRIBUTION OF DOLLY VARDEN AND CUTTHROAT TROUT CAUGHT IN 10 M. FLOATING NETS SET IN MARION LAKE MAY 15 – SEPTEMBER 15, 1967. SUMMARIZED DATA INCLUDES 3 NIGHT SETS.

in the day. Consequently, day and night data were pooled.

The proportions of Cutthroat caught during the summer (23 May-22 September, 1967) in shallow (0-3) and deep intervals (4-10 m.) differ significantly from the proportions of Dolly Varden caught in the same depth intervals. The same applies to the distribution of the two species in the five meter nets. Cutthroat were associated with surface waters whereas Dolly Varden were caught in deeper waters. For example, in the 10 m. nets, 75% of the Cutthroat were caught in the interval 0-4 m. whereas only 15% of the Dolly Varden were caught in this same interval.

Figure 11b summarizes the data from a single sample taken from Phyllis Lake (adjacent to Marion Lake) on 15 August, 1967. The pattern of spatial segregation in the two species of fish resembles that for the summer in Marion Lake.

Results of three day sets made in September 1967 (Fig. 13) were separated from the rest of the summer data because of the apparent change in Dolly Varden distribution. Although spatial segregation was still evident there was no longer a concentration of Dolly Varden at the deepest depths. Cutthroat distribution remained relatively unchanged.

No fish were caught during day sets in November and rising fish which were commonly seen in the summer were not observed during either visit. Night sets on two occasions (Fig. 13) caught few fish

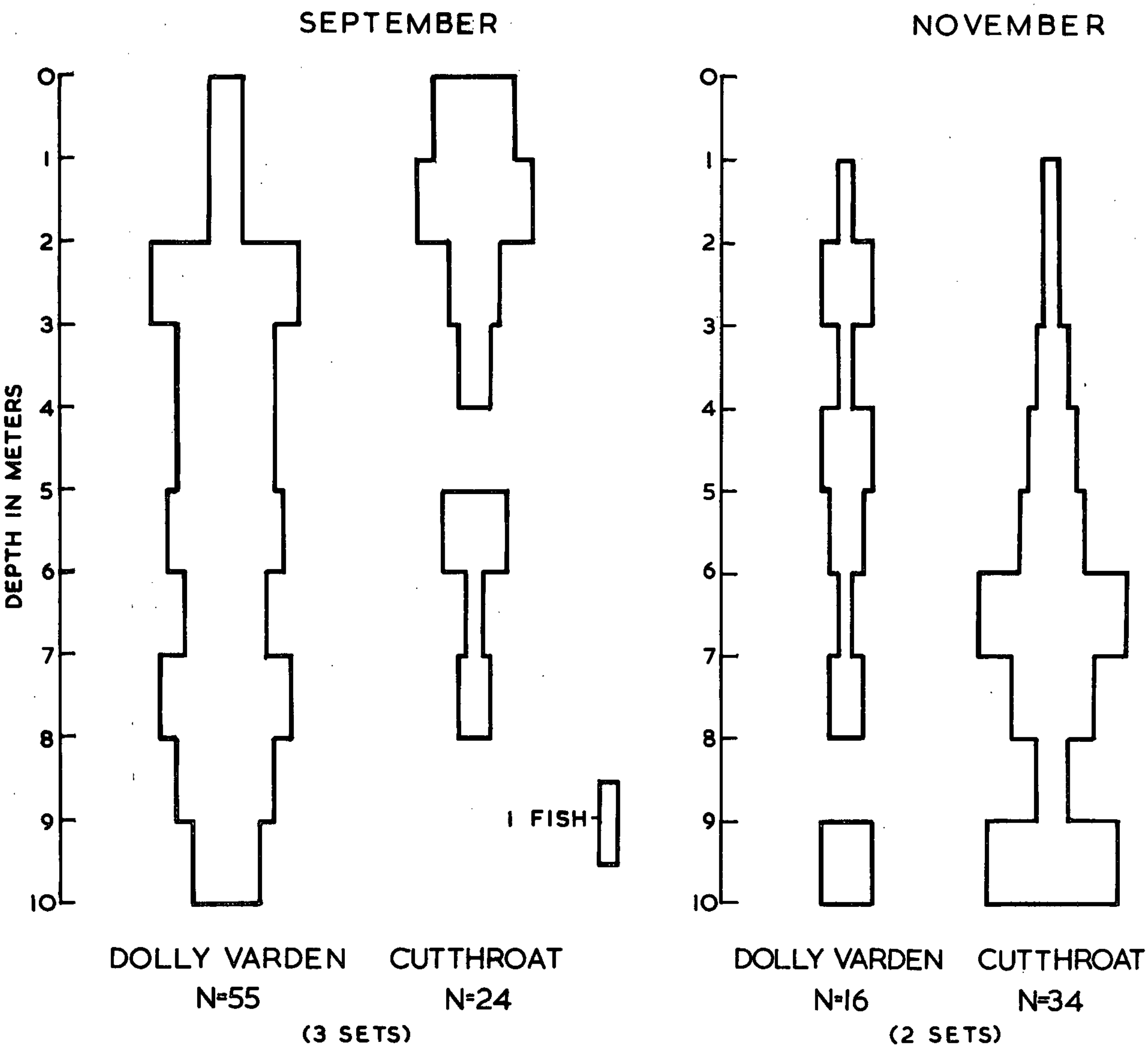

FIG. 13 VERTICAL DISTRIBUTION OF DOLLY VARDEN AND CUTTHROAT TROUT CAUGHT IN 10M. FLOATING NETS IN MARION LAKE SEPT. & NOV. 1967.

but suggested that Cutthroat had moved deeper while Dolly Varden were distributed as in September.

ii) Horizontal Distribution

Results of three meter net sets made parallel to shore in the littoral zone are shown in Figure 11a. Throughout summer twice as many Cutthroat as Dolly Varden were caught in these littoral sets. In contrast, the ratio of catches from the ten meter nets were about three Dolly Varden for every Cutthroat caught. This suggests a horizontal difference in distribution. In an analysis of variance, there is a significant difference ($F = 3.81$ 2, 15 df) between the mean numbers of Cutthroat caught in the onshore, middle and offshore 10 m. nets (Fig 14), with the greatest mean for the inshore nets. For Dolly Varden ($F = 0.32$ 2, 15 df) the differences were not significant, - the mean catch was the same in the onshore, middle and offshore nets.

iii) Randomness within nets

Throughout the summer it was observed that Dolly Varden were caught in clusters in the nets whereas Cutthroat were usually alone or rarely in two's or three's. Dolly Varden caught in the 25.4 mm. and 38.1 mm. mesh of the 10 m. nets were highly clumped in distribution ($\chi^2 = 21.1$ for 2 d. f. and $\chi^2 = 37.3$ for 2 d. f.).

Cutthroat caught in the 38.1 mm. mesh of the 10 meter nets (first four meters) were moderately dispersed ($\chi^2 = 10.8$, 2 d. f.),

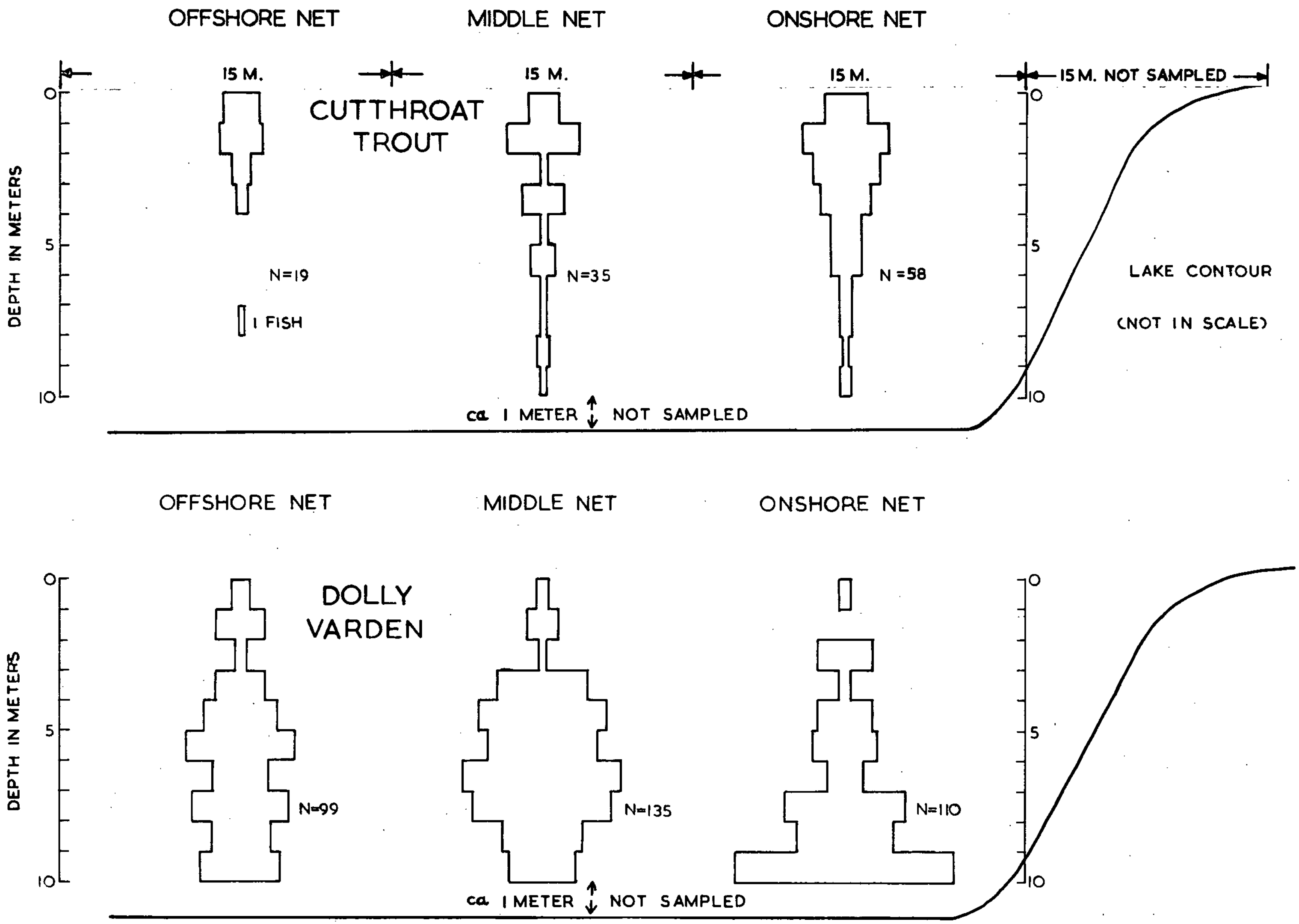

FIG.14 VERTICAL AND HORIZONTAL DISTRIBUTION OF DOLLY VARDEN AND CUTTHROAT TROUT CAUGHT IN THREE NETS (EACH 10M. DEEP, 15 M. LONG) AT STATION 1 IN MARION LAKE, JUNE - SEPTEMBER, 1967.

but in the 5 meter and 3 meter nets (25. 4 mm.) were randomly distributed (X^2=5. 36 and 2. 98 respectively both with 2 d. f.).

iv) Size class distribution differences

Cutthroat (n=13) taken at depths greater than 6 m. were larger than average and 10 were over 230 mm.

During summer the Dolly Varden caught in shallow waters (less than 3 meters) were often small (100-150 mm.). Chi-square analysis of proportions caught in the 25. 4 and 38. 1 mm. mesh for the respective depth intervals of 0-3 and 4-10 m. did not suggest any significant differences at the 5% level. However, for September proportionately more small fish from the 25. 4 mm. mesh were caught in shallow depths.

5) Age

Specific ages could not be determined conclusively with the data available - particularly for Dolly Varden whose scales were difficult to interpret due to indistinct circuli. It is reasonably certain, however, that most were two years and older. Most Cutthroat taken involved three-and four-year-old fish while some two-year-olds were caught in late summer and fall.

6) Stomach Analysis

a) Placid Lake

A marked seasonal feeding pattern is quite apparent for the Placid

Lake Cutthroat trout (Fig. 15).

In May and early June chironomid pupae were the most important food organisms. As summer progressed there was a change to zooplankters and bottom fauna. In the latter part of June and throughout July Diaptomus spp. and caddis larvae were the most important food items. During late summer chironomid larvae became the major food item. This seasonal change in diet from planktonic foods to bottom dwelling forms coincided with the shift in vertical distribution of the fish (Fig. 8).

By early December, just prior to ice-formation, the main food items were bottom dwelling forms such as caddis larvae, chironomid larvae and some dragonfly nymphs. The zooplankton consumed in December, as well as in September, were mainly cladocerans, in particular, Daphnia rosea and Diaphanosoma leuchtenbergianum.

Winged insects never represented a major portion of the diet of the sampled population but were extensively eaten by a few individuals. This seems paradoxical considering their abundance on the surface of Placid Lake (especially chironomid adults and coleopterans).

Although Cutthroat in Placid Lake took only small amounts of surface insects it is obvious that these fish did utilize a considerable variety of food during the summer months. Throughout the season no particular type of organism was exclusively selected although there was a considerable dependence upon bottom organisms.

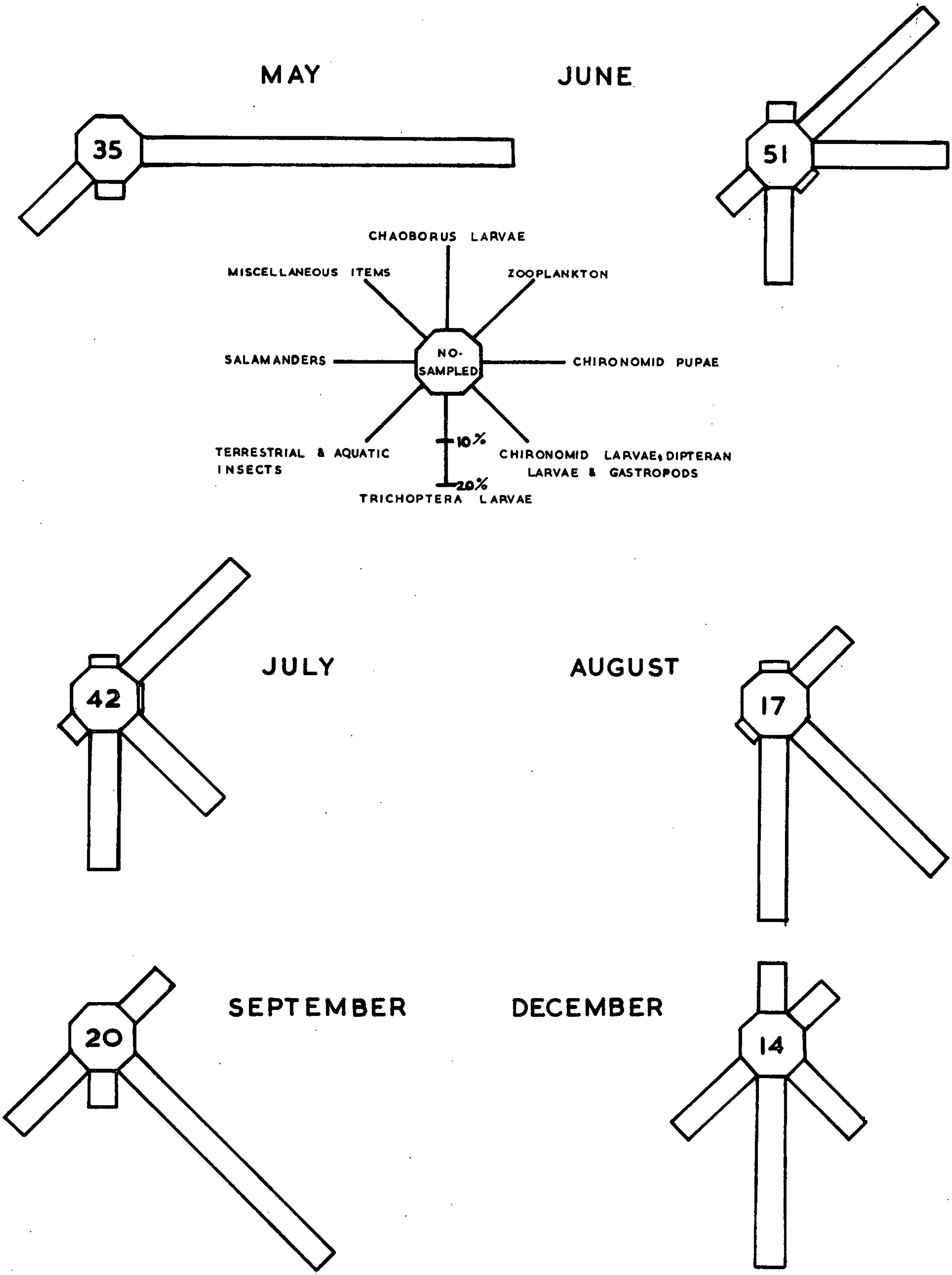

FIG. 15 STOMACH ANALYSIS OF PLACID LAKE CUTTHROAT TROUT IN AVERAGE PERCENT VOLUME, MAY – DECEMBER, 1967.

b) Dickson Lake

Heavy utilization of terrestrial insects by Dickson Lake Dolly Varden for June and July (85 and 50% respectively) is illustrated in Figure 16 (also Appendix Table VI). Because these fish were only caught as they moved upward to the surface toward evening, the stomachs do not necessarily reflect food habits over a 24-hour period. However, if these fish had been feeding heavily on zooplankton or bottom fauna during the day, one would expect these to be more heavily represented in the stomachs of the fish caught at dusk.

In October, zooplankton was the predominant food source (68% by volume) with terrestrial insects and bottom fauna both of secondary importance (13% each by volume).

c) Marion Lake

i) Bottom organisms

Trichoptera larvae and pupae were important food items for both species during July and November (Fig. 17). In the remaining months trichopteran larvae were found regularly only in Cutthroat.

In July day samples, Cutthroat and Dolly Varden stomachs contained trichopteran larvae to the extent of 33 and 32% total volume, respectively. These larvae were almost exclusively <u>Mystacides alafimbriata</u> with very few Limnephilidae. Note that the vertical distribution of <u>M. alafimbriata</u> found in the Ekman samples was 0-6m. Stomach samples of both species from night sets in July (Fig. 17) contained more

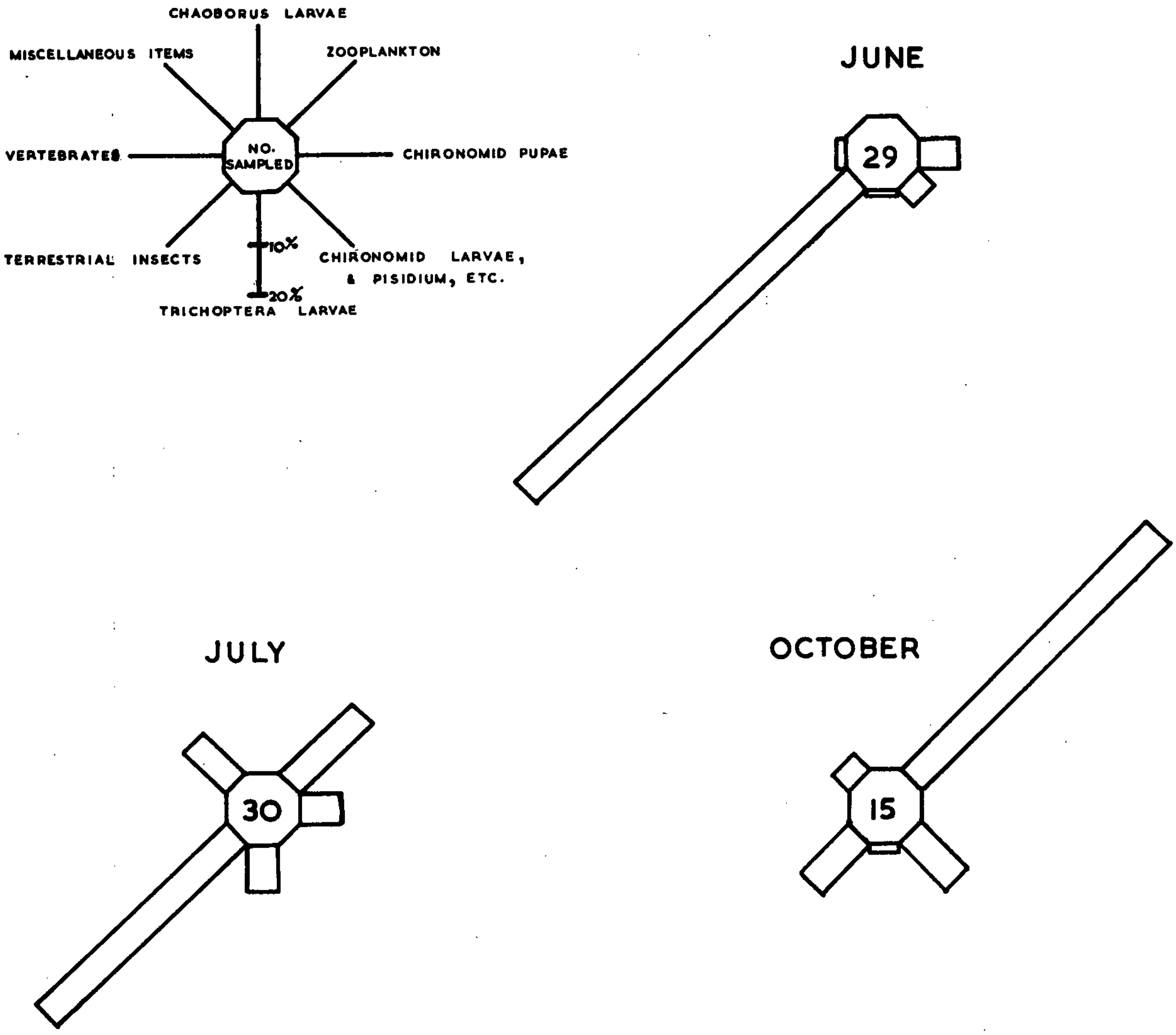

FIG. 16 STOMACH ANALYSIS OF DICKSON LAKE DOLLY VARDEN IN AVERAGE PERCENT VOLUME. 1967

emerging trichopteran pupae than larvae. Unfortunately the pupae could not be identified.

In November, large volumes of caddisfly larvae were found in both species (61% and 79% respectively for Cutthroat and Dolly Varden). Limnephilidae and Glyposyche irrorata were quite numerous with counts ranging from 25-50 larvae per stomach. Only an occasional M. alafimbriata was found.

During May trichopteran larvae were over half the diet (56%) of the Cutthroat with Ptilostomis sp., Glyphosyche irrorata and limnephilini represented in considerable numbers. For the rest of the summer, Mystacides alafimbriata were consumed by Cutthroat most frequently. It is not surprising to find caddisfly larvae of considerable importance to Cutthroat since bottom samples (Appendix table I) suggest them to be in greatest abundance in the littoral areas and figure 11 show that Cutthroat were located in the shallow depths and onshore during the entire summer.

All remaining food items normally associated with the bottom were grouped together. Chironomid larvae, Pisidium and other dipteran larvae were the main food items by volume in this category.

It is obvious (Fig. 17) that these bottom organisms were of primary importance only to the Dolly Varden. This category of food never exceeded 2% of the average volume of the Cutthroat diet during the sampling program. In May, August and September 74%, 58% and

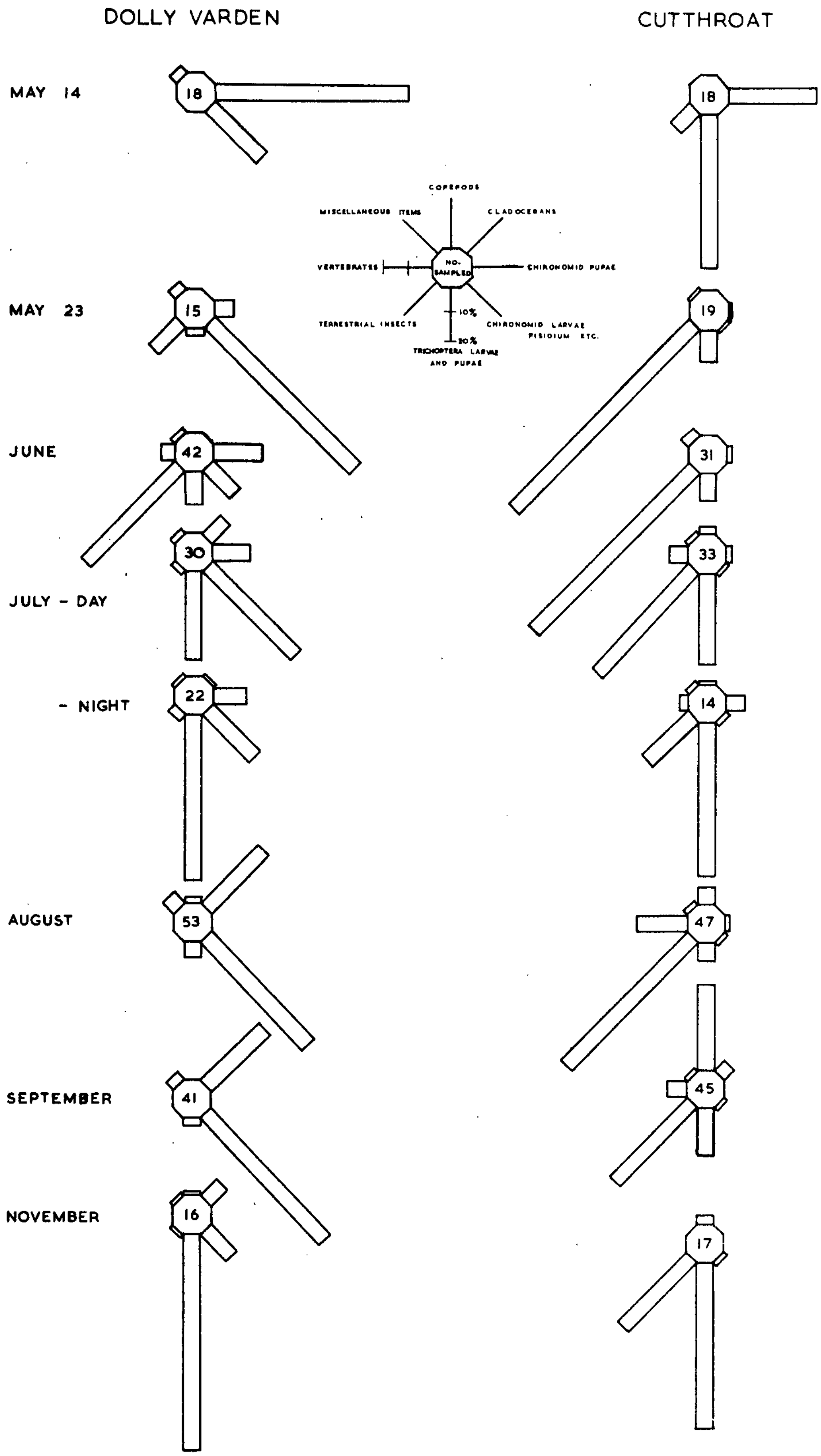

FIG. 17 STOMACH ANALYSIS OF MARION LAKE DOLLY VARDEN AND CUTTHROAT TROUT IN AVERAGE PERCENT VOLUME, SPRING-AUTUMN, 1967.

62% respectively of the entire Dolly Varden diet was composed of benthic organisms, predominantly chironomid larvae.

Pisidium contributed appreciably to the Dolly Varden diet throughout the summer, as well as November. By occurrence, they were found in one of every three fish analyzed (Appendix Table VIII) and 25-30 per stomach were common. In contrast, not a single *Pisidium* was found in the Cutthroat stomachs during the entire study. Ceratopogonidae and Tipulidae larvae were found occasionally in the stomachs of both species, more frequently in Dolly Varden.

ii) Chironomidae pupae

Chironomidae pupae were of considerable importance to the diets of both species in early May (Fig. 17). These high percentages (69% - Dolly Varden; 32% - Cutthroat) of pupal consumption were probably in response to initial spring emergence of chironomids since the percentage volume and average volume percentages (Appendix Table VII) both decrease after early May. Chironomid pupae were of some importance to the Dolly Varden diet during June (19% volume, 36% by average of volume percent) and diminished in importance as summer progressed. They were completely absent in the stomachs after early August.

iii) Zooplankton

Zooplankton does not appear to become abundant in Marion Lake until mid-July (Fig. 17) and does not contribute appreciably to the diet of either species until August. In general, Dolly Varden consumed cladocerans, whereas Cutthroat preyed almost exclusively on the copepod *Diaptomus leptopus.* *Holopedium gibberum* was the dominant cladoceran consumed by Dolly Varden during July and early August. In late August and September, however, *Daphnia rosea* and *Ceriodaphnia sp.* became dominant plankters in their diet. *Polyphemus pediculus* and *Bosmina sp.* were found occasionally. The cladocerans, although available, did not form an appreciable percentage (less than 5%) of the Cutthroat diet at any time.

iv) Terrestrial Insects

With the exception of June, terrestrial insects played a very minor role in the diet of Dolly Varden. In contrast, the Cutthroat diet at times consisted exclusively of insects caught at the surface. In May, June and August, more than 65% of the entire volume was composed of winged insects. The greatest contributor to these large volumes were coleopterans (Staphylinidae, Cantharidae, Carabidae and Elateridae). These beetles were most numerous in May and June with *Zylodromus concinnus*, *Pelecomalium testaceum*, and *Podabrus diversipes* being exceedingly abundant.

Second in importance were dipteran adults represented primarily by Chironomidae, Simulidae, Culicidae, and Empididae. These soft-bodied forms were consumed throughout the summer but were most common during early summer.

Hymenoptera were also of importance to the Cutthroat diet - particularly in May and early June when Camponotus herculeanus (Family Formicidae) contributed considerably.

The percentage occurrence and importance of terrestrial insects in the Cutthroat diet decreased as the summer advanced. Heteroptera and Homoptera did, however, increase substantially during late summer with leaf hoppers (Family Cicadellidae) contributing in considerable quantities during mid-summer whereas stink bugs (Family Pentatomiidae) were common during August and September.

The negligible amount (10% of the volume) of terrestrial insects consumed on 14 May 1967 as compared to the large volume (86%) on 23 May 1967 probably was a result of the differences in the limnological conditions within the lake and or, the meteorological conditions outside it. As stated earlier, 13 May was the last day of ice-cover and this would give little chance for insects to accumulate on the surface waters. Ten days later, however, and with several days of warm weather, over-wintering adult insects would have had a chance to fly and be blown onto the lake hence becoming available to the fish. This possible increase in terrestrial insect availability may have brought about a switch in the Cutthroat diet and also may have been at least partly responsible for the concomitant change in the Cutthroat distribution (fig. 10).

v) Vertebrates

Due to the advanced state of digestion vertebrate remains were difficult to identify. Increased vertebrate predation by larger Cutthroat occurred as summer advanced (Appendix Table VIII), but this could be attributed to nothing more than sampling variation. The opportunistic feeding behaviour of larger Cutthroat was evidenced by the occurrence of a shrew (genus Sorex) and a salamander (genus Ambystoma) in two large fish caught in September. In all other cases the vertebrate remains appeared to be younger fish. Vertebrate predation by Dolly Varden was almost negligible (only two fish contained vertebrate material during the sampling program).

vi) Miscellaneous Items

Included in this category were plant material, dirt, and some unidentifiable food organisms. Although difficult to quantify, it was often noted that in the Dolly Varden stomachs where chironomid larvae and Pisidium sp. were present, plant material, sticks, seeds, and dirt were also present. This gives indirect evidence that Dolly Varden may "grub around" in the mud when searching for food.

7) Food Habit Variation

Throughout the summer variation in the Cutthroat diet was negligible with terrestrial insects and caddisfly larvae totalling 65%

or more of the volume. However, during September these two items only total 57% as _Diaptomus leptopus_ composed 31% of the diet.

As indicated in Appendix Table VIII, the dominant food of Dolly Varden varied considerably with chironomid pupae and larvae, _Pisidium_, trichopteran larvae-pupae and cladocerans all being dominant at some time during the summer months.

Food types commonly shared (greater than 10% of the total volume) were chironomid pupae and terrestrial insects in early summer, and trichopteran larvae in July and November. During August and September no food items were shared to any extent although limited predation by both species on _Daphnia rosea_ and _Ceriodaphnia_ occurred during early September.

8) Seasonal Variation

Some insight into seasonal change in diet can be gained by comparing early May and November samples with the rest of the summer data. Greatest changes occurred within the Cutthroat diet where surface insects dominated throughout summer, but trichopteran larvae were predominant before and after the summer months. These changes appear to closely follow the seasonal occurrence of insects on the surface water. Very little seasonal change in diet occurred within the Dolly Varden. They depended upon bottom organisms throughout the period studied with predation on chironomid pupae and zooplankton being important exceptions.

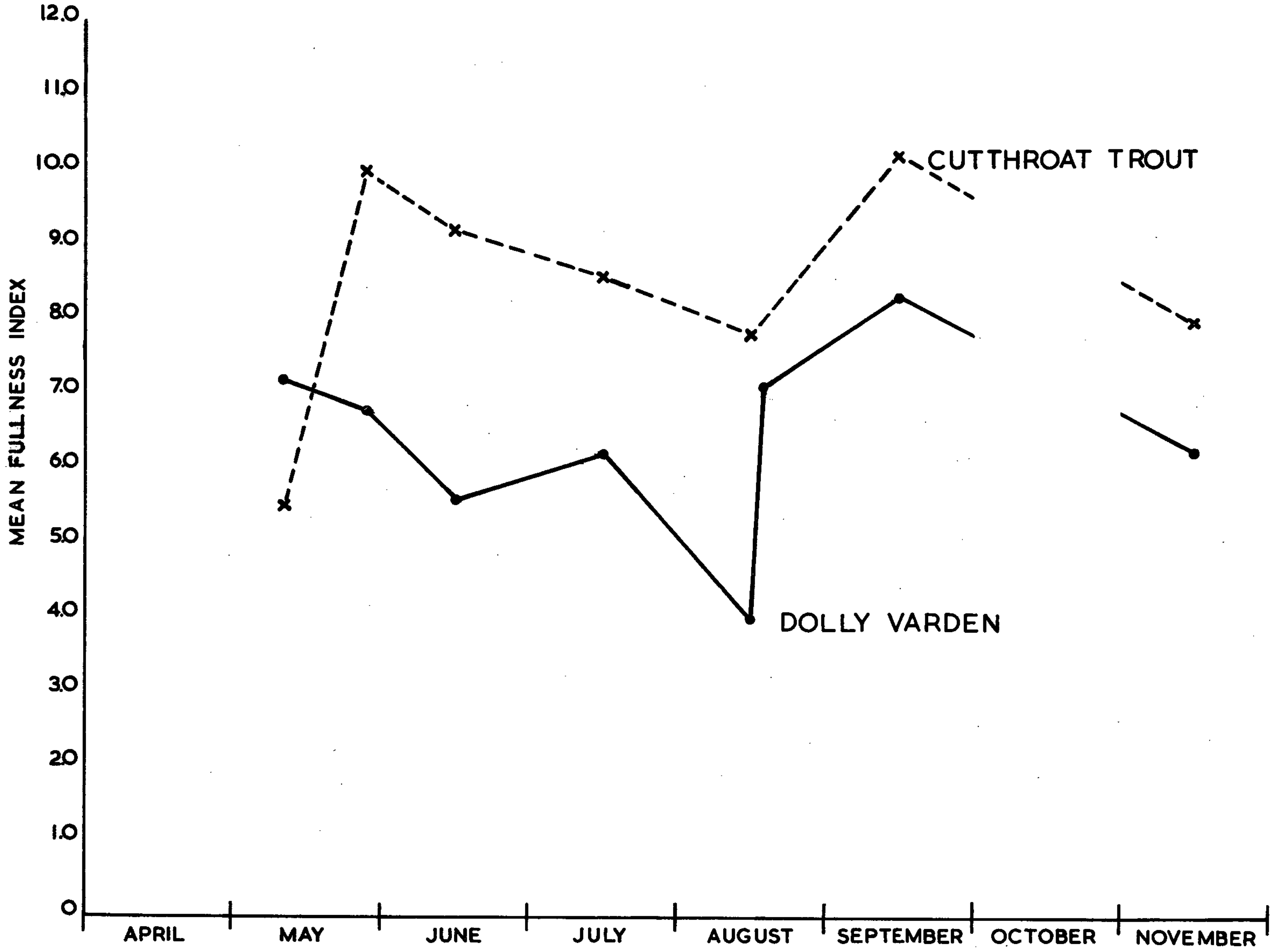

FIG. 18 MEAN FULLNESS INDEX VALUES FOR DOLLY VARDEN AND CUTTHROAT IN MARION LAKE, 1967.

Figure 18 graphically represents mean fullness index changes which occurred in both species throughout the sampling program. High values in early spring were followed by gradual decreases as summer advanced. Lowest values were recorded in August for both species when the highest incidence of empty stomachs was encountered. Except for mid-May, Dolly Varden stomachs consistently had smaller volumes of food in comparison to the Cutthroat.

9) Variation Between Size Classes

Figure 19 suggests differences in feeding habits between various size classes of Dolly Varden and Cutthroat. Very little difference is apparent between the 100-150mm and 150-200mm size groups of Cutthroat trout. However, fish greater than 200mm tended to be more predaceous on small fish and other vertebrates.

The smaller size class of Dolly Varden tended to feed heavily on plankton during the late summer months, whereas the 150-200mm size group feed primarily on bottom fauna. This rather marked difference in feeding habits between size classes was not apparent, however, when zooplankton was relatively sparse, e.g., in July.

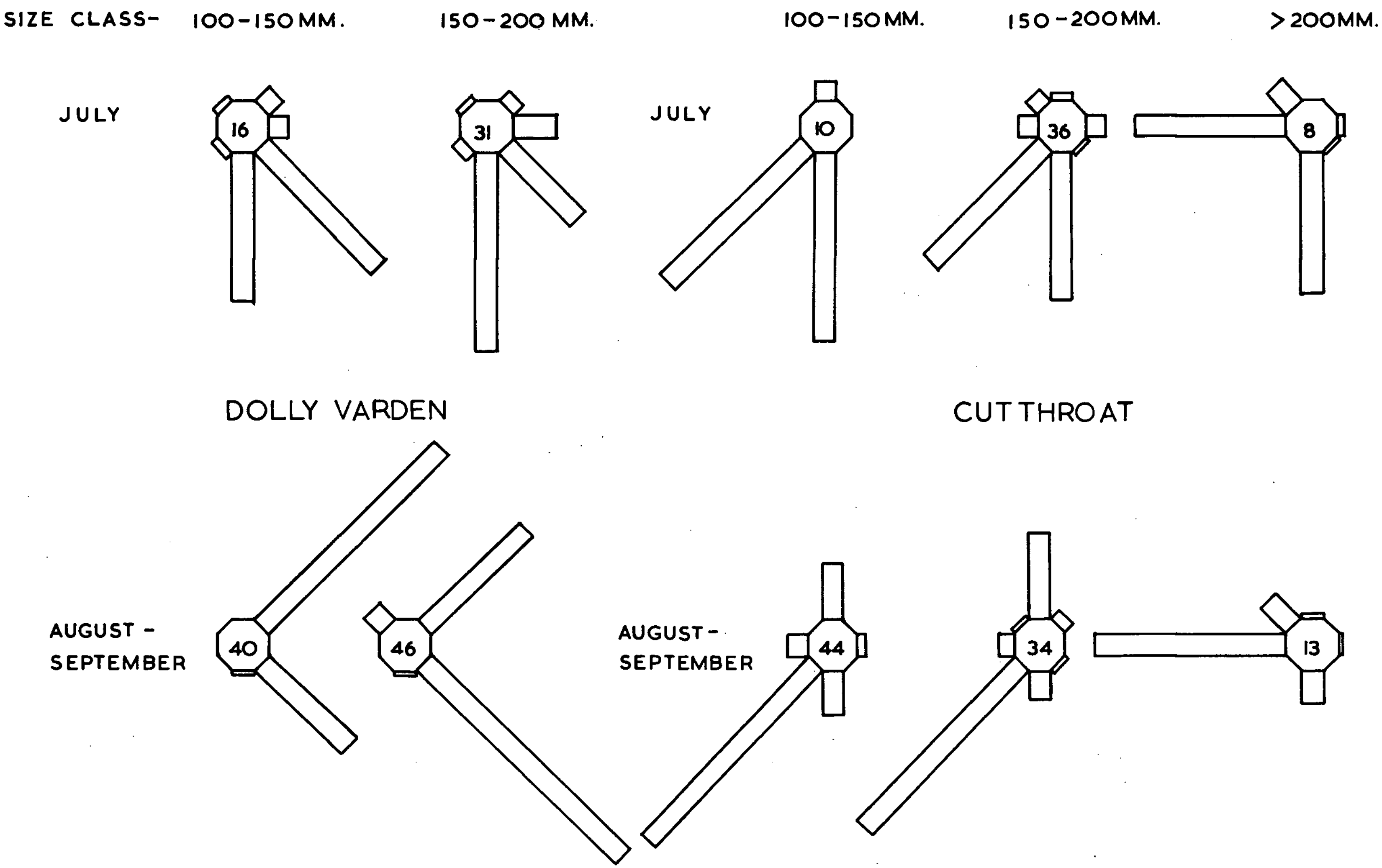

FIG. 19 SIZE CLASS FOOD HABITS FOR MARION LAKE DOLLY VARDEN AND CUTTHROAT FOR JULY AND AUGUST - SEPTEMBER, 1967. REFER TO KEY OF FIG. 17.

TABLE I. A summary of spatial distributions and feeding habits of Cutthroat trout and Dolly Varden in the three study lakes, spring, summer and fall, 1967.

	Dickson Lake	Marion Lake		Placid Lake
	Dolly Varden	Dolly Varden	Cutthroat	Cutthroat
Spring				
Distribution	not sampled	concentrated near bottom	concentrated near bottom	near surface
Food Habits	not sampled	chironomid pupae and bottom organisms	caddis larvae and chironomid pupae	chironomid pupae
Summer				
Distribution	deeper during day, surface at night	concentrated near bottom	surface and littoral areas	near surface and later near bottom
Food Habits	terrestrial insects and zooplankton	bottom organisms	terrestrial insects	zooplankton and bottom organisms
Fall				
Distribution	deeper during day, surface at night	near bottom and mid-water	concentrated near bottom	concentrated near bottom
Food Habits	zooplankton	zooplankton and caddis larvae	caddis larvae	bottom organisms

V. DISCUSSION

Spatial distribution and food habits of Cutthroat and Dolly Varden from the three lakes studied suggest marked differences between the two when coexisting and when living separately (Table I).

Summer vertical distributions of the allopatric char and trout are considerably different. Dolly Varden from Dickson Lake undergo nocturnal vertical and horizontal migration into shallow areas during dusk and evening.

Cutthroat in Placid Lake show no noticeable diel change in distribution, but they did change their distribution seasonally. During early summer these trout were caught in surface waters, but in late summer they were largely restricted to deeper parts of the lake (4-6 meters). Factors governing their distribution appear to be limnological in nature. Very warm surface waters and low oxygen levels at 4-5 meters were recorded during the summer and appeared to force the fish into a depth where oxygen and temperature were tolerable.

Vertical distributions of the two coexisting species in Marion Lake clearly illustrate striking differences during the summer (Fig. 12). Cutthroat trout remained near the surface and shore throughout the summer, whereas Dolly Varden inhabited greater depths. Spatial segregation between sympatric species of fish has also been demonstrated by Nilsson (1955, 1961) for brown trout and arctic char. Everhart and Waters (1965) have recorded a similar phenomenon for arctic char and brook trout in some lakes in Maine.

Hartman (1965) has demonstrated that spring and summer microhabitat segregation of juvenile coho salmon and steelhead trout broke down during fall and winter. Nilsson (1967) points out that Hartman's field and experiment evidence suggests interactive segregation may be seasonal in occurrence. The vertical distributions of Cutthroat and Dolly Varden in Marion Lake (Figs. 10-14) support this view. In spring, vertical distributions of both species were very similar; both were found together in the deeper areas of the lake. As summer progressed, spatial segregation was quite obvious. In fall the distribution of at least the Cutthroat had changed with the largest portion of the catch taken at the greatest depths. Indeed, the fall distributions appear more similar to early spring (14 May 1967) than to the summer distributions. Furthermore, these fall distributions suggest that both species might be associated with the bottom at onset and during winter. Although offered only as speculation, this view seems logical since it would be of little advantage to either species to be surface orientated (immediately underneath the ice) where little food may be present.

As implied earlier, the three lakes used in this study were dissimilar. Nevertheless, it seems relevant to compare catch distributions from all three lakes. Dickson Lake Dolly Varden undergo vertical movements towards surface at dusk during summer and autumn. No such movement was detected in Marion Lake Dolly Varden and this evidence suggests that some factor(s) may be operating to restrict their movements. Presence of a competitor or shallow depth of the lake are two possibilities. However, any explanation accounting for different distributions of Dolly Varden in the two lakes must also take into account those factors which stimulate vertical movements such as spawning migrations, specific response to a migratory invertebrate or others as discussed recently by Northcote (1967).

Cutthroat from Placid Lake appeared to have a similar early summer distribution to those in Marion Lake. Furthermore, neither population showed obvious diel vertical or horizontal movements. Cutthroat from Placid Lake did, however, change their distribution by mid-summer whereas those from Marion Lake remained near the surface. Distribution changes within a season were noted for allopatric Cutthroat and daily changes for allopatric Dolly Varden. Neither of these two phenomena were evident in the summer distribution of Marion Lake fish.

Food habits of Placid Lake Cutthroat were considerably different from those of Dickson Lake Dolly Varden. Terrestrial insects and zooplankton were predominant in the diets of Dolly Varden whereas Cutthroat fed primarily on planktonic and bottom dwelling organisms. These results are contrary to those of Nilsson (1965) who studied allopatric populations of brown trout and arctic char and concluded that "trout and char show considerable similarities in feeding habits when living in separate populations."

The assumption made by Nilsson in formultating the above statement was that the lakes and their faunas be reasonably similar and such was the case in Nilsson's work (Nilsson, 1965). Placid and Dickson Lakes differ considerably however in their morphometry and limnology and, consequently, some caution must be made in comparing their fish populations. For example, because the bottom fauna of Dickson Lake was relatively poor, the Dolly Varden fed opportunistically, therefore consuming large quantities of surface insects during June and July (87% and 50% respectively). Because the lakes are dissimilar there is no reason to expect the food habits of the respective fish populations to be similar. However, for the purposes of this study, it is important in itself that these fish do respond differently to variable environmental and biological conditions.

Further insight into the process of segregation can be gained by analyzing food habits of the species where they occur together. Nilsson (1965), on the basis of extensive stomach analysis, has hypothesized that food habits of sympatric salmonid species would be dissimilar whereas allopatric populations have similar food habits. Stomach analysis from the Marion Lake fish adds further support to this hypothesis.

As might be anticipated from viewing the distribution data, the "surface orientated" Cutthroat during the summer fed primarily on surface foods. Dolly Varden fed on a much wider range of food but concentrated on bottom fauna (especially chironomid larvae and Pisidium) and plankton. In general, the food habits reflect the respective spatial distributions of the two species. This is indicated by the diets of fish caught on 14 May 1967. Cutthroat consumed large numbers of tricopteran larvae and chironomid pupae while Dolly Varden consumed large numbers of chironomid pupae. The distributions of the char and trout were very similar when both were near the bottom. Ten days later when spatial segregation was evident there was a corresponding change in the diets of both species as shown in Figure 17.

The relatively high percentage of terrestrial insects found in the Dolly Varden stomachs as well as the Cutthroat during June can possibly be explained by what Nilsson (1965), Keast (1965) and others refer to as superabundance or mass development of a food type. They suggest that when a food is in obvious superabundance, feeding habits of fish species will be similar - a readily imagined situation when terrestrial insects fall onto lake surfaces in great numbers during the summer (Norlin, 1967). Coleopteran and Hymenopteran adults were in fact observed in considerable numbers on the surface of Marion Lake during June and early July. Norlin (1967) has substantial evidence on terrestrial insects found on the surface of Lake Blåsjön, Sweden, which supports these observations. He found the peak of numbers occurred in early summer and suggests that variation in abundance will depend upon such factors as air temperature, winds, ice cover, and the life history of the insects.

Nilsson (1960) has presented evidence that food segregation in arctic char and brown trout became most pronounced as the summer advanced. Gee and Northcote (1962) suggest a similar phenomenon with sympatrically occurring leopard dace and longnose dace in the lower Fraser River. In the present study a similar process was recorded in the diets of the Dolly Varden and Cutthroat from Marion Lake. In late summer, Dolly Varden concentrated on Daphnia rosea and chironomid larvae whereas Cutthroat fed on terrestrial insects and Diaptomus leptopus. As shown in Appendix table VII, late summer was the only time that no food item was shared to any extent, indicative of intesified food segregation.

The stomach analysis results from November indicate that food segregation was less pronounced then than during the summer. Both species consumed trichopteran larvae in sizable quantities (Cutthroat-61%, Dolly Varden - 79%) and, although this could be a temporary response to a superabundance of these larvae, the marked changes in diet support the view that the segregation process is a temporary phenomenon. This switch to bottom dwelling organisms also suggests pre-winter feeding conditions since zooplankton and terrestrial insects had diminished by this time.

Another aspect of the feeding habits of the two sympatric species to be considered is the variation in food habits of different size classes. During mid-summer little difference was apparent in the food habits of adults of either species. However, during August-September differences were observed (Fig. 19). The small size class of Dolly Varden fed mainly on cladocerans (60%) whereas the larger fish fed on bottom fauna. There was no marked differences in the diets of small and moderate-sized Cutthroats, but the largest Cutthroat (> 200 mm.) were more piscivorous. Differences in size class food habits have been well documented in the literature. Keast (1965) discusses at some length how intraspecific food competition may be overcome by differences in diets of various sizes of fish in Lake Opinicon, Ontario.

Interspecific competition for food has been adequately described by Larkin (1956) as "the demand, typically at the same time, of more than one organism for the same resources of the environment in excess of immediate supply." But as Northcote (1954) has pointed out, it is extremely difficult to measure whether the demand is greater than the supply. As a result it is rarely possible to demonstrate directly from field work that food competition occurs between fish species. Results from this study were no exception and, at best, only inferences can be made concerning food competition between the sympatric Dolly Varden and Cutthroat trout. For example, during July both species of fish preyed on Mystacides alafimbriata in considerable quantities. Bottom samples did not reveal any "superabundance" of trichopteran larvae during July hence competition for these larvae may have occurred. Because the two species were spatially segregated they could conceivably have eaten these larvae in two separate parts of the lake. Furthermore, since the Ekman dredge does not sample all types of fauna adequately, there is no means of knowing for sure whether the demand was greater than the supply.

It was not the object of this study to distinguish which mechanisms were operating in the segregation process but there may be some value in speculating on what may be functional in segregation of the Marion Lake fish. Nilsson (1967) summarizes his previous papers and proposes that the mechanisms possibly working in the process of interactive segregation are terroriality, exploitation, food fighting, predation and other interference.

In this study, as previously stated, it can only be inferred that food competition occurred and is a factor operating in food segregation of Dolly Varden and Cutthroat trout. In the absence of a fish competitor, Cutthroat consumed bottom dwelling organisms and zooplankton, but concentrated on terrestrial insects and caddisfly larvae in the presence of Dolly Varden. Presumably in the sympatric situation a species restricts itself to those food items which it is best adapted for obtaining (Nilsson 1955, 1960, 1965, 1967; Brian 1956). These authors as well as others have stated that the food optima of sympatric species are not necessarily the ones which seem most favorable to the species when living alone. This appears to be the case in at least the Cutthroat studied in Marion and Placid Lakes.

Nilsson (1961, 1965, 1967) has discussed how certain preferences for a particular food item, learning to avoid competitors and learning to switch from one food type to another may all be functional in segregation of co-existing species. Morphological differences may also be very important in determination of food optima of competing species of fish. Northcote (1954) has discussed the importance of minor differences in mouth parts of two cottid species and Keast and Webb (1966) have considered in some detail mouth and body forms relative to the feeding habits of 14 co-habiting species of fish in a small lake in Ontario. They conclude that structural specializations give certain species ecological advantages over others but at the same time these specializations are not so restricitive as to not allow considerable flexability in feeding habits. According to D. C. Schutz (pers. comm.) large differences occur between mouth parts of Marion Lake Dolly Varden and Cutthroat trout. These differences may aid in specialized feeding and therefore promote segregation.

It is of special interest to note that an occasional Cutthroat or Dolly Varden had eaten predominantly a specific food organism (eg. ceratopogonid larvae) which would, in numbers at least, be much higher than expected. Since the fish appeared to have actively sought out this particular food item over a wide range of choices the question arises as to why and how this occurs. As indicated earlier, Nilsson (1961, 1965, 1967) and others have stressed the importance of learning in fishes as part of the segregation process. I agree with this, and although purely speculative, suggest that part of this learning may be a very special process similar to the "hunting by searching image" principle discussed by N. Tinbergen (1967) and first presented by L. Tinbergen (1960). There is good evidence from bird studies which indicate that once a bird finds a prey item an intensified effort follows in the immediate area seeking to find similar prey items. De Ruiter (1952) has demonstrated such a phenomenon in the case of jays Garrulus glandularius L.) seeking camouflaged stick caterpillars.

It is conceivable that such a searching image principle may be operating in feeding fish. Perhaps the ability to search for specific food items is in part responsible for determining the food optimum of a species and therefore functional in the segregation process.

Territoriality may also be a factor involved in the segregation of Marion Lake Cutthroat and Dolly Varden. Cutthroat distribution within the nets were shown to be either random or dispersed in contrast to the clumped distribution of Dolly Varden. Such distributions in Cutthroat can be interpreted as an indication of either aggressiveness or territoriality, or both. The inference of Cutthroat agressiveness is supported by preliminary laboratory studies (D. C. Schutz, pers. comm.) whereas Newman's lab observations (Newman 1960) on juvenile Cutthroat support the idea of Cutthroat being territorial. These inferences, however, need further confirmation from laboratory studies of adult Cutthroat. In any event, occasional or even rare aggressiveness in the natural environment could reinforce spatial segregation of the two species.

Finally, predation appears to be a mechanism in the segregation process for the two species studies. Both were observed to have fish remains in their stomachs and unless cannibalism was high predation probably would aid in segregation of the two species. This might be expected since Godfrey (1955) has shown both species to be predaceous in Lakelse Lake, British Columbia.

In conclusion, this type of field study has not allowed for an effective test of Nilsson's hypothesis. Food and spatial segregation has been demonstrated for the Marion Lake fish and speculations made as to the possible explanations. However, because of considerable differences between the three lakes it was impossible to positively demonstrate that "--ecological differences between species are often magnified through interaction" (Nilsson, 1967). Unless the lakes are reasonably similar considerable restriction is placed on comparing the behaviour of allopatric and sympatric populations of fish. A means of avoiding this problem is to study several lakes and determine the "average" behavior of the species living alone and compare this to the "average" interaction of coexisting species from several lakes.

Another method of testing interactive segregation aside from those suggested by Nilsson (1967) would be to use one lake and divide it off with enclosures and form allopatric and sympatric populations within the same lake. This theoretical approach overcomes many of the problems faced when comparing lakes and requires serious consideration in future work. Obviously the lake would need to be uniformly shallow and of special dimensions for this type of experiment to work. Alternatively, species taken singly and in combination could be observed in the same lake at different times, although this would require a long time.

VI CONCLUSIONS

1. The vertical distribution and food habits of allopatric populations of Cutthroat trout and Dolly Varden studied were quite dissimilar.
2. Co-existing Dolly Varden and Cutthroat trout in Marion Lake were spatially segregated with Cutthroat being surface and littorally "orientated" while the Dolly Varden were benthically "orientated."
3. The respective spatial distributions of both species corresponded with marked food segregation between the two. Cutthroat consumed surface-caught insects and littoral trichopteran larvae whereas the Dolly Varden ate mainly bottom organisms.
4. Food segregation was maximal during August and September when no common food items were shared to any great extent.
5. Food and spatial segregation of the Dolly Varden and Cutthroat was seasonal, the segregation process not being evident during late spring and fall.
6. The hypothesis of interactive segregation in sympatric species of fish advanced by Nilsson (1960, 1963, 1965, 1967) is supported by data from this study.

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APPENDIX TABLE I. Mean number of bottom organisms per square meter and range of numbers per Ekman sample for Marion Lake, May-September 1967, and Dickson Lake, June 1967.

Month	Depth Interval	chironomid larvae	Pisidium spp.	oligochaetes	Hyallela azteca	ceratopogonid larvae	caddis larvae	other dip-teran larvae	gastropods	numbers of samples
MARION LAKE										
May	0-2m	3386 3-170	977 0-21	1221 6-65	1510 1-89	178 1-11	78 0-4	44 0-3	11 0-1	4
	3-4m	7977 117-287	481 3-25	792 9-37	81 0-4	126 0-15	59 0-3	7 0-1	15 0-1	6
	5-6m	2944 51- 89	502 7-15	296 4- 9	---	15 0- 1	30 0-1	---	---	3
	8-11m	1731 24- 48	89 0- 7	426 2-22	---	---	9 0-1	---	---	5
June-July	0-2m	400 0- 27	573 1-26	2264 20-85	666 5-28	11 0- 6	44 0-4	22 0-2	11 0-1	8
	3-4m	4492 21-252	625 7-29	766 6-40	222 0-20	163 0- 6	7 0-1	19 0-2	7 0-1	12
	5-6m	5398 59-252	585 4-19	270 0-11	---	4 0- 1	11 0-2	4 0-1	---	12
August-Sept.	0-2m	8947 74-528	1254 4-85	799 4-50	1166 1-74	100 1- 3	100 0-4	11 0-1	---	4
	3-4m	4159 60-126	244 1- 8	355 0-12	7 0- 1	---	81 0-4	---	---	6
	5-6m	2449 25-114	318 0-14	192 0-10	---	---	89 0-6	---	7 0-1	6
	8-11m	1257 10- 39	142 0-13	651 7-25	---	---	9 0-1	---	---	6
DICKSON LAKE										
June	0-3m	901 13- 28	344 0-15	---	255 0-23	155 0- 7	100 0-5	44 0-15	---	5
	5-9m	1066 12- 40	244 1-16	---	---	---	44 0-3	---	---	5

APPENDIX TABLE II. Partial list of organisms identified from stomach contents of Marion Lake fish, 1967.

Bottom Organisms		
Amphipods	*Hyalella azteca*	
Trichoptera	Family Limnephilidae	
	Tribe limnephilini sp.?	
	Glyphopsyche irrorata	
	Family Psychomyiidae	
	G. polycentropus sp.?	
	Family Phryganeidae	
	G. ptilostomis sp.?	
	Family Leptoceridae	
	Mystacides alafimbriata	
Zooplankton	*Daphnia rosea*	*Holopedium gibberum*
	Ceriodaphnia sp.?	*Cyclops* sp.?
	Bosmina sp.?	
	Polyphemus pedidculus	*Diaptomus leptopus*
Insects		
Coleoptera	Family Staphylinidae	Family Hydrophilidae
	Zylodromus concinnus	Family Lycidae
	Pelecomalium testaceum	Family Scolytidae
	Family Cantharidae	Family Elmidae
	Podabrus diversipes	Family Dytiscidae
	Family Elateridae	Family Oedemeridae
	Megspinthis sp.?	
	Family Carabidae	
Diptera	Family Chironomidae	Family Ephydridae
	Family Empididae	Family Stratiomyiidae
	Family Asilidae	Family Phoridae
	Family Simuliidae	Family Mycetophilidae
	Family Muscidae	Family Culicidae
	Family Dolichopodidae	Family Syrphidae
Hymenoptera	Family Formicidae	
	Camponontus herculeanus	
	Family Tenthredinidae	
	Family Ichneumonidae	
	Family Apidae	
	Family Cynipidae	

APPENDIX TABLE II. continued

Insects (continued)

Homoptera	Family Cicadellidae
	Family Delphasidae
	Family Pentatomidae
Heteroptera	Family Coreidae
Trichoptera	Family Limnephilidae

APPENDIX TABLE III. Summary of Chi-square tests for vertical distributions of Marion Lake fish for May-September 1967.

Date	Test	Net	Depth Intervals	No. of Fish	Degrees of Freedom	Chi-square	Ho- that the proportions are not different*
14 May	Proportions of cutthroat and Dolly Varden	5m	0-2m 3-5m	c.t. = 40 D.V.= 85	1	0.3	Accept Ho
June-Sept.	Proportions of cutthroat and Dolly Varden	5m	0-2m 3-5m	c.t. = 38 D.V.= 40	1	17.5	Reject Ho
May - Sept.	Proportions of cutthroat and Dolly Varden	10m	0-3m 4-10m	c.t. = 112 D.V.=372	1	126	Reject Ho
July - Aug.	Proportions of cutthroat in day and night - same also for Dolly Varden	10m	0-3m 4-10m	c.t. = 35 D.V. = 174	1 1	0.1 2.9	Accept Ho Accept Ho
June - Sept.	Proportions of Dolly Varden in 25.4 and 38.1 mm mesh	10m	0-3m	D.V.= 405	1	3.2	Accept Ho
Sept.	Proportions of Dolly Varden in 25.4 and 38.1 mm.	10m	0-3m	D.V.= 55	1	9.3	Reject Ho

*5% level of significance c.t. = cutthroat D.V. = Dolly Varden

APPENDIX TABLE IV. Analysis of variance results for horizontal distribution of Cutthroat and Dolly Varden caught in 10 meter nets (Station 1) in Marion Lake, June-September 1967. Data in square root values.

Species	Source	Degrees of Freedom	Mean Square	F
Cutthroat	Time	15	1.064	2.00
	**Place	2	1.9198	3.81*
	Error	30	.50371	
	Total	47		
Dolly Varden	Time	15	1.267	1.94
	**Place	2	.435	0.32
	Error	30	1.3714	
	Total	47		

* Significant at 5% level

** Place = Onshore, Middle and Offshore nets.

APPENDIX TABLE V. Summary of tests of randomness within a mesh size for Cutthroat and Dolly Varden caught in 25.4mm and 38.1mm meshes in Marion Lake, 1967.

Species	Date	Net (meter floating)	Tested Interval	Mesh Size	No. of Fish	d.f.	χ^2	Ho distribution is random *
Cutthroat	May-Nov.	10	0-4m	38.1mm	43	2	10.8	Reject (dispersed)
Cutthroat	June-Nov.	3	0-3m	38.1mm	30	2	2.98	Accept (random)
Cutthroat	June-Sept.	5	0-5m	38.1mm	30	2	5.4	Accept (random)
Dolly Varden	May-Nov.	10	0-5m	25.4mm	84	2	21.1	Reject (clumped)
Dolly Varden	May-Nov.	10	0-10m	38.1mm	124	3	37.3	Reject (clumped)

* 5% level of significance

APPENDIX TABLE VI. Mean volume, percent total volume and average volume percent of stomach contents for Placid Lake cutthroat (May-September and December 1967), and Dickson Lake Dolly Varden (June-July and October 1967). See methods for explanation of terms.

			Caddis larvae + pupae, Mayflies, Dragonfly nymphs			Chironomid larvae, Pisidium spp? etc.			Chironomid pupae			Chaoborus larvae			Zooplankton			Terrestrial Insects			Vertebrates			Miscellaneous Items		
	Species	Number of Stomachs	Mean Volume	% Total Volume	% Average Volume	Mean Volume	% Total Volume	% Average Volume	Mean Volume	% Total Volume	% Average Volume	Mean Volume	% Total Volume	% Average Volume	Mean Volume	% Total Volume	% Average Volume	Mean Volume	% Total Volume	% Average Volume	Mean Volume	% Total Volume	% Average Volume	Mean Volume	% Total Volume	% Average Volume
PLACID LAKE																										
May	c.t.	44	.05	3	3	.01	T	1	1.39	80	88	-	-	-	-	-	-	.29	17	6	-	-	-	T	T	1
June	c.t.	51	.08	21	19	T	1	-	.12	29	35	.02	4	4	.14	37	28	.04	9	13	-	-	-	-	-	-
July	c.t.	42	.12	30	25	.11	26	18	T	1	2	.01	2	5	.14	35	40	.02	4	9	.01	2	1	-	-	-
August	c.t.	17	.16	40	32	.17	43	29	-	-	-	.01	2	7	.06	14	18	.01	2	4	-	-	-	-	-	-
September	c.t.	20	.03	8	6	.22	61	51	T	1	1	-	-	-	.04	11	18	.07	20	24	-	-	-	-	-	-
December	c.t.	14	.14	42	52	.06	18	13	-	-	-	.03	10	17	.03	9	6	.07	22	12	-	-	-	-	-	-
DICKSON LAKE																										
June	D.V.	29	.01	1	1	.02	4	5	.06	7	16	-	-	-	-	-	-	.76	87	75	.02	2	3	-	-	-
July	D.V.	30	.02	9	5	-	-	-	.02	8	7	-	-	-	.04	19	31	.11	50	47	.01	2	3	.03	11	7
October	D.V.	15	.01	2	1	.05	13	9	-	-	-	-	-	-	.25	68	67	.05	13	18	-	-	-	.01	4	5

c.t. = cutthroat   D.V. = Dolly Varden   T = trace

APPENDIX TABLE VII. Mean volume, percent total volume and average volume percent of stomach contents of Marion Lake cutthroat and Dolly Varden (May-September and November 1967). See methods for explanation of terms.

			Caddis larvae plus pupae, mayfly and dragonfly nymphs			Chironomid larvae Pisidium spp. etc.			Chironomid pupae			Copepods Diaptomus leptopus			Cladocerans			Terrestrial Insects			Vertebrates			Miscellaneous Items		
	Species	Number of Stomachs	Mean Volume	% Total Volume	% Average Volume	Mean Volume	% Total Volume	% Average Volume	Mean Volume	% Total Volume	% Average Volume	Mean Volume	% Total Volume	% Average Volume	Mean Volume	% Total Volume	% Average Volume	Mean Volume	% Total Volume	% Average Volume	Mean Volume	% Total Volume	% Average Volume	Mean Volume	% Total Volume	% Average Volume
May 14	c.t.	18	.11	56	30	-	-	-	.06	32	49	-	-	-	-	-	-	.02	10	18	-	-	-	T	1	3
May 14	D.V.	18	-	-	-	.11	27	32	.30	69	59	-	-	-	-	-	-	T	1	3	-	-	-	.01	3	6
May 23	c.t.	19	.23	12	12	.01	1	5	.02	1	2	-	-	-	-	-	-	1.64	86	81	-	-	-	.01	1	1
May 23	D.V.	15	.01	3	6	.32	74	67	.03	7	10	-	-	-	-	-	-	.06	14	10	-	-	-	.01	2	1
June	c.t.	31	.14	10	15	T	-	-	.03	2	4	-	-	-	-	-	-	1.13	84	82	-	-	-	.05	4	2
	D.V.	42	.07	12	7	.08	14	21	.11	19	36	-	-	-	-	-	-	.29	48	29	.03	5	2	.01	2	6
July	c.t.	33	.23	33	36	.01	2	2	.01	2	2	.02	3	3	-	-	-	.32	52	49	.04	7	4	.01	2	6
	D.V.	30	.06	32	16	.09	45	46	.03	13	16	-	-	-	.02	7	11	T	2	2	-	-	-	T	2	-
Night	c.t.	14	.58	57	43	.02	2	3	.08	7	5	.01	1	2	-	-	-	.26	26	34	.03	3	5	.04	2	7
	D.V.	22	.24	60	47	.09	23	23	.05	12	18	-	-	-	.01	1	4	.01	3	2	-	-	-	T	1	6
August	c.t.	47	.03	7	8	T	1	2	T	1	1	.02	6	15	-	-	-	.21	65	58	.07	18	12	.01	2	5
	D.V.	53	.01	6	2	.09	58	42	-	-	-	T	2	-	.04	29	-	-	-	-	-	-	-	.01	6	3
September	c.t.	45	.03	17	18	T	1	-	-	-	-	.05	31	26	.01	4	8	.07	40	43	.01	7	4	T	1	1
	D.V.	41	T	3	3	.07	62	43	-	-	-	-	-	-	.04	32	53	-	-	-	-	-	-	.01	4	1
November	c.t.	17	.32	61	66	.01	1	2	-	-	-	.02	3	4	-	-	-	.18	35	27	-	-	-	-	-	-
	D.V.	16	.35	79	51	.06	13	25	-	-	-	.01	1	6	.02	1	6	.01	1	-	-	-	-	.01	1	-

c.t. = cutthroat D.V. = Dolly Varden T = Trace

APPENDIX TABLE VIII. Approximate percent occurrence of food items in stomach contents of Marion Lake cutthroat and Dolly Varden (May-September and November 1967). See methods for explanation of terms.

Date	Fish Species	Caddis larvae	Caddis pupae	Odonata nymphs	Stonefly nymphs	*Hyalella azteca*	Chironomid larvae	Simulium larvae	Cranefly larvae	Ceratopogonid larvae	*Pisidium spp.*	Gastropods	Leeches	Chironomid pupae	*Ceriodaphnia* and *Daphnia rosea*	*Holopedium gibberum*	*Polyphemus pediculus*	*Bosmina sp.*	*Diaptomus leptopus*	Coleoptera	Hymenoptera	Diptera	Arachnida	Trichoptera	Heteroptera	Homoptera	Odonata	Plecoptera	Vertebrata
May	c.t.	86	3	3	5	14	16	3	3	3	-	-	-	76	-	-	-	-	-	57	41	32	3	11	-	8	-	3	-
June	c.t.	19	22	-	-	-	22	3	3	3	-	3	-	78	-	-	-	-	-	100	60	69	16	16	9	13	3	-	-
July	c.t.	49	36	8	24	8	49	8	2	18	-	2	-	75	-	4	4	2	6	90	39	69	26	20	10	24	4	-	10
August	c.t.	28	8	8	14	-	26	2	-	2	-	-	-	24	6	6	4	4	26	54	52	38	14	32	12	20	4	24	12
September	c.t.	32	10	2	-	6	6	-	2	-	-	-	-	10	22	2	4	-	42	28	40	28	22	14	10	38	16	-	6
November	c.t.	90	20	-	-	5	5	-	-	-	-	-	-	-	5	-	-	-	41	16	41	16	16	16	20	-	-	-	7
May	D.V.	9	-	-	6	9	55	3	9	18	33	6	6	73	-	-	-	-	-	24	18	6	-	-	-	-	-	-	-
June	D.V.	26	52	-	2	-	51	12	12	16	30	5	2	88	9	14	-	-	-	53	19	28	5	7	2	-	-	-	2
July	D.V.	49	36	2	19	21	77	38	15	18	32	9	11	83	2	27	2	2	-	13	-	3	2	2	-	-	-	-	-
August	D.V.	2	-	-	-	-	48	2	-	10	24	8	-	10	56	52	18	16	14	-	-	-	-	2	-	-	-	-	-
September	D.V.	11	-	-	-	5	37	-	3	9	22	4	7	1	45	19	23	15	5	-	1	-	-	-	-	-	-	-	-
November	D.V.	75	-	-	6	13	81	-	6	13	31	13	-	-	44	-	-	-	6	6	-	-	-	-	-	-	-	-	-

c.t. = cutthroat

D.V. = Dolly Varden