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CHARACTER DISPLACEMENT AND VARIABILITY
IN LACUSTRINE SYMPATRIC AND ALLOPATRIC
DOLLY VARDEN (Salvelinus malma)
POPULATIONS

by

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B.A., Oxon., 1970

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

in the Department
of
Zoology

We accept this thesis as conforming to the
required standard

THE UNIVERSITY OF BRITISH COLUMBIA

May, 1973

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ABSTRACT

The object of this study was to investigate character displacement (Brown and Wilson, 1956) and reduction of phenotypic variability with reduction in niche width (Van Valen, 1965). Dolly Varden from one sympatric (Loon Lake) and two allopatric (Dickson and Foley Lake) populations were compared.

Field studies showed that the niche width of sympatric Dolly Varden was less than that of allopatric Dolly Varden owing to food and spatial segregation, confirming results of an earlier study (Andrusak and Northcote, 1971).

Character displacement was evident in pyloric caeca numbers and in certain behavioural responses (spatial distribution and feeding) observed in the laboratory. These were accompanied by reduced variability, also apparent in length distributions within year classes, in the sympatric population compared with an allopatric population (Dickson Lake).

However, character displacement and reduced variability could not be demonstrated for most morphometric characters, presumably because of the complexity of growth processes involved. Effects of overlapping adjacent year classes and of continuous growth of fish body parts (in contrast to comparable studies with birds) obscured interpretation of such characteristics.

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ACKNOWLEDGEMENTS

Financial support for this study came from a National Research Council grant to my supervisor, while I was supported on a Canadian Commonwealth Scholarship.

I am most grateful to my supervisor, Dr. T.G. Northcote, for his encouragement and guidance during this study. Drs. N.J. Wilimovsky, J.D. McPhail and R. Liley read the manuscript and offered useful suggestions.

I thank Mr. Harvey Andrusak for the loan of original data from Dickson and Marion Lakes.

I am grateful to Mr. J. Walters and members of the U.B.C. Research Forest staff for access to and accomodation at Loon Lake; also Canadian Forest Products Ltd. for arranging access to Dickson Lake, and to the B.C. Fish and Wildlife Branch for the loan of much field equipment.

I am particularly grateful to the many individuals who gave me assistance in the field; Mr. Kim Waterman and Miss Regina Clarotto also assisted with analysis of benthos and plankton samples. My thanks go to Mr. Bill Dunford for help with analysis of stomach contents, to Mrs. Dolores Lauriente for the computer data analysis, to Mrs. Gayle Burnison for assistance with figures and to Miss Alice Fedorenko for translation of Russian papers.

Finally I wish to thank my wife Frances for her continual encouragement, patience and assistance throughout the study and for typing the manuscript.

INTRODUCTION

Coexisting populations of trout and char differ considerably in their spatial distribution and diets, both from one another and from populations of the same species living singly in allopatry. This has been shown for brown trout (Salmo trutta) and Arctic char (Salvelinus alpinus) by Nilsson (summarized in Nilsson, 1967) and for cutthroat (Salmo clarki clarki) and Dolly Varden (Salvelinus malma) by Andrusak and Northcote (1971). Schutz and Northcote (1972) showed in laboratory experiments that Dolly Varden from a population coexisting with cutthroat in Marion Lake, near Squamish, B.C., were more substrate oriented and more efficient substrate feeders than trout; the trout, in contrast, hovered in midwater and were more efficient surface feeders. Ecological character displacement (Brown and Wilson, 1956; Kohn and Orians, 1962) or ecological segregation certainly appears to occur when the two species are living in sympatry.

Nilsson (1967), using Brian's (1956) terminology, describes the segregation between trout and char as 'interactive' as opposed to 'selective'. Differences between the two species, when cohabiting, are magnified by interaction, either through direct interference between individuals or by one species exploiting prey with greater efficiency. Selective segregation, in contrast, refers to situations where species are segregated either because of

differences evolved incidentally in allopatry or through reinforcement of existing differences in sympatry, involving a period of interactive segregation until preferences for the reduced ecological niches (Hutchinson, 1957) are stabilized in their respective genotypes. Schutz and Northcote (1972), although acknowledging that 'it is difficult to decide at what point interactive segregation becomes selective segregation if continuous evolutionary differentiation is involved', state that interaction between the two species is probably a minor factor and that innate morphological and behavioural differences seem largely responsible for their segregation when cohabiting in small coastal lakes.

The aim of this study is to examine in more detail the ecological segregation of Dolly Varden coexisting with cutthroat trout, and to determine whether morphological or behavioural character displacement occurs, in order to reveal, if possible, mechanisms of segregation. Morphological character displacement may indicate whether selection for greater specialization has occurred. In addition, phenotypic variability may be decreased by reduction in 'niche width' (Van Valen, 1965) due to the presence of the second species or to the absence of major prey types. This possibility is considered in terms of morphological and behavioural characters.

Populations from three lakes were chosen for the

study; Loon and Dickson Lakes are similar limnologically and contain sympatric and allopatric populations of Dolly Varden respectively. Foley Lake, quite distinct limnologically from the other two lakes, contains an allopatric population of Dolly Varden.

II. DESCRIPTION OF THE STUDY AREAS

1. Loon Lake

Loon Lake ($49^{\circ} 18' 20''$ N, $122^{\circ} 35' 45''$ W) is located in the U.B.C. Research Forest, approximately 47 kilometres east of Vancouver at an altitude of 343 metres. The lake consists of two basins - a steep-sided main basin with a maximum depth of 62 metres and a smaller outlet basin with a maximum depth of 15 metres (Fig. 1). The two basins are connected by a shallow arm, the most extensive littoral area in the lake. Bottom sediments consist mainly of soft mud. The lake contains Dolly Varden and a large population of cutthroat trout but no other species of fish.

2. Dickson Lake

Dickson Lake ($49^{\circ} 19' 0''$ N, $122^{\circ} 5' 30''$ W) is located 84 kilometres east of Vancouver at an altitude of 671 metres (Fig. 2). It is deep, with a maximum depth of 76 metres, and steep-sided, except near the outlet and in the south-east bay which was used as the study area.

Much of the east side of the watershed was logged

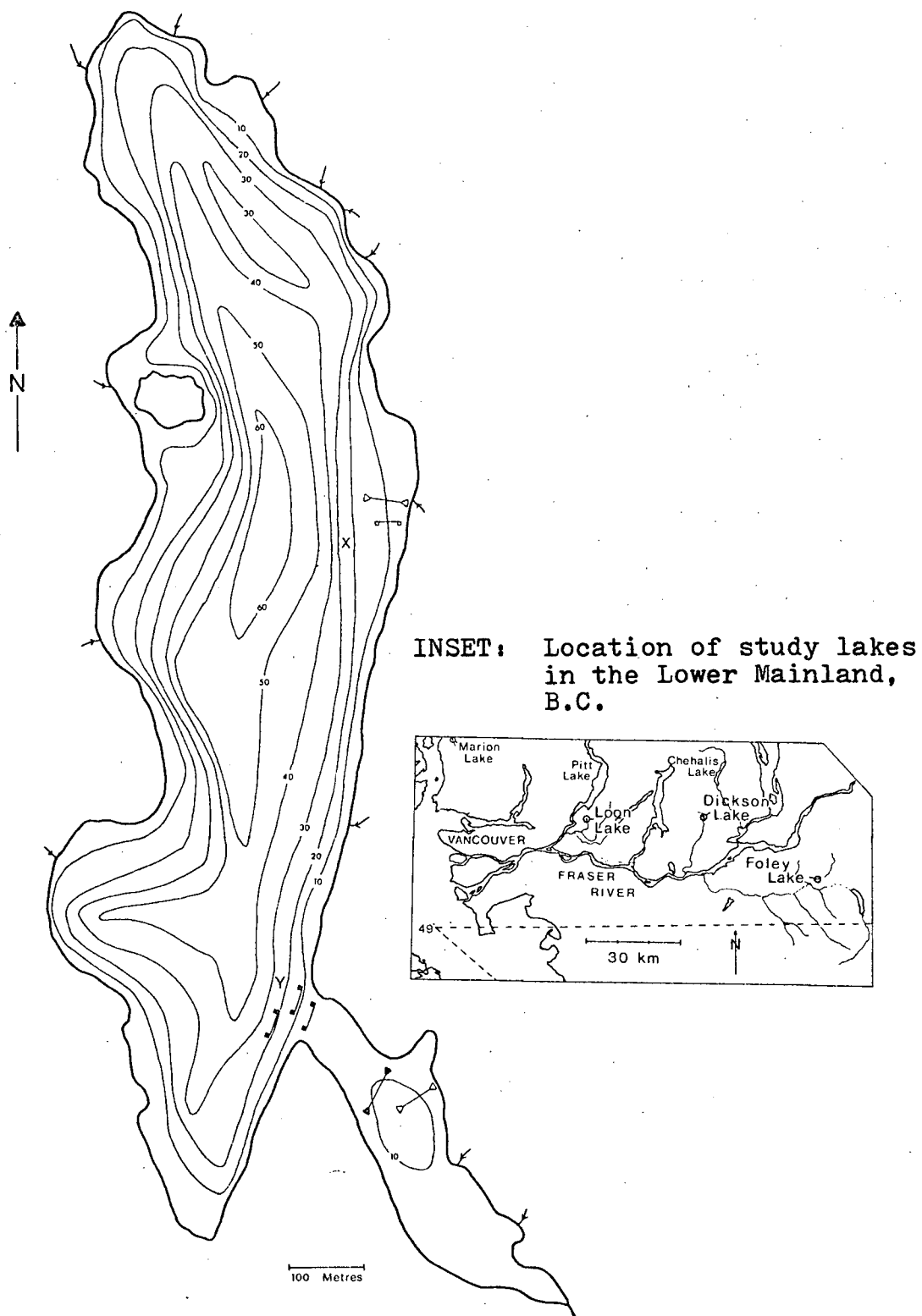


FIGURE 1. Morphometry of Loon Lake. X and Y indicate 1971 and 1972 limnological stations respectively; — and —•— indicate surface-bottom and bottom fished nets respectively, in 1971 (open) and 1972 (solid). Depth contours in metres.

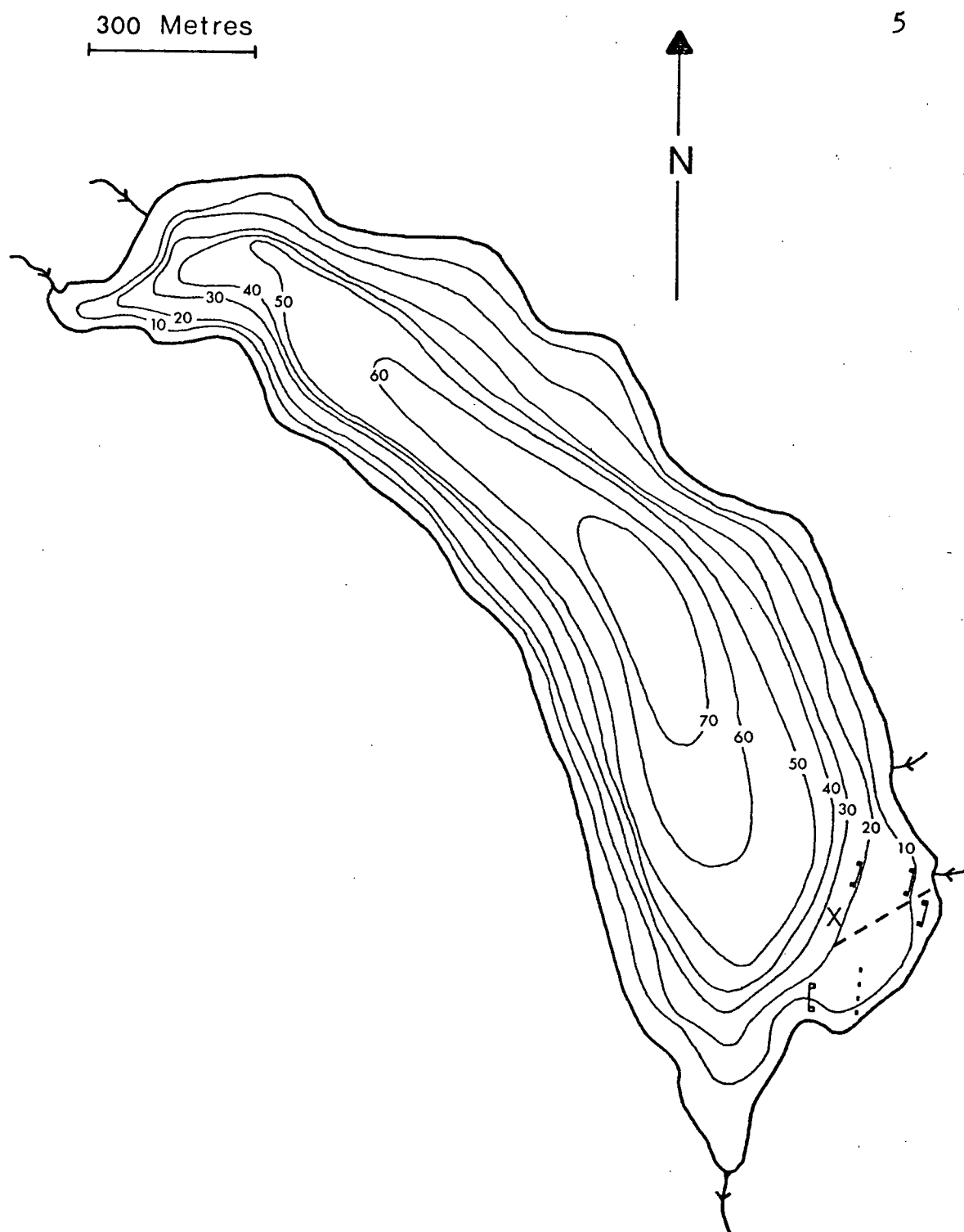


FIGURE 2. Morphometry of Dickson Lake (adapted from Andrusak, MS 1968). Map shows limnological station (X), netting sites in 1971 (□) and 1972 (■) and echo sounding transects in 1971 (----) and 1972 (—). Depth contours in metres.

in 1963. Gravel deltas and sand beaches have formed near the mouths of creeks owing to the friable nature of the surrounding granite. Sediments in the littoral area consist of mud and sand or leaf litter. Further offshore, they consist of mud mixed with flakes of clay.

The lake has a large population of Dolly Varden, the only species of fish present. A study of these was made in 1967 (Andrusak and Northcote, 1971).

3. Foley Lake

Foley Lake ($49^{\circ} 7' 30''$ N, $121^{\circ} 24' 45''$ W) is located 120 kilometres E-S-E of Vancouver at an altitude of 550 metres (Fig. 3). It was apparently formed about a century ago by a rockslide which dammed Foley Creek, a major tributary of the Chilliwack River. Large stands of trees, mainly Western Red Cedar, remain in the eastern half of the lake, flooded to a depth of 20 metres; most have been trimmed to lake level by logging operators.

The major inflow is Foley Creek which enters the lake at the east end; a secondary inflow enters on the north side. The drainage area of the lake is relatively large which, together with its small surface area, contributes to its short retention time (Table I) and to its rapidly fluctuating turbidity and level during the spring runoff. The eastern half of the lake is steep-sided, falling rapidly to 20 metres. The western half of the lake is shallower with more extensive littoral areas; this was

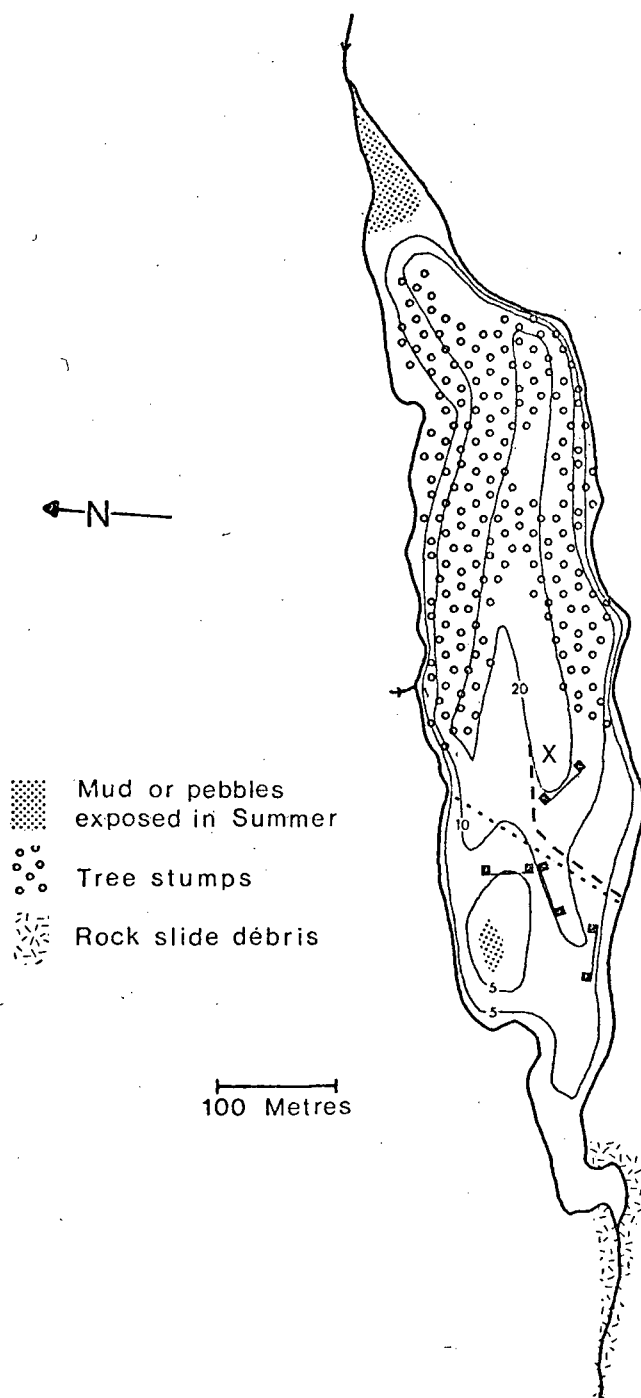


FIGURE 3. Morphometry of Foley Lake. Map shows limnological station (X), netting sites (■) and spring (-----) and summer/fall (—) echo sounding transects. Depth contours in metres.

used as the study area. Bottom sediments here consisted of soft mud.

Water leaves the lake through some wide, shallow pools and then plunges over rockslide debris for several hundred metres before returning to the original stream gradient. This constitutes an effective barrier to upstream migration; rainbow trout (Salmo gairdneri) occur below the rapids but not above (Hartman and Gill, 1968). There is a small population of Dolly Varden, the only fish species present, in the lake.

TABLE I. Morphometric and discharge characteristics of the study lakes.

<u>Lake</u>	<u>Area (m²)</u>	<u>Volume (m³)</u>	<u>Approximate drainage area (km²)</u>	<u>Estimated retention time*</u>
LOON	4.5×10^5	10.8×10^6	4.5	1 year
DICKSON	9.7×10^5	38×10^6	9	6 months
FOLEY	1.1×10^5	1.4×10^6	45	3 days

*based on very approximate estimates of average annual discharge

III. MATERIALS AND METHODS

A. Field Study

1. Temperature

Temperature was recorded with a Lakes Instrument Co. combined oxygen-temperature probe Mark 2. Readings

were taken every metre down to 10 metres and usually at greater intervals thereafter at limnological stations shown on Figures 1, 2 and 3.

2. Bottom fauna

Benthos samples were collected with an Ekman dredge (225 cm^2) near each of the main netting sites. Spring and summer samples were stirred thoroughly; a 1200 ml subsample of the approximately 3800 ml collected was sieved through a screened-bottom bucket (0.85 mm square mesh opening). Fall samples were sieved in entirety. Material remaining in the sieve was preserved with 10% formalin and was sorted later using a binocular microscope (20-30x magnification). The macrobenthos was identified, grouped into five major categories, and expressed as numbers per 100 cm^2 .

3. Zooplankton

Plankton samples were taken in the spring, summer and early fall at Loon and Foley Lakes and in the summer only at Dickson Lake in 1972.

Collections were made using a Wisconsin net with 25 cm internal diameter and 100 micron mesh size. Vertical hauls from 5 m to the surface, from 15 to 10 and from 10 to 5 m were made close to the 20 m netting sites. Vertical hauls were also made from 5 m to the surface close to the 5 m netting sites, in water about 6 m deep. Samples were collected at midday and midnight.

Samples were preserved in the field with 5% formalin. Zooplankton were identified into major categories using a binocular microscope (20 x 30x magnification). Numbers in each category in the Loon Lake fall samples were estimated by dividing the sample into six equal subsamples by volume, analysing one subsample, and returning it to the original sample which was then stirred and subsampled again; the mean of the two subsamples was taken for each of the categories. Numbers in each category for all other samples were counted directly.

Average numbers of major categories were calculated for day and night samples at each depth range. Sample sizes were small, so no significant differences could be established between day and night samples or between inshore and offshore samples. The average of day and night samples was calculated for each depth range; results for the uppermost 5 m are given as the average of inshore and offshore results.

4. Use of gill nets

Floating monofilament gill nets, 5 or 10 m deep, were marked horizontally every metre to determine capture depth of each fish. Each net was composed of three 5 m sections with stretched mesh sizes of 25.4, 38.1 and 50.8 mm. One of the 10 m floating nets was converted for use as a sinking net by the addition of an extra lead line during the spring and summer series at Loon Lake.

Sinking nets were 1.4 m deep, 35 m long, and composed of five 7 m sections of stretched mesh sizes 25.4, 38.1, 63.5, 79.8 and 95.2 mm.

Floating nets, 3 and 6 m deep (smallest stretched mesh size 38.1 mm) and sinking nets, 5 m deep (stretched mesh size 38.1 mm) and 2 m deep (stretched mesh sizes 25.4, 38.1, 50.8 and 63.5 mm) were used in Loon Lake in July 1970 only.

During the fall of 1970, two netting series were made in Loon Lake using replicate floating nets set parallel to shore and sinking nets set perpendicular to shore. Nets were set from midday to dusk in both series and, in one, for a further five hours starting from dusk.

During the summer of 1971, three netting series were made in Loon Lake and one in Dickson Lake; single nets were usually fished for three hour periods and, when pulled, were immediately replaced with identical nets. Nets were set perpendicular to the shore (Figs. 1 and 2).

During 1972, nets were set parallel to the shore to fish the whole water column at 5 m and at 10 m in each lake; 1.4 m nets were sunk to fish the bottom at 10 m in Loon Lake and, in the spring and summer, in Foley Lake (Figs. 1, 2 and 3). At 20 m, 1.4 m sinking nets were fished at the bottom and 5 m floating nets were fished at the surface except in the spring and summer Loon Lake series when a sinking 10 m and a floating 10 m net were fished

close together to sample the whole water column; no nets were fished at 20 m in Foley Lake during the fall of 1972. Day and night nets were usually set for about ten hours each.

5. Echo sounder records

A Furuno Model FM-22D echo sounder with a 50 kHz transducer was used to obtain bottom profiles for depth contour maps of Loon and Foley Lakes and to provide additional information on fish distribution. The zero band on the sounder obscured the upper one to three metres. All traces were made in a boat moving at approximately 2 km/hour.

6. Fish collections

All nets were picked immediately after they were pulled, with the exception of the September 1970 night series. A number-coded waterproof tag was slipped into the mouth of each fish, following its removal from the net, and the code number and depth of capture of each fish were recorded together with pertinent net set data.

All Dolly Varden were fixed in 10% formalin, as were all trout from Loon Lake prior to the 1972 summer series. During the summer and fall series in Loon Lake, all trout from bottom-fished nets were immediately fixed. All trout from surface-to-bottom nets were measured (fork length) to the nearest millimetre; those captured in the same depth interval as char, and subsamples from other depths, were then fixed to provide shrinkage and stomach content data.

Following several weeks in formalin, the fish were rinsed and transferred to 40% isopropanol for storage; preservation schedules were kept as similar as possible for all specimens.

7. Morphometrics and meristics

All counts and measurements follow Hubbs and Lagler (1958) except snout-to-eye; this was measured from the tip of the snout to the hindmost border of the orbit. All measurements were made on the left side of the specimen with dial calipers reading to 0.1 mm, except for gill raker counts and measurements which were made on the first right-hand gill arch; this was dissected out of the specimen and examined under a stereo-binocular microscope (12x magnification) using a seeker, where necessary, to detect rudimentary gill rakers. Measurements from males and females were not treated separately.

8. Age analysis of fish

Length frequency distributions were analysed using fork length data from separate netting series. Data were plotted on probability paper (Cassie, 1954). Males and females were not distinguished.

Scales taken from the right side behind the dorsal fin were examined under a stereo-binocular microscope at 80x magnification. Interpretation was very difficult as the scales were so small. Otoliths were taken from a number of fish for comparison.

9. Stomach analysis

Contents of the digestive tract from the oesophagus to the pyloric sphincter were taken for food analysis. The material from individual stomachs was either preserved in 40% isopropanol and filtered with a 100 micron mesh prior to examination, or removed directly from the stomach prior to examination.

The damp material was sorted under 20x magnification into the same major food categories as used by Andrusak (MS 1968), except that gastropods and Simulium larvae were included with the more motile benthic forms such as amphipods and nymphs, and Chaoborus larvae were placed in the 'static benthos' category with chironomid larvae and Pisidium. If a sizeable amount of a given category was present, it was transferred to a graduated centrifuge tube and its volume measured to the nearest 0.05 ml by volume displacement, adding a known volume of water from a graduated pipette.

The volume of small amounts of material was measured using a method based on that of Hellowell and Abel (1971). Two microscope slides were glued onto the sides of a glass plate, 80 x 100 mm, to form a cell approximately 1 mm deep. Stomach material of a given category was placed, slightly moist, on the plate and covered with an identical upper plate, squashing out the material. The number of squares of mm graph paper covered by the area of the squash was counted and recorded.

The cell was calibrated by pipetting known volumes of water onto it, covering it with the second plate and counting the number of squares covered by the water. From the resulting calibration curve, volumes as small as 0.001 ml could be estimated.

Numbers of prey items in each food category were counted under 12-20x magnification. Items that were too thoroughly digested to be identified were ignored.

Results are presented as the average of volume percentages (Andrusak, MS 1968).

B. Laboratory Study

1. Methods of capture

Dolly Varden from Dickson Lake were captured in August and October 1971, by angling with a surface-fished lure. Those from Loon Lake were captured in August and September 1971 with sinking nets fished at 10-12 m. Fish were removed as quickly as possible from the net and placed in cold oxygenated water. Table II shows the average sizes of the fish held.

TABLE II. Sizes of Dolly Varden held, December 1971.

<u>Lake</u>	<u>Fork length, mm</u>		<u>Number held</u>
	<u>Mean</u>	<u>Range</u>	
LOON	197	170-230	9
DICKSON	198	175-265	18

2. Holding facilities

Dickson and Loon Lake fish were always kept separate. Initially, they were held in outdoor wooden flume tanks, through which a slow flow of water was maintained. All Loon and some Dickson Lake fish were later transferred to laboratory fibreglass holding tanks; the average number to a tank was three, the maximum six.

Holding tanks were 110 cm long and 60 cm wide, with a central standpipe 35-40 cm high. Lighting was completely artificial, being provided by 60 watt incandescent bulbs controlled by an Intermatic T101 time switch at approximately natural photoperiod; daylength was adjusted every two weeks. All tanks were covered with wire mesh screens over which was stretched black polyethylene sheeting with openings 50 x 50 cm by the lights, which were between 50 and 100 cm from the water surface.

City water was fed into each tank at 1 to 3 litres per minute; its temperature ranged from 6°C in winter to 12°C in summer. Water pipes passed through a large thermostatically controlled water bath to minimise temperature fluctuation. Aeration was provided in every tank using Metaframe Bubble-up corner filters.

All fish were conditioned to feed on small pieces of chicken liver, which floated on the surface. They were occasionally fed live plankton.

3. Observation facilities

Two observation tanks of grey painted plywood with plexiglass fronts, each 122 x 61 x 61 cm, also used by Schutz (MS 1969), were set side by side 1.3 m from a wall of the laboratory, behind which was an observation chamber. This section of the laboratory was totally screened off with black polyethylene sheeting to minimise disturbance.

Water was run through the tanks at approximately $\frac{1}{2}$ litre/minute and the tanks were aerated prior to introduction of a fish. Lighting was provided by two 60 watt incandescent light bulbs 20 cm above the water and 22 cm from the ends of the tank; this gave uniform lighting 11 cm above the bottom of the tank, as measured by a GM submersible photometer.

The substrate was grey painted wood for the spatial tests and the earthworm feeding tests. Chironomid and Chaoborus feeding tests were conducted with a substrate composed of sand, gravel and debris sieved from lake mud.

4. Stomach pump

This was used only for the Chaoborus feeding experiments. Its basic design followed that of Seaburg (1957). The sampler used had a 0.8 mm internal diameter plastic inlet tube and a 6.35 mm i.d. plastic outlet tube.

Rather than stomach pump fish to standardize hunger prior to experimentation, as done by Schutz (MS 1969),

fish were tested at least three days after feeding. Fish were usually fed to satiation every three to four days.

5. Experimental procedures

For the spatial tests, a horizontal line on the plexiglass front divided the tank into equal upper and lower halves and a vertical line similarly divided the tank into two halves, right and left. Trials were run during the winter of 1971, usually in the mornings prior to feeding. Fish were tested singly and once only; an individual was transferred from a holding tank to one of the observation tanks, and observations were started after thirty minutes when the fish began to show exploratory cruising behaviour. During the thirty minute trial the time of each trip into the upper half was recorded cumulatively on a stopwatch. Each complete journey from one end of the tank to the other was recorded as one activity unit, using a mechanical counter; a sortie into the other half of the tank of no more than one body length from the middle of the tank, followed by a return, was also recorded as a single activity unit.

Chaoborus feeding experiments were conducted during the summer of 1972 with water temperatures between 13 and 16°C in the observation tank. Two hundred 4th instar Chaoborus trivittatus larvae were introduced to the tank and the water flow was cut off during the test to minimise loss of larvae through the outflow pipe.

Fish were introduced individually to the tank. The time that elapsed before the first grab at prey and the total number of grabs during the following 10 minutes were recorded. Following the test, the fish were anaesthetized in dilute MS-222 until they were limp and then their stomachs were flushed with three aspirator bulbs-full of water (total 75 ml) using the stomach pump. Nearly all the Chaoborus larvae were washed out in the first 25 ml and none were in the last; it was therefore assumed that recovery was 100%.

Following recovery from the anaesthetic, fish were returned to their holding tanks and an hour later each individual was fed approximately one quarter of the satiation volume of chicken liver recorded for it during tests in the preceding month. The next test was run two days later and only traces of liver appeared in the washings. Tests were repeated three times for each fish.

The number of larvae taken by the fish was replaced with fresh Chaoborus to bring the number to 200 again. As each series took two days, the water flow through the tank was switched on again in the evenings to maintain the temperature at approximately 13°C and a net was set at the end of the outflow pipe to collect those larvae that were washed out; the number in the tank was made up to approximately 200 in the morning before tests were started again. Four sympatric Dolly Varden from Loon Lake and

five allopatric Dolly Varden from Dickson Lake were tested. All had been feeding regularly on chopped chicken liver. Three of the sympatric fish (#2, #3 and #4) were recent captures.

C. Statistical Analysis

1. Meristics

Means, 95 and 99% confidence limits were calculated for the raw data. Variances were calculated from log-transformed data to correct for the effects of unequal means on the variances (cf. Van Valen, 1965; Lewontin, 1966) and the two tailed F test was used to test whether variances differed significantly from one another.

2. Morphometrics and length-weight relationships

Regressions were calculated for various body parts and weight against standard length, using log-transformed data. The log-transformation was used to investigate the presence of allometric growth (Huxley, 1932), and to correct for the size related change in variance (Lewontin, 1966). Pairs of lines were compared using analysis of covariance.

3. Canonical correlation

Canonical correlation analysis is used to relate one set of random variables, U, to another set of random variables, V, where

$$U = \sum_{i=1}^K a_i x_i \quad \text{and}$$

$$V = \sum_{j=1}^J b_j y_j \quad (i \leq j).$$

The coefficients are chosen to give the largest possible correlation between the sets U and V (Lee, 1971), with the restriction that they be independent of previously derived linear combinations of coefficients (Green, 1972).

This was used as an exploratory tool to determine if relationships existed between diet and meristic counts. Diet was expressed as a linear combination of eight major food categories.

Calculations were performed on the IBM 360 computer using a program available at the U.B.C. computing centre, BMD: 06M.

Canonical correlations were tested for significance using Bartlett's criterion (Lee, 1971) for detection of the simultaneous departure of several roots from zero:

$$\chi^2 = -[N - \frac{1}{2}(p_1 + p_2 + 1)\log_e \Lambda]$$

where $\Lambda = \prod_{i=r+1}^{p_1} (1 - \lambda_i)^2$

which follows approximately a Chi-square distribution with $(p_1 - r + 1)(p_2 - r + 1)$ degrees of freedom. N is the total number in the sample, p_1 and p_2 the number of random variables in the first or second set respectively, and λ_i is the i^{th} canonical root.

4. Comparison of means using a modified 't' test
to correct for unequal sample variances

Variances differed significantly in the spatial

distribution laboratory tests and the following approximation was used for the comparison of means (Bailey, 1959):

$$d = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{(s_1^2/n_1 + s_2^2/n_2)}}$$

is treated as being distributed approximately as 'Student's' t with f degrees of freedom where

$$f = \frac{1}{u^2/(n_1 - 1) + (1 - u)^2/(n_2 - 2)}$$

$$\text{and } u = \frac{s_1^2/n_1}{s_1^2/n_1 + s_2^2/n_2} .$$

IV. RESULTS

A. Field Study

1. Temperature

Loon Lake is usually frozen from mid-December to mid-February though ice cover is not always complete during this period (information from U.B.C. Research Forest staff). A thermocline may develop by the end of May and stratification is well developed for the whole summer. The thermocline becomes deeper as the summer progresses and at the end of September 1970 it lay between 8 and 10 m (Fig. 4).

Dickson Lake usually does not become icefree until the middle of May and ice may remain on the surface until early June (L. Liberty, pers. comm.). The lake

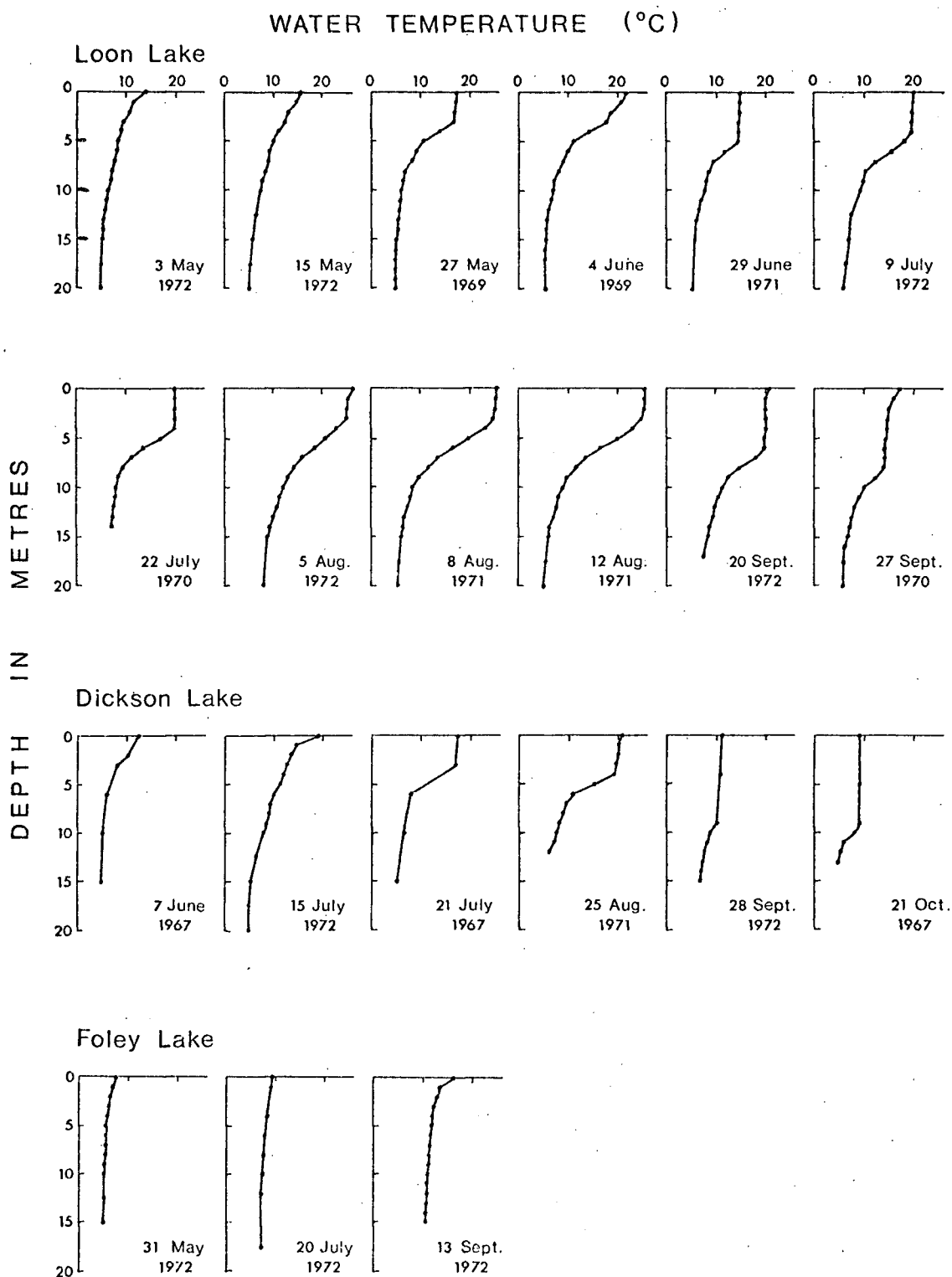


FIGURE 4. Temperature profiles of the three study lakes.

developed a thermocline between 3 and 6 m by the end of July in 1967 (Andrusak and Northcote, 1971), but not by mid-July in 1972. At the end of August 1971 the surface temperature had risen to 21.0°C , with a thermocline at 5 m (Fig. 4). A weak thermocline persisted between 9-11 m at the end of September 1972 and as late as mid-October in 1967.

Foley Lake usually freezes over in mid-December and becomes icefree at the end of February. However, in 1972 the lake had ice cover until the end of March following a hard winter (B. Walton, pers. comm.). During the summer of 1972, no stratification developed (Fig. 4), probably because of the short retention time of the lake (Table I). The temperature at 15 m rose steadily from 4.9°C in the spring to 10.6°C in early fall, and the maximum recorded surface temperature was 15.5°C .

2. Bottom fauna

Densities of bottom organisms at 10 and 20 m were lower in Loon and Dickson Lakes than in Foley Lake (Fig. 5) as they decreased with increasing depth, while in Foley Lake the density of bottom fauna increased with increasing depth.

In Loon Lake at 5 m oligochaetes made up most of the fauna followed by chironomid larvae. At 10 m, chironomid larvae were most common; Pisidium spp. and Chaoborus larvae were also taken in small numbers at this depth. The only organisms recorded at 20 m were chironomid larvae. Small

amounts of motile benthos were obtained at 5 m; this category included amphipods, Sialis and caddis larvae, although the last were only represented by their empty larval cases.

In Dickson Lake, Pisidium spp. were more abundant than in Loon Lake but densities of other categories were similar. Motile benthos, consisting of amphipods, planorbid gastropods and caddis larvae were collected in small numbers at 5 and 10 m.

Pisidium spp. were abundant in Foley Lake, particularly in littoral areas. Densities of chironomid larvae were greatest at 10 m and were much more abundant at this depth and at 5 m than in the other two lakes. Oligochaetes became more common with increasing depth and at 10 and 20 m accounted for much of the increased density of bottom fauna in Foley Lake relative to the other two lakes. In the motile benthos category, caddis larvae and planorbid gastropods were collected; mayfly nymphs were not taken in benthos samples but were evident in submerged vegetation in the littoral area.

Both chironomid larvae and Pisidium spp. were separated into two distinct size classes. Chironomid larvae longer than 10 mm and Pisidium spp. with shell diameter greater than 1.5 mm were classified as 'large'. All Loon Lake chironomid larvae and Pisidium were in the small category. Foley Lake had proportionately more large

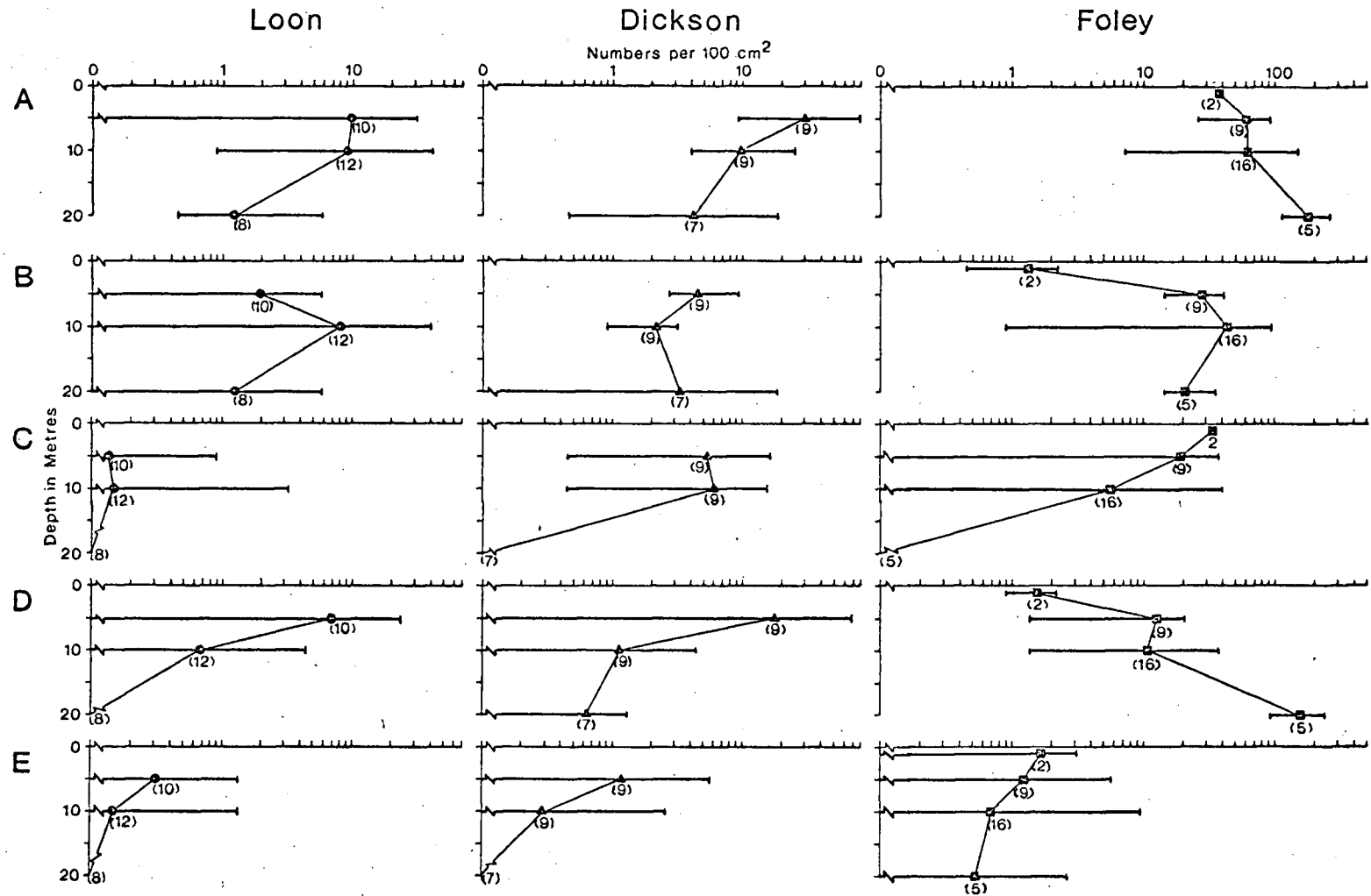


FIGURE 5. Depth distributions of major benthic organisms in the three study lakes during summer 1972. Sample sizes in parentheses; mean and range of numbers per 100 cm² shown. A. Total B. *Pisidium* C. Chironomids D. Oligochaetes E. Motile Benthos.

chironomid larvae and Pisidium spp. than Dickson Lake (Table III).

TABLE III. Size frequency of bottom organisms from Foley and Dickson Lake fall samples, separated by eye.

	<u>FOLEY</u>	<u>DICKSON</u>	<u>Chi-square</u>	<u>Significance with 1 d.f.</u>
chironomids >10 mm	382	5	430	p < 0.001
<10 mm	220	82		
<u>Pisidium</u> >1.5 mm	107	6	400	p < 0.001
<1.5 mm	478	137		

3. Zooplankton

Zooplankton is considerably more abundant in Loon Lake than in Dickson Lake, and Foley Lake contains only small amounts (Fig. 6). Loon Lake also shows a significant increase in numbers per haul in the top 5 m as the season progresses (Fig. 6A).

Calanoid (Diaptomus spp.) and cyclopoid copepods formed a considerable percentage of the plankton in Loon Lake in each sampling series (Fig. 7). Numbers of Daphnia spp. increased through the season; Bosmina longirostris showed a peak in the summer and Diaphanosoma leuchtenbergianum were most abundant in the fall. Other species present included Holopedium gibberum, Polyphemus pediculis, Leptodora kindti and Scapholebris kingi. Water mites (Acarini) were taken occasionally. In Loon Lake, numbers of cladocerans

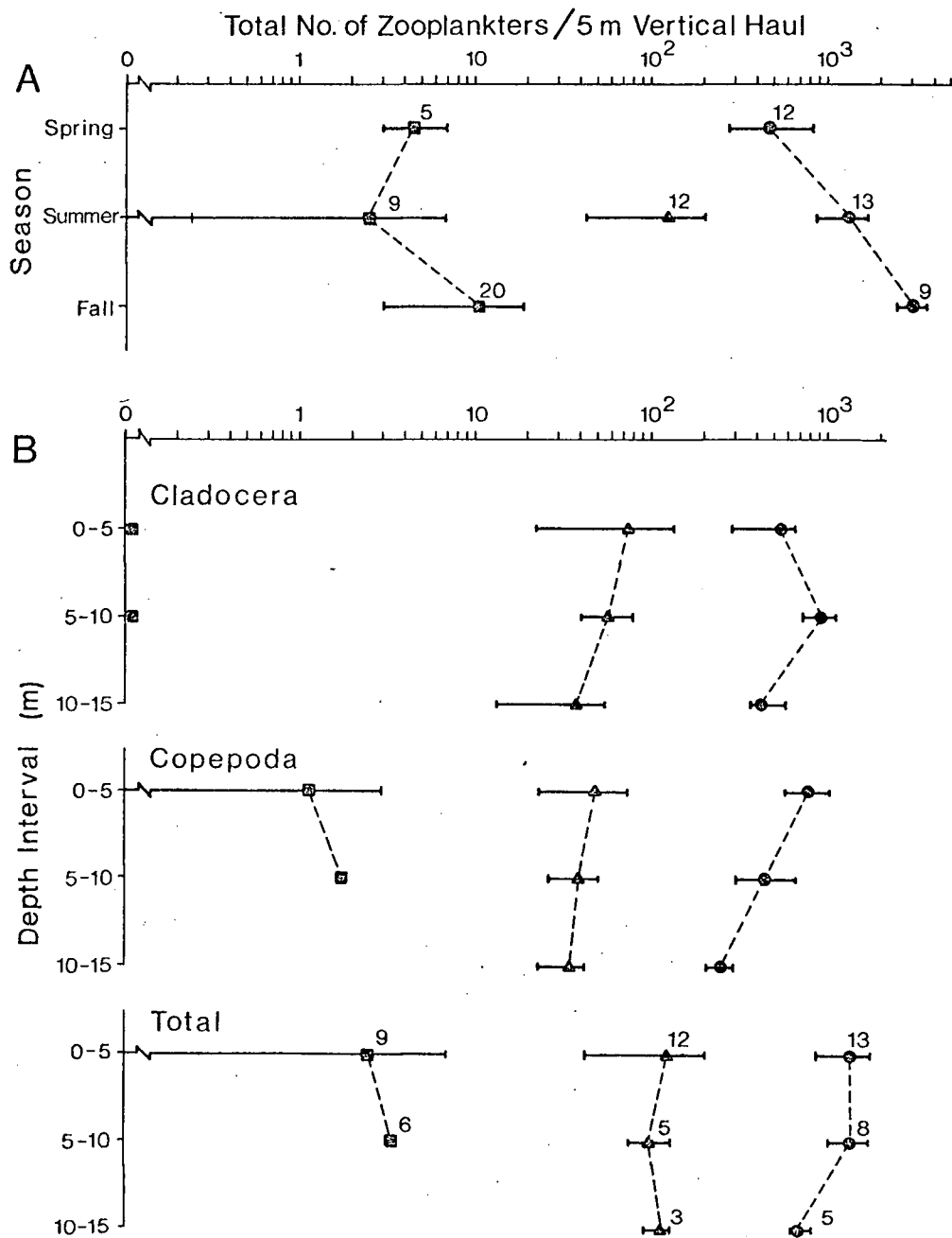


FIGURE 6. Zooplankton abundance in Loon (●), Dickson (▲) and Foley (■) Lakes. Mean numbers and range per 5 metre vertical stage haul shown; number of samples indicated.

A. Seasonal changes.

B. Depth distribution during summer.

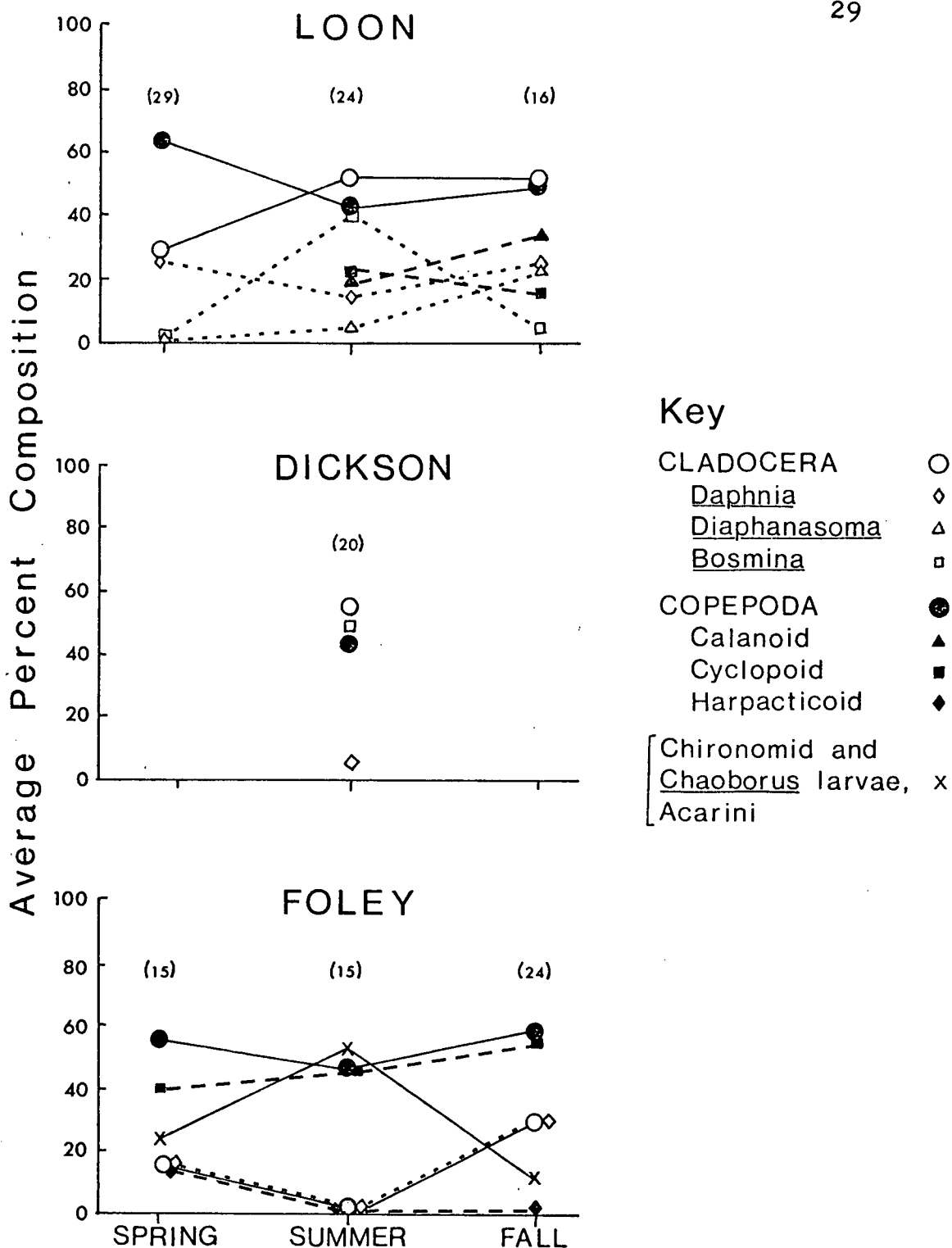


FIGURE 7. Seasonal changes in average percent composition of zooplankton samples in the three study lakes during 1972. Number of samples in parentheses.

were highest between 5 and 10 m, while copepod numbers decreased with increasing depth (Fig. 6B).

In the one Dickson Lake sampling series, Bosmina longirostris was the most abundant species present (Fig. 7). Calanoid copepods (several Diaptomus spp.) were common; cyclopoid copepods were scarce. Daphnia were present; Diaphanosoma, Holopedium and Scapholebris were not recorded in plankton samples but were present in fish stomachs. Cladocerans and copepods were fairly evenly distributed in the top 15 m of Dickson Lake.

In Foley Lake, cyclopoid copepods were the most important items in the sparse plankton, followed by Daphnia. Turbulence, caused by spring runoff water, was probably responsible for the appearance of harpacticoid copepods, chironomid larvae and nematodes as important constituents of the plankton in the spring and summer samples.

4. Fish distribution

i. Loon Lake

Sympatric Dolly Varden were mainly associated with the bottom in May 1972 (Fig. 8). Most were captured inshore, and here some were taken in midwater. They were also taken in large numbers in bottom nets at 10 m (Table IV); more were captured in the lower than in the upper half of these nets (Chi-square = 7.53; $p < 0.01$). Cutthroat trout were taken in large numbers throughout the water column inshore (Fig. 8). Offshore, they were predominantly

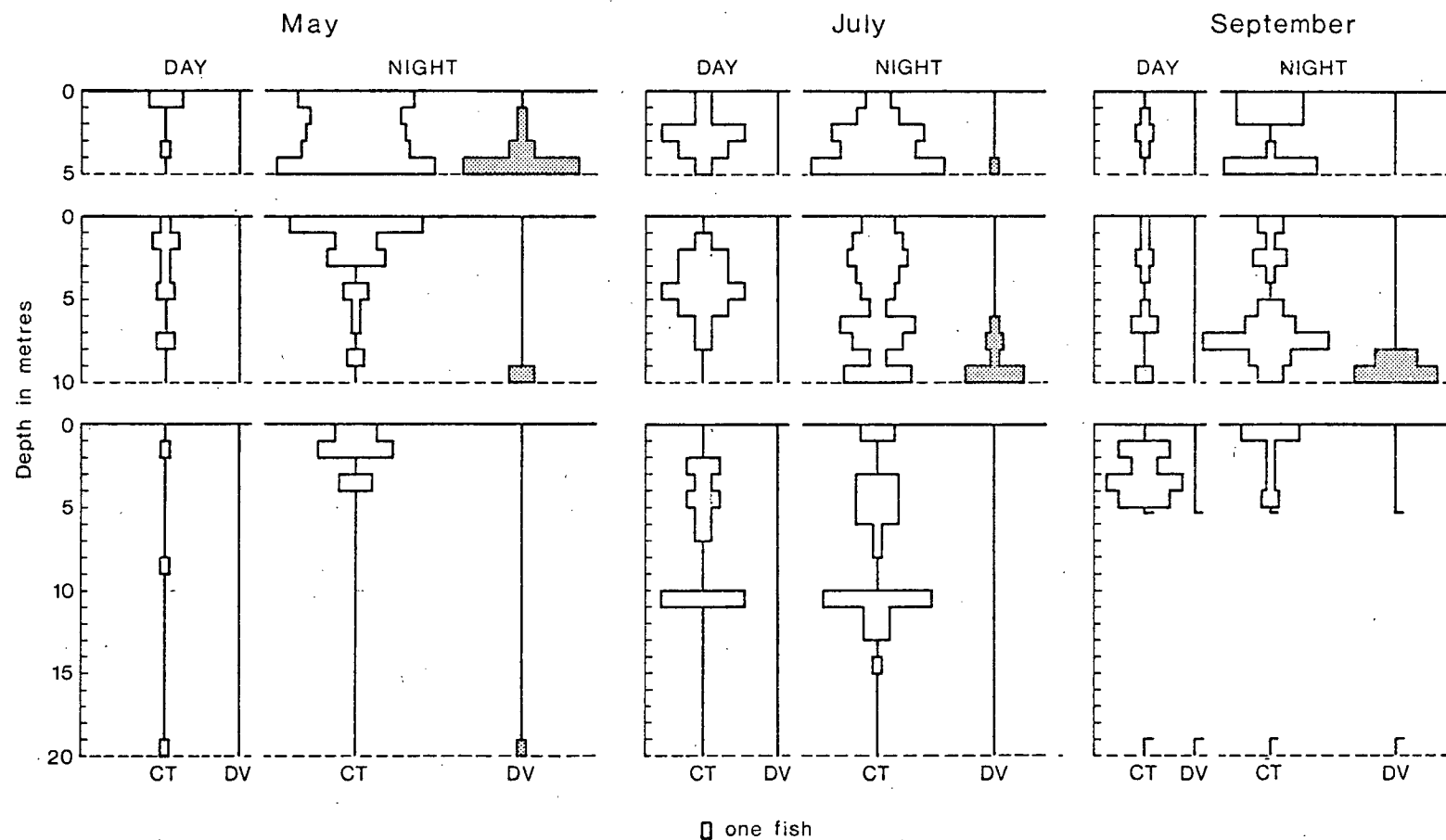


FIGURE 8. Vertical distribution of sympatric Loon Lake Dolly Varden (DV, shaded) and cutthroat trout (CT, blank) in nets set from surface to bottom at 5, 10 and 20 m, day and night, in 1972. Catches expressed as number per pair of nets.

associated with the surface. During the day, cutthroat trout were taken in smaller numbers than at night; Dolly Varden were taken only at night.

Dolly Varden had moved into deeper water by July 1972 and remained near the bottom (Fig. 8). Here, they were taken in about equal numbers with cutthroat trout (Table IV). Summer netting series in previous years confirmed that Dolly Varden were only taken in nets that fished the bottom and that cutthroat were not excluded from this region (Table V). Cutthroat were deeper than in May and were the only species taken during the day.

TABLE IV. Numbers of Dolly Varden and cutthroat trout captured in duplicate 1.4 m deep gill nets fished on the bottom at 10 m in Loon Lake in 1972.

<u>Month</u>	<u>Dolly Varden</u>	<u>Cutthroat trout</u>
May	42	4
July	24	19
September	55	9

TABLE V. Numbers of Dolly Varden and cutthroat trout captured in summer netting series in Loon Lake during 1970 and 1971.

<u>Depth range fished</u>	<u>Depth at netting site</u>	<u>Effort*</u>	<u>Dolly Varden</u>	<u>Cutthroat trout</u>
0 - 5 m	12 m	900	0	5
5 - 10 m	12 m	360	0	36
Bottom 1.4 m	10 - 15 m	4340	79	33

*Effort: product of the length of net (metres) and the time fished (hours)

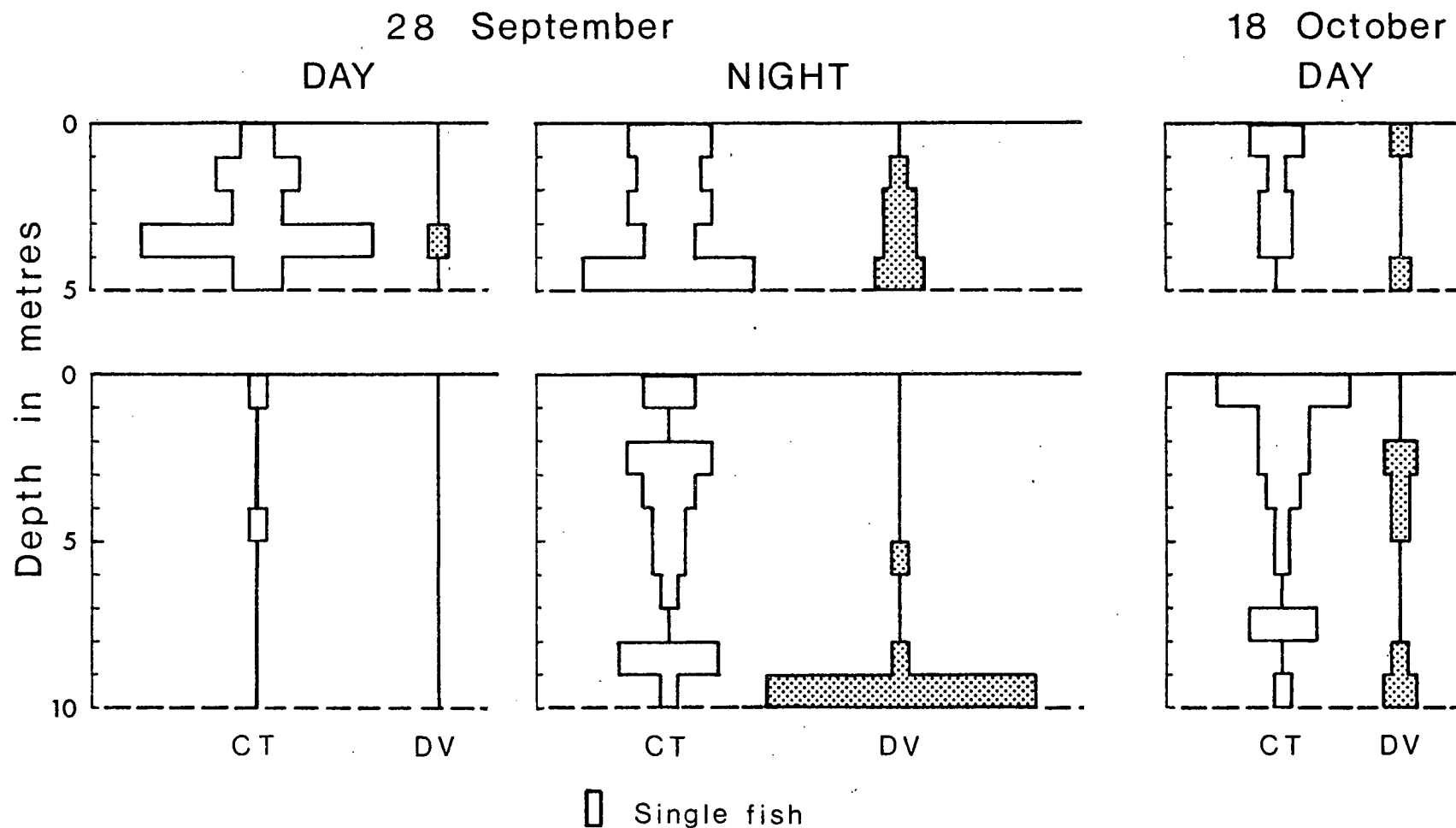


FIGURE 9. Vertical distribution of sympatric Loon Lake Dolly Varden (DV, shaded) and cutthroat trout (CT, blank) in nets set from surface to bottom at 5 and 10 m, day and night, in fall 1970. Catches expressed as number per three nets.

In mid-September 1972, Dolly Varden were confined to the bottom at 10 m (Fig. 8). Few cutthroat trout were captured in this region (Table IV), but they were often taken in midwater and at the surface, both day and night.

In late September 1970 (Fig. 9), more Dolly Varden were captured inshore and in the water column than in July and mid-September 1972 netting series. However, a preference for the bottom was still evident, but this disappeared by October 1970. Cutthroat trout were widely distributed in the water column, both day and night in the fall.

In summary, Dolly Varden were closely associated with the substrate in Loon Lake during the summer, and this association was far more distinct than that reported by Andrusak and Northcote (1971) for Dolly Varden in Marion Lake. Although Dolly Varden appeared to be confined to the bottom few metres from spring to early fall, cutthroat were not excluded from this part of the water column. Later in the fall, Dolly Varden moved into the water column and were also taken during the day.

ii. Dickson Lake

Allopatric Dolly Varden in Dickson Lake were widely distributed throughout the water column, inshore and offshore, both day and night during the summer and fall. Gill netting results and echo sounding records (Figs. 10, 11 and 12) both showed this pattern.

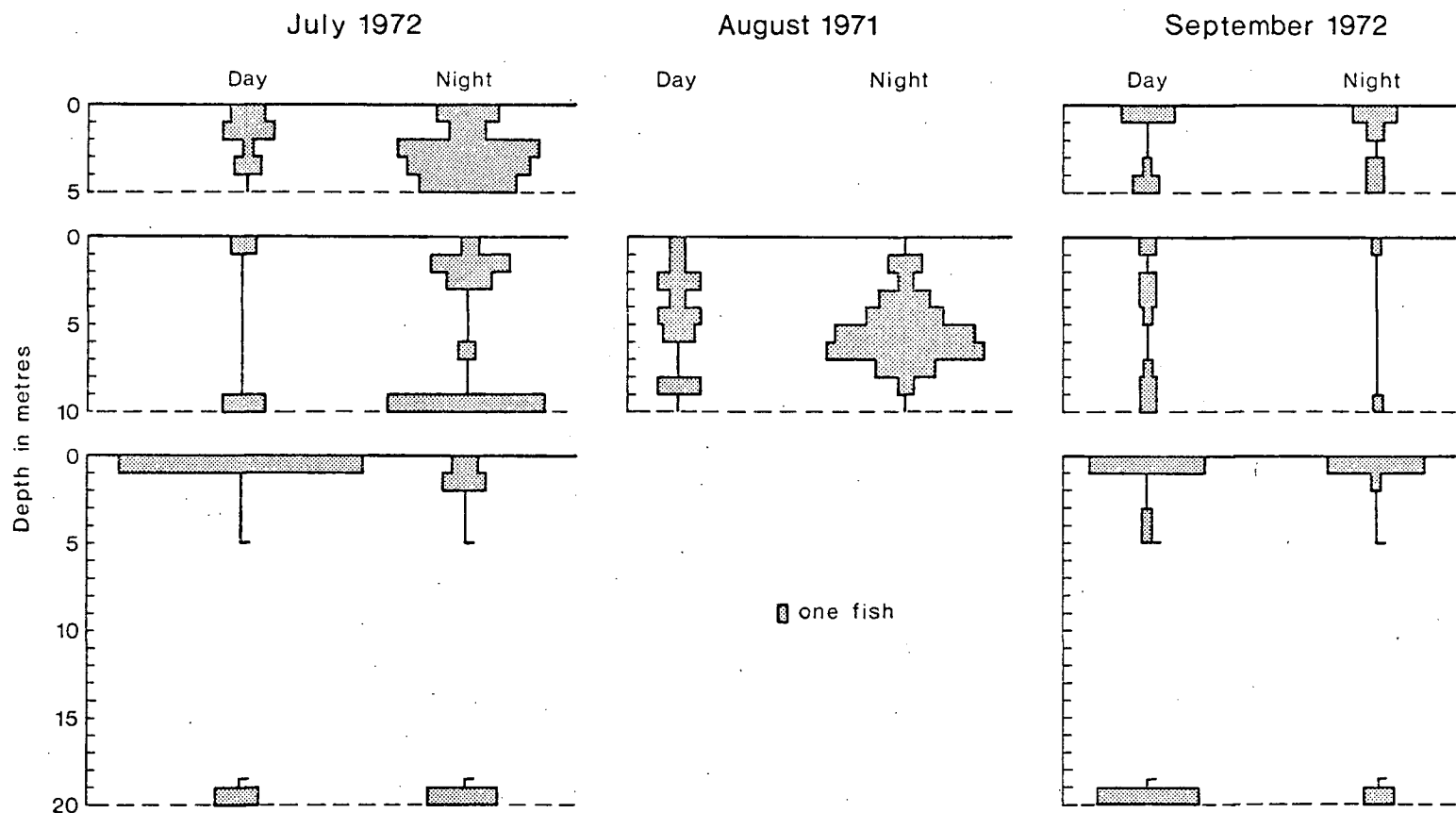


FIGURE 10. Vertical distribution of allopatric Dickson Lake Dolly Varden in nets set from surface to bottom at 5, 10 and 20 m, day and night, in summer 1971 and 1972. Catches expressed as number per pair of nets.

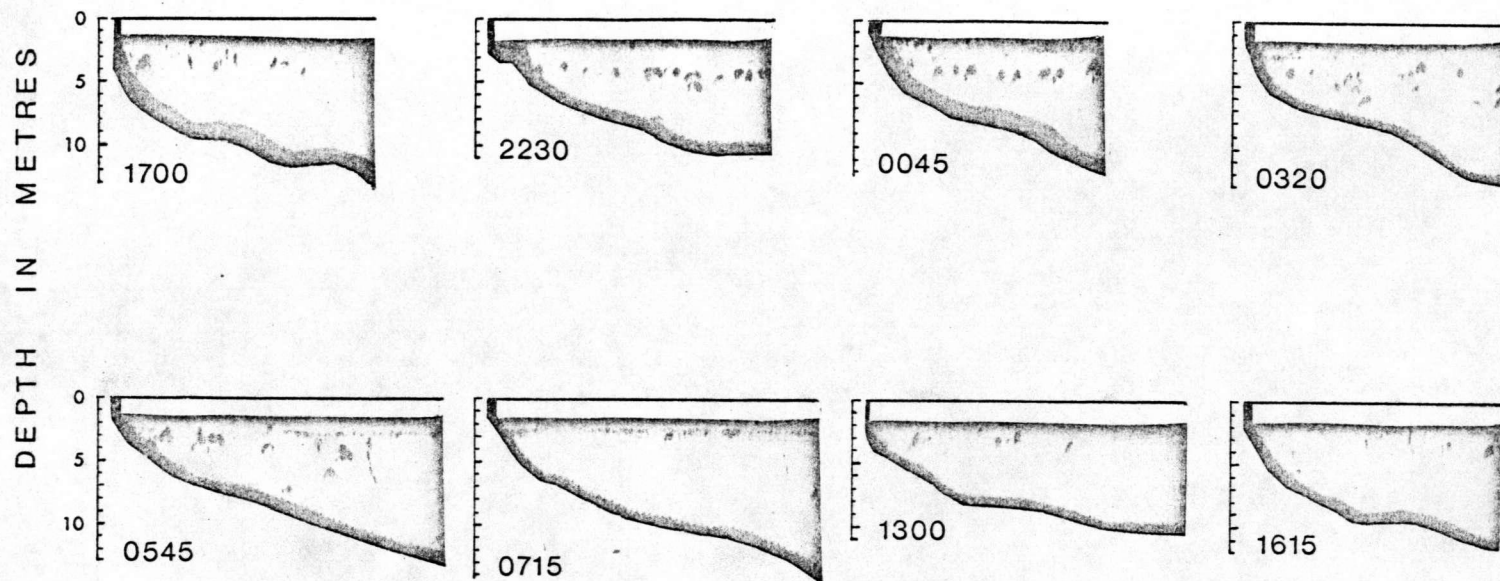


FIGURE 11. Echo sounding traces made on a standard transect in Dickson Lake over a 24 hour period in August 1971, showing onshore movements of allopatric Dolly Varden at night. Thermocline present from 4 to 6 metres.

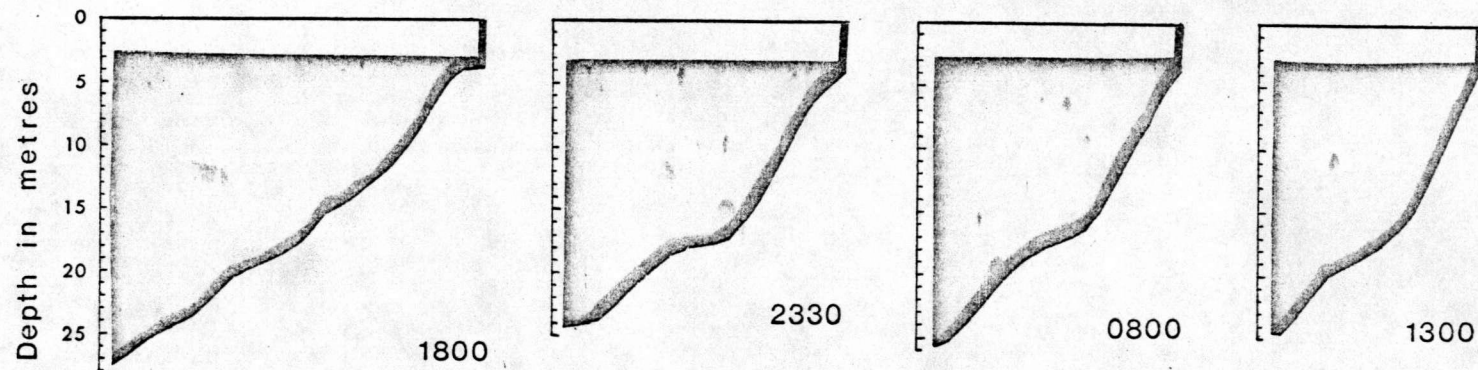


FIGURE 12. Echo soundings made on a standard transect in Dickson Lake over a 24 hour period in July 1972. No thermocline present.

Wide distribution of Dolly Varden in the upper 10 m of Dickson Lake at night was also shown in a previous study (Andrusak and Northcote, 1971). However, numbers captured during the day (Fig. 13) were small compared with the present study; the short duration of day net sets (average 3 hours, maximum 6 hours; Andrusak, MS 1968) may be part of the reason that so few were taken then in that study.

Echo sounding records in 1967 showed no evidence of fish above 25 m during the day (Andrusak and Northcote, 1971). However, the upper 1-2 m are always obscured by the 'zero band' on the echo sounding record. In 1972, the majority of fish taken in 5 m surface nets offshore at the 20 m depth contour, both day and night in July and September, were captured in the uppermost 2 metres (Fig. 10). Numerous observations of fish rising at the surface, particularly for several hours after dawn and at dusk, in 1971 and 1972, also showed that allopatric Dolly Varden in Dickson Lake were not confined to deeper water during the day.

Although there was no evidence for extensive diel vertical movements of fish within the lake from gill netting or echo sounding results, netting results from July 1972 (Table VI) and echo sounding records made over 24 hours in August 1971 (Fig. 11) suggest that an onshore migration occurred at night during the summer. It was not

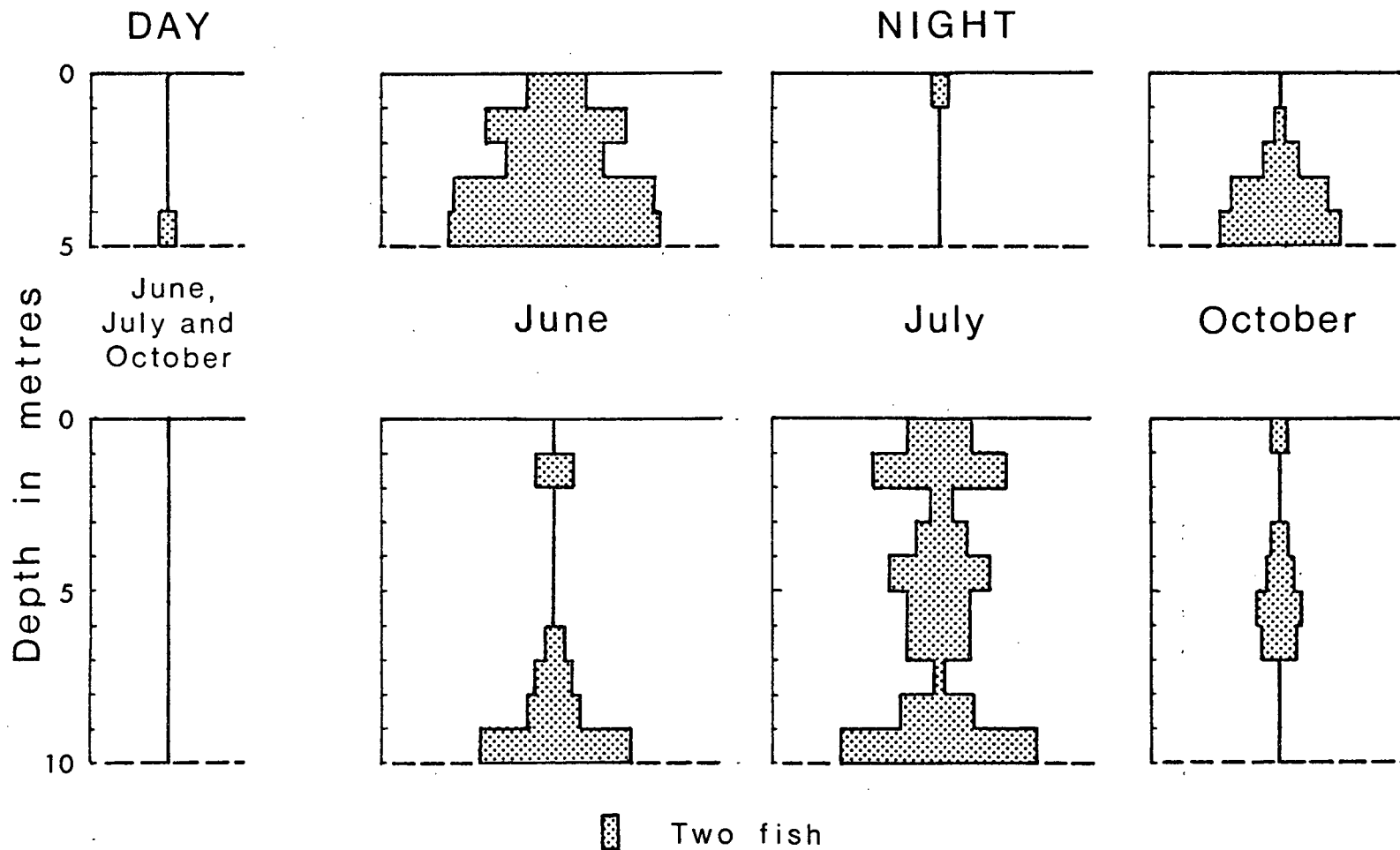


FIGURE 13. Vertical distribution of allopatric Dolly Varden in nets set in Dickson Lake by Andrusak in 1967 (Andrusak, MS 1968).

TABLE VI. Numbers of Dolly Varden in onshore and offshore gill nets in the upper 5 m of Dickson Lake in 1972.

	<u>July</u>		<u>September</u>	
	<u>Onshore</u>	<u>Offshore</u>	<u>Onshore</u>	<u>Offshore</u>
Day	17	28	17	15
Night	68	8	17	12
Chi-square	42		0.05	

apparent in late September 1972 (Table VI).

To conclude, in contrast to the sympatric Loon Lake population, allopatric Dolly Varden in Dickson Lake were widely distributed throughout the water column during summer and autumn.

iii. Foley Lake

Catches of Dolly Varden were small relative to netting effort in each of the sampling series. Day and night distributions did not differ significantly from one another, so were combined for each series; similarly spring and summer distributions did not appear to differ from one another and these results were also combined (Fig. 14).

In the spring and summer series, the majority of fish were captured within one metre of the bottom ('bottom fish'). In the fall series, more fish were captured in the water column ('midwater fish') and fewer near the bottom (Table VII). The small number of 'midwater fish' in the spring and summer series may be an underestimate

Spring and Summer

Fall

41

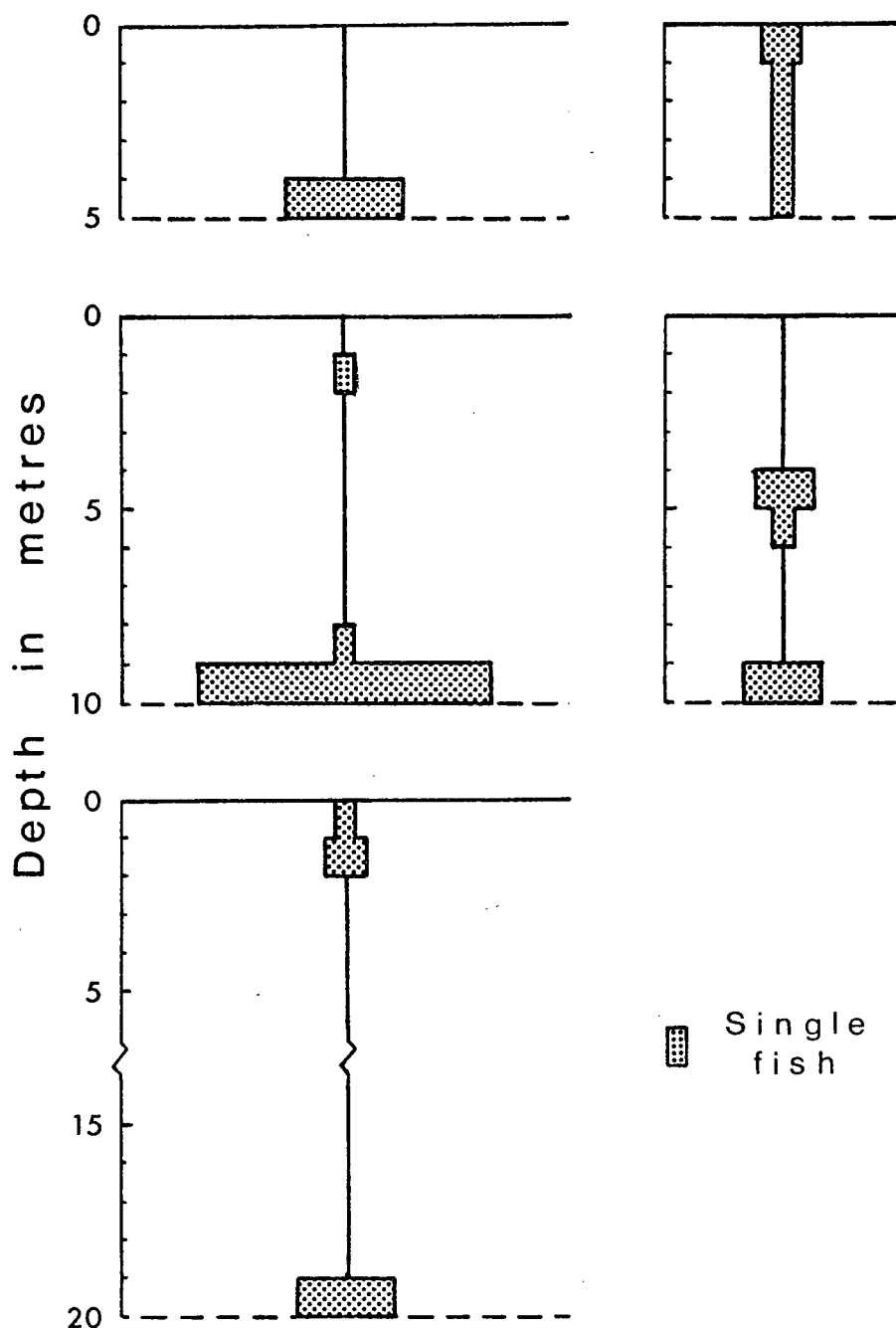


FIGURE 14. Vertical distribution of allopatric Foley Lake Dolly Varden in nets set from surface to bottom at 5, 10 and 20 m during 1972. Day and night data combined; catches expressed as number per four nets.

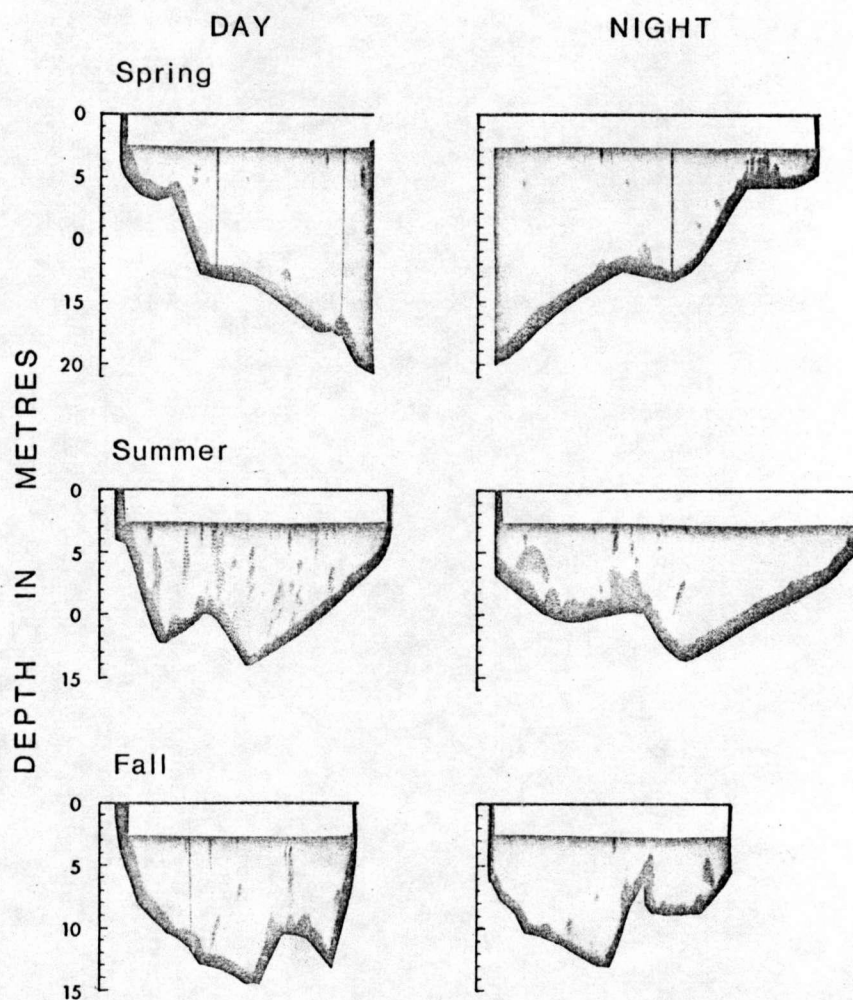


FIGURE 15. Echo sounding records showing evidence of allopatric Dolly Varden throughout the water column in Foley Lake in 1972. Long vertical marks may be submerged logs; vertical reference lines should be ignored.

TABLE VII. Seasonal differences in vertical distribution of Dolly Varden in surface-bottom gill nets set at 5 and 10 m in Foley Lake.

	<u>Spring and Summer</u> <u>(pooled data)</u>	<u>Fall</u>
'Midwater fish'	2	8
'Bottom fish'	21	4

Distributions differ: $p < 0.001$ (Fisher Exact Test)

of the actual proportion present in the water column as marks, probably representing fish, were present here on the spring and summer echo sounding records (Fig. 15); fine red silt, which accumulated on the meshes of the gill nets, rendering them conspicuous, may have been partly responsible for low net catches in midwater during the spring and summer series.

In summary, although data were limited, allopatric Dolly Varden in Foley Lake appeared to be present throughout the water column; they were, however, more closely associated with the bottom than those in Dickson Lake, but not nearly as definitely as the sympatric population in Loon Lake.

5. Food

i. Seasonal changes

Loon Lake

Sympatric Dolly Varden in Loon Lake took a progressively greater proportion of benthic prey from spring

to early fall; this was composed increasingly of organisms taken from within the substrate, such as chironomids and Chaoborus larvae and Pisidium spp. (Fig. 16). The proportion of indigestible items taken (mud, seeds and leaf debris) increased concomitantly. Water column prey, solely zooplankton, decreased in importance from spring to early fall, but in October, when Dolly Varden were present throughout the water column, zooplankton again became the major prey category. 'Motile benthos', an important food in the spring, was a minor item in early fall, when Dolly Varden were absent from inshore regions.

Cutthroat trout caught in the same depths as Dolly Varden were subject to special study (Fig. 16); they took an increasing amount of benthic prey from spring to early fall. In contrast, benthic prey was of little importance to cutthroat trout caught in midwater, surface and onshore regions of Loon Lake (Fig. 16).

Cutthroat trout throughout the lake fed predominantly on water column prey (Fig. 16), mainly zooplankton and, to a small extent, chironomid pupae. The percent occurrence of cladocerans decreased whereas copepods increased from spring to early fall, although cladocerans were always more commonly taken (Fig. 17). In the spring, when cutthroat trout were not present in as large numbers as Dolly Varden at the 10 m depth zone (Table IV), planktivorous Dolly Varden fed mostly on cladocerans.

LOON LAKE

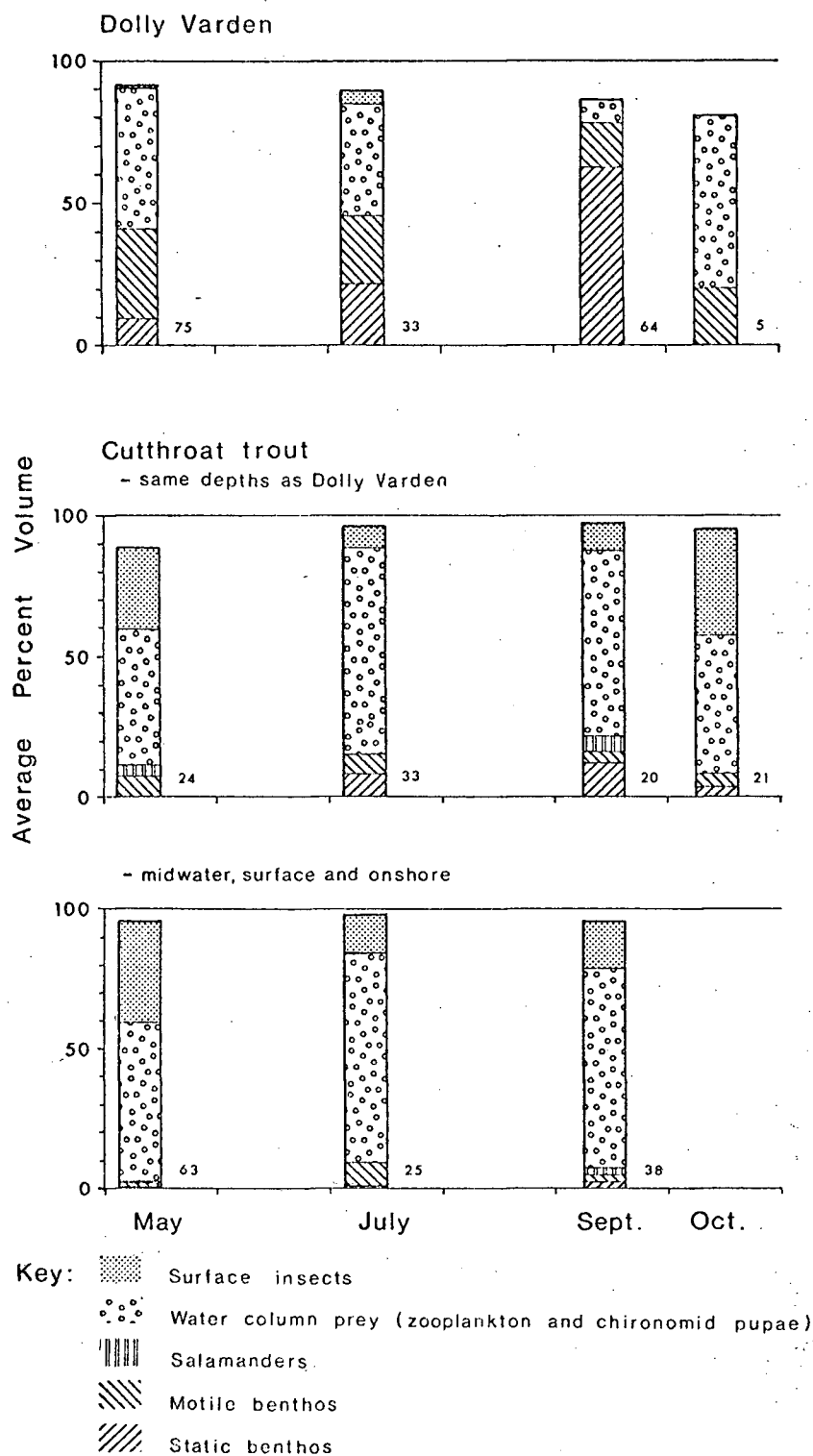


FIGURE 16. Stomach contents (average percent volume) of adult sympatric Dolly Varden and cutthroat trout in Loon Lake in 1970 (October) and 1972. Number sampled indicated; balance (unshaded) composed of indigestible material e.g. seeds, mud.

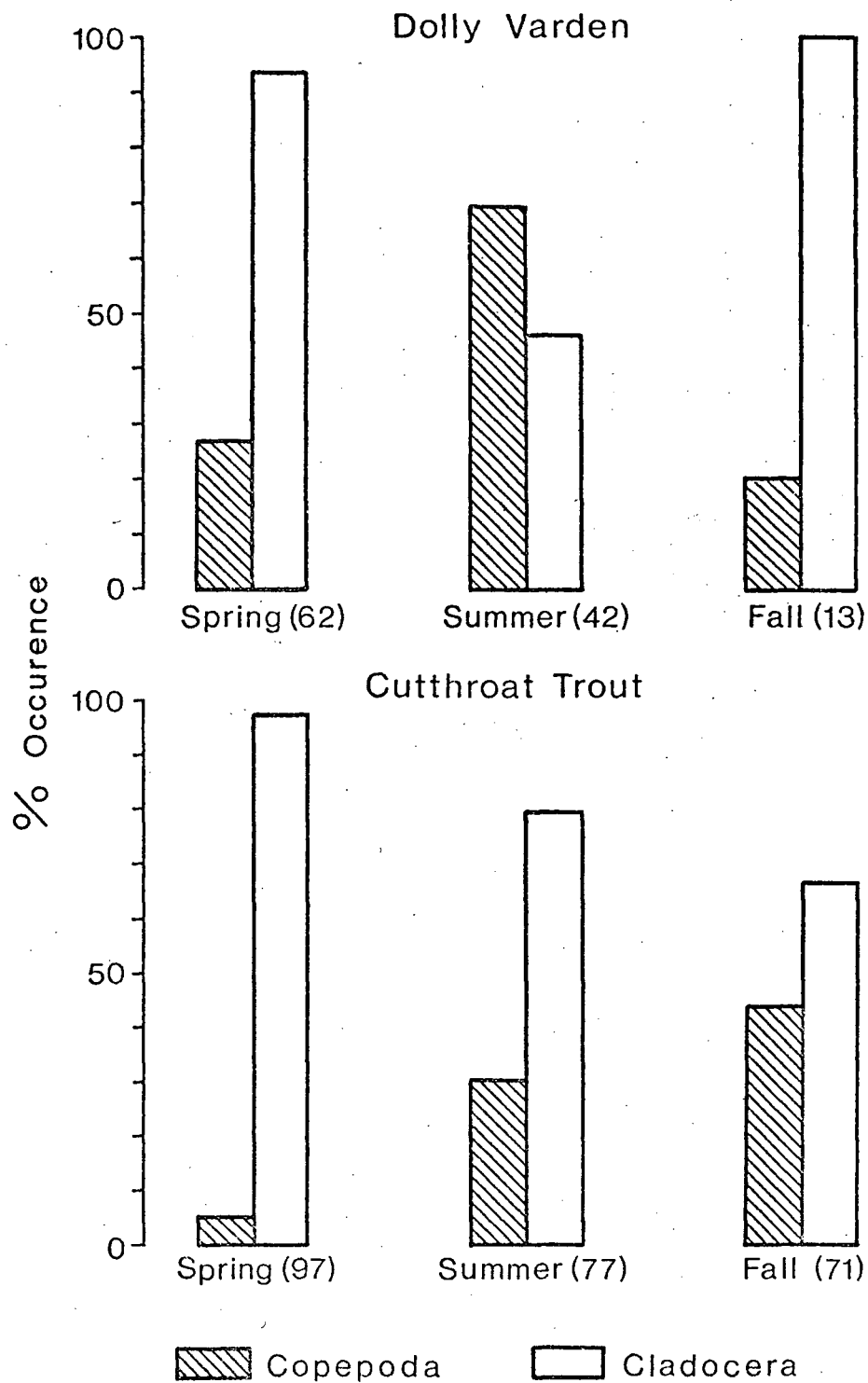


FIGURE 17. Percent occurrence of copepods and cladocerans in stomach contents of planktivorous Dolly Varden and cutthroat trout from all regions sampled in Loon Lake. Percent occurrence of planktivores in parentheses.

In the summer, when cutthroat and Dolly Varden were taken in about equal numbers there, fewer Dolly Varden fed on zooplankton and, in those that did, the percent occurrence of copepods was greater than that of cladocerans. In early fall, when spatial segregation between the two species was most pronounced (Table IV; Fig. 8), the few planktivorous Dolly Varden fed largely on cladocerans (Fig. 17). This suggests that in the summer, when the two species overlapped spatially and fed on the same general food category, zooplankton in the water column, they nevertheless concentrated on different prey items within that category.

Cutthroat trout throughout the lake, particularly in spring and fall, fed on surface insects. These were of little importance to Dolly Varden. A few larger cutthroat trout took salamanders, but Dolly Varden did not eat any vertebrate prey.

In summary, sympatric Dolly Varden in Loon Lake fed primarily on bottom fauna in summer and early fall; zooplankton was predominant in their diets in spring and in October. Their diet differed most from that of cutthroat in early fall.

Dickson Lake

Water column prey became increasingly important in the diet of allopatric Dickson Lake Dolly Varden as the season progressed (Fig. 18). Surface insects, the most important food category in the spring (Andrusak and Northcote,

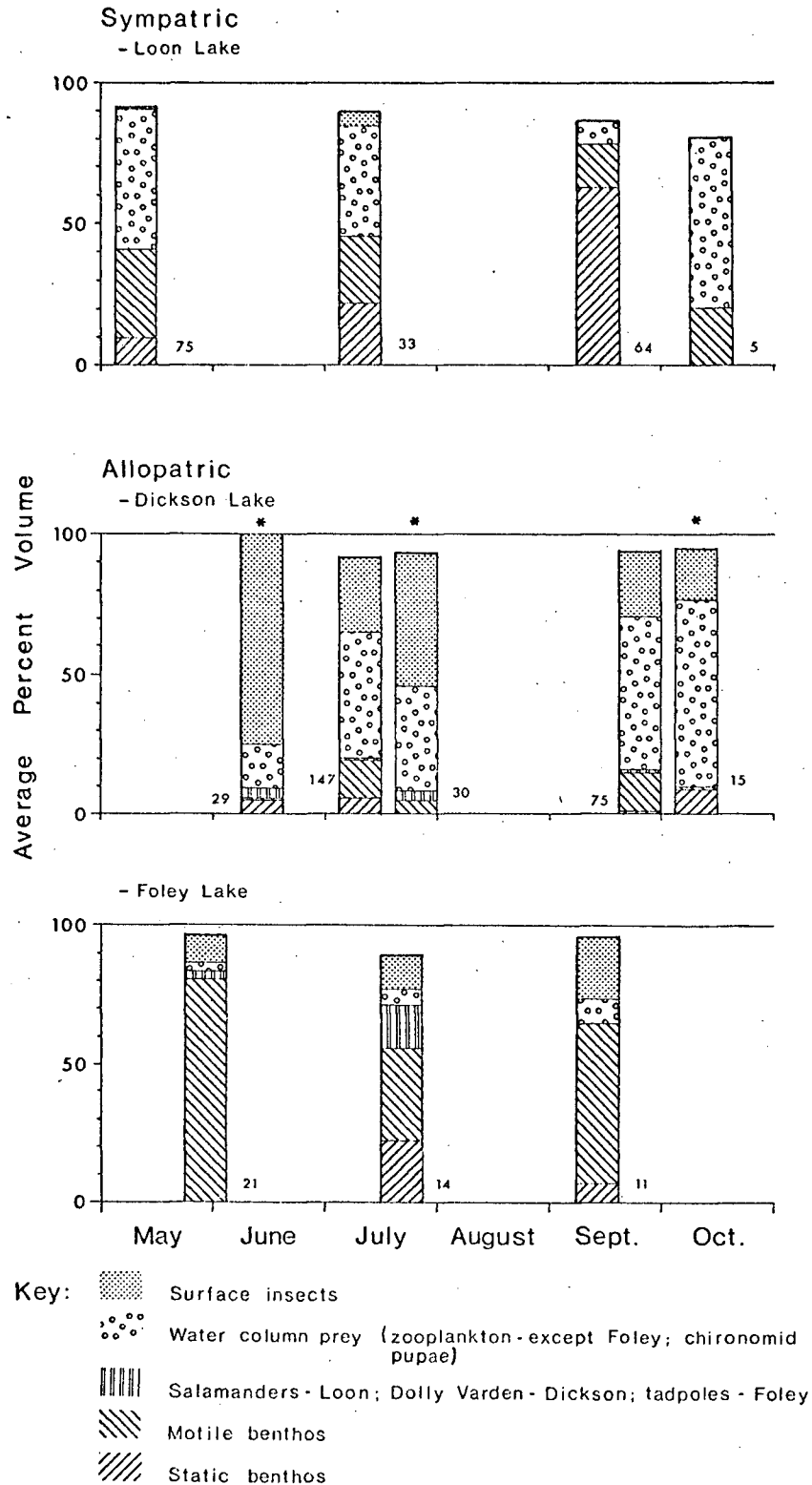


FIGURE 18. Stomach contents (average percent volume) of adult sympatric (Loon Lake) and allopatric (Dickson and Foley Lakes) Dolly Varden. Sample sizes indicated; balance (unshaded) composed of indigestible material e.g. seeds, mud.
*data from Andrusak (MS 1968)

1971), decreased in importance during summer and autumn. Water column prey was composed increasingly of zooplankton, largely Bosmina and Daphnia spp., and decreasingly of chironomid pupae between June and October. Benthic organisms were of little importance. Individual Dolly Varden started to feed on members of their own species when as small as 140 mm (fork length); exceptionally large fish taken in 1967 and 1972 (360 and 380 mm fork length respectively) had both fed exclusively on fish. Cannibalism, however, was uncommon and the average percent occurrence of fish remains in 371 adults examined in 1967, 1971 and 1972 was only 3.3%.

The most marked differences between diets of sympatric Loon and allopatric Dickson Lake Dolly Varden were the importance of benthic prey to the former and of surface insects to the latter (Fig. 18). They differed most in early fall when Loon Lake Dolly Varden took mostly benthos and very little water column prey.

Foley Lake

Motile benthos, mainly Heptageniidae (Ephemeroptera) larvae with a few large plecopteran and trichopteran larvae, was the most important prey category of allopatric Foley Lake Dolly Varden (Fig. 18). It comprised 80% of the average percent volume in the spring, but dropped to 33% in the summer when 22% of the average percent volume was static benthos; this was largely composed of chironomid larvae

with some large Pisidium. Surface insects, and to a lesser extent chironomid pupae, increased in importance through the season. Tadpoles were an important constituent of the diet in the summer; individual fish preyed heavily on them.

ii. Number of food categories taken per fish

Allopatric Dolly Varden from Dickson and Foley Lakes took a wider range of major food categories per fish than sympatric Dolly Varden from Loon Lake (Fig. 19). Dolly Varden from Loon Lake showed a decrease in the range of food categories taken as the season progressed; in the fall, the range taken per individual was significantly less ($p < 0.05$) than that in the spring.

Variability in range of food categories taken between individuals was greatest for Foley Lake Dolly Varden (Appendix Table III); in the summer and fall the variance of the number of major categories taken was greater for Foley Lake Dolly Varden than for Dolly Varden from Dickson and Loon Lakes (F ratios give $p < 0.01$ in all cases).

iii. Factors affecting food taken

The diet of sympatric Dolly Varden in Loon Lake was evidently influenced by their association with the bottom, benthos being important at all times in their diet and surface insects negligibly so. In contrast, cutthroat trout captured in the same depth intervals as Dolly Varden were not so restricted and fed on insects as well as

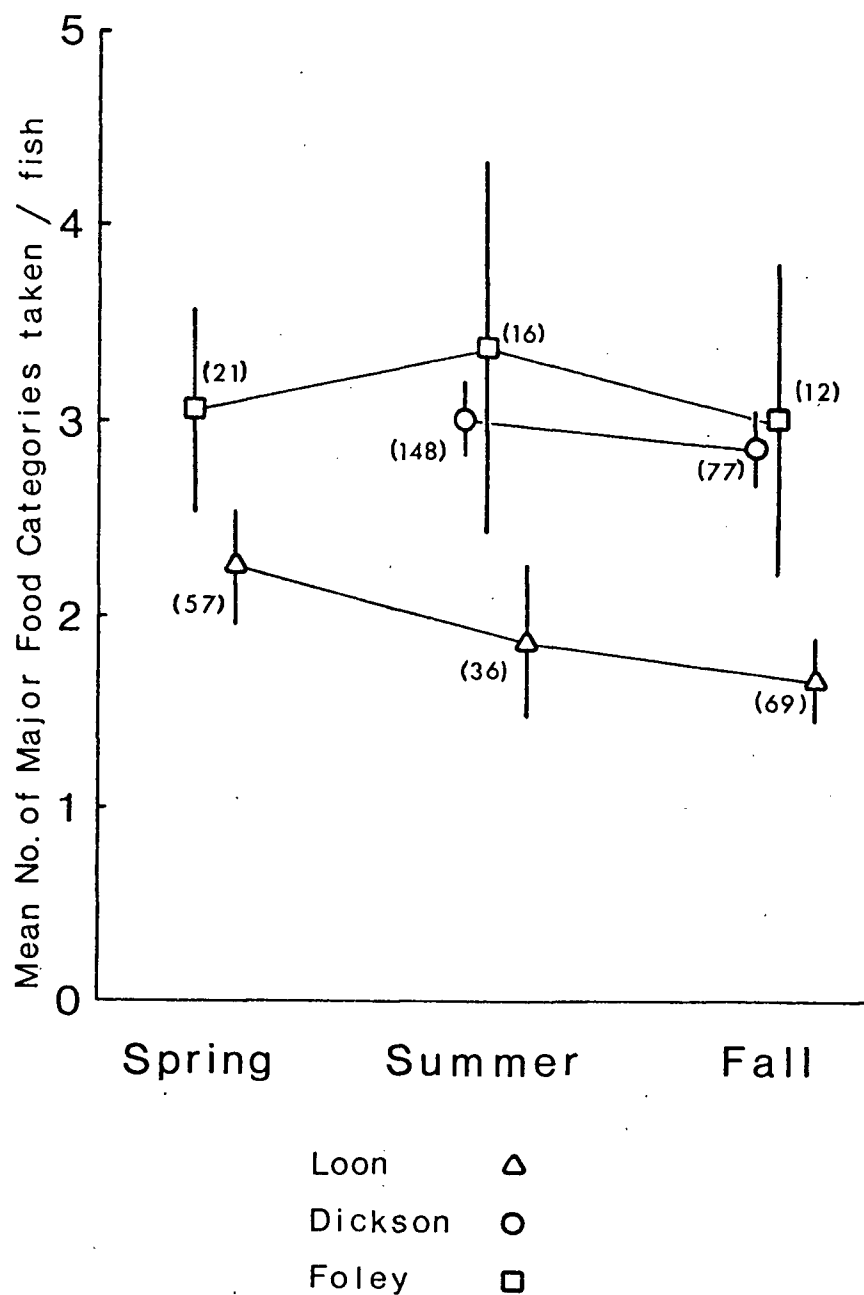


FIGURE 19. Mean number of major food categories taken per individual Dolly Varden. 95% confidence limits of mean shown; sample size in parentheses. (See Appendix Table III)

zooplankton and benthos (Fig. 18)

Relative proportions of food categories eaten by sympatric Dolly Varden in Loon Lake changed with increasing body size. Fish larger than 155 mm fork length, a critical length as shown in the morphological section (Fig. 31), ate a greater proportion of benthos (Fig. 20) than smaller fish. Average numbers of chironomids taken per fish by large and small fish in Loon Lake in the fall were 98 (12 fish sampled) and 6.7 (10 fish sampled) respectively; the average volume of individual chironomids eaten by large Dolly Varden was over twice that of those taken by small fish. More mud and debris was also taken by the large fish. Small fish took more zooplankton. The same changes with increasing size were reported for Marion Lake (Andrusak, MS 1968).

Food taken by allopatric Dolly Varden in Dickson Lake was not clearly related to the depth at which they were captured. Some fish caught at the bottom at 20 m had eaten insects and motile benthos, and others caught at the surface at 20 m had eaten static and motile benthos prey types. This suggests considerable vertical and onshore-offshore movement by Dolly Varden in Dickson Lake, a behavioural pattern corroborated by netting data there.

Allopatric Dickson Lake Dolly Varden, with fork length less than 155 mm, took more zooplankton both in the summer and in the fall than larger fish (Fig. 20). In the summer, larger fish took a greater proportion of insects

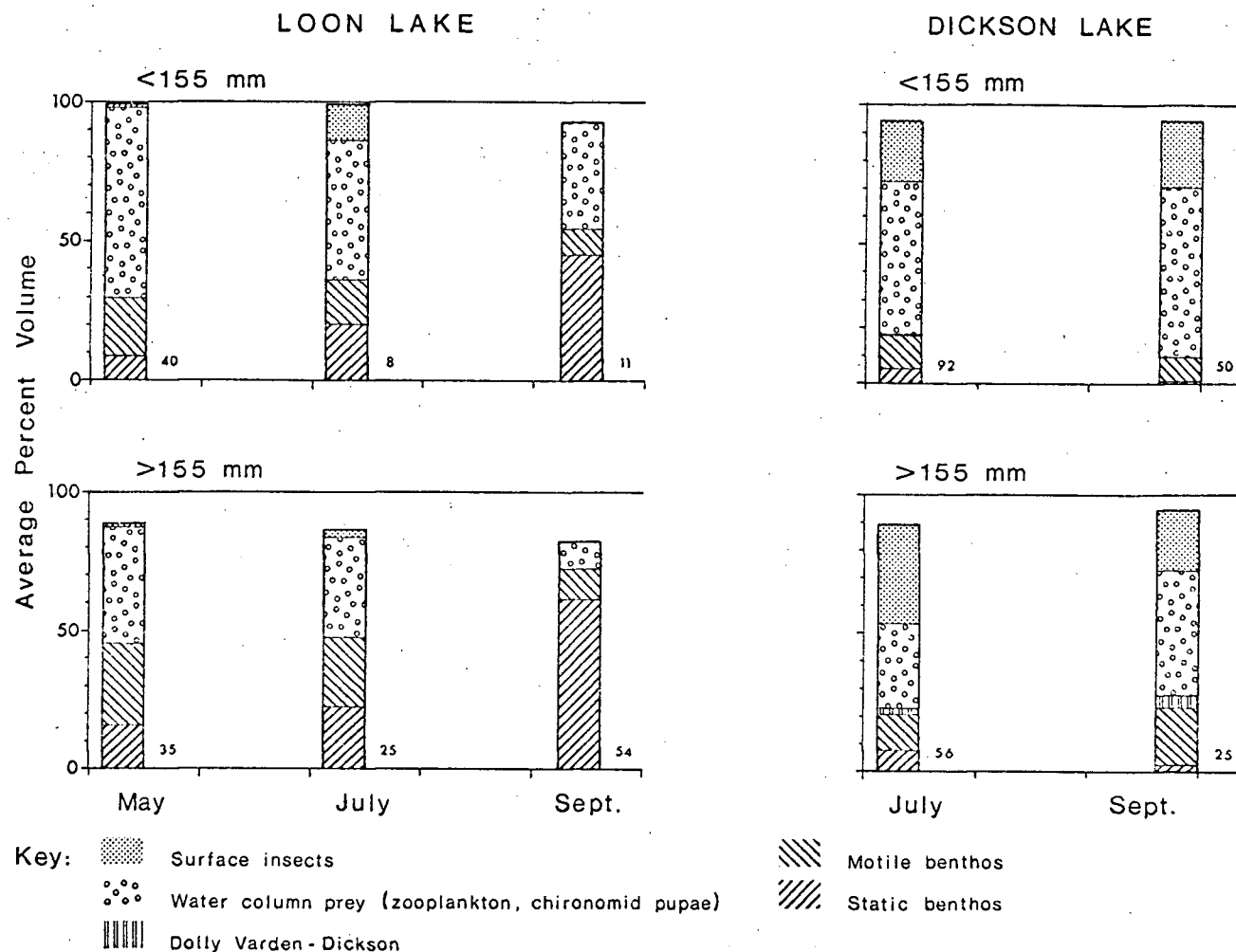


FIGURE 20. Size related differences in stomach contents (average percent volume) of sympatric Loon Lake and allopatric Dickson Lake Dolly Varden in 1972. Sample sizes indicated; balance (unshaded) composed of indigestible material e.g. seeds, mud.

than smaller ones but this was reversed in the fall, when larger fish took more motile benthos. Static benthos and fish were proportionately more important in the diets of large fish than small in both summer and fall.

In Foley Lake, individual allopatric Dolly Varden made similar vertical movements to those in Dickson Lake. Fish taken at 17 m depth in the summer, close to the substrate, had eaten insects shortly before capture; others that had freshly eaten insects were taken at 10 m in the spring and fall. Most fish were captured close to the substrate and the amount of benthos eaten was correspondingly high.

Canonical correlations (Lee, 1971) showed that food of individual Dolly Varden was not correlated with the number of gill rakers or pyloric caeca in any of the three lakes (Table VIII).

TABLE VIII. Relationship of numbers of pyloric caeca and gill rakers to diet; data within lakes are combined.

<u>Lake</u>	<u>N</u>	<u>Canonical correlations and their significance</u>							
		<u>I</u>	<u>Chi²</u>	<u>d.f.</u>		<u>II</u>	<u>Chi²</u>	<u>d.f.</u>	
LOON	160	0.272	17.5	27	NS	0.190	5.7	16	NS
DICKSON	205	0.177	10.8	27	NS	0.148	4.4	16	NS
FOLEY	47	0.442	14.8	27	NS	0.368	6.0	16	NS

6. Length-frequency and age categories

The length frequency distributions of Loon Lake Dolly Varden (Fig. 21) are distinctly more polymodal than

those of Dickson Lake fish (Fig. 22). This distinction is shown well when frequency distributions of Dolly Varden captured in July over a number of years from Loon and Dickson Lakes are plotted on probability paper (Fig. 23). These suggest that there is less variability in fork length within year classes in Loon Lake than in Dickson Lake. Scale samples taken from a small number of Loon Lake Dolly Varden in the fall showed that the winter checks corresponding to the first, second and third winters occurred when fish were approximately 80, 125 and 175 mm in fork length respectively. This showed that yearling fish (1+) started to enter the catch in the fall (Fig. 21).

Most cutthroat trout captured in Loon Lake were between 160 and 200 mm in fork length; winter checks corresponded to fork lengths of approximately 60, 110 and 160 mm. Fork lengths for a given year class appeared to overlap considerably with those of Dolly Varden from the same year class.

Dickson Lake Dolly Varden were difficult to separate into year classes using length frequency histograms owing to the variability in length within year classes and the overlap between adjacent year classes (Figs. 22 and 23). Ageing with otoliths proved impractical as they were difficult to clear; an individual of fork length 173 mm was shown to have overwintered three times (J.D. McPhail, pers. comm.). A few scales were read, but results were uncertain;

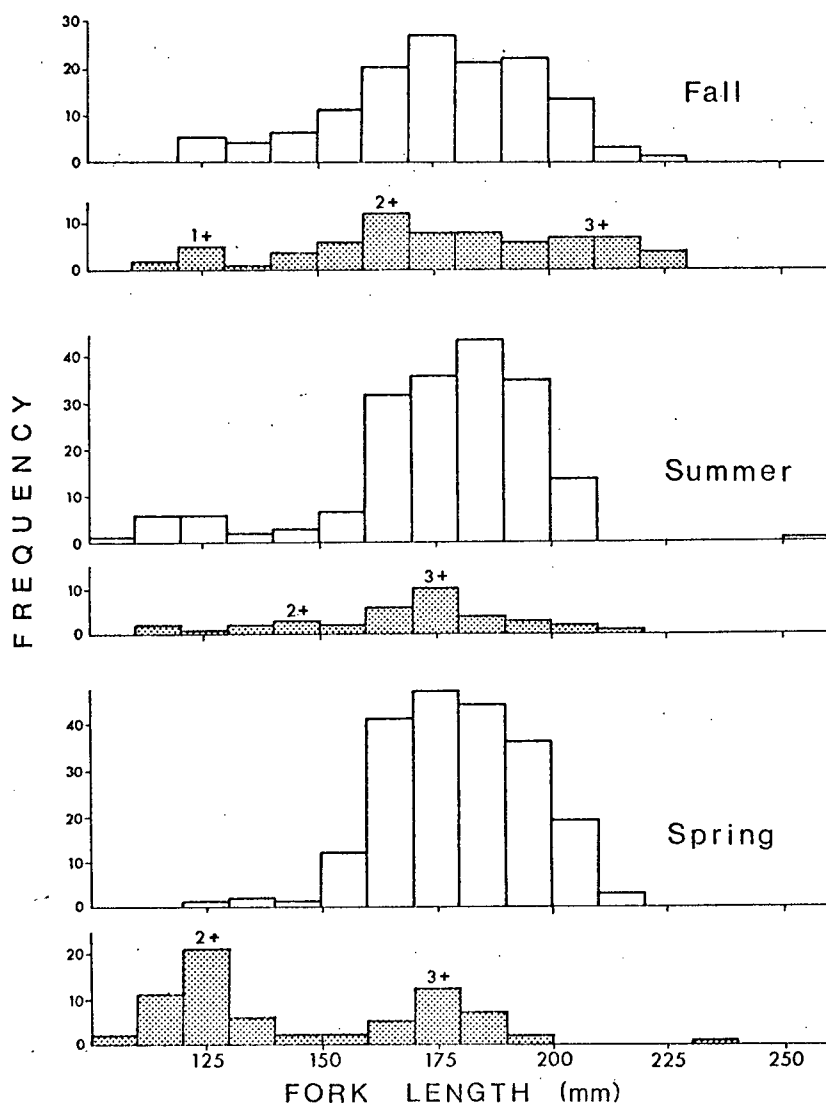


FIGURE 21. Seasonal changes in length frequency distribution of Dolly Varden (shaded) and cutthroat (blank) in Loon Lake during 1972. Probable age categories shown on some histograms.

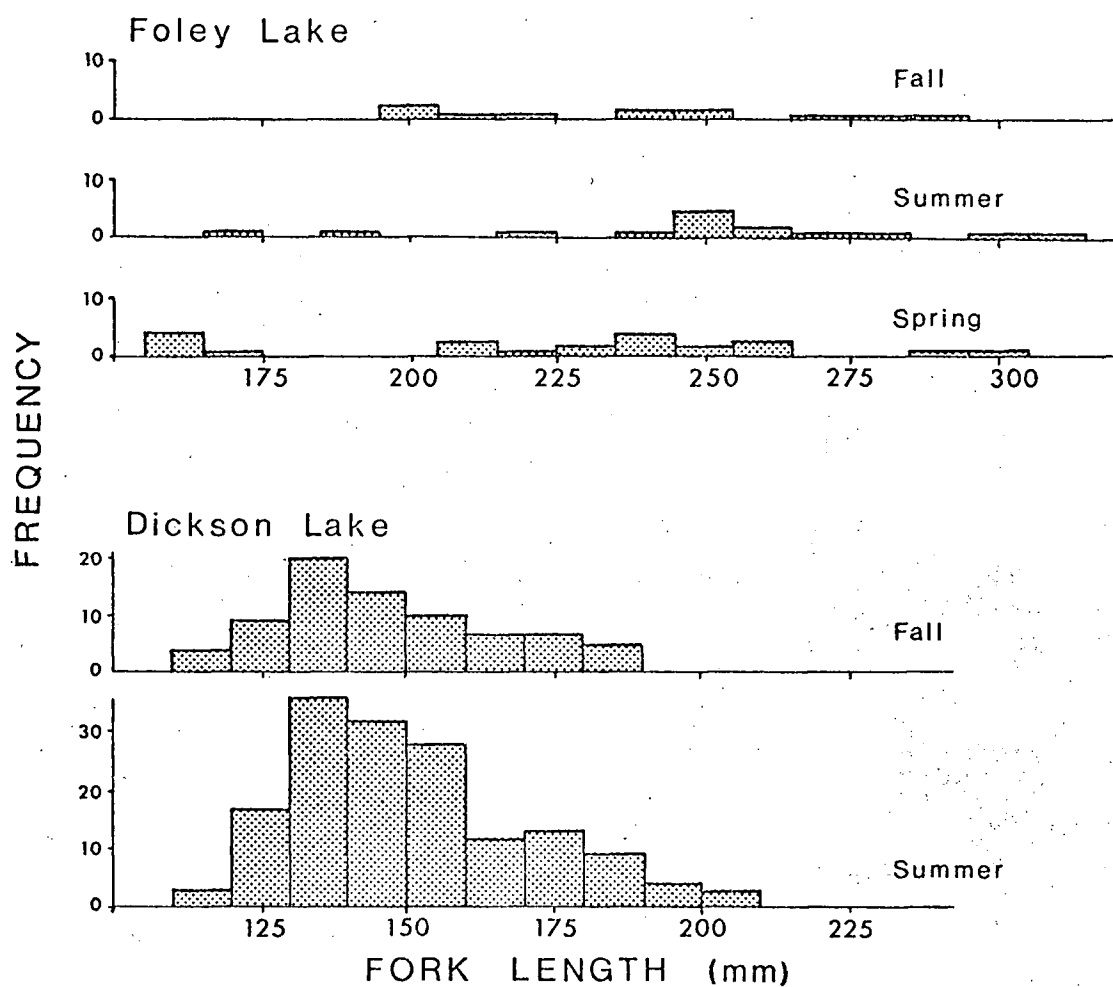


FIGURE 22. Length frequency histograms for Dolly Varden captured in Foley and Dickson Lakes in 1972.

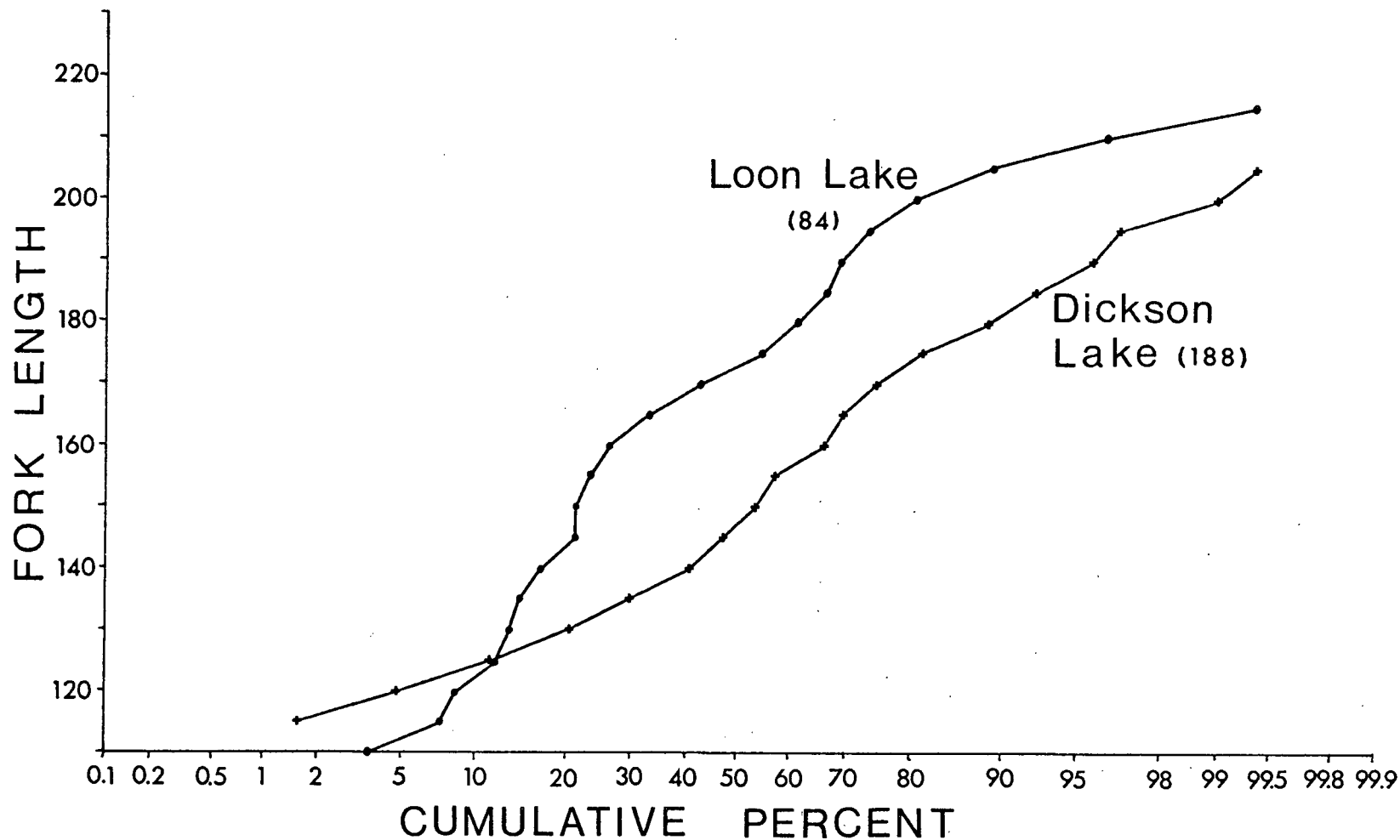


FIGURE 23. Fork length distributions of July samples of Dolly Varden from Loon and Dickson Lakes. Samples from several years are pooled in each case. Sample sizes in parentheses.

probably most of the fish taken in 1972 netting with fork lengths between 130 and 160 mm were fish that had overwintered twice. In August 1971, a sample of young of the year was collected by dip netting in an inflow creek mouth; they ranged in fork length from 28 to 50 mm with a mean of 37 mm.

Foley Lake Dolly Varden were considerably larger than Dolly Varden from Loon and Dickson Lakes (Fig. 22). Young of the year, with fork length of approximately 50 mm, were observed in side channels of the main inflow, Foley Creek, in September 1972.

7. Meristic counts

Numbers of pyloric caeca are not correlated with fork length for Loon and Foley Lake Dolly Varden, but correlation is evident for the Dickson Lake population (Fig. 24). This may account for part of the greater variability in pyloric caeca number of the Dickson Lake population (Table IX). Mean numbers of pyloric caeca are greater in both allopatric populations than in the sympatric Loon Lake population.

Gill raker numbers are correlated with fork length for Loon Lake Dolly Varden (Fig. 25); this may account in part for the high variability in gill raker numbers of the Loon Lake population (Table IX). Numbers reach an asymptote at approximately 140 mm fork length. Gill raker numbers are not correlated with fork length for the two allopatric

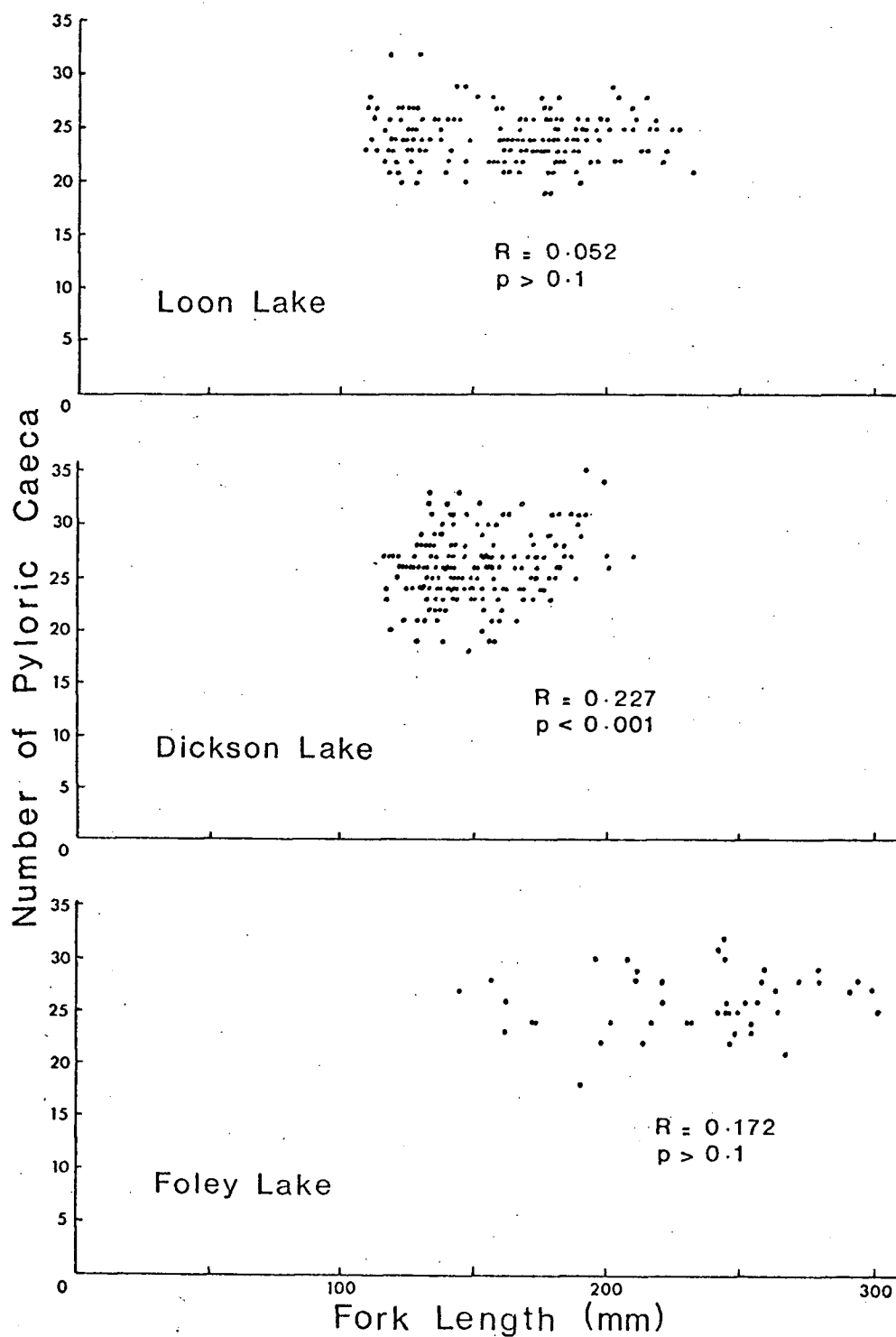


FIGURE 24. Relationship of pyloric caeca numbers to fork length; correlation coefficients (R) and probability of significance (p) are shown.

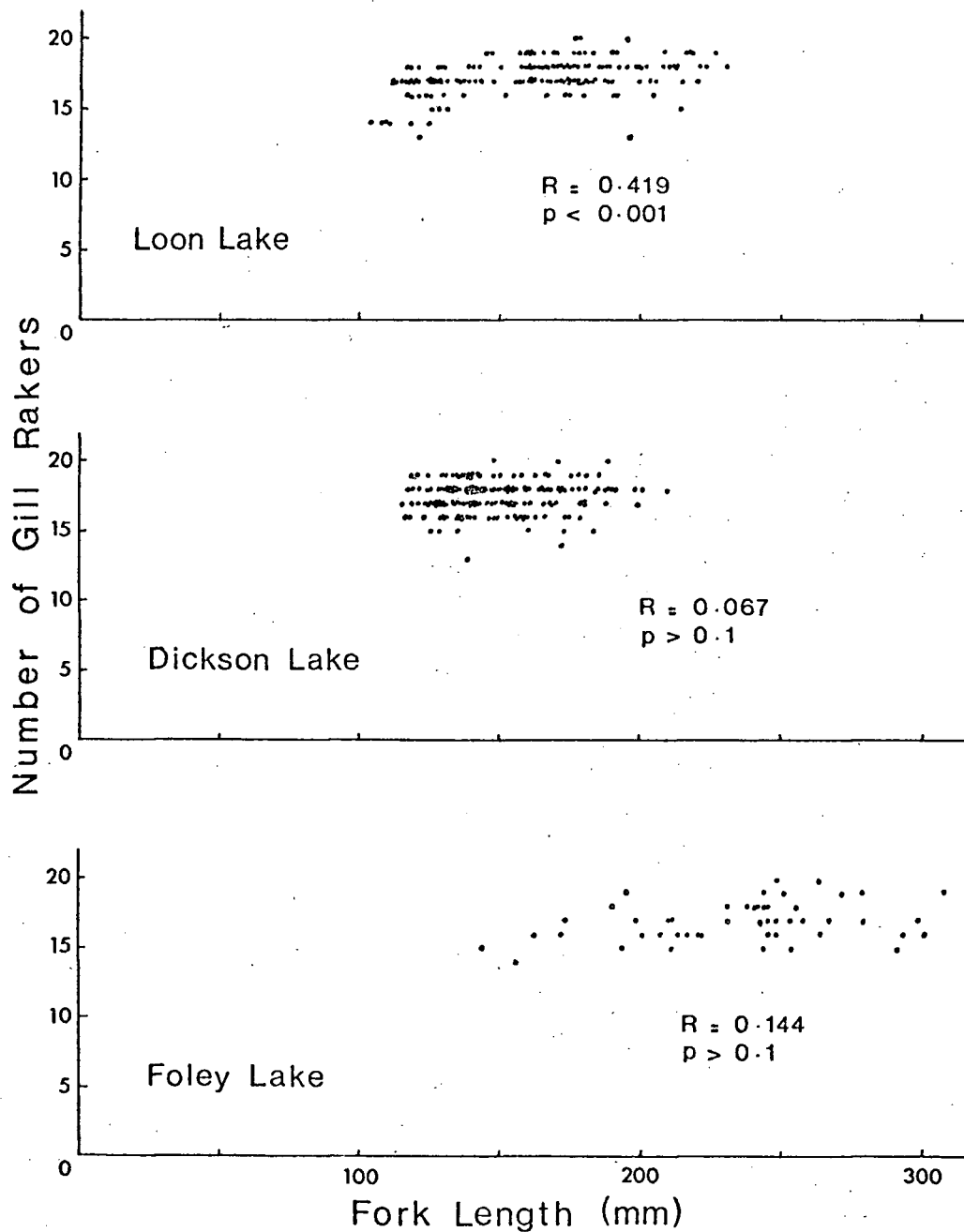


FIGURE 25. Relationship of gill raker numbers to fork length; correlation coefficients (R) and probability of significance (p) are shown.

TABLE IX. Means and variances of meristic counts for Dolly Varden from Loon, Dickson and Foley Lakes.

1. Pyloric caeca

<u>Population</u>	<u>Mean</u>	<u>99% confidence range of mean</u>	<u>Variance of log (count)</u>	<u>N</u>
LOON	24.23	23.77 - 24.68	0.0088	168
DICKSON	25.90	25.35 - 26.46	0.0145	209
FOLEY	25.89	24.76 - 27.02	0.0128	46

DICKSON and FOLEY means > LOON mean, 1% significance.

F ratio (two tailed test) to compare variances:

DICKSON: LOON = 1.648; $p < 0.01$

FOLEY: LOON = 1.454; $p < 0.05$

DICKSON: FOLEY = 1.133; NS

2. Gill rakers on the anteriormost right hand gill arch

<u>Population</u>	<u>Mean</u>	<u>99% confidence range of mean</u>	<u>Variance of log (count)</u>	<u>N</u>
LOON	17.31	17.06 - 17.56	0.0058	177
DICKSON	17.46	17.27 - 17.66	0.0043	221
FOLEY	17.00	16.47 - 17.52	0.0056	49

There is no significant difference between the means.

F ratio (two tailed test) to compare variances:

LOON: DICKSON = 1.349; NS

LOON: FOLEY = 1.036; NS

FOLEY: DICKSON = 1.302; NS

See Figures 26 and 27.

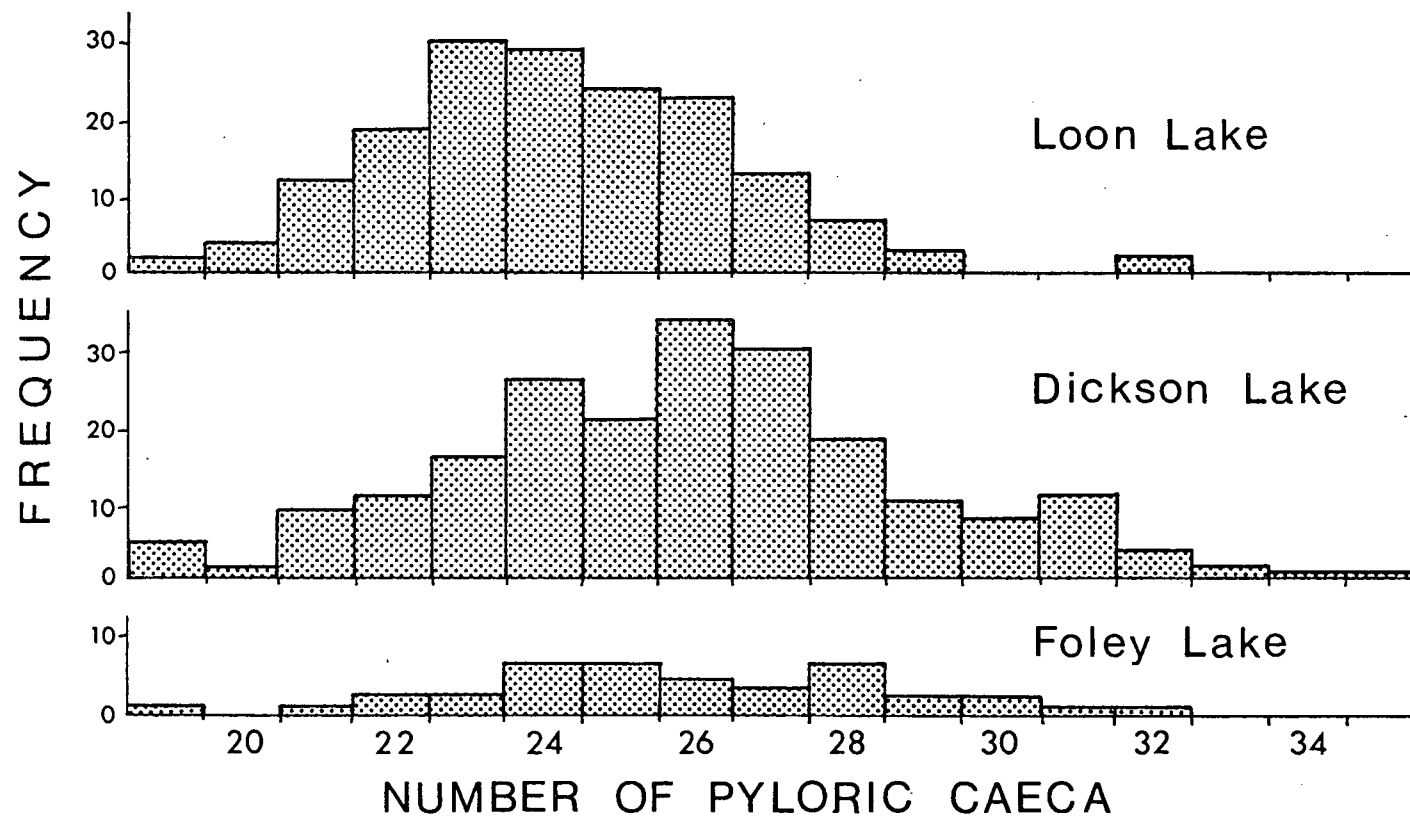


FIGURE 26. Distribution of pyloric caeca numbers in Dolly Varden from Loon, Dickson and Foley Lakes.

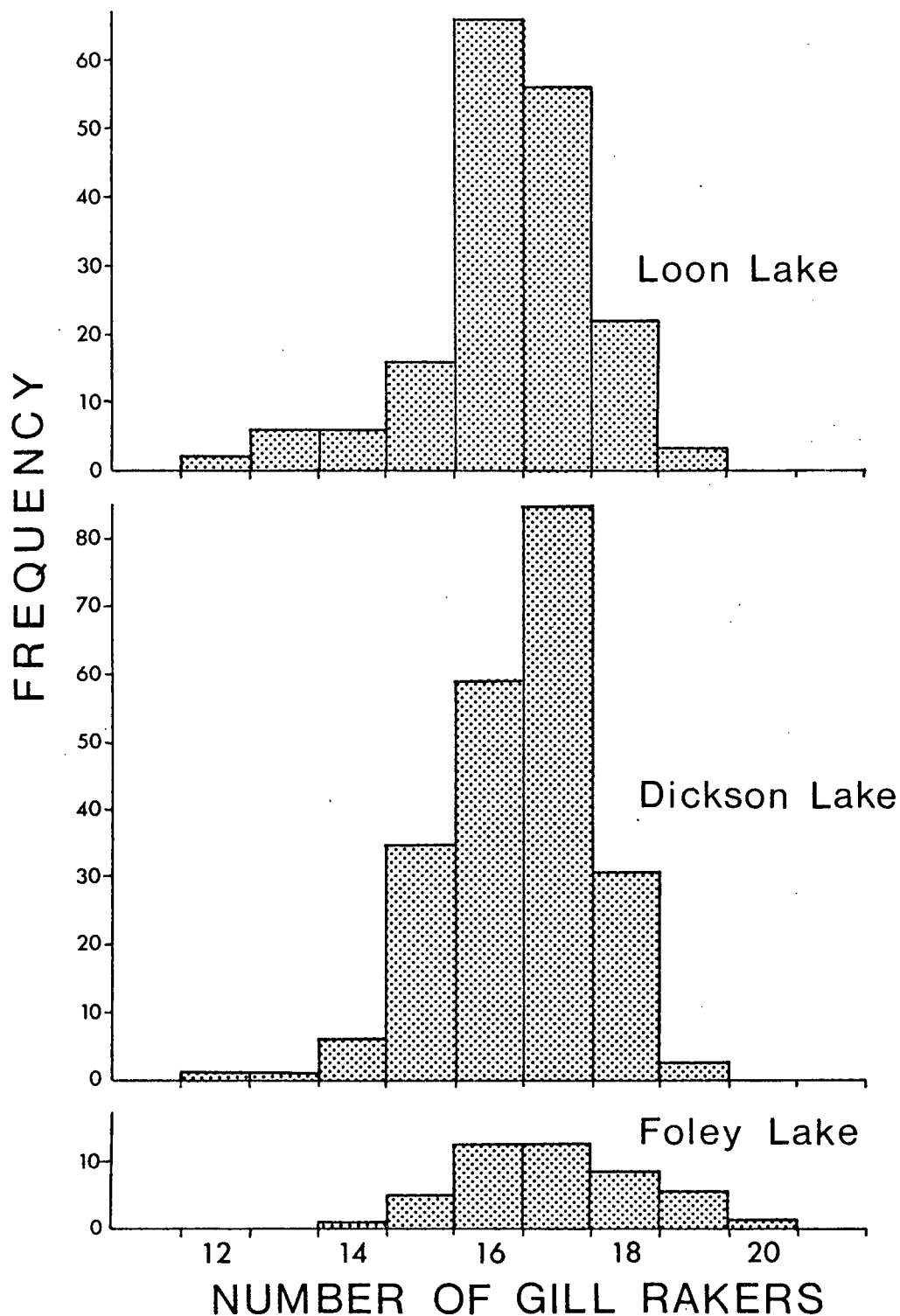


FIGURE 27. Distribution of gill raker numbers on the anteriormost right hand gill arch in Dolly Varden from Loon, Dickson and Foley Lakes.

populations. Mean numbers of gill rakers do not differ significantly between the three populations.

8. Morphometric comparison of the three Dolly Varden populations

Growth of the head (Fig. 28) and predorsal length in relation to standard length is greatest for Loon Lake Dolly Varden and least for the Foley Lake population (Table X). Similar differences in relative growth of other head parts, upper jaws, snout-to-back-of-eye, eye (Fig. 29) and longest gill raker (Fig. 30) are found between the three populations.

Although relative growth rates of these body parts are greater for Loon and Dickson Lake Dolly Varden, in most cases they are proportionately smaller than in the Foley Lake fish for much of the size range captured. For example, upper jaws of Loon Lake Dolly Varden are smaller than those of Foley Lake fish of corresponding size until they reach 230 mm standard length (Fig. 29). Relative growth rates of the eye vary greatly between the populations, that of Loon Lake Dolly Varden being the greatest; both Loon and Dickson Lake Dolly Varden have larger eyes than similar sized Foley Lake fish over the size range captured (Fig. 29) as the growth rates of their eyes in relation to standard length are so much larger than that of Foley Lake Dolly Varden (Appendix Table VIII).

Contrary to expectation, variability (mean square

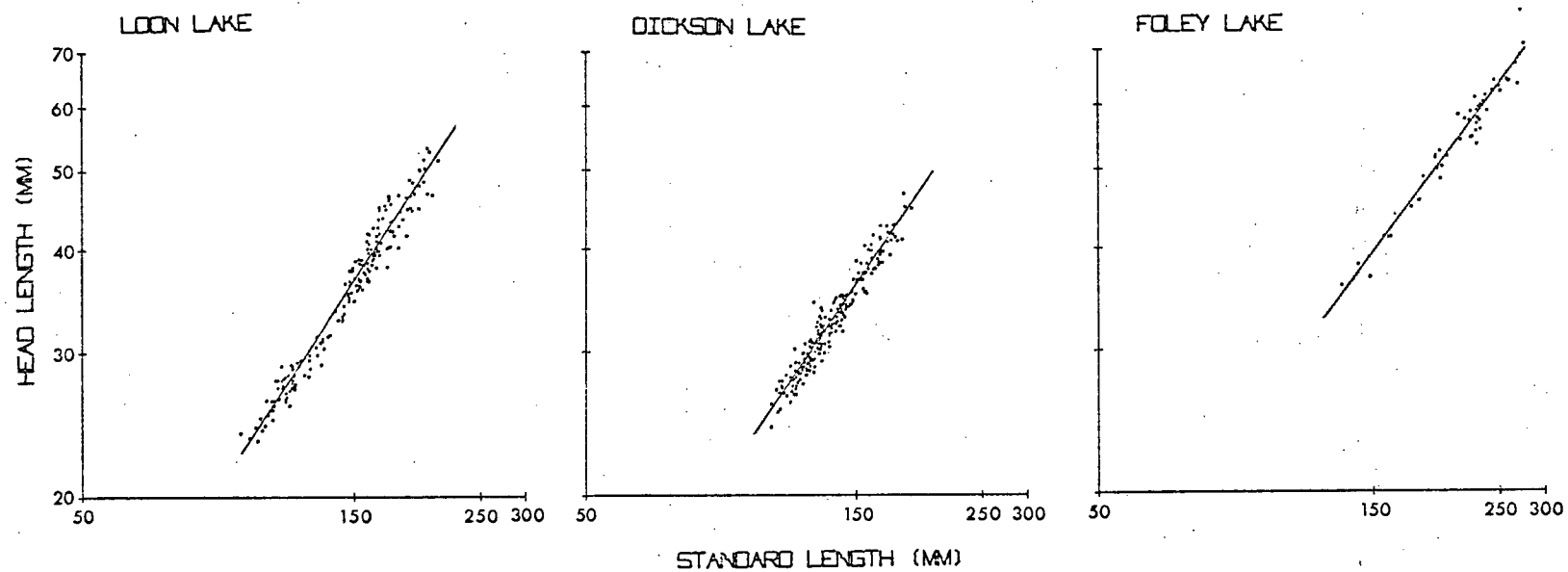


FIGURE 28. Relationship of head length to standard length for the three Dolly Varden populations.

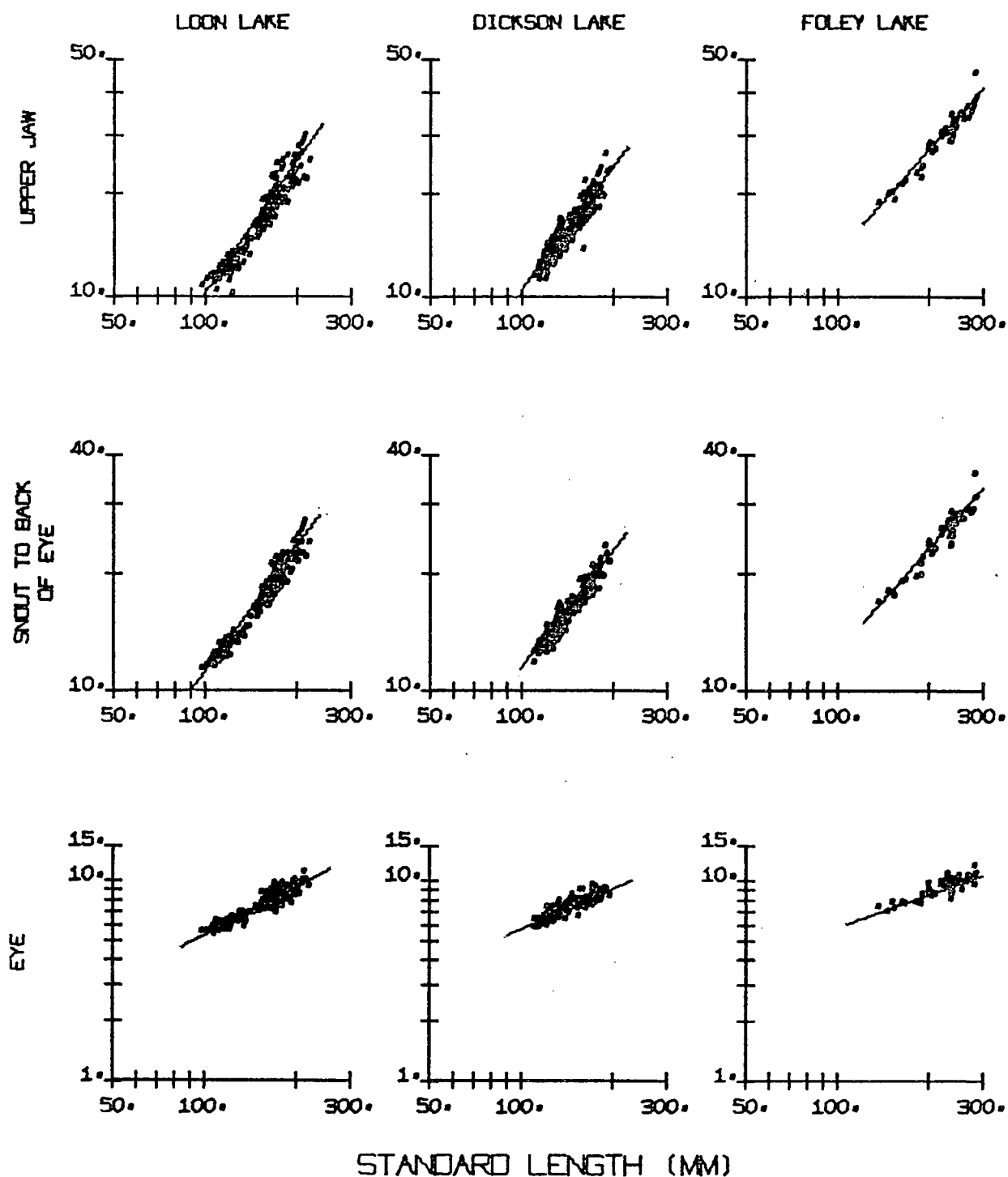


FIGURE 29. Relationship of upper jaw length, distance from snout to back of eye, and eye length to standard length for the three Dolly Varden populations.

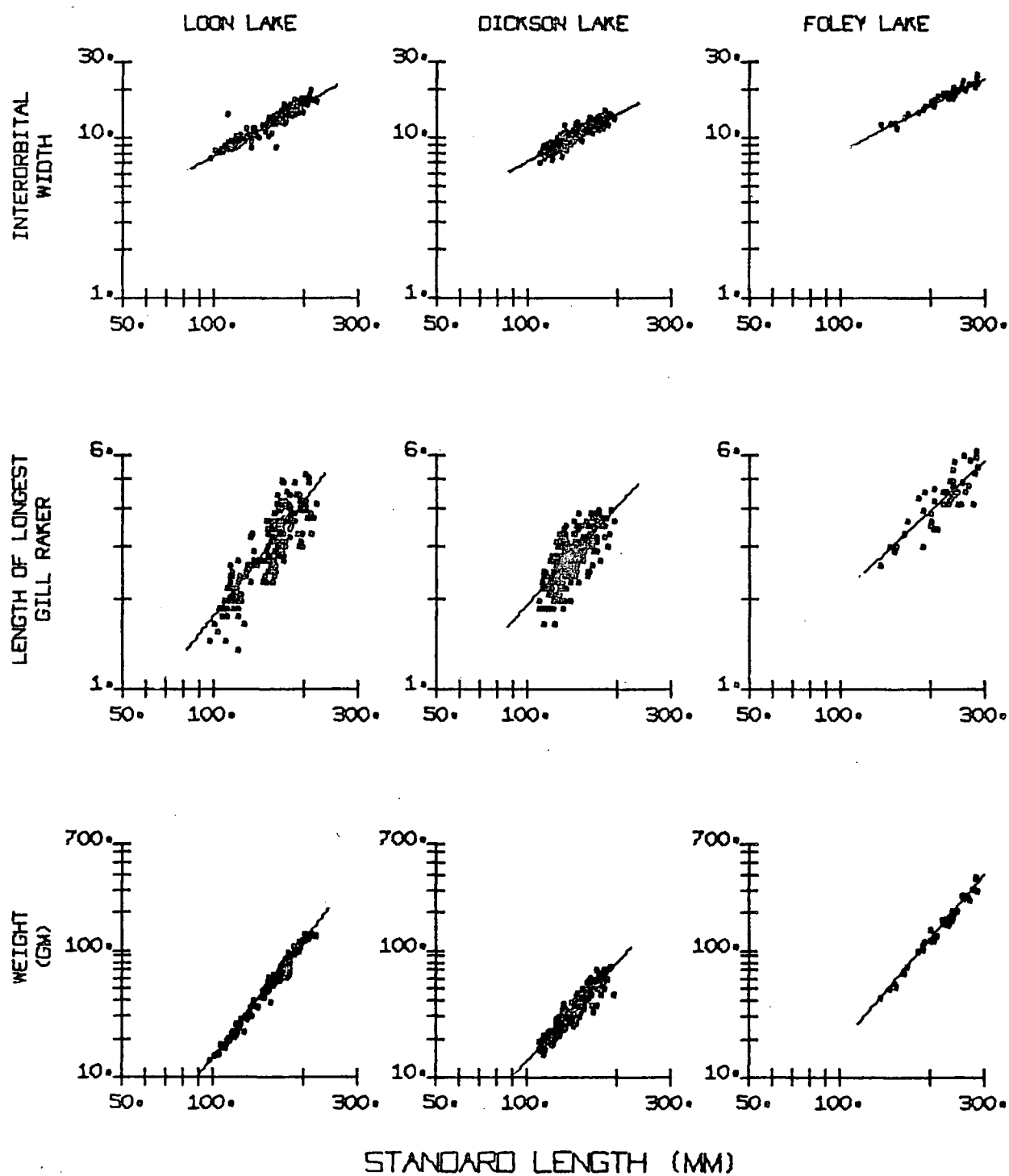


FIGURE 30. Relationship of least fleshy interorbital width, length of longest gill raker, and weight to standard length for the three Dolly Varden populations.

deviation) about the regression is greatest for the sympatric Loon Lake population for head, predorsal, upper jaw, snout-to-back-of-eye, eye and longest gill raker lengths (Table X). The variability is significantly greater than that of Dickson Lake Dolly Varden in every case and it is greater than that of Foley Lake Dolly Varden in upper jaw, longest gill raker and predorsal lengths. Examination of the regressions of head (Fig. 28), upper jaw, snout-to-back-of-eye and eye (Fig. 29) lengths on standard length for Loon Lake Dolly Varden suggests an inflection, particularly marked for the upper jaw, at 140 mm (approximately 155 mm fork length) towards greater relative growth of each of these body parts in larger fish. The inflection must contribute considerably to the increased mean square deviations of these body parts of the Loon Lake population with respect to the allopatric populations. Regressions calculated separately for fish smaller than and larger than 140 mm (Fig. 31) eliminate the effect of the inflection, and variability within each size group of the Loon Lake fish is no longer significantly greater than that of fish from equivalent size classes from the other two populations (Appendix Table XIII). The inflections noted for the relative growth of the head, snout-to-back-of-eye and eye lengths for Loon Lake Dolly Varden suggest that all these characters are interrelated with upper jaw length in the same 'morphogenetic field of influence'

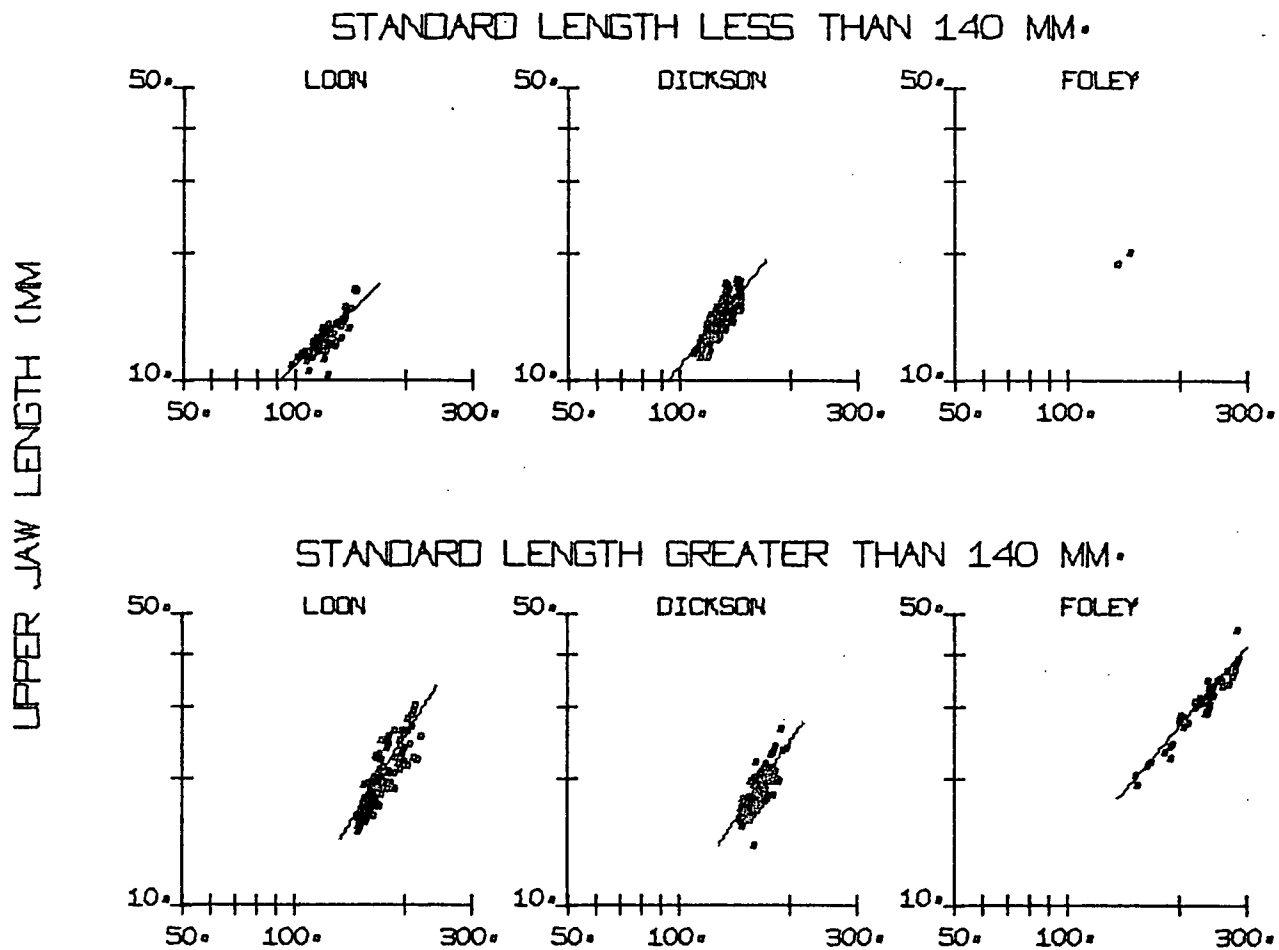


FIGURE 31. Relationship of upper jaw length to standard length for Dolly Varden smaller than and larger than 140 mm (approximately 155 mm fork length) for the three populations.

TABLE X. Summary of morphometric comparisons of the three Dolly Varden populations.

<u>Body part</u>	<u>Slope</u>	<u>Relative size of body part at given standard length</u>		<u>Variability</u>	<u>Appendix Table</u>
Head	L and D > F	F > L > D	for all lengths measured	L > D	V
Upper jaw	L > D > F	F > L F > D	for fish > 300 mm for fish > 300 mm	L > F and D	VI
Snout-to-back- of-eye	L > D > F	F > L and D for fish > 250 mm		L and F > D	VII
Eye	L > D > F	F > D F > L D > L	for fish > 110 mm for fish > 150 mm for fish > 160 mm	L and F > D	VIII
Length of longest gill raker	L > D and F	F > D > L L > D > F	for fish > 150 mm for fish > 150 mm	L > D and F	IX
Predorsal	L > D > F	F > L > D	for all lengths measured	L > D > F	X
Interorbital width	No differences	F > L > D	for all lengths measured	L > D > F	XI
Anal to pectoral fin base	F > D > L	F > D > L	for all lengths measured	F > D > L	XII

L = Sympatric Loon Lake Dolly Varden
D = Allopatric Dickson Lake Dolly Varden
F = Allopatric Foley Lake Dolly Varden

All differences are significant at $p \leq 0.05$.

(Huxley, 1932).

The three populations do not differ in relative growth of the interorbital width (Fig. 30; Table X), a measure of head width. However, Dickson Lake Dolly Varden have considerably narrower heads than Dolly Varden from the other two lakes in the size ranges measured. Foley Lake Dolly Varden smaller than 180 mm standard length have relatively wider heads than Loon Lake Dolly Varden of corresponding sizes; larger Foley Lake fish have relatively narrower heads. Loon Lake Dolly Varden again vary most for this character (Table X).

The distance from the anal base to the pectoral fin base, a measure of body length, is greatest in Foley Lake fish and least for Loon Lake Dolly Varden for fish of any size in the range measured. Growth of this character in relation to standard length, and its variability about the regression line are greatest in allopatric Foley Lake Dolly Varden and least in sympatric Loon Lake Dolly Varden, the reverse of the situation for the head-related body parts (Table X).

9. Length-weight relationships

The coefficients (b) in the equation

$$\log W = \log a + b(\log L)$$

are 3.071, 2.835 and 2.573 for the Loon, Foley and Dickson Lake populations respectively and these differ significantly (Appendix Table XIV). The Loon Lake Dolly Varden grow

heavier for their length with increasing length (slope departs from isometry, where $b = 3.0$; $p < 0.05$); fish from Foley and Dickson Lakes become lighter for their length at increasing lengths ($p < 0.01$ and $p < 0.001$ respectively).

For all standard lengths captured, Dickson Lake Dolly Varden are lighter than similar sized fish from the other two populations, and have a significantly greater mean square deviation about the regression indicating greater variability (Fig. 30). Foley Lake fish with standard lengths less than 300 mm are heavier than similar sized Loon Lake fish.

10. Morphometric differences between cutthroat trout and Dolly Varden

The average rate of growth of the upper jaw in relation to standard length (Fig. 32) is the same for both cutthroat and Dolly Varden from Loon Lake (Appendix Table XV), but the upper jaw length of cutthroat is proportionately larger than that of similar sized Dolly Varden, comparing smaller fish. This situation also occurred in Marion Lake (Schutz and Northcote, 1972); Dolly Varden there, like small Loon Lake Dolly Varden, had smaller maxillaries than cutthroat and differed from the general description in Clemens and Wilby (1961) in having small subterminal mouths. However, owing to the marked increase in relative growth of the upper jaw of Loon Lake Dolly Varden larger than 140 mm standard length (Fig. 32), their jaw length approaches that

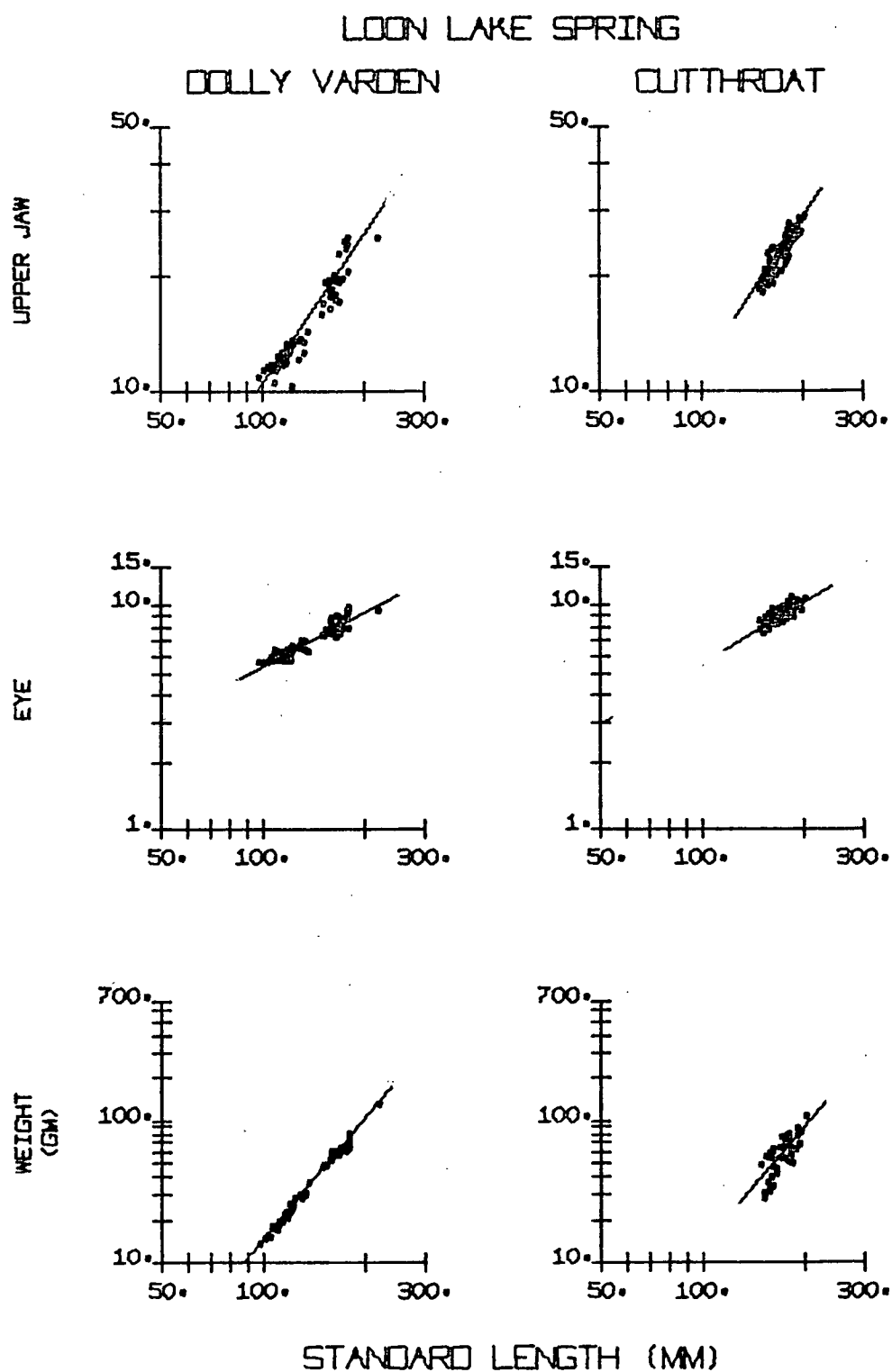


FIGURE 32. Relationship of upper jaw length, eye length, and weight to standard length for Loon Lake Dolly Varden and cutthroat taken in May 1972.

of cutthroat at standard lengths greater than 220 mm. Foley Lake Dolly Varden smaller than 170 mm standard length (Fig. 29) have larger jaws than similar sized cutthroat; the upper jaws of Dickson Lake Dolly Varden, on the other hand, are proportionately smaller than those of cutthroat at all lengths measured.

Relative growth of the eyes of the two species do not differ in Loon Lake, but cutthroat have proportionately larger eyes.

Cutthroat trout are proportionately heavier than Dolly Varden in Loon Lake but the rate of increase of body weight with length is the same for both populations.

B. Laboratory Observations

1. Spatial distribution

Allopatric Dickson Lake Dolly Varden spent a greater percentage of a test period in the upper half of the tank than sympatric Loon Lake Dolly Varden (Table XI). The former also showed significantly more variability between individuals in the amount of time spent in the upper half than the latter.

The amount of time spent in the upper half of the tank by sympatric Dolly Varden was not correlated with activity, but was so for allopatric Dolly Varden (Fig. 33), because one individual was exceptionally active and spent over 70% of the trial in the upper half, and another rested frequently on the substrate. The mean

TABLE XI. Results of spatial distribution and activity comparisons.

A. Spatial distribution:

<u>Population</u>	<u>Arcsin transformed data</u>		<u>% Mean time up</u>	<u>Number tested</u>
	<u>Mean time up</u>	<u>Variance</u>		
LOON	36.46	36.94	35.3	9
DICKSON	48.62	171.74	56.3	13

Mean time up: DICKSON > LOON; $p < 0.01$ from $d = 2.925$ with 18 d.f. using a modified 't' test to compare means of small samples with unequal variances (Bailey, 1959).

Variance of time spent up: DICKSON > LOON
 $F = 4.648$; one tailed test gives $p < 0.02$.

B. Activity:

<u>Population</u>	<u>Mean</u>	<u>Variance</u>	<u>Number tested</u>
LOON	77.2	415	9
DICKSON	98.9	2413	13

Mean activity: No difference. $p > 0.10$ from $d = 1.426$ with 17 d.f. using the modified 't' test.

Variance of activity: DICKSON > LOON
 $F = 5.807$; one tailed test gives $p < 0.01$.

C. Correlation of time spent in upper half with activity:

	<u>All fish</u>	<u>Allopatric</u>	<u>Sympatric</u>
R (correlation coefficient)	0.61	0.73	0.05
p	< 0.01	< 0.01	NS

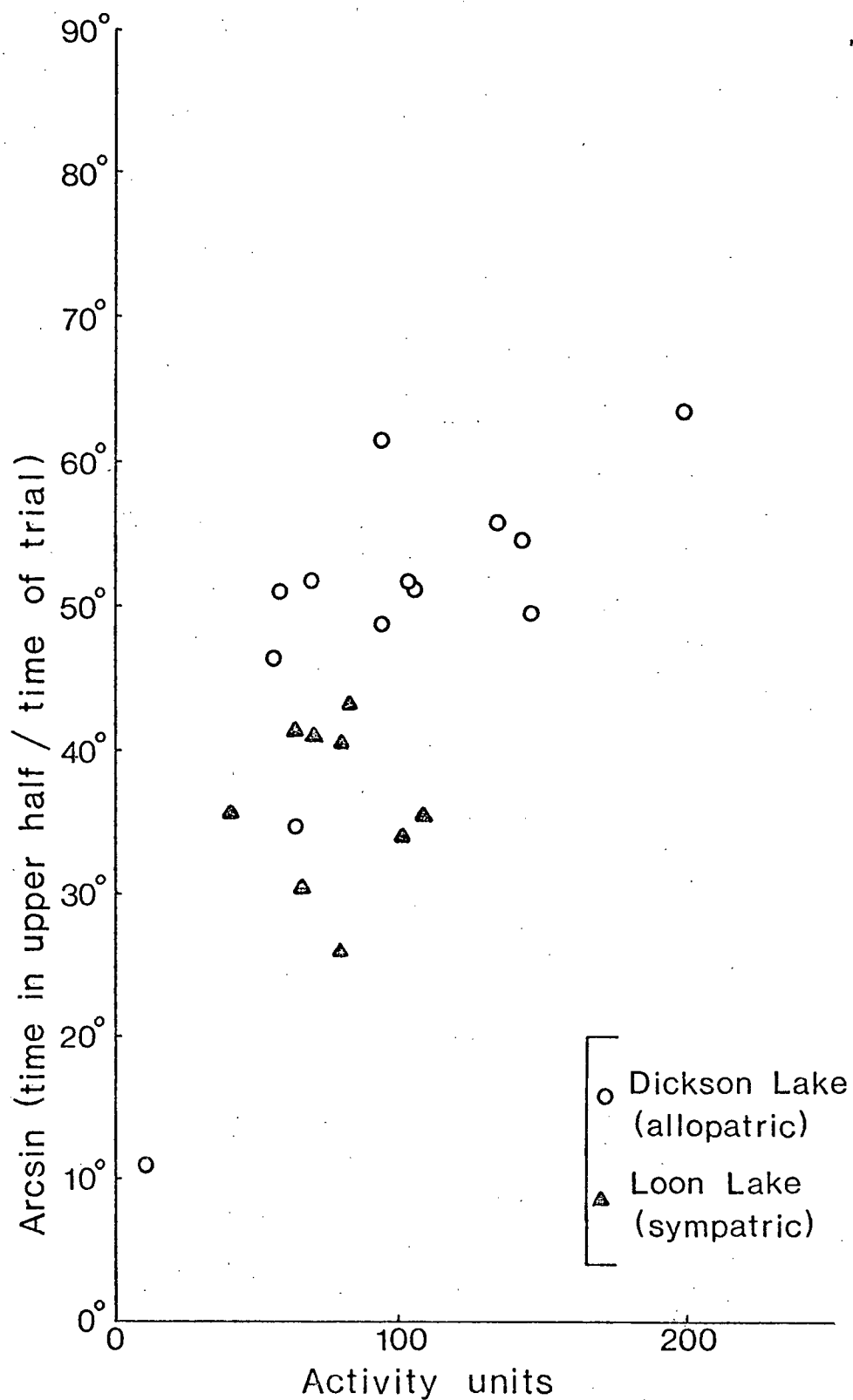


FIGURE 33: Correlation of time spent in upper half of observation tank with activity.
(See Table XI C)

activities of the two populations did not differ significantly; however, allopatric Dolly Varden showed more variability in activity between individuals than did the sympatrics.

2. Presentation of novel prey

Following capture and while being held in outdoor stream tanks, Dolly Varden from Loon Lake took longer to condition to feed on small cubes of chicken liver, presented still frozen at the surface where initially they floated. All Dickson Lake fish were eating such items within 5 days of capture (18 individuals observed) while Loon Lake fish required 14 days before all were feeding (12 individuals observed). Dickson Lake fish rapidly learned to take liver at the surface or while it sank but usually rejected it on the substrate. Loon Lake Dolly Varden initially took liver as it sank but took 30 days to condition to take liver from the surface; their surface grabs were rapid and they frequently missed the food item.

Two experiments were conducted in the observation tanks in the spring of 1972 to test whether allopatric Dolly Varden responded faster to novel prey than sympatric Dolly Varden after 6 months feeding on chicken liver. All fish had been fed to satiation on chicken liver three days before the test in an attempt to standardize hunger levels.

i. Earthworms

Ten earthworms of uniform size were placed on the

bare substrate of the observation tank prior to the introduction of a test fish. The fish was allowed ten minutes in the tank to respond to the prey, before being returned to its holding tank. Three out of five allopatric fish and none of the five sympatric fish ate earthworms ($p = 0.085$, Fisher Exact Test); although this was not statistically significant, the difference was in the expected direction.

ii. Chironomid larvae

Twenty larvae were scattered randomly over the sand and leaf litter substrate. Fish were introduced individually for a 10 minute test period. The time to the first grab was recorded (Appendix Table XVI). At the end of the test period the fish was removed and the remaining chironomid larvae were counted to determine how many had been eaten. Following the test, each fish was fed to satiation with chicken liver, and the test was repeated three to four days later.

Allopatric fish responded faster to the prey than sympatric fish, considering up to three successive tests to encourage unresponsive fish to feed (Appendix Table XVI).

Allopatric Dolly Varden appeared to eat larvae more readily during the first 10 minute test than did sympatric Dolly Varden (Table XII). The one allopatric fish which did not feed then fed immediately when it was tested a second time, as did one of the sympatric Dolly

TABLE XII. Comparison of numbers of allopatric and sympatric Dolly Varden eating chironomid larvae during their first 10 minute exposure to 20 larvae scattered on a sand and leaf litter substrate.

	<u>Allopatric</u>	<u>Sympatric</u>
Feeding	7	1
Not feeding	1	3

$p = 0.065$, Fisher Exact Test

Varden. The latter, however, only took one larva and failed to eat on the third test. The two remaining sympatric Dolly Varden failed to feed on chironomid larvae during any of the three tests although, like all the other fish, they were active during the test period.

The one sympatric individual that fed on the first test ate 75% of the larvae presented; most of the allopatric fish took more than this. Allopatric Dolly Varden took more larvae on the first test than sympatric Dolly Varden ($p = 0.014$; Mann Whitney U test for non-normal data, where $U = 3$, $n_1 = 8$, $n_2 = 4$; Siegel, 1956).

3. Efficiency of feeding on planktonic Chaoborus larvae by sympatric and allopatric Dolly Varden

In three successive exposures of sympatric and allopatric Dolly Varden to planktonic Chaoborus larvae, the capture efficiency of the sympatric fish lay well within the range of that of the allopatric fish, considering only tests

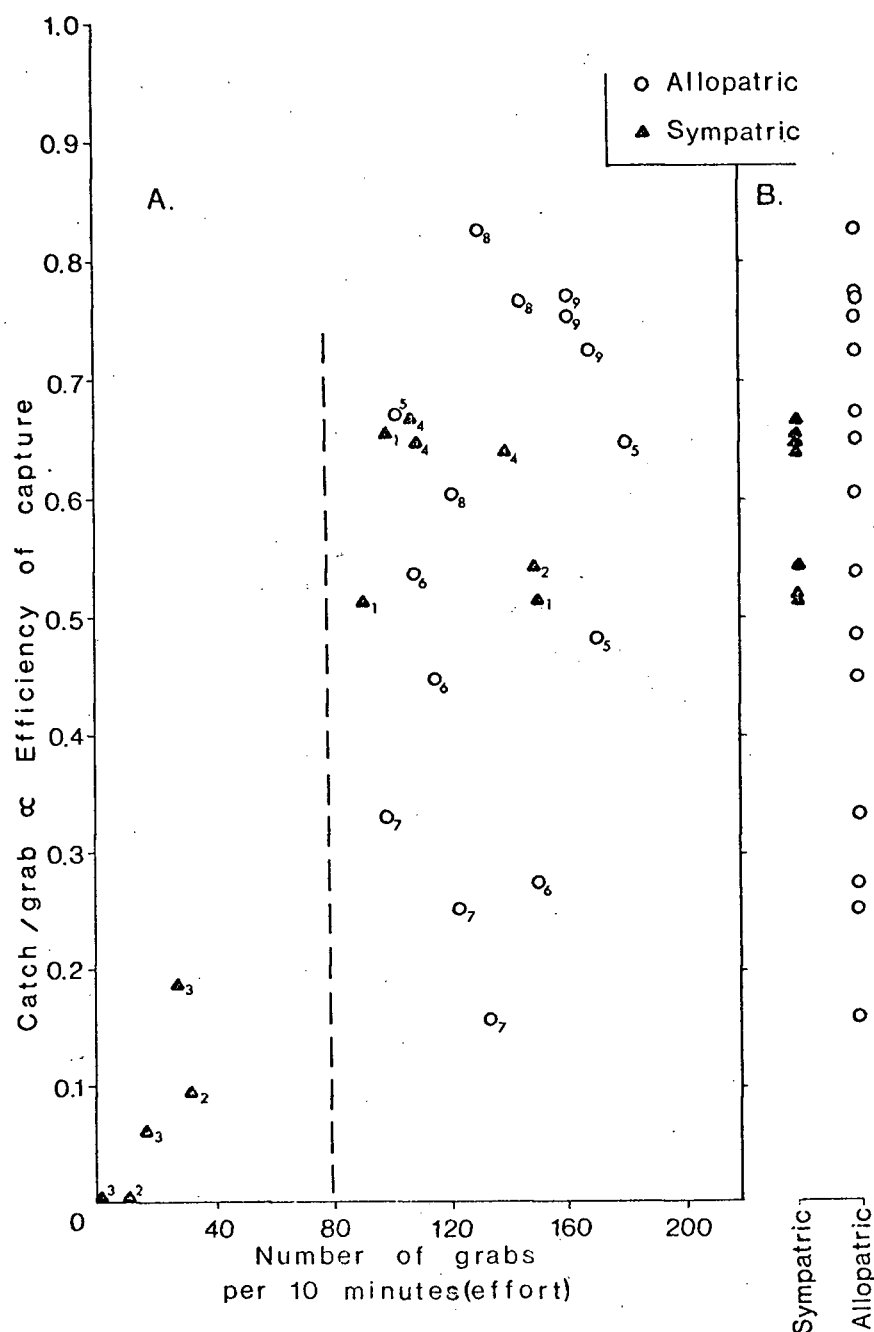


FIGURE 34. Efficiency of capture of *Chaoborus* larvae by sympatric and allopatric Dolly Varden. A. In relationship to effort. B. For those individuals making an effort greater than 8 grabs/minute.

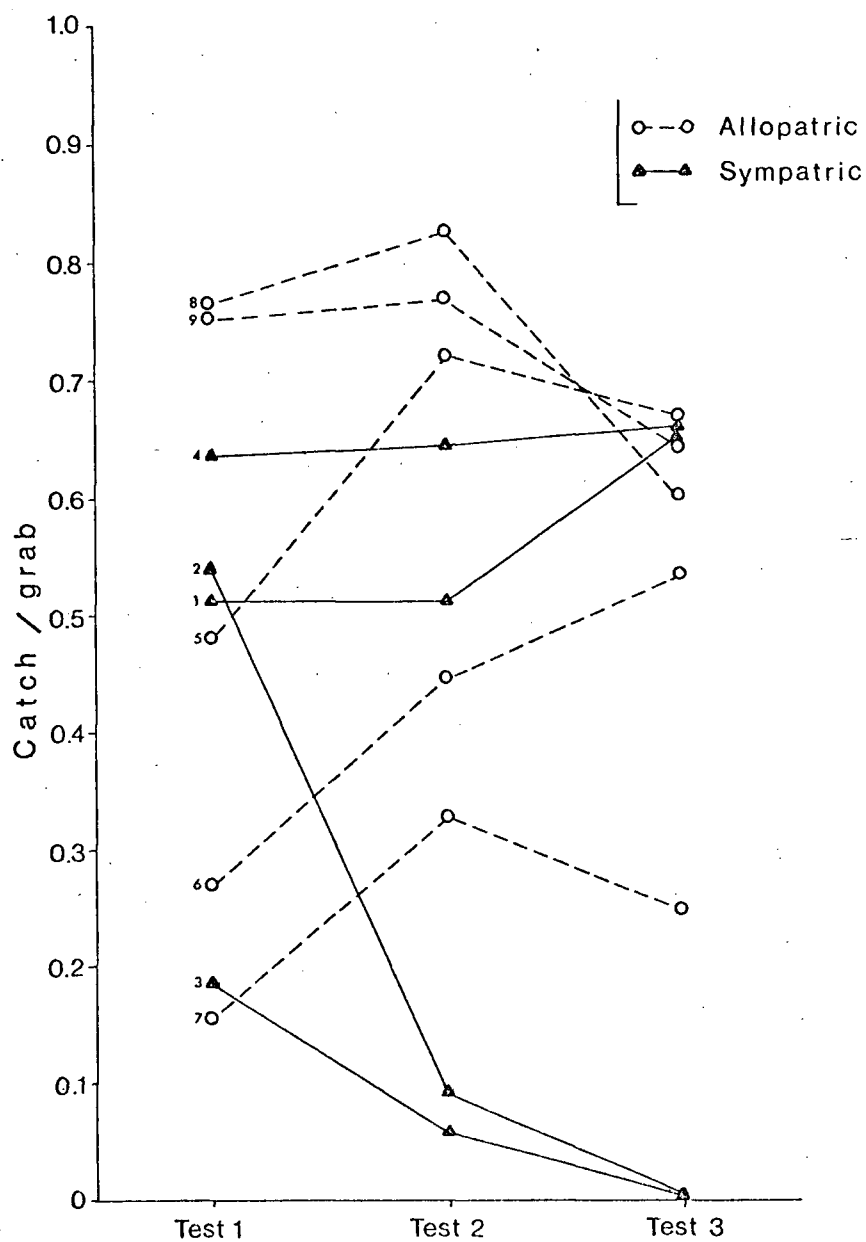


FIGURE 35. Efficiency of capture (catch/grab) of *Chaoborus* larvae by sympatric and allopatric Dolly Varden in successive trials.

in which individuals made more than 8 grabs per minute (Fig. 34). This level of effort was chosen to eliminate results from two sympatric individuals (#2, #3), whose catch efficiencies decreased markedly through the test series, neither of them capturing any prey in the final test (Fig. 35). Both fish were recent captures and presumably were unused to handling.

V. DISCUSSION

The aim of this study was to investigate the nature and extent of the character displacement evident in sympatric and allopatric Dolly Varden populations in small lakes. This follows from studies conducted by Andrusak (MS 1968) and Schutz (MS 1969); more emphasis was placed on fish from allopatric populations, both in the field and in laboratory observations.

Loon and Dickson Lake Dolly Varden populations were chosen for the primary comparison as these two lakes were fairly similar in their limnology, although Dickson Lake had a shorter summer and plankton abundance was less in the summer than in Loon Lake. Foley Lake was quite different, with abundant benthos and negligible amounts of zooplankton.

Dolly Varden were associated with the substrate in Loon Lake and moved out of the sublittoral zone into deeper water in late summer. In autumn, they were found

inshore again and also in the water column, showing a similar breakdown in spatial segregation to that reported by Andrusak (MS 1968) for Marion Lake. Spatial segregation in summer was far more apparent in Loon than in Marion Lake. Cutthroat trout were more abundant in Loon than in Marion Lake; capture ratios of char to trout were 3.25 and 0.34 respectively. In Marion Lake, Dolly Varden were captured in the water column throughout the summer, mainly in the lower half. In Loon Lake, Dolly Varden were confined to the substrate during the summer and early fall; cutthroat were not excluded from this region although numbers here were low in early fall.

In Dickson Lake, Dolly Varden were captured throughout the water column in July, August and September both day and night. These results appear to conflict with those of Andrusak (MS 1968), but re-examination of his original data suggests that fish may have been captured during the day. Stomach contents provided indirect evidence for vertical migration of some individuals and this may be a thermoregulatory mechanism for energy conservation in the face of limited food resources, similar to that proposed by Brett (1971) for juvenile sockeye salmon (Oncorhynchus nerka). The close association of the fish with the thermocline in August 1971 and their more random distribution in July and September 1972, when thermoclines were absent or only weakly present, suggests a possible relationship

of their distribution with temperature. Nilsson (1965) points out that Salvelinus alpinus are eurythermal: Arctic char captured at 30 m had freshly caught imagines of Lycoridae in their stomachs. Dolly Varden captured in Dickson Lake at 20 m had eaten adult dipterans. Groups of Dolly Varden were observed feeding at the surface for several hours at a time when the surface temperature was 21°C in August 1971, showing that they were not excluded by these high temperatures from any portion of the lake.

Dolly Varden from Foley Lake were mostly captured close to the substrate but they were not confined there; some were caught at the surface in the middle of the lake. Echo sounding records suggest a more midwater distribution than do the netting results.

In general, the sympatric Dolly Varden were associated with the substrate and with greater depths, as reported for a number of other lakes in British Columbia where they coexist with trout species (Andrusak and Northcote, 1970), while the allopatric Dolly Varden were not so spatially restricted.

Loon Lake Dolly Varden fed increasingly on benthos and less on zooplankton as the season progressed, until October, when they moved back into the water column and zooplankton became more important. Large fish became even more benthophagic than small fish in the summer and fall; they took less zooplankton than small fish presumably

because at their size, it was no longer efficient to do so. Andrusak (MS 1968) showed similar size related changes in the diet of Marion Lake Dolly Varden. As summer progressed and they became more benthophagic, Loon Lake Dolly Varden became less similar in diet to Dickson Lake Dolly Varden as well as to cutthroat trout. The diet of the cutthroat trout is fairly similar to that of Dickson Lake Dolly Varden although zooplankton, more abundant in Loon Lake, is more important for trout.

Cutthroat trout mainly took zooplankton, the percentage occurrence of copepods increasing, as in Marion Lake (Andrusak, MS 1968), and of cladocerans decreasing through the season. As in Marion Lake, many Dolly Varden took cladocerans and there was a similar peak percent occurrence of copepods in midsummer. Insects were important to cutthroat in the spring and fall and some chironomid pupae were eaten in the spring and summer, but far less than in Marion Lake.

Increasing amounts of chironomids and Chaoborus larvae taken by trout caught at the same depths as Dolly Varden in early fall suggest that competition may start to occur for this prey category as cutthroat invade the food refuge. However, Andreasson (1971) states that similarity of diet indicates lack of competition owing to superabundance of a common prey. One would have to determine levels of prey production and requirements of the two competitors to be able

to state whether competition is occurring or not; however, it is difficult to determine whether demand exceeds supply in the field (Northcote, 1954).

Dickson Lake Dolly Varden fed on all categories of food that were available. Cannibalism occurred but was not common. The small sizes of prey available in Dickson Lake may put a limit on the size to which Dolly Varden grow, owing to energy expenditure required to capture sufficient food, unless the fish become piscivorous (Andreasson, 1971; Nikolsky, 1963, p. 277). Fish larger than 210 mm were rare, although two fish of 360 and 380 mm fork length were caught in 1967 and 1972 respectively.

The absence of smaller fish in Foley Lake may be explained on this basis; there were negligible amounts of zooplankton and the remaining prey items were probably all too large for small fish to capture or to handle efficiently, especially large nymphs. These made up a large proportion of the food taken throughout the season. Small fish presumably stayed in the inflow creek until they were over at least 150 mm fork length before entering the lake. The wide range of prey exploited, particularly by some individuals, is probably partly due to the large size of these fish compared to those from Loon and Dickson Lakes, as well as to the absence of a competitor in Foley Lake.

Reduction in niche width is well illustrated by the average number of prey categories taken per individual

in the three lakes. The two allopatric populations take consistently more categories than the sympatric Dolly Varden population. The reduction in average number of prey categories per individual as the season progresses in Loon Lake is probably a result of lower amounts of insects and motile benthos being taken by sympatric Dolly Varden, which are no longer present in surface and onshore regions of the lake.

Around Loon Lake there appeared to be few suitable spawning sites. Loon Lake Dolly Varden entered the creeks in the fall and cutthroat moved into the creeks later in the winter (Provincial Fish and Wildlife trap records, 1969-70). It is possible that spawning trout interfered with Dolly Varden redds; the low population levels of Dolly Varden in Loon Lake may result partly from this.

Loon Lake Dolly Varden became proportionately heavier with increasing length suggesting that food was readily available for the larger size classes. The size classes were distinct from one another even in older age classes; this may be due both to the small population and to the probable short spawning season.

Spawning sites appeared to be abundant in Dickson Lake. Absence of a competitor may result in a longer spawning season; this, coupled with marked growth depensation (Brown, 1946; Poliakov, 1958; Magnuson, 1962) owing to high recruitment and concomitant low food availability would

result in considerable size differences among the fry in the spawning creeks. Interactions among similar sized fry are greatest (Chapman and Bjornn, 1968); dominant fish can establish higher growth rates (Onodera, 1967) which enable them to feed on larger organisms, as the size of food taken is related to the size of the predator. Spreading of the length frequency distribution in the allopatric situation may allow the population as a whole to exploit a wider size range of foods. Adjacent year classes start to overlap as fast growing individuals catch up with slow growing individuals of the previous year class; this can be seen from the length frequency data presented for Dickson Lake where year classes were hardly separable on such a basis.

Variability about the regression of weight on standard length was significantly greater for Dickson Lake Dolly Varden than for the other two populations; this may be another expression of growth depensation. In addition, Dickson Lake fish departed considerably from isometry and grew proportionately lighter with increasing length. These effects could both be due to low food levels in the lake, the plankton being one tenth the abundance of Loon Lake and largely composed of small Bosmina in the summer.

Although corresponding age classes of Loon Lake Dolly Varden and cutthroat were fairly similar in length throughout the season, adult cutthroat trout had

proportionately larger upper jaws than sympatric Dolly Varden for most of the length range measured; trout in Marion Lake also had proportionately larger jaws (Schutz, MS 1969). This may enable them to take a larger range of prey sizes (Northcote, 1954; Keast and Webb, 1966) than Dolly Varden of the same age; both Marion and Loon Lake cutthroat trout took vertebrates while Dolly Varden in these lakes did not. Schutz (MS 1969) suggested that the small scoop-like mouths of Dolly Varden were well adapted to bottom feeding. However, Dolly Varden from Foley Lake had proportionately larger jaws than cutthroat, comparing fish smaller than 170 mm standard length; from the time they enter the lake, Foley Lake Dolly Varden must specialize on relatively large benthic prey whereas the other Dolly Varden populations and the cutthroat population can take zooplankton when small. Unlike relative growth of the upper jaws of both cutthroat and Loon and Dickson Lake Dolly Varden, which was positively allometric, growth of the upper jaw in relation to standard length in Foley Lake fish was isometric in the range measured (suggesting an earlier growth stanza in which relative growth may have been much greater in response to the large prey available (Martin, 1949)). The proportional size of the jaws of Dickson Lake Dolly Varden increased regularly with increasing standard length; concomitantly, more benthic prey and other larger items such as the occasional conspecific were taken. In

contrast, the Loon Lake Dolly Varden showed a marked shift to benthic prey at standard lengths greater than 140 mm (155 mm fork length); before attaining this size, relative growth of their upper jaws was negatively allometric, but a marked inflection was evident at this length. Relative growth became so strongly positively allometric that upper jaw lengths of the largest Loon Lake Dolly Varden captured were almost the same as those of cutthroat of the same length.

Relative interorbital width, probably a fair measure of jaw width, appears similarly to reflect the influence of benthic feeding. That of Dickson Lake Dolly Varden was smallest while Foley Lake fish had wider heads than Loon Lake Dolly Varden up to a standard length of 180 mm. A benthic form of stickleback, Gasterosteus sp. in Paxton Lake, B.C., with a proportionately wider mouth than a coexisting limnetic form took largely macrobenthos while the latter took largely zooplankton (Larson, MS 1972).

Martin (1949) showed that differences in body form could be produced by controlling diet during early growth in rainbow trout (Salmo gairdneri). Relatively large eyes and heads resulted from malnutrition. Whereas most differences in body proportions were related to different body sizes at the time of earlier growth inflections, differences in this case appeared to result from changes in regression slope. It appears that the

different relative growth rates reported here for the three Dolly Varden populations may also be related to changes in diet. The proportions of these body parts and their relative growth histories are affected by environmental factors and must certainly also be influenced by the genotype.

The growth inflection contributed considerably to the increased variability (mean square deviation) of the upper jaw length of sympatric Loon Lake Dolly Varden in relation to standard length when compared with the allopatric populations. Comparisons of relative upper jaw growth of Loon Lake Dolly Varden smaller than 140 mm (standard length) with fish of similar size from Dickson Lake, and of fish larger than 140 mm with fish of similar sizes from Dickson and Foley Lakes showed that the variability within each stanza of the upper jaws of the sympatric Dolly Varden was no greater than that of the allopatric populations.

Similar inflections were apparent in the relative growth of several other head parts of the Loon Lake Dolly Varden. These head parts are probably all interrelated in the same 'morphogenetic field of influence' (Huxley, 1932; Kanep, 1971); McCart (MS 1963) demonstrated that heads, eyes and jaws of different whitefish populations showed parallel relative growth patterns. Such growth inflections may also contribute towards the higher variability of these

head parts compared with those of the allopatric populations. Phenotypic variability, if expressed as the mean square deviation about regression of the body part on standard length, is not reduced in the population with reduced niche width, ie. in sympatric Loon Lake Dolly Varden. However, owing to more distinct modality of the length distribution within year classes in Loon Lake Dolly Varden, jaw lengths are also distributed as a series of modes (Fig. 32); in the allopatric Dickson Lake population, jaw lengths are more evenly distributed (Fig. 29) over the size range of fish captured, owing partly to the large population size but also to the greatly increased growth depensation in this lake. This allows exploitation of a wider range of prey by each year class with overlap of prey size requirements of adjacent year classes. Thus, in effect, it appears that Van Valen's (1965) hypothesis may be supported; the phenotypic variability, if expressed as the variability of jaw size within a year class, may be less in the population with reduced niche width.

It can be seen that continuous growth of fish leads to complicated interpretations of character displacement and of variability changes resulting from the presence of competing species, even though one species may be compared in the presence or absence of only one competitor. Work with birds usually involves a large number

of other species present, but complications owing to continuous growth are minimised. Van Valen (1965) compared the variabilities of bill measurements of several species of birds on mainland Africa and on the Canaries or Azores and showed increased variability on the islands where he assumed niche widths were greater. This approach has been used by numerous other authors (eg. Crowell, 1962; Grant, 1968).

Use of meristic counts lessens the problems associated with growth as the counts were not, in most cases, correlated with body length for these sizes of fish. Loon and Dickson Lake Dolly Varden populations did not differ significantly from one another in gill raker numbers, nor from Loon Lake cutthroat. Gill rakers in both species were relatively short unlike the long gill rakers associated with planktivores like Coregonus peled (Kanep, 1971), where numbers of gill rakers correspond to actual conditions of feeding and growth in lakes. Foley Lake Dolly Varden, which took no zooplankton, had a slightly lower (NS) average number of gill rakers; insufficient numbers of lakes were studied to determine if correlation between diet and gill raker number existed as shown by Kliever (1969) for Coregonus.

The allopatric Dickson and Foley Lake populations, which consumed vertebrates and considerable amounts of insects, had higher numbers of pyloric caeca, although

food specialization by individuals correlated with their caeca numbers was not evident. Variability was also greater in the allopatric populations. Pitt and Chehalis Lake Dolly Varden resemble Loon Lake Dolly Varden in having low mean pyloric caeca numbers of 22.1 and 24 respectively (McPhail, 1961); in both lakes, one or more species of trout is present.

Pyloric caeca act as extensions to the anterior end of the intestine and have been shown to have proteolytic functions (Dobrovolsky, 1966). Piscivorous Baikal grayling (Thymallus arcticus baicalensis) have an average of 19.1 caeca while grayling (T. arcticus baicalensis infrasubsp. brevipinnis) which feed on amphipods and caddis larvae have an average of 15.3 (Svetovidov, 1953). Savvaitova (1961) reported a correlation of pyloric caeca number with diet in Kamchatka Salvelinus alpinus. The piscivorous form had most pyloric caeca; the form feeding on aquatic insect larvae had the least, while numbers were intermediate in the form that ate molluscs. Martin and Sandercock (1967), however, could not find a correlation in diet with pyloric caeca number in the three populations of S. namaycush that they studied.

Diet is probably not the only factor determining pyloric caeca numbers (McPhail, MS 1959). Winters are more severe in Dickson and Foley Lakes and lower temperatures are often correlated with an increase in meristic counts

(Barlow, 1961). If, as is suggested above, allopatric Dolly Varden spawn over a longer period also, some will develop in warmer weather, but no warmer than in Loon, Pitt or Chehalis Lakes. This should set a lower limit on the range of pyloric caeca numbers; it is 19 for all but the Chehalis Lake population, where it is 22.

In the laboratory, individual Loon Lake Dolly Varden spent a smaller proportion of a test period in the upper half of an observation tank compared with Dickson Lake Dolly Varden. This parallels their behaviour in the field; however, it cannot be argued that this demonstrates selective segregation. The Loon Lake fish, captured as adults, may have learnt to avoid unpleasant encounters with trout or to exploit benthos more efficiently than trout by cruising close to the substrate; Loon Lake Dolly Varden and cutthroat trout were held together in the laboratory so reinforcement for such behaviour probably continued. Sympatric and allopatric Dolly Varden should be reared under identical conditions in laboratory stream tanks and then tested to determine whether such behaviour patterns persist. Similar experiments could be performed on groups of each population reared with similar sized cutthroat.

The stenophagia shown by Loon Lake Dolly Varden may reflect the low average number of prey items per individual in the lake. Prey switching does, however, occur in the field as seasonal changes in stomach contents

suggest; 'superabundant' insects in the spring on the surface of Marion Lake are preyed on by Dolly Varden but, unlike the cutthroat, they did not feed on them immediately (Andrusak and Northcote, 1971). In the laboratory, they were slower than trout to switch to surface prey and increased steadily in efficiency over four days (Schutz and Northcote, 1972). Dickson Lake Dolly Varden were, however, relatively euryphagic and learned to switch prey rapidly; this plasticity of behaviour may be advantageous when food availability is low (Nikolsky and Pikuleva, 1958) as well as probably reflecting the wide range of food items taken by fish in the lake.

Both Dickson and Loon Lake Dolly Varden hunted the substrate in a similar way to that described for Marion Lake Dolly Varden (Schutz and Northcote, 1972), with fast cruising and frequent turning especially following a prey capture; they both fed on planktonic Chaoborus with similar efficiency if they made more than a threshold amount of effort. With no food present on the bottom in the spatial tests, sympatric Dolly Varden still swam closer to the substrate than allopatric Dolly Varden. The only difference in treatment was that they had been held with trout while the allopatric fish had been held with other allopatric individuals, or alone in several cases; thus sympatric Dolly Varden may eat largely benthic food because

they swim closer to the substrate than allopatric Dolly Varden.

Evidence provided in this study confirms work by Andrusak (MS 1968) which showed that coexisting Dolly Varden and cutthroat are segregated, though not completely, with respect to food and space, in particular during the summer. The patterns of change of growth rate of the upper jaw may be connected with changes in the diet, larger jaws giving an obvious advantage in feeding on larger and more varied prey. Diet is influenced to a large extent by the presence or absence of a competitor, but as can be seen from comparisons of Dickson and Foley Lakes, population numbers, availability of small sized prey for small fish and availability of intermediate and large prey sizes for larger fish also influence the diet of the fish, complicating discussion of character displacement as a response to the presence of a competing species. Pyloric caeca numbers are also influenced by diet, but again this character may be influenced to a greater or lesser extent by environmental factors such as the temperature regime of development. As body form is determined by both genetic and environmental effects and behaviour by both the genotype and the effects of learning, it is impossible to state categorically to what extent the segregation observed between the two coexisting species is 'interactive' or 'selective'.

VI. CONCLUSIONS

1. Coexisting Dolly Varden and cutthroat trout were spatially segregated in Loon Lake; Dolly Varden were confined to deep water close to the bottom during the summer while cutthroat trout were widely distributed throughout the lake. Allopatric Dolly Varden in Dickson and Foley Lakes were present throughout the water column during the summer.

2. The average number of prey categories taken per individual by sympatric Dolly Varden was less than that taken by allopatric Dolly Varden. Sympatric Dolly Varden ate mainly benthos; smaller individuals took more zooplankton. Dickson Lake Dolly Varden took mainly water column and surface food, although larger individuals took more benthos and some cannibalism occurred. Foley Lake fish took largely benthic prey, though chironomid pupae, tadpoles and surface insects were also eaten.

3. Loon Lake Dolly Varden grew proportionately heavier with increasing length. The year classes remained distinct and the population size was small, possibly due to limited spawning facilities and interference of redds by later-spawning cutthroat.

Considerable overlap in length between year classes occurred in Dickson Lake. The small coefficient and large mean square deviation from regression

in the allometric length-weight equation are probably further indications of the unfavourable relationship of population size to food.

Few small fish were taken in Foley Lake, possibly due to scarcity of suitable small sized food.

4. Allopatric populations of Dolly Varden had higher mean pyloric caeca counts than did the sympatric population. This was interpreted in terms of character displacement resulting from a wider spread of diet in the absence of trout.

5. Proportionately larger upper jaws appeared to be correlated with increased consumption of benthic prey. Separation of the growth stanzas showed that variability of the relative upper jaw length within each stanza of the sympatric Loon Lake population was no greater than that of the allopatric Dickson Lake fish of corresponding sizes. Relative growth of the upper jaws in Foley Lake Dolly Varden differs from that of the other two populations, perhaps owing to the need for larger jaws in small fish when faced only with relatively large prey items.

6. Laboratory studies showed that allopatric Dolly Varden were less substrate oriented and more variable in spatial preferences than sympatric Dolly Varden. They

were also more euryphagic, taking novel prey more readily. Both populations could feed with similar efficiencies on planktonic Chaoborus when they exerted more than a threshold amount of effort. These studies suggest that behavioural character displacement occurs in the sympatric population. Whether these traits have been selected for in the sympatric population, stabilizing them in the genotype, was not established.

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APPENDIX TABLE I. Seasonal changes of stomach contents (average percent volume) of Loon Lake Dolly Varden and cutthroat in 1972.

<u>Season</u>	<u>N</u>	<u>Benthic prey</u>			<u>Water column prey</u>		<u>Surface insects</u>	<u>Miscellaneous</u>
		<u>Static</u> ¹	<u>Motile</u> ²	<u>Vertebrates</u> ³	<u>Chironomid pupae</u>	<u>Zooplankton</u>		
Dolly Varden:								
Spring	75	9.5	32.0	0	0.8	53.4	1.1	4.7
Summer	33	22.1	23.0	0	tr	39.3	4.9	9.7
Fall	64	62.4	10.8	0	0.2	13.1	0	13.4
Cutthroat captured in the same depth intervals as Dolly Varden:								
Spring	24	0	7.7	4.2	6.6	41.4	28.4	11.7
Summer	33	8.0	7.2	0	9.1	64.4	7.8	3.8
Fall	20	12.8	3.4	6.1	2.0	63.6	9.6	2.4
Cutthroat captured in midwater and at the surface:								
Spring	63	0.1	2.3	0.1	9.5	47.1	36.3	4.6
Summer	25	0.7	8.1	0	16.1	59.1	14.7	1.4
Fall	38	2.1	2.3	2.5	0.6	71.0	16.7	4.6

1. Chironomid and Chaoborus larvae and Pisidium spp.
2. Aquatic insect larvae, amphipods, planorbid gastropods.
3. Salamanders.

APPENDIX TABLE II. Seasonal changes of stomach contents (average percent volume) of allopatric Dolly Varden from Dickson and Foley Lakes.

<u>Month</u>	<u>N</u>	<u>Benthic prey</u>			<u>Water column prey</u>		<u>Surface insects</u>	<u>Miscellaneous</u>
		<u>Static</u> ¹	<u>Motile</u> ²	<u>Vertebrates</u> ³	<u>Chironomid pupae</u>	<u>Zooplankton</u>		
Dickson Lake:								
*June	29	5	1	3	16	0	75	0
July	147	6.2	12.8	1.0	9.8	36.3	26.8	7.1
*July	30	0	5	3	7	31	47	7
September	75	1.7	13.4	1.3	4.9	49.8	22.7	6.2
*October	15	9	1	0	0	67	18	5
Foley Lake:								
May	21	0.4	80.2	2.5	4.0	0	9.8	3.2
July	14	22.4	32.8	16.0	5.9	0	12.2	10.7
September	11	7.7	56.5	0	9.0	0	22.9	3.9

1. Chironomid larvae, Pisidium spp.

2. Aquatic insect larvae, amphipods (Dickson Lake only), planorbid gastropods, Simulium larvae (Foley Lake only).

3. Dolly Varden (Dickson Lake only), tadpoles (Foley Lake only).

* 1967 data from Andrusak (MS 1968). All other data from 1972.

APPENDIX TABLE III. Average number of major food categories taken per individual Dolly Varden.

<u>Lake</u>	<u>Season</u>	<u>Number of fish</u>	<u>Mean and 99% confidence limits</u>	<u>Variance</u>
LOON	Spring	57	2.24 \pm 0.30	1.37
	Summer	36	1.89 \pm 0.37	1.31
	Fall	69	1.68 \pm 0.20	0.69
DICKSON	Summer	148	3.00 \pm 0.19	1.42
	Fall	77	2.86 \pm 0.18	0.69
FOLEY	Spring	21	3.05 \pm 0.53	1.55
	Summer	16	3.37 \pm 0.94	3.72
	Fall	12	3.00 \pm 0.80	2.00

As Simulium larvae were not present in Loon or Dickson Lakes, Simulium occurring in Foley Lake fish stomachs were grouped together with 'motile benthos' as this was the category with which they were most often associated.

APPENDIX TABLE IV. Size related differences of stomach contents (average percent volume) of Loon and Dickson Lake Dolly Varden in 1972.

<u>Season</u>	<u>Size</u> ¹	<u>N</u>	<u>Benthic prey</u>		<u>Vertebrates</u> ⁴	<u>Water column prey</u>		<u>Surface insects</u>	<u>Miscellaneous</u>
			<u>Static</u> ²	<u>Motile</u> ³		<u>Chironomid pupae</u>	<u>Zooplankton</u>		
Loon Lake:									
Spring	>155	35	15.9	29.4	0	1.0	40.9	1.3	9.8
	<155	40	8.3	31.3	0	0.6	58.0	1.0	0.2
Summer	>155	25	22.6	25.2	0	tr	36.0	2.4	12.5
	<155	8	20.4	16.3	0	0	50.0	12.5	0.8
Fall	>155	54	61.6	11.0	0	tr	10.0	0	14.5
	<155	11	55.8	9.1	0	0.9	27.0	0	7.1
Dickson Lake:									
Summer	>155	56	7.5	3.3	1.7	13.4	17.9	34.6	9.9
	<155	92	5.1	12.3	0.5	7.6	47.2	21.8	5.3
Fall	>155	25	2.5	21.3	3.9	7.3	37.8	21.2	5.7
	<155	50	1.0	8.7	0	3.7	56.7	23.9	5.8

1. Fork length (mm).

2. Chironomids, Pisidium spp. and Chaoborus larvae (Loon Lake only).

3. Aquatic insect larvae, amphipods, planorbid gastropods (Dickson Lake only).

4. Dolly Varden (Dickson Lake only).

For APPENDIX TABLES V - XIV:

Relationships of body parts or weight (y) to standard length (x) are given using log-transformed 1972 data.

$Y = A + b(X - \bar{X})$ was calculated where

$Y = \log_e y$ and

$X = \log_e x.$

Differences in mean square, slope and A between the Dolly Varden populations are shown when significant at $p \leq 0.05$, calculated using analysis of covariance.

APPENDIX TABLE V. Relationship of head length to standard length.

<u>Lake</u>	<u>Mean square</u>	<u>Slope</u>	<u>A</u>	<u>Number of fish</u>
LOON	1.772×10^{-3}	1.057	3.560	177
DICKSON	1.057×10^{-3}	1.015	3.475	232
FOLEY	1.430×10^{-3}	0.932	3.991	49

Differences significant at $p \leq 0.05$:

Mean square: LOON > DICKSON

Slope: LOON and DICKSON > FOLEY

A: FOLEY > LOON > DICKSON

See Figure 28.

APPENDIX TABLE VI. Relationship of upper jaw length to standard length.

<u>Lake</u>	<u>Mean square</u>	<u>Slope</u>	<u>A</u>	<u>Number of fish</u>
LOON	6.327×10^{-3}	1.288	2.799	177
DICKSON	3.762×10^{-3}	1.200	2.710	231
FOLEY	2.798×10^{-3}	1.024	3.355	49

Differences significant at $p \leq 0.05$:

Mean square: LOON > FOLEY and DICKSON

Slope: LOON > DICKSON > FOLEY

A: FOLEY > LOON and DICKSON

See Figure 29.

To determine the significance of departures from isometry, i.e. $B = 1.00$ (Bailey, 1959):

<u>Lake</u>	<u>b</u>	<u>s_b^2</u>	<u>$t=(b-B)/s_b$</u>	<u>d.f.=n-2</u>	<u>Significance</u>
LOON	1.288	9.26×10^{-4}	9.0	175	$p < 0.01$
DICKSON	1.200	10.05×10^{-4}	6.3	229	$p < 0.01$
FOLEY	1.024	18.03×10^{-4}	0.565	47	NS

APPENDIX TABLE VII. Relationship of snout-to-back-of-eye length to standard length.

<u>Lake</u>	<u>Mean square</u>	<u>Slope</u>	<u>A</u>	<u>Number of fish</u>
LOON	2.700×10^{-3}	1.057	2.805	177
DICKSON	1.761×10^{-3}	0.993	2.732	233
FOLEY	2.367×10^{-3}	0.868	3.188	49

Differences significant at $p \leq 0.05$:

Mean square: LOON and FOLEY > DICKSON

Slope: LOON > DICKSON > FOLEY

A: FOLEY > DICKSON

See Figure 29.

APPENDIX TABLE VIII. Relationship of eye length to standard length.

<u>Lake</u>	<u>Mean square</u>	<u>Slope</u>	<u>A</u>	<u>Number of fish</u>
LOON	4.476×10^{-3}	0.809	1.969	177
DICKSON	2.588×10^{-3}	0.677	1.949	233
FOLEY	4.702×10^{-3}	0.550	2.176	49

Differences significant at $p \leq 0.05$:

Mean square: LOON and FOLEY > DICKSON

Slope: LOON > DICKSON > FOLEY

A: FOLEY > LOON > DICKSON

See Figure 29.

APPENDIX TABLE IX. Relationship of maximum gill raker length to standard length.

<u>Lake</u>	<u>Mean square</u>	<u>Slope</u>	<u>A</u>	<u>Number of fish</u>
LOON	2.367×10^{-2}	1.291	1.023	177
DICKSON	1.715×10^{-2}	1.097	0.974	219
FOLEY	1.167×10^{-2}	0.936	1.426	49

Differences significant at $p \leq 0.05$:

Mean square: LOON > DICKSON and FOLEY

Slope: LOON > DICKSON and FOLEY

A: FOLEY > LOON > DICKSON

See Figure 30.

APPENDIX TABLE X. Relationship of predorsal length to standard length.

<u>Lake</u>	<u>Mean square</u>	<u>Slope</u>	<u>A</u>	<u>Number of fish</u>
LOON	1.012×10^{-3}	1.020	4.086	28
DICKSON	0.938×10^{-3}	0.974	4.099	28
FOLEY	0.825×10^{-3}	0.955	4.535	14

Differences significant at $p \leq 0.05$:

Mean square: LOON > DICKSON > FOLEY

Slope: LOON > DICKSON > FOLEY

A: FOLEY > DICKSON > LOON

Not illustrated.

APPENDIX TABLE XI. Relationship of interorbital width to standard length.

<u>Lake</u>	<u>Mean square</u>	<u>Slope</u>	<u>A</u>	<u>Number of fish</u>
LOON	5.486×10^{-3}	1.080	2.442	177
DICKSON	4.291×10^{-3}	1.002	2.263	233
FOLEY	1.780×10^{-3}	0.964	2.827	49

Differences significant at $p \leq 0.05$:

Mean square: LOON > DICKSON > FOLEY

Slope: No differences

A: LOON and FOLEY > DICKSON

See Figure 30

APPENDIX TABLE XII. Relationship of the distance from the anal fin base to the pectoral fin base to standard length.

<u>Lake</u>	<u>Mean square</u>	<u>Slope</u>	<u>A</u>	<u>Number of fish</u>
LOON	0.813×10^{-3}	1.053	4.187	28
DICKSON	1.173×10^{-3}	1.068	4.247	28
FOLEY	1.554×10^{-3}	1.085	4.632	14

Differences significant at $p \leq 0.05$:

Mean square: FOLEY > DICKSON > LOON

Slope: FOLEY > DICKSON > LOON

A: FOLEY > DICKSON > LOON

Not illustrated.

APPENDIX TABLE XIII. Size related differences in the relationship of upper jaw length to standard length for the three Dolly Varden populations.

<u>Standard length (mm)</u>	<u>Lake</u>	<u>Mean square</u>	<u>Slope</u>	<u>A</u>	<u>Number of fish</u>
140	LOON	2.900×10^{-3}	0.866	2.499	64
	DICKSON	2.952×10^{-3}	1.081	2.620	154
140	LOON	7.398×10^{-3}	1.401	2.968	113
	DICKSON	5.314×10^{-3}	1.285	2.891	77
	FOLEY	2.785×10^{-3}	1.062	3.373	47

The following differences were shown to be significant at $p \leq 0.05$:

- i) Small fish Mean square: No difference
Slope: DICKSON > LOON
A: DICKSON > LOON
- ii) Within Loon Lake Mean square: large fish > small fish
Slope: large fish > small fish
A: No difference
- iii) Within Dickson Lake Mean square: large fish > small fish
Slope: No difference
A: No difference
- iv) Large fish Mean square: LOON and DICKSON > FOLEY
Slope: LOON > FOLEY; DICKSON intermediate
A: FOLEY > LOON and DICKSON

APPENDIX TABLE XIV. Relationship of weight to standard length.

<u>Lake</u>	<u>Mean square</u>	<u>Slope</u>	<u>A</u>	<u>Number of fish</u>
LOON	7.020×10^{-3}	3.071	3.793	177
DICKSON	1.604×10^{-2}	2.573	3.383	224
FOLEY	6.098×10^{-3}	2.835	4.978	46

Differences significant at $p \leq 0.05$:

Mean square: DICKSON > FOLEY and LOON

Slope: LOON > FOLEY > DICKSON

A: FOLEY > LOON > DICKSON

See Figure 30.

To determine significance of departure from isometry

i.e. $B = 3.00$ (Bailey, 1959):

<u>Lake</u>	<u>b</u>	<u>s_b^2</u>	<u>$t=(b-B)/s_b$</u>	<u>d.f.=n-2</u>	<u>Significance</u>
LOON	3.071	10.26×10^{-4}	2.22	175	$p < 0.05$
DICKSON	2.573	43.79×10^{-4}	6.48	222	$p < 0.01$
FOLEY	2.835	40.30×10^{-4}	2.60	44	$p < 0.01$

APPENDIX TABLE XV. Relationship of upper jaw length, eye length and weight to standard length for cutthroat and Dolly Varden using log-transformed spring 1972 data from Loon Lake.

A. Upper jaw length against standard length:

<u>Species</u>	<u>Mean square</u>	<u>Slope</u>	<u>A</u>	<u>Number of fish</u>
Dolly Varden	6.085×10^{-3}	1.312	2.682	71
Cutthroat	2.447×10^{-3}	1.338	3.101	105

Differences significant at $p \leq 0.05$:

Mean square: Dolly Varden > cutthroat

Slope: No difference

A: Cutthroat > Dolly Varden

B. Eye length against standard length:

<u>Species</u>	<u>Mean square</u>	<u>Slope</u>	<u>A</u>	<u>Number of fish</u>
Dolly Varden	3.231×10^{-3}	0.795	1.889	71
Cutthroat	2.252×10^{-3}	0.905	2.161	105

Differences significant at $p \leq 0.05$:

Mean square: Dolly Varden > cutthroat

Slope: No difference

A: Cutthroat > Dolly Varden

C. Weight against standard length:

<u>Species</u>	<u>Mean square</u>	<u>Slope</u>	<u>A</u>	<u>Number of fish</u>
Dolly Varden	3.160×10^{-3}	2.832	3.430	71
Cutthroat	4.601×10^{-3}	2.763	3.929	44

Differences significant at $p \leq 0.05$:

Mean square: Cutthroat > Dolly Varden

Slope: No difference

A: Cutthroat > Dolly Varden

Regressions and analyses of covariance calculated as on p.111.

APPENDIX TABLE XVI. Times to first bottom grab (seconds) during 10 minute exposure period to red chironomid larvae on sand and leaf litter substrate.

<u>Allopatric</u>	<u>Sympatric</u>
72	375
135	980*
35	1800+**
65	1800+**
600*	
90	
0	
130	

*Fish which did not respond during the first 10 minute test but did during a subsequent test.

**Fish which were tested three times but did not respond to the chironomid larvae on any of these occasions.

The time to the first grab is less for allopatrics than for sympatrics, significant at $p < 0.01$ using the Mann Whitney U test; $U = 1$, $n_1 = 8$, $n_2 = 4$.