Growth and Food Habits of Strains of Rainbow Trout (*Salmo gairdneri* Richardson) in Winterkill Lakes of Western Manitoba

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GROWTH AND FOOD HABITS OF STRAINS OF RAINBOW TROUT (*Salmo gairdneri* Richardson) IN WINTERKILL LAKES OF WESTERN MANITOBA

by

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This is the eighth Manuscript Report
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FOREWORD

Claude Holmstrom did his undergraduate work at Guelph University and during those summers worked for the Ontario Ministry of Natural Resources in the Kenora area - his home. It was here he met and married Lynne-Anne White. Following this he did graduate work through the University of Manitoba and the Freshwater Institute, under the supervision of Dr. G.H. Lawler, studying the feeding behavior of rainbow trout in the prairie pothole lakes south of Riding Mountain National Park. Upon completion of his Master's degree in 1972, Claude became a regional biologist with the Manitoba Department of Mines, Resources and Environmental Management. A short time later, on July 25, 1973, Claude was killed in a helicopter crash while carrying out a waterfowl survey in the marshes at the south end of Lake Winnipeg.

Claude's untimely death left a permanent void in the lives of those who knew him well. He is remembered for a fairness and open-mindedness that we could all emulate.

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Fingerlings of different strains of rainbow trout, stocked in winterkill lakes, gained an average of 200 g in approximately 160 days (May to October). Seasonal growth was best described by the Gompertz growth curve. Within a lake the domestic strains, Idaho and Nisqually, had the same growth rates, though there was some variability in growth between lakes at harvest time. The wild strain, Tunkwa, was smaller at harvest time than the Idaho domestic strain. The three strains of trout showed the same general pattern of seasonal change in specific growth rate and this pattern was influenced by water temperature.

Amphipods were the major food organism consumed by trout in one lake in 1970 and 1971, but studies in 1973 and 1974 showed marked seasonal differences in food organisms consumed between lakes and harvest years. Amphipods were important to the trout diet but other organisms such as corixids, Odonata nymphs, *Chaoborus* and other fish were also of importance. The changes in food habits are discussed in relation to changes in growth.

Key words: trout,rainbow; growth; feeding; genetic strains.

RESUME

Bernard, D. and C. Holmstrom. 1978. Growth and food habits of rainbow trout (*Salmo gairdneri* Richardson) in winterkill lakes of western Manitoba. Can. Fish. Mar. Serv. MS Rep. 1477: iv + 20 p.

Des alevins de différentes souches de truite arc-en-ciel, qui ont servi à ensemencer des lacs où le taux de mortalité due aux rigueurs de l'hiver est très élevé, ont pris 200 g en moyenne, pendant environ 160 jours (de mai à octobre). La courbe de croissance Gompertz a fourni la meilleure description de la croissance saisonnière. Dans un même lac, les souches domestiques, Idaho et Nisqually, ont eu le même taux de croissance, bien que la taille des poissons ait varié quelque peu d'un lac à l'autre, au moment de la pêche. A cette même époque, la souche sauvage, Tunkwa, était plus petite que la souche domestique Idaho. Le taux de croissance spécifique des trois souches de truite a suivi le même modèle général de variation saisonnière, influencé par la température de l'eau.

Les amphipodes ont été le principal organisme consommé par la truite dans un lac, en 1970 et en 1971, mais des études effectuées en 1972 et 1974 ont montré que le genre d'organismes consommés variait de façon prononcée selon les lacs et les années de pêche. Les amphipodes ont constitué une part importante du régime de la truite, mais d'autres organismes, comme les corises, les nymphes d'odonates, les *Chaoborus* et d'autres poissons ont également compté pour beaucoup. Les changements d'habitudes alimentaires sont étudiés en rapport avec les variations de la croissance.

Mots-clés: truite,arc-en-ciel; croissance; alimentation; souches génétiques.

INTRODUCTION

In 1968 the Freshwater Institute began studying the feasibility of stocking rainbow trout, *Salmo gairdneri*, in prairie winterkill lakes. Trout fingerlings (3-4 g) stocked May grew to marketable size (>200 g) by the fall, feeding only on natural food organisms (Johnson et al. 1970; Sunde et al. 1970; Lawler et al. 1974). This resulted in the development of a small cottage industry across the Canadian prairies: but while annual production has expanded to over 267,000 kg, large-scale industrial development is hampered by a number of biological and non-biological factors (Ayles and Brett 1978).

The productivity of these lakes is very high but quite variable. It is possible that differences in food available in the lakes could be the cause of this variability. The objective of this study was twofold:

- firstly, to determine what the trout were feeding on; and
- secondly, to determine when differences in growth rates occurred and whether they could be associated with differences in feeding.

In 1970-71 the food habits, feeding periodicity, feeding selectivity, rates of gastric digestion in relation to several factors and the estimation of daily ration during the growing season were determined. In 1973-74, in conjunction with a genetics program directed toward the production of a strain of trout better suited to these lakes, comparison was made between seasonal growth rates and food habits of matched plantings of one wild and two domestic strains of rainbow trout in three different lakes.

METHODS

The geography of the study area is described by Sunde and Barica (1975) and the morphometry and water chemistry of the lakes in this study are given by Barica (1975).

STOCKING OF FISH

In the 1970-71 study rainbow trout fingerlings were stocked in Lake 103 on 15 May in 1970 and 5 May 1971 (Table 1). In 1970 eyed eggs were obtained from Pennask Lake, British Columbia, and the trout were reared at the Freshwater Institute in Winnipeg to fingerling size. In 1971 fingerlings were purchased from Livingston Hatchery, Montana.

In 1973 and 1974 plantings of 3 strains (one wild and two domestic) were made in 3 lakes (Table 1). The wild strain was obtained from Tunkwa Lake, British Columbia, in 1973. The two domestic strains were obtained from commercial hatcheries in the United States. One strain was obtained from a private hatchery in Idaho and the other from Nisqually Hatchery in the State of Washington. All 3 strains were received as eyed eggs and were reared under identical conditions at the Freshwater Institute's Rockwood Experimental Hatchery. In 1973 Tunkwa and Idaho fish were planted in each of the 3 lakes and in 1974 the Nisqually and Idaho fish were planted in each lake. Before stocking the strains were marked for identification. In 1973 they were marked by a hot-wire brand (Bernard and van der Veen 1974), while in 1974 a coded wire nose tag was used (Jefferts et al. 1963). Trout size was controlled so that for each lake the strains were approximately the same weight at the time of planting. The stocking time was between 4-11 May in 1973 and between 16-23 May in 1974. Both strains were planted on the same date in each lake except for Lake 318 in 1973. A severe storm at Lake 318 on the day when the Idaho fish were planted in 1973 resulted in nearly complete mortality of this strain.

COLLECTION OF SAMPLES

During 1970-71, 24-hour gillnetting experiments were conducted on Lake 103. All fish were taken with nylon gillnets. For each diel sampling two joined nets (50 m) were set perpendicular to shore at 3-hour intervals and left for not more than 15 minutes. This usually was sufficient to catch the preselected quota of 10 trout. In May and June nets were left in for the entire 24-hour sampling period and checked every 3 hours. Fish from the May and June experiments were combined to provide a sufficiently large sample. If less than 7 fish were caught at any given interval the set was repeated the following day. When more than 10 fish were taken, a random selection of 10 was used for stomach analysis.

In 1973-74, trap nets, which were assumed to be less selective than gillnets, were used to catch trout. Usually, two trap nets were fished per lake per sampling period and these nets were checked daily until a satisfactory sample of trout was obtained (at least 10 fish per strain per lake). If more than 15 fish per strain per lake were caught a random sample of 10 fish per strain in 1973 and 15 fish per strain in 1974 were taken for stomach analysis. Fork length and weight were taken for all fish caught (Appendices 2 and 3). Stomach samples were collected approximately once a month from July to September in 1973 and June till September in 1974 from each lake. Growth data in 1974 were obtained from a separate population dynamics study (Ayles et al. 1976). Gillnets were used in the summers of 1973 and 1974 when no fish could be caught by the trap nets. Gillnets and trap nets were used for the final harvest in the fall.

ANALYSIS OF GROWTH RATES

Differences in final harvest size between fish of different strains and fish from different lakes in 1973 and 1974 were examined by means of an unweighted analysis of variance (Snedecor and Cochran 1967).

Seasonal growth of trout in 1974 was analyzed by means of an asymptotic regression analysis computer program BMOOGR (Dixon 1974) on mean weights (log transformed) of trap-netted fish. Gompertz curves, which are S-shaped curves with a lower and upper asymptotic, gave the best fit to the data and were used to compare seasonal differences between strains and between lakes.

The seasonal changes in specific growth rate (% wet body weight/day, after Brown 1957 and Ricker 1975) were compared between each strain of 1973-74 trout in each lake except for Lake 318 in 1973 where partial summerkill (Barica 1975) developed.

Changes in specific growth rates were compared to the mean daily water temperature. Water temperature (surface and bottom) was recorded continuously with a Weksler recording thermometer. Mean daily temperature was calculated by summing the max and min values for each depth for each day and dividing by four. Due to daily fluctuations the data were analyzed in terms of five-point moving averages to provide smoother graphical presentation. In 1973 the water temperature of Lake 154, which is comparable to the lakes studied, was monitored and in 1974 Lake 318 was used.

ANALYSIS OF FOOD HABITS

In 1973 and 1974 captured trout were identified as to strain, measured and weighed, and individual stomachs were preserved in 10% formalin.

Food analysis initially involved the determination of number and weight of various food organisms present in individual stomachs. Absolute counts in some cases were difficult. Consequently it was often necessary to count head capsules or eyes rather than whole food items. In 1970-71 when cladocerans were the predominant food organism, the contents were subsampled because of the large number involved. Food items in 1970-71 were dried in an oven for 48 hours, at a temperature of 100 C. A freeze-drier was used in 1973-74 and the samples were dried for 24 hours. The dried samples were then weighed on an analytical balance.

Percent frequency of occurrence, total number and total dry weight were determined for each type of food organism. To compare the food habits of the two strains of trout and to compare food habits in different lakes a coefficient of similarity (Whittaker and Fairbanks 1958) was determined. This coefficient is based on the percent contribution of a consumption index (percent C.I.) for each food item, or simply the sum of the minimum values (percent C.I.) for a particular food organism eaten by both strains. Data were grouped according to the sampling interval, date and year. The consumption index (C.I.) was calculated using numerical and gravimetric values of food habit results, similar to that proposed by Godfrey (1955). The square root of the product of the number of fish in the sample that had consumed the organism and the average weight of that organism in the stomachs of all the fish in the sample were determined. This value was converted to a percentage of the total stomach content for the intervals under consideration. The total diet of each strain was also compared for each lake in 1973 and 1974 using Spearman rank correlation coefficient (Fritz 1974; Snedecor and Cochran 1967).

RESULTS AND DISCUSSION

GROWTH OF RAINBOW TROUT

The winterkill lakes in the Erickson area are highly productive lakes (Barica 1975). Rainbow trout fingerlings stocked in these lakes grew to the following size by fall with no supplemental feeding.

		Mean Weight (grams)	
Year	Days in Lake	at Stocking	at Harvest
1970	180	4.5	212
1971	183	1.7	217
1973*	184	8.7	372
1974	143	1.9	219

* Excluding Lake 318

Harvest weight was similar among years except in 1973 where larger fingerlings produced larger trout. An analysis of variance of the final size at harvest for both strains, in lakes 587 and 721 (Appendix 1), showed that Idaho were significantly heavier than Tunkwa trout but the trout were not significantly different between the two lakes. However, there was a significant interaction etween lakes and strains. Ayles (1975) found that the domestic strain, Idaho, grew better than the wild strain, Tunkwa, and that there were significant effects of the environment (lakes) and the genotype-environment interactions. He concluded that the environmental differences were mostly responsible for the variation in growth and survival but these have not yet been identified. The present results are in disagreement with Smith (1957) and Cordone and Nicole (1970) who suggested that wild trout do better in a vigorous environment than domestic trout. An analysis of variance comparing the final harvest size of the Idaho and Nisqually strains in each lake (Appendix 1) showed no significant difference in weight between strains in each lake but a significant difference was found in the size of trout between lakes.

The weights the fish reached in this study are within the range reported by Lawler et al. (1974) for rainbow trout stocked in the Erickson area from 1969 to 1972. Other studies have shown this great potential for trout production in underutilized lakes, such as Myers (MS. 1973) who obtained reasonable growth for rainbow trout fingerlings stocked in similar environments in south central North Dakota with mean weight gains of 270.6 and 128.6 g for 1.4 g fingerlings in 1971 and 208.7 for 6.9 g trout in 1972. Brynildson and Kempinger (1973) working in a soft-water lake in Wisconsin produced rainbow trout of mean weight of 242 g from 8 g fingerlings in 152 days. However, Johnson and Hasler (1954) obtained relatively poor growth ($\bar{x}$ = 104, 128, 154 g) for trout of 5.5 g stocked in three dystrophic lakes near the Wisconsin-Michigan border.

Trout growth in these natural water bodies with no supplemental feeding compares favorably with growth of trout reared in intensive culture situations where fish are grown under "optimum" conditions. For instance Murai and Andrews (1973) in a cage culture experiment obtained 256 g rainbow trout from 60 g fish in 112 days in fresh water of 21.3 C, but in brackish water of 30 o/oo trout grew to only 217 g at 13.5 C. This is only a mean weight gain of 196 and 157 g respectively, while at Erickson the mean gain in weight was 210 g. However, Tatum (1973) was able to provide trout of mean weight gain of 261 g from 93.8 g fish in 120 days when they were reared in cages at low density and high food ration in water of 20 o/oo salinity. Brett (1974) produced pan-size sockeye and pink salmon of 230 g from 4 g fish from tank culture; however, it took 280 days to grow such fish.

SEASONAL CHANGES IN GROWTH AND IN SPECIFIC GROWTH RATES

The seasonal changes in growth of different strains of rainbow trout are given in Appendices 2, 3 and 4. As discussed above, there were ignificant differences in seasonal growth between the Idaho and Tunkwa fish but not between the Idaho and Nisqually fish. For 1974 the growth curves of trout (strains combined) were:

Lake 318	$\ln Y = 6.157 - (5.360)(.988)^x$
Lake 587	$\ln Y = 6.185 - (5.494)(.988)^x$
Lake 721	$\ln Y = 7.535 - (6.927)(.992)^x$
Common curve	$\ln Y = 6.696 - (5.945)(.989)^x$ (Fig. 1)

where Y = mean weight and x = growing days. Superimposing the growth curve of trout of each lake yielded very similar curves for the first 100 growing days; thereafter the trout of Lake 721 appeared to grow faster, followed by trout of Lake 318 and then Lake 587 trout.

Variability of growth of trout between lakes encountered in this study is a recognized problem and some of the factors responsible are discussed by Lawler et al. (1974), Ayles et al. (1976), Johnson and Hasler (1954) and Larkin et al. (1957). A possible explanation for the lower growth in Lake 587 is the occurrence of a partial summerkill in July, which has been described by Ayles et al. (1976). This condition killed an estimated 60% of the trout. This probably stressed the surviving fish which may have produced a growth depression, resulting in the lower growth by fall. However, removing this lake from the analysis of variance previously discussed still showed a significant difference in harvest size between trout of Lake 318 and 721. Ayles (1975) suggested that interspecific competition between trout and other fish (stickleback or minnows) may be an important factor. But in 1974 neither Lake 318 or 721 had other fish than trout. There are probably many factors such as "characteristic availability of food organisms" discussed by Larkin et al. (1957), and other physical factors and/or the interaction of several factors which are responsible for variability in growth.

An important factor in variable growth is the growth potential of different strains of trout. Vincent (1960), Flick and Webster (1964), Cordone and Nicole (1970) and Rawstron (1973) have observed differences in growth between strains of trout grown in natural environments. The variable growth observed in the 1974 study was not entirely due to genetic differences since the growth rate between the two domestic strains was not significantly different. There was a significant difference in size between lakes and also a significant strain-lake interaction, particularly when Lake 587 was included in the analysis. This shows that environmental differences were most likely the important factor in 1974.

The specific growth rate (% wet wt/day) of the 1973 and 1974 trout showed a marked seasonal change in both years and the pattern was similar (Fig. 2A) between strains within a lake and also between lakes for both years. There was a general decrease in specific growth rate with growing days (or aging), a low by the beginning of August, a sharp increase thereafter, then a drop to below 1% g/day by October. In 1973 the specific growth rate was lower than in 1974 during most of the season, and the second peak in growth rate was shifted to a much later time in the season. Similar observations of peaks and depressions of growth rates have been reported before for rainbow trout in a natural environment, notably by Johnson and Hasler (1954), Coche (1967) and Brynildson and Kempinger (1973). They related this variation to changes in water temperature since water temperature is one of the most important external environmental factors influencing the growth rate (Swift 1961).

As Johnson and Hasler (1954) and Brynildson and Kempinger (1973) showed, high water temperatures in July-August appear to severely affect the growth rate of trout (Fig. 2). In 1974 a low specific growth of 1.6% g/day was reached between day 200 and day 225 when the average mean daily water temperature was 20.7 C. In 1973 the specific growth rate was lower and the water temperature was 19.9 C. The trout seemed to grow best in June when the lake waters were warming up, averaging 15.2 C, and again in late summer when the water temperature was dropping. This second pulse of growth occurred at different times in 1973 and 1974 and it can be explained by the following table on the average mean daily water temperature.

Day	1973	1974
230-255	19.0(16.5 to 21.6)	14.2(10.8 to 17.8)
255-273	13.0(11.4 to 16.5)	10.7(8.8 to 12.2)

The growth pulses appear at approximately the same water temperature. Both the spring and late summer temperature of 15 C and 13-14 C are within the range of 11-16 C of preferred temperature of rainbow trout calculated by Garside and Tait (1958). However, Schaeperclaus (in Johnson and Hasler 1954) stated that rainbow trout grew most rapidly at 10 C and its optimum for rapid growth is within 15 to 20 C in fish ponds in Germany. Rainbow trout at Erickson tolerated very high water temperatures (24 C) and even grew well at high temperatures of 19 C, but it appears that the optimum temperature for growth for 1973-74 trout is within 12-16 C.

The lake waters of 1973 appeared to be warm for a longer period than in 1974 which may account for the differences in specific growth rate between years (Fig. 2B). However, the 1973 fingerlings were much larger at stocking than the 1974 fingerlings (Table 1). Brown (1946), Brett and Shelbourn (1975) and Elliott (1975) found that specific growth rate decreases with increasing size. This probably accounts for the lower seasonal specific growth rates in 1973 and also for differences between the spring and late summer pulses of growth observed in both years. The small trout in the spring would have a higher specific growth rate than large trout in late summer when grown at approximately the same temperature.

Brett and Shelbourn (1975) described the growth rate-weight relation of three salmonids, fed on full ration and grown at optimum temperatures, by the equation $\ln G = \ln a + b \ln W$ where G = specific growth rate and W = weight. The mean slope of the line for this relationship was $b = -.41 \pm 0.04$. This relationship was calculated for rainbow trout, assuming that is applicable for this species raised in a natural uncontrollable environment, and compared to the observed specific growth rate-weight relation of 1974 trout (Fig. 3). It showed that the 1974 trout at Erickson generally followed the expected decrease in growth rate with increase in size, and also that growth of trout in these lakes is as good if not better than trout reared reared under optimum conditions. However, the general pattern of seasonal variation in specific growth rate was maintained which strongly suggests the important influence of temperature on growth.

The growth curves of trout in the three lakes studied in 1974 were found to diverge after 100 days of introduction into the lake. This occurs at the same time as the appearance of the second pulse of growth. The model on changes of specific growth rate probably masks these differences in the growth curves. There is no direct evidence to explain this divergence, however Elliott (1975a,b) found that in brown trout food ration size, temperature and fish size are all very important in influencing growth rates. It is likely that food availability played an important role during the second pulse of growth since water temperature in all three lakes was likely in the optimum range and fish were approximately equal in size.

FOOD HABITS OF TROUT IN PRAIRIE WINTERKILL LAKES

Rainbow trout caught in the first four diel gillnetting periods of 1971 showed very little difference in food consumed within a 24-hour period (Fig. 4A). Therefore the stomach contents were pooled for each period (Appendices 5 & 6).

There was a marked, though regular, variation in food habits during the period of July to September 1970 and May through October in 1971 (Fig. 4B). Amphipods were the most important food organism consumed by trout except for May 25-26 and June 2-3 when young fish (4-6 g) fed heavily on chironomid larvae and cladocerans. However, both declined in the diet during the season, rarely occurring after August in 1971, but gained in importance through August and September in 1970.

A comparison of consumption indices, using the coefficient of similarity to express similarity of trout caught in similar periods in different years is shown in Fig. 4B. The diet is at least 66% similar, being most similar in July. The difference in August and September is due to the consumption of cladocerans and the increased evidence of corixids and *Chaoborus* larvae in 1970.

The seasonal variations in consumption are probably entirely related to changes in the relative abundance of the food organisms and/or to changes in size of the stocked trout. During May to September there was a marked reduction in the abundance of cladocerans and a corresponding increase in amphipods in samples taken from the limnetic zone (Holmstrom 1972). This zone was the region in which trout fed previously (Holmstrom 1972). Also the density of chironomid larvae was found to decrease steadily from a high of 9,970/m^2 on June 22 to 2,870/m^2 on August 30. This may account for the extent to which these organisms were utilized by trout. However there may be a size-dependent response ty rainbow trout as has been observed by Hartman (1958) and Galbraith (1967), where smaller trout consume smaller foods. Whatever the mechanism this lower consumption of amphipods in the spring is significant because it corresponds to the reproductive period of *Gammarus* (Biette 1969). This would allow for the perpetuation of *Gammarus* and also provide trout with a large prey population after spring.

The food organisms consumed in 1973 and 1974 by the different strains in any of the lakes studied was at least 66% similar (Appendices 7 & 8). Therefore, data from the different strains were combined for each lake. Mention of the food organisms eaten by some of the strains is made for dates when significant differences were apparent.

The food habits of 1973 trout showed marked differences between the 3 lakes studied as well as seasonal changes in diet (Fig. 5). The diet of the trout in each of these lakes can be described as follows:

1) In Lake 318 corixids were the dominant food organism, comprising from 44 to 92% C.I. by August. By September sticklebacks, *Culaea inconstans*, were also important but they were fed upon only by Idaho trout. Amphipods were fed upon in variable amounts in the season but never formed more than 24% C.I. for any period.

2) The trout of Lake 587 showed a progressive decrease in the consumption of amphipods in the season, from 80% to 5% C.I. by September. Sticklebacks, *Culaea inconstans*, and corixids became more important with the advancing season. Idaho trout consumed relatively more fish and at an earlier time in the season than Tunkwa trout.

3) In Lake 721, which had no fish other than trout, the trout fed mainly on amphipods and odonate naiads. This food comprised between 75 and 90% C.I. of the seasonal diet except for July (small sample size) when corixids formed 51% C.I. of the food eaten.

4) Zooplankton appeared in small amounts in the diet of trout and only in the early sample of July.

The differences between lakes were quantified by calculating and comparing the percentage similarity of each sampling period of each lake (Table 2). Almost all of the comparisons between time and lakes had a percentage similarity of less than 50%. Only Lake 318 showed some similarity to other lakes. In particular the September sample was similar to Lake 587 August and September samples where fish, corixids and amphipods formed about 84% C.I. of the diet. Also the July fish of Lake 318 had a diet similar to most of the Lake 721 fish. This was due to the importance of corixids, amphipods and partly to chironomids in their diet. Surprisingly fish from lakes 587 and 721 had little similarity in diet (Table 2) though in both lakes fish fed on amphipods they ate them at different times in the season.

Similarly in 1974 the trout showed marked seasonal differences in diet in the lakes studied (Fig. 5). Their diets are described as follows:

1) For all lakes in June cladocerans were an important food for the young fish, comprising at least 30% C.I.. They were also consumed thereafter

but to a much smaller extent.

2) In Lake 318 chironomids were also eaten by young fish in June and early July. However, *Chaoborus* became the dominant food in July, at least 60% C.I. By August and September *Chaoborus* Odonata naiads and amphipods became of equal importance to the trout.

3) Similarly in Lake 587 chironomids were highly fed upon by young fish. In July, the only other month that the lake was sampled, the trout had shifted to amphipods and corixids. Trout also fed on stickleback during this month. Only this lake had fish other than trout in 1974.

4) Odonata naiads and amphipods were the most important foods of Lake 721 fish. They amounted to at least 60% C.I. except for July when *Chaoborus* comprised 80% C.I.

Differences in diet in time and between lakes were quantified and it was found that 75% of the comparisons had less than 50% similarity (Table 3). In particular lakes 587 and 721 were different with not more than 38% similarity. Lakes 587 and 318 were also different except for June when fish in both lakes were feeding on cladocerans, *Chaoborus* and chironomids. The most similarity occurred between lakes 318 and 721. For example the June sample of Lake 721 was 57% similar to the August and September samples of Lake 318 because amphipods and Odonata naiads were eaten in both lakes. And in July fish from both lakes were feeding largely on *Chaoborus*. In August and September fish of both lakes were feeding primarily on these organisms, *Chaoborus*, amphipods and Odonata naiads.

The food habits of rainbow trout in the three lakes studied in 1973 and 1974 show clear differences between lakes within and between years. These differences clearly demonstrate that rainbow trout are versatile, opportunistic feeders, capable of exploiting a variety of food sources such as McAfee (1966) described them. This response is most likely dependent on prey availability and/or a size-dependent response as discussed for the 1971 trout. The diet in 1973-74 appeared to be more varied than in 1971, though the studies are not directly comparable since different sampling techniques were used.

There appeared to be a size-dependent response for food habits as the trout grew which was most notable in lakes which had other fish with trout. Generally the diet of the young trou- was composed of a mixture of plankton and insects, then as it grew it shifted to insects and crustaceans. This pattern is similar to that described by Scott and Crossman (1973) for rainbow trout.

RELATIONSHIP BETWEEN FOOD HABITS AND GROWTH PATTERNS

The changes in food habits relative to the changes in -rowth pattern of 1973-74 trout seems not to be related as the literature would suggest. For instance Scott anc Crossman (1973) stated that "the availability of other fish as food is often considered necessary for the attainment of large size by rainbow trout". In this study larger trout were obtained in 1973 and in Lake 587 trout fed partly on fish, with Idaho trout eating relatively more fish and at an earlier time than Tunkwa trout. The Idaho and Tunkwa trout, though significantly different in weight at harvest, were at the same size as those of Lake 721. Yet in Lake 721 only crustaceans and insects were available. This evidence is also striking because Lake 587 had a large population of sticklebacks, a highly probable competitor for the same food resource, yet it produced the same size trout as in Lake 721. Therefore food does not appear to be limiting, at least not for the density of trout stocked in these lakes, and this abundance of food appears able to support strains of rainbow trout with behavioral differences in feeding habits, such as lakes 587 and 721 suggest, with no detrimental effect on growth.

Also Larkin et al. (1957) found that when other fish besides rainbow trout were present in lakes, instantaneous growth rates were not linearly related to size. For example, they found in Paul Lake that trout grew slowly at small size because of competition with shiners for food, but when trout a-tained a larger size, preying on shiners, they embarked on a new growth relationship. But the seasonal change in specific growth rate observed in 1973-74 (Fig. 2) cannot be explained by change in feeding habits since this pattern occurred in trout living in lakes which had no other fish. However, the differences in the diets of trout in the lakes observed in this study may be as Larkin et al. (1957) suggested that "in each lake, a characteristic availability of food organisms determines the ratio of energy gained from food intake to energy expended in living processes". And the availability of food organisms can change within a season like Lake 103 in 1971 but remain the same between years, 1970-71, or change between years, 1973-74, and also vary between lakes in a year as lakes 318 and 721, 1974.

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Table 1. Lake morphometry, planting rates and sizes of trout, of lakes stocked with different strains of rainbow trout in 1970, 1971, 1973 and 1974.

Lake	Year	Area (ha)	Depth (m) Max.	Depth (m) Mean	Strains	Trout planting: Date planted	Trout planting: No/ha	Trout planting: Mean Size (g)
103	1970	10.1	1.5	0.6	Pennask	May 15	750	4.50
.	1971	.	.	.	Livingstone	May 5	.	1.70
318	1973	21.9	2.4	1.2	Idaho	May 4	238	4.40
.	.	.	.	.	Tunkwa	.	.	4.88
.	1974	.	.	.	Idaho	May 23	.	1.93
.	.	.	.	.	Nisqually	.	.	2.15
587	1973	6.9	4.0	2.5	Idaho	May 11	247	10.80
.	.	.	.	.	Tunkwa	.	.	9.45
.	1974	.	.	.	Idaho	May 18	.	1.87
.	.	.	.	.	Nisqually	.	.	1.93
721	1973	6.5	3.0	1.6	Idaho	May 11	216	6.67
.	.	.	.	.	Tunkwa	.	.	7.96
.	1974	.	.	.	Idaho	May 16	.	1.87
.	.	.	.	.	Nisqually	.	.	1.93

Table 2. The percentage similarity in food habits of the combined Idaho and Tunkwa rainbow trout strains stocked in 1973 in lakes 318, 587 and 721.

	L. 318				L. 587				L. 721			
	July 5	July 26	Aug. 14	Sept. 19	July 5	July 26	Aug. 14	Sept. 19	July 5	July 26	Aug. 14	Sept. 19
L. 318												
July 5	100.0	49.9	49.0	47.6	36.5	30.7	42.6	39.6	26.6	77.1	27.9	27.5
July 26		100.0	89.9	36.3	6.1	14.6	39.2	42.6	5.8	56.8	5.8	4.0
Aug. 14			100.0	31.1	8.1	11.8	34.0	37.5	5.0	56.0	5.0	5.0
Sept.19				100.0	26.5	40.1	82.1	74.8	14.8	46.3	20.1	21.5
L. 587												
July 5					100.0	67.3	16.6	9.4	21.6	31.6	48.2	32.7
July 26						100.0	34.2	23.6	23.9	33.0	44.6	29.3
Aug. 14							100.0	82.4	16.1	42.6	13.5	13.5
Sept.19								100.0	5.1	37.6	5.1	5.1
L. 721												
July 5									100.0	19.8	70.2	75.8
July 26										100.0	31.6	29.0
Aug. 14											100.0	81.4
Sept.19												100.0

Table 3. The percentage similarity in food habits of the combined Idaho and Nisqually rainbow trout strains stocked in 1974 in lakes 318, 587 and 721.

	L. 318					L. 587			L. 721			
	June 26	July 9	July 23	Aug. 22	Sept. 19	June 20	July 9	July 18	June 14	July 12	Aug. 8	Sept. 13
L. 318												
June 26	100.0	23.2	16.6	24.3	22.0	73.9	12.8	4.0	32.0	9.7	18.5	13.6
July 9		100.0	60.7	14.6	13.0	32.7	12.9	4.0	2.1	69.8	19.0	12.4
July 23			100.0	15.2	15.2	6.2	7.6	4.4	7.6	77.0	15.2	14.9
Aug. 22				100.0	79.2	21.2	32.7	24.8	57.7	27.4	57.2	79.5
Sept.19					100.0	18.8	24.8	29.3	57.1	27.4	64.0	74.6
L. 587												
June 20						100.0	21.5	4.0	38.1	11.8	18.5	10.4
July 9							100.0	56.6	25.4	10.7	28.0	19.9
July 18								100.0	33.6	2.0	35.5	23.5
L. 721												
June 14									100.0	14.1	60.3	59.2
July 12										100.0	30.5	27.4
Aug. 8											100.0	60.7
Sept.13												100.0

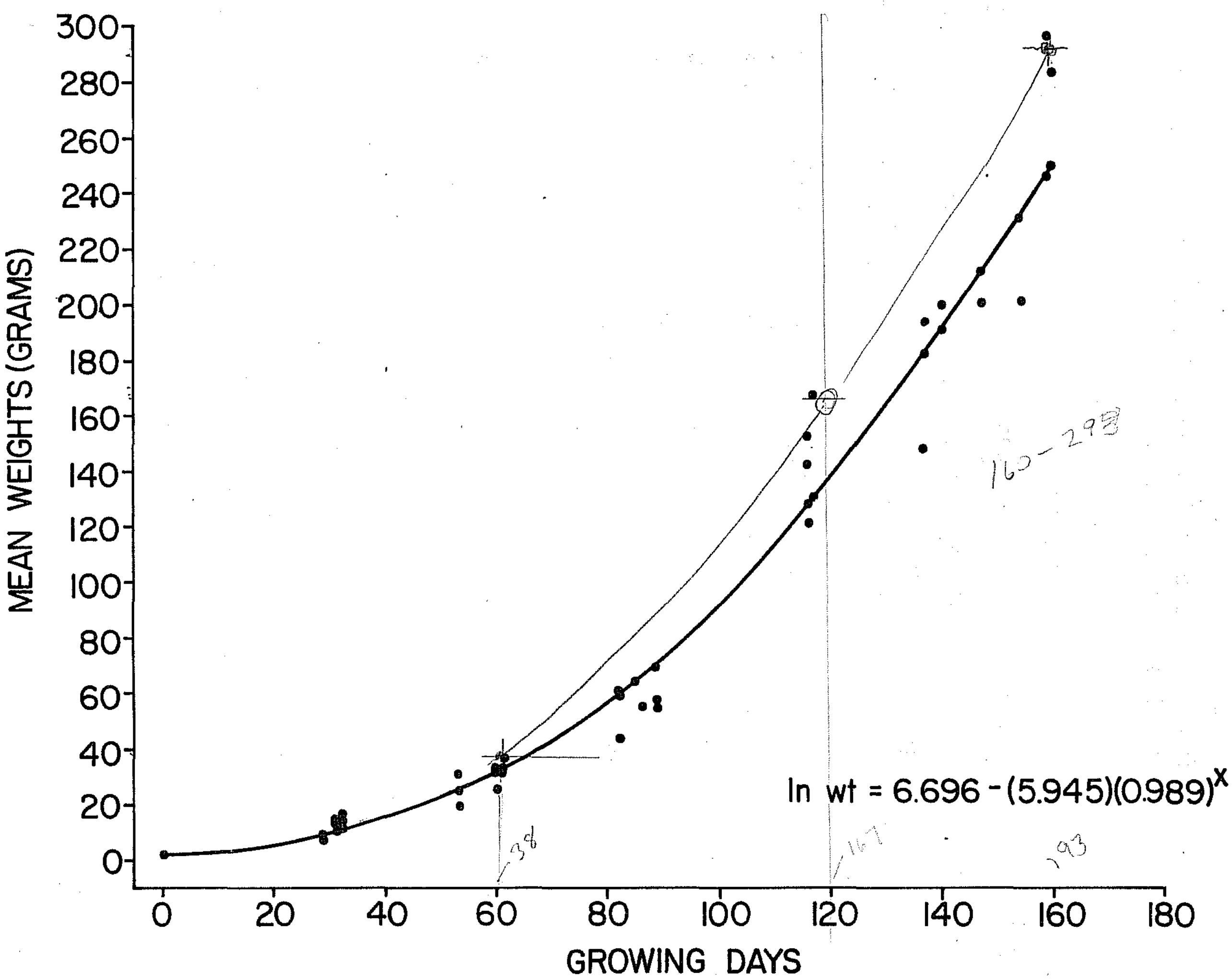

Fig. 1. The growth curve of the 1974 trout expressed by the Gompertz growth curve.

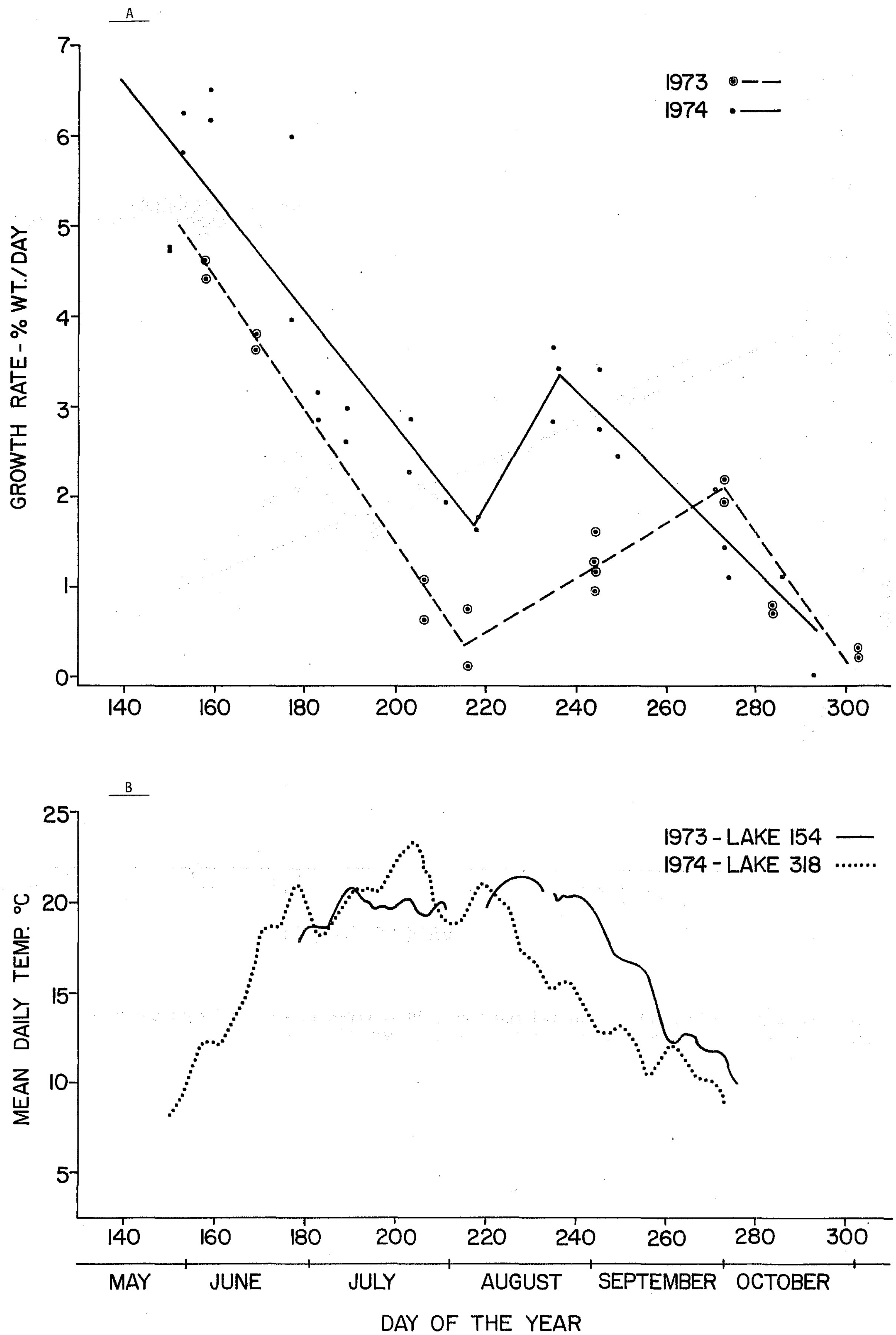

Fig. 2 A. The seasonal change in specific growth rate of rainbow trout in 1973 and 1974.
B. The mean daily water temperature of Lake 154 in 1973 and Lake 318 in 1974.

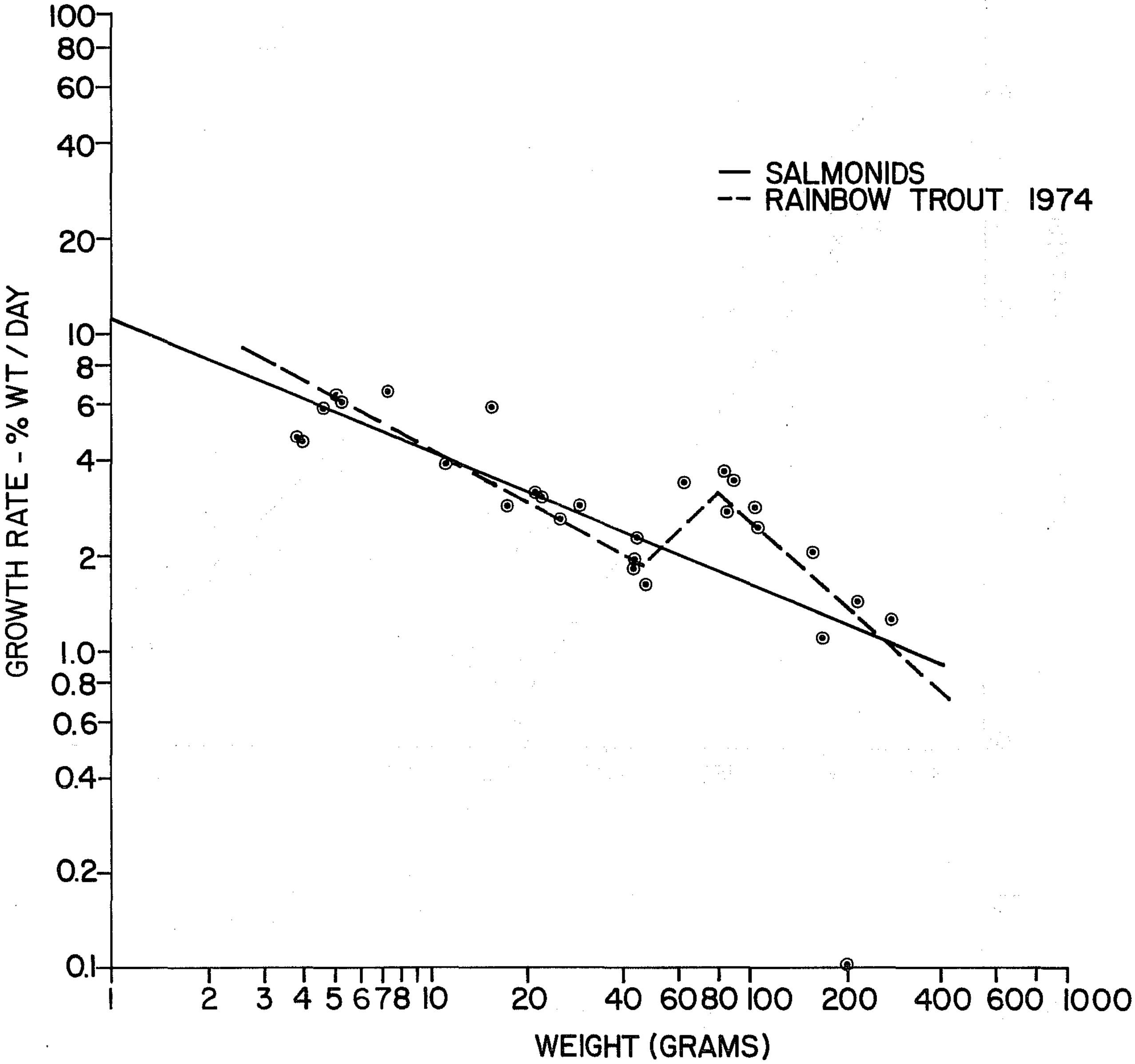

Fig. 3. The growth rate-weight relation of rainbow trout, 1974, grown in a natural environment and compared to the relationship calculated for salmonids grown under optimum temperature from Brett and Shelbourn (1975).

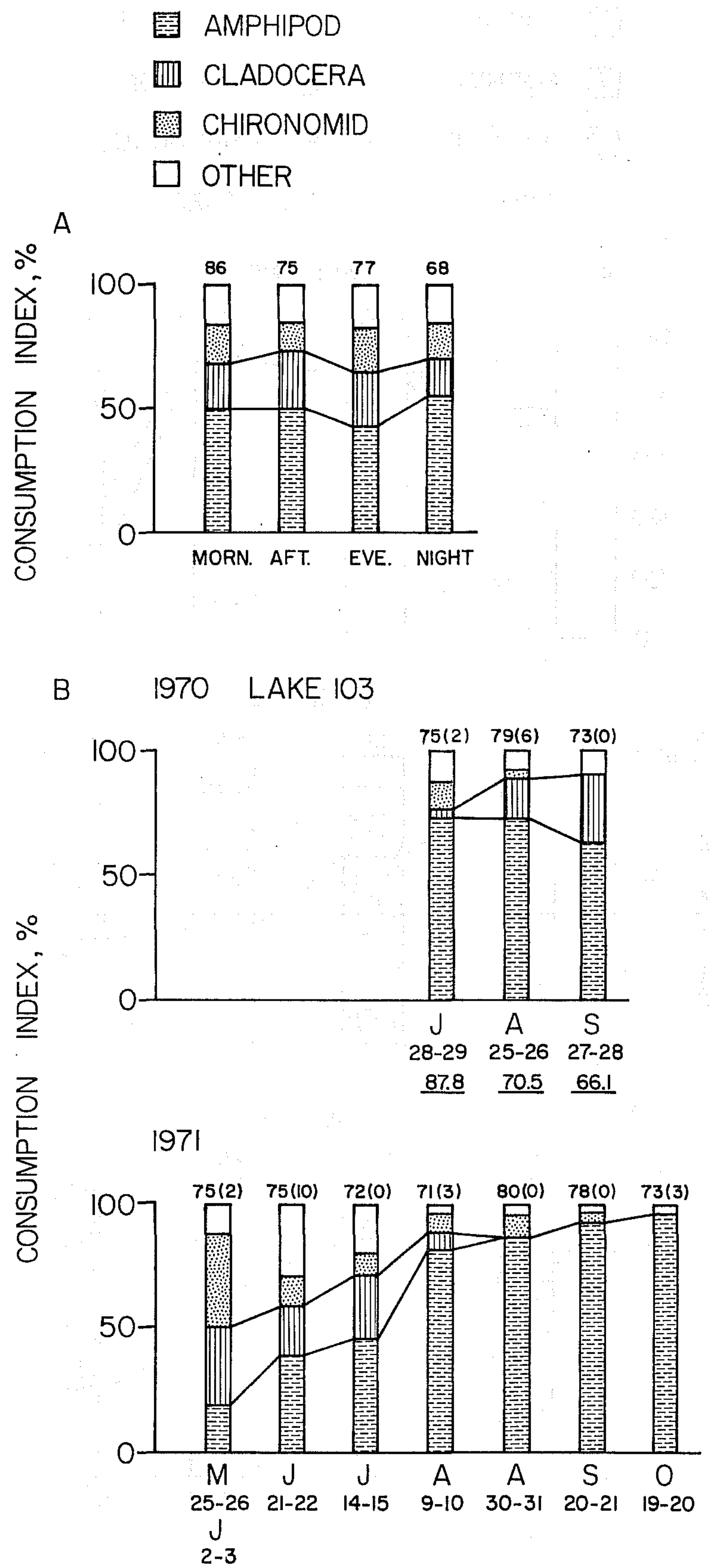

Fig. 4. Relative importance of major food organisms in Lake 103 trout stomachs.

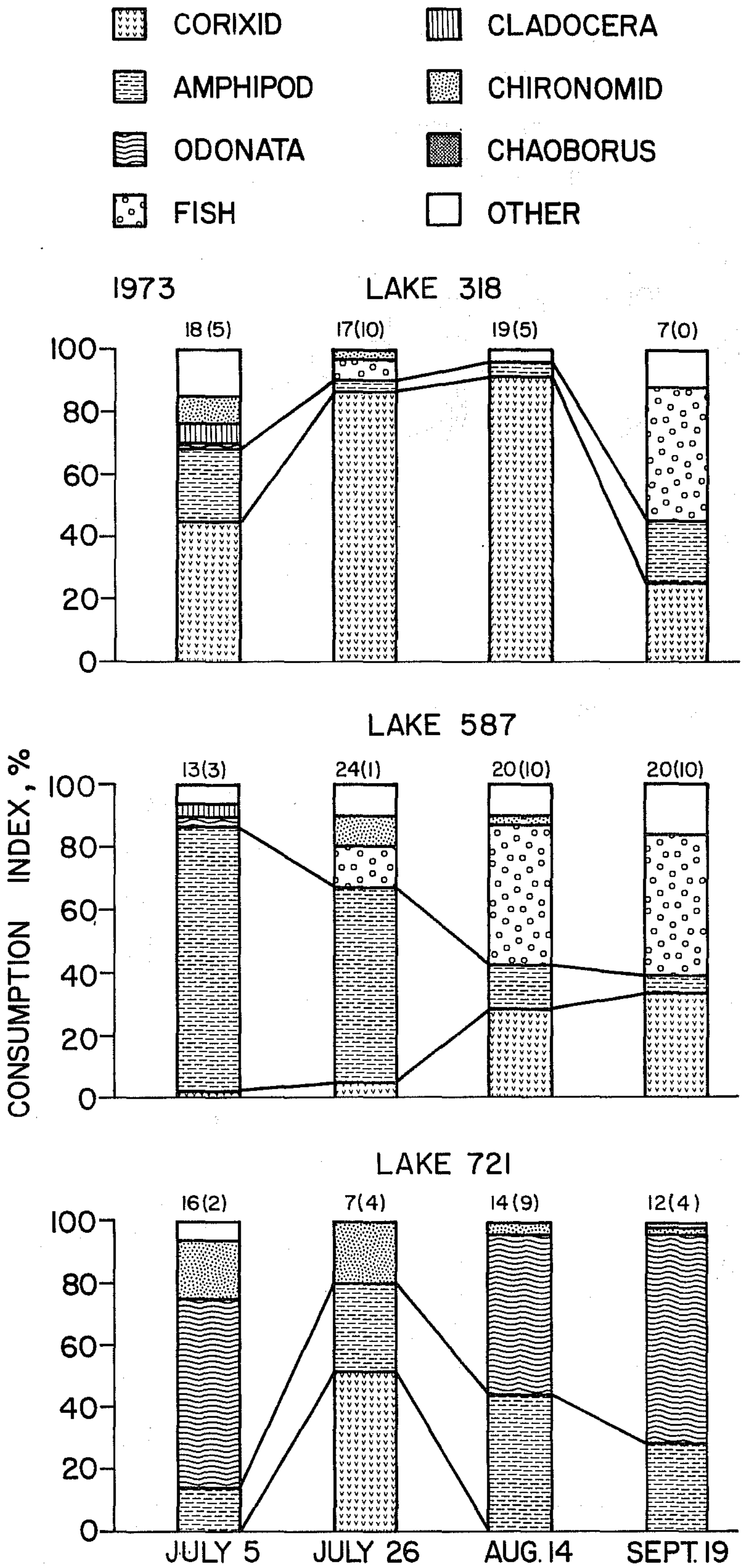

Fig. 5. Relative importance of major food organisms in stomachs of trout of 1973 in lakes 318, 587 and 721, based on consumption index and expressed as a percentage.

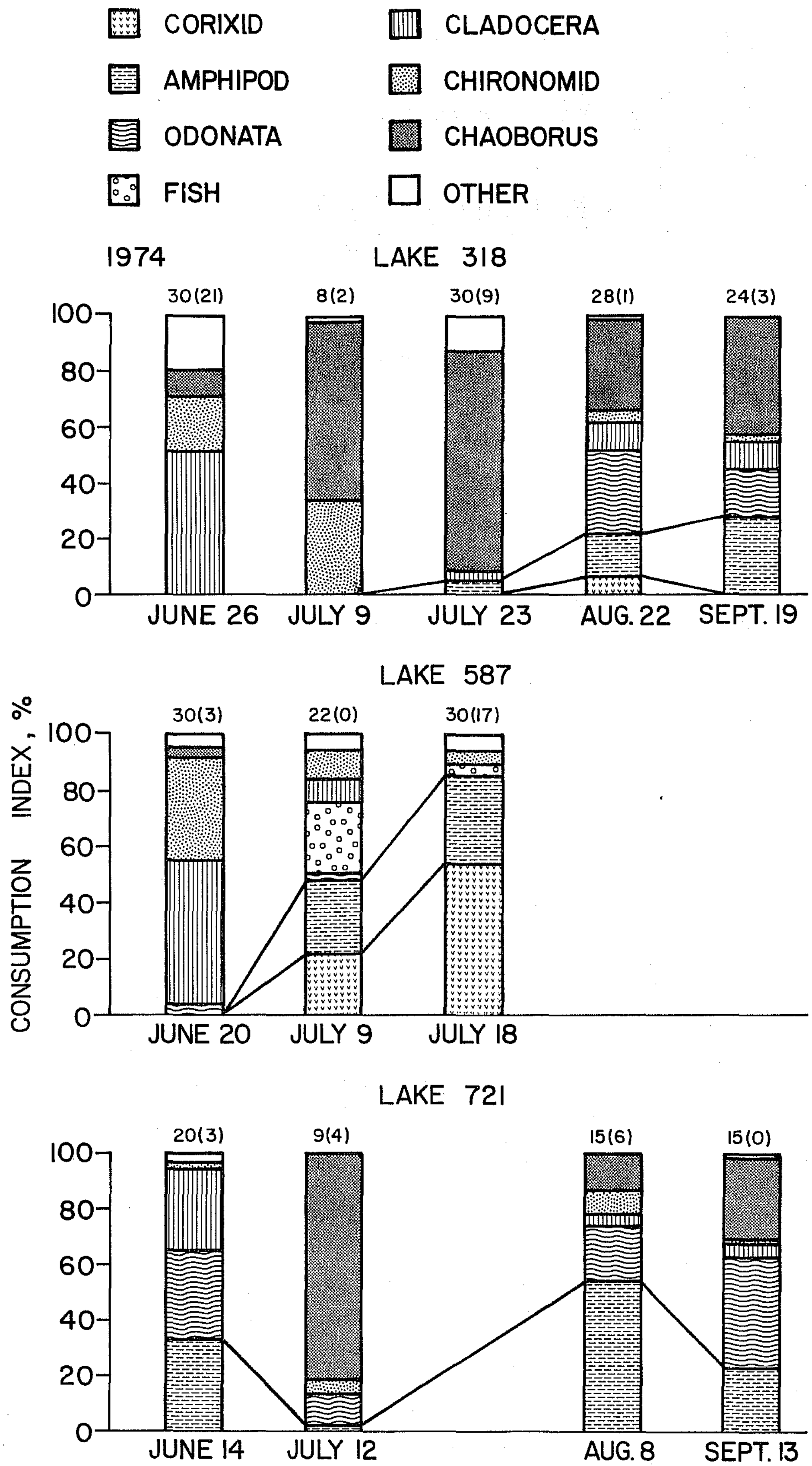

Fig. 6. Relative importance of major food organisms in stomachs of trout in 1974 in lakes 318, 587 and 721, based on consumption index and expressed as a percentage.

Appendix 1.

Analysis of variance of the weight (log transformed) of rainbow trout at the time of harvest in 1974 for lakes 318, 587 and 721.

Source	df	SS	MS	F
Lakes	2	1.676	.838	35.609**
Strains	1	0.026	.026	1.120
L x S interaction	2	0.181	.091	3.850*
Within	373		.023	

Analysis of variance of the weight (log transformed) of rainbow trout at the time of harvest in 1974 for lakes 318 and 721 only.

Source	df	SS	MS	F
Lakes	1	0.840	.840	72.431**
Strains	1	0.002	0.002	.215
L x S interaction	1	0.009	0.009	.774
Within	145		0.012	

Analysis of variance of weight (log transformed) of rainbow trout at the time of harvest in 1973 for lakes 587 and 721 only.

Source	df	SS	MS	F
Lakes	1	0.077	0.077	0.462
Strains	1	2.178	2.178	130.044**
L x S interaction	1	0.730	0.730	43.723II
Within	372		0.017	

* indicates P <.10

** indicates P <.01

Appendix 2. Comparison of growth rate data for Lake 103 rainbow trout in 1970 and 1971.

1970			1971		
Sampling date	Sample size	Mean wet wt.(g)	Sampling date	Sample size	Mean wet wt.(g)
[1] May 15		4.5	[1] May 5		1.7
			May 25	46	5.8
			June 2	36	6.6
			June 22	167	42.4
July 8	25	73.9	July 14	91	61.3
July 28	224	84.8	July 29	17	103.1
			Aug. 9	190	107.7
Aug. 25	193	115.7	Aug. 30	123	133.5
Sept. 27	105	209.6	Sept. 10	108	184.8
			Oct. 20	87	210.1
[2] Oct. 6 - Dec. 17	2207	216.4	[2] Oct. 14 - Nov. 25	1758	219.1

[1] Date of stocking

[2] Range of harvest dates

Appendix 3. Summary of the growth of two strains of rainbow trout in 1973.

Strain	Lake	Gear*	Day sampled	Days of growth	Number of fish	Weight (grams) Mean	Weight (grams) S D	Weight (grams) Range	Fork length (mm) Mean	Fork length (mm) S D	Fork length (mm) Range
Idaho	318		May 4	0	5200	4.40					
		1	July 5-6	62	4	38.25	20.22	19- 65	135.5	24.28	109-162
		1	July 26-27	83	5	89.80	38.64	36-132	181.60	28.17	138-211
		1	Aug 14-15	102	7	114.43	22.02	83-150	196.57	15.93	173-221
		1	Sept 19	138	2	153.50	34.65	129-178	221.50	6.36	217-226
Tunkwa	318		May 4	0	5200	4.88					
		1	July 5-6	62	12	47.00	16.99	23- 70	159.67	15.21	126-190
		1	July 26-27	83	16	72.75	25.55	14-110	181.13	22.74	115-207
		1	Aug 14-15	102	28	69.07	29.96	32-162	181.18	25.01	115-224
		1	Sept 19	138	5	46.20	17.18	25- 60	169.60	19.17	144-185
		2	Nov 2	182	5	77.60	37.15	43-128	194.80	30.97	163-233
Idaho	587		May 11	0	1700	10.80					
		1	July 5-6	55	9	132.89	40.77	70-205	196.89	18.82	174-228
		2	July 27	77	11	180.73	40.14	110-234	219-36	14.83	195-240
		1	Aug 14	95	10	212.50	66.11	136-349	235.70	22.81	200-275
		1	Sept 19	131	10	377.80	108.04	207-470	286.20	24.78	238-316
		1	**Nov 4	177	50	521.12	149.61	135-871	310.76	29.88	207-369
Tunkwa	587		May 11	0	1700	9.45					
		1	July 5-6	55	4	87.00	39.68	30-122	187.50	31.51	141-211
		2	July 27	77	12	160.17	35.28	105-230	228.58	17.21	201-260
		1	Aug 14	95	10	137.60	31.23	94-190	222.40	16.10	197-243
		1	Sept 19	131	10	192.70	58.14	101-326	250.80	19.66	213-290
		1	**Nov 4	177	50	269.98	90.03	113-567	279.66	23.16	221-339
Idaho	721		May 11	0	1400	6.67					
		2	July 5-6	55	9	106.44	21.62	74-135	186.33	14.64	168-204
		1	July 26-27	77	4	119.00	14.28	104-138	198.25	1.71	196-200
		1	Aug 14-15	95	5	137.00	30.43	106-172	209.60	13.28	196-223
		1	Sept 19	131	3	218.33	27.06	195-248	236.67	10.41	225-245
		2	Oct 11	153	38	355.32	93.38	142-522	273.55	22.22	222-312
		2	***Nov 19	192	30	397.83	80.93	243-632	286.97	18.04	248-327
Tunkwa	721		May 11	0	1400	7.96					
		2	July 5-6	55	7	107.71	14.55	94-134	197.71	8.58	188-213
		1	July 26-27	77	4	126.00	22.38	110-159	218.00	10.10	215-233
		1	Aug 14-15	95	9	128.89	54.08	62-214	219.67	26.87	177-266
		1	Sept 19	131	9	196.78	80.21	106-330	250.00	32.27	211-298
		2	Oct 11	153	100	296.73	85.16	113-551	275.12	24.93	196-329
		2	***Nov 19	192	101	334.55	84.07	122-532	290.30	23.47	216-343

* Gear 1-Trap nets 2-Gillnets
** pooled Nov 2 and 6 samples
*** pooled Nov 17, 19 and 21 samples

Appendix 4. Summary of the growth of two strains of rainbow trout in 1974.

Strain	Lake	Gear*	Day sampled	Days of growth	Number of fish	Weight (grams) Mean	S D	Range	Fork length (mm) Mean	S D	Range
Idaho	318		May 23	0	5400	1.93					
		1	June 24	32	40	13.98	3.18	8- 20	9.78	0.75	7.6-11.2
		2	July 9	47	2	11.00	1.41	10- 12	9.55	0.64	9.1-10.0
		1	July 23	61	72	33.19	7.26	10- 48	12.79	0.99	9.7-14.6
		1	Aug 19	88	26	58.62	20.87	15- 88	15.21	1.71	10.5-17.4
		1	Aug 21	90	17	51.06	24.09	12- 85	14.50	2.42	10.5-17.1
		1	Sept 16	116	36	142.47	42.59	70-208	17.34	3.86	8.0-22.5
		1	Oct 17	148	19	200.11	43.37	141-306	22.68	1.76	19.7-26.3
		2	Oct 19	149	17	197.24	30.67	145-253	23.26	1.05	21.2-24.6
		2	Oct 30	160	13	204.15	59.13	95-304	23.22	2.34	18.2-26.0
Nisqually	318		May 23	0	5400	2.15					
		1	June 24	32	107	17.26	11.47	7- 26	10.30	1.05	6.4-14.3
		2	July 9	47	6	15.17	4.75	10- 22	10.88	0.92	10.1-12.3
		1	July 23	61	78	36.72	9.11	14- 61	13.41	1.11	10.3-16.0
		1	Aug 19	88	108	61.19	24.95	15-112	15.37	2.29	10.0-18.9
		1	Aug 21	90	15	54.73	32.08	30-116	14.91	2.23	12.2-19.0
		1	Sept 16	116	80	121.37	36.06	40-187	19.40	2.83	5.5-23.7
		1	Oct 10	140	50	199.94	48.18	85-328	23.47	1.83	17.5-28.5
Idaho	587		May 18	0	1700	1.87					
		1	June 18	31	12	11.33	2.10	4- 16	8.81	0.56	8.1- 9.7
		2	July 9	52	5	15.60	5.55	10- 24	10.78	0.85	9.8-12.0
		1	July 17	60	14	26.00	4.74	15- 32	12.19	1.02	9.4-13.6
		2	Oct 2	137	24	148.08	52.28	84-250	20.99	2.19	16.6-24.8
Nisqually	587		May 18	0	1700	1.93					
		1	June 18	31	91	13.40	3.82	7- 25	9.53	0.93	6.7-11.7
		2	July 9	52	17	31.53	15.82	10- 64	12.81	1.66	10.2-15.7
		1	July 17	60	96	33.74	9.93	9- 63	13.17	1.40	7.0-16.9
		1	Aug 12	86	7	55.57	26.48	30-100	15.39	1.86	13.0-18.2
		2	Oct 2	137	208	193.73	74.01	48-408	20.69	2.54	15.3-27.8
Idaho	721		May 16	0	1600	1.87					
		1	June 14	29	10	7.40	2.63	4- 10	8.57	0.74	7.3- 9.5
		1	July 8	53	8	19.13	8.37	9- 34	11.05	1.39	9.1-13.3
		2	July 12	57	1	49.0	-	-	14.10	-	-
		1	Aug 6	82	8	43.87	9.31	25- 55	14.46	1.07	12.2-15.4
		1	Sept 9	116	4	152.00	22.04	125-170	20.70	0.95	19.3-21.4
		2	Oct 22	159	33	297.12	57.76	150-402	24.63	2.79	14.7-28.1
Nisqually	721		May 16	0	1600	1.93					
		1	June 14	29	7	7.57	4.08	3- 14	9.01	1.28	6.7-10.2
		1	July 8	53	49	31.84	9.28	10- 54	13.00	1.13	10.2-15.0
		2	July 12	57	8	45.00	9.44	32- 56	13.81	0.89	12.8-15.1
		1	Aug 6	82	49	61.32	15.81	31-107	16.13	1.32	13.2-19.5
		1	Sept 9	116	25	151.92	49.07	25-240	20.93	2.82	12.0-24.2
		1	Sept 12	119	32	181.81	39.36	83-240	21.94	1.56	17.3-24.5
		1	Oct 23	160	15	284.27	87.04	119-440	25.15	2.59	19.9-28.5

* Gear 1-Trap nets, 2-Gillnets

Appendix 5. Number and dry weight of major food organisms in the stomachs of 1973 rainbow trout (strains combined).

Lake	Date	No. of fish	Chironomids		Chaoborus		Corixidae		Odonata		Amphipods		Cladocerans		Fish		Other	
			No.	Wt(g)	No.	Wt(g)	No.	Wt(g)	No.	Wt(g)	No.	Wt(g)	No.	Wt(g)	No.	Wt(g)	No.	Wt(g)
318	0507	13	21	0.012			52	0.168	1	.001	45	.071	69	.028			8	.066
	2607	7	1	.002			72	.302			1	.002			2	.012		
	1408	14					211	1.122			10	.046					3	.013
	1909						21	.130			20	.103			21	.688	5	.026
587	0507	10					1	.007	1	.009	86	.526	27	.003			4	.011
	2607	23	77	.228			19	.042	1	.001	773	3.404	24	.001	14	.767	33	.300
	1408	10	2	.006			26	.127			46	.163			6	.606	2	.044
	1909	10	1	--			76	.596			34	.043			15	1.474	8	.123
721	0607	14	111	.163	3	.001			198	1.549	117	.133	5	.001			23	.071
	2707	3	10	.008			18	.024			10	.005						
	1408	5	1	.001					20	.058	69	.053						
	1909	8	1	.001					100	.442	58	.071					1	.001

Appendix 6. Number and dry weight of major food organisms in the stomachs of 1974 rainbow trout (strains combined).

Lake	Date	No. of fish	Chironomids		Chaoborus		Corixidae		Odonata		Amphipods		Cladocerans		Fish		Other	
			No.	Wt(g)	No.	Wt(g)	No.	Wt(g)	No.	Wt(g)	No.	Wt(g)	No.	Wt(g)	No.	Wt(g)	No.	Wt(g)
318	2606	9	10	.001	5	.001							120	.004			4	.004
	0907	6	81	.051	251	.183							4	--			3	.002
	2307	9	79	.069							2	.001	10	.001			7	.008
	2208	27	18	.025	1775	.737	24	.089	273	.581	175	.175	903	.082			16	.006
	1909	21	7	.013	3035	1.536	36	.241	92	.428	229	.708	954	.133			2	.001
587	2006	27	211	.074	16	.002	2	.001	2	.005			2098	.094			28	.010
	0907	22	29	.049			227	.293	1	.006	24	.098	194	.042	15	.434	9	.019
	1807	13	2	.002			33	.068			12	.029			1	.006	2	.004
721	1406	17	5	.001					54	.065	27	.097	610	.054			2	.003
	0907	5	3	.004	201	.141			2	.010	2	.001						
	0808	9	2	.002	13	.006	1	.001	5	.013	78	.029	6	.001				
	1309	15	4	.004	978	.542			201	1.039	271	.359	35	.008			6	.002

Appendix 7. Comparison of the food consumed by each strain of trout in 1973 in each of the three lakes. (% C.I. = percentage of total consumption index, Nr = number of ranks, r = Spearman rank correlation coefficient.)

Food organisms	Lake 318 Idaho % C.I.	Lake 318 Tunkwa % C.I.	Lake 587 Idaho % C.I.	Lake 587 Tunkwa % C.I.	Lake 721 Idaho % C.I.	Lake 721 Tunkwa % C.I.
Diptera (adult)				1.6		
Chironomidae	1.6	2.5	1.2	8.0	13.2	13.4
Chaoborinae						
Hemiptera (adult)			1.5	2.3		
Corixidae	49.0	75.0	11.0	19.4		4.7
Coleoptera			0.9	1.1		
Dytiscidae	5.2	2.9		0.7	7.2	
Haliplidae		2.9	0.01	1.4		0.8
Gyrinidae		3.8	0.4	1.1		
Odonata						
Zygoptera			1.0		62.4	55.3
Maphipoda	10.3	15.4	36.7	49.5	17.2	26.0
Cladocera		2.3	0.9	.01		
Gastropoda				1.6		
Hirudinea	2.4		2.3			
Salamander			3.2			
Fish	31.4		41.0	10.7		
Number of fish	14	27	28	25	16	14
Percentage similarity	60.9		62.4		85.7	
Nr	9		15		6	
r	0.1000		0.3221		0.8114	
t - test	0.2659		1.2267		2.7766	
Probability	>0.1		>0.1		>0.1	

Appendix 8. Comparison of the food consumed by each strain of trout in 1974 in each of the three lakes. (% C.I. = percentage of total consumption index, Nr = number of ranks, r = Spearman rank correlation coefficient.)

Food organisms	Lake 318 Idaho % C.I.	Lake 318 Nisqually % C.I.	Lake 587 Idaho % C.I.	Lake 587 Nisqually % C.I.	Lake 721 Idaho % C.I.	Lake 721 Nisqually % C.I.
Diptera						
Chironomidae	3.1	5.4	27.2	12.1	1.9	1.9
Chaoborinae	42.7	40.9			6.9	29.9
Hemiptera						
Corixidae	7.9	3.0	27.6	28.4		
Coleoptera	0.01	0.01				
Dytiscidae			3.4		2.7	.01
Haliplidae			1.8			
Gyrinidae	1.1	.01				
Odonata						
Zygoptera	11.8	21.7	1.8	1.6	28.8	38.1
Ephemeroptera				4.9		
Amphipoda	17.6	20.6	12.9	12.8	33.9	24.2
Cladocera	15.7	7.8	23.6	16.3	25.8	5.2
Gastropoda						
Hirudinea						
Salamander						
Fish			1.8	23.4		
Number of fish	27	45	27	35	10	36
Percentage similarity	84.2		72.2		67.0	
Nr	8		9		6	
r	0.8857		0.5200		0.6572	
t - test	4.6708		1.6107		1.7439	
Probability	<0.01		>0.1		>0.1	