

THE UNIVERSITY OF MANITOBA

FOOD HABITS, FEEDING SELECTIVITY, GASTRIC DIGESTION  
RATES, AND DAILY RATION OF RAINBOW TROUT, Salmo  
gairdneri RICHARDSON, IN WESTERN MANITOBA  
WINTERKILL LAKES

by

CLAUDE C. HOLMSTROM

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES  
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE  
OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

WINNIPEG, MANITOBA

OCTOBER, 1972



## TABLE OF CONTENTS

	PAGE
ACKNOWLEDGEMENTS .....	vii
ABSTRACT .....	viii
INTRODUCTION .....	1
DESCRIPTION OF STUDY AREA .....	3
MATERIALS AND METHODS .....	10
Sampling .....	10
Treatment of Samples .....	16
Food Habits and Feeding Periodicity .....	17
Feeding Selectivity .....	18
Laboratory experiments .....	19
Field experiments .....	20
Rates of Gastric Digestion .....	23
Food Consumption .....	27
RESULTS .....	30
Food Habits .....	30
Feeding Periodicity .....	36
Feeding Selectivity .....	38
Laboratory experiments .....	38
Field experiments .....	41
Rates of Gastric Digestion .....	45
Effect of meal size .....	46
Effects of water temperature .....	48
Effect of food type .....	51
Effect of fish size .....	51
Food consumption .....	55

	PAGE
DISCUSSION .....	58
Food Habits .....	58
Temporal food habits .....	58
Diel food habits .....	61
Feeding Periodicity .....	62
Feeding Selectivity .....	64
Laboratory experiments .....	64
Feeding selectivity of Lake 3 trout .....	66
Digestion Rates .....	69
Effect of meal size .....	70
Effect of water temperature .....	71
Effect of food type .....	73
Effect of fish size .....	74
Effects of other variables .....	75
Food Consumption .....	75
SUMMARY .....	81
LITERATURE CITED .....	83
APPENDIX A .....	89
APPENDIX B .....	92
APPENDIX C .....	96
APPENDIX D .....	101
APPENDIX E .....	108

## LIST OF FIGURES

FIGURE		PAGE
1.	Weekly oxygen concentrations (ppm) and mean weekly water temperatures at a depth of 1 m. on Lake 3 .....	5
2.	Relative importance of major food organisms in Lake 3 trout stomachs for the 1971 diel netting experiments, based on consumption index .....	31
3.	Relative importance (consumption index) of major food organisms in Lake 3 trout stomachs for the morning, afternoon, evening, and night samples .....	32
4.	Relative importance (consumption index) of major food organisms in Lake 3 trout stomachs for similar sampling dates in 1970 and 1971 .....	34
5.	Diel pattern of indices of rainbow trout stomach fullness for each 24 hour sampling of the Lake 3 population completed during the 1971 growing season .....	37
6.	Stomach depletion rates of rainbow trout fed 3 different size meals of amphipods at a constant water temperature of 17C .....	47
7.	Percent depletion of amphipods from rainbow trout stomachs at temperature acclimations of 5, 12, 17, and 22C .....	49
8.	Relation between time to 95% digestion, instantaneous depletion rates, and acclimation temperature for similar size rainbow trout .....	50
9.	Comparison of gastric digestion rates for similar size rainbow trout fed different foods .....	54

## LIST OF TABLES

TABLE		PAGE
1.	Physical-chemical data from a series of study area lakes compared with those of Lake 3 .....	6
2.	A partial list of fauna and flora of Lake 3 .....	7
3.	Summary of 1971 Lake 3 invertebrate sampling schedule .....	22
4.	Summary of dates, water temperatures, food, fish size, and variables considered in laboratory experiments on digestion rates of rainbow trout .....	26
5.	Comparison of rainbow trout food habits in 6 study area lakes during July and August, 1971 .....	35
6.	Percent composition of the ration of rainbow trout allowed to feed for 2 hours in a clear, concealment-free aquarium (Rp) and in an aquarium simulating natural conditions (Rn)..	40
7.	Comparison of selectivity indices(S) with their respective preference (P) and availability (A) components for six different food organisms .....	40
8.	Percent abundance of various food organisms in the Lake 3 limnetic zone (L) and in Lake 3 trout stomachs (F) for 3 sets of day-night samples taken during the summer of 1971...	43
9.	Comparison of selectivity indices for amphipods, cladocerans and chironomid larvae, assuming that feeding of Lake 3 rainbow trout was restricted to the limnetic zone .....	44
10.	Comparison of selectivity indices for various food organisms in Lake 3, assuming the trout fed only in the littoral zone	44
11.	Summary of analysis of covariance tests for differences in gastric digestion rates of rainbow trout .....	53
12.	Comparison of estimated daily food consumption of Lake 3 rainbow trout using 4 methods of computation .....	57

## LIST OF PLATES

PLATE		PAGE
1.	Aerial view of Lake 3 facing north. Transects with sampling stations are indicated .....	13
2.	Aerial view of Lake 3 facing west .....	13
3.	F.R.B. Multiple Corer used for sampling Lake 3 benthos ...	14
4.	Schindler trap used for taking zooplankton samples in Lake 3 limnetic zone .....	14
5.	Cylindrical iron tank, diaphragm pump, and sieve net used for sampling Lake 3 littoral zone .....	15

## LIST OF APPENDICES

TABLE		PAGE
A-1	Comparison of growth rate data for Lake 3 rainbow trout in 1970 and 1971 .....	89
A-2	Dry weights of equal samples of <u>Gammarus lacustris</u> preserved in 10% and full strength formalin for varying periods of time .....	90
A-3	Summary of wet and dry weights for samples of different size rainbow trout caught in Lake 3 during 1971 .....	91
B-1	Number and dry weight of major food organisms in the stomachs of Lake 3 rainbow trout caught during 1970 and 1971 diel gillnetting experiments .....	92
C-1	Analysis of variance test for differences in consumption of several aquatic invertebrates by rainbow trout in a clear, concealment-free aquarium .....	96
C-2	Analysis of variance test for differences in consumption of several aquatic invertebrates by rainbow trout in a simulated natural environment .....	96
C-3	Summary of data for day and night benthic samples taken with a multiple corer on Lake 3 during the summer of 1971 .	97
C-4	Summary of data for day and night water column samples taken with a Schindler trap on Lake 3 during the summer of 1971 .....	98
C-5	Number of organisms recovered in daytime littoral zone samples taken with the Whitaker tank on Lake 3 during the summer of 1971 .....	99
C-6	Summary of stomach content information used in the assessment of day and night feeding selectivity of Lake 3 rainbow trout .....	100
D-1	Summary of data from digestion rate experiments conducted on rainbow trout during the summers of 1970 and 1971 .....	101
D-2	Summary of regression analysis data for rainbow trout digestion rate experiments .....	104
D-3	Summary of analysis of covariance test for significant differences in slopes of the regressions of natural log of percent food remaining in the stomach on time linear ...	105
E-1	Summary of data from 1971 gillnetting experiments used in calculation of daily ration of Lake 3 rainbow trout .....	108

## ACKNOWLEDGEMENTS

The author wishes to express his gratitude to Dr. G. H. Lawler, Research Scientist, Fisheries Research Board of Canada (Freshwater Institute) and Adjunct Professor of Zoology, University of Manitoba, for making this project possible and also for the encouragement and constructive suggestions he willingly offered during the course of the study. I also appreciate the advice and critical review of the manuscript given by Dr. R. H. Green, Assistant Professor of Zoology, University of Manitoba and Dr. K. Patalas, Research Scientist, Freshwater Institute, Winnipeg.

I am deeply indebted to many of the professional and technical staff of the Freshwater Institute for their unselfish contributions to the study. In particular, I would like to thank Messrs. J. Whitaker, L. Sunde, E. Pessah, G. Pryznyk, C. Haight, J. Flannagan, A. Salki, S. Zettler, and Miss H. Kling. The assistance of Dr. D. P. Scott with the mathematical and statistical analyses was invaluable. Thanks are also due to summer assistants L. Siemieniuk, L. Decter, and J. Janzen and especially to my wife, Lynne-Anne without whose encouragement and infinite patience this investigation would not have been completed.

The financial support provided by the Fisheries Research Board of Canada, the National Research Council, and the University of Manitoba is gratefully acknowledged.

## ABSTRACT

Food habits, feeding selectivity, digestion rates, and daily rations were determined for stocked rainbow trout in a Western Manitoba winterkill lake. Amphipods, cladocerans, and chironomid larvae were the most important food items with amphipods comprising more than 90% by weight of the food consumed from August to October in 1970 and 1971. Rainbow trout were diurnal in their feeding habits and fed more or less continuously throughout the day and early evening. Peak stomach fullness occurred in late afternoon. Food consumption was reduced or absent from about midnight to 6:00 a.m. The type of food organisms eaten at different times of the day did not change appreciably. Evidence suggested that feeding was limited primarily to the limnetic zone.

Laboratory and field experiments on feeding selectivity indicated that prey availability was the most important factor in determining which foods were eaten while predator preference was of minor significance. Chironomid larvae, although apparently preferred by the trout, were negatively selected because of their inaccessibility. The more easily captured amphipods were positively selected. Terrestrial invertebrates, plant material, and many littoral organisms were avoided entirely.

The relationship between state of digestion and time approximated a negative exponential. The number of hours required for 95% digestion at 5, 12, 17, and 22C was 54, 16, 14, and 9 respectively. Digestion rates were independent of meal size, food type, and fish size for the range of food items and fish weights used in the experiments.

Several methods of determining daily ration were evaluated. Estimates based on the balanced equation of Winberg (1956) were considerably higher than those derived from data on digestion rates and diel feeding intensities. Food consumption rates of 3.8% to 5.9% of body weight per day were calculated by the former method for July, August, September, 1971.

## INTRODUCTION

A research program, designed to determine the feasibility of stocking rainbow trout, Salmo gairdneri, in prairie winterkill lakes, was undertaken by the Fisheries Research Board of Canada in 1968. Initial investigations demonstrated that rainbow fingerlings 2 -  $3\frac{1}{2}$  in. in length, stocked in early May, would attain a marketable size of 8 or more oz. by October of the same year (Johnson et al. 1970).

During May, 1970, 20 small lakes in the Erickson area of Western Manitoba were stocked with 2 - 3 in. rainbow trout at densities ranging from 25 to 860 per acre. Success was highly variable with some lakes yielding as much as 80 to 110 lbs./acre while a few others failed completely. The mean yield was 43 lbs. / acre and the mean weight of fish harvested, 7.0 oz. Corresponding data for the 22 lakes stocked in 1971 show a significantly greater degree of success with a mean yield of 64 lbs. / acre and a mean harvest weight of 8.9 oz. (Sunde, pers. comm.).

Before trout farming in pothole lakes can become a viable, commercially successful operation, a management program based on a knowledge of the physical and chemical limnology of the lakes and of the stocking densities required to produce the maximum sustained yield, must be developed. The purpose of this investigation was to evaluate, qualitatively and quantitatively, various aspects of the feeding ecology of the stocked rainbow trout as an initial contribution to this program. The primary objectives were as follows:

1. to assess the daily, seasonal, and annual variations in food habits and to identify the more important food organisms.
2. to determine the diel feeding periodicity.
3. to evaluate feeding selectivity.

4. to experimentally determine the rates of gastric digestion in rainbow trout with respect to differences in water temperature, food type, meal size, and fish size.

5. to estimate the daily ration of a population of rainbow trout at regular intervals throughout the growing season.

## DESCRIPTION OF STUDY AREA

The study area is located immediately south of Riding Mountain National Park in Western Manitoba between latitudes  $50^{\circ} 30'$  -  $50^{\circ} 40'$  north and longitudes  $95^{\circ} 55'$  -  $100^{\circ} 30'$  west. A Fisheries Research Board field station is situated in the southeast corner of the area, near the town of Erickson.

The physiography of the region has been described by Goodwin (1930), Munro (1963), Princic (1971), and Fedoruk (1971). A mantle of unconsolidated material, deposited by the receding Wisconsin glacier, overlies a sedimentary shale bedrock of Cretaceous origin. The characteristic "knob and kettle" topography results from the uneven deposition of till in the form of moraines. The till is a heterogeneous mixture of boulders, gravel, sand, silt, and clay. Soil types are grey wooded, black, or variations of the two (Jenkins 1970). The natural vegetation reflects the transition from grassland to boreal forest which occurs here with broadleaf forest predominating in uncleared areas (Jenkins 1970).

Pothole or kettle lakes are extremely abundant in the study area. Most are relatively small in size; those between 2 and 5 acres account for about 50% of the total water area, while lakes of 20 acres or more constitute only 15% (Fedoruk 1971). They are characteristically shallow (15 ft. or less) and self-contained. Water levels are maintained by precipitation, run-off, and groundwater seepage. They are also highly productive with substantial concentrations of dissolved salts (primarily magnesium sulphate and sodium bicarbonate) and high levels of phosphate and nitrate nutrients (Sunde et al. 1971). Winterkill, the gradual reduction of dissolved oxygen to lethal levels resulting from oxidation reactions beneath the ice cover, is an annual phenomenon in all but the deeper lakes and accounts for the absence of indigenous fish populations.

Partial or complete summerkill occurred in some stocked lakes as a result of oxygen depletion during July and August. Decaying algal blooms probably account for this depletion.

Lake 3 (Plates 1 and 2), located adjacent to the Erickson field station, was used extensively during the ice-free seasons of 1970 and 1971 for investigations of rainbow trout food habits, feeding selectivity and feeding periodicity. Physical and chemical features of this lake and of other experimentally stocked lakes are described in Table 1. Weekly oxygen and temperature data are illustrated in Fig. 1. Several authors, including Greenbank (1945), Rozkowska and Rozkowski (1969), and Nickum (1971), provide more detailed information on the limnological characteristics of winterkill lakes.

Flora and fauna lists of the study area lakes are as yet incomplete. A partial list for Lake 3 is given in Table 2. The most abundant invertebrates are the crustacean amphipods, Gammarus lacustris lacustris and to a lesser extent, Hyalella azteca. Tiger salamanders, Ambystoma tigrinum are relatively abundant throughout the area. Population estimates of this species in two small lakes yielded densities of 127 and 282 individuals per hectare (Macklem, pers. comm.). Fathead minnows, Pimephales promelas and brook stickleback, Culaea inconstans are also commonly found. Heavy blooms of the blue-green alga Aphanizomenon flos-aquae occur regularly during the warm summer months in many study area lakes.

Figure 1. Weekly oxygen concentrations (ppm) and mean weekly water temperatures at a depth of 1 m. on Lake 3.

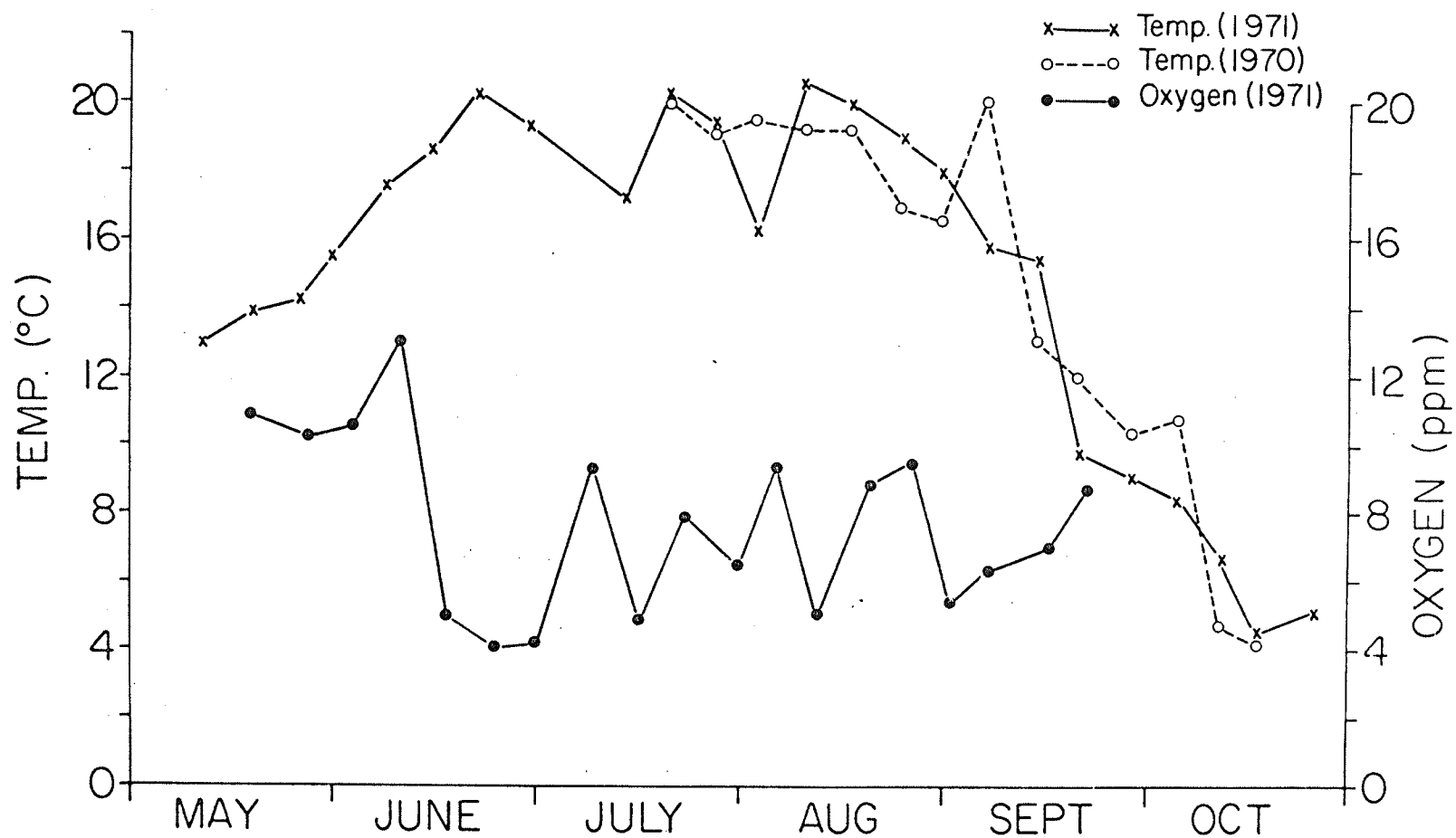


Table 1. Physical - chemical data from a series of study area lakes compared with those of lake 3.

Feature	Time of year	Lake 3	Other lakes	
			Min.	Max.
Lake area (hectares)		10	1	28
Max. depth (m.)		1.5	1	8
Spec. cond. ( $\mu\text{mho}/\text{cm}^2$ )	March	2160	700	4100
	July	1000	-	-
Total diss. solids ( $\mu\text{mho}/\text{cm}^2$ )	March	1790	1170	3960
	July	810	-	-
Calcium (mg/l)	March	97	31	215
	July	90	-	-
Magnesium (mg/l)	March	180	60	747
	July	55	-	-
Sodium (mg/l)	March	269	15	496
	July	53	-	-
Sulphate (mg/l)	March	745	72	2065
	July	285	-	-
Total phosphorus ( $\mu\text{g}/\text{l}$ )	March	2172	33	310
	July	900	-	-
Total nitrogen ( $\mu\text{g}/\text{l}$ )	March	3740	1465	4205
	July	860	-	-
pH	July	-	8.5	9.2

Table 2. A partial list of fauna and flora of Lake 3.

Phylum/Division	Class, Order	Family	Scientific Name	Identification <sup>1</sup>
Mollusca	Gastropoda		<u>Gyraulus</u>	C. Holmstrom
			<u>Helisoma</u>	"
			<u>Lymnaea</u>	"
Annelida	Hirudinea			"
Arthropoda	Amphipoda	Gammaridae	<u>Gammarus lacustris</u>	J. Flannagan
		Talitridae	<u>Hyalella azteca</u>	"
	Copepoda		<u>Diaptomus sicilis</u>	K. Patalas
			<u>Cyclops vernalis</u>	"
			<u>Cyclops bicuspidatus</u>	"
			<u>Diaptomus siciloides</u>	"
			<u>Mesocyclops edax</u>	"
	Cladocera		<u>Bosmina longirostris</u>	A. Salki
			<u>Daphnia pulex</u>	"
			<u>Daphnia magna</u>	"
	Odonata	Lestidae	<u>Lestes</u>	C. Holmstrom
		Coenagrionidae	<u>Ischnura</u>	"
	Hemiptera	Gerridae	<u>Gerris</u>	"
		Corixidae		"
		Belostomatidae	<u>Belostoma</u>	"
		Notonectidae	<u>Notonecta</u>	"
	Coleoptera	Dytiscidae	<u>Dytiscus</u>	"
		Haliplidae		"
		Gyrinidae	<u>Gyrinus</u>	"

Table 2. Cont'd.

Phyllum/Division	Class, Order	Family	Scientific Name	Identification <sup>1</sup>
	Trichoptera	Hydrophilidae		C. Holmstrom
		Limnephilidae		"
	Diptera	Culicidae	<u>Chaoborus</u>	"
		Tendipedidae		"
		Tipulidae		"
		Syrphidae		"
Cyanophyta	Myxophyceae		<u>Microcystis flos-aquae</u>	H. Kling
			<u>Aphanizomenon flos-aquae</u>	"
Chlorophyta	Chlorophyceae		<u>Pandorina</u>	"
			<u>Pediastrum Boryanum</u>	"
			<u>Pediastrum duplex</u>	"
			<u>Oocystis lacustris</u>	"
			<u>Oocystis crassa</u>	"
			<u>Oocystis submarina</u>	"
			<u>Nephrocytium limneticum</u>	"
			<u>Nephrocytium Agardhianum</u>	"
			<u>Scenedesmus quadricauda</u>	"
			<u>Quadrigula closteroides</u>	"
			<u>Ankistrodesmus falcatus</u>	"
			<u>Crucigenia quadrata</u>	"
			<u>Coelastrum microporum</u>	"
			<u>Dictyosphaerium pulchellum</u>	"
			<u>Dictyosphaerium Ehrenbergianum</u>	"
			<u>Dimorphococcus lunatus</u>	"

Table 2. Cont'd.

Phyllum/Division	Class, Order	Family	Scientific Name	Identification
Euglenophyta	Euglenophyceae		<u>Euglena Ehrenbergii</u>	H. Kling
			<u>Lepocinclis ovum</u>	"
			<u>Phacus</u>	"

<sup>1</sup>With the exception of the author, all of the personnel listed below are members of the staff of the Freshwater Institute and are qualified in the taxonomy of the invertebrate group with which their name is associated.

## MATERIALS AND METHODS

### Sampling

Rainbow trout were stocked in Lake 3 on May 15, 1970 and May 5, 1971 at a mean initial size of 3.1 g. and 1.5 g. respectively. The stocking density in both years was approximately 750 fish/hectare.

Although information on food habits and growth rates was obtained from samples of trout collected in several stocked lakes, only Lake 3 fish were used in studies on feeding periodicity, feeding selectivity and food consumption rates. During 1970, 24 hour gill netting experiments were conducted on Lake 3 on the following dates: July 28-29, August 25-26, and September 27-28. In 1971 the sampling was extended to cover a broader period and was carried out on May 25-26, June 2-3, June 21-22, July 14-15, August 9-10, August 30-31, September 20-21, and October 19-20. All fish were taken with graduated mesh, nylon gill nets since the submergent vegetation and soft, silty bottom precluded the use of other types of fishing gear. For each diel sampling two joined 50 m. nets were set perpendicular to shore at consecutive 3 hour intervals and left for not more than 15 minutes. This very brief fishing time was usually 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. Data from the May 25-26 and June 2-3 experiments were combined to provide a sufficiently large sample for that time of year. 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 and, for the remainder, only length-weight information was recorded. It was assumed that the data obtained were representative of the total population and that regurgitation of stomach contents did not occur.

Complete records of water temperature fluctuations were essential in estimating digestion rates and daily ration of the trout. These were obtained with a continuous recording thermometer (Wekslar, model 06MN1) stationed near the centre of Lake 3 with the probe fixed at a depth of 1m. Weekly oxygen profiles were taken with an oxygen meter (YSI, model 54) and Hach kit.

The invertebrate fauna of Lake 3 was sampled during the summer of 1971. Although quantitative determinations were taken with the original intention of estimating secondary production of amphipods, these determinations are presented here only in so far as they pertain to the feeding selectivity of stocked rainbow trout. Two perpendicular transects were established, each traversing the breadth of the lake. Stakes were driven into the bottom at contour intervals of 0.3 m. along the transects and these served as sampling stations (Plates 1 and 2).

To obtain adequate samples of the substrate, water column, and inshore zone of dense vegetation, 3 separate sampling devices were used. A multiple corer, described by Hamilton et al. (1970) and employed successfully by Flannagan (1970), was used for the benthic fauna (Plate 3) and a 28 l., self-activating plexiglass trap, described and tested by Schindler (1969), was used for the water column samples (Plate 4). Dense vegetative growth posed special problems in sampling the littoral zone. An apparatus designed by J. Whitaker of the Fisheries Research Board was an effective alternative to other available gear (Plate 5). It consisted of a cylindrical iron tank, 152 cm. by 30 cm. with a serrated bottom edge and handles welded at the top. The sampling procedure was as follows: At each sampling station the tank was lifted about 0.5 m. above and perpendicular to the water surface and released thereby sealing off a volume of water proportional to the tank diameter and the water depth.

In tall stands of Scirpus the emergent vegetation was clipped prior to dropping the tank. By twisting the handles the tank was securely anchored and the enclosed substrate well separated from its surroundings. As much vegetation as possible was removed by hand, each piece being rinsed thoroughly within the confines of the tank before discarding. A diaphragm pump, bolted to a plywood base and clamped to the stern of the boat, quickly extracted the water, loose pieces of vegetation, and the surface layer of substrate. All material was pumped into an adjacent sieve net, washed, emptied into a large plastic bag, and fixed in formalin. The paucity of organisms observed from repeated fillings suggested a high recovery rate on the first extraction. The tremendous number of invertebrates present necessitated sub-sampling. Consequently only one-sixth by volume of the actual sample was analyzed.

Plate 1. Aerial view of Lake 3 facing north.  
Transects with sampling stations are  
indicated.

Plate 2. Aerial view of Lake 3 facing west. Note  
dense mats of submergent vegetation and  
partial ice cover. (Photographs taken  
late October, 1971.)



Plate 1.

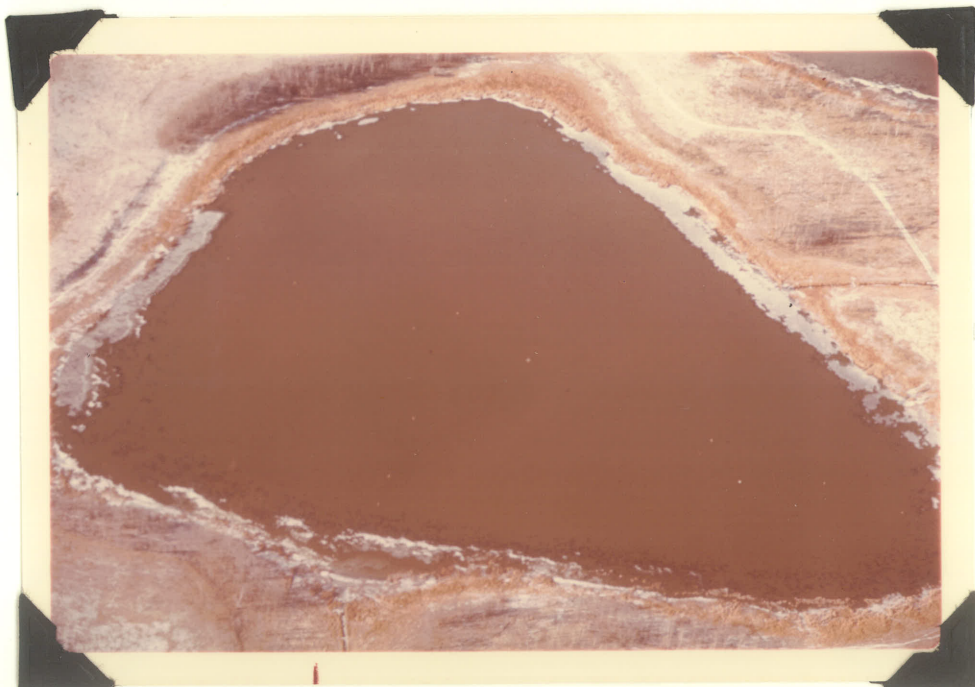


Plate 2.

Plate 3. F.R.B. Multiple corer used for sampling  
Lake 3 benthos.

Plate 4. Schindler trap used for taking zooplankton  
samples in Lake 3 limnetic zone.



Plate 3.



Plate 4.

Plate 5. Cylindrical iron tank, diaphragm pump,  
and sieve net used for sampling Lake 3  
littoral zone.



Plate 5.

#### Treatment of Samples:

Trout caught during the diel netting experiments were immediately returned to the field laboratory where length and weight information was recorded and stomachs removed for preservation. Fish weights were recorded to the nearest 0.1 g on a top loading balance (Mettler, P 1200). Stomachs plus contents were placed in vials containing 10% formalin and stored for future analysis.

Food analysis initially involved the determination of number and weight of various food organisms present in individual stomachs. Although basic identification was relatively simple, absolute counts became difficult when food was in an advanced state of digestion. Consequently it was often necessary to count head capsules or eyes rather than whole food items. When cladocerans were the predominant food organism the sorting dish was divided in quarters and the contents sub-sampled. Food samples were distributed in small aluminum dishes and dried in a vacuum oven for 48 hours at a temperature of 100C and a pressure of 15 p.s.i. The dried material was weighed to the nearest 0.01 mg on an analytical balance (Mettler, H6T).

To facilitate the expression of stomach content weight as a percentage of fish body weight, the dry weights of various size rainbow trout were taken. Since it was not possible to dry all the fish caught, dry weight information is based on a sample of 79 trout ranging in size from 3.8 to 256 g wet. An equation based on the linear regression analysis of the resultant data was used for all subsequent determinations of dry fish weight (Appendix A-3).

Howmiller (pers. comm.) reported substantial weight losses of aquatic invertebrates preserved in 70% alcohol and in 10% formalin. An effort was made to compensate for this potential error in stomach content

weights by preserving 20, 10.0 g. (wet wt.) samples of amphipods in 10% formalin and determining dry weights at regular intervals over a 21 week period. The results obtained (Appendix A-2) were used to correct dry weights of the stomach samples taken from Lake 3 trout.

Multiple corer and tank samples were sorted in white enamel trays containing a sugar solution of specific gravity 1.12, as recommended by Anderson (1959). Each water column sample was analyzed by emptying the contents into glass petri dishes and counting the invertebrates directly. Although individual counts have been recorded for each sampling device and for each station, the results used in the selectivity study represent pooled data.

#### Food Habits and Feeding Periodicity.

Percent frequency of occurrence, total number, and total dry weight were determined for each type of food organism consumed by Lake 3 trout. These data were separated according to the sampling interval, date, and year. Individually, numerical and gravimetric presentations of food habit results can often produce biases in the interpretation of the relative importance of a particular food item. Consequently a consumption index, similar to that proposed by Godfrey (1955), was calculated for all Lake 3 fish. The index was calculated by taking the square root of the product of the number of fish in the sample that have consumed the organism in question and the average weight of that organism in the stomachs of all the fish in the sample and converting this value to a percentage of the total stomach contents for the interval under consideration. The combination of numerical and gravimetric data into a single consumption index eliminates the bias which is otherwise introduced when fish consume a few very large food organisms or conversely when they consume many

small ones. It therefore provides a more acceptable measure of the importance of a given food item in a fish's diet.

An index of stomach fullness was also determined for each interval of the 1970 and 1971 diel netting experiments on Lake 3. This index is simply the dry stomach content weight expressed as a percentage of dry body weight. When plotted for each of the 8 sampling intervals over a 24 hr. period these indices provide a graphic expression of the diel feeding rhythm of Lake 3 trout.

#### Feeding Selectivity.

Both laboratory and field studies were carried out on the feeding selectivity of rainbow trout. Selectivity is expressed as an index with values from -1 to +1, an index of 0 indicating that the food organism under consideration is consumed in about the same proportion as it is available. This index, used initially by Ivlev (1961) and more recently by Starostka and Applegate (1970) is calculated using the equation,

$$S = (r_i - p_i)/(r_i + p_i)$$

where  $S$  = index of selectivity,  $r_i$  = the abundance of a given food item in the ration, expressed as a percentage of the total ration, and  $p_i$  = the abundance of the same food item in the lake, expressed as a percentage of the total food complex. It should be emphasized that this index is a measure of the selectivity shown for a food item in relation to its particular abundance and does not necessarily indicate the importance of that food item in the trout diet.

Selectivity is actually a function of two closely related factors:

- (1) the preference ( $P$ ) shown by a fish for a particular food item, and
- (2) the accessibility ( $A$ ) of the food organism itself. Differences in prey size, mobility, and habitat prevent the absolute separation of

these factors under natural conditions. The purpose of the laboratory experiments was to obtain some understanding of the relative contribution of each factor to the observed feeding habits of the stocked trout.

#### Laboratory Experiments

A 100 l. aquarium, connected to an adjacent 500 l. holding tank by a small water pump and siphon, was used for the laboratory experiments. This arrangement provided a continuous flow-through with a constant water temperature of  $17 \pm 0.5$  C. In the first series of experiments a clear, concealment-free aquarium was used while in the second series a natural situation was duplicated by introducing a 5 cm. layer of silt and organic debris as well as several aquatic plants. Theoretically the clear aquarium afforded equal accessibility of food items to the fish and subsequent measures of selectivity were a function of preference only. With concealment available to the prey, as in the latter arrangement, selectivity was a function of both preference and availability. A comparison of selectivity indices obtained using both set-ups provides at least a superficial assessment of the importance of availability and preference as components of feeding selectivity.

For each experiment a single trout, ranging in size from 17 to 45 g., was introduced into the aquarium 15-20 min. after 75 of each of the following organisms had been added: amphipods, corixids, Chaoborus larvae, chironomid larvae, zygoptera naiads, and small gastropods. After feeding for two hours the fish was removed, autopsied, and its stomach contents enumerated. Eight replicates were run for each series of experiments.

### Field experiments

Data on the relative abundance of food organisms in the trout stomachs and in the Lake 3 food complex were used to determine the feeding selectivity of Lake 3 rainbow trout. Invertebrate samples were taken between 1300 - 1700 hours and between 2400 - 0400 hours on June 21-22, July 29-30, and August 30-31, 1971. These samples ran concurrent with diel netting experiments except on July 29-30. Consequently, the number of organisms present in the ration can be directly related to their availabilities in the lake during the same interval. Stomach content data from August 9-10 were combined with the invertebrate sample taken on July 29-30 to arrive at selectivity indices for this period.

The multiple corer, Schindler trap, and iron tank were employed for all daylight samples but only the former two were used at night. Information on sampling is summarized in Table 3. Bottom sample counts were combined for all depths and expressed as mean number/m<sup>2</sup> for the entire vegetation-free portion of the lake. The densities of pelagic invertebrates, expressed initially as mean number/m<sup>3</sup>, were converted to number/m<sup>2</sup> of lake surface area by assuming an average water depth of 1 m in the limnetic zone. The availabilities of benthic and pelagic organisms could then be expressed in similar terms of number/m<sup>2</sup> of lake surface area. Tank samples taken from the littoral zone were treated independently of the limnetic samples. As a result, two sets of selectivity indices have been calculated, the first for the limnetic invertebrates and the second for the littoral organisms. Estimates of  $r_i$ , the relative abundance of any given food item in the ration of the fish, were determined from analysis of trout stomachs obtained in the diel netting experiments. Results of the 1200, 1500 and 1800 hr. net sets were used to calculate

daytime selectivity while nighttime selectivity was determined from fish caught at 2100, 2400 and 0300 hrs. It was assumed that the 25-30 stomachs analyzed were representative of the population of stocked fish during that sampling interval.

Table 3. Summary of 1971 Lake 3 invertebrate sampling schedule.

Date	Sampling interval(hrs.)	Gear used	Number of samples	Depth of samples(m)
June 22	1530-1630	Multiple corer	3	0.9,1.2,1.5
"	"	Schindler trap	8	0.6,0.9,1.2,1.5
"	1630-1715	Tank	1	0.5
June 23	0015-0130	Multiple corer	3	0.9,1.2,1.5
"	"	Schindler trap	8	0.6,0.9,1.2,1.5
July 29	1300-1500	Multiple corer	6	0.9,1.2,1.5
"	"	Schindler trap	18	0.6,0.9,1.2,1.5
"	1030-1130	Tank	2	0.3,0.7
July 30	0100-0230	Multiple corer	6	0.9,1.2,1.5
"	"	Schindler trap	18	0.6,0.9,1.2,1.5
Aug. 30	1630-1715	Multiple corer	6	0.9,1.2,1.5
"	1345-1445	Schindler trap	18	0.6,0.9,1.2,1.5
"	1500-1545	Tank	2	0.3,0.7
Aug. 31	0100-0345	Multiple corer	3	0.9,1.2,1.5
"	"	Schindler trap	18	0.6,0.9,1.2,1.5

## Rates of Gastric Digestion

Gastric digestion rates of rainbow trout were determined during the summers of 1970 and 1971 using field laboratory facilities. Two large, 500 l. rectangular tanks ("Living Streams"<sup>1</sup>) each equipped with a 1 h.p. cooling and circulating unit ("Min-O-Cool"<sup>2</sup>) were used for all experiments. When greater than ambient water temperatures were required, an immersible water heater was employed. It was thus possible to obtain fairly precise control of water temperature; resultant fluctuations did not exceed  $\pm 0.5^{\circ}\text{C}$ . The tanks were cleaned and refilled with filtered Lake 3 water upon completion of each digestion experiment. Rainbow trout were held in a nylon mesh cage in Lake 3 and transferred to the laboratory when required.

A total of 17 experiments were completed in assessing the effects of water temperature, meal size, food type, and fish size on the rate of gastric digestion in rainbow trout. Pertinent information on the experiments undertaken is given in Table 4. The experimental procedure used was similar to that of Brett and Higgs (1970) in which a large group of fish, fed initially to satiation, was sampled at regular intervals until digestion was complete. A sample taken immediately after the fish had been fed provided an estimate of the average amount of food consumed by the fish. Four or more subsequent samples were usually taken, each consisting of 6-10 fish. The trout were starved for 36-72 hours before testing to ensure that the stomachs were completely empty.

---

<sup>1</sup>Model MT 700, Frigid Units Inc., Toledo, Ohio

<sup>2</sup>Model DL 100, Frigid Units Inc., Toledo, Ohio

Fish transferred from the caged stock were acclimated gradually to the laboratory conditions. Water temperatures were increased or decreased at the rate of 1-2C per day until the required temperature was reached. The fish were fed daily, always with the food type to be used in the digestion experiment. Small fish became readily accustomed to the artificial environment and fed voluntarily at all times. This was not the case with the larger fish, however, and several experiments were terminated because of the reluctance of many individuals to consume the food offered. It was possible to complete only one experiment using large fish ( $\bar{x} = 99\text{g.}$ ) and for this a somewhat different approach was taken. Using the same set-up as outlined for the selectivity experiments, individual trout were transferred from their holding tank to the clear aquarium once or twice a day and offered quantities of live amphipods. After  $2\frac{1}{2}$  weeks most fish fed voluntarily and it was then possible to complete the digestion experiment. Each fish was fed a predetermined weight of fresh amphipods and then autopsied at the desired interval. Fish from each sample were weighed and their stomach contents transferred immediately to labelled vials containing 10% formalin. The contents from each sample were pooled and dry weights determined. Data were compiled as the dry weight of food remaining in the stomach expressed as a percentage of dry body weight (index of stomach fullness). Each measurement was then converted to a percentage of initial food consumption to facilitate graphic comparisons. This was considered necessary because satiation levels for trout at different temperatures varied considerably, making direct comparison of digestion curves difficult.

Differences between slopes of the linear regressions of the natural logarithm of percent digestion on time were tested by the analysis of covariance. Appropriate tests were made to evaluate the effects of water

temperature, food type, meal size, and fish size on rates of gastric digestion.

Table 4. Summary of dates, water temperatures, food, fish size, and variables considered in laboratory experiments on digestion rates of rainbow trout.

Experiment	Date	Mean wt. of fish(g)	Temp. (C)	Food	Number of fish in expt.	Initial ration as % body wt.	Experimental variable
A	May, 1971	4	5	amphipods	71	4.2	Temp., fish size
B	Aug., 1970	23	5	amphipods	30	-	"
C	Aug., 1970	4	12	amphipods	20	-	"
D	May, 1971	3	12	amphipods	60	4.4	"
E	June, 1971	39	12	amphipods	49	1.2	"
F	June, 1971	4	17	amphipods	71	6.2	Temp., meal size
G	July, 1971	8	17	amphipods	65	4.1	"
H	July, 1971	6	17	amphipods	50	1.9	Meal size
I	Sept., 1970	20	17	amphipods	20	-	Temp.
J	Aug., 1971	99	17	amphipods	14	-	Temp., fish size
K	June, 1971	8	17	cladocerans	50	2.1	Food type
L	Aug., 1971	19	17	<u>Chaoborus</u>	23	1.5	Food type
M	July, 1971	7	17	artificial	60	8.9	Food type
N	May, 1971	20	17	amphipods	52	1.0	Temp., fish size
O	July, 1971	8	17	artificial	68	8.9	Food type
P	May, 1971	3	22	amphipods	50	2.5	Temp., fish size
Q	June, 1971	35	22	amphipods	50	1.4	"

## Food Consumption

Estimates of daily and seasonal food consumption of Lake 3 rainbow trout were obtained from knowledge of the diel pattern of stomach fullness and of gastric evacuation rates. Only results from the 1971 diel netting experiments were considered. The method used involved the determination of the amount of food consumed for each 3 hour interval over a 24 hr. period and the subsequent summing of each quantity to obtain a figure for daily consumption. A generalized form of the equation employed is as follows:

$$C = \sum_{i=1}^n [(I_i - I_{i-1}) + D]$$

where:

C = daily food consumption as a % of dry body weight

$I_i$  = index of stomach fullness at the end of the  $i^{th}$  interval  
(i.e. g dry wt food/100 g dry wt. fish).

$I_{i-1}$  = index of stomach fullness at the start of the  $i^{th}$  interval

D = amount digested during the interval (expressed as g.  
dry wt digested/100 g dry wt. fish).

n = number of intervals.

When  $(I_i - I_{i-1}) + D$  was a negative quantity, consumption for the interval was taken to be zero. The regression coefficient required to calculate D was obtained from Figure 8 by interpolation and inserted into the exponential equation  $\ln W = \ln W_0 - bT$ . Since the average water temperatures in Lake 3 at the time of each diel netting usually deviated from the laboratory temperatures used in the digestion experiments, the need for interpolating "b" values become obvious.

The validity of the results obtained using this method is

dependent on the following assumptions:

1. the diel pattern of stomach fullness for each sampling period, as indicated by gill net catches, is quantitatively representative of the Lake 3 trout population at that time.

2. the results of laboratory experiments on rates of gastric digestion are applicable under actual field conditions.

To evaluate this technique, determinations of daily food consumption were completed using 3 other methods. Foerester and Ricker (1948) estimated the food turnover rate of Cultus Lake sockeye to be approximately 4 during the summer months. This method was applied to Lake 3 trout by multiplying the mean stomach content weight for each of the June-Sept. diel experiments by a factor of 4. A modification of this approach, as described by Sandercock (1969), was also applied to the Lake 3 results using the equation,

$$\text{Daily ration} = \frac{\text{Wt. of food in digestive tract(g)}}{\text{wt. of fish(g)}} \times \text{Turnover rate} \times 100$$

where, weight of food in the digestive tract = weight of stomach contents x 2.6. A turnover rate of 3.0 was considered reasonable for trout at 19C.

A third series of determinations was undertaken using Winberg's (1956) balanced equation

$$R = (G + T)/p$$

where R = daily ration in percent dry weight, G = daily growth in percent dry weight, T = expenditure for metabolism, and p = correction for the incomplete utilization of the ration (=0.8). The expenditure for metabolism, T, can be determined from the well documented parabolic relationship between weight and metabolism given by,

$$Q = aW^k$$

where Q = rate of oxygen consumption (ml. O<sub>2</sub>/hr.), W = weight of the fish

(g) and a, k are constants. Average values of  $a = 0.30$  and  $k = 0.81$  are suggested for freshwater fish at 20C (Winberg 1956). The resting metabolism was corrected for water temperature using appropriate conversion factors and then multiplied by 2.0 to estimate metabolism in nature (Winberg 1956). Although several assumptions and generalizations are made, this method has the singular advantage of requiring only growth rate information since all other values can be extracted from the literature.

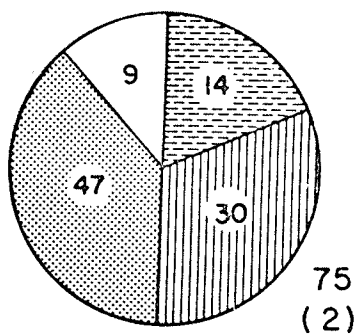
## RESULTS

### Food Habits

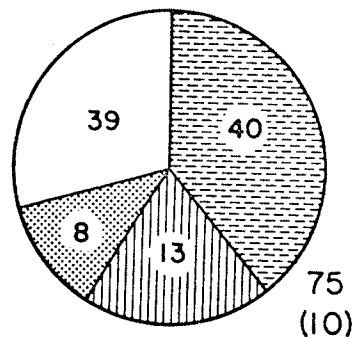
Stomach analysis of 529 rainbow trout caught during periodic diel gill netting on Lake 3 revealed a marked, though regular, variation in food habits during the period May through October, 1971 (Fig. 2). Amphipods, cladocerans, and chironomid larvae together comprised over 85% by weight of the total food eaten except on June 21-22 when dytiscid larvae and zygoptera naiads accounted for 38% of consumption. Food organisms which were consumed infrequently and therefore grouped together in one category include corixids, Chaoborus larvae, leeches, halipid beetles, Trichoptera larvae and gastropods. Terrestrial invertebrates, bottom debris, and plant material were found in the stomachs very rarely. Only 18 empty stomachs, 10 from the June 21-22 catches, were noted in the entire analysis. The incidence of amphipods increased with each sampling, comprising over 90% of the dry weight of food eaten from August through October. Young fish ( $\bar{x} = 6g$ ) relied heavily on chironomid larvae; however, by June 21-22 their incidence had declined to 8% by weight (consumption index of 12) and continued to decline over the remainder of the season. Cladocerans were utilized frequently until July but were rarely noted in the trout diet from August on.

Diel changes in the food consumption index, determined from the first four sampling periods, are illustrated in Figure 3. The diagrams indicate the relative importance of the various food organisms as a percentage of the total for each interval but in no way reflect the quantities of food consumed during different times of the day. There was little difference in the consumption index between morning, afternoon, evening, and night, the values for amphipods ranging from 41-57. The indices for chironomid larvae ranged from 12-19 and for cladocerans from

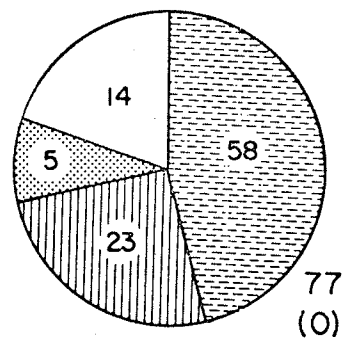
Figure 2. Relative importance of major food organisms in Lake 3 trout stomachs for the 1971 diel netting experiments, based on consumption index. Each diagram represents pooled results from 8 separate samples taken at 3 hr. intervals over a 24 hr. period. The number of stomachs examined and the number of empty stomachs is indicated at the lower right. Percent by weight (if  $>5\%$ ) is shown within each section.



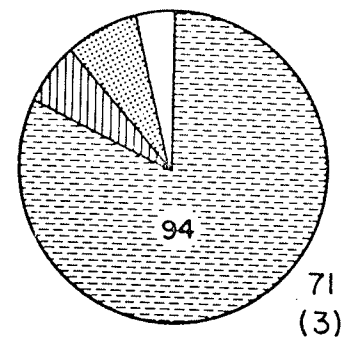
MAY 25-26, JUNE 2-3



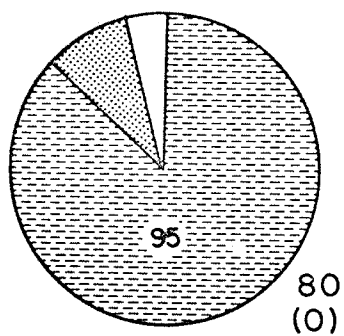
JUNE 21-22



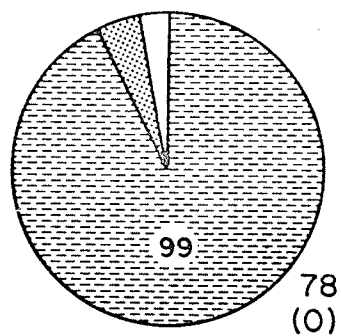
JULY 14-15



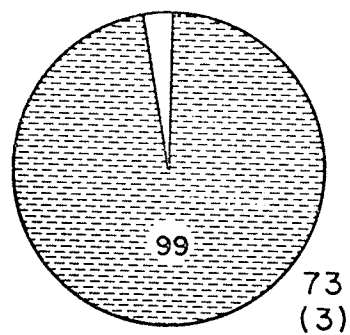
AUG. 9-10



AUG. 30-31



SEPT 20-21



OCT. 19-20

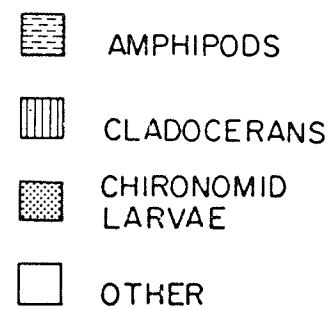
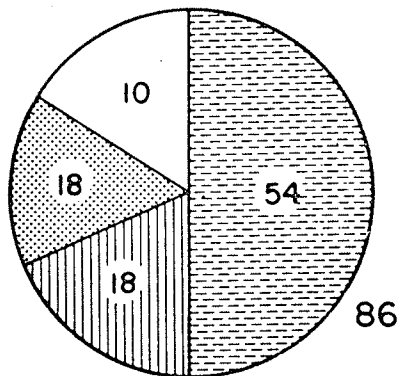
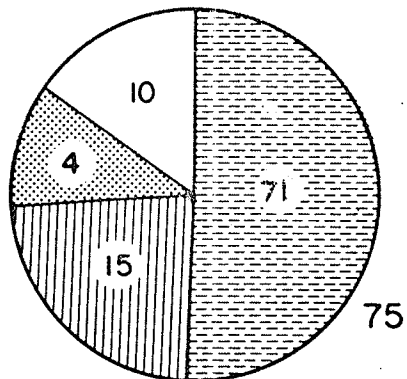


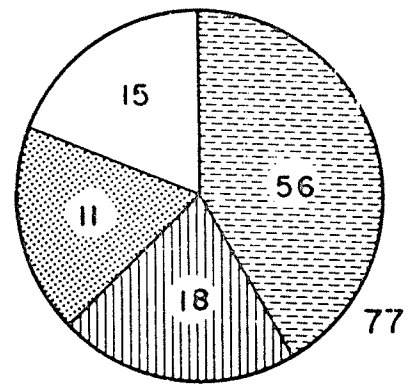
Figure 3. Relative importance (consumption index) of major food organisms in Lake 3 trout stomachs for the morning (0600 + 0900 hrs.), afternoon (1200 + 1500 hrs.), evening (1800 + 2100 hrs.), and night (2400 + 0300 hrs.) samples. Each diagram represents the combined data from the May 25-26 + June 2-3, June 21-22, July 14-15, and Aug. 9-10 diel netting experiments. The number of stomachs analyzed appears at the bottom right of each diagram and the % by weight (dry) of each organism is given within the appropriate section.



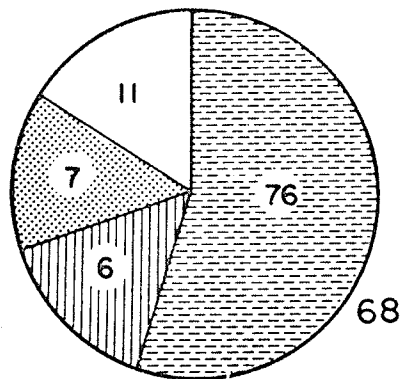
MORNING



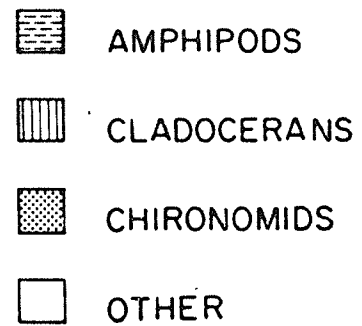
AFTERNOON



EVENING



NIGHT

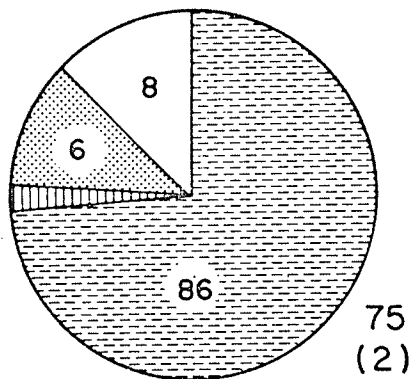


18-24. The highest and lowest values, for amphipods and cladocerans respectively, occurred at night. The importance of "other" items, mainly dytiscid larvae and zygoptera naiads remained remarkably constant.

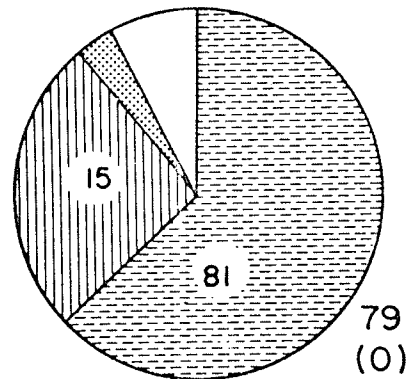
A comparison of consumption indices for Lake 3 trout caught during diel netting experiments on similar dates in two different years is shown in Figure 4. While cladocerans were absent from the late August and September fish in 1971 they constituted 15 and 23% by weight of the trout diet in 1970 (consumption indices of 26 and 27 respectively). The consumption index for chironomids changed little for the 3 dates during 1971 but a progressive reduction from 12 to 0 was evident in 1970. The increased incidence of corixids and Chaoborus larvae in 1970 is reflected in the slightly higher indices for the "other" category. Amphipods remained the most important food item.

Although other study area lakes were similar limnologically, there was considerable variation in the food habits of the trout populations (Table 5). The small number of stomachs analyzed and the absence of gravimetric data severely limits interpretation of these results, however, some general observations can be made. Except in Lake 58 on which Chaoborus larvae and gastropods were the main food items in July and August respectively, amphipods chironomid larvae and cladocerans comprised the bulk of the trout ration. In nearly every sample amphipods had a frequency of occurrence of 100% although it appeared that they did not constitute as large a portion of the total diet as in Lake 3 trout. The extent to which chironomid larvae were utilized appeared similar with the exception of Lakes 39 and 4 where their numbers were proportionately greater. For any given lake cladocerans were the major food items in either July or August but not both, with no consistent monthly pattern. All of the other aquatic invertebrates, shown to occur

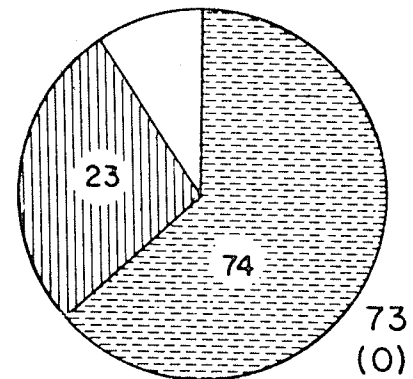
Figure 4. Relative importance (consumption index) of major food organisms in Lake 3 trout stomachs for similar sampling dates in 1970 and 1971. The total number of stomachs analyzed and the number of empty stomachs is given at the bottom right of each diagram. Percent by weight (if >5%) of each organism appears in the appropriate section.



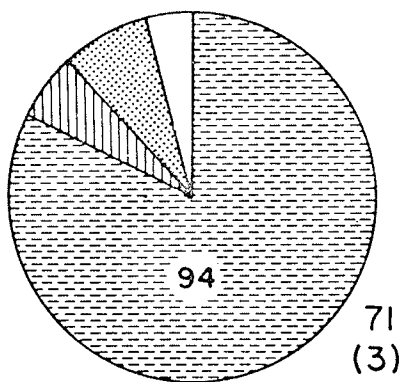
JULY 28-29, 1970



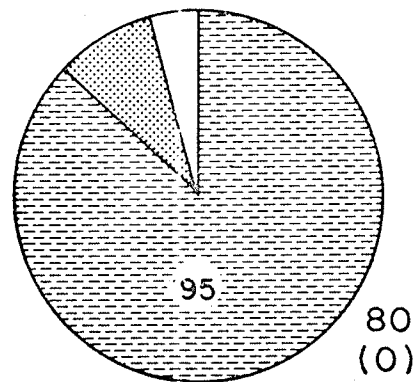
AUG. 25-26, 1970



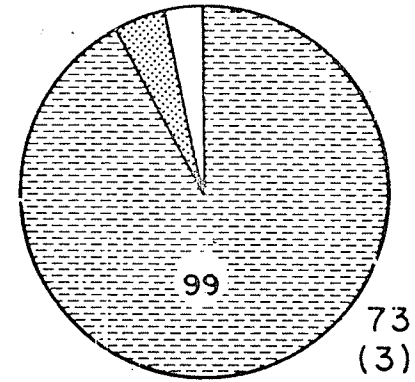
SEPT. 27-28, 1970



AUG. 9-10, 1971



AUG. 30-31, 1971



SEPT. 20-21, 1971

Table 5. Comparison of rainbow trout food habits in 6 study area lakes during July and August 1971.\*

ORGANISMS	LAKE 4				LAKE 41				LAKE 101				LAKE 9				LAKE 58				LAKE 39						
	July		August		July		August		July		August		July		August		July		August		July		August				
	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F	N	F			
Amphipoda	45	40	60	6	100	88	31	100	158	4	100	223	100	652	100	123	80	653	100	7	60	99	80	410	60	1098	100
Chironomidae	93	100	28	100	2	20	-	-	25	100	29	60	7	40	14	80	1	20	8	60	654	100	64	80			
Cladocera	1427	80	-	-	60	20	9	40	44	80	418	60	-	-	843	60	-	-	144	20	332	20	-	-			
Corixidae	4	60	-	-	30	60	1	20	-	-	10	40	256	80	1	20	145	100	-	-	11	80	-	-			
Chaoborinae	-	-	-	-	-	-	-	-	311	100	255	100	-	-	-	-	2014	80	-	-	6	20	-	-			
Dytiscidae	1	20	-	-	-	-	-	-	1	20	-	-	1	20	-	-	7	60	-	-	5	20	-	-			
Gastropoda	66	80	14	60	1	20	1	20	-	-	-	-	-	-	11	80	-	-	666	100	3	20	-	-			
Haliplidae	-	-	1	20	-	-	-	-	-	-	-	-	4	20	-	-	1	20	2	40	4	40	2	20			
Hirudinea	-	-	2	20	-	-	1	20	-	-	8	20	-	-	52	80	-	-	-	-	-	-	-	-			
Trichoptera	3	40	2	20	-	-	-	-	-	-	-	-	1	20	-	-	-	-	-	-	-	-	-	-			
Zygoptera	-	-	12	80	-	-	-	-	-	-	8	40	4	60	34	100	2	40	6	80	-	-	56	80			

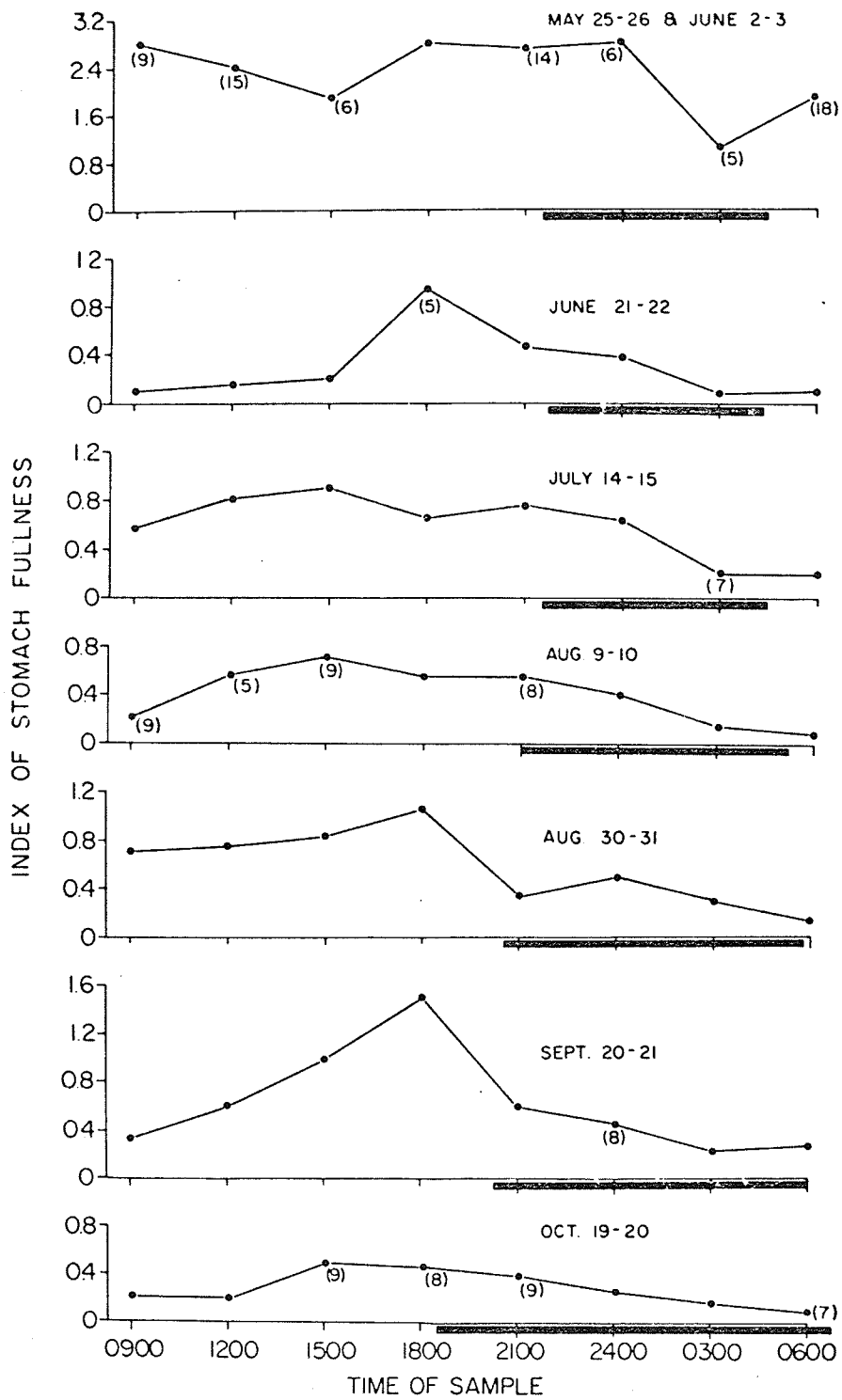
\*Based on analysis of 10 stomachs per lake. N = total number; F = percent frequency of occurrence.

infrequently in Lake 3 fish, appeared at one time or another in stomach analysis of fish from these other lakes but generally they made up a very small portion of the diet.

#### Feeding Periodicity

The diel pattern of feeding intensity, as indicated by changes in the index of stomach fullness over a 24 hour period, remained essentially the same for all sampling dates during 1971 (Fig. 5). With the exception of small, newly stocked trout (May 25-26 + June 2-3 sample) feeding appeared to be restricted to daylight hours. Minimum values of the index of stomach fullness invariably occurred at 0300 and 0600 hours indicating virtual cessation of feeding activity from 2400 to 0600 hrs. Feeding resumed prior to 0900, continuing throughout the day and into the evening. Peak periods of stomach fullness usually occurred between 1500 and 2100 hrs. although abrupt increases were the exception rather than the rule. Care must be exercised in associating stomach fullness with feeding intensity since erroneous conclusions could be drawn without knowledge of digestion rates, food size and sample size. Nonetheless it is clear that rainbow trout in Lake 3 exhibit a diurnal feeding periodicity with more or less continuous food consumption during daylight hours. The average quantity of food present in the trout stomachs as a percentage of body weight was highest for the small fish taken in late May and early June at 2.35. Average indices of stomach fullness for the other six sampling dates were 0.30, 0.57, 0.40, 0.58, 0.62 and 0.30. Fish size, water temperature and weather conditions at the time of sampling probably account for the observed differences.

Figure 5. Diel pattern of indices of rainbow trout stomach fullness for each 24 hour sampling of the Lake 3 population completed during the 1971 growing season. Unless otherwise indicated each point represents pooled results from 10 stomachs. Dark lines below time axis indicate hours of darkness.



## Feeding Selectivity

### Laboratory Experiments

Analysis of variance tests on feeding selectivity of similar size rainbow trout were completed for all laboratory experiments. The mean number of the various types of organisms consumed was significantly different for trout in the concealment-free and in the "natural" aquarium ( $F = 3.59, 4.20; P < 0.05$ ).

The average percent composition of the ration for both series of experiments is summarized in Table 6. In the clear aquarium the following organisms were consumed in decreasing abundance: chironomid larvae, amphipods, zygoptera naiads, Chaoborus larvae, and corixids. No gastropods were eaten. Observations of prey activity after their introduction into the clear aquarium, indicated that the assumption of equal accessibility did not entirely hold. Amphipods quickly sought out the corners and were captured by the trout only when they ventured into the water column or swam across the bottom of the aquarium. Corixids were usually very active swimmers and paused only briefly at the surface for air. Chironomid larvae were distributed more or less randomly about the bottom and, aside from periodic twisting and bending movements, were not particularly active. When zygoptera naiads left the bottom they swam slowly and appeared to be easy prey for the trout.

Composition of the ration changed considerably in the simulated natural environment (Table 6). Concealment was now available for the amphipods and zygoptera naiads as well as for the bottom dwelling chironomid larvae. This is clearly reflected in the very low consumption of chironomids (2% of the total) and in the greatly reduced consumption of amphipods and zygoptera naiads. Under these conditions corixids became the predominant food item, followed closely by Chaoborus larvae. It would

therefore appear that accessibility is the more important determinant in selective feeding and that preference plays a relatively minor role. Transformation of the results from Table 6 into selectivity indices clarifies this relationship (Table 7). Food preference (P) is calculated directly from the first series of experiments while selectivity (S) is determined from the second series. Since  $S = P + A$ , the accessibility factor (A) is easily tabulated. In all cases the value of S is influenced primarily by the accessibility component. The most outstanding result is that both chironomid larvae and amphipods have a strongly negative index in spite of their positive preference component. Zygoptera naiads also had a negative index as did the gastropods which were avoided in both experiments. The positive selectivity index for corixids and Chaoborus larvae probably results from the high availability component of each.

Table 6. Percent composition of the ration of rainbow trout allowed to feed for 2 hours in a clear, concealment-free aquarium ( $R_p$ ) and in an aquarium simulating natural conditions ( $R_n$ ). Each value is an average of 8 separate determinations.

Ration	Food Organism					
	Amphipods	Corixids	<u>Chaoborus</u>	Zygoptera	Chironomid larvae	Gastropods
$R_p$	23	11	17	21	28	0
$R_n$	5	42	41	10	2	0

Table 7. Comparison of selectivity indices (S) with their respective preference (P) and availability (A) components for six different food organisms.

	Food organism					
	Amphipods	Corixids	<u>Chaoborus</u>	Zygoptera	Chironomid larvae	Gastropods
S	-0.56	0.44	0.42	-0.26	-0.83	-1.00
P	0.16	-0.22	0.02	0.11	0.25	-1.00
A	-0.72	0.66	0.40	-0.37	-1.00	0

### Field experiments

To assess the feeding selectivity of the Lake 3 trout population techniques similar to those outlined above, were applied to the results of the invertebrate samples and corresponding diel netting experiments. It was necessary to calculate two series of selectivity indices, one for the large, open water area of the lake and another for the area of vegetation. The relative abundance of various invertebrates in the Lake 3 limnetic zone, determined from multiple corer and Schindler trap samples, is summarized in Table 8 along with the corresponding data on the trout ration. The submergent vegetation in Lake 3, consisting more or less exclusively of Ceratophyllum and Myriophyllum, was extremely dense and almost certainly excluded penetration by fish. This was confirmed by catches from gill nets set from within the vegetation to the open water area of the lake. Although most of the fish were taken well out from the edge of the vegetation, some were recovered in the transition zone, between littoral and limnetic water. Assuming that the majority of feeding occurred within the non-vegetated limnetic zone, as observation of gill net catches and analysis of stomach contents would suggest, the actual selectivity indices should closely approximate those presented in Table 9. Chironomid larvae had a strongly negative index on all sampling dates. Negative selectivity indices were also recorded for cladocerans on all but one sampling date. With a single exception, amphipods were positively selected. A few fish with a very large number of cladocerans in their stomachs account for the inconsistent index recorded for amphipods and cladocerans on August 30 and should be regarded as atypical.

If the assumption was made that trout feed only in the littoral zone, the selectivity indices for amphipods, chironomid larvae, and cladocerans become completely altered (Table 10). The indices for chironomid

larvae and cladocerans are then strongly positive while those for amphipods become negative. The -1 value for corixids, Trichoptera larvae, gastropods and leeches has little meaning and shows only that these organisms were not eaten. Allen (1941-b) considers the phenomenon of selectivity to apply only to those organisms which are abundant in the environment and are frequently encountered by the fish.

Table 8. Percent abundance of various food organisms in the Lake 3 limnetic zone (L) and in Lake 3 trout stomachs (F) for 3 sets of day-night samples taken during the summer of 1971.

Date	Time	Food organism													
		Amphipods		Cladocerans		Chironomids(l.)		Corixids		Dytiscids		Zygoptera		Chaoborus(l.)	
		L	F	L	F	L	F	L	F	L	F	L	F	L	F
June 22	Day	4.6	53.4	78.0	35.6	17.2	3.2	0.1	-	<0.1	6.9	-	1.0	<0.1	-
June 23	Night	5.5	14.3	80.2	77.8	14.1	0.1	0.1	-	<0.1	5.4	-	2.4	-	-
July 29	Day	37.8		41.1		20.9		0.1		-		-		<0.1	
Aug. 9	Day		64.1		30.0		5.8		-		-		-		<0.1
July 30	Night	56.6		20.4		23.0		<0.1		-		-		<0.1	
Aug. 10	Night		80.9		15.7		2.7		-		-		0.2		-
Aug. 30	Day	77.4	54.0	13.9	41.2	8.5	4.4	<0.1	-	-	-	-	0.3	<0.1	<0.1
Aug. 31	Night	73.3	99.2	18.5	-	7.9	0.7	<0.1	-	-	-	-	0.1	<0.1	-

Table 9. Comparison of selectivity indices for amphipods, cladocerans and chironomid larvae, assuming that feeding of Lake 3 rainbow trout was restricted to the limnetic zone. Index values were determined from data in Table 8.

Date	Time	Food Organism		
		Amphipods	Cladocerans	Chironomid larvae
June 22	Day	0.84	-0.37	-0.69
June 23	Night	0.44	-0.02	-0.99
Aug. 9	Day	0.26	-0.16	-0.57
Aug. 10	Night	0.18	-0.13	-0.80
Aug. 30	Day	-0.18	0.50	-0.32
Aug. 31	Night	0.15	-1.00	-0.84

Table 10. Comparison of selectivity indices for various food organisms in Lake 3 assuming the trout fed only in the littoral zone.

Food Organism	Date		
	June 22	August 9	August 30
Amphipods	-0.19	-0.22	-0.29
Cladocerans	0.33	1.00	1.00
Chironomid larvae	0.56	0.78	0.76
Corixids	-1.00	-1.00	-1.00
Trichoptera	-1.00	-1.00	-1.00
Hirudinea	-1.00	-1.00	-1.00
Gastropods	-1.00	-1.00	-1.00

## Rates of Gastric Digestion

The relationship between quantity of food remaining in the stomach and the time interval after feeding clearly was not linear. Curvilinear regressions were applied to the data using the equations,

$$W = W_0 T^b \quad (1)$$

$$W = W_0 e^{-bT} \quad (2)$$

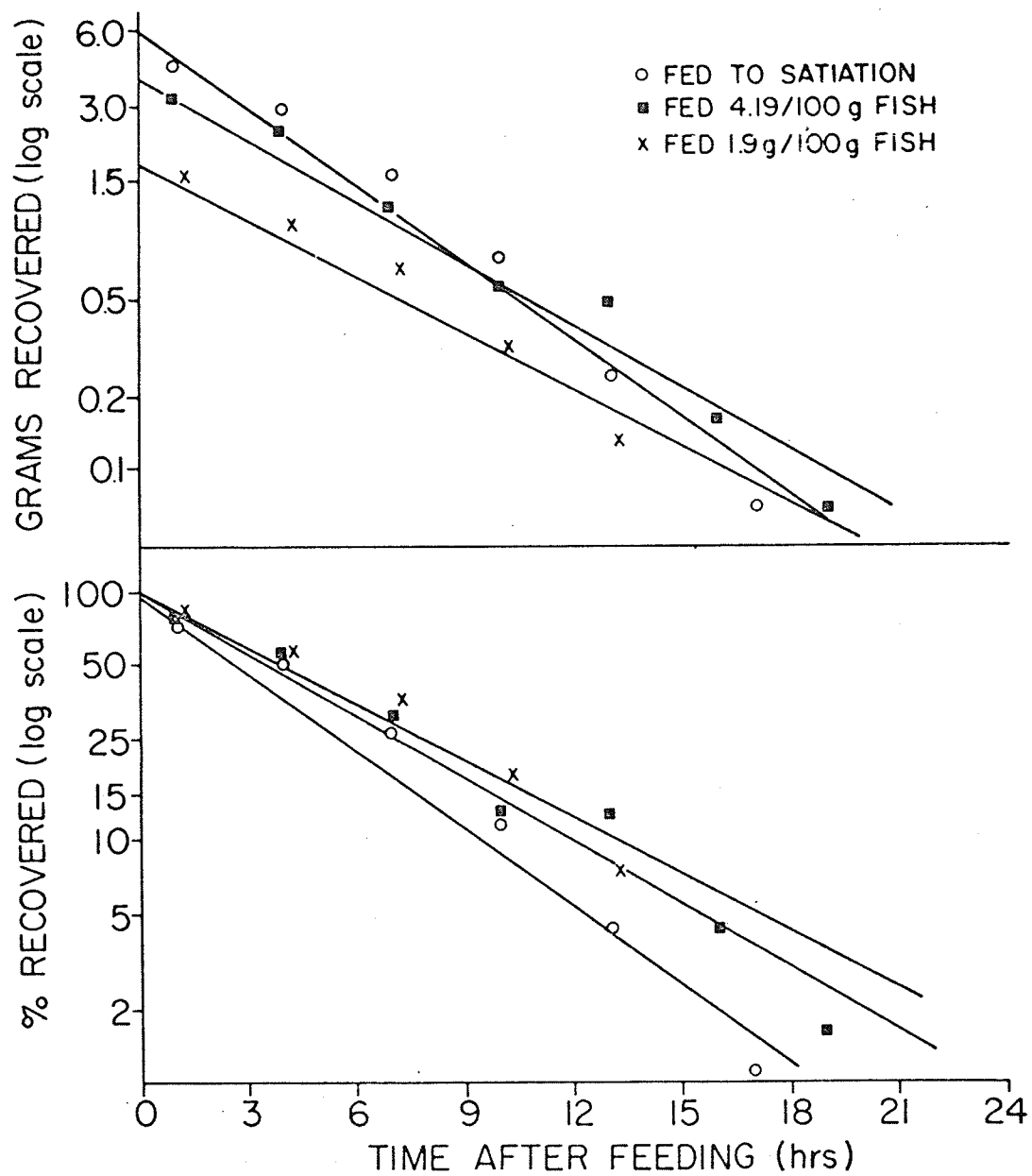
where  $W$  = grams dry weight of food remaining in the stomach per 100 g dry weight of fish,  $W_0$  = initial quantity of food consumed (g.food/100g fish),  $b$  = regression coefficient and  $T$  = time after feeding. The correlation coefficients in all cases were much higher using the negative exponential (2). The range of  $r$  values for all 18 digestion experiments, based on the exponential regression, was 0.92 to 0.99. Logarithmically transformed values of the dependent variable however, when plotted against time did not produce a straight line as expected but showed a slightly curved response. The curvilinearity was due mainly to the initial values being somewhat higher than predicted by an exponential. The consistency of this phenomenon in the digestion experiments indicates that there exists a definite lag in digestive activity after food is consumed. Using the method described by Snedecor and Cochran (1968), tests of the significance of departure from linear regression of the transformed data were made on experiments at all temperatures. In 6 of 8 experiments tested, linear regression could not adequately account for the observed relationship between percentage depletion and time. This implies that an equation of the form,  $W = a_0 + a_1 T + a_2 T^2$  more accurately describes the relationship and that the exponential is not really a valid model. Although superior for predictive purposes, the polynomial was rejected for use in this study; it is an empirical rather than a rational equation and is therefore not representative of any real biological phenomenon (Alger 1969; Sokal and

Rohlf 1969). Considering the substantial variation in digestion rate of individual fish, even under identical conditions, and the basic nature of the study itself, the errors incurred by using the somewhat imperfect exponential model are not great. The primary consequence of its use is to increase the error mean square in covariance analysis, thereby reducing the opportunity for detecting significant differences.

#### Effect of meal size

The effect of meal size on depletion rates of small trout (3-10g) was tested in 3 experiments in which the water temperature was a constant 17C. Amphipods were used as food. In the first experiment the fish were allowed to feed to satiation, the average initial consumption being 6.19g dry weight of amphipods per 100g dry weight of fish, while in the other two, feeding was terminated short of satiation, at levels of 4.06 g/100g and 1.86g/100g. Quantities remaining after successive 3 hour intervals are plotted in Figure 6, first as dry weight of food per 100g dry weight of fish and subsequently as percentage of initial meal size. Regression analysis of the data from the 3 experiments yielded instantaneous depletion rates (b values) of -0.240, -0.193, and -0.178 respectively. When tested by the analysis of covariance the slopes were not significantly different ( $F = 3.03$ ,  $P > 0.05$ ). Since the percentage depletion curves (Fig. 6, panel 2) are statistically indistinguishable, it appears that the rate at which food leaves the stomach is independent of meal size for any given temperature. In other words, rate of depletion is proportional to the remaining mass of undigested food. Although this theoretically implies that digestion would never be complete, the mechanical action of peristalsis is capable of eliminating small quantities of food which remain in the stomach (Brett and Higgs 1969).

Figure 6. Stomach depletion rates of rainbow trout fed 3 different size meals of amphipods at a constant water temperature of 17C. Depletion is plotted first as g dry wt. food/100g. dry wt. fish and subsequently as % initial meal size vs. time. Each point is based on the mean dry weight of amphipods recovered from 8-10 stomachs. Lines are fitted negative exponentials.



Assuming the above results valid, all indices of stomach fullness (g dry wt. of food/100 g dry wt. of fish) were converted to percentages of initial consumption to facilitate graphic comparisons. Because of the previously mentioned lag in digestion, "a" values were consistently higher than 100 when regressions were rerun using percentages. To force the regression through 100 percent at 0 time the duration of this initial lag was calculated for each experiment and the independent variable adjusted accordingly. Although this had the effect of eliminating the lag phase from the regression analysis, the resultant differences in regression coefficients were very slight. The length of the lag in each case was determined by fixing  $P_0$  at  $\ln 100$  and calculating T in the linear equation,  $\ln P = \ln P_0 - bT$ , where  $P = \% \text{ remaining at time } T$  and  $P_0 = \% \text{ remaining at 0 time}$ . Generally, the time lag decreased with increasing temperature but all determinations fell within the range 0.5 to 3.0 hours.

#### Effect of water temperature

Data from experiments repeated within temperature acclimation levels were pooled and a single regression calculated for each. This was done after analysis of variance F tests revealed no significant difference between depletion rates of the individual regressions. The results of experiments at four water temperatures are illustrated in Figures 7 and 8. The 5, 12, 17, and 22°C curves represent combined data from 2, 3, 4, and 2 experiments respectively. Amphipods were used as food in all cases. As expected, the rate of gastric evacuation increased with temperature, the proportional increase being greatest at the lower temperatures. For example, evacuation was approximately 3 times more rapid at 12°C than at 5°C but only 1.7 times more rapid at 22°C compared to 17°C. The corresponding regression coefficients (instantaneous depletion rates), also plotted in

Figure 7. Percent depletion of amphipods from rainbow trout stomachs at temperature acclimations of 5,12,17, and 22C. Each point represents the dry weight of amphipods recovered from 6-10 stomachs, expressed as a % of initial consumption. Repeated experimental values are indicated by separate symbols. Curves are fitted negative exponentials.

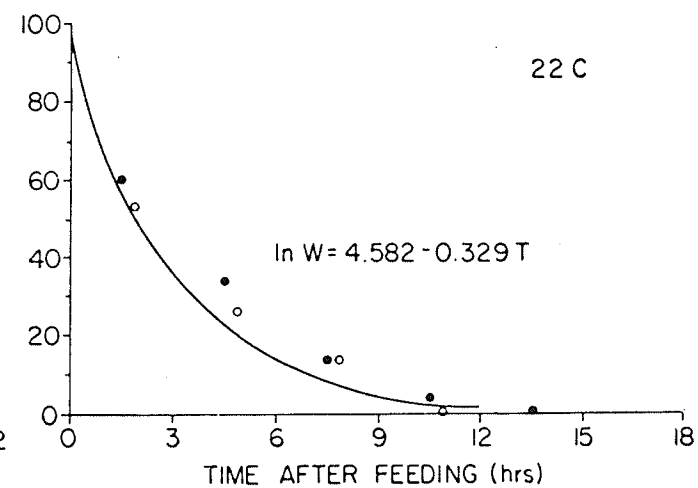
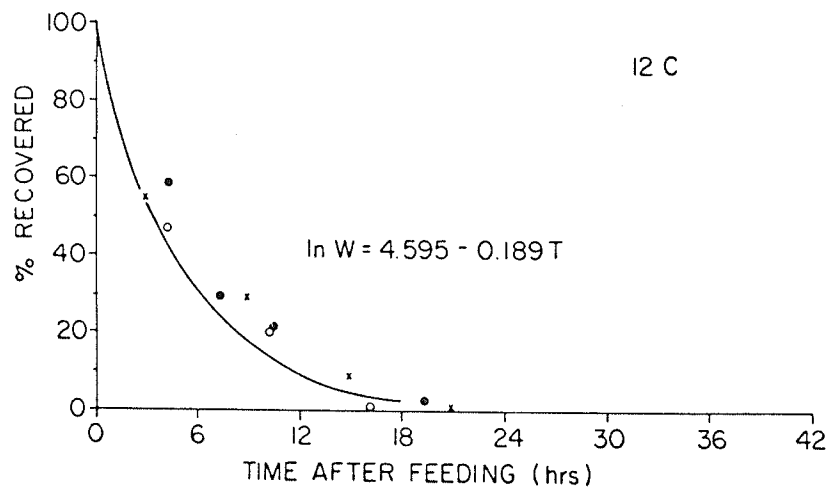
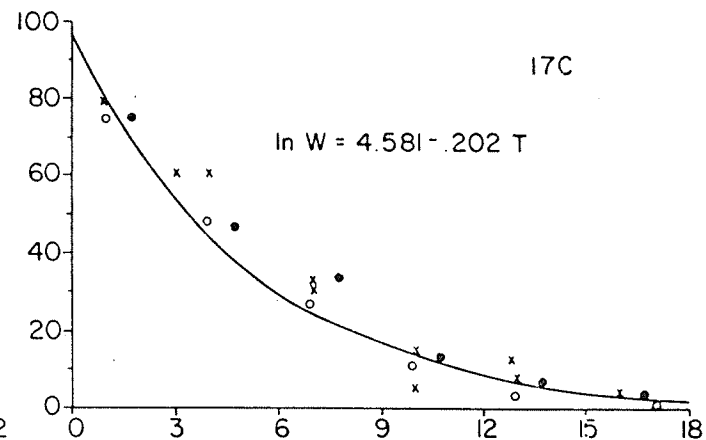
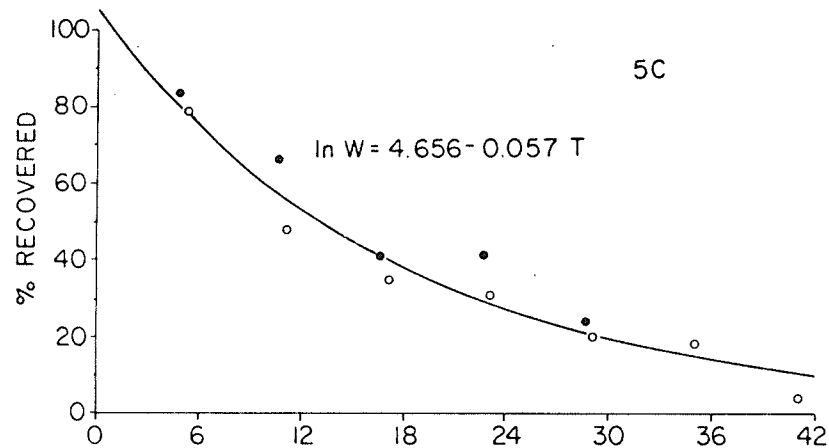


Figure 8. Relation between time to 95% digestion, instantaneous depletion rates, and acclimation temperature for similar size rainbow trout. Curves are fitted by eye.

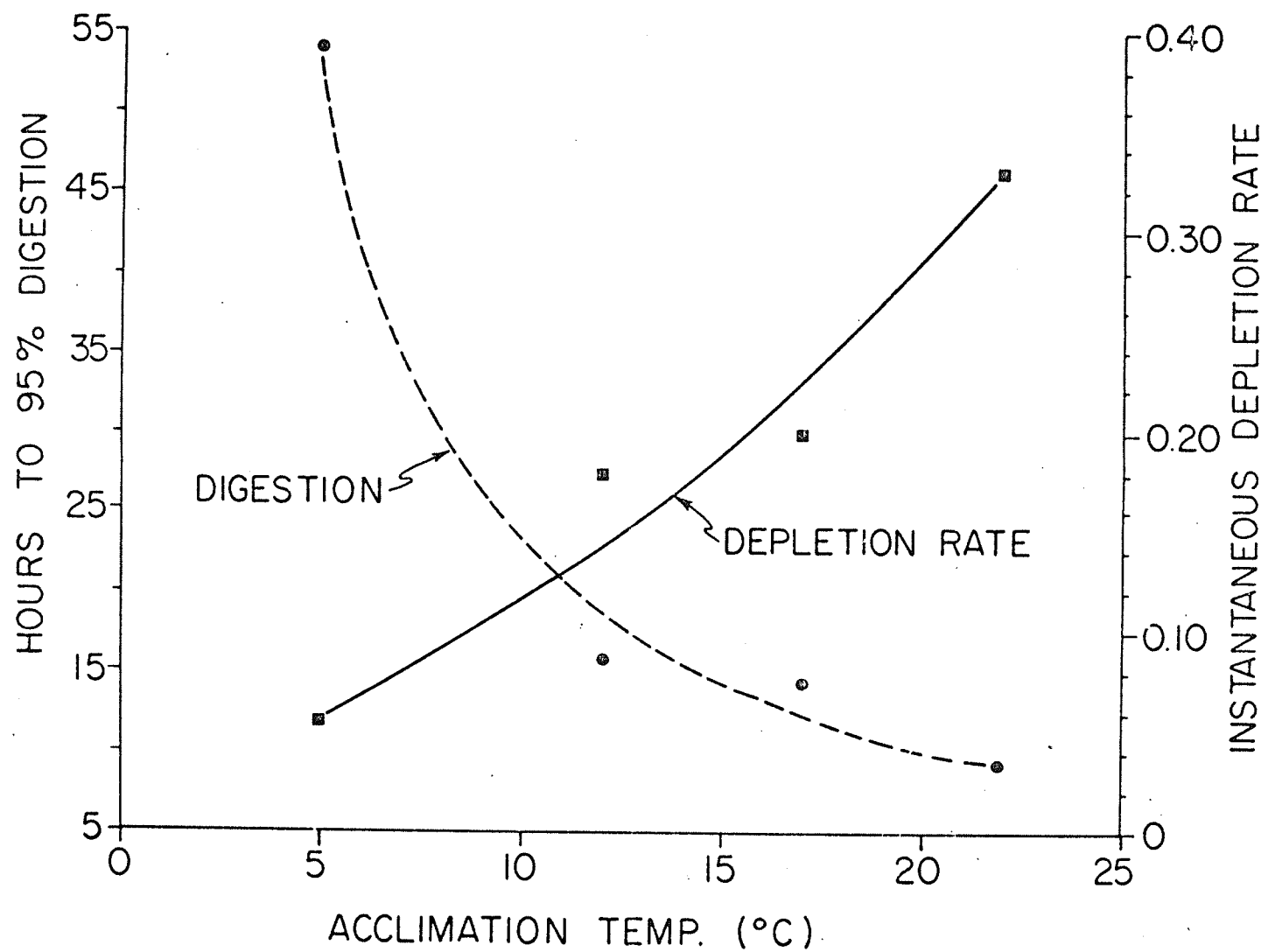


Fig. 8, in addition to confirming this relationship, provide a means of estimating digestion rates at other temperatures. This is necessary in order to calculate daily consumption when there is a deviation between actual and experimental water temperatures. More experiments at intermediate temperatures are required to give these estimates greater reliability. To determine whether observed differences in gastric evacuation at the four acclimation temperatures were statistically significant, analysis of covariance tests were performed on the appropriate combinations. The results are summarized in Table 11. No significant difference in instantaneous depletion rate could be detected between the 12 and 17°C experiments ( $F = 0.40$ ;  $P > 0.05$ ). However, the differences between 5 and 12°C and between 17 and 22°C were highly significant at the 0.01 level ( $F = 51.04$  and  $19.54$ ).

#### Effect of food type

Amphipods, cladocerans, Chaoborus larvae, and artificial food were used in separate experiments to evaluate the possible influence of food type on digestion. Instantaneous depletion rates for the natural organisms were very similar (Fig. 9) and no significant difference could be detected between them (Table 11). Replicated experiments using artificial food indicated a highly significant decrease in evacuation time ( $F = 107.6$ ;  $P < 0.01$ ). The pellets required 37 hours, as compared to about 15 hours for natural foods, to undergo 95% digestion at a water temperature of 17°C.

#### Effect of fish size

Within the range of fish size tested in the laboratory experiments it was not possible to relate digestion rate to fish size. The highest  $F$  value resulted from a comparison of 12.8 and 98.8 g trout held at 17°C but the difference was not statistically significant (Table 11). Comparison

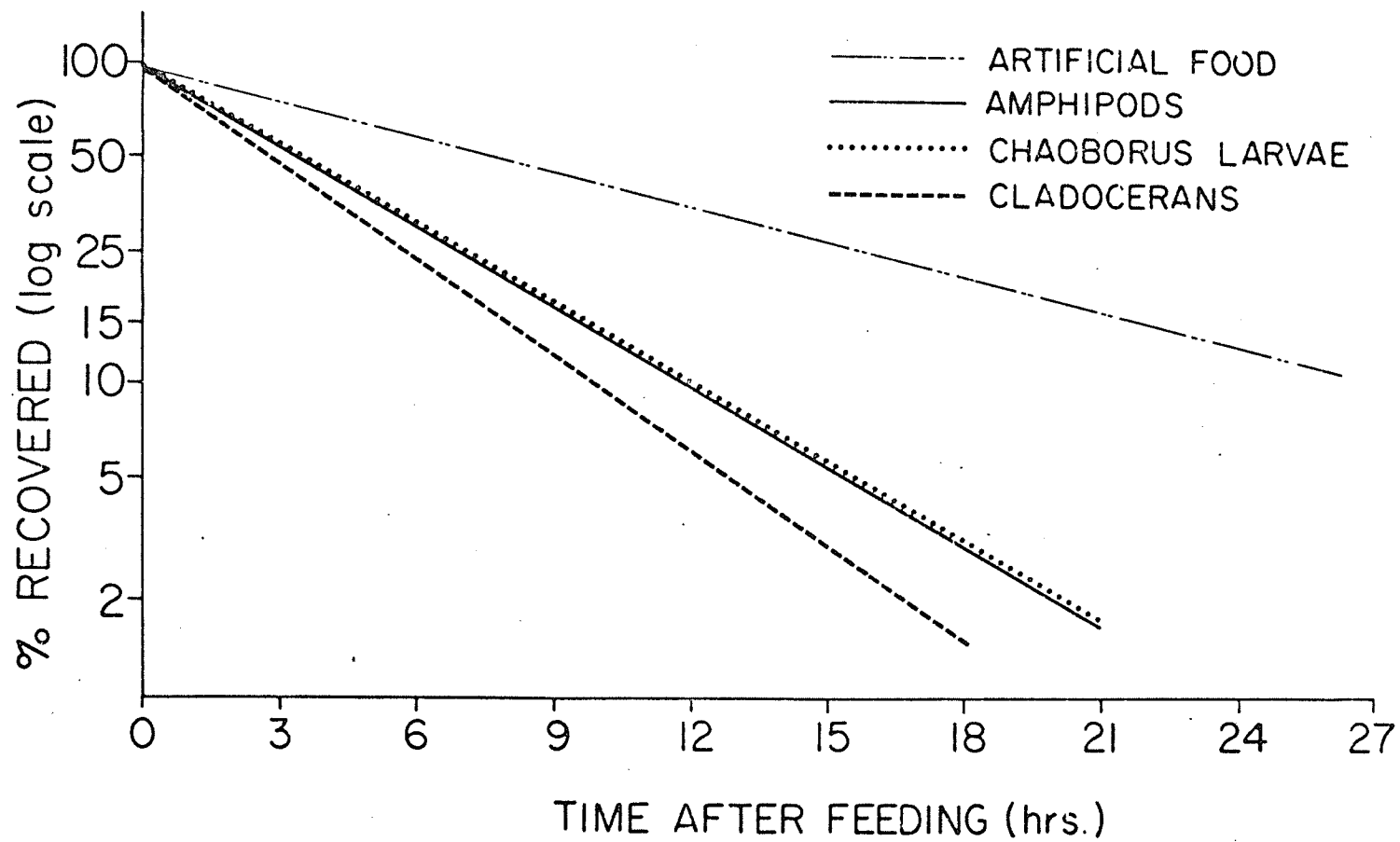
at 12C and 22C yielded F values of 0.64 and 0.04 respectively. Further experimentation, especially with larger fish, might possibly reveal a significant relationship here.

Table 11. Summary of analysis of covariance tests for differences in gastric digestion rates of rainbow trout.

Variable	Comparison	F
Meal size	6.2 g vs. 4.1 g. vs. 1.9 g	3.03
Temperature	5C vs. 12C	51.04**
	12C vs. 17C	0.40
	17C vs. 22C	19.54**
Food type	Amphipods vs. cladocerans	0.04
	Amphipods vs. <u>Chaoborus</u>	0.07
	Amphipods vs. artificial food	107.60**
Fish size	3.3g vs. 38.6g (12C)	0.64
	5.9g vs. 19.7g (17C)	0.54
	12.8g vs. 98.8g(17C)	2.91
	3.3g vs. 35.2g (22C)	0.04

\*\*P < 0.01

Figure 9. Comparison of gastric digestion rates for similar size rainbow trout fed different foods. All experiments were conducted at 17C. Lines are fitted negative exponentials.



## Food Consumption

A summary of the estimated daily food consumption of Lake 3 rainbow trout, obtained by four separate methods of calculation, is shown in Table 12. The individual results, presented for all 7 diel sampling periods, reflect seasonal variations in water temperature and fish size as well as variability due to local conditions at the time of sampling. The first three methods are similar in that they are based on observed quantities of food in the trout stomachs while Winberg's method is dependent only on a knowledge of growth rate. Since the turnover rate of stomach contents given by Foerster and Ricker (1948) for Cultus Lake sockeye salmon was estimated for a mean water temperature of 19C, use of their method was restricted to similar thermal periods in Lake 3. From the estimates of daily consumption completed in this way it is obvious that this approach yields results which are consistently lower than any of the others. Values derived using the method proposed in this study are somewhat higher but not nearly as high as those obtained using Sandercock's computational technique. The difference between the two latter methods appears to diminish with decreasing temperature. Clearly the estimates of daily ration produced by Winberg's balanced equation are considerably greater than those using the Foerster-Ricker method or those obtained by the study method but generally only a little higher than estimates using Sandercock's equation. Further interpretation of these results and possible reasons for the observed variations will be presented later.

The available data on daily ration were applied to the determination of total seasonal food consumption and the corresponding food utilization coefficient for Lake 3 trout. Two estimates of each were obtained, one using results from the study method and the other from Winberg's balanced

equation. The resultant estimates of total food consumed, on a wet weight basis, from May 5 to October 20, 1971 for a single fish were 277g and 593g respectively, a difference of nearly 120%. The corresponding food utilization coefficients, that is, the percentage of the total ration used for growth, were 76% and 35%.

Table 12. Comparison of estimated daily food consumption of Lake 3 rainbow trout using four different methods of computation.

Sampling date	Mean Fish wt(g)	Water Temp. (c)	Daily ration as % dry body weight			
			Study method	Foerster & Ricker	Sandercock	Winberg
May 25-26 + June 2-3	6.3	14.5	8.43	-	11.96	-
June 21-22	40.6	18.8	1.39	1.19	2.32	10.06
July 14-15	61.3	18.5	2.73	2.30	4.48	5.52
Aug. 9-10	107.7	19.0	1.77	1.60	3.12	5.87
Aug. 30-31	133.5	19.1	2.66	2.33	4.54	4.13
Sept. 20-21	184.8	14.1	2.36	-	3.31	3.77
Oct. 19-20	210.1	8.1	0.67	-	0.90	1.36

## DISCUSSION

### Food Habits

A variety of techniques have been developed for the express purpose of assessing the importance of various food organisms in a fish's diet. These methods have been evaluated by Lagler (1956), Hynes (1950), and Windell (1968) and will not be discussed here. Since each method has its own advantages and disadvantages the one(s) chosen for a study should reflect the particular requirements of that study. The consumption index used in the present study has not received wide application but is considered superior to methods in which numerical and gravimetric (or volumetric) data are presented separately. However, an analysis of food habits per se may be quite meaningless unless the characteristics of the predator and prey species and the dynamics of the invertebrate populations are considered. For this reason, food habits and feeding selectivity of Lake 3 trout cannot be discussed separately without some degree of overlap. Nonetheless, to maintain consistency and organization of format, these topics have been dealt with independently.

#### Temporal food habits

Amphipods were the most important food organism consumed by Lake 3 trout on all 1971 sampling dates except May 25-26 + June 2-3 when chironomid larvae and cladocerans predominated. All food organisms, other than amphipods, declined steadily in importance from May through October and after mid-August constituted a negligible portion of the total diet.

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. It is difficult to establish which of the above factors is responsible for the observed variations in the consumption index of cladocerans and amphipods. From 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. This alone may account for the extent to which these organisms were utilized by the trout. It is also possible that the higher consumption index of zooplankton in May and June is directly related to fish size, i.e. the smaller trout consumed smaller food organisms. Similar size-dependent responses have previously been recorded for rainbow trout by Swift (1970), Ide (1943) and Hartman (1958). Regardless of the explanation, the lower consumption of amphipods during May and June is significant in terms of the breeding habits of these crustacean invertebrates. Gammarus lacustris has an annual life cycle with each female usually bearing a single brood, the size of which is dependent on body length (Menon 1966). According to Biette (1969) most of the young gammarids in West Blue Lake, Manitoba had been released by late June and reproduction was complete by early July. Because water temperature in study area lakes increased rapidly, recruitment of new individuals occurred somewhat earlier than in West Blue Lake. The effect of water temperature on incubation time in amphipods is well documented (Clemens 1950; Cooper 1965). Predation on the Gammarus population is less intense during the reproductive period; thus there is a larger prey population available to the trout in subsequent months. There is also a greater potential for maintaining high population levels since more adults are likely to overwinter and be available to reproduce the following spring.

The continuous temporal reduction in the consumption index of larval chironomids is almost certainly a function of availability since their density decreased steadily from a high of  $9,970/\text{m}^2$  on June 22 to  $2,870/\text{m}^2$  on August 30. The fairly high consumption of dytiscid larvae indicated in the June 21-22 samples likely reflects the susceptibility of this

organism to predation, as well as their high incidence of occurrence at that time. When observed in the aquarium they underwent regular vertical movements and swam with slow, exaggerated motion.

Rainbow trout have been described by Leonard and Leonard (1949) and McAfee (1966) as versatile, opportunistic feeders, capable of exploiting a variety of food sources. The restricted number of species utilized by the Lake 3 trout is probably indicative of an abundant food supply. Other studies report high percentages of vegetation (Wales 1946; Surber 1937) and terrestrial insects (Swift 1970) in the stomachs of lake dwelling rainbow. Except for isolated cases both these food components were absent from the diet of Lake 3 fish, however both were certainly available. Although some adult chironomids were found in the stomachs of the June 21-22 samples, corresponding to an extremely heavy emergence near that time, their importance, as a percentage of total food consumed, was negligible. There was no apparent shortage of available food as only 18 of 529 trout stomachs from Lake 3 were empty in all 1971 samples. This represents a much lower percentage than normally recorded for lake dwelling fish (Ball 1948; Falk 1971). The majority of empty stomachs were noted in the June 21-22 samples when feeding activity appeared to be much below the expected level. Unusually high water temperatures may have contributed to this depression in food consumption.

Little difference was noted in the food habits of Lake 3 trout in 1970 and 1971 except that an increased consumption of cladocerans, Chaoborus larvae, and corixids was evident in 1970. Although invertebrate samples were not taken in 1970 the increase in consumption of cladocerans is likely a function of availability (i.e. abundance). The reduced growth of Lake 3 trout in 1970 (Appendix A-1) may have been related to this variation in food habits. Nikolsky (1963) suggests that the energy

expended in obtaining food is much greater when large fish are required to consume numerous small organisms and, as a result, most maturing, predaceous fishes abandon zooplankton as a food source and switch to larger organisms. In a Swedish lake where zooplankton afforded the only major food supply, Nilsson (1965) found that char growth was markedly reduced.

It is difficult to present a meaningful interpretation of the food habit information collected from other study area lakes since sample size was limited and only numerical data were recorded. It would appear that, in comparison with Lake 3 fish, a wider range of food organisms was utilized. However, without some knowledge of their relative abundance, one cannot postulate whether the increased consumption of food items other than amphipods and cladocerans is indicative of lower amphipod populations. Many of the invertebrates which Table 5 shows were consumed in greater numbers, such as corixids, gastropods, zygoptera naiads, and leeches, are usually found in the littoral zone. Since the littoral vegetation in these lakes was not nearly as dense as in Lake 3 it is possible that the trout could more easily inhabit this region and make better use of the food available there. If the similarities rather than differences in Table 5 data are examined it is evident that amphipods, chironomid larvae, and, to a lesser extent, cladocerans still constitute the most important food items.

#### Diel feeding habits

Consumption indices for Lake 3 trout showed little divergence when food habits were compared for the morning, afternoon, evening and night. This comparison is not entirely valid because of differences in absolute quantities consumed during the respective intervals and also because many of the organisms assigned to a particular time period had probably been

consumed during the preceding interval. Major differences in diel food consumption could, however, be expected to alter the consumption indices considerably. It is apparent that such major differences did not occur and that the food items eaten varied little throughout the day. Feeding does not appear to be related to the activity patterns of aquatic invertebrates, especially chironomids and amphipods. Chironomid larvae are known to migrate closer to the mud-water interface during darkness (Nikolsky 1963; Mundie 1959) thereby rendering them more susceptible to predation by fish. However, Figure 3 shows that chironomid larvae did not constitute a more important food source during hours of darkness than during daylight. Since amphipods are negatively phototrophic they tend to more readily vacate the shelter of the vegetation or substrate at night (Clemens 1950). This is evident from water column samples taken in mid-afternoon (1300-1600 hrs.) and early morning (0100-0400 hrs.). The slightly increased nighttime consumption index for amphipods and the corresponding decrease for cladocerans might be a reflection of this phenomenon.

#### Feeding Periodicity

Rainbow trout are considered to be visual feeders and this is reflected in the results shown in Figure 5. Feeding of Lake 3 trout was much reduced from midnight to about 6:00 a.m. but resumed shortly thereafter and continued throughout the day and early evening with a peak intensity occurring around 6:00 p.m. This observation can be considered valid and reliable since the pattern was consistent throughout the May to October sampling period. Feeding often continued well into the evening when light intensity was much reduced but never seemed to resume prior to 6:00 a.m. even though full daylight had been available for some time. A similar response is reported for stream dwelling brown trout (Hoar 1942). Visual

orientation may not be the only factor controlling feeding activity and this is confirmed to some extent by Jenkins (1969) who was unable to detect any increase in the feeding activity of stream rainbows even under conditions of bright moonlight. Hoar (1942) found that caged brook trout were equally capable of consuming food in total darkness. He suggests that the absence of night feeding under natural conditions is most likely an adaptation to lower levels of food abundance at this time rather than an uncontrollable restriction imposed by low light intensity. This is not a plausible explanation for the feeding periodicity of Lake 3 trout since amphipods were more abundant in the water column at night and thus would be more subject to predation. Some stomachs from trout caught at night were examined immediately after capture. These often contained recently ingested amphipods and other invertebrates but quantities were usually small. There is, perhaps, little reason to expect feeding activity and prey availability to correspond closely, especially when food is abundant and interspecific competition absent. Chaston (1969) found the peak feeding periods of stream dwelling brown trout differed entirely from the times of maximum prey availability.

Other studies of fish feeding periodicity often reveal a bimodal consumption pattern with morning and evening peaks and a midday depression (Carlander and Cleary 1949; Hoar 1942). Hoar (ibid.) associates the reduced midday consumption with restrictively high light intensities. The fact that feeding of Lake 3 trout remained more or less continuous throughout the day suggests that the turbid and discoloured water reduced light penetration to the extent that there was no light-associated inhibition in feeding.

## Feeding Selectivity

Differences in the relative proportion of food consumed compared to the total available supply have been revealed in numerous studies on the feeding and food habits of fishes. Various indices or ratios have been developed to quantitatively evaluate these differences. A "forage ratio" for some of the food organisms in a stream and in a lake was determined by Hess and Swartz (1941) and Ball (1948) respectively. The ratio for any given food item is equal to the percentage that food item constitutes of the total food consumed by a population of fish, divided by its percentage abundance in the food complex. This is equivalent to the "Availability factor" of Allen (1941-a). The selectivity index proposed by Ivlev (1961) and used in this study is simply a modified form of the forage ratio and, for reasons already given, is considered superior to it. The purpose of these ratios and indices is to express the relationship between available food and food eaten in quantitative terms and to estimate the importance of a given food organism to the fish.

### Laboratory experiments

Most investigators agree that selectivity is a function of two major variables, prey availability and predator preference and there is equal agreement on the difficulty of separating these components (Frost 1945; Lewis et al. 1961; Ivlev 1961). Attempts to isolate them were made by Allen (1941-6) who determined selectivity ratios only for those food organisms considered equally accessible to the young salmon being studied. Differences in morphology and activity make it unlikely that even two food organisms could be found which are truly of equal accessibility to the fish. Compounded by inevitable differences in abundance, Allen's field technique for separating availability and preference is far from definitive. These

problems were overcome, to a degree, in the present study by carrying out laboratory experiments using concealment-free and "natural" aquaria, as suggested by Ivlev (1961). However, it is obvious from observations made in this study that the activity patterns of the various food organisms are such that equal accessibility is never really possible. For this reason the indices given for P in Table 7 cannot be considered precise measurements of the preference component. The results given in Table 6, however, are quite convincing in their implication that food consumption by rainbow trout is a function of predator preference in situations where the food organisms are, essentially, equally accessible to them. Support for this hypothesis is provided by the evidence that corixids, which appeared to be the most capture-prone invertebrates in the concealment-free system, were consumed in much smaller quantities than the less mobile chironomid larvae. Despite their relative inactivity, chironomid larvae were the most intensively cropped organism under the equal accessibility conditions and should be regarded as the preferred food of the trout. Having derived values for the preference component of several of the more common aquatic invertebrates it is still not known if the features dictating this preference are of a physiological or ecological nature, or both. It was noted in the aquarium observations that trout were initially rather unselective and consumed whatever they came across but as their appetite was appeased they tended to confine their attention to one or two types of organisms. This suggests that the degree of preference shown for a food item depends largely on the state of hunger. This is in agreement with observations made by Nebol'sina (1968) and Ivlev (1961) in similar studies. Pearse (1929) however, found that several sunfish had very strong preferences for certain foods and refused to consume others, which they apparently did not like, even when hungry. Conditioning, as a result of repeated consumption

of a particular food, also has a marked effect on the preference component of selectivity (Ivlev 1961; Ware 1971).

The consumption pattern and selectivity indices were altered considerably in the selectivity experiments repeated using a simulated natural environment (Tables 5 and 7). A comparison of the respective availability (A) and preference (P) components of selectivity shows that, under the conditions imposed, availability is by far the most important determinant in selective feeding and that preference plays a relatively minor role. Similar conclusions were drawn by Neill (1938) and Hess and Swartz (1941) for natural situations.

No effort has been made in this study to quantitatively evaluate the factors which affect the availability of food organisms to rainbow trout. A very thorough and comprehensive series of experiments undertaken by Ivlev (1961), with several species of fish, clearly show that prey density, patchiness of distribution, concealment, and mobility are the most important variables in this respect.

#### Feeding selectivity of Lake 3 trout

Selectivity indices obtained for the food organisms in the littoral and limnetic zones of Lake 3 support the original assumption that feeding is essentially restricted to the open water portion of the lake. For example, significant numbers of cladocerans occurred in the stomachs of trout on all 3 sampling dates but were absent from the July 29 and August 30 littoral zone tank samples, resulting in an impossible index of +1 for these dates. Although it is possible for corixids, Trichoptera larvae, gastropods, and leeches to possess indices of -1, it seems entirely unlikely that all species would be completely avoided by the trout, as Table 10 suggests. A more reasonable explanation is that these characteristically littoral organisms are spatially separated from the trout.

The limited consumption of the amphipod, Hyalella azteca, in relation to its overall abundance, supports this explanation. Hyalella was rarely found in samples from the limnetic zone but was often quite abundant in the littoral samples. The propensity of this amphipod to occupy shallow, vegetated areas of a lake has been noted by Buschermi (1961) and Biette (1969). As few fish stomachs contained this species, it is suggested that the trout did not generally invade its habitat. If this is correct it would appear that Hyalella azteca, by virtue of its preferred natural habitat, has a selective advantage over the sympatrically occurring Gammarus lacustris. Continued stocking over a period of years might result in a shift in relative abundance of these species.

The negative selectivity indices indicated for chironomid larvae on all of the sampling dates is in general agreement with laboratory determinations. The burrowing habit of these benthic invertebrates obviously precludes intense predation by trout. Swift (1970) also found chironomid larvae to be poorly utilized by rainbow trout in a California lake. Other fish species, especially those adopted for bottom feeding, show strong selection for this food item (Ball 1948). The lower indices noted for the night samples may indicate that the ability of rainbow trout to capture chironomid larvae in darkness is impaired to a greater extent than is their ability to capture amphipods or cladocerans.

Although the values for amphipods are inconsistent with the laboratory determinations, the two results are not really comparable since concealment, in the form of vegetation was available to the aquarium fish. If trout restrict their feeding to the limnetic zone where amphipods do not have this concealment, the selectivity index would have positive availability and preference components. In his stream study of young Atlantic salmon Allen (1941-b) reports a negative selection for one species

of Gammarus and relates this to the shelter afforded by the gravel stream bed.

Cladocerans, although not used in the laboratory experiments, would likely possess a negative preference component simply because of the predator-prey size differential. The negative indices observed for cladocerans in Lake 3 reflect the general principle that it is energetically inefficient for large fish to consume such small food items. Aside from several reports that rainbow trout do feed on zooplankton, there is little information in the literature from which to draw comparisons. Galbraith (1967) noted that rainbow trout exerted a size selective pressure on a population of Daphnia by consuming only the larger individuals. This selection could not be entirely related to gill raker spacing and it was suggested that the trout discriminated to some extent in the size of Daphnia which they ingested. No attempt was made to determine if there was size selective predation of cladocerans by Lake 3 trout. It was evident from stomach samples that copepods were not ingested even though they were periodically quite abundant. A similar observation was made in a study of the feeding habits of char (Lindstrom 1955).

Generally, it appears that rainbow trout utilize primarily those organisms which are most accessible to them and on which they are morphologically adapted to feed. There is no indication to date that the stocked trout in Lake 3 are exerting undue pressure on any particular aquatic invertebrate. This is not to say that such pressure will not exist in the future or that it does not already exist in other study area lakes. More information is obviously required on the population dynamics of the important food organisms, especially amphipods, before realistic predictions can be made as to the effects of stocking on the overall food resource.

## Digestion Rates

Windell (1967) defines time for gastric digestion as "the number of hours necessary for passing all the food from the stomach to the intestine "and considers digestion to be complete "when the stomach becomes devoid of all measurable remains." Brett and Higgs (1970) suggest that " gastric evacuation" would be a more correct description since it avoids the implication of absorption within the stomach itself. In this study the terms are considered synonymous and have been used interchangeably.

The various techniques employed for following gastric evacuation in fish have been reviewed by Windell (1968). The serial slaughter method used in this study has gained the widest acceptance although several variations in approach are common. Some investigators, including Battle et al. (1936), Magnuson (1969) and Brett and Higgs (1970) measured depletion by subsampling, at regular intervals, a fairly large group of fish fed initially to satiation, while Pandian (1967), Shrable et al. (1969), and Herting and Witt (1968) sequentially autopsied small numbers of spatially isolated fish which had been fed a measured meal. Stomach x-rays of briefly anesthetized, living fish enabled Molnar and Tolg (1962) to follow the digestive disintegration of bleak in the stomach of largemouth bass. This method is presently restricted in application to piscivorous species.

The negative exponential is an appropriate descriptive model for stomach depletion rate provided a constant percentage of the stomach contents is digested per unit time (i.e. there is a constant digestion rate). If the data are plotted on a semi-logarithmic scale any pronounced deviation from linearity would indicate a varying digestion rate with time. This could result from changes in digestive efficiency with quantity or quality of food remaining in the stomach.

Not all of the depletion curves reported in the literature approach the theoretically expected negative exponential. The model appears to be least applicable to largemouth bass (Hunt 1960), channel catfish (Shrable et al. 1969) and bluegill sunfish (Windell 1966) but provides a fairly precise expression of digestion rate in sockeye salmon (Brett and Higgs 1970) and young cod (Tyler 1970). Magnuson (1969) applied a polynomial regression to his data on skipjack tuna.

If it is assumed that digestion in closely related species follows a similar pattern, the sockeye salmon results provide some support for the depletion model used in this study for rainbow trout. It is difficult to render additional comparisons since little information is available on digestion in Salmo gairdneri, especially with respect to natural food organisms. Experiments conducted by Windell and Norris (1969) and Windell et al. (1969) on this species are not considered comparable because only artificial diets were used. A visual inspection of their results, however, suggest that a negative exponential would not provide a good fit to the data. This inconsistency is difficult to rationalize if it ~~is~~ presupposed that the depletion pattern (not rate) is independent of food type.

A lag phase is evident in the depletion curves of bluegill sunfish (Windell 1966), skipjack tuna (Magnuson 1969) and rainbow trout (Windell and Norris 1969) but not in young cod (Tyler 1970). A delay in the secretion of gastric juices after food is consumed may possibly account for this lag (D. P. Scott, pers. comm.).

#### Effect of meal size

Barrington (1957) and Molnar et al. (1967) suggest that a small meal may be expected to undergo more rapid elimination from the stomach than a large meal. The experimental results of this study contradict

this hypothesis as they indicate that gastric evacuation in rainbow trout is independent of meal size. The percentage decrease of a satiation meal of amphipods was not significantly different from the decrease recorded for a meal which was less than one half the satiation quantity. Similar observations have been made on bluegill (Windell 1966), pumpkinseed (Kitchell and Windell 1968), and young cod (Tyler 1970). Windell and Norris (1969) noted that an increase in meal size resulted in an accelerated stomach depletion rate for rainbow trout given artificial pellet diets.

The rate of stomach depletion, then, is proportional to the quantity of food present in the stomach at any given time; for equal time intervals, equal percentages of the total mass of food are passed from the stomach. Knowing the satiation ration and the slope of the digestion curve, a maximum rate of evacuation (and therefore a maximum rate of food consumption) can be easily calculated.

#### Effect of water temperature

Instantaneous depletion rates increased rapidly as the water temperature was raised from 5C to 12C, the increase becoming less pronounced at acclimation temperatures of 17 and 22C. This response approximates a negative exponential and possibly reflects the relationship between enzyme activity and temperature (Tyler 1970) but may also be related to peristaltic action (Brett and Higgs 1970). Although the literature does not contain comparable data for rainbow trout, the results of experiments on several other species support these observations. Molnar et al. (1967) noticed little variation in the general shape of the curve for 4 piscivorous species examined and was able to linearize the data with semilog transformations. A similar relationship is reported for fingerling sockeye salmon (Brett and Higgs 1970). According to Tyler (1970), it is possible that experiments at higher temperatures would reveal a levelling off or perhaps a

decline in depletion rate.

Brett and Higgs (1970) examined digestion rate in relation to food intake, growth, and conversion efficiency of sockeye salmon over their full range of temperature tolerance. Some interesting relationships were observed which, if applicable to rainbow trout, would help clarify the overall effects of water temperature on growth and yield in stocked lakes. At low temperatures digestive efficiency was much reduced, resulting in poor conversion and slow growth. All systems, especially growth rate, increased rapidly with rising temperature until an optimum was reached at 15C. Beyond this, digestion rate continued to climb while food intake, conversion, and growth rate dropped precipitously. It seems logical to assume that similar mechanisms operate in rainbow trout although the respective inflections in the curve are likely to occur at slightly higher temperatures. Since food intake of experimental fish held at 22C was consistently lower than at 17C it is apparent that the former temperature is beyond the optimum for this species. McAfee (1966) reports a preferred temperature range for rainbow trout of 15-20C while Garside and Tait (1958) quote a lower range of 13-16C. It would seem that the increased capacity of the trout to digest food at higher temperatures is of little value to them since appetite, growth, and conversion efficiency are substantially reduced. It can be expected that prolonged periods of water temperatures greater than 20C, especially if accompanied by low oxygen levels, will ultimately result in poor yields. This has been confirmed, in part, by Johnson and Hasler (1954) for rainbow trout stocked in several dystrophic Wisconsin lakes.

### Effect of food type

Differential rates of digestion for different food organisms might be expected on the basis of food particle size (Tyler 1970) and/or chemical composition (Hess and Rainwater 1939; Nikolsky 1963). In this study no significant difference could be detected in the gastric evacuation rate of several natural food organisms, possibly indicating that differences in size and chemical composition were not sufficiently great to alter depletion time. Heavily chitinized aquatic invertebrates such as dragonfly naiads and Trichoptera larvae have been shown to delay stomach emptying (Kionka and Windell 1972; Hess and Rainwater 1939; Kitchell and Windell 1968) but these organisms did not comprise a significant portion of Lake 3 trout consumption and were not used in digestion experiments. In rainbow trout, Kionka and Windell (1972) observed that small pieces of chitin, such as appendages, moved at essentially the same rate as the digestible organic matter while pieces larger than the diameter of the pylorus were delayed. This may account for the fact that amphipods, though more heavily chitinized than the other experimental food organisms, were evacuated from the stomach at very nearly the same rate. Evidence of the effects of chemical composition on gastric digestion is given by Windell et al. (1969) who fed rainbow trout encapsulated meals of commercial pellet food as well as various pure diets including corn oil, saturated fat, and methyl cellulose. The percentage depletion at 12 hours for the four food types was 65.8, 42.6, 28.8, and 50.3 respectively.

In this study it was noted that artificial food, in the form of dried pellets, was digested at a considerably slower rate than natural food organisms. This is confirmed by Windell and Norris (1969) who suggest that the delayed evacuation may result from the lower water and higher fat content of the artificial food.

Although differential rates of digestion of different food organisms did not appear to be a major consideration in the assessment of feeding selectivity as food consumption rates of Lake 3 trout, this factor should be given additional attention in future studies on digestion in fish.

#### Effect of fish size.

Few attempts have been made to relate stomach depletion rate to fish size, probably because of the difficulties encountered in feeding and maintaining large fish under laboratory conditions. Much of the information to date is contradictory, sometimes even within the same study (Hunt 1960; Seaburg and Moyle 1964). Neither Windell (1966) nor Tyler (1970) could detect a significant difference in emptying time for different size fish in their experiments. In a more comprehensive study Pandian (1967) related food intake, digestion, absorption, and conversion to fish size. He found that digestion rate for Megalops cyprinoides decreased as fish weight increased and compared the relationship to that existing between fish size and feeding rate.

In the current study it was not possible to distinguish size-dependent differences in digestion rate for rainbow trout. Since only one experiment was completed on fish greater than 50g mean weight this observation must be accepted with reservation. If significant differences do exist between large and small fish, calculations of daily food consumption based on laboratory determinations of evacuation rate in small fish may under- or overestimate the true values. Further experimentation is required to elucidate the exact nature of the relationship existing here.

### Effects of other variables

Several variables, other than those examined, have been implicated as potential factors influencing rate of digestion in fish. Continuous feeding may accelerate stomach emptying by forcing partially digested food into the intestine. Windell (1966) recognized this possibility but emphasized that accelerated emptying did not occur in bluegill sunfish. Tyler (1970) found that stomach evacuation of young cod fed 3 meals in overlapping succession was more rapid than would be predicted from single meal experiments. However, the discrepancy was not considered serious enough to prevent estimates of daily ration.

Prolonged starvation and force feeding have been shown to retard digestion (Windell 1966) while the effects of other variables, such as photoperiod, confinement, and physical handling are, as yet, unknown.

### Food Consumption

Determination of daily food consumption by combining information on observed indices of stomach fullness and gastric digestion rates is by no means unique to this study. The usefulness of this method has been pointed out by Davis and Warren (1968), Windell (1967) and Popova (1967) and is probably the most frequently employed approach to measuring daily ration. However, comparison between studies is extremely difficult because of the variety of ways in which rates of food passage through the stomach have been determined.

Bajkov (1935) proposed a field method for estimating daily ration whereby a large sample of fish was captured over a minimum time interval and placed in a food-free container in the lake. The rate of food passage was determined by subsampling at time zero and at appropriate intervals thereafter until digestion was complete. The method is only valid if it is assumed that feeding throughout the day is continuous and that handling

does not interfere with the digestive process. Equally unrealistic assumptions are inherent in the methods of Keast and Welch (1968), Pinskii (1967) and Mikhman (1969) who based their estimates of food passage rates on differences in the diel feeding pattern. The method does not consider food ingested during periods of declining stomach fullness nor food digested during increases and is restricted in application to fish which have pronounced peaks in feeding intensity. Other authors, including Seaburg and Moyle (1964), Tsunikova (1970) and Nebol'sina (1968), measured digestion over a short interval (e.g. 4 hrs.), at a given water temperature, and multiplied the result by the number of such intervals in a day and by the mean stomach fullness to arrive at a figure for daily ration. Essentially the same method was used by Sandercock (1969) who determined a stomach emptying time interval using marker organisms and multiplied this by the number of these time intervals in a day and by the mean stomach fullness. Similarly, Darnell and Meierotto (1962), using amphipods as food items, established an arbitrary classification of digestion stages and from this calculated daily food consumption of black bullheads. Only Tyler (1970) and Falk (1971) completed estimates of daily ration using values from experimentally derived digestion curves. This is rather surprising in light of the number of studies undertaken on the rates of digestion in fish. Equations describing the rate of depletion of food from the stomachs of juvenile perch were derived by Falk (1971) who combined this information with data on diurnal feeding intensity to obtain estimates of daily ration. Data on the diel feeding rhythm and indices of stomach fullness were not available to Tyler (1970), however, he computed a theoretical maximum ration for cod by extrapolating the mean rate of stomach depletion for the first 5 hours to a 24 hour period. The method used in this study is similar to Tyler's except that food consumption was calculated on an

interval basis from direct measurements of the indices of stomach fullness and then summed for a 24 hour period.

The substantial differences reported for the daily ration of Lake 3 rainbow trout in Table 12 are difficult to comprehend if it is assumed that all of the described methods are valid. It seems reasonable to reject the empirical method of Ricker and Foerster (1948) since it was proposed only as a general approximation and does not adequately consider the seasonal changes in water temperature. A fairly obvious explanation exists for the difference in the estimates of daily ration derived using the study method and the method proposed by Sandercock (1969). In the latter case 8 hours is given as the time required for rainbow trout to clear their entire intestinal tract at 19°C although no explanation is provided as to how this determination was completed. Numerous experiments undertaken for the present study repeatedly indicate that, for trout at this temperature, approximately 16 hours are needed to clear the stomach alone. Although there is little data available from the literature with which these findings can be compared, Windell and Norris (1969) show that 28-36 hours are required for rainbow trout to digest a meal of oligochaetes at 15°C. If Sandercock's formula is adjusted for a more realistic turnover rate of 1.5 at 19°C, the resultant estimates of daily ration are reduced by 50%. These estimates would not differ greatly from those calculated by the study method nor for that matter from those determined by the Ricker-Foerster technique. However, when extrapolated to total seasonal food consumption and related to overall growth by the coefficients of food utilization it becomes clear that the study method significantly underestimates daily ration of Lake 3 fish. The possible reasons for this will be discussed shortly.

Estimates of daily ration based on Winberg's (1956) balanced equation present a reasonable alternative to the previously mentioned techniques and, in spite of the many assumptions required, it has been widely accepted by fishery biologists. Since many of the necessary parameters such as metabolic rate and food assimilation efficiencies have been determined in numerous other studies, it is quite feasible to predict, from a knowledge of growth rate only, the levels of food consumption. The assumption that energy expended for metabolism in nature is approximately twice the level of energy expenditure of a minimally active laboratory fish is the most difficult to justify and likely accounts for most of the error involved in this method (Mann 1967).

In the few situations where daily ration has been measured using gastric digestion rates and stomach content data, in conjunction with Winberg's balanced equation, the results obtained are comparable (Pinskii 1967; Foerster 1968; Falk 1971). Although this is quite obviously not true for this particular study, it is suggested that the differences result, not from inconsistencies in the rationale of the methods used but rather from the nature of the observed indices of stomach fullness. However, no adequate explanation can be given to account for the abnormally low stomach content indices, especially since each estimate is based on 70-80 fish. It is possible that the gillnets did not take representative samples of the fish population and that only fish which were actively moving about in search of food were caught. If this was true, the observed indices of stomach fullness would likely be less than the true values. It seems totally unlikely that the stomachs were, by coincidence, abnormally deficient in food during all 7 of the sampling periods. Unquestionably, the feeding intensity of the trout was influenced to some extent by weather conditions at, or near, the time of sampling. For example, during the June 21-22

sampling, Lake 3 water temperatures reached a summer high of 23C and this may have inhibited feeding activity. Sampling dates were chosen according to the day of the week and therefore were not biased in favour of any particular weather conditions.

If one considers, then, the amount of effort required to obtain accurate information on gastric digestion rates and the variability which is likely to arise from short term observations of diel feeding intensity, little justification can be given for the estimation of daily ration using the method presented here. This is not to suggest that the method used is inadequate for its designed purpose but rather that Winberg's balanced equation can produce reliable results with much less effort.

It was previously stated that a major goal in the trout farming program was to establish a range of suitable stocking densities which would facilitate management on a maximum sustained yield basis. To accomplish this, a knowledge of the secondary production of food organisms (particularly amphipods) and the food consumption rates of stocked trout is necessary. Part of the purpose of this study was to obtain quantitative estimates of the latter. Observations during 1970 and 1971 on yield, survival, and growth of trout in study area lakes tend to negate the importance of food supply as a major factor in the overall suitability of any given lake for stocking. Data from 1971 indicate that no significant relationship existed between survival or growth, and stocking density. In fact 3 of the 5 most successful lakes had stocking densities greater than 1000 fish per hectare (Sunde, pers. comm.). At the present time the most important factor operating to reduce production appears to be oxygen depletion associated with high water temperatures and algal die-offs. In lakes where oxygen stress was known to occur, slower growth rates were observed and survival was lowered. These problems appear more critical to

effective management at present than does a complete understanding of feeding relationships,

## SUMMARY

Food habits and feeding selectivity of rainbow trout in a small, Western Manitoba winterkill lake were studied during the ice-free periods of 1970 and 1971. Annual, seasonal, and diel changes in type and quantity of food consumed were determined. Laboratory experiments were conducted on rates of, and factors influencing, gastric digestion and the results applied to estimates of daily ration.

1. The most important food organisms of Lake 3 trout were amphipods, cladocerans and chironomid larvae, however their relative contribution to the diet changed over the season. The latter two organisms, abundant in the stomachs during May and June, became less important as the season progressed. The food utilized by the stocked trout did not differ greatly from one year to the next with the exception of an increased consumption of cladocerans during August and September, 1970.

2. Rainbow trout were diurnal in their feeding habits. Feeding activity was more or less continuous throughout the day and evening with a maximum index of stomach fullness occurring in late afternoon. Consumption was greatly reduced from about midnight to 6:00 a.m. Little change was noted in the types of food items eaten at different times of the day.

3. Considerable variation was observed in food habits of trout stocked in other lakes; however results are based on a limited number of samples. Although amphipods were still the most important food item it was evident that a wider range of invertebrates were consumed.

4. Feeding selectivity, a function of prey availability and predator preference, was evaluated for rainbow trout in laboratory and field experiments. Availability was clearly the most important factor in determining which foods were eaten. Chironomid larvae, although a preferred food item, were negatively selected. The inaccessibility of this benthic

invertebrate probably accounted for its limited consumption. Selection for cladocerans was slightly negative while several organisms including corixids, caddisfly larvae, snails, and leeches were almost exclusively avoided. Amphipods were negatively selected in the laboratory experiments where vegetation was available for concealment but positively selected in the open water portion of Lake 3. The feeding of Lake 3 trout appeared to be limited primarily to the limnetic zone.

5. The relationship between state of digestion and time was curvilinear, the response approximating a negative exponential. Rates of gastric digestion were independent of meal size but greatly affected by temperature. The number of hours required for 95% digestion at 5, 12, 17 and 22C was 54, 16, 14, and 9 respectively. No significant difference was detected in the rate of digestion of several natural food organisms but digestion of artificial food was 2.5 times slower. Digestion rates were not significantly affected by fish size within the size range examined.

The daily ration of Lake 3 trout was estimated for several sampling periods using information on gastric digestion rates and diel feeding intensities. The daily ration varied from 1.4 to 2.7 percent of body weight during the interval from mid-June to late August when mean weekly water temperatures were relatively constant. Although the estimates derived using this method were definitely too low, it was felt that the errors were attributable to variations in the indices of stomach fullness rather than to any inconsistency in the basic theory. Several other methods of determining daily food consumption were employed for comparative purposes. It was concluded that adequate estimates of daily ration could be obtained with much less effort by using the balanced equation method of Winberg (1956).

LITERATURE CITED

- Alger, P. L. 1969. Mathematics for science and engineering. McGraw-Hill, New York. 374 p.
- Allen, K. R. 1941-a. Comparison of bottom faunas as sources of available fish food. Trans. Amer. Fish. Soc. 71: 275-283.
- . 1941-b. Studies on the biology of the early stages of the salmon (Salmo salar). 2. Feeding habits. Anim. Ecol. 10: 47-76.
- Anderson, R. O. 1959. A modified flotation technique for sorting bottom fauna samples. Limnol. Oceanogr. 4: 223-225.
- Bajkov, A. D. 1935. How to estimate the daily food consumption of fish under natural conditions. Trans. Amer. Fish. Soc. 65: 288-289.
- Ball, R. C. 1948. Relationship between available fish food, feeding habits of fish and total fish production in a Michigan lake. Mich. State Coll. Agr. Expt. Stat. Tech. Bull. 206. 56 p.
- Barrington, C. J. W. 1957. The alimentary canal and digestion, p. 109-161. In M. E. Brown (ed.) The physiology of fishes. Vol. 1. Academic Press, New York.
- Battle, H. I., A. G. Huntsman, A. M. Jeffers, G. W. Jeffers, W. H. Johnson, and N. A. McNairn. 1936. Fatness, digestion and food of Passamaquoddy young herring. J. Biol. Bd. Canada 2: 401-429.
- Biette, R. M. MS, 1969. Life history and habitat differences between Gammarus lacustris lacustris Sars and Hyaella azteca (Saussure) in West Blue Lake, Manitoba. M.Sc. Thesis. Univ. Manitoba. 98 p.
- Brett, J. R., and D. A. Higgs. 1970. Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon, Oncorhynchus nerka. J. Fish. Res. Bd. Canada 27: 1767-1779.
- Buschermi, P. A. 1961. Ecology of the bottom fauna of Parvin Lake, Colorado. Trans. Amer. Microscop. Soc. 80: 266-307.
- Carlander, K. D., and R. E. Cleary. 1949. The daily activity patterns of some freshwater fishes. Amer. Midl. Nat. 41: 447-452.
- Chaston, I. 1969. Seasonal activity and feeding pattern of brown trout (Salmo trutta) in a Dartmoor stream in relation to availability of food. J. Fish. Res. Bd. Canada 26: 2165-2171.
- Clemens, H. P. 1950. Life cycle and ecology of Gammarus fasciatus Say. Ohio State University, The Franz Theodore Stone Laboratory, Contribution no. 12. 63 p.
- Cooper, W. E. 1965. Dynamics and production of a natural population of a freshwater amphipod, Hyaella azteca. Ecol. Monogr. 35: 377-394.

- Darnell, R. M., and R. M. Meierotto. 1962. Determination of feeding chronology in fishes. Trans. Amer. Fish. Soc. 89: 206-211.
- Davis, G. E., and C. E. Warren. 1968. Estimation of food consumption rates, p. 204-225. In W. E. Ricker (ed.) Methods for assessment of fish production in fresh waters. Blackwell Scientific Publications, Oxford and Edinburgh.
- Falk, M. R. MS, 1971. Food habits, gastric digestion and food consumption rates of yellow perch, Perca fluviatilis flavescens (Mitchill), in West Blue Lake, Manitoba. M.Sc. Thesis. Univ. Manitoba. 175 p.
- Fedoruk, A. N. 1971. Water and fish capability, ARDA project area no. 7038, South side Riding Mountain National Park. Manitoba Dept. Mines and Nat. Res., Canada Land Inventory project No. 8.
- Flannagan, J. F. 1970. Efficiencies of various grabs and corers in sampling freshwater benthos. J. Fish. Res. Bd. Canada 27: 1691-1700.
- Foerster, R. E. 1968. The sockeye salmon. Bull. Fish. Res. Bd. Canada 162. 422 p.
- Frost, W. E. 1945. River Liffey survey-VI. Discussion on the results obtained from investigations on the food and growth of brown trout (Salmo trutta L.) in alkaline and acid waters. Proc. Roy. Irish Acad. (B) 50: 321-342.
- Galbraith, M. G. 1967. Size-selective predation on Daphnia by rainbow trout and yellow perch. Trans. Amer. Fish. Soc. 96: 1-10.
- Garside, E. T., and J. S. Tait. 1958. Preferred temperature of rainbow trout (Salmo gairdneri Richardson) and its unusual relationship to acclimation temperature. Canadian J. Zool. 36: 563-567.
- Godfrey, H. 1955. On the ecology of Skeena River whitefishes, Coregonus and Prosopium. J. Fish. Res. Bd. Canada 12: 499-531.
- Goodwin, W. L. 1930. Geology and minerals of Manitoba. Industrial and Educational Publishing Co., Gardenvale, Quebec. 260 p.
- Greenbank, J. 1945. Limnological conditions in ice-covered lakes, especially as related to winterkill of fish. Ecol. Monogr. 15: 343-392.
- Hamilton, A. L., W. Burton, and J. F. Flannagan. 1970. A multiple corer for sampling profundal benthos. J. Fish. Res. Bd. Canada 27: 1867-1869.
- Hartman, G. F. 1958. Mouth size and food size in young rainbow trout, Salmo gairdneri L. Copeia 1958: 233-234.
- Herting, G. E., and A. W. Witt. 1968. Rate of digestion in the bowfin. Progr. Fish-Cult. 30: 26-38.

- Hess, A. D., and J. H. Rainwater. 1939. A method for measuring the food preference of trout. *Copeia* 1939: 154-157.
- Hess, A. D., and A. Swartz. 1941. The forage ratio and its use in determining the food grade of streams. *Trans. Fifth N. A. Wildl. Conf.*: 162-164.
- Hoar, W. S. 1942. Diurnal variations of feeding activity of young salmon and trout. *J. Fish. Res. Bd. Canada* 6: 90-101.
- Hunt, B. P. 1960. Digestion rate and food consumption of Florida gar, warmouth, and largemouth bass. *Trans. Amer. Fish. Soc.* 89: 206-211.
- Hynes, H. B. N. 1950. The food of freshwater sticklebacks (Gasterosteus aculeatus and Pygosteus pungitius) with a review of methods used in studies of the food of fishes. *J. Anim. Ecol.* 19: 36-58.
- Ide, F. P. 1943. Availability of aquatic insects as food of the speckled trout, Salvelinus fontinalis. *Trans. Seventh N. A. Wildl. Conf.*: 442-450.
- Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, Conn. 302 p.
- Jenkins, G. C. 1970. Land use study, ARDA project no. 7038, South side Riding Mountain National Park. Manitoba Dept. Mines and Nat. Res., Canada Land Inventory report no. 9. 93 p.
- Jenkins, T. M. 1969. Night feeding of brown and rainbow trout in an experimental stream channel. *J. Fish. Res. Bd. Canada* 26: 3275-3278.
- Johnson, L., G. H. Lawler, and L. A. Sunde. 1970. Rainbow trout farming in Central Canada. *Fish. Res. Bd. Canada Tech. Rept.* 165. 17 p.
- Johnson, W. E., and A. D. Hasler. 1954. Rainbow trout production in dystrophic lakes. *J. Wildl. Mgmt.* 18: 113-134.
- Keast, A., and L. Welsh. 1968. Daily feeding periodicities, food uptake rates and dietary changes with hour of day in some lake fishes. *J. Fish. Res. Bd. Canada* 25: 1133-1144.
- Kionka, B. C., and J. T. Windell. 1972. Differential movement of digestible and indigestible food fractions in rainbow trout, Salmo gairdneri. *Trans. Amer. Fish. Soc.* 101: 112-115.
- Kitchell, J. F., and J. T. Windell. 1968. Rate of gastric digestion in pumpkinseed sunfish, Lepomis gibbosus. *Trans. Amer. Fish. Soc.* 97: 489-492.
- Lagler, K. F. 1956. Freshwater fishery biology. Wm. C. Brown Co., Dubuque, Iowa. 421 p.

- Leonard, J. W., and F. A. Leonard. 1949. An analysis of the feeding habits of rainbow trout and lake trout in Birch Lake, Cass County, Michigan. *Trans. Amer. Fish. Soc.* 76: 301-314.
- Lewis, W. M., G. E. Gunning, E. Lyles, and W. L. Bridges. 1961. Food choice of largemouth bass as a function of availability and vulnerability of food items. *Trans. Amer. Fish. Soc.* 90: 277-280.
- Lindström, T. 1955. On the relation fish size - food size. *Rept. Inst. Freshwater Res. Drottningholm* 36: 133-147.
- Magnuson, J. J. 1969. Digestion and food consumption of skipjack tuna (Katsuwonus pelamis). *Trans. Amer. Fish. Soc.* 98: 379-392.
- Mann, K. H. 1967. The cropping of the food supply, p. 243-257. *In* S. D. Gerking (ed.) *The biological basis of freshwater fish production*. Blackwell Scientific Publications, Oxford and Edinburgh.
- McAfee, W. R. 1966. Rainbow trout, p. 192-215. *In* A. Calhoun (ed.) *Inland fisheries management*. State of California, The Resources Agency, Dept. Fish and Game.
- Menon, P. S. MS, 1966. Population ecology of Gammarus lacustris lacustris Sars in Big Island Lake. Ph.D Thesis. Univ. Alberta. 109 p.
- Mikhman, A. S. 1969. Some new data on the larval feeding of the Azov tyul'ka (Clupeonella delicatula, Nordm.) and on the role of the nutritional factor in fluctuations in its abundance. *Problems of Ichthyology* 9: 666-673.
- Molnár, Gy., E. Tamássy, and I. Tölgy. 1967. The gastric digestion of living, predatory fish, p. 135-149. *In* S. D. Gerking (ed.) *The biological basis of freshwater fish production*. Blackwell Scientific Publications, Oxford and Edinburgh.
- Molnár, Gy., and I. Tölgy. 1962. Relation between water temperature and gastric digestion of largemouth bass (Micropterus salmoides Lacépède). *J. Fish. Res. Bd. Canada* 19: 1005-1012.
- Mundie, J. H. 1959. The diurnal activity of larger invertebrates at the surface of Lac la Ronge, Saskatchewan. *Canadian J. Zool.* 37: 945-956.
- Munro, D. A. 1963. Ducks and the Great Plains wetlands. *Canadian Audubon magazine*. Sept. - Oct.
- Nebol'sina, T. K. 1968. Daily food intake and feeding pattern of the carp-bream (Abramis brama L.) in the Volgograd Reservoir. *Problems of Ichthyology* 8: 101-106.
- Neill, R. M. 1938. The food and feeding habits of brown trout (Salmo trutta L.). *Trans. Roy. Soc. Edinburgh* 59: 481-520.

- Nickum, J. C. 1971. Limnology of winterkill lakes in South Dakota, p. 19-25. In E. Schneberger (ed.) A symposium on the management of midwestern winterkill lakes. North Central Division, Amer. Fish. Soc., Special publication.
- Nikolsky, G. W. 1963. The ecology of fishes. Academic Press, London and New York. 352 p.
- Nilsson, N-A. 1965. Food segregation between salmonid species in North Sweden. Rept. Inst. Freshwater Res. Drottningholm 46: 58-78.
- Pandian, T. J. 1967. Intake, digestion, absorption and conversion of food in the fishes Megalops cyprinoides and Ophiocephalus striatus. Mar. Biol 1: 16-32.
- Pearse, A. S. 1924. Amount of food eaten by four species of freshwater fishes. Ecology 5: 254-258.
- Pinskii, F. Y. 1967. Daily feeding rhythm and diets of young of the salmon, Salmo salar L. when raised in ponds. Fish. Res. Bd. Canada Trans. Series 1143. 11 p.
- Popova, O. A. 1967. The 'predator-prey' relationship among fish (A survey of Soviet papers), p. 359-376. In S. D. Gerking (ed.) The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford and Edinburgh.
- Princic, R. MS, 1971. The economic feasibility of rainbow trout farming in the natural ponds of Western Canada. M.N.R.M. Practicum. Univ. Manitoba. 64 p.
- Ricker, W. E., and R. E. Foerster. 1948. Computation of fish production. Bull. Bingham Oceanogr. Coll. 11(4): 173-211.
- Rózkowska, A. D., and A. Rózkowski. 1969. Seasonal changes of slough and lake water chemistry in Southern Saskatchewan (Canada). J. Hydrology 7: 1-13.
- Sandercock, F. K. MS, 1969. Bioenergetics of the rainbow trout (Salmo gairdneri) and the kokanee (Oncorhynchus nerka) populations of Marion Lake, British Columbia. Ph.D. Thesis. Univ. British Columbia. 114 p.
- Schindler, D. W. 1969. Two useful devices for vertical plankton and water sampling. J. Fish. Res. Bd. Canada 26: 1948-1955.
- Seaburg, K. G., and J. B. Moyle. 1964. Feeding habits, digestion rates, and growth of some Minnesota warmwater fishes. Trans. Amer. Fish. Soc. 93: 269-285.
- Shrable, J. B., O. W. Tiemeier, and C. W. Deyoe. 1969. Effects of temperature on rates of digestion by channel catfish. Progr. Fish-Cult. 31: 131-138.

- Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods. 6th ed. Iowa State Univ. Press, Ames, Iowa. 465 p.
- Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco. 776 p.
- Starostka, V. J., and R. L. Applegate. 1970. Food selectivity of Bigmouth Buffalo, Ictiobus cyprinellus, in Lake Poinsett, South Dakota. Trans. Amer. Fish. Soc. 99: 571-576.
- Sunde, L. A., J. Whitaker, and G. H. Lawler. 1971. Rainbow trout production in winterkill lakes, p. 57-63. In E. Schneberger (ed.) A symposium on the management of midwestern winterkill lakes. North Central Division, Amer. Fish. Soc., Special publication.
- Surber, E. W. 1937. Rainbow trout and bottom fauna production in one mile of stream. Trans. Amer. Fish. Soc. 66: 193-202.
- Swift, M. C. 1970. A qualitative and quantitative study of trout food in Castle Lake, California. Calif. Fish and Game 56: 109-120.
- Tsunikova, Ye. P. 1970. Daily food consumption of young pike-perch and Azov roach (Taran) in the Kuban fish farms. J. Ichth. 10: 658-661.
- Tyler, A. V. 1970. Rates of gastric emptying in young cod. J. Fish. Res. Bd. Canada 27: 1177-1189.
- Wales, J. H. 1946. Castle Lake trout investigation. First phase: interrelationships of four species. Calif. Fish and Game 32: 109-143.
- Ware, D. M. 1971. Predation by rainbow trout (Salmo gairdneri): the effect of experience. J. Fish. Res. Bd. Canada 28: 1847-1852.
- Winberg, G. G. 1956. Rate of metabolism and food requirements of fishes. Fish. Res. Bd. Canada Trans. Series 194. 220 p.
- Windell, J. T. 1966. Rate of digestion in the bluegill sunfish. Invest. Indiana Lakes Streams 7: 185-214.
- \_\_\_\_\_. 1967. Rates of digestion in fishes, p. 151-173. In S. D. Gerking (ed.) The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford and Edinburgh.
- \_\_\_\_\_. 1968. Food analysis and rate of digestion, p. 196-203. In W. E. Ricker (ed.) Methods for assessment of fish production in fresh waters. Blackwell Scientific Publications, Oxford and Edinburgh.
- Windell, J. T., and D. O. Norris. 1969. Gastric digestion and evacuation in rainbow trout. Progr. Fish-Cult. 31: 20-26.
- Windell, J. T., D. O. Norris, J. F. Kitchell, and J. S. Norris. 1969. Digestive response of rainbow trout, Salmo gairdneri, to pellet diets. J. Fish. Res. Bd. Canada 26: 1801-1812.

## APPENDICES

Table A-1. Comparison of growth rate data for Lake 3 rainbow trout in 1970 and 1971.

1970			1971		
Sampling date	Sample size	Mean wet wt.(g)	Sampling date	Sample size	Mean wet wt.(g)
<sup>1</sup> May 15		4.5	<sup>1</sup> May 5		1.7
			May 25	46	5.8
			June 2	36	6.6
			June 22	167	42.4
July 8	25	73	July 14	91	61.3
July 28	203	84	July 29	17	103.1
			Aug. 9	190	107.7
Aug. 25	193	114	Aug. 30	123	133.5
Sept. 27	115	210	Sept. 19	108	184.8
			Oct. 20	87	210.1
<sup>2</sup> Oct.20-25	2155	232	<sup>2</sup> Oct.22-30	2623	240.0

<sup>1</sup>Date of stocking.

<sup>2</sup>Approximate range of harvest dates.

Table A-2. Dry weights of equal samples of Gammarus lacustris preserved in 10% (A) and full strength (B) for malin for varying periods of time.

No. of days preserved	Preservative	Dry weight(g)
0	Not preserved	1.655
3	A	1.558
	B	1.737
10	A	1.469
	B	1.658
17	A	1.458
	B	1.659
24	A	1.441
	B	1.659
31	A	1.448
	B	1.645
45	A	1.455
	B	1.623
59	A	1.437
	B	1.629
95	A	1.412
	B	1.586
142	A	1.393
	B	1.556

Table A-3. Summary of wet and dry weights for samples of different size rainbow trout caught in Lake 3 during 1971.

Wet wt(g)	Dry wt(g)	Dry/wetx100	Wet wt(g)	Dry wt(g)	Dry/wetx100
4.14	0.812	19.6	22.93	6.285	27.4
6.19	1.199	19.4	22.84	6.266	27.8
5.62	1.058	18.8	24.50	6.373	26.0
7.29	1.450	19.9	17.63	4.304	24.4
5.81	1.206	20.8	10.38	2.666	25.7
6.85	1.375	20.1	20.07	4.888	24.4
5.94	1.161	19.6	19.67	4.692	23.8
4.34	0.820	18.9	18.33	5.251	18.6
6.19	1.247	20.1	18.24	4.09	22.4
6.00	1.076	17.9	29.98	9.32	31.1
4.30	0.834	19.4	38.23	9.30	24.3
7.28	1.473	20.2	42.67	12.01	28.1
3.14	0.617	19.6	54.47	13.70	25.1
4.46	0.919	20.6	52.66	13.52	25.7
5.63	1.060	18.8	62.54	16.84	26.9
5.52	1.015	18.2	70.96	20.43	28.8
3.81	0.623	16.3	116.27	42.30	25.4
8.64	1.595	18.5	130.87	32.30	24.7
7.58	1.484	19.6	119.56	30.92	25.9
7.20	1.335	18.5	117.18	33.91	28.9
7.76	1.597	20.6	83.50	25.98	31.1
8.13	1.479	18.2	101.42	28.03	27.6
11.34	2.102	18.5	114.50	27.02	23.6
6.54	1.408	21.5	114.99	29.76	25.9
5.32	1.106	20.8	107.28	33.63	31.3
7.85	1.687	21.5	158.70	47.24	29.8
8.47	1.876	22.1	151.95	44.46	29.3
8.18	1.677	20.5	118.06	35.82	30.3
7.13	1.324	18.6	81.42	22.54	27.7
12.82	2.556	19.9	130.88	34.52	26.4
7.55	1.636	21.7	261.49	68.64	26.2
21.32	5.426	25.2	126.85	30.08	23.7
24.66	5.753	23.3	95.77	37.66	31.3
255.71	69.41	27.1	198.45	62.51	31.5
116.70	36.59	31.4	147.10	43.42	29.7
116.93	33.29	28.5	173.03	53.36	30.8
140.30	39.90	28.4	155.43	46.40	29.8
140.60	43.85	31.2	142.67	42.68	29.9
147.79	42.89	29.0	137.48	42.31	30.8
139.49	41.47	29.8			

Table B-1. Number and dry weight of major food organisms in the stomachs of Lake 3 rainbow trout caught during 1970 and 1971 diel gill netting experiments.

Date	Time	No. of fish	Dry wt(g)	Food organisms							
				Amphipods		Cladocerans		Chironomids(l.)		Other*	
				No.	wt(g)	No.	wt(g)	No.	wt(g)	No.	wt(g)
July 28-29 1970	2100	10	309	221	0.288	-	-	2	-	26	0.047
	2400	10	238	279	0.353	66	-	1	-	9	0.042
	0300	10	254	191	0.296	-	-	-	-	41	0.074
	0600	10	230	83	0.159	-	-	4	0.003	11	0.050
	0900	6	153	65	0.135	-	-	9	0.008	27	0.065
	1200	10	240	127	0.228	-	-	34	0.021	41	0.006
	1500	8	218	142	0.350	-	-	99	0.050	5	0.001
	1800	10	278	425	0.849	-	-	45	0.056	26	0.014
Aug. 25-26 1970	1500	10	421	290	0.260	742	0.114	1	-	26	0.033
	1800	10	360	118	0.156	1472	0.150	5	0.003	20	0.039
	2100	10	357	85	0.059	5363	0.315	-	-	42	0.078
	2400	10	344	848	1.385	215	0.037	1	-	3	-
	0300	10	351	420	0.730	271	0.053	3	-	-	-
	0600	10	278	784	1.316	344	0.066	67	0.092	2	-
	0900	9	257	162	0.255	1477	0.153	3	-	30	0.036
	1200	10	368	194	0.281	917	0.102	6	0.004	18	0.030
Sept. 27-28 1970	1800	10	608	249	0.422	8996	1.242	-	-	34	0.052
	2100	7	385	439	0.610	837	0.305	-	-	18	0.022
	2400	10	609	454	1.037	-	-	-	-	6	0.004
	0300	10	582	691	1.544	-	-	-	-	3	-
	0600	10	629	724	1.859	-	-	-	-	10	0.018
	0900	6	533	177	0.369	3925	0.593	-	-	22	0.049
	1200	10	346	755	1.787	965	0.152	2	-	8	0.004
	1500	10	531	696	1.299	4700	0.750	5	-	20	0.037

Table B-1. Cont'd.

Date	Time	No. of fish	Dry wt(g)	Food organisms							
				Amphipods		Cladocerans		Chironomids(l.)		Other*	
				No.	wt(g)	No.	wt(g)	No.	wt(g)	No.	wt(g)
May 26-27+	0900	9	12	20	0.023	315	0.020	313	0.111	10	0.030
June 2-3,1971	1200	15	17	78	0.070	1417	0.088	179	0.069	34	0.004
"	1500	6	7	8	0.011	1023	0.052	25	0.014	12	-
"	1800	10	13	10	0.011	2212	0.105	266	0.068	14	0.026
"	2100	14	20	35	0.061	1105	0.068	656	0.167	14	-
"	2400	6	8	10	0.015	211	0.020	358	0.076	24	0.044
"	0300	5	5	4	0.012	-	-	-	-	-	-
"	0600	18	25	13	0.018	1045	0.075	624	0.160	19	0.011
June 21-22	1500	10	111	143	0.038	526	0.029	14	0.004	98	0.051
1971	1800	5	62	614	0.222	23	-	32	0.016	64	0.091
"	2100	10	152	290	0.073	419	0.033	2	-	165	0.280
"	2400	10	112	45	0.048	1123	0.066	-	-	71	0.119
"	0300	10	113	29	0.014	440	0.021	-	-	4	0.007
"	0600	10	121	28	0.045	71	0.003	1	-	22	0.013
"	0900	10	162	128	0.053	304	0.015	-	-	13	0.015
"	1200	10	146	116	0.104	33	0.002	6	-	2	0.005
July 14-15	1500	10	176	191	0.393	1143	0.157	13	0.008	436	0.173
1971	1800	10	228	357	0.607	429	0.060	65	0.067	105	0.114
"	2100	10	192	100	0.288	3613	0.452	14	0.008	123	0.073
"	2400	10	191	435	0.635	45	-	3	-	9	0.039
"	0300	7	87	37	0.030	159	0.007	39	0.055	1	-
"	0600	10	153	63	0.099	423	0.034	6	0.003	8	0.021
"	0900	10	150	310	0.262	1408	0.141	18	0.122	51	0.064
"	1200	10	169	192	0.509	694	0.106	72	0.019	227	0.108

Table B-1. Cont'd.

Date	Time	No. of fish	Dry wt(g)	Food Organisms							
				Amphipods		Cladocerans		Chironomids(l.)		Other*	
				No.	wt(g)	No.	wt(g)	No.	wt(g)	No.	wt(g)
Aug. 9-10 1971	1500	9	289	569	1.077	527	0.069	2	-	2	-
	1800	10	294	492	0.787	84	0.006	50	0.096	1	-
	2100	8	207	332	0.563	161	0.017	26	0.020	10	0.018
	2400	10	305	342	0.699	-	-	-	-	-	-
	0300	10	285	164	0.246	-	-	-	-	-	-
	0600	10	388	99	0.181	-	-	3	0.003	-	-
	0900	9	281	151	0.304	25	0.002	1	-	2	0.003
	1200	5	186	244	0.565	-	-	7	0.005	2	0.002
Aug. 30-31 1971	1500	10	400	766	1.708	1014	0.089	23	0.027	10	0.051
	1800	10	377	718	2.135	-	-	73	0.088	4	0.012
	2100	10	501	388	0.967	-	-	5	0.004	3	0.012
	2400	10	370	419	1.082	-	-	2	-	-	-
	0300	10	398	256	0.659	-	-	-	-	-	-
	0600	10	418	141	0.319	-	-	-	-	-	-
	0900	10	446	459	1.664	-	-	55	0.046	4	0.012
	1200	10	467	571	1.804	553	0.045	70	0.065	7	0.007
Sept. 19-20 1971	1500	10	705	1177	3.912	105	0.012	23	0.025	5	-
	1800	10	651	1532	5.449	-	-	44	0.038	2	-
	2100	10	579	762	1.952	-	-	8	0.014	3	-
	2400	8	506	468	1.300	14	-	5	0.006	2	-
	0300	10	505	268	0.626	-	-	5	0.015	3	-
	0600	10	548	286	0.820	15	-	1	-	1	-
	0900	10	569	294	0.965	-	-	6	0.008	3	-
	1200	10	590	568	1.892	370	0.033	10	0.012	2	-

Table B-1. Cont'd.

Date	Time	No. of fish	Dry wt(g)	Food Organisms							
				Amphipods		Cladocerans		Chironomids(l.)		Other*	
				No.	wt(g)	No.	wt(g)	No.	wt(g)	No.	wt(g)
Oct. 20-21	1500	9	564	440	1.637	-	-	2	-	2	0.019
1971	1800	8	510	405	1.354	-	-	-	-	-	-
"	2100	9	531	391	1.189	-	-	-	-	-	-
"	2400	10	586	270	0.842	-	-	-	-	1	0.018
"	0300	10	680	226	0.670	-	-	1	-	-	-
"	0600	7	395	91	0.246	-	-	-	-	-	-
"	0900	10	609	232	0.756	-	-	-	-	1	-
"	1200	10	617	219	0.676	-	-	1	-	-	-

\*Depending on time of year, this group consisted mainly of Dytiscus Larvae, Zygoptera naiads, Chaoborus Larvae and Corixids.

Table C-1. Analysis of variance test for differences in consumption of several aquatic invertebrates by rainbow trout in a clear, concealment-free aquarium.

Source	d.f	SS	MS	F
Total	39	7382.6		
Between	4	2286.4	457.3	3.59*
Residual	35	5096.3	127.4	

\* $P < 0.05$

Table C-2. Analysis of variance test for differences in consumption of several aquatic invertebrates by rainbow trout in a simulated natural environment.

Source	d.f	SS	MS	F
Total	39	4457.5		
Between	4	1534.2	308.9	4.20*
Residual	35	2923.3	73.1	

\* $P < 0.05$

Table C-3. Summary of data for day and night benthic samples taken with a multiple corer on Lake 3 during the summer of 1971. Only the dominant invertebrates are considered.

Date	Time	No. of cores	Amphipods		Chironomid larvae	
			Total no.	no./m <sup>2</sup>	Total no.	no./m <sup>2</sup>
June 21	Day	11	48	2153	207	9285
June 22	Night	12	86	3536	259	10,649
July 29	Day	24	508	10,443	284	5838
July 30	Night	23	673	14,437	306	6564
Aug. 30	Day	24	1626	33,427	178	3659
Aug. 31	Night	12	421	17,309	48	1974

Table C-4. Summary of data for day and night water column samples taken with a Schindler trap on Lake 3 during the summer of 1971. Only dominant invertebrates are considered.

Date	Time	No. of samples	Amphipods		Cladocerans		Copepods		Corixids	
			No.	No/m <sup>3</sup>	No.	No/m <sup>3</sup>	No.	No/m <sup>3</sup>	No.	No/m <sup>3</sup>
June 21	Day	6	53	315	7092	42,214	62	369	9	54
June 22	Night	6	104	619	10,160	60,476	56	333	13	77
July 29	Day	12	28	83	3846	11,446	489	1449	10	30
July 30	Night	13	638	1753	2120	5824	379	1041	4	11
Aug. 30	Day	13	10	27	2179	5986	577	1420	1	3
Aug. 31	Night	13	405	1113	1689	4640	575	1580	2	5

Table C-5. Number of organisms recovered in daytime littoral zone samples taken with the Whitaker tank on Lake 3 during the summer of 1971.

Organism	June 22	July 29		Aug. 30	
	51 cm.	30 cm.	69 cm.	33 cm.	66 cm.
<u>Gammarus</u>	2526	708	1578	258	840
<u>Hyalella</u>	84	24	-	750	156
Corixidae	90	-	-	-	12
Zygoptera	-	-	-	-	12
<u>Dytiscus</u>	7	-	-	-	-
Trichoptera	2	-	-	-	-
Chironomidae	60	-	36	-	30
Cladocera	594	-	-	-	-
Hirudinea	26	-	-	18	-
Gastropoda	-	-	-	-	6

Table C-6. Summary of stomach content information used in the assessment of day<sup>1</sup> and night<sup>2</sup> feeding selectivity of Lake 3 rainbow trout.

Date	Time	No. of Stomachs	Amphipods		Cladocerans		Chironomids(1.)		Dytiscids(1.)	
			No.	%total	No.	%total	No.	%total	No.	%total
June 21	Day	25	873	53	582	36	52	3	113	7
June 22	Night	30	364	14	1982	78	2	-	39	5
Aug. 9	Day	24	1305	64	611	30	119	6	-	-
Aug. 10	Night	28	828	81	161	16	26	3	-	-
Aug. 30	Day	30	2055	54	1567	41	168	4	-	-
Aug. 31	Night	30	1064	99	-	-	7	1	-	-

<sup>1</sup>Daytime results are based on stomach contents of trout captured at 1200, 1500, and 1800 hours

<sup>2</sup>Nighttime " " " " " " " " " " 2100, 2400, and 0300 hours

Table D-1. Summary of data from digestion rate experiments conducted on rainbow trout during the summers of 1970 and 1971.

Expt.	Time after feeding(hrs.)	No. of fish	Dry wt of fish(g)	Dry wt of food(g)	% of initial food remaining
A	0.2	9	8.11	0.341	100.0
	6	10	9.03	0.320	84.3
	12	10	7.77	0.218	66.9
	18	10	8.71	0.150	41.2
	24	10	8.05	0.139	41.0
	30	10	9.03	0.092	24.3
B	0.2	4	24.1	0.140	100.0
	7.5	4	23.0	0.112	78.7
	13.5	4	24.0	0.075	48.0
	19.5	4	27.8	0.062	34.4
	25.5	4	20.5	0.042	31.5
	31.5	4	27.3	0.035	19.6
	38.0	4	21.3	0.026	18.4
	43.5	4	20.0	0.007	5.6
C	0.2	2	12.4	0.059	100.0
	6	2	11.3	0.034	58.1
	9	2	15.0	0.023	30.2
	12	2	10.3	0.012	21.8
	21	2	11.0	0.002	3.0
D	0.2	10	6.93	0.302	100.0
	6	10	6.49	0.157	55.5
	12	10	6.47	0.082	29.1
	18	10	6.42	0.025	8.9
	24	10	6.46	0.003	1.1
	30	10	5.94	0.001	0.2
E	0.2	7	67.5	0.758	100.0
	6	6	57.6	0.316	47.8
	12	8	78.8	0.179	20.0
	18	8	84.9	0.004	0.9
F	0.2	9	7.07	0.437	100.0
	3	11	7.87	0.364	74.6
	6	10	8.40	0.251	48.3
	9	10	6.94	0.116	27.0
	12	10	7.55	0.054	11.5
	15	10	6.77	0.017	4.0
	19	10	8.60	0.006	1.1

Table D-1. Cont'd.

Expt.	Time after feeding(hrs.)	No. of fish	Dry wt of fish(g)	Dry wt. of food(g)	% of initial food remaining
G	0.2	8	12.0	0.488	100.0
	3	9	12.5	0.401	79.1
	6	8	12.3	0.298	59.6
	9	8	12.8	0.159	30.8
	12	8	13.2	0.074	13.8
	15	8	14.1	0.071	12.3
	18	8	12.9	0.022	4.2
	21	8	13.6	0.010	1.7
H	0.2	7	8.95	0.166	100.0
	3	7	7.72	0.126	83.9
	6	8	9.27	0.093	54.3
	9	8	8.49	0.057	36.0
	12	8	7.11	0.046	16.1
	15	6	7.65	0.010	7.0
	18	5	6.64	0.006	5.4
I	0.2	2	10.1	0.116	100.0
	3	2	11.0	0.086	74.4
	6	2	6.2	0.054	46.9
	9	2	5.9	0.047	33.6
	12	2	8.1	0.013	12.9
	15	2	8.6	0.008	6.8
	18	2	6.7	0.005	4.5
J	4	2	50.7	0.32	56.5
	8	3	75.0	0.15	30.4
	12	3	81.2	0.27	23.2
	18	3	75.0	0.07	5.5
K	0.2	10	16.7	0.358	100.0
	3	8	12.9	0.262	95.3
	6	8	11.8	0.140	55.1
	9	8	12.6	0.073	27.1
	12	8	12.9	0.055	19.6
	15	8	12.3	0.013	5.1
L	0.2	3	29.8	0.443	100.0
	6	3	25.8	0.262	67.8
	12	3	23.4	0.052	14.8
	18	3	29.6	0.014	3.4

Table D-1. Cont'd.

Expt.	Time after feeding(hrs.)	No. of fish	Dry wt. of fish(g)	Dry wt. of food(g)	% of initial food remaining
M	0.2	7	12.4	1.101	100.0
	6	8	13.1	0.765	65.8
	12	8	13.3	0.705	59.9
	18	8	11.9	0.441	41.9
	24	8	12.9	0.446	38.9
	30	7	12.7	0.134	12.0
	36	8	12.4	0.059	5.4
	42	7	7.4	0.026	4.1
	48	7	11.8	0.021	1.9
N	0.2	8	40.2	0.395	100.0
	4	7	49.0	0.292	61.2
	8	8	41.6	0.126	30.6
	12	10	48.8	0.027	6.1
	16	10	40.3	0.032	8.2
	20	10	53.1	0.009	1.6
O	0.2	8	12.1	1.072	100.0
	6	8	11.7	0.762	73.3
	10	7	11.5	0.632	61.9
	15	6	8.8	0.342	43.6
	21	7	10.3	0.242	26.4
	27	7	8.8	0.140	18.0
	33	4	5.7	0.034	6.9
	39	5	6.8	0.033	5.5
P	0.2	10	6.67	0.165	100.0
	3	10	5.86	0.077	53.4
	6	10	7.18	0.049	27.5
	9	12	7.55	0.025	13.8
	12	10	6.17	0.002	1.2
Q	0.2	9	72.8	0.989	100.0
	3	8	60.5	0.496	60.3
	6	8	76.4	0.351	33.8
	9	8	85.4	0.163	14.0
	12	9	79.1	0.042	3.7
	15	8	83.0	0.006	0.7

Table D-2. Summary of regression analysis data for rainbow trout digestion rate experiments.

Expt.	slope(b)	d.f.(n-2)	$t_{0.05}$	$S_b$	C.I. ( $b \pm t_{0.05} S_b$ )
A	-0.0522	4	2.78	0.0050	-0.0384 to -0.0662
B	-0.0582	6	2.45	0.0070	-0.0411 to -0.0753
C	-0.1698	3	3.18	0.0175	-0.1140 to -0.2256
D	-0.2084	4	2.78	0.0268	-0.1338 to -0.2830
E	-0.2500	2	4.30	0.0670	+0.0382 to -0.5382
F	-0.2408	6	2.45	0.0205	-0.1906 to -0.2910
G	-0.1934	6	2.45	0.0161	-0.1539 to -0.2329
H	-0.1572	4	2.78	0.0339	-0.0630 to -0.2514
I	-0.1831	5	2.57	0.0130	-0.1498 to -0.2164
J	-0.1543	3	3.18	0.0158	-0.1041 to -0.2045
K	-0.2296	3	3.18	0.0294	-0.1362 to -0.3230
L	-0.1944	2	4.30	0.0319	-0.0571 to -0.3317
M	-0.0840	7	2.37	0.0080	-0.0651 to -0.1029
N	-0.2023	4	2.78	0.0267	-0.1281 to -0.2765
O	-0.0786	6	2.45	0.0052	-0.0658 to -0.0914
P	-0.3400	3	3.18	0.0692	-0.1200 to -0.5600
Q	-0.3244	4	2.78	0.0387	-0.2168 to -0.4320
A+B <sup>1</sup>	-0.0567	12	2.18	-0.0050	-0.0458 to -0.0676
C+D+E	-0.1893	13	2.16	-0.0206	-0.1448 to -0.2338
P+Q	-0.3290	9	2.26	-0.317	-0.2574 to -0.4006
M+O	-0.0824	15	2.13	-0.0048	-0.0722 to -0.0926
I+N+F+G	-0.2023	36	2.06	-0.0109	-0.1798 to -0.2248

<sup>1</sup>An analysis of covariance test for difference in slopes was performed on each set of data prior to combining them.

Table D-3. Summary of analysis of covariance tests for significant differences in slopes of the regressions of ln percent food remaining in the stomach on time linear.

Test comparison	Source of variation	d.f	SS(X)	SP(XY)	SS(Y)	Deviations from regression			
						d.f	SS(Dev)	MS(Dev)	F
Meal size (FvsGvsH)	F	6	271	-65	16	5	0.36		
	G	7	378	-73	15	6	0.58		
	H	5	158	-28	5	4	0.28		
	Within					15	1.22	0.08	3.03
	Reg.coef.					2	0.49	0.25	
	Common	18	808	-165	37	17	1.72		
5C vs 12C (AB vs CDE)	AB	13	2360	-134	8	12	0.70		
	CDE	14	805	-152	33	13	4.47		
	Within					25	5.17	0.21	51.0*
	Reg.coef.					1	10.56	10.56	
	Common	27	3165	-286	41	26	15.73		
12C vs 17C (CDE vs INFG)	CDE	14	805	-152	33	13	4.47		
	INFG	27	1197	-242	53	26	3.70		
	Within					39	8.18	0.21	0.40
	Reg.coef.					1	0.08	0.08	
	Common	41	2002	-394	86	40	8.26		
17C vs 22C (INFG vs PQ)	INFG	27	1197	-242	53	26	3.70		
	PQ	10	251	-83	29	9	2.27		
	Within					35	5.97	0.17	19.5*
	Reg.coef.					1	3.33	3.33	
	Common	37	1448	-325	82	36	9.31		

Table D-3. Cont'd.

Test comparison	Source of variation	d.f.	SS(X)	SP(XY)	SS(Y)	Deviations from regression			
						d.f.	SS(Dev)	MS(Dev)	F
Amphipods vs cladocerans (INFG vs K)	INFG	27	1197	-242	53	26	3.70		
	K	3	90	-21	5	2	0.23		
	Within Reg.coef. common	30	1287	-263	58	28 1 29	3.94 0.06	0.14 0.06	0.44
Amphipods vs <u>Chaoborus</u> (INFG vs L)	INFG	27	1197	-242	53	26	3.70		
	L	3	180	-35	7	2	0.36		
	Within Reg.coef. common	30	1377	-277	60	28 1 29	4.07 0.01 4.08	0.15 0.01	0.07
Amphipods vs artificial food (INFG vs MO)	INFG	27	1197	-242	53	26	3.70		
	MO	16	3451	-283	24	15	1.20		
	Within Reg.coef. common	43	4648	-525	77	41 1 42	4.90 12.87 17.77	0.12 12.87	107.6*
33g.fish vs 38.6g.fish (D vs E)	D	5	630	-132	29	4	1.81	0.45	
	E	3	180	-45	13	2	1.62	0.81	

Table D-3. Cont'd.

Test comparison	Source of variation	d.f.	SS(X)	SP(XY)	SS(Y)	Deviations from regression			
						d.f.	SS(Dev)	MS(Dev)	F
	Within					6	3.43	0.57	0.19
	Reg.coef.					1	0.11	0.11	
	Common	8	810	-177	42	7	3.32		
5.9g.fish vs.	FG	14	657	-138	31	13	2.21		
19.7g.fish	IN	12	540	-104	22	11	1.41		
(FG vs IN)									
	Within					24	3.62	0.15	0.54
	Reg.coef.					1	0.08	0.08	
	Common	26	1197	-242	53	25	3.70		
12.8g. fish vs	INFG	27	1197	-242	53	26	3.70		
98.8g. fish	J	4	195	-30	5	3	0.15		
(INFG vs J)									
	Within					29	3.85	0.13	2.91
	Reg.coef.					1	0.39	0.39	
	Common	31	1392	-272	58	30	4.23		
3.3g.fish vs	M	4	90	-31	12	3	1.29		
35.2g. fish	O	5	158	-51	18	4	0.94		
(M vs O)									
	Within					7	2.24	0.32	0.44
	Reg.coef.					1	0.01	0.01	
	Common	9	248	-82	30	8	2.24		

\*P&lt;0.05

Table E-1. Summary of data from 1971 gill netting experiments used in calculation of daily ration of Lake 3 rainbow trout.

Date	Time Interval	No. of fish	Index stomach fullness	Amt. digested during interval	Interval consumption
May 25-26 + June 2-3	0430				
	-0730	18	1.906	0.789	1.633
	-1030	9	2.790	1.155	0.741
	-1330	15	2.376	0.984	0.539
	-1630	6	1.931	0.799	1.870
	-1930	10	3.002	1.243	0.946
	-2230	14	2.705	1.120	1.408
	-0130	6	2.993	1.239	-
	-0430	5	1.053	0.436	1.289
Daily ration = 8.426					
June 21-22	0430				
	-0730	10	0.090	0.049	0.053
	-1030	10	0.094	0.051	0.094
	-1330	10	0.137	0.074	0.133
	-1630	10	0.196	0.106	0.871
	-1930	5	0.961	0.519	0.017
	-2230	10	0.459	0.248	0.165
	-0130	10	0.376	0.203	-
	-0430	10	0.067	0.036	0.059
Daily ration = 1.392					
July 14-15	0430				
	-0730	10	0.187	0.101	0.486
	-1030	10	0.572	0.309	0.548
	-1330	10	0.821	0.443	0.524
	-1630	10	0.740	0.400	0.328
	-1930	10	0.668	0.361	0.460
	-2230	10	0.767	0.414	0.284
	-0130	10	0.637	0.344	-
	-0430	7	0.198	0.107	0.096
Daily ration = 2.726					

Table E-1. Cont'd.

Date	Time interval	No. of fish	Index stomach fullness	Amt. digested during interval	Interval consumption
Aug. 9-10	0430				
	-0730	10	0.085	0.046	0.159
	-1030	9	0.198	0.107	0.463
	-1330	5	0.554	0.299	0.460
	-1630	9	0.715	0.386	0.216
	-1930	10	0.545	0.294	0.287
	-2230	8	0.538	0.291	0.167
	-0130	10	0.414	0.224	-
	-0430	10	0.155	0.084	0.014
Daily ration = 1.766					
Aug. 30-31	0430				
	-0730	10	0.137	0.074	0.632
	-1030	10	0.695	0.375	0.420
	-1330	10	0.740	0.400	0.504
	-1630	10	0.844	0.456	0.679
	-1930	10	1.067	0.576	-
	-2230	10	0.347	0.187	0.366
	-0130	10	0.526	0.284	0.057
	-0430	10	0.299	0.161	-
Daily ration = 2.658					
Sept. 19-20	0430				
	-0730	10	0.270	0.110	0.148
	-1030	10	0.308	0.126	0.408
	-1330	10	0.590	0.241	0.641
	-1630	10	1.010	0.413	0.920
	-1930	10	1.517	0.620	-
	-2230	10	0.610	0.249	0.103
	-0130	8	0.464	0.190	-
	-0430	10	0.229	0.094	0.135
Daily ration = 2.355					
Oct. 20-21	0430				
	-0730	7	0.112	0.028	0.139
	-1030	10	0.223	0.055	0.030
	-1330	10	0.198	0.049	0.380
	-1630	9	0.529	0.131	0.081
	-1930	8	0.479	0.119	0.043
	-2230	9	0.403	0.100	-
	-0130	10	0.265	0.066	-
	-0430	10	0.178	0.044	-
Daily ration = 0.673					