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A Comparison of the Diet and Growth of the Trout from the Upper Au Sable and Upper Manistee Rivers, Michigan

James W. Strogen, Jr.

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A COMPARISON OF THE DIET AND GROWTH OF THE TROUT FROM THE UPPER AU SABLE AND UPPER MANISTEE RIVERS, MICHIGAN *

By James W. Strogen, Jr.

* This is a reprint of a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fisheries, in the School of Natural Resources, The University of Michigan, 1979.

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TABLE OF CONTENTS

	Page
ACKNOWLEDGMENTS	ii
LIST OF TABLES	v
LIST OF FIGURES	vii
LIST OF APPENDICES	viii
ABSTRACT	ix
INTRODUCTION	1
METHODS	3
RESULTS	7
Trout diet	18
Upper Au Sable 3.0- to 5.9-inch brook trout	18
Upper Au Sable 7.0- to 9.9-inch brook trout	20
Upper Manistee 3.0- to 5.9-inch brown trout	20
Upper Manistee 7.0- to 9.9-inch brown trout	22
Total stomach volume--total length relationship	22
Growth as measured by length	24
Growth as measured by weight	30
Length-weight relationship	30
Total volume-total weight relationship	32
Trout populations	33
Trout density	33
DISCUSSION	37
Seasonal changes in trout diet	37
Upper Au Sable 3.0- to 5.9-inch brook trout	38
Upper Au Sable 7.0- to 9.9-inch brook trout	39
Upper Manistee 3.0- to 5.9-inch brown trout	40
Upper Manistee 7.0- to 9.9-inch brown trout	40

Page

Total stomach volume-total length relationship 41

Growth as measured by length 42

Growth as measured by weight 43

Length-weight relationship 43

Quantity vs. quality 43

Total stomach volume-total weight relationship 46

Trout populations 47

Trout density 48

LITERATURE CITED 51

APPENDIX 53

LIST OF TABLES

Table		Page
1.	Mean volume of stomach contents (milliliters) of brook trout 3.0-5.9 inches total length from the upper Main Au Sable River, May-September 1976	8
2.	Mean volume of stomach contents (milliliters) of brook trout 7.0-9.9 inches total length from the upper Main Au Sable River, May-September 1976	10
3.	Mean volume of stomach contents (milliliters) of brown trout 3.0-5.9 inches total length from the upper Manistee River, May-September 1976	12
4.	Mean volume of stomach contents (milliliters) of brown trout 7.0-9.9 inches total length from the upper Manistee River, May-September 1976	14
5.	The natural log of total stomach volume and the natural log of total length measurements with 95% confidence limits for the upper Au Sable, upper Manistee, South Branch, and lower Au Sable rivers to accompany Figure 3. R^2 values and number of fish sampled are included	23
6.	Mean lengths (inches) at various ages for brook and brown trout on the upper Au Sable and upper Manistee rivers, May-September 1976 and weighted mean lengths, fall 1976	25
7.	Mean weights (grams) at various ages for brook and brown trout on the upper Au Sable and upper Manistee rivers, May-September 1976	26
8.	Mean lengths (inches) at various ages for brown trout on the South Branch Au Sable, lower Au Sable, and upper Manistee rivers, May-September 1976 and weighted mean lengths, fall 1976	27

Table		Page

9. Mean weights (grams) at various ages for brown trout on the South Branch Au Sable, lower Au Sable, and upper Manistee rivers, May-September 1976 28

10. Number of trout per acre for the upper Au Sable and upper Manistee rivers, fall 1976 34

11. Pounds of trout per acre for the upper Au Sable and upper Manistee rivers, fall 1976 35

LIST OF FIGURES

Figure		Page
1.	Location of sampling sites on the upper Au Sable and upper Manistee rivers	4
2.	Total monthly mean stomach volumes (milliliters) of upper Au Sable, upper Manistee, South Branch and lower Au Sable trout 3.0-5.9 inches and 7.0-9.9 inches with 95% confidence limits	16
3.	Regression of the natural log of total stomach volume vs. the natural log of total length for upper Au Sable brook trout, upper Manistee brown trout, South Branch brown trout, and lower Au Sable brown trout, May-September 1976	17
4.	Percent composition of the diet of brook trout from the upper Main Au Sable River, May-September 1976	19
5.	Percent composition of the diet of brown trout from the upper Manistee River, May-September 1976	21

LIST OF APPENDICES

Appendix Page

1. Mean volume of stomach contents (milliliters) of brown trout 3.0-5.9 inches total length from the South Branch Au Sable River, May-September 1976 (unadjusted figures) 53

2. Mean volume of stomach contents (milliliters) of brown trout 7.0-9.9 inches total length from the South Branch Au Sable River, May-September 1976 (unadjusted figures) 54

3. Mean volume of stomach contents (milliliters) of brown trout 3.0-5.9 inches total length from the lower Au Sable River, May-September 1976 (unadjusted figures) 55

4. Mean volume of stomach contents (milliliters) of brown trout 7.0-9.9 inches total length from the lower Au Sable River, May-September 1976 (unadjusted figures) 56

ABSTRACT

Brook trout from the upper Au Sable River and brown trout from the upper Manistee River, the dominant species, were sampled from May through September 1976. Equal numbers of small (3.0-5.9 inches) and large (7.0-9.9 inches) trout were sampled. Diet composition, various growth parameters, and population estimates were determined. These data were then compared to the results obtained by Stauffer (1977) on the brown trout populations of the South Branch and lower Au Sable rivers.

The diet of the trout sampled in each river was heavily dependent on one food item. Hexagenia limbata accounted for about 35% of the total consumption in the upper Au Sable brook trout diet, while trichopterans, especially Brachycentrus accounted for about 45% of the total upper Manistee brown trout diet. Fish became an increasingly important food source in both rivers as the trout attained greater lengths.

Some food items were more important at certain times of the year. Hexagenia limbata consumption by all trout on the upper Au Sable occurred almost entirely in June. Trichoptera and other Ephemeroptera consumption remained relatively constant from month to month in the smaller trout diet, but these insects were of varying degrees of importance to the larger trout throughout the summer. On the upper Manistee River, Ephemeroptera supplemented the diet early in the season, while Diptera became more important later in the season. Diptera consumption was highest in the month of June for the larger upper Manistee brown trout.

The upper Au Sable brook trout ate more than the brown trout from the upper Manistee, South Branch, and lower Au Sable in the smaller size range, but had less food in their stomachs than the brown trout at the greater lengths. The upper Manistee and South Branch total stomach volumes were essentially identical for the entire range sampled, yet the South Branch brown trout were found to be longer and heavier than the upper Manistee brown trout at any given age. There was no significant difference found in the lengths and weights of the upper Au Sable brook trout and the upper Manistee brown trout.

The upper Au Sable was estimated to contain 276.8 trout per acre and the upper Manistee to contain approximately 1148.9 trout per acre. Density of trout was not found to be a factor in determining trout weight on these rivers or the South Branch. Density was thought to be a factor in the lower Au Sable River where the number of brown trout in the stream apparently influenced the weight of the brown trout in the stream.

INTRODUCTION

The Au Sable and Manistee rivers are among the most prestigious trout streams in Michigan. Much of their fame comes from fishing success in the middle and lower sections of the rivers but little has been reported about the upper sections. This report will focus on the upper sections of these two rivers.

These wooded upper regions are largely uninhabited. Soils of the area are comprised mainly of sand and gravel (Burgis 1977; Coopes 1974), which lead to a high degree of water infiltration into the water table. This provides a stable stream discharge, even during the summer months, which is an important factor in maintaining conditions suitable for the fine trout populations that dominate these rivers (Benson 1953b).

The upper Au Sable trout population is predominantly brook trout (Salvelinus fontinalis) with a few brown trout (Salmo trutta) also present. The upper Manistee is dominated by brown trout with some brook trout and a few rainbow trout (Salmo gairdneri).

This study was threefold in scope. First, the stomach contents of the dominant trout species in each of the rivers were analyzed to determine diet composition. Second, different growth parameters were determined and compared. Third, population estimates were made and age structures determined. In addition to this baseline information a comparison was made between the brown trout of the upper Manistee and the brown trout in the lower Au Sable and the South Branch of the Au Sable (Stauffer 1977).

METHODS

Monthly samples were taken from May through September 1976 which is when most feeding and growth of trout occurs (Leonard 1941; Benson 1953a; Alexander and Shetter 1969; Alexander and Gowing 1976). The sampling sites for the upper Au Sable were Forks, Cameron Bridge Road, 612 Bridge, Wakui Canoe Livery, Animal Land, Wakui Campground, MacAurthur's, Pollak Bridge and several locations between Pollak Bridge and M-72 Bridge, and for the upper Manistee they were Mancelona Road, Triangle, Ford, Loop, Arbor vitae, Ogemaw Trail, Deward, Lower Deward, High Banks, and Cameron Bridge Road (Fig. 1). These sites were spaced through the study area to better represent the stream types prevalent in the rivers.

Samples were taken from the two rivers at approximately the same day and time of day each month using a 230-volt d-c generator (Shetter 1947). Samples from each river totaled 50 fish per month. Twenty-five of the fish were in the 3.0- to 5.9-inch group; twenty-five fish were in the 7.0- to 9.9-inch group. The fish taken from the upper Au Sable River were brook trout, while the fish taken from the upper Manistee River were brown trout. Sampling the same species from both rivers would have been more desirable and would have afforded more meaningful comparisons, but unfortunately sufficient numbers of a single species were not found in both rivers.

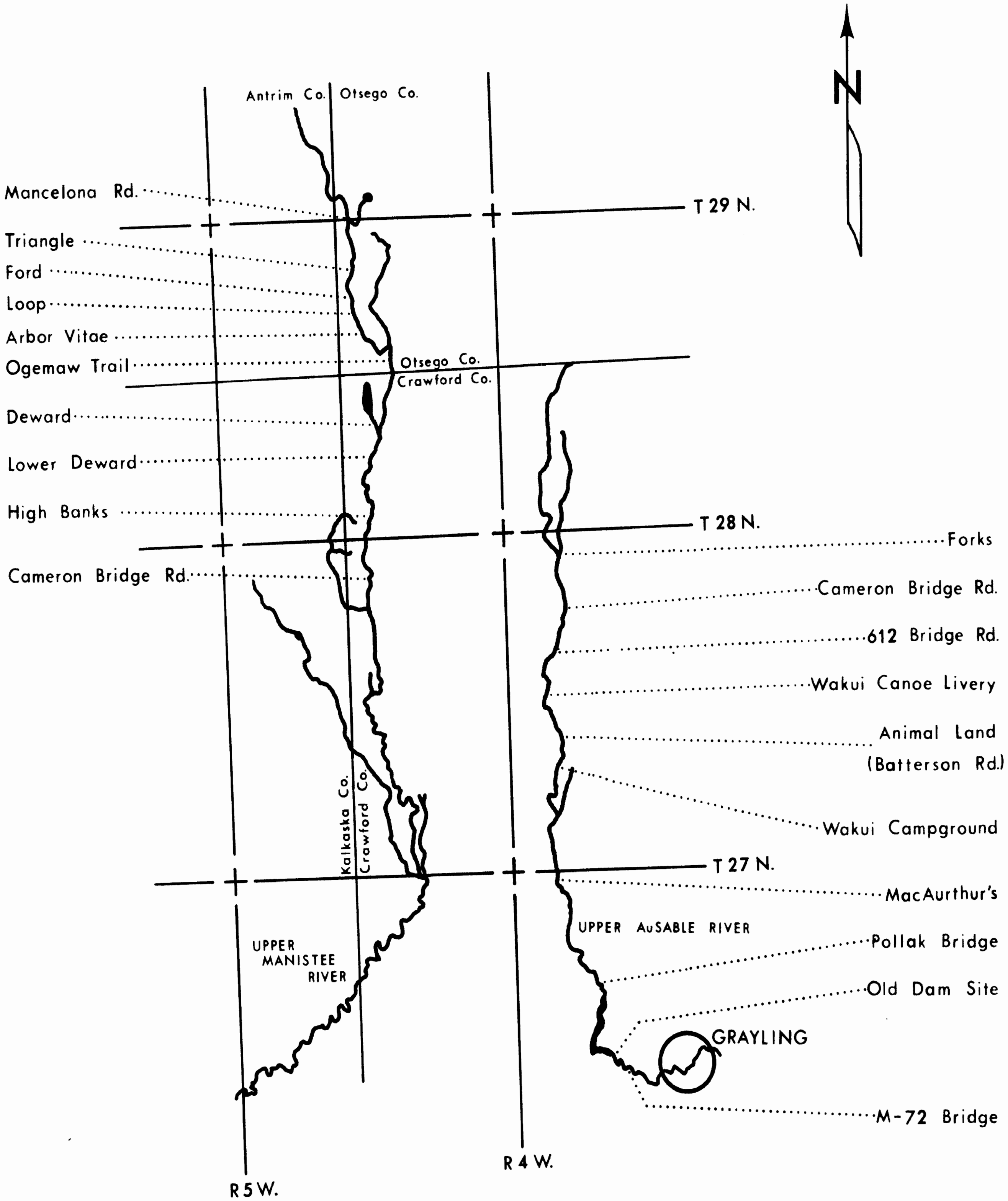

Figure 1.--Location of sampling sites on the upper Au Sable and upper Manistee rivers.

Once the proper number and size fish were secured, they were transferred on ice to the laboratory where they were measured to the nearest 0.1 inch (total length), weighed to the nearest 0.1 gram and the sex was determined. A scale sample was taken from the caudal peduncle area of each fish (Cooper 1949). Impressions of trout scales were made on cellulose acetate squares and examined with a microprojector. Age (number of annuli) was determined for each fish according to the procedure outlined by Cooper (1951).

Stomach samples were processed in the manner described by Alexander and Gowing (1976) and Stauffer (1977). Identification tags including pertinent data were inserted into the esophagus of the fish. Fish 5 inches and less were slit along the sides and preserved whole in a 10% formalin solution. Gills, stomach, and intestines were removed from the larger fish and preserved in the formalin solution. After a period of time sufficient to harden the viscera and contents, the stomachs were cut open and the contents and the accompanying identification tag were placed in a vial containing 70% alcohol. The contents were identified to the family level. The number of individuals present and the total volume of displacement for each group were determined to the nearest 0.025 ml. The stomach contents were thought to represent food eaten in the previous 6-8 hours before capture (Windell and Norris 1969; Bryan and Larkin 1972).

Fall population estimates on the two rivers were run from October through November 1976 by personnel of the Fisheries Division, Michigan Department of Natural Resources. The fall population sites on the upper Au Sable were Cameron Bridge Road, Wakui Campground, MacAurthur's, and the Old Dam site above M-72 Bridge (Fig. 1). On the upper Manistee, the fall sampling sites were Mancelona Road, Loop, Deward, and Cameron Bridge Road. Twelve-hundred-foot sections were sampled using electrofishing equipment. During the first run fish were captured, fin clipped and returned to the river. Later, a second sampling run was made and the number of marked and unmarked fish captured was recorded. These data were then used to estimate the trout population by inch group according to the Petersen mark-recapture method. Scale samples were taken of fish from each inch group to determine age compositions of the populations.

RESULTS

Presented in Tables 1 to 4 are the observed stomach contents of the upper Au Sable brook trout and the upper Manistee brown trout. Total monthly mean volumes also are presented in Figure 2, with 95% confidence limits, to illustrate more clearly the significant changes from month to month, river by river, and size by size.

Stauffer (1977) used a correction factor to compare his data on the South Branch and lower Main Au Sable. This correction factor was based on a curve of mean stomach volume against total fish length that was fitted by eye. The upper Manistee and upper Main Au Sable data were analyzed by comparison of the regression of the natural log (ln) of the average total stomach volume against the natural log (ln) of the total fish length. When Stauffer's uncorrected data (Appendices 1 to 4) were analyzed by this method the resultant regression line of the South Branch was essentially identical to that of the Manistee (Fig. 3). The lower Main Au Sable and upper Main Au Sable also were included in Figure 3. The 95% confidence limits of the Manistee and South Branch brown trout values overlapped for the entire range of the graph, as did the lower Au Sable brown trout values for much of this range. The upper Au Sable values for brook trout 6 inches and longer also overlapped. For this reason, a correction factor seemed unnecessary and was not applied.

Table 1.--Mean volume of stomach contents (milliliters) of brook trout 3.0-5.9 inches total length from the upper Au Sable River, May-September 1976 (sample sizes in parentheses), with 95% confidence levels.

Organism	Month: May (25)	June (31)	July (25)	Aug (25)	Sep (25)	Seasonal mean volume	Percent composition
Trichoptera	0.036 ±0.010	0.035 ±0.010	0.023 ±0.010	0.020 ±0.010	0.033 ±0.010	0.029 ±0.010	10.3 ±5.6
Hexagenia limbata	0.000 ±0.095	0.478 ±0.094	0.006 ±0.095	0.000 ±0.095	0.000 ±0.095	0.097 ±0.092	34.4 ±35.6
Other Ephemeroptera	0.057 ±0.024	0.028 ±0.024	0.011 ±0.024	0.022 ±0.024	0.011 ±0.024	0.026 ±0.023	9.2 ±9.0
Plecoptera	0.000 ±0.003	0.000 ±0.003	0.000 ±0.003	0.000 ±0.003	0.000 ±0.003	0.000 ±0.003	0.0 ±0.0
Odonata	0.008 ±0.008	0.000 ±0.008	0.000 ±0.008	0.000 ±0.008	0.000 ±0.008	0.002 ±0.007	0.7 ±0.0
Hemiptera	0.000 ±0.001	0.005 ±0.001	0.004 ±0.001	0.001 ±0.001	0.000 ±0.001	0.002 ±0.001	0.7 ±0.0
Coleoptera	0.002 ±0.012	0.008 ±0.012	0.008 ±0.012	0.000 ±0.012	0.006 ±0.012	0.005 ±0.012	1.8 ±4.2
Megaloptera	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.0 ±0.0
Diptera, larvae and pupae	0.002 ±0.007	0.021 ±0.006	0.004 ±0.007	0.005 ±0.007	0.004 ±0.007	0.007 ±0.006	2.5 ±2.3
Diptera adults	0.000 ±0.008	0.002 ±0.008	0.006 ±0.008	0.011 ±0.008	0.000 ±0.008	0.004 ±0.008	1.4 ±2.9
Mollusca	0.024 ±0.003	0.003 ±0.003	0.004 ±0.003	0.001 ±0.003	0.018 ±0.003	0.010 ±0.003	3.5 ±1.8
Fish	0.000 ±0.068	0.000 ±0.068	0.043 ±0.068	0.000 ±0.068	0.006 ±0.068	0.010 ±0.066	3.5 ±22.9
Isopoda Amphipoda	0.014 ±0.003	0.006 ±0.003	0.000 ±0.003	0.000 ±0.003	0.000 ±0.003	0.004 ±0.003	1.4 ±1.2
Decapoda	0.000 ±0.006	0.000 ±0.006	0.000 ±0.006	0.000 ±0.006	0.000 ±0.006	0.000 ±0.006	0.0 ±0.0
Terrestrials	0.000 ±0.010	0.001 ±0.010	0.004 ±0.010	0.003 ±0.010	0.032 ±0.010	0.008 ±0.009	2.9 ±3.4
Annelida	0.094 ±0.016	0.000 ±0.016	0.000 ±0.016	0.000 ±0.016	0.005 ±0.016	0.020 ±0.015	7.1 ±6.1

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Table 1.--concluded

Organism	Month May (25)	June (31)	July (25)	Aug (25)	Sep (25)	Seasonal mean volume	Percent compo-sition
Vegetable mineral matter	0.036 ±0.008	0.000 ±0.008	0.003 ±0.008	0.000 ±0.008	0.013 ±0.008	0.010 ±0.007	3.5 ±2.8
Other	0.004 ±0.002	0.000 ±0.002	0.000 ±0.002	0.000 ±0.002	0.000 ±0.002	0.001 ±0.002	0.4 ±0.0
Unidentified	0.057 ±0.009	0.040 ±0.009	0.037 ±0.009	0.060 ±0.009	0.041 ±0.009	0.047 ±0.009	16.7 ±7.6
Monthly mean volumes	0.334 ±0.122	0.627 ±0.120	0.153 ±0.122	0.123 ±0.122	0.169 ±0.122	0.282 ±0.117	100.0 ±58.6

Table 2.--Mean volume of stomach contents (milliliters) of brook trout 7.0-9.9 inches total length from the upper Main Au Sable River, May-September 1976 (sample sizes in parentheses), with 95% confidence levels.

Organism	Month					Seasonal mean volume	Percent composition
	May (25)	June (37)	July (25)	Aug (25)	Sep (26)		
Trichoptera	0.124 ±0.010	0.036 ±0.010	0.029 ±0.010	0.043 ±0.010	0.092 ±0.010	0.065 ±0.010	6.3 ±1.2
Hexagenia limbata	0.032 ±0.095	1.809 ±0.094	0.023 ±0.095	0.000 ±0.095	0.000 ±0.095	0.373 ±0.092	36.1 ±9.8
Other Ephemeroptera	0.069 ±0.024	0.015 ±0.024	0.240 ±0.024	0.058 ±0.024	0.002 ±0.024	0.077 ±0.023	7.4 ±2.4
Plecoptera	0.016 ±0.003	0.001 ±0.003	0.000 ±0.003	0.000 ±0.003	0.000 ±0.003	0.003 ±0.003	0.3 ±0.0
Odonata	0.030 ±0.008	0.001 ±0.008	0.014 ±0.008	0.044 ±0.008	0.007 ±0.008	0.019 ±0.007	1.8 ±0.7
Hemiptera	0.001 ±0.001	0.007 ±0.001	0.011 ±0.001	0.001 ±0.001	0.000 ±0.001	0.004 ±0.001	0.4 ±0.0
Coleoptera	0.050 ±0.012	0.042 ±0.012	0.008 ±0.012	0.006 ±0.012	0.008 ±0.012	0.023 ±0.012	2.2 ±1.2
Megaloptera	0.000 ±0.000	0.001 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.0 ±0.0
Diptera, larvae and pupae	0.008 ±0.007	0.032 ±0.006	0.001 ±0.007	0.002 ±0.007	0.001 ±0.007	0.009 ±0.006	0.9 ±0.7
Diptera adults	0.000 ±0.008	0.005 ±0.008	0.087 ±0.008	0.025 ±0.008	0.000 ±0.008	0.023 ±0.008	2.2 ±0.8
Mollusca	0.010 ±0.003	0.003 ±0.003	0.001 ±0.003	0.002 ±0.003	0.019 ±0.003	0.007 ±0.003	0.7 ±0.0
Fish	0.194 ±0.068	0.089 ±0.067	0.176 ±0.068	0.397 ±0.068	0.464 ±0.068	0.264 ±0.066	25.6 ±7.0
Isopoda Amphipoda	0.020 ±0.003	0.001 ±0.003	0.000 ±0.003	0.000 ±0.003	0.000 ±0.003	0.004 ±0.003	0.4 ±0.0
Decapoda	0.016 ±0.006	0.000 ±0.006	0.013 ±0.006	0.000 ±0.006	0.040 ±0.006	0.014 ±0.006	1.4 ±0.6
Terrestrials	0.000 ±0.010	0.007 ±0.010	0.031 ±0.010	0.016 ±0.010	0.074 ±0.010	0.026 ±0.009	2.5 ±0.9
Annelida	0.146 ±0.016	0.000 ±0.015	0.000 ±0.016	0.023 ±0.016	0.000 ±0.016	0.034 ±0.015	3.3 ±1.5

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Table 2.--concluded

Organism	Month May (25)	June (37)	July (25)	Aug (25)	Sep (26)	Seasonal mean volume	Percent composition
Vegetable mineral matter	0.046 ±0.008	0.016 ±0.008	0.000 ±0.008	0.017 ±0.008	0.044 ±0.008	0.025 ±0.007	2.4 ±0.7
Other	0.012 ±0.002	0.000 ±0.002	0.000 ±0.002	0.000 ±0.002	0.000 ±0.002	0.002 ±0.002	0.2 ±0.0
Unidentified	0.064 ±0.009	0.054 ±0.009	0.068 ±0.009	0.054 ±0.009	0.064 ±0.009	0.061 ±0.009	5.9 ±1.1
Monthly mean volumes	0.838 ±0.122	2.119 ±0.120	0.702 ±0.122	0.688 ±0.122	0.815 ±0.122	1.033 ±0.117	100.0 ±16.1

Table 3.--Mean volume of stomach contents (milliliters) of brown trout 3.0-5.9 inches total length from the upper Manistee River, May-September 1976 (sample sizes in parentheses), with 95% confidence levels.

Organism	Month: May (25)	June (25)	July (25)	Aug (25)	Sep (25)	Seasonal mean volume	Percent composition
Trichoptera	0.049 ±0.030	0.064 ±0.030	0.127 ±0.030	0.050 ±0.030	0.025 ±0.030	0.063 ±0.029	46.7 ±28.9
Hexagenia limbata	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.0 ±0.0
Ephemeroptera	0.035 ±0.003	0.007 ±0.003	0.004 ±0.003	0.011 ±0.003	0.008 ±0.003	0.013 ±0.003	9.6 ±4.5
Plecoptera	0.000 ±0.002	0.000 ±0.002	0.000 0.002	0.012 0.002	0.000 0.002	0.002 ±0.002	1.5 ±1.5
Odonata	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.0 ±0.0
Hemiptera	0.000 ±0.002	0.000 ±0.002	0.000 ±0.002	0.000 ±0.002	0.000 ±0.002	0.000 ±0.002	0.0 ±0.0
Coleoptera	0.000 ±0.006	0.005 ±0.006	0.000 ±0.006	0.000 ±0.006	0.001 ±0.006	0.001 ±0.006	0.7 ±0.0
Megaloptera	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.0 ±0.0
Diptera, larvae and pupae	0.001 ±0.015	0.004 ±0.015	0.049 ±0.015	0.001 ±0.015	0.018 ±0.015	0.015 ±0.014	11.1 ±11.3
Diptera adults	0.001 ±0.002	0.000 ±0.002	0.000 ±0.002	0.008 ±0.002	0.005 ±0.002	0.003 ±0.002	2.2 ±1.7
Mollusca	0.000 ±0.003	0.000 ±0.003	0.000 ±0.003	0.000 ±0.003	0.000 ±0.003	0.000 ±0.003	0.0 ±0.0
Fish	0.000 ±0.050	0.006 ±0.050	0.002 ±0.050	0.002 ±0.050	0.000 ±0.050	0.002 ±0.048	1.5 ±33.9
Isopoda Amphipoda	0.011 ±0.002	0.004 ±0.002	0.001 ±0.002	0.000 ±0.002	0.003 ±0.002	0.004 ±0.002	3.0 ±1.9
Decapoda	0.000 ±0.001	0.000 ±0.001	0.000 ±0.001	0.000 ±0.001	0.000 ±0.001	0.000 ±0.001	0.0 ±0.0
Terrestrials	0.000 ±0.005	0.002 ±0.005	0.000 ±0.005	0.000 ±0.005	0.001 ±0.005	0.001 ±0.005	0.7 ±0.0
Annelida	0.000 ±0.007	0.010 ±0.007	0.000 ±0.007	0.000 ±0.007	0.000 ±0.007	0.002 ±0.006	1.5 ±4.3

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Table 3.--concluded

Organism	Month					Seasonal	Percent
	May (25)	June (25)	July (25)	Aug (25)	Sep (25)	mean volume	compo-sition
Vegetable mineral matter	0.002 ±0.009	0.030 ±0.009	0.007 ±0.009	0.002 ±0.009	0.004 ±0.009	0.009 ±0.009	6.7 ±7.2
Other	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.0 ±0.0
Unidentified	0.013 ±0.008	0.020 ±0.008	0.022 ±0.008	0.017 ±0.008	0.029 ±0.008	0.020 ±0.008	14.8 ±8.5
Monthly mean volumes	0.112 ±0.058	0.152 ±0.058	0.212 ±0.058	0.103 ±0.058	0.094 ±0.058	0.135 ±0.056	100.0 ±58.6

Table 4.--Mean volume of stomach contents (milliliters) of brown trout 7.0-9.9 inches total length from the upper Manistee River, May-September 1976 (sample sizes in parentheses), with 95% confidence levels.

Organism	Month: May (26)	June (25)	July (25)	Aug (25)	Sep (26)	Seasonal mean volume	Percent composition
Trichoptera	0.245 ±0.030	0.174 ±0.030	0.547 ±0.030	0.154 ±0.030	0.497 ±0.030	0.323 ±0.029	44.9 ±5.3
Hexagenia limbata	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.0 ±0.0
Ephemeroptera	0.010 ±0.003	0.010 ±0.003	0.002 ±0.003	0.001 ±0.003	0.001 ±0.003	0.005 ±0.003	0.7 ±0.0
Plecoptera	0.006 ±0.002	0.000 ±0.002	0.000 ±0.002	0.000 ±0.002	0.000 ±0.002	0.001 ±0.002	0.1 ±0.0
Odonata	0.002 ±0.000	0.001 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.001 ±0.000	0.1 ±0.0
Hemiptera	0.000 ±0.002	0.002 ±0.002	0.000 ±0.002	0.005 ±0.002	0.010 ±0.002	0.003 ±0.002	0.4 ±0.0
Coleoptera	0.004 ±0.006	0.058 ±0.006	0.012 ±0.006	0.001 ±0.006	0.004 ±0.006	0.016 ±0.006	2.2 ±0.8
Megaloptera	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.0 ±0.0
Diptera, larvae and pupae	0.013 ±0.015	0.179 ±0.015	0.024 ±0.015	0.000 ±0.015	0.002 ±0.015	0.044 ±0.014	6.1 ±2.0
Diptera adults	0.000 ±0.002	0.002 ±0.002	0.000 ±0.002	0.001 ±0.002	0.008 ±0.002	0.002 ±0.002	0.3 ±0.0
Mollusca	0.021 ±0.003	0.016 ±0.003	0.013 ±0.003	0.005 ±0.003	0.002 ±0.003	0.011 ±0.003	1.5 ±0.4
Fish	0.125 ±0.049	0.164 ±0.050	0.177 ±0.050	0.311 ±0.050	0.106 ±0.049	0.177 ±0.048	24.6 ±6.9
Isopoda Amphipoda	0.006 ±0.002	0.004 ±0.002	0.004 ±0.002	0.000 ±0.002	0.000 ±0.002	0.003 ±0.002	0.4 ±0.0
Decapoda	0.002 ±0.001	0.002 ±0.001	0.000 ±0.001	0.000 ±0.001	0.000 ±0.001	0.001 ±0.001	0.1 ±0.0
Terrestrials	0.004 ±0.005	0.004 ±0.005	0.018 ±0.005	0.025 ±0.005	0.010 ±0.005	0.012 ±0.005	1.8 ±0.7
Annelida	0.003 ±0.007	0.002 ±0.007	0.028 ±0.007	0.002 ±0.007	0.012 ±0.007	0.009 ±0.006	1.3 ±0.9

(continued, next page)

Table 4.--concluded

Organism	Month: May (26)	June (25)	July (25)	Aug (25)	Sep (26)	Seasonal mean volume	Percent compo-sition
Vegetable mineral matter	0.019 ±0.009	0.040 ±0.009	0.067 ±0.009	0.040 ±0.009	0.071 ±0.009	0.047 ±0.009	6.5 ±1.3
Other	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.000 ±0.000	0.0 ±0.0
Unidentified	0.060 ±0.008	0.074 ±0.008	0.043 ±0.008	0.062 ±0.008	0.085 ±0.008	0.065 ±0.008	9.0 ±1.3
Monthly mean volumes	0.520 ±0.058	0.732 ±0.058	0.935 ±0.058	0.607 ±0.058	0.808 ±0.058	0.720 ±0.056	100.0 ±10.8

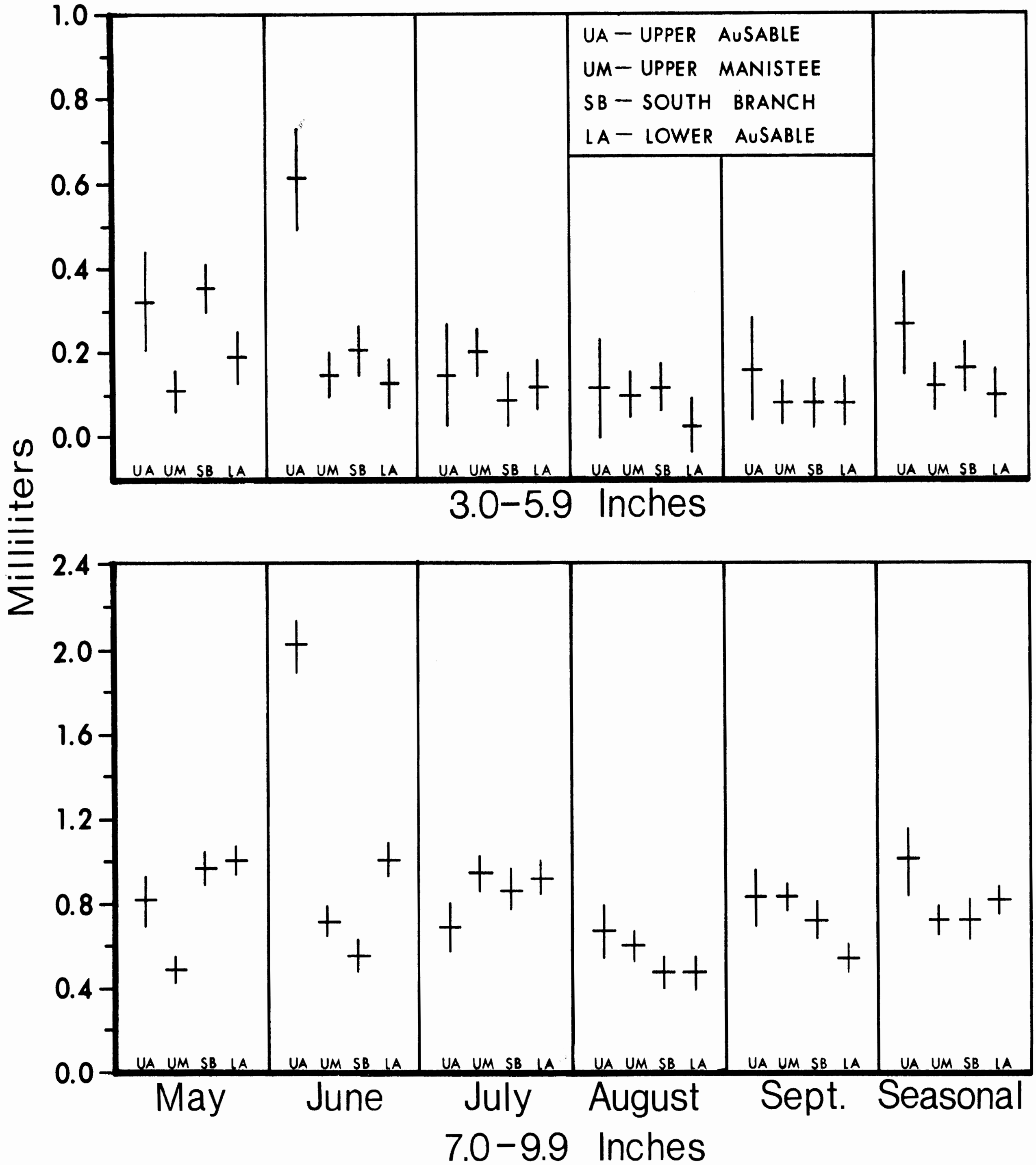


Figure 2.--Total monthly mean stomach volumes (milliliters) of upper Au Sable, upper Manistee, South Branch, and lower Au Sable trout 3.0-5.9 inches and 7.0-9.9 inches with 95% confidence limits.

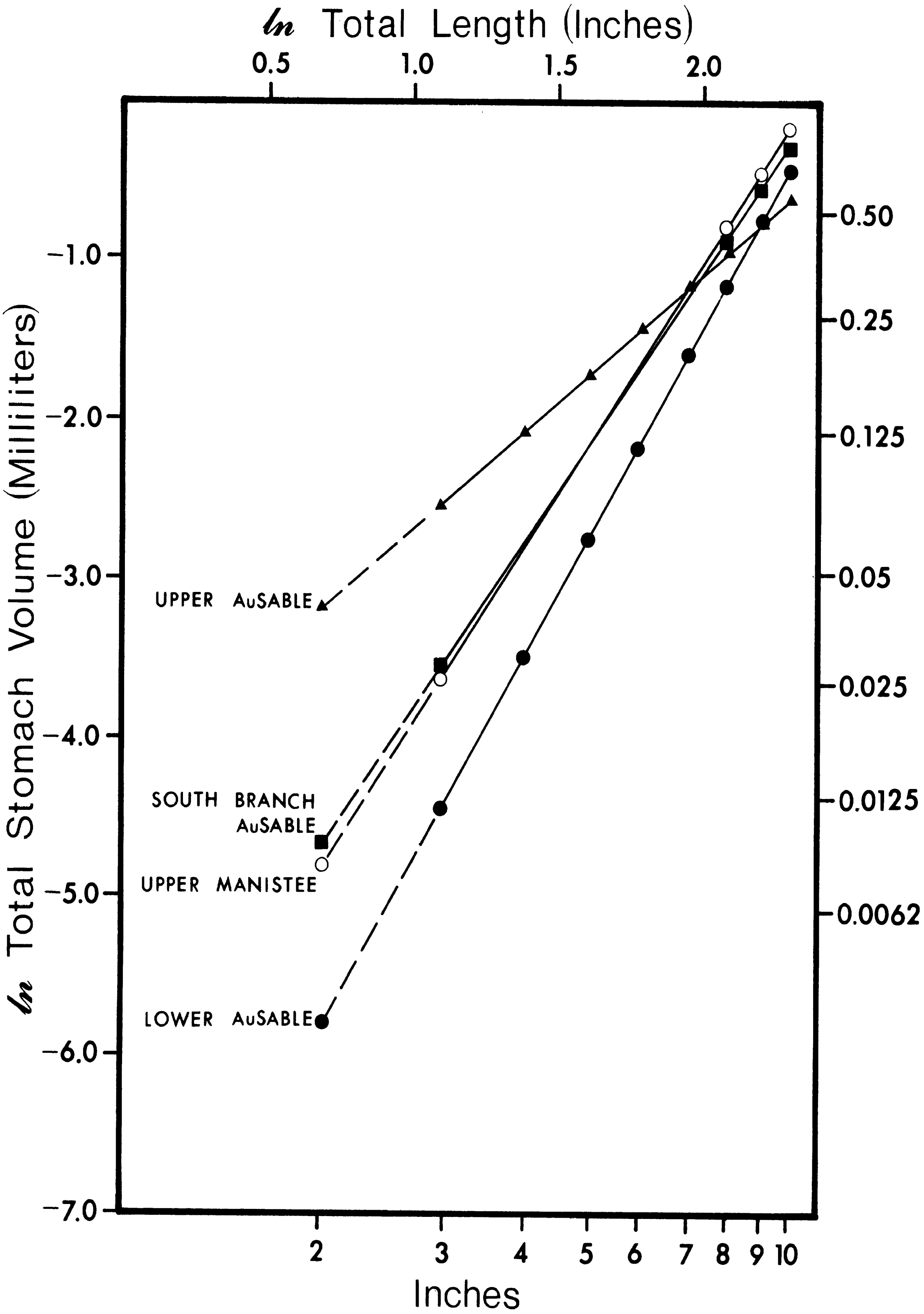


Figure 3.--Regression of natural log total stomach volume vs. natural log total length for upper Au Sable brook trout, upper Manistee brown trout, South Branch brown trout, and lower Au Sable brown trout May-September 1976.

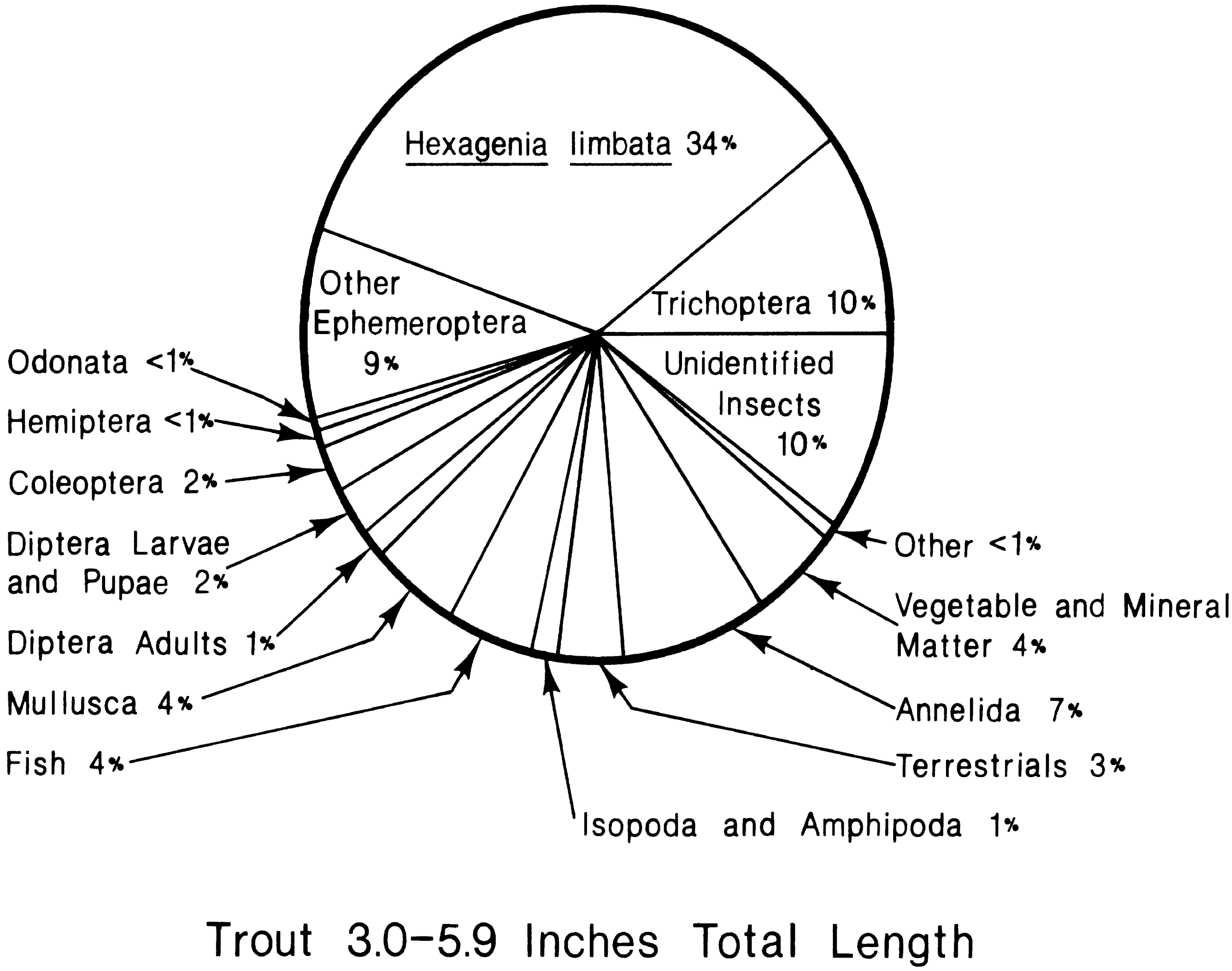
Trout diet

In addition to total stomach volume measurements, individual diet constituents for the two size ranges of fish in each river were recorded with 95% confidence limits (Tables 1 to 4, Appendices 1 to 4). To determine the importance of certain food items in streams it is important to keep in mind both the presence or absence of certain organisms in the stream and the availability of these organisms to the trout (Frost 1945; Allen 1951; Alexander and Gowing 1976). If the trout cannot utilize the food source, it is of little value.

Upper Au Sable 3.0- to 5.9-inch brook trout

In the upper Main Au Sable the composition of the brook trout stomach contents in both the large and small fish reflected a diet composition that was dependent on primarily five items (Fig. 4). *Hexagenia limbata* was separated from other Ephemeroptera because of their tremendous importance to the total diet of the upper Main Au Sable brook trout. As indicated in Figure 4, *Hexagenia limbata* was the dominant food source in the 3.0- to 5.9-inch size range, while Trichoptera, other Ephemeroptera, and Annelida were moderately important.

Hexagenia limbata consumption accounted for over 75% of the total June stomach volume for the 3.0- to 5.9-inch fish (Table 1). This single species in effect dominated the diet of these trout for the entire season, since the total mean volume for June was greater than for any month sampled (Fig. 2).



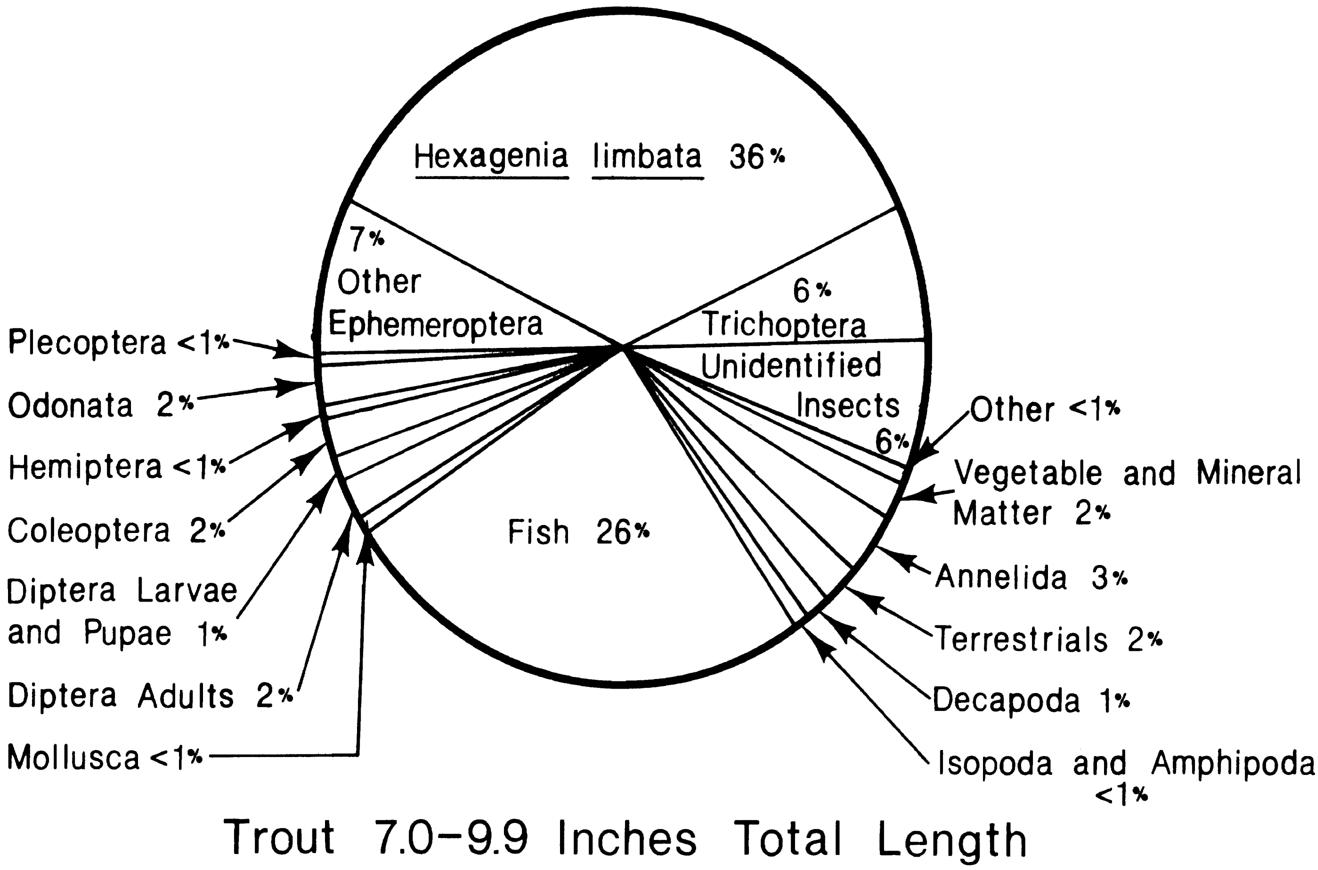


Figure 4.--Percent compositions of the diet of brook trout from the upper Main Au Sable River, May-September 1976.

Upper Au Sable 7.0- to 9.9-inch brook trout

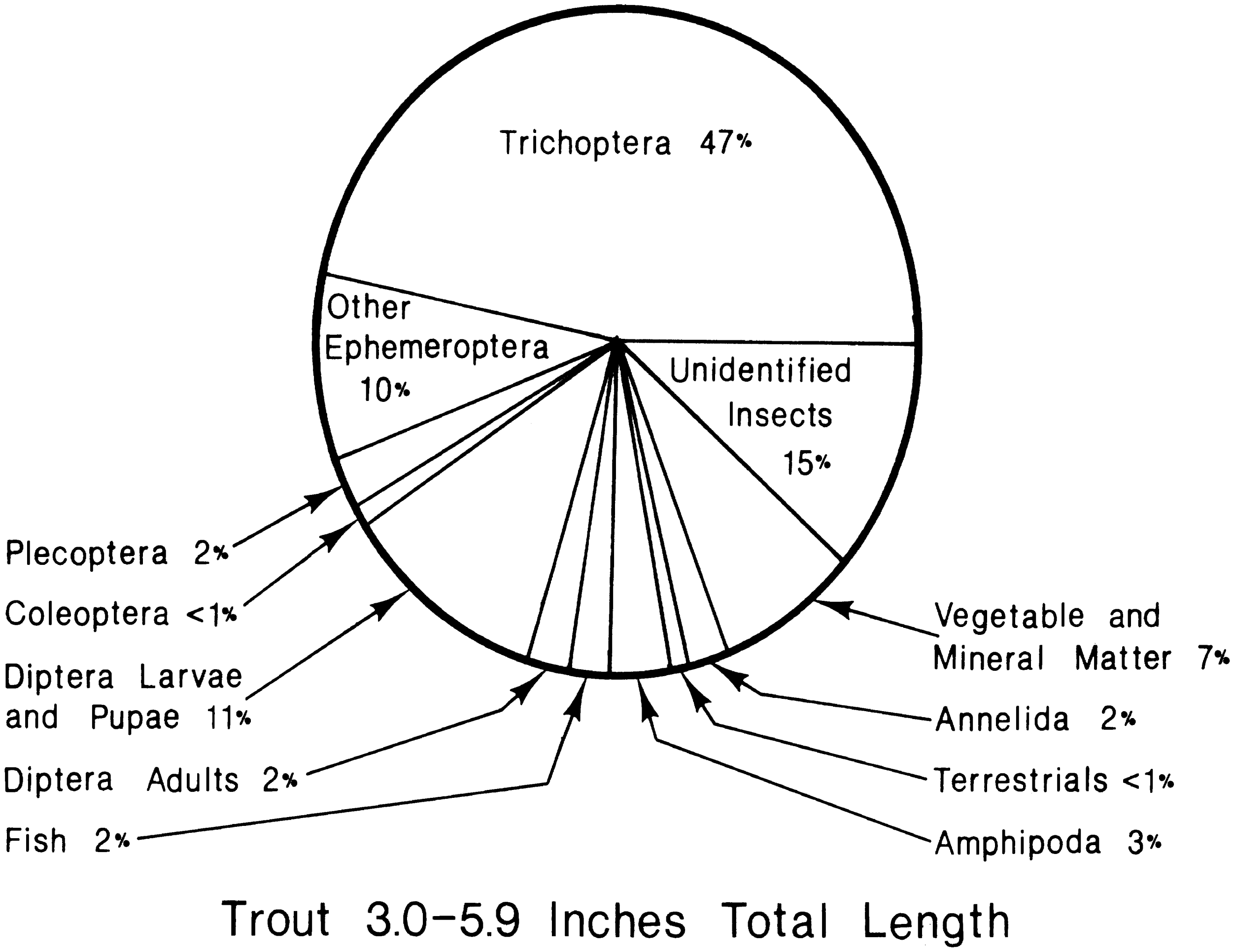
As with the smaller fish, Hexagenia limbata accounted for the largest percentage of the total diet in the 7.0- to 9.9-inch range (Fig. 4). Total food consumption for the summer was highest in June (Fig. 2), of which over 85% of the month's volume was supplied by Hexagenia limbata (Table 2).

Fish were the second most important food source and constituted over 25% of the total stomach volume (Fig. 4). Other Ephemeroptera and Trichoptera comprised much of the rest of the 7.0- to 9.9-inch brook trout diet.

Upper Manistee 3.0- to 5.9-inch brown trout

Again, one group far surpassed the others in importance in terms of diet composition. Trichoptera, largely Brachycentrus, comprised over 45% of the total diet of the 3.0- to 5.9-inch brown trout (Table 3). Diptera, especially larvae and pupae, and Ephemeroptera accounted for a large percentage of the remainder of the total volume (Fig. 5).

Vegetable and mineral matter also contributed to the total volume and remained at a constant percentage of the total diet, as did Trichoptera, even in the larger fish (Fig. 5). It was assumed that since the stomach contents were often in varying degrees of decomposition that this category probably represented to a large extent, Trichoptera cases that had been reduced to a less recognizable state.



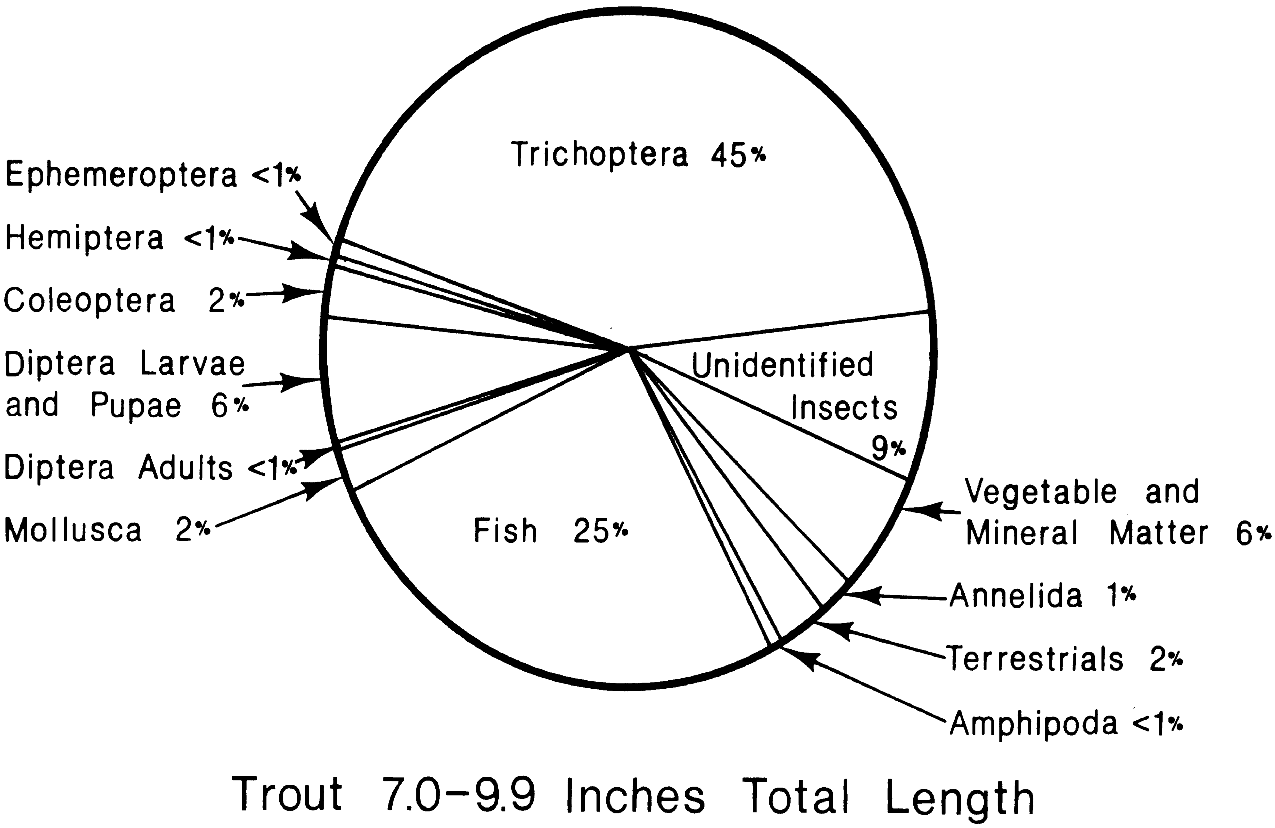


Figure 5. --Percent composition of the diet of brown trout from the upper Manistee River, May-September 1976.

Upper Manistee 7.0- to
9.9-inch brown trout

Although consumption of Trichoptera remained extremely important to the larger upper Manistee brown trout, Diptera and Ephemeroptera usage was less (Fig. 5). Fish emerged as the second most important food source, as it had in the larger upper Au Sable trout. Again, fish contributed about 25% to the total trout diet (Table 4).

Total stomach volume--
total length relationship

An important consideration when discussing diet is the relationship of diet to trout growth. As trout grow larger they eat more food. The regression of the natural log of total stomach volume against the natural log of total fish length demonstrated this relationship for all four rivers (Fig. 3). Ninety-five percent confidence limits for lengths of trout 2 inches through 10 inches are included in Table 5. In addition, R^2 values and the number of fish sampled in each river are given. The slope and constant of the regressions were significant for all four rivers, and a difference among the regressions from 6 inches and up could not be identified. The R^2 values for all of the rivers, especially the upper Au Sable, were not extremely high, but such a large number of trout were sampled that the relationship was considered a sound one.

Table 5.--The natural log total length and natural log stomach volume measurements with 95% confidence limits for the upper Au Sable, upper Manistee, South Branch, and lower Au Sable rivers to accompany Figure 3. R^2 values and number of fish sampled are included.

Total length with natural log values (inches)	(ln)	Natural log total stomach volume (ml) with 95% confidence limits	
		Upper Au Sable R^2 = 0.0854; N = 269	Upper Manistee R^2 = 0.4960; N = 252
2.0	0.69	-3.1800 ± 0.7270	-4.8048 ± 0.4243
3.0	1.10	-2.5270 ± 0.4854	-3.6242 ± 0.2860
4.0	1.39	-2.0651 ± 0.3283	-2.7892 ± 0.1964
5.0	1.61	-1.7148 ± 0.2339	-2.1557 ± 0.1424
6.0	1.79	-1.4281 ± 0.1986	-1.6374 ± 0.1211
7.0	1.95	-1.1732 ± 0.2171	-1.1767 ± 0.1293
8.0	2.08	-0.9662 ± 0.2610	-0.8023 ± 0.1525
9.0	2.20	-0.7751 ± 0.3151	-0.4568 ± 0.1821
10.0	2.30	-0.6158 ± 0.3658	-0.1688 ± 0.2104
		South Branch Au Sable R^2 = 0.3742; N = 210	Lower Au Sable R^2 = 0.3479; N = 210
2.0	0.69	-4.7316 ± 0.5615	-5.8321 ± 0.7504
3.0	1.10	-3.5954 ± 0.3787	-4.4500 ± 0.5116
4.0	1.39	-2.7916 ± 0.2646	-3.4746 ± 0.3581
5.0	1.61	-2.1800 ± 0.2024	-2.7337 ± 0.2665
6.0	1.79	-1.6831 ± 0.1851	-2.1275 ± 0.2291
7.0	1.95	-1.2397 ± 0.2030	-1.5887 ± 0.2395
8.0	2.08	-0.8794 ± 0.2362	-1.1509 ± 0.2759
9.0	2.20	-0.5468 ± 0.2764	-0.7467 ± 0.3244
10.0	2.30	-0.2697 ± 0.3143	-0.4100 ± 0.3716

Growth as measured by length

Mean lengths at various ages with 95% confidence limits were determined for the upper Au Sable brook trout and the upper Manistee brown trout (Table 6). This same procedure was applied to the brown trout data of the South Branch and lower Au Sable (Stauffer 1977), and the upper Manistee (Table 8).

The weighted mean length from the fall data for the various ages in the four rivers were also included in Tables 6 and 8. This weighting procedure was done in the following manner. The fall population estimates were arranged by inch group. In each inch group scale samples were taken of at least the first ten fish in that inch group. Lengths were recorded for the various ages of fish sampled in each inch group to determine a mean length for a particular age in a given inch group. This mean length was multiplied by the calculated number of trout present in the river in that inch group of the appropriate age. The values obtained for all inch groups that contained members of that given age were then totaled, and that total was divided by the total calculated number of trout in each inch group of a given age. This value represented the weighted mean length for a given age group.

Values derived in this manner are somewhat different, often less than the values obtained when mean lengths are determined when no weighting system is applied. These weighted values gave a more accurate picture of the mean sizes of the fish in the various ages. For this reason Stauffer's (1977) fall data in Tables 6 and 8 were recalculated in this weighted mean average form for more meaningful comparisons to the upper Manistee and upper Au Sable values.

Table 6.--Mean lengths (inches) at various ages for brook and brown trout on the upper Au Sable and upper Manistee rivers, May-September 1976, and weighted mean lengths, fall 1976.

Age, and month		Mean length: Brook trout, Upper Main Au Sable	Mean length: Brown trout, Upper Manistee	$\bar{X}$ by month	95% CL
0	May				
	June	3.1		3.10	
	July	3.4	3.0	3.20	±1.52
	Aug	4.0	3.3	3.65	±1.52
	Sep	4.3	3.9	4.10	±1.52
$\bar{X}$ by river		3.70	3.40	3.57	
95% CL		±0.38	±0.52	±0.29	
Fall weighted means		3.56	3.72		
I	May	5.0	4.8	4.90	±2.15
	June	5.7	5.2	5.45	±2.15
	July	6.3	5.2	5.75	±2.15
	Aug	7.3	5.5	6.40	±2.15
	Sep	6.8	6.9	6.85	±2.15
$\bar{X}$ by river		6.22	5.52	5.87	
95% CL		±0.47	±0.47	±0.38	
Fall weighted means		6.12	6.40		
II	May	8.0	8.1	8.05	±1.30
	June	8.4	8.0	8.20	±1.30
	July	8.6	8.1	8.35	±1.30
	Aug		8.4	8.40	
	Sep	8.3	8.8	8.55	±1.30
$\bar{X}$ by river		8.32	8.28	8.30	
95% CL		±0.33	±0.28	±0.24	
Fall weighted means		8.35	8.64		
III	May	9.1	9.2	9.15	±1.72
	June		9.4	9.40	
	July	8.7	9.1	8.90	±1.72
	Aug				
	Sep	9.7	8.7	9.20	±1.72
$\bar{X}$ by river		9.17	9.10	9.13	
95% CL		±0.58	±0.43	±0.33	
Fall weighted means		11.20	10.98		
IV					
Fall weighted means			13.21		

Table 7.--Mean weights (grams) at various ages for brook and brown trout on the upper Au Sable and upper Manistee rivers, May-September 1976.

Age, and month		Mean weight: Brook trout, Upper Main Au Sable	Mean weight: Brown trout, Upper Manistee	$\bar{X}$ by month	95% CL
0	May				
	June	5.1		5.10	
	July	6.5	4.2	5.35	±8.68
	Aug	9.6	5.8	7.70	±8.68
	Sep	12.8	9.8	11.30	±8.68
$\bar{X}$ by river		8.50	6.60	7.68	
95% CL		±2.17	±2.94	±1.67	
I	May	21.2	17.5	19.35	±47.91
	June	35.2	23.1	29.15	±47.91
	July	49.6	24.1	36.85	±47.91
	Aug	67.4	27.8	47.60	±47.91
	Sep	51.3	53.3	52.30	±47.91
$\bar{X}$ by river		44.94	29.16	37.05	
95% CL		±10.47	±10.47	±8.53	
II	May	87.8	82.2	85.00	±55.07
	June	116.5	86.6	101.55	±55.07
	July	116.2	87.0	101.60	±55.07
	Aug		94.2	94.20	
	Sep	95.3	106.3	100.80	±55.07
$\bar{X}$ by river		103.95	91.26	96.90	
95% CL		±13.79	±12.03	±9.99	
III	May	118.1	124.6	121.35	±65.68
	June		131.6	131.60	
	July	114.2	118.6	116.40	±65.68
	Aug				
	Sep	152.6	110.0	131.30	±65.68
$\bar{X}$ by river		128.30	121.20	124.24	
95% CL		±22.24	±16.45	±12.65	

Table 8.--Mean lengths (inches) at various ages for brown trout on the South Branch Au Sable, lower Au Sable, and upper Manistee rivers, May-September 1976, and weighted mean lengths, fall 1976.

Age, and	month	Mean length: Au Sable: South Branch	Mean length: Au Sable: Lower Main stream	Mean length: Upper Manistee	$\bar{X}$ by month	95% CL
0	May					
	June		3.8		3.80	
	July	3.1	3.1	3.0	3.07	±0.07
	Aug	3.6	3.7	3.3	3.53	±0.07
	Sep	3.9	3.9	3.9	3.90	±0.07
$\bar{X}$ by river		3.53	3.62	3.40	3.53	
95% CL		±0.07	±0.05	±0.07	±0.04	
Fall weighted means		4.01	3.66	3.72		
I	May	5.0	4.9	4.8	4.90	±0.55
	June	5.4	5.3	5.2	5.30	±0.55
	July	6.6	5.6	5.2	5.80	±0.55
	Aug	7.8	5.8	5.5	6.37	±0.55
	Sep	7.9	6.7	6.9	7.17	±0.55
$\bar{X}$ by river		6.54	5.66	5.52	5.91	
95% CL		±0.36	±0.36	±0.36	±0.28	
Fall weighted means		7.53	6.86	6.40		
II	May	8.9	8.6	8.1	8.53	±0.33
	June	9.2	9.1	8.0	8.77	±0.33
	July	9.4	8.8	8.1	8.77	±0.33
	Aug	8.6	8.5	8.4	8.50	±0.33
	Sep	9.0	8.8	8.8	8.87	±0.33
$\bar{X}$ by river		9.02	8.76	8.28	8.68	
95% CL		±0.21	±0.21	±0.21	±0.16	
Fall weighted means		10.76	9.37	8.64		
III	May		9.6	9.2	9.40	±0.93
	June		9.4	9.4	9.40	±0.93
	July		9.6	9.1	9.35	±0.93
	Aug		9.4		9.40	
	Sep		9.5	8.7	9.10	±0.93
$\bar{X}$ by river			9.50	9.10	9.32	
95% CL			±0.20	±0.23	±0.17	
Fall weighted means		13.54	11.14	10.98		
IV						
Fall weighted means		15.65	12.64	13.21		

Table 9.--Mean weights (grams) at various ages for brown trout on the South Branch Au Sable, lower Au Sable, and upper Manistee rivers, May-September 1976.

Age, and month		Mean weight: Au Sable: South Branch	Mean weight: Au Sable: Lower Main stream	Mean weight: Upper Manistee	$\bar{X}$ by month	95% CL
0	May					
	June		10.2		10.20	
	July	5.1	5.0	4.2	4.77	±0.68
	Aug	7.8	8.7	5.8	7.43	±0.68
	Sep	11.2	10.4	9.8	10.47	±0.68
$\bar{X}$ by river		8.03	8.58	6.60	7.82	
95% CL		±0.68	±0.50	±0.68	±0.36	
I	May	21.4	19.5	17.5	19.47	±11.71
	June	26.6	26.0	23.1	25.23	±11.71
	July	49.6	30.3	24.1	34.67	±11.71
	Aug	75.2	33.4	27.8	45.47	±11.71
	Sep	81.5	51.8	53.3	62.20	±11.71
$\bar{X}$ by river		50.86	32.20	29.16	37.41	
95% CL		±7.56	±7.56	±7.56	±5.84	
II	May	116.9	106.8	82.2	101.97	±10.99
	June	107.1	121.3	86.6	105.00	±10.99
	July	119.6	110.3	87.0	105.63	±10.99
	Aug	91.4	98.5	94.2	94.70	±10.99
	Sep	115.2	107.0	106.3	109.50	±10.99
$\bar{X}$ by river		110.04	108.78	91.26	103.36	
95% CL		±7.09	±7.09	±7.09	±5.48	
III	May		165.1	124.6	144.85	±41.42
	June		133.5	131.6	132.55	±41.42
	July		144.0	118.6	131.30	±41.42
	Aug		141.2		141.20	
	Sep		121.4	110.0	115.70	±41.42
$\bar{X}$ by river			141.04	121.20	132.22	
95% CL			±9.05	±10.37	±7.52	

The results from the regression analysis of the natural log of the lengths of the trout against the natural log of the age of the trout were also obtained.

The equation of the line for the upper Au Sable with 95% confidence limits was:

$$\ln \text{total length} = 1.3439 + 0.6803\,(\ln \text{age of the trout}) \pm 0.3327\sqrt{0.0038 + \frac{(0.6743 - \ln \text{age of the trout})^2}{40.6855}}$$

The equation of the line for the upper Manistee with 95% confidence limits was:

$$\ln \text{total length} = 1.2107 + 0.7662\,(\ln \text{age of the trout}) \pm 0.2708\sqrt{0.0040 + \frac{(0.7939 - \ln \text{age of the trout})^2}{39.8342}}$$

When this regression was performed on Stauffer's (1977) uncorrected data, the following equations of the line were obtained.

The equation of the line for the South Branch with 95% confidence limits was:

$$\ln \text{total length} = 1.2726 + 0.8275\,(\ln \text{age of the trout}) \pm 0.3418\sqrt{0.0048 + \frac{(0.6112 - \ln \text{age of the trout})^2}{35.0182}}$$

The equation of the line for the lower Au Sable with 95% confidence limits was:

$$\ln \text{total length} = 1.2401 + 0.7838\ (\ln \text{age of the trout})$$

$$\pm\ 0.2603\sqrt{0.0048 + \frac{(0.7541 - \ln \text{age of the trout})^2}{39.1508}}$$

The respective R^2 values were 0.8310, 0.7099, 0.7912, and 0.8676.

Growth as measured by weight

Weight was another important consideration in the determination of trout growth. Mean weights at various ages with 95% confidence limits were determined for the upper Au Sable and upper Manistee (Table 7). Ninety-five percent confidence limits were added to Stauffer's (1977) data in Table 9, and were then analyzed with the upper Manistee brown trout results.

Length-weight relationship

In addition to the length by age, and weight by age relationships described above, the length-weight relationships for the upper Au Sable and upper Manistee were determined. The length-weight relationships for Stauffer's (1977) uncorrected results were also determined. Length was measured in inches and weight was measured in grams.

The equation of the line for the upper Au Sable with 95% confidence limits was:

$$\ln \text{weight} = 0.2801 + 0.5238\,(\text{total length}) \pm 0.3143\sqrt{0.0037 + \frac{(6.3985 - \text{total length})^2}{952.9625}}$$

The equation of the line for the upper Manistee with 95% confidence limits was:

$$\ln \text{weight} = 0.4494 + 0.4852\,(\text{total length}) \pm 0.3632\sqrt{0.0040 + \frac{(6.5131 - \text{total length})^2}{1024.6874}}$$

The equation of the line for the South Branch with 95% confidence limits was:

$$\ln \text{weight} = 0.3102 + 0.5064\,(\text{total length}) \pm 0.3309\sqrt{0.0048 + \frac{(6.3352 - \text{total length})^2}{1014.3206}}$$

The equation of the line for the lower Au Sable with 95% confidence limits was:

$$\ln \text{weight} = 0.5267 + 0.4744\,(\text{total length}) \pm 0.3175\sqrt{0.0048 + \frac{(6.6429 - \text{total length})^2}{1035.7969}}$$

The respective R^2 values were 0.9744, 0.9656, 0.9777, and 0.9771.

Total volume-total weight relationship

Regression analysis was performed to determine the effect of stomach volume upon weight of the trout. The equations of the line for the upper Au Sable brook trout with 95% confidence limits were:

$$\ln \text{weight} = 6.7262 + 1.9594 (\ln \text{stomach volume}) \pm 1.1122 \sqrt{0.0833 + \frac{(\ln \text{stomach volume} + 1.2850)^2}{9.5692}}$$

and for the Manistee brown trout:

$$\ln \text{weight} = 6.3402 + 1.3916 (\ln \text{stomach volume}) \pm 1.7726 \sqrt{0.0526 + \frac{(\ln \text{stomach volume} + 0.3793)^2}{65.4048}}$$

Analysis of Stauffer's (1977) South Branch and lower Au Sable uncorrected results yielded the following equations of the line:

$$\ln \text{weight} = 6.1008 + 1.2636 (\ln \text{stomach volume}) \pm 1.3821 \sqrt{0.0667 + \frac{(\ln \text{stomach volume} + 0.9758)^2}{41.6394}}$$

and

$$\ln \text{weight} = 6.0317 + 0.9741 (\ln \text{stomach volume}) \pm 1.2941 \sqrt{0.0667 + \frac{(\ln \text{stomach volume} + 1.2681)^2}{61.4874}}$$

respectively. The R^2 values were 0.9365, 0.9135, 0.9259, 0.9259, respectively.

Trout populations

The third aspect of the study involved estimates of the trout populations in the rivers. Stomach content analysis and the various growth parameters are of limited value until they are put into proper perspective by population estimates.

The number of trout per acre for the upper Au Sable and upper Manistee are listed in Table 10. The estimated number of trout per acre in the upper Au Sable was 276 fish, almost entirely brook trout. The estimate for the upper Manistee was 1148 fish per acre (70% brown trout, 29% brook trout, and about 1% rainbow trout).

Stauffer (1977) reported population estimates for the South Branch and lower Au Sable. There were 506 trout per acre in the South Branch, 57% of which were brown trout, and 43% brook trout. The lower Au Sable contained an estimated 1091 trout per acre. Brown trout accounted for 65% of this value, brook trout 24%, and rainbow trout 11%.

These data were further analyzed to obtain estimates of pounds of trout per acre. These estimates were included in Table 11 for the upper Au Sable and upper Manistee. The figures for the South Branch and lower Au Sable were presented in Stauffer (1977).

Trout density

Trout density was thought to have a potential effect on weight of the trout. A multiple regression analysis was done for all four rivers in which the dependent variable was the natural log of the weight of the dominant

Table 10.--Number of trout per acre for the upper Au Sable and upper Manistee rivers, fall 1976.

Inch group	Brown trout		Brook trout		Rainbow trout		Total trout	
	Upper Au Sable	Upper Manistee	Upper Au Sable	Upper Manistee	Upper Au Sable	Upper Manistee	Upper Au Sable	Upper Manistee
2		86.0	26.0	18.8			26.0	104.8
3		248.4	136.3	183.0		2.9	136.3	434.3
4		101.2	51.8	81.2		0.4	51.8	182.8
5		47.9	20.8	24.0		0.4	20.8	72.3
6		84.4	22.1	16.3		2.5	22.1	103.2
7		59.2	10.7	7.8		1.6	10.7	68.6
8		48.2	3.7	2.8		1.2	3.7	52.2
9	0.2	47.0	1.5	0.8		1.1	1.7	48.9
10	0.7	28.9	0.5	0.6		0.4	1.2	29.9
11	0.5	21.2	0.5				1.0	21.2
12	0.6	15.8	0.1				0.7	15.8
13		5.2	0.3				0.3	5.2
14	0.2	4.4					0.2	4.4
15		2.2						2.2
16		0.7						0.7
17		1.0						1.0
18	0.2	0.4					0.2	0.4
19		0.6						0.6
20								
21+	0.1	0.4					0.1	0.4
Total	2.5	803.1	274.3	335.3		10.5	276.8	1148.9

Table 11.--Pounds of trout per acre for the upper Au Sable and upper Manistee rivers, fall 1976.

Inch group	Brown trout		Brook trout		Rainbow trout		Total trout	
	Upper Au Sable	Upper Manistee	Upper Au Sable	Upper Manistee	Upper Au Sable	Upper Manistee	Upper Au Sable	Upper Manistee
2		0.5	0.1	0.1			0.1	0.6
3		3.5	2.1	2.8			2.1	6.3
4		3.1	1.7	2.6			1.7	5.7
5		2.7	1.2	1.4			1.2	4.1
6		7.7	2.2	1.6		0.2	2.2	9.5
7		8.6	1.6	1.2		0.2	1.6	10.0
8		10.1	0.8	0.6		0.2	0.8	10.9
9	0.1	13.6	0.5	0.2		0.3	0.6	14.1
10	0.3	11.3	0.2	0.2		0.1	0.5	11.6
11	0.3	10.8	0.3				0.6	10.8
12	0.4	10.5	0.1				0.5	10.5
13		4.4	0.2				0.2	4.4
14	0.2	4.6					0.2	4.6
15		2.8						2.8
16		1.0						1.0
17		1.9						1.9
18	0.4	0.9					0.4	0.9
19		1.5						1.5
20								
21+	0.4	0.7					0.4	0.7
Total	2.1	100.2	11.0	10.7		1.0	13.1	111.9

species in each river and the independent variables were the total number of the dominant trout species per acre, and the natural log of the total average stomach volume of the dominant trout species. This same analysis was performed with the total number of dominant trout species per acre replaced by the total number of trout per acre.

DISCUSSION

The trout populations of the upper Au Sable and upper Manistee rivers have been virtually unstudied. The data included here will provide future workers with baseline information on these two streams, but in addition it was thought that although the conditions for comparisons were not ideal, it would be useful and informative to compare the brook trout data on the upper Au Sable with those of the upper Manistee brown trout. Also the upper Manistee data were compared with data on brown trout gathered the same year on the South Branch and lower Au Sable by Stauffer (1977).

The findings generally centered around three areas. The first area was diet composition and the monthly and seasonal importance of certain major food items. The second area, growth of the trout, as determined by length and weight measurements was examined. The third area, population estimates, and age structures based on these estimates, was considered. All of these components were then examined together in an attempt to determine the effect of trout density on diet and growth.

Seasonal changes in trout diet

An important consideration when measuring diet composition is the availability of food items. Certain food items are available, or more easily utilized at certain times of the year (Benson 1953a; Needham 1930;

Surber 1936). Such was the case with Hexagenia limbata consumption on the upper Au Sable in June. This was when the nymphs emerged and transformed to the sub-imago stage. Much of the Hexagenia limbata found in the stomach samples were either in the nymphal or sub-imago stage. It is likely that the imago stage was also heavily utilized by the trout but sampling runs did not correspond as well to these mating flights.

Diet composition was also dependent on the availability of food items in the rivers as a whole. As indicated in Figures 4 and 5, and Stauffer (1977), certain items dominated diet composition and this dominance was different from river to river.

In the future it is hoped that extensive work will be done to analyze the fauna of these two rivers. Unfortunately, such a study was not included in this project. It can only be assumed that the trout ate what was most prevalent in the stream or what was most accessible.

To get a better idea of the importance of different food sources in the upper Au Sable and Manistee trout diets, it is helpful to look at the trends of these sources simultaneously throughout the season.

Upper Au Sable 3.0- to 5.9-inch brook trout

In the upper Au Sable, the diet of the 3.0- to 5.9-inch brook trout was dominated by Ephemeroptera, Trichoptera, and Annelida (Table 1). Annelida are known to be important food sources in the diet of trout in many rivers of northern lower Michigan (Alexander and Gowing 1976). This importance was not evident in the diet of the trout of these rivers for the summer of 1976. Only in the 3.0- to 5.9-inch brook trout on the upper Au Sable did Annelida account for as much as 7% of the total diet. Most of the Annelida consumption on the upper Au Sable both in the 3.0- to 5.9-inch and 7.0- to 9.9-inch size ranges occurred in May (Tables 1 and 2). In the other rivers and in both size categories Annelida comprised a much smaller percentage of the total diet composition.

The 3.0- to 5.9-inch upper Au Sable brook trout depended most heavily on Annelida and moderately on Ephemeroptera and Trichoptera in May. Ephemeroptera dominated the diet in June, with Trichoptera remaining somewhat important, and Annelida not of any importance until September. Fish was the staple food in July, and was supplemented by Trichoptera and Ephemeroptera. The lowest total volume of the season occurred in August. Trichoptera and Ephemeroptera values, though relatively low, were the dominant diet components during this month. In September, Trichoptera was the most important food source. The diet of the trout in September was supplemented by Annelida, Ephemeroptera and terrestrials. Although the summer diet of the 3.0- to 5.9-inch brook trout was dominated overwhelmingly by _Hexagenia limbata_, Trichoptera and other Ephemeroptera maintained relatively constant levels from month to month and thus were considered the staple foods of the 3.0- to 5.9-inch upper Au Sable brook trout.

Upper Au Sable 7.0- to 9.9-inch brook trout

Fish and Ephemeroptera contributed heavily to the 7.0- to 9.9-inch brook trout diet on the upper Au Sable (Table 2 and Fig. 4). Ephemeroptera, Trichoptera, and Annelida supplemented fish as important food sources in May. In June, Hexagenia limbata, accounted for the majority of the diet composition. Other Ephemeroptera, along with fish and Diptera made up the July diet. Fish consumption dominated the August diet composition values, while Ephemeroptera, Trichoptera, and Odonata contributed modestly to the total food consumption. Like August, the September diet was dominated largely by fish. Trichoptera contributed to the total consumption as did terrestrials and Decapoda to a minor extent.

Upper Manistee 3.0- to
5.9-inch brown trout

The 3.0- to 5.9-inch upper Manistee brown trout diet was dominated by Trichoptera (Table 3 and Fig. 5). In May, the diet was predominantly Trichoptera supplemented by Ephemeroptera. Trichoptera was almost the exclusive diet component in June. The other items of any importance in June were vegetable and mineral matter and unidentified insect parts. Diptera values were moderately high in July, but again the diet was dominated by Trichoptera. Though Trichoptera was still the most important food source in August, Ephemeroptera, Plecoptera, and Diptera (mostly Simulidae) also contributed to the diet. September samples were dominated by Trichoptera and Diptera consumption.

Upper Manistee 7.0- to
9.9-inch brown trout

The 7.0- to 9.9-inch trout of the upper Manistee, although depending a great deal on forage fish still ate large quantities of Trichoptera (Table 4 and Fig. 5). The May diet was predominantly Trichoptera, while fish accounted for much of the remainder of the diet. Diptera, Trichoptera, and fish accounted for much of the June diet; while in July, although the trout ate a lot of fish, the diet was comprised overwhelmingly of Trichoptera. Fish heavily dominated the August values, though Trichoptera was still important. September values were similar to the July values in that Trichoptera consumption again dominated, although this size brown trout also ate a lot of fish.

Total stomach volume-total length relationship

The larger trout on all four rivers ate more than their smaller counterparts (Fig. 3). Perhaps more important were the comparisons at selected sizes across rivers (Table 5). The graph showed that in the smaller size range (3.0-5.9 inches), the upper Au Sable brook trout ate more than did the brown trout from any of the other three rivers.

The slope of the upper Au Sable brook trout line (Fig. 3) is such that in the upper size range, the brook trout showed a tendency to have less food in their stomachs than did the same size brown trout from the other rivers. It was not clear from this study whether these differences in consumption were due to the difference in species or the difference in fauna available to all sizes of the population from river to river.

Growth as measured by length

Measurements of mean lengths of the trout populations of the upper Au Sable and upper Manistee indicated no significant difference in lengths at ages 0 through III (Table 6), which is all that the summer data included. Comparisons of the brown trout summer population data of the upper Manistee, lower Main Au Sable, and South Branch showed some significant differences in lengths at certain ages (Table 8). In the age-0 class, brown trout of the lower Au Sable were significantly longer than the brown trout of the South Branch and upper Manistee. Age-I brown trout from the South Branch were significantly longer than either the lower Au Sable or the upper Manistee brown trout, while the age-II brown trout from both the South Branch and lower Au Sable were significantly longer than the age-II upper Manistee brown trout. No age-III trout were taken from the South Branch during the summer, and though the lower Au Sable brown trout averaged slightly longer than the upper Manistee brown trout, there was no significant difference between the average lengths of the two populations at that age.

Regression analysis yielded essentially the same results, but when the results of this test were graphed, it allowed for easier comparisons from river to river. These equations of the line with 95% confidence limits, when plotted, indicated that at the end of 1 year, the upper Au Sable brook trout were slightly longer than the brown trout from the other three rivers. After 3 years, the growth rates were more evident. The average South Branch brown trout was almost 9 inches long, while the lower Au Sable, and upper Manistee trout were closer to 8 inches long.

Growth as measured by weight

As may be expected from the length against age results, weight against age also showed no significant difference between the trout populations of the upper Au Sable and upper Manistee (Table 7). The upper Manistee brown trout, which were generally shorter than the South Branch and lower Au Sable brown trout, also weighed less than the trout from these two rivers (Table 9).

Length-weight relationship

The length-weight relationship of the brown trout populations in the upper Manistee, lower Au Sable, and South Branch were very similar. The 2-inch upper Manistee and lower Au Sable brown trout were slightly heavier than the 2-inch South Branch brown trout. Conversely, the 10-inch upper Manistee and lower Au Sable brown trout were slightly lighter than the 10-inch South Branch brown trout. Even the upper Au Sable brook trout length-weight relationship was similar between 2 and 7 inches. However, the larger upper Au Sable brook trout weighed significantly more than brown trout of the same length from the other rivers.

Quantity vs. quality

Baldwin (1956) found that the more trout ate, the better they grew. By collectively examining the total volume-total length results (Fig. 3) with the other growth parameters discussed above, this relationship was analyzed with respect to the trout populations of the Au Sable and Manistee rivers.

This correlation of trout growth to the quantity of food eaten was especially apparent with the upper Au Sable brook trout. As the trout reached greater lengths, the amount of food found in their stomachs decreased (Fig. 3). At the same time growth rate, as measured by the regression of the natural log of the length of the trout against the natural log of the age of the trout, slowed at these same longer lengths.

It was believed that the brook trout ate relatively high quality food for their entire life, but were limited by their environment in obtaining adequate amounts of food at the greater lengths. The limiting factor for the upper Au Sable trout may well have been that Hexagenia limbata were only available for 1 month of the year, and that this was the only month when high stomach volumes were consistently observed.

Alexander and Gowing (1976) found that often natural populations do not feed up to their full potential; frequently the environment cannot provide enough food to satiate the trout. Under these conditions they argue that quantity of food, not quality, determines the extent of trout growth. They do concede, however, that certain foods may be better than others in terms of digestibility and caloric value for the trout.

Quality of food items does come into play even when trout are not eating up to their maximum physical potential. It is assumed that trout eat as much as their particular environment allows, but often the food source may not be particularly nutritious, or the food item requires a great deal of energy to be utilized. If this is the case, then the food item may be present in large quantities but is of little value to the trout in terms of growth.

This condition seemed to be the case with the brown trout in the upper Manistee River. These trout contained almost identical stomach volumes of food as the brown trout in the South Branch (Fig. 3), yet their rate of growth (Table 8) appeared slower than the South Branch brown trout.

The upper Manistee brown trout diet seemed different from the South Branch brown trout diet in two respects (Fig. 5, and Stauffer 1977, Fig. 2). Fish constituted about 25% of the total diet composition of the upper Manistee brown trout but only about 7% of the total diet composition of the South Branch brown trout in the 7.0- to 9.9-inch size range. Fish were of little consequence on either river in the 3.0- to 5.9-inch range. It seemed unlikely that the addition of fish to the Manistee diet would cause poorer growth as Schneider (1973) found fish to be an excellent food source in his study of yellow perch and bluegills. Furthermore, South Branch brown trout tended to have a better growth rate than the upper Manistee brown trout even in the smaller size range, where fish were not a factor in the diet.

The second major difference between the diets of the upper Manistee brown trout and the South Branch brown trout was the consumption of Trichoptera. Almost half of the total diet composition of the upper Manistee brown trout in both the 3.0- to 5.9-inch and 7.0- to 9.9-inch size ranges was Trichoptera; while on the South Branch Trichoptera accounted for only 27% of the total composition in the 3.0- to 5.9-inch brown trout and 17% in the 7.0- to 9.9-inch brown trout. Brachycentrus larvae dominated on the upper Manistee, with other cased forms making up the majority of the remainder. On the South Branch, Brachycentrus was also a major trichopteran but was supplemented largely by Hydropsychidae, an uncased trichopteran. In addition, adult trichopterans were far more common in the stomach samples of the South Branch brown trout than they were in the stomach samples from the upper Manistee.

Trichoptera with cases are digested at a much slower rate than most other food items, and they do not furnish as much caloric advantage as many other trout foods (Alexander and Gowing 1976). Given the importance of cased trichopterans to the upper Manistee brown trout diet, it seemed likely that they did not provide the trout in the upper Manistee with the same nutritional benefit that the food staples in the South Branch provided.

Total stomach volume-total weight relationship

As in the total volume-total length relationship it was not completely apparent from this study whether differences in consumption were due to the difference in species, or food availability from river to river. When the equations of the line were plotted for the natural log of weight against the natural log of stomach volume, the lines for the upper Manistee and South Branch were again found to be almost identical. At the lowest total stomach volume measurement the lower Au Sable brown trout were found to weigh slightly more than the upper Manistee and South Branch brown trout, and significantly more than the upper Au Sable brook trout. The reverse was found to occur at the highest total stomach volume. At this volume, the lower Au Sable brown trout weighed slightly less than the upper Manistee and South Branch brown trout; while the upper Au Sable brook trout were found to be heavier than the brown trout of the other three rivers, especially the lower Au Sable.

Trout populations

The third segment of this study involved estimates of the trout populations in these streams (Tables 10 and 11, and Stauffer 1977, Table 12). Of the four rivers, the upper Au Sable had the lowest number of trout per acre (276.8 per acre) and the upper Manistee the largest (1148.9 per acre). Both rivers supported populations dominated heavily by one species.

Though brook trout and brown trout are similar in many respects, there are some factors in which they tend to differ. Brook trout do not tend to live as long as brown trout, and are more easily exploited by angling (Cooper 1953). It is also known that brook trout mature and spawn at an earlier age than brown trout (Cooper 1952). Optimum spawning material is fine and coarse gravel for brook trout, while brown trout utilize coarse gravel and rubble (Benson 1953b). Although spawning sites for both species are most prevalent in areas of groundwater seepage, this correlation is most apparent with brook trout (Benson 1953b).

It would seem that the upper Au Sable would have a sufficient flow of groundwater coming into the stream as it is part of the same aquifer system as the upper Manistee. Both rivers appeared to remain cold throughout the summer, although no comprehensive temperature data were recorded. The upper Au Sable, more than any of the other three rivers, has several areas of broad, relatively shallow pools, some of which were caused by old dams. The combination of silt buildup and the possibly slightly less stable water temperatures which may result in these areas could be enough to restrict the availability of sufficiently good spawning sites on the upper Au Sable. There is no obvious explanation why brook trout dominate the upper Au Sable while brown trout dominate the lower Au Sable, and why the numbers of trout in this river are fewer than in the other river sections considered.

Trout density

It was found that density (total number of the dominant species in each river per acre, total trout per acre) had no measurable effect on the natural log of the weight in any of the streams, except in the lower Au Sable. In the upper Au Sable, upper Manistee, and South Branch, the natural log of the weight was mainly influenced by the natural log of the volume eaten. In the lower Au Sable, while total trout per acre demonstrated no measurable effect on the natural log of the weight, the total number of brown trout per acre had a significant effect upon the natural log of the weight of brown trout at the 0.9773 level. The equation of the line was:

$$\ln \text{weight} = 6.3844 - 0.0118\,(\text{brown trout/acre}) + 0.8066\,(\ln \text{stomach volume})$$

The inclusion of density into the natural log of the weight-natural log of the volume eaten relationship improved the R^2 by 0.0257. The inclusion of density in this relationship on the upper Au Sable, upper Manistee, and South Branch only improved the R^2 values by 0.00034, 0.00045, and 0.00082, respectively. This means that only in the case of the lower Au Sable did the number of brown trout in the stream influence the weight of the brown trout in the stream.

Apparently due to the high intraspecific competition in the lower Au Sable brown trout population, the brown trout in this river weighed less than the trout from the other three rivers at the highest stomach volume measured. It is likely that there are more demands metabolically on larger and older fish, and that nutritional deficiencies may manifest themselves more at these larger sizes when density is a factor. Seaburg and Moyle (1964) found in their study of bluegills that often the larger fish were out-competed by smaller fish of the same species for the most nutritious food, and thus were forced to eat foods of less nutritional quality.

Perhaps a more meaningful measure of trout populations than the total number of trout per acre would be the total number of trout per volume of the river. The upper Manistee and lower Au Sable had very similar trout species composition and total numbers per acre yet the lower Au Sable brown trout weights were affected by density and the Manistee brown trout weights were not.

The upper Manistee seemed much deeper overall than did the lower Au Sable. Consequently, the trout of the upper Manistee would seem to have more space in which to feed and grow than would the lower Au Sable trout.

No single factor is responsible for the productivity or vigor of a population of trout in a river. The stream fauna, quantity and quality of food eaten, the size of the river, the number of fish present, the age structure, habitat preference, inter- and intraspecific competition, and predation are some of the elements responsible for determining productivity. This report has attempted to deal with some of these factors. It is hoped that future workers will continue in this endeavor to provide a more thorough understanding of the workings of the trout populations of the upper Au Sable and upper Manistee rivers.

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Appendix 1.--Mean volume of stomach contents (milliliters) of brown trout 3.0-5.9 inches total length from the South Branch Au Sable River, May-September 1976 (unadjusted figures) (sample sizes in parentheses), with 95% confidence levels.

Organism	Month					Seasonal mean volume
	May (21)	June (25)	July (25)	Aug (25)	Sep (25)	
Trichoptera	0.142 ±0.020	0.014 ±0.020	0.027 ±0.020	0.013 ±0.020	0.046 ±0.020	0.048 ±0.019
Ephemeroptera	0.060 ±0.015	0.060 ±0.015	0.011 ±0.015	0.086 ±0.015	0.007 ±0.015	0.045 ±0.015
Diptera	0.033 ±0.005	0.029 ±0.005	0.007 ±0.005	0.019 ±0.005	0.012 ±0.005	0.020 ±0.005
Mollusca	0.002 ±0.008	0.000 ±0.008	0.000 ±0.008	0.000 ±0.008	0.004 ±0.008	0.001 ±0.008
Fish	0.001 ±0.034	0.000 ±0.034	0.000 ±0.034	0.000 ±0.034	0.000 ±0.034	tr ±0.032
Isopoda Amphipoda	0.000 ±0.005	0.000 ±0.005	0.002 ±0.005	0.000 ±0.005	0.000 ±0.005	tr ±0.005
Monthly mean volumes	0.362 ±0.062	0.212 ±0.062	0.095 ±0.062	0.131 ±0.062	0.090 ±0.062	0.178 ±0.059

Appendix 2.--Mean volume of stomach contents (milliliters) of brown trout 7.0-9.9 inches total length from the South Branch Au Sable River, May-September 1976 (unadjusted figures) (sample size in parentheses), with 95% confidence levels.

Organism	Month					Seasonal mean volume
	May (25)	June (25)	July (25)	Aug (25)	Sep (25)	
Trichoptera	0.289 ±0.020	0.073 ±0.020	0.065 ±0.020	0.060 ±0.020	0.146 ±0.020	0.127 ±0.019
Ephemeroptera	0.031 ±0.015	0.029 ±0.015	0.105 ±0.015	0.013 ±0.015	0.001 ±0.015	0.036 ±0.015
Diptera	0.007 ±0.005	0.029 ±0.005	0.001 ±0.005	0.049 ±0.005	0.014 ±0.005	0.020 ±0.005
Mollusca	0.037 ±0.008	0.038 ±0.008	0.001 ±0.008	0.055 ±0.008	0.080 ±0.008	0.042 ±0.008
Fish	0.000 ±0.034	0.000 ±0.034	0.037 ±0.034	0.171 ±0.034	0.055 ±0.034	0.053 ±0.032
Isopoda Amphipoda	0.000 ±0.005	0.000 ±0.005	0.000 ±0.005	0.000 ±0.005	0.000 ±0.005	0.000 ±0.005
Monthly mean volumes	0.981 ±0.062	0.581 ±0.062	0.840 ±0.062	0.507 ±0.062	0.728 ±0.062	0.727 ±0.059

Appendix 3.--Mean volume of stomach contents (milliliters) of brown trout 3.0-5.9 inches total length from the lower Main Au Sable River, May-September 1976 (unadjusted figures) (sample size in parentheses), with 95% confidence levels.

Organism	Month					Seasonal
	May (25)	June (25)	July (29)	Aug (25)	Sep (25)	mean volume
Trichoptera	0.040 ±0.020	0.039 ±0.020	0.011 ±0.020	0.004 ±0.020	0.019 ±0.020	0.023 ±0.019
Ephemeroptera	0.021 ±0.015	0.032 ±0.015	0.055 ±0.015	0.007 ±0.015	0.011 ±0.015	0.025 ±0.015
Diptera	0.012 ±0.005	0.014 ±0.005	0.005 ±0.005	0.001 ±0.005	0.000 ±0.005	0.006 ±0.005
Mollusca	0.002 ±0.008	0.000 ±0.008	0.013 ±0.008	0.006 ±0.008	0.000 ±0.008	0.004 ±0.008
Fish	0.026 ±0.034	0.000 ±0.034	0.000 ±0.034	0.001 ±0.034	0.000 ±0.034	0.005 ±0.032
Isopoda Amphipoda	0.058 ±0.005	0.008 ±0.005	0.018 ±0.005	0.000 ±0.005	0.054 ±0.005	0.028 ±0.005
Monthly mean volumes	0.198 ±0.062	0.136 ±0.062	0.126 ±0.062	0.036 ±0.062	0.095 ±0.062	0.118 ±0.059

Appendix 4.--Mean volume of stomach contents (milliliters) of brown trout 7.0-9.9 inches total length from the lower Au Sable River, May-September 1976 (unadjusted figures) (sample size in parentheses), with 95% confidence levels.

Organism	Month					Seasonal mean volume
	May (25)	June (25)	July (26)	Aug (25)	Sep (25)	
Trichoptera	0.275 ±0.020	0.104 ±0.020	0.187 ±0.020	0.058 ±0.020	0.127 ±0.020	0.150 ±0.019
Ephemeroptera	0.027 ±0.015	0.173 ±0.015	0.030 ±0.015	0.000 ±0.015	0.008 ±0.015	0.048 ±0.015
Diptera	0.012 ±0.005	0.010 ±0.005	0.000 ±0.005	0.002 ±0.005	0.000 ±0.005	0.005 ±0.005
Mollusca	0.060 ±0.008	0.038 ±0.008	0.055 ±0.008	0.045 ±0.008	0.134 ±0.008	0.066 ±0.008
Fish	0.221 ±0.034	0.140 ±0.034	0.232 ±0.034	0.183 ±0.034	0.171 ±0.034	0.189 ±0.032
Isopoda Amphipoda	0.065 ±0.005	0.073 ±0.005	0.018 ±0.005	0.004 ±0.005	0.006 ±0.005	0.033 ±0.005
Monthly mean volumes	1.031 ±0.062	1.012 ±0.062	0.907 ±0.062	0.495 ±0.062	0.557 ±0.062	0.800 ±0.059