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A COMPARISON OF THE DIET AND GROWTH OF BROWN TROUT (*Salmo trutta*) FROM THE SOUTH BRANCH AND THE MAIN STREAM, AU SABLE RIVER, MICHIGAN.

THOMAS E. STAUFFER

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A COMPARISON OF THE DIET AND GROWTH OF BROWN TROUT (SALMO TRUTTA) FROM THE SOUTH BRANCH AND THE MAIN STREAM, AU SABLE RIVER, MICHIGAN *

By Thomas E. Stauffer

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ABSTRACT

Samples of brown trout were collected monthly from the South Branch and the Main Stream, Au Sable River, Michigan, from May through September, 1976. Stomach contents were analyzed to determine the type and volume of organisms present.

The mean stomach volumes for smaller fish (mean total length = 4.56 inches) were 0.180 ml and 0.125 ml for the South Branch and Main Stream, respectively. Total volumes for larger fish (mean total length = 8.81 inches) averaged 0.885 ml and 0.768 ml for the South Branch and Main Stream, respectively. The major diet components for both rivers were Trichoptera, Ephemeroptera, Diptera, and Mollusca. Also, Main Stream fish ate an abundance of Isopoda.

There was a marked shift between the diet of younger and older fish. Small food items such as Ephemeroptera and Isopoda which were so important to smaller fish were replaced in the diet of larger fish by higher amounts of Mollusca, Decapoda, Odonata, and especially by more fish.

A great difference in diet was observed between different months. Total stomach volume and the volumes of Trichoptera, Isopoda, and Amphipoda were highest in the early part of the growing season, especially in May. In contrast to this were the volumes of Mollusca, which were highest late in the season.

South Branch trout were in better condition and grew faster than Main Stream trout. This difference probably resulted from the greater volume of food per individual trout of the South Branch. Because the population of trout per acre for the Main Stream was more than twice that of the South Branch, intense competition for food probably accounted for the lower volumes of food per fish observed for the Main Stream. The estimated total volume of food consumed per acre for the entire growing season was 133,871.4 ml for the South Branch and 260,580.6 ml for the Main Stream.

INTRODUCTION

The Au Sable River System in Crawford County, Michigan, has received much recognition for its excellent recreational value. Trout fishing has undoubtedly contributed much to the Au Sable's fame, especially with regard to the management philosophies developed through great public interest and scientific research.

A section of the Au Sable system which has received much attention is the Main Stream from Burton's Landing downstream to Wakeley Bridge. This 8.9-mile stretch has been designated as a "special regulation" or "quality fishing" area, with fly-fishing only, a 12-inch size limit for brown trout, an 8-inch size limit for brook trout, and a three-trout creel limit. Another section with fly-fishing only regulations is the Mason Tract on the South Branch, however here the minimum size for brown trout is only 10 inches, and the creel limit is five trout. This popular section was originally set aside as a "wilderness" area, and offers few access sites to its 9.7 miles of river. Although both the Main Stream and South Branch are excellent trout fishing rivers, the total number and size composition of their trout populations differ. Both rivers have excellent water quality and diverse insect populations. Coopes (1974) gave a thorough description of the two rivers with respect to habitat (bottom type and trout cover), water quality, and human impact and use.

The present study seeks to aid both anglers and biologists who have an interest in the rivers. Knowing the major types of food actually eaten by the trout will aid fishermen in selecting appropriate imitations. These results, coupled with knowledge of the number and sizes of brown trout in each river, will enable the serious angler to plan his trips more effectively. These same population and diet data will also help biologists understand the Main Stream and the South Branch trout populations.

The specific objections of the study were to identify the kinds of organisms eaten seasonally by different sizes of trout, to determine the mean volume of food eaten per trout and to compare food, growth and numbers of South Branch trout with Main Stream trout.

METHODS

Monthly samples of trout were taken from May through September 1976. These months represent the major portion of the growing season for wild trout (Cooper 1953; Alexander and Gowing 1976). The stations sampled on the Main Stream were Burton's Landing, Louie's Landing, Keystone Landing, Wa Wa Sum, Stephan's Bridge, Pine Road, Thunderbird Club, and Wakeley Bridge; stations on the South Branch were Chase Bridge, Marlbar, Castle, Downey's, Dogtown, and Smith Bridge (Figure 1). The gear consisted of a 230-volt DC generator mounted on a small boat. The copper-sheeted bottom of the boat served as the negative electrode, and was used with two portable positive electrodes.

Each month, 25 brown trout from 3.0-5.9 inches total length and the same number from 7.0-9.9 inches were taken from each river. Immediately after collection, the trout were transferred to an ice chest and then transported to the laboratory, where they were measured to the nearest 0.1 inch (total length), weighed to the nearest 0.1 gram, and scale-sampled. Stomachs were removed from larger fish and preserved in 10% formalin, while the smaller fish were slit along the side and preserved whole. A label containing pertinent data was inserted in each stomach. After one week, the contents of each stomach and the respective label were transferred to a vial containing 80% alcohol. Each

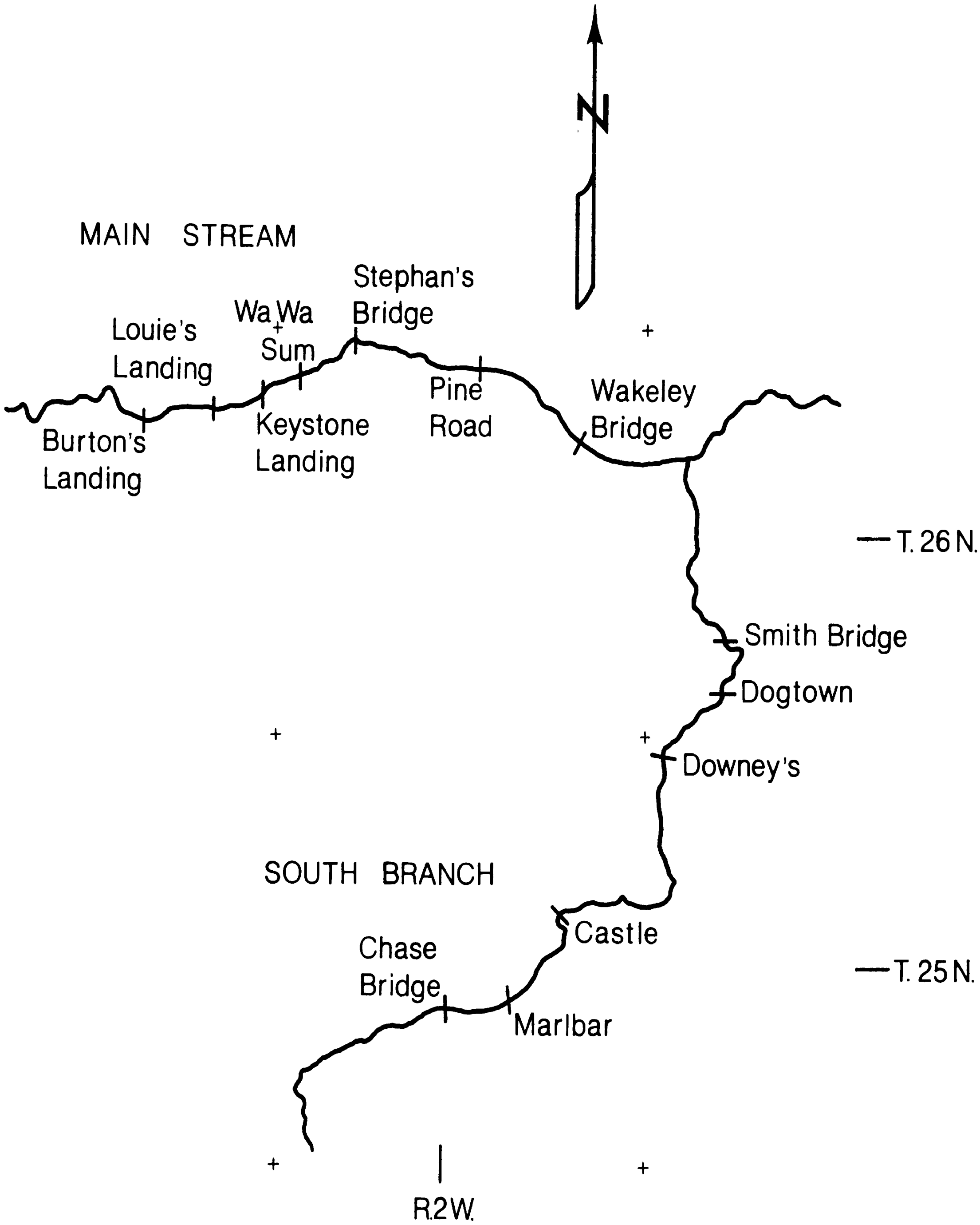

Figure 1.--Location of sampling sites on the South Branch and Main Stream, Au Sable River, Crawford County, Michigan.

sample was then sorted to taxonomic order and family, and the number of individuals was counted. The volume of each familial type was determined by liquid displacement to the nearest 0.025 ml. Impressions of trout scales were made on cellulose acetate squares and were magnified with a microprojector. Age (number of annuli) was determined for each fish.

Fall population estimates for several stations on the two rivers were run by the Michigan Department of Natural Resources Fisheries Division. At each station, trout were captured with an electroshocker, fin-clipped, and returned to the river. Later, a second sampling with the electrofishing gear yielded the number of marked and unmarked trout. These data were then used for Peterson estimates of total population size. The results were made available for this study, and included the population size of brook, brown, and rainbow trout in each inch group. Representative scale samples collected in the fall estimates were used to determine the age of trout as described above.

RESULTS

Stream-side Observations

From observations made on the monthly sampling trips, it appeared that the surface-feeding of trout on insects differed noticeably between the South Branch and Main Stream. Although the monthly trips occurred during the bright daylight hours, they were supplemented by occasional evening visits to the two rivers. Without fail every month on the Main Stream, daytime or evening, trout were surface-feeding to some extent. Most of these fish appeared to be brook trout, with a few smaller brown trout involved. These fish fed throughout the season on the small black dance flies (Diptera: Empididae), but switched their attention to larger insects during sizable emergences. These "hatches" also stimulated the larger brown trout to surface-feed, especially toward dusk. In May and June the fish fed intensively on emerging gray caddis flies (Hydropsychidae, Brachycentridae). Small- to medium-sized mayflies were eaten to a lesser extent. Much less surface-feeding on dance flies occurred on the South Branch, and was confined to the evening. Fairly good hatches of the mayflies *Isonychia* and *Tricorythodes* took place, but the major event of the season, the *Hexagenia* (Michigan mayfly) hatch, probably overshadowed all the others. The emergence of these big insects prompted even the largest trout to surface-feed.

Ironically, I found no adult Hexagenia in the stomach samples, although I did find some nymphs. The reasons for this were probably two: (1) the sampling dates of June 15 and July 16 missed the peak of the emergence; (2) adult Hexagenia eaten during the evening periods were digested by the time we captured the fish on the following day. The latter reason probably also explained why very few adults of other types of mayflies were found in stomach samples. Nonetheless, I believe that the South Branch trout benefitted greatly from Hexagenia, while Main Stream fish did not have them as a food source. Although several nymphs were found in the stomachs of trout from one station on the Main Stream, the reports of knowledgeable anglers indicate that significant populations of Hexagenia do not exist in the section of the river studied here.

Stomach Sample Analysis

Summaries of the data of brown trout diet for the Main Stream and South Branch are presented in Tables 1 to 4. The most common families of each order may be found in Table 5. For those who are unfamiliar with insect taxonomy, this table also gives the common names of the orders and families. Comparing the contribution of each taxon in trout diet by percentages demonstrates, that in general, the types of food eaten in both rivers were very similar. Also, it appears that shifts in diet as the trout grow from small to large are of a similar nature in both rivers. Comparisons of this sort may be more easily visualized in Figures 2 and 3. (Notice that the label "others" in these figures was a

Table 1.--Mean volume of stomach contents (ml) of brown trout 3.0-5.9 inches total length from the South Branch Au Sable River, May-September, 1976 (sample size in parentheses).

Organism	Month					Seasonal mean volume	Percent composition
	May (21)	June (25)	July (25)	Aug. (25)	Sept. (25)		
Trichoptera	0.175	0.023	0.025	0.012	0.047	0.052	28.2
Ephemeroptera	0.062	0.064	0.023	0.079	0.007	0.046	25.0
Plecoptera	0.014	0.000	0.000	0.000	0.000	0.002	1.3
Odonata	0.014	0.014	0.028	0.000	0.000	0.011	6.0
Hemiptera	0.000	0.000	0.001	0.004	0.000	0.001	0.6
Coleoptera	0.002	0.002	0.000	0.000	0.005	0.002	1.0
Megaloptera	0.000	0.010	0.000	0.000	0.000	0.002	1.1
Diptera	0.038	0.027	0.008	0.016	0.011	0.019	10.4
Mollusca	0.002	0.000	0.000	0.001	0.003	0.001	0.7
Fish	0.001	0.000	0.000	0.000	0.000	0.000	0.1
Isopoda + Amphipoda	0.000	0.000	0.001	0.000	0.000	0.000	0.1
Decapoda	0.000	0.000	0.000	0.000	0.000	0.000	0.0
Terrestrial	0.000	0.008	0.007	0.001	0.001	0.004	1.9
Other	0.000	0.001	0.000	0.000	0.000	0.000	0.1
Unidentified	0.052	0.097	0.019	0.013	0.014	0.039	20.8
Annelida	0.019	0.000	0.008	0.000	0.000	0.005	2.7
Monthly mean volume	0.381	0.246	0.120	0.126	0.088	0.186	100.0

Table 2.--Mean volume of stomach contents (ml) of brown trout 7.0-9.9 inches total length from the South Branch Au Sable River, May-September, 1976 (sample size in parentheses).

Organism	Month					Seasonal mean volume	Percent composition
	May (22)	June (25)	July (25)	Aug. (25)	Sept. (25)		
Trichoptera	0.281	0.073	0.059	0.065	0.133	0.118	16.9
Ephemeroptera	0.034	0.029	0.094	0.059	0.001	0.044	6.2
Plecoptera	0.018	0.021	0.004	0.000	0.024	0.013	1.9
Odonata	0.173	0.038	0.072	0.032	0.007	0.062	8.8
Hemiptera	0.000	0.006	0.011	0.006	0.086	0.022	3.2
Coleoptera	0.000	0.028	0.003	0.005	0.005	0.008	1.2
Megaloptera	0.016	0.000	0.000	0.000	0.010	0.005	0.7
Diptera	0.007	0.033	0.001	0.053	0.018	0.023	3.3
Mollusca	0.038	0.036	0.018	0.044	0.069	0.041	5.9
Fish	0.000	0.012	0.031	0.144	0.054	0.049	7.1
Isopoda + Amphipoda	0.000	0.000	0.000	0.000	0.000	0.000	0.0
Decapoda	0.061	0.000	0.137	0.004	0.024	0.045	6.4
Terrestrial	0.009	0.062	0.027	0.044	0.104	0.050	7.2
Other	0.198	0.008	0.016	0.006	0.011	0.053	7.6
Unidentified	0.116	0.240	0.285	0.056	0.112	0.163	23.3
Annelida	0.009	0.000	0.000	0.000	0.000	0.002	0.2
Monthly mean volume	0.959	0.586	0.758	0.518	0.702	0.698	99.9

Table 3.--Mean volume of stomach contents (ml) of brown trout 3.0-5.9 inches total length from the Main Stream Au Sable River, May-September, 1976 (sample size in parentheses).

Organism	Month					Seasonal mean volume	Percent composition
	May (25)	June (25)	July (29)	Aug. (25)	Sept. (25)		
Trichoptera	0.042	0.047	0.016	0.003	0.019	0.025	20.0
Ephemeroptera	0.024	0.035	0.042	0.006	0.011	0.024	19.4
Plecoptera	0.000	0.000	0.000	0.000	0.000	0.000	0.0
Odonata	0.000	0.000	0.000	0.000	0.000	0.000	0.0
Hemiptera	0.000	0.000	0.000	0.000	0.001	0.000	0.2
Coleoptera	0.000	0.000	0.000	0.001	0.000	0.000	0.2
Megaloptera	0.004	0.000	0.000	0.000	0.000	0.001	0.6
Diptera	0.010	0.014	0.011	0.001	0.000	0.007	5.9
Mollusca	0.002	0.000	0.015	0.005	0.000	0.005	3.7
Fish	0.022	0.000	0.000	0.001	0.000	0.004	3.6
Isopoda + Amphipoda	0.069	0.011	0.025	0.000	0.054	0.032	25.3
Decapoda	0.000	0.000	0.002	0.000	0.000	0.000	0.3
Terrestrial	0.004	0.002	0.002	0.001	0.000	0.002	1.4
Other	0.004	0.006	0.004	0.000	0.000	0.003	2.3
Unidentified	0.025	0.025	0.023	0.016	0.011	0.020	16.1
Annelida	0.000	0.006	0.000	0.000	0.000	0.001	0.9
Monthly mean volume	0.206	0.146	0.140	0.034	0.096	0.125	99.9

Table 4.--Mean volume of stomach contents (ml) of brown trout 7.0-9.9 inches total length from the Main Stream Au Sable River, May-September, 1976 (sample size in parentheses).

Organism	Month					Seasonal mean volume	Percent composition
	May (25)	June (25)	July (26)	Aug. (25)	Sept. (25)		
Trichoptera	0.319	0.097	0.171	0.079	0.135	0.160	20.9
Ephemeroptera	0.023	0.210	0.043	0.000	0.007	0.057	7.4
Plecoptera	0.000	0.002	0.000	0.000	0.000	0.000	0.1
Odonata	0.020	0.018	0.000	0.000	0.000	0.008	1.0
Hemiptera	0.000	0.000	0.000	0.000	0.019	0.004	0.5
Coleoptera	0.000	0.007	0.004	0.001	0.000	0.002	0.3
Megaloptera	0.024	0.010	0.000	0.000	0.000	0.007	0.9
Diptera	0.010	0.038	0.173	0.002	0.000	0.047	5.9
Mollusca	0.050	0.032	0.047	0.051	0.113	0.059	7.6
Fish	0.186	0.038	0.188	0.246	0.149	0.177	23.1
Isopoda + Amphipoda	0.055	0.061	0.016	0.003	0.005	0.028	3.6
Decapoda	0.056	0.096	0.017	0.005	0.000	0.035	4.5
Terrestrial	0.002	0.167	0.004	0.008	0.030	0.042	5.4
Other	0.085	0.054	0.043	0.023	0.026	0.046	6.0
Unidentified	0.158	0.122	0.109	0.050	0.044	0.097	12.6
Annelida	0.000	0.008	0.000	0.000	0.000	0.002	0.2
Monthly mean volume	0.988	1.040	0.815	0.468	0.528	0.768	100.0

Table 5.--The most common families of aquatic organisms in stomach samples and their common names.

Order and Family	Common Name	Occurrence South Branch	Occurrence Main Stream
Trichoptera	Caddis flies		
Brachycentridae		*	*
Helicopsychidae		*	*
Goeridae		*	*
Glossosomatidae		*	*
Hydropsychidae		*	*
Lepidostomatidae		*	*
Leptoceridae		*	*
Philopotamidae			*
Ephemeroptera	Mayflies [1]		
Ephemerellidae	Hendrickson, Sulfur, Blue-winged olive	*	*
Ephemeridae	Brown drake and Michigan mayfly	*	
Baetiscidae		*	
Baetidae	Blue-winged olive, Quill Gordon, Sulfur	*	*
Heptageniidae	Cahill, Quill Gordon, Sulfur, March brown, Ginger quill, Grey fox	*	*
Siphlonuridae	Isonychia, Lead-wing coachman	*	*
Tricorythidae	Tricorythodes, Tiny white-winged black	*	*

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Table 5.--continued

Order and Family	Common Name	Occurrence	
		South Branch	Main Stream
Plecoptera	Stoneflies		
Perlidae		*	
Chloroperlidae		*	
Perlodidae		*	*
Pteronarcidae		*	
Odonata	Dragonflies and Damselflies		
Gomphidae	Darners	*	*
Hemiptera	True bugs		
Corixidae	Water boatmen	*	*
Belostomatidae	Giant water bugs	*	*
Coleoptera	Beetles		
Hydrophilidae		*	*
Dytiscidae		*	*
Neuroptera			
Corydalidae	Fishflies	*	*
Diptera	Two-winged flies		
Chironomidae	Midges	*	*
Simuliidae	Black flies	*	*
Rhagionidae	Snipe flies	*	
Empididae	Dance flies	*	*
Mollusca	Molluscs		
Physidae		*	*
Limnaeidae		*	*

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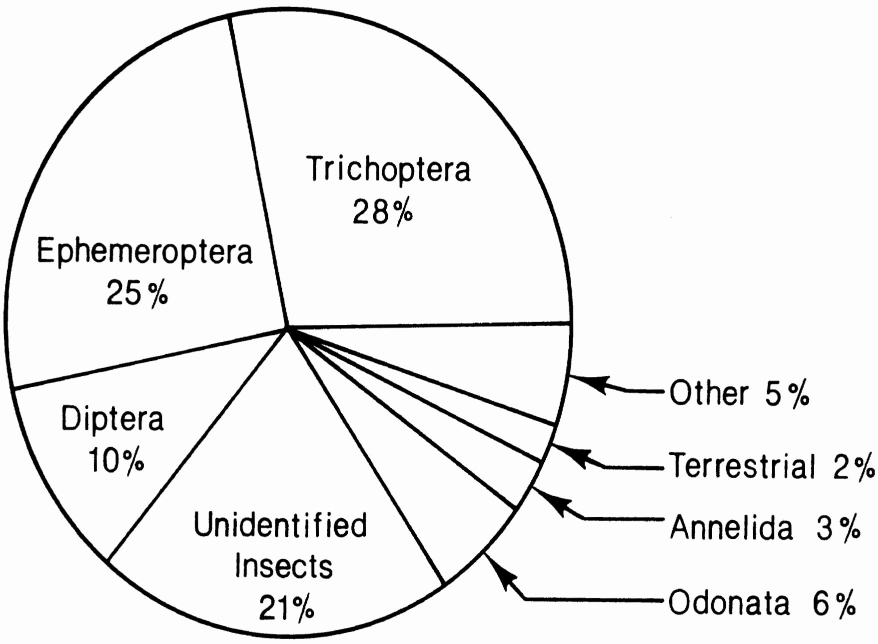
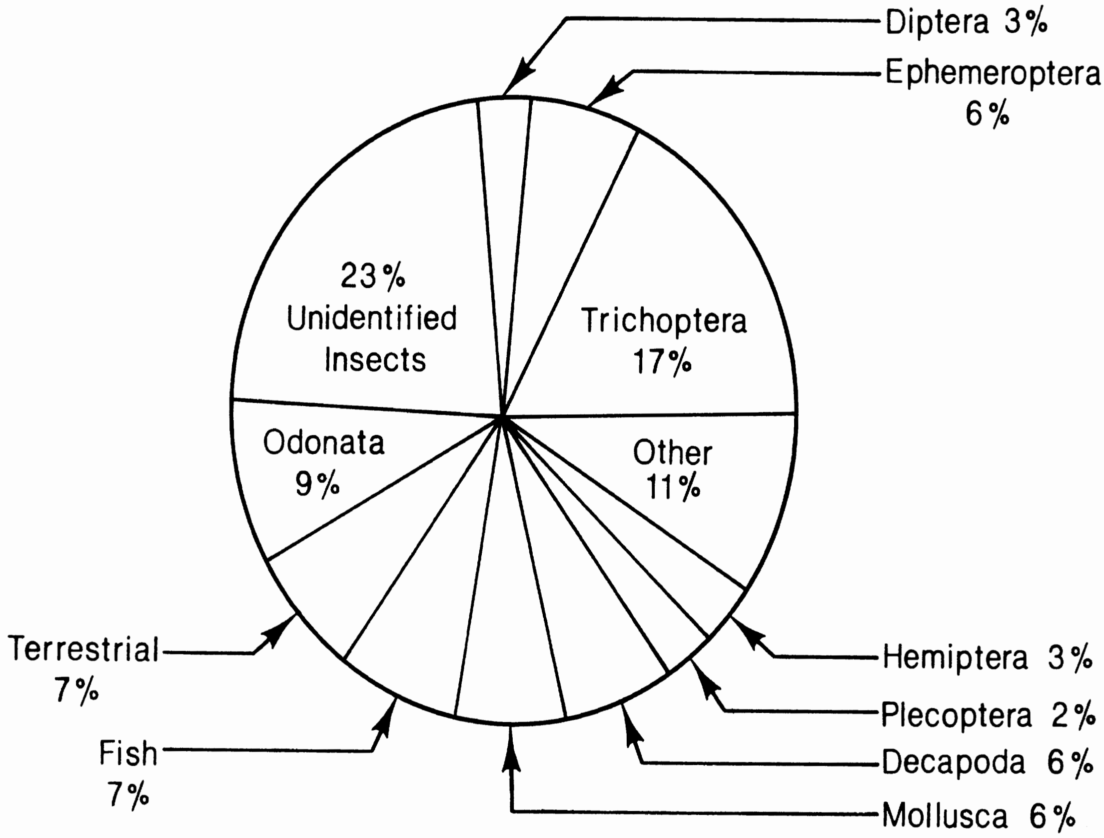
Table 5.--concluded

Order and Family	Common Name	Occurrence South Branch	Occurrence Main Stream
Perciformes			
Cottidae	Sculpins or Muddlers	*	*
Percidae	Darters		*
Isopoda			
Asellidae	Aquatic sow bugs		*
Amphipoda			
Gammaridae	Scuds		*
Decapoda	Crayfish	*	*

[1] Common names of families of mayflies were taken from Caucci and Nastasi (1975).



Trout 3.0-5.9 Inches Total Length



Trout 7.0-9.9 Inches Total Length

Figure 2. --Percent composition of the diet of brown trout from the South Branch Au Sable River, May-September, 1976.

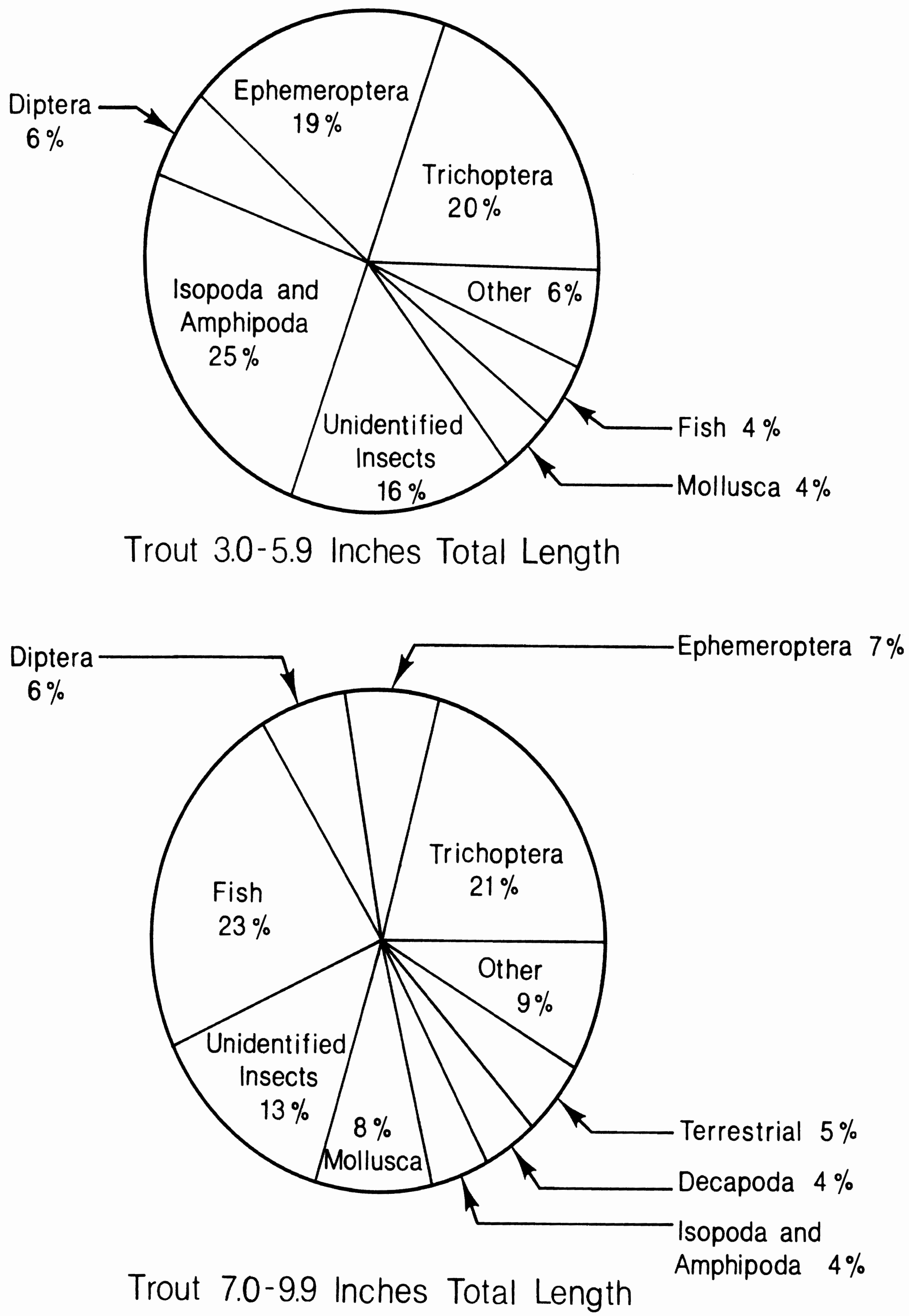


Figure 3.--Percent composition of the diet of brown trout from the Main Stream Au Sable River, May-September, 1976.

pooled category consisting of the "other" category in Tables 1 to 4 plus all taxa with percentages less than 2%.)

Comparing the diet of small fish of the South Branch to the Main Stream, the percentages of Trichoptera, Ephemeroptera, and Diptera were very similar. The major difference appeared to be Isopoda and Amphipoda, which on the Main Stream comprised 25% of the diet while being virtually absent from the South Branch. Odonata provided a fair amount of food in the South Branch and not in the Main Stream; fish were eaten in the Main Stream and not in the South Branch.

Small organisms were phased out of the diet of the larger fish and were replaced by more substantial items. Specifically, Ephemeroptera lost importance as a major source of food in both rivers; Isopoda and Amphipoda declined drastically in the Main Stream. Trichoptera did not lose importance in the Main Stream but were reduced moderately in the South Branch. Replacing the small food items in the Main Stream were Mollusca, Decapoda, and especially fish. In the South Branch, Odonata and terrestrials increased in importance; also fish, Mollusca, and Decapoda were major food items. Overall, the types of organisms present in the diet of Au Sable brown trout were very similar to the findings of Allen (1951), Lorz (1974), and Alexander and Gowing (1976).

Tables 1 to 4 show the average stomach volumes monthly and over the entire growing season for each component taxon. The average total volumes per fish for the entire 5-month period for the small and large fish in the South Branch were 0.186 ml and 0.698 ml, respectively;

Main Stream small fish averaged 0.125 ml and large fish averaged 0.768 ml. As previously discussed, the sampling scheme randomly selected trout in the intervals 3.0-5.9 and 7.0-9.9 inches. Due to this method, a difference in mean length of trout in the categories arose between the two rivers. South Branch and Main Stream small fish averaged 4.41 and 4.56 inches, respectively; South Branch large fish averaged 8.24 inches while Main Stream large fish averaged 8.81 inches. In order to compare stomach volumes between the two rivers, correction was made for this difference in length, because stomach capacity increases with an increase in fish length.

To determine this length-volume relationship, I calculated the mean stomach volume for each inch group of trout for each river, plotted the corresponding points, and fit the curves by eye (Figure 4). These curves adequately represented the mean stomach volumes for trout of all sizes between 3.0-9.9 inches, so a suitable correction factor was employed on this basis. I arbitrarily elected the South Branch to undergo correction using the following procedure. The mean length of small Main Stream fish was 4.56 inches, so the mean stomach volume corresponding to this length on the curve for the South Branch fish was equivalent to 0.180 ml. Likewise, the mean length of large Main Stream fish was 8.81 inches, so the mean stomach volume for this length on the South Branch curve was 0.885 ml. In effect, the corrected stomach volumes were those volumes which would have been observed had the mean lengths of South Branch and Main Stream fish been equal.

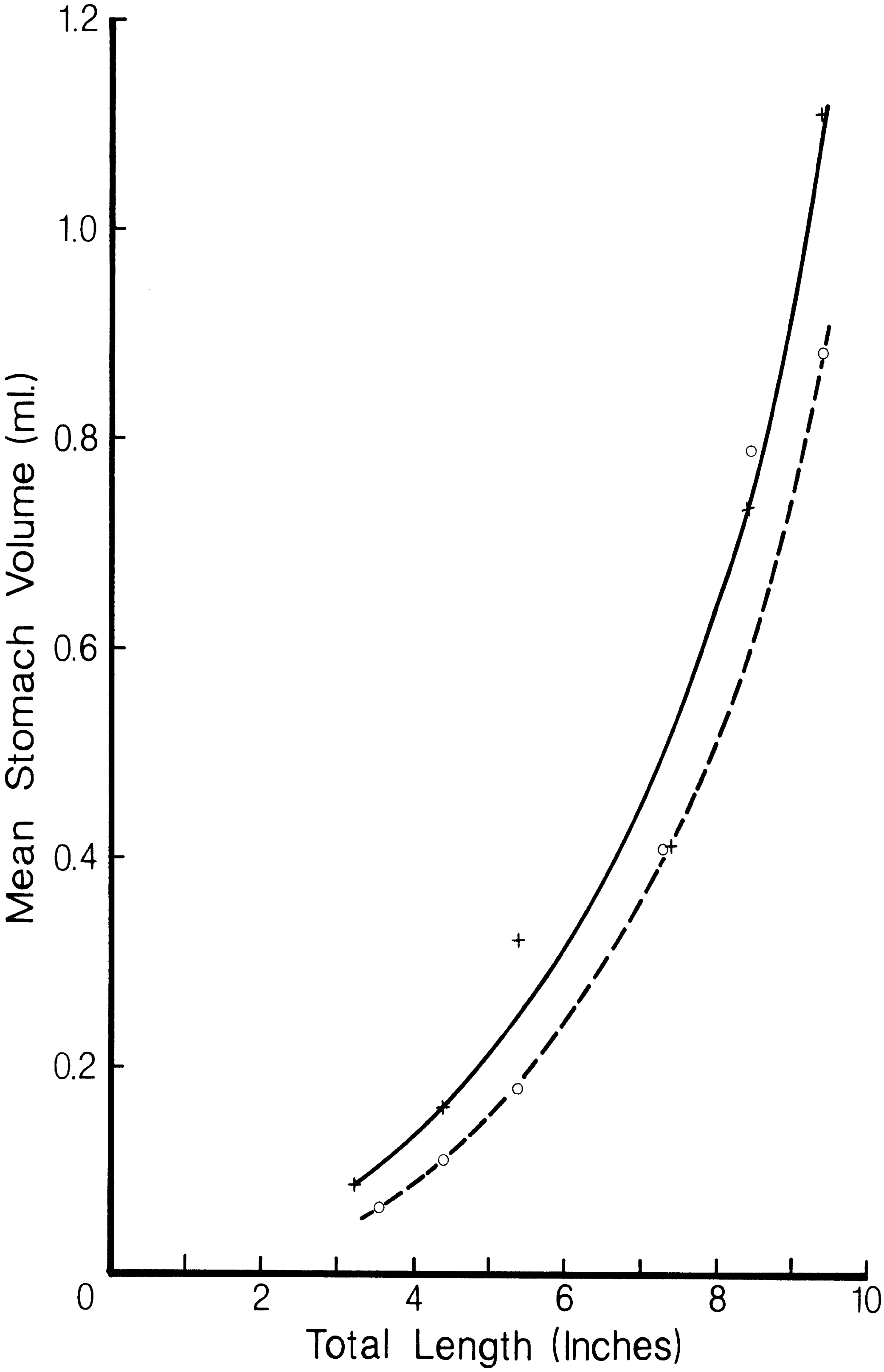


Figure 4.--Mean stomach volume versus total length for brown trout from the South Branch (solid line) and Main Stream (broken line), Au Sable River, May-September, 1976.

Comparison of these corrected stomach volumes showed that South Branch trout ate more than Main Stream trout. For small fish the comparison was 0.180 ml to 0.125 ml, which yielded a ratio of 1.44:1 for South Branch: Main Stream. The South Branch: Main Stream ratio for large fish was less striking--0.885 ml to 0.768 ml, or 1.15:1. However, the absolute difference between the volumes for the two rivers is greater for large fish (difference = 0.117 ml) than for small fish (difference = 0.055 ml).

Age Structure

The mean weight and length for fish in each age group as determined by scale readings are shown in Tables 6 and 7. Plotting the average total length against age yielded growth histories for South Branch and Main Stream trout (Figures 5 and 6). Knowledge concerning the periodicity of wild trout growth (Cooper 1953 and 1961) permitted the plotting of these curves by eye, thus depicting the most probable pattern of growth for trout in the two rivers. Also, smoothing of the curves was necessary because of the bias in the summer sampling scheme. Sampling was designed to obtain fish in certain length intervals; stratifying these fish by age introduced a bias to the fish at the lower and upper size boundaries. The data from fish sampled in the fall population work were not biased in this way, and were further strengthened by the large sample sizes. Therefore in drawing the smoothed curves, more emphasis was given to the fall data. These smoothed curves showed the inherent difference between the growth in length of South Branch and Main Stream trout. At first the difference was slight, but gradually became greater.

Table 6.--Monthly averages of length and weight for brown trout from the South Branch, Au Sable River, 1976.

Summer					Late fall (November)		
Age	Month	Number of fish	Mean total length (inches)	Mean weight (grams)	Age	Number of fish	Mean total length (inches)
0	May	...	...	...	0	115	4.1
	June	...	...	...	I	82	7.6
	July	19	3.1	5.1	II	29	10.9
	Aug.	24	3.6	7.8	III	47	13.2
	Sept.	23	3.9	11.2	IV	11	17.0
					V	1	26.0
	Mean	...	3.6	8.2			
I	May	21	5.0	21.4			
	June	27	5.4	26.6			
	July	17	6.6	49.6			
	Aug.	23	7.8	75.2			
	Sept.	23	7.9	81.5			
	Mean	...	6.5	50.6			
II	May	23	8.9	116.9			
	June	23	9.2	107.1			
	July	13	9.4	119.6			
	Aug.	2	8.6	91.4			
	Sept.	3	9.0	115.2			
	Mean	...	9.1	113.0			

Table 7.--Monthly averages of length and weight for brown trout from the Main Stream, Au Sable River, 1976.

Summer					Late fall (Sept.-Oct.)		
Age	Month	Number of fish	Mean total length (inches)	Mean weight (grams)	Age	Number of fish	Mean total length (inches)
0	May	...	...	...	0	79	3.5
	June	2	3.8	10.2	I	74	6.7
	July	10	3.1	5.0	II	63	9.5
	Aug.	16	3.7	8.7	III	46	11.5
	Sept.	21	3.9	10.4	IV	9	13.0
	Mean	...	3.7	8.7	V	1	16.3
I	May	25	4.9	19.5			
	June	24	5.3	26.0			
	July	21	5.6	30.3			
	Aug.	11	5.8	33.4			
	Sept.	10	6.7	51.8			
	Mean	...	5.5	28.9			
II	May	24	8.6	106.8			
	June	22	9.1	121.3			
	July	22	8.8	110.3			
	Aug.	20	8.5	98.5			
	Sept.	15	8.8	107.0			
	Mean	...	8.8	109.1			
III	May	1	9.6	165.1			
	June	2	9.4	133.5			
	July	2	9.6	144.0			
	Aug.	2	9.4	141.2			
	Sept.	4	9.5	121.4			
	Mean	...	9.5	135.3			

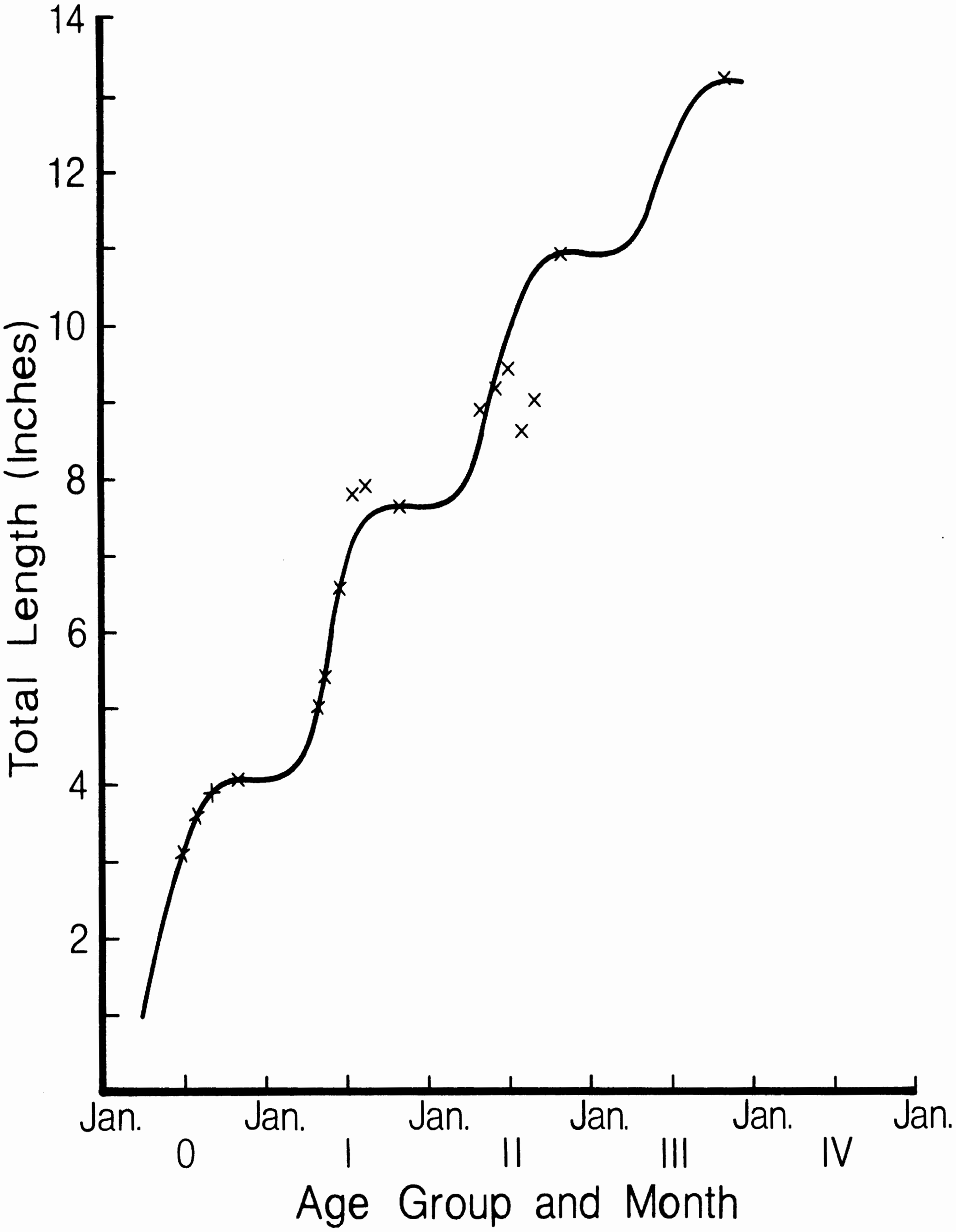


Figure 5.--Seasonal growth of brown trout from the South Branch Au Sable River, based on summer and fall sampling, 1976.

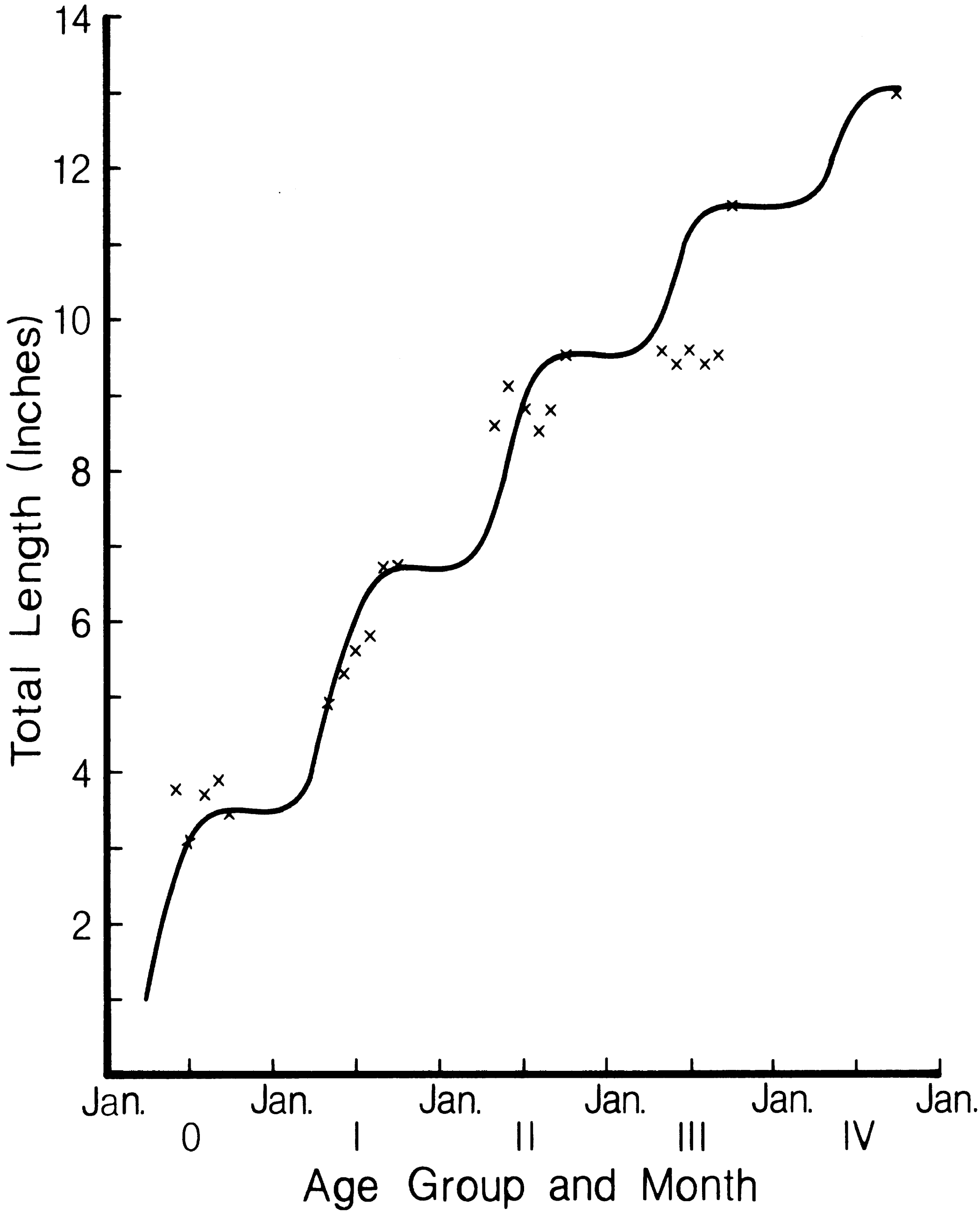


Figure 6.--Seasonal growth of brown trout from the Main Stream Au Sable River, based on summer and fall sampling, 1976.

STATISTICAL ANALYSIS

The two sources of brown trout observations--the summer sampling and fall population runs--provided information to statistically compare various aspects of diet and growth for the two rivers. Although most monthly summer samples consisted of 25 each of small (3.0-5.9 inches) and large (7.0-9.9 inches) trout from each river, the first South Branch sample had only 21 small fish. Therefore to make all sample sizes equal, a characteristic which simplified the application of some statistical techniques, the appropriate numbers of samples were randomly deleted from each category so that the total number of samples for the summer data was 21 samples × 2 sizes × 2 rivers × 5 months = 420 samples. Due to the different statistical treatment of the fall population samples, there was no need for equal sample sizes. Thus none of the 557 fall brown trout samples were eliminated.

Stomach Sample Analysis

A three-way analysis of variance was run for the mean stomach volume and for the mean volume of each of six major organisms in the diet. The three components of the test were river, month, and size; the number of replicates in each cell was 21. This design tested the hypothesis that the mean volume of food type was different for each of the components included in the study. The components tested were as follows: river, month, size, river × month, river × size, month × size, and river × month × size. For example, in the test of total volume, the hypothesis for the "river" main effect was as follows: the mean stomach volumes of South Branch and Main Stream fish were significantly different. For the river × size interaction, the hypothesis was that the difference in mean volume between South Branch fish and Main Stream fish was different for small fish than it was for large fish. All possible interactions were tested. As in the previous section, correction factors for comparing stomach volumes between the South Branch and Main Stream were derived from Figure 4. This correction was again arbitrarily applied to South Branch fish, and was calculated as follows:

$$\text{correction factor} = \frac{\text{mean stomach volume at length equal to Main Stream mean length}}{\text{mean stomach volume at observed mean length}}$$

This equation yielded the following factors for small and large trout:

$$\text{c.f. (for small fish)} = \frac{0.18}{0.17} = 1.06$$

$$\text{c.f. (for large fish)} = \frac{0.88}{0.69} = 1.28$$

In order to make the analysis of variance tests meaningful, the correction factors were applied to the stomach volumes prior to running the tests. This consisted simply of multiplying the South Branch small fish stomach volumes by 1.06 and the South Branch large fish volumes by 1.28.

The results of all seven of the analysis of variance tests appear in Table 8. Total volume, the most important test, showed a significant difference between months and between sizes, but not between rivers as I had anticipated. Therefore, the difference in total stomach volume between the South Branch and Main Stream as calculated in the previous section could have been due to the variability between samples. The significant size interaction simply reflected the greater capacity of large fish's stomachs. The test of Trichoptera yielded results similar to the total volume test. The amount of Diptera eaten was significantly higher in the South Branch, probably because of the abundance of Rhagionidae larvae. Like the tests of total volume and Trichoptera, the test of Mollusca showed significant differences between months and between sizes. However, the seasonality was reversed from the trend of the first two tests; instead of higher volumes in the early season, more mollusks were eaten in the late season. This probably indicated that as the caddis and other preferred foods became scarce, more food of lower preference, i.e., mollusks, were eaten. As expected, the test for volume of fish eaten showed that large brown trout ate more fish than did small trout. Also as expected, Main Stream fish ate significantly more isopods and amphipods than did the South Branch fish. Monthly means showed that more were eaten early in the season.

An overview of Table 8 shows that major differences occur between months and between the two size categories. For the most part, significant differences were not found between the South Branch and Main Stream with respect to total volume or types of food eaten.

Table 8.--Results of the analysis of variance of stomach volume data for brown trout from the South Branch and Main Stream, Au Sable River, May to September, 1976 (degrees of freedom are in parentheses).

Test	Component						
	River (1,400)	Month (4,400)	Size (1,400)	River × Month (4,400)	River × Size (4,400)	Month × Size (4,400)	River × Month × Size (4,400)
Total volume		***	***				
Trichoptera volume		***	***				
Ephemeroptera volume							*
Diptera volume	***						
Mollusca volume		*	***			**	
Fish volume			***				
Isopoda and Amphipoda volume	***	**		***		*	*

* Significant at the 0.05 level.

** Significant at the 0.01 level.

*** Significant at the 0.005 level.

The analysis of variance described above tested the hypothesis that there was a difference between the South Branch and Main Stream for stomach volume on the basis of one mean value computed from the entire size range of trout. Because this test lumped the fish from each river into one category, I employed an alternate test to determine any difference between mean stomach volumes between the two rivers. This method, the analysis of covariance, determines significant differences between two regression lines on the basis of slope and adjusted means (Steel and Torrie 1960). The regression lines which I used were log-log relationships derived from Figure 4. By testing the regression line for the South Branch against that of the Main Stream, I attempted to establish a difference between the respective volumes of food eaten for all inch groups of trout (between 3.0 and 9.9 inches).

For South Branch brown trout, the regression equation was as follows:

$$\log_e \text{(stomach volume)} = -6.6439 + 2.7714 \log_e \text{(length)}.$$

The coefficient of determination (r^2) was 0.374. For Main Stream brown trout, the equation was as follows:

$$\log_e \text{(stomach volume)} = -8.1559 + 3.3678 \log_e \text{(length)},$$

$$r^2 = 0.348.$$

Table 9 shows the covariance test of these regressions. The test for equality of slopes was accepted at the 0.05 level of significance, while the test for equal adjusted means was rejected. This indicated that the

Table 9.--Covariance test of the regressions of $\log_e$ stomach volume on $\log_e$ total length for brown trout from the South Branch and Main Stream, Au Sable River.

Source	Degrees of freedom	Sum of squares	Mean square	F	P
Total	419	1533.40			
Overall regression	1	530.07			
Equal regressions	2	24.91	12.45	5.3	0.05
Equal slopes	1	5.15	5.15	2.2	0.05
Equal adjusted means	1	19.76	19.76	8.4	0.05
Error	416	978.45	2.35		

South Branch fish ate significantly more food than did the Main Stream fish of the same sizes. The three assumptions for the analysis of covariance are as follows:

(1) the X's are fixed and measured without error,

(2) the regression of Y on X after removal of block and treatment differences is linear and independent of treatments and blocks, and

(3) the residuals are normally and independently distributed with zero mean and a common variance. The assumption of normality is not necessary for estimating components of the variance of Y, but does affect the validity of the F-test (Steel and Torrie 1960). In this case, the residuals were not quite normally distributed. This stemmed from transforming stomach volumes to logarithms--fish with empty stomachs were arbitrarily assigned a volume of 0.001 ml, so the logarithms for "empty" stomachs were quite low compared to those with measurable quantities. As a result, residuals for "empty" stomachs were clustered on the lower tail of the distribution, causing the mode of the residuals to be somewhat greater than zero (about 0.5 log units). I thought that this could have been responsible for the low coefficient of determination for both regressions ($r^2 = 0.374$ and 0.348). Therefore, I ran regressions of the same data excluding fish with empty stomachs. The resulting r^2 values were not much better, leading me to believe that the inherently high variability between stomach samples accounted for the low r^2 values. Since trout from both rivers showed similar variablity, I felt that the results of this covariance test were valid.

Length-weight Relationship

In the past few years, controversy arose concerning the condition of brown trout in the "quality water" of the Main Stream. Fishermen reported that trout caught in this area were "skinnier" than normal. White et al. (1975) compared the growth and condition factor of brown trout in the "quality water" with those in adjacent sections of the Main Stream. They documented the abnormally thin condition of the trout in and below the special regulation water, noting that the condition factor decreased from age I to age IV, whereas the condition of fish upstream increased for older trout. Because this aspect of the trout's biology was relevant to my investigation, I compared the length-weight relationship of South Branch and Main Stream trout sampled during the summer. I employed the analysis of covariance technique similar to Cooper's (1961) treatment, except that I used semi-log rather than log-log regressions. The regression equation for the South Branch took the form $\log_e (\text{weight}) = 0.31018 + 0.5064\ (\text{length})$, and for the Main Stream, $\log_e (\text{weight}) = 0.52666 + 0.4744\ (\text{length})$. The coefficients of determination were 0.978 and 0.977, respectively. The analysis of covariance for these regressions appears in Table 10. The hypothesis of equal slopes was rejected at the 0.05 level of significance, which precluded the need for the test of adjusted means. This showed the inherent difference between the condition of South Branch and Main Stream fish. Although Main Stream trout were heavier for their length in the lower sizes, South Branch trout were heavier for their length in the upper size ranges. The intersection of the two regression lines

Table 10.--Covariance test of the regressions of $\log_e$ weight on length for brown trout from the South Branch and Main Stream, Au Sable River.

Source	Degrees of freedom	Sum of squares	Mean square	F	P
Total	419	507.36			
Overall regression	1	495.44			
Equal regressions	2	0.53	0.27	9.7	0.05
Equal slopes	1	0.52	0.52	19.1	0.05
Error	416	11.39	0.03		

occurred around 6.0 inches of length. Because of the high coefficients of determination, I applied the regression lines to fish longer than 9.9 inches (the limit of my data). This extrapolation showed the increased difference between points on the two regression lines in the range of legal-sized fish (over 12 inches). This evidence supports the findings of White et al. (1975) for fish over 6.0 inches.

Seasonal Growth

An apparent difference in growth between South Branch and Main Stream trout is shown in Figures 5 and 6. These curves were drawn on the basis of both summer and fall samples of trout. Because of the limitations of the summer data as discussed above, the statistical treatment of growth data was confined to the fall samples. The analysis of covariance was used to test the hypothesis that South Branch and Main Stream trout had equal total lengths at the end of successive growing seasons for all lengths of fish sampled (2.0-26.0 inches), or in other words, that South Branch and Main Stream fish grew at the same rate. The regression equations used for this test were log-log transformations of the fall data from Figures 5 and 6. The regression equation for the South Branch was $\log_e (\text{length}) = 1.3966 + 0.8716 \log_e (\text{age} + 1)$; the equation for the Main Stream was $\log_e (\text{length}) = 1.2592 + 0.8863 \log_e (\text{age} + 1)$. The r^2 values were 0.896 and 0.837, respectively. The results of the covariance test of these regressions appear in Table 11. The test for equality of slopes was accepted at the 0.05 level of

Table 11.--Covariance test of the regressions of $\log_e$ length on $\log_e$ growing season for brown trout from the South Branch and Main Stream, Au Sable River.

Source	Degrees of freedom	Sum of squares	Mean square	F	P
Total	556	150.71			
Overall regression	1	128.41			
Equal regressions	2	2.24	1.12	30.9	0.05
Equal slopes	1	0.01	0.01	0.2	0.05
Equal adjusted means	1	2.23	2.23	61.6	0.05
Error	553	20.07	0.04		

significance; the test for equality of adjusted means was rejected. This indicates that South Branch trout were significantly longer at the end of successive growing seasons than were Main Stream trout.

TROUT POPULATION SIZE AND FOOD PRODUCTIVITY

The preceding treatment has compared the diet, condition, and growth of individual trout sampled from the South Branch and Main Stream. All of these factors reflect the availability of food in the streams, since condition and growth arise from diet. However, this investigation to be complete needs to consider also the effects of population size on the individual trout's diet.

The results of fall population estimates by inch group for the South Branch and Main Stream for 1976 are given in Table 12. It was readily apparent that the Main Stream had a much higher population than the South Branch, especially for brown trout. However, I previously showed that individual South Branch trout ate more than did Main Stream trout of the same size. Therefore to understand the relationship between population size and the amount of food per fish, I compared the total amount of food consumed by the trout in each river in the following way:

$$\text{volume of food eaten per acre for the growing season} = \frac{\text{number of fish}}{\text{acre}} \times \frac{\text{average volume consumed per fish}}{\text{day}} \times \text{number of days in growing season} \qquad \text{(Equation 1)}$$

Table 12.--Number of fish per acre for the South Branch and Main Stream Au Sable River, September 27-November 9, 1976.

Inch group	Brown trout		Brook trout		Rainbow trout		Total	
	South Branch	Main Stream	South Branch	Main Stream	South Branch	Main Stream	South Branch	Main Stream
2	9.6	48.8	7.2	79.7	...	47.5	16.8	176.0
3	76.0	139.4	95.7	120.7	...	44.4	171.7	304.5
4	97.8	101.0	77.8	12.0	...	2.2	175.6	115.2
5	17.5	33.5	13.9	12.2	...	1.2	31.4	46.9
6	6.0	78.6	8.8	15.8	...	7.8	14.8	102.2
7	19.8	85.0	11.0	12.1	...	7.0	30.8	104.1
8	12.8	59.9	4.0	3.4	...	1.7	16.8	65.0
9	7.1	56.2	0.2	1.2	...	2.8	7.3	60.2
10	5.8	60.6			...	1.7	5.8	62.3
11	7.4	28.4			...	0.3	7.4	28.7
12	7.0	17.4			...	1.4	7.0	18.8
13	4.9	3.4			...	0.3	4.9	3.7
14	8.6	1.2					8.6	1.2
15	2.9	2.3					2.9	2.3
16+	4.8	0.6					4.8	0.6
Total	288.0	716.3	218.6	257.1	0.0	118.3	506.6	1091.7

The present study yielded values for the number of fish per acre and for the instantaneous stomach volume. To convert the latter into volume consumed per day (daily ration), I used the method described by Alexander and Gowing (1976). They analyzed stomach and scale samples of brook, brown, and rainbow trout from many lakes and streams in northern lower Michigan. They estimated that the growing season lasted 180 days. To determine the average volume consumed per fish per day or daily ration they used the following equation:

$$\text{daily ration} = \left(\begin{array}{c}\text{annual}\\ \text{weight}\\ \text{gain}\end{array} \times \begin{array}{c}\text{food}\\ \text{conversion}\\ \text{ratio}\end{array}\right) \div 180 \text{ days} \qquad \text{(Equation 2)}$$

They cited findings by Ball (1948), who determined that for stomach contents, 1 ml was equivalent to 1 g wet weight. The food conversion ratio which they used was 5.0. The data which I used to compute daily ration are shown in Table 13. The "mean weight" values in Table 13 were derived by using the length-weight relationship of fish sampled in summer and the mean length of fish sampled in late fall. I assumed that the average weight did not change between late fall and early spring. The "mean summer stomach volume" values represented the volumes which were present in the upcoming growing season. For example, the stomach volume for fish which were age I* in early spring (age I in the coming summer) was 0.430 for South Branch fish. Most of the ratios of daily ration to stomach volume fell between 3.05 and 4.37. I obtained much higher values for the higher-aged fish, but I disregarded

Table 13.--Annual weight gain (g), mean stomach volume (ml), estimated daily ration (ml) and ratio of daily ration to stomach volume for brown trout from the South Branch and Main Stream, Au Sable River.

Age in early spring	Mean weight	Annual weight gain	Estimated daily ration	Mean summer stomach volume	Ratio of daily ration to stomach volume
			SOUTH BRANCH		
Newly-hatched	0	10.9	0.339	0.101	3.36
I*	10.9	53.1	1.475	0.430	3.43
II*	64.0	276.3	7.675	0.839	9.15
III*	340.3	...	...	...	...
			MAIN STREAM		
Newly-hatched	0	8.9	0.247	0.081	3.05
I*	8.9	31.8	0.883	0.202	4.37
II*	40.7	112.8	3.133	0.813	3.85
III*	153.5	242.8	6.744	0.631	10.69

them on the basis of the biased summer sampling as explained earlier. Therefore I averaged the daily ration: stomach volume values for South Branch fish of the first two ages and for Main Stream fish of the first three ages, and obtained values of 3.40 and 3.76, respectively. The same calculations for the data of Alexander and Gowing (1976) yielded values of 2.17 (for trout in streams) and 2.50 (for trout in lakes).

On the basis of the entire population of trout broken down by inch group, equation 1 was computed for each river (Table 14). A major assumption made was that brook and rainbow trout ate similar amounts as brown trout of the same size. The instantaneous stomach volume values for the 3- to 5- and 7- to 9-inch classes were taken from the observed data of Figure 4. Values for all other inch classes were taken from extrapolations of the curves in Figure 4. The Main Stream trout population consumed 260,580.6 ml of food, almost twice as much as the South Branch population, which consumed only 133,871.4 ml.

The different levels of food consumption by trout populations of the two rivers prompted questions about the effects of grazing on the benthos, about which very little research has been done. In Coopes (1974), Quigley sampled the benthos at some of the same sites on the South Branch and Main Stream used in my study. The mean number of organisms per square foot was 412 for two stations on the South Branch and 144 for three stations on the Main Stream. Because the composition of organisms from the two rivers was very similar, I assumed that the weight of organisms per square foot was greater for the South Branch than for the Main Stream, and corresponded to the 412:144 ratio for

Table 14.--Estimated volume of food eaten (ml) per acre during the 1976 growing season (May-October) for the South Branch and Main Stream, Au Sable River.

Inch group	South Branch			Main Stream		
	Mean stomach volume	Volume per acre per day	Volume per acre per growing season	Mean stomach volume	Volume per acre per day	Volume per acre per growing season
2	0.02	1.14	205.2	0.02	13.24	2,383.2
3	0.08	46.70	8,406.0	0.06	68.70	12,366.0
4	0.16	95.53	17,195.4	0.11	47.65	8,577.0
5	0.32	34.16	6,148.8	0.18	31.74	5,713.2
6	0.37	18.62	3,351.6	0.30	115.28	20,750.4
7	0.41	42.94	7,729.2	0.41	160.48	28,886.4
8	0.73	116.16	20,908.8	0.79	193.08	34,754.4
9	1.11	27.55	4,959.0	0.88	199.19	35,854.2
10	1.38	27.21	4,897.8	1.15	269.39	48,490.2
11	1.73	43.53	7,835.4	1.44	155.39	27,970.2
12	2.08	49.50	8,910.0	1.72	121.58	21,884.4
13	2.50	41.65	7,497.0	2.04	28.38	5,108.4
14	2.98	87.14	15,685.2	2.42	10.92	1,965.6
15	3.62	35.69	6,424.2	2.82	24.39	4,390.2
16+	4.67	76.21	13,717.8	3.66	8.26	1,486.8
Total		743.73	133,871.4		1,447.67	260,580.6

the number of individuals. This meant that the standing crop of benthos from the South Branch was almost three times that of the Main Stream, which probably reflected the intense grazing on the benthos by the Main Stream trout population. This may continually depress the benthic community in this part of the Main Stream. The overall effect of this situation, in comparison to the South Branch, is a lower standing crop of invertebrates at any given time with perhaps a higher yearly productivity and turnover rate.

In a study of brown trout from the Horokiwi, Allen (1951) found a negative relation between the standing crop of benthos and the amount consumed yearly by the trout population. He concluded that the bottom fauna played an important role in regulating the population of trout by a self-regulating mechanism which tended to maintain the weight of the stock at a constant level by increasing or decreasing the trout's growth rate. Trout in the Main Stream and South Branch also demonstrated the same density-dependent process. Apparently, trout in the Main Stream consumed nearly twice the amount of food per acre than did South Branch trout, and as a result the standing crop of benthos in the Main Stream was lower than in the South Branch. Furthermore, the growth of individual trout in the Main Stream was slower to compensate for the lower standing crop of benthos.

The slower growth of Main Stream trout may not have been caused solely by competition for food. Brown (1945) found that in overcrowded brown trout populations, growth was retarded by mutual mechanical disturbance in addition to competition for food. Apparently the high level of disturbance caused an increase in activity and resulted in higher food requirements. Within every group of fish, she found a social hierarchy based on size. Removal of the larger, faster-growing fish allowed the growth rates of remaining fish to increase. This effect was attributed solely to behavioral factors and not to competition for food.

DISCUSSION

Population size was the outstanding difference between the South Branch and Main Stream trout, and consequently led to inequalities in diet, condition, and growth. These factors and several others were treated separately in this study. Tying them all together presents a useful picture of the two trout populations.

The South Branch population, about half the density of the Main Stream population, consisted of more brown than brook trout. The Main Stream had quite a few more brown than brook trout, plus a significant number of rainbow trout. The South Branch brown trout were in better condition than Main Stream browns, and grew faster. These differences arose from the diet of individual fish--over all lengths of trout sampled (3.0-9.9 inches), South Branch trout ate more than Main Stream trout of the same size. Although they ate different total amounts, the types of food eaten were very similar, with Trichoptera and Ephemeroptera heading the list. Very few adult insects were found in the stomach samples. The difference in types of food eaten was that South Branch trout ate more Diptera and Main Stream trout ate more Isopoda and Amphipoda.

The Main Stream trout populations are denser than those of the South Branch because of better spawning success. Both rivers have abundant substrate suitable for spawning, however the amount of groundwater percolation is much less on the South Branch (Alexander, personal communication). Because percolation is very important to egg development, many more eggs spawned in the Main Stream survive to the hatching of fry than survive in the South Branch. Less groundwater in the South Branch probably allows temperatures in winter to fall below optimum. This causes high egg mortalities and results in a low density of trout fry.

Benefitting from the sparse populations which result, individual South Branch trout find plenty of suitable food and grow quickly. On the other hand, early survival in the Main Stream is high, which allows for dense trout populations, thus causing slower growth from competition for the limited food supply. South Branch trout overtake Main Stream trout in condition at a length of about 6 inches. From this point on, Main Stream fish undergo intense competition for food. This situation is aggravated by the special regulations which protect 10- to 12-inch fish from anglers. As a result, the Main Stream nowhas a large population of smaller, thinner fish because of the longer time necessary for trout to attain legal size in comparison to trout of the South Branch. Although this section of the Main Stream was put under special regulations for the purposes of reducing exploitation and producing trophy-size fish, apparently overcrowding prevents many fish from reaching legal size. Harvesting brown trout of 10 to 12 inches or smaller might result in a population of faster-growing, plumper fish.

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Report approved by W. C. Latta

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