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Consumption of Small Trout by Large Predatory Brown Trout in the North Branch of the Au Sable River, Michigan

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CONSUMPTION OF SMALL TROUT BY LARGE PREDATORY BROWN TROUT IN THE NORTH BRANCH OF THE AU SABLE RIVER, MICHIGAN[1]

By Gaylord R. Alexander

Abstract

Stomachs of large wild brown trout collected from the North Branch of the Au Sable were analyzed for foods eaten. High proportions of fish, particularly brook trout were found. Working from the partially digested remains of the prey trout, the daily ration of predator brown trout was determined. Also estimates of the total daily ration and the proportion of coarse fish in the ration were made.

Using the estimated daily rations of prey trout along with knowledge of the magnitude of the predator trout stocks, the number of prey trout by age class consumed per mile of river was calculated. The predator brown trout kill of small trout was 7,626 fish per mile of river in the normal angling regulation water (7.0-inch minimum size, any lure, 10 trout creel limit) and 3,579 fish per mile in the special angling regulation water (9.0-inch minimum size, flies-only, 5 trout creel limit). Kills of small brown trout were relatively low in both the normal and special regulation waters and amounted to only 217 and 218 fish per mile for the respective waters.

Brown trout are the most significant natural predator yet identified on the Au Sable in terms of total trout killed. However, because the brown trout eat only small trout they are not in direct competition with anglers, as are the American Merganser, Great Blue Heron, mink, and otter which kill more large trout.

Brown trout predation is probably detrimental to brook trout populations where brook trout fisheries are the primary management objective. However, brown trout predation is probably beneficial in controlling slow growth in high population densities of small trout. Further, if older brown trout lacked smaller trout as prey they would grow slower and fewer large "trophy" size fish would be produced. Also, the predation of the brown trout on coarse fish populations is beneficial to all trout.

Many of the trout spared from the anglers' hooking mortality and not caught due to special regulations, are subsequently eaten by natural predators. However, in the normal regulation waters the kill of trout by natural predators is also high.

[1] Contribution from Dingell-Johnson Project F-35-R, Michigan.

Introduction

The implementation of "special," more restrictive, angling regulations gained momentum in Michigan and elsewhere in the United States following hooking mortality studies on trout by Shetter and Allison (1955, 1958). These studies revealed mortality rates as high as 40% for natural bait-caught sublegal fish that were returned to the water. By comparison, mortality of only 2% was found for artificial flies and 5% for hardware lures. In the 1950's and 1960's a number of streams in Michigan and Wisconsin were placed under a variety of special fishing regulations, i.e., higher minimum size limits and lure restrictions. The intent was to reduce trout mortality rates by reducing the kill of sublegal trout by hooking, and encourage survival of larger trout by raising the size limit. Fisheries managers hypothesized that these regulations would result in larger trout populations and angler catches of legal-size fish.

Studies to evaluate the alleged benefits of these special regulations were carried out on a number of streams in Michigan (Shetter and Alexander 1962, 1966; Latta 1973; and Alexander and Ryckman 1976). Hunt (1970) reported upon a similar study in Wisconsin. In general, these studies found that trout survival was increased slightly during the summer fishing season. This resulted in somewhat higher fall trout populations, but gains were erased during the winter between trout angling seasons. The anticipated greater trout catches and populations did not materialize.

It has been known for years, by both biologist and angler that large brown trout prey heavily on fish in general and on small trout in many waters. To my knowledge, however, no one has attempted to quantify the kill of small trout or other prey fish by the brown trout. Thus my predator investigations were initiated in Michigan in the early sixties to determine the relationship of large brown trout as well as other predators to trout losses. It was my intent to identify and quantify losses of trout to predators and thereby possibly provide an explanation for the failure of special regulations to produce anticipated benefits.

Predator studies were focused on the North Branch of the Au Sable River because extensive trout population data were available. A study documenting significant losses of trout in this river, to American Mergansers, Great Blue Herons, and Belted Kingfishers has been reported by Alexander (1974).

The objective of this study is to document the proportion of the total mortality of small brook and brown trout attributable to large predatory brown trout.

Methods

The study sections of the North Branch of the Au Sable consisted of 12.9 miles of stream (average width 111.2 feet) fished under special regulations, and 6.9 miles (average width 106.0 feet) fished under normal (statewide) regulations. Special regulations were: artificial flies only, 9.0-inch minimum size, and 5 trout creel limit. Normal angling regulations were: any lure, 7.0-inch minimum size limit, and 10 trout creel limit.

From 1961 to 1967, semi-annual estimates of the trout population were made by electrofishing, one in the spring prior to the angling season and one in the fall after the season closed, in nine sub-sections of river. These sub-sections ranged from 913 to 1,300 feet long. Estimates were calculated by the Peterson mark-and-recapture method as described by Shetter (1957). Average estimates from these sub-sections were then transformed into numbers per mile of river for the two regulation waters. The size of the population was derived by summing estimates of trout in each inch class. Age groups within each inch class were then determined by age assessment of scales from representative samples of trout.

The predator population of brown trout was considered to be that portion of the total brown trout population, 12.0 inches long or longer. Brown trout smaller than 12.0 inches rarely prey on small trout in the North Branch of the Au Sable.

Samples of predatory size brown trout for stomach analysis were collected over a period of 10 years (1962-1971) from some 27 different stream areas. The sampling procedure was to collect the first 10 fish

12.0 inches or longer in each sampling area. Fish were accumulated over the years until I had at least 15 trout for each month of the year from each of the normal and special regulation areas. A total of 676 predator-size brown trout were eventually accumulated for analysis.

To be able to estimate the numbers of small trout eaten from predator brown trout stomachs collected in the field, I needed to know the gastric digestion rates of various sizes of prey trout eaten at different water temperatures. This information was obtained from extensive controlled laboratory feedings of known-size prey trout to large brown predator fish held at various water temperatures. Digestion rates for both force feeding and voluntary feeding were gathered. With this information, tables were constructed giving the percentage of digestion after 24, 48, and 72 hours of various size prey, at various water temperatures, and when eaten by various predator-size brown trout. To account for seasonal differences in weight of like-size prey trout (coefficient of condition), a summer and winter length-weight relationship was recognized.

The approach used to determine the daily meal of wild predatory brown trout was to examine the stomach contents. The remains of a prey trout found in the stomach was measured and assigned to a length class and the undigested portion was weighed. Knowing the average weight of trout of various lengths (length-weight relationship) and the residual weight of the partially digested prey, I could determine whether the prey was eaten within the last 24-, 48-, or 72-hour period. Only trout ingested within the last 24 hours, however, were used to estimate the daily ration and size frequency of prey trout eaten.

An estimate of the average daily ration was calculated for each month. The average daily ration for the periods November-April and May-October was calculated and multiplied by the number of days in the period, times the number of predator-size brown trout per mile of river to arrive at the total weight of prey-size trout consumed during the period. This total weight consumed was then divided into the proportions of brook and brown trout. Observed size-frequency data of prey trout in stomachs were then used to transform weight of prey into numbers of prey eaten. Finally, trout-scale reading information was used to apportion trout numbers into appropriate age categories.

Results

The empirical and real diet composition of large brown trout in waters of the North Branch of the Au Sable River are given in Tables 1, 2, 3, and 4. These tables also show the adjustments made to the empirical diets for relative gastric evacuation rates due to differences in seasonal water temperatures and taxa of food eaten to derive the estimated real diet, following procedures of Alexander and Gowing (1976).

The real diet of large brown trout, in the normal regulation water, for the summer period, was composed of 75% fish. Small brook trout made up 30% of the diet; no brown trout were found (Table 1). The winter diet consisted of 80% fish. Small brook trout comprised 37% and small brown trout 2% of the diet (Table 2).

By comparison, large brown trout in the special regulation water ate 82% fish during the summer. Some 61% of the diet was small brook trout, but again no brown trout were found in the summer diet. The winter diet of large brown trout in the special regulation water was composed of 77% fish. Brook trout made up 42% and brown trout 5% of the diet.

Winter diet composition was very similar in the normal and special regulation waters. Summer diet was also similar, except that the fish fraction was composed of more trout and less coarse fish in the special regulation waters. Mean volume of food per trout stomach, adjusted for water temperature and taxa, were very similar for the normal and special waters. Summer volumes were 2.22 g in normal compared to 2.04 g in special waters and winter volumes were 1.28 g versus 1.54 g, respectively. Note that the empirical volumes of food per stomach were larger in winter than summer. This is a distortion of the real diet and daily ration because of slower digestion rates due to low water temperature.

It is obvious that large brown trout are very predacious on fish in general, and small trout in particular, in the North Branch of the Au Sable. However, diet composition by itself does not tell the story quantitatively of the impact of large brown trout on the small trout population. To calculate the quantities of trout eaten by the brown trout predators, I reconstructed their consumption of small trout from analyses of stomach contents of the randomly collected wild fish. The needed knowledge on gastric evacuation rates for large brown trout that had eaten small trout of various sizes at various water temperatures was accumulated by experimental feeding studies at the Hunt Creek Fisheries Research Station.

My feeding studies showed that water temperature played a very important role in rate of gastric evacuation. These data showed average gastric digestion was greatest around 57 F (Fig. 1). For example, gastric evacuation is only 65% as fast at 40 F and only 88% as fast at 65 F as compared to 57 F. It is interesting to note that the fastest gastric evacuation occurred near the temperature preferendum of brown trout and for that matter salmonids in general (Ferguson 1958). Most early feeding tests were obtained by force feeding the large brown trout. Later, voluntary test feeding was conducted which revealed that gastric digestion averaged 38% faster than when fish were force fed. Thus, the force feeding data were adjusted upwards. Nearly 1,400 feedings were conducted in these laboratory tests.

The gastric rate of evacuation of small trout (2-7 inches) from the stomachs of various size predator brown trout held at various water temperatures and time intervals is given in Table 5. Findings in general were: (1) the larger the meal the greater the amount of flesh digested, (2) digestion rate increased with rising water temperature up to about 57 F and then dropped off, (3) the more flesh, of course, that is digested the greater the time interval, and (4) the larger the predatory fish the more flesh digested per unit of time.

Using the data in Table 5 and knowledge of the length-weight relationships of brook and brown trout prey, for both summer and winter (coefficients of condition), I constructed tables giving the percentage of digestion of prey after 24-, 48-, and 72-hour intervals. In turn, these tables were used to determine the time of ingestion of each trout found in the stomachs of field-collected brown trout. To determine the daily ration of small trout, I used the 24-hour time interval as the cut off point. This had to be done to obtain the correct size-frequency distribution of trout eaten. If a longer time interval had been used some of the smaller prey (2- and 3-inch trout) would be digested beyond the point of detection. Consequently the size-frequency information would be biased toward large prey.

In estimating the daily ration of prey trout, I assumed that the digestion rate of wild river fish was the same as wild laboratory fish that had been allowed to feed voluntarily. There are two possible biases, however, that I have not corrected for: (1) digestion of laboratory trout even when feeding voluntarily may be slowed somewhat and (2) when wild river fish had invertebrate food in their stomachs along with trout flesh this undoubtedly slowed digestion. However, in most instances, when small trout were found in the stomach of predator brown trout it was the only food present making the gastric evacuation rates applicable. Further the diet composition of North Branch Au Sable trout is 70 to 80% fish, thus this latter source of bias is probably minimal.

Estimates of the average daily ration of prey trout are given in Table 6. The average monthly daily rations were combined to obtain the average daily ration of predatory trout for the summer and winter seasons, and for the normal and special regulation waters. These semi-annual mean daily rations of prey trout were then multiplied by the number of days in the semi-annual period and then times the average number of predator brown trout per mile of river (Table 7).

Predator brown trout in the normal regulation water during the period May-October, ate an estimated 54,118 g of trout per mile of river. For the November-April period, their consumption was 24,750 g. The predator brown trout population in the special regulation water from May to October ate 22,934 g per mile of river. During the November-April period consumption was 26,122 g per mile of river.

These quantities of trout prey were then partitioned into proportion of brook and brown trout. The weight of each species was then apportioned into numbers by size class and then into numbers by age class following the procedure outlined by Alexander (1974).

The numerical kill of small brook trout by predatory brown trout in the normal regulation water totaled 7,626 fish per mile of river (Table 8). The kill of small brown trout amounted to only 217 fish per mile (Table 9).

In the special regulation water the large brown trout consumed 3,579 small brook trout and only 218 small brown trout per mile of river (Tables 10 and 11).

Obviously considerable quantities of small trout, particularly brook trout, are eaten by large brown trout. Also shown in Tables 8, 9, 10, and 11 are the trout populations per mile of river by age class. Total trout mortalities for various age-class intervals are also given in these tables.

Total losses of brook trout to predatory brown trout amounted to 6.6% of the total annual mortality of the brook trout population, in the normal regulation water, and 2.8% in the special regulation water. Annual losses of small brown trout to predator brown trout amounted to only 0.2% in the normal and 0.3% in the special water. Even though the overall effect of brown trout predation might appear to be small, judging from the above discussion, the impact on first and second growing season brook trout is considerable in both the normal and special waters (Tables 8 and 10). In the normal water from 4 to 84% of the semi-annual mortalities of these age categories is due to brown trout predation. Similarly, from 1 to 53% of the brook trout losses in the special waters is attributable to brown trout predation. Compared to losses identified with avian and mammalian predators cited by Alexander (1974, 1976), the brown trout is the most significant predator on small brook and brown trout in the North Branch of the Au Sable River (Tables 8, 9, 10, and 11).

The estimated daily total ration (all food types) of predator brown trout during the summer period, in the normal water, was 3.77 g per day in comparison with 2.50 g per day in the special water. Fish in the normal water had higher total rations in the summer because of the greater intake of coarse fish and invertebrates. Daily total ration of the predator brown trout in the winter period for the normal water was 1.38 g per day compared to a much larger ration of 3.75 g per day in the special waters. These greater rations in the special water in the winter are due to the greater consumption of small trout, coarse fish, and invertebrates, than in the normal waters. The average annual daily total ration, per individual predator brown trout, for the normal water was 2.58 g per day and 3.12 g per day for the special water. Thus each large trout fares somewhat better in the special water probably because of the lower population densities of large fish.

The consumption of coarse fish by predator brown trout was substantial. Many muddlers, blacknose dace, creek chubs, shiners, darters, and some suckers and lamprey were eaten. The average size of coarse fish was 2.45 inches long and 2.5 g in weight. I calculated the daily ration of coarse fish as a direct proportion of the percent of trout in the real diet to the percent of coarse fish in the real diet, to the daily ration of trout to the daily ration of coarse fish. The total weight of coarse fish eaten was then calculated by the same procedure used for trout.

In the normal regulation waters about 80,702 g (32,288 fish) of coarse fish were eaten in the summer period and 26,618 g (10,647 fish) during the winter period. For the special waters predator brown trout consumed 7,846 g (3,138 fish) in the summer period and 16,920 g (6,768 fish) during the winter period.

Discussion

Large brown trout consume considerable numbers of small trout and are a significant source of mortality, particularly on the brook trout. If the management goal in a stream is to maximize the brook trout population, then the presence of large brown trout may not permit this. This would be particularly so where high exploitation of the older and larger brook trout by anglers occurs, due to low size limits. Predator brown trout may be one of the most important factors bringing about reduced brook trout populations, where brown trout have been introduced. However reduction of large brown trout (about 60%) and some American Merganser control on a portion of the North Branch of the Au Sable resulted in more large brook trout, but no change in small trout numbers (Shetter and Alexander 1970). Possibly the numbers of small trout did not increase because the predator brown trout left in the river ate higher daily rations of the small trout. The daily ration of trout would only have to change from 2 g to 5 g per day to accomplish this and a large trout's potential to eat food is much greater than 5 g per day. If this was the reason, then to attain a significant increase in the survival of small trout, predator numbers might have to be reduced considerably more than 60%.

Large brown trout are not very cannibalistic on small brown trout however. This is evident in both the data on relative diet composition and the proportion of small brook and brown trout that are lost to brown trout predators. This differential kill could be due to the relative preference or availability of the two species to the predator. I suggest that it is preference for brook trout, or rather a rejection of brown trout. In some of my experimental voluntary feeding tests I offered predatory brown trout small brown trout and they did not eat them. In some tests I put small brook and brown trout of similar size in the same tank and the brown trout ate only the brook trout.

Where the management goal is to enhance the brown trout populations, then predation by large brown trout is probably good. In fact, without the small trout as a source of food the growth of older brown trout would undoubtedly be much slower. Fewer large trophy trout would be produced. Further, without the significant impact of large brown trout on the small trout population in the North Branch of the Au Sable and other rivers, many more small trout and other fish would survive which could result in slower growth rates for all trout.

More restrictive special regulations (12 inch minimum size, 3 trout creel limits, and flies only) imposed on a portion of the Main Branch of the Au Sable resulted in increased trout survival and enlarged stocks of 7- to 11-inch fish. Commensurate growth reductions have occurred. Growth is significantly faster in sections of the Main Au Sable both upstream and downstream from the special waters (White 1975; Stauffer 1976). Few trout over 15 inches are presently being grown in the special waters. However, all of the increased survival might not be due to the special regulations. This portion of the Main Au Sable has more human habitation along its banks, compared to the other waters of the Au Sable. Thus, the impact of predators such as the Great Blue Heron, American Merganser, mink and otter might be minimal because they tend to avoid areas with heavy human activity.

The large brown trout eat considerable numbers of muddlers, minnows, darters, and suckers which undoubtedly compete with trout for food and space. Without brown trout predation, these coarse fish stocks would be much more competitive than at present.

The relative kills of trout by most of the natural predators and anglers indicate that the anglers are responsible for much of the mortality of older trout (third growing season fish and older) of both species. The exception being relatively few losses of brook trout to anglers in the special regulation waters. This is due to the effectiveness of the special regulations in reducing the take by anglers. Angling regulations on brown trout, however, apparently do not alter the angler kill much, except for age-III brown trout. However, for both species of trout, those size and age classes saved from the angler, due mainly to the higher size limit of the special regulation water, are subsequently lost to natural predators. The predators responsible are mainly the Great Blue Herons, American Mergansers, and Belted Kingfishers. However, kills also occur from mink and otter, but I have not been able to quantify their predation because of meager knowledge on population levels of these mammals that frequent the river. Further, predation estimates presented here are based on consumption only and are judged by me to be minimal because all of these predators injure some prey which escape to die later from the wounds. It is not the predator size brown trout that are in direct competition with the angler because these fish crop the small trout. It is, however, the American Merganser, Great Blue Heron, mink, and otter that compete most with the angler, by frequently cropping the larger size trout.

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Table 1. - Procedures used to derive average real diet (grams) and diet composition (percent) per trout from the observed diet of brown trout from the North Branch Au Sable River, normal regulation water, for the summer period (monthly mean water temperatures (F) in parentheses).

	Month (water temperature and temperature factor)[1]											
	May (55F-1.00)		June (63F-0.93)		July (65F-0.83)		August (62F-0.96)		September (57F-1.00)		October (48F-0.88)	
	O	A	O	A	O	A	O	A	O	A	O	A
Brook	1.06	1.06	0.75	0.70	1.07	0.89	0.25	0.24	0.46	0.46	0.76	0.67
Brown	....	....	....	....	....	....	....	....	....	....	....	....
Muddlers	0.08	0.08	0.37	0.34	0.60	0.50	0.33	0.32	0.21	0.21	0.03	0.03
Minnows	0.12	0.12	0.07	0.07	0.80	0.66	1.37	1.32	1.71	1.71	....	....
Lamprey and darters	0.02	0.02	....	....	0.45	0.37	....	....	0.02	0.02	0.07	0.06
Unidentified fish	0.08	0.08	....	....	0.01	0.01	....	....	0.13	0.13	0.02	0.02
Crustacea	0.71	0.71	1.14	1.06	0.71	0.59	0.87	0.84	0.43	0.43	0.05	0.04
Mollusca	0.05	0.05	0.13	0.12	0.01	0.01	0.05	0.05	0.18	0.18	....	....
Insects	0.75	0.75	0.99	0.92	0.53	0.44	0.17	0.16	0.36	0.36	0.41	0.36
Amphibians	....	....	....	....	0.63	0.52	....	....	....	....	....	....
Mammals	0.07	0.07	....	....	....	....	....	....	0.07	0.07	....	....
Veg. debris unidentified	0.24	0.24	0.16	0.15	0.02	0.02	0.12	0.12	0.04	0.04	0.02	0.02
Annelida	0.17	0.17	....	....	0.10	0.08	....	....	0.01	0.01	....	....
Total	3.35	3.35	3.61	3.36	4.93	4.09	3.16	3.05	3.62	3.62	1.36	1.20

	Adjusted mean (May - September)	Taxa factor	Real diet	Percent of all diet	Empirical mean diet	Empirical diet composition (%)
Brook	0.67	1.00	0.67	30.2	0.72	21.6
Brown	....	1.00	....	....	....	....
Muddlers	0.25	1.00	0.25	11.3	0.27	8.1
Minnows	0.65	1.00	0.65	29.3	0.68	20.3
Lamprey and darters	0.08	0.80	0.06	2.7	0.10	3.0
Unidentified fish	0.04	1.00	0.04	1.8	0.04	1.2
Crustacea	0.61	0.17	0.10	4.5	0.65	19.4
Mollusca	0.07	0.66	0.05	2.2	0.07	2.1
Insects	0.50	0.37	0.18	8.1	0.54	16.2
Amphibians	0.09	1.00	0.09	4.0	0.10	3.0
Mammals	0.02	1.00	0.02	0.9	0.02	0.6
Veg. debris Unidentified	0.09	0.50	0.04	1.8	0.10	3.0
Annelida	0.04	1.68	0.07	3.2	0.05	1.5
Total	3.11	....	2.22	100.0	3.34	100.0

[1] O = observed; A = adjusted.

Table 2.--Procedure used to derive average real diet (grams) and diet composition (percent) per trout from the observed diet of brown trout from the North Branch Au Sable River, normal regulation water, for the winter period (monthly mean water temperatures (F) in parentheses).

	Month (water temperature and temperature factor)[1]											
	November (40F-0.65)		December (33F-0.19)		January (32F-0.06)		February (32F-0.06)		March (35F-0.39)		April (43F-0.75)	
	O	A	O	A	O	A	O	A	O	A	O	A
Brook	0.42	0.27	6.10	1.16	1.45	0.09	2.09	0.13	2.12	0.83	0.42	0.32
Brown	....	....	....	....	0.17	0.01	....	....	0.25	0.10	....	....
Muddlers	0.67	0.44	0.55	0.10	0.73	0.04	0.93	0.06	0.76	0.30	0.79	0.59
Minnows	1.02	0.66	0.10	0.02	0.13	0.01	0.28	0.02	1.00	0.39	0.27	0.20
Lamprey and darters	0.21	0.14	....	....	....	....	0.11	0.01	0.02	tr	0.01	0.01
Unidentified fish	0.13	0.08	0.10	0.02	0.16	0.01	0.01	tr	0.13	0.05	0.09	0.08
Crustacea	0.01	0.01	0.08	0.02	0.08	tr	0.04	tr	0.26	0.10	0.19	0.14
Mollusca	0.03	0.02	0.04	0.01	0.05	tr	tr	tr	0.02	tr	0.03	0.02
Insects	0.36	0.23	0.22	0.04	1.03	0.06	1.20	0.07	6.39	2.49	0.57	0.43
Amphibians	....	....	....	....	....	....	....	....	....	....	....	....
Mammals	....	....	....	....	....	....	....	....	....	....	....	....
Veg. debris unidentified	0.09	0.06	0.07	0.01	0.13	0.01	0.13	0.01	0.74	0.29	0.20	0.15
Annelida	....	....	....	....	....	....	....	....	0.01	tr	....	....
Total	2.94	1.91	7.26	1.38	3.93	0.23	4.79	0.30	11.70	4.55	2.57	1.94

	Adjusted mean (November - April)	Taxa factor	Real diet	Percent of all diet	Empirical mean diet	Empirical diet composition (%)
Brook	0.47	1.00	0.47	36.7	2.10	37.9
Brown	0.02	1.00	0.02	1.6	0.07	1.3
Muddlers	0.25	1.00	0.25	19.5	0.74	13.4
Minnows	0.22	1.00	0.22	17.2	0.46	8.3
Lamprey and darters	0.03	0.80	0.02	1.6	0.07	1.3
Unidentified fish	0.04	1.00	0.04	3.1	0.09	1.6
Crustacea	0.04	0.17	0.01	0.8	0.11	2.0
Mollusca	0.01	0.66	0.01	0.8	0.03	0.5
Insects	0.55	0.37	0.20	15.6	1.63	29.4
Amphibians	....	1.00	....	....	....	....
Mammals	....	1.00	....	....	....	....
Veg. debris unidentified	0.09	0.50	0.04	3.1	0.23	4.2
Annelida	tr	1.68	....	....	tr	0.1
Total	1.72	....	1.28	100.0	5.53	100.0

[1] O = observed; A = adjusted.

Table 3.--Procedure used to derive average real diet (grams) and diet composition (percent) per trout from the observed diet of brown trout from the North Branch Au Sable River, special regulation water, for the summer period (monthly mean water temperature (F) in parentheses).

	Month (water temperature and temperature factor)[1]											
	May (55F-1.00)		June (63F-0.93)		July (65F-0.83)		August (62F-0.96)		September (57F-1.00)		October (48F-0.88)	
	O	A	O	A	O	A	O	A	O	A	O	A
Brook	3.34	3.34	0.89	0.83	1.65	1.37	0.84	0.81	0.91	0.91	0.23	0.20
Brown	....	....	....	....	....	....	....	....	....	....	....	....
Muddlers	....	....	0.14	0.13	....	....	....	....	0.07	0.07	0.28	0.25
Minnows	0.72	0.72	0.02	0.02	....	....	0.05	0.05	0.19	0.19	0.33	0.29
Lamprey and darters	0.18	0.18	....	....	....	....	....	....	0.03	0.03	0.15	0.13
Unidentified fish	0.12	0.12	0.06	0.06	....	....	0.27	0.26	....	....	0.09	0.08
Crustacea	0.50	0.50	0.62	0.58	2.44	2.03	0.71	0.68	0.21	0.21	0.04	0.04
Mollusca	....	....	0.24	0.22	tr	....	0.03	0.03	tr	tr	....	....
Insects	0.19	0.19	0.52	0.48	0.02	0.02	0.07	0.07	0.16	0.16	0.03	0.03
Amphibians	....	....	....	....	....	....	0.04	0.04	0.14	0.14	....	....
Mammals	....	....	....	....	....	....	....	....	....	....	....	....
Veg. debris unidentified	0.12	0.12	0.17	0.16	0.02	0.02	0.98	0.94	0.06	0.06	0.09	0.08
Annelida	....	....	....	....	0.02	0.02	....	....	0.03	0.03	....	....
Total	5.17	5.17	2.66	2.48	4.15	3.46	2.99	2.88	1.80	1.80	1.24	1.10

	Adjusted mean (May - September)	Taxa factor	Real diet	Percent of all diet	Empirical mean diet	Empirical diet composition (%)
Brook	1.24	1.00	1.24	60.8	1.31	43.7
Brown	....	1.00	....	....	....	....
Muddlers	0.08	1.00	0.08	3.9	0.08	2.7
Minnows	0.21	1.00	0.21	10.3	0.22	7.3
Lamprey and darters	0.06	0.80	0.05	2.4	0.14	4.7
Unidentified fish	0.09	1.00	0.09	4.4	0.09	3.0
Crustacea	0.67	0.17	0.11	5.4	0.75	25.0
Mollusca	0.04	0.66	0.03	1.5	0.04	1.3
Insects	0.16	0.37	0.06	2.9	0.17	5.7
Amphibians	0.03	1.00	0.03	1.5	0.03	1.0
Mammals	....	1.00	....	....	....	....
Veg. debris unidentified	0.23	0.50	0.12	5.9	0.16	5.3
Annelida	0.01	1.68	0.02	1.0	0.01	0.3
Total	2.82	....	2.04	100.0	3.00	100.0

[1] O = observed; A = adjusted.

Table 4.--Procedure used to derive average real diet (grams) and diet composition (percent) per trout from the observed diet of brown trout from the North Branch Au Sable River, special regulation water, for the winter period (monthly mean water temperature (F) in parentheses).

	Month (water temperature and temperature factor)[1]											
	November (40F-0.65)		December (33F-0.19)		January (32F-0.06)		February (32F-0.06)		March (35F-0.39)		April (43F-0.75)	
	O	A	O	A	O	A	O	A	O	A	O	A
Brook	2.05	1.33	4.00	0.76	1.87	0.11	1.89	0.11	2.08	0.81	1.05	0.79
Brown	0.09	0.06	0.02	tr	....	....	1.35	0.08	....	....	0.35	0.26
Muddlers	0.10	0.06	0.48	0.09	0.23	0.01	0.49	0.03	0.54	0.21	1.05	0.79
Minnows	0.06	0.04	0.68	0.13	0.04	tr	0.68	0.04	0.47	0.18	1.19	0.89
Lamprey and darters	0.04	0.03	0.11	0.02	0.07	0.01	0.04	tr	0.21	0.08	0.04	0.03
Unidentified fish	0.03	0.02	0.04	0.01	0.01	tr	0.04	tr	0.17	0.07	0.12	0.09
Crustacea	0.14	0.09	0.01	tr	0.05	tr	0.13	0.01	0.08	0.03	0.14	0.11
Mollusca	tr	....	0.06	0.01	0.01	tr	....	....	0.02	0.01	tr	tr
Insects	1.33	0.86	0.20	0.04	0.27	0.02	1.23	0.07	3.65	1.42	0.92	0.69
Amphibians	....	....	0.24	0.05	....	....	0.11	0.01	0.96	0.37	0.33	0.25
Mammals	....	....	....	....	....	....	....	....	....	....	....	....
Veg. debris unidentified	0.11	0.07	0.09	0.02	0.03	tr	0.21	0.01	0.22	0.09	0.12	0.09
Annelida	....	....	....	....	....	....	0.36	0.02	0.08	0.03	0.06	0.04
Total	3.95	2.56	5.93	1.13	2.58	0.15	6.53	0.38	8.48	3.30	5.37	4.03

	Adjusted mean (November-April)	Taxa factor	Real diet	Percent of all diet	Empirical mean diet	Empirical diet composition (%)
Brook	0.65	1.00	0.65	42.2	2.16	39.5
Brown	0.07	1.00	0.07	4.6	0.30	5.5
Muddlers	0.20	1.00	0.20	13.0	0.48	8.8
Minnows	0.21	1.00	0.21	13.6	0.52	9.5
Lamprey and darters	0.03	0.80	0.03	2.0	0.08	1.5
Unidentified fish	0.03	1.00	0.03	2.0	0.07	1.3
Crustacea	0.04	0.17	0.01	0.6	0.09	1.6
Mollusca	tr	0.66	tr	....	0.02	0.4
Insects	0.52	0.37	0.19	12.3	1.27	23.2
Amphibians	0.11	1.00	0.11	7.1	0.27	4.9
Mammals	....	1.00	0.00	....	0.00	0.0
Veg. debris unidentified	0.05	0.50	0.02	1.3	0.13	2.4
Annelida	0.01	1.68	0.02	1.3	0.08	1.4
Total	1.92	....	1.54	100.0	5.47	100.0

[1] O = observed; A = adjusted.

Table 5.--Grams of trout evacuated from the stomachs of experimentally fed predator brown trout at the end of 24, 48, and 72 hours, employing an array of prey and predator-size trout, at four water temperatures.

Length of prey (inches)	35F Number of hours			45F Number of hours			55F Number of hours			65F Number of hours	
	24	48	72	24	48	72	24	48	72	24	48
12.0- to 14.9-inch brown trout predators											
2	2.9	...	...	2.8	3.9	...	3.3	...	...	...	...
3	2.6	5.5	7.2	4.3	6.6	7.3	6.3	8.4	...	5.0	8.0
4	2.5	6.6	10.6	6.8	10.8	14.6	8.7	13.2	14.6	6.5	11.6
5	2.8	7.2	14.4	8.3	15.3	20.6	8.3	19.7	20.1	8.6	19.2
15.0- to 17.9-inch brown trout predators											
3	3.0	5.7	7.7	4.1	6.9	7.3	7.3	8.7	...	5.6	8.6
4	3.9	8.4	11.2	7.2	13.7	16.1	9.9	15.3	14.6	7.2	12.6
5	3.6	10.4	18.4	9.1	18.5	23.5	12.8	26.4	29.3	10.5	23.9
6	3.6	10.6	21.1	10.1	23.2	33.4	12.7	33.8	34.6	11.2	28.7
7	3.3	12.0	24.8	...	...	...	...	...	...	...	...
18.0+ -inch brown trout predators											
3	3.4	5.5	7.9	5.2	8.6	9.1	6.6	8.9	...	4.9	7.7
4	4.4	8.8	12.3	11.0	14.1	14.9	10.5	16.7	13.8	10.8	16.8
5	5.1	11.0	21.9	14.4	25.1	32.3	18.6	30.2	31.3	15.2	27.6
6	4.7	13.0	26.5	15.7	31.9	45.4	17.4	38.8	56.2	15.6	36.2
7	4.7	12.8	28.3	15.3	31.5	44.6	21.3	39.5	53.5	16.9	31.7

Table 6.--Estimated average daily meal (grams) of prey trout eaten by predatory brown trout for various months and semi-annual seasonal periods, for the normal and special regulation river areas.

Month	Normal regulation area	Special regulation area
May	0.95	3.76
June	1.37	1.41
July	2.07	1.59
August	0.88	0.41
September	0.58	1.65
October	1.00	0.32
Average May-October	1.14	1.52
November	0.55	2.30
December	0.53	2.89
January	0.60	1.73
February	0.42	1.44
March	0.38	0.35
April	0.72	1.87
Average November-April	0.53	1.76

Table 7.--Procedure used to estimate weight of prey trout eaten by predatory brown trout, per mile of river, normal and special regulation waters.

Semi-annual period	Average daily meal of prey trout (g)	Days during seasonal interval	Number of predator trout	Weight of prey trout eaten (g)
Normal regulation water				
May-October	1.14	184	258	54,118
November-April	0.53	181	258	24,750
Special regulation water				
May-October	1.52	184	82	22,934
November-April	1.76	181	82	26,122

Table 8.--Semiannual brook trout numbers per mile of river in the North Branch of the Au Sable River, under normal fishing regulations, with estimated numbers and percentages (in parentheses) lost to predators and anglers.

Trout age[a]	Estimated number	Total mortality during interval	Source of mortality: Angler catch	American Merganser	Great Blue Heron	Belted King-fisher	Brown trout	Total natural predators
Eggs	154,647							
		38,584	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Fry	116,063							
		108,779	0 (0)	0 (0)	50 (tr)	1017 (0.9)	4107 (3.8)	5,174 (4.8)
0	7,284							
		3,531	0 (0)	212 (5.7)	6 (0.2)	152 (4.3)	2966 (84.0)	3,336 (94.5)
I*	3,754							
		2,422	395 (16.3)	0 (0)	276 (11.4)	106 (4.4)	485 (20.0)	867 (35.8)
I	1,332							
		255	0 (0)	134 (52.6)	1 (0.4)	1 (0.4)	61 (23.9)	197 (77.2)
II*	1,077							
		944	542 (57.4)	0 (0)	26 (2.8)	0 (0)	7 (0.7)	33 (6.1)
II	133							
		43	0 (0)	6 (14.0)	0 (0)	0 (0)	0 (0)	6 (14.0)
III*	90							
		85	39 (45.9)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
III	5							
		-1	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
IV*	6							
		6	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
IV	0							
Total	129,744[b]	116,064[b]	976	352	359	1276	7626	9,613[b]

[a] * indicates spring estimates; lack of *, fall estimates.

[b] Only fry and older trout.

Table 9.--Semiannual brown trout numbers per mile of river in the North Branch of the Au Sable River, under normal fishing regulations, with estimated numbers and percentages (in parentheses) lost to predators and anglers.

Trout age[a]	Estimated number	Total mortality during interval	Source of mortality: Angler catch	American Merganser	Great Blue Heron	Belted King-fisher	Brown trout	Total natural predators
Eggs	253,512							
		118,645	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Fry	134,867							
		132,569	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
0	2,298							
		967	0 (0)	143 (14.8)	0 (0)	0 (0)	215 (22.2)	358 (37.0)
I*	1,331							
		366	91 (24.9)	0 (0)	55 (15.0)	0 (0)	0 (0)	55 (15.0)
I	965							
		196	0 (0)	117 (59.7)	4 (2.0)	0 (0)	2 (1.0)	123 (62.8)
II*	769							
		369	324 (87.8)	0 (0)	69 (18.7)	0 (0)	0 (0)	69 (18.7)
II	400							
		159	0 (0)	4 (2.5)	3 (1.9)	0 (0)	0 (0)	7 (4.4)
III*	241							
		156	83 (53.2)	0 (0)	8 (5.1)	0 (0)	0 (0)	8 (5.1)
III	85							
		19	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
IV*	66							
		32	19 (59.4)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
IV	34							
		7	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
V-VIII*	27							
		4	7 (175.0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
V-VIII	23							
Total	141,106[b]	134,844[b]	524	264	139	0	217	620[b]

[a] * indicates spring estimates; lack of *, fall estimates.

[b] Only fry and older trout.

Table 10.--Semiannual brook trout numbers per mile of river in the North Branch of the Au Sable River, under special fishing regulations, with estimated numbers and percentages (in parentheses) lost to predators and anglers.

Trout age[a]	Estimated number	Total mortality during interval	Source of mortality					Total natural predators
			Angler catch	American Merganser	Great Blue Heron	Belted Kingfisher	Brown trout	
Eggs	169,395							
		42,264	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Fry	127,131							
		120,071	0 (0)	0 (0)	47 (tr)	565 (0.5)	1479 (1.2)	2,091 (1.7)
0	7,060							
		3,945	0 (0)	82 (2.1)	3 (tr)	214 (5.4)	1539 (39.0)	1,838 (46.6)
I*	3,115							
		1,646	1 (tr)	0 (0)	186 (11.3)	64 (3.9)	283 (17.2)	533 (32.4)
I	1,469							
		511	0 (0)	112 (21.9)	2 (0.4)	5 (1.0)	269 (52.6)	388 (75.9)
II*	958							
		736	43 (5.8)	0 (0)	111 (15.1)	0 (0)	2 (0.3)	113 (21.2)
II	222							
		85	0 (0)	11 (12.9)	0 (0)	0 (0)	7 (8.2)	18 (21.2)
III*	137							
		130	9 (6.9)	0 (0)	3 (2.3)	0 (0)	0 (0)	3 (9.2)
III	7							
		-1	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
IV*	8							
		8	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
IV	0							
Total	140,107[b]	127,131[b]	53	205	352	848	3579	4,984[b]

[a] * indicates spring estimates; lack of *, fall estimates.

[b] Only fry and older trout.

Table 11.--Semiannual brown trout numbers per mile of river in the North Branch of the Au Sable River, under special fishing regulations, with estimated numbers and percentages (in parentheses) lost to predators and anglers.

Trout age[a]	Estimated number	Total mortality during interval	Source of mortality: Angler catch	American Merganser	Great Blue Heron	Belted King-fisher	Brown trout	Total natural predators
Eggs	121,909							
		57,053	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Fry	64,856							
		61,598	0 (0)	0 (0)	21 (tr)	0 (0)	0 (0)	21 (tr)
0	3,258							
		1,998	0 (0)	75 (3.8)	0 (0)	0 (0)	156 (7.8)	231 (11.6)
I*	1,260							
		444	2 (0.4)	0 (0)	76 (17.1)	0 (0)	0 (0)	76 (17.1)
I	816							
		363	0 (0)	109 (30.0)	4 (1.1)	0 (0)	62 (17.1)	175 (48.2)
II*	453							
		193	100 (51.8)	0 (0)	43 (22.3)	0 (0)	0 (0)	43 (22.3)
II	260							
		128	0 (0)	24 (18.8)	5 (3.9)	0 (0)	0 (0)	29 (22.7)
III*	132							
		80	21 (26.2)	0 (0)	10 (12.5)	0 (0)	0 (0)	10 (12.5)
III	52							
		30	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
IV*	22							
		8	8 (100.0)	0 (0)	2 (25.0)	0 (0)	0 (0)	2 (25.0)
IV	14							
		6	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
V-VIII*	8							
		1	1 (100.0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
V-VIII	7							
Total	71,138[b]	64,849[b]	132	208	161	0	218	587[b]

[a] * indicates spring estimates; lack of *, fall estimates.

[b] Only fry and older trout.

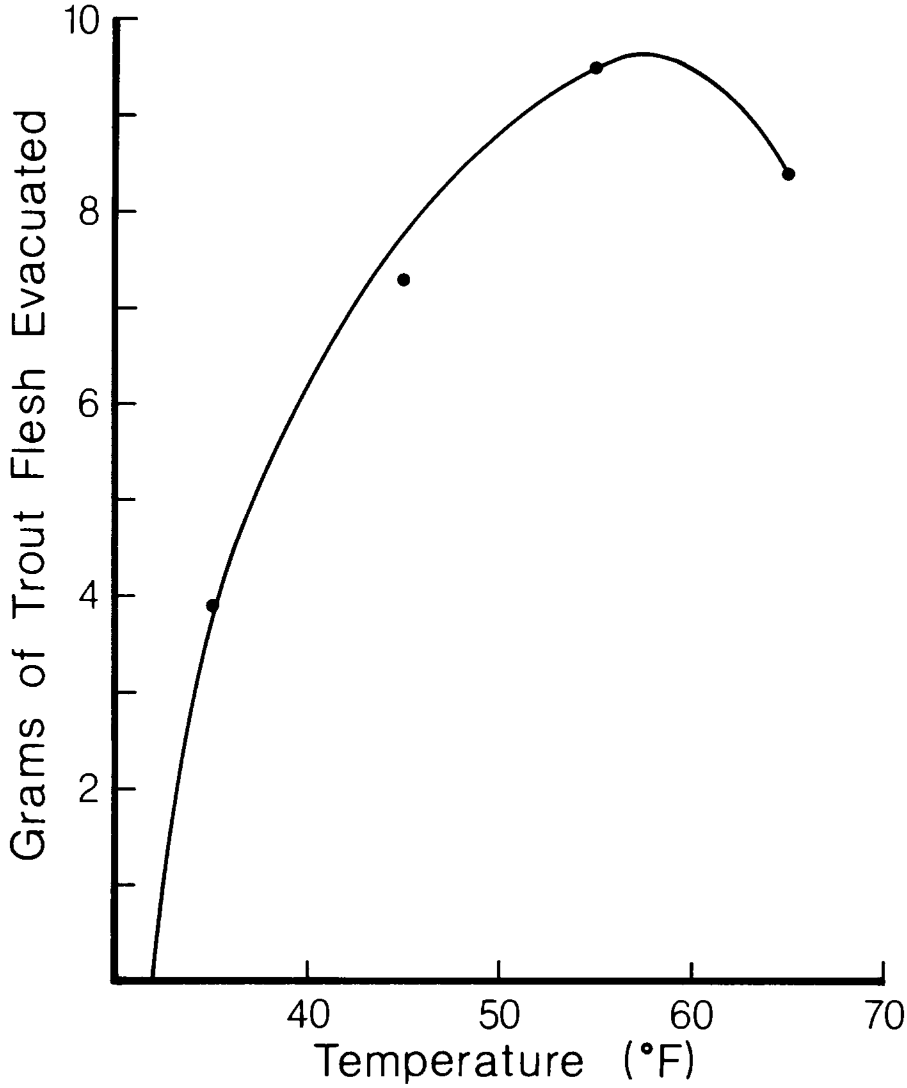

Figure 1.--Estimated average grams of trout flesh evacuated from stomachs of experimentally fed predator brown trout, per 24 hours, at various water temperatures.

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