Original: To Ecology,
for publication
cc: Fish Division
Education-Game
Inst. for Fish. Res.
R. J. Ellis
H. Gowing
D. S. Shetter
Rifle River

December 4, 1956

Report No. 1496

Relationship Between Food Supply and Condition of Wild Brown Trout (*Salmo trutta*) in a Michigan Stream

By Robert J. Ellis and Howard Gowing

December 4, 1956

Report No. 1496

Relationship Between Food Supply and Condition of Wild Brown Trout (*Salmo trutta*) in a Michigan Stream

By Robert J. Ellis and Howard Gowing

Abstract

The coefficient of condition is a useful measurement in studies of trout populations because it marks the season when growth is most rapid and is a means for comparing the relative well being of the fish. Although the seasonal change in condition of salmonids has been established repeatedly, its cause has remained uncertain.

Field study during 1950 and 1951 revealed great differences in the biological productivity of two adjacent sections of a Michigan trout stream, Houghton Creek in Ogemaw County. The difference presumably was a result of domestic sewage from Rose City entering the downstream section. This situation offered an opportunity to investigate the influence of differing food supplies on the condition and growth of native brown trout in two stream sections whose physical-chemical features were nearly identical.

Monthly samples were collected from the two stream areas to determine the seasonal cycles in abundance of bottom fauna, feeding habits, and coefficient of condition of the brown trout. Results indicated that, in the less productive area, a paucity of food of aquatic origin caused a sharp decline in condition, a reduction in the quantity of food per stomach, and a shift to a diet containing a considerable portion of terrestrial organisms. This belief was substantiated when trout from the productive area and the unproductive area were compared. Trout from the productive area (which, throughout the year, had a

greater volume of bottom fauna than the unproductive area) maintained significantly higher and much less variable condition than trout from the less productive area. Stomachs from the productive area contained more food in midsummer and did not show the increase in terrestrial foods.

Relationship Between Food Supply and Condition of Wild Brown Trout (*Salmo trutta*) in a Michigan Stream

By

Robert J. Ellis and Howard Gowing

Michigan Department of Conservation, Ann Arbor, Michigan

Introduction

It has been observed that the length-weight ratio or coefficient of condition of stream trout varies during the year (Went and Frost, 1942; Cooper and Benson, 1951; Cooper, 1953). It has been demonstrated that the length-weight ratio of trout is related to growth in that when the fish are relatively heavy they are growing faster than when they are relatively light (Went and Frost, 1942; Allen, 1940; and Brown, 1946a). Coefficient of condition is a useful measurement in studies of trout populations, because it marks the season when growth is most rapid, and is a means for comparing the relative well being of the fish.

Brown (1946a) reported that brown trout raised in the laboratory under constant conditions of food, light, and temperature exhibited an annual growth rate cycle and that the specific rate of growth in length was directly proportional to the condition of the fish. Benson (1953), Allen (1940), and Neil (1938) demonstrated that in a natural stream environment there was a direct correlation between volume of stomach contents and seasonal changes in condition for brook trout, young salmon, and brown trout. Allen (1940) and Neil (1938) both examined the relationship between growth of stream fish and seasonal abundance (but not volume) of food, and found no correlation.

While the seasonal change in condition in the salmonids has been established repeatedly, its cause has remained uncertain. Field study during 1950 and 1951 revealed great differences in the biological productivity of two adjacent portions of Houghton Creek, a trout stream in Michigan. This situation offered an opportunity to investigate the influence of differing food supplies on the condition and growth of native brown trout in the two stream sections.

Study Area

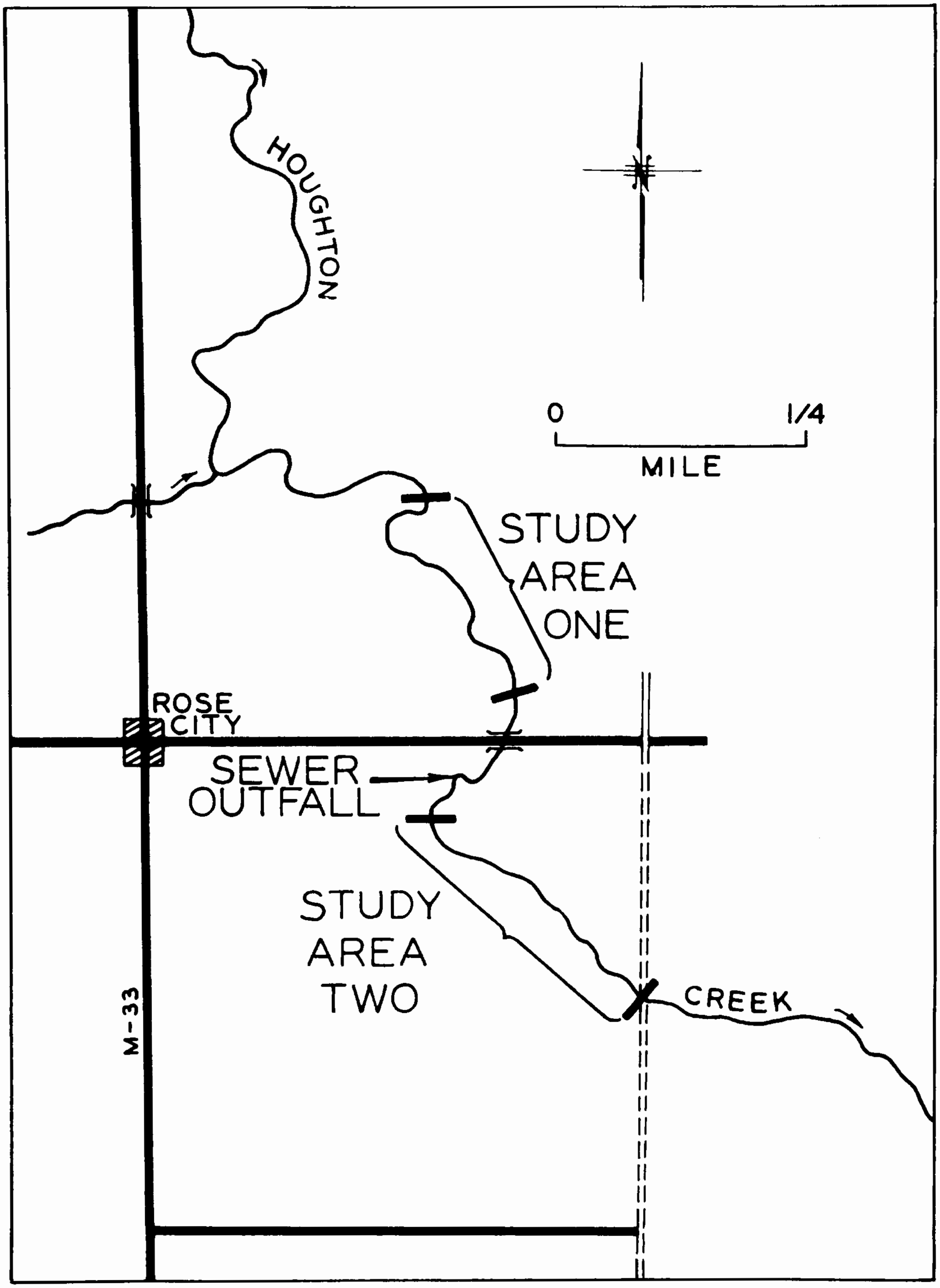
Houghton Creek, Ogemaw County, Michigan was the site of the investigation. The accompanying map (Figure 1) shows the area. The stream is approximately 9.7 miles long and is a tributary of the Rifle River. The village of Rose City (population 500) is located about midway between source and mouth of the stream and untreated sewage from this community is discharged into Houghton Creek. A survey was conducted by the Michigan Water Resources Commission in August and October, 1950 to determine the degree of pollution of the stream by sewage from Rose City. This survey indicated a maximum biochemical oxygen demand of 3.6 p.p.m. coincident with a dissolved oxygen supply of 9.8 p.p.m. at a temperature of 56° F., and it was concluded that the sewage did not decrease the oxygen sufficiently to harm fish life. A re-survey of the stream by the Michigan Water Resources Commission in October of 1956 verified this conclusion.

Two study areas were selected. The upstream one (Area One) began at a point about 1,300 feet above the sewer outfall and extended 1,700 feet upstream. The lower area (Area Two) began 300 feet below the sewer outfall and extended about 1,900 feet downstream.

Physically, the two stream sections were similar. The upstream section had an average width of 24 feet and an average depth of 1.1 feet; the other averaged 24.4 feet in width and 1.6 feet in depth. Percentages of each type of bottom soil and amount of trout cover were essentially the same in the two sections.

Checks showed water temperatures to be in close agreement in the two sections, and these temperatures were nearly identical with those recorded on

Figure 1. Map of Houghton Creek, Ogemaw County, Michigan,showing relationships between study areas and sewer outfall.


HOUGHTON
0
1/4
MILE
STUDY
AREA
ONE
ROSE
CITY
SEWER
OUTFALL
STUDY
AREA
TWO
CREEK
M-33

a thermograph housed on Houghton Creek about 4 miles downstream. Mean maximum and minimum water temperatures recorded at the gaging station during the period of this study are listed in Table I and Figure 2.

Analyses showed that chemically there was little difference in the water of the two sections, except for additional nitrogen and phosphorus resulting from the sewage entering the lower area. Results of the chemical analyses are shown in Table II.

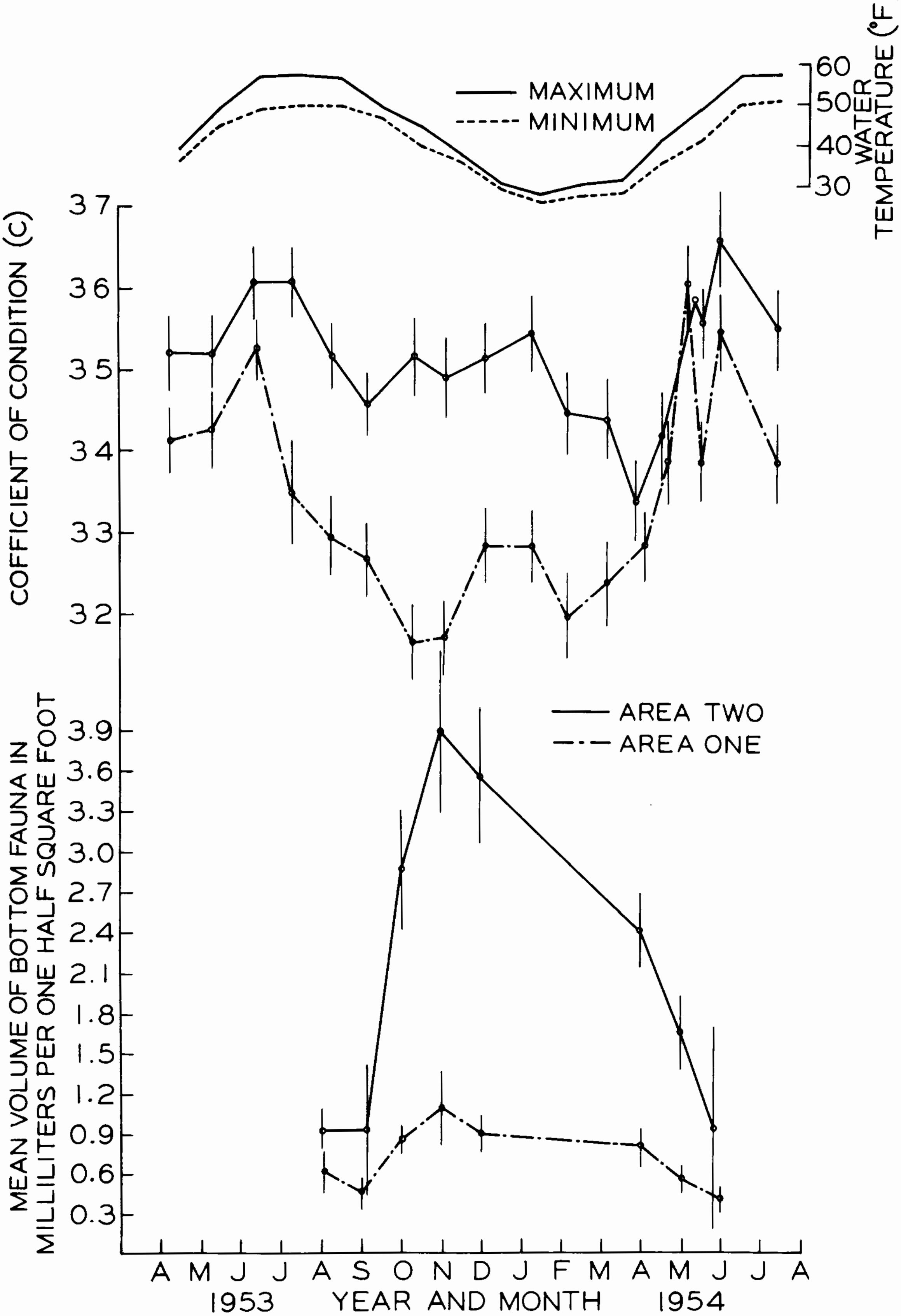
Bottom Fauna

A modified Surber stream bottom sampler was used to collect samples of bottom fauna for quantitative and qualitative analysis. All samples were collected from riffle areas. It was recognized that organisms were present in other habitats but for practical reasons only riffle areas were considered. Each month four samples (each 1/2 square foot) were taken from each of two gravely riffles in each stream section. Organisms were sorted out of the bottom samples, and the total volume of all organisms in each sample was determined by displacement of fluid in a 15-ml. centrifuge tube.

The results of the bottom sampling are summarized in Table III and Figure 2. The three categories presented in the table were used for convenience of presentation and because these were the most important taxonomic groups in the bottom fauna samples.

There are three aspects of Table III and Figure 2 which are of particular importance: (1) The volumes of bottom fauna samples show a marked seasonal variation, with a summer minimum followed by a fall and winter increase and a sharp decline in the spring and early summer; (2) Each month, for every major category of bottom fauna, the samples from Area Two had a greater volume of organisms than Area One. (3) For most monthly samples it was demonstrated

Figure 2. Seasonal variation of water temperature (monthly averages), of condition (C) of wild brown trout, and of bottom fauna abundance in Houghton Creek, Ogemaw County. Vertical line represents two standard errors above and below the mean for coefficient of condition, and one standard error for abundance of bottom fauna.



MAXIMUM
MINIMUM
60
50
40
30
WATER TEMPERATURE (°F)
COFFICIENT OF CONDITION (C)
3 7
3 6
3 5
3 4
3 3
3 2
AREA TWO
AREA ONE
MEAN VOLUME OF BOTTOM FAUNA IN MILLILITERS PER ONE HALF SQUARE FOOT
3.9
3.6
3.3
3.0
2.7
2.4
2.1
1.8
1.5
1.2
0.9
0.6
0.3
A M J J A S O N D J F M A M J J A
1953 YEAR AND MONTH 1954

Table I. Monthly mean maximum and minimum water temperatures of Houghton Creek for the period April, 1953 to July, 1954. (Courtesy of U. S. Geological Survey, Grayling, Michigan)

Year	Month	Water temperatures	
		maximum °F	minimum °F
1953	April	46	42
	May	55	50
	June	61	56
	July	63	57
	August	61	57
	September	55	52
	October	50	47
	November	43	42
	December	37	36
1954	January	34	32
	February	37	35
	March	38	35
	April	47	41
	May	54	48
	June	62	56
	July	62	57

Table II. Chemical analysis of water from two areas of Houghton Creek.

Date	Study area	pH	Alkalinity $CaCO_3$	Soluble phosphorus	Total nitrogen
July 2	One		172	0.008	0.60
	Two		164	0.004	0.68
July 31	One		161	0.005	0.08
	Two		164	0.049	0.20
Aug. 25	One		171	0.005	0.45
	Two		169	0.009	0.57
Nov. 27	One		172	0.002	0.57
	Two		176	0.012	0.80
Average	One	8.4[1]	169	0.005	0.425
	Two	8.3[1]	168	0.018	0.562

[1] pH determinations were not coincident with other determinations.

Table III. Mean volumes (ml. per 1/2 square foot) of four one-half square-foot bottom samples collected in each of eight months from Houghton Creek, Ogemaw County, Michigan

Date	Asellus[2]			Gammarus[2]			All other[2]			Entire sample		
	Mean volume		t	Mean volume		t	Mean volume		t	Mean volume		t
	Area One	Area Two	value[3]	Area One	Area Two	value	Area One	Area Two	value	Area One	Area Two	value
1953												
Aug.	0.038	0.287	3.45	0.003	0.084	2.43	0.577	0.559	0.035	0.618	0.930	1.47
Sept.	0.044	0.338	2.58	0.006	0.084	2.26	0.425	0.515	2.20	0.475	0.934	2.23
Oct.	0.083	1.021	3.77	0.026	0.331	2.58	0.756	1.566	3.02	0.865	2.884	8.23
Nov.	0.091	1.472	3.39	0.009	0.284	2.49	1.012	2.138	2.46	1.112	3.893	3.79
Dec.	0.106	0.956	3.77	0.031	0.081	1.41	0.894	2.491	4.15	1.031	3.528	4.35
1954												
Apr.	0.006	0.488	3.125	trace	0.022	...	0.769	1.888	3.85	0.775	2.396	4.67
May	trace	0.031	...	0.0	trace	...	0.531	1.600	2.75	0.531	1.631	3.72
[1]June	0.009	0.041	0.85	trace	trace	...	0.366	0.894	1.36	0.375	0.934	1.17
Average	0.047	0.579		0.009	0.111		0.666	1.456		0.719	2.141	

[1]N = 4, all other N = 8.

[2]Asellus = A. intermedius Forbes; Gammarus = G. fasciatus Say; other = over 90 percent aquatic insects.

[3]Dixon, W. J., and Massey, F. J. Jr. 1951. Introduction to Statistical Analysis. McGraw Hill Book Company Inc., page 104.

statistically that Area Two was richer than Area One in both total volume of all bottom fauna and in volume of Asellus.

Investigations into the life history of Asellus intermedius Forbes revealed that in the late spring the breeding population of the riffles makes a definite migration to the stream margins and to protected places in deeper water. As suggested by Allee (1912), there seemed to be a change in the rheotactic response of the breeding population of Asellus. Thus the sharp drop in abundance of Asellus in samples collected during late spring or summer months was largely due to the migration and was not a true indication of a change in abundance of this animal in the stream.

The summer minimum in volume of bottom fauna, excluding Asellus, in the gravely riffles was largely due to the emergence of aquatic insects as adults. Their volume had not yet been replaced by the growth of their offspring.

The most important difference between the two study areas was the more stable food supply in the lower section (Area Two). In summer, when the supply of other aquatic foods was low, Asellus and Gammarus were much more numerous in the area below the sewer outfall than above.

Coefficient of Condition

Samples of 100 brown trout were collected in each area at approximately monthly intervals between April 17, 1953 and May, 1954. In May and June of 1954 additional samples were collected at semi-monthly intervals, and sampling was terminated on July 13, 1954. All samples were collected with electrofishing gear powered by a 220-volt D.C. generator.

Each fish in the sample was measured and weighed and returned to the stream. Total length was recorded in tenths of inches and weight was measured in grams on a Chatillon dietary scale. Grams were later converted to hundredths of a pound. Fish less than 5.0 inches in total length were excluded from the samples because of the difficulty in accurately weighing such small individuals.

The following relationship between weight in pounds (W) and total length in inches (L) was used in determining the coefficient of condition (C) of trout: $C = W/L^3 \times 10^5$. Average C values were computed for samples of trout collected in each area during a 16-month period. Results are plotted (Figure 2) and tabulated (Table IV). It will be noted that the seasonal trends in condition are similar in Area One and Area Two. In both areas condition improved to a maximum with the advance of spring and declined during the summer months. During fall and early winter the condition factor of the trout again rose before falling off to a minimum in midwinter or later.

Earlier studies of salmonids in lotic environments have shown a seasonal trend in condition similar to the one observed in Houghton Creek (Went and Frost, 1942; Cooper and Benson, 1951; Cooper, 1953). As a corollary of these studies, Went and Frost (1942) and Cooper (1953) showed a correlation between growth and condition. Periods of rapid growth were associated with high condition, and during periods of little or no growth condition was poor. This correlation was elaborated upon by Allen (1940) in his study of the biology of the early stages of salmon. He found that if at the onset of the growth period condition was low, weight increased more rapidly than length, while if condition was high at the beginning of the growing period, length would increase more rapidly than weight. This aspect of growth and condition was corroborated experimentally under laboratory conditions by Brown (1946a).

In comparing the 16-month trend in condition of trout in the two areas, two principal differences were apparent. First, the average condition of trout in Area Two exceeded that in Area One, a single sample excepted. These differences are statistically significant at the 95 percent level except for

Table IV. Average coefficient of condition (C), at monthly intervals, for samples of 100 native brown trout, Houghton Creek, Ogemaw County.

Date	Area One			Area Two		
	Size range (inches)	Mean (C)	Std. error of mean	Size range (inches)	Mean (C)	Std. error of mean
4-7-53	5.0-11.7	34.17	0.229	5.0-23.2	35.24	0.249
5-11-53	5.1-13.8	34.25	0.291	5.0-15.0	35.23	0.224
6-10-53	5.0-14.0	35.37	0.218	5.0-24.1	36.14	0.273
7-7-53	5.0-12.3	33.52	0.338	5.0-18.6	36.13	0.264
8-6-53	5.1-12.1	32.94	0.250	5.0-24.3	35.21	0.243
9-3-53	5.1-11.5	32.71	0.239	5.5-14.3	34.61	0.202
10-9-53	5.1-14.5	31.67	0.238	5.0-24.3	35.22	0.258
11-3-53	5.1-13.1	31.73	0.282	5.0-12.3	34.91	0.251
12-2-53	5.0-11.6	32.84	0.259	5.0-14.6	35.19	0.246
1-8-54	5.0-11.6	32.80	0.237	5.0-14.7	35.48	0.260
2-5-54	5.0-14.5	32.00	0.268	5.0-13.9	34.49	0.279
3-5-54	5.0-12.3	32.42	0.276	5.0-12.3	34.42	0.252
3-29-54	5.0-12.1	32.79	0.236	5.0-15.7	33.41	0.281
4-15-54	5.0-13.0	33.79	0.278	5.0-15.9	34.22	0.320
5-4-54	5.0-11.9	36.11	0.254	5.0-13.2	35.88	0.297
5-17-54	5.0-12.0	33.83	0.254	5.1-13.1	35.59	0.228
6-1-54	5.0-12.1	35.49	0.280	5.0-15.8	36.67	0.332
7-13-54	5.0-15.0	33.80	0.228	5.0-15.6	35.52	0.282

the samples of March 29, April 17, and May 4, 1954. Secondly, the annual range of condition was greater in Area One than in Area Two.

Other features of these seasonal trends in condition are worthy of note. Brown trout in both areas entered early April of 1954 in poorer condition than in April of the preceding year. However, the improvement in condition during April of 1954 was much more rapid than during April of the previous year. An anomaly occurred between the May and June samples of 1954. The mid-May sample of trout from Area One showed a marked drop in condition over a relatively short period of time while trout from Area Two showed only an insignificant loss of condition.

Water Temperature

During the investigation water temperatures in Houghton Creek increased rapidly during April, May, and June, reaching a maximum (67° F.) in July and thereafter decreased slowly to a minimum (32° F.) in January.

A general upward trend in condition of trout was coincident with an increase in water temperatures during the spring. After attaining the spring maximum in condition, a downward trend in condition preceded a comparable downward trend in water temperature. During a period of slowly falling water temperatures in the fall and early winter, condition of trout tended to recover somewhat. Finally, condition declined to a low during the later half of the winter.

Trout in both areas were subject to similar water temperatures. The influence of water temperature on trout condition was masked somewhat by the effects of other environmental factors. According to Allen (1940) water temperature was the stimulus that initiated activity and growth of salmon smolts in the spring of the year. He cited 7° C. (45° F.) as the critical water temperature. Brown (1946b) reared two-year-old brown trout at different constant water temperatures and in water of changing temperature and found specific growth rates to be high between 7° C. and 9° C. (45°-48° F.) and between 16° C. and 19° C. (61°-66° F.). Above, between, and below these temperatures specific growth rates were low. At Houghton Creek, the spring rise in condition of brown trout occurred with maximum water temperatures of 41° to 67° F. in 1953 and 41° to 61° F. in 1954.

Mean minimum and maximum stream temperatures during June (56°-60° F.), July (57°-63° F.) and August (57°-61° F.) were similar. In spite of nearly optimum temperatures for growth during the summer, the condition of trout in Area One declined after the middle of June and in Area Two the decline took place during the first week in July. In Area Two trout maintained better condition than the trout from Area One. Apparently temperature was not the primary cause of the summer decline in condition.

Sexual maturity appeared to influence condition values in autumn, particularly during October and November. During this spawning period when water temperatures ranged between 38° F. and 52° F., mature trout (9.0 inches or longer) showed a drop in condition. Immature trout (shorter than 9.0 inches) tended to improve slightly in condition during the late fall months.

During late winter, between the January and late March sampling dates, temperatures ranged between 32°-42° F. The condition of trout was comparatively poor during this period.

Population Density

To test whether population density might influence the condition factor of trout, population estimates were made for both stream sections during the fourth week of August, 1954. Area One (1,734 feet in length) was estimated to contain 1,259 brown trout, or about 120 pounds per acre. For Area Two

(1,900 feet) the estimate was 1,693 brown trout, or about 127 pounds per acre. It can be seen that the numerical abundance of brown trout was approximately the same in both areas, with perhaps a slightly more numerous population in Area Two. Size distribution of the trout in the two sections was similar, and all one-inch size groups between 2 and 14 inches were represented in the samples. The effect of population density, per se, on trout condition cannot be discussed here, but evidently population density may be eliminated as a factor accounting for the disparity in condition between trout in the two areas.

Feeding Habits, and Utilization of Bottom Fauna

Stomachs from trout in both stream sections were collected to determine if major components of the bottom fauna contributed significantly to the food of trout, and particularly if the abundant Asellus was an important item in the diet.

Trout for stomach analyses were collected from each of the two areas with electro-fishing gear powered by a 220-volt D.C. generator. Two stomachs from fish in each one-inch size group (7 through 12 inches) were collected from each area each month from April through August. The stomachs were removed from freshly killed fish and preserved in 85 percent alcohol for several months before the contents were examined. Only the material in the stomach was examined. Organisms were identified only to the smallest taxonomic group, usually genus, easily recognized by the investigators. Since there is a considerable difference in the rate of digestion of the different kinds of food organisms eaten by trout (Ellis, unpublished), it was felt that a direct volumetric determination of the stomach contents would be invalid, and only the number of each kind of organism was recorded.

The results of examination of the stomachs of trout from the two areas is presented graphically in Figure 3. It was readily apparent that brown trout fed on Asellus, and that this animal was possibly a preferred food item. From 33.7 to 87.5 percent of the organisms contained in the stomachs of trout from Area Two were Asellus. For Area One these percentages were 0.8 to 44.7.

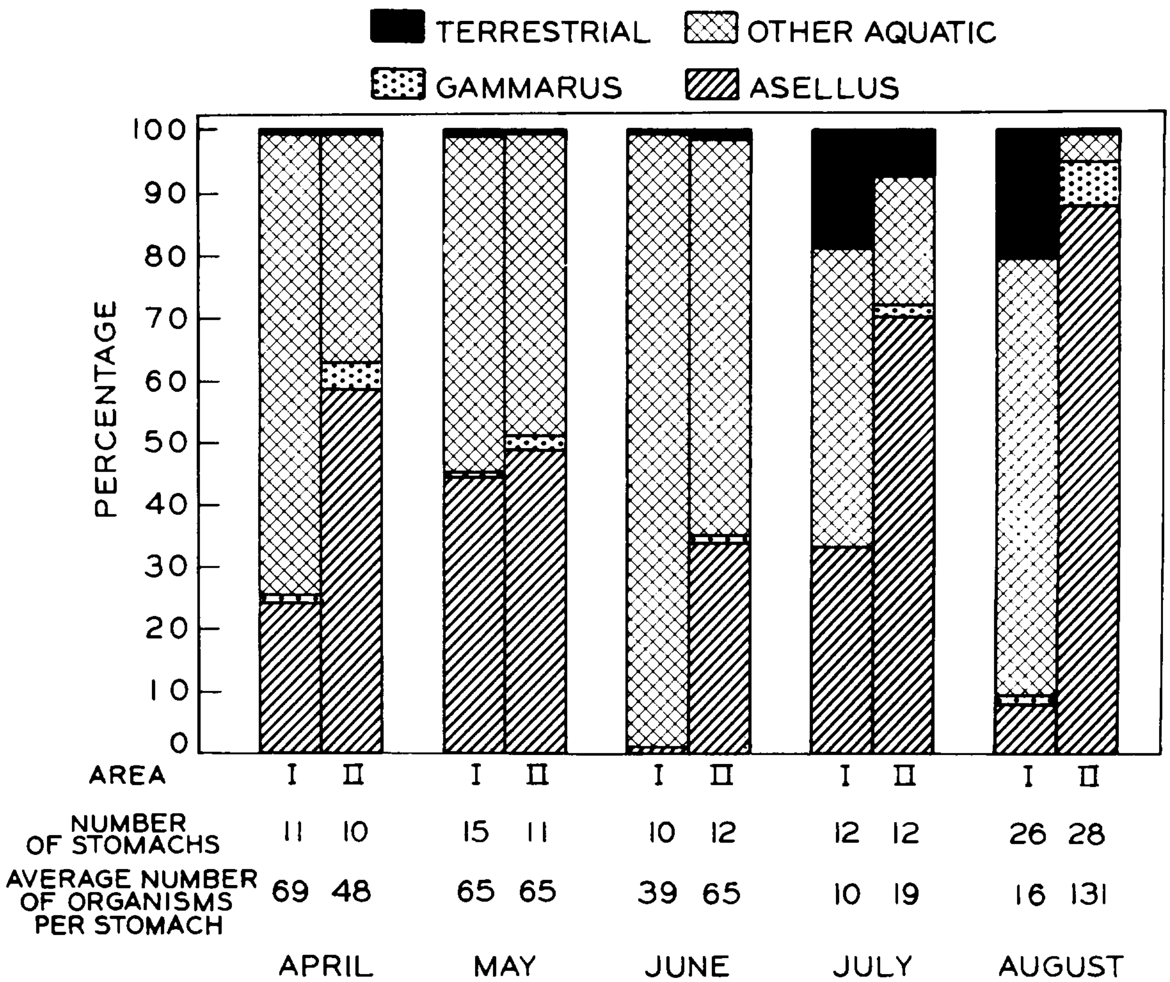
The numerical percentage of Asellus in the trout stomachs (Figure 3) may be misleading. If Asellus in stomachs were assumed to have volumes identical with those in bottom samples, their volumetric percentage would exceed their numerical percentage. This concept was tested and verified for the stomach samples collected in April. The importance of Asellus, by volume, would be even more apparent later in the season when mature insects had emerged and their young began to enter the trout's diet.

The average number of food organisms per stomach (Area One, Figure 3) shows a marked seasonal decline. This occurred at the time, July and August, when the fish in this area were directing more effort to surface feeding on terrestrial organisms and seems to indicate that the supply of food of aquatic origin was low. Parallel collections from Area Two however, do not show this marked shift to food of terrestrial origin nor was there a continued reduction in the numbers of food organisms per stomach. This difference in the pattern of feeding seems to indicate that some difference existed in the food supply of the two areas.

Discussion

Seasonal variation in the volume of bottom fauna has been described frequently. Ball and Hayne (1952) and Eggleton (1931) reported such variations in lakes. Seasonal variation in the volume of stream bottom fauna has also received some attention.

Figure 3. Numerical abundance (percentage), and number of organisms per stomach--brown trout, Houghton Creek, Ogemaw County.



TERRESTRIAL
OTHER AQUATIC
GAMMARUS
ASELLUS
PERCENTAGE
0
10
20
30
40
50
60
70
80
90
100
AREA
I II I II I II I II I II
NUMBER OF STOMACHS
11 10 15 11 10 12 12 12 26 28
AVERAGE NUMBER OF ORGANISMS PER STOMACH
69 48 65 65 39 65 10 19 16 131
APRIL
MAY
JUNE
JULY
AUGUST

Surber (1937) presented data on an eastern trout stream which showed a late spring maximum in volume of bottom fauna followed by a decline during the summer and a rise during the fall and winter. Needham (1938) reported that two maxima in volume of bottom fauna occurred, one in the spring and another in early winter. Allen (1951) described two maxima from the Horokiwi in New Zealand, one in the spring and the other in early winter. Other investigators have not observed this periodicity in volume of bottom fauna. The work of Pennak and Van Gerpen (1947), though based on limited sampling in a Colorado trout stream, indicated that no seasonal periodicity in volume of bottom fauna occurred. Surber (1951) gave data which indicated no seasonal trend in volume of bottom fauna in a Virginia trout stream.

In his study of the ecology of streams in Yellowstone National Park, Muttkowski (1925) showed the annual food cycle of mountain trout to be divided into two sharply defined periods. First, the "water food" period of October to July and second, the "surface food" period of summer. He observed that during the short period of summer, trout become dependant upon food of terrestrial origin following the depletion of the primary food supply through emergence of the insects.

Our data demonstrated a definite seasonal trend in the volume of bottom fauna in gravely riffles. Bottom fauna was at peak abundance during the winter months and declined gradually until sometime in April. During April and May a sharp reduction in the volume of animals occurred which lasted until early fall when the volume of bottom fauna increased rapidly to a winter high (Figure 2).

This investigation revealed that the aquatic sowbug, Asellus intermedius Forbes, was an important item of difference between the bottom faunas of the two areas. For example, during the August-April period, the volume of Asellus in samples from Area Two varied from nearly one-half, to more than the total volume, of all organisms in the samples from Area One. From Figure 3 it can be seen that many Asellus were eaten by brown trout, particularly in Area Two. From Figure 4 and from a comparison between Table 3 and Figure 3, it may be seen that the abundance of Asellus in stomachs was disproportionate to its abundance in bottom samples. This phenomenon is especially evident for Area One.

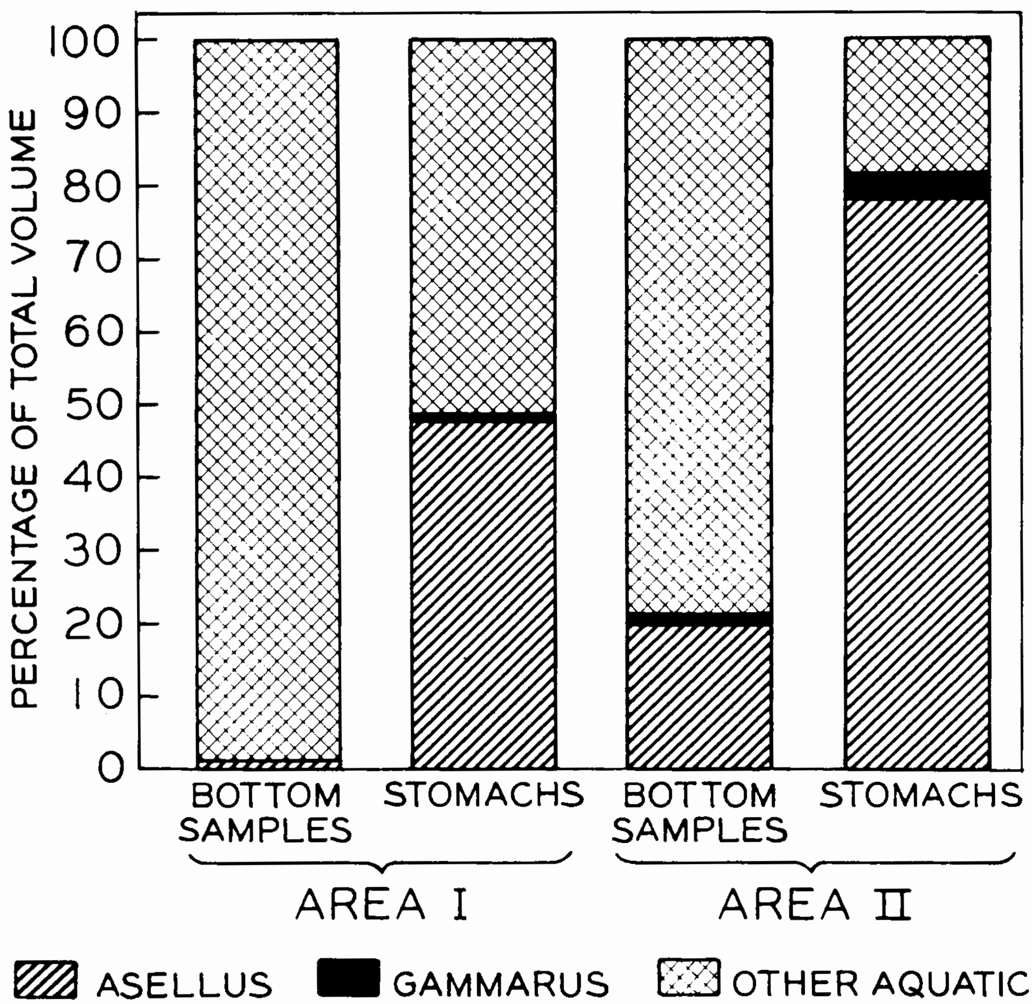
Information obtained indicated that either: (1) Asellus are readily available to brown trout, (2) are preferred by brown trout, (3) sampling methods did not give a reliable index of their relative abundance, or (4) a combination of these factors.

Frost (1939) noted that in the River Rye, where an abundance of Asellus aquaticus occurred, brown trout fed to a great extent on this animal; but in the River Liffey where Asellus was common, but not abundant, it was of little importance as a trout food. Frost concluded that in the River Liffey trout preferred the larval forms of aquatic insects to the crustaceans, Asellus and Gammarus. Results at Houghton Creek seemed to indicate that brown trout preferred Asellus and Gammarus over the aquatic insects (Figure 3).

During July and August, and probably most of June, Area One was characterized by a paucity of food. At this time of year abundance of bottom fauna was at its minimum, trout in Area One fed extensively on terrestrial foods, and the number of organisms per stomach was sharply reduced (Figure 3). Fewer organisms per stomach during late summer has been observed repeatedly. Neil (1938) and Frost (1939) have reported it for brown trout, Benson (1953) for brook trout, and Allen (1940) for salmon smolt.

None of these investigators attempted to correlate abundance of bottom food with numbers (or volume) of organisms per stomach. Surber (1936) found

Figure 4. Percentage composition (by volume) of various groups in bottom samples and brown trout stomachs for April, 1954. Terrestrial animals (less than 1 percent) omitted. Houghton Creek, Ogemaw County.



PERCENTAGE OF TOTAL VOLUME
100
90
80
70
60
50
40
30
20
10
0
BOTTOM SAMPLES
STOMACHS
BOTTOM SAMPLES
STOMACHS
AREA I
AREA II
ASELLUS
GAMMARUS
OTHER AQUATIC

that rainbow trout, from a stream with no shortage of aquatic food, switched to terrestrial foods in midsummer.

Our belief is that in Area One of Houghton Creek the change to a diet consisting of a considerable proportion of terrestrial organisms, the reduction in the quantity of food per stomach, and the sharp drop in condition were all due to the same thing--a paucity of food of aquatic origin. The belief is substantiated when the data from the two areas are compared in regard to the volume of bottom fauna available, amount of food in the stomach samples, the use of terrestrial animals as food, and the changes in the coefficient of condition of trout. More bottom food was available in Area Two at all times, stomach samples from this area contained more food during the summer months and did not show the sharp increase in numbers of terrestrial organisms observed in Area One, and the coefficient of condition of the fish of Area Two was significantly higher and much less variable than in Area One.

The contrast between the growth of the two groups of fish, as expressed by coefficient of condition, does not support Brown's (1946a) hypothesis of an intrinsic physiological growth cycle during that part of the year when temperatures are suitable for growth. These findings indicate that growth at this season is regulated by the quantity and kinds of food available. An important difference in the food supply of these two areas was the comparative stability of a crustanean food source as contrasted to the marked seasonal fluctuation in abundance of insect food. The importance of the type of animal food present is further emphasized by the evidence that brown trout ate crustacean food even when it may have been less abundant than aquatic insects.

References

Allee, W. C. 1912. An experimental analysis of the relation between physiological states and rheotaxis in isopods. Jour. Exp. Zool., 13: 270-344.

Allen, K. R. 1940. Studies on the biology of the early stages of salmon (Salmo salar). Jour. Anim. Ecol., 9 (No. 1): 1-23.

_____. 1951. The Horokiwi Stream. New Zealand Dept. Fish., Fish. Bull., No. 10: 1-231.

Ball, R. C. and D. W. Hayne. 1952. Effects of the removal of the fish population on the fish food organisms of a lake. Ecology 33: 41-48.

Benson, N. G. 1954. Seasonal fluctuations in the feeding of brook trout in the Pigeon River, Michigan. Trans. Am. Fish. Soc., 83 (1953): 76-83.

Brown, M. E. 1946a. The growth of brown trout (Salmo trutta Linn.), II. The growth of two-year-old trout at a constant temperature of 11.5 degrees C. Jour. Exp. Biol., 22: 130-144.

_____. 1946b. The growth of brown trout (Salmo trutta Linn.), III. The effect of temperature on the growth of two-year-old trout. Ibid: 145-155.

Cooper, E. L. 1953. Periodicity of growth and change of condition of brook trout (Salvelinus fontinalis) in three Michigan trout streams. Copeia, 1953 (2): 107-114.

Cooper, E. L., and N. G. Benson. 1951. The coefficient of condition of brook, brown, and rainbow trout in the Pigeon River, Otsego County, Michigan. Prog. Fish-Cult., 13: 181-192.

Eggleton, F. E. 1931. A limnological study of the profundal bottom fauna of certain fresh-water lakes. Ecol. Monogr., 1: 231-332.

Frost, W. E. 1939. River Liffey Survey II. The food consumed by the brown trout (Salmo trutta Linn.) in acid and alkaline waters. Proc. Roy. Irish Acad., 45 (Sec. B, No. 7): 139-206.

Muttkowski, R. A. 1925. The food of trout in Yellowstone National Park. Roosevelt Wildlife Bull., Vol. 2, No. 4: 470-497.

Needham, P. R. 1938. Trout Streams. Comstock Pub. Co., Inc., Ithaca, New York. 233 pp.

Neill, R. M. 1938. The food and feeding of brown trout (Salmo trutta L.) in relation to the organic environment. Trans. Roy. Soc. Edinburgh, 59 (Part II, No. 18): 481-520.

Pennak, R. W. and E. D. Van Gerpen. 1947. Bottom fauna production and physical nature of the substrate in a northern Colorado trout stream. Ecology 28: 42-48.

Surber, E. W. 1937. Rainbow trout and bottom fauna production in one mile of stream. Trans. Am. Fish. Soc., 66 (1936): 193-202.

_____. 1951. Bottom fauna and temperature conditions in relation to trout management in St. Mary's River, Augusta County, Virginia. Va., Jour. Sci., 2 (No. 3): 190-202.

Went, A. E. J. and W. E. Frost. 1942. River Liffey Survey V. Growth of brown trout (Salmo trutta L.) in alkaline and acid waters. Proc. Roy. Irish Acad., 68 (Sec. B, No. 7): 67-84.

INSTITUTE FOR FISHERIES RESEARCH
Robert J. Ellis and Howard Gowing

Approved by: G. P. Cooper

Typed by: Anne E. Kruse

Acknowledgments

Appreciation is extended to Dr. David C. Chandler, Department of Zoology, University of Michigan, and to Dr. Frank F. Hooper, Institute for Fisheries Research, who read the paper critically. Mr. Walter R. Crowe gave freely of his time in editing the paper and many other members of the staff of the Institute for Fisheries Research aided in sampling the trout populations.