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THE COMPARATIVE RATES OF DIGESTION OF CERTAIN
FISH FOOD ORGANISMS BY BROOK TROUT

by

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Many attempts have been made to establish the comparative importance of the various organisms in the natural diet of fishes. Two methods commonly used have been to compare either the numbers or volumes of the kinds of organisms found in stomach samples. In employing either of these methods one encounters the problem that all organisms are not digested at the same rate; it is not logical to assume that a heavily chitinized organism such as a beetle would be digested as rapidly as a soft-bodied animal like a mayfly nymph. Furthermore, Hess and Rainwater (1939) demonstrated differences in the rates of movement of different kinds of food organisms through the stomachs of brook trout.

The purpose of the present work was to devise a method for measuring and expressing differences in the rates of digestion of various food organisms by brook trout. If these differences could be established and compared quantitatively, it would be possible to make more positive statements as to the food habits of fishes. Hess and Rainwater (1939) proposed to solve this problem by establishing the length of time it takes for different organisms to pass out of the stomach of the fish.

In the present study, individual fish were fed many of at least two kinds of organisms and measurements were made of the changes in the volume

of each kind caused by digestion. These data were used to compute the proportion of the original volume lost by each kind of organism and, by comparison of these proportions, comparative rates of digestion were calculated.

The work was conducted during the summer of 1950 at the Hunt Creek Fisheries Station of the Institute for Fisheries Research, Michigan Department of Conservation. Guidance and assistance were received from Dr. J. W. Leonard and Dr. D. S. Shetter of the Institute for Fisheries Research.

Materials and Methods

The fish used were brook trout, Salvelinus fontinalis, of hatchery stock ranging in total length from about 12.5 cm. to 17.5 cm. The food organisms used were midge larvae (over 0.6 mm. in length) of the tribe Tendipedinae, nymphs of the mayfly Ephemerella and the stonefly Isoperla, adults of the beetle Halipus, larvae and pupae of the case-building caddisfly Brachycentrus, and larvae of the non-case-building caddisfly Hydropsyche. These organisms were collected from trout streams near the Hunt Creek Station. Although some of the organisms were held for several days they were active and appeared to be in good condition at the time of feeding.

The volumes of the food organisms were determined by water displacement in a 15-ml. centrifuge tube. Before measurement, the organisms were placed on damp absorbent tissue paper to remove surface moisture. It had been noted that dry paper was discolored with body juices from the organisms

being measured after removal from the digestive tract. The use of damp paper greatly reduced this loss.

The food organisms were fed to the fish by means of a syringe consisting of a glass tube $1/4$ inch in diameter and 4 inches long, and a close-fitting plunger about $1/2$ inch longer. The food organisms were placed in the forward end of the tube and the plunger introduced into the opposite end. The fish was held in one hand, and the syringe containing the food organisms was operated with the other. The syringe was inserted into the mouth of the fish and down its throat until the open end of the tube was in the stomach. The plunger was then pushed gently until it extended past the open end of the tube. The syringe was then slowly withdrawn, care being taken to remove any organisms that might have adhered to the tube.

It was necessary to limit the volume of organisms placed in the tube at each "feeding" because too large a volume made it difficult to push the organisms out of the tube without crushing them. Crushing of the food organisms was believed to be undesirable as the fish's digestive fluids then had unnatural access to the soft parts of the organism.

The fish were held in a white enameled pan during feeding and then placed in a pail for transfer to the holding trough. The fish were lifted from the pan to the pail and from the pail to the trough by hand. The pan and pail were then examined for any regurgitated organisms.

During the test periods the first fish was held in a trough in the basement of the laboratory, the second in a live box in the stream, and succeeding fish were placed in a trough of running water set up in Hunt Creek. Only in the trough in the stream was it possible to search

for defecated or regurgitated organisms and this trough was examined carefully for such items. Water temperatures were determined with a maximum-minimum thermometer.

At the termination of the experimental period each fish was placed in a white enameled pan, and the entire digestive tract excised and its contents removed.

A summary of the data for the seven experimental feedings is presented in Table 1. In many instances the number of organisms fed was greater than the number recovered from the digestive tract. These differences resulted from miscounting of recovered organisms due to fragmentation or in some instances from the fact that organisms had actually left the digestive tract. Both living and dead organisms, especially midge larvae, were occasionally recovered from the holding trough.

Some organisms remained alive for periods of 3 to 17 hours in the digestive tracts of trout. Survival of food organisms was greatest in the heavily chitinized Haliphus (39 percent), rather high for the Brachycentrus in their protective cases (50 percent), and less (but still a remarkable 3.5 percent) for the seemingly unprotected Tendipedinae larvae. Both living and well-digested organisms were often found together throughout the entire digestive tract. (None of the Ephemerella, Isoperla or Hydropsyche were alive when removed from the digestive tract.)

It is recognized that this survival of food organisms occurred at rather low temperatures (49°-59° F.) and that force-feeding may have disturbed the normal digestive processes. However, this would not seem to invalidate comparisons of the rates of digestion of the organisms fed to the same fish.

Table 1.--Numbers and volumes of organisms fed to and recovered from seven brook trout, Hunt Creek Station, 1950

Fish no.	Time (hours)	Temperature (°F.)	Food organisms																							
			Tendipedinae				Ephemerella				Isoperla				Hydropsyche				Brachycentrus				Halipius [✓]			
			Fed		Recovered		Fed		Recovered		Fed		Recovered		Fed		Recovered		Fed		Recovered		Fed		Recovered	
No.	Vol. (ml.)	No.	Vol. (ml.)	No.	Vol. (ml.)	No.	Vol. (ml.)	No.	Vol. (ml.)	No.	Vol. (ml.)	No.	Vol. (ml.)	No.	Vol. (ml.)	No.	Vol. (ml.)	No.	Vol. (ml.)	No.	Vol. (ml.)	No.	Vol. (ml.)			
1	8	49-52	45	0.10	44	0.08	10	0.10	10	0.05	6	0.10	6	0.06	
2	8	50-51	20	0.20	18	0.15	6	0.10	6	0.05	9	...	9	
3	8	56-59	45	0.42	[✓] 0.12	17	0.20	[✓] 0.08	14	0.20	14	0.20	10	...	9	
4	16	46-50	115	0.40	69	0.30	30	0.30	29	0.19	7	0.10	7	0.05	10	0.20	10	0.18	10	...	9	
5	16	52-57	50	0.20	41	0.05	13	0.43	13	0.40	11	...	10	
6	16	52-59	50	0.40	27	0.10	30	0.30	29	0.20	
7	17	52-59	19	0.10	17	0.08	18	0.30	16	0.16	[✓] 14	...	14	

[✓] No digestion occurred.

[✓] Too fragmented to count.

³ 11 larvae, 3 pupae all in cases, no digestion occurred.

Comparative Rates of Digestion

The rates of digestion of the food organisms tested were calculated by comparing the proportionate losses of volume during digestion. Comparisons were made only between organisms fed to the same fish and therefore in the same physical and chemical environment.

By expressing the rates of digestion of all organisms in terms of a standard organism fed in each trial, it would be possible to compare the speed of digestion of different organisms without their having been fed to the same fish. In Table 2 the rate of digestion of each group has been compared to that of the Tendipedinae fed to each group.

The derivation of these figures for the Ephemerella : Tendipedinae column for fish Number 1 will illustrate the use of the formulae in footnote 1 of Table 2, and will help explain the significance of these comparisons of the rates of digestion. Using the values from Table 1, the proportionate loss of volume of all the Tendipedinae larvae fed to fish Number 1 was calculated thus:

$$\frac{0.10 \text{ ml. (original volume)} - 0.08 \text{ ml. (recovered volume)}}{0.10 \text{ ml. (original volume)}} = 0.20.$$

The same value for the Ephemerella nymphs was:

$$\frac{0.10 \text{ ml.} - 0.05 \text{ ml.}}{0.10 \text{ ml.}} = 0.50.$$

The rate of digestion or rate of loss of volume of all the Ephemerella nymphs as compared to all the Tendipedinae larvae, "Total" column, was

$$\frac{0.50}{0.02} = 2.5.$$

This means that the Ephemerella lost volume during digestion 2.5 times as fast as the Tendipedinae.

The sub-column headed "Total" is based on the loss of volume of the entire group and therefore includes the loss due to some animals having left

Table 2.--Comparison of the rates of digestion of three genera of immature aquatic insects with the rate of digestion of Tendipedinae larvae²

Fish no.	<u>Ephemerella : Tendipedinae</u>		<u>Isoperla : Tendipedinae</u>		<u>Hydropsyche : Tendipedinae</u>	
	Total	Individual	Total	Individual	Total	Individual
1	2.5	2.8	2.0	2.2
4	1.5	-1.4 ²	2.0	-2.0	0.4	-0.4
5	0.1	0.1
6	0.4	0.6
7	2.4	3.6

↓ Formulae for computing:

$$\frac{\text{Original volume} - \text{recovered volume}}{\text{Original volume}} = \text{Proportionate loss of volume}$$

$$\frac{\text{Proportionate loss of volume for organism A}}{\text{Proportionate loss of volume for organism B}} = \text{Rate of digestion of organism A in terms of organism B.}$$

² Negative due to increase in average volume per individual Tendipedinae.

the digestive tract. The other sub-column, headed "Individual" differs from the total column in that it is based on the average volume per individual fed and recovered from the digestive tract. The former would seem to be the more useful value for it takes into account both the movement of organisms out of the digestive tract and the loss of volume per individual.

An example will illustrate the use that might be made of these factors for rate of digestion. Assume that stomach samples yield volumes of Ephemerella nymphs, Isoperla nymphs and Tendipedinae larvae in ratios 1:1:1. Using the digestion factors for the entire group for fish Number 1 in Table 2, the actual ratios of volumes consumed would be 2.5:2:1.

Conclusions

A number of trials sufficient for statistical evaluation is necessary for any positive statement as to the practicability of this suggested method for determining rate of digestion factors. The very limited number of trials in the present work do however indicate certain conclusions.

1. With suitable care force feeding of insects to trout with a syringe is feasible.
2. Some aquatic organisms survived for extended periods in a trout's alimentary tract at water temperatures of 49°-59° F.
3. Some organisms passed through the entire alimentary tract without being digested.
4. Differences were found in the rate of digestion of natural trout food organisms.
5. Evaluation of the numbers of food organisms in trout stomach samples should take into consideration the different rates of digestion.

Literature Cited

Hess, A. D. and J. H. Rainwater

1939. A method for measuring the food preference of trout. *Copeia*,
1939, No. 3, pp. 154-157.