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FEEDING HABITS OF THE MONTANA GRAYLING (Thymallus montanus Milner)
IN FORD LAKE, MICHIGAN*

Justin W. Leonard

Fisheries investigators have long been asking themselves what factors have been responsible for the disappearance of the Michigan grayling (Thymallus tricolor Cope), and for the current marked annual diminution of the once abundant Montana grayling (Thymallus montanus Miln.) in its native waters; the grayling in each instance seeming to fail under the effects of increasing human activity, and of propagation of trout, which may be detrimental to grayling through competition, active predation, or both. This condition is all the more puzzling when one considers the fact that the closely related European grayling has not only survived the activities of human agencies and existence of various salmonid fishes in the same waters, but persists in such numbers as to be considered a "weed fish" by many anglers, and in consequence subjected to stern control measures.

On May 18, and from October 18-20, 1937, Drs. A. S. Hazzard and R. W. Fschmeyer collected small samples of the Montana grayling population which was introduced into Ford Lake, Pigeon River State Forest (T. 32 N., R. 1 W., Sec. 8, Otsego County, Michigan) during the fall of 1936. Owing to the keen interest with which fisheries biologists

* Contribution from the Institute for Fisheries Research, Michigan Department of Conservation and University of Michigan.

have been following the fate of Montana grayling stockings of Michigan waters, the fishes collected in the above sampling series have been considered deserving of special study. The present report is concerned with an analysis of the feeding habits. It is to be hoped that this and additional studies to be carried out during the progress of the Ford Lake experiment may yield facts with which to answer some of the perplexing questions and speculations brought on by the failure and probably extinction of the native Michigan grayling.

Early accounts of the Michigan grayling include only sketchy observations on its feeding habits, but comments on its numbers seem almost incredible to present-day readers. Thaddeus Norris (1833), writing of a boat trip down the Au Sable River made in 1874, mentions that: "On our second day we killed and salted down--heads and tails off--a hundred and twenty pounds of fish [grayling] , besides eating all we wanted." Again, on the same trip: "I took at five casts fifteen fish [grayling] , averaging three-quarters of a pound each." Of the feeding habits, he simply states that: "The various orders of flies which lay their eggs in running waters, and the larvae of such flies, appear to be their only food." Parker (1889), while discussing a vain attempt to take grayling spawn, states that stomachs of several grayling taken by angling contained a large amount of vegetable material, particularly oat grains, a quantity of which had been spilled in the stream. He suggests, rather hesitantly, that vegetation might be a normal complement to the diet, adducing the supposed thyme-like odor and flavor of the graylings in support of this. Milner (1874) mentions that stomachs of grayling taken by him from the Au Sable contained Coleoptera, Neuroptera, and nymphs of various species of Odonata. Also present were leaves of the white cedar, which he believed were taken by mistake and not selected as food.

In a paper dealing with artificial propagation of the Montana grayling, Henshall (1907) writes very briefly that the food consists of insects and their larvae.

According to Heckel and Kner (1858), the European grayling (Thymallus thymallus) feeds upon worms, snails, insect larvae, spawn, young fish fry, and various small minnows. Dealing with the same species, von Siebold (1863) mentions further that such seasonally available insects as beetles, bugs, leaf-hoppers, grasshoppers, wasps and ants are taken.

Svetovidov (1931), in an account of the habits of the grayling of Lake Baikal, states that the diet of the black grayling is formed of amphipods, caddisflies, and adult winged insects, while the white grayling feeds chiefly upon fish and amphipods.

Since a description of Ford Lake has been given by Eschmeyer (1937), it will be sufficient at this time to mention a few of its more salient characteristics. The lake is situated in the midst of rolling, sandy country grown with jack pine and aspen, and receives a relatively small amount of surface drainage. In a survey made by Mr. J. B. Schwerdt, Project Superintendent of Camp Vanderbilt, U. S. Parks Service, during the summer of 1936, the surface area was determined as 10.66 acres. In a survey conducted by the Institute for Fisheries Research, the bottom in the deeper portions of the lake was found to be composed uniformly of pulpy peat. The rather extensive shoal areas, averaging 175 feet in width, were composed of sand on the north, east and south sides, separated from the peat by a belt of marl of approximately equal width. The maximum depth was 10 meters; slope 20-30 degrees; Secchi disc reading 5.5 meters; pH at all levels 8.2. At the time of survey (August 1, 1932) a thermocline was formed between the five and six meter levels. There were 9.4 p.p.m. of dissolved oxygen at the surface, 8.6 p.p.m. at the bottom.

There are appended tables recording the results of stomach analyses. These give some indication of the feeding habits of the fish over a 24-hour period. They also reveal some rather unusual organism dominances. It will not be possible to state to what extent the diet is determined by selection or by necessity until further information has been gathered on the numbers and availability of food organisms actually present in the lake. An attempt will be made at a future date to determine the condition factor for the grayling, in hope of shedding additional light on the adequacy of their available food supply. The tabulations of food organisms, listed by taxonomic order, are briefly discussed as follows:

Collections: (1) May 18, 1937 (Table 1). This sample was taken by a single haul of a 100-foot bag seine through water from two to eight feet in depth, over a sparsely-weeded section of shoal at the east end of the lake. Fifty specimens were examined, ranging from 67-111 mm. in standard length, average 89 mm., or approximately 3 1/4 - 5 inches total length.

It will be seen that well over one-half of the diet was composed of aquatic Diptera. Complete tabulation of all the components of this order is not feasible; but it may be stated that 48 fish contained no other Diptera than larvae and pupae of midges (Chironomidae and Ceratopogonidae), while two contained larvae of the culicid phantom midge Chaoborus (Corethra) punctipennis. Of greater interest is the unusually large showing made by two other orders, Odonata and Coleoptera. The former is represented by many nymphs of the zygopterous species Enallagma carunculatum and E. Hageni, and by four nymphs of the anisopterous genus Tetragoneuria. The Coleoptera are represented by a

few terrestrial dung-beetles of the family Scarabaeidae, chiefly of the genus Aphodius. By far the more numerous, however, are minute adult dytiscid water beetles of the genus Bidessus. These insects seldom exceed 2 mm. in length, but were present in numbers sufficient to account for most of the 8.5% of total volume made up by aquatic Coleoptera. All the mayflies taken are nymphs of the family Baetidae. All the Amphipoda, or scuds, have been determined as Hyaella knickerbockeri. In passing, it is deserving of notice that among the aquatic Hemiptera taken are backswimmers of the relatively rare species Plea striola, one water bug, Belostoma sp., and one water strider. Past work has shown that representatives of these three groups are seldom eaten by fish, possibly because of their musky odor and the fact that some are capable of inflicting painful stings.

(2) October 18, 1937, evening (Table 2). Sample, collected by seining in shoal water at the east end of the lake, consists of 11 specimens ranging in standard length from 148-176 mm., average 165 mm., approximately 6 3/4 - 8 inches total length.

Of particular interest in this sample are: (a) the large number of Odonata nymphs (belonging, as in each instance following, to the same species of Enallagma recorded for Collection 1), these occurring in sufficient quantity to compose almost one-half of the total amount of food taken; (b) the appreciable amount (16%) of terrestrial insects, indicating readiness of grayling of this size to feed on surface food when it is available; and (c) the appearance of plankton, in the form of Cladocera, or water fleas. The large volume of Enallagma nymphs is the more striking in view of the fact that at this time of year all such nymphs are in early instars, each nymph having but a small fraction of the bulk attained by late spring. One stomach contained 85 nymphs. Powerfully stinging backswimmers, Notonecta insulata,

appear in surprising quantities.

(3) October 19, 1937, morning (Table 2). The sample, collected by seining in shoal water at the east end of the lake, consists of 8 specimens ranging in standard length from 147-179 mm., average 163 mm., approximately $6 \frac{7}{8}$ - $8 \frac{1}{2}$ inches total length.

In this series scuds proved to be the most important food item. It may be pointed out that since it is probable that the stomachs in this sample were filled with organisms taken during night feeding, the scanty amount of terrestrial organisms found is what would be expected. This is one of two collections in which two caddis larvae appear. Here again examples of Notonecta insulata occur in an abundance which accounts for most of the volume ascribed to aquatic Hemiptera in the table. Larvae of the phantom midge, Chaoborus (Corethra) punctipennis occur in significant numbers for the first time, being responsible for all the measurable volume of aquatic Diptera, although larvae and pupae of the Chironomidae are present in small numbers. One stomach contained a statoblast of the polyzoon Cristatella mucedo.

(4) October 19, 1937, 10:15 a.m. to 7:00 p.m. (Table 2). Sample, collected by means of a gill-net set, consists of 7 individuals ranging in standard length from 151-183 mm., average 163 mm., approximately $7 \frac{1}{8}$ - $8 \frac{1}{2}$ inches total length.

This collection is of interest for the large amount of plankton and the very small amount of midge larvae and pupae taken. The aquatic Hemiptera is again an important group due to the number of backswimmers consumed. The very low volume of terrestrial organisms encountered indicates that little surface feeding had been carried on immediately prior to capture.

(5) October 19, 7:30 p.m. to October 20, 1:00 p.m., 1937

(Table 2). This sample, also collected by means of a gill-net set, consists of 6 specimens ranging in standard length from 148-165 mm., average 159 mm., approximately 7 - 7 5/8 inches total length.

As in Collection 2, Enallagma nymphs exceed all other groups in total volume. Aside from the fact that Odonata and Cladocera occupy transposed ranks, this collection conforms rather closely with the pattern recorded for the other gill-net haul, Collection 4. In the present instance, only one phantom midge larva (Chaoborus) was encountered, the low total percentage of aquatic Diptera being made up by a small number of larvae and pupae of two subfamilies of true midges, Chironominae and Tanypodinae.

Table 1 shows results obtained by combining findings for the four October collections. Calculated on this basis, it will be seen that scuds and odonate nymphs share the position of first importance, with a difference of only 0.7%. A few points worthy of attention are the low percentage of total diet composed of midge larvae and pupae when considered from the standpoint of all the October samples; the relatively high percentage of aquatic Hemiptera; and the very small amount of mayfly nymphs utilized. Three groups of organisms were taken in quantities too small to affect the percentages. These are Copepoda, members of the plankton; Hydracarina, free swimming water mites; and Corrodantia, represented by the Psocidae, a family of terrestrial insects allied to the book lice.

General Considerations: Because no previous work dealing with the natural feeding habits of lake-inhabiting Montana grayling has been

published, it is impossible to state whether or not the Ford Lake specimens were subsisting on a normal diet. Thus, the rather surprising low percentage of midge larvae and pupae taken in the October collections (this group having far outstripped all others in the May sample) may be due to seasonal decrease in the midge population, or to a change in diet preference connected with size increase on the part of the fish.

The most surprising finding is the very large quantity of predacious forms consumed.* Nymphs of the Odonata are predatory in habits from birth to maturity. The nymphs of Enallagma, which made up the bulk of the Odonata taken in both the May and October samples, feed upon animal plankton when young, but soon change to a diet composed chiefly of smaller insect larvae. The aquatic Hemiptera are represented almost exclusively by Notonecta insulata, one of the largest backswimmers in the state, known for its voracity which extends to small fish as well as to a variety of aquatic insects and small crustaceans. The aquatic Coleoptera are best represented by the Dytiscidae, a group whose feeding habits are predacious in both larval and adult stages.

* Since the above study was completed, a single winter-caught specimen from Ford Lake has been examined, and found to agree with the others in containing a large amount of predacious insect larvae. The specimen, having a standard length of 196 mm., a total length of 8 7/8 inches, and a weight of 100 gms., was collected through the ice on February 27, 1938, by Dr. A. S. Hazzard, using hook and line with a stonefly nymph for bait. The stomach was found to contain 10 scuds (Amphipoda), remains of 6 dragonfly nymphs (Anax junious), and a single chironomid midge larva. The dragonfly nymphs accounted for 98.6%, the scuds 1.4%, and the midge larva a trace, of the total volume.

Further study of food consumed and of food organisms present in the lake are demanded to demonstrate whether such a diet is determined by necessity or preference. The need for such studies is further emphasized by comparing the tabulations for May and the combined October data in Table 1. While Odonata nymphs hold second place in the percentage columns in both instances, wide discrepancies appear in the positions of various other groups, especially the aquatic Diptera and the scuds. No sure explanation can now be offered for the absence, in the May sample, of plankton which is well represented (by the Cladocera) in the October collections. Examinations of seasonal plankton abundance, as well as that of larger food organisms, should be made to afford added information on the important question of selection versus availability in determining feeding habits.

UNIVERSITY OF MICHIGAN

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TABLE 1

AMOUNTS AND DISTRIBUTION OF FOOD ORGANISMS FOR MAY AND COMBINED OCTOBER COLLECTIONS

Organism	May 18, 1937				October 18-20, 1937			
	Per cent of stomachs containing organism	Average number per stomach	Total volume in cubic centimeters	Per cent by volume	Per cent of stomachs containing organism	Average number per stomach	Total volume in cubic centimeters	Per cent by volume
Cladocera (Water fleas)	87.5	...	2.865	15.8
Copepoda (Copepods)	15.6	...	trace	...
Amphipoda (Scuds)	16.0	0.24	0.025	0.4	90.6	67.8	4.730	26.0
Ephemeroptera (Mayfly nymphs)	14.0	0.16	0.130	1.9	6.2	0.003	0.025	0.1
Odonata (Dragonfly nymphs)	30.0	1.68	1.300	19.6	43.7	10.4	4.610	25.3
Aquatic Hemiptera (Water bugs)	28.0	0.34	0.090	1.4	60.6	1.4	2.000	11.0
Terrestrial Hemiptera (Land bugs)	6.2	0.1	0.075	0.4
Homoptera (Aphids)	53.1	19.8	1.003	5.5
Corrodentia (Psocids)	25.0	0.8	trace	...
Aquatic Coleoptera (Water beetles)	60.4	8.60	0.560	8.5	43.7	0.8	0.600	3.3
Terrestrial Coleoptera (Land beetles)	10.0	0.10	0.050	0.8	50.0	1.3	0.375	2.0
Trichoptera (Caddis flies)	9.4	0.1	0.250	1.4
Aquatic Lepidoptera (Aquatic moths)	2.0	0.04	0.025	0.4
Hymenoptera (Ants & wasps)	12.0	0.12	0.115	1.6	5.0	1.1	0.100	0.5
Aquatic Diptera (Midge larvae & pupae)	96.0	44.40	4.340	65.4	93.7	28.4	1.540	8.5
Terrestrial Diptera (Land flies)	4.0	0.04	trace	...	28.1	0.4	0.045	0.2
Hydracarina (Water mites)	14.0	0.46	trace	...	15.6	0.4	trace	...
Terrestrial Araneae (Spiders)	6.2	0.1	trace	...

TABLE 2

	Cladocera (water fleas)	Copepoda (Copepods)	Amphipoda (Scuds)	Ephemeroptera (Mayfly nymphs)	Odonata (Dragonfly nymphs)	Aquatic Hemiptera (Water bugs)	Aquatic Coleoptera (Water beetles)	Trichoptera (Caddis larvae)	Aquatic Diptera (Midge larvae & pupae)	Hydracarina (Water mites)	Corrodentia (Psocids)	Terrestrial Hemiptera (Land bugs)	Homoptera (Aphids)	Terrestrial Coleoptera (Land beetles)	Terrestrial Diptera (Land flies)	Hymenoptera (Ants & wasps)	Araneae (Spiders)
Oct. 18, evening																	
Per cent of stomachs containing organism	90.9	45.5	90.9	9.1	45.5	54.5	27.2	18.2	100.0	18.2	45.5	9.1	72.7	63.6	45.5	72.7	0
Average number of organisms per stomach	10.2	0.1	21.6	1.6	0.3	0.2	55.4	0.6	2.3	0.1	48.6	2.1	0.8	1.2	0
Total volume in cubic centimeters	0.760	trace	0.180	0.025	2.850	0.525	0.050	trace	1.120	trace	trace	0.025	0.775	0.200	0.025	0.100	0
Per cent by volume	10.8	...	2.6	0.4	46.1	7.5	0.7	...	15.9	0.4	11.0	2.8	0.4	1.4	0
Oct. 19, morning																	
Per cent of stomachs containing organism	100.0	0	100.0	0	50.0	62.5	62.5	12.5	100.0	0	0	0	87.5	75.0	25.0	62.5	25.0
Average number of organisms per stomach	...	0	99.0	0	1.1	1.2	1.8	0.2	23.8	0	0	0	18.7	1.7	0.4	0.9	0.4
Total volume in cubic centimeters	0.225	0	2.248	0	0.240	0.825	0.400	0.250	0.345	0	0	0	0.197	0.125	0.020	trace	0.125
Per cent by volume	4.5	0	45.0	0	4.8	16.5	8.0	5.0	6.9	0	0	0	3.9	2.5	0.4	...	2.5
October 19, 10:15 a.m.-7:00 p.m.																	
Per cent of stomachs containing organism	71.4	0	85.7	0	28.5	71.4	71.4	0	85.7	14.2	0	0	28.5	28.5	14.2	42.8	0
Average number of organisms per stomach	...	0	154.8	0	1.6	1.4	1.0	0	9.6	0.1	0	0	3.3	0.6	0.1	0.4	0
Total volume in cubic centimeters	1.750	0	1.500	0	0.125	0.425	0.150	0	0.100	trace	0	0	0.025	0.050	trace	trace	0
Per cent by volume	42.4	0	36.4	0	3.0	10.3	3.6	0	2.4	...	0	0	0.60	1.2	0
Oct. 19, 7:30 a.m. - Oct. 20, 1:00 p.m.																	
Per cent of stomachs containing organism	83.3	0	83.3	0	66.6	66.6	16.6	0	83.3	83.3	0	0	0	16.6	16.6	0	0
Average number of organisms per stomach	...	0	53.8	0	12.7	1.0	0.2	0	5.3	1.0	0	0	0	0.3	0.2	0	0
Total volume in cubic centimeters	0.085	0	0.755	0	0.710	0.300	0.050	0	trace	trace	0	0	0	trace	trace	0	0
Per cent by volume	4.5	0	39.7	0	37.4	15.8	2.6	0	0	0	0	0	0