Diet of brook trout (Salvelinus fontinalis MITCHILL) and brown trout (Salmo trutta L.) in an alpine stream

J. DAVID ALLAN

With I figure and 3 tables in the text

Introduction

Several studies have compared the frequency of prey items in the diet of salmonids to the abundance of prey in a stream environment. A close correspondence has been reported between the diet of trout and the abundance of prey, especially of drifting invertebrates, for brown trout Salmo trutta and rainbow trout S. gairdneri (Elliott 1970, 1973). Other studies of rainbow trout (Jenkins et al. 1970) and juvenile coho salmon Onchorhynchus kisutch (Mundie 1969) showed a similar pattern, although some exceptions also were observed. The present study compares prey eaten by brown trout and brook trout Salvelinus fontinalis to the abundance of invertebrates in the stream drift over 24 hours, and to a sample of the benthos. The principle objectives were to determine (1) whether the two trout species fed primarily on the most abundant prey, or whether additional factors seemed to affect prey consumption; (2) whether the two species of trout fed on similar prey.

Description of stream

Cement Creek, Gunnison County, Colorado is a high elevation, stony bottom stream which originates in snow melt at 3600 m and joins the East River at 2602 m. At least 40 species of aquatic insects occur in the stream, although usually fewer than 25 taxa are observed at any one locality. Three species of salmonids, cutthroat trout Salmo clarki, S. trutta and Salvelinus fontinalis maintain breeding populations, and a fourth species Salmo gairdneri is stocked for fishermen. S. trutta is abundant at elevations below 2,900 m and Salvelinus fontinalis above 2,900 m, while Salmo clarki is common only above 3,200 m. The three salmonids which breed in Cement Creek are for the most part separated altitudinally, with rather narrow zones of overlap (Allan 1975).

The study site was located in a meadow at an elevation of 2,820 m; the main stream bank vegetation was Salix spp. This site was close to the upper limit of Salmo trutta and the lower limit of Salvelinus fontinalis, and was chosen for that reason.

Methods

Drift, benthos and trout samples were collected from Cement Creek on 5 and 6 August 1975. Drift samples were collected by a single net of 300 m μ mesh submerged for 3 hour intervals over 24 hours. The net was 0.1 m² in area and sampled 8.6% of total flow, which was 0.77 m³/second. All samples were sorted and analysed in their entirety. Benthos was sampled once at mid-day by making 12 Surber collections using a net of 300 m μ mesh and 0.093 m² sampling area. Trout were collected by electroshocking at roughly 3 hour intervals over 24 hours. At each sampling interval an attempt was made to collect 6 trout of each species, two each of small (<10 cm), medium (10—15 cm) or large (>15 cm) size. All trout were measured for length and weight, and stomachs were preserved for later analysis.

PRIVATE LIBRARY

OF WILLIAM L PETERS

Over the 24 hour collection interval, water temperature varied from 6 to 14 $^{\circ}C.$ Light levels were <1 lux from 20.15 to 05.45, and there was no moon.

Results

There did not appear to be much variation among the several drift samples collected during the day or those collected during the night (except that abundance were highest immediately after nightfall compared to subsequent night sam-

Table 1. Composition of invertebrates in the stream (drift and benthos) compared to that in trout stomachs, 5—6 August 1975. Numbers drifting per hour are for the entire stream.

	Drift				Trout s	(0/0)		
				_	Salveli		Salmo	
	Numbers/hour			Benthos fonti			$\frac{trutta}{}$	
	Day	Night	Drift	(0/0)	Day	Night	Day	Night
Baetis bicaudatus	730	12,206	45.7	35.4	10.5	20.6	21.1	33.5
Cinygmula sp.	152	2,558	9.6	25.0	7.9	16.3	7.8	20.7
Epeoris longimanus	70	1,651	6.1	9.2	0.1	1.0	1.8	1.3
Rhithrogena spp.	2	65	0.3	1.6	0	0	0.6	1.3
Ephemerella coloradensis	2	27	0.1	0.9	0.5	1.3	0.9	2.0
E. inermis	2	29	0.1	0.2	0.8	0.7	2.7	5.3
Paraleptophlebia vaciva	2	31	0.1	0.4	0.3	0.3	0	0
Ameletus velox	0	124	0.4	0	0.3	0.3	0.6	2.6
Total Ephemeroptera	961	16,695	62.5	73.0	20.4	40,5	36.1	66.7
Alloperla spp.	40	1,028	3.8	5.5	2.2	1.7	2.7	0.6
Zapada haysi	120	479	2.1	2.1	0.7	1.0	0	. 0
Kogotus modestus	5	17	0.1	0	0.3	0	0.3	0.6
Pteronarcella badia	14	27	0.1	0	0	0	0	0
Total Plecoptera	182	1,564	6.2	7.7	3.2	2.7	3.6	1.2
Brachycentrus sp.	28	39	0.2	0	3.4	4.0	4.2	0.6
Rhyacophila spp.	28	93	0.4	1.5	0	0	1.5	0.6
Total Trichoptera	58	140	0.6	1.5	3.4	4.0	6.6	1.2
Simulium spp.	923	4,437	18.9	7.7	25.4	22.8	11.4	14.1
Chironomidae	355	2,198	9.0	1.7	26.2	16.3	0.9	2.6
Total Diptera	1,278	6,635	27.9	9.4	51.6	39.1	12.3	16.7
Heterliminus sp.	41	33	0.3	4.6	0	0	0	0
Total Coleoptera	53	44	0.4	4.6	1.6	0	1.8	0
Acari	21	5	0.1	0	0	0	0.3	0
Oligochaeta	0	0	0	3.7	0	0	0	0
Total non-Insecta	192	124	1.1	3.8	0	0	2.1	0
Emerging aquatic insects	103	103	0.7	0	13.9	9.6	28.4	13.5
Total aquatic invertebrates	2,827	25,305	99.4	-	94.0	95.9	90.9	99.3
Terrestrial invertebrates	99	116	0.6		6.0	4.2	9.0	0.7
Total drift	2,926	25,421						
Numbers/m² in benthos				1137				
Number of trout inspected					18	14	20	12
Number of prey consumed					779	328	332	148
Number of prey/trout					43.3	23.4	16.6	12.3

ples), so all daytime samples were averaged, as were all nighttime samples, for both drift and the stomach contents of trout (Table 1). As is typical, drift during the night far exceeded drift during the day. The most frequent taxa were nymphs of Ephemeroptera and larvae of Diptera, which together comprised over 80 $^{\rm 0}/_{\rm 0}$ of the drift total. In the benthos, Ephemeroptera were by far the most abundant group. Dipterans were less common in benthic than in drift samples, but this may be a sampling error due to very strongly clumped distributions in the benthos. The rank orders of invertebrates in the drift and the benthos were highly correlated (Spearman's $r_{\rm s}=0.82,~P\leq.01$).

A total of 33 brook and 32 brown trout were collected for stomach analysis. The average size of brook trout was 12.3 cm (range 8.0 to 29.4 cm) and 17.4 g (range 4.2 to 84.3 g). The average size of brown trout was 15.3 cm (range 6.8 to 29.5 cm) and 35.0 g (range 2.7 to 253.0 g). Thus brown trout were larger on the average. Both species fit satisfactorily the equation $W = aL^b$, where W is weight in g, L is length in cm. For brook trout the equation was $W = 0.0164 \ L^{2.78}$ ($r^2 = 0.96$), and for brown trout $W = 0.0081 \ L^{3.07}$ ($r^2 = 0.995$). The weight of brown trout increased more rapidly per unit length than occurred in brook trout, but the difference was not significant (95% confidence intervals for slopes were 2.78 \pm 0.11 and 3.07 \pm 0.10).

Both species of trout consumed most of the invertebrate taxa which were present in the stream. Sperman rank correlation coefficients between trout diet and drift or benthos were significant in each instance (Table 2). Both species of trout consumed similar prey (Table 3). The number of prey per trout was greatest in the afternoon (13.00, 17.00 hours) and evening samples (19.00, 23.00 hours) in both species, but some prey were observed in stomachs throughout the 24 hour period.

A number of observations can be made by inspecting the data in Table 1. Ephemeroptera were less frequent in the stomachs of both species of trout than would be expected from their frequency in the drift and benthos. Diptera larvae,

Table 2. Spearman rank correlation coefficient (r_s) between relative abundance of items in the environment (drift or benthos) and in the diet of trout. Only one benthic sample was collected, during mid-day. Drift samples are from day, night or total (day and night combined), as are stomach contents. r_s between benthos and total drift = 0.82 °°.

	Salvelinus fontinalis			Salmo trutta		
	Day	Night	Total	Day	Night	Total
drift	0.46*	0.61**	0.74**	0.65**	0.55**	0.61**
benthos	_	—	0.55*		_	0.60**

^{*} p < .05, ** p < .01

Table 3. Spearman rank correlation coefficient (r_s) between diet of brown trout (Salmo trutta) and brook trout (Salvelinus fontinalis).

		 	
Day	Night	Total	
0.93**	0.62**	0.71**	

emerging aquatic insects and terrestrial items were more frequent in stomachs of trout than in the drift or benthos. Brown trout differed from brook trout in consuming more Ephemeroptera and fewer Diptera, especially of the Chironomidae. Brown trout also consumed more of certain taxa which were relatively large but rare, including species of the genera *Ephemerella*, *Rhithrogena* and *Rhyacophila*.

To determine whether size of prey had a detectable effect on its likelihood of being eaten, I compared the size distribution of nymphal head widths of the mayfly *Baetis bicaudatus* in the drift and in trout stomachs. This avoids the complication of comparing two different species which may vary in additional factors such as body form. Results (Fig. 1) demonstrate that only the larger nymphs are heavily fed upon by trout. The modal sizes were drift by day, 0.70 mm; drift by night, 0.77 mm; in stomachs of brook trout, 0.90 mm; in stomachs of brown trout, 0.96 mm. Differences between trout species were not significant. Differences between day and night drift also were not significant

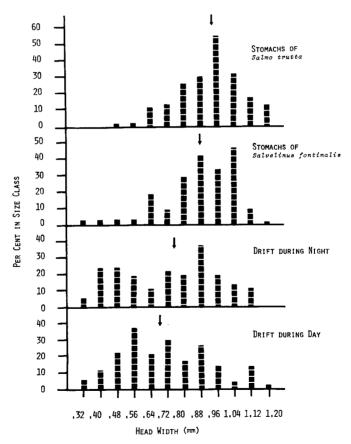


Fig. 1. The size distribution of nymphs of the mayfly *Baetis bicaudatus* in the stomachs of trout, and in the drift. Arrows denote median size. Trout fed upon the larger nymphs (p < 0.005).

although I have reported elsewhere that the size of nymphs of *B. bicaudatus* drifting by night typically is greater than the size of nymphs drifting by day, often significantly so (Allan 1978). However, the difference between the size composition of the drift and that in the stomachs of trout was highly significant ($p \le .005$ by G test, Sokal & Rohlf 1969, p. 599).

Discussion

This study is in agreement with the work of others (Elliott 1970, 1973; Jenkins et al. 1970) which shows that stream salmonids feed most heavily on the most abundant prey. Whether trout were feeding primarily from the drift, as Elliot (1970) has argued, or from the benthos is difficult to determine because of the high correlation among all possible comparisons (Tables 2, 3). However, the over-representation of emerging and terrestrial prey argues for drift feeding, as does the over-representation of dipteran larvae in trout diets, since dipteran larvae were more abundant in drift than in benthic samples. Only the presence of Trichoptera in trout stomachs seems to require a reliance on bottom feeding (Table 1).

In addition to prey abundance, prey size appears to be a major factor underlying the choice of food by trout. Within one species, the mayfly *Baetis bicaudatus*, large nymphs are much more likely to be fed upon than small nymphs (Fig. 1). Comparisons between taxa also indicate that prey which are consumed in excess of their frequency in the environment tend to be large, or in the surface drift (Table 1). Both factors enhance visibility of prey to salmonids, as Mundie (1969), Ware (1972) and Metz (1974) have documented.

Brook trout Salvelinus fontinalis and brown trout Salmo trutta showed some minor differences in consumption of prey, with brown trout feeding more upon the surface drift of emergent and terrestrial groups, and less upon dipteran larvae. However brook trout were somewhat smaller in this study, which may contribute to the greater reliance upon Chironomidae. Habitat differences between the trout were not examined, and it is also possible that differences between species in food consumed stems from feeding in different micro-habitats. In general, the results of Elliott (1973) that the diets of S. trutta and S. gairdneri are similar appears to extend to Salvelinus fontinalis as well.

In conclusion, based on this and earlier studies, salmonids dwelling in streams are quite similar in their choice of foods. The relative abundance of a given item in the environment is a good approximation to its frequency in the diet of trout, while large size or presence in the surface drift helps to explain the over-representation of particular prey.

Acknowledgements

I thank J. Kuhar for assistance in data collection and the Colorado Division of Wildlife for permission to collect trout. Research supported by a grant from NSF.

References

- Allan, J. D., 1975: The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. Ecology 56: 1040—1053.
 - 1978: Trout predation and the size composition of stream drift. Limnol. Oceanogr. (in press).
- ELLIOTT, J. M., 1970: Diet changes in invertebrate drift and the food of trout Salmo trutta L. J. Fish. Biol. 2: 161—165.
 - 1973: The food of brown and rainbow trout (Salmo trutta and S. gairdneri) in relation to the abundance of drifting invertebrates in a mountain stream. Oecologia 12: 329—347.
- Jenkins, T. M. Jr., Feldsmith, C. R. & Elliott, G. V., 1970: Feeding of rainbow trout (Salmo gairdneri) in relation to abundance of drifting invertebrates in a mountain stream. J. Fish. Res. Bd. Canada 27: 2356—2361.
- METZ, J. P., 1974: Die Invertebratendrift an der Oberfläche eines Voralpenflusses und ihre selektive Ausnutzung durch die Regenbogenforellen (Salmo gairdneri). — Oecologia 14: 247—267.
- Mundle, J. H., 1969: Ecological implications of the diet of juvenile Coho in streams.

 In: T. G. Northcote (ed.), Symposium on salmon and trout in streams:
 135—152. Univ. of British Columbia, Vancouver.
- SOKAL, R. R. & ROHLF, F. J., 1969: Biometry. Freeman, San Francisco.
- WARE, D. M., 1972: Predation by rainbow trout (Salmo gairdneri): the influence of hunger, prey density and prey size. — J. Fish Res. Bd. Canada 29: 1193—1201.

Author's address:

Dr. J. D. Allan, Department of Zoology, University of Maryland, College Park, Maryland 20742, U. S. A.