

The Food of Brown and Rainbow Trout (*Salmo trutta* and *S. gairdneri*) in Relation to the Abundance of Drifting Invertebrates in a Mountain Stream

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Summary. The diet of *Salmo gairdneri* and *S. trutta* in a Pyrenean stream was very similar, and was also similar to the percentage composition of the drift but not the benthos. There was a good correlation between diel changes in the amount of food (both numbers and biomass) in the stomachs and diel changes in the abundance of drifting invertebrates. The major feeding period was in the early hours of the night when the trout fed chiefly on benthic invertebrates in the drift. This was the only feeding period in experiments 1 and 2 (mean water temperatures 4.7 and 7.3°C) but in experiment 3 (10.8°C), there was a second feeding period in the day when terrestrial invertebrates and emerging aquatic insects formed a large proportion of the diet.

Neither species was consuming a greater amount of food than the other. The weight of food consumed/trout/day increased with water temperature, and was close to the daily food requirements for resting metabolism in experiment 1, for twice resting metabolism (active metabolism) in experiment 2, and for four times resting metabolism in experiment 3. Therefore the energy of the second meal in experiment 3 was available for growth.

The effect of temperature on rates of gastric evacuation was the chief factor which determined the number of meals/day; the availability of food organisms in the drift determined the time of feeding; and the requirements for metabolism (affected by temperature and body weight) determined the amount of energy left for growth.

Introduction

Numerous studies have shown that large numbers of benthic invertebrates drift downstream, especially at night. Elliott (1965) suggested that brown trout (*Salmo trutta* L.) utilise some of this readily available drift food, especially in the early hours of the night; and several studies have now supported this hypothesis (Elliott, 1967a, 1970; Tuša, 1969; Jenkins, 1969). Rainbow trout (*Salmo gairdneri* Richardson) also feed on invertebrate drift during the night (Jenkins, 1969; Jenkins *et al.*, 1970), and can take drifting foods at light intensities greater than 0.035 lux (Tanaka, 1970). However, Chaston (1969) has suggested that brown trout feed chiefly on terrestrial invertebrates, and rarely on the emerging

aquatic insects and benthic invertebrates in the drift. This work was strongly criticised by Elliott (1970) who worked on the same population of brown trout.

There is clearly a need for more comparative studies on diel changes in the food of trout. The present study describes the diet of *Salmo gairdneri* and *S. trutta* in a Pyrenean stream, compares diel changes in the food with diel changes in the abundance of drifting invertebrates, and examines quantitative differences in the amount of food eaten by the trout.

Description of Stream and Experimental Sites

Estibère is a mountain stream in the catchment area of the Neste d'Aure (river of the wind) in the central Pyrénées. As Décamps (1967) has described this area in detail, only a brief account is included here.

Estibère is about 3.5 km from source to mouth and rises in the north-west end of the valley from a series of lakes and small streams at altitudes between 2060 m and 2450 m. Two major tributaries from the northwest join at about 2 km from the source and a third major tributary from the south joins the main stream at about 2.5 km from the source. Site 2 was in this third tributary immediately upstream from the junction and site 1 was in the main stream immediately downstream from the junction (altitude 2050 m). The substratum was large stones (modal width 20–30 cm) over smaller stones (width <10 cm) and gravel at site 2, and chiefly gravel and mud at site 1. The gradient is steep (fall about 16%) for the first 2.5 km, but is considerably reduced near the junction (fall about 2%) where the stream meanders across a moorland plateau. This section ends after about 0.5 km and there is a final steep section (fall about 18%) of about 0.5 km.

Total discharge is highest in June and then decreases throughout July to a low level in August. Therefore depth, water velocity and total discharge were considerably higher in experiments 1 and 2 (29 June–1 July) than in experiment 3 (1–2 August). Water temperature also varied considerably between experiments (Table 1). Although the basic rock of the valley is granite, bands of calcareous material are present and the pH of the stream is high (range 7.4–8.4 at site 1 for period from May to October). Water analyses are compared in Table 1, and the following values were also obtained in August (experiment 3): magnesium 0.016 m — equiv/l, sodium 0.035 m — equiv/l, potassium 0.005 m — equiv/l.

The only species of fish in Estibère are brown trout (*Salmo trutta*) and rainbow trout (*S. gairdneri*). Brown trout are indigenous, but rainbow trout were introduced between 1958 and 1960, and spawn in June and July. Both species were present at sites 1 and 2, but rainbow trout were always the most numerous.

Table 1. Physical and chemical conditions for each experiment (95% confidence limits are given in parentheses)

	Experiment 1	Experiment 2	Experiment 3
Length of section (m)	90	89	120
Width (range in m)	2–8	2–10.5	1.5–9.0
Depth (range in m)	0.1–1.5	0.1–1.2	0.04–0.6
Mean water velocity:			
near Net 1 (cm/sec)	50.5 (± 2.9)	98.3 (± 17.1)	16.1 (± 2.3)
near Net 2 (cm/sec)	46.3 (± 0.6)	37.3 (± 0.9)	<1.0 (± 1.0)
Total discharge (m ³ /sec)	0.81 (± 0.12)	0.49 (± 0.10)	0.05 (± 0.01)
Volume sampled by:			
Net 1 (m ³ /sec)	0.022 (± 0.001)	0.033 (± 0.001)	0.005 (± 0.001)
Net 2 (m ³ /sec)	0.016 (± 0.0003)	0.013 (± 0.0003)	0.001 (± 0.001)
Water temperature:			
mean (°C)	4.7 (± 0.5)	7.3 (± 0.7)	10.8 (± 1.0)
range (°C)	4–6	6–9	9–13
Alkalinity (HCO ₃ ⁻) (m-equiv/l)	0.208	0.310	0.380
Total hardness (m-equiv/l)	0.250	0.280	0.376
Calcium (Ca ⁺⁺) (m-equiv/l)	0.205	0.251	0.376
Nitrates (NO ₃ ⁻) (m-equiv/l)	0.006	0.006	0.002
Total ions ³ (m-equiv/l)	0.304	0.370	0.425

Sampling Procedure and Methods

Three experiments were performed in 1972 on the following dates: 29–30 June (experiment 1 at site 1), 30 June–1 July (experiment 2 at site 2), 1–2 August (experiment 3 at site 2). Each experiment was over 24 h and was divided into four periods of 6 h (14:30–20:30 h, 20:30–02:30 h, 02:30–08:30 h, 08:30–14:30 h). The light intensity was less than 1 lux from 21:00–05:00 h in experiments 1 and 2, and from 20:45–05:15 h in experiment 3. Drifting invertebrates were caught in surface nets (described by Elliott, 1967b) which sampled a small proportion of the total discharge (Table 1). Net 1 was at the upstream end and net 2 at the downstream end of the experimental section. Two drift samples (sampling period 2.5 h) were taken with each net over 5 h. The surface nets were removed from the stream for one hour and a sample of about 20 trout was obtained by means of an electrical shocker. This procedure was repeated for each 6 h-period, and fish samples were therefore taken just before dusk, at night, after dawn, and in the afternoon. The trout were killed, weighed (to nearest g) and measured (length from nose to fork of tail in cm) soon after capture, and their stomachs were removed and preserved in formaldehyde. In the laboratory, the amount of food in each stomach was estimated by a simple points method: 0 for empty stomach, 1 for only pyloric

Table 2. Numbers in the night and day catches of drifting invertebrates, and the samples in

	Experiment 1			Benthos (%)
	Drift			
	Night	Day	(%)	
<i>Baëtis alpinus</i> Pictet	394	45	(25)	(2)
<i>Baëtis muticus</i> L.	60	36	(6)	(25)
<i>Epeorus</i> spp.	1	0		(0)
<i>Ecdyonurus</i> spp.	4	0		(<1)
<i>Rhithrogena</i> spp.	16	1		(4)
Total Ephemeroptera	482	82	(33)	(32)
<i>Amphinemura sulcicollis</i> (Steph.)	74	24	(6)	(9)
<i>Protonemura</i> spp.	9	3		(<1)
<i>Leuctra</i> spp.	28	5	(2)	(<1)
<i>Isoperla</i> sp.	37	1	(2)	(2)
Total Plecoptera	155	33	(11)	(12)
<i>Agapetus fuscipes</i> Curtis	0	0	(0)	(0)
<i>Drusus rectus</i> McL.	0	1		(6)
<i>Sericostoma personatum</i> (Spence)	0	0	(0)	(2)
Total Trichoptera	8	4		(9)
<i>Pericoma</i> sp.	185	201	(22)	(0)
<i>Dicranota</i> sp.	2	1		(5)
<i>Simulium</i> spp.	142	79	(13)	(<1)
Chironomidae	51	80	(7)	(23)
Total Diptera	401	364	(43)	(30)
<i>Elmis aenea</i> (Müll.)	162	38	(12)	(1)
<i>Elodes</i> sp.	17	0		(<1)
Total Coleoptera	180	39	(13)	(2)
<i>Polycelis felina</i> (Dalyell)	1	2		(2)
Oligochaeta	5	2		(12)
Total non-Insecta	6	5		(15)
Total benthic invertebrates as % of total drift	1232	527	(100) (73)	(100)
Emerging aquatic insects	158	203	(15)	
Terrestrial invertebrates	42	235	(12)	
Nos/m² in benthos (95 % confidence limits)				671 (283–1589)

half of stomach with some food, 2P for full pyloric half of stomach, 2 for pyloric and cardiac with some food, 3 for pyloric full and cardiac half with some food, 4 for full stomach. After the invertebrates in each stomach had been identified and counted, they were dried at 85°C on a single pan balance until a constant dry weight was obtained.

percentage composition of the drift (values <1% are not given) and bottom each experiment

Experiment 2				Experiment 3			
Drift			Benthos (%)	Drift			Benthos (%)
Night	Day	(%)		Night	Day	(%)	
412	5	(29)	(4)	76	2	(26)	(3)
54	9	(4)	(13)	22	3	(8)	(6)
6	0		(<1)	2	0		(4)
32	1	(2)	(4)	5	0	(2)	(1)
3	0		(<1)	3	0	(1)	(2)
519	16	(37)	(23)	111	5	(39)	(17)
98	4	(7)	(5)	0	0	(0)	(0)
16	2	(1)	(<1)	20	3	(8)	(2)
56	4	(4)	(11)	1	0		(1)
0	0	(0)	(0)	0	0	(0)	(0)
170	10	(12)	(19)	23	3	(9)	(5)
0	0	(0)	(3)	0	0	(0)	(1)
0	0	(0)	(0)	0	0	(0)	(0)
0	0	(0)	(<1)	0	0	(0)	(1)
14	4	(1)	(7)	3	3	(2)	(3)
25	24	(3)	(0)	0	0	(0)	(<1)
1	0		(2)	0	0	(0)	(0)
415	55	(33)	(6)	8	0	(3)	(<1)
43	96	(10)	(30)	71	53	(42)	(59)
489	175	(46)	(38)	79	53	(45)	(65)
23	9	(2)	(<1)	8	0	(3)	(1)
3	0		(<1)	0	0	(0)	(0)
27	9	(2)	(1)	8	0	(3)	(1)
0	0	(0)	(3)	0	0	(0)	(<1)
0	0	(0)	(8)	0	0	(0)	(7)
1	2		(12)	2	5	(2)	(9)
1222	217	(100)	(100)	226	69	(100)	(100)
		(52)				(65)	
44	198	(9)		10	104	(25)	
198	865	(39)		17	30	(10)	
			1737				1782
			(939-3213)				(891-3563)

Bottom samples were taken with a Surber sampler (mesh width 0.09-0.10 mm) which covered 0.07 m² of bottom. A random sample of 5 sampling units was taken from the section at the end of an experiment. A small Ott current meter was used to measure water velocity, and both total discharge and the volume of water sampled by each net were estimated in each experiment.

Invertebrates in the Drift and Benthos

More than 50 species were taken in the drift and bottom samples, and Table 2 includes all taxa which contributed more than 1% to the total numbers in at least one experiment. Several taxa could not be identified to species, and the following species were combined under the generic name: *Epeorus assimilis* Eaton and *Ep. torrentium* Eaton; *Ecdyonurus angelieri* Thomas and *Ec. forcipula* Pictet; *Rhithrogena* sp. and *R. semicolorata* (Curtis); *Protonemura beatensis* Despax, *P. pyrenaica* Mosely and *P. umbrosa intricata* (Pictet); *Leuctra prima* Kempny, *L. lamellosa* Despax and *L. alosi* Navas. Rarer taxa not listed in the table included the following Ephemeroptera: *Baëtis rhodani* (Pictet), *Habrophlebia berthelemyi* Thomas; Plecoptera: *Nemoura erratica* Claassen, *Dinocras cephalotes* (Curtis), *Perla marginata* (Panzer), *Siphonoperla torrentium* (Pictet); Trichoptera: *Rhyacophila evoluta* McL., *R. tristis* Pictet, *Philopotamus montanus* (Don.), *Hydropsyche pellucidula* (Curt.), *Potamophylax latipennis* (Curtis), *Melampophylax mucoreus* (Hagen); Coleoptera: *Hydraena emarginata* Rey, *Limnius perrisi* Duf; Diptera: *Liponeura* sp., *Dixa puberula* Loew.; Megaloptera: *Sialis lutaria* L.; non-Insecta: Hydrachnellae, *Pisidium* sp.

Most taxa taken in the bottom samples were also taken in the drift samples, and the only exceptions were *Dinocras cephalotes*, larvae of *Agapetus fuscipes* and *Sericostoma personatum*, *Limnius perrisi*, Ceratopogonidae, and *Pisidium* sp. Larvae of *Dixa puberula* were only taken in the drift samples. The numbers of benthic invertebrates in the drift increased at night for all taxa except *Pericoma* sp., Chironomidae, and Hydrachnellae, but the catches of emerging aquatic insects and terrestrial invertebrates were always higher in the day samples (Table 2). Chironomidae predominated in the catches of emerging aquatic insects, but *Sericostoma personatum* was also important in experiment 3.

As the experiments were performed at different sites on adjacent dates (experiments 1 and 2), and in different months at the same site (experiments 2 and 3), it is not surprising that the percentage composition of the drift and benthos varied between experiments. There were, however, some consistent differences in each experiment. Percentages for *Baëtis alpinus*, total Ephemeroptera, and *Simulium* spp. were higher in the drift than in the benthos, whereas the converse was usually true for *Baëtis muticus*, Trichoptera, Chironomidae and non-Insecta. Therefore some taxa were swept into the drift more easily than others, but these differences cannot be explained until more is known about the ecology of each species. However, the different drift rates of *Baëtis* species can be explained. *Baëtis alpinus* lives chiefly on large stones, whereas *B. muticus* lives interstitially amongst small stones and gravel. Therefore the probability that a nymph will be swept into the drift is only high for *B. muticus* when the nymphs move onto the exposed surface of the substratum, but is always high for *B. alpinus*, especially at night when most nymphs probably move onto the upper surfaces of large stones and graze on the periphyton.

The density of the benthos was much lower at site 1 (experiment 1) than at site 2 (experiments 2 and 3), but did not significantly vary within one month at site 2 (cf. experiments 2 and 3 in Table 2). Total

numbers of benthic invertebrates in the drift samples were very similar in experiments 1 and 2, but decreased markedly in experiment 3. This decrease was related to the large decrease in total discharge and the volumes sampled by the surface nets in experiment 3 (Table 1). In all experiments, the two surface nets sampled a small proportion of the total discharge (4.7% in experiment 1, 9.4% in experiment 2, 12% in experiment 3). Therefore estimates of the total numbers of invertebrates drifting past the sampling point in 24 h were 51 000 in experiment 1, 29 191 in experiment 2 and 3 800 in experiment 3. These estimates are similar to those obtained for other small streams and rivers, but are lower than those obtained for larger rivers (see list in Elliott and Corlett, 1972).

The Trout and Diel Changes in Their Food

A wide size range of trout was taken in each experiment (Fig. 1), and the relationship between live weight (Wg) and length (L cm) was described by the regression equation:

$$W = a L^b \quad \text{or} \quad \log W = \log a + b \log L \quad (1)$$

where a and b are constants. Although the numbers of *Salmo trutta* were low and their mean length and mean weight were less than the corresponding values for *S. gairdneri*, the constants a and b were not significantly different ($P > 0.05$) for the two species in each experiment (Table 3). Therefore trout of the same length were a similar weight for each species. The constants a and b were not significantly different ($P > 0.05$) in experiments 1 and 2, but a was significantly higher ($P < 0.05$) and b significantly lower ($P < 0.001$) in experiment 3. Therefore trout of similar length were heavier in experiment 3 than in experiments 1 and 2, and the increase in weight was greatest for the smallest trout. The mean length ($\pm 95\%$ confidence limits) of *Salmo gairdneri* at the end of each year of the life cycle was 6.9 ± 2.2 cm for first year, 12.4 ± 3.2 cm for second year, 17.0 ± 2.8 cm for third year, and 22.2 ± 2.5 cm for fourth year (Dumas, unpublished). As there is no comparable information for *S. trutta*, it is not known if the two species were growing at similar rates.

The diel changes in the amount of food in the stomachs were shown by the points method of assessing "stomach fullness" (Table 4). Most trout had full stomachs in the night samples (1:30–2:30 h) of each experiment and in the afternoon sample (13:30–14:30 h) of experiment 3. The decrease in "stomach fullness" was slowest in experiment 1, more rapid in experiment 2 and most rapid in experiment 3. As the samples with full stomachs must have been taken just after or within a major

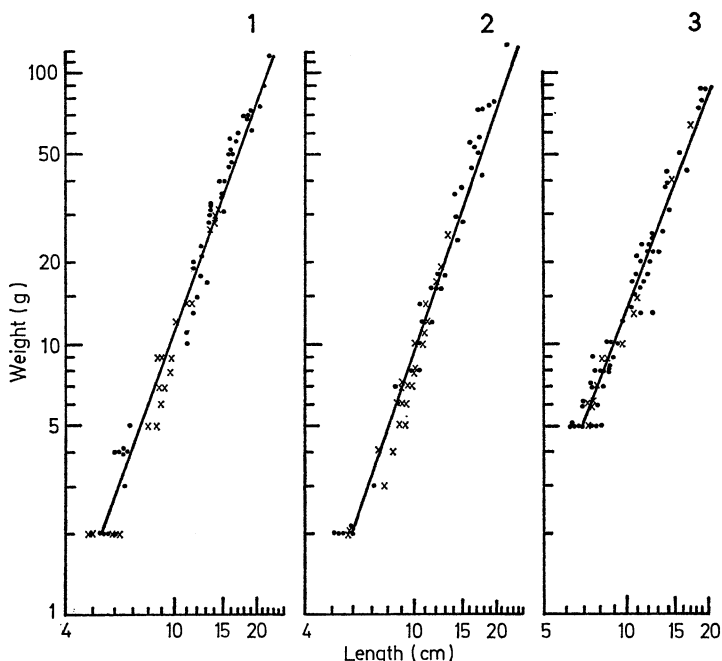


Fig. 1. Relationship between weight (g live weight) and length (cm) of *Salmo gairdneri* (•) and *S. trutta* (×) in experiments 1, 2, 3 [regression lines were calculated from Eq. (1)]

feeding period, the trout were feeding in the early hours of the night in each experiment and also during the day in experiment 3.

The diet of the two species was very similar at night, and was also similar to the percentage composition of the drift but not the benthos (cf. Tables 2 and 5). There was good agreement between the drift and diet of *Salmo gairdneri* in the afternoon sample of experiment 3, but the diet of *S. trutta* was slightly different with a lower percentage for Chironomidae, and higher percentages for *Baëtis* spp. and *Protonemura* spp. As only three *S. trutta* were present in the sample, these differences were possibly not significant and were simply due to the variability between individual trout. There were several other notable differences between the diet and drift. Percentages for *Pericoma* sp., *Elmis aenea*, and emerging Chironomidae in experiment 1, and *Simulium* spp. in experiment 2 were lower in the diet than in the drift, whereas the converse was true for *Amphinemura sulcicollis*. Therefore some taxa in the drift were more available to the trout than others. The low availability of the first four taxa was probably due to their small size

Table 3. Number of trout in each experiment, and values of the constants *a* and *b* ($\pm 95\%$ confidence limits) in regression Eq. (1)

	Experiment 1		Experiment 2		Experiment 3				
	No.	<i>a</i>	<i>b</i> ± 95% CL	No.	<i>a</i>	<i>b</i> ± 95% CL	No.	<i>a</i>	<i>b</i> ± 95% CL
<i>Salmo gairdneri</i>	58	0.0185	2.80 ± 0.09	48	0.0103	2.96 ± 0.16	68	0.0377	2.54 ± 0.12
<i>Salmo trutta</i>	22	0.0171	2.79 ± 0.23	28	0.0129	2.82 ± 0.26	12	0.0290	2.66 ± 0.52
Both species	80	0.0167	2.83 ± 0.08	76	0.0095	2.98 ± 0.12	80	0.0363	2.56 ± 0.11

Table 4. Percentage of stomachs in each category of "stomach fullness" (see methods for explanation of points 1-3) in each sample

Sampling time (h)	Experiment 1				Experiment 2				Experiment 3			
	19:30-20:30	1:30-2:30	7:30-8:30	13:30-14:30	19:30-20:30	1:30-2:30	7:30-8:30	13:30-14:30	19:30-20:30	1:30-2:30	7:30-8:30	13:30-14:30
<i>Salmo gairdneri</i>												
Stomach full	4	64	33	14		83	33			65	82	
	3	29				17				35	18	
	2	7		7			25		12		6	
2P	33		60	36	40		25	28	35		29	
1	33		7	43	20		17	44	53		65	
Stomach empty	0	27			40			28				
<i>Salmo trutta</i>												
Stomach full	4	67	20	17		50	17			67	100	
	3	33				50				33		
2							16					
2P	20		60	33	10		17	17	33		33	
1	20		20	50	30		50	33	67		67	
Stomach empty	0	60			60			50				

Table 5. Percentage composition of the drift samples and stomach contents of *Salmo gairdneri* (S.g.) and *S. trutta* (S.t.) in the night samples (20:30-02:30 h) of all experiments and in the afternoon sample (08:30-14:30 h) of experiment 3

Sampling time	Experiment 1		Experiment 2		Experiment 3		Experiment 3					
	20:30-02:30 h		20:30-02:30 h		20:30-02:30 h		08:30-14:30 h					
	Drift	S.g.	S.t.	Drift	S.g.	S.t.	Drift	S.g.	S.t.			
<i>Baëtis alpinus</i>	28	41	36	28	38	35	30	24	20	1	2	8
<i>Baëtis muticus</i>	4	6	3	4	7	8	9	7	5	1	<1	4
Heptageniidae	1	2	5	3	3	3	4	6	2	0	0	0
Total Ephemeroptera	34	49	44	35	49	46	44	37	28	2	2	12
<i>Amphinemura sulciatilis</i>	5	21	15	7	19	18	0	0	0	0	0	0
<i>Protonemura</i> spp.	<1	<1	<1	1	2	2	8	12	12	1	4	8
<i>Leuctra</i> spp.	2	3	1	4	4	9	<1	3	2	0	0	0
<i>Isoperla</i> sp.	3	7	6	0	0	0	0	0	0	0	0	0
Total Plecoptera	11	33	24	12	25	29	9	18	17	1	4	8
Total Trichoptera	<1	<1	2	<1	2	<1	1	<1	<1	1	3	8
<i>Pericoma</i> sp.	13	<1	2	2	<1	0	0	0	0	0	0	0
<i>Simulium</i> spp.	10	8	12	28	8	12	3	6	8	0	0	0
Chironomidae	4	5	9	3	3	3	28	22	27	26	27	5
Total Diptera	28	14	27	33	14	16	31	28	35	26	27	5
<i>Elmis aenea</i>	11	<1	<1	2	<1	<1	3	<1	<1	0	0	0
<i>Elodes</i> sp.	1	0	0	<1	<1	<1	0	0	0	0	0	0
Total Coleoptera	12	<1	<1	2	1	<1	3	<1	<1	0	0	0
Total non-Insecta	<1	0	0	<1	0	0	<1	0	0	2	0	0
Total benthic invertebrates	86	97	98	83	92	91	89	83	83	34	35	33
<i>Sericostoma personatum</i>	0	0	0	0	0	0	0	<1	<1	4	11	2
Chironomidae	11	1	2	3	4	5	4	11	12	41	24	26
Total emerging	11	2	2	3	4	5	4	11	12	51	43	46
Diptera	1	0	0	4	2	2	3	2	2	8	9	6
Hymenoptera	<1	0	0	<1	<1	<1	2	2	1	2	8	10
Coleoptera	<1	<1	0	<1	2	2	0	0	0	0	0	0
Total terrestrial	3	<1	0	14	4	4	7	6	5	15	22	21

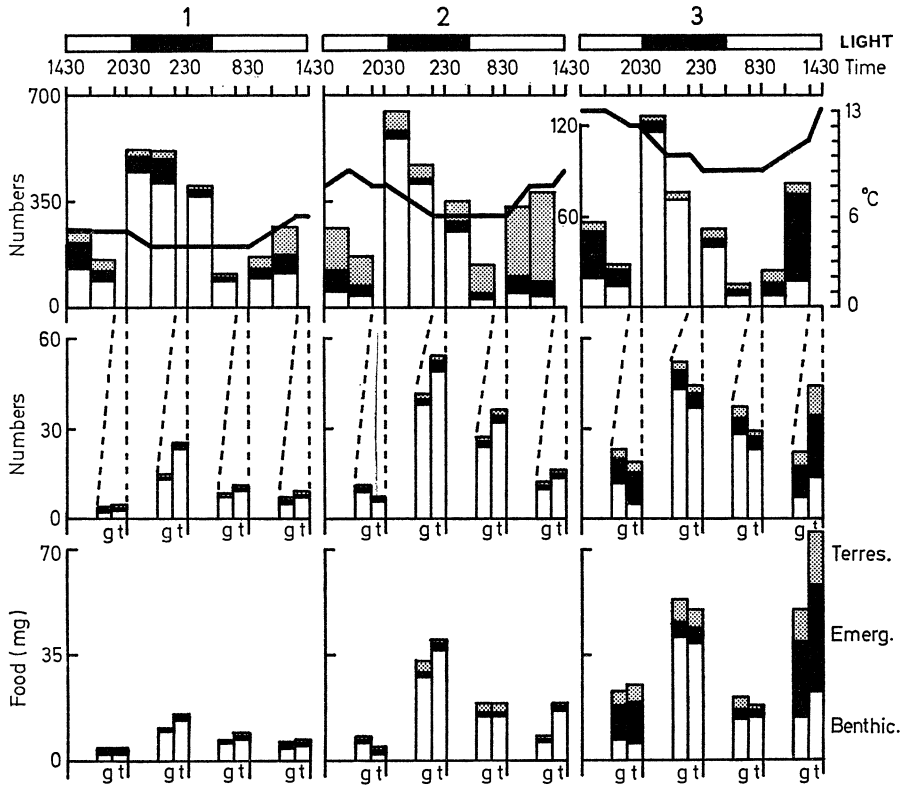


Fig. 2. Diel changes in the numbers of invertebrates in the drift, and in both mean numbers and mean dry weight (mg) of food organisms per 10 g live weight of *Salmo gairdneri* (g at foot of column) and *Salmo trutta* (t) in each experiment. Each column is divided into benthic invertebrates (clear), emerging aquatic insects (shaded), and terrestrial invertebrates (stippled). Changes in water temperature (°C) are given, and the shaded portion at the top of each figure indicates the period of darkness (light intensity < 1 lux)

and their behaviour in the drift, and the high availability of *A. sulcirostris* was probably due to the large size of the nymphs prior to their emergence. In spite of these differences, there was generally good agreement between the diet and the drift, and it was therefore concluded that the trout were feeding chiefly on the drift rather than on the benthos.

The diel periodicity of benthic invertebrates in the drift followed the usual pattern with higher numbers throughout the night and maximum numbers after dusk (Fig. 2). Emerging aquatic insects and terrestrial invertebrates in the drift were more abundant in the day samples. When the numbers in the drift were compared with both the mean

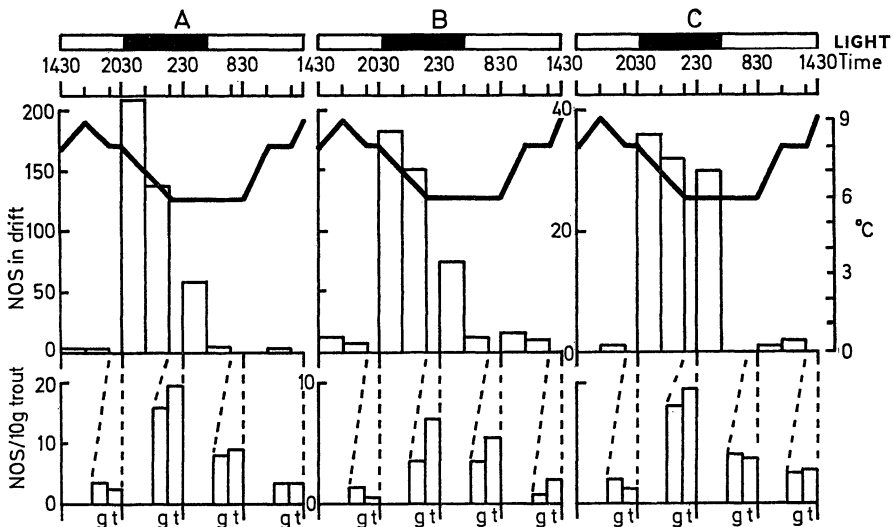


Fig. 3. Diel changes in the numbers of *Baëtis alpinus* (A), *Simulium* spp. (B), and *Amphinemura sulcicollis* (C) in the drift, and in their mean numbers per 10 g live weight of *Salmo gairdneri* (g at foot of column) and *Salmo trutta* (t) in experiment 2. Changes in water temperature (°C) are given, and the shaded portion at the top of each figure indicates the period of darkness (light intensity < 1 lux)

numbers and mean dry weight (mg) of food organisms per 10 g live weight of trout, there was a clear correlation between diel changes in the amount of food in the stomachs and diel changes in the abundance of drifting invertebrates. This close relationship between the food and the drift was also shown by the more abundant taxa and three examples are included in Fig. 3. Therefore the major feeding period was in the early hours of the night when the trout fed chiefly on benthic invertebrates in the drift. In experiment 3, there was a second feeding period in the day (08:30–14:30 h) when terrestrial invertebrates and emerging aquatic insects formed a large proportion of the diet.

Quantitative Differences in the Amount of Food Eaten by the Trout

As the amount of food in a full stomach increases with the size of a fish, the unit chosen for comparisons with the drift was mean numbers (or weight) of food organisms per 10 g live weight of trout, rather than mean numbers per trout. The chosen unit assumes a linear relationship between the amount of food and the live weight of the trout. Alternative relationships (exponential and log/log) were examined by regression analyses with total numbers or weight of terrestrial invertebrates,

emerging aquatic insects, benthic invertebrates and all invertebrates considered separately as dependent variables and live weight of trout as the independent variable. Apart from one exception, none of these regressions was significantly better than a linear relationship, probably because there was a high variability in the data. Therefore the principle of Occam's razor was followed and the simplest hypothesis was accepted for comparisons with the drift.

The one exception was the dry weight (Q mg) of all the invertebrates in the stomach, and the relationship to the live weight (W g) of trout was described by the regression equation:

$$Q = a W^b \quad \text{or} \quad \log Q = \log a + b \log W \quad (2)$$

where a and b are constants. This equation was a good fit to the data in nearly all samples (Table 6), and the non-significance in a few samples was due to a high proportion of empty stomachs or to the small sample size. The percentage ($P\%$) of the total sum of squares attributable to the regression indicated that variability in the data was negatively correlated with the amount of food in the stomachs, and was greatly reduced in the samples with full stomachs. When comparisons were possible, the constants a and b were not significantly different ($P > 0.05$) for the two species in each experiment. Therefore the apparent differences between the amount of food in the stomachs of the two species (Figs. 2 and 3) were not significant, and were chiefly due to the bias towards smaller fish in the samples of *S. trutta*. This bias is shown in Fig. 4 which also illustrates the excellent fit of the regression lines to the data from the four samples with full stomachs. Therefore the weight of food expressed as a proportion of the fish's body weight is higher for smaller trout than for larger trout (cf. values for 10 g and 100 g trout in Table 6).

From an extensive review of the literature, Winberg (1956) showed that the relationship between resting metabolism and body weight is well described by Eq. (2) where Q is the rate of metabolism measured as cm^3 of oxygen consumed per fish per hour at a standard temperature. He further demonstrated that the values of the level of metabolism (a) and weight exponent (b) were fairly constant for different taxonomic groupings with values for Salmonidae of $b = 0.76$ and $a = 0.50$ at a body weight of 1 g and a standard temperature of 20°C . The value of the constant a , and hence the level of metabolism, at various temperatures follows the curve of Krogh (1916), and therefore it is possible to predict the resting metabolic rate of a trout at any combination of body size and temperature. If it is assumed that the energy of egestion and excretion is about 20% of the energy intake, that the calorific values of fish flesh and food are similar, and that the consumption of $1 \text{ cm}^3 \text{ O}_2$ is equivalent to the expenditure of about 1 mg of dry body

Table 6. Values of the constants *a* and *b* in regression Eq. (2) for each experiment, the percentage (*P*%) of the total sum of squares attributable to the regression, the significance levels of the regression (**P*<0.05, ***P*<0.01, N.S. not significant *P*>0.05), and estimates of the dry weight of food (mg with 95% confidence limits) in the stomachs of trout with a live weight of 10 g and 100 g

Sampling time (h)	Experiment 1				Experiment 2				Experiment 3			
	19:30– 20:30	1:30– 2:30	7:30– 8:30	13:30– 14:30	19:30– 20:30	1:30– 2:30	7:30– 8:30	13:30– 14:30	19:30– 20:30	1:30– 2:30	7:30– 8:30	13:30– 14:30
<i>Salmo gairdneri</i>												
<i>a</i>	0.55	3.04	1.42	0.92		6.95	2.96		3.30	11.30	4.28	11.91
<i>b</i>	0.81	0.72	0.81	0.86		0.78	0.86		0.80	0.76	0.73	0.76
<i>P</i> %	35*	94**	92**	88**	N.S.	98**	86**	N.S.	77**	94**	64**	98**
<i>Salmo trutta</i>												
<i>a</i>		3.14	1.31	1.01		6.32				9.77		12.82
<i>b</i>		0.72	0.81	0.80		0.79				0.81		0.73
<i>P</i> %	N.S.	96**	76*	76*	N.S.	86**	N.S.	N.S.	N.S.	98*	N.S.	98*
Both species												
<i>a</i>	0.55	3.08	1.38	0.92	0.93	6.64	2.58	1.51	2.94	11.07	4.48	12.19
<i>b</i>	0.82	0.72	0.81	0.85	0.78	0.79	0.89	0.78	0.80	0.77	0.71	0.75
<i>P</i> %	46**	94**	90**	86**	24*	96**	83**	24*	76**	96**	66**	98**
mg food/10 g trout												
95% CL	3.6 (1.3– 10.1)	16.2 (14.7– 17.8)	8.9 (7.4– 10.7)	6.5 (5.0– 8.5)	4.6 (2.3– 9.3)	41.0 (37.3– 45.1)	20.0 (16.7– 24.0)	9.1 (4.8– 17.3)	18.6 (15.5– 22.3)	65.2 (59.3– 71.7)	23.0 (19.2– 27.6)	68.5 (62.3– 75.4)
mg food/100 g trout												
95% CL	24.0 (15.0– 38.4)	84.8 (70.7– 101.8)	57.5 (41.1– 80.5)	46.1 (30.7– 69.1)	32.8 (7.0– 154.5)	252.5 (210.4– 303.0)	155.5 (86.4– 279.9)	54.8 (10.7– 280.0)	117.0 (65.0– 210.6)	383.8 (319.8– 460.6)	117.8 (65.4– 212.0)	385.4 (350.4– 423.9)

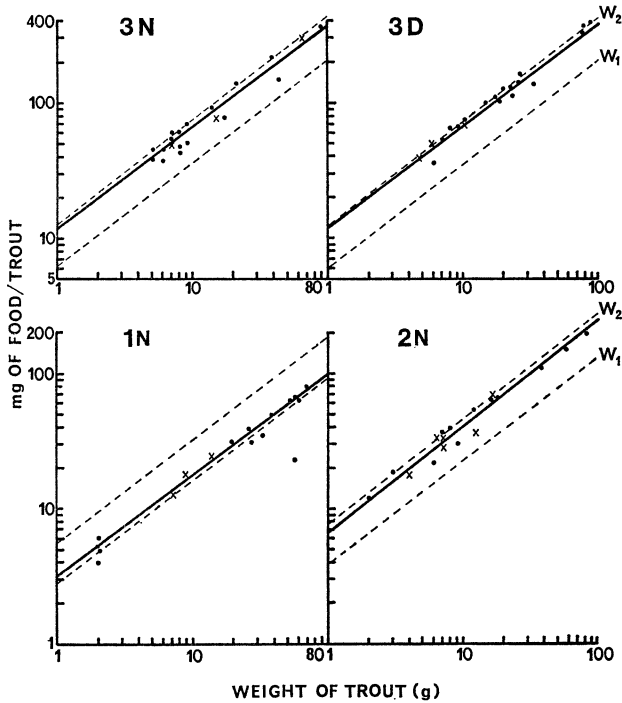


Fig. 4. Relationship between the dry weight (mg) of food in the stomachs and the live weight (g) of *Salmo gairdneri* (•) and *S. trutta* (×) in the night samples of experiment 1 (1N), experiment 2 (2N), experiment 3 (3N), and in the afternoon sample of experiment 3 (3D). Regression lines were calculated from Eq. (2), and estimates of the daily food requirements for resting metabolism (W_1) and twice resting metabolism (W_2) are shown as broken lines

substance; then Q can be also expressed in mg dry weight of food and the amount of food required for resting metabolism is 1.25 energy of metabolism. These approximations were justified by Winberg and more recently by Paloheimo and Dickie (1966). Winberg also proposed that the metabolic rate of fish in nature is about twice the resting level. Therefore two values for the dry weight of the ration were calculated, one based on resting metabolism (Winberg 1) and the other based on twice that value (Winberg 2). The final values were the dry weight of food required per fish per day at the mean water temperature of the experiment (see two broken lines W_1 and W_2 in Fig. 4).

These estimates revealed some interesting differences between experiments. The weights of food in the stomachs were close to the daily food requirements for resting metabolism in the night sample of experi-

Table 7. Daily energy budgets for 10 g and 100 g trout in each experiment (values in cal./trout/day) with energy value of food consumed (Q_c), energy of egestion and excretion ($Q_w = Q_c/5$), energy of resting metabolism (Q_r), additional energy for swimming activity (Q_a), and energy for growth (Q_g). Q_a in experiment 2 and Q_g in experiment 3 were obtained by difference. It was assumed that maximum $Q_a = Q_r$

	$Q_c -$	$Q_w = Q_r + Q_a + Q_g$				Comments
Experiment 1						
10 g trout	81	16	65	0	0	One meal provides energy for Q_r only
100 g trout	424	85	339	0	0	
Experiment 2						
10 g trout	205	41	89	75	0	One meal provides energy for Q_r but not max. Q_a
100 g trout	1262	252	513	497	0	
Experiment 3						
10 g trout	668	134	141	141	252	Two meals provide energy for Q_r , Q_a and Q_g
100 g trout	3846	769	811	811	1455	

ment 1, and for twice resting metabolism in the night samples of experiments 2 and 3, and the afternoon sample of experiment 3. There was only one major feeding period per day in experiments 1 and 2, and therefore the amount of food in the stomach was only sufficient for metabolism with no surplus for growth. As there were two feeding periods per day in experiment 3 and the daily food requirements for twice resting metabolism were fulfilled during one feeding period, the energy of the second meal was available for growth. This explains why trout of similar length were significantly heavier in experiment 3 than in experiments 1 and 2 (Fig. 1).

As agreement with Winberg's predictions was very good, an attempt was made to construct daily energy budgets for 10 g and 100 g trout (Table 7). It was assumed that the oxy-calorific coefficient was 4.8 cal/cm³ of oxygen, and that the calorific value of the food was 5 cal/mg dry weight. Although these budgets are only approximate, they clearly illustrate the major differences between experiments.

Discussion

The results of the present study provide strong evidence that *Salmo gairdneri* and *S. trutta* were feeding on invertebrate drift in Estibère, and therefore support the hypothesis of Elliott (1965). Both species had a similar diet and neither species was consuming a greater amount of food than the other. The major differences were between the weights of food consumed by the trout in each experiment. Agreement with Winberg's predictions showed that trout of different sizes fed at rates

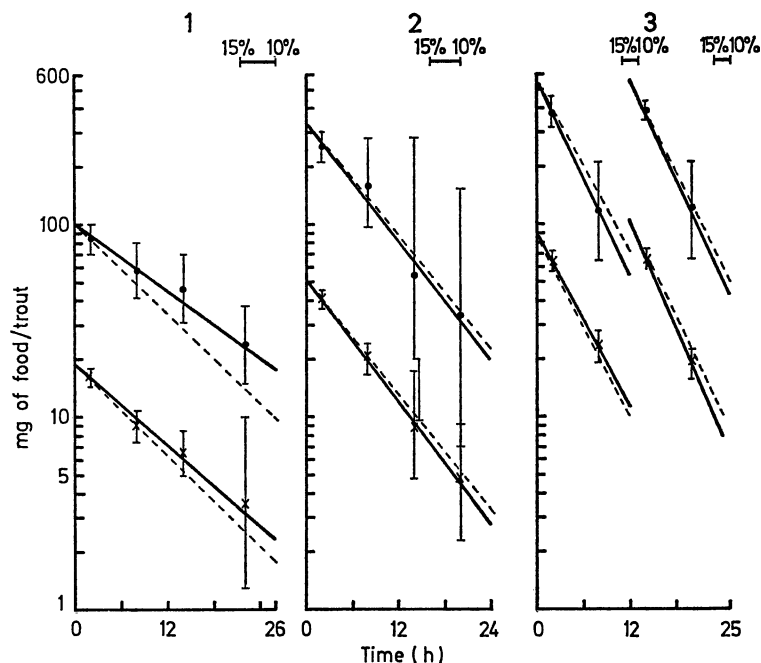


Fig. 5. Relationship between the mean (\pm 95% confidence limits) dry weight (mg) of food in the stomachs of 10 g trout (\times) and 100 g trout (\bullet) and time (hours after midnight) in each experiment. The expected rates of gastric evacuation are shown as broken lines, and the expected times at which 15% and 10% of the food should be left in the stomach are shown at the top of each figure

which resulted in the maintenance of a value of the weight exponent (b) characteristic of the two species, and a level of metabolism (a) which was possibly affected by the level of food supply and environmental conditions. As large numbers of invertebrates drifted downstream in Estibère, especially during the major feeding period in the early hours of the night, the food supply was probably not an important limiting factor for the level of metabolism.

The most important environmental factor affecting the level of metabolism was probably water temperature. As temperature increased from experiment 1 (mean 4.7°C) to experiment 2 (mean 7.3°C) to experiment 3 (mean 10.8°C), the weight and energy value of food consumed per trout per day also increased (Tables 6 and 7). This increase was due partially to the increased capacity of the stomach, but chiefly to the increased rate of gastric evacuation. The increase in stomach capacity (cf. the weights of food in full stomachs of trout of similar size in Figs. 4

and 5) cannot be explained, but a similar effect has been observed in feeding experiments with *S. trutta* (Elliott, unpublished).

The marked effect of water temperature on rates of gastric evacuation was shown by the comparisons of "stomach fullness" (Table 4), and by the estimates of the weight of food in the stomachs of 10 g and 100 g trout (Table 6) when these estimates were arranged in decreasing order (Fig. 5). If the effect of temperature is similar for *Salmo gairdneri* and *S. trutta*, then the rates obtained in the present study can be compared with expected rates estimated from the exponential model for rates of gastric evacuation in *S. trutta* (Elliott, 1972). It was assumed that feeding had finished by midnight, and the weight of food in the stomachs at midnight was therefore the starting point for the expected rates of gastric evacuation (broken lines in Fig. 5). The expected rates are the most rapid at the mean temperature of the experiment (i.e. food organisms in group 1 in Elliott, 1972), and evacuation rates are slower for some food organisms, especially those with a high fat content, e.g. larvae of *Hydropsyche*. The presence of these food organisms may explain the slower observed rates for 100 g trout in experiment 1, but in the other comparisons there was good agreement between observed and expected rates. *S. trutta* with full stomachs will feed again when about 10–15% of the first meal is left in the stomach (Elliott, unpublished). The estimated times for the 10–15% points (Fig. 5) show that trout with full stomachs could feed only once a day at the temperatures in experiments 1 and 2, but twice a day in experiment 3. Therefore temperature ultimately determined the number of meals per day, and probably the capacity of the stomach; the availability of food organisms in the drift determined the time of feeding; and the requirements for metabolism (affected by temperature and body weight) determined the amount of energy left for growth.

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References

- Chaston, I.: Seasonal activity and feeding pattern of brown trout (*Salmo trutta*) in a Dartmoor stream in relation to availability of food. J. Fish. Res. Bd Can. **26**, 2165–2171 (1969).
- Décamps, H.: Écologie des trichoptères de la vallée d'aure (hautes-pyrénées). Ann. Limnol. **3**, 399–577 (1967).
- Elliott, J. M.: Daily fluctuations of drift invertebrates in a Dartmoor stream. Nature (Lond.) **205**, 1127–1129 (1965).
- Elliott, J. M.: The food of trout (*Salmo trutta*) in a Dartmoor stream. J. appl. Ecol. **4**, 59–71 (1967a).

- Elliott, J. M.: Invertebrate drift in a Dartmoor stream. *Arch. Hydrobiol.* **63**, 202–237 (1967b).
- Elliott, J. M.: Diel changes in invertebrate drift and the food of trout *Salmo trutta* L. *J. Fish Biol.* **2**, 161–165 (1970).
- Elliott, J. M.: Rates of gastric evacuation in brown trout, *Salmo trutta* L. *Freshwat. Biol.* **2**, 1–18 (1972).
- Elliott, J. M., Corlett, J.: The ecology of Morecambe Bay IV. Invertebrate drift into and from the River Leven. *J. appl. Ecol.* **9**, 195–205 (1972).
- Jenkins, T. M.: Night feeding of brown and rainbow trout in an experimental stream channel. *J. Fish. Res. Bd Can.* **26**, 3275–3278 (1969).
- Jenkins, T. M., Feldmeth, C. R., Elliott, G. V.: Feeding of rainbow trout (*Salmo gairdneri*) in relation to abundance of drifting invertebrates in a mountain stream. *J. Fish. Res. Bd Can.* **27**, 2356–2361 (1970).
- Krogh, A.: Respiratory exchange of animals and man. London: Longmans, Green & Co. 1916.
- Paloheimo, J. E., Dickie, L. M.: Food and growth of fishes. II. Effects of food and temperature on the relation between metabolism and body weight. *J. Fish. Res. Bd Can.* **23**, 869–908 (1966).
- Tanaka, H.: On the nocturnal feeding activity of rainbow trout (*Salmo gairdnerii*) in streams. *Bull. Freshwat. Fish. Res. Lab. (Tokyo)* **20**, 73–82 (1970).
- Tuša, I.: On the feeding biology of the brown trout (*Salmo trutta* m. *fario* L.) in the course of day and night. *Zool. Listy* **18**, 275–284 (1969).
- Winberg, G. G.: Rate of metabolism and food requirements of fish. *Fish. Res. Bd Can. Transl. Ser. No 194* (1956).

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