Ref ID: 88453

THE FOOD OF TROUT (*SALMO TRUTTA*) IN A DARTMOOR STREAM

By J. M. ELLIOTT*

Department of Zoology, University of Exeter

Salmonids in lakes are known to take surface food of terrestrial origin plus emerging aquatic insects. In lotic systems, salmonids also feed on this surface drift especially in the summer months.

Norbäck (1884) first noted 'drift feeding' by young salmon fry on small crustaceans and later Nilsson (1957) showed that trout fry fed mainly on zooplankton washed out of a lake. In systems devoid of lakes, salmonids have been observed feeding on invertebrate drift of aquatic origin and Müller (1954), Nilsson (1957) and Kalleberg (1958) concluded that *Salmo trutta* L. and young *S. salar* L. feed substantially on this 'drift food'.

The purpose of the present investigation was to assess the importance of invertebrate drift in a Dartmoor stream and this included a study of the food of salmonids in relation to the invertebrate drift and the benthos. The amount and composition of invertebrate drift was the subject of an earlier paper (Elliott 1967).

METHODS

The Walla Brook, a tributary of the East Dart, is slightly acid (pH 6·4–6·8) and has a good population of *Salmo trutta* (Horton 1961), with the occasional young *S. salar*. Samples of fish, bottom and drift were all taken from a run where the bottom was chiefly small stones and gravel with *Myriophyllum spicatum* L. as the dominant aquatic plant (site 2 in Elliott 1967), and all were taken as close as possible in each month so that the trout diet could be compared with the invertebrate drift and benthos.

Using an electrical stunning machine, fish samples were taken from June 1963 to October 1964. Each monthly sample was separated into 1st year (0+), 2nd year (1+) and 3rd year and older (2+) categories, using length data from the population studied by Horton (1961), and six pairs were taken for stomach analyses; these pairs covered the size range of the sample. There were usually two pairs per year class, except in March, April, May and June, when there were three pairs in 1+ and 2+ categories, and no 0+ fish. Ten per cent formaldehyde was pipetted into the stomach of each fish and the whole sample preserved in formaldehyde.

To determine the number of items in the stomachs, parts of animals were utilized as well as whole individuals. It was not always possible to identify the stomach contents down to species and the following animals were counted under single genera: *Baetis* spp., *Leuctra* spp., *Polycentropus* spp. and *Simulium* spp. Similarly Ecdyonuridae, Tipulidae, Dytiscidae, Chironomidae and Hydrachnellae were grouped as families. The dry weight of these component groups was determined. Lots of ten individuals of each size class in each component generic or family group were dried in an oven for 3 days at 65° C (Allen 1951). Freeze-dried individuals gave similar results to oven-dried individuals of the same size class and species. For incomplete animals in the stomachs, e.g. chironomid larvae, the size of the head usually gave a good indication of the original size of the animal.

* Present address: Freshwater Biological Association, Far Sawrey, Ambleside, Westmorland.

During this investigation it became apparent that invertebrate drift increased during the early hours of the night (Elliott 1965, 1967). Samples of fish taken at night were necessary to discover if this large potential 'drift food' was being taken by the salmonids. The time taken for food to pass through the stomach depends on the rate of digestion, and this determines the minimum period after sunset when fish can be taken whose stomachs contain only food ingested during the hours of darkness.

Very little direct work exists on the rate of digestion in salmonids. Heavily chitinized animals take longer to digest than those with little cuticle (Hess & Rainwater 1939; Reimers 1957), and the digestion time increases with a decrease in water temperature (Reimers 1957).

In the present study, the fish samples were taken at least 4 h after sunset, and it was hoped that all day food had passed out of the stomach by this time. Night samples were taken in April, May, June, August and October 1964, all samples being taken within 12 h of the corresponding day samples.

RESULTS

1. *Differences in the food of the* 0+, 1+ *and* 2+ *trout*

The stomach contents of 208 *Salmo trutta* were analysed. All the common members of the benthos and drift occurred in the trout stomachs, except nymphs of *Leptophlebia vespertina* and *Paraleptophlebia submarginata*. Although empty cases of *Sericostoma personatum* were occasionally present in the lower gut, the larvae were never found in the stomachs. Table 1 lists those invertebrates which were present in the stomachs of the different year classes. Only the stomachs of the 1+ and 2+ trout contained the larger members of the benthos and drift, these being chiefly adults of the Dytiscidae, large nymphs of the Ecdyonuridae, large oligochaetes, large larvae of the Tipulidae and stone-cased Trichoptera, and the larger terrestrial invertebrates. It appears that the 0+ trout could not utilize these larger invertebrates, but this did not explain the absence of the small Hydrachnellae and *Hydroptila* sp. from their stomachs.

In March and April 1964 trout fry were found in several 1+ and 2+ fish, but in all other months trout were present in the stomachs of only four 2+ fish.

To determine the most important food items in a year, mean values have been calculated for dry weight and numbers of invertebrates per ten trout stomachs (Table 2). Food items have been arranged according to their contribution to the total dry weight in the stomachs of the 2+ trout and have been given to the nearest 0·5%: the + sign indicates that the item constitutes less than 0·25% of the stomach contents. Dry weight probably gives a reasonable indication of the nutritional value of the food present in the stomachs. Numbers alone can be very misleading, and expressing biomass in wet weight exaggerates the importance of items with a high water content, e.g. Oligochaeta.

Of the twenty-nine items listed in Table 2, items 1–12 (down to *Leuctra* spp.) contributed 94, 92·5 and 84·2% to the total mean biomass in the stomachs of the 2+, 1+ and 0+ trout (only ten items for the 0+ trout). Although the remaining seventeen items contributed little to the mean biomass for the year, their importance often increased for one or more months.

There was a marked difference in the principal foods of the three fish classes. Large larvae of Limnephilidae (over 5 mm long) were almost exclusive to the 2+ trout and contributed the greatest biomass to the diet (stone cases were not included in the dry weights). Terrestrial invertebrates were next in importance in the 2+ fish and were

with Oligochaeta the pr
similar amounts in all f
the 0+ trout owing to t

Table 1. *Inverteb*

0+, 1+, 2+

AQUATIC
Plecoptera
Protonemura meyeri
Amphinemura sulcicol
Leuctra inermis
L. hippopus
Chloroperla torrentiun
Isoperla grammatica
Ephemeroptera
Baetis niger
B. scambus
B. rhodani
Trichoptera
Limnephilidae (under 5 long)
Rhyacophila munda
R. dorsalis
Hydropsyche instabilis
Polycentropus kingi
P. flavomaculatus
Oxyethira sagittifera
Megaloptera
Sialis lutaria
Diptera
Chironomidae (larvae ar
Simulium spp.
Coleoptera
Helmidae
Helmis maugei
Limnius tuberculatus
EMERGING AQUATIC INSECTS
Ephemeroptera
Trichoptera
Chironomidae
TERRESTRIAL INVERTEBRATES
Collembola
Hemiptera
Diptera
Thysanoptera
Psocoptera
Araneida
Acarina

of large limnephilid larv
diet probably reduced co
Generally, the biomas
of the trout. The total n
times that of the 1+ tro
reflection of the food rec

with Oligochaeta the principal items in the diet of the 1+ trout. Although present in similar amounts in all fish classes, nymphs of *Baetis* sp. became the principal food of the 0+ trout owing to the minor importance of terrestrial invertebrates and the absence

Table 1. *Invertebrates present in the stomachs of both night and day fish samples, June 1963 to October 1964*

	0+, 1+, 2+	1+, 2+	2+
AQUATIC	Plecoptera *Protonemura meyeri* *Amphinemura sulcicollis* *Leuctra inermis* *L. hippopus* *Chloroperla torrentium* *Isoperla grammatica* Ephemeroptera *Baetis niger* *B. scambus* *B. rhodani* Trichoptera Limnephilidae (under 5 mm long) *Rhyacophila munda* *R. dorsalis* *Hydropsyche instabilis* *Polycentropus kingi* *P. flavomaculatus* *Oxyethira sagittifera* Megaloptera *Sialis lutaria* Diptera Chironomidae (larvae and pupae) *Simulium* spp. Coleoptera Helmidae *Helmis maugei* *Limnius tuberculatus*	Ephemeroptera *Ephemerella ignita* Ecdyonuridae *Ecdyonurus venosus* *Rhithrogena semicolorata* Trichoptera Limnephilidae (over 5 mm long) *Hydroptila* spp. Coleoptera Hydroporini *Oreodytes rivalis* Arachnida Hydrachnellae Mollusca *Ancylastrum fluviatile* Oligochaeta	Plecoptera *Perlodes microcephala* Trichoptera *Silo pallipes* Diptera Tipulidae *Dicranota bimaculata* *Limnophila* sp. Coleoptera Helmidae *Latelmis volckmari* Dytiscidae *Deronectes 12-pustulatus* *Oreodytes septentrionalis* *Hydroporus erythrocephalus* *Agabus bipustulatus* *Orectochilus villosus*
EMERGING AQUATIC INSECTS	Ephemeroptera Trichoptera Chironomidae	Plecoptera	
TERRESTRIAL INVERTEBRATES	Collembola Hemiptera Diptera Thysanoptera Psocoptera Araneida Acarina	Hemiptera *Velia caprai* Hymenoptera Coleoptera Lepidoptera Isopoda *Oniscus asellus* Arachnida *Neobisium muscorum*	Diplopoda *Cylindrojulus punctatus* Chilopoda Arachnida *Leiobunum blackwalii* Mollusca *Arion circumscriptus*

of large limnephilid larvae and oligochaetes from their diet. These major differences in diet probably reduced competition for food between the fish classes.

Generally, the biomass and numbers of each item in the diet increased with the size of the trout. The total mean biomass in the stomachs of the 2+ trout was about 3·5 times that of the 1+ trout and 7 times that of the 0+ trout. If these values were a true reflection of the food requirements, then the latter must have increased markedly with the size of the trout, especially from 1+ to 2+. Although this was true in all months except December 1963, the increases in numbers in the diet were often less pronounced than increases in biomass (Table 3). This was due to the older trout taking larger invertebrates and therefore the numbers required for unit biomass decreased from 0+ to 2+ trout (see ratio of biomass : numbers in Table 3). The mean biomass per stomach

Table 2. *Mean biomass and numbers of invertebrates per ten fish over the period October* 1963 *to October* 1964 (*biomass in mg dry weight, numbers in parentheses and percentage contribution of each item to total biomass*)

	2+			1+			0+		
Mean lengths of trout:		>15 cm			7–12 cm			<7 cm	
	mg	(No.)	%	mg	(No.)	%	mg	(No.)	%
Limnephilidae (over 5 mm long)	274·5	(27·5)	50	5	(0·5)	3	0		
Terrestrial invertebrates	89	(25·5)	16	37	(15)	22·5	4	(4·5)	5
Protonemura meyeri	29	(24)	5	14	(10)	8·5	6	(7)	7·5
Baetis spp.	20·5	(22)	4	17	(17)	10	18·5	(19·5)	23
Isoperla grammatica	20·5	(18·5)	4	9	(8)	5·5	5	(4·5)	6
Rhyacophila spp.	19·5	(4)	3·5	7	(1·5)	4	6	(1)	7·5
Oligochaeta	19·5	(2)	3·5	37	(4)	22·5	0		
Emerging aquatic insects	14·5	(11·5)	2·5	10	(8·5)	6	7	(6)	9
Chironomidae (larvae)	12·5	(62·5)	2	9	(45·5)	5·5	6	(33·5)	7·5
Polycentropus spp.	9	(6)	1·5	4	(2·5)	2	10	(7)	12·5
Chironomidae (pupae)	6	(15)	1	3	(6)	2	3	(6)	4
Leuctra spp.	6	(11)	1	2	(2)	1	2	(3·5)	2·5
Perlodes microcephala	6	(1)	1	0			0		
Limnephilidae (under 5 mm long)	3	(14)	0·5	5	(0·5)	3	1	(5)	1
Simulium spp.	2·5	(8)	0·5	1	(3·5)	0·5	2	(7)	2·5
Dytiscidae	2·5	(1·5)	0·5	1	(0·5)	0·5	0		
Ancylastrum fluviatile	2·5	(1)	0·5	1	(+)	0·5	0		
Ecdyonuridae	2·5	(0·5)	0·5	1	(+)	0·5	0		
Chloroperla torrentium	1·5	(3)	+	0·5	(1)	+	0		
Helmidae	1·5	(2)	+	0·5	(2)	+	3	(4)	4
Ephemerella ignita	1	(1)	+	+	(+)	+	0		
Silo pallipes	1.	(1)	+	0			0		
Hydropsyche instabilis	1	(0·5)	+	3	(1·5)	2	3·5	(2)	4·5
Amphinemura sulcicollis	0·5	(4·5)	+	+	(2·5)	+	0·5	(4)	0·5
Hydrachnellae	0·5	(2·5)	+	+	(2)	+	0		
Tipulidae	0·5	(0·5)	+	0			0		
Oxyethira sagittifera	+	(1·5)	+	+	(2·5)	+	0·5	(6)	0·5
Hydroptila sp.	+	(1·5)	+	+	(1)	+	0		
Sialis lutaria	+	(+)	+	0			1	(0·5)	1
Total mean biomass (No.)	547	(273·5)		165	(152)		79	(121)	
No. of trout		91			61			26	

showed least variation in the 2+ trout and only in this class were monthly variations in biomass less than those in numbers. The mean biomass showed no definite seasonal pattern, and there was no correlation between mean water temperature and the amount of food per stomach.

The stomachs of six young *Salmo salar* (5·5–6·9 cm) were examined during the course of this work. The diet of the young salmon appeared to be very similar to that of the 0+ trout.

2. *Seasonal changes in diet*

The proportion of each item in the diet of trout collected during daylight has been calculated as a percentage of the total stomach contents, using both numbers and biomass. These proportions for 0+, 1+ and 2+ trout are compared with those in the monthly drift and bottom samples (Fig. 1). As the composition of the drift differed considerably from day to night, only day samples were used in determining the proportions in the drift.

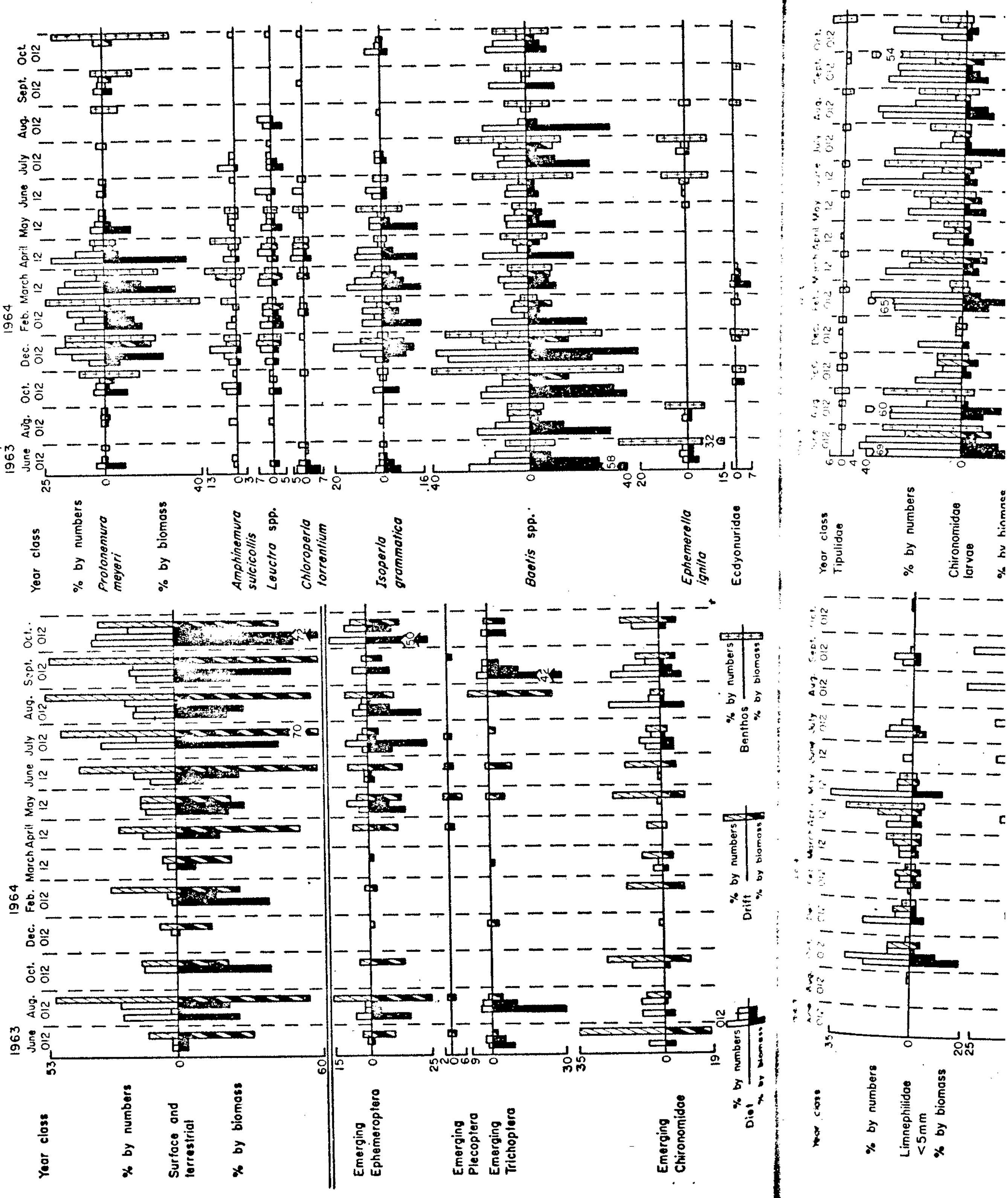
Table 3. *Mean biomass (mg dry weight) and number of invertebrates per fish stomach for day samples only*

	2+		1+		0+		Mean water temperature
No. of trout	82		46		23		(°C)
	mg	(No.)	mg	(No.)	mg	(No.)	
1963 June	58	(39)	19	(33)	5	(11)	14·3
August	64	(33)	26	(32)	13	(19)	13·2
October	23	(14)	7	(14)	3	(5)	10·2
December	24	(12)	4	(5)	14	(12)	5·0
1964 February	71	(64)	20	(39)	13	(21)	4·7
March	71	(49)	15	(17)			6·6
April	61	(23)	15	(15)			8·4
May	48	(22)	7	(13)			10·9
June	70	(24)	44	(22)			12·0
July	56	(21)	14	(19)	6	(14)	14·4
August	36	(11)	7	(12)	5	(10)	16·0
September	84	(25)	15	(12)	5	(11)	13·7
October	25	(15)	26	(10)	2	(4)	9·0
Mean	53	27	17	19	7	11·8	
Biomass: numbers	1:0·5		1:1·1		1:1·6		
Coefficient of variability (%)	37	54	59	51	63	44	

There was a marked seasonal change in the food habits of the trout. Nymphs of Plecoptera, especially *Protonemura meyeri* and *Isoperla grammatica*, small larvae (under 5 mm long) of Limnephilidae and larvae of *Hydropsyche instabilis* were important foods in winter (November to April) and were replaced in summer (May to October) by nymphs of *Ephemerella ignita*, Helmidae (adults and larvae of *Helmis maugei*, *Limnius tuberculatus* and *Latelmis volkmari*), chironomid pupae, emerging aquatic insects, and terrestrial invertebrates (Fig. 1).

Nymphs of *Baetis* spp., large larvae (over 5 mm long) of Limnephilidae, larvae of *Rhyacophila* spp., *Polycentropus* spp., Chironomidae, and *Simulium* spp. were important foods throughout the year. Of the three *Baetis* spp. (*B. rhodani*, *B. niger*, *B. scambus*) in the diet in summer, only *B. rhodani* appeared to be present in the stomachs in winter. Although rare in the diet, some animals increased in importance in one month, e.g. Hydroptilidae in October 1963 and 1964, Dytiscidae in August 1963 and 1964, *Ancylastrum fluviatile* in October 1963, Hydrachnellae in October 1964, and larvae of *Sialis lutaria* in October 1963 (forming 40% of the biomass in the stomachs of 0+ trout).

It was also possible to estimate the relative importance of invertebrate drift and benthos in the day food of the trout.


1963
1964
June
Aug.
Oct.
Dec.
Feb.
March
April
May
July
Sept.
Year class
% by numbers
% by biomass
Protonemura meyeri
Amphinemura sulcicollis
Leuctra spp.
Chloroperla torrentium
Isoperla grammatica
Baetis spp.
Ephemerella ignita
Ecdyonuridae
Tipulidae
Chironomidae larvae
Surface and terrestrial
Emerging Ephemeroptera
Emerging Plecoptera
Emerging Trichoptera
Emerging Chironomidae
Limnephilidae <5mm
Diet
Drift
Benthos

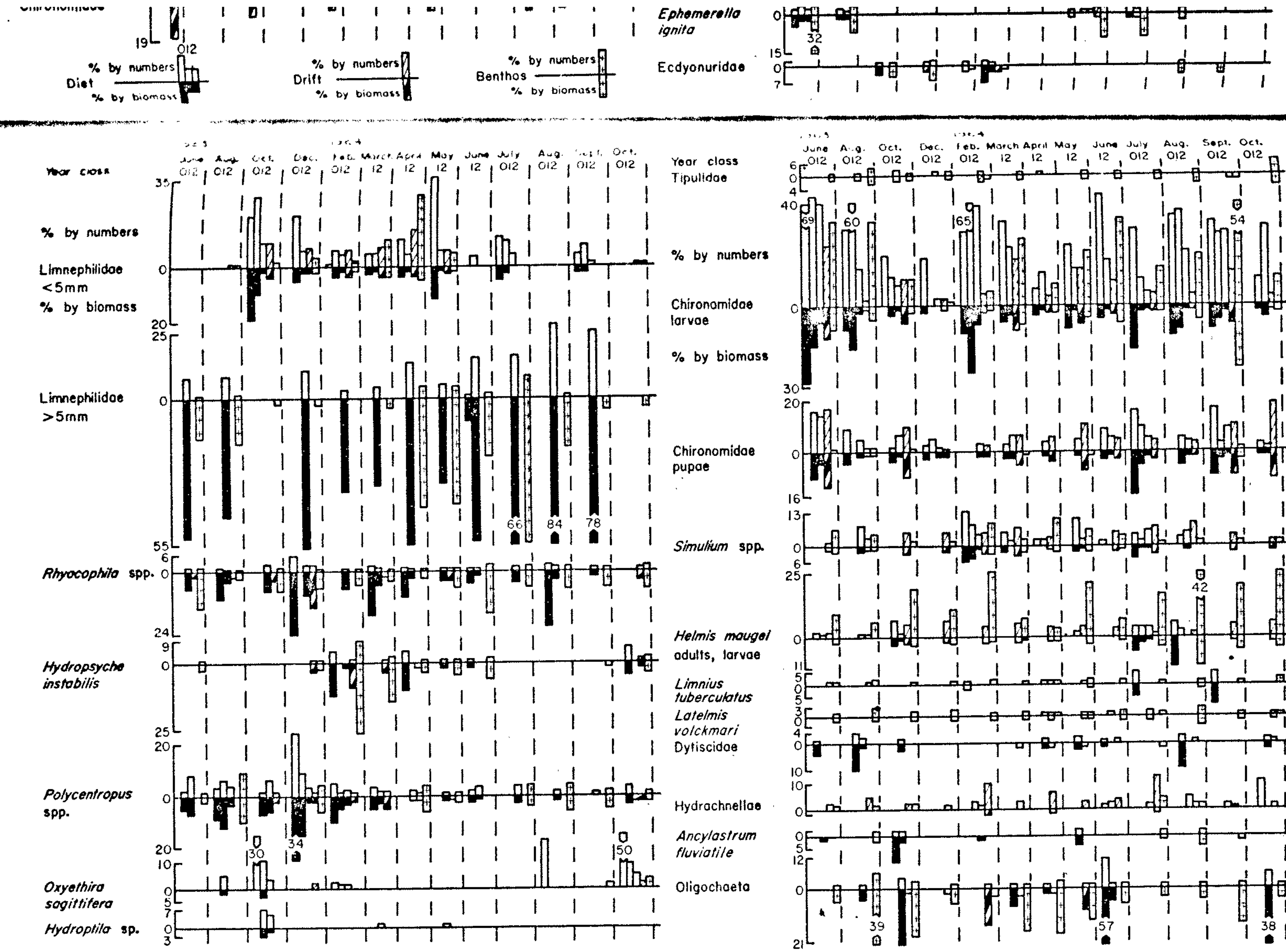


FIG. 1. The diet of the 0+, 1+ and 2+ trout compared with the monthly drift and bottom samples. All proportions given as percentages, both by numbers and biomass.

Terrestrial invertebrates and emerging aquatic insects were only present in the drift and formed an important part of the day food, especially in summer (Fig. 1, upper left). Chironomid pupae, Hydrachnellae and *Simulium* spp. formed a small proportion of the benthos but were important in both the day food and the drift. Although often abundant in the benthos, *Ephemerella ignita* and *Helmis maugei* formed a small proportion of both diet and drift. Either these animals were taken directly from the benthos in small numbers or they were only available to the trout when in the drift.

Large limnephilid larvae with stone cases were never in the drift and formed an important food of the 2+ trout. Other exclusively benthic animals (*Ancylastrum fluviatile* and larvae of *Silo pallipes, Sericostoma personatum*) were occasionally taken by the 1+ and 2+ trout. Oligochaetes were almost exclusive to the benthos and formed a significant proportion of the diet in October 1963, June 1964 and October 1964. It is likely that chironomid larvae also were taken in considerable numbers from the benthos as they often represented a far greater proportion of the diet than in the drift. This was probably also true of *Protonemura meyeri*, *Rhyacophila* spp., *Hydropsyche instabilis* and *Polycentropus* spp., which often formed a small proportion of the day drift but a large proportion of both diet and benthos.

Whereas most of the animals taken exclusively from the drift were only important as constituents of the diet in summer, those taken chiefly from the benthos were important in both summer and winter (*Protonemura meyeri* and *Hydropsyche instabilis* only in winter). Although, at first, invertebrate drift appears to be unimportant as a food in winter, there were animals which were probably taken from both drift and benthos in large numbers, e.g. *Baetis* spp., nymphs of Plecoptera (except *Protonemura meyeri*) and small larvae of Limnephilidae. The latter often occurred in the drift and the absence of later instars from the drift was associated with the change from vegetable to stone cases (Elliott 1967).

3. *The night food of the trout*

At night there was a large increase in the number of aquatic invertebrates in the drift and this section deals with the night food of the trout in relation to this large potential 'drift food'.

Mean values were calculated for biomass and numbers of invertebrates per ten fish. If the assumed digestion time of 4 h was correct, the presence of animals in the stomachs indicated that trout were feeding in the early hours of the night. This was supported by differences between the stomach contents of trout collected at night and during the day. In Table 4 the food items have been divided into two groups according to their importance in the diet during the day or at night.

Terrestrial invertebrates, emerging Ephemeroptera and Hydrachnellae were present in greatest numbers in the drift during the day and this probably explains their greater importance in the diet during the day than at night. Large limnephilid larvae, oligochaetes, *Perlodes microcephala*, *Silo pallipes* and *Ancylastrum fluviatile* were also more important in the diet during the day and were only taken from the benthos.

Most of the Plecoptera, Trichoptera and Chironomidae emerged during the early hours of the night (Elliott 1967) and were more important in the night food than in the day food (Table 4). This was strong evidence for 'drift feeding' in the early hours of the night, and was supported by the presence of fifteen trout fry in six trout of the April night sample contrasted with only one fry in the day sample. Downstream movement of trout fry occurred at this time of year and was at a maximum in the early hours of the night (Elliott 1966).

The remaining food items in the second group in Table 4 (*Baetis* spp. to *Helmis maugei*) all increased in importance at night. Although many of these aquatic invertebrates could have come from either drift or benthos, it is suggested that their increased

Table 4. *Comparison of day and night samples for April, May, June, August, and October 1964 (mean biomass and numbers of invertebrates per ten fish)*

	2+		1+		0+	
	Day mg(No.)	Night mg(No.)	Day mg(No.)	Night mg(No.)	Day mg(No.)	Night mg(No.)
MORE IMPORTANT IN DIET DURING DAY						
Ephemeroptera (emerging)	13(7)	3(2)	5(3)	4(2)	10(5)	0
Terrestrial invertebrates	110(30)	97(42)	48(18)	23(8)	10(13)	5(2)
Limnephilidae (over 5 mm long)	250(25)	153(15)	10(1)	5(+)	0	0
Oligochaeta	20(2)	0	75(8)	0	0	0
Chironomidae (pupae)	4(9)	3(7)	3(7)	2(4)	0	1(1)
Perlodes microcephala	7(1)	0	0	0	0	0
Silo pallipes	3(2)	0	0	0	0	0
Ancylastrum fluviatile	3(1)	0	0	0	0	0
Hydrachnellae	+(2)	0	+(4)	0	0	0
Total per ten fish	410(79)	256(66)	141(41)	34(14)	20(18)	6(3)
MORE IMPORTANT IN DIET AT NIGHT						
Plecoptera (emerging)	0(+)	27(12)	0	7(6)	0	0
Trichoptera (emerging)	0	37(8)	2(+)	0	0	19(4)
Chironomidae (emerging)	2(4)	3(9)	1(4)	2(7)	0	0
Baetis spp.	13(13)	69(73)	17(17)	25(26)	8(8)	30(30)
Ephemerella ignita	1(1)	2(2)	1(1)	1(2)	0	0
Protonemura meyeri	16(12)	24(16)	12(8)	13(9)	0	6(4)
Isoperla grammatica	15(13)	17(15)	9(8)	8(8)	0	1(1)
Chloroperla torrentium	2(4)	2(4)	1(2)	1(2)	0	0
Leuctra spp.	5(9)	6(11)	2(3)	4(7)	0	0
Amphinemura sulcicollis	+(3)	2(9)	+(2)	2(10)	0	0
Ecdyonuridae	0	8(2)	0	2(+)	0	0
Limnephilidae (under 5 mm long)	2(10)	4(18)	3(12)	3(10)	0	0
Rhyacophila spp.	10(2)	33(7)	10(2)	10(2)	0	6(2)
Polycentropus spp.	5(3)	9(6)	3(2)	5(3)	0	2(1)
Hydropsyche instabilis	1(+)	4(2)	6(3)	6(4)	0	5(2)
Chironomidae (larvae)	7(35)	7(31)	6(28)	9(47)	3(15)	6(35)
Simulium spp.	2(8)	2(8)	+(2)	3(7)	0	21(69)
Dytiscidae	+(1)	2(1)	+(1)	4(3)	0	0
Helmis maugei	+(1)	1(5)	+(+)	1(4)	2(2)	1(4)
Total per ten fish	81(119)	259(239)	73(95)	106(157)	13(25)	97(152)
No. of trout	29	29	20	20	4	8

importance in the diet was associated with the increase in numbers in the drift at night. It was therefore concluded that whilst feeding in the early hours of the night the trout had utilized some of the large potential 'drift food'.

DISCUSSION

Few workers have attempted to assess the availability (accessibility) of aquatic invertebrates to salmonids. Neill (1938) divided the benthos into five categories according to its accessibility to trout. Allen (1941) determined the 'availability factor' for each invertebrate by comparing the percentage by number of each animal in the diet with percentage by number of the same animal in the benthos. Both Hynes (1950) and Maitland (1964) have criticized Allen's sampling techniques and use of numbers rather than biomass. Hynes (1950) concluded that percentage by bulk should be used to determine availability factors and this method has been used by Maitland (1965).

In the Walla Brook, the variation in diet between trout of the same year class and sample was often considerable, especially with the larger fish. Macan, McCormack &

Table 5. *The availability factors of the aquatic invertebrates in the diet (a + indicates < 0·1)*

	Benthos (% by weight)	2+		1+		0+	
		Day	Night	Day	Night	Day	Night
AF GREATER IN DAY THAN AT NIGHT							
Limnephilidae (over 5 mm long)	20·0	3·4	2·2	0·3	0·2	0	0
Oligochaeta	7·2	0·8	0	6·6	0	0	0
Perlodes microcephala	10·5	0·2	0	0	0	0	0
Silo pallipes	1·4	0·6	0	0	0	0	0
Ancylastrum fluviatile	0·9	0·9	0	0	0	0	0
Hydrachnellae	0·1	+	0	+	0	0	0
AF GREATER AT NIGHT THAN IN DAY							
Baetis spp.	10·5	0·3	1·9	1·0	2·3	5·9	3·6
Chloroperla torrentium	0·6	0·8	1·0	1·0	1·7	0	0
Protonemura meyeri	12·0	0·4	0·6	0·6	1·0	0	0·6
Amphinemura sulcicollis	0·5	0·2	1·2	0·1	4·0	0	0
Rhyacophila spp.	8·8	0·3	1·1	0·7	1·1	0	0·9
Polycentropus spp.	3·0	0·5	1·0	0·7	1·7	0	0·8
Ecdyonuridae	0·7	0	3·3	0	2·9	0	0
Dytiscidae	0·2	+	3·0	+	19·0	0	0
Limnephilidae (under 5 mm long)	0·8	0·6	1·4	2·4	3·8	0	0
Simulium spp.	0·9	0·7	0·7	0·1	3·3	0	29·6
Leuctra spp.	0·5	2·8	3·4	2·6	7·6	0	0
Isoperla grammatica	2·0	2·1	2·5	2·9	3·9	0	0·5
Chironomidae (pupae)	0·2	5·0	5·0	9·5	9·5	0	0·5
Chironomidae (larvae)	3·5	0·5	0·6	1·1	2·5	6·6	2·4
Hydropsyche instabilis	3·2	0·1	0·3	1·2	1·9	0	2·0
Ephemerella ignita	2·0	0·2	0·3	0·3	0·5	0	0
Helmidae	5·9	+	0·1	+	0·2	2·6	0·2
Others	4·6	0	0	0	0	0	0
No. of trout		29	29	20	20	4	8

Maudsley (1966) have also found that availability factors varied considerably from year to year in Hodson's Tarn. Therefore availability factors can only be used to show general tendencies in the feeding pattern of trout.

Availability factors (AF) were calculated for aquatic invertebrates in the diet during the 5 months when both day and night fish samples were taken. These values were obtained by using the formula AF = d/b, where d is the percentage by biomass in the diet and b is the percentage by biomass in the benthos. As terrestrial invertebrates and emerging aquatic insects were not included in the total biomass for the diet, the aquatic invertebrates formed 100% of both diet and benthos. Therefore an availability factor of 1 indicates that an invertebrate was taken strictly in accordance with its occurrence in the benthos. The aquatic invertebrates were divided into two groups according to their availability factor (Table 5).

All the animals in the first group (large Limnephilidae to Hydrachnellae) were more available to the trout during the day than at night, and all except the Hydrachnellae were only taken from the benthos. The greatest numbers of Hydrachnellae were in the drift during the day (Elliott 1967) and this agrees with their availability to the trout. At night the large limnephilid larvae were still readily available to the 2+ trout (AF 2·2). Although these larvae were an easily available food and were often seen crawling across the bottom of the stream, they were only fully utilized by the 2+ trout. As the 1+ trout fully utilized the larger oligochaetes, the low availability factor for limnephilid larvae was not due to their large size. The stone cases appeared to be the only possible reason for the low availability factor.

Table 6. *The different groups of availability factors for those animals which increased in availability at night*

2+	1+
AF < 1 IN DAY AND 1 OR MORE AT NIGHT	
Baetis spp.	*Baetis* spp.
Chloroperla torrentium	*Chloroperla torrentium*
Amphinemura sulcicollis	*Protonemura meyeri*
Rhyacophila spp.	*Amphinemura sulcicollis*
Polycentropus spp.	*Rhyacophila* spp.
Ecdyonuridae	*Polycentropus* spp.
Dytiscidae	Ecdyonuridae
Limnephilidae > 5 mm	Dytiscidae
	Simulium spp.
AF > 1 IN BOTH DAY AND NIGHT	
Leuctra spp.	Limnephilidae < 5 mm
Isoperla grammatica	*Leuctra* spp.
Chironomidae (pupae)	*Isoperla grammatica*
	Chironomidae (pupae and larvae)
	Hydropsyche instabilis
AF < 1 IN BOTH DAY AND NIGHT	
Protonemura meyeri	*Ephemerella ignita*
Simulium spp.	Helmidae
Chironomidae (larvae)	
Hydropsyche instabilis	
Ephemerella ignita	
Helmidae	

Although the availability of all the animals in the second group (*Baetis* spp. to Helmidae) increased at night, the magnitude of the availability factors varied considerably and three distinct groups were recognized (Table 6). As only four 0+ fish were taken in the day samples, this year class was not included in Table 6.

As a day food, the animals in the first group (AF < 1 in day) were not easily available to the trout, whereas those in the second group (AF > 1 in day) were readily available. At night, all animals in both groups were readily available to the trout (AF 1 or more at night) and most of the animals in the first group were taken in accordance with their occurrence in the benthos whilst those in the second group were more available than in the day. Animals in the third group (AF < 1 in both day and night) were not easily available to the trout. Some of the animals were only in this group for 2+ trout, and were readily available to the 1+ trout in both day and night (chironomid larvae and *Hydropsyche instabilis*) or only at night (*Protonemura meyeri* and *Simulium* spp.). There was no apparent reason why these animals were only readily available to the smaller trout.

It was only at night that most of the aquatic invertebrates had availability factors of 1 or more (Tables 5 and 6) and this indicates a definite change in the habits of these invertebrates. All these animals were often in the drift and the increase in availability factors at night was associated with a nocturnal increase in invertebrate drift. The presence of more aquatic invertebrates on the tops of stones at night (Elliott 1967) could also account for the higher availability factors. Brett (1957) has shown that young coho salmon can feed at a light intensity of 0·0001 ft-candles and there is no reason why trout should have inferior scotopic vision. Young salmon were observed to feed at a high intensity during the light nights of the summer (Kalleberg 1958) and the salmonids investigated by Hoar (1942) fed well into the night. In the summer months of the present study, large numbers of trout were frequently observed at night in midwater and at the surface. They were usually fairly stationary and always faced upstream.

It is concluded that the availability of many benthic animals increased at night and that the trout were utilizing this readily available food either as drift or from the tops of stones. Although this may occur throughout the night in all months of the year, the observations in the Walla Brook are only for the early hours of the night during the summer months.

ACKNOWLEDGMENTS

I wish to express my sincere thanks to the following for their help in this work: Professor L. A. Harvey, under whose supervision this work was carried out; The Devon River Authority, especially Mr M. E. Wilson and Mr B. R. Letts, for their assistance in the field and the loan of all fishing gear; my colleague Dr M. R. Rudge for his frequent assistance in the field; and Dr R. W. Edwards and Dr T. T. Macan for all their help in the preparation of this paper.

The work was supported by a grant from the Development Commission.

SUMMARY

1. The food of trout (*Salmo trutta*) was investigated in relation to the invertebrate drift and the benthos.

2. Using an electrical stunning machine, fish samples were taken from June 1963 to October 1964 in the day and from April to October 1964 at night.

3. Nearly all the common members of the benthos and drift occurred in the trout stomachs, but only the 1+ and 2+ trout contained the larger members of the benthos and drift. The biomass and numbers of most items in the stomachs increased with the size of the trout, and showed no definite pattern when compared on a monthly basis.

4. The principal day foods were nymphs of *Baetis* spp. for 0+ trout, terrestrial invertebrates and oligochaetes for 1+ trout, and large larvae of Limnephilidae for 2+ trout. It is suggested that this marked difference in the principal foods reduced the competition for food between the fish classes.

5. Most of the animals taken exclusively from the drift were only important as constituents of the diet in summer, and those taken chiefly from the benthos were important in both winter and summer. Some animals were taken from both drift and benthos in large numbers, especially in winter.

6. The fish samples taken at night indicated that the trout were feeding in the early

hours of the night during the summer months. It is concluded that the availability of many benthic animals increased at night and that the trout were utilizing this readily available food either as drift or from the tops of stones.

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(*Received* 14 *April* 1966; *revision received* 1 *September* 1966)