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A quantitative study of the invertebrate fauna of the River Tees below Cow Green Reservoir

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Summary

Monthly samples were taken in the River Tees below Cow Green dam from four sites differing in flow conditions, by means of trays containing stones from the river, which were immersed for a period of 1 month. Information on the distribution, abundance and biomass of the benthos of the River Tees is given with additional data on the life-histories of some of the more common species, during the period May 1971 to May 1972.

Of the seventy-two taxa found, fourteen made up 95% of the total numbers. Hydra, Polycentropodidae, and the molluscs Limnaea peregra and Ancylus fluviatilis were the most abundant animals in the slower-flowing water (10–26 cm s⁻¹) and Simuliidae, Orthocladiinae, and Baetis rhodani dominate the riffle (50–75 cm s⁻¹) fauna numerically. Some organisms, Nais spp., Caenis rivulorum and Baetis scambus favoured intermediate flows of 20–60 cm s⁻¹. The slowest-flowing water contained the largest number of taxa and the site with the fastest flow supported the least. A mean monthly weight per square metre of 14·56 g (95% limits from 7 to 31) was calculated using data from all four sites.

The frequency distribution of nymphal size-classes is given for B. scambus, C. rivulorum, Ephemerella ignita, and Brachycentrus subnubilus, and the association of certain nymphal size-classes with a particular site is analysed.

The composition and distribution of the fauna is discussed. It is suggested that the relative richness of the fauna in terms of biomass is attributable to the organic enrichment of the river following the building of the Cow Green dam. The regulation of the flow has allowed the dense growth of algae and mosses, and the development of large molluscan populations, and the reservoir itself provides a rich source of food, particularly zooplankton and phytoplankton, for the river benthos.

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Introduction

Cow Green reservoir was completed in the summer of 1970 and at this time a programme of studies on invertebrates was initiated to monitor any changes in the benthos of the Tees below the dam after impoundment. This programme included studies of drift and longitudinal zonation and the purpose of the present study is to supply background information on life-histories, absolute abundance and biomass of the benthos for a period of 1 year between May 1971 and May 1972.

Previous work on invertebrates in the upper part of the Tees is limited to a survey (Butcher, Longwell & Pentelow, 1937) which was rather cursory in the present study area and which suffered from a lack of suitable keys to identification; and a recent general survey (Armitage, MacHale & Crisp, 1974) which dealt mainly with annual and seasonal changes in the relative abundance of the benthos before impoundment.

Study area and methods

The Tees rises on the eastern slope of Cross Fell in the North Pennines at an altitude of 772 m and flows over the Carboniferous mountain-limestone series, which also contains basalt intrusions, to the Cow Green basin now occupied by the reservoir. Glacial drift is widespread in the area. About 180 m below the dam the river falls 60 m down a ravine of basalt known as Cauldron Snout. Below the falls there is a large deep pool and from here the Tees is a fast-flowing stream generally not exceeding 1 m in depth and ranging in width from 20 to 30 m during normal flow. 200 m downstream from the foot of the fall, the Tees is joined by a major tributary, Maize Beck. The present study area was situated midway between the foot of the falls and the junction with Maize Beck, (National Grid Reference NY 814284), and lies at an altitude of 430 m. The bottom consists of solid rock with firmly bedded large stones and emergent boulders. Normal discharges from the reservoir range from 0·45 to 2·0 $m^3\ s^{-1}$ and the frequency of spates in the Tees is reduced. However, during the winter when the reservoir reaches top water level and flows down the spillway high flows (23·4 $m^3\ s^{-1}$) can occur. These flows do not carry the pre-impoundment sediment load because coarse particles settle out in the reservoir and therefore do not scour the bottom. It is possible that the high winter flows will remove small stones from the riffle areas and these will not be replaced from upstream because of the dam. Loose stones and gravel are uncommon and areas suitable for 'kick-sampling' are restricted. The larger stones and boulders support algal and moss growth for most of the year with particularly dense growths of filamentous algae during the summer months. Mats of the blue-green alga *Oscillatoria* sp. occur on the bottom of some of the deeper pools.

Observations on diel temperature and oxygen changes were made during the summer period in the Tees and Maize Beck. Table 1 shows the ranges and means for both during five 24-h periods. Measurements in the reservoir by Dr D. T. Crisp (personal communication) indicated that there was little difference between top and bottom-water temperatures and the reservoir temperatures approximate closely to those taken in the Tees below Cauldron Snout. This results in a reduction of diel fluctuations as compared with the large fluctuations recorded in the unregulated Maize Beck.

Table 1. The range and mean of temperature and dissolved oxygen readings taken every hour during 24 h (noon–noon) sampling periods in the Tees below Cauldron Snout (TBCS) and in Maize Beck (MzB) in 1971

		Temperature (°C)		Oxygen (% saturation)	
Date	River	Range	$\bar{x}$	Range	$\bar{x}$
13–14 May	MzB	7·5–13·7	10·5	86·5– 99·0	95·6
	TBCS	7·9– 8·9	8·2	95·5–100·0	97·6
10–11 June	MzB	7·8–11·7	9·2	89·5– 93·0	91·2
	TBCS	10·4–10·7	10·5	92·0– 96·5	94·5
8–9 July	MzB	14·8–25·1	19·4	87·0– 99·0	91·9
	TBCS	12·5–13·3	13·2	97·5–103·0	99·5
12–13 Aug.	MzB	11·6–14·2	12·6	93·0–100·0	95·3
	TBCS	13·6–14·8	13·9	91·0–100·0	94·9
9–10 Sept.	MzB	11·3–18·1	13·8	93·0–100·0	95·8
	TBCS	12·3–13·6	12·7	93·0–100·5	96·5

Table 2. Depth and current speed (cm s^{-1}) at the four sampling sites at flows of 0·9 and 2·4 $m^3\ s^{-1}$ (in parentheses). The anomalous readings at P1 are due to eddies and back-wash. No reading could be obtained at R2 due to the fast flow (2·4 $m^3\ s^{-1}$) causing turbulence

		Current speed	
Site	Depth (cm)	Surface	Tray depth
P1	60	20 (15)	26 (10)
P2	30	28 (57)	20 (17)
R1	40	58 (90)	60 (50)
R2	30	143 (—)	53 (75)

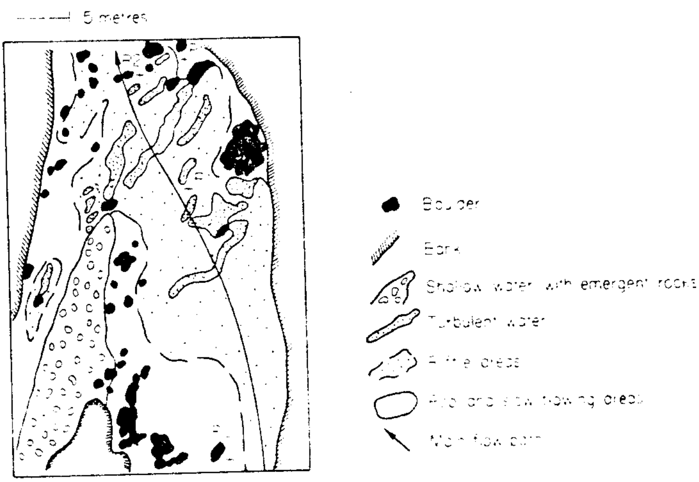

Fig. 1. Sketch map of study area showing the relative positions of sites P1, P2, R1, and R2.

Because of the fast flow in riffle areas, and the depth and substratum characteristics it was not possible to use the usual sampling methods for stony streams (Macan, 1958) and instead, trays containing stones from the river were submerged for 1 month at four sites differing in flow conditions (see Fig. 1 and Table 2). An important factor in the selection of the sites was that the trays should rest as flatly as possible on the bottom to increase stability and maintain close contact between the tray and the river substratum. All sites had substrata composed of firmly bedded rocks, with gravel and coarse sand rather scarce. The pool sites P1 and P2 received large amounts of silty sand and sites P2 and R1 supported the densest algal growth. The bottom deposit at site R2, because of the current speed, contained few particles less than 4 mm in diameter.

Trays have been used by several workers (Moon 1935; Wene & Wickliff, 1940; Egglishaw, 1964). They have been criticized by Hynes (1970) as being unsuitable for production studies, but often they are the only way to obtain large numbers of species.

In the present study, seed trays made of grey plastic with perforated bottoms were used and each measured 21·5 × 35·5 cm and was 5·5 cm deep. In order to standardize the trays as much as possible, forty-eight stones (ranging from 10 to 15 cm in diameter) were selected, measured and grouped to make up sixteen trays each containing three stones together having a surface area ranging from 1000 to 1100 cm^2. The stones rested on some gravel and sand, all components being taken from the river-bed near the sampling sites. The trays were fitted with polypropylene rope handles. Since this material floats, the handles were clear of the tray surface and easy to grasp. During removal of the trays, a net (25 threads/cm) was held downstream to catch any animals swimming or drifting away, though observations during lifting indicated that the great majority of the fauna stayed with the tray. Plastic is known to encourage settlement of some organisms, particularly simuliid larvae, (Wolfe & Peterson, 1958; Williams & Obeng, 1962), and therefore animals were never taken from the sides of the trays; collections being restricted to organisms present on and within the stone and gravel substratum.

After lifting, the stones were washed and scrubbed, and the gravel and sand elutriated and sieved through screens of mesh apertures 1·0, 0·5 and 0·25 mm. The 0·25-mm mesh will allow very young instars of some of the groups, especially chironomids, to pass through (Jonasson, 1955), but some of these would not appear in tray samples since they are found deep in the substratum. The advantages of the 0·25-mm mesh is that by reducing sorting time it allows more samples to be taken. Despite this, limitations in time and man-power made it impossible to lift more than one tray per month at each of the four sites, P1, P2, R1 and R2.

The washed residues were preserved in 70% methanol. Large numbers of small animals present in the 250-μm sieve were sub-sampled. The animals were identified, measured (head-capsule width) and weighed to the nearest mg, giving 'preserved wet-weight' which is approximately the same as the wet-weight of fresh specimens (Mackay & Kalff, 1969).

One tray was lifted from each site every month, except in August when the trays were destroyed by vandals and in winter months when some trays in the riffle areas were carried away by extreme flows over the top of the dam. At these times, non-quantitative samples were taken by disturbing the substratum. The results from these samples were not used to compare numbers and biomass at each station.

Results

The total numbers of animals taken at each site during the study period are shown in Table 3. Of the seventy-two taxa found, fourteen make up 95% of the total. The remaining fifty eight taxa occurred at low densities. Site P1 contained the most taxa (sixty-three) and site R2 the least (forty-four). Of the twenty-seven rarer taxa occurring in one or two sites, seventeen were found only in the pool sites, three in both riffles and pools and seven only in riffles.

In a previous survey in the area, covering the period 1968–70 (Armitage *et al.*, 1974), most of the samples taken in the Tees were qualitative. Table 4 gives the taxa which were present in this pre-inundation survey but which were not found in the present study, and also the additional taxa found in the tray samples.

Amongst the stoneflies, *Perla bipunctata* which usually occurs on unstable bottoms was absent, but the other large perlid *Dinocras cephalotes* which favours stable substrata (Hynes, 1941) was found occasionally, and *Perlodes microcephala* which used to be present before the dam was built, no longer occurs. Its absence may be due to the lack of large

Table 3. The total numbers of animals caught in trays at sites, P1, P2, R1 and R2 during the study period. Part (a) lists the abundant and common taxa and part (b) lists the rarer forms. (The non-quantitative August, January, February, March and April samples are excluded from the totals. + indicates presence of a species in a non-quantitative sample)

(a) Abundant and common species

	P1	P2	R1	R2	Total
Hydra vulgaris	7494	3394	964	91	11943
Nematoda	14	1	15	—	30
Naididae*	1136	3685	4578	2378	11777
Lumbriculidae	1	9	11	1	22
Enchytraeidae	7	19	34	2	62
Leuctra inermis Kempny	4	14	12	22	52
Leuctra fusca (L.)	10	18	11	8	47
Amphinemura sulcicollis (Stephens)	1	7	10	12	30
Caenis rivulorum Eaton	116	189	249	103	657
Ephemerella ignita (Poda)	15	44	44	24	127
Baetis rhodani (Pict.)	527	837	1345	1186	3895
Baetis scambus/bioculatus	69	93	142	31	335
Baetis muticus (= *pumilus*) (Burm.)	1	8	12	13	34
Ecdyonurus dispar (Curt)	6	6	13	8	33
Ecdyonurus torrentis Kimmins	5	8	2	1	16
Rhithrogena semicolorata (Curt.)	3	28	107	19	157
Rhyacophila dorsalis (Curt.)	15	29	82	63	189
Hydropsyche sp.	7	9	22	42	80
Polycentropus flavomaculatus	153	33	26	4	216
Plectrocnemia geniculata (McLachlan)	14	7	28	1	50
Neureclipsis bimaculata (L.)	25	1	2	—	28
Brachycentrus subnubilus (Curt.)	19	11	17	4	51
Limnius volckmari Panz.	23	61	17	7	108
Elmis aenea (Müll.)	11	25	32	26	94
Esolus parallelepipedus (Müll.)	11	14	18	31	74
Orthocladiinae	1012	740	1226	1146	4124
Tanytarsini	257	61	13	8	339
Tanypodinae	83	66	50	49	248
Simuliidae†	125	214	3663	2551	6553
Clinocera sp.	7	7	3	14	31
Dicranota sp.	3	3	6	3	15
Hydrachnellae	15	2	15	5	37
Lymnaea peregra (Müll.)	1155	1078	390	89	2712
Ancylus fluviatilis (Müll.)	330	417	277	71	1095
	12674	11138	13436	8013	45261

(b) Rarer species

	P1	P2	R1	R2	Total
Tricladida	1	1	–	–	2
Eiseniella tetraedra (Savigny)	1	3	3	–	7
Peloscolex ferox (Eisen)	1	4	5	–	10
Glossiphonia complanata (L.)	2	–	1	+	3
Taeniopteryx nebulosa (L.)	2	3	1	–	6
Nemoura cinerea (Retz.)	1	–	–	–	1
Nemoura cambrica (Stephens)	–	–	–	1	1
Leuctra nigra (Oliver)	–	–	–	1	1
Leuctra hippopus (Kempny)	+	–	–	–	+
Leuctra moselyi Morton	–	–	4	–	4
Capnia sp.	+	–	–	–	+
Isoperla grammatica (Poda)	+	2	2	4	8
Dinocras cephalotes (Curt.)	1	1	1	7	10
Chloroperla torrentium (Pict.)	1	2	–	–	3
Ecdyonurus venosus (Fabr.)	+	–	–	–	+
Heptagenia lateralis (Curt.)	1	3	–	–	4
Paraleptophlebia submarginata (St ph.)	–	–	1	–	1
Leptophlebia sp.	1	–	1	–	2
Siphlonurus lacustris Etn.	+	–	–	–	+
Cyrnus trimaculatus (Curt.)	1	–	–	–	1
Agapetus sp.	–	–	1	–	1
Drusus annulatus (Steph.)	–	1	–	–	1
Hydroptila sp.	1	3	1	–	5
Limnephilidae	1	1	2	–	4
Callicorixa woolastoni (D & S)	+	–	–	–	+
Oulimnius tuberculatus (Müll.)	1	–	6	+	7
Riolus cupreus (Müll.)	1	2	–	1	4
Hydrophilidae	–	1	–	–	1
Diamesa sp.	–	1	1	1	3
Chironomini	2	2	–	–	4
Pedicia sp.	–	–	1	–	1
Tipulidae	1	1	–	–	2
Ceratopogonidae	3	–	–	1	4
Empididae	1	1	–	–	2
Oribatoidea	–	+	–	2	2
Lymnaea truncatula (Müll.)	+	–	–	–	+
Pisidium sp.	+	–	–	–	+
	24	32	31	18	105

* Includes *Nais alpina* Sperber, and *Nais elinguis* Müller.
† Includes *Simulium variegatum* Meigen and *Simulium monticola* Friederichs.

loose stones under which it is commonly found, (Hynes, 1941). *Ameletus inopinatus* usually found in stony streams (Macan, 1957) was absent and may be less tolerant of post-inundation conditions than *Siphlonurus lacustris* which was found only at P1. The polycentropodids, *Neureclipsis bimaculata* usually present below lake outflows (Edington, 1964) and *Cyrnus trimaculatus*, have appeared since the dam was built.

In 1970 the last year of the pre-inundation survey a kick-sampling technique was used to obtain samples of the Tees benthos and this method has been used subsequently in a post-inundation survey. Though this latter survey has not yet been completed it is instructive to compare the fauna in 1970 (the year the dam was completed) with the fauna sampled by trays and kicks in 1971–72 (Table 4).

Amongst the more common taxa, changes have occurred since the building of the dam. The most obvious of these is the overall increase in numbers of animals, such as *Hydra* and *Nais* spp. which are able to develop large populations due to the lack of spates.

Table 4 (a). The numbers per square metre and percentage composition of the bottom fauna of the Tees below Cauldron Snout based on data collected in May, August and October 1970 and August, October 1971 and May 1972

	Kicks 1970		Kicks 1971–72		Trays 1971–72	
	No.m^{-2}	%	No.m^{-2}	%	No.m^{-2}	%
Hydra vulgaris	—	—	33	2·18	522	3·10
Naididae	—	—	150	9·90	7265	43·11
Tubificidae	8	1·31	40	2·64	2	0·01
Leuctra fusca	7	1·15	35	2·31	42	0·25
Leuctra inermis	18	2·95	13	0·86	20	0·12
Caenis rivulorum	2	0·33	10	0·66	59	0·35
Ephemerella ignita	1	0·16	35	2·31	92	0·55
Ecdyonurus dispar	39	6·38	18	1·19	37	0·22
Rhithrogena semicolorata	23	3·76	12	0·79	131	0·78
Baetis rhodani	82	13·42	185	12·21	1520	9·02
Baetis scambus/bioculatus	22	3·60	45	2·97	66	0·38
Rhyacophila dorsalis	11	1·80	2	0·13	138	0·82
Polycentropodidae	19	3·11	42	2·77	101	0·60
Brachycentrus subnubilus	5	0·82	32	2·11	44	0·26
Chironomidae	98	16·04	323	21·32	1590	9·44
Simuliidae	3	0·49	—	—	3446	20·45
Elmis aenea	12	1·96	20	1·32	59	0·35
Limnius volckmari	37	6·06	102	6·73	20	0·12
Lymnaea peregra	129	21·11	247	16·31	861	5·11
Ancylus fluviatilis	12	1·96	63	4·16	513	3·04
Others	83	13·59	108	7·13	323	1·92
	611	100·00	1515	100·00	16851	100·00

(b) Species occurring before but not after inundation and additional taxa found in the present tray samples.

Species present before		Species found only after
Brachyptera risi	*Hydra vulgaris*	*Leptophlebia* sp.
Protonemura meyeri	Tricladida	*Neureclipsis bimaculata*
Protonemura praecox	Nematoda	*Cyrnus trimaculatus*
Perlodes microcephla	Naididae	*Agapetus* sp.
Perla bipunctata	*Glossiphonia complanata*	Hydrophilidae
Ameletus inopinatus	*Nemoura cinerea*	*Riolus cupreus*
Hydraena gracilis	*Leuctra nigra*	*Clinocera* sp.
	Leuctra hippopus	*Pedicia*
	Capnia sp.	Tipulidae
	Dinocras cephalotes	Empididae
	Chloroperla torrentium	Ceratopogonidae
		Lymnaea truncatula
		Pisidium spp.

Table 4 also compares the catches by kick samples and tray samples over the same period of time. Despite differences in the mesh sizes of the nets used, (10 threads cm^{-1} in the kick samples and 25 threads cm^{-1} in the present study) the composition of the fauna is similar for both methods. The higher proportions of Naididae and Simuliidae in the tray samples are attributable to the smaller mesh-size (retaining the minute *Nais* spp.), the generally faster current of the riffle sites which supported the largest numbers of Simuliidae, and the difficulty of removing simuliid larvae by 'kick-sampling'.

Abundance and biomass

The total numbers and weights of major groups in all four sites are shown in Fig. 2. It is apparent from this figure that *Hydra* sp., Oligochaeta (mostly *Nais* spp.), Ephemeroptera, Diptera and Mollusca are the numerically dominant groups and that Diptera, Trichoptera, Ephemeroptera and Mollusca contribute most of the total biomass. At stations P1 and P2 *Hydra* and Oligochaeta were the most abundant organisms respectively but contributed little to the biomass. Mollusca, however, at both these stations formed about 72% of the total biomass. In the riffle stations R1 and R2, Diptera, particularly simuliid larvae, were most abundant and this group together with Ephemeroptera, Trichoptera and Mollusca made up about 80% of the total biomass, each group contributing about 20% to the total.

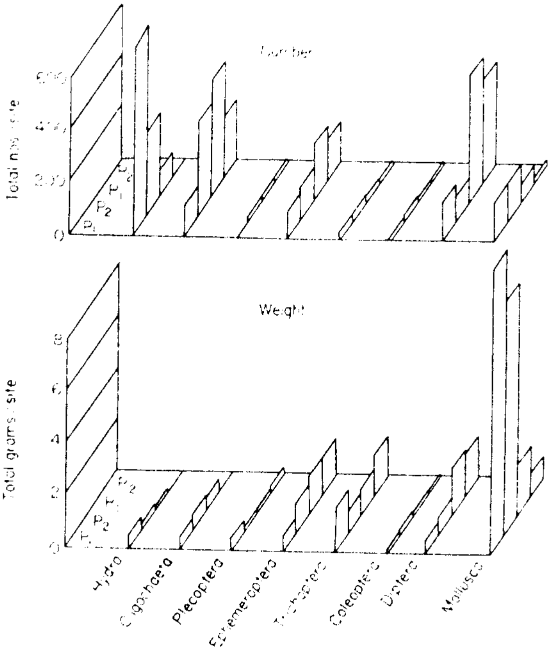

Fig. 2. The total numbers and weight (preserved wet-weight) of animals in each major group at the four sites P1, P2, R1 and R2. (August, January, February, March and April excluded from the totals.)

Seasonal variation in abundance and biomass of major faunal groups is illustrated in Figs. 3 and 4, for both riffles and pools. *Hydra* sp. is most abundant in September at a time when large numbers of micro-crustacea are being washed out of the reservoir. Annelids, chiefly *Nais* spp., reach their peak density between July and September. These worms appear to be associated with algae and mosses which are at their most abundant at this time. Mollusca, *Lymnaea peregra* and *Ancylus fluviatilis*, were most abundant in July when eggs of both species hatched. In the Diptera, simuliid larvae reached a pronounced peak in December at sites R1 and R2. A small peak did occur at this time at P1 and P2 but is masked in Fig. 4 by large numbers of chironomids. The simuliid peak was made up of large numbers of very small larvae (mean weights of larvae in October, November and December were 0·11, 0·18 and 0·32 mg respectively). In January the mean weight of a larva was 1·31 mg and growth during the rest of the winter was slow. In May when sampling stopped the larvae had reached a mean weight of 1·95 mg. The monthly changes in the densities of the common taxa in riffles and pools are presented in more detail in Table 5. The annual total numbers and weights (in grams) for sites P1, P2, R1 and R2 were respectively 12 698, 11 170, 13 467 and 8031, and 15·02, 12·51, 6·81 and 5·65. Total numbers showed a significant difference between sites (χ^2 21 529 $P<0{\cdot}001$) but total weights showed no such difference (χ^2 6·06 $P>0{\cdot}05$). This agrees with Leonard (1939) who has shown that total numbers per unit area are less consistent than total volume (weight), and Maitland (1964) has shown that the average standing crop is a better parameter to use in comparing different rivers than numerical abundance. The standing crop (mean monthly weight m^{-2}) was calculated for the study area based on total catches from each site and was found to be 14·6 g with 95% coincidence limits ranging from 6·9 to 30·7 g.

Distribution

The distribution of species between sites was investigated using chi-square. Of the thirty-five

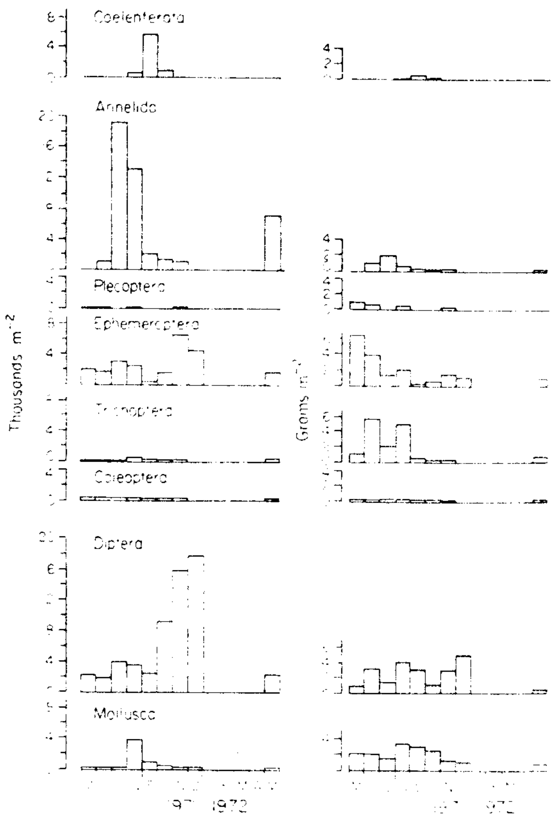

Fig. 3. Monthly changes in numbers and biomass per square meter, of invertebrate groups at the riffle sites, R1 and R2. (August, January, February, March and April excluded as no quantitative samples were available.)

Table 5. The mean density of the invertebrate fauna m^{-2} at sites P1/P2 (Pools) and R1/R2 (Riffles) between May 1971 and May 1972. No quantitative samples were taken from January to April in the riffle sites because of high flows

Fauna	Pools													
	3/5	1/6	28/6	27/7	20/9	19/10	22/11	16/12	17/1	8/2	13/3	19/4	25/5	Total
Hydra vulgaris	—	—	—	1028	58525	8542	605	—	—	—	—	—	2455	71155
Naididae	13	1474	9126	9466	2856	1644	2994	197	—	85	—	—	3813	31688
Other Oligochaeta	73	14	21	111	21	26	7	60	21	14	—	—	—	368
Amphinemura sulcicollis	26	13	—	—	—	13	—	—	—	—	—	—	7	59
Leuctra inermis	7	—	7	—	7	53	26	13	26	46	26	39	7	257
Leuctra fusca	—	—	—	184	—	—	—	—	—	—	—	—	—	184
Caenis rivulorum	164	492	1068	203	7	13	7	—	—	—	—	—	46	2000
Ephemerella ignita	—	157	197	33	—	—	—	—	—	—	—	—	—	387
Ecdyonurus spp.	27	46	—	59	112	20	13	—	—	7	13	—	7	304
Rhithrogena semicolorata	—	26	138	7	—	20	13	—	7	13	—	—	—	224
Baetis muticus	—	13	—	—	—	39	7	—	—	—	—	13	—	72
Baetis scambus	—	302	596	158	—	7	—	—	—	—	—	—	—	1063
Baetis rhodani	66	105	203	79	72	1140	4822	2450	734	734	708	144	210	11467
Rhyacophila dorsalis	7	20	13	20	20	92	72	20	13	33	26	13	26	375
Hydropsyche sp.	7	26	—	—	13	26	7	13	—	7	—	13	13	125
Polycentropidae	216	243	282	72	1094	282	33	—	40	—	13	210	374	2859
Brachycentrus subnubilus	—	—	7	111	53	—	7	—	7	13	—	52	20	270
Simuliidae	—	33	7	171	13	288	1212	498	321	26	39	—	—	2608
Orthocladiinae	603	688	1848	695	2103	387	2287	2254	885	1133	1402	3184	950	18419
Tanytarsini	7	98	59	210	1068	151	315	144	243	26	13	39	33	2406
Tanypodinae	46	256	308	79	190	33	20	20	20	13	—	—	26	1011
Elmis aenea	—	7	13	131	138	7	—	13	—	13	—	—	—	322
Limnius volckmari	79	92	229	72	40	7	—	—	13	—	—	13	53	598
Esolus parallelepipedus	13	7	26	46	92	—	7	7	26	—	—	—	20	244
Lymnaea peregra	138	531	282	9820	2208	826	354	112	170	203	92	472	360	15568
Ancylus fluviatilis	—	92	256	1946	1920	308	111	46	53	13	92	236	216	5289
Others	67	66	86	408	21	66	54	34	93	20	46	46	46	1053
Totals	1559	4801	14772	25109	70573	13990	12973	5881	2672	2399	2470	4474	8682	170355

Fauna	Riffles									
	3/5	1/6	28/6	23/7	20/9	19/10	22/11	16/12	25/5	Total
Hydra vulgaris	—	—	—	465	5280	1087	66	—	13	6911
Naididae	20	1713	19149	13115	2319	1428	1048	66	7252	45570
Other Oligochaeta	111	7	13	145	33	14	72	7	—	402
Amphinemura sulcicollis	98	46	—	—	—	—	—	—	—	144
Leuctra inermis	—	7	—	—	72	59	66	20	—	224
Leuctra fusca	—	—	—	125	—	—	—	—	—	125
Caenis rivulorum	419	1022	682	144	7	20	—	—	13	2307
Ephemerella ignita	—	20	144	275	—	—	7	—	—	446
Ecdyonurus spp.	33	7	—	171	46	—	7	—	—	264
Rhithrogena semicolorata	66	46	249	367	26	20	33	13	7	827
Baetis muticus	66	52	13	13	13	—	—	7	—	164
Baetis scambus	—	203	734	197	—	—	—	—	—	1134
Baetis rhodani	1671	531	1114	1376	269	1540	6518	4337	1644	19000
Rhyacophila dorsalis	20	99	118	216	125	164	144	33	33	952
Hydropsyche sp.	20	39	13	7	72	20	13	—	236	420
Polycentropidae	26	7	33	190	164	40	7	—	72	539
Brachycentrus subnubilus	—	—	—	131	—	—	—	—	7	138
Simuliidae	118	387	380	1717	1946	8621	12021	15507	13	40710
Orthocladiinae	2208	1212	3322	1520	452	636	3839	2169	2260	17618
Tanytarsini	7	7	7	—	59	13	26	—	20	139
Tanypodinae	7	197	112	302	—	13	—	13	7	651
Elmis aenea	26	13	111	112	39	13	13	—	53	380
Limnius volckmari	7	39	46	46	7	—	—	—	13	158
Esolus parallelepipedus	46	66	13	26	33	13	—	—	125	322
Lymnaea peregra	20	26	13	2326	218	249	131	131	7	3121
Ancylus fluviatilis	—	20	20	1454	623	39	40	40	46	2282
Others	59	85	211	179	197	27	14	7	92	871
Totals	5048	5311	26497	24619	12000	14016	24065	22350	11913	145819

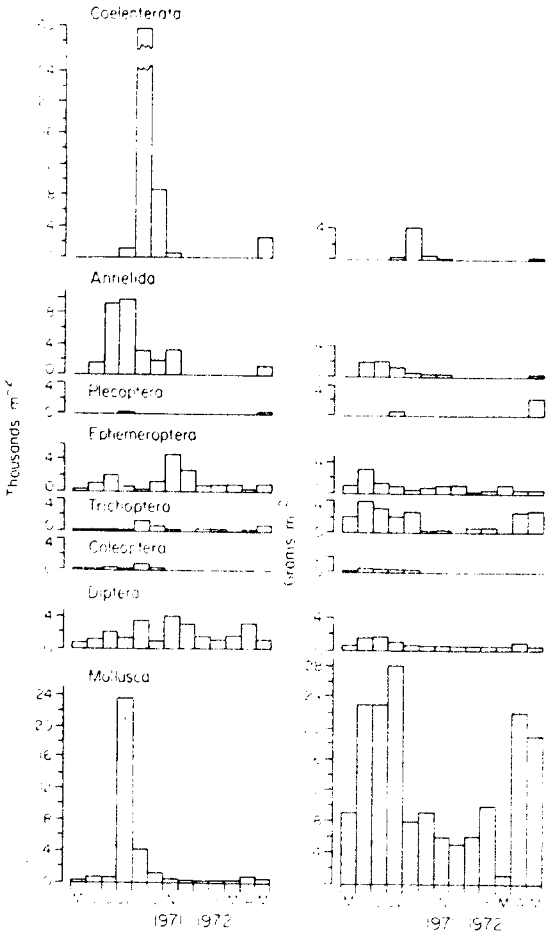

Fig. 4. Monthly changes in numbers and biomass per square metre, of invertebrate groups at the pool sites, P1 and P2.

taxa tested, only four, *Leuctra fusca*, *Ecdyonurus dispar*, *Elmis aenea* and *Esolus parallelepipedus* showed equal proportions in each site ($P>0{\cdot}05$). *Leuctra inermis*, *Brachycentrus subnubilus*, empidid larvae and Tanypodinae, neither showed definite preferences for any site, nor were they in equal proportions at each site. The remaining groups generally showed strong preferences for one or a combination of sites and these are listed below.

Pools (P1 & P2)	Riffles (R1 & R2)
Hydra vulgaris	*Baetis rhodani*
Polycentropodidae	*Rhyacophila dorsalis*
Limnius volckmari	*Hydropsyche* sp.
Tanytarsini	Simuliidae
Lymnaea peregra	Orthocladiinae
Ancylus fluviatilis	

Intermediate (P2 & R1)
Nais spp.
Caenis rivulorum
Ephemerella ignita
Rhithrogena semicolorata
Baetis scambus

Life histories and distribution of nymphal size-classes

Certain taxa which it was possible to identify to the species level occurred in sufficient numbers to allow observations to be made on their life-history.

Baetis rhodani. The general pattern of growth agrees with that observed by other workers (Macan, 1957; Elliott, 1967; Ulfstrand, 1968) despite the presence of the dam which causes cooler summer temperatures and warmer winter temperatures which might have affected development time. Association of nymphal size-classes with a particular sampling site was tested using chi-square. Tests were carried out on November, May and total counts of all nymphs taken during the study period, (January to April counts excluded). The total and May counts showed no association (χ^2 4·2218, d.f.4, and χ^2 2·5033, d.f.3, respectively, $P>0{\cdot}05$) but in November when the population consisted mainly of small nymphs there appeared to be a definite association, (χ^2 37·0900, d.f.3, $P<0{\cdot}001$), with riffle areas supporting a larger proportion of small nymphs than the pools.

Baetis scambus/bioculatus. Nymphs of this species occurred only in the summer months, (Fig. 5). Hatching probably took place in late June and July and no mature nymphs were found in August. A few very small nymphs occurred in August when they made up 58% of the total found but no further specimens were found in September or subsequently during the study period. Again the pattern of growth and emergence agrees with the findings of previous workers (Hynes, 1961; Elliott, 1967), despite the presence of the dam. Tests revealed a strong association between site and nymphal size-class when total counts were considered (χ^2 53·0439, d.f.9, $P<0{\cdot}001$). Larger nymphs occurred more commonly at site P1 where water velocity was lower than at any other site.

Caenis rivulorum. Nymphs grew rapidly (Fig. 5) in May, June and July, and probably emerged in June and July. In August, the population was made up of medium-sized specimens. From December to March, nymphs were absent from the samples but in April they occurred again and were slightly larger than those taken in August. It is very likely that the nymphs burrow deeply into the substratum during

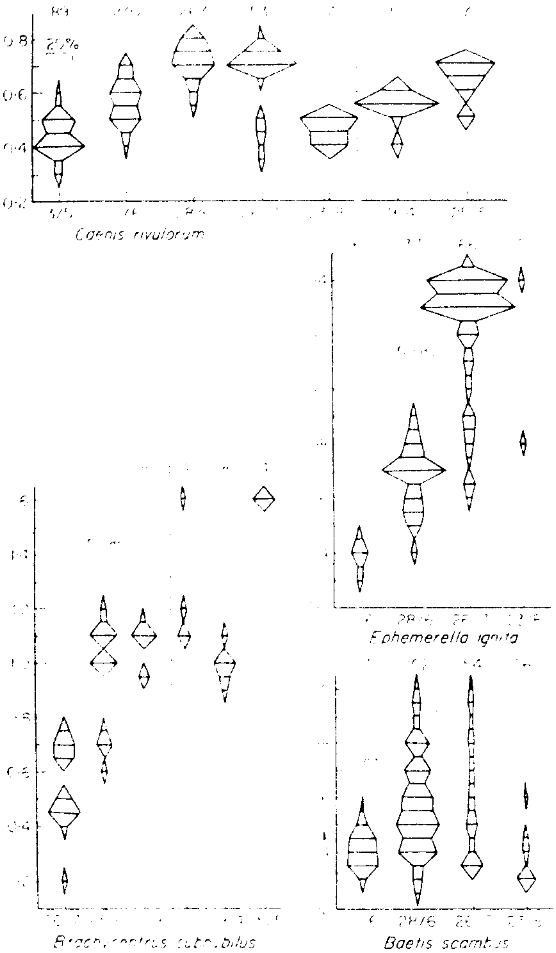

Fig. 5. The monthly distribution of nymphal size-classes. Head capsule width in mm on vertical axis and Date on horizontal axis. The number of animals measured is given above each polygon.

the winter and will not be sampled by the trays. An association test on the distribution of nymphal size-classes in riffles (R1 & R2) and pools (P1 & P2) showed that the pattern was not the same in the two areas (χ^2 32·4519, d.f.5, $P<0·001$) and that the proportion of larger nymphs (head width 0·70–0·85 mm) was greater in pools than in riffles.

Ephemerella ignita. This is another species which in the Tees is most abundant in samples taken in the summer months, and which hatches in July and August. These observations agree with those of other workers in the British Isles (Macan, 1957; Maitland, 1965; Elliott, 1967). The analysis of nymphal size-class association with site in the present study, revealed no association, (χ^2 1·6533, d.f.1, $P>0·05$).

Rhyacophila dorsalis and *Polycentropus flavomaculatus.* The life-histories of these species have been described by Mackereth (1960) and Elliott (1968), and the observations made in the present study, despite the relatively low numbers of specimens available for analysis, support their results. One difference is that although the same net mesh-size (24 meshes cm^{-1}) as in the present work was used by Elliott, more small larvae (head width $<0·4$ mm) of *P. flavomaculatus* were taken by him using a shovel sampler than in the present study using trays. Small larvae of *R. dorsalis* were however taken regularly by both methods. This may indicate that the first two instars of *P. flavomaculatus* are either at the extreme edge of the river or are more intimately associated with the deeper substratum than those of *R. dorsalis* and therefore unlikely to be sampled efficiently by the trays.

Brachycentrus subnubilus. Larvae of this species did not occur in the samples until July (Fig. 5) when they grew rapidly up to September. Growth appeared to stop during the winter. No catches of adults were made but from the presence of final instars in samples taken between March and May it is likely that emergence took place during those months. Macan (1973) gives March and April as the months in which adults are usually found.

Discussion

The substratum of the Tees in the study area presents many sampling problems due to the depth of the water and the firmly bedded boulders. Usual methods such as Surber-sampling and 'kick-sampling' are not feasible as the bottom can be disturbed only with great difficulty. It was for this reason that trays were used in the present study. They sampled all the main taxa and proved effective for the main objects of the work, which were to describe seasonal changes in abundance and biomass and provide general information on distribution and life-histories.

Considering the distribution of individual groups and taxa in the study area it was seen that some were associated more commonly with one site than another. The pool sites P1 and P2 were characterized by a greater species diversity and higher biomass than the riffles sites R1 and R2. Highest numbers of animals were also found in the pools if the sites were considered together, but the fauna at riffle site R1 was as abundant numerically as that at site P1. Biomass showed the greatest difference between sites due to large populations of *Lymnaea peregra* and *Ancylus fluviatilis*. In contrast Egglishaw & Mackay (1967) found greater numbers of animals in riffles than in pools and no significant difference in biomass in the two habitats. However, their faunas did not contain high densities of molluscs, hydra and *Nais* spp., which in the Tees greatly influenced weights and numbers in pools and riffles. Egglishaw (1964) demonstrated that increases in organic detritus led to increases in the numbers of certain species. Trays from sites P1 and P2 were always observed to contain much more silty sand after a month's immersion than trays from site R1, and R2 generally had all the finer particles in the tray removed by the current. *Baetis* spp. were shown by Egglishaw (1964) to increase in numbers with increase in organic detritus. In the present study such a correlation was not apparent and both numbers and biomass were greater in the fast-flowing sites R1 and R2. Ulfstrand (1967) noted that *B. rhodani* preferred strong current (>75 cm s^{-1}) but did not distinguish between moderate (25–75 cm s^{-1}) and weak current (<25 cm s^{-1}). In the Tees *B. rhodani* favoured the faster-flowing reaches which are equivalent to Ulfstrand's moderate category. The quality of the detritus in the pool areas may not have been suitable for *B. rhodani* and the nymphs may prefer detritus trapped by algae and mosses in the riffle sites. The existence of local races of *B. rhodani* differing in feeding habits is postulated by Brown (1961) but in the absence of data on feeding in the present study it can only be said that *B. rhodani* in contrast to observations by Brown (1961) and Egglishaw (1964) appears to favour sites with the least detritus and the fastest flows.

Several forms which one may expect to occur rather commonly are poorly represented in the study area, the chief examples of which are Plecoptera and Ecdyonuridae. Spence & Hynes (1971) noted a complete absence of Plecoptera below a dam and attributed this to a diminution of dissolved oxygen especially at night when the respiratory demand of heavy periphyton communities is high. In the present study no such diminution of dissolved oxygen occurred at night in spite of dense algal growth and this explanation for low numbers of plecopterans has to be rejected. Most of the species which are present have a wide distribution on different types of substratum but two, *Dinocras* associated with stable bottoms and sluggish rivers, respectively (Hynes, 1941). With little evidence it is not possible to say why Plecoptera are relatively rare in the Tees below Cauldron Snout but it may well be that the substratum with heavy algal growth and silting in places is in some way unsuitable for most of the available species.

Ecdyonuridae were never very abundant in this part of the Tees (Armitage *et al.*, 1974) but were abundant and still are in the adjacent tributary, Maize Beck. Although five species occurred in the present area none made up a large proportion of the fauna. *Rhithrogena semicolorata* was the most common species making up 1% of the fauna at site R1. Butcher *et al.* (1937) found that in the Tees, *R. semicolorata* was scarce below the confluence of a polluted tributary, the Skerne, where the substratum supported growth of sewage fungous and *Cladophora*. Percival & Whitehead (1930) noted that *R. semicolorata* was abundant where stones were bare with no visible vegetation, and prone to movement during spates. Harker (1953) noted the complete disappearance of the mayfly fauna of a stony stream following an enormous increase in the number of blue–green algae and diatoms. In the Tees below Cauldron Snout the bottom was always relatively more stable than that of the adjacent Maize Beck, due to the generally larger rocks and boulders embedded in the river bottom. The stability increased after the building of the dam as did algal growth, and yet very high flows (23·4 m^3 s^{-1}) do occur when the reservoir overflows down the spill-way. The chief difference is that these high flows do not carry the coarser particles, which settle in the reservoir, and consequently do not have a marked scouring effect on the river bottom. This growth of vegetation in the Tees may create unsuitable conditions for *R. semicolorata*, and the current speed and general size of the river could create conditions unfavourable to *Heptagenia lateralis* which is usually found in the upper parts of moorland becks (Macan, 1957) and is intolerant of floods (Harker, 1953). *Ecdyonurus torrentis* is also largely confined to smaller streams and becks (Macan, 1957). The scarcity of *Ecdyonurus dispar* and *E. venosus*, which one might expect to be more common than *R. semicolorata* under these conditions is not possible to explain at present, particularly since both species are found in large rivers (Macan, 1957).

The present study area has a fauna in which few species account for most (90%) of the numbers and high for a stream at this altitude; though it should be stressed that the biomass of organisms living in the trays could be higher than that of the surrounding fauna. However, instability and separation from the deep river-substratum may counteract the beneficial features of the tray environment and provided no collections are made from the plastic sides, the biomass recorded in the trays may approximate quite closely to the surrounding biomass.

Maitland (1964) estimated the mean standing crop of the fauna on a stony substratum in the River Endrick to be 16 g m^{-2} and using Lagler's (1949) standards considers this to be average in richness. The estimate for the Tees in the present study (14·6 g m^{-2}) also places it in this category. This relatively high value for an upland stream may be related to organic enrichment of the river. The presence of the dam reduces spate velocity and frequency and this encourages the development of dense algal and moss growth with its associated species, *Nais* spp. and Orthocladiinae. The regulated flow leads to deposition of silt in the quieter reaches allowing the establishment of populations of Tanytarsini larvae. The less extreme flows also encourage large *Lymnaea peregra* populations and the reservoir itself provides a rich source of food in the form of plankton, particularly zooplankton (Armitage & Capper, 1976) which is fed upon by the large *Hydra* population.

Briggs (1948) noted a doubling of the average density of the fauna in Stevens Creek, California, below a dam. In Europe, Müller (1955) and Økland (1963) have recorded similar increases in numbers and biomass of the fauna below lakes and impoundments. Spence & Hynes (1971) working on benthos below an impoundment noted that alteration of the temperature regime, abundant development of periphyton and addition of plankton from the reservoir work together and affect the benthos in the same general way as does mild organic pollution. All these features are seen in the Tees below the Cow Green dam. However, the detrimental effects of organic enrichment are lessened considerably by the fact that the reservoir outflow water is never significantly deoxygenated. This is because the water in the reservoir itself is well mixed by winds, and the gradient, including the fall of Cauldron Snout, ensures a rapid flow through most of the section from the dam to the junction with Maize Beck. The build-up of blue-green algal mats on the bottom of certain pools is one feature on the debit side of the organic enrichment, which may eventually reduce faunal numbers in these areas, because the mats form a barrier to organisms which spend part of their life-history in the deeper substrata.

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