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LONG-TERM FAUNAL CHANGES IN A REGULATED AND AN UNREGULATED STREAM—COW GREEN THIRTY YEARS ON

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ABSTRACT

Cow Green dam is situated in Northern England on the River Tees in a region with high average wind speeds (24 km h^{-1}), low average annual temperatures (circa 5°C) and average rainfall of 1800 mm. The River Tees was impounded by the Cow Green dam in 1970 and early studies revealed significant changes arising from flow regulation. This study compares macroinvertebrate communities in 2004 with those recorded in the first 5 years after impoundment in the Tees and in the unregulated Maize Beck. Nineteen of the 31 common taxa in the regulated sites declined in abundance by a factor of 5 or more. These included *Hydra* sp., *Ancylus fluviatilis*, Naididae, Heptageniidae, Leuctridae and *Brachycentrus subnubilus*. Some taxa, *Lymnaea peregra*, *Ephemerella ignita*, *Hydroptila* sp. increased in numbers, and others Hydropsychidae and *Gammarus pulex* declined at sites nearest the dam but increased downstream. In Maize Beck there were fewer changes. The changes in faunal communities in the Tees were evident from multivariate analyses where the Tees sites sampled in 2004 were separated from those sampled in the period 1972–1975, as a result of abundance changes in common taxa and the appearance of taxa not previously recorded. Maize Beck in contrast was characterized by few changes in abundance and no new taxa and samples from all years grouped together. The results suggest that the Tees communities have changed since 1975 and are still possibly undergoing change, although without evidence from intervening years this cannot be proved. A narrower range of environmental conditions and increased flow stability have led to a dynamically fragile community (indicated by observed changes in community diversity and abundance) which is very susceptible to perturbations because it has developed in their absence. Periphyton and reservoir plankton play an important role in structuring the faunal composition by creating an environment where biotic interactions are more likely. Increased interaction between components of the faunal community may account for the observed changes since 1975 in the regulated sites in contrast to the situation in the unregulated Maize Beck where there has been little change in faunal community between the original study and the 2004 survey. An unregulated natural flow regime continues to dominate the Maize Beck environment and the variable and unpredictable conditions have resulted in a dynamically robust faunal community. Copyright © 2006 John Wiley & Sons, Ltd.

KEY WORDS: regulated river ecology; aquatic invertebrates; plankton; microcrustacea; periphyton; biotic interactions; long-term studies; ecological assessment

INTRODUCTION

Efficient management of streams and rivers, to maximize resource use while minimizing ecological impacts, requires information gathered over long periods of time in order to separate natural changes in ecosystems from those associated with anthropogenic disturbances (Resh and Rosenberg, 1989; Elliott, 1990; Voelz *et al*., 2000). It is important to know how community stability, measured by the resistance and resilience of assemblages, varies in natural and disturbed systems (Weatherley and Ormerod, 1990; Grossman *et al*., 1990; Death and Winterbourn, 1994; Armitage and Gunn, 1996; Robinson *et al*., 2000; Bradley and Ormerod, 2001; Minshall *et al*., 2001; Woodward *et al*., 2002; Scarsbrook, 2002; Wagner and Schmidt, 2004). In particular, with the increasing regulation of world river flows (Petts, 1989, Dynesius and Nilsson, 1994) it is necessary to obtain information on the long-term effects of impoundment to identify and alleviate adverse impacts. Recent long-term studies below dams have examined a number of aspects including geomorphology (Petts and Greenwood, 1985; Décamps *et al*., 1995;

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Gilvear, 2004; Lloyd *et al*., 2004), fish assemblages (Gido *et al*., 2002, Quinn and Kwak, 2003), and invertebrate communities (Greenwood *et al*., 1999; Voelz *et al*., 2000; Vinson, 2001).

In 1970 the Cow Green Dam in Upper Teesdale in Northern England was closed and the Tees impounded. Investigations at that time followed the development of the reservoir fauna (Armitage, 1977a; Armitage, 1983), and changes in the physico-chemical characteristics, and macroinvertebrate and fish populations, below the dam and in an unregulated tributary Maize Beck (Armitage, 1976, Armitage, 1977a, Armitage, 1977b, Crisp, 1977, Armitage, 1978, Crisp *et al*., 1983, Crisp, 1984, Armitage and Blackburn, 1990). The macroinvertebrate studies covered the period 1968 to 1975 and demonstrated major changes in faunal communities at the regulated sites in the first 5 years following impoundment (Armitage *op. cit*.). In 2004 the site was re-visited to examine any further changes in the composition and structure of the benthic invertebrate faunal communities which had occurred over the past 30 years and to compare the output of plankton from the reservoir with that observed in the original study (Armitage and Capper, 1976).

STUDY AREA

Cow Green Reservoir is surrounded by Pennine moorland and lies at an altitude of 489 m above sea level. The region is strongly influenced by the prevailing Atlantic climate with cool summers and mild winters. However the altitude of upper Teesdale (between 500 and 900 m above sea level) offsets the oceanic influence on temperatures in winter and exaggerates it in summer and the area is typified by high average wind speeds (24 km h^{-1}), low average annual temperatures (circa 5°C) and average rainfall of 1800 mm (Manley, 1936). Details of the surrounding area and its history are given in Clapham (1978) and physical and chemical data are presented by Crisp (1977).

The main use of the reservoir has been to maintain flows in the river to provide industrial Teeside with water during dry periods. Before impoundment, the Tees was subject to severe fluctuations in discharge following heavy rainfall. These spatey flows carried high loads of suspended solids, which scoured the bed, restricting the growth of aquatic plants and algae. With completion of the impoundment in June 1970 the reservoir began to fill and the first overflow over the dam wall occurred in January 1972. In operation, water is drawn off simultaneously from the upper and lower levels of the reservoir. This in conjunction with the altitude, high and frequent winds and relatively shallow depth (maximum 23 m) of the reservoir, results in considerable mixing and the outflow water is cold and well oxygenated.

The Tees just below the dam is about 20–30 m wide with a stony bottom. After about 100m the stream narrows, passes over a weir, and flows rapidly for about 100m. A short section with little gradient follows before the river drops about 40m in 135m down the waterfall, Cauldron Snout. For about 200m downstream of this, the river is rocky-bottomed and braided before joining the unregulated tributary Maize Beck. Below the junction with Maize Beck the river curves and flows rapidly over large boulders (Figures 1a, 1b). The substratum of the Tees and Maize Beck is mainly dominated by boulders but in Maize Beck the boulders are smaller and the bottom less stable with little algal cover (Table I). pH in both the Tees and Maize Beck ranged between 6.56 and 6.93 and total phosphorous from 25–49 micrograms per litre. Nitrates (NO_3-N) were undetectable in April and September samples but concentrations of 0.101 and 0.02 mg/l were recorded in July spot samples in the Tees below Cauldron Snout and Maize Beck, respectively. These values compare with maximum and minimum values recorded by Crisp (1977) in

Table I. Summary of basic features recorded in 2004 at sites **a**, **b**, **c** and **d** on the R.Tees and site **e** on Maize Beck. The algal and moss growth was assessed visually and the numbers indicate ranks where 1 represents the least cover. Temperature data are spot readings taken on each sample visit (April, July and September)

Site	Distance below dam (m)	Mean substratum	Depth cm	Velocity m/s	Algae/Moss	Temperature °C
a	20	Cobbles	30–50	0.25–0.98	2	6.5:13.8:11.0
b	239	Boulders	30–60	0.4–1.25	4	6.7:13.8:11.0
c	400	Boulders	22–53	0.79–0.95	5	11.5:13.8:11.0
d	600	Boulders	40–50	0.4–0.9	3	8.3:13.7:10.1
e	n/a	Boulders	20–37	0.25–0.55	1	7.3:11.5:7.2

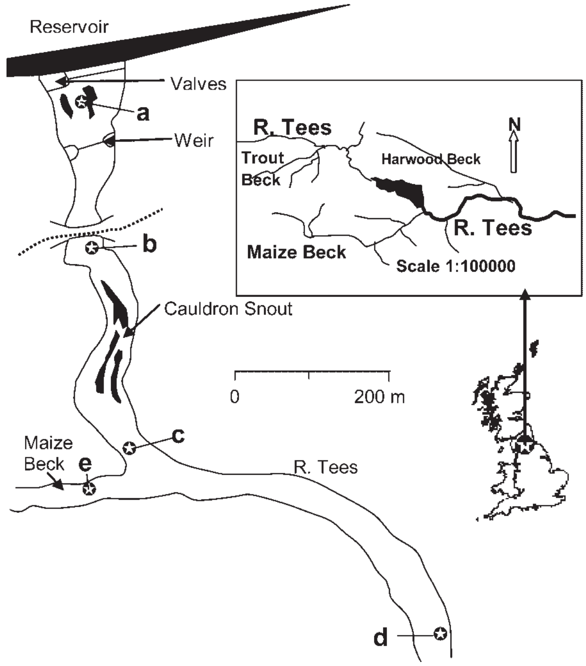

Figure 1 (a). Sketch map showing the location of Cow Green reservoir (solid black), in upper Teesdale, Northern England, together with major tributaries and the position of sites **a**, **b**, **c** and **d** on the Tees and **e** on Maize Beck

Cow Green Reservoir between 1971 and 1975, of 0.16 and 0.09. Current velocity values in 2004 fall within those observed in the earlier study (Armitage, 1978) and there were no obvious changes to channel shape.

METHODOLOGY

Samples

Samples of benthic invertebrates were taken in spring, summer and autumn (April 24, July 24 and September 24) at the five sites examined in the 1970's by the same operator in exactly the same manner. Evidence from other sampling programmes (Armitage, 1976) indicated that these sample periods provided a comprehensive assessment of the faunal community. The substratum was disturbed with the foot for 60 s immediately upstream of a net (250 mm in diameter with a mesh aperture of 800 microns). Details of the method and its consistency are presented in Armitage *et al*. (1974). Two of these kick samples were collected at each site. In addition, another set of single samples was taken using the standard methodology used in national monitoring in the UK (Wright *et al*., 1993, Murray-Bligh *et al*., 1997) at site **e** (Maize Beck) and site **c** on the Tees in order to provide a 'modern' assessment of ecological quality. These samples consisted of 3 min kicking and sweeping in all available aquatic habitats in proportion to their occurrence. A further set of 'plankton' samples was collected at three sites (**a**, **c** and **d**) using the methods described in Armitage and Capper (1976). Three samples, each of 60 s duration, were taken at each site with a plankton net (diameter 15 cm, mesh 250 μm) attached to a pole and held vertically off the bottom and at right angles to the current. Samples were preserved in 5% formalin and identified to family level. All sites were sampled in 1972, 1973, 1974, 1975 and 2004. Site **c** was also sampled in 1970 and 1971 and site **e** also in 1968 and 1969.

Discharge data for the period 1971 to 2004 (mean daily discharge) was provided by the Environment Agency for the Tees below Cow Green Dam and for an unregulated tributary Trout Beck. This latter stream provides information on the pattern of discharge in both the unregulated Tees and Maize Beck (Crisp, 1977).

Figure 1 (b). (A) Junction of the Tees (left) with Maize Beck (right). (B) The Tees at site 'c'. (C) Maize Beck site 'e'. (D) Spillway from Cow Green Dam. (E) Site 'a' next to outflow from Dam. This figure is available in colour online at www.interscience.wiley.com/journal/rra

Treatment of data

The data used for analyses of benthic invertebrates in the early study were restricted to samples collected from riffles. This present study uses the same data but includes some additional samples taken in the seventies from riffle-pool habitats and takes account of changes in taxonomy and nomenclature in the past 30 years. In addition Oligochaeta have been downgraded from species level to family and Orthocladiinae combined with Diamesinae. The site/taxa matrix used for analysis consists of the mean number of animals per 60 s kick $\times$ 10 for April, July and September. (January samples were not taken in 2004). Year codes 1–9 were assigned to sites where 1 is 1968 and 9 is 2004. The plankton data were expressed as numbers per m^3 using information on the volume filtered per sample.

Analyses

The coefficient of variation ($CV = SD/mean \times 100$) was used to examine temporal variability of common taxa using abundance data for each taxon (Grossman *et al*., 1990). Freeman *et al*. (1988) have proposed the following classification scheme where $CV \leq 25\%$ represents a highly stable situation, from 25 to $\leq 50\%$ moderately stable, 50 to $\leq 75\%$ moderately fluctuating, and $\geq 76\%$ highly fluctuating. ANOVA was used to test for differences in the numbers of taxa and overall macroinvertebrate abundance between sites and years. Data were transformed ($\log x + 1$) prior to analyses to enhance normality. Wilcoxon matched-pairs signed-ranks tests (Siegel, 1956, Lowry, 2006) were used to examine the hypothesis that there was no mean difference between paired observations in the population between years.

Five macroinvertebrate functional feeding groups (predators, scrapers, collector/gatherers, filterers and shredders) were assigned to the recorded taxa in accordance with Cummins and Klug (1979), Merritt and Cummins (1984), Moog (1995) and Wright *et al*. (2002). The percentage composition of functional feeding groups was calculated from abundance data.

Differences in macroinvertebrate community composition were examined with non-metric multidimensional scaling ordination (MDS) on a Bray Curtis similarity matrix of square root transformed taxon abundance data using the software package PRIMER (Plymouth marine Laboratory, UK). The statistical significance of differences between years and sites was tested using the simulation/permutation test ANOSIM2 (Clarke and Green, 1988, Clarke and Warwick, 1994) a sub-routine within PRIMER.

Ecological assessment samples were analysed using RIVPACS (River Invertebrate Prediction and Classification System), a software programme used by government organizations in the UK to assess the ecological quality of streams by comparing the macroinvertebrate fauna observed at a site with a prediction of the fauna expected at that site in the absence of major environmental stress (Wright *et al*., 1993, Murray-Bligh *et al.*, 1997). The 'expected' fauna is derived by RIVPACS using a small suite of environmental attributes which characterize the site, these include substratum features, width and depth, distance from source, slope, discharge and conductivity. The system is based on 614 reference sites which represent all major types of geology and topography in Great Britain and provides a method of setting a standard against which to assess the fauna of new sites and also places the site in a national context.

In this study, combined data from all seasons sampled were used to predict the expected probability of occurrence of each family, the numbers of taxa, and BMWP biotic score and Average Score Per Taxon (Armitage *et al*., 1983) using the latest widely available version of RIVPACS (RIVPACS III, Cox *et al*., 1995). Sites are classified into one of 6 categories, based on the ratios of observed to expected values for ASPT and total numbers of taxa where 'a' is very good and 'f' is bad (Hemsley-Flint, 2000).

RESULTS

Discharge

The pattern of discharge reported by Crisp, 1977 has continued to the present. Flow records are not available for Maize Beck but discharge is recorded for Trout Beck, a major unregulated tributary of the Tees which enters the main river about 8.8 km upstream of the dam. Trout Beck has a similar slope to that of Maize Beck and arises in an

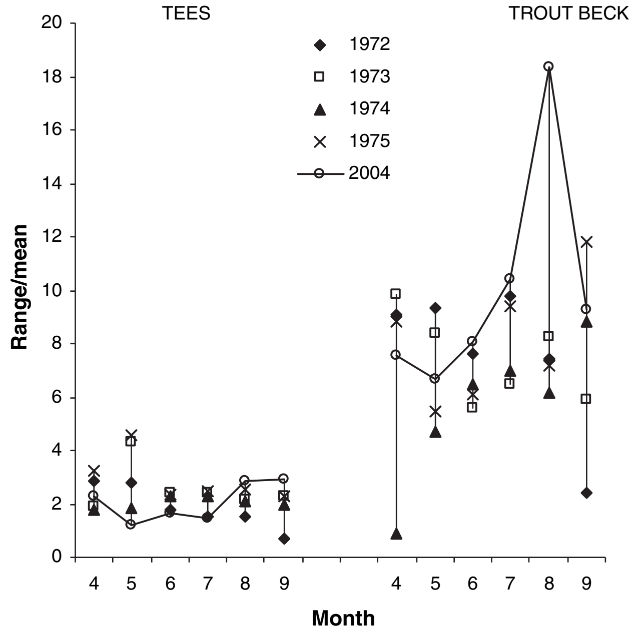

Figure 2. A comparison of monthly ranges /means for the period April to September for the five main study years at the Tees and at Trout Beck. The figures represent Maximum–minimum discharges for each month divided by the mean for the period April to September for each year. Square roots of the ratios are plotted to show low values

adjacent valley and although its catchment area is about a third of that of Maize Beck it provides a good indication of the unregulated flow pattern. A comparison of the frequency distribution of daily means as fractions of the annual mean for Trout Beck and the regulated Tees was made for the years 1972, 1973, 1974, 1975 and 2004. A Chi squared test on the two distributions showed that they differed significantly (Chi 55.421, $df = 6$, $P < 0.0001$). The difference between maximum and minimum flow in each month as a fraction of the mean flow for the period April to September (Figure 2) illustrates the greater variability of the unregulated flows over the study period and shows the position of the year 2004 in relation to 1972–1975. 2004 was characterized by two short periods of unusually high discharge in August and September associated with valve maintenance procedures, when flows greater than three times the median were recorded. However the water was released from the reservoir in a controlled manner and is unlikely to have had as extreme an effect as that associated with spatey flows in the unregulated Maize Beck.

Discharge parameters over the period 1972–1975 were compared with those of the 4 years up to and including 2004 (Table II). These included median, maximum and minimum flow (based on daily mean flows for each year in $m^3 s^{-1}$) and measures of flow variability, the number of times the median flow was exceeded by a factor of three

Table II. A comparison of flow parameters in the periods 1972–1975 and 2001–2004 in the unregulated Trout Beck and the regulated Tees. Median, maximum and minimum values are shown for each 4-year period together with the coefficient of variation (CV) and the number of occasions where flows equal to or exceeding 3 times the median ($n > m \times 3$) or less than or equal to half the median value ($n < m/2$) were recorded

	Trout Beck		Tees	
Period	72–75	01–04	72–75	01–04
Median $m^3 s^{-1}$	0.474	0.548	2.201	2.443
Maximum $m^3 s^{-1}$	4.962	7.641	12.855	18.73
Minimum $m^3 s^{-1}$	0.021	0.013	0.474	0.45
CV	152.43	169.36	78.92	78.9
$n > m \times 3$	98.5	97	13	8.5
$n < m/2$	109.5	107.5	94	44.5

(n > m × 3), the number of times a flow of half the median flow (n < m/2) was recorded and the coefficient of variation (CV = standard deviation/mean × 100) (Clausen and Biggs, 1997). A Mann-Whitney test revealed no significant differences between parameters in the two periods in either the unregulated Trout Beck (U = 7, $p = 0.443$) or the regulated Tees (U = 5.5, $p = 0.293$).

The fauna

Table III compares common (comprising >1% of total numbers) macroinvertebrates taken in 1975 with those taken in 2004. Nineteen of the thirty-one common taxa in the regulated sites **a, b, c** and **d** have declined in numbers by a factor of 5 or more; these include *Hydra* sp., *Ancylus fluviatilis*, Naididae, Heptageniidae, *Leuctra fusca*, *Leuctra inermis* and *Brachycentrus subnubilus*. Some taxa have increased in numbers, *Lymnaea peregra*, *Ephemerella ignita*, *Hydroptila* sp. and Hydropsychidae and *Gammarus pulex* declined at site **b** but increased at **c**

Table III. The mean numbers of common (>1%) animals per 60s kick sample × 10, based on data collected in April July and September in 1975 and 2004 at the five sites

Site	**a**		**b**		**c**		**d**		**e**	
Year	1975	2004	1975	2004	1975	2004	1975	2004	1975	2004
Hydra	700	33	1757	72	148	128	17	5	0	0
Lymnaea peregra (Muller)	372	160	232	78	89	1230	3	135	0	0
Ancylus fluviatilis	2	5	168	30	294	3	30	2	32	2
Nematoda	0	0	0	0	97	5	0	2	0	0
Lumbriculidae	16	18	55	12	171	58	82	20	36	65
Enchytraeidae	6	25	72	30	69	75	17	7	3	8
Naididae	232	13	4345	25	2089	32	320	10	20	3
Tubificidae	3	13	0	20	69	33	48	8	19	3
Lumbricidae	3	0	32	0	9	0	13	2	10	18
Gammarus pulex (L.)	356	330	1058	328	47	253	3	2	3	0
Baetis rhodani (Pictet)	2	10	198	133	134	173	180	167	196	225
Baetis scambus Eaton	0	0	23	0	39	8	63	8	17	2
Rhithrogena semicolorata (Curtis)	0	0	0	0	1	0	167	13	132	172
Ecdyonurus spp.	0	0	3	0	36	3	118	7	49	90
Ephemer*ella ignita* (Poda)	37	32	110	160	30	162	57	45	8	5
Caenis rivulorum Eaton	0	5	193	20	197	60	57	10	4	23
Amphinemura sulcicollis (Stephens)	0	0	2	0	11	3	0	0	13	3
Leuctra fusca (L.)	9	0	7	5	40	5	73	3	50	25
Leuctra inermis Kempny	0	0	113	7	81	20	82	17	72	32
Elmis aenea (Muller)	0	0	0	12	53	157	15	57	11	3
Limnius volckmari (Panzer)	2	2	437	67	238	157	75	22	25	75
Rhyacophila dorsalis (Curtis)	2	2	55	8	38	15	12	23	3	7
Hydroptila	0	22	7	12	14	440	13	78	9	2
Polycentropus flavomaculatus (Pictet)	0	0	5	0	46	10	27	5	22	12
Hydropsyche pellucidula (Curtis)	0	0	0	30	0	32	0	7	0	3
Hydropsyche siltalai Dohler	0	0	5	73	99	60	2	17	0	7
Brachycentrus subnubilus Curtis	2	0	8	3	233	13	475	8	125	3
Simuliidae	0	0	0	0	1	0	13	3	17	3
Orthocladiinae + Diamesinae	137	18	1080	48	1166	173	188	105	52	5
Tanytarsini	9	0	70	0	34	0	43	10	19	7
Empididae	5	0	13	5	74	3	10	3	0	2
No.taxa > 1%	18	15	25	22	30	27	28	30	25	27
Total taxa	22	21	40	27	52	46	51	47	37	38
Nos of common taxa	1895	688	10048	1178	5647	3311	2203	801	947	805
Total nos	1925	703	10157	1207	5748	3475	2343	864	987	853

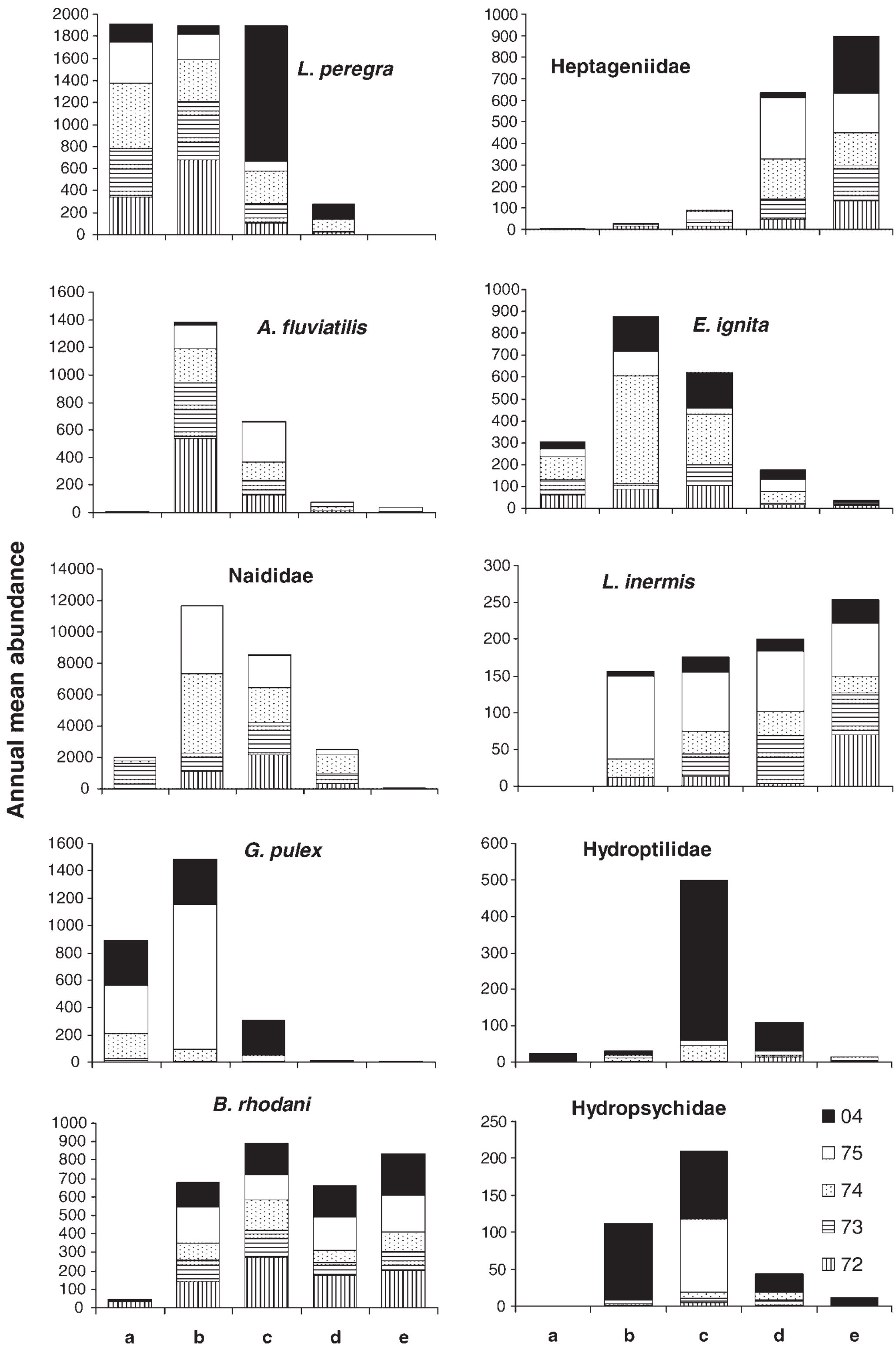

Figure 3. Annual contributions to total abundance of 10 common taxa showing a range of response to regulation at the five sites **a–e**

by a factor of 3. In the unregulated tributary Maize Beck there have been fewer changes with *Ancylus fluviatilis*, Tubificidae, *Baetis scambus*, *B. subnubilus* and Simuliidae showing decreases and Hydropsychidae and *Caenis rivulorum* increasing.

The following rarer taxa were recorded for the first time in 2004. Microturbellaria, *Crenobia alpina*, *Agapetus* sp., *Mystacides azurea*, *Sericostoma personatum, Hexatoma* sp. at site **c,** *Polycelis felina* at **c** and **d**, Aelosomatidae at **a** and **c,** *Heptagenia sulphurea* at **b** and *Elodes marginata* at **d**.

Shifts in numerical dominance have occurred in the regulated sites **a, b** and **c** from *Hydra* sp. to *Gammarus pulex* at **a,** Naididae to *Gammarus pulex* at **b** and Naididae to *Lymnaea peregra* at **c**. The site **d,** below the junction with Maize Beck, was dominated by *B. subnubilus* in 1975 and by *Baetis rhodani* in 2004, although Ephemeroptera as a whole dominated the site in both years. Ephemeroptera were dominant in both 1975 and 2004 at **e**. The annual contributions to the total abundance at each site are illustrated for 10 of the common taxa for the years 1972–1975 and 2004 (Figure 3). If there were no change between years at each site each shaded block would be of similar size. For example *B. rhodani* shows little difference between years at all sites except at **a** immediately below the dam where abundances were very low. In contrast, *L. peregra* Hydroptilidae and Hydropsychidae show marked changes with 2004 contributing a high proportion of the total. *G. pulex* is abundant at site **c** only in 2004 whereas *A. fluviatilis* and Naididae contributed less than 5% to the total catch in 2004.

Table IV summarizes the mean relative abundances and CV's for 21 taxa comprising >1% of the fauna at least one site over the period 1972 to 2004. These taxa comprised over 80% of the total fauna at all sites (96, 94, 93, 89 and 83% at **a, b, c, d** and **e,** respectively). The numbers of most taxa fluctuated widely over the study period but the amplitude varied from site to site. The greatest stability in terms of numbers of taxa with CV's ≤75% was observed at sites **d** and **e** and these sites also had the lowest mean CV (86, 82, respectively compared with 137, 105 and 87 at **a, b** and **c**).

Temporal and spatial differences in faunal composition were demonstrated in the relative abundances of functional feeding groups (Figure 4). It is clear that the proportions of the functional feeding groups are highly variable at sites **a** and **b** over the period 1972–2004. This is particularly marked for predators, scrapers and

Table IV. The mean relative abundance and coefficient of variation (cv) for 21 taxa comprising >1% of the fauna at atleast one site over the period 1972-1975, 2004

Taxa	a		b		c		d		e	
	mean	cv	mean	cv	mean	cv	mean	cv	mean	cv
Hydra sp.	33.17	**83**	24.60	**106**	11.88	**100**	5.05	**136**	0.00	—
Lymnaea peregra	20.50	**24**	6.21	**59**	9.40	**155**	4.32	**150**	0.04	**224**
Ancylus fluviatilis	0.19	**160**	4.17	**74**	2.34	**77**	0.69	**69**	0.79	**173**
Lumbriculidae	0.85	**121**	0.63	**48**	1.60	**58**	3.16	**46**	3.56	**69**
Naididae	15.37	**159**	27.24	**81**	30.28	**54**	24.28	**77**	1.67	**69**
Gammarus pulex	14.28	**138**	7.74	**151**	1.64	**194**	0.10	**93**	0.11	**143**
Baetis rhodani	0.87	**138**	3.59	**118**	3.56	**37**	9.10	**74**	22.34	**15**
Baetis scambus	0.14	**103**	0.32	**66**	0.44	**66**	2.12	**129**	1.42	**117**
Rhithrogena semicolorata	0.03	**224**	0.01	**224**	0.05	**111**	2.51	**108**	17.49	**28**
Ecdyonurus spp.	0.01	**224**	0.04	**114**	0.24	**92**	3.40	**48**	7.65	**40**
Ephemerella ignita	3.36	**40**	4.21	**129**	2.54	**67**	2.19	**84**	0.92	**48**
Caenis rivulorum	0.19	**159**	1.15	**67**	1.67	**70**	1.99	**49**	2.24	**45**
Leuctra fusca	0.37	**101**	0.26	**51**	0.46	**48**	2.77	**56**	2.99	**53**
Leuctra inermis	—	—	0.41	**109**	0.66	**67**	2.22	**75**	7.01	**42**
Elmis aenea	—	—	0.24	**167**	2.59	**59**	3.07	**110**	0.93	**54**
Limnius volckmari	0.06	**160**	3.99	**51**	3.48	**26**	2.20	**39**	3.71	**79**
Hydroptila sp.	0.63	**220**	0.24	**174**	2.73	**203**	2.14	**182**	0.39	**95**
Polycentropus flavomaculatus	0.05	**224**	0.09	**100**	0.54	**51**	0.69	**45**	1.67	**64**
Brachycentrus subnubilus	0.13	**124**	0.60	**137**	3.78	**134**	6.85	**123**	3.18	**167**
Orthocladiinae + Diamesinae	4.53	**54**	7.56	**72**	12.11	**48**	7.65	**37**	3.88	**52**
Tanytarsini	1.41	**146**	0.93	**117**	0.52	**113**	2.07	**85**	1.19	**69**

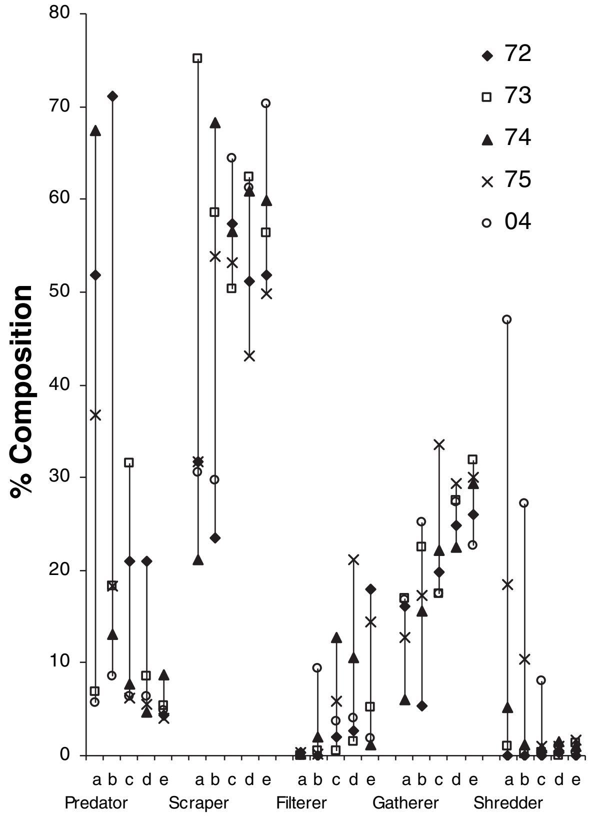

Figure 4. The range of annual variations in the proportions of functional feeding groups at sites **a**, **b**, **c**, **d** and **e** for the years 1972–1975 and 2004

shredders and is due to large changes in the abundance of 3 taxa which dominate these groups respectively, Hydridae, Naididae and *Gammarus pulex*. The unregulated Maize Beck shows little change in the proportions of shredders or predators over the 30-year period. Scrapers and filterers do show some fluctuations however due to changes in the abundance of *Baetis rhodani* and Heptageniidae (scrapers) and Simuliidae and *Brachycentrus subnubilus* (filterers). The occurrence of *B. subnubilus* (only in 1975) is unusual in a river of this type and is probably related to the high populations recorded in the adjacent Tees site (**c**). In general, scrapers dominated all sites with the exception of **a** however the types of scraper differed between the regulated and unregulated sites with *Lymnaea peregra*, *Ancylus fluviatilis* and Naididae in the Tees and Heptageniidae in Maize Beck. *Baetis rhodani* was common in both streams.

Changes in the numbers of taxa and abundance over the study period were marked (Figure 5). Abundance fluctuated widely at all the regulated Tees sites in contrast to the situation in Maize Beck where there was little change in numbers of animals between samples taken in 1975 and those in 2004. The numbers of taxa caught varied least at site **a** immediately below the dam. This site had a very restricted fauna due mainly to the extreme conditions of fluctuating discharge and the difficulties for colonizing organisms. The remaining sites showed moderate fluctuations in both the regulated Tees (**b**, **c** and **d**) and the unregulated Maize Beck (**e**).

The observed changes in total abundance and total taxa between years and sites were statistically significant (Table V) with inter-site differences more pronounced than those between years. Wilcoxon matched-pairs signed-ranks tests were used to examine the hypothesis that the mean difference in abundance between paired observations in the population was nil between years (Table VI). Significant changes in abundance were observed at the regulated sites **b**, **c** and **d** between the two years 1975 and 2004 but the unregulated Maize Beck (site **e**) showed no significant change throughout the period of study. At site **a,** although there were changes in the community the decrease of Hydra in 2004 was offset by increase in Gammarus pulex. Similar shifts in taxa dominance accounted for the lack of significance between 1972 and 2004 at sites **d** and **c.**

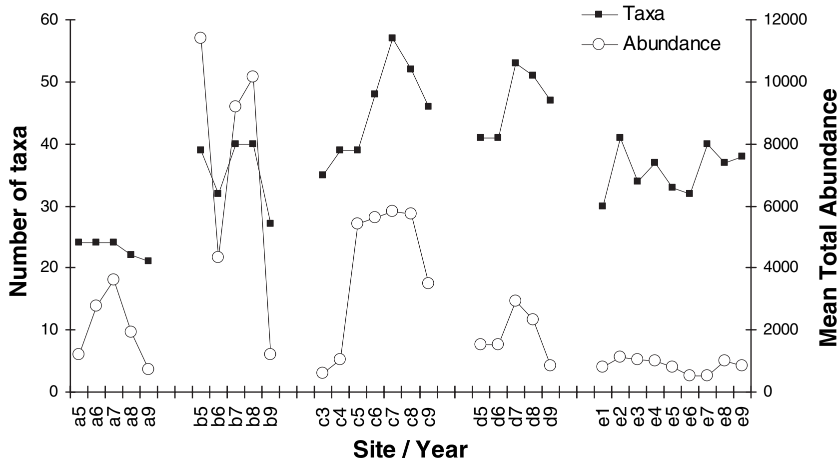

Figure 5. The mean total abundance and mean numbers of taxa per year at sites **a–e**

Table V. Results of two-way ANOVA's comparing the total numbers of taxa and total abundance between years and sites for the years 1972, 1973, 1974, 1975 and 2004

Response	Variable	SS	df	MS	*F*	*P*
Taxa	Year	0.026017	4	0.006504	3.157168	0.043
Taxa	Site	0.32863	4	0.082157	39.88004	<0.0001
Numbers	Years	0.599887	4	0.149972	3.678645	0.026
Numbers	Sites	2.815124	4	0.703781	17.26299	<0.00001

Table VI. Wilcoxon tests for the significance of differences in abundance in paired observations between years based on annual mean values for all fauna at the 5 sites, **a**, **b**, **c**, **d** and **e**

Year pairs	*N*	*W*	*z*	*P*
a72-a04	28	−80	0.91	0.3628
a75-a04	27	−97	1.16	0.246
b72-b04	44	370	2.16	0.0308
b75-b04	44	595	3.47	0.0005
c70-c04	56	−925	−3.77	0.0002
c72-c04	57	−178	−0.71	0.4777
c75-c04	67	554	1.73	0.0836
d72-d04	47	190	1	0.3173
d75-d04	59	963	3.63	0.0003
e68-e04	49	−110	−0.54	0.5892
e70-e04	46	−88	−0.48	0.6312
e72-e04	40	−52	10.35	0.7263
e75-e04	45	108	0.61	

(*N* number of matched pairs, W = *sum of signed ranks, Wilcoxon z and associated probability for two-tail test*).

Community composition

Changes in community structure over the period 1972 to 2004 are illustrated by the cluster diagram based on Bray Curtis indices applied to the site/taxa matrix and an MDS ordination of the derived Bray Curtis dissimilarity matrix (Figure 6).

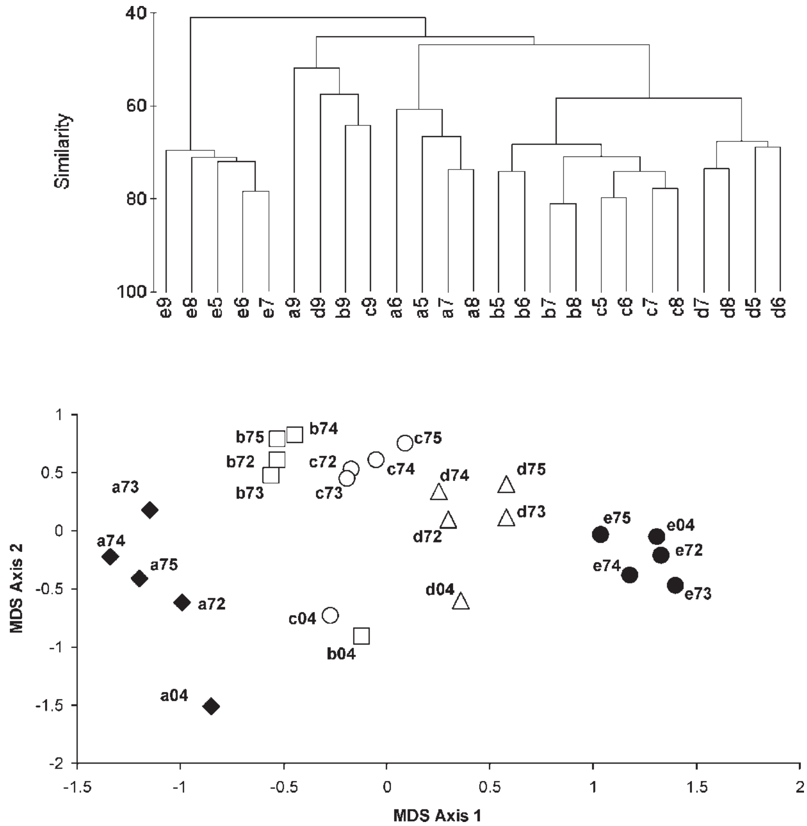

Figure 6. The cluster diagram based on Bray Curtis indices and an MDS ordination of the derived Bray Curtis dissimilarity matrix based on data for the years 1972–1975 and 2004 at all sites

The two salient points to emerge from the dendrogram are the faithfulness of the samples from site **e** throughout the study period and the grouping of the 2004 samples from **a, b, c** and **d**. The remaining samples also show a high degree of site faithfulness. The stress in the MDS two-axis plot of 0.11 indicates that the ordination provides a good representation of dissimilarities in community structure between years (Clarke and Warwick, 1994). The MDS plot shows the interrelationships between site samples and illustrates the separation of the 2004 samples from **a, b, c** and **d** from those taken in the 1972–1975 period. ANOSIM2 tests indicated that there were significant differences between year groups (Sample statistic Rho 0.611, significance level 0.2%) and between site groups (Rho 0.813, significance level 0.1%).

Ecological Assessment

RIVPACS analyses of combined seasons samples from the unregulated Maize Beck (**e**) and the regulated Tees (**c**) (Table VII) show that both sites are classified as 'good' with Maize Beck in the 'very good' (General Quality Assessment) category. A closer look at the predicted taxa shows that the number of 'false' predictions is greatest at the regulated site, **c**. Here 9 taxa were expected to occur at a probability of >50% but were not found in the RIVPACS samples. In contrast, only 3 expected taxa were not found at the unregulated site **e**. A further 9 taxa occurred in the Tees despite a low expected occurrence. Of these Gammaridae, Brachycentridae, Hydroptilidae and Hydridae were common with Psychomyiidae, Glossiphoniidae, Sphaeriidae and Sericostomatidae occurring only as singletons. At Maize Beck only 2 taxa, Brachycentridae and Leptophlebiidae, with low expected occurrence were found as singletons.

Table VII. Ecological Quality Indices (1) and predicted occurrence of taxa (2) based on combined seasons data from RIVPACS samples collected in 2004 from site **c**, Tees below Cauldron Snout and **e**, Maize Beck

1.

Site	Taxa (O)	taxa (E)	taxa (O/E)	aspt(O/E)	EQI taxa	EQIaspt	GQA
c	22	23.6	0.93	0.91	*a*	*b*	*b*
e	21	24	0.88	1.05	*a*	*a*	*a*

2.

Tees (**c**)		Maize Beck (**e**)	
Not found but $P > 50\%$	**Taxa**	**Not found but P $> 50\%$**	**Taxa**
99.90%	Heptageniidae	90.30%	Limnephilidae
91.10%	Simuliidae	71.90%	Dytiscidae
84.80%	Hydracarina	59.00%	Hydrophilidae
88.40%	Limnephilidae		
85.60%	Chloroperlidae		
84.20%	Perlidae		
81.00%	Polycentropodidae		
71.10%	Dytiscidae		
56.10%	Hydrophilidae		
Found but with $P < 50\%$		**Found but with $P > 50\%$**	
4.40%	Psychomyiidae	9.20%	Brachycentridae
5.30%	Hydridae	37.40%	Leptophlebiidae
10.50%	Brachycentridae		
15.30%	Glossiphoniidae		
16.70%	Sphaeriidae		
33.70%	Sericostomatidae		
45.40%	Lymnaeidae		
45.90%	Planariidae		
48.40%	Gammaridae		

Plankton

Large numbers of microcrustacea and *Hydra* were found at the three sites **a, c** and **d** in 2004 with densities varying according to site and season (Figure 7). The data were compared with that obtained in 1973 using ANOVA (Table VIII). Cladocera showed significant differences between years with greater densities occurring in 2004 in July. Between site differences were significant in all months with site **a** > **c** and **d** in April and September. In 1973 Daphniidae made up the highest proportion of cladocerans with only rare occurrence of Bosminidae. In 2004, Bosminidae made up 60% of the total Cladocera at sites **c** and **d** in the summer samples. Copepoda were less abundant in 2004 than in 1973. Site **a** supported higher densities than either **c** or **d**. *Hydra* densities were significantly greater in 2004 but between site differences were not significant although there was a tendency for numbers to be higher at site **c** in 2004. Between month densities were significantly different for all taxa with Cladocera and Copepoda being more abundant in July samples and *Hydra* more abundant in September samples.

DISCUSSION

Discharge

The importance of flow regime has long been recognized (Hynes, 1970) and its central role as a key driver of river ecology and a major determinant of physical habitat has received much attention in recent years (Bunn and Arthington, 2002). The pattern of flow release from Cow Green reservoir has remained similar over the years since impoundment with maintained minimum flows in summer and with occasional overtopping during the winter

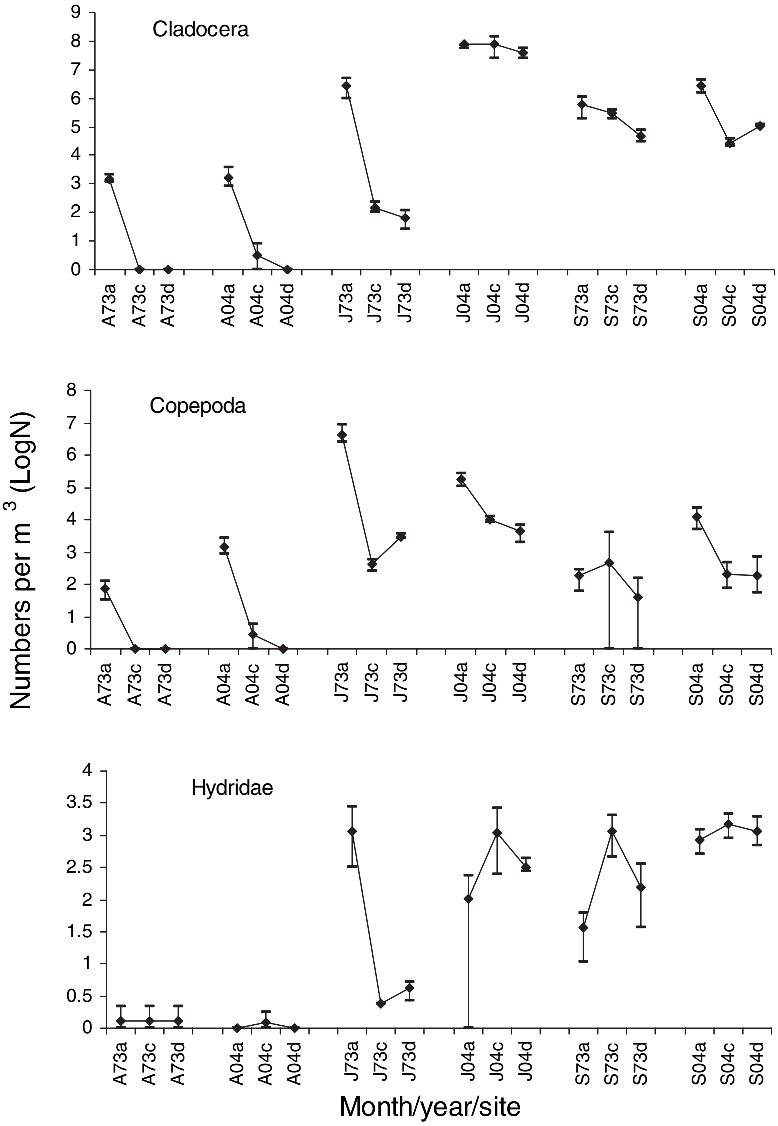

Figure 7. Seasonal changes (A April, J July, S September) in the longitudinal distribution of numbers and ranges of microcrustacea and Hydridae in the Tees in the years 1973 and 2004 at sites **a**, **c** and **d**

Table VIII. F ratios from two-way ANOVA's comparing densities of microcrustacea and 'Hydra' in 1973 and 2004 at 3 sites, **a**, **c** and **d** for each season

Taxa	Year	Month	Site	Year/Month	Year/Site	Month/Site		
Cladocera	64.41***	238.98***	60.42***	57.83***	4.69*	3.86*		
Copepoda	8.93**	103.8***	50.98***	2.36ns	0.43ns	2.03ns		
Hydridae	10.99**	69.58***	0.51ns	2.91ns	3.05ns	2.03ns		
Parameter	1973	2004	**a**	**c**	**d**	April	July	September
Cladocera	146.46	910.46	701.40	506.78	377.20	7.90	1324.86	252.62
Copepoda	90.77	42.09	170.89	15.06	13.33	4.67	177.44	17.17
Hydridae	5.98	10.96	8.05	10.66	6.70	0.04	9.86	15.51

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. Also shown are the mean parameter values for year, site and month.

period. Similarly the disposition of the large substratum particles, boulders and cobbles, in the Tees and Maize Beck has not changed markedly and, thus, water velocity distribution patterns (which have a direct affect on biota) will not have altered. Some of the observed changes in faunal composition might have been attributable to a markedly different flow regime in the years preceding the 2004 sampling but the available evidence suggests that the flow quantities and flow variability in the two 4-year periods, 1972–1975 and 2001–2004 were not significantly different in either the unregulated Trout Beck (a surrogate for Maize Beck) or the regulated Tees. Thus, any observed variations in faunal community composition and abundance since 1975 are more likely to be attributable to temporal changes arising from the regulated flow regime.

Benthos

The changes in composition and abundance of the benthic macroinvertebrate fauna noted in the first 5 years of the reservoirs existence were dramatic and involved major shifts in community composition in the regulated Tees and the extent and type of changes varied with distance from the dam. In general, these involved reductions in the abundance of Heptageniidae and Plecoptera and large increases particularly of Naididae, Hydridae and *Lymnaea peregra*, and the appearance of *Gammarus pulex*, not found in the Tees in a pre-impoundment study (Armitage *et al*., 1974). These changes after dam closure were related to the reservoir, as a source of colonisers (*G. pulex*) and enriched seston (microcrustacea) (Armitage, 1984), and a reduction in extreme flows, with a resultant increase in periphyton (Armitage, 1978). The stability of the substratum and stable flows are typically associated with high average periphyton biomass (Poff *et al*., 1990, Clausen and Biggs, 1997). At Cow Green conditions below the dam still support an abundant periphyton.

Now, 30 years later, community changes have taken place in the Tees and the main differences at site **c** since 1975 have been an increase in *Pisidium* sp., *Lymnaea peregra*, *Gammarus pulex*, *Ephemerella ignita*, *Hydroptila* sp. and Hydropsychidae and reductions in the abundance of *Ancylus fluviatilis*, Naididae, Lumbricidae, Heptageniidae, *Caenis rivulorum*, *Leuctra inermis*, *Brachycentrus subnubilus* and Orthocladiinae/Diamesinae. There are insufficient data to explain all these fluctuations but habitat changes due to increased fines in the absence of scouring flows may favour *Pisidium* sp. *L. peregra* is known to take a wide range of foodstuffs including periphyton and dead animal tissue (Nazrul Islam *et al*., 2001) both of which are plentiful. Increases in Amphipoda below dams have been well documented (Spence and Hynes, 1971, Ward and Stanford, 1979, Vinson, 2001) and at Cow Green the *G. pulex* population appears to be moving downstream, decreasing at the two sites nearest to the dam which were colonized first (from the reservoir), despite less than optimum flow and substratum characteristics, and increasing at site **c** where the breakdown of filamentous algae and mosses provide a rich source of food. *Ephemerella ignita* is reported to be tolerant to regulated conditions partly due to its life-history with a long period of egg development and hatching and short period of late spring and summer nymphal growth which allows the species to avoid extreme flows (Alba-Tercedor, 1990, Céréghino and Lavandier, 1998). In addition, its food (algal fragments and detritus) will also be abundant. Dense growths of filamentous algae will also favour large *Hydroptila* populations (Nielsen, 1948, Keiper *et al*., 1998) and Hydropsychidae should benefit from the enriched seston (Armitage, 1984; Winget, 1984).

Of those taxa that showed reductions in abundance many require a substratum without dense periphyton growth (Heptageniidae, *C.rivulorum*, Leuctridae, *Ancylus fluviatilis*, Lumbricidae). The observed reduction in Naididae, Chironomidae (Orthocladiinae, Tanytarsini) and the filter feeding *B. subnubilus* is harder to explain in the absence of extreme flows and more detailed data on possible biotic interactions are needed. *Gammarus*, although classified predominantly as a shredder (Wright *et al*., 2002), is known to consume insect eggs and small instars (MacNeil *et al*., 1997, Krisp and Maier, 2005) and it is possible that increased amphipod abundance is reducing numbers of naid worms and chironomids. *B. subnubilis* reached peak densities in 1974 and already by 1975 its population had fallen by a factor of three. This species is a filterer and a grazer and showed a rapid increase after impoundment. Its subsequent decline may be attributable to increased predation by *G. pulex* (Krisp and Maier, 2005) following changes in overall community composition or possibly to changes in the quality of seston or substratum characteristics. At site **d** below the junction with Maize Beck, the community is influenced by both regulated and unregulated flow conditions. *Hydroptila* increased in abundance and Heptageniidae and Plecoptera decreased since the 1972–1975 period in response to the regulated flow whereas *Gammarus pulex* whose abundance increased at the Tees sites above the confluence was adversely affected by the unregulated flows from Maize Beck.

The observed changes in faunal composition after 30 years are consistent with a community continuing to adapt to a periphyton/bryophyte rich substratum, which offers a large complex three-dimensional habitat (Lee and Hershey, 2000) with considerable hydraulic diversity (Dodds and Biggs, 2002) and a rich food resource supplemented with enriched seston from the reservoir (Armitage, 1984). The role of flow regulation in affecting biotic interactions by subtly altering habitat characteristics has been the focus of studies by Power *et al*., 1995, 1996 and Vinson (2001) suggests that in the long-term it is these subtle changes which may determine the ability of species to maintain a viable population. Certainly at Cow Green in the 30 years since the last study on macroinvertebrates there have been no apparent further changes in physical conditions in the Tees below the dam but the faunal community has changed.

In marked contrast to the situation in the regulated Tees, the unregulated Maize Beck (**e**) showed little change over the 30-year period. An early indication of the persistence of the Maize Beck fauna was the greater variability of chironomid assemblages in the regulated Tees as compared with the unregulated stream (Armitage and Blackburn, 1990). A number of studies have shown that invertebrate assemblages in 'pristine' systems are persistent over multiple years (Ward, 1975, Robinson *et al*., 2000, Scarsbrook, 2002) and that constancy in habitat conditions supports a persistent stream community (Weatherley and Ormerod, 1990, Death and Winterbourn, 1994, Armitage and Gunn, 1996, Scarsbrook, 2002). Environmental conditions in Maize Beck are not stable, that is to say there is a wide fluctuation in temperature, flow and to a lesser extent water chemistry, but despite this there is a constancy of conditions from year to year. The substratum is composed largely of boulders and cobbles and although these move in response to floods there is no overall change in substratum characteristics. It is these factors that most likely account for the persistence of the Maize Beck community.

In the Tees there appears to be a continuing adjustment to the prevailing predictable and low disturbance environment. Other workers (Palmer *et al*., 1996, Vinson, 2001) have stressed that such conditions in conjunction with low rates of dispersal and colonization provide the greatest opportunity for local biotic interactions. In the Tees the dam effectively cuts off dispersal of lotic taxa and reduces colonization from upstream and the absence of extreme physical events has created an environment markedly different from the pre-impoundment state. Boulders instead of being bare through frequent scouring have developed a complex periphyton and bryophyte community, which although showing seasonal fluctuations, is never removed. With the absence of extreme physical changes it would be expected that community composition would be largely governed by biotic interactions. Community composition may also be influenced by long-term geomorphological adjustment often reported where flows are regulated (Petts, 1980, Petts and Greenwood, 1985, Greenwood *et al*., 1999, Grant *et al*., 2003). However, the confined, steeply sloped channels and coarse substrata in both the Tees and Maize Beck may mitigate against geomorphological change in this particular river sector but this does not preclude the possibility of subtle changes here and more obvious changes further downstream but this has not been studied. The temporal changes in faunal community are evident from the results from the MDA where the Tees sites sampled in 2004 are separated from those sampled in the period 1972–1975, as a result of abundance changes in common taxa and the appearance of taxa not previously recorded. Maize Beck in contrast was characterized by few changes in abundance and no new taxa.

Ecological Assessment

Armitage (1989) examined the macroinvertebrate fauna in the tailwaters of 29 reservoirs used for supply purposes. Extremes of discharge were reduced but compensation flows were released to maintain flows. Conditions were broadly similar therefore to those at Cow Green. Indications from quality assessments carried out using an early version of RIVPACS showed that 23 of the 29 sites were of good to very good quality based on the ratio of observed to expected number of taxa. This is similar to the current situation recorded at Cow Green and indicates that quality as assessed by RIVPACS does not appear to have been much affected by regulation. This contrasts with work in Australia using a similar assessment model (Marchant and Hehir, 2002) where all observed/expected indices were below the threshold considered equivalent to unregulated reference sites. This is not unexpected given the major climatic differences between the two countries but does point up the dangers of drawing general conclusions on the effects of regulation. Despite no demonstration of reduced quality at Cow Green there are strong indications from the analysis that there have been major shifts in community composition. The list of expected taxa which were not recorded and those that occurred despite a low probability of occurrence, if considered with knowledge of their food and habits, can provide clues as to how regulation is affecting the ecology of the stream (Armitage, 1987). In this case the results from RIVPACS support the findings of the main study and correctly identified taxa, which have been responsive to regulation such as decreases in Heptageniidae and Simuliidae and increases in Gammaridae, Hydroptilidae and Hydridae.

A site situated 2 km below site **c** has been monitored on a regular basis by the Environment Agency throughout the 1990's until the present. Currently samples are collected in spring and summer only. RIVPACS predictions based on these seasons data collected in 2003 placed the site in the 'very good' GQA category. The equivalent category, based on spring and summer data for both Maize Beck and the Tees, was 'good'. These results indicate that although there is a tendency for the GQA to be slightly lower in the Tees at site **c** just before its confluence with Maize Beck, the river quickly recovers and the highest band is reached 2km further downstream.

Plankton

Increases in zooplankton abundance in subarctic reservoirs have been linked to increased phytoplankton production following release of nutrients often reported in newly flooded systems (Ostrofsky, 1978). While Cow Green cannot be considered a subarctic reservoir, the development of a zooplankton community in the newly formed reservoir was expected and very high densities of microcrustacea were recorded in the littoral zone in the first year after filling (Armitage, 1977a) and high densities were recorded below the dam in 1972 and 1973 (Armitage and Capper, 1976). What is surprising is that thirty years on, the abundance of microcrustacea is still high despite an expected reduction and erosion of flooded vegetation. The overall pattern of abundance and transport downstream of microcrustacea and *Hydra* recorded in 2004 was similar to the situation 30 years ago (Armitage and Capper, 1976) but Cladocera and *Hydra* densities increased and Copepoda decreased.

Particulate matter retained during drift sampling in the Tees (Armitage, 1977b) was composed largely of detritus and filamentous algae, supplemented with microcrustacea and *Hydra* in contrast to that in Maize Beck which consisted mainly of eroded peat and mineral particles. The mean C:N ratios for the eight sampling occasions in the Tees and Maize Beck were 11.63 and 27.00, respectively (Armitage, 1984) indicating the potentially higher nutritional value of Tees seston. The transport downstream of these organisms will therefore continue to influence the benthic communities below the dam by providing a protein rich food source.

CONCLUSIONS

The main findings of this study are:-

- Faunal communities in the regulated Tees below Cow Green Reservoir showed marked changes between the original study in 1972–1975 and 2004. It is likely, but unproved, that this represents a continuing change in community structure where no equilibrium has been reached. A narrower range of environmental conditions and increased flow stability have led to a dynamically fragile community which is very susceptible to physical perturbations because it has developed in their absence. The evidence suggests that in this relatively physically stable environment biotic interactions may be exerting a dominant influence on community structure and dynamics.
- The unregulated stream Maize Beck has shown little change in faunal community composition between the original study and the present observations. A natural spatey flow regime continues to dominate the environment and the variable and unpredictable conditions have resulted in a dynamically robust faunal community.
- The role of periphyton and reservoir plankton in structuring the faunal composition in the regulated sites in the Tees seems to be paramount. The effects were noted immediately after impoundment and their influence is still apparent. Periphyton and moss attenuate water velocity and create a three-dimensional habitat, which offers a wide range of niches for the invertebrate community and provides an abundant food resource. The effects of this are likely to increase opportunities for a wide range of organisms to colonize this habitat and increase the

probability of biotic interactions between members of the faunal community and with the biotic substratum itself. These interactions are likely to result in continuing shifts in faunal composition at the regulated sites.

- Observations in this cool temperate system have revealed long-term effects of impoundment on the macroinvertebrate communities, which although not as drastic as those observed in some reservoirs experiencing continental climates are nonetheless clearly demonstrated.

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