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DOWNSTREAM CHANGES IN THE COMPOSITION, NUMBERS AND BIOMASS OF BOTTOM FAUNA IN THE TEES BELOW COW GREEN RESERVOIR AND IN AN UNREGULATED TRIBUTARY MAIZE BECK, IN THE FIRST FIVE YEARS AFTER IMPOUNDMENT

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Abstracts

Changes in composition, numbers and biomass of benthic fauna of the Tees below Cow Green Reservoir and an unregulated tributary Maize Beck were followed between 1972 and 1975 and pre- and post-impoundment conditions were compared. Species diversity was lowest just below the dam and numbers and biomass were highest 240 m downstream of the dam. Faunal densities increased in the Tees after impoundment but in Maize Beck no major changes were observed.

Introduction

This present work forms part of a general study of the effects of Cow Green reservoir on the invertebrate fauna of the Tees below the dam. Previous studies include a pre-impoundment survey of the benthos in the Tees and its tributaries (Armitage *et al.*, 1974), and post-impoundment studies on benthos (Armitage, 1976), downstream movement of zooplankton (Armitage & Capper, 1976) and invertebrate drift (Armitage, 1977a). This present study was designed to determine longitudinal changes in the fauna below the dam over a four-year period (1972-1975), and to compare pre- and post-impoundment conditions.

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Study area

The Cow Green dam (Upper Teesdale, N. England) was completed in the summer of 1970. The reservoir is situated in Pennine moorland and lies at an altitude of 489 m above sea level. Some temperature and discharge data are presented in Armitage (1976) and Armitage & Capper (1976), and Crisp (1977) gives physical and chemical data.

The reservoir is used to regulate the flow of the Tees in order to provide industrial Teeside with water during dry conditions. Water is drawn-off simultaneously from upper and lower levels of the reservoir. The combination of high and frequent winds and altitude of the reservoir result in considerable mixing of its waters and the outflow from the valves is cold and well-oxygenated. Below the dam the river is wide with a stony bottom and undisturbed flow. About 100 m below the dam the river narrows at a weir and flows rapidly for about 100 m. There is then a short section with relatively little gradient before the river drops about 40 m in 135 m down a ravine of basalt, known as Cauldron Snout. Below this the river flows as a rocky-bottomed braided stream and 200 m downstream it is joined by a tributary, Maize Beck.

Samples were taken in riffles by disturbing the substratum with the foot for 60 s immediately upstream of a net (250 mm in diameter with a mesh aperture of 800 μ) held vertically on the bed of the stream. This method was described by Hynes (1961) and found to give consistent results (Morgan & Egglishaw, 1965). Armitage *et al.* (1974) used this method in a pre-impoundment survey

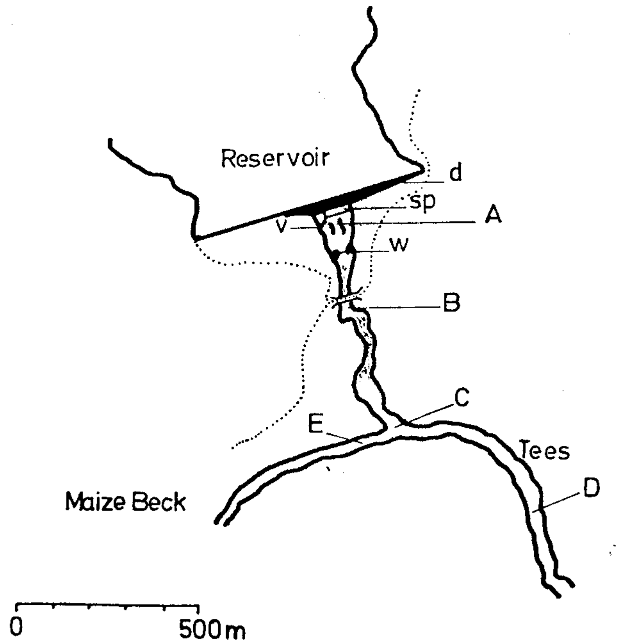

Fig. 1. Sketch map of study area showing location of sample sites. (d = dam wall, s.p. = stilling pool, v = valves, w = weir).

and found that one kick sample covered an area of 95200 mm^2. The location of the sample sites is shown in Fig. 1.

Site A is situated just below and to the right of the outflow valves (looking upstream) and so does not receive the full force of the water. The velocity of the current ranges from 0.33 to 1.11 m s^{-1} with a mean of about 0.70 m s^{-1}. The substratum consists of stones not > 100 mm in diameter with slight algal cover, resting on sand and clay.

Site B is 239 m below the dam and the substratum is made up of relatively large stones (up to 250 mm in diameter resting on gravel and sand). Current speed ranged from about 0.40 to 1.50 m s^{-1} with a mean of 0.80 m s^{-1}. Algal and moss cover was great especially during the summer months.

Site C is near the junction with Maize Beck and the area probably recieves Maize Beck water when flow in the Tees is low and Maize Beck is in spate. The substratum is similar to that at site B and algal and moss cover is great. However, the velocity of the water at this point is slightly less, ranging from 0.39 to 1.06 with a mean of 0.70 m s^{-1}. Substratum and current speed at site D, about 300 m below the Maize Beck confluence are similar to those at site B.

Site E is subject to the greatest range in current velocity (0.40-2.00 m s^{-1}, mean 0.87 m s^{-1}). The boulders comprising the bottom are similar in size to those at sites B, C, and D but are more rounded, looser-packed and devoid of dense algal and moss cover.

Two samples were taken at each site 4 times a year in January, April/May, July and September.

Table 1. The mean numbers of animals per 60 s kick sample x 10, at sites A-E, based on data collected in January, May, July and September in the years 1972-1975.

Taxa	A	B	C	D	E
Hydra vulgaris Pallas	772	2277	151	84	–
Naididae	386	2215	1119	468	14
Enchytraeidae	18	68	22	12	6
Tubificidae	7	3	42	26	15
Lumbriculidae	9	46	91	48	13
Lumbricidae	1	24	14	8	8
Gammarus pulex L.	106	230	5	2	1
Leuctra inermis Kempny	–	35	35	38	57
Leucta fusca L.	7	14	28	53	19
Ecdyonurus dispar (Curt.)	+	3	19	60	47
Rhithrogena semicolorata (Curt.)	+	2	6	57	141
Baetis rhodani (Pict.)	27	162	161	95	131
Baetis scambus Eaton	4	25	21	32	10
Caenis rivulorum Eaton	2	78	58	35	11
Ephemerella ignita (Poda)	54	134	73	25	6
Rhyacophila dorsalis (Curt.)	4	43	24	9	5
Polycentropodidae	1	2	27	12	11
Hydroptila sp.	+	3	15	6	3
Brachycentrus subnubilus (Curt.)	2	44	175	153	28
Limnephilidae	3	5	10	6	1
Limnius volckmari Panz.	+	228	153	33	15
Esolus parallelepipedus (Mull.)	+	45	9	13	1
Elmis aenea (Mull.)	–	7	92	44	8
Orthocladiinae	61	476	369	89	23
Tanytarsini	40	94	13	43	7
Dicranota sp.	1	1	10	14	6
Simuliidae	1	–	3	8	33
Lymnaea peregra (Mull.)	510	473	59	28	+
Ancyclus fluviatilis (Mull.)	+	314	139	14	7
Others	13	44	70	62	34
Totals	2029	7095	3013	1577	661

Table 2. The numbers of species/taxa in each faunal group at the 5 study sites based on data collected between 1972 and 1975.

Group	A	B	C	D	E
Hydrozoa	1	1	1	1	–
Tricladida	–	–	1	–	1
Nematoda	1	1	1	1	–
Annelida	9	7	9	7	7
Amphipoda	1	1	1	1	1
Plecoptera	3	11	15	16	14
Ephemeroptera	6	7	11	11	11
Trichoptera	7	11	9	9	8
Coleoptera	4	4	6	7	4
Diptera	10	11	10	10	8
Hydrachnellae	–	–	1	1	1
Mollusca	3	2	3	3	3
Totals	45	56	68	67	58

Results

The fauna

Tables 1 and 2 present data on the fauna of the five sites studied between 1972 and 1975 and Fig. 2 shows the percentage composition of major taxa at all the sites. The differences between the stations are due more to changes in the proportions of component species or taxa than to the presence of widely differing faunas. Thus, with some few exceptions most sites share taxa in common. Thirty of the 67 main taxa recorded were found in all five stations.

The inter-relationships between the five sites were investigated by using the Mountford Index of Similarity (Mountford, 1962) on taxa at the species level. The results are presented in the form of a diagram (Fig. 3). The most similar sites are D and C. Site E (Maize Beck) stands separately but has similarities with sites D and C. The two sites just below the dam stand on their own. Site A is characterised by a fauna which is dominated numerically by *Hydra, Lymnaea peregra,* Naididae, *Gammarus pulex* and Orthocladiinae. Plecoptera, Trichoptera and Coleoptera are poorly repŗesented and occur at low mean densities (< 1 per 60 s kick). *Ephemerella ignita* and *Baetis rhodani* are the only common ephemeropterans and occur at low mean densities of 3-5 animals per 60 s kick. Site B has a similar fauna but Coleoptera (Elminthidae) are more abundant and *Ancylus fluviatilis* makes up 4.5% of the total mean numbers. The abundance of *Gammarus pulex* at both A and B is probably directly due to the

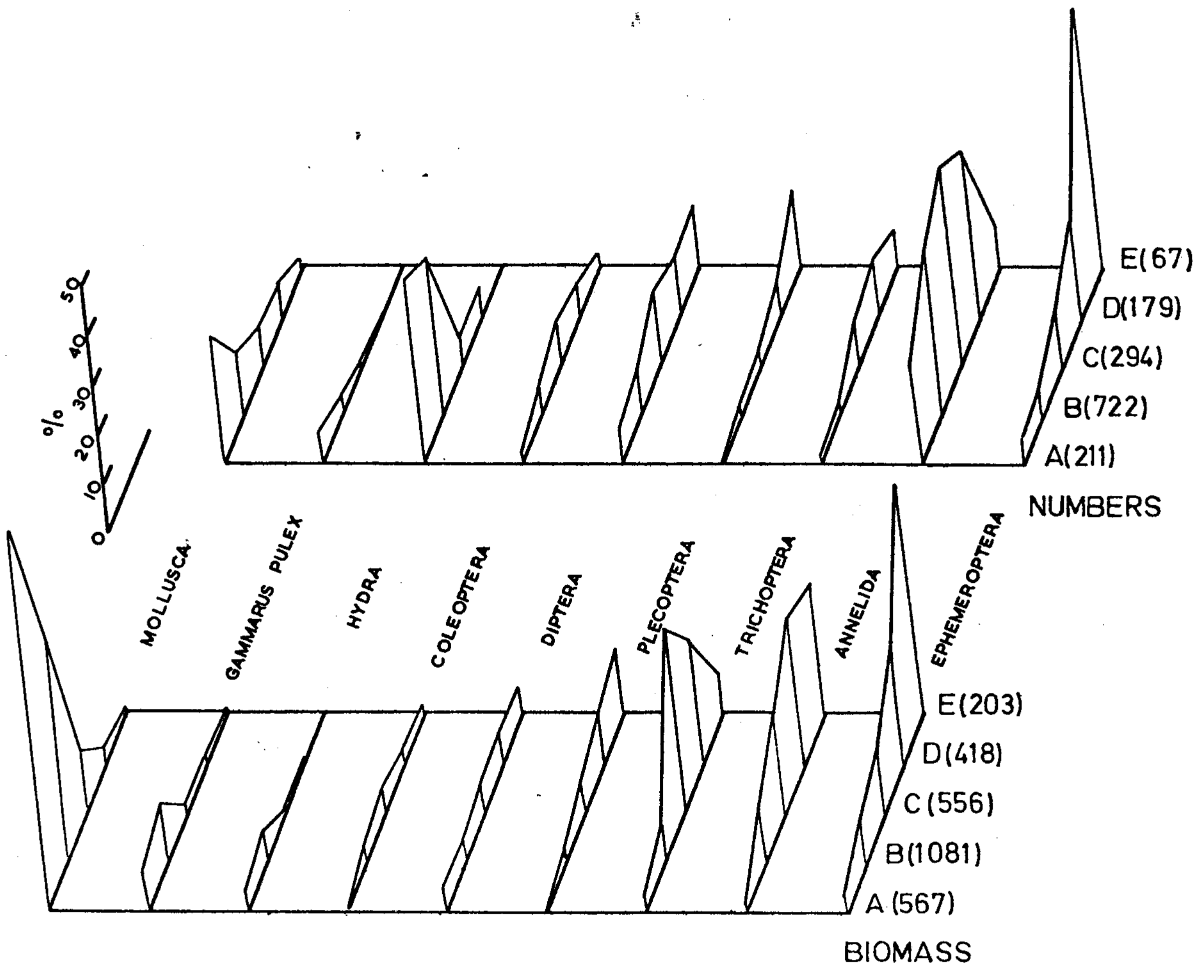

Fig. 2. The composition of the fauna at sites A-E based on mean numbers and biomass of major groups and taxa in January, May, July and September in the years 1972-1975. (Figures in parentheses represent mean numbers and biomass (mg, wet-weight) per 60 s kick sample for total fauna).

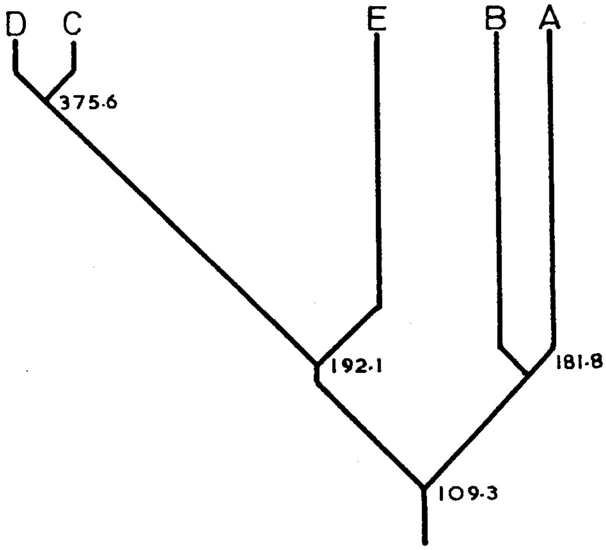

Fig. 3. Diagram showing the relationship of one site to another based on Mountford indices of similarity.

large numbers of this species found in the reservoir (Armitage, 1977b). *G. pulex* was not found in the Tees in this area in a pre-impoundment study (Armitage *et al.*, 1974) and it is very likely that the species now occurs there because colonization downstream is facilitated by the presence of the reservoir.

A preliminary look at the species lists for all 5 sites indicates that sites A and B have less diverse faunas than the other three sites. In order to test this observation the information index of Shannon & Weaver (1949) was adopted to express the diversity of the fauna at each station using the formula $H(S) = -\sum_{i=1}^{s} Pi \log_2 Pi$ (Southwood, 1966) where S = total number of species in the sample and Pi is the proportion of the ith species in the sample. The index (H) was calculated for January, May, July and September for the four years, 1972-1975, at each of the 5 sites, Table 3. The Wilcoxon matched pairs signed ranks test (Siegel, 1956) was used to test the significance of

Table 3 a) The mean values of diversity indices for January, May, July and September based on estimates in the four years 1972-1975 at sites A through E.
b) Summary of results of Wilcoxon T tests for the significance of the difference in faunal diversity between pairs of adjacent sites (N = number of matched pairs, T = Wilcoxon T statistic, P = probability associated with calculated T value for the null hypothesis that there is no difference in diversity between pairs of adjacent sites, R = result of test).

a)	A	B	C	D	E
January	1.45	3.02	3.92	3.34	2.26
May	1.73	3.19	3.74	3.28	3.08
July	2.00	2.39	2.48	3.16	3.65
September	1.12	2.06	3.24	3.52	3.09

b)	A/B	B/C	C/D	C/E	D/E
N	16	16	14	16	14
T	6	17	49	52	22
P	0.01	0.01	n.s.	n.s.	0.05
R	B>A	C>B			D>E

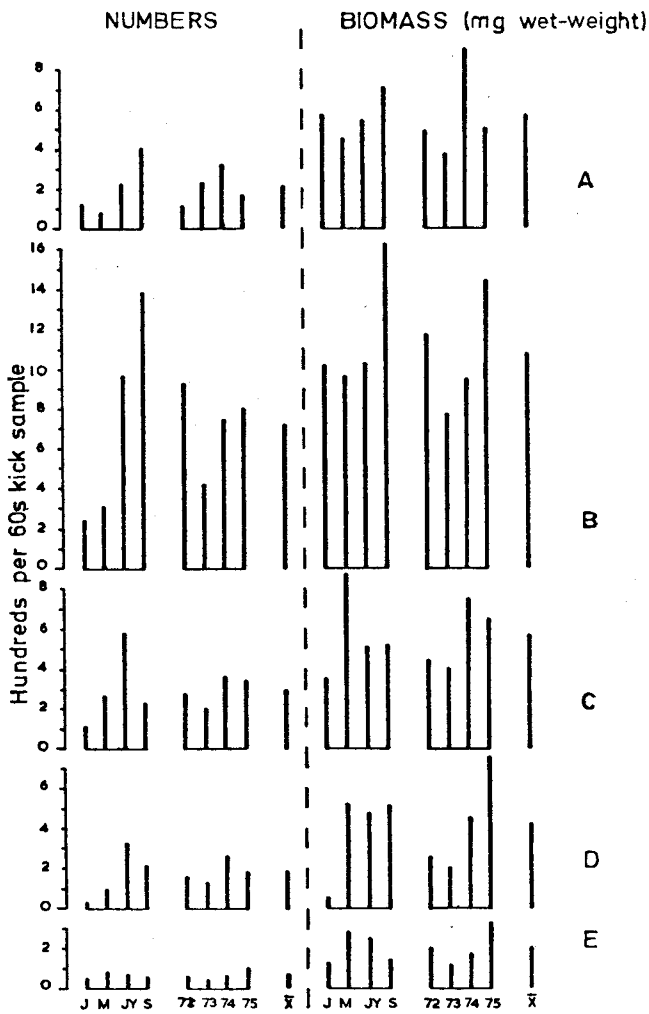

Fig. 4. Seasonal and annual fluctuations in total numbers and biomass at sites A-E. The values for January, May, July and September are means for the period 1972-1975, and each annual mean is based on samples taken in those months. x̄ is the overall annual mean for the period 1972-1975.

differences in diversity between adjacent stations. The results indicate that faunal diversity is least at A (1.57), slightly greater at B (2.67) and greatest at C and D (3.34 and 3.32 respectively). Diversity at E (3.02) was significantly less than at D but no differences could be detected between C and E. A Krustall-Wallis one-way analysis of variance test (Siegel, 1956) was employed to test if there were significant differences between indices for January, May, July and September and also between indices for the four years. No significant annual or seasonal differences could be detected ($P > 0.05$).

The low values of the indices for sites A and B reflect the relatively high numbers of few species at these sites, for example over the period 1972-1975 5 species accounted for 90% of the numbers at A and 8 species made up a similar percentage at B. The number of taxa making up 90% of the numbers at C, D, and E were 15, 19 and 19 respectively.

Seasonal and annual changes in abundance and biomass

Fig. 4 shows fluctuations in total numbers and biomass at the 5 study sites. The significance of differences between years months and sites was examined by using the Friedman test (Siegel, 1956). Significant differences in total numbers were observed between months ($\chi_T^2 = 8.28$, d.f. = 3. $P < 0.05$) and between sites ($\chi_T^2 = 14.2$, d.f. = 4, $P < 0.01$) but not between years. Total biomass showed significant differences between sites ($\chi_T^2 = 13.4$, d.f. = 4, $P < 0.01$) and between years ($\chi_T^2 = 11.16$, d.f. = 3, $P < 0.02$).

Table 4. Results of Wilcoxon T tests for the significance of differences in numbers and biomass of major groups and taxa, between pairs of adjacent sites; based on samples taken in January, May, July and September in the 4 years 1972-75. The null hypothesis that numbers and biomass at adjacent sites are not significantly different was rejected at P < 0.05. (The probabilities (P) are indicated for each test, * < 0.05, ** < 0.02, *** < 0.01, ns = not significant)

Numbers	AB	BC	CD	CE	DE
Hydra vulgaris	B>A *	B>C ***	C>D ***	C>E ***	D>E **
Naididae	B>A ***	ns	C>D ***	C>E ***	D>E ***
Other Annelida	B>A ***	ns	C>D *	C>E ***	D>E **
Gammarus pulex	ns	B>C *	ns	C>E *	ns
Plecoptera	B>A ***	C>B *	ns	ns	ns
Baetis rhodani	B>A ***	ns	ns	ns	E>D ***
Ecdyonuridae	ns	C>B **	D>C ***	E>C ***	ns
Trichoptera	B>A ***	C>B *	ns	C>E ***	D>E ***
Coleoptera	B>A ***	ns	C>D **	C>E ***	D>E ***
Orthocladiinae	B>A ***	ns	C>D ***	C>E ***	D>E ***
Mollusca	ns	B>C ***	C>D ***	C>E ***	D>E ***
Total fauna	B>A ***	B>C ***	C>D ***	C>E ***	D>E **

Biomass	AB	BC	CD	CE	DE
Hydra vulgaris	B>A *	B>C ***	ns	C>E ***	D>E **
Annelida	B>A ***	ns	ns	ns	ns
Gammarus pulex	ns	B>C *	C>D *	C>E *	ns
Plecoptera	B>A ***	ns	ns	ns	ns
Ephemeroptera	B>A ***	ns	ns	ns	ns
Trichoptera	B>A ***	ns	ns	C>E ***	ns
Coleoptera	B>A ***	ns	C>D ***	C>E ***	D>E ***
Diptera	B>A ***	ns	ns	C>E ***	ns
Mollusca	ns	B>C ***	C>D ***	C>E ***	D>E ***
Total fauna	B>A ***	B>C ***	ns	C>E ***	ns

Further analysis of monthly fluctuations in total numbers using the Wilcoxon T test showed that at sites A and B highest numbers were found in September or in September and July ($P < 0.02$). At sites C and D greatest numbers were found in July ($P < 0.001$) and site E showed no significant differences between months.

Amongst the major groups and taxa some showed distinct seasonal and/or annual trends. *Hydra* was always most abundant in September. *Gammarus pulex* first appeared in July 1972 at site B and increased steadily in numbers and biomass during the study period, both parameters being greatest in September 1975. Naididae were most abundant in July in the years 1974 and 1975. The numbers of Plecoptera were highest in May and July due respectively to populations of *Leuctra inermis* and *Leuctra fusca,* and densities were generally greatest in 1974 and 1975. Trichoptera were most abundant at site C due mainly to a population of *Brachycentrus subnubilus* which reached its greatest numbers in July in 1974 and 1975. *B. subnubilus* is a filter-feeder and it is possible that its high density is due in part to the availability of seston consisting of nutrient rich algal filaments and microcrustaceans (Armitage, 1977a).

The significance of the differences in abundance between pairs of adjacent sites of the major groups and taxa are indicated in Table 4. Most groups occurred at higher densities in the regulated Tees' sites, exceptions were Ecdyonuridae which were more abundant at E than at C

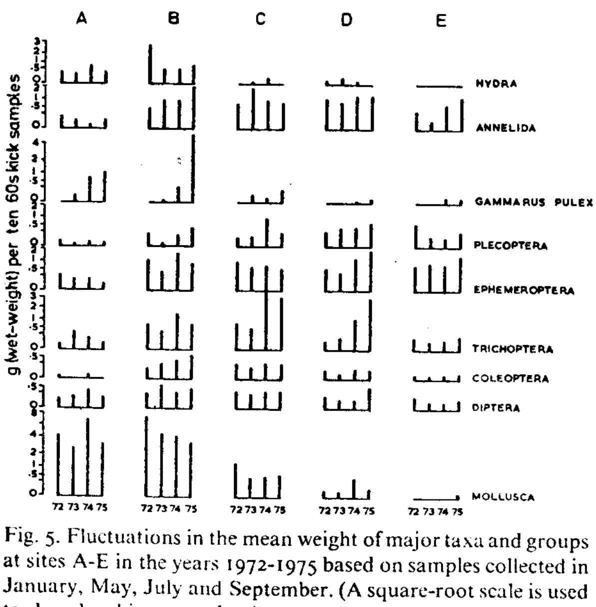

Fig. 5. Fluctuations in the mean weight of major taxa and groups at sites A-E in the years 1972-1975 based on samples collected in January, May, July and September. (A square-root scale is used to show low biomass values).

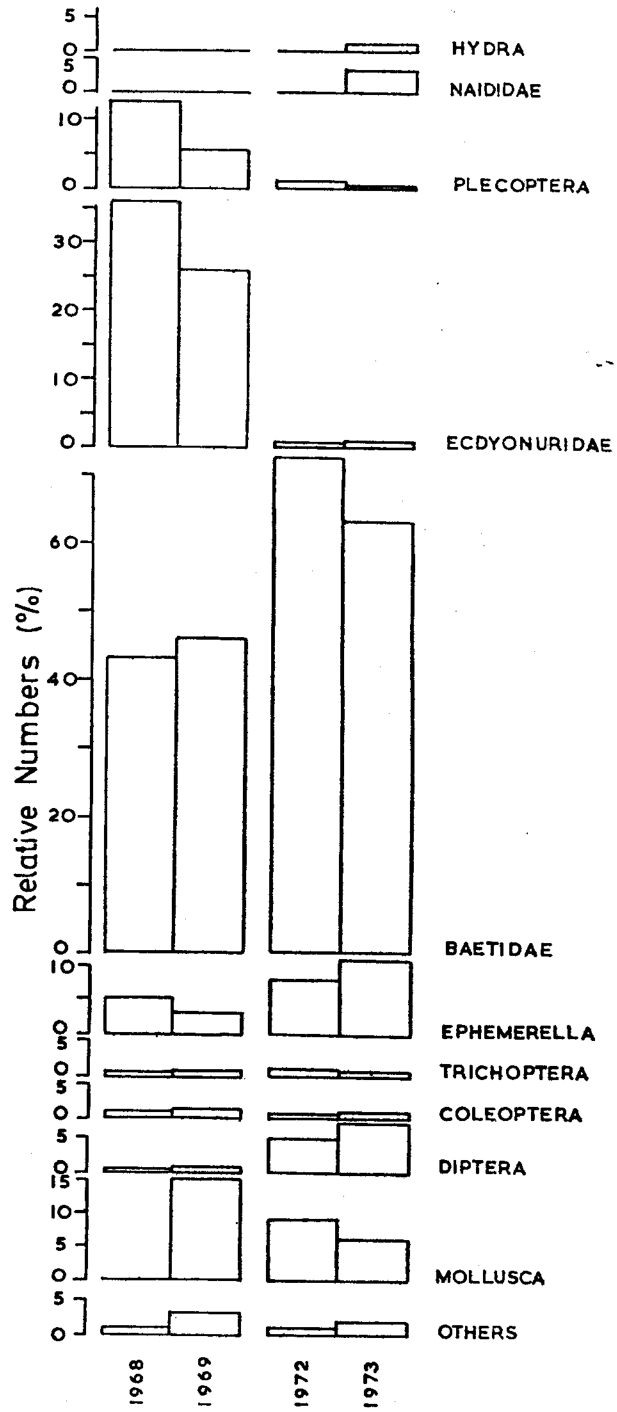

Fig. 6. The relative abundance of taxa taken in nets during electrofishing in pre- (1968, 1969) and post-impoundment (1972, 1973) periods. The proportions for each year are based on the mean of May, July and September samples.

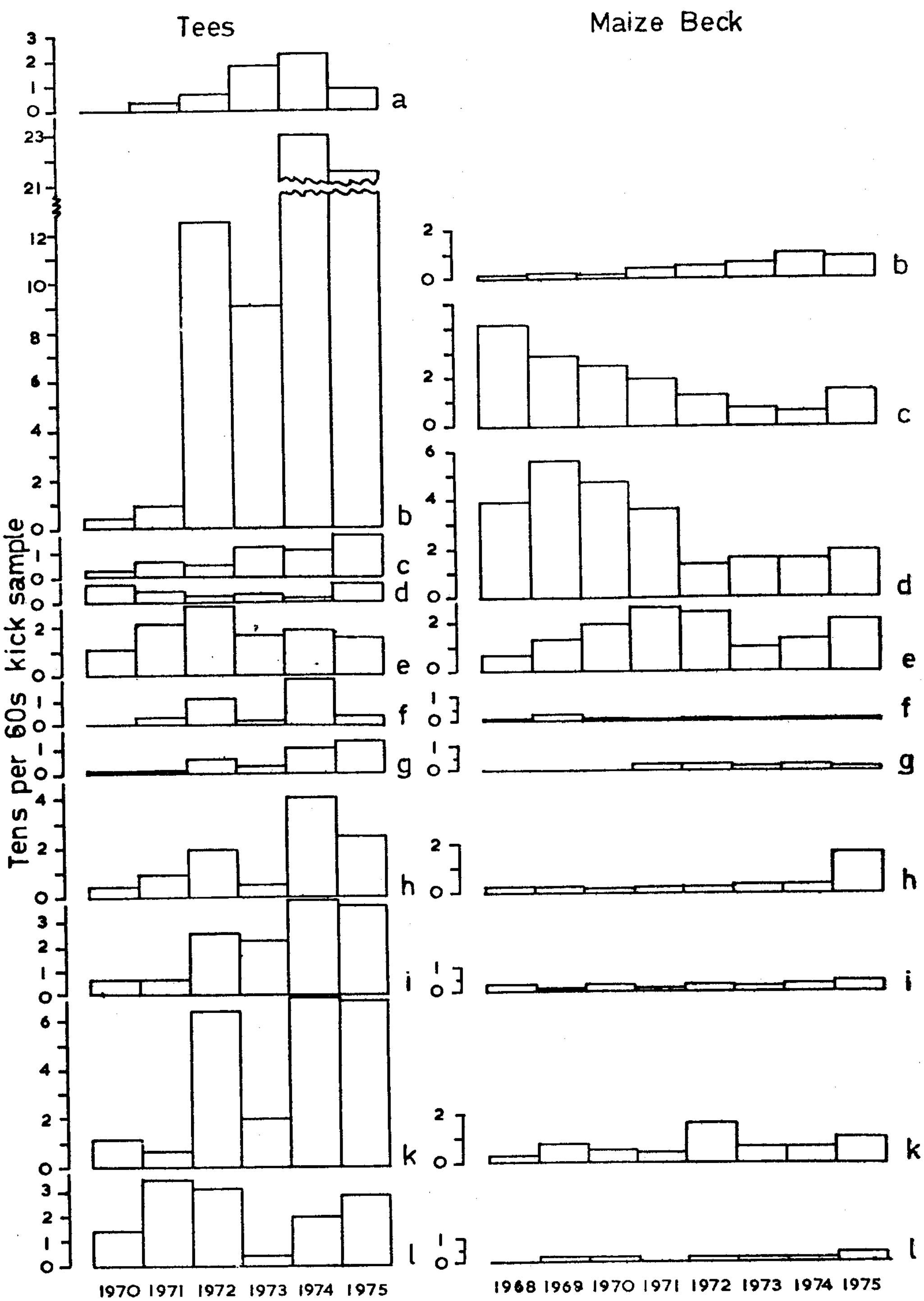

Fig. 7. The mean numbers of animals per 60 s kick samples taken in May, July and September in the years 1970-1975 in the Tees (site C) and 1968-1975 in Maize Beck (site E). (a = *Hydra*, b = Annelida, c = Plecoptera, d = Ecdyonuridae, e = Baetidae, f = *Ephemerella ignita*, g = *Caenis*, h = Trichoptera, i = Coleoptera, k = Diptera, l = Mollusca).

and *Baetis rhodani* which was more abundant at E than at D. No significant differences in the abundance of Plecoptera were found between sites C, D and E.

Fig. 5 shows annual fluctuations in the weight of major groups at the 5 sites. Significant differences between adjacent sites were less than for numbers. Most significant differences occurred between sites A and B with the biomass of all groups except molluscs and *Gammarus pulex* being greater at B. At site C the biomass of *G. pulex,* Trichoptera, Coleoptera, Diptera and Mollusca was greater than at E; and between sites C and D only molluscs, coleopterans and *G. pulex* showed significant differences (Table 4), all being greatest at C.

Changes since impoundment at sites C (Tees) and E (Maize Beck)

Before 1970, the year of the completion of the reservoir, the benthos of the Tees was studied by analysing samples of invertebrates taken in nets while electro-fishing. The results of this work are given in Armitage *et al.* (1974). Samples taken by this method were not considered to be truly representative of the bottom fauna, but provided a species list and a means of comparing pre- and post-impoundment faunas. Fig. 6 shows faunal composition, based on this method, in the Tees before and after construction of the dam. Since impoundment *Hydra* and Naididae have appeared, the proportions of Plecoptera and Ecdyonuridae have decreased and Baetidae, *Ephemerella ignita* and Diptera appear to have increased. The diversity of the fauna also decreased in the electro-fishing samples since impoundment from a mean value of 3.4 in 1968 and 1969 (mean of May, July and September samples) to 1.7 in 1972-1973.

Sampling by the kick method in the Tees below Cauldron Snout has proved difficult due to high flows and large firmly-bedded rocks, hence the use of trays in a previous survey in the area (Armitage, 1976). Site C, near the junction of the Tees with Maize Beck is one of the few places where kick samples can be taken efficiently. Sampling at site C began in 1970 and Fig. 7 shows the annual changes in the numbers of the major faunal groups up to 1975; also shown are changes in Maize Beck (site E) since 1968 which, because it was unregulated served as a control. *Hydra,* Annelida and Diptera have increased since impoundment in the Tees. Plecoptera which appeared to decrease in proportion in the electro-fishing samples have actually shown a steady increase from 1970 to 1975. Ecdyonuridae decreased in 1972 and 1973 but returned to their 1970 level in 1975. Baetidae have not shown any definite trends since impoundment. *Caenis* appears to have increased in numbers since 1971. Trichoptera have also increased in numbers due particularly to *Brachycentrus subnubilus* which increased from a mean density of 0.5 per 60 s kick in 1970 to 62 per 60 s kick in 1974. The net-spinning Polycentropodidae which might have been expected to increase in numbers in the outflow from a reservoir did not in fact show a rise in density. Elminthidae increased in numbers in the period 1970-1975 and Mollusca have maintained their numbers and have not increased since 1970.

Corresponding changes in Maize Beck (site E) have been relatively small and apart from the sudden appearance of *Caenis* (at low densities) in 1971, any observed trends have been gradual. Annelida show a slight but steady increase in numbers and Plecoptera and Ecdyonuridae show a decrease. The main steps in the decrease of Plecoptera and Ecdyonuridae occur after 1971 and a comparison of pre-1971 and post-1971 using the Mann-Whitney test shows that numbers of both groups were significantly less after 1971 ($P < 0.05$). The remaining groups showed no demonstrable changes over the eight-year period. The high numbers of Trichoptera in Maize Beck in 1975 are due to the appearance of small *Brachycentrus subnubilus* larvae in the summer. By the autumn their density had fallen from 365 m^{-2} to 15 m^{-2}. Comparing total numbers of all faunal groups per kick sample at Maize Beck in 1968, 1969, 1970 with those in 1972-1975 using a Mann-Whitney test on May July and September data showed that there was no significant difference in any month ($P > 0.05$) between the pre-and post-impoundment periods. A similar test comparing total numbers in

Table 5. The total mean numbers per 60s kick for May, July and September in pre- and post-impoundment periods in the regulated river Tees (site C) and the unregulated tributary Maize Beck (site E). Also shown are the results of Mann-Whitney tests for the significance of the difference in pre- and post-impoundment means (U = Mann-Whitney statistic and $n_1 : n_2$ are the respective number of kick samples used to calculate U. Significant values of U, P = ≤ 0.05, are indicated by *).

River Tees	Month	Pre-1970	Post-1971-1975	'U'	n_1 :	n_2
	May	95	239	0*	2	10
	July	21	538	0*	2	10
	September	53	483	0*	2	9
Maize Beck	**Month**	**1968-1970**	**1971-1975**	**'U'**	**n_1 :**	**n_2**
	May	158	108	13	6	10
	July	65	60	31	6	10
	September	75	63	22¼	6	10

the Tees in 1970 with those in succeeding years showed that numbers were significantly greater in every month in the post-impoundment period ($P < 0.05$). Table 5 summarises the results of these tests.

Faunal diversity indices as calculated from kick samples were similar in 1970 and in subsequent years. In the Tees the mean value of the index based on May, July and September data was 3.25 in 1970 and 3.15 in 1972-1975. In Maize Beck there was a slight increase in the index from 2.66 in 1970 to 3.27 in 1972-1975. These results contrast with those from the electro-fishing samples but there the low post-impoundment values were due to the selectivity of the method which resulted in Baetidae making up about 90% of the total numbers in 1972 and 1973. Hughes (1974) recorded low diversity indices for 'electro-shock' samples.

Estimates of standing crop

The total weight of organisms sampled each year was used as a base for the calculation of the mean biomass m^{-2}. Annual biomass totals for the 4 years 1972-1975 were transformed to logarithms and the geometric mean and 95% confidence limits calculated for each station. This total annual mean biomass is derived from 8 kick samples, 2 each in January, May, July and September. Dividing the mean by 8 gives a biomass per kick which can be converted approximately to mean biomass m^{-2} by multiplying by 10.5 which is the number of kicks which

Table 6. The mean and range of numbers (n) and biomass (b) per m^2, based on kick samples taken in January, May, July and September in the years 1972-1975, (see text for details).

Site		min	mean	max
A	n	1036	2066	4124
	b	3.04	5.61	10.35
B	n	4179	7267	12633
	b	7.22	11.06	16.93
C	n	1983	3004	4547
	b	3.72	5.77	8.96
D	n	990	1719	2990
	b	1.27	3.60	10.17
E	n	404	672	1117
	b	1.00	1.99	3.97

Table 7. Estimates of standing crop (g m^{-2} wet-weight) of total benthic fauna above and below lakes and reservoirs. Shown also are the chief contributors (taxa) to the total biomass. ((1) Müller 1956, (2) Illies 1956, (3) Ulfstrand 1968, (4) Briggs 1948, (5) Peňáz *et al.* 1968, (6) Radford & Hartland-Rowe 1971, (7) Ward 1974, (8) Ward 1976a, (9) this study)

	Locus	Sample period	g m^{-2}	Taxa
(1)	Annsjön, above lake	Sept.	1.76	Ephemeroptera
	outlet	,,	52.50	*Hydropsyche*
	6.0 km below outlet	,,	4.14	*Hydropsyche*
(2)	Anajaure, above lake	July	3.13	*Baetis*
	0.15 km below outlet	,,	54.24	Simuliidae
(3)	Stora Tjulträsk, outlet	May-Sept.	36.06	Simuliidae
	7.50 km below outlet	,, ,,	3.96	Ephemeroptera/Trichoptera
	Gauträsk, 5.0 above lake	,, ,,	4.40	Ephemeroptera/Trichoptera
	outlet	,, ,,	11.64	Simuliidae/Trichoptera
(4)	Stevens Creek, above reseroivr	Oct.-June	3.76	Ephemeroptera
	0.8 km below dam	,, ,,	8.06	Trichoptera
(5)	Vir, above reservoir	Annual mean	10.73	Trichoptera
	7.7 km below dam	,, ,,	30.24	Trichoptera
(6)	Lusk Creek, unregulated tributary	April-Nov.	2.91	Ephemeroptera
	Kananaskis River, 13 km below dam	,, ,,	1.67	Ephemeroptera
(7)	Cheesman Dam, 0.25 km below dam	Annual mean	15.30	Diptera/Ephemeroptera
	5.0 km below dam	,, ,,	38.40	Diptera
(9)	Maize Beck, unregulated tributary	May, Aug., Sept.	1.99	*Baetis*/Ecdyonuridae
	River Tees, 0.2 km below dam	,, ,, ,,	11.06	Gastropoda
	River Tees, 0.6 km below dam	,, ,, ,,	5.77	Trichoptera*

* *Brachycentrus subnubilus*

were found to make up one square metre (Armitage *et al.*, 1974). Treatment of the minimum and maximum estimates of the geometric mean in a similar manner provide a range based on the original 95% confidence limits. Table 6 shows the mean and range of total numbers and biomass for all sites. There is some overlap of estimates at each site and these are probably a result of the clumped distribution of the bottom fauna and the relatively small number of samples taken at each site. However, it is possible to state with some confidence that total numbers and biomass are greatest at site B in the regulated river Tees and least in the unregulated Maize Beck. Table 7 compares estimates of standing crop at Cow Green with those from other areas below lakes and reservoirs.

Discussion

The effect of a reservoir on the river fauna below the dam will depend to a large extent on the flow regime and the point at which water is drawn-off. Hydro-electric schemes generally result in widely fluctuating daily flows to which few species can adapt (Radford & Hartland-Rowe, 1971; Fisher & Lavoy, 1972; Trotsky & Gregory, 1974) and the result on the benthos is low diversity and density. Storage and regulating reservoirs may, through the release of cold hypolimnial water reduce faunal diversity (Spence & Hynes, 1971; Lehmkuhl, 1972; Ward, 1974) but here the stabilised flow may result in increased faunal densities below the dam (Briggs, 1948; Spence & Hynes, 1971).

At Cow Green the reservoir is used to regulate the flow of the Tees. Water in the reservoir is well mixed and is taken from the upper and lower levels simultaneously. These conditions have resulted in low diversity and high biomass at the two sites nearest the dam.

Many workers on outflows from lakes and reservoirs (Berg, 1948; Knöpp, 1952; Müller, 1956; Illies, 1956; Cushing, 1963; Ulfstrand, 1968; Spence & Hynes, 1971) have found large numbers of filter feeding organisms, particularly net-spinning caddis larvae and Simuliidae, probably as a result of the supply of plankton. At Cow Green filter-feeders occur in relatively low numbers despite a supply of zooplankton from the reservoir (Armitage & Capper, 1976). This is difficult to explain because even though substratum conditions at A may not have been suitable owing to the small size of the stones, those at B would have offered a suitable environment. Ward (1975) found that filter-feeders did not 'dominate' the fauna below Cheesman Dam despite available plankton and suggests that hypolimnial plankton is not a reliable enough food source for the build-up of a fauna depending on suspended matter.

It is known that the kick-sampling method is inefficient for Simuliidae (Armitage, 1976) but observations during sampling revealed no larvae at B. Spence & Hynes (1971) using this method found large numbers of simuliid larvae below a dam. A possible factor for their rarity at this site could be the very high densities of *Hydra* which would compete for settlement with simuliid larvae. From a previous study just above site C (Armitage, 1976) it is known that first instar larvae of Simuliidae occur in October at a time when *Hydra* was very abundant. These small larvae would have difficulty competing with established *Hydra* populations except where fast flows prevent the development of such populations. This, together with the possible reduction in micro-seston loads in the Tees (Armitage, 1977a) may help to account for the lack of simuliid larvae in the present study area, but cannot explain the low numbers of net-spinning caddis larvae and this remains an anomaly. Polycentropodidae and Hydropsychidae are very common below lake outflows (Müller, 1956) and there appears to be no reason why they should not be abundant at site B. Hydropsycidae were rare before and after the reservoir was built (Armitage *et al.*, 1974; Armitage, 1976), but Polycentropodidae occurred widely at low densities before impoundment; and after impoundment one species *Polycentropus flavomaculatus* was relatively abundant particularly in pools (Armitage, 1976) and the low numbers recorded in this study are possibly due to sampling in riffles only. Low numbers of Hydropsychidae were found in a regulated river by Ward (1976a) and he attributes this to the clarifying effect of the reservoir and consequent reduction in particle size diversity. Ward (1976a) found that another filter-feeder *Brachycentrus americanus* was absent 5 km downstream of a dam but present 32 km below it and in unregulated streams. This is in marked contrast to the situation at Cow Green where a species of similar habits, *Brachycentrus subnubilus*, was very abundant on rocks at sites C and D, 600 and 900 m below the dam. Cursory observations of the gut contents of *B. subnubilus* larvae revealed the presence of large amounts of algal filaments. These are a major constituent of the macro-seston during the summer months and it is possible that this regular supply of food material together with reduced spate frequency and velocity have allowed dense populations to develop.

The enriching effect of lake outflows does not persist very far. Müller (1956) noted a reduction in standing crop from 52 g m^{-2} (wet-weight) in an outflow to 4 g m^{-2} 6 km downstream and Illies (1956) has shown that there can be a large change in species composition of the benthos in a lake outlfow in a distance as little as 20 m. Spence & Hynes (1971) studied two sites, 28 and 107 m below a dam and recorded their highest densities at the 107 m site. Ward (1974) working below a hypolimnial release reservoir recorded his highest biomass 5 km downstream and highest densities 8.5 km downstream. At Cow Green benthos numbers and biomass were greatest about 200 m below the dam. Thereafter both parameters decreased and species diversity increased.

Some authors have reported reduced numbers of species of Plecoptera (Pearson *et al.*, 1968; Spence & Hynes, 1971), Ephemeroptera (Lehmkuhl, 1972; Spence & Hynes, 1971) and Trichoptera (Hilsenoff, 1971; Spence & Hynes, 1971), below dams. However, at Cow Green at site C there was no reduction in the number of species in any of these groups and no group has shown a significant decrease in density since impoundment. Conditions at Cow Green are generally similar to those below other storage or regulating reservoirs with hypolimnial release. The water flowing out from the reservoir is well oxygenated, colder in summer and warmer in winter, and diel fluctuations in temperature rarely exceed 1°C 620 m downstream of the dam (Armitage, 1976). Flow is stabilised and algal growth is dense particularly during the summer months. One feature which differentiates Cow Green from some other reservoirs is the presence of the rapids section known as Cauldron Snout. It is possible that the turbulence resulting from this rapid flow over a heterogeneous bottom is sufficient to maintain a relatively silt-free hyporheic habitat in the riffle areas and prevent clogging of interstitial spaces. The turbulent flow may also redistribute sediment which has collected during periods of low flow. The importance of the hyporheal zone has been stressed by a number of authors (Coleman & Hynes, 1970; Williams & Hynes, 1974; Stanford & Gaufin, 1974; Ward, 1976b) and its 'flushing-out' by turbulent water will maintain the variety of ecological niches necessary for a diverse fauna. The relatively high diversity indices at site C may also be due to the close proximity of Maize Beck which carries a large number of species, some of which will be able to maintain populations in the Tees. Sites A and B being nearer the dam are more influenced by the reservoir but it is only at A that there are appreciably fewer species and this may be attributable to lack of turbulence and the relatively homogeneous nature of the substratum which does not offer a wide range of niches for colonizing organisms. The low diversity index at site B is due mainly to the large numbers of *Hydra* and Naididae. Thus the overall effect of the reservoir on the Tees has been to increase numbers and biomass of certain taxa but not at the expense of the previous fauna. In contrast changes in the unregulated Maize Beck have been slight and although diversity is as high as in the Tees C and D sites, the numbers and biomass are in general lower.

Summary

Changes in the composition, numbers, and biomass of the benthic invertebrate fauna of the River Tees were followed between 1972-1975 at sites approximately 2, 240, 500, and 900 m below Cow Green dam, and compared with observations in the unregulated tributary Maize Beck. Species diversity was lowest at the site nearest the dam and numbers and biomass were greatest 240 m downstream. *Lymnaea peregra, Hydra,* and Naididae were all abundant at these two sites. Downstream, species diversity increased and values in the Tees were not significantly different to those in Maize Beck. Numbers and biomass of the fauna were lowest in Maize Beck where *Baetis rhodani* and Ecdyonuridae were the most abundant organisms. In the Tees, Naididae, *Baetis rhodani, Brachycentrus subnubilus* and Orthocladiinae were all abundant 500 and 900 m downstream of the dam. A comparison of faunal density before and after impoundment in Maize Beck and the Tees indicated that numbers were greatest in the Tees after closure of the dam in 1970, and in Maize Beck there was no difference in the pre-and post-impoundment densities. It is suggested that the particular release pattern from Cow Green Reservoir coupled with the heterogeneous nature of the substratum have created conditions which have resulted in increases in the numbers and biomass of certain taxa without displacing the previous fauna.

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