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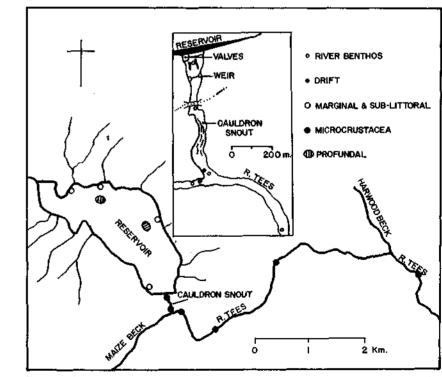
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THE IMPACT OF COW GREEN RESERVOIR ON INVERTEBRATE POPULATIONS IN THE RIVER TEES

P. D. ARMITAGE

Cow Green is a new reservoir situated in Pennine moorland (Fig. 1). It has an area of 312 ha, a capacity of 40.9×10^6 m³ and a maximum depth of 22.8 m. The reservoir began filling in June 1970 and was 2 m below top water level (489 m above sea level) in March 1971. The climate at this altitude is characterized by high annual mean wind speeds (24 km h⁻¹), high rainfall (1800 mm a⁻¹) and low annual mean temperatures (5 °C). Because of its exposed location, the reservoir water is well mixed and oxygenated. Water derived from the peaty catchment is coloured brown and about 90% of surface light intensity is extinguished in the first 2 m and no light penetrates further than about 5 m depth (Dr R. Fisher pers. comm.). More physical and chemical data are given by Crisp (1977).



F10. 1. Sketch map of the general study area and, inset, detail of the River Tees below the dam, showing position of the sample sites.

The function of the reservoir is to regulate flow in the River Tees to provide industrial Teesside with sufficient water during dry spells. Regulation causes maximum drawdowns to occur during the period August-October and these may range from 3 to 8 m below top water level and exceptionally as much as 19 m.

The main object of the invertebrate work in the Tees was to monitor changes resulting from the construction of the reservoir both in the flooded basin and below the dam. Limitations in the amount of manpower available for the project precluded the use of intensive methods of study and a more general survey approach was adopted in order to cover all major areas where changes might occur. The results will have practical relevance in so much as they will provide a base with which to compare observations on faunal changes resulting from the construction of other upland reservoirs.

The reservoir basin

The development of marginal (shore-line), sub-littoral (3-6 m) and profundal (15-18 m) fauna was followed using timed collections in shallow water and artificial substrata in deeper regions (Armitage 1977b). Corers and light grabs used for sampling lake benthos were unsuitable at Cow Green because of the lack of soft sediment and the presence of the flooded vegetation which prevented the jaws of a grab from closing.

At the start of the investigation in February 1971 the only animals found in the marginal zone were drowned terrestrial organisms and some chydorid cladocerans. By October, copepods and cladocerans formed 98% of the faunal numbers and chironomids and oligochaetes were abundant. Peak population densities of microcrustaceans were reached in the summer of 1971 but oligochaetes and chironomids were most abundant in the second year after filling: thereafter, the abundance of all groups declined. Of the three marginal sites sampled regularly, the most sheltered supported the largest numbers of animals and lowest densities were recorded from a site on the windward shore. At a stream mouth the rheophilic fauna (Plecoptera and Ephemeroptera) present in April 1971 was completely replaced with limnophilic organisms (Chironomidae and Tubificidae) by September 1971.

In the sub-littoral, faunal development was slow during 1971 and the most abundant groups were chironomids (Orthocladiinae), oribatoid mites and oligochaetes. In 1972 Chironomidae were again the most abundant organisms, oribatoid mites declined and *Hydra* and *Gammarus pulex* became more numerous. The biomass (wet-weight) of the total fauna reached a maximum in mid-September 1972 of 7.5 g m⁻². In 1973 there was a decline in the numbers and biomass of all animals except *Hydra* and Ostracoda.

In the profundal (15-18 m) chironomid populations were slow to develop in 1971 and Naididae and Tubificidae were the most numerous organisms.

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Peak biomass was recorded in 1972 following increases in Gammarus pulex and oligochaetes, and the appearance of the leeches Glossiphonia complanata and Helobdella stagnalis. In 1975 the numbers of Gammarus and Hirudinea dropped and chironomids (Chironomini) and Oligochaeta (Naididae) were the most abundant organisms. Annual fluctuations in total numbers and biomass of fauna at sub-littoral and profundal sites are shown in Fig. 2.

Changes in bottom fauna are linked to changes in the substratum. In the early stages of colonization newly-flooded vegetation provides shelter and in littoral regions quickly becomes covered with algae which provide a food source for a number of animals. At this time relatively high standing crops are recorded but these high values are not maintained and as nutrient

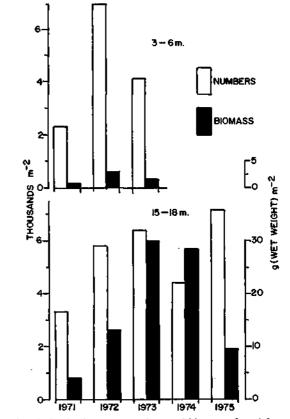


Fig. 2. Annual variation in the mean numbers and biomass of total fauna at sub-littoral and profundal sites in Cow Green, based on data collected in May, July and September.

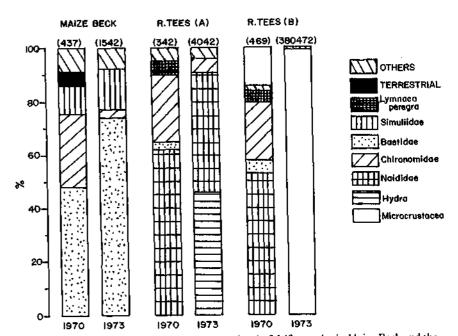
release lessens, so biomass drops. At Cow Green there is still much undecomposed matter (particularly heather shoots) on the reservoir floor and this may continue to provide shelter and support for some taxa (e.g. *Gammarus* and leeches). When the shore vegetation and subsoil have eroded completely, the main input of dissolved nutrients and organic detritus will be via the Tees and afferent streams of the reservoir basin and one may expect a fall in standing crop at this time. Chironomidae (particularly Chironomini) and oligochaetes are likely to resume dominance of the bottom fauna as the numbers of *Gammarus pulex* and leeches fall in response to changes in the substratum involving decomposition of the flooded vegetation which had formerly provided shelter and support.

River Tees below the dam

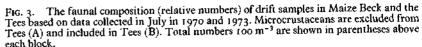
The water flowing out from the reservoir is well oxygenated, colder in the summer and warmer in the winter than adjacent unregulated streams, and diel variations in temperatures rarely exceed 1 °C at 620 m below the dam (Armitage 1976). Crisp (1977) has noted that one of the main temperature effects was to delay the seasonal cycle by about one month. The flow is stabilized and discharges in spring, summer and autumn do not generally exceed 4 m³ s⁻¹. High discharges (20 m³ s⁻¹) are occasionally recorded during the winter when the reservoir overflows down the spillway, but these do not carry the coarse particles which are usually associated with high flows over stony-bottomed rivers. The result of this is that scouring spates are rare and this has allowed the build-up of dense algal and moss growth on boulders on the river bottom especially during the summer months. The effects of these conditions on invertebrate drift and benthos are described below.

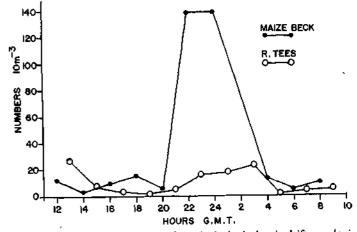
Invertebrate drift

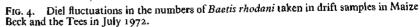
This was studied in both the Tees and Maize Beck in order to compare the regulated river with an unregulated tributary (Armitage 1977a). The faunal composition of the drift samples in the two rivers was very different (Fig. 3) and whereas Maize Beck remained similar in composition between 1970 and 1973 the Tees changed markedly, with microcrustaceans from the reservoir completely dominating numbers and biomass in 1973. Seasonal fluctuations in both numbers and biomass of drifting organisms originating from the river benthos were similar in both rivers. Diel fluctuations, particularly of baetids, were however most pronounced in Maize Beck and peaks of abundance of nymphs appeared to be depressed in the Tees (Fig. 4). Benthos densities were similar in the two rivers and the low numbers in Tees drift samples may in part be due to the presence of algae and moss on the Tees boulders (not abundant in Maize Beck) which enables animals which enter the drift to regain their 'footing' relatively rapidly.



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In addition to drifting fauna, non-faunal matter was also sampled and this revealed a major difference between the rivers. In the unregulated Maize Beck this material (coarse particulate seston retained by a filter with a mesh aperture of 0.275 mm) consisted of peat and mineral particles. In the Tees, detritus and fragments of filamentous algae made up the bulk of the sample. Maize Beck released greater quantities of material than the Tees (Fig. 5) at high discharges, and fluctuations in concentration were much wider. On the eight occasions when seston was sampled simultaneously from the two rivers, concentration (g dry-weight 1000 m^{-3}) ranged from 1 to 500 in Maize Beck and from 7 to 145 in the Tees. At peak discharges the seston load is likely to be greater still in Maize Beck. The absence of peat and mineral particles in Tees seston, despite a catchment area similar to that of Maize Beck, indicates that these components of the seston are deposited in the reservoir. Using data on total output of seston from the two rivers it was possible to estimate that at least 91.5% of these suspended solids are retained in the reservoir.

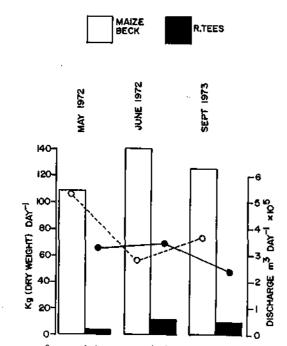


FIG. 5. The output of suspended coarse particulate matter from the Tees and Maize Beck on three occasions when discharge (O = Maize Beck; $\bullet = Tees$) was greater than 2×10^5 m³ day⁻¹

Generally speaking, regulation of the Tees has resulted in an increase in the numbers and biomass of organisms in the drift, due mainly to microcrustaceans from the reservoir. It seems probable that these, together with the algal filaments and moss fragments which form the seston, are likely to provide a more readily available source of energy and protein for detritus feeders on the river bottom than the peat and mineral particles which are the usual components of the seston in unregulated streams and rivers in the area (Crisp 1966; Armitage 1977a).

As noted above, the discharge of microcrustaceans from the reservoir was the single most important feature affecting composition, numbers and biomass of the drift. Because of this the transport downstream of these organisms was studied in more detail. Observations made in 1972 and 1973 (Armitage & Capper 1976) showed that 98% of the total annual output (149 kg dry-weight) occurs between July and October. During periods of peak abundance, up to 2% of the total of this drifting fauna is found 6.5 km below the dam. Greatest losses of organisms occurred in the first 400 m below the dam (Fig. 6) and it was estimated that the river bottom there receives about 160 mg m⁻² day⁻¹ (dry-weight) in the August-September period.

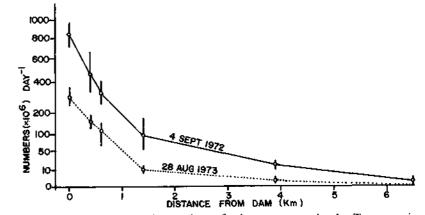


FIG. 6. The reduction in the numbers of microcrustaceans in the Tees at points downstream of the Cow Green dam in September 1972 and August 1973. Mean and confidence limits are given for each site.

Benthos

Changes in the benthic fauna of the Tees since impoundment were followed at riffle sites approximately 2, 240, 500 and 900 m below the dam, and compared with observations in the unregulated tributary Maize Beck (Armitage 1978).

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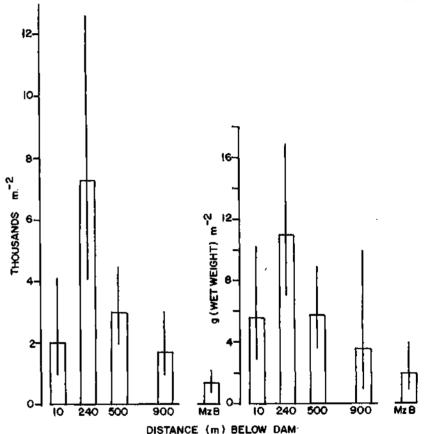
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A comparison of mean faunal density before and after impoundment based on May, July and September samples indicated significant (P<0.05) increases in the numbers of total fauna in the Tees adjacent to Maize Beck from 56 to 420 animals per one minute kick sample and no significant change in Maize Beck (99–77 animals per one minute kick sample).

Species diversity, calculated using an adaptation of the information index of Shannon & Weaver (1949), was lowest (1.5) at the site nearest the dam. Downstream, species diversity increased and values in the Tees (3.3) were not significantly different from those in Maize Beck (3.0).

Lymnaea peregra, Hydra and Naididae were all abundant at the two sites nearest the dam. Gammarus pulex first appeared in the Tees after impoundment, in July 1972 and has increased steadily in numbers and biomass during the study period. Large populations of this species are present in the reservoir (Armitage 1977b) and this has facilitated its spread below the dam. Filter-feeders, often associated with reservoir outflows (Spence & Hynes 1971), were uncommon in this area. Ward (1975) also noted relatively low densities of filter-feeders below Cheesman dam. However, about 500 m below Cow Green dam the density of one filterfeeding caddis larva, Brachycentrus subnubilus, increased steadily over the study period. Examination of the gut contents of several larvae showed the presence of large quantities of algal filaments, a major component of the seston in the Tees. Orthocladiinae and Naididae were particularly abundant where algal and moss growth was dense and appeared to be associated with detritus trapped by the vegetation. The fauna of Maize Beck differed from that of the Tees both above and below the junction of the two streams. Algae and mosses were uncommon and their associated fauna was absent; instead, Ecdyonuridae and Baetidae dominated numbers and biomass. Fig. 7 shows the mean and range of total faunal numbers and biomass at all sites.

The situation below Cow Green dam differs somewhat from that described by other workers. Some authors (Pearson et al. 1968; Spence & Hynes 1971; Lehmkuhl 1972; Hilsenoff 1971) have reported reduced numbers of species of Plecoptera, Ephemeroptera and Trichoptera below dams. However, at the only site on the Tees to have been examined continuously before and after impoundment (just above the junction with Maize Beck), although there have been some changes in the species present there has been no reduction in the total number of species in any of these groups and no group has shown a significant decrease in density since impoundment. In contrast, the overall effect of the reservoir on the Tees has been to increase the numbers and biomass of certain taxa but generally not at the expense of the previous fauna. Some of these positive effects, i.e. increase in numbers and biomass and maintenance of faunal diversity, may in part be attributable to the presence of the rapids and waterfall known as Cauldron Snout. Turbulence resulting from this rapid flow over a



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FIG. 7. The mean and range of total numbers and biomass m^{-2} based on kick samples taken in January, May, July and September in the years 1972–1975 at sites on the Tees below the dam and at Maize Beck (MzB).

heterogeneous bottom is sufficient to prevent clogging of interstitial spaces by silt and to maintain the variety of ecological niches necessary for a diverse fauna.

I wish to acknowledge the facilities provided by the Northumbrian Water Authority; the fishery owners – Mr P. B. Oughtred and the Raby Castle and Strathmore Estates; the Teesdale Trust; the Nature Conservancy at Teesdale and at Moor House; and assistance provided by my colleagues in the Cow Green Unit. Special thanks are due to two sandwich students, M. H. Capper (University of Bath) and A. O. Davis (Liverpool Polytechnic) for all their help. Some of this work formed part of a contract from the Department of the Environment (Contract No. DGR 480 34).

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WATER CHEMISTRY AND OSMOREGULATION IN SOME ARTHROPODS, ESPECIALLY MALACOSTRACA

D. W. SUTCLIFFE

Introduction

All animals (and plants) need to osmoregulate their salt and water content. Failure to do so leads to hydration or dehydration of the tissue cells, with fatal consequences. In the case of aquatic animals, it is convenient to immediately introduce three commonplace observations. First, many marine animals die rapidly when placed in fresh water. Second, the principal inorganic solutes in ocean and sea waters are sodium (c.460mM Na or $10.8 \text{ g} (l^{-1})$ and chloride (c. 535 mM Cl or $19.4 \text{ g} (l^{-1})$). Water is fresh to the taste when it contains about 5 mM NaCl, approximately 1% sea water. Fresh waters in general contain 0.2-0.5 mM NaCl, three orders of magnitude less than the concentration in ocean waters. Third, the proportions of major ions in the oceans and seas are similar and remain relatively constant. These three observations can be matched with three that are less commonplace. First, many freshwater animals die rapidly when placed in certain types of fresh water. Second, the principal inorganic solutes in fresh waters are sodium and/or calcium chloride, sulphates and (bi)carbonates. The range of sodium chloride concentrations in fresh waters is three orders of magnitude, from 1-5 mM down to 0.001-0.005 mM. Third, the proportions of major ions in fresh waters differ widely depending on their location, and the actual concentrations may also vary widely (e.g. daily or seasonally) in any one locality.

Thus fresh waters represent a range of salinities and a series of physiological challenges equalling those which confront marine organisms when they enter brackish water. In the latter case the major challenge is to combat hydration resulting from osmotic water uptake and diffusional ion loss. Freshwater organisms face the same challenge. This article briefly summarizes some chief characteristics of osmoregulatory systems in malacostracan crustaceans, evolved to combat hydration, and the limitations thereby imposed on the salinity tolerance and distribution of these animals.

It should be noted that for simplicity in the following account all concentrations, rates and similar quantities are approximations only; more precise data may be obtained from the original papers cited in the account.

Osmoregulation in arthropods

The primary objective is to maintain the constancy of several basic types of intracellular fluid, characteristic of nerves, muscles, and other excitable tissues. Osmoregulatory control is mediated via feed-back systems which operate ion transporting sites located in excretory systems and in other

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