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Comparative limnology of differentially regulated sections of a Colorado mountain river

By JAMES V. WARD

With 5 figures and 10 tables in the text

Abstract

Studies of one-year duration were conducted from 1972—75 on four sections of the South Platte River in the Colorado mountains to elucidate the effects and extent of influence of deep release dams on stream macroinvertebrates. Study sites represented a gradient from highly regulated to unregulated by dams. Macroinvertebrates exhibited lower standing crops but much higher diversity at unregulated sites. *Gammarus* and gastropods were restricted to regulated sites, whereas filipalpian stoneflies, heptageniid mayflies, and certain dipterans were not found below the dam. Restriction of taxa to regulated or unregulated sites is explained by differences in (1) chemical limiting factors, (2) distribution and abundance of submerged angiosperms and epilithic algae, (3) diversity of organic matter inputs, (4) predation pressure and competitive interactions, (5) environmental stability and predictability, and (6) thermal signals.

Introduction

A year-round study conducted in 1972—73 on the stream ecosystem immediately below a hypolimnial release reservoir in the Colorado mountains showed that the reservoir had a great influence on the biological and physicochemical parameters of the receiving stream (WARD, 1974). Large standing crops of macroinvertebrates and epilithic algae were present nearly year-round. Macroinvertebrate diversity, however, was extremely low and this was attributed largely to the modified thermal pattern, since a generally favorable physicochemical environment was demonstrated. Many biotic and abiotic factors exhibited progressive downstream changes of considerable magnitude considering the limited extent (8.5 km) of the study section. The effects of the dam on the stream ecosystem were still apparent at the most downstream site. For this reason, in the 22 months subsequent to the completion of that study, the writer conducted similar studies in another canyon section 32 km below the dam and at stations above the confluence of an unregulated tributary.

It was the purpose of the additional studies to provide data of comparative value in an attempt to further elucidate the effects and extent of influence of deep release dams on receiving streams, especially on the composition and diversity of macroinvertebrate communities.

Study Areas

The South Platte River originates on the East Slope of the Continental Divide in the Rocky Mountains of Colorado and flows through Antero Reservoir, Elevenmile Canyon Reservoir and Cheesman Lake (Fig. 1). Confluence with

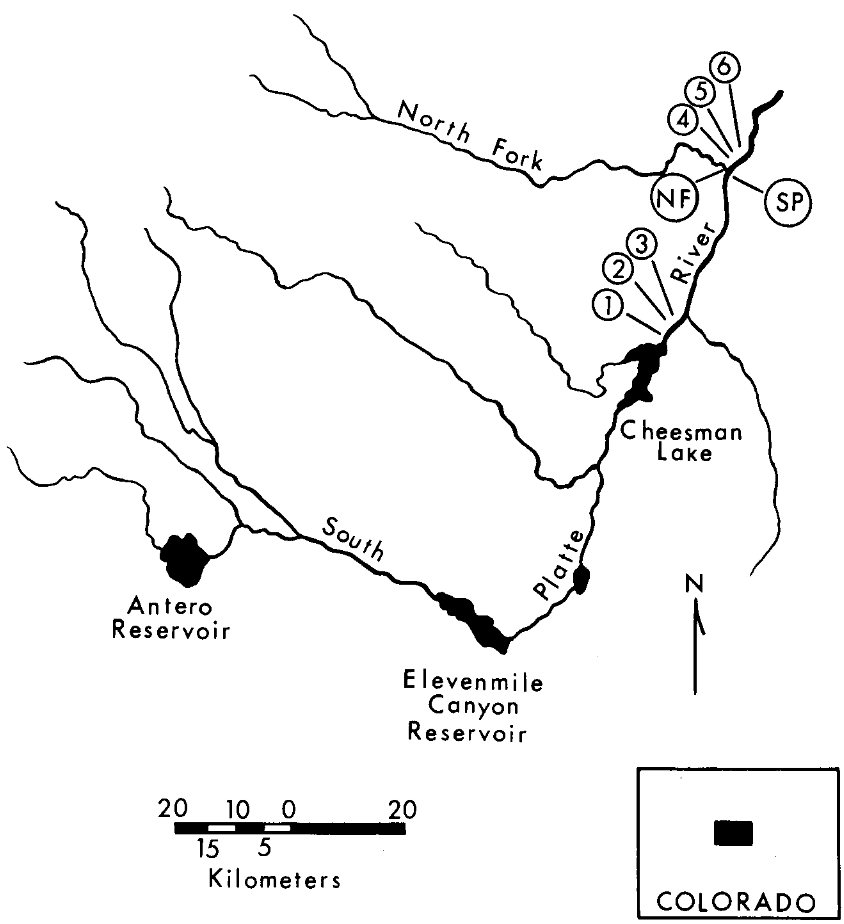

Fig. 1. Map of study locations on the South Platte River, Colorado. Sites 1, 2, and 3 are in Cheesman Canyon in the section below a deep release dam. Sites 4, 5, and 6 are in Waterton Canyon 32 km downstream. Sites SP and NF are immediately above the confluence of the North Fork and the South Platte River.

the North Fork is 32 km below Cheesman Lake, and the stream flows another 15 km as a foothills canyon stream before dropping to the plains.

The North Fork originates on the slopes of Mount Evans and is unregulated by dams, although its natural flows are sometimes augmented with West Slope water. This water is carried through a tunnel system and enters the North Fork 65 km above confluence with the South Platte River. However, this source was utilized only two days during the one-year study of the lower canyon section. The South Platte River and the North Fork are streams of similar size at their confluence.

Sites 1, 2, and 3 in Cheesman Canyon are 0.25, 2.4, and 5 km below the dam. Cheesman Lake is a deep (65 m) storage reservoir which releases water into the stream from a combination of 46 and 60 m depths. These study sites were accessible only by foot trail. A fourth site (8.5 km below the dam) was eliminated from consideration in the present paper, since it exhibited ecotonal properties (WARD, in press), to allow a better comparison with the three sites in the less regulated downstream canyon.

Sites 4, 5, and 6 in Waterton Canyon are 0.5, 4.4, and 6 km below the North Fork, and were accessible only by private road.

Cheesman and Waterton Canyons have steep, rocky walls with an only poorly developed riparian vegetation of grasses and willows in some sections.

Sites SP and NF are immediately above the mouth of the North Fork. Site SP has little riparian vegetation other than streamside grasses and willows, whereas Site NF has a dense riparian vegetation dominated by Rocky Mountain alder *(Alnus tenuifolia).* The substrate at Site SP had a dense algal Aufwuchs much of the year, whereas at Site NF allochthonous leaf litter was the primary energy source.

All sites were located on rubble riffles in quality trout water sections of granitic foothills streams. Elevation ranged from 2013 m (Site 1) to 1757 m (Site 6).

These study locations represent a gradient from highly regulated in Cheesman Canyon to essentially unregulated conditions at Site NF.

Methods and Materials

All sites were sampled year-round for one year. Sites 1, 2, and 3 were sampled about every 28 days from June 1972 through May 1973. Sites 4, 5, and 6 were sampled every three weeks during the summer and once a month thereafter from June 1973 through May 1974 (except January when Sites 5 and 6 were inaccessible). Samples for physicochemical analysis were also taken at SP and NF four times during this period (July, October, January, April). Macroinvertebrates, temperature, and pH were sampled monthly at Sites SP and NF from April 1974 through March 1975.

The methods used for field collection and laboratory analyses are described in detail in WARD (1974). Macroinvertebrates were collected with a Surber sampler. A timed scraping technique was used to sample the Aufwuchs. Free and bound CO_2 were determined titrimetrically using phenolphthalein and methyl orange indicators. Suspended and dissolved matter were determined by filtration and subsequent evaporation of one liter water samples. Daily flow data were procured from Denver Water Board and U. S. Geological Survey records.

Diversity indices were applied to the macroinvertebrate communities at each site using the Shannon-Weaver function with logarithms to base 2 (bits per individual).

Results and Discussion

Physicochemical Analyses

Table 1 compares the physical and chemical parameters of Cheesman and Waterton Canyons. Since the North Fork and the South Platte have

Table 1. Physicochemical data[1] for Cheesman and Waterton Canyons, South Platte River, Colorado.

Parameter	Cheesman Canyon			Waterton Canyon		
	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Free CO_2 (ppm)	—2.0	—3.7	—5.5	—0.8	—1.0	—1.0
Bound CO_2 (ppm)	55.6	55.0	54.7	26.6	28.8	29.1
pH (median)	8.2	8.4	8.4	7.6	7.6	7.7
Flow (m^3/min)	206	—	—	739	—	—
Temperature (°C)	5.8	7.2	7.9	6.5	7.1	7.5
O_2 (ppm)	11.2	—	—	11.3	—	10.7
Total suspended (mg/l)	2.2	4.2	7.4	29.5	37.4	36.0
L. O. I.	0.8	1.0	1.8	4.3	4.9	4.8
Total dissolved (mg/l)	356.9	—	—	140.8	—	160.6
L. O. I.	56.1	—	—	35.3	—	39.0

[1] Annual means.

Table 2. Physicochemical data[1] for sampling sites on the South Platte River, Colorado (SP) and the North Fork (NF) immediately above their confluence.

Parameter	SP	NF
Free Co_2 (ppm)	—1.4	+0.8
Bound CO_2 (ppm)	36.0	15.0
pH (median)	7.9	7.3
Temperature (°C)	6.3	5.2
O_2 (ppm)	10.0	11.5
Total suspended (mg/l)	24.3	21.2
L. O. I.	3.4	5.7
Total dissolved (mg/l)	191.5	67.6
L. O. I.	47.5	19.9

[1] Means of 27 VII 1973, 13 X 1973, 19 I 1974, and 19 IV 1974, except temperature and pH which are based on monthly samples.

comparable discharge at their confluence, reference to Table 2 elucidates their contributions to conditions at Waterton Canyon sites.

Free CO_2 exhibited negative values at all sites on all sampling dates in both canyons with the exception of a 0.5 ppm value at Site 4 in June. The lower values in Cheesman Canyon reflect the greater photosynthetic uptake of CO_2 by the well-developed algal Aufwuchs and macrophytes in the section below the dam. The difference in free CO_2 between Sites SP and NF (Table 2) corresponds to the greater development of epilithic algae at the former site.

The high pH values in Cheesman Canyon were undoubtedly a result of high levels of photosynthetic activity. Waterton Canyon values represent an approximate average of the more autotrophic Site SP and the more heterotrophic Site NF.

Bound CO_2 values place Cheesman Canyon waters in the "hard" category of PENNAK (1971), whereas Waterton Canyon exhibited "medium" hardness. The mean value of 55.1 ppm in Cheesman Canyon decreased to 36.0 ppm at Site SP, which was still well over two times higher than in the unregulated North Fork. The mean value of 28.2 ppm in Waterton Canyon represents an approximate average of Sites SP and NF.

Waters were always fully saturated with dissolved oxygen wherever sampled with the exception of a 90 % value at Site 6 in December. Air valves in Cheesman Dam prevent an oxygen deficit at Site 1.

Suspended matter was extremely low at Site 1 (2.2 mg/l), due to the clarifying effect of the reservoir, but increased downstream. Lentic zooplankton released from the reservoir were also collected, but were rapidly eliminated downstream (WARD, 1975). Means for suspended matter were over seven times greater in Waterton Canyon. Loss on ignition values comprised from 24 to 36 % of the total suspended matter in Cheesman Canyon and from 13 to 15 % in Waterton Canyon. Total suspended matter was similar at Sites SP and NF, but relative loss on ignition values were nearly twice as high (14 versus 27 %) in the more heterotrophic North Fork.

Site 1 exhibited dissolved matter values (357 mg/l) over twice as great as those at Sites 4 (141 mg/l) or 6 (161 mg/l). This is attributed to a concentration of ions in the deep waters of Cheesman Reservoir and subsequent uptake by downstream biota. Loss on ignition fractions averaged 15, 25, and 24 per cent at Sites 1, 4, and 6, respectively.

Total dissolved matter was still high (191.5 mg/l) at Site SP, 32 km below the dam, which contrasted with the 67.6 mg/l in the North Fork. The loss on ignition fractions were similar, 25 and 29 % at Sites SP and NF, respectively.

Figure 2 compares the flow regimes of Sites 1 and 4 in consecutive years. The flow in Cheesman Canyon, which is regulated by the dam, averaged 206 m^3/min during the period of study. The high mean flow at Site 4 (739 m^3/min), normally slightly more than twice that of Cheesman Canyon, was a result of an exceptionally large spring runoff.

The effect of the storage reservoir (Cheesman Lake) is to spread the flow more evenly throughout the year and to produce long periods of constant flow below the dam (e. g. late March to early May). The constant flow has an important influence on certain floral and faunal components in Cheesman Canyon.

Flow averaged 308 and 279 m^3/min, respectively, at Sites NF and SP from April 1974 through March 1975.

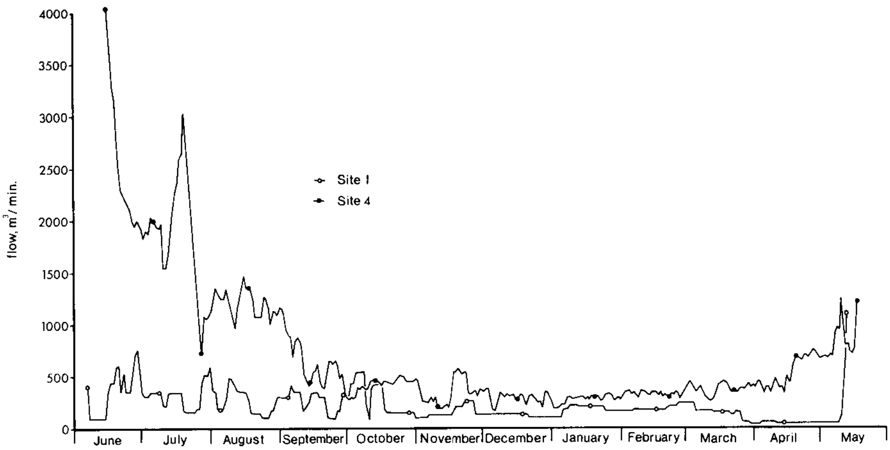

Fig. 2. Flow regimes of Cheesman (Site 1) and Waterton (Site 4) Canyons, South Platte River, Colorado.

The modified temperature regime in Cheesman Canyon has been postulated (Ward, in press) as having a major influence on the biotic community. Unusual thermal features included (1) low summer temperatures, (2) high winter temperatures and absence of ice, (3) diurnal constancy, (4) seasonal constancy, (5) a delayed seasonal maximum. However, annual mean temperatures were remarkably similar in Cheesman and Waterton Canyons (Table 1). This agrees with the findings of Jaske & Goebel (1967) who reported that although dams altered the thermal patterns on the Columbia River, the annual mean temperature was little affected. Thermal constancy, temperature range, and time of seasonal maximum did differ between the canyons and may be of considerable ecological significance.

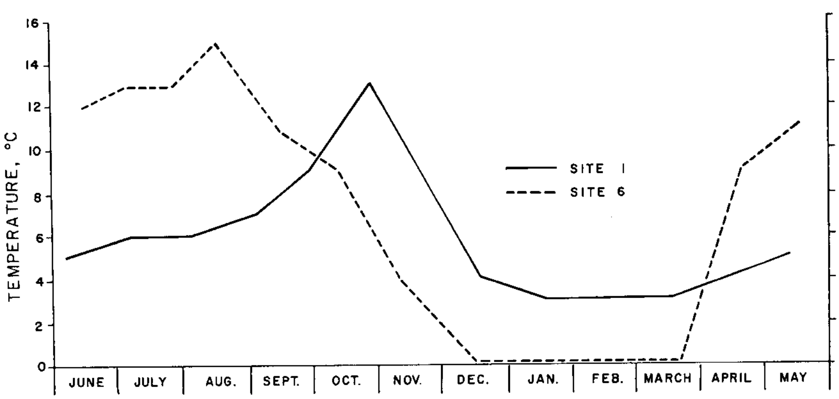

Fig. 3. Seasonal patterns of water temperature in Cheesman and Waterton Canyons, South Platte River, Colorado.

Figure 3 compares the seasonal temperature pattern at Sites 1 and 6. Although temperature data for Site 1 represent morning values, temperatures fluctuate very little diurnally at this location immediately below the dam. Site 6 temperatures approximate the daily maxima. In Cheesman Canyon the temperature ranged from 3 to 13°, and the maximum occurred on 28 October at the time of reservoir overturn. In Waterton Canyon the range was 0 to 15°, and the maximum occurred in mid-August. While the differences in these temperature ranges are not great, several authors have stressed the importance to the stream biota of small temperature alterations (IDE, 1935; COUTANT, 1968; NEBEKER, 1971; LEHMKUHL, 1972, 1974).

The rapid spring rise from near freezing to 9° in Waterton Canyon contrasts with spring temperatures in Cheesman Canyon. This difference may have great significance for some stream organisms (LEHMKUHL, 1972).

The winter warm conditions in Cheesman Canyon and the absence of ice contrasted sharply with conditions in Waterton Canyon, where an ice axe was sometimes required to procure samples. HYNES (1970 a) suggested that winter warm conditions may have a greater effect on stream organisms than summer cold conditions.

Although 24-hour temperature cycles were not measured, diurnal fluctuations as great as 6 °C occurred at a location only 8.5 km below the dam and contrasted sharply with the nearly constant temperatures at Site 1 (WARD, 1974).

Cheesman Lake did not exert any discernible effect on temperatures at SP, 32 km downstream. Temperatures at Sites SP and NF (Table 2) are means of mid-morning values. The slightly lower mean temperature at NF is a result of its more shaded situation in a narrower canyon with overhanging riparian vegetation.

Epilithic Algae

Epilithic algae were collected from the upper surfaces of rubble at Cheesman and Waterton Canyon sites. A much greater standing crop of epilithic algae occurred at sites in the regulated section below the dam (Table 3), although part of this difference was undoubtedly a result of the high spring runoff during the study of Waterton Canyon. The clarifying effect of the reservoir, the more stable substrate, the increased nutrients, and the higher winter temperatures are factors responsible for the enhanced algal crop below the dam. Moreover, whereas the loss on ignition fraction averaged 19 % in Cheesman Canyon, it averaged only 8 % in Waterton Canyon, reflecting the greater proportion of inorganic silt.

Chlorophyceae were a more important component of the epilithon in Cheesman (Table 3), but the composition of green algae was similar in both

Table 3. Epilithon standing crop and percentage composition values for Cheesman and Waterton Canyons, South Platte River, Colorado[1].

Site	Dry weight (g) per 5-minute sample	L. O. I. (g)	Percentage composition				
			C	M	B	H	D
1	9.73	2.02	72	1	11	5	11
2	7.51	1.65	50	1	18	16	15
3	12.02	1.86	38	1	20	13	27
4	0.64	0.05	14	1	21	4	60
5	0.70	0.04	17	<1	16	3	64
6	2.25	0.19	23	<1	13	2	61

C — Chlorophyceae, M — Myxophyceae, B — Bacillariophyceae, H — *Hydrurus*, D — Detritus.

[1] Annual means.

canyons. *Cladophora* and *Ulothrix* were the most common genera. *Microthamnion, Microspora,* and several desmids were also common to both canyons.

Bacillariophyceae exhibited similar relative abundance in Cheesman and Waterton Canyons. *Hantzschia,* found only in Waterton, was the only common genus not found in both canyons. *Diatomella, Synedra, Frustulia,* and *Cocconeis* were the most common diatoms in Cheesman Canyon; *Gomphonema, Tabellaria, Frustulia,* and *Cocconeis* in Waterton Canyon.

Myxophyceae were not important in either canyon, comprising 1 % or less of the epilithon samples. *Lyngbya, Nostoc,* and *Stigonema* were the only genera noted.

Hydrurus, a cold stenotherm, was more important in Cheesman Canyon.

The detrital fraction was considerably lower in Cheesman Canyon, and, unlike Waterton Canyon, increased progressively downstream.

Submerged angiosperms, abundant at some locations in Cheesman Canyon, were not encountered at any of the lower sites.

Macroinvertebrates

The macroinvertebrate communities of Cheesman and Waterton Canyons differed greatly whether standing crop or species diversity is considered (Table 4). Cheesman sites exhibited rich density and biomass with annual means of 2784 organisms and 29.5 grams wet weight per m^2, but species diversity was low. Waterton sites were poor in standing crop, averaging only 716 organisms and 8.2 grams per m^2, but species diversity was much higher than in Cheesman Canyon.

Sites SP and NF exhibited highly contrasting standing crops. Biomass

Table 4. Summary of macroinvertebrate standing crop and diversity data for locations on the South Platte River, Colorado.

	Cheesman[1]	Waterton[1]	SP	NF
organisms/m^2	2784	716	4786	406
biomass[2] g/m^2	29.5	8.2	30.9	7.6
No. of species	32	70	64	49

[1] Means of 3 sites.
[2] Wet weight.

values at SP were comparable to Cheesman Canyon; NF values were similar to Waterton Canyon. It should be emphasized that, whereas values from canyon sections represent annual means of three sites, confluence values are based on one study location.

Macroinvertebrate composition

Species composition also varied greatly between Cheesman and Waterton Canyons. From a total of 82 taxa, only 20 were common to both canyons, whereas 62 taxa were found in only one of the canyon sections (Table 5). Several families and even higher groups were restricted to one canyon.

Table 5. Number of species in major taxa found in only one canyon section of the South Platte River, Colorado.

Taxon	Cheesman Canyon	Waterton Canyon
Plecoptera	0	12
Ephemeroptera	0	11
Trichoptera	0	5
Coleoptera	2	1
Diptera	6	17
Odonata	0	1
Amphipoda	1	0
Gastropoda	2	0
Others	1	3
Total	12	50

A total of 41 taxa were common to SP and NF; however, despite their contiguity, 31 taxa were limited to one of these sites.

Figure 4 compares the study locations based upon the percentage composition of the major groups. Plecoptera, Ephemeroptera, Diptera, and Trichoptera comprised 97.1 % and 95.4 % of the macroinvertebrates, by numbers, in Cheesman and Waterton Canyons, respectively. These same groups made up 94.6 % and 92.6 % of the biomass. They were the four most abundant groups in Waterton Canyon, but in Cheesman Canyon

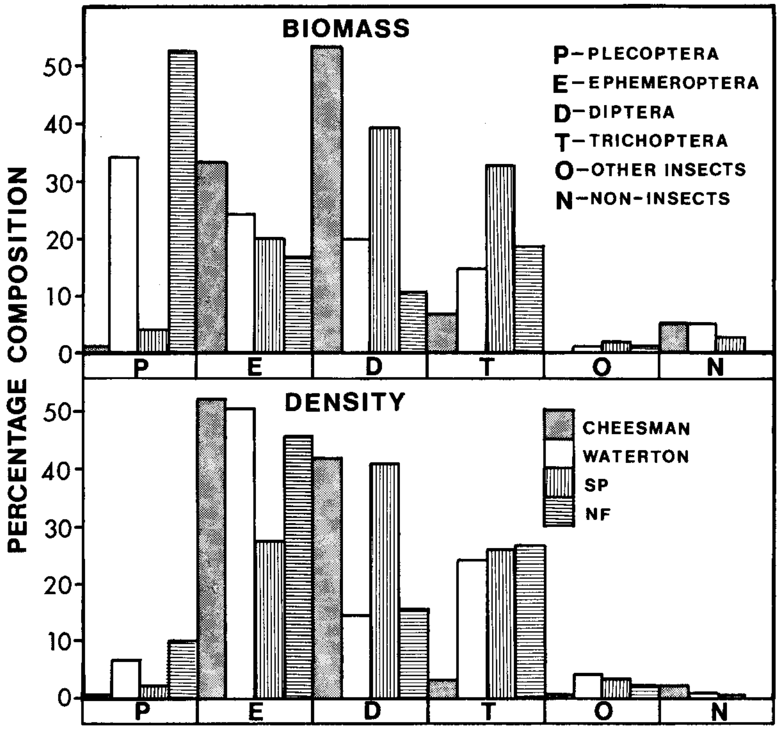

Fig. 4. Percentage composition by biomass and density of major macroinvertebrate taxa at four locations on the South Platte River, Colorado.

plecopterans were poorly represented (< 1.0 %) and were exceeded in either density or biomass by amphipods, annelids, gastropods (shells excluded) and coleopterans. Dipterans and ephemeropterans dominated the Cheesman macroinvertebrate community, comprising 93.7 % of the numbers and 86.8 % of the biomass. In Waterton Canyon, biomass and, to some extent, density were more evenly distributed among the four major taxa.

Except for ephemeropterans, Cheesman and Waterton differed considerably in the relative importance of major taxa (Fig. 4). Plecopterans, for example, were the most important taxon by biomass in Waterton Canyon (34.1 %), but comprised less than 1.0 % of the Cheesman biomass.

Waterton trichopterans exhibited a relative density over eight times greater and a biomass more than twice that of Cheesman Canyon.

Dipterans were much more abundant in Cheesman with relative density and biomass values nearly three times greater than Waterton. Chironomids and tipulids were much more important in Cheesman; simuliids exhibited comparable relative abundance in both canyons.

Table 6. Plecoptera distribution and annual mean density values and biomass totals for locations on the South Platte River, Colorado.

	Number of individuals[1] per m²			
	Cheesman[2]	Waterton[2]	SP	NF
Isoperla patricia	14.2	3.3	31.6	+
Isoperla fulva	—	+	2.2	3.1
Isogenus expansus	—	2.8	25.1	+
Arcynopteryx parallela	—	3.4	3.6	2.5
Acroneuria pacifica	—	+	+	+
Claassenia sabulosa	—	2.1	1.4	3.6
Pteronarcys californica	—	8.8	+	10.4
Pteronarcella badia	—	19.4	7.1	15.8
Nemoura (Amphinemura)	—	+	1.6	—
Nemoura sp.	—	+	+	2.2
Alloperla signata	—	+	+	—
Alloperla sp.	—	2.5	22.5	1.6
Hastaperla sp.	—	+	+	—
Total density	14.2	45.5	98.0	40.7
Total biomass (g/m²)	0.3	2.8	1.2	4.0

[1] + = present but less than 1.0/m².
[2] Means of 3 sites.

Table 7. Ephemeroptera distribution and annual mean density values and biomass totals for locations on the South Platte River, Colorado.

	Number of individuals[1] per m²			
	Cheesman[2]	Waterton[2]	SP	NF
Ephemerella g. grandis	—	10.0	3.9	5.6
Ephemerella inermis	273.0	96.0	838.6	19.4
Ephemerella doddsi	—	1.3	—	—
Baetis sp.	1162.8	145.1	331.4	49.1
Pseudocloeon sp.	—	6.2	7.5	2.7
Ameletus sp.	—	+	—	—
Siphlonurus sp.	—	+	—	—
Paraleptophlebia sp.	—	+	4.1	+
Choroterpes sp.	—	+	—	—
Tricorythodes fallax (?)	11.7	+	11.8	—
Rhithrogena doddsi	—	98.1	110.4	103.6
Epeorus longimanus	—	1.5	+	2.3
Cinygmula sp.	—	+	+	—
Heptagenia elegantula	—	1.3	4.3	+
Total density	1447.5	360.4	1312.7	183.7
Total biomass (g/m²)	9.9	2.0	6.2	1.3

[1] + = present but less than 1.0/m².
[2] Means of 3 sites.

Sites SP and NF also differed greatly in the relative composition of some major taxa. Although stoneflies were more important at SP than Cheesman, the difference between SP and NF was still considerable (Fig. 4). Chironomids, tipulids, simuliids, and total dipterans were relatively more abundant at SP than NF. Trichopterans exhibited similar percentage composition at SP and NF.

While sampling inadequacies may account for the apparent distribution of some rare species, other groups of some importance in one canyon were absent from the other.

Filipalpian stoneflies, absent from Cheesman Canyon, were of major importance at Waterton Sites (Table 6). Perlids and chloroperlids were also absent from Cheesman.

Heptageniid mayflies, important in Waterton Canyon, were absent from Cheesman (Table 7). The large mayfly, *Ephemerella g. grandis*, which comprised a significant portion of the Waterton mayfly biomass, was not found in Cheesman Canyon. Several other mayfly species occurred in Waterton but not Cheesman. *Tricorythodes* was the only mayfly (with one

Table 8. Trichoptera and Coleoptera distribution and annual mean density values and biomass totals for locations on the South Platte River, Colorado.

	Number of individuals[1] per m²			
	Cheesman[2]	Waterton[2]	SP	NF
Arctopsyche grandis	—	2.0	+	3.1
Hydropsyche sp.	64.1	160.6	1178.7	84.2
Rhyacophila coloradensis	11.2	1.4	10.7	2.3
Glossosoma sp.	—	1.6	7.8	4.7
Agapetus sp.	—	—	+	4.3
Brachycentrus americanus	—	3.7	3.9	9.0
Lepidostoma sp.	—	1.3	14.5	+
Sericostoma sp.	+	+	1.8	—
Stactobiella sp.	4.3	+	15.6	+
Agraylea sp.	—	+	+	—
optioservus	15.8	22.3	82.0	6.8
Zaitzevia sp.	1.5	5.9	80.2	1.0
Narpus sp.	—	+	—	+
Donacia sp.	—	—	—	+
Helichus sp.	—	—	+	+
Galerucella sp.	+	—	—	—
Agabus sp.	+	—	—	—
Total Trichoptera	79.9	172.7	1233.8	108.2
Total biomass (g/m²)	2.0	1.2	10.1	1.4
Total Coleoptera	17.8	28.3	162.4	9.1
Total biomass (g/m²)	0.1	+	0.2	0.1

[1] + = present but less than 1.0 organism or 0.1 g per m².
[2] Means of 3 sites.

Table 9. Diptera distribution and annual mean density values and biomass totals for locations on the South Platte River, Colorado. Values in parentheses indicate number of taxa.

	Number of individuals[1] per m[2]			
	Cheesman[2]	Waterton[2]	SP	NF
Atherix variegata	2.7	26.6	39.8	12.8
Simulium arcticum	62.4	25.7	795.3	31.7
Prosimulium sp.	—	+	+	—
Protanyderus margarita	—	+	—	+
Tipulidae	150.1 (3)	5.6 (7)	95.0 (6)	8.8 (5)
Chironomidae	941.8 (3)	42.4 (9)	1023.3 (11)	3.2 (5)
Euparyphus sp.	+	—	—	—
Tabanus sp.	+	—	—	—
Limnophora aequifrons	+	—	—	—
Palpomyia sp.	+	—	+	—
Hemerodromia sp.	3.2	+	—	+
Pericoma sp.	—	+	—	—
Agathon sp.	—	+	—	5.6
Deuterophlebia coloradensis	—	+	—	—
Total density	1161.3	103.5	1954.4	62.9
Total biomass (g/m²)	15.7	1.6	12.1	0.8

[1] + = present but less than 1.0/m².
[2] Means of 3 sites.

Table 10. Distribution and density values of miscellaneous taxa for locations on the South Platte River, Colorado. Values in parentheses indicate number of taxa.

	Number of individuals[1] per m[2]			
	Cheesman[2]	Waterton[2]	SP	NF
Pyralidae	—	—	—	+ (1)
Ophiogomphus sp.	—	+	1.3	—
Dugesia tigrina	10.0	+	4.4	—
Gordionus sp.	—	+	—	—
Helobdella sp.	—	+	—	—
Eiseniella tetraedra	9.2	3.3	17.9	—
Allolobophora chlorotica	—	+	—	—
Microdrili	7.1 (2)	+ (1)	2.2 (3)	+ (1)
Gammarus lacustris	33.4	—	+	—
Subterranean amphipod	—	—	—	+
Lymnaea auricularia	1.5	—	—	—
Physa anatina	2.8	—	—	—

[1] + = Present but less than 1.0/m².
[2] Means of 3 sites.

exception) found in Cheesman but not Waterton Canyon. Only one *Tricorythodes* was found at the three Waterton sites in one year of sampling.

Several species of trichopterans were found in Waterton but not Cheesman, but none were of great numerical importance (Table 8).

The canyons did not exhibit any major difference in coleopteran species composition (Table 8). The Elmidae were the only group of any importance.

While the composition of dipterans was quite different in the two canyons, only a few of these difference were numerically important (Table 9). Several genera of chironomids important in Waterton Canyon were not found in Cheesman Canyon. *Deuterophlebia* (Deuterophlebiidae) and *Agathon* (Blepharoceridae), members of families restricted to mountain streams, occurred only in Waterton Canyon, but never in abundance.

Amphipods (*Gammarus*) and gastropods (*Physa* and *Lymnaea*) were of some importance in Cheesman Canyon, but were not encountered in Waterton (Table 10).

Several differences are noted when NF and SP are compared on the basis of specific taxa present. Although some stoneflies were rare at one confluence site and abundant at the other (e.g. *Isoperla patricia*), no species of numerical importance was found at only one site (Table 6). A similar situation occurred with mayflies (Table 7). Some species (e.g. *Ephemerella inermis*) were much more abundant at one site, but only *Tricorythodes* was absent at one site but exhibited some importance at the other location. Trichopterans and coleopterans (Table 8) exhibit this same pattern with few or no species important at one site being absent from the other, but with some species differing greatly in their abundance. Among the dipterans (Table 9), the most notable difference is the abundance of chironomids at SP (1023 organisms/m^2) and the paucity of this family at NF (3 organisms/m^2). Despite this, only two genera (*Microtendipes* and *Parachironomus*) were abundant at SP but absent from NF. A large species of *Tipula* comprised a major portion of the dipteran biomass at SP, but was not found at NF.

Table 10 includes the remaining taxa, only one (*Eiseniella tetraedra*) of which is abundant at one confluence site but absent at the other. Truly aquatic populations of this lumbricid earthworm appear restricted to the stretch of the South Platte River from a few kilometers below Cheesman Dam to the confluence of the North Fork (Ward, 1976). Small, opaque white, eyeless amphipods were collected in the North Fork and are presumed to be hyporheic forms. Their taxonomic status is being investigated.

Despite their contiguity, the macroinvertebrate communities at SP and NF were quite different, and species which occurred at both sites were often rare at one location but relatively abundant at the other.

Species diversity

Only 32 species of macroinvertebrates were found at the three sites in Cheesman Canyon (Table 4). At Site SP this number had increased to 64, and 70 species were collected at the three sites in Waterton Canyon. The unregulated North Fork yielded 49 species at one site over the one-year sampling period.

To further elucidate community structure, the Shannon-Weaver diversity index was applied to the macroinvertebrate data of the South Platte River. In Figure 5 the study locations are arranged by the degree of

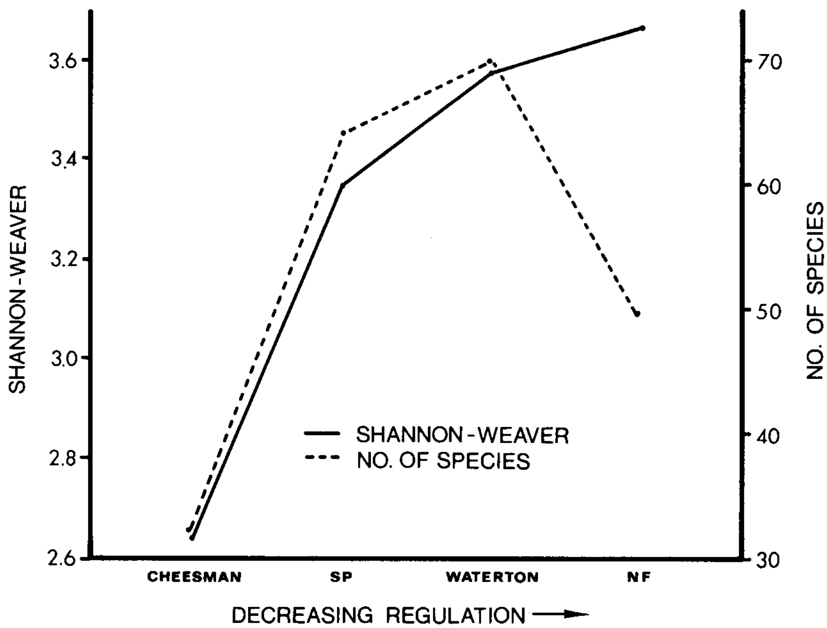

Fig. 5. Macroinvertebrate diversity as a function of regulation at locations on the South Platte River, Colorado.

regulation by dams. The number of species increased with decreasing regulation from Cheesman to Waterton Canyons, but decreased at NF. Even though the North Fork did not contain the largest number of species, the macroinvertebrate community of this unregulated section exhibited an index value which exceeded all other locations because of the more even distribution of individuals among the species. Other authors have also noted a reduced macroinvertebrate diversity in streams below deep release dams (Pearson et al., 1968; Hilsenhoff, 1971; Hoffman & Kilambi, 1971; Isom, 1971; Spence & Hynes, 1971; Fisher & LaVoy, 1972; Lehmkuhl, 1972, 1974).

Macroinvertebrate communities below deep release dams may have characteristics similar to streams with mild organic enrichment (Spence & Hynes, 1971). Wilhm (1970) found that unpolluted streams generally have diversity index values between 3.0 and 4.0 The highly regulated Cheesman sites exhibited a diversity index (2.6) which is similar to values found in organic pollution recovery zones.

Effects of Regulation on Macroinvertebrates

Effects on Standing Crop

The rich standing crop in Cheesman Canyon and at Site SP contrasted sharply with the low numbers and biomass of macroinvertebrates in Waterton Canyon and at Site NF (Table 4). Although the large spring runoff may have suppressed Waterton values, more organisms with a much larger biomass were collected in June of 1973 during high water conditions than in May of the following year. In addition, the great differences in standing crop between NF and SP indicate that other factors are involved. The following factors, conducive to large macroinvertebrate populations, are thought to be largely a result of regulation by Cheesman Dam: (1) large crops of epilithic algae, (2) presence of aquatic angiosperm beds, (3) hard water and high dissolved salts, (4) long periods of constant flow, (5) warm winter temperatures and associated ice-free conditions, (6) low turbidity, and (7) reduced bank and bed erosion. Although these factors changed with increasing distance below the dam, even 32 km downstream at SP conditions had not reached the same levels as at NF (Table 2). The water was still higher in dissolved salts than at NF, harder, and had a much greater development of benthic algae.

Biomass was similar at SP and Cheesman (although numbers differed), indicating a similar carrying capacity in these two sections of the South Platte River. Any decrease in favorable conditions (e.g. hardness) from Cheesman to SP was apparently compensated for by the lower growth efficiency (Ward, in press) associated with the low summer temperatures in the stream section below the dam. The low dissolved oxygen and siltation effects which limit macroinvertebrates below some deep release dams (Neel, 1963; Wright, 1967; Hynes, 1970 a; Isom, 1971) were not encountered here.

Effects on Composition and Diversity

The composition and diversity of the macroinvertebrate communities varied between study locations, and these differences were sometimes great. For example, amphipods and gastropods were important in Cheesman Canyon but were not found in Waterton Canyon. Conversely, major taxa of Waterton Canyon, such as filipalpian stoneflies, were not collected in Cheesman. Over twice as many macroinvertebrate taxa occurred in Waterton than in Cheesman Canyon. Whereas only one stonefly (*Isoperla patricia*) occurred in Cheesman Canyon, 13 species were collected in Waterton Canyon. Many other examples can be seen in Tables 6—10.

What factors are responsible for these differences in the macroinvertebrate communities? The answers to this question are thought to relate to several different phenomena which result from regulation by dams and will be discussed under the following headings: (1) Limiting factors, (2) trophic relationships, (3) environmental stability and competitive interactions, and (4) thermal effects.

Limiting factors

Some species may be restricted to or prevented from inhabiting a study section simply because environmental conditions are inappropriate. Gastropods, for example, are limited by calcium and pH, which may explain their restriction to Cheesman Canyon. Most Lymnaeidae are restricted to waters where bound carbon dioxide exceeds 15 ppm and where pH is 7.0 or higher (PENNAK, 1953). *Gammarus lacustris*, in addition to being confined to streams of high alkalinity (TITCOMB, 1927), is limited to waters which are cool to cold in summer (BOUSFIELD, 1958). Other species may find the summer cool conditions below the dam quite inappropriate although they may occupy warmer downstream sites.

The restriction of submerged angiosperms to the South Platte River above the confluence of the North Fork is apparently the reason for the restriction of *Tricorythodes* to this section.

The dense covering of epilithic algae on virtually all rock surfaces in Cheesman Canyon may have prevented the establishment of certain forms which utilize suckers or friction pads. Blepharocerids, the only stream insects with true suckers, were confined to Waterton and NF. The larvae of this family are restricted to streams with smooth rock surfaces (HORA, 1936), hardly the situation below the dam. The lack of smooth rock surfaces below the dam may also explain the absence of *Ephemerella doddsi* and heptageniid mayflies. PERCIVAL & WHITEHEAD (1929) found that *Rhithrogena*, which has the gills modified as a holdfast organ, was virtually eliminated in the *Cladophora*-covered stone zone. *Rhithrogena doddsi* did not occur in Cheesman Canyon, but was the most abundant species in the unregulated North Fork.

Trophic relationships

CUMMINS et al. (1972) stated that the organic matter input of a stream must be chemically diverse in order to maintain a biologically diverse ecosystem. It is unlikely that a high degree of chemical diversity exists below most deep release dams.

Particle size diversity was also reduced by the dam and because of the steep rocky walls of Cheesman Canyon and the paucity of riparian vegetation, allochthonous input was limited. The near absence of terrestrial leaf litter below the dam may explain the restriction of certain taxa to downstream locations. This could be the case for large particle detritivores, such as filipalpian stoneflies, which feed on decomposing vascular plants. It is, however, unlikely that food is limiting even for these species since aquatic angiosperms and filamentous algae were readily available. Lack of food is certainly not responsible for the absence of predaceous plecopterans below the dam. Other factors must therefore account for the great reductions in plecopterans at highly regulated sites.

The low macroinvertebrate diversity below the dam may result from the absence of a key predator which maintains species richness by preventing monopolization of resources by one or a few prey species (PAINE, 1966). A few species with high densities comprised a large majority of the benthic community of Cheesman Canyon, a situation which may result from low predation pressure (PATRICK, 1970).

The clarifying effect of Cheesman Lake greatly reduces the total suspended matter, and this effect extends several kilometers downstream except when bankfull level is exceeded (WARD, 1974). An enhancement of filter-feeding benthos in lake outflows has been attributed to the release of lentic plankton (ILLIES, 1956; MÜLLER, 1956; CUSHING, 1963). It appears that plankton is not a reliable enough food source below deep release dams to allow the buildup of large populations of filter-feeders (WARD, 1975). The clarifying effect of the dam may indeed be detrimental to this trophic component. *Hydropsyche*, for example, was relatively unimportant in Cheesman Canyon, but was the most abundant organism at Waterton and SP and second in abundance at NF (Table 8). *Brachycentrus*, another filter-feeder, was absent from Cheesman sites, but was present at all downstream locations.

Environmental stability and competitive interactions

Natural stream environments are subject to great temporal variations in ecological parameters, such as flow, temperature, and the kinds and amounts of potential food materials. Changes in these parameters in turn cause variations in other factors. For example, changes in discharge are accompanied by variations in turbidity, among other things. Different organisms will be favored as conditions change, resulting in species replacement over time and a relatively diverse community (PATRICK, 1970). Competitive exclusion does not therefore operate to the extent that it does in environments with more constant and predictable conditions (HUTCHINSON, 1953). Cheesman Canyon and certain other streams below hypolimnial release dams display relatively constant and predictable conditions quite unlike unregulated streams.

The abundant and constant algal food source below the dam has already been mentioned as has the sparse, but uniform, supply and composition of suspended particulate matter. PATRICK (1970) states that in natural streams competition among benthic plants is relatively unimportant, since monopolization of a given resource is less likely to occur where the composition and amount of nutrients fluctuate in an unpredictable manner, and this should also apply to benthic stream animals. Conversely, in environments with constant and predictable resources, competitive interactions would be expected to intensify, resulting in the elimination of opportunistic species and reduced community diversity. Species for which ecological factors are within tolerance limits, but not optimal, may also be eliminated under conditions of more intense competition.

The effect of Cheesman Dam on the flow regime of the South Platte River is to dampen the effects of spates and spring runoff and create long periods of constant flow. In addition, increased flow (within limits) is not necessarily accompanied by large increases in suspended materials. The variations in flow and associated parameters in unregulated streams, if not too extreme, alternately favor different species and increase diversity.

Thermal effects

Water temperature exhibited a high degree of diurnal and seasonal constancy below the dam compared with downstream locations. Absence of ice in Cheesman Canyon reduced the large seasonal fluctuations in benthic algae characteristic of Waterton Canyon. These thermal effects contribute to the environmental stability discussed in the preceding section.

Sublethal and indirect effects of thermal constancy on aquatic macroinvertebrates have been discussed in detail elsewhere (WARD, in press) and will only be summarized here.

Many life cycle phenomena, such as hatching, growth and emergence, depend on thermal cues. The thermal constancy and seasonal temperature pattern below deep release dams may not provide the thermal signals essential for completion of the life cycle for certain species (NEBEKER, 1971; LEHMKUHL, 1972). The number of degree days, for example, may not be sufficient. Only species able to complete their life cycles under relatively constant thermal conditions would be able to occupy the steam below deep release dams in temperate regions. Diurnal constancy and the seasonal timing of temperature phenomena may also be important. HYNES (1970 b) feels that the temperature pattern may be more important than absolute temperatures in controlling the distribution of stream insects. Site 1 below the dam exhibited a quite different thermal pattern than Site 6 in Waterton Canyon (Fig. 3). The time of the seasonal maximum and the pattern of spring temperature increase may be as important for some species as temperature constancy (LEHMKUHL, 1972; WARD, in press).

Whether deep release dams improve or degrade the receiving stream ecosystem depends on many factors, and much more data are required before definitive answers will be possible. For example, advantages may be derived from a more constant flow regime but only if a relatively natural seasonal flow pattern is maintained. The trophic state of the reservoir is a major determiner of the effects of deep release on the receiving stream. Other factors to consider are retention time, drawdown levels, and the temperature profile of the reservoir. It should be determined whether reduced growth of gamefish during summer cool conditions would be compensated for by higher winter temperatures and an abundant year-round food supply.

While increases in macroinvertebrate standing crop may be beneficial, it is difficult to assess the effects of associated reductions in species diversity. Perhaps the position of Cairns (1974) is the most rational at the present time. He stresses that, until it is clearly demonstrated that reduced diversity is not associated with reduced ecosystem stability, the natural diversity of an area should not be disrupted.

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Summary

Over a 34-month period from 1972—75 year-round studies were conducted at four locations on the South Platte River in the mountains of central Colorado. Each location was studied for one year to determine differences in ecological parameters at study sites differentially regulated by deep release dams. The greater development of algae and submerged angiosperms at more regulated sites was reflected in lower free CO_2 and higher pH values. Bound CO_2 and total dissolved salts progressively decreased downstream from the dam, exhibiting lowest values at unregulated sites. Mean annual temperatures were remarkably similar in regulated and unregulated canyons, but thermal regimes were quite different. The seasonal and diurnal temperature range was greater at less regulated sites; the summer maximum occurred earlier, and the temperature rise in spring was much more rapid. Low standing crop associated with high macroinvertebrate diversity was characteristic of unregulated sites; the converse was true of regulated locations.

Only ephemeropterans exhibited similar percentage composition in both canyons. Plecopterans were especially reduced by regulation. Trichopterans were more important and dipterans less important in the downstream section. Taxa important below the dam but absent downstream include, *Gammarus*, gastropods, and a mayfly associated with submerged angiosperms. Important taxa found only in the downstream canyon include filipalpian stoneflies, heptageniid mayflies, and two chironomids. Despite their contiguity, macroinvertebrate composition also differed considerably at two sites immediately above the confluence of an unregulated tributary with the regulated stream.

Some species may be prevented from inhabiting a location because environmental conditions are inappropriate, and this may be a function of regulation. Some species, for example, may be unable to tolerate the summer cool conditions below dams. Enhanced algae favors some species, but prevents establishment of forms utilizing suckers or friction pads. Low diversity of particulate and dissolved organic matter may limit macroinvertebrate diversity at sites below dams and could explain the absence of large particle detritivores. Moderate predation pressure at downstream sites maintains species richness by preventing monopolization of resources by one or a few species, unlike the situation below dams where predators are scarce.

Temporal, unpredictable variations in temperature, flow, and the kinds and amounts of food materials increase diversity of unregulated streams by allowing temporary colonization by opportunistic species. The greater environmental stability in regulated sections increases competitive interactions and reduces diversity, especially where predation pressure is low.

Thermal conditions below deep release dams not only contribute to environmental stability, but also have sublethal and indirect effects on certain species.

Zusammenfassung

Während 34 Monaten (1972—1975) wurden am South Platte River in Central-Colorado an vier Stellen kontinuierliche Untersuchungen durchgeführt. Jede Stelle wurde ein Jahr lang untersucht, um die unterschiedlichen ökologischen Parameter in Abhängigkeit von der Entfernung des tiefen Stausee-Ausflusses zu bestimmen. Die intensivere Entwicklung von Algen und Unterwasserpflanzen an Stellen, die vom Stausee stark beeinflußt sind, zeigte sich am niederen freien CO_2-Gehalt und an höheren pH-Werten. Der Gehalt an gebundenem CO_2 und die Menge der total gelösten Salze nahm progressiv flußabwärts vom Stausee ab und zeigte den tiefsten Wert an den Stellen, die vom Staugewässer unbeeinflußt waren. Die mittleren jährlichen Temperaturen von regulierten und unregulierten Canyons sind bemerkenswert ähnlich, die Temperaturschwankungen jedoch sind

ganz unterschiedlich. Die saisonalen und täglichen Temperaturschwankungen waren größer an weniger regulierten Stellen; das Sommermaximum trat früher ein, und der Temperaturanstieg im Frühling war viel schneller. Charakteristisch für die unregulierten Stellen war eine niedrige Biomasse, verbunden mit einer hohen Arten-Diversität der Macro-Invertebraten; an den regulierten Stellen traf gerade das Gegenteil zu.

Nur Ephemeropteren waren in beiden Canyons in ähnlichen prozentualen Mengen vorhanden. Besonders Plecopteren wurden stark durch die Regulierung vermindert. Stromabwärts dominierten Trichopteren, während Dipteren weniger stark vertreten waren. Einige wichtige „Taxa", die unterhalb des Stausees vorhanden waren, aber stromabwärts fehlten, waren *Gammarus*, Gastropoden und eine Ephemeride assoziert mit Unterwasserpflanzen. Die einzigen wichtigen „Taxa" weiter stromabwärts beinhalteten filipalpe Plecopteren, heptageniide Ephemeriden und zwei Chironomiden. Trotz enger Nachbarschaft variierte die Zusammensetzung der Macro-Invertebraten beträchtlich an zwei Stellen unmittelbar oberhalb der Einmündung eines unregulierten Nebenflusses in den regulierten Strom.

Einige Arten mögen einer bestimmten Stelle fernbleiben, weil die Umgebungsbedingungen ungünstig sind, was eine Folge der Regulierung sein kann. So können sich z. B. einige Arten den kühlen Bedingungen im Sommer unterhalb des Stausees nicht anpassen. Ein erhöhter Algenbestand begünstigt einige Arten, verhindert aber die Ansiedlung von Arten, die Wurzelsprosse benötigen. Ein niedriger Gehalt an organischem Material (gelöst und ungelöst) kann die Arten-Diversität der Macro-Invertebraten an Stellen unterhalb des Stausees begrenzen und erklärt die Abwesenheit von Lebewesen, die sich von großen organischen Partikeln ernähren. Ein gemäßigter Einfluß von Raubformen an Stellen stromabwärts erhält den Artenreichtum, indem verhindert wird, daß eine oder weniger Arten die Nahrungsstellen beherrschen; unterhalb eines Stausees sind räuberische Organismen selten.

Gelegentliche, unvoraussehbare Änderungen der Temperatur, der Fließgeschwindigkeit und der Futtermenge etc. erhöhen die Arten-Diversität in unregulierten Strömen, da sich zeitweilig „opportunistische" Arten ausbreiten können. Die stabileren Umweltsbedingungen in regulierten Sektoren führen zu einem härteren Wettbewerb und reduzieren die Arten-Diversität besonders dort, wo der Einfluß der Räuber niedrig ist.

Die Temperaturbedingungen unterhalb des Stauseeausflusses tragen nicht nur zur Stabilität der Umweltbedingungen bei, sondern haben auch einen sublethalen und indirekten Einfluß auf gewisse Arten.

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Address of the author:

Dr. JAMES V. WARD, Dept. of Zoology and Entomology, Colorado State University, Fort Collins, Colorado 80523, U.S.A.