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INFLUENCE OF REGULATION ON ENVIRONMENTAL CONDITIONS AND THE MACROINVERTEBRATE COMMUNITY IN THE UPPER COLORADO RIVER

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ABSTRACT

The influence of stream regulation on environmental conditions and concomitant alterations of macroinvertebrate community structure was determined from field studies conducted from September 1981–June 1983 at three sites on the upper Colorado River. Site 1 (reference site) was located above Granby and Shadow Mountain Reservoirs, a deep-release storage impoundment, whereas sites 2 (regulated site) and 3 (recovery site) were located 0·4 and 4·0 km, respectively, below the dam.

Although macroinvertebrate diversity was reduced at the regulated site compared to both the reference and recovery sites, the number of taxa (43) was considerably higher than values reported from studies of other regulated streams in the Rocky Mountains. Macroinvertebrate mean annual density in the regulated site was twenty times higher than at the reference site and slightly higher than the recovery site. The regulated site was characterized by the absence of heptageniid mayflies, reductions in stoneflies, caddisflies, shredders, and predators, and high densities of *Baetis* spp., *Ephemerella infrequens*, chironomids, and non-insect taxa. Many of these faunal changes are attributed to alterations in the temperature regime induced by regulation and to changes in the source and temporal sequencing of organic detritus. Although the number of annual degree days was actually greater below the dam than above the reservoir, other components of the thermal regime was severely altered by regulation. At the regulated site the primary source of coarse organic detritus was autochthonous (decaying algae) with a vernal pulse, in contrast to the typical autumnal pulse of allochthonous leaf litter. There was no evidence that the greater substrate permeability and flow predictability below the dam directly influenced the reduction of species.

KEY WORDS Regulated streams Colorado River Macroinvertebrates

INTRODUCTION

On a world-wide scale the number of large dams continues to increase (Petts, 1984), thereby interrupting the river continuum (Ward and Stanford, 1983). In some countries (e.g. India) dams have been built on virtually every feasible location (Stanford and Ward, 1979a). Despite this proliferation, it was only since the early 1970s that data were presented which began to clearly demonstrate the influence of large dams upon channel morphology, riparian vegetation, aquatic plants, fish populations, and benthic invertebrate assemblages. Ward and Stanford (1979a), Ward (1982), Petts (1984), and Lillehammer and Saltviet (1984) provide reviews on the general effects of stream regulation.

In the early 1940s the United States government developed a scheme of reservoirs and diversion canals designed to facilitate the delivery of water to several western states (Stanford and Ward, 1979b). Included in this plan was construction of Granby Reservoir high in the mountains near the headwaters of the Colorado River. The Colorado River drains one twelfth of the United States and is fed by snowmelt from the western slope of the southern Rocky Mountains (Stanford and Ward, 1986). Granby dam (91 m high) was specifically built to divert the headwaters of the Colorado River through the Continental Divide via a

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21 km tunnel (Pennak, 1963). The reservoir is a deep-release storage impoundment with a capacity of 666 hm^3 located at 2460 m a.s.l. near the southwest corner of Rocky Mountain National Park (Figure 1). It is ice-covered in the winter and thermally stratified during the summer and early fall.

The objectives of this research were: (1) to document the changes in the macroinvertebrate assemblage induced by stream regulation and (2) to quantify and characterize alterations in the major environmental factors responsible for such changes.

SITE DESCRIPTIONS AND METHODS

Three sampling sites with similar characteristics, except for the influence of stream regulation, were selected for study. The sites were located in the upper Colorado River in the vicinity of Granby Reservoir (Figure 1). All three sites were located in rubble riffles of similar gradient (0·006–0·009), canopy cover, geology, and riparian vegetation at similar elevations (2,426–2,593 m a.s.l.).

An unregulated location (site 1) was selected as a reference station. Site 2, 0·4 km downstream from Granby Dam, was located in an intensely regulated stream segment. Site 3 was located a sufficient distance below Granby Dam (4·0 km) to exhibit at least partial recovery from the altered conditions engendered by the upstream impoundment. These three sampling stations will henceforth be referred to as the reference site (site 1), the regulated site (site 2), and the recovery site (site 3).

Macroinvertebrates

Four to eight benthic sampling units were collected monthly for twenty months at each site using both a modified Surber sampler (0·09 m^2) equipped with side panels and a 1 m net with 240 μm mesh and

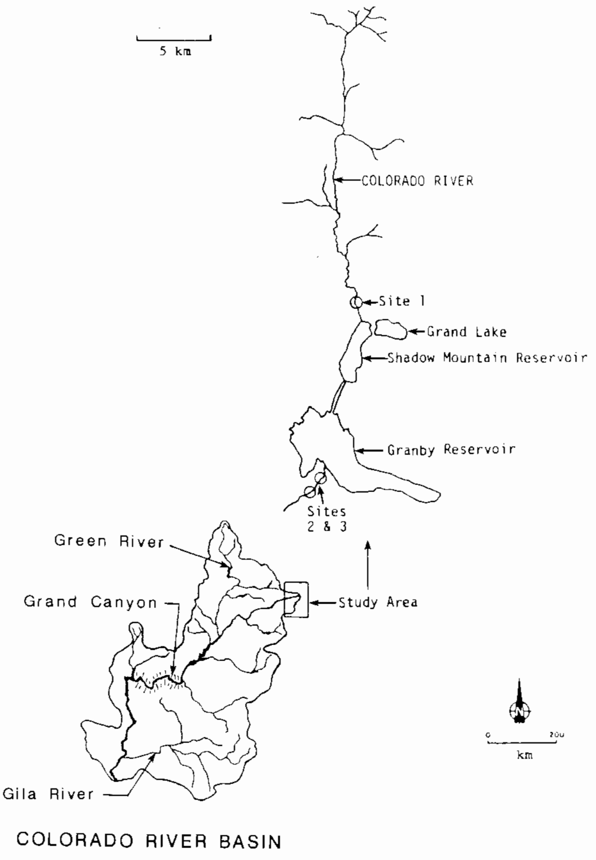

Figure 1. The Colorado Basin and the upper portion of the Colorado River showing the locations of the study sites.

artificial substrates. Four Surber samples, taken across the width of the stream, were collected monthly at each site. The substrata delineated by the Surber sample was stirred down to approximately 10 cm. Artificial substrates, consisting of clay bricks (23 × 19 × 9·5 cm), were allowed a one month colonization period before being sampled. Sampling consisted of sweeping the macroinvertebrates from the entire area of a specific surface (top, side, etc.) into a small net (240 μm mesh) held immediately downstream. An artificial substratum sampling unit consisted of combining the density of organisms from each surface (top, side, etc.), plus organisms in the top 10 cm of sediment below the brick. The combined area sampled by a brick and a Surber sampler were approximately equal. Therefore, sample units from both techniques were used to estimate macroinvertebrate densities. Each sampling unit was preserved in 5 per cent formalin. Specimens were identified to species or genus, except midge larvae (identified to family), water mites, ostracods, nematodes, and oligochaetes. All individuals from artificial substrate samples and Surber samples from the reference site were fully sorted, identified and enumerated. Fifty per cent of the Surber samples collected at the regulated and recovery sites were subsampled (½ or ¼ subsamples) because of the large numbers of organisms present. Ten samples which had been subsampled were remixed and completely sorted to assess the precision of the technique. A paired t-test indicated that there was not a significant difference ($p = 0{\cdot}35$) in the density estimates of abundant mayflies and caddisflies between subsamples and completely sorted samples.

Statistical differences between sites with respect to the abundances of specific taxa and functional groups was determined using a non-parametric analysis; the Friedman two-way analysis of variance by ranks (Daniel, 1978). Each site represented 3 treatment levels and the mean density (#'s m^{-2}) for each month (12) for specific taxa or groups represented statistical blocks. When abundances between sites were significantly different, a multiple-comparison procedure for the Friedman test (Daniel, 1978) was used to determine which sites were statistically different.

Floral Analysis

Periphyton was sampled monthly by scraping a 10 cm^2 area delineated with a shallow plastic cylinder from the top surface of three rocks at each site. Rocks to be sampled were haphazardly selected from the thalweg. Each sample was preserved in 5 per cent formalin. Most algae were identified to species. Quantitative estimates of the density (#'s mm^{-2}) of each taxon were determined by strip counts in a Sedgwick-Rafter cell.

Macrophyte dominance, estimated as per cent cover, was determined four times during the study (February, April, June, and September of 1982). Eight to ten 1 m^2 quadrats were randomly placed along a transect that spanned the width of the river. Sampling occurred along two transects per site per sampling period.

Water Temperature Analysis

Water temperature was measured continuously at each site for eighteen months using Ryan ninety-day thermographs. Each thermograph was checked against a Weksler hand-held thermometer on a monthly basis and calibrated in an ice bath prior to placement and following retrieval. Annual mean daily temperatures, annual coefficients of variation, annual degree days, summer maximum and winter minimum values, and the rates of vernal rise and autumnal decline were determined from daily mean temperatures.

Mineral Substrata Analysis

Four samples were taken at each site; two replicates before and two replicates following snowmelt runoff. A steel cylindrical coring device (28 cm in diameter) was driven 15 cm into the substrata and all sediment and water were removed using a hand-operated bilge pump. Samples were dry-sieved into size fractions based on Cummins' (1962) modification of the Wentworth scale. The fredle index was used to estimate substrate permeability of the riffles at each site (Lotspeich and Everest, 1981). Cobble and boulder sized particles, which have little influence on permeability and would have incorrectly inflated the mean particle diameter, were excluded from the permeability analysis.

Calculations of disturbance flows, defined here as the flow necessary to transport the mean particle diameter, were based on all substrate size categories, including boulders and cobbles. Core samples were used to estimate the weight of the cobble through clay size categories. The mean number of boulder sized particles (greater than the core diameter) per metre were estimated by determining the number of boulders touching a 10 m transect located in the middle of each riffle at each site. For each boulder counted the longest diameter was measured and used to determine the mean diameter of the boulder category at each site. Three rocks from each site representing the mean boulder diameter were brought back to the laboratory and weighed. The mean diameter and weight of the boulder size category was included in calculations of the geometric mean particle diameter of the boulder through clay size fractions at each site.

Flow Analysis

United States Geological Survey (U.S.G.S.) gauging stations were located a short distance upstream from the reference and regulated sites. A third U.S.G.S. gauging station was located approximately 1 km downstream from the recovery site. Thirty years (1952 to 1982) of mean daily flow records were used to determine annual mean daily flow, annual coefficient of variation, flow predictability, and key attributes of the flow disturbance regime.

Colwell's (1974) index of predictability (constancy and contingency) was used to compare flow predictability above and below Granby Reservoir. Because the standard deviation for flow values within established categories covaried with the long-term mean, a natural log transformation of the flow values was necessary (Colwell, 1974). The transformed mean daily flow values were organized into eight categories corresponding to the eight rows of a frequency matrix with three hundred and sixty-five columns representing the days in a year. Category intervals for both flow and time were chosen to maximize the resolution of the analysis.

Before estimating the disturbance flow at each site, it was necessary to estimate the critical tractive force capable of transporting the mean particle diameter; the tractive force ($\mathrm{kg\,m^{-2}}$),

$$t = 1000\,(D)\,(S),$$

is related to the specific weight of water ($1000\,\mathrm{kg\,m^{-3}}$), water depth D (m), and the slope of the energy gradient S. The tractive force, an estimate of the lift and drag exerted on a given particle at the point of incipient motion, was determined from a graph describing the empirical relationship between the mean diameter of rounded particles and the tractive force (Newbury, 1984). Once the tractive force equation was solved, the flow necessary to transport the mean particle diameter at each site was calculated by inserting the critical water depth into the flow equation:

$$Q = (W)\,(D)\,(V),$$

(W) is the stream width, (D) is the critical water depth, and (V) is the current velocity at approximately 10 cm above the stream bottom at the critical water depth. Both the current velocity at the critical water depth and the stream width were measured during flood events at each site. High flows ($Q > 30\,\mathrm{m^3\,s^{-1}}$) were released from the dam in 1983 and 1984 following the termination of field sampling. Using flow records from above and below the dam a computer program was written to determine the average number of times per year that the flow equaled or exceeded the critical value for incipient motion of the mean particle size. The average interval (in days) between critical flow events was also calculated. The variance associated with the average interval between disturbances was used as a relative estimate of the predictability of disturbance events. A site with a high variance in the intervals between disturbances would be relatively less predictable than a site with a low variance. This analysis provided an estimate of the rate of disturbances (frequency) and an estimate of their predictability.

Water Chemistry Analysis

Dissolved oxygen, free and bound carbon dioxide concentrations, and pH were measured monthly in the field using standardized procedures (Ward and Dufford, 1979).

Table 1. Mean and ranges (in parentheses) of chemical variables over the period of study

Variable	Reference site	Regulated site	Recovery site
Dissolved oxygen, mg l^{-1}	9·9 (7·6–9·9)	9·4 (7·1–11·4)	9·6 7·3–11·5)
Free CO_2, mg l^{-1}	0·7 (0·3–1·0)	1·4 (0·3–4·4)	0·1 (−5·0–0·8)
Bound CO_2, mg l^{-1}	12·7 (10·5–15·0)	10·1 (5·3–14·0)	13·8 (11·0–18·5)
pH Units	7·1 (7·0–7·4)	7·0 (6·6–7·4)	7·4 (7·1–8·2)

Sedimentary Detritus Analysis

Sedimentary detritus standing crop was determined eleven times over two years on a seasonal basis with more intensive sampling during the fall of the year. Samples were collected by driving a cast iron core sampler (24 cm diameter) 15 cm into the substrate. Samples were processed, using procedures described by Short and Ward (1981), into four size classes (>1000 μm, 250–1000 μm, 75–250 μm and 0·45–75 μm). Ash-free dry weight (AFDW) of the detrital material in each size class was determined following combustion at 550°C for 24 h in a muffle furnace (Petersen and Cummins, 1974). Results are expressed as g m^{-2} AFDW for each size class.

RESULTS AND DISCUSSION

Water Chemistry

'Run-of-the-river reservoirs' may have only minor effects on downstream water chemistry (Ward, 1982), as was found in the present study. Dissolved oxygen was near saturation at all times, with the somewhat higher maxima at both downstream sites (Table 1) attributable to the dense aquatic flora below the dam. Other chemistry values were also similar between sites, with a few exceptions. The pH was circumneutral at the three sites during most of the year. During August and September, water high in free CO_2 (up to 4·4 mg l^{-1}) released from the dam depressed the pH (down to 6·6) at the regulated site. At the recovery site, the highest pH values (8·1 and 8·2) occurred during September of both years when free CO_2 values were negative, suggesting that the pH was elevated by high photosynthetic activity (*cf.* Ward, 1976). All bound CO_2 values were in the 'soft' category, or the lower end of the 'medium' water hardness category (Pennak, 1971).

Temperature

The temperature regime at the unregulated reference site was characterized by a relatively rapid vernal increase and autumnal decline, an annual maximum of 18°C, four months of ice cover, and five months at 0°C (Figure 2 and Table 2). The relatively high coefficient of variation (Table 2) reflects the responsiveness of the reference stream to short-term changes in atmospheric conditions.

The vernal rise and autumnal decline were less abrupt at the regulated site, where temperature only varied from 2°C to 9°C over the annual cycle (Figure 2). Summer cool and winter warm conditions characterize temperature regimes in streams below deep-release reservoirs (Ward, 1982, 1985). Faster leaf litter decomposition at this location, compared to an unregulated tributary, were attributed to the higher autumn and winter water temperatures (Short and Ward, 1980).

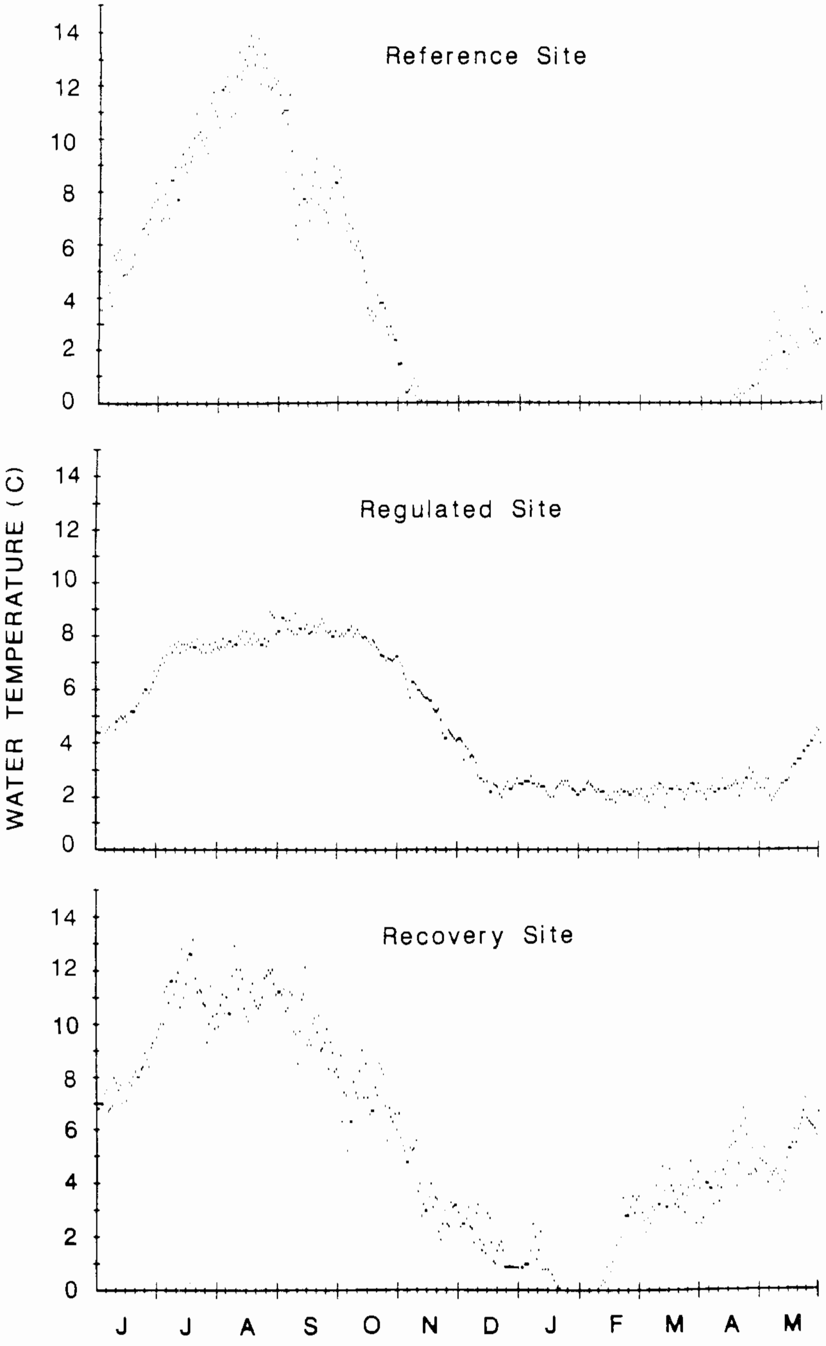

Figure 2. Temperature regimes of the study sites during 1981–1982. Individual points represent daily means.

The temperature regime at the recovery site exhibited characteristics intermediate between those prevailing at the reference and regulated sites (Figure 2). Although the annual range was similar, the duration of minimum temperature and rates of vernal rise and autumnal decline were reduced at the recovery site compared to the reference site.

The thermal energy available for growth, maturation, and emergence can be estimated by the number of annual degree days (Sweeney, 1984). Annual degree days (above 0°C) and mean annual temperatures

Table 2. Temperature characteristics and the elevation of each site

	Elevation (m a.s.l.)	Annual degree days (C)	Mean annual temperature (C)	C.V. (%)	Minimum (C)	Maximum (C)
Reference Site	2590	1130	3·6	119	0·0	18·0
Regulated Site	2450	1729	4·7	53	1·8	9·8
Recovery Site	2426	2082	5·7	64	0·0	18·2

were considerably higher at the regulated and recovery sites compared to the reference site (Table 2). Lower summer maximum temperatures were compensated for by higher autumn and winter temperatures in the regulated site (Figure 2). The greater number of degree days at the regulated site compared to the unregulated site probably resulted in the faster rates of leaf decomposition (Short and Ward, 1980).

Mineral Substrata

Although the pebble to clay size fractions generally constituted similar proportions at the three sites, the amount of sand, silt, and clay was lower at the regulated and recovery sites compared to the reference site (Table 3).

Table 3. Mineral substrate size fractions based on core samples for sites above and below Granby Reservoir. Values in the body of the table represent the mean weight, in grams, of each category except boulders. Standard errors were all less than 10 per cent of the mean. Boulder abundance was measured as the mean number along 1-metre transects. Values in parentheses represent the per cent by weight of the pebble through clay categories. The sorting coefficient, mean particle diameter, and Fredle index were calculated for each site using the size categories below the dashed line

Size categories		Reference	Regulated	Recovery
>256 mm (Boulder) (mean #/m)		1·1	3·4	3·8
64–256 mm (Cobble)		4965·6 g	3743·0 g	4162·9 g
16–64 mm (Pebble)		1820·8 g (43·0)	2145·0 g (48)	1870·3 (44·5)
2–16 mm (Gravel)		1378·0 g (32·6)	1489·4 g (33·3)	1537·9 g (36·6)
0·0625–2 mm (Sand)		810·1 g (19·1)	659·2 g (14·7)	696·3 g (16·6)
0·0039–0·0625 mm (Silt)		125·1 g (3·0)	90·8 g (2·0)	52·5 g (1·2)
<0·0039 mm (Clay)		90·9 g (2·2)	88·4 g (1·98)	42·9 g (1·1)
Total sample weight		9190·5 g	8215·8 g	8362·5 g
Sorting coefficient	(S_o)	4·10	2·28	2·18
Geometric mean particle diameter	(d_g)	8·1 mm	10·4 mm	10·5 mm
Fredle index	(f_i)	1·98	4·56	4·82

Fredle index values were similar at the regulated and recovery sites, but the unregulated reference location exhibited a much lower value (Table 3). The lower Fredle index value at the reference site compared to the regulated and recovery sites was caused by a higher sorting coefficient and lower geometric mean particle diameter of the pebble–clay size categories at the reference site. Fredle index values greater than five indicate relatively good permeability or interstitial flow (Lotspeich and Everest, 1981). Therefore, compared to the unregulated site, the sites below the dam exhibited increased substrate permeability despite a reduction in flow (especially flood level discharges) and armoring (Simon, 1974) by abundant large particles below the dam (Table 3). Large reservoirs reduce downstream sediment loads over 95 per cent compared to preimpoundment levels (Leopold *et al.*, 1964). The clear, sediment-free water released below dams has a high erosive potential which can entrain fine particles and increase permeability.

Flow

The mean daily flow and variation in mean daily flow were greater above the dam (Table 4). Flow below the dam was much more constant due to the absence of annual snowmelt discharge (Figure 3). Colwell's (1974) predictability index was greater below the dam primarily due to a high constancy component (Table 4). Mean minimum flows were maintained near 0·6 $m^3 s^{-1}$ for six months of each year (Figure 3). Minimum flow values at the reference site were often only 50 per cent of those below the reservoir. Predictability component (Table 4). Contingency was high above the reservoir primarily because peak run-off occurred early in June nearly every year on record.

Disturbances, defined as flow events necessary to transport the mean substrate particle diameter, occurred far more frequently above the reservoir (Table 4). Sousa (1984) defined disturbances as 'discrete, punctuated killing, displacement, or damaging of one or more individuals that directly or indirectly creates an opportunity for new individuals to become established'. Discharges less than disturbance flows, as defined here, can undoubtedly cause scouring and result in the death of individuals of some species; however, flows large enough to transport the mean particle diameter must certainly adversely influence most members of the benthic assemblage. Most disturbance flows above the reservoir can be attributed to annual snowmelt run-off and spates that often occurred in July. Flows required to create a disturbance were greater at sites below the dam because the mean particle diameter was larger and the stream bed was wider with a more gradual slope (Table 5). However, the relative lack of disturbance flows below the reservoir were due to the absence of snowmelt run-off. There were only three short periods of disturbance flows below the dam over the thirty-year period of record and they were caused by unexpectedly high run-offs which forced temporary releases of water over the spillway.

The mean interval between disturbances and its standard deviation (Table 4) provide a relative estimate of the predictability of disturbance events. However, the relative absence of disturbances below the dam makes this analysis ambiguous. Although disturbance events were unpredictable (the intervals between disturbances were extremely variable) below the dam, this pattern may have no biological

Table 4. Flow characteristics below Granby Dam (regulated) and at the unregulated reference site based on U.S.G.S. records over a 30-year period (1952–1982)

			Colwell's Index*			Disturbance†		
	Mean daily flow ($m^3 s^{-1}$)	C.V. (%)	Predictability	Constancy (%)	Contingency (%)	Mean # yr^{-1}	Mean interval (days)	S.D. interval (days)
Unregulated regime	1·75	167	0·62	42	58	2·6	93	129
Regulated regime	1·24	72	0·87	66	34	0·1	3,285	3,613

*Colwell (1974)
†Flow events which transport the mean substrate particle size

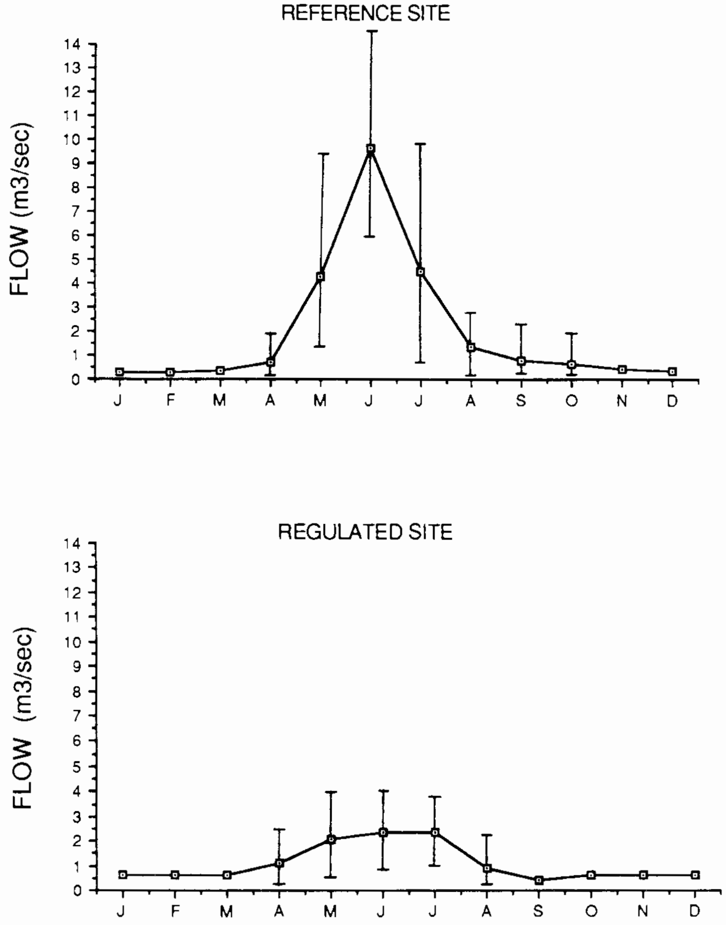

Figure 3. Mean monthly flow values (1952–1982). The upper and lower dashes on the vertical lines represent mean monthly maximum and minimum flow values over the 30-year period.

Table 5. Various stream characteristics, including the estimated flow necessary to transport the mean particle diameter (disturbance flow)

Stream characteristic	Reference	Regulated	Recovery
Mean particle diameter (cm)	6·5	8·5	9·9
Riffle width (m)	18	34	24
Riffle slope	0·009	0·007	0·006
Disturbance flow ($m^3 s^{-1}$)	7·9	29·8	27·0

meaning because the rate of disturbances was very low relative to the life cycle turn-over rates (generation times) of the macroinvertebrate assemblage.

Flora

In general, hypolimnetic release reservoirs impart an overall favourable environment for downstream flora (e.g. Holmes and Whitton, 1977; Lowe, 1979; Ward, 1976). Although the number of species of aquatic plants were reduced below the reservoir, floral densities increased. Filamentous green algae

(*Ulothrix zonata* and *Spirogyra* sp.) were enhanced at both regulated and recovery sites during the summer and fall (Table 6). However, Bryophyta were abundant only at the regulated site (Table 6). Flow constancy, which increases bed stability, enables mosses and filamentous algae to dominate rock surfaces below most deep release storage reservoirs (Armitage, 1977; Dufford *et al.*, 1987; Ward, 1976).

Mean annual diatom density was highest at the regulated site with much lower and similar values at the reference and recovery sites (Figure 4). Ward (1976) found epilithon standing crops three to twenty times greater in a regulated section of the South Platte River in Colorado below Cheesman Reservoir. Many of the dominant diatom species at the regulated site of the present study were either planktonic and originated in the reservoir or they were epiphytic on filamentous green algae (Table 6). Most regulated streams support an abundance of the same epiphytic diatom genera (Dufford *et al.*, 1987; Lowe, 1979; Spence and Hynes, 1971). Diatom density peaked in July at the reference site (Figure 4). However, the highest per cent diatom densities in the regulated and recovery sites occurred in the autumn and winter (Figure 4). Regulated streams apparently favour the growth of cool-water stenotherms (Lowe, 1979). High winter densities of diatoms below Granby Dam support this conclusion.

Aquatic angiosperms were rare at the regulated site, where mosses were the predominant macrophytes, but abundant at the recovery site (Table 6). A greater proportion of the substrate surface

Table 6. A qualitative summary of the floral data for each site. Only species pertinent to the discussion are included

	Reference	Regulated	Recovery
# OF TAXA	163	117	137
SPERMATOPHYTA			
Ranunculus sp.	—	R	A
Elodea canadensis	—	—	C
BRYOPHYTA			
Fontinalis sp.	—	A	—
CHLOROPHYTA			
Microspora sp.	R	A	R
Ulothrix zonata	R	A	R
Spirogyra sp.	C	C	A
CHRYSOPHYTA			
Hydrurus foetidus	R	R	A
CYANOPHYTA			
Oscillatoria sp.	A	A	A
Nostoc parmeloides	R	—	A
BACILLARIOPHYTA			
Achnanthes spp.	A	C	C
Fragilaria spp.	A	A	A
Melosira spp.*	R	A	C
Cymbella spp.†	C	C	A
Cocconeis spp.†	C	C	A

R = RARE—Constitute <10 per cent of total floral density
C = COMMON— Constitute between 10 per cent and 40 per cent of total floral density
A = ABUNDANT—Constitute between 40 per cent and 70 per cent of total floral density
* = PHYTOPLANKTON
† = EPIPHYTIC on *Fontinalis* and *Ranunculus*

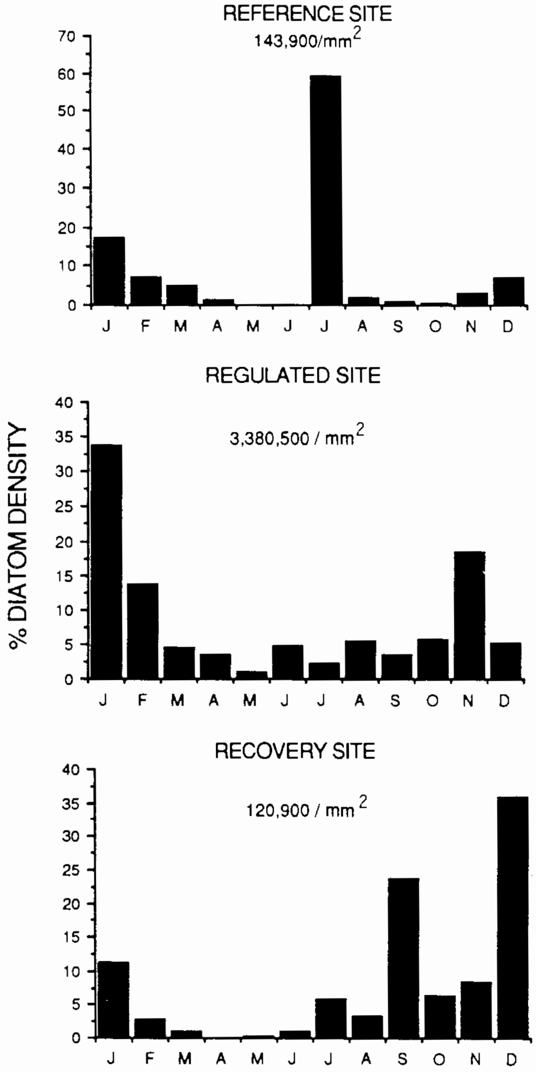

Figure 4. Monthly diatom percentages based on density values at each site (1982). Numbers at the top of each graph represent the mean annual density of diatoms.

was clear of aquatic angiosperms and/or filamentous green algae at the recovery site compared to the moss-covered substrate at the regulated site. There were no aquatic angiosperms, abundant mosses or thick mats of filamentous green algae at the reference site.

Sedimentary Detritus

Peak standing crop in the reference site corresponded to riparian leaf abscission in October (Figure 5) and was primarily composed of coarse particulate organic matter (Figure 6). Detritus standing crop values during the winter and spring were similar in the reference site (Figure 5). The lowest levels of detritus occurred in July and August following spring run-off. Short and Ward (1981) found similar seasonal fluctuations in benthic detritus in Little Beaver Creek, a free-flowing stream (2410 m a.s.l.) located in north central Colorado. However, in addition to a fall peak and post run-off depletion, detritus standing crop was also relatively high early in the spring as ice-cover receded and fine detritus from the banks entered the stream (Short and Ward, 1981). A spring peak was not detected at the reference site in the Colorado River.

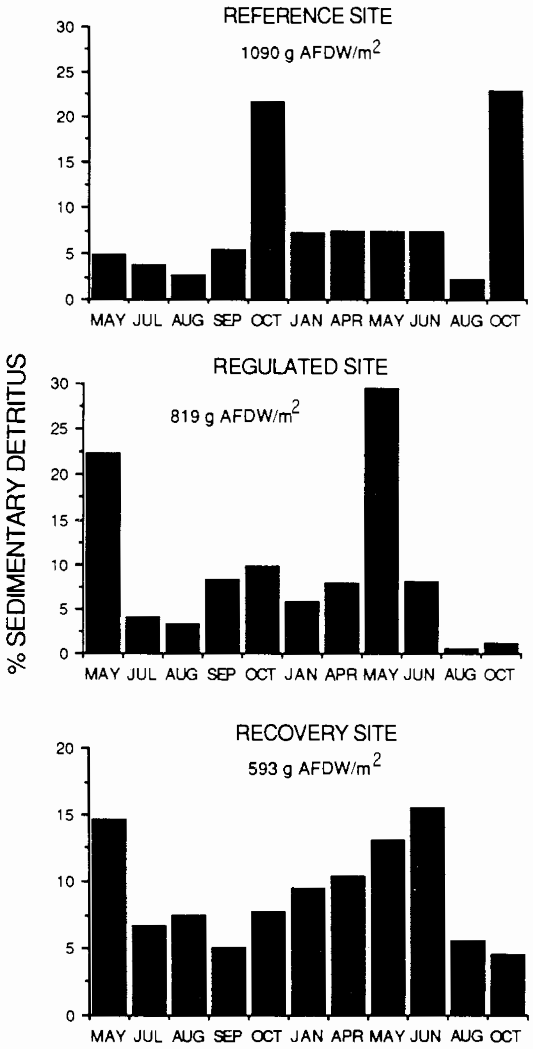

Figure 5. Monthly percentages of sedimentary detritus standing crop for each site (1981–1982). Mean annual standing crop values are indicated at the top of each graph.

Clearly, the downstream transport of organic detritus is disrupted by stream regulation (e.g. Ward, 1974; Webster *et al.*, 1979). However, the effects of stream regulation on sedimentary detritus standing crop and particle size composition is poorly documented (Ward, 1982). As expected, annual standing crop of detritus was higher in the reference site than either sites below the dam (Figure 5). However, annual detritus standing crop was higher in the regulated site compared to the recovery site (Figure 5) because of the abundance of refractory moss stems. Ward (1976) demonstrated that epilithic detritus progressively increased downstream from Cheesman Reservoir on the South Platte River. However, the epilithon in the intensely regulated section of the South Platte River was not dominated by moss.

The temporal occurrence of periods of peak detritus standing crop may have an important influence on stream energetics and community structure and function (e.g. Cummins, 1974; Malmqvist *et al.*, 1978; Vannote *et al.*, 1980). Peak detritus standing crop in both the regulated and recovery sites occurred in the spring (Figure 5) because mosses and filamentous algae, rather than terrestrial leaves, constituted the major portion of detrital input. Although introduced leaf litter rapidly decomposes below Granby Reservoir (Short and Ward, 1980), most sedimentary detritus was decaying aquatic vegetation.

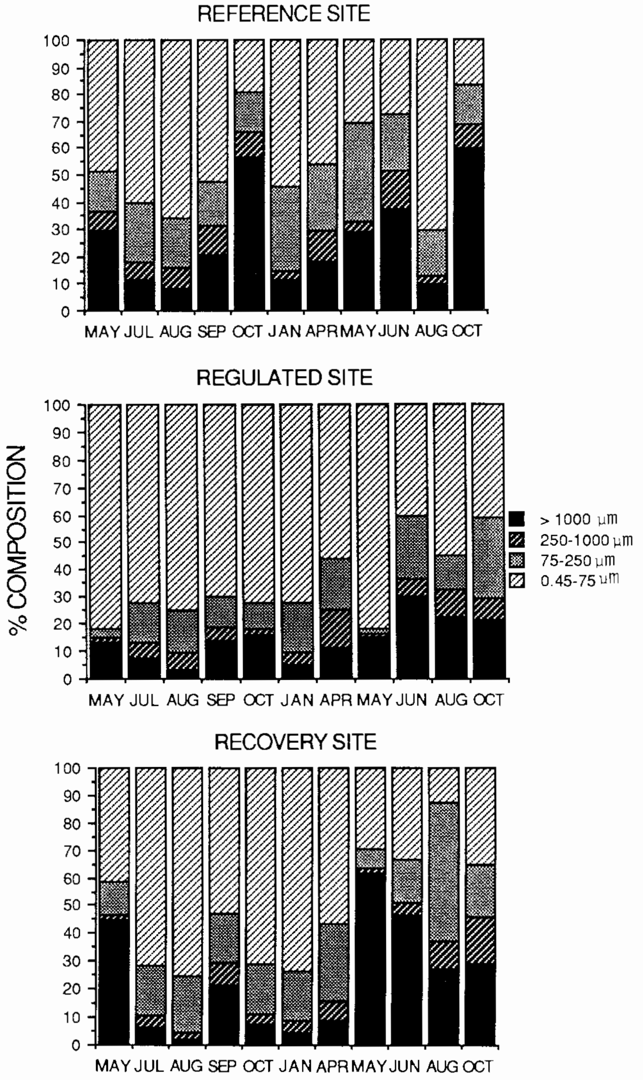

Figure 6. Particle size distribution patterns of sedimentary detritus at each site (1981–1982).

Therefore, not only did the detrital pool above and below the dam differ in abundance and origin (terrestrial leaf material versus filamentous algae), but periods of peak detrital input to the system were also different (spring versus fall).

The smallest size class (0·45–75 µm) comprised the largest fraction of total detritus in the reference site, except in October when >1000 µm size class increased because of the input of terrestrial leaves (Figure 6). Except during leaf abscission, the 0·45–75 µm size class also comprised the largest fraction of detritus in a third order Rocky Mountain stream (Little Beaver Creek; Short and Ward, 1981). As the >1000 µm size fraction (detritus) in the reference site decomposed during the winter and spring, the per cent composition of the 75–250 µm size class increased (Figure 6). Except for September and October, the >1000 µm size fraction was primarily composed or refractory detritus material (e.g. branches, bark, and needles). The 250–1000 µm size class consistently comprised the smallest fraction of total detritus in both the reference site and Little Beaver Creek (Short and Ward, 1981).

The 0·45–75 µm size class comprised the largest fraction of total detritus throughout the year in the regulated site, while the 250–1000 µm size class consistently comprised the smallest size fraction (Figure 6). Compared to the reference site, the >1000 µm size fraction in the regulated site did not increase with leaf abscission in the fall. In fact, the per cent composition of the >1000 µm size class in the regulated site did not fluctuate on a consistent basis during the course of this study. However, the >1000 µm size class in the recovery site increased in May and June as decomposing filamentous algae from the previous year drifted into the recovery site from upstream reaches. Utilization of decaying filamentous green algae by *Arctopsyche grandis* larvae was observed in the Mainstream channel of the Flathead River Basin (Hauer and Standford, 1981). Although more terrestrial leaf material was present in the >1000 µm size category in the recovery site compared to the regulated site, its annual pattern was obscured by the more abundant inputs of decaying aquatic plants. The 0·45–75 µm size class comprised the largest fraction of detritus in the recovery site, except when the >1000 µm size class increased, as was the case in both the reference and regulated sites (Figure 8).

Macroinvertebrates

Species diversity is almost invariably reduced and the taxonomic composition altered below storage reservoirs (e.g. Armitage, 1984; Isom, 1971; Hilsenhoff, 1971; Spence and Hynes, 1971; Ward, 1974, 1976, 1982). Several diversity indices were computed for each site in order to facilitate comparisons between this study and previous research (Table 7).

As expected, diversity was similar at the reference and recovery sites but was reduced at the regulated site (Table 7). However, the total number of taxa at the regulated site was considerably higher than values reported for most other regulated streams below deep release storage reservoirs in the Rocky Mountains (e.g. Cline and Ward, 1984; Ward, 1974; Ward and Short, 1978; Stanford and Ward, 1984; Zimmermann and Ward, 1984). For example, Ward (1974) found only nineteen taxa in a regulated section below Cheesman reservoir. The number of abundant taxa in the regulated site (nine species), however, was similar to the number of abundant taxa in regulated sites from other studies (e.g. Armitage, 1976; Hilsenhoff, 1971; Zimmermann and Ward, 1984). The lower diversity at the regulated site below Granby Dam, compared to the recovery and reference sites, was primarily caused by a low evenness (Table 7). Therefore, the regulated Colorado River site was characterized by a few very abundant species as expected, but also contained an unusually high number of rare species.

The taxonomic composition of the macroinvertebrate assemblages in the regulated and recovery sites exhibited greater similarity than the macroinvertebrate assemblages in the more diverse reference and recovery sites (Table 8). This result suggested that recovery at site 3 was not necessarily an addition of species present in the reference site but eliminated immediately below the dam. Several taxa common in

Table 7. Several measures of macroinvertebrate diversity and evenness for each site. See Washington (1984) for a review of each index

Index	Reference	Regulated	Recovery
# of Taxa	62	43	61
Margalef's Index	13·01	9·36	13·30
Menhinick's Index	0·61	0·25	0·42
Simpson's Dominance	0·07	0·31	0·13
Simpson's Diversity	0·93	0·69	0·87
Simpson's Evenness	0·95	0·71	0·88
Simpson's Maximum Diversity	0·98	0·98	0·98
Shannon Diversity (Base E)	3·12	1·69	2·63
Shannon Evenness	0·79	0·45	0·65
Shannon Maximum Diversity	3·93	3·76	4·06

Table 8. Several measures of similarity (based on taxonomic composition) between site pair combinations for the macroinvertebrate assemblages (site 1 = reference site; site 2 = regulated site; site 3 = recovery site). See Washington (1984) for a review of each index

Index	Sites 1 and 2	Sites 1 and 3	Sites 2 and 3
Jaccard Coefficient	0·36	0·46	0·48
Sorensen Coefficient	0·53	0·63	0·65
Percent Similarity	33·94	41·60	62·57
Dissimilarity	0·87	0·85	0·85
Morisita's Index	0·33	0·54	0·85
Horn's Index	0·47	0·62	0·77

high gradient mountain streams were absent or reduced in the regulated and recovery sites (e.g. stoneflies of the families Perlidae and Capniidae). Insects represented 98 per cent of the fauna at the reference site, 90 per cent at the regulated site, and 92 per cent in the recovery site (Figure 7).

The mean annual density at the regulated site was twenty times higher than at the reference site and slightly higher than the recovery site (Figure 7). In fact, the mean annual density of mayflies at the regulated site was higher than the mean annual density of the entire macroinvertebrate fauna in the reference site. Although ephemeropterans and dipterans had the highest relative abundances in the reference site, plecopterans, trichopterans, and coleopterans were well represented (Figure 7). The non-Insecta (e.g. Mollusca, Annelida, and Nematoda) was the only poorly represented group in the reference site. Plecoptera, Trichoptera, and Coleoptera were either rare or absent in the regulated site, which was numerically dominated by a few Ephemeroptera species and dipterans. Ephemeropterans and dipterans comprised 89 per cent of the total macroinvertebrate density in the regulated site. The relative abundances of ephemeropterans and dipterans were not significantly different in the recovery site compared to the reference site (p = 0·35). However, the proportion of Plecoptera and Coleoptera were significantly lower (p = 0·05) while the proportion of Trichoptera and non-Insecta were significantly higher (p = 0·05) in the recovery site compared to the reference site.

Mayflies in the reference site were represented by eleven species, five of which were abundant. In the regulated site, however, only two mayfly taxa (*Baetis* spp. and *Ephemerella infrequens*) were abundant while three were rare. Heptageniid mayflies, absent at the regulated site in this study, are often eliminated in regulated streams (Armitage *et al.*, 1987; Ward and Stanford, 1979b; Ward, 1982). Mayflies in the recovery site were represented by six abundant and nine rare species, including three heptageniid mayflies (*Cinygmula ramaleyi, Epeorus longimanus*, and *Epeorus memorialis*).

The reference site was represented by a diverse fauna of stoneflies (approximately fifteen species) with similar relative abundances. However, only rare individuals of *Amphinemura banksi*, two chloroperlid, and three isoperlid species represented the stonefly taxa at the regulated site. A general reduction in stoneflies and the occasional appearance of *Amphinemura* and *Isoperla* is common below dams in Colorado (Ward and Short, 1978; Zimmermann and Ward, 1984). Eight stonefly species were collected at the recovery site; however, only two (*Amphinemura banksi* and *Pteronarcella badia*) were consistently represented in samples.

The reference site was represented by twelve species of caddisflies, including relatively abundant populations of *Arctopsyche grandis* and *Rhyacophila acropedes*. Trichopterans at the regulated site, however, were represented by nine rare and three slightly more abundant caddisflies (*Hydoptila* sp., *Brachycentrus americanus*, and *Hesperophylax designatus*). The abundance of net-spinning caddisflies was significantly reduced in the regulated site compared to both reference and recovery locations (p = 0·05), as has been reported by several workers (Armitage and Capper, 1976; Müller, 1962; Ward, 1987).

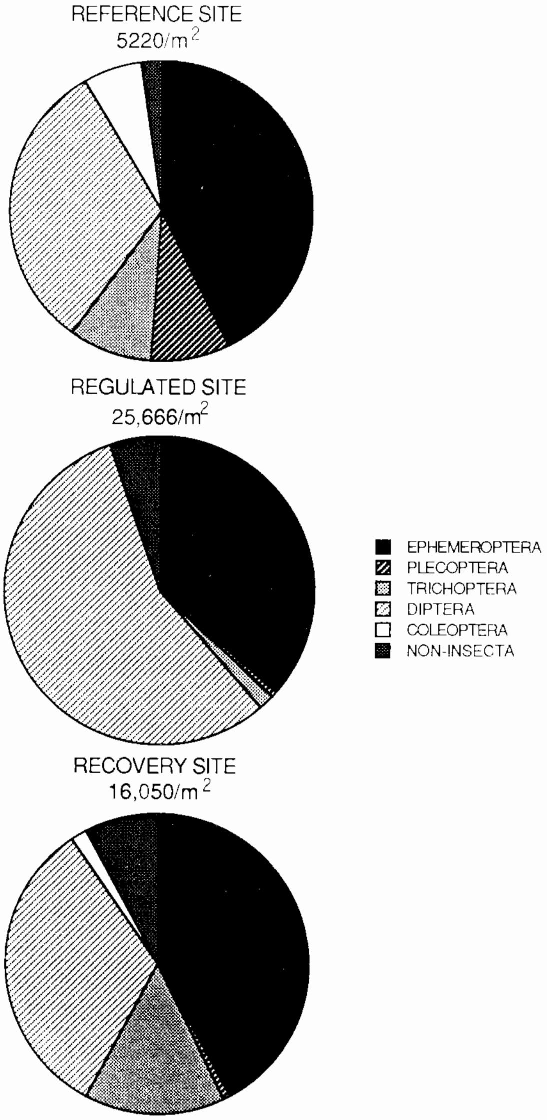

Figure 7. Percentage composition of major macroinvertebrate taxa based on density estimates at each site. Mean annual density values are indicated above each diagram.

The thirteen species of Trichoptera in the recovery site included four of the most abundant species of macroinvertebrates at that site: *Glossosoma ventrale*, *Brachycentrus americanus*, *Lepidostoma ormeum*, and *Oligophlebodes minutus*. Ward (1987) summarized the effects of regulation on Trichoptera in Rocky Mountain streams and concluded that *Rhyacophila* and *Hydropsyche* were the only genera commonly occurring at both regulated and reference locations, whereas *Brachycentrus*, *Glossosoma*, *Arctopsyche*, and *Lepidostoma* were often reduced or absent in regulated segments. With the exception of *Brachycentrus americanus*, which was significantly more abundant in the regulated and recovery sites, compared to the reference site ($p = 0{\cdot}05$), data from this study concur with previous conclusions concerning the influence of regulation on Trichoptera (Ward, 1987).

Riffle beetles in the family Elmidae, the only coleopterans collected in this study, were absent from the regulated site and significantly reduced in the recovery site ($p = 0{\cdot}01$). The mean annual density of coleopterans was three times greater in the reference site compared to the recovery site.

Chironomids and simuliids were the most abundant dipterans at all three sites. Chironomid mean annual density at the regulated site was an order of magnitude higher than the reference site and three times higher than at the recovery site. The abundance of simulids was not significantly different between sites ($p > 0{\cdot}35$). Dipterans in the family Blephariceridae were present in the reference site but absent at both locations below the dam. Ward (1976) noted the same distributional pattern for blephariceridae in the South Platte River.

The major non-insects in the regulated site were *Hydra* sp., zooplankton from the reservoir, ostracods, water mites, and oligochaetes. Oligochaetes, water mites and the triclad *Polycelis coronata* were the abundant non-insects in the recovery site, whereas this category contained only water mites and *Polycelis coronata* at the reference site (Figure 7).

The regulated site in this study conforms with other intensely regulated streams below deep-release dams which are also characterized by the absence of heptageniid mayflies, reductions in stoneflies and net-spinning caddisflies, and high abundances of baetid and ephemerellid mayflies, chironomids, and non-insect taxa (e.g. Armitage *et al.*, 1987; Petts, 1984; Ward and Stanford, 1979b; Ward, 1982).

The trophic structure of the macroinvertebrate assemblage, based on functional feeding groups (Merritt and Cummins, 1984), was altered by stream regulation. The relative abundance of shredders ($p = 0{\cdot}01$) and to a lesser extent predators ($p = 0{\cdot}05$) was significantly reduced in the regulated site compared to the recovery and reference sites (Figure 8). Reductions in nemourid stoneflies and shredding caddisflies (e.g. *Lepidostoma*) accounted for the lower relative abundance of shredders, whereas the absence of stonefly predators (e.g. Perlidae) accounted for the reduction in predators. Predators in the regulated site consisted primarily of empidids and other dipterans, whereas stoneflies were the dominant predators in the reference site. Stoneflies, dipterans, and *Polycelis coronata* were the abundant predators in the recovery site.

Black flies and net-spinning caddisflies accounted for the highest relative abundance of filterers in the reference site (Figure 8). The relative abundance of filterers was higher in the regulated site compared to the recovery site ($p = 0{\cdot}05$) because of slightly more abundant populations of black flies and much higher densities of *Hydra* spp. *Arctopsyche grandis* density was very low at the regulated site. Although the densities of net-spinning caddisflies began to increase in the recovery site compared to the regulated site, both simuliid and *Hydra* densities decreased. High densities of glossomatid caddisflies, which were rare in both the regulated and reference sites, accounted for the high relative abundance of scrapers in the recovery site. Relatively dense populations of hydroptilid caddisflies accounted for the significantly higher relative abundance of algal piercers in the regulated site compared to the reference and recovery sites ($p = 0{\cdot}01$). Data from several regulated streams below deep-release reservoirs in Colorado showed reductions in the relative abundance of trichopteran shredders, scrapers, and collectors, and increases in filter-feeders and predators (Ward, 1987). The abundant Trichoptera in the regulated site in this study were primarily scrapers/collector-gatherers and filter-feeders. Shredders and predators were significantly reduced ($p = 0{\cdot}05$) in the regulated site compared to the reference and recovery sites in this study.

CONCLUSIONS

Studies of macroinvertebrate communities in regulated streams may provide considerable insight into the ecological requirements of the benthic fauna (Armitage, 1984; Ward, 1982; Ward and Stanford, 1979b). Figure 11 outlines several factors important to macroinvertebrates which may be altered in streams below deep release storage reservoirs. Factors which probably had no influence or a minor influence on the macroinvertebrate assemblage below Granby Reservoir are indicated using dashed lines. Factors with potentially strong effects are indicated with solid lines. Water chemistry is excluded because the three sites were generally similar, and because no extreme or adverse chemical conditions are known to occur.

The following major features characterize the macroinvertebrate community at the regulated site: (1) absence of heptageniid mayflies, (2) reductions of net-spinning caddisflies, (3) reductions in shredders, and (4) reductions in predaceous stoneflies. The factors potentially responsible for each of these differences will be discussed in turn.

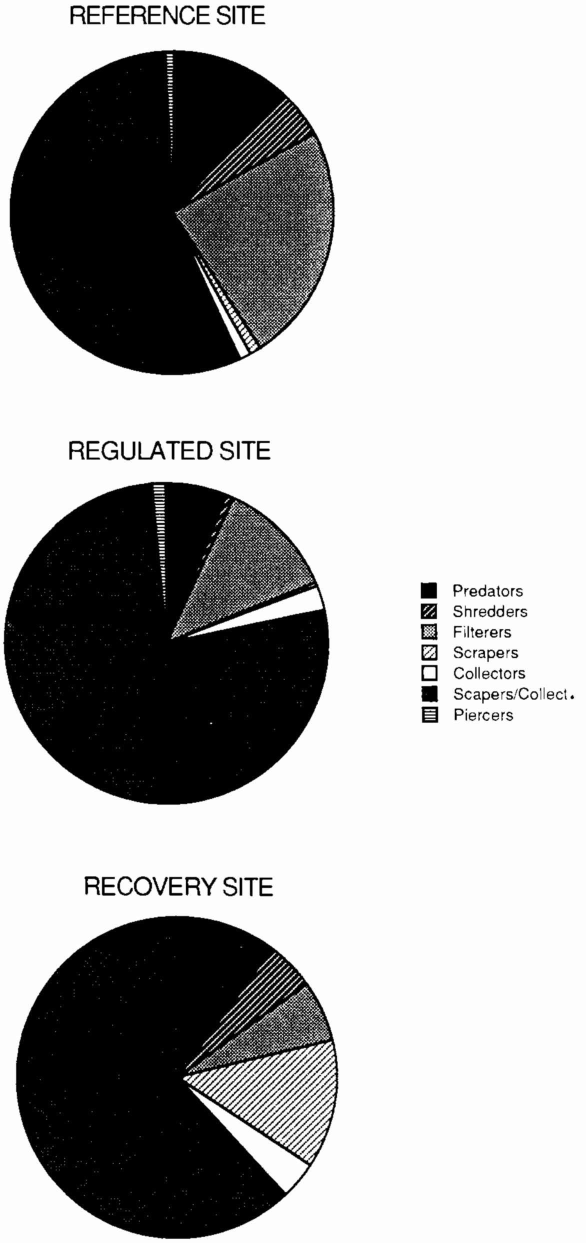

Figure 8. Relative abundance of macroinvertebrate functional feeding groups based on density estimates at each site. Species not examined for food habits are assigned to categories based on Merritt and Cummins (1984) for insects and Pennak (1978) for non-insects.

Food availability for scraper/collector-gatherers probably did not contribute to the absence of heptageniid mayflies at the regulated site. Although amounts of sedimentary detritus were reduced and seasonal fluctuations altered, stable substrate conditions enhanced periphyton growth and, therefore, food availability. Blephariccerids, which were absent below the dam, may be limited by an absence of clean rock surfaces due to the abundance of moss and periphyton in the regulated and recovery sites. Ward (1976) suggested that blephariccerids, which utilize hydraulic suckers for movement, were absent below Cheesman Reservoir because of thick growths of *Cladophora*. Recently, Dudley *et al.* (1986) have

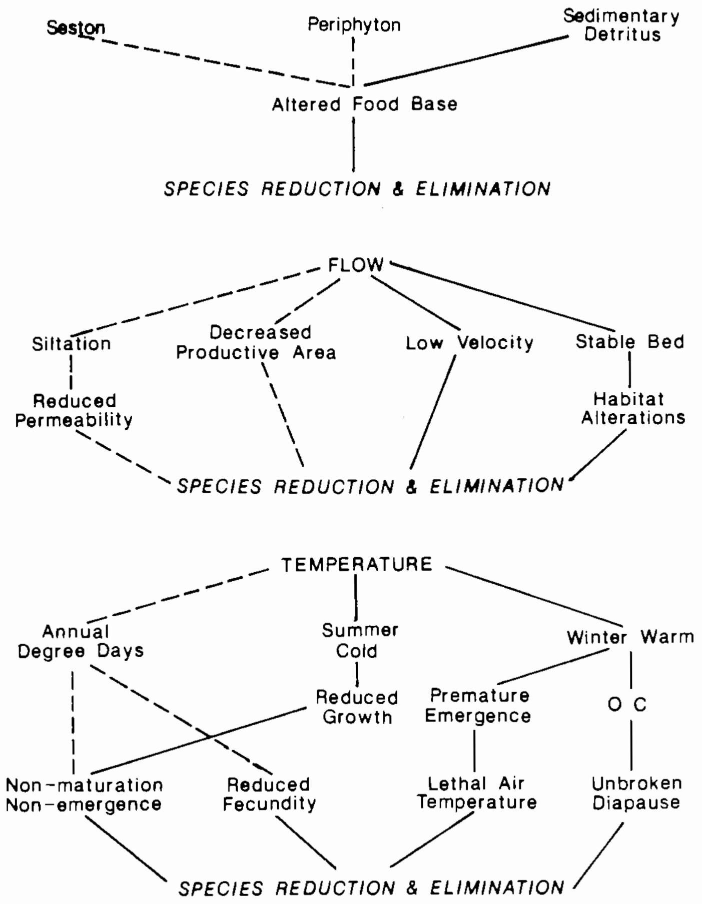

Figure 9. Summary of the major factors that may lead to the reduction or elimination of particular species of macroinvertebrates in lotic reaches below hypolimnetic release storage reservoirs. Interactions suggested as largely responsible for the altered macroinvertebrate community in the regulated site of the present study are indicated by solid lines (modified from Ward and Stanford, 1979b).

demonstrated that both blepharicerids and simuliids were associated with bare substrate and could not occupy habitats modified by abundant growths of macroalgae.

Both summer cold and winter warm conditions may have prevented heptageniid populations from becoming established in the regulated site. Critical temperatures necessary to initiate development, maturation, or emergence may never be reached because of summer cold temperatures (Ward and Standford, 1982). Even when maturation and emergence is attained, the developmental process may be delayed, preventing its completion; or fecundity may be reduced (Lemkuhl, 1974). Winter warm temperatures may increase growth rates, or truncate or eliminate diapause periods which can result in premature development and emergence into lethal (cold) air temperatures (e.g. Rupprecht, 1975). In addition, winter warm temperatures may eliminate species that require winter chill (0°C) to break egg or larval diapause (e.g. Lehmkuhl, 1972). Therefore, winter warm and summer cold conditions probably had an important influence on heptageniid populations and the macroinvertebrate assemblage in general.

Summer cold conditions often reduce the number of annual degree days below hypolimnetic release reservoirs compared to unregulated sites (e.g. Ward and Stanford, 1979b). The number of annual degree days may have an important influence on macroinvertebrate development, maturation, and body size (Ward and Stanford, 1982). However, the number of annual degree days in the regulated site below Granby Reservoir was higher compared to the reference site. Therefore, the influence of a reduced number of degree days in the regulated site appeared unimportant. However, the seasonal distribution of degree days was altered by regulation, which may be an important difference between sites.

Food availability may not have influenced the reduction of net-spinning caddisflies in the regulated site because of the abundance of zooplankton and phytoplankton. However, summer cold and winter warm conditions may have influenced their distribution and abundance. Also, increased bed stability with corresponding habitat alterations (thick mats of filamentous algae) may have reduced microcurrent velocities and, therefore, net-spinning caddisfly habitat. Net-building caddisflies have preferred current velocities in relation to net construction, and many species will not spin nets below a certain velocity (Edington, 1965).

Thermal alterations and food limitations may account for the reduction of shredders, both stoneflies and caddisflies, in the regulated site where decomposing filamentous algae and some leaf material were the primary food resources. Although the standing crop of detritus was low at the regulated site, the failure of the spring pulse of detritus to correspond with the growth and maturation of shredders may also be important. Therefore, the timing of food availability and food abundance may have had an adverse effect on shredder populations in the regulated site.

Perennially high abundances of baetid mayflies and chironomid larvae indicated that food availability was not limiting for predatory stoneflies (e.g. Perlidae) in the regulated site. Despite abundant food resources, winter warm and summer cold conditions probably accounted for the reduction of predatory stoneflies in the regulated site. Predatory stoneflies are often absent in regulated streams even where conditions other than temperature are favourable (Lehmkuhl, 1972; Ward, 1976; Ward and Short, 1978).

Based on the results of this study and other work done below Granby Reservoir (Ward, 1984), it appears that most environmental conditions (flow, water quality, periphyton, and seston) were favourable for the macroinvertebrate assemblage at the regulated site. In fact, Ward (1984) concluded that the braided stream channel below Granby Dam provide thermal refugia that could account for the maintenance of small populations of species that would be unable to complete their life cycles if confined to the thalweg. Annual and diel temperature patterns of the side channels are probably comparable to those of unregulated streams.

Alterations of temperature, microhabitat and detrital input probably had the greatest influence on the elimination and reduction of species in the regulated site. Both the downstream increase in species diversity corresponding to the downstream recovery of the thermal regime, and the primarily favourable conditions prevalent below the dam, suggested that temperature (winter warm and summer cold conditions) was the single most important factor accounting for alterations in the macroinvertebrate assemblage in the regulated site.

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