EPHEMEROPTERA OF THE GUNNISON RIVER, COLORADO, U.S.A.

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ABSTRACT

Samples were taken year-round at eleven sites (2900–1400 m a.s.l.) along the Gunnison River, a 329 km long tributary of the Colorado River, to examine the longitudinal distribution of Ephemeroptera and to assess the response of the mayfly fauna to dams in the headwaters and middle reaches. Nymphal abundance increased from headwaters (791 organisms and 333 mg dry weight m^{-2} at Site 1) to lower reaches (2610 organisms and 873 mg at Site 11). Abundance was slightly elevated immediately below the headwater dam (Site 2) whereas damming the middle reaches greatly reduced mayfly density and biomass. Five families (Baetidae, Ephemerellidae, Heptageniidae, Leptophlebiidae, Tricorythidae) comprised from > 98% to 100% of the mayfly fauna at each site. Leptophlebiids and tricorythids were abundant only in the lower reaches. Mayfly species richness exhibited a unimodal pattern with the maximum at Site 4. Both headwater and middle reach dams greatly reduced species richness immediately downstream. Scrapers and collector-gatherers comprised the majority of the mayfly fauna at all sites. Filter-feeders were abundant only at Site 11 where *Traverella albertana* attained high densities.

INTRODUCTION

The Gunnison River system in the Rocky Mountains of Colorado provided an opportunity to examine longitudinal patterns of lotic zoobenthos over an extensive elevation gradient. In addition, dams in the headwaters and middle reaches allowed analysis of faunal responses to impoundment and subsequent spatial recovery. A study of physicochemical conditions, including dissolved and particulate organic carbon dynamics, provided a detailed data base of habitat conditions along the longitudinal profile (Stanford and Ward 1983).

The purpose of this paper is to examine the altitudinal distribution of Ephemeroptera along the Gunnison River system and the differential responses of the mayfly fauna to damming upper and middle reaches.

STUDY AREA

The Gunnison River heads (as the Taylor R.) on the Western Slope of the Continental Divide (38°50'N, 106°25'W) at 3609 m a.s.l. and drops 2224 m in 329 km to its confluence with the Colorado River at 1385 m a.s.l. The upper basin (above the Black Canyon) is mesic and consists of relatively insoluble crystalline bedrock, whereas the lower basin drains the mineral-rich sedimentary formations characterizing the semi-arid Colorado plateau.

Taylor Park Reservoir in the upper basin (Fig. 1) is a deep-release storage impoundment. A series of three deep-release reservoirs occur in the middle reaches. Crystal Reservoir serves as a re-regulation unit to dampen the extreme flow fluctuations resulting from hydropower generation from Blue Mesa and Morrow Point Reservoirs.

I.C. Campbell (ed.) Mayflies and Stoneflies, 215–220.

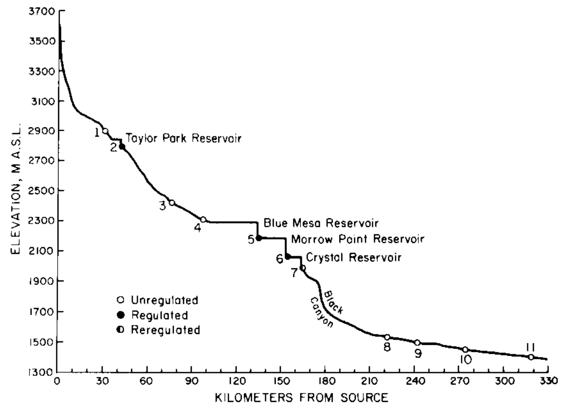

Fig. 1. Longitudinal profile of the Gunnison River system, Colorado, showing sampling sites.

METHODS

Sampling locations were selected to enable examination of the fauna from three perspectives. Unregulated sites (open circles in Fig. 1) were situated above reservoirs of a sufficient distance below dams (Site 3 was 33 km below Taylor Park Dam; Site 8 was 56 km below Crystal Dam) to eliminate or minimize the effects of stream regulation (Ward and Stanford 1984). In addition, major tributaries enter the river below the dams (the East R. between Sites 2 and 3; the North Fork between Sites 7 and 8; the Uncompahgre R. between Sites 8 and 9). The presupposition was that these "unregulated" sites contained a mayfly fauna not unlike the preimpoundment community at those locations. Regulated sites (solid circles) were selected to analyze the response of lotic ephemeropterans to the altered environmental conditions induced by upstream impoundment. The reregulated site (hybrid circle) allowed an assessment of the ecological efficacy of this ameliorative strategy.

Sampling was conducted on eleven occasions

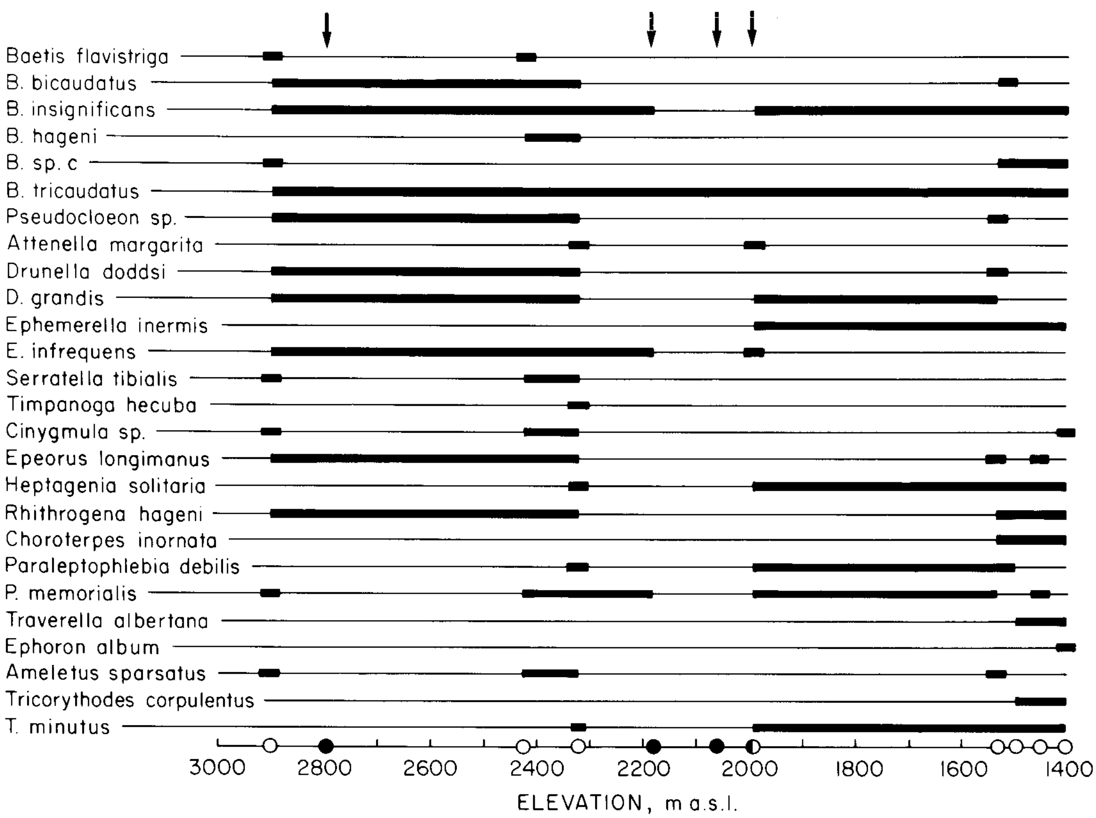

Fig. 2. Altitudinal distribution of mayflies, Gunnison River, Colorado. Locations of sampling sites (2900–1400 m a.s.l.) indicated by circles near bottom of figure ((symbols as in Fig. 1). Arrows indicate locations of dams. Reservirs considered dimensionless points on this figure.

during the period September 1979 to October 1980. Sampling was confined to rubble-boulder riffles at each site. Because of the coarse nature of the substrate, a special sampling device was used. The device is essentially a large Surber-type sampler, employing 150 μm mesh, that delineates 0.5 m^2 of substrate (Hauer and Stanford 1981). Three 0.5 m^2 samples were collected at each site.

RESULTS

Five families (Baetidae, Ephemerellidae, Heptageniidae, Leptophlebiidae, Tricorythidae) comprised from > 98% to 100% of total mayflies (by numbers and biomass) at each sampling site. Twenty-six mayfly species were identified (Fig. 2), a species richness comparable to that reported for a pristine river system in Colorado (Ward 1986). In the ensuing discussion, the mayfly fauna of unregulated and regulated (including reregulated) sites are treated separately.

Longitudinal patterns at unregulated sites

Species diversity at unregulated sites (solid line in Fig. 3) exhibited a unimodal pattern with the maximum at Site 4. Fifty percent of the mayflies were upper basin species, being restricted to or abundant only at upper basin sites (e.g. *Drunella grandis,* Fig. 4). Nine mayflies were lower basin species (e.g. *Traverella albertana,* Fig. 4). Only four species were abundant at both upper and lower basin sites (*Baetis tricaudatus, B. insignificans, Rhithrogena hageni* and *Paraleptophlebia memorialis*). *B. tricaudatus,* the most abundant species of both upper and lower basins, was the only mayfly that occurred at all eleven sites.

Total density and biomass values exhibited similar longitudinal patterns (Fig. 3). When mayfly density and biomass for unregulated upper basin sites (means of Sites 1, 3 and 4) are compared with unregulated lower basin sites (means of Sites 8-11), composite values are *ca.* three times greater for the lower basin (659 versus 2180 nymphs m^{-2}; 259 versus 745 mg dry weight m^{-2}). Higher values for the lower basin result

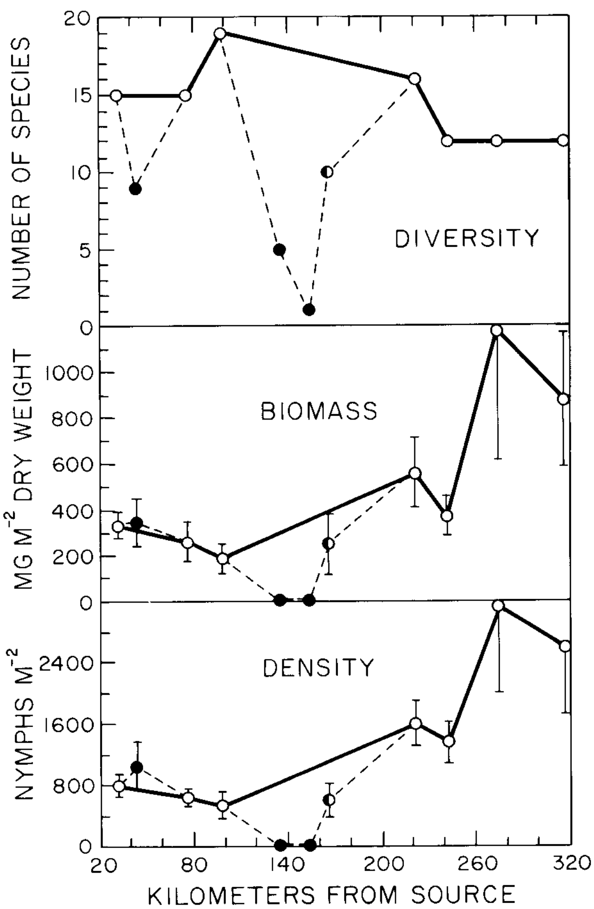

Fig. 3. Total diversity (cumulative species richness), and biomass and density values ($\bar{x} \pm 1$ s.e.) for the mayfly fauna, Gunnison River, Colorado. Site symbols as in Fig. 1.

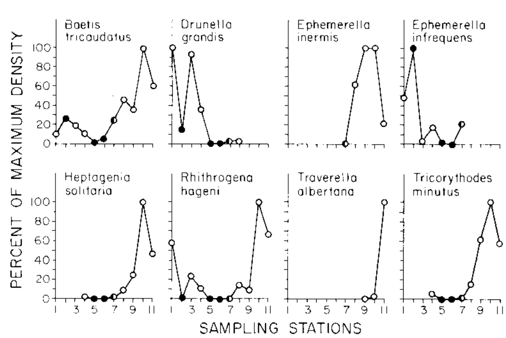

Fig. 4. Spatial patterns of relative abundance for selected mayflies, Gunnison River, Colorado. Site symbols as in Fig. 1.

both from the high densities attained by some lower basin species (e.g. *T. albertana, T. minutus)* and from the downstream increases exhibited by abundant euryzonal species (e.g. *B. tricaudatus* means of 256 m^{-2} and 167 m^{-2} for upper and lower basins). Euryzonal species all exhibited density maxima at Sites 10 or 11.

Response to regulation

If the solid lines in Fig. 3 approximate unregulated conditions, deviations from these longitudinal patterns (the dashed lines) are attributable to stream regulation (*sensu* Ward and Stanford 1979). Mayfly diversity was reduced from 15 species at Site 1 to 9 species at Site 2 below the headwater storage reservoir, but returned to the original level by Site 3. Most of the species missing from Site 2 were rare at Site 1; mean densities ranged from 1 nymph m^{-2} (*Serratella tibialis* and *Baetis* sp. C) to 40 nymphs m^{-2} (*Cinygmula* sp.). Several additional species were considerably reduced, but not eliminated below the headwater dam (*D. grandis* and *R. hageni,* Fig. 4). Three additional species, none of which were abundant, exhibited similar (low) densities at Sites 1 and 2. The small increases in total mayfly biomass and density below the headwater dam (Fig. 3) are attributable to two very abundant species that more than doubled in density from Site 1 to Site 2 (*B. tricaudatus* and *E. infrequens,* Fig. 4). Note that Fig. 4 shows relative, not absolute abundances. Overall, baetids and ephemerellids increased from Site 1 to Site 2, whereas heptageniids decreased.

The dams of the middle reaches had a much greater effect on the mayfly fauna (Fig. 3). Only four species were collected at Site 5 below Blue Mesa Reservoir, all at mean densities much less than 1 nymph m^{-2}. Below Morrow Point Reservoir only *B. tricaudatus* remained.

Argyle and Edmunds (1962) collected mayflies from eight locations in the segment of the Gunnison River now inundated by Blue Mesa and Morrow Point Reservoirs. In spite of the limited duration (28 June – 19 July 1961) of their study, the preimpoundment mayfly fauna is remarkably similar to the species we found at unregulated Site 4 (Fig. 2). *Drunella doddsi* and *Paraleptophlebia,* reported only from tributaries in the preimpoundment study, most certainly also occurred in the Gunnison River. It appears, however, that *Epeorus albertae* and the two unidentified species of *Heptagenia* found by Argyle and Edmunds (1962) no longer occur in the mainstream.

A much more diverse and abundant mayfly fauna occurred below Crystal Reservoir than the other two regulated sites of the middle reaches (Fig. 3). *B. tricaudatus* (491 nymphs m^{-2}) and *E. infrequens* (101 nymphs m^{-2}) were the most abundant species at Site 7 below the reregulation dam. Most of the species present at Site 7 continued to increase in abundance downstream, although Site 7 was the lower distributional limit for *E. infrequens* which was replaced by *E. inermis* at Sites 8-11 (Figs 2, 4).

Scrapers and collector gatherers comprised virtually 100% of the mayfly functional feeding groups at all but Site 11 where the filter feeder *Traverella albertana* attained maximum abundance (Fig. 5). There is a tendency for decreased importance of mineral scrapers at sites below dams, a common functional response to stream regulation (Ward 1987), but the trend is not consistent for Gunnison River Ephemeroptera.

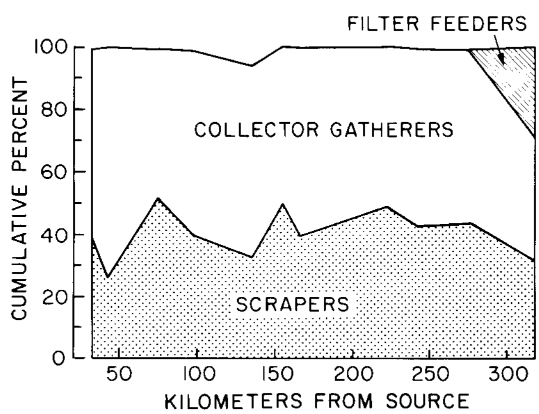

Fig. 5. Relative abundance of filter feeders, collector gatherers, and scrapers for the mayfly fauna, Gunnison River, Colorado.

DISCUSSION

The diversity curve of Ephemeroptera at unregulated sites (solid line, Fig. 3) conforms to the longitudinal pattern of biotic diversity proposed by the River Continuum Concept (Vannote *et al.* 1980); deviation from that pattern at regulated locations (dashed lines, Fig. 3) generally corresponds to the predictions of the Serial Discontinuity Concept (Ward and Stanford 1983).

The moderate depression of diversity below the deep-release storage reservoir in the upper reaches is largely attributable to altered temperature, substratum, and trophic conditions (Ward 1982, Ward and Stanford 1982). In addition, flow constancy, substrate stability, clear water, and winter warm conditions resulted in dense accumulations of periphyton below the dam to the detriment of species, such as *Drunella doddsi* and heptageniids, that are adapted to "clean" rock surfaces (Ward 1976a, Dudley *et al.* 1986).

The virtual elimination of mayflies at sites below hydroelectric dams in the middle reaches (Fig. 3) is indicative of the dramatic short-term flow fluctuations (Ward 1976b). The substantial recovery at Site 7 below the reregulating dam demonstrates the ecological efficacy of this ameliorative strategy in this situation.

Differences in total mayfly abundance between unregulated upper and lower reaches (solid lines, Fig. 3) correspond to the cool, oligotrophic character of the upper basin and the warmer, richer trophic conditions at sites in the lower basin. Indeed mean annual particulate organic carbon (seston) increased from 0.20 mg l^{-1} below the last dam to 0.80 mg l^{-1} at Site 9. Slightly elevated abundance values below the upper basin dam reflect large population increases by those few species favoured by the altered conditions, presumably including reduced predation and competition. The extreme environments below the hydroelectric dams in the middle reaches, however, were colonized by small numbers of only the most tolerant species. Below the reregulation dam, abundance values had recovered to levels comparable to those obtaining at unregulated upper basin sites.

The preimpoundment Gunnison River system was clearly divided into an upper rhithron segment and a lower potamon segment. This general pattern remains, but rhithron conditions have been considerably displaced downstream. The dams of the middle reaches have transformed much of the lower basin from warm, turbid potamon habitat to cool, clear rhithron conditions. This is clearly reflected by the fish fauna (Stanford and Ward 1986). Based solely on temperature, the prime determinant of Illies and Botosaneanu's (1963) zonation scheme, the rhithron/potamon boundary has shifted from the vicinity of Site 6 to Site 8, a discontinuity distance (*sensu* Ward and Stanford 1983) of 68 km involving a drop in elevation of over 500 m.

Although basin-wide preimpoundment data are unavailable for lotic zoobenthos, it is likely that their response to regulation was similar to that of the fishes (Stanford and Ward 1986). Prior to damming the Gunnison River, the typical rhithron fishes (salmonids) were largely restricted to the upper basin; the lower basin was occupied by endemic potamon species. Now salmonids are well established in the lower basin and the specialized potamon species are absent or restricted to the lowermost reaches.

Several typical rhithron mayflies extend well into the lower basin, some reaching Site 11 and one even attaining maximum abundance in the lower basin (*R. hageni,* Fig. 4). *Traverella albertana,* the only common potamon mayfly collected, is now restricted to the lowermost sites and is abundant only at Site 11 (Fig. 4). This species extends at least 150 km up the Colorado River above its confluence with the Gunnison River (Ward *et al.* 1986), and it is likely that it was once abundant over most of the lower basin of the Gunnison. One of the most remarkable riverine mayfly communities known occurred in the Green River, another major tributary of the Colorado (Edmunds 1973). That unique community was eliminated as its habitat was altered by stream regulation. We will probably never know whether the lower basin of the Gunnison once supported a similar highly-specialized riverine mayfly community.

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