

Influence of impoundments on mayfly diets, life histories, and production

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Abstract. We investigated the influence of stream regulation on the dietary composition, life histories, and production of four mayfly species (*Drunella grandis*, *Ephemera infrequens*, *Paraleptophlebia heteronea*, and *Baetis tricaudatus*) at three sites in the Upper Colorado River. Sites (unregulated, intensely regulated, and recovery) were selected based upon degree of regulation (i.e., upstream, 0.4 km downstream, and 4.0 km downstream from a deep-release reservoir). Although levels of food abundance (diatom density and sedimentary detritus) varied between sites, the dietary compositions of *B. tricaudatus* (primarily diatoms) and *P. heteronea* (detritus) did not change. However, *D. grandis* and *E. infrequens* consumed diatoms downstream from the reservoir whereas their diet was strictly detritivorous at the upstream site. The number of degree days and mean annual water temperatures at the downstream sites were greater than at the free-flowing unregulated site. *Baetis tricaudatus* responded to regulated conditions by higher rates of development, altered voltinism, and extended emergence. *Ephemera infrequens* and *P. heteronea* were univoltine at each site. However, development of *E. infrequens* and *P. heteronea* was poorly synchronized and emergence was extended at both downstream sites. *Drunella grandis* was univoltine and well synchronized with a short emergence period at each site. Life history flexibility, in rates of egg development, growth, maturation, and emergence, at the population level may be determined by a lack of dependence by individuals upon temperature or photoperiod cues to synchronize the developmental process. Annual production estimates at downstream sites were higher for all four species than at the upstream site. Annual production of *D. grandis* (15.38 g/m²) at the recovery site and of *E. infrequens* (15.89 g/m²) at the regulated site are the highest production estimates recorded for mayflies.

Key words: stream regulation, mayflies, production, life histories, diet composition.

Dams alter, to various degrees, the dominant abiotic variables (flow and temperature) of streams and rivers (e.g., Ward and Stanford 1979a). Production data for invertebrates from lotic habitats below impoundments have been determined primarily for filter-feeding caddisflies below surface-release reservoirs (Macfarlane and Waters 1982, Parker and Voshell 1983, Richardson 1984, Voshell and Parker 1985, Mackay and Waters 1986). Only a few studies have included estimates of mayfly production in regulated rivers (McClure and Stewart 1976, Macfarlane and Waters 1982, Perry et al. 1986) despite the numerical dominance of mayflies below most reservoirs (e.g., Ward and Stanford 1979b) and their importance as food for drift-feeding fish (Hynes 1970). We are not aware of any studies specifically designed to determine the influence of stream regulation on mayfly production below deep-release, storage reservoirs.

Both temperature and nutritional alterations in stream reaches below reservoirs can influence life history patterns of lotic macroinvertebrates (Nebeker 1971, Ward and Stanford 1982, Raddum 1985), including stoneflies (Radford and Hartland-Rowe 1971, Vaught and Stewart 1976), caddisflies (Rhame and Stewart 1976, Mackay 1979, 1984, Hauer and Stanford 1982, Parker and Voshell 1983) and mayflies (Konratieff and Voshell 1981, Perry et al. 1986). However, species-specific life history responses of macroinvertebrates to stream regulation are difficult to predict and are probably most critically related to altered temperature patterns. Although stream regulation may alter macroinvertebrate food resources, such as periphyton composition (Lowe 1979) and detritus standing crop (Webster et al. 1979), the effect of such alterations on mayfly diet has not been investigated.

The objective of this study was to relate differences in production, life history patterns and diet composition of four mayfly species to temperature, flow, and food at an unregulated ref-

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erence site and two regulated sites located downstream from an impoundment on the upper Colorado River.

Study Sites

The study was conducted in the upper Colorado River in the vicinity of Granby Reservoir (Fig. 1), a large (666 km³) deep-release storage reservoir. Three sampling sites were selected that had similar characteristics except for the influence of stream regulation. All three sites were in rubble riffles of similar gradient (0.006–0.009) and elevation (2426–2593 m a.s.l.), and were characterized by similar canopy cover, geology, and riparian vegetation.

A free-flowing reach (site 1) upstream from the impoundment 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 allow at least partial recovery from the impoundment. Table 1 summarizes various biological and physico-chemical comparisons among the sites (see Rader and Ward [1988] for further descriptions of study sites).

Methods

The life histories, production, and diets of *Ephemera infrequens* (McDunnough), *Drunella grandis* (Eaton), a *Baetis* species complex, and *Paraleptophlebia heteronea* (McDunnough) (abundant only at sites 1 and 3) were estimated at each site. Although the *Baetis* complex at each site comprised primarily *B. tricaudatus* (Dodds), a small number of adult *B. bicaudatus* (Dodds) and *B. insignificans* (McDunnough) were also collected at sites 1 and 3.

Population densities for production estimates were based on four Surber samples (240- μ m mesh) collected monthly at each site for one year (1983). Samples from introduced bricks were also used to increase replication (see Rader and Ward [1989] for methods used with artificial substrates). Each sample (Surber and bricks) was preserved in 5% formalin before and after sorting, identification, and enumeration.

Food quality was estimated by determining diatom densities and sedimentary detritus standing crop at each site. Diatom density and sedimentary detritus estimates were deter-

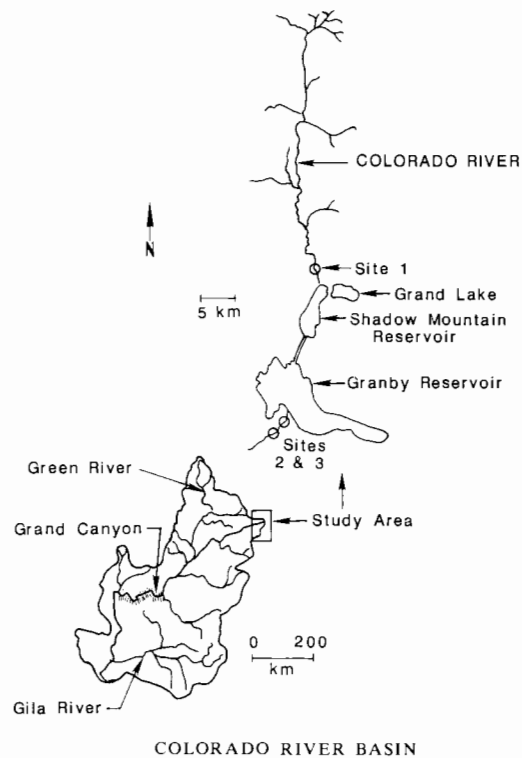


FIG. 1. The Colorado Basin showing the location of the upper Colorado River, Shadow Mountain Reservoir, Granby Reservoir, Grand Lake and the study sites.

mined by scraping a known area and by replicate cores from the stream bed, respectively (Rader and Ward 1988).

The size frequency method (Benke 1984) was used to estimate annual production of each species at each site. Following identification, all nymphs were divided into 0.1-mm interval size classes based on maximum head capsule width. Head capsule widths were measured with an ocular micrometer to the nearest 0.05 mm for large instars and 0.03 mm for small instars. The mean biomass of individuals within size classes was obtained by drying at least 10 individuals in larger size classes and at least 30 individuals in smaller size classes at 60°C for 48 hours. Biomass estimates were multiplied by a relatively small correction factor of 1.2 (Mortensen and Simonsen 1983) which corresponded to an approximately 15–20% weight loss due to preservation (Howmiller 1972, Dermott and Pater-son 1974). When necessary, annual production

TABLE 1. Biological comparisons at each site plus mean and ranges (in parentheses) of physico-chemical variables over the period of study.

Variable	Site 1	Site 2	Site 3
Simpson's diversity (macroinvertebrates)	0.93	0.69	0.87
Simpson's evenness (macroinvertebrates)	0.95	0.71	0.88
Number of taxa (macroinvertebrates)	62	43	61
Mean annual diatom density (No./mm ²)	143,900	3,380,500	120,900
Mean annual detritus standing crop (g AFDW/m ²)	1090	819	593
Dissolved oxygen (mg/L)	9.9 (7.6-9.9)	9.4 (7.1-11.4)	9.6 (7.3-11.5)
Free CO ₂ (mg/L)	0.7 (0.3-1.0)	1.4 (0.3-4.4)	0.1 (-5.0-0.8)
Bound CO ₂ (mg/L)	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)
Annual mean temperature (°C)	3.6 (0.0-18.0)	4.7 (1.8-9.8)	5.7 (0.0-17.2)
Daily flow (m ³ /s)	1.75 (0.1-10.2)	1.24 (0.6-4.0)	1.24 (0.6-4.5)

values were corrected to reflect the cohort production interval (CPI) (Benke 1979).

Head-capsule measurements used to calculate production estimates were also used to construct size-frequency plots for life history determinations. Although the *Baetis* complex was used to calculate production, only nymphs identified as *Baetis tricaudatus* were used in the life history analysis. Adult mayflies were collected with black-light traps during the summer and fall and by sweeping the riparian vegetation at monthly intervals to confirm species identifications and patterns of emergence. Nymphs with swollen, black wing pads were also used to confirm patterns of emergence.

Gut contents from the larger instars of each species collected during the summer and early autumn at each site were analyzed to determine diet. The fore-gut of sample individuals was dissected and the contents were teased onto a depression slide (after Cummins 1973). All material on the slide was dispersed in a beaker containing 25 ml of distilled water and then drawn onto a 0.45 µm Millipore filter. A drop of immersion oil was added to the filter which was allowed to clear for 24 hr before being mounted on a slide. The slide was scanned at 200× and 400× to identify food items as either detritus, diatoms, filamentous algae, or animal material. The percentage composition of food

material was determined from areal measurements using an ocular Whipple grid in ten fields per slide. Fields were chosen by randomly selecting microscope stage settings. After following the same procedure, Gray and Ward (1979) found that slide contents were adequately represented by ten fields; standard error estimates were less than 30% of the mean for each food category.

Results

Diets

The impoundment did not alter the dietary compositions of *Baetis* spp. and *P. heteronea*. *Baetis* spp. ingested primarily diatoms at each site with a small proportion of detritus, whereas *P. heteronea* ingested primarily detritus at each site with small proportions of diatoms (Fig. 2). *Drunella grandis* and *E. infrequens* ingested primarily detritus at site 1 (Fig. 2); however, in contrast to *Baetis* and *P. heteronea*, both species had different diets at the downstream sites where they had a greater proportion of diatoms in their guts. Filamentous green algae were rarely found in guts despite algal abundance at sites 2 and 3 (Rader and Ward 1988).

Mean annual diatom density was highest at site 1 and similar at sites 1 and 3 (Table 1). Diatom densities peaked in July at site 1, where-

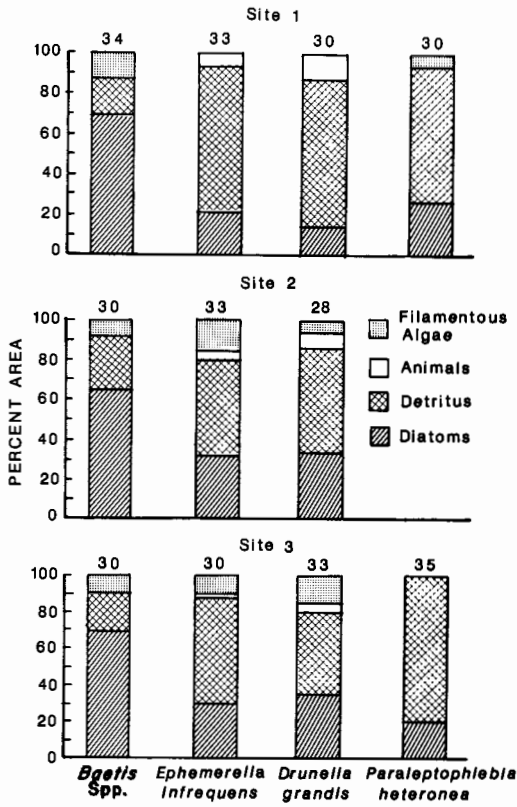


FIG. 2. Percent of area on microscope slides covered by each food type (diatoms, detritus, animal material, and filamentous algae) from guts of *Baetis* spp., *Ephemerella infrequens*, *Drunella grandis*, and *Paraleptophlebia heteronea* at each site. Numbers of individuals are shown above each bar.

as the highest diatom densities at the downstream sites occurred during winter. The annual mean standing crop of detritus was highest at the upstream site (Table 1). The largest standing crop of detritus occurred in the late fall (October) at site 1, whereas the highest values at the downstream sites occurred in the spring. More information concerning the algal flora and standing crop estimates for sedimentary detritus size categories can be found in Rader and Ward (1988).

Life histories

Baetis tricaudatus was univoltine at site 1; however, it appeared to be multivoltine (probably bivoltine) at both downstream sites (Fig. 3). A high frequency of early instars in August and

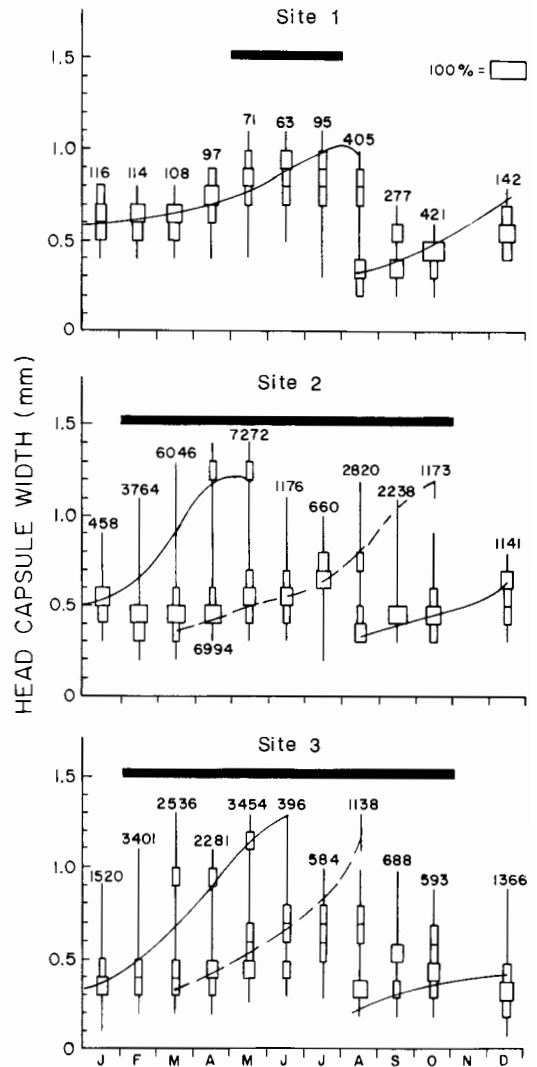


FIG. 3. Size-frequency distributions for *Baetis tricaudatus* at each site. Width of each bar represents the relative proportion of total animals found in a size class. Size classes of 10% or less are represented by a vertical line. Presence of adults is shown by a horizontal bar at the top of each graph. Numbers of individuals used to calculate frequencies are shown above or below each bar.

September characterized the univoltine life cycle at the upstream site (Fig. 3). Although *B. tricaudatus* populations were poorly synchronized at both sites below the dam, a distinct pulse of early instars appeared in August and September, and in March, April, and May (Fig.

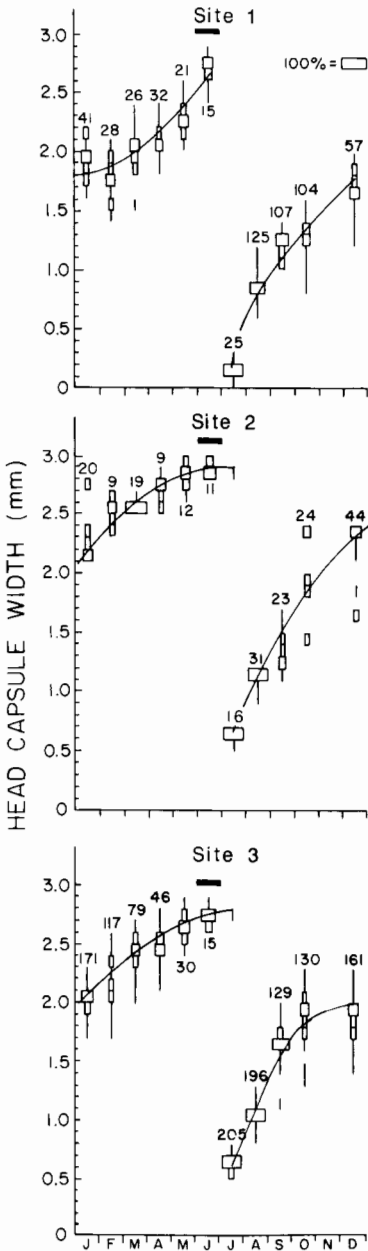


FIG. 4. Size-frequency distributions for *Drunella grandis*. For further description, see Figure 3 legend.

3). Both generations appeared to complete nymphal growth in about six months. Emergence occurred during May, June, and July at site 1, but was extended (February through October) at sites 2 and 3 (Fig. 3).

Growth patterns for *Baetis* at the downstream sites were more difficult to analyze because of

high population densities. If *Baetis* were univoltine, with several poorly synchronized cohorts, instead of bivoltine, then its production at the downstream sites would be reduced by half. However, based on our interpretation of the life history data, *Baetis* had a CPI equal to 6 mo and its production was multiplied by a correction factor of 2.

Drunella grandis was a univoltine, slow seasonal species (Clifford 1982) represented by a single well synchronized cohort at all three sites (Fig. 8). Therefore, a correction factor equal to 1 was used to calculate production for this species. *Drunella grandis* emerged at approximately the same time in June at all three sites (Fig. 4).

Paraleptophlebia heteronea and *E. infrequens* at sites 1 and 3 were also univoltine slow seasonal species (Figs. 5, 6), with a CPI equal to 12 mo. However, production of *E. infrequens* at site 2 was multiplied by a correction factor of 1.09 because its CPI there was equal to 11 months. Although both species were represented by a single poorly synchronized cohort at site 1, at the downstream sites they appeared to have two poorly synchronized cohorts (Figs. 5, 6). *Paraleptophlebia heteronea* early instars were abundant in July at site 1; however, at site 3 they were abundant in June and July and again in April and May (Fig. 5). *Ephemera infrequens* had a similar pattern with a single cohort at site 1 and two poorly synchronized cohorts at the downstream sites (Fig. 6). Emergence of both species was extended at the downstream sites compared with site 1.

The presence of two *Paraleptophlebia* species, rather than a single species with two cohorts, is an alternative explanation for the life history data in Figure 5. However, the only other *Paraleptophlebia* species identified (*Paraleptophlebia memorialis*) was too rare to produce the relatively large recruitment of nymphs found in either cohort at the downstream sites. At sites 2 and 3, *P. heteronea* had mean annual densities of 51 and 889 individuals/m², respectively, whereas *P. memorialis* had mean annual densities of 3.3 (site 2) and 4.0 individuals/m² (site 3).

Annual production

Production was higher for each species at the downstream sites compared with the upstream site (Table 2; *P. heteronea* was too rare at site 2

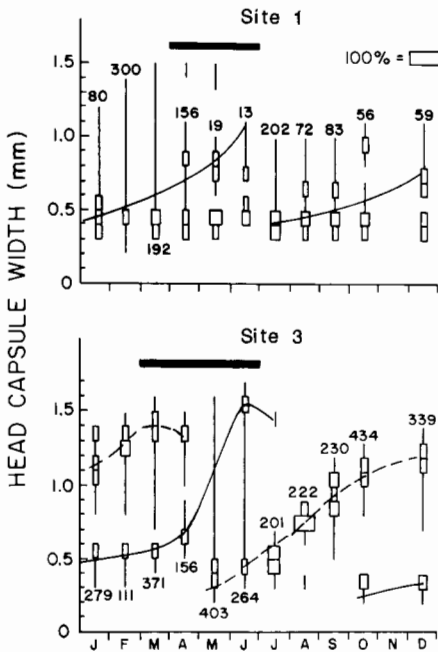


FIG. 5. Size-frequency distributions for *Paraleptophlebia heteronea*. For further description, see Figure 3 legend.

for production to be calculated). Maximum annual production for *Baetis* spp. and *E. infrequens* occurred at site 2 (Table 2). However, maximum annual production for *D. grandis* and *P. heteronea* occurred at site 3. Annual P/B ratios ranged from 2.6 for univoltine populations to 9.9 for the bivoltine *Baetis* population.

Discussion

Diets

Temperature patterns and food quantity and quality may influence rates of growth and development and therefore body size, voltinism, population density, and production (e.g., Anderson and Cummins 1979, Vannote and Sweeney 1980, Sweeney 1984, Sweeney et al. 1986). Even though food levels (diatom densities and detritus standing crops) varied from site to site, the diet composition of the baetid complex (algivorous) and *P. heteronea* (detritivorous) was consistent at each of the three sites. However, the proportion of diatoms consumed by *D. grandis* and *E. infrequens* nymphs below the dam was $\approx 2\times$ greater than at site 1 (Fig. 2). Although both species were almost exclusively detriti-

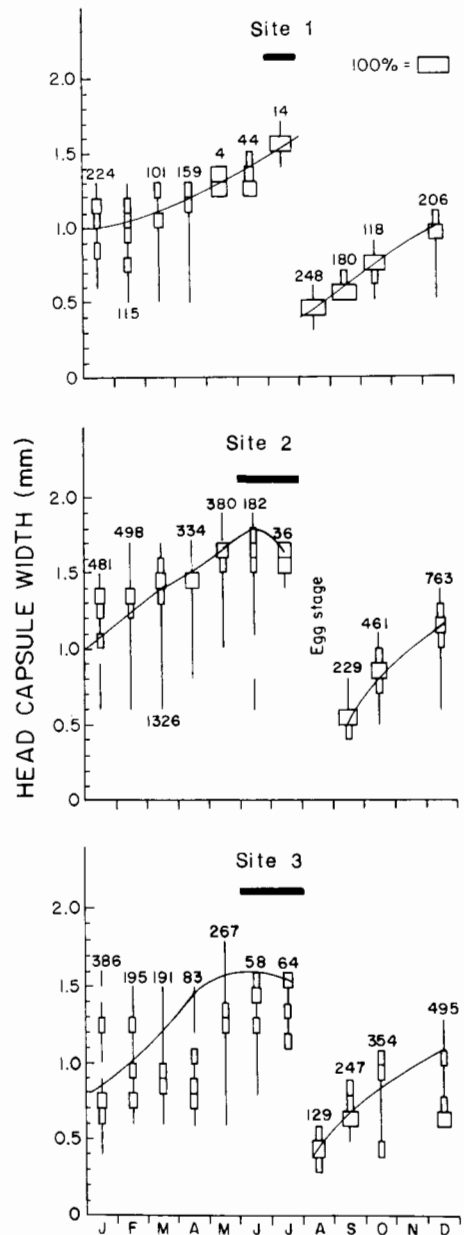


FIG. 6. Size-frequency distributions for *Ephemerella infrequens*. For further description, see Figure 3 legend.

vores in the upstream site, at the downstream sites they ingested a greater proportion of diatoms probably because of the increased availability of diatoms below the reservoir. The abundance of filamentous green algae at sites 2 and 3 (Rader and Ward 1988) may have altered micro-current velocities on the upper surfaces

TABLE 2. Production ($\text{g dry wt m}^{-2} \text{ yr}^{-1}$), mean standing crop (g/m^2) and P/B ratios for four mayfly species at the upstream site (1), and both downstream sites (2 and 3).

Species	Mean Biomass			Annual Production			Annual P/B		
	1	2	3	1	2	3	1	2	3
<i>Baetis</i> spp.	0.14	1.50	1.16	0.62	7.48	5.01	4.4	9.9	8.6
<i>E. infrequens</i>	0.50	4.96	1.18	2.29	15.89	3.96	4.6	3.2	3.4
<i>D. grandis</i>	1.58	2.37	3.36	6.90	9.26	15.38	4.4	3.9	4.6
<i>P. heteronea</i>	0.20	—	1.29	0.51	—	4.25	2.6	—	3.3

of substrates (Newbury 1984), allowing typically cryptic mayflies to move onto upper surfaces to strip entrained and epiphytic diatoms from algal filaments. Typically, lentic phytoplankton species from the reservoir were the most abundant diatoms found in the periphyton below the dam (Rader and Ward 1988).

Filamentous algae were rarely consumed despite their abundance below the dam. Since cell walls of filamentous algae are generally thick, nitrogen and lipid levels are low compared with microscopic diatoms (Lamberti and Moore 1984). Gray and Ward (1979) determined that filamentous algae (primarily *Cladophora*) had a calorific content approximately half that of allochthonous detritus. Filamentous algae may occasionally have been consumed while being stripped for epiphytic diatoms (Gray and Ward 1979); otherwise mayflies probably ignored living filaments as a food item.

Life histories

The thermal energy available for growth, maturation and emergence can be estimated by the number of annual degree days (Ward and Stanford 1982, Sweeney 1984). Annual degree-day accumulations (above 0°C) and mean annual temperatures, respectively, were 1330°C and 3.6°C in the reference site, 1729°C and 4.7°C in the regulated site, and 2082°C and 5.7°C in the recovery site. Winter-warm conditions accounted for the greater number of degree-days in the regulated and recovery sites, compared with the reference site which was ice covered for approximately five months of the year (Rader and Ward 1988). *Baetis tricaudatus* appeared to complete two generations below the dam compared with one at site 1. When other life history requirements have been met (e.g., critical threshold temperatures that break egg dia-

pause or initiate development and/or emergence) then the number of degree days may be the most important factor determining the number of generations produced by some aquatic insects. The number of degree days accumulated beyond threshold temperatures (Ward and Stanford 1982) may determine the number of generations produced. Increased degree days associated with winter warm conditions in springbrook habitats and warm rivers in general, often increase the number of generations for mayflies and other aquatic insects (Thorup and Lindegaard 1977, Newell and Minshall 1978, Freeman and Wallace 1984, Rutherford and Mackay 1986).

Development in three of the four species (*D. grandis* excluded) was poorly synchronized below the dam which probably accounts for the extended emergence patterns at the downstream sites compared with site 1. *Drunella grandis* development was equally synchronized at each site and its emergence was not extended or temporally displaced below the dam. Even when an additional number of degree days are available for development, specific temperatures or photoperiod cues may be required to initiate maturation and/or emergence (Peters and Peters 1977, LeSage and Harrison 1980, Ward and Stanford 1982, Sweeney 1984). Therefore, excess degree days (additional degree days beyond the number necessary to complete development) may not alter population synchronization and/or emergence patterns for some species.

Life history flexibility at the population level (flexibility in rates of egg development, growth, maturation, and emergence) may be determined by a lack of dependence by individuals upon specific temperature or photoperiod cues to synchronize the developmental process. Life history flexibility allows some mayfly popula-

tions to increase voltinism by increasing the rate of development in response to changing or unusual environmental conditions, such as the altered temperature regime below the dam. However, this flexibility may also impart certain disadvantages associated with poor population synchronization; for example, the largest numbers of males and females may not coincide temporally, and adult mortality may increase owing to a lack of predator satiation (Butler 1984). Species-specific characteristics (e.g., body size) may determine the types of selection forces that have influenced life history attributes (e.g., flexibility versus synchrony). For example, selection on large mayfly species (e.g., *D. grandis*) may have produced inflexible synchronized developmental patterns because of the increased probability of finding a mate and decreased adult mortality due to predation. However, selection for developmental synchrony in small mayfly species (e.g., *B. tricaudatus*) may have been unimportant because mating difficulties and adult mortality due to predation were unimportant. Selection for flexible life history attributes capable of exploiting changing environmental conditions may be more important for small species.

Annual production

Production values at the upstream site were similar to other production values for mayflies in the Rocky Mountains (Rader and Ward 1987) and elsewhere (McClure and Stewart 1976, Macfarlane and Waters 1982, Mortensen and Simonsen 1983, Benke et al. 1984, Smock et al. 1985, Tokeshi 1985). However, the high annual production values for *E. infrequens* at site 2 and *D. grandis* at site 3 (15.89 and 15.38 g/m², respectively) are considerably higher than those previously published for mayflies (Benke 1984).

The magnitude of production is a function of the population biomass and the rate of biomass turnover. Both population density and the biomass of individual organisms determine the population biomass, whereas the cohort production interval influences the biomass turnover rate (Benke 1979). Higher population densities and heavier individual organisms accounted for the higher production of the *Baetis* complex at sites 2 and 3. In fact, the largest baetid instars at the downstream sites had over twice the biomass of the largest individuals at

the upstream site. In addition, *B. tricaudatus* was probably bivoltine at the downstream sites and, therefore, had a higher biomass turnover rate compared with site 1 where this species was univoltine.

Biomass turnover rates for *P. heteronea*, *E. infrequens*, and *D. grandis* at sites 1 and 3 were the same because each species was univoltine with a CPI of approximately 365 days. Therefore, differences in annual production estimates between sites were due primarily to differences in population biomass estimates. *Drunella grandis* production was higher at site 3 than at site 2 because of a higher population density at site 3 since individual biomass means were similar. Both individual biomass estimates and population densities for *E. infrequens* and *P. heteronea* were higher at sites below the dam.

The substrate at both sites below the reservoir has rarely been moved or disturbed since the dam was built in the late 1940s (Rader and Ward 1989). In contrast, substrate particles 6.5 cm in diameter and less were rolled on an average of 2-3 times per year (over 30 years of flow records) at the free-flowing upstream site (Rader and Ward 1989). Therefore, the substrate in both sites below Granby Dam, and below other storage reservoirs, provide stable attachment sites for dense growths of filamentous algae and macrophytes (e.g., Dufford et al. 1987). Although living filamentous algae and macrophytes are rarely used directly as a food resource by aquatic insects, they enhance food abundance by entraining plankton from the reservoir and providing attachment sites for high quality epiphytic algae, mainly diatoms.

Because water is released from deep in the reservoir, the temperature regime below the dam has been altered. In particular, winter warm conditions increase the amount of thermal energy available for growth and development. Therefore, mayfly species that can tolerate the altered annual temperature pattern find an environment with a long growing season and rich with food. The high production values reported in this paper reflect these favorable conditions.

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