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# A REVIEW OF THE EFFECT OF RIVER REGULATION ON MAYFLIES (EPHEMEROPTERA)

JOHN E. BRITTAIN AND SVEIN JAKOB SALTVEIT
*Freshwater Ecology and Inland Fisheries Laboratory, University of Oslo, Sarsgt. 1, 0562 Oslo 5, Norway*

## ABSTRACT

Impoundment and diversion of watercourses for power production and water supply can have profound effects on the mayfly fauna. To explain such effects a species-specific approach is adopted on account of differing habitat requirements and life histories in the order and even within genera. Environmental conditions such as discharge and flow patterns, temperature, food availability, and predation may be changed. This leads to changes in the density and species composition of the mayfly community, especially when there is a hypolimnion drain from reservoirs. Temperature changes below such reservoirs may remove obligatory life cycle thresholds. Prolonged periods of low discharge lead to the dominance of genera, such as *Paraleptophlebia*, *Choroterpes*, *Siphlonurus*, and *Pseudocloen*, typical of slow-flowing and lentic habitats.

The life cycle plasticity and opportunism shown by *Baetis rhodani* in Europe and *B. tricaudatus* in North America have undoubtedly contributed to their success in regulated rivers. The life history characteristics of *Tricorythodes* are also advantageous below dams. The increased growth of periphyton and mosses below many dams favour certain Ephemerellidae, but restrict or eliminate many Heptageniidae. In order to survive adverse conditions, flexible life cycles or a short period of rapid nymphal growth coupled with a long period of egg development, are advantageous.

KEY WORDS Ephemeroptera Mayflies Regulated rivers Dams Water temperature Life cycles

## INTRODUCTION

Mayflies (Ephemeroptera) are a major order of benthic insects in running waters. They form an important link between primary production and secondary consumers such as fish. They are often the most abundant taxa in macroinvertebrate drift (Brittain and Eikeland, 1988). The majority of species are herbivore collector-grazers, feeding on detritus and periphyton (Brittain, 1982). They are recorded from a wide range of freshwater habitats, from the tropics to the Arctic. Recently their potential as indicators of pollution and environmental change has attracted increasing attention.

River regulation invariably modifies both flow patterns and discharge (Ward, 1976a). Changes in discharge may affect many other environmental parameters such as current, substrate, and water quality (Armitage, 1984). In such instances it is often difficult to separate cause and effect. Temperature, a major factor controlling the distribution, abundance and life cycles of aquatic insects (Ward and Stanford, 1982), is also frequently modified in regulated rivers downstream of dams.

In the present review we summarize the known effects of river regulation on mayflies and put forward hypotheses to explain its differing effect under various regulation schemes.

## DISCHARGE AND FLOW PATTERNS

Discharge and flow patterns are invariably modified in regulated rivers. Ward (1976a) recognized four major types of flow regime: reduced flow, seasonal flow constancy, increased flow, and short-term flow fluctuations. As mayfly species have certain preferential and absolute limits with respect to current

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velocity, water depth, and hydraulic conditions (Gore, 1978; Gaschignard and Berly, 1987), the mayfly fauna will be changed by river regulation.

### *Short-term fluctuations*

Few species can adapt to widely fluctuating daily flows and current velocities and this therefore results in lower benthic densities and diversity (Ward, 1976a). River faunas are also adversely affected by rapid changes in water level, probably because many mayflies occur in the shallow waters along the edge of rivers and rapid rise or fall increases drift and stranding (Ciborowski *et al.*, 1977; Graham *et al.*, 1980; Perry and Perry, 1986; Brittain and Eikeland, 1988).

In a Swedish river, short-term regulation of flow reduced the positive effect of phytobenthos, causing *Baetis* either to be restricted to the deeper parts of the river or to be totally eliminated (Henricson and Sjöberg, 1984), although in another river *Ephemerella mucronata* (Bengtsson) and *Heptagenia sulphurea* (Müller) were able to survive (Henricson and Müller, 1979).

Despite being subject to irregular high discharges, Ephemeroptera were a major taxa in the regulated River Rheindol. The dominant species, *Baetis rhodani* Pictet, *B. scambus* Eaton, and *Rhithrogena semicolorata* (Curtis), were the same as in the neighbouring unregulated River Ystwyth, although maximum densities were lower (Brooker and Morris, 1980). In New Zealand, Irvine and Henriques (1984) studied the effects of fluctuating flows and were unable to demonstrate any changes in benthic densities of the mayfly genus *Delatidium.*

In North America there have been several studies of the effects of peaking flows below dams and power stations. In the Skagit River, Washington, a change from diel flow fluctuations in 1976 to a relatively stable flow in 1977, when peaking was curtailed, greatly enhanced populations of *Ephemerella inermis* Eaton, *Baetis* spp., and *Rhithrogena* spp. (Gislason, 1985). Only three species of mayfly, *Attenella attenuata* McDunnough, *Pseudocloeon* sp., and *Stenonema integrum* (McDunnough) were recorded immediately below a peaking hydropower station on the Savannah River, compared to ten and twelve, respectively, at 4·5 and 12·5 km downstream (Hudson and Nichols, 1986). *Ephemerella infrequens* McDunnough attained high densities below Dworshak Dam, Idaho, due to the abundance of aquatic mosses, which trapped food particles on which it feeds (Brusven, 1984). The highly mobile *Paraleptophlebia* became more abundant in a Maine river subject to artificially high and low flows, especially at unseasonal times, but the low flows were limiting for heptageniids (Trotzky and Gregory, 1974).

Consistent with many drift studies in unregulated rivers (Brittain and Eikeland, 1988), drift densities of *Pseudocloeon* exhibited a definite nocturnal increase in the Lake Hartwell tailwater, U.S.A. (Matter *et al.*, 1983). However, another peak was recorded in the afternoon during the initial phase of the peaking discharge.

Ephemeropteran drift densities and species diversity in the impounded River Elan, U.K., were significantly lower than in the unregulated main River Wye, reflecting the lower benthic densities (Hemsworth and Brooker, 1981). In contrast, Baetidae were more common in the drift of an unregulated tributary than in the regulated River Tees, despite similar benthic densities (Armitage, 1977). An increased discharge from the River Elan produced no immediate effect on the numbers of drifting *Ephemerella ignita* (Poda) in the River Wye, but the night-time peak was significantly enhanced (Brooker and Hemsworth, 1978).

### *Reduced discharge and cessation of flow*

Zelinka (1984) found that strong decrease in flow in an experimental stream caused a considerable fall in densities of mayfly nymphs after a few days. However, the shorter the time of reduced flow, the quicker recolonization occurred.

In a Danish stream, Iversen *et al.* (1978) found that the mayfly, *Baetis rhodani*, was almost eliminated by a suspension of flow for two weeks. In another Danish stream, a major reduction in flow stranded the burrowing mayfly, *Ephemera danica* Müller, although *Baetis rhodani* and *Heptagenia sulphurea* easily escaped (Jensen and Jensen, 1984).

In experimental channels, discharge was reduced in two stages, first from 0·57 to 0·28 $m^3$ $s^{-1}$ and subsequently down to 0·03 $m^3$ $s^{-1}$ (Corrarino and Brusven, 1983). After the initial reduction only a few insects were stranded, but the second more drastic reduction resulted in considerably more insects being stranded, including large numbers of *Rhithrogena hageni* Eaton. Kroger (1973) reported stranding of large numbers of *R. hageni* following a rapid reduction of water flow in a regulated river. In experimental channels, however, *Baetis tricaudatus* Dodds largely avoided stranding (Corrarino and Brusven, 1983). When flows were reduced from 0·57 to 0·28 $m^3$ $s^{-1}$, there was little immediate effect on drift in *B. tricaudatus*, but the night-time peak increased. A further decrease in flow to 0·03 $m^3$ $s^{-1}$ generally produced an immediate drift response, although peak drift was still delayed until midnight.

After a reduction in discharge of 90 per cent during winter and 10–70 per cent during summer in a Norwegian river, Søre Osa, mayflies increased their density and biomass (Garnås, 1985). There was, however, a shift from a dominance of larger species, *Ephemerella mucronata* and *E. aurivilli* (Bengtsson), to greater numbers of the smaller species, *Baetis rhodani*. Similar findings were also reported from the Strawberry River, U.S.A., where a drastic reduction in flow led to *Drunella grandis* Eaton being replaced by *Baetis* sp. (Williams and Winget, 1979).

In certain cases reduction in discharge leads to complete cessation of flow. Generally, mayflies surviving drought are considered to be either able to go into a diapause as eggs or are capable of going into the hyporheic (Williams and Hynes, 1976; Canton *et al.*, 1984), although so far no nymphal diapause or drought resistent egg stage has been documented (Brittain, 1982; Suter, in press), although suggested several times. Nevertheless, at least two species of *Paraleptophlebia* are able to survive in intermittent streams (Williams and Hynes, 1976; Wright *et al.*, 1984).

In a Welsh river a period of low flow reduced the abundance of *Rhithrogena semicolorata* and *Ephemerella ignita* (Cowx *et al.*, 1984), while *Baetis* sp. and *Heptagenia sulphurea* were eliminated in a Norwegian regulated river, the Nøra, which dried up from October to May/June (Josefsen, 1953). In another Norwegian river, the Nea, a severe reduction in discharge, coupled with periods with virtual drought, led to a reduction in mayfly species. *Heptagenia journensis* (Bengtsson) also common in lakes, became the dominant mayfly (Langeland and Haukebø, 1979).

Low winter flows virtually eliminated the winter generation of *Baetis rhodani* downstream of a dam on the Norwegian River Glomma (Brittain *et al.*, 1984). The low flow rates also permitted colonization by species more typical of the slower reaches of the river, such as *Centroptilum luteolum* Müller. Similarly, below a deep release dam in Sweden, *Baetis* spp. were replaced by species, such as *Siphlonurus lacustris* Eaton, *Paraleptophlebia strandii* (Eaton), and *Metretopus borealis* (Eaton), that are tolerant of low flows (Henricson and Müller, 1979).

### *Seasonal flow constancy*

The elimination of high seasonal discharges on the Strawberry River, Utah, U.S.A., by permitting ehnanced algal growth, allowed a substantial increase in *Baetis* spp. (Williams and Winget, 1979). At the same time, numbers of the shredder/predator, *Drunella grandis*, were drastically reduced. A large increase in another ephemerellid, *Ephemerella inermis*, was perhaps surprising, but it is much more of an algal scraper than *D. grandis* (Hawkins, 1984). The low discharge also produced an increase in species, such as *Paraleptophlebia*, which is tolerant of low flows and able to utilize detrital material from a wide range of sources (Mattingly, 1987).

The reduction in extremes of discharge by the Cow Green Reservoir, U.K., which allowed dense growth of algae and mosses, increases ephemeropteran densities in the downstream River Tees (Armitage, 1976). There was an increase in numbers and biomass of *Baetis rhodani*, *Ephemerella ignita*, and *Caenis rivulorum* Eaton and a reduction in *Rhithrogena semicolorata* and *Ecdyonurus dispar* (Curtis). Similar reduction in extreme flows in Norway, France, and Spain also favoured Baetidae at the expense of Heptageniidae (Gregoire and Champeau, 1981; Lillehammer and Saltveit, 1984; Puig *et al.*, 1987; Casado *et al.*, in press).

### *Increased discharge*

Examples of more or less stable increase in discharge are characteristic of irrigation schemes in warm, dry countries. After dam construction had already reduced diversity, high summer irrigation flows in an Australian river caused a further reduction in mayfly species at sites near the dam (Doeg, 1984).

Interbasin transfer of water from the Orange River/Fish River basin to the Great Fish River in South Africa changed its flow from very irregular seasonal flow to perennial, increasing the annual runoff by 500–800 per cent. The mayfly fauna changed from species preferring backwaters and marginal vegetation such as *Cloeon africanum* (Esben–Petersen) and *Austrocaenis capensis* (Barnard) to species preferring stones and fast-flowing current, such as *Baetis harrisoni* Barnard and *B. glaucus* Agnew (O'Keefe and DeMoor, 1988).

Three mayflies adapted to torrential conditions, *Epeorus longimanus* (Eaton), *Drunella doddsi* Needham, and *Rhithrogena hageni*, comprised about 65 per cent of the insect fauna in the regulated Kananaskis River, Alberta, compared to only about 20 per cent in the unregulated Lusk Creek, despite it having a greater gradient (Radford and Hartland-Rowe, 1971). *Cinygmula* spp. and *R. hageni* were dominant in the drift of both rivers, but high discharges from the dam also introduced species of riverside pools, such as *Siphlonurus occidentalis* Eaton, into the drift.

## TEMPERATURE

Temperature regime in regulated streams may be modified in several ways (Ward and Stanford, 1982). Thermal changes are most pronounced just below deep release dams, with decreasing river temperatures during summer and increasing during winter. Surface release usually leads to increase in summer temperatures.

### *Hypolimnetic release*

Many of the studies of hypolimnetic release dams have been carried out in North America, where this is the most common regulation type (Stanford and Ward, 1979). Although the average number of mayfly taxa usually decreases below deep-release reservoirs, mean density often increases. Species such as *Ephemerella infrequens*, *E. inermis*, *Tricorythodes minutus* Traver, *Baetis tricaudatus*, and *Choroterpes* spp. commonly attained high densities below such reservoirs (Ward, 1974; Young *et al.*, 1976; Gore, 1977, 1980; Zimmermann and Ward, 1984).

A hypolimnion release dam on the South Saskatchewan River, Canada caused a dramatic reduction in the mayfly fauna. Even over 100 km below the dam only 40 per cent of the species present above the dam and in a control tributary were recorded. This large scale elimination of mayfly species was studied by Lehmkuhl (1972) and related to the changed temperature regime. Several mayflies from the study area, including *Ephoron album* (Say), had univoltine summer cycles, in which the eggs have a long period of diapause, followed by rapid growth until emergence. Using Britt's (1962) data on the life cycle of *E. album*, Lehmkuhl clearly showed that the temperature requirements of this species were not met on three counts: the eggs were not exposed to temperatures at or near freezing, a prerequisite for development; the eggs will not hatch unless near-zero temperatures are followed by 10–13°C; and the nymphs will not reach maturity unless they receive several months of warm temperatures. Other species had univoltine winter cycles, in which egg development is short and nymphal development takes almost a year. One of these, *Ephemera simulans* Walker, requires a specific number of degree-days to complete nymphal development (Britt, 1962), but near the dam the warm periods of the year are curtailed and the required degree-days are not met.

Immediately below a hypolimnion drain impoundment in Wisconsin both *Baetis quebecensis* McDunnough and *B. brunneicolor* McDonnough were severely reduced in numbers (Hilsenhoff, 1971), although 3 km below the dam the effect was less obvious.

Regulation of the Flathead and Kootenai Rivers in Montana had differing effects on the density and growth of two ephemerellid mayflies (Perry *et al.*, 1986). Temperature changes were moderate due to selective withdrawal systems. The mayfly, *Drunella flavilinea* McDunnough, responded to within-river differences and appeared sensitive to the effects of regulation. *Serratella tibialis* McDonnough, on the other hand, had its highest densities in the regulated Kootenai River, where it was able to take advantage of the high biomass of periphyton and seston.

Impoundment of the Brazos River, Texas, resulted in a much more even flow, and during base discharge changes in temperature were quickly modified by air temperatures. The leptophlebiid mayfly, *Choroterpes mexicanus* Allen, was very abundant (McClure and Stewart, 1976), although mayflies generally declined in abundance (Stanford and Ward, 1979).

Reduced summer and increased winter temperatures in Aurlandselva, Norway, gave greater densities of mayflies, but with a reduced biomass (Raddum, 1978). This was due to a shift to smaller individual size, possibly caused by the drift of the largest, more active, individuals out of the area during the increased winter discharges. Penáz *et al.* (1968) also reported an increase in the number of small animals, especially *Baetis*, below a Czechoslovakian dam. *Ephemerella ignita* occurred in high numbers both before and after impoundment. Below a German dam, with reduced summer temperatures, there was an increase in *E. ignita*, but a decrease in *Baetis* spp. and *Rhithrogena semicolorata* compared to upstream sites (Rehfeldt, 1987). In the River Surna, Norway, colder water in the river below the power station in summer lead to a decrease in densities of the mayflies, *Ameletus inopinatus* Eaton, *Baetis rhodani*, and *Ephemerella aurivilli*, although there were no differences in species composition (Brittain and Saltveit, 1988).

The benthos below two Welsh dams were compared by Petts (1984). Below Clywedog Dam, with a hypolimnion release, *Baetis rhodani* was the dominant mayfly. In contrast, below Lake Vyrnwy, an intermediate-release water supply dam, *B. rhodani* was far less important and was only half as abundant as another mayfly, *Ecdyonurus dispar*. This occurred despite a generally stable discharge regime, often disadvantageous for heptageniids, but monthly artificial freshets (Douglas, 1988) probably rendered the downstream section more suitable.

Depressed water temperatures below Flaming Gorge Dam, Utah, U.S.A., delayed hatching in *Baetis* sp. and were the cause of the almost complete failure of the summer generation (Pearson *et al.*, 1968).

### *Surface release*

While mayfly densities generally increased below deep release reservoirs in Colorado, their densities decreased below surface release reservoirs (Ward and Short, 1978; Zimmermann and Ward, 1984). Only *Tricorythodes* increased in abundance below surface release dams.

Surface release from a shallow reservoir on the Madison River, Montana, caused an increase in summer water temperatures (Fraley, 1979). *Drunella grandis* was three to four times more abundant above the reservoir. Adults of *Rhithrogena undulata* Banks and *Epeorus* sp. were commonly taken above the reservoir, but not below. In contrast *Choroterpes albiannulata* McDunnough and *Tricorythodes minutus* only occurred below the dam and thus showed a positive respose to the higher temperatures. *Ephemerella inermis* and Baetis sp. had similar densities above and below the dam and were considered eurythermal species.

In Virginia, U.S.A., *Heterocloeon curiosum* (McDunnough) was bivoltine with two rapid summer generations and a probable overwintering egg stage, in both a free-flowing river and a river below a surface release dam (Kondratieff and Voshell, 1981). However, densities were twice as great in the unregulated river. Reduced fecundity produced by non-optimal temperatures during nymphal growth was put forward as the main explanation.

## WATER CHEMISTRY

The chemical environment may be modified in regulated rivers, especially below hypolimnion release dams (Petts, 1984). Depletion of dissolved oxygen and low pH induce other chemical changes, such as increase in dissolved iron and manganese and elevated $H_2S$ levels.

In the regulated Rivers Elan and Tywi, U.K. low ephemeropteran densities, including those of *Ecdyonurus dispar*, *Rhithrogena semicolorata*, *Baetis rhodani*, and *B. scambus*, have been attributed to the deposition of sediments rich in iron and manganese, enhanced by the stable flow regime below the reservoir (Scullion, 1983; Inverarity *et al.*, 1983).

Changes in mayfly distribution along the regulated Arkansas River, U.S.A., were correlated among other things with changes in zinc concentrations (Gore and Bryant, 1986). Weatherley *et al.* (1975) found zinc to be particularly toxic to Ephemeroptera. Species which appeared tolerant of such conditions included *Baetis bicaudatus* Dodds, *B. tricaudatus*, and *Tricorythodes minutus*.

Nymphs of the mayfly, *Cloeon*, appear to be very tolerant of external gas bubbles caused by gas supersaturation (Montgomery and Fickeisen, 1979). However, under simulated tailrace conditions they experience floatation and exhibit abnormal swimming patterns. Nymphs of an ephemerellid, *Timpanoga hecuba* Eaton, were relatively sensitive to high oxygen levels and have a 96 h LC-50 value of 129 per cent, while none successfully emerged above 135 per cent saturation (Nebeker *et al.*, 1981). Low concentrations of $H_2S$ over long periods have also been shown to be toxic to mayflies (Oseid and Smith, 1975). *Baetis* appears to be less tolerant of $H_2S$ than either *Ephemera* or *Hexagenia* (Oseid and Smith, 1974).

## SUBSTRATE, SEDIMENTATION, AND SCOURING

The morphometric characteristics of the streambed influence the diversity, density, and distribution of benthic animals (Petts and Greenwood, 1985). Changes in substrate composition through sedimentation or scouring may therefore dramatically alter species composition and community structure.

The addition of sand and silt from dam construction usually results in a decrease in the mayfly fauna (Briggs, 1948; Blyth *et al.*, 1984; Cline and Ward, 1984). Some mayflies seem especially sensitive to introduced sediments, while burrowing species seem to benefit. The absence of certain species is apparently due to sediment filling the substrate interstices and reducing the effective size of the surface cobbles (McClelland and Brusven, 1980) and by increasing drift (Rosenberg and Wiens, 1978).

Increased sedimentation resulting from the flushing of an upstream reservoir on the River Rhône, France, significantly reduced densities of the mayfly, *Heptagenia sulphurea* (Bournaud *et al.*, 1987). However, their numbers returned to normal two months later. Following flusing of a reservoir on the North Platte River, U.S.A., *Tricorythodes minutus*, a species characteristic of warm, turbid streams, increased in density, while *Baetis insignificans* McDunnough showed no significant change (Gray and Ward, 1982).

Sedimentation in the Australian Mitta Mitta and Thomson Rivers due to construction activity depressed both the total numbers of species and their density (Blyth *et al.*, 1984; Doeg *et al.*, 1987). The mayflies, *Atalophlebioides* sp. and *Coloburiscoides* sp., widespread in both rivers prior to construction, were adversely affected. Downstream of another Australian dam, *Baetis* spp. decreased in abundance and the burrowing leptophlebiid, *Jappa* sp., increased due to increased sedimentation during construction (Chessman *et al.*, 1987).

Species of *Cinygmula* are among the more sediment tolerant in the Heptageniidae and returned in increasing numbers after some of the fine sediments produced during the construction of a dam on the Huntington River, Utah, U.S.A., had been washed out in the early discharges (Winget, 1984). However, another heptageniid, *Rhithrogena robusta* Dodds, was unable to tolerate the increased sedimentation and algal growth below the dam and became absent. Another species adversly affected by sedimentation, both during construction and operation of the dam, was *Drunella doddsi*. Densities of two *Brachycercus* species were adversely affected, possibly due to the scouring effect of the unseasonal flushing flows in July and August on the small nymphs present at that time. Downstream of other river impoundments, the erosive effects of highly variable discharge have resulted in the washout of fine particles and general reductions in invertebrate abundance (Radford and Hartland-Rowe, 1971; Trotzky and Gregory, 1974; Ward and Short, 1978).

## COMMUNITY STRUCTURE AND TROPHIC RELATIONSHIPS

Change in community structure may arise in regulated rivers, often as an indirect result of changes in discharge (e.g. Krzyzanek, 1986). Reviewing British and American literature, Logan and Brooker (1983) found significantly higher ephemeropteran densities in riffles compared to pools, although at the family level only Baetidae showed significantly higher densities in riffles.

Shortly after the building of weirs in Norway to reduce the effects of low flows, *Baetis rhodani*, became far more abundant outside the weir basin (Baekken *et al.*, 1984). There was also a subsequent increase in the densities of *Siphlonurus aestivalis* (Eaton), *S. lacustris*, and *Ameletus inopinatus* within the weir basin (Fjellheim *et al.*, 1987). These latter species benefitted from the increase in detritus and the slow-flowing conditions within the basin.

Below a Minnesota impoundment, MacFarlane and Waters (1982) found that the mayflies *Caenis simulans* McDunnough and *Stenonema neopotellum* (McDunnough) were replaced by *Stenacron interpunctatum* (Say). The production of the latter species below the dam was so high that total mayfly production was three times greater than above the dam. The large quantities of FPOM and the course substrate as well as the higher summer temperatures (McCafferty and Pereira, 1984) were probably favourable for *S. interpunctatum*.

Algae are an important food source for *Baetis* nymphs and Fuller *et al.* (1986) demonstrated a marked reduction in densities and adult size in a population of *Baetis tricaudatus* reared in areas with experimentally reduced algal standing crop. Increased algal densities caused by a reduction in discharge below a dam on the river Rhône, France, favoured *Ephemerella ignita* Poda (Gaschingnard and Berly, 1987).

It has been suggested that the number and abundance of predators is reduced below dams, allowing taxa such as *Baetis*, to reach extremely high densities (Ward, 1976a; Winget, 1984). However, below Cow Green Reservoir, U.K., brown trout consumed more ephemeropteran nymphs after impoundment (Crisp *et al.*, 1978) and Baetidae increased in numerical abundance relative to the Ecdyonuridae both in trout and bullhead stomachs.

## DISCUSSION

Major alterations occur in the macroinvertebrate fauna, including mayflies, in regulated rivers (Ward and Stanford, 1979). The relative abundance of mayflies may not change appreciably, but species diversity and composition are generally strongly modified. Enhanced growth of algae and macrophytes below dams, due to more stable flow conditions and decreased grazer diversity, provides an important food resource (Figure 1). The increase below dams of *Baetis rhodani* and *Ephemerella ignita* in Europe and *B.*

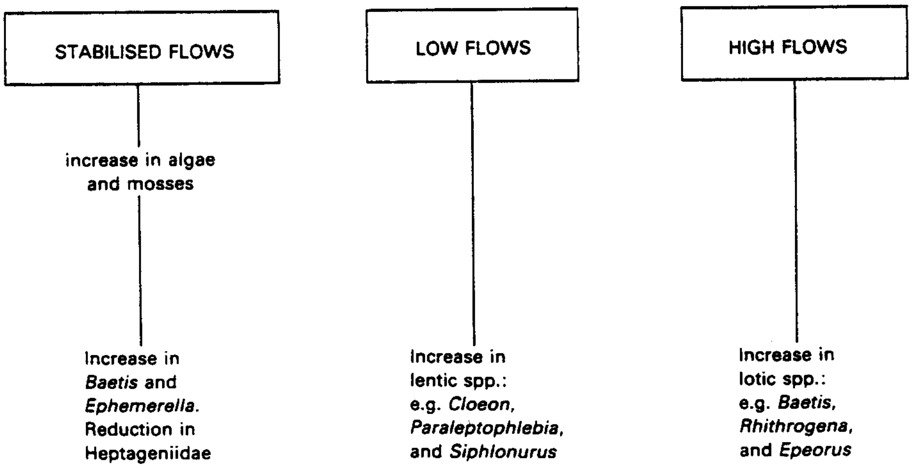

Figure 1. Generalized changes in the mayfly community of regulated rivers as a result of modifications in the discharge regime

*tricaudatus* and *E. inermis* in North America, has often been related to enhanced algal and moss growth (e.g. Penáz *et al.*, 1968; Spence and Hynes, 1971; Ward, 1976a; Williams and Winget, 1979; Zimmermann and Ward, 1984; Gaschingnard and Berly, 1987). As well as providing a direct source of food, such growth acts as a seston trap and as a refuge from predation and environmental extremes.

Although increased periphyton may be advantageous for some mayflies, it often excludes species typical of clean rock surfaces which utilize suckers or friction pads for attachment, such as several genera of the Heptageniidae and *Drunella doddsi* (Ward, 1976b; Trotzky and Gregory, 1977; Winget, 1984; Armitage *et al.*, 1987). Nevertheless, heptageniids may dominate the fauna below dams when discharges are high (Radford and Hartland-Rowe, 1971).

By hindering both downstream drift and the upstream movement of adults and nymphs, dams and above lying reservoirs are potential barriers to dispersal and gene flow. Below two New York dams, Sweeney *et al.* (1986) attempted to assess this, using protein electrophoresis. No evidence of any barrier was found in *Eurylophella verisimilis*, while the evidence for *Ephemerella subvaria*, which showed significant geographical variation, was inconclusive. Nevertheless, changes in life history characteristics above and below the reservoirs were observed. Adult size and fecundity of *E. subvaria* gradually increased almost two-fold at sites downstream of the reservoirs. Conversely, adult size and fecundity of *E. verisimilis* exhibited a gradual two-fold decrease in a downstream direction below the dams. Consistent with these trends *E. subvaria* was rarer at sites below the dams, whereas *E. verisimilis* was least abundant at the site furthest downstream. Similar temperature effects below dams have also been reported by Fraley (1979) and Kondratieff and Voshell (1981).

Ward and Stanford (1982) stressed that high species diversity among aquatic insects is usually associated with wide annual temperature range. Moreover, Vannote and Sweeney (1980) have suggested that the course of biotic diversity along a stream closely parallels that of thermal variation. Thus a reduction in both diel and annual thermal ranges in regulated rivers will lead to a reduction in species diversity. These effects may be greater in continental areas with high species diversity, such as certain parts of North America, and less marked in oceanic areas with low species diversity, such as northwestern Europe (see Saltveit *et al.*, 1987).

Necessary temperature and other environmental cues may also not be reached after regulation (e.g. Lehmkuhl, 1972). Rivers below deep-release dams are also characterized by a high degree of diurnal thermal constancy (Ward, 1976a). The development of eggs and growth in some species of Ephemeroptera has been correlated to the degree of diel temperature fluctuation (Sweeney, 1978).

The considerable success of *Ephemerella ignita* in European regulated rivers may be partly due to the long period of egg development and hatching (Bohle, 1972; Elliott, 1978) coupled with a short period of summer nymphal growth (Bournaud *et al.*, 1987). Such species are only exposed to flow fluctuations for a short time as active, growing nymphs and thus better suited to the temporal instability of many regulated rivers (*cf.* Hawkins; in press). The North American, *Ephemerella inermis*, has a univoltine winter cycle (Hawkins, 1986), but is capable of surviving a wide range of temperature conditions and has been found below both hypolimnion and epilimnion release dams (Ward, 1974; Ward and Short, 1978; Fraley, 1979). *E. ignita* and *E. inermis*, together with other members of the family recorded below dams, such as *E. infrequens*, *E. aurivillii*, and *Seratella tibialis*, are favoured by enhanced growth of mosses and periphyton. *E. infrequens* has also been reported to be basically univoltine, but relatively unsynchronized, with more than one cohort per generation and a short period of rapid growth (Rader and Ward, 1987; Hawkins, in press). In contrast, *Drunella grandis* and *D. doddsi*, negatively affected by regulation, have well-synchronized univoltine cycles with nymphal growth spread over much of the year (Radar and Ward, 1987; Hawkins, in press).

In addition to temperature, changes in flow conditions seem to be the main factor responsible for changes in the mayfly community of regulated rivers (Figure 1). Rapid fluctuations in discharge have the most pronounced effect and many mayflies are either stranded or enter the drift. Low discharge and/or reduced current velocity gives rise to major changes in community structure, and mayfly species typical of more lentic habitats often increase in importance. Among these are the genera, *Paraleptophlebia*, *Choroterpes*, *Siphlonurus*, *Centroptilum*, *Pseudocloeon*, and *Heterocloeon*.

Table I. A summary of mayfly life history attributes generally advantageous or disadvantageous in regulated rivers

| | Advantageous | Disadvantageous |
|---|---|---|
| Life cycle | Flexible<br>Bivoltine/multivoltine | Fized<br>Univoltine |
| Temperature relationships | Eurytherm | Stenotherm |
| Nymphal development | Asynchronous | Synchronous |
| Egg development | Long | Short |
| Feeding | Scraper | Collector/shredder |
| Nymphal size | Small | Large |

The life cycle plasticity of *Baetis rhodani* and *B. tricaudatus* (Clifford, 1982) has undoubtedly contributed to their success in regulated rivers and running waters in general (Tables I and II). Their life cycles range from a fairly synchronous univoltine cycle in cold water habitats to a wide range of more or less synchronous multivoltine cycles, sometimes with overlapping cohorts (see Clifford, 1982). This gives the potential to maintain a viable population, even though one cohort or generation may be decimated by unfavourable environmental conditions (e.g. Brittain *et al.*, 1984), and to exploit new and favourable conditions (e.g. Wallace and Gurtz, 1986). Mayflies are among the most fecund insects (Brittain, 1982) and together with their frequency in drift and their aerial adult stage, makes them among the first colonizers of virgin habitats (e.g. Ladle *et al.*, 1980; Sagar, 1983).

Other baetid genera often reported from regulated rivers, such as *Centroptilum* and *Pseudocloeon*, have multivoltine life cycles (Clifford, 1982). *Choroterpes mexicanus*, abundant in the regulated Brazos River, is a seasonal polyvoltine species, with three overlapping generations per year (McClure and Stewart, 1976). In contrast, most Heptageniidae are reported as having univoltine winter life cycles, whereby they are present as nymphs throughout much of the year. Thus, in addition to the deleterious effects of increased algal growth below dams, most Heptageniidae do not appear to have life cycle strategies suited to river regulation.

The occurrence of *Tricorythodes*, often a dominant mayfly genus, below North American dams has been related to the distribution of well-developed submerged angiosperms (Ward, 1976a; Ward and Short, 1978). However, other facets of this genus are advantageous. As with baetids, *Tricorythodes minutus* is flexible in its voltinism (Newell and Minshall, 1978a). *Tricorythodes* spp. also have very high growth and ingestion rates and can therefore rapidly complete their life cycles in warm waters (McCullough *et al.*, 1979; Benke and Jacobi, 1986). They may also live interstitially, protected from the extremes of current and temperature. Like the Caenidae, which also have operculate gills, they are also well able to withstand silting. Additionally, *T. minutus* is well adapted to changes in temperature regime. For a mayfly, its egg development is surprisingly little affected by changes in temperature (Newell and Minshall, 1978b; Brittain, in press).

## CONCLUSIONS

The mayfly community, although perhaps not reduced in biomass or numbers, may be greatly changed in terms of species composition and diversity as a result of river regulation (Table II). Temperature and discharge regime are two major factors changed in many river regulation schemes. These same two factors have a profound effect in determining the species composition of the mayfly community in a particular river. Thus, when the discharge regime is altered the mayfly community will change. For example, a reduction in discharge will often lead to a predominance of species typical of slow-flowing

Table II. Mayfly taxa generally favoured by river regulation and those often reduced or absent in regulated rivers, based on reports in the literature. Taxa specifically affected by dam construction are not included

| | |
|---|---|
| Mayfly taxa generally favoured by regulation: | |
| *Baetis rhodani* | Armitage, 1977; Brooker and Morris, 1980; Lillehammer and Saltveit, 1984; Petts, 1984. |
| *Baetis tricaudatus* | Gore, 1977; Gore and Bryant, 1986. |
| *Paraleptophlebia* spp. | Trotzky and Gregory, 1974; Williams and Winget, 1979; Mattingly, 1987. |
| *Choroterpes* spp. | McClure and Stewart, 1976; Fraley, 1979. |
| *Ephemerella ignita* | Penaz *et al.*, 1968; Armitage, 1977; Gaschignard and Berly, 1987; Rehfeldt, 1987. |
| *Ephemerella inermis* | Pearson *et al.*, 1968; Kroger, 1973; Ward, 1974, 1976a; Williams and Winget, 1979; Gislason, 1985. |
| *Ephemerella infrequens* | Brusven, 1984; Zimmermann and Ward, 1984. |
| *Seratella tibialis* | Perry *et al.*, 1986. |
| *Tricorythodes minutus* | Canton *et al.*, 1984; Gore and Bryant, 1986. |
| Mayfly taxa often reduced or eliminated by regulation: | |
| *Isonychia sicca* | Lehmkuhl, 1972; Stanford and Ward, 1979. |
| *Epeorus* spp. | Trotzky and Gregory, 1974; Ward, 1976b; Fraley, 1979. |
| *Ecdyonurus* spp. | Armitage, 1977; Unverarity *et al.*, 1983; Winget, 1984; Rehfeldt, 1987. |
| *Rhithrogena* spp. | Trotzky and Gregory, 1977; Armitage, 1977. |
| *Traverella albertana* | Lehmkuhl, 1972; Gore, 1980. |
| *Drunella grandis* | Fraley, 1979; Williams and Winget, 1979. |
| *Ephemera simulans* | Lehmkuhl, 1972. |
| *Ephoron album* | Lehmkuhl, 1972. |

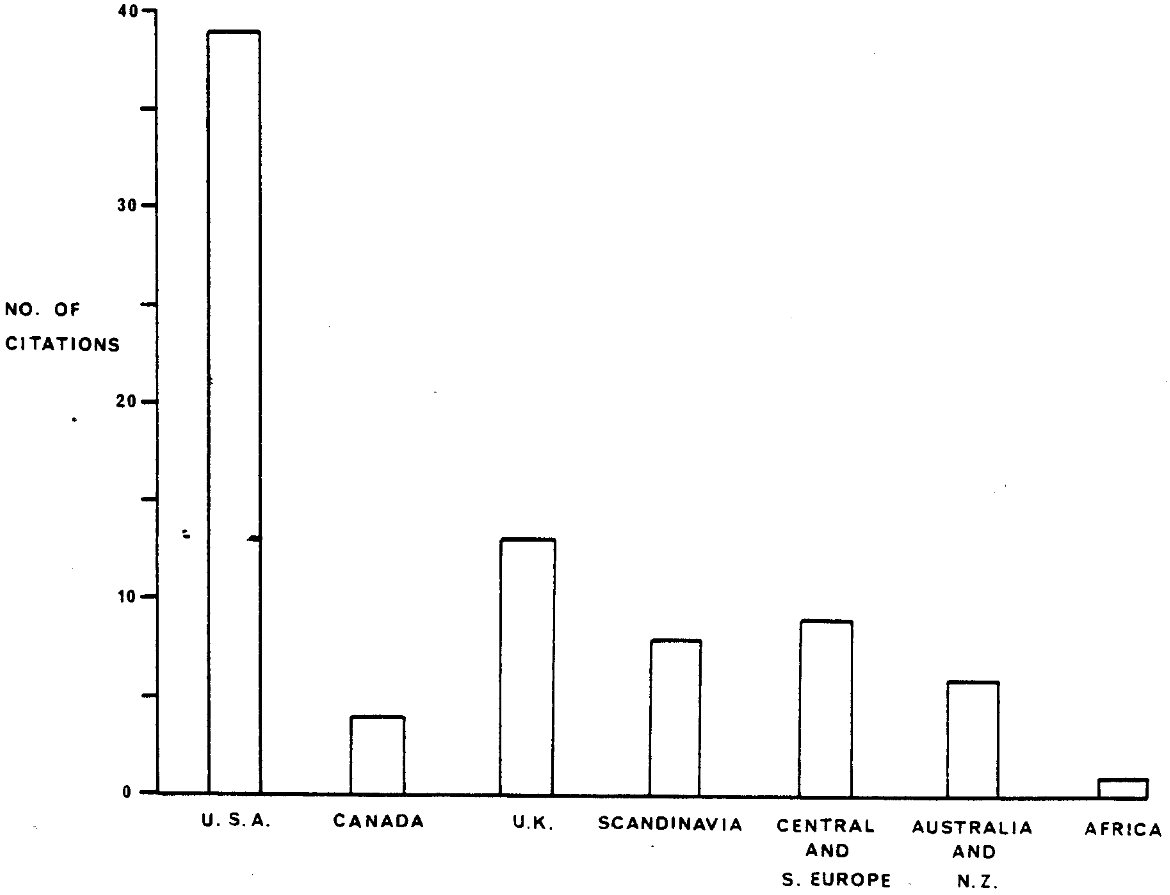

Figure 2. Geographical distribution of studies concerning the effects of river regulation on mayflies, based on citations in international journals

waters, such as *Cloeon* or *Siphlonurus*. These and similar changes associated with increased discharge and stabilization of discharge are illustrated diagramatically in Figure 1.

Within these constraints of discharge regime and adaptation to a particular current flow, certain life cycle attributes appear to be of advantage in regulated rivers (Table 1). The unpredictable and at times harsh conditions favour opportunisitc species, with either flexible, asynchronous life cycles, or a short, active nymphal stage able to take advantage of favourable conditions of short duration.

In the future, there is a need for critical experimental studies on the effects of river regulation on mayflies and for more basic knowledge of their life cycle parameters. A species-specific approach is also necessary, as different species even within the same genus can exhibit different reactions to a particular environmental change.

Most of our information on the effects of river regulation on mayflies comes from Europe and North America (Figure 2). There is clearly need for more data from Asia, Africa, and the southern hemisphere in general. As well as being necessary to document the environmental effects of river regulation in these regions, it is important to verify the significance of life history characteristics and adaptation to discharge regime in determining the effect of river regulation on mayfly communities.

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