

Effects of hydropower-induced flow perturbations on mayfly (Ephemeroptera) richness and abundance in north Swedish river rapids

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Abstract

Mayfly species richness and abundance were investigated at 52 Swedish river rapids. These were either unregulated, or regulated with or without reduced discharge. Sites impacted by regulation had lower mayfly richness and abundances than unregulated reference sites. The relative importance of reduced discharge, daily fluctuations in flow, flow constancy, and the distance to nearest rapid (as a measure of isolation) was evaluated in multiple regression analyses. These indicated negative effects of diel fluctuations on both abundance and richness, whereas flow constancy was favourable for richness. Neither the distance to nearest rapid nor reduced flow were significantly related to mayfly richness and abundance. In total, 26 mayfly species were recorded. Only *Baetis rhodani* was found at all sites, but another 11 species were present at more than 40 sites. The strongest effects were found for species within the Heptageniidae. Nineteen of 20 mayfly species present in both the regulated (with unreduced flow) and unregulated reference rapids were on average more common in the unregulated ones. Mayfly assemblage structure was primarily influenced by regional factors and nutrient status, although daily fluctuations in flow together with rapids dimensions also had a significant influence. No rare species appears to be threatened by hydropower regulation though it is conceivable that depressed abundances in regulated rivers indirectly influence predators and periphyton.

Introduction

River regulation for hydroelectric power inevitably affects discharge patterns over downstream benthic habitats. Typically the seasonal and diel dynamics of the flow reflect the periods of electricity demand leading to a reduced spring flood and elevated winter discharge, and sometimes also to high daytime/weekday flow and low nighttime/weekend flow. Frequently discharge is also reduced to a fraction of the natural flow because of water diversion. Studies on the effects of river regulation on downstream communities have mainly been conducted on single systems, often as upstream-downstream (e.g. Troitzky & Gregory, 1974; Rader & Ward, 1988; Saltveit et al., 1995) or before-after (e.g. Armitage, 1978; Williams & Winget, 1979) comparisons. In addition, a few studies have attempted controlled modification of flow conditions (e.g. Gislason, 1985; Perry & Perry, 1986). Almost exclusively

the effects have been studied within a limited distance downstream of the dam (but see Hauer et al., 1989).

Natural lotic habitats are heterogeneous systems with flow patterns of varying predictability (Poff & Ward, 1989). In central Scandinavia, where this study was carried out, river hydrographs are strongly affected by snowmelt, but occasional spates may occur following heavy rain in any of the ice-free seasons. Flow variation is also affected by hydroelectric schemes, which in addition to changing flow regimes cause habitat loss and fragmentation, and a general change from lotic to lentic environments. In total, about 70% of Sweden's rivers are exploited through water regulation (Grundsten, 1991). It is obvious that regulation-related flow alterations must cause fundamental changes of the river habitats, and thereby, of their entire biotas. In Swedish river systems, such effects have been demonstrated for the overall species richness and abundance of benthic macroinvertebrates (Englund & Malmqvist, 1996),

Table 1. Predicted changes and underlying mechanisms hypothesized to follow water regulation for mayfly community parameters and selected taxa.

Effects on	Predicted change	Mechanism	Source
Diversity	–	Reduced flow	Langeland & Haukebo, 1979
	–	Diel fluctuations in flow	Ward, 1976
	–	Isolation	This study
Density	–	Reduced flow	Garnås, 1985
	–	Diel fluctuations in flow	Ward, 1976
<hr/>			
<i>Ephemera mucronata</i>	–	Reduced flow	Garnås, 1985
<i>E. aurivilli</i>	–	Reduced flow	Garnås, 1985
<i>E. ignita</i>	–	Reduced flow	Cowx et al., 1984
<hr/>			
<i>Heptagenia joernensis</i>	+	Reduced flow	Langeland & Haukebo, 1979
<i>Baetis rhodani</i>	+	Reduced flow	Garnås, 1985; Raddum & Fjellheim, 1993
	–	Diel fluctuations in flow	Brooker & Morris, 1980
	+	Seasonal flow constancy	Armitage, 1976; Raddum & Fjellheim, 1993
<i>Ephemera ignita</i>	+	Seasonal flow constancy	Armitage, 1976
<i>C. rivulorum</i>	+	Seasonal flow constancy	Armitage, 1976

and specifically for certain animal groups (Hydropsychidae/Arctopsychidae, Englund et al., in press, and Diptera: Simuliidae, Zhang et al., manuscript), and also for moss communities (Englund et al., 1996).

Mayflies are common inhabitants of all sorts of freshwater bodies. Their distribution is controlled by a number of historical and abiotic factors, temperature, water quality, and current speed (see Brittain, 1982 for a review). In addition, biotic factors are likely to further influence some species. The larvae of many species of mayflies graze epibenthic and epiphytic algae. This life style makes mayfly larvae directly exposed to flow perturbations, perhaps more than most other lotic invertebrates, and therefore their occurrence could be expected to reflect the degree of flow stress accompanying frequent and/or rapid flow fluctuations (Brusven et al., 1974).

Brittain & Saltveit (1989) reviewed a number of changes in mayfly communities following water regulation. Their compilations show that replicate studies involving affected and unaffected river sites are few (but see Armitage et al., 1987, Ward & García de Jalón 1991). Instead, most information has been derived from case studies, often reported in the 'grey' literature. Our approach is to formulate testable predictions, partly taking Brittain & Saltveit's review as a starting point, to investigate whether our data from Swedish river rapids would support a series of predic-

Table 2. Means, standard deviations (SD) and results of one-way ANOVAs on mayfly species richness and abundance in relation to hydropower exploitation (upper panel) and regulation regime (lower panel).

Factor	N	Means	SD	F	p-level
<i>Species richness</i>					
Unaffected	14	13.6	2.79	4.87	0.032
Affected	38	11.6	2.91		
<i>Abundance</i>					
Unaffected	14	152	26.7	19.32	<0.0001
Affected	38	110	31.2		
<hr/>					
<i>Species richness</i>					
Unaffected	14	13.6	2.79	2.54	0.089
Regulated	15	11.3	3.53		
Reduced	23	11.8	2.50		
<i>Abundance</i>					
Unaffected	14	149	33.4	7.31	0.0017
Regulated	15	109	33.5		
Reduced	23	113	28.7		

tions (Table 1). These address effects of (1) flow reduction, (2) seasonal flow constancy, and (3) diel fluctuations in flow on the diversity and density of mayflies, and on individual species. We also consider a fourth hypothesis. We observed that hydropower exploitation

Table 3. Multiple linear regression models for mayfly species richness (upper panel) and abundance (lower panel) at sites with reduced flow. Partial correlation coefficients, degrees of freedom (df) and *p*-levels are indicated.

Variable	Partial correlation	df	<i>p</i>
Model (richness)		4,18	0.046
Distance	-0.235		0.318
Flow constancy	0.428		0.059
Diel variation	-0.474		0.033
Flow reduction	-0.213		0.366
Model (abundance)		3,19	0.038
Flow constancy	-0.196		0.395
Diel variation	-0.547		0.010
Flow reduction	-0.163		0.479

makes rapids more rare and therefore also more isolated from each other. This could, in case of extinctions, reduce recolonisation rates leading to lower species richness, especially for taxa with limited dispersal capabilities. Since mayflies, although often competent fliers, are principally restricted to their stream of origin because of extremely short adult lives (Hynes, 1970), we consider isolation as a potentially important factor in the relationship between mayfly species richness and hydropower regulation. Finally, we examine the possibility that the same species occur in regulated as in unregulated rivers, but in reduced densities, as was suggested by Brooker & Morris (1980).

Materials and methods

Study area and site selection

Regulated, large rivers in central and northern Sweden have natural or man-made reservoirs near the source areas in the western mountains. These reservoirs are usually filled by snow melt during the summer while the release is highest in winter, when demand for electricity is high. Many rivers have several run-of-the-river plants creating a series of impoundments. These rivers have a regulated but unreduced flow. Flow patterns in such rivers typically include a reduced springflood and an elevated winter discharge. A second type of regulation regime is found where river water is diverted. Here hydropower plants are located at the

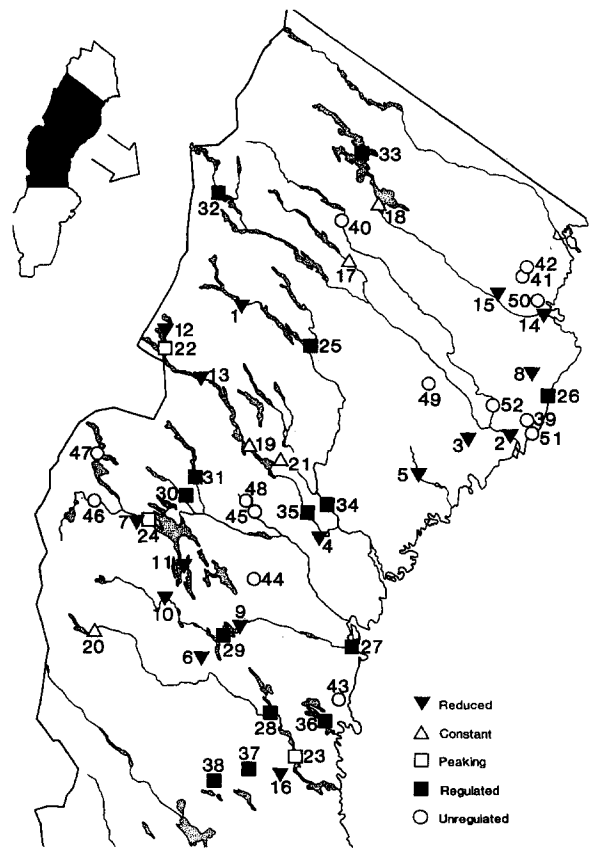


Figure 1. Map of North Sweden showing the study sites. The numbers refer to sites that were unregulated (1–14), regulated without reduction (15–29), and reduced (30–52).

end of a canal or tunnel away from the dam, leaving as much as several km of the original channel with only a fraction of the original flow, usually a stipulated compensation flow in addition to local run-off. In contrast to the run-of-the-river systems, such sections with reduced flow often show a high degree of flow disturbance (see below; Englund & Malmqvist, 1996). Release depth in this study was always shallow. In addition to 14 unregulated reference sites, we studied mayfly richness and abundance of the two regulation regimes in regulated rivers at 15 sites with regulated but unreduced flow, and at 23 sites with regulated and reduced flow (Figure 1).

In addition to a curtailed discharge, the flow regime at sites affected by diversions typically results in: (1) extended periods of nearly constant flow and (2) erratic spikes when flow may increase several hundred percent from one day to the next. Spikes usually are associated with the opening of all gates when

reservoirs are brimful and precipitation occurs, or is forecast, usually in late summer or autumn. Peaking schemes (reduced nighttime flow) are rare but occurred at three of the sites studied. Due to the presence of different and largely independent flow factors, viz. reduced flow, diel flow variation and constancy, we attempted to separate their respective effects on the mayfly communities in subsequent analyses.

Forests and mires make up 70–80% and 5–15% respectively of these catchments, except in the western mountains where a large proportion is above the timber line. The proportion of urban and agricultural land is low, and the main human impacts, apart from hydroelectric exploitation, include ditching, forestry, peat mining, and acid rain. The altitudinal gradient ranges from 0 to 500 m a.s.l. Mean flow varies between 0.5 and 258 m³ s⁻¹, and the length of the rapids between 40 and 5000 m. Values for selected environmental variables are given in Appendix 1.

Site selection aimed at maintaining orthogonality in variables affected by hydropower exploitation such as flow variability, habitat size and isolation. This was also considered in relation to drainage area, upstream distance to lake, and to latitude and longitude (Figure 1). We made preliminary estimates of these variables for a large number of sites (>150) and from this sample we chose sites to minimise correlations between key variables ($r < 0.2$).

Data collection

Sampling was performed twice at each site: in Aug–Sep and again in Oct–Nov. Half of the sites were visited in 1992 and half in 1993. In both years precipitation was above normal in August. We sampled invertebrates and measured environmental variables in three 50 m segments situated at the upstream, middle, and downstream ends of each rapid. We took seven samples per site and sampling occasion by disturbing the substratum upstream of a hand net (mesh 0.5 mm), with each sample consisting of several smaller samples totally covering about 1 m² and distributed in as many microhabitats as could be identified, and with the seven samples dispersed among the three 50 m segments. Sampling over a relatively large area of each rapid increased the likelihood to recover all of the species present. We did not analyse the relationships between individual samples and abiota, since the focus of this report is on site-specific rather than microhabitat patterns. We did not either consider differences between early and late autumn, and therefore combined the samples from the

two occasions to a total of 14 per site. All invertebrates, including mayfly larvae, were sorted immediately in a white tray and preserved in 70% ethanol for later identification.

We recorded a large number of environmental variables, including conductivity, pH, total phosphorous and nitrogen, slope, and width. Substratum composition was rated into six categories (<0.2 mm, 0.2–2 mm, 2–20 mm, 20–80 mm, 80–200 mm, and >200 mm). From maps we estimated the percentage land use for each drainage area, the length of each rapid and the distance to nearest rapid. Measurements of mean daily flow for 300 days preceding our second visit were obtained from nearby hydroelectric power plants or from gauging stations run by the Swedish Meteorological and Hydrological Institute. Flow data were based on recordings from January to October in the year of sampling. Temperature sums (degree days, threshold 5 °C) were obtained from maps in Odin et al., 1983. Most other environmental variables could be assumed to remain fairly constant over time, viz. substratum, altitude, longitude, latitude, rapid and catchment areas, slope, width, and distance to nearest rapid. Only water quality data, including total phosphorus and nitrogen, water colour (absorbance at 420 nm), and conductivity were spot readings. Although these are likely to vary, we assumed that they would be representative.

Pre-treatment of data

Data from the benthic samples were used to calculate an abundance index and to estimate species richness. For each sample we rated the abundance of each taxon in three categories: 0 = not occurring, 1 = one specimen, 2 = more than one specimen. The ratings were summed over the 14 samples from each site, resulting in an index ranging from 0–28 used throughout the paper as 'abundance'. Identifications were aided with the key by Svensson (1986). Larvae of *Cloeon* are here referred to the species *dipterum*, although other species may have been present. Larvae of *Baetis fuscatus* and *B. scambus* could not be separated with certainty and were therefore combined.

Records of mean daily flow for 300 days (Jan–Oct) were used to calculate several measures of variability. Flow constancy was defined as the number of days in which the flow differed <5% from the discharge of the previous day. For three of the sites which had day–night regulation, we calculated the nighttime reduction in percentage of normal daytime flow.

Effects of daily flow fluctuations, constancy, and reduction were analysed graphically. The percentage change in abundances at sites with peaking flow ($N=3$), high flow constancy ($N=5$), and reduced flow (and not present in the former two categories) ($N=16$) was related to the abundances at unregulated sites ($N=14$) according to:

$$100 \cdot (A - U)/U,$$

where A is the abundance at affected sites, and U at unregulated sites.

Statistical methods

In addition to graphical analysis, we tested the hypotheses listed in Table 1 using analysis of variance and regression techniques. Univariate (ANOVA) and multivariate (MANOVA) analyses of variance were performed to compare mayfly abundances at sites of reduced flow with abundances at the reference sites. We used Rao's R in multivariate tests of MANOVA models for species belonging to the same family to test whether the abundances at sites with reduced flow were different from those at reference sites. On significance, we examined the univariate F tests for each species. Multiple regression analyses were used to examine the effects of flow (amount of remaining flow, diel flow regulation, and flow constancy) and isolation (distance to nearest rapid) factors on mayfly abundance at all the sites, and on species richness and abundance at sites with reduced flow. All species either listed for hypothesis testing in Table 1, indicating strong responses in the graphical analysis, or providing partial correlation coefficients with p -values < 0.10 in multiple regression were tabulated.

The number of species that were more common in the reference rapids were compared with the number that were commoner in regulated rapids in Chi-square tests, where equal numbers were expected values. Rare species were only considered in the general description of the material. In all these statistical analyses the software package Statistica 4.0 (Statsoft) was used.

For analyses of the assemblage structure we used canonical correspondence analysis (CCA; CANOCO version 3.11.5, ter Braak 1987). We used the option of 'forward selection', which is a procedure selecting, for each step, the environmental variable that adds most to the explained variance of the species abundance data. Only those variables were included that were statistically significant in Monte Carlo permutation tests (we used 1000 permutations) after each step (ter Braak,

1990). Three species, viz. *Baetis vernus*, *Metretopus borealis* and *Paraleptophlebia strandii*, were only found at single sites and were therefore excluded from the CCA analysis.

Further information on the design of the investigation can be found in Englund & Malmqvist (1996) and Englund et al., (1996).

Results

In total, 26 species of mayflies were recorded (Appendix 2). Only one species, *Baetis rhodani*, was found at all sites. Another five (in decreasing order) were collected at 40 or more sites, viz. *Heptagenia dalecarlica*, *Ephemerella mucronata*, *Centroptilum luteolum*, *H. sulphurea*, and *Leptophlebia marginata*. Five species were recorded at four or fewer sites. The mean abundances of each species in the three main categories (unregulated, reduced flow, regulated but unreduced flow) are shown in Figure 2.

Sites impacted by hydropower exploitation had significantly lower abundances and species richness than unimpacted sites (Table 2). Type of regime (unregulated; reduced flow; regulated but unreduced) significantly influenced mayfly abundance, but not richness ($p=0.089$). A post-hoc test (Tukey's test) showed that abundances were significantly lower at sites with reduced flow in comparison with unregulated sites ($p<0.01$).

To address the question of which mechanisms could generate the negative effects on mayfly richness and abundances at sites with reduced flow we used multiple regression analyses. In particular, we inspected the partial correlation coefficients of the flow variables, viz. flow constancy, diel flow variation, and flow reduction, and for richness also distance to the nearest rapid. The partial correlation coefficients indicated significant effects of diel flow variation for abundances, but not for constancy nor flow reduction (Table 3). For species richness, constancy and diel fluctuations appeared to be more influential than flow reduction (Table 3). On average, the distance to nearest rapid was 2.3 km at unregulated sites, and about 50% longer at regulated sites. The partial correlation for distance to nearest rapid did however not indicate any importance for this factor.

Heptageniids, baetids, ephemereids and *Caenis rivulorum* all became sparser in response to flow reduction in MANOVA (families) and ANOVA (*C. rivulorum*). In univariate tests, the following species indi-

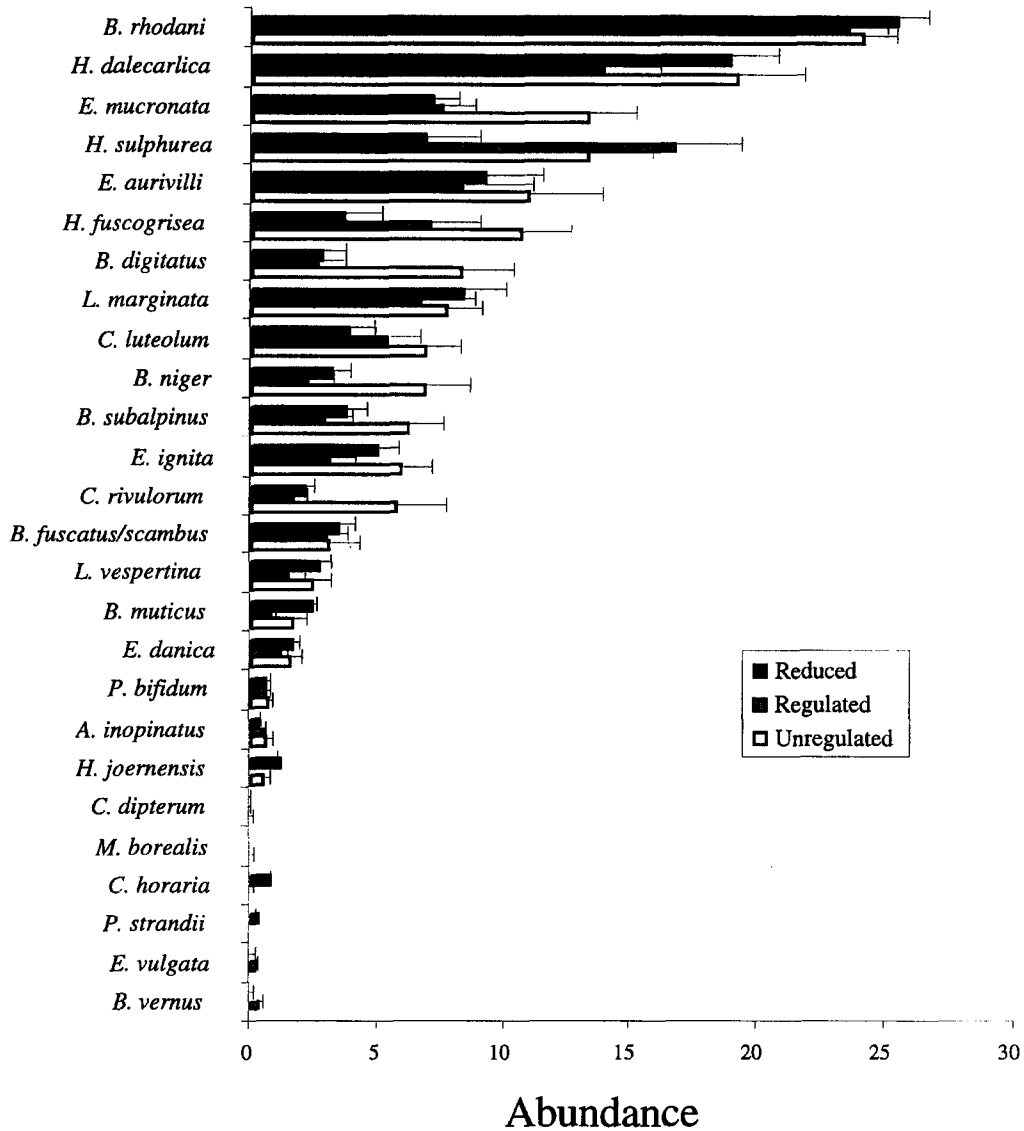


Figure 2. Mean abundances of mayfly larvae in the three regimes. Species ordered with respect to decreasing abundance at unregulated river sites. Error bars denote one standard error. Maximum average abundance is 28 (when ≥ 2 ind were found in each sample).

cated significant effects: *H. fuscogrisea*, *B. digitatus*, *B. niger*, *C. luteolum*, *E. mucronata*, and *Caenis rivulorum* (Table 4).

Sites with high flow constancy, peaking flow, and reduced flow had lowered abundance of most species in comparison to reference sites (Figure 3). The few exceptions include *H. joernensis* for all categories, and *E. ignita* for constant flow. In multiple regression, however, only a few species showed significant effects. Examination of the partial correlation coefficients indicated that daily fluctuations in flow were negative to

H. dalecarlica and *B. rhodani*. Percentage remaining discharge was positive to *H. fuscogrisea* and *H. sulphurea* (i.e. a negative response to reduced flow), but negative to *H. joernensis*, and flow constancy positive to *B. rhodani* and *Leptophlebia marginata* (Table 5). Several species, for which effects were predicted from the literature (Table 1), were not significantly impacted in this study.

Twenty species occurred at both unregulated and regulated sites. Of these species, nineteen were more common at the reference sites, whereas only one

Table 4. Effect of flow reduction shown in MANOVA of the abundances of species of three mayfly families (a–c) and ANOVA for *Caenis rivulorum* (d). The factor used was flow regime with the levels unaffected and reduced flow, respectively.

(a) Heptageniidae					
Test		Value	p-level		
Wilks' Lambda		0.579			
Rao's R (4,32)		5.650	0.001		
Dependent variable	Mean Sqr Effect	Mean Sqr Error	F df (1,35)	p-level	
<i>H. dalecarlica</i>	46.04	109.60	0.42	0.521	
<i>H. fuscogrisea</i>	535.36	29.68	18.04	<0.001	
<i>H. joernensis</i>	3.71	2.97	1.25	0.271	
<i>H. sulphurea</i>	175.66	90.62	1.94	0.173	
(b) Baetidae					
Test		Value	p-level		
Wilks' Lambda		0.430			
Rao's R (9,27)		5.486	0.0004		
Dependent variable	Mean Sqr Effect	Mean Sqr Error	F df (1,35)	p-level	
<i>B. digitatus</i>	322.00	44.94	7.16	0.011	
<i>B. fuscatus/scambus</i>	0.003	19.79	0.00	0.990	
<i>B. muticus</i>	1.95	14.99	0.13	0.721	
<i>B. niger</i>	159.52	36.45	4.38	0.044	
<i>B. rhodani</i>	0.69	25.34	0.03	0.870	
<i>B. subalpinus</i>	27.65	27.12	1.02	0.320	
<i>Centroptilum luteolum</i>	116.56	23.89	4.88	0.034	
(c) Ephemerellidae					
Test		Value	p-level		
Wilks' Lambda		0.769			
Rao's R (4,32)		3.295	0.0325		
Dependent variable	Mean Sqr Effect	Mean Sqr Error	F df (1,35)	p-level	
<i>E. aurivilli</i>	63.33	112.96	0.56	0.459	
<i>E. ignita</i>	0.26	38.77	0.01	0.935	
<i>E. mucronata</i>	471.09	46.46	10.14	0.003	
(d) <i>Caenis rivulorum</i>					
Univariate Test	Sums of Squares	df	Mean Square	F	p-level
Effect	143.04	1	143.04	4.51	0.041
Error	1109.88	35	31.71		

Table 5. Multiple regression analyses performed on the abundances of individual mayfly species from all sites using flow variables as predictors. The significance levels of the multiple regression models and the partial correlation coefficients of variables with p -values < 0.1 are shown. The percentage of flow remaining after flow reduction is indicated as 'Remaining flow', peaking flow in terms of percentage night-time reduction as 'Diel variation', and number of days with $< 5\%$ deviation between consecutive days as 'Constancy'.

Species	Model (p)	Variable	Partial correlation coeff.	p -level
<i>Heptagenia fuscogrisea</i>	0.025	Remaining flow	0.385	0.006
<i>H. joernensis</i>	0.245	Remaining flow	-0.252	0.080
<i>H. sulphurea</i>	0.062	Remaining flow	0.393	0.006
<i>H. dalecarlica</i>	0.239	Diel variation	-0.267	0.063
<i>Baetis digitatus</i>	0.587	—	—	—
<i>B. niger</i>	0.749	—	—	—
<i>B. rhodani</i>	0.049	Constancy	0.270	0.061
		Diel variation	-0.298	0.038
<i>Centroptilum luteolum</i>	0.239	—	—	—
<i>Ephemerella aurivilli</i>	0.904	—	—	—
<i>E. ignita</i>	0.408	—	—	—
<i>E. mucronata</i>	0.251	—	—	—
<i>Caenis rivulorum</i>	0.906	—	—	—
<i>Leptophlebia marginata</i>	0.276	Constancy	0.300	0.036

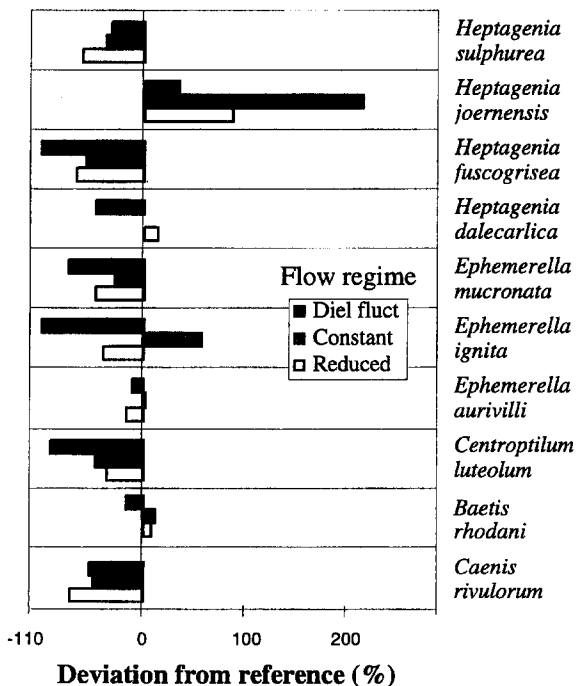


Figure 3. Deviations in the abundance of selected mayfly species relative to unregulated sites for three different types of impacted sites.

(*H. sulphurea*) was more common at sites of regulated (but unreduced) flow. This difference was significant (Chi-square = 8.1, $p < 0.01$). In contrast, there was no similar difference in abundance patterns between unregulated sites and those with reduced flow (13 vs 7, Chi-square = 0.9, $p > 0.05$).

The canonical correspondence analysis provided a significant species-environment relationship (F-ratio for the overall test = 3.25, $p < 0.01$) into which seven variables were incorporated. Strongest factors were related to climate (temperature sum), geography (latitude and longitude), and overall nutrient levels as indicated by conductivity (Figure 4). Weak, however significantly contributing factors were the width and area of rapids, and diel variation in flow. Flow constancy was marginally insignificant ($p = 0.067$).

A summary of all responses found on community, family and species levels with the different methods is presented in Table 6.

Discussion

In unregulated rivers different measures of flow patterns typically are strongly interrelated (Richards, 1990). River sites can accordingly be classified along a gradient from relative constancy to flashy conditions.

Table 6. Summary of the three regulation effects, viz. flow reduction, flow constancy and diel fluctuations on the total abundance and richness, and on families and species of Ephemeroptera. 0 = no effect, + = positive effect, - = negative effect, nt = not tested. MRA = multiple regression analysis (flow reduction only), F = univariate F in MANOVA, CCA = Canonical correspondence analysis. Signs within brackets indicate the results of the graphical analysis.

Mayfly category	Reduced flow	Flow constancy	Diel fluctuations	Test method
Total richness	0	+	-	MRA
Total abundance	0	0	-	MRA
Assemblage structure	0	0 ¹	sign effect	CCA
Heptageniidae	-	nt	nt	MANOVA
<i>H. fuscogrisea</i>	-(-)	0(-)	0(-)	MRA, F
<i>H. joernensis</i>	+(+)	0(+)	0(+)	MRA, F
<i>H. sulphurea</i>	-(-)	0(-)	0(-)	MRA, F
<i>H. dalearlica</i>	0(+)	0(0)	-(-)	MRA, F
Baetidae	-	nt	nt	MANOVA
<i>B. rhodani</i>	0(+)	+(+)	-	MRA, F
<i>B. digitatus</i>	-	nt	nt	MRA, F
<i>B. niger</i>	-	nt	nt	MRA, F
<i>C. luteolum</i>	-(-)	nt(-)	nt(-)	MRA, F
Ephemerellidae	-	nt	nt	MANOVA
<i>E. aurivilli</i>	0(-)	0(0)	0(-)	MRA, F
<i>E. ignita</i>	0(-)	0(+)	0(-)	MRA, F
<i>E. mucronata</i>	-(-)	0(-)	0(-)	MRA, F
Caenidae				
<i>C. rivulorum</i>	-(-)	nt(-)	nt(-)	ANOVA
Leptophlebiidae				
<i>L. marginata</i>	0	+	0	MRA

¹ Flow constancy was marginally insignificant ($p=0.067$)

In regulated systems, however, such measures often are considerably less correlated. This difference is important to recognise if the goal is to mitigate the conditions in regulated rivers.

This study clearly showed that the abundances and species richness of mayfly communities in Swedish rivers are affected by hydroelectric regulation. It also demonstrated that different species are influenced to a varying extent, and that different mechanisms affect different species. Thus, we found support for a number of the predictions deduced from Brittain & Saltveit's (1989) review. Peaking flow did reduce mayfly diversity and density (Ward, 1976), and curtailed the abundance of *Baetis rhodani* (Brooker & Morris, 1980). Reduced flow strongly affected *Ephemerella mucronata* (Garnås, 1985), though possibly favoured *Heptagenia joernensis* (Langeland & Haukebo, 1979). Contrary to predictions, reduced flow did not, however, reduce *E. aurivilli* (Garnås, 1985) or *E. ignita* (Coxw

et al., 1984), nor benefit *Baetis rhodani* (Garnås, 1985; Raddum & Fjellheim, 1993). We saw indications of lower densities of *E. aurivilli* and *E. ignita* in the analyses of the three regimes (Figure 3), but the reduced flow factor itself was not significant (Table 5). Flow constancy was not an influential factor for overall mayfly density, but it was significantly beneficial to *B. rhodani* as also found by Armitage (1976) and Raddum & Fjellheim (1993). The anticipated positive effect of river regulation on *E. ignita* and *C. rivulorum* was not observed (Armitage, 1976). In addition to the predicted effects we found negative effects on *H. fuscogrisea* and *H. sulphurea* by reduced flow and on *H. dalearlica* by flow constancy, showing that the reversal of constancy, i.e. flow stress, can be detrimental.

In addition to the negative effects on abundance, we saw evidence for only a moderate decline in richness, which supports the contention of Brooker & Morris (1980), who suggested that the species constellation

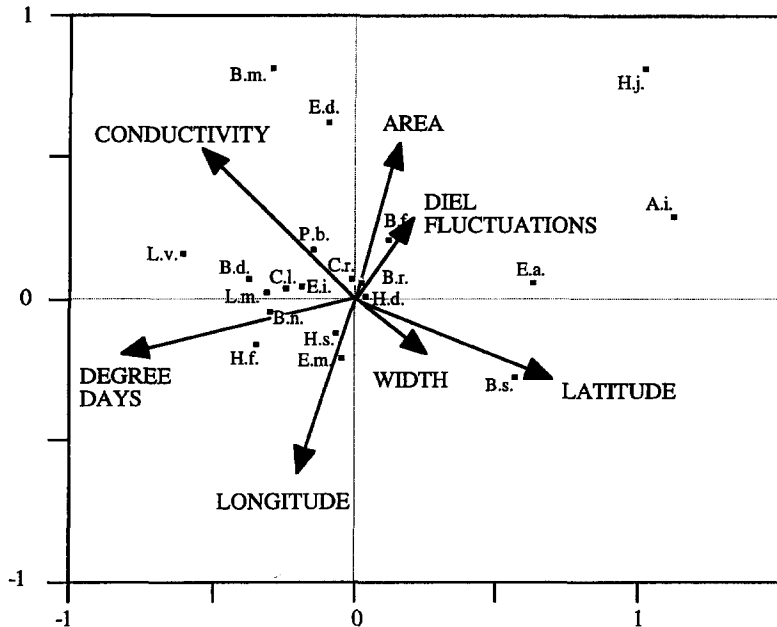


Figure 4. Ordination diagram of species from the canonical correlation analysis showing the first two axes. Significant environmental variables are represented by arrows. The species are indicated with squares and the abbreviations are A.i.=*Ameletus inopinatus*, B.d.=*Baetis digitatus*, B.f.=*B. fuscatus*, B.m.=*B. muticus*, B.n.=*B. niger*, B.r.=*B. rhodani*, B.s.=*B. subalpinus*, C.r.=*Caenis rivulorum*, C.l.=*Centropilum luteolum*, E.d.=*Ephemerella danica*, E.a.=*Ephemerella aurivillii*, E.i.=*E. ignita*, E.m.=*E. mucronata*, H.d.=*Heptagenia dalecarlica*, H.f.=*H. fuscogrisea*, H.j.=*H. joernensis*, H.s.=*H. sulphurea*, L.m.=*Leptophlebia marginata*, L.v.=*L. vespertina*, and P.b.=*Procladius bifidus*. Species with low weight (<5) were not included in the graph.

remains the same after regulation, but with abundances scaled down. Ward & García de Jalón (1991) observed much stronger alterations in mayfly taxonomic composition in a comparative study of mayflies in regulated rivers in Spain and the USA, especially below deep-release dams. Release depth importantly influences water quality and temperature, and although the effects on macroinvertebrates may reveal certain similarities in response to epilimnial and hypolimnial releases, the latter appear to cause the most drastic effects (Petts, 1984). In our study, no site was affected by hypolimnial release.

Contrary to expectation, isolation did not significantly affect mayfly richness. Either the distances between rapids in the regulated rivers were within the capacity for dispersal of any species, or extinctions simply have not taken place.

Our samples did not contain any of the rarest species in Sweden; none of the collected species has been reported to occur at fewer than 80 sites in an extensive survey of >5000 lake and stream sites (Degerman et al., 1994). Therefore, hydroelectric development in Sweden appears not to be a direct threat to any

of these species. This is not to say that dams do not have negative effects on the riverine biota. Possibly the effects of reduced abundances will influence other parts of the trophic systems, such as grazing effects on epibenthic algae and in predator-prey systems. It has been shown experimentally that mayfly larvae can exert substantial suppression of periphyton standing crop (Hill & Knight, 1987). Likewise, mayfly larvae may be important links to predaceous fish (Dudgeon, 1991) and invertebrate predators (Lancaster, 1990). To evaluate the indirect effects on trophic processes is an important challenge for future studies.

Effects on baetid and ephemerellid densities were limited to certain species. In contrast, most heptageniids showed clear and strong responses, especially to flow reduction. This family also was the most susceptible to regulation of British rivers (Armitage et al., 1987). These authors suggested that the effects may be the result of increased siltation and algal growth. In the present study, flow reduction was the strongest factor, and is associated with sedimentation of transported fines as a result of lower current velocities. Troelstrup and Hergenrader (1990) reported that hep-

Appendix 1. Environmental characteristics of the study sites.

Site number	Site name	Latitude	Longitude	Altitude (m a.s.l.)	Rapids area (m ²)	Distance to nearest rapid (m)	Conductivity ($\mu\text{S cm}^{-1}$)	pH	totP ($\mu\text{g l}^{-1}$)	totN ($\mu\text{g l}^{-1}$)	Discharge (m ^{3 s} -1)	Consistency (days)	Diel variation (% night-time reduction)	Catchment area (km ²)	Slope (cm per 50 m)	Width (m)	Substrate (index)	Absorbance (%, 420 nm)	Remaining discharge (%)	Temp sum (degree days)
Reduced																				
1	Kaitsjån	7200	1487	486	9694	1500	30.3	7.10	4.7	117	11	265	0	1870	57	39	6.00	0.012	6.04	650
2	Baggböle	7088	1712	10	22167	1000	34.9	7.05	5.3	249	24	219	0	26499	76	44	6.15	0.026	1.93	1100
3	Agnäs	7087	1670	100	11333	3000	25.8	6.66	4.8	341	24	178	0	2580	102	38	5.52	0.064	0.50	960
4	Lodlingeån	7006	1555	125	11733	100	47.8	7.23	4.4	469	1	182	0	730	53	15	5.48	0.052	1.00	1000
5	Björna	7053	1639	130	3833	200	33.9	7.00	8.1	331	8	234	0	3017	38	26	5.41	0.049	3.46	980
6	Hoan	6895	1458	253	6978	2000	26.6	6.76	3.5	261	6	224	0	1060	116	35	5.93	0.051	0.75	990
7	Storbodströmmen	7017	1395	380	60000	200	56.1	7.28	2.7	168	2	134	0	1350	58	30	5.33	0.021	2.94	800
8	Ålgård	7141	1730	115	13100	100	35.0	7.05	3	333	3	275	0	1400	70	13	5.96	0.036	7.88	1050
9	Alby	6932	1485	180	36244	2000	43.8	6.60	8.3	389	10	255	0	5290	122	26	6.00	0.042	6.67	980
10	Trångforsen	6953	1418	415	86944	500	27.2	6.72	7.1	319	4	260	0	2610	75	35	5.81	0.005	1.25	820
11	Billstaån	6979	1437	325	2400	300	89.8	7.00	4.7	258	3	297	0	510	30	12	6.00	0.007	5.11	1050
12	Blågåsilven	7176	1422	390	211111	1500	24.6	7.09	1.3	95.1	7	69	0	1070	52	42	5.78	0.005	7.22	720
13	Blågåle	7138	1452	290	13711	1000	25.4	6.92	2.8	158	14	225	0	4000	89	69	6.26	0.007	4.06	830
14	Myckle	7192	1738	20	30444	25000	28.9	6.90	13.5	235	28	262	0	7340	48	30	5.85	0.013	0.71	1100
15	Pettån	7211	1700	165	2387	4500	42.2	6.56	18.4	471	8	245	0	740	365	20	6.59	0.064	7.14	920
16	Alfa	6803	1512	120	53000	6000	30.8	6.61	8.6	343	4	253	0	3080	68	18	6.19	0.031	1.43	1200
Constant																				
17	Juktån	7241	1575	360	6422	200	36.4	6.51	1.7	111	4	272	0	1880	71	32	5.48	0.026	8.92	770
18	Slagnäs	7278	1609	412	13767	200	23.9	7.30	2.7	118	24	199	0	7360	44	46	5.70	0.005	13.96	750
19	Ulriksfors	7080	1491	282	26756	1000	31.4	7.26	1.5	147	3	279	0	6432	55	67	5.41	0.011	2.61	900
20	Lossen	6926	1356	510	39028	800	63.5	7.00	4.4	180	1	275	0	1390	63	16	5.74	0.015	1.59	730
21	Vångelilven	7070	1501	270	10633	3000	32.8	6.59	3.5	197	8	290	0	6510	45	18	5.56	0.012	1.42	950
Peaking flow																				
22	Junsterforsen	7162	1420	320	30133	13000	25.9	7.08	1.3	117	1	291	100	1350	153	38	6.63	0.004	3.94	740
23	Arbrå	6817	1531	100	1100	9000	32.8	6.46	8.6	386	36	248	83	14580	123	17	6.33	0.036	0.20	1200
24	Indalsilven	7020	1403	295	59222	500	27.5	7.00	1.6	94	258	108	40	8780	27	118	6.15	0.014	100.00	980
Regulated																				
25	Vojmán	7164	1544	340	6650	6000	34.7	7.00	2.3	194	67	237	0	3910	18	44	5.85	0.025	100.00	800
26	Nätungforsen	7119	1750	2	6800	1500	37.1	6.85	4.9	420	15	216	0	1673	107	34	5.56	0.038	100.00	1100
27	Ljungan E4	6907	1582	1	15133	300	56.4	7.31	2.4	194	123	137	0	12076	15	76	5.44	0.011	100.00	1160
28	Ljusnan	6856	1510	135	196944	600	32.0	7.10	3.2	213	127	194	0	11690	32	79	5.07	0.026	100.00	1100
29	Köfällire	6920	1469	250	11867	700	42.8	7.24	2.2	137	57	241	0	4910	113	59	5.52	0.016	100.00	1030
30	Långan	7047	1429	300	9783	700	41.2	7.25	0.9	128	45	242	0	1530	18	65	5.74	0.008	100.00	850
31	Hårkan	7053	1446	280	123333	6000	30.8	7.16	1	136	97	240	0	3850	121	206	5.85	0.012	100.00	840
32	Krokforsen	7298	1469	454	15433	5000	28.6	6.85	1.1	104	60	218	0	1270	22	51	5.81	0.003	100.00	530
33	Arjeplog	7329	1594	420	11400	5000	23.6	6.94	3	184	127	240	0	3610	67	38	6.00	0.005	100.00	730
34	Moforsen	7029	1559	55	17222	12000	28.7	7.60	19	541	522	126	0	23400	5	172	4.78	0.026	100.00	1030
35	Meåforsen	7022	1542	110	24800	3500	38.2	6.85	4.5	219	203	174	0	7580	16	62	3.67	0.011	100.00	1020
36	Forsa	6847	1560	34	11567	2500	46.1	7.04	7.2	415	19	291	0	1940	24	39	5.48	0.009	100.00	1230
37	Finnstuguforsen	6805	1488	200	22500	3000	26.7	6.63	6.1	335	26	274	0	2220	89	45	5.63	0.036	100.00	1180
38	Ore	6790	1465	210	7200	1000	21.2	6.26	5.1	335	22	243	0	1229	10	48	4.48	0.034	100.00	1110
Unregulated																				
39	Laxgårdsforsen	7100	1734	20	15722	500	40.9	7.15	5.5	235	9	264	0	970	63	31	5.56	0.036	100.00	1100
40	Stensundsforsen	7271	1577	340	31111	700	33.2	7.55	1.1	92.8	162	248	0	6110	28	78	5.93	0.037	100.00	800
41	Åbyilven	7245	1733	170	35667	1000	27.5	7.10	3.4	206	7	250	0	790	52	24	5.63	0.032	100.00	880
42	Byskälilven	7238	1728	170	7133	300	31.0	7.16	3.9	254	44	235	0	3470	37	48	5.41	0.022	100.00	880
43	Harmångersån	6875	1566	45	6547	1500	41.4	7.00	3.9	179	7	226	0	520	193	55	5.74	0.021	100.00	1200
44	Gimån	6967	1495	260	82320	2000	94.3	8.02	2	215	19	269	0	2260	18	69	4.67	0.007	100.00	950
45	Ammerån	7034	1488	265	16590	2000	84.8	7.54	2.4	296	48	178	0	2060	81	55	6.30	0.027	100.00	880
46	Tegeforsen	7035	1358	375	30433	1000	30.7	6.94	3.6	159	83	201	0	2940	59	101	5.81	0.016	100.00	750
47	Yckån	7083	1363	400	10250	500	13.9	6.60	3.6	167	10	142	0	160	53	41	6.04	0.009	100.00	700
48	Edeforsen	7048	1482	300	4750	8000	71.4	7.19	7.5	365	55	222	0	1800	46	53	5.37	0.034	100.00	860
49	Lomforsen	7138	1642	220	2093	1000	32.1	6.90	18.3	433	26	173	0	1560	16	52	5.26	0.057	100.00	900
50	Håkansforsen	7203	1741	20	17344	1800	45.3	6.93	12.3	456	17	192	0	950	57	25	5.63	0.051	100.00	1100
51	Sikvar utloppet	7086	1735	0.5	1213	10000	36.1	6.55	16.7	393	14	287	0	1100	46	20	5.63	0.061	100.00	1100
52	Lilforsen	7112	1701	100	16844	800	34.0	7.16	2.3	161	212	258	0	11897	11	84	4.81	0.036	100.00	970

Appendix 1.

tagniids recolonised sites after cessation of diel flow fluctuations.

Assemblage structure was primarily related to gradients in climate and geography. Diel variation in flow did, however, significantly contribute to the pattern observed. These results suggest that the structure

of mayfly assemblages relate to hydropower schemes chiefly within the limits set by regional features.

Since the focus of this study was on autumnal mayfly communities in river rapids it is not possible to predict the results for other habitats or for summer species. It is likely, however, that hydropower regulation will have an effect also in summer because the

stranding, flow stress, and indirect effects via siltation, food, and perhaps, predators. Increasing distance between remaining rapids was not found to be of any significance. Judging from our results, attempts to moderate regulation impacts on mayflies should examine the possibility of increasing residual flow and adopting natural flow dynamics.

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