

ROLE OF DISCHARGE AND TEMPERATURE VARIATION IN DETERMINING INVERTEBRATE COMMUNITY STRUCTURE IN A REGULATED RIVER

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ABSTRACT

This paper quantifies patterns of discharge and temperature variation in the regulated river Lyon and the adjacent, unregulated river Lochay (Scotland) and assesses the importance of these patterns for benthic invertebrate community structure. Invertebrates were sampled at sites in each catchment in autumn, winter and spring during the 2002–2003 hydrological year. Metrics were used to characterize the discharge and temperature regimes in the period immediately preceding invertebrate sample collection. Metric values were then used in a canonical correspondence analysis (CCA) of the invertebrate sample data, in order to assess the significance of individual metrics and the overall importance of flow and temperature variability for community structure. The variance in the invertebrate data explained by this CCA was compared to that from a CCA using a range of environmental data from the sites (stream-bed algal cover, channel hydraulic, sedimentary and water quality characteristics). This comparison allowed assessment of the relative importance of environmental variables versus hydrologic and thermal regimes.

Invertebrate communities in the Lyon were relatively poor and uneven, with Ephemeroptera, Plecoptera and Coleoptera poorly represented. Distinct site and seasonal clusters were evident in the CCA ordination biplots, with Lyon and Lochay sites separated in dimensions represented by geometric mean sediment size, water temperature and algal cover. The cumulative variance values from ordinations using the discharge and temperature metrics were consistently highest, suggesting that differences in invertebrate communities showed a stronger relation to patterns of discharge and temperature variability than to the broader suite of environmental conditions. Although there were marked thermal differences between sites, temperature metrics appeared no more important than discharge metrics in explaining differences in invertebrate community structure. A number of the temperature and discharge metrics appeared similarly important, suggesting that no one aspect of the hydrothermal regime was any more important than others in helping to understand differences in invertebrate community between the study sites. Copyright © 2007 John Wiley & Sons, Ltd.

KEY WORDS: invertebrates; discharge; temperature; variability; metrics; hydropower

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INTRODUCTION

More than 45 000 large dams and a further 800 000 small dams are now estimated to exist worldwide (Abramovich, 1995; McCully, 1996; Pringle, 2000; WCD, 2000). Research has indicated that there are some generalized patterns of ecological change that tend to follow impoundment (Brittain and Saltveit, 1989). For example, invertebrate species richness typically has been found to decrease below dams, although total abundance may increase; certain mayfly species are sensitive to flow regulation and so may disappear below dams, while taxa such as oligochaetes that are tolerant of flow change often reach high abundance. Thus, there are alterations to invertebrate community structure that, to some extent, are now predictable. Nonetheless, location-specific factors related to geography and the design and operational use of a given dam dictate that studies are needed on a case-by-case basis in order to assess regulation impacts.

A parallel research agenda has focussed on developing so-called ecologically acceptable or environmental flows for regulated rivers (Brown and King, 2000; Gibbins *et al.*, 2001a). Environmental flows seek to re-establish more natural patterns of flow variability and, in so doing, help maintain or restore ecological integrity. In Europe, the

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Water Framework Directive (2000/60EC) seeks to maintain and, where necessary, improve the ecological status of freshwater habitats. Thus, for many rivers affected by impoundment, the Directive is likely to require agencies involved in river management to develop environmental flow regimes. Numerous indices and metrics that help characterize patterns of flow variability now exist (Richter *et al.*, 1997; Clausen and Biggs, 1998; Archer and Newson, 2002; Olden and Poff, 2003). These can be used to provide insights into the way in which regulation has affected discharge regimes and to identify targets for re-naturalization as part of the development of environmental flow regimes.

Despite broad recognition of the importance of discharge variability, relatively few studies have explicitly linked changes to patterns of variability, quantified using indices or metrics, to community structure in regulated rivers. Even fewer studies have characterized patterns of thermal variability using such metrics (Tetzlaff *et al.*, 2005) and linked ecological changes following impoundment to changes in temperature metric values. Because thermal alterations below dams have been known for some time to contribute to ecological change (Boon, 1987), it is important that the development of environmental flow regimes is based on an understanding of the ecological significance of both discharge and temperature variability.

This paper aims to assess the impacts of flow regulation on the invertebrate fauna of the River Lyon, Scotland (Figure 1). It quantifies patterns of discharge and temperature variability in the river and assess the importance of these patterns for invertebrate community structure. The Lyon is typical of many rivers that have been regulated for some time, in that no pre-impoundment hydrologic, thermal or ecological data exist. For this reason, a true Before-After-Control-Impact (BACI) monitoring programme was not possible. An unregulated but otherwise similar river was therefore used as a surrogate for the unregulated Lyon; this allows inferences to be made as to the extent to which physical and chemical conditions and patterns of discharge and thermal variability in the Lyon have been affected by regulation and whether these differences are responsible for differences in invertebrate communities. The focus of the paper is on community structure rather than the distribution and abundance patterns of individual species.

STUDY AREA AND SITES

The River Lyon is 49 km long and has a catchment area of 391 km² (Figure 1). Mean annual discharge in the Lyon at the Comrie Bridge gauge is 12.10 m³ s⁻¹ (1958–1999 data). Flows in the Lyon have been regulated since the completion of the Breadalbane Scheme in 1953. The scheme comprises a series of dams and water diversions in the Lyon and its tributaries, as well as several adjacent catchments. Two HEP dams are located on the mainstem Lyon. Electricity production at the uppermost dam (which impounds the river to form Lubreoch Reservoir) results in a hydropeaking flow regime in the downstream reach (Figure 2). This reach extends for 4 km before flowing into the second reservoir, Stronuich. Although Stronuich also produces HEP, water used to generate the electricity is not

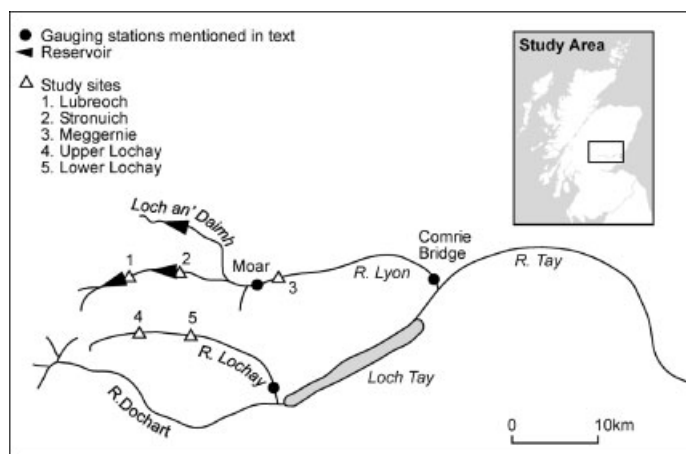


Figure 1. Location of the study area and sites

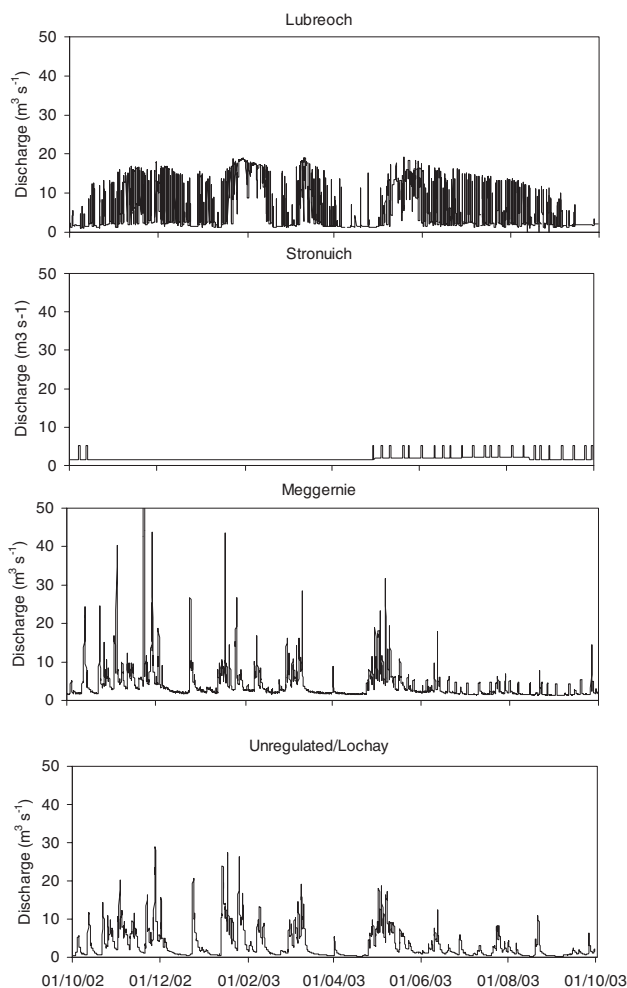


Figure 2. Discharge regimes for the 2002/2003 hydrologic year. Note that because hydrographs for both the Lochay sites were constructed by multiplying discharge from the nearest gauge by a conversion factor related to respective catchment areas, patterns of discharge change at the two sites are identical; only magnitude differs. Thus, for clarity, only one Lochay hydrograph is shown

released into the river; rather, it is pumped directly out of the catchment and used to support HEP production elsewhere. Flows in the Lyon immediately downstream from Stronuich are dominated by the reservoir's compensation discharge ($1.5\text{--}2.0\text{ m}^3\text{ s}^{-1}$), punctuated by freshet releases (approximately $5\text{ m}^3\text{ s}^{-1}$) designed to encourage upstream migration and spawning of Atlantic salmon *Salmo salar*. HEP production at the two dams is supported by intra- and inter-basin water transfers. Water from a number of Lyon tributaries that would otherwise discharge into the river further downstream are diverted into one or other of the two dams, as is water held in Loch an' Daimh Reservoir.

The Lochay is the adjacent catchment and has the same general topography and climate as the Lyon. It lies at a similar altitude and has similar land-use characteristics. The Lochay differs from the Lyon principally in its smaller catchment area (132 km^2) and lack of impoundment in its upper catchment (although its lower section is regulated to produce HEP).

The two study sites located immediately downstream from the two Lyon dams (Figure 1) allowed characterization of environmental conditions and invertebrate communities in reaches with contrasting regulated discharge regimes. The site on the Lyon at Meggernie was located approximately 5 km downstream from Stronuich Reservoir. Several large, unregulated tributaries below Stronuich contribute to the flow regime at Meggernie. This site was used to assess the extent of any downstream recovery in hydrologic, thermal and environmental conditions

Table I. Summary statistics for the five study sites

Site name	National grid reference	Altitude (m.a.s.l.)	Catchment area (km ²)	Distance from source (km)
Lubreoch	NN466418	310	83.61	9
Stronuich	NN509421	280	107.95	13
Meggernie	NN548459	220	170.95	18.5
Upper Lochay	NN454356	220	45.75	9.5
Lower Lochay	NN489368	190	68.22	12

and in invertebrate communities. The two sites on the Lochay were located at equivalent catchment positions to the two upper Lyon sites (as far as possible, integrating distance from source and altitude) and were used as reference sites (Table I). They are located in the upper part of the catchment where there are no impoundments.

METHODS

Hydrologic and thermal regimes

The study period extended from April 2002 to September 2003. River discharge data for this period were available from flow gauges (gauge sites located in Figure 1) and from information on release regimes from Lubreoch and Stronuich. Hydrographs for study sites that were not adjacent to a gauge or immediately downstream from a dam were constructed by adjusting data from the nearest gauge site according to any differences in catchment area. Temperature loggers (Gemini Tinytalk) were placed in the river at the five study sites for the duration of the study. These were housed in white plastic tubes and logged temperatures at hourly intervals to an accuracy of $\pm 0.2^{\circ}\text{C}$. Malfunction and/or loss of some loggers resulted in periodic data gaps.

Invertebrates and environmental conditions

Invertebrates were sampled in spring/early summer (May), autumn (September) and winter (February). Sampling in each of three seasons allowed assessment of whether patterns of site similarity differed between seasons. The May sampling date coincided with the time that Atlantic salmon fry in the Lyon emerge from the gravels and first require an external food source. Thus, the May data provided an insight in the food available to young fish at this critical stage in their life cycle. The sampling programme focussed on riffle habitats. Each site was a pool-riffle reach, of a length necessary to include five separate riffles. Individual riffles were typically separated by several tens of metres of river length, so each site consisted of a 100–200 m reach of river. Six weeks before each sampling date, 25 plastic colonization baskets were dug into the stream bed at each site (Figure 3). In each riffle at each site, five baskets were placed in a square cluster, covering approximately 10 m². Sediments removed from the bed to create each hole were placed inside respective baskets, acting as the colonization substrate. The sediment was denuded of invertebrates first by the drift that resulted from the initial digging process and then by hand cleaning before being placed in the baskets. Sediments placed in each basket were not controlled or sorted by size in any way; they were simply the materials excavated from each location. Only after invertebrate samples were collected was the size distribution of sediment quantified (see below). This size data was then used in a canonical correspondence analysis (CCA) to determine the importance of sediment for invertebrate community characteristics.

On the day of sampling, a single basket was randomly selected from each riffle cluster and removed for analysis; thus, five replicate samples were collected from each site. This protocol meant that the experimental inference space (the 'site') was of a scale appropriate to the treatment effects being tested for (differences between sites). Collecting all samples from a single riffle at each site would have resulted in pseudo-replication, as defined by Hurlburt (1984). On the day of sampling, each selected basket was lifted from the bed and the whole of its contents placed in a plastic bag and taken back to the laboratory. The remaining unused baskets were also removed. Although not used in the analysis, these spares allowed for the loss of some baskets during the colonization period (e.g. due to scouring flows) or mishaps during the process of removal (e.g. accidental spillage of basket contents).

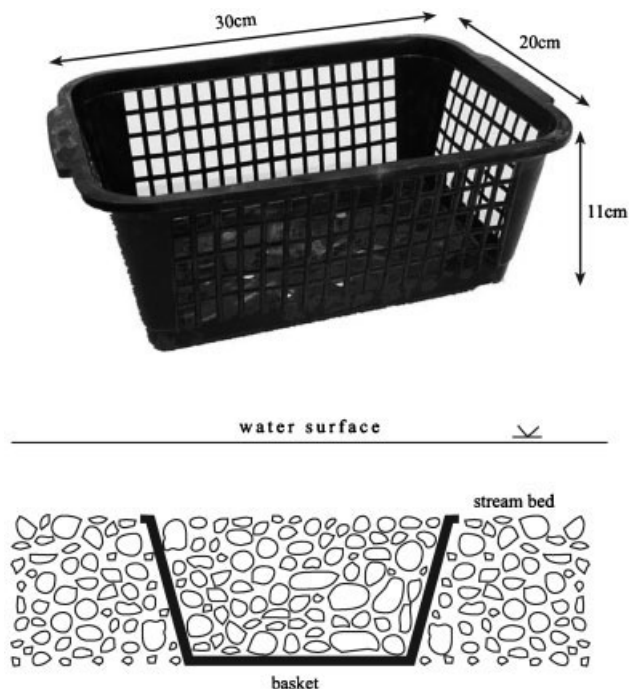


Figure 3. Colonization baskets used to sample invertebrates. A basket is shown *in situ* in the lower part of the figure

Their presence meant that it was always possible to randomly select five replicate samples from each site. The process of basket placement, colonization and random removal was repeated in each season.

Invertebrates colonizing each basket were counted and identified to species level, except for certain difficult groups (oligochaetes were identified to subclass and Simuliidae, Chironomidae, Ceratopogonidae, Culicidae, Antocha, Tipula and Dicranota were identified to genus level). At the time of removal, water depth, velocity, dissolved oxygen (DO), temperature, conductivity, turbidity and pH were measured at each basket location. Water samples were collected from the water column above each basket and analyzed in the laboratory to determine gran alkalinity. Algal cover was assessed visually as per cent cover in a 1 m² area centred on each basket. All of the substrate from each basket was sieved into size fractions and the geometric mean sediment size determined. Thus, environmental variables used in the analyses consisted of hydraulic, hydro-chemical, sedimentary and algal data, with a measurement of each variable corresponding to each replicate invertebrate sample.

Statistical treatment of the data

Two-way ANOVA (log transformed data) was used to test for differences in taxon richness and total abundance between sites and seasons. Species were also aggregated into major groups, some known to be sensitive (e.g. Coleoptera) and some tolerant (e.g. Oligochaeta) to changes in flow regimes (Armitage *et al.*, 1987; Munn and Brusven, 1991; Extence *et al.*, 1999; Grown and Grown, 2001). The relative abundance of these groups was assessed to provide an indication of community evenness.

Principal components analysis (PCA) was used to summarize and compare site environmental conditions on the day invertebrate samples were collected. A single PCA was produced, so as to show relations between sites and seasons. Prior to PCA, a correlation matrix of the environmental variables was produced. Alkalinity and pH proved to be significantly correlated ($p < 0.05$), so only the former was used in the PCA. In total, nine variables were included in the PCA.

CCA was used to assess the relative importance of environmental, hydrologic and thermal conditions in determining differences in invertebrate community structure between sites and seasons. Two CCA ordinations were produced: the first assessed the importance of environmental conditions on the day of sampling while the second

assessed the importance of hydrologic and thermal regimes over the period preceding invertebrate sample collection (i.e. during the colonization period). The first ordination was a simple analysis of invertebrate sample data and the environmental data values associated with each sample. The second was more complicated and involved several preliminary steps. First, discharge and thermal regimes for 2-week period preceding sample collection were characterized using a number of metrics (Table II). These metrics have been shown from previous studies either to best represent the critical attributes of a flow regime (Olden and Poff, 2003) or to correlate with invertebrate community structure (Clausen and Biggs, 1998; Gibbins *et al.*, 2001b). The initial number of metrics (13 for discharge and 11 for temperature) was then reduced using PCA to identify those that differed most between the sites (highest component loadings on PCA Axes 1 and 2). Values of these key metrics (13 in total) were then used as the environmental data matrix values in the CCA. A 2-week period was used simply because this was the longest period across which continuous temperature and discharge data were available at the same temporal resolution.

For each of the two CCAs, all data were analyzed together; that is, each ordination captured both spatial (within and between sites) and temporal (between seasons) variation. On a CCA biplot, the length of the arrow representing an environmental variable indicates the strength of the correlation between that variable and the ordination axes (McCune and Mefford, 1995); the longer the arrow the stronger the relationship between a variable and the species data. In the current study, arrow lengths were used to make inferences about the relative importance of environmental variables and the flow and temperature metrics. The objective of producing two ordinations was to determine the relative importance of environmental conditions versus hydrologic/thermal regimes.

RESULTS

Environmental conditions and thermal regimes at the study sites

PCA of replicate measurements of environmental variables on the days that colonization baskets were removed produced distinct site and seasonal clusters (Figure 4). Conductivity, alkalinity, depth and temperature accounted for most of the variation in the environmental data (highest component loadings on Axis 1). Within each season, the Lochay sites separated from the Lyon sites across Axis 1. With respect to Axis 1 scores, Meggernie typically occupied an intermediate position, sitting between the Lochay and remaining Lyon sites.

The thermal regimes of the study sites differed across daily, weekly and seasonal time-steps, as well as in the magnitude of instantaneous maximum and minimum temperatures. Temperatures at the Lochay sites were consistently more variable in terms of both mean daily values and daily rhythms (Figure 5). Typically the mean daily temperatures in the Lochay differed by 1–2°C to the Lyon sites, although occasionally differences were much greater (e.g. in early June the Lochay mean daily temperature was 5–6°C warmer than the Lyon sites). In terms of daily rhythms, mean daily and instantaneous high and low temperatures, the Lyon at Meggernie was intermediate between the Lochay and the other two Lyon sites. PCA of the temperature and discharge metrics indicated both seasonal and between-site differences (Figure 6). Seasonal separation was principally across Axis 1; for example, winter samples from each site were located more to the positive end of the axis. These seasonal differences were driven most by the mean and median temperature as well as the temperature exceeded for 5% of the time (T_5) (highest component loadings on Axis 1). There was much overlap between the 3 Lyon sites with respect to Axis 1 scores; separation of sites was clearer across Axis 2, an axis representing the minimum specific discharge value and the duration of time that temperature was less than 50% and 20% of the mean temperature.

Invertebrate community structure

In total, 57 taxa were recorded in the Lyon and 72 in the Lochay. Patterns of relative site taxon richness and abundance differed between the seasons (Figure 7). For both taxon richness and abundance, two-way ANOVA indicated significant differences between sites (taxon richness $p < 0.001$, df 74, F 35.46; abundance $p < 0.001$, df 74, F 29.14) and between seasons (taxon richness $p < 0.001$, df 74, F 17.48; abundance $p < 0.001$, df 74, F 23.39). There were also significant interactions between site and season (taxon richness $p < 0.001$, df 74, F 4.63; abundance $p < 0.001$, df 74, F 6.71). Results of multiple comparison tests of difference (Tukey's HSD at $p < 0.01$) are indicated by the horizontal bars on Figure 7. Taxon richness was consistently less at Lubreoch and Stronich than the other sites. Patterns in total abundance were less consistent, but in general Lubreoch had fewest individuals.

Table II. Complete list of metrics of discharge and thermal variation (and their abbreviations) used in PCA and CCA analyses

	Hydrologic metrics	Thermal metrics
(a) Statistics	<p>Specific mean flow (Smean)¹</p> <p>Specific median flow (Smed)</p> <p>Specific hourly maximum flow (Smax)</p> <p>Specific hourly minimum flow (Smin)</p> <p>Specific Q₉₅ (discharge exceeded for 95% of the time) (SQ₉₅)</p> <p>Specific Q₅ (Discharge exceeded for 5% of the time) (SQ₅)</p> <p>Skewness-Q</p>	<p>Mean temperature (Tmean)</p> <p>Median temperature (Tmed)</p> <p>Maximum hourly temperature (Tmax)</p> <p>Minimum hourly temperature (Tmin)</p> <p>T₉₅ (temperature exceeded for 95% of the time) (T₉₅)</p> <p>T₅ (temperature exceeded for 5% of the time) (T₅)</p> <p>Skewness-T</p>
(b) Distribution	<p>Low flow measures:</p> <p>Duration flows less than 20% of mean (DM < 20%)</p> <p>Duration flows less than 50% of mean (DM < 50%)</p>	<p>Low temperature measures:</p> <p>Duration temperatures were less than 20% of mean (DMT < 20%)</p> <p>Duration temperatures were less than 50% of mean (DMT < 50%)</p>
(c) Duration (% time)	<p>High flow measures:</p> <p>Duration that flows were greater than 3 times the median flow (DQ > 3×)</p> <p>Duration that flows were greater than 7 times the median flow (DQ > 7×)</p> <p>The frequency that flows exceeded 3 times the median (FC3×)</p> <p>The frequency that flows exceeded 7 times the median (FC7×)</p>	<p>High temperature measures:</p> <p>Duration that temperatures were greater than 3 times the median (DT > 3×)</p> <p>Duration that temperatures were greater than 7 times the median (DT > 7×)</p> <p>The frequency that temperatures exceeded 3 times the median (FT3×)</p> <p>The frequency that temperatures exceeded 7 times the median (FT7×)</p>
(d) Frequency (number of times crossing threshold)		

¹Specific discharge was used to remove the potentially dominating influence of between-site differences in absolute discharge.

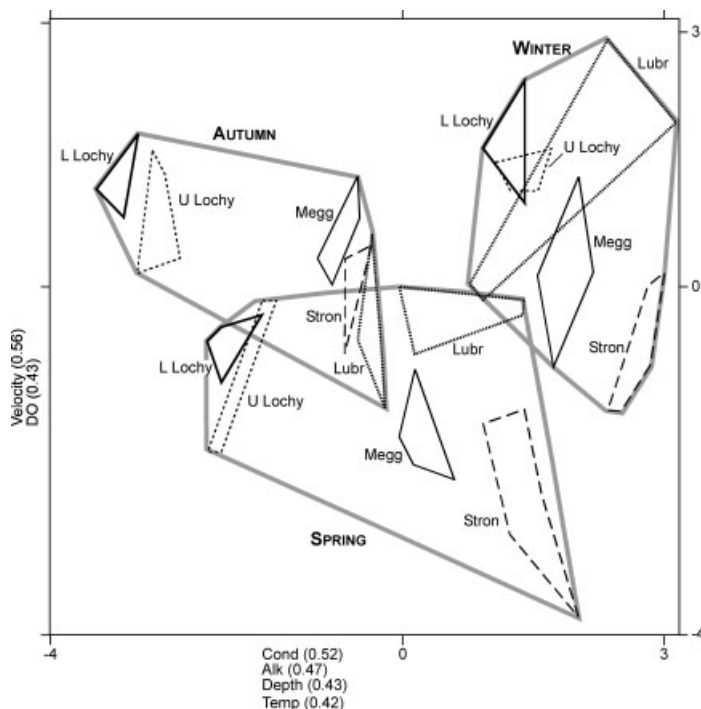


Figure 4. Principal components analysis (PCA) of environmental conditions at study sites on spring, autumn and winter sampling dates. The five samples collected from each site have been grouped to produce a polygon. For clarity, individual samples are not shown. The larger grey polygons group sites according to season. Environmental variables with the highest component loadings are shown for each axis (component loadings are given in parentheses). Cumulative per cent variance for Axes 1 and 2 is 54.5%

There were some marked differences in the taxonomic composition of communities present at each site (Figure 8). Ephemeroptera were consistently scarce at the sites immediately below the Lyon dams, particularly Lubreoch. The relative abundance of Plecoptera was similar to Ephemeroptera: they were scarce below the dams but comprised a consistently higher proportion of the community at the other sites. Coleoptera were not found at any of the Lyon sites but, while never abundant, were consistently present at the Lochay sites. Conversely, Oligochaeta and Diptera were consistently numerous in the Lyon, particularly at Lubreoch and Stronuich, but scarce or absent from the Lochay. Overall, the patterns depicted in Figure 8 illustrate the relatively uneven community present in the Lyon, a community dominated by oligochaetes and diptera.

CCA of the invertebrate samples and the environmental data collected on the day of sampling produced a seasonal separation across ordination space (Figure 9). The autumn sample data were the most distinct, separating from the spring and winter in dimensions represented by conductivity, alkalinity and DO, as well as water velocity and depth. Within each season, samples clustered neatly by site, with little or no overlap between Lyon and Lochay site polygons. Lochay sites either overlapped or were each other's closest neighbours, with separation of these from the Lyon sites being in dimensions represented by mean sediment size, temperature and per cent algal cover. The Lyon sites immediately below the two dams were either close together or overlapping on ordination space.

The CCA using temperature and discharge metrics (Figure 10) explained slightly more (19%) of the variance in the invertebrate sample data than that using the environmental data (16%). The positions of site polygons with respect to individual flow and temperature metrics differed between seasons. No single flow or temperature metric exerted a dominant influence on the invertebrate data, with a number of flow and temperature metrics having similar arrow lengths. Variables with the least influence (shortest arrows) were all temperature metrics (the maximum temperature (T_{max}), the temperature value exceeded for 5% of the time (T_5) and the skewness of the temperature distribution). CCA ordinations depicted in Figures 9 and 10 capture both seasonal and site related variation in invertebrate community composition. Table III gives results of CCAs conducted for each of the seasons separately; for each season it gives an indication of how much of the variation in community composition within and between

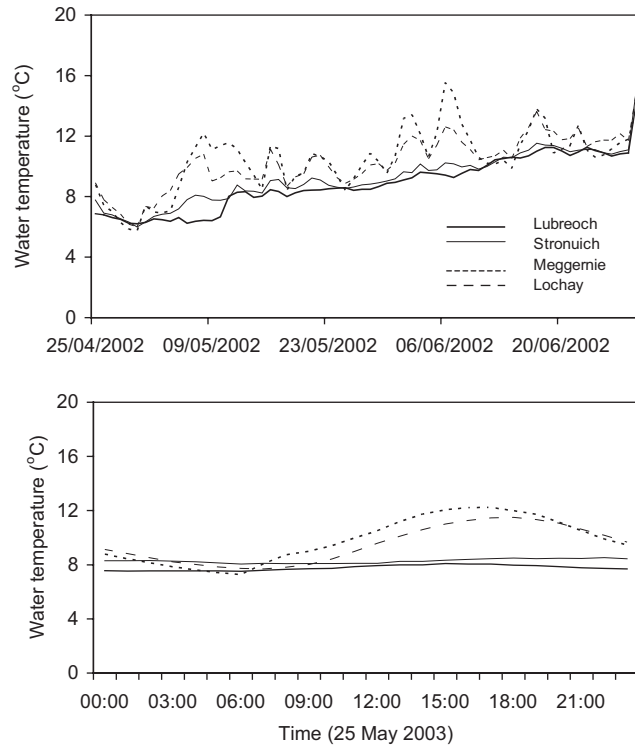


Figure 5. An example to illustrate key differences in site thermal regimes. The figure shows the spring period, centred on the time that invertebrate samples were collected; May 25 is used to illustrate patterns over a 24-h cycle

sites can be accounted for by the environmental variables and the discharge/temperature metrics. The cumulative variance values from ordinations using the discharge and temperature metrics were consistently highest, suggesting that differences in invertebrate communities showed a stronger relation to patterns of discharge and temperature variability than to the broader suite of environmental conditions.

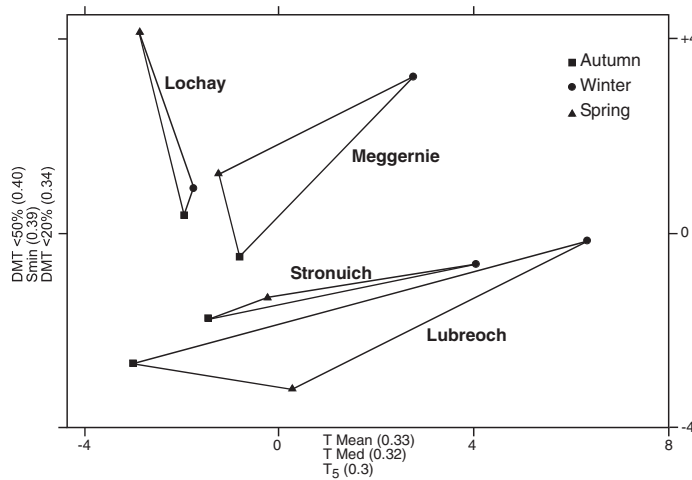


Figure 6. Principal components analysis (PCA) of the discharge and thermal characteristics of study sites in the spring, autumn and winter periods. The PCA was produced using data for the 2-week period preceding invertebrate sample collections. Water temperature and discharge over this period were characterized using the suite of metrics listed in Table II. Note that due to periodic data gaps, Lochay data are for the upper site only. Cumulative variance for Axes 1 and 2 is 61%

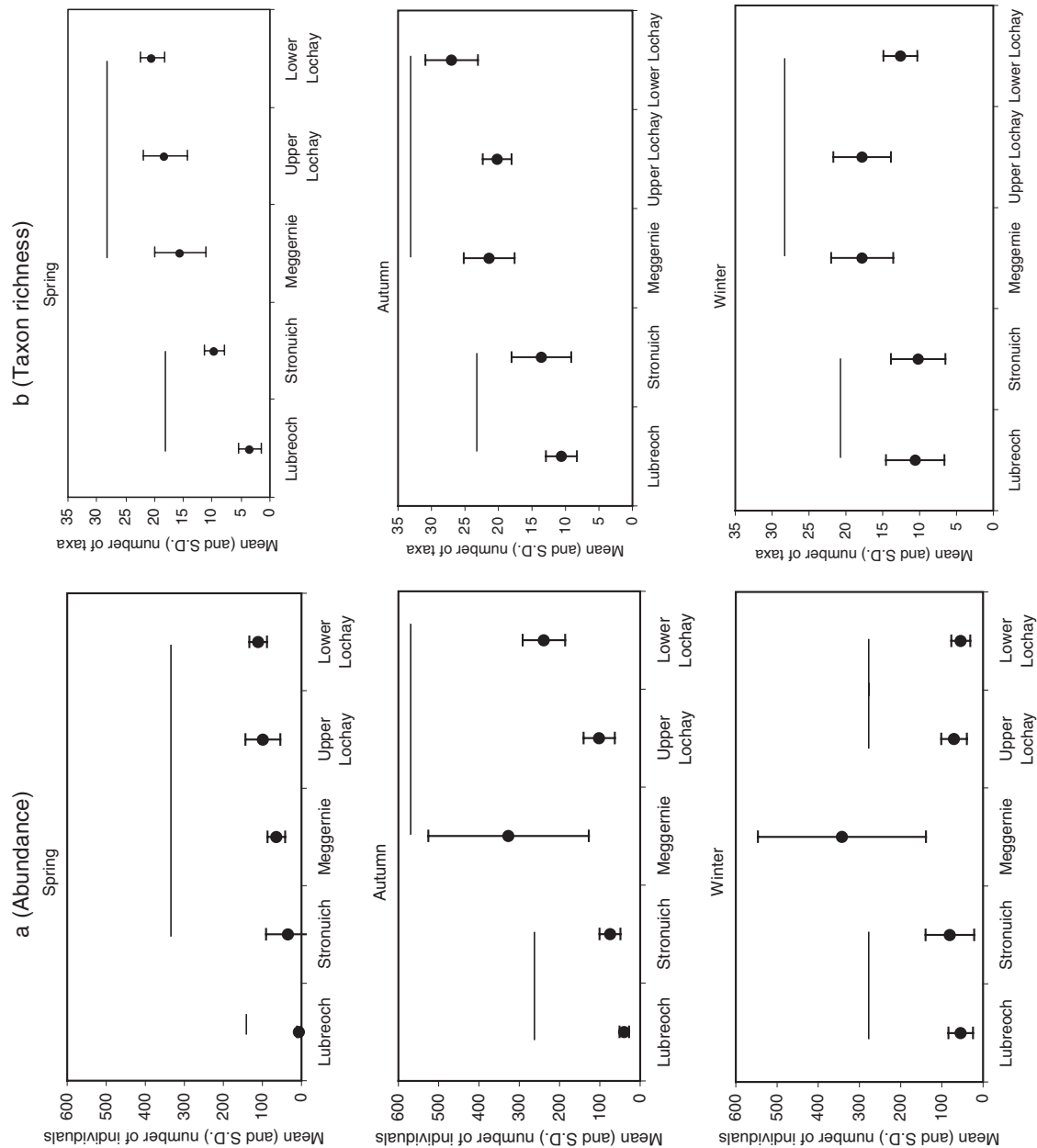


Figure 7. Invertebrate abundance and taxon richness per sampling basket for spring, autumn and winter sampling dates. Taxon richness values are from identification to mixed taxonomic levels; most animals were identified to species though more difficult groups were identified to Genus or Family level (detailed in methods section). Horizontal bars indicate the results of ANOVA and Tukey's HSD tests at $p = 0.01$

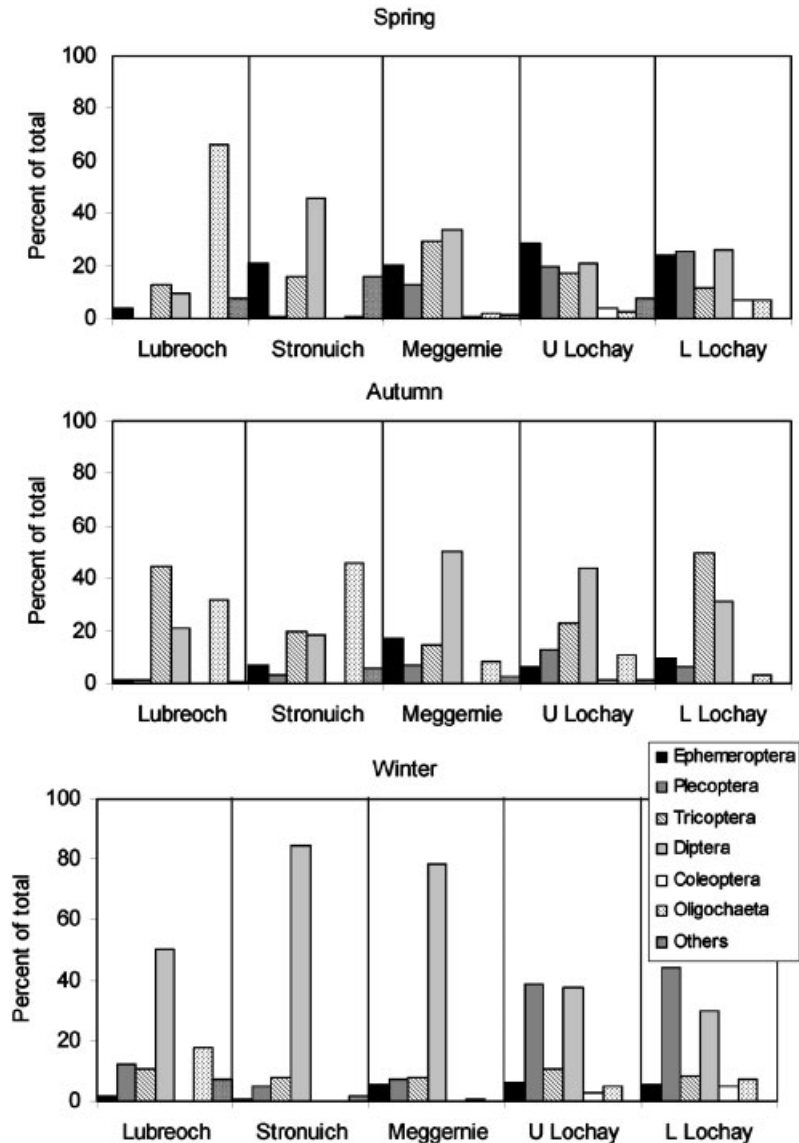


Figure 8. Relative abundance of major taxonomic groups in spring, autumn and winter. Per cent values are for the abundance pooled across the five replicate samples collected from each site on each date

DISCUSSION AND CONCLUSIONS

The European Union Water Framework Directive (WFD) is providing the impetus for much new research (Bratrich *et al.*, 2004; Gilvear *et al.*, 2004). Under the terms of the WFD, certain water bodies may be designated as Heavily Modified. In rivers designated as Heavily Modified, management needs only to have the objective of creating 'Good Ecological Potential', rather than creating 'Good Ecological Status'. Central to deliberations over whether a river should be designated as Heavily Modified is assessment of the ecological impact of human activity. The current study provides such an assessment and so represents the starting point determining the extent of management likely to be required in the River Lyon under the terms of the WFD.

Because of the absence of pre-impoundment data, invertebrate communities and environmental, hydrologic and thermal conditions in the Lyon were compared to those in the unregulated River Lochay. This use of an adjacent

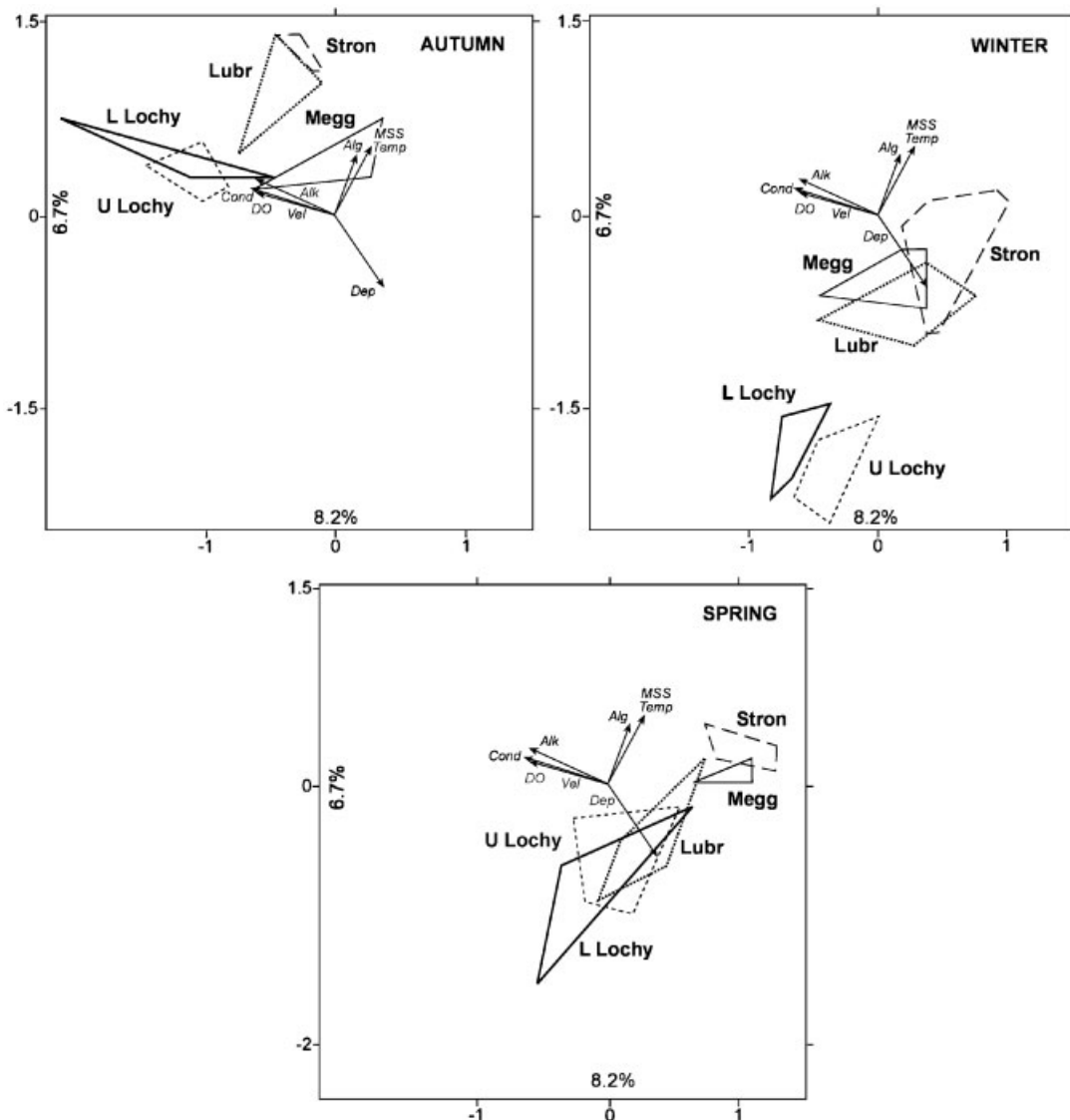


Figure 9. Canonical correspondence analysis ordinations of site invertebrate communities and environmental data for spring, autumn and winter sampling dates. Cumulative variance in the invertebrate data explained by Axes 1 and 2 is 14.9%. Polygons group the five replicate samples collected from each site on each occasion. Note that the CCA was performed on the whole data set simultaneously (i.e. sites and seasons were analyzed together). However, the resulting biplot was extremely cluttered. For the sake of clarity, data for each season are plotted separately; as can be seen from the scales on the axes, the overall ordination space represented on each biplot is the same. Sites not plotted are those where gaps in environmental data prevented inclusion in the analysis

unregulated catchment mirrors recent work by Ahearn *et al.* (2005). Comparison of the three Lyon sites with those in the Lochay, as well as between Lyon sites subject to different reservoir release regimes, suggests that the 50 years of HEP operations have resulted in highly modified communities at sites immediately below the two dams. The invertebrate community below Lubreoch dam was consistently the most impoverished of the study sites. It was species poor and uneven: Ephemeroptera and Plecoptera were either relatively scarce or completely absent from the site in each of the three seasons, with the community dominated by the oligochaete families Lumbricidae and Lumbriculidae. However, data for Meggernie suggest that communities in the Lyon begin to resemble those that might be expected in the unregulated river (as referenced by the Lochay) within 10 km downstream of the lower dam.

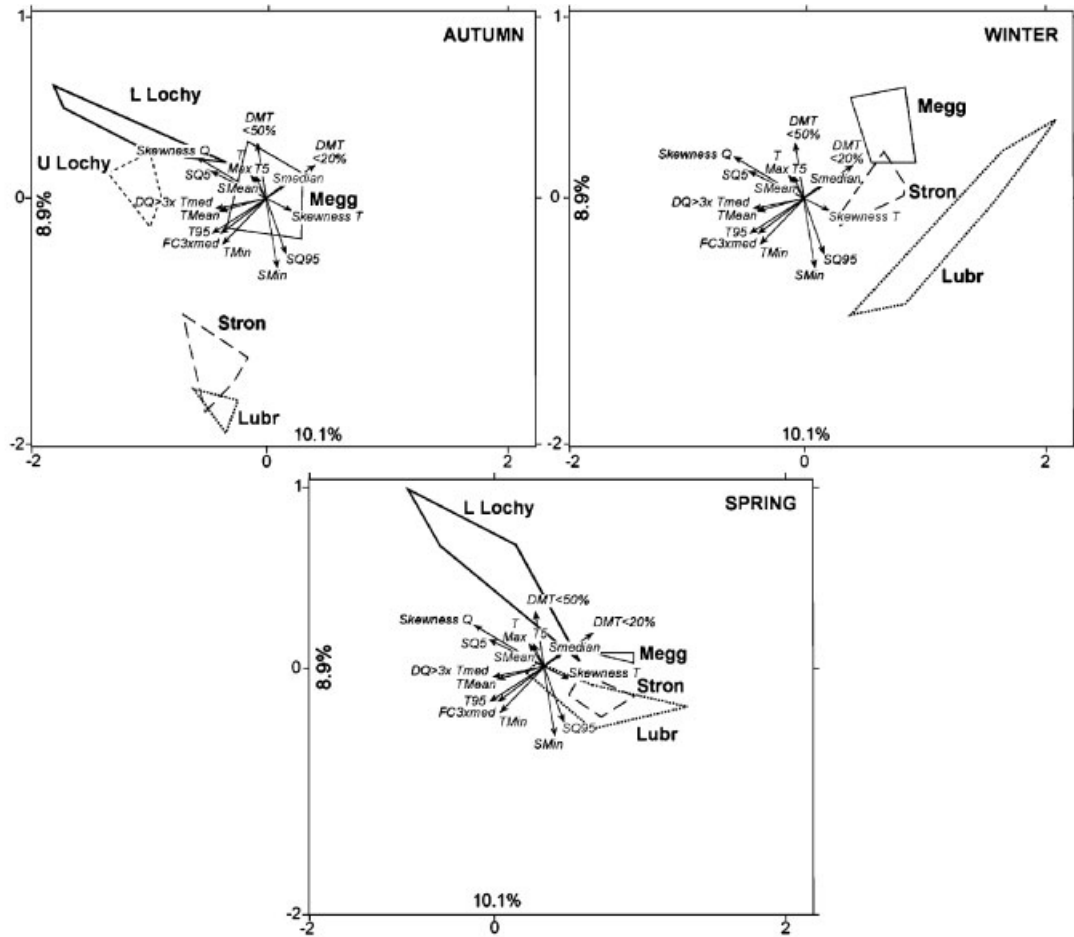


Figure 10. Canonical correspondence analysis ordinations of invertebrate communities and metrics of discharge and thermal variability calculated for the 2-week period preceding invertebrate sample collection. Cumulative variance in the invertebrate data explained by Axes 1 and 2 is 19%. Note that the CCA was performed on the whole data set simultaneously (sites and seasons analyzed together). However, the resulting single biplot was extremely cluttered. For the sake of clarity seasons are plotted separately, though their positions are those determined by the simultaneous ordination. Sites not plotted are those where gaps in environmental data prevented inclusion in the analysis

Invertebrate communities differed between sites in ways that corresponded to changes often associated with regulation. Algae is frequently abundant below impoundments (Inverarity *et al.*, 1983; Allan, 1995; Penaz *et al.*, 1999), principally in circumstances where the absence of high flows reduces bed scour. The increased growth of algae in the Lyon has been a notable feature of the river since the construction of the dams (Summers, 2000).

Table III. Cumulative per cent variance explained by CCA ordinations of (a) invertebrate communities and environmental conditions on the day of sample collection, and (b) invertebrate communities and hydrologic and thermal conditions in the 2 weeks preceding sample collection

	(a) Day of sampling	(b) Preceding 2-week period
Spring	27.8	53.4
Autumn	33.7	49.1
Winter	45.0	56.6

Unlike those presented in Figures 9 and 10, statistics given in the table are from separate CCA ordinations conducted for each season. In this way, values represent the per cent of variance between samples and sites that can be accounted for by the variables used to constrain respective ordinations. Eleven variables were used in (a) while 13 were used in (b).

Per cent algal cover was important structuring variable in the PCA of site environmental conditions, while CCA suggested that algae were important in helping to explain differences in invertebrate community structure between individual sites and the two catchments.

Algae provide microscale flow refugia for benthic invertebrates, a trap for organic material, a potential food resource and material for case construction (Moog, 1993). However, extensive growth of periphyton can lead to declines in abundance or the disappearance of species requiring clean rock surfaces (Petts, 1984). Simuliidae larvae use clean surfaces for attachment and are known to avoid substrate covered with detritus or algae (Hershey and Hiltner, 1988; Doeg *et al.*, 1989). In a manipulative study in the Lyon, Jackson (2006) found that Simuliidae reached high abundance on clean stream bed surfaces but were replaced by Chironomidae on algal-covered substrate. Periphyton and mosses below dams have been shown to restrict or eliminate *Rhithrogena semicolorata* (Armitage, 1980). This species was not present at the sites immediately below the two Lyon dams, where algae is most abundant, but was recorded further downstream at Meggernie and in the Lochay.

The Lotic-invertebrate Index for Flow Evaluation (LIFE) (Extence *et al.*, 1999) provides a further basis upon which patterns of species presence and absence in the Lyon can be interpreted. Within the LIFE system, species are allocated to groups according to their velocity preferences. Group I taxa are those which have traits which allow them to exist in high velocity environments (velocity $>1 \text{ m s}^{-1}$) and so are anticipated to decline if flow modification reduces the availability of such environments. The reservoir compensation flow dominates the hydrology of the Stronuich site for much of the year. At this discharge, mean column velocity ($0.4 \times \text{depth}$) across the site averages only 0.38 m s^{-1} (SD 0.18; values from 40 measurements across 5 transects). Even during freshets, velocities average only 0.5 m s^{-1} (Jackson, 2006). The mayflies *Ecdyonurus torrentis* and *Heptagenia sulphurea* (Heptageniidae) are LIFE Group I taxa. Both species were absent from the highly regulated Stronuich and Lubreoch sites but present further downstream in the Lyon as well as in the Lochay. Several stonefly species belonging to LIFE Group I were also absent from Lubreoch and Stronuich but present at the other sites (*Perlodes microcephala*, *Amphinemura sulcicollis* and *Leuctra inermis*). These patterns suggest the absence of suitably high velocity microhabitats below the dams. However, without controlled, manipulative studies, it is difficult to be confident about the causal mechanisms involved. Moreover, there is a need to consider both direct and indirect influences on species distribution patterns. For example, *R. semicolorata* is also a Group I taxa, so its absence from Stronuich may be related directly to the absence of suitably high velocities. However, its absence may be as an indirect result of reduced velocities which limit scour and permit algal growth.

Comparisons between the study sites suggest that water released from the reservoirs at Lubreoch and Stronuich reduces variability in temperatures in the Lyon. At the seasonal timescale, typical reservoir-induced winter warming and summer cooling (Petts, 1984) was evident in the Lyon downstream from the two dams. Instantaneous temperatures differed markedly between the Lyon and Lochay catchments. In spring for example, the maximum daily temperature was as much as 14°C higher in the Lochay than at Stronuich and Lubreoch; conversely, minimum temperature in the Lochay dropped to 0.8°C while Lyon temperatures did not fall below 5°C . Despite the marked and consistent thermal differences between sites, metrics characterizing patterns of temperature variability did not appear to exert a dominant influence on site invertebrate community structure (arrow lengths for discharge and temperature metrics were similar; Figure 10) while temperature was no more important than other the environmental variables used in the initial CCA (arrow lengths for all variables were similar; Figure 9). Thus, rather than driving species presence/absence or abundance at the study sites, the ecological impact of thermal modification in the Lyon may be more subtle, influencing growth rates or life cycles.

Patterns of invertebrate community structure in the Lyon and Lochay need to be interpreted not just in the context of flow regulation but in relation to natural differences in water chemistry. There is a greater frequency of limestone in the Lochay catchment. Conductivity and alkalinity had high component loadings on Axis 1 of the PCA, the axis that separated the two Lochay sites from the three Lyon ones. CCA using the environmental data separated catchment invertebrate communities in a dimension that was related to conductivity and alkalinity. Thus, data suggest differences in invertebrate community structure may partly reflect geological differences between the catchments.

Discharge and thermal variability in the 2-week period preceding sample collection explained more of the invertebrate community variability than a broad suite of environmental conditions. Thus, the technique of using metric values in CCAs may provide a useful insight into the ecological importance of patterns of flow and

temperature variability. Nonetheless, levels of explanation provided by CCA depend on the time period used (Gibbins *et al.*, 2001b). A period of 2 weeks was used in the current study largely for practical reasons; data gaps dictated that it was not possible to calculate the full range of metrics for longer and potentially more instructive time periods. Per cent variance values for the CCAs using environmental data may also increase if metrics characterizing patterns of variability were to be used. While this was not possible in the current study because only spot measurements were taken, such an analysis would improve comparison of the relative importance of environmental conditions versus hydrologic and thermal regimes.

At the broadest of levels, the patterns of reduced taxon richness and the dominance of certain tolerant groups below the Lyon dams are consistent with results of other reservoir impact studies (reviewed by Brittain and Saltveit, 1989). However, the precise impacts of an individual impoundment depend upon its depth and surface area, the chemistry of inflowing waters, water residence times and dam operations, as well as regional geographic factors such as climate (Ahearn *et al.*, 2005). The Lyon system is interesting because the two online dams are only a few kilometres apart but have markedly different discharge regimes. This provided an unusual opportunity to assess the long-term effects of different regulated discharge regimes on benthic invertebrates in the same river. Cortes *et al.* (2002) compared invertebrate community structure in two sections of the river Lima (Portugal) subjected to different regulated regimes; as in the Lyon, one section experienced relatively low and stable flows, the other higher and more variable flows. They found that species diversity (as indexed by H') did not differ significantly between the sections. In the Lyon, patterns of taxon richness below Lubreoch and Stronuich differed between the seasons, but in general fewer taxa were found in the section below Lubreoch where flows were more variable. The lack of detectable patterns in diversity in the Lima led Cortes *et al.* (2002) to suggest that this measure is probably not the most appropriate for assessing the effects of regulation; they argued that species replacement was a more sensitive and appropriate measure. In the case of the Lyon, it appears that impacts are of a magnitude that changes not only extend to species replacement (as indicated by differences in community structure represented on the CCA ordinations) but through to reductions in taxon richness.

The lengths of CCA arrows characterizing aspects of the site discharge and thermal regimes were similar, suggesting that no one metric exerts an overriding influence on community structure. This suggests that whole regime changes, rather than alterations to one particular aspect of the regime, are responsible for the impoverishment observed in the Lyon. In turn, this suggests that small modifications to reservoir release programmes (e.g. introducing occasional high flows) may not lead to noticeable improvement in the ecological status of the river. Krause *et al.* (2005) found that modifications to a regulated discharge regime designed to improve instream physical habitat for trout would reduce the occurrence of optimal growth temperatures. Their research also found that the best management option for improving one temperature criterion for the fish was not the best for improving other criteria. This helps emphasize how the interaction between discharge and temperature and between different aspects of the temperature regime in the Lyon would require careful analysis before any changes to reservoir operation could be safely implemented. Thus, while the current study has provided important information about the impacts of flow regulation in the Lyon, much more research is needed before management programmes aimed at meeting the requirements of the WFD could be implemented. In particular, there is a need for detailed studies of the impact of impoundment on groups other than invertebrates as well as studies of the habitat requirements of different life stages at different times of the year. Such information provides the basis for a building block approach to developing an environmental flow regime for the river (Acreman and Dunbar, 2004). Currently, however, a more pressing debate concerns whether hydropower rivers such as the Lyon should be designated as Heavily Modified; depending on its outcome, this debate may negate the requirement for environmental flow regimes.

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APPENDIX I. LIST OF ABBREVIATED SPECIES NAMES USED IN FIGURE 11

Abbreviation	Species
Nerr	<i>Nemoura erratica</i>
Npic	<i>Nemoura pictecti</i>
Ncin	<i>Nemoura cinerea</i>
Unem	Unidentified <i>Nemoura</i>
Pmey	<i>Protonemura meyeri</i>
Ppra	<i>Protonemura praecox</i>
Asul	<i>Amphinemura sulcicollis</i>
Uamp	Unidentified <i>Amphinemura</i>
Unem	Unidentified <i>Nemouridae</i>
Lhip	<i>Leuctra hippopus</i>
Line	<i>Leuctra inermis</i>
Lnig	<i>Leuctra nigra</i>
Uleu	Unidentified <i>leuctridae</i>
Ctri	<i>Chloroperla tripunctata</i>
Ctor	<i>Chloroperla torrentium</i>
Uchl	Unidentified <i>chloroperlidae</i>
Pbip	<i>Perla bipunctata</i>
Pmic	<i>Perlodes microcephala</i>
Igra	<i>Isoperla grammatica</i>
Iobs	<i>Isoperla obscura</i>
Dcep	<i>Dinocras cephalotes</i>
Tnebs	<i>Taeniopteryx nebulosa</i>
Bris	<i>Brachyptera risi</i>
Brho	<i>Baetis rhodani</i>
Bmut	<i>Baetis muticus</i>
Ubae	Unidentifiable <i>Baetidae</i>
Criv	<i>Caenis rivulorum</i>
Etor	<i>Ecdyonurus torrentis</i>
Hlat	<i>Heptagenia lateralis</i>
Hsul	<i>Heptagenia sulphurea</i>
Uhep	Unidentified <i>Heptagenidae</i>
Rsem	<i>Rhithrogena semicolorata</i>
Uecd	Unidentified <i>Ecdyonurus</i>
Lept	<i>Leptophlebia</i> sp
Ulep	Unidentified <i>leptophlebid</i>
Ipal	<i>Isotomurus palustris</i>
Pota	<i>Potamophylax cingulatus/latipennis</i>
Chae	<i>Chaetopteryx</i> sp
Acin	<i>Anthripsodes cinereus</i>
Uant	Unidentified <i>Anthripsodes</i>
Myst	<i>Mystacides</i> sp
Lhir	<i>Lepidostoma hirtum</i>
Sper	<i>Sericostoma personatum</i>
Aaur	<i>Allogamus auricollis</i>
Abil	<i>Anthripsodes bilineatus</i>
Hydr	<i>Hydroptila</i> sp
Oalb	<i>Odontocerum albicorne</i>
Oxys	<i>Oxyethira</i> sp
Glos	<i>Glossosoma</i> sp

(Continues)

Appendix. (Continued)

Abbreviation	Species
Ulim	Unidentified Limnephilidae
Utri	Unidentified Tricoptera
Hsil	<i>Hydropsyche siltalai</i>
Hpel	<i>Hydropsyche pellucidula</i>
Hins	<i>Hydropsyche instabilis</i>
Uhyd	Unidentified Hydropsyche
Pcon	<i>Plectrocnemia conspersa</i>
Pbre	<i>Plectrocnemia brevis</i>
Pgen	<i>Plectrocnemia geniculata</i>
Uple	Unidentified Plectrocnemia
Eten	<i>Ecnomus tenellus</i>
Rdor	<i>Rhyacophila dorsor</i>
Rmun	<i>Rhyacophila munda</i>
Rsep	<i>Rhyacophila septentrionis</i>
Urhy	Unidentified Rhyacophilidae
Ppus	<i>Psychomyia pusilla</i>
Pkin	<i>Polycentropus kingi</i>
Lred	<i>Lype reducta</i>
Mfra	<i>Metalype fragilis</i>
Twae	<i>Tinodes waeneri</i>
Upsy	Unidentified Psychomyidae
Upol	<i>Unidentified Polycentropidae</i>
Nbim	<i>Neureclipsis bimaculata</i>
Sims	Simuliidae
Tips	Tipulid
Dics	Dicranota
Ants	Antocha
Rhas	Rhagionid
Elas	Elaeophila
Utip	Unidentified Tipulidae
Tanp	Tanypodinae
Chir	Chironomini
Tant	Tanytarsini
Orth	Orthocladinae
Culs	Culicidae
Cers	Ceratopogonidae
Tubs	Tubificidae
Lum1	Lumbriculidae
Lum2	Lumbriculidae
Nais	Nais
Styl	Stylaria
Uoli	Unidentified Oligochaeta
Ases	<i>Asellus aquaticus</i>
Ouli	<i>Oulimnius</i> sp
Lvol	<i>Limnais volckmari</i>
Epar	<i>Esolus parallelepipedus</i>
Riol	<i>Riolus</i> sp
Uhel	Unidentified Helodidae
Clac	<i>Criodrilus lacuum</i>
Gamm	Gammarus
Moll	Mollusca
Crus	Crustacean