Recognition of stream drying based on benthic macroinvertebrates: a new tool in Central Europe

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Abstract

Many streams in the extensive Central European region have an intermittent flow regime. Conventional hydrological methods used to identify zero-flow conditions, and in particular drying events, have limited use when assessing large areas dominated by low-order streams. We developed a novel multimetric index to recognise antecedent stream drying based on the analysis of benthic macroinvertebrate communities. The data used to develop the index were collected in pristine streams with different flow permanence regimes between 2012 and 2014, using standard sampling methods for ecological status assessment. The data include 64 perennial, 19 near-perennial and 27 intermittent benthic macroinvertebrate samples. Metrics considered for the index included variables based on (i) the occurrence of indicator taxa, (ii) the proportion of biological and ecological traits, and (iii) structural community metrics. Linear discriminant analysis identified the metric combinations that best discriminated among the three flow permanence categories. Different metrics were used in the final multimetric index calculation for the autumn and spring season that followed stream drying. In both seasons, the index included the proportion of indicator taxa and the proportion of taxa with high body flexibility. In addition, the autumn index included the proportion of taxa with a preference for organic substrates, whereas in spring the index included total abundance. Independent data from regulatory monitoring activity were used to validate the accuracy of the index. The correct classification of independent samples was 92% and 96% for samples from perennial and non-perennial sites, respectively. The index can be calculated using data collected by routine monitoring programmes used to assess ecological status and provides information about stream intermittence where conventional hydrological monitoring is limited. As intermittent streams increase in extent in global regions including Central Europe, the tool may be of particular interest to those who use invertebrates to monitor or manage these ecosystems.

1. Introduction

Intermittent rivers and ephemeral streams (i.e. streams with periodic flow cessation and/or drying; IRES) are mostly associated with arid and semi-arid regions. However, they are also common and widespread in temperate and continental regions with cooler, wetter climates (Datry, et al. 2014a; Stubbington et al., 2017). IRES are typically managed using methods developed for perennial waterways, or as if they were part of the terrestrial ecosystems (Acuña et al., 2014; Stubbington et al., 2018), and the need for more effective policies and management strategies has been highlighted around the world (Datry et al., 2017; Marshall et al., 2018). In the European Union, a major objective for water management is the assessment of ecological status in water bodies, to meet the legislative requirements of the EU Water Framework Directive (European Commission, 2000). The characterisation of 'biological quality elements' such as benthic macroinvertebrates is one important approach used to evaluate ecological status.

Aquatic macroinvertebrates are routinely used as indicator organisms for determining ecological status and diagnosing specific environmental pressures (e.g. Rosenberg and Resh, 1993; Birk et al., 2012). However, even short-term (i.e. days to weeks) stream drying can substantially alter benthic macroinvertebrate community composition (Datry et al., 2014b;

Hille et al., 2014; Lancaster and Ledger, 2015). The interpretation of ecological status based on metrics developed in perennial streams can thus be misleading (Munné and Prat, 2009; Menció and Mas-Pla, 2010; Wilding et al., 2018). Information about flow permanence is crucial to accurately interpret data used to evaluate status and thus inform effective IRES management. In addition, knowledge about stream intermittence is needed, to anticipate the effects of climate change, to assess human pressures such as water abstraction and to manage protected species and habitats (Wilby et al., 2010).

Using flow gauging stations to monitor the flow permanence of small streams is expensive and technically impractical, because small streams (Strahler orders 1-4) comprise a substantial part of the stream network length (e.g. 92% in Czech Republic; Zahrádková et al., 2015). Moreover, even where hydrological data are collected, they may not distinguish between lentic and dry zero-flow conditions, and alternative methods are therefore needed to recognize IRES and characterize their water regimes (Gallart et al., 2016; Beaufort et al., 2018), for example using stream biota. Loss of surface water acts as an ecological filter (Poff 1997) and benthic macroinvertebrates have taxon-specific quantitative responses to drying (Datry et al., 2014b; Leigh and Datry, 2017). Dry phases can therefore be detected through both structural (i.e. taxonomic) and functional (i.e. trait-based) changes in community composition (Bogan et al., 2013; Schriever et al., 2015; Leigh et al., 2016; Chadd et al., 2017). Presence/absence of indicator taxa of benthic invertebrates has also been used to recognize stream flow duration (NC Division of Water Quality, 2010; Nadeau, 2015), and both taxonomic structure and species trait information have been used to assess flow connectivity in Mediterranean regions (Cid et al., 2016). Such tools may enable the data routinely collected during biomonitoring programmes to provide information about flow intermittence, even if hydrological data are absent. However, no method to detect drying events has been developed for the extensive continental-climate region of Central Europe.

Different metrics can be sensitive to different aspects of stream drying, and a combination of structural, functional and indicator-taxa metrics may therefore provide robust and sensitive insight into the responses of an assemblage to drying (Li et al., 2010). Here, our aim was to develop and test a new multimetric index to identify antecedent stream drying events based on the structural and functional composition of benthic macroinvertebrate communities. We evaluated three groups of metrics as indicators of stream drying: (i) the occurrence of indicator taxa; (ii) the proportion of biological and ecological traits; and (iii) structural community metrics. We identified the metrics and metric combinations that most effectively indicated antecedent stream drying.

2. Materials and Methods

2.1. Study area

The study was conducted in 23 small (order 2-4) streams in the Czech Republic (Fig. 1). All were classified as reference streams, i.e. exposed to minimal anthropogenic impacts. Catchment land use was dominated by woodland, with smaller proportions of agricultural land, and with at least 10-m riparian buffer strips of deciduous bushes and trees. The study area has a warm-summer humid continental climate (Köppen-Geiger classification *Dfb*; Peel et al., 2007) and spans the Hercynian (17 streams) and West-Carpathian (6 streams) biogeographical subprovinces (Culek, 2013), which approximately correspond with ecoregions 9 (Central Highlands) and 10 (Carpathians; Illies, 1967). To facilitate comparison of macroinvertebrate communities from different sites, streams were paired, with each pair comprising one non-perennial and one perennial stream of comparable altitude, size, geology and hydromorphology. In one case, a single perennial stream was paired with two non-perennial streams. A sampling site representative of typical conditions was selected in each stream. The altitude of the sampling sites ranged from 250 m to 560 m a.s.l. and the maximum distance between paired sites was 13 km.

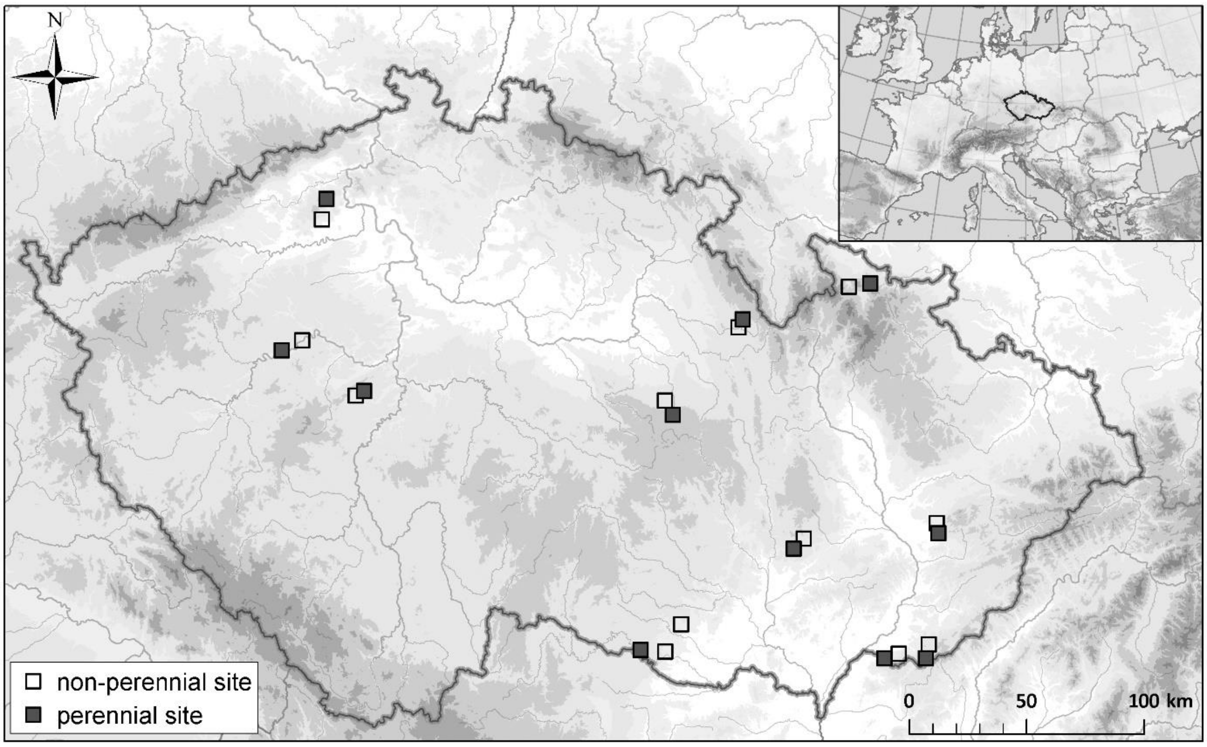

Fig. 1. Location of the study sites in the Czech Republic. Open squares represent non-perennial (i.e. near-perennial and intermittent) sites and filled squares represent perennial sites.

2.2. Sampling strategy

Benthic macroinvertebrate assemblages were sampled in spring (March-April) in 2013 and 2014 and in autumn (September-October) in 2012, 2013 and 2014. Proportional multi-habitat three-minute kick samples were collected with a hand net (25 × 25 cm aperture, 0.5-mm mesh size) according to the standard method used for ecological status assessments in the Czech Republic (Kokeš et al., 2006; Kokeš and Němejcová, 2006). Samples were preserved in 4% formaldehyde and processed in the laboratory. All macroinvertebrates were identified to the lowest possible taxonomic level: 292 out of 421 to species level, 117 to genus level, and the remaining 12 to a higher taxonomic level.

Sites were classified as non-perennial or perennial a priori, based on expert knowledge. In addition, observed instream conditions were recorded from summer 2012 to autumn 2014, including determination of the dry period duration using a water-level logger (Solinst Levelogger Edge) and photo-trap (Acorn 5310MG) installed at each site. Each water-level logger was placed in the lowest part of the streambed, to account for the persistence of surface water in isolated pools. Photo-traps were installed in trees in the adjacent riparian zone (at 3 m height) and were facing a water-level gauge board. Logger and photo-trap data were collected every 15 minutes and every 4 hours, respectively.

We divided individual samples into three intermittence categories: *perennial*, *intermittent* and an intermediate *near-perennial* category. The allocation of samples into the three categories was based primarily on the dry period duration: i) perennial sites were defined as those which experienced more than one year of continuous flow prior to sample collection; ii) near-perennial sites lost surface water for hundreds of meters for <7 d in the summer prior to sampling, with disconnected pools occasionally present; and iii) intermittent sites dried for >1 km for 7-86 d before sampling. The cut-off between near-perennial and intermittent sites was arbitrary, reflecting the gradual nature of stream drying. In total, we collected 27 perennial, 7 near-perennial and 12 intermittent samples in spring and 34 perennial, 12 near-perennial and 15 intermittent samples in autumn. Spring samples from intermittent and near-perennial streams were taken 175-224 d after flow resumption and autumn samples were taken 2-63 d after flow resumption.

2.3. Identification of perennial flow indicators and flow intermittence tolerant taxa

To identify taxa associated with either perennial or intermittent streams, we performed Indicator Species Analysis (IndVal; Dufrêne and Legendre, 1997) using samples from spring 2013 and autumn 2012 and 2013. IndVal was performed using the multipatt function in the R package indicspecies (Cáceres and Legendre, 2009), which identifies taxa with a strong association with each group based on their abundance and frequency. The calculated indicator value (IV) of a given taxon for its preferred group ranges from zero (no affinity) to one (strongest affinity). Best-matching patterns were tested for statistical significance of the associations. Taxa significantly associated with either perennial or intermittent and near-perennial samples were considered as reliable indicators and were assigned a reliability value of 2 (see "Proportion of indicator taxa" section). Taxa with non-significant IV but found exclusively in either perennial or intermittent and near-perennial streams in at least 10% of samples were considered as indicators with lower reliability and were assigned a reliability value of 1.

To support the IndVal analyses, we conducted a literature review of primary research papers comparing macroinvertebrate assemblages at perennial and non-perennial sites during flowing phases. From these studies, a taxon was identified as indicative of perennial flow if it was absent from intermittent stream assemblages. A taxon was considered as intermittence tolerant if it was found in intermittent stream assemblages. Literature sources describing the autecology of macroinvertebrate taxa were also reviewed to explore taxon-specific responses to intermittence. If a taxon's relationship with stream intermittence was described once in data-based published sources then the species was assigned a reliability value of 1, and if it was published two or more times, a value of 2 was assigned. The review focused on taxa living in the Czech Republic area; consulted literature is listed in Appendix A. If information in different published sources were contradictory or unclear, then a taxonomic expert decided the reliability of the taxa based on the available evidence.

2.4. Metrics used for index development

Three groups of potential metrics that indicate flow intermittence were calculated, to inform subsequent development of the multimetric index:

i) Proportion of indicator taxa

The proportion of indicator taxa was calculated as the sum of the reliability values of perennial flow indicators present in a sample divided by the sum of the reliability values of all (perennial + intermittence-tolerant) indicators present. The proportion of indicators was rescaled to zero and the resultant values are within the range -1 to +1.

$$\text{Proportion of indicator taxa}=\left(\frac{\sum \quad values\ of\ perennial\ flow\ indicators}{\sum \quad values\ of\ all\ indicators}\times 2\right)-1$$

ii) Proportion of macroinvertebrate traits in community

The macroinvertebrate community was characterized using traits extracted from available databases (IS ARROW, 2014; Schmidt-Kloiber and Hering, 2015), supplemented by information from the literature review and from experts in different taxonomic groups. Information about fine-sediment-sensitive invertebrates was taken from Extence et al. (2013). To describe the ability to penetrate substrata, taxonomic experts assigned each taxon to one of three body flexibility modalities: (i) none, body flexibility is limited by shell or exoskeleton, e.g. molluscs, adult beetles; (ii) low, body is flexible but cannot turn around, e.g. mayflies, stoneflies; (iii) high, body can turn 360 degrees, e.g. Oligochaetes, Chironomidae (Omesová et al. 2008). Preferences for organic substrate were calculated as preferences for pelal (organic mud) and particulate organic matter. For each trait coded in a single-category assignment system or presence/absence assignment system (Schmidt-Kloiber and Hering, 2015), the community-level trait value was calculated as the number of individuals within the trait modality divided by the total macroinvertebrate abundance of a sample. The community-level trait value of traits coded in ten-point assignment system (Schmidt-Kloiber and Hering, 2015) was calculated as the sum of the trait values multiplied by the abundance of each taxon and divided by the total abundance (Schmera et al., 2014).

iii) Community structure metrics

The number of taxa, ln(x+1)-transformed total abundance, and abundances and proportion in the community of the most abundant higher taxonomic units was calculated for each sample. This was done also for three drying-sensitive taxonomic groups (Bonada et al., 2007; Datry et al., 2014b): the family Heptageniidae, ET taxa (Ephemeroptera and Trichoptera) and EPT taxa (Ephemeroptera, Plecoptera and Trichoptera).

2.5. Index development

We performed exploratory data analysis to inform later identification of metrics that discriminate among intermittence classes. We used dot charts to assess metric distribution, and pair plots to assess their collinearity. We used nonmetric multidimensional scaling (NMDS) of a Bray-Curtis distance matrix calculated using ln(x+1)-transformed abundance data to visualize variability in community composition in relation to year, season, subprovince and intermittence. We used the adonis function from the vegan package (Oksanen et al., 2017) to run permutational multivariate ANOVA (PERMANOVA; Anderson,

2001) to identify differences in community composition between seasons (*spring*, *autumn*), subprovinces (*Hercynian*, *West-Carpathian*) and intermittence categories (*intermittent*, *near-perennial*, *perennial*). Because only autumn samples were available for 2012, the difference between years was not tested. One-way ANOVA was used to examine differences in total abundance and taxa richness between perennial, near-perennial, and intermittent samples.

To reduce the number of potential metrics selected for inclusion in the final multimetric index (hereafter, the *Biodrought index*) a pre-selection process was conducted. To identify candidate metrics, values of each potential metric were plotted against intermittence categories. Those that effectively discriminated between intermittent and perennial samples were retained as candidate metrics (Table 1), with Mann-Whitney U tests used to identify differences in metric values between perennial and intermittent samples.

To identify the metric combination that best discriminated among perennial, near-perennial and intermittent sites, we identified linear combinations of candidate metrics using a sequence of linear discriminant analyses (LDA). Because macroinvertebrate community composition differs among seasons (e.g. Straka et al., 2012) we expected different metrics to reflect stream intermittence in autumn and spring. Therefore, all possible combinations of 2-4 metrics were tested for their discriminatory power using the leave-one-out cross-validation procedure (lda function, MASS package; Venables and Ripley, 2002) in each season. The combination of metrics with the best discrimination power was selected and its equation noted. The final index is this equation centred to zero and can be used to calculate a 'discrimination score' for an independent sample. To relate the discrimination score to the intermittence categories, we calculated discrimination scores for all samples and fitted probability density functions of a normal distribution to each category, from which the probability of belonging to each category could be derived. Normality of distribution of LDA discriminant scores for each sample category was tested by Shapiro-Wilk tests. The effects of season and sample category on LDA discriminant score were tested using ANOVA. All statistical analyses and graphs were performed using R open-source software version 3.4.4 (R Core Team, 2018).

2.6. Validation by independent samples

The ability of the index to identify antecedent stream drying was tested on an external dataset, provided by the former Czech Agricultural Water Management Authority, and collected using the same method as the original dataset (Kokeš and Němejcová, 2006). The dataset comprised 117 (59 autumn + 58 spring) samples from 59 perennial sites and 26 (16 autumn + 10 spring) samples from 16 non-perennial sites. We could not distinguish between intermittent and near-perennial sites, and all samples for at which stream drying was observed were therefore classified as non-perennial. Samples were taken from 2nd to 4th order streams distributed across the Czech Republic (Fig. 2), at an altitude of 210 to 460 m a.s.l. The streams were not polluted or morphologically modified and monthly observations of hydrological instream conditions in the summer prior to sampling were available. The value of the Biodrought index was calculated for each sample and the probability of its classification as intermittent, near-perennial or perennial was calculated using the probability density function of the normal distribution. The sample was assigned to the category with the highest probability.

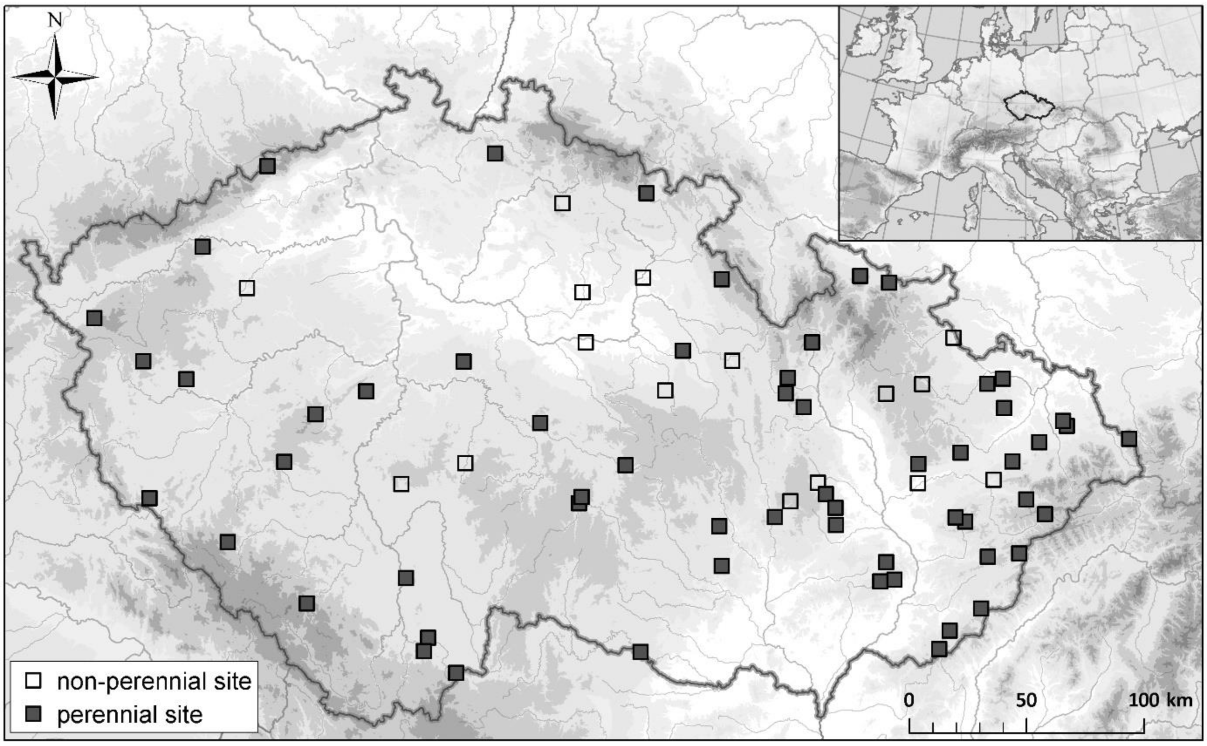

Fig. 2. Location of the sites used for validation within the Czech Republic. Open squares represent non-perennial sites and filled squares represent perennial sites.

3. Results

3.1 Community structure across years, seasons, and regions

In total, 532 552 benthic macroinvertebrate individuals from 421 taxa were collected (Appendix B). Individual sample abundance values ranged from 307 to 57 581 (mean ± SE, 4997 ± 591) individuals per sample and taxa richness values from 28 to 108 (60.7 ± 1.5) taxa per sample. Macroinvertebrate abundance decreased with increasing flow intermittence (Fig. 3), with significant differences among intermittence categories (one-way ANOVA, $F_{2,104}$ = 3.71, p = 0.028). Taxa richness was also lowest in intermittent samples ($F_{2,104}$ = 15.11, p < 0.001). The five most abundant taxa were *Gammarus fossarum* (30% of all individuals), *Micropsectra atrofasciata*-Gr. (9.5%), *Nemoura* sp. (3.5%), *Baetis rhodani* s.l. (3.1%) and *Habroleptoides confusa* (2.9%). Twenty-six taxa were identified as significant indicators of intermittent and near-perennial samples and 33 were identified as significant indicators of perennial samples (Appendix A). The five taxa with the highest IV were *Eiseniella tetraedra*, *Brachyptera risi*, *Parametriocnemus stylatus*, *Paraphaenocladius* sp. and *Marionina* sp. for non-perennial sites and *Dugesia gonocephala*, *Baetis muticus*, *Baetis rhodani* s.l., *Leuctra* sp. and *Hydropsyche* sp. for perennial sites.

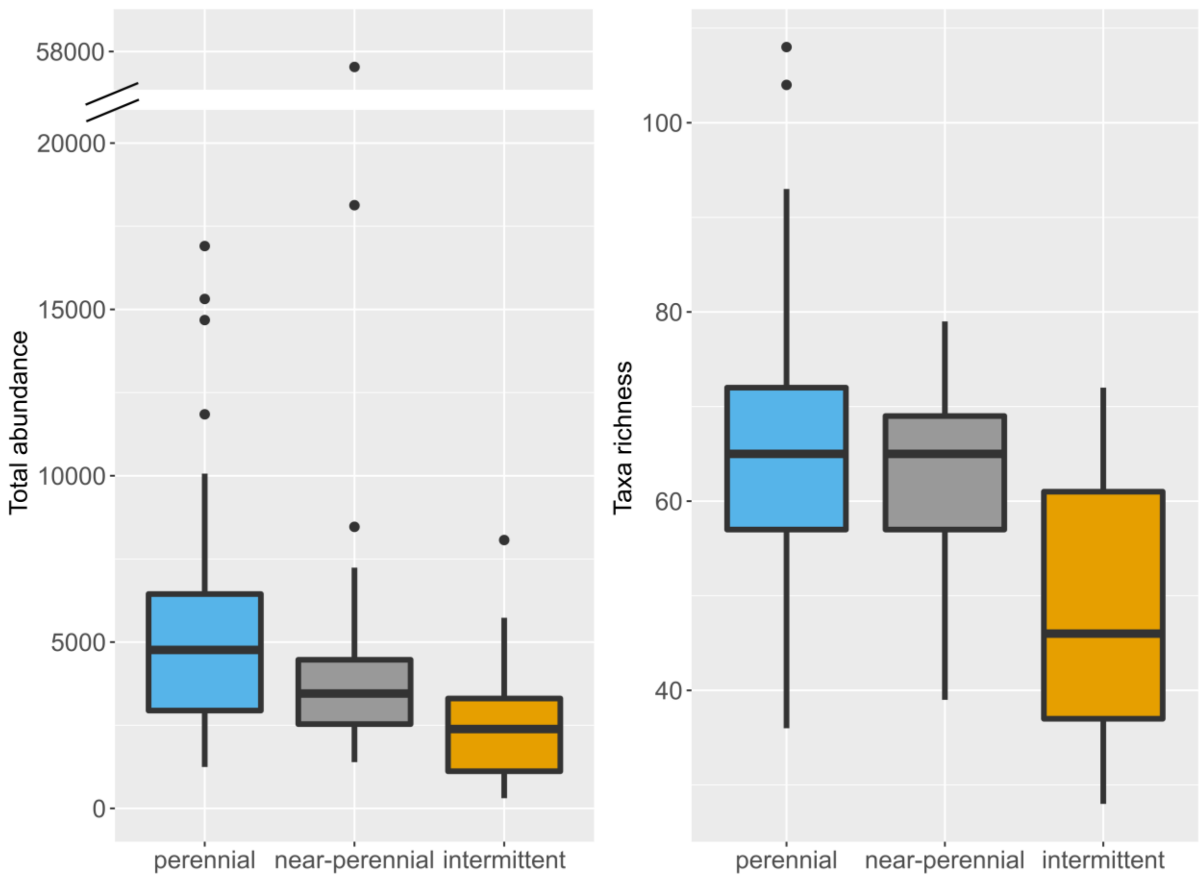

Fig. 3. *(colour figure)* Total invertebrate abundance (number of individuals) and taxa richness (number of taxa) in samples classified into three flow intermittence categories: i) perennial; ii) near-perennial; iii) intermittent. The box area indicates the first and third quartiles, the central line indicates the median, whiskers represent 95% confidence intervals and circles indicates outliers.

Non-metric multidimensional scaling analyses produced a two-dimensional solution (stress = 0.1998; Fig. 4). Community composition differed among perennial, near-perennial and intermittent samples (PERMANOVA; $F_{2,104} = 7.4$, $p < 0.001$). Despite considerable overlap, we detected differences in community composition both between seasons (PERMANOVA; $F_{1,105} = 6.0$, $p < 0.001$) and subprovinces ($F_{1,105} = 5.6$, $p < 0.001$).

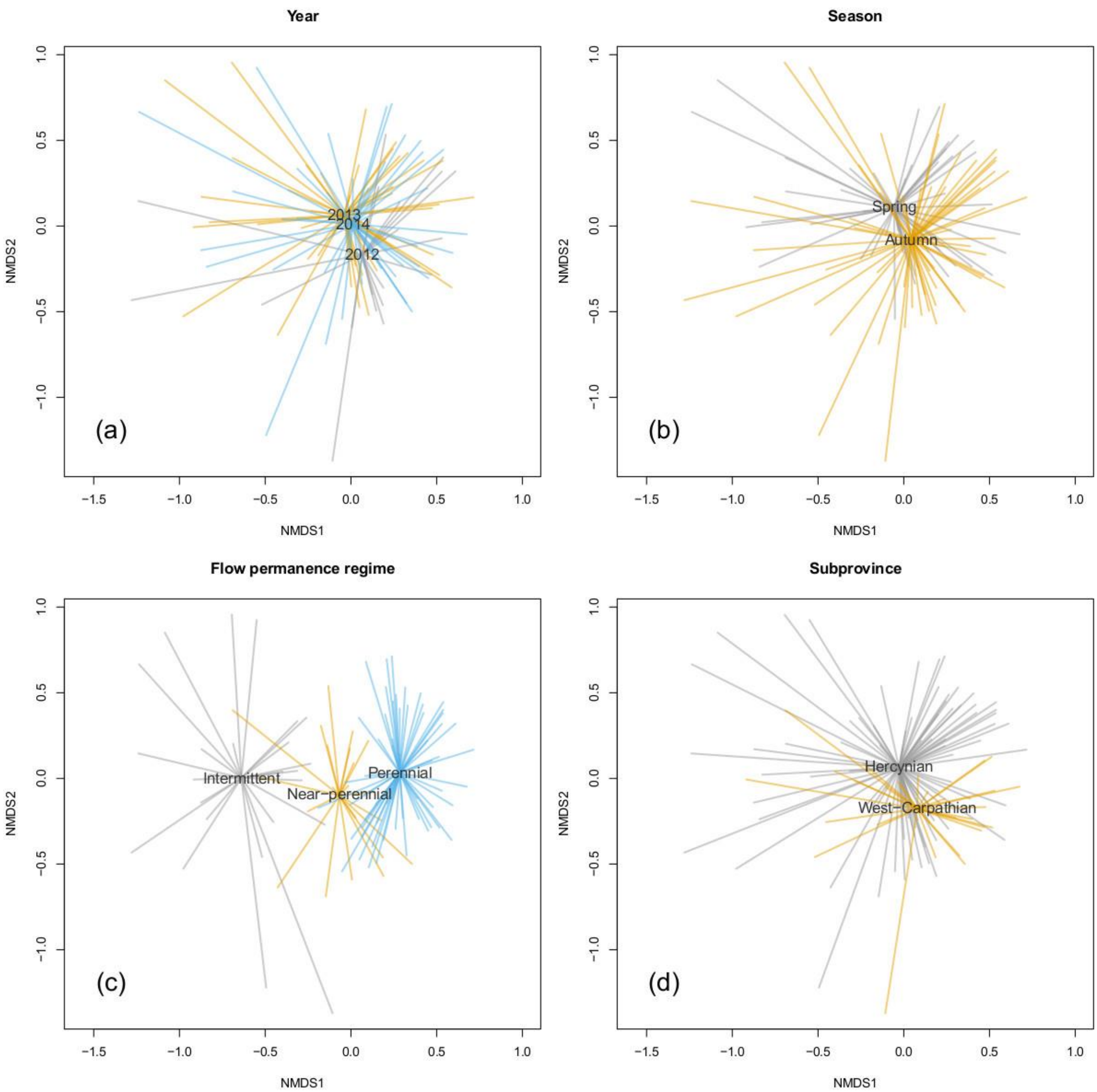

Fig. 4. *(colour figure)* Non-metric multidimensional scaling ordinations of all samples, showing differences in community composition between: (a) years (2012, 2013, 2014); (b) seasons (autumn, spring); (c) intermittence categories (intermittent, near-perennial, perennial); and (d) biogeographical subprovinces (Hercynian, West-Carpathian). Each point (sample) is connected to the group centroid.

3.2. Discrimination of samples from each intermittence category

Because PERMANOVA identified differences in community composition among perennial, near-perennial and intermittent samples, we investigated the metrics that most effectively discriminated between these intermittence categories. Because many potential metrics differed between intermittent and perennial samples, we plotted all calculated potential metrics and selected a subset of candidate metrics based on their ability to discriminate between categories (Table 1).

Table 1: Candidate metrics tested as discriminators of macroinvertebrate communities from sites in different intermittence categories. Differences between perennial/intermittent samples were tested with Mann-Whitney U-tests. ***<0.001, **<0.01, *<0.05

Metrics selected for index development	Autumn	Spring	Observed state at intermittent sites
% of lithal preference	***	***	lower
% of organic substrate preference	**	**	higher
% of rheophilic preference	***	n.s.	lower
% taxa with respiration with gills	***	***	lower
% taxa with high body flexibility	***	**	higher
% of rhithral preference	***	*	lower
% of epirhithral preference	***	*	lower
Weighted mean of sediment-sensitive invertebrates	***	n.s.	higher
Number of taxa	**	**	lower
Number of ET taxa	***	***	lower
Number of EPT taxa	***	***	lower
Total abundance	***	*	lower
Abundance of Heptageniidae	***	***	lower
Abundance of EPT	***	n.s.	lower
Proportion of Heptageniidae	***	***	lower
Proportion of Oligochaeta	***	n.s.	higher
Proportion of indicator taxa	***	***	lower

From the set of candidate metrics (Table 1), successive LDA revealed important metrics for sample separation. Three metrics were selected for discrimination in autumn: the proportion of indicator taxa, the proportion of individuals with high body flexibility, and the proportion of taxa with a preference for organic substrates. The formula for calculating the autumn index is:

*Biodrought index = (4.23*Proportion_of_indicator_taxa) + (-1.69*Proportion_of_high_body_flexibility) + (-2.94*Proportion_of_organic sediment preference) - 0.26*

Three metrics were also selected as discriminators of spring samples: the proportion of indicator taxa, the proportion of individuals with high body flexibility, and the total abundance. The formula for calculating the spring season index is:

*Biodrought index = (4.09*Proportion_of_indicator_taxa) + (-1.76*Proportion_of_high_body_flexibility) + (0.47*Total_abundance) - 4.01*

The Biodrought index was calculated for each sample (Fig. 5b) and the probability function for perennial, near-perennial and intermittent samples was approximated based on the distribution of index values within the intermittence categories. LDA discriminant scores (i.e. the Biodrought index) for each category were normally distributed (Shapiro-Wilk tests, $p >$

0.05). Mean discriminant scores varied between samples in the three intermittence categories ($F_{2,\ 101}$ = 215.9; p < 0.001) but not between spring and autumn samples ($F_{1,\ 101}$ = 0.009; p = 0.926), and there was no interaction between intermittence category and season ($F_{2,\ 101}$ = 0.328, p = 0.721). Because there was no difference in the distribution of sample discriminant scores between spring and autumn, it was possible to calculate probability functions independently of season (Fig. 5a). Values for the probability function were derived from the dataset for intermittent (mean = -3.36, SD = 1.398), near-perennial (mean = -0.231, SD = 0.926) and perennial (mean = 1.559, SD = 0.777) sites.

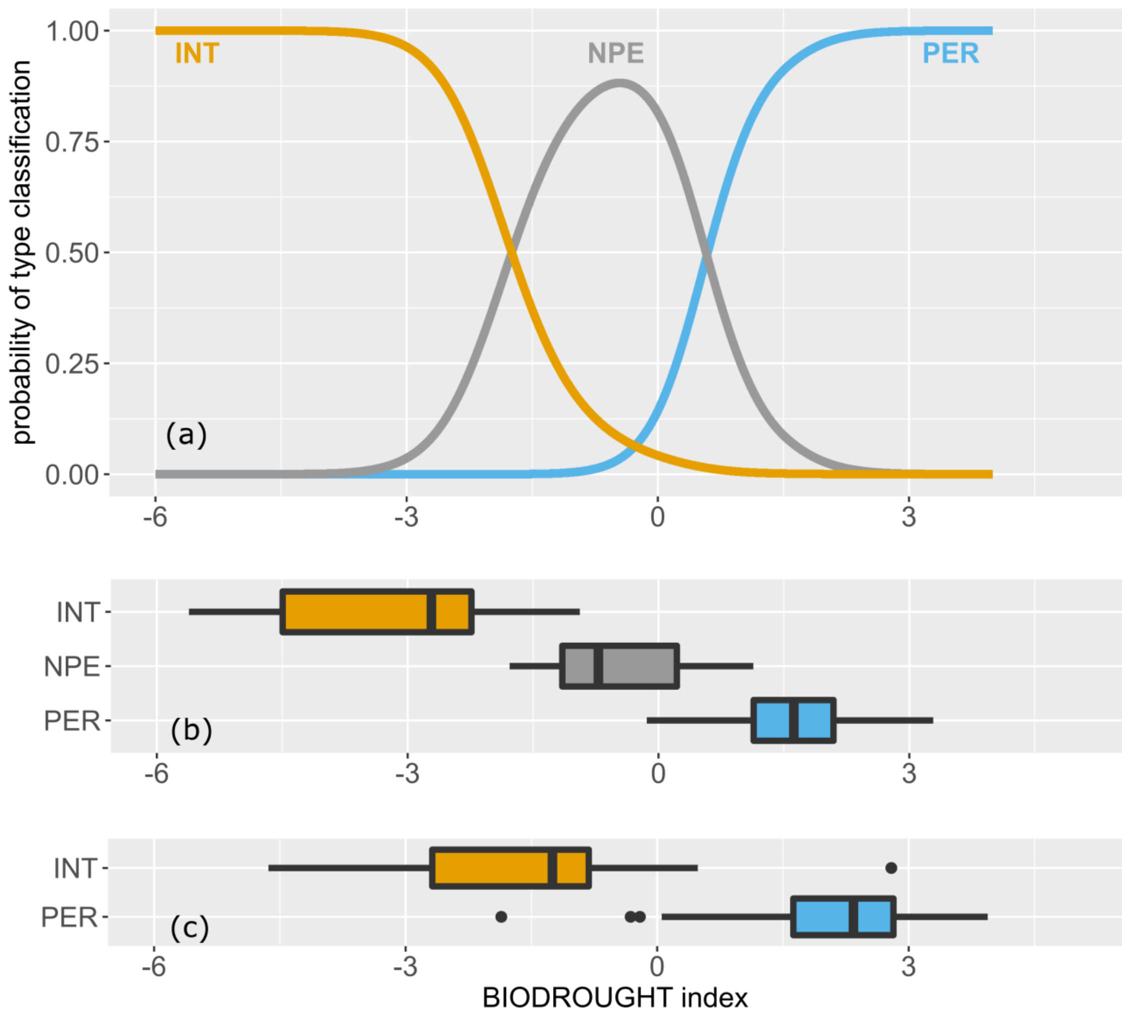

Fig. 5. *(colour figure)* Biodrought index values for each flow intermittence category: (a) Probability of classification to each category according to the index; index values for each category, for (b) samples used for index development and (c) independent samples used for index validation. INT – intermittent, NPE – near-perennial, PER – perennial.

3.3. Validation by independent samples

To evaluate the performance of the method, we calculated the Biodrought index values for a dataset not used for index development (Fig. 5c). Of 117 perennial samples, 108 (92%) had a probability >50% of being classified correctly by the index, with eight and one samples classified as near-perennial and intermittent, respectively. The index classified 1 of 26 samples from non-perennial streams incorrectly, with 15 and 10 correctly classified as near-perennial and intermittent, respectively. Because it was not possible to distinguish between intermittent and near-perennial categories in this independent dataset, the correct classification of non-perennial samples was 96%.

4. Discussion

Our results agree with previous research demonstrating that benthic macroinvertebrate community composition reflects stream flow intermittence (Arscott et al., 2010; Datry, 2012; Soria et al., 2017) and that the effects of relatively short (7-86 day) drying events can be detected even after seven months after flow resumption (Ledger and Hildrew, 2001; Chester and Robson, 2011). Previous studies from other regions have distinguished perennial and non-perennial streams using the proportional representation of different macroinvertebrate taxonomic groups (Mazzacano and Black, 2009; Nadeau, 2015; Cid et al., 2016; Cañedo-Argüelles et al., 2016) and using traits (Serra et al., 2017; Kelso and Entrekin, 2018). Our results confirm that macroinvertebrate communities in Central Europe can also be explored to identify stream intermittence, and specifically drying events. Our Biodrought index provides a new tool to identify antecedent drying events, which may facilitate interpretation of ecological data including the results of ecological status assessments, especially when hydrological data are missing. The method was developed and validated using Czech Republic data, but it has considerable potential for wider uptake due to the extensive distribution of the continental climate zone across Central Europe

4.1. Metrics used for index calculations

Biotic responses to environmental stress (e.g. water loss) can be species-specific (Lake, 2003) and we examined available information about responses to flow continuity mainly at the species level, and summarized the most sensitive/tolerant indicator taxa (Appendix A). The proportion of these indicator taxa was one of the most effective metrics to distinguish among intermittence categories. Flow intermittence tolerant taxa usually possess behavioural, morphological, physiological and/or life-history adaptations to survive dry phase (Lytle and Poff, 2004). For example, one species strongly associated with intermittent streams in this study was *Brachyptera risi*. This stonefly has the eggs with summer diapause, allowing the species to remain in the sediments in a viable egg stage during dry phases (Khoo, 1964). However, the selective loss of taxa sensitive to flow intermittence (and specifically drying) rather than selection for desiccation-resistant specialists is the primary driver of differences in community composition between perennial and non-perennial sites (Datry, 2012; Vidal-Abarca et al., 2013; Cid et al., 2016).

Although high body flexibility is not typically reported as a crucial trait in relation to stream drying (e.g. Bonada et al., 2007; Díaz et al., 2008; Walters, 2011) our results indicated its relevance. Organisms with flexible body shapes can respond to drying by moving into the subsurface interstices, which may maintain high humidity and can thus act as refuge for aquatic invertebrates during dry phases (Stubbington, 2012; Strachan et al., 2015). Moreover, a highly flexible body enables organisms including oligochaetes and leeches to form globular, desiccation-tolerant cysts (Montalto and Marchese, 2005; Shikov, 2011). Intermittent streams also supported a higher proportion of invertebrates with a preference for organic substrates, which may reflect their dry-phase survival in moisture-retaining patches of organic matter (Stubbington et al., 2009). Invertebrates that use such organic-rich habitats during flowing conditions can therefore persist in this substrate, which acts as a refuge that limits desiccation during dry phases (Boulton, 1989).

The Biodrought index calculated for the spring season also included total abundance. The relationship between total abundance and flow permanence in streams has previously been indicated by several studies (Rüegg and Robinson, 2004; Fenoglio et al., 2007; Datry, 2012). The lower abundance in our study was caused in particular by high mortality of *Gammarus* species, known to be sensitive to stream drying (Meyer and Meyer, 2000; Smith et al., 2003; Pařil et al., 2019).

4.2. Utility of the developed tool

Our index addresses the recognized need (Datry et al., 2011; Cid et al., 2016) for methods to identify antecedent drying events using biological metrics, and thus without using gauging stations or other prohibitively costly infrastructure. Even where gauging station data are available, biotic approaches such as our index complement the continuous, long-term hydrological information by distinguishing dry from lentic zero-flow states (Gallart et al., 2012). Sampling and processing of benthic invertebrate samples is methodologically well-managed and is routinely practised within the scope of monitoring programmes (Smith et al., 1999; Birk et al., 2012; Hill et al., 2017). The method used for taking samples (Kokeš et al., 2006) is comparable to other commonly used European methods such as AQEM/STAR method (Lorenz and Clarke, 2006), and the Biodrought index therefore has high potential for testing and use in other countries within the extensive continental climate zone that spans Central and Eastern Europe. The study dataset spans two biogeographical subprovinces (Hercynian and West-Carpathian; Culek, 2013) and the discriminatory power of the index was sufficient to correctly classify evaluated samples from the independent dataset from whole Czech Republic with high probability. Although working at a finer geographical resolution (e.g. within one subprovince) may achieve higher levels of correct assignment, we also recommend testing of our index in other Central European countries to explore the geographical limits of its reliability. A saprobic system based on common taxa is used in many Central and Eastern European countries (Rolauffs et al., 2004) and the Biodrought index may therefore be useable in Central European region without extensive taxonomic adjustment.

Our index was developed in pristine streams where only a single, natural stressor (drying) was known to influence macroinvertebrate community composition. Elsewhere, factors that may affect index performance include interactions between the hydrological stressor of drying (both natural and anthropogenic) with other human pressures, interactions which can have antagonistic or additive effects on biological communities (Folt et al., 1999; Matthaei et al., 2010; Ormerod et al., 2010). In particular, the typical sequence of hydrological conditions from low flows, to flow cessation and gradual drying can reduce oxygen concentrations, and intermittence and organic pollution can therefore have comparable effects by eliminating sensitive invertebrates (Pardo and Garcia, 2016). Moreover, a reduction in oxygen availability and low flow can have synergistic effects on benthic invertebrates (Calapez et al., 2017). Disentangling the effects of stream drying and anthropogenic stressors (including organic pollution) is therefore challenging, but consideration of the Biodrought index alongside physico-chemical quality elements may improve the accuracy of ecological status assessments that might otherwise incorrectly classify IRES as polluted. Wider testing is needed to explore how the index performs in streams exposed to human stressors.

The spatial distribution of intermittent reaches in relation to perennial reaches and other refuges may have a considerable influence on the rate and extent of community recovery after drying events (Sedell et al., 1990; Bogan et al., 2017; but see Datry et al., 2014b). The spatial proximity of extensive refuges, in particular upstream perennial reaches, may enable rapid recolonization and community reestablishment within weeks to obscure the occurrence of an antecedent dry phase (Fowler, 2004; Fritz and Dodds, 2004; Pařil et al., 2019). In our dataset, the intermittent sites were at least 0.5 km downstream of a perennial reach and the samples were taken at most 7 months after flow resumed. However, recovery at highly isolated sites (e.g. >10 km from perennial refuges) may take multiple years with repeated drying events often preventing aquatic communities from reaching a stable state (Bogan and Lytle, 2011; Bogan et al., 2017). Our index and comparable tools thus have higher potential for strong performance in IRES with relatively short dry phases, compared to those which may remain dry for years.

4.3. Conclusions and recommendations for index use

We developed the Biodrought index: a novel index to characterize the effect of stream drying on aquatic invertebrate communities. The index enable calculation of the probability of the antecedent stream drying, based on benthic invertebrates sampled using standard methods. We demonstrated the index as robust at national scale. The robustness of our index is evidenced by its registration by the Ministry of Environment of the Czech Republic, and we recommend its testing and adoption (with required adaptation) in other European countries within continental-climate region. In particular, the Biodrought index is intended for use by those with responsibility for monitoring and management of river ecosystems, including water management boards, environmental agencies and private water companies. We recommend adoption of the Biodrought index by such managers, to improve their interpretation of the macroinvertebrate assemblage data collected during ecological status assessments. The index can help avoid misinterpreting a deviation of community composition from reference status caused by a preceding dry phase (Reyjol et al., 2014; Cid et al., 2016; Stubbington et al., 2018). Environmental agencies could employ this tool for characterization of dry phase effects on macroinvertebrate communities in protected areas or for evaluation of the effectiveness of projects intended to restore naturally perennial flow at sites impacted by water resource pressures such as over-abstraction. The index can also be useful when identifying the impacts of water resource use in naturally perennial streams. However, since the method was developed in naturally intermittent streams, its use in non-natural IRES must be carefully assessed and the performance of Biodrought index in such conditions remains to be tested.

Our approach was essentially qualitative, identifying if a drying event had or had not occurred in the the one-year period preceding sample collection. Further research is needed to explore variability within ‘intermittent’, ‘near-perennial’ and other flow intermittence categories, in particular to identify species-specific responses to dry phases of differing durations. Identification of such thresholds is crucial to predict biotic responses to increasing intermittence in the context of ongoing climate change, which is interacting with increasing water resource pressures.

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Appendix A

Table A.1: List of flow intermittence tolerant taxa and the reasons for their inclusion in the list. The reliability of indicators is based on stronger (value 2) or weaker (value 1) evidence. Indicator values (IV) and their significance are shown separately for spring and autumn seasons for taxa that were associated with intermittent and near-perennial samples in Indicator Species Analysis. The frequency of taxa at intermittent and near-perennial samples is shown. Published sources in which information was found is shown. * - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$, n.s. – not significant

Taxon	Reliability	IV Spring/Autumn	Significance of IV Spring/Autumn	Frequency Spring/Autumn	References
Platyhelminthes					
Mesostoma lingua	1				Young, 2001
Nematomorpha	1	-/0.06	-/n.s.	0/0.06	Clifford, 1966
Gordiidae Gen. sp.	1				Clifford, 1966
Gordius sp.	1				Clifford, 1966
Mollusca					
Anisus leucostoma	2				Piechocki, 1979; Jurkiewicz-Karnkowska, 2011; Costil et al., 2001
Anisus septemgyratus	2				Jurkiewicz-Karnkowska, 2008; Jurkiewicz-Karnkowska, 2011
Anisus sp.	1				Costil et al., 2001
Anisus spirorbis	1				Jurkiewicz-Karnkowska, 2008
Aplexa hypnorum	2				Jurkiewicz-Karnkowska, 2008; Costil et al., 2001
Bathyomphalus contortus	1				Jurkiewicz-Karnkowska, 2011
Bithynia leachii	2				Jurkiewicz-Karnkowska, 2008; Piechocki, 1979
Bythinella austriaca agg.	2	0.44/0.46	*/*	0.45/0.56	
Galba truncatula	2	0.24/0.18	n.s./n.s.	0.27/0.19	Meyer and Meyer, 2000; Acuña et al., 2005; Stubbington et al., 2009; Costil et al., 2001; Falkner et al., 2001
Gyraulus riparius	1				Jurkiewicz-Karnkowska, 2008
Musculium lacustre	1				Piechocki, 1993
Pisidium casertanum	1				Piechocki, 1993
Pisidium obtusale	1				Piechocki, 1993
Pisidium personatum	1				Piechocki, 1993
Planorbarius corneus	1				Jurkiewicz-Karnkowska, 2011
Planorbis planorbis	2				Jurkiewicz-Karnkowska, 2011; Falkner et al., 2001
Potamopyrgus antipodarum	1	0.09/-	n.s./-	0.09/0.06	Costil et al., 2001
Radix peregra	2	-/0.06	-/n.s.	0/0.06	Costil et al., 2001; Extence, 1981
Segmentina nitida	2				Jurkiewicz-Karnkowska, 2011; Falkner et al., 2001
Stagnicola fuscus	1				Falkner et al., 2001
Stagnicola occultus	1				Falkner et al., 2001
Stagnicola palustris	1				Jurkiewicz-Karnkowska, 2011
Valvata cristata	2				Jurkiewicz-Karnkowska, 2008; Jurkiewicz-Karnkowska, 2011; Falkner et al., 2001.
Valvata macrostoma	2				Jurkiewicz-Karnkowska, 2008; Jurkiewicz-Karnkowska, 2011; Falkner et al., 2001
Oligochaeta					

Eiseniella tetraedra	2	0.54/0.64	n.s./*	0.82/0.75	Fenoglio et al., 2007; Hynes, 1958; Dumnicka and Kozsalka, 2005
Enchytraeus sp.	2	0.24/0.25	n.s./*	0.27/0.25	
Epirodrilus pygmaeus	1	0.18/0.2	n.s./n.s.	0.18/0.25	
Haplotaxis gordioides	2	0.29/0.32	n.s./*	0.36/0.38	
Marionina sp.	2	0.61/0.12	*/n.s.	0.73/0.13	
Nais elinguis	2	0.18/0.3	n.s./**	0.18/0.31	
Stylodrilus heringianus	2	0.56/0.52	n.s./n.s.	0.64/0.63	Dumnicka and Koszałka, 2005; Nijboer et al., 2004
Hirudinea					
Dina lineata	1				Elliott and Mann, 1979
Haemopis sanguisuga	2	0.18/0.19	n.s./*	0.18/0.19	Elliott and Mann, 1979
Crustacea					
Asellus aquaticus	2	0.07/0.04	n.s./n.s.	0.09/0.06	Iversen et al., 1978; Extence, 1981
Ephemeroptera					
Cloeon dipterum s. lat.	1	0.09/0.13	n.s./n.s.	0.09/0.13	
Ecdyonurus picteti	1	0.18/-	n.s./-	0.18/0	
Habrophlebia fusca	2	-/-	-/-	0.09/0.06	Bohle, 2000; Řezníčková et al., 2010
Metreletus balcanicus	2	0.09/-	n.s./-	0.09/0	Bauernfeind and Soldán, 2012; Soldán and Zahrádková, 2000; Bohle, 2000
Paraleptophlebia werneri	1				Soldán and Zahrádková, 2000
Siphlonurus aestivalis	2	0.25/-	n.s./-	0.27/0	Bauernfeind and Soldán, 2012; Řezníčková et al., 2010
Siphlonurus armatus	2	0.09/-	n.s./-	0.09/0	Bauernfeind and Soldán, 2012; Soldán and Zahrádková, 2000; Bohle, 2000
Siphlonurus lacustris	2				Fenoglio et al., 2007; Hynes, 1958
Odonata					
Pyrrhosoma nymphula	1				Opatrilova et al., 2005
Plecoptera					
Brachyptera risi	2	0.76/0.06	*/n.s.	0.82/0.06	Bohle, 2000; Hynes, 1941; Wagner et al., 2011; Mackereth, 1957
Capnia bifrons	2	0.45/0.5	*/n.s.	0.45/0.56	Bohle, 2000
Isoperla tripartita	2	0.55/0.19	**/n.s.	0.55/0.25	
Nemoura cinerea	2				Bohle, 2000; Malicky, 1989; Meyer and Meyer, 2000; Iversen et al., 1978; Hynes, 1958
Coleoptera					
Agabus guttatus	2	0.36/0.54	*/**	0.36/0.56	Bohle, 2000; Hynes, 1958
Agabus sp.	2				Bohle, 2000; Hynes, 1958; Meyer and Meyer, 2000
Anacaena globulus	2	-/0.25	-/*	0/0.25	Bohle, 2000; Hynes, 1958
Cyphon sp.	1	-/0.13	-/n.s.	0/0.13	
Esolus angustatus	2	0.15/0.25	n.s./*	0.27/0.25	
Helophorus aquaticus	1				Bohle, 2000
Helophorus brevipalpis	2				Bohle, 2000; Smith and Wood, 2002; Stubbington et al., 2009
Helophorus flavipes	1				Hynes, 1958
Helophorus grandis	1				Bohle, 2000
Helophorus sp.	2				Wood et al., 2005
Hydraena melas	1	-/-	-/-	0/0.06	Fenoglio et al., 2007
Hydraena nigrita	1	0.3/0.19	n.s./n.s.	0.55/0.38	Bohle, 2000
Hydroporus planus	1	-/0.06	-/n.s.	0/0.06	Opatrilova et al., 2005
Hydroporus pubescens	1				Opatrilova et al., 2005
Limnebius truncatellus	2	-/-	-/-	0/0.06	Bohle, 2000; Jackson, 1973

Platambus maculatus	2	0.18/0.53	n.s./*	0.18/0.63	Bohle, 2000; Hynes, 1958; Meyer and Meyer, 2000
Trichoptera					
Agrypnia varia	1				Moretti et al., 1976
Beraea pullata	1				Bohle, 2000
Beraeidae Gen. sp.	1				Fenoglio et al., 2007
Beraeodes minutus	2	0.09/0.19	n.s./*	0.09/0.19	Bohle, 2000
Glyphotaelius pellucidus	2	0.25/0.19	n.s./n.s.	0.27/0.19	Bohle, 2000; Acuña et al., 2005; Svensson, 1974
Grammotaulius nigropunctatus	2				Novák and Sehnal, 1963; Hiley, 1978
Chaetopteryx villosa	1	0.18/0.15	n.s./n.s.	0.18/0.19	
Ironoquia dubia	2	0.09/-	n.s./-	0.09/0	Bohle, 2000; Sommerhäuser et al., 1995
Leptocerus tineiformis	1				Moretti et al., 1976
Limnephilus affinis	1				Hiley, 1978
Limnephilus auricula	2				Novák and Sehnal, 1963; Hiley, 1978; Bohle, 2000; Smith et al., 2003; Pastuchová, 2008; Sommerhäuser et al., 1995; Svensson, 1974
Limnephilus bipunctatus	2				Novák and Sehnal, 1963; Moretti et al., 1976; Bohle, 2000; Meyer and Meyer, 2000
Limnephilus centralis	2				Hiley, 1978; Bohle, 2000; Smith et al., 2003; Wood et al., 2005; Svensson, 1974
Limnephilus coenosus	1				Hiley, 1978
Limnephilus flavicornis	1				Novák and Sehnal, 1963
Limnephilus griseus	2				Novák and Sehnal, 1963; Hiley, 1978; Svensson, 1974; Gislason, 1993
Limnephilus incisus	1				Hiley, 1978
Limnephilus lunatus	2				Bohle, 2000; Meyer and Meyer, 2000; Smith et al., 2003
Limnephilus sparsus	2				Novák and Sehnal, 1963; Hiley, 1978; Moretti et al., 1976; Bohle, 2000; Svensson, 1974
Limnephilus stigma	2				Novák and Sehnal, 1963; Hiley, 1978; Svensson, 1974
Limnephilus vittatus	2				Novák and Sehnal, 1963; Hiley, 1978; Moretti et al., 1976; Svensson, 1974
Micropterna lateralis	2				Bohle, 2000; Smith et al., 2003; Wood et al., 2005; Pastuchová, 2008; Sommerhäuser et al., 1995
Micropterna nycterobia	2	0.49/-	*/-	0.55/0	Pastuchová, 2008; Meyer and Meyer, 2000; Moretti et al., 1976
Micropterna sequax	2				Bohle, 2000; Meyer and Meyer, 2000; Smith et al., 2003; Wood et al., 2005
Micropterna testacea	1				Meyer and Meyer, 2000
Oligostomis reticulata	1				Sommerhäuser et al., 1995
Rhadicoleptus alpestris	1				Hiley, 1978
Stenophylax permistus	2				Bohle, 2000; Meyer and Meyer, 2000; Smith et al., 2003; Wood et al., 2005
Trichostegia minor	2				Novák and Sehnal, 1963; Svensson, 1974
Diptera					
Diplocladius cultriger	2	0.34/0.55	n.s./**	0.36/0.56	
Eukiefferiella claripennis	1	-/0.13	-/n.s.	0/0.13	
Hydrobaenus sp.	1	0.27/-	n.s./-	0.27/0	
Chironomus sp.	2	-/0.31	-/**	0/0.31	
Krenosmittia camptophleps	1	0.27/-	n.s./-	0.27/0	
Macropelopia sp.	2	0.45/0.08	*/n.s.	0.45/0.13	
Micropsectra atrofasciata-Gr.	2	-/0.89	-/*	1/0.94	
Natarsia sp.	2	0.58/0.42	*/*	0.64/0.5	
Orthocladius rivicola-Gr.	2	0.28/0.19	n.s./*	0.36/0.19	
Parametriocnemus stylatus	1	0.71/0.35	n.s./n.s.	0.91/0.63	Rüegg and Robinson, 2004
Paraphaenocladius sp.	2	0.64/0.25	*/*	0.82/0.25	

Paratrichocladius rufiventris	1	-/-	-/-	0.18/0	Moller Pillot, 2013
Procladius sp.	1	0.18/0.24	n.s./n.s.	0.18/0.25	
Rheocricotopus atripes	1	0.27/0.13	n.s./n.s.	0.27/0.13	
Rheocricotopus effusus	2	0.44/0.3	*/*	0.45/0.31	
Rheocricotopus effusus	2	0.44/0.3	*/*	0.45/0.31	
Rhypholophus haemorrhoidalis	1	0.41/0.13	n.s./n.s.	0.45/0.13	
Simulium noelleri	1	0.09/0.19	n.s./n.s.	0.09/0.19	
Zavrelimyia sp.	2	0.7/-	**/-	0.82/0	Opatrilova et al., 2005

Table A.2: List of perennial flow indicators and the reasons for their inclusion in the list. The reliability of indicators is based on stronger (value 2) or weaker (value 1) evidence. Indicator values (IV) and their significance are shown separately for spring and autumn seasons for taxa that were associated with perennial samples in Indicator Species Analysis. The frequency of taxa at perennial samples is shown. Published sources in which information was found are shown. * - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$, n.s. – not significant

Taxon	Reliability	IV Spring/Autumn	Significance of IV spring/autumn	Frequency spring/autumn	References
Platyhelminthes					
Crenobia alpina	2				Fenoglio et al., 2007; Rüegg and Robinson, 2004; Hynes, 1958
Dugesia gonocephala	2	0.82/0.73	**/**	0.83/0.74	Meyer and Meyer, 2000
Dugesia sp.	1				Fenoglio et al., 2007
Phagocata vitta	1				Hynes, 1958
Polycelis nigra	1				Sarriquet et al., 2007
Polycelis sp.	1				Fenoglio et al., 2007
Polycelis tenuis	1	-/-	-/-	0/0.04	Sarriquet et al., 2007
Mollusca					
Ancylus fluviatilis	2	0.46/0.25	*/n.s.	0.5/0.26	Meyer and Meyer, 2000; Wood et al., 2005; Stubbington et al., 2009 ; Fenoglio et al., 2007
Lithoglyphus naticoides	2				Jurkiewicz-Karnkowska, 2008; Falkner et al., 2001
Lymnaea stagnalis	1				Falkner et al., 2001
Myxas glutinosa	1				Falkner et al., 2001
Oligochaeta					
Aulodrilus japonicus	1	0.17/0.12	n.s./n.s.	0.17/0.15	
Nais alpina	2	0.33/0.47	n.s./*	0.33/0.48	
Ophidonais serpentina	1	0.25/0.11	n.s./n.s.	0.25/0.11	
Pristinella rosea Gr.	1	0.17/0.35	n.s./n.s.	0.17/0.37	
Propappus volki	2	0.25/0.3	n.s./*	0.25/0.3	
Rhyacodrilus coccineus	1	0.25/0.05	n.s./n.s.	0.25/0.15	
Hirudinea					
Erpobdella octoculata	2	0.17/0.14	n.s./n.s.	0.17/0.15	Meyer a Meyer, 2001; Sarriquet et al., 2007
Glossiphonia complanata	1				Sarriquet et al., 2007
Piscicola geometra	2				Wood et al., 2005; Elliott and Mann, 1979
Acari					
Hydracarina	2	0.56/0.53	n.s./*	0.58/0.59	
Crustacea					
Gammarus fossarum	1	-/0.46	-/n.s.	0.75/0.78	Meyer and Meyer, 2000
Ephemeroptera					
Baetis alpinus	1				Rüegg and Robinson, 2004
Baetis muticus	2	0.87/0.8	**/**	0.92/0.81	Řezníčková et al., 2010
Baetis niger	1	0.17/0.17	n.s./n.s.	0.17/0.19	
Baetis rhodani s.l.	2	0.96/0.87	**/**	1/0.93	Iversen et al., 1978; Pastuchová, 2008; Morrison, 1990
Baetis sp.	2				Bohle, 2000; Wood et al., 2005; Stubbington et al., 2009; Pastuchová, 2008
Baetis vernus	1	-/0.11	-/n.s.	0/0.22	Pastuchová, 2008
Centroptilum luteolum	1	0.5/-	n.s./-	0.75/0.67	Fenoglio et al., 2007

Ecdyonurus austriacus	1	-/0.11	-/n.s.	0.08/0.11	
Ecdyonurus starmachi	1				Řezníčková et al., 2010
Ecdyonurus subalpinus	1	0.16/0.26	n.s./n.s.	0.17/0.3	Pastuchová, 2008
Ecdyonurus torrentis	2	0.33/0.48	n.s./*	0.33/0.48	
Ecdyonurus venosus	1	-/0.04	-/n.s.	0/0.04	Hynes, 1958
Epeorus assimilis	1	0.33/0.22	n.s./n.s.	0.33/0.22	
Ephemera danica	2	0.65/0.63	*/**	0.75/0.78	Meyer and Meyer, 2000; Pastuchová, 2008; Řezníčková et al., 2010
Ephemerella mucronata	1	0.17/0.07	n.s./n.s.	0.17/0.07	
Habroleptoides confusa	2	0.55/0.7	n.s./*	0.67/0.81	Řezníčková et al., 2010; Pastuchová, 2008
Habrophlebia lauta	2	0.69/0.63	*/*	0.92/0.81	Řezníčková et al., 2010; Meyer and Meyer, 2000
Heptagenia sulphurea	1				Wood et al., 2005
Leptophlebia marginata	1				Opatrilova et al., 2005
Paraleptophlebia submarginata	2	0.48/0.59	*/n.s.	0.5/0.67	
Rhithrogena carpatoalpina	2	0.21/0.19	n.s./n.s.	0.25/0.19	Pastuchová, 2008; Řezníčková et al., 2010
Rhithrogena iridina	2				
Rhithrogena iridina/picteti	2	0.76/0.63	*/**	0.83/0.63	
Rhithrogena picteti	2				Meyer and Meyer, 2000; Pastuchová, 2008
Rhithrogena semicolorata	2	0.17/0.07	n.s./n.s.	0.17/0.07	Pastuchová, 2008; Řezníčková et al., 2010; Hynes, 1958
Serratella ignita	2				Meyer and Meyer, 2000; Stubbington et al., 2009; Pastuchová, 2008; Hynes, 1958
Torleya major	2	0.25/0.33	n.s./*	0.25/0.33	Meyer and Meyer, 2000
Plecoptera					
Amphinemura sp.	1	0.41/0.22	n.s./n.s.	0.42/0.22	
Dinocras cephalotes	2	0.08/0.07	n.s./n.s.	0.08/0.07	Fenoglio et al., 2007; Hynes, 1941
Dinocras sp.	2				Fenoglio et al., 2007; Hynes, 1941
Diura bicaudata	2	-/0.04	-/n.s.	0/0.04	Stubbington et al., 2009; Hynes, 1958
Chloroperla sp.	2				Fenoglio et al., 2007; Hynes, 1941
Chloroperla tripunctata	2				Fenoglio et al., 2007; Hynes, 1941
Isoperla oxylepis	1	0.25/0.17	n.s./n.s.	0.25/0.22	
Isoperla rivulorum	1	0.06/0.11	n.s./n.s.	0.08/0.11	
Leuctra digitata	1				Pastuchová, 2008
Leuctra fusca	1				Wood et al., 2005; Hynes, 1941
Leuctra handlirschi	1				Hynes, 1941
Leuctra inermis	2				Hynes, 1958
Leuctra pseudosignifera	1	0.08/0.11	n.s./n.s.	0.08/0.11	
Leuctra sp.	2	0.5/0.87	n.s./**	0.5/0.89	Stubbington et al., 2009
Perla sp.	2				Fenoglio et al., 2007; Hynes, 1941; Mackereth, 1957
Perlodes microcephalus	1	0.17/0.11	n.s./n.s.	0.17/0.11	
Protonemura sp.	2	0.38/0.44	n.s./**	0.42/0.44	Pastuchová, 2008
Siphonoperla sp.	1	0.17/0.25	n.s./n.s.	0.17/0.26	
Heteroptera					
Velia saulii	1	-/0.11	-/n.s.	0/0.11	
Coleoptera					
Elmis aenea	2	0.49/0.44	*/*	0.5/0.44	Wood et al., 2005; Stubbington et al., 2009
Elodes marginata	2	0.33/0.3	n.s./*	0.33/0.3	
Esolus parallelepipedus	1	0.08/0.15	n.s./n.s.	0.08/0.15	
Hydraena saga	1	-/0.11	-/n.s.	0/0.11	
Hydraena schuleri	1	0.17/0.09	n.s./n.s.	0.17/0.11	
Hydroporus nigrita	1				Opatrilova et al., 2005
Limnius perrisi	2	0.5/0.33	*/*	0.5/0.33	
Limnius volckmari	1	0.27/0.46	n.s./n.s.	0.33/0.74	Wood et al., 2005
Orectochilus villosus	2	0.17/0.11	n.s./n.s.	0.17/0.11	Meyer and Meyer, 2000
Oreodytes sanmarkii	1	-/0.07	-/n.s.	0/0.07	Fenoglio et al., 2007
Riolus subviolaceus	1	0.07/0.09	n.s./n.s.	0.08/0.11	Wood et al., 2005

Trichoptera					
Agapetus fuscipes	2	0.25/-	n.s./-	0.25/0	Sommerhäuser et al., 1995; Wood et al., 2005
Anabolia nervosa	1				Sommerhäuser et al., 1995
Athripsodes aterrimus	2				Hiley, 1978; Sommerhäuser et al., 1995
Athripsodes bilineatus	1	0.18/0.21	n.s./n.s.	0.25/0.3	Sommerhäuser et al., 1995
Athripsodes cinereus	1				Sommerhäuser et al., 1995
Cyrnus flavidus	1				Bohle, 2000
Drusus annulatus	1	0.16/-	n.s./-	0.25/0.04	Stubbington et al., 2009
Ecclisopteryx madida	1	0.17/-	n.s./-	0.17/0	
Goera pilosa	2				Iversen et al., 1978; Sommerhäuser et al., 1995
Hagenella clathrata	1				Opatrilova et al., 2005
Halesus digitatus	2				Pastuchová, 2008; Sommerhäuser et al., 1995
Halesus radiatus	2				Hiley, 1978; Pastuchová, 2008; Sommerhäuser et al., 1995
Hydropsyche angustipennis	2				Iversen et al., 1978; Sommerhäuser et al., 1995
Hydropsyche bulbifera	1				Pastuchová, 2008
Hydropsyche contubernalis	1				Sommerhäuser et al., 1995
Hydropsyche fulvipes	1				Pastuchová, 2008
Hydropsyche instabilis	1				Pastuchová, 2008
Hydropsyche pellucidula	2				Meyer and Meyer, 2000; Sommerhäuser et al., 1995; Pastuchová, 2008
Hydropsyche saxonica	2				Sommerhäuser et al., 1995; Pastuchová, 2008
Hydropsyche siltalai	1				Sommerhäuser et al., 1995
Hydropsyche sp.	2	0.87/0.89	**/**	0.92/0.93	
Hydropsychidae Gen. sp.	1				Bohle, 2000
Hydroptilidae Gen. sp.	2				Fenoglio et al., 2007; Wallace et al., 2003
Chaetopteryx fusca/villosa	1				Pastuchová, 2008
Lasiocephala basalis	2	0.08/0.11	n.s./n.s.	0.08/0.11	Sommerhäuser et al., 1995
Lepidostoma hirtum	1	0.17/0.07	n.s./n.s.	0.17/0.07	
Lype phaeopa	1				Sommerhäuser et al., 1995
Lype reducta	1				Sommerhäuser et al., 1995
Lype sp.	1	0.46/0.31	n.s./n.s.	0.5/0.41	Sommerhäuser et al., 1995
Micrasema longulum	1	-/0.11	-/n.s.	0/0.11	
Molanna angustata	1				Sommerhäuser et al., 1995
Mystacides azurea	2	0.08/0.09	n.s./n.s.	0.08/0.11	Sommerhäuser et al., 1995
Neureclipsis bimaculata	1				Sommerhäuser et al., 1995
Notidobia ciliaris	1				Sommerhäuser et al., 1995
Odontocerum albicorne	2	0.55/0.64	*/**	0.67/0.67	Pastuchová ,2008; Meyer and Meyer, 2000; Fenoglio et al., 2007
Oecismus monedula	1	0.21/0.19	n.s./n.s.	0.25/0.19	
Philopotamidae Gen. sp.	1				Bohle, 2000
Philopotamus montanus	2	0.33/0.22	n.s./n.s.	0.33/0.22	Pastuchová, 2008
Polycentropus flavomaculatus	2	0.57/0.5	*/*	0.58/0.56	Meyer and Meyer, 2000; Wood et al., 2005
Polycentropus irroratus	2	0.17/0.11	n.s./n.s.	0.17/0.11	Sommerhäuser et al., 1995
Potamophylax cingulatus	2				Hiley, 1978; Sommerhäuser et al., 1995
Potamophylax luctuosus	1				Sommerhäuser et al., 1995
Potamophylax nigricornis	2				Pastuchová, 2008; Meyer and Meyer, 2000
Potamophylax rotundipennis	2				Sommerhäuser et al., 1995; Pastuchová, 2008
Potamophylax sp.	2	0.44/0.4	n.s./*	0.75/0.41	
Psychomyia pusilla	1				Meyer and Meyer, 2000
Psychomyiidae Gen. sp.	1				Fenoglio et al., 2007
Rhyacophila dorsalis	2				Wood et al., 2005; Hynes, 1958
Rhyacophila fasciata	2				Pastuchová, 2008; Sommerhäuser et al., 1995
Rhyacophila nubila	2	0.25/-	n.s./-	0.25/0	Meyer and Meyer, 2000
Rhyacophila obliterata	1				Hynes, 1958

Rhyacophila polonica	1	0.14/-	n.s./-	0.17/0	Pastuchová, 2008
Rhyacophila sp.	1				Bohle, 2000
Rhyacophila tristis	1	0.25/-	n.s./-	0.25/0	
Sericostoma personatum	2				Pastuchová, 2008; Sommerhäuser et al., 1995
Sericostoma sp.	2	0.52/0.64	n.s./*	0.83/0.81	Meyer and Meyer, 2000
Silo pallipes	1	0.44/-	n.s./-	0.58/0	Pastuchová, 2008
Silo piceus	1				Pastuchová, 2008
Synagapetus iridipennis	1	-/-	-/-	0.08/0	Pastuchová, 2008
Tinodes assimilis	1				Sommerhäuser et al., 1995
Tinodes pallidulus	1				Sommerhäuser et al., 1995
Tinodes rostocki	1				Pastuchová, 2008
Tinodes waeneri	1				Sommerhäuser et al., 1995
Wormaldia occipitalis	1				Pastuchová, 2008
Diptera					
Ablabesmyia sp.	1	0.17/-	n.s./-	0.17/0.04	
Atherix ibis	2	-/0.11	-/n.s.	0/0.11	Meyer and Meyer, 2000
Berdeniella sp.	2	0.42/0.15	*/n.s.	0.42/0.15	
Brillia longifurca	1	0.22/0.15	n.s./n.s.	0.33/0.15	
Ceratopogonidae Gen. sp.	1	0.33/-	n.s./-	0.33/11	
Dicranota sp.	2	0.82/0.47	**/n.s.	0.92/0.67	Meyer and Meyer, 2000
Eloeophila sp.	1	-/0.41	-/n.s.	0.67/0.7	Meyer and Meyer, 2000
Eukiefferiella devonica/ilkleyensis	1	0.17/0.04	n.s./n.s.	0.17/0.04	
Hemerodromia sp.	2	0.5/0.24	**/n.s.	0.5/0.26	Opatrilova et al., 2005
Ibisia marginata	2	0.57/0.44	**/*	0.58/0.44	
Microtendipes rydalensis-Gr.	1	0.25/0.19	n.s./n.s.	0.25/0.19	
Paratrissocladius excerptus	1	0.27/0.19	n.s./n.s.	0.42/0.19	
Peripsychoda sp.	1	0.17/0.04	n.s./n.s.	0.17/0.04	
Pilaria sp.	1	-/0.15	-/n.s.	0/0.15	
Polypedilum albicorne	1	0.13/0.11	n.s./n.s.	0.25/0.11	
Polypedilum convictum-Gr.	2	-/0.49	-/*	0.25/0.56	
Polypedilum pedestre-Gr.	1	-/0.15	-/n.s.	0/0.15	
Potthastia longimana	2	0.25/0.37	n.s./*	0.25/0.37	
Prosimulium hirtipes	1	0.33/-	n.s./-	0.33/0	
Rheotanytarsus sp.	2	0.17/0.22	n.s./n.s.	0.17/0.22	Meyer and Meyer, 2000
Scleroprocta sp.	1	0.17/0.1	n.s./n.s.	0.17/0.11	
Simulium angustitarse	1	0.17/-	n.s./-	0.17/0.07	
Simulium variegatum	1	0.25/0.11	n.s./n.s.	0.25/0.11	
Stempellinella brevis	1	0.3/0.15	n.s./n.s.	0.67/0.15	
Stratiomyidae Gen. sp.	1				Fenoglio et al., 2007
Thienemanniella sp.	2	0.58/0.24	*/n.s.	0.58/0.3	
Thienemannimyia sp.	2	0.42/0.12	*/n.s.	0.42/0.15	
Tvetenia bavarica/calvescens	2	0.44/0.41	n.s./*	0.5/0.41	Moller Pillot, 2013

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Appendix B

Table B.1: List of benthic macroinvertebrates collected during the study and their frequency of occurance and mean density in three flow intermittence categories.

	Frequency			Density		
	Perennial	Near-perennial	Intermittent	Perennial	Near-perennial	Intermittent
Coelenterata						
Hydra sp.	0.02	0.00	0.00	0.13	0.00	0.00
Turbellaria						
Crenobia alpina	0.02	0.05	0.04	0.33	0.11	0.07
Dendrocoelum lacteum	0.02	0.05	0.00	0.02	0.42	0.00
Dugesia gonocephala	0.80	0.26	0.07	42.82	1.89	0.15
Dugesia polychroa	0.10	0.00	0.00	2.66	0.00	0.00
Polycelis tenuis	0.02	0.05	0.00	0.03	0.42	0.00
Mollusca						
Ancylus fluviatilis	0.31	0.32	0.07	12.79	6.11	0.19
Bythinella austriaca agg.	0.16	0.42	0.56	2.51	2.58	29.22
Galba truncatula	0.11	0.16	0.33	0.36	3.16	5.81
Gyraulus albus	0.02	0.05	0.00	0.13	0.11	0.00
Gyrinus substriatus	0.03	0.00	0.00	0.11	0.00	0.00
Musculium lacustre	0.00	0.00	0.04	0.00	0.00	0.04
Pisidium sp.	0.77	1.00	0.89	113.05	254.16	76.67
Potamopyrgus antipodarum	0.05	0.16	0.04	0.89	0.84	6.56
Radix ovata	0.08	0.05	0.00	6.90	0.26	0.00
Radix peregra	0.00	0.00	0.11	0.00	0.00	5.67
Nematoida						
Nematoda	0.31	0.26	0.26	1.89	0.95	3.04
Nematomorpha	0.02	0.00	0.04	0.02	0.00	0.11
Oligochaeta						
Achaeta sp.	0.00	0.00	0.07	0.00	0.00	0.22
Aulodrilus japonicus	0.15	0.16	0.04	2.57	10.53	0.30
Aulodrilus limnobius	0.00	0.05	0.00	0.00	0.11	0.00
Aulodrilus pluriseta	0.00	0.00	0.04	0.00	0.00	0.04
Bryodrilus sp.	0.00	0.00	0.04	0.00	0.00	1.04
Cernosvitoviella sp.	0.07	0.11	0.04	0.43	1.26	0.59
Cognettia glandulosa	0.13	0.16	0.33	1.15	1.74	6.52
Cognettia sphagnetorum	0.23	0.00	0.19	2.82	0.00	7.70
Eiseniella tetraedra	0.57	0.79	0.89	5.34	6.74	41.30
Enchytraeus sp.	0.05	0.11	0.22	0.39	0.21	22.59
Epirodrilus pygmaeus	0.08	0.32	0.15	0.36	4.21	3.33
Haplotaxis gordioides	0.20	0.16	0.41	0.46	0.42	1.85
Henlea/Fridericia sp.	0.52	0.47	0.89	6.48	4.05	56.63
Limnodrilus claparedeanus	0.05	0.00	0.00	0.48	0.00	0.00
Limnodrilus hoffmeisteri	0.38	0.37	0.22	7.69	9.16	3.89
Limnodrilus profundicola	0.00	0.05	0.00	0.00	0.05	0.00

	Frequency			Density		
	Perennial	Near-perennial	Intermittent	Perennial	Near-perennial	Intermittent
Limnodrilus udekemianus	0.03	0.05	0.00	0.16	0.16	0.00
Lumbricidae Gen. sp.	0.26	0.21	0.52	0.57	0.32	1.89
Lumbriculus variegatus	0.33	0.37	0.11	4.10	2.26	0.93
Marionina sp.	0.13	0.26	0.33	1.48	1.58	6.44
Mesenchytraeus armatus	0.10	0.00	0.33	0.72	0.00	2.48
Nais alpina	0.38	0.16	0.04	17.67	10.26	0.07
Nais barbata	0.02	0.00	0.00	0.07	0.00	0.00
Nais bretscheri	0.10	0.05	0.00	0.92	0.95	0.00
Nais communis	0.36	0.32	0.30	6.02	20.37	5.63
Nais elinguis	0.18	0.37	0.33	11.13	22.58	122.59
Nais christinae	0.02	0.00	0.00	0.07	0.00	0.00
Nais pardalis	0.02	0.05	0.00	0.13	1.00	0.00
Nais stolci	0.05	0.00	0.00	2.56	0.00	0.00
Nais variabilis	0.02	0.16	0.07	0.03	14.53	2.74
Ophidonais serpentina	0.16	0.05	0.04	3.77	0.32	1.19
Pristina aequiseta	0.03	0.11	0.00	0.13	1.05	0.00
Pristinella rosea Gr.	0.25	0.16	0.22	3.74	1.00	0.81
Propappus volki	0.28	0.00	0.00	33.89	0.00	0.00
Psammoryctides barbatus	0.26	0.32	0.11	7.39	16.84	3.00
Rhyacodrilus coccineus	0.15	0.16	0.00	2.00	4.26	0.00
Rhyacodrilus falciformis	0.23	0.26	0.26	1.08	0.58	1.59
Rhyacodrilus subterraneus	0.05	0.00	0.00	0.79	0.00	0.00
Rhypholophus haemorrhoidalis	0.03	0.05	0.37	0.10	0.42	1.19
Slavina appendiculata	0.05	0.05	0.00	3.84	0.42	0.00
Spirosperma ferrox	0.02	0.00	0.00	0.07	0.00	0.00
Stylodrilus brachystylus	0.28	0.26	0.07	47.69	82.42	38.67
Stylodrilus heringianus	0.64	0.53	0.67	48.97	37.63	289.52
Trichodrilus sp.	0.23	0.05	0.15	6.74	0.63	0.59
Trichodrilus strandi	0.11	0.11	0.04	12.98	3.26	0.89
Tubifex tubifex	0.54	0.63	0.22	72.00	7.00	2.89
Hirudinea						
Erpobdella octoculata	0.13	0.11	0.07	0.87	0.16	0.19
Erpobdella vilnensis	0.20	0.21	0.07	0.54	0.47	0.19
Glossiphonia complanata	0.03	0.11	0.04	0.10	0.16	0.07
Glossiphonia nebulosa	0.02	0.05	0.00	0.07	0.11	0.00
Glossosoma conformis	0.05	0.00	0.00	0.34	0.00	0.00
Haemopis sanguisuga	0.02	0.11	0.11	0.03	0.21	0.48
Helobdella stagnalis	0.02	0.00	0.00	0.02	0.00	0.00
Acari						
Hydracarina	0.43	0.32	0.15	9.43	1.21	0.48
Crustacea						
Asellus aquaticus	0.05	0.16	0.07	0.21	8.32	0.26
Copepoda	0.07	0.00	0.11	0.56	0.00	1.07

	Frequency			Density		
	Perennial	**Near-perennial**	**Intermittent**	**Perennial**	**Near-perennial**	**Intermittent**
Gammarus fossarum	0.79	0.89	0.63	1811.13	2533.32	43.26
Gammarus roeselii	0.10	0.16	0.11	3.39	3.37	0.96
Niphargus aquilex	0.02	0.00	0.19	0.02	0.00	4.89
Ephemeroptera						
Baetis alpinus	0.02	0.00	0.00	0.15	0.00	0.00
Baetis buceratus	0.03	0.00	0.00	0.18	0.00	0.00
Baetis fuscatus	0.02	0.11	0.00	0.03	1.37	0.00
Baetis liebenauae	0.02	0.00	0.00	0.07	0.00	0.00
Baetis muticus	0.84	0.47	0.11	83.92	9.68	1.70
Baetis niger	0.16	0.16	0.00	3.95	0.37	0.00
Baetis rhodani	0.97	0.89	0.44	229.98	103.63	11.93
Baetis vernus	0.11	0.26	0.07	3.07	9.47	0.48
Caenis luctuosa	0.00	0.00	0.04	0.00	0.00	0.07
Caenis macrura	0.02	0.05	0.04	0.13	0.05	0.15
Caenis pseudorivulorum	0.02	0.00	0.00	0.03	0.00	0.00
Centroptilum luteolum	0.64	0.53	0.44	26.44	58.63	43.44
Centroptilum pennulatum	0.02	0.00	0.00	0.03	0.00	0.00
Cloeon dipterum s. lat.	0.00	0.05	0.11	0.00	0.68	11.19
Ecdyonurus aurantiacus	0.02	0.05	0.00	0.28	0.21	0.00
Ecdyonurus austriacus	0.07	0.00	0.07	0.66	0.00	1.07
Ecdyonurus dispar	0.00	0.00	0.04	0.00	0.00	0.04
Ecdyonurus helveticus-Gr.	0.07	0.05	0.04	0.80	0.21	0.04
Ecdyonurus macani	0.02	0.00	0.00	0.03	0.00	0.00
Ecdyonurus picteti	0.05	0.05	0.04	0.75	0.37	0.04
Ecdyonurus starmachi	0.00	0.00	0.04	0.00	0.00	0.11
Ecdyonurus subalpinus	0.36	0.26	0.22	50.46	13.63	1.78
Ecdyonurus submontanus	0.02	0.00	0.00	0.20	0.00	0.00
Ecdyonurus torrentis	0.43	0.32	0.00	24.41	2.95	0.00
Ecdyonurus venosus	0.07	0.00	0.00	0.57	0.00	0.00
Electrogena lateralis	0.05	0.11	0.00	0.62	0.21	0.00
Electrogena quadrilineata	0.03	0.00	0.07	6.64	0.00	1.30
Electrogena ujhelyii	0.57	0.58	0.26	87.93	118.37	2.81
Epeorus assimilis	0.28	0.00	0.00	7.72	0.00	0.00
Ephemera danica	0.75	0.63	0.04	40.80	26.68	0.44
Ephemerella mucronata	0.10	0.00	0.00	5.02	0.00	0.00
Ephemerella notata	0.02	0.00	0.04	0.33	0.00	0.07
Habroleptoides confusa	0.79	0.74	0.44	211.72	120.89	16.96
Habrophlebia fusca	0.11	0.32	0.15	1.95	5.84	5.15
Habrophlebia lauta	0.87	0.79	0.30	78.84	72.63	16.48
Leptophlebia marginata	0.02	0.00	0.00	0.02	0.00	0.00
Metreletus balcanicus	0.00	0.00	0.07	0.00	0.00	0.63
Paraleptophlebia submarginata	0.56	0.53	0.22	18.00	7.11	10.19
Rhithrogena carpatoalpina	0.28	0.32	0.04	29.02	1.68	0.04

	Frequency			Density		
	Perennial	Near-perennial	Intermittent	Perennial	Near-perennial	Intermittent
Rhithrogena iridina/picteti	0.70	0.32	0.30	121.93	1.16	1.89
Rhithrogena semicolorata	0.08	0.00	0.04	5.61	0.00	0.07
Siphlonurus aestivalis	0.05	0.05	0.19	0.25	0.68	18.52
Siphlonurus armatus	0.00	0.00	0.04	0.00	0.00	0.07
Siphlonurus lacustris	0.00	0.05	0.00	0.00	0.21	0.00
Torleya major	0.26	0.00	0.00	11.51	0.00	0.00
Odonata						
Aeshna cyanea	0.00	0.00	0.04	0.00	0.00	0.07
Calopteryx virgo	0.15	0.05	0.07	0.66	0.11	0.26
Cordulegaster bidentata	0.00	0.05	0.00	0.00	0.11	0.00
Cordulegaster boltonii	0.13	0.11	0.00	0.66	0.11	0.00
Plecoptera						
Amphinemura sp.	0.30	0.16	0.07	21.28	0.53	1.44
Brachyptera risi	0.28	0.21	0.41	8.03	26.63	83.52
Brachyptera seticornis	0.03	0.00	0.00	1.00	0.00	0.00
Capnia bifrons	0.26	0.37	0.41	11.39	44.58	94.26
Dinocras cephalotes	0.08	0.00	0.00	2.84	0.00	0.00
Diura bicaudata	0.05	0.00	0.00	0.08	0.00	0.00
Isoperla grammatica	0.11	0.16	0.19	6.64	7.00	27.19
Isoperla oxylepis	0.23	0.21	0.00	11.70	20.42	0.00
Isoperla rivulorum	0.10	0.05	0.00	1.77	0.47	0.00
Isoperla tripartita	0.11	0.37	0.41	4.61	16.63	35.85
Leuctra braueri	0.05	0.00	0.04	0.18	0.00	0.07
Leuctra nigra	0.15	0.11	0.04	1.11	0.68	0.22
Leuctra pseudosignifera	0.10	0.00	0.00	0.46	0.00	0.00
Leuctra sp.	0.72	0.79	0.33	163.98	7.74	2.56
Nemoura sp.	0.84	1.00	0.74	179.26	188.84	152.00
Nemurella picteti	0.02	0.00	0.00	0.15	0.00	0.00
Perla burmeisteriana	0.07	0.00	0.00	0.25	0.00	0.00
Perla marginata	0.03	0.00	0.00	0.13	0.00	0.00
Perlodes microcephalus	0.10	0.00	0.00	0.13	0.00	0.00
Protonemura sp.	0.48	0.11	0.11	47.62	0.63	1.93
Siphonoperla sp.	0.20	0.16	0.00	7.59	1.79	0.00
Taeniopteryx sp.	0.02	0.00	0.00	0.03	0.00	0.00
Heteroptera						
Aquarius paludum	0.02	0.00	0.00	0.02	0.00	0.00
Gerris lacustris	0.05	0.05	0.00	0.18	0.05	0.00
Gerris odontogaster	0.00	0.00	0.04	0.00	0.00	0.07
Micronecta sp.	0.07	0.05	0.04	2.44	1.58	0.11
Velia caprai	0.03	0.05	0.04	0.07	0.05	0.04
Velia saulii	0.05	0.05	0.07	0.07	0.26	0.30
Neuroptera						
Osmylus fulvicephalus	0.02	0.00	0.00	0.02	0.00	0.00

	Frequency			Density		
	Perennial	Near-perennial	Intermittent	Perennial	Near-perennial	Intermittent
Megaloptera						
Sialis fuliginosa	0.49	0.63	0.26	4.30	10.32	2.44
Trichoptera						
Agapetus fuscipes	0.08	0.00	0.00	4.79	0.00	0.00
Allogamus auricollis	0.00	0.05	0.00	0.00	0.05	0.00
Allogamus uncatus	0.00	0.00	0.04	0.00	0.00	0.07
Athripsodes bilineatus	0.26	0.21	0.19	3.98	1.47	0.33
Beraeodes minutus	0.00	0.16	0.15	0.00	0.32	0.22
Brachycentrus montanus	0.08	0.00	0.00	1.02	0.00	0.00
Crunoecia irrorata	0.00	0.00	0.07	0.00	0.00	0.19
Cyrnus trimaculatus	0.07	0.05	0.00	0.21	0.11	0.00
Drusus annulatus	0.08	0.26	0.11	0.61	1.58	0.22
Ecclisopteryx dalecarlica	0.07	0.00	0.07	0.79	0.00	0.07
Ecclisopteryx madida	0.05	0.05	0.00	1.34	0.11	0.00
Glyphotaelius pellucidus	0.05	0.05	0.30	0.16	0.05	2.30
Halesus sp.	0.31	0.32	0.22	12.25	5.26	1.78
Hydatophylax infumatus	0.02	0.00	0.00	0.02	0.00	0.00
Hydropsyche sp.	0.93	0.63	0.19	93.03	11.63	0.96
Chaetopteryx fusca	0.02	0.05	0.00	0.02	3.63	0.00
Chaetopteryx major	0.16	0.05	0.11	3.20	5.53	0.96
Chaetopteryx villosa	0.07	0.11	0.30	0.46	0.21	0.48
Ironoquia dubia	0.00	0.00	0.07	0.00	0.00	0.11
Lasiocephala basalis	0.11	0.00	0.00	0.48	0.00	0.00
Lepidostoma hirtum	0.10	0.00	0.00	7.30	0.00	0.00
Limnephilus lunatus	0.00	0.05	0.00	0.00	0.11	0.00
Limnephilus rhombicus	0.02	0.05	0.00	0.13	0.05	0.00
Limnephilus sp.	0.02	0.11	0.04	0.07	0.16	0.04
Lithax obscurus	0.03	0.00	0.00	0.05	0.00	0.00
Lype sp.	0.43	0.32	0.04	2.75	1.47	0.07
Micrasema longulum	0.05	0.00	0.00	0.30	0.00	0.00
Micrasema minimum	0.02	0.00	0.00	0.07	0.00	0.00
Micropterna nycterobia	0.02	0.26	0.26	0.07	1.32	1.41
Micropterna sp.	0.02	0.05	0.26	0.03	0.42	12.37
Mystacides azurea	0.10	0.05	0.00	1.05	0.21	0.00
Odontocerum albicorne	0.62	0.32	0.07	8.33	1.16	0.30
Oecismus monedula	0.21	0.00	0.04	1.16	0.00	0.15
Oligostomis reticulata	0.02	0.00	0.00	0.02	0.00	0.00
Philopotamus ludificatus	0.08	0.00	0.00	2.03	0.00	0.00
Philopotamus montanus	0.26	0.00	0.00	20.95	0.00	0.00
Plectrocnemia brevis	0.00	0.00	0.04	0.00	0.00	0.07
Plectrocnemia conspersa	0.18	0.32	0.30	7.97	12.53	8.11
Polycentropus flavomaculatus	0.49	0.37	0.04	14.56	4.84	0.07
Polycentropus irroratus	0.11	0.05	0.00	1.13	0.42	0.00

	Frequency			Density		
	Perennial	Near-perennial	Intermittent	Perennial	Near-perennial	Intermittent
Potamophylax sp.	0.59	0.37	0.15	8.95	2.53	0.89
Psychomyia pusilla	0.02	0.00	0.00	0.03	0.00	0.00
Ptilocolepus granulatus	0.02	0.00	0.00	0.03	0.00	0.00
Rhyacophila cf. *fasciata*	0.21	0.11	0.04	1.77	0.84	0.07
Rhyacophila nubila	0.11	0.05	0.00	1.66	0.79	0.00
Rhyacophila polonica	0.08	0.00	0.07	0.69	0.00	0.22
Rhyacophila tristis	0.11	0.05	0.00	2.33	0.05	0.00
Sericostoma sp.	0.82	0.68	0.19	21.85	15.63	0.41
Silo nigricornis	0.02	0.00	0.00	0.07	0.00	0.00
Silo pallipes	0.21	0.11	0.00	1.93	1.05	0.00
Stenophylax permistus	0.00	0.11	0.11	0.00	0.26	0.19
Synagapetus iridipennis	0.03	0.00	0.04	0.26	0.00	0.15
Synagapetus moselyi	0.07	0.11	0.22	0.23	1.89	18.67
Tinodes sp.	0.46	0.37	0.04	7.34	2.79	0.15
Coleoptera						
Agabus guttatus	0.03	0.32	0.67	0.13	1.21	12.22
Anacaena globulus	0.02	0.11	0.11	0.03	0.16	0.19
Contacyphon sp.	0.00	0.00	0.11	0.00	0.00	1.11
Deronectes latus	0.05	0.00	0.00	0.10	0.00	0.00
Elmis aenea	0.46	0.37	0.15	25.64	1.16	1.19
Elmis latreillei	0.00	0.00	0.04	0.00	0.00	0.07
Elmis maugetii	0.93	0.84	0.67	86.97	138.89	14.37
Odeles sp.	0.25	0.00	0.04	1.34	0.00	0.15
Elodes sp.	0.43	0.84	0.26	5.74	19.16	0.48
Esolus angustatus	0.11	0.21	0.22	2.07	1.84	7.78
Esolus parallelepipedus	0.16	0.00	0.15	1.72	0.00	0.30
Haliplus lineatocollis	0.00	0.00	0.04	0.00	0.00	0.04
Haliplus sp.	0.00	0.00	0.04	0.00	0.00	0.07
Hydraena belgica	0.05	0.00	0.00	1.20	0.00	0.00
Hydraena dentipes	0.11	0.00	0.04	4.23	0.00	0.07
Hydraena excisa	0.23	0.32	0.41	3.20	13.63	5.04
Hydraena gracilis	0.89	0.79	0.52	71.30	58.37	13.33
Hydraena melas	0.05	0.00	0.07	0.46	0.00	0.15
Hydraena nigrita	0.23	0.42	0.41	2.36	5.00	2.00
Hydraena paganettii	0.00	0.05	0.00	0.00	0.21	0.00
Hydraena pygmaea	0.05	0.00	0.00	0.38	0.00	0.00
Hydraena riparia	0.41	0.32	0.26	9.13	5.37	1.93
Hydraena rufipes	0.02	0.00	0.04	0.07	0.00	0.07
Hydraena saga	0.13	0.00	0.00	0.66	0.00	0.00
Hydraena schuleri	0.11	0.05	0.00	0.74	0.21	0.00
Hydraena subimpressa	0.03	0.00	0.00	0.15	0.00	0.00
Hydraena truncata	0.00	0.00	0.04	0.00	0.00	0.04
Hydrocyphon deflexicollis	0.02	0.00	0.00	0.03	0.00	0.00

	Frequency			Density		
	Perennial	Near-perennial	Intermittent	Perennial	Near-perennial	Intermittent
Hydroporus palustris	0.00	0.05	0.00	0.00	0.05	0.00
Hydroporus planus	0.00	0.00	0.04	0.00	0.00	0.04
Ilybius sp.	0.02	0.05	0.00	0.07	0.32	0.00
Laccobius bipunctatus	0.02	0.00	0.00	0.07	0.00	0.00
Laccobius obscuratus	0.02	0.00	0.00	0.07	0.00	0.00
Limnebius truncatellus	0.13	0.00	0.04	0.49	0.00	0.04
Limnius perrisi	0.39	0.11	0.07	54.25	0.37	0.96
Limnius volckmari	0.82	0.79	0.33	34.20	49.63	4.48
Orectochilus villosus	0.15	0.05	0.00	2.57	0.32	0.00
Oreodytes sanmarkii	0.03	0.00	0.00	0.05	0.00	0.00
Oulimnius tuberculatus	0.28	0.21	0.04	3.41	1.58	0.11
Platambus maculatus	0.33	0.68	0.44	2.80	26.74	7.07
Riolus cupreus	0.02	0.05	0.00	0.07	1.58	0.00
Riolus subviolaceus	0.08	0.16	0.00	3.72	4.53	0.00
Diptera (excl. Chironomidae)						
Acanthocnema glaucescens	0.02	0.00	0.00	0.03	0.00	0.00
Antocha sp.	0.10	0.05	0.00	0.62	0.11	0.00
Atherix ibis	0.05	0.00	0.00	0.34	0.00	0.00
Berdeniella sp.	0.15	0.00	0.00	2.21	0.00	0.00
Beris vallata	0.02	0.00	0.00	0.03	0.00	0.00
Bezzia sp.	0.51	0.47	0.33	6.18	10.84	3.33
Ceratopogonidae	0.21	0.16	0.19	1.54	0.84	1.37
Clinocera/Wiedemannia sp.	0.11	0.05	0.00	1.87	0.53	0.00
Clytocerus sp.	0.00	0.00	0.07	0.00	0.00	0.37
Dicranomyia sp.	0.00	0.00	0.04	0.00	0.00	0.30
Dicranota sp.	0.70	0.63	0.30	20.48	11.21	0.81
Dixa sp.	0.28	0.21	0.07	1.48	1.32	0.15
Dolichopodidae	0.10	0.11	0.04	0.49	0.21	0.07
Eloeophila sp.	0.69	0.63	0.19	8.95	14.26	0.59
Ephydridae	0.03	0.00	0.00	0.10	0.00	0.00
Erioptera sp.	0.02	0.00	0.00	0.07	0.00	0.00
Fannia sp.	0.00	0.00	0.04	0.00	0.00	0.07
Gonomyia sp.	0.03	0.00	0.00	0.10	0.00	0.00
Hemerodromia sp.	0.28	0.11	0.04	11.26	0.37	0.15
Hexatoma sp.	0.36	0.16	0.37	2.49	3.05	3.30
Chelifera sp.	0.44	0.42	0.37	11.87	7.95	15.63
Chrysopilus auratus	0.10	0.05	0.26	0.48	0.11	0.74
Chrysops sp.	0.38	0.47	0.33	3.05	9.47	1.89
Ibisia marginata	0.46	0.16	0.07	47.87	0.42	0.26
Jungiella sp.	0.02	0.00	0.00	0.46	0.00	0.00
Limnophila sp.	0.03	0.00	0.07	0.20	0.00	0.11
Limonia sp.	0.03	0.00	0.11	0.16	0.00	0.30
Molophilus sp.	0.11	0.26	0.26	0.54	1.16	22.56

	Frequency			Density		
	Perennial	Near-perennial	Intermittent	Perennial	Near-perennial	Intermittent
Muscidae	0.08	0.05	0.11	0.46	0.11	0.56
Nemotelus sp.	0.00	0.00	0.04	0.00	0.00	0.07
Neolimnomyia sp.	0.05	0.11	0.00	0.13	0.21	0.00
Orimarga sp.	0.00	0.00	0.04	0.00	0.00	0.07
Oxycera sp.	0.10	0.11	0.22	0.31	1.42	6.89
Pedicia sp.	0.31	0.53	0.19	1.90	3.95	1.00
Pericoma sp.	0.11	0.37	0.19	2.18	6.26	0.56
Peripsychoda sp.	0.07	0.05	0.00	0.59	0.84	0.00
Pilaria sp.	0.11	0.11	0.11	0.46	0.26	0.41
Pneumia sp.	0.07	0.11	0.00	0.52	0.16	0.00
Prosimulium hirtipes	0.10	0.00	0.00	19.67	0.00	0.00
Prosimulium latimucro	0.00	0.00	0.04	0.00	0.00	1.96
Prosimulium rufipes	0.00	0.00	0.04	0.00	0.00	1.04
Prosimulium tomosvaryi	0.33	0.42	0.37	130.51	65.21	86.96
Psychoda sp.	0.02	0.00	0.04	0.03	0.00	0.04
Ptychoptera sp.	0.41	0.32	0.04	13.93	17.58	0.07
Sciomyzidae	0.00	0.00	0.07	0.00	0.00	0.15
Scleroprocta sp.	0.20	0.16	0.04	0.85	0.32	0.04
Simulium angustipes	0.15	0.26	0.19	7.20	6.11	4.63
Simulium angustitarse	0.08	0.05	0.11	0.28	0.84	0.30
Simulium argyreatum	0.08	0.05	0.07	5.84	0.11	0.11
Simulium brevidens	0.02	0.00	0.00	1.05	0.00	0.00
Simulium carpathicum	0.00	0.00	0.04	0.00	0.00	0.04
Simulium costatum	0.10	0.05	0.04	2.48	0.05	0.15
Simulium cryophilum	0.16	0.11	0.07	3.89	1.16	12.78
Simulium equinum	0.02	0.00	0.00	0.03	0.00	0.00
Simulium noelleri	0.00	0.11	0.11	0.00	1.16	1.33
Simulium ornatum	0.28	0.42	0.19	3.10	131.68	0.63
Simulium reptans	0.05	0.00	0.00	1.44	0.00	0.00
Simulium trifasciatum	0.00	0.00	0.04	0.00	0.00	0.33
Simulium variegatum	0.11	0.00	0.04	7.67	0.00	0.11
Simulium vernum	0.31	0.58	0.37	7.54	10.11	5.26
Tabanus miki	0.00	0.00	0.04	0.00	0.00	0.07
Tabanus sp.	0.03	0.00	0.04	0.05	0.00	0.07
Tipula lateralis	0.00	0.05	0.00	0.00	0.21	0.00
Tipula maxima	0.28	0.68	0.44	1.66	9.37	1.41
Tipula saginata	0.20	0.16	0.07	0.82	1.89	0.15
Tipula unca	0.02	0.00	0.07	0.07	0.00	0.15
Tipula vittata	0.00	0.00	0.04	0.00	0.00	0.19
Chironomidae						
Ablabesmyia sp.	0.08	0.05	0.07	1.41	0.47	0.37
Apsectrotanypus trifascipennis	0.39	0.53	0.15	3.28	51.00	0.78
Brillia bifida	0.62	0.89	0.78	25.57	69.26	29.11

	Frequency			Density		
	Perennial	**Near-perennial**	**Intermittent**	**Perennial**	**Near-perennial**	**Intermittent**
Brillia longifurca	0.21	0.11	0.07	0.87	0.32	0.15
Bryophaenocladius sp.	0.02	0.05	0.00	0.13	0.11	0.00
Cladotanytarsus vanderwulpi-Gr.	0.03	0.00	0.00	0.26	0.00	0.00
Conchapelopia sp.	0.74	0.74	0.48	24.93	36.63	10.96
Corynoneura coronata-Gr.	0.02	0.00	0.04	0.23	0.00	0.07
Corynoneura lobata	0.31	0.37	0.37	2.95	5.21	4.41
Cricotopus albiforceps	0.00	0.05	0.00	0.00	0.11	0.00
Cricotopus bicinctus	0.03	0.00	0.04	0.30	0.00	0.15
Cricotopus patens/flavocinctus	0.02	0.00	0.00	0.26	0.00	0.00
Cricotopus sp.	0.10	0.05	0.00	1.66	0.11	0.00
Cricotopus sylvestris-Gr.	0.00	0.00	0.04	0.00	0.00	0.07
Cricotopus tremulus-Gr.	0.07	0.11	0.00	1.21	0.47	0.00
Cricotopus trifascia	0.02	0.00	0.00	0.79	0.00	0.00
Cryptochironomus sp.	0.03	0.00	0.00	0.10	0.00	0.00
Demicryptochironomus sp.	0.03	0.00	0.00	0.20	0.00	0.00
Diamesa cinerella-Gr.	0.20	0.26	0.30	30.69	21.68	51.41
Dicrotendipes sp.	0.00	0.00	0.04	0.00	0.00	0.59
Diplocladius cultriger	0.16	0.53	0.52	0.97	19.95	24.37
Epoicocladius ephemerae	0.51	0.32	0.00	5.10	9.32	0.00
Eukiefferiella brevicalcar	0.34	0.32	0.30	7.11	5.84	5.52
Eukiefferiella claripennis	0.00	0.21	0.04	0.00	2.42	0.37
Eukiefferiella cf. *clypeata*	0.03	0.00	0.00	0.08	0.00	0.00
Eukiefferiella devonica/ilkleyensis	0.10	0.16	0.00	0.98	1.37	0.00
Eukiefferiella gracei-Gr.	0.07	0.05	0.04	0.39	0.95	0.15
Eukiefferiella minor/fittkaui	0.00	0.00	0.04	0.00	0.00	0.30
Eukiefferiella rectangularis-Gr.	0.03	0.05	0.00	0.23	0.11	0.00
Eukiefferiella similis	0.02	0.00	0.00	0.20	0.00	0.00
Georthocladius luteicornis	0.02	0.00	0.00	0.03	0.00	0.00
Gymnometriocnemus sp.	0.00	0.00	0.04	0.00	0.00	0.07
Heleniella ornaticollis	0.33	0.32	0.11	7.54	2.47	2.30
Heterotrissocladius cf. *scutellatus*	0.00	0.00	0.04	0.00	0.00	0.15
Heterotrissocladius marcidus	0.18	0.16	0.19	3.13	2.42	4.93
Hydrobaenus sp.	0.00	0.00	0.11	0.00	0.00	1.85
Chaetocladius dentiforceps-Gr.	0.02	0.00	0.04	0.07	0.00	0.11
Chaetocladius piger-Gr.	0.05	0.11	0.19	0.67	1.16	1.59
Chaetocladius vitellinus-Gr.	0.03	0.00	0.00	0.16	0.00	0.00
Chironomus sp.	0.05	0.11	0.15	0.21	0.68	47.89
Krenopsectra sp.	0.11	0.05	0.19	6.49	1.58	28.78
Krenosmittia camptophleps	0.00	0.00	0.15	0.00	0.00	4.44
Limnophyes sp.	0.11	0.26	0.30	0.62	0.84	5.00
Macropelopia sp.	0.05	0.21	0.26	0.43	0.89	15.30
Metriocnemus fuscipes-Gr.	0.00	0.05	0.00	0.00	0.42	0.00
Micropsectra apposita-Gr.	0.13	0.21	0.44	3.21	14.74	13.93

	Frequency			Density		
	Perennial	Near-perennial	Intermittent	Perennial	Near-perennial	Intermittent
Micropsectra atrofasciata-Gr.	0.80	0.89	0.89	161.33	1816.00	223.70
Microtendipes pedellus-Gr.	0.59	0.63	0.30	19.36	54.00	19.48
Microtendipes rydalensis-Gr.	0.13	0.05	0.00	11.80	0.11	0.00
Monodiamesa bathyphila	0.05	0.00	0.00	0.20	0.00	0.00
Nanocladius parvulus/rectinervis	0.05	0.11	0.07	0.16	0.95	0.15
Natarsia sp.	0.25	0.42	0.59	0.90	3.74	4.44
Nilotanypus dubius	0.02	0.00	0.00	0.07	0.00	0.00
Orthocladius lignicola	0.10	0.05	0.19	0.36	0.42	0.63
Orthocladius obumbratus/oblidens	0.34	0.37	0.33	69.77	21.16	25.07
Orthocladius rivicola-Gr.	0.11	0.26	0.26	6.31	2.42	39.56
Orthocladius rivulorum	0.07	0.11	0.04	4.57	0.63	0.22
Orthocladius rubicundus	0.11	0.26	0.11	3.31	5.05	0.37
Paracladopelma sp.	0.02	0.00	0.00	0.02	0.00	0.00
Paracricotopus niger	0.02	0.00	0.00	0.07	0.00	0.00
Parakiefferiella sp.	0.02	0.11	0.00	0.03	0.47	0.00
Paramerina sp.	0.03	0.05	0.00	0.10	0.42	0.00
Parametriocnemus stylatus	0.80	0.95	0.70	41.02	60.05	193.67
Paraphaenocladius sp.	0.05	0.21	0.48	2.00	3.47	14.44
Parasmittia sp.	0.00	0.00	0.04	0.00	0.00	0.04
Paratendipes albimanus-Gr.	0.03	0.00	0.04	0.08	0.00	0.15
Paratrichocladius rufiventris	0.13	0.21	0.07	5.70	0.95	0.44
Paratrissocladius excerptus	0.25	0.16	0.22	3.43	3.58	1.63
Parorthocladius sp.	0.00	0.00	0.07	0.00	0.00	3.74
Phaenopsectra sp.	0.07	0.05	0.11	0.15	0.16	1.70
Polypedilum albicorne	0.18	0.11	0.26	1.25	0.53	3.26
Polypedilum convictum-Gr.	0.48	0.42	0.33	27.10	10.95	5.48
Polypedilum cultellatum	0.02	0.00	0.00	0.07	0.00	0.00
Polypedilum laetum-Gr.	0.00	0.05	0.00	0.00	0.68	0.00
Polypedilum pedestre-Gr.	0.10	0.05	0.07	0.38	0.11	0.52
Polypedilum scalaenum-Gr.	0.28	0.21	0.11	1.67	2.11	0.44
Potthastia longimana	0.26	0.00	0.00	2.46	0.00	0.00
Procladius sp.	0.08	0.26	0.22	0.28	6.16	1.52
Prodiamesa olivacea	0.33	0.42	0.41	5.34	4.11	17.52
Psectrocladius sp.	0.00	0.00	0.04	0.00	0.00	0.07
Pseudorthocladius sp.	0.05	0.11	0.07	0.15	0.63	0.74
Pseudosmittia sp.	0.00	0.00	0.04	0.00	0.00	0.22
Rheocricotopus atripes	0.02	0.05	0.19	0.07	0.21	1.41
Rheocricotopus effusus	0.07	0.26	0.63	0.23	5.00	9.48
Rheocricotopus fuscipes	0.62	0.79	0.63	19.79	35.89	13.19
Rheocricotopus chalybeatus	0.00	0.05	0.00	0.00	0.11	0.00
Rheotanytarsus sp.	0.20	0.11	0.04	6.97	0.16	0.04
Smittia sp.	0.00	0.00	0.04	0.00	0.00	0.07
Stempellinella brevis	0.48	0.26	0.37	24.36	41.47	2.22

	Frequency			Density		
	Perennial	**Near-perennial**	**Intermittent**	**Perennial**	**Near-perennial**	**Intermittent**
Stictochironomus sp.	0.15	0.11	0.00	0.84	2.37	0.00
Synorthocladius semivirens	0.20	0.11	0.11	3.38	0.53	0.30
Tanytarsus brundini/curticornis	0.11	0.11	0.04	4.23	0.32	0.07
Tanytarsus sp.	0.48	0.74	0.22	27.61	50.58	3.07
Thienemannia sp.	0.02	0.11	0.00	0.03	0.84	0.00
Thienemanniella sp.	0.34	0.21	0.19	7.20	8.53	0.70
Thienemannimyia sp.	0.21	0.11	0.04	5.02	0.63	0.15
Trissopelopia sp.	0.13	0.26	0.19	2.25	34.42	4.63
Tvetenia bavarica/calvescens	0.39	0.32	0.07	40.90	7.79	2.89
Tvetenia discoloripes-Gr.	0.49	0.42	0.22	17.28	19.26	2.00
Zavrelimyia sp.	0.43	0.47	0.59	7.07	22.89	19.15