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Short communication

Seasonal predictability of benthic macroinvertebrate metrics and community structure with maturity-weighted abundances in a Missouri Ozark stream, USA

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A B S T R A C T

Benthic macroinvertebrates in lotic habitats are influenced by a wide range of physical and chemical environmental factors that change over a temporal continuum. Within a year, different species can occupy the same space at different points in time. Thus, the community structure itself is in flux from season to season. This study analyzed the structure of a riffle macroinvertebrate community in a single stream from a series of monthly samples over a year cycle. The goals of this study were to: (1) identify community measures that were least variable over the continuum and predict them in test samples from the next year; (2) explore the usefulness of maturity data in analyzing community structure; (3) construct a temporal River Invertebrate Prediction and Classification System like (RIVPACS-like) model that classifies seasons based on biota and predicts an expected community for any season. From a set of 120 metrics, nine metrics representing 5 measurement categories displaying low variability over the annual continuum were selected for multiple regression analysis. The Biotic Index was fairly predictable between years, regardless of season, whereas other measures were less so. Metrics with standard abundances compared to their maturity-weighted analogues revealed that measures based on finer taxonomic resolution or functional groups were more likely to differ. Three biologically determined seasons were identified from cluster analysis during the process of creating a multivariate predictive model. Temporal environmental variables were used to determine test date group membership and comparisons of expected to observed communities revealed that 1 of 3 test dates was predicted well by the model. Our results demonstrate that macroinvertebrate community structures can express high variability over a short period of time and this phenomenon deserves more understanding with regard to interpreting biological assessment results.

1. Introduction

Aquatic macroinvertebrate communities in temperate lotic systems are influenced by seasonal changes. Many aquatic insect life histories and development rates are influenced by temperature (Vannote and Sweeney, 1980; Sweeney, 1984; Ward, 1992; Williams and Feltmate, 1992) and other physico-temporal factors (Wohl et al., 1995; Robinson and Minshall, 1998), while thermal conditions temporally partition resources (Cummins and Merrit, 1996). Seasonal precipitation and discharge have been shown to be significant factors influencing community structure from year to year (McElravy et al., 1989). Differences in disturbance rates can dictate the number and types of species (obligate vs. specialist) that may coexist within a habitat (Ward, 1989). Stream 'patches' change temporally (Wiens, 2002) and a snapshot of environmental conditions measured at the time of sampling may not reflect important events that could have affected the community prior to sampling (Cooper and Barmuta, 1993). It is important to recognize that macroinvertebrate communities fluctuate and samples from one point in time may appear quite different from other points in time.

Macroinvertebrate metrics are common components of biological water quality assessment studies. In general, metrics require rigorous testing in order to provide the most meaningful understanding of their relationships with environmental factors (Norris, 1995). Screening of metrics as a step in developing measures of biological condition usually includes examination of metric variability at reference sites as recommended in designing a Benthic Index of Biotic Integrity (B-IBI) (Barbour et al., 1999; Flotemersch et al., 2006). Even though many monitoring programs specify an index period for sampling, temporal effects within that period may be unaccounted. Some studies have investigated annual variation in community structure (e.g., McElravy et al., 1989; Robinson et al., 2000). However, relatively few studies have investigated seasonal

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differences in metric values (Hilsenhoff, 1977; Murphy, 1978; Jones et al., 1981; Armitage et al., 1983; Lenat, 1993; Zamora-Muñoz et al., 1995; Linke et al., 1999; Maloney and Feminella, 2006; Leunda et al., 2009). Metrics with the least variability within a single year are most favorable as measures for biological assessment because they will be more consistent with regard to seasonal differences.

Many macroinvertebrate species exhibit ontogenetic shifts in habitat preferences (Minshall, 1984; Buffagni et al., 1995; Lloyd and Sites, 2000; Reich and Downes, 2004) and feeding strategies or prey items (Norris, 1995), even between immature stages (Snellen and Stewart, 1979; Gibbs and Mingo, 1986). Many aquatic macroinvertebrates are r-select and display high mortality, therefore high abundances of individuals can be observed during early stages of a population's development. It stands to reason that an early instar compared to a conspecific later instar will feed on less material and will represent less of a nutritive food source for predators. Weighting individuals according to a set of maturity classifications can provide data with less emphasis to early instars and possibly better precision for analyzing the functional composition of the community. Classifications based on maturity have been used in life histories studies to characterize population growth (Clifford, 1969; Bretschko, 1985; Kosnicki and Burian, 2003), however, maturity data has not been used to weight community structure.

Multivariate techniques for predictive modeling in applied stream ecology have received considerable attention since the development of the River Invertebrate Prediction and Classification System (RIVPACS) (Wright et al., 1984). Contemporary RIVPACS-like models utilize presence–absence data to obtain expected assemblages from each taxon's frequency of occurrence within classified groups, and thus the probability of any taxon occurring is between 0 and 1 (but see Clarke et al., 2003). Rather than predicting the expected assemblage based on the probability of a taxon's occurrence, it is also possible to use relative abundance data in constructing an expected community. This would allow the use of abundance based similarity indices in comparing an observed community to an expected community predicted by the model (see Flotemersch et al., 2006).

A RIVPACS-like model designed for a temporal gradient will cluster taxa of sampling dates into seasons. Discriminant functions may best utilize temporal variables (i.e., degree days) as a means of predicting group membership to season. The capture probability for test sites could be calculated based on the probability of belonging to each season and the taxonomic frequencies within those seasons. Defining seasons based on biological data may be useful for comparing communities from different years.

The goal of this investigation was to explore the seasonal variability of communities at a single site. Specifically, we (1) identify metrics that exhibit minimal seasonal variation and attempt to predict their values; (2) demonstrate the potential utility of maturity structured data; (3) develop a temporal RIVPACS-like model for examining and predicting seasonal community structure.

2. Material and methods

2.1. Sampling and processing

The Burris Fork is a temperate 2nd order wadeable stream in the Inner Ozark Border subsection of the Ozark Highlands ecoregion of the United States (Omernik, 1987; Nigh and Schroeder, 2002) and has been designated by the state of Missouri as a reference stream for development of regional biocriteria (Rabeni et al., 1997; Sarver et al., 2002). Samples were taken from a 300 m reach 11 km south of California, Missouri, USA (38°33′10.24″N; 92°34′13.66″W; 236 m in elevation). Macroinvertebrates were sampled from 3 separate riffles with a 500 μm mesh D-frame kick net by physically disturbing 1 m of substrate upstream of the net (ca. 0.3 m^2) for 1 min. Each sample was transferred to a container containing 95% ethanol and taken to the laboratory for identification and enumeration. Dissolved oxygen (mg/L and percent), conductivity (μS), pH, temperature (°C) (YSI 85 and YSI 60, Yellow Springs, OH, USA), and current velocity (m/s) (AR 2000) were measured at each sample point. Two StowAway TidbiT temperature data loggers (Onset Computer Corporation, Bourne, MA, USA) bolted to metal stakes were positioned just above the substrate surface and programmed to record every 40 min starting at 12:01 am on the winter solstice (21 December 2002). Daily precipitation data were obtained from the United States Department of Commerce, National Oceanic and Atmospheric Administration, weather station in California, Missouri.

Samples were taken ca. monthly for 12 dates from 20 December 2002 to 28 November 2003. This time frame was designated as the Model Development Period (MDP). Three test dates (t1, t2, and t3) were sampled on 21 December 2003, 23 March 2004, and 3 October 2004 to represent different time points for the purpose of validating models constructed from data collected during the MDP.

Means of environmental variables were calculated for each date. Cumulative degree days > 0 °C were calculated from temperature logger data. Due to logger malfunction and loss, in-stream temperature data were available only until 25 March 2004. Degree days from this point on were estimated using linear regression with data from loggers at this site and loggers deployed in a nearby stream ($n = 461$, $R^2 = 0.99$). Fixed period cumulative precipitation and degree days were calculated for periods of 4, 7, and 14 days previous to the sampling dates. Back calculations for fixed count degree days for 20 December 2002 were estimated from a second order polynomial regression of daily mean water temperatures and daily mean air temperatures obtained from the weather station ($n = 461$, $R^2 = 0.92$).

Whole samples of macroinvertebrates were sorted and identified to the genus or species level, except for oligochaetes which were left at class. Chironomids were counted at the family level, then at least 11% of the individuals were subsampled. Subsampled chironomids were cleared in 10% KOH overnight, transferred to 100% ethanol, and slide-mounted with Euparal. Relative abundances from these identifications were calculated for each sample. Macroinvertebrates from each kick sample were numerically pooled, representing ca. 1 m^2 of riffle community for each date.

When clear taxonomic associations between sample dates could be made, coarse level identifications were elevated to finer levels, but when associations were not apparent, taxa were collapsed into coarser level identifications (usually from species to genus). In this way, operational taxonomic units (OTUs) were established, allowing for control of ambiguous taxa among sample dates (Cuffney et al., 2007). OTUs and their abundances were joined to a database with functional feeding group (FFG), tolerance values, and other taxonomic information obtained from the Missouri Department of Natural Resources (Sarver, 2001) and other sources (Merritt and Cummins, 1996; Barbour et al., 1999; Bode et al., 2002).

During the identification process, each non-oligochaete individual was assigned to a maturity class (I: early; II: middle; III: late; IV: pupae/adult, for Trichoptera, Coleoptera and Diptera). Classifications were based on qualitative observation of size and morphological development of each specimen following the guidelines in Table 1. The classes were used to weight abundances in thirds; the total number of individuals in class I was multiplied by 0.33, class II by 0.67, and classes III and IV were counted 1 for 1. Thus, a second dataset was created with maturity-weighted (MW) abundances. Transient non-benthic OTU's (e.g., Veliidae, Cladocera), singletons, and taxa with an average relative abundance < 0.1% were eliminated before analysis.

Table 1
Morphological attributes per taxonomic group used for determining individual maturity classifications.

Taxonomic group	Attributes
Turbelaria	Presence or absence of gonadopores and relative size.
Bivalvia	Relative size; presence of immatures in the mantle.
Gastropoda	Relative size and shell morphology.
Crustacea	Relative size and morphological development.
Ephemeroptera	Development of wingpads.
Odonata	Development of wingpads.
Plecoptera	Development of wingpads and relative size.
Hemiptera	Development of wingpads and relative size.
Megaloptera	Relative size.
Trichoptera	Relative size, morphological development, and its case.
Coleoptera	Relative size of immatures.
Diptera	Relative size and morphological development.
Other groups[a]	Relative size.

[a] Hydrozoa, Hirudinea.

2.2. Metric assessment

We calculated 120 metrics (MW and non-weighted abundances) for each sample date, representing commonly used community measures (Resh and Jackson, 1993; Barbour et al., 1999) and others independently developed for this study (Appendix A). We reduced this set to a smaller suite representing the categories of FFG, tolerance, diversity, richness, and composition by first selecting metrics with a coefficient of variation (CV) < 20 over the MDP. When more than one derivative of a metric met the criteria (e.g., DOM2, DOM3, DOM4), only one was chosen. Standard metrics were selected for model construction when both the standard and MW analogues met the variability criteria. Stepwise multiple regression (SWMR) was used to find models that explained metric values for each sampling date with physico-chemico-temporal factors (Table 2), their squares, and the single interactions of all predictors. In most cases the simplest significant model was selected, but when an additional factor increased the R^2 by ca. 0.10 or greater, the more complex model for that metric was considered. Observed and expected values for each metric were plotted for sampling dates taken during the MDP and for each test sample. The mean squared prediction error (MSPE) of the test samples was compared to the mean square error (MSE) of each regression model as a means of validating predictive ability (Neter et al., 1996).

2.3. Maturity-weighted vs. standard abundance

For comparisons between standard and MW abundances, metrics utilizing standard abundances were recalculated to only include non-oligochaete taxa. Means and standard deviations for tolerance, diversity, percentage FFG, and relative abundance metrics were calculated with standard and MW data over the MDP. The difference of the standard metric subtracted from its maturity analogue was taken for each sampling date to determine if maturity weighting tended to increase or decrease the metric value. Maturity weightings were also examined to determine if the metric value changed by more than 5%, 10%, and 20% as compared to the standard for each date.

2.4. Multivariate assessment

The construction of our RIVPACS-like model followed 3 steps (Fig. 1) (Moss et al., 1987; Wright, 1995; Hawkins et al., 2000; Simpson and Norris, 2000; Flotemersch et al., 2006). (1) Stepwise discriminant analysis (SDA) was used to reduce OTUs into a suitable set of taxa for sample date classification (biologically determined seasons); MW and standard datasets were considered, separately. Cluster analysis (Ward method) was used to classify dates of the MDP into discrete seasons (d). The taxonomic frequency of occurrence (f) and relative abundance (a) of pre-SDA OTUs (x) was found for each seasonal grouping d. Correspondence analysis was used to show the relationship of MDP sample dates and taxa used to cluster dates into seasons.

(2) SDA was also used to reduce the set of physico-chemico-temporal variables into a discrete set of predictors suitable for discriminant function analysis (DFA). DFA of the seasonal groupings d was used to create discriminant functions for estimating the probability of sampling date group membership (p_d) for MDP and test sampling dates.

(3) Sampling date probability of group membership for each OTU (p_d, x) was multiplied by the expected OTU f and a for corresponding seasonal groups, separately. The products of each group d were added to find the probability of occurrence frequency capture (P_{fc}) and relative abundance capture (P_{ac}) of each OTU, respectively. The summation of P_{fc} for all OTUs was taken for each date where $P_{fc} > 0$ and $P_{fc} \geq 0.5$, separately, to determine two sets of observed to expected (O/E_0 and O/E_{50}) scores. The P_{ac} of each OTU x was the predicted relative abundance of that OTU expected to occur at each sample date. The percentage similarity index (Whittaker and Fairbanks, 1958) and non-weighted Pinkham and Pearson's index (Pinkham and Pearson, 1976) were used to compare the similarity of the observed community to the expected, for all sampling dates. All statistical procedures were conducted in SAS (Version 8, Cary, NC).

3. Results

3.1. Metric assessment

Fourteen metrics representing richness, diversity, and tolerance measurement categories had a CV < 20 over the MDP (Appendix A). Because FFG and composition metrics did not generate CVs

Table 2
Physico-chemico-temporal factors considered for metric multiple regressions and discriminant function analysis of RIVPACS models.

Symbol	Name	Definition
g	Dissolved oxygen	Dissolved oxygen (mg/L) taken at the time of sampling.
θ	Pctg dissolved oxygen	Percentage of dissolved oxygen taken at the time of sampling.
h	pH	pH taken at the time of sampling.
c	Specific conductance	Specific conductance (μS) taken at the time of sampling.
f	Flow	Current velocity (m/s) taken at the time of sampling.
p_4	Precipitation 4	Cumulative precipitation (in.) 4 days before the sample was taken.
p_7	Precipitation 7	Cumulative precipitation (in.) 7 days before the sample was taken.
p_{14}	Precipitation 14	Cumulative precipitation (in.) 14 days before the sample was taken.
t	Temperature	Water temperature (°C) taken at the time of the sampling.
d	Degree days	Cumulative degree days (daily mean > 0 °C) from Julian day 1.
d_7	Degree days 7	Cumulative degree days (daily mean > 0 °C) 7 days before sampling.
d_{14}	Degree days 14	Cumulative degree days (daily mean > 0 °C) 14 days before sampling.
j	Julian days	Number of days starting 20 December.

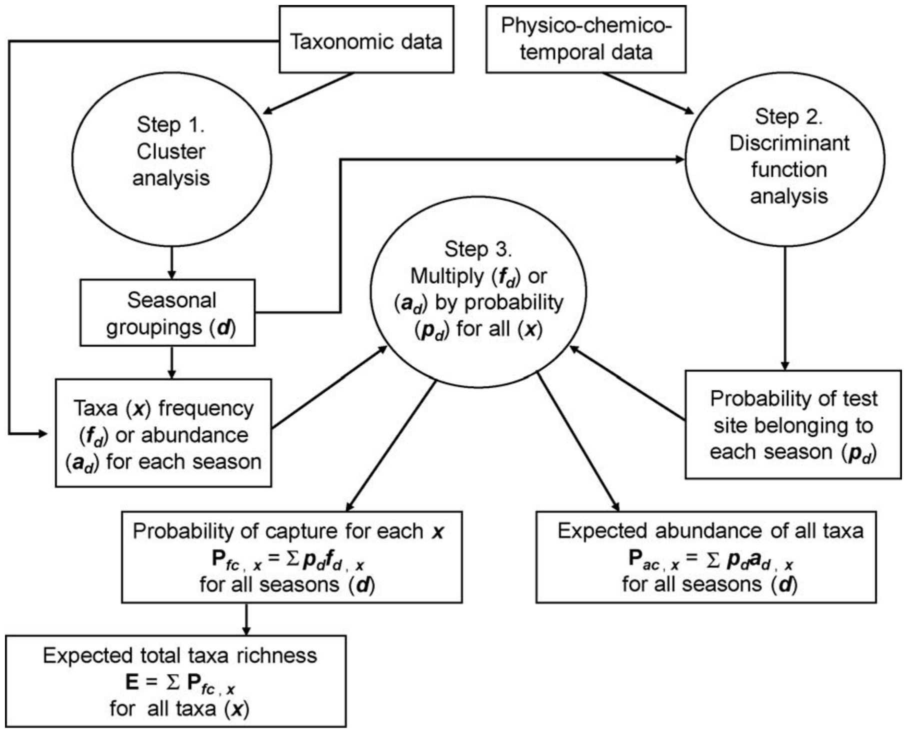

Fig. 1. Flow chart showing the steps to construct a temporal RIVPACS model showing different pathways for constructing expected communities based on occurrence frequency and relative abundances. Taken after Flotemersch et al. (2006).

less than 20, GATHMAT (CV = 31.5) and NOINMAT (CV = 27.1) were added to this dataset so that representatives of these categories could be included for model development. Maturity abundance weighted metrics were chosen because they had CVs closer to the criteria compared to those of their standard analogues GATHER (CV = 36.7) and NOINSECT (CV = 33.0). Nine of these metrics were selected for SWMR with physico-chemico-temporal variables.

The MOBI and richness metrics were more predictable and consistent over the annual continuum, whereas diversity, composition, functional, and other tolerance measures were not (Fig. 2). The RICH and EPTRICH metrics were most variable between 14 April and 27 September. CHIRICH values tended to be consistent, in part because many chironomid taxa were considered rare or transient and were eliminated from the dataset. Both diversity measures had similar observed values over the study period, but were not accurate at predicting test dates. The pattern of DOM3, from sampling date to sampling date, was opposite of the diversity indices and its predictive ability was not accurate. The GATHMAT and the NOINMAT represented some of the most variable metric types.

The MSPE of the MOBI test samples was not substantially different from the MSE of the model, indicating that the predictive ability of the model was unbiased (Table 3). The MSPE for EPTRICH was about twice that of the MSE. The MSPEs compared to the MSEs for the rest of the metrics were 3–10 times higher, indicating that the predictive ability of the models were not reliable.

3.2. Maturity-weighted vs. standard abundance

MW metrics tended to be more variable than standard metrics over the MDP (Table 4). Ten pairwise comparisons showed that 75% or more sampling dates had at least a ±5% change in value. Four pairwise comparisons increased in value for 75% or more sampling dates when maturity structured data were applied, whereas 7 other pairwise comparisons decreased in value for 75% or more sampling dates.

3.3. Multivariate assessment

A cluster dendrogram was produced (Fig. 3) with a set of MW abundances for the OTUs in Fig. 4 and was obtained after the removal of the 30 June sampling date (see Section 4). The cluster analysis classified dates into three seasonal groups, roughly described as winter, summer, and autumn. Correspondence analysis showed that winter dates were best characterized by the presence of *Isoperla* sp. (Plecoptera: Perlodidae), *Cricotopus*/*Orthocladius* sp. (Diptera: Chironomidae), and

Table 3
Multiple regression models of environmental parameters used for predicting test date metric values for Burris Fork in the Missouri Ozarks, USA. MSE = mean square error; MSPE = mean square predicted error. Environmental parameters are listed in Table 2.

Metric and equation	*F*-Value	*p*-Value	Error df	R^2	MSE	MSPE
RICH = $32.05 - 27.34p_{14} - 0.037cf + 3.76hp_{14}$	9.69	0.005	8	0.78	2.700	10.230
EPTRICH = $9.39 + 0.0033jp_{14}$	8.58	0.015	10	0.46	1.310	2.499
CHIRICH = $5.02 + 0.14gp_{14} - 0.16gf$	8.26	0.009	9	0.65	0.323	1.614
SDI = $4.87 + 0.94f^2 - 0.041h^2$	7.63	0.012	9	0.63	0.034	0.319
PLJ = $1.49 - 0.012h^2$	12.09	0.006	10	0.55	0.003	0.011
MOBI = $6.39 - 0.031g^2 + 0.94gf - 6.81f^2$	66.03	< 0.001	8	0.96	0.016	0.023
DOM3= $-32.20 + 1.37h^2$	6.40	0.030	10	0.39	77.278	267.492
GATSUMAT = $25.54 + 0.53fd_7 - 0.65tp_4$	12.50	0.003	9	0.74	46.231	352.079
NOINSMAT = $23.35 + 0.014\theta t$	18.94	0.001	10	0.65	39.012	217.544

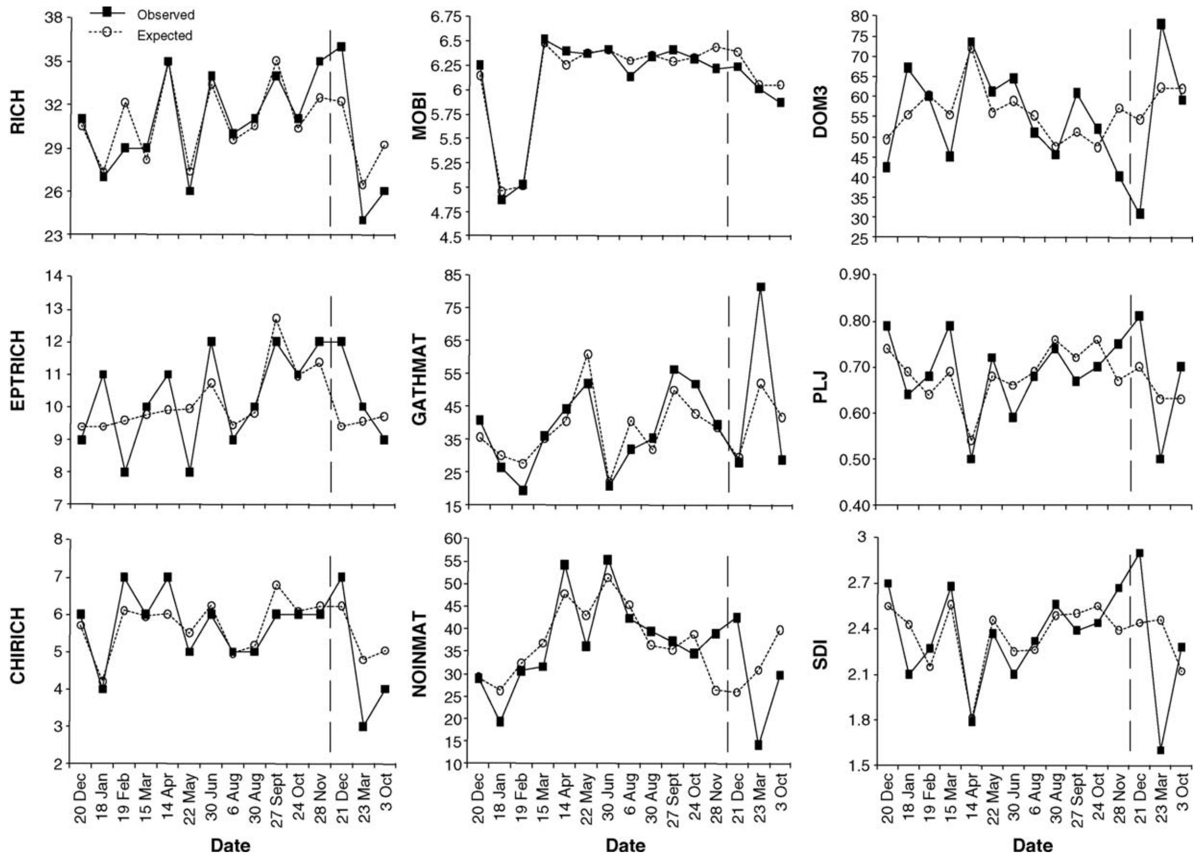

Fig. 2. Observed and expected multiple regression trends for selected metrics. Vertical lines indicate the end of the Model Development Period (20 December 2002–28 November 2003) and the beginning of the test dates.

Stenonema femoratum (Ephemeroptera: Heptageniidae) (Fig. 4). Summer was best explained by *Baetis* sp. (Ephemeroptera: Baetidae), *Rheotanytarsus* sp. (Diptera: Chironomidae) and *Berosus* sp. (Coleoptera: Hydrophilidae). Autumn was best characterized by *Bezzia*/*Palpomyia* sp. (Diptera: Ceratopogonidae) and Planariidae (Tricladida).

The SDA of the physico-chemico-temporal variables identified degree days, degree days 14, and precipitation 7 (Table 2) as environmental variables suitable for DFA. DFA correctly classified the samples of the MDP into their designated seasonal groups (Table 5) (Wilks $\lambda < 0.001$). Functions 1 and 2 accounted for 75.8% and 24.8% of the variation, respectively. The probability of group membership to seasons was calculated for dates of the MDP and each test date, respectively (Table 5). Both t1 and t2 plotted within the range of the MDP winter group, whereas t3 showed departure from autumn towards the summer MDP group (Fig. 5).

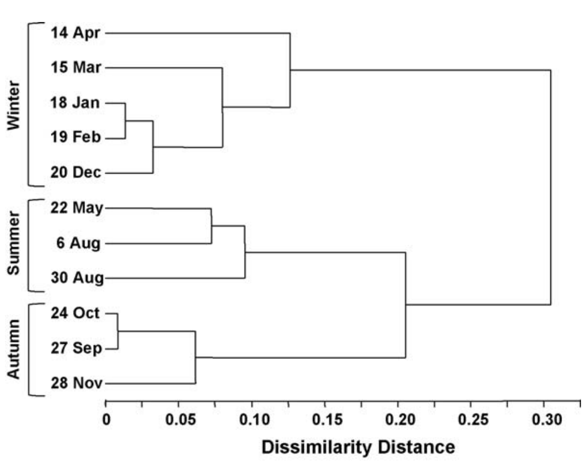

Fig. 3. Cluster dendrogram showing sampling date classifications and biologically derived seasons from select operational taxonomic units, based on semi-partial R^2 dissimilarity distance.

4. Discussion

4.1. Metric assessment

Short-term temporal sampling showed great variability in community structure over the continuum as displayed by metric values. In general, multiple regression models did not accurately predict metric values for test dates; they appeared over fit in part because of the small sample size ($n = 12$).

The predictor coefficients for richness measures were less influential than the *Y*-intercept (Table 3), indicating that the variables had little influence. Species within a family (Hauer and Resh, 2006) or unrelated species with similar functional traits (Cummins et al., 1989; Townsend, 1989; Wiens, 2002) may replace one another over the temporal continuum, leading to consistent richness measures. Thus, as environmental conditions change over the temporal continuum, taxa replace one another, yielding a fairly consistent number of species.

The similar patterns of the diversity metrics were not surprising because the Shannon Diversity Index is the numerator of Pielou's J (Washington, 1984). Regardless, the models did not predict well for the test dates. The reciprocal behavior of DOM3 to the diversity

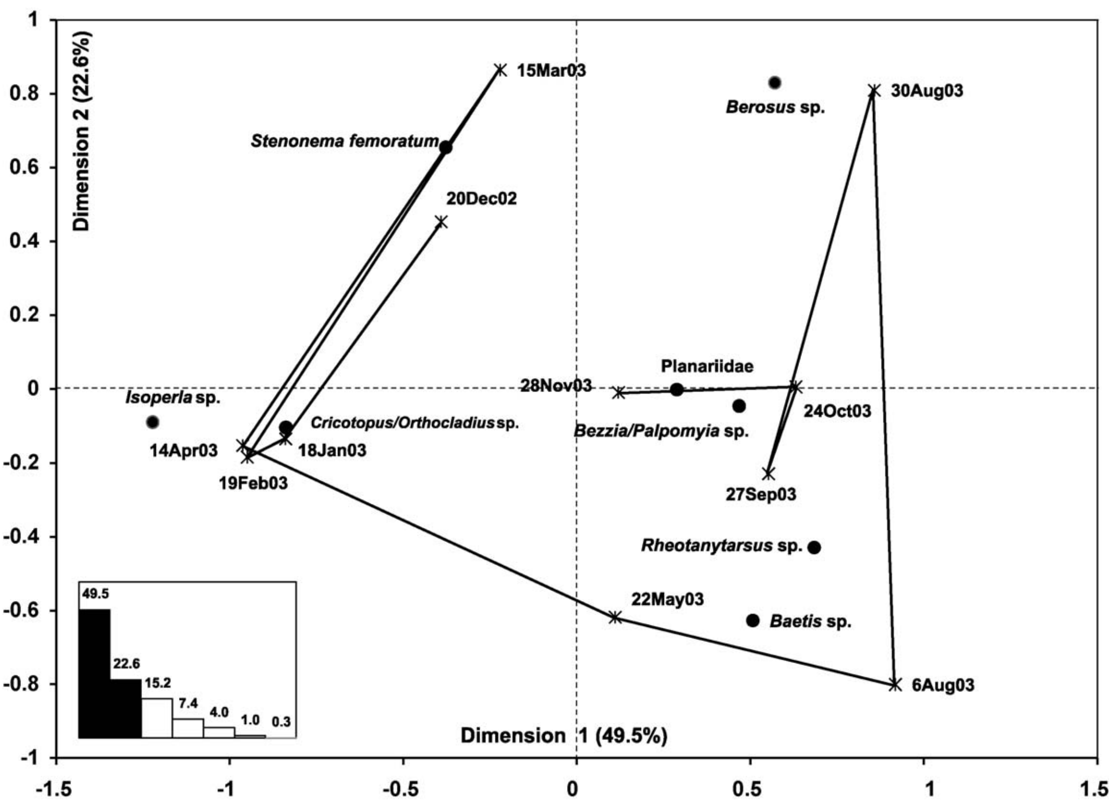

Fig. 4. Correspondence analysis ordination diagram of the sample dates of the Model Development Period (20 December 2002–28 November 2003) and macroinvertebrate operational taxonomic units used in cluster analysis for the Burris Fork in the Missouri Ozarks, USA. The insert histogram gives the percentage of variance explained by the eigenvalues of the successive dimensions. The line shows the succession of sample dates.

metrics should be expected because increases in dominant taxa will decrease the diversity and evenness of the community.

Resources are destined to change over the temporal continuum and feeding strategies of the biota are expected to shift in response to those changes (Vannote et al., 1980). This appeared to be true particularly for the GATHMAT (Fig. 2) as there were distinct troughs during periods when the shredders *Allocapnia* sp. (Plecoptera: Capniidae) and *Polypedilum* sp. (Diptera: Chironomidae) were abundant in winter and summer months, respectively.

The observed values for t2 were outside of the MDP range for 7 of the 9 metric models. Closer inspection revealed that the current velocity was outside the range of observed values of the MDP (Table 6) and, therefore, our metric estimates for this date may be unjustifiable (Zar, 1999). Although current velocity was not a predictor for all models, it implied that the environmental conditions at t2 were outside the MDP range of variability and the models may not be valid for predicting metric values of this date.

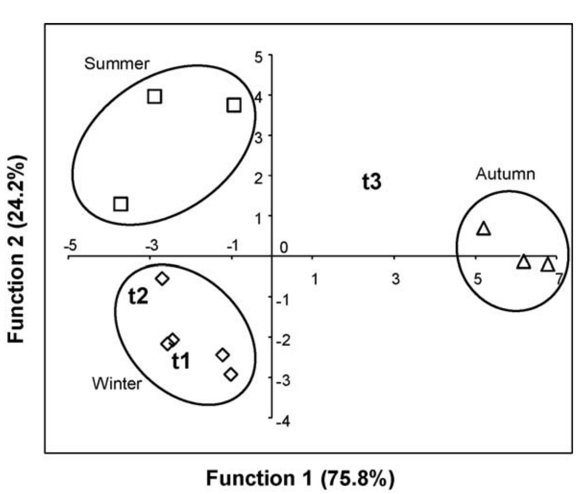

Fig. 5. Discriminant function analysis scatter plot of Model Development Period sampling dates (20 December 2002–28 November 2003) and test dates (t1, t2, and t3) for the Burris Fork in the Missouri Ozarks, USA.

These results demonstrate some of the difficulty in explaining environmental variability in field studies and emphasize the challenges incurred by a dynamic environment. Samples collected during the early part of a sampling index period may not be comparable to samples taken near the later portion of that period and samples may not be comparable year to year unless long-term variability has been taken into account (see Mazor et al., 2009). For instance, the Missouri biological assessment protocols recommend that macroinvertebrate samples be taken from mid-March to mid-April for evaluating stream condition (Sarver et al., 2002). However, members of 'winter' stonefly groups have fast univoltine life cycles (see Stewart and Stark, 1993), and emerge in mid-March (Poulton and Stewart, 1991), which is probably attributable to temperature increases (see Sweeney, 1984). Large numbers of Capniidae and Leuctridae (Plecoptera) could be captured at the beginning of the sampling period but not at the later end of the sampling period, or not at all from samples taken during warm years. In this study, 144 nymphs of *Allocapnia* sp. were collected on 15 March 2003, but none on 15 April 2003 and only 2 individuals were collected on 23 March 2004. As mentioned above, this taxon had a substantial influence on the MOBI, but also contributed to the EPTRICH, two of the four primary metrics used by Missouri for evaluating aquatic life impairments. Potentially, a sampling protocol could utilize ambient temperature data from local weather stations to predict a more optimal sampling period based on accumulated degree days. For example, the cumulative air temperature degree

Table 4
Metrics calculated from standard data and their maturity-weighted analogues in the Burris Fork in the Missouri Ozarks, USA. Standard metrics were calculated after the removal of OTUs that were not maturity weighted. Means and standard deviations (SD) were based on sampling dates for which the target groups of the metric were present (n). The number of n sampling dates that were positive as a result of the standard metric subtracted from its maturity-weighted analogue and the number of sampling dates where the maturity analogue represented a ±5%, 10%, and 20% change is given. Pctg = percentage.

Metric	n	Mean ± SD		+[a]	5%[b]	10%[b]	20%[b]
		Standard	Maturity				
Pctg EPT	12	44.7 ± 17.3	44.4 ± 18.1	3	4	0	0
Pctg Ephemeroptera	12	21.3 ± 10.6	20.3 ± 9.8	3	7	3	0
Pctg Plecoptera	10	10.9 ± 14.8	12.3 ± 17.1	7	10	8	3
Pctg Trichoptera	12	14.3 ± 8.1	13.8 ± 8.2	4	6	4	2
Pctg Hydropsychidae	12	8.8 ± 5.3	8.4 ± 5.1	4	8	4	3
Pctg Philopotamidae	12	4.8 ± 3.5	4.6 ± 3.5	3	9	4	2
Pctg Chironomidae	12	30.0 ± 11.9	29.0 ± 12.7	4	8	3	0
Pctg Tanypodinae	12	4.2 ± 3.5	4.3 ± 4.2	5	10	7	5
Pctg Orthocladiinae	11	7.1 ± 7.0	7.3 ± 7.5	5	9	8	4
Pctg Chironomini	11	15.0 ± 9.5	14.3 ± 10.6	3	9	6	4
Pctg Tanytarsini	12	5.6 ± 4.3	4.9 ± 4.2	4	10	8	6
Tanypodinae/Chironomidae	12	15.2 ± 10.1	15.3 ± 10.1	5	10	10	8
Orthocladiinae/Chironomidae	11	27.3 ± 23.1	30.4 ± 27.7	7	7	5	3
Chironomini/Chironomidae	11	45.6 ± 22.4	44.3 ± 26.9	5	6	6	3
Tanytarsini/Chironomidae	12	18.0 ± 8.9	16.2 ± 9.3	3	11	6	3
Pctg Elmidae	12	14.3 ± 12.5	15.9 ± 13.2	10	10	8	6
Pctg Diptera and noninsects	12	38.8 ± 9.3	37.3 ± 10.1	4	6	3	0
Biotic Index	12	6.11 ± 0.55	6.05 ± 0.61	1	1	0	0
Pctg dominant taxon	12	26.5 ± 7.1	27.6 ± 9.5	6	6	2	0
Pctg dominant 2 taxa	12	42.6 ± 8.6	44.1 ± 11.2	8	5	2	0
Pctg dominant 3 taxa	12	54.3 ± 9.5	55.8 ± 11.3	10	2	1	0
Pctg dominant 4 taxa	12	63.4 ± 9.0	64.5 ± 10.8	9	2	1	0
Pctg dominant 5 taxa	12	70.6 ± 8.1	71.2 ± 9.2	9	2	0	0
Simpson's Diversity Index	12	0.14 ± 0.04	0.15 ± 0.05	8	5	2	1
Shannon Diversity Index	12	2.39 ± 0.22	2.35 ± 0.26	4	2	1	0
Pielou's J	12	0.70 ± 0.06	0.69 ± 0.07	4	2	1	0
Pctg shredder	12	27.6 ± 12.1	28.6 ± 14.7	6	7	5	0
Pctg predator	12	8.1 ± 4.5	8.4 ± 5.2	6	10	8	2
Pctg scraper	12	3.3 ± 3.4	3.2 ± 3.6	3	9	6	1
Pctg filterers	12	22.7 ± 12.0	21.2 ± 12.1	4	8	4	2
Pctg gatherers	12	37.7 ± 10.8	37.9 ± 12.0	6	6	2	0

[a] '+' indicates number of n for which the standard metric value subtracted from the maturity analogue was positive.
[b] 5%, 10%, and 20% indicate the number of n that changed >5%, 10%, and 20%, respectively, in metric value as a result of maturity weighting.

days (based on daily lows) for 15 March 2003, 15 April 2003, and 23 March 2004 were 22.2, 108.2, and 93.3 °C, respectively. A sampling period <90.0 °C cumulative air temperature degree days might be better for assuring these organisms are obtainable (long-term data would be needed to establish a cap).

4.2. Maturity-weighted vs. standard abundance

Differences between metric values calculated with standard abundances vs. MW analogues tended to average out over the annual continuum (Table 4). Metrics that incorporate the larger portions of the community were less likely to change >5% with maturity weightings, but tended to be consistent in the direction they changed. Metrics that were based on a more specific subset of the community tended to weigh differently when maturity data were used. For example, the percentage Plecoptera increased for 7 of 10 sampling dates and changed >5% in value for all sample dates. The percentage Elmidae (Coleoptera) changed >20% for 8 of 12 pairwise comparisons. Metric values of percentage EPT (Ephemeroptera, Plecoptera, Trichoptera) showed fewer changes compared to its composite orders considered as metrics on their own. Moreover, percentage Hydropsychidae and percent-

Table 5
Group membership probabilities, similarity, and O/E model results for communities sampled from the Burris Fork in the Missouri Ozarks, USA. Discriminant function analysis was used to find the probability of group membership to seasons (winter, summer, autumn) determined from temporal variables from all dates covering the Model Development Period (MDP) (20 December 2002–28 November 2003). Probabilities of season membership for test dates (t1, t2, and t3) were determined from the MDP discriminant functions.

Date	Predicted season	Probability winter	Probability summer	Probability autumn	Pinkham and Pearson's	Percentage similarity	O/E_0	O/E_{50}
20-Dec-02	Winter	1.00	0	0	0.49	70.50	1.03	1.06
18-Jan-03	Winter	1.00	0	0	0.36	68.56	0.89	0.88
19-Feb-03	Winter	1.00	0	0	0.43	70.63	0.96	1.02
15-Mar-03	Winter	1.00	0	0	0.41	71.98	0.96	0.95
14-Apr-03	Winter	0.99	0.01	0	0.41	56.80	1.16	1.09
22-May-03	Summer	0.01	0.99	0	0.34	70.74	0.90	0.87
6-Aug-03	Summer	0	1.00	0	0.45	83.24	1.05	1.06
30-Aug-03	Summer	0	1.00	0	0.50	80.62	1.05	1.06
27-Sep-03	Autumn	0	0	1.00	0.54	74.19	1.01	1.01
24-Oct-03	Autumn	0	0	1.00	0.56	86.86	0.92	0.95
28-Nov-03	Autumn	0	0	1.00	0.56	79.02	1.07	1.04
21-Dec-03 (t1)	Winter	1.00	0	0	0.49	75.57	1.13	1.09
23-Mar-03 (t2)	Winter	1.00	0	0	0.18	30.27	0.71	0.66
3-Oct –03 (t3)	Autumn	0	0.01	0.99	0.17	30.49	0.66	0.59

Table 6
Physico-chemico-temporal variable measurements from Burris Fork in the Missouri Ozarks, USA used for metric multiple regressions and discriminant function analysis of RIVPACS models. Dates covering the Model Development Period (20 December 2002–28 November 2003) and test dates (t1, t2, and t3) are given.

Date	Dissolved oxygen (mg/L)	Percentage dissolved oxygen	pH	Flow (m/s)	Specific conductance	Precip 4	Precip 7	Precip 14	Temp (°C)	Degree days (°C)	Degree days7 (°C)	Degree days14 (°C)	Julian days
20-Dec-02	8.8	70.3	7.7	0.39	225.5	0.98	0.98	0.98	5.8	5.0	66.7	105.8	1
18-Jan-03	13.9	101.1	8.0	0.46	293.1	0.11	0.11	0.11	2.0	101.0	19.4	44.5	29
19-Feb-03	10.6	87.6	8.2	0.26	370.1	0.29	1.00	1.00	7.2	195.3	25.6	50.1	61
15-Mar-03	9.7	87.6	8.0	0.60	345.3	1.19	1.19	1.34	10.8	324.6	56.4	91.5	85
14-Apr-03	6.7	76.9	8.7	0.30	425.2	0.00	0.92	1.37	22.3	744.5	93.9	191.6	116
22-May-03	6.2	68.9	8.0	0.52	417.4	0.21	0.47	1.11	19.9	1407.7	137.8	275.3	153
30-Jun-03	5.0	66.3	8.2	0.37	429.6	2.10	2.10	2.12	29.7	2322.9	189.8	373.8	192
6-Aug-03	4.0	52.8	8.0	0.15	473.9	0.06	0.06	0.06	29.2	3372.2	199.0	398.6	228
30-Aug-03	2.9	35.9	7.6	0.14	449.5	0.46	0.46	0.51	25.4	4076.5	194.1	402.2	253
27-Sep-03	3.9	42.5	7.8	0.40	304.3	0.41	2.75	3.61	19.7	4692.2	139.8	288.4	281
24-Oct-03	6.1	63.0	7.6	0.30	353.8	0.00	0.91	1.54	17.1	5127.9	108.5	221.7	308
28-Nov-03	6.9	53.4	8.1	0.49	278.9	0.00	0.32	1.75	3.8	5500.1	49.7	123.8	343
21-Dec-03 (t1)	7.7	56.5	8.0	0.43	245.4	0.11	0.40	1.56	3.1	2.5	18.0	42.6	1
23-Mar-04 (t2)	6.5	56.6	8.3	0.69	301.5	0.02	0.26	0.51	9.1	406.2	71.7	129.4	94
3-Oct-04 (t3)	7.9	78.1	8.3	0.30	381.0	0.34	0.34	0.34	14.7	4664.3	121.6	273.5	288

age Philopotamidae (Trichoptera) had a higher incidence of percent change compared to their parent metric percentage Trichoptera. Composition metrics based on the family Chironomidae were also more likely to change in value when finer taxonomic groups of the family (tribes and subfamilies) were considered. Dominance measures with 1 or 2 taxa were more subject to change then those with 3, 4, or 5 taxa. More specialized FFGs were more influenced by maturity weighting than were generalist groups; values for percentage predators and percentage scrapers changed by >10% more frequently than the collector metrics.

One of the more notable metrics to show a significant difference between the standard and maturity analogue was the modified Missouri Biotic Index. Although only one of the sampling dates showed a change >5%, all but one date were lower for the MW metric. Similar results were exhibited by the standard and MW analogues of Shannon's Diversity Index and Pielou's J.

It might be better to use a different weighting scheme, such as biomass. Consider the comparison of two shredders, *Polypedilum* sp. and *Pteronarcys* sp. (Plecoptera: Pteronarcyidae). Such a comparison may not be an equivalent 1 to 1 between taxa, considering that an individual *Pteronarcys* sp. could be 1200 times the biomass of an individual *Polypedilum* sp. (Benke et al., 1999), and it is longer lived. Thus, it might be better to weight *Pteronarcys* sp. higher than *Polypedilum* sp. Grubaugh et al. (1996) demonstrated that biomass weighted functional groups were better at explaining the River Continuum Concept (Vannote et al., 1980) compared to raw abundances. Other studies have shown that biomass estimates are as good as or better than abundance measures for explaining habitat differences or conditions (e.g., Smith and Kaster, 1983; Hutchens et al., 1998; Flinn et al., 2008). However, many studies do not employ biomass estimates (Huryn and Wallace, 2000), probably because of the extra processing time (see Wallace et al., 1996). Maturity weightings assigned by experienced macroinvertebrate biologists could offer a less intensive yet practical alternative.

4.3. Multivariate assessment

Biologically delineating seasons offered insights into the fluctuation of community structure but presented us with challenges. Whole counting samples tended to be cumbersome due to the high numbers of individuals (Fig. 6). Because total abundance was especially high during June–August additional summer samples were not pursued. Fixed subsample counts may have provided reasonable estimates of density, but because repeated samples were taken from the same system, we were interested in more precise measures of taxa abundances and individual maturity levels. If more sampling dates in June and July were included in the analysis, we expect the summer season may have resolved better and a fourth season representing spring would have been realized from the sampling dates classified as winter. The 30 June sampling date tended to cluster by itself, creating noise, and was eliminated to enable distinct biological classifications.

Variables used for the DFA portion of RIVPACS models are normally based on physical parameters that are not highly alterable by human activities. Clarke et al. (2003) pointed out that the predictors should 'fit the purpose' of the model. The SDA found three temporal variables (degree days, degree days 14, and precipitation 7) appropriate for the purpose of this study. Cumulative degree days and precipitation are ideal for studying short-term temporal community structure as they represent recent environmental changes that have had a direct influence on the community, yet are not directly influenced by human activities.

The percentage similarity index is sensitive to structural-functional similarity whereas the Pinkham and Pearson's index tends to be more sensitive to changes in less common taxa (Brock, 1977; Washington, 1984). The percentage similarity index showed moderate changes among the sampling dates of the MDP with date 14 April showing a marked deviation from expected community composition (Table 5). The Pinkham and Pearson's index indicated that considerable changes in the less common taxa occurred throughout the sampling dates of the MDP with the most notable differences at 18 January and 22 May. Both similarity indices and

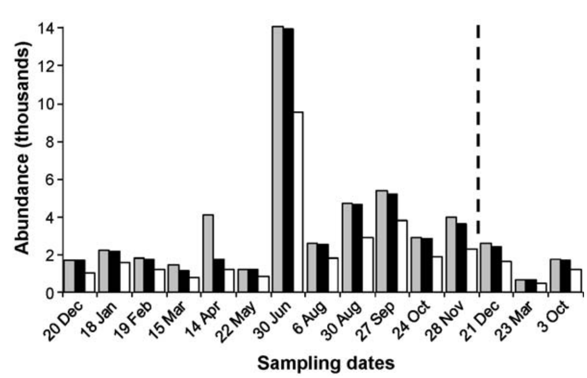

Fig. 6. Abundance in thousands per sampling date at the Burris Fork in the Missouri Ozarks, USA. Grey bars indicate total abundance, solid black bars indicate total abundance minus taxa without maturity weightings (e.g., Oligochaeta), and white bars indicate maturity-weighted abundance. The dotted line separates dates of the Model Development Period (left) from the test dates (right).

O/E models found t1 to be similar to the expected community of the winter classification. Test dates t2 and t3 showed considerable departure from expected community relative abundances and frequencies of occurrence. Reasons given for t2 departure from expected metric values are implicated as the same reasons for the difficulty of the metric models to predict an expected community. It is unclear why the models were not able to predict an expected community similar to that observed for t3 other than the fact that more temporal information is probably needed.

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Appendix A.

List of metrics and their coefficients of variation for Burris Fork, Missouri, USA, over the Model Development Period (20 December 2002–28 November 2003, $n = 12$). Abbreviations and measure type are also given. EPT = Ephemeroptera + Plecoptera + Trichoptera, abn = abundance, MW = maturity weighted, FFG = functional feeding group.

Metric name	Abbreviation	Type of measure	Coefficient of variation
Total taxonomic richness	RICH[a]	Richness	9.7
EPT richness	EPTRICH[a]	Richness	14.5
Ephemeroptera richness	ERICH	Richness	25.4
Plecoptera richness	PRICH	Richness	70.3
Trichoptera richness	TRICH	Richness	20.4
Chironomidae richness	CHIRICH[a]	Richness	15.1
Total abn	TOTAL	Composition	90.8
EPT abn	EPT	Composition	88.3
Ephemeroptera abn	ESUM	Composition	65.6
Plecoptera abn	PSUM	Composition	160.9
Trichoptera abn	TRSUM	Composition	155.8
Hydropsychidae abn	HYDROSUM	Composition	169.0
Philopotamidae abn	PHILSUM	Composition	139.7
Elmidae abn	ELMSUM	Composition	110.1
Chironomidae abn	CHI	Composition	144.3
Tanypodinae abn	TANYPOD	Composition	79.4
Orthocladiinae abn	ORTHO	Composition	89.8
Chironmini abn	CHA	Composition	176.6
Tanytarsini abn	TANY	Composition	185.9
Diptera + noninsect abn	NOINSUM	Composition	109.6
Oligochaeta abn	OLIGO	Composition	222.1
EPT abn/Chironomidae abn	EPTCHI	Composition	79.5
Tanypodinae abn/Chironomidae abn	TPODCHI	Composition	66.5
Othocladiinae abn/Chironomidae abn	ORTHOCHI	Composition	93.3
Chironomini abn/Chironomidae abn	MINICHI	Composition	60.1
Tanytarsini abn/Chironomidae abn	TANYCHI	Composition	49.2
Shredder abn	SHREDSUM	FFG	122.9
Predator abn	PREDSUM	FFG	70.7
Scraper abn	SCRAPSUM	FFG	73.0
Filterer abn	FILTSUM	FFG	152.6
Gatherer abn	GATHSUM	FFG	70.0
Pctg EPT	PEREPT	Composition	45.1
Pctg Ephemeroptera	E	Composition	53.9
Pctg Plecoptera	P	Composition	161.6
Pctg Trichoptera	TR	Composition	60.6
Pctg Hydropsychidae	PERHYDRO	Composition	63.7
Pctg Philopotamidae	PHIL	Composition	75.2
Pctg Elmidae	ELMIDAE	Composition	93.8
Pctg Chironomidae	PERCHI	Composition	40.8
Pctg Tanypodinae	TPODTOT	Composition	64.8
Pctg Orthocladiinae	ORTHOTOT	Composition	89.3
Pctg Chironomini	MINITOT	Composition	80.0
Pctg Tanytarsini	TANYTOT	Composition	82.2
Pctg Diptera + noninsect	NOINSECT	Composition	33.0
Pctg Oligochaeta	PEROLIGO	Composition	189.4
Modified Missouri Biotic Index	MOBI[a]	Tolerance	9.0
Dominant taxon abn	DOMTAX	Tolerance	103.7
Dominant two taxa abn	PREDOM2	Tolerance	104.1
Dominant three taxa abn	PREDOM3	Tolerance	104.3
Dominant four taxa abn	PREDOM4	Tolerance	101.1
Dominant five taxa abn	PREDOM5	Tolerance	100.7
Pctg dominant taxon	DOM1	Tolerance	36.9
Pctg dominant two taxa	DOM2	Tolerance	23.8
Pctg dominant three taxa	DOM3[a]	Tolerance	19.4
Pctg dominant four taxa	DOM4[a]	Tolerance	15.5
Pctg dominant five taxa	DOM5[a]	Tolerance	12.4
Simpson's Diversity Index	D	Diversity	44.3
Shannon Diversity Index	SDI[a]	Diversity	11.6
Pielou's J	J[a]	Diversity	12.0
Pctg shredders	SHREDDER	FFG	50.4
Pctg predators	PREDATOR	FFG	46.5
Pctg scrapers	SCRAPER	FFG	103.0
Pctg filterers	FILTER	FFG	56.2
Pctg gatherers	GATHER	FFG	36.7
MW total abn	TOTALMAT	Composition	100.8
MW EPT abn	EPTSMAT	Composition	88.3
MW Ephemeroptera abn	ESUMMAT	Composition	66.5
MW Plecoptera abn	PSUMMAT	Composition	164.9
MW Trichoptera abn	TRSUMMAT	Composition	158.7
MW Hydropsychidae abn	HYDRSMAT	Composition	167.2
MW Philopotamidae abn	PHILSMAT	Composition	151.9
MW Elmidae abn	ELMSUMAT	Composition	108.0
MW Chironomidae abn	CHISMAT	Composition	151.8
MW Tanypodinae abn	TANPDMAT	Composition	84.6
MW Orthocladiinae abn	ORTHOMAT	Composition	92.9
MW Chironomini abn	CHAMAT	Composition	184.7
MW Tanytarsini abn	TANYMAT	Composition	204.8
MW Diptera + noninsect abn	NOINSMAT	Composition	135.9
MW EPT/MW Chironomidae	EPTCHIMAT	Composition	76.5
MW Tanypodinae abn/MW Chironomidae abn	TPODCHIM	Composition	65.9
MW Orthocladiinae abn/MW Chironomidae abn	ORTHCHIM	Composition	99.7
MW Chironomini abn/MW Chironomidae abn	MINICHIM	Composition	70.5
MW Tanytarsini abn/MW Chironomidae abn	TANYCHIM	Composition	57.7
MW shredder abn	SHRDSMAT	FFG	124.3
MW predator abn	PRDSMAT	FFG	66.0
MW scraper abn	SCRPSMAT	FFG	73.6
MW filterer abn	FSUMMAT	FFG	161.2
MW gatherer abn	GATSUMAT	FFG	76.4
MW pctg EPT	PREPTMAT	Composition	40.7
MW pctg Ephemeroptera	EMAT	Composition	48.1
MW pctg Plecoptera	PMAT	Composition	157.4
MW pctg Trichoptera	TRMAT	Composition	59.3
MW pctg Hydropsychidae	HYDROMAT	Composition	61.0

MW pctg Philopotamidae	PHILMAT	Composition	76.6
MW pctg Elmidae	ELMMAT	Composition	83.3
MW pctg Chironomidae	PERCHIM	Composition	43.8
MW pctg Tanypodinae	TPODTOTM	Composition	97.1
MW pctg Orthocladiinae	ORTHTOTM	Composition	110.3
MW pctg Chironomini	MINITOTM	Composition	83.1
MW pctg Tanytarsini	TANYTOTM	Composition	86.6
MW pctg Diptera + noninsects	NOINMAT[a]	Composition	27.1
MW modified Missouri Biotic Index	MOBIMAT[a]	Tolerance	10.1
MW dominant taxon abn	DOMTAXMT	Tolerance	119.7
MW dominant two taxa abn	PREDOM2M	Tolerance	114.4
MW dominant three taxa abn	PREDOM3M	Tolerance	115.3
MW dominant four taxa abn	PREDOM4M	Tolerance	112.5
MW dominant five taxa abn	PREDOM5M	Tolerance	111.4
MW pctg dominant taxon	DOM1MAT	Tolerance	34.3
MW pctg dominant two taxa	DOM2MAT	Tolerance	25.4
MW pctg dominant three taxa	DOM3MAT	Tolerance	20.3
MW pctg dominant four taxa	DOM4MAT[a]	Tolerance	16.7
MW pctg dominant five taxa	DOM5MAT[a]	Tolerance	12.9
MW pctg shredders	SHREDMAT	FFG	51.5
MW pctg predators	PREDMAT	FFG	62.6
MW pctg scrapers	SCRAPMAT	FFG	112.7
MW pctg filterers	FILTMAT	FFG	57.1
MW pctg gatherers	GATHMAT[a]	FFG	31.5
MW Simpson's Diversity Index	DMAT	Diversity	36.1
MW Shannon Diversity Index	SDIMAT[a]	Diversity	11.1
MW Pielou's J	JMAT[a]	Diversity	10.5

[a] Metrics considered for multiple regression.

References

Armitage, P.D., Moss, D., Wright, J.F., Furse, M.T., 1983. The performance of a new biological water-quality score system based on macroinvertebrates over a wide-range of unpolluted running-water sites. Water Res. 17, 333–347.

Barbour, M.T., Gerritsen, J., Snyder, B.D., Stribling, J.B., 1999. Rapid Bioassessment Protocols for Use in Wadeable Streams and Rivers: Periphyton, Benthic Macroinvertebrates and Fish, 2nd ed. EPA 841-B-99-002. Office of Water, United States Environmental Protection Agency, Washington, DC.

Benke, A.C., Huryn, A.D., Smock, L.A., Wallace, J.B., 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. J. N. Am. Benthol. Soc. 18, 308–343.

Bode, R.W., Novak, M.A., Abele, L.E., Heitzman, D.L., Smith, A.J., 2002. Quality Assurance Work Plan for Biological Stream Monitoring in New York State. New York State Department of Environmental Conservation, Division of Water, Stream Biomonitoring Unit.

Bretschko, G., 1985. Experimental analysis of the development of overwintering larvae of *Siphlonurus aestivalis* Eaton (Ephemeroptera) from a karstic lake. Arch. Hydrobiol. 104, 111–128.

Brock, D.A., 1977. Comparison of community similarity indices. J. Water Pollut. Control Fed. 36, 650–653.

Buffagni, A., Crosa, G., Marchetti, R., 1995. Size-related shifts in the physical habitat of two mayfly species (Ephemeroptera). Freshwater Biol. 34, 297–302.

Clarke, R.T., Wright, J.F., Furse, M.T., 2003. RIVPACS models for predicting the expected macroinvertebrate fauna and assessing the ecological quality of rivers. Ecol. Model. 160, 219–233.

Clifford, H.F., 1969. Limnological features of a northern brown-water stream, with special reference to the life histories of the aquatic insects. Am. Midl. Nat. 82, 578–597.

Cooper, S.D., Barmuta, L.A., 1993. Field experiments in biomonitoring. In: Rosenberg, D.M., Resh, V.H. (Eds.), Freshwater Biomonitoring and Benthic Macroinvertebrates. Routledge, Chapman and Hall, Inc., New York, NY, pp. 399–441.

Cuffney, T.F., Bilger, M.D., Haigler, A.M., 2007. Ambiguous taxa: effects on the characterization and interpretation of invertebrate assemblages. J. N. Am. Benthol. Soc. 26, 286–307.

Cummins, K.W., Merrit, R.W., 1996. Ecology and distribution of aquatic insects. In: Merritt, R.W., Cummins, K.W. (Eds.), An Introduction to the Aquatic Insects of North America. Kendall/Hunt Publishing Co., Dubuque, IW, pp. 74–86.

Cummins, K.W., Wilzbach, M.A., Gates, D.M., Perry, J.B., Taliaferro, W.B., 1989. Shredders and riparian vegetation. BioScience 39, 24–30.

Flinn, M.B., Adams, S.R., Whiles, M.R., Garvey, J.E., 2008. Biological responses to contrasting hydrology in backwaters of Upper Mississippi River. Environ. Manag. 41, 468–486.

Flotemersch, J.E., Stribling, J.B., Paul, M.J., 2006. Concepts and approaches for the bioassessment of non-wadeable streams and rivers. EPA 600-R-06-127. United States Environmental Protection Agency, Cincinnati, Ohio.

Gibbs, K.E., Mingo, T.M., 1986. The life history, nymphal growth rates, and feeding habits of *Siphlonisca aerodromia* Needham (Ephemeroptera: Siphlonuridae) in Maine. Can. J. Zool. 64, 427–430.

Grubaugh, J.W., Wallace, J.B., Houston, E.S., 1996. Longitudinal changes of macroinvertebrate communities along an Appalachian stream continuum. Can. J. Fish. Aquat. Sci. 53, 896–909.

Hauer, F.R., Resh, V.H., 2006. Macroinvertebrates. In: Hauer, F.R., Lamberti, G.A. (Eds.), Methods in Stream Ecology. Academic Press, Burlington, MA, pp. 435–463.

Hawkins, C.P., Norris, R.H., Hogue, J.N., Feminella, J.W., 2000. Development and evaluation of predictive models for measuring the biological integrity of streams. Ecol. Appl. 10, 1456–1477.

Hilsenhoff, W.L., 1977. Use of arthropods to evaluate water equality of streams. Wisconsin Department of Natural Resources Technical Bulletin 100.

Huryn, A.D., Wallace, J.B., 2000. Life history and production of stream insects. Annu. Rev. Entomol. 45, 83–110.

Hutchens Jr., J.J., Chung, K., Wallace, J.B., 1998. Temporal variability of stream macroinvertebrate abundance and biomass following pesticide disturbance. J. N. Am. Benthol. Soc. 17, 518–534.

Jones, J.R., Tracy, B.H., Sebaugh, J.L., Hazelwood, D.H., Smart, M.M., 1981. Biotic Index tested for ability to assess water quality of Missouri Ozark streams. Trans. Am. Fish. Soc. 110, 627–637.

Kosnicki, E., Burian, S., 2003. Life history aspects of the mayfly *Siphlonurus typicus* (Ephemeroptera: Siphlonuridae) with a new application for measuring nymphal development and growth. Hydrobiologia 510, 131–146.

Lenat, D.R., 1993. A biotic index for the southeastern United States: derivation and list of tolerance values, with criteria for assigning water-quality ratings. J. N. Am. Benthol. Soc. 12, 279–290.

Leunda, P.M., Oscoz, J., Miranda, R., Ariño, A.H., 2009. Longitudinal and seasonal variation of the benthic macroinvertebrate community and biotic indices in an undisturbed Pyrenean river. Ecol. Indic. 9, 52–63.

Linke, S., Bailey, R.C., Schwindt, J., 1999. Temporal variability of stream bioassessments using benthic macroinvertebrates. Freshwater Biol. 42, 575–584.

Lloyd, F., Sites, R.W., 2000. Microhabitat associations of three species of Dryopoidea (Coleoptera) in an Ozark stream: a comparison of substrate, and simple and complex hydraulic characters. Hydrobiologia 439, 103–114.

Maloney, K.O., Feminella, J.W., 2006. Evaluation of single- and multi-metric benthic macroinvertebrate indicators of catchment disturbance over time at the Fort Benning Military Installation, Georgia, USA. Ecol. Indic. 6, 469–484.

Mazor, R.D., Purcell, A.H., Resh, V.H., 2009. Long-term variability in Bioassessments: a twenty-year study from two Northern California streams. Environ. Manag. 43, 1269–1286.

McElravy, E.P., Lamberti, G.A., Resh, V.H., 1989. Year-to-year variation in the aquatic macroinvertebrate fauna of a northern California stream. J. N. Am. Benthol. Soc. 8, 51–63.

Merritt, R.W., Cummins, K.W., 1996. An Introduction to the Aquatic Insects of North America. Kendall/Hunt Publishing Co., Dubuque, IW.

Minshall, G.W., 1984. Aquatic insect-substratum relationships. In: Resh, V.H., Rosenburg, D.M. (Eds.), The Ecology of Aquatic Insects. Praeger, New York.

Moss, D., Furse, M.T., Wright, J.F., Armitage, P.D., 1987. The prediction of the macroinvertebrate fauna of unpolluted running-water sites in Great Britain using environmental data. Freshwater Biol. 17, 41–52.

Murphy, P.M., 1978. The temporal variability in biotic indices. Environ. Pollut. 17, 227–236.

Neter, J.M., Kutner, H., Nachtsheim, C.J., Wasserman, W., 1996. Applied Linear Regression Models. IRWIN Books, Chicago, IL.

Nigh, T.A., Schroeder, W.A., 2002. Atlas of Missouri Ecoregions. Missouri Department of Conservation, Jefferson City, MO.

Norris, R.H., 1995. Biological monitoring: the dilemma of data analysis. J. N. Am. Benthol. Soc. 14, 440–450.

Omernik, J.M., 1987. Ecoregions of the conterminous United States. Ann. Assoc. Am. Geogr. 77, 118–125.

Pinkham, C.F., Pearson, J.G., 1976. Applications of new coefficient of similarity to pollution surveys. J. Water Pollut. Control Fed. 48, 717–723.

Poulton, B.C., Stewart, K.W., 1991. The stoneflies of the Ozark and Ouachita mountains (Plecoptera). Memoirs of the American Entomological Society, no. 38. The American Entomological Society at the Academy of Natural Sciences, Philadelphia, PA.

Rabeni, C.F., Saver, R.J., Wang, N., Wallace, G.S., Weiland, M., Peterson, J.T., 1997. Development of Regionally Based Biological Criteria for Streams of Missouri. Final Report. Missouri Department of Natural Resources, Jefferson City, MO.

Reich, P., Downes, B.J., 2004. Relating larval distributions to patterns of oviposition: evidence from lotic hydrobiosid caddisflies. Freshwater Biol. 49, 1423–1436.

Resh, V.H., Jackson, J.K., 1993. Rapid assessment approaches to biomonitoring using benthic macroinvertebrates. In: Rosenberg, D.M., Resh, V.H. (Eds.), Freshwater Biomonitoring and Benthic Macroinvertebrates. Routledge, Chapman, and Hall, Inc., New York, NY, pp. 195–223.

Robinson, C.T., Minshall, G.W., 1998. Macroinvertebrate communities, secondary production, and life history patterns in two adjacent streams in Idaho, USA. Arch. Hydrobiol. 142, 257–281.

Robinson, C.T., Minshall, G.W., Royer, T.V., 2000. Inter-annual patterns in macroinvertebrate communities of wilderness streams in Idaho, U.S.A. Hydrobiologia 421, 187–198.
Sarver, R., 2001. Semi-quantitative macroinvertebrate stream bioassessment. Missouri Department of Natural Resources, Division of Environmental Quality, Environmental Services Program. MDNR-FSS-209. Jefferson City, MO.
Sarver, R., Harlan, S., Rabeni, C., Sowa, S.P., 2002. Biological Criteria for Wadeable/Perennial Streams of Missouri. Missouri Department of Natural Resources, Jefferson City, MO.
Simpson, J.C., Norris, R.H., 2000. Biological assessment of river quality: development of the AUSRIVAS models and outputs. In: Wright, J.F., Sutcliffe, D.W., Furse, M.T. (Eds.), Assessing the Biological Quality of Freshwaters: RIVPACS and Other Techniques. Freshwater Biological Association, Ambleside, Cumbria, UK, pp. 125–142.
Smith, M.E., Kaster, J.L., 1983. Effect or rural highway runoff on stream benthic macroinvertebrates. Environ. Pollut. (Series A) 32, 157–170.
Snellen, R.K., Stewart, K.W., 1979. The life cycle of *Perlesta placida* (Plecoptera: Perlidae) in an intermittent stream in northern Texas. Ann. Entomol. Soc. Am. 72, 659–666.
Stewart, K.W., Stark, B.P., 1993. Nymphs of North American Stonefly Genera (Plecoptera). University of North Texas Press, Denton, TX.
Sweeney, B.W., 1984. Factors influencing life-history patterns of aquatic insects. In: Resh, V.H., Rosenberg, D.M. (Eds.), The Ecology of Aquatic Insects. Praeger Publishers, New York, NY, pp. 56–100.
Townsend, C.R., 1989. The patch dynamics concept of stream community ecology. J. N. Am. Benthol. Soc. 8, 36–50.
Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E., 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37, 130–137.
Vannote, R.L., Sweeney, B.W., 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insects communities. Am. Nat. 155, 667–695.
Wallace, J.B., Grubaugh, J.W., Whiles, M.R., 1996. Biotic indices and stream ecosystem processes: results from an experimental study. Ecol. Appl. 6, 140–151.
Ward, J.V., 1989. The four-dimensional nature of lotic ecosystems. J. N. Am. Benthol. Soc. 8, 2–8.
Ward, J.V., 1992. Aquatic Insect Ecology I. Biology and Habitat. John Wiley and Sons, New York.
Washington, H.G., 1984. Diversity, biotic and similarity indices. Water Resour. 18, 653–694.
Whittaker, R.H., Fairbanks, C.W., 1958. A study of plankton copepod communities in the Columbia Basins, southeastern Washington. Ecology 39, 46–65.
Wiens, J.A., 2002. Riverine landscapes: taking landscape ecology into the water. Freshwater Biol. 47, 501–515.
Williams, D.D., Feltmate, B.W., 1992. Aquatic Insects. CAB International, Wallingford, UK.
Wohl, D.B., Wallace, J.B., Meyer, J.L., 1995. Benthic macroinvertebrate community structure, function and production with respect to habitat type, reach and drainage basin in the southern Appalachians (U.S.A.). Freshwater Biol. 34, 447–464.
Wright, J.F., 1995. Development and use of a system for predicting the macroinvertebrate fauna in flowing waters. Aust. J. Ecol. 20, 181–197.
Wright, J.F., Moss, D., Armitage, P.D., Furse, M.T., 1984. A preliminary classification of running-water sites in Great Britain based on macro-invertebrate species and the prediction of community type using environmental data. Freshwater Biol. 14, 221–256.
Zamora-Muñoz, C., Sainz-Cantero, C.E., Sanchez-Ortega, A., Alba-Tercedor, J., 1995. Are biological indices BMPW' and ASPT' and their significance regarding water quality seasonally dependent? Factors explaining their variations. Water Res. 29, 285–290.
Zar, J.H., 1999. Biostatistical Analysis. Prentice-Hall, Upper Saddle River, New Jersey.