AN ANALYSIS OF THE DISTRIBUTION AND DIVERSITY OF THE EPHEMEROPTERA OF MAINE, U.S.A.

STEVEN K. BURIAN

Department of Biology, Southern Connecticut State University, New Haven, Connecticut, 06515, USA

Although Maine has the best documented mayfly fauna of all the New England States, there have been no detailed analyses of species distributions or patterns of diversity. Data used in this study were obtained from an extensive survey of Maine's mayfly fauna conducted from 1985-1987. Distributional data for 157 species from 239 sites was analyzed using Two-way Indicator Species Analysis (TSA) to search for block structure in the data matrix. Most site classes produced by TSA showed little or no correlation to the present landscape classification for Maine. Further analysis on a subset of 66 sites, located in all major physiographic regions and containing 129 species, was conducted using TSA. At six levels of division TSA produced 18 site classes. Seven of these classes broadly align with one or more major landscape units. Species-environment relationships of this subset were examined using Canonical Correspondence Analysis (CCA). Results of CCA showed that 49.9% of the variance in species distributions was accounted for by the first four ordination axes. Environmental variables of the first two axes important in accounting for species distributions were: aquatic vegetation, water depth, water velocity, water temperature, and site elevation. Results of these analyses indicate that a majority (81%) of species are not constrained within the narrow context of the current climatic/biophysical zones identified in Maine.

Analysis of species diversity conducted on a state-wide basis, for drainage basins, and climatic/biophysical zones indicated that the central-southern region of the State had the greatest diversity. About 60% of all species recorded for Maine had ranges that overlapped in this region.

INTRODUCTION

Mayflies (Ephemeroptera) are ecologically important components of aquatic ecosystems throughout Maine (BURIAN, 1990), but no landscape-level analyses of their distribution or diversity are available. Recently, conservation and environmental biologists have begun to evaluate aquatic biodiversity and develop management proposals for species that are perceived to be at risk of extirpation or for which risk is unknown. This work has emphasized the importance of understanding the distribution and diversity of the mayflies at the landscape-level. Without such knowledge it is not possible to answer even the simplest questions posed by conservationists or understand the deficiencies of our existing data. Maine has a rich mayfly fauna composed of about 157 species (BURIAN & GIBBS, 1991), and developing a landscape-level understanding of the distribution and diversity of these species will be the focus of this paper. Analyses presented here will form the basis for future studies of the mayflies of Maine and adjacent areas of New England and Atlantic Canada.

MATERIALS AND METHODS

Study Area

Maine is the northernmost of the New England States (extending from 43°N to 47° 30'N) and it has a surface area of 84,769 km² (Fig. 1). Maine has a diverse physiography that ranges from mountains with alpine summits in the west to low lying coastal bogs in the east. Distributed across this landscape is a diverse array of aquatic habitats (BURIAN, 1990). Except for large deep rivers with clean shifting sand bottoms, most types of aquatic habitat capable of supporting mayflies are present in Maine.

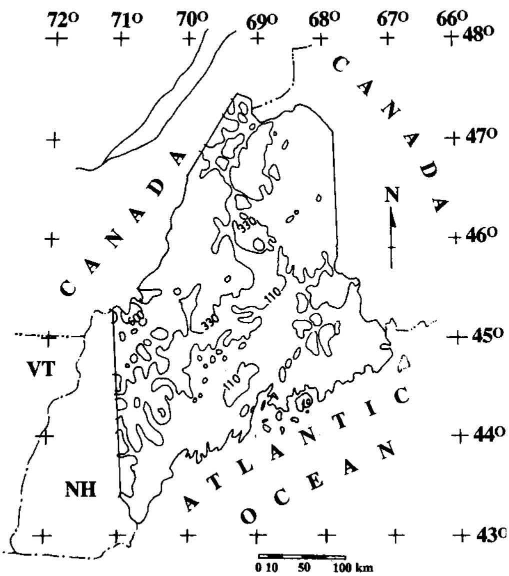

Fig. 1. Map of Maine showing major topographic changes. Contours indicated are in meters above sea level.

© MTL, Fribourg - 1997. P. Landolt & M. Sartori (Eds).
Ephemeroptera & Plecoptera: Biology-Ecology-Systematics.

Species data

Species records compiled by BURIAN & GIBBS (1991) and MACK (1988) along with recent records obtained by the author were the source of data for this study. Species names from these sources were corrected to conform to recently published systematic changes for the Baetidae (MCCAFFERTY & WALTZ, 1990, 1995; MCCAFFERTY *et al.*, 1994), *Eurylophella* (FUNK & SWEENEY, 1994), *Timpanoga* (MCCAFFERTY & WANG, 1994) and *Choroterpes* (BURIAN, 1995). For analysis, distribution data were compiled into binary (absence/presence) and interval (numbers of occurrence) forms. The primary (all species and all sites) data matrix was composed of 157 rows (species) and 239 columns (sites). Secondary matrices were compiled in a similar manner for species distributions in 15 biophysical regions (MCMAHON, 1990), nine climatic zones (BRIGGS & LEMIN, 1992), and eight major drainage basins (unpublished report from Maine State Planning Office). Codes and landscape divisions are presented in Fig. 2. Landscape units (e.g., biophysical regions) were columns among secondary matrices. Further, a subset of the primary data matrix was produced that was composed of 129 rows and 66 columns to examine species distributions among a group of sites that were repeatedly and extensively sampled in a similar manner. Sites selected for this subset were mostly those sampled during 1986 and 1987 (BURIAN, 1990; MACK, 1988). This subset was also used in multivariate analysis of species-environment relationships.

Faunal Analysis

An important goal in the analysis of species distributions is to identify block structures within data-sets that may be associated with ecological factors or distinct landscape units. To accomplish this, the Two-way Indicator Species Analysis (TSA) (GAUCH, 1982) via the computer program TWINSPAN (HILL, 1979) was used to examine the structure of the primary data matrix and its subset. Block structures, appearing as groups of sites produced by assemblages of species with similar distributions among those sites, would be the product of the biological or ecological attributes of species, because TSA uses no geographic data in analysis of species occurrences. Repeated TSA runs were completed to search for patterns of convergence, as described by FURSE *et al.* (1984). Sites are from BURIAN & GIBBS (1991).

Aquatic habitat variables that may affect the distribution of mayflies were investigated using Canonical Correspondence Analysis (CCA) (TER BRAAK, 1986) via the computer program CANOCO 3.12 (TER BRAAK, 1990). This direct gradient multivariate technique allows species data (which is nonlinear) to be analyzed with corresponding environmental data (which is linear); the only critical assumption is that species data is monotonic. Current evidence suggests that mayflies are generally monotonic (CORKUM & CIBOROWSKI, 1988). CCA was conducted using the 129 by 66 (species by sites) subset of the primary data matrix and habitat data for 10 environmental variables recorded for the

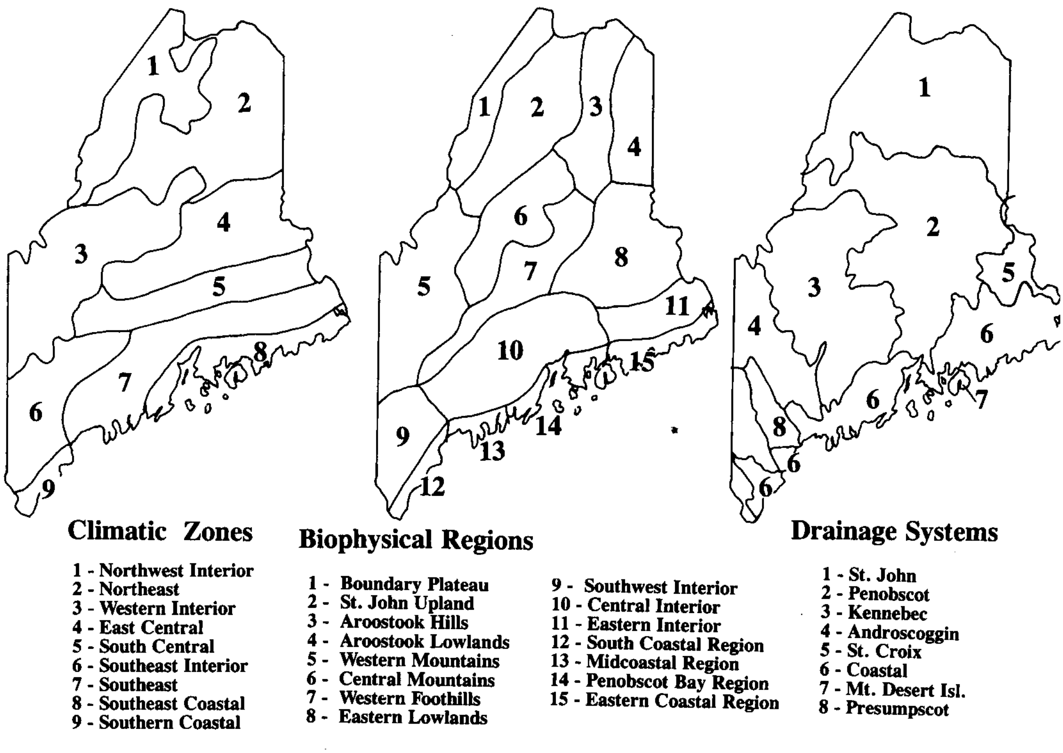

Fig. 2. Maps of major landscape classifications presented by MCMAHON (1990) for biophysical regions; BRIGGS & LEMIN (1992) for climatic zones; and drainage systems (Maine State Planning Office as represented by BURIAN 1990).

same 66 sites. Environmental variables and codes are explained in Appendix 1. Species names and codes are listed in Appendix 2. Percent variation in species data explained by corresponding environmental variables was calculated in the form of intraset correlation coefficients. Species and sites were ordinated along axes produced by linear combinations of environmental variables. Environmental variables are shown on plots as arrows; the longer the arrow and the closer it is to an axis the more important it is in defining that axis. Significance of relations inferred by CCA were tested using a Monte Carlo Random Resampling Test using 100 random permutations. Results of CCA were plotted for the first two canonical axes using the computer program CANODRAW (SMILAUER, 1990).

Analysis of Species Richness

Mayfly beta-level diversity of major landscape classifications (biophysical regions, climatic zones, and drainage basins) was examined by calculating association coefficients for secondary matrices and by clustering the results using the Unweighted Pair Group Mathematical Averaging (UPGMA). Because mutual occurrences of species were a priori determined to be of greater information value than mutual absences, Dice's Coefficient of association (DICE, 1945) was selected to evaluate faunal similarity. Association coefficients and clusters were generated via the computer program NTSYS pc ver. 1.7 (ROHLF, 1992).

Patterns of mayfly species richness over the entire state were determined by overlaying range maps of species on a grid of 317 (20 by 20 km) quadrats. The grid size was chosen because it was previously adopted for botanical studies by MCMAHON (1990) and will facilitate future comparisons with other data-sets. Rules for indicating a species presence in a quadrat determined by MCMAHON (1990) for woody plants were also adopted. Numbers of species recorded per month, per family per month, per biophysical region, per climatic zone, and per drainage basin were compiled. Species with apparently restricted or disjunct distributions within Maine were noted and discussed.

RESULTS

Faunal Analysis of the Primary Data Matrix

TSA of the primary data matrix, using six division levels, produced 11 site classes. Nine site classes were small containing from one to four species. Most of these smaller site classes were produced by sites defined by one species with no other occurrences in the data-set. These singleton records provided minimal information and used up most of the division levels in the first TSA runs. One site class contained 22 species, but was primarily defined by the presence of *Hexagenia limbata* at almost every site in the class. The final site class contained 207 species. Maps of biophysical regions, climatic zones, and major drainage systems overlaid on plots of these site classes revealed no stable block structures that corresponded to landscape units. Additional TSA runs using up to 12 division levels (maximum possible is 15) failed to substantially improve site class resolution or reveal any landscape patterns. The failure of TSA to resolve site classes for most species of

Table 1. Summary of TWINSPAN analysis of subset data matrix (129 rows [species] by 66 columns[sites]). Landscape classification code numbers are defined in Fig. 2. Site codes for faunal patterns are defined in BURIAN & GIBBS (1991).

TSA Site Classes and Pattern Type	Number of Sites in Class and Codes	TSA Indicator Species	Biophysical Region	Climatic Zone	Drainage
Moosehead Plateau					
2	1 (S4)	*Baetis veteris*	5, 6	3	3
5	1 (S1)	*Heptagenia pulla*	5, 6	3	3
7	4 (F7, F9, F13, Ps5)	*Acerpenna macdunnoughi* *Ephemera varia*	5, 6	3	3
13	4 (F1, Ps1, Ps8, Ps10)	*Arthroplea bipunctata*	5, 6	3	3
South-Central					
9	5 (K1, L1, P3, P8, P23)	*Ephemerella rotunda* *Serratella deficiens* *Siphlonurus marginatus*	8, 10	4, 5, 7	–
14	3 (P9, W9, Wn6)	*Procloeon simplex*	8, 10	4, 5, 7	–
Eastern Aroostook					
11	1 (AK1)	*Nixe horrida*	4	2	1

the primary data matrix was believed to be related to the large number of singleton records, the large number of sites with few species records, and the large number of overall zero occurrences in the data matrix relative to the number of sites being analyzed.

Faunal Analysis of the Subset Data Matrix

TSA of the subset data matrix, using six division levels, produced 18 site classes. Maps of biophysical regions, climatic zones, and major drainage systems overlaid on plots of these site classes showed that 11 site classes had no correlation to landscape units, but seven site classes did correspond to one or more landscape units (Table 1). Site classes 2, 5, 7, and 13 were represented by 10 sites all located either in biophysical region 5 or 6, contained within climatic zone 3 and located in the upper part of drainage system 3. Indicator species determined by TSA for these site classes are presented in Table 1.

Site classes 9 and 14 were represented by eight sites all located either in biophysical region 8 or 10, and contained within one or more of three broad climatic regions (5, 7, or 8) that collectively represent the climate of the central interior of Maine. No restrictions to major drainage systems were observed. Indicator species determined by TSA are presented in Table 1.

Site class 11 was represented by a single site located in biophysical region 4, climatic region 2, and drainage system 1. The indicator species for this site class is *Nixe horrida*.

There seems to be three distinct patterns among these groups of site classes. First, a western mountain pattern that broadly corresponds with aquatic habitats of the central Moosehead Plateau (Fig. 2, Biophysical regions 5 & 6). Second, a central southern pattern that broadly corresponds with the warmer lower elevation aquatic habitats of the south-central part of Maine (Fig. 2, Biophysical regions 8 & 10). Finally, a unique assemblage of species associated with aquatic habitats of eastern Aroostook County and the Aroostook River system (Fig. 2, Biophysical region 4).

Analysis of Species-Environment Relationships

The results CCA ordination for 129 species of mayflies, 66 sites, and 10 environmental variables showed that 49.9% of the variance in species occurrences was accounted for by the first four ordination axes (Table 2). Most of the variance was explained by variables of the first two axes. This was expected because of the high level of environmental noise intrinsic to this type of data. Significance of the relationship of the first axis was marginal with an *F*-ratio of 1.96 (P = 0.10). However, overall significance of relationships indicated by all ordination axes was high with a calculated *F*-ratio of 1.29 (P<0.01). Intraset correlation coefficients for the environmental variables are summarized in Fig. 3.

The first ordination axis reflected a gradient mostly related to the occurrence of aquatic vegetation, water depth, and current velocity (Fig. 3). The presence of aquatic vegetation decreases from the positive to the negative end of the axis. Water depth decreases in the same manner from positive to negative ends of the axis. Water current velocity, however, decreases from the negative end of the axis toward the positive end.

Along axis one the increasing occurrence of aquatic plants is correlated with increased water depth and lower current velocities or standing water conditions. Shallow habitats with few aquatic plants correlated with higher velocities at the negative extreme of axis one.

The second ordination axis indicated that site elevation above sea level and water temperature had the next largest effect on the occurrence of species (Fig. 3). Site elevation above sea level decreases from the negative to the positive end of axis two. Water temperature decreases from the positive to the negative end of axis two.

Table 2. Eigenvalues and percent variance explained for the first four ordination axes of CCA. *F*-ratio statistics are listed for the first axis and all axes combined.

Axis	Eigenvalues	% Variance
1	0.352 (F = 1.96, P = 0.10)	15.8
2	0.305	29.5
3	0.241	40.3
4	0.214	49.9
Sum of all Canonical Eigenvalues = 2.229		
Overall Significance, F = 1.29 (P<0.01)		

Thus warmest temperatures occurred at the positive extreme correlated with lower elevations. Cooler water temperatures at the negative extreme correlated with the position of higher elevation sites.

Ordination of species with regards to the first two axes is presented in Fig. 4. Species typical of higher elevation and cool streams were positioned in the lower left quadrat. Species of fast flowing waters occurred in the upper left quadrat. Species occurring in warmer, deeper aquatic habitats with aquatic vegetation were positioned in the upper right quadrat. Species in the lower right quadrat of the plot were typical of the slower flowing areas of streams, stream flowages, and the margins of ponds and lakes.

Patterns of Diversity and Species Richness

Results of cluster analysis of 157 species of mayflies in 12 of the 15 biophysical regions are presented in Fig. 5a. Biophysical regions 13

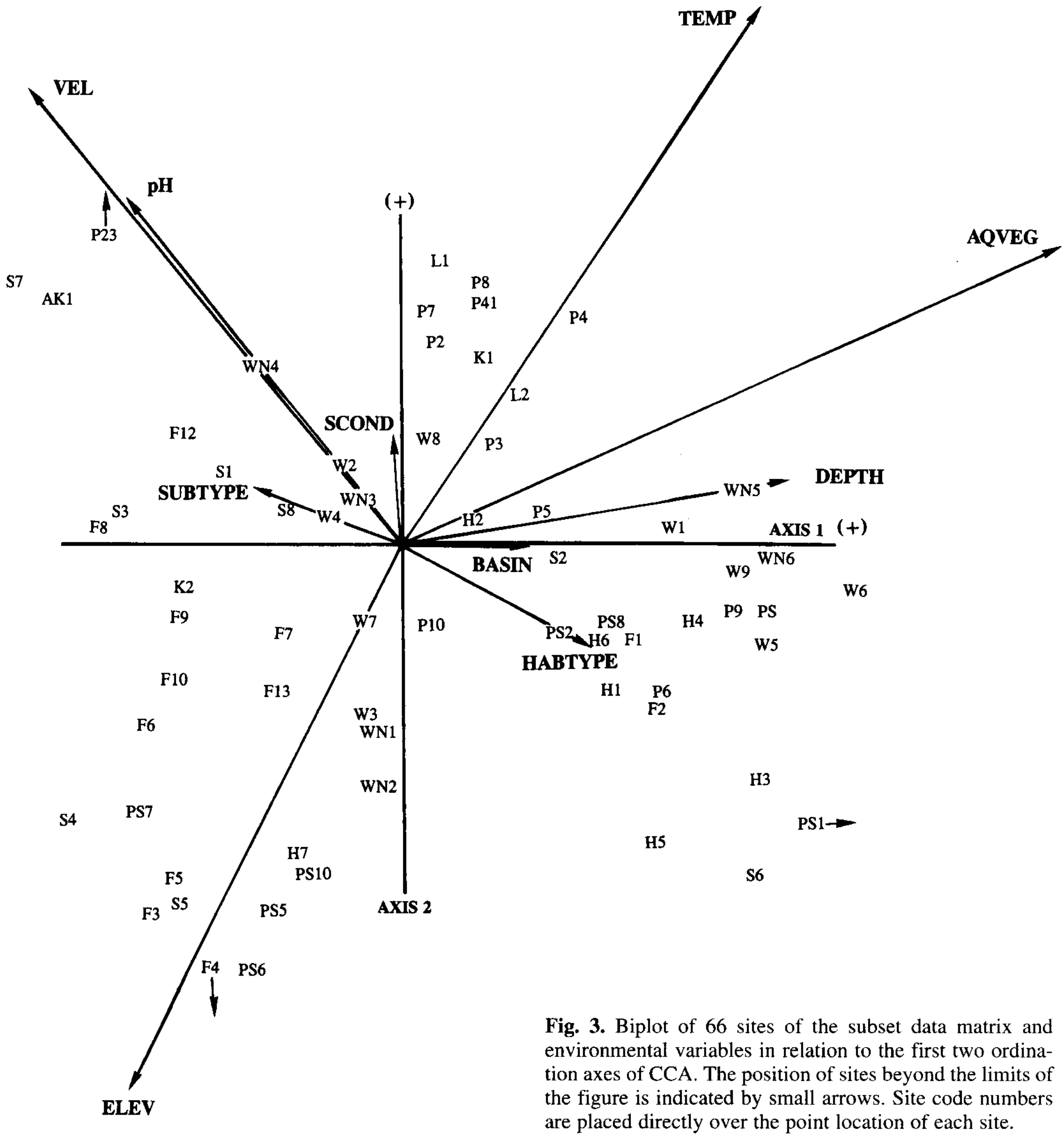

Fig. 3. Biplot of 66 sites of the subset data matrix and environmental variables in relation to the first two ordination axes of CCA. The position of sites beyond the limits of the figure is indicated by small arrows. Site code numbers are placed directly over the point location of each site.

and 14 were omitted from the analysis because there was only one species recorded for each of these regions. Biophysical regions 1, 11, and 2 form a cluster, indicating a similar fauna and a disjunct pattern between species in north-western and eastern Maine. The cluster formed between biophysical regions 8 and 10 had the highest association coefficient of any cluster. The cluster formed by biophysical regions 9 and 12 form had the lowest association coefficient of any cluster, but the close geographic position of these regions to each other lends credibility to the grouping.

Patterns of faunal similarity for climatic zones are presented in Fig. 5b. Climatic zones 1 and 2 form a distinct cluster indicating a similar, but disjunct fauna between these areas. Climatic zones 4 and 5 had the highest similarity value. Results of cluster analysis of major drainage systems are presented in Fig. 5c. The Saco and Piscataqua drainage systems were omitted because no species records were available for these areas. Three distinct clusters were evident among the areas studied. The largest cluster composed of drainage systems 2, 3, 5, 6, and 7 had the highest association coefficient. Drainage 1 was the most distinctive single system and was only weakly associated with the drainages of central and eastern Maine. The final cluster had the lowest association value, but is credible because of the proximity of these areas to each other.

General patterns of species richness for 157 species of mayflies are presented in Fig. 6. In this plot the central interior region had the greatest species richness with most quadrats containing from 80 to 100 species. Moving outward from this area species richness dropped

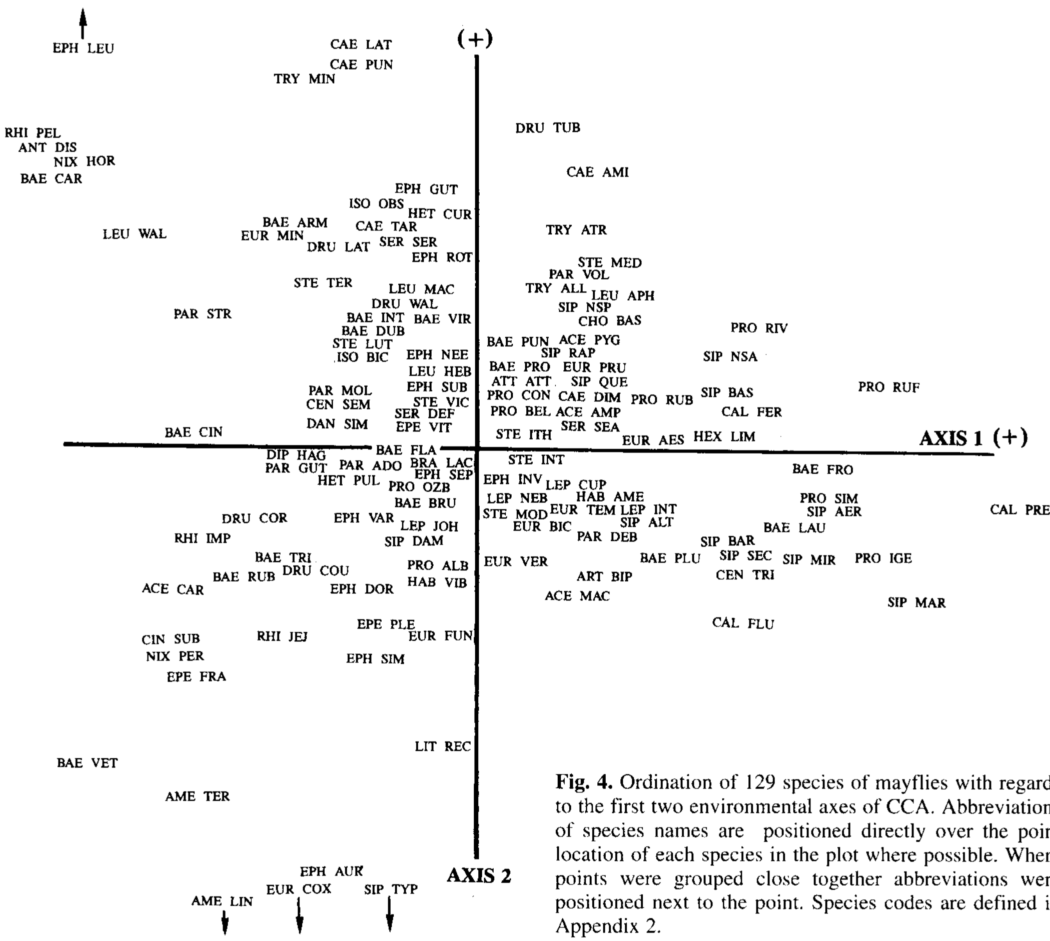

Fig. 4. Ordination of 129 species of mayflies with regards to the first two environmental axes of CCA. Abbreviations of species names are positioned directly over the point location of each species in the plot where possible. Where points were grouped close together abbreviations were positioned next to the point. Species codes are defined in Appendix 2.

progressively to areas outside the limits of current range maps. Areas with no species represent places for which no species records are available, but all such areas had suitable habitats for mayflies. Currently, the most diverse families were Baetidae and Heptageniidae each contained 23.5% and 22.0% of all species, respectively. Within the Baetidae the most diverse genera were *Baetis* and *Procloeon* each contained 11 species. In the Heptageniidae generic diversity was more equally distributed, four of the nine genera recorded contained between five and eight species. Among the other 12 families recorded most of the diversity was localized in one or two genera.

Numbers of species occurring in major landscape units are presented in Table 3. Biophysical region 5 and 10 had the greatest numbers of species. However, the same number of species (i.e., 95) recorded in both regions was recorded from only 31 sites in region 5 vs. 66 sites in region 10. Regarding climatic zones, zone 3 had the highest species richness with 112 species. For drainage systems, drainage 3 had the highest species richness with 120 species. Drainage system 2 was next with 103 species.

A temporal plot of species richness and sites sampled is presented in Fig. 7. The most species rich month was June (102 species), followed closely by July (94 species).

The months of May-August had the largest number of different sites sampled. Numbers of sites sampled per major landscape unit are summarized in Table 3. Biophysical region 10 had the largest number of different sites (66). Coastal regions had among the fewest sites with the exception of region 15, which had 20 sites.

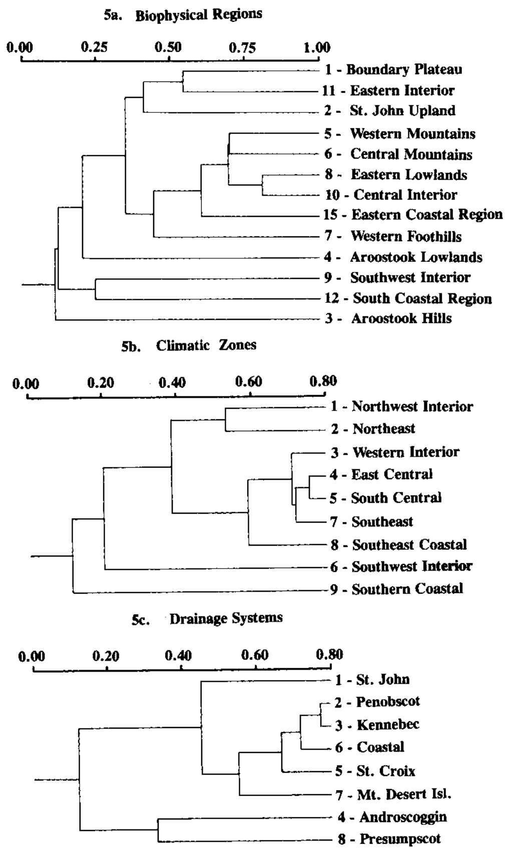

Fig. 5. Results of cluster analysis using Dice's Coefficient of faunal similarity of major landscape units for 157 species of mayflies: 5a, biophysical regions, 5b. climatic zones, and 5c. major drainage systems.

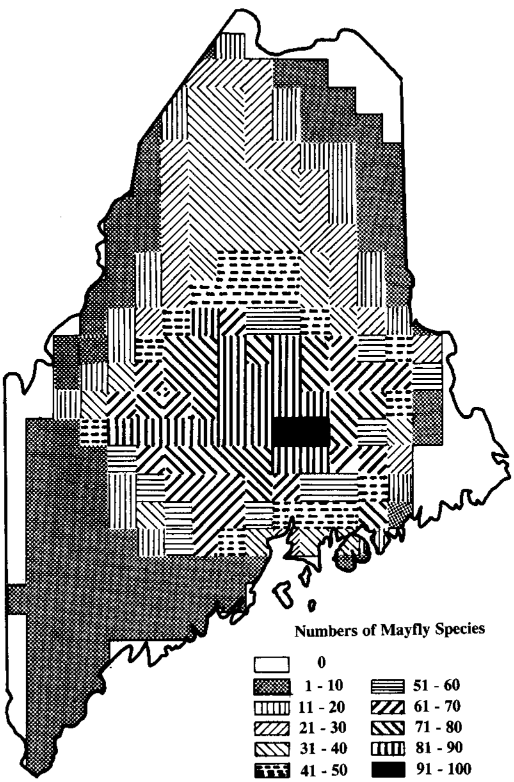

Fig. 6. Synopsis of spatial patterns of species richness for 157 species of mayflies.

Sites were more evenly distributed among climatic zones. Zone 9 was the only area with less than 10 sites. Among drainage systems, drainages 2 and 3 had the majority of sites. The southernmost drainages were not represented.

Restricted and Disjunct Species

About 35 species of mayflies showed some type of a restricted occurrence (complete list of restricted species is available from the author on request). Generally, these species were considered rare in the primary data-set with only one or a few records. No biophysical region had more than five restricted species. Most of the restricted species occurred in biophysical regions 5, 7, 10, and 11. Climatic zone 3 had eight restricted species, the highest for any climatic zone. Numbers of restricted species were more evenly distributed among major drainage systems. The drainage systems 1, 2, and 3 had between five and nine restricted species.

About 15 species of mayflies showed some type of broad disjunct distribution within Maine (complete list of disjunct species is available from the author on request). The pattern held in common by these species is one of occurrences in western or northern Maine and eastern or southeastern Maine with no records in the central part of the State. Some examples of species that best represented this pattern were *Metretopus borealis, Cinygmula subaequalis* and *Hexagenia rigida*.

Table 3. Synopsis of species richness of major landscape divisions and sampling effort per region defined by numbers of sites yielding species records.

Landscape Units	Number of Species	Number of Sites
Biophysical Regions		
5	95	31
10	95	66
6	86	32
8	84	25
15	58	20
11	53	9
7	41	13
1	35	14
2	22	8
4	15	3
9	10	7
3	6	5
12	6	4
13	1	1
14	1	1
Total		239
Climatic Zones		
3	112	56
5	97	34
7	94	54
4	78	23
8	64	25
1	39	16
2	36	13
6	19	14
9	6	4
Total		239
Drainages		
3	120	61
2	103	73
6	96	41
5	70	6
1	52	22
7	47	15
4	15	14
8	3	3
Total		239

DISCUSSION

Analyzing existing databases for landscape patterns is usually a difficult task because of varying information content of species records (HUGHES *et al.*, 1987). The TSA of the primary data matrix clearly showed that not all mayfly species records were useful in identifying patterns. Singleton records, although important in terms of estimates of gamma-level diversity, provided little information in resolving block structures. These types of records should be treated separately in analyses for landscape

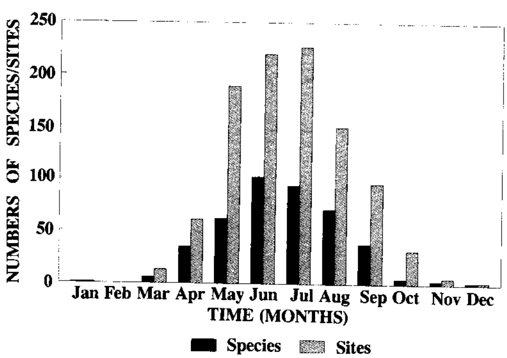

Fig. 7. Synopsis of overall temporal species richness and temporal sampling effort.

patterns. Initial analyses indicated species records need to be carefully screened and specific criteria adopted for inclusion of records in analysis of landscape patterns. From these analyses, I recommend that data for analysis should be from a site that was sampled more than once and sampled using a standard methodology. Among the current data-set only about 28% of the 239 sites were found acceptable for analysis using these criteria.

The analysis of the subset data matrix showed that there were distinct block structures present among species distributions. These block structures broadly corresponded to landscape divisions of the central Moosehead Plateau, the lower elevation central interior, and lower elevation area of eastern Aroostook County. The lack of close agreement of patterns identified for western and central Maine with the boundaries of a single biophysical region or climatic zone is reflective of the wide range of aquatic habitats in these areas, which are not restricted in their distribution. Species of mayflies comprising these patterns occur broadly throughout these areas and their occurrence seems most affected by the interaction between local climate and aquatic habitat structure. Only TSA site classes that were defined by a single site were completely restricted within the boundaries of landscape divisions. Further, it is clear that the broad distribution patterns elucidated by TSA can only be partially explained by some attributes of the landscape classifications studied here. This conclusion cautions against the uncritical use of these landscape classifications for planning the location of water quality reference sites or aquatic biodiversity reference sites for mayflies or other aquatic insects with similar ecological requirements.

Based on CCA a majority (81%) of the mayflies occurring in Maine seem to be distributed along two environmental gradients. One was mostly defined by the presence aquatic vegetation, water depth, and current velocity. The other by site elevation above sea level and water temperature. Similar variables were identified by CORKUM (1989, 1990) as being important in predicting assemblages of benthic invertebrates in western Canada. Except for the variables of site elevation, which was controlled by topography, and water temperature, which was affected by topography interacting with local climate, other habitat variables were not correlated with features of landscape divisions. Aquatic habitats with varying aquatic plant growth, depth, and current velocity are broadly distributed across Maine. Most species of mayflies seem to have a good chance of occurring wherever local aquatic habitats provide the correct mix of ecological conditions regardless of geographic position. This is probably why landscape classifications lacked explanatory power for mayfly species distributions. Currently, all the species in this study have continental ranges that extend beyond Maine. It is expected that unless aquatic habitats in other areas are or become geographically restricted that environmental variables, presented here, will operate in a similar manner to affect species occurrences.

Cluster analysis of mayfly species assemblages among biophysical regions, climatic zones, and major drainage systems produced a number of patterns depending on the landscape units. The biophysical region classification contained 15 regions that split up broad geographic areas and produced a complex plot. The other two landscape classifications had fewer, but larger areas that tended to lump sites and produced less complex plots. Although patterns differed among landscape classifications, the same broad patterns elucidated by TSA of the subset data matrix were evident. However, cluster analysis revealed a strong association between western/northern areas and eastern areas of the State that was not detected by TSA. This association represented a clear disjunct distribution between species of these areas. Although not confirmed, this pattern was suspected during the extensive survey of the mayflies conducted from 1985-1987. At that time, species known from these areas were specifically sought between the known localities, but no additional populations were found. This combined with results from cluster analysis suggests that the disjunction is real and not an artifact of collecting effort.

Understanding spatial and temporal patterns of species richness is important in assessing faunal change and in identifying areas and times that are poorly documented. MACK & GIBBS (1991), provided the first such assessment of mayflies in Maine by reviewing the changes in the mayfly fauna of Mount Desert Island. The overall pattern of species richness presented here showed the area of highest species richness was located in central Maine; the epicenter close to the University of Maine at Orono. The gradual reduction in species richness outward from this area (decreasing with increasing distance from Orono) suggests that the high species richness recorded for this area may be related more to a greater sampling effort in the vicinity of the University and that much of Maine is still in need of intensive study. This is especially true in the far northern and southwestern areas of the state. However, some areas well away from the University have been well collected. For example, the central Moosehead Plateau and Mount Desert Island. Although only a few sites have been sampled in eastern Aroostook County indications from analyses presented in this paper suggest that this area holds a unique mayfly fauna and should be more broadly sampled. Equally in need of study are the areas south of the River Kennebec. Most of this part of Maine has 10 or fewer species records.

Spatial patterns of species richness for major landscape divisions illustrated, on a finer scale, the same general trends typical of the entire state. However, when numbers of sites per region are considered with species counts a clearer understanding of the general pattern is possible. Biophysical regions 5 and 10 had the same number of species (i.e., 95), but the number of sites sampled in region 10 was more than double those sampled in region 5. Further both region 5 and 10 had comparable surface areas of 10726.01 and 9762.06 km^2, respectively. Considering these results with regards to sampling effort and total area it seems that the same number of sites need not be sampled in all areas to record most species present. Although area measurements were not available for climatic zones, a sites/species relationship similar to that observed for biophysical regions was detected for climatic zones 5 and 7. Drainage systems 2 and 3 showed a similar, but slightly reversed sites/species relationship. In drainage 2 fewer species were recorded from a greater number of sites compared to drainage 3, which had a greater overall species diversity. Based on counts from all landscape areas it seems that the detection of maximal species richness was achieved between 56 and 66 sites. This suggests a general number of sites necessary for estimating maximal species richness of under sampled areas, providing sites are distributed among a variety of habitat types.

Temporal patterns of overall species richness combined with counts of different sites sampled per month showed that greater sampling effort corresponded with higher numbers of species recorded during months of June and July. Number of sites sampled in May was only slightly less than June, but 40 fewer species were recorded compared with June. Despite this difference it is difficult to determine if the numbers of sites recorded for June and July represent numbers necessary to estimate maximal monthly species richness because earlier months and later months will likely contain larvae of many genera that cannot be identified to species regardless how many sites are sampled. Temporal patterns of species richness for families of mayflies with more than a few species parallel overall temporal patterns. Families represented in Maine by only one or a few species had a dispersed pattern without a distinct temporal peak. This is most likely related to the relative ease of recognizing larvae to species compared to the difficult task of doing this in some species rich families.

The interpretation of so called rare or regionally restricted species is difficult when complete geographic coverage is lacking. Most of the species listed as restricted were only recorded at one or a few sites and are considered rare with regards to their occurrence in the species database, but not necessarily with regards to their true distribution. Currently, it is best to consider the status of these species as uncertain pending additional sampling. Details of the biology and ecology of several of these species are unknown or poorly known making it difficult to identify potential habitats to sample. Recently, two species with rare occurrences in western Maine were unexpectedly collected in coastal eastern Maine (BURIAN *et al.*, 1995).

In conclusion, it is clear that much work remains to be done to achieve a reasonably complete landscape-level understanding of the mayfly fauna of Maine. Although enough data are available to detect broad landscape patterns, many areas need to be more extensively sampled to fill in the gaps in the current database. Analyses presented here suggest that environmental variables largely unconstrained by landscape features may be the key to understanding mayfly distributions. More intensive multivariate ecological studies should be conducted to test species-environment relationship inferred here. Patterns of species richness for the entire State and landscape divisions should provide a good starting point for planning future studies of the diversity of mayflies in Maine and for tracking changes of the fauna of currently well sampled areas.

ACKNOWLEDGEMENTS

I would like to thank Dr. K.E. Gibbs for her help and support during the initial data collection phase of this project. I would like to thank all those individuals who contributed species records, especially Terry Mingo who compiled many of the early species records. Technical support, computer facilities and research release time was provided by the Department of Biology, Southern Connecticut State University. Information on landscape divisions was provided by Bill Duffy of the Maine State Office of G.I.S.

REFERENCES

BRIGGS, R.D. & LEMIN, R.C., JR. 1992. Delineation of climatic regions in Maine. Can. J. For. Res. 22: 801-811.

BURIAN, S.K. 1990. The Mayflies (Ephemeroptera) of Maine: A Faunal Survey, Part 1 and Taxonomy of the Leptophlebiidae, Potamanthidae, Polymitarycidae, and Ephemeridae, Part 2. Ph.D. Dissertation, Univ. of Maine, Orono, Maine. U.S.A. 409 p.

BURIAN, S.K. 1995. Taxonomy of the eastern Nearctic species of *Choroterpes* EATON (Ephemeroptera: Leptophlebiidae). *In*: CORKUM, L.D. & CIBOROWSKI, J.H. (Eds), pp. 433-453. Current directions in research on Ephemeroptera. Canadian Scholar's Press, Inc., Toronto.

BURIAN, S.K. & GIBBS, K.E. 1991. The Mayflies of Maine: An Annotated Faunal List. Maine Agricultural Experiment Stat. Tech. Bull 142. 109 p.

BURIAN, S.K., BLACKBURN, K.A. & JUENTES-MOLACK, L. 1995. An update on the occurrence of three species of mayflies (Ephemeroptera) in Maine. Maine Nat. 3: 49-54.

CORKUM, L.D. 1989. Patterns of benthic invertebrate assemblages in rivers of northwestern North America. Freshwater Biol. 21: 191-205.

CORKUM, L.D. 1990. Intrabiome distributional patterns of lotic macroinvertebrate assemblages. Can. J. Fish. Aquat. Sci. 47: 2147-2157.

CORKUM, L.D. & CIBOROWSKI, J.J.H. 1988. Use of alternative classifications in studying broad-scale distributional patterns of lotic invertebrates. J. N. Am. Benthol. Soc. 7: 167-179.

DICE, L.R. 1945. Measures of the amount of ecologic association between species. Ecology 26: 297-302.

FUNK, D.H. & SWEENEY, B.W. 1994. The larvae of eastern North American *Eurylophella* (Ephemeroptera: Ephemerellidae). Trans. Am. Entomol. Soc. 120: 209-286.

FURSE, M.T., MOSS D., WRIGHT, J.F. & ARMITAGE, P.D. 1984. The influence of seasonal and taxonomic factors on the ordination and classification of running water sites in Great Brittain and on the prediction of macroinvertebrate communities. Freshwater Biol. 14: 257-280.

GAUCH, H.G., JR. 1982. Multivariate analysis in community ecology. Cambridge Univ. Press, New York. 298 p.

HILL, M.O. 1979. TWINSPAN-A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individual attributes. Cornell Univ., Ithaca, New York. 60 p.

HUGHES, R.M., REXSTAD, E. & BOND, C.E. 1987. The relationship of aquatic ecoregions, river basins and physiographic provinces to ichthyogeographic regions of Oregon. Copeia 2: 423-432.

MACK, R.G. 1988. Faunal Survey and Observed Biology of the Mayflies of Acadia National Park. M.S. Thesis, University of Maine, Orono, Maine. U.S.A. 102 p.

MACK, R.G. & GIBBS, K.E. 1991. Mayflies of Acadia National Park, Maine, U.S.A. *In*: ALBA-TERCEDOR, J. & SANCHEZ-ORTEGA, A. (Eds) Overview and Strategies of Ephemeroptera and Plecoptera, pp. 277-287, Sandhill Crane Press, Inc., Gainesville, Florida.

MCCAFFERTY, W.P. & WALTZ, R.D. 1990. Revisionary synopsis of the Baetidae (Ephemeroptera) of North America. Trans. Am. Entomol. Soc. 116: 769-799.

MCCAFFERTY, W.P. & WALTZ, R.D. 1995. *Labiobaetis* (Ephemeroptera: Baetidae): new status, new North American species, and related new genus. Entomol. News. 106: 19-28.

MCCAFFERTY, W.P. & WANG, T-Q. 1994. Phylogenetics and the classification of the *Timpanoga* complex (Ephemeroptera: Ephemerellidae). J. N. Am. Benthol. Soc. 13: 569-579.

MCCAFFERTY, W.P., WIGLE, M.J. & WALTZ, R.D. 1994. Systematics and biology of *Acentrella turbida* (MCDUNNOUGH) (Ephemeroptera: Baetidae). Pan-Pacific Entomol. 70: 301-308.

MCMAHON, J.S. 1990. The Biophysical Regions of Maine: Patterns in the Landscape and Vegetation. M.S. Thesis, University of Maine, Orono, Maine. U.S.A. 119 p.

ROHLF, J.F. 1992. NTSYS pc, Numerical taxonomy and multivariate analysis system (version 1.70). Exeter Software, Setauket, New York.

SMILAUER, P. 1990. CANODRAW-A companion program to CANOCO for publication-quality graphical output (version 2.10). Microcomputer Power, Ithaca, New York. 33 p.

TER BRAAK, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167-1179.

TER BRAAK, C.J.F. 1990. CANOCO-A FORTRAN program for canonical community ordination by partial detrended canonical correspondence analysis, principal components analysis, and redundancy analysis (version 3.10). Agricultural and Mathematics Group, Wageningen. The Netherlands. 35 p.

Appendix 1. Explanation of environmental variables used in CCA.

Environmental Variables	CCA Code	Units	Notes
Water Temperature	TEMP	°C	
pH	pH	Std. Units	
Specific Conductance	SCOND	µohms cm^{-1} @ 25 °C	
Mean Depth	DEPTH	meters	1
Mean Current Velocity	VEL	m sec^{-1}	2
Site Elevation	ELEV	meters	
Habitat Type	HABTYPE	Eleven Categories	3
Aquatic Vegetation	AQVEG	Two Categories	4
Substrate Type	SUBTYPE	Six Categories	5
Drainage Basin	BASIN	Eight Categories	6

1. For a wadable stream, mean was determined by three measurements, one at midchannel and the other two about one meter from each bank. For small pools and brooks less than one meter wide, three-five measurements were used. For ponds, lakes, and deep rivers, three measurements were used at the location where the sample was taken.
2. Mean of three-five measurements made at midchannel just below the surface of the water.
3. Habitat units were: 1: lotic first-second order streams; 2: lotic second-third order streams; 3: lotic third-fourth order streams; 4: fourth and larger order streams; 5: river/lake confluence; 6: marsh/flowage; 7: cold forest pools/small spring brooks; 8: pond/lake outlet; 10: ponds/lakes; 11: marsh streams.
4. Aquatic vegetation units were: 1: submerged or emergent or floating-leaf plants present; 0: aquatic plants absent except for periphyton.
5. Aquatic substrate units were: 1: lakes (littoral zones), coarse large particles with some fines; 2: lakes (littoral zones), few coarse large particles, mostly fines and organic detritus; 3: marshes, mostly muck composed of fine mineral particles and organic detritus; 4: lotic, erosional, mostly large to medium coarse particles intermixed with a variety of smaller particles, few fines; 5: lotic bedrock with boulders and large coarse particles, few fines; 6: lotic depositional, mostly small fines and organic detritus with few large particles.
6. Drainage basin units were: 1: St. John; 2: St. Croix; 3: Penobscot; 4: Kennebec; 5: Androscoggin; 6: Presumpscot; 7: Saco; 8: Piscataqua.

Appendix 2. List of species codes and full species names used in CCA. Asterisk indicates species whose names were changed after the code list was constructed.

1 AME LIN *Ameletus lineatus*
2 AME TER *Ameletus tertius*
3 SIP AER *Siphlonisca aerodromia*
4 SIP ALT *Siphlonurus alternatus*
5 SIP BAR *Siphlonurus barbaroides*
6 SIP DAM *Siphlonurus damarayi*
7 SIP MAR *Siphlonurus marginatus*
8 SIP MIR *Siphlonurus mirus*
9 SIP QUE *Siphlonurus quebensis*
10 SIP NSP *Siphlonurus* n.sp
11 SIP RAP *Siphlonurus rapidus*
12 SIP SEC *Siphlonurus securifer*
13 SIP TYP *Siphlonurus typicus*
14 ACE AMP *Acentrella ampla*
15 ACE CAR *Acentrella turbida**
16 ACE MAC *Acerpenna macdunnoughi*
17 ACE PYG *Acerpenna pygmaea*
18 BAE ARM *Baetis armillatus*
19 BAE BRU *Baetis brunneicolor*
20 BAE CIN *Baetis cinctutus*
21 BAE DUB *Baetis dubius*
22 BAE FLA *Baetis flavistriga*
23 BAE FRO *Labiobaetis frondalis**
24 BAE INT *Baetis intercalaris*
25 BAE PLU *Baetis pluto*
26 BAE PRO *Labiobaetis propinquus**
27 BAE PUN *Baetis punctiventris*
28 BAE TRI *Baetis tricaudatus*
29 BAE VET *Baetis veteris*
30 BAE VIR *Baetis virile*
31 CAL FER *Callibaetis ferrugineus*
32 CAL FLU *Callibaetis fluctuans*
33 CAL PRE *Callibaetis pretiosus*
34 CEN SEM *Centroptilum semirufum*
35 CEN TRI *Centroptilum triangulifer*
36 DIP HAG *Diphetor hageni*
37 HET CUR *Heterocloeon curiosum*
38 PRO ALB *Procloeon album*
39 PRO BEL *Procloeon bellum*
40 PRO CON *Procloeon convexum*
41 PRO IGE *Procloeon ingens*
42 PRO OZB *Procloeon ozburni*
43 PRO RIV *Procloeon rivulare*
44 PRO RUB *Procloeon rubropictum*
45 PRO RUF *Procloeon rufostrigatum*
46 PRO SIM *Procloeon simplex*
47 SIP BAS *Siphloplecton basale*
48 SIP NSA *Siphloplecton* n. sp.
49 ISO BIC *Isonychia bicolor*
50 ISO OBS *Isonychia obscura*
51 ART BIP *Arthroplea bipunctata*
52 CIN SUB *Cinygmula subaequalis*
53 EPE FRA *Epeorus fragilis*
54 EPE PLE *Epeorus pleuralis*
55 EPE VIT *Epeorus vitreus*
56 HET PUL *Heptagenia pulla*
57 LEU APH *Leucrocuta aphrodite*
58 LEU HEB *Leucrocuta hebe*
59 LEU MAC *Leucrocuta maculipennis*
60 LEU WAL *Leucrocuta walshi*
61 NIX HOR *Nixe horrida*
62 NIX PER *Nixe perfida*
63 RHI IMP *Rhithrogena impersonata*
64 RHI JEJ *Rhithrogena jejuna*
65 RHI PEL *Rhithrogena pellucida*
36 STE INT *Stenacron interpunctatum*
67 STE ITH *Stenonema ithaca*
68 STE LUT *Stenonema luteum*
69 STE MED *Stenonema mediopunctatum*
70 STE MOD *Stenonema modestum*
71 STE TER *Stenonema terminatum*
72 STE VIC *Stenonema vicarium*
73 CHO BAS *Choroterpes basalis*
74 HAB VIB *Habrophlebia vibrans*
75 HAB AME *Habrophlebiodes americana*
76 LEP CUP *Leptophlebia cupida*
77 LEP INT *Leptophlebia intermedia*
78 LEP JOH *Leptophlebia johnsoni*
79 LEP NEB *Leptophlebia nebulosa*
80 PAR ADO *Paraleptophlebia adoptiva*
81 PAR DEB *Paraleptophlebia debilis*
82 PAR GUT *Paraleptophlebia guttata*
83 PAR MOL *Paraleptophlebia mollis*
84 PAR STR *Paraleptophlebia strigula*
85 PAR VOL *Paraleptophlebia volitans*
86 ANT DIS *Anthopotamus distinctus*
87 EPH LEU *Ephoron leukon*
88 EPH GUT *Ephemera guttulata*
89 EPH SIM *Ephemera simulans*
90 EPH VAR *Ephemera varia*
91 LIT REC *Litobrancha recurvata*
92 HEX LIM *Hexagenia limbata*
93 ATT ATT *Attenella attenuata*
94 DAN SIM *Timpanoga simplex**
95 DRU COR *Drunella cornuta*
96 DRU COU *Drunella cornutella*
97 DRU LAT *Drunnella lata*
98 DRU TUB *Drunella tuberculata*
99 DRU WAL *Drunella walkeri*
100 EPH AUR *Ephemerella aurivillii*
101 EPH DOR *Ephemerella dorothea*
102 EPH INV *Ephemerella invaria*
103 EPH NEE *Ephemerella needhami*
104 EPH ROT *Ephemerella rotunda*
105 EPH SEP *Ephemerella septentrionalis*
106 EPH SUB *Ephemerella subvaria*
107 EUR AES *Eurylophella aestiva*
108 EUR BIC *Eurylophella bicolor*
109 EUR COX *Eurylophella coxalis*
110 EUR FUN *Eurylophella funeralis*
111 EUR MIN *Eurylophella minimella*
112 EUR PRU *Eurylophella prudentalis*
113 EUR TEM *Eurylophella temporalis*
114 EUR VER *Eurylophella verisimilis*
115 SER DEF *Serratella deficiens*
116 SER SER *Serratella serrata*
117 SER SEA *Serratella serratoides*
118 TRY ALL *Trycorythodes allectus*
119 TRY ATR *Trycorythodes atratus*
120 TRY MIN *Trycorythodes minutus*
121 BRA LAC *Brachycercus lacustris*
122 CAE AMI *Caenis amica*
123 CAE DIM *Caenis diminuta*
124 CAE LAT *Caenis latipennis*
125 CAE PUN *Caenis punctata*
126 CAE TAR *Caenis tardata*
127 BAE CAR *Baetisca carolina*
128 BAE LAU *Baetisca laurentina*
129 BAE RUB *Baetisca rubescens*