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BIODIVERSITY OF MINNESOTA CADDISFLIES (INSECTA: TRICHOPTERA)

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DAVID CHARLES HOUGHTON

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Ralph W. Holzenthal, Advisor

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ABSTRACT

Over 300,000 caddisfly specimens were examined based on 317 light trap samples collected during 1999-2001, and from museum records. Two hundred-eighty four caddisfly species were determined to occur in Minnesota, representing 20 families and 74 genera. The relative occurrence in different regions, habitat types, and levels of upstream disturbance is documented for each species.

Detrended Correspondence Analysis and a UPGMA dendogram of caddisfly relative abundance data from 58 Minnesota watersheds delineated five regions of caddisfly biodiversity. Caddisfly species richness and diversity were significantly highest in the Lake Superior and Northern regions, lowest in. the Northwestern and Southern regions, and intermediate in the Southeastern region. These determined regions had nearly double the classification strength of a priori ecological regions or watersheds in partitioning the natural variation of the caddisfly fauna. Classification strength also decreased with increasing spatial scale and decreasing taxonomic resolution.

Canonical Correspondence Analysis found that temperature, percentage of disturbed habitat, and stream gradient were related to caddisfly species composition, although the correlation between temperature and disturbed habitat made determination of the relative importance of those variables difficult. Caddisfly species richness correlated negatively with percentage of disturbed upstream habitat for small and medium-sized streams in the Northern, Northwestern, and Southern regions.

Change in the composition of trophic feeding groups based on habitat type generally followed a pattern predicted by the river continuum concept in the Lake Superior, Northern, and Southeastern regions, whereas fine particle filtering collectors dominated all sizes of lakes and streams in the Northwestern and Southern regions. Binomial regression analysis determined three fine particle filtering collectors as indicators of habitat disturbance-particularly that of lakes and small streams- independent of other environmental variables.

Although the absence of historical data makes it difficult to separate the relative importance of natural and anthropogenic factors, loss of caddisfly biodiversity and homogenization of feeding ecology has probably occurred in at least the Northwestern and Southern regions due to human disturbance. With baseline data now in place, potential future changes can be evaluated with greater confidence.

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CHAPTER I

INTRODUCTION

Biodiversity Research. Baseline organismal biodiversity research is necessary for an understanding of ecosystem ecology, organism conservation, and cladistic biogeography (Readka-Kudla et al. 1997, McKamey 1999, Mickevich 1999, Solis 1999). The conservation aspect of this type of research is becoming increasingly important due to a measured decline in worldwide organismal biodiversity and concern over the potential ecological implications of this decline (e.g., Readka-Kudla et al. 1997). Biodiversity databases include both organismal distribution data and the environmental data associated with such distributions. These data are crucial to proposing hypotheses on the factors contributing to organismal biodiversity, particularly changes in biodiversity over time (Mickevich 1999).

Documenting the biodiversity of insects is of particular importance due to the species richness of the group and the general lack of knowledge about insects relative to less diverse groups such as birds or mammals (Wheeler 1990, Mickevich 1999). Documenting the biodiversity of aquatic insects takes on yet an additional measure of importance due to the utility of the group in water quality biomonitoring. In this technique, taxonomic data are collected from an aquatic habitat and combined with known information on the pollution tolerance, habitat affinity, and trophic functional group of individual taxa to assess potential habitat disturbances (e.g., Rosenberg and Resh 1993, Karr and Chu 1999). Documenting these data for specific aquatic insect taxa in different areas, therefore, is necessary to refine water quality biomonitoring techniques.

Overview of the Caddisflies. The caddisflies (Trichoptera) are an order of holometabolous insects found on every continent except Antarctica. Larvae are aquatic and occupy virtually all types of freshwater ecosystems. There are currently approximately 10,000 species of caddisflies known from the world (Morse 2002) with many new species being described every year, primarily from the Neotropical and Oriental regions (e.g., Flint 1991, Malicky and Chantaramongkol 1999).

The scientific name of the caddisflies *(Trichos* = hair, *optera = wing)* refers to the covering of unmodified setae over the wing surfaces of most species. This characteristic allies the caddisflies phylogenetically with the Lepidoptera ("scale-wings"). Unlike Lepidoptera (butterflies and allies), whose scales are often configured into elaborate and colorful patterns, caddisfly adults tend towards drab coloration. Caddisfly adults, as well as other life stages of the order, are often mimicked by the artificial lures of fly-fishers who attempt to imitate caddisfly emergences during trout fishing (LaFontaine 1981, McCafferty 1981).

Caddisflies are probably best known for their ability as larvae to produce silk from modified glands of the labium. This silk is used to attach together various combinations of mineral and organic materials, and construct portable cases and stationary retreats. These structures can be simple portable tubes, "saddle-cases" that superficially resemble tortoise shells, silken purses, fixed retreats with attached silken filter nets, and even helical cases that closely resemble snail shells (Wiggins 1996a). The ability of the order to utilize silk to produce these structures is thought to be an important factor contributing to their ecological success as it allows them to fill different niches (Mackay and Wiggins 1979). Caddisflies are important in aquatic ecosystems as secondary producers, cycling nutrients and being preyed upon by insectivorous fish and other animals (Rhame and Stewart 1976, Wiggins and Mackay 1978, Benke and Wallace 1980, Ross and Wallace 1983, Robison and Buchanan 1988, Wiggins 1996a, b).

Among aquatic insects caddisflies exhibit taxonomic richness and ecological diversity. The order contains almost as many North American species (1,556) as do the Ephemeroptera (836), Plecoptera (577), Odonata (380), and Megaloptera (46)-the other wholly aquatic insect orderscombined (Merrit and Cummins 1996). Among the five major trophic functional groups: gathering collectors, filtering collectors, predators, scrapers, and shredders, the caddisflies exhibit a greater ecological diversity than the other aquatic orders, all of which are dominated by one or two trophic groups (Figure 1.1) (Merrit and Cummins 1996). There are, however, some aquatic families of Diptera that may surpase the Trichoptera in taxonomic richness and aquatic diversity (Merrit and Cummins 1996).

Due to the taxonomic richness and ecological diversity of the cadisflies, along with their varying susceptibilities to pollution and abundance in virtually all freshwater ecosystems, the order has high potential value as a water quality biomonitoring taxon (Mackay and Wiggins 1979, Rosenberg and Resh 1993, Merritt and Cummins 1996, Barbour et al. 1999, Dohet 2002). The ability to predict specific caddisfly assemblages in specific aquatic ecosystems, therefore, will likely improve water quality biomonitoring techniques. The state of Minnesota contains a rich diversity of aquatic ecosystems, including over 10,000 natural lakes, several thousand kilometers of streams of various sizes and gradients, and several thousand acres of wetlands (e.g., Tester 1995). It is crucial, therefore, that the biodiversity of aquatic organisms such as caddisflies is understood so that science-based decisions can be made on Minnesota water quality management.

Previous Caddisfly Taxonomic Research. In most of the United States and adjacent Canadian provinces caddisflies are either barely known, or known from only a basic species checklist (Figure 1.2). Comprehensive treatments of the Alabama (Harris et al. 1991), California (Denning 1956), Illinois (Ross), New York (Betten 1934), and North and South Carolina (Unzicker et al. 1982) faunas provide good anecdotal information about the distributions and habitat affinities of the caddisflies within those areas. They do not, however, rigorously evaluate hypotheses on the important environmental variables affecting overall caddisfly distribution patterns in those regions. Only Moulton and Stewart's (1996) study of the caddisflies of the Interior Highlands of North America-primarily Arkansas and Missouri-assessed caddisfly distribution data 'With modern statistical methods. That study determined two regions of caddisfly biodiversity corresponding to the Ozark and Oachita ranges and ascertained that latitude, geology, and the presence of high-volume springs were the most important variables affecting caddisfly distributions within the studied region.

Within the northcentral U.S. and southcentral Canada, Ross' (1944) study of the Illinois fauna remains the only comprehensive faunal treatment of the caddisflies. Basic checklists are available for the Indiana (Waltz and McCaffery 1985), Manitoba

(Flannagan and Flannagan 1982), Minnesota (Houghton et al. 2001), North Dakota (Harris et al. 1980), and Wisconsin (Longridge and Hilsenhoff 1973) faunas (Figure 1.2). None of these studies attempted to address relationships between caddisfly distributions and environmental conditions.

Caddisfly taxonomic research in Minnesota has generally been that of non-comprehensive individual studies (Figure 1.3). Elkins (1936) published the first study of Minnesota caddisflies, documenting 31 species and hypothesizing that the fauna may include "at least 100 species". Papers mainly by Ross (1938a, b, 1941 a, b, 1944, 1946, 1947, 1950, 1956) and Denning (1937, 1941, 1942, 1943, 1947a, b, c) in the middle part of the 1900s reported an additional 118 species. Etnier (1956) published the first comprehensive checklist of the fauna, documenting 208 species. In the latter portion of the 1900s, regional taxonomic studies (Etnier 1968, Lager et al. 1979, Phillippi and Schuster 1987, MacLean 1995, Monson 1997), generic and familial revisions (Nimmo 1971, Morse 1972, Denning and Blickle 1972, Schuster and Etnier 1978, Blickle 1979, Nimmo 1986), and new species descriptions (Wiggins 1975, Monson and Holzenthal 1993, Sykora and Harris 1994) added an additional 48 species to the known fauna.

Houghton et al. (2001) updated the checklist of Minnesota caddisflies, documenting a total of 284 species including 28 new state species records, and removing 21 doubtful species. They reported known species based on five geographic areas and found that the northeastern and southeastern areas of the state appeared to have the highest levels of caddisfly biodiversity relative to their areas. They hypothesized that relative statewide biodiversity was probably affected by both historical and contemporary factors. Beyond this, no attempt has been made to document the biodiversity and distribution patterns of Minnesota caddisflies or to test hypotheses on the factors contributing to these patterns.

Study Objectives. This research had five main objectives: (1) inventory the caddisflies of Minnesota to ascertain the distributions of all species and group these distributions into overall regions; (2) compare the biological diversity and trophic functional group ecology of the caddisflies of these determined regions; (3) determine the environmental variables potentially important to influencing overall caddisfly distribution patterns (4); compare the classification strength of determined caddisfly regions with those of other geographic classifications such as ecological region and watershed, while also considering the effects of spatial scale and taxonomic resolution; and (5) document the affinities of individual species with habitat type and level of anthropogenic disturbance. Collectively, such results will establish the baseline data for Minnesota caddisflies needed to evaluate potential future changes to the fauna, and refine the use of caddisflies in biological water quality assessment, both in Minnesota and in adjacent states and provinces. Objectives 1-3 are covered in Chapter 2 and the last two in Chapters 3 and 4, respectively.

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Figure 1.1. Comparison of the percent of genera of the five wholly aquatic insect orders in five trophic functional groups (Merrit and Cummins 1996). Number of genera in parentheses. GC = Gathering Collectors, FC = Filtering Collectors, PR = Predators, SC = Scrapers, SH = Shredders.

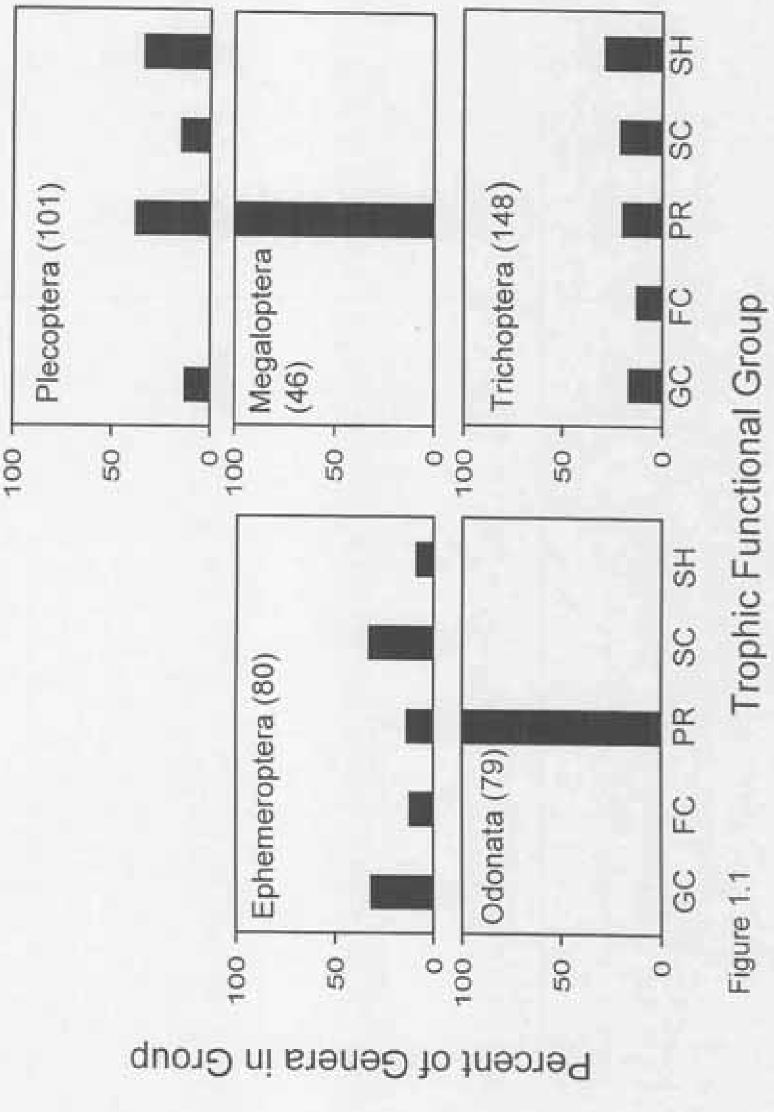
Percent of Genera in Group
Trophic Functional Group
Ephemeroptera (80)
Odonata (79)
Plecoptera (101)
Megaloptera (46)
Trichoptera (148)
100
50
0
GC
FC
PR
SC
SH

Figure 1.1

Figure 1.2. Caddisfly taxonomic studies of the United States and adjacent Canadian provinces (Wiggins 1996b). White areas = piecemeal studies or none at all, light grey = basic species checklist, dark grey = faunal study.

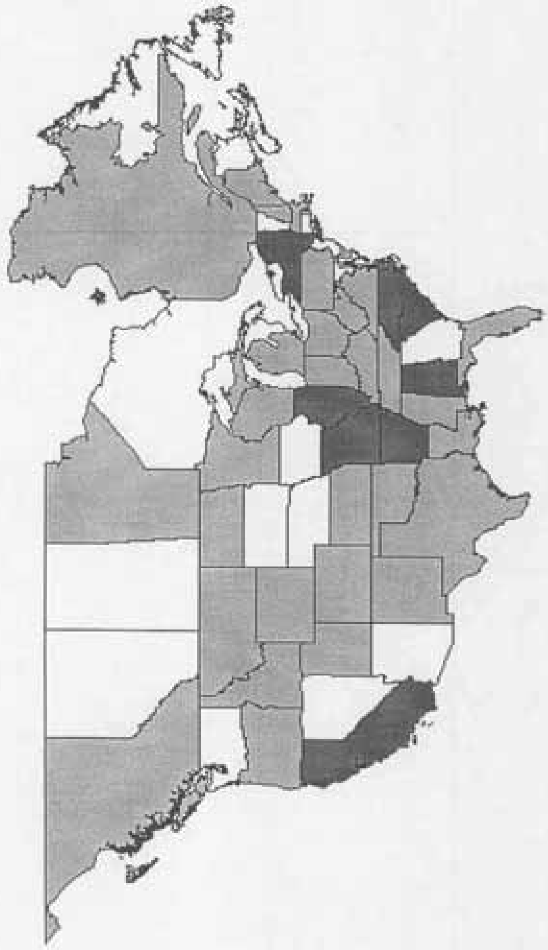

Figure 1.2

Figure 1.3. Progression of Minnesota caddisfly discovery from 1930 to 2001.

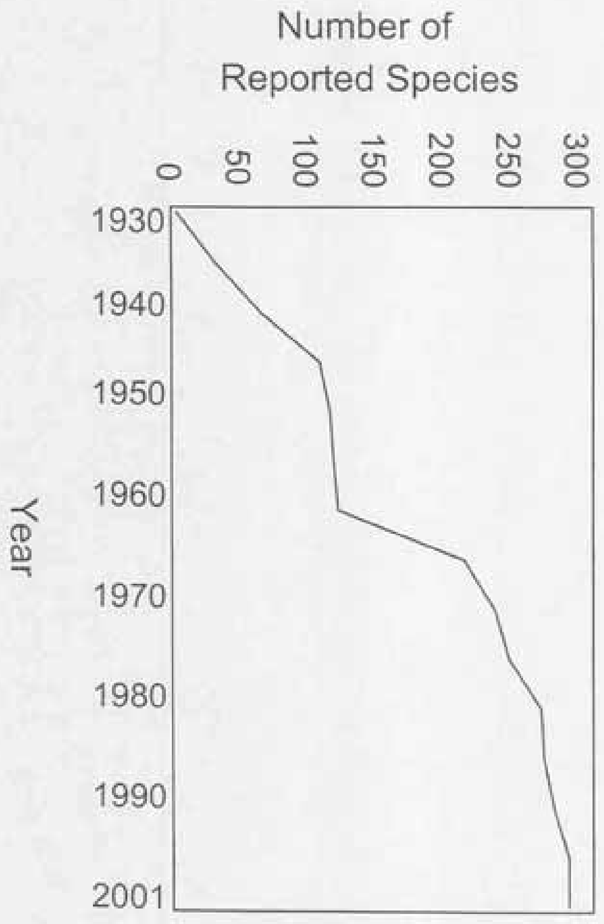
Number of
Reported Species
0
50
100
150
200
250
300
1930
1940
1950
1960
1970
1980
1990
2001
Year

Figure 1.3

CHAPTER 2

DELINEATION AND CHARACTERIZATION OF MINNESOTA CADDISFLY REGIONS

ABSTRACT

Over 300,000 adult caddisfly specimens representing 224 species were collected and analyzed from samples of 248 Minnesota aquatic habitats within 58 watersheds. Detrended Correspondence Analysis and a flexible unweighted pair-group method using arithmetic averages (UPGMA) dendogram of caddisfly relative abundance data determined that five regions of caddisfly exist within the state. Species richness and diversity were significantly highest in the Lake Superior and Northern regions, lowest in the Northwestern and Southern regions, and intermediate in the Southeastern region. Canonical Correspondence Analysis determined that caddisfly species composition was related to temperature, percentage of disturbed habitat, and stream gradient. A strong correlation between temperature and percentage of disturbed habitat made determination of the relative importance of those variables difficult. Caddisfly species richness in small and medium-sized streams correlated negatively with percentage of disturbed upstream habitat in the Northern, Northwestern, and Southern regions. Change in the composition of trophic functional groups based on habitat type generally followed a pattern predicted by the river continuum concept in the Lake Superior, Northern, and Southeastern regions, whereas fine particle filtering collectors dominated all sizes of lakes and streams in the Northwestern and Southern regions. Although the absence of historical data makes it difficult to separate the relative importance of natural and anthropogenic factors, loss of

caddisfly biodiversity and homogenization of feeding ecology has probably occurred in at least the Northwestern and Southern regions due to human disturbance.

INTRODUCTION

Anthropogenic disturbance of freshwater lakes and streams is one of the largest environmental problems currently facing both Minnesota and much of the United States (Heiskary and Wilson 1989,1990; Tester 1995; Karr and Chu 1999). Quantifying the composition of aquatic organism assemblages-such as those of phytoplankton, insects, or fish-is a powerful technique for evaluating aquatic disturbance because it directly measures ecosystem function (e.g., Rosenberg and Resh 1993, Karr and Chu 1999). An array of water quality metrics using aquatic organism data has, therefore, been developed (Barbour et al. 1999). These metrics use taxonomic data collected from a site, coupled with known information on each organism's pollution tolerance, habitat affinity, and trophic functional group, to assess the nature of potential habitat disturbance of the collection site (e.g., Rosenberg and Resh 1993, Karr and Chu 1999).

The caddisflies (Trichoptera) have potential value for aquatic biomonitoring due to their taxonomic richness, ecological diversity, abundance in virtually all types of freshwater ecosystems, and varying susceptibilities to different types of aquatic disturbances (Mackay and Wiggins 1979, Resh 1993, Rosenberg and Resh 1993, Merritt and Cummins 1996, Barbour et al. 1999, Dohet 2002). Unfortunately, only six North American studies (Betten 1934, Ross 1944, Denning 1956, Unzicker et al. 1982, Harris et al. 1991, Moulton and Stewart 1996) have thoroughly assessed the caddisflies of any region. Of these, only Moulton and Stewart's (1996) study of the caddisflies of the Interior Highlands region of the United States attempted to quantify environmental factors for their potential to influence caddisfly distribution patterns. They determined that two regions of caddisfly biodiversity corresponded to the Ozark and Oachita ranges, and concluded that latitude, geology, and the presence of high-volume springs were important factors affecting regional caddisfly distributions and diversity.

Aside from Ross' (1944) landmark study of the Illinois species, the caddisflies of the northcentral U.S. and southcentral Canada are known only from basic checklists of the Indiana (Waltz and McCaffery 1985), Manitoba (Flannagan and Flannagan 1982), Minnesota (Houghton et al. 2001), North Dakota (Harris et al. 1980), and Wisconsin (Longridge and Hilsenhoff 1973) faunas. None of these studies attempted to address relationships between caddisfly distributions and environmental conditions. The state of Minnesota is situated at the intersection of the three largest biotic provinces of the northcentral U.S.: Coniferous Forest, Deciduous Forest, and Prairie (Figure 2.1) (Bailey 1980). Caddisflies collected from the state may, therefore, be indicative of the northcentral U.S. as a whole. This fact makes assessment of the statewide fauna particularly important.

Houghton et al. (2001) updated the checklist of Minnesota caddisflies, documenting a total of 284 species. They reported known species based on five geographic areas and found that the northeastern and southeastern areas of the state appeared to have the highest levels of caddisfly biodiversity relative to their areas. They hypothesized that relative statewide biodiversity was probably affected by both historical and contemporary factors. Beyond this, no attempt has been made to document the biodiversity and distribution patterns of Minnesota caddisflies or to test hypotheses on the factors contributing to these patterns.

The current study had three main objectives: (1) combine distributions of the Minnesota caddisflies into overall regions; (2) compare the biological diversity and trophic functional group ecology of the caddisflies among regions; and (3) assess the environmental variables potentially important to influencing the determined caddisfly distribution patterns. Collectively, such results will establish the baseline data for Minnesota caddisflies needed to evaluate potential future changes to the fauna, and refine the use of caddisflies in biological water quality assessment, both in Minnesota and in adjacent states and provinces.

MATERIALS AND METHODS

Sampling. Several recent studies (see Hawkins et al. 2000) have determined that watershed basins are appropriate units for sampling the aquatic biota, although their classification strength tends to decrease as their size increases. To characterize spatial diversity within Minnesota, the state's 81 major watersheds were treated as primary sampling units (Figure 2.2). These watersheds are defined by all of the land area draining into a single river, except for the Lake Superior North and Lake Superior South watersheds (Nos 1 and 2 on Figure 2.2), which are actually groupings of several smaller watersheds draining directly into Lake Superior (USGS 2002). Twenty minor watersheds had at least 50% of their area outside of the state and were not sampled.

Secondary sampling units were sites within watersheds, which were divided into six constructed site classes (Table 2.1); five of the classes were based on stream width estimated from the sampling site, the sixth constituted lakes and wetlands. Site classes were not synonymous with hydrologic stream order (Strahler 1964). At least four samples were taken from most watersheds, representing one small stream (Class 1-2), one medium stream (3), one large river (4-5), and one lake or wetland (Table 1). Many watersheds had sample sizes greater than this. Watersheds lacking certain habitats, such as small streams, lakes, or large rivers had sample sizes of three.

Sampling sites were located using the Minnesota Atlas and Gazetteer (DeLorme 1994) and more detailed State Park maps. Advice from Minnesota Department of Natural Resources officials as well as area residents was also used to identify sampling sites. Sampling sites were perceived to be the least disturbed of their respective watershed and most came from State Parks, State Forests, or National Forests.

Samples of adult caddisflies were collected during June and July, the peak period of adult emergence and flight activity (Monson 1996). Adults were sampled with an ultraviolet light trap which consisted of an 8-watt portable ultraviolet light placed over a white pan filled with 70% EtOH. Traps were placed adjacent to aquatic habitats at dusk and retrieved approximately two hours after dusk. To standardize weather conditions in this study, samples were collected only if the peak daytime temperature was >22°C, dusk temperature was > 13 °C, and there was no noticeable wind or precipitation at dusk. Dispersals of adults between sampling; sites were considered unimportant, and dispersals between entire watershed sampling units even more. so (see "Discussion" for more detail on sampling strategies).

Data Entry. All specimens were identified to the species level except for some females of the Hydropsychidae, Hydroptilidae, and Polycentropodidae, which lack characters necessary for species-level identification. Such specimens were not included in any analysis. These three families were common throughout the state, so it was unlikely that the inability to identify female specimens affected statewide distribution analyses. All identified specimens were counted and entered into the relational database Biota (Colwell 1996). Each vial of specimens was affixed with a barcode label, thus allowing direct scanning into Biota, and the permanent association of all known ecological information about specimens with their unique code and number. Locality and ecological data. were exported from Biota to statistical programs. Unless otherwise mentioned, data analyses were performed using the Statistical Analysis System for Windows@ (SAS Institute .1989). All specimens collected during this study were deposited in the University of Minnesota Insect Museum (UMSP).

Species Ordination. Patterns of caddisfly biodiversity were examined with Detrended Correspondence Analysis (DCA) using the program PC-ORD for Windows@ (McCune and Medford 1997). DCA its a multivariate gradient analysis that reduces complex patterns inherent in large data sets into several determined axes of ecological interest, (e.g., Gauch 1982). Unlike other ordination techniques (e.g., Principle Components Analysis) DCA does not produce a spurious third axis based on a data arch effect, and can ordinate species and watersheds simultaneously (Gauch 1982, Kremen 1992, Kovach 1993, Palmer 1993). DCA essentially produces a plot of watersheds in "species-space", which allows visual expression of pure gradients of species assemblages, with distances between watersheds corresponding to differences in species composition (Gauch 1982, Økland 1996, Rabeni and Doisy 2000).

The DCA analysis was performed on a two-dimensional data matrix of watersheds by species relative abundance values. Relative abundances were determined by calculating the arithmetic mean of specimens per watershed for each species based on the 3-4 samples taken. Determined means for each species were then categorized for each watershed by coding 0 specimens as "0", 1-10 as "1 ", 11-100 as "2", 101-1000 as "3", and 1001-10,000 as "4". Such data coding accounted for variation in species abundance between watersheds and was a more powerful measure than simple presence or absence data (van Tongeren 1987, Magurran 1988, Feminella 2000). Because watersheds, not sample sites, were considered primary. sampling units, means were calculated before data coding. The natural differences between site. classes for each watershed were, therefore, maximized. By coding on a log10 scale, however, the effects of outlier samples often associated with light-trapping data were mitigated, as was the influence of highly abundant species (Jackson 1993, Cao et al. 1997; Anderson and Vondracek 1999, Dohet 2002). All species were weighted equally in the analysis.

A mean similarity dendogram was also computed for the same watershed by species relative abundance data matrix using a flexible unweighted pair-group method using arithmetic averages (UPGMA) algorithm in PC-ORD. UPGMA is a phenetic clustering method that calculates between-group dissimilarities as the average of all possible pairs within each group (Gauch 1982, Jongman et al. 1995, Oswood 2000). It produces a branching diagram of groups of watersheds based on caddisfly species composition,. with distances between groups expressed as percent dissimilarity (e.g., Gauch 1982). The UPGMA algorithm in PC-ORD automatically sets the base node of the tree to 0% similarity and the end nodes to 100%. Longer branch lengths indicate a greater degree of dissimilarity and suggest that clusters at the end of such long branches constitute "significant" groups (Oswood et al. 2000). The determined dendogram clarified groupings established by the DCA analysis. Delineation of regions of caddisfly biodiversity was accomplished using the output of both the DCA and UPGMA analyses.

Biodiversity Comparison. C Once regions were established, several biodiversity indices were calculated., Mean. species richness per watershed was determined for each region, as was mean species richness in each site class for each region. The number and percentage of species unique within Minnesota was calculated for each region. The Shannon diversity index (H') was calculated for each region. This is an overall representation of a species assemblage based on both species richness and proportional specimen abundance within the pooled sample (Margurran 1988). The Shannon index was calculated using Estimates for Windows® software (Colwell 1997).

Species accumulation curves were calculated for each region along with two nonparametric estimators of true regional species richness: the abundance-based coverage estimator (ACE), and the incidence-based coverage estimator (ICE) (Lee and Chao 1994). Assuming that information on undiscovered species can be found using rare species, ACE predicts the number of species that occur in a defined area based on the proportion of species in each sample with 10 or fewer specimens and ICE predicts the number of species based on the proportion of species occurring in 10 or fewer samples (Chao et al. 1993, Lee and Chao 1994, Chazdon et al. 1998). Unlike earlier nonparametric models, ACE and ICE do not appear to overestimate species richness when sample sizes are low (Chao and Lee 1992, Colwell and Coddington 1994, Chazdon et al. 1998).

Species accumulation curves, ACE, ICE, and the number of singletons-species with only one individual in all pooled samples-were calculated with EstimateS using total abundance data for all samples taken from each region. EstimateS calculates these indices by random resampling without replacement, with subsequent recalculation of indices as samples are added. Fifty random resamplings-the default setting in EstimateS-were done for each regional data set.

The modified Morista-Horn index of biotic similarity (Wolda 1983) was calculated for each region also using :Estimates. This is an estimate of ß, or differential diversity, and measures the degree of similarity between pairs of samples (Whittaker 1960, Margurran 1988). Unlike other estimators of B, the Morisita-Horn index does not appear to be strongly influenced by species richness, sample size, or highly abundant species (Wolda 1981, Wolda 1983, Margurran 1988). The mean Morisita-Horn index was calculated from species total abundance data for all pairwise sample comparisons for each region, giving an overall index of regional species heterogeneity.

Environmental Analysis. Continuous environmental variables potentially important to affecting statewide caddisfly biodiversity were assessed with Canonical Correspondence Analysis (CCA) (Ter Braak 1986, 1994), using PC-ORD. CCA is a direct multivariate gradient analysis which ordinates a main data matrix (species data) based on a multiple regression on variables of a second matrix (environmental data) (McCune and Medford 1997). Because ordination of species data is constrained by the values of the environmental data, CCA excels at determining which variables are potentially important for predicting species composition, provided meaningful environmental data are measured (Økland 1996).

The main CCA analysis matrix consisted of the same watershed by species relative abundance values as in the DCA and UPGMA analyses described earlier. The second matrix was of watersheds by the mean values of continuous environmental data for each watershed sampling unit. The following environmental variables were selected a priori as potentially important in affecting caddisfly biodiversity: latitude, longitude, annual precipitation, elevation, stream gradient, temperature, soil type, amount of disturbed habitat, and amount of habitat under agricultural cultivation.

Latitude and longitude coordinates were determined from the center of each watershed (Delorme 1994). Mean annual precipitation (Baker and Kuehnast 1978, Tester 1995) and elevation (Borchert and Yeager 1968) were determined for each watershed. The total change in watershed elevation per watershed area was considered a measure of stream gradient (Borchert and Yeager 1968, USGS 2002). The mean amount of organic carbon in the soil of each watershed (USDA 2002) was considered to be a measure of overall soil type (Buol et al. 1989). Because this study addressed landscape-level faunal changes and included aquatic habitats of differing thermal profiles in each watershed sampling unit, mean air temperature from June to August-important to warming aquatic ecosystems and, therefore, affecting species assemblages-was determined for each watershed and considered a descriptor of the overall range of aquatic ecosystem temperatures (Baker et al. 1985).

Human landuses such as agriculture, urbanization, mining, or intensive logging were determined from USGS (1999) data, and the amount occurring in each watershed sampling unit was calculated using the "Tabulate Area" function of ArcView for Windows® software (ESRI 1996). The combined area of these landuses was expressed as the percentage of disturbed habitat. This measure has been shown to be an adequate descriptor of human effect on aquatic ecosystems, even without quantification of the severity of disturbances (Meeuwing and Peters 1996, Karr and Chu 1999). Percentage of watershed area under agricultural cultivation was also determined as this is the most common landuse practice in Minnesota (USGS 1999).

Eigenvalues of the data axes determined by CCA were then correlated with species data and the determined r-values tested for significance using a Monte Carlo procedure in PC-ORD. Probability (p) values of the Monte Carlo test were estimated from the proportion of randomized runs with correlations between species and environmental values greater than or equal to the observed species-environmental data correlation of the data set (McCune and Medford 1997). CCA also reported r-values between axis scores and values of specific environmental variables. The significance of a particular environmental variable was assessed by its association with data axes (Ter Braak and Prentice 1988, Kremen 1992).

Landuse and Species Richness. To further assess the potential effects of habitat disturbance on caddisfly biodiversity, the percentage of disturbed habitat was determined for the area upstream of the sampling points of Class 2-3 streams. Small streams (Class 1) and lentic habitats were not included in the analysis due to the difficulty of determining the land area constituting upstream habitat. Large rivers (Class 4-5) were also excluded due to the imprecision of selecting the large areas constituting their upstream habitat. Class 2-3 rivers comprised almost half of all samples taken (Table 1). Also, limiting the analysis to these streams likely eliminated some of the natural variation associated with different ecosystem types (e.g., Allan 1995).

The land area upstream of each analyzed stream was determined by selecting and grouping each of the minor watersheds (USGS 2002) upstream of the site using ArcView. The amount of each landuse type (USGS 1999) occurring in each watershed group was calculated using the "Tabulate Area" function of ArcView, and the amount of land area used for agriculture, urbanization, mining, or intensive logging was considered disturbed habitat. Correlations between percentage of disturbed upstream habitat and the caddisfly species richness were determined using a Pearson Correlation test. A loss of species richness is one of the most reliable indicators of human disturbance of aquatic ecosystems, particularly when monitoring large taxonomic groups such as the Trichoptera (Ford 1989, Barbour et al. 1995, DeShon 1995, Karr and Chu 1999). Correlations were assessed for these streams in different established caddisfly regions.

Trophic Comparison. The relative abundance of five different trophic functional groups: gathering collectors, filtering collectors, shredders, predators, and scrapers, was compared between site classes of the five caddisfly regions. Larval feeding preferences were determined at the genus level based on Wiggins (1996a, b). Algal piercers were considered to be gathering collectors (Cummins and Klug 1979, Wilzbach et al. 1988). The total number of specimens within each feeding group in a sample was determined for each individual sampling site. Sampling sites were grouped into site classes within each region. The mean number of specimens per site class per region was then calculated.

Means of trophic group abundance within each region and site class were compared with One-way Analysis of Variance with a Student-Neuman-Keuls test. This analysis placed mean values into statistically distinct groups, thus the relative abundance of trophic groups within each region and site class was assessed. A trophic group was considered to have high, moderate, or low relative abundance within each region and site class based on the group in which its mean was placed. This analysis was used to compare regional ecosystem functioning based on the river continuum concept (Vannote et al. 1980, Merrit et al. 1984). While these analyses of ecosystem processing were not exhaustive without the inclusion of other aquatic invertebrate taxa, the abundance and ecological diversity of the caddisflies alone can give important information about relative ecosystem functioning (Mackay and Wiggins 1979, Rosenberg and Resh 1993, Barbour et al. 1999, Dohet 2002).

RESULTS

Samples of adult caddisflies were collected from 248 aquatic habitats in 58 Minnesota watersheds (Figure 2.2). Four samples were collected in 1989, 23 in 1999, 175 in 2000, and 46 in 2001. A total of 306,541 specimens representing 224 species were identified. This is approximately 80% of all the species known in Minnesota through historical collecting (Houghton et al. 2001).

Species Ordination. The Detrended Correspondence Analysis (DCA) suggested five clusters of watersheds based on caddisfly relative abundance (Figure 2.3). Two large clusters corresponded to the northern (28 watersheds) and southern (20) portions of Minnesota, and three smaller clusters corresponded to the Lake Superior (2), northwestern (5), and southeastern (3) portions (Table 2.2). Axes 1 and 2 had eigenvalues of 0.323 and 0.178, respectively; indicating that half of the variance in the data set was explained by these two axes (McCune and Medford 1997). Since DCA searched for the maximum possible resolution on the first two axes it is unlikely that other axes were highly informative in assessing caddisfly distributional patterns (Matthews and Robinson 1988).

These clusters were clarified by the UPGMA dendogram (Figure 2.4). It showed two groupings based on approximately 25% dissimilarity; one corresponded to the Northern and Lake Superior regions, and the other to the South, Southeast, and Northwest regions. The. two watersheds of the Lake Superior region were separated from those of the Northern region by 62% dissimilarity, confirming their status as distinct groupings. The Southern region was approximately 25% dissimilar from the Southeastern and Northwestern Regions, while the latter regions were separated by approximately 50% dissimilarity. Although the Lower Saint Croix watershed (#56) was near the Southern region in the DCA output (Figure 2.3), its placement in the similarity dendogram suggested that its proper classification was with the Southeastern region. Likewise the relatively short branch lengths (~10°/o) separating the watersheds of the Northwestern region confirmed their placement together despite some separation in Figure 2.3. Extrapolating the results to the 22 unsampled watersheds yielded Figure 2.5. Unsampled watersheds were grouped with sampled watersheds based on geographic location.

Biodiversity Comparison. The northern region the largest of the five-had the highest total caddisfly species richness (197 species), followed by the South (110), Lake Superior (107), Southeast (73), and Northwest (52) regions (Table 2.2). The Lake Superior (74) and Northern (73) regions had the highest mean number of species per watershed sampling unit, the South (31) and Northwest (27) regions the lowest, and

Southeast (47) had an intermediate mean (One-way Analysis of Variance with Students Neuman-Keuls test, $p < 0.001$) (Table 2.2). The number of species caught per watershed did not correlate with watershed area (Pearson Correlation Test, $p = 0.35$). There was no significant difference in the mean number of species caught per watershed between the areas of the Prairie and Deciduous Forest biotic provinces within the Southern region (Student's t-test, $p = 0.49$). As a portion of total species richness, the Northern region had the highest level of unique species (25% of total species), followed by the Lake Superior (13), South (7), Southeast (4), and Northwest (0) (Table 2.2).

The Northern region had relatively high species richness (30-50 species) in all but Class 1 streams, with steadily increasing diversity in larger streams (Figure 2.6). The Lake Superior region exhibited its highest diversity (~30) in medium sized streams (Figure 2.6). The South, Southeast, and Northwest regions all averaged less than 20 species in all site classes, and there was no discernible trend towards higher or lower species richness in any particular site class (Figure 2.6). The Lake Superior Region had the lowest mean modified Morisita-Horn index of biological similarity (0.14), the Northwest region had the highest (0.37), and the Southeast (0.21), North (0.21), and South (0.24) regions had an intermediate mean (One-way Analysis of Variance with Students-Neuman-Keuls test, $p < 0.001$) (Table 2.2). The Northern region had the highest Shannon diversity index (3.7 $\log_e$ units) followed by the Lake Superior (3.4), Southeastern (3.0), Southern (2.9), and Northwestern (2.3) (Table 2.2)

All five regions exhibited the same trends in species accumulation and richness based on the scale at which they were graphed (Figure 2.7). All five species accumulation curves appeared to be asymptotic or nearly so; all singleton curves were level or decreasing slightly; and both :richness estimators followed the same asymptotic pattern as the species curve for all regions. These patterns suggested that sampling effort in each region was sufficient to recover the majority of species diversity (e.g., McKamey 1999). The initial rise of ICE on all graphs was due to the high number of species with only one individual-the singleton curve-relative to the total number of samples. ICE leveled off as samples were added.

Environmental Analysis: Canonical Correspondence Analysis (CCA) detected two axes with significant correlations between species assemblages and environmental data (Table 2.3). A third determined axis was not significant. As these axes explained over half of the variance in the species matrix, it is unlikely that additional axes would have been highly informative (Table 2.3) (McCune and Medford 1997). Axis 1 correlated most strongly with percent disturbed habitat (r = 0.864), temperature (0.854), percent agricultural habitat (0.851), latitude (-0.549), and soil type (0.502), and axis 2 with stream gradient (r = 0.869) and elevation (r = 0.577) (Table 2.4).

Several of the variables of both axes exhibited strong correlations with each other (Table 5). These correlations suggested that some variables were redundant (McCune 1997). Variables that correlated with another variable in Table 2.5 and had the lower of the two correlation coefficients from Table 2.4 were removed from the environmental data matrix. These variables included percent agricultural habitat, which correlated with percent disturbed habitat because it is the most common landuse practice in the state (USGS 1999); elevation, which correlated with stream gradient and described a similar landscape feature; and latitude, which correlated negatively with temperature-such an inverse relationship between these two variables in the Northern Hemisphere is well established (Table 2.5). Precipitation and longitude did not correlate strongly with either axis (Table 2.4) and were also removed.

A CCA analysis containing temperature, soil type, stream gradient, and percent disturbed habitat determined two axes with significant correlations between species assemblages and environmental data I; Table 2.3); again, a third determined axis was not significant. Temperature and percent disturbed habitat correlated strongly with axis 1, whereas stream gradient correlated strongly with axis 2 (Table 2.4). A third CCA analysis contained temperature, stream gradient, and percent disturbed habitat, and yielded two significant axes with temperature and percent disturbed habitat correlated with axis 1 and stream gradient correlated with axis 2 (Tables 2.3-2.4).

A biplot ordination of the 58 watersheds constrained by temperature, percent disturbed habitat, and stream gradient showed the same five regions of caddisfly biodiversity exhibited in Figure 2.3 (Figure 2.8). The arrows in Figure 2.8 indicate the direction and strength of environmental gradients, with axis 1 correlated with temperature and percent disturbed habitat, and axis 2 correlated with stream gradient (Table 2.4) (Figure 2.9). The greater degree of clustering between the watersheds of the Lake Superior, Northwestern, and Southeastern regions than seen in the DCA output (Figure 2.3) indicated that these regions were particularly distinct; the Lake Superior region with high stream gradient, low temperature, and little disturbed habitat; the Southeastern region with high stream gradient, high temperature, and a moderate to high level of disturbed habitat; and the Northwestern region with low stream gradient, moderate temperature, and a high level of disturbed habitat. The Northern and Southern regions were less distinct, and their environmental conditions appeared to describe a continual gradient over a large area, particularly regarding temperature and percent disturbed habitat (Figure 2.8).

Landuse and Species Richness. The number of caddisfly species caught exhibited a strong negative correlation with the percentage of disturbed habitat upstream of all Class 2-3 streams in the Northern ($r = -0.617$) and Northwestern ($r = -0.770$) regions (Figure 2.10) ($p < 0.001$ for both). The number of caddisfly species caught also exhibited a strong negative correlation with the percentage of disturbed habitat upstream of all Class 2-3 streams in areas of the Southern region within both the Prairie ($r = 0.657$) and Deciduous Forest ($r = -0.845$) biotic provinces (Figure 2.10) ($p <0.001$ for both). The Northern, Northwestern, and Southern regions accounted for 85% of Class 23 streams sampled. Thus, plotting data for all streams would have displayed redudant information. Other regions were not analyzed due to sample sizes <10 sites.

Trophic Comparison. Caddisfly feeding group composition within the different site classes exhibited marked differences between caddisfly regions (Figure 2.11). In the Northern and Lake Superior regions shredders-invertebrates whose larvae typically consume coarse allochthonous material such as leaf litter-had high relative mean abundance in small-medium streams (Classes 1-3) and in lakes (L). Shredders decreased in abundance relative to the other feeding groups as stream width increased. Filtering collectors-those that filter suspended particles from the water column-exhibited the opposite trend. This group increased in relative abundance as stream width increased and had high mean abundance only in large rivers (Class 5). Predators-organisms that consume other animals, and scrapers--those that consume periphyton from exposed substrates-exhibited low-moderate relative abundance in all site classes and did not show a clear trend. Predators did, however, have high mean abundance in lakes of the Northern region. Gathering collector,,,-generalist feeders that consume organic material from the substrate-had moderate to high relative abundance in all sizes of lakes and streams.

In the Northwestern and Southern regions, filtering collectors had high mean abundance in all site classes, including lakes and small streams (Figure 2.11). Shredders, predators, and scrapers exhibited a low to moderate relative abundance in all sites classes. Gathering collectors exhibited moderate to high relative abundance in all site classes. The same pattern was found in areas of the Southern region within both the Prairie and Deciduous Forest biotic provinces (Figure 2.12). In the Southeastern region, filtering collectors had high relative abundance in all site classes as they did in the Northwestern and Southern regions (Figure 2.11). Of these filtering collectors, 65-80% were subclassified as macrofiltering collectors (particles size = 1-4 mm) in Class 1-3 streams, whereas in all other regions microfilterers (particle size <0.25mm) composed 100% of the filtering collector trophic group. The remaining feeding groups of the Southeastern region exhibited the same trends in abundance seen in the Northern and Lake Superior regions (Figure 2.11).

DISCUSSION

Sampling. Larval caddisflies were not collected during this study due to the difficulty of obtaining a representative sample with larval collecting methods such as kick-netting, Hess sampling, or Surber sampling. Such methods are labor-intensive, difficult to standardize, often fail to find rare species, or may not sample all microhabitats representatively (Erman and Erman 1990, Merritt et al. 1996, Barbour 1999). Most larvae are not identifiable to the species level resulting in a loss of information (Resh and Unzicker 1975, Hawkins and Norris 2000, Hawkins and Vinson 2000, Hawkins et al. 2000). The light traps used in this study were not exhaustive collecting devices-some caddisflies are day-flying or simply not attracted to light (Myers and Resh 1999, Nakano and Tanida 1999). But by standardizing the time of collection, wattage of the light source, and size of collecting pan, the technique likely yielded a representative sample of the nocturnally active caddisfly adults and allowed for comparisons between sites.

Air temperature, wind speed, precipitation, and humidity have been observed to affect the abundance and composition of light trap samples. In several studies, dusk temperature was determined to be a significant factor affecting specimen abundance, species diversity, and sex ratios in caddisfly light trap samples, with dusk temperatures below 10°C lowering abundance and diversity, and increasing the proportion of males (Resh et al. 1975, Anderson 1978, Usis and MacLean 1986, Waringer 1989, Anderson and Vondracek 1999). Waringer (1991) found that air temperature at dusk had a significant effect on caddisfly composition and abundance in light traps, with a dusk temperature greater than 7°C necessary to obtain a representative sample. He did not observe an upper temperature threshold nor did he find precipitation or wind speed to have significant effects on catch success. Weather conditions were standardized in this study based on these previous studies, although a more conservative approach was taken.

Several studies have suggested that dispersal of adult caddisflies between habitats is of only minimal importance. Sode and Wiberg-Larson (1993) found that malaise traps placed within 2 m of a stream caught a significantly higher number of caddisfly species and specimens than did traps placed >2 m from the stream, and that traps placed 40 m from the stream caught significantly fewer. They also found that over 95% of specimens caught in traps were known to occur as larvae in the sampled stream. Petersen et al. (1999) placed a total of 15 malaise traps at 15 m intervals from a studied stream and found that over 90% of caddisfly specimens were caught within 15 m of the sampled stream. They further found an exponential decline in caddisfly specimen abundance as distance from the stream increased.

Several other studies using light traps found that almost all caddisfly species fly <100 m from their natal stream, although a few species have been found up to 1000 m away (Nielsen 1942, Swenson 1974, Garlicky 1987, Gothberg 1973). Sommerhauser et al. (1999) found that samples of adult caddisflies were appropriate for classifying aquatic habitat types. Based on studies of Lepidopteron, Malicky (1987) suggested that light traps have an attraction distance of 40-100 m for adult caddisflies. Virtually all of the sampling sites in this study were separated by at least 5000 m and most were covered by forest canopy. Thus, dispersals were considered unimportant.

Regional Comparisons. The Northern region contains a total of 32 watersheds and over 100,000 km^2 (USGS 1999). It is composed of mostly Coniferous Forest with a band of Deciduous Forest in its southern portion (Figure 2.5). The Northern region contains approximately 85% of Minnesota's natural lakes, most of which are small, deep, and oligotrophic (Heiskary and Wilson 1989, 1991). Most streams are low gradient and connect lakes (e.g., Tester 1995). Nearly 75% of the land area remains forested although much of the original coniferous forest has been replaced with early- to mid-succesional trembling aspen *(Populas tremuloides)* and paper birch *(Betula papyrifera)* forests (Stearns 1988, USGS 1999).

The Lake Superior region encompasses almost 6,000 km2 and is composed of two areas draining directly into Lake Superior (Figure 2.5). It was originally composed of entirely Coniferous Forest, much of which-as in the Northern Region-has been replaced by deciduous forest stands (Steams 1988). Although a few small towns and mining operations occur in this region, around 95% of the land area remains forested (Tester 1995, USGS 1999). Lakes are cold, deep, and oligotrophic, and many of the streams adjacent to Lake Superior are high gradient, containing numerous waterfalls (Heiskary and Wilson 1989, Tester 1995).

The Northwestern region contains 10 watersheds and encompasses approximately 16,000 km2; all of its streams drain into the Red River of the North. It is composed approximately equally of Prairie and Coniferous Forest (Figure 2.5). This region is now dominated by agriculture, with around 82% of the land area under cultivation, and has had almost all of its prairie vegetation removed and lakes, wetlands, and small streams modified to accommodate this landuse practice (Waters 1977, Tester 1995, USGS 1999, Waters 2000). Virtually all aquatic habitats are low gradient medium to large rivers with high levels of sediments and nutrients (Stoner et al. 1998). The region experiences considerable flooding during the spring season of most years (e.g., Waters 2000).

The Southeastern region is made up of eight watersheds and almost 10,000 km2, primarily composed of Deciduous Forest (Figure 2.5). It is semi-discontinuous, containing most of the watersheds draining into the lower Saint Croix and Mississippi Rivers. The region is dominated by streams and has virtually no natural lakes except in its extreme northern portion (Heiskary and Wilson 1989). Approximately 70% of the land area is under agricultural cultivation, although many of the valleys of small and medium rivers are protected by the State Park system (USGS 1999). Streams are spring fed, moderate-high gradient, and many support naturally reproducing stocks of brook trout *(Salvelinus fontinalis)* (e.g., Tester 1995).

The Southern region contains 29 watersheds and nearly 70,000 km^2 (USGS 1999). It is composed of approximately equal amounts of Deciduous Forest and Prairie (Figure 2.5). As with the Northwest Region, much of the natural vegetation and many of the lakes, wetlands, and small streams have been replaced with agriculture, which accounts for 85% of landuse (Tester 1995, USGS 1999). This region also includes nearly 70% of Minnesota's human population (Minnesota Office of the State Demographer, personal communication). Aquatic habitats are mostly low gradient medium to large rivers although some small streams remain, primarily in State Parks. Existing lakes are almost entirely eutrophic or hypereutrophic (Heiskary and Wilson 1989, 1990).

Differences in regional caddisfly biodiversity indices appeared to reflect the natural and anthropogenic differences among habitats of the five determined regions (Table 2.2). The Lake Superior region had high overall species richness and heterogeneity; different types of aquatic ecosystems yielded disparate faunal assemblages. The Northern region contained high species richness and moderate heterogeneity; a rich faunal assemblage composed of similar species occurred in most habitats. The Southeastern region exhibited moderate species richness and heterogeneity. The Southern region contained low species richness and moderate heterogeneity. The Northwestern region exhibited low species richness and low heterogeneity. These trends in species composition within the state were noted by Houghton et al. (2001), who hypothesized that both natural and anthropogenic factors may be important in affecting caddisfly biodiversity in Minnesota.

Environmental Analysis. Axis 1 of the CCA analysis described a northeast to southwest environmental gradient that correlated significantly with changes in caddisfly species composition (Table 2.3) (Figure 2.9). The direction and gradual nature of this axis likely explains why latitude correlated with these variables in the first CCA analysis (Table 2.4). Garono and MacLean (1988), and Moulton and Stewart (1996) found that latitude was significantly correlated with changes in caddisfly species composition in Ohio bog communities and the Interior Highlands region of North America, respectively. Neither authors used CCA, but rather correlated changes in environmental variables with DCA axis scores using Spearman Rank Correlation. In both cases, latitude may be describing the landscape-level change in another variable such as temperature. Due to the correlations between temperature and percent disturbed habitat (Table 2.5) in this study, it is difficult to separate their relative importance in determining caddisfly distributions. Both appeared to describe independent environmental gradients that change in the same direction within Minnesota (Figure 2.9), and both are well established in their effects on the aquatic biota.

Air temperature and the number of frost-free days decrease in a northeasterly direction in Minnesota as do overall lake and stream temperatures (Figure 2.9) (Baker and Strub 1963, Baker et al. 1985, Tester 1995). Furthermore, the forests of northern and central Minnesota may provide a greater level of stream shading than do the prairie and agricultural vegetation of the south and west, leading to a more pronounced difference in the temperatures of aquatic ecosystems (e.g., Tester 1995). Water temperature is an important factor in determining distributions of aquatic invertebrates, with most species restricted to a fairly stenothermic range (e.g., Allan 1995). Changes in the environmental temperature of Minnesota, with corresponding changes in aquatic habitat temperature, are likely to promote changes in the caddisfly fauna.

The relative level of human landuse also decreased in a northeasterly direction, with northeastern Minnesota less than 20% disturbed, and with over 80% of southern Minnesota converted to agricultural or urban environments (Figure 2.9). Changes in the species compositions of aquatic organisms are a common result of aquatic ecosystem degradation by human landuses such as logging, mining, agriculture, or urbanization; an overall loss of biological diversity and increases in the populations of tolerant species are typical effects (see Karr and Chu 1999). Several recent studies (Sommerhauser et al. 1999, Berlin and Thiele 2002, Dohet 2002) used CCA to determine the level of disturbed habitat as an important environmental variable affecting caddisfly species composition. The current study appeared to confirm this previous research.

Axis 2 did not describe a gradual environmental gradient running east and west, but rather an abrupt change from the low gradient streams that dominate most of the state to the relatively high gradient streams of the eastern border (Figure 2.9). Axis 2 also correlated with .significant changes in caddisfly species composition (Table 2.4). Longitude did not correlate with stream gradient in the original CCA analysis, due to the abruptness of change (Table 2.4). As with temperature, stream gradient was measured on a landscape level as an overall measure of stream velocity per watershed. Stream velocity affects substrate particle size, availability of food sources, and exerts a physical force on the aquatic organisms, representing one of the most important factors influencing the fauna of a particular habitat (e.g., Allan 1995). In a Luxembourg study Dohet (2002) used CCA to determine stream gradient as one of the most important environmental variables affecting the species composition of caddisflies. Changes in the overall stream gradient of Minnesota habitats, with corresponding changes in stream velocity, are likely to promote changes in the caddisfly fauna.

Biodiversity and Landuse. The Northwestern and Southern regions had the lowest mean species richness per watershed (Table 2.2, Figure 2.7). This lack of richness could be explained by much of both regions being located within the Prairie biotic province (Figure 2.5). Prairie aquatic ecosystems in Minnesota tend to be low gradient, flood-prone, and with relatively little heterogeneity in substrate or streamflow relative to those of the Coniferous and Deciduous Forest biotic provinces (Tester 1995). These factors could naturally lead to low species richness in the Northwestern and Southern regions.

This lack of species richness in the Northwestern and Southern regions could also have been caused by human disturbance, as much of these regions have been converted to agriculture or urban landuse (Figure 2.9). Although the mechanisms of species loss depend on the nature of the impact, native taxa tend to decline as human disturbance increases. In North America declines have been documented with periphyton (Bahls 1993, Pan et al. 1996), phytoplankton. (Schelske 1984), zooplankton (Stemberger and Lazorchak 1994), invertebrates (Ohio EPA 1988, Reynoldson and Metcalfe-Smith 1992, Kerans and Karr 1994, DeShon 1995, Kleindl 1995, Fore et al. 1996, Thorne and Williams 1997), fish (Karr 1981, Karr et al. 1985, Miller et al. 1988, Minns et. al 1994, Lyons et. al 1996, Wang et al. 1997), and amphibians (Corn and Bury 1989). A decrease in the species richness of caddisflies with an increase in a variety of human activities has been documented in Oregon, Washington, Wyoming, Tennessee, Germany, and Japan, among other places (Kerans and Karr 1994, Kleindl 1995, Rossano 1995, Patterson 1996, Karr and Chu 1999, Berlin and Thiele 2002).

Separating the natural and anthropogenic influences on modern Minnesota prairie aquatic ecosystems is difficult as over 99% of the natural prairie has been removed and replaced by agricultural and urban environments (Tester 1995). Most remnant prairie habitats are less than 100 acres in size, precluding a watershed-level analysis (Tester 1995). Representative historical caddisfly data from the original prairie ecosystems of Minnesota are, unfortunately, lacking.

Although it was difficult to differentiate between the possible effects of natural and anthropogenic factors on caddisfly species biodiversity, it is likely that habitat disturbance has led to a decrease in species richness throughout the state. It is possible that caddisfly species richness was naturally higher in the Northern region than in the Northwestern and Southern regions, yet the negative correlation between richness and habitat disturbance in all three suggests a loss of species after habitat disturbance regardless of initial level (Figure 2.10). No significant difference was found between the current level of species richness of the Prairie and Deciduous Forest habitats of the Southern region. Furthermore, even within aquatic prairie habitats species richness correlated negatively with level of habitat disturbance, again suggesting a loss of species in disturbed habitats regardless of initial level of species richness (Figure 2.10). These results suggest that natural differences between deciduous forest and prairie ecosystems have less effect on caddisfly species richness than does habitat disturbance.

In Minnesota, agriculture is the most common landuse practice (USGS 1999). In such environments common disturbances include soil erosion, ditching and draining of streams and wetlands, removal of riparian vegetation, and input of fertilizer and pesticides (Gianessi et al. 1986, Lowe-McConnell 1987, Gregory et al. 1991, Turner and Rabalais 1991). Urban environments produce similar disturbances in addition to municipal and industrial wastes (Osborne and Wiley 1988, Allan 1995). These factors likely promote extirpations of species intolerant of such disturbances, and an increase of tolerant species populations (Roth 1994, Barbour et al. 1999). While it is not the objective of the current study to describe mechanisms of species loss, the documentation of reduced species richness in areas primarily disturbed by agriculture and urbanization suggests that anthropogenic factors have decreased caddisfly biodiversity in at least portions of Minnesota. .

Trophic Comparison. It appears that aquatic habitats of the Lake Superior, Northern, and Southeastern regions fit the river continuum concept (RCC), whereas habitats of the Northwestern and Southern regions do not (Figure 2.11). According to the RCC (Vannote et al. 1980, Merrit et al.. 1984), shredders are most abundant in small streams (Class 1-2) because the canopy of riparian vegetation over the narrow stream channel promotes high levels of their coarse allochthonous food source. Scrapers typically exhibit their highest abundance in medium-sized streams (Class 2-3) as the widening stream allows solar radiation to penetrate to the water surface and stimulate growth of periphyton. In large rivers I; Class 4=5), filtering collectors typically exhibit high abundance as the breakdown of detritus from upstream reaches promotes high levels of their fine particle source. In lakes - particularly oligo- and mesotrophic lakes -

shredders show a high relative abundance due to the influence of shoreline canopy cover while scrapers and filtering collectors;, although sometimes present, are rarely abundant. Predators typically, show little change in abundance in different ecosystems as their primary food source, animal tissue, is common in all types of lotic and lentic systems. The preferred food type of gathering collectors-substrate-deposited organic material-is also common in all types of aquatic ecosystems, hence gathering collectors usually exhibit high abundance in all ecosystem types.

In the Northern and Lake Superior regions, relative abundance of trophic functional groups-particularly the changes in relative abundance of shredders and filtering collectors-followed a general pattern predicted by the RCC (Figure 2.11). In the Southeastern region, filtering collectors dominate in most types of streams (Figure 2.11). This observation, however, may be misleading. Filtering collectors can be further subdivided based on the size of particle consumed. Macrofiltering collectors consume large (1-4 mm) particulate organic matter such as the leaf fragments and woody debris disturbed by fast-moving current, while microfiltering collectors consume small (<0.25 mm) detrital fragments, feces, and free-living microorganisms (Cummins 1974, Boiling et al. 1975). In the Southeastern region macrofilterers composed 65-85% of the filtering collectors caught in Class 1-3 streams, and were absent in Class 4-5 streams (Figure 2.11). The high-gradient streams of the southeastern region likely promoted a naturally high abundance of macrofilterers (Figure 2.9)

The abundance of macrofiltering collectors in the southeastern was due mainly to a high abundance of *Brachycentrus americanus* (Banks) Brachycentridae. While *B. americanus* exhibits the feeding behavior of a filtering collector-grasping suspended particles with their meso- and metathoracic legs (Wiggins 1996a)-the size and nature of food consumed could place *B. americanus* in other trophic functional groups. Mecom (1972) found that *B. americanus* was an opportunistic omnivore, consuming plant fragments, animal fragments, diatoms, and woody debris. Mecom and Cummins (1964) likewise found a positive correlation between the gut contents of *B. americanus* and the food available on the substrate during the feeding period. While the precise niche of *B. americanus* may be unclear, it is probably not appropriate to classify them with fine particle filter feeders, thus their separation in Figure 2.11.

In the Southern and Northwestern regions, caddisfly trophic feeding composition was contrary to the RCC (Vannote et al. 1980); microfiltering collectors dominated in all site classes including small streams and lakes (Figure 2.11). It is possible that the observed pattern could have been caused by the predominance of prairie ecosystems in the Northwestern and Southern regions. Several authors (Statzner and Higler 1985, Wiley et al. 1990, Allan 1995) have suggested that streams within natural prairie ecosystems do not fit into the RCC model; instead exhibiting increasing canopy cover into the middle stream reaches (Class 3). Erosion of nutrient-rich prairie soil may lead to naturally high levels of dissolved nitrogen and phosphorous in prairie streams (Anderson and Grigal 1984, Buol et al. 1989). The combination of limited canopy cover and high nutrient availability may promote ecosystem autotrophy, a lower than expected abundance of shredders, and a higher than expected abundance of filtering collectors in small and medium streams (Class 1-3) of the Northwestern and Southern regions. Many of the sampling sites of these regions were within the Prairie biotic province (Figure 2.2).

It also may be that the high relative abundance of microfiltering collectors in all types of aquatic habitats within the Northwestern and Southern regions is due to human disturbance. Intensive agriculture probably has the most extensive impact of any human landuse on aquatic ecosystems (Omernik 1977, Karr and Schlosser 1978, Karr et al. 1985, Allan 1995). Agriculture often leads to stream channelization, draining of wetlands, modification or loss of the surrounding floodplain, and removal of riparian canopy cover with subsequent loss of allochthonous input (Lowe-McConnell 1987, Gregory et al. 1991, Allan 1995). Agricultural runoff into aquatic habitats often contains large amounts of sediments, nutrients, and pesticides (Gianessi et al. 1986, Turner and Rabalais 1991). Collectively these impacts promote homogenization of stream microhabitats and an increase in autotrophic production, especially in small to medium streams (Berkman and Rabeni 1987; Feminella et al. 1989; Delong and Brusven 1992, 1993; Pringle et al. 1993). Nutrient input and loss of habitat due to large urban environments can cause similar effects (Osborne and Wiley 1988). The Northwestern and Southern regions are dominated by agricultural and urban landuse, whereas much of the Northern, Lake Superior, and portions of the Southeastern region are composed of forest (Figure 2.9).

Separating the natural and anthropogenic influences on modern Minnesota prairie aquatic ecosystems is difficult; as mentioned earlier almost all of the prairie vegetation has been removed and replaced by agricultural and urban environments and only small remnants remain, precluding a watershed-level analysis (Tester 1995). Filtering collectors, however, had a high relative abundance in Class 2-4 streams in both prarie and deciduous forest areas of the Southern caddisfly region (Figure 2.12). This result suggests that natural differences between these areas are less important than contemporary factors in affecting trophic functional group composition.

These results confirm previous studies. Wiley et al. (1990) found that agricultural and urban landuse contributed more nutrient input into prairie streams in Illinois than did natural processes. Several recent studies of the Red River of the North basin=a mainly prairie ecosystem approximating the boundaries of the Northwestern caddisfly region have determined that insect and fish populations are affected by both instream environmental conditions and agricultural cultivation with its resulting input of nutrients and fine sediment into streams (Stoner et al. 1993, 1998; Goldstein et al. 1995, 1996). It may be that agricultural and urban environments=and their corresponding physical and chemical changes to the watershed-may be an important influence on caddisfly feeding group composition in Minnesota. The inclusion of other aquatic insect taxa would undoubtedly add value to these observations; however, the differences in the feeding group ecology of caddisflies alone were striking.

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Table 2.1. The six site classes constructed for this study and the total number of samples taken from each. Stream width was estimated at each sampling site.

Class	Description	Width	Sample Size
1.	Small Stream	<2m	24
2.	Small/medium Stream	2-4m	37
3.	Medium River	4-10m	71
4.	Medium/large River	10-30m	54
5.	Large River	>30m	20
L.	Lake or Wetland	N/A	42

Table 2.2. Summary statistics for five regions of Minnesota caddisfly biodiversity (Figure 6). Unsampled watersheds were placed into regions based on geographic location and perceived habitat similarity to sampled watersheds. H' = Shannon's Diversity Index, ß = mean Morisitia-Horn index for all pairs of samples within each region. Total and Relative Uniques refer to unique species in each region within Minnesota, not actual endemism. Superscript letters denote statistically significant groupings based on a One-way Analysis of Variance with Student-Newman-Keuls test ($\alpha = 0.05$).

Region	Total Watersheds	Watersheds Sampled	Total Samples	Total Species	Species/ Watershed	H'	ß	Total Uniques	Relative Uniques
Lake Superior	2	2	17	107	74^A	3.4	0.14^A	14	13%
Northern	32	28	119	197	73^A	3.7	0.21^B	49	25%
Southeastern	8	3	15	73	47^B	3.0	0.21^B	3	4%
Southern	27	20	75	110	31^C	2.9	0.24^B	8	7%
Northwestern	10	5	17	52	27^C	2.3	0.37^C	0	0%

Table 2.3. Eigenvalues, species/environment correlations, and their respective probability (p) values for axes of ecological interest determined by three runs of a Canonical Correspondence Analysis of environmental and caddisfly species data for 58 Minnesota watersheds.

Run	Axis	Eigenvalue	p	Species/Environmental Correlation	p
1	1	0.268	0.02	0.936	0.02
	2	0.200	0.02	0.963	0.02
	3	0.085	0.02	0.832	0.14
2	1	0.262	0.02	0.932	0.02
	2	0.196	0.02	0.956	0.02
	3	0.077	0.02	0.816	0.10
3	1	0.260	0.02	0.930	0.02
	2	0.194	0.02	0.952	0.02
	3	0.070	0.10	0.800	0.10

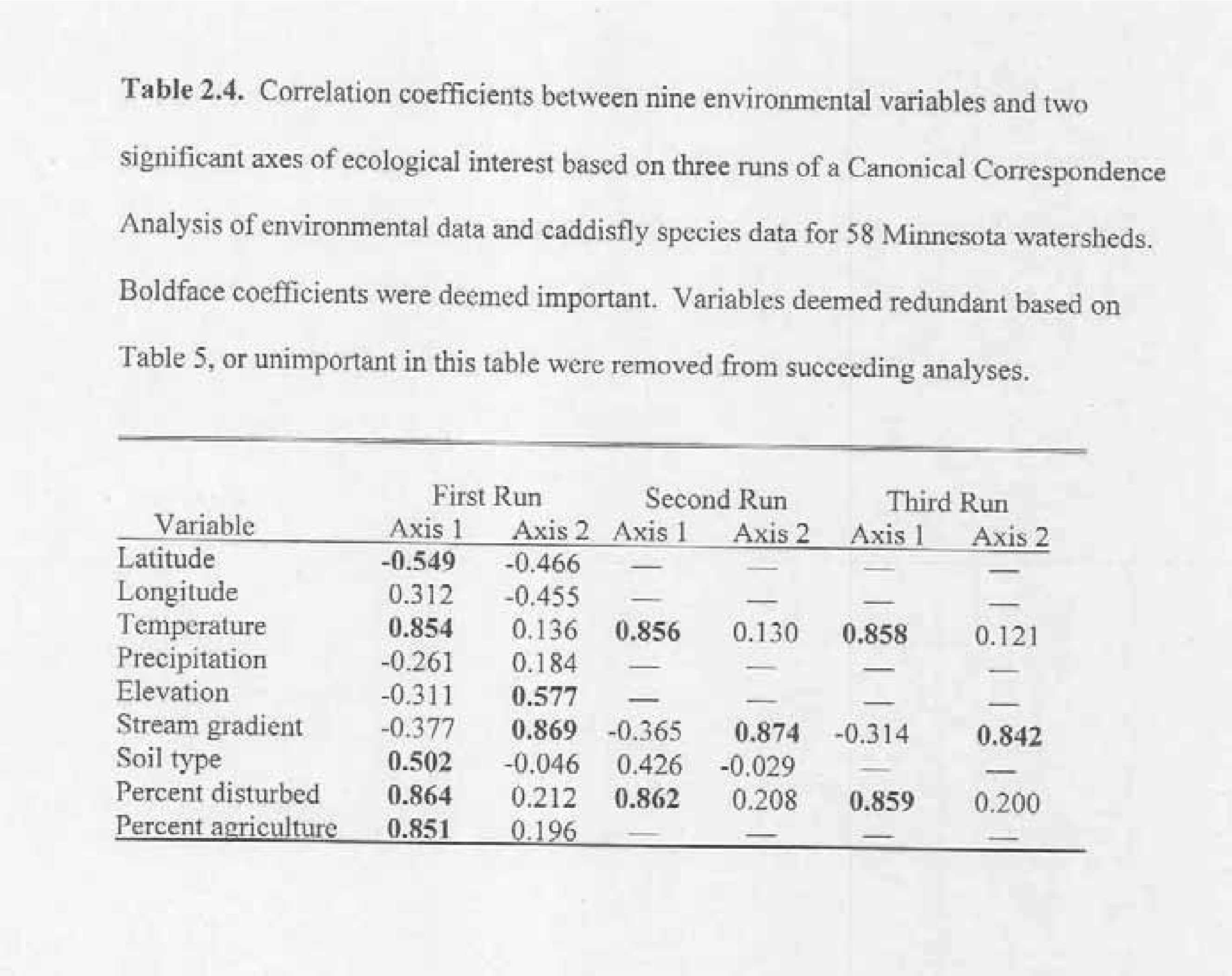


Table 2.4. Correlation coefficients between nine environmental variables and two significant axes of ecological interest based on three runs of a Canonical Correspondence Analysis of environmental data and caddisfly species data for 58 Minnesota watersheds. Boldface coefficients were deemed important. Variables deemed redundant based on Table 5, or unimportant in this table were removed from succeeding analyses.

Variable	First Run		Second Run		Third Run	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Latitude	**-0.549**	-0.466	—	—	—	—
Longitude	0.312	-0.455	—	—	—	—
Temperature	**0.854**	0.136	**0.856**	0.130	**0.858**	0.121
Precipitation	-0.261	0.184	—	—	—	—
Elevation	-0.311	**0.577**	—	—	—	—
Stream gradient	-0.377	**0.869**	-0.365	**0.874**	-0.314	**0.842**
Soil type	**0.502**	-0.046	0.426	-0.029	—	—
Percent disturbed	**0.864**	0.212	**0.862**	0.208	**0.859**	0.200
Percent agriculture	**0.851**	0.196	—	—	—	—

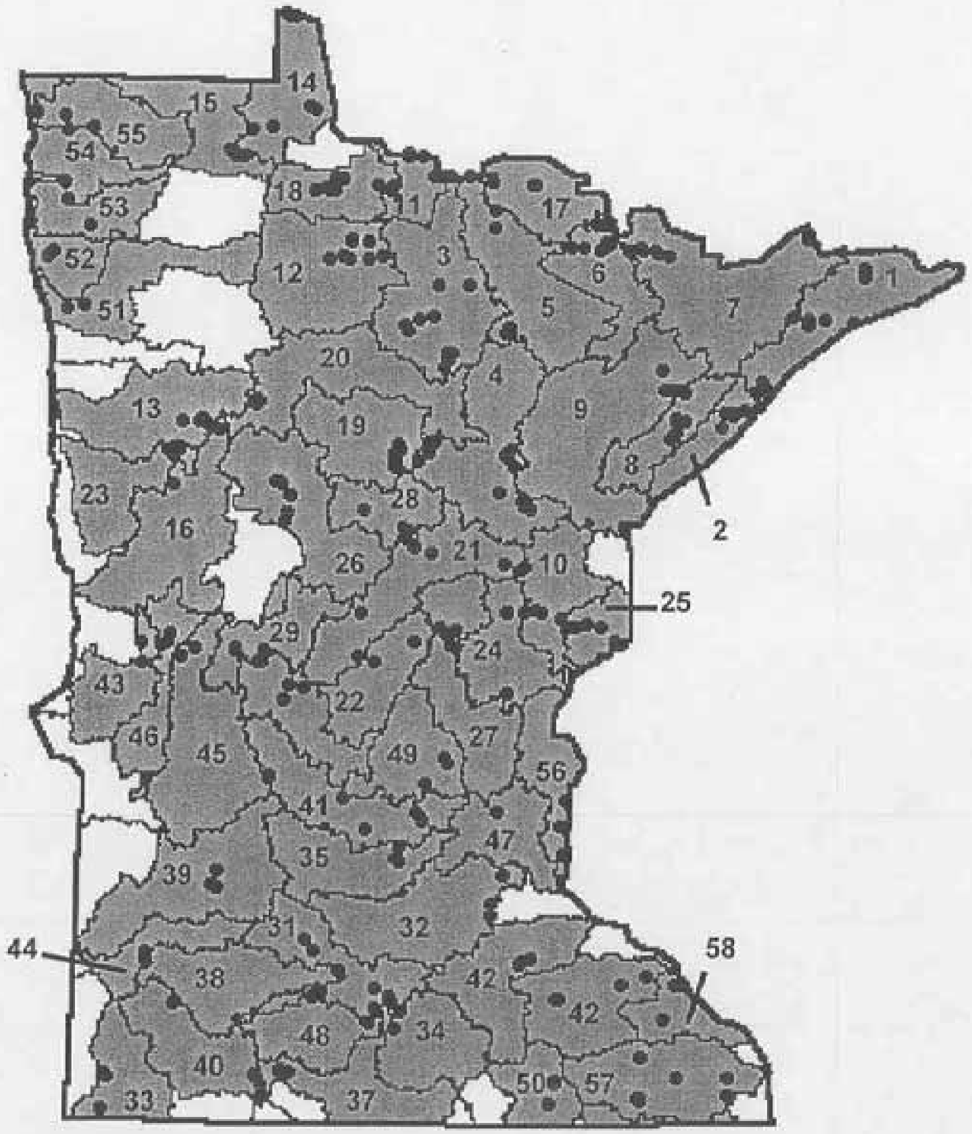
Table 2.5. Correlation coefficients among nine environmental variables based on a Canonical Correspondence Analysis of environmental data and caddisfly species data for 58 Minnesota watersheds. Boldface coefficients denote important correlations between variables giving potentially redundant information.

	Lat	Long	Temp	Precip	Elev	Grad	Soil	%Dist	%Ag
Lat	—	0.078	**-0.764**	-0.289	-0.158	-0.260	-0.285	-0.624	-0.590
Long		—	0.391	-0.605	-0.495	-0.605	0.639	0.456	0.482
Temp			—	-0.052	-0.148	-0.079	0.566	0.827	0.792
Precip				—	0.369	0.415	-0.467	-0.237	-0.256
Elev					—	**0.689**	-0.257	-0.188	-0.188
Gradient						—	-0.398	-0.219	-0.228
Soil							—	0.773	0.798
% Dist								—	**0.986**
% Ag.									—

Figure 2.1. The convergence of the Coniferous Forest, Deciduous Forest, and Prairie biotic provinces in the northcentral United States and southcentral Canada.

Figure 2.1

Figure 2.2. The 81 major watersheds of Minnesota (USGS 2002) showing the 58 watersheds sampled (shaded and numbered) during this study, and the corresponding 248 sampling sites. Overlap occurs between sample markers. Watershed names are in Figure 2.4.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37

Figure 2.2

Figure 2.3. Detrended Correspondence Analysis ordination of 58 Minnesota watersheds based on relative abundance of 224 caddisfly species, showing determined geographic regions of caddisfly biodiversity. Watershed names are in Figure 2.4.

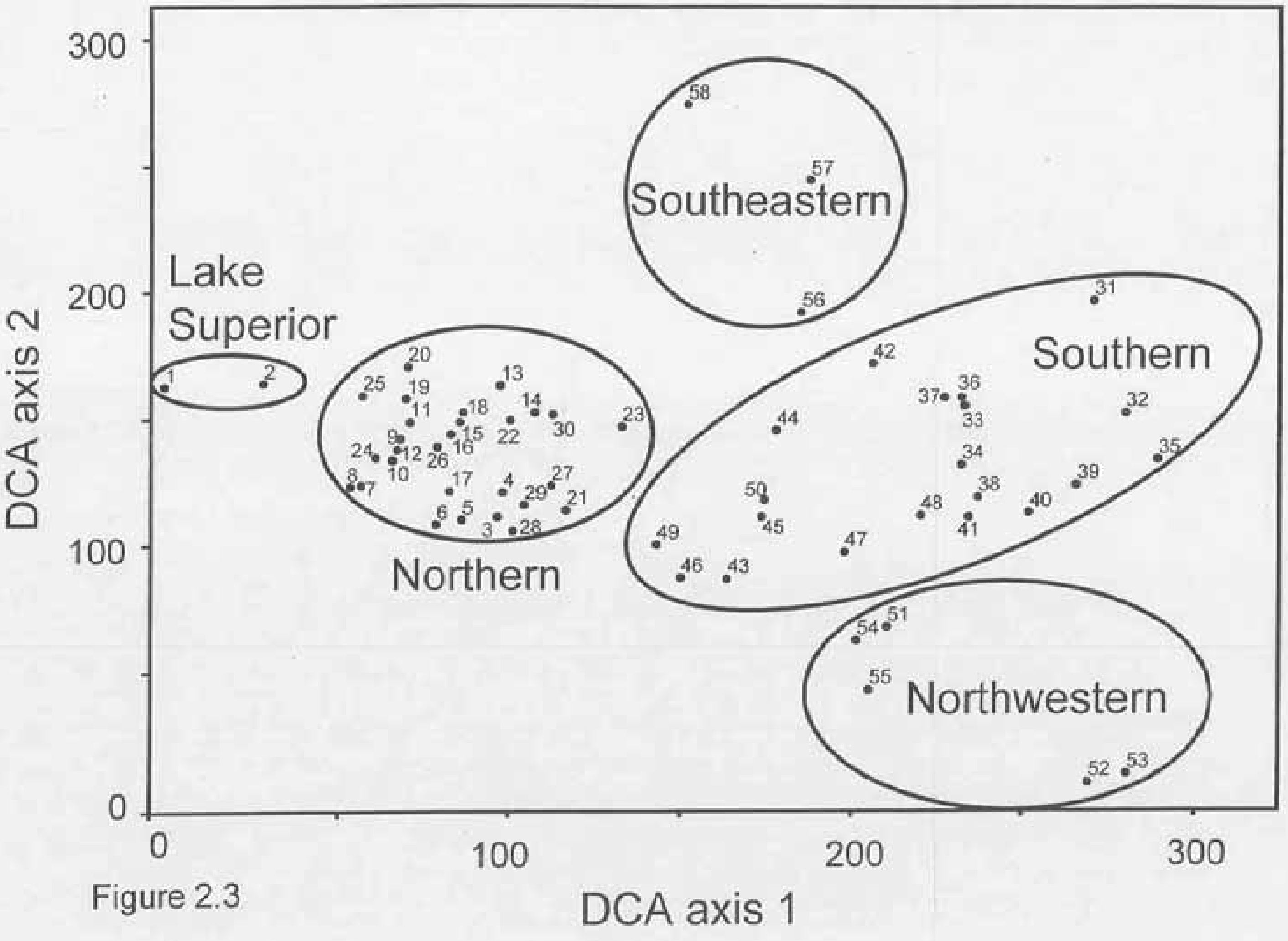
DCA axis 2
DCA axis 1
0
100
200
300
0
100
200
300
Lake Superior
Northern
Southeastern
Southern
Northwestern
1
2
3
4
5
6
7
8
9
10
11
12
13
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Figure 2.3

Figure 2.4. Flexible unweighted pair-group method using arithmetic averages (UPGMA) dendogram of 58 watersheds, based on relative abundance data for 224 Minnesota caddisfly species, showing determined regions of caddisfly biodiversity. Terminal branches were set to 0% and 100% similarity. Regions: LS = Lake Superior, NO = Northern, NW = Northwestern, SE = Southeastern, SO = Southern.

Figure 2.4

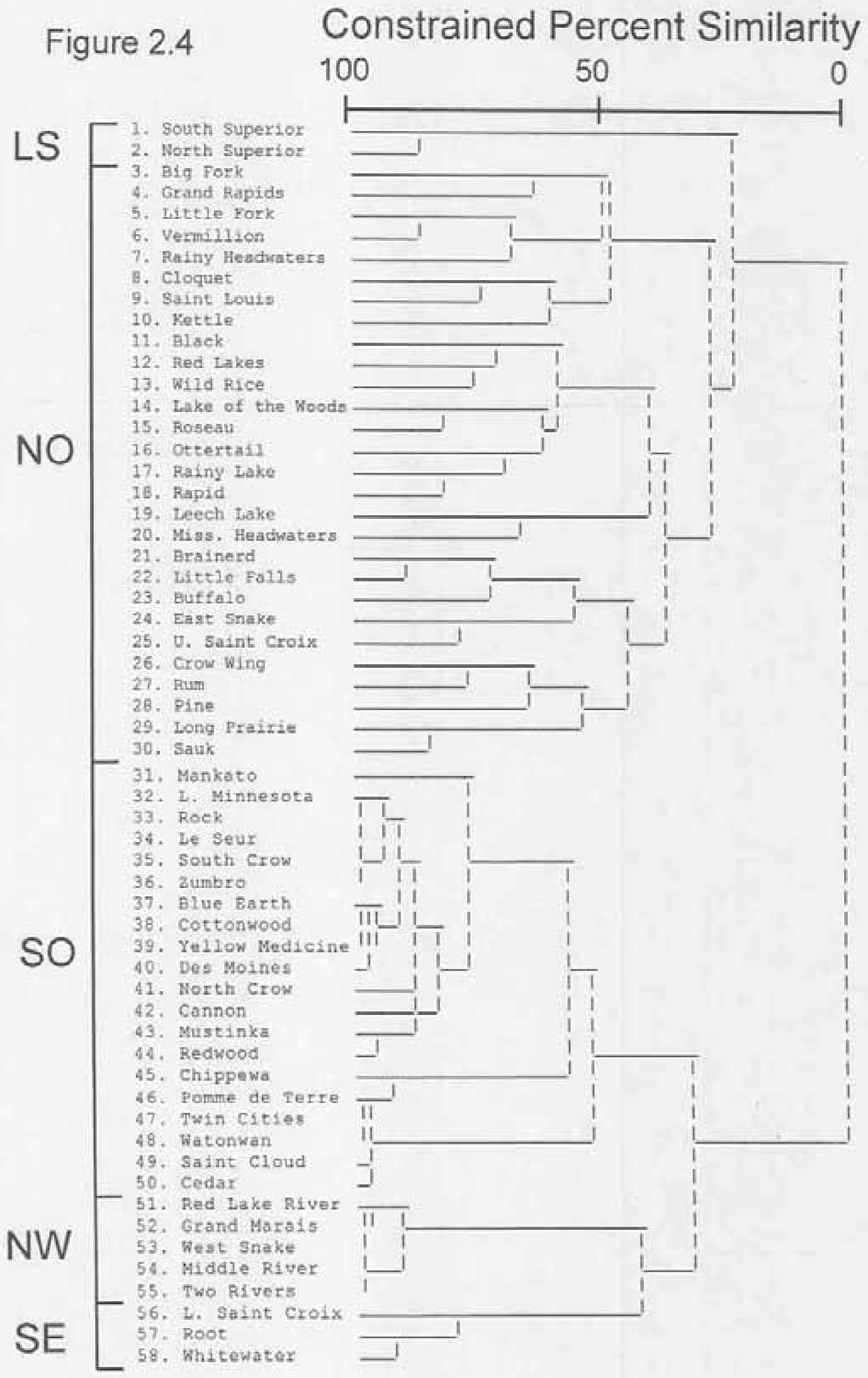

Constrained Percent Similarity
100
50
0
LS
NO
SO
NW
SE
1. South Superior
2. North Superior
3. Big Fork
4. Grand Rapids
5. Little Fork
6. Vermillion
7. Rainy Headwaters
8. Cloquet
9. Saint Louis
10. Kettle
11. Black
12. Red Lakes
13. Wild Rice
14. Lake of the Woods
15. Roseau
16. Ottertail
17. Rainy Lake
18. Rapid
19. Leech Lake
20. Miss. Headwaters
21. Brainerd
22. Little Falls
23. Buffalo
24. East Snake
25. U. Saint Croix
26. Crow Wing
27. Rum
28. Pine
29. Long Prairie
30. Sauk
31. Mankato
32. L. Minnesota
33. Rock
34. Le Seur
35. South Crow
36. Zumbro
37. Blue Earth
38. Cottonwood
39. Yellow Medicine
40. Des Moines
41. North Crow
42. Cannon
43. Mustinka
44. Redwood
45. Chippewa
46. Pomme de Terre
47. Twin Cities
48. Watonwan
49. Saint Cloud
50. Cedar
51. Red Lake River
52. Grand Marais
53. West Snake
54. Middle River
55. Two Rivers
56. L. Saint Croix
57. Root
58. Whitewater

Figure 2.5. The 81 major watersheds in Minnesota grouped into regions of caddisfly biodiversity based on a Detrended Correspondence Analysis (Figure 2.3) and UPGMA dendogram (Figure 2.4) of 58 watersheds and 224 caddisfly species. The 23 nonsampled watersheds were grouped with sampled watersheds based on geographic location. See Figure 2.4 for regional abbreviations. Biotic provinces of inset figure, CF = Coniferous Forest, DF = Deciduous Forest, PR = Prairie.

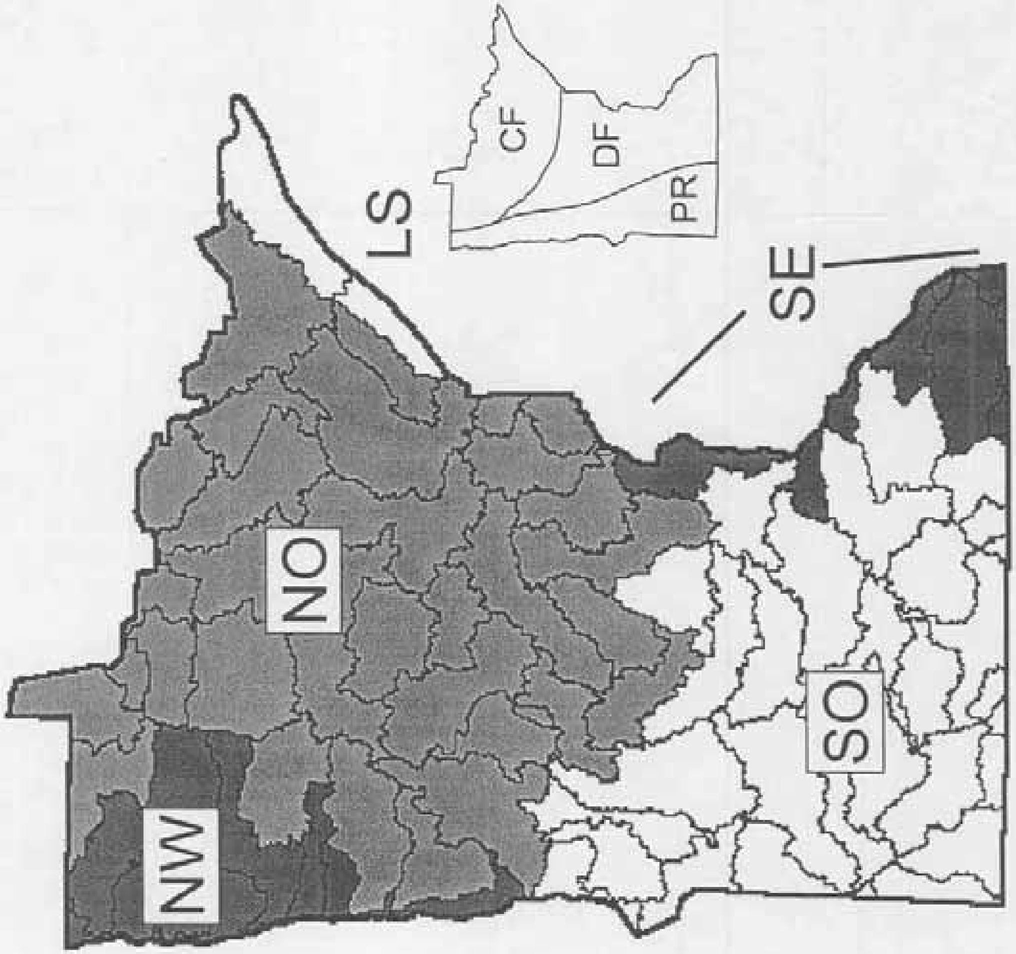


Figure 2.5

Figure 2.6. The mean number of caddisfly species collected from six different site classes within five regions of Minnesota caddisfly biodiversity (Figure 2.5). 1-5 = progressively larger streams, L = Lakes (Table 1). Sample sizes above each bar. Classes with sample sizes <2 were omitted.

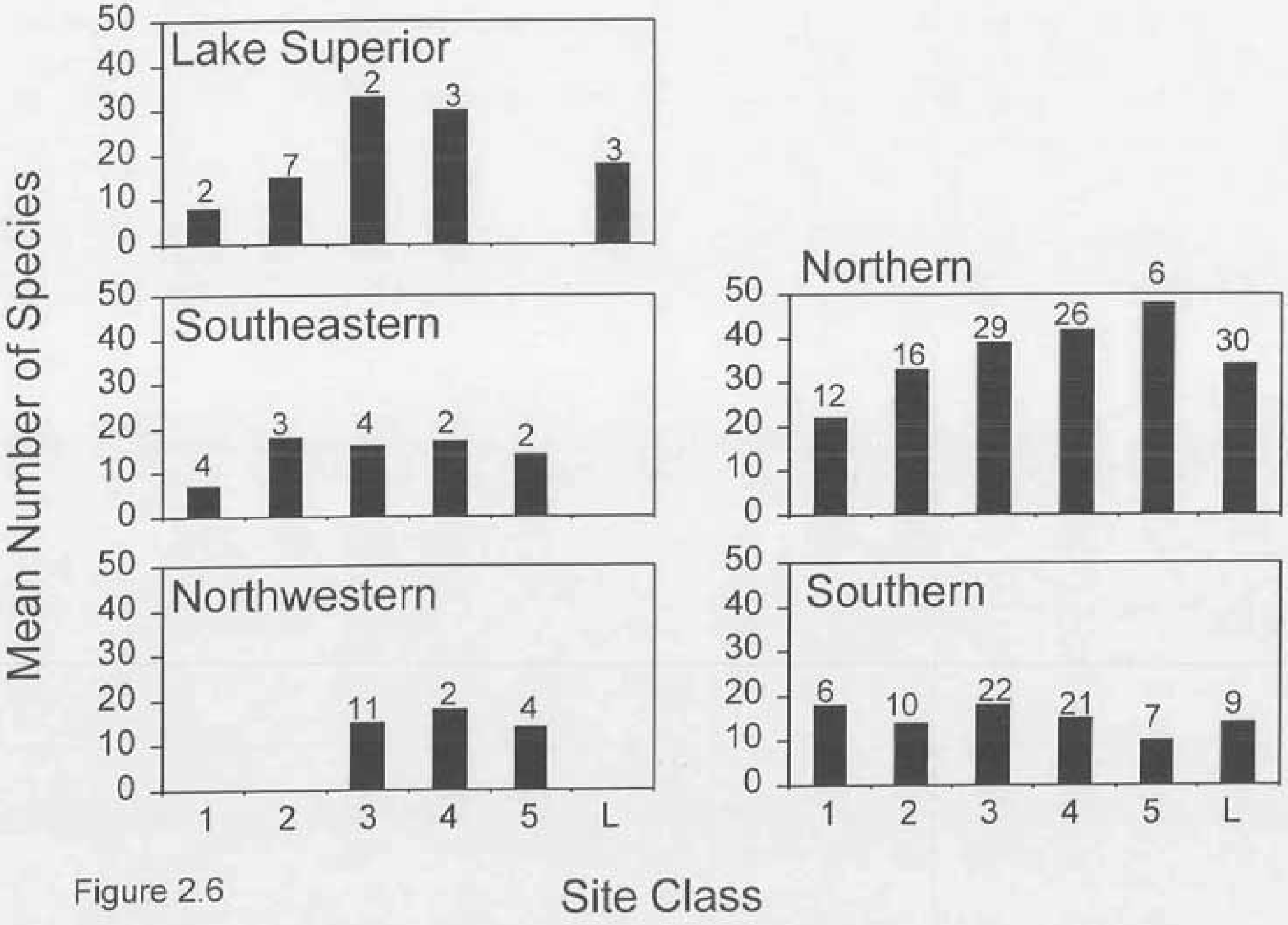
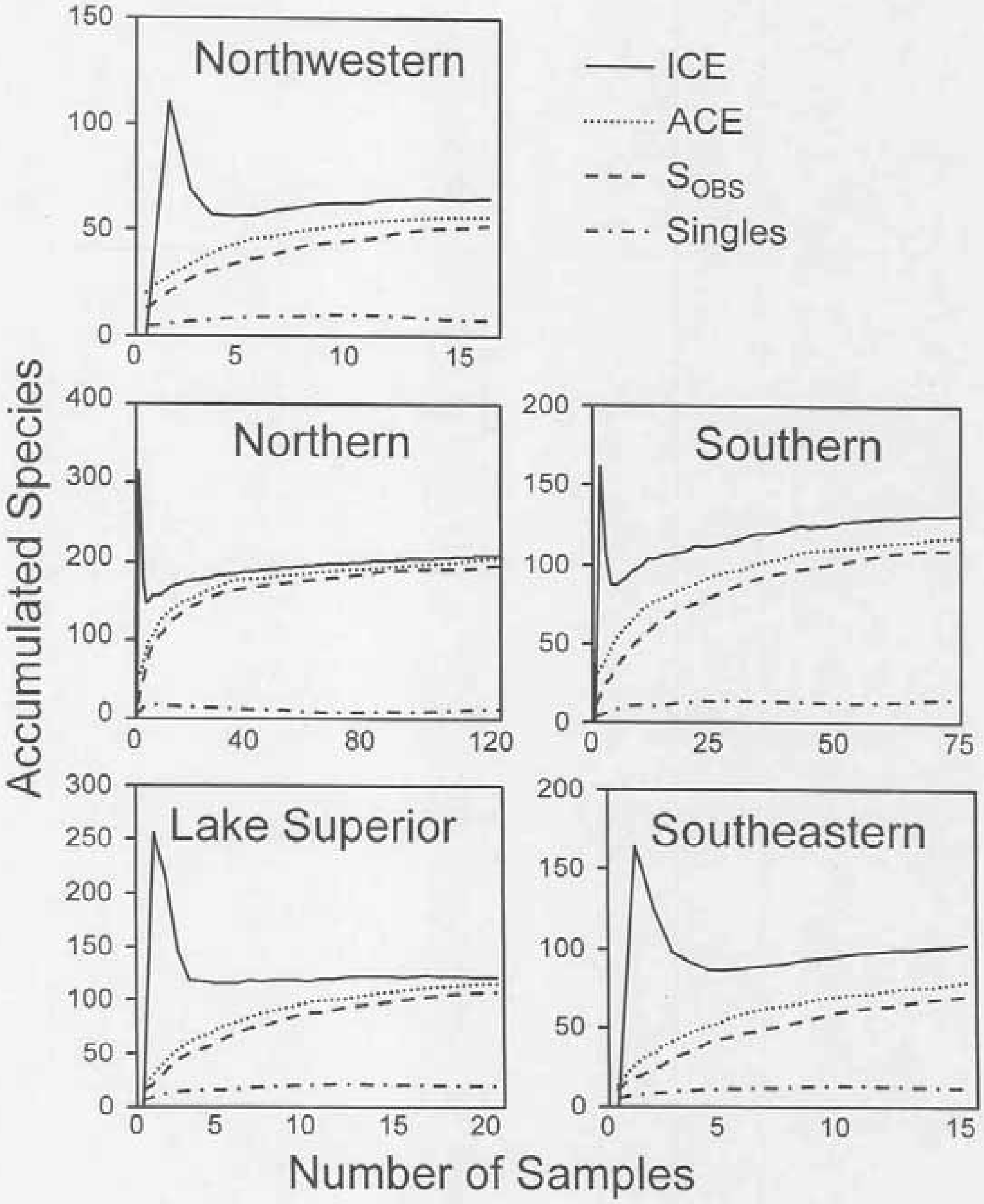

Mean Number of Species
Lake Superior
Southeastern
Northwestern
Northern
Southern
50
40
30
20
10
0
2
7
2
3
3
4
3
4
2
2
11
2
4
12
16
29
26
6
30
6
10
22
21
7
9
1
2
3
4
5
L
Site Class

Figure 2.6

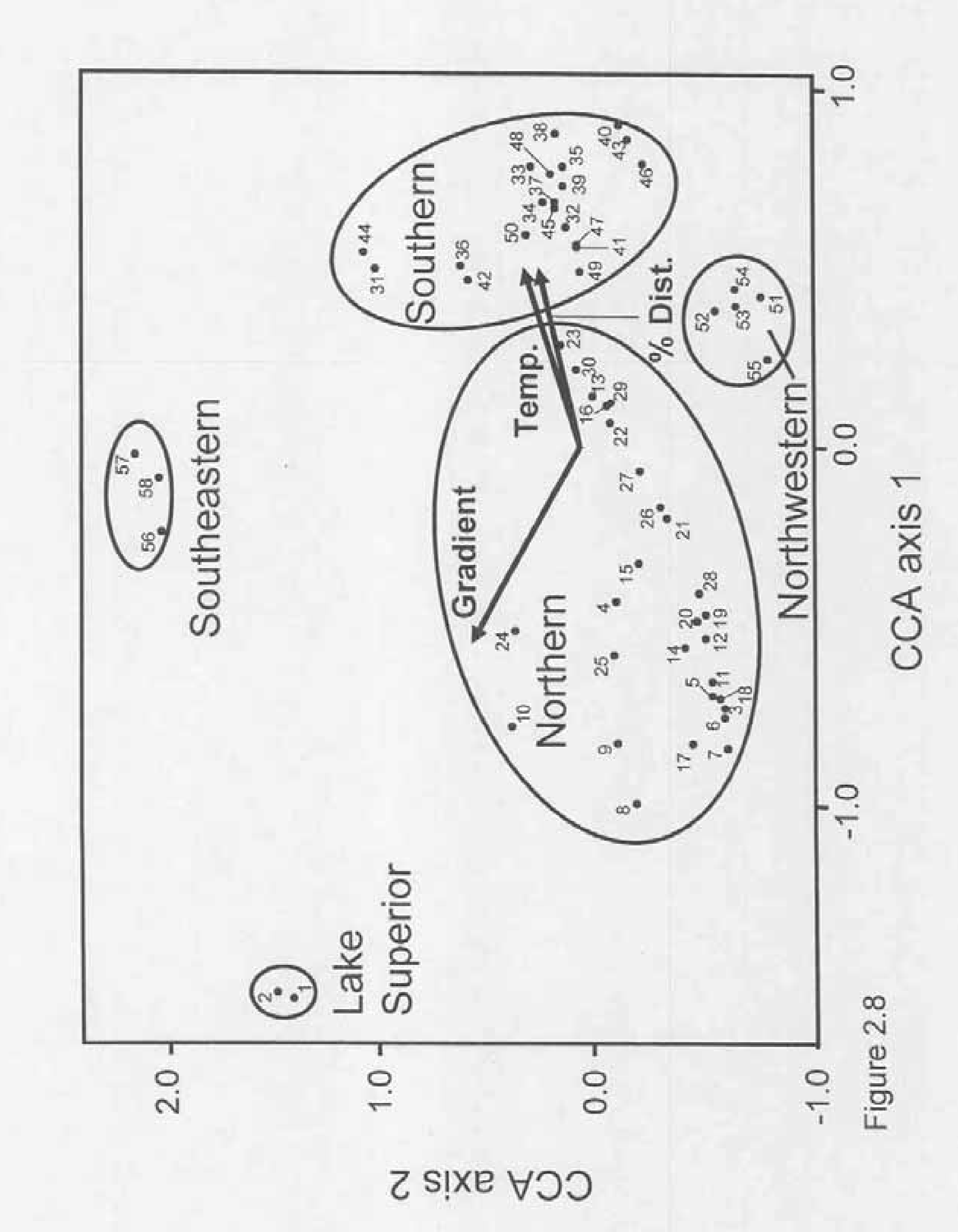
Figure 2.7. Curves of abundance-based coverage estimator of species richness (ACE), incidence-based coverage estimator of species richness (ICE), observed species accumulation (Sobs), and observed singletons (Singles) for five regions of Minnesota caddisfly biodiversity (Figure 2.5). Based on 50 random resamplings.

Figure 2.7



Northwestern
Northern
Southern
Lake Superior
Southeastern
ICE
ACE
S_{OBS}
Singles
Accumulated Species
Number of Samples
150
100
50
0
0
5
10
15
400
300
200
100
0
0
40
80
120
200
150
100
50
0
0
25
50
75
300
250
200
150
100
50
0
0
5
10
15
20
200
150
100
50
0
0
5
10
15

Figure 2.8. Canonical Correspondence Analysis biplot ordination of 58 Minnesota watersheds constrained according to the variables mean summer temperature (Temp.), percentage of disturbed habitat (% Dist.), and stream gradient (Gradient) (Table 2.4). Arrows indicate strength and direction of gradient. Temperature and percentage of disturbed habitat correlated with axis 1, whereas stream gradient correlated with axis 2 (Table 2.4).



CCA axis 2
CCA axis 1
2.0
1.0
0.0
-1.0
-1.0
0.0
1.0
Lake Superior
Southeastern
Northern
Southern
Northwestern
Gradient
Temp.
% Dist.
1
2
3
4
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10
11
12
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Figure 2.8

Figure 2.9. Mean summer temperature (Baker et al. 1985), percentage of disturbed habitat (USGS 1999), and stream gradient (Borchert and Yaeger 1968, USGS 1999) for 81 Minnesota watersheds showing approximate placement of two axes of caddisfly species composition gradient determined by the third run of Canonical Correspondence Analysis (Table 2.4). Mean summer temperature and percentage of disturbed habitat correlated with axis 1, stream gradient correlated with axis 2.

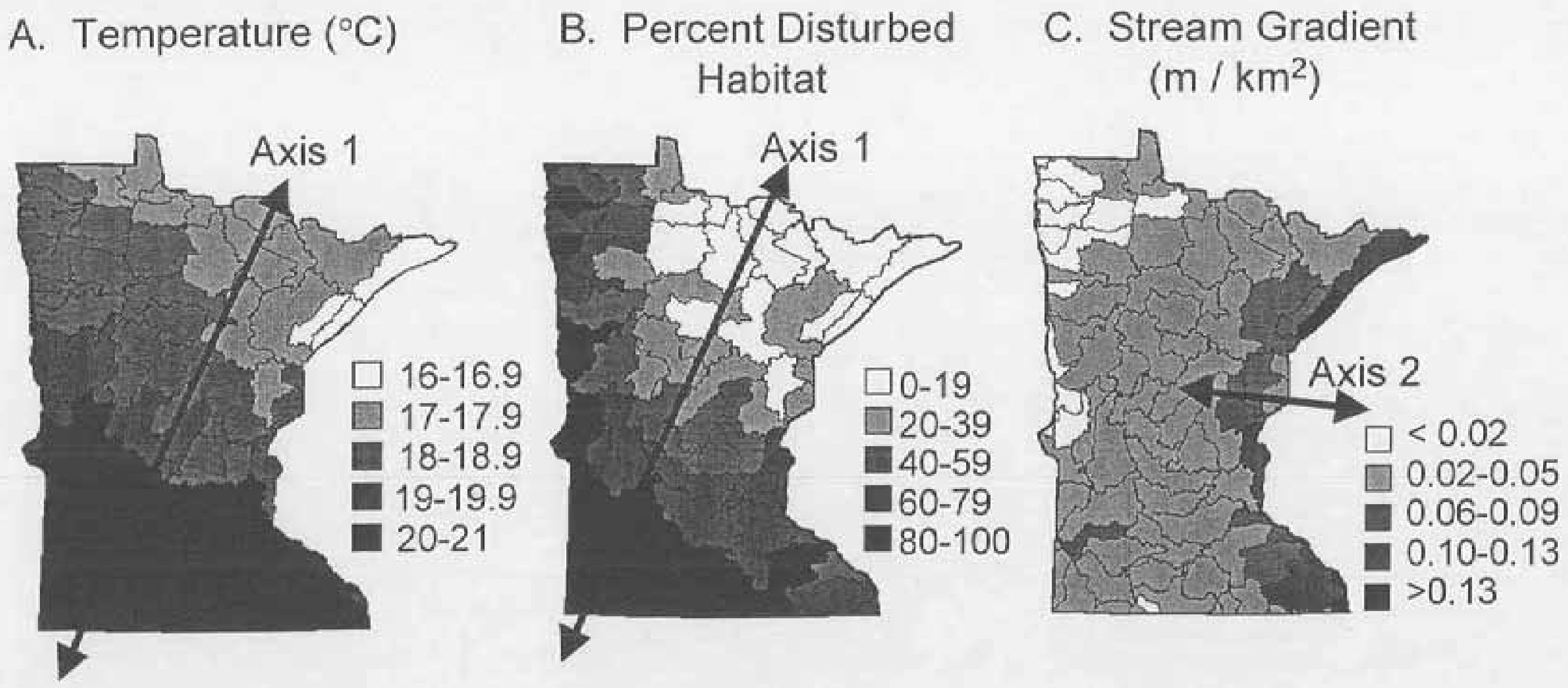
A. Temperature (°C)
Axis 1
☐ 16-16.9
▨ 17-17.9
■ 18-18.9
■ 19-19.9
■ 20-21
B. Percent Disturbed Habitat
Axis 1
☐ 0-19
▨ 20-39
■ 40-59
■ 60-79
■ 80-100
C. Stream Gradient (m / km2)
Axis 2
☐ < 0.02
▨ 0.02-0.05
■ 0.06-0.09
■ 0.10-0.13
■ >0.13

Figure 2.9

Figure 2.10. Plots of caddisfly species richness based on the percentage of disturbed habitat (USGS 1999) for three Minnesota caddisfly regions. A. Northern region (n = 45, r = -0.617), Northwestern region (n == 11, r = -0.770). B. Southern region: Prairie biotic province (n = 17, r = -0.657), Deciduous Forest province (n = 16, r = -0.845). All plots had p-values <0.001. Percentage of disturbed habitat was calculated from all land area upstream of the sampling point. All individual streams were in Class 2-3 (SmallMedium) (Table 2.1). Regions correspond to Figure 2.5.

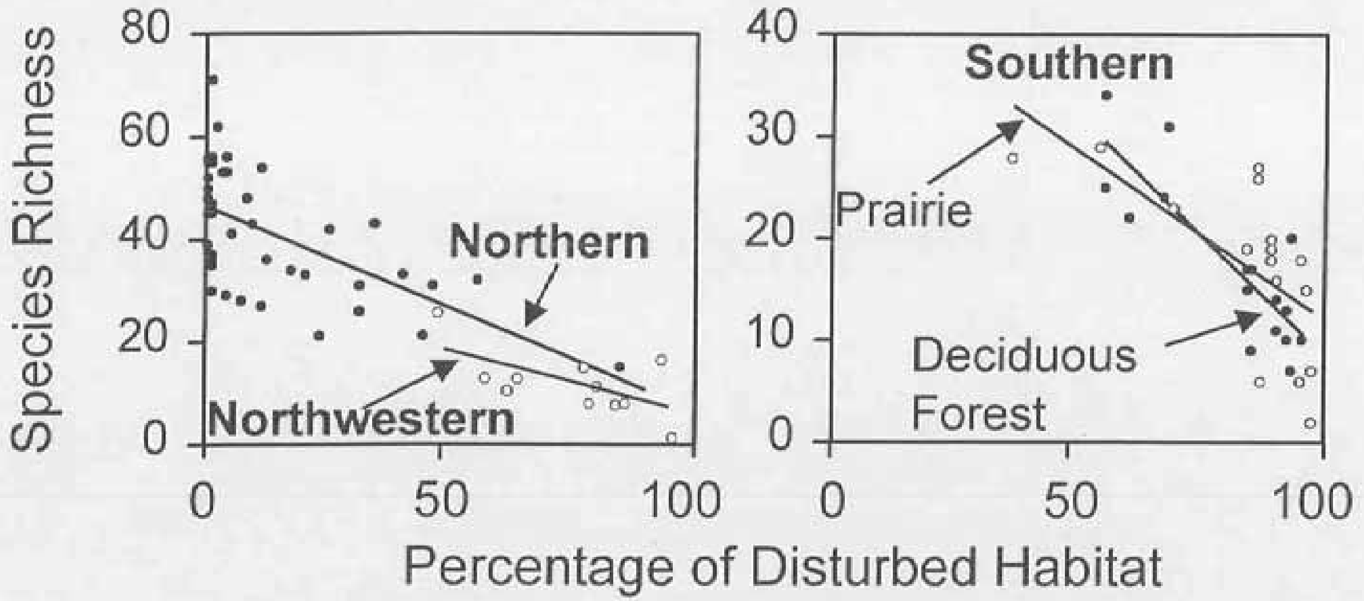
Species Richness
80
60
40
20
0
Northern
Northwestern
0
50
100
40
30
20
10
0
Southern
Prairie
Deciduous
Forest
0
50
100
Percentage of Disturbed Habitat

Figure 2.10

Figure 2.11. The percentage of mean specimen abundance for five trophic functional groups (Wiggins 1996a, b) within sip different sites classes (Table 1) of five different caddisfly regions (Figure 2.5). Classes with sample sizes <2 were omitted. Numbers above each graph denote statistically distinct means within each region and site class (One-way Analysis of Variance with Student-Neuman-Keuls test, p <0.05 for all).

Trophic functional groups: GC = Gathering Collectors, FC = Filtering Collectors, C = coarse particle filterer, F = fine particle filterer, PR = Predators, SC = Scrapers, SH = Shredders. All other filtering collectors were microfilterers. Regions: LS = Lake Superior, NO = Northern, NW = Northwestern, SO = Southern, SE = Southeastern.

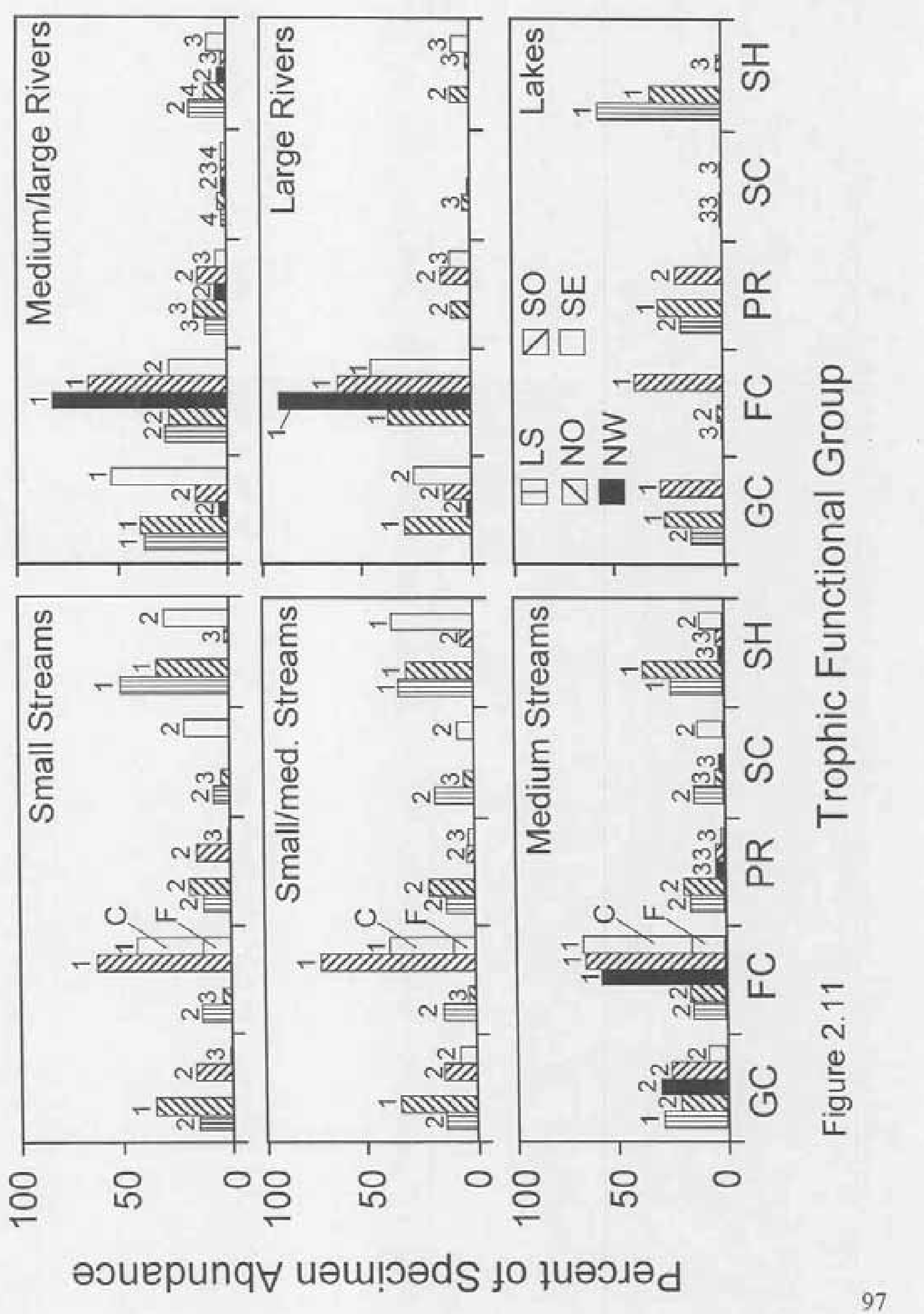
Percent of Specimen Abundance
100
50
0
Small Streams
Small/med. Streams
Medium Streams
Medium/large Rivers
Large Rivers
Lakes
C
F
LS
NO
NW
SO
SE
GC
FC
PR
SC
SH
Trophic Functional Group

Figure 2.11

Figure 2.12. The percentage of mean specimen abundance for five trophic functional groups (Wiggins 1996a, b) within three different sites classes (Table 2.1) of areas of prairie and deciduous forest within the Southern caddisfly region (Figure 2.5). Numbers above each graph denote statistically distinct means within each region and site class (1way Analysis of Variance with Student-Neuman-Keuls test). Trophic functional groups: GC = Gathering Collectors, FC = Filtering Collectors, PR = Predators, SC = Scrapers, SH = Shredders. All filtering collectors were fine particle feeders.

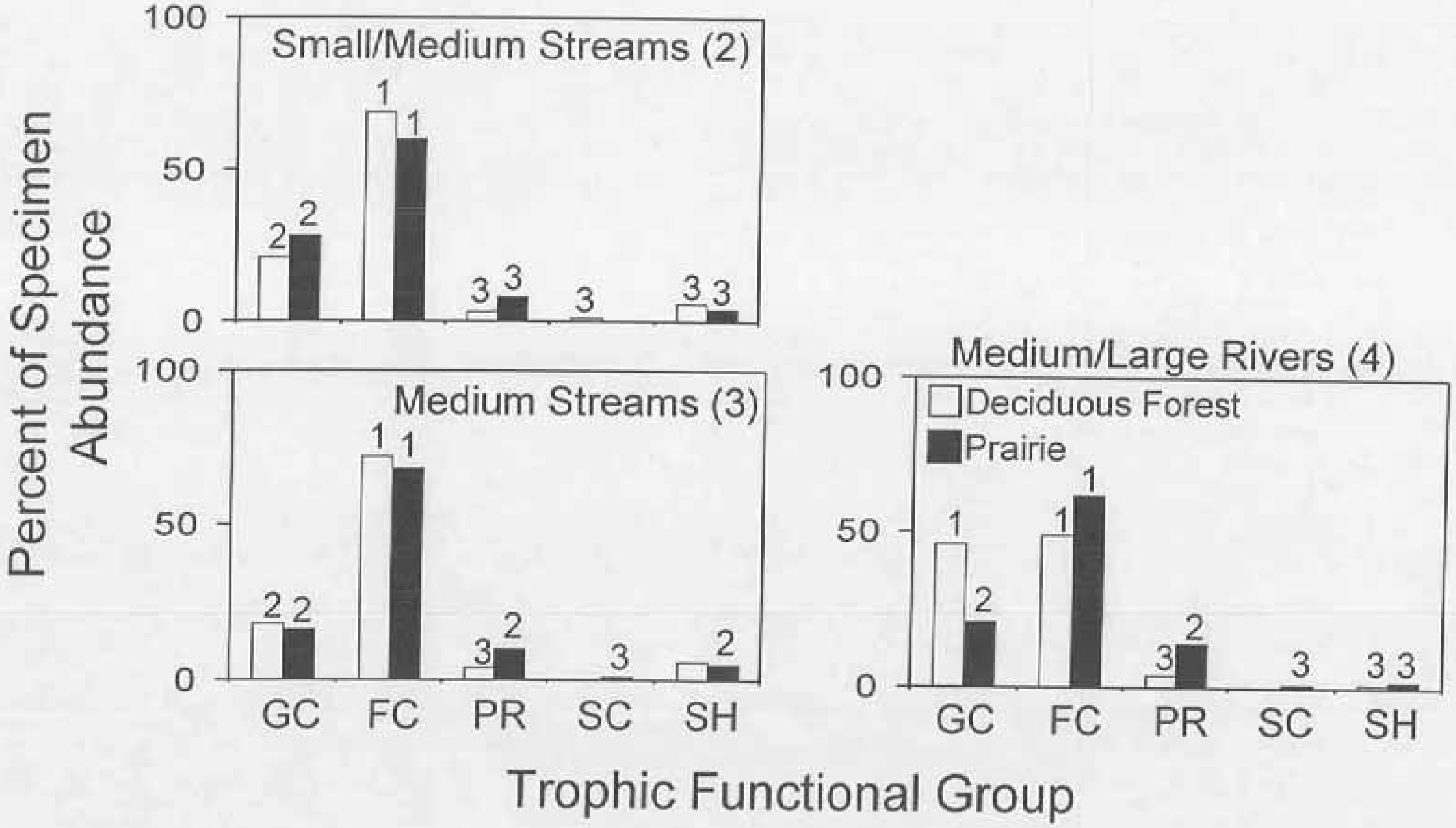
Percent of Specimen Abundance
100
50
0
Small/Medium Streams (2)
1
1
2
2
3 3
3
3 3
Medium Streams (3)
1 1
2 2
3
2
3
2
Medium/Large Rivers (4)
Deciduous Forest
Prairie
1
2
1
1
3
2
3
3 3
GC
FC
PR
SC
SH
Trophic Functional Group

Figure 2.12

CHAPTER 3

EVALUATION OF MINNESOTA GEOGRAPHIC CLASSIFICATIONS BASED ON CADDISFLY DATA

ABSTRACT

The ability to partition the variation of faunal assemblages into homogenous units is referred to as classification strength (CS). In this study, the CSs of three types of geographic classifications: watershed basin, ecological region, and caddisfly region, were compared based on 254 light trap samples of adult caddisflies collected in Minnesota during 1999-2001. The effect on CS of three different levels of taxonomic resolution: family, genus, and species, was also assessed. Primary (broadest possible) *a priori* classifications by watershed basin and ecological region had a lower CS than did secondary classifications by these regions. Caddisfly region, an *a posteriori* classification based directly on caddisfly distribution data, had nearly twice the CS of the *a priori* classifications. CS decreased approximately 20% with a decrease in taxonomic resolution from species to genus, and from genus to family. These results suggest that geographic classification, spatial scale, and taxonomic resolution are all important factors to consider when sampling aquatic insects.

INTRODUCTION

A premise underlying geographic classifications, such as watershed basins, is that sites within each determined class are similar to each other in their physical and biological properties (Omernik 1987, Omernik and Griffith 1991). If effective, natural biological variation among sites within each class can, therefore, be predicted based on measured environmental variables. This idea is important for biomonitoring because it implies that biological responses to human disturbance of a site can be measured by comparing the organismal assemblages of a disturbed site to those of an undisturbed site within the same class (Hughes and Larson 1988, Hughes 1989, Omernik and Bailey 1997). For this implication to hold, classes must successfully partition the variation within a fauna into homogenous regions.

Two of the most commonly used *a priori* geographic classifications pertaining to aquatic biomonitoring are ecological region (e.g., Coniferous Forest) and watershed basin. The former is based on factors such as geology, vegetative cover, and climate, whereas the latter consists of all of the geographic area that drains into a common river (Bailey 1980, Omernick 1987). Both of these classifications can be applied at different spatial scales. Primary or first-level watershed basins (e.g., the Mississippi River) drain directly into the ocean and are the largest determinable hydrologic units. Secondary and succeeding-level watersheds are then subsets of the broader watershed classes. Primary ecological regions, often termed biotic provinces or biomes, are the broadest ecological classifications possible, with succeeding levels nested within them (Bailey 1980).

Since neither watershed basin nor ecological region is created using aquatic organismal distribution data, they may not provide optimal separation of taxa assemblages (Sokal 1974). It becomes important, therefore, to test the relative strength of these classifications in providing such separation before using them as units to sample aquatic biota. Otherwise, comparisons between disturbed and undisturbed sites within classes will be of little value (Hughes and Larson 1988, Hughes 1989, Omernik and

Bailey 1997). The ability of a classification scheme to partition the variation in faunal assemblages into homogenous units is referred to as its classification strength.

Classification strength (hereafter designated "CS") can be calculated as CS = W - B, where W is the mean of all individual within-class site similarities (W;) weighted by sample size, and B is the mean of all between-class site similarities (Smith et al. 1990, Van Sickle 1997). A value of W that is large relative to the value of B means that the classes contain sites that are more similar to each other than they are to sites in other classes (Van Sickle 1997, Van Sickle and Hughes 2000). Thus, classes have successfully partitioned natural variation into homogenous units and, consequently, have a high CS. The value of CS can be tested for statistical significance against the null hypothesis of no class structure by using a permutation procedure (Mielke et al. 1987, Clarke and Green 1988, Smith et al. 1990). In this procedure, the determined CS of a chosen classification scheme is compared with a CS determined by a random grouping of the same sites. The probability value (p) of the test is estimated from the proportion of 10,000 randomly chosen groups having a larger CS than the tested classification (Jackson and Somers 1989, Van Sickle 1997).

Hawkins et al. (2000) reviewed the literature on CS testing, summarizing both aquatic vertebrate and invertebrate studies. They found that watersheds and ecological regions typically had similar CSs. Both classification schemes applied at secondary or higher levels tended to have higher CS than did those applied at primary levels. Regions created from distribution data of studied organisms, termed *a posteriori* classifications, almost always had higher CS than did *a priori* regions. Increasing the level of taxonomic resolution from family to genus or species almost always increased CS, regardless of the classification scheme used.

The state of Minnesota is situated at the intersection of the three largest biotic provinces of North America: Coniferous Forest, Deciduous Forest, and Prairie (Figure 3.1) (Bailey 1980). These three provinces are subdivided into 10 ecological sections (secondary ecological regions) (Hanson and Hargrove 1996). Minnesota is likewise at the intersection of three primary watersheds: Hudson Bay, Mississippi River, and Saint Lawrence Seaway (Figure 3.1), which are divided into eight secondary and 81 tertiary watersheds, often termed watershed provinces and major watersheds, respectively (Schwartz and Thiel 1954, USES 2002). Several environmental variables, including climate, geology, soil type, vegetative cover, topographic relief, and level of human disturbance vary notably from north to south or east to west within Minnesota (Borchert and Yaeger 1968, Wright 1972, Anderson and Grigal 1984, Baker et al. 1985, Coffin 1988, Tester 1995). The ecological and aquatic diversity of the state, therefore, provides several different criteria for classification.

The caddisflies (Trichoptera) are an important group for biomonitoring due to their high species richness, ecological diversity, varying susceptibilities to different types of human disturbances, and abundance in virtually all types of freshwater ecosystems (Mackay and Wiggins 1979, Rosenberg and Resh 1993, Merritt and Cummins 1996, Barbour et al. 1999, Dohet 2002). For biomonitoring purposes it is, therefore, important to find a classification scheme that successfully partitions natural variation of the Minnesota caddisflies into homogenous regions. A classification that does so will have a have high caddisfly CS and will be appropriate units for caddisfly sampling.

Houghton (Chapter 2) used Detrended Correspondence Analysis and a flexible unweighted pair-group method using arithmetic averages (UPGMA) dendogram to group 58 Minnesota watersheds into five regions of caddisfly biodiversity based on caddisfly relative abundance (Figure 3.2). As an a posteriori classification created using caddisfly data, caddisfly region was assumed to be the optimal partitioning of faunal variation within Minnesota. It should, therefore, have a higher CS than a priori classifications that ignore caddisfly distribution data.

This study had three main objectives. The first was to compare the CSs of caddisfly region, ecological region, and watershed basin based on caddisfly data. This comparison will determine if the created caddisfly regions have a greater value as caddisfly sampling units than alternative a priori classifications. The second objective was to compare the CSs of first and second-level watershed and ecological region classifications to assess the effects of spatial scale. The third was to assess the effects of three levels of taxonomic resolution-family, genus, and species-on CS of all classifications.

MATERIALS AND METHODS

Sampling. Adult caddisflies were sampled during June and July, the peak period of emergence and flight activity (Monson 1996). Larvae were not collected as most are not identifiable to the species level and species-level identification was necessary for this study. Between three and 12 samples were collected from 58 of Minnesota's 81 major watersheds yielding a broad distribution of sampling sites (Figure 3.2). Several studies have suggested that most adult caddisflies disperse <100 m from the natal habitat (Sode and Wiberg-Larsen 1993, Petersen et al. 1999). Since virtually all of the sampling sites in this study were separated by >5000 m, dispersal of adults between sites was assumed to be negligible. To standardize weather conditions, samples were taken only on days with peak daytime temperature >22°C, dusk temperature >13°C, and without precipitation or noticeable wind at dusk (Waringer 1991, Anderson and Vondracek 1999). Caddisflies were sampled at each site with an ultraviolet light trap, which consisted of an 8-watt portable ultraviolet light placed over a white pan filled with 70% EtOH. These traps were placed adjacent to aquatic habitats at dusk and retrieved approximately two hours after dusk. By standardizing the time of collection, wattage of the light source, and size of collecting pan, the technique likely yielded a representative sample of the nocturnally active caddisfly adults and allowed comparisons between sites.

To characterize caddisfly diversity within different types of habitats, sampling sites were divided into six site classes (Table 3.1); five of these classes were based on stream width estimated at the sampling sites; the sixth class constituted lakes and wetlands. Site classes were not synonymous with hydrologic stream order (Strahler 1964). Samples were collected from at least one small stream (Class 1-2), one medium stream (Class 3), one large river (Class 4-5), and one lake or wetland (Class L) from each of the 58 watersheds that contained such habitats. All sampling sites were perceived to be the least disturbed among their representative watershed.

Adults were collected from 254 aquatic habitats during 1999-2001. A total of 306,541 specimens were identified and counted, representing 224 species. Females that were not readily identifiable to the species level were ignored. All identified specimens were entered into the relational database Biota (Colwell 1996). Each vial of specimens was affixed with a barcode label, thus allowing direct scanning into Biota, and the permanent association of all known ecological information about specimens with their unique code. All specimens collected during this study were deposited in the University of Minnesota Insect Museum (UMSP).

Analysis. Sorensen coefficients (Sorensen 1948) were calculated for all pairwise combinations of samples using caddisfly species presence/absence data. This is a commonly used expression of the similarity of taxa between sites, and ranges from 0 (no species in common) to 1 (all species on common). Calculations of W; and W were made for each classification using the MRPP function of the program PC-ORD for Windows,@ (Mielke et al. 1976, McCune and Medford 1997). Calculations of B and overall CS for each classification were made using the freeware program MEANSIM6 for Windows® (http://www.epa.gov/wed), which uses output from the MRPP function to make these calculations.

Values of W;, W, B, and overall CS were determined for each classification scheme. These values were plotted as mean similarity dendograms, with W; - B for each individual class represented as individual branch length on a dendogram. This allowed for graphic comparison of the relative CSs of the various classifications and classes, since relative CS could not be tested for statistical significance (Feminella 2000, Van Sickle and Hughes 2000).

RESULTS AND DISCUSSION

CSs ranged from 2% to 15% and all tested groupings exhibited a statistically significant CS (Figures 3.3-3.5). Statistical significance, however, may have been misleading. Van Sickle and Hughes (2000) argued that permutation tests for CS are too powerful, especially with sample size >50, and that even weak CSs will likely be deemed significant. Sample size for this study was 254 sites. Because tests of CS are against a model of no class structure-a completely random grouping of sites-it is difficult to translate statistical significance into biological significance. A CS of 2% may be statistically significant, yet is only 2% better at partitioning faunal variation than is a random site grouping. For this reason several workers have suggested that the no class structure model is not particularly informative, and that considerably more information can be learned from comparing the biological significance (dendogram branch lengths) of competing classifications rather than by testing the statistical significance of a single classification (Green 1980, Gordon 1981, Yocoz 1991, Stewart-Oaten et al. 1992, Hillborn and Mangel 1997, Van Sickle and Hughes 2000).

Caddisfly Regions. As expected, CS of caddisfly region was the highest (12-17%) among classifications across the three taxonomic levels, exhibiting approximately twice the CS of any other classification (Figures 3.3-3.5). All individual classes had CS >5% at the species level. At all taxonomic levels the Lake Superior and Southeastern regions had consistently lower values of W; than the other classes and, therefore, lower CSs. Houghton (Chapter 2) found that these two regions had a lower Morita-Horn index of biological similarity (Margurran 1988) than did the other regions due to greater topographical variation and subsequent heterogeneity of sampling sites. Site heterogeneity lowered W; in these regions.

Caddisfly regions were created using caddisfly data specifically, as opposed to other physical or biological data. This classification should, therefore, have yielded an optimal partitioning of the fauna. Furthermore, since the regions were determined from collections made during 1999-2001, they automatically incorporated anthropogenic disturbance, whereas watersheds and ecological regions were based entirely on the best determination of natural conditions (Bailey 1980, Omernik 1987, USGS 2002). `All samples in this study were taken from the least disturbed habitats within the individual ecosystems. "Least disturbed", however, may be relative. Much of northeastern Minnesota remains forested while almost all of northwestern and southern Minnesota-has been converted to agricultural or urban environments (USGS 1999). True reference sites may not exist in these areas. Houghton (Chapter 2) found that the relative level of disturbed habitat correlated with caddisfly species composition in Minnesota, likely contributing to the higher CS of caddisfly region.

Despite the perceived best possible partitioning of the caddisfly fauna by caddisfly region, these regions still had relatively weak (<20%) CSs. These values were consistent with those of previous studies; only rarely were CS values >20%, even for a posteriori classifications (see Hawkins et al. 2000). This low CS may leave the majority of faunal variation unaccounted for by even the best determined classifications. Individual species distributions are continuous, and forcing a discrete model on to a series of such continuous distributions is artificial (Hawkins and Vinson 2000). Wide-ranging species that occur in more than one class raise the value of B, which lowers overall CS. Secondly, within-class environmental heterogeneity-whether caused by natural or anthropogenic factors-lowers the value of W, which also lowers CS. Some of this heterogeneity may have been mitigated because caddisfly regions incorporated anthropogenic factors. Watersheds and ecological regions likely had lower CSs because they did not incorporate such factors. All classifications may simply have been too coarse to successfully partition the caddisfly fauna. A substantial amount of within-class heterogeneity was likely added to all classifications including caddisfly regions by intentionally sampling different types of aquatic habitats (Table 3.1). Sampling only medium-sized streams, for example, would likely have yielded a higher CS value for all classifications. This strategy, however, is impractical for biomonitoring unless only one type of habitat is of interest.

Ecological Regions and Watersheds. At a similar spatial scale, ecological region had a higher CS than watershed at all taxonomic levels (Figures 3.3-3.5). Biotic province had a higher CS than primary watershed while ecological section had a higher CS than secondary watershed. Biotic province had approximately the same CS as secondary watershed (Figures 3.3-3.5). This pattern was not surprising. Ecological regions include a variety of physical and biological data such as climate, vegetative cover, and geology. These variables could potentially affect caddisfly distributions. In contrast, watershed basins are simply hydrologic units and do not incorporate ecological data. This phenomenon was noted by Hawkins et al. (2000) who found that watersheds had a higher CS than ecological regions only when they were smaller than the corresponding ecological regions (see "Spatial Effects").

Previous studies using aquatic organismal data have found that the highest CSs (>10) of ecological regions occurred in areas with notable topographic and climatic variation, such as the South Platte River Basin (Tate and Heiny 1995), Ozark Highlands and Plains (Rabeni and Doisy 2000), Australian Highlands and Lowlands (Marchant et al. 2000), Alaska Range (Oswood et al. 2000), Rocky Mountains and Wyoming Basin, and the Victoria region of Australia (Newall and Wells 2000). Climate and topographic relief appeared to be more important to partitioning the variation of the aquatic biota than vegetative cover, geology, or the other common variables used in forming ecological regions. Many aquatic organisms can exist in only a limited temperature range; likewise, the change in the physical force of strearnflow promoted by topographic variation is an important factor in determining aquatic organismal assemblages (e.g., Allan 1995).

In Minnesota, environmental temperature decreases in a northeasterly direction (Baker et al. 1985). Minimal topographic variation exists in Minnesota up to the eastern border where the Lower Saint Croix and Mississippi River gorges, as well as the Lake Superior Rift Zone promote relatively high relief (Borchert and Yaeger 1968). Level of disturbed habitat also decreases in an approximately northeasterly direction (USGS 1999). Houghton (Chapter 2) found that temperature, stream gradient, and level of disturbed habitat correlated with caddisfly species assemblages in Minnesota. The Red River Valley ecological section likely had the highest CS among ecological sections because it encompassed an area of similar temperature, topography; and landuse, thereby increasing W; and overall CS (Figure 3.1). The borders of this region were similar to those of the Northwestern caddisfly region and included almost identical sampling points (Figures 3.1-3.2). The Minnesota and Iowa Morainal ecological section contained considerable temperature variation because of its length from north to south for most of the length of the state. It, therefore, had a W_i value lower than B and, thus, negative CS (Figure 3.1).

A similar situation occurred with watershed basins. Among primary watersheds, the Saint Lawrence Seaway had by far the highest CS (Figure 3.1j. This region corresponded closely to the Lake Superior caddisfly region (Figure 3.2). It was also the smallest of the three primary watersheds (see "spatial effects"). The Lake Superior, Red River Valley, and Saint Croix secondary watersheds all had consistently higher than average CS among secondary watersheds. The first two had borders similar to the Lake Superior and Northwestern caddisfly regions (Figure 3.1-3.2) and encompassed areas of similar temperature, topography, and landuse (Figure 3.1). The same was true for the Saint Croix watershed, even though it was not by itself similar to a caddisfly region (Figure 3.1). The Mississippi River watershed likely had the lowest W; and CS due to variations in temperature and landuse (Figure 3.1).

Spatial Effects. At all three levels of taxonomic resolution, secondary groupings of both watersheds and ecological regions had higher CSs than did primary groupings (Figures 3.3-3.5). For both watersheds and ecological regions, values of B were similar for both primary and secondary groupings. Values of W; were, in general, higher with secondary groupings (Figures 3.3-3.5). These results demonstrated that the smaller regions were more successful at partitioning the variation into homogenous units. Several previous studies (see Hawkins et al. 2000) had similar results when comparing primary and secondary classifications.

The higher CS of smaller regions may have been due to several factors. Smaller regions have less environmental heterogeneity relative to that which occurs between the regions. Ecological regions and watersheds that encompassed areas of similar temperature, stream gradient, and landuse had higher CS than those that encompassed areas with a range of these values. Regardless of the exact placement of a region, however, smaller units are likely to have less environmental variation simply because they are smaller (e.g., Hawkins at al. 2000) and this will increase the value of W;.

Smaller regions may also have had a higher CS because sampling sites were more contiguous. Van Sickle and Hughes (2000) found that geographic clusters had a higher CS than did any a priori classification. McCormack et al. (2000) determined that similarity between sites decreased as a function of the distance between sites. Smaller regions will have, on average, less distance between samplng sites than will large regions. This close proximity of sites will likely decrease the value of B and increase CS in small regions even if the sites are grouped without consideration of environmental variables. This may be particularly true with watershed basins. Although differences in physical variables that determine aquatic organismal distributions such as stream gradient, water chemistry, or substrate may exist between watersheds, such regions are essentially geographic, not biological partitions (Hawkins et al. 2000).

Taxonomic Resolution. CS increased with increased taxonomic resolution for all classifications (Figures 3.3-3.5). For all classifications, both B and W decreased with increased taxonomic resolution; there; was less chance of any two sites having a lower taxon in common than a higher taxon. W exhibited a smaller decrease than B with increasing resolution; a lower taxon was more likely to be unique to a region than a higher taxon. Within caddisfly regions 12% of CS was lost when decreasing the taxonomic resolution from species (CS = 0.17) to genus (CS = 0.14), and another 20%

was lost from genus to family (CS = 0.12) (Figure 3.6). A similar trend emerged with both watersheds and ecological regions at both primary and secondary scales (Figure 3.6). On average, CS decreased by approximately 0.02 between levels of resolution for all classifications. Individual classes of all classifications generally maintained their CS relative to other classes at the different levels of resolution (Figures 3.3-3.5).

The majority of CS studies to date have found that increasing taxonomic resolution increases CS of the sampling grouping with both vertebrates (Van Sickle and Hughes 2000) and invertebrates (Marchant et al. 1995, Hawkins and Norris 2000, Hawkins and Vinson 2000, Feminella 2000, Hawkins et al. 2000, Waite et al. 2000). Identification to the lowest taxon possible has the greatest ability to discern biological differences among sites, thereby increasing the power of biological water quality monitoring (Resh and Unzicker 1975, Cranston 1990, Resh and McElravy 1993). Some workers argue, however, that this increase in CS is of minimal importance compared to the added difficulty and expense of species-level identification, and that general trends in family data parallel those of species data (Warwick 1993, Bowman and Bailey 1997, Feminella 2000). For many aquatic invertebrates, including caddisflies, species-level identification is not possible with larvae.

In their review of CS literature, Hawkins et al. (2000) found a typical decrease in CS of 0.03-0.10 (ca. 10-25%) when decreasing taxonomic resolution from genus-species to family. Those results are consistent with the current study. It is difficult to judge the biological significance of this documented decrease. While probably important, the 20% decrease in CS with decreasing taxonomic resolution is certainly less than the 5,,50% decrease in CS when using any classification other than caddisfly region. Hawkins et al.

(2000) likewise found that classification was more important than level of taxonomic resolution.

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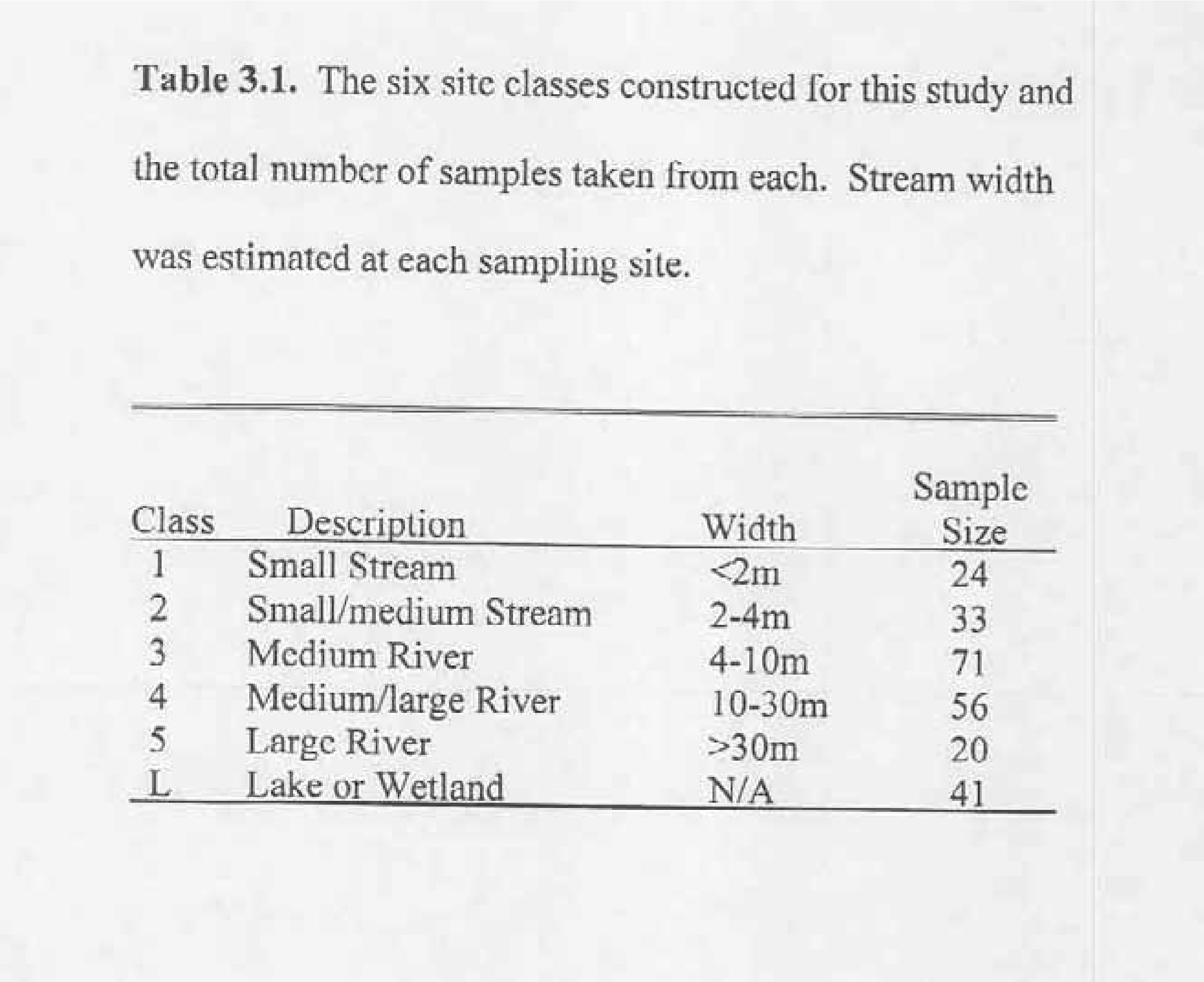

Table 3.1. The six site classes constructed for this study and the total number of samples taken from each. Stream width was estimated at each sampling site.

Class	Description	Width	Sample Size
1	Small Stream	<2m	24
2	Small/medium Stream	2-4m	33
3	Medium River	4-10m	71
4	Medium/large River	10-30m	56
5	Large River	>30m	20
L	Lake or Wetland	N/A	41

Figure 3.1. Location of Minnesota showing two geographic classifications. A. Primary watersheds (boldface type), HB = Hudson's Bay, MR = Mississippi River, SL = Saint Lawrence Seaway, divided into secondary watersheds (regular type), LS = Lake Superior, MN = Minnesota River, MS = Mississippi River, RA = Rainy River, RE = Red Rver, SC = Saint Croix River (USGS 2002). B. Biotic provinces (boldface type), CF = Coniferous Forest, DF = Deciduous Forest, PR = Prairie, divided into ecological sections (regular type), DLP = Drift and Lake Plains, GP = Glaciated Plains, MIM = Minnesota and Iowa Morainal, NS = Northern Superior Uplands, PE = Peatlands, PP = Paleozoic Plateau, RRV = Red River Valley, WS = Western Superior Uplands (Bailey 1980, Hanson and Hargrove 1996). Darkened areas correspond to the Missouri secondary watershed, and to the Aspen Parkland and Southern Superior Uplands ecological sections, respectively. These areas had insufficient sample size to be included in any analyses.

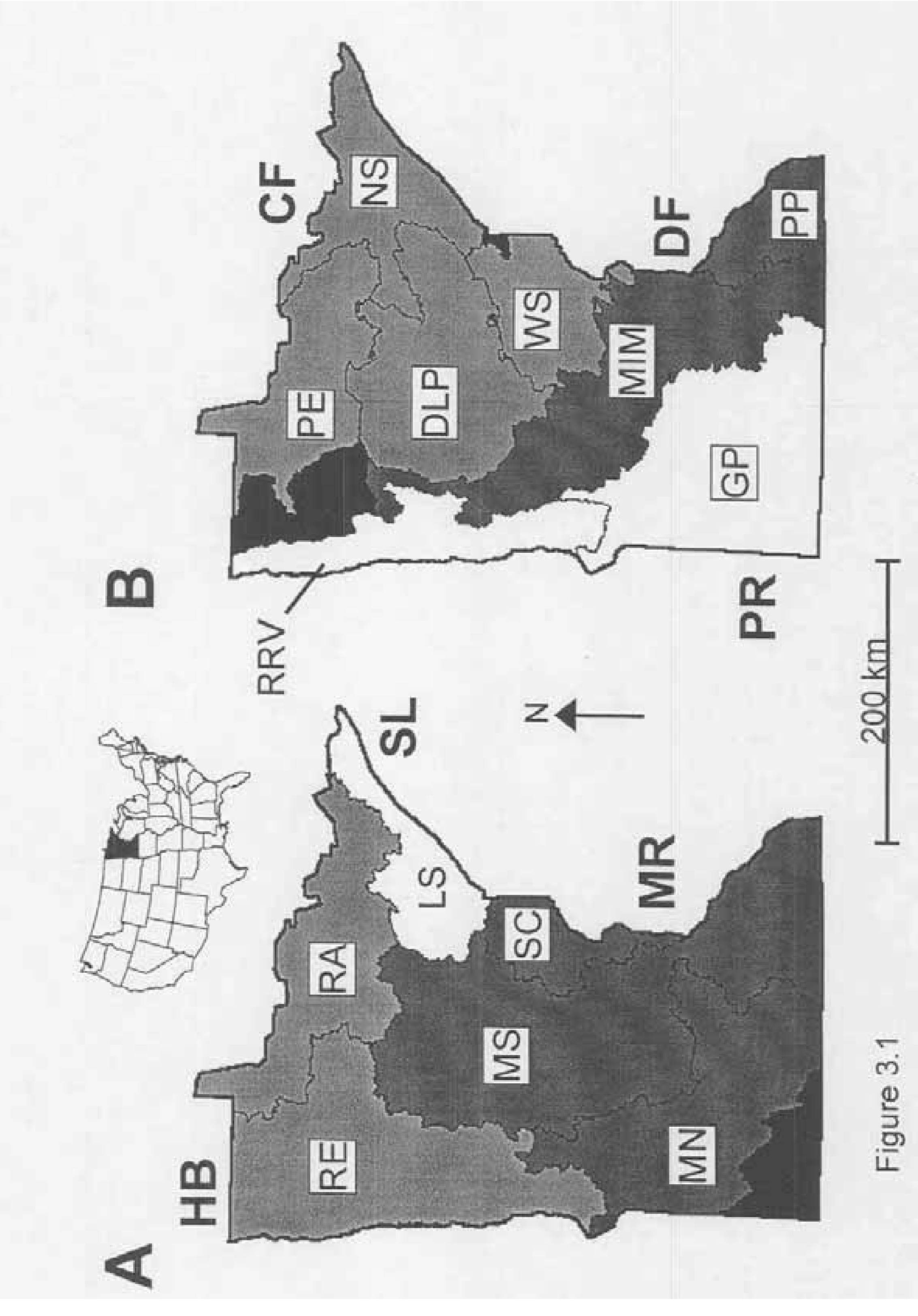
A
HB
RE
RA
MS
SC
LS
SL
MN
MR
B
RRV
PE
DLP
CF
NS
WS
MIM
DF
GP
PR
PP
N
200 km

Figure 3.1

Figure 3.2. The five caddisfly regions of Minnesota determined by grouping together Minnesota's 81 major watersheds (Chapter 2) and the 254 sampling sites of this study. Overlap occurs between sample markers. Regions: LS = Lake Superior, NO = Northern, NW = Northwestern, SE = Southeastern, SO = Southern.

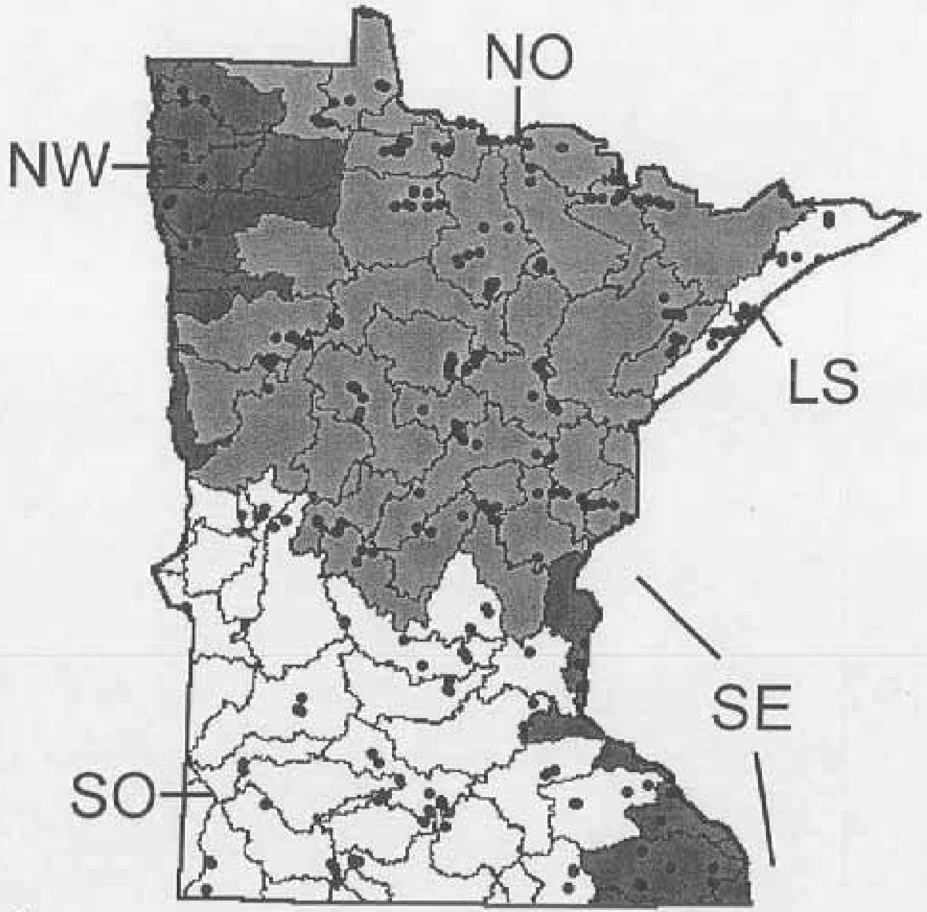

Figure 3.2

Figure 3.3. Mean similarity dendograms for caddisfly region (Figure 3.2), watershed, and ecological regions (Figure 3.1) using presence or absence of Minnesota caddisfly species. For each dendogram, the node (vertical line) is plotted at the mean betweenclass similarity (B) for each grouping, and the end of each horizontal branch is plotted at the mean within-class similarity for the individual class (W;). Classification Strength (CS) is the mean length of dendogram branches for each class weighted by sample size, and is calculated with the formula CS = W - B.

Figure 3.3

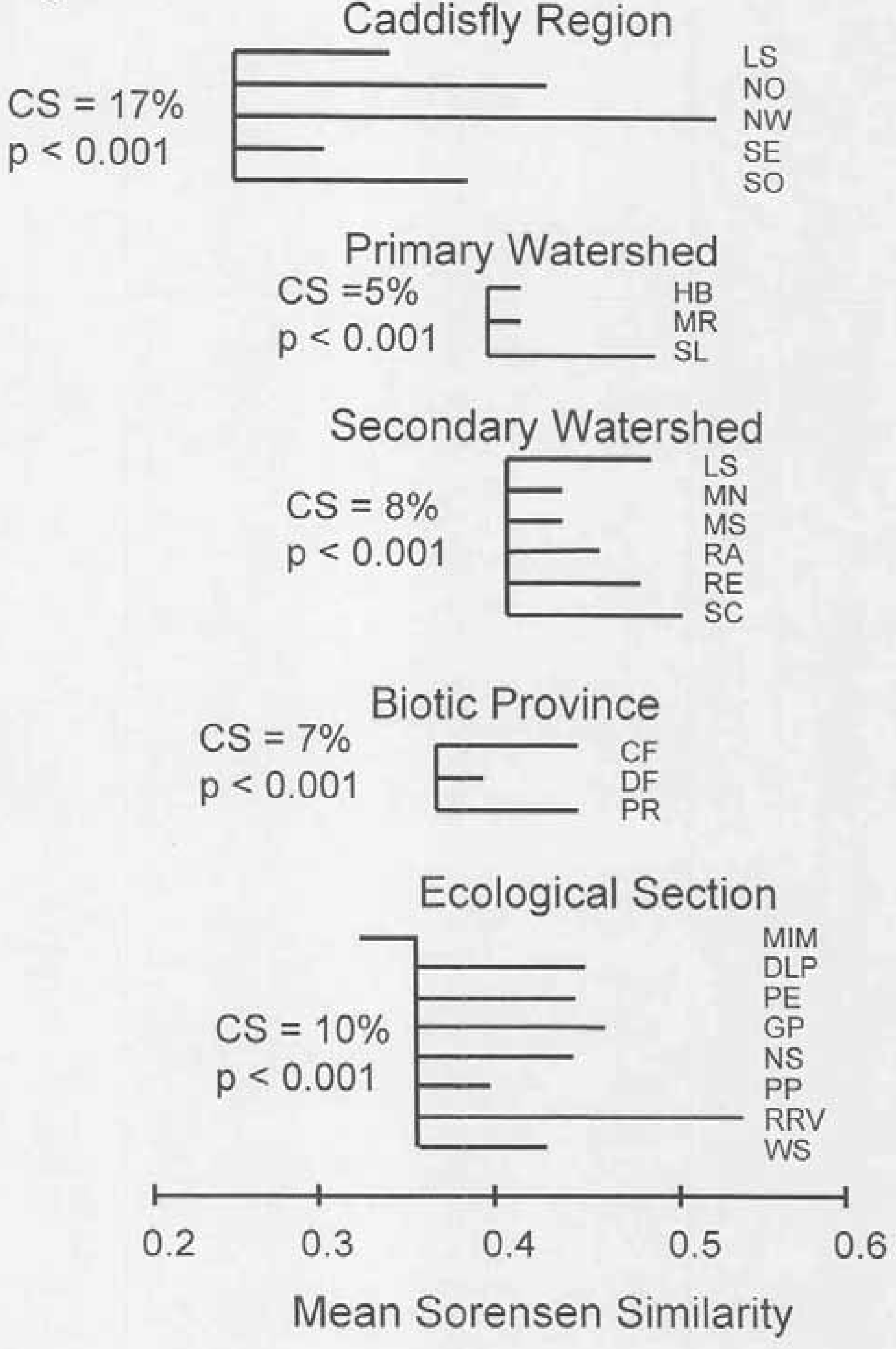
Caddisfly Region
CS = 17%
p < 0.001
LS
NO
NW
SE
SO
Primary Watershed
CS =5%
p < 0.001
HB
MR
SL
Secondary Watershed
CS = 8%
p < 0.001
LS
MN
MS
RA
RE
SC
Biotic Province
CS = 7%
p < 0.001
CF
DF
PR
Ecological Section
CS = 10%
p < 0.001
MIM
DLP
PE
GP
NS
PP
RRV
WS
0.2
0.3
0.4
0.5
0.6
Mean Sorensen Similarity

Figure 3.4. Mean similarity dendograms for caddisfly region (Figure 3.2), watershed, and ecological regions (Figure 3.1) using presence or absence of Minnesota caddisfly genera. See Figure 3.3 for further explanation.

Figure 3.4

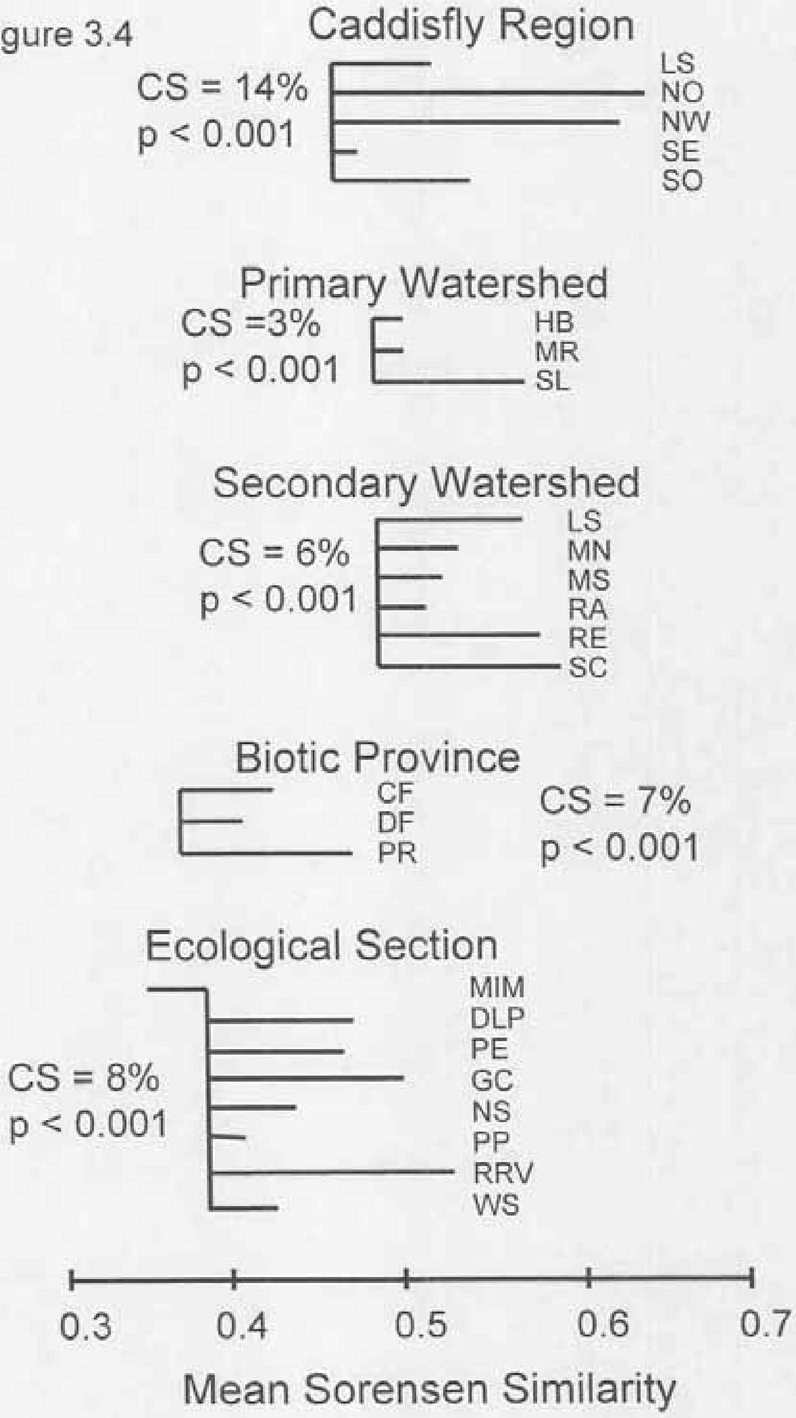
Caddisfly Region
CS = 14%
p < 0.001
LS
NO
NW
SE
SO
Primary Watershed
CS =3%
p < 0.001
HB
MR
SL
Secondary Watershed
CS = 6%
p < 0.001
LS
MN
MS
RA
RE
SC
Biotic Province
CF
DF
PR
CS = 7%
p < 0.001
Ecological Section
MIM
DLP
PE
GC
NS
PP
RRV
WS
CS = 8%
p < 0.001
0.3
0.4
0.5
0.6
0.7
Mean Sorensen Similarity

Figure 3.5. Mean similarity dendograms for caddisfly region (Figure 3.2), watershed, and ecological regions (Figure 3.1) using presence or absence of Minnesota caddisfly families. See Figure 3.3 for further explanation.

Figure 3.5

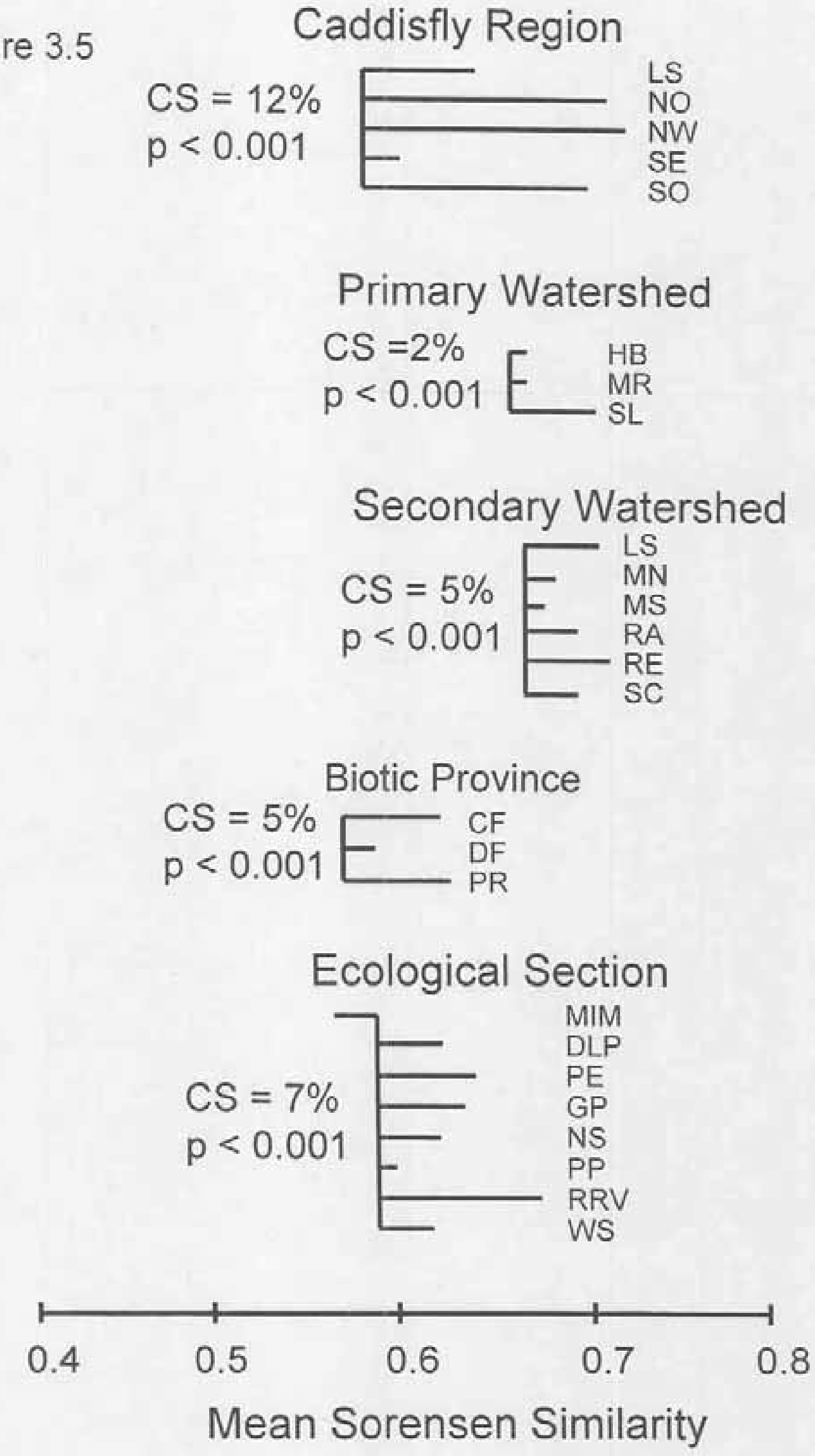
Caddisfly Region
CS = 12%
p < 0.001
LS
NO
NW
SE
SO
Primary Watershed
CS =2%
p < 0.001
HB
MR
SL
Secondary Watershed
CS = 5%
p < 0.001
LS
MN
MS
RA
RE
SC
Biotic Province
CS = 5%
p < 0.001
CF
DF
PR
Ecological Section
CS = 7%
p < 0.001
MIM
DLP
PE
GP
NS
PP
RRV
WS
0.4
0.5
0.6
0.7
0.8
Mean Sorensen Similarity

Figure 3.6. CS at three levels of taxonomic resolution for the three strongest geographic classifications, based on Minnesota caddisfly presence or absence.

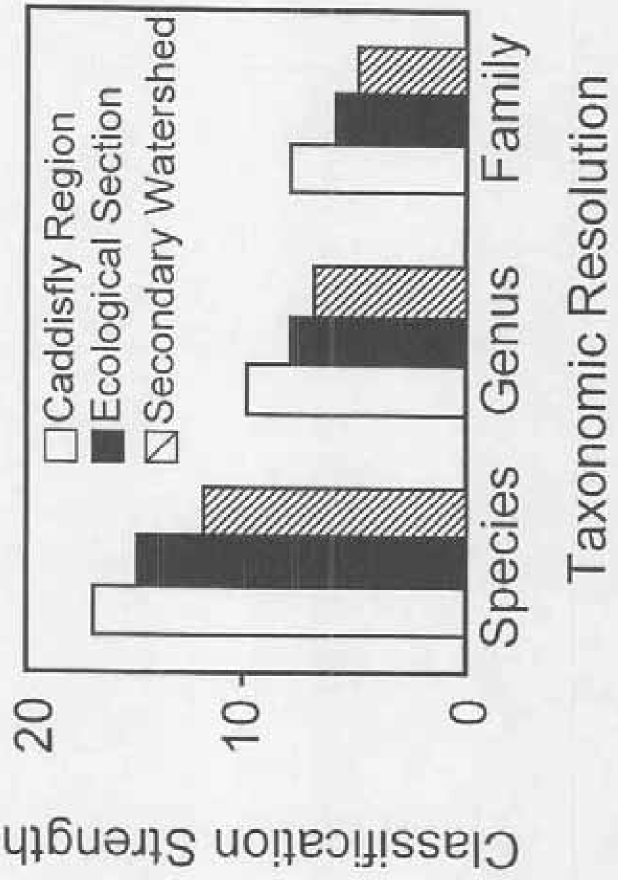
Classification Strength
20
10
0
□ Caddisfly Region
■ Ecological Section
▨ Secondary Watershed
Species
Genus
Family
Taxonomic Resolution

Figure 3.3

CHAPTER 4

PHENOLOGY AND HABITAT AFFINITIES OF THE MINNESOTA CADDISFLIES (INSECTA: TRICHOPTERA)

ABSTRACT

Over 300,000 caddisfly specimens were examined from 317 light trap samples collected during 1999-2001, and from museum and literature records. Two hundred-eighty four caddisfly species were determined to occur in Minnesota, representing 20 families and 74 genera. The distribution and relative occurrence in different regions, habitat types, and levels of upstream disturbance was documented for each species. The majority of Minnesota species appeared to be univoltine, with adult emergence and flight occurring in June and July. There were, however, other species that were detected in the spring, fall, winter, or during multiple seasons. Fifty-three percent of all specimens were represented by eight species, whereas 81 species were known from <10 specimens. Seven of the 13 species with official protective status in Minnesota were located during 1999-2001. Two were more widespread than previously thought. Binomial regression determined that 16 species were statistical indicators of particular habitats and site conditions in Minnesota. Presence of three species appeared to indicate habitat disturbance, particularly the disturbance of lakes and small streams. Presence of the remaining 13 species was related to both latitude and habitat disturbance. These species may be valuable as indicators of undisturbed habitats, but their response to latitude must first be separated from their response to habitat disturbance.

INTRODUCTION

The biological diversity of organisms, or biodiversity, has become an important scientific topic over the last 15-20 years, largely due to a measured decline in worldwide organismal biodiversity and concern over the potential ecological implications of such a decline (e.g., Reaka-Kudla et al. 1957). Biodiversity studies include both species population data, and also the physical and biological factors contributing to the documented populations (e.g., Mickevich 1999). Such data are crucial for a basic understanding of ecosystem ecology, organism conservation, and cladistic biogeography (Readka-Kudla et a1.1997, McKamey 1999, Mickevich 1999, Solis 1999). Constructing baseline biodiversity databases is necessary so that potential future changes in organismal distributions can be evaluated scientifically. This necessity is particularly profound with insects, a diverse group that is historically poorly known relative to less diverse taxa such as birds and mammals (Mickevich 1999). Documentation of aquatic insect biodiversity takes on an additional measure of importance due to the group's association with water quality monitoring.

The caddisflies (Trichoptera) are an important water quality indicator group due to the order's taxonomic richness, ecological diversity, and abundance in virtually all freshwater ecosystems (Mackay and Wiggins 1979, Rosenberg and Resh 1993, Merritt and Cummins 1996, Barbour et al. 1999, Dohet 2002). Almost 80% of the taxa for which data are available are thought to be intolerant to organic pollution (Barbour et al. 1999). A loss of caddisfly species richness, therefore, may indicate habitat disturbances such as agriculture, grazing, logging., or urbanization (Ford 1989, Resh 1993, Barbour et al. 1995, DeShon 1995, Karr and Chu 1999); all of these landuses can increase organic matter in aquatic habitats (Gianessi et al. 1986, Turner and Rabalais 1991, Allan 1995, Karr and Chu 1999).

Although generally classified as intolerant, populations of some caddisfly species may actually increase with increased organic pollution (Barbour et al. 1999). Establishing the characteristic caddisfly faunal assemblages of different habitat types and levels of disturbance, therefore, will increase the utility of Trichoptera in biomonitoring. Several recent studies have attempted this by using a variety of multivariate approaches such as correspondence analysis (Sommerhauser 1999, DeMoor 1999, Dohet 2002) or discriminant function analysis (Resh et al. 2002). Such analyses result in the ability to predict the characteristic caddisfly assemblages based on natural and anthropogenic site variables and, ideally, the ability to predict site conditions based on sampled caddisfly assemblages (Reynoldson et al. 2001). Even basic checklists that document species occurrences in various habitat types and levels of disturbance have value, however, as such studies suggest species that warrant further study as potential environmental indicators.

Six studies in North America have thoroughly assessed the caddisflies of a region (Betten 1934, Ross 1944, Denning 1956, Unzicker et al. 1982, Harris et al. 1991, Moulton and Stewart 1996). All of these studies provide 'at least anecdotal associations between caddisfly species presence and habitat types, whereas Moulton and Stewart (1996) document the specific habitat affinities and general adult flight phenology for the caddisflies of the North American Interior Highlands. Although a recent checklist has been compiled for the Minnesota caddisflies (Houghton et al. 2001), specific habitat preference data are not available for individual species. The main objectives of this study were to document the general flight phenology of the Minnesota caddisfly fauna, to determine associations between species assemblages and both natural and anthropogenic variables, and to attempt to identify species whose presence may statistically indicate various habitat types, disturbance levels, or both.

MATERIALS AND METHODS

Sampling. Caddisfly adults were sampled primarily by an ultraviolet light trap which consisted of an 8-watt portable ultraviolet light placed over a white pan filled with 70% EtOH. These traps were placed adjacent to aquatic habitats at dusk and retrieved approximately two hours after dusk. By standardizing the time of collection, wattage of the light source, and size of collecting pan, the technique likely yielded a representative sample of the nocturnally active caddisfly adults and allowed for comparisons between sites. Larvae were not collected as most are not identifiable to the species level. Other sporadic adult collecting techniques included sweep netting and aspiration from riparian rocks and vegetation. These techniques were used mainly to find species that emerge during winter and early spring and rarely fly to lights due to cold weather. Caddisfly specimens from the University of Minnesota Insect Museum (UMSP) were also examined.

Several studies have suggested that dispersal of adults is minimal, and that most species fly <100 m from the natal habitat (Sode and Wiberg-Larsen 1993, Petersen et al. 1999). Since virtually all of the sampling sites in this study were separated by >5000 m, dispersal of adults between sites was considered unimportant. To standardize weather conditions, samples were collected only if the peak daytime temperature was >22°C, dusk temperature was >13°C, and there was no perceptible wind or precipitation at dusk (Waringer 1991, Anderson and Vondracek 1999).

To characterize caddisfly diversity within different types of habitats, sampling sites were divided into six site classes (Table 4.1); five of these classes were based on stream width estimated at the sampling site, the sixth class constituted lakes and wetlands. Site classes were not synonymous with hydrologic stream order (Strahler 1964). Samples were collected from at least one small stream (Class 1-2), one medium stream (Class 3), one large river (Class 4-5), and one lake or wetland (Class L) from each of the 58 watersheds that contained such habitats. All sampling sites were perceived to be the least disturbed possible of their representative watershed.

Data Entry and Table Preparation. Females of specimens that were not readily identifiable to the species level were ignored. All identified specimens were counted and entered into the relational database Biota (Colwell 1996). Each vial of specimens was affixed with a barcode label, thus allowing direct scanning into Biota to permanently associate all known ecological information about specimens with their unique code and number. All specimens examined during this study were deposited in the UMSP.

The period of adult capture for each species was noted and represented as Winter (November-February), Spring (March-May), Summer (June-July) or Fall (September-October). Species were referenced based on four environmental classifications: caddisfly region (Figure 4.1) (Chapter 2), site class (Table 4.1), estimated stream gradient based on the appearance of the site and on the change in elevation per area of the surrounding watershed (Borchert and Yaeger 1968, USGS 2002), and the percentage of disturbed habitat upstream of each collecting site (USGS 1999). Houghton (Chapters 2-3) concluded that caddisfly region was the most appropriate geographic classification to represent caddisfly diversity on a statewide level. He also concluded that stream gradient and percentage of disturbed upstream habitat were related to the overall distribution of Minnesota caddisflies. The same variables likely influence individual species distributions. Species were represented as either not occurring in a class of environmental variable, occurring in <50% of samples taken from the class, or occurring in >50% of samples taken from the class.

Indicator Species Analysis. Binomial regression models were calculated for summer-emergent species using the freeware program Arc for Windows® (http://www.wiley.com/mathematics). A detailed discussion of this technique can be found in Cook and Weisberg (1999). Unlike most regression models where the value of the response (Y) is continuous-taking any value within a given interval-binomial regression responses can take only two values, species presence (1) or species absence (0). Calculated models predicted the occurrence of each species based on the values of predictor variables, assuming such responses were linear. Predictor variables were tested for statistical significance by assessing if the slope relating the predictor and each response variable was significantly different from zero.

Latitude, stream gradient, and percentage of disturbed upstream habitat were considered likely candidates for predicting the presence or absence of species. Houghton (Chapter 2) concluded that the latter two variables were related to distributions of Minnesota caddisflies when measured on a watershed level. Percentage of disturbed upstream habitat was determined for each site (USGS 1999). Stream gradient was estimated at the site and placed into one of four classes-low, medium, high and none (lakes and wetlands). To a degree, this classification took into account differences due to site class (Table 4.1), as it separated lakes and streams, as well as streams of differing gradient. Latitude-measured at each site with a handheld GPS unit-was used as a surrogate for environmental temperature, the third variable relating to Minnesota caddisfly distributions (Chapter 2). Latitude and temperature correlate strongly negatively in Minnesota (Chapter 2). While this replacement neglected differences in the temperatures of individual sampling sites, overall trends in temperature likely followed trends in latitude, and measuring the temperature of individual sampling sites was not practical due to diel and seasonal temperature variation (e.g., Allan 1995). Caddisfly region, an important predictor of overall caddisfly distributions in Minnesota (Chapter 2) was not analyzed. The predictive ability of these regions likely approximates that of latitude, stream gradient, and level of disturbed upstream habitat combined since these variables related to distributions of the Minnesota caddisflies and, thus, were used to delineate caddisfly regions.

Models were fit for all species that occurred in >_10 summer samples. For each modeled species, all two-way and three-way interactions were calculated for the three predictor variables using the "Make Interactions" function in Arc. A full model was then fit for each species using all variables and interactions with the "Fit Binomial Response" function. Variables and interactions ,were deleted sequentially by the "Backwards Elimination" option of the "Examine Submodels" function. Variables were only included in the final model if their coefficients differed from zero (a = 0.05) and if their coefficients made biological sense.

To test the adequacy of determined models, plots were made of residuals - the difference between the observed and predicted response values - versus individual predictor variables, and a *lower* smooth line was fitted to the plot. The *lowess* smoother (Cleveland 1979, Härdle 1990) is a locally weighted scatterplot smoothing function that computes the fitted value of each observed data point based on the values of points adjacent to it. The values of the residuals in any model should have an average of zero, and an ideal model is one where residual values remain constant throughout all values of the predictor variable (Cook and Weisberg 1982, 1999; Cook 1998). Pseudo R^2 values were also calculated for each model, to evaluate each model's explanatory value.

RESULTS AND DISCUSSION

A total of 244 samples of adult caddisflies were collected during June and July, the peak period of emergence and flight activity for the majority of Minnesota species (Monson 1996). Between three and 112 samples were collected from 58 of Minnesota's 81 major watersheds, yielding a broad distribution of sampling sites (Figure 4.1). An additional 73 samples were collected during September and early October, the peak period of emergence and flight activity for a minority of species. The brevity of this period and the lack of warm evenings precluded collecting as many samples as were collected during June and July. A grand total of 317 samples were taken from 294 different sites; 23 sites were sampled in both summer and fall.

A total of 284 caddisfly species, 74 genera, and 20 families were determined to occur in Minnesota (Table 4.2). Two hundred and fifty species 88% of the known total-were collected during the current study and represented by 306,541 specimens.

An additional 25,235 museum specimens - collected primarily from 1940 to 1965 - were also examined during the current study. The greatest species richness was represented by the families Hydroptilidae (60), Limnephilidae (51), Leptoceridae (50), Hydropsychidae (34), and Polycentropodidae (25); the highest diversity within genera by *Hydroptila* (27), *Limnephilus* (20), *Hydropsyche* (20), *Ceraclea* (19), and *Polycentropus* (17) (Table 2).

Flight Periodicity. Most of the 284 caddisfly species known to occur in Minnesota appeared to exhibit univoltine life cycles. This conclusion cannot be stated definitively, however, without detailed life history information for each species; adults may have been present during periods when samples were not taken. Adults of 260 species-92% of the fauna-were present during the summer flight period (June and July) (Table 4.2). Of these summer species 25 were also present during the fall period (September and October), and seven were present during the spring period (March-May); no species were present in three periods (Table 4.2). Most of the species present only during the summer were likely univoltine, exhibiting a single emergence period and decreasing in adult abundance throughout the summer. Of the seven Minnesota summer-emergent species for which detailed life history data are available, all appeared univoltine except for possibly *Cheumatopsyche pettiti* (Hydropsychidae); this species' high abundance throughout the summer made determination of voltinism difficult (Krueger and Cook 1984, Mackay 1986)

Common species present during both summer and fall periods, such as *Oecetis inconspicua, Leptocerus americanus* (Leptoceridae), or *Cheumatopsyche campyla* (Hydropsychidae), may have exhibited asynchronous emergence of a single generation; adults were abundant for the entire summer and did not begin decreasing in abundance until fall (Table 4.2). It is also possible that these species may have been multivoltine, with several short generations during the summer. Two Canadian populations of *O. inconspicua* were determined to be univoltine despite the species' abundance throughout the summer and into early fall (Winterbourn 1971, Richardson and Clifford 1986). Other summer/fall species, such as *Agraylea multipunctata* (Hydroptilidae) or *Chimarra obscurra* (Philopotamidae) were likely bivoltine as they exhibited large emergences during both the summer and fall periods (Table 4.2).

Most of the spring/summer species, such as *Hesperophylax designatus* (Limnephilidae) or *Brachycentrus americanus* (Brachycentridae), were likely univoltine and simply emerged before the main summer fauna. Adults of these species were rarely present into late summer. A notable exception may have been *Dolophilodes distinctus* (Phil opotamidae); adults of this species-including apterous females-emerged in early spring. Macropterous females were found during the summer months, suggesting either two distinct generations or else asynchronous cohort growth with differing developmental responses to the prevailing weather or photoperiod. This species is known to be multivoltine in Georgia and North Carolina (Benke and Wallace 1980, Huryn and Wallace 1988). *Glossosoma intermedium* (Glossossomatidae) also appeared to exhibit bivoltinism, as adults were present from early spring until late summer. Krueger and Cook (1984) determined bivoltinism with distinct spring and summer generations for this species in a southern Minnesota stream.

Adult presence of 24 species appeared limited to the fall period. These included the family Uenoidae (three species), 18 species of Limnephilidae, two of Lepidostomatidae, and one of Phryganeidae (Table 4.2). The brevity of this flight period and past studies strongly suggest univoltinism for these species (Beam and Wiggins 1987, Wisseman and Anderson 1987, Roeding and Smock 1989). Some of these species, such as *Agrypnia staminea* (Phryganeidae) or several species of *Pycnopsyche* (Limnephilidae) were common and easy to collect throughout the fall whereas others, such as the three species of *Neophylax* (Uenoidae), were rare in light traps relative to their larval presence in streams during the summer (personal observation). Adults of these species may have been present for only a brief period during the fall. It is also possible that the cool evening weather during the fall limited flight of some species.

Adults of a few species exhibited unusual emergence periods. *Parapsyche apicalis* (Arctopsychidae) was present as an adult only during the spring. Larval data and literature records (Wiggins 1998) suggest a similar life cycle for *Oligostomis sp.* (Phryganeidae) although adults have not yet been found in Minnesota. Adults of *Frenesia missa* (Limnephilidae) were collected from late fall into the winter, often emerging from open riffles on to the snow. Adults of *Chilostigma itascae* (Limnephilidae) were found exclusively during the winter, also emerging and mating on the snow.

Water temperature may be an important factor in influencing life histories of Minnesota caddisflies. Warming water temperatures in the spring and summer have been shown to synchronize growth and emergence of many aquatic insect species including caddisflies (Ward and Stanford 1982., Sweeney 1984, Houghton and Stewart 1998). In Oklahoma, Vaughn (19$5) found that a population of *Helicopsyche borealis* (Helicopsychidae) in a springfed stream was exposed to a near-constant water temperature and exhibited multivoltinism. In the same study, another Oklahoma population of *H. borealis* in a stream of seasonally changing water temperature was univoltine. Even in springfed streams, the seasonal changes in ambient temperature within Minnesota likely promoted synchrony in emergence and univoltinsm. The brevity of the Minnesota summers relative to those of southern states and neotropical environments also likely promoted univoltinsm due to a shorter growing season. Many species that appeared to be univoltine in Minnesota, such as *Glossossoma nigrior* (Glossossomtidae), *Cheumatopsyche pasella* and *Macrostemum zebratum* (Hydropsychidae), and *Neureclipsis crepuscularis* and *Polycentropus centralis* (Polycentropodidae) have been shown to be bivoltine in southern states (Cudney and Wallace 1980, Parker and Voshell 1982, Georgian and Wallace 1983, Bowles and Allen 1992).

Abundant Species. The distribution of both specimen abundance and sample presence per species exhibited an exponential change as species became more common and abundant (Figure 4.2). Over half (53%) of the total specimen abundance for the state was represented by eight species The five most abundant species were *Psychomyia flavida* (22,744 specimens), *Chimarra obscura* (19,217), *Leptocerus americanus* (18,225), *Oecetis avara* (14,588), and *Oecetis inconspicua* (12,638) (Table 4.2). Some species that were not identifiable as females, such as *Cheumatopsyche campyla*, *Hydropsyche morosa* (Hydropsychidae), and several species of Hydroptilidae, may have been as abundant.

The five most common species were *Oecetis inconspicua* (collected in 230 samples), *Ceraclea tarsipunctata* (194), *O. cinerascens* (136), *Psychomyia flavida* (126), and *O. avara* (119) (Table 4.2). These species emerged during the summer, and considerably more samples were taken in the summer relative to other seasons. Some fall emerging species, such as *Pycnopsyche guttifer,* may be as common given an equal seasonal sampling effort.

Rare Species. Eighty-one species were represented by <10 specimens and 103 species were collected in <10 samples (Table 4.2). An additional 34 species have not been collected during the last 10 years (Table 4.2). Some species such as *Diplectrona modesta* (Hydropsychidae) and *Oecetis dittisa* (Leptoceridae) are common throughout much of the eastern United States and may be at the edge of their range in Minnesota (Harris et al. 1991). Others, such as *Limnephilus parvulus* (Limnephilidae), *Oxyethira ecornuta* (Hydroptilidae), and *Polycentropus milaca* (Polycentropodidae), appeared restricted to certain geographic areas of Minnesota without a clear correspondence with habitat type. The former two species exhibit distributions throughout their ranges that are widespread but localized, whereas *P. milaca* appears endemic to Minnesota (Armitage and Hamilton 1990, Monson 1994, Ruiter 1995). Other species, such as *Frenesia missa* and *Neophylax* spp.*,* may have appeared rare because they emerge in the late fall and may not have been able to fly to lights in cold weather. Several species of *Protoptila* (Glossosomatidae) and Hydroptilidae likely appeared uncommon because males are rarely found in light traps and females could not be identified to the species level.

Many rare species appeared to be restricted to certain types of habitats that were uncommon in Minnesota, difficult to locate, or else occur only in certain areas of the state. Some examples include *Apatania zonella* (Apataniidae), *Hydroptila salmo*

(Hydroptilidae), and *Limnephilus sackeni* (Limnephildae), which were only found at large oligotrophic lakes; *Asynarchus montanus* (Limnephilidae), *Lepidostoma libum* (Lepidostomatidae), and *Parapsyche apicalis* (Arctopsychidae), collected exclusively at small springs; and several species that were found only near fast-moving rocky streams. This last habitat type may be particularly important as faunas of the Lake Superior and Southeastern region appeared distinct from those of the other regions due mainly to the presence of higher-gradient streams (Figure 4.1) (Chapter 2). Minnesota populations of many species found in these habitats are disjunct from other known populations. These species include *Agapetus rossi* (Glossosomatidae*), Oecetis disjuncta* (Leptoceridae), *Onocosmoecus unicolor* (Limnephilidae), *Rhyacophila angelita, R. fuscula*, and *R. vibox* (Rhyacophilidae), which are otherwise known from the Appalachian Mountains, Rocky Mountains, or both (Schmid 1988, Harris et al. 1991, Houghton 2001, Prather and Morse 2001). The fast-moving rocky streams of the Lake Superior region appeared especially similar to those typically found in mountainous areas and this similarity likely promoted a similar fauna.

Listed Species. Seven caddisfly species listed either as "Endangered" or "Species of Special Concern" by the Minnesota Department of Natural Resources (MNDNR 1996) were collected during this study. Three (*Chilostigma itascae, Oxethira ecornuta, Polycentropus milaca*) appeared rare, two (*Agapetus tomus, Asynarchus rossi*) appeared rare but possibly locally abundant, and two (*Hydroptila novicola, Oxethira itascae*) were found throughout northern Minnesota. The five other listed species: *Ceraclea brevis, C. vertreesi* (Leptoceridae), *Protoptila talola* (Glossosomatidae), *Hydroptila metoeca*; and *H. tortosa* (Hydroptilidae) have not been collected since 1965. Their conservation status in discussed on the Minnesota Department of Natural Resources Ecological Services website (<http://www.dnr.state.mn.us/ecological_services>).

A single male specimen of *Chilostigma itascae* (Limnephilidae) was collected from its type locality, a wet meadow near Nicollet Creek in Lake Itasca State Park, during February 2001 (Figure 4.3). This species is known only from its type locality and is unique in its exclusively winter adult emergence. This species was first collected in 1974 and again in 1995.

A total of 14 males of *Oxeythira ecornuta* (Hydroptilidae) were collected from the White Earth River, Mahnomen County, and Pike Lake, Becker County, during July 2000. This species was previously known in Minnesota from a single male specimen collected from LaSalle Creek, Lake Itasca State Park in 1988 (Monson and Holzenthal 1993). All collecting sites are within 50 km (Figure 4.3). This species is known from both Canada and Europe, but is rare and localized throughout its range (Monson and Holzenthal 1993).

Three males of *Polycentropus milaca* were collected in June 2000 from Mabel and Big Rice Lakes in Cass County. This species was known previously only from the holotype collected at Link (Lynx) Lake, Itasca County in 1965 (Etnier 1968). All sites are within 75 km and are small meostrophic lakes with abundant littoral vegetation (Figure 4.4).

Agapetus tomus (Glossossomatidae), previously known from a single collection in Pine County, was collected from Aitkin, Morrison, and Pine Counties in eastcentral Minnesota (Figure 4.4). A total of 194 specimens was identified from six collections during 2000 and 2001. Collection sites are within 150 km of each other and range from low to high-gradient small and medium streams. Minnesota populations are disjunct from the other known populations of *A. tomus* in the southeastern U.S. where the species typically occurs in high-gradient mountain streams (Harris et al. 1991). The rarity, habitat disparity, and local abundance of *A. tomus* make it difficult to hypothesize about the specific habitat requirements of this species in Minnesota.

Asnarchus rossi (Limnephilidae) adults were collected from Valley Creek, Washington County, in October of 1996 (74 specimens) and in September of 1997 (11 specimens). An additional male was collected from Grand Portage Creek, Cook County in August of 2000. Although widely separated geographically, both collecting sites are high-gradient streams (Figure 4.4). This species is also known from Michigan, Wisconsin, and Quebec and is rare and localized throughout its range (Monson 1994).

Hydroptila novicola (Hydroptilidae), known previously in Minnesota from a single specimen from Pine County, was found at 28 sites throughout northern Minnesota (Figure 4.3). *Oxethira itascae* (Hydroptilidae), previously thought to be endemic to sites in Lake Itasca State Park, was found at 14 sites in northern Minnesota (Figure 4.4). Both of these species appeared throughout the Northern caddisfly region and the few previous collections may reflect a lack of collecting effort or the difficulty of collecting and identifying hydroptilid species.

Indicator Species. The distributions of almost 95% of the Minnesota species could not be analyzed using a regression model. Rare species, even those found exclusively in certain types of habitats, did not occur at a high enough frequency to analyze. Conversely, some abundant species occurred in most or all habitats and were, therefore, not characteristic of any particular type. Some highly abundant species appeared to generate spurious statistical significance for certain habitat types simply due to their high sample size. It was probably not appropriate to model either especially rare or especially abundant species statistically. Instead, prediction of their occurrence in particular habitat types is best accomplished using a tabular approach (Table 4.2).

Binomial regression analysis indicated 16 species whose presence or absence was statistically related to certain habitats or site conditions in Minnesota (Tables 4.3-4.4). Of these species, distributions of 13 appeared to relate to latitude and percentage of disturbed upstream habitat, and three to percentage of disturbed upstream habitat exclusively (Table 4.3-4.4). No species correlated significantly with stream gradient or with interactions between predictor variables.

All of the 13 species that related to latitude and percentage of disturbed upstream habitat exhibited a similar response: the predicted proportion decreased between 0.02 and 0.04 for each percent increase of disturbed upstream habitat (Table 4.3). Species presence increased with latitude for all 13 species (Table 4.3). Probability (p) values for both variables in each model were <0.05 (Table 4.3). These relationships were confounding; percentage of disturbed upstream habitat generally decreases with increasing latitude in Minnesota (Chapter 2). It was difficult to determine, therefore, if these species responded to latitude, percentage of disturbed upstream habitat, or both.

Probability values for percent disturbed habitat were higher than for latitude for all species models (Table 4.3). This result suggests that disturbed habitat may be a better predicter of the distributions of these species than latitude. Species that had a relatively high pseudo R2 value, such as *Banksiola crotchi, Ceraclea cancellata,* and *Helicopsyche* *borealis,* may have the highest value as indicator species. The last species has been determined to be intolerant of organic pollution, as has *Micrasema wataga,* another of the 13 species that decreased with increased habitat disturbance (Barbour et al. 1999). All of the 13 species may be good indicators of undisturbed aquatic habitats. Further research, however, will be needed to differentiate between the effects of disturbance and latitude on their distributions.

The proportion of occurrence of three species: *Cheumatopsyche campyla, Hydropsyche bidens,* and *Potamyia flava,* was best predicted by percentage of disturbed upstream habitat only (Table 4.4, Figure 4.5).' All three species responded positively to percentage of disturbed upstream habitat in small streams (Class 1-2), medium streams (Class 3-4), and lakes (Class L) when analyzed separately, except C. *campyla (*$p = 0.07$*)* for small streams (Table 4.4, Figure 4.5). None of the species, however, was related to percentage of disturbed upstream habitat in large rivers ($p > 0.20$) (Table 4.4). Pseudo R2 values ranged from 0.14 to 0.49, suggesting that the majority of the variation in distribution of these three species in Minnesota was explained by factors other than the fit models. Thus, conclusions drawn from these models should probably be considered tentative.

Conclusions drawn from these models should also be considered tentative due to the consistent decrease in residual values as percent of disturbed upstream habitat increased (Figure 4.6). This pattern suggests that the model may have underestimated the proportion of occurrence of these species at low disturbance, and overestimated it at high disturbance (Cook and Weisberg 1999). Because all three species were predicted to occur at a low proportion (0.05-0.20) in undisturbed habitats, a sporadic presence of species yielded a high (positive) residual. In disturbed habitats, species were predicted to occur at a high proportion (0.70-0.90), thus sporadic absence resulted in a low (negative) residual (Figures 4.5-4.6). This pattern led to the decreasing residual scores with increasing habitat disturbance in Figure 4.6. There was, however, not a great deal of curvature in the *lowess* smooth line in Figure 4.6 relative to the variation in the residuals. This relationship suggested that, despite some non-constancy, the plot may have been consistent with the assumptions of the model and, therefore, the percentage of disturbed upstream habitat may have been an acceptable predictor of the presence or absence of *C. campyla*, *H. bidens,* and P. flava in Minnesota (Cook and Weisberg 1999).

All three of these species are widespread throughout the eastern and eastcentral U.S. (Gordon 1974, Wiggins 1996a, Schmid 1998) and are found in all Minnesota caddisfly regions except the Lake Superior (Table 4.2). All three are fine particle filtering collectors that consume particles <0.25 mm in diameter and are, therefore, typically found in the large, warm, slow-moving rivers that provide such food sources (Fremling 1960; Cummins 1974; Boiling et al. 1975; Rhame and Stewart 1976; Vannote et al. 1980, Wiggins 1996a, b). In Minnesota, all three are more common in larger rivers (Class 4-5 streams) than in other habitat types (Table 4.2).

In Minnesota, the presence of *C. campyla*, *H. bidens,* and *P. flava* in small to medium streams or lakes may indicate organic pollution. Agricultural or urban runoff into aquatic habitats often contains large amounts of sediments and nutrients, which promote an increase in autotrophic production, especially in small to medium streams (Gianessi et al. 1986; Feminella et al. 1989; Turner and Rabalais 1991; Delong and Brusven 1992, 1993; Pringle et al. 1993; Karr and Chu 1999). Nutrient and sediment input may, therefore, modify lakes and small to medium streams into habitats suitable for fine particle filtering collectors. This fact may explain the response of these species to percentage of disturbed upstream habitat in small to medium streams and lakes (Figure 4.5); in Minnesota, agriculture and urbanization are the predominant habitat disturbances (USGS 1999). In large rivers, these species did not respond to percentage of disturbed upstream habitat. This lack of response was likely because large rivers naturally contained the fine organic particles that constitute the species' food source and additional habitat disturbance was likely of little importance (Vannote et al. 1980).

Houghton (Chapter 2) found that in areas of Minnesota with >80% upstream habitat disturbance fine particle filtering collectors dominated in lakes and small to medium streams. This phenomenon occurred mostly in the Northwestern and Southern regions of the state (Figure 4.1) and included both prairie and deciduous forest ecosystems; habitats in which *C. campyla, H. bidens,* and *P. flava* are found. It is possible that small to medium prairie streams may naturally support populations of these species as the lack of forest canopy cover and erosion of the nutrient-rich prairie soils may increase the amount of their fine organic particle food source (Anderson and Grigal 1984, Buol et al. 1989, Wiley et al. 1990, Allan 1995). In the absence of historical data and without undisturbed prairie ecosystems remaining in Minnesota it is difficult to determine whether *C. campyla, H. bidens,* and *P. flava* occur naturally in all types of prairie lakes and streams, whether habitat disturbance has increased their presence in such habitats, or both.

Wiley et al. (1990) found that agricultural and urban landuse in Illinois contributed more nutrient input into prairie streams than did natural processes. Houghton

(Chapter 2) found no difference in the trophic feeding composition between prairie and deciduous forest ecosystems in Minnesota and suggested that any natural differences that may have existed between them are less important than the contemporary effects of disturbance. While it is possible that the occurrence of *C. campyla*, *H. bidens,* and *P. flava* in small to medium prairie streams may be explained by natural phenomena, it is likely that human disturbance is increasing their presence and abundance in such habitats. Certainly their presence in lakes and small to medium streams of other ecosystem types may indicate disturbed habitat.

While a species whose presence indicates undisturbed habitat may disappear soon after a disturbance. renders the site uninhabitable (Karr and Chu 1999), the reverse may not be true. Species like C. campyla, *H. bidens,* and P. (lava whose presence indicates a disturbed site may not colonize such a site immediately after disturbance unless the species are already present in the general area. Several studies have shown that caddisfly dispersal is rarely >1000 m from the natal stream and that this limits the ability to recolonize aquatic habitats whose quality has improved (Sode and Wiberg-Larsen 1993, Petersen et al. 1999). The same lack of vagility may limit the usefulness of *C. campyla*, *H. bidens,* and *P. flava* as indicators of organic pollution in areas without naturally occurring large river populations of these species.

Further research is needed to determine the applicability of *C. campyla*, *H. bidens,* and *P. flava* to biomonitoring in Minnesota. The 13 species responding negatively to percentage of disturbed habitat are also likely good indicator taxa once responses to percentage of disturbed habitat and latitude can be separated. Other species, particularly those associated with only certain types of habitats (Table 4.2), may also have value as indicator taxa. Sampling on a smaller spatial scale or measuring environmental variables with greater precision may clarify such value and be amenable to statistical testing.

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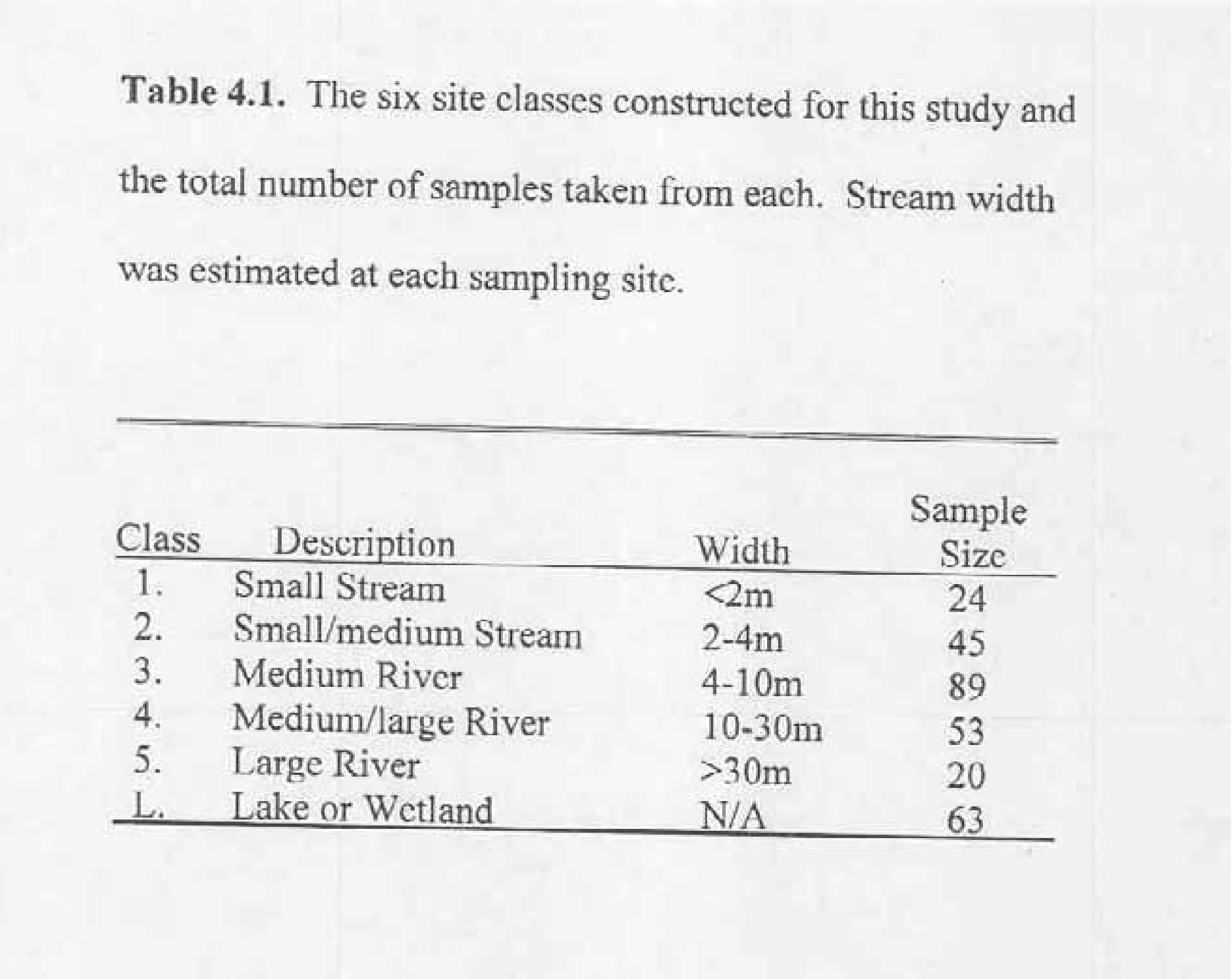
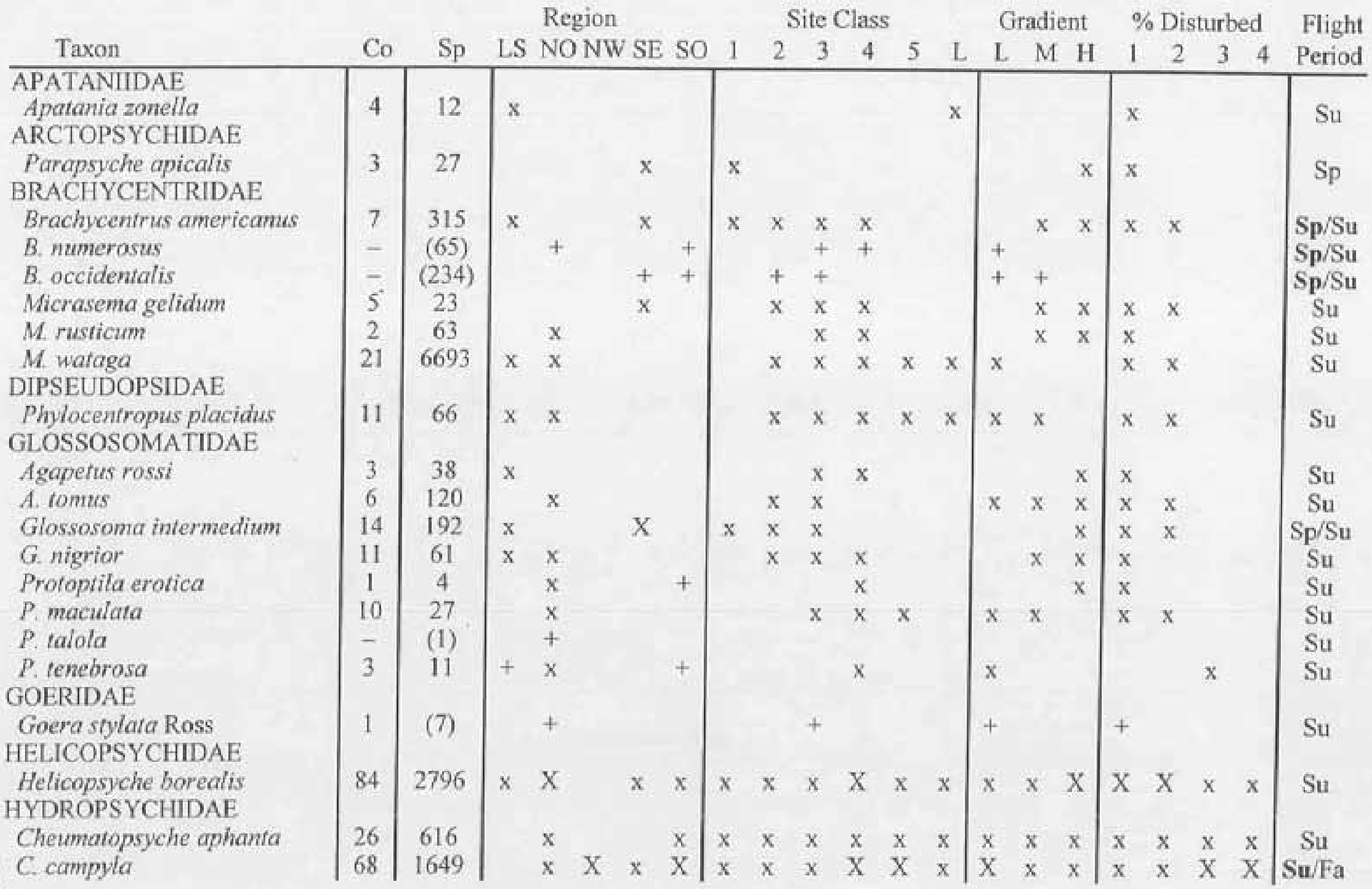


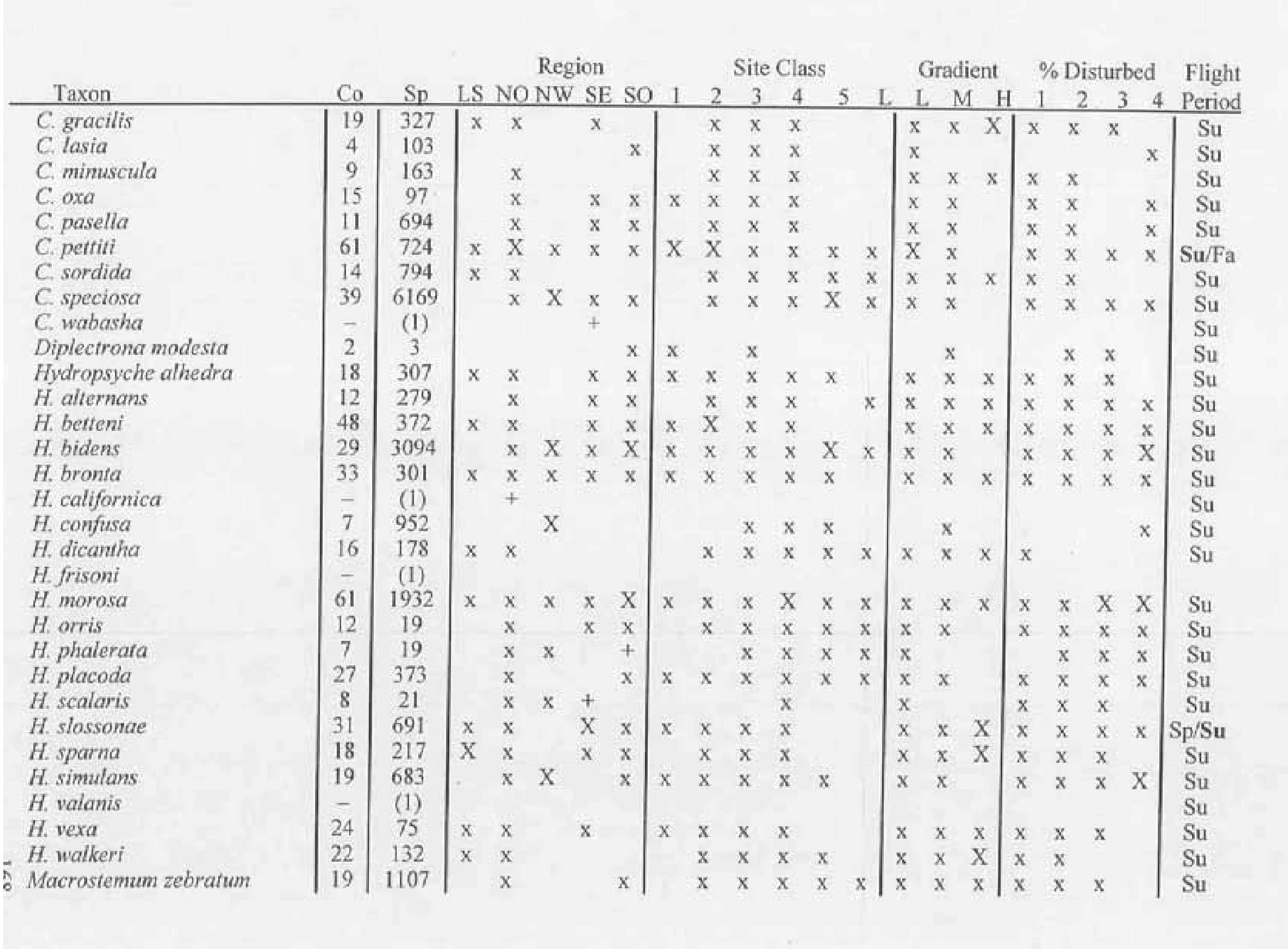
Table 4.1. The six site classes constructed for this study and the total number of samples taken from each. Stream width was estimated at each sampling site.

Class	Description	Width	Sample Size
1.	Small Stream	<2m	24
2.	Small/medium Stream	2-4m	45
3.	Medium River	4-10m	89
4.	Medium/large River	10-30m	53
5.	Large River	>30m	20
L.	Lake or Wetland	N/A	63

Table 4.2. The 284 caddisfly species confirmed from Minnesota with corresponding habitat affinities and abundances based on 317 samples collected from 294 localities during 1999–2001. Author names omitted to conserve space. Co = number of samples in which individual species were collected. Sp = number of specimens collected during sampling regime; species known from Minnesota but not collected during sampling regime have number of specimens examined listed in parentheses. Region (Figure 4.1), LS = Lake Superior, NO = Northern, NW = Northwestern, SE = Southeastern, SO = Southern; Site Class (Table 4.1) 1–5 = progressively larger streams, L = Lakes and wetlands; Stream Gradient based on perceived site conditions (Borchert and Yaeger 1968, USGS 2001), L = Low, M = Medium, H = High; % Disturbed Habitat (USGS 1999), 1 = 0–24%, 2 = 25–49%, 3 = 50–74%, 4 = 75–100%; Flight Period, Sp = Spring (March–May), Su = Summer (June–August), Fa = Fall (September–October), Wi = Winter (November–February). If species were present in more than one flight period boldface text indicates the period of greater abundance; two periods in regular type indicate approximately equal abundance. x = adults present in < 50% of samples taken from respective class; X = adults present in > 50% of samples from respective class; + = museum record. For summer emergent species, Xs refer to relative presence in summer samples; Xs refer to relative presence in fall samples for fall-emergent species.



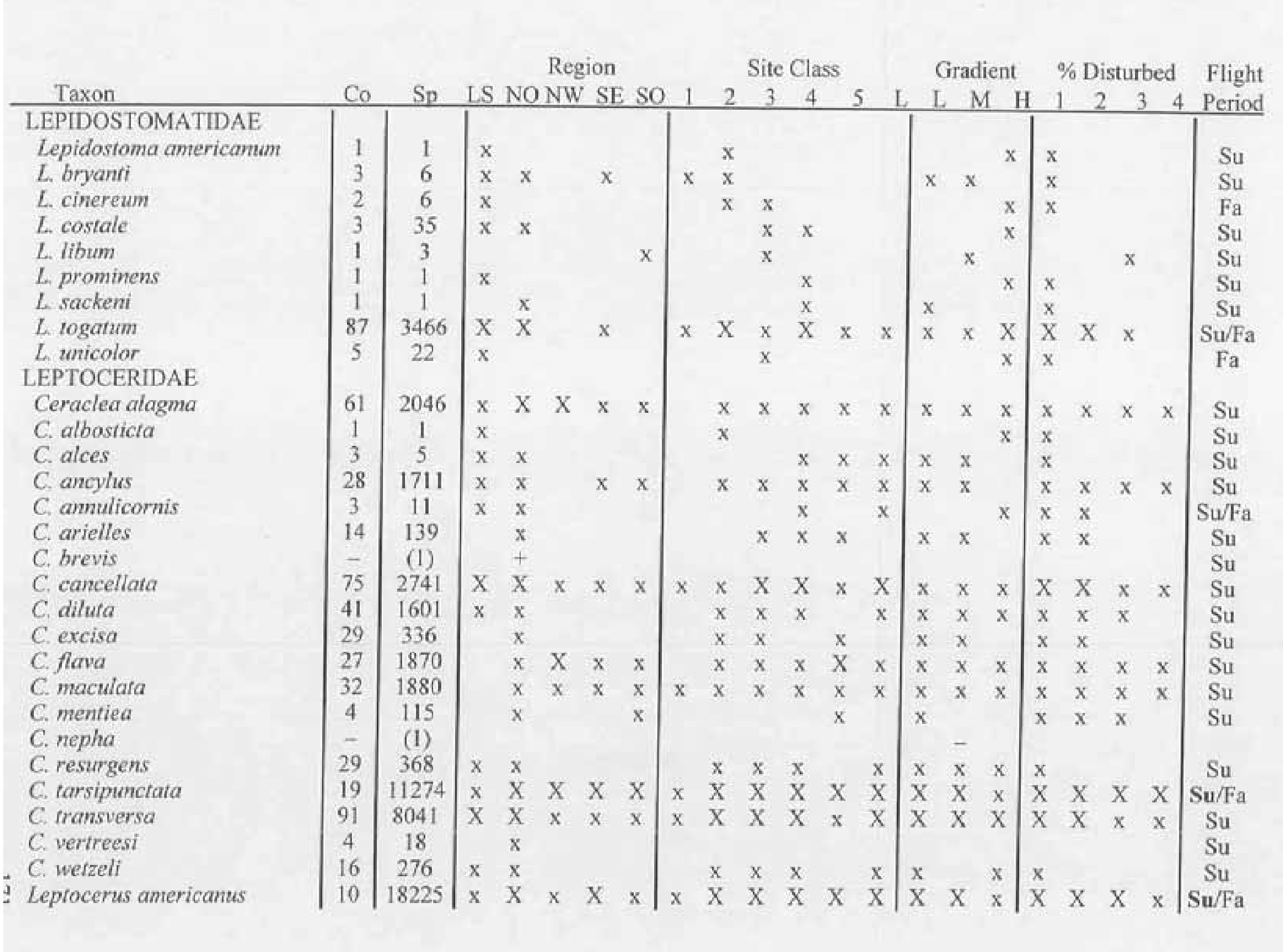
Taxon	Co	Sp	Region LS	NO	NW	SE	SO	Site Class 1	2	3	4	5	L	Gradient L	M	H	% Disturbed 1	2	3	4	Flight Period
APATANIIDAE																					
Apatania zonella	4	12	x										x				x				Su
ARCTOPSYCHIDAE																					
Parapsyche apicalis	3	27				x		x								x	x				Sp
BRACHYCENTRIDAE																					
Brachycentrus americanus	7	315	x			x		x	x	x	x				x	x	x	x			Sp/Su
B. numerosus	–	(65)		+			+			+	+			+							Sp/Su
B. occidentalis	–	(234)				+	+		+	+				+	+						Sp/Su
Micrasema gelidum	5	23				x			x	x	x				x	x	x	x			Su
M. rusticum	2	63		x						x	x				x	x	x				Su
M. wataga	21	6693	x	x					x	x	x	x	x	x			x	x			Su
DIPSEUDOPSIDAE																					
Phylocentropus placidus	11	66	x	x					x	x	x	x	x	x	x		x	x			Su
GLOSSOSOMATIDAE																					
Agapetus rossi	3	38	x							x	x					x	x				Su
A. tomus	6	120		x					x	x				x	x	x	x	x			Su
Glossosoma intermedium	14	192	x			X		x	x	x						x	x	x			Sp/Su
G. nigrior	11	61	x	x					x	x	x				x	x	x				Su
Protoptila erotica	1	4		x			+				x					x	x				Su
P. maculata	10	27		x						x	x	x		x	x		x	x			Su
P. talola	–	(1)		+																	Su
P. tenebrosa	3	11	+	x			+				x			x					x		Su
GOERIDAE																					
Goera stylata Ross	1	(7)		+						+				+			+				Su
HELICOPSYCHIDAE																					
Helicopsyche borealis	84	2796	x	X		x	x	x	x	x	X	x	x	x	x	X	X	X	x	x	Su
HYDROPSYCHIDAE																					
Cheumatopsyche aphanta	26	616		x			x	x	x	x	x	x	x	x	x	x	x	x	x	x	Su
C. campyla	68	1649		x	X	x	X	x	x	x	X	X	x	X	x	x	x	x	X	X	Su/Fa



Taxon	Co	Sp	Region LS	NO	NW	SE	SO	Site Class 1	2	3	4	5	L	Gradient L	M	H	% Disturbed 1	2	3	4	Flight Period
C. gracilis	19	327	x	x		x			x	x	x			x	x	X	x	x	x		Su
C. lasia	4	103					x		x	x	x			x						x	Su
C. minuscula	9	163		x					x	x	x			x	x	x	x	x			Su
C. oxa	15	97		x		x	x	x	x	x	x			x	x		x	x		x	Su
C. pasella	11	694		x		x	x		x	x	x			x	x		x	x		x	Su
C. pettiti	61	724	x	X	x	x	x	X	X	x	x	x	x	X	x		x	x	x	x	**Su/Fa**
C. sordida	14	794	x	x					x	x	x	x	x	x	x	x	x	x			Su
C. speciosa	39	6169		x	X	x	x		x	x	x	X	x	x	x		x	x	x	x	Su
C. wabasha	–	(1)				+															Su
Diplectrona modesta	2	3					x	x		x					x			x	x		Su
Hydropsyche alhedra	18	307	x	x		x	x	x	x	x	x	x		x	x	x	x	x	x		Su
H. alternans	12	279		x		x	x		x	x	x		x	x	x	x	x	x	x	x	Su
H. betteni	48	372	x	x		x	x	x	X	x	x			x	x	x	x	x	x	x	Su
H. bidens	29	3094		x	X	x	X	x	x	x	x	X	x	x	x		x	x	x	X	Su
H. bronta	33	301	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	Su
H. californica	–	(1)		+																	Su
H. confusa	7	952			X					x	x	x			x					x	Su
H. dicantha	16	178	x	x					x	x	x	x	x	x	x	x	x				Su
H. frisoni	–	(1)																			
H. morosa	61	1932	x	x	x	x	X	x	x	x	X	x	x	x	x	x	x	x	X	X	Su
H. orris	12	19		x		x	x		x	x	x	x	x	x	x		x	x	x	x	Su
H. phalerata	7	19		x	x		+			x	x	x	x	x				x	x	x	Su
H. placoda	27	373		x			x	x	x	x	x	x	x	x	x		x	x	x	x	Su
H. scalaris	8	21		x	x	+					x			x			x	x	x		Su
H. slossonae	31	691	x	x		X	x	x	x	x	x			x	x	X	x	x	x	x	Sp/**Su**
H. sparna	18	217	X	x		x	x		x	x	x			x	x	X	x	x	x		Su
H. simulans	19	683		x	X		x	x	x	x	x	x		x	x		x	x	x	X	Su
H. valanis	–	(1)																			Su
H. vexa	24	75	x	x		x		x	x	x	x			x	x	x	x	x	x		Su
H. walkeri	22	132	x	x					x	x	x	x		x	x	X	x	x			Su
Macrostemum zebratum	19	1107		x			x		x	x	x	x	x	x	x	x	x	x	x		Su

Taxon	Co	Sp	Region					Site Class						Gradient			% Disturbed				Flight
			LS	NO	NW	SE	SO	1	2	3	4	5	L	L	M	H	1	2	3	4	Period
Potamyia flava	72	12200		x	X	x	X	x	x	x	x	X	x	x	x		x	x	X	X	**Su/Fa**
HYDROPTILIDAE																					
Agraylea multipunctata	60	2112		X	x	x	x		x	x	X	x	x	x	x	x	x	X	x	x	Su/Fa
Hydroptila ajax	14	284		x		x	x		x	x	x	x		x	x			x	x	x	Su
H. albicornis	11	62		x						x	x	x		x		x	x	x			Su
H. amoena	3	4		x						x			x	x			x				Su
H. ampoda	1	1		x						x				x			x				Su
H. angusta	16	92		x			x	x	x	x	x	x		x				x	x	x	Su
H. antennopedia	6	787		x									x				x				Su
H. armata	12	84		x					x	x			x	x			x	x			Su
H. callia	–	(1)													–						Su
H. consimilis	31	500	x	x	x	X	x	x	x	x	x	x	x	x	x	x	x	x	x	x	Su
H. delineata	4	14		x							x					x	x				Su/Fa
H. grandiosa	24	109		x	x		x	x	x	x	x		x	x	x		x	x	x	x	Su
H. hamata	1	3		x					x						x		x				Su
H. jackmanni	27	623	x	x		x			x	x	x	x		x	x	X	x	x			Su
H. metoeca	–	(1)		+																	Su
H. novicola	28	236	x	x					x	x	x		x	x	x	X	x	x			Su
H. perdita	6	11		x		x	x	x		x	x				x	x		x	x	x	Su
H. quinola	5	16		x			x			x				x			x		x		Su
H. rono	1	2					x			x					x				x		Su
H. salmo	1	15		x									x								Su
H. scolops	13	92					x			x	x			x				x	x	x	Su
H. spatulata	14	44		x					x	x	x		x	x	x		x	x	x		Su
H. tortorsa	–	(1)		+																	Su
H. valhalla	30	1366	x	x					x	x	x		x	x	x	X	x	x			Su
H. waskesia	1	1		x					x					x			x				Su
H. waubesiana	26	812	x	x		x	x			x	x	x	x	x	x		x	x	x	x	Su/Fa
H. wyomia	21	106		x					x	x	x	x	x	x		x	x	x			Su
H. xera	17	101	x	x		x		x	x	x	x			x	x	x	x	x	x		Su
Ithytrichia clavata	9	148		x		x				x	x		x	x			x				Su

			Region					Site Class						Gradient			% Disturbed				Flight
Taxon	Co	Sp	LS	NO	NW	SE	SO	1	2	3	4	5	L	L	M	H	1	2	3	4	Period
Leucotrichia pictipes	–	(120)	+	+						+	+		+		+	+					Su
Mayatrichia ayama	21	1112		x		x	x	x	x	x	x	x		x	x	x	x	x	x	x	Su
Neotrichia falca	5	24		x						x	x			x			x	x	x		Su/Fa
N. halia	3	92	x	x						x	x					x	x	x			Su
N. minutisimella	7	119		x	x					x	x	x		x			x			x	Su
N. okopa	12	133		x			x		x	x	x	x		x			x		x	x	Su
N. vibrans	9	296		x					x	x	x	x			x		x				Su
Ochrotrichia spinosa	1	5		+		x	+		x						x			x			Su
O. tarsalis	23	2682		x	x		x			x	x	x		x	x	x	x	x	x	x	Su
Orthotrichia aegerfasciella	31	471		x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	Su
O. balduft	19	144	x	x					x	x	x	x	x	x	x	x	x	x	x	x	Su
O. curta	–	(1)		+																	Su
O. cristata	46	647	x	x			x	x	x	x	x		x	x		x	x	x	x	x	Su
Oxeythira aeola	3	11		x					x	x	x			x			x				Su
O. anabola	2	3	x	x							x		x			x	x				Su
O. arraya	2	5		x									x				x				Su
O. coercens	23	296		x					x	x	x	x	x	x	x	x	x	x	x		Su
O. ecornuta	2	14		x						x	x		x	x			x	x			Su
O. forcipata	57	2560	x	X		x	x	x	x	x	x	x	x	x	x	x	x	x	x		Su/Fa
O. itascae	14	50		x					x	x	x		x	x			x				Su
O. michiganensis	4	19		x					x	x	x		x			x	x				Su/Fa
O. obtatus	16	239		x						x		x	x	x			x				Su
O. pallida	11	25		x			x	x		x	x	x	x	x	x		x	x	x		Su
O. rivicola	45	311		x					x	x	x		x	x	x		x	x	x		Su
O. rossi	1	1	x								x					x	x				Su
O. serrata	26	224		x			x		x	x	x		x	x			x	x			Su
O. sida	39	1140	x	x					x	x	x		x	x	x	x	x	x			Su
O. verna	14	107		x			x		x	x			x	x			x	x			Su
O. zeronia	7	16		x			x						x				x				Su
Stactobiella delira	2	3	x	x						x	x					x	x	x			Su
S. palmata	6	27		x					x	x	x			x			x	x	x		Su

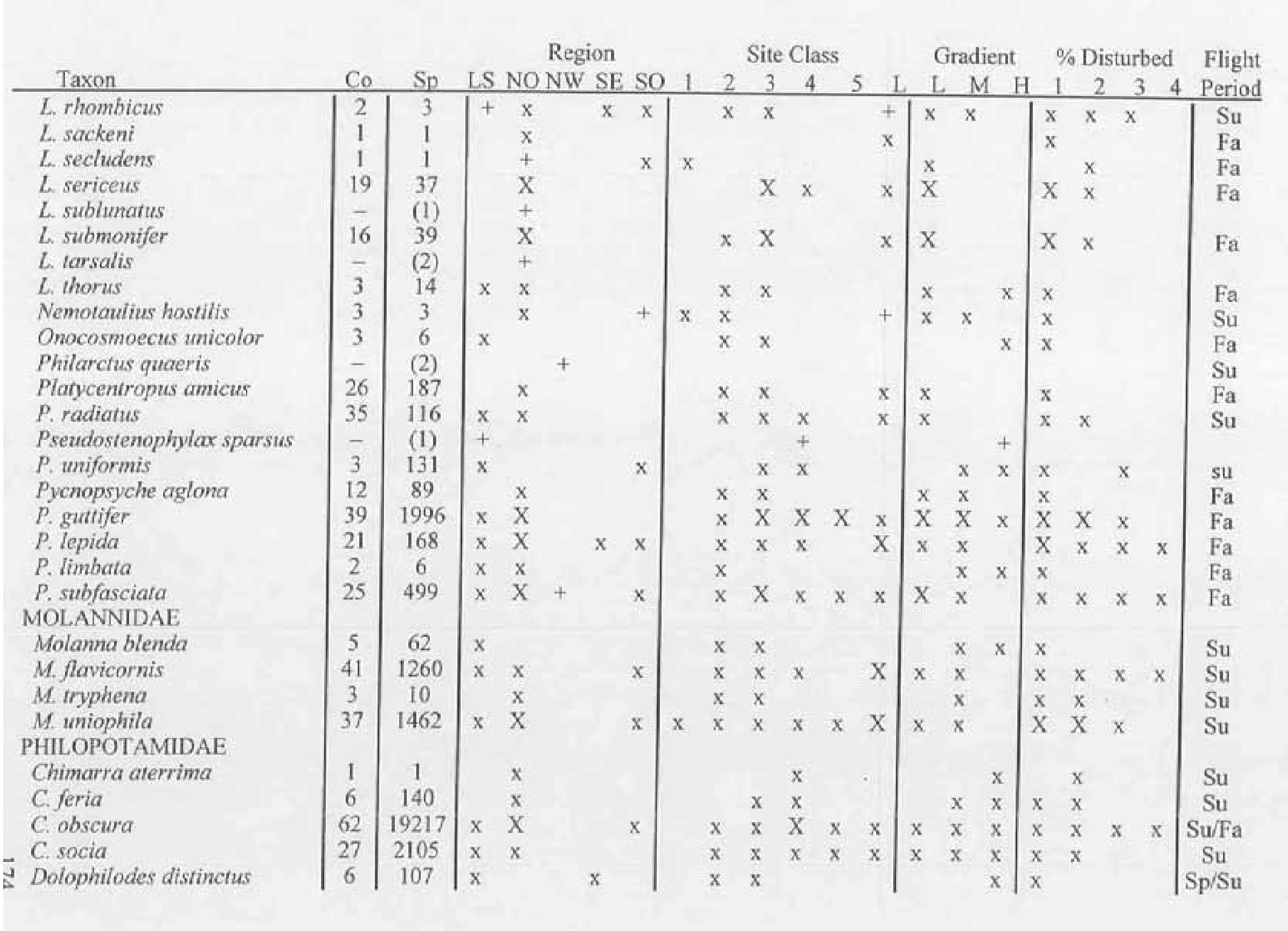


Taxon	Co	Sp	Region LS	NO	NW	SE	SO	Site Class 1	2	3	4	5	L	Gradient L	M	H	% Disturbed 1	2	3	4	Flight Period
LEPIDOSTOMATIDAE																					
Lepidostoma americanum	1	1	x						x							x	x				Su
L. bryanti	3	6	x	x		x		x	x					x	x		x				Su
L. cinereum	2	6	x						x	x						x	x				Fa
L. costale	3	35	x	x						x	x					x					Su
L. libum	1	3					x			x					x				x		Su
L. prominens	1	1	x								x					x	x				Su
L. sackeni	1	1		x							x			x			x				Su
L. togatum	87	3466	X	X		x		x	X	x	X	x	x	x	x	X	X	X	x		Su/Fa
L. unicolor	5	22	x							x						x	x				Fa
LEPTOCERIDAE																					
Ceraclea alagma	61	2046	x	X	X	x	x		x	x	x	x	x	x	x	x	x	x	x	x	Su
C. albosticta	1	1	x						x							x	x				Su
C. alces	3	5	x	x							x	x	x	x	x		x				Su
C. ancylus	28	1711	x	x		x	x		x	x	x	x	x	x	x		x	x	x	x	Su
C. annulicornis	3	11	x	x							x		x			x	x	x			Su/Fa
C. arielles	14	139		x						x	x	x		x	x		x	x			Su
C. brevis	–	(1)		+																	Su
C. cancellata	75	2741	X	X	x	x	x	x	x	X	X	x	X	x	x	x	X	X	x	x	Su
C. diluta	41	1601	x	x					x	x	x		x	x	x	x	x	x	x		Su
C. excisa	29	336		x					x	x		x		x	x		x	x			Su
C. flava	27	1870		x	X	x	x		x	x	x	X	x	x	x	x	x	x	x	x	Su
C. maculata	32	1880		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	Su
C. mentiea	4	115		x			x					x		x			x	x	x		Su
C. nepha	–	(1)													–						
C. resurgens	29	368	x	x					x	x	x		x	x	x	x	x				Su
C. tarsipunctata	19	11274	x	X	X	X	X	x	X	X	X	X	X	X	X	x	X	X	X	X	**Su**/Fa
C. transversa	91	8041	X	X	x	x	x	x	X	X	X	x	X	X	X	X	X	X	x	x	Su
C. vertreesi	4	18		x																	Su
C. wetzeli	16	276	x	x					x	x	x		x	x		x	x				Su
Leptocerus americanus	10	18225	x	X	x	X	x	x	X	X	X	X	X	X	X	x	X	X	X	x	**Su**/Fa

			Region					Site Class						Gradient			% Disturbed				Flight
Taxon	Co	Sp	LS	NO	NW	SE	SO	1	2	3	4	5	L	L	M	H	1	2	3	4	Period
Mystacides interjecta	65	2740	x	x			x	x	x	x	x	x	X	x	x		x	x	x	x	Su
M. sepulchralis	42	793	x	x			x	x	x	x	x	x	x	x	x	x	x	x		x	Su
Nectopsyche albida	53	594	x	X	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	Su
N. candida	19	143		x			x		x	x	x	x	x	x	x		x	x	x		Su
N. diarina	61	712	x	X	x	x	X	x	x	x	x	x	x	X	x	x	x	x	x	x	Su
N. exquisita	14	183	x	x			x			x	x	x	x	x	x	x	x	x			Su
N. pavida	16	1336		x		x			x	x	x	x	x	x	x	x	x	x			Su
Oecetis avara	11	14588	x	X		x	x	x	x	x	X	x	x	X	x	x	x	X	x	x	**Su**/Fa
O. cinerascens	13	2210	x	X	x	x	X	x	x	X	X	x	X	X	x		X	X	X	X	**Su**/Fa
O. disjuncta	3	8	x			x			x	x	x				x	x	x	x			Su
O. ditissa	1	1					x			x					x				x		Su
O. immobilis	41	1220	x	x		x	x	x	x	x	x	x	x	x	x	x	x	X	x	x	Su
O. inconspicua	23	12638	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	**Su**/Fa
O. nocturna	27	423	x	x		x	x	x	x	x	x	x	x	x	x		x	x	x	x	**Su**/Fa
O. ochracea	18	146		x	x		x		x	x	x	x	x	x	x		x	x	x	x	**Su**/Fa
O. osteni	26	3479	x	x		x	x		x	x	x	x	X	x	x		x	x	x	x	Su
O. persimilis	34	2662	x	X	x		x	x	x	x	x	x	x	x	x	x	X	x	x	x	Su
Setodes incertus	19	313		x						x	x			x	x		x				Su
S. oligius	23	267		x					x	x	x		x	x			x	x			Su
Triaenodes abus	28	134		x				x	x	x	x		x	x			x	x	x		Su
T. baris	1	6		x									x				x				Su
T. dipsius	89	2361	x	X			x	x	x	x	x	x	x	x	x	x	x	x	x	x	Su
T. flavescens	2	7		x					x					x			x				Su
T. ignitus	14	97		x					x	x	x			x	x		x	x			Su
T. injustus	86	2741	x	X		x	x		x	x	x	x	X	x	x	x	X	X	x	x	**Su**/Fa
T. marginatus	94	2306	x	X	x			x	x	x	x	x	x	x	x		X	x	x	x	**Su**/Fa
T. nox	22	96		x		x		x	x	x	x		x	x	x		x	x	x		Su
T. tardus	11	1054	x	X	x	X	X	X	x	X	X	X	x	X	x		x	X	X	X	**Su**/Fa
Ylodes frontalis	1	1		x			+						x				x				Su
Y. reuteri	6	27		x	x		x			x	x	x		x			x		x	x	**Su**/Fa

LIMNEPHILIDAE

			Region					Site Class						Gradient			% Disturbed				Flight
Taxon	Co	Sp	LS	NO	NW	SE	SO	1	2	3	4	5	L	L	M	H	1	2	3	4	Period
Anabolia bimaculata	37	119	x	x	x		x	x	x	x	x	x	x	x			x	x	x	x	Su
A. consocia	42	69		x	x		x	x	x	x	x		x	x	x		x		x	x	Su
A. ozburni	4	5		x					x				x	x			x				Su
A. sordida	–	(33)			+																Su
Arctopora pulchella	–	(4)		+									+								Su
Asynarchus montanus	4	4	x	x				x	x	x					x	x	x				Su
A. mutatus	–	(2)	+																		Su
A. rossi	3	75	x			x			x							x	x	x			Fa
Chilostigma itascae	2	3		x									x				x				Wi
Frenesia missa	2	3				x			x	x					x	x	x	x			**Fa**/Wi
Glyphopsyche irrorata	1	1	x						x							x	x				Su
Grammotaulius interogationis	–	(1)																			Su
Hesperophylax designatus	14	39	x			x		x	x	x						x	x	x			**Sp**/Su
Hydatophylax argus	5	6	x	x					x	x				x	x	x	x	x			Su
Ironoquia lyrata	1	3		x			x	x	x						x		x				Fa
I. punctatissima	1	5					x	x						x				x			Fa
Lenarchus crassus	1	1	x						x							x	x				Su
L. keratus	–	(1)	+																		Su
Leptophylax gracilis	–	(5)		+	+	+					+										Su
Limnephilus argenteus	6	7	x	x						x	x				x	x	x				Su
L. canadensis	25	37		x					x	x	x	x		x	x		x	x	x		Su
L. dispar	–	(1)		+									+								Su
L. hyalinus	28	44		x	x					x	x			x			x				Fa
L. indivisus	7	9		x			x	x		x	x		x	x	x		x				Su
L. infernalis	32	66	x	x					x	x			x	x			x				Fa
L. janus	1	1		x					x					x			x				Su
L. moestus	11	14	x	x					x	x	x		x		x	x	x				Su
L. ornatus	6	7		x						x	x		x		x		x				Su
L. partitus	–	(1)		+																	
L. parvulus	3	22		x					x				x	x			x				Su
L. perpusillus	4	19		x	+		+		x	x	x			x			x				Su



			Region					Site Class						Gradient			% Disturbed				Flight
Taxon	Co	Sp	LS	NO	NW	SE	SO	1	2	3	4	5	L	L	M	H	1	2	3	4	Period
L. rhombicus	2	3	+	x		x	x		x	x			+	x	x		x	x	x		Su
L. sackeni	1	1		x									x				x				Fa
L. secludens	1	1		+			x	x						x				x			Fa
L. sericeus	19	37		X						X	x		x	X			X	x			Fa
L. sublunatus	–	(1)		+																	
L. submonifer	16	39		X					x	X			x	X			X	x			Fa
L. tarsalis	–	(2)		+																	
L. thorus	3	14	x	x					x	x				x		x	x				Fa
Nemotaulius hostilis	3	3		x			+	x	x				+	x	x		x				Su
Onocosmoecus unicolor	3	6	x						x	x						x	x				Fa
Philarctus quaeris	–	(2)			+																Su
Platycentropus amicus	26	187		x					x	x			x	x			x				Fa
P. radiatus	35	116	x	x					x	x	x		x	x			x	x			Su
Pseudostenophylax sparsus	–	(1)	+								+					+					
P. uniformis	3	131	x				x			x	x				x	x	x		x		su
Pycnopsyche aglona	12	89		x					x	x				x	x		x				Fa
P. guttifer	39	1996	x	X					x	X	X	X	x	X	X	x	X	X	x		Fa
P. lepida	21	168	x	X		x	x		x	x	x		X	x	x		X	x	x	x	Fa
P. limbata	2	6	x	x					x						x	x	x				Fa
P. subfasciata	25	499	x	X	+		x		x	X	x	x	x	X	x		x	x	x	x	Fa
MOLANNIDAE																					
Molanna blenda	5	62	x						x	x					x	x	x				Su
M. flavicornis	41	1260	x	x			x		x	x	x		X	x	x		x	x	x	x	Su
M. tryphena	3	10		x					x	x					x		x	x			Su
M. uniophila	37	1462	x	X			x	x	x	x	x	x	X	x	x		X	X	x		Su
PHILOPOTAMIDAE																					
Chimarra aterrima	1	1		x							x					x		x			Su
C. feria	6	140		x						x	x				x	x	x	x			Su
C. obscura	62	19217	x	X			x		x	x	X	x	x	x	x	x	x	x	x	x	Su/Fa
C. socia	27	2105	x	x					x	x	x	x	x	x	x	x	x	x			Su
Dolophilodes distinctus	6	107	x			x			x	x						x	x				Sp/Su

Taxon	Co	Sp	Region					Site Class						Gradient			% Disturbed				Flight
			LS	NO	NW	SE	SO	1	2	3	4	5	L	L	M	H	1	2	3	4	Period
Wormaldia moesta	–	(29)	+																		Su
PHRYGANEIDAE																					
A. deflata	1	1		x					x					x			x				Su
A. glacialis	–	(13)		+	+						+			+							Su
A. improba	36	73	x	x				x	x	x	x		x	x	x	x	x	x			Su
A. macdunnoughi	–	(6)	+								+		+			+					Su
A. straminea	27	226	x	X			x		x	x	x		X	x			x	x			Fa
A. vestita	16	28		x			x	x		x	x		x	x	x		x	x	x	x	Su
Banksiola crotchi	78	1093	x	X		x	x	x	X	x	x	x	X	X	x	x	X	x	x	x	Su
B. dossuaria	–	(5)	+	+						+					+						Su
B. smithi	–	(1)		+																	Su
Beothukus complicatus	1	1	x						x							x	x				Su
Fabria inornata	–	(26)		+			+														Su
Hagenella canadensis	3	3		x						x	x		x	x			x				Su
Oligostomis sp.	1	3					L		L					L					L		
Phryganea cinerea	69	389	x	X	x		x	x	x	x	x	x	X	x	x	x	X	X	x	x	Su
Ptilostomis ocellifera	56	157	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	Su
P. semifasciata	74	466	X	X	x	x	x	x	X	X	X	x	X	X	x	X	X	x	x	x	Su
POLYCENTROPODIDAE																					
Cyrnellus fraternus	4	32				x	x			x	x	x		x	x	x	x		x	x	Su
Neureclipsis bimaculata	16	980		x	x		x		x	x	x	x	x	x			x	x	x	x	Su
N. crepuscularis	29	301	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	Su
N. valida	12	100		x					x	x	x		x	x			x	x			Su
Nyctiophylax affinis	52	1290	x	x	x	x	x	x	x	x	x	x	X	x	x	x	x	x	x	x	Su
N. banksi	1	1		x									x				x				Su
N. celta	9	136	x	x					x	x	x			x	x	x	x	x			Su
N. moestus	41	615	x	x		x		x	x	x	x	x	x	x	x	X	x	x	x		Su
Polycentropus albipunctatus	16	37	x	x					x	x	x		x	x			x	x			Su
P. aureolus	5	11		x					x	x	x		x	x			x	x			Su
P. centralis	3	5	x						x	x	x					x	x				Su
P. cinereus	63	2736	X	X	x	x	x	x	x	x	x	X	X	x	x	X	X	X	x	x	Su/Fa

			Region					Site Class						Gradient			% Disturbed				Flight
Taxon	Co	Sp	LS	NO	NW	SE	SO	1	2	3	4	5	L	L	M	H	1	2	3	4	Period
P. clinei	–	(2)		+						+				+							
P. confusus	11	17	x	x					x	x	x		x		x	x	x				Su
P. crassicornis	3	7	x	x					x	x					x	x	x				Su
P. flavus	6	9		x					x	x	x		x	x			x	x			Su
P. glacialis	3	5		x									x					x			Su
P. iculus	–	(2)		+						+				+							
P. interruptus	52	680		x		x	x		x	x	x	x	X	x	x		x	x	x	x	Su
P. melanae	14	75		x					x	x	x		x	x			x				Su
P. milaca	2	3		x									x				x				Su
P. pentus	17	46				x	x	x	x	x				x	x		x	x	x		Su
P. picicornis	2	2	x				x				x		x	x			x			x	Su
P. remotus	12	32		x			x		x	x	x		x	x	x		x				Su
P. weedi	3	4		x					x	x	x			x	x		x				Su
PSYCHOMYIIDAE																					
Lype diversa	9	21		x					x	x	x			x	x		x	x			Su
Psychomyia flavida	12	22744	x	X	x	x	x	x	x	x	x	x	x	x	x	x	X	X	x	x	Su
RHYACOPHILIDAE																					
Rhyacophila angelita	1	1	x						x							x	x				Su
R. fuscula	13	63	x						x	x	x					x	x				Su
R. vibox	1	1	x						x							x	x				Su
SERICOSTOMATIDAE																					
Agarodes distinctus	18	200	x	x					x	x	x		x	x	x	x	x	x			Su
UENOIDAE																					
Neophylax concinnus	8	31				x			x	x					x	x	x	x			Fa
N. fuscus	2	2		x							x	x			x	x	x				Fa
N. oligius	11	37	x	x					x	x	x				x	x	x				Fa

Table 4.3. The 13 Minnesota caddisfly species whose presence was best predicted by latitude (Lat) and percentage of disturbed upstream habitat (Dist), with calculated binomial regression models for each species. Based on fit of y = logit (p). Probability (p) values are for each variable separately; all models were also significant ($p < 0.05$). C = regression coefficient for each variable.

Species	Intercept (±SE)	C_{Lat} (±SE)	p	C_{Dist} (±SE)	p	Pseudo R^2
Agrypnia improba	-13.19 (6.31)	0.49 (0.007)	0.01	-0.03 (0.134)	<0.001	0.23
Anabolia bimaculata	-14.81 (6.23)	0.33 (0.006)	0.03	-0.02 (0.128)	<0.001	0.22
Banksiola crotchi	-13.59 (7.65)	0.52 (0.008)	0.001	-0.02 (0.163)	<0.001	0.36
Ceraclea cancellata	-14.59 (6.11)	0.35 (0.006)	0.001	-0.03 (0.133)	<0.001	0.28
Ceraclea transversa	-13.53 (6.21)	0.30 (0.006)	0.00	-0.02 (0.130)	<0.001	0.15
Helicopsyche borealis	-16.23 (6.43)	0.40 (0.008)	0.02	-0.02 (0.141)	<0.001	0.25
Lepidostoma togatum	-16.54 (7.07)	0.51 (0.007)	0.03	-0.04 (0.172)	<0.001	0.21
Micrasema wataga	-14.29 (6.36)	0.35 (0.007)	0.02	-0.02 (0.145)	<0.001	0.16
Molanna uniophila	-12.65 (6.18)	0.29 (0.006)	0.01	-0.04 (0.187)	<0.001	0.18
Oecetis persimils	-14.27 (6.97)	0.47 (0.008)	0.03	-0.02 (0.167)	<0.001	0.13
Ptilostomis semifasciata	-15.92 (6.12)	0.34 (0.006)	0.01	-0.02 (0.130)	<0.001	0.15
Triaenodes injusta	-12.24 (6.73)	0.32 (0.007)	0.01	-0.04 (0.152)	<0.001	0.12
Triaenodes marginata	-14.15 (6.72)	0.42 (0.006)	0.01	-0.03 (0.164)	<0.001	0.10

Table 4.4. The three species of Minnesota caddisfly species whose presence was best predicted by percentage of disturbed upstream habitat (Dist), with calculated binomial regression models, pseudo R^2 values, and probability (p) values for each model for five different site classes. Based on fit of y = logit (p). Small streams = Class 1–2, medium streams = Class 3–4, large rivers = Class 5 (Table 4.1).

Species	Intercept (±SE)	C_{Dist} (±SE)	Pseudo R^2	p
Cheumatopsyche campyla				
All sites	-1.38 (0.37)	0.03 (0.007)	0.18	<0.001
Small Streams	-4.44 (0.56)	0.06 (0.006)	0.14	0.07
Medium Streams	-2.96 (0.39)	0.05 (0.007)	0.18	<0.001
Large Rivers		N/A		0.20
Lakes	-2.56 (0.41)	0.04 (0.005)	0.19	<0.001
Hydropsyche bidens				
All Sites	-2.19 (0.33)	0.04 (0.005)	0.21	<0.001
Small Streams	-1.96 (0.46)	0.03 (0.006)	0.23	<0.001
Medium Streams	-2.18 (0.35)	0.03 (0.007)	0.20	<0.001
Large Rivers		N/A		0.36
Lakes	-1.55 (0.32)	0.04 (0.006)	0.19	<0.001
Potamyia flava				
All sites	-2.58 (0.32)	0.05 (0.008)	0.42	<0.001
Small streams	-4.61 (0.43)	0.17 (0.010)	0.35	0.004
Medium Streams	-3.96 (0.36)	0.07 (0.009)	0.41	0.001
Large Rivers		N/A		0.63
Lakes	-4.25 (0.30)	0.10 (0.006)	0.49	<0.001

Figure 4.1. The five caddisfly regions of Minnesota determined by grouping together Minnesota's 81 major watersheds (Chapter 2) and showing the 294 sampling sites of this study. Overlap exists between markers. LS = Lake Superior, NO = Northern, NW = Northwestern, SE = Southeastern, SO = Southern.

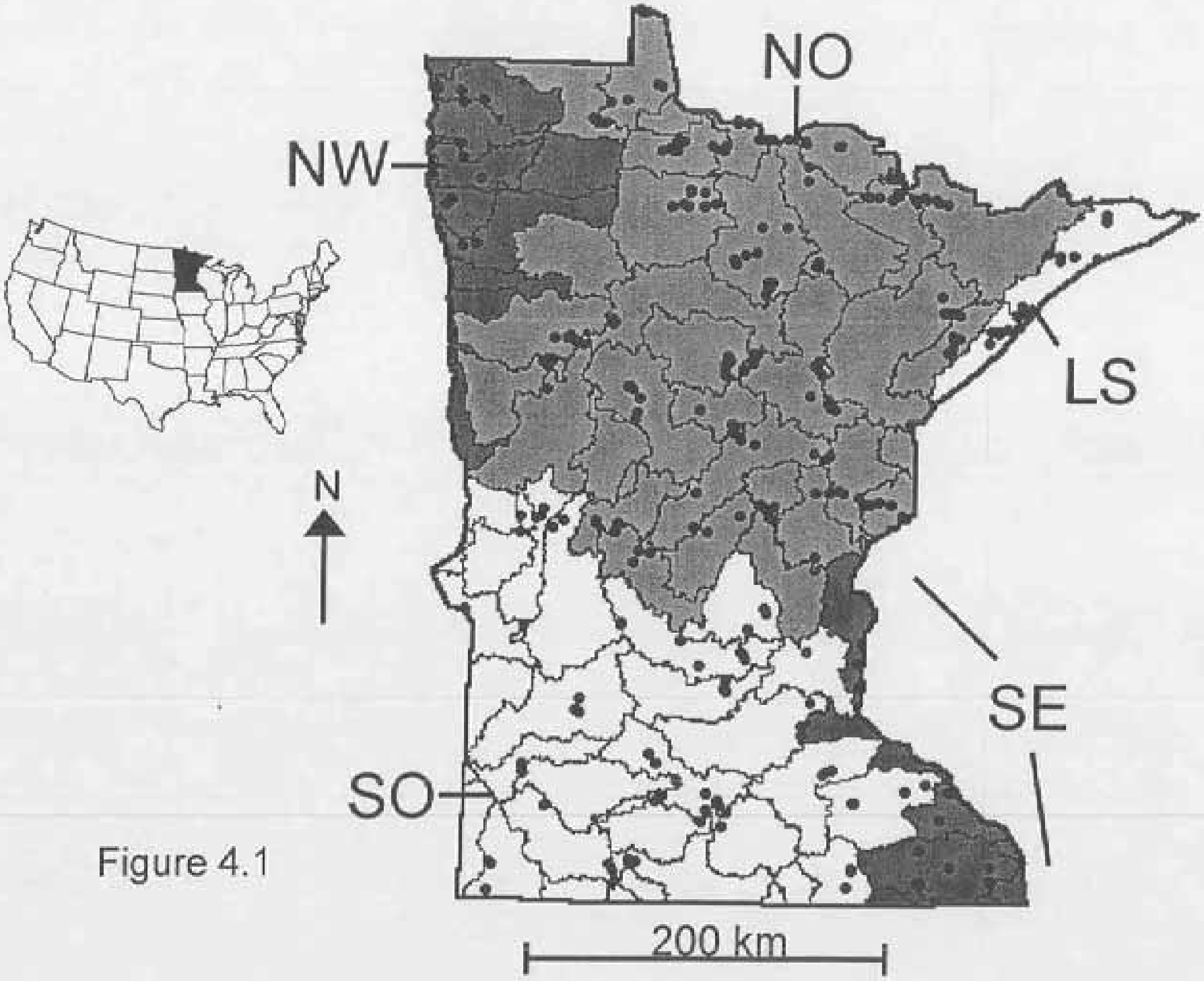


Figure 4.1

Figure 4.2. Species ranked in descending order of incidence (# samples) and abundance (# specimens) in the 317 samples collected.

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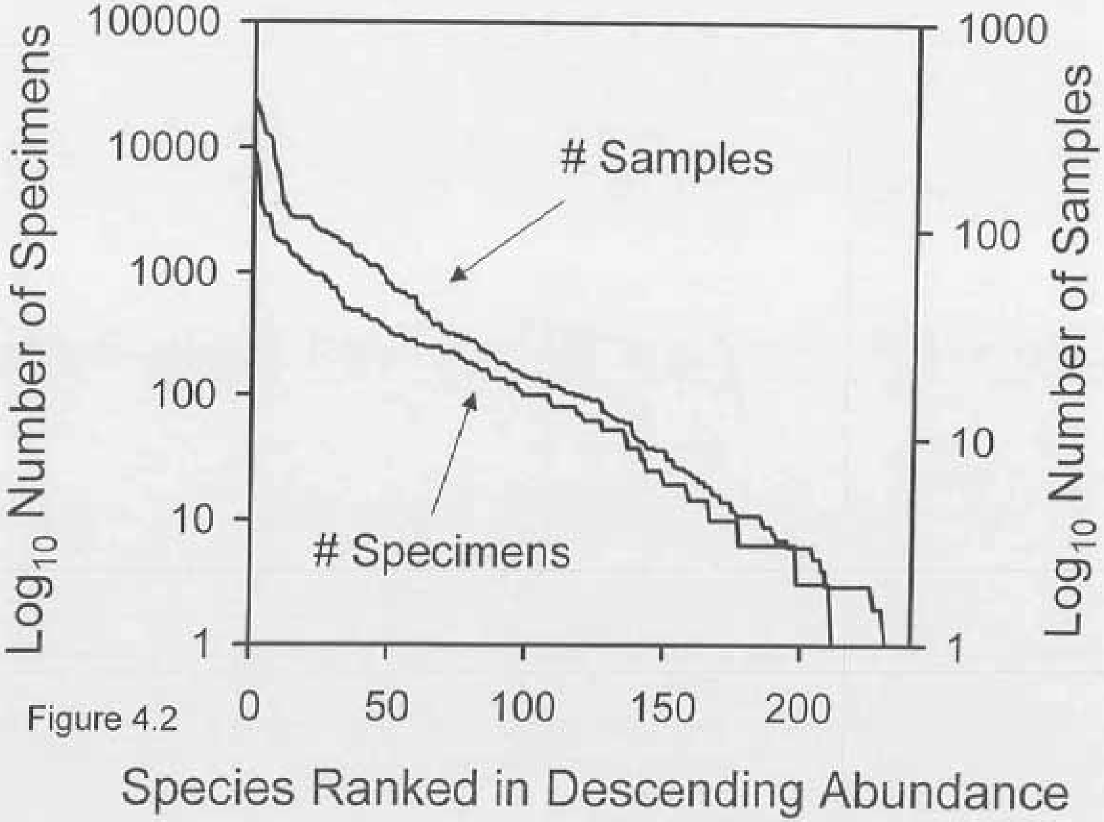
Log10 Number of Specimens
100000
10000
1000
100
10
1
Samples
Specimens
1000
100
10
1
Log10 Number of Samples
0
50
100
150
200
Species Ranked in Descending Abundance

Figure 4.2

Figure 4.3. Known distributions of three rare caddisfly species: *Hydroptila novicola* (circles), *Chilostigma itascae* (triangle), and *Oxyethira ecornuta (Xs)* within the five caddisfly regions of Minnesota (Chapter 2) based on all collecting.

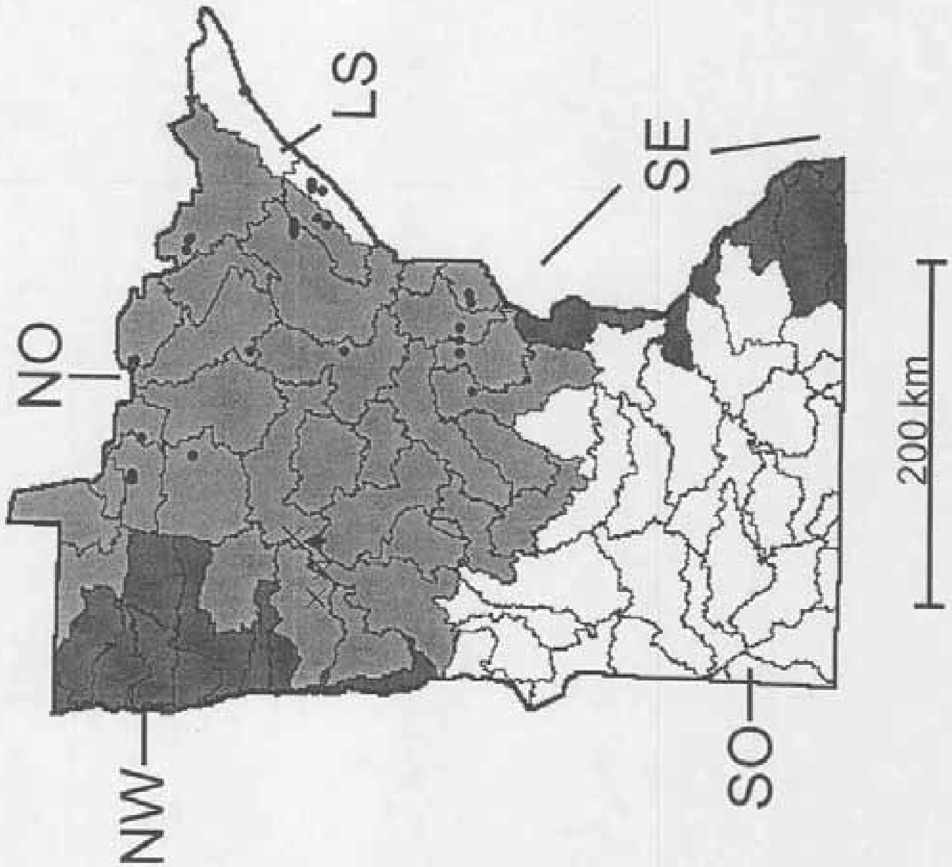

Figure 4.3

Figure 4.4. The known distributions of four rare caddisfly species: *Oxyethira itascae* (circles), *Agapetus tomus* (squares), *Polycentropus milaca* (triangles), and *Asynarchus rossi* (arrows) within the five caddisfly regions of Minnesota (Chapter 2) based on all collections.

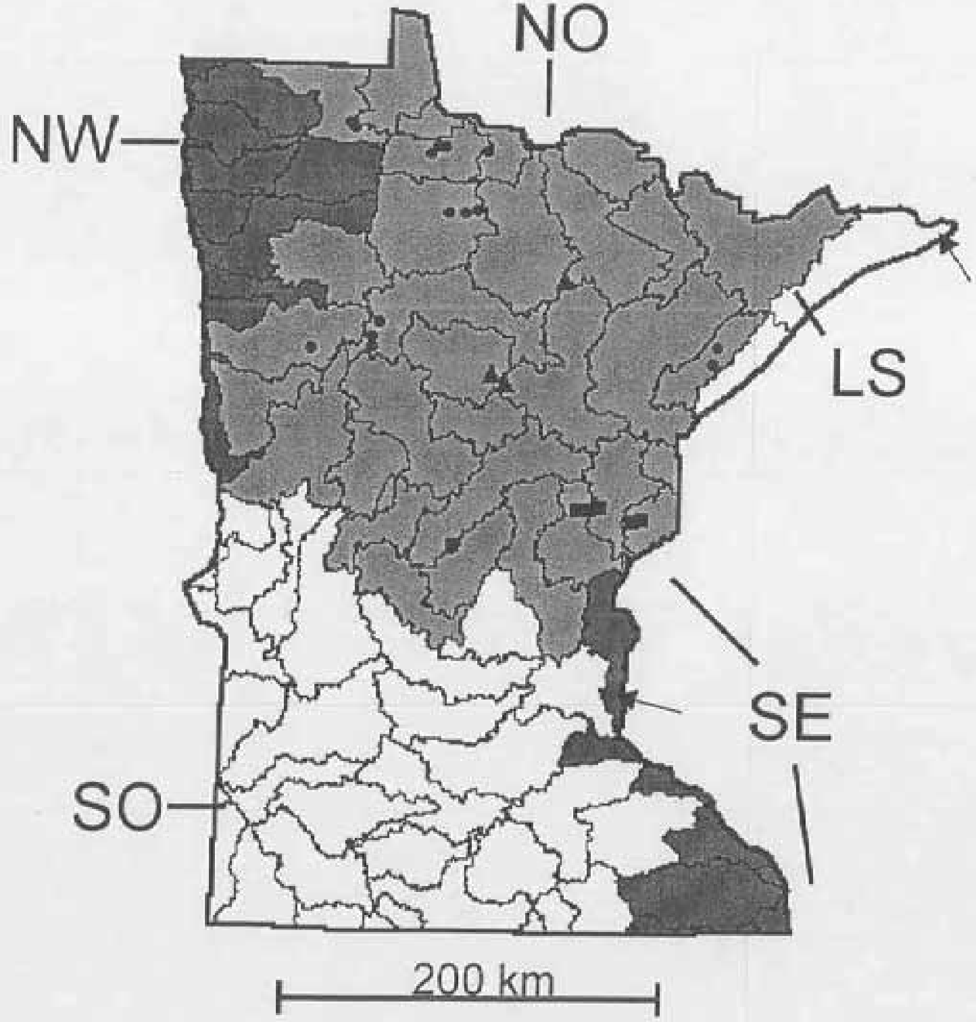

Figure 4.4

Figure 4.5. Binomial regression models of the occurrence of *Cheumatopsyche campyla, Hydropsyche bidens,* and *Potamyiaflava* in Minnesota based on percentage of disturbed upstream habitat for four different habitat types. Calculated models are in Table 4.4.

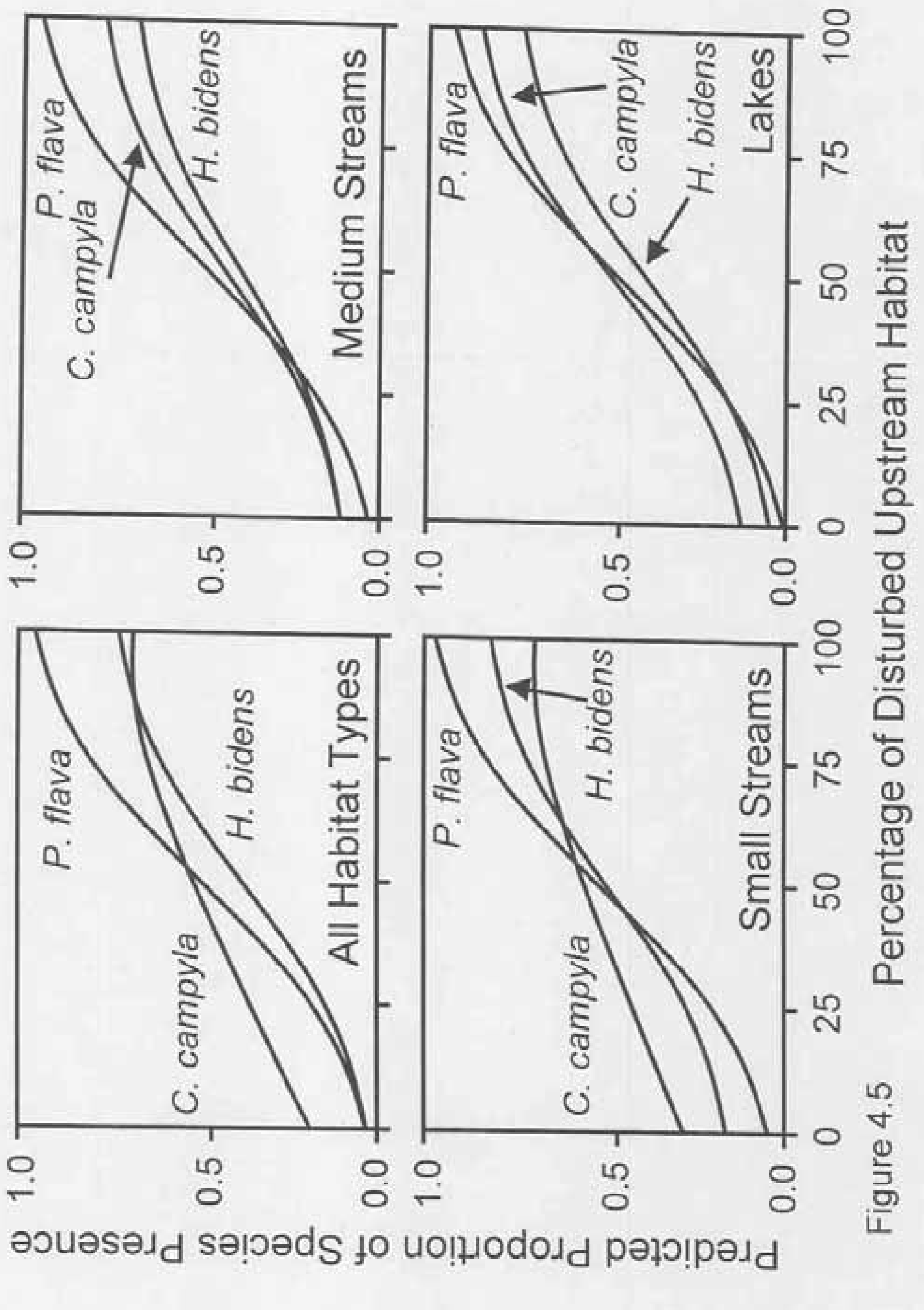
Predicted Proportion of Species Presence
Percentage of Disturbed Upstream Habitat
All Habitat Types
P. flava
C. campyla
H. bidens
Medium Streams
P. flava
C. campyla
H. bidens
Small Streams
P. flava
C. campyla
H. bidens
Lakes
P. flava
C. campyla
H. bidens
0.0
0.5
1.0
0
25
50
75
100

Figure 4.5

Figure 4.6. Chi-residuals and *lowess* smooth line for *Cheumatopsyche campyla* (closed circles), *Hydropsyche bidens* (plus signs), and *Potamyiaflava* (open circles) based on a binomial regression of species presence or absence on the percentage of disturbed upstream habitat for all combined habitat types.

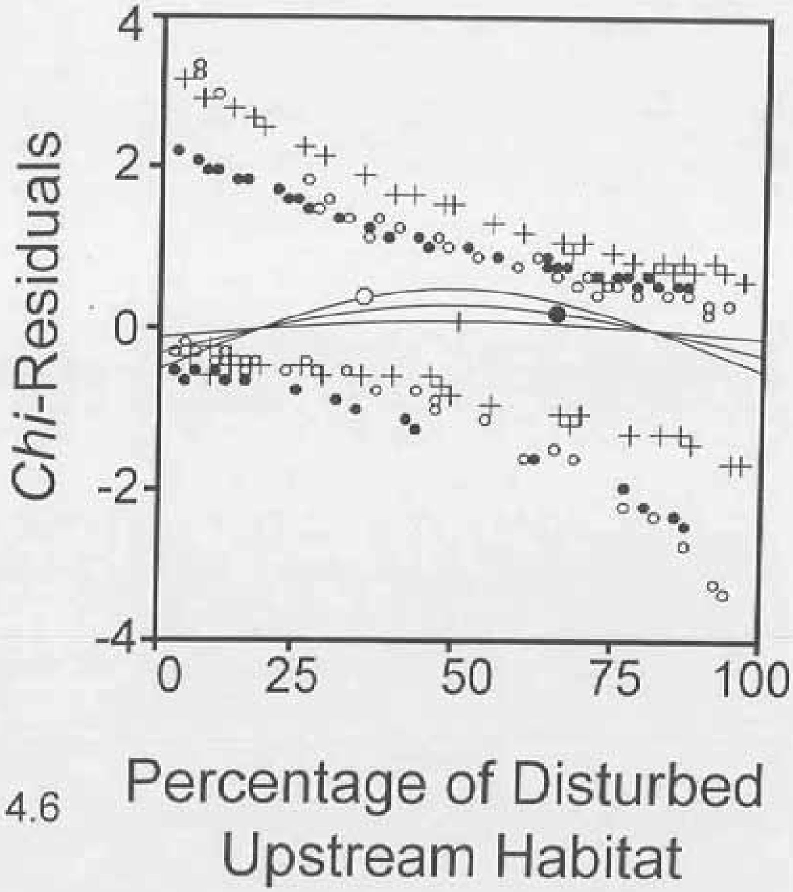
Chi-Residuals
4
2
0
-2
-4
0
25
50
75
100
Percentage of Disturbed
Upstream Habitat

Figure 4.6

CHAPTER 5

CONCLUSIONS

Conclusion 1. Distributions of Minnesota caddisflies can be separated into distinct faunal regions corresponding to the Northern, Southern, Northwestern, Southeastern, and Lake Superior regions of the state. These regions were supported by both Detrended Correspondence Analysis and a flexible unweighted pair-group method using arithmetic averages (UPGMA) dendogram using caddisfly relative abundance data per watershed.

Conclusion 2. These determined regions have nearly twice the classification strength at partitioning the variation of the caddisfly fauna than do a priori geographic classifications of watersheds and ecological regions. Higher taxonomic resolution and smaller spatial scale also increase classification strength, although not to as great a degree as using caddisfly regions instead of other classifications.

Conclusion 3. Differences exist in the species richness, diversity, and trophic feeding ecology of the caddisflies within the five determined regions. The Lake Superior, Northern, and Southeastern regions have relatively high richness and diversity, as well as feeding group ecology based on habitat types as predicted by the River Continuum Concept. The Northwestern and Southern regions, conversely, have relatively low richness and diversity, and are dominated in all types of lakes and streams by fine particle filtering collectors.

Conclusion 4. These differences in caddisfly assemblages between different regions are likely caused by both natural and anthropogenic factors. Temperature, percentage of disturbed habitat, and stream gradient all related to caddisfly distributions. A distinct fauna exists in the high-gradient region of eastern Minnesota, exhibiting similarities to those of mountainous areas. In contrast, the strong negative correlation between temperature and percentage of disturbed habitat made it difficult to separate the relative importance of these variables in affecting caddisfly distributions.

Quantifying potential loss of biodiversity and changes in. trophic feeding ecology due to human influence are impeded by the lack of historical caddisfly data within disturbed areas, and the possibility that prairie ecosystems may naturally exhibit less biodiversity and atypical trophic feeding ecology. The strong negative correlations between species richness and percentage of disturbed habitat for both relatively disturbed and undisturbed areas, however, adds further support to the possibility of species loss due to human activities. Furthermore, no differences were found in either species richness or feeding ecology between Prairie and Deciduous Forest ecosystems within disturbed regions, suggesting that any natural variation between these ecosystems is less important than the effects of human disturbance.

Conclusion 5. Three species, *Cheumatopsyche campyla, Hydropsyche bidens,* and *Potamyia flava* (Hydropsychidae) are likely good indicators of disturbed habitat in Minnesota, especially those of disturbed lakes and small-medium streams. The proportion of occurrence of all three species is best predicted by percentage of disturbed upstream habitat using binomial regression analysis, and does not respond to other variables. All three species are fine particle filtering collectors typically found in large rivers. They may move into lakes and small-medium streams when organic pollution raises the level of their fine particle food source.

Conclusion 6. Finding additional species that indicate certain habitat types or level of disturbance will likely necessitate more through sampling and higher precision of environmental measurements. Many species that were exclusive to certain habitats were not found frequently enough in these habitats to generate statistical significance using binomial regression modeling. Of the 16 species whose response did generate statistical significance, 13 responded positively to increasing latitude and negatively to increasing percentage of upstream habitat disturbance. Some of these species are good likely indicators of undisturbed habitats, but responses to latitude and percentage of disturbed habitat must be first separated due to the strong negative correlation between these variables in Minnesota.

Overall Conclusions. The utility of the caddisflies in biomonitoring was confirmed during this study, as was the importance of baseline biodiversity data for biomonitoring. As a group, Minnesota caddisflies responded to gradients of both habitat type and level of disturbance. Separating out the natural and anthropogenic components of this response is difficult in the absence of historical caddisfly biodiversity data. It does appear, however, that caddisfly biodiversity and feeding ecology have been negatively affected in at least the Northwestern and Southern regions due to human disturbance. Further research will be needed to clarify these changes, as well as their potential implications for the overall health and functioning of Minnesota aquatic ecosystems.

With baseline caddisfly biodiversity data now in place, future changes to the fauna can be evaluated with greater confidence. The overall documented patterns of caddisfly biodiversity in Minnesota, as well as the habitat affinities of the individual species, should serve as a foundation for the use of caddisflies in the aquatic biomonitoring in Minnesota by predicting general caddisfly assemblages on a regional level.