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Bioassessment and the Partitioning of Community Composition and Diversity Across Spatial Scales in Wetlands of the Bonneville Basin

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BIOASSESSMENT AND THE PARTITIONING OF COMMUNITY COMPOSITION AND DIVERSITY ACROSS SPATIAL SCALES IN WETLANDS OF THE BONNEVILLE BASIN

by:

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GRADUATE COMMITTEE APPROVAL

of a dissertation submitted by

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This dissertation has been read by each member of the following graduate committee and by majority vote has been found to be satisfactory.

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DEPARTMENT AND COLLEGE ACCEPTANCE

As chair of the candidate's graduate committee, I have read the dissertation of Mary Jane Keleher in its final form and found that (1) its format, citations and bibliographical style are consistent and acceptable and fulfill university and department style requirements; (2) its illustrative materials including figures, tables, and charts are in place; and (3) the final manuscript is satisfactory to the graduate committee and is ready for submission to the university library.

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ABSTRACT

Bioassessment and the Partitioning of Community Composition and Diversity Across Spatial Scales in Wetlands of the Bonneville Basin

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Doctor of Philosophy

The Bonneville Basin encompasses an area that was covered by ancient Lake Bonneville and which today lies within the Great Basin province. The Bonneville Basin is distinguished geologically by its characteristic parallel north-south mountain ranges that are separated by broad, alluviated desert basins and valleys. Benches and other shoreline features of ancient Lake Bonneville prominently mark the steep, gravelly slopes of these ranges. Numerous artesian desert springs are present at the base of the mountains and in the valley floors that form various sizes of both isolated wetlands and wetland complexes. Many these wetlands are some of the most unique and currently some of the most threatened wetlands in the United States.

Several aquatic species and communities have maintained an existence as relict populations and communities in these wetlands since the receding of Lake Bonneville over 10,000 years ago. For example, Hershler has described 58 previously undescribed species of hydrobiid snails, 22 of which are endemic to single locations. Like hydrobiid snails, numerous other species, such as the least chub, *Iotichthys phlegethontis* and the

Columbia spotted frog, *Rana luteioventris*, depend on these wetlands for their continued existence, many of which are already imperiled. The continued decline and loss of these wetlands would further push many of these species toward endangerment and/or extinction.

Several factors have already eliminated or altered many of these habitats including capping and filling, water depletions, agricultural practices, livestock grazing, and introduction of nonnative species. In recent years, the significant loss and degradation of wetlands resulting in sensitive species designations have provided impetus for resource agencies to develop and implement management plans to conserve and protect these vital ecosystems. One problem facing appropriate management is the lack of biological information for determining which wetlands should receive protection priorities based on the presence of viable, functioning characteristics.

The purpose of this dissertation project was to obtain biological information needed to support defensible decisions concerning conservation, protection, acquisition, restoration, and mitigation of the artesian springs in the Bonneville Basin. The primary objectives of this project were to 1) Develop bioassessment procedures for artesian wetlands of the Bonneville Basin using macroinvertebrates and 2) Determine patterns of community composition and diversity for macroinvertebrates and metaphyton algae at multiple scales in Bonneville Basin artesian wetlands.

Keywords: Bonneville Basin, bioassessment, macroinvertebrates, metaphyton algae, community composition, community diversity, desert wetlands, artesian springs

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CHAPTER ONE - BIOASSESSMENT OF ARTESIAN SPRINGS IN THE BONNEVILLE BASIN, UTAH - USA

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ABSTRACT

In recent years, the degradation and loss of desert artesian springs has resulted in several sensitive species designations. Information (e.g. physico-chemical, biological) needed to determine the health and integrity of these wetlands is lacking. Bioassessment procedures have not been developed for groundwater-fed springs in the United States and elsewhere. Assessing the integrity of artesian springs was a challenge because of variable physico-chemical conditions between springs coupled with their unique hydrologic characteristics (a constant inflow of clean, unpolluted water). We collected physico-chemical data and macroinvertebrates from 125 springs. Thirty-three springs clustered into three minimally impacted reference classes. We were able to match and compare 39 disturbed sites with one of these three classes, which was critical for identifying bioindicators of degradation. An integrated approach combining diversity indices, and aspects of multivariate analyses, multimetrics, and HGM was valuable in assessing the health and integrity of these artesian springs. Multivariate analyses (NMDS, ANOSIM and SIMPER) were particularly valuable in detecting trends at the community level and identifying specific indicator taxa (e.g. amphipods and dipterans). We developed an Index of Biological Integrity (IBI) that can be used to distinguish reference sites from severely impacted sites. Many macroinvertebrates appeared to have a threshold response to the effects of degradation as their diversity increased along the disturbance gradient, often being greater in Severely Impacted sites than in Reference sites. Odum's subsidy-stress gradient provides a theoretical explanation for this paradox.

Key words: bioassessment, desert artesian springs, Bonneville Basin, macroinvertebrates, bioindicators, multimetrics, IBI, multivariate analyses, HGM,

reference classification

INTRODUCTION

Environmental degradation attributed to human intervention can reduce the capacity of natural ecosystems to provide valuable goods and services (e.g. Randall 1988). Bioassessment is the practice of using living organisms to detect environmental degradation attributed to human activities (Rosenberg and Resh 1993). Bioassessment requires an understanding of how habitats and living organisms respond to environmental change. It is particularly valuable if it can detect the early signs of degradation before ecosystems shift to alternative states with lower diversity and a reduced functional capacity (Rader and Shiozawa 2001).

Desert artesian springs of the Great Basin are some of the most unique and threatened wetlands in the United States. Many have been eliminated (capped and filled) and others have been altered by urbanization, water depletions, livestock use, agricultural inputs, and the introduction of nonnative species. These wetlands are critical habitats for many endemic aquatic taxa (e.g. Meffe and Marsh 1983, Hershler 1994). In recent years, the degradation and loss of these springs has resulted in several species receiving sensitive designations (e.g. Perkins et al. 1988). Efforts to protect artesian springs of the arid west lack the information needed to determine their health and integrity (e.g. chemical, physical, and biological).

Researchers have developed a variety of methods to assess the integrity of aquatic ecosystems in an effort to meet the objectives of the Clean Water Act. Bioassessment methods range from simple diversity indices (Simpson 1949) to more complex techniques involving hydrogeomorphic functions (e.g. Brinson 1993, Brinson 1996), biological metrics (e.g. Karr 1981, Kerans and Karr 1994, Karr 2000, Simon 2003) and

multivariate predictive models (e.g. Hawkins et al. 2000, Hawkins and Carlisle 2001).

The hydrogeomorphic model (HGM) uses a variety of variables to assess the integrity of functions performed by specific types of wetlands (Brinson 1996). For example, the capacity of riverine wetlands to store nutrients from lotic ecosystems (the function) can be estimated by: 1) wetland area, 2) frequency and length of inundation, 3) density of macrophytes, and 4) density of retention structures of organic matter. A diverse assemblage of macroinvertebrates is also a function that is frequently included in an HGM assessment. All functions are typically compared between minimally impacted reference sites versus potentially impacted test sites (sites of unknown ecological condition) to assess wetland integrity.

A *metric* is a measurable biological characteristic that responds to human disturbance in a predicable way (Barbour et al. 1995). Multimetric indices are sets of aggregated indicators ranging from the response of individual species to the response of entire communities (Karr 1981, Kerans and Karr 1994, Barbour et al. 1995, Barbour et al. 1999, Stevenson 2001, US EPA 2002). The first multimetric analysis was applied to stream fish in the Index of Biological Integrity (IBI - Karr 1981). Since then IBI's have been developed using a variety of taxa including birds (e.g. O'Connell et al. 2000), aquatic macroinvertebrates (e.g. Kerans and Karr 1994, Klemm et al. 2003), algae (e.g. Stevenson 2001), and wetland macrophytes (e.g. Simon et al. 2001, DeKeyser et al. 2003).

Multivariate techniques assess environmental condition by comparing the observed species composition of potentially disturbed test sites to the predicted species composition from minimally impacted reference sites (e.g. Reynoldson et al. 1997). A

variety of multivariate analyses may be used to predict reference conditions and compare reference sites and test sites. Non-metric multidimensional scaling (O'Conner et al. 2000, Clarke and Warwick 2001), canonical correspondence analysis (Kingston et al. 1992, Dufréne and Legendre 1997), and discriminant analysis (e.g. Armitage et al. 1987) are common procedures.

All three approaches to bioassessment (HGM, multimetrics, multivariate analyses) have the same goal, to detect degradation before diversity declines and ecosystem functions fail. They often require the same data collected using similar techniques (e.g. quantitative biological and physico-chemical data). They primarily differ in the way test sites are compared to reference sites (e.g. Reynoldson et al. 1997).

The greatest challenge for any bioassessment procedure is to discern the signal of degradation through the haze of natural variation (Rader and Shiozawa 2001). This can be a daunting task since populations and communities tend to vary in complex ways at multiple spatial and temporal scales (e.g. White and Walker 1997). Distinguishing natural variation in populations from variation due to human intervention is vital to correctly interpreting bioassessment results (White and Walker 1997, Rader and Shiozawa 2001, Niemi and McDonald 2004). Variability is addressed to some extent through standardized procedures (Resh et al. 1995). However, it is usually necessary to classify aquatic systems into groups with similar physico-chemical characteristics (e.g., hydroperiod and temperature), and to compare reference sites to test sites within the same class.

The unusual challenge in artesian springs of the Bonneville Basin is to find taxa that respond to common types of environmental degradation (e.g. urbanization, cattle

grazing, agricultural runoff, and introduced species) despite the constant inflow of clean groundwater. Water levels are stable and independent of local, short-term precipitation patterns (Deacon and Minckley 1974). Isotopic analyses from a subset of springs in the Bonneville Basin have shown that inflows are primarily comprised of "old water" derived from deep aquifers that filled during former pluvial periods in the Pleistocene (Smith et al. 2000, Anderson et al. 2005). Thus, much of the groundwater inflow is uncontaminated by human activity. Bioassessment may be difficult because many freshwater biological indicators typically respond to a reduction in water quality. For example, the quality of surface waters (e.g. streams and rivers) can be severely affected by watershed impacts (e.g. erosion, sedimentation and pollutants from runoff). However, current watershed impacts will have little effect on the quality of "old" groundwater derived from the Pleistocene. Thus, indicators used for streams and rivers may not work in groundwater-fed wetlands.

The purpose of this study was to develop bioassessment procedures based on macroinvertebrates in desert artesian springs of the Bonneville Basin. Our objectives were to: 1) group springs into classes based on the physico-chemical attributes correlated with variation in macroinvertebrate community composition, 2) define minimally impacted reference conditions for springs in each class, and 3) determine macroinvertebrate indicators for each class using diversity indices, and aspects of HGM, multimetrics, and multivariate approaches. Specifically, we explored three hypothesis: 1) that physico-chemical conditions between springs will vary requiring the development of indicators specific to different classes of spring systems, 2) that some springs will defy classification and our efforts to develop indicators of degradation, and 3) multiple

approaches (e.g. diversity indices, HGM, multimetrics, and multivariate analyses) rather than any single technique will be required to detect degradation.

METHODS

We followed general bioassessment procedures (e.g. Rader and Shiozawa 2001): 1) predict reference and disturbed sites prior to (*a priori*) and following sampling (*a postori*) using specific criteria (e.g. grazing allotments and onsite habitat assessments), 2) classify reference sites into groups based on physico-chemical attributes that do not respond to human intervention (e.g. groundwater temperature), 3) match disturbed sites with an appropriate reference class based on similar physico-chemical attributes to reduce natural variation, and 4) search for macroinvertebrate indicators of degradation that differ between reference and disturbed sites in the same class.

Study Area and Site Selection

The Bonneville Basin is the eastern-most internal drainage basin of the Great Basin Province. It encompasses an area approximately 51,722 km^2, which was the area covered by ancient Lake Bonneville more than 15,000 years ago. The basin is characterized by north-south mountain ranges separated by broad, alluviated desert valleys (Christiansen 1951, Maxey 1968, Wilberg and Stolp 1985). Wetlands that range in size from small isolated springs (1.0 m^2) to large spring complexes (> 600 km^2) occur in the foothills and valley floors. Twenty hydrologic units (United States Geological Survey, 1982) lie within the boundaries of ancient Lake Bonneville. Eleven valleys within these units contained wetlands that met our *a priori* criteria: groundwater-fed

springs that occurred below the shoreline of ancient Lake Bonneville (approximately 1,555 meters above sea level; Figure 1).

A site was defined as the area encompassed by a spring wellhead and the surrounding strip of riparian vegetation (Figure 2). Some sites consisted of isolated springs, which were easy to sample. We used a randomized sampling design to select sites within large wetland complexes. Wetland complexes consisted of multiple spring wells and associated marshes connected by flowing channels. Aerial photographs were examined to identify two transects spanning the maximum length and width of each complex. We then randomly selected segments (100 m) along both transects and searched a 50 m radius for potential sampling sites. This procedure was repeated until we had sampled a maximum of five springs in each wetland complex. Site-specific inventories were conducted during the summer of 2001 and 2002 in order to collect both physico-chemical and biological data.

Physical and Chemical Data

Physico-chemical data were collected at each site in order to determine the environmental variables that best explained variation in the macroinvertebrates of reference sites and subsequent reference classes. We therefore recorded the location (UTMs), elevation (Garmin GPS 60CS), maximum and average water depth, and general substrate type (organic, clay, silt, sand, and gravel) at each site. We also measured water temperature, salinity, conductivity, dissolved oxygen (YSI Model 85 water quality meter), and pH (Hanna pHep pH meter) at the wellhead approximately 0.3 m from the surface of the water.

Macroinvertebrates

We assumed that habitat degradation, as in other freshwater ecosystems, could cause changes to the diversity and species composition of the macroinvertebrate community (Ball 1982; Ohio EPA 1987; Plafkin et al., 1989). Standard assessment protocols were used to collect macroinvertebrates (Rader and Richardson 1992, Resh and Jackson, 1993, Batzer et al. 2001). Three samples were collected at most sites using a standard D-frame sweep net (1 mm mesh). At very small sites only two samples could be taken (e.g. surface area < 1 m^2). A sample consisted of three 1-meter sweeps through all microhabitats; emergent vegetation (e.g. *Eleocharis* spp.), undercut banks, submersed vegetation (e.g., *Potamogeton* spp.), floating vegetation (e.g. *Lemna* spp.), metaphyton, and detrital material. Macroinvertebrates were also removed by hand from woody debris. The same field technician collected all samples to avoid potential bias. All samples were combined into a single composite for each site, preserved in 90 % ethanol, and returned to the laboratory for processing.

In the laboratory, macroinvertebrate samples were placed in a 23 cm x 33 cm tray and subsampled using randomly selected quadrats (6 cm^2) until 300 individuals were recorded (Hannaford and Resh 1995, Barbour et al. 1999, King and Richardson 2002). Large-rare organisms were removed prior to sub-sampling and were included in the 300 count to document the species composition (Rader and Richardson 1992). All invertebrates were identified to the lowest possible taxonomic level (usually genus or species), except for ostracods and prosobranch gastropods, which were identified to the order level. However, native spring snails (Hydrobiidae) were separated from the rest of

the gastropods and sent to experts for identification because we suspected their potential as a useful indicator of degradation.

Reference Classification

Landscape Criteria

We determined reference criteria at the scale of individual valleys prior to visiting specific sites for habitat assessment and collecting macroinvertebrates. We stratified the Bonneville Basin into large landscape units using maps (e.g. DOI-USGS - Hydrologic Unit Maps 1982, BLM Land-Use maps), previous field observations (Utah Division of Wildlife Resources monitoring data), and variables such as valley average elevation and general hydrology. We used topographic maps to identify springs in each unit that occurred below 1,555 m.a.s.l. and located areas that might contain sites that could meet both reference and disturbed conditions. We used aerial photographs, the expertise of resource managers, and personal experience to gather background information on each area (e.g. grazing allotments, years since grazed, urbanization, nonnative species). We then visited the least disturbed and most disturbed areas in each valley to locate individual springs and collect site-specific information to describe minimally impacted reference sites and potentially disturbed test sites.

Habitat Assessment

In order to evaluate the health of each site independent from data used for bioassessment (macroinvertebrates), we developed a scoring system based on livestock use, agricultural inputs, nonnative species, and degree of urbanization (Table 1). These are the most common sources of degradation in spring systems of the Bonneville Basin. This scoring

system was developed prior to visiting sites and collecting data to assess habitat condition.

Data were collected at each site using visual estimates of livestock use, presence of nonnative species, and urban impacts (fences, buildings, water diversions etc.). We used cluster analysis to determine reference classes using the sites that received a score of 3. Disturbed sites (moderately and severely impacted) were matched with reference sites in the same class and macroinvertebrates were collected from each of the three types of sites within each class. The cluster analysis of minimally impacted reference sites and ranking procedures used to determine Reference, Moderately Impacted, and Severely Impacted sites in each class are described below.

Livestock use was divided into three categories: 1) the percent of the site grazed, 2) the percent area trampled, and 3) the percent area containing cattle excrement (Table 2). The area included the wellhead and the wetted riparian vegetation surrounding the wellhead. These were visual estimates made by the same field technician at each site. Each category was divided into five degrees of impact with an associated value (e.g. 1 = < 10 % impact). The values for each category were summed for each site to obtain the overall rank for livestock use (Table 2). Any site that received a total value of 3 - 5 with no single value greater than 2 (e.g. 1 + 1 + 1, or 1 + 1 + 2, or 1 + 2 + 2) was designated as minimally impacted and received an overall rank of 1 for livestock use. Sites with values totaling between 6 and 9 represented moderately impacted conditions and received a rank of 2, whereas any site with a total value ≥ 10 represented severely impacted conditions and received a rank of 3.

Each site was assigned one of three ranks representing the affects of non-native

taxa. A rank of 1 was assigned to a site where no nonnative species were detected, a rank of 2 was assigned to a site where nonnative species were present, but their affect was either benign or minimal. This category included species that would not affect macroinvertebrates, such as small patches of purple loosestrife (*Lythrum salicaria*) or small stands of Russian olives (*Elaeagnus angustifolia*). A rank of 3 was assigned to sites where nonnative species were present and that likely could affect the aquatic macroinvertebrates. Species in this category included mosquitofish, sunfish, and bass, amphibians (e.g. bullfrogs, *Rana catesbiena*,), mollusks (*Melanoides tuberculata*), and dense canopies of plants that could reduce overall oxygen concentrations (e.g. *Elaeagnus angustifolia*).

The urbanization category was based on the presence of dwellings, roads, water development, and recreational uses near to and upslope from the site. Urbanization was divided into three ranks with a 1 representing minimally impacted conditions. Minimally impacted sites showed no visible sign of recent human activity. If human activities were observed, but likely had minimal impact (e.g. nearby fence, small water diversions, etc.) the site received a rank of 2. Sites receiving a rank of 3 had multiple effects, such as roads, agricultural fields, urban developments (e.g. buildings), recreation (e.g. trampling), or water development (e.g. capping/diversions) upslope from a spring or in the near vicinity.

Statistical Procedures

A taxonomic list of macroinvertebrates was used to group minimally impacted sites into reference classes based on community similarity using Euclidian distances (MINITAB 2000). Stepwise discriminant analysis was used to determine which physical and

chemical variables (e.g. water temperature, pH, and salinity) were best correlated with variation between classes. This analysis was performed using Proc STEPDISC (SAS 1997) with entry and exit level set at $p = 0.15$. Although ineffective, we also experimented with reducing the number of physico-chemical variables to a smaller sub-set of principal components (Proc PRINCOMP, SAS 1997). A discriminant function analysis (Proc DISCRIM, SAS 1997) was then performed to examine how well the physico-chemical variables from the stepwise discriminant analysis correctly discriminated wetland classes by assigning sites to the correct class.

Biological Indicators

Diversity Indices

We used richness, evenness, and taxonomic distinctness to compare macroinvertebrate diversity between reference and disturbed sites within each class. Although we used a fixed number of individuals from each sample, some composite samples had fewer than 300 individuals (e.g. very small springs) and since we unavoidably sampled a different number of reference and disturbed sites in each class, we used EcoSim (Version 7.72 - Gotelli and Entsminger 2006) to calculate rarified species accumulation curves (e.g. Sanders 1968, Gotelli and Colwell 2001). Richness was standardized using the site with the fewest individuals and smallest area sampled (e.g. Clarke and Gorley 2006, Krebs 2002). Interpretations of statistical significance between reference and disturbed sites were based on simulated 95 % confidence intervals generated by EcoSim (McCabe and Gotelli 2000, Gotelli and Entsminger 2006).

We used Simpson's Index of diversity (SI - Simpson 1949) to determine

differences between reference and disturbed sites attributed to species evenness and not just richness. SI also accounts for differences in sampling effort between sites (PRIMER Version 6.0, Clarke and Gorley 2006). Several authors suggest that it is the best index to combine evenness and richness because of its intuitive appeal (e.g. May 1975, Lande et al. 2000). Simpson's Index is calculated as:

$$SI = 1 - \sum \left[n_i (n_i - 1)/N (N-1) \right] \text{ where,}$$

n_i is the number of individuals in the ith species and N is the total number of individuals in a sample. This equation calculates the probability that any two individuals drawn at random from different sites (reference versus disturbed) will belong to the same taxa. It ranges between 0 (no taxa in common) and 1 (all taxa in common between sites).

We also used taxonomic distinctness (TD -Clarke and Warwick 1998) with six levels of classification (Phylum, Class, Order, Family, Genus and Species) to further evaluate diversity as a potential indicator of degradation because it provides information absent in traditional diversity indices based on richness and evenness (e.g. SI). TD incorporates information on phylogenetic diversity. For example, a site with 10 species each in the same genus will have a lower diversity than a site with 10 species each from a different family. The mean value of this statistic is independent of sampling effort allowing comparisons between reference and test sites where sampling effort varies (e.g. Rogers et al. 1999). We used a form of taxonomic distinctness based on the presence/absence of taxa at a single test site (Δ^+) compared to the distinctness of the macroinvertebrate taxa for an entire reference class:

$$\Delta^+ = \left[\sum\sum_{i<j} \omega_{ij} \right] / [S(S-1)/2].$$

"S" is the observed number of taxa and ω_{ij} is the weight given to the path length linking species *i* and *j* in the taxonomy of a site or class. This equation measures the average distance (path length) between all pairs of taxa, traced through a taxonomic tree (Warwick and Clarke 2001). We can test the departure of Δ^+ for a test site compared to Δ^+ obtained by randomly selected taxa from the macroinvertebrate list for the entire reference class (Clarke and Warwick 1998). The null hypothesis states that the distinctness of a test site should fall within 95% confidence intervals for the reference class. Since the mean TD within a reference class remains constant while the variance decreases as more taxa are added, the 95% confidence intervals take the form of a "funnel". Δ^+ determines the position of a test site relative to the "funnel" for a reference class and is used to gauge the extent to which a test site falls below (lower TD) or above (greater TD) the expected value for a reference class. These analyses were performed on all sites (Reference, Moderately and Severely Impacted) in each of the three reference classes using PRIMER Version 6.0 (Clarke and Gorley 2006).

Community Composition

Non-metric multidimensional scaling (NMDS) was used to produce ordination plots of the community similarity between reference and disturbed sites (moderately and severely) in each reference class using the Bray-Curtis (dis)-similarity index (Primer Version 6.0, Clarke and Warwick 2001, Clarke and Gorley 2006). Bray-Curtis similarity (*BC*) is:

$$BC = 1 - \frac{\sum_{i=1}^{n} \left| X_{ij} - X_{ik} \right|}{\sum_{i=1}^{n} \left(X_{ij} + X_{ik} \right)}, \text{ where}$$

X_{ij} = the number of individuals in species i in sample j, X_{ik} = the number of individuals in species i in sample k, and n = the number of species. It ranges between 0 (no taxa in common) and 1 (all taxa in common between sites). The Bray-Curtis index gives less weight to outliers and is the recommended distance measure for NMDS (McCune and Mefford 1999, Southwood and Henderson 2000). Differences in community composition between each type of site within each class were tested for significance using analysis of similarity (ANOSIM, PRIMER Version. 6.0, Clarke and Warwick 2001). ANOSIM is based on random permutations and the R_{ANOSIM} statistic, is analogous to an F-statistic in ANOVA. Finally we used an analysis of species contributions (SIMPER, PRIMER V 6.0, Clarke and Warwick 2001, Clarke and Gorley 2006) to explore the relative contribution of individual species to the dissimilarity among reference and disturbed sites within each class. SIMPER shows which taxa might be valuable indicators of degradation.

Multimetrics

We examined numerous potential metrics but only four emerged as potential indicators of degradation: 1) average relative abundance of specific taxa, 2) dominance of the three most abundant taxa, 3) dominance of sensitive, semi-sensitive, semi-tolerant and tolerant taxa, and 4) richness and abundance of functional feeding groups (FFG). Dominance was the percent representation of each group based on the total number of individuals in a sample for each site. Tolerant taxa inhabit a wide range of habitats and tolerate a wide range of physico-chemical conditions. The number of tolerant taxa may not change with disturbance (U.S. EPA 2002). Sensitive taxa however, are more likely to decline or disappear under impaired conditions; hence their presence typically indicates good

conditions (U.S. EPA 2002). Taxa were classified as sensitive, semi-sensitive, semi-tolerant, or tolerant based on information derived primarily from stream ecosystems (Hilsenhoff 1988, Plafkin et al. 1989, Hauer and Lamberti 1996, Mandaville 2002). Potential tolerance metrics were calculated with and without taxa in the family Chironomidae as their sensitivity to degradation can be difficult to determine in surface water systems (Rabeni and Wang. 2001). The tolerance values for each taxon can be found on Russell Rader's web page (www.inbio.byu.edu).

We compared the average richness of macroinvertebrates in each functional feeding group (predator, collector/gatherer, collector/filterer, shredder, or scraper) between reference and disturbed sites (Moderately and Severely Impacted) within each class using Analysis of Variance (ANOVA, SAS 2004). All taxa were assigned to a feeding group using Merritt and Cummins (1996), Merritt et al. 1999, and Mandaville (2002).

We used macroinvertebrate metrics that either increased (positive response) or decreased (negative response) along a disturbance gradient from reference to disturbed sites (moderately or severely). We combined and summed metrics to form IBI scores for each site to indicate degraded conditions (Karr 1981). IBI scores were also plotted for each site (Reference, Moderately Impacted and Severely Impacted) to identify potentially misclassified sites. For example, some sites could have been classified as reference sites based on habitat assessment but failed to show reference conditions based on their macroinvertebrate IBI score. Misclassified sites were dropped from the analysis.

RESULTS

One hundred and twenty-five sites representing a range of physico-chemical conditions were sampled throughout the Bonneville Basin. Twenty and fifty-six sites were moderately and severely impacted, respectively. Livestock use was the only identifiable disturbance in moderately impacted sites, whereas severely impacted sites were affected by more than one of the three disturbance categories (livestock use, nonnative species and urban impacts).

Reference Classification

We stratified the eleven valleys into four groups based on historical land use information (e.g. grazing allotments). We used this information along with onsite habitat evaluations to *a priori* define the condition of a site as either reference or disturbed. Physico-chemical attributes collected during site-specific sampling showed considerable variation among springs of the Bonneville Basin even within the same valley (Keleher and Rader, unpublished data). However, these data were still effective at clustering most reference sites into specific classes to reduce the effects of natural variation.

Forty-nine of the 125 sites were minimally impacted and of these 33 were classified as reference sites. The remaining sixteen minimally impacted sites could not be grouped into a specific class using cluster analysis. Thus, reference sites were only from two valleys (Snake and Ibapah). Reference sites clustered into four classes ranging from 83 % to 80 % within-class similarity (Figure 3). The discriminant function analysis indicated that the physico-chemical properties of sites within Classes B, C, and D were strongly correlated. Stepwise discriminant analyses showed that water temperature ($p = < .0001$), valley ($p = .0005$), pH ($p = .0245$), and conductivity ($p = .0881$) accounted for

most of the natural variation between Classes B, C, and D. These factors correctly classified 67 % of the sites in B and 89 % of the sites in Classes C and D. However the physico-chemical properties of sites within Class A were not correlated even though the macroinvertebrate communities showed a high similarity (Figure 3). The poorly defined physico-chemical properties of Class A prevented matching test sites with this reference class. Thus, Class A was dropped from the analysis. Also, principal components of physico-chemical attributes were not used to define reference classes because they did not account for additional variation beyond that provided by the individual measurements.

Class B was comprised of sites from Ibapah and Snake Valleys, whereas Classes C and D consisted of sites from a large complex in Snake Valley. Class B had the highest water temperatures and the lowest average conductivity, whereas Class D had the coldest water temperatures and the highest conductivity (Table 3). Twelve of the moderately impacted sites could be matched with one of the three reference classes; four with Class B, three with Class C, and five with Class D. Eleven, four, and twelve of the severely impacted sites were matched based on physico-chemical similarity with Classes B, C, and D, respectively.

Diversity Indices

Three hundred and two macroinvertebrate taxa were collected in the Bonneville Basin of which 132 were collected from reference sites (Appendix A). All three rarefaction curves (Reference, Moderately and Severely Impacted) began to level-off suggesting that our sampling procedures provided an adequate estimate of total richness

(Figure 4). Differences in the rate of species accumulation between reference and moderately impacted sites were not significant for all three classes. However, species accumulation was faster ($P < 0.05$) in severely impacted sites than in reference and moderately impacted sites in all three classes (Figure 4).

There were no significant differences in Simpson's Index of richness between Reference, Moderately Impacted and Severely Impacted sites in Classes B and C (Table 4). However, SI was significantly greater in the Severely Impacted sites than Reference and Moderately Impacted sites in Class D.

Taxonomic distinctness (TD) was similar between sites (Reference, Moderately and Severely Impacted) in all three classes (Figure 5). The only sites that fell outside of the 95 % confidence funnels were severely impacted. All of these severely impacted sites had a greater than average TD.

Community Composition

The taxomonic composition of macroinvertebrates based on NMDS showed a clear separation between the reference sites and the severely impacted sites of all three classes in ordination space (Figure 6, Table 5). The variation in species composition was low among reference sites. In contrast, the separation between Reference sites and Moderately Impacted sites was less distinct, and only significant in Class C (Figure 6, Table 5). For example, four of the five Moderately Impacted sites were overlapping with the distinct cluster of Reference sites in Class D.

Potential indicator taxa should: 1) account for variation between reference and disturbed sites (Moderately and Severely Impacted) with a high dissimilarity, 2) account

for a comparably large percentage of the dissimilarity, and 3) show a substantial difference in average abundances between reference and disturbed sites. SIMPER showed that the dissimilarity in species composition between Reference and Moderately Impacted sites was lower than between Reference and Severely Impacted sites in each class (Table 6). In Classes B and D no taxa had both a high percent contribution to dissimilarity and a comparably large difference in average abundance between Reference and Moderately Impacted sites. *Hyalella azteca*, *Pyrgulopsis kolobensis* and Ostracoda however, are potentially good indicator taxa separating Reference from Moderately Impacted sites in Class C. Together they accounted for 36% of the dissimilarity with large differences in average abundances between the classes (Table 6).

In contrast, Reference and Severely Impacted sites showed a large dissimilarity and at least three species in each class that accounted for a large percentage of the dissimilarity and showed large differences in abundances (Table 6). All of these taxa except for *H. azteca* in Class D were investigated as potential indicators of degradation between Reference and Severely Impacted sites. Differences in the average abundances of *H. azteca* between Reference and Severely Impacted sites in Class D were not sufficient to warrant further analysis. We also examined the relative abundance of orders, families and other taxa not identified by SIMPER and found that Diptera, the family Chironomidae, and *Micropsectra* spp. (Chironomidae) were also useful metrics.

Multimetrics

The abundance of amphipods decreased with increasing disturbance in all classes (Figure 7), but was only significant for *H. azteca* ($F_{2,16} = 4.96$, $P = 0.02$) in Class C, and

G. lacustris in Class D ($F_{2,25}$ = 45.44, P = <0.001). The decrease of *G. lacustris* was not significant ($F_{2,18}$ = 2.32, P = 0.130) in Class B, but it was included in the IBI because it accounted for 6 % and 4 % of the dissimilarity between Reference and Moderately Impacted sites and Reference and Severely Impacted sites, respectively.

Dipterans were also useful indicators because their abundance increased with disturbance in Class D ($F_{2,25}$ = 4.87, P = 0.015) and decreased ($F_{2,16}$ = 1.40, P = 0.28) in Class C (Figure 8a). The decrease in Class C was considered biologically significant though it was not statistically significant. Two chironomid genera also proved to be valuable indicators. The average relative abundance of *Micropsectra* spp. ($F_{2,16}$ = 4.56, P = 0.03) and *Micropsectra spp*. + *Cricoptopu*s spp. ($F_{2,16}$ = 11.12, P = <0.001) significantly decreased with increasing disturbance in Class B (Figure 8b).

The percent dominance of the three most abundant taxa (Figure 9) decreased in Classes C ($F_{2,14}$ = 3.24, P = 0.07), and D ($F_{2,25}$ = 8.04, P = 0.002) but showed no trend in Class B ($F_{2,16}$ = 0.26, P = 0.77). The relative abundance of sensitive, semi-sensitive, semi-tolerant and tolerant taxa provided useful indicators in Classes B and D, but not in Class C (Figure 10). The combined relative abundance of semi-sensitive and sensitive taxa decreased in Classes B ($F_{2,18}$ = 3.38, P = 0.06) and D ($F_{2,25}$ = 19.50, P = < 0.001), whereas the semi-tolerant and tolerant taxa increased in Classes B ($F_{2,18}$ = 4.10, P = 0.03) and D ($F_{2,25}$ = 19.84, P = < 0.001).

There were no significant differences in the richness of FFG between reference and disturbed sites (Moderately and Severely Impacted) in Class B and for most groups in Classes C and D. However, the average richness of collector-gatherers (Figure 11a) increased at Severely Impacted sites in Classes C ($F_{2,16}$ = 3.45, P = 0.06) and D ($F_{2,27}$ =

2.27, P = 0.003). Predators in Class D also showed an increase in richness with increasing disturbance ($F_{2,27}$ = 4.70, P = 0.02). In contrast, the average relative of abundance of collector-gatherers decreased with increasing disturbance in Classes C ($F_{2,18}$ = 2.32, P = 0.07) and D ($F_{2,26}$ = 9.51, P = < 0.001) along the disturbance gradient (Figure 11b).

Index of Biological Integrity (IBI)

Based on results from the previous section, we identified thirteen metrics as good indicators of degradation for spring-fed wetlands in the Bonneville Basin (Table 7). All but three of the metrics were based on patterns of relative abundance with some showing a negative and others a positive response to increasing degradation (Table 7).

The highest possible IBI scores for Classes B, C, and D, were 35, 25 and 40, respectively (Table 8). Scores close to these high values indicated healthy biological conditions, whereas scores close to 7, 5, and 8 in Classes B, C, and D, respectively, indicated poor biotic conditions. Table 8 shows how the condition of a site is related to the range in IBI values for each class. Cut-off points separating the condition estimates of a site are a subjective decision made by the investigators.

We used stacked bars to show the contribution of each metric to the total IBI score for all sites in each class to test the accuracy of our procedure (Figure 12). Because we designated sites as reference or disturbed independent from data used to develop the IBI scores (macroinvertebrate samples), this plot was a test of how many sites we could accurately identify. All of the reference sites in each class had a Very Good or Good condition with 91% in the Very Good category. Similarly, 78 % of the Severely

Impacted sites had a condition of Poor to Very Poor with 48% falling within the Very Poor group. These data indicate a 91 % and 78 % accuracy of correctly identifying healthy sites (Very Good and Good) and degraded sites (Poor and Very Poor), respectively. However, we were much less successful at identifying moderately impacted sites as all fell either within the Very Good to Good categories or Poor to Very Poor categories (Figure 12). This suggests a threshold of disturbance intensity beyond which these macroinvertebrates made detectable changes in either abundance or richness. It may be difficult to separate healthy sites from moderately degraded sites prior to reaching this hypothetical threshold.

DISCUSSION

An integrated approach combining diversity indices, and aspects of multivariate analyses, multimetrics, and HGM was valuable in assessing the health and integrity of these artesian springs. Multivariate techniques made it possible to detect trends at the community level that helped identify metrics based on individual taxa (Leland et al. 1986, Wright et al. 1993, Gower et al. 1994, Zamora-Muñoz and Alba-Tercedor 1996). NMDS and ANOSIM showed clear differences in species composition between Severely Impacted sites and References sites, whereas SIMPER showed which species accounted for the greatest dissimilarity between the reference and impacted sites. This was an efficient and objective method of identifying taxa that were subsequently used as metrics to create an IBI for groundwater springs of the Bonneville Basin. An integrated approach that utilizes a variety of bioassessment techniques was more useful for identifying indicators of degradation than any single method. This may often be case in any

bioassessment program.

Classification of multiple reference sites followed by matching of disturbed sites was necessary to detect the signal of degradation through the haze of natural variation. As hypothesized, assessing the integrity of groundwater-fed wetlands was a challenge because of variable physico-chemical conditions between springs. Identifying numerous references springs, creating reference classes based on the species composition of macroinvertebrates, and matching degraded sites with a specific reference class was critical in identifying metrics of degradation. Most of these metrics would otherwise not have been detected. Matching test sites with reference classes should be necessary for many types of wetlands because of the high degree of physico-chemical variation in wetland ecosystems (e.g. Batzer and Sharitz 2006).

Finding a sufficient number of reference sites spanning the full range of physico-chemical conditions in potentially degraded test sites is a challenge in all bioassessment studies. Eighty-six of the 125 springs sampled in the Bonneville Basin were either moderately or severely degraded by human intervention. Only 33 met minimally impacted criteria and were used to identify three reference classes. Although we were able to assess the integrity of 39 test sites by matching them with one of the three reference classes, 47 moderately or severely disturbed springs defied classification and our efforts to develop metrics of degradation. Several of these springs had warm temperatures at the inflow (≥ 20 C). Expanding the scope of this study to artesian springs of the entire Great Basin Province may produce additional reference classes and thus, provide a way to assess the integrity of all springs.

Macroinvertebrates in desert springs of the Bonneville Basin did not respond to

the potentially adverse effects of moderate livestock grazing. In all of our analyses none of the moderately impacted sites could be distinguished from minimally impacted, reference sites, and all of the moderately impacted sites were only affected by livestock. We suggest two possible explanations: 1) macroinvertebrates are adapted to the effects of moderate levels of grazing, and 2) the adverse effects of livestock are most important in surface water systems not groundwater springs. Historically, a variety of large ungulates undoubtedly frequented these springs as a source of water (buffalo, elk, deer, etc.). As such, macroinvertebrates may be adapted to the effects of moderate levels of livestock use (grazing, trampling, and nutrient increases attributed to excrement). Also, livestock may have their greatest impact on surface water systems where grazing can increase rates of erosion and sedimentation (Waters 1995). Artesian springs are resistant to watershed impacts because they are fed by a constant inflow of clean groundwater.

Many macroinvertebrates, especially collector-gatherers, in these springs appeared to have a threshold response to the effects of degradation. Diversity (richness, evenness, and TD) showed a general trend of increasing along the disturbance gradient, often being greater in Severely Impacted sites than in Reference sites. Odum et al. (1979) described a subsidy-stress gradient where moderate levels of stress (e.g. increased nutrient inputs) enhanced the diversity of a system because of increased rates of primary and secondary production. This is a performance curve where diversity peaks at some intermediate threshold of perturbation (nutrient input) and then begins to decline. In springs of the Bonneville Basin, cattle excrement and agricultural inputs are two types of stressors that can increase nutrient levels. We suggest that the increased diversity in the Severely Impacted sites represents an increase in nutrients, primary production, and

secondary production that may affect the abundance of rare taxa. Rare taxa are difficult to detect until their densities increase. Increased nutrients can increase primary production and the availability of algal and detrital resources for secondary consumers, such as macroinvertebrates (Boone et al. 1988, Mackey 1979). If we assume that many macroinvertebrates are rare because they are food-limited, then the probability of detecting rare taxa would increase as their densities increased, which would result in detecting a greater diversity in impacted versus reference sites. Rader and Richardson (1992) and King et al. 2000 have shown similar increases in macroinvertebrate richness as nutrient levels increased in the Everglades. We emphasize, however, that this may be a threshold effect. Continued stress beyond the threshold level will eventually result in a decline in diversity. Such declines may not be reversible if the system shifts to a new alternative stable state (e.g. Gunderson et al. 2002, Folke et al. 2004). Odum's subsidy-stress gradient may explain why diversity can increase along a disturbance gradient in this study as well as in other wetland ecosystems.

Different taxa may have different thresholds depending on their natural history requirements and the specific type of disturbance. For example, decreases in the abundance of Diptera generally occurred in sites (e.g. in Class C) with high densities of small introduced fish (e.g. *Gambusia affinis*, *Fundulis zebrinus*), whereas increases in the abundance of Diptera was associated with increased livestock use and agricultural inputs (Class D). Similarly, amphipods showed a decrease in abundance in springs impacted by livestock and agricultural inputs. Other studies have also shown that amphipods decrease in response to an increase in agricultural activity, especially an increase in nutrient inputs (Pearson and Rosenberg 1978, Dewitt et al. 1988). In contrast, the relative abundance of

P. kolobensis increased with increasing agricultural inputs. Many hydrobiid snails have been found to be relatively tolerant of agricultural stress (Barbour et al. 1999, VTDEC 2004). Spring snails are gill-breathers which means they are mostly restricted to the area immediately surrounding the inflow of fresh, clean water (Hershler 1994), as such they may be minimally impacted by many forms of human degradation. Also, two chironomid genera were valuable indicators of degradation in Class B (*Micropsectra* spp. and *Cricotopus* spp.) where their abundances decreased with increasing disturbance. These indicators would not have been detected without a relatively fine level of taxonomic resolution. Failure to identify complex groups (e.g. Chironomidae) to a fine taxonomic resolution may miss valuable indicators of degradation.

Groundwater springs and associated wetlands occur in a variety of biomes and ecoregions around the world. This study is the first attempt to use biological indicators to determine their health and integrity. Maybe bioassessment has not been applied to these ecosystems because of the obvious challenges associated with physico-chemical variation and clean groundwater inflows. We have shown however, that an integrated approach combined with classification and matching of test sites with reference sites can produce valuable indicators of degradation even in groundwater systems that appear to resist typical forms of degradation found in many surface water systems. Future research should expand on our results and extend bioassessment to a variety of groundwater ecosystems around the world.

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REFERENCES CITED

Anderson, K., S. Nelson, A. Mayo and D. Tingey. 2005. Interbasin flow revisited: the contribution of local recharge to high-discharge springs, Death Valley, CA. Journal of Hydrology 323:276-302.

Armitage, P. D., R. J. M. Gunn, M. T. Furse, J. F. Wright, and D. Moss. 1987. The use of prediction to assess macroinvertebrate response to river regulation. Hydrobiologia 144: 25-32.

Ball, J. 1982. Stream classification guidelines for Wisconsin. Wisconsin Department of Natural Resources Technical Bulletin. Wisconsin Department of Natural Resources, Madison, WI.

Barbour, M. T., J. B. Stribling and J. R. Karr. 1995. The multimetric approach for establishing biocriteria and measuring biological condition. p. 121-146, *In* W. S. Davis and T. P. Simon (eds.) Biological Assessment and Criteria: Tools for Water Resource Planning and Decision-making. Lewis Publishers, Chelsea, Michigan.

Barbour, M. T., J. Gerritesen, B. D. Synder and J. B. Stribling. 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates, and fish, second edition. Report EPA 841-B-99-002. U.S. Environmental Protection Agency, Office of Water, Washington, DC.

Batzer, D. P., R. B. Rader and S. A. Wissinger. 2001. Invertebrates in freshwater wetlands of North America: ecology and management. Wiley, New York.

Batzer, D. P. and R. R. Sharitz (eds.). 2006. Ecology of Freshwater and Estuarine Wetlands. University of California Press, Berkeley, Los Angeles California.

Boone, P. I., P. C. Morris, L. S. Hughes and K. Morris. 1988. The implications of

nutrient enrichment for wetland management. *In* W. D. Williams (ed.) Wetlands in a dry land: understanding management.

Brinson, M. M. 1993. A hydrogeomorphic classification for wetlands. Wetlands Research Program Report TR-WRPDE-4. U.S. Army Corps of Engineers, Waterways Experiment Station, Vickburg, MS.

Brinson, M. M. 1996. Assessing Wetland Functions Using HGM. National Wetlands Newsletter 18(1):10-16.

Christiansen, F. W. 1951. Geology of the Canyon, House and Confusion ranges, Millard County, Utah. Guidebook to the Geology of Utah 6:68-80.

Clarke, K. R. and R. M. Warwick. 1998. A taxonomic distinctness index and its statistical properties. Journal of Applied Ecology 35:523-531.

Clarke, K.R. and R.N. Gorley. 2006. Primer v6 User Manual/Tutorial. Primer-E, Plymouth, UK.

Cummins, K. W. and R. W. Merritt. 2001. Application of invertebrate functional feeding groups to wetland ecosystem function and biomonitoring. p. 167-185. *In* Rader, R. D., D. B. Batzer and S. A. Wissinger (eds.) Bioassessment and management of freshwater wetlands. John Wiley and Sons Publishers, New York, New York.

Deacon, J. E. and W. L. Minckley. 1974. Desert fishes. p. 385-488. *In* G. W. Brown Jr. (ed.) Desert Biology 2. Academic Press, New York, NY.

DeKeyser, E. S., D. R. Kirby and M. J. Ell. 2003. An index of plant community integrity: development of methodology for assessing prairie wetland plant communities. Ecological Indicators 3:119-133.

DOI (Department of the Interior), United States Geological Survey. 1982. Hydrologic

Unit Map – 1981. State of Utah. Published by the U.S. Geological Survey. Reston, Virginia 22092.

DeWitt, T. H., G. R. Ditsworth and R. C. Swartz. 1988. Effects of natural sediment features on survival of the Phoxocephalid Amphipod, *Rhepoxynius abronius*. Marine Environmental Research 25:99124.

Dufréne, M., P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67:345-366.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology, Evolution and Systematics 35:557-581.

Gotelli, N. J. and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379-391.

Gotelli, N. J. and G. L. Entsminger. 2006. EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. and Kesey-Bear. Jericho, Vermont 054065.

Gower, A. M., G. Myers, M. Kent and M. E. Fowlkes. 1994. Relationships between macroinvertebrate communities and environmental variables in metal-contaminated streams in south-west England. Freshwater Biology 32:199-221.

Gunderson, L. H., C. S. Holling, L. Pritchard Jr. and G. D. Peterson. 2002. A summary and synthesis of resilience in large systems. p. 249-266. *In* L. H. Gunderson and L. Pritchard Jr. (eds.) Resilience and Behavior of Large-scale Systems. Island Press, Washington, DC.

Hannaford, M. J. and V. H. Resh. 1995. Variability in macroinvertebrate rapid-bioassessment surveys and habitat assessments in a northern California stream. Journal of the North American Benthological Society 14:430-439.

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

Hawkins, C. P. and D. M. Carlisle. 2001. Use of predictive models for assessing the biological integrity of wetlands and other aquatic habitats. p. 59-83. *In* R. B. Rader, D. P. Batzer and S. A. Wissinger (eds.) Bioassessment and management of North American freshwater wetlands. John Wiley and Sons, Inc. New York.

Hauer, F. R. and G. A. Lamberti. 1996. Methods in Stream Ecology. Academic Press.

Hershler, R. 1994. A systematic review of the North America freshwater snail genus, *Pyrgulopsis* (Hydrobiidae). Smithsonian Contributions to Zoology. Washington D.C., Smithsonian Institute 554.

Hilsenhoff, W. L. 1988. Rapid field assessment of organic pollution with a family-level biotic index. Journal of the North American Benthological Society 7(1):65-68.

Karr, J. R. 1981. Assessment of biotic integrity using fish communities. Fisheries 6:21-27.

Karr, J. R. 2000. Heath, integrity, and biological assessment: the importance of measuring whole things. p. 209-226. *In* D. Pimentel, L. Westra and R. F. Noss (eds.) Ecological integrity: integrating environment, conservation, and health. Island Press. Washington D.C.

Kerans, B. L. and J. R. Karr. 1994. A benthic index of biotic integrity (B-IBI) for rivers

of the Tennessee Valley. Ecological Applications 4:768-785.

King, R. S., K. T. Nunnery and C. J Richardson. 2000. Macroinvertebrate assemblage responses to highway crossings in forested wetlands: implications for bioassessment. Wetlands Ecological Management 8:81-94.

King, R. S. and C. J. Richardson. 2002. Evaluating subsampling approaches and macroinvertebrate taxonomic resolution for wetland bioassessment. Journal of the North American Benthological Society 21(1):150-171.

Kingston, J. C., H. J. B. Birks, A. J. Uutala, B. F. Cumming and J. P. Smol. 1992. Assessing trends in fishery resources and lake water aluminum from paleolimnological analyses of siliceous algae. Canadian Journal of Fisheries and Aquatic Sciences 49:116-127.

Klemm, D. J., K. A. Blocksom, F. A. Fulk, A. T. Herlihy and R. Hughes. 2003. Development and evaluation of a macroinvertebrate biotic integrity index (MBII) for regionally assessing Mid-Atlantic highlands streams. Environmental Management 31:656-669.

Krebs, C. J. 2002. Ecological programs that compliment Ecological Methodology, second edition. 1999. Addison-Welsey Educational Publishers, Inc.

Lande, R., P. J. DeVries and T. Walla. 2000. When species accumulation curves intersect: implications for ranking diversity using small samples. Oikos 89: 601-605.

Leland, H. V., J. L. Carter and S. V. Fend. 1986. Use of detrended correspondence analysis to evaluate factors controlling spatial distribution of bentic insects. Hydrobiologia 131:113-123.

Mackey, A. P. 1979. Trophic dependencies of some larval chironomidae and fish species in the River Thames. Hydrobiologia 62(3):241-247.

Mandaville, S. M. 2002. Benthic macroinvertebrates in fresh waters – taxa tolerance values, metrics, and protocols. Soil and Water Conservation Society of Metro Halifax. Project H-1.

Maxey, G. B. 1968. Hydrogeology of desert basins. 1968. Ground Water 6:10-22.

May, R. M. 1975. Patterns of species abundance and diversity. P. 81-120. *In* M. L. Cody and J. M. Diamond (eds.) Ecology and Evolution of Communities. Harvard University Press, Cambridge, MA.

McCabe, D. J. and N. J. Gotelli. 2000. Effects of disturbance frequency, intensity and area on assemblages of stream macroinvertebrates. Oecologia 124:270-270.

McCune, B. and M. J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data, version 4. MjM Software Design, Gleneden, Oregon.

Meffe, G. K. and P. C. Marsh. 1983. Distribution of aquatic macroinvertebrates in three Sonoran desert springbrooks. Journal of Arid Environments 6(4):363-371.

Merritt, R. W. and K. W. Cummins. 1996. An introduction to the aquatic insects of North America, third edition. Kendall/Hunt Publishing Company.

Niemi, G. J. and M. E. McDonald. 2004. Application of Ecological Indicators. Annual Review of Evolutionary Systematics 24:89-111.

O'Connell, T. J., L. E. Jackson and R. P. Brooks. 2000. Bird guilds as indicators of ecological condition in the central Appalachians. Ecological Applications 10:1706-1721.

O'Conner, R. J., T. E. Walls and R. M. Hughes. 2000. Using multiple taxonomic groups to index the ecological condition of lakes. Environmental Monitoring and Assessment 61:207-228.

Odum, E. P., J. T. Finn, and E. H. Franz. 1979. Perturbation theory and the subsidy-stress gradient. BioScience 29(6):349-352.

Ohio EPA (Ohio Environmental Protection Agency). 1987. Biological criteria for the protection of aquatic life. Volume I-III, Surface Water Section, Division of Water Quality Monitoring and Assessment, Columbus, Ohio.

Pearson, T. H. and R. Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology, Annual Review 16:229-311.

Perkins, M. J., L. D. Lentsch and J. Mizzi. 1998. Conservation agreement and strategy for least chub (*Iotichthys phlegethontis*) in the State of Utah. Utah Division of Wildlife Resources, Salt Lake City, Utah. Publication Number 98-25.

Plafkin, J. L., M. T. Barbour, K. D. Porter, S. K. Gross and R. M. Hughes. 1989. Rapid bioassessment protocols for use in streams and rivers. Benthic macroinvertebrates and fish. EPA/444/4-89/001. Office of Water Regulations and Standards, U.S. Environmental Protection Agency, Washington D.C.

Rabeni, C. F. and N. Wang. 2001. Bioassessment of streams using macroinvertebrates. Are the chironomidae necessary? Environmental Monitoring and Assessment 71(2):177-185.

Rader, R. B. and C. J. Richardson. 1992. The effects of nutrient enrichment on macroinvertebrates and algae in the Everglades: a review. Wetlands 12:34-41.

Rader, R. B. and D. Shiozawa. 2001. General principles of establishing a bioassessment program. p. 13-43. *In* R. B. Rader, D. P. Batzer and S. A. Wissinger (eds.) Bioassessment and management of North American freshwater wetlands. John Wiley and Sons, Inc., New York.

Randall, A. 1988. What mainstream economists have to say about the value of biodiversity. p. 329 – 344, *In* E. O. Wilson (ed.) Biodiversity. National Academy Press, Washington, D.C.

Resh V. H. and J. K. Jackson. 1993. Rapid assessment approaches to biomonitoring using benthic macroinvertebrates. p. 195-233. *In* D. M. Rosenberg and V. H. Resh (eds.) Freshwater biomonitoring and benthic macroinvertebrates. Chapman and Hall, New York.

Resh, V. H., Norris, R. H. and M. T. Barbour. 1995. Design and implementation of rapid assessment approaches for water resource monitoring using benthic macroinvertebrates. Australian Journal of Ecology 20:108-121.

Reynoldson, T. B., R. H. Norris, V. H. Resh, K. E. Day and D. M. Rosenberg. 1997. The reference condition. A comparison of multimetric and multivariate approaches to assess water quality impairment using benthic macroinvertebrates. Journal of North American Benthological Society 16:833-852.

Rogers, S. I., K. R. Clarke and J. D. Reynolds. 1999. The taxonomic distinctness of coastal bottom-dwelling fish communities of the North-east Atlantic. Journal of Animal Ecology 68(4):769-782

Rosenberg, D. M. and V. H. Resh. 1993. Introduction to freshwater biomonitoring and benthic macroinvertebrates. p. 1-9. *In* D. M. Rosenberg and V. H. Resh (eds.)

Freshwater biomonitoring and benthic macroinvertebrates. Chapman and Hall, New York.

Sanders, H. L. 1968. Marine benthic diversity: a comparative study. American Naturalist 10:243-282.

SAS Institute Inc. 2004. SAS/STAT 9.1 User's Guide. SAS Institute Inc., Cary, North Carolina.

Simon, T. P. 2003. Biological response signatures: indicator patterns using aquatic communities. Boca Raton, FL:CRC.

Simon, T. P., P. M. Stewart and P. L. Rothrock. 2001. Development of an index of biotic integrity for plant assemblages (P-IBI) in southern Lake Michigan. Aquatic Ecosystem Health Management 4:293-309.

Simpson, G. H. 1949. Measurement of diversity. Nature 163:688.

Smith, G. I., I. Friedman, G. Veronda and C. A. Johnson. 2000. Stable isotope compositions of waters in the Great Basin, United States. Comparison of groundwater with modern precipitation. Journal of Geophysical Research 107(D19):4403.

Southwood, R. and P.A. Henderson. 2000. Ecological Methods. Oxford University Press, Blackwell Science Publications, Oxford, England.

Stevenson, R. J. 2001. Using algae to assess wetlands with multivariate statistics, multimetric indices, and an ecological risk assessment framework. p. 113-140. *In* Rader, R. D., D. B. Batzer and S.A. Wissinger (eds.) Bioassessment and management of freshwater wetlands. John Wiley and Sons Publishers., New York, New York.

U.S. EPA (United States Environmental Protection Agency). 2002. Methods for evaluating wetland condition: developing an invertebrate index of biological integrity for wetlands. Office of Water Regulations and Standards, Washington, D.C. EPA-822-R-02-019.

VTDEC (Vermont Department of Environmental Conservation). 2004. Biocriteria for fish and macroinvertebrate assemblages in Vermont wadeable streams and rivers. Water Quality Division, Biomonitoring and Aquatic Studies Section. February 14, 2004 Version.

Warwick, R. M. and K. R. Clarke. 2001. Practical measures of marine biodiversity based on relatedness of species. Oceanography and Marine Biology, Annual Review 39:207-231.

Waters, T. F. 1995. Sediment in streams: sources, biological effects and control. American Fisheries Society Monograph 7:251 pp. American Fisheries Society, 5410 Grovsner Lane, Suite 110, Bethesda, Maryland, 20814.

White, P. S. and J. L. Walker. 1997. Approximating nature's variation: selecting and using reference information in restoration ecology. Restoration Ecology 5:338-349.

Wilberg, D. E. and B. J. Stolp. 1985. Physical characteristics and chemical quality of selected springs in parts of Juab, Millard, Tooele, and Utah counties, Utah. USGS Water-Resource Investigations Report 85-4324. 39pp.

Wright, J. F., M. T. Furse and P. D. Armitage. 1993. RIVPACS – a technique for evaluating the biological quality of rivers in the UK. European Water Quality Control 3:15-25.

Zamora-Muñoz, C. and J. Alba-Tercedor. 1996. Bioassessment of organically polluted Spanish Rivers using a biotic index and multivariate methods. Journal of the North American Benthological Society 15(3):332-352.

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number of individuals or the total number of Chironomidae at a site.

Table 8. Cut-off values of IBI scores showing the condition of sites in each class.

Table 1. Scoring system used to determine the degree of impact at each site prior to sampling for macroinvertebrates.

Disturbance	Ranks		
Livestock Use	1	2	3
Nonnative Species	1	2	3
Urbanization	1	2	3
Overall Disturbance Score	3	4 – 6	7 – 9
A *priori* Condition	Minimally Impacted	Moderately Impacted	Severely Impacted

Table 2. Scoring system used to rank all sites according to the degree of livestock impact. Total scores between 3 to 5, 6 to 9, or ≥ 10 were designated as minimally, moderately, and severely impacted, respectively.

Livestock Use Category	Degree of Impact				
	<10 %	10-25%	26-50%	51-75%	>75%
Grazing	1	2	3	4	5
Trampling	1	2	3	4	5
Excrement	1	2	3	4	5

Table 3. Means of physico-chemical variables best correlated with three macroinvertebrate reference classes. N, is the number of sites, and one standard error is shown in parentheses.

Reference Class	Valley	Temperature °C	pH	Conductivity
B, N = 6	Snake and Ibapah	15.4 (± 0.80)	8.0 (± 0.26)	317 (± 96)
C, N = 10	Snake	13.8 (± 0.54)	7.8 (± 0.19)	419 (± 99)
D, N = 11	Snake	11.5 (± 0.16)	8.0 (± 0.16)	644 (± 69)

Table 4. The average of Simpsons' Index of diversity (SI) for reference, moderately impacted, and severely impacted sites in all three classes. Different letters as superscripts indicate sites that were significantly different. "N" is the number of sites.

Class	Reference	Moderately Impacted	Severely Impacted	Statistics
Class B	0.85^{a} (N = 6)	0.78^{a} (N = 4)	0.81^{a} (N = 11)	$F_{2,24} = 3.44$, P = 0.47
Class C	0.50^{a} (N = 10)	0.55^{a} (N = 3)	0.36^{a} (N = 4)	$F_{2,11} = 4.26$, P = 0.35
Class D	0.41^{a} (N = 11)	0.41^{a} (N = 5)	0.73^{b} (N = 12)	$F_{2,16} = 3.73$, P = 0.05

Table 5. Analysis of similarity (ANOSIM) showing significant differences between sites in ordination space (Reference, Moderately and Severely Impacted).

Class	Comparison	R-value	P-value
B	Reference vs. Moderately	0.095	0.25
B	Reference vs. Severely	0.173	0.1*
C	Reference vs. Moderately	0.488	0.03*
C	Reference vs. Severely	0.841	0.003*
D	Reference vs. Moderately	-0.086	0.646
D	Reference vs. Severely	0.316	0.02*

Table 6. Taxa that accounted for the greatest amount of dissimilarity between sites (Reference, Moderately and Severely Impacted) in all three classes. Ab_{ref} and Ab_{dis} are the average abundance in reference sites and disturbed sites, respectively. "% Contribution" is the percentage of the total dissimilarity between sites due to each taxa.

Class/Comparison	Dissimilarity	Taxa	Ab 1	Ab 2	% Contribution
CLASS B					
Reference vs. Moderately Impacted	57.29	*Cricotopus* spp.	4.14	2.72	6.63
		Gammarus lacustris	3.51	3.01	5.93
		Hyalella azteca	4.81	5.78	4.80
Reference vs. Severely Impacted	71.64	*Micropsectra* spp.	6.98	1.94	6.40
		Pyrgulopsis kolobensis	1.75	4.94	4.96
		Cricotopus spp.	4.14	0.98	4.08
CLASS C					
Reference vs. Moderately Impacted	55.78	*Hyalella azteca*	13.52	7.27	15.64
		Pyrgulopsis kolobensis	0.72	6.16	12.46
		Ostracoda	1.98	5.22	8.21
Reference vs. Severely Impacted	71.33	*Hyalella azteca*	13.52	6.40	11.54
		Pyrgulopsis kolobensis	0.72	4.90	6.81
		Caecidotea	0.00	3.61	6.65
		Gammarus lacustris	7.18	3.54	6.61
CLASS D					
Reference vs. Moderately Impacted	46.19	*Gammarus lacustris*	14.06	13.22	12.61
		Hyallela azteca	6.80	5.81	10.86
		Gastropods	1.34	2.29	6.76
		Caecidotea	0.12	2.53	5.80
Reference vs. Severely Impacted	77.69	*Gammarus lacustris*	14.06	3.97	14.25
		Caecidotea	0.12	6.54	9.19
		Hyalella azteca	6.80	5.91	6.25
		Cricotopus spp.	0.08	3.31	4.18

Table 7. Scoring criteria of macroinvertebrate metrics for springs in the Bonneville Basin. RA is the relative abundance of each taxa or group based on the total number of individuals or the total number of Chironomidae at a site.

Class	Metric Description	Range for Metric Score		
		1	3	5
Class B	RA of Chironomidae	< 35 %	35 % - 40 %	> 40 %
	RA of *Pyrgulopsis kolobensis*	> 20 %	10 % - 20 %	< 10 %
	RA of *Micropsectra* spp. within Chironomidae	< 20 %	20 % - 35 %	> 35 %
	RA of *Micropsectra* spp. + *Cricoptopus* spp.	< 20 %	20 % - 30 %	> 30 %
	RA of *Gammarus lacustris*	< 2 %	2 % - 7 %	> 7 %
	RA of Semi-sensitive + Sensitive Taxa	< 10 %	10 % - 20 %	> 20 %
	RA of Semi-Tolerant + Tolerant Taxa	> 90 %	80 % - 90 %	< 80 %
Class C	Richness of Collector/Gatherers	> 10	6 - 10	< 6
	RA of Collector/Gatherers	< 60 %	60 % - 75 %	> 75 %
	RA of Diptera	< 5 %	5 % - 10 %	> 10 %
	RA of *Hyallela azteca*	< 25 %	25 % - 40 %	> 40 %
	RA of 3 most abundant taxa	< 75 %	75 % - 85 %	> 85 %
Class D	Richness of Collector/Gatherers	> 10	6 - 10	< 6
	Richness of Predators	> 10	5 - 10	< 5
	RA of Collector/Gatherers	< 75 %	75 %– 90 %	> 90 %
	RA of Diptera	> 50 %	15 % – 50 %	< 15 %
	RA of *Gammarus lacustris*	< 50 %	50 % - 65 %	> 65 %
	RA of 3 most abundant taxa	< 75 %	75% – 90 %	> 90 %
	RA of Semi-sensitive + Sensitive Taxa	< 30 %	30 % – 70 %	> 70 %
	RA of Semi-tolerant + Tolerant Taxa	> 50%	25 % – 50 %	< 25 %

Table 8. Cut-off values of IBI scores showing the condition of sites in each class.

Condition	Site Score by Class		
	B	C	D
Very Good	30 - 35	21 – 25	34 - 40
Good	24 – 29	17 – 20	27 – 33
Fair	18 – 23	13 – 16	20 – 26
Poor	12 – 17	9 – 12	14 – 19
Very Poor	7 – 11	5 – 8	8 – 13

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Figure 7. Amphipod average relative abundance based on the total number of individuals in a sample between sites (Reference, Moderately Impacted and Severely Impacted) in all three classes.

Figure 8. Comparisons between sites (Reference, Moderately and Severely Impacted) in the average percent abundance of Diptera based on the total number of invertebrates in a sample in all three classes (a), and selected chironomid taxa only in Class B (b). *Microptsectra* spp. was calculated from all chironomids in a sample, whereas *Microptsectra* spp. + *Cricoptopus* spp. were calculated from the total number of invertebrates in a sample.

Figure 9. The percent dominance of the three most abundant taxa for all sites (Reference, Moderately and Severely Impacted) in each Class.

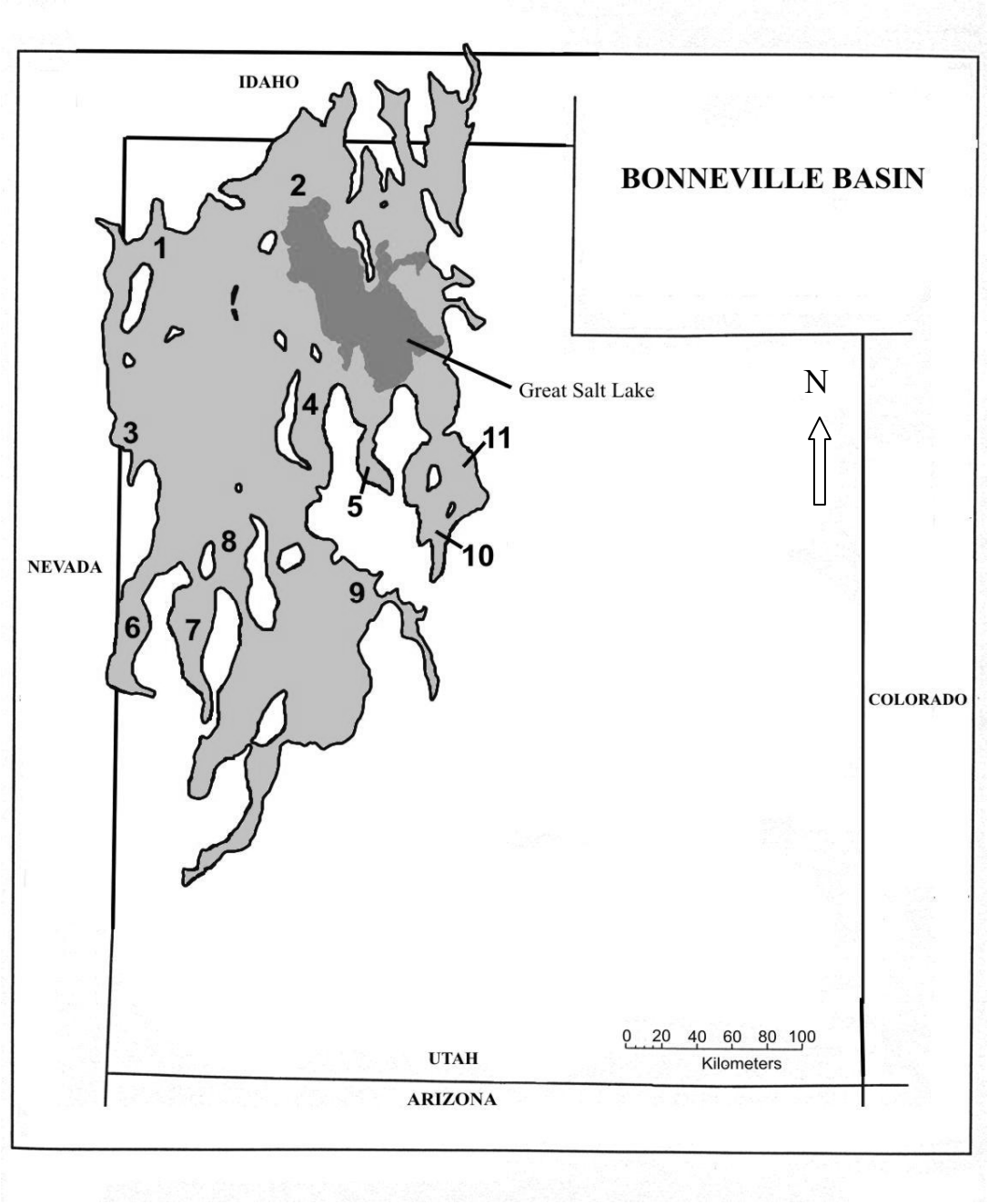
Figure 10. Average percent abundance of sensitive + semi-sensitive (SS/S) and semi-tolerant + tolerant taxa (ST/T) for all sites (Reference, Moderately and Severely Impacted) in each class.

Figure 11. Average richness of collector-gatherers (CG) and predators (PRD) between sites (Reference, Moderately and Severely Impacted) in Classes C and D (a), and average percent abundance of collector-gatherers between sites (Reference, Moderately and Severely Impacted) in each

class (b).

Figure 12. IBI scores for Reference (R), Moderately Impacted (M) and Severely Impacted (S) sites. Scores above 23, 16, and 26 in Classes B, C, and D, respectively, represented good or very good conditions.

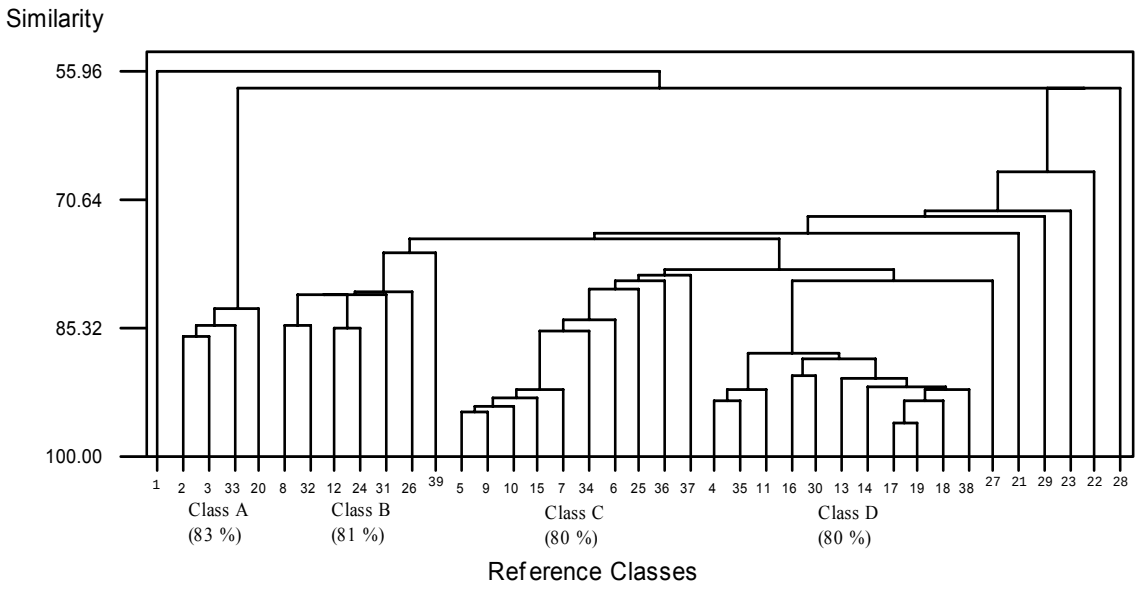
Figure 1.



1 = Grouse Creek, 2 = Curlew, 3 = Ibapah, 4 = Skull, 5 = Rush, 6 = Snake,
7 = Tule, 8 = Fish Springs Flat, 9 = Mills, 10 = Goshen, 11 = Utah

Figure 2.

Figure 3.



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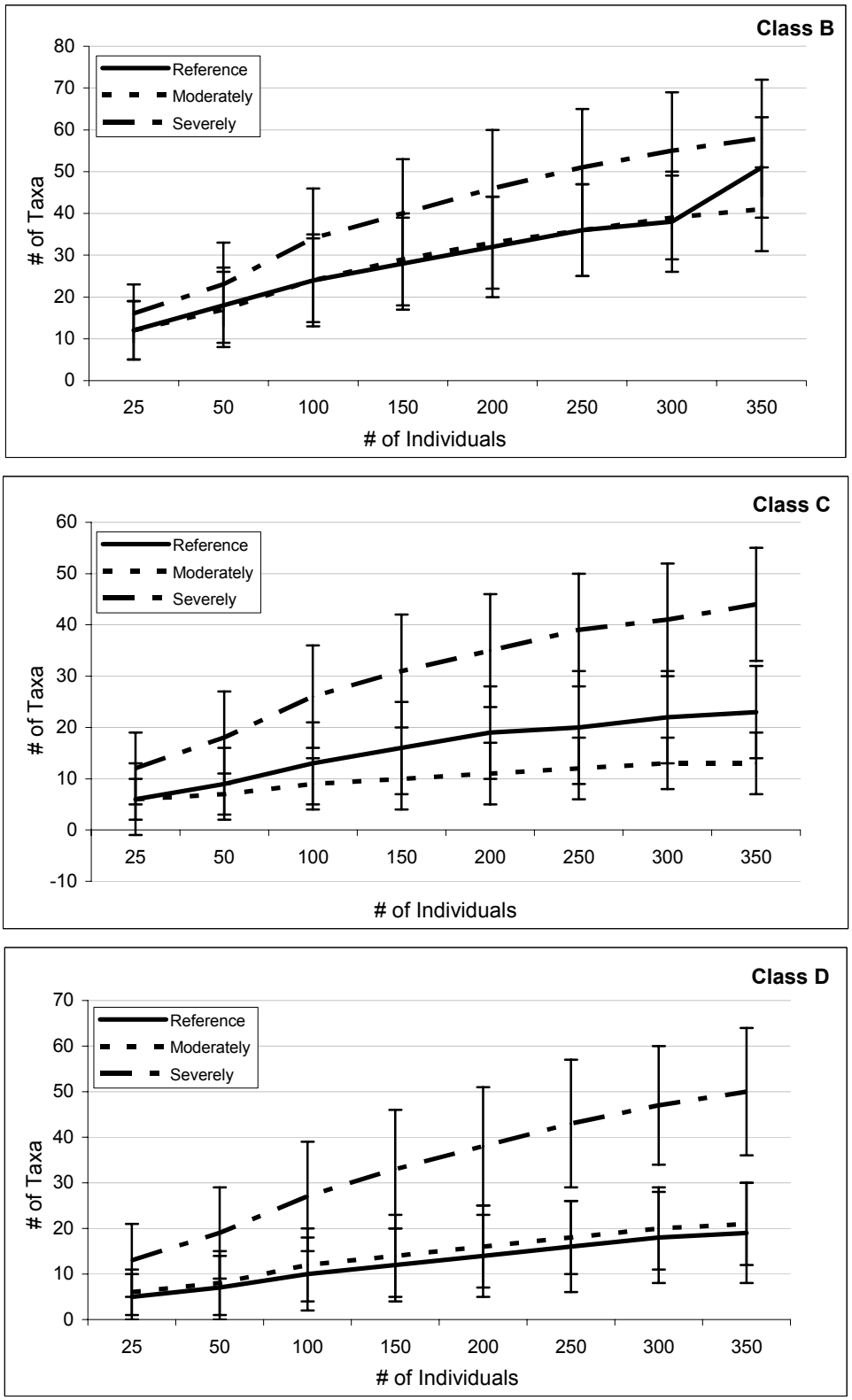

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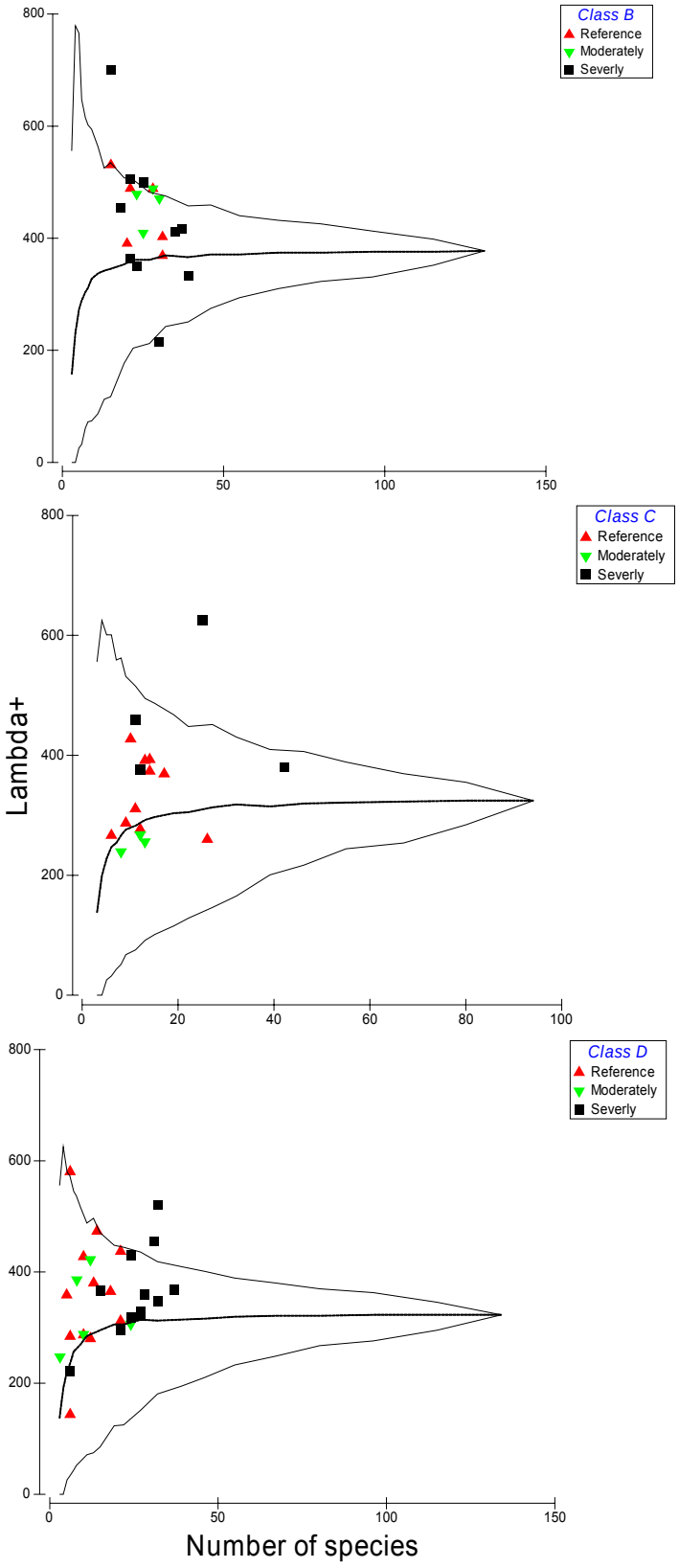

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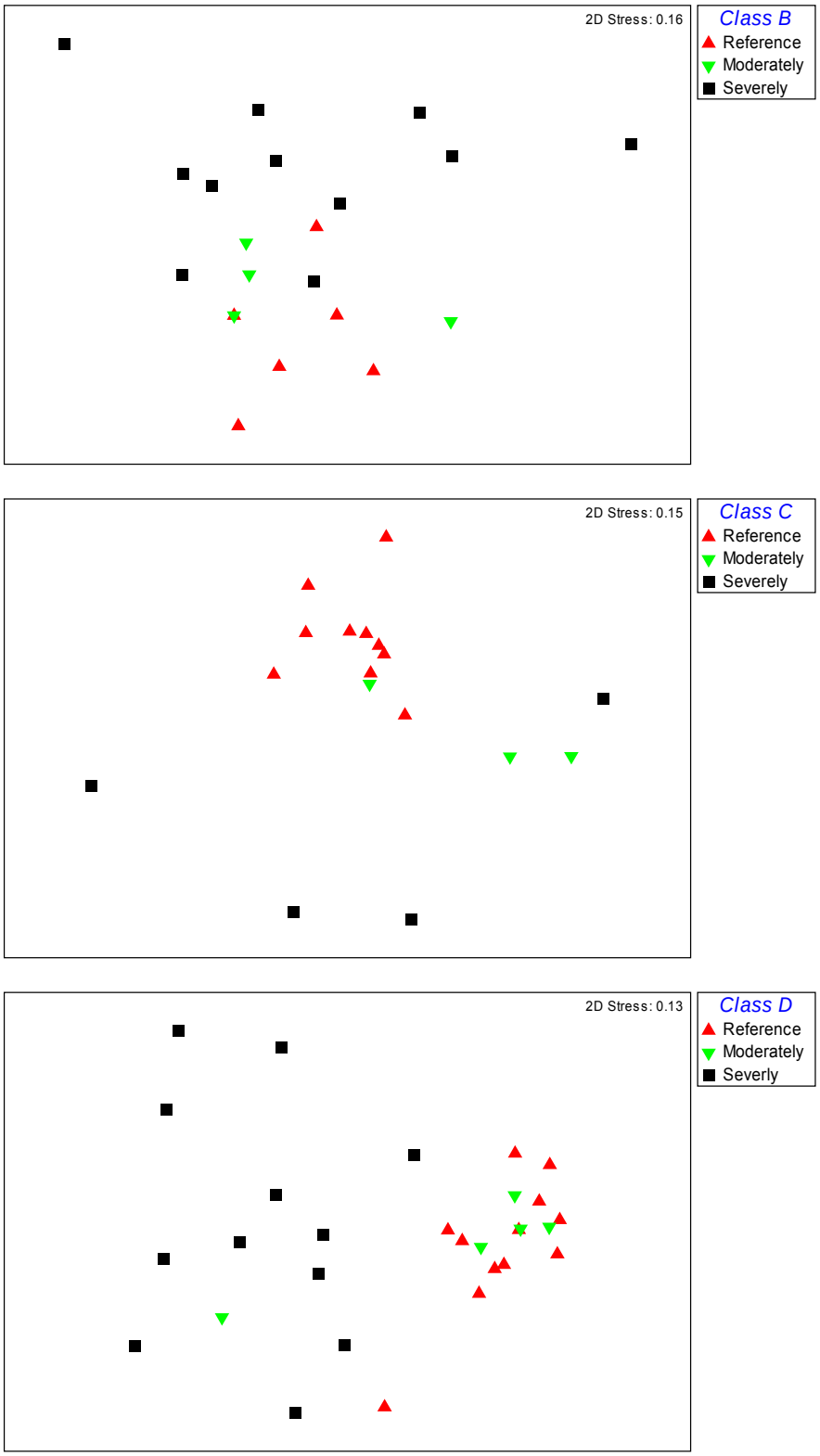

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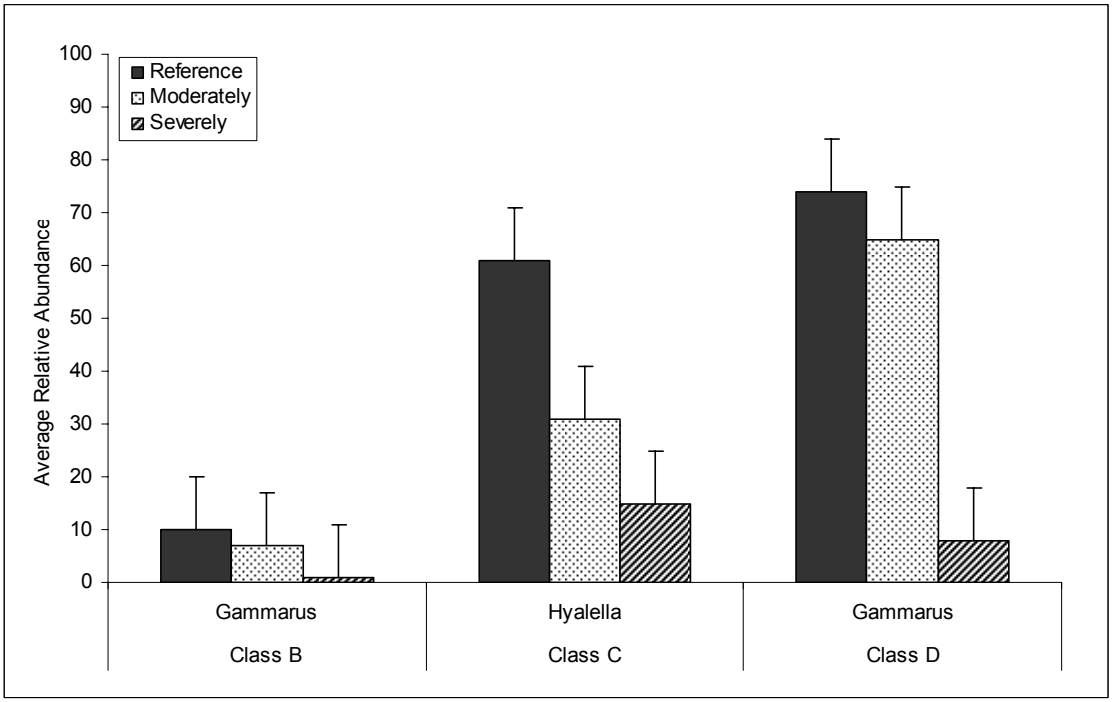

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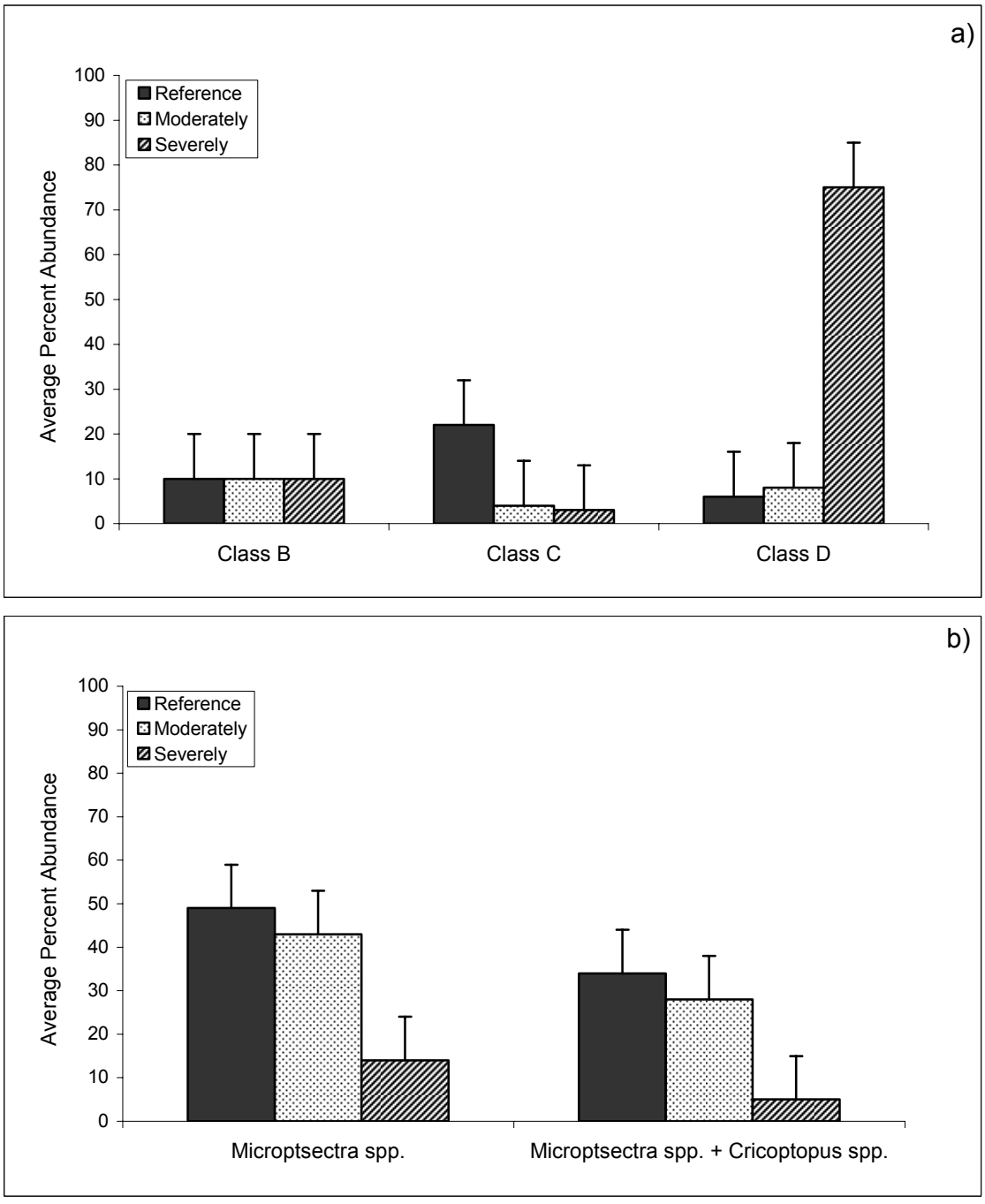

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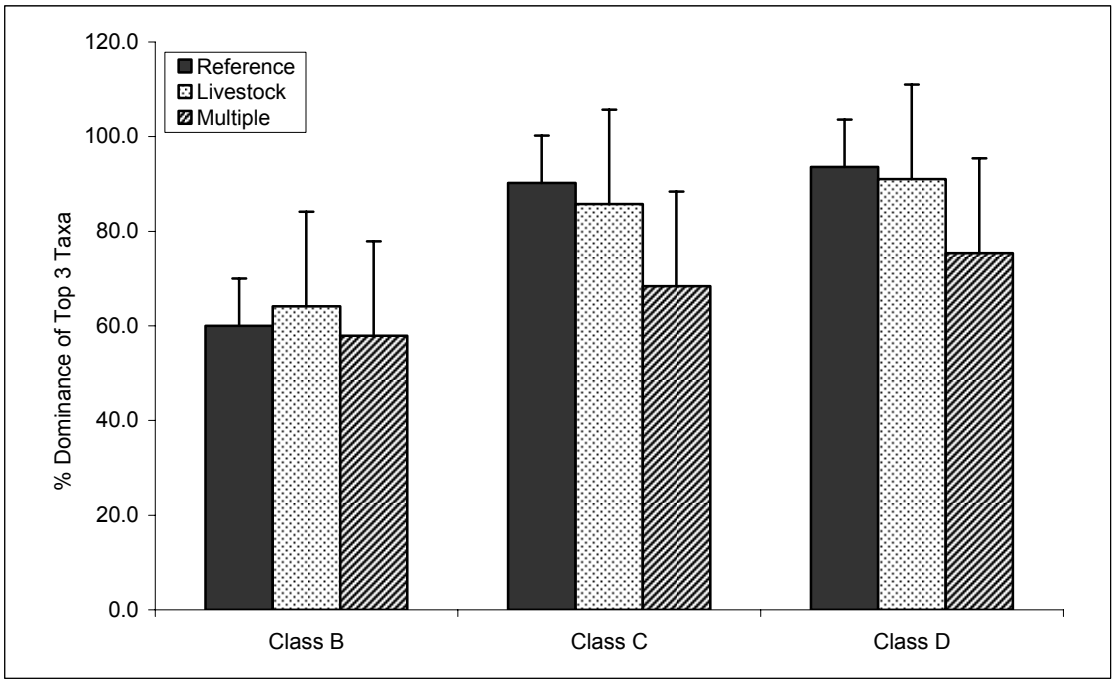

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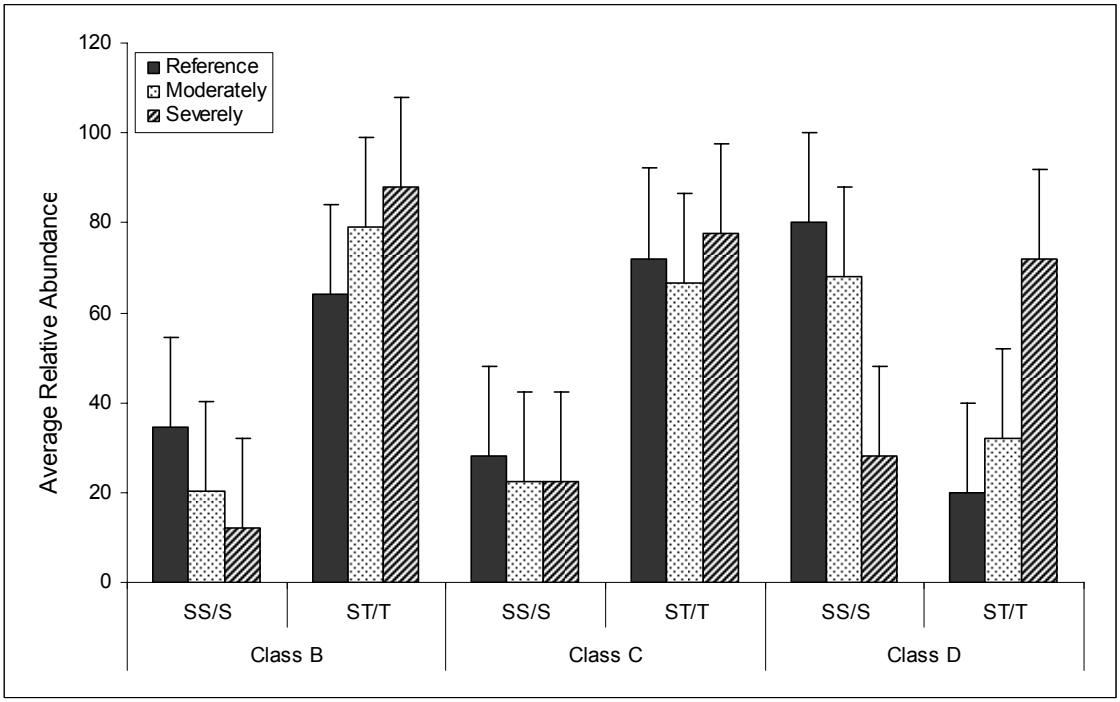

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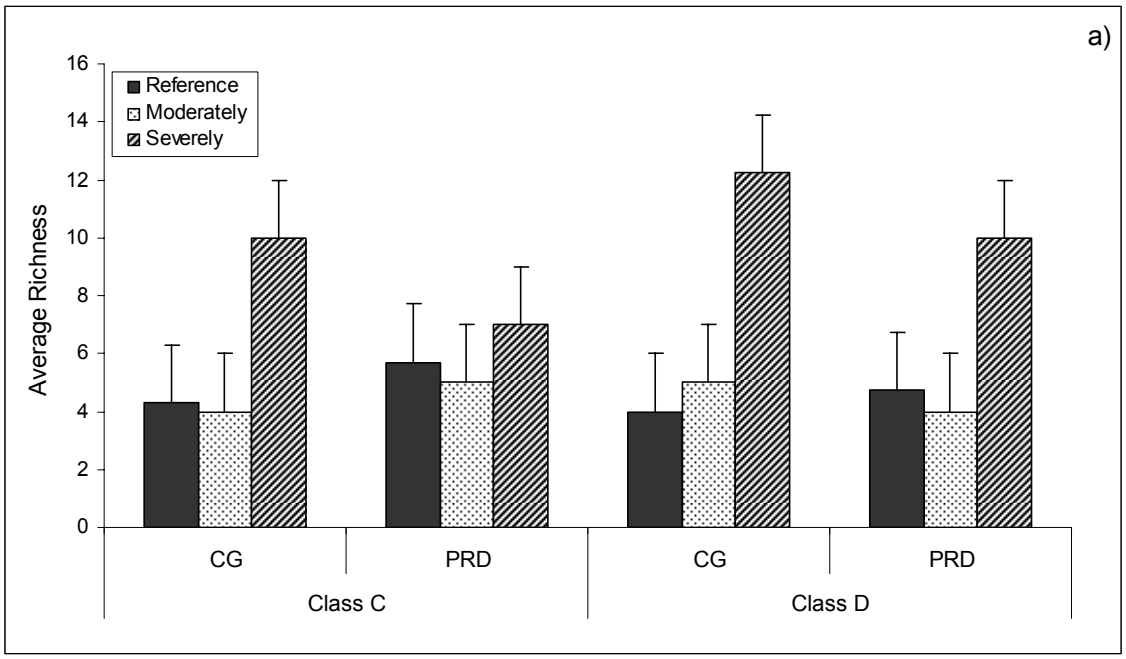


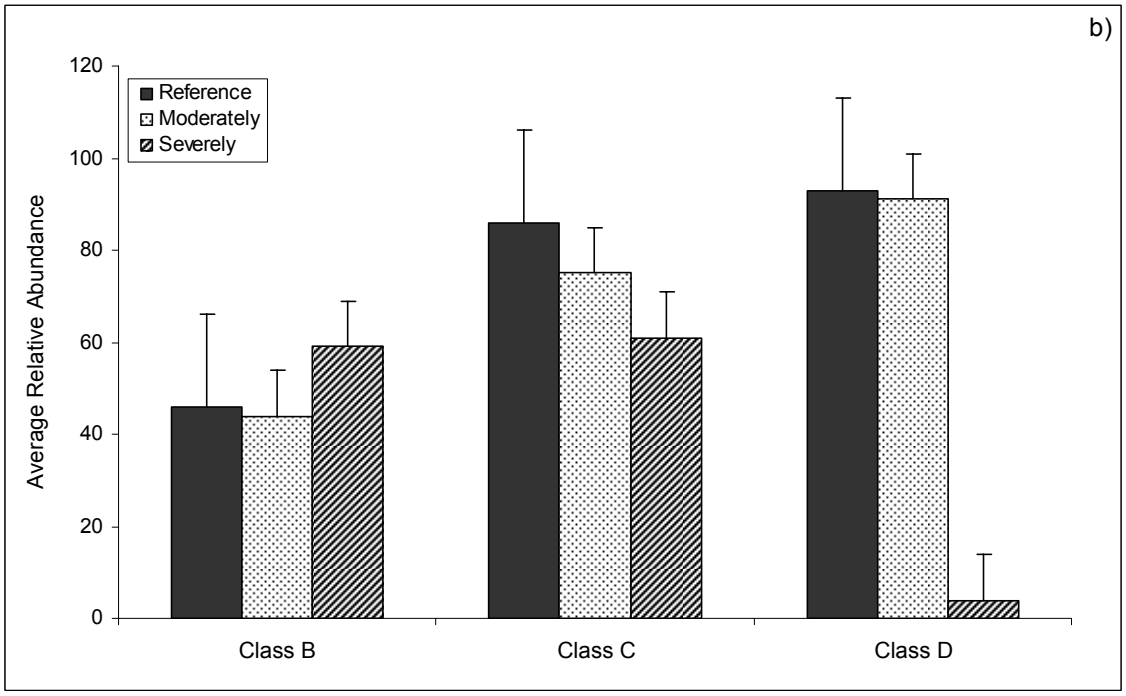
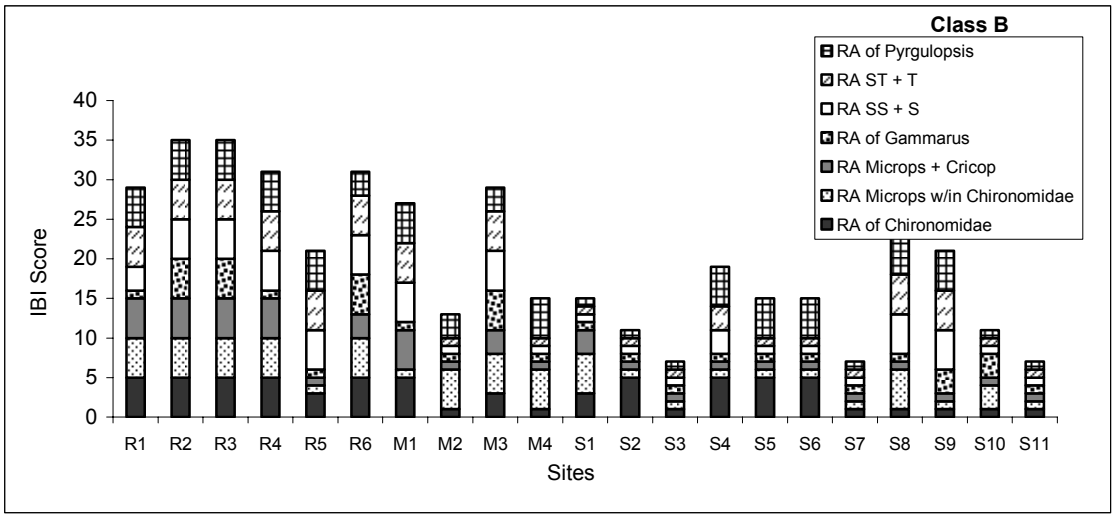
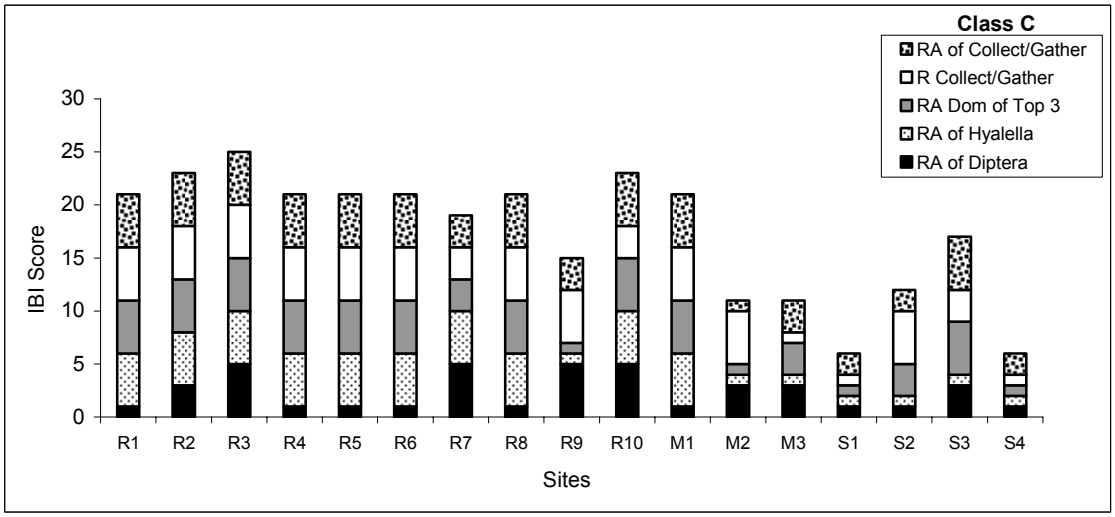
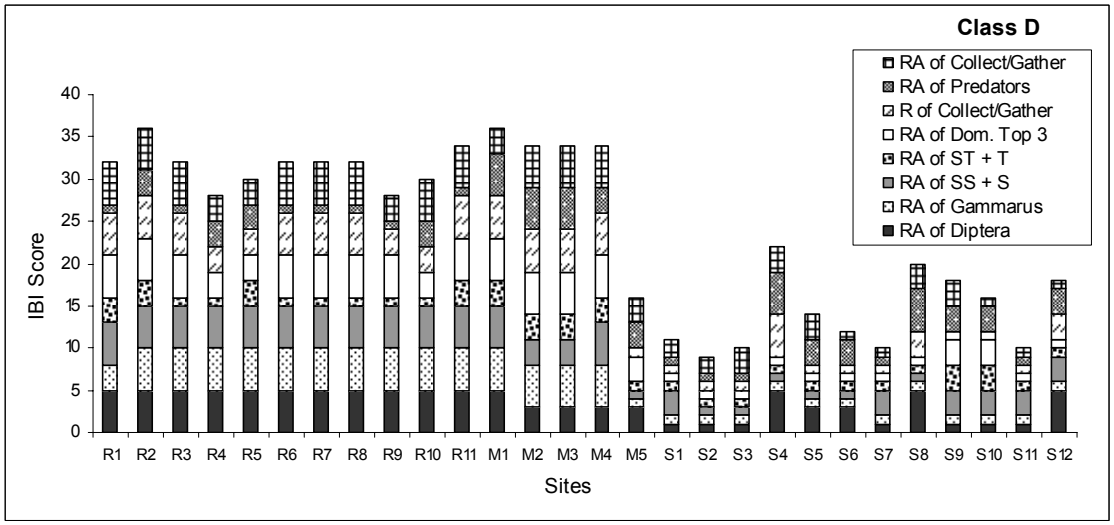


Figure 12.







APPENDIX A:

Macroinvertebrates collected in the Bonneville Basin. Functional feeding group (FGG), tolerance levels (0 = least sensitive, 10 = most tolerant), reference class occurrence, and macroinvertebrate occurrence in reference sites by class. FFG were completed after Merritt and Cummins (1996) and Mandaville (2002). Tolerances were compiled after Mandaville 2002; Hauer and Lamberti 1996; Hilsenhoff 1988; and Plafkin et al. 1989.

Taxa	Order	FFG	Tolerance Value	Class of Occurrence	Reference Site Occurrence		
					B	C	D
Ablabesmyia spp.	Diptera	PRD	10	B	0	0	0
Acricotopus spp.	Diptera	CG	10	B, C,D	X	0	0
Aedes spp.	Diptera	CG	8	B	0	0	0
Aeshna spp.	Odonata	PRD	5	B, C,D	X	X	X
Aeshnidae	Odonata	PRD	5	B, C,D	X	0	X
Agabus disintegratus	Coleoptera	PRD	5	B, D	0	0	0
Agabus griseipennis	Coleoptera	PRD	5	B, C,D	X	X	X
Agabus obliteratus obliteratus	Coleoptera	PRD	5	B, D	0	0	X
Agabus spp.	Coleoptera	PRD	5	B, C,D	X	X	0
Agabus tristis	Coleoptera	PRD	5	D	0	0	0
Amphiagrion abbreviatum	Odonata	PRD	9	B, C,D	X	X	0
Anopheles spp.	Diptera	CF	8	B, C,D	X	0	0
Apedilum spp.	Diptera	CG	6	B	0	0	0
Argia spp.	Odonata	PRD	6	B,C	0	0	0
Arrenurus spp.	Acara	PRD	?	B, D	0	0	0
Belostoma flumineum	Hemiptera	PRD	5	B, C,D	X	X	X
Berosus fraternus	Coleoptera	CG	5	D	0	0	X
Berosus spp.	Coleoptera	CG	5	B	0	0	0
Bezzia spp.	Diptera	PRD	6	B, C,D	X	0	0
Brillia spp.	Diptera	SHR	5	B	0	0	0
Caecidotea	Isopoda	CG	8	B, C,D	0	0	X
Caenis spp.	Ephemeroptera	CG	6	B	0	0	0
Callibaetis spp.	Ephemeroptera	CG	8	B, C,D	X	0	0
Callicorixa audeni	Hemiptera	PRD	5	B, C,D	0	X	X
Caloparyphus spp.	Diptera	CG	7	B, D	X	0	0
Carbabidae	Coleoptera	PRD	5	B, C,D	0	0	X
Cenocorixa wileyae	Hemiptera	PRD	5	D	0	0	0
Ceratopogon spp.	Diptera	PRD	6	B, C,D	X	X	X
Ceratopogonidae	Diptera	PRD	6	B, C,D	X	0	0
Chaetocladius spp.	Diptera	CG	6	B,C	X	0	0
Chaetogaster diastrophus	Tubificida	CG	7	B, D	0	0	0
Chironomus spp.	Diptera	CG	10	B, C,D	X	0	X
Chrysomelidae	Coleoptera	SHR	5	D	0	0	X
Chrysops spp.	Diptera	CG	5	C	0	0	0

Appendix A Continued

Taxa	Order	FFG	Tolerance Value	Class of Occurrence	Reference Site Occurrence B	C	D
Cladopelma spp.	Diptera	CG	5	B	0	0	0
Coenagrion / Enallagma spp.	Odonata	PRD	9	B, D	0	0	0
Coenagrionidae	Odonata	PRD	9	B, C,D	X	0	0
Colymbetes incognitus	Coleoptera	PRD	5	B, C,D	0	X	X
Colymbetes sculptilis	Coleoptera	PRD	5	C,D	0	X	X
Corisella decolor	Hemiptera	PRD	5	B, D	0	0	0
Corixidae	Hemiptera	PRD	5	B, C,D	X	X	0
Corynoneura spp.	Diptera	CG	4	B, C,D	X	X	X
Cricotopus spp.	Diptera	SHR	7	B, C,D	X	X	X
Culex spp.	Diptera	CF	8	B	0	0	0
Culicidae	Diptera	CF	8	B, D	0	0	0
Culiseta spp.	Diptera	CF	8	B	0	0	0
Curculionidae	Coleoptera	SHR	5	D	0	0	0
Cybister explanatus	Coleoptera	PRD	5	B	X	0	0
Cymbiodyta spp.	Coleoptera	PRD	5	C	0	0	0
Dasyhelea spp.	Diptera	CG	6	B, C,D	X	0	0
Dero spp.	Tubificida	CG	10	B	X	0	0
Derotanypus spp.	Diptera	PRD	5	B, C,D	X	X	X
Dicrotendipes spp.	Diptera	CG	8	B, D	X	0	0
Dixella spp.	Diptera	CG	8	C,D	0	0	X
Dixidae	Diptera	CG	8	C	0	0	0
Dugesia spp.	Tricladida	CG	6	B, D	0	0	X
Dytiscus marginicollis	Coleoptera	PRD	5	C,D	0	X	X
Dytiscus spp.	Coleoptera	PRD	5	C,D	0	X	X
Enchytraeidae	Lumbriculida	CG	10	B	0	0	0
Enochrus californicus	Coleoptera	CG	5	B	0	0	0
Enochrus carinatus	Coleoptera	CG	5	B	X	0	0
Enochrus hamiltoni	Coleoptera	CG	5	B, C,D	0	X	X
Enochrus spp.	Coleoptera	CG	5	B, D	X	0	X
Ephemerella spp.	Ephemeroptera	CG	1	D	0	0	0
Ephydridae	Diptera	SHR	6	B, D	0	0	0
Erpobdellidae	Arhynchobdellida	PRD	8	B, C,D	0	0	X
Erythemis spp.	Odonata	PRD	2	B, D	0	0	0
Eukiefferiella spp.	Diptera	CG	4	B	0	0	0
Euparyphus spp.	Diptera	CG	7	D	0	0	0
Eylais spp.	Acara	PRD	?	D	0	0	0
Gammarus lacustris	Amphipoda	CG	4	B, C,D	X	X	X
Gastropods	Prosobranch	SCR	8	B, C,D	X	X	X
Gerridae	Hemiptera	PRD	5	D	0	0	0
Gerris gillettei	Hemiptera	PRD	5	C	0	0	0
Gerris incognitus	Hemiptera	PRD	5	B, D	X	0	X
Glossiphoniidae	Rhynchobdellida	PRD	8	B	0	0	0
Glyptotendipes spp.	Diptera	SHR	8	B	0	0	0
Gyrinus picipes	Coleoptera	PRD	5	C,D	0	X	0

Appendix A Continued

Taxa	Order	FFG	Tolerance Value	Class of Occurrence	Reference Site Occurrence		
					B	C	D
Haemopis spp.	Arhynchobdellida	PRD	8	B,C	0	X	0
Haliplus immaculicollis	Coleoptera	SHR	5	B, C,D	0	0	0
Haliplus spp.	Coleoptera	SHR	5	B, C,D	0	0	0
Helobdella stagnalis	Rhynchobdellida	PRD	8	B, C,D	X	X	X
Helophorus orientalis	Coleoptera	SHR	5	B	0	0	0
Helophorus spp.	Coleoptera	SHR	5	B, C,D	X	X	X
Hesperophylax spp.	Trichoptera	CG	3	D	0	0	0
Hyalella azteca	Amphipoda	CG	8	B, C,D	X	X	X
Hybomitra spp.	Diptera	PRD	5	B	0	0	0
Hydrachna spp.	Acara	PRD	?	B	0	0	0
Hydrobiidae	Prosobranch	SCR	8	B, C,D	X	X	X
Hydrobius fuscipes	Coleoptera	CG	5	D	0	0	0
Hydroporinae	Coleoptera	PRD	5	B, D	0	0	0
Hydroporus spp.	Coleoptera	PRD	5	B, C,D	X	X	X
Hydroptila spp.	Trichoptera	CG	6	D	0	0	0
Hydrozetes spp.	Acara	PRD	?	B, C,D	X	X	0
Hygrotus impressopunctatus	Coleoptera	PRD	5	B,C	0	X	0
Hygrotus lutescens	Coleoptera	PRD	5	B, C,D	X	X	0
Hygrotus sayi	Coleoptera	PRD	5	D	0	0	0
Ilybius fraterculus	Coleoptera	PRD	5	B,C	X	X	0
Ischnura spp.	Odonata	PRD	8	B, C,D	X	X	0
Laccobius spp.	Coleoptera	PRD	5	B, C,D	X	X	X
Laccophilus maculosus decipiens	Coleoptera	PRD	5	B,C	0	0	0
Laccophilus mexicanus	Coleoptera	PRD	5	B,C	0	X	0
Laccophilus spp.	Coleoptera	PRD	5	B, C,D	0	0	0
Lebertia spp.	Acara	PRD	?	D	0	0	0
Lestes spp.	Odonata	PRD	6	D	0	0	0
Libellula spp.	Odonata	PRD	9	B, C,D	X	X	0
Libellulidae	Odonata	PRD	9	B, C,D	X	0	0
Limnephilidae	Trichoptera	CG	3	C	0	0	0
Limnephilus spp.	Trichoptera	SHR	3	B, C,D	X	X	X
Limnesia spp.	Acara	PRD	?	B	0	0	0
Limnochares spp.	Acara	PRD	?	B	0	0	0
Limnophyes spp.	Diptera	CG	8	B, C,D	X	X	X
Limonia spp.	Diptera	SHR	6	B	0	0	0
Liodessus obscurellus	Coleoptera	PRD	5	B, C,D	X	X	X
Lumbriculidae	Lumbriculida	CG	10	D	0	0	X
Merragata heboides	Hemiptera	PRD	5	B, D	0	0	0
Metriocnemus spp.	Diptera	CG	8	B, C,D	0	0	0
Micropsectra spp.	Diptera	CF	7	B, C,D	X	X	X
Microtendipes spp.	Diptera	SHR	6	D	0	0	0
Microvelia cerifera	Hemiptera	PRD	5	B	X	0	0
Microvelia spp.	Hemiptera	PRD	5	D	0	0	0
Nais communis	Tubificida	CG	8	B	0	0	0

Appendix A Continued

Taxa	Order	FFG	Tolerance Value	Class of Occurrence	Reference Site Occurrence		
					B	C	D
Nais simplex	Tubificida	CG	8	D	0	0	0
Nais spp.	Tubificida	CG	8	B	0	0	0
Nais variabilis	Tubificida	CG	10	B, D	X	0	0
Natarsia spp.	Diptera	PRD	8	C	0	X	0
Neoplasta spp.	Diptera	PRD	6	B	0	0	0
Nephelopsis obscura	Arhynchobdellida	PRD	8	C,D	0	0	0
Notonecta kirbyi	Hemiptera	PRD	5	D	0	0	0
Notonecta spp.	Hemiptera	PRD	5	B, D	X	0	0
Notonecta spinosa	Hemiptera	PRD	5	D	0	0	0
Notonecta undulata	Hemiptera	PRD	5	D	0	0	0
Notonecta unifasciata	Hemiptera	PRD	5	B,C	X	X	0
Ochthebius aztecus	Coleoptera	SCR	5	B	0	0	0
Ochthebius discretus	Coleoptera	SCR	5	C,D	0	0	0
Ochthebius kaszabi	Coleoptera	SCR	5	B, C,D	0	0	0
Ochthebius lineatus	Coleoptera	SCR	5	D	0	0	0
Ochthebius rectus	Coleoptera	SCR	5	B, C,D	X	X	X
Ochthebius spp.	Coleoptera	SCR	5	B	0	0	0
Odontomyia spp.	Diptera	CG	7	C,D	0	X	0
Ophidonais serpentina	Tubificida	CG	6	B	0	0	0
Optioservus castanipennis	Coleoptera	SCR	5	C	0	0	0
Optioservus divergens	Coleoptera	SCR	5	C	0	0	0
Optioservus spp.	Coleoptera	SCR	4	B, C,D	0	0	0
Ostracoda	Ostracoda	CG	8	B, C,D	X	X	X
Oxyethira spp.	Trichoptera	CG	3	B, D	X	0	0
Paracymus confusus	Coleoptera	CG	5	D	0	0	0
Paracymus spp.	Coleoptera	CG	5	B, C,D	X	X	X
Parakiefferiella spp.	Diptera	CG	4	C,D	0	0	0
Paramerina spp.	Diptera	PRD	6	B, C,D	X	0	0
Paraphaenocladius spp.	Diptera	CG	4	D	0	0	0
Paratanytarsus spp.	Diptera	CF	6	B, C,D	X	0	0
Paratendipes spp.	Diptera	CG	6	B, C,D	X	0	0
Peltodytes callosus	Coleoptera	SHR	5	B, C,D	X	0	0
Peltodytes spp.	Coleoptera	SHR	5	B, C,D	X	0	X
Pericoma spp.	Diptera	CG	4	C,D	0	X	X
Phaenopsectra spp.	Diptera	SCR	7	D	0	0	0
Polypedilum spp.	Diptera	SHR	4	C	0	0	0
Psectrocladius spp.	Diptera	PRD	8	B, D	X	0	X
Pseudochironomus spp.	Diptera	CG	5	B, C,D	X	0	0
Pseudosmittia spp.	Diptera	CG	6	B, D	0	0	0
Psychoglypha spp.	Trichoptera	CG	0	D	0	0	0
Quistadrilus multisetosus	Tubificida	CG	10	D	0	0	0

Appendix A Continued

Taxa	Order	FFG	Tolerance Value	Class of Occurrence	Reference Site Occurrence B	C	D
Radotanypus spp.	Diptera	PRD	6	C	0	0	0
Radotanypus spp.	Diptera	PRD	6	D	0	0	0
Rhantus binotatus	Coleoptera	PRD	5	B, D	X	0	X
Rhantus spp.	Coleoptera	PRD	5	D	0	0	0
Scirtidae	Coleoptera	SCR	5	C	0	X	0
Sigara alternata	Hemiptera	CG	5	D	0	0	0
Sigara washingtonensis	Hemiptera	CG	5	C,D	0	0	0
Sminthuridae	Collembola	CG	?	B, D	X	0	0
Sphaeriidae	Venroidea	CG	6	B, C,D	X	X	X
Staphylinidae	Coleoptera	PRD	5	B, C,D	0	0	X
Stictotarsus griseostriatus	Coleoptera	PRD	5	B, C,D	X	X	X
Stratiomys spp.	Diptera	CG	7	D	0	0	0
Tabanidae	Diptera	PRD	6	C,D	0	X	X
Tanypus spp.	Diptera	PRD	10	B,C	X	0	0
Tanytarsus spp.	Diptera	CF	6	B, D	0	0	0
Thienemannimyia group	Diptera	PRD	6	B, C,D	X	0	X
Tribelos spp.	Diptera	CG	6	B	0	0	0
Tropisternus columbianus	Coleoptera	CG	5	B, D	0	0	0
Tropisternus lateralis marginatus	Coleoptera	CG	5	B	0	0	0
Tropisternus spp.	Coleoptera	CG	5	B, C,D	X	X	X
Tropisternus sublaevis	Coleoptera	CG	5	D	0	0	X
Tubificidae with hair chaetae	Tubificida	CG	10	B, D	X	0	0
Tubificidae without hair chaetae	Tubificida	CG	10	B, C,D	X	X	X
Tvetenia spp.	Diptera	CG	5	B	0	0	0

CF = Collector-filterers, CG = Collector-Gatherer, PPD = Predator, SCR = Scraper, SHR = Shredder

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CHAPTER TWO -
PARTITIONING DIVERSITY ACROSS MULTIPLE SPATIAL SCALES IN ARTESIAN SPRINGS OF THE BONNEVILLE BASIN, USA

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ABSTRACT

An important goal of ecology is to assess the factors that influence the spatial distribution of diversity ranging from local sites (α diversity) to the regional species pool (γ diversity). This often requires examining patterns of diversity at progressively larger scales in a nested design. We partitioned β-diversity of invertebrates into contributions by different sites nested within habitats (springs, channels, and marshes), habitat types within spring complexes, different complexes within valleys and different valleys nested within the Bonneville Basin of Utah, USA. A site was one of the three habitat types. We found that 50% of 288 total taxa collected from 280 sites across the entire basin/region occurred in six or fewer sites. Twenty percent were collected from a single site. Fifty percent of the total regional diversity was attributed to differences between valleys, 20% to differences between wetlands within valleys and the remainder was attributed to differences between habitats within wetlands (10%), locations within habitat types (10%) and alpha richness within locations (10%). Wetland size and isolation were scale dependent. Area effects were important at smaller scales, such as between individual springs, whereas isolation and dispersal limitations were more important within and between valleys. Although each level of the spatial hierarchy contributed to the total diversity in spring ecosystems of the Bonneville Basin, differences between valleys was especially important. Historical biogeography associated with the drying of ancient Lake Bonneville and dispersal limitations between valleys were the most important processes determining patterns of β-diversity. Thus, spring ecosystems in different valleys contained a different complement of species many of which are unique to individual springs. However, conservation measures should be applied at all scales because many

sites, all three habitat types, some wetlands, and all valleys contributed unique taxa to the basin's diversity.

Key words: diversity partitioning, desert artesian springs, Bonneville Basin, macroinvertebrates, α diversity, β diversity, γ diversity, island biogeography

INTRODUCTION

Species diversity is affected by processes that occur at a variety of spatial scales from local habitats to the entire globe (Gaston 2003, Soberon et al. 2007). For example, species interactions affect diversity within local communities; whereas historical events (e.g. biogeographic range contraction and expansion of species) associated with climate change can affect the number of species in the regional pool at large geographic scales (e.g. Wiens and Donoghue 2004). Conversely, environmental heterogeneity at any scale can promote diversity by increasing the number of available niches (e.g. Davies et al. 2005).

Whittaker (1960) was the first to emphasize that regional species diversity (γ) could be partitioned into two components: within site (α) and between site diversity (β). Beta-diversity is often called the rate of species turnover along environmental gradients. This terminology is consistent with the perspective that one community gradually grades into another and that species distributions overlap along environmental continua (e.g. Gleason 1926 and 1939, Whittaker 1962). Beta-diversity is also the dissimilarity in species composition between sites. This terminology is more consistent with the perspective that communities along environmental gradients can be separated into discrete units (e.g. Clements 1916 and 1936). Beta-diversity increases as the degree of dissimilarity between sites increases or as the fraction of shared species between sites decreases.

The additive partitioning of species diversity ($\gamma = \alpha + \beta$) utilizes Whittaker's concepts of α, β, and γ diversity, but expresses α- and β-diversity in the same units so that their relative importance can be easily quantified and interpreted (Lande 1996, Crist et al.

2003, Crist and Veech 2006). Recently, ecologists have used additive partitioning to analyze hierarchal patterns of species diversity primarily in terrestrial landscapes (Loreau 2000, Wagner et al. 2000, Crist et al. 2003, Gering et al. 2003, Summerville and Crist 2005).

We can gain valuable insight into the processes that drive patterns of diversity by partitioning regional diversity into β-diversity components corresponding to different geographic scales (sites, habitats, wetland complexes, and valleys), which is similar in concept to a standard statistical analysis of variance (ANOVA). For example, if there is high dissimilarity in species composition between sites nested in habitats, then we might infer the importance of local environmental heterogeneity (e.g. differences in physico-chemical characteristics between habitats) and/or species interactions. However, if species composition is similar between sites nested in the same habitat but dissimilar between sites in different valleys then we can infer the importance of processes operating at the valley scale (e.g. dispersal limitations).

Our study is the first attempt to use additive partitioning of species diversity in a freshwater environment. We partitioned β-diversity in a hierarchical design where the diversity of macroinvertebrates in spring ecosystems of the Bonneville Basin were examined at progressively larger geographic scales to infer the relative importance of processes operating at each scale to the total regional diversity. Individual sites were nested in habitats (springs, channels and marshes), nested in wetland complexes, nested in valleys, nested in the Bonneville Basin of Utah, USA. Geographic units (e.g. valleys) that contain sites with the smallest fraction of shared species will make the greatest contribution to the total regional diversity. For example, β-diversity may be small

between sites within the same wetland complex but large between sites in different valleys. Conserving species diversity depends on identifying and preserving landscape units and the processes that account for the greatest amount of the total regional diversity.

Artesian springs of the Bonneville Basin provide a valuable perspective on the partitioning of β-diversity because: 1) each spatial scale can be delineated into discrete geographic units, 2) sites in different habitat types represent extremes along a permanency/constancy gradient and 3) island effects on diversity (size and isolation) are not confounded with habitat permanency.

Landscape units with clearly defined boundaries reduce potential bias compared to more arbitrary attempts to circumscribe scales along gradually changing environmental continua (e.g. Rahbek 2005). When spatial scales correspond with clearly delineated geographic boundaries (valleys in the Bonneville Basin), we can infer the importance of known historical events (e.g. the draining of ancient Lake Bonneville) in effecting patterns of diversity, specifically the partitioning of β-diversity.

These artesian springs are unique aquatic environments because constant and variable habitat types occur in the same system. Water levels and physico-chemical factors in springs have been stable for 100s to 1000s of years with only slight seasonal and inter-annual variation (e.g. Deacon and Minkley 1974, Hubbs and Miller 1948, Waring 1965). Shallow marshes are fed by surface flows from springs but are generally located 10 to 100s of meters from the spring source and thus, are influenced by external conditions (e.g. solar insolation). Marshes are one of the most variable aquatic environments in the world (e.g. Mitch and Gosselink 2000) with fluctuating water levels, frequent drying, and variable chemical conditions (e.g. oxygen and pH) that fluctuate

orders of magnitude on a daily basis (e.g. Euliss et al. 1999, Rader and Richardson 1992, Wetzel 2001). Thus, we expected that marshes versus springs would select for a different suite of species. Consequently, we expected β-diversity to be high between springs and marshes.

In many environments, including most wetlands, both the size and the permanency of a site have a direct positive relationship with diversity at a site making it difficult to separate their effects. Groundwater springs ranging in size from less than one meter in diameter to fifty meters in diameter are characterized by constant water levels (Deacon and Minkley 1974). Thus, we can test for island effects (size and isolation) without the confounding influence of environmental permanency.

We quantified diversity of spring ecosystems at four scales (sites, habitat types, wetlands and valleys) in a desert landscape for one of the most diverse groups of organisms in aquatic systems, macroinvertebrates. Specifically, we explored three hypotheses. First, α-diversity would be greater in variable marshes than in more constant springs. Second, all scales would contribute a significant proportion to the total β-diversity in the basin and third, processes operating at each scale from local habitats to entire valleys would be important in maintaining diversity in the Bonneville Basin.

METHODS

Study Area

The Bonneville Basin is the eastern-most endorheic drainage basin of the Great Basin Geological Province in western North America. Approximately 17,000 years ago,

Lake Bonneville was formed and covered most of the state of Utah (Oviatt et al. 1992). The lake breached its northern border 15,000 years ago, and subsequent drying fragmented the lake into present-day remnants (lakes, rivers and springs). Artesian springs occur in the valleys at points of groundwater discharge in areas that have been influenced by geologic activity such as folding or faulting (Maxey, 1968). Water levels in springs of the Bonneville Basin are very stable due to constant groundwater inflows, which are independent of local, short term precipitation patterns (Deacon and Minckley 1974, Hovingh 1993, Anderson et al. 2005).

Site Selection

Artesian springs below the water-level of ancient Lake Bonneville were sampled in 11 valleys of the Bonneville Basin, Utah (Keleher and Rader, in review). We distinguished two types of wetlands: isolated and complexes. Isolated wetlands were generally small (0.05 m to 10s of meter in diameter), had a single water source, were rarely associated with channels or marshes, and were separated from other sources of water by 10s to 100s of kilometers. Wetland complexes were large (1 to 10s of km^2) and contained multiple spring sources with both channels and marshes. A site was defined as one of three habitat types (springs, channels, marshes) located within either complexes or isolated wetlands. Springs consisted of a groundwater inflow source (wellhead), slow flowing lentic conditions and the wetted riparian area surrounding the wellhead. Channels contained flowing water that originated from a spring and marshes were identified by shallow, stagnant water. Channels often connected springs to marshes and springs to springs in a wetland complex. We used aerial photographs, resource

managers, and personal experience to locate isolated wetlands and wetland complexes within each valley.

Selecting sites in isolated wetlands was simple as most consisted of a single spring. However, we used a randomized sampling design to select sites in large complexes. Aerial photographs were used to identify two transects that spanned the maximum length and width of each complex. Both transects were divided into 100 m segments. We randomly selected multiple segments and searched a 50 m radius for habitats associated with springs (marshes, spring wells, channels). This procedure was repeated until we had sampled 3 to 5 sites containing three habitat types if all three were present. A maximum transect length of 30 m was sampled in channels and a 30 m x 30 m quadrate was selected for collecting samples in marshes.

Physico-chemical Data

We recorded the location (UTMs), elevation, maximum water depth and general substrate type (organic, clay, silt, sand, and gravel) at each site. We estimated the maximum surface area (maximum length * maximum width) at each spring and measured the maximum width of each channel. We also recorded water temperature, salinity, dissolved oxygen (YSI Model 85 water quality meter) and pH (Hanna pH meter) at the source in all springs.

We only compared the chemical attributes of springs because physico-chemical composition of groundwater inflows is very constant over 24 hrs and on a seasonal basis (e.g. Todd and Mays 2005). In contrast, single measurements taken at different times of the day in marshes have no comparative value because temperature, dissolved oxygen

and pH fluctuate over 24 hrs (e.g. Wetzel 2001). Measurements of physco-chemical factors over 24 hrs in hundreds of sites was beyond the scope of this study.

Macroinvertebrates

Three macroinvertebrate samples were collected at most sites using a standard D-frame sweep net with a 1 mm mesh (Rader and Richardson 1992, Batzer et al. 2001). However, only two samples could be taken at very small sites (e.g. surface area < 5 m^2). A sample consisted of three 1-meter sweeps through a variety of microhabitat types; emergent vegetation (e.g. *Eleocharis* spp.), undercut banks, submersed vegetation (e.g., *Potamogeton* spp.), floating vegetation (e.g. *Lemna* spp.), metaphyton, and detritus. Macroinvertebrates were also removed by hand from woody debris when present. All samples were combined into a single composite at each site, preserved in 90 % ethanol and returned to the laboratory for processing. The same field technician collected all macroinvertebrate samples to avoid potential bias.

In the laboratory, macroinvertebrates were placed in a 23 cm x 33 cm tray and subsampled using randomly selected quadrats (6 cm^2) until 300 individuals were recorded (Vinson and Hawkins 1996, Barbour et al. 1999, King and Richardson 2002). Large-rare organisms were visually removed prior to sub-sampling and were included in the 300 count to document diversity. All invertebrates were identified to the lowest feasible taxonomic level (usually genus or species), except for ostracods and prosobranch gastropods, which were identified to the order level. However, native spring snails (Hydrobiidae) were sent to experts for species identifications. The proportion of the 300 individuals represented by each taxa was used to show patterns of relative abundance.

Although we used a fixed number of individuals from each sample, we unavoidably collected fewer samples in smaller springs and unavoidably sampled a different number of sites within some wetlands and a different number of wetlands within valleys. Thus, we used rarefaction to calculate richness as if sample sizes had been equal (e.g. Gotelli and Colwell 2001). Richness at each scale (sites within habitat types, habitat types within wetlands and wetlands within valleys) was standardized using the site, wetland type, or valley with the fewest individuals (EstimateSWin700, Krebs 2002).

Analyses of α diversity

We used a general linear model (PROC GLM, SAS 1997) to analyze a nested, 3-factor ANOVA to determine differences in average within-site macroinvertebrate richness (α-diversity) between habitat types (marshes, springs, channels), between wetland types (complexes versus isolated springs) and between the eleven valleys using rarefied richness. Alpha diversity was the sum of the taxa at each site. We also analyzed the effects of all 2-way interactions between each of the three factors (habitats, wetlands and valleys), and temperature at the spring well was included as a covariate. Each of the three main effects were fixed variables (valleys, wetland types and habitat types). We re-ran the same analysis using a reduced model after deleting non-significant interactions from the full model. We used Tukey pair-wise comparisons to determine differences between levels of each factor and Type III sums of squares to generate P values for the interpretation of results. Standard tests were used to verify compliance with parametric assumptions (PROC GLM, SAS 1997).

Analysis of β-diversity

If the overall β-diversity in the Bonneville Basin is low then most species will occupy most sites. However, if β-diversity is high then most species will only occupy a small fraction of the total sites. We calculated the number of sites occupied by each species in the entire basin.

We used the software program PARTITION (Crist et al. 2003) to quantify β-diversity of spring macroinvertebrates at each level of the hierarchy (sites, habitats, wetland complexes and valleys). PARTITION uses a statistical approach to compare the observed β-diversity at each scale or level in the hierarchy to the expected β-diversity generated by random permutations. The program calculates an average alpha diversity for each level of the hierarchy (*i*) as,

$$\alpha_i = \sum_{j=1}^{n_i} S_{ij} q_{ij} ,$$

where S_{ij} is the species richness of each site *j* of hierarchical level *i*, n_i is the number of sites at level *i*, and q_{ij} is the site weight or the proportion of the total number of individuals found in each site *j*. The formula for obtaining the observed β-diversity at each level of the hierarchy (*i)* is,

$$\gamma = \alpha_1 + \sum_{i=1}^{m} \beta_i ,$$

where *m* is the number of levels in the hierarchy.

We used a square-root transformation because the program is limited to analyzing less than 60,000 total individuals. Expected null-distributions were generated for α_1 and β_i diversity at each level of the hierarchy using 1,000 individual-based randomizations to

calculate the probability that the observed α_1 and β_i components were obtained by the random distribution of individuals among samples.

Test of Island Effects

We examined how island effects influenced patterns of diversity (MacArthur and Wilson 1967) at each level of the hierarchy using different analyses for the effects of size/area separate from isolation. We examined the effects of isolation by calculating the similarity in species composition between sites regressed against the distance between sites using Bray-Curtis' index:

$$C_s = \frac{2j}{a+b}$$

where j is the number of species common between two sites, a is the number species in site A, and b is the number of species in site B. Beta diversity can be measured as $1 - C_s$. An inverse relationship between distance and the similarity between sites provides evidence of dispersal between near sites and diminishing dispersal as distance increases (e.g. Condit et al. 2002). The probability that individuals drawn at random between sites will be from the same species should be high as species freely disperse between near sites and diminish with the distance between sites. We tested for dispersal limitations at different scales by calculating all pairwise comparisons of similarity versus distance between sites within valleys, between sites in adjacent valleys, and between pairs of sites in non-adjacent valleys. This analysis was run separately for each habitat type to remove the confounding effects of calculating similarity versus distance between different habitats where we expected a high dissimilarity. Only valleys with eight or more sites

within a given habitat were included. There were three adjacent pairs of valleys separated by a mountain range, and 24 pairs of non-adjacent valleys consisting of site comparisons of the same habitat type involving seven of the eleven valleys.

The affects of area on patterns of β-diversity at each scale was analyzed according to Crist and Veech (2006). However, we restricted this analysis to spring habitats because of the difficulty of measuring the total area of marshes and channels. Thus, the levels in the hierarchy were reduced to sites/springs, wetlands and valleys. We summed the area of each spring within wetland complexes and each spring within valleys to estimate area at these larger scales. The α, β, and γ-components were defined as before, only now we assessed how much of the total β-diversity was attributed to area (β_{area}) and how much was attributed to other factors ($\beta_{replace}$). We estimated β_{area} as,

$$\beta_{area} = \frac{1}{r}\sum_{j=1}^{r}(s_{\max} - s_j)$$

where r is the number of springs, s_j is the observed species richness in sample j, and s_{max} is the species richness of the largest spring. Crist and Veech (2006) defined $\beta_{replace}$ as the portion of the β–diversity due to factors other than sample area, including historical events.

RESULTS

Analyses of α diversity

We identified sixteen orders and 288 taxa of aquatic macroinvertebrates (Appendix A) from 280 sites in the Bonneville Basin (γ-diversity). Sixty-nine percent of the gamma richness was attributed to Diptera (31 %), Coleoptera (27 %), and Hemiptera

(11 %; Table 1). Rarefied richness of complexes accumulated across the entire basin was 1.5x greater than isolated wetlands, whereas the rarefied accumulated richness of channels was greater than springs, which was greater than marshes (Table 1).

Temperature ($F_{1,236} = 2.29$, $P = 0.13$), wetland types ($F_{1,236} = 0.01$; $P = 0.92$), and all three interactions did not account for significant variation in mean rarefied α-richness (valley*wetland type $F_{4,236} = 1.45$, $P = 0.22$; valley*habitat type $F_{16,236} = 1.56$, $P = 0.09$; wetland type*habitat type $F_{2,236} = 0.58$, $P = 0.56$). Valley was the only significant factor in the full-model analysis ($F_{10,236} = 2.96$, $P = 0.0002$). Thus, we re-ran the analysis using a reduced model with only the main effects (valley, wetland type, and habitat type). Mean rarefied α-richness differed between valleys ($F_{10,263} = 4.64$, $P = <0.0001$) and between habitat types nested in wetlands ($F_{2,263} = 6.14$, $P = 0.003$) but not between wetland types within valleys ($F_{2,263} = 6.14$; $P = 0.78$). Tukey pairwise comparisons showed that α-richness was greater ($P = 0.03$) in marshes than channels and springs ($P = 0.0006$), which did not differ ($P = 0.42$; Table 1). Thus, marshes had the greatest α-richness, but the lowest richness of the three habitat types accumulated across the Bonneville Basin (Table 1).

The average α-richness for all sites in the Bonneville Basin was 20 taxa. The most diverse site was a spring in Goshen (46 taxa), whereas the least diverse site was a spring in Snake Valley (3 taxa). There were no obvious physico-chemical differences between these sites. Both were associated with a wetland complex and were similar in elevation, size, temperature, and water depth. However, Goshen Valley is positioned between two large lakes connected by a temporary stream, which may influence rates of macroinvertebrate dispersal and colonization.

Goshen Valley had the greatest rarefied α-richness and the greatest accumulated rarefied richness in the Bonneville Basin (Table 2). Tukey pairwise comparisons showed that mean rarefied α-richness was greater in Goshen Valley than all other valleys except Ibapah and Grouse Creek (P ranged from < 0.0001 to 0.04). Although Snake Valley had the second greatest accumulated rarefied richness, it had one of the lowest values of rarefied α-richness. Snake Valley (26) and Utah Valley (18) had the greatest number of taxa that were not collected in other valleys. The number of "unique" taxa varied from 0 to 9 in the other valleys.

Analyses of β-diversity

The overall β–diversity in the Bonneville Basin was high because approximately half of the 288 taxa were found in 6 or fewer sites (Figure 1). Thus, half of the taxa had a very restricted distribution, with twenty percent collected from a single site. When we partitioned the overall β–diversity we found that 31% of the total species richness (γ-diversity) was due to within- and among-site components and among-habitat components (α_1, β_1, and β_2 in Figure 2). The among-wetland component (β_3) accounted for 21 % of the total species richness, whereas the among-valley component (β_4) accounted for nearly half of the total diversity (48%) in the Bonneville Basin. Only β_4 was significantly greater than expected; all other components were significantly lower than expected by chance ($P < 0.001$). The average β-diversity within valleys ranged from 14 taxa in Skull Valley to a remarkable 30.1 taxa in Goshen Valley (Table 2). That is, sites in Goshen Valley differed on average by 30 taxa.

Test of Island Effects

Comparisons of α-richness and accumulated richness between large wetland complexes and small isolated springs provided contrasting evidence concerning the importance of island effects in determining patterns of diversity. Wetland type (complexes versus isolated) did not account for significant variation in mean rarefied α-richness. However, rarefied accumulated richness of larger complexes was over 1.5x greater than in smaller isolated wetlands. Although accumulated richness suggests the importance of island effects, these analyses averaged across levels within the spatial hierarchy. Thus, we analyzed the community similarity-distance relationship at each scale to further explore the importance of island effects.

The relationship between the similarity in species composition and distance between sites within valleys provided support for the importance of island effects and dispersal in determining patterns of diversity at this scale. However, evidence for island effects was stronger for springs than marshes. All five valleys showed a significant inverse relationship between the community similarity of spring sites versus distance between springs within a valley (Table 3 and Figure 3). However, only two out of four valleys showed a significant inverse relationship between the community similarity of marsh sites versus distance suggesting the absence of dispersal limitations for marshes in Snake and Tule valleys (Table 4 and Figure 4).

Patterns of community similarity within versus between valleys suggested that mountain ranges were important barriers to dispersal. There was no relationship between community similarity and the distance between either springs or marshes in adjacent valleys (Table 5 and Figure 5). Community dissimilarity between sites separated by 10s

of kilometers across a mountain range was no different than sites separated by 100s of kilometers of desert and multiple mountain ranges. Also, the overall mean similarity of sites within a valley of the same habitat type (0.42) was almost 2x greater than the mean similarity between the same habitat types in adjacent valleys (0.22). Lower similarity between sites in adjacent valleys versus between sites within a valley, and no relationship between similarity and distance between sites separated by a mountain range suggested the importance of mountains as barriers to dispersal. Plus, the mean similarity between sites in non-adjacent valleys separated by 100s of kilometers across the Bonneville Basin (0.26) was similar to comparisons between sites in adjacent valleys (Table 6 and Figure 6). Also, there was no relationship between similarity and distance between sites in non-adjacent valleys.

Area effects on β-diversity decreased with increasing scale (Figure 7). Area accounted for 56 % of the variation in the dissimilarity between springs nested in wetlands, 26 % of wetlands nested in valleys, and 1 % of valleys in the Bonneville Basin. That is, the area of a spring can have a large effect on the number of species that colonize and persist at local scales. However, the size of a wetland complex or especially the size of all groundwater springs in a valley is not important in determining the species that colonize and persist. Thus, $\beta_{replace}$, or factors other than area-related effects, accounted for the majority of the observed β-diversity of wetlands in valleys and especially between valleys.

DISCUSSION

Processes Affecting Local Patterns of Diversity

We suggest that temporal variability primarily determined differences in α-diversity between habitats nested in wetlands of the Bonneville Basin. We hypothesize that marshes had a greater α-diversity than springs or channels because they show a greater diel range in physico-chemical conditions. That is, we suggest that marshes have a greater number of niches than springs or channels. Both theoretical and empirical evidence indicates that spatial and temporal variability as manifest by physico-chemical diversity begets species diversity (e.g. Hutchinson 1961, Tilman 1994, Chesson 2000, Amarasekare 2003, Snyder and Chesson 2003, Amarasedkare et al. 2004). Also, temporal variability in the form of disturbances (Connell 1961 and 1978) may prevent competitive exclusion in marshes (seasonal drawdown and drying), and sustain a greater diversity than in springs and channels. By contrast, temporal variation is reduced in springs and channels, which are the most constant freshwater environments on Earth. Constant conditions and a lack of natural disturbances can reduce the number of niches and promote competitive exclusion.

We suggest that species-environment relationships explain why marshes have the lowest accumulated diversity across the basin, even though they had the greatest α-diversity within a site. As we tally species in each habitat type across the entire basin, marshes do not accumulate species as fast as springs or channels because marshes select for a specific group of taxa with good dispersal abilities. This is shown by the weak relationship between distance and community similarity for marshes within valleys. The variable nature of marshes selects for generalist taxa adapted to harsh conditions (e.g. Wissinger 1999). Good dispersal ability is one of the most important traits of taxa that inhabit ephemeral environments.

Area effects played a prominent role in determining levels of β-diversity between springs within wetlands. Island Biogeography theory predicts that smaller islands will have lower diversity than larger islands because smaller islands have faster rates of extinction and slower rates of immigration and successful colonization (MacArthur and Wilson 1967). Wetlands embedded in a dry desert matrix are like islands in the sea because of the risks associated with dispersal across an inhospitable matrix. Several studies have plotted wetland size versus species diversity as evidence supporting (Stout 1964, Reisen 1973, Ebert and Balko 1987, Spencer et al. 1999, Brooks 2000) and refuting (Driver 1997, Lake et al. 1989, March and Bass 1995, Schneider and Frost 1996, Hall et al. 2004) the importance of area effects in determining diversity in wetland communities. However, most of these analyses have confounded wetland permanency (length of inundation) with wetland size because increased permanency and size are both correlated with greater species diversity. Size and permanency are not confounded in desert springs because small and large springs are fed by constant groundwater inflows.

Thus, a large proportion of the turnover in species between springs in wetlands is attributed to area. The species-area relationship is generally attributed to habitat heterogeneity and island effects. Explanations invoking habitat heterogeneity suggest that large springs will have more species than small springs because large springs contain a greater variety of habitat types than small springs. Island effects suggest that large springs contain more species than small springs because of the effects of spring size on rates of immigration and extinction independent from possible differences in habitat heterogeneity (MacArthur and Wilson 1967).

According to Island Biogeography theory, small springs are colonized by a

similar group of taxa that are good at dispersal to remote locations. Thus, small springs have a high similarity. Larger springs, however, are colonized by a greater fraction of the total species arriving in a valley both poor and good dispersers. Poorer dispersers reach some large springs and not others thus, decreasing the proportion of shared taxa between large springs and increasing β-diversity in large springs relative to small springs.

Processes Affecting Patterns of Diversity within Valleys

We suggest that isolation and dispersal limitations determined the turnover of species between wetlands within a valley. Wetlands in this desert landscape appeared to be well suited for the application of island biogeography theory. Some wetlands were larger complexes close to other sources of water, while others were smaller more isolated, 10 to 100s of kilometers from other sources of water. Island Biogeography predicts that 1) community similarity would decrease with increasing distance between sites, and 2) area would account for a significant portion of the total β-diversity.

We suggest that Island Biogeography theory is best applied to sites and wetlands within valleys. That is, the size and isolation of a spring are useful characteristics in predicting macroinvertebrate diversity and the dissimilarity in macroinvertebrates community composition within valleys. Although wetlands within valleys accounted for a relatively small proportion of the total β-diversity in the Bonneville Basin, it was considerably larger than that contributed by sites within habitats, and different habitat types. The similarity by distance analysis showed that much of the variation in species composition or turnover of species within a valley was attributed to a decline in dispersal with distance, especially in springs. Distant sites had an overall greater dissimilarity than

near sites.

Patterns of α-diversity at the valley scale could have also been affected by their position on the landscape, which may influence rates of colonization to a valley. Macroinvertebrates reached their greatest accumulated diversity and average within-site diversity in Goshen Valley. Goshen Valley is situated between two permanent lakes, Mona Reservoir to the south and Utah Lake to the north, connected by a temporary stream. Both lakes and the stream contained extensive wetland habitat. Thus, springs in Goshen Valley are 10s to 100s of meters from the nearest source of colonists, whereas wetlands in all of the other valleys are 10s to 100s of kilometers from the nearest source of colonists. Most of these other valleys open into the Great Salt Lake, the salt flats surrounding the Great Salt Lake, or are endorheic. The Great Salt Lake is a hyper-saline environment and thus, it is not a source of colonists for macroinvertebrates that inhabit freshwater springs. Increased colonization rates can increase local diversity within Goshen Valley by the "rescue effect". Small populations that are prone to extinction can be rescued by a frequent influx of new colonists causing local and total accumulated diversity within Goshen Valley to increase relative to other valleys in the basin (e.g. Erman and Erman 1995).

Processes Affecting Patterns of Diversity between Valleys

Historical biogeography and dispersal limitations best account for the high dissimilarity in species composition between valleys in the Bonneville Basin. Differences between valleys accounted for the greatest variation in both α- and β-diversity. The valley scale explained nearly 50% of the total macroinvertebrate β-

diversity. Thus, processes at this scale have the greatest impact on the total regional diversity.

Wetlands in the Bonneville Basin have been isolated since ancient Lake Bonneville dried more than 9,500 year ago. If species could readily disperse between valleys we would expect to see an inverse relationship with distance between sites. Nearer sites would have a greater similarity in species composition than distant sites. Similarity would decrease in distant sites because of the difficulty of dispersing through a dry desert landscape. However, our similarity by distance analysis showed that there was no relationship between sites in adjacent and non-adjacent valleys. This suggests that wetlands within different valleys have been isolated from each other since Lake Bonneville drained.

Evidence from the distribution and genetics of individual species supports this assertion. For example, Hovingh (1993) found that Snake Valley and Tule Valley contained unique species of leeches absent in the other valleys of the basin. He suggested that these species were isolated by the intervening mountains before Lake Bonneville drained and have been unable to disperse between valleys since that time. Hershler and Sada (2002) showed a similar pattern with spring snails. Long isolation coupled with slow dispersal has led to local speciation and extinction, and thus high endemism within valleys. Also a similar pattern is seen in the genetic variation of a small minnow, the least chub (*Iotichthys phlegothontis*), which is endemic to the Bonneville Basin and limited to wetlands in only a few valleys. A high proportion of the genetic variation in this species is attributed to differentiation between populations in separate valleys (Mock and Miller 2005). Indeed, wetlands resemble patterns of diversity

on oceanic islands which are rich in endemics but impoverished in species compared to the regional species pool (Whittaker 1998), a pattern that is amplified at the valley scale.

Management Implications

Wetlands with a variety of different habitat types will support a greater variety of niches and thus, species. Preservation of biodiversity depends on maintaining the full range of natural variation to which organisms have evolved (Paine et al. 1998, Gunderson and Holling 2002). Natural variation within spring ecosystems of the Bonneville Basin extends across multiple scales from different habitats to different valleys because of environmental variation between habitat types (e.g. marshes versus springs), historical biogeography, and dispersal limitations.

Managers often balance human demands (e.g. water resources, agriculture, grazing) with biodiversity conservation. Our study suggests that in order to preserve biodiversity within the Bonneville Basin, a variety of habitats with different physical-chemical attributes will need to be protected within all of the valleys. Over 50% of the total macroinvetebrate species occurred in less than 6 sites. Although we are aware of some endemic species, many sites, especially springs, may contain unidentified endemic taxa.

We suggest caution when planning conservation actions (e.g. habitat protection) for single species as they often require a narrow range of habitats and conditions. Action plans should preserve the full range of biological diversity in these unique environments. Maintaining biodiversity at all scales, but especially at the valley scale, will help to ensure that the processes (re-colonization, migration etc.) that maintain the functional

integrity at the community level (e.g. food webs) are conserved.

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LITERATURE CITED

Amarasekare, P. Competitive coexistence in spatially structured environments: a synthesis. Ecology Letters 6:1109-1122.

Amarasekare, P., M.F. Hoopes, N. Mouquet, and M. Holyoak. 2004. Mechanisms of coexistence in competitive metacommunities. American Naturalist 164:310-326.

Anderson, K., S. Nelson, A. Mayo, and D. Tingey. 2006. Interbasin flow revisited: The contribution of local recharge to high-discharge springs, Death Valley, CA. *Journal of Hydrology* 323:276-302.

Barbour, M. T., J. Gerritsen, B. D. Snyder and J. B. Stribling. 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates and fish, second edition. EPA 841-B-99-002. U.S. Environmental Protection Agency: Office of Water; Washington, D.C.

Batzer, D. P., R. B. Rader, and S. A. Wissinger. 2001. Invertebrates in freshwater wetlands of North America: ecology and management. Wiley, New York.

Brooks, R. T. 2000. Annual and seasonal variation and the effects of hydroperiod on benthic macroinvertebrates of seasonal forest ("vernal") ponds in central Massachusetts, USA. Wetlands 20:707-715.

Chesson P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343-366.

Clements, F. E. 1916. Plant succession: An analysis of the development of vegetation. Washington D.C.: Carnegie Institution of Washington, Publication 242.

Clements, F. E. 1936. Nature and structure of the climax. Journal of Ecology 24:252-284.

Condit, R., N. Pitman, E. G. Leigh Jr., J. Chave, J. Terborgh, R.B. Foster, P. Núñez, S. Aguilar, R. Valencia, G. Villa, H. C. Muller-Landau, E. Losos and S. P. Hubbell. 2002. Beta-Diversity in Tropical Forest Trees. Science 295(5555):666-669.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42:710-723.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.

Crist, T. O., and J. A. Veech. 2006. Additive partitioning of rarefaction curves and species-area relationships: unifying α-, β-, and γ-diversity with sample size and habitat area. Ecology Letters 9:923-932.

Crist, T. O., J. A. Veech, J. C. Gering and K. S. Summerville. 2003. Partitioning species diversity across landscapes and regions: a hierarchical analysis of α, β, and γ diversity. American Naturalist 162:734-743.

Davies, K.F., P. Chesson, S. Harrison, B.D. Inouye, B.A. Melbourne, and K.J. Rice. Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. Ecology 86:1602-1610.

Deacon, J. E. and W. L. Minckley. 1974. Desert fishes. p. 385-488. *In* G.W. Brown Jr. (ed) Desert Biology volume 2. Academic Press, New York, NY.

Driver, E. A. 1997. Chironomid communities in small prairie ponds: some characteristics and controls. Freshwater Biology 7:121-133.

Ebert, T. A. and M. L. Balko. 1987. Temporary pools as islands in space and time: the biota of vernal pools in San Diego, Southern California, USA. Archiv für

Hydrobiologie 110:101-123.

Erman, N. A. and D. C. Erman. 1995. Spring permanence, Trichoptera species richness, and the role of drought. Journal of the Kansas Entomological Society 68:50-64.

Euliss N.H., D.A. Wrubleski, and D.M. Mushet. 1999. Wetlands of the Prairie Pothole region: Invertebrate species composition, ecology, and management. *In* Batzer, D.P., R.B. Rader, and S.A. Wissinger (eds.) Invertebrates in freshwater wetlands of North America: ecology and management. Wiley, New York.

Gaston, K. J. 2003. The how and why of diversity. Nature 421:200-201.

Gering, J. C., T. O. Crist and J. A Veech. 2003. Additive partitioning of species diversity across multiple spatial scales: implications for regional conservation of biodiversity. Conservation Biology 17:488-499.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53:1-20.

Gleason, H.A. 1939. The individualistic concept of the plant association. American Midland Naturalist 21:92-110.

Gotelli, N. J. and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379-391.

Gunderson, L. and C. S. Holling 2001. Panarchy, understanding transformations in humans and natural systems. Island Press, New York, N.Y. USA.

Hall, D. L., M. R. Willig, D. L. Moorehead, R. W. Sites, E. B. Fish and T. R. Mollhagan. 2004. Aquatic macroinvertebrate diversity of playa wetlands: the role of landscape and island biogeographic characteristics. Wetlands 24:77-91.

Hershler R. and D. W. Sada. 2002. Biogeography of Great Basin aquatic snails of the genus *Pyrgulopsis*. P. 255-276. In Hershler, R., Madison D. B., Currey D. R. (eds.) Great Basin Aquatic Systems History. Smithsonian Contributions to the Earth Sciences, 33. Smithsonian Institute Press, Washington, D.C.

Hovingh, P. 1993. Aquatic habitats, life history observations, and zoogeographic considerations of the spotted frog (*Rana pretiosa*) in Tule Valley, Utah. Great Basin Naturalist 53:168-179.

Hubbs, C. L. and R. R. Miller. 1948. Correlation between fish distribution and hydrographic history in the desert basins of the western United States. Bulletin of University of Utah, Biological Services 38:17-166.

Hutchinson, G.E. 1961. The paradox of plankton. American Naturalist 95:137-145

King, R. S., and C. J. Richardson. 2002. Evaluating subsampling approaches and macroinvertebrate taxonomic resolution for wetland bioassessment. Journal of North American Benthological Society 21(1):150-171.

Krebs, C. J. 2002. Programs for Ecological Methodology, second edition. Department of Zoology, University of British Columbia.

Lake, P. S., I. A. E. Bayly and D. W. Morton. 1989. The phenology of a temporary pond in western Victoria, Australia with special reference to invertebrate succession. Archiv für Hydrobiologie 115:171-202.

Lande, R. 1996. Statistics and partitioning of species diversity and similarity among multiple communities. Oikos 76:5-13.

Loreau, M. 2000. Are communities saturated? On the relationship between α, β, and γ

diversity. Ecology Letters 3:73-76.

MacArthur, R. H. and E. O. Wilson. 1967. An equilibrium theory of insular zoogeography. Evolution 17:373-387.

March, F. and D. Bass. 1995. Application of island biogeography theory to temporary pools. Journal of Freshwater Ecology 10:83-85.

Maxey, G. B. 1968. Hydrogeology of desert basins. Ground water 6:10-22.

Mitch, W. J. and J. G. Gosselink. 2000. Wetlands, third edition. Wiley, New York.

Mock, K. E. and M. P. Miller. 2005. Patterns of molecular diversity in naturally occurring and refugial populations of least chub. Transactions of the American Fisheries Society 134:267-278.

Oviatt, C. G., D. R. Currey and D. Sack. 1992. Radiocarbon chronology of Lake Bonneville, Eastern Great Basin, USA. Palaeogeography, Palaeoclimatology and Palaeoecology 99:225-241.

Paine, R. T., M. J. Tegner and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. Ecosystems **1**: 535-545.

Rader, R. B. and C. J. Richardson. 1992. The effects of nutrient enrichment on macroinvertebrates and algae in the Everglades: a review. Wetlands 12:34-41.

Reisen, W. K. 1973. Invertebrate and serial progression in temporary pool communities at Turner's Falls, Murray County, Oklahoma. Journal of the Kansas Entomological Society 46:294-301.

Rhabek, C. 2005. The role of scale and the perception of large-scale species-richness

patterns. Ecology Letters 8:224-239.

SAS Institute Inc. 2004. SAS/STAT 9.1 User's Guide. SAS Institute Inc., Cary, North Carolina.

Schneider, D. W. and T. M. Frost. 1996. Habitat duration and community structure in Temporary ponds. Journal of the North American Benthological Society 15:64-86.

Snyder, R.E. and P. Chesson. 2003. Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. Ecology Letters 6:301-309.

Soberon, J., R. Jimenez, J. Golubov and P. Koleff. 2007. Assessing completeness of biodiversity databases at different spatial scales. Ecography. Doi: 10.1111/j20060906-7590.04627.

Spencer, M., L. Blaustein, S. S. Schwartz and J. E. Cohen. 1999. Species richness and the proportion of predatory animal species in temporary freshwater pools; relationships with habitat size and permanence. Ecology Letters 2:157-166.

Stout, V. M. 1964. Studies on temporary ponds in Canterbury, New Zealand. Verhandlungen der Internationalen Vereinigung fur Theoretische Angewandte Limnologie XV:209-214.

Summerville, K. S. and T. O. Crist. 2005. Temporal scaling of species accumulation in forest Lepidoptera: Biodiversity Conservation 14:3393-3406.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75:2-16.

Todd, D. K. and L. W. Mays. 2005. Groundwater Hydrology, third edition. John Wiley

and Sons Inc. New York, New York, USA.

Vinson, M. R. and C. P. Hawkins. 1996. Effects of sampling area and subsampling procedure on comparisons of taxa richness among streams. Journal of North American Benthological Society 15:392-399.

Wagner, H. H., O. Wildi and K. C. Ewald. 2000. Additive partitioning of plant species diversity in an agricultural mosaic landscape. Landscape Ecology 15:219-227.

Waring, G. H. 1965. Thermal springs of the United States and other countries of the world: A summary. U.S. Geological Survey Professional Papers 492:1-383.

Wetzel, R. G. 2001. Limnology: Lake and River Ecosystems, third edition. Academic Press, New York, NY.

Whittaker, R. H. 1962. Classification of natural communities. Botanical Review 28:1-239.

Whittaker, R. H. 1998. Island biogeography: ecology, evolution, and conservation. Oxford University Press, Oxford.

Wiens, J. A. and M. J. Donoghue. 2004. Historical biogeography, ecology, and species richness. Trends in Ecological Evolution 19:639-644.

Wissinger, S.A. 1999. Ecology of wetland invertebrates: Synthesis and applications for conservation and management. *In* Batzer, D.P., R.B. Rader, and S.A. Wissinger (eds.) Invertebrates in freshwater wetlands of North America: ecology and management. Wiley, New York.

LIST OF TABLES

Table 5. Regression results of all pairwise similarity comparisons of spring and marsh sites versus distance between sites in adjacent valleys separated by a mountain range. "Range" is the range of distances between sites.

Table 6. Regressions of all pairwise comparisons of spring and marsh sites versus distance between non-adjacent valleys. "Range" is the distances between sites.

Table 1. Accumulated rarefied richness (RR), and mean rarified α-richness of macroinvertebrates in wetland types (Complexes and Isolated) and in habitats of the Bonneville Basin. Mean rarified α-richness with different letters indicate significantly different values ($P < 0.05$). Values in parentheses represent one standard error and the number of sites are shown in brackets. Complexes and isolated wetlands were rarefied separate from marshes, channels, and springs.

Order	Complexes [263]	Isolated [17]	Marshes [88]	Channels [67]	Springs [125]	Basin [280]
Diptera	87	60	63	66	75	94
Coleoptera	82	34	54	54	72	81
Hemiptera	33	10	21	21	24	32
Oligochaeta	16	9	8	12	16	17
Odonata	17	13	13	15	14	17
Trichoptera	15	3	4	12	11	16
Gastropoda	11	5	10	9	10	11
Acari	13	4	9	5	9	13
Hirudinea	9	4	6	8	8	9
Ephemeroptera	5	1	4	4	3	5
Amphipoda	2	2	2	2	2	2
Bivalvia	2	1	1	2	1	2
Cnidaria	1	0	0	0	1	1
Turbellaria	1	1	1	1	1	1
Isopoda	1	1	1	1	1	1
Accumulated RR	228	148	188	212	201	-
Rarified α–Richness	19.6[a] (1.0)	19.1[a] (1.9)	23.4[a] (1.1)	18.7[b] (1.1)	17.8[b] (0.9)	19.7 (1.2)

Table 2. Average rarefied α-richness, accumulated rarefied richness (RR), and average β-diversity of macroinvertebrates in valleys of the Bonneville Basin. Different letters indicate significantly different values ($P < 0.05$). Values in parentheses represent one standard error,and the number of sites is shown in brackets.

Valley	Rarified α–Richness	Accumulated RR	Average β-diversity
Goshen [21]	27.2^{a} (1.8)	82	30.1
Ibapah [6]	22.8^{ab} (2.9)	49	24.5
Grouse Creek [10]	20.8^{ab} (2.7)	72	22.6
Mills [24]	20.6^{b} (1.7)	65	22.3
Curlew [2]	18.4^{b} (4.0)	39	18.0
Rush [6]	18.1^{b} (1.7)	38	17.5
Utah [30]	17.8^{b} (1.5)	60	18.8
Fish Springs [35]	17.3^{b} (1.4)	59	19.3
Snake [114]	17.1^{b} (1.1)	74	26.3
Tule [28]	16.5^{b} (1.5)	64	18.0
Skull [4]	16.1^{b} (3.6	33	14.0

Table 3. Regression results of all pairwise comparisons of community similarity of spring sites versus distance within valleys. "Range" is the range of the distances between sites.

Valley	Range (m)	Mean	Significance	Slope	R^2
Goshen	13 – 17,944	0.38	$F_{1,34} = 4.3$; $P = 0.04$	-0.00005	0.11
Utah	12 – 39,780	0.30	$F_{1,134} = 3.9$; $P = 0.04$	-0.00006	0.02
Fish Springs	59 – 16,327	0.51	$F_{1,89} = 37.9$; $P < 0.0001$	-0.00005	0.30
Snake	4.5 – 70,265	0.36	$F_{1,1511} = 104.4$; $P < 0.0001$	-0.00003	0.06
Tule	31.3 - 4326	0.43	$F_{1,26} = 7.7$; $P = 0.009$	-0.00005	0.23

Table 4. Regression results of all pairwise similarity comparisons of marsh sites versus distance within valleys. "Range" is the range of the distances between sites.

Valley	Range (m)	Mean	Significance	Slope	R^2
Mills	50.6 – 65,427	0.49	$F_{1,103} = 16.9$; $P < 0.0001$	-0.000002	0.14
Fish Springs	154 - 8172	0.50	$F_{1,34} = 5.3$; $P < 0.03$	-0.00003	0.13
Snake	48.4 – 70,491	0.39	$F_{1,463} = 1.2$; $P = 0.28$	-0.0000001	0.002
Tule	28.5 – 100,053	0.33	$F_{1,53} = 3.5$; $P = 0.07$	0.0000001	0.06

Table 5. Regression results of all pairwise similarity comparisons of spring and marsh sites versus distance between sites in adjacent valleys separated by a mountain range. "Range" is the range of distances between sites.

Comparison	Habitat	Range (km)	Mean	Significance	Slope	R^2
Snake vs Tule	Spring	183 - 352	0.23	$F_{1,34} = 4.4$; $P = 0.06$	0.0000005	0.18
Fish Springs vs Tule	Spring	43 - 63	0.18	$F_{1,110} = 0.4$; $P = 0.50$	0.000001	0.004
Utah vs Goshen	Spring	8.5 - 66	0.23	$F_{1,151} = 0.6$; $P = 0.43$	0.0000005	0.004
Snake vs Tule	Marsh	30 - 168	0.24	$F_{1,339} = 20$; $P < 0.001$	0.0000006	0.06
Fish Springs vs Tule	Marsh	46 - 153	0.23	$F_{1,97} = 0.5$; $P = 0.5$	0.0000003	0.004

Table 6. Regressions of all pairwise comparisons of spring and marsh sites versus distance between non-adjacent valleys. "Range" is the distances between sites.

Comparison	Habitat	Range (km)	Mean	Significance	Slope	R^2
Utah vs Grouse Cr.	Spring	203 - 251	0.22	$F_{1,83} = 0.06$; P = 0.8	0.00000	0.000
Utah vs Fish Springs	Spring	136-159	0.22	$F_{1,236}$=1.33; P = 0.56	0.00000	0.001
Utah vs Tule	Spring	162-190	0.20	$F_{1,134}$=0.0002; P = 0.98	0.00000	0.000
Utah vs Snake	Spring	160-214	0.23	$F_{1,933} = 45.4$; P = 0.000	0.00001	0.046
Utah vs Mills	Spring	65-158	0.25	$F_{1,49} = 8.23$; P = 0.006	0.00003	0.143
Utah vs Ibapah	Spring	186-348	0.25	$F_{1,66} = 6.52$; P = 0.0129	0.00000	0.090
Grouse vs Goshen	Spring	233-263	0.28	$F_{1,43} = 0.42$; P = 0.52	0.00000	0.009
Grouse vs Mills	Spring	264-291	0.29	$F_{1,13} = 0.053$; P = 0.821	0.00000	0.004
Goshen vs Tule	Spring	149-159	0.24	$F_{1,70} = 0.139$; P = 0.71	0.00000	0.002
Goshen vs Mills	Spring	39-112	0.32	$F_{1,25} = 1.90$; P = 0.179	0.00000	0.071
Goshen vs Ibapah	Spring	183-352	0.36	$F_{1,34} = 7.44$; P = 0.010	0.00000	0.179
Mills vs Tule	Spring	62-128	0.26	$F_{1,21} = 14.73$; P= 0.0009	0.00009	0.412
Ibapah vs Tule	Spring	83-499	0.26	$F_{1,30} = 2.72$; P = 0.1095	0.00000	0.083
Mills vs Ibapah	Spring	82-427	0.31	$F_{1,12} = 3.90$; P = 0.071	0.00000	0.245
Fish Springs vs Mills	Spring	97-129	0.32	$F_{1,40} = 14.1$; P = .00056	0.00000	0.26
Fish Springs vs Goshen	Spring	130-135	0.29	$F_{1,124} = 2.54$; P = 0.112	-.00001	0.020
Grouse vs Fish Springs	Spring	171-208	0.25	$F_{1,68} = 17.18$; P = 0.000	0.00000	0.202
Grouse vs Tule	Spring	227-254	0.22	$F_{1,38} = 0.025$; P = 0.873	0.00000	0.000
Grouse vs Ibapah	Spring	154-551	0.29	$F_{1,18} = 2.13$; P = 0.162	0.00000	0.105
Fish Springs vs Ibapah	Spring	50-484	0.29	$F_{1,54} = 23.9$; P = 0.0000	0.00002	0.307
Snake vs Grouse	Spring	154-247	0.24	$F_{1,273} = 1.79$; P = 0.182	0.00000	0.007
Snake vs Ibapah	Spring	26-532	0.29	$F_{1,218} = 9.33$; P = 0.003	0.00000	0.041
Snake vs Goshen	Spring	157-186	0.27	$F_{1,493} = 77.17$; P = 0.001	0.00000	0.135
Snake vs Mills	Spring	113-163	0.27	$F_{1,163} = 28.01$; P = 0.000	0.00006	0.147
Snake vs Fish	Spring	26-67	0.22	$F_{1,768} = 22.33$; P = 0.000	0.00004	0.028
Fish vs Snake	Marsh	26-67	0.32	$F_{1,277} = 6.91$; P = 0.009	0.00000	0.024
Utah vs Mills	Marsh	87-159	0.24	$F_{1,73} = 10.92$; P = 0.001	0.00000	0.130
Utah vs Fish	Marsh	146-159	0.21	$F_{1,43} = 4.484$; P = 0.040	0.00000	0.094
Utah vs Tule	Marsh	177-250	0.19	$F_{1,53} = 0.369$; P = 0.546	0.00000	0.007
Goshen vs Mills	Marsh	40-102	0.32	$F_{1,58} = 0.950$; P = 0.334	0.00000	0.016
Goshen vs Fish	Marsh	130-134	0.33	$F_{1,34} = 0.262$; P = 0.612	0.00000	0.008
Goshen vs Tule	Marsh	144-197	0.29	$F_{1,42} = 4.701$; P = 0.036	0.00000	0.101
Mills vs Fish	Marsh	101-129	0.36	$F_{1,133} = 0.026$; P = 0.87	0.00000	0.000
Mills vs Tule	Marsh	79-162	0.30	$F_{1,163} = 1.31$; P = 0.253	0.00000	0.008
Utah vs Snake	Marsh	164-214	0.28	$F_{1,153} = 0.127$; P = 0.72	0.00000	0.000
Goshen vs Snake	Marsh	157-180	0.37	$F_{1,122} = 16.42$; P = 0.00	0.00002	0.119
Mills vs. Snake	Marsh	110-163	0.36	$F_{1,463} = 0.184$; P = 0.67	0.00000	0.000

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adjacent valleys separated by a mountain range showing spring sites in Fish Springs Valley versus Tule Valley (a) and marsh sites in Snake Valley versus Tule Valley (b).

Figure 6. Examples of the fraction of shared species versus distance between sites in non- adjacent valleys across the Bonneville Basin showing spring sites in Utah and Snake valleys (a) and marsh sites in Mills and Snake valleys (b).

Figure 7. Partitioning of β-diversity between β_{area} and $\beta_{replace}$ for macroinvertebrate communities in springs at each level of the spatial hierarchy.

Figure 1.

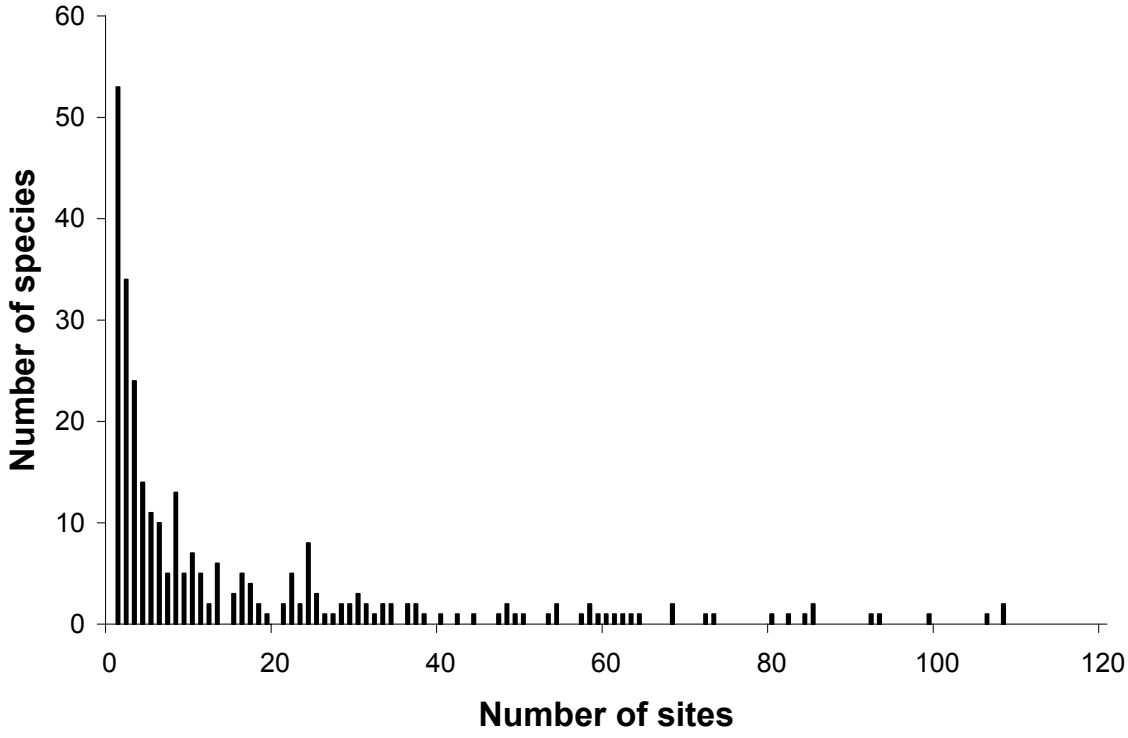


Figure 2.

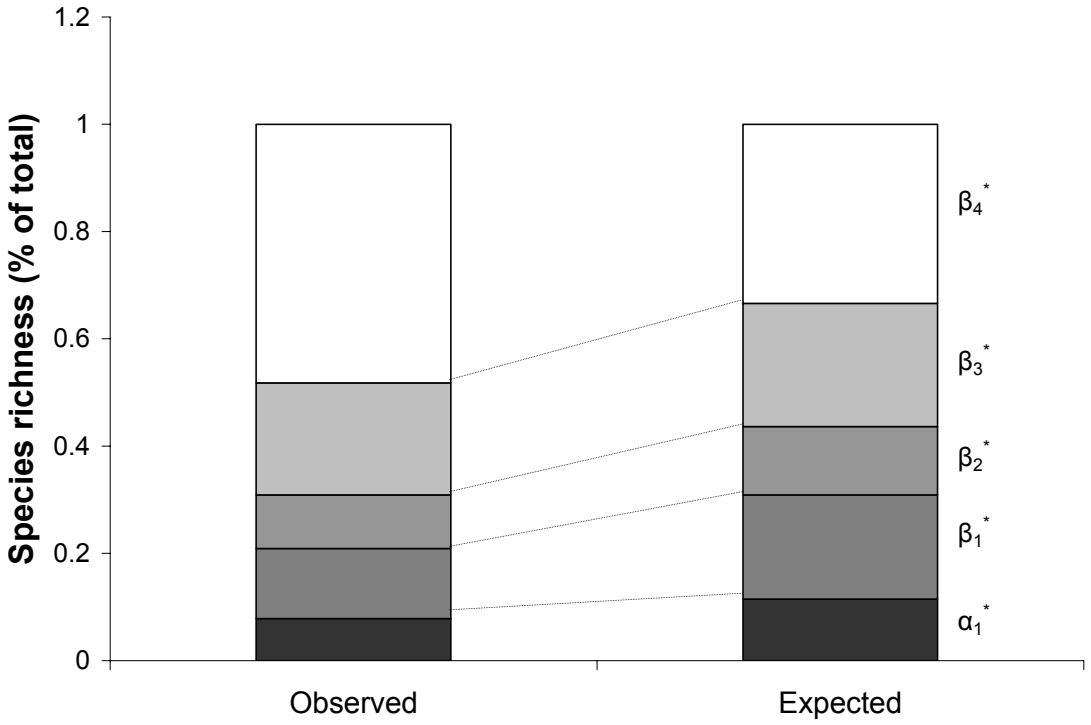


Figure 3.

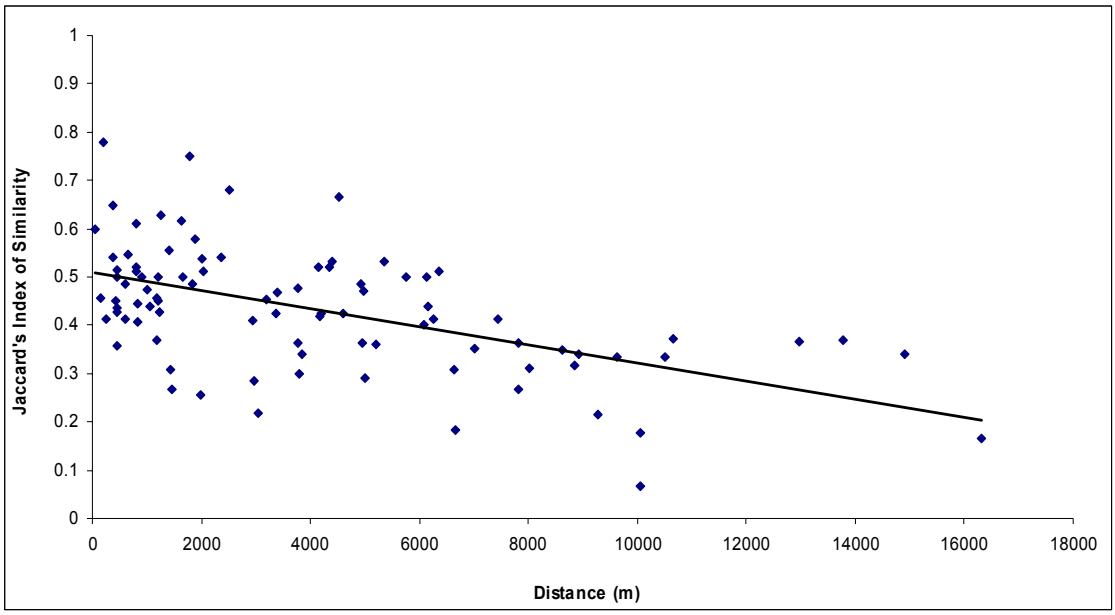


Figure 4.

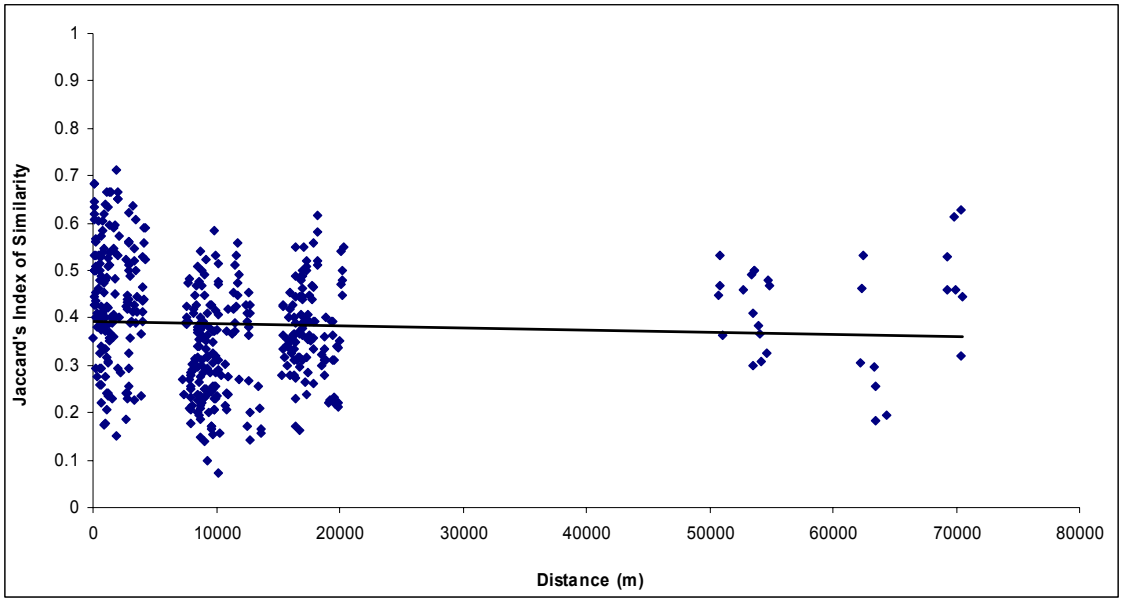
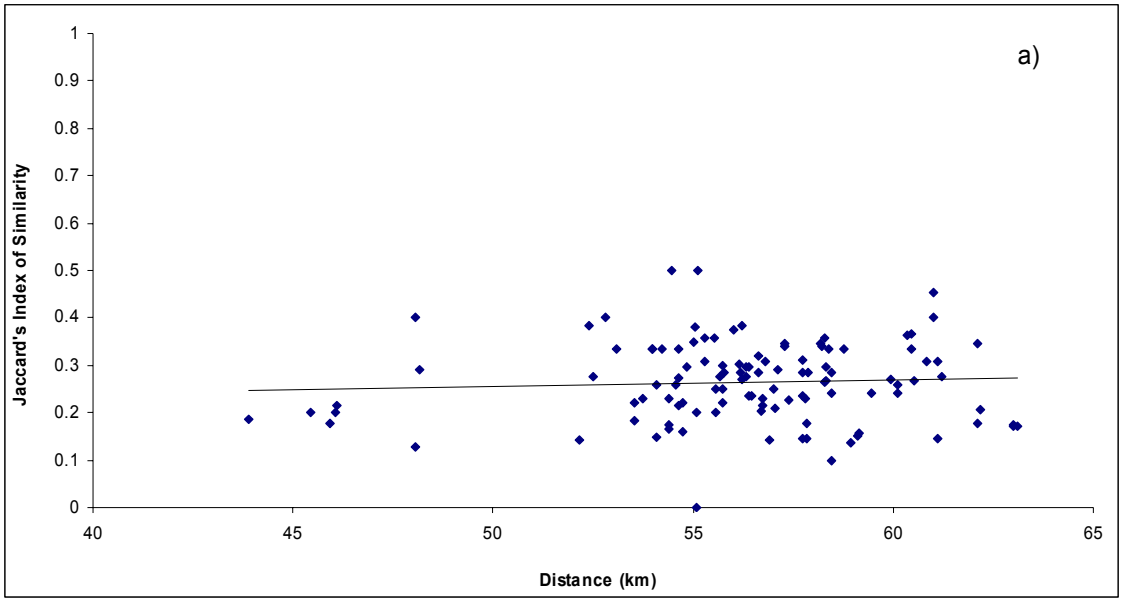


Figure 5.



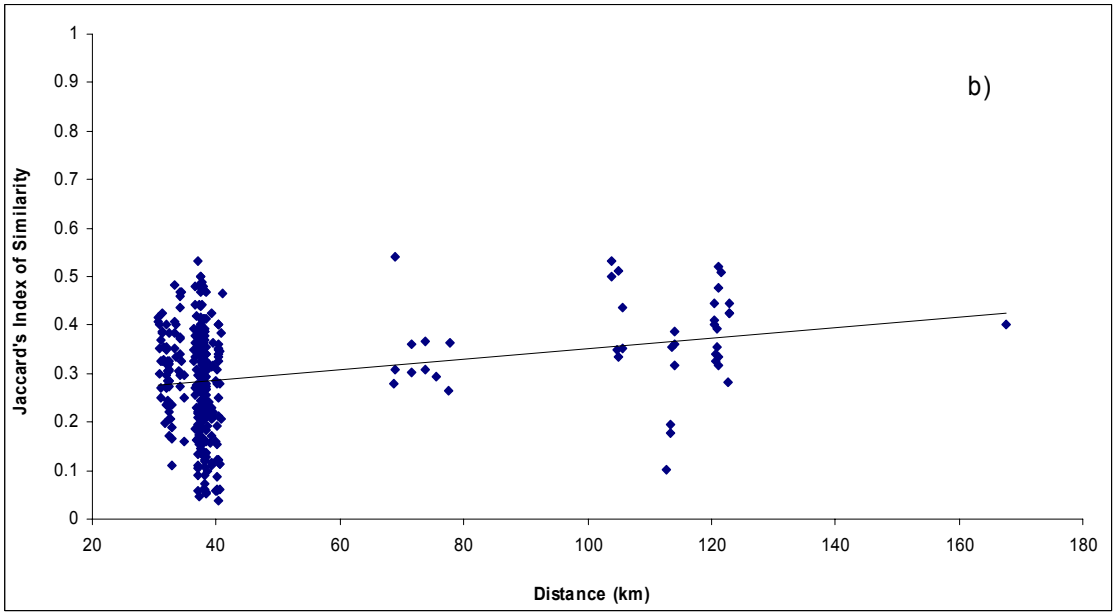


Figure 6.

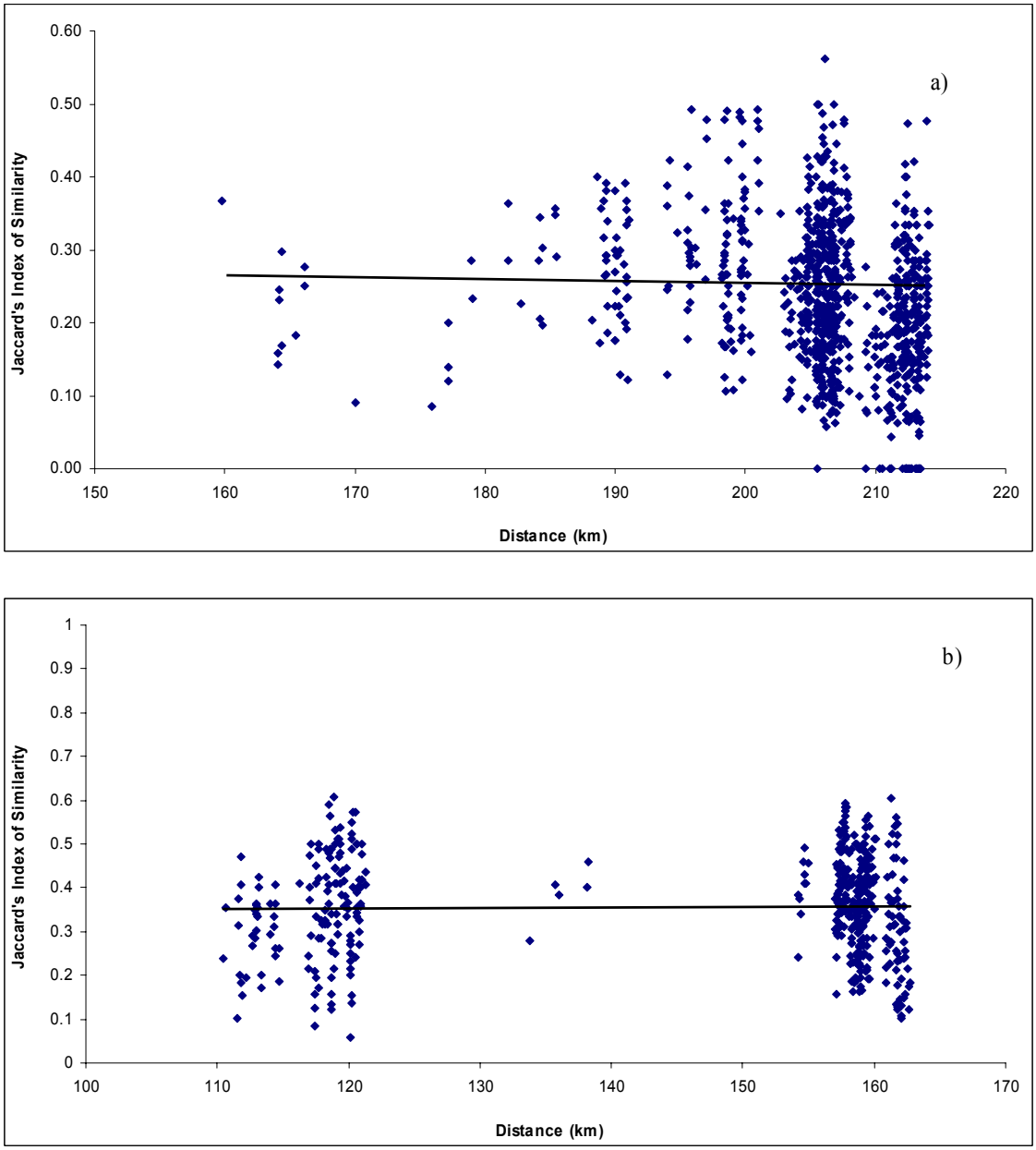
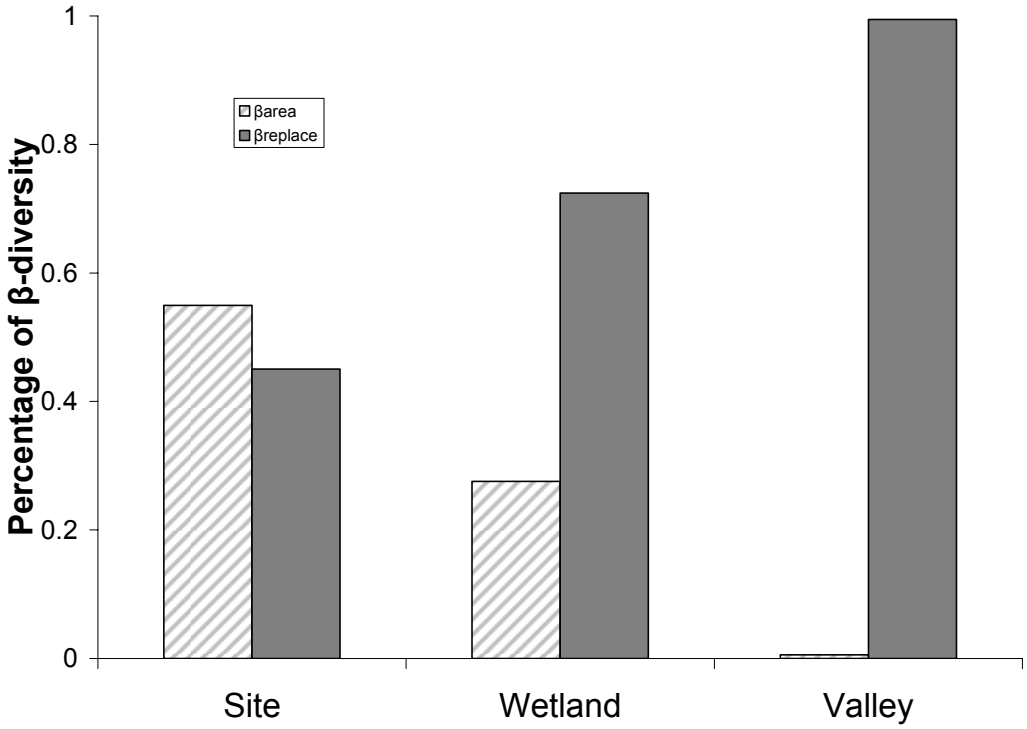


Figure 7.



APPENDIX A:

Lowest taxonomic resolution of macroinvertebrates collected in eleven valleys in the Bonneville Basin.

Grouse Creek	Order	Grouse Creek	Order
Hyalella azteca	Amphipoda	Corynoneura spp.	Diptera
Gammarus lacustris	Amphipoda	Psectrocladius spp.	Diptera
Erpobdellidae	Arhynchobdellida	Thienemannimyia group	Diptera
Mooreobdella fervida	Arhynchobdellida	Empididae	Diptera
Agabus spp.	Coleoptera	Chrysops spp.	Diptera
Tropisternus spp.	Coleoptera	Ceratopogon spp.	Diptera
Agabus o. obliteratus	Coleoptera	Polypedilum spp.	Diptera
Sanfilippodytes spp.	Coleoptera	Dixa spp.	Diptera
Laccophilus spp.	Coleoptera	Sciomyzidae	Diptera
Enochrus spp.	Coleoptera	Syrphidae	Diptera
Cymbiodyta spp.	Coleoptera	Ceratopogonidae	Diptera
Agabus seriatus	Coleoptera	Nilotanypus spp.	Diptera
Hydroporinae	Coleoptera	Radotanypus spp.	Diptera
Haliplus spp.	Coleoptera	Tanytarsus spp.	Diptera
Peltodytes callosus	Coleoptera	Dixidae	Diptera
Agabus tristis	Coleoptera	Caloparyphus spp.	Diptera
Hydroporus spp.	Coleoptera	Callibaetis spp.	Ephemeroptera
Laccophilus maculosus	Coleoptera	Notonecta spp.	Hemiptera
Peltodytes spp.	Coleoptera	Corixidae	Hemiptera
Laccobius spp.	Coleoptera	Gerridae	Hemiptera
Derotanypus spp.	Diptera	Notonecta kirbyi	Hemiptera
Acricotopus spp.	Diptera	Lumbriculidae	Lumbriculida
Culiseta spp.	Diptera	Argia spp.	Odonata
Metriocnemus spp.	Diptera	Amphiagrion abbreviatum	Odonata
Pericoma spp.	Diptera	Coenagrionidae	Odonata
Micropsectra spp.	Diptera	Ischnura spp.	Odonata
Chironomus spp.	Diptera	Libellula spp.	Odonata
Paramerina spp.	Diptera	Aeshna spp.	Odonata
Cricotopus spp.	Diptera	Aeshnidae	Odonata
Paratendipes spp.	Diptera	Anax spp.	Odonata
Chaetocladius spp.	Diptera	Lestes spp.	Odonata
Paraphaenocladius spp.	Diptera	Ostracoda	Ostracoda
Culex spp.	Diptera	Hydrobiidae	Prosobranch
Tabanidae	Diptera	Gastropods	Prosobranch
Alotanypus spp.	Diptera	Helobdella stagnalis	Rhynchobdellida
Pseudochironomus spp.	Diptera	Oxyethira spp.	Trichoptera
Paratanytarsus spp.	Diptera	Limnephilidae	Trichoptera
Limnophora spp.	Diptera	Tubificidae w/o hair chaetae	Tubificida
Limnophyes spp.	Diptera	Tubificidae w/ hair chaetae	Tubificida
Aedes spp.	Diptera	Sphaeriidae	Veneroida
Dixella spp.	Diptera		

Utah Valley	Order	Utah Valley	Order
Arrenurus spp.	Acara	Dasyhelea spp.	Diptera
Hydrozetes spp.	Acara	Psectrocladius spp.	Diptera
Hygrobates spp.	Acara	Limnophyes spp.	Diptera
Tyrrellia spp.	Acara	Corynoneura spp.	Diptera
Hyalella azteca	Amphipoda	Bezzia spp.	Diptera
Gammarus lacustris	Amphipoda	Derotanypus spp.	Diptera
Nephelopsis obscura	Arhynchobdellida	Ceratopogonidae	Diptera
Erpobdellidae	Arhynchobdellida	Euparyphus spp.	Diptera
Haliplus immaculicollis	Coleoptera	Chaetocladius spp.	Diptera
Curculionidae	Coleoptera	Tanytarsus spp.	Diptera
Hydroporinae	Coleoptera	Pseudochironomus spp.	Diptera
Helophorus spp.	Coleoptera	Metriocnemus spp.	Diptera
Enochrus spp.	Coleoptera	Caloparyphus spp.	Diptera
Agabus spp.	Coleoptera	Paratanytarsus spp.	Diptera
Peltodytes spp.	Coleoptera	Eukiefferiella spp.	Diptera
Haliplus spp.	Coleoptera	Phaenopsectra spp.	Diptera
Peltodytes callosus	Coleoptera	Radotanypus spp.	Diptera
Tropisternus spp.	Coleoptera	Brillia spp.	Diptera
Optioservus spp.	Coleoptera	Paramerina spp.	Diptera
Tropisternus columbianus	Coleoptera	Paratendipes spp.	Diptera
Hygrotus sayi	Coleoptera	Anopheles spp.	Diptera
Optioservus castanipennis	Coleoptera	Neoplasta spp.	Diptera
Dytiscus spp.	Coleoptera	Ephydridae	Diptera
Sanfilippodytes spp.	Coleoptera	Odontomyia spp.	Diptera
Ochthebius rectus	Coleoptera	Cladopelma spp.	Diptera
Paracymus spp.	Coleoptera	Prodiamesa spp.	Diptera
Carbabidae	Coleoptera	Stictochironomus spp.	Diptera
Agabus griseipennis	Coleoptera	Tvetenia spp.	Diptera
Agabus o. obliteratus	Coleoptera	Culicidae	Diptera
Agabus seriatus	Coleoptera	Stratiomys spp.	Diptera
Laccophilus mexicanus	Coleoptera	Tabanidae	Diptera
Rhantus binotatus	Coleoptera	Apedilum spp.	Diptera
Optioservus divergens	Coleoptera	Tanypus spp.	Diptera
Heteroceridae	Coleoptera	Dixa spp.	Diptera
Berosus fraternus	Coleoptera	Dixella spp.	Diptera
Enochrus hamiltoni	Coleoptera	Syrphidae	Diptera
Tropisternus lateralis	Coleoptera	Limonia spp.	Diptera
Staphylinidae	Coleoptera	Callibaetis spp.	Ephemeroptera
Sminthuridae	Collembola	Corixidae	Hemiptera
Micropsectra spp.	Diptera	Merragata heboides	Hemiptera
Dicrotendipes spp.	Diptera	Belostoma flumineum	Hemiptera
Cricotopus spp.	Diptera	Sigara alternata	Hemiptera
Pseudosmittia spp.	Diptera	Sigara washingtonensis	Hemiptera
Chironomus spp.	Diptera	Corisella decolor	Hemiptera
Acricotopus spp.	Diptera	Notonecta spp.	Hemiptera

Utah Valley	Order	Utah Valley	Order
Callicorixa audeni	Hemiptera	Nais communis	Tubificida
Notonecta kirbyi	Hemiptera	Naididae	Tubificida
Hesperocorixa laevigata	Hemiptera	Sphaeriidae	Veneroida
Microvelia spp.	Hemiptera		
Cenocorixa wileyae	Hemiptera	**Goshen Valley**	**Order**
Gerridae	Hemiptera	Hydrozetes spp.	Acara
Mesovelia mulsanti	Hemiptera	Limnochares spp.	Acara
Notonecta spinosa	Hemiptera	Eylais spp.	Acara
Notonecta undulata	Hemiptera	Lebertia spp.	Acara
Microvelia cerifera	Hemiptera	Hydrachna spp.	Acara
Caecidotea	Isopoda	Piona spp.	Acara
Lumbriculidae	Lumbriculida	Hyalella azteca	Amphipoda
Enchytraeidae	Lumbriculida	Gammarus lacustris	Amphipoda
Coenagrionidae	Odonata	Erpobdellidae	Arhynchobdellida
Ischnura spp.	Odonata	Haemopis spp.	Arhynchobdellida
Aeshnidae	Odonata	Helophorus spp.	Coleoptera
Aeshna spp.	Odonata	Ochthebius kaszabi	Coleoptera
Amphiagrion abbreviatum	Odonata	Tropisternus spp.	Coleoptera
Erythemis spp.	Odonata	Peltodytes spp.	Coleoptera
Libellulidae	Odonata	Haliplus spp.	Coleoptera
Libellula spp.	Odonata	Haliplus immaculicollis	Coleoptera
Argia spp.	Odonata	Helophorus orientalis	Coleoptera
Coenagrion / Enallagma spp.	Odonata	Microcylloepus pusillus	Coleoptera
Ostracoda	Ostracoda	Enochrus spp.	Coleoptera
Gastropods	Prosobranch	Tropisternus lateralis	Coleoptera
Hydrobiidae	Prosobranch	Laccophilus spp.	Coleoptera
Helobdella stagnalis	Rhynchobdellida	Staphylinidae	Coleoptera
Glossiphonia complanata	Rhynchobdellida	Liodessus obscurellus	Coleoptera
Theromyzon spp.	Rhynchobdellida	Peltodytes callosus	Coleoptera
Oxyethira spp.	Trichoptera	Agabus o. obliteratus	Coleoptera
Psychoglypha spp.	Trichoptera	Hydroporinae	Coleoptera
Limnephilus spp.	Trichoptera	Hydroporus spp.	Coleoptera
Hesperophylax spp.	Trichoptera	Rhantus binotatus	Coleoptera
Hydroptila spp.	Trichoptera	Ochthebius discretus	Coleoptera
Limnephilidae	Trichoptera	Ochthebius rectus	Coleoptera
Lepidostoma spp.	Trichoptera	Ochthebius spp.	Coleoptera
Dugesia spp.	Tricladida	Curculionidae	Coleoptera
Dero spp.	Tubificida	Agabus griseipennis	Coleoptera
Tubificidae w/o hair chaetae	Tubificida	Agabus spp.	Coleoptera
Nais variabilis	Tubificida	Laccophilus maculosus	Coleoptera
Tubificidae w/ hair chaetae	Tubificida	Enochrus carinatus	Coleoptera
Nais simplex	Tubificida	Laccobius spp.	Coleoptera
Quistadrilus multisetosus	Tubificida	Paracymus spp.	Coleoptera
Ophidonais serpentina	Tubificida	Tropisternus columbianus	Coleoptera
Chaetogaster diaphanus	Tubificida	Carbabidae	Coleoptera

Goshen Valley	Order	Goshen Valley	Order
Agabus disintegratus	Coleoptera	Polypedilum spp.	Diptera
Rhantus spp.	Coleoptera	Chrysops spp.	Diptera
Enochrus hamiltoni	Coleoptera	Chaetocladius spp.	Diptera
Agabus tristis	Coleoptera	Tanytarsus spp.	Diptera
Colymbetes incognitus	Coleoptera	Culiseta spp.	Diptera
Hygrotus impressopunctatus	Coleoptera	Pericoma spp.	Diptera
Hygrotus lutescens	Coleoptera	Psychoda spp.	Diptera
Ilybius fraterculus	Coleoptera	Cladopelma spp.	Diptera
Optioservus spp.	Coleoptera	Microtendipes spp.	Diptera
Heteroceridae	Coleoptera	Tribelos spp.	Diptera
Ochthebius aztecus	Coleoptera	Culicidae	Diptera
Ochthebius lineatus	Coleoptera	Culex spp.	Diptera
Berosus spp.	Coleoptera	Sciomyzidae	Diptera
Tropisternus sublaevis	Coleoptera	Tabanidae	Diptera
Sminthuridae	Collembola	Hybomitra spp.	Diptera
Cricotopus spp.	Diptera	Limonia spp.	Diptera
Dicrotendipes spp.	Diptera	Callibaetis spp.	Ephemeroptera
Tanypus spp.	Diptera	Ephemerella spp.	Ephemeroptera
Micropsectra spp.	Diptera	Caenis spp.	Ephemeroptera
Paratanytarsus spp.	Diptera	Corixidae	Hemiptera
Acricotopus spp.	Diptera	Sigara washingtonensis	Hemiptera
Corynoneura spp.	Diptera	Corisella decolor	Hemiptera
Dasyhelea spp.	Diptera	Belostoma flumineum	Hemiptera
Limnophyes spp.	Diptera	Sigara alternata	Hemiptera
Paratendipes spp.	Diptera	Notonecta spp.	Hemiptera
Psectrocladius spp.	Diptera	Gerridae	Hemiptera
Pseudochironomus spp.	Diptera	Hesperocorixa laevigata	Hemiptera
Chironomus spp.	Diptera	Merragata heboides	Hemiptera
Radotanypus spp.	Diptera	Saldidae	Hemiptera
Ceratopogon spp.	Diptera	Gerris gillettei	Hemiptera
Paramerina spp.	Diptera	Notonecta unifasciata	Hemiptera
Pseudosmittia spp.	Diptera	Caecidotea	Isopoda
Ceratopogonidae	Diptera	Enchytraeidae	Lumbriculida
Glyptotendipes spp.	Diptera	Lumbriculidae	Lumbriculida
Dixella spp.	Diptera	Ischnura spp.	Odonata
Anopheles spp.	Diptera	Coenagrionidae	Odonata
Ephydridae	Diptera	Amphiagrion abbreviatum	Odonata
Bezzia spp.	Diptera	Aeshnidae	Odonata
Derotanypus spp.	Diptera	Libellula spp.	Odonata
Metriocnemus spp.	Diptera	Libellulidae	Odonata
Paraphaenocladius spp.	Diptera	Argia spp.	Odonata
Apedilum spp.	Diptera	Lestes spp.	Odonata
Parakiefferiella spp.	Diptera	Aeshna spp.	Odonata
Phaenopsectra spp.	Diptera	Erythemis spp.	Odonata
Dixidae	Diptera	Ostracoda	Ostracoda

Goshen Valley	Order	Curlew Valley	Order
Gastropods	Prosobranch	Limonia spp.	Diptera
Hydrobiidae	Prosobranch	Micropsectra spp.	Diptera
Helobdella stagnalis	Rhynchobdellida	Ephydridae	Diptera
Glossiphonia complanata	Rhynchobdellida	Aedes spp.	Diptera
Glossiphoniidae	Rhynchobdellida	Bezzia spp.	Diptera
Oxyethira spp.	Trichoptera	Cladotanytarsus spp.	Diptera
Lepidostoma spp.	Trichoptera	Derotanypus spp.	Diptera
Hesperophylax spp.	Trichoptera	Glyptotendipes spp.	Diptera
Hydroptila spp.	Trichoptera	Paramerina spp.	Diptera
Limnephilidae	Trichoptera	Paraphaenocladius spp.	Diptera
Dugesia spp.	Tricladida	Dixidae	Diptera
Tubificidae w/o hair chaetae	Tubificida	Tabanidae	Diptera
Tubificidae w/ hair chaetae	Tubificida	Callibaetis spp.	Ephemeroptera
Nais communis	Tubificida	Caenis spp.	Ephemeroptera
Pristina leidyi	Tubificida	Cenocorixa spp.	Hemiptera
Dero spp.	Tubificida	Enchytraeidae	Lumbriculida
Chaetogaster limnaei	Tubificida	Coenagrionidae	Odonata
Chaetogaster diaphanus	Tubificida	Libellulidae	Odonata
Quistadrilus multisetosus	Tubificida	Aeshnidae	Odonata
Sphaeriidae	Veneroida	Amphiagrion abbreviatum	Odonata
		Ostracoda	Ostracoda
Curlew Valley	**Order**	Gastropods	Prosobranch
Hydrozetes spp.	Acara	Hydrobiidae	Prosobranch
Hyalella azteca	Amphipoda	Helobdella stagnalis	Rhynchobdellida
Gammarus lacustris	Amphipoda	Limnephilidae	Trichoptera
Cymbiodyta spp.	Coleoptera	Nais communis	Tubificida
Agabus o. obliteratus	Coleoptera	Tubificidae w/ hair chaetae	Tubificida
Agabus griseipennis	Coleoptera	Nais variabilis	Tubificida
Agabus spp.	Coleoptera	Tubificidae w/o hair chaetae	Tubificida
Enochrus spp.	Coleoptera	Sphaeriidae	Veneroida
Paratanytarsus spp.	Diptera		
Chironomus spp.	Diptera	**Mills Valley**	**Order**
Ceratopogonidae	Diptera	Limnochares spp.	Acara
Acricotopus spp.	Diptera	Arrenurus spp.	Acara
Dasyhelea spp.	Diptera	Hydrozetes spp.	Acara
Pseudochironomus spp.	Diptera	Hygrobates spp.	Acara
Cricotopus spp.	Diptera	Limnesia spp.	Acara
Dicrotendipes spp.	Diptera	Hyalella azteca	Amphipoda
Endochironomus spp.	Diptera	Gammarus lacustris	Amphipoda
Apedilum spp.	Diptera	Erpobdella punctata	Arhynchobdellida
Ablabesmyia spp.	Diptera	Tropisternus spp.	Coleoptera
Ceratopogon spp.	Diptera	Hygrotus lutescens	Coleoptera
Limnophyes spp.	Diptera	Laccobius spp.	Coleoptera
Euparyphus spp.	Diptera	Hygrotus impressopunctatus	Coleoptera
Corynoneura spp.	Diptera	Haliplus spp.	Coleoptera

Mills Valley	Order	Mills Valley	Order
Enochrus spp.	Coleoptera	Dasyhelea spp.	Diptera
Tropisternus columbianus	Coleoptera	Apedilum spp.	Diptera
Ochthebius kaszabi	Coleoptera	Chaetocladius spp.	Diptera
Enochrus diffusus	Coleoptera	Cryptochironomus spp.	Diptera
Scirtidae (Cyphon spp.)	Coleoptera	Tabanidae	Diptera
Curculionidae	Coleoptera	Psectrocladius spp.	Diptera
Liodessus obscurellus	Coleoptera	Radotanypus spp.	Diptera
Ochthebius discretus	Coleoptera	Ephydridae	Diptera
Hygrotus sayi	Coleoptera	Bezzia spp.	Diptera
Microcylloepus pusillus	Coleoptera	Paratendipes spp.	Diptera
Paracymus spp.	Coleoptera	Stratiomyidae	Diptera
Hydroporinae	Coleoptera	Stratiomys spp.	Diptera
Hydroporus spp.	Coleoptera	Corynoneura spp.	Diptera
Haliplus immaculicollis	Coleoptera	Paramerina spp.	Diptera
Peltodytes spp.	Coleoptera	Pseudosmittia spp.	Diptera
Ochthebius rectus	Coleoptera	Thienemanniella spp.	Diptera
Enochrus hamiltoni	Coleoptera	Sciomyzidae	Diptera
Agabus spp.	Coleoptera	Callibaetis spp.	Ephemeroptera
Dubiraphia spp.	Coleoptera	Caenis spp.	Ephemeroptera
Gyrinus bifarius	Coleoptera	Corixidae	Hemiptera
Berosus spp.	Coleoptera	Corisella decolor	Hemiptera
Hydrobius fuscipes	Coleoptera	Notonecta spp.	Hemiptera
Colymbetes sculptilis	Coleoptera	Hesperocorixa laevigata	Hemiptera
Laccophilus spp.	Coleoptera	Notonecta unifasciata	Hemiptera
Gyrinus picipes	Coleoptera	Belostoma flumineum	Hemiptera
Berosus stylifer	Coleoptera	Ambrysus spp.	Hemiptera
Tropisternus lateralis	Coleoptera	Gerridae	Hemiptera
Sminthuridae	Collembola	Trichocorixa verticales	Hemiptera
Tanypus spp.	Diptera	Gerris buenoi	Hemiptera
Cladotanytarsus spp.	Diptera	Cenocorixa spp.	Hemiptera
Chironomus spp.	Diptera	Mesovelia mulsanti	Hemiptera
Cricotopus spp.	Diptera	Ischnura spp.	Odonata
Paratanytarsus spp.	Diptera	Coenagrionidae	Odonata
Dicrotendipes spp.	Diptera	Libellula spp.	Odonata
Derotanypus spp.	Diptera	Amphiagrion abbreviatum	Odonata
Acricotopus spp.	Diptera	Anax spp.	Odonata
Tanytarsus spp.	Diptera	Aeshna spp.	Odonata
Micropsectra spp.	Diptera	Enallagma spp.	Odonata
Glyptotendipes spp.	Diptera	Aeshnidae	Odonata
Parakiefferiella spp.	Diptera	Libellulidae	Odonata
Ceratopogonidae	Diptera	Argia spp.	Odonata
Procladius spp.	Diptera	Erythemis spp.	Odonata
Limnophyes spp.	Diptera	Sympetrum spp.	Odonata
Pseudochironomus spp.	Diptera	Ostracoda	Ostracoda
Polypedilum spp.	Diptera	Gastropods	Prosobranch

Mills Valley	Order	Fish Springs	Order
Hydrobiidae	Prosobranch	Tropisternus sublaevis	Coleoptera
Helobdella stagnalis	Rhynchobdellida	Pseudochironomus spp.	Diptera
Oxyethira spp.	Trichoptera	Tanypus spp.	Diptera
Oecetis spp.	Trichoptera	Paratanytarsus spp.	Diptera
Tubificidae w/o hair chaetae	Tubificida	Chironomus spp.	Diptera
Tubificidae w/ hair chaetae	Tubificida	Dasyhelea spp.	Diptera
Nais variabilis	Tubificida	Ceratopogonidae	Diptera
Nais communis	Tubificida	Cricotopus spp.	Diptera
Chaetogaster limnaei	Tubificida	Tanytarsus spp.	Diptera
Sphaeriidae	Veneroida	Micropsectra spp.	Diptera
Corbiculidae	Veneroida	Cladotanytarsus spp.	Diptera
		Nimbocera spp.	Diptera
Fish Springs	**Order**	Ephydridae	Diptera
Arrenurus spp.	Acara	Corynoneura spp.	Diptera
Hydrozetes spp.	Acara	Acricotopus spp.	Diptera
Limnochares spp.	Acara	Thienemannimyia group	Diptera
Hyalella azteca	Amphipoda	Dicrotendipes spp.	Diptera
Gammarus lacustris	Amphipoda	Paratendipes spp.	Diptera
Erpobdella punctata	Arhynchobdellida	Apedilum spp.	Diptera
Peltodytes callosus	Coleoptera	Limnophyes spp.	Diptera
Laccophilus maculosus	Coleoptera	Radotanypus spp.	Diptera
Peltodytes spp.	Coleoptera	Tabanidae	Diptera
Tropisternus spp.	Coleoptera	Bezzia spp.	Diptera
Hygrotus impressopunctatus	Coleoptera	Ceratopogon spp.	Diptera
Tropisternus columbianus	Coleoptera	Paramerina spp.	Diptera
Hygrotus lutescens	Coleoptera	Pseudosmittia spp.	Diptera
Enochrus carinatus	Coleoptera	Dolichopodidae	Diptera
Enochrus spp.	Coleoptera	Odontomyia spp.	Diptera
Cybister explanatus	Coleoptera	Limonia spp.	Diptera
Agabus griseipennis	Coleoptera	Callibaetis spp.	Ephemeroptera
Curculionidae	Coleoptera	Caenis spp.	Ephemeroptera
Ochthebius aztecus	Coleoptera	Hesperocorixa laevigata	Hemiptera
Enochrus hamiltoni	Coleoptera	Belostoma flumineum	Hemiptera
Laccophilus mexicanus	Coleoptera	Notonecta kirbyi	Hemiptera
Liodessus obscurellus	Coleoptera	Corisella decolor	Hemiptera
Hydrovatus brevipes	Coleoptera	Notonecta unifasciata	Hemiptera
Ilybius fraterculus	Coleoptera	Notonecta spp.	Hemiptera
Haliplus fulvus	Coleoptera	Corixidae	Hemiptera
Ochthebius rectus	Coleoptera	Rhagovelia distincta	Hemiptera
Paracymus spp.	Coleoptera	Sigara washingtonensis	Hemiptera
Carbabidae	Coleoptera	Gerridae	Hemiptera
Rhantus binotatus	Coleoptera	Merragata heboides	Hemiptera
Haliplus spp.	Coleoptera	Mesovelia mulsanti	Hemiptera
Laccobius spp.	Coleoptera	Saldidae	Hemiptera
Tropisternus lateralis	Coleoptera	Microvelia cerifera	Hemiptera

Fish Springs	Order	Tule Valley	Order
Caecidotea	Isopoda	Enochrus spp.	Coleoptera
Coenagrionidae	Odonata	Scirtidae (Cyphon spp.)	Coleoptera
Erythemis spp.	Odonata	Colymbetes incognitus	Coleoptera
Ischnura spp.	Odonata	Ilybius fraterculus	Coleoptera
Libellula spp.	Odonata	Hygrotus impressopunctatus	Coleoptera
Libellulidae	Odonata	Thermonectes intermedius	Coleoptera
Argia spp.	Odonata	Peltodytes spp.	Coleoptera
Aeshna spp.	Odonata	Enochrus diffusus	Coleoptera
Anax spp.	Odonata	Carbabidae	Coleoptera
Aeshnidae	Odonata	Colymbetes sculptilis	Coleoptera
Sympetrum spp.	Odonata	Dytiscus marginicollis	Coleoptera
Coenagrion / Enallagma spp.	Odonata	Hygrotus lutescens	Coleoptera
Amphiagrion abbreviatum	Odonata	Laccophilus maculosus	Coleoptera
Pachydiplax longipennis	Odonata	Rhantus binotatus	Coleoptera
Ostracoda	Ostracoda	Ochthebius rectus	Coleoptera
Gastropods	Prosobranch	Enochrus hamiltoni	Coleoptera
Hydrobiidae	Prosobranch	Pseudochironomus spp.	Diptera
Oxyethira spp.	Trichoptera	Micropsectra spp.	Diptera
Hydropsyche spp.	Trichoptera	Chironomus spp.	Diptera
Oecetis spp.	Trichoptera	Ceratopogonidae	Diptera
Hydroptila spp.	Trichoptera	Acricotopus spp.	Diptera
Nais variabilis	Tubificida	Paramerina spp.	Diptera
Tubificidae w/o hair chaetae	Tubificida	Dasyhelea spp.	Diptera
Nais communis	Tubificida	Thienemannimyia group	Diptera
Tubificidae w/ hair chaetae	Tubificida	Culex spp.	Diptera
		Nimbocera spp.	Diptera
Tule Valley	**Order**	Paratanytarsus spp.	Diptera
Hydrozetes spp.	Acara	Polypedilum spp.	Diptera
Arrenurus spp.	Acara	Tanypus spp.	Diptera
Hydrachna spp.	Acara	Tanytarsus spp.	Diptera
Limnochares spp.	Acara	Paraphaenocladius spp.	Diptera
Hyalella azteca	Amphipoda	Culiseta spp.	Diptera
Gammarus lacustris	Amphipoda	Ephydridae	Diptera
Erpobdellidae	Arhynchobdellida	Bezzia spp.	Diptera
Erpobdella punctata	Arhynchobdellida	Cricotopus spp.	Diptera
Hydrovatus brevipes	Coleoptera	Pericoma spp.	Diptera
Tropisternus columbianus	Coleoptera	Limonia spp.	Diptera
Hydroporinae	Coleoptera	Ceratopogon spp.	Diptera
Curculionidae	Coleoptera	Limnophyes spp.	Diptera
Tropisternus spp.	Coleoptera	Paratendipes spp.	Diptera
Laccophilus spp.	Coleoptera	Dixella spp.	Diptera
Cybister explanatus	Coleoptera	Aedes spp.	Diptera
Laccophilus mexicanus	Coleoptera	Atrichopogon spp.	Diptera
Paracymus spp.	Coleoptera	Corynoneura spp.	Diptera
Hygrotus sayi	Coleoptera	Parakiefferiella spp.	Diptera

Tule Valley	Order	Tule Valley	Order
Ablabesmyia spp.	Diptera	Hydroptilidae	Trichoptera
Apedilum spp.	Diptera	Oxyethira spp.	Trichoptera
Procladius spp.	Diptera	Tubificidae w/o hair chaetae	Tubificida
Psectrocladius spp.	Diptera	Nais variabilis	Tubificida
Psectrotanypus spp.	Diptera	Tubificidae w/ hair chaetae	Tubificida
Pseudosmittia spp.	Diptera	Nais communis	Tubificida
Culicidae	Diptera	Sphaeriidae	Veneroida
Anopheles spp.	Diptera		
Caloparyphus spp.	Diptera	**Skull Valley**	**Order**
Syrphidae	Diptera	Hydrozetes spp.	Acara
Tabanidae	Diptera	Limnochares spp.	Acara
Tipulidae	Diptera	Hyalella azteca	Amphipoda
Callibaetis spp.	Ephemeroptera	Ochthebius rectus	Coleoptera
Notonecta spp.	Hemiptera	Enochrus spp.	Coleoptera
Belostoma flumineum	Hemiptera	Enochrus carinatus	Coleoptera
Corixidae	Hemiptera	Peltodytes spp.	Coleoptera
Hesperocorixa laevigata	Hemiptera	Enochrus hamiltoni	Coleoptera
Notonecta unifasciata	Hemiptera	Dicrotendipes spp.	Diptera
Notonecta undulata	Hemiptera	Cricotopus spp.	Diptera
Corisella decolor	Hemiptera	Tanypus spp.	Diptera
Mesovelia mulsanti	Hemiptera	Chironomus spp.	Diptera
Hydrometra spp.	Hemiptera	Micropsectra spp.	Diptera
Microvelia buenoi	Hemiptera	Dasyhelea spp.	Diptera
Merragata heboides	Hemiptera	Pseudochironomus spp.	Diptera
Buenoa spp.	Hemiptera	Ceratopogonidae	Diptera
Notonecta spinosa	Hemiptera	Cryptochironomus spp.	Diptera
Microvelia cerifera	Hemiptera	Corynoneura spp.	Diptera
Coenagrionidae	Odonata	Procladius spp.	Diptera
Ischnura spp.	Odonata	Tabanidae	Diptera
Argia spp.	Odonata	Callibaetis spp.	Ephemeroptera
Libellulidae	Odonata	Corixidae	Hemiptera
Erythemis spp.	Odonata	Corisella decolor	Hemiptera
Aeshna spp.	Odonata	Ambrysus spp.	Hemiptera
Aeshnidae	Odonata	Merragata heboides	Hemiptera
Anax spp.	Odonata	Coenagrionidae	Odonata
Libellula spp.	Odonata	Libellulidae	Odonata
Sympetrum spp.	Odonata	Libellula spp.	Odonata
Enallagma spp.	Odonata	Hydrobiidae	Prosobranch
Amphiagrion abbreviatum	Odonata	Gastropods	Prosobranch
Ostracoda	Ostracoda	Tubificidae w/o hair chaetae	Tubificida
Hydrobiidae	Prosobranch	Nais communis	Tubificida
Gastropods	Prosobranch	Tubificidae w/ hair chaetae	Tubificida
Helobdella stagnalis	Rhynchobdellida		
Phryganeidae	Trichoptera		
Oecetis spp.	Trichoptera		

Ibapah Valley	Order	Ibapah Valley	Order
Limnochares spp.	Acara	Paratanytarsus spp.	Diptera
Arrenurus spp.	Acara	Radotanypus spp.	Diptera
Hydrozetes spp.	Acara	Culicidae	Diptera
Hyalella azteca	Amphipoda	Trichoclinocera spp.	Diptera
Gammarus lacustris	Amphipoda	Caloparyphus spp.	Diptera
Haemopis spp.	Arhynchobdellida	Tabanidae	Diptera
Liodessus obscurellus	Coleoptera	Callibaetis spp.	Ephemeroptera
Helophorus spp.	Coleoptera	Belostoma flumineum	Hemiptera
Agabus griseipennis	Coleoptera	Corixidae	Hemiptera
Agabus o. obliteratus	Coleoptera	Sigara omani	Hemiptera
Laccobius spp.	Coleoptera	Notonecta spp.	Hemiptera
Tropisternus columbianus	Coleoptera	Corisella decolor	Hemiptera
Tropisternus spp.	Coleoptera	Lumbriculidae	Lumbriculida
Laccophilus mexicanus	Coleoptera	Ischnura spp.	Odonata
Rhantus binotatus	Coleoptera	Amphiagrion abbreviatum	Odonata
Peltodytes callosus	Coleoptera	Argia spp.	Odonata
Peltodytes spp.	Coleoptera	Aeshna spp.	Odonata
Enochrus spp.	Coleoptera	Coenagrionidae	Odonata
Hydrobius fuscipes	Coleoptera	Ostracoda	Ostracoda
Hydroporus spp.	Coleoptera	Gastropods	Prosobranch
Hygrotus lutescens	Coleoptera	Hydrobiidae	Prosobranch
Ilybius fraterculus	Coleoptera	Helobdella stagnalis	Rhynchobdellida
Laccophilus maculosus	Coleoptera	Oxyethira spp.	Trichoptera
Heteroceridae	Coleoptera	Limnephilus spp.	Trichoptera
Enochrus carinatus	Coleoptera	Dero spp.	Tubificida
Paracymus spp.	Coleoptera	Tubificidae w/o hair chaetae	Tubificida
Sminthuridae	Collembola	Sphaeriidae	Veneroida
Cricotopus spp.	Diptera		
Micropsectra spp.	Diptera	**Rush Valley**	**Order**
Limnophyes spp.	Diptera	Hydryphantes spp.	Acara
Pseudochironomus spp.	Diptera	Arrenurus spp.	Acara
Acricotopus spp.	Diptera	Thyopsis spp.	Acara
Tanypus spp.	Diptera	Gammarus lacustris	Amphipoda
Anopheles spp.	Diptera	Hyalella azteca	Amphipoda
Pseudosmittia spp.	Diptera	Haemopis spp.	Arhynchobdellida
Corynoneura spp.	Diptera	Erpobdellidae	Arhynchobdellida
Dasyhelea spp.	Diptera	Erpobdella punctata	Arhynchobdellida
Derotanypus spp.	Diptera	Helophorus spp.	Coleoptera
Paramerina spp.	Diptera	Agabus spp.	Coleoptera
Apedilum spp.	Diptera	Hydroporus spp.	Coleoptera
Chironomus spp.	Diptera	Staphylinidae	Coleoptera
Ceratopogonidae	Diptera	Curculionidae	Coleoptera
Bezzia spp.	Diptera	Agabus o. obliteratus	Coleoptera
Ceratopogon spp.	Diptera	Ochthebius rectus	Coleoptera
Chaetocladius spp.	Diptera	Hydrobius fuscipes	Coleoptera

Rush Valley	Order	Rush Valley	Order
Tropisternus columbianus	Coleoptera	Sphaeriidae	Veneroida
Chaetocladius spp.	Diptera		
Acricotopus spp.	Diptera	**Snake Valley**	**Order**
Apedilum spp.	Diptera	Limnochares spp.	Acara
Micropsectra spp.	Diptera	Hydrozetes spp.	Acara
Paratendipes spp.	Diptera	Arrenurus spp.	Acara
Metriocnemus spp.	Diptera	Eylais spp.	Acara
Caloparyphus spp.	Diptera	Thyas spp.	Acara
Diamesa spp.	Diptera	Limnesia spp.	Acara
Rheocricotopus spp.	Diptera	Gammarus lacustris	Amphipoda
Dasyhelea spp.	Diptera	Hyalella azteca	Amphipoda
Thienemannimyia group	Diptera	Erpobdellidae	Arhynchobdellida
Culiseta spp.	Diptera	Erpobdella punctata	Arhynchobdellida
Paratanytarsus spp.	Diptera	Mooreobdella fervida	Arhynchobdellida
Tabanidae	Diptera	Haemopis spp.	Arhynchobdellida
Ceratopogon spp.	Diptera	Ochthebius rectus	Coleoptera
Orthocladius spp.	Diptera	Agabus griseipennis	Coleoptera
Paraphaenocladius spp.	Diptera	Scirtidae (Cyphon spp.)	Coleoptera
Dolichopodidae	Diptera	Stictotarsus griseostriatus	Coleoptera
Ceratopogonidae	Diptera	Tropisternus spp.	Coleoptera
Corynoneura spp.	Diptera	Hydroporus spp.	Coleoptera
Heleniella spp.	Diptera	Enochrus spp.	Coleoptera
Odontomesa spp.	Diptera	Laccophilus spp.	Coleoptera
Parametriocnemus spp.	Diptera	Peltodytes spp.	Coleoptera
Radotanypus spp.	Diptera	Hygrotus lutescens	Coleoptera
Dicrotendipes spp.	Diptera	Hydroporinae	Coleoptera
Polypedilum spp.	Diptera	Liodessus obscurellus	Coleoptera
Pseudochironomus spp.	Diptera	Paracymus spp.	Coleoptera
Pseudosmittia spp.	Diptera	Laccobius spp.	Coleoptera
Culicidae	Diptera	Agabus spp.	Coleoptera
Aedes spp.	Diptera	Agabus o. obliteratus	Coleoptera
Nemotelus spp.	Diptera	Dytiscus spp.	Coleoptera
Hesperocorixa laevigata	Hemiptera	Colymbetes incognitus	Coleoptera
Cenocorixa spp.	Hemiptera	Laccophilus mexicanus	Coleoptera
Lumbricidae	Lumbriculida	Enochrus hamiltoni	Coleoptera
Coenagrionidae	Odonata	Helophorus spp.	Coleoptera
Amphiagrion abbreviatum	Odonata	Tropisternus columbianus	Coleoptera
Ostracoda	Ostracoda	Staphylinidae	Coleoptera
Gastropods	Prosobranch	Colymbetes sculptilis	Coleoptera
Hydrobiidae	Prosobranch	Tropisternus sublaevis	Coleoptera
Limnephilus spp.	Trichoptera	Hygrotus impressopunctatus	Coleoptera
Dugesia spp.	Tricladida	Hydrobius fuscipes	Coleoptera
Tubificidae w/o hair chaetae	Tubificida	Gyrinus picipes	Coleoptera
Tubificidae w/ hair chaetae	Tubificida	Chrysomelidae	Coleoptera
Nais communis	Tubificida	Cybister explanatus	Coleoptera

Snake Valley	Order	Snake Valley	Order
Microcylloepus pusillus	Coleoptera	Pericoma spp.	Diptera
Anacaena spp.	Coleoptera	Rheotanytarsus spp.	Diptera
Enochrus carinatus	Coleoptera	Ceratopogon spp.	Diptera
Carbabidae	Coleoptera	Culex spp.	Diptera
Curculionidae	Coleoptera	Paratendipes spp.	Diptera
Hygrotus infuscatus	Coleoptera	Pseudosmittia spp.	Diptera
Ilybius fraterculus	Coleoptera	Procladius spp.	Diptera
Rhantus binotatus	Coleoptera	Simulium vittatum complex	Diptera
Cymbiodyta spp.	Coleoptera	Stempellinella spp.	Diptera
Enochrus californicus	Coleoptera	Bezzia spp.	Diptera
Enochrus diffusus	Coleoptera	Dicrotendipes spp.	Diptera
Agabus disintegratus	Coleoptera	Chaetocladius spp.	Diptera
Dytiscus marginicollis	Coleoptera	Eukiefferiella spp.	Diptera
Laccophilus maculosus	Coleoptera	Radotanypus spp.	Diptera
Peltodytes callosus	Coleoptera	Culicidae	Diptera
Cercyon spp.	Coleoptera	Dixella spp.	Diptera
Hygrotus sayi	Coleoptera	Ephydridae	Diptera
Ochthebius spp.	Coleoptera	Tabanidae	Diptera
Lampyridae	Coleoptera	Cladotanytarsus spp.	Diptera
Agabus confinis group	Coleoptera	Thienemanniella spp.	Diptera
Colymbetinae	Coleoptera	Aedes spp.	Diptera
Helophorus oblongus	Coleoptera	Parakiefferiella spp.	Diptera
Helophorus orientalis	Coleoptera	Psectrotanypus spp.	Diptera
Berosus fraternus	Coleoptera	Anopheles spp.	Diptera
Berosus spp.	Coleoptera	Odontomyia spp.	Diptera
Crenitis spp.	Coleoptera	Stratiomys spp.	Diptera
Paracymus confusus	Coleoptera	Ablabesmyia spp.	Diptera
Micropsectra spp.	Diptera	Cryptochironomus spp.	Diptera
Cricotopus spp.	Diptera	Metriocnemus spp.	Diptera
Pseudochironomus spp.	Diptera	Microtendipes spp.	Diptera
Chironomus spp.	Diptera	Pentaneura spp.	Diptera
Tanypus spp.	Diptera	Paraphaenocladius spp.	Diptera
Derotanypus spp.	Diptera	Hemerodromia spp.	Diptera
Acricotopus spp.	Diptera	Trichoclinocera spp.	Diptera
Tanytarsus spp.	Diptera	Sciomyzidae	Diptera
Paratanytarsus spp.	Diptera	Nemotelus spp.	Diptera
Corynoneura spp.	Diptera	Glyptotendipes spp.	Diptera
Psectrocladius spp.	Diptera	Lauterborniella spp.	Diptera
Dasyhelea spp.	Diptera	Natarsia spp.	Diptera
Ceratopogonidae	Diptera	Orthocladius spp.	Diptera
Thienemannimyia group	Diptera	Dixidae	Diptera
Limnophyes spp.	Diptera	Caloparyphus spp.	Diptera
Paramerina spp.	Diptera	Euparyphus spp.	Diptera
Apedilum spp.	Diptera	Chrysops spp.	Diptera
Polypedilum spp.	Diptera	Tipulidae	Diptera

Snake Valley	Order	Snake Valley	Order
Limonia spp.	Diptera	Helobdella stagnalis	Rhynchobdellida
Callibaetis spp.	Ephemeroptera	Limnephilus spp.	Trichoptera
Tricorythodes spp.	Ephemeroptera	Cheumatopsyche spp.	Trichoptera
Fallceon quilleri	Ephemeroptera	Phryganeidae	Trichoptera
Caenis spp.	Ephemeroptera	Oxyethira spp.	Trichoptera
Corixidae	Hemiptera	Hydroptila spp.	Trichoptera
Corisella decolor	Hemiptera	Triaenodes spp.	Trichoptera
Notonecta spp.	Hemiptera	Dugesia spp.	Tricladida
Callicorixa audeni	Hemiptera	Tubificidae w/o hair chaetae	Tubificida
Belostoma flumineum	Hemiptera	Nais variabilis	Tubificida
Hesperocorixa laevigata	Hemiptera	Tubificidae w/ hair chaetae	Tubificida
Notonecta unifasciata	Hemiptera	Nais simplex	Tubificida
Gerris gillettei	Hemiptera	Nais communis	Tubificida
Gerridae	Hemiptera	Dero spp.	Tubificida
Mesovelia mulsanti	Hemiptera	Chaetogaster diastrophus	Tubificida
Notonecta spinosa	Hemiptera	Nais spp.	Tubificida
Cenocorixa spp.	Hemiptera	Chaetogaster diaphanus	Tubificida
Gerris incognitus	Hemiptera	Naididae	Tubificida
Notonecta kirbyi	Hemiptera	Sphaeriidae	Veneroida
Microvelia cerifera	Hemiptera		
Gerris incurvatus	Hemiptera		
Ambrysus spp.	Hemiptera		
Microvelia buenoi	Hemiptera		
Hydra spp.	Hydroida		
Caecidotea	Isopoda		
Lumbriculidae	Lumbriculida		
Coenagrionidae	Odonata		
Ischnura spp.	Odonata		
Lestes spp.	Odonata		
Argia spp.	Odonata		
Libellula spp.	Odonata		
Amphiagrion abbreviatum	Odonata		
Libellulidae	Odonata		
Aeshna spp.	Odonata		
Aeshnidae	Odonata		
Erythemis spp.	Odonata		
Hetaerina spp.	Odonata		
Enallagma spp.	Odonata		
Sympetrum spp.	Odonata		
Coenagrion / Enallagma spp.	Odonata		
Anax spp.	Odonata		
Gomphidae	Odonata		
Ostracoda	Ostracoda		
Gastropods	Prosobranch		
Hydrobiidae	Prosobranch		

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CHAPTER THREE -
FACTORS AFFECTING THE COMMUNITY COMPOSITION OF METAPHYTON IN DESERT SPRINGS OF THE BONNEVILLE BASIN, UTAH, USA: A MULTISCALE ANALYSIS

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ABSTRACT

We examined patterns of metaphyton taxonomic composition from 150 sites in springs of the Bonneville Basin, Utah across three spatial scales: valleys, wetlands nested in valleys, and habitat types nested in wetlands (springs, channels, and marshes). Our objective was to determine which spatial scale(s) accounted for the greatest variation in metaphyton community composition. We expected local processes at the habitat scale, especially physico-chemical heterogeneity, to account for the majority of variation in local community composition. To our surprise, we found that the valley scale accounted for 6.3x more variation in metaphyton community composition than the habitat scale and that community composition did not differ between wetlands in the same valley. Also, the community composition of isolated springs differed from the community composition of springs in large complexes. We discuss the potential importance of large scale processes that operate at the valley scale, such as historical events (i.e. the draining of ancient Lake Bonneville) and island effects (dispersal limitations). We suggest that dispersal limitations have an important effect on metaphyton community composition despite the world-wide distribution of many freshwater algal taxa. Also, bioassessment based on metaphyton in spring ecosystems of the Bonneville Basin should compare potentially disturbed test sites to minimally impacted reference sites in the same valley to minimize variation. Although outward appearances suggested that metaphyton might have a simple community composition, we found 242 taxa with an average Bray-Curtis similarity between sites of only 14.1 %. It is important to protect all habitat types in multiple wetlands in each valley to preserve this rich diversity in these unique ecosystems.

Keywords: algal biodiversity, metaphyton community composition, desert springs, multiscale analysis

INTRODUCTION

Desert springs around the world are centers of biological diversity embedded in a dry terrestrial landscape (e.g. Curtis et al. 1998, Fensham 2003). Spring ecosystems on all major continents are the focus of intense conservation because they are threatened by a variety of anthropogenic stressors (e.g. Ashley et al. 2002, Fensham and Price 2004). Our ability to preserve these ecosystems depends in part, on our understanding of their unique biological properties. We examined patterns of taxonomic composition in springs of the Bonneville Basin across multiple spatial scales for one of the most diverse groups of organisms in aquatic ecosystems, algae.

The Bonneville Basin is the eastern-most endorheic drainage in the Great Basin Geological Province. It is distinguished by parallel north-south mountain ranges separated by broad, alluviated valleys (Christiansen 1951) where rates of evaporation (60 cm/year to 106.7 cm/year) are three to five times greater than rates of precipitation (14.8 cm/year to 28.7 cm/year; Desert Research Institute, Western Regional Climate Center, www.wrcc.dri.edu). Wetlands that range in size from small individual springs (< 1.0 m^2) to large spring complexes (> 100 km^2) are scattered along the base of the mountains and throughout the valley floors. These artesian springs are characterized by stable water levels attributed to constant groundwater inflows. Several springs in large complexes are often connected by flowing channels and shallow marshes. These three habitat types (springs, channels, and marshes) have very different physico-chemical characteristics known to effect community composition in freshwater ecosystems (e.g. Keleher and Rader, in review, Wetzel 2001).

Distinct algal associations can be identified (e.g. epilithon, epipelon, epiphytic)

based on the type of substrate to which they are best adapted (Round 1981). Metaphyton consists of macroscopic stalks that float up from the bottom during the spring to form partially suspended masses of filamentous green algae and associated microscopic epiphyton (e.g. Goldsborough and Robinson 1996, Stevenson et al. 1996). Wetlands around the world with a stable water column are characterized by metaphyton, which undoubtedly plays a critical role in these ecosystems (e.g. rates of nutrient cycling) because of its large biomass (e.g. Goldsborough and Robinson 1996, Borchardt 1996). Spring wellheads, channels, and marshes in the Bonneville Basin can be choked with metaphyton throughout the growing season (April – October). Thus, we decided to study metaphyton in these artesian springs because it is the most conspicuous type of algae.

Local community composition is determined by multiple processes operating at different scales (e.g. Wiens 1989, Cooper et al. 1998). For example, physico-chemical conditions (e.g. water chemistry) and biotic interactions (grazing) can exclude species at local scales, whereas historical events and dispersal limitations can restrict local community composition at large scales (MacArthur and Wilson 1967, Rosenzweig 1995, Connelly and Roughgarden 1999). We can infer the processes important in determining membership in a local community by sampling numerous sites of the same community type (e.g. artesian desert springs) across multiple spatial scales and determining the scale(s) that account for the greatest variation in local community composition (sensu Li et al. 2001, Heino et al. 2004). For example, we can infer the importance of processes operating at the valley scale if community composition differs between valleys but not between local sites within valleys.

Freshwater algae are commonly thought to possess exceptional powers of

dispersal because of the cosmopolitan distribution of taxa within temperate, tropical, and polar zones (e.g. Round 1981). Wind-driven, resistant spores and algal fragments may be distributed over long distances (e.g. Schlichting 1969, Brown et al. 1976). Except for the drift of benthic algae in streams (Stevenson and Peterson 1989, 1991), dispersal is rarely studied and algologists tend to emphasize the importance of local factors in determining freshwater algal community composition. Consequently, we expected local processes, especially physico-chemical heterogeneity between habitats (springs, channels, and marshes), to be most important in determining local community composition. However, our multiscale design also allowed us to infer the potential importance of large scale processes, such as historical events (i.e. the draining of ancient Lake Bonneville) and dispersal limitations.

No studies have examined the processes that effect wetland algal communities across multiple spatial scales. Although studies have examined the community composition of diatoms in multiple springs of the Great Basin (Grimes et al, 1980, Kaczmarska and Rushforth 1984), the community composition of metaphyton in spring wetlands of the Bonneville Basin has also never been explored. Our study will help fill this void and lay the foundation for future research. We described the community composition of metaphyton across three scales: valleys nested in the Bonneville Basin, wetlands nested in valleys, and habitat types nested in wetlands (springs, channels, and marshes). Our objective was to determine the spatial scale(s) that account for the greatest variation in metaphyton community composition.

Specifically, we tested two hypotheses. First, metaphyton community composition would show little variation among sites in the Bonneville Basin except for

the effects of habitat heterogeneity. That is, community composition would differ between habitat types (springs, channels, marshes) more than between wetlands within valleys, or between valleys in the Bonneville Basin. Also, macroscopic appearances suggest that metaphyton is a comparatively simple algal association based on a few species of filamentous green algae. Second, metaphyton community composition would not differ between isolated springs and large spring complexes. Island effects attributed to isolation (dispersal limitations) would not affect local community composition because algae have exceptional powers of dispersal.

METHODS

Study Area and Site Selection

The Bonneville Basin includes the area that was once covered by Lake Bonneville during the Pleistocene. Nearly 16,000 years ago Lake Bonneville reached its maximum level of 1,626 m a.s.l., covered approximately 51,720 km^2 and had depths up to 370 m (Figure 1; Currey et al. 1984, Benson et al. 1990). About 14,500 years ago the waters of Lake Bonneville cut through the lowest point along it shore (Red Rock Pass) and drained to an elevation of about 1,319 m a.s.l. in less than one year. For the next 4,000 years, Lake Bonneville experienced climatically induced declines resulting in only a few modern lakes (e.g. Great Salt Lake, Sevier Lake) and the exposing of the artesian springs of this study (Currey et al. 1984, Oviatt, C.G 1988, Benson et al. 1990, Grayson 1993).

Sites were the smallest scale in our spatial hierarchy. They consisted of one of the three habitat types (spring basins, channels, and marshes) nested within either an

isolated wetland or a wetland complex. Wetlands were nested in valleys, and valleys in the Bonneville Basin. We defined the Bonneville Basin as the regional scale.

Habitats in spring ecosystems of the Bonneville Basin feature two classic contrasts known to effect community composition in freshwater environments: 1) lentic versus lotic and 2) constant versus variable environmental conditions (e.g. Ward 1992). In particular, springs and marshes are lentic habitats, whereas channels contain running water and rheophilic taxa (Myers and Resh 1999). Also, spring wells are one of the most constant aquatic habitats on Earth, while marshes are one of the most variable (Mitsch and Gosselink 2000). Water levels in springs are stable and independent of short term precipitation patterns, and water chemistry shows only slight daily, seasonal, and interannual variability (Deacon and Minckley 1974, Hovingh 1993, Anderson et al. 2005). In contrast, the chemical conditions of marshes (e.g. oxygen, pH and nutrients) fluctuate on a daily and seasonal basis as photosynthesis and total community respiration respond to changes in solar irradiation (Wetzel 2001, Rader and Richardson 1992). Also, water levels in marshes fluctuate seasonally because of variation in rates of evaporation and precipitation. Thus, we expected pronounced differences in community composition between each of the three habitats.

Isolated wetlands had a single spring and were rarely associated with channels or marshes, whereas wetland complexes contained multiple springs connected by channels and marshes. Isolated springs were separated by 10s of kilometers to 100s of kilometers of desert to the nearest aquatic habitat, whereas springs in complexes were separated by 10s of meters to 100s of meters. Springs consisted of a groundwater inflow (wellhead), slow flowing lentic conditions, and a narrow band of riparian vegetation surrounding the

basin (Figure 2). We used aerial photographs, resource managers, and personal experience to locate spring wetlands within each valley. Physico-chemical data and metaphyton were sampled at all sites beginning the last week of May and continued through August in both 2001 and 2002.

Eleven valleys contained artesian springs below the shoreline of ancient Lake Bonneville (Fig. 1). Selecting habitat types (sites) in isolated wetlands was simple as most consisted of a single spring. However, we used a randomized sampling design to select sites in large complexes. Aerial photographs of each complex were examined prior to sampling to identify two transects that spanned the maximum length and width. Both transects were divided into 100 m segments. We randomly selected multiple segments and searched a 50 m radius for potential habitats to sample. This procedure was repeated until we had sampled 3 to 5 of the three habitat types if all three were present. A maximum length of 30 m was sampled in channels and a 30 m x 30 m area was selected for collecting samples in marshes.

Physico-chemical Data

We recorded the location (UTMs), elevation, maximum water depth, and general substrate type (organic, clay, silt, sand, and gravel) at each site. We estimated the maximum surface area (maximum length * maximum width) at each spring and measured the maximum width of each channel. We also recorded water temperature, salinity, dissolved oxygen (YSI Model 85 water quality meter), and pH (Hanna pH meter) at the source in all springs.

We only compared the chemical attributes of springs because physico-chemical

composition of groundwater inflows is very constant (e.g. Todd and Mays 2005). In contrast, water temperature, dissolved oxygen, and pH fluctuate over 24 hrs in shallow stagnant habitats (e.g. marshes) as photosynthesis and total community respiration respond to diel fluctuations in solar irradiation (e.g. Wetzel 2001). Thus, measurements of most physico-chemical attributes taken at different times of the day in marshes have no comparative value.

Marshes were generally located several meters from the spring source and were more influenced by external conditions. To verify this assumption, we placed thermographs (*StowAway*, Onset Corporation) at the spring outflow (2 m deep), in the marsh (25 cm deep), and in the channel (25 cm deep) at the Fish Springs complex to determine differences in temperature variation in each habitat. Mean temperature was recorded every three hours for one year at each location.

Metaphyton

Three metaphyton samples were taken from different locations but from a similar shallow depth (<10 cm deep) at each site, combined into a single composite, preserved in 3 % formalin, and returned to the laboratory for identification and enumeration. A sample consisted of extracting a similar amount of algae trapped between the thumb and forth finger. To minimize bias, the same technician collected all metaphyton samples at each site. All taxa were identified to the lowest feasible taxonomic level. Identification and enumeration was made with an inverted phase contrast microscope of subsamples consisting of 10 ml aliquots (Utermohl 1958). Samples were homogenized in a blender for 30 s before subsamples were exacted with a wide-bore pipette (Wetzel and Likens,

1991). Larger taxa were first enumerated at a magnification of 125x, whereas smaller algae were counted at 500x and 1250x using a standard strip count technique (APHA, 1989). A fixed number of 500 units were counted in each sample, where a unit was defined as a single cell, colony, or filament of intact cells containing protoplasm. Diatoms were identified separately after clearing in 30 % hydrogen peroxide and mounted in Hyrax Mounting Medium (Lowe and LaLiberte 1996).

Twenty-five cells per species were used to determine average cell dimension (ACD) using an ocular micrometer. We used ACD to estimate the biovolume of all taxa based on the geometric shape that best approximated the cell shape of each species (Wetzel and Likens 1991, Hillibrand et. al. 1999). The biovolume of each taxa in a sample was determined by multiplying the number of units by the biovolume of a single unit (e.g. individual cell). Biovolume is the most accurate estimate of algal biomass (Wetzel and Likens 1991).

Statistical Analyses

We used non-metric multidimensional scaling (NMDS) to test both hypotheses. We used NMDS to plot differences in species composition between sites using three spatial models: 1) habitat types (springs, channels and marshes), 2) wetlands, and 3) valleys. Thus, each site was assigned to a habitat type, then a wetland, and finally a valley in one of the three separate analyses. We also used NMDS to plot differences in community composition between isolated springs and spring habitats in complexes to test the second hypothesis.

NMDS provides a visual representation of how well a model accounts for

variation in taxonomic composition between sites. The best model will cluster sites into distinct groups based on taxonomic similarity. NMDS ordinations were run using abundance data with a Log e (x + 1) transformation and was obtained using Primer v6 (Primer-E Users Manual, Clarke and Warwick 2001; Clarke and Gorley 2006) and the Bray-Curtis index (same as Sørensen's index) of community similarity (McCune and Mefford 1999). Bray-Curtis similarity (*BC*) is:

$$BC = 1 - \frac{\sum_{i=1}^{n} \left| X_{ij} - X_{ik} \right|}{\sum_{i=1}^{n} \left(X_{ij} + X_{ik} \right)}, \text{ where}$$

X_{ij} = the number of individuals in species i in sample j, X_{ik} = the number of individuals in species i in sample k, and n = the number of species. This index ranges from 0 (no taxa in common) to 1, where both sites share the same taxa in the same rank order of abundance. The Bray-Curtis index gives less weight to outliers and is the recommended distance measure for NMDS (McCune and Mefford 1999, Southwood and Henderson 2000). We also used an analysis of species contributions (SIMPER, Primer E) to determine which taxa accounted for the greatest percentage of similarity in community composition between the classes of each model (Clarke and Warwick 2001). Although ordinations show the similarity in community composition among sites, it cannot test hypotheses.

We used an analysis of similarities permutation procedure (ANOSIM) to test for differences in community composition between the classes of each model. That is, between habitat types in Model 1, different wetlands in Model 2, between valleys in the Bonneville Basin in Model 3, and between isolated springs and springs in complexes.

ANOSIM is a non-parametric, distance-based procedure that measures the extent to which communities in the classes of a model overlap based on the observed compared to the permutated average within-group distance among sites (Biondini et al. 1991; Mielke and Berry 2001). The output is an R statistic which ranges from -1 to 1. Values significantly different from 0 indicate differences in community composition greater than expected by chance ($P < 0.05$). Comparisons with the largest R value show the greatest difference in community composition (Clarke and Warwick 2001). Comparisons of community composition were based on the Bray-Curtis coefficient of similarity (McCune and Grace 2002), which was used to create a pair-wise matrix between each pair of sites (Bray and Curtis 1957). This matrix was also used to calculate the classification strength of each model.

Classification strength can compare how well each model accounted for variation in metaphyton community structure (Van Sickle 1997, Van Sickle and Hughes 2000). Classification strength (CS) is the average similarity of sites *within* each class j (W_j) of a model minus the average similarity of sites *between* all classes in a model ($\overline{B}$) or $CS = \overline{W} - \overline{B}$, with:

$$\overline{W} = \sum \frac{n_j}{N} W_j \text{ where,}$$

n_j = the number of samples in class j and N = the total number of classes in the model. Both within- and between-class similarity range from 0 to 1, with 0 indicating that none of the sites within or between classes have any taxa in common and 1 indicating that all sites within or between classes share the same species. In an ideal model $\overline{B}$ would

approach 0 and W_j would approach 1. Models with CS = 0 do not account for variation in the data and all classes have the same community composition, whereas CS = 1 indicates that each class has a unique community composition (Van Sickle 1997).

Classification strength cannot be compared between models consisting of a different number of classes. We judged the performance of each model by comparing their CS values to the CS value of a reference model created from the species lists for each site, which was the maximum CS attainable for a particular model. We used Bray-Curtis similarities and the flexible UPGMA agglomerative, hierarchical clustering to create a dendrogram that was used to locate invertebrate classes that showed the maximum within-class and minimum between-class similarity for each model. We determined the relative classification strength of each model by dividing its CS value by the CS value of the reference model with the same number of classes (Van Sickle and Hughes 2000, Pyne et al. 2007). For example, we created a reference model with 3 classes (springs, channels, and marshes) to compare to the Habitat model. Models with a relative classification strength of 100 % would perfectly correspond with the reference model and would account for 100 % of the variation in community composition. Relative CS provides a standardized percentage which can be compared across models with different numbers of classes.

RESULTS

Physico-chemical Attributes

One hundred and fifty sites were sampled within the Bonneville Basin: 71 springs, 33 channels, and 47 marshes. Most of the sites (89 %) were within wetland

complexes, while only 11 % were from isolated wetlands. Eighty-five percent of the sites had primary substrate types consisting of silt and/or organic material, whereas the remainder consisted of clay or sand. Channels ranged in width from 0.5 m in Rush Valley to 17.5 m in Fish Springs, but were typically narrow (4.0 m wide) and shallow (34 cm deep) with steep sides. Marshes throughout the basin were typically shallow with a mean depth of 28 cm.

Physico-chemical attributes at the spring well showed considerable variation between sites. Elevations ranged from 1294 m a.s.l. to 1778 m a.s.l. with an average of 1450 m a.s.l. across the entire basin (Table 1). Water temperatures varied from 9.0 C in Rush Valley, which had the highest elevations, to 32.0 C in Fish Springs, which were fed by thermal groundwater inflows (Table 1). The largest spring complexes in the Bonneville Basin occurred in Snake Valley, Tule Valley, and Fish Springs. Maximum water depth was occasionally greater than 2.5 m, but averaged only 0.84 m (Table 1). Average salinity ranged from < 0.001 ppt to 2.1 ppt with an overall mean of 0.9 ppt (Table 1). pH varied from 6.7 (Utah Valley) to 9.1 (Snake Valley), whereas dissolved oxygen concentrations (DO) ranged from 0.3 mg/l in Snake Valley to 14.0 mg/l in Grouse Creek. Springs in Curlew and Mills Valley had the highest mean concentration of DO (11.0 mg/l and 7.7 mg/l), whereas springs in Tule Valley had the lowest (1.4 mg/l).

As expected, environmental variation was much greater in marshes versus springs. In particular, water temperature variation was much more constant at the spring inflow and increased with distance from the spring source through the channel and into the marsh (Fig. 3). The annual range and annual coefficient of variation was greater in

marshes (31.5 C; 50.8%) than in channels (13.7 C; 15.0 %) or at the spring outflow (7.7 C; 12.5%). The mean annual temperature in marshes was lower (13.5 C) than channels (16.9 C) or springs (16.3 C) despite warmer summer temperatures because of freezing winter conditions in the marsh.

The Bonneville Basin

We sampled metaphyton in each habitat type in all eleven valleys. Four metaphyton divisions and 242 taxa were collected (Appendix A). Although diatoms (Bacillariophyta; 48 %) and blue-green algae (Cyanophyta; 30 %) accounted for 78 % of the total richness, Chlorophytes were the most abundant division (Table 2).

Size and growth form were the primary factors that determined the percent representation by biovolume of each division. Green algae (Chlorophyta) had the greatest relative abundance (80 %) in all habitats (Table 2) and valleys (Table 3). Specifically, species in two common genera (*Cladophora* and *Spirogyra*) were the dominant taxa. Although single-celled epiphyte reached high densities, their biovolume was always much lower than the large filamentous stalks of the chlorophyte taxa. However, some non-chlorophyte taxa were well represented in the Bonneville Basin (Table 3). *Synedra ulna var. subaequalis* (Bacillariophyta) produce narrow, needle-shaped, solitary cells that attach one end of their frustule to a stalk of filamentous algae producing dense, erect clusters. *Merismopedia elegans* (Cyanophyta) grow in flat, rectangular colonies covered in mucilage that can form large visible sheets, whereas *Vaucheria geminate* are filamentous golden-brown algae (Chysophyta) that also form mats comprised of large stalks.

Contrary to our first hypothesis, metaphyton community composition showed considerable variation among sites. The maximum average Bray-Curtis similarity between sites within groups was only 29.6 % in the wetland reference model with 14 classes and 24.8 % in the valley model with seven classes. Also, thirty-two different metaphyton species were the single most dominant taxa in at least one site. Most of these taxa were filamentous green algae. Similarly, 67 % of the total number of taxa occurred in three or fewer sites (162 species).

Habitat Comparisons

Springs were dominated by four chlorophytes (*Spirogyra* sp., *C. glomerata*, *C. oligoclona*, and *S. porticalis*) that comprised 75 % of the biovolume, plus two non-chlorophytes, *Synedra ulna var. subaequali* and *Gomphosphaeria aponina* (Cyanophyta). Channels were dominated by *C. glomerata* (31.5 %) and *C. oligoclona* (19.2 %), plus *V. geminate* (11.4 %) and a filamentous cyanophyte, *Oscillatoria sancta* (12.9 %). Marshes were dominated by *C. glomerata*, (31.5 %) and *S. porticalis* (9.6 %), plus the blue-green alga, *M. elegans* (22.6 %). Thus, *G. aponina* was the most abundant blue-green alga in springs, *O. sancta* in channels, and *M. elegans* in marshes. *Synedra ulna var. subaequali* was the most abundant diatom in all three habitats, whereas the most abundant chrysophytes were *Tribonema bombycinum* in springs, and *V. geminate* in both channels and marshes. Despite such differences; however, community composition only differed between two of the three habitats.

ANOSIM showed that metaphyton community composition differed between springs and marshes (R = 0.059, P = 0.02) but springs and channels (R = 0.056, P = 0.10)

and channels versus marshes (R = -0.025, P = 0.70) were not significant. Even though community composition differed between springs and marshes, there was considerable overlap attributed to within-group variability (Figure 4a). The average Bray-Curtis similarity among sites in springs, channels, and marshes was 11.8 %, 11.9 %, and 8.8 %, respectively.

SIMPER showed that the dissimilarity in community composition between springs and marshes was attributed to rarer taxa. For example, the biovolume of *Denticula kuetzingii* (Bacillariophyta) and *C. glomerata* was nearly 3 times greater in springs, whereas the biovolume of *Rhizoclonium hieroglyphicum* (Chlorophyta) was nearly 4 times greater in marshes. Also, we collected 22 taxa from marshes that were absent in springs and 14 taxa in springs that were absent from marshes.

Overall, springs contained 57 species that were not collected in other habitat types (27 diatoms, 18 cyanophytes, 11 chlorophytes, and 1 chrysophyte), marshes contained 37 potentially unique species (21 diatoms, 11 cyanophytes, and 5 chlorophytes), and channels had 11 (5 diatoms, 4 cyanophytes, and 2 chlorophytes). Perhaps it is not surprising that channels contained the fewest number of "unique" taxa because metaphyton in channels tended to accumulate in slow water microhabitats with intermediate physico-chemical conditions between marshes and springs.

Wetland Comparisons

Four valleys were dropped from comparisons at the wetland and valley scales because of an insufficient number of sites. Although there was considerable overlap among groups, the wetland scale accounted for significant variation in community

composition of metaphyton in the Bonneville Basin (Figure 4b). Community similarity was different (51.6 %; $P < 0.05$) in 47 of the 91 pairwise comparisons among wetlands. All of these significant comparisons were between wetlands in different valleys. All 11 of the comparisons between wetlands in the same valley were not significant. Comparisons between wetlands in Snake Valley were not significant, even though it contains four large complexes with different physico-chemical properties. For example, average temperature ranges from 12.0 in the northern most complex (Miller Spring Complex) to 18.6 in the southern most complex (Bishop Spring Complex). This result suggests that habitat heterogeneity at the wetland scale was not important in determining differences in community composition.

Valley Comparisons

Again there was considerable variation in community composition within a valley and considerable overlap between valleys (Figure 4c). However, 11 of 21 pairwise comparisons of community composition (52.0 %) were significantly different ($P < 0.05$). Much of this variation was attributed to differences in biovolume amongst the dominant taxa. For example, two valleys (Curlew and Ibapah) were dominated by filamentous chlorophytes that were rare (< 5 % relative abundance) in all other valleys (*Sirogonum floridanum*, *Mougeotia* sp. and *Rhizoclonium hieroglyhicum*). Similarly, *V. geminate* was abundant in Grouse Creek and Utah valleys, whereas six valleys had no chrysophyte species with relative abundances > 1 %. The same pattern was seen with diatoms and blue-green algae where many species reached a relatively high biovolume in two or three valleys but were otherwise rare throughout the rest of the region.

Isolation Effects

Despite large variation within groups, metaphyton community composition was significantly different (R = 0.126, P = 0.05) between isolated springs and springs in complexes (Figure 5). The average Bray-Curtis similarity among isolated springs was 11.6 %, whereas the average similarity among springs in complexes was 12.1 %. We were surprised to find significant isolation effects because algae are presumed to have good dispersal abilities.

Model Comparisons

The valley and wetland models accounted for the greatest variation in metaphyton community composition among sites (Table 4). However, neither model accounted for the majority of the variation in metaphyton community composition. Contrary to our predictions (Hypothesis 2), the habitat model was least effective at accounting for variation in community composition, whereas the isolation model was nearly as effective as the wetland and valley models.

DISCUSSION

Efforts to describe the processes that determine patterns of community composition in freshwater algae invariably focus on local factors. Recent summaries devote chapters to describing the effects of light, water temperature, micro-current dynamics, substrate types, nutrient concentrations, resource competition, and grazing on community composition of freshwater algae (e.g. Round 1981, Stevenson et al. 1996).

This is certainly appropriate considering the fact that the scale(s) at which organisms respond to environmental variation is determined by their size and mobility (Addicott et al. 1987). Even macroscopic algae are small and most species are immobile or only capable of very limited movement (Round 1981). Thus, we expected local factors to play a major role in accounting for variation in metaphyton community composition between sites in artesian springs of the Bonneville Basin. In particular, we expected the distinct physico-chemical differences between habitats to account for the majority of variation in community composition. To our surprise, the valley model accounted for 6.3x more variation than the habitat model. We suggest two potential explanations: 1) metaphyton respond to environmental variation at a micro-habitat scale rather than the habitat scale as defined in this study and, 2) processes operating at the valley scale are important in determining differences in metaphyton community composition.

The composition of algal communities is clearly effected by small scale processes, even by physico-chemical gradients operating at the micron scale (e.g. Jørgensen et al. 1979, Wetzel 1996). For example, slow flowing micro-currents can influence algal communities by altering the thickness of the boundary layer and consequently rates of gas and nutrient exchange (e.g. Wetzel 1993). Although measuring such factors at a microhabitat scale was not practical at the numerous sites in this study, it may be necessary to account for greater variation in metaphyton community structure. However, the potential importance of factors operating at the microscale does not diminish the importance of factors operating at the valley scale.

Two results support the assertion that factors operating at the valley scale can influence the local community composition of metaphyton: 1) the valley model

accounted for the greatest variation in metaphyton community composition, and 2) the only comparisons that were significantly different at the wetland scale were between wetlands in different valleys. Metaphyton community composition did not differ between wetlands in the same valley. Historical events related to the draining of ancient Lake Bonneville, dispersal limitations, and physico-chemical heterogeneity at the valley scale may explain these results.

Lake Bonneville breached its northern border 15,000 years ago. Subsequent drying exposed present-day lakes, rivers, and springs (Currey et al. 1984, Benson et al. 1990, Grayson 1993). The first metaphyton propogules to colonize these newly exposed springs were likely derived from the littoral zone of Lake Bonneville as the shoreline receded. Spatial and temporal variation in the composition of the metaphyton in the littoral zone of the lake probably caused different springs to be inoculated with different taxa. Springs in different valleys were probably exposed to the lake littoral zone at different times because springs have similar elevation within a valley but different elevations between valleys. Springs in the same valley may have been inoculated with a similar suite of taxa at the same time. Subsequent dispersal between springs within the same valley would have had an additional homogenizing effect on community composition within valleys. Thus, differences in community composition between valleys but not between wetlands within valleys may have been reinforced by more frequent dispersal within a valley than between valleys.

Dispersal limitation is widely recognized as one of the most important processes determining patterns of community composition (e.g. MacArthur and Wilson 1967, Holyoak et al. 2005). The importance of dispersal limitations in constraining the

membership of algal communities in freshwater environments has rarely been investigated (Round 1981). We are not aware of any studies that have investigated the dispersal abilities of metaphyton. However, the community composition of isolated springs in our study differed from the community composition of springs in large complexes. This result suggests that some metatphyton taxa may not be capable of dispersing to isolated habitats. Also, the localized distribution of many taxa in this study and stream investigations of benthic algae (e.g. Stevenson and Peterson 1989) indicate a gradient in dispersal abilities between algal taxa with different growth forms and life history traits. The paucity of information on dispersal in wetland algal communities is likely related to the difficulty of studying this process and the prevailing opinion that most algae have excellent powers of dispersal (e.g. McCormick 1996). Evidence supporting dispersal limitation in algae based on examining patterns of community composition from local habitats to the regional scale, as done in this study, is also rare, especially in wetland environments.

Environmental heterogeneity between valleys was the least likely explanation for why the valley scale accounted for the greatest variation in community composition. Physico-chemical attributes would have to be comparatively uniform between wetlands within a valley and different from wetlands in other valleys. Although most of the coldest springs were in Rush Valley and the warmest were in Fish Springs, most physico-chemical attributes differed as much between wetlands within a valley as between wetlands in different valleys. In fact, water chemistry (e.g. dissolved oxygen) often varied greatly between springs in the same wetland complex.

Future research should explore if and how dispersal limitations might limit the

membership of local algal communities. Different taxa must certainly have different dispersal capabilities. Determining the traits that promote dispersal may explain patterns of community composition, especially at larger scales. Desert springs are ideal for such investigations because of the extreme challenges associated with dispersing over mountain ranges through a dry desert landscape.

Management Implications

Bioassessment is the practice of using living organisms to indicate the health of natural ecosystems (Barbour et al. 1999, Karr 2000). Algae are commonly used to assess the integrity of freshwater ecosystems because they can rapidly respond to human degradation (e.g. Lowe and Pan 1996, Stevenson 2001). However, spatio-temporal variation in algal populations and communities can limit their use in bioassessment. The greatest challenge in bioassessment is to find indicators of degradation that distinguish the signal of human degradation through the haze of natural variation (e.g. Karr and Chu 1999, Rader and Shiozawa 2001). Outward appearances of metaphyton in springs of the Bonneville Basin suggested a simple community composition that varied little between sites. We found just the opposite. The average Bray-Curtis similarity between all sites was only 14.1 %. The metaphyton community varied between sites because of differences in the dominant filamentous species and their microscopic epiphytes. Bioassessment based on metaphyton in spring ecosystems of the Bonneville Basin should compare potentially disturbed test sites to minimally impacted reference sites in the same valley to minimize variation.

Desert springs in the Bonneville Basin are threatened by a variety of

anthropogenic stressors such as, groundwater extraction, agricultural runoff, livestock grazing, and introduced plant and animal species. Preservation of biodiversity depends on maintaining the full range of natural or historic environmental variation to which organisms have evolved (Gunderson and Holling 2001). Our study suggests the importance of protecting all habitat types in multiple wetlands in each valley to preserve the rich diversity of metaphyton in these unique ecosystems.

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LITERATURE CITED

Addicott, J. F., Aho J. M., Antolin M. F., Padilla D. K., Richardson J. S. and D.A. Soluk. 1987. Ecological neighborhoods: scaling environmental patterns. Oikos 49:340-346.

APHA (American Public Health Association). 1989. Standard Methods for the Examination Wasterwater. 17th Ed. American Public Health Association. Washington, D.C. 1550 pp.

Anderson, K., S. Nelson, A. Mayo and D. Tingey. 2005. Interbasin flow revisited: the contribution of local recharge to high-discharge springs, Death Valley, CA. Journal of Hydrology 323:276-302.

Ashley, G.M., M. Goman, V.C. Hover, R.B. Owen, R.W. Renaut, and A.M. Muassya. 2002. Artesian Blister Wetlands, a Perennial Water Resource in the Semi-arid Rift Valley of East Africa. Wetlands 22(4):686-695.

Barbour, M. T., J. Gerritesen, B. D. Synder and J. B. Stribling. 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates, and fish, second edition. Report EPA 841-B-99-002. U.S. Environmental Protection Agency, Office of Water, Washington, DC.

Benson, L.V., D. R. Currey, R. I. Dorn, K. R. Lajoie, C. G. Oviatt, S.W. Robinson, G.I. Smith and S. Stine. 1990. Chronology of expansion and contraction of four Great Basin lake systems during the past 35,000 years. Paleogeography, Paleoclimatology, Paleoecology 78:241-286.

Biondini, M.E., P.W. Mielke and E.F. Redente. 1991. Permutation techniques based on euclidian analysis spaces: a new and powerful statistical method for ecological

research. Pp. 221-240. *In* Computer Assisted Vegetation Analysis. E. Feoli and L. Orloci (eds). Kluwer Academic Publishers. The Netherlands.

Borchardt, M.A. 1996. Nutrients. Pp. 183-218. *In* R. J. Stevenson, M. K. Bothwell and R. L. Lowe (eds) Algal ecology: freshwater benthic ecosystems. Academic Press, San Diego, CA.

Bray, J. R. and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs, 27, 325-349.

Brown, R. M., D. A. Larson and H. C. Bold. 1976. Air-borne algae. Their abundance and heterogeneity. Science 143:583-585.

Christiansen, F. W. 1951. Geology of the Canyon, House, and Confusion ranges, Millard County, Utah. Guidebook to the Geology of Utah. No. 6:68-80.

Clarke, K. R. and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation (second edition). Primer-E, Plymouth, UK

Clarke, K .R. and R. N. Gorley. 2006. Primer v6 User Manual/Tutorial. Primer-E, Plymouth, UK.

Connelly, S. R. and J. Roughgarden. 1999. Theory of marine communities: competition, predation, and recruitment-dependent interaction strength. Ecological Monographs 69: 277-296.

Cooper, S. D., Diehl S., Kratz K. and Sarnelle O. (1998) Implications of scale for patterns and processes in stream ecology. Australian Journal of Ecology 23: 27-40.

Currey, D. R., C. G. Oviatt and J. E. Czarnomski. 1984. Late Quaternary geology of Lake Bonneville and Lake Waring. Utah Geological Association Publications 13:227-238.

Curtis, B., K. S. Roberts, M. Griffin, S. Bethune, C. J. Hay and H. Kolberg. 1998. Species richness and conservation of Nambian freshwater macro-invertabrates, fish and amphibians. Biodiversity and Conservation 7:447-466.

Deacon, J. E. and W. L. Minckley. 1974. Desert fishes. pp. 385-488. *In* Desert Biology, Volume 2. G.W. Brown Jr. (ed). Academic Press, New York, NY.

Desert Research Institute, Western Regional Climate Center, www.wrcc.dri.edu

Fensham, R. J. 2003. Spring Wetlands of the Great Artesian Basin, Queensland, Australia. Wetlands Ecology and Management 11(5):343-363

Fensham, R. J. and R. J. Price. 2004. Ranking Spring Wetlands in the Great Artesian Basin of Australia using endemicity and isolation of plant species. Biological Conservation 119(1):41-50.

Goldsborough, L. G. and G. G. C. Robinson. 1996. Patterns in wetlands. Pp. 77-117. *In* R. J. Stevenson, M. K. Bothwell and R. L. Lowe (eds.). Algal ecology: freshwater benthic ecosystems. Academic Press, San Diego, CA.

Grayson, D. K. 1993. The desert's past. A natural prehistory of the Great Basin. Smithsonian Institution Press, Washington DC.

Grimes, J. A., L. L. St. Clair and S. R. Rushforth. 1980. A comparison of epiphytic diatom assemblages on living and dead stems of the common grass *Phragmites australis*. Great Basin Naturalist 40(3):223-228.

Gunderson, L. and C. S. Holling. 2001. Panarchy, understanding transformations in humans and natural systems. Island Press, New York, N.Y. USA.

Heino, J., P. Louhi and T. Muotka. 2004. Identifying the scales of variability in stream macroinvertebrate abundance, functional composition and assemblage structure.

Freshwater Biology 49:1230-1239.

Hillebrand, H., C. D. Durselen, D. Kirschtel, U. Pollingher and T. Zohary. 1999. Biovolume calculation for pelagic and benthic microalgae. J. Physcol. 35:403-424.

Holyoak, M., M. A. Leibold and R. D. Holt. 2005. Metacommunities: Spatial Dynamics and ecological Communities. The University of Chicago Press. Chicago, IL.

Hovingh, P. 1993. Aquatic habitats, life history observations, and zoogeographic considerations of the spotted frog (*Rana pretiosa*) in Tule Valley, Utah. *Great* Basin Naturalist 53:168-179.

Jorgensen, B. B., N. P. Revsbech, T. H. Blackburn and Y. Cohen. 1979. Diurnal cycle of oxygen and sulfide microgradients and microbial photosynthesis in a cyanobacterial mat sediment. Applied Environmental Microbiology 38: 46-58.

Kaczmarska, I. and S. R. Rushforth. 1984. Diatom associations in Blue Lake Warm Spring, Utah. USA. Bibliotheca Diatomologica 2(1):1-123.

Karr, J. R. and E. W. Chu. 1999. Restoring Life in Running Waters: Better Biological Monitoring. Island Press. Washington, DC.

Karr, J. R. 2000. Health, integrity and biological assessment: the importance of measuring whole things. Pp. 209-226. *In* D. Pimentel, L. Westra and R. F. Noss (eds.) Ecological integrity: integrating environment, conservation, and health. Island Press. Washington D.C.

Keleher, M. J. and R. B. Rader. In review. Bioassessment of Artesian Springs in the Bonneville Basin, Utah. Submitted to "Wetlands".

Li, J., A. Herlihy, W. Gerth, P. Kaufmann, S. Gregory, S. Urquhart and D.P. Larsen.

2001. Variability in stream macroinvertebrates at multiple spatial scales. Freshwater Biology 46: 87-97.

Lowe, R. L. and G. D. LaLiberte. 1996. Benthic stream algae: distribution and structure. Pp. 269-294. *In* F.R. Hauer and G.A. Lamberti (eds). Methods in Stream Ecology. Academic Press, New York, New York, USA.

Lowe, R .L. and Y. Pan. 1996. Benthic algal communities as biological monitors. Pp. 705-739. *In* R. J. Stevenson, M. K. Bothwell and R. L. Lowe (eds). Algal ecology: freshwater benthic ecosystems. Academic Press, San Diego, CA.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton New Jersey, USA.

McCormick, P. V. 1996. Resource competition and species coexistence in freshwater benthic algal assemblages. Pp. 229-249. *In* R. J. Stevenson, M. K. Bothwell and R. L. Lowe (eds). Algal ecology: freshwater benthic ecosystems. Academic Press, San Diego, CA.

McCune, B. and M. J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data, version 4. MjM Software Design, Gleneden, Oregon.

McCune, B. and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden, Oregon.

Mielke, P. W. and K. J. Berry. 2001. Permutation methods: A distance function approach. New York: Springer-Verlag.

Mitch, W. J. and J. G. Gosselink. 2000. Wetlands, third edition. Wiley, New York.

Myers, M. J. and V. H. Resh. 1999. Spring-formed wetlands of the arid west. Pp. 811 -828. *In* Invertebrates in Freshwater Wetlands of North America: Ecology and

Management, D. P. Batzer, R. B. Rader and S. A. Wissinger (Eds). Wiley, New York.

Oviatt, C.G. 1988. Late Pleistocene and Holocene lake fluctuations in the Sevier Lake Basin, Utah, USA. Journal of Paleolimnology 1:9-21.

Pyne, M. I., R. B. Rader and W.F. Christensen. 2007. Predicting local biological characteristics in streams: a comparison of landscape classifications. Freshwater Biology 52:1302-1321.

Rader, R. B. and C. J. Richardson. 1992. The effects of nutrient enrichment on macroinvertebrates and algae in the Everglades: a review. Wetlands 12:34-41.

Rader, R. B. and D. Shiozawa. 2001. General principles of establishing a bioassessment program. pp. 13-43. *In* R. B. Rader, D. P. Batzer and S. A. Wissinger (eds.) Bioassessment and management of North American freshwater wetlands. John Wiley and Sons, Inc., New York.

Rosenzweig, M. L. 1995. Species Diversity in Space and Time. Cambridge University Press. Cambridge, UK.

Round, F. E. 1981. The ecology of algae. Cambridge University Press, London.

Schlichting, H. E. 1969. The importance of airborne algae and protozoa. F. Air Pollut. Cont. Ass. 19:946-51.

Southwood, R. and P. A. Henderson. 2000. Ecological Methods. Oxford University Press, Blackwell Science Publications, Oxford, England.

Stevenson, R. J., M. L. Bothwell, R. L. Lowe. 1996. Algal Ecology: Freshwater Benthic Ecosystems. Academic Press, San Diego, CA.

Stevenson, R. J. and C. G. Peterson. 1989. Variation in benthic diatom

(Bacillariophyceae) immigration with habitat characteristics and cell morphology. J. Phycol. 25:120-129.

Stevenson, R. J., and C. G. Peterson. 1991. Emigration and immigration can be important determinants of benthic diatom assemblages in streams. Freshwater Biology 26: 279-294.

Stevenson R .J. 2001. Using algae to assess wetlands with multivariate statistics, multimetric indices and an ecological risk assessment framework. Pp. 113-140. *In* Bioassessment and management of freshwater wetlands. Rader, R. D., D. B. Batzer, and S. A. Wissinger (eds). John Wiley and Sons Publishers., New York, New York.

Todd, D. K. and L. W. Mays. 2005. Groundwater Hydrology (Third edition). John Wiley and Sons Inc. New York, New York, USA, pp. 625.

Utermohl, H. 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. Mitt. Int. Ver. Limnol. 9. 38 pp.

Van Sickle, J. 1997. Using mean dendrograms to evaluate classifications. Journal of Agricultural Biological and Environmental Statistics 2:370-388.

Van Sickle, J. and Hughes R. M. 2000. Classification strengths of ecoregions, catchments and geographic clusters for aquatic vertebrates in Oregon. Journal of the North American Benthological Society 19**:**370-384.

Ward, J. V. 1992. Aquatic insect ecology: biology and habitat. John Wiley & Sons, Inc. New York, New York, USA.

Wetzel, R. G. 1993. Land-water interfaces: Metabolic and limnological regulators. Verh.- Int. Ver. Theor. Angew. Limnol. 24:6-24

Wetzel, R. G. 1996. Benthic algae and nutrient cycling in lentic freshwater ecosystems. Academic Press, Inc. San Diego, California, USA.

Wetzel, R. G. 2001. Limnology: Lake and River Ecosystems. Third edition. Academic Press, New York, NY.

Wetzel, R. G. and G. E. Likens. 1991. Limnological analyses. Second edition, Springer-Verlag, New York, New York, USA.

Wiens, J.A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397

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Table 1: Mean and range (in parentheses) of physico-chemical measurements in springs of the Bonneville Basin. Number of springs is shown in brackets. Dashes indicate missing data.

Valley	Elevation (m a.s.l)	Surface Area (m^2)	Maximum Depth (m)	Water Temp (C)	Salinity (ppt)	pH	DO (mg/l)
Grouse Creek [6]	1618 (1378 - 1778)	438 (64 - 1200)	1.0 (0.3 - >3.0)	16.8 (12 - 21)	0.6 (0.1-1.0)	7.7	6.6 (2.1 - 14.0)
Curlew [2]	1294	900	1.0 (0.1 - 2.0)	20	2.1	8.8	11.1
Ibapah [4]	1626 (1625 - 1632)	16 (5 - 25)	1.4 (0.5 - >2.0)	16.1 (13 - 19)	1.0 (1.0-1.0)	7.5-7.8	4.9 (3.6 - 7.5)
Skull [2]	1311 (1307 - 1314)	717 (33 - 1400)	1.5 (2.0 - >3.0)	25.2 (25 - 26)	0.2 (0.1 - 0.3)	-	6.5 (4.3 - 8.7)
Rush [2]	1696 (1686 - 1703)	35 (15 - 60)	1.4 (1.3 - 1.5)	9.5 (9 - 10)	0.5 (0.5 - 0.6)	7.5 - 7.7	5.4 (4.0 - 6.8)
Snake [57]	1446 (1457 - 1490)	101 (1 - 600)	1.6 (0.2 - 4.0)	14.3 (11 - 22)	0.9 (0.2 - 1.0)	7.1 - 9.1	3.8 (0.3 - 9.4)
Tule [8]	1357 (1347 - 1369)	100 (50 - 200)	1.4 (0.3 – 2.3)	28.9 (18 - 30)	0.9 (0.8 - 1.0)	7.6 - 8.1	1.4 (1.3 - 1.8)
Fish Springs [14]	1323 (1315 - 1332)	420 (50 - 850)	2.2 (0.6 - >3.5)	25.5 (16 - 32)	1.1 (0.2 - 1.7)	7.5 - 7.7	4.3 (1.6 - 7.0)
Mills [3]	1484 (1342 - 1524)	33 (25 - 50)	0.8 (0.6 – 1.0)	18.3 (15 - 25)	1.0 (1.0 - 1.0)	7.6 - 8.8	7.7 (4.7 - 13.3)
Goshen [11]	1482 (1391 - 1509)	204 (5 - 900)	1.1 (0.5 - >3.0)	18.1 (12 - 21)	0.9 (0.5 - 1.3)	7.4 - 8.0	4.1 (2.7 - 6.6)
Utah [16]	1394 (1387 - 1512)	138 (2 - 711)	1.3 (0.1 - >3.0)	12.9 (11 - 19)	0.7 (0.1- 1.0)	6.7 - 8.3	5.2 (0.4 - 10.0)

Table 2. Relative abundance of metaphyton divisions (percent of the total biovolume) by habitat types and for the entire Bonneville Basin.

Habitat Type	Chlorophyta	Cyanophyta	Bacillariophyta	Chrysophyta
Springs	90.0	0.4	9.5	< 0.1
Channels	72.5	12.9	3.2	11.4
Marshes	67.3	24.3	5.7	2.7
Basin	80.0	9.2	6.8	4.0

Table 3. Dominant metaphyton taxa for each valley and in the Bonneville Basin. Percent representation based on the total biovolume for a valley is shown in parentheses.

Valley	Dominant Species
Grouse Cr.	*Spirogyra dubia* (26.3), *Vaucheria geminata* (25.1) *Zygnema insigne* (23.5), *Spirogyra porticalis* (19.6)
Curlew	*Sirogonum floridanum* (46.7), *Mougeotia* sp. (44.1)
Ibapah	*Rhizoclonium hieroglyphicum* (28.1), *Spirogyra porticalis* (25.7), *Spirogyra dubia* (20.1), *Cladophora oligoclona* (16.0)
Skull	*Cladophora glomerata* (50.2), *Pleurosira laevis* (23.9), *Enteromorpha flexuosa* (7.7), *Cladophora oligoclona* (5.9), *Denticula kuetzingii* (5.1)
Rush	*Vaucheria geminate* (47.0), *Synedra rumpens* (16.5), *Microspora stagnorum* (14.7), *Spirogyra dubia* (12.8)
Snake	*Cladophora oligoclona* (49.1), *Spirogyra porticalis* (15.8), *Rhizoclonium hieroglyphicum* (7.3), *Spirogyra decimina* (6.1), *Cladophora glomerata* (4.7)
Tule	*Cladophora oligoclona* (48.0), *Spirogyra* sp. (26.8), *Rhizoclonium hieroglyphicum* (17.0)
Fish Springs	*Oscillatoria sancta* (23.9), *Spirogyra porticalis* (23.5), *Cladophora glomerata* (21.0), *Cladophora oligoclona* (14.0), *Klebsormidium sp.* (5.5)
Mills	*Cladophora glomerata* (52.6), *Merismopedia elegans* (37.6)
Goshen	*Cladophora glomerata* (56.5), *Cladophora oligoclona* (10.2), *Synedra fasciculate* (7.3), *Synedra ulna* (5.0)
Utah	*Spirogyra sp.* (54.3), *Cladophora oligoclona* (13.6), *Vaucheria geminata* (8.5)
Basin	*Cladophora oligoclona* (20.1), *Cladophora glomerata* (18.9), *Spirogyra sp.* (13.8), *Spirogyra porticalis* (10.5), *Merismopedia elegans* (5.0)

Table 4. The classification strength (CS) and relative CS of each spatial model (Habitat, Wetland, and Valley) and the isolation model based on the average within and between class similarity (Bray-Curtis) in the community composition of metaphyton. Reference models show the maximum CS. Relative CS is the percentage of the maximum CS attributed to each model.

Models	Number of Classes	Within	Between	CS	Relative CS (%)
Habitat	3	10.8	10.1	0.7	7.0
Habitat Reference	3	16.5	6.4	10.1	-
Wetland	14	17.0	9.3	7.7	38.5
Wetland Reference	14	29.6	9.6	20.0	-
Valley	7	16.7	8.5	8.2	43.9
Valley Reference	7	24.8	6.1	18.7	-
Isolation	2	11.9	9.4	2.8	37.3
Isolation Reference	2	15.8	8.3	7.5	-

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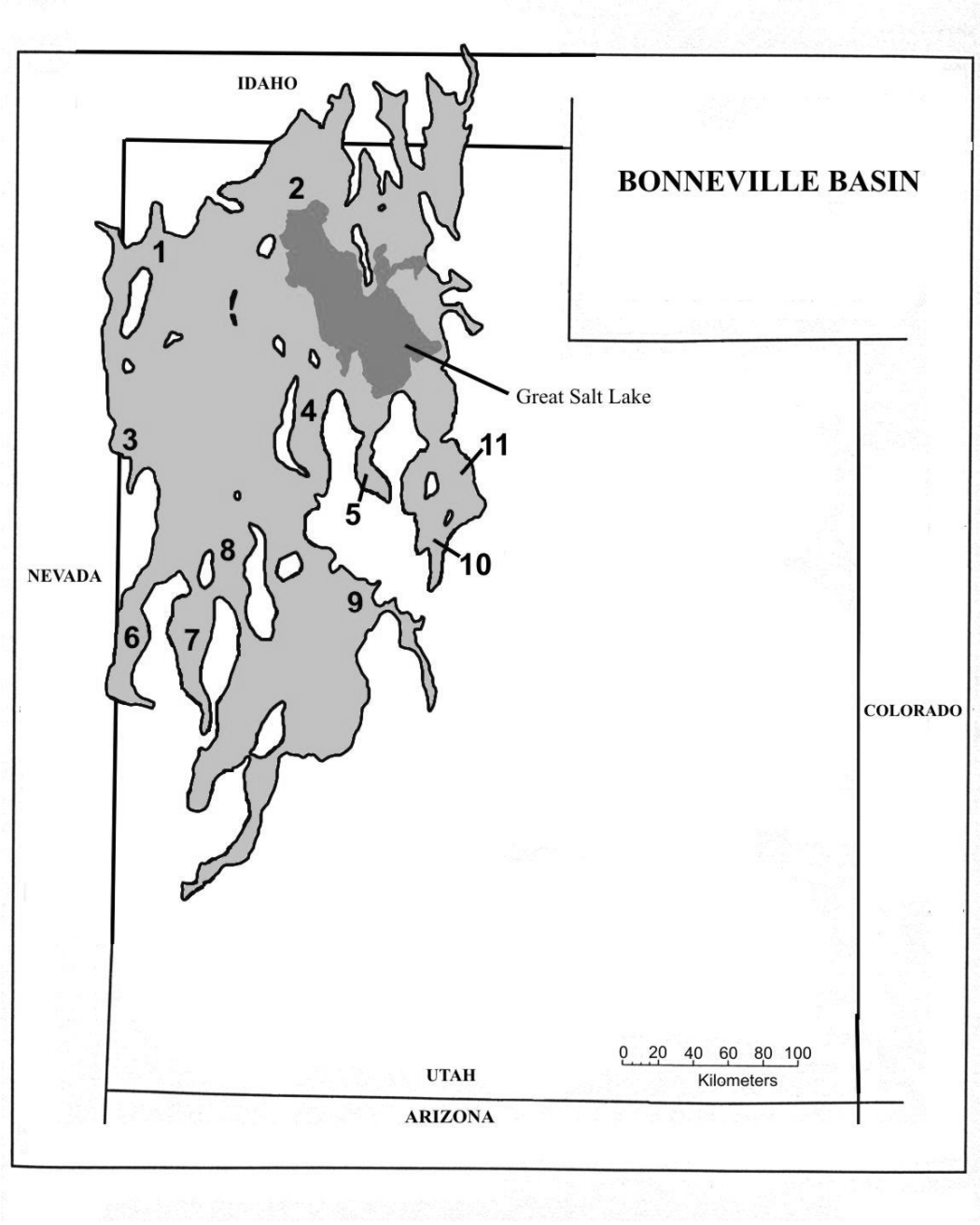
Figure 1:



1 = Grouse Creek, 2 = Curlew, 3 = Ibapah, 4 = Skull, 5 = Rush, 6 = Snake,
7 = Tule, 8 = Fish Springs Flat, 9 = Mills, 10 = Goshen, 11 = Utah

Figure 2.

Figure 3.

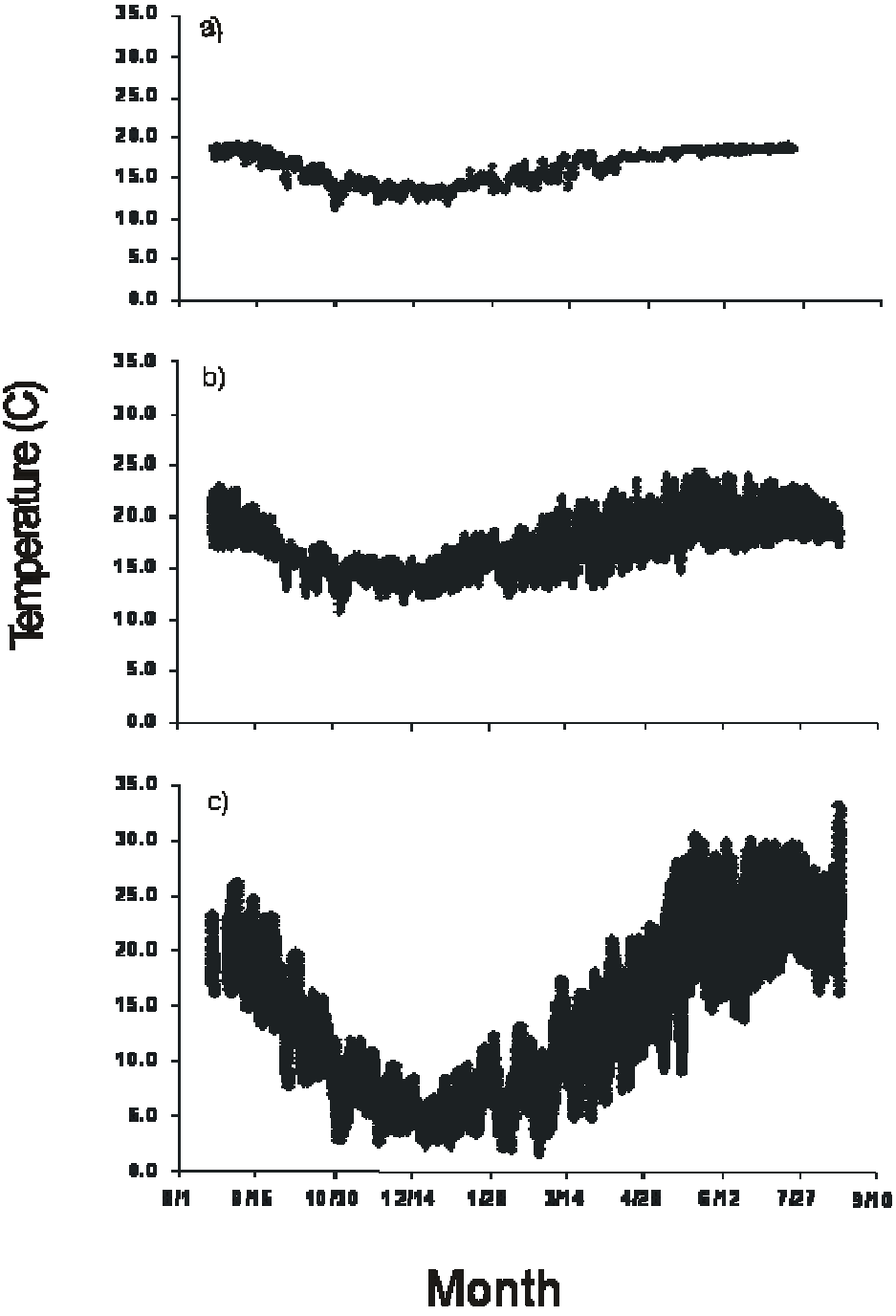


Figure 4.

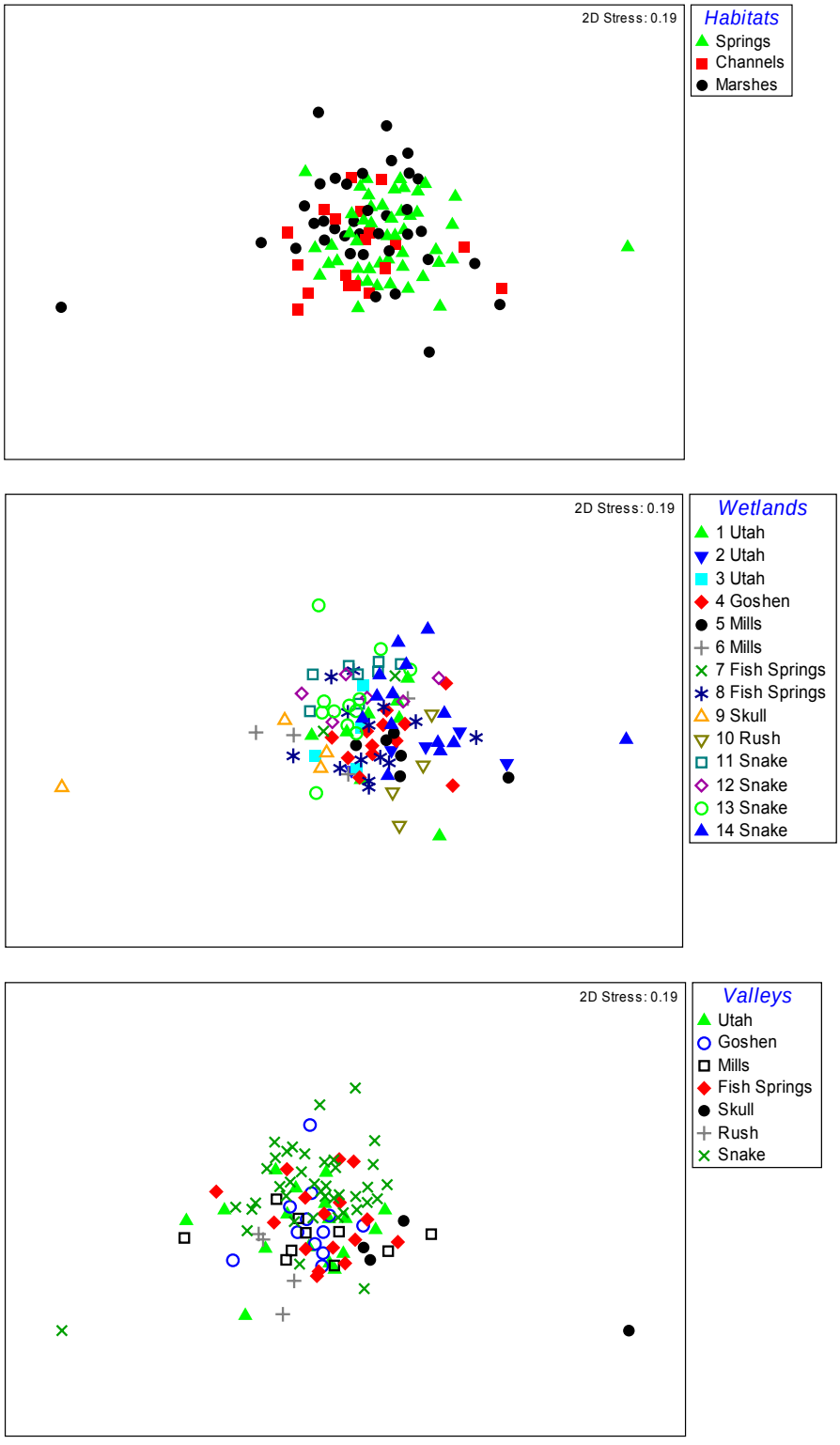
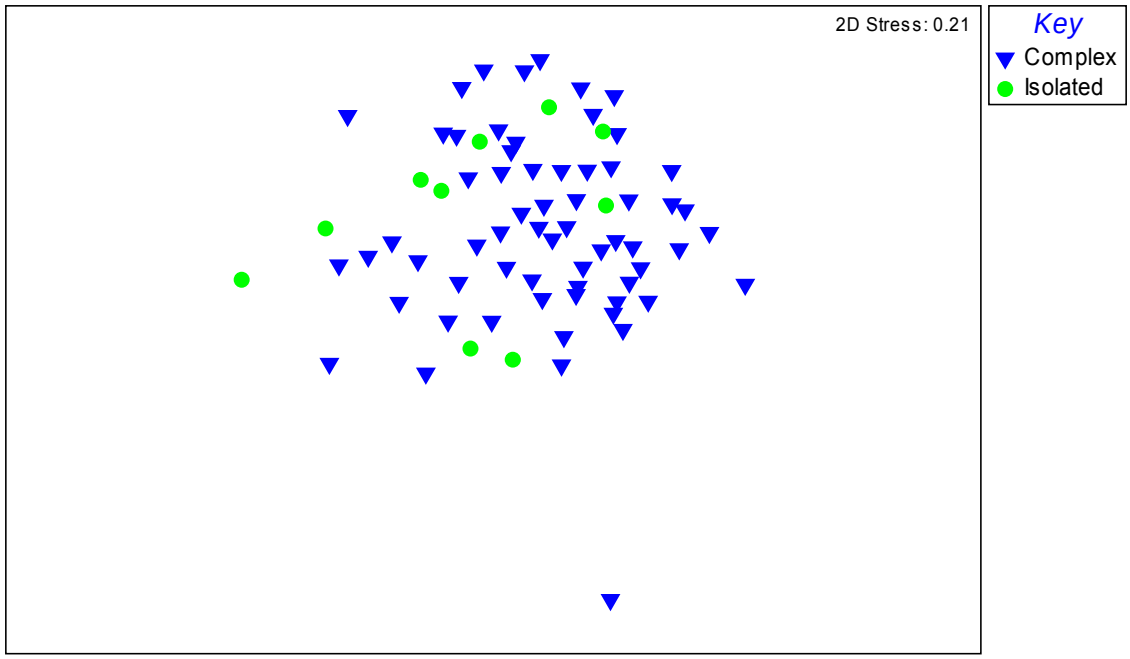


Figure 5.



APPENDIX A:

Lowest taxonomic resolution of metaphyton algae collected in eleven valleys in the Bonneville Basin.

Grouse Creek	Division	Grouse Creek	Division
Spirogyra dubia	Chlorophyta	*Rhopalodia musculus*	Chrysophyta
Zygnema insigne	Chlorophyta	*Cymbella silesiaca*	Chrysophyta
Spirogyra porticalis	Chlorophyta	*Anabaena catenula*	Cyanophyta
Sirogonum floridanum	Chlorophyta	*Oscillatoria agardhii*	Cyanophyta
Cladophora spp.	Chlorophyta	*Anabaena variabilis*	Cyanophyta
Spirogyra spp.	Chlorophyta	*Lyngbya diguetii*	Cyanophyta
Spirogyra neglecta	Chlorophyta	*Hapalosiphon* spp.	Cyanophyta
Mougeotia spp.	Chlorophyta	*Lyngbya aestuarii*	Cyanophyta
Mougeotia genuflexa	Chlorophyta	*Aphanothece smithii*	Cyanophyta
Oedogonium spp.	Chlorophyta	*Nostoc* spp.	Cyanophyta
Stigeoclonium spp.	Chlorophyta	*Gloeocapsa* spp.	Cyanophyta
Chlorella minutissima	Chlorophyta	*Synechocystis* spp.	Cyanophyta
Vaucheria geminata	Chrysophyta	*Chroococcus minutus*	Cyanophyta
Cocconeis placentula var. euglypta	Chrysophyta	*Chroococcus* spp.	Cyanophyta
Pinnularia maior	Chrysophyta	*Synechococcus* spp.	Cyanophyta
Melosira varians	Chrysophyta	*Chamaesiphon incrustans*	Cyanophyta
Fallacia pygmaea	Chrysophyta		
Craticula cuspidata	Chrysophyta	**Curlew Valley**	**Division**
Denticula kuetzingii	Chrysophyta	*Mougeotia* spp.	Chlorophyta
Tryblionella victoriae	Chrysophyta	*Rhizoclonium hieroglyphicum*	Chlorophyta
Navicula circumtexta	Chrysophyta	*Oedogonium* spp.	Chlorophyta
Navicula cryptotenella	Chrysophyta	*Synedra fasciculata*	Chrysophyta
Navicula veneta	Chrysophyta	*Mastogloia smithii*	Chrysophyta
Epithemia argus	Chrysophyta	*Navicula radiosa*	Chrysophyta
Rhoicosphenia abbreviata	Chrysophyta	*Denticula kuetzingii*	Chrysophyta
Synedra minuscula	Chrysophyta	*Achnanthes minutissima*	Chrysophyta
Achnanthes minutissima var. minutissima	Chrysophyta	*Cocconeis pediculus*	Chrysophyta
Navicula erifuga	Chrysophyta	*Navicula cryptotenella*	Chrysophyta
Navicula radiosa	Chrysophyta	*Epithemia argus*	Chrysophyta
Epithemia adnata var. proboscidea	Chrysophyta	*Cymbella tumida*	Chrysophyta
Gomphonema acuminatum	Chrysophyta	*Cymbella cistula*	Chrysophyta
Gomphonema truncatum	Chrysophyta	*Rhopalodia gibba*	Chrysophyta
Anomoeoneis vitrea	Chrysophyta	*Cymbella lunata*	Chrysophyta
Nitzschia acicularis	Chrysophyta	*Lyngbya aestuarii*	Cyanophyta
Nitzschia linearis	Chrysophyta	*Nostoc* spp.	Cyanophyta
Rhopalodia gibba	Chrysophyta	*Aphanocapsa conferta*	Cyanophyta
Gomphonema maclaughlinii	Chrysophyta	*Chroococcus minutus*	Cyanophyta
Fragilaria brevistriata	Chrysophyta	*Lyngbya nordgaardii*	Cyanophyta

Curlew Valley	Division	Utah Valley	Division
Heteroleibleinia kuetzingii	Cyanophyta	*Cocconeis pediculus*	Chrysophyta
Aphanocapsa incerta	Cyanophyta	*Gomphonema angustum*	Chrysophyta
Aphanothece minutissima	Cyanophyta	*Fragilaria vaucheriae*	Chrysophyta
Aphanothece smithii	Cyanophyta	*Gomphonema angustatum*	Chrysophyta
		Anomoeoneis vitrea	Chrysophyta
Utah Valley	**Division**	*Navicula salinarum*	Chrysophyta
Spirogyra spp.	Chlorophyta	*Denticula kuetzingii*	Chrysophyta
Cladophora oligoclona	Chlorophyta	*Gomphonema dichotomum*	Chrysophyta
Spirogyra porticalis	Chlorophyta	*Gomphonema truncatum*	Chrysophyta
Spirogyra crassa	Chlorophyta	*Rhoicosphenia abbreviata*	Chrysophyta
Spirogyra decimina	Chlorophyta	*Gomphonema parvulum*	Chrysophyta
Cladophora glomerata	Chlorophyta	*Navicula cryptotenella*	Chrysophyta
Zygnema sterile	Chlorophyta	*Cyclotella distinguenda*	Chrysophyta
Spirogyra novae-angliae	Chlorophyta	*Gyrosigma acuminatum*	Chrysophyta
Spirogyra neglecta	Chlorophyta	*Nitzschia acicularis*	Chrysophyta
Zygnema insigne	Chlorophyta	*Navicula erifuga*	Chrysophyta
Zygnema spp.	Chlorophyta	*Achnanthes flexella*	Chrysophyta
Spirogyra dubia	Chlorophyta	*Navicula capitata*	Chrysophyta
Chlorococcum spp.	Chlorophyta	*Nitzschia nana*	Chrysophyta
Scenedesmus bicaudatus	Chlorophyta	*Eunotia* spp.	Chrysophyta
Spirogyra pratensis	Chlorophyta	*Cymbella cistula*	Chrysophyta
Ankistrodesmus falcatus	Chlorophyta	*Cymbella microcephala*	Chrysophyta
Closterium moniliferum	Chlorophyta	*Cymbella lunata*	Chrysophyta
Oedogonium spp.	Chlorophyta	*Stauroneis smithii*	Chrysophyta
Pediastrum boryanum	Chlorophyta	*Lyngbya aerugineo-coerulea*	Cyanophyta
Mougeotia parvula	Chlorophyta	*Oscillatoria agardhii*	Cyanophyta
Chlorella minutissima	Chlorophyta	*Oscillatoria splendida*	Cyanophyta
Scenedesmus spp.	Chlorophyta	*Oscillatoria prolifica*	Cyanophyta
Stigeoclonium spp.	Chlorophyta	*Chamaesiphon incrustans*	Cyanophyta
Chaetophora spp.	Chlorophyta	*Oscillatoria tenuis*	Cyanophyta
Vaucheria geminata	Chrysophyta	*Oscillatoria limosa*	Cyanophyta
Synedra ulna var. subaequalis	Chrysophyta	*Pleurocapsa* spp.	Cyanophyta
Synedra ulna	Chrysophyta	*Heteroleibleinia kuetzingii*	Cyanophyta
Synedra minuscula	Chrysophyta	*Chamaesiphon confervicolus*	Cyanophyta
Achnanthes minutissima var. minutissima	Chrysophyta	*Homoeothrix* spp.	Cyanophyta
Cocconeis placentula var. euglypta	Chrysophyta	*Lyngbya epiphytica*	Cyanophyta
Gomphonema maclaughlinii	Chrysophyta	*Chroococcus* spp.	Cyanophyta
Synedra delicatissima var. angustissima	Chrysophyta	*Aphanocapsa incerta*	Cyanophyta
Gomphonema acuminatum	Chrysophyta	*Aphanothece smithii*	Cyanophyta
Synedra rumpens var. familiaris	Chrysophyta	*Chroococcus minutus*	Cyanophyta
Synedra radians	Chrysophyta	*Anabaena* spp.	Cyanophyta
Sellaphora pupula	Chrysophyta	*Clastidium setigerum*	Cyanophyta

Goshen Valley	Division	Mills Valley	Division
Chroococcus spp.	Cyanophyta	*Gomphonema parvulum*	Chrysophyta
Nostoc spp.	Cyanophyta	*Synedra minuscula*	Chrysophyta
Chroococcus minutus	Cyanophyta	*Gomphonema maclaughlinii*	Chrysophyta
Lyngbya epiphytica	Cyanophyta	*Gomphonema intricatum*	Chrysophyta
Oscillatoria limnetica	Cyanophyta	*Gomphonema dichotomum*	Chrysophyta
Chroococcus turgidus	Cyanophyta	*Navicula veneta*	Chrysophyta
Lyngbya diguetii	Cyanophyta	*Rhoicosphenia abbreviata*	Chrysophyta
Lyngbya nordgaardii	Cyanophyta	*Amphipleura pellucida*	Chrysophyta
Oscillatoria nigra	Cyanophyta	*Epithemia adnata var. proboscidea*	Chrysophyta
Lyngbya limnetica	Cyanophyta	*Amphora veneta*	Chrysophyta
Chroococcus limneticus	Cyanophyta	*Navicula erifuga*	Chrysophyta
Aphanothece smithii	Cyanophyta	*Cymbella cistula*	Chrysophyta
Clastidium setigerum	Cyanophyta	*Cymbella fonticola*	Chrysophyta
Aphanocapsa nubilum	Cyanophyta	*Cymbella silesiaca*	Chrysophyta
Gomphosphaeria aponina	Cyanophyta	*Amphora coffeaeformis*	Chrysophyta
Synechocystis spp.	Cyanophyta	*Cymbella microcephala*	Chrysophyta
Phormidium tenue	Cyanophyta	*Merismopedia elegans*	Cyanophyta
Aphanothece minutissima	Cyanophyta	*Heteroleibleinia kuetzingii*	Cyanophyta
Chamaesiphon incrustans	Cyanophyta	*Chamaesiphon incrustans*	Cyanophyta
Aphanocapsa conferta	Cyanophyta	*Limnothrix* spp.	Cyanophyta
		Lyngbya epiphytica	Cyanophyta
Mills Valley	**Division**		
Cladophora glomerata	Chlorophyta	**Rush Valley**	**Division**
Zygnema pectinatum	Chlorophyta	*Microspora stagnorum*	Chlorophyta
Spirogyra dubia	Chlorophyta	*Spirogyra dubia*	Chlorophyta
Rhizoclonium hieroglyphicum	Chlorophyta	*Mougeotia* spp.	Chlorophyta
Spirogyra decimina	Chlorophyta	*Spirogyra porticalis*	Chlorophyta
Mougeotia laetevirens	Chlorophyta	*Chlorella minutissima*	Chlorophyta
Cladophora oligoclona	Chlorophyta	*Vaucheria geminata*	Chrysophyta
Spirogyra porticalis	Chlorophyta	*Synedra rumpens var. rumpens*	Chrysophyta
Zygnema insigne	Chlorophyta	*Synedra* spp.	Chrysophyta
Mougeotia genuflexa	Chlorophyta	*Gomphonema angustatum*	Chrysophyta
Oedogonium spp.	Chlorophyta	*Fragilaria crotonensis*	Chrysophyta
Enteromorpha flexuosa	Chlorophyta	*Achnanthes lanceolata*	Chrysophyta
Oedogonium spp.	Chlorophyta	*Navicula erifuga*	Chrysophyta
Synedra ulna var. subaequalis	Chrysophyta	*Achnanthes linearis*	Chrysophyta
Synedra radians	Chrysophyta	*Meridion circulare*	Chrysophyta
Denticula kuetzingii	Chrysophyta	*Navicula cryptotenella*	Chrysophyta
Synedra delicatissima	Chrysophyta	*Achnanthes minutissima var. minutissima*	Chrysophyta
Synedra fasciculata	Chrysophyta	*Navicula lanceolata*	Chrysophyta
Achnanthes minutissima var. minutissima	Chrysophyta	*Nitzschia communis*	Chrysophyta
Mastogloia pumila	Chrysophyta	*Craticula cuspidata*	Chrysophyta

Rush Valley	Division	Fish Springs Flat	Division
Gyrosigma acuminatum	Chrysophyta	*Cladophora* spp.	Chlorophyta
Nostoc spp.	Cyanophyta	*Spirogyra dubia*	Chlorophyta
Lyngbya epiphytica	Cyanophyta	*Oedogonium* spp.	Chlorophyta
Chroococcus spp.	Cyanophyta	*Zygnema* spp.	Chlorophyta
Chamaesiphon incrustans	Cyanophyta	*Microspora willeana*	Chlorophyta
Oscillatoria acutissima	Cyanophyta	*Chlorella minutissima*	Chlorophyta
Anabaena catenula	Cyanophyta	*Spirogyra tenuissima*	Chlorophyta
		Synedra fasciculata	Chrysophyta
Skull Valley	**Division**	*Synedra ulna var. subaequalis*	Chrysophyta
Cladophora glomerata	Chlorophyta	*Campylodiscus noricus*	Chrysophyta
Enteromorpha flexuosa	Chlorophyta	*Achnanthes minutissima var. minutissima*	Chrysophyta
Cladophora oligoclona	Chlorophyta	*Tribonema bombycinum*	Chrysophyta
Rhizoclonium hieroglyphicum	Chlorophyta	*Entomoneis paludosa*	Chrysophyta
Pleurosira laevis	Chrysophyta	*Gomphonema intricatum*	Chrysophyta
Denticula kuetzingii	Chrysophyta	*Mastogloia elliptica*	Chrysophyta
Melosira spp. (*moniliformis?*)	Chrysophyta	*Denticula kuetzingii*	Chrysophyta
Cocconeis pediculus	Chrysophyta	*Anomoeoneis vitrea*	Chrysophyta
Rhoicosphenia abbreviata	Chrysophyta	*Synedra radians*	Chrysophyta
Mastogloia smithii	Chrysophyta	*Achnanthes linearis*	Chrysophyta
Achnanthes minutissima var. minutissima	Chrysophyta	*Gomphonema parvulum*	Chrysophyta
Achnanthes brevipes var. intermedia	Chrysophyta	*Diploneis oblongella*	Chrysophyta
Navicula tripunctata	Chrysophyta	*Mastogloia smithii*	Chrysophyta
Nitzschia nana	Chrysophyta	*Thalassiosira weissflogii*	Chrysophyta
Amphora coffeaeformis	Chrysophyta	*Navicula veneta*	Chrysophyta
Amphora veneta	Chrysophyta	*Cymbella silesiaca*	Chrysophyta
Cymbella lunata	Chrysophyta	*Gomphonema maclaughlinii*	Chrysophyta
Amphora ovalis	Chrysophyta	*Pleurosigma delicatulum*	Chrysophyta
Oscillatoria princeps	Cyanophyta	*Cocconeis placentula var. euglypta*	Chrysophyta
Chroococcus limneticus	Cyanophyta	*Navicula cryptotenella*	Chrysophyta
Hapalosiphon spp.	Cyanophyta	*Gomphonema dichotomum*	Chrysophyta
Lyngbya major	Cyanophyta	*Nitzschia* spp.	Chrysophyta
Heteroleibleinia kuetzingii	Cyanophyta	*Craticula halophila*	Chrysophyta
Lyngbya epiphytica	Cyanophyta	*Cymbella cistula*	Chrysophyta
Chamaesiphon incrustans	Cyanophyta	*Amphora veneta*	Chrysophyta
		Cymbella lunata	Chrysophyta
Fish Springs Flat	**Division**	*Cymbella microcephala*	Chrysophyta
Spirogyra porticalis	Chlorophyta	*Rhopalodia gibba*	Chrysophyta
Cladophora glomerata	Chlorophyta	*Oscillatoria sancta*	Cyanophyta
Cladophora oligoclona	Chlorophyta	*Oscillatoria nigra*	Cyanophyta
Klebsormidium spp.	Chlorophyta	*Oscillatoria chalybea*	Cyanophyta
Spirogyra decimina	Chlorophyta	*Gomphosphaeria aponina*	Cyanophyta
Rhizoclonium hieroglyphicum	Chlorophyta	*Chroococcus turgidus*	Cyanophyta

Fish Springs Flat	Division	Tule Valley	Division
Lyngbya aestuarii	Cyanophyta	*Navicula tripunctata*	Chrysophyta
Aphanocapsa incerta	Cyanophyta	*Achnanthes minutissima var. minutissima*	Chrysophyta
Chroococcus spp.	Cyanophyta	*Epithemia turgida*	Chrysophyta
Heteroleibleinia kuetzingii	Cyanophyta	*Navicula cryptotenella*	Chrysophyta
Aphanothece smithii	Cyanophyta	*Rhopalodia gibba*	Chrysophyta
Lyngbya epiphytica	Cyanophyta	*Epithemia adnata var. proboscidea*	Chrysophyta
Chamaesiphon confervicolus	Cyanophyta	*Rhopalodia musculus*	Chrysophyta
Synechocystis spp.	Cyanophyta	*Rhopalodia gibberula*	Chrysophyta
Aphanocapsa fonticola	Cyanophyta	*Chamaesiphon confervicolus*	Cyanophyta
Chroococcus dispersus	Cyanophyta	*Lyngbya* spp.	Cyanophyta
Chroococcus limneticus	Cyanophyta	*Nostoc* spp.	Cyanophyta
Lyngbya diguetii	Cyanophyta	*Cylindrospermum* spp.	Cyanophyta
Nostoc spp.	Cyanophyta	*Oscillatoria formosa*	Cyanophyta
Aphanocapsa nubilum	Cyanophyta	*Anabaena variabilis*	Cyanophyta
Oscillatoria splendida	Cyanophyta	*Nodularia* spp.	Cyanophyta
Homoeothrix spp.	Cyanophyta	*Aphanothece stagnina*	Cyanophyta
Lyngbya nordgaardii	Cyanophyta	*Lyngbya martensiana*	Cyanophyta
Chroococcus minutus	Cyanophyta	*Lyngbya diguetii*	Cyanophyta
Lyngbya limnetica	Cyanophyta	*Heteroleibleinia kuetzingii*	Cyanophyta
Cyanobium spp.	Cyanophyta	*Aphanothece smithii*	Cyanophyta
Pseudanabaena spp.	Cyanophyta	*Lyngbya epiphytica*	Cyanophyta
Oscillatoria spp.	Cyanophyta	*Oscillatoria splendida*	Cyanophyta
Aphanothece minutissima	Cyanophyta	*Lyngbya nordgaardii*	Cyanophyta
Chamaesiphon incrustans	Cyanophyta	*Chroococcus limneticus*	Cyanophyta
Synechococcus spp.	Cyanophyta	*Lyngbya aerugineo-coerulea*	Cyanophyta
Gloeocapsa spp.	Cyanophyta	*Microcoleus* spp.	Cyanophyta
Calothrix spp.	Cyanophyta	*Oscillatoria tenuis*	Cyanophyta
		Calothrix spp.	Cyanophyta
Tule Valley	**Division**	*Chroococcus minutus*	Cyanophyta
Cladophora oligoclona	Chlorophyta	*Merismopedia elegans*	Cyanophyta
Rhizoclonium hieroglyphicum	Chlorophyta	*Chroococcus dispersus*	Cyanophyta
Spirogyra spp.	Chlorophyta	*Lyngbya aestuarii*	Cyanophyta
Spirogyra porticalis	Chlorophyta	*Gomphosphaeria aponina*	Cyanophyta
Spirogyra aequinoctialis	Chlorophyta	*Oscillatoria prolifica*	Cyanophyta
Mougeotia genuflexa	Chlorophyta	*Calothrix epiphytica*	Cyanophyta
Oedogonium spp.	Chlorophyta	*Oscillatoria agardhii*	Cyanophyta
Mougeotia parvula	Chlorophyta	*Pseudanabaena* spp.	Cyanophyta
Mougeotia spp.	Chlorophyta	*Oscillatoria limnetica*	Cyanophyta
Epithemia argus	Chrysophyta		
Epithemia adnata	Chrysophyta	**Ibapah Valley**	**Division**
Denticula kuetzingii	Chrysophyta	*Rhizoclonium hieroglyphicum*	Chlorophyta
Mastogloia smithii	Chrysophyta	*Spirogyra porticalis*	Chlorophyta

Ibapah Valley	Division	Snake Valley	Division
Spirogyra dubia	Chlorophyta	*Aphanochaete repens*	Chlorophyta
Cladophora oligoclona	Chlorophyta	*Zygnema insigne*	Chlorophyta
Spirogyra spp.	Chlorophyta	*Microspora willeana*	Chlorophyta
Oedogonium spp.	Chlorophyta	*Stigeoclonium spp.*	Chlorophyta
Zygnema spp.	Chlorophyta	*Chlorella minutissima*	Chlorophyta
Bulbochaete spp.	Chlorophyta	*Coenocystis* spp.	Chlorophyta
Achnanthes minutissima var. minutissima	Chrysophyta	*Uronema* spp.	Chlorophyta
Denticula kuetzingii	Chrysophyta	*Ankistrodesmus falcatus*	Chlorophyta
Gomphonema maclaughlinii	Chrysophyta	*Chlamydomonas* spp.	Chlorophyta
Fragilaria brevistriata	Chrysophyta	*Synedra ulna var. subaequalis*	Chrysophyta
Gomphonema minutum	Chrysophyta	*Synedra capitata*	Chrysophyta
Synedra ulna	Chrysophyta	*Synedra ulna*	Chrysophyta
Amphora montana	Chrysophyta	*Synedra fasciculata*	Chrysophyta
Gomphonema acuminatum	Chrysophyta	*Vaucheria geminata*	Chrysophyta
Cymbella microcephala	Chrysophyta	*Epithemia adnata*	Chrysophyta
Cymbella silesiaca	Chrysophyta	*Tribonema bombycinum*	Chrysophyta
Chroococcus minutus	Cyanophyta	*Denticula kuetzingii*	Chrysophyta
Tolypothrix spp.	Cyanophyta	*Synedra radians*	Chrysophyta
Heteroleibleinia kuetzingii	Cyanophyta	*Navicula* spp.	Chrysophyta
Lyngbya epiphytica	Cyanophyta	*Mastogloia smithii*	Chrysophyta
Nostoc spp.	Cyanophyta	*Synedra rumpens var. familiaris*	Chrysophyta
Chamaesiphon incrustans	Cyanophyta	*Gomphonema acuminatum*	Chrysophyta
		Synedra rumpens var. rumpens	Chrysophyta
Snake Valley	**Division**	*Aulacoseira valida*	Chrysophyta
Cladophora oligoclona	Chlorophyta	*Fragilaria brevistriata*	Chrysophyta
Spirogyra porticalis	Chlorophyta	*Achnanthes minutissima var. minutissima*	Chrysophyta
Rhizoclonium hieroglyphicum	Chlorophyta	*Cocconeis pediculus*	Chrysophyta
Spirogyra decimina	Chlorophyta	*Cymbella cistula*	Chrysophyta
Cladophora glomerata	Chlorophyta	*Epithemia turgida*	Chrysophyta
Spirogyra dubia	Chlorophyta	*Navicula radiosa*	Chrysophyta
Spirogyra pratensis	Chlorophyta	*Fragilaria crotonensis*	Chrysophyta
Spirogyra spp.	Chlorophyta	*Gomphonema truncatum*	Chrysophyta
Ulothrix zonata	Chlorophyta	*Gomphonema dichotomum*	Chrysophyta
Mougeotia genuflexa	Chlorophyta	*Pinnularia subgibba*	Chrysophyta
Mougeotia parvula	Chlorophyta	*Eunotia* spp.	Chrysophyta
Oedogonium spp.	Chlorophyta	*Gomphonema maclaughlinii*	Chrysophyta
Zygnema leiospermum	Chlorophyta	*Gomphonema parvulum*	Chrysophyta
Oedogonium spp.	Chlorophyta	*Gomphonema angustum*	Chrysophyta
Mougeotia spp.	Chlorophyta	*Synedra delicatissima*	Chrysophyta
Chaetophora attenuata	Chlorophyta	*Cocconeis placentula var. euglypta*	Chrysophyta
Ulothrix spp.	Chlorophyta	*Neidium affine*	Chrysophyta
Zygnema sterile	Chlorophyta	*Craticula cuspidata*	Chrysophyta

Snake Valley	Division	Snake Valley	Division
Navicula tripunctata	Chrysophyta	*Lyngbya aerugineo-coerulea*	Cyanophyta
Anomoeoneis vitrea	Chrysophyta	*Gomphosphaeria aponina*	Cyanophyta
Epithemia argus	Chrysophyta	*Tolypothrix* spp.	Cyanophyta
Navicula cryptotenella	Chrysophyta	*Lyngbya martensiana*	Cyanophyta
Aulacoseira italica	Chrysophyta	*Scytonema crispum*	Cyanophyta
Gomphonema intricatum	Chrysophyta	*Calothrix epiphytica*	Cyanophyta
Fragilaria capucina var. mesolepta	Chrysophyta	*Nostoc* spp.	Cyanophyta
Aulacoseira subarctica	Chrysophyta	*Oscillatoria limosa*	Cyanophyta
Melosira varians	Chrysophyta	*Chroococcus dispersus*	Cyanophyta
Fragilaria construens	Chrysophyta	*Lyngbya epiphytica*	Cyanophyta
Navicula erifuga	Chrysophyta	*Synechococcus* spp.	Cyanophyta
Cymbella lunata	Chrysophyta	*Chroococcus limneticus*	Cyanophyta
Anomoeoneis sphaerophora	Chrysophyta	*Calothrix stagnalis*	Cyanophyta
Gomphonema minutum	Chrysophyta	*Heteroleibleinia kuetzingii*	Cyanophyta
Pleurosigma delicatulum	Chrysophyta	*Cyanobium* spp.	Cyanophyta
Sellaphora laevissima	Chrysophyta	*Oscillatoria bornetii*	Cyanophyta
Navicula lacustris	Chrysophyta	*Oscillatoria tenuis*	Cyanophyta
Achnanthes linearis	Chrysophyta	*Aphanothece saxicola*	Cyanophyta
Cymbella turgidula	Chrysophyta	*Oscillatoria agardhii*	Cyanophyta
Cymbella minuta	Chrysophyta	*Oscillatoria splendida*	Cyanophyta
Epithemia adnata var. proboscidea	Chrysophyta	*Coelosphaerium aerugineum*	Cyanophyta
Synedra acus	Chrysophyta	*Aphanothece stagnina*	Cyanophyta
Navicula salinarum	Chrysophyta	*Lyngbya diguetii*	Cyanophyta
Rhoicosphenia abbreviata	Chrysophyta	*Oscillatoria nigra*	Cyanophyta
Amphipleura pellucida	Chrysophyta	*Pseudanabaena* spp.	Cyanophyta
Rhopalodia gibba	Chrysophyta	*Stigonema* spp.	Cyanophyta
Diatoma vulgaris	Chrysophyta	*Aphanocapsa incerta*	Cyanophyta
Tryblionella apiculata	Chrysophyta	*Chroococcus* spp.	Cyanophyta
Cymbella silesiaca	Chrysophyta	*Cylindrospermum* spp.	Cyanophyta
Nitzschia closterium	Chrysophyta	*Lyngbya versicolor*	Cyanophyta
Cymbella microcephala	Chrysophyta	*Aphanothece smithii*	Cyanophyta
Fragilaria construens var. veneta	Chrysophyta	*Synechocystis* spp.	Cyanophyta
Ctenophora pulchella	Chrysophyta	*Lyngbya limnetica*	Cyanophyta
Nitzschia paleacea	Chrysophyta	*Microcystis* spp.	Cyanophyta
Ophiocytium cochleare	Chrysophyta	*Chroococcus turgidus*	Cyanophyta
Nitzschia frustulum	Chrysophyta	*Synechococcus sigmoideus*	Cyanophyta
Amphora veneta	Chrysophyta	*Chamaesiphon incrustans*	Cyanophyta
Navicula cincta	Chrysophyta	*Chamaesiphon confervicolus*	Cyanophyta
Nitzschia spp.	Chrysophyta	*Oscillatoria acutissima*	Cyanophyta
Achnanthes exigua	Chrysophyta	*Anabaena* spp.	Cyanophyta
Amphora coffeaeformis	Chrysophyta	*Homoeothrix* spp.	Cyanophyta
Rhopalodia gibberula	Chrysophyta	*Komvophoron* spp.	Cyanophyta
Rhopalodia musculus	Chrysophyta	*Coelomoron pusillum*	Cyanophyta