

Dispersal limitations and history explain community composition of metaphyton in desert springs of the Bonneville Basin, Utah: A multiscale analysis

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Abstract

We examined patterns of metaphyton community composition from 150 sites in spring wetlands of the Bonneville Basin across three spatial scales: valleys, wetlands nested in valleys, and habitat types nested in wetlands (springs, channels, and marshes) to determine which scale(s) accounted for the greatest variation in metaphyton community composition. We expected local processes at the habitat scale, especially physico-chemical differences between springs and marshes, to account for the majority of variation in local community composition but found that the valley scale accounted for 6.3 times more variation than the habitat scale. We suggest the importance of factors that operate at the valley scale, such as historical events (i.e., the draining of ancient Lake Bonneville) and island effects (dispersal limitations) in determining metaphyton community composition. We emphasize that dispersal limitations among valleys may have an important effect on metaphyton community composition despite the prevailing opinion that algae have exceptional powers of dispersal attributed to the worldwide distribution of some species. We base this assertion on three observations: first, the absence of species in isolated springs compared to springs associated with large complexes; second, 67% of the taxa in the Bonneville Basin occurred in only three or fewer sites; and third, the average Bray-Curtis similarity between all sites based on all taxa (242) was only 14.1%, which is an unlikely low value if metaphyton taxa can freely disperse between sites. Future studies should incorporate the potential importance of history and dispersal limitations as researchers continue to explore patterns of algal community composition across multiple scales.

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

The Bonneville Basin is distinguished by parallel north-south mountain ranges separated by broad, alluviated valleys (Christiansen 1951) where evaporation (60 cm yr⁻¹ to 106.7 cm yr⁻¹) greatly exceeds precipitation (14.8 cm yr⁻¹ to 28.7 cm yr⁻¹; Desert Research Institute, annual average minimum and maximum values from 1960 to 2005). Wetlands that range in size from small individual springs (<1.0 m²) to large spring complexes (>100 km²)

are scattered along the base of the mountains and throughout the valley floors. Multiple springs in large complexes are often connected by natural channels that flow between springs and into shallow marshes.

Habitats in spring ecosystems of the Bonneville Basin (springs, channels, and marshes) feature one of the most important contrasts known to effect community composition: constant vs. variable environmental conditions (e.g., Southwood 1977). Spring wells are one of the most constant aquatic habitats on Earth, whereas 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; Anderson et al. 2005). By contrast, the chemical conditions of marshes (e.g., oxygen, pH, and nutrient levels) fluctuate on a daily basis as photosynthesis and total community respiration respond to changes in solar irradiation (Wetzel 2001). Also, marshes tend to dry as the summer progresses. Hydrodynamics (water level fluctuation) is one of the most important local factors effecting algal community composition in wetlands (Goldsborough and Robinson 1996).

Benthic algal associations can be identified (e.g., epilithon, epipelon, epiphytic) based on their preferred substratum (Round 1981). Metaphyton consists of macroscopic stalks that float up or away from solid surfaces (e.g., vascular plants) during the spring to form partially suspended masses of filamentous green algae and associated microscopic epiphyton (e.g., Borchardt 1996; Goldsborough and Robinson 1996). We decided to study metaphyton because it is the most conspicuous type of algae in springs of the Bonneville Basin. Goldsborough and Robinson (1996) described the factors that produce four

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stable states in wetland algal communities (Open, Dry, Sheltered, and Lake). Springs around the world epitomize the “sheltered state” which is characterized by metaphyton (Goldsborough and Robinson 1996). To our knowledge, the community composition of metaphyton in spring ecosystems has not been explored, although epiphytic diatoms have been identified from two springs in the Great Basin (Grimes et al. 1980; Kaczmarek and Rushforth 1984).

Local community composition is determined by multiple factors operating at different scales (e.g., Wiens 1989). For example, physico-chemical conditions (water chemistry) and biotic interactions can exclude species at local scales, whereas historical events and dispersal limitations can restrict local community composition at large scales (MacArthur and Wilson 1967; 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.

Local factors are often emphasized as the primary determinants of algal community composition in freshwaters (e.g., Stevenson et al. 1996). Consequently, we expected local processes, especially physico-chemical heterogeneity between habitats (springs and marshes), to determine local community composition of metaphyton in springs of the Bonneville Basin. However, our multiscale design allowed us to infer the potential importance of large-scale processes, such as historical events and dispersal limitations. Freshwater algae are commonly thought to possess exceptional powers of dispersal because many taxa have a cosmopolitan distribution (e.g., Round 1981; Finley and Clarke 1999). 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 1991), algal dispersal is rarely studied in freshwater ecosystems.

This is the first study to explore the processes that effect community composition of freshwater benthic algae across multiple spatial scales. 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) accounting for the greatest variation in metaphyton community composition.

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. We expected the greatest variation in community composition between habitat types (springs vs. marshes) more than between wetlands within valleys, or between valleys in the Bonneville Basin. Second, metaphyton community composition would not differ between

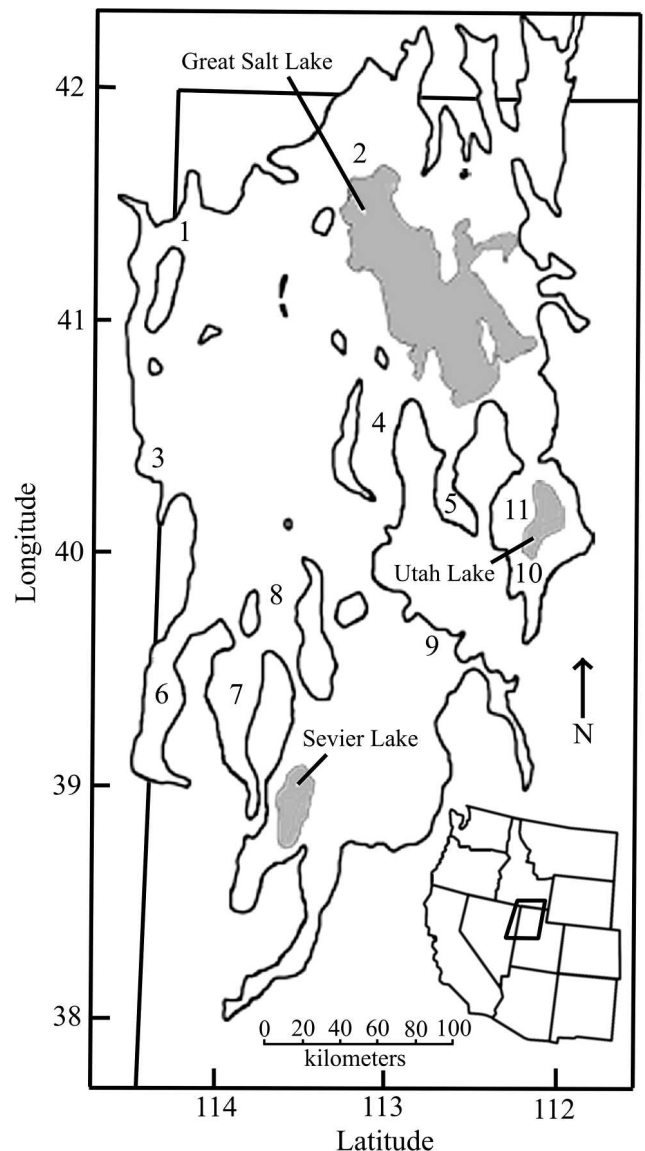


Fig. 1. Eleven valleys sampled in the Bonneville Basin of Utah. The solid boundary shows ancient Lake Bonneville at its highest level (16,000 years ago). The shaded areas show extant remnants of Lake Bonneville. (1) Grouse Creek, (2) Curlew, (3) Ibapah, (4) Skull, (5) Rush, (6) Snake, (7) Tule, (8) Fish Springs, (9) Mills, (10) Goshen, (11) Utah.

isolated springs and large spring complexes. We expected that island effects attributed to isolation (dispersal limitations) would not affect local community composition because of the prevailing impression that algae have a cosmopolitan distribution attributed to exceptional powers of dispersal (e.g., Fritsch 1953; Kristiansen 1996).

Methods

Study area and site selection—The Bonneville Basin is the eastern-most drainage in the Great Basin geological province. It is defined by the area once covered by Lake Bonneville during the Pleistocene (Fig. 1). The scope of this study was restricted to springs below the highest shoreline

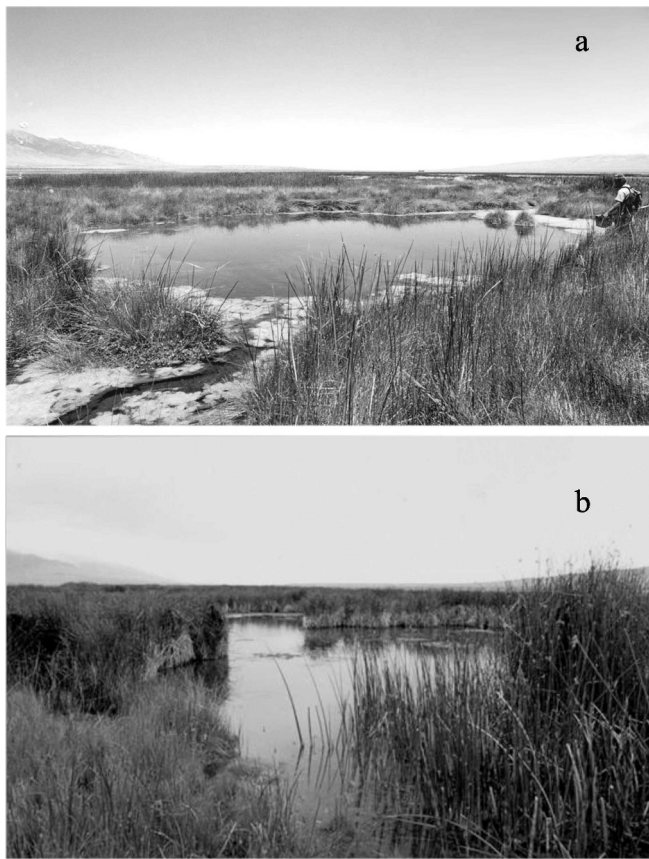


Fig. 2. Photograph of typical (a) spring with outflow channel and (b) marsh.

of ancient Lake Bonneville. Nearly 16,000 years ago Lake Bonneville reached its maximum level of 1,626 m a.s.l., covered $\sim 51,720$ km², and had depths up to 370 m (Benson et al. 1990). About 14,500 years ago the lake breached its northern rim and drained to an elevation of 1,320 m a.s.l. in less than one year (Benson et al. 1990). Over the next 4,000 years, it gradually declined, leaving current remnants (e.g., Great Salt Lake, Utah Lake) including the springs of this study (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 11 valleys, and valleys were nested in the Bonneville Basin, which we defined as the regional scale. Wetland complexes contained multiple springs connected by channels and marshes, whereas isolated wetlands usually consisted of a single spring. Isolated springs were separated from the nearest aquatic habitat by tens of kilometers to hundreds of kilometers, whereas springs in complexes were only separated by tens of meters to hundreds of meters.

Springs consisted of a groundwater inflow (wellhead), slow flowing lentic conditions, and a narrow band of riparian vegetation surrounding a quasi-circular basin (Fig. 2). We used aerial photographs, resource managers,

and personal experience to characterize the effects of humans on each valley (e.g., grazing allotments, years since grazed, urbanization, nonnative species). We used this information to locate springs that we expected to be least affected by human activities in each valley. We then determined the condition of each site based on visual estimates of livestock use (e.g., percent of area grazed or trampled), presence of nonnative species, and urban effects (e.g., distance to fences and water diversions) to locate the least-affected springs in each valley (Keleher and Rader unpubl. data).

Metaphyton was sampled once during the summer at all sites. Winter dieback of metaphyton is common in these systems. Thus, we avoided sampling during periods of rapid change (spring and autumn) to minimize seasonal effects. Samples were collected over three months from the last week in May through the second week in August in 2001 and 2002.

Selecting habitat types (sites) in isolated wetlands was simple because 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 in order 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 three to five of the three habitat types if all three were present.

Physico-chemical data—We recorded the location (using a Universal Transverse Mercator [UTM] grid) and recorded elevation, maximum water depth, and general substrate type at each site (organic, clay, silt, sand, and gravel). We estimated the maximum surface area (maximum length \times 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 model HI-8314 pH meter) at the source in all springs.

We compared only 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 from day to night 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 recorded mean temperatures every 3 h for 1 yr (*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 between habitats. Fish Springs is a nature preserve and a typical representative of large complexes.

Metaphyton—Our sampling scheme integrated across microspatial differences in metaphyton community composition. Three samples were taken at different locations from metaphyton suspended at a similar depth at each site (<10 cm deep), 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 index finger and trimmed to the same length with scissors. Samples were pulled from the center to the periphery of the suspended material to integrate across differences in species composition attributed to depth. Other procedures were less reliable at providing an integrated sample (e.g., lifting a Styrofoam pad through the metaphyton). 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 125 \times , whereas smaller algae were counted at 500 \times and 1,250 \times 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; Hillebrand et al. 1999). The biovolume of each taxon 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 living algal biomass (Wetzel and Likens 1991).

Statistical analyses—To test the first hypothesis, we used nonmetric multidimensional scaling (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, and then a wetland, and finally a valley in one of the three 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 was run using algal biovolume with a $\ln(x + 1)$ transformation and was obtained using Primer v6 (Primer-E Users Manual, Clarke and Warwick 2001; Clarke and Gorley 2006) and

the Bray-Curtis index (*BC*) of community similarity:

$$BC = 1 - \frac{\sum_{i=1}^n |X_{ij} - X_{ik}|}{\sum_{i=1}^n (X_{ij} + X_{ik})} \quad (1)$$

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 (Southwood and Henderson 2000). We also used an analysis of similarities permutation procedure (ANOSIM) and an analysis of species contributions (SIMPER, Primer E) to test for differences in community composition and to determine which taxa accounted for the greatest percentage of similarity, respectively, in community composition between the classes of each model (Clarke and Warwick 2001). ANOSIM is a non-parametric permutation procedure that measures the extent to which communities in the classes of a model overlap (Mielke and Berry 2001).

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 (\bar{W}_j) of a model minus the average similarity of sites *between* all classes in a model (\bar{B}) or $CS = \bar{W} - \bar{B}$, with

$$\bar{W} = \sum \frac{n_j}{N} W_j \quad (2)$$

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. 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. Thus, we judged the relative effectiveness of each model in accounting for variation in metaphyton community composition by comparing their *CS* values with the *CS* value of a reference model created from the species list 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 metaphyton 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). Models with a relative classification strength of 100% would

Table 1. Mean and range (in italics) of physico-chemical measurements of springs in valleys 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	pH	DO (mg L ⁻¹)
Grouse Creek (6)	1,618 <i>1,378–1,778</i>	438 <i>64–1200</i>	1.0 <i>0.3–>3.0</i>	16.8 <i>12–21</i>	0.6 <i>0.1–1.0</i>	7.7	6.6 <i>2.1–14.0</i>
Curlew (2)	1,294	900	1.0 <i>0.1–2.0</i>	20	2.1	8.8	11.1
Ibapah (4)	1,626 <i>1,625–1,632</i>	16 <i>5–25</i>	1.4 <i>0.5–>2.0</i>	16.1 <i>13–19</i>	1.0 <i>1.0–1.0</i>	7.5–7.8	4.9 <i>3.6–7.5</i>
Skull (2)	1,311 <i>1,307–1,314</i>	717 <i>33–1400</i>	1.5 <i>2.0–>3.0</i>	25.2 <i>25–26</i>	0.2 <i>0.1–0.3</i>	—	6.5 <i>4.3–8.7</i>
Rush (2)	1,696 <i>1,686–1,703</i>	35 <i>15–60</i>	1.4 <i>1.3–1.5</i>	9.5 <i>9–10</i>	0.5 <i>0.5–0.6</i>	7.5–7.7	5.4 <i>4.0–6.8</i>
Snake (57)	1,446 <i>1,457–1,490</i>	101 <i>1–600</i>	1.6 <i>0.2–4.0</i>	14.3 <i>11–22</i>	0.9 <i>0.2–1.0</i>	7.1–9.1	3.8 <i>0.3–9.4</i>
Tule (8)	1,357 <i>1,347–1,369</i>	100 <i>50–200</i>	1.4 <i>0.3–2.3</i>	28.9 <i>18–30</i>	0.9 <i>0.6–1.0</i>	7.6–8.1	1.4 <i>1.3–1.8</i>
Fish Springs (14)	1,323 <i>1,315–1,332</i>	420 <i>50–850</i>	2.2 <i>0.6–>3.5</i>	25.5 <i>16–32</i>	1.1 <i>0.2–1.7</i>	7.5–7.7	4.3 <i>1.6–7.0</i>
Mills (3)	1,484 <i>1,342–1,524</i>	33 <i>25–50</i>	0.8 <i>0.6–1.0</i>	18.3 <i>15–25</i>	1.0 <i>1.0–1.0</i>	7.6–8.8	7.7 <i>4.7–13.3</i>
Goshen (11)	1,482 <i>1,391–1,509</i>	204 <i>5–900</i>	1.1 <i>0.5–>3.0</i>	18.1 <i>12–21</i>	0.9 <i>0.5–1.3</i>	7.4–8.0	4.1 <i>2.7–6.6</i>
Utah (16)	1,394 <i>1,387–1,512</i>	138 <i>2–711</i>	1.3 <i>0.1–>3.0</i>	12.9 <i>11–19</i>	0.7 <i>0.1–1.0</i>	6.7–8.3	5.2 <i>0.4–10.0</i>

perfectly correspond with the reference model and would account for 100% of the variation in community composition.

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 showed considerable variation between sites. Elevations ranged from 1,294 m a.s.l. to 1,778 m a.s.l. with an average of 1,450 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 occurred in Snake Valley, Tule Valley, and Fish Springs. Maximum water depth was occasionally 2.5 m, but averaged only 0.84 m (Table 1). All springs in this study were fed by fresh groundwater typically ranging from 0.1 to 1.0 with an overall mean of 0.9 (Table 1). The pH varied from 6.7 (Utah Valley) to 9.1 (Snake Valley), whereas dissolved oxygen concentrations (DO) ranged from 0.3 mg L⁻¹ in Snake Valley to 14.0 mg L⁻¹ in

Grouse Creek. Springs in Curlew and Mills Valley had the highest mean concentration of DO (11.0 mg L⁻¹ and 7.7 mg L⁻¹), whereas springs in Tule Valley had the lowest (1.4 mg L⁻¹). Except for elevation, physico-chemical attributes varied as much between springs in the same valley as they did between springs in different valleys (Table 1).

As expected, environmental variation was much greater in marshes vs. springs and intermediate in channels. In particular, water temperature variation was low at the spring inflow and increased with distance from the spring source through the channel and into the marsh. 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 inflow (7.7°C; 12.5%).

The Bonneville Basin—We sampled metaphyton in each habitat type in all 11 valleys. Four metaphyton divisions and 242 taxa were collected. Although diatoms (Bacillariophyta; 48%) and blue-green algae (Cyanophyta; 30%) accounted for 78% of the total richness, Chlorophytes comprised the majority of the algal biovolume (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 epiphytes reached high densities, their biovolume was always much lower than the large filamentous stalks of the chlorophyte taxa. However, some non-chlorophyte taxa were also well represented (Table 3). For example, *Synedra ulna* var. *subaequalis* (Bacillario-

Table 2. Relative abundance of metaphyton divisions (percent of the total biovolume for all sites) 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

phyta) produce narrow, needle-shaped, solitary cells with one end of their frustule attached 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 geminata* are filamentous golden-brown algae (Chrysophyta) that also form mats comprised of large stalks.

Contrary to our first hypothesis, metaphyton community composition showed considerable variation among sites.

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

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

The average Bray-Curtis similarity between all sites was only 14.1%. Thirty-two different metaphyton species were the single most dominant taxa in at least one site. 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. geminata* (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%). *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. geminata* in both channels and marshes. Despite such differences, however, community composition only differed between two of the three habitats.

As predicted, ANOSIM showed that metaphyton community composition differed between springs and marshes ($R = 0.059$, $p = 0.02$), but differences between springs and channels ($R = 0.056$, $p = 0.10$) and between channels vs. 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 (Fig. 3a). The average Bray-Curtis similarity among sites in springs, channels, and marshes was 11.8%, 11.9%, and 8.8%, respectively.

Similarity percentage (SIMPER) analysis showed that the dissimilarity in community composition between springs and marshes was partially attributed to three taxa. The biovolume of *Denticula kuetzingii* (Bacillariophyta) and *C. glomerata* was nearly three times greater in springs, whereas the biovolume of *Rhizoclonium hieroglyphicum* (Chlorophyta) was nearly four times greater in marshes.

Overall, springs contained 57 species that were not collected in other habitat types; marshes contained 37 potentially unique species, and channels had 11 species. Channels contained the fewest number of “unique” taxa presumably because species from both springs and marshes could find suitable conditions in channels because physico-chemical conditions in channels were intermediate between marshes and springs.

Wetland comparisons—Four valleys were dropped from comparisons at the wetland and valley scales because of an

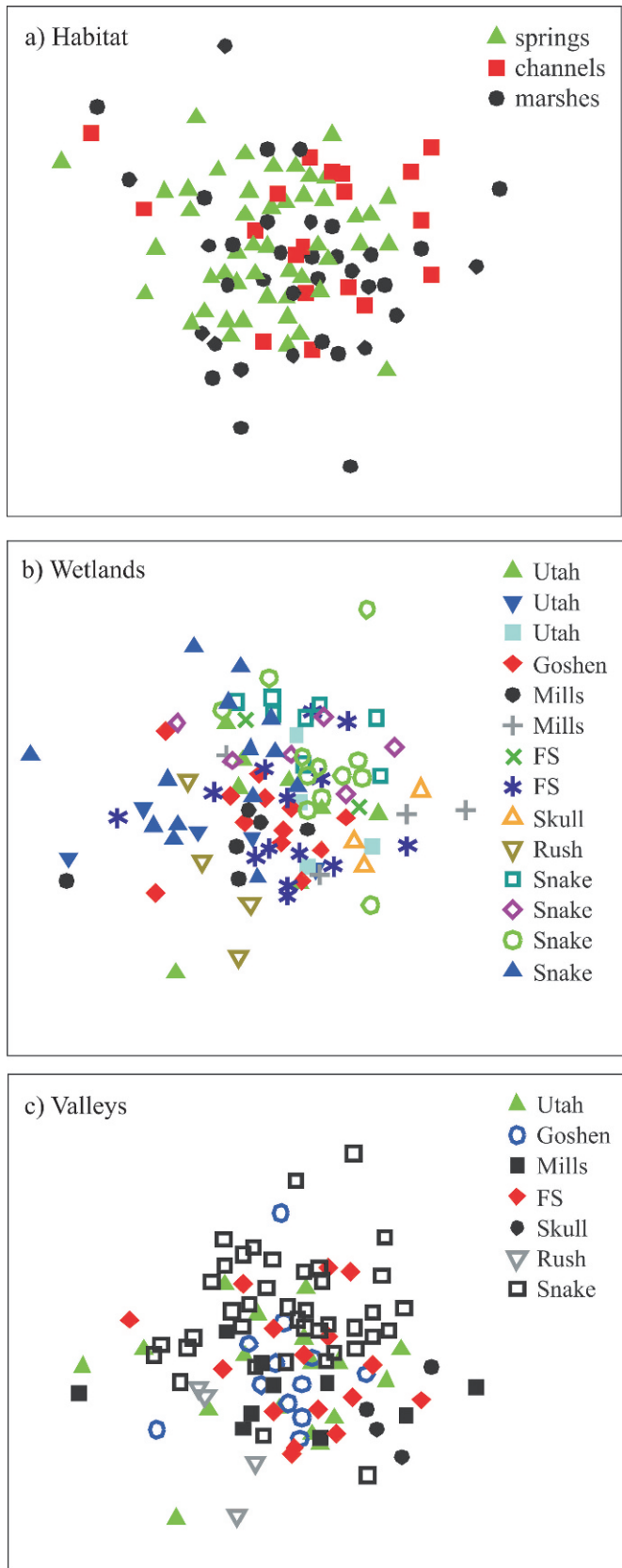


Fig. 3. Ordination biplots showing all sites grouped by (a) habitat type, (b) wetlands, and (c) valleys for metaphyton in the Bonneville Basin. The stress is 0.19 for all three plots and FS shows the wetlands in Fish Springs Valley.

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 (Fig. 3b). Community similarity was different (51.6%; $p < 0.05$) in 47 of the 91 pairwise comparisons among wetlands. Interestingly, 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. Thus, differences between wetlands were attributed to differences at the valley scale.

Valley comparisons—Again there was considerable variation in community composition within a valley and considerable overlap between valleys (Fig. 3c). However, 11 of 21 pairwise comparisons of community composition were significantly different ($p < 0.05$). Much of this variation was attributed to differences in biovolume among the dominant taxa. For example, two valleys (Curlew and Iapah) were dominated by filamentous chlorophytes that were rare (<5% relative abundance) in all other valleys (*Sirogonum floridanum*, *Mougeotia* sp., and *Rhizoclonium hieroglyphicum*). 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 (Fig. 4). Four isolated springs are clearly similar to springs that occur with large complexes presumably because they occur in valleys with large complexes. The remaining isolated springs occur in valleys without large complexes. Differences between isolated springs and springs in complexes primarily reflect the absence of taxa in isolated springs. We identified 173 taxa from springs in complexes and 50 taxa from isolated springs. One hundred and thirty taxa collected from springs in complexes were absent in isolated springs, whereas only seven taxa collected in isolated springs were absent from springs in complexes. We were surprised to find significant isolation effects because of the prevailing opinion that algae have exceptional dispersal capabilities.

Model comparisons—The valley and wetland models accounted for the greatest variation among sites in metaphyton community composition (Table 4). Contrary to our predictions, the habitat model was least effective at accounting for variation in community composition, whereas the isolation model was nearly as effective as the valley model.

Discussion

Discussions about the factors that determine patterns of community composition in freshwater algae invariably

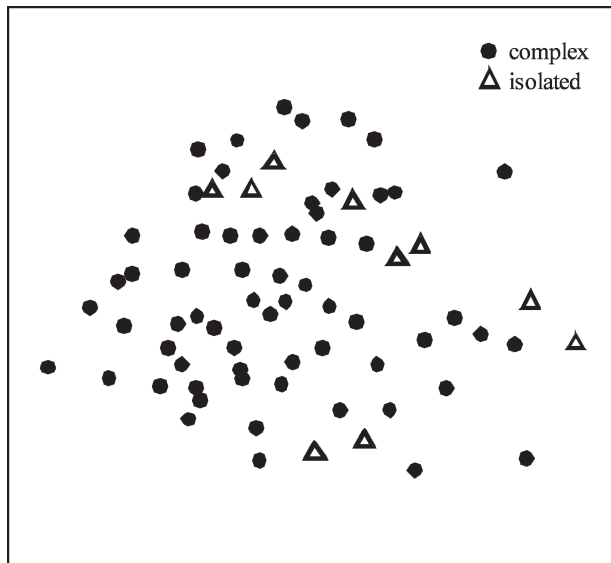


Fig. 4. An ordination biplot showing differences in the community composition of metaphyton in isolated springs vs. springs in complexes of the Bonneville Basin. The stress for this plot is 0.21.

focus on local factors. Recent summaries devote chapters to describing the effects of light, water temperature, microcurrents, 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 (springs and marshes) to account for the majority of variation in community composition. Instead, the same habitat type in different wetlands and especially in different valleys showed considerable variation in community composition. To our surprise, the valley model accounted for 6.3 times more variation than the habitat model.

We suggest that factors operating at the valley scale are important in determining differences in metaphyton community composition. Two results support this assertion. First, the valley model accounted for the greatest variation in metaphyton community composition and second, 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 within the same valley. That is, the only reason that the wetland scale accounted for significant variation was because of differences between valleys.

Historical events and dispersal limitations are common explanations when patterns of local community composition emerge at large scales (Connelly and Roughgarden 1999; Webb et al. 2002). We offer three explanations for why the valley scale accounted for the greatest variation in local metaphyton community composition: (1) habitat heterogeneity and species sorting at the valley scale, (2) dispersal limitations between valleys, and (3) differences in the respective histories of the valleys. The habitat heterogeneity hypothesis describes how a subset of species from the region pool is able to persist in some valleys but not others. It assumes that all species can freely disperse to all valleys and that physico-chemical attributes at the valley scale determine which species ultimately gain membership in the community. The validity of this hypothesis depends on whether physico-chemical attributes are more uniform within valleys than between valleys. We found that physico-chemical attributes lacked uniformity at the valley scale. Instead, physico-chemical conditions differed between wetlands in the same valley and even between springs in the same wetland complex. For example, temperatures in springs at the Fish Springs Nature Preserve (a large wetland complex) varied from 16°C to 32°C. Thus, we found no evidence to support the habitat heterogeneity explanation.

Island biogeography theory describes how island isolation and size are important in limiting rates of colonization because of the difficulty of dispersing over long distances to small islands (MacArthur and Wilson 1967). We suggest that dispersal limitation between valleys is a plausible explanation for why the valley scale accounted for the greatest variation in community composition. First, the isolation model was almost as strong as the valley model. That is, community composition in isolated springs differed from springs in large complexes because of the absence of

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	—

species in isolated springs that occurred in larger complexes. Also, 67% of the taxa in the Bonneville Basin had a localized distribution and only occurred in three or fewer sites. Thus, the average Bray-Curtis similarity between all sites was very low (14.1%). If metaphyton can freely disperse between sites, then there should be no difference between isolated springs and springs in complexes, and the overall community similarity between sites with similar physico-chemical attributes (e.g., marshes) should be high but was instead very low (8.8%).

The importance of dispersal limitations in constraining the membership of algal communities has rarely been investigated (Round 1981; Foissner 2006). The paucity of information on dispersal in algal communities is related to the difficulty of studying this process and the prevailing opinion that most algae have excellent powers of dispersal (e.g., Kristiansen 1996; McCormick 1996). Recent studies have suggested that free-living microbial species, including algae, have a global distribution because of their vast numbers and small size, which facilitate dispersal (e.g., Finlay 2002; Fenchel and Finlay 2004; Londry et al. 2005). However, a recent review suggests that many microorganisms also have a restricted geographic distribution and that some taxa appear to be endemic (Foissner 2006). Endemic algal species are common in wetlands of Antarctica (Sabbe et al. 2003) and in lakes and springs of Australia (Tyler 1996). Foissner (2006) suggested that about 30% of microorganisms might be morphological and/or genetic endemics. We found that 67% of metaphyton taxa in desert springs of the Bonneville Basin appear to have restricted distributions. Based on Foissner's (2006) estimation, half of these may be endemic to individual springs or wetlands. Endemism is common among vertebrates and invertebrates in desert springs (e.g., Dumont 1982; Sluys et al. 2007). For example, species of spring snails (Hershler 1998) and amphipods (Witt et al. 2006) are endemic to single springs.

Stream investigations of benthic algae indicate a gradient in dispersal abilities between algal taxa with different growth forms and life-history traits (e.g., Stevenson and Peterson 1991). Although stream studies on dispersal have not been duplicated in wetlands, it is likely that wetland taxa also show a gradient in dispersal abilities. Traits that may promote dispersal in algae should increase resistance to desiccation and digestion in the guts of potential vectors (e.g., Kristiansen 1996). They may include: (1) thick-celled spores and cysts, (2) gelatinous envelopes in the vegetative stage, (3) majority of the life cycle in the encysted stage, (4) tolerant of a wide range of water quality conditions, and (5) lacking adhesive compounds that bind the cells to solid substrates.

History is also a plausible explanation for why valleys accounted for the greatest variation in community composition. Many of the vertebrates and invertebrates in springs of the Great Basin are relic taxa that took refuge in springs as desertification expanded nearly 10,500 years ago (Hubbs et al. 1974). If all springs started with the same complement of metaphyton species then we do not expect differences in community composition at the valley scale or between isolated springs and springs in complexes.

The first metaphyton propagules to colonize these springs were likely derived from the littoral zone of Lake

Bonneville as the shoreline receded. Spatial and temporal variation in the composition of metaphyton in the littoral zone could have caused different springs to be inoculated with different taxa. Initial colonists can have lasting effects on community composition. For example, Drake (1991) found that identical artificial ponds developed very different plankton communities when inoculated with different initial colonists. Springs in the same valley may have been inoculated with a similar suite of taxa at the same time because springs tend to occur at similar elevations within a valley but at different elevations between valleys. Subsequent dispersal between springs within the same valley would have had an additional homogenizing effect on community composition within valleys. Thus, differences in metaphyton community composition between valleys but not between wetlands within valleys in this study may have been set by the initial colonists and reinforced by more frequent dispersal within a valley than between valleys.

The influence of historical events and dispersal limitations on large scale patterns of species composition is widely recognized for a variety of terrestrial and aquatic communities (e.g., Menge and Olson 1990; Webb et al. 2002; Wiens and Donoghue 2004). Future research should incorporate the potential importance of history and dispersal limitations as we continue to explore patterns of algal community composition across multiple scales in freshwater communities.

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