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DIVERSITY OF BRYOZOANS IN THE UPPER MISSISSIPPI RIVER WATERSHED

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DIVERSITY OF BRYOZOANS IN THE UPPER MISSISSIPPI RIVER WATERSHED

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ABSTRACT

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The Mississippi River undergoes constant change, most notably through agriculture, irrigation, and damming. Physical and chemical factors within habitats affect food availability and habitat sustainability for existing native species. Disturbances in aquatic systems allow for establishment of non-native species, contributing to further changes to the ecosystem. Bryozoans are relatively unexplored in the Upper Mississippi River (UMR) watershed. Understanding bryozoan distributions across habitats and latitudes in this watershed will help lay groundwork for understanding how flow patterns, water usage, and temperature changes affect native and invasive bryozoans. My research provides a broad-scale distribution map of bryozoans within the UMR watershed by determining their relative abundance among five habitats: river main channels, backwaters, marshes, lakes, and vernal pools. Results indicate there are thirteen species of bryozoans in the UMR. While community composition was not significantly different across latitudes within the UMR, richness, abundance, and diversity of these species is significantly higher in lakes compared to river main channels and vernal pools. Bryozoans were mostly absent from vernal pools. While different aquatic habitats showed significant differences in bryozoan composition, environmental parameters (temperature, DO, specific conductivity, and pH) did not dictate trends in bryozoan community.

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INTRODUCTION

The connectivity between aquatic and terrestrial systems within the Upper Mississippi River watershed creates a mosaic of habitat types, from main channel systems to backwater habitats, marshes, lakes, and vernal pools. Habitat diversity, differences in substrate, and variations in flow regime supports the wide variety of organisms observed in the river (Wiener et al. 1998). The Upper Mississippi River (UMR Figure 1) is an ecologically, economically, and socially valuable system.

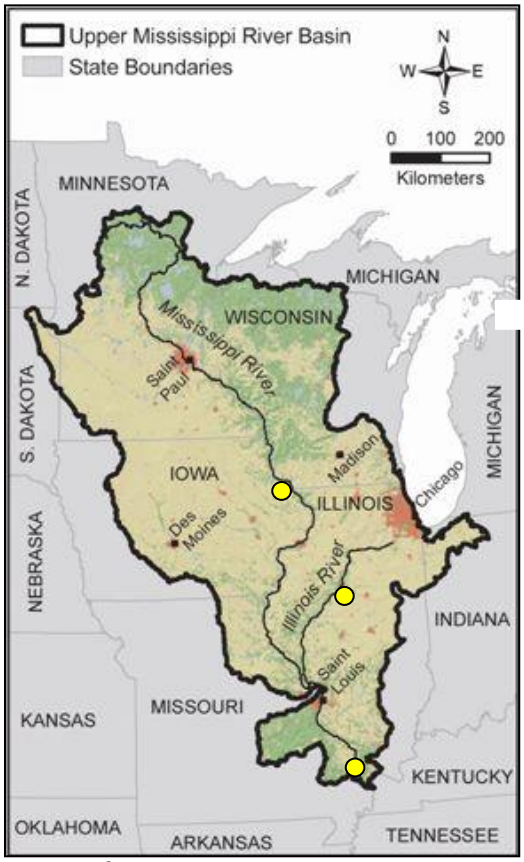

Figure 1. Map of the Upper Mississippi River Watershed (United States Fish and Wildlife Service). Circles indicate three latitudes sampled.

However, alteration through land clearance, irrigation, damming, and other anthropogenic uses have drastically changed the river over time. Prior to European settlement, the system was surrounded by a relatively untouched prairie-forest mosaic. Human-driven alteration of the river had already begun by the 1870's, and much of the floodplain forest that once framed the river was lost to farming, urbanization, and timber hauling. During the 1930's a lock-and-dam system was constructed along the UMR to provide a 2.7m deep navigation channel that could support commercial transportation and trade along the river (Wiener et al. 1998). The construction of the Lock and Dam system, along with land clearance and development, caused a significant increase in open water habitats, sediment deposition, and island loss. This drastic alteration of the Mississippi River resulted in the inundation of terrestrial habitats, thus extending the network of aquatic floodplains (Belby et al. 2015).

River systems are impacted globally by sediment loading, eutrophication, toxic pollution, and degradation of habitats (Hill et al. 2007). These disturbances allow for the establishment of non-native and invasive species. Large disturbance events, both natural and anthropogenic, decrease species richness and reduce the competitive advantage of native species, allowing exotics to establish (Bulleri et al. 2016). Changes in habitat and species invasion often result in the alteration of species assemblages and can be linked to high extinction rates (Ricciardi and Rasmussen 1999). These differences are evident across taxa, ranging from an increase in aquatic plant diversity and changes in fish species to changes in zooplankton abundance (Weiner et al. 1998).

One group of economically and ecologically significant, but extremely understudied, organisms are the Bryozoa (Animalia, Lophotrochozoa). Bryozoans are a

diverse group of sessile, filter feeding aquatic invertebrates that contains about 8,000 extant species (Waeschenbach 2012). Of these 8000 species, only 88 have successfully established in freshwater systems (Massard and Geimer 2008). They grow as colonies, composed of genetically identical individuals called zooids. Colonies grow in a number of forms, from mossy to gelatinous, and can grow up to a meter in size (Wood 2010). Bryozoans are found across a wide range of aquatic habitat types, including marshes, streams, lakes, and ponds, and can quickly become a nuisance.

In addition to being effective biofoulers, bryozoans can be successful exotic and invasive species. Since its introduction to the United States in the 1930's, *Lophopodella carteri* is thought to have been dispersed via the leaves of aquatic plants, which can often harbor statoblasts. It is now found across a wide range in North America (Wood and Marsh 1996). Other bryozoans are prime future invaders due to the ease of dispersal via statoblasts, an arrested developmental stage that aids in temporal and spatial movement. Eleven bryozoans species, including one established exotic species (*Lophopodella carteri*) and two species that had not been observed previously in the Great Lakes region were present in sediments found in the tanks of trans-oceanic ships in the Great Lakes, (Kipp et al. 2009). Both native and nonnative bryozoans rely on annual variations in temperature and photoperiod for prompts to germinate (Wood 2010). Modifications to the UMR have changed water residence time of aquatic systems and turbidity which can influence how bryozoans perceive germination cues. These modifications can impact migration times, hatching events, and spawning times (Walther et al. 2002).

There are nineteen species of bryozoan from the class Phylactolaemata found in North America. Of these species, three are endemic, one is introduced, and seven are

thought to be found in Wisconsin (Watermolen 2004). Another eleven species have been reported in the lakes of Indiana (Barnes 2003). However, species distribution of bryozoans across habitat types in the UMR watershed remains unexplored. Understanding the current distribution of bryozoans across the region is important to establish baseline information that will allow us to identify future points of invasion and to predict where certain species might become a nuisance. Additionally, this information will help us understand how altered flow patterns, changing water usage, and changing temperatures across latitudes may change patterns in bryozoan diversity and abundance in the UMR watershed. Here I present a regional survey of bryozoan communities in the UMR watershed. These data are used to test whether there are differences in species assemblages across five habitat types (lakes, river main channels, backwaters, marshes, and vernal pools) and three latitudes (at La Crosse, WI, Savannah, IL, and Alton, IL) that will help define bryozoan communities in terms of thermal gradients along the UMR. My hypothesis is that bryozoans will be more abundant in slower moving systems, such as lakes, backwater habitats, and marshes because these systems will allow statoblasts to settle, adhere to the substrate, and germinate.

MATERIALS AND METHODS

Description of study organisms: Bryozoa

There are 25 known species of bryozoans in North America. Fourteen species of bryozoan were found in eastern Canada, *Fredericella indica, Plumatella casmiana, Plumatella emarginata, Plumatella fruticosa, Plumatella fungosa, Plumatella orbisperma, Plumatella repens, Plumatella reticulata, Hyalinella punctata, Lophopodella carteri, Pectinatella magnifica, Cristatella mucedo,* and two species from the class Gymlactolaemata that do not produce statoblasts and are not of interest in this study (Ricciardi and Reiswing 1994). Prior research regarding bryozoans in the class Phylactolaemata and their distribution in the United States is limited. *Plumatella bushnelli, Plumatella vaihiriae, Plumatella casmiana,* and *Plumatella* sp. were found in a Florida lake (Taticchi et al. 2009). Species found in Michigan were *Plumatella repens, Plumatella fruticosa, Plumatella emarginata, Hyalinella punctata, Hyalinella orbisperma, Fredericella sultana, Paludicella articulata, Cristatella mucedo, Lophopodella carteri, Stephanella indica, and Stoella evelinae* (Bushnell 1965). Thirteen species of bryozoans (12 phylactolaemate) were found in northern Indiana lakes: *Fredericella indica, Fredericella browni, Hyalinella punctata, Plumatella casmiana, Plumatella emarginata, Plumatella fungosa, Plumatella orbisperma, Plumatella nitens, Plumatella reticulata, Pectinatella magnifica, Cristatella mucedo,* and *Paludicella articulata* (Barnes et al. 2003).

Bryozoans can reproduce sexually by producing sperm and egg clusters within the colony, but most reproduce asexually by creating new buds from existing colonies, splitting the existing colony, and the production of statoblasts, seed-like capsules filled with material capable of sprouting a new colony (Wood 2010). Statoblasts consist of two valves that contain a capsule with germinal tissue and a food source. The annulus contains chitinous, gas-filled chambers and can be produced at a rate of 1-20 statoblasts per zooid (Bushnell and Rao 1974, Hirose et al. 2011). Bryozoan statoblasts are either categorized as floatoblasts (floating resting structures), piptoblasts (simplified resting structures) or sessoblasts (sessile resting structures that are floating within the colony) (Wood and Marsh 1999, Bailey-Brock and Hayward 1984). Floatoblasts allow for large-scale dispersal in these passively-transported migrators. Simplified reproductive structures like piptoblasts may have evolved because they are less energetically expensive than more complex statoblasts. Sessoblasts allow for colonies to reestablish colonies in habitats known to be favorable.

Bryozoan statoblasts vary in morphology between species and, despite being highly variable within species, are a useful mode of species identification that can be conducted at any point during the season (Bushnell and Rao 1974). Statoblasts can be collected from the water column and sediment as well as from substrate scraping and epiphyte collections, which reduces the likelihood of overlooking small and concealed colonies (Ryland 1972, Hill et al. 2007, Sanzhak et al. 2012). Statoblasts are also easy to store and can withstand long periods in storage without marked degradation.

Site overview

Bryozoan communities were surveyed at three latitudes along the UMR to determine whether the species present in different habitat types varied along the thermal gradient along the watershed. Sampling sites were originally targeted using Google Earth and were clustered around three latitudes: La Crosse, Wisconsin (43.8°N); Savannah, Illinois (42°N); Alton, Illinois (38°N) (Figure 2: A, B and C respectively). Latitudes were selected based on river hydrology and the presence of each of the targeted five habitat types at each location. The goal was to select three latitudes that were equidistantly apart within the UMR watershed. Sites at each latitude were within approximately 20 miles from each other and latitudes were approximately 2° apart (Appendix A).

To compare bryozoan distributions across a range of habitat types, sample habitats were chosen to represent a range of lotic vs. lentic habitats that varied in connectivity to the main channel of the UMR. . The main channel of the UMR was sampled at each latitude. Backwater habitats were well-connected to the main channel and did not exhibit periods of significant drying, but had slower currents and shallower water than the main channel. Marshes were even more removed from the main channel, with periods of drying throughout the season. Lakes were not directly connected to the main channel and are systems with high water resident times. Some lakes, such as Neshonoc Lake and Perch Lake, had small river inflows and outfalls. Vernal pools were completely disconnected from the river; sites were far enough removed to ensure the river could not inundated during periods of high water level. They exhibit periodic drying throughout the year.

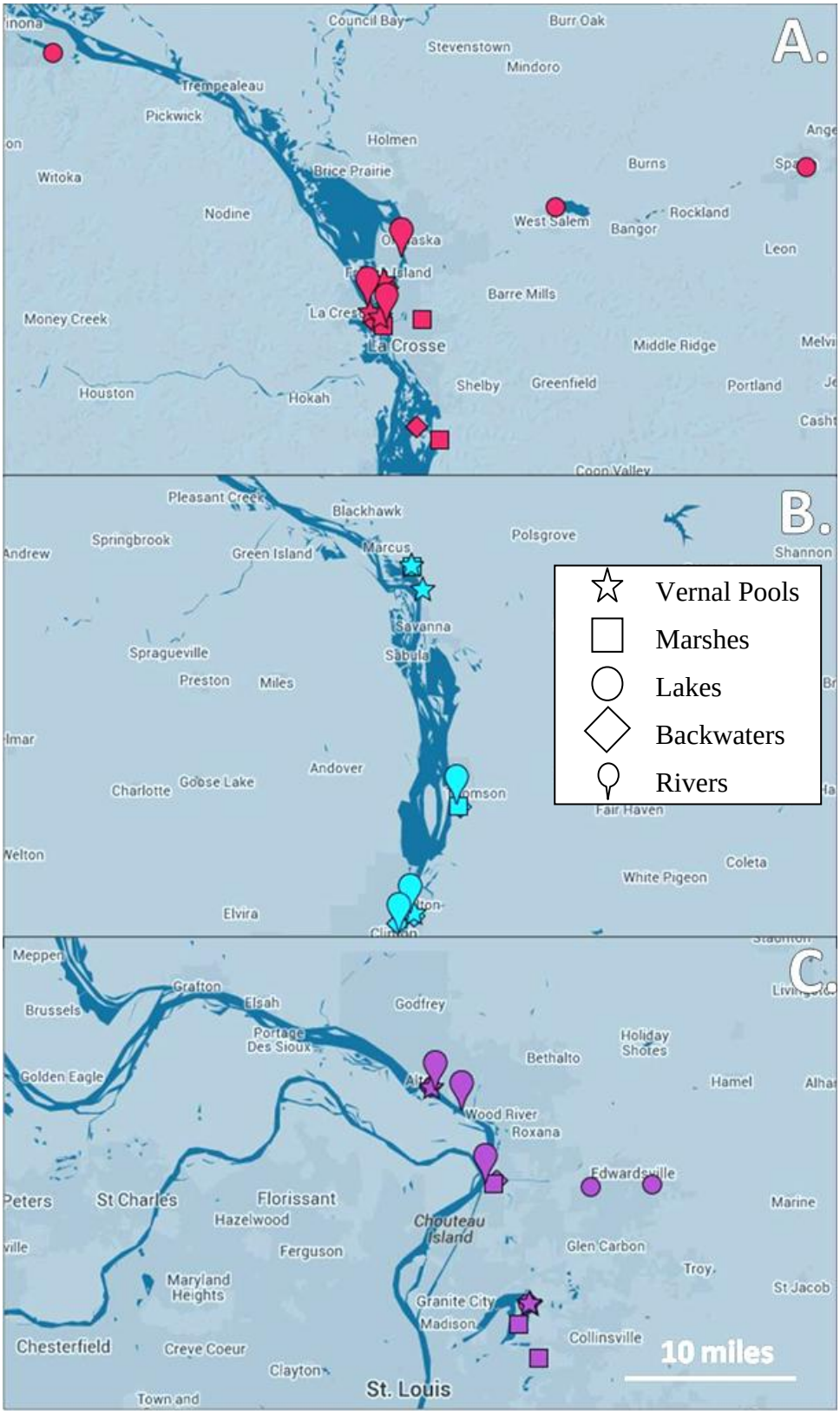

Figure 2. Sampling sites at A: La Crosse, WI, B: Savannah, IL, and C: Alton, IL.

Forty sites were sampled in total: nine vernal pools, eight marshes, eight backwaters, six lakes, and nine main channel habitats (Table 1).

Table 1. Sites sampled across three latitudes and five habitats

Habitat	Latitudes		
	La Crosse, WI	Savannah, IL	Alton, IL
River Main channel	Mississippi Main Channel La Crescent	Thomson Main Channel	Marina Main Channel
	Mississippi Main Channel Pettibone	Clinton Main Channel	Museum Main Channel
	Black River Beach	Fulton Main Channel	Lewis and Clark Main Channel
Backwater	Richmond Bay	Thomson Backwater	Alton Marina
	Goose Island Backwater	Clinton Marina	Lewis and Clark Canal
	La Crescent Backwater	Fulton Marina	Not-sampled
Marsh	Myrick Marsh	Hidden Slough Marsh	Lewis and Clark Marsh
	Pettibone Marsh	Palisades Marsh	Horseshoe Marsh
	Goose Island Marsh	Not sampled	Cahokia Marsh
Lake	Lake Winona	Not sampled	Horseshoe Lake
	Neshonoc Lake	Not sampled	Dunlap Lake
	Perch Lake	Not sampled	Tower Lake
Vernal Pool	Summit Frog Pond	Kiwanis Park Roadside	Marina Bridge Pool
	Shore Acres Vernal Pool	Great River Roadside	Granite City Roadside
	Pettibone Vernal Pool	Palisades Roadside	Horseshoe Vernal Pool

Fifteen sites were sampled near La Crosse, fourteen near Alton, and eleven near Savannah. Three of each of the five habitats were targeted at each latitude. However, some sites were inaccessible. Only two backwater habitats were sampled in Alton, IL as the UMR has been severely channelized at this latitude, restricting the number of suitable backwater habitats. Lakes were not sampled at Savannah, IL due to a lack of access points. Lakes visited at this latitude were surrounded by mostly private land. Only two marshes were sampled at Savannah, IL due to a lack of access points.

Sample collection

To develop a consistent sampling protocol that provided the maximum diversity of bryozoan statoblasts, a preliminary study was conducted in the La Crosse River (Myrick) Marsh to compare sampling methods. Four sampling methods were tested: 1) substrate scraping and sediment sieving; 2) shore and Ekman sediment sieving; 3) substrate scraping and wind row sieving; and 4) shoreline algae sieving and water sieving. A combination of sediment sieving, substrate scraping, water sieving, and aquatic vegetation sampling was chosen for use when sampling additional sites. Ekman dredging did not result in a more diverse sample and was difficult to conduct, so was not done during the final sampling method. Sampling is biased toward freshwater species that produce floating statoblasts (Class Phylactolaemata, excluding *Fredericella* species). One composite sample was taken at each site.

Statoblasts were collected from water and sediment at each site using a sieve (125µm sieve size). I filtered sediment from five locations along the shore to increase the likelihood that statoblasts deposited at different water heights were collected. I also scraped any prominent substrates (rocks, trees, etc.) at each site and washed the scrapings

through the sieve. Sediment and substrate scrapings were rinsed using water from the site, except for vernal pool sites that had dried earlier in the season. Sediment from dry vernal pool sites was rinsed using DI water back in the lab. Water and sediment was combined to make one composite sample per site. Once the sample had been rinsed, contents on the sieve were transferred into plastic containers. Samples were labeled and stored at room temperature until returning to the lab (within approximately 24 hours). Since statoblasts remain identifiable after germination and are capable of remaining intact in sediment cores for many decades, no degradation was expected during this 24 hour period.

Upon returning to the lab, approximately 25mL ethanol was added to each sample to slow the degradation of organic material. Water in each sample was exchanged and sediment was re-rinsed through a sieve using deionized water as needed to remove any decaying plant material in the sample. After each water exchange, an additional 25mL ethanol were added to preserve the sample. Each sample was then labeled and stored at 4°C until processing.

Using a dissecting microscope at 40x magnification, I repeatedly scanned the water surface, as well as the sediment and large detritus in each sample for statoblasts. Samples were searched for statoblasts in their storage container to reduce the likelihood of losing statoblasts during transfer between containers. All observed statoblasts were removed using a transfer pipet and placed in a petri dish and dried at room temperature. During preliminary sampling, no new species were encountered after 100 statoblasts were identified. Because of this, 100 statoblasts was the target sample size for species identifications. Up to 100 of the total statoblasts collected from each sample were

mounted using glycerin jelly between cover slips. Many samples did not have 100 total statoblasts. In those cases, all statoblasts were mounted. Only two sites had more than 100 statoblasts present. In those cases, only the first 100 encountered were identified. Identification took place using a light microscope at 100x magnification, a dichotomous key (Wood 2010), and images provided in Hartikainen et al. (2013).

Environmental Data Collection

Prior to sample collection, I calibrated the pH, dissolved oxygen (DO) and specific conductivity (SpC) probes according to the University of Wisconsin - La Crosse standard operating procedure. Approximately 0.5m from the shore at each site, I measured pH, temperature, DO, and SpC near the location at which sediment was collected using a Hydrolab Quanta multiprobe, allowing the reading to stabilize before recording each measurement.

Data analysis

Mean statoblast abundance, species richness (based on statoblast representation) and Shannon diversity were compared across habitat types and latitudes. Since less than 100 statoblasts were collected at all but 2 sites, overall mean statoblast abundance was averaged for each habitat type at each latitude. Species richness was calculated by summing the total number of species represented in the statoblast collection at each site. The Shannon index is a measure of diversity at each site and represents of the number of species present at each site in relation to distribution of species across sites and is computed as follows: $H = -\sum_{i=1}^{S} p_i * lnp_i$ where p is the proportion of individuals of one species divided by the total individuals and s is the number of species. Each response

variable (abundance, richness and Shannon's H) was evaluated independently using a two-way ANOVA with habitat type and latitude as independent variables.

To determine whether specific species of bryozoans varied across latitudes and habitat types I conducted two-way ANOVAs for each bryozoan species encountered. Relative abundances of bryozoan species were calculated by dividing the mean number of statoblasts of a given species by the total number of statoblasts collected at each site. Statoblast relative abundance, the dependent variable in these analyses, was normalized using arcsine square root transformation prior to statistical analysis. Habitat and latitude were used as the independent variables.

Bray-Curtis estimation was also performed to determine the degree of similarity between sites according to the relative abundances of species present at each site. This involves summing the differences between abundance values at two sites and dividing this by the sum of the differences between all sites. Lastly, I used a Bray-Curtis estimation to calculate habitat similarities based on measured environmental variables (pH, dissolved oxygen, temperature, and specific conductivity). Because environmental variables were collected at different times across latitudes, data was standardized by dividing measured values by latitude means. Bray-Curtis similarity estimations for relative abundance of bryozoans across sites were regressed with similarity of environmental variables to determine if sites with higher similarity in environmental factors also contained more similar bryozoan communities.

RESULTS

Habitat types showed significant differences in diversity, richness, and abundance, while latitudes were not significantly different (Table 2). Since diversity, richness, and abundance were not significantly different across latitudes, data were collapsed across latitudes and graphed only in terms of habitat type. Shannon diversity, richness, and abundance were significantly higher in lakes compared with vernal pools (Shannon Tukey's $p = 0.01$, richness Tukey's $p = 0.006$, abundance Tukey's $p = 0.034$)(Figure 3). In general, lakes contained the highest number of bryozoan statoblasts however the number was variable across systems.

Table 2. Summary of two-way ANOVA values testing the interactive effects of latitude and habitat on bryozoan Shannon index (H'), species richness, and abundance. df: degree of freedom, MS: mean squares, F: F-statistic, p: p-value. Bolded values are significant.

	Shannon index (H')				Richness				Abundance			
	df	MS	F	p	df	MS	F	p	df	MS	F	p
Intercept	1	11.3	35.63	0.00	1	237.5	38.27	0.00	1	19456.2	18.55	0.00
Habitat	4	1.2	3.76	**0.01**	4	25.6	4.12	**0.01**	4	2852.8	2.72	**0.05**
Latitude	2	0.3	0.86	0.43	2	0.4	0.06	0.94	2	360.4	0.34	0.71
Habitat * Latitude	7	0.1	0.38	0.91	7	1.8	0.29	0.95	7	463.4	0.44	0.86
Error	26	0.3	-	-	26	6.2	-	-	26	1048.5	-	-

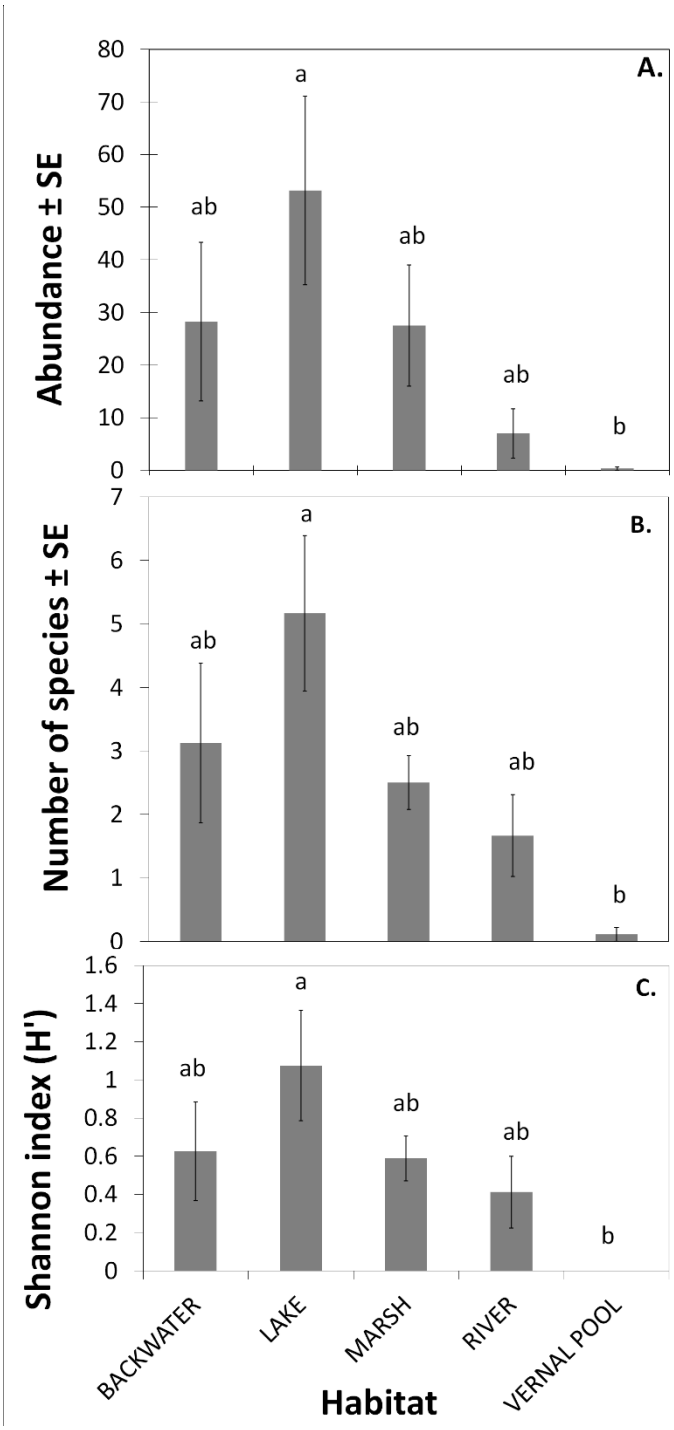

Figure 3. Bryozoan statoblast indices for five habitat types averaged across latitudes and replicate habitats sampled within latitudes. N=40. Bars indicate mean values ± standard deviation. A: Statoblast abundance, B: Species richness, C: Shannon index (H').

While overall data trends are better explained by habitat type, some species varied significantly across latitudes and habitat types. Statoblasts were found in 25 of the 40 sites sampled representing twelve species of bryozoans: *L. carteri, P. reticulata, P. emarginata, P. magnifica, P. vaihiriae, C. mucedo, P. fungosa, S. hina, P. casmiana, P. nitens, H. punctata,* and *P. fruticosa* (Table 2). I also identified a thirteenth category of bryozoans that I was unable to classify to species because their distinguishing characteristics could only be seen using a scanning electron microscope. These statoblasts were simply described as *Plumatella* spp. and include the species *P. rugosa, P. nodulosa, P. repens,* and *P. semilirepens.* These species are similar to those found in other surveys in the Upper Midwest.

Based on two-way ANOVA tests of relative abundance for species across habitat types and latitudes, the relative abundances of *C. mucedo*, *H. punctata*, *P. emarginata, P. fruticosa, P. fungosa, P. nitens*, *P. reticulata, P. vaihiriae, and S. hina* did not differ significantly across habitat types or latitudes ($p > 0.05$).

Two-way ANOVA tests did reveal significant trends in relative abundance of the four remaining bryozoan species. *L. carteri, P. casmiana, Plumatella* spp., and *P. magnifica* did exhibit trends based on latitude and/or habitat (see * in Table 2 and Figure 4). *L. carteri* was significantly higher in La Crosse, WI marshes (habitat: df=7, F=3.035, p=0.018) (Figure 4a). *P. casmiana* relative abundance was significantly higher in lakes compared to marshes, rivers, and vernal pools (Tukey post hoc comparisons: df= 4, F= 0.261, p=0.021; df= 4, F= 0.261, p=0.030; df= 4, F= 0.261, p=0.017, respectively) (Figure 4b). There was a significant difference in relative abundance of *Plumatella* spp. across latitudes (latitude: df= 2, F= 4.523, p=0.021), as well as a significant difference in

relative abundance between lakes: rivers, lakes:vernal pools, marshes: rivers, and marshes:vernal pools (Tukey post hoc comparisons: p=0.042, 0.015, 0.039, and 0.013 respectively)(Figure 4c). *P. magnifica* was present at eight sites. Relative abundance of *P. magnifica* was significantly higher in Savannah, IL compared to Alton, IL (latitude: p=0.036)(Figure 4d).

Table 3. List of the thirteen bryozoan species with overall N observed. All habitats and all latitudes in which each species were observed are listed. Asterisks represent habitats or locations where each species significantly differed in abundance. L: lake, M: marsh, B: backwater, R: river main channel, V: vernal pool. ALT: Alton, IL, LSE: La Crosse, WI, SAV: Savannah, IL.

Species	Overall N	Habitat observations	Latitude observations
H. punctata	138	L, M, B	ALT, LSE, SAV
P. vaihiriae	119	B, L*, M, R	ALT, LSE, SAV
L. carteri	110	M*	LSE*
Plumatella spp.	109	B, L, M	ALT*, LSE*, SAV*
P. nitens	99	R, L, M	ALT, LSE
P. emarginata	76	B, L, R, M	ALT, SAV, LSE
P. casmiana	70	B, L*, R	ALT, LSE, SAV
P. reticulata	50	B, L, R	ALT, LSE, SAV
P. magnifica	25	L, M, B, R	LSE, SAV*
P. fungosa	19	B, L, M, R	ALT, LSE
P. fruticosa	12	B	ALT
C. mucedo	3	L, M	LSE
S. hina	1	B	ALT

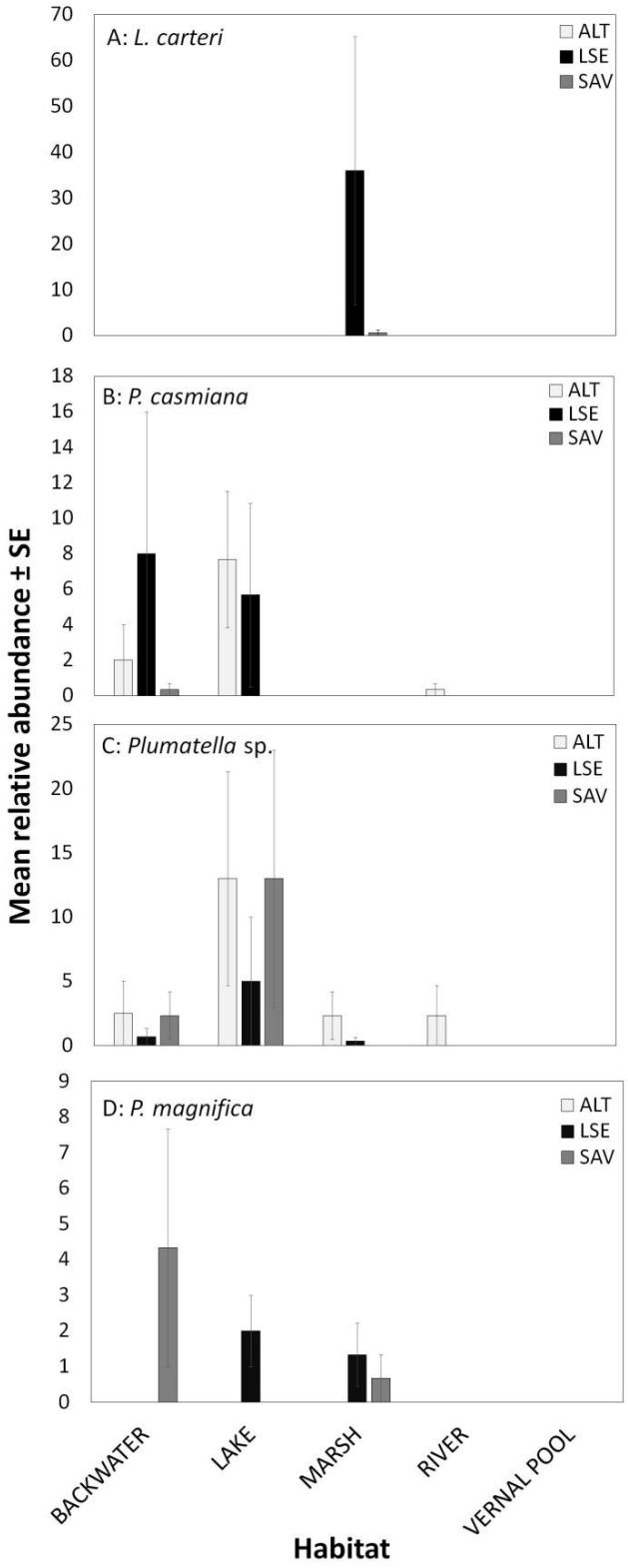

Figure 4. Mean relative abundance of all species that showed significant differences in distributions across latitudes or habitats A: *L. carteri*, B: *P. casmiana*, C: *Plumatella* spp., D: *P. magnifica*.

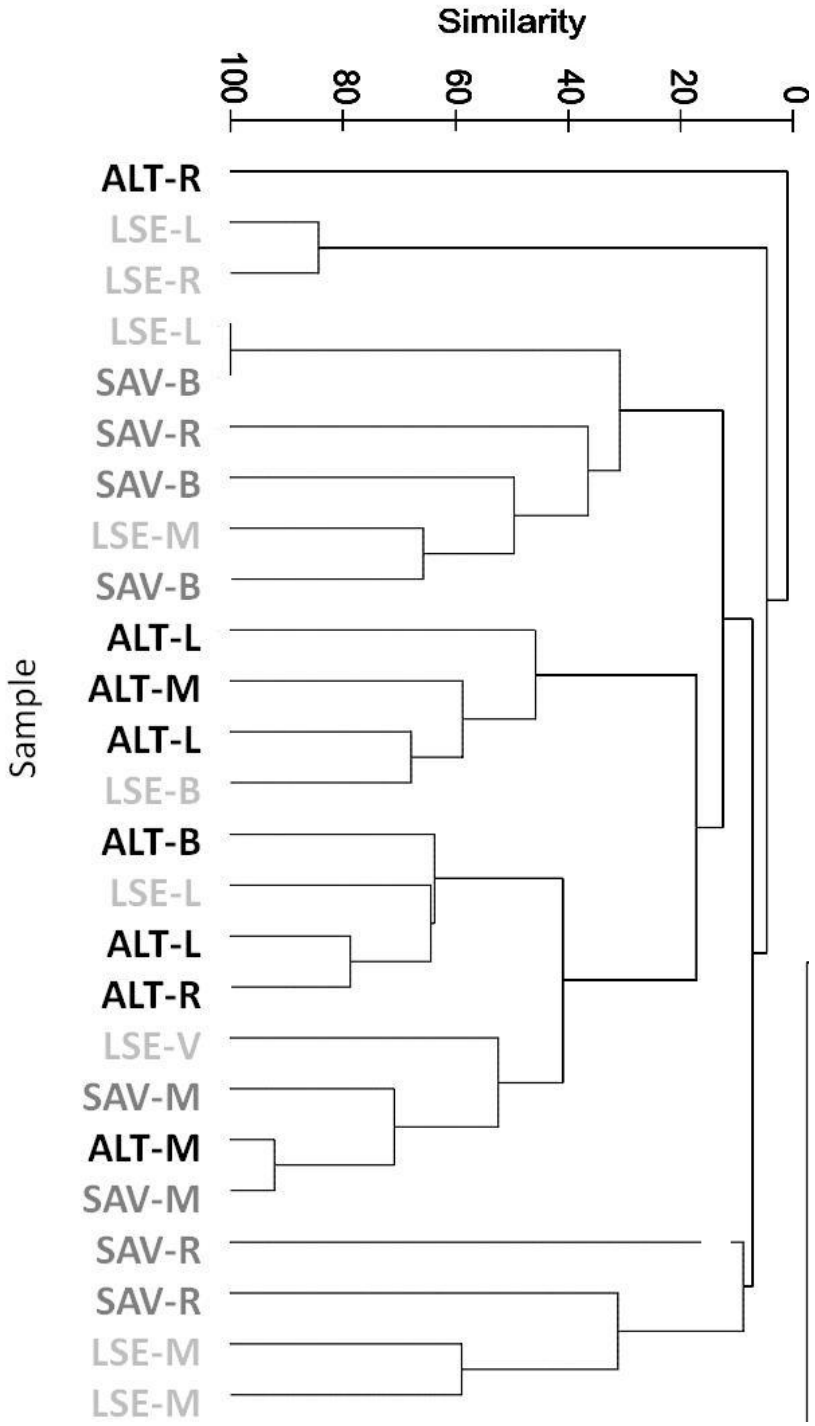

Figure 5. Cluster tree based on Bray-Curtis similarities of bryozoan community assemblage calculated from species relative abundances. All habitats and latitudes that contained bryozoan statoblasts are included. Branch lengths are based on an additive hierarchical clustering of similarity estimates. L: lake, M: marsh, B: backwater, R: river main channel, V: vernal pool. ALT: Alton, IL, LSE: La Crosse, WI, SAV: Savannah, IL.

Using Bray-Curtis similarity estimations in Primer (Clarke and Gorley 2015), there is 100% similarity in species assemblage between Perch Lake, La Crosse, WI and Fulton Marina, Savannah IL. Four relationships were found to be 75% similar or greater. Twenty-six relationships between sites were 50% similar or greater. There was some clustering of marsh sites from Savannah and Alton, IL, as well as rivers and marshes from Savannah and La Crosse, respectively, despite being from different latitudes (Figure 5). However, there were no marked groupings of sites based on community assemblages from the same habitat or latitude.

Environmental factors

Since environmental conditions change markedly diurnally and across seasons, we cannot directly compare physical traits across latitudes. However, it is possible to compare similarity in variation of environmental conditions at each site against similarity in bryozoans community composition. After standardizing values for environmental factors around the mean value from each latitude, there was no significant difference in temperature, SpC, DO, or pH among habitats ($df=4$, $p= 0.173$, 0.555, 0.241, and 0.378, respectively). There is no apparent relationship between similarity of bryozoan community composition and similarity of environmental factors in paired sampling sites (Figure 6).

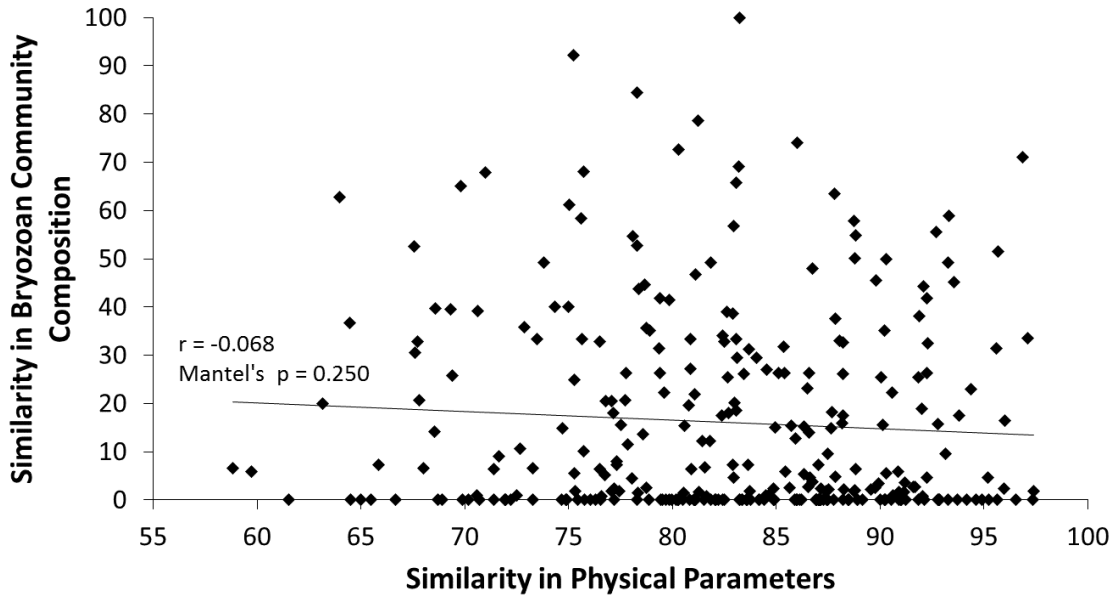

Figure 6. Similarity in bryozoan community composition vs. similarity in physical parameters for 25 sites sampled in the UMR watershed.

DISCUSSION

Previous studies targeting bryozoans have provided significant evidence of shifts in abundance and diversity in accordance with damming and other disturbance events in the UMR (Belby et al. 2015). Since lake habitats support the highest bryozoan diversity, they should be considered key environments for conservation efforts in order to preserve the rich diversity of bryozoans in the UMR. As rivers undergo changes toward these more impounded habitats, there could be an increase in bryozoan abundance and diversity.

Disturbance events can often result in changes in diversity and succession in invertebrate populations by opening niches for colonizing organisms and favoring the establishment of ephemeral, fast-colonizing species (Cardinale and Palmer 2002, Death 1995). While some succession events rely on disturbance, others rely on seasonal variation and geographical separation for ecological transitions. In an English Midland lake, midges and caddisflies were found to alternate spatially and temporally within the same microhabitat (Harrison and Hildrew 2001). This habitat heterogeneity allows for greater overall species diversity in a given location. While floods tend to homogenize aquatic systems, habitat heterogeneity is maximized through a combination of intermediate disturbance, the presence of ecotones, and connectivity in the hydrologic system (Thomaz et al 2006). Secondary effects from changes in hydrology include increased sedimentation and changes in plant morphology, which may result in additional changes in habitat suitability and the availability of appropriate substrates for aquatic invertebrate colonization (Frederickson and Reed 1988). Lakes do not share many

transitional zones with other aquatic habitats unless fed by streams and rivers or surrounded by marshes. Because of this, higher bryozoan diversity, abundance, and richness in these habitats are related to factors other than habitat heterogeneity.

Dam removal is a popular river restoration tool and can restore biotic diversity. It also eliminates the lake-like impounded areas above the dam, as well as the consistently inundated floodplain (Bednarek 2001). Although dam removal may eliminate important bryozoan habitat, it does restore a natural flood pulse pattern to the system (Bednarek 2001). Many organisms with quiescent stages rely on flood pulses for dispersal through the watershed. The extent and success of colonization as a result of these dispersal events rely on both life-history traits of the species as well as hydraulic and hydrologic characteristics of the aquatic system (Boedeltje et al. 2004). Life-histories that include a floating quiescent stage allow for an increase in dispersal range for many aquatic organisms. In *Daphnia,* dormant stages that quickly settle into egg banks can experience extended periods of dormancy if they settle in deeper water with shallow light penetration, low temperatures and poor oxygen concentrations (Carvalho and Wolf 1989). Alternately, floating propagules like the floatoblasts of bryozoans benefit from being present in more aerated water, quickly experiencing environmental cues for germination. Dormant stages can easily adhere to waterfowl and boats, which creates the potential for long-distant dispersal and movement to more removed systems such as lakes.

Reliance on waterfowl as a dispersal mechanism is common in passively-transported organisms. Propagules can be transported both externally and internally, with up to 36% of waterfowl droppings containing at least one dormant stage (Leeuwen et al.

2012). In some species of bryozoans, timing of release of bryozoan statoblasts and hibernacules coincides with migration patterns of waterfowl (Økland 2005). This reliance on waterfowl and other mobile organisms for dispersal can often result in isolated habitats such as lakes becoming temporary sinks for these species, as the extinction rate in isolated locations can be substantial (Okamura et al. 2013). Evidence supports that lakes can act as sinks for aquatic invertebrates that rely on propagule dispersal (Leeuwen et al. 2012). Observed bryozoan distributions in the UMR (Figure 3) support findings from previous studies (Økland 2005) that find greater bryozoan numbers and diversity in lake systems.

Since bryozoan species are globally distributed, there is international interest in gene flow of local and global metapopulations (Freeland et al. 2000)(Okamura et al. 2013)(Figuerola et al. 2005). Freeland et al. (2000) determined there was significant genetic diversity among and between populations of *C. mucedo* in northwestern Europe, with a lack of correlation between genetic similarity and distance between populations. Waterfowl dispersal has been found to alter genetic patterns among populations of *C. mucedo,* a trend that persists across other taxa that utilize a dormant stage (Figuerola et al. 2005). Subsequent genetic studies related to metapopulation analyses along the UMR would provide more information as to gene flow within or between bryozoan species in different habitat types and latitudes.

Lack of degradation of statoblasts in cores allows for multi-decade diversity and abundance studies. Cores also provide a biological timeline that can relate major events in an aquatic system, such as dam construction, urbanization, and changes in species abundance and distribution. Previous work in the UMR has demonstrated the long-

standing presence of *P. magnifica, Plumatella* sp., and *C. mucedo* in Pool 8 and the subsequent invasion of the exotic *L. carteri* after the construction of this dam site in 1937 (Belby et al. 2015). Statoblasts from cores cannot only be used to determine gene flow within and among populations, but can also correlate community composition and environmental factors across time. Given that environmental variables fluctuate daily and seasonally, especially due to the harsh northern winters it is challenging to determine trends in species distribution and abundance based on environmental chemistry and hydrology. A more comprehensive study examining core sediment chemistry and statoblast abundance would improve the current known relationship between bryozoan community composition and environmental factors. These studies would allow for the determination of interconnection between bryozoan community composition and hydrologic events recorded over previous decades in different aquatic habitats, as well as establish successional changes in aquatic invertebrate communities. These data could help determine indicator species for large-scale variation in habitat and what can be expected for future changes to bryozoan community composition in the UMR or internationally.

CONCLUSION

The Upper Mississippi River hosts a diverse assemblage of bryozoans, representing seven families and thirteen species. These data have created a knowledge-base for bryozoan distribution and abundance in this region, information that was previously unknown. It pinpoints lentic systems as rich bryozoan habitat, as well as diminishes the importance of vernal pools to bryozoan community structure. Further, information on present ranges allows us to track future changes in species occurrence in relation to habitat modification and changing climate. Floating quiescent stages are an important reproductive strategy for plants, *Daphnia*, and other aquatic invertebrates; statoblast dispersion can be useful in predicting movement and establishment of other passively-transported taxa. While the UMR watershed is ecologically unique due to a distinctive geological history, these trends in bryozoan diversity extend globally and can be witnessed as far as northern Europe. Continuing trends in statoblast dispersal and bryozoan presence will be dictated by migratory bird movement, as well as the alteration of form and ecological function of the Mississippi River. Future research should focus on gene flow patterns of metapopulations across habitats and latitudes, expansion of distributional data for North American Bryozoa, as well as determining possible environmental factors that restrict establishment and dispersal of species of interest.

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APPENDIX

SITE INFORMATION

Names, codes, coordinates, and descriptions of 40 collection sites.

Site Code	Site Name	Latitude	Longitude	Description
LSE-L-01	Lake Winona	44.03233	-91.62792	Much vegetation, surrounded by bike paths
LSE-L-02	Neshonoc Lake	43.91058	-91.07605	Boat launch, recreational area, along La Crosse River
LSE-L-03	Perch Lake	43.94224	-90.80225	Along La Crosse River
LSE-B-01	Richmond Bay	43.84754	-91.26025	Many eagles, recreational boating area
LSE-B-02	Goose Island Backwater	43.73712	-91.22918	Camping area, abundant waterfowl
LSE-B-03	La Crescent Backwater	43.82023	-91.27625	
LSE-M-01	Myrick Marsh	43.82266	-91.22407	Waterfowl area, hiking trails
LSE-M-02	Pettibone Marsh	43.81752	-91.2657	
LSE-M-03	Goose Island Marsh	43.72699	-91.20375	
LSE-V-01	Summit Frog Pond	43.85239	-91.26452	Ditch near Summit School
LSE-V-02	Shore Acres Vernal Pool	43.82773	-91.27987	Roadside in residential area
LSE-V-03	Pettibone Vernal Pool	43.82325	-91.2696	Low area in forest at Pettibone Park
LSE-R-01	Mississippi Main	43.83226	-91.28267	Near railroad bridge

	Channel La Crescent			
LSE-R-02	Mississippi Main Channel Pettibone	43.81929	-91.26188	
LSE-R-03	Black River Beach	43.87119	-91.24548	
ALT-L-01	Horseshoe Lake	38.70044	-90.06905	Many duck blinds
ALT-L-02	Dunlap Lake	38.80272	-89.93219	Park in suburban area
ALT-L-03	Tower Lake	38.8002	-90.0006	Lake in the center of SIUE campus
ALT-B-01	Alton Marina	38.88532	-90.17632	Marina, many boats docked, drainage pipes
ALT-B-02	Lewis and Clark Canal	38.8054	-90.10231	Canal flowing into Mississippi, clay sediment
ALT-B-03	Not sampled - Mississippi River too channelized			
ALT-M-01	Lewis and Clark Marsh	38.803	-90.10768	
ALT-M-02	Horseshoe Marsh	38.68318	-90.zaw208029	
ALT-M-03	Cahokia Marsh	38.65453	-90.05832	
ALT-V-01	Marina Bridge Pool	38.88452	-90.17409	
ALT-V-02	Granite City Roadside	38.6994	-90.06579	

ALT-V-03	Horseshoe Vernal Pool	38.70008	-90.0669
ALT-R-01	Marina MC	38.88217	-90.17006
ALT-R-02	Museum MC	38.86579	-90.14144
ALT-R-03	Lewis and Clark MC	38.80358	-90.11491
SAV-L-01	Not sampled - no available habitat		
SAV-L-02	Not sampled - no available habitat		
SAV-L-03	Not sampled - no available habitat		
SAV-B-01	Thomson Backwater	41.94782	-90.11516
SAV-B-02	Clinton Marina	41.85345	-90.18366
SAV-B-03	Fulton Marina	41.8592	-90.16668
SAV-M-01	Hidden Slough Marsh	41.94885	-90.11849
SAV-M-02	Palisades Marsh	42.14454	-90.16887
SAV-M-03	Not sampled - no access		
SAV-V-01	Kiwanis Park Roadside	41.86134	-90.16583
SAV-V-02	Great River Roadside	42.12443	-90.15697
SAV-V-03	Palisades	42.14407	-90.16859

	Roadside		
SAV-R-01	Thomson MC	41.95032	-90.12016
SAV-R-02	Clinton MC	41.84631	-90.18263
SAV-R-03	Fulton MC	41.86131	-90.17046