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Macroinvertebrate communities in restored and natural Platte River slough wetlands

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Abstract. Wetlands in the central Platte River basin provide numerous ecosystem services but have been diminished and degraded by agricultural practices and development. Wetland restoration is increasingly common in this region, but the success of restorations is virtually unknown. We sampled macroinvertebrates during spring 2003 and 2004 in restored (5–16 y old) and natural slough wetlands to assess restoration success. Simple measures (e.g., total abundance, biomass, diversity) were all similar in restored and natural wetlands. Communities were similar in natural and restored wetlands, but we observed some taxonomic differences. For example, abundances of *Helisoma* and *Pisidium* and abundance and biomass of amphipods were higher in natural than in restored wetlands, and leeches were collected only in natural wetlands. These results suggest that dispersal ability is a biotic filter limiting recovery and that these noninsects are good candidates for assessing recovery. Functional structure on the basis of abundance was similar between natural and restored wetlands, but some differences in biomass-based estimates were evident. For example, relative biomass of collector-filterers was higher in natural than in restored wetlands in 2003. Multivariate analyses indicated that factors such as hydroperiod might be more important than restoration status in shaping wetland macroinvertebrate communities. Furthermore, drought conditions constrained our sampling efforts and influenced temporal patterns, thereby underscoring the need for multiyear studies, especially under extreme environmental conditions. Our results indicate that wetland macroinvertebrate communities in this region are resilient and recover rapidly after restoration, but that ongoing restoration and management efforts should focus on hydrology, which might limit recovery in restorations and is a critical factor shaping wetland macroinvertebrate communities.

Key words: recovery, restoration, function, hydrology, dispersal, community composition.

Wetlands provide many valuable ecosystem services, including flood control, groundwater discharge or recharge, and removal or transformation of nutrients, such as N through denitrification and microbial immobilization (Schlesinger 1997). Wetlands also provide important habitat for fish and wildlife and can harbor diverse nongame communities, many of which are unique to intermittent habitats (e.g., Williams 1996, Semlitsch and Bodie 1998, Batzer et al. 1999). Despite their inherent ecological and economic value, >½ of the original wetland area that once existed within the contiguous 48 states of the United States has been lost (Vileisis 1997).

The central Platte River Valley (PRV) in Nebraska consists of the braided channels of the Platte River and adjacent wet meadows, which are a matrix of mesic prairie with meandering, linear sloughs. This region is a focus for wetland conservation efforts because of its importance to migratory birds, including the federally endangered interior least tern (*Sterna antillarum*) and whooping crane (*Grus americana*) (US Fish and Wildlife Service 1997). Despite their importance, agricultural activities, impoundments, and other anthropogenic activities have severely reduced and degraded wetland habitats in this region. For example, 23 to 45% of wet meadows were lost between 1938 and 1982 in the PRV (Sidle et al. 1989).

Heightened awareness of the importance of wetlands in the PRV has resulted in increased efforts to create and restore wetlands by federal and state agencies and private groups, which have been implementing restorations for >12 y by land contouring and introduction of seeds and seedlings collected

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from nearby natural systems. Wetland restorations are an increasingly common feature in the region and implementation is expensive and laborious. However, habitat quality, biotic communities, and overall function in restorations have not been evaluated adequately to compare restored and natural systems.

The proximity of restored and natural slough wetlands in the PRV provides an opportunity to test hypotheses regarding restoration and community development. Community assembly is thought to be affected by site conditions and species traits that act as filters and might limit the dispersal or survival of species (e.g., Weiher and Keddy 1995). Hobbs and Norton (2004) discuss types of filters, ranging from abiotic to biotic to socioeconomic, and how they should be considered in restoration projects. Abiotic filters include factors such as climate or substrate and biotic filters include interactions such as competition, predation, and dispersal-related availability of propagules (Hobbs and Norton 2004). Socioeconomic filters are related to goals and financial considerations of the proximal human population (Hobbs and Norton 2004). Ultimately, community development at a given site is dictated by the interaction between existing species pools and the kinds of filters in place (e.g., Díaz et al. 1998).

Our main objective was to assess wetland restorations in the PRV by comparing macroinvertebrate abundance, biomass, richness, diversity, and functional structure in restored wetlands to those in natural systems. Macroinvertebrates can colonize and recover relatively quickly after restoration in some wetlands (e.g., Brown et al. 1997). Hence, we predicted that most macroinvertebrate taxa with high dispersal capabilities (e.g., beetles, hemipterans, dipterans) would do so in these systems because of numerous nearby source areas for colonists. However, habitat features in restored sloughs (e.g., hydrology, substrates) and recovery of other groups, such as plants, also should influence recovery of macroinvertebrate communities. Therefore, we predicted that these abiotic and biotic filters would limit recovery of some taxa, particularly those that lacked aerial dispersal mechanisms.

Methods

Study region

The study region is a 90-km stretch of the central Platte River in south-central Nebraska, roughly from 10 km east of Grand Island, Hall County, to south of Elm Creek, in Phelps County. The landscape is a series of wet meadows with dendritic systems of linear sloughs. These sloughs are periodically inundated channels within low-lying areas. Hydrology of these sloughs ranges from ephemeral to perennial, and water levels are affected by local precipitation and river discharge through groundwater (Wesche et al. 1994, Whiles and Goldowitz 1998). Vegetation within the meadows is dominated by sedges (e.g., *Carex emoryi* Dewey, *Carex molesta* Mackenzie ex Bright) and grasses (e.g., *Spartina pectinata* Bosc ex Link), with a substantial component of forbs (e.g., *Verbena hastata* L., *Alisma subcordatum* Raf.). Climate is temperate with warm summer temperatures (July daily average temperature: 24°C) and cold winter temperatures (January daily average temperature: –7°C), often resulting in ice-covered surface waters from November through March. Mean annual precipitation is 63 cm/y, most of which falls in May and June (National Weather Service; http://www.weather.gov/climate/index.php?wfo=oax).

Study sites

We chose 3 natural wetland sites and 4 restored sites, ranging from 5 to 16 y old at the onset of this study for comparisons (Table 1). Natural sites were located on 2 adjacent islands formed by the braided channels of the Platte River near Grand Island, Nebraska (lat 40°48′29.57″N, long 98°26′45.01″W). Mormon East and Mormon Middle are on Mormon Island and Wild Rose East is located on Shoemaker Island, directly west of Mormon Island. The restored sites all were located on areas within 1.5 km of the main river channel of the Platte River. Management histories (e.g., grazing, burning) were similar among all sites chosen, and restoration procedures (e.g., land contouring, seeding) were similar, except for the Johns Clearing site, which was a previously existing slough located on a forested (predominantly *Salix* L. and *Populus* L.) island of the Platte River. Restoration at Johns Clearing involved removal of trees in 1987 and did not include seeding or land contouring. We included Johns Clearing in our study because it is the oldest site owned by the Platte River Whooping Crane Maintenance Trust, and thus, represented one of the oldest restorations in the region.

Sloughs chosen for our study included 2 semipermanent sites (1 restored, 1 natural). The rest were intermittent, with dry periods typically occurring in late summer (Table 1). For the past 3 to 4 y, the PRV has been under drought conditions, which caused increased frequencies and durations of dry periods during our study. Growing season precipitation (April through September) was ~280 mm in 2002, ~420 mm in 2003, and ~380 mm in 2004 (National Weather Service).

Table 1. Physical characteristics of the 3 natural (N1 = Mormon East, N2 = Mormon Middle, N3 = Wild Rose East) and 4 restored (R1 = Johns Clearing, R2 = Nature Center, R3 = Johns Restoration, R4 = Studnicka) wetlands sampled during spring 2003 and 2004. All sites are representative 20- to 30-m reaches of linear sloughs. All measurements are means of monthly data from March to June in each year when water was present. Hydroperiod is a list of months (Jan = 1, Feb = 2, etc.) during which sites held water. Measurements began in March of 2003. Estimated minimum distance is the distance from a restored wetland to the nearest natural wetland or Platte River channel that represents a potential source for colonization of aquatic invertebrates. NK = age not known, DO = dissolved O_2, NA = not applicable.

	Natural			Restored			
Characteristics	N1	N2	N3	R1	R2	R3	R4
Site age in 2003 (y)	NK	NK	NK	16	5	5	7
Maximum depth (cm)							
2003	65.2	46.0	13.4	40.0	59.0	32.0	50.9
2004	68.9	52.0	16.0	34.0	32.0	7.0	34.0
Average area (m^2)							
2003	220.3	209.8	44.0	103.7	316.1	61.7	138.3
2004	187.8	201.0	44.0	94.2	233.2	10.3	214.0
Maximum area (m^2)							
2003	291.3	269.3	46.0	105.3	356.0	79.3	215.0
2004	293.3	275.0	46.7	104.0	287.3	10.4	214.0
Maximum volume (m^3)							
2003	68.8	75.2	3.4	28.2	136.8	12.0	42.1
2004	85.5	99.1	3.6	23.0	61.8	0.5	32.9
Hydroperiod							
2003	3–6	3–6	1–12	1–12	3–6	4–5	4–6
2004	3–4, 11–12	3–4, 11	1–12	1–12	3–6	3	3
Temperature (°C)							
Spring maximum							
2003	41.1	34.5	34.8	27.1	28.7	27.5	43.9
2004	46.8	30.2	26.7	24.4	34.8	38.7	44.4
Spring minimum							
2003	0.0	0.0	5.7	4.4	4.1	9.4	8.2
2004	0.0	0.9	0.0	8.8	3.7	0.0	0.0
Average daily temperature (°C)							
2003	17.1	15.7	12.1	10.7	16.9	18.8	19.9
2004	13.2	11.3	12.0	11.7	14.2	12.4	12.1
Inorganic substrates (%)							
Gravel	0	0	5	6	5	0	0
Sand	15	25	45	34	52	50	50
Silt	85	75	50	60	43	50	50
Water chemistry							
pH	7.5	7.7	6.2	7.8	8.5	7.1	6
DO (mg/L)	10.8	9.4	7.9	4.6	11.6	6.7	4.8
Conductivity (µS/cm)	1423	1435	808	955	738	1136	1111
Estimated minimum distance (km)	NA	NA	NA	0.6	0.5	1.4	1.3

Physical habitat variables

We sampled within permanently marked 20- to 30-m representative reaches of each site. We installed staff gauges in the deepest points in each study slough. We read gauges at approximately monthly intervals from March 2003 to December 2004 when water was present. We measured annual hydroperiods for the sites as the sum of all months during which standing water was present at each site. We do not know whether water was present in sites before March in 2003, but we assumed water had been present during January and February at the 2 wettest, intermittently exposed sites, and included them in annual hydroperiod measurements (Table 1). All other reported hydrologic measurements were spring averages

(March–June) for 2003 and 2004 at each site when water was present.

We established reference transects for wetted width and depth measurements at 10-m intervals perpendicular to the slough in each study reach. We measured wetted width along each perpendicular transect and measured depth at 1-m intervals. We estimated water volume in sloughs from wetted width and depth transects. We placed a thermograph in each site to record temperature at 60-min intervals when water was present. We measured dissolved O_2, conductivity (YSI model 85; Yellow Springs Instruments, Yellow Springs, Ohio), and pH (Orion Quikchek model 106; Thermo Scientific-Orion, Beverley, Massachusetts) and visually estimated inorganic substrate size composition in 3 random locations in each slough during monthly invertebrate sampling.

Benthic invertebrate sampling and processing

We collected 3 monthly macroinvertebrate dip-net (340 mm wide) samples from random locations in each site when water was present during the spring hydroperiod (March–June) of 2003 and 2004. To standardize area sampled and minimize invertebrate avoidance of the net, we used a drop trap (1 m tall, 0.43 m wide, 0.5 m long), covered on 4 sides with 0.5-mm Nytex™ mesh (Nytex, Geneva, Switzerland). During sampling, we bounced the net along the substrate within the trap in alternating directions for a total of 5 sweeps. We rinsed samples through the net, placed remaining materials in plastic bags, and preserved them in 8% formalin.

We washed samples through nested sieves to divide them into coarse (>1 mm) and fine (<1 mm, >0.5 mm) fractions. We separated invertebrates from debris in coarse fractions under a dissecting microscope. We subsampled invertebrates in fine fractions with a Folsom wheel sample splitter, usually to $^1/_4$ to $^1/_{32}$ of the original volume. To facilitate identification, we subsampled coarse samples containing large numbers of oligochaetes and chironomids by picking them from sections of a gridded petri dish until $\geq$100 individuals were selected. When samples contained large amounts of filamentous algae that could not be split with the Folsom wheel, we subsampled in sorting trays (see Meyer 2007).

We measured invertebrates (total millimeters body length) and identified them to the lowest practical taxonomic level. We identified most insects and other taxa to genus, oligochaetes and some crustaceans (i.e., Ostracoda, Copepoda) to class, and chironomids to subfamily. We determined functional feeding group assignments on the basis of Merritt and Cummins (1996), Smith (2001), or our knowledge of local fauna. We used length–mass relationships (Bottrell et al. 1976, Benke et al. 1999) to estimate biomass (ash-free dry mass/m^2) of individuals.

We also calculated a leech and mollusk ratio because we observed differences in noninsect groups (i.e., leeches, bivalves, and mollusks) between natural and restored wetlands. We calculated the ratio as the biomass of leeches plus bivalves divided by snail biomass.

Analysis of macroinvertebrate data

We compared macroinvertebrate community measures among wetland types (natural vs restored) and over time (2003 vs 2004) using the mixed model procedure with repeated measures (SAS version 9.0; SAS Institute, Cary, North Carolina). This procedure uses Satterthwaite's method to estimate denominator degrees of freedom (Littell et al. 1996). We used orthogonal contrast statements to test whether wetland types differed within a year and whether changes occurred within a wetland type over time ($\alpha = 0.05$; p-values < 0.10 are reported because of high variability and low replication). We did not include dates on which water was not present at a site, so spring averages for each site represent different sample sizes in some cases. We arcsine$\sqrt{(x)}$-transformed percentages and $\log_e(x)$-transformed other values before analysis when appropriate to decrease heteroscedasticity and satisfy normality assumptions.

We tested for differences in total spring average abundance, total spring average biomass, average and total taxon richness, and Shannon diversity (H', base e). We also tested for differences in abundance and biomass of functional feeding groups and average predator size (for total predatory taxa, Coleoptera, and Diptera). To test for differences at finer taxonomic scales (class, order, and family), we compared groups that accounted for $\geq$10% of abundance or biomass in 1 of the wetland types. These groups included Oligochaeta, Branchiopoda, Ostracoda, Amphipoda, Coleoptera, Trichoptera, Diptera, Lymnaeidae, Physidae, Planorbidae, and Sphaeriidae. We also tested for differences in the leech and mollusk ratio.

Community composition

We used nonmetric multidimensional scaling (NMDS) (Minchin 1987) to compare macroinvertebrate community composition among sites. Sampling units were spring averages (March–June of both 2003 and 2004) of macroinvertebrate community composition on the basis of abundance or biomass at each site, and we standardized the output to unit maxima. We calculated

TABLE 2. Average macroinvertebrate abundance and biomass, functional structure, and measures of diversity in 3 natural and 4 restored wetland sites during spring 2003 and 2004. Values are means (1 SE). Percentages are the contributions of each functional feeding group to total abundance and total biomass. Numbers followed by different letters are significantly different: a and b denote differences between natural and restored wetlands within a year, x and y denote differences between years within a wetland type. No asterisk = $p < 0.10$, * = $p < 0.05$. AFDM = ash-free dry mass.

	2003						2004					
Variable	Natural	SE	%	Restored	SE	%	Natural	SE	%	Restored	SE	%
Abundance (no./m^2)	12,870.6	5426.8		16,119.7	8334.1		21,561.9	9200.2		13,953.9	12,321.4	
Collector-filterers	5242.0	4357.1	41	2707.9	1415.6	17	1681.2	647.3	8	1093.6	1138.2	8
Collector-gatherers	7065.8	1547.0^{x}	55	11,329.9	8605.9	70	18,997.7	9975.5^{y}	88	11,722.9	10,634.3	84
Predators	93.4	29.7^{x}	<1	599.8	350.2	4	249.0	120.9^{y}	1	464.3	314.2	3
Scrapers	339.2	133.4	3	181.9	88.9	1	310.4	240.4	1	487.3	312.9	3
Shredders	24.9	24.8^{x*}	<1	11.0	5.9	<1	234.1	$155.6^{a,y}$	1	19.6	4.6b	<1
Herbivore-piercers	7.4	3.7	<1	3.4	2.6	<1	10.7	9.6	<1	1.6	1.1	<1
Biomass (mg AFDM/m^2)	988.5	99.6^{x}		1772.2	418.3		2476.2	783.5^{y}		1530.6	969.8	
Collector-filterers	99.1	32.4^{a}	10	39.5	19.9^{b}	2	54.2	29.0	2	16.4	17.4	1
Collector-gatherers	441.0	117.3	45	714.4	645.4	40	1178.5	1080.0	48	655.4	589.9	43
Predators	190.5	72.3	19	676.0	327.6^{x}	38	511.4	316.6	21	175.1	128.9^{y}	11
Scrapers	212.9	88.6	22	318.1	240.6	18	475.5	437.3	19	636.8	645.8	42
Shredders	21.9	12.9^{x*}	2	13.2	6.7	<1	182.0	$113.0^{a*,y}$	7	29.7	10.8^{b}	2
Herbivore-piercers	10.5	6.6	1	5.8	2.3	<1	51.6	50.2^{a}	2	4.2	3.7^{b}	<1
Average taxon richness	13.5	1.4		14.2	2.9		15.7	1.1		13.8	3.4	
Total taxon richness	34.3	4.3		33.5	6.4		37.0	5.1		27.5	9.2	
Shannon diversity (H')	1.3	<0.1		1.5	0.3		1.3	<0.1		1.3	0.4	
Unique taxa	12			21			13			11		

dissimilarities using the Bray–Curtis index (Bray and Curtis 1957), did the analysis in 1 to 6 dimensions, and used 100 random starting configurations.

We used analysis of similarity (ANOSIM; Clarke and Green 1988) to detect differences between a priori groups of samples (restored vs natural wetlands) for both macroinvertebrate abundance and biomass. ANOSIM is calculated as:

$$R = (r_B - r_W)/(M/2)$$

where r_B = the rank similarity between groups, r_W = the rank similarity within groups, $M = n(n-1)/2$, where n = the number of sampling units. Values in ANOSIM range from −1 to 1. R approaches 1 if samples are more similar within groups than among groups. We used vector fitting (Dargie 1984, Faith and Norris 1989, Kantvilas and Minchin 1989) to examine correlations between macroinvertebrate community composition and the following potential explanatory variables: wetland type, restoration age, average depth, average area, annual hydroperiod, average temperature, percentage sand, and conductivity. Wetland type was a comparison of natural and restored sites. The restoration age variable excluded natural sites and was the age (y) of each restored site. Annual hydroperiod was the number of months during the year in which the site held standing water. All other vectors were averages of monthly measurements taken during the spring hydroperiods of 2003 and 2004. We used DECODA software (version 3.00 b38; Minchin 1989) to conduct all ordination, ANOSIM, and vector-fitting procedures.

Results

Macroinvertebrate abundance and diversity

Annual average macroinvertebrate abundance was not significantly different between natural and restored wetlands in either year (Table 2). Similarly, total biomass did not differ significantly between natural and restored wetlands, but was higher in 2004 than in 2003 in natural wetlands ($F_{1,5} = 4.3$, $p = 0.09$; Table 2). During the 2003 spring hydroperiod, macroinvertebrate abundance peaked in May in natural sites and in March in restored sites (Fig. 1A). Biomass peaked in June in natural sites but was similar through time in restored sites (Fig. 1B). During 2004, both abundance and biomass peaked dramatically in both wetland types in June (Fig. 1A, B). A total of 86 macroinvertebrate taxa was collected at all sites combined. Total and average taxon richness and H' were similar between natural and restored wetlands (Table 2).

Dominant groups were more temporally variable in restored than in natural wetlands. In restored wetlands in 2003, most individuals were annelids (42%) or crustaceans (34%), followed by insects (only 15%)

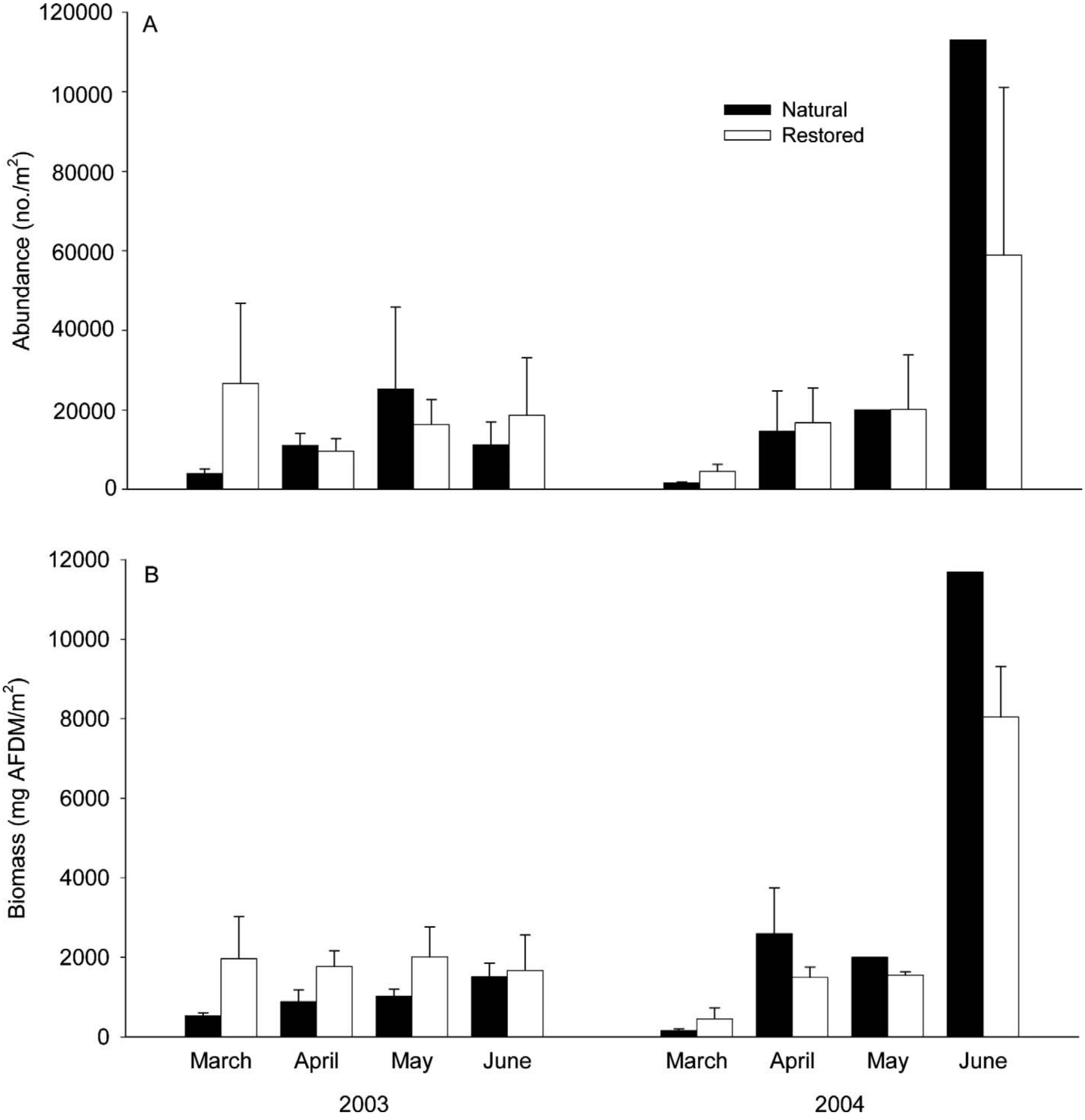

FIG. 1. Mean (+1 SE) monthly averages of total macroinvertebrate abundance (A) and biomass (B) in 3 natural and 4 restored wetlands during spring 2003 and 2004. Samples with no error bar occurred in May and June 2004, when only 1 natural wetland held water. AFDM = ash-free dry mass.

(Table 3). However, in restored wetlands in 2004, most individuals were insects (37%), followed by crustaceans (32%) and annelids (28%) (Table 3). In restored wetlands in both years, most insects belonged to Diptera (88–98%), and most were chironomids or ceratopogonids. Stratiomyid flies (mostly *Odontomyia* and *Nemotelus*) were found in all restored sites except 1 (Johns Clearing), but were found in only 1 natural site (Wild Rose East). Odonates (mostly *Sympetrum*, *Anax*, *Enallagma*, and *Lestes*) were abundant in restored sites,

TABLE 3. Average abundance (no./m^2) and % contribution of macroinvertebrate taxa in natural and restored wetlands during spring 2003 and 2004. Values are means (1 SE). Percentage contribution of major groups is the % of total macroinvertebrate abundance. Percentage contribution of each taxon within a group is % contribution to that group. Numbers followed by different letters are significantly different: a and b denote differences between natural and restored wetlands within a year, x and y denote differences between years within a wetland type. No asterisk = $p < 0.10$, * = $p < 0.05$.

	2003						2004					
	Natural			Restored			Natural			Restored		
Taxon	no./m^2	SE	%	no./m^2	SE	%	no./m^2	SE	%	no./m^2	SE	%
Tricladida	17.7	13.0	<1	14.5	16.7	<1	7.9	5.1	<1	65.9	54.0	<1
Nematoda	54.4	23.2	<1	1239.6	1182.8	8	33.3	9.9	<1	106.9	57.3	<1
Annelida	1556.7	384.9	12	6724.1	6222.7	42	4734.1	4343.7	22	3914.0	2474.0	28
Oligochaeta	1555.6	386.3	100	6724.1	6222.7	100	4729.7	4338.3	100	3914.0	2474.0	100
Hirudinea	1.2	1.4	<1	0.0	0.0	0	4.4	5.4	<1	0.0	0.0	0
Crustacea	7347.0	5739.9	57	5452.3	2037.1	34	8540.5	4140.0	40	4435.6	4835.0	32
Branchiopoda	5058.3	4487.1	69	2705.5	1417.2	50	1471.5	890.5	17	1091.6	1138.6	25
Ostracoda	1769.3	1155.3^{x*}	24	1804.9	1242.3	33	5882.7	2709.1^{y}	69	617.9	627.9	14
Copepoda	434.4	151.5	6	932.7	529.9	17	1009.8	936.5	12	2719.1	3063.3	61
Amphipoda	85.0	65.7^{x}	1	9.2	6.0	<1	176.5	94.4^{a*,y}	2	7.1	8.2^{b}	<1
Hydrachnidia	1.7	1.8	<1	10.2	4.8	<1	59.9	69.6	<1	18.9	5.8	<1
Insecta	3409.2	1982.2	26	2496.1	1207.5	15	7671.4	8573.1	36	5142.3	5064.3	37
Collembola	0.5	0.6	<1	118.1	123.7	5	0.8	1.0	<1	20.6	12.2	<1
Odonata	5.6	5.0	<1	94.1	96.6	4	7.5	2.8	<1	53.5	61.6	1
Ephemeroptera	0.0	0.0	0	10.7	9.3	<1	2.1	2.5	<1	6.5	5.3	<1
Hemiptera	10.6	3.0	<1	22.3	25.3	<1	1.0	0.8	<1	4.0	2.8	<1
Coleoptera	49.5	10.4	1	63.8	40.3	3	111.3	68.3	1	34.6	19.6	<1
Trichoptera	22.2	24.2^{x*}	<1	0.0	0.0	0	221.5	146.5^{y}	3	4.8	5.6	<1
Lepidoptera	0.0	0.0	0	0.0	0.0	0	0.7	0.5	<1	<0.1	<0.1	<1
Diptera	3320.5	2002.1	97	2187.0	1290.0	88	7325.5	8715.0	95	5017.6	5085.7	98
Mollusca	483.0	58.3	4	183.0	87.5	1	514.7	294.2	2	270.4	(220.9)	2
Lymnaeidae	140.0	112.5	29	124.4	80.6	68	71.6	86.7	14	128.3	129.2	47
Physidae	42.0	39.9	9	43.2	27.3	24	173.5	114.7	34	141.7	102.2	52
Planorbidae	145.3	125.6^{a}	30	14.0	12.8^{b}	8	62.8	57.7^{a}	12	0.3	0.3^{b}	<1
Sphaeriidae	155.6	184.0^{a}	32	1.5	1.7^{b}	<1	206.9	239.7^{a}	40	0.1	0.1^{b}	<1

particularly the Nature Center site, but were found sporadically in only 2 of the natural sites (Mormon East and Mormon Middle).

Abundance of most invertebrate groups did not differ between wetland types, but 3 groups of flightless invertebrates were significantly more abundant in natural than in restored wetlands. Amphipods were more abundant in natural than in restored wetlands in both years, and this trend was significant during 2004 ($F_{1,7.8} = 9.1$, $p = 0.02$; Table 3). Planorbid snails (*Helisoma*) were ~10× more abundant in natural than in restored wetlands in 2003 ($F_{1,10} = 3.80$, $p = 0.08$) and ~200× more abundant in natural than in restored wetlands in 2004 ($F_{1,5} = 4.4$, $p = 0.09$; Table 3). Sphaeriid clams (all *Pisidium*) were generally more abundant in natural than in restored wetlands in both 2003 ($F_{1,6.3} = 3.8$, $p = 0.10$) and 2004 ($F_{1,6.3} = 4.6$, $p = 0.07$; Table 3), and were collected from only 1 restored wetland (Johns Clearing). In addition, leeches (*Erpobdella* and *Placobdella*) were present in 1 natural wetland (Wild Rose East), but were not found in any restored wetlands (Table 3).

Statistical comparisons of biomass at the order/family level between wetland types and between years showed patterns similar to abundance. Oligochaetes, branchiopods, coleopterans, dipterans, and all mollusk families did not differ between wetland types (Table 4). However, amphipods had higher biomass in natural than in restored wetlands in both 2003 ($F_{1,5.6} = 4.2$, $p = 0.09$) and 2004 ($F_{1,5.6} = 12.7$, $p = 0.01$; Table 4). Biomass of ostracods ($F_{1,7.3} = 8.9$, $p = 0.02$) and trichopterans ($F_{1,9.7} = 10.2$, $p = 0.01$) was higher in natural than in restored wetlands during 2004 (Table 4). No temporal differences in biomass of any group were evident in restored sites, but ostracods ($F_{1,5} = 12.4$, $p = 0.02$), amphipods ($F_{1,5} = 14.5$, $p = 0.01$), and trichopterans ($F_{1,5} = 9.4$, $p = 0.03$) had higher biomass in 2004 than in 2003 in natural wetlands (Table 4).

TABLE 4. Average biomass (mg ash-free dry mass [AFDM]/m^2) and % contribution of macroinvertebrate taxa in natural and restored wetlands during spring 2003 and 2004. Values are means (1 SE). Percentage contribution of major groups is the % of total macroinvertebrate biomass. Percentage contribution of each taxon within a group is % contribution to that group. Numbers followed by different letters are significantly different: a and b denote differences between natural and restored wetlands within a year, x and y denote differences between years within a wetland type. No asterisk = $p < 0.10$, * = $p < 0.05$.

	2003						2004					
	Natural			Restored			Natural			Restored		
Taxon	mg/m^2	SE	%	mg/m^2	SE	%	mg/m^2	SE	%	mg/m^2	SE	%
Tricladida	2.9	2.4	<1	1.9	2.2	<1	1.6	1.5	<1	2.7	2.0	<1
Nematoda	7.9	9.6	<1	0.9	0.8	<1	12.7	15.5	<1	7.6	8.7	<1
Annelida	58.6	27.6	6	464.7	475.4	26	135.3	55.1	5	260.4	251.0	17
Oligochaeta	58.1	28.1	99	464.7	475.4	100	134.2	54.1	99	260.4	251.0	100
Hirudinea	0.5	0.6	<1	0.0	0.0	0	1.1	1.3	<1	0.0	0.0	0
Crustacea	96.6	47.9	10	52.7	19.9	3	112.7	49.3	5	24.0	25.8	2
Branchiopoda	59.9	48.2	62	39.3	20.0	75	19.5	12.1	17	16.3	17.4	68
Ostracoda	9.2	6.0^{x*}	9	9.4	6.4	18	30.4	14.2^{a*,y}	27	3.2	3.3^{b}	13
Copepoda	0.5	0.1	<1	1.1	0.6	2	1.2	1.1	1	3.1	3.5	13
Amphipoda	27.0	21.3^{a,x*}	28	2.9	3.3^{b}	6	61.6	37.3^{a*,y}	55	1.4	1.7^{b}	6
Hydrachnidia	<0.1	<0.1	<1	<0.1	<0.1	<1	0.1	0.1	<1	<0.1	<0.1	<1
Insecta	576.9	160.1	58	934.3	321.1	53	1703.9	974.5	69	599.1	406.0	39
Collembola	0.1	0.1	<1	6.6	7.2	<1	0.3	0.3	<1	1.0	0.5	<1
Odonata	2.3	2.8	<1	49.1	38.5	5	3.2	2.0	<1	49.5	54.7	8
Ephemeroptera	0.0	0.0	0	2.0	2.2	<1	0.1	0.1	<1	4.3	4.3	<1
Hemiptera	11.9	4.9	2	5.2	5.5	<1	1.5	0.9	<1	3.9	3.4	<1
Coleoptera	212.4	63.0	37	542.1	349.0	58	593.8	409.8	35	104.6	73.9	17
Trichoptera	17.7	10.7^{x*}	3	0.0	0.0	0	165.0	100.5^{a*,y}	10	8.0	9.2^{b}	1
Lepidoptera	0.0	0.0	0	0.0	0.0	0	1.8	1.8	<1	<0.1	<0.1	<1
Diptera	332.3	175.4	58	329.2	267.7	35	937.4	1098.1	55	427.7	375.2	71
Mollusca	245.5	67.2	25	317.7	240.0	18	509.9	426.1	21	636.7	645.8	42
Lymnaeidae	134.2	104.2	55	264.2	243.1	83	27.7	33.2	5	553.7	633.9	87
Physidae	46.5	37.2	19	49.2	29.0	15	432.8	392.8	85	82.7	61.4	13
Planorbidae	32.1	27.4	13	4.3	2.9	1	14.9	13.1	3	0.3	0.4	<1
Sphaeriidae	32.7	38.5	13	0.1	0.2	<1	34.4	40.2	7	<0.1	<0.1	<1

The leech and mollusk ratio was consistently higher in natural (2003: 0.30 ± 0.29, 2004: 0.15 ± 0.14) than in restored wetlands (2003: 0.01 ± <0.001, 2004: 0.01 ± <0.001) in both years, but differences were not significant because of site variability.

Macroinvertebrate functional structure

Functional structure on the basis of abundance was similar between natural and restored wetlands, and communities were numerically dominated by collector-gatherers (Table 2). Functional structure on the basis of biomass was more evenly distributed among groups in both natural and restored wetlands (Table 2). There were few differences in functional groups between natural and restored wetlands during 2003, except for collector-filterer biomass, which was higher in natural than in restored wetlands ($F_{1,9.7} = 4.4$, $p = 0.06$) (Table 2). In 2004, most groups did not differ between wetland types, but shredder biomass ($F_{1,9.6} = 7.5$, $p = 0.02$) and herbivore-piercer biomass ($F_{1,9.4} = 3.7$, $p = 0.09$) were higher in natural than in restored wetlands (Table 2).

Predator biomass decreased between years in restored wetlands ($F_{1,5} = 5.6$, $p = 0.07$) (Table 2), and this corresponded to a decrease in individual predator size. Average individual predator size did not differ between natural and restored wetlands in 2003, but was lower in restored than in natural wetlands in 2004 ($F_{1,9.9} = 8.8$, $p = 0.01$; Fig. 2A). In addition, average individual predator size in restored wetands decreased between 2003 and 2004 ($F_{1,5} = 4.4$, $p = 0.09$; Fig. 2A). Average individual size of predatory Coleoptera did not differ between natural and restored wetlands in either year (Fig. 2B). However, average individual size of predatory Coleoptera decreased between 2003 and 2004 in both natural and restored wetlands, and this trend was most pronounced in restored wetlands ($F_{1,5}$

$= 4.7$, $p = 0.09$; Fig. 2B). Average individual size of predatory Diptera was lower in restored than in natural wetlands in both 2003 ($F_{1,8.1} = 4.8$, $p = 0.06$) and 2004 ($F_{1,7.6} = 3.9$, $p = 0.09$), and no temporal changes in average individual predatory dipteran size were observed in either wetland type (Fig. 2C).

Community composition

ANOSIM results failed to show significant differences in community composition with respect to abundance ($R = 0.02$, $p = 0.44$) or biomass ($R = -0.09$, $p = 0.59$) between natural and restored wetlands.

Two-dimensional NMDS was used for both macroinvertebrate abundance and biomass ordinations. In the abundance ordination, the fitted vectors of maximum correlation with hydroperiod ($r = 0.90$, $p < 0.0001$) and restoration age ($r = 0.85$, $p = 0.05$) were significant (Fig. 3A). The vectors for hydroperiod and restoration age were separated by 39.4° (Fig. 3A). Wetland type ($r = 0.11$, $p = 0.95$), average depth ($r = 0.33$, $p = 0.53$), average temperature ($r = 0.20$, $p = 0.79$), % sand ($r = 0.21$, $p = 0.62$), conductivity ($r = 0.34$, $p = 0.52$), and average area ($r = 0.12$, $p = 0.87$) vectors were not significant and were not included in the abundance ordination.

The vector of maximum correlation with hydroperiod was highly significant in the biomass ordination ($r = 0.88$, $p < 0.0001$; Fig. 3B). Restoration age showed a weak correlation with community composition ($r = 0.77$, $p = 0.11$), and the vectors for hydroperiod and restoration age were separated by 17.5° (Fig. 3B). Vectors for wetland type ($r = 0.12$, $p = 0.93$), average depth ($r = 0.57$, $p = 0.12$), average temperature ($r = 0.11$, $p = 0.93$), % sand ($r = 0.21$, $p = 0.78$), conductivity ($r = 0.28$, $p = 0.62$), and average area ($r = 0.08$, $p = 0.95$) were not significant.

Discussion

Restored and natural wetland comparisons

Our study is the first intensive investigation of invertebrate communities in restored wetlands in the PRV. Our results are an important step toward assessing the effectiveness of current restoration practices in this region and should be applicable to similar situations in other regions. Some metrics (e.g., total abundance and biomass, diversity) suggested that restored wetlands were similar to natural wetlands, but other metrics (e.g., functional structure) indicated persistent differences, suggesting that recovery in restorations might take longer than the 5 to 16 y considered in our study.

Wetland macroinvertebrate diversity recovers quickly after restoration and can surpass that found in natural wetlands in some systems. For example, macroinvertebrate richness in a reconstructed salt marsh was similar to richness in a natural marsh

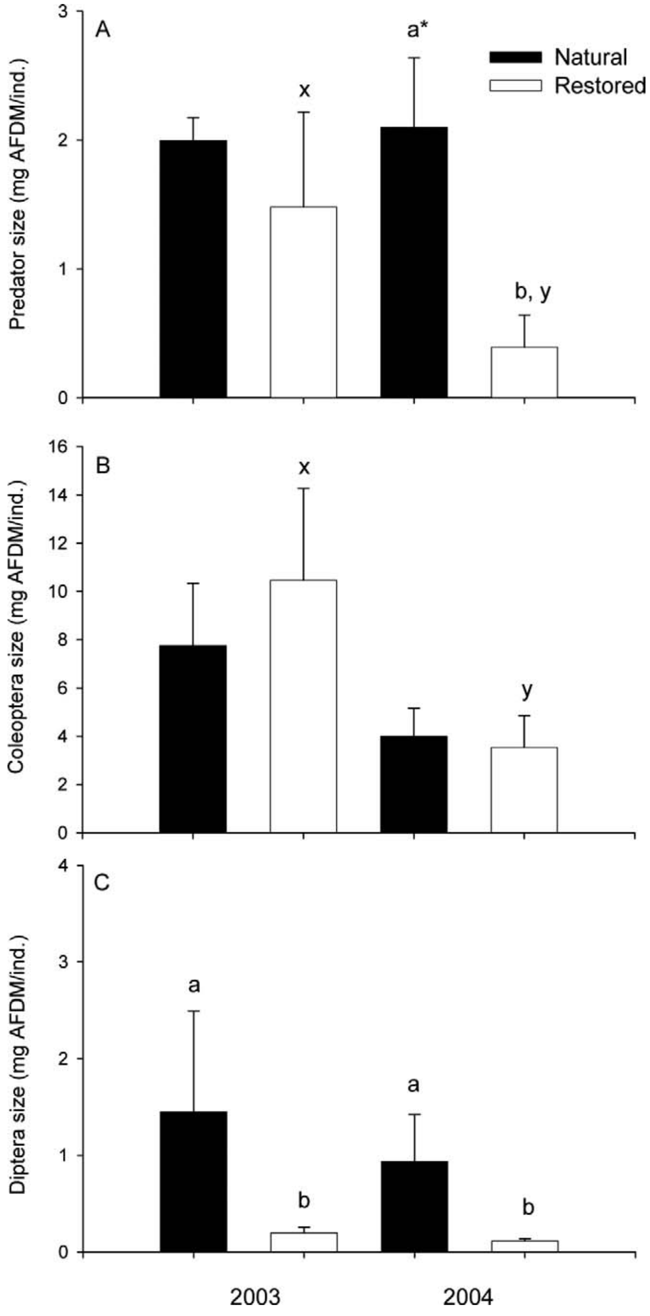

FIG. 2. Mean (+1 SE) individual size of all predators (A), predaceous Coleoptera (B), and predaceous Diptera (C) in natural and restored wetlands during spring 2003 and 2004. Bars with different letters are significantly different. a and b denote differences between natural and restored wetlands within a year, x and y denote differences between years within a wetland type. No asterisk = $p < 0.10$, * = $p < 0.05$. AFDM = ash-free dry mass, ind. = individual.

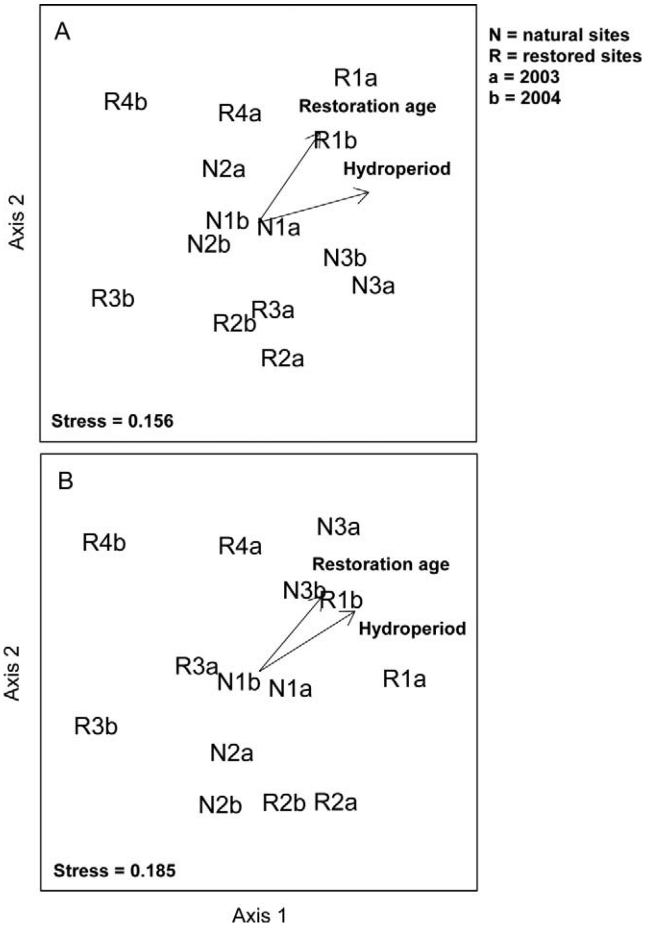

FIG. 3. Ordinations of macroinvertebrate community structure using abundance (A) and biomass (B). Samples were taken from 3 natural and 4 restored wetlands during spring 2003 and 2004. Significantly correlated environmental variables are shown as vectors. Vector length is proportional to the correlation of the macroinvertebrate community with that explanatory variable. Hydroperiod was the number of months of the year during which the site held standing water. Restoration age excluded natural sites and is the age of each restoration (y). See Table 1 for wetland names.

within 4 y (Levin et al. 1996). Macrophyte communities and primary productivity in a North Carolina *Spartina* marsh recovered to natural marsh levels 5 y after restoration, and density and richness of benthic fauna exceeded that of natural sites after 15 to 25 y (Craft et al. 1999). Given the extent to which our restored sites had been degraded before the restoration process (e.g., row-cropped fields before restoration; US Fish and Wildlife Service 1981, Sidle et al. 1989), we were surprised that some metrics (e.g., total abundance, biomass, and diversity) showed recovery within a time frame similar to that observed in other studies (Levin et al. 1996, Craft et al. 1999).

Taxonomic differences between natural and restored wetlands were evident despite similarities in some metrics. Abundance and biomass of amphipods, *Pisidium*, and *Helisoma* were lower in restored than in natural wetlands; biomass of ostracods was lower in restored than in natural wetlands; and leeches were absent from restored wetlands. These results indicate lack of recovery by these groups. Furthermore, the only restored wetland in which *Pisidium* was collected was the Johns Clearing site, a slough that existed before restoration. Recovery of these groups probably is limited by a biotic filter (sensu Hobbs and Norton 2004) associated with the lack of aerial dispersal capabilities of these taxa. Abundances of *Pisidium* were significantly lower in restored Ohio wetlands than in nearby natural systems (Stanczak and Keiper 2004), presumably because of limited dispersal capabilities of both larvae and adults (McMahon 1991). Invertebrates, such as leeches and pygmy backswimmers (Pleidae), with low dispersal abilities had significantly lower abundances in restored than in natural wetlands in New York (Brown et al. 1997).

In contrast to taxa that failed to recover, physid and lymnaeid snails were abundant in restored wetlands. Physid snails also were higher in mitigation than reference wetlands in seasonally to permanently flooded wetlands in West Virginia (Balcombe et al. 2005). This response might be attributable to aspects of physiology that, according to Smith (2001), make pulmonate snails good dispersers and colonizers. For example, many lymnaeid and physid snails are tolerant of poor conditions such as high temperatures and low dissolved O_2 (Smith 2001). Our results suggest that proportions of noninsect groups (i.e., leech and mollusk ratio) might be useful assessment metrics in these and similar wetland systems, although our ability to detect statistical differences between natural and restored wetlands was limited by high variability among sites.

Some taxa, especially odonates and stratiomyid flies, were more abundant in restored than in natural wetlands. Newly created wetlands in Ohio supported odonate taxa that rarely were found in nearby natural wetlands (Roush and Amon 2003). Dragonflies have high dispersal abilities (Corbert 1999) that allow them to colonize newly formed habitats rapidly. Dragonflies base habitat choice on visual cues that include the presence of vegetation and surface water reflection (Corbert 1999), and pond size has been positively correlated with dragonfly colonization (Oertli et al. 2002, Kadoya et al. 2004). In our study, odonates were particularly abundant in the Nature Center restoration. This wetland consistently had the highest average and maximum area among wetlands in our study (Table 1), and these characteristics probably positively influenced odonate abundance. In addition, this wetland had relatively dense stands of emergent plants (e.g., *Typha*; CKM, personal observation) that might have attracted ovipositing adults (Corbert 1999). Stratiomyid abundances also were high at the Nature Center site and this result also might have been related to plant structure because stratiomyids often are associated with emergent vegetation (Merritt and Cummins 1996).

Ordinations and related ANOSIM tests did not reflect significant differences between communities in natural and restored wetlands. Furthermore, vectors that related shifts in macroinvertebrate community to wetland type were not significant, probably because of high variability in macroinvertebrate community composition among restored wetlands. However, vectors relating community shifts to restoration age and to hydroperiod were significant and closely associated because of a positive relationship between hydroperiod length and restoration age. This association occurred partially because the oldest restored site in our study was an existing, intermittently exposed slough before restoration. However, other factors, particularly soil development with restoration age, appear important as well. During a simultaneous companion study at many of the same wetland sites, we observed a strong correlation between organic content of substrates and restoration age. In addition, older restorations with higher organic matter content held water longer (Meyer et al. 2008). Thus, hydrology is a significant factor shaping macroinvertebrate communities in these systems (e.g., Whiles and Goldowitz 2001, 2005) and can be considered an important abiotic filter for macroinvertebrate colonization and recovery. This relationship must be taken into account in restoration planning and management.

Functional structure

We observed differences in functional feeding groups, particularly with respect to biomass, between natural and restored wetlands. These differences are potentially important because macroinvertebrate functional structure is linked closely to ecosystem processes and function in freshwater systems (e.g., Wallace and Webster 1996).

Collector-gatherers consistently dominated abundance and biomass in both natural and restored wetlands, but functional feeding groups exhibited differential recovery patterns and were temporally dynamic. For example, the difference in biomass of collector-filterers between wetland types in 2003, and the concurrent decrease in collector-filterer abundance and increase in collector-gatherer abundance from 2003 to 2004, were driven, in part, by a shift in microcrustacean assemblages in the natural wetlands. This shift was from mostly cladocerans (69%) in 2003 to mostly ostracods (69%) in 2004 and probably was related to differences in hydroperiod between years. In general, 2004 was drier than 2003, indicated by shorter spring hydroperiods in most sites (Table 1). The length of the previous dry phase was a significant predictor of the presence or absence of most species of microcrustaceans in a series of constructed temporary ponds in the UK (Jeffries 2003).

Abundance and biomass of shredders and biomass of herbivore-piercers were higher in natural than in restored wetlands in 2004. The higher shredder abundance and biomass in natural systems was driven almost solely by *Ironoquia plattensis*, which was not found in restored wetlands in 2003 and had higher abundance and biomass in natural than in restored wetlands in 2004. The abundance of *I. plattensis* in some sites is notable because shredders often are underrepresented in wetland habitats (Wissinger 1999) and because this species has been collected in only a handful of intermittent wetlands in the region (Whiles et al. 1999, Alexander and Whiles 2000, Whiles and Goldowitz 2001, 2005). We collected *I. plattensis* at 3 sites, 2 natural (Mormon Middle and Wild Rose East) and 1 restored (Nature Center), in which it had not been found previously. *Ironoquia plattensis* has a limited range, so it is not surprising that this species is not yet abundant in the macroinvertebrate communities of restored wetlands. The changing distribution of *I. plattensis* probably is linked to changes in hydrology of wetland sites over the past decade (Whiles et al. 1999). Long-term sampling in these and other potentially suitable sites will be necessary to understand the apparently dynamic distribution of this insect.

The higher biomass of herbivore-piercers in natural sites was attributable to adult hydrophilid beetles. Hydrophilid larvae leave the water to pupate in nearby organic debris or moist soil (Merritt and Cummins 1996). Soils in restored wetlands were generally sandy and lacked organic materials (Meyer et al. 2008), characteristics that probably limited completion of this step in the hydrophilid life cycle. This abiotic filter probably decreased the presence of adult hydrophilids in restorations. In addition, hydroperiod might limit hydrophilid pupation success in restored habitats. Abundance and biomass of the hydrophilid *Berosus* in Mississippi River floodplain wetland sites were linked to hydrologic differences between sites (Flinn et al., in press).

Body size of predatory macroinvertebrates, many of which are gape-limited, can affect prey selection (e.g., Mittelbach and Persson 1998), predation rates (e.g., Malmquist and Sjöström 1980), and community dynamics (Peckarsky 1982, and references therein) by altering top-down effects. The decrease in individual predator size in restorations and the decrease in predatory beetle size in both wetland types during 2003 to 2004 were related to decreases in hydroperiod duration over this period. Recovery of predators in temporary waters often has a lag time (Williams 1996). Decreased hydroperiods during dry years might limit colonization potential of large-bodied predators, such as adult dytiscid beetles (e.g., Wiggins et al. 1980). Also, average individual size of predatory flies was consistently lower in restored wetlands than natural wetlands, probably because restored wetlands, especially Johns Clearing, had a much higher proportion of tanypodine chironomids, a relatively small-bodied predator taxon, than did natural wetlands.

Drought conditions constrained our study because hydroperiods were significantly shortened, as evidenced by a 50 to 65% decrease in hydroperiods of the Mormon sites from those reported by Whiles and Goldowitz (2001) during 1997 to 1998. In addition, Wild Rose East, which historically had been considered a permanent slough (Whiles and Goldowitz 2001, B. Goldowitz, Platte River Trust, personal communication), dried for ~3 wk during September and October 2003. The spring hydroperiod was shorter in 2004 than in 2003 in all but the intermittently exposed sites in our study, and the shortened hydroperiod constrained our sampling efforts. These differences in annual hydrology probably drove many of the temporal patterns we observed in macroinvertebrate communities, and our results underscore the importance of multiyear studies to account for the dynamic nature of these and similar systems.

Management implications

Our results suggest that many components of wetland macroinvertebrate communities, particularly simple measures such as total abundance and biomass, recover in a relatively short time frame. However, taxonomic and functional differences between wetland types remained evident several years after restoration. In particular, taxa that lack aerial adult stages generally were less abundant or absent from restorations. Augmenting restorations with sediments from natural wetlands, which would contain macroinvertebrate propagules, might overcome the biotic filter of decreased dispersal and might speed recovery of these less-vagile taxa. This process also would introduce organic substrates, which were lacking in newer restorations and appeared related to water-holding capacity (Meyer 2007, Meyer et al. 2008), into resorations.

Results of our study and other studies in the region (Whiles and Goldowitz 2001, 2005, Davis et al. 2006) all underscore the importance of hydrology in shaping macroinvertebrate communities and the restoration process. Restoring and maintaining a natural hydrologic regime should be a central focus in the restoration and management of these wetlands. However, obstacles to restoring hydrology on a local scale (e.g., lack of deep organic horizons in substrates, altered groundwater connections) and upstream impoundments and other anthropogenic decreases in stream flow already have resulted in drastic departures from historic hydrologic conditions in natural systems in the region. Further departures are likely because of increased water use in the region and climate-change predictions, and these changes might further impede successful restoration of these systems.

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