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## MACROINVERTEBRATE COMMUNITIES IN CENTRAL PLATTE RIVER WETLANDS: PATTERNS ACROSS A HYDROLOGIC GRADIENT

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**Abstract:** Wetlands provide critical wildlife habitat in the central Platte River basin of Nebraska, USA, but little is known about their macroinvertebrate communities or how factors such as hydrology affect them. In 1997, we quantified macroinvertebrate abundance, biomass, and community structure and organic matter resources in four natural wetlands that represented a gradient from ephemeral to permanent flooding. All four wetlands had abundant macroinvertebrate communities when flooded, and we observed unique taxa at all sites. Mean annual macroinvertebrate abundance and biomass increased with hydroperiod length, but taxon richness and diversity were greatest in intermittent sites. Non-insect groups, mostly crustaceans, annelids, and mollusks, were important at all sites, and their taxonomic composition shifted across the hydrologic gradient. Insect communities were dominated by dipterans (mostly Chironomidae and Ceratopogonidae) and Coleopterans (mostly Hydrophilidae and Dytiscidae), and these also varied across the hydrologic gradient. Collector-gatherers, scrapers, and predators were the dominant functional groups in terms of biomass, and biomass was most evenly distributed among these groups in intermittent sites. Macroinvertebrate communities in these riparian wetlands vary across natural hydrologic gradients, and diversity peaks in intermittent sites. Patterns of abundance, biomass, and diversity, along with seasonal patterns, suggest that, at a landscape level, a diversity of wetland habitats with different hydrologic regimes will maximize abundance and diversity of freshwater macroinvertebrate communities in this region.

**Key Words:** intermittent, backwater, floodplain, aquatic invertebrate, Platte River

### INTRODUCTION

Wetlands are productive habitats that are important for biodiversity and providing valuable ecosystem services such as flood control and maintenance of water quality. Although now widely regarded as important habitats, wetlands are one of the most beleaguered habitats in North America, and less than 50% of the historical wetlands in the lower forty-eight states of the United States remain (Vileisis 1997). Concerns over the loss of wetland habitats and associated ecosystem services have led to increased management of remaining wetlands and restoration of degraded systems. However, proper management and restoration require an understanding of factors that influence the structure and function of natural systems. Studies have examined factors influencing the productivity and/or

diversity of plants (e.g., Wallen et al. 1988, Pollock et al. 1998, Ervin and Wetzel 2002), invertebrates (e.g., Batzer et al. 1999, Whiles and Goldowitz 2001, Jenkins et al. 2003), and amphibians (e.g., Snodgrass et al. 2000) in wetlands, and hydrology and predation are often important factors.

The influence of hydrology on the structure and function of freshwater ecosystems has received considerable attention (e.g., van der Valk 1981, Matthews 1988, Resh et al. 1988, Stanley and Fisher 1992, Poff and Allan 1995, Wellborn et al. 1996, Dodds et al. 2004), and numerous studies provide evidence that hydrology can have a profound impact on the biological diversity and productivity of wetlands (e.g., Batzer and Wissinger 1996, Corti et al. 1997, Kohler et al. 1999, Zimmer et al. 2000, Whiles and Goldowitz 2001). Further, along with direct effects, hydrology can influence

Table 1. Physical characteristics of the four study sites at Mormon Island (MI) and Wild Rose Ranch (WR) during 1997-1998. Study sites are arranged in order of increasing annual hydroperiod. All sites are 20-m reaches of linear wetlands. Maximum depth, area, and volume are max. readings obtained between 5 April 1997 - 4 April 1998.

Characteristics	Study Site			
	WR1	MI2	MI1	WR2
Maximum depth (cm)	21	54	68	43
Maximum wetted area (m <sup>2</sup> )	262	300	386	43
Maximum volume (m <sup>3</sup> )	19	149	151	17
Annual hydroperiod (days)	158	296	331	365
*No. dry periods/yr	11	4	3	0
Longest dry period (days)	77	48	29	—
**Annual degree days (>0° C)	939	2150	2939	3173
**Max. daily avg. temp. (°C)	22	27	28	18
**Min. daily avg. temp. (°C)	0	0	0	4
Inorganic substrates:				
% gravel	0	0	0	8
% sand	33	24	24	53
% silt	67	76	76	39

\* Calculated as number of periods  $\geq$  3 days without surface water present.

\*\* Calculated from daily means for periods with water; a daily mean of 0°C was assumed for periods with extensive ice cover (25 November 1997 – 22 February 1998 for all sites except WR2).

important biological factors (e.g., predator-permanence gradients) (Wellborn et al. 1996, Wissinger et al. 1999). Understanding the influence of hydrology and associated factors on wetland function is critical for successful wetland management and restoration.

In the central Platte River basin of Nebraska, USA, there is great interest in wetland management and restoration of riparian wetlands because they are critical habitats and important stopover points for migratory birds in the central flyway, including the federally endangered Whooping Crane (U.S. Fish and Wildlife Service 1997). Due to agricultural development, the once extensive wetland system of the central Platte River valley is now among the most diminished and degraded habitats in the region (Sidle et al. 1989). Although these wetlands are critical habitats and provide important food resources for migrating birds (e.g., Reinecke and Krapu 1986), little is known about their aquatic communities and the influence of factors such as hydrology on their diversity and productivity. To address this lack of knowledge, we compared macroinvertebrate communities in four wetlands in the central Platte River basin that represented a hydrologic gradient ranging from ephemeral to permanent water. We predicted that these wetlands would harbor abundant macroinvertebrate communities and that hydrology would influence the abundance, biomass, and diversity of macroinvertebrates.

#### STUDY SITES

We selected four study sites, comprised of 20-m reaches of linear wetlands, located on two adjacent

islands in the central Platte River, Hall County, Nebraska. Sites were located on either the Wild Rose Ranch (WR) or Mormon Island (MI) properties owned by the Platte River Whooping Crane Maintenance Trust. The dominant habitat on these islands is mesic prairie, dominated by grasses, sedges, and forbs typical of tallgrass prairie, with linear wetlands located in low areas. The wetlands are connected to the braided river channels during wet periods and high flows but disconnect as flows recede. Substrates are silt and detritus overlying sand and gravel. Based on Cowardin et al. (1979), these systems are palustrine, emergent wetlands that range from non-persistent to persistent habitats.

Hydrology of the four study sites ranged from ephemeral to perennial (Table 1, Figure 1). Water was about 0.25–1.0 m deep, and flows were slow (<5 cm/s) when wetlands were full but ceased when water level decreased. Riparian vegetation is a mixture of grasses, sedges, rushes, and mixed forbs; no woody vegetation is present. Macrophytes (e.g., *Typha*, *Scirpus*, *Sparganium*, *Eleocharis*, *Lemna*, *Potamogeton*, and others) and filamentous algae were common in MI1, MI2, and WR2 during spring and summer but less abundant in the ephemeral site (WR1) where grasses and other prairie plants encroached into the wetland. Water chemistry was generally similar among the study sites. Annual average pH = ~7.7 and dissolved oxygen = ~6.0 mg/L. Conductivity was somewhat lower in the ephemeral site (WR1 annual average = ~500  $\mu$ S/cm) than the three wetter sites (= ~1400  $\mu$ S/cm) (Goldowitz and Whiles 1999, Whiles and Goldowitz 2001).

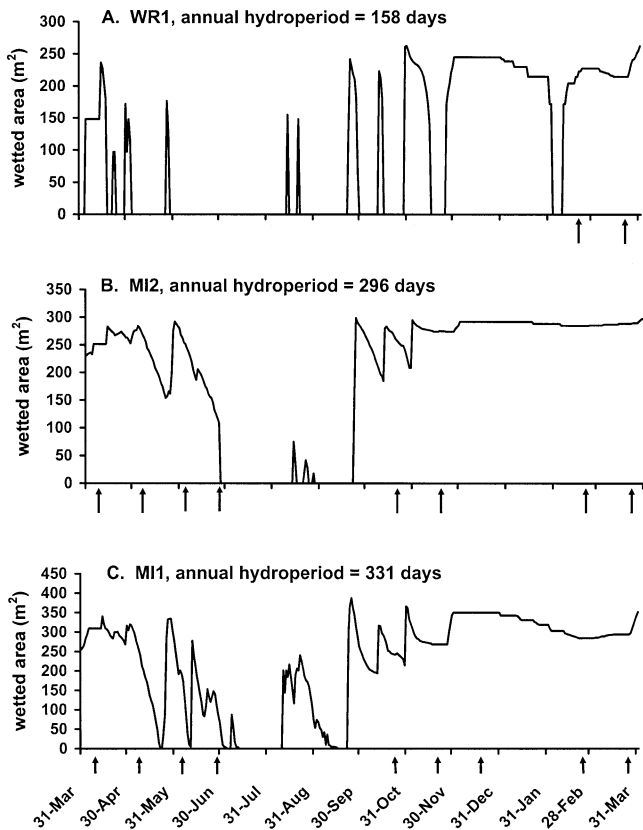


Figure 1. Annual hydrographs, based on wetted area, for the ephemeral (WR1) and the two intermittent (MI1, MI2) study sites during the 1997–1998 study period. The permanent site (WR2) is not shown because its morphology is such that wetted surface area does not fluctuate significantly with depth and is nearly constant at 43 m<sup>2</sup>. Arrows indicate sampling dates in each site (WR2 was sampled every month during the year).

The two wettest sites (WR2 and MI1) harbored fish communities during this study. *Hybognathus hankinsoni* Hubbs, *Fundulus sciadicus* Cope, and to a lesser extent, *Cyprinus carpio* Linnaeus used the intermittent site (MI1) for spawning and nursery habitat during spring and also migrated back into the site during fall. A year-round community consisting of *Etheostoma exile* (Girard), *Semotilus atromaculatus* (Mitchill), *Culaea inconstans* (Kirtland), *F. sciadicus*, and other species was present in the perennial site (WR2) (Whiles and Goldowitz 1998).

Climate in this region is typical of the central Great Plains, with warm summers (July mean air temp. = 24°C) and cold winters (January mean air temp. = -7°C). Significant ice cover is often present on surface waters from November to March. Average annual precipitation is 63 cm/yr, with most occurring in May and June. Precipitation during our study was greater than average (81 cm, or 128% of the long-term average),

mostly due to above average rainfall during late summer and fall 1997.

Both precipitation and the adjacent Platte River influence hydrology of these wetlands (Wesche et al. 1994, Whiles and Goldowitz 1998). In addition, upstream dams, canals, and power plants have reduced flows and altered seasonal patterns in the Platte River. In its current state, flows in this section of the Platte River generally peak in June, with lowest levels during the July to September irrigation season. River discharge was relatively high during our study (total annual runoff = 178% of the long term average) due to above average rainfall during summer and fall.

## METHODS

### Hydrology and Physical Habitat

Wetted area, volume, and water temperature were monitored continuously in the study sites for one year beginning March 1997. Staff gauges were installed at the deepest point in each site, and transects for wetted width and depth measurements were established at 0, 10, and 20 m along the length of each linear wetland. Wetted width and depth measurements were taken weekly and more frequently during periods of fluctuating water levels. Water depth was recorded daily when water levels fluctuated and every 1–2 weeks during periods of little fluctuation or ice cover. Staff gauge readings and wetted width and depth transect measurements were used to predict daily wetted surface area of each site following procedures of Whiles and Goldowitz (2001). Significant logarithmic relationships ( $r^2 > 0.90$ ,  $p < 0.01$ ,  $n > 25$  for each) were obtained for depth vs. surface area at WR1, MI2, and MI1. Depth and surface area were not correlated at the perennial site (WR2) because water levels did not fluctuate as much and the morphology of this site is such that wetted surface area changes very little with depth. Thus, we used an average wetted surface area of 43 m<sup>2</sup> based on field measurements for WR2. Annual hydroperiods at each site were calculated as total days with water for the one-year study period.

Thermographs (Onset Computer Corporation, Bourne, MA) recorded water temperatures continuously in each site whenever sufficient water was present and not frozen. When sites were frozen, we assumed temperature to be 0°C from the formation of sufficient ice cover (thermographs removed 28 November 1997) until spring thaw (thermographs replaced 15 February 1998). Thermographs were also removed from sites when they dried and were replaced following rewetting. Daily average water temperatures were used to estimate annual degree days (>0°C).

### Macroinvertebrate Abundance and Biomass

Beginning on 5 April 1997, three stovepipe core samples were collected at ~30-d intervals in each site for one year when water was present and not extensively frozen. Because of differences in hydroperiod among sites, the number of monthly sampling dates varied greatly among sites (WR1 = 2, MI2 = 8, MI1 = 9, WR2 = 13). Samples were obtained by driving a stovepipe coring device (20-cm diameter, 91-cm depth, 314-cm<sup>2</sup> sampling area) into the substrate at three locations in each site. On each sampling date, the three samples were taken along a 20-m transect aligned mid-way between the shoreline and deepest area of each site moving from the downstream (core 1) to upstream (core 3) end so that a sample was taken in a random location within the lower, middle, and upper part of each wetland, all at mid-depth. The corer was inserted ~20 cm into the substrate so that water could not enter, and all sediments and vegetation down to ~10 cm below the sediment surface were removed by hand into a holding bucket. All water within the corer was then bailed into the bucket, and the water/sediment mixture was stirred and elutriated through a 250- $\mu$ m sieve. Material retained on the sieve was preserved in 7–8% formalin. This sampling procedure allowed us to sample invertebrates associated with sediments and plants along with those in the water column quantitatively.

Samples were washed through nested sieves and divided into very coarse (>4 mm), coarse (<4 mm>1 mm), and fine (<1 mm>250  $\mu$ m) fractions. Invertebrates were removed from very coarse and coarse fractions under a dissecting microscope. Fine fractions occasionally were subsampled (up to 1/16 of total) with a Folsom wheel prior to removing invertebrates. All invertebrates were identified, counted, and measured (total body length). Identifications to the lowest practical taxonomic unit (usually genus) were made using keys provided by Thorp and Covich (1991), Merritt and Cummins (1996), and Smith (2001). Notable exceptions were oligochaetes (class) and chironomids (family or subfamily). Functional designations were based on Thorp and Covich (1991) and Merritt and Cummins (1996). Body length measurements were used to estimate dry mass (DM) following procedures of Benke et al. (1999). Taxon-specific length-mass relationships were obtained from Bottrell et al. (1976), Benke et al. (1999), and Whiles et al. (1999).

### Organic Matter Estimates

Following removal of invertebrates from samples, one sample date per season was analyzed for organic matter content (spring: 2 May 1997; summer: 28 June

1997; autumn: 23 October 1997; winter: 22 February 1998). The driest site (WR1) was only sampled in winter, and no estimates of organic matter were available for the other periods. Coarse particulate organic materials (CPOM) from each sample (>1mm) were sorted into living macrophytes, filamentous algae, dead leaves and stems, seeds, and miscellaneous material. Each fraction was then dried (55° C for 5 d), weighed, ashed (500°C for 5 h), and reweighed to estimate g ash-free dry mass (AFDM)/m<sup>2</sup>. Fine fractions of each sample (<1mm>250 $\mu$ m) were designated fine particulate organic matter (FPOM), and AFDM was determined in the same manner as for CPOM. Our benthic FPOM estimates underestimate actual FPOM standing stocks because we did not collect fine particles that passed through the 250- $\mu$ m sieve while processing samples in the field.

### Statistical Analyses

Individual sampling locations in each wetland (i.e., core 1, 2, and 3) were treated as replicate samples (n=3 for each wetland). Invertebrate and organic matter values for each location were averaged over the entire year to estimate annual averages for each sample location. In order to compare sites on the only two dates when all four held water and were sampled, averages for the February and March 1998 sampling dates were also calculated. Differences in invertebrate communities and organic matter were compared among sites using one-way analysis of variance (ANOVA), and individual means were compared using Tukey's multiple comparison procedure ( $\alpha=0.05$ ). Where necessary, values were log-transformed to satisfy normality assumptions and correct for heteroscedasticity. All values used in our analyses and presented here are based only on periods when water was present (e.g., when a wetland was dry, no samples were collected and that date was not included in the calculation of means). Hence, the natural hydrologic gradient we examined dictated different sampling intensities among the sites. Because individual wetlands cannot be replicated, our design involved simple pseudoreplication (e.g., Hurlbert 1984, Hurlbert and White 1993). Thus, our inference is limited, and we cannot strictly attribute any differences we found to any specific factor.

## RESULTS

### Macroinvertebrate Abundance and Diversity

Annual average macroinvertebrate abundance ranged from 26,989 individuals/m<sup>2</sup> in the ephemeral site (WR1) to 152,741 individuals/m<sup>2</sup> in the permanent site (WR2); total abundance in WR2 was greater than

Table 2. Macroinvertebrate mean abundance, mean biomass, percent functional composition\*, and measures of diversity at the four wetlands during 1997–1998. Sites are arranged in order of increasing hydroperiod. Values in parentheses are 1 standard error. Across rows, values with different superscript letters are significantly different ( $p < 0.05$ ).

Metric	WR1	MI2	MI1	WR2
Abundance (no./m <sup>2</sup> )	26989.3 (3874.4) <sup>a</sup>	66595.0 (18672.7) <sup>a</sup>	57070.8 (7994.0) <sup>a</sup>	152741.1 (17255.3) <sup>b</sup>
Collector-filters	1%	10%	11%	3%
Collector-gatherers	88%	65%	69%	92%
Predators	11%	16%	17%	3%
Scrapers	<1%	9%	2%	1%
Shredders	0	1%	1%	1%
Biomass (mg DM/m <sup>2</sup> )	127.2 (30.0) <sup>a</sup>	4364.3 (223.3) <sup>b</sup>	2449.2 (251.9) <sup>c</sup>	9472.2 (623.2) <sup>d</sup>
Collector-filters	1%	2%	4%	7%
Collector-gatherers	62%	14%	26%	59%
Predators	6%	35%	19%	12%
Scrapers	31%	49%	38%	19%
Shredders	0	<1%	14%	3%
Average taxon richness	7.3 (0.4) <sup>a</sup>	34.3 (4.1) <sup>b</sup>	32.7 (3.5) <sup>b</sup>	20.3 (0.8) <sup>c</sup>
Total taxon richness	10	55	54	34
Shannon diversity (H')	1.1 (0.1) <sup>a</sup>	2.1 (0.1) <sup>b</sup>	1.7 (0.2) <sup>bc</sup>	1.4 (0.2) <sup>ac</sup>
Unique taxa	2	14	12	7

\* Functional group values do not include herbivore-piercers and herbivore miners, which did not represent more than 1% at any site.

all other sites ( $F=24.1$ ;  $df=3,8$ ;  $P<0.0001$ ) (Table 2). Biomass showed a similar pattern, with the lowest annual average at WR1 (127 mg DM/m<sup>2</sup>) and highest at WR2 (9,472 mg DM/m<sup>2</sup>). Annual average biomass was different among all sites ( $F=188.8$ ;  $df=3,8$ ;  $P<0.0001$ ) (Table 2). Average abundance during February and March, when all sites held water, did not differ significantly among sites. However, biomass differed across sites during this period ( $F=13.6$ ;  $df=3,8$ ;  $P=0.002$ ), and was lowest in the ephemeral site (WR1).

Macroinvertebrate abundance peaked in WR2 and the intermittent (MI1, MI2) sites in May–June 1997 (Figure 2A). Biomass showed a similar but less pronounced pattern in these three sites (Figure 2B). The ephemeral site held water long enough for sampling only in February–March 1998, precluding meaningful comparisons with the other sites.

Seventy-nine macroinvertebrate taxa were collected during this study. Total and average taxon richness ( $F=26.1$ ;  $df=3,8$ ;  $P<0.0001$ ) and Shannon diversity ( $F=12.9$ ;  $df=3,8$ ;  $P=0.002$ ) varied across sites and were highest in the intermittent sites (Table 2). Diversity and richness values were lowest in the ephemeral site and intermediate in the permanent site. Richness ( $F=99.9$ ;  $df=3,8$ ;  $P<0.001$ ) and diversity ( $F=11.9$ ;  $df=3,8$ ;  $P=0.003$ ) during March and February only also differed across sites, with values in WR1 significantly lower than all other sites. At least two unique taxa were present in each site, with greatest numbers of unique taxa in the intermittent sites (Table 2).

Non-insect groups were major contributors to abun-

dance at all four sites, with annelids (mostly oligochaetes) and crustaceans (mostly cyclopoid copepods) constituting the bulk of abundance at all sites (Table 3). Non-Tanypodinae chironomids in the permanent site, which accounted for 39% of total abundance, were the only insect group to represent more than 2% of total abundance at any site. In contrast to abundance, insect groups were substantial contributors to biomass at all sites (Table 4). Mollusks, particularly gastropods, were also important contributors to total biomass. Biomass showed greater differences among sites than abundance; mollusks and insects dominated biomass at all sites, but the composition of these groups and dominant taxa within them varied considerably across sites (Table 4).

Diptera, mostly non-Tanypodinae Chironomidae and Ceratopogonidae, dominated insect abundance across sites, but other groups, particularly coleopterans (mostly *Agabus* and *Tropisternus*) were important contributors to insect biomass in the intermittent and permanent sites (Tables 3, 4). Trichopterans, 99% of which were the limnephilid caddisfly, *Ironoquia platensis* Alexander and Whiles, accounted for 9% of total macroinvertebrate biomass in the wetter intermittent site (MI1) but were absent from the other three sites.

Copepods (mostly Cyclopoida) and cladocerans (mostly *Simocephalus* and *Daphnia*) dominated crustacean abundance in all except the permanent site, where copepods and amphipods were most abundant (Table 3). Copepods dominated crustacean biomass in the ephemeral site, but cladocerans and amphipods accounted for most crustacean biomass in the two inter-

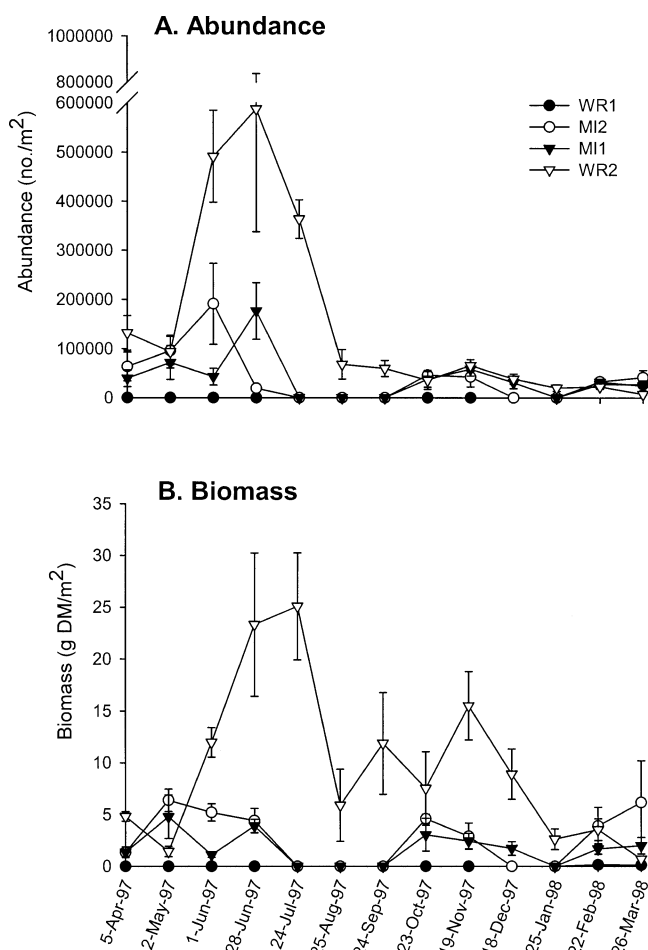


Figure 2. Monthly average (+ 1 standard error) total macroinvertebrate abundance (A) and biomass (B) in the study sites during the 1997–1998 study period.

mittent sites and amphipods (56% *Crangonyx*, 44% *Hyalella*) alone accounted for ~97% of total crustacean biomass in the permanent site (Table 4).

Cladocerans were only present in the two intermittent sites, and there were large differences in cladoceran communities between these sites. *Simocephalus*, *Daphnia*, Chydoridae, *Ceriodaphnia*, and *Scapholeberis* were all abundant in the drier intermittent site (MI2), whereas *Simocephalus* constituted 100% of the cladoceran community in the wetter intermittent site (MI1).

Mollusk communities showed distinct trends across the hydrologic gradient. Among gastropods, there was a shift from 100% Lymnaeidae (all *Fossaria*) in the ephemeral site to 100% Physidae (all *Physella*) in the permanent site (Tables 3,4). The fingernail clam, *Pisidium*, was only abundant in the permanent site, where it represented 7% of total macroinvertebrate biomass (Tables 3, 4).

## Macroinvertebrate Functional Structure

Based on abundances, functional structure was fairly similar across sites because collector-gatherers dominated macroinvertebrate abundance (65–92% of total abundance), and predators were the second most abundant group at all sites (Table 2). In contrast, functional structure based on biomass varied across sites (Table 2). Collector-gatherers accounted for most biomass in the ephemeral (WR1) and perennial (WR2) sites, whereas scrapers had greatest biomass in the two intermittent sites (MI1, MI2). Shredders were not present or poorly represented in three of the four sites but accounted for 14% of biomass in MI1 because of the presence of a single species of shredder, the limnephilid caddisfly *I. plattensis*. Numbers and biomass of functional groups were generally more evenly distributed across groups in the two intermittent sites.

## Organic Matter

There were no significant differences in FPOM across sites, although annual average FPOM in the perennial site (WR2) was only about half that of the other three sites (Table 5). In contrast, annual average total CPOM values differed among sites ( $F=4.84$ ;  $df=3,8$ ;  $P=0.033$ ), with highest values in the intermittent sites (MI1, MI2) (Table 5). This pattern was primarily a result of differences in living ( $F=9.93$ ;  $df=3,8$ ;  $P=0.005$ ) and senesced ( $F=4.8$ ;  $df=3,8$ ;  $P=0.033$ ) macrophytes, both of which were greatest in the two intermittent sites. Seeds and miscellaneous CPOM showed similar, non-significant trends of highest values in the two intermittent sites. Filamentous algae contributed significantly to organic matter pools only at the ephemeral (12% of total CPOM) and perennial (3% of total CPOM) sites.

## DISCUSSION

Macroinvertebrate communities in these central Platte River wetlands were similar to those of other wetland types in the Great Plains and adjacent regions (e.g., Euliss et al. 1999, Lovvorn et al. 1999), particularly the Playas of the Southern Great Plains (Hall et al. 1999). These other studies, along with ours, suggest that non-insect groups, particularly oligochaetes, crustaceans such as amphipods and copepods, and gastropods, are often numerically dominant components of the macroinvertebrate communities. Among insects, taxa with rapid life cycles (e.g., many dipterans including chironomids, ceratopogonids, and culicids) and air-breathers such as the hemipterans, most of the coleopterans, and some dipterans (e.g., stratiomyids) are also abundant. In sites with longer hydroperiods

Table 3. Average abundance (no./m<sup>2</sup>) and percent contribution of macroinvertebrate taxa in the study sites. Percent contribution of major groups is the percent of total macroinvertebrate abundance; percent contribution of individual taxa within groups is percent contribution to that group. Sites are presented from left to right in order of increasing hydroperiod.

Taxon	WR1		MI2		MI1		WR2	
	No./m <sup>2</sup>	%	No./m <sup>2</sup>	%	No./m <sup>2</sup>	%	No./m <sup>2</sup>	%
<b>Tricladida</b>	<b>0.0</b>	<b>0</b>	<b>1.3</b>	<b>&lt;1</b>	<b>0.0</b>	<b>0</b>	<b>86.2</b>	<b>&lt;1</b>
<b>Nematoda</b>	<b>2840.0</b>	<b>11</b>	<b>9897.3</b>	<b>15</b>	<b>9454.2</b>	<b>17</b>	<b>3707.3</b>	<b>2</b>
<b>Annelida</b>	<b>5061.3</b>	<b>19</b>	<b>20798.2</b>	<b>31</b>	<b>19175.7</b>	<b>34</b>	<b>64345.7</b>	<b>42</b>
Oligochaeta	5061.3	100	20771.5	100	19149.3	100	64163.5	100
Hirudinea	0.0	0	26.7	<1	26.4	0	182.2	<1
<b>Crustacea</b>	<b>17797.3</b>	<b>66</b>	<b>29260.8</b>	<b>44</b>	<b>25361.8</b>	<b>44</b>	<b>17015.1</b>	<b>11</b>
Cladocera	0.0	0	6203.5	21	5097.5	20	0.0	0
Ostracoda	0.0	0	878.7	3	1141.3	5	256.0	2
Copepoda	17797.3	100	21793.3	74	19069.6	75	14171.1	83
Amphipoda	0.0	0	385.3	1	53.3	<1	2588.0	15
<b>Hydrachnidia</b>	<b>0.0</b>	<b>0</b>	<b>25.3</b>	<b>&lt;1</b>	<b>11.9</b>	<b>&lt;1</b>	<b>0.0</b>	<b>0</b>
<b>Insecta</b>	<b>1248.0</b>	<b>5</b>	<b>2365.3</b>	<b>4</b>	<b>2168.9</b>	<b>4</b>	<b>60735.7</b>	<b>40</b>
Collembola	0.0	0	88.0	4	72.3	3	52.5	<1
Odonata	21.3	2	36.0	2	126.8	6	103.4	<1
Ephemeroptera	0.0	0	98.7	4	41.5	2	38.6	<1
Hemiptera	0.0	0	60.0	3	9.5	<1	13.1	<1
Coleoptera	0.0	0	128.0	5	21.3	1	73.0	<1
Trichoptera	0.0	0	0.0	0	629.3	29	0.0	0
Diptera	1226.7	98	1954.7	83	1268.1	58	60455.1	100
<b>Molluska</b>	<b>42.7</b>	<b>&lt;1</b>	<b>4246.7</b>	<b>6</b>	<b>898.4</b>	<b>2</b>	<b>6851.3</b>	<b>4</b>
Hydrobiidae	0.0	0	53.3	1	19.0	2	0.0	0
Lymnaeidae	42.7	100	1728.0	41	219.3	24	0.0	0
Physidae	0.0	0	2321.3	55	155.3	17	1938.7	28
Planorbidae	0.0	0	144.0	3	502.5	56	0.0	0
Sphaeriidae	0.0	0	0.0	0	2.4	<1	4912.6	72

(e.g., those that hold surface water more often than they are dry), larger predatory taxa such as odonates become increasingly abundant.

Although the communities we observed are common in wetlands in the Great Plains, there were some interesting exceptions. In particular, the abundance of a CPOM-shredding caddisfly, *I. plattensis*, in one of our intermittent sites (MI1) is unusual. In a review of numerous studies of wetland invertebrate communities across North America, Wissinger (1999) noted that CPOM shredders were rare in wetlands, and thus nutrients and energy from detrital resources must enter food webs via other pathways. *Ironoquia plattensis* are an exception, as our current investigation showed that this caddisfly accounts for 9% of macroinvertebrate biomass in the MI1 wetland. Further, our prior investigations demonstrated that this trichopteran is productive, consumes about 13% of the annual standing stock of CPOM in this site (Whiles et al. 1999), and represents over half of the insect emergence production from this wetland (Whiles and Goldowitz 2001). Although an important component of the MI1 wetland,

this caddisfly was not present in any of our other sites. To date, *I. plattensis* is known only from a handful of intermittent wetlands in the region, and this is likely linked to its adaptation to a fairly specific intermittent hydrologic regime (Whiles et al. 1999).

#### Patterns Across the Hydrologic Gradient

We cannot strictly attribute the patterns we observed to hydrology because our study design did not limit confounding variables. However, other studies (e.g., Batzer and Wissinger 1996, Wellborn et al. 1996, Corti et al. 1997, Wissinger 1999, Whiles and Goldowitz 2000, Zimmer et al. 2000), combined with the patterns we observed during our study, suggest that hydrology is a primary factor influencing macroinvertebrate communities in wetlands. Based on the present study and our simultaneous investigation of insect emergence patterns (Whiles and Goldowitz 2001), we noted strong shifts in community structure along the hydrologic gradients we examined, and these patterns are evident at both relatively coarse (e.g., total macroin-



Table 4. Average biomass (mg dry mass/m<sup>2</sup>) and percent contribution of macroinvertebrate taxa in the study sites. Percent contribution of major groups is the percent of total macroinvertebrate biomass; percent contribution of individual taxa within groups is percent contribution to that group. Sites are presented from left to right in order of increasing hydroperiod.

Taxon	WR1		MI2		MI1		WR2	
	mg/m <sup>2</sup>	%	mg/m <sup>2</sup>	%	mg/m <sup>2</sup>	%	mg/m <sup>2</sup>	%
<b>Tricladida</b>	<b>0.0</b>	<b>0</b>	<b>0.4</b>	<b>&lt;1</b>	<b>0.0</b>	<b>0</b>	<b>26.6</b>	<b>&lt;1</b>
<b>Nematoda</b>	<b>2.0</b>	<b>2</b>	<b>6.9</b>	<b>&lt;1</b>	<b>6.6</b>	<b>&lt;1</b>	<b>2.6</b>	<b>&lt;1</b>
<b>Annelida</b>	<b>15.5</b>	<b>12</b>	<b>467.6</b>	<b>11</b>	<b>549.0</b>	<b>23</b>	<b>907.5</b>	<b>10</b>
Oligochaeta	15.5	100	441.4	94	532.4	97	834.5	92
Hirudinea	0.0	0	26.3	6	16.6	3	73.0	8
<b>Crustacea</b>	<b>24.2</b>	<b>19</b>	<b>142.7</b>	<b>3</b>	<b>119.3</b>	<b>5</b>	<b>698.2</b>	<b>7</b>
Cladocera	0.0	0	56.6	40	76.4	64	0.0	0
Ostracoda	0.0	0	5.1	4	6.6	6	1.5	<1
Copepoda	24.2	100	24.7	17	20.7	17	18.9	3
Amphipoda	0.0	0	56.4	39	15.6	13	677.8	97
<b>Hydrachnidia</b>	<b>0.0</b>	<b>0</b>	<b>0.0</b>	<b>0</b>	<b>0.0</b>	<b>0</b>	<b>0.0</b>	<b>0</b>
<b>Insecta</b>	<b>46.1</b>	<b>36</b>	<b>1624.0</b>	<b>37</b>	<b>828.8</b>	<b>34</b>	<b>5349.6</b>	<b>56</b>
Collembola	0.0	0	0.7	<1	1.4	<1	2.0	<1
Odonata	1.7	4	101.9	6	36.8	4	3.3	<1
Ephemeroptera	0.0	0	38.5	2	11.8	1	4.8	<1
Hemiptera	0.0	0	12.2	1	38.0	5	9.5	<1
Coleoptera	0.0	0	1307.5	81	437.5	53	918.1	17
Trichoptera	0.0	0	0.0	0	231.9	28	0.0	0
Diptera	44.4	96	163.3	10	71.4	9	4411.8	82
<b>Molluska</b>	<b>39.4</b>	<b>31</b>	<b>2115.7</b>	<b>49</b>	<b>919.7</b>	<b>38</b>	<b>2487.7</b>	<b>26</b>
Hydrobiidae	0.0	0	7.7	<1	3.3	<1	0.0	0
Lymnaeidae	39.4	100	1161.9	55	391.4	43	0.0	0
Physidae	0.0	0	880.5	42	260.1	28	1795.5	72
Planorbidae	0.0	0	65.5	3	260.5	28	0.0	0
Sphaeriidae	0.0	0	0.0	0	4.4	<1	692.2	28

vertebrate communities) and fine (e.g., genera of Cladocera, Molluska, and Gastropoda) taxonomic scales.

Hydrology is often confounded with other factors that influence invertebrate communities. As is the case in other systems, hydrology is linked to the presence,

abundance, and diversity of vertebrate predators. Fish, and other vertebrate predators such as salamanders, can have a strong influence on macroinvertebrate communities in wetlands (Huener and Kadlec 1992, Mallory et al. 1994, Corti et al. 1997, Wissinger 1999,

Table 5. Annual average CPOM and FPOM standing stocks (g AFDM/m<sup>2</sup>) in the study sites. Sites are presented in order of increasing annual hydroperiod. Values in parentheses are 1 standard error. Means were calculated from benthic core samples collected seasonally during 1997–1998 at each site (n = 12) except for WR1 where water was present and not frozen only during spring 1998 (n = 3). Across rows, values with different superscript letters are significantly different (p < 0.05).

Category	Study Site			
	WR1	MI2	MI1	WR2
Total FPOM	159.7 (58.9)	181.4 (23.1)	199.5 (26.2)	82.4 (10.6)
Total CPOM	104.7 (22.0) <sup>a</sup>	270.5 (51.0) <sup>ab</sup>	416.5 (40.4) <sup>b</sup>	151.2 (23.0) <sup>a</sup>
Macrophytes				
living	0.0 <sup>a</sup>	65.6 (24.6) <sup>ab</sup>	109.7 (18.3) <sup>b</sup>	10.5 (4.1) <sup>a</sup>
senesced	17.0 (6.1) <sup>a</sup>	52.7 (15.0) <sup>ab</sup>	177.0 (48.2) <sup>b</sup>	46.7 (11.2) <sup>ab</sup>
Filamentous algae	12.2 (9.1)	0.1 (0.1)	0.0	4.7 (2.6)
Seeds	0.0	4.7 (3.2)	5.5 (1.4)	0.2 (0.1)
Miscellaneous	75.5 (7.7)	147.2 (30.9)	124.3 (24.9)	89.1 (15.5)

Wissinger et al. 1999, Zimmer et al. 2001, Wissinger et al. 2003). Salamanders were not present in our wetlands, but fish were present year-round in our perennial site, and a seasonal community was present in our wettest intermittent site (MI1). As with other studies, we cannot completely separate the effects of hydrology and fish on macroinvertebrate communities in these wetlands. However, the presence or absence of fish in these systems is ultimately a product of hydroperiod length (e.g., predator-permanence gradients), and thus, we consider hydrology the primary factor underlying patterns that we observed.

Results of our study add to growing evidence that intermediate hydroperiods support greater diversity in Platte River wetlands. In our concurrent study of insect emergence from the same wetlands, plus an additional ephemeral site, Whiles and Goldowitz (2001) found greatest insect diversity (measured as richness) in the same intermittent sites that harbored greatest total macroinvertebrate richness in the current study (MI1, MI2). Both results suggest that both emerging insects and total macroinvertebrates respond similarly to the hydrologic gradient and show similar patterns of greater diversity in intermittent sites.

The short and unpredictable hydroperiod in our ephemeral site (WR1) resulted in reduced sampling intensity (only sampled in February and March 1998) for this site. Although this constrained our study, an analysis of only the February and March 1998 data across all sites showed that patterns of macroinvertebrate biomass, richness, and diversity across sites were the same as when data from all dates and sites were used. Only total abundance failed to show the same pattern as for the full year because small-bodied taxa, primarily copepods, oligochaetes, and chironomids, rapidly colonized WR1 when water was present. In a concurrent investigation of insect emergence from these wetlands, we sampled an additional ephemeral site on Mormon Island and found that insect abundance, biomass, and richness values from both ephemeral sites were significantly lower than intermittent and permanent sites (Whiles and Goldowitz 2001), substantiating patterns we observed in this study (e.g., reduced biomass and diversity in ephemeral sites).

In contrast to macroinvertebrate patterns, differences in living macrophyte biomass in WR1 samples compared to the other sites were influenced by sampling constraints because we only sampled this site when water was present during late winter and early spring, before most annual macrophyte growth occurs in these wetlands. Nonetheless, patterns we report here reflect conditions when water and aquatic macroinvertebrates are present in these wetlands. Differences in plant communities across the hydrologic gradient we examined likely influenced our results because wetland

plant communities influence invertebrates by serving as both structural habitat and food (Batzer and Wissinger 1996). However, as with other biotic factors such as the presence or absence of fish, plant communities in these wetlands are also a function of hydrology (e.g., Pollock et al. 1998).

Whiles and Goldowitz (2001) found that insect emergence production peaked in intermittent sites (MI1, MI2) and was lower in ephemeral and perennial sites, suggesting that intermittent sites were most productive. In contrast, our current investigation showed a trend of increasing invertebrate biomass along the same hydrologic gradient, with significantly greater biomass in the perennial site, suggesting that perennial sites might be most productive. This apparent discrepancy could be related to a variety of factors. For one, the current study included non-insect groups that did not contribute to emergence production, although the perennial site had the highest % of biomass represented by insects (mostly Chironomidae); thus, the inclusion of non-insect groups does not provide a complete explanation. Additionally, predation by fish likely influenced the differences we observed. The perennial site contained a diverse, year-round fish community, many of which feed on invertebrates (e.g., *Culea inconstans*, *Etheostoma exile*, *Lepomis cyanelus*, *Fundulus sciadicus*, *Semotilus atromaculatus*) (Whiles and Goldowitz 1998, Goldowitz and Whiles 1999). Fish consume some portion of available aquatic insect biomass before adults emerge and thus account for some portion of this apparent "loss" of biomass. The intermittent site with largest emergence production did not contain fish, and the intermittent site with the second largest emergence production contained only a seasonal fish community. Further, the sampling methods used for the two studies were different and likely did not sample all taxa with the same efficiency. In particular, culicids were major contributors to emergence production at the two most productive intermittent sites, but they were only occasional in the stove-pipe samples collected during the same year for this study. This suggests that the stove-pipe sampler underestimated culicid densities.

Organic matter analyses during this study support the productivity relationship observed by Whiles and Goldowitz (2001) (highest productivity in intermittent sites) because higher organic matter values for the two intermittent sites suggest greater primary production in these sites. This pattern was attributable primarily to macrophytes because filamentous algae did not account for a large fraction of annual averages of organic materials in any of the sites, and we did not measure phytoplankton production. Although not reflected in the annual average values because they were not present for much of the year, filamentous algae were very

abundant in the perennial site periodically during summer. Conversely, we likely overestimated the importance of filamentous algae in the ephemeral site because we only collected samples in late winter and early spring when water was present.

Invertebrate communities in all wetlands were numerically dominated by collector-gatherers. However, patterns based on biomass were different among wetlands. Based on biomass, the wettest and driest sites were dominated by collector-gatherers, followed by scrapers. The intermittent sites showed a more even distribution of biomass among functional groups, and collector-gatherers and scrapers were again well-represented. Based on these functional patterns, food webs in these wetlands are mostly supported by FPOM resources and periphyton, although the presence of the CPOM-shredding caddisfly, *I. plattensis*, in the MII intermittent site represents a link with CPOM resources in that site.

#### Management Implications for Central Platte River Wetlands

Management of remaining wetlands in the central Platte River basin requires a holistic approach because the hydrology of these systems is influenced by in-stream flows of the Platte River. Consideration of upstream hydrologic influences such as impoundments, dewatering for irrigation, and channel modifications will be required to ensure long-term sustainability of wetland resources in the region. Given the established linkages between in-stream flows, regional ground-water levels, and wetland hydrology (Wesche et al. 1994, Goldowitz and Whiles 1999), our results suggest that anthropogenic activities that alter river hydrology can alter the abundance, biomass, and structure of macroinvertebrate assemblages in these wetlands.

Results of this study, combined with results of our prior investigations on these same systems, suggest that intermittent wetlands with longer hydroperiods are most diverse and that productivity is greatest in intermittent and perennial sites. This does not suggest that management and restoration activities should target longer hydroperiods. We found unique taxa in every wetland site we examined, and the temporal patterns of macroinvertebrate abundance and biomass differed among sites as well. Hence, management and restoration activities that promote diverse hydrologic gradients across wetlands will most likely maximize the abundance, biomass, and diversity of macroinvertebrates on larger spatial and temporal scales.

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#### LITERATURE CITED

- Batzer, D. P., R. B. Rader, and S. A. Wissinger. 1999. Invertebrates in freshwater wetlands of North America: ecology and management. John Wiley & Sons, New York, NY, USA.
- Batzer, D. P. and S. A. Wissinger. 1996. Ecology of insect communities in nontidal wetlands. *Annual Review of Entomology* 41: 75–100.
- Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society* 18:308–343.
- Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson, and T. Weglenska. 1976. A review of some problems in zooplankton production studies. *Norwegian Journal of Zoology* 24:419–456.
- Corti, D., S. L. Kohler, and R. E. Sparks. 1997. Effects of hydroperiod and predation on a Mississippi River floodplain invertebrate community. *Oecologia* 109:154–165.
- Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U. S. Fish and Wildlife Service, Washington, DC, USA. FWS/OBS-79/31.
- Dodds, W. K., K. B. Gido, M. R. Whiles, K. M. Fritz, and W. J. Matthews. 2004. Life on the edge: the ecology of Great Plains prairie streams. *Bioscience* 54:205–216.
- Ervin, G. N. and R. G. Wetzel. 2002. Influence of a dominant macrophyte, *Juncus effusus*, on wetland plant species richness, diversity, and community composition. *Oecologia* 130:626–636.
- Euliss, N. H., Jr., D. A. Wrubleski, and D. M. Mushet. 1999. Wetlands of the prairie pothole region: invertebrate species composition, ecology, and management. p. 471–514. *In* D. P. Batzer, R. B. Rader, and S. A. Wissinger (eds.) *Invertebrates in Freshwater Wetlands of North America, Ecology and Management*. John Wiley and Sons, New York, NY, USA.
- Goldowitz, B. S., and M. R. Whiles. 1999. Investigations of fish, amphibians, and aquatic invertebrate species within the middle Platte River system. Final Report, Platte Watershed Program Cooperative Agreement X99708101. USEPA region VII, Kansas City, MO, USA.
- Hall, D. L., R. W. Sites, E. B. Fish, T. R. Molhagen, D. L. Moorhead, and M. R. Willig. 1999. Playas of the southern High Plains: the macroinvertebrate fauna. p. 635–666. *In* D. P. Batzer, R. B. Rader, and S. A. Wissinger (eds.) *Invertebrates in Freshwater Wetlands of North America, Ecology and Management*. John Wiley and Sons, New York, USA.
- Huener, J. D. and J. A. Kadlec. 1992. Macroinvertebrate response to marsh management strategies in Utah. *Wetlands* 12:72–78.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–211.
- Hurlbert, S. H. and M. D. White. 1993. Experiments with freshwater invertebrate zooplanktivores: quality of statistical analyses. *Bulletin of Marine Science* 53:128–153.
- Jenkins, D. G., S. Grissom, and K. Miller. 2003. Consequences of prairie wetland drainage for crustacean biodiversity and metapopulations. *Conservation Biology* 17:158–167.
- Kohler, S. L., D. Corti, M. C. Slamecka, and D. W. Schneider. 1999. Prairie floodplain ponds: mechanisms affecting invertebrate community structure. p. 711–732. *In* D. P. Batzer, R. B. Rader, and S. A. Wissinger, (eds.) *Invertebrates in Freshwater Wetlands of*

- North America: Ecology and Management. John Wiley & Sons, New York, NY, USA.
- Lovvorn, J. R., W. M. Wolheim, and A. H. Hart. 1999. High plains wetlands of southeast Wyoming: salinity, vegetation, and invertebrate communities. p. 603–634. *In* D. P. Batzer, R. B. Rader, and S. A. Wissinger (eds.) *Invertebrates in Freshwater Wetlands of North America, Ecology and Management*. John Wiley and Sons, New York, NY, USA.
- Mallory, M. L., P. J. Blancher, P. J. Weatherhead, and D. K. McNicol. 1994. Presence or absence of fish as a cue to macroinvertebrate abundance in boreal wetlands. *Hydrobiologia* 279–280: 345–351.
- Matthews, W. J. 1988. North American prairie streams as systems for ecological study. *Journal of the North American Benthological Society* 7:387–409.
- Merritt R. W. and K. W. Cummins (eds.). 1996. *An Introduction to the Aquatic Insects of North America*, 3<sup>rd</sup> ed. Kendall-Hunt Publishing, Dubuque, IA, USA.
- Poff, N. L. and J. D. Allan. 1995. functional organization of stream fish assemblages in relation to hydrologic variability. *Ecology* 76: 606–627.
- Pollock, M. M., R. J. Naiman, and T. A. Hanley. 1998. Plant species richness in riparian wetlands—a test of biodiversity theory. *Ecology* 79:94–105.
- Reinecke, K. J. and G. L. Krapu. 1986. Feeding ecology of sandhill cranes during spring migration in Nebraska. *Journal of Wildlife Management* 50:71–79.
- Resh, V. H., A. B. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7:433–455.
- Sidle, J. G., E. D. Miller, and P. J. Currier. 1989. Changing habitats in the Platte River valley of Nebraska. *Prairie Naturalist* 21:91–104.
- Smith, D. G. 2001. *Pennak's Freshwater Invertebrates of the United States, Porifera to Crustacea*. 4<sup>th</sup> ed. John Wiley and Sons, New York, NY, USA.
- Snodgrass, J. W., M. J. Komoroski, A. L. Bryan, jr., and J. Burger. 2000. Relationships among isolated wetland size, hydroperiod, and amphibian species richness: implications for wetland regulations. *Conservation Biology* 14:414–419.
- Stanley, E. H. and S. G. Fisher. 1992. Intermittency, disturbance, and stability in stream ecosystems. p. 271–280. *In* R. D. Robarts and M. L. Bothwell (eds.) *Aquatic Ecosystems in Semi-Arid Regions: Implications for Resource Management*. Environment Canada, Saskatoon, Saskatchewan, Canada.
- Thorp, J. H. and A. P. Covich. 1991. *Ecology and Classification of North American Freshwater Invertebrates*. Academic Press, New York, NY, USA.
- U.S. Fish and Wildlife Service. 1997. Biological opinion on the Federal Energy Regulatory Commission's preferred alternative for the Kingsley dam project and North Platte/Keystone dam project. U.S. Fish and Wildlife Service, Grand Island, NE, USA.
- van der Valk, A. G. 1981. Succession in wetlands: a Gleasonian approach. *Ecology* 62:688–696.
- Vileisis, A. 1997. *Discovering the Unknown Landscape: a History of America's Wetlands*. Island Press, Washington, DC, USA.
- Wallen, B., U. Falkengren-Grerup, and N. Malmer. 1988. Biomass, productivity and relative rate of photosynthesis of sphagnum at different water levels on a South Swedish peat bog. *Holarctic Ecology* 11:70–76.
- Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* 27:337–363.
- Wesche, T. A., Q. D. Skinner, and R. J. Henszey. 1994. *Platte River wetland hydrology study: final report*. Wyoming Water Resources Center, Laramie, WY, USA.
- Whiles, M. R. and B. S. Goldowitz. 1998. Biological response to hydrologic fluctuation in wetland sloughs of the central Platte River. p. 3–18. *In* G. Lingle (ed.) *Proceedings of the Ninth Platte River Ecosystem Symposium*. University of Nebraska Cooperative Extension-Platte Watershed Program, Kearney, NE, USA.
- Whiles, M. R. and B. S. Goldowitz. 2001. Hydrologic influences on insect emergence production from central Platte River wetlands. *Ecological Applications* 11:1829–1842.
- Whiles, M. R., B. S. Goldowitz, and R. E. Charlton. 1999. Life history and production of a semi-terrestrial limnephilid caddisfly in an intermittent Platte River wetland. *Journal of the North American Benthological Society* 18:533–544.
- Wissinger, S. A. 1999. Ecology of wetland invertebrates: synthesis and applications for conservation and management. p. 1043–1086. *In* D. Batzer, R. B. Rader, and S. A. Wissinger (eds.) *Invertebrates in Freshwater Wetlands of North America: Ecology and Management*. John Wiley and Sons, New York, NY, USA.
- Wissinger, S. A., W. S. Brown, and J. E. Jannot. 2003. Caddisfly life histories along permanence gradients in high-altitude wetlands in Colorado (USA). *Freshwater Biology* 48:255–270.
- Wissinger, S. A., H. H. Whiteman, G. B. Sparks, G. L. Rouse, and W. S. Brown. 1999. Foraging trade-offs along a predator-permanence gradient in subalpine wetlands. *Ecology* 80:2102–2116.
- Zimmer, K. D., M. A. Hanson, and M. G. Butler. 2000. Factors influencing invertebrate communities in prairie wetlands: a multivariate approach. *Canadian Journal of Fisheries and Aquatic Sciences* 57:76–85.
- Zimmer, K. D., M. A. Hanson, M. G. Butler, and W. G. Duffy. 2001. Size distribution of aquatic invertebrates in two prairie wetlands, with and without fish, with implications for community production. *Freshwater Biology* 46:1373–1386.

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