

WILEY



---

Hydrologic Influences on Insect Emergence Production from Central Platte River Wetlands

Author(s): Matt R. Whiles and Beth S. Goldowitz

Source: *Ecological Applications*, Vol. 11, No. 6 (Dec., 2001), pp. 1829-1842

Published by: Wiley on behalf of the Ecological Society of America

Stable URL: <http://www.jstor.org/stable/3061099>

Accessed: 18-01-2018 18:35 UTC

#### REFERENCES

Linked references are available on JSTOR for this article:

[http://www.jstor.org/stable/3061099?seq=1&cid=pdf-reference#references\\_tab\\_contents](http://www.jstor.org/stable/3061099?seq=1&cid=pdf-reference#references_tab_contents)

You may need to log in to JSTOR to access the linked references.

---

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at

<http://about.jstor.org/terms>



JSTOR

Wiley, Ecological Society of America are collaborating with JSTOR to digitize, preserve and extend access to *Ecological Applications*

## HYDROLOGIC INFLUENCES ON INSECT EMERGENCE PRODUCTION FROM CENTRAL PLATTE RIVER WETLANDS

MATT R. WHILES<sup>1,3</sup> AND BETH S. GOLDOWITZ<sup>2</sup>

<sup>1</sup>Department of Entomology, Kansas State University, Manhattan, Kansas 66506-4004 USA

<sup>2</sup>Platte River Whooping Crane Maintenance Trust, Inc., 6611 W. Whooping Crane Drive,  
Wood River, Nebraska 68883 USA

**Abstract.** The physical template of freshwater ecosystems has a pervasive influence on biological communities and processes. To examine the influence of hydrology on wetland insect communities, we quantified insect emergence from five riparian sloughs in the central Platte River valley. Annual hydroperiods of the wetlands ranged from 94 to 365 d/yr, and frequency and magnitude of drying events were inversely proportional to hydroperiod length. Three emergence traps were placed in each wetland from April through November 1997. Most insects collected in traps were identified to genus, and individual dry mass (DM) also was determined. Abundance of emerging insects (24 124 individuals/m<sup>2</sup>) and emergence production (5.1 g DM·m<sup>-2</sup>·yr<sup>-1</sup>) were highest from the site with an intermediate hydroperiod of 296 d. Sites with longer and shorter hydroperiods had lower emergence abundance and production. Emergence production from the perennial site, which contained fish year-round, was only 0.26 g DM·m<sup>-2</sup>·yr<sup>-1</sup>. Diptera generally dominated emergence trap catches. Chironomidae, Culicidae, and Ceratopogonidae were among the dominant contributors to abundance, whereas Sciomyzidae and Muscidae were important contributors to biomass at most sites.

Quadratic equations best described relationships between taxa richness and annual hydroperiod ( $r^2 = 0.78$ ,  $P < 0.05$ ) or number of drying events/yr ( $r^2 = 0.81$ ,  $P < 0.05$ ), reflecting a peak in richness at intermediate levels of both. These relationships followed predictions of the intermediate disturbance hypothesis, but specific mechanisms underlying patterns were difficult to discern. Like emergence production, taxa richness was also highest at intermediate hydroperiods. Hence, insect diversity (measured as richness) and emergence production were positively correlated ( $r^2 = 0.85$ ,  $P < 0.05$ ). Results indicate that the hydrology of central Platte River wetlands exerts a strong influence on insect species richness and emergence production, and that intermittent sites harbor the highest insect diversity and produce more emergent insect biomass. However, trends in seasonal emergence patterns and taxonomic shifts across the hydrologic gradient in this study suggest that a landscape containing a mosaic of hydrologically distinct wetlands will maximize aquatic insect diversity and productivity at larger spatial and temporal scales.

**Key words:** aquatic invertebrates; central Platte River (USA); disturbance; diversity; floodplain; hydrology; insect emergence; productivity; wetland management; wetlands.

### INTRODUCTION

Wetlands can be highly productive systems that are also rich in biological diversity. This, coupled with their well-documented value for maintaining water quality, has made wetlands a recent focus of research, management, and restoration activities. Recent investigations have documented invertebrate community structure in a variety of wetland systems (see reviews by Batzer and Wissinger 1996, Batzer et al. 1999), but much less is known about wetland invertebrate productivity and the dynamics and relative importance of insect emergence from wetlands. Factors influencing invertebrate diversity and productivity also are not well understood for many types of wetlands, although hy-

drology and/or the presence of vertebrate predators are often implicated as primary factors structuring invertebrate communities in wetlands (Wissinger 1999).

Identifying factors that structure and control wetland invertebrate communities (e.g., hydroperiod, biotic interactions) is of basic and applied relevance, because it allows for testing of current ecological paradigms and is of great relevance to prudent management of the biotic diversity and productivity of remaining wetland systems. Identifying these factors is also an important consideration for proper planning of wetland restorations. Both manipulations (e.g., Neckles et al. 1990, Batzer and Resh 1992, Wissinger et al. 1999) and natural experiments (e.g., Bataille and Baldassarre 1993, Schneider 1999) have been used to examine factors controlling invertebrate productivity and/or diversity in wetlands, but results are sometimes contradictory. For example, while some studies suggest that wetland invertebrate diversity increases with water permanence

Manuscript received 12 May 2000; revised 23 January 2001; accepted 1 February 2001; final version received 2 April 2001.

<sup>3</sup> Present address: Southern Illinois University, Department of Zoology, Carbondale, Illinois 62901-6501 USA.

(Driver 1977, Evans et al. 1999, Hall et al. 1999, Taylor et al. 1999, Williams and Williams 1999), others indicate that intermittent systems are most diverse (Goldaday et al. 1999, Leslie et al. 1999). Some of this disparity is due to correlation among the mechanisms structuring wetland invertebrate communities (e.g., predator–permanence gradients), making identification of the importance of specific factors difficult, but it also suggests that mechanisms governing diversity and productivity of wetlands may vary both spatially and temporally.

The few studies that have examined wetland insect emergence suggest that it may be a significant process and, in some cases, may exceed many estimates from lotic and open water lentic systems where more studies have been conducted (Wrubleski and Rosenberg 1990, Stagliano et al. 1998). Emergence of adult aquatic insects represents the culmination of their production in the aquatic environment and a potential transfer of energy and nutrients from aquatic to terrestrial systems. Adult aquatic insects are important prey items for consumers such as birds, amphibians, spiders, and other insects, and, in some cases, numerical responses to aquatic insect emergences have been demonstrated (Street 1977, Orians 1980, Gray 1993). Although generally considered an important process, the overall significance of aquatic insect emergence to consumer groups and ecosystem dynamics in many systems remains poorly quantified. However, studies in some regions suggest that aquatic insect emergence production may greatly exceed insect production in surrounding terrestrial environments (Jackson and Fisher 1986, Gray 1989). Thus, aquatic environments may represent hot spots of prey production for terrestrial insectivores.

Floodplain wetlands of the central Platte River consist of sloughs, with varying hydrologic regimes, in a matrix of mesic prairie. Although biotic communities inhabiting these sloughs are poorly studied, there is evidence that they are biologically diverse and productive systems (Whiles and Goldowitz 1998, Goldowitz and Whiles 1999, Whiles et al. 1999). They also are critical habitats for a variety of species, including numerous migratory waterfowl and the federally endangered Whooping Crane (*Grus americana*; Johnson 1980, Reinecke and Krapu 1986, U.S. Fish and Wildlife Service 1997). Despite their apparent ecological significance, mesic prairies and the slough wetlands that dissect them represent some of the most seriously degraded and diminished habitats in the region. River regulation, combined with increasing agriculture in the basin, has resulted in the destruction of the majority of wet meadows, and this habitat currently comprises <5% of the land area in the Platte River valley (Sidle et al. 1989, U.S. Fish and Wildlife Service 1997). As a result, several conservation organizations actively engage in wet meadow and wetland protection and restoration efforts in the region, but lack of information about the structure and function of these systems makes

evaluating the effectiveness of conservation and restoration activities difficult.

The objective of this investigation was to examine the influence of wetland hydrology on diversity, abundance, biomass, and phenology of emerging aquatic insects. We hypothesized that hydrologic fluctuation would exert a strong influence on insect emergence, and we tested this hypothesis with a natural experiment utilizing similar, nearby floodplain sloughs representing a hydrologic gradient ranging from ephemeral to perennial. We also characterized and quantified aquatic insect emergence from floodplain wetlands of the central Platte River basin; these systems are imperiled and poorly studied, but are considered vital to the ecological integrity of the region.

#### STUDY SITES

We selected five study sites comprising 20-m reaches of sloughs within a large wet meadow complex located on two adjacent islands in the central Platte River, Hall County, Nebraska. The landscape is a series of ridges and swales, with linear sloughs in low areas. This habitat is a mesic prairie dominated by grasses, sedges, and forbs typical of tallgrass prairie. Climate in this region is typical of the central Great Plains with warm, generally dry summers (July mean air temperature = 24°C). Winters are cold (January mean air temperature = -7°C), with significant ice cover on surface waters generally occurring from November through March. Mean annual precipitation is 63 cm/yr, with most of this occurring in May and June. During this study, precipitation was somewhat higher than the mean (81 cm, or 128% of the long term mean), and this was primarily a result of above mean rainfall during late summer and fall.

Both precipitation and the adjacent Platte River influence hydrology of these wetland systems, and annual hydroperiod increases with connectivity to the river (Whiles and Goldowitz 1998). Discharge in this region of the Platte River is influenced by upstream dams, canals, and power plants that provide water for irrigation and hydroelectric power and significantly reduce flows and alter seasonal patterns. Currently, flows generally peak in June with lowest levels during the July–September irrigation season. River discharge was high during most of the study period (total annual runoff = 178% of the long term mean). Much of this was a result of above mean flows during summer and fall.

Hydrology of the five study sloughs ranges from ephemeral to perennial. In nonpermanent sites, drying generally occurs during summer, and water is present at least occasionally from autumn through spring. Water is ~0.25–1.0 m deep and flows slowly (usually <5 cm/s) in these wetlands when they are full, but flow ceases as water levels decline. Substrates are primarily a mixture of silt and sand covered with detritus (Table 1). Riparian growth around sloughs is a mixture of mainly grasses, sedges, rushes, and mixed forbs; no

TABLE 1. Physical characteristics of the study sites at Mormon Island (MI) and Wild Rose Ranch (WR).

Characteristic	Study site				
	MI3	WR1	MI2	MI1	WR2
Maximum depth (cm)	40	21	54	68	43
Maximum wetted area (m <sup>2</sup> )	152	262	300	386	43
Maximum volume (m <sup>3</sup> )	43	19	149	151	17
Annual hydroperiod (d)	94	158	296	331	365
No. dry periods/yr†	10	11	4	3	0
Longest dry period (d)	117	77	48	29	...
Annual degree days (>0°C)‡	822	939	2150	2939	3173
Max. daily mean temp. (°C)‡	22	22	27	28	18
Min. daily mean temp. (°C)‡	0	0	0	0	4
Inorganic substrates (%)					
Gravel	0	0	0	0	8
Sand	26	33	24	24	53
Silt	74	67	76	76	39

Notes: Study sites are arranged in order of increasing annual hydroperiod. All sites are 20-m reaches of wetland sloughs. Maximum depth, area, and volume are maximum readings obtained between 5 April 1997 and 4 April 1998.

† Number of periods  $\geq 3$  consecutive days without any water.

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

woody vegetation is present. Dense growths of macrophytes (*Typha*, *Scirpus*, *Sparganium*, *Eleocharis*, *Lemna*, *Potamogeton*, and others) and filamentous algae are evident in spring and summer in sites with longer hydroperiods (MI1, MI2, and WR2).

The two wettest sites (WR2 and MI1) harbored fish communities during this study. *Hybognathus hankinsoni*, *Fundulus sciadicus* and, to a lesser extent, *Cyprinus carpio* used the intermittent site (MI1) for spawning and rearing of young during spring; these species also migrated in during fall. A diverse, year-round community consisting of *Etheostoma exile*, *Semotilus atromaculatus*, *Culaea inconstans*, *Fundulus sciadicus*, and other species was present in the perennial site (WR2; Whiles and Goldowitz 1998). Salamander larvae, predators that are often abundant in wetlands and can have a significant impact on invertebrate communities (e.g., Wellborn et al. 1996, Wisinger et al. 1999), did not occur in our study wetlands.

Water chemistry is generally similar at all sites, except that specific conductance is much lower at the two ephemeral sites ( $\sim 500$   $\mu\text{S}/\text{cm}$  at MI3 and WR1) compared to the wetter sites ( $\sim 1400$   $\mu\text{S}/\text{cm}$  at MI1, MI2, and WR2). Dissolved oxygen in these sloughs fluctuates greatly with water depth and temperature and has a mean of  $\sim 6.0$  mg/L. The pH in these wetlands averages  $\sim 7.7$ . The ephemeral (WR1, MI3) and intermittent (MI1, MI2) sites exhibit a wide range of annual temperature extremes (Table 1). Temperature is less variable in the perennial site (WR2; Table 1), and this site is the only one that does not freeze extensively in the winter.

#### METHODS

##### *Slough hydrology and physical habitat*

Wetted area, volume, and water temperature were monitored continuously in the study wetlands for one

year. In March 1997, staff gauges were installed at the deepest point in each slough, and reference transects for wetted width and depth measurements were established. Wetted width and depth transects were located 10 m apart along the length of sloughs at 0, 10, and 20 m. Wetted width and depth (at 1-m intervals across the width of each transect) were measured approximately weekly, and more frequently during periods of fluctuating water levels. Staff gauges were usually read daily when water was present and not frozen, but were measured at longer intervals (1–2 wk) during periods of ice cover or little fluctuation in water level. Staff gauge readings were then used to predict daily wetted surface area. Wetted surface area estimates were calculated from wetted width and depth transect measurements that spanned a variety of conditions, including high and low extremes, and then were regressed against staff gauge readings to develop predictive equations. Significant logarithmic relationships ( $r^2 > 0.90$ ,  $P < 0.01$ ,  $n > 25$  for each) were obtained for depth vs. surface area at four of the five sites. A significant relationship between depth and surface area could not be obtained at the perennial site (WR2) because the morphology of this site is such that wetted surface area changes very little with depth. Thus, we used mean wetted surface area from field measurements for WR2. Annual hydroperiods at each site were calculated as total days with water for the yearlong study period.

A thermograph recorded water temperatures in each site at 30-min intervals for the study period whenever sufficient water was present and not frozen. During winter 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 mean water temperatures were used to estimate annual degree-days ( $>0^{\circ}\text{C}$ ). Spot measurements of conductivity, pH, and dissolved oxygen were obtained monthly in winter through spring 1998. Inorganic substrate composition was estimated visually (to  $\sim 10$  cm deep) from three sediment core samples (313  $\text{cm}^2$  area each) collected monthly at each site when water was present (M. R. Whiles and B. S. Goldowitz, unpublished data).

#### *Aquatic insect emergence*

To quantify abundance and production (biomass) of insects emerging from the study wetlands, three emergence traps (625  $\text{cm}^2$  sampling surface area each) were placed in each of the sloughs from 15 April through 14 November 1997. Emergence traps were constructed from inverted plastic buckets with the bottom removed, and Nitex caps (0.5-mm mesh) which tapered into U-shaped PVC tubes formed the tops of each trap. Emerging insects were collected in 250-mL plastic bottles, filled with a 50% ethylene glycol or 7% formalin solution, that screwed into PVC tubes. Traps were mounted on two electric fence posts, which were driven into the sediments in a manner that allowed adjusting the height of the trap to correspond with changing water levels. Emergence trap heights were adjusted every 1–3 d so that the bottom 6–10 cm of each was under the water surface. A wire strung between fence posts supported tubes and collection bottles. Traps most closely resembled the design of Corbet (1965) for shallow standing water.

Emergence trap collection bottles were emptied at least once every two weeks. Trap locations at each site were randomly selected within the wetted area of the slough and were changed every 1–3 wk so that oviposition by adults was not inhibited. Traps were moved in or out from the center of each site following significant changes in wetted area of sloughs. When sloughs dried, traps were lowered flush with the ground and left in place until the soil surface was completely dry. Following extended dry periods when traps were removed from the slough, they were replaced immediately when water returned. Traps were inspected and routine maintenance was performed (repair of holes, addition of preservative, removal of spiders and webs, and removal of algae and associated material on submerged trap parts) at least once each week throughout the study period. Emergent vegetation was allowed to grow into traps but was trimmed back when it reached the top of the mesh cones.

Aquatic and semi-aquatic adult insects collected in traps were identified to genus whenever possible, sexed, measured (total body length), and counted. Four to ten male and female individuals of most common taxa, which were preserved in formalin, were oven dried ( $60^{\circ}\text{C}$  for 24–48 h) and weighed to obtain gender-specific estimates of mean dry mass (DM). Exceptionally small taxa were sometimes weighed in groups of

two to four individuals. Gender-specific dry mass estimates for Chironomidae (Diptera) genera were obtained using mean dry masses and regressions from Stagliano et al. (1998). For Tipulidae (Diptera), we used a similar, unpublished regression based on total body length (D. M. Stagliano and A. C. Benke, unpublished data). For some small taxa (e.g., Ceratopogonidae [Diptera]), infrequently collected taxa (e.g., some Sciomyzidae and Ephydriidae genera [Diptera]), and taxa for which only one sex was collected (e.g., *Psorophora* females [Diptera: Culicidae]), gender-specific DM was not determined, and we used a mean DM for all individuals collected regardless of sex.

Abundance and biomass values from the three traps at each site were standardized to 1  $\text{m}^2$  and averaged to generate emergent numbers and production for each sampling interval. For total emergence numbers and production at each site, mean abundance and biomass values were multiplied by mean wetted surface area during sampling intervals. Because we sampled the entire nonfreezing period of 1997, we assume our estimates of emergent numbers and production reflect annual values. However, some Chironomidae and other taxa may emerge from these sites during mild periods in winter, so our annual estimates may be conservative. *Ironoquia plattensis* (Trichoptera: Limnephilidae), a recently described species of caddisfly that emigrates from the water as a final instar and then aestivates and pupates on land (Alexander and Whiles 2000), was abundant at MI1, but was not present at other study sites (Whiles et al. 1999). Because emigration of *I. plattensis* larvae from this slough represents a transfer from the slough to the surrounding terrestrial habitat, numbers and biomass of larvae leaving MI1, which are presented by Whiles et al. (1999), were included in MI1 emergence abundance and production values. However, because these data were collected in a different manner, the values were not included in statistical comparisons between sites.

Differences in annual emergent numbers and biomass were compared among sites with one-way ANOVA, and the least squares means procedure was used for multiple comparisons of individual means ( $P < 0.05$ ). Logarithmic ( $\ln[x + 1]$ ) transformations were used to normalize data and eliminate heteroscedasticity prior to analysis (Zar 1996). Seasonal patterns of emergence production among sites were analyzed with repeated measures ANOVA performed on transformed ( $\ln[x + 1]$ ) spring, summer, and autumn emergence biomass totals for each site. Mauchly's test for sphericity was used to confirm that data satisfied Huynh-Feldt conditions for univariate procedures (Milliken and Johnson 1992). Since Mauchly's test was not significant ( $P = 0.33$ ,  $df = 2$ ), data were analyzed with a univariate repeated measures design to test for a significant interaction between seasonal patterns and site ( $P < 0.05$ ). Statistical analyses were performed using SAS software for personal computers (SAS 2000). This

study, like many whole-system field studies, involves simple pseudoreplication (e.g., Hurlbert 1984, Hurlbert and White 1993). Because these wetland systems cannot be replicated, individual traps in each site were treated as experimental units ( $n = 3$  for each site). Thus, we tested for difference among sites but cannot strictly attribute differences in insect emergence patterns to any specific factor.

Simple linear correlation was used to compare richness and productivity in sites. Polynomial regression techniques were used to examine nonlinear relationships between taxonomic richness of wetlands and annual hydroperiod and number of drying events  $\geq 3$  d/yr. A forward stepwise procedure and a  $t$  test were used to determine equations most appropriate for fitting nonlinear relationships (Zar 1996). Shannon diversity ( $H'$ ) and percentage similarity indices were calculated with emergence abundance data (total numbers of each taxon from each site) according to Brower et al. (1997).

## RESULTS

### Hydrology

Hydrology varied greatly among the five sloughs during this study, with annual hydroperiod ranging from 94 d in the driest ephemeral site (MI3) to 365 d in the perennial site (WR2; Fig. 1, Table 1). The two ephemeral sites contained water 26% (MI3) and 43% (WR1) of the days during the study year, whereas the two intermittent sites contained water 81% (MI2) and 91% (MI1) of the time. For the ephemeral and intermittent sites, the number of dry periods  $\geq 3$  d ranged from 11 (WR1) to 3 (MI1). Maximum length of dry periods varied from 117 d (MI3) to 29 d (MI1). Degree days accumulated increased with increasing annual hydroperiod (Table 1).

### Insect abundance and emergence production

In general, emergence abundance was highest at intermediate hydroperiods and declined with increasing or decreasing days with water/yr. Total numbers of insects emerging from the five sites ranged from 375 individuals·m<sup>-2</sup>·yr<sup>-1</sup> at WR1, an ephemeral site, to 24 124 individuals·m<sup>-2</sup>·yr<sup>-1</sup> at MI2, an intermittent site that lacked fish and had an annual hydroperiod that was intermediate among the five study sites (Table 2).

Emergence production showed this same trend, with higher levels at the intermittent sites and decreasing levels at drier or wetter sites. Emergence production at MI2 (intermittent site without fish) was significantly higher than at all other sites ( $P < 0.05$ ), and the lowest production occurred at the driest site, MI3 (Table 2). When emergence production values were corrected for wetted surface area during sampling intervals (total emergence production), this same trend was evident, but relative differences between sites changed as a result of correcting for concentration/dilution of insects with changing wetted area and overall size differences

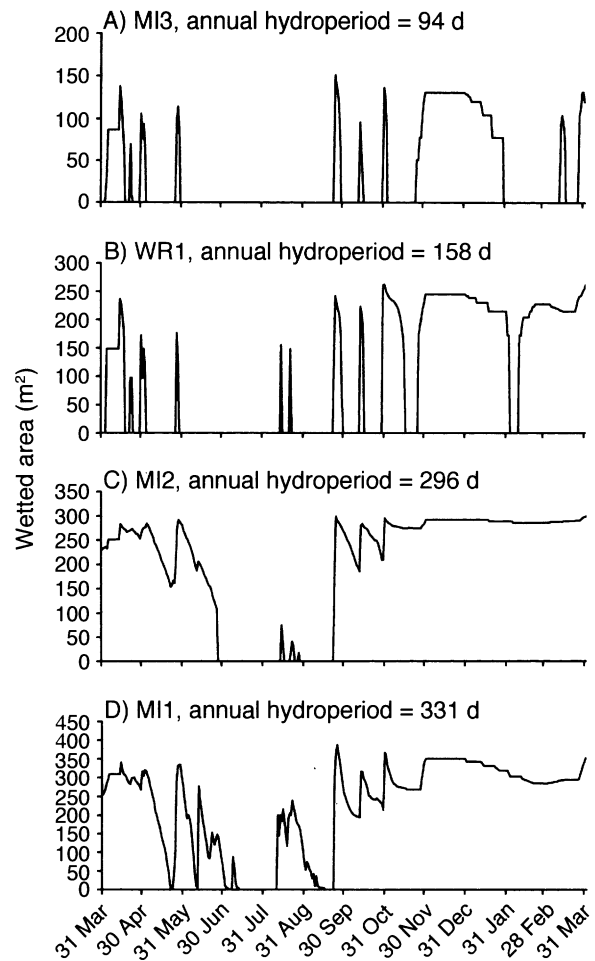


FIG. 1. Hydrographs of the study wetlands showing daily wetted area (m<sup>2</sup>) of the ephemeral sites (A) MI3 and (B) WR1, and the intermittent sites (C) MI2 and (D) MI1 during March 1997–March 1998. Because wetted area remains nearly constant at 43 m<sup>2</sup>, the perennial site (WR2) is not shown.

between sites. For example, emergence production per unit area at MI2 was 11× higher than that of MI1, but total emergence production at MI2 was only 4× greater than total emergence production in MI1, because wetted surface area during sampling intervals was generally higher in MI1 than MI2. Total emergence production in the two intermittent sites, MI2 and MI1 (excluding *I. plattensis* in MI1; see *Methods: Aquatic insect emergence*), was significantly higher than the other three sites. Total emergence production in MI3, the driest site, was significantly lower than all other sites except WR1, the second driest ( $P < 0.05$ ; Table 2).

Emergence production varied seasonally at most sites, and those patterns were significantly different among sites ( $P < 0.01$ ; Fig. 2). Production at both ephemeral sites (WR1 and MI3) peaked in spring and autumn, whereas emergence production at the perennial site (WR2) remained fairly constant. Mormon Island 1, the wetter of the intermittent sites, showed relatively constant emer-

TABLE 2. Abundance, emergence production, and richness of insects emerging from the five study wetlands (mean  $\pm$  1 SE,  $n = 3$  for each site), and Shannon diversity and number of taxa unique to each site.

Variable	Study site				
	MI3 [94]	WR1 [158]	MI2 [296]	MI1 [331]	WR2 [365]
Abundance (no. $\cdot$ m <sup>-2</sup> .yr <sup>-1</sup> )	456 (163) <sup>a</sup>	374 (91) <sup>a</sup>	24 124 (21 025) <sup>b</sup>	1739 (263) <sup>ab</sup>	1619 (361) <sup>a</sup>
Production (mg. $\cdot$ m <sup>-2</sup> .yr <sup>-1</sup> )	135 (34) <sup>a</sup>	183 (74) <sup>a</sup>	5 099 (4 208) <sup>b</sup>	440 (68) <sup>a</sup>	256 (47) <sup>a</sup>
Total production (g/yr)	3.2 (0.5) <sup>a</sup>	6.1 (1.5) <sup>ac</sup>	279.3 (171.4) <sup>b</sup>	65.3 (8.5) <sup>b</sup>	11.0 (2.0) <sup>c</sup>
Richness	7 (0.6) <sup>a</sup>	12 (0.6) <sup>b</sup>	25 (1.2) <sup>c</sup>	19 (0.7) <sup>d</sup>	17 (0.3) <sup>e</sup>
Shannon diversity ( $H'$ )	2.1	2.3	0.3	2.7	1.7
Unique taxa	2	2	9	6	5

Notes: Total production values are corrected for mean wetted area during sampling intervals. Values in brackets next to site names are the annual hydroperiods (d). Lowercase superscript letters indicate groups of values that are significantly different (ANOVA,  $P < 0.05$ ). For purposes of statistical comparisons, values for *Ironoquia plattensis* (presented in Table 3) are not included in MI1 abundance and biomass values in this table.

gence production throughout the study period, similar to the perennial site (Fig. 2). The drier intermittent site that did not contain fish (MI2) was the only site where emergence production peaked in summer.

#### Taxonomic patterns

Taxonomic composition varied greatly between sites, and total taxa richness, much like abundance and production, was highest at the intermittent sites (MI2 and MI1; Table 2). There was a significant quadratic relationship between taxa richness and hydroperiod for all sites ( $P < 0.05$ ; Fig. 3A), suggesting that intermittent wetlands with annual hydroperiods between 250 and 300 d support the highest insect richness. Number of drying events ( $\geq 3$  d) was inversely proportional to annual hydroperiod during 1997 (Table 1), and thus there was also a significant quadratic relationship between insect taxa richness and number of drying events/yr ( $P < 0.05$ ; Fig. 3B).

A significant, positive correlation between richness

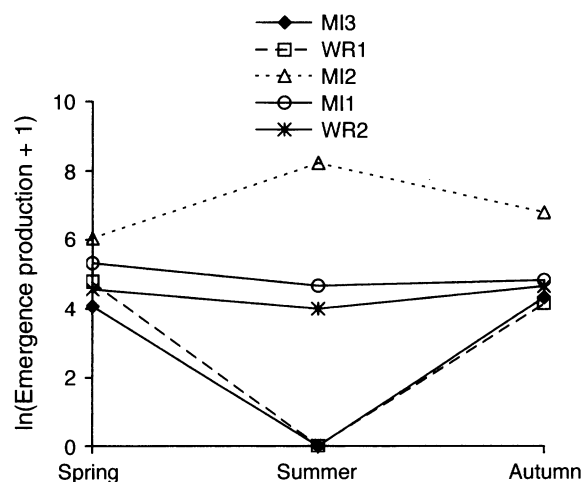


FIG. 2. Seasonal patterns of emergence production from the five study wetlands during 1997. Seasonal totals (mg DM $\cdot$ m<sup>-2</sup>.season<sup>-1</sup>) are plotted as transformed values ( $\ln[x + 1]$ ). Quadratic responses across seasons were significantly different among sites (repeated-measures ANOVA,  $P < 0.01$ ).

of emerging insects and emergence production indicated that a diversity–productivity gradient (diversity measured as richness) was present in these wetlands ( $P < 0.05$ ; Fig. 4A). The slope of this line was reduced and this relationship was not significant when the dominant contributor to emergence production was removed from all sites except the one with lowest richness (site with lowest richness used as the baseline for comparison), indicating that individual taxa caused this pattern ( $P > 0.10$ ; Fig. 4B). Shannon diversity ( $H'$ ) was lowest at the intermittent site that had the highest richness (Table 2). This occurred primarily because culicids dominated emergence at MI2, thus decreasing evenness. The perennial site (WR2) also had relatively low Shannon diversity as a result of high dominance by a few genera of chironomids. Shannon diversity was highest at the wetter intermittent site where fish were present (MI1), followed by the two ephemeral sites (WR1 and MI3; Table 2).

Diptera dominated emergence abundance and production at all sites except MI1, where biomass of emigrating final instar *I. plattensis* larvae accounted for over half of the total emergence production and 11% of emergent numbers (Table 3). At three of the five sites examined (MI3, MI2, and WR2), Chironomidae were numerically dominant; they were the second most abundant taxon at the remaining sites (WR1 and MI1; Table 3). Overall, Chironomidae were most abundant at the perennial site, where members of this family accounted for 96% of total emergent numbers and 94% of biomass (Table 3). However, chironomids did not contribute significantly to emergence production at the other four sites because of their relatively small size.

Differences in the relative contribution of chironomid subfamilies to total emergence abundance were evident across the five sloughs. In general, Orthocladiinae (primarily *Corynoneura*) made up a larger fraction of chironomid emergence abundance at drier sites, whereas Chironominae dominated in wetter sites (Fig. 5). The exception to this trend was at the intermittent site with fish (MI1), where Orthocladiinae outnumbered Chironominae as a result of large contributions by two unidentified Orthocladiinae. *Microspectra* and

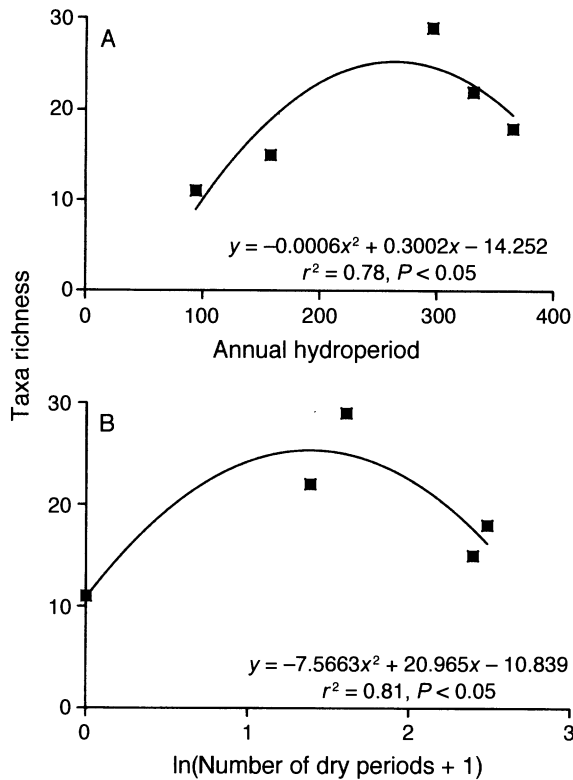


FIG. 3. Taxa richness of insects emerging from the study wetlands compared to (A) annual hydroperiods and (B) number of dry periods/yr that were  $\geq 3$  d. Values for number of dry periods are transformed ( $\ln[x + 1]$ ). Coefficients of determination are for second-order polynomial correlations.

*Chironomus* dominated Chironominae catches in the ephemeral sites (MI3 and WR1). *Polypedilum*, *Pseudochironomus*, and *Chironomus* were most abundant in MI2 traps, and *Dicrotendipes* and *Parachironomus* dominated the wetter intermittent site, MI1. The perennial site (WR2) had the greatest richness of Chironominae, dominated by *Dicrotendipes*, *Polypedilum*, and *Microspectra*. Tanytopodinae (primarily *Procladius*) contributed a small portion to trap catches from the two intermittent sites (MI2 and MI1) but were not collected at the other sites (Fig. 5).

Sciomyzidae (primarily *Pherbellia* and *Elgiva*), Muscidae, and Tipulidae (primarily *Erioptera*), which are relatively heavy-bodied dipterans, were important contributors to emergence production at most sites, particularly those with shorter annual hydroperiods (Table 3). *Culex* and *Psorophora* (Diptera: Culicidae) dominated emergence abundance and production at the intermittent site that lacked fish (MI2), accounting for  $\sim 4600$  mg DM $\cdot$ m $^{-2}$ ·yr $^{-1}$  emergence production there (Table 3). Mass culicid emergences were the primary reason for the summer emergence production peak at MI2 (Fig. 2). Culicids were also important, but less dominant, at the other intermittent site that contained a seasonal fish community (MI1), but were not a sig-

nificant contributor to emergence abundance or production at the remaining sites. Exopterygotes were poorly represented in trap catches from all sites; *Calibaetis* (Ephemeroptera: Baetidae) in MI2 was the only hemimetabolous insect that contributed significantly to total emergence production at a site (Table 3).

A dendrogram based on a percentage similarity matrix (calculated with emergence abundance values for each taxon from each site) showed that insect emergence patterns grouped according to the general hydrologic regimes of the five sites. However, no two sites were  $>55\%$  similar (Fig. 6). The two most similar sites were ephemeral ones, followed by the two intermittent sites. The perennial site, WR2, was the most dissimilar of all sites. The two sites that contained fish (MI1 and WR2) did not cluster closely, indicating little similarity (Fig. 6).

## DISCUSSION

### Diversity patterns

The relationship we observed between the taxonomic richness of aquatic insects and wetland hydrology follows predicted patterns of the intermediate disturbance hypothesis (IDH) (Connell 1978). The IDH has been explored in the context of lotic systems, generally with

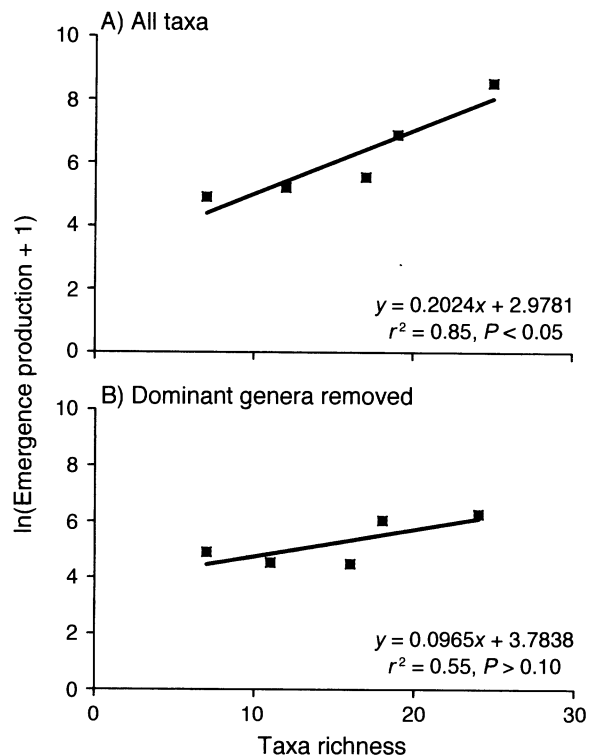


FIG. 4. Annual emergence production ( $\ln[x + 1]$ -transformed) during 1997 compared to taxa richness in the study wetlands calculated with (A) all taxa and with (B) the dominant contributor to emergence production removed from all except the site with lowest richness. Coefficients of determination are for simple linear correlations.



TABLE 3. Taxa (summarized by family) contributing the greatest amounts to annual (A) insect emergence abundance (no.·m<sup>-2</sup>·yr<sup>-1</sup>) and (B) production (mg DM·m<sup>-2</sup>·yr<sup>-1</sup>) at each study site.

Study site					
MI3 [94]		WR1 [158]		MI2 [296]	
A) Abundance					
Family (%)	No.	Family (%)	No.	Family (%)	No.
Chironomidae (33%)	152.1	Tipulidae (28%)	103.2	Culicidae (95%)	23 021.1
Sciaridae (27%)	125.0	Chironomidae (19%)	70.6	Chironomidae (1%)	331.4
Sciomyzidae (8%)	38.0	Sciaridae (17%)	65.2	Ceratopogonidae (1%)	211.9
Dolichopodidae (8%)	38.0	Muscidae (16%)	59.8	Muscidae (1%)	146.7
Total	456.4	Total	374.9	Total	24 124.1
B) Emergence production					
Family (%)	mg	Family (%)	mg	Family (%)	mg
Sciomyzidae (45%)	60.6	Muscidae (35%)	64.7	Culicidae (90%)	4590.4
Muscidae (20%)	27.6	Sciomyzidae (25%)	45.9	Muscidae (3%)	171.9
Sciaridae (12%)	16.0	Tipulidae (12%)	22.3	Sciomyzidae (2%)	80.5
Tipulidae (10%)	13.9	Chironomidae (7%)	12.6	Baetidae (1%)	55.4
Total	134.7	Total	183.4	Total	5099.4

Notes: Numbers in parenthesis show the percentage of contribution of each family to the total at that site. Values in brackets next to site names are annual hydroperiods (d).

† Limnephilidae values are abundance and biomass of final-instar *I. plattensis* that emigrated from MI1.

regard to spates. Ward and Stanford (1983) suggested that diversity patterns of stream macroinvertebrates across disturbance gradients could be explained by the IDH. In New Zealand streams, Death and Winterborne (1995) found highest invertebrate species richness at sites with highest stability (least disturbed), but highest evenness occurred at intermediately disturbed sites, and they suggested that time since the last disturbance was most important in determining diversity. Townsend et al. (1997) found that aquatic insect richness in streams followed predictions of the intermediate disturbance hypothesis, with highest richness at intermediate levels of disturbance. In contrast, Reice (1984, 1985) saw no relationship between disturbance frequency and insect species richness or Shannon diversity in stream sediments. Resh et al. (1988) reviewed stream disturbance studies and concluded that the dynamic equilibrium model (Huston 1979) and IDH were both applicable to a variety of situations because results of many studies suggested that recurrence intervals of disturbances influence biotic interactions, and thus diversity. However, demonstration of competitive hierarchies in many freshwater systems is lacking, limiting interpretations (Reice 1985, Resh et al. 1988).

Annual hydroperiods were inversely proportional to the frequency and magnitude of drying disturbances in the wetlands we examined, and a strong, significant relationship indicated that the frequency of drying events was an important factor governing insect richness in these wetlands. At MI2, the site with the highest richness, annual hydroperiod and frequency and magnitude of drying events both were roughly intermediate across the range we examined (see Table 1). Thus, our results indicate that insect diversity, measured as taxonomic richness of emerging adults, peaks in these wetlands at intermediate levels of disturbance; in this

case, annual hydroperiods of 250–300 d. However, lack of information on biotic interactions in these wetlands precludes a direct test of the IDH.

Our analyses focused on drying as a disturbance because insects that complete at least a portion of their life cycle in water were the focus of this study. We considered drying a disturbance because it has a marked negative impact on the aquatic environment of the sloughs. However, wetting might also be considered a disturbance for some taxa that inhabit these systems. For example, the life cycle of *Ironoquia plattensis*, which was found only in MI1, is closely linked to the intermittent hydrology of this site (Whiles et al. 1999), and it is not present in wetter sites that we examined. Hence, for this caddisfly, wetter conditions might constitute a disturbance. Nonetheless, wetting and drying patterns are antagonistic, so the direction of the quadratic relationship we observed would be reversed, but otherwise essentially the same, if wetter sites were considered more disturbed.

In wetlands, hydroperiod is considered one of the most important components of the physical template influencing invertebrate communities (Wissinger 1999). Previous investigations suggest that richness of wetland invertebrate taxa increases with water permanence (Driver 1977, Evans et al. 1999, Hall et al. 1999, Taylor et al. 1999, Williams and Williams 1999). However, the presence of fish, which is generally positively correlated with water permanence, has been shown to limit wetland invertebrate richness and biomass (Huener and Kadlec 1992, Mallory et al. 1994). Neckles et al. (1990) also suggested that some invertebrates are simply adapted to semipermanent hydrologic regimes and that longer hydroperiods may eliminate cues vital to reproduction, hatching, etc. of many wetland invertebrates. Results of our study support a

TABLE 3. Extended.

Study site			
MI1 [331]		WR2 [365]	
Family (%)	No.	Family (%)	No.
Chironomidae (32%)	635.7	Chironomidae (96%)	1553.9
Culicidae (19%)	364.0	Ceratopogonidae (1%)	21.7
Limnephilidae (11%)†	219.0	Sciaridae (1%)	16.3
Ceratopogonidae (7%)	141.3	Tipulidae (1%)	10.9
Total	1957.7	Total	1619.1
Family (%)	mg	Family (%)	mg
Limnephilidae (57%)†	560.0	Chironomidae (94%)	239.8
Culicidae (14%)	137.9	Ephydriidae (3%)	7.0
Sciomyzidae (11%)	112.6	Tipulidae (2%)	4.7
Leptoceridae (5%)	50.3	Sciaridae (1%)	2.1
Total	982.3	Total	255.7

combination of these observations and indicate that, at least in Platte River wetlands, both insect richness and productivity are maximized in intermittent sites without fish.

This natural experiment did not allow us to quantify the influence of specific biotic interactions (e.g., competition and predation). However, we observed patterns indicating that the presence of fish was important. For example, both taxa richness and productivity in these wetlands increased with length of hydroperiod until fish were present (sites MI1 and WR2) and then declined. Fish predation has been shown to reduce aquatic invertebrate diversity and productivity in wetlands (Huener and Kadlec 1992, Mallory et al. 1994), and fish and invertebrates can also compete for resources (Morin et al. 1988). Culicids, which are generally intolerant of fish predation (Wood et al. 1979, Walker and Newson 1996), dominated emergence at the fishless intermittent

site (MI2), but their abundance at the most hydrologically similar site (MI1), which contained fish seasonally, was only 1.5% that of MI2, and they were absent altogether from the perennial site where fish were present year-round (WR2). Although some culicids require dry/wet cycles for successful oviposition and hatching, *Culex* dominated the culicid fauna in these wetlands, and females of this genus lay eggs in the water (Walker and Newson 1996). Thus, the dramatic decrease in the abundance of culicids in MI1, and their complete absence from WR2, were most likely related to the presence of predators, indicating biotic interactions such as fish predation in wetter sites did have an effect on community structure and emergence production in these wetlands.

One interesting aspect of this study was the inclusion of two intermittent sites with similar hydrologic regimes, one that harbored a seasonal fish community (MI1) and one that did not (MI2). Floodplain wetlands, like the Platte River systems, are unique in that even temporary sites can harbor fish, because they are connected to the river during wet periods (e.g., Kohler et

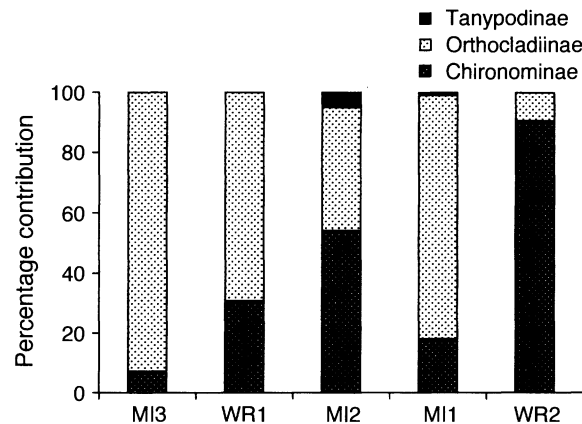


FIG. 5. Percentage contribution of chironomid subfamilies to total chironomid emergence abundance at each study site. Sites are arranged in order of increasing annual hydroperiod.

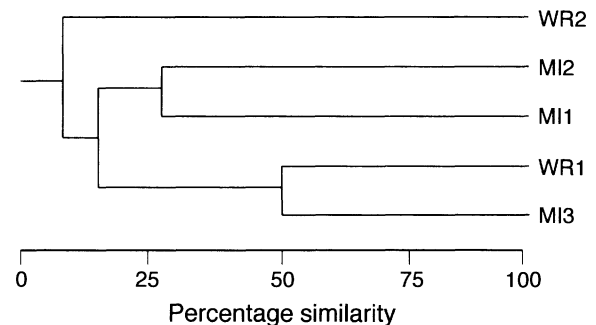


FIG. 6. Percentage similarity dendrogram based on total annual emergence densities of all insect taxa in the five study wetlands.

al. 1999). Although fish were absent from three of our five wetlands during this study, during flooding they invade some areas that normally do not harbor fish (B. S. Goldowitz, *unpublished data*). Based on results from this study, invasions by fish could result in changes in insect communities and emergence dynamics. However, the surprising lack of community similarity between the two wetlands with fish (MI1 and WR2) combined with the greater similarity between hydrologically similar sites (see Fig. 6), suggest that hydrology was the primary factor underlying the patterns we observed.

Taxa richness and emergence production estimates generated during this study indicate there is a positive diversity–productivity relationship for emerging aquatic insects in these wetlands. The mechanism for this relationship resembles the sampling effect model (Huston 1997, Tilman et al. 1997), wherein the chance of having a productive species in a community increases with taxonomic richness. Emergence production at the two most diverse and productive sites (MI2 and MI1) was dominated by *Culex* and *I. plattensis*, respectively. If these two taxa were removed from these respective wetlands, their emergence production would fall much closer to the range of the other, less productive sites. With the dominant taxon removed from all but the site with lowest richness, the slope of this relationship decreased and no significant correlation between richness and productivity was evident (see Fig. 4B). Thus, this positive diversity–productivity relationship was a result of individual taxa that were highly productive, as opposed to higher production by many taxa in more productive sites.

We know of no other studies that have addressed diversity–productivity relationships of aquatic insects, and a recent review by Schlöpfer and Schmid (1999) indicated there was a lack of information on diversity and productivity relationships among consumer groups. However, there is evidence that this pattern may not be common in streams. Benke's (1993) review of stream invertebrate production demonstrated generally higher production in large, anthropogenically impacted systems where taxonomic richness was likely to be low. Grubaugh et al. (1996) examined macroinvertebrate taxa richness and biomass along the longitudinal gradient of an Appalachian stream, and their results indicate that biomass was highest at downstream sites where taxa richness also was comparatively low. Hence, the diversity–productivity pattern for emerging aquatic insects that we observed might be unique to wetlands, or possibly the specific type of wetlands we examined.

Although it has been suggested that floodwaters from adjacent rivers can be an important source of invertebrate colonists in wetlands (Kohler et al. 1999), and thus more connectivity with a river may result in higher species richness, our results do not support this observation. Connectivity between these floodplain wetlands

and the Platte River is positively correlated with hydroperiod (Goldowitz and Whiles 1998) and thus not with taxa richness of emerging insects. At least for these riparian wetlands, other factors, such as hydrology and biotic interactions, have greater influence than river proximity on insect taxa richness. However, it is important to consider that our richness measures were based on emergence trap collections, and thus included only taxa that successfully complete life cycles in the wetlands and emerge as adults. It is possible that, during wet periods, colonists from the river may occasionally alter richness and diversity patterns in these wetlands. However, they may not successfully emerge as adults unless they are in the proper environment.

Besides relationships with hydrology and the presence of fish, insect taxa richness in these Platte River wetlands also may be linked to patterns of diversity and productivity of other groups. Species richness and productivity of macrophytes varied among our study sites and appeared highest at intermittent sites where insect richness also peaked (MI1 and MI2). Macrophytes increase structural habitat in wetlands, serve as a food source for phytophagous invertebrates, provide substrate for periphyton, and ultimately produce detrital food resources (Batzer and Wissinger 1996). Although macrophyte diversity and productivity may influence insect richness in these wetlands, it is also quite possible that macrophytes and insects respond to the same variables (e.g., hydrology).

Emergence traps can sometimes underestimate the abundance and diversity of aquatic insects (Davies 1984). In particular, our traps were probably inadequate for sampling some larger odonates that crawl out of the water before eclosion. Immature and adult odonates were observed at our intermittent and perennial sites, but they were rarely present in our traps. Only *Ischnura verticalis* (Odonata: Coenagrionidae), a relatively small damselfly, was occasionally collected in traps. Hemipterans, including corixids and belostomatids, were also present seasonally in some study sites, but they were infrequent in trap collections. Among holometabolous groups, some coleopterans such as hydrophilids were also observed in the wetlands but rarely collected in traps because larvae leave the aquatic environment to pupate. Therefore, we may not have accounted for the entire insect community in each slough we examined and our emergence production estimates are likely conservative. However, there is evidence that we accounted for the majority of taxa present. The emergence traps that we used sample from the surface of the water, and it has been shown that this method is efficient for sampling aquatic insects in lentic situations (McCauley 1976). We collected a total of 48 taxa, representing 18 insect families, in emergence traps during this study, and this represents >80% of the aquatic/semi-aquatic insects that we have observed or collected in these wetlands using a variety of techniques since 1997 (M. R. Whiles and B. S. Goldowitz,

*unpublished data*). Further, many taxa that were not collected, or were poorly represented, can be transient in these wetlands (e.g., some adult Hemiptera and Coleoptera that fly into wetlands when water is present, but may not complete their entire life cycles in them), and quantifying their contribution to diversity and productivity of a given site is problematic. Thus, our diversity and emergence production estimates reflect the majority of insect taxa in each wetland, and are focused on those that complete their life cycles in specific wetlands and then emerge from them.

#### *Emergence production estimates*

Few studies have examined the emergence production of entire insect communities from wetlands. Recently, however, Stagliano et al. (1998) quantified emergence of the total insect community from a beaver impoundment in Alabama, and they estimated that emergence production from the open water and shallower *Nymphaea* zones was  $0.59 \text{ g DM}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$  and  $2.39 \text{ g DM}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ , respectively. Like our WR2 site, the wetland they examined was perennial, contained insectivorous fish, and had midges dominating insect emergence. However, their abundance and production estimates from the *Nymphaea* zone (more similar in depth and macrophyte abundance to our systems) exceeded both our respective estimates from WR2 by  $\sim 9\times$ . This disparity may be related to climate, since aquatic insects generally have shorter life cycles and longer periods of emergence at lower latitudes (Armitage 1995, Tokeshi 1995). The annual mean temperature of the Alabama wetland was substantially higher than at WR2 ( $17.5^\circ\text{C}$  vs.  $12^\circ\text{C}$ , respectively; Stagliano et al. 1998). In addition, insects emerged year-round from the warmwater subtropical system in Alabama (Stagliano et al. 1998). Although we did not trap in WR2 during winter months, cold winter temperatures and extensive ice cover in our region undoubtedly limit emergence of adult insects, reducing annual totals compared to lower latitudes.

Although our perennial site produced lower annual emergence production than the Alabama wetland, MI2, an intermittent site without fish that accumulated fewer annual degree days, had emergence production approximately twice that of the Alabama wetland. Culicids (*Culex* and *Psorophora*), dipterans that are vulnerable to predators and often favor intermittent sites (Wood et al. 1979, Walker and Newson 1996), dominated emergence abundance and production in MI2. This suggests that factors such as hydrology and/or the presence of fish may override differences in climate and can exert a strong influence on insect taxonomic composition in wetlands, and thus emergence patterns. Large pulses of insect emergence from northern-latitude sites like MI2 during warm months can be significant, resulting in substantial annual production even though emergence periods are abbreviated by a short growing season.

Our annual emergence production estimates are generally within the range of the few published values from more northern latitudes. For example, emergence production from peatland bogs in Finland ranged from 0.5 to  $2.5 \text{ g/m}^2$  during the growing season (Paasivirta et al. 1988), which is similar to the range we observed across our study sites. In contrast, emergence of chironomids only from the pondweed zone of a Manitoba pond greatly exceeded total insect emergence production from all of our wetlands, even the most productive intermittent site (Wrubleski and Rosenberg 1990); however, values from the less productive cattail and bulrush zones of the same system were in the range of our intermittent sites (MI1 and MI2).

Numerous investigations have focused on chironomids (Rosenberg et al. 1988, Wrubleski and Rosenberg 1990, Iwakuma 1992), and/or determined that they are the dominant contributors to emergence production in wetlands (Leeper and Taylor 1998, Paasivirta et al. 1988, Stagliano et al. 1998). Although they were important contributors to abundance in all of our Platte River wetlands, chironomids contributed significantly to emergence production only at the perennial site (WR2). This suggests that focusing on emergence abundance only, or chironomids exclusively, may underestimate aquatic-terrestrial linkages and/or the importance of other insect groups. Further, emergence production at each of our study wetlands was dominated by members of different families, demonstrating that the relative importance of various insect groups to the export of energy and nutrients from wetlands can change dramatically across a hydrologic gradient, even within a limited geographic area.

#### *Conservation and restoration of Platte River wetlands*

When managing habitat to conserve and promote diversity, insects are an excellent focal group, as they often comprise the bulk of diversity in ecosystems. Further, the importance of emerging aquatic insects to vertebrate groups, such as birds, is well documented (Orians 1964, 1980, Street 1977, Sjöberg and Danell 1982, Gray 1993, Cox and Kadlec 1995). Current management and restoration objectives in the central Platte River basin focus on migratory waterfowl, Sandhill Cranes, and the federally endangered Whooping Cranes that utilize this region each year. These birds represent an important ecological and economic resource in the region (Eubanks et al. 1998, Eubanks 1999), and they depend on wetland habitats during their stay on the Platte. Managing and restoring wetlands to enhance aquatic insect diversity and productivity should have a positive influence on these focal groups, as well as other organisms. Because hydrology influences insect diversity and productivity in these systems, and water levels in the wetlands are, in turn, influenced by flow in the Platte River (Whiles and Goldowitz 1998, Goldowitz and Whiles 1999), maximizing insect diversity

and productivity in central Platte River wetlands will require appropriate management of the Platte River system as a whole, including instream flows.

Our results suggest that management strategies for conserving and restoring Platte River wetlands which strive to maximize aquatic insect diversity and productivity should target intermediate (~250–300 d) annual hydroperiods. However, emergence abundance and production at the most diverse and productive wetland in this study was dominated by culicids. Culicids are generally considered a nuisance and are important disease vectors, and this often overshadows any positive contributions of this group, such as their importance as prey for a variety of predators. Our results suggest that management efforts may need to consider tradeoffs between highest productivity and diversity of insects and pest management in these wetlands. Culicids were much less abundant in the second most diverse and productive wetland (MI1), which had a slightly longer annual hydroperiod (+35 d) and supported a seasonal fish community. This indicates that an appropriate hydrologic regime and/or the presence of insectivorous fish may reduce culicids in these systems while still resulting in relatively high insect diversity and productivity compared to perennial and ephemeral systems.

Temporal patterns of insect emergence production observed during this study show that sites with different hydrology generate peaks of adult insect biomass at different times of the year. This suggests that, at the landscape level, a mosaic of wetlands with different hydrologic regimes should enhance the annual availability of adult aquatic insect production to consumers. A landscape of wetlands with different annual hydroperiods also facilitates the process of cyclic colonization, whereby colonists from wetter sites colonize more temporary systems when they become inundated (Batzer and Wissinger 1996, Wissinger 1997). Although insect diversity during this study was highest at intermittent sites, every study site harbored at least two taxa not found elsewhere, including a formerly undescribed species of caddisfly (*I. plattensis* at MI1) that is currently known to exist in only a handful of intermittent sloughs in this immediate area. Thus, a landscape with a mosaic of wetlands with different hydrologic regimes should also maximize wetland insect diversity in the central Platte River valley. Because the management goal in this region is to provide resources for all migratory birds that depend on the Platte River, and because different types of wetlands harbor different insect communities and have different patterns of emergence production, we conclude that management and restoration efforts in the region should focus on maintaining a landscape with an array of wetlands with varying hydrologic regimes.

#### ACKNOWLEDGMENTS

R. Charlton provided valuable assistance with all aspects of this study. Field assistance by S. Bergman, M. Kearns, C.

Morgan, R. Presgraves, and M. Wolfe was essential to successful completion of this project, and P. Currier and other Platte River Whooping Crane Maintenance Trust personnel provided lodging and additional field help. R. Brown and D. M. Stagliano assisted with insect identifications, and K. D. Alexander, S. G. Baer, and L. J. Gray provided essential materials and advice. J. A. Stanford and two anonymous reviewers made valuable comments that greatly improved this manuscript. This work was funded in part by the USEPA.

#### LITERATURE CITED

- Alexander, K. D., and M. R. Whiles. 2000. A new species of *Ironoquia* (Trichoptera: Limnephilidae) from an intermittent slough the central Platte River, Nebraska. *Entomological News* 111:1–7.
- Armitage, P. D. 1995. Behavior and ecology of adults. Pages 194–224 in P. Armitage, P. S. Cranston, and L. C. V. Pinder, editors. *The Chironomidae: the biology and ecology of non-biting midges*. Chapman and Hall, London, UK.
- Bataille, K. J., and G. A. Baldassarre. 1993. Distribution and abundance of aquatic macroinvertebrates following drought in three prairie pothole wetlands. *Wetlands* 13:260–269.
- Batzer, D. P., R. B. Rader, and S. A. Wissinger, editors. 1999. *Invertebrates in freshwater wetlands of North America*. John Wiley and Sons, New York, New York, USA.
- Batzer, D. P., and V. H. Resh. 1992. Wetland management strategies that enhance waterfowl habitats can also control mosquitoes. *Journal of the American Mosquito Control Association* 8:117–125.
- 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. 1993. Concepts and patterns of invertebrate production in running waters. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 25:15–38.
- Brower, J. E., J. H. Zar, and C. N. Von Ende. 1997. *Field and laboratory methods for general ecology*. Fourth edition. McGraw-Hill, Boston, Massachusetts, USA.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.
- Corbet, P. S. 1965. An insect emergence trap for quantitative studies in shallow ponds. *Canadian Entomologist* 97:845–848.
- Cox, R. R., and J. A. Kadlec. 1995. Dynamics of potential waterfowl foods in Great Salt Lake marshes during summer. *Wetlands* 15:1–8.
- Davies, I. J. 1984. Sampling aquatic insect emergence. Pages 161–227 in J. A. Downing and F. H. Rigler, editors. *A manual on methods for the assessment of secondary productivity in fresh waters*. IBP Handbook 17, Blackwell Scientific Publications, Oxford, UK.
- Death, R. G., and M. J. Winterborne. 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. *Ecology* 76:1446–1460.
- Driver, E. A. 1977. Chironomid communities in small prairie ponds: some characteristics and controls. *Freshwater Biology* 7:121–133.
- Eubanks, T. 1999. *Wildlife-associated recreation along Nebraska's Platte River: the economic impact of hunting and fishing on the middle Platte River in Nebraska*. Platte Watershed Program, USEPA region VII, Kansas City, Missouri, USA.
- Eubanks, T., R. Ditton, and J. Stoll. 1998. *Platte River nature recreation study: the economic impact of wildlife watching on the Platte River in Nebraska*. Platte Watershed Program, USEPA region VII, Kansas City, Missouri, USA.
- Evans, D. L., W. J. Streever, and T. L. Crisman. 1999. Natural flatwoods marshes and created freshwater marshes of Florida: factors influencing aquatic invertebrate distribution and comparison between natural and created marsh com-

- munities. Pages 81–104 in D. P. Batzer, R. B. Rader, and S. A. Wissinger, editors. *Invertebrates in freshwater wetlands of North America*. John Wiley and Sons, New York, New York, 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, Missouri, USA.
- Golladay, S. W., S. Entekin, and B. W. Taylor. 1999. Forested limesink wetlands of southwest Georgia: invertebrate habitat and hydrologic variation. Pages 197–216 in D. P. Batzer, R. B. Rader, and S. A. Wissinger, editors. *Invertebrates in freshwater wetlands of North America*. John Wiley and Sons, New York, New York, USA.
- Gray, L. J. 1989. Emergence production and export of aquatic insects from a tallgrass prairie stream. *The Southwestern Naturalist* **34**:313–318.
- Gray, L. J. 1993. Response of insectivorous birds to emerging aquatic insects in riparian habitats of a tallgrass prairie stream. *American Midland Naturalist* **129**:288–300.
- Grubaugh, J. W., J. B. Wallace, and E. S. Houston. 1996. Longitudinal changes of macroinvertebrate communities along an Appalachian stream continuum. *Canadian Journal of Fisheries and Aquatic Science* **53**:896–909.
- Hall, D. L., R. W. Sites, E. B. Fish, T. R. Mollhagen, D. L. Moorehead, and M. R. Willig. 1999. Playas of the southern High Plains: the macroinvertebrate fauna. Pages 635–666 in D. P. Batzer, R. B. Rader, and S. A. Wissinger, editors. *Invertebrates in freshwater wetlands of North America*. John Wiley and Sons, New York, 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.
- Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* **113**:81–101.
- Huston, M. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**:449–460.
- Iwakuma, T. 1992. Emergence of Chironomidae from the shallow eutrophic Lake Kasumigaura, Japan. *Hydrobiologia* **245**:27–40.
- Jackson, J. K., and S. G. Fisher. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran Desert stream. *Ecology* **67**:629–638.
- Johnsgard, P. A. 1980. A revised list of birds of Nebraska and adjacent plains states. *Nebraska Ornithological Union Occasional Papers* Number 6, Lincoln, Nebraska, USA.
- Kohler, S. L., D. Corti, M. C. Slamecka, and D. W. Schneider. 1999. Prairie floodplain ponds: mechanisms affecting community structure. Pages 711–732 in D. P. Batzer, R. B. Rader, and S. A. Wissinger, editors. *Invertebrates in freshwater wetlands of North America*. John Wiley and Sons, New York, New York, USA.
- Leeper, D. A., and B. E. Taylor. 1998. Abundance, biomass, and production of aquatic invertebrates in Rainbow Bay, a temporary wetland in South Carolina, USA. *Archiv für Hydrobiologie* **143**:335–362.
- Leslie, A. J., J. P. Prenger, and T. L. Crisman. 1999. Cypress domes in North Florida: invertebrate ecology and response to human disturbance. Pages 105–120 in D. P. Batzer, R. B. Rader, and S. A. Wissinger, editors. *Invertebrates in freshwater wetlands of North America*. John Wiley and Sons, New York, New York, 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.
- McCauley, V. J. E. 1976. Efficiency of a trap for catching and retaining insects emerging from standing water. *Oikos* **27**:339–345.
- Milliken, G. A., and D. E. Johnson. 1992. *Analysis of messy data*. Chapman and Hall, London, UK.
- Morin, P. J., S. P. Lawler, and E. A. Johnson. 1988. Competition between aquatic insects and vertebrates: interaction strength and higher order interactions. *Ecology* **69**:1401–1409.
- Neckles, H. A., H. R. Murkin, and J. A. Cooper. 1990. Influence of seasonal flooding on macroinvertebrate abundance in wetland habitats. *Freshwater Biology* **23**:311–322.
- Orians, G. H. 1964. Food of nestling yellow-headed blackbirds, Caribou Parklands, British Columbia. *Condor* **68**:321–337.
- Orians, G. H. 1980. *Some adaptations of marsh-nesting blackbirds*. Princeton University Press, Princeton, New Jersey, USA.
- Paasivirta, L., T. Lahti, and T. Perätie. 1988. Emergence phenology and ecology of aquatic and semi-terrestrial insects on a boreal raised bog in central Finland. *Holarctic Ecology* **11**:96–105.
- Reice, S. R. 1984. The impact of disturbance frequency on the structure of a lotic riffle community. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* **22**:1906–1910.
- Reice, S. R. 1985. Experimental disturbance and the maintenance of species diversity in a stream community. *Oecologia* **67**:90–97.
- 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. V. 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.
- Rosenberg, D. M., A. P. Wiens, and B. Bilyj. 1988. Chironomidae (Diptera) of peatlands in north-western Ontario, Canada. *Holarctic Ecology* **11**:19–31.
- SAS Institute. 2000. *SAS for Windows 7.0*, SAS Institute, Cary, North Carolina, USA.
- Schläpfer, F., and B. Schmid. 1999. Ecosystem effects of biodiversity: a classification of hypotheses and extrapolation of empirical results. *Ecological Applications* **9**:893–911.
- Schneider, D. W. 1999. Snowmelt ponds in Wisconsin: influence of hydroperiod on invertebrate community structure. Pages 299–318 in D. P. Batzer, R. B. Rader, and S. A. Wissinger, editors. *Invertebrates in freshwater wetlands of North America*. John Wiley and Sons, New York, New York, USA.
- Side, J. G., E. D. Miller, and P. J. Currier. 1989. Changing habitats in the Platte River valley of Nebraska. *Prairie Naturalist* **21**:91–104.
- Sjöberg, K., and K. Danell. 1982. Feeding activity of ducks in relation to diel emergence of chironomids. *Canadian Journal of Zoology* **60**:1383–1387.
- Stagliano, D. M., A. C. Benke, and D. H. Anderson. 1998. Emergence of aquatic insects from two habitats in a small wetland of the southeastern USA: temporal patterns of numbers and biomass. *Journal of the North American Benthological Society* **17**:37–54.
- Street, M. 1977. The food of mallard ducklings in a wet gravel quarry and its relation to duckling survival. *Wildfowl* **28**:113–125.

- Taylor, B. E., D. A. Leeper, M. A. McClure, and A. E. DeBiase. 1999. Carolina bays: ecology of aquatic invertebrates and perspectives on conservation. Pages 167–196 in D. P. Batzer, R. B. Rader, and S. A. Wissinger, editors. *Invertebrates in freshwater wetlands of North America*. John Wiley and Sons, New York, New York, USA.
- Tilman, D., C. L. Lehman, and K. T. Thomson. 1997. Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences (USA)* **94**:1857–1861.
- Tokeshi, M. 1995. Life cycles and population dynamics. Pages 225–268 in P. Armitage, P. S. Cranston, and L. C. V. Pinder, editors. *The Chironomidae: the biology and ecology of non-biting midges*. Chapman and Hall, London, UK.
- Townsend, C. R., M. R. Scarsbrook, and S. Doledec. 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnology and Oceanography* **42**:938–949.
- 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, Nebraska, USA.
- Walker, E. D., and H. D. Newson. 1996. Culicidae. Pages 571–590 in R. W. Merritt and K. W. Cummins, editors. *An introduction to the aquatic insects of North America*. Third edition. Kendall/Hunt, Dubuque, Iowa, USA.
- Ward, J. V., and J. A. Stanford. 1983. The intermediate disturbance hypothesis: an explanation for biotic diversity patterns in lotic ecosystems. Pages 347–356 in T. D. Fontaine, III and S. M. Bartell, editors. *Dynamics of lotic ecosystems*. Ann Arbor Science, Ann Arbor, Michigan, USA.
- 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.
- Whiles, M. R., and B. S. Goldowitz. 1998. Biological response to hydrologic fluctuation in wetland sloughs of the central Platte River. Pages 3–18 in G. Lingle, editor. *Proceedings of the ninth Platte River ecosystem symposium*. University of Nebraska Cooperative Extension, Platte Watershed Program, Kearney, Nebraska, USA.
- 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.
- Williams, D. D., and N. E. Williams. 1999. Canadian springs: postglacial development of the invertebrate fauna. Pages 447–470 in D. P. Batzer, R. B. Rader, and S. A. Wissinger, editors. *Invertebrates in freshwater wetlands of North America*. John Wiley and Sons, New York, New York, USA.
- Wissinger, S. A. 1997. Cyclic colonization and predictable disturbance: a template for biological control in ephemeral crop habitats. *Biological Control* **10**:4–15.
- Wissinger, S. A. 1999. Ecology of wetland invertebrates: synthesis and applications for conservation and management. Pages 1043–1086 in D. P. Batzer, R. B. Rader, and S. A. Wissinger, editors. *Invertebrates in freshwater wetlands of North America*. John Wiley and Sons, New York, New York, USA.
- 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.
- Wood, D. M., P. T. Dang, and R. A. Ellis. 1979. The mosquitoes of Canada (Diptera: Culicidae). Publication Number 1686. Biosystematics Research Institute, Ottawa, Ontario, Canada.
- Wrubleski, D. A., and D. M. Rosenberg. 1990. The Chironomidae (Diptera) of Bone Pile Pond, Delta Marsh, Manitoba, Canada. *Wetlands* **10**:243–275.
- Zar, J. H. 1996. *Biostatistical analysis*. Third edition. Prentice Hall, Upper Saddle River, New Jersey, USA.