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Life history and production of a semi-terrestrial limnephilid caddisfly in an intermittent Platte River wetland

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Abstract. The life history and ecosystem significance of a recently discovered species of *Ironoquia* (Trichoptera:Limnephilidae) were examined in a riparian slough of the central Platte River, Nebraska, USA. Monthly benthic samples were collected for 1 y and adult emergence was monitored to examine *I. plattensis* life history in this harsh, intermittent habitat. Ecosystem significance of this caddisfly was assessed by estimating larval secondary production and consumption of coarse particulate organic matter (CPOM), biomass exported from the slough during larval migration onto land, and adult emergence production from the riparian prairie where pupation occurred. The life cycle of *I. plattensis* appeared intimately linked to the hydroperiod, with larval migration to land and adult emergence coinciding with drying and inundation of the slough, respectively. Total larval production in a 20-m reach of slough, adjusted for average wetted area during sampling intervals, was 429–536 g ash-free dry mass (AFDM)/y, depending upon the method of calculation. Biomass that left the slough via larval migration to land was estimated at 109 g AFDM (~23% of larval production), and total adult emergence was 69 g AFDM (~16% of larval production). Turnover rate of larval biomass was 10–12/y. CPOM consumption estimates indicated that larvae in the study site consumed 8690 g AFDM/y, ~13% of the annual average CPOM standing stock in the site. Results demonstrate that this leaf-shredding trichopteran is a productive component of this prairie wetland system, representing an abundant invertebrate food resource for aquatic and terrestrial predators and facilitating decomposition processes. However, its distribution along the central Platte River may be limited because of habitat destruction and its adaptation to a specific hydrologic regime.

Key words: aquatic invertebrates, Trichoptera, secondary production, wetlands, insect emergence, benthic macroinvertebrates, *Ironoquia*, life history.

Intermittent aquatic habitats are common features of the Great Plains region (Dodds 1997) that often exhibit hydrologic extremes and may harbor distinct, less-diverse aquatic communities than perennial systems (Matthews 1988, Williams 1996). Because of abiotic and biotic differences, rates of ecosystem processes can vary between intermittent and perennial systems. For example, some investigators have documented reduced rates of litter decomposition in intermittent systems compared to perennial ones (Tate and Gurtz 1986, Hill et al. 1988). Nevertheless, ecosystem processes and exchanges with surrounding terrestrial systems may still be of great importance in intermittent aquatic habitats, although their productivity and overall significance in the Great Plains remain poorly known.

Central Platte River sloughs are slow-flowing, primarily lentic habitats that exhibit a wide variety of hydrologic regimes ranging from ephemeral to perennial. These wetland systems have various degrees of hydrologic connection with the main channel of the Platte River, and hydroperiod generally increases with the degree of connection. Whiles and Goldowitz (1998) recently demonstrated that hydroperiod in these systems exerts a strong influence on aquatic vertebrate assemblages, which likely also applies to invertebrates and ecosystem processes. These wetlands are also a vital component of an ecosystem that is an important stopover point on

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the central flyway for migrating waterfowl, shorebirds, and wading birds, including the federally endangered whooping crane (*Grus americana*) (Johnsgard 1980, Reinecke and Krapu 1986). During spring and fall, myriad migrating birds use sloughs and surrounding wet meadows for feeding, watering, resting, and pair bonding (Johnsgard 1980).

Recent investigations in wetlands of the central Platte revealed the presence of a previously undescribed species of limnephilid caddisfly, *Ironoquia plattensis*, in an intermittent slough (Alexander and Whiles, in press). Similar to other *Ironoquia* species (Flint 1958, Williams and Williams 1975) *I. plattensis* migrates from the water as a final (5th) instar, aestivates for ~4 mo on land, and then pupates. This site currently harbors one of the few known populations of this species. Our objective was to examine the life cycle of this trichopteran in the harsh physical conditions imposed by its intermittent habitat. Further, we assessed its energetic role in this wetland system by examining larval production and consumption, biomass transfer to the riparian prairie by emigrating final instars, and adult emergence production.

Study Site

The study area is in a riparian wet meadow on Mormon Island Crane Meadows, a large (890 ha) island in the central Platte River, Hall County, Nebraska. This area is primarily lowland tallgrass prairie that is dominated by warm-season grasses, such as big bluestem (*Andropogon gerardii*), indiangrass (*Sorghastrum nutans*), prairie cordgrass (*Spartina pectinata*), and switch grass (*Panicum virgatum*), along with sedges (*Carex* spp.). Occasional patches of riparian forest, consisting of cottonwood (*Populus deltoides*), willow (*Salix* sp.), and elms (*Ulmus* spp.) are present along the banks of the river. Wet meadows in the Platte River are dissected by sloughs that are fed by a high groundwater table and surface runoff from precipitation; the sloughs vary from being ephemeral to permanent wetlands. Most of the annual precipitation falls during spring and summer. Flows of the Platte River are highest in late spring and lowest in late summer. Winters are harsh, with significant ice cover on surface waters often occurring from November to March.

The study site is a 20-m linear reach of slough and is an intermittent wetland that is filled with water most of the year, but is dry from early summer through autumn. Hydrology is influenced by both precipitation and the adjacent Platte River (Whiles and Goldowitz 1998). Riparian growth is a mixture of mainly grasses, sedges, rushes, and mixed forbs; woody vegetation is absent. Maximum wetted width of the study area is ~16 m. The substrate of the slough is a mixture of silt and sand covered with a 4–12 cm layer of detritus. Water chemistry is typical of the region, with an average pH of 8.03 and specific conductance of 1270 μS/cm. Dissolved oxygen concentration fluctuates greatly with water level, temperature, and season, and averages ~6.0 mg/L. Mean water column velocity is 3–10 cm/s, and flow ceases as the site dries. Dense growth of macrophytes (*Typha, Scirpus, Sparganium, Eleocharis, Ludwigia,* and others) and filamentous algae is evident in spring and summer. Fishes (primarily *Hybognathus hankinsoni, Fundulus sciadicus,* and *Cyprinus carpio*) are present in the slough seasonally (autumn and spring, Whiles and Goldowitz 1998).

Methods

Slough hydrology and physical habitat

In March 1997, a staff gauge was installed at the deepest point in the slough and 3 reference transects for wetted width and water depth measurements were established. Wetted width and depth transects were located 10 m apart along the length of the slough at 0, 10, and 20 m. Wetted width and depth readings (1-m intervals across the width of each transect) were collected at approximately weekly intervals, and more frequently during periods of fluctuating water levels. Staff gauge readings generally were taken daily when water was not frozen, but were taken at longer intervals (1–3 wk) during periods of ice cover or limited fluctuation in water level. Wetted surface area and volume estimates (calculated from wetted width and depth transect measurements) spanning a variety of conditions, including high and low extremes, were regressed against staff gauge readings to develop predictive equations for each. Significant logarithmic ($r^2 = 0.95$, $p < 0.01$, $n = 26$) and exponential ($r^2 = 0.95$, $p < 0.01$, $n = 26$) relationships were obtained for surface area and volume estimates, respectively. Staff gauge readings were then used to predict daily volume and wetted surface area.

A submerged thermistor datalogger was used to measure water temperature in the middle of the water column at 30-min intervals when water was not frozen. During winter when the site was frozen, we assumed temperature to be 0°C from the 1^{st} hard freeze (thermistor removed on 28 November) until spring thaw (thermistor replaced on 15 February). Spot measurements of conductivity, pH, and dissolved oxygen concentration were made monthly with standard handheld meters beginning in spring 1998.

Larval abundance, biomass, and production

Three benthic core samples were collected at ~30-d intervals for 1 y beginning on 5 April 1997 (36 samples total), except during January 1998, when extensive ice cover prevented collecting. Sampling began after larvae started developing in the slough in April 1997, so our 1-y sampling regime followed the remainder of development and adult emergence for 1997 and post-hatching development through March 1998. We used November 1997 (appearance of 1st instars) as a starting point for data presentation and production calculations.

A stovepipe coring device (20-cm diameter, 91-cm depth, 314-cm^2 sampling area) was used to sample *I. plattensis* larvae. Samples were obtained by driving the corer through the water and into the substrate at 3 random locations in the slough. After making contact with the bottom of the slough, the corer was inserted ~20 cm into the substrate so that water could not enter or leave. All sediment and vegetation down to ~10 cm below the sediment surface was removed by hand and placed 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-μm sieve. Material retained on the sieve was preserved in 7–8% formalin.

Samples were washed through nested sieves and divided into very coarse (>4 mm), coarse (<4 mm >1 mm), and fine (<1 mm >250 μm) fractions. Larvae 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 sample splitter prior to removing larvae (Waters 1969). Larvae were counted, and total body length and head capsule width were measured with a graduated stage and ocular micrometer, respectively. Size-frequency plots of head capsule width were used to identify instars, and body length measurements were used to estimate biomass of larval size classes. Formalin-preserved larvae of each body length class (2–5 per size class) were oven dried (55°C for 48 h), weighed, ashed in a muffle furnace (500°C for 4 h), and reweighed to obtain ash-free dry mass (AFDM, i.e., difference between dry mass and ash mass) for each size class (1–10 mm). A length-mass regression (ln-transformed length vs ln-transformed AFDM) ($r^2 = 0.98$, $p < 0.01$, $n = 27$) was then used to develop the following predictive equation for mg AFDM based on total body length:

$$\mathrm{AFDM} = 0.00056 \cdot (\mathrm{L})^{3.73294}$$

where L = length in mm.

We estimated production with both the increment summation and instantaneous growth methods because cohort development for *I. plattensis* was relatively synchronous (see Benke 1984). The former is designed for synchronous cohorts, and the latter can be applied to species with asynchronous development (Benke 1984, 1993). Although Benke (1993) demonstrated that results obtained from both methods are generally similar, cohort methods usually are considered more accurate. Thus, our results focused on the estimate obtained with the increment summation method, and we used the instantaneous growth method to validate it.

Estimates of 13% and 38% for shredder assimilation efficiency and net production efficiency, respectively, were obtained from Perry et al. (1987) and used to estimate *I. plattensis* ingestion. Ingestion was derived by dividing production by the product of assimilation efficiency and net production efficiency (see Benke and Wallace 1980).

The average number of 5th instars in samples (present in May and June 1997) was used as an estimate of total number and biomass of larvae that emerged from the slough onto riparian prairie. This estimate is likely conservative because some 4th instars, which also presumably grew and emigrated, were collected on the last sampling date when larvae were present in the slough (1 June 1997) but were not included in our estimate. Because emigration began in late

May and the 2 sample dates used for this estimate were 1 mo apart, we assumed final instars were not counted twice in this estimate. Estimates of areal density, biomass, and production were multiplied by the average wetted area during sampling intervals to calculate totals for the study reach of slough.

The land area occupied by larvae that emigrated from the slough was determined by examining the litter layer and soil surface on each side of the slough. Four transects (5 m apart) perpendicular to the slough were searched for larvae on each side in July 1997. For each transect, we recorded the distances from the water line where larvae were 1st encountered and where larvae were no longer found. This procedure allowed for estimation of surface area occupied by aestivating larvae.

Organic matter estimates

Following removal of larvae from core samples, 1 sample date per season was analyzed for organic matter content (spring: 2 May; summer: 28 June; autumn: 17 October; winter: 18 December 1997). Coarse fractions of each sample (i.e., material retained by a 1-mm sieve) 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 obtain g AFDM/m^2 estimates. Dead leaves and stems, seeds, and the miscellaneous category were combined to estimate total CPOM. Fine fractions of each sample (material that passed through a 1-mm sieve but retained by a 250-μm sieve) were designated fine particulate organic matter (FPOM) and processed in the same manner as CPOM. Values from the 3 cores per date were averaged to obtain seasonal average g AFDM/m^2 estimates. We recognize that our benthic FPOM estimates probably were lower than actual FPOM standing stocks in the slough because we did not collect fine particles that passed through the 250-μm sieve while processing samples in the field. Values from all 12 cores were averaged to obtain estimates of annual standing stocks. Total CPOM and FPOM standing stocks in the study site were derived by applying seasonal estimates of g AFDM/m^2 to average wetted area during each season.

Adult emergence production

We used emergence traps placed over the riparian prairie to estimate *I. plattensis* adult emergence production. Three traps (625 cm^2 sampling surface area each) were placed flush with the ground at randomly selected points within the area occupied by pupae. Traps were plastic cylinders capped with a fine Nitex® mesh cone that directed trapped insects into a collecting bottle filled with 7–8% formalin. Each trap was secured to 2 fence posts driven into the ground. Posts held traps in contact with the ground and supported the mesh cone and collecting bottle. Traps were placed in the field in mid-August and checked every 2–3 d until the emergence started. Trap bottles were changed every 1–2 d until emergence ceased. Two mesh cages (0.9 m × 0.9 m × 1.3 m high) were used for additional qualitative collections to increase numbers of adults collected, estimate sex ratio, and quantify the duration of emergence. These cages were erected in the vicinity of quantitative traps during the same time interval. Adults in qualitative collection cages were removed every 1–2 d during the emergence period, preserved in 80% ethyl alcohol, sexed, and counted.

Estimates of mean individual AFDM were obtained separately for adult male and female *I. plattensis*. Ten individuals of each sex (from formalin collections) were dried, weighed, ashed, and reweighed as described above for larvae. Mean individual mass was applied to data from quantitative emergence traps to estimate emergence production.

Results

Slough hydrology and physical habitat

When benthic sampling commenced in April 1997, slough wetted surface area and volume averaged 300 m^2 and 84 m^3, respectively. Water level generally decreased through the spring and the site dried completely by 2 July 1997 (Fig. 1). Water returned for 29 d in August following summer thunderstorms, but complete drying occurred again by 10 September. The slough filled again following late-September rains, and remained wet for the remainder of the study period. The annual hydroperiod (total no. of d with water from May 1997 to May 1998) for this site was 321 d.

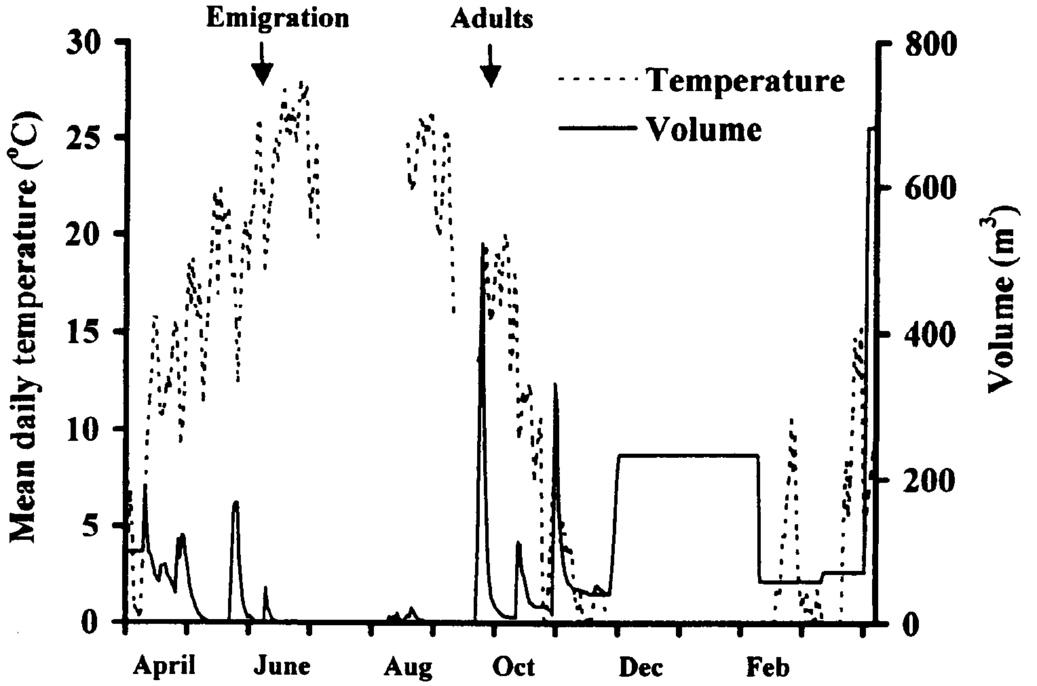

FIG. 1. Slough hydrograph (daily volume in m^3) and average daily water temperature from April 1997 to March 1998. Winter values are estimates based on conditions before and after extensive ice cover formed. Arrows indicate dates when *Ironoquia plattensis* larvae left the slough (Emigration) and when adults 1st appeared in emergence traps (Adults).

Temperature in the slough fluctuated greatly during the study, but a steady increase was evident beginning in April 1997 (Fig. 1). Temperatures peaked as water levels dropped in June, with a maximum daily average of 27.9°C recorded on 28 June 1997 and a maximum 30-min interval recording of 37.6°C recorded as the site was drying on 1 July 1997. Substantial ice cover formed in late November 1997, which persisted with little interruption until 15 February 1998. Degree days accumulated (>0°C) during 1997–1998 when water was present = 2967.

Organic matter

Both FPOM and CPOM standing stocks were somewhat higher in spring than other seasons (Table 1). Totals of FPOM and CPOM for the entire wetted area of the slough also were highest in spring, and lowest in summer when average wetted surface area was lowest (Table 1).

Based on annual average standing stocks, dead leaves and stems of aquatic macrophytes accounted for 58% of CPOM, followed by miscellaneous detritus (40%) and seeds (2%). Living macrophyte tissue averaged 110 g AFDM/m^2 annually but was not included in our CPOM estimates. Visual examination of CPOM, including miscellaneous detritus, indicated that riparian grasses and forbs contributed little to the benthic organic matter pool in the site.

Larvae and pupae

First instars were 1st encountered in mid-November 1997. Larval growth was slow during winter, and 1st instars still accounted for ~40% of the population by late February (Fig. 2). Growth rates increased with increasing water temperatures in spring, and final instars migrated from the slough from late May to early June (Figs 1, 2). Larvae spent the remainder of the summer up to late August through early September aestivating under the litter layer of prairie surrounding the slough. Field and laboratory observations of aestivating larvae revealed that they remained somewhat active (i.e., they retained mobility) but did not feed. Pupation occurred in the same area during early September.

Density of larvae was 288 ± 225/m^2 (mean ± 1 SE) in November, when 1st instars were collected, and peaked at 1547 ± 655/m^2 in February. Annual average density of larvae was 469 ± 162/m^2, and average density for the 7-mo production interval was 805 ± 194/m^2. Standing stock biomass peaked at 1.16 ± 0.16 g AFDM/m^2 in early May. Annual and cohort

TABLE 1. Mean coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) standing stocks (g ash-free dry mass/m^2) in the study site calculated from benthic core samples (n = 3 on each date) during winter (18 December), spring (2 May), summer (28 June), and autumn (13 October) and annual average (n = 12 cores). Values in parentheses are 1 SE. Totals are seasonal m^2 values applied to averaged wetted surface area.

Season	FPOM	CPOM	Total FPOM	Total CPOM
Winter	119.0 (58.9)	257.9 (29.2)	39,827	86,314
Spring	283.8 (31.8)	448.8 (94.7)	75,088	118,744
Summer	217.3 (55.8)	312.1 (26.0)	19,114	27,452
Autumn	177.7 (18.3)	208.2 (67.6)	37,470	43,901
Annual avg.	199.5 (26.2)	306.8 (37.7)	42,875	69,103

standing stock biomass averaged 0.15 ± 0.09 and 0.27 ± 0.15 g AFDM/m^2, respectively.

Estimates of larval production generated with the instantaneous growth and increment summation methods were somewhat similar, with the instantaneous growth estimate being 23% higher (Tables 2 and 3). Both methods indicated highest production and growth rates during April (5 April–2 May), and no production during the 1^{st}-mo interval (mid November–mid December). The difference between the 2 estimates was most likely a result of large increases in biomass over some sampling intervals (Tables 2 and 3), which amplified differences between the exponential (instantaneous growth) and linear (increment summation) models used. Unusually low production and growth rates were evident for the short interval between 26 March to 5 April, even though production in intervals before and after this period was relatively high. This result suggests that error associated with merging points when sampling began and ended between years (March 1998 and April 1997) may have artificially reduced our estimates during this short, 10-d interval. Depending on the production calculation method, cohort and annual production to biomass ratios (P/B) ranged from 5.5 to 6.8 and 10.0 to 12.3, respectively. Areal production estimates generated from both methods applied to wetted surface area during intervals indicated that larval *I. plattensis* production was ~429 to 536 g AFDM/y (Tables 2

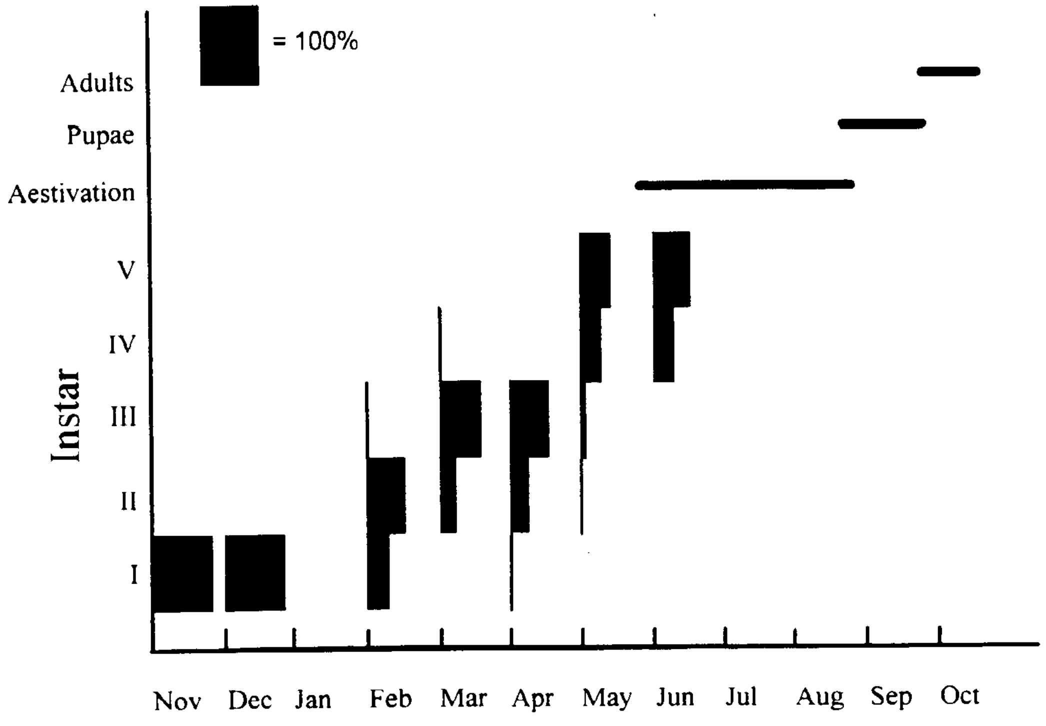

FIG. 2. Size-frequency plot of *Ironoquia plattensis* larvae during April 1997 to March 1998. Width of bars represents % in each instar (I–V) on a given sampling date. Horizontal lines indicate periods of larval aestivation on land, pupation, and adult emergence. No samples were collected in January.

TABLE 2. Instantaneous growth production calculations for *Ironoquia plattensis* during 1997–1998. Initial standing stock biomass was not included with this method but was added to production in intervals to obtain total annual production (see Benke 1984). Production in the slough was interval production (g/m²) multiplied by the average wetted area of the slough (m²) over the sampling interval. Biomass (B) and production (P) units are ash-free dry mass.

Date	Interval (d)	Avg. biomass (mg/m²)	Daily growth rate[a] (d⁻¹)	Interval production (g/m²)	Avg. wetted area (m²)	Production in slough (g)
19 Nov						
	29	4.60	0	0	322.5	0
18 Dec						
	66	26.34	0.021	0.036	345.6	12.44
22 Feb						
	32	170.86	0.064	0.348	287.7	100.12
26 March						
	10	232.86	0.003	0.007	288.6	2.02
5 April						
	27	662.59	0.072	1.294	302.4	391.31
2 May						
	30	690.65	0.005	0.110	195.0	21.45
1 June						
	27	112.91	0.017	0.052	145.0	7.54
28 June						
	Avg. =	271.54				
Cohort P/B = 6.8		Annual P/B = 12.3	+ Initial biomass	0.003 g/m²		0.97 g
			Total production	1.849 g m⁻² y⁻¹		535.85 g/y

[a] Instantaneous rates of growth: $\ln(W_t/W_{(t-1)})/t$, where W = weight in mg, t = time in d

and 3). Data from the 2 sampling dates when final instars were present (2 May and 1 June 1998) showed that 219 individuals/m² reached the final instar and emigrated from the slough. Based on an average wetted area of 195 m² during this interval, 42,633 final instars (109 g AFDM larval biomass) migrated into mesic prairie surrounding the slough by mid-June (Fig. 3).

Based on the lower (i.e., more conservative) production estimate obtained with the increment summation method (1.5 g AFDM/m²), *I. plattensis* larvae consumed 30.36 g AFDM m² y⁻¹ CPOM (8690 g AFDM/y in the entire study site). This amount represents 13% of the 1997–1998 annual average CPOM standing stock in the study site.

Adult emergence

The 1st *I. plattensis* adults were qualitatively collected on 24 September. Emergence peaked on 30 September, when 93 individuals were collected. Qualitative and quantitative collections showed that the emergence was highly synchronous, lasting only 10 d; >70% of total emergence occurred in a 3-d span from 29 September to 1 October (Fig. 4). Collections from qualitative mesh cages revealed that males were numerically dominant during the first 4 d of emergence (Fig. 4).

Adult females (1.76 ± 0.18 mg AFDM, mean ± 1 SE) weighed >2× more than males (0.71 ± 0.03). Emergence production estimated from quantitative traps was 0.026 ± 0.007 g AFDM m⁻² d⁻¹, or 0.26 g AFDM/m² emergence production over the 10-d period. Total emergence production for the entire 267 m² area surrounding the slough in which larvae pupated was estimated at 69.4 g AFDM/y (Fig. 3).

Discussion

Production estimates

Although relatively small in size compared with other limnephilid caddisflies, *I. plattensis* is a productive component of the Platte River floodplain ecosystem. High densities and production of *I. plattensis* larvae represent an abundant potential food source for aquatic and terrestrial predators foraging in sloughs. Emigration of 109 g AFDM final instars from the slough and emergence of 69 g AFDM adults from riparian prairie represent substantial fluxes of energy and nutrients to riparian habitats. This single population generated 260 mg AFDM/m² of adult emergence production in 10 d., representing ~40% of total aquatic insect

TABLE 3. Increment summation production calculations for *Ironoquia plattensis* during 1997–1998. Initial standing stock biomass was not included with this method but was added to production in intervals to obtain total annual production (see Benke 1984). Production in the slough was interval production (g/m^2) multiplied by the average wetted area of the slough (m^2) over the sampling interval (presented in Table 2). All biomass (B) and production (P) units are ash-free dry mass.

Date	Avg. density (no./m^2)	Avg. individual weight (mg)	Δ weight (mg)	Interval production (g/m^2)	Production in slough (g)
19 Nov		0.0075			
	613.33		0	0	0
18 Dec		0.0075			
	1242.67		0.022	0.027	9.33
22 Feb		0.0295			
	1429.33		0.196	0.280	80.56
26 March		0.2257			
	1018.67		0.007	0.007	2.02
5 April		0.2330			
	714.67		1.408	1.006	304.21
2 May		1.6413			
	410.67		0.283	0.116	22.62
1 June		1.9246			
	58.67		1.124	0.066	9.57
28 June		3.0487			
			+ Initial biomass	0.003 g/m^2	0.97 g
Cohort P/B = 5.54		Annual P/B = 10.0	Total production	1.505 g m^{-2} y^{-1}	429.28 g/y

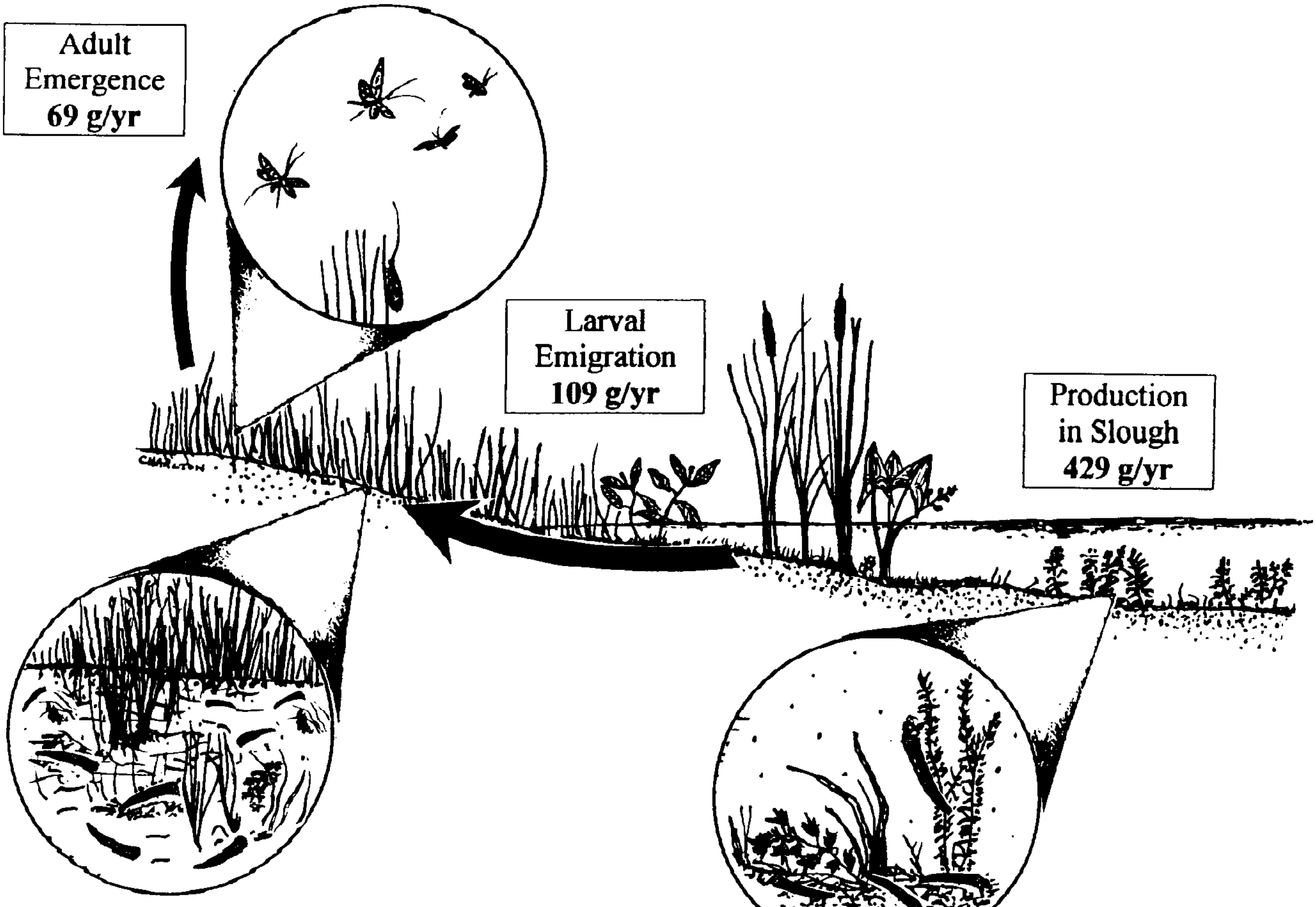

FIG. 3. *Ironoquia plattensis* larval production, biomass transfer by emigration of final instars to land, and adult emergence production. Arrows indicate direction of transfer, and values in boxes are total g ash-free dry mass.

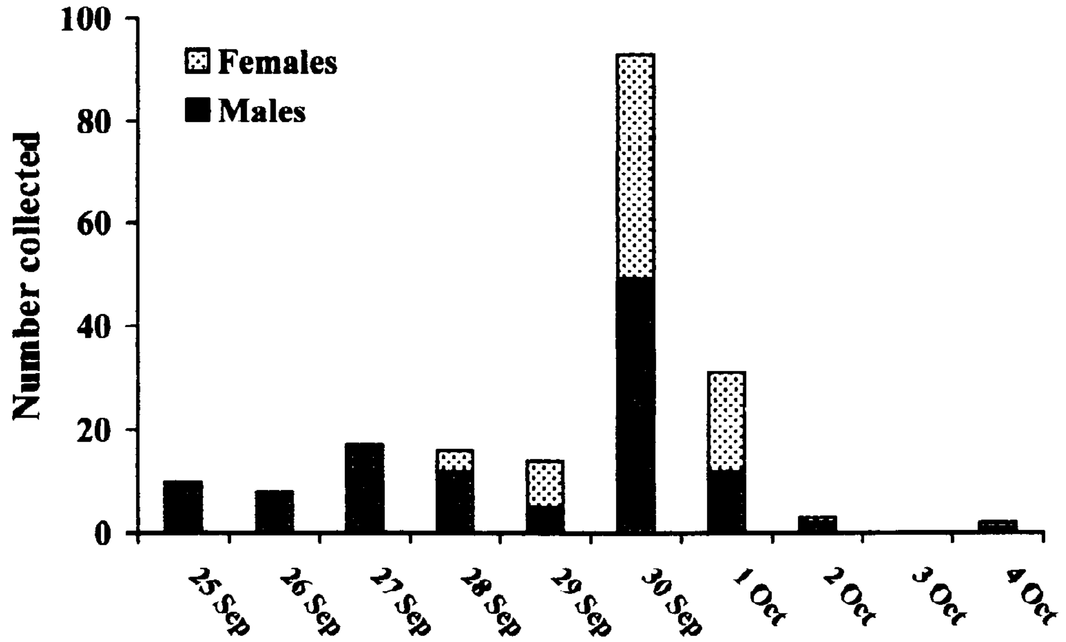

FIG. 4. Sequence of *Ironoquia plattensis* adult emergence showing proportion of males and females collected in emergence traps from 24 September to 4 October 1997.

emergence production from the study site during 1997 (M. R. Whiles and B. S. Goldowitz, unpublished data). Compared to other emergence production estimates, *I. plattensis* represent ~1/2 of the 580 mg dry mass m^{-2} y^{-1} for nearly the entire aquatic insect community in the open-water zone of an Alabama wetland, and 11% of the total from the shallower and more productive *Nymphaea* zone (Stagliano et al. 1998). Further, our adult emergence estimate did not include biomass export from the slough by emigrating final instars. Although substantial compared to some estimates, *I. plattensis* emergence production measured during this study is only 1% of total emergence production from Sycamore Creek (Jackson and Fisher 1986), a highly productive Sonoran Desert stream.

Differences between *I. plattensis* larval production, biomass leaving the slough as final instars, and adult emergence suggest that ~320 g AFDM (75% of larval production) was lost to mortality as larvae and another 40 g (9% of larval production) was lost during aestivation and pupation (see Fig. 3). Thus, our estimates indicate ~16% of *I. plattensis* production emerged as adults. Although not measured during this study, a portion of this mass lost between stages, and adult emergence production, was likely passed on to secondary consumers. The relationship between adult emergence and larval production (E/P) we observed for *I. plattensis* falls within the range of previously reported values for a variety of taxa. Our E/P estimate of 16% is lower than the 27% reported for a hydropsychid caddisfly in Sycamore Creek (Jackson and Fisher 1986), but greatly exceeds the 4% calculated for *Agapetus fuscipes* (Trichoptera: Glossosomatidae) in a German stream (Castro 1975).

Our production estimates of 1.5 g m^{-2} y^{-1} (increment summation method) and 1.9 g m^{-2} y^{-1} (instantaneous growth method) are high compared to estimates of other *Ironoquia* species and limnephilid caddisflies. Roeding and Smock (1989) estimated that production of *I. parvula* was <1 mg m^{-2} y^{-1} in a Virginia coastal plain stream. Roeding and Smock (1989) estimated that production of 2 larger leaf-shredding limnephilids in the same system, *Pycnopsyche luculenta* and *P. scabripennis*, was 458 and 459 mg m^{-2} y^{-1}, respectively. Huryn and Wallace (1988) estimated *P. gentilis* production to be 136 mg m^{-2} y^{-1} in a southern Appalachian stream, the 2nd highest production of 28 trichopteran species they examined. None of these estimates approach that obtained for *I. plattensis* in our study, and based on Benke's (1993) review of secondary production studies, *I. plattensis* occurs within the top 10% of estimates for shredding invertebrates. Factors contributing to high production may include an abundance of food (CPOM derived from dense macrophyte growth), low abundance of other competing shredders in this system (M. R. Whiles and B. S. Goldowitz, unpublished data), and high water temperatures during late spring.

Cohort P/B ratios obtained with both production calculation methods are near the value of 5 commonly obtained from field estimates (Waters 1979). However, the annual P/Bs of 10 to 12 estimated for *I. plattensis,* which are related directly to individual growth rates, suggest fairly rapid growth and biomass turnover. This annual P/B estimate is somewhat inflated, however, because larvae are in the slough for just over half the year before emigration (~7 mo), resulting in low annual average biomass relative to production. Thus, relatively high production by *I. plattensis* is a function of high abundance and biomass during the cohort production interval, rather than rapid growth per se.

Life history

The life cycle of *I. plattensis* appears highly adapted to its intermittent habitat. During our study, final instars migrated from the slough within 3 wk of drying, during a period when water temperatures steadily increased (Fig. 1). Flint (1958) and Williams and Williams (1975) reported that final instars of *I. parvula* and *I. punctatissima,* respectively, also migrated from intermittent habitats shortly before drying. It is not clear from these studies what cues initiate emigration, or if there is plasticity associated with the timing of this behavior. However, we failed to find *I. plattensis* in 4 nearby sloughs with different hydroperiods, despite similar sampling intensity over the same time period. These other sites include a similar, nearby (>1.5 km) reach of slough, also on Mormon Island, with an annual hydroperiod ~30 d less than that of our study site and that dried only 19 d prior to our site in spring 1997 (Whiles and Goldowitz 1998). We also did not find this species during monthly benthic sampling for >1 y in a similar permanent slough located on an adjacent island in the central Platte River. The apparent absence of *I. plattensis* populations in nearby sloughs with different hydrologic regimes suggests that this species may exist within a narrow range of physical habitats. The few nearby sites where we found this species have intermittent hydrologic regimes very similar to our study site. In addition, *I. plattensis* appeared associated with dense growths of the macrophyte *Ludwigia polycarpa,* which did not occur in other sloughs where *I. plattensis* was absent. This observation suggests either a possible relationship between the 2 species, or that both species are responding to the same hydrologic regime.

Adult emergence during 1997 corresponded with heavy rains and the return of water to the slough, but this occurrence may have been coincidental. We did not collect 1st- instar *I. plattensis* until the mid-November sampling, ~45 d after the end of the adult emergence period. Clifford (1966) and Williams and Williams (1975) reported that *I. punctatissima* eggs could be deposited prior to inundation and still remain viable. Thus, the presence of water during adult flight and oviposition may not be critical.

Although the life history of *I. plattensis* is similar to that of other *Ironoquia* species (Flint 1958, Flint 1960, Williams and Williams 1975), at least 1 important difference is evident. Williams and Williams (1975) reported that in Ontario 1st-instar *I. punctatissima* appeared in early October and underwent a period of rapid growth in the fall (most rapid from October to early November), with some final instars occurring by January. In sharp contrast, during our study *I. plattensis* grew little until late winter (February), and final instars were not evident until May. This difference in growth-rate phenology between the 2 species in different regions may stem from differences in climate. Although our adult *I. plattensis* were emerging by late September and water was already present in the slough, 1st instars were not collected until mid-November. Thus, larvae had not hatched in our slough during the period of highest growth reported for *I. punctatissima* in Ontario, and water temperatures were already quite low by the time 1st instars were present (0.9°C daily average on 19 November when samples were collected, Fig. 1). This observation indicates that the eggs of *I. plattensis* did not hatch, regardless of the presence of water, until temperatures were too low for rapid growth. Delayed egg hatching may be a safeguard in a relatively dry geographic region where inundation may occur late, or false starts may occur before water returns for the duration of the fall to spring period.

Feeding and consumption

Periodic examination of guts from fresh larvae revealed that although larvae appeared to be associated with living macrophytes, in particular dense growths of *L. polycarpa,* they fed on senescent or moribund, rather than living, plant tissue. Thus, like other species of *Ironoquia* (Merritt and Cummins 1996), *I. plattensis* is a CPOM shredder. However, unlike many lotic systems in the eastern USA that other *Ironoquia* species inhabit, where a large portion of CPOM is derived from allochthonous sources, CPOM available to *I. plattensis* in the system we examined is primarily autochthonous material derived from aquatic plants. Our consumption estimate suggests that *I. plattensis* consume a significant portion of the CPOM standing stock in this system, but are not food limited as has been shown for some aquatic detritivores (Richardson 1991). Further, total CPOM standing stock in our site was lowest in summer when wetted surface area was greatly reduced (dry for much of this period), and larvae were not present in the slough. As a result, total CPOM available to larvae when they were in the slough (autumn to spring average = 82,986 g AFDM) was actually higher than the annual average we reported. Consumption of CPOM by leaf-shredding invertebrates, which typically show low assimilation efficiencies and high ingestion rates, creates fine particles that are important to other consumers, such as gathering collectors and filter feeders (Short and Maslin 1977, Anderson and Sedell 1979, Grafius and Anderson 1980, Mulholland et al. 1985). Feeding activities of shredders can also generate dissolved organic carbon (Meyer and O'Hop 1983). *Ironoquia plattensis* feeding activities in this wetland system, in which other shredders are scarce, represent a potentially significant invertebrate-mediated decomposition pathway.

In summary, our study illustrates the unique life history of a recently discovered inhabitant of a poorly studied system. Because of its high abundance and productivity, *I. plattensis* represents a potentially significant resource for terrestrial and aquatic secondary consumers, including large numbers of migratory birds. Further, this trichopteran facilitates decomposition processes and energy flow in a wetland system where few other species of shredders exist. However, because this species appears adapted to a narrow hydrologic regime, and little of the wet-meadow habitat where it is found remains, the distribution of populations may be highly restricted. Only 25% of native lowland grassland habitats in the Platte River valley of Nebraska remain, and these are highly fragmented (Sidle et al. 1989). Hydrologic regimes, which are increasingly altered by regulation of the Platte River for hydroelectric and agricultural purposes, appear to be major factors dictating distribution of this unique species. Future management of the Platte River and its remaining riparian wetlands should take into consideration potential hydrologic influences on biotic diversity and productivity, including effects on species that may be easily overlooked and whose significance may be underestimated.

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