

## LONG-TERM EMERGENCE PATTERNS OF CHIRONOMIDAE (DIPTERA) FROM AN INTERMITTENT STREAM

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### Abstract

In non-perennial aquatic habitats, dry periods influence the aquatic community by filtering organisms based on their ability to survive periods of drying or to recolonize the habitat quickly. Although intermittent streams often support interesting, specialized species, they often support a less species-rich community compared to perennial habitats. I collected Chironomidae from an intermittent, 3rd order stream biweekly for 6 years using surface floating pupal exuviae. The stream regularly dried in the summer every year, but the duration of the dry period varied among years (15-146 days). In total, 158 non-biting midge taxa were identified, but many species (65) were rare and only occurred in 1-2 samples. Most common taxa had regular seasonal emergence patterns, but some taxa had irregular emergence patterns that differed year to year. Following dry periods, Chironomidae resumed emergence within 2-3 weeks after the stream began flowing again and, in some years, sample richness was higher after flow resumed than before. The length of the dry period in the stream did not affect annual taxa richness, but lower annual taxa richness was observed in years with higher accumulated discharge and more frequent summer spates. Comparison of midge communities from this intermittent site to a downstream perennial site found no difference in taxonomic richness. However, the emergence period was shorter and the number of taxa present in individual samples was lower at the intermittent site. The equivalent richness was achieved in the intermittent site through higher temporal  $\beta$  diversity. This pattern may have been the result of higher disturbance in the intermittent site due to spates and drying which could contribute to greater habitat heterogeneity and promote colonization of new taxa. Most taxa at the perennial site were also found in the intermittent site indicating that many midge taxa in these habitats are facultative. Intermittent streams are usually expected to only support a depauperate community of facultative species, but these habitats can support interesting and diverse communities that should be conserved.

### Introduction

Intermittent and ephemeral streams comprise more than half of stream miles in the United States with the proportion of non-perennial aquatic habitats increasing in arid regions (Levick et al. 2008, Fesenmyer et al. 2021). However, society often assigns lower value to intermittent and ephemeral streams, wetlands, and lakes compared to perennial habitats. As a result, non-perennial habitats are afforded less stringent protections from human activities including prevention of water quality degradation or destruction through dredging and filling (Fesenmyer et al. 2021). The importance of these habitats is often minimized because they are thought to provide fewer benefits to humans and wildlife. Non-perennial habitats are often considered to support lower biodiversity and have limited human uses such as fishing and boating. However, they provide many important benefits such as flood mitigation, processing and sequestration of pollutants, habitat for aquatic and terrestrial life, and cultural or aesthetic benefits (Koundouri et al. 2017). Given the large proportion of stream miles that can be classified as non-perennial and the important benefits these waters provide, there is value in protecting these habitats.

Undervaluation of intermittent streams is associated with the most obvious characteristic of these waters – they are dry for part of the year. These dry periods suggest that for part of the year, the habitat does not provide the benefits that would typically be supported by an environment with surface water (e.g., fishing, boating, aesthetics). Drying streams may also be viewed negatively as they may become pooled and a source for organisms that can be harmful to humans (e.g., mosquitoes; Williams 1987). Furthermore, dry periods in intermittent habitats appear to make the habitat unsuitable for aquatic organisms which reduces biodiversity. This assumption is not unreasonable because the drying of an aquatic habitat is a type of disturbance that can have negative impacts on aquatic organisms. Stream discharge can also be more variable in non-perennial streams, and these

habitats may be exposed to both dry periods and disruptive spates. In addition to hydrology, chemical and physical parameters are also more variable in intermittent streams which create additional challenges for organisms in these waters (Williams 1987). Temperature and dissolved oxygen can vary more seasonally and daily than in perennial streams due to smaller water volumes and periods of low flow. The challenges of surviving in intermittent streams creates a filter that eliminates many aquatic organisms not adapted to such conditions (Wiggins et al. 1980). As a result, ephemeral and intermittent streams have been demonstrated to support lower species richness and diversity compared to similar perennial habitats (Williams 1996, Williams 2006, Meyer and Meyer 2000, Rüegg and Robinson 2004). However, species inhabiting non-perennial habitats have a variety of physiological and behavioral attributes that allow survival during dry periods (e.g., drying resistant life stages [eggs, cocoons], movement to hyporheic zones, rapid colonization). As a result, non-perennial habitats can still support a diverse and unique assemblage or aquatic organisms.

The family Chironomidae includes species that are fully aquatic, semiaquatic, and terrestrial. Although most species are considered fully aquatic, there are aquatic species that are facultative and can survive dry periods. Drought-resistance strategies observed in Chironomidae include drought resistant larvae, formation of cocoons, movement to wetted habitats (e.g., hyporheic zone or pools), and rapid recolonization (Blanchart et al. 1987, Frouz et al. 2003, Frouz and Matěna 2015). However, many detailed studies of drought resistance in chironomids have focused on unusual ephemeral habitats (e.g., Hinton 1960, Kitching 1972, McLachlan and Ladle 2001). As a result, the specific mechanisms used by most chironomid species in ephemeral and intermittent streams are not as well studied or known (Frouz et al. 2003). Generally, chironomids in intermittent streams likely use a variety of strategies observed in other aquatic invertebrates and in chironomids in other habitats. Studies documenting the chironomid diversity from temporary streams have reported both lower (Boulton and Suter 1986, Rüegg and Robinson 2004) or equivalent (Feminella 1996, Casas and Langton 2008) taxa richness in temporary streams compared to perennial streams. In some cases, the richness of chironomids exceeded 100 taxa in intermittent streams (e.g., Casas and Langton (2008)). Given the high diversity in this family and the range of strategies for surviving dry conditions observed in the Chironomidae, this family is an important component of intermittent habitats

(e.g., Williams 1996, Rüegg and Robinson 2004).

The objective of this study was to document the diversity and emergence patterns of chironomids from an intermittent stream over multiple years. Long-term studies of aquatic insects are limited due to the effort required, but they may provide additional insight into how environmental factors, particularly antecedent conditions, influence the diversity of aquatic communities and the phenology of species. I studied the emergence of chironomids over six years from an intermittent stream site to document the diversity of midges in an intermittent habitat and to determine if there are species that are dependent on these habitats. In addition, by sampling this stream for six years, the annual variability in hydrology can be documented and linked to attributes of the chironomid community (e.g.,  $\alpha$  and  $\beta$  diversity, phenology). In this study, I also compared Chironomidae emergence from the intermittent stream reach to a perennial reach on the same stream. Overall, the objective is to characterize chironomid communities in intermittent streams and to describe how changes in hydrology affect this biological assemblage. This information is important to develop strategies to conserve these habitats as they face risks from anthropogenic alteration, water pollution, and climate change.

## Materials and Methods

### *Site descriptions*

The main study site was located on the Credit River, a 3<sup>rd</sup> order stream with a 60 km<sup>2</sup> drainage area (Figure 1a; Table 1). The watershed is dominated by forest, row crop, and open field, but the stream at the sample site is located within or borders a regional park and is protected. The riparian zone at the sample site and approximately 2 km upstream from the sample site is forested. As a result, the site was largely shaded, and extensive leaf matter was present in the stream after leaf abscission. Although the stream was well shaded, periphyton, filamentous algae, and mosses were present and sometimes in high abundance. When flow was present, the stream width was on average 6.1 m wide. The proportion of different substrate types was visually estimated during sampling and was comprised of 16% boulder, 30% cobble, 24% gravel, 20% sand, and 11% silt. During periods when the stream was flowing, the sample reach consisted of 55% run, 35% riffle, and 10% pool. During three sampling visits, no flow was detected and only pool habitats were present.

Intermittent streams are defined as channels that do not flow during certain times of the year, but during the rest of the year have sustained flows



Figure 1. Credit River sampling sites on May 19, 2004: a) intermittent site and b) perennial site.

Table 1. Description of study sites.

Stream name	Hydrology	County	Coordinates (WGS 84)	Elevation (m)	SampleYear(s)
Credit River	Intermittent	Scott	44.7086°, -93.3506	280	2003-2008
Credit River	Perennial	Scott	44.7608°, -93.3424°	240	2004

(USEPA and USACE 2020). This contrasts with ephemeral streams which may only flow in response to precipitation events. The intermittent stream studied here meets this definition as it did not only flow in response to rainfall but rather it flowed during much of the year and regularly dried in the late summer or fall (Figure S1). The length of the period the stream was dry varied from year to year and ranged from 15-146 d. This stream is surface-water fed and receives most of its water from surface runoff and shallow subsurface flow and not thermally, buffered groundwater. As a result, the stream was completely frozen during the winter although during warm periods some winters, the stream was open or there were small openings in the ice cover. For example, the winter of 2005/2006 was warmer than other years and the stream was only frozen for the first part of the winter (December-January). Typically, this reach of the Credit River was frozen during the entire winter. It thawed in March and flowed continuously until it dried in July or August. The stream remained dry until it rewetted in September (often following fall leaf abscission) except for fall 2003 when it did not flow again until the following March. Although there was normally only one dry period, in 2008 the summer and fall was drier than usual and there were multiple drying events in the fall. After the stream began flowing again in the fall, it became partially or wholly ice covered in December.

A perennial site on the Credit River was also sampled for comparison with the intermittent site (Figure 1b; Table 1). The perennial site was approximately 14 km downstream of the intermittent

site and was also a 3<sup>rd</sup> order stream although the drainage area was twice as large as the upstream site (120 km<sup>2</sup>). The watershed was dominated by developed land, open field, forest, and row crop. Although surrounded by a developed watershed, the stream near the sample site had a largely forested riparian zone. The stream was on average 4.8 m wide. Substrates were visually estimated during sampling and were comprised of 4% boulder, 26% cobble, 28% gravel, 23% sand, and 19% silt. The sample reach consisted of 30% run, 27% riffle, and 44% pool. The downstream site on the Credit River was similar to the upstream site in many regards, but differed in one important attribute for this study, the downstream site was perennial. Discharge differed between the two stream sites in 2004, although the stream widths were similar. Discharge during sample events averaged 0.18 (0.00-1.23) m<sup>3</sup>/s at the intermittent site and 0.42 (0.06-3.27) m<sup>3</sup>/s at the perennial site. There were some other differences between these stream sites that could have affected aquatic life. This downstream reach likely receives more groundwater and is warmer in the winter than the upstream reach. As a result, parts of the perennial stream reach remained open most of the winter and some emergence of midges were observed throughout the winter when air temperatures were suitable. The composition of substrates also differed slightly, and water quality may also differ but both sites are affected by anthropogenic impacts including increased nutrient loading and elevated chloride (MPCA 2018). Although these differences were present between the two sites, it was assumed that hydrological differences would be the most impor-

tant difference affecting the Chironomidae communities between sites.

*Stream discharge measurement and modelling*

Stream discharge for the intermittent site on the Credit River was measured or modeled using several methods. Discharge was directly measured during 13 sampling visits using a Marsh-McBirney Flo-Mate 2000. To determine stream discharge, water velocity was measured 4/10 from the bottom of the stream at a minimum of eight locations along a cross-section transect in a stream run. Discharge was calculated by multiplying the water velocity for each interval by the interval area (i.e., depth multiplied by the interval width) and summing these values. For 67 visits, the stream cross-section area was measured, and stage height was measured during 21 visits. Flow was not measured when ice cover or extensive edge ice was present or when the stream was pooled or dry. In addition, on four visits no stream discharge information was collected. To estimate stream discharge for all sample events when discharge was not directly measured at the intermittent site on the Credit River, several models were developed including: 1) cross section area to stream discharge, 2) stage to cross section area, and 3) Credit River stream discharge from a nearby, continuously-gaged stream site (Vermillion River). A linear model was initially considered for the cross-section area to stream discharge model, but it was apparent that despite a high  $R^2$ , the relationship was nonlinear. The best fit was determined to be a combination of models (Figure 2a). At cross-section areas below 1 m<sup>2</sup>, a second-order, polynomial model was used (Dis-

charge = 0.2138 • Cross Section Area<sup>2</sup> - 0.0152 • Cross Section Area - 0.0001,  $R^2 = 0.97$ ) and above a cross-section area of 1 m<sup>2</sup>, a logarithmic model was used (Discharge = 1.0642 • ln(Cross Section Area) + 0.1961;  $R^2 = 0.99$ ). This approach approximated the results of a generalized additive model but permitted extrapolation for visits when the cross-section area was >2 m<sup>2</sup>. A least-squares regression was fitted to estimate stream cross-section area from stage height (Cross Section Area = 6.0268 • Stage + 0.6183;  $R^2 = 0.99$ ; Figure 2b). To estimate daily discharge at the Credit River site, stream discharge data was obtained from a nearby stream site with continuous discharge measurements during the sampling period (2003-2008). A United States Geological Survey (USGS) station on the Vermillion River (near Empire, MN; station number: 05345000) was selected as this was the closest station (24 km) with continuous data and on a similarly sized stream. A segmented regression model (Figure 3) was used to estimate stream discharge at the Credit River site using the Vermillion River gage data (< 4.836 °C: Credit Discharge = 0.0142 • Vermillion Discharge - 0.0237; > 4.836 °C: Credit Discharge = 0.1121 • Vermillion Discharge - 0.4974;  $R^2 = 0.82$ ). Using the Vermillion River model, stream discharge at the intermittent Credit River site could be estimated for days when the site was not visited or not measured. Stream discharge was not estimated for days the stream was frozen. Polynomial and logarithmic models were fitted using the “lm” function (R Core Team 2025). Segmented regression was performed using the “segmented” function in the segmented package (Muggeo 2008).

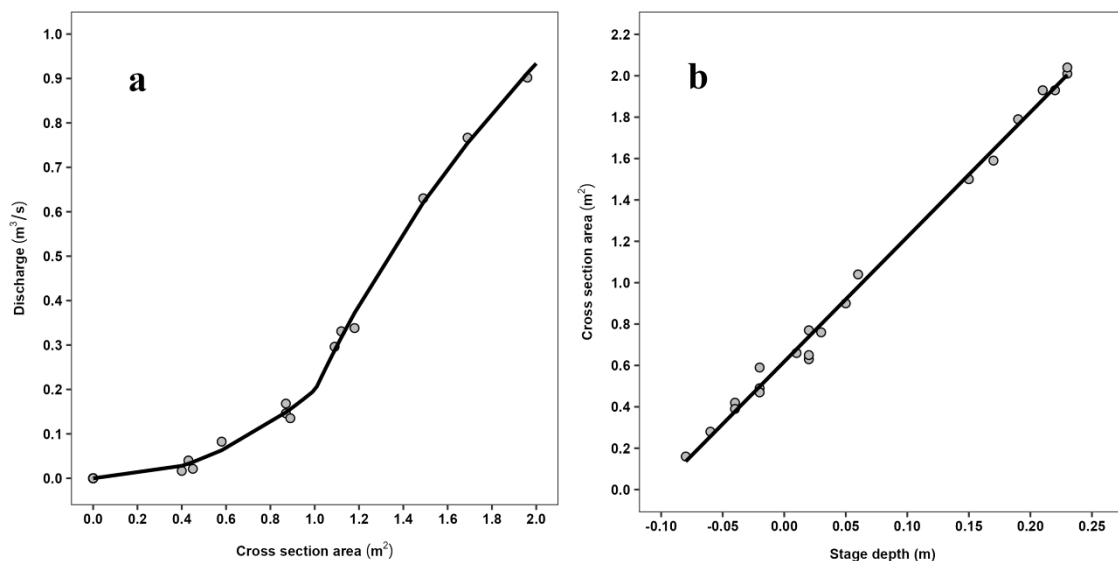


Figure 2. Models used to estimate discharge at the intermittent sites on the Credit River using a) cross section to model discharge ( $R^2 = 0.97-0.99$ ,  $n = 54$ ) and b) stage to model cross section area ( $R^2 = 0.99$ ,  $n = 21$ ).

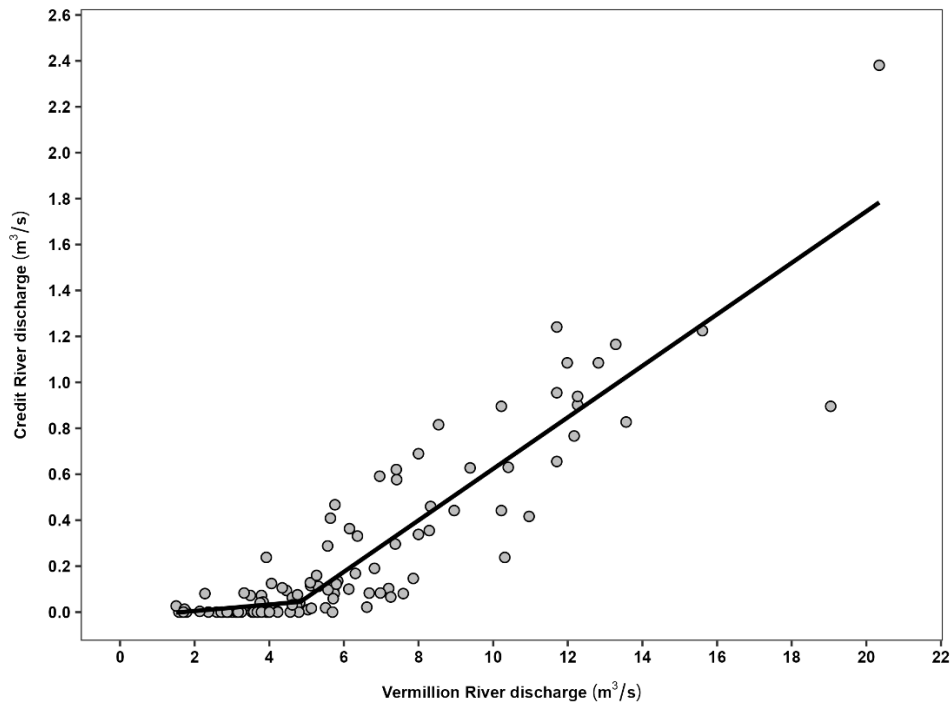


Figure 3. Model used to estimate flow at the intermittent site on the Credit River using stream gage data from a site on the Vermillion River ( $R^2 = 0.82$ ,  $n = 109$ ).

#### *Water temperature measurement and modelling*

Onset HOBO TidbiT temperature loggers were deployed in both Credit River sites. In the intermittent Credit River site, a temperature logger was deployed from March 27, 2003 through September 8, 2004. A temperature logger was deployed in the perennial site from January 9, 2024 through September 8, 2004. Water temperature was measured every 15 minutes during deployment. Using the 15-minute interval readings mean daily temperatures were determined by averaging temperature readings during each 24-hour period. In the intermittent site, there were periods when the temperature logger recorded air temperature, and these measurements were removed from the dataset.

To estimate water temperatures in both stream sites when water temperature was not directly measured, models were developed to estimate water temperature using air temperature data from a station at the Minneapolis Flying Cloud Airport (Midwestern Regional Climate Center 2024). This station was 11 km (perennial site) and 15 km (intermittent site) from the sampling stations. A least squares regression was used to fit the relationship between the three-day average of air temperature and water temperature (Water Temperature =  $1.0455 \cdot 3\text{-Day Average Air Temperature} - 0.54869$ ;  $R^2 = 0.92$ ; Figure 4a). When this model predicted negative mean water temperatures, these values were replaced with  $0\text{ }^\circ\text{C}$  as it was assumed

that water temperatures would not be much below  $0\text{ }^\circ\text{C}$ . A simple linear regression was used for the intermittent site because there were few recordings at low air temperatures due to the lack of flow during the winter of 2003. However, this was not the case for the perennial site and a segmented regression was used to fit the broken-stick relationship. Linear models were fitted using the “lm” function (R Core Team 2025). Segmented regression was performed using the “segmented” function in the segmented package (Muggeo 2008). The breakpoint was determined to be at a three-day average of air temperature of  $-2.189\text{ }^\circ\text{C}$  and different linear regressions were fitted to the data on either side of this breakpoint ( $< -2.189\text{ }^\circ\text{C}$ : Water Temperature =  $0.0063 \cdot 3\text{-Day Average Air Temperature} + 0.4007$ ;  $> -2.189\text{ }^\circ\text{C}$ : Water Temperature =  $0.8198 \cdot 3\text{-Day Average Air Temperature} + 2.1819$ ;  $R^2 = 0.95$ ; Figure 4b).

#### *Collection and processing of surface-floating pupal exuviae samples*

Chironomids are often the most taxonomically rich group in many aquatic habitats (Coffman 1973) and this high richness, along with challenges with identifying chironomid larvae, make the study of whole midge communities in detail difficult. Sampling of surface floating pupal exuviae (SFPE) is more effective relative to common methods of collecting larval chironomids from benthic sediments because it is easier to collect taxa from a

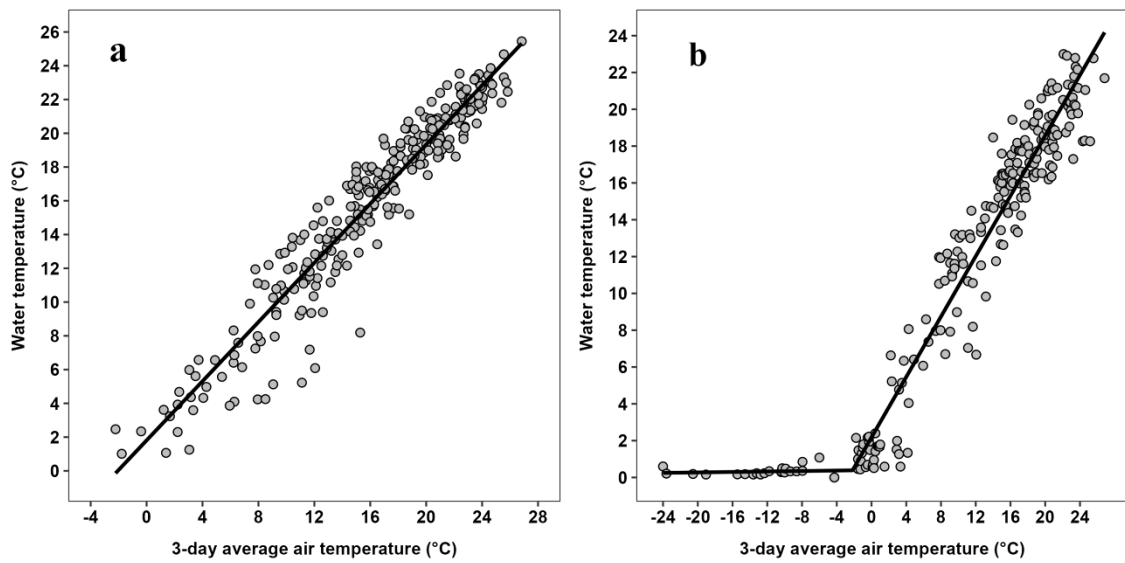


Figure 4. Regression of 3-day mean daily air temperature measures from Minneapolis Flying Cloud Airport and mean daily water temperatures from a) intermittent and b) perennial Credit River sites.



Figure 5. a) Sampling surface floating pupal exuviae from vegetation and b) accumulation of pupal exuviae behind woody debris.

wide range of habitats, including those difficult to sample with a kick net (e.g., wood, hyporheos, deep water; Wilson 1994, Raunio et al., 2007, Ruse 2010, Kranzfelder et al., 2015). This method permits determination of timing of emergence and can largely produce species-level data. Chironomidae SFPE samples were collected bi-weekly following the methods of Ferrington et al. (1991) and Kranzfelder et al. (2015). The intermittent site was visited 154 times and the perennial site 26 times. If the stream was dry or completely frozen, no sample was collected. Samples consisted of a timed 10-minute sampling period within an approximately 100 m sample reach. Working upstream, SFPE were sampled by scooping exuviae into a pan from areas where they collect (e.g., snags, in vegetation, eddies) and pouring this material

through a 125- $\mu$ m sieve (i.e., standard testing sieve no. 120) (Figure 5). Samples were transferred to 118-ml jars and preserved with 75% ethanol.

In the laboratory, samples were sieved and rinsed in a 125- $\mu$ m sieve to remove the preservative. A small portion of the sample was placed in a picking tray, and under a dissecting microscope, SFPE were picked from the sample into 3.7-ml vials with 75% ethanol. After a complete pass of the sample tray, the sample was swirled and scanned again. This was repeated until two successive passes did not recover any additional SFPE. Picking of specimens was halted when the entire sample was picked or the total number reached 300 specimens (Bouchard and Ferrington 2011). Specimens that were broken, covered in extensive fungal hyphae, or dried and compressed were not picked or

counted to avoid identification problems or uncertainty regarding the age of the SFPE. Whole pupae or SFPE with adults still attached were also not counted; however, this material was picked from the sample to aid with identification of SFPE. Before slide mounting, specimens were divided into morphotaxa under a dissecting microscope. Exuviae were dehydrated in 95% ethanol, dissected, and slide mounted in Euparal as described by Ferrington and Berg (2019). In cases where a particular morphotype was abundant (>40 specimens), only 25% of these specimens were slide mounted and identified. The identity of the remaining unmounted specimens was estimated based on the proportions of each taxon in the slide mounted material. Identifications were made under a compound microscope at 100-400X. Genus-level and some species group identifications were made using Ferrington and Berg (2019) and Wiederholm (1986). Species-level identifications and species-group identifications were based on numerous additional sources. Morphospecies that did not match known pupae were assigned morphospecies codes. Morphospecies with “RWB” are part of the author’s taxon numbering system for North American pupal exuviae and morphospecies with “NA” are from Langton (2023).

### *Analyses*

All statistical analyses and plots were generated using R 4.4.2 (R Core Team, 2024). Species richness estimates for the cumulative dataset and for each sampling year were calculated using the nonparametric Chao1 estimator from the “wqid” package (Meredith 2022). The relationship between annual accumulated discharge and temperature (water and air) on annual taxa richness was assessed using generalized additive models. Accumulated degree days for air and water temperature was calculated by summing the mean daily temperature above a reference temperature of 10 °C. Accumulated annual discharge was determined by estimating the total discharge (cubic hectometers) per year. Generalized additive models were fitted using the “gam” function in the “mgcv” package (Wood 2017).

Taxa richness and taxon specific patterns were visually assessed against temperature, stream discharge, and seasonal timing to identify emergence patterns that may be related to exogenous cues (e.g., temperature and discharge). Emergence patterns were categorized based on the timing of emergence peaks. Emergence pattern categories included: winter, winter/spring, spring, spring/summer, spring/fall, summer, summer/fall, fall, continuous,

and irregular. Continuous emerging taxa were present through much of the spring, summer, and fall. Taxa with irregular emergence patterns emerged during different seasons year to year. Some of these taxa with irregular emergence patterns may have had relatively synchronous emergence peaks, but the timing varied among years. Some taxa had low total abundance and there is lower confidence in the assigned emergence patterns for these taxa.

To analyze how the community changed as a function of time between samples (i.e., taxonomic turnover), dissimilarity between sample pairs was calculated using Bray-Curtis dissimilarity coefficients for 2004 samples for both the intermittent and perennial sites. Calculation of dissimilarity was limited to sample pairs during the period of observed emergence from the intermittent site (April 7 through November 17). The winter, early spring, and late fall samples were eliminated to compare sample dissimilarities for the same time period from both sites. Time between samples was used as a variable so it was important that the time frame was consistent between the two sites. Bray-Curtis dissimilarity coefficients were calculated using “vegdist” function in the “vegan” package (Oksanen et al., 2020). The average dissimilarity values were graphed as a function of the number of weeks between each sample pair.

## **Results**

### *Discharge and temperature patterns*

Discharge and water temperature followed largely predictable patterns across the 6 years of sampling from the intermittent site (Figure 6). The thermal regime in the intermittent site followed a regular seasonal pattern with mean daily water temperatures in the winter near 0 °C and summer maximum temperatures usually >20 °C (Figure 6). Discharge was not as predictable as water temperature, but in general discharge was higher in the spring and lower in late summer and fall (Figure 6). Every year a series of spates were observed, but their timing varied among years. There were always a series of spates during the spring and summer, however, in some years, e.g., 2004 and 2005, there were also late summer/fall spates. The number of days the stream flowed each year varied from 219 to 350 days (Table 2). The length of individual dry periods also varied between years and lasted from 2 weeks (2005) to 7 months (2003/2004); however, in most years, the dry period lasted 4 to 6 weeks (2004, 2006, 2007, 2008). The intermittent site regularly dried in July or August and in most years rewetted in August or September. In two years (2003, 2008), the late summer or fall

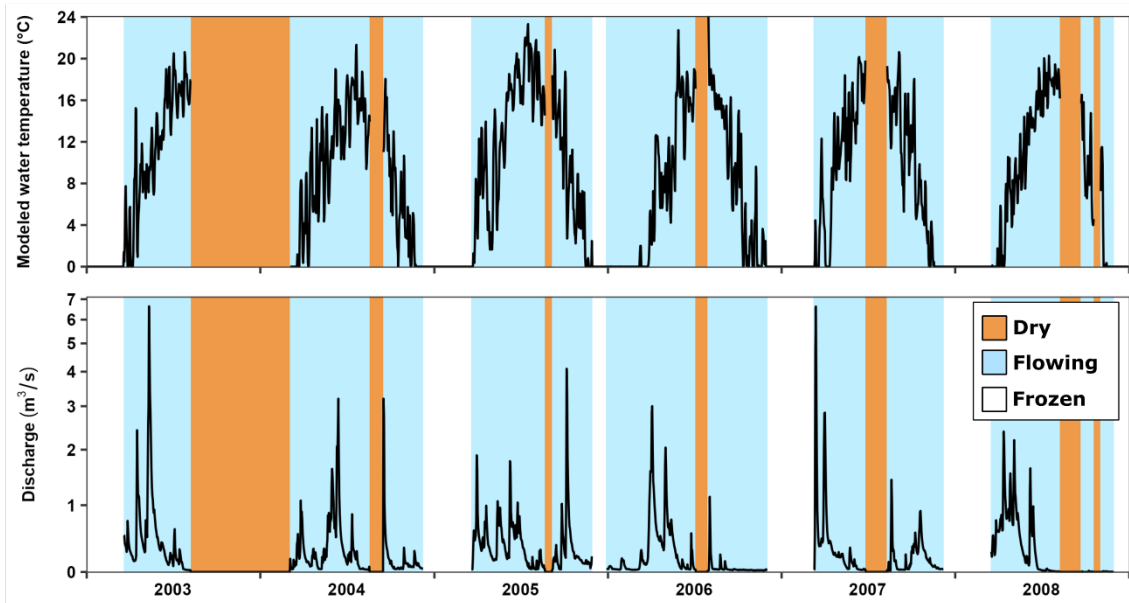


Figure 6. Long-term (2003-2008) estimated temperature (top) and discharge (bottom) for the intermittent Credit River site.

Table 2. Annual taxa richness patterns from the intermittent site on the Credit River.

Year	Days with flow	Total taxa	% Cumulative site richness	New taxa	Cumulative taxa	Unique taxa
2003	219	67	42%	67	67	5
2004	273	90	57%	38	105	5
2005	350	61	39%	6	111	3
2006	340	103	65%	22	133	14
2007	320	91	58%	19	152	17
2008	307	87	55%	7	158	7

was drier than normal. In 2003, the stream did not rewet until the next spring and in 2008, there were multiple dry periods with discharge remaining low when flow resumed.

#### *Intermittent stream emergence patterns*

The intermittent site on the Credit River was visited 154 times and a SFPE sample was collected on 99 of these visits. Samples were not collected during 55 visits because the stream was dry (27 visits) or frozen (28 visits). In 14 of the SFPE samples collected, no exuviae were present. The remaining 85 samples produced at least one specimen. Over 6 years of sampling, a total of 14,560 specimens were picked and identified, which included 158 species and morphotaxa. The number of taxa collected each year ranged from 61 to 103 taxa (Table 2). On average, 83 (15 std. dev.) taxa or approximately half of the cumulative 6-year total, was collected each year. New taxa were collected each sample year indicating that not all taxa at this site were detected over the 6 years of sampling (Table 2; Figure 7). The Chao1 richness estimator, projected that 199 taxa (175-256) were present at

the intermittent site during the 6-year sample period and therefore (Table 3), 41 taxa were missed by this sampling effort. The plurality of taxa (32%) were only collected in a single year, but 19% of taxa were collected in all six years (Table S1).

Taxa richness per sample followed a regular seasonal pattern with higher taxa richness in samples from late spring to early fall and lower richness in the early spring and late fall (Figure 8). Although richness was low in the spring, emergence was detected immediately or shortly after the stream thawed or began flowing again in the spring. The timing of the highest richness observed differed between years, and occurred in late spring, summer, or early fall (May, June, July, August, or September; Figure 8). For example, peak emergence richness was detected in May in 2005, but in 2006 the greatest richness was in August. In most years, the peak in richness of emerging chironomids occurred before the stream dried in July or August (Figure 8). However, in some years higher (2006) or equal (2007) richness was observed in the late summer or fall after the stream began to flow again

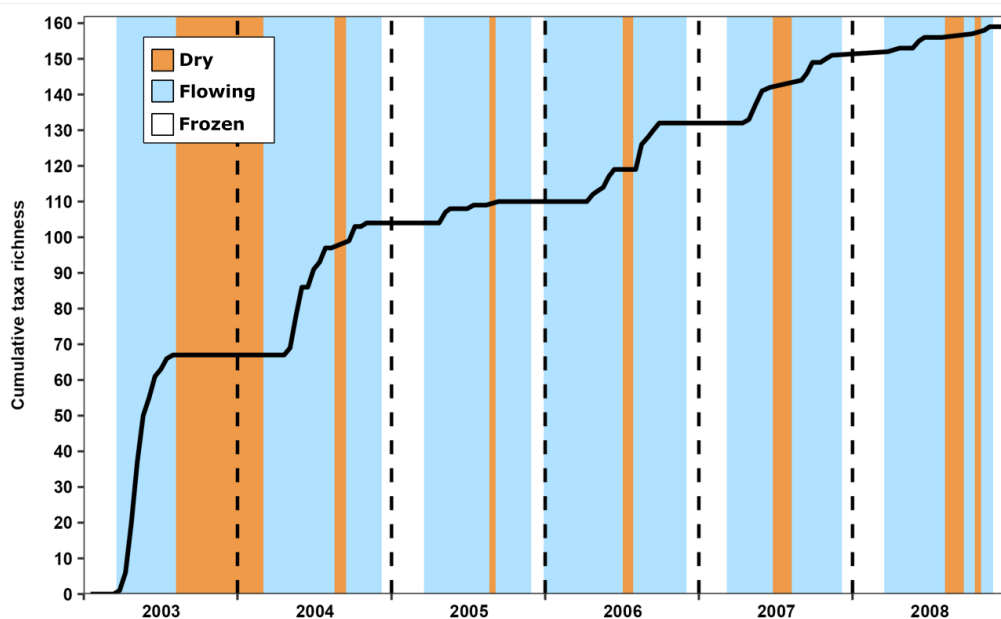


Figure 7. Taxa accumulation curve as a function of time for samples collected from the intermittent site on the Credit River.

Table 3. Total number of taxa collected each year with species richness estimates and 95% confidence intervals.

Year	Number of taxa	Chao estimate	Lower estimate	Upper estimate
2003	67	92	74	160
2004	90	119	101	169
2005	61	75	65	108
2006	103	175	131	287
2007	91	121	103	172
2008	87	126	101	195
All	158	199	175	256

following the dry period. After the stream resumed flowing in August or September, Chironomidae emergence quickly resumed and in most years, emergence was detected in the first sample collected after flow resumed (Figure 8). Emergence halted at or shortly before the stream became ice covered in December.

Total annual taxa richness was assessed against accumulated annual discharge, water temperature, and air temperature. Although 6 years of biweekly monitoring data is a relatively large dataset, when aggregated to annual totals, it results in only 6 data points and limited conclusions can be drawn from these results. However, there are possibly some patterns that can be observed with these data. The year with the lowest accumulated stream discharge (2006) had the highest taxa richness and the year with the highest accumulated stream discharge (2005) had the lowest taxa richness. Taxa richness declined with increasing annual discharge (adjusted  $R^2 = 0.60$ ) although this pattern was largely driven by 2 years (2003, 2005; Figure 9a). Exami-

nation of discharge patterns over time in relation to sample taxa richness indicated a possible effect of spates on taxa richness. Sample taxa richness often declined following a spate ( $> 2\text{m}^3/\text{s}$ ) although this pattern was not observed following every spate (Figure 10). There was a unimodal taxa richness pattern along a gradient of increasing annual water temperature (adjusted  $R^2 = 0.84$ ), although much of this pattern was due to a single year (2005). Finally, there was a weak, negative relationship between annual taxa richness and accumulated air temperature (adjusted  $R^2 = 0.06$ ). Both accumulated temperature and stream discharge were highest in 2005, the year with the fewest taxa collected.

Different emergence patterns could be documented in the more abundant species which broadly included seasonal, continuous, and irregular emergence patterns (Table S1). Most taxa had distinct seasonal peaks that were generally consistent in terms of timing from year to year as would be expected in a temperate stream. The most common taxon in the study, *Hydrobaenus* RWB pe1, had a very large

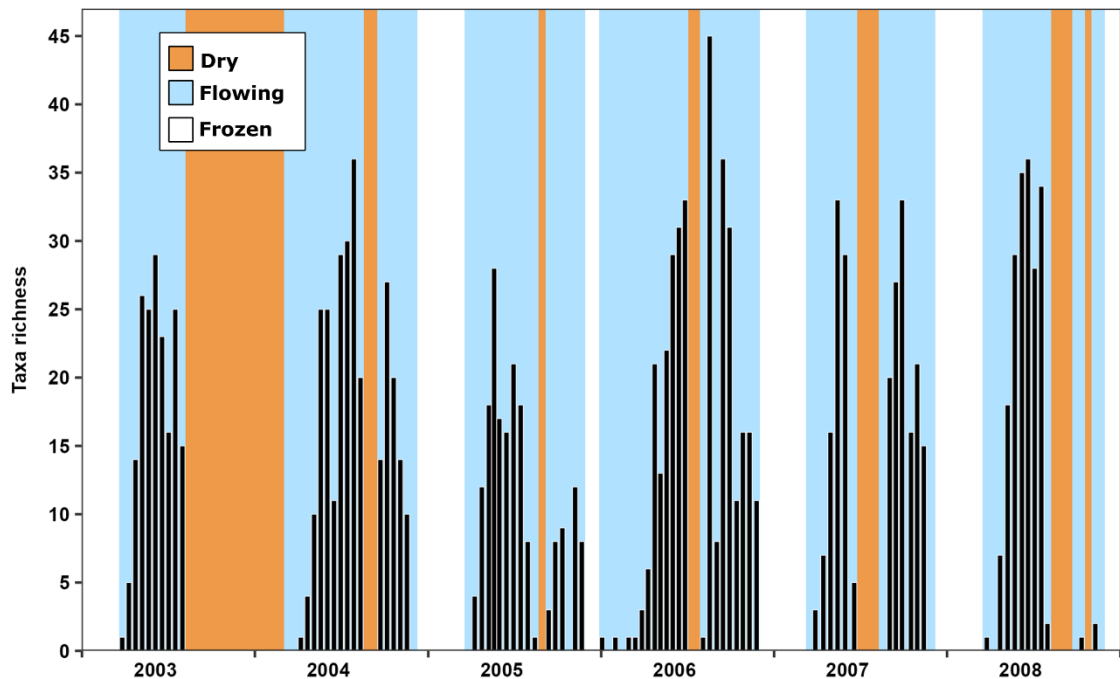


Figure 8. Taxa richness for individual samples from the intermittent site on the Credit River.

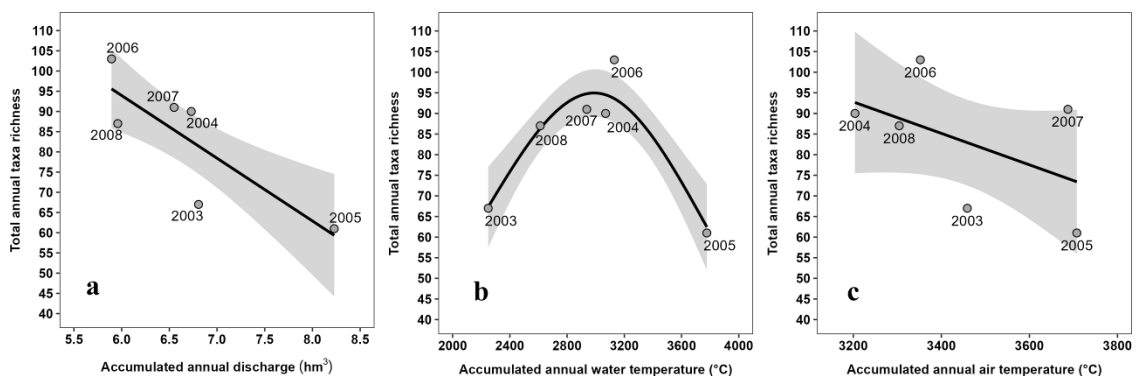


Figure 9. Total annual taxa richness as a function of accumulated a) annual discharge (modeled), b) water temperature (modeled), and c) air temperature (Minneapolis Flying Cloud Airport station).

and distinct emergence in the spring (Figure 11a). Other species that had a distinct spring emergence period included *Chaetocladius* RWB pe5, *Orthocladius* (*O.*) *clarkei*, and *Polypedilum* RWB pe8 (Table S1). Some species had two distinct emergence peaks during the spring and fall (Figure 11b; e.g., *Orthocladius* (*O.*) *obumbratus*, *Orthocladius* (*O.*) *mallochii*). Several species were restricted to summer emergence (Figure 11c; *Polypedilum* (*U.*) *obtusum*, *Microtendipes* RWB pe1, *Tanytarsus* RWB pe10, *Orthocladius* (*O.*) *carlatus*, and *Corynoneura* RWB pe3). Interestingly, several of these summer emerging taxa were absent or had low abundance in 2005 (*P. (U.) obtusum* (absent), *Microtendipes* RWB pe1 (absent), *Tanytarsus* RWB pe10 (low abundance)). Many of the most common taxa were categorized as having continuous emergence patterns as they were present dur-

ing much of the open water season (Figure 11d; e.g., *Thienemanniella* RWB pe1, *Orthocladius* (*O.*) *oliveri*, *Hydrobaenus pillipes*, *Corynoneura* RWB pe1, *Parametriocnemus* RWB pe1, *Cricotopus* (*C.*) *bicinctus*, *Eukiefferiella* RWB pe2, *Tvetenia* RWB pe1, *Micropsectra nigripila*, *Paratanytarsus inopertus* gr. RWB pe1, *Parametriocnemus* RWB pe4). Many taxa had inconsistent emergence timing year to year (i.e., irregular) which was only detectable due to the long-term sampling effort (Figure 11e; e.g., *Tanytarsus lobiger*, *Orthocladius* (*Euorthocladius*) *abiskoensis*). Some taxa did appear to have patterns that suggested extirpation or colonization patterns. For example, *Rheotanytarsus exiguus* and *Polypedilum* (*Tripodura*) RWB. pe2 were present in high number in 2003, absent or largely absent from 2004–2006, and reappeared in 2007 and 2008. *Paratanytarsus inopertus* gr.

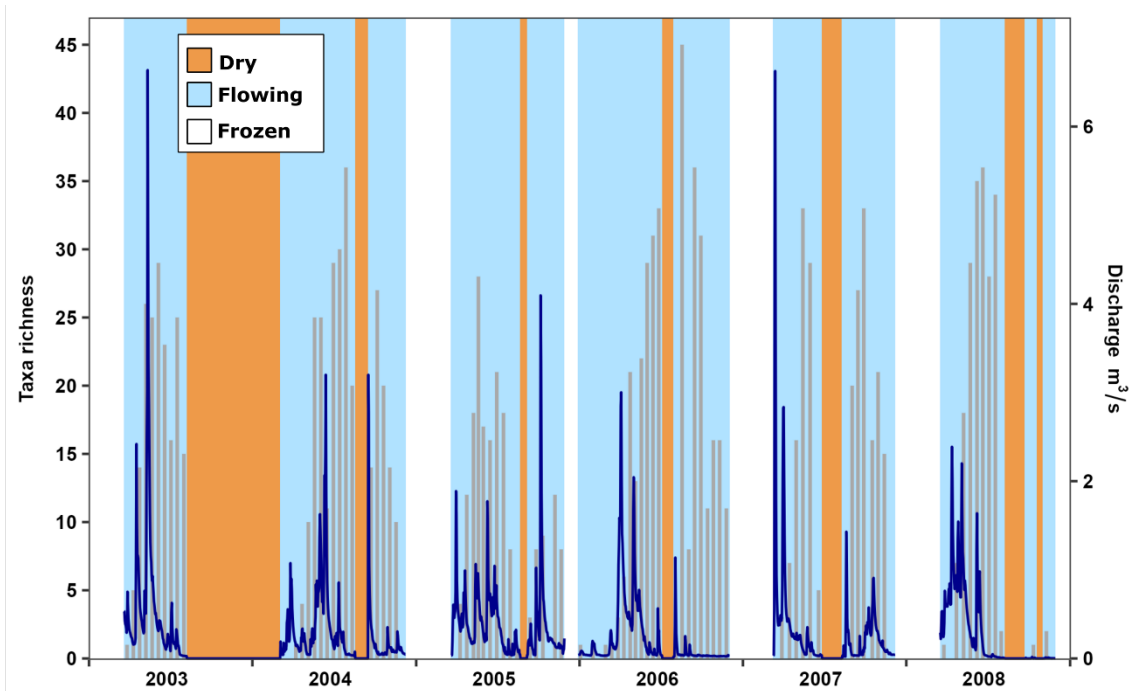


Figure 10. Sample taxa richness and modeled discharge (dark blue line) from the intermittent site on the Credit River.

RWB. pe3 was absent in 2003 but had a steady increase in abundance from 2004 to 2008. The specific drivers for these patterns in presence and abundance on an annual basis were not obvious.

#### *Comparison with a perennial stream site*

Seasonal trends in water temperature were similar between the intermittent and perennial sites on the Credit River, but water temperatures were more variable in the perennial site (Figure 12). The number of sample events from which SFPE were collected differed between the two sites (Figure 12). Fifteen samples from the intermittent site contained SFPE in 2004 compared to 23 samples with SFPE in the perennial site. The smaller number of sample events which produced SFPE in the intermittent site was due to greater ice cover during winter and the drying of the stream in late summer/early fall. The number of taxa present in samples differed between the two stream sites. At the perennial site, taxa richness of individual samples equaled or exceeded 25 taxa in 12 samples but at the intermittent site only 6 samples had at least 25 taxa (Figure 12). The average number of taxa per sample was 21 in the perennial site and 18 in the intermittent site. Despite these differences, total annual richness was identical at these sites in 2004 (90 taxa). The composition and pattern of Chironomidae subfamilies were similar between the two sites with Orthoclaadiinae taxa richness dominating most samples followed by Chironominae. Orthoclaadiinae was a large component of most

samples throughout the year whereas Chironominae were only a high proportion of taxa richness during the spring, summer, and early fall. Tanypodinae, Diamesinae, and Prodiamesinae were a low proportion of the taxa with Tanypodinae occurring in spring and summer, Diamesinae largely limited to winter, early spring, and late fall, and Prodiamesinae collected sporadically throughout the year (Figure 12).

A total of 124 taxa were collected from both sites on the Credit River in 2004. Fifty-six (45.2%) of the taxa collected were shared between the two sites. A total of 68 taxa were only found at one site or the other with 34 (27.4%) taxa were unique to each site. When all 6 years of sampling from the intermittent site is included, 21 additional taxa that were collected from the perennial site were recorded from the intermittent site (13 taxa still not observed). Several of the taxa which were unique to the intermittent site are taxa associated with intermittent habitats including *Hydrobaenus* RWB pe1, *O. (Eu.) abiskoensis*, *Paraphaenocladus nasthecus*, and *Allocladius* sp. *Hydrobaenus* RWB pe1 was the most common species collected at the intermittent site, but it was completely absent from the perennial site. The most abundant taxon at the perennial site was *Parakiefferiella* RWB pe3 but this taxon was also present in moderate numbers in the intermittent site.

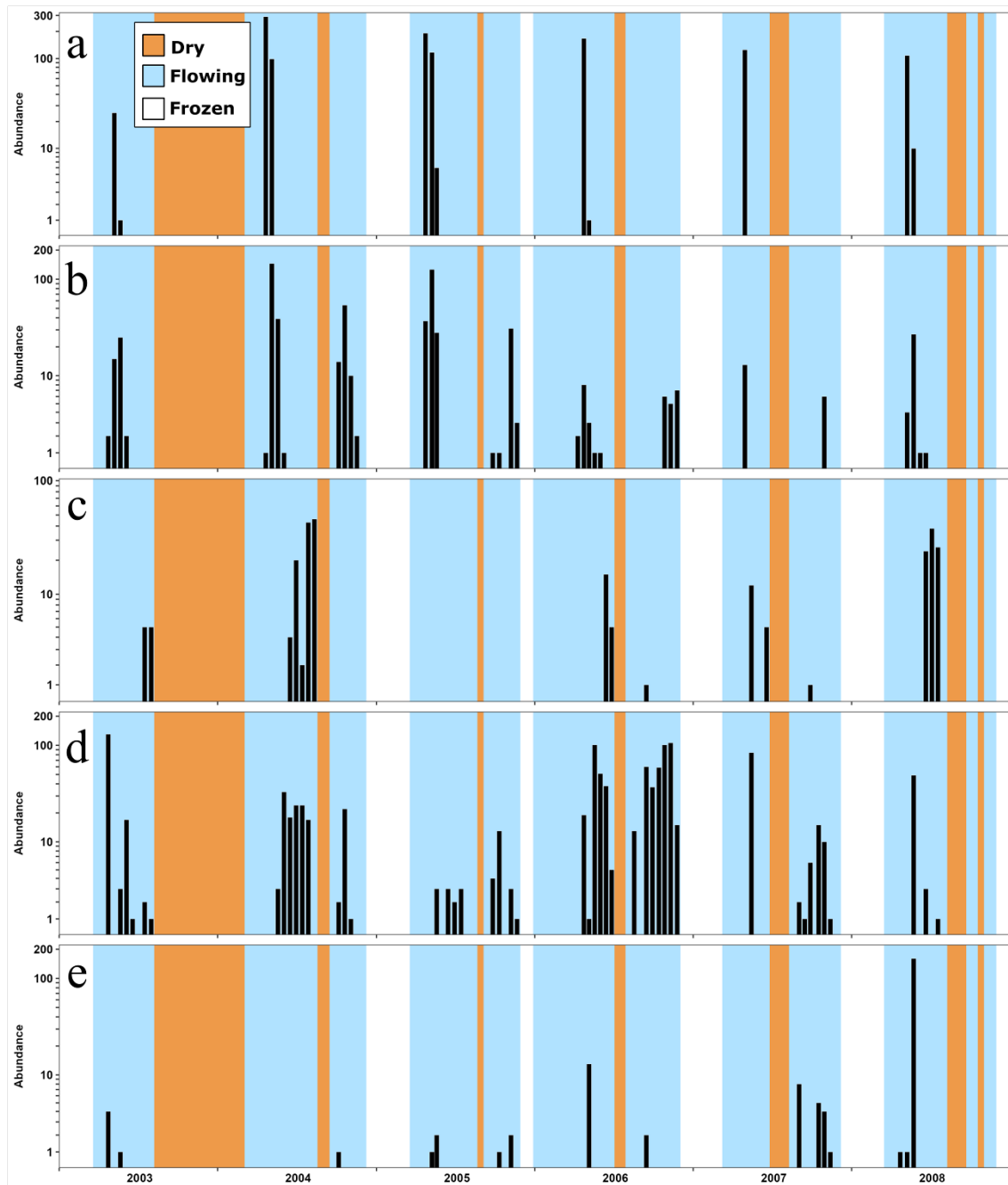


Figure 11. Relative abundance per sample during the six-year sampling period for example species: a. *Hydrobaenus* RWB pe1 (spring), d. *Orthocladius* (*O.*) *obumbratus* (spring/fall), c. *Microtendipes* RWB pe1 (summer), d. *Thienemanniella* RWB pe1 (continuous), and e. *Orthocladius* (*Euorthocladius*) *abiskoensis* (irregular).

Dissimilarity in taxa composition between sample dates was higher overall at the intermittent site (Figure 13). At the intermittent site, dissimilarity between samples was on average very high (0.88) and exceeded 0.90 when paired samples were separated by 8-18 weeks. Average dissimilarity for the perennial site was also high (0.72) with a largely consistent increase in dissimilarity as the time interval between samples increased. Both the intermittent and perennial sites had a drop in

dissimilarity when paired samples were collected between 20 and 28 weeks apart. This decline was smaller and occurred at a higher temporal separation of samples in the perennial site. This decline in dissimilarity corresponded to a comparison of spring and fall samples indicating that these samples were more similar to each other than less temporally separated summer samples.

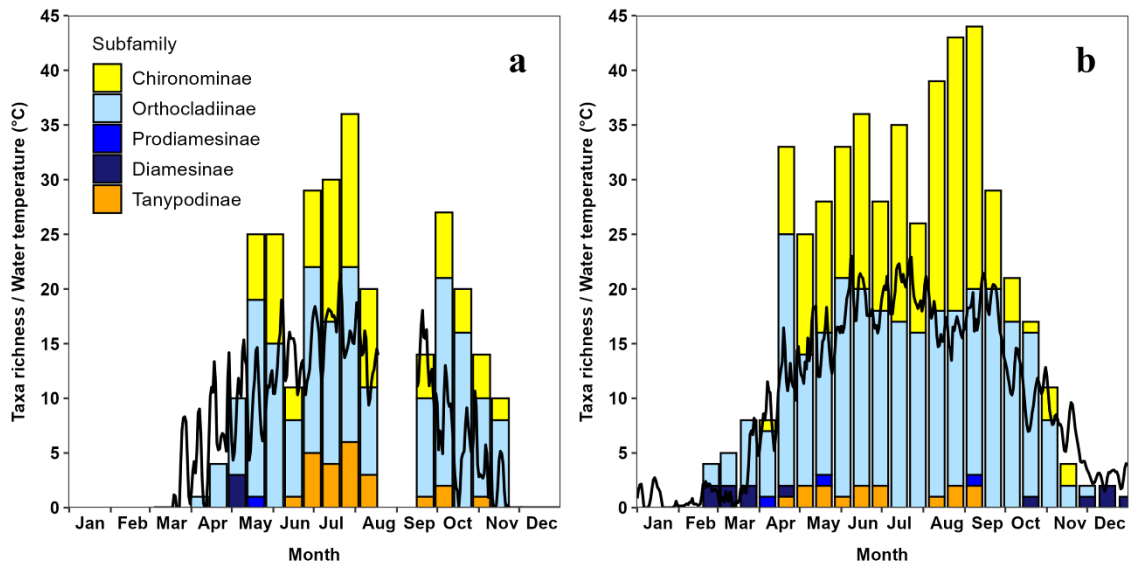


Figure 12. Subfamily taxa richness for each surface-floating pupal exuviae sample collected from a) intermittent and b) perennial sites on the Credit River. The black lines are daily mean water temperatures.

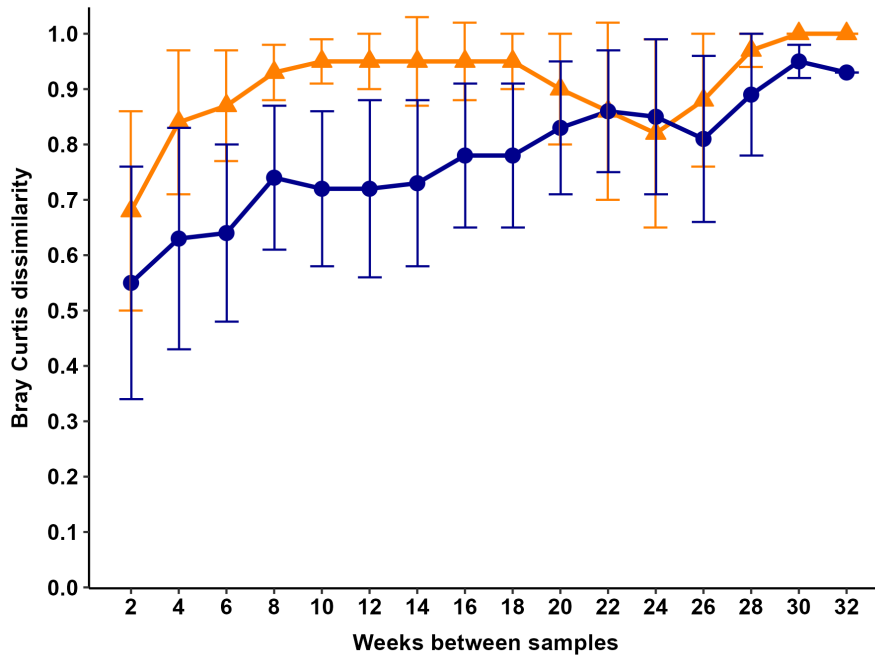


Figure 13. Average Bray Curtis dissimilarity as a function of time between samples for the intermittent (orange triangles) and perennial (blue circles) sites on the Credit River (bars bracketing the points are standard deviation).

## Discussion

### *Comparison with a perennial stream site*

Both intermittent and perennial sites were sampled on the Credit River in 2004 to provide a comparison of Chironomidae diversity patterns between intermittent and perennial stream reaches. The most distinct and presumably most important difference between these sites is stream discharge. There were other differences in the characteristics of these sites including thermal regime, substrates, and water quality that could affect the

midge community. However, these factors only differed minimally between sites and were assumed to affect chironomids less than discharge. Furthermore, these smaller differences in stream attributes should not obscure important changes in the midges resulting from hydrological differences. Contrary to expectations, total annual taxa richness was identical at the intermittent and perennial sites during 2004 (90 taxa). The intermittent site matched the taxa richness at the perennial site even though there were 8 fewer samples containing SFPE from the intermittent site (15 sample

intermittent, 23 samples perennial). In addition, there were on average fewer taxa in individual samples from the intermittent site compared to the perennial site. The equal total annual taxa richness was achieved in the intermittent site through higher temporal  $\beta$  diversity between samples. This attribute was also apparent in the higher dissimilarity between paired samples, especially between paired samples separated by short temporal gaps (2-18 weeks). The more variable discharge (e.g., more disruptive spates and dry periods) may have contributed to the high dissimilarity between summer samples at the intermittent site. Higher species turnover and diversity in intermittent streams may be the result of more colonization of new species due to spates that alter and disrupt substrates and dry periods (Boulton and Suter 1986, Chou et al. 1999, Casas and Langton 2008).

Aquatic insect species may be divided into different categories based on their tolerance of flow permanence including: 1) taxa found only in perennial habitats, 2) facultative taxa that are found both in perennial and temporary habitats, and 3) specialist taxa in temporary habitats (Williams and Hynes 1977, Feminella 1996). Examination of the taxa present in the intermittent and perennial sites on the Credit River permits categorization of taxa into these types of tolerance to flow permanence. Forty-five percent of taxa were collected from both sites and therefore these stream reaches shared a high proportion of their chironomid communities. However, the majority of taxa were only collected at one of the sites indicating differences between the intermittent and perennial sites. Large differences between the aquatic insect and chironomid communities in perennial and intermittent streams have been documented (Dance and Hynes 1979, Wiggins et al. 1980, Williams 1987, Williams 1996). However, some of the differences between the two sites in my study could be a failure to detect some rare species that are actually present at both sites. When including all 6 years of sampling at the intermittent site, only 13 taxa recorded at the perennial site did not occur in the intermittent site samples. This does not consider additional taxa that would have been likely collected from the perennial site if 5 more years of sampling was performed, but it suggests that given a sufficient sampling effort, most taxa likely occur at both sites. If the taxa collected at the intermittent site are compared to a larger study of 12 perennial streams in the region (Bouchard 2007), only 10% (28 taxa) of the taxa collected in the intermittent site were not collected from the perennial streams. Many of the species inhabiting perennial streams appear to be tolerant

to dry periods or at least capable of recolonization following dry periods. My study supports the patterns observed by others demonstrating that most species are facultative and occur in both perennial and intermittent streams (e.g., Boulton and Suter 1986, Feminella 1996, Casas and Langton 2008).

#### *Richness and diversity*

Documentation of species diversity supports species conservation work and the use of these species in ecological and biological assessment studies. Habitats with high diversity or unique taxa will be given greater priority for protection. Conversely, habitats with low diversity, whether actual or perceived, will be assigned lesser value and be at greater risk of degradation or destruction. Such is the case for non-perennial habitats. This long-term study of Chironomidae emergence from an intermittent stream demonstrated that non-perennial streams can support a high diversity of Chironomidae (158 taxa). Several studies have documented more than 100 species of chironomids from single stream sites in temperate regions (e.g., Coffman (1973): 141 taxa; Siebert (1980) 134 taxa; Boerger (1981): 112 taxa; Becker and Wagner (2004): 110 taxa; Bouchard (2007): five streams – 107–131 taxa; Casas and Langton (2008): 159 taxa). However, most of these studies are from perennial streams and only include a single year of study. The high estimate in the current study of an intermittent stream was influenced by the higher-than-typical effort which spanned 6 years. On an annual basis, 61-103 taxa were recorded and only one year exceeded 100 taxa. Most studies of Chironomidae in streams only include a single year or season of sampling, but there are several that spanned multiple years (e.g., Siebert 1980, Feminella 1996), including several that studied non-perennial streams (Chou et al. 1999, Langton and Casas 1999, Casas and Langton 2008). All three of the studies on intermittent streams also used a similar methodology (i.e., biweekly collections of SFPE) which allows a good comparison between studies. Chou et al. (1999) collected SFPE exuviae from an intermittent stream in Kansas over three years, but only 55 taxa were recorded which was assumed to be due to the small stream size (1<sup>st</sup> order). Casas and Langton (2008) is more comparable to the current study because it compared intermittent and perennial stream sites over multiple years (5 years). No difference in total taxa richness was identified between the two habitats (159 taxa) (Casas and Langton 2008) and their total taxa richness was very similar to the intermittent stream in Minnesota (158 taxa). The current study and Casas and Langton (2008) both studied intermittent

streams that remained flowing for a relatively high proportion of the year for at least some years. The taxa richness observed in these detailed studies of chironomid emergence from temporary streams indicates that high taxa richness, comparable to that in perennial streams, is likely maintained until the length of the dry period is sufficiently long (e.g., >2 months) to filter out facultative species. Although relatively short dry periods in streams do not appear to eliminate facultative species, this short dry period does appear to create a suitable habitat for species adapted to temporary habitats. Additional research is needed to determine how aquatic insect communities in lotic habitats shift along gradients of intermittency (e.g., Feminella 1996).

Virtually any sampling design will fail to detect species that are actually present in the study area. Estimation of true taxa richness can be useful to identify sampling effectiveness or for conservation purposes. In the intermittent stream, the taxa accumulation curve and species richness estimator indicated that despite a high sampling effort, chironomid taxa were missed in this study (Figure 7). One hundred and ninety-nine taxa (95% confidence interval: 175-256 taxa) were estimated to be present in the intermittent site during the 6-year study, although there is uncertainty with the results of species richness estimators. The presence of rare taxa creates difficulties for determining species richness. Many of the taxa collected from the intermittent site can be considered rare because they were only collected during one (27%) or two (14%) sample events. The high proportion of rare species increases uncertainty in species richness estimators (Gotelli and Chao 2013). Sample size is also an important factor for a study's ability to detect species. This study relied on a 300-count subsample to maintain a reasonable processing effort as SFPE samples can often contain 1000s of specimens. Bouchard and Ferrington (2011) determined that a 300-count subsample will be sufficient to capture most taxa. However, compared to a 1000-count sample, a 300-count subsample will miss on average 21% of the taxa richness in a sample from a surface-water fed stream. Therefore, it can be concluded that taxa were missed because of the subsample size used in this study. Regardless of the true number of taxa in this habitat during the 6-year sample period, individual years only documented 39-65% of the cumulative 6-year taxa richness indicating that a single year is not sufficient to fully characterize the total richness at a site over a longer period.

The high taxa richness recorded from this inter-

mittent stream raises questions regarding how the diversity from this site ( $\alpha$  diversity) compares to regional diversity ( $\gamma$  diversity). Casas and Langton (2008) determined that 36% of the known Iberian fauna was represented in a 5-year study of the chironomids from an intermittent stream. A similar comparison cannot be made for the intermittent site on the Credit River because a comprehensive catalogue of Chironomidae in the Great Lakes Region of North America has not been produced. However, a narrower comparison of the intermittent site on the Credit River can be made by comparing the taxa collected from the intermittent stream to the cumulative richness from 12 perennial streams in the region (Bouchard 2007). Based on this comparison, 54% of the total pool (290 taxa) were present in the intermittent site. However, this is an overestimate of the proportion of regional  $\gamma$  diversity at the intermittent site as the taxa list from the 12 streams does not include chironomids that occur in other habitats such as lakes, wetlands, large rivers, phytotelmata, and terrestrial habitats. In general, the diversity of Chironomidae based on pupal exuviae is less well documented in the Nearctic compared to the Palearctic. Although considerable work toward this effort by researchers such as Ferrington and Berg (2019) and Langton (2023) has improved our knowledge of pupal taxonomy in the Nearctic, considerable work is still required. In particular, fewer species names can be assigned to pupal morphotypes which create difficulty when harmonizing nomenclature between studies. This demonstrates a need to better understand regional diversity patterns, even in regions such as the Great Lakes Region of North America where many studies on the Chironomidae have been carried out. To conserve species, a reasonable determination of regional  $\gamma$  diversity is valuable, but this is an area of research that is lacking especially for taxonomically challenging groups like the Chironomidae.

The high chironomid diversity in the intermittent Credit River is surprising given the challenges aquatic insects face in non-perennial habitats. This indicates that many of these species can either survive dry periods through physiological or behavioral mechanisms or they can rapidly recolonize the habitat. This stream flowed for much of the summer providing a long window for colonization of the habitat with sufficient time to complete at least one generation. However, many taxa appear to have the ability to survive the mid-summer dry periods. For example, after the stream began flowing again in late summer or fall, emergence usually resumed within 1-3 weeks following the

dry period. This suggests that many taxa were present in the stream during the dry period and were able to rapidly resume and complete development once water was present in the stream again. Many chironomid species can survive periods of drying through physiological or behavioral mechanisms (e.g., anhydrobiosis, cocoon building, migration to the hyporheos; Frouz et al. 2003), which may also explain the diversity of this family in the stream. The intermittent site of the Credit River was dominated by areas of coarse substrates which suggest that Chironomidae larvae at this site can retreat to the hyporheos during dry periods. There were several taxa that were specifically related to non-permanent habitats (e.g., *Hydrobaenus* RWB pe1, *O. (Eu.) abiskoensis*, *P. nasthecus*, and *Allocladius* sp.). These species were absent from the perennial site and their known natural history also suggests they have adaptations to semiaquatic or intermittent habitats (e.g., drying resistant life stages, ability to rapidly colonize habitats; Cranston et al. 2007, Casas and Langton 2008, Andersen et al. 2013). One of these taxa, *Hydrobaenus* RWB pe1, was the most abundant taxon collected in the intermittent stream due to large, synchronized pulses of emergence in the early spring. Langton and Casas (1999) identified a species (*Orthocladius calvus*) which was a dominant taxon in an intermittent stream but absent from a nearby perennial stream; *O. calvus* is documented as an early colonizer of rewetted habitats. *Hydrobaenus* RWB pe1 was present in all years and is likely a permanent resident of the intermittent stream with adaptations for surviving dry periods. Some species of *Hydrobaenus* are well known to colonize intermittent habitats (e.g., Grodhaus 1980, Kondo 1996, Cranston et al. 2007). *Orthocladius (Eu.) abiskoensis*, a species largely collected at high latitudes in the Holarctic region (Soponis 1990), was relatively abundant at this intermittent site. This species has also been collected from an intermittent site in Kansas (Chou et al. 1999). This suggests that at lower latitudes it may be largely limited to non-perennial habitats. Surprisingly, there were 4 species of *Diaamesa* present at the intermittent site (Table S1). Although this genus is known from non-perennial habitats (e.g., Langton and Casas 1999, Williams 2006), this cold-adapted genus is more commonly encountered in Minnesota from groundwater fed streams. Because its emergence is limited to winter and early spring, it is likely that larvae aestivate in the stream in the hyporheic zone. Although there is evidence for the drought resistance traits in this midge community, the specific mechanisms used by many of the midges to successfully occupy a non-perennial habitat cannot be determined here.

#### *Discharge and water temperature effects on Chironomidae diversity*

Temperature is often considered to be the most important factor influencing the timing of growth and development of aquatic insects in temperate streams (Ward and Stanford 1982). In streams that experience strong seasonal gradients in temperature (e.g., with daily mean temperatures 0-25 °C), water temperatures will be outside of the thermal optima for a given species for some part of the year. As a result, species inhabiting these streams will have periods of diapause or quiescence when growth or development is halted. These regular periods of inactivity serve to synchronize the phenology of species and often species will emerge at predictable times based on their thermal optima. The seasonal emergence patterns in the intermittent stream were typical for a temperate, surface-water fed stream. Taxa richness was low in the winter, early spring, and late fall and was dominated by Orthocladiinae and Diamesinae. Orthocladiinae also dominated much of the rest of the year with Chironominae and Tanypodinae reaching their highest diversity in the summer. This seasonal pattern of richness among the subfamilies is commonly observed in perennial temperate streams (e.g., Armitage 1995, Coffman and de la Rosa 1998, Bouchard 2007). This pattern differs from that of tropical streams which have weaker seasonal variability temperature (Coffman and de la Rosa 1998, Bouchard and Ferrington 2023). However, there are other factors in streams that influence the timing of development including stream discharge and input of allochthonous matter.

The hydrology of a stream is an important factor that influences the composition and life history of aquatic insects. Discharge can have acute disruptive impacts on aquatic invertebrates during high flows (e.g., spates), low flows, and dry periods. Stream intermittency has obvious and direct effects on Chironomidae and other aquatic insects. When a stream dries, this halts emergence of aquatic species and could disrupt the life cycle if refugia are not available or if the species is not adapted to periods of drying. Longer periods of drying are expected to have a greater impact on aquatic species so less taxonomic diversity would be predicted to be supported in habitats or during years with less flow. For example, an intermittent stream in Kansas studied for 3 years had a much longer dry period one year (134 days of streamflow) and only 6 chironomid species were collected compared to 29 and 49 taxa in two other wetter years. There is a decrease in the richness of species emerging from these habitats even when water is retained in pools,

but flow ceases (Chou et al. 1999, Casas and Langton 2008). In the present study, a similar pattern was observed with only 0-8 taxa present during sampling events when the stream was pooled. The decline in species richness during periods of no or low flow and an absence of emergence when the stream is dry suggests that the years of this study with longer dry periods should support lower taxa richness. However, this was not the case and there was no clear relationship between the number of days the stream was dry each year and the number of taxa collected. In fact, the opposite pattern was observed when accumulated annual flow was compared against annual taxa richness (Figure 9). Higher flows or spates are disruptive to chironomids which may explain this pattern. The lowest taxa richness was recorded in 2005, a year with numerous spates throughout spring and summer (Figure 6). Taxa richness in 2003 was also low and although this year did not have a series of summer spates, the discharge was high ( $> 6 \text{ m}^3/\text{s}$ ) in May. In 2007, taxa richness was high (91 taxa) and there were also some spates with very high flows, but these occurred in March and April. This suggests that the frequency and timing of spates is important in determining taxa richness in intermittent streams. If there are spates associated with late winter and early spring snow melt or rainfall, this may be less disruptive than spates during periods when temperatures are warmer and more species are active (e.g., late spring and summer). A negative relationship between spates and chironomid richness was also noted by Chou et al. (1999) who suggested that lower richness during wetter years may be due to scouring flows. This has also been hypothesized to be a determinant of abundance in tropical streams (Ramírez and Pringle 1998, Silva et al. 2009). However, the magnitude and timing of spates may result in different effects on chironomid communities. Scouring spates, especially during periods when chironomids are not dormant, may reduce diversity for days or weeks following the spate. Chironomids and other invertebrates in intermittent streams may be resistant to long-term effects of spates and recover within weeks (Miller and Golladay 1996), but repeated spates during the growing season could have an accumulative, negative effect.

Spates may have a positive effect on macroinvertebrate richness under some conditions. Casas and Langton (2008) hypothesized that spates in an intermittent stream increased temporal  $\beta$  diversity and increased  $\alpha$  diversity. In the Credit River, the increased  $\beta$  diversity may be due to spates, but the effects of intermittency could also be impor-

tant. The combined periodic disturbance caused by spates and drying may allow for the colonization of new species and therefore increase  $\alpha$  diversity in the long-term. How this might impact intermittent systems as climate change alters their hydrology is not clear; however, this study does indicate negative relationships between increased flows and temperatures and chironomid taxa richness. Increases in peak flows and decreases in base flows are predicted to occur in the midwestern United States (Demaria et al. 2016) which will impact aquatic insect communities. However, forecasting specific long-term trends in species diversity is more difficult because there are effects that can be observed at different time scales and the relationships between hydrology, temperature, and species diversity can differ depending on the scale.

## Conclusions

Disturbance caused by high variability in discharge, including spates and periods of drying, has an important effect on Chironomidae communities. High flows disrupt substrates and can cause displacement or a need for aquatic insects to move to protected habitats within the stream (e.g., hyporheic zone). Although aquatic insects, particularly Chironomidae, have demonstrated resilience to such disturbances (Miller and Golladay 1996, Anderson and Ferrington 2013), they have short-term impacts on communities (Casas and Langton 2008). Low flows and drying can also be a form of disturbance which require migration to the hyporheic zone or resistance to drying. Regardless of the mechanism for survival, dry periods will be disruptive through energetic costs (e.g., movement, cocoon construction) and delays in growth and development. For some chironomid species, dry periods will cause extirpation or at least a decline in the population and the species will need to recolonize the habitat. For species that cannot survive dry periods and require a year or more to develop, they will be limited to perennial sites. Thus, species attributes determine the species that occupy the habitat and their phenologies. However, many Chironomidae species are apparently facultative and capable of inhabiting both perennial and intermittent streams. There is also a smaller subset of taxa that are more abundant or are only found in intermittent streams. Together these taxa demonstrate that intermittent streams can support diverse aquatic insect communities, including unique taxa that do not occur in other habitats.

The long-term study of an intermittent stream in Minnesota (USA) has demonstrated that non-perennial streams contain unique taxa and these habi-

tats can support a high diversity of aquatic insects comparable to that of perennial systems. However, non-perennial habitats are less often studied which highlights the need for additional research on non-perennial habitats. Long-term studies of aquatic habitats are also important to understand the effects of antecedent conditions. Due to the constraints of time and funding, it is not common for aquatic studies to extend beyond a year or two, but long-term patterns in flow and other variables affect aquatic insect communities. This is especially true in intermittent habitats which are more dynamic and have more variability in the aquatic insect community over time. A failure to account for such variability in sampling design and analysis can result in an underestimation of diversity and could affect the identification of other important factors such as pollution. This study also adds to the research demonstrating the importance of non-perennial, freshwater habitats (e.g., high species diversity, unique species) and the need for their conservation (Williams 1996, Casas and Langton 2008). However, this requires a shift in opinions as many consider non-perennial habitats to be less valuable. Conservation becomes more important for non-perennial habitats in this region as climate change is expected to increase temperatures and extreme weather events including droughts and heavy rain events. These threats, coupled with a low priority for conservation, has the potential to cause widespread disruption and extirpation to the diverse communities and unique taxa supported by non-perennial habitats.

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