



Seasonal Mass Migration of Water Boatmen (Hemiptera: Corixidae) as a Wetland–River Linkage and Dietary Subsidy to Riverine Fish

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ABSTRACT

Cross-boundary movements of organisms can act as important ecosystem linkages by subsidizing food webs. We investigated the magnitude and implications of a little understood food web subsidy in the form of migrating aquatic insects, corixids (Hemiptera: Corixidae), that fly from geographically isolated wetlands into large rivers in the Prairie Pothole Region (PPR) of North America every fall, to overwinter. We found that these migrations can lead to drastically increased riverine corixid densities as high as $\sim 3,000$ individuals/m² within areas of standing or slow-moving water, with ~ 500 g of corixid material entering every meter of water immediately adjacent to the banks of rivers, where landings are concentrated. This movement shifts the species assemblage in rivers to one dominated by wetland-breeding species, namely *Callicorixa audeni*, *Sigara bicoloripennis*, and

Sigara decoratella. Stomach content analyses of fish reveal that goldeye (*Hiodon alosoides*), mooneye (*Hiodon tergisus*), longnose sucker (*Catostomus catostomus*), and white sucker (*Catostomus commersoni*) make heavy use of this forage subsidy, with corixids occurring in 97% to 100% of these fishes and accounting for 38% to 97% of stomach contents by weight during the corixid migration period in fall. We estimate that seasonal migrations could result in ~ 1500 metric tons of corixids entering the North and South Saskatchewan rivers within Saskatchewan, and $\sim 12,000$ tons of biomass moving between wetlands and rivers across the entire PPR. Our study has demonstrated an extensive cross-boundary flux that occurs between spatially separated wetland and river ecosystems, highlighting a need for conservation to ensure that this connection is maintained.

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GRAPHIC ABSTRACT



Key words: ecosystem linkage; subsidy; insect flux; aquatic insect; Corixidae; seasonal migration; wetland; river; food web; fish diet.

INTRODUCTION

Ecosystems are linked by transfers of organic material, which can strongly affect community and food web dynamics. For example, external prey subsidies may allow consumers to increase in abundance beyond what could be supported by autochthonous production alone, initiating trophic cascades and affecting the stability of recipient food webs (Polis and others 1997). Such coupling of habitats via prey subsidies can result from animal migrations (Bauer and Hoyer 2014; Uno and Power 2015).

The movements and emergence of aquatic insects can link the productivity of aquatic ecosystems to both the surrounding terrestrial environment (Gratton and Vander Zanden 2009; Wesner and others 2020) and other waterbodies (Kraus and others 2011). Aquatic invertebrates are known to link the productivity of lentic and lotic ecosystems that are connected by surface flows, such as backwater or floodplain wetlands that are connected to rivers (Fisher and others 2001; Farly and others 2019). Less well understood, however, are biological links between waterbodies that are not connected by surface flows, such as rivers and non-floodplain wetlands (US EPA 2015). Such geographically isolated wetlands usually have no

surface water connections, but receive inputs via groundwater, snowmelt, and rain. This includes most wetlands in the Prairie Pothole Region (PPR) of North America (Tiner 2003; Doherty and others 2018).

The PPR is a large freshwater wetland complex encompassing an area over 770,000 km² in the western plains of Canada and the USA (Doherty and others 2018). The PPR contains approximately 5–8 million wetlands, many of which are small, shallow, and only hold water for part of the year (Johnson and others 2010). These wetlands are typically productive and have few fish, owing to frequent drying and a general lack of surface connections, which can lead to high secondary production of macroinvertebrates (Bataille and Baldassare 1993; Covich and others 1997; McCauley and others 2015).

Insect species in small wetlands often possess strong dispersal abilities (Fernando and Galbraith 1973; Williams 1996) and are able to migrate to more permanent waterbodies as needed to complete life cycles or in response to changing habitat conditions (Batzer and Wissinger 1996). Such seasonal insect migrations may have a pulsed, predictable nature, and can result in the regular concentration of massive amounts of biomass in recipient habitats (Uno and Power 2015; Satterfield and others 2020). One group of aquatic insects that regularly travels between wetlands and larger waterbodies during seasonal migrations are water boatmen, or corixids (Hemiptera: Corixidae).

The Corixidae are a diverse and highly adaptable family of aquatic insects, with at least 41 known species in Alberta, Saskatchewan, and Manitoba (Brooks and Kelton 1967). Different corixid species are able to exist in a wide range of lentic and lotic environments; however, they typically prefer areas of standing or slow-moving water (Hungerford 1948; Stonedahl and Lattin 1986) and reach the highest abundances in fishless, macrophyte-dense habitats (Tolonen and others 2003; Schilling and others 2009) such as prairie pothole wetlands. Many corixid species are thought to feed primarily on algae and detritus, while others are predatory or employ multiple feeding strategies (Hädicke and others 2017). In temperate waters, most corixid species breed during the spring and summer and produce one to two generations per year; however, this may vary depending on species and climate (Hungerford 1948; Stonedahl and Lattin 1986).

Many corixid species will migrate in anticipation of the freezing or drying of habitats (Fernando and Galbraith 1973; Hilsenoff 1975; Pajunen and Salmi 1988; Boda and Csabai 2013); however, the precise distance that they are capable of travelling is unknown (Scudder 1976). Corixid flight estimates range from 10 to 90 km/day, with wind potentially playing an important role in the distance and direction travelled (Popham 1943, 1951, 1952, 1964; Scudder 1976). In northern latitudes of North America, a number of corixid species migrate every autumn from small, shallow breeding wetlands, many of which will freeze through, into larger habitats for overwintering, later moving back into these wetlands to reproduce in spring (Hungerford 1948; Hilsenoff 1984). These fall migrations can lead to immense numbers of corixids concentrating in rivers and streams (Hilsenoff 1970; Stoaks and others 1980). However, the ecological importance of this transfer of insect material between wetlands and rivers is not well understood.

Fishes influence ecosystem functioning and resilience, with the consumption of external subsidies affecting their ability to control other organisms through feeding, act as ecosystem engineers, and mediate nutrient cycling (Holmund and Hammer 1999; Villéger and others 2017). A number of fish species from North American river systems are known to prey on corixids, and some studies have noted an increase in corixid feeding in fall (Glenn 1975; Donald and Kooyman 1977; Little and others 1998). Yet, to our knowledge, no study has connected fish predation on corixids to their seasonal migrations and examined these phenomena in the context of an ecosystem linkage with corixid source habitats.

The large number of wetlands in the PPR that are capable of producing corixids in high abundances, but are unsuitable as overwintering sites, makes this an area in which a large annual flux of corixids moving between wetlands and rivers could occur. We have previously observed large aggregations of corixids in both the North and South Saskatchewan rivers throughout Saskatchewan, as well as in Alberta (John Acorn, personal communication), and in the Red River in Manitoba (S. Srayko, personal observation) in the fall. It is unknown to what extent this migration changes the abundance and species composition of corixids in these habitats, and whether or not these wetland-based, migratory corixids subsidize the diets of riverine fish. In this study, we characterized the seasonal corixid migration by describing changes in abundance and species composition in wetland and river habitats

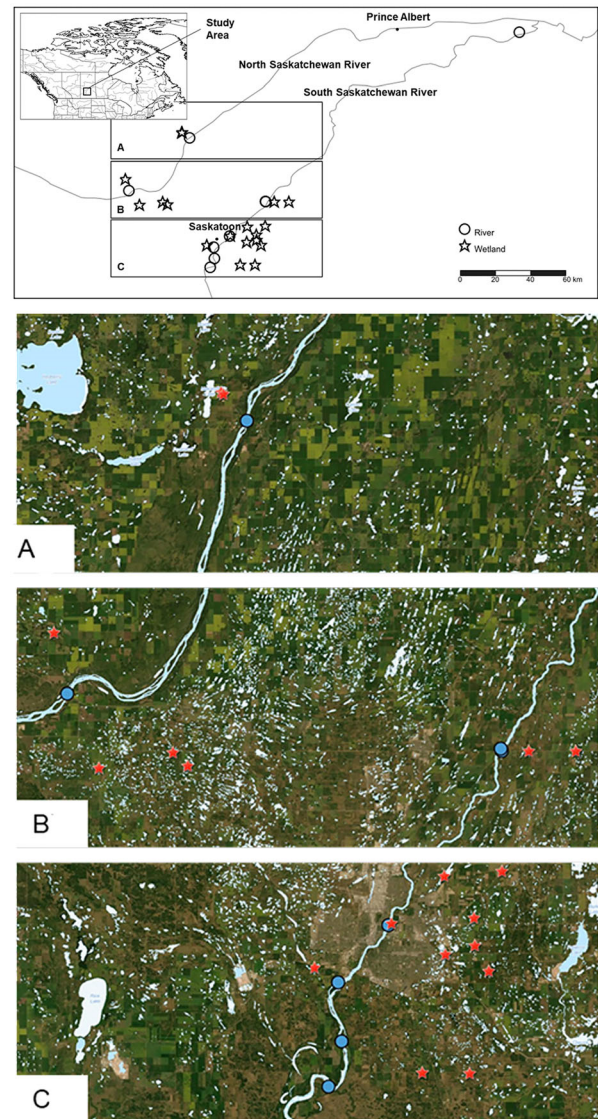


Figure 1. Map of the study area in central Saskatchewan, Canada, with river (circles) and wetland (stars) sampling locations. Blown up portions A–C detail the study area near Saskatoon, with waterbodies in blue.

from spring to fall. We then assessed the importance of this potential subsidy to the diets of riverine fish communities by examining the stomach contents of several fish species before and during the times when large numbers of migratory corixids were present in our study rivers. Finally, we contextualized the magnitude of this flux on a larger scale by estimating the number and biomass of corixids that could be moving annually across the PPR during these migrations.

Table 1. Average (\pm SD) and Range of the Number of Adult Corixids Collected per 5 m D-frame Net Sweep From All River or Wetland Sites Each Month From 2015 to 2016, with Post-hoc Tukey Test Groupings for Each Habitat Type in Both Years

Year	Month	River			Wetland			Number of Sites (Sweeps)	Range	Number of Sites (Sweeps)	Post-hoc Tukey Results	Number of Sites (Sweeps)	Post-hoc Tukey Results
		Adults per 5 m	Range	Adults per 5 m	Adults per 5 m	Range	Adults per 5 m						
2015	Aug	178 (181)	13–488	55 (61)	4–230	6 (12)	A	6 (12)	4–230	6 (12)	A		
	Sept	216 (175)	38–441	131 (216)	0–679	6 (6)	A	6 (12)	0–679	6 (12)	A		
	Oct	4009 (3291)	331–10,978	17 (22)	1–61	6 (12)	B	6 (6)	1–61	6 (6)	AB		
	Nov	4466 (6433)	228–16,048	2 (2)	1–5	6 (6)	B	6 (6)	1–5	6 (6)	B		
2016	April	3045 (3296)	56–10,951	12 (16)	0–55	5 (15)	D	6 (18)	0–55	6 (18)	A		
	May	139 (197)	9–708	4 (4)	0–17	5 (15)	AB	6 (18)	0–17	6 (18)	A		
	June	28 (32)	0–98	14 (27)	0–117	5 (15)	A	6 (18)	0–117	6 (18)	AB		
	July	32 (30)	1–130	69 (113)	4–476	7 (21)	A	6 (18)	4–476	6 (18)	C		
	Aug	64 (66)	0–232	38 (59)	1–280	6 (18)	AB	18 (54)	1–280	18 (54)	BC		
	Sept	206 (234)	29–1012	72 (122)	5–517	6 (18)	BC	6 (18)	5–517	6 (18)	C		
	Oct	1404 (1952)	9–7045	9 (12)	0–61	7 (21)	CD	15 (45)	0–61	15 (45)	AB		
	Nov	2555 (3091)	1–13,017	16 (24)	0–94	6 (18)	CD	9 (27)	0–94	9 (27)	AB		

METHODS

Study Area

This study was carried out in central Saskatchewan from 2015 to 2017. Corixid samples were taken from a total of nine sites in the North and South Saskatchewan rivers and 18 wetlands within 15 km of these rivers. Fish samples were collected from sites in the North and South Saskatchewan rivers throughout spring (April 2016), summer (August 2015 and July to August 2016), and fall (September to November 2015 and 2016), at the same sites where corixids were collected (Figure 1; Table S3).

Sample Collection

Corixid D-Frame Net Samples

To estimate abundances at wetland and river sites, corixids were sampled with a D-frame sweep net (mesh size = 500 μm , mouth = 30.5 \times 25.4 cm) along 5.0 m transects, with each sweep representing an area of approximately 1.5 m^2 . A single sweep was performed at each site at two- to three-week intervals from August to November 2015, and three sweeps at sites at either monthly intervals from April to November 2016, or with a two- to three-month interval between sampling for select sites from July to November 2016 (Table 1; Table S2). Corixids were frozen after collection and thawed prior to counting and identification.

River sites consisted of areas of standing or slow-moving water such as backwaters, areas downstream of bridge piers, rocky embankments, beaver dams, or along river margins (Table S1). Within each river site, specific sweep locations were selected haphazardly based on landmarks on shore, and performed where there was substrate other than bare sand or mud, such as rocks, sticks or macrophytes, with sweeps taken parallel to shore at depths of 0.3 to 1.0 m.

Wetland sites consisted primarily of shallow, semipermanent class 4 or permanent class 5 wetlands (Stewart and Kantrud 1971) bordered by gravel roads and agriculture. While prone to fluctuation, the primarily agricultural region of southern Saskatchewan in which this study was conducted contains approximately 1.5 million wetlands, over 80% of which are less than 1 ha in area, with an estimated 20 wetlands/ km^2 (Adams 1988; Huel and others 2000). Our study wetlands were in keeping with this size range, with all except three sites being less than 5 ha in area and less than 2 m deep at the center (Table S1). Wetlands ranged from fresh to brackish (Stewart and Kantrud 1971)

with conductivity ranging between 416 and 9780 $\mu\text{S}/\text{cm}$, averaging (\pm SD) 2460 ± 2389 $\mu\text{S}/\text{cm}$. These values are similar to those observed by Adams (1988) in a survey of 39 wetlands in southern Saskatchewan, ranging from 260 to 11,400 $\mu\text{S}/\text{cm}$ (average 1730 $\mu\text{S}/\text{cm}$). With the exception of the largest sites that had open water absent of vegetation in the central area of the wetland, all other sites exhibited mostly uniform conditions throughout, consisting of more or less even depth and abundant submerged vegetation for most of the year. D-net sweeps were taken perpendicular to the edge of the wetland, moving from the center to the edge, at depths of 0.3 to 1.0 m, with specific locations for D-net sweeps selected haphazardly based on landmarks on the shore.

Fish Sampling

Fish were collected by gill netting and angling. Gill netting consisted of overnight sets of 5–20-m-long panels of 4–10-cm mesh, set perpendicular or parallel to the riverbank in wadeable sections of standing or slow-moving water. We collected two Hiodontidae species, goldeye (*Hiodon alosoides*) and mooneye (*Hiodon tergisus*); three Catostomidae species, longnose sucker (*Catostomus catostomus*), white sucker (*Catostomus commersoni*), and short-head redhorse (*Moxostoma macrolepidotum*); as well as northern pike (*Esox lucius*) and walleye (*Stizostedion vitreum*). These species encompass multiple feeding groups, with the Hiodontidae documented as midwater to surface-feeding invertivores and piscivores, the three catostomid species classified as predominantly benthic invertivores, and northern pike and walleye being classified as mainly piscivorous; however, these latter species will also feed on invertebrates, particularly when young, while northern pike feed opportunistically (Scott and Crossman 1973; Stewart and Watkinson 2004). These seven species represent some of the more common large-bodied fishes from this river system in Saskatchewan (71 to 91% of catch; Merkowsky 1987; Miles and Sawchyn 1988; Table S5).

After collection and euthanization, fish were placed on ice for transport to the laboratory. Prior to collection, the University Animal Care Committee Animal Research Ethics Board (UACC AREB) at the University of Saskatchewan reviewed and approved our sampling procedures in compliance with the Canadian Council on Animal Care (CACC) guidelines (UACC AREB Protocol number: 20160046).

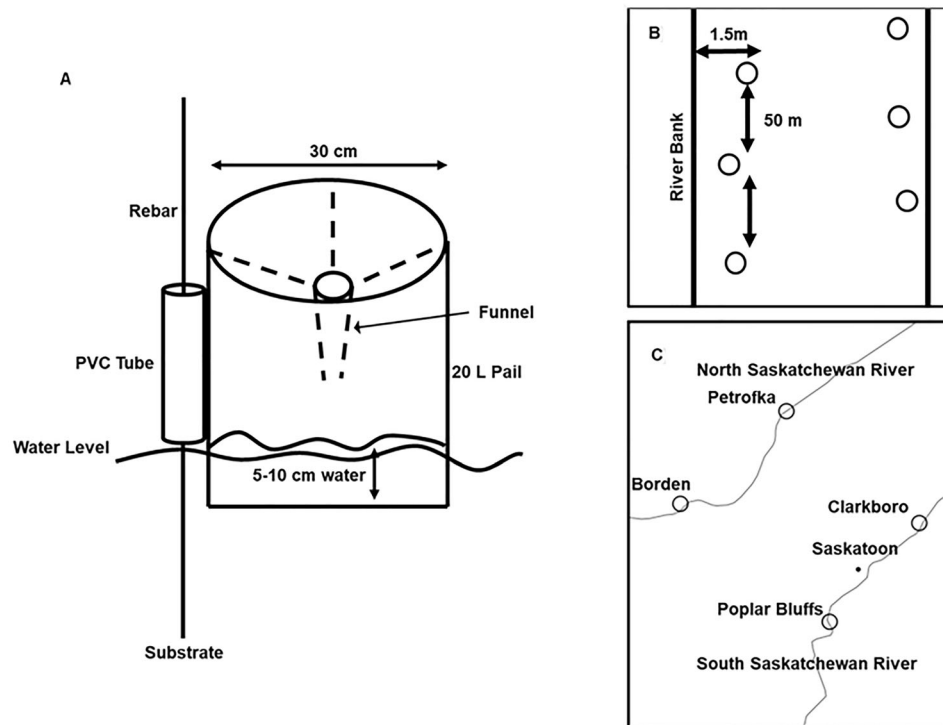


Figure 2. Details of the passive sampling method. (A) Sampler design. (B) Layout of all six samplers at each site in 2017. (C) The four sites in both the North and South Saskatchewan rivers where samplers were placed in 2017.

Corixid Passive Samplers

To estimate migratory inputs, passive samplers were deployed in 2017 to collect corixids as they attempted to enter the rivers, following preliminary tests and observation of sampling methods in 2016. Samplers consisted of a black, plastic funnel, 0.305 m in diameter (0.073 m² in area), placed on top of a 20-L pail that floated on the water's surface, tethered in an upright position to a piece of rebar (Figure 2A). Corixids would hit the funnel as they attempted to enter the surrounding water from the air. These samplers were set in the water within 1.5 m of the riverbank, as corixids in the previous years of this study had been observed concentrating their entry almost entirely along the edge of the rivers, with very few landing mid-channel. We speculate that this may be an adaptation to avoid fish predation and enter the river near areas of standing or slow-flowing water. Twenty-four samplers were set out at four sites in the North and South Saskatchewan rivers, with six samplers per site, three on each bank and ~ 50 m between samplers (Figure 2B-C). These were in place from September 12 to October 26, 2017, emptied of corixids once per week, and removed several days before ice appeared on the rivers and the onset of winter conditions halted migration. A

brief experiment supported our hypothesis that the passive samplers were not acting as an attractant for flying corixids (Appendix 5).

Sample Processing

Corixid Abundance, Biomass, and Species Composition Adult corixids were identified to species using Brooks and Kelton (1967). Identifications were completed for corixids from a single representative net sweep at each river site in 2015 and 2016, from all wetland sweeps in both years, and from two passive samplers at each site (one on each bank) in 2017. Passive sampler collections were weighed after counting and/or identification, with a subset of specimens used to determine species-specific weights (Appendix 6; Table S7).

Fish Stomach Content Analyses After collection, fish were weighed to the nearest 5–10 g and measured to the nearest 0.1 cm (fork length). Stomachs were dissected out, opened with a razor and contents scraped into vials. The fullness of each stomach that was not completely empty was assessed using a stomach content weight index (SCWI), with $SCWI = (\text{stomach content weight (g)}/\text{body weight (g)}) \times 1000$ (Hyslop 1980; Liu and others 2020). Fish with stomachs that were completely empty were omitted from all calculations. After extrac-

tion, stomach contents were frozen, then later thawed prior to examination. For the Catostomidae, the contents of the entire digestive tract were examined, as these fish lack a distinctive stomach (Ahlgren 1990), whereas intestinal contents were not examined in other species. Thawed stomach contents were visually identified to the lowest taxonomic level possible and separated into different categories of material with forceps under a dissecting microscope. Excess moisture was then blotted away with paper towel and mucous removed before items were weighed to the nearest 0.01 g (wet weight) (see Appendix 4, Table S6 for greater detail on fish size, stomach fullness, and stomach content information).

Stomach content categories were characterized using the frequency of occurrence (%O) and percent total weight (%W) of every category in the stomachs of each fish species from spring (April), summer (July–August) and fall (September–November), with fish from different sites and years pooled together by season. In regard to food item *i*, %O = the percentage of all non-empty stomachs from a particular species/season containing food in which prey *i* occurred, and %W = the percentage that the mass of prey taxon *i* contributed to the total mass of food in the stomach contents of all individuals of a fish species from a particular season (Hynes 1950; Hyslop 1980). The number of corixids in the stomachs of goldeye, mooneye, and longnose sucker was also estimated by counting head capsules.

Data Analysis

Corixid D-net Abundance

To examine changes in corixid abundance in wetland and river habitats before and after migration, we performed a three-way ANOVA on log-transformed abundance data from D-net sweeps separately for each habitat, examining the effects of month, year (2015 vs. 2016), and site, with site as a random factor. Post-hoc Tukey tests were used to reveal groupings. Statistical analyses were conducted in SPSS 28 (SPSS Inc., IBM) with $\alpha = 0.05$.

Corixid Flux Calculations

To produce estimates of the abundance and biomass of corixids that could potentially be (1) entering the North and South Saskatchewan rivers in Saskatchewan, (2) entering several major rivers in the PPR, and (3) leaving wetlands in the PPR, we ran three Monte Carlo simulations, each with 1000 iterations, with parameters based on values mea-

sured in this study and obtained from the literature.

To estimate the biomass of corixids moving between habitats, a subset of specimens identified from D-net and passive sampler collections was weighed after counting and identification. Specimens to be weighed at the species level were selected based on which samples contained large quantities of the different species in question. Potential migratory corixid species ranged in average weight (wet) from the smallest species, *Trichocorixa borealis* ($n = 175$) at 0.002 g/corixid, to the largest, *Hesperocorixa atopodonta* ($n = 1131$) at 0.022 g/corixid (Table S7).

The number of corixids that could be entering large rivers in the PPR during the fall migration was estimated based on passive sampler collections. In 2017, the 24 samplers collected a range of 586 to 9908 corixids per sampler throughout the fall migratory period, equating to a range of 8027 to 135,726 corixids/m², or landing at the edges of rivers per meter of shoreline.

To estimate the number and biomass of corixids that could be entering the water along the banks of rivers during fall migrations, we drew from a range of between 8027 and 135,726 corixids per meter of shoreline, with a weight range between 0.002 and 0.022 g/corixid. This was then applied to the combined lengths of (1) both banks of the North and South Saskatchewan rivers within the study area (province of Saskatchewan), totaling ~ 2400 river km, and (2) the combined lengths of both banks from multiple large rivers within the PPR including the North and South Saskatchewan, Battle, Oldman, Bow, Red Deer, Souris, Qu'Appelle, Assiniboine, Red and Missouri rivers (~ 18,686 river km).

For the estimate of corixid biomass that could be leaving wetlands across the PPR (3), we drew random numbers from a range of 9–18 corixids/m². These values were based on average numbers of individuals of known migratory species (species other than *Cymatia americana* and *Trichocorixa verticalis interiores*; see Discussion), collected from study wetlands in the months prior to fall migration. The same weight range of corixids as above (0.002 to 0.022 g/corixid) was applied. The simulation drew from a range of 5.0×10^{10} to 11.6×10^{10} m² of wetland area in the entire PPR (3.7×10^{10} m² in the US portion, plus 4.6×10^{10} m² in Canada, $\pm 3.3 \times 10^{10}$ m² (three times the estimated standard deviation of wetland area in the Canadian PPR, to account for potential fluctuations in wetland area between years)) (Watmough and Schmoll 2007; Doherty and others 2018).

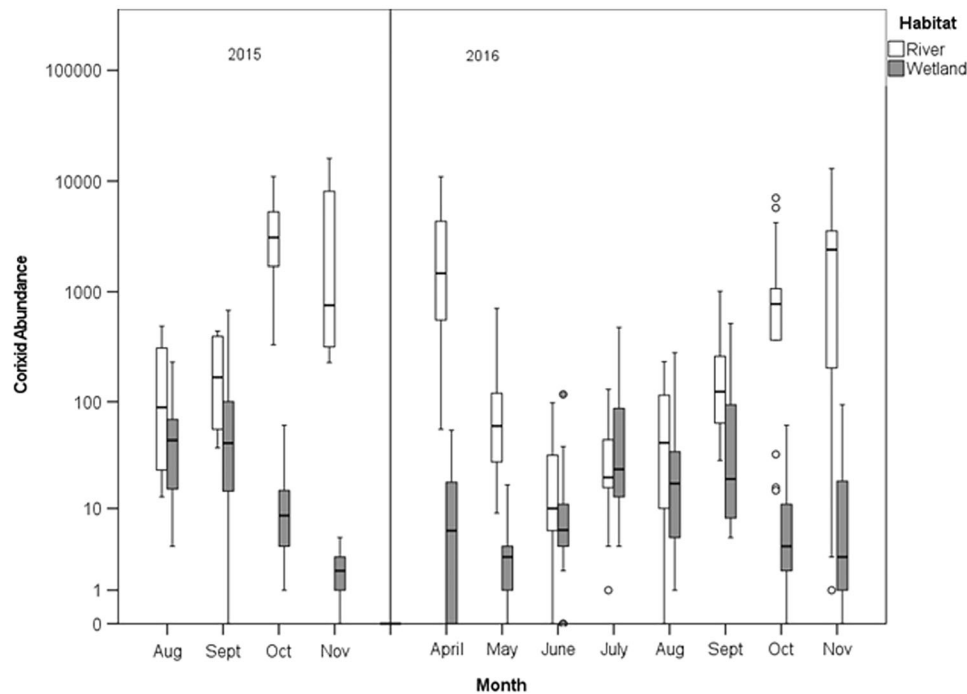


Figure 3. Variation in corixid abundance in D-frame net sweeps from August to November 2015 and April to November 2016, in river and wetland sites.

RESULTS

Corixid Abundance

D-Frame Net Samples

The number of corixids in the rivers was affected significantly by interactions between year and month ($F_{3,115} = 3.088$, $P = 0.030$) and site and month ($F_{39,115} = 2.891$, $P < 0.001$), in which October and November abundances differed significantly from August and September in 2015, and April, October, and November differed from May to August in 2016 (Figure 3; Table 1). Corixid abundances in the river sites greatly increased from summer to fall after corixids began landing in the rivers starting in September in both years, as average adult abundances per 5.0 m D-net sweep increased by approximately 18 times from mid-September to October in 2015 and seven times from September to October in 2016. From this time until freeze-up, average numbers (\pm SD) at each sampling interval in both years remained at values upwards of 1000 individuals per sweep, ranging from 1404 (\pm 1952) to 4466 (\pm 6433) corixids per 5 m sweep, or approximately 921 (\pm 128) to 2929 (\pm 4218) corixids/m².

The average number of adult corixids per sweep in April 2016 after ice-break was similar to that in the river sites sampled in the previous November

before freeze-up, averaging 3045 (\pm 3296) corixids per sweep. At this time, corixids were observed leaving the rivers and entering wetland sites, as well as temporary meltwater puddles and ditches en route. Average abundances decreased in the river sites by over 20 times from April to May, to an average of 139 (\pm 197) corixids per sweep, a decline similar in magnitude to the increase that had occurred from summer to fall in 2015. Abundances in 2016 continued to decrease until June, after which average numbers remained lower than in 2015 through July and August (Figure 3; Table 1).

The number of corixids in the wetlands was affected by significant interactions between year and month ($F_{3,167} = 3.870$, $P = 0.010$), year and site ($F_{5,167} = 5.128$, $P < 0.001$), and month and site ($F_{51,167} = 3.499$, $P < 0.001$). In 2015, August and September abundances differed significantly from November, while in 2016, July and September differed from April, May, June, October, and November (Figure 3; Table 1). In contrast to the rivers, corixid abundances in wetland sites declined from summer to fall in both 2015 and 2016. The average number of adults declined by approximately 65 times in 2015 and five times in 2016 from the highest number of corixids per sweep, seen in September of both years, to the last samples taken in November. The average number of adult corixids per sweep in April 2016 was higher than in

the wetlands sampled in the previous November before freeze-up, declined in May, and then increased moving into the summer, as the new generations of adults reached maturity (Figure 3; Table 1).

Average nymphal corixid abundances, which were not included in analyses, peaked in abundance in river sites in August 2015 and June 2016 at 20 (\pm 30) (range 0–90) and 23 (\pm 36) (range 0–119) nymphs per sweep, and in wetlands in September 2015 and July 2016 at 14 (\pm 40) (range 0–137) and 97 (\pm 231) (range 0–946) nymphs per sweep, respectively (Table S4).

Corixid Species Composition

D-Frame Net Samples and Passive Samplers

Three migratory species, *Callicorixa audeni*, *Sigara bicoloripennis*, and *Sigara decoratella*, were most responsible for the migratory flux in all years of this study. In the river sites, these three species made up 9.0% of adult corixids in the summer of 2015 (Figure 4B) and 1.0% in the summer of 2016 (Figure 4H). These species numerically increased in river sites in the fall by approximately 87 times in 2015 and over 4000 times in 2016 compared to their presence in the summer months in the representative sweeps used for identification, composing 86.7% of corixids in the fall of 2015 (Figure 4D) and 78.3% in the fall of 2016 (Figure 4J) (as well as 82.9% in the spring of 2016, prior to migration back into wetlands (Figure 4F)). Of these time periods, *C. audeni* was most abundant in all but the fall river samples from 2016, in which *S. bicoloripennis* was most numerous. These species also made up 92.0% and 85.8% of corixids from passive samplers in 2016 and 2017, respectively (Figure S6). Between both wetland and river sites, the number of species collected was always highest in the rivers in fall and spring (20–23 species; Figure 4D, F, J).

C. audeni, *S. bicoloripennis*, and *S. decoratella* declined in abundance in the wetland sites from summer to fall in both years, together accounting for 41.4% of adults in the summer of 2015 (Figure 4A) and 28.3% of adults in the summer of 2016, (Figure 4G) and decreasing to 15.9% and 14.5% of adults in these sites in the fall of both years (Figure 4C, I). This represented a decrease in abundance by approximately 93% in 2015 and 87% in 2016 from their collective numbers in summer. These species also composed the majority of corixids in wetlands in the spring of 2016 (Figure 4E).

Fish Stomach Content Analyses

Hiodontidae

The two Hiodontidae species fed primarily on a mix of aquatic invertebrates (Table S6). Corixids were fed on in summer and fall by both species (with only one fish collected in spring, which had also eaten corixids). In summer, corixids occurred in 46.2% of goldeye and 80.0% of mooneye, but they accounted for less than 0.1% of the total weight of all stomach contents for both species. In fall, average SCWI values doubled for both species (Table S6), and corixids became the most important prey item, occurring in all fish sampled and making up over 85% and 75% of all stomach contents by weight in goldeye and mooneye, respectively (Table 2). For the goldeye, this amounted to a total of 53.8 g of corixid material from an estimated 4914 corixids, averaging (\pm SD) 3.8 (\pm 1.8) g and 351.0 (\pm 201.6) corixids per stomach. For mooneye, corixid material totalled 13.9 g from an estimated 817 corixids, averaging 3.5 (\pm 2.2) g and 204.3 (\pm 74.7) corixids per stomach.

Catostomidae

The stomach contents of the three sucker species were mostly a mix of aquatic invertebrates and other miscellaneous material (Table S6). For the longnose sucker, only one individual with stomach contents was collected in the spring and summer months. In fall, corixids were the dominant prey item, occurring in all longnose sucker sampled and accounting for approximately 97% of all stomach contents by weight (Table 2). This amounted to a total of 210.5 g of corixid material from an estimated 9,868 corixids, or an average (\pm SD) of 21.1 (\pm 9.6) g and 986.8 (\pm 494.2) corixids per stomach.

White sucker fed on corixids in all seasons. In spring, corixids occurred in 75.0% of fish and composed approximately 7% of the total stomach content weight. In summer, corixids occurred in over 80% of white sucker but accounted for less than 0.5% of the total weight. In fall, average SCWI values tripled (Table S6) and corixids occurred in 97.4% of white sucker sampled, accounting for 38.1% of all stomach contents by weight (Table 2). This amounted to a total of 206.8 g of corixid material, averaging (\pm SD) 5.6 (\pm 7.4) g per fish. Corixids were not found in the stomachs of any of the shorthead redhorse.

Northern Pike and Walleye

The diets of the northern pike and walleye consisted mostly of fish in all three seasons, accounting for 80% to 98% of total stomach content weight and occurring in at least half of the fish from any season, with aquatic invertebrates of lesser importance (Table S6). Only two corixids were found in the stomachs of northern pike, one in the summer and fall, while a single corixid was found in the stomach of a walleye in fall (Table 2).

Despite a lack of direct corixid predation, corixid remains were found within the intact digestive tracts of prey fish within the stomachs of these species. Corixid remains were found within these prey fish from inside the stomachs of two walleye from spring, a single walleye from summer, and five walleye and a single northern pike from fall. The identity of these prey fish was not determined, as the remains, despite having intact digestive tracts, were otherwise highly degraded.

Corixid Flux Estimates

In 2017, the 24 passive samplers collected a total of 71,949 corixids throughout the fall migratory period, averaging (\pm SD) 2998 ± 2317 corixids per sampler ($41,068 \pm 31,738$ corixids/m²), ranging from 586 to 9908 corixids per sampler (8027 to 135,726 corixids/m²). The total corixid biomass (wet) collected by all passive samplers was 930.52 g, with an average weight per corixid 0.013 g/individual. The average biomass (\pm SD) collected by each sampler was 38.77 ± 25.67 g (531.64 ± 351.64 g/m²), ranging from 8.57 to 93.03 g (117.39 to 1274.38 g/m²).

With the given parameters of 0.002 to 0.022 g/corixid and 8027 to 135,726 corixids/m², 1000 runs of the Monte Carlo simulation produced a median estimate of 70,986 corixids/m² with a median weight of 0.012 g/corixid, which would result in 852 g of corixid material entering the water along every meter of shoreline. This resulted in a median estimate of 1.6×10^6 kg of corixid material entering the two study rivers in Saskatchewan, ranging from 4.2×10^4 kg to 7.1×10^6 kg. If all of the PPR rivers accounted for in this study were to receive a similar amount of corixid material, this could result in inputs ranging from 3.3×10^5 kg to 5.2×10^7 kg, with a median value of 1.3×10^7 kg. Estimates of the biomass of corixids that could be expected to leave wetlands across the PPR in fall ranged from 9.8×10^5 kg to 4.4×10^7 kg, with a median value of 1.2×10^7 kg (Table 3).

Figure 4. Species composition of adult corixids from representative sweeps used for identification. (A, B) Summer 2015 (August). (C, D) Fall 2015 (wetland: October to November; river: late September to October). (E, F) Spring 2016 (April). (G, H) Summer 2016 (July to August). (I, J) Fall 2016 (October to November). *Callicorixa audeni* (CAUD), *Sigara bicoloripennis* (SBIC) and *Sigara decoratella* (SDEC), the three species most abundant in river sites in spring and fall samples, are shaded in grey when they occurred in the top 90% of corixids. Other species which composed the remaining top 90% of corixids in each habitat type/season are as follows: *Cenocorixa bifida* (CB), *Cymatia americana* (CAM), *Dasycorixa hybrida* (DH), *Hesperocorixa atopodonta* (HA), *Sigara fallenoidea* (SF), *Sigara lineata* (SLIN), *Sigara trilineata* (STRI), *Sigara solensis* (SSOL), *Trichocorixa sexcincta* (TS), *Trichocorixa borealis* (TBOR), and *Trichocorixa verticalis interiores* (TVI).

DISCUSSION

This study has demonstrated a significant linkage between spatially separated wetland and river ecosystems through the seasonal migration of an aquatic insect. We quantified the increase in corixid numbers that occurs due to migration from wetland habitats into the Saskatchewan River system in the fall, determined which species were most responsible for the migratory flux, and confirmed that this subsidy is being used by several fish species. In this way, corixids are acting to transfer wetland productivity into fish production in rivers. Across the entire PPR, we estimate that this seasonal corixid migration could result in thousands of tons of biomass moving between wetlands and rivers every year, redistributing energy from source wetlands across the landscape.

Corixid Abundance and Species Composition

After migration began in fall, average corixid abundances in the study rivers increased to an order of magnitude higher than were present prior to migration (Figure 3; Table 1). Corixids formed dense aggregations along the banks of the study rivers, often gathering in areas of little to no flow around structures such as sticks, rocks, or macrophytes, or extending in a band along river margins. *C. audeni*, *S. bicoloripennis*, and *S. decoratella* composed the vast majority of corixids in the river sites in fall and spring (Figure 4), and were also the three most abundant species in passive samplers (Figure S6). These three species also occurred in the wetlands in the summer, and declined in abun-

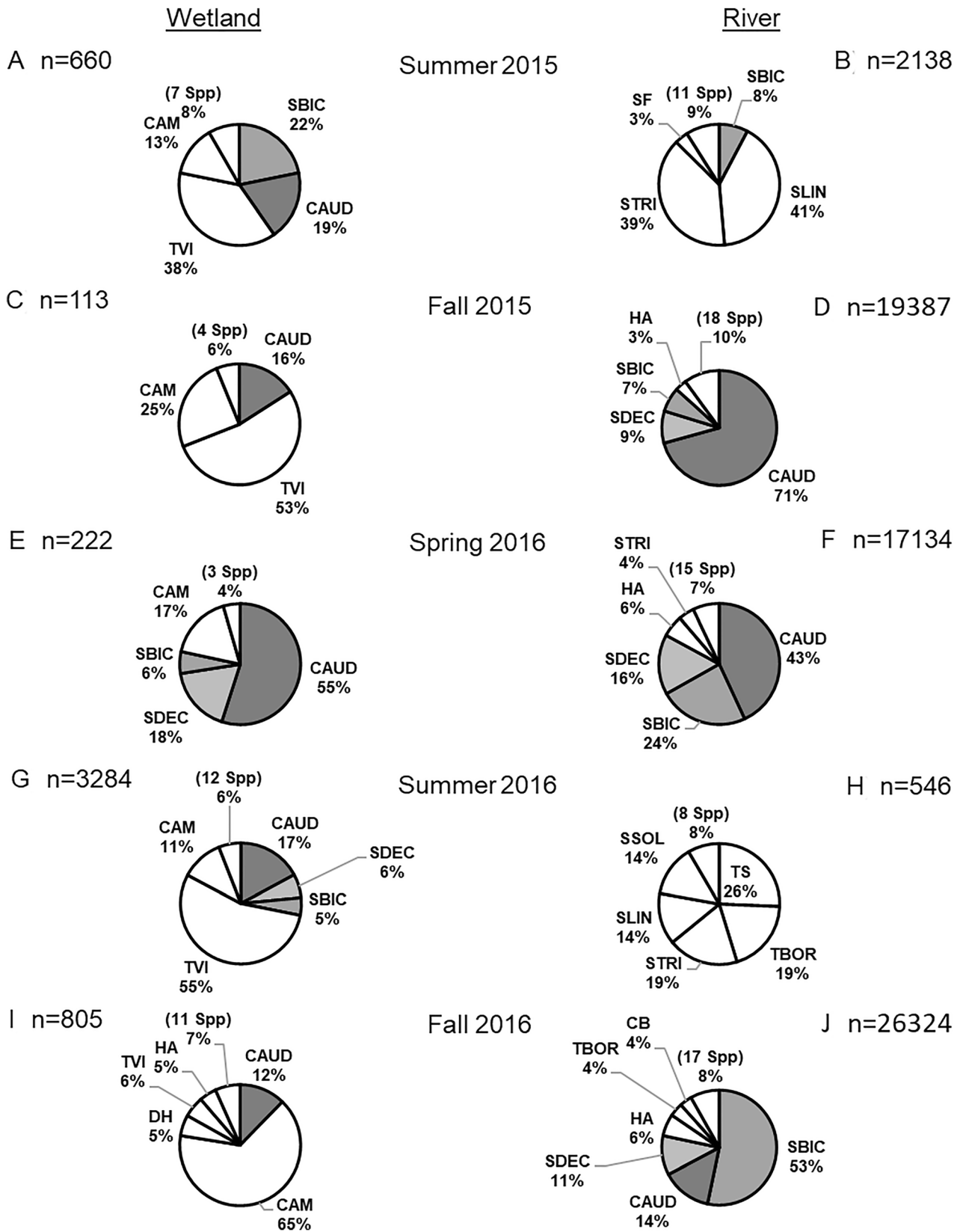


Table 2. Frequency of Occurrence (%O) and Percent Total Weight (%W) of Corixids in the Stomachs of Different Fish Species, in Individuals Without Completely Empty Stomachs (N), Collected From Both the North and South Saskatchewan Rivers During Spring (April 2016), Summer (August 2015, July to August 2016) and Fall (September to November 2015 and 2016)

Species	Fish size		Spring			Summer			Fall			Fall corixid stomach contents			
	FL (cm)	Wt(g)	N	%O	%W	N	%O	%W	N	%O	%W	Total #	Avg #	Total Wt(g)	Avg Wt(g)
Goldeye	37.6 ± 3.9	690.0 ± 213.9	1	100.0	49.4	13	46.2	< 0.1	14	100.0	86.8	4914	351.0 ± 201.6	53.8	3.8 ± 1.8
Mooneye	32.4 ± 2.9	558.3 ± 144.3	-	-	-	5	80.0	< 0.1	4	100.0	76.0	817	204.3 ± 74.7	13.9	3.5 ± 2.2
Longnose sucker	40.9 ± 7.1	895.2 ± 340.5	1	100.0	< 0.1	1	0	0	10	100.0	97.3	9868	986.8 ± 494.2	210.5	21.1 ± 9.6
White sucker	43.1 ± 6.1	1291.7 ± 436.5	8	75.0	6.7	11	81.8	0.2	38	97.4	38.1	-	-	206.8	5.6 ± 7.4
Shorthead redhorse	38.5 ± 4.0	867.2 ± 235.8	1	0	0	3	0	0	5	0	0	0	0	0	0
Northern pike	55.1 ± 8.7	1411.7 ± 701.5	3	0	0	2	50.0	< 0.1	13	7.7	< 0.1	1	-	< 0.1	-
Walleye	35.0 ± 8.6	518.2 ± 330.4	5	0	0	9	0	0	30	3.3	< 0.1	1	-	< 0.1	-

For species that consumed corixids in fall, the total and average number (#) of corixids (with the exception of white sucker, for which corixids were not counted) and the total and average weight (wet weight; Wt) of corixid material found in stomachs are provided. Also shown for each species is the average fork length (FL) and weight (Wt) of all fish collected that did not have empty stomachs. Average (Avg) values are presented ± SD.

Table 3. Estimated Range and Median Values of the Annual Corixid Flux Both Into Rivers and Out of Wetlands in the PPR Every Fall After 1000 Runs of a Monte Carlo Simulation

North and South Saskatchewan Rivers within SK (Inputs)	Number of Corixids	Biomass (metric tons)
Total Length (combined banks): 2400 km	Range: 19.4 billion–325.7 billion	42–7118
	Median: 170.4 billion	1594
All PPR Rivers (Inputs)	Number of Corixids	Biomass (metric tons)
Total Length (combined banks): 18,686 km	Range: 152.0 billion–2.5 trillion	334–51,949
	Median: 1.3 trillion	12,512
All PPR Wetlands (Exports)	Number of Corixids	Biomass (metric tons)
Total Wetland Area: Range: 5.0–11.6 million ha	Range: 436.1 billion– 2.1 trillion	979–43,649
Median: 8.6 million ha	Median: 1.1 trillion	11,838

dance in these habitats after migrations began in September. This created a shift in species composition, where species that were previously most abundant in the rivers such as *Sigara lineata*, *Sigara trilineata*, and others, became vastly outnumbered.

In contrast to the rivers, average corixid numbers in wetlands declined considerably from the time of migration into the rivers until freeze-up. However, mortality, and not just migration, may also have contributed to the total declines of wetland corixids as conditions grew harsher in fall. This is especially true for *Trichocorixa verticalis interiores*, the most abundant wetland corixid in this study, which is unique among most corixid species in that it overwinters in the egg stage, with adults dying off in late fall (Tones 1977). Numbers may also have remained high in some wetlands as a result of corixids that did not manage to leave in time or that were incapable of flight. Notably, *Cymatia americana* does not appear to migrate en masse, but remains in the wetlands, as this species is capable of overwintering encased in ice (Hussey 1920; Mihalicz 2015).

Our findings coincide with those by Stoaks and others (1980) and Hilsenoff (1970; 1984), who observed extremely high abundances of corixids migrating into streams in North Dakota and Wisconsin to overwinter, accumulating in areas of standing or slow-moving water. These studies also noted increased species richness in fall owing to the occurrence of wetland-breeding species. Stoaks and others (1980) observed a shift in species composition similar to this study, with *C. audeni*, *S. decoratella*, and other migrants greatly outnumbering the species that were previously dominant in summer.

Fish Predation

Wetland-based energy and nutrients entered the riverine food webs in this study through predation

on migratory corixids by several species of fish. Goldeye and mooneye fed primarily on a mix of aquatic and terrestrial invertebrates in summer, with both species shifting to corixids as the dominant prey item once the fall migration had begun. In the fall, longnose sucker fed almost exclusively on corixids, while corixids became an important prey item by weight for many of the white sucker (Table 2). Goldeye, mooneye, longnose sucker, and white sucker also appeared to feed the most during the fall, with stomachs that were at least twice as full as in summer (Table S6). Corixids were not fed on by the shorthead redhorse and were of little direct importance to the diets of northern pike and walleye, with fish being the dominant prey items for both species in all seasons. Relatively few fish were collected in spring, because this could only be done once ice had melted from the rivers, by which point most of the migratory corixids appeared to have left (fish sampling in April 2016 was carried out between two and three weeks after corixid sampling in that month; see Tables S2, S3).

Several studies have shown an increase in corixid predation by hiodontids during the fall in riverine ecosystems and connected lentic habitats. In waterbodies of the Peace-Athabasca Delta, Alberta, Donald, and Kooyman (1977) found that corixids became a major food item for certain age classes of goldeye in October and November, whereas Little and others (1998) also noted an increase in the importance of corixids to the diets of goldeye collected in October versus during the summer in the Slave River, Northwest Territories. In the Assiniboine River, Manitoba, Glenn (1975) found that corixids formed the majority of material ingested by mooneye, which also consumed the most food in spring (April to May) and fall (October to November), which would coincide with the times of peak corixid abundance due to migration that was observed in this study. However, none of these studies indicated that an increase in corixid abun-

dance had occurred due to migration into these habitats.

Despite the importance of corixids to the diets of white and longnose sucker shown here, other studies have found limited evidence for predation on corixids by these species (for example, Salt River, Little and others 1998; Missouri River, Fisher and others 2001). It is also interesting that the shorthead redhorse did not appear to use this subsidy, when its diet is expected to be similar to other sucker species (Scott and Crossman 1973; Stewart and Watkinson 2004). Future studies that examine changes in prey abundance, and which also extend into the fall or early spring, would be valuable in detecting the occurrence and use of migratory corixid subsidies by these and potentially other fish species in different river systems.

Corixids proved to be of indirect importance to northern pike and walleye by being consumed by fish that these species are known to prey on, such as goldeye and suckers (Little and others 1998; Fisher and others 2001), and as evidenced by corixid remains found in the guts of prey fish that were eaten by northern pike and walleye in this study. Smaller fish species such as shiners and stickleback, also common prey for walleye and northern pike (Little and others 1998), have been shown to feed on corixids (Savage 1989; Batzer and Resh 1992; McCulloch 2003) but were not examined here. Future work assessing the importance of the fall migratory corixid flux to the diets of these smaller fish species in rivers will be necessary to understand the full significance of this subsidy.

Feeding on corixids may convey substantial nutritional benefits to predators. Even low quality but highly abundant subsidies can drive food webs (Marcarelli and others 2011) and the fall corixid flux into rivers may provide both, potentially transferring large quantities of energy and nutrients between habitats (Table S8). For example, migratory corixids may be exceptionally high in lipid content relative to other insects (Ghioni and others 1996; Sushchik and others 2016). In an examination of essential long-chain n-3 polyunsaturated fatty acid (PUFA) content of various Heteropteran species from wetlands in Central Siberia, Sushchik and others (2016) found that corixids contained the highest docosahexaenoic acid (22:6n-3 DHA) and eicosapentaenoic acid (20:5n-3, EPA) content relative to all other species examined and compared to the literature reports for other aquatic insects. Previous research based on elemental carbon to nitrogen ratios has indicated that wetland corixids in Saskatchewan tend to accumulate lipids toward the end of the summer

prior to migration (S. Srayko, unpublished data) as lipid reserves allow for survival in some Hemipterans during periods of non-feeding (Steinbauer 1998) and in corixids are also used for flight muscle and ovarian development (Smith 1977). Consumption of migratory corixids could aid in lipid accumulation by fish, a common strategy for winter survival (Biro and others 2004; Houston and others 2014) which would make this flux a valuable food source in the prewinter period.

Food Web Effects

Energy and nutrients derived from a combination of sources including headwaters (Vannote and others 1980), floodplains (Junk and others 1989), and other local autochthonous and allochthonous inputs (Thorpe and Delong 1994) are known to support fish production in rivers (Dettmers and others 2001; Humphries and others 2020). However, one source not accounted for in these models of riverine energy flow is an influx of migratory prey from distant, external systems such as geographically isolated and highly productive PPR wetlands. The transfer of subsidies can level the productivity of different habitats, with more productive habitats fuelling the growth of consumers in less productive systems, decoupling them from local energetic pathways (Polis and others 1997), and may also add resilience to recipient communities by providing nutrients and energy after a disturbance (Lundberg and Moberg 2003; Bauer and Hoyer 2014; Uno and Power 2015). For example, Uno and Power (2015) found that adult mayflies (*Ephemera maculata*) migrate from sunny, productive river mainstems to cold, shaded, and unproductive tributaries of the South Fork Eel River in California, and provide an important subsidy to young of the year steelhead trout (*Oncorhynchus mykiss*), greatly enhancing growth relative to those fish that did not have access to this food source, and also lessening antagonistic interactions between fish related to competition for food. The large flux of migratory, wetland-based corixids has the potential to act on riverine fish communities in such a capacity, bolstering production in certain species and alleviating competition by providing an overabundance of food (Little and others 1998). However, if populations of riverine fish that are subsidized by migratory corixids are able to achieve greater abundances than would be possible relying solely on local prey sources, this could also result in apparent competition between the wetland-based corixids and riverine invertebrate communities, with these fish

subsequently increasing predation pressure on resident invertebrates when corixids migrate away or in years when corixid inputs arrive in lesser amounts (Polis and others 1997; Bauer and Hoye 2014).

In addition to impacts on fish, future studies examining predator–prey or competitive dynamics between migratory corixids and riverine invertebrate communities would be valuable to understanding the full impact of this flux on riverine food webs. Subsidies to terrestrial consumers may also be worthy of study. For example, gulls and waterfowl have been observed feeding on riverine corixid aggregations, bats and other birds are known to prey on corixids while in flight (Bird 1961; Reimer and others 2010; John Acorn, personal communication), and riparian spiders have been observed preying on corixids when they climb onto riverbanks in preparation for spring flights (S. Srayko, personal observation).

Flux Transfer from Wetlands to Rivers

We estimate that thousands of corixids, potentially amounting to hundreds of grams of biomass, could be entering every square meter of water along riverbanks in Saskatchewan during fall migrations. Our findings of 117 to 1274 g/m² (wet mass) entering passive samplers in the rivers over a one to two-month period in the fall may match or exceed the typical inputs of terrestrial invertebrates into streams and wetlands in temperate regions, which have been estimated to range from 10 to 54 g per m² (dry mass) per year (Kraus and others 2011).

If corixid migrations occur across the PPR in a similar extent to what was measured in our study area, we estimate that fall corixid fluxes could amount to ~1500 tons of biomass entering the North and South Saskatchewan rivers within Saskatchewan, and over 12,000 tons of biomass entering several major rivers over the entire PPR every year. The biomass of migratory corixid species present in wetlands across the PPR may also near 12,000 tons when wetland area totals approximately 8.5 million ha (Table 3). The area of wetlands in the PPR has been estimated at 8.3 million ha (Doherty and others 2018); however, this is prone to fluctuations between years, as wetlands in the Canadian portion of the PPR may exceed 30 million ha alone in years with abundant precipitation (Ducks Unlimited Canada Wetland Inventory). The significance of wetlands across the landscape to this corixid flux into rivers also depends on the distance that corixids can fly, the limits of which have not been clearly defined. All of

the wetlands in this study fell within 15 km of a large river, which has been estimated as the limit of how far some European corixid species may be capable of flying under windless conditions in a single day (Popham 1951, 1952; Scudder 1976; Stonedahl and Lattin 1986). However, it is likely that some corixids may be able to fly much further, especially if aided by wind, with other estimates ranging from 65 to 90 km/day (Popham 1964). For example, Hu and others (2016) found that insects larger than 10 mg (the weight of at least several corixid species; see Table S7) can make use of seasonal tailwinds for dispersal, and may be able to travel over 200 km in four hours. Future studies examining corixid species composition and migration patterns in a wider range of wetlands, some further from suitable overwintering sites, would allow for further assessment of which habitats are the most important contributors to this seasonal flux.

The corixid flux estimated in this study matches or exceeds several recent estimates of other notable cross-ecosystem fluxes, including estimates of the biomass of insects that fly over the southern UK on a yearly basis (3200 tons, Hu and others 2016) and the biomass of Pacific salmon (*Oncorhynchus* spp.) that return to the Pacific Northwest states of Oregon, Idaho, and California (11,800–13,700 tons, Gresh and others 2000; Table S9). Large seasonal corixid migrations also occur well outside the PPR in North America, as corixids have been observed mass migrating into lotic habitats as far north as Alaska (Cummins 2011) and between overwintering and breeding sites as far south as Arizona (Stevens and others 2007), indicating that mass movements by this family of insects may be linking food webs in regions beyond our study area.

Implications for Conservation

The loss and degradation of wetlands in the PPR may affect the strength of the linkage that exists between these habitats and rivers via corixid migration. It is estimated that up to 70% of natural prairie pothole wetlands have been lost due to agriculture and urban development (Dale-Burnett and Anderson 2003; Dahl 2014). Small, temporary, and seasonal wetlands are more readily lost (McCauley and others 2015), which could be of particular consequence to corixid species that rely on these small, shallow habitats. However, the aquatic Hemiptera of the prairies are typically adaptable, ecological generalists, and may be capable of adjusting to the loss of natural wetlands in

part by using habitats such as human-made dug-outs (Scudder and others 2010).

Wetlands provide many critical ecosystem services, such as habitat for wildlife, drought and flood protection, carbon storage, and mitigating the effects of pollution (US EPA 2015; Doherty and others 2018). Another ecosystem service provided by wetlands is the transfer of valuable subsidies to external food webs. This study has revealed one such subsidy in the form of an aquatic insect that migrates en masse between wetland and river habitats every year. Both river and wetlands ecosystems must be conserved together to ensure that this connection is not lost.

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DATA AVAILABILITY

Data is available at Srayko, S., Jardine, T., Phillips, I., Chivers, D. (2022) Seasonal mass migration of water boatmen (Hemiptera: Corixidae) as a wetland–river linkage and dietary subsidy to riverine fish. Federated Research Data Repository. <https://doi.org/10.20383/102.0541>

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