

UNIVERSITY OF WISCONSIN-LA CROSSE

Graduate Studies

INSECT EMERGENCE FROM A LARGE RIVER SYSTEM IN THE PRESENCE
AND ABSENCE OF BIGHEAD (*HYPOPHthalmichthys nobilis*) AND SILVER
(*H. molitrix*) CARP

A Research Thesis Submitted in Partial Fulfillment of the Requirement for the Degree of
Master of Science

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Biology – Aquatic Science

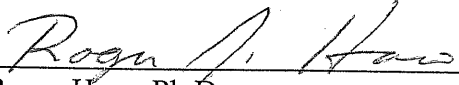
May 2012

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By Patrick Kelly

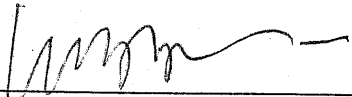
We recommend acceptance of this thesis in partial fulfillment of the candidate's requirements for the degree of Master of Science in Aquatic Science

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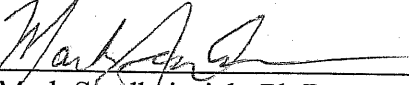
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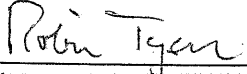
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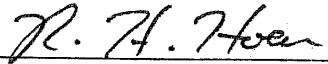
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ABSTRACT

Kelly, P.T. Insect emergence from a large river system in the presence and absence of bighead (*Hypophthalmichthys nobilis*) and silver (*H. molitrix*) carp. MS in Aquatic Science, May 2012, 66 pp. (R. Haro)

Aquatic insect emergence is an important resource for terrestrial insectivores that rely on aquatic insects while raising young, or when terrestrial production is low. Emerging insects also transfer valuable high-energy lipids from phytoplankton to terrestrial consumers. The objectives of this project were to: (1) quantify insect emergence in two large-river systems that differed in primary productivity, and (2) determine the impacts of bighead and silver carp on the emergent insect community. Floating traps (surface area = 0.25 m²) were used to sample emerging adult insects, and were placed in study sites with and without Asian carp. Insects were sorted, identified to family, and individually weighed to determine emergent biomass rates. Sites with carp displayed the greatest insect flux; however, insect diversity was greatest at sites without carp, and lowest at the sites with carp. Emergent insect diversity was correlated with the presence of aquatic vegetation. Insect abundance was also linearly related to algal standing stock (measured as chlorophyll *a*). This suggests that primary productivity in large river systems have a positive impact on the magnitude of insect emergence, and that the diversity of insects increases with aquatic vegetation. Bighead and silver carp may positively impact insect emergence by removing zooplankton competitors, but may decrease insect diversity by a reduction in large-sized phytoplankton food resources.

ACKNOWLEDGEMENTS

I thank my advisor, Dr. Roger Haro for all of the guidance in the research project as well as in the assembly of this manuscript. I also thank my committee members: Drs. William Richardson, Mark Sandheinrich, and Robin Tyser for their input and support. A special thanks to all of those who assisted me in the field, as well as with data preparation and manuscript editing including: Sara Erickson, Shawn, Joe, and Doyn, and Jim Coloso. I thank the University of Wisconsin – La Crosse graduate school and the biology program for the 7 years spent at a wonderful institution, and to all of the people along the way who have helped me in some capacity, especially my fellow graduate students. Thank you to my funding sources of the University of Wisconsin – La Crosse Research, Service, Education, and Learning grant as well as the United States Geological Survey, as well as the Nature Conservancy for their support of access to Emiquon Preserve. Last, but definitely not least, I thank and dedicate this thesis to my family. To my parents Tom and Cecelia Kelly for their unending support, to my sister Erin Luckey for always giving me the motivation I needed to succeed and a person to look up to, and to my wife Erin Kelly for the support, love, and understanding during the long days and late nights throughout this process.

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INTRODUCTION

Aquatic insects are characterized by an aquatic larval stage, which eventually develops into a terrestrial or aerial adult. This adult stage is spent predominantly outside of the water column, often times in the terrestrial environment in order to feed or reproduce. Because of this emergence, aquatic insects are not only a large part of the aquatic food web in terms of resources for upper trophic levels, but also make up a significant portion of the terrestrial food web as they emerge as adults (Ballinger and Lake 2006). This flux of insect biomass to land links the two ecosystems, and may supply a very important energy subsidy to terrestrial consumers (Power and Dietrich 2002; Baxter *et al.* 2005). Examples of resource subsidies include the movement of terrestrial carbon to lakes and streams and terrestrial insect inputs into the water (Polis *et al.* 1997; Lamberti *et al.* 2010). The flux of insects from the water column to the landscape, however, is a less reported and less studied but, perhaps, locally important resource subsidy. Insect emergence also provides a flow and a fate for river production, through the transfer of exuviae and adult biomass. This resource subsidy supplies prey otherwise unavailable to terrestrial predators, and may support riparian communities during periods when terrestrial resources are scarce (Nakano and Murakami 2001; Uesugi and Murakami 2007).

Several studies have shown the importance of emerging insects as food for reptiles (Sabo and Power 2002), terrestrial predatory insects (Burdon and Harding 2007),

and birds (McCloskey *et al.* 2009; Murakami and Nakano 2002). Migratory phenologies for many birds coincide with periods of major insect emergence (MacKenzie 2005; Smith *et al.* 2007), and the quantity of insect biomass from the aquatic environment may have an effect on the distribution of insectivorous bird species. McCarty and Winkler (1999) found that emerging aquatic Diptera comprised the majority of tree swallow (*Tachycineta bicolor*) diets, with emergent Odonata making up a second significant dietary contribution. These subsidies appear to be especially important to young nestlings. Gray-crowned Rosy Finches (*Leucosticte tephrocotis dawsoni*) were observed changing their diets from primarily seeds to emergent aquatic insects while feeding their young (Epanchin *et al.* 2010). The benefit of switching diets provides the nestlings with a more lipid-rich and nutritious food source than would be offered by a completely seed-based diet. Similar behaviors are also seen in Wilson's snipe (*Gallinago delicata*), which are observed to change their diets from oligochaetes and seeds in the non-breeding periods, to a diet consisting primarily of adult aquatic insects during the spring (McCloskey *et al.* 2009). Emergent insects ingested by terrestrial predators provide a flux of an abundant food mass, but also nutrients and high quality lipids produced in the aquatic environment and transferred to the terrestrial environment

The ultimate contribution of these subsidies is largely dependent on the secondary production of aquatic insects. Aquatic insects serve as an intermediary between aquatic primary producers and higher land-based trophic levels. Secondary production in aquatic habitats that emerges to the terrestrial environment supplies a critical source of biomass and high-quality carbon to the landscape, and represents an important flow of resources

from one ecosystem to another. The quality of this resource subsidy to the recipient system depends heavily on the species composition of the primary producers of the donor system. For example, primary production derived from algal communities dominated by diatoms, chryptophytes, and chrysophytes contain higher concentrations of polyunsaturated fatty acids (PUFAs), relative to those dominated by cyanobacteria (Kainz, *et al.* 2010). Invertebrates, including aquatic insect larvae, grazing on phytoplankton will produce tissues rich in PUFAs and will provide lipid-rich prey for terrestrial predators via emergence (Gladyshev *et al.* 2009).

A more productive system may provide a higher quantity of high quality food resources for insect consumers (Polis *et al.* 1997), and can therefore support the riparian community with this high-quality carbon source. Although most aquatic insects derive a large amount of their bulk fatty acids (FA) from allochthonous material, autochthonous food sources generally have a greater amount of fatty acids available per unit mass, and are of greater quality (Torrez-Ruiz *et al.* 2007). Fatty acids supplied by phytoplankton and periphyton are important for support of the insect's growth and reproductive output (Vanderploeg *et al.* 1996; Goedkoop *et al.* 2007). These essential fatty acids (EFAs) are assimilated into the tissues of aquatic insects through their diet, and are transferred via emergence to the terrestrial ecosystem for potential consumption by birds and other organisms (Gladyshev *et al.* 2009). Essential fatty acids are so termed because of the necessity to assimilate them through the diet, as the organisms themselves cannot synthesize them *de novo*. The quality of fatty acids available is largely dependent on the

availability of algal resources in the aquatic ecosystem; any reduction or alteration of this food resource may affect the transfer of these EFAs to the terrestrial consumers.

Much research has shown the importance of emergent insects as a subsidy to terrestrial ecosystems in streams (Li *et al.* 2011; Nakano and Murakami 2001; Malison and Baxter 2010), lakes (Epanchin *et al.* 2010; Pope *et al.* 2009; Finlay and Vredenburg 2007), and wetlands (MacKenzie and Kaster 2004; Whiles and Goldowitz 2001), however, little is known about insect emergence from large-river ecosystems. Large rivers are often characterized by high levels of primary production, but the secondary productivity of aquatic insects in these large systems has yet to be fully investigated.

Large rivers provide important environmental and economic resources. They are critical transit routes for goods, services, recreation, and are valuable ecosystems for sport and commercial fisheries (Baker *et al.* 1991; Keddy *et al.* 2009; Mac *et al.* 1998). River floodplains also supply water resources and arable soil for agriculture (Verhoeven and Setter 2010). Large rivers supply important habitat for fish, invertebrates and waterfowl, and also provide habitat to migratory birds and other riparian and wetland organisms (Stafford *et al.* 2007; Kirsch 1995; King *et al.* 2006; USACE 2005). Rivers are important downstream-transport systems for nutrients and sediments, moving loads hundreds or thousands of kilometers to their ultimate receiving waters (Poff *et al.* 1997).

Large rivers often contain side channels and backwater areas that are productive and biological drivers for, and play a pivotal role in, the general productivity of the system. Backwaters are sites of increased uptake and removal of nitrogen supplied by main channel water (Richardson *et al.* 2004; Strauss *et al.* 2004). As main channel water

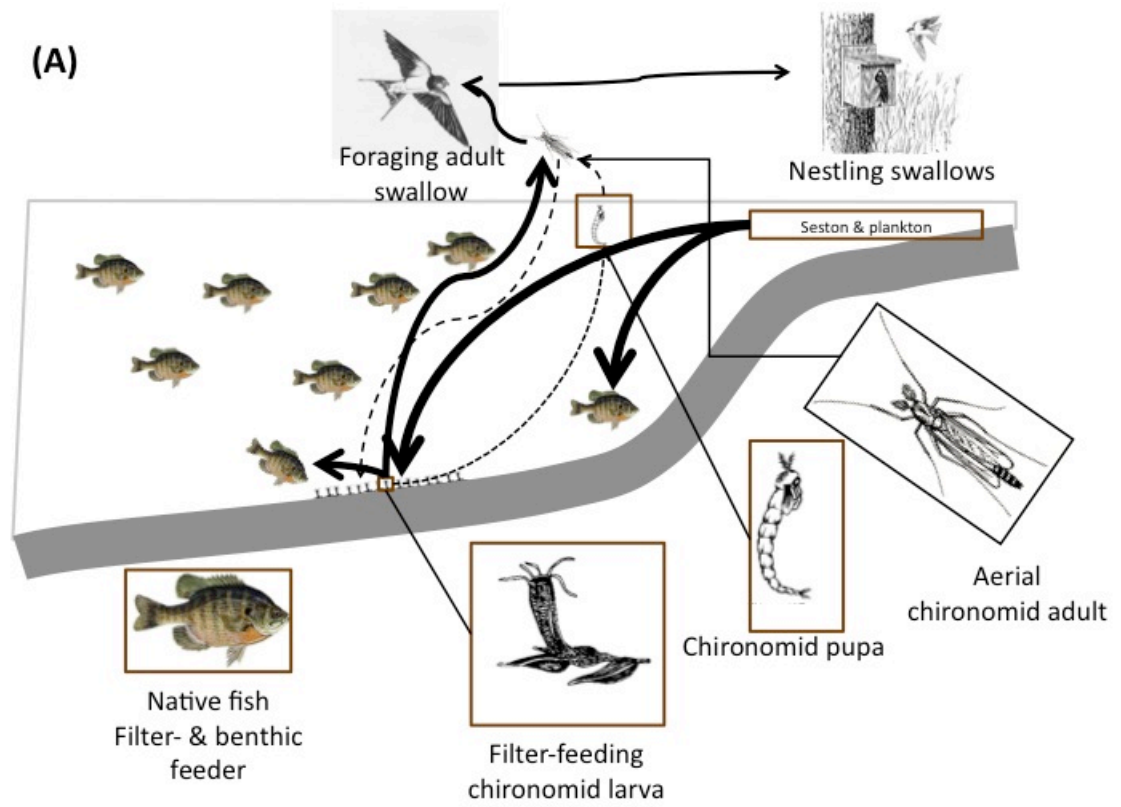
enters side channels and backwaters areas, velocities decrease, suspended particles drop out of the water column, and carbon-rich sediments and anoxia develop. Nutrients and carbon-rich sediments promote development of dense and diverse macrophyte beds, promoting habitat heterogeneity and increased biodiversity (Bukaveckas 2007). These conditions also create areas where the biogeochemical cycling of nitrogen and phosphorus is high, with elevated rates of denitrification and sediment phosphorus release (Houser and Richardson 2010). Yet, the ecology of these river systems has often been interrupted by human alteration, in particular with the introduction of invasive species.

Invasive fish have major effects on stream and river environments, short-circuiting energy flow of local food webs and altering energy flow to resident native species. An invasive planktivorous fish will likely have far reaching effects by diminishing the foundation of food chains (Irons *et al.* 2007). Consequently much of the rest of the local food web will be altered. Aquatic insects, while diverse as a collection of species, are predominantly grazers and filterers, relying on phytoplankton, periphyton, and detritus. Alteration of the quantity or quality of these resources by an invading species would likely impact insect production and emergence. For example, stocked exotic trout species have greatly reduced the amount of emerging aquatic insect species in experimental lakes, significantly reducing biomass available to predators on the landscape (Pope *et al.* 2009). Although studies have shown the direct effect of invasive insectivorous fish species on the flux of emergent insects to the landscape (Epanchin *et al.* 2010; Baxter *et al.* 2004, Finlay and Vradenburg 2007), the indirect effect of an invasive fish altering the base of the aquatic food web is largely unstudied.

Phytoplanktivorous invasive fish may lower phytoplankton abundance and alter its composition, indirectly affecting the production of aquatic insects, and ultimately the number of aquatic insects emerging to the terrestrial ecosystem.

Bighead (*Hypophthalmichthys nobilis*) and silver (*H. molitrix*) carp are two invasive species of Asian carp currently found in North America. The full extent of their range is uncertain, but these species have had undesirable impacts on aquatic ecosystems across the Mississippi River basin. Because of their efficient filter-feeding behavior, both bighead and silver carp were introduced to the United States to control excess phytoplankton blooms in aquaculture facilities. Silver carp are notorious for their impacts on recreational boating due to their tendency to jump from the water when distressed. The carp have also had effects on the native fish communities, significantly decreasing the condition of the native filter feeders in the areas in which the carp have invaded (Irons *et al.* 2007; Sampson *et al.* 2009). The carp have been known to cause a sharp decline in some species of zooplankton in freshwater communities, and may change the community structure of the remaining zooplankton to smaller and more evasive species (Ke *et al.* 2009). Similarly, silver carp can reduce the size of available phytoplankton by efficient filter feeding, which leads to a decrease in size of the remaining phytoplankton (Ma *et al.* 2009). A reduction of the size and abundance of phytoplankton and zooplankton can significantly reduce resources available to native filter-feeding fish, and may also have an effect on aquatic insects that use this plankton as a food source (Figure 1). Little is known about the impact that these fish will have on the

(A)



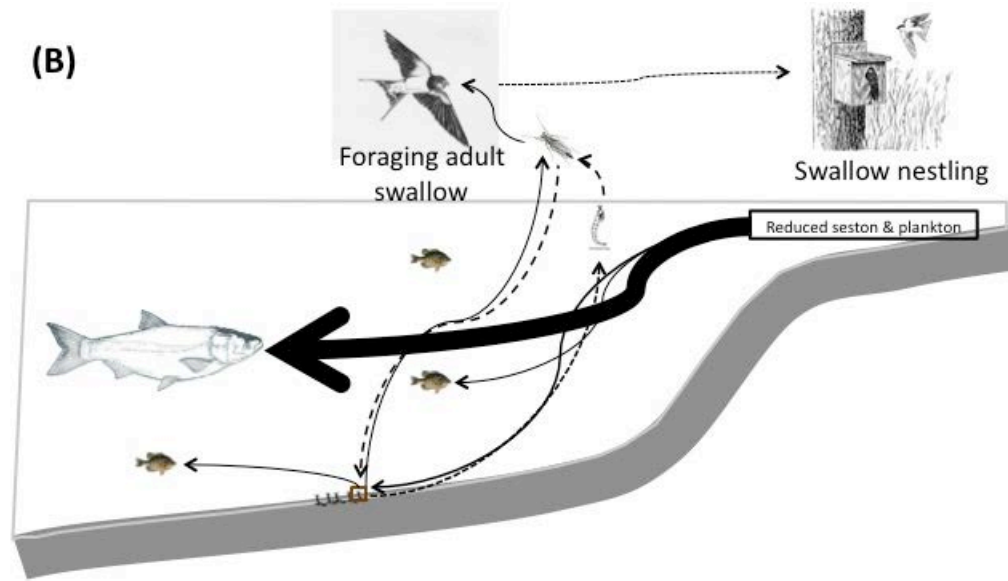


Fig 1. Hypothetical diagram of the biomass fluxes between seston and consumers (red arrows) in the (A) absence and in the (B) presence of invasive Asian carp. The thickness of the red arrows indicates estimated flux magnitude. The dashed, black arrows show the life cycle of aquatic insects (a chironomid midge) including the emergence of aerial adults.

native macroinvertebrate communities, and similarly the impact on the flux of insect biomass from these large river systems is unknown.

OBJECTIVES AND HYPOTHESES

My goal was to quantify the magnitude of insect flux from a large river system, and to determine the impact of an invasive filter-feeding fish on insect emergence. My objectives were to measure insect emergence in two large river ecosystems, quantifying emergent biomass flux from the Upper Mississippi and Illinois Rivers; rivers that vary in 1) productivity and 2) presence of invasive Asian Carp.

The first objective of this project was to determine insect flux in a large river ecosystem in sites of varying primary productivity. Insects were collected in different sites in the upper Mississippi (mesotrophic) and Illinois Rivers (eutrophic). Abundance, taxonomic differences, and biomass fluxes were determined. I hypothesized that areas of greater primary production (characterized as water column chlorophyll *a* concentration) would also have a larger flux of insect abundance and biomass because of the abundant resources available to stimulate secondary production.

The second objective was to determine the effect of an invasive planktivorous fish on insect emergence. I hypothesized an indirect effect of a filter-feeding fish such that a significant part of the lower food web would be diminished. Because of the possible decline of plankton abundance, the quantity of emergent biomass between sites with the invasive carp and sites without the carp was expected to be significantly lower. In

addition to the hypothesized decrease in insect biomass flux, the decrease in resources or shift in phytoplankton size structure may cause a change in the community structure or decrease diversity in the affected area.

METHODS

Study area

The study sites for this project were located in Navigation Pool 8 of the Upper Mississippi River and La Grange Pool in the Illinois River, a major tributary of the Mississippi. The upper Mississippi River is defined as the section from origin at Lake Itasca, Minnesota to the confluence with the Ohio River near Cairo, Illinois. The upper Mississippi is approximately 1300 km long, and is joined by a number of major tributaries including the Wisconsin, Missouri and Ohio Rivers. The drainage area for the upper Mississippi River is approximately 489,500 km², and the average discharge ranges from 260 m³ s⁻¹ (near St. Paul, Minnesota), to approximately 5800 m³ s⁻¹ at Thebes, Illinois (UMBRA 2011). The river has had a long history of human interactions and alterations including the construction of 29 locks and dams for navigation, consistent dredging to maintain a shipping canal, and the introduction of numerous invasive species including zebra mussels (*Dreissena polymorpha*), common carp (*Cyprinus carpio*) and the New Zealand mud snail (*Potamopyrgus antipodarum*). The study sites in the Mississippi River were located in Pool 8, the navigation pool created by lock and dam 7

(Genoa, Wisconsin), to the upstream extent at lock and dam 8 (Dresbach, Minnesota).

The study sites in the Illinois River (ILR) were conducted in the La Grange Pool, an impoundment created by La Grange Lock and Dam, extending from south of Beardstown, IL to Peoria, IL.

Six sites were sampled for insect emergence, four in the Illinois River and two from Pool 8 of the Upper Mississippi River. Sites in the ILR were selected based on the presence or absence of bighead and silver carp; bighead and silver carp have not established populations in Navigation Pool 8. Carp sites on the ILR were located at a northern (Big Lake North; 40°27'17.8668 N 90°3'26.86 W) and southern (Big Lake South; 40°26'44.718 N 90°3'6.275 W) ends of Big Lake. Big Lake is a backwater of the Illinois River located near Havana, Illinois. Two sites without Asian carp were in the Emiquon National Wildlife Preserve, also at a northern (Emiquon North; 40°21'33.7824 N 91°55'0.473 W) and southern (Emiquon South; 40°19'14.0268 N 91°55'0.325 W) part of a flooded agricultural field that was once a lakebed of the Illinois River. Although formerly connected to the Illinois River, Emiquon has been disconnected for approximately 100 years, and therefore has not been invaded by the carp. The two sites selected in Pool 8 were Lawrence Lake (43°43'42.1788 N 92°37'46.51 W) and Shellhorn (43°38'42.1728 N 92°43'38.518 W); neither site contained Asian carp. Lawrence Lake is a backwater lake of the upper Mississippi River located near Brownsville, Minnesota, and is connected to the main channel on the southern end of the lake. Shellhorn is an off-

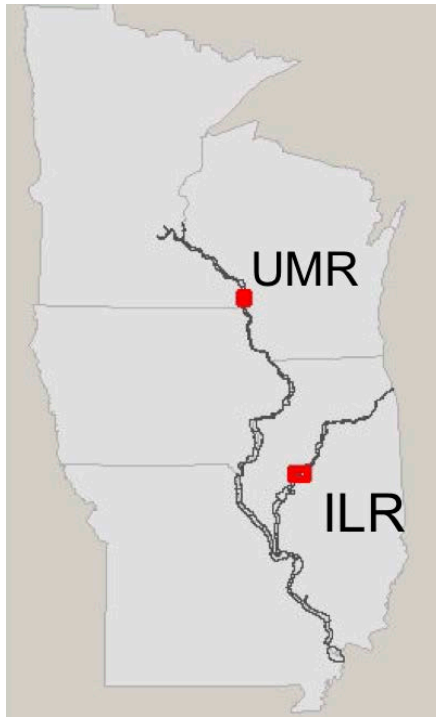


Fig 2. Map of relative locations of study sites. Lawrence Lake and Shellhorn located in the upper Mississippi River (UMR), and Big Lake North, Big Lake South, Emiquon North and Emiquon South located in the Illinois River (ILR).

channel area of the Mississippi River, just south of Lawrence Lake, and is separated from the main channel by an island complex (Figure 2). Insect emergence sampling period was based on the presence of tree swallow nestlings; it commenced during the first appearance of hatchlings, and was terminated after the fledging of the chicks.

Water chemistry

Dissolved oxygen and temperature were measured once every two weeks (Yellow Springs Instrument Company, Yellow Springs, Ohio, USA) at a depth of approximate 0.5 m. Water for analysis of nutrients and chlorophyll *a* concentrations were collected in 1-L brown Nalgene bottles at a depth of approximately 0.5 m, and transferred to smaller 100-mL sample bottles for analysis of total nitrogen (TN), ammonium (NH₄-N), nitrate (NO₃-N), total phosphorus (TP), and soluble reactive P (SRP). Water samples for analysis of total suspended solids, volatile suspended solids and chlorophyll *a* were filtered and analyzed in the lab within 3 hours of collection. Water nutrients, chlorophyll *a*, TSS and VSS were analyzed by the USGS-Upper Midwest Environmental Sciences (UMESC) water quality laboratory according to APHA (1992) methods: Total nitrogen (persulfate digestion, copper-cadmium reduction), NH₄-N (automated phenate), NO₃-N (copper-cadmium reduction), total phosphorous (persulfate digestion, ascorbic acid reduction), soluble reactive phosphorous (ascorbic acid reduction), and chlorophyll *a* (fluorometric determination of chlorophyll-a), and total suspended solids and volatile suspended solids (gravimetric).

Insect emergence

Insects were collected from 27 May 2011 to 9 July 2011 at the four Illinois sites and from 20 May 2011 to 25 June 2011 in Pool 8. Floating emergence traps were placed approximately 50 meters from shoreline at each site to sample insects likely selected by adult tree swallows (McCarty and Winkler 1999). All traps were placed on top of a water depth of about 0.5 to 3.50 meters. The traps were made from transparent 1-mm thick polycarbonate plastic (Lexan) and were formed into a cone shape. Two triangular holes were cut from the sides of the plastic traps and were enclosed with a 500 μm mesh netting to allow for airflow and for perching sites for the insects, but did not allow for insects to escape. Inverted screw-top glass jars were secured on top of a polypropylene funnel and were used to trap the emerging insects. The screw-top glass jar contained a 70% ethanol solution to preserve the insects. The plastic cones were attached with cable ties to a 2-m² PVC square base that floated on the water surface. Each trap was attached to a 4.3-m PVC pipe that was anchored to the sediment to hold the traps in place, but is designed for movement with changes in the water level. Traps were attached with a 1-m plastic-covered metal cable, and were designed to be able to rotate 360° around the PVC pole. This allowed the traps to be able to collect a standard area of about 3.1 m². Anchors were made from PVC and filled with cement, with metal rebar inserted through bottom of the anchor to be inserted into the sediment (Figure 3). Traps were above the water surface, with a portion of the base below the water surface to prevent insects escaping from changing water levels and wave action. Emergence traps were modeled

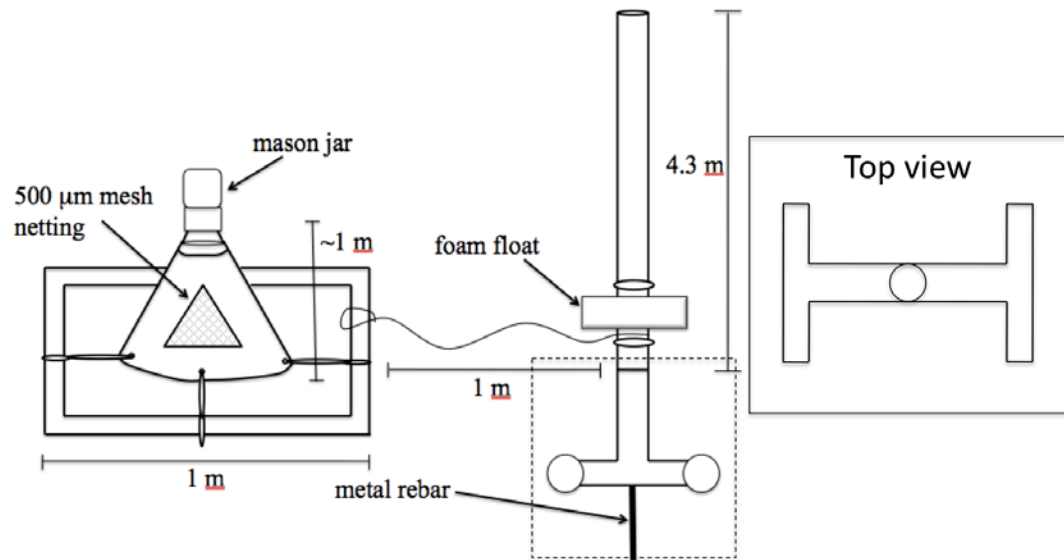


Fig 3. Schematic of emergence trap design. Emergence trap (left) rotates around PVC pole, which is attached to an anchor that is pushed into the sediment (dashed-boxed region).

after similar traps used by Stagliano *et al.* (1998) and Davies (1984), and modified by Lemke *et al.* (2007). Traps were visited by kayak approximately every 3 days at all sites except Lawrence Lake, which was sampled weekly due to few insects per trap. All traps were cleaned of algal growth and debris when sampled, but were allowed to remain in patches of vegetation that later developed. Insects were removed from the traps with a hand-held aspirator (Bioquip, Rancho Dominguez, California, USA) and placed into separate clear-plastic bags for storage in the field. Upon return to the laboratory, bags were stored in the freezer overnight to allow samples to freeze for easy sorting. All insect from each trap were transferred to separate scintillation vials containing 70% ethanol, and stored at the lab until the end of the sampling period.

Abundance and biomass estimates

Using keys from Merritt *et al.* (2008), insects were counted and sorted from each trap by taxonomic family. Individual insects were placed on small, pre-weighed sections of tin foil and dried in an oven at 60°C for 24 hours. Each insect was weighed individually to the nearest 0.1 mg on an analytical balance (Ohaus, Parsippany, New Jersey, USA). Samples with >30 individuals in a given taxonomic family were subsampled; 30 individuals were weighed, and the remaining number of individuals multiplied by average weight to estimate the remaining sample mass. Insect “flux” ($\text{mg dry weight} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) was calculating by dividing the sampled mass by trap area sampled and total length of time during which the trap collected insects.

Data analysis

Repeated measures analysis of variance (RM-ANOVA) was used to compare insect emergence (abundance and biomass flux) among study sites. Emergence data from each trap were pooled and summed for comparison among each sampling date for each site. Emergence rates were scaled using time between sampling, and compared among study sites as the between-treatment factor ($n = 6$). Emergence rates were also separated into sites with carp and sites without carp ($n = 2$ and 4 , respectively) and used as within-treatment factors. Study sites with and without carp were nested within the treatments, falling into categories of “carp site” or “no carp site”. Data was log-transformed prior to statistical analysis in order to meet assumptions for parametric analysis (Shapiro-Wilk test), and checked for outliers using the Dixon test. If any statistical differences were seen in analysis of study sites or regions, Tukey’s multiple comparisons test was used to determine treatment differences. Relationships between mean abundance or biomass flux and average water chemistry variables were modeled using linear regression. Water chemistry parameters were log transformed in order to meet assumptions of normality. Cumulative mass and abundance were also analyzed by carp treatment with a Welch two-sample t-test ($n = 2$ vs. 4). For cumulative analysis, study sites were nested within “carp” and “no carp” treatments. All comparisons were made using $\alpha = 0.05$, and statistical tests were made using R statistics software (R Development Core Team, Vienna, Austria 2008).

RESULTS

Water chemistry

Of all water quality parameters measured, dissolved oxygen, total suspended solids, volatile suspended solids, nitrate and chlorophyll *a* were the most notably variable when observing differences among study sites (Table 1). Average daytime dissolved oxygen was highest in Big Lake South at 14.48 mg L⁻¹, and lowest at Shellhorn at 7.35 mg L⁻¹. Average total suspended solids were greatest at Big Lake South and Shellhorn, possibly due to their connectivity with the main channel of the Illinois and Mississippi Rivers, respectively. Volatile suspended solids followed a similar trend. Average nitrate concentrations were greatest in Shellhorn and Big Lake South, and all other sites were similarly low. Nitrate was significantly different among study sites (RM-ANOVA, $F_{5,17} = 3.70$, $p = 0.02$; treatment x time $p = 0.41$), with Shellhorn and Big Lake South greater than the other sites (Figure 4). Chlorophyll *a* was also significantly different among sites among different times (RM-ANOVA, $F_{5,51} = 240.80$, $p < 0.01$, treatment x time $p < 0.01$). Big Lake South had the highest chlorophyll *a* concentration, with an average of 79.44 µg L⁻¹; the next highest was Big Lake North at 14.05 µg L⁻¹ (both sites with carp). All sites fluctuated drastically throughout the sampling period, however Big Lake South always remained highest in concentration (Figure 5). No site had significantly high concentrations of ammonium, total phosphorous, or soluble reactive phosphorous.

Table 1. Mean (\pm SE) water temperature, dissolved oxygen, total suspended solids, volatile suspended solids, and chlorophyll *a* for all study sites.

Site	Temp °C	DO mg L ⁻¹	TSS mg L ⁻¹	VSS mg L ⁻¹	Chl <i>a</i> µg L ⁻¹
Big Lake North	27.3 (0.48)	8.05 (0.82)	5.48 (0.23)	4.34 (0.28)	14.05 (4.81)
Big Lake South	26.9 (1.12)	14.48 (2.96)	15.99 (1.65)	11.52 (1.04)	79.44 (8.24)
Emiquon North	26.3 (1.25)	11.63 (1.56)	2.46 (0.39)	2.18 (0.30)	5.00 (0.67)
Emiquon South	25.5 (0.87)	10.75 (1.33)	4.84 (1.20)	3.07 (0.75)	9.62 (2.79)
Lawrence Lake	22.8 (1.89)	9.63 (1.19)	3.34 (1.31)	2.40 (0.28)	6.54 (3.04)
Shellhorn	21.3 (1.89)	7.35 (0.82)	13.04 (1.92)	3.39 (0.31)	4.99 (1.42)

Table 1 (extended). Mean (\pm SE) total phosphorous, soluble reactive phosphorous, total nitrogen, nitrate, and ammonium for all study sites.

Site	TP mg L ⁻¹	SRP mg L ⁻¹	TN mg L ⁻¹	NO ₃ mg L ⁻¹	NH ₄ mg L ⁻¹
Big Lake North	0.03 (0.00)	0.00 (0.00)	0.61 (0.06)	0.11 (0.08)	0.02 (0.00)
Big Lake South	0.11 (0.01)	0.00 (0.00)	2.59 (0.35)	1.60 (0.21)	0.08 (0.03)
Emiquon North	0.31 (0.06)	0.14 (0.00)	1.03 (0.11)	0.03 (0.02)	0.03 (0.01)
Emiquon South	0.07 (0.01)	0.01 (0.00)	1.13 (0.10)	0.02 (0.01)	0.03 (0.00)
Lawrence Lake	0.05 (0.02)	0.01 (0.00)	0.78 (0.11)	0.01 (0.02)	0.03 (0.00)
Shellhorn	0.11 (0.02)	0.05 (0.02)	3.00 (0.22)	2.55 (0.35)	0.01 (0.03)

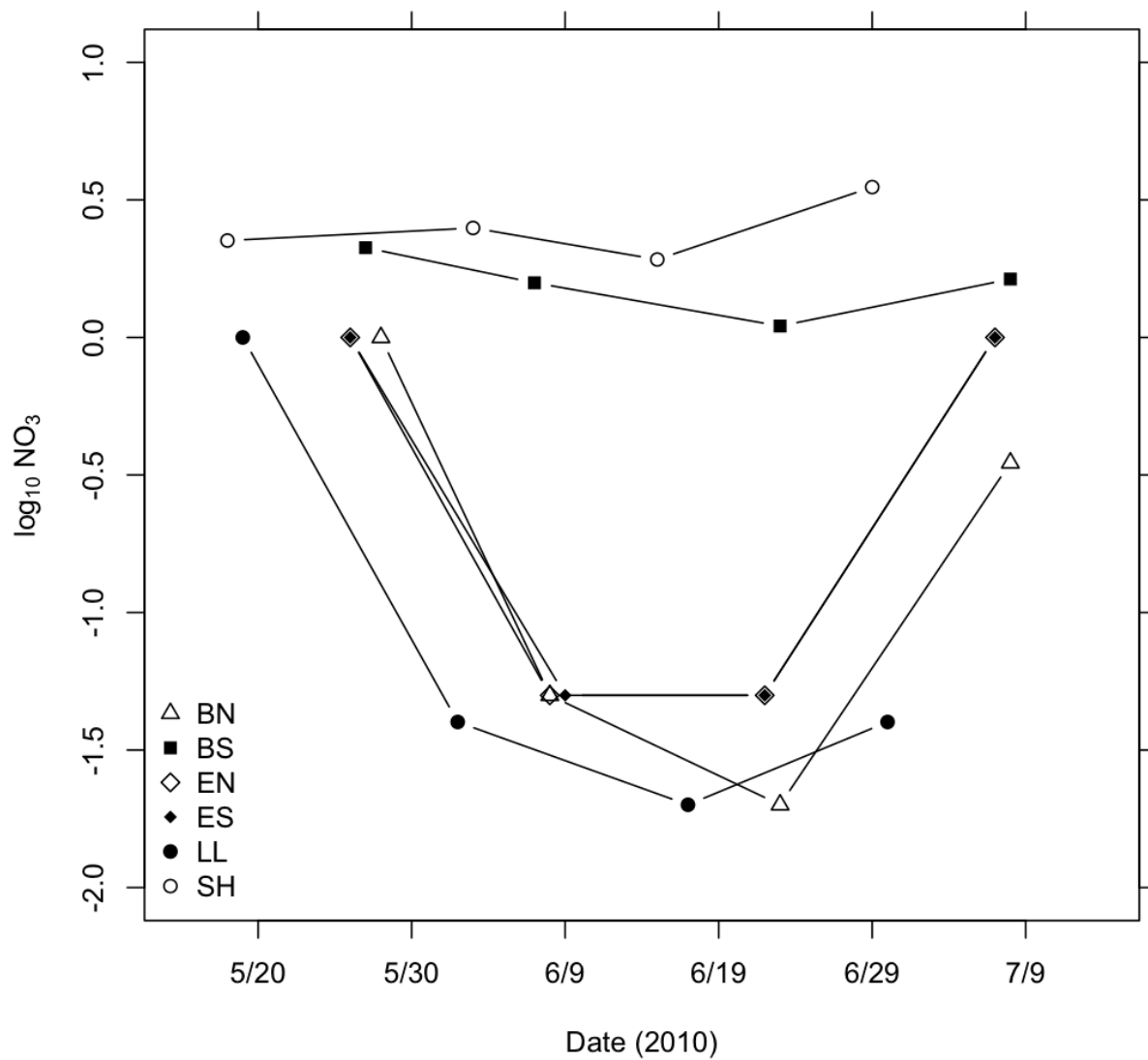


Fig 4. Plot of log-transformed nitrate (mg L^{-1}) for Big Lake North (BN), Big Lake South (BS), Emiquon North (EN), Emiquon South (ES), Lawrence Lake (LL), and Shellhorn (SH). No replicates taken.

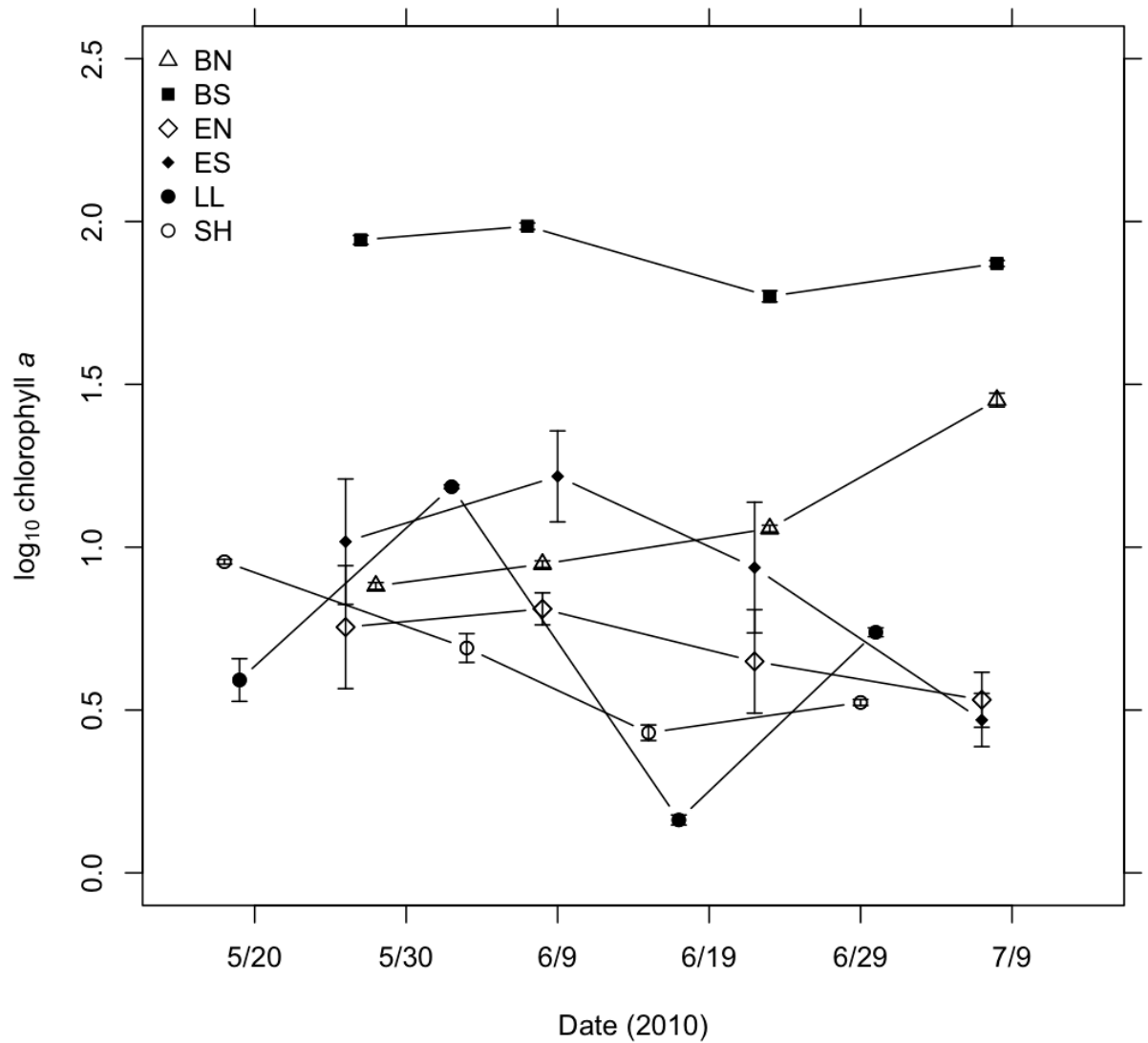


Fig 5. Plot of log-transformed chlorophyll *a* ($\mu\text{g L}^{-1}$; mean \pm SE) for Big Lake North (BN), Big Lake South (BS), Emiquon North (EN), Emiquon South (ES), Lawrence Lake (LL), and Shellhorn (SH)

Taxonomic composition and diversity of emerging insects

The orders Ephemeroptera, Odonata, Lepidoptera, Trichoptera, Coleoptera, Hymenoptera and Diptera were collected. Diptera were the most common taxa, comprising 90.8% of all insects collected. Trichoptera were the second most abundant order comprising 6.9% of insects collected. A total of 54 families were collected across the study sites; the greatest number of families (32) was collected at Big Lake North, and the least at Lawrence Lake and Shellhorn (25; Table 2). Chironomids were the most common family collected across study sites, ranging from 60.1% of the flux at Lawrence Lake to 96.2% of the flux at Big Lake South. Ephydrid flies were the second-most abundant family ranging from 0.9% of the flux at Big Lake South to 14.0% of the flux at Lawrence Lake. (Appendix A).

Assemblages of emerging insects were most diverse (family-level) in Lawrence Lake (Shannon-Wiener index (H'): 1.52 ± 0.02), with the second most diverse community found at Emiquon South ($H' = 1.12 \pm 0.02$). The least diverse community was collected at Big Lake South ($H' = 0.26 \pm 0.02$) (Table 3). Diversity and evenness were calculated with pooled samples across all sampling dates and all traps.

Table 2. Summary of mean emergence rates (\pm SE) for study sites on the upper Mississippi and Illinois River collected from 20 May 2010 to 7 July 2010.

Study site	# families	abundance	biomass
		(ind. \cdot m ⁻² \cdot day ⁻¹)	(mg dry wt. \cdot m ⁻² \cdot day ⁻¹)
Big Lake North	32	314.53 (63.47)	30.46 (6.20)
Big Lake South	30	380.27 (84.59)	39.23 (6.80)
Emiquon North	30	154.09 (26.79)	29.67 (6.50)
Emiquon South	29	204.30 (29.29)	23.08 (3.66)
Lawrence Lake	25	88.50 (20.52)	10.99 (1.91)
Shellhorn	25	235.08 (57.79)	29.86 (4.77)

Table 3. Shannon-Wiener diversity indices (mean \pm SE) for each site.

Study site	H'
Big Lake North	0.386 (0.003)
Big Lake South	0.259 (0.002)
Emiquon North	0.751 (0.006)
Emiquon South	1.119 (0.015)
Lawrence Lake	1.520 (0.017)
Shellhorn	0.982 (0.011)

Insect abundance and biomass flux

Abundance was significantly different among study sites (RM-ANOVA, $F_{5,34} = 10.64$, $p < 0.01$; abundance x date $p < 0.01$), with Big Lake North (Tukey's HSD, $p < 0.01$), Big Lake South (Tukey's HSD, $p < 0.01$), and Emiquon South (Tukey's HSD, $p = 0.02$) significantly greater than Lawrence Lake, and Big Lake South greater than Emiquon North (Tukey's HSD, $p = 0.04$).

In terms of biomass flux ($\text{mg dry wt. m}^{-2} \text{ day}^{-1}$), Chironomidae was the most common family captured at all sites ranging from 43.4 to 95.4% of total biomass collected at Lawrence Lake and Big Lake South, respectively. Chironomidae was the only family with a significant flux from all sites, and no other family was noticeably dominant across all sites (Appendix B). Chironomids collectively contributed to a majority of the numerical flux, but individually were quite small in terms of biomass. Some groups contained much larger individuals (some Coleoptera and Odonata), but because of their low abundance did not contribute much to the overall flux.

Biomass flux differed among study sites (RM-ANOVA, $F_{5,31} = 3.68$, $p = 0.02$; flux x date $p = 0.44$). The differences occurred between Big Lake North and Lawrence Lake (Tukey's HSD, $p = 0.04$), Big Lake South and Lawrence Lake (Tukey's HSD, $p < 0.01$), and Shellhorn and Lawrence Lake (Tukey's HSD, $p = 0.04$). Big Lake South had the greatest average flux at $39.23 \text{ mg dry wt. m}^{-2} \text{ day}^{-1}$, with the second highest flux observed at Big Lake North with an average flux of

30.46 mg dry wt. $\text{m}^{-2} \text{day}^{-1}$. Lawrence Lake had the lowest flux at just 10.99 mg dry wt. $\text{m}^{-2} \text{day}^{-1}$ (Table 2).

Mean abundance of insect emergence was positively related to chlorophyll *a* concentration (linear regression, $R^2 = 0.66$, $p = 0.05$; Figure 6), and volatile suspended solids (linear regression, $R^2 = 0.62$, $p = 0.04$). Primary production was the main source of VSS, as chlorophyll *a* concentrations and VSS were highly correlated (linear regression, $R^2 = 0.97$, $p < 0.01$). Biomass flux did not show any significance with any of the water chemistry variables.

Temporal patterns

Peak emergence was asynchronous across sites. Big Lake South had the highest emergence numbers, and peaked later in the sampling period, while Lawrence Lake had the lowest emergence and did not show a defined peak (Figure 7; a-f). The sites without carp, both Emiquons (N,S) and UMR (SH, LL), showed an eventual decline in emergence rates, while emergence in Big Lake North and Big Lake South did not plateau during the sampling period. Sampling was terminated due to fledging of tree swallow nestlings in the Big Lake sites prior to an observed leveling-off of emergence rates. Big Lake South and Emiquon South had larger emergences than their sister-sites of Big Lake North and Emiquon North. Insects from the Emiquon sites showed a difference in emergence phenology between the northern and southern sites; Emiquon North had a large early peak emergence and a slight leveling off,

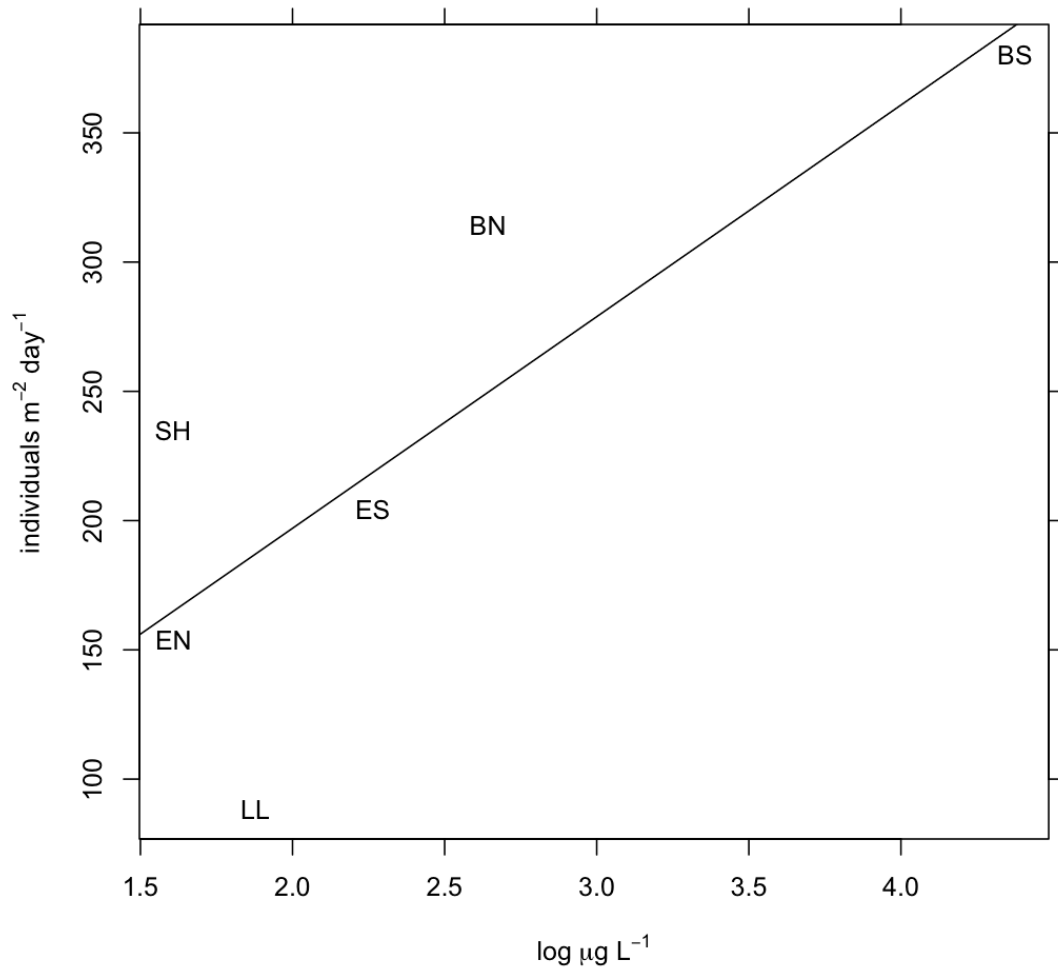


Fig 6. Bivariate plot of log-transformed chlorophyll *a* and mean emergent insect abundance (linear regression, $r^2 = 0.66$, $p = 0.05$; $y = 81.88x + 33.27$). Text on graph indicates study site.

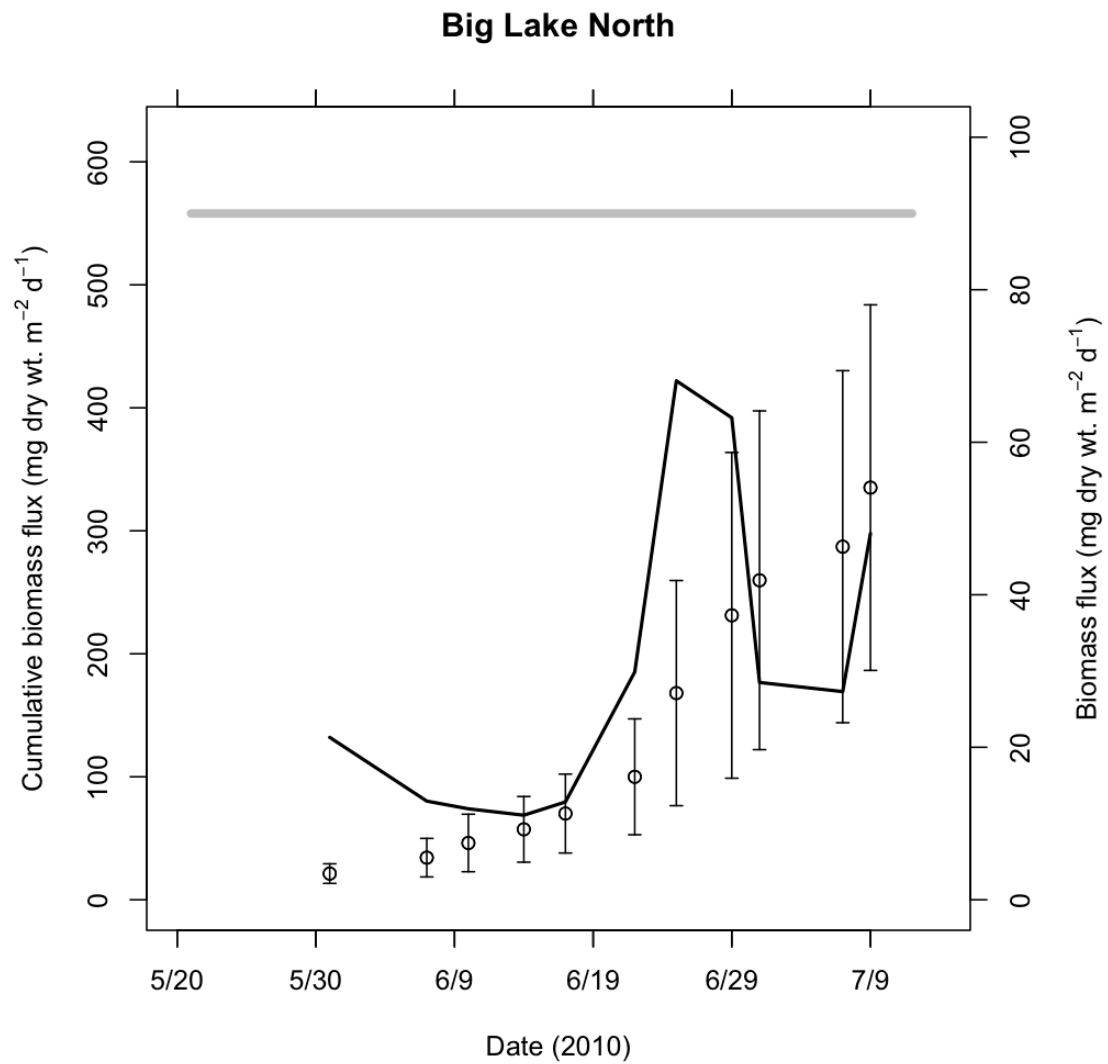


Fig 7. (a) Plots of cumulative biomass flux (points; mean \pm SE) and instantaneous biomass flux (black lines) for Big Lake North. Gray line represent time period of tree swallows feeding nestlings.

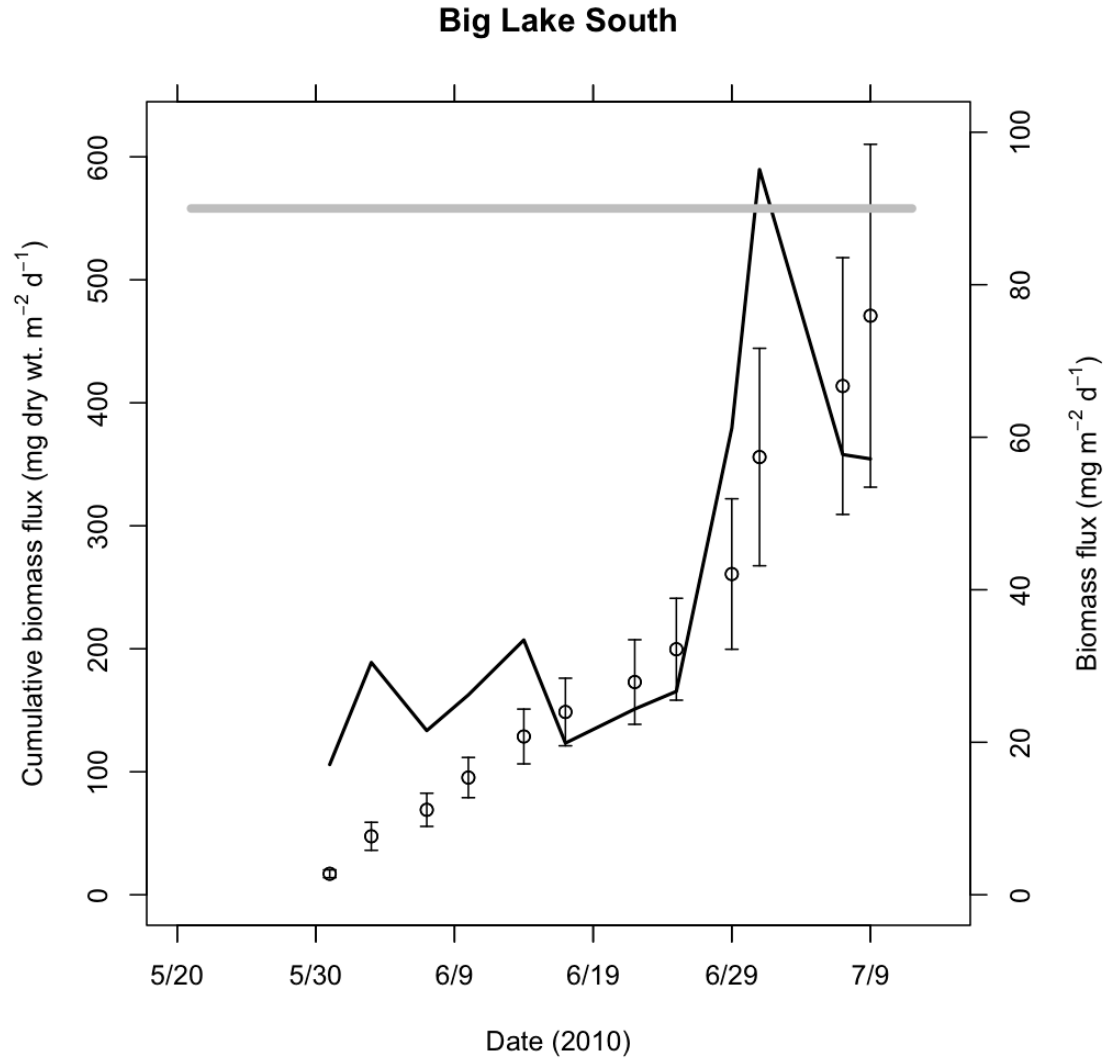


Fig 7. (b) Plots of cumulative biomass flux (points; mean \pm SE) and instantaneous biomass flux (black lines) for Big Lake South. Gray line represent time period of tree swallows feeding nestlings.

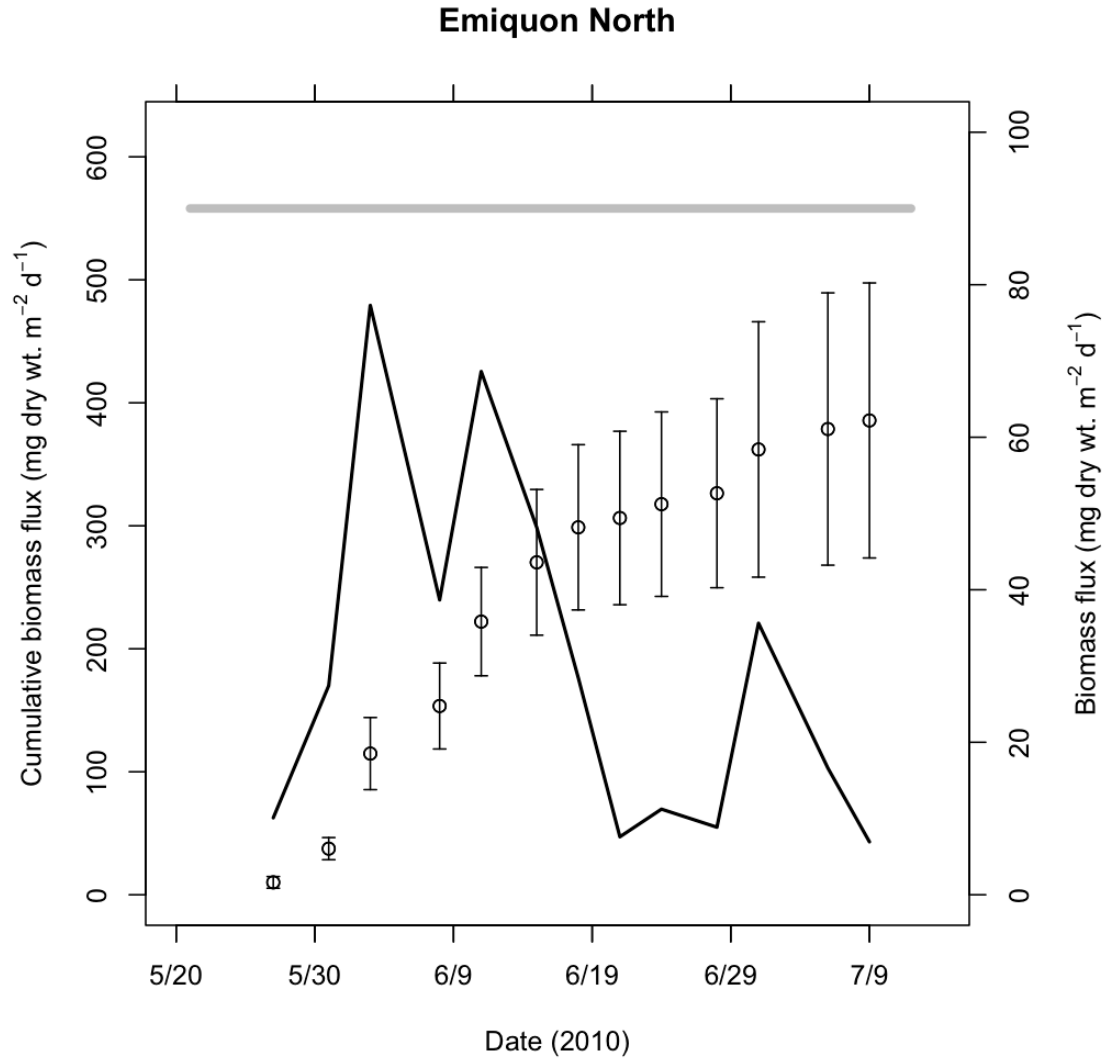


Fig 7. (c) Plots of cumulative biomass flux (points; mean \pm SE) and instantaneous biomass flux (black lines) for Emiquon North. Gray line represent time period of tree swallows feeding nestlings.

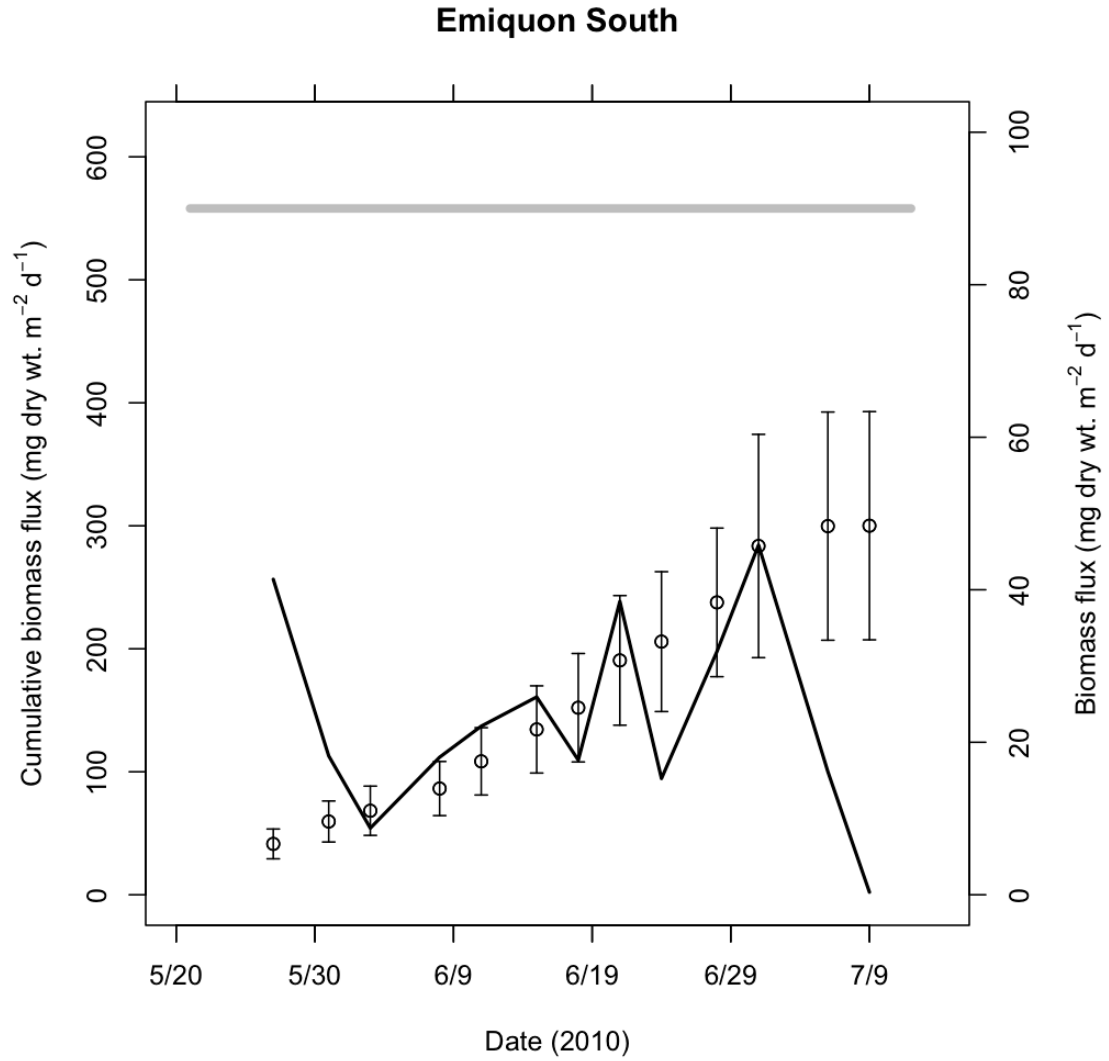


Fig 7. (d) Plots of cumulative biomass flux (points; mean \pm SE) and instantaneous biomass flux (black lines) for Emiquon South. Gray line represent time period of tree swallows feeding nestlings.

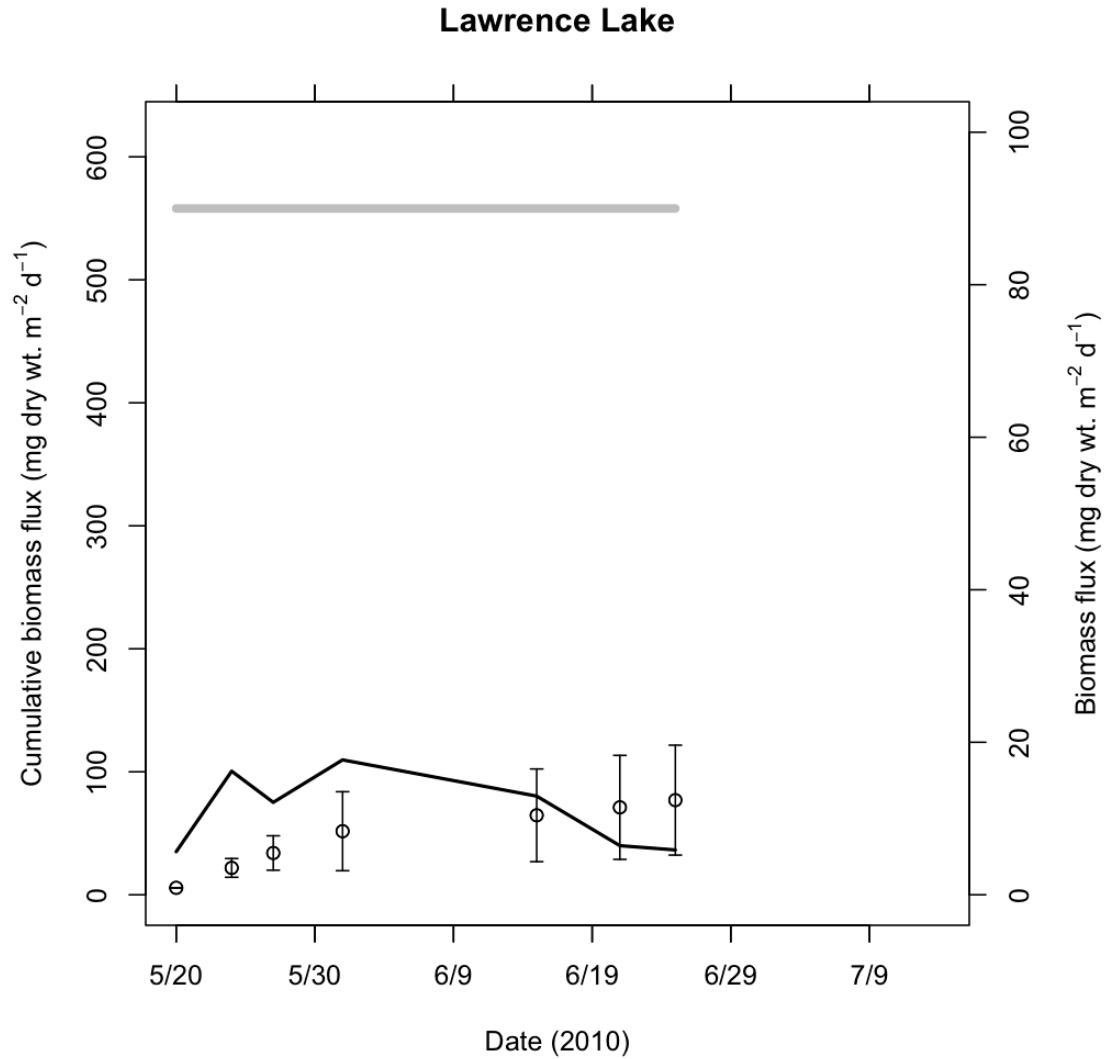


Fig 7. (e) Plots of cumulative biomass flux (points; mean \pm SE) and instantaneous biomass flux (black lines) for Lawrence Lake. Gray line represent time period of tree swallows feeding nestlings.

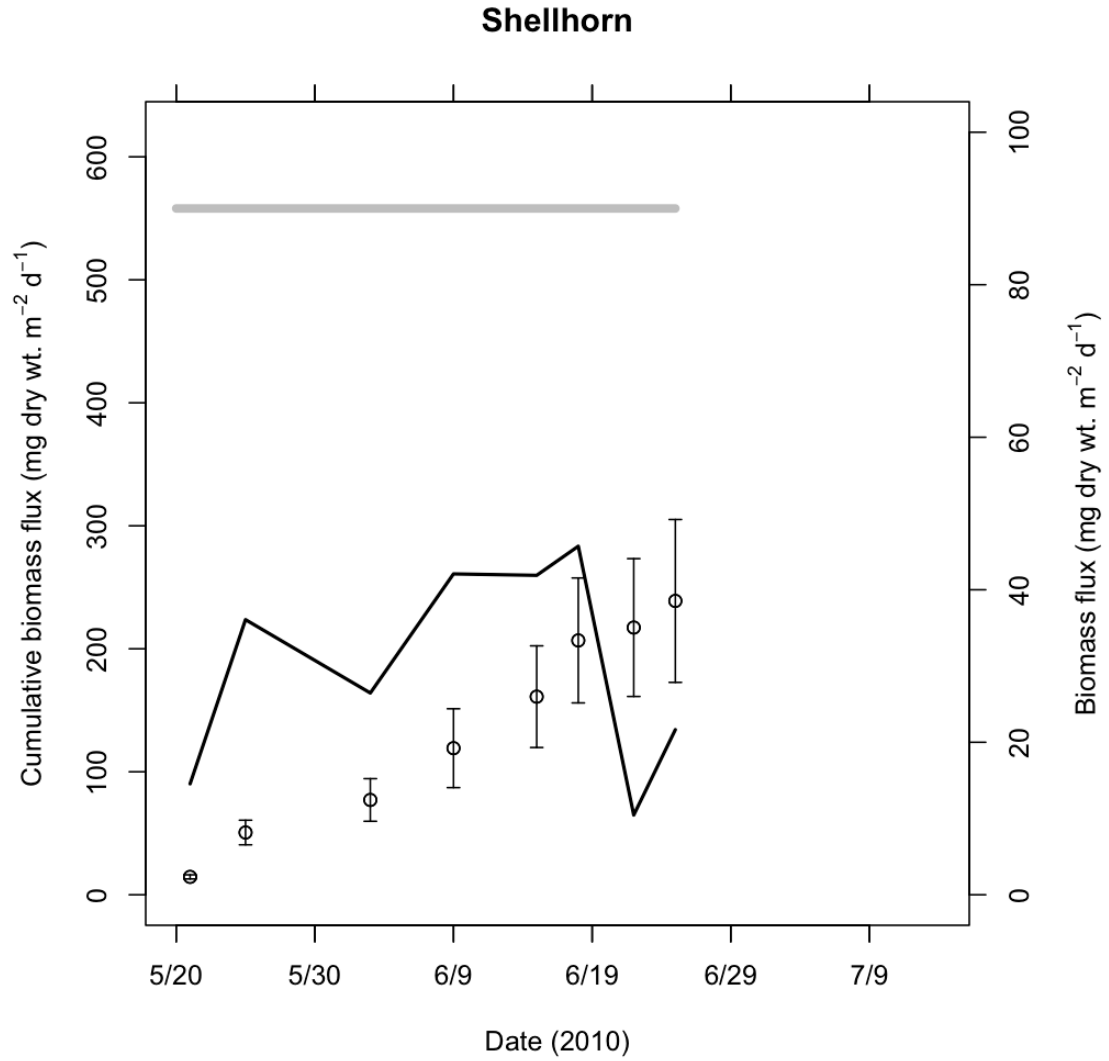


Fig 7. (f) Plots of cumulative biomass flux (points; mean \pm SE) and instantaneous biomass flux (black lines) for Shellhorn. Gray line represent time period of tree swallows feeding nestlings.

while a more gradual and consistent flux with a rather noticeable plateau was observed at Emiquon South.

Sites with carp vs. sites without carp

The presence of carp significantly affected the rate of biomass flux ($F_{1,35} = 2.16$, $p = 0.03$; flux x date $p = 0.42$), and abundance ($F_{1,38} = 25.87$, $p < 0.01$; abundance x date $p < 0.01$) among sites. Carp sites had the largest average flux and highest total abundance compared to no-carp sites; however, these sites collectively were significantly less diverse with $H' = 0.32$ compared to sites without carp ($H' = 1.15$; Welch's two sample t-test, $df = 1$, $t = -4.44$, $p = 0.01$). This trend is evident in the emergence of specific taxon. While Chironomidae dominated flux in Big Lake South and Big Lake North, the flux at the sites without carp was more taxonomically even. Cumulative mass flux of emerging insects did not differ significantly across sites with carp (t-test, $df = 2$ vs. 4, $t = 1.63$, $p = 0.21$: 402.9 mg dry wt. m^{-2} for carp sites and 250.4 mg dry wt. m^{-2} for no-carp sites). Cumulative abundance was, however, significantly higher in sites with carp (t-test, $df = 2$ vs. 4, $t = -4.17$, $p = 0.02$). Average cumulative abundance was 4168.8 individuals m^{-2} for carp sites and 1811.97 individuals m^{-2} for no-carp sites.

DISCUSSION

Influence of primary production on emergence

The high primary productivity of the Mississippi and Illinois Rivers was hypothesized to drive secondary production, and result in a significant energy subsidy to the landscape via insect emergence. As predicted, sites with the greatest primary production (as determined by chlorophyll *a* concentrations) also displayed the greatest insect emergences. This suggests greater primary production may impact the number of insects emerging and the biomass flux from the system. The transfer of this biomass from an area rich in autochthonous material may also represent a higher quality food resource, as important fatty acids are more readily available for assimilation in systems with greater primary production (Torres-Ruiz *et al.* 2007). Big Lake South, in particular, had the greatest primary production and insect emergence. This site likely supplied a higher quality carbon source to the surrounding terrestrial consumers because of both the quantity of material emerging, as well as the associated fatty acids incorporated into the tissues of insects living in an environment rich in high-lipid phytoplankton. Emergence from Lawrence Lake, however, was significantly lower than all other sites, possibly due to the limitation of high-quality resources for insect consumers with low levels of primary production. The low nutritional value of emerged insects from areas with low primary productivity, in combination with the low flux, may force terrestrial predators to

forage longer or more often to meet their dietary needs. This study provides evidence supporting the importance of aquatic primary production to the surrounding landscape via the increase in the quantity of a cross-ecosystem subsidy.

In addition to the study sites displaying a gradient of primary production, there were observed differences the density of in submerged vegetation densities among sites. Although no quantitative measurements of aquatic vegetation were made, a *post hoc* qualitative assessment of the macrophyte density of the study sites was performed. Big Lake is a large backwater ecosystem with little vegetation and a sandy substrate. Conversely, the Emiquon sites are part of a complex of restored agricultural land, now flooded, but unconnected to the Illinois River (Havera *et al.* 2003). The site is now a converted wetlands dominated by native macrophytes (Michaels and Sass 2009). Upper Mississippi River sites were also heavily vegetated, with Shellhorn similar to Emiquon, and Lawrence Lake highly vegetated with submerged macrophytes. The macrophyte abundance, or even the presence or absence of macrophytes in a system can have large impacts on the physical nature of the substrate and light irradiance in the water column, as well as provide habitat and protection from predators for aquatic insects (Dewey et al 1997; Madsen *et al.* 2001; Okun and Mehner 2003).

The density of macrophytes in a system can be important for aquatic insects because of the refuge that is provided from predation. The presence of insectivorous fish may reduce emergence rates by directly reducing the density of juvenile insects in the water column. Mallory *et al.* (1994) determined that fish presence predicted 76% of differences in insect abundance among different wetlands, with the fishless

areas having significantly higher densities of aquatic invertebrates. This direct predation on larval and pupating insects could ultimately suppress adult emergence. Although the high densities of macrophytes in the Emiquon and UMR did not contribute to greater emergence rates compared to Big Lake, there was an observed correlation between the diversity of emergent insects and the density of submerged vegetation. For example, the highly vegetated sites in Emiquon (North, South) and Lawrence Lake also had the greatest diversity ($H' = 0.75, 1.12$, and 1.52 , respectively), whereas the less vegetated sites of Big Lake (North, South) had the lowest diversity ($H' = 0.386$ and 0.259 , respectively). The differences in insect diversity may be attributed to the reduction of large insects in the Big Lake sites compared to other, more heavily vegetated sites. Wesner (2010) showed the presence of fish reduced insect emergence biomass by 55% in experimental mesocosms. Although fish reduced biomass, it did so mainly by altering the size structure of the insect community through size-selective predation, leaving the number of smaller insects (i.e., Chironomids) unchanged. Wesner (2010) also observed a 57% reduction in a predatory Odonate emergence, without significant reduction in the abundance of Ephemeropterans, Trichopterans, and Chironomids. Other studies have supported these findings and have further shown fish alteration of insect assemblages (Baxter *et al.* 2004; Flinn *et al.* 2005 Epanchin *et al.* 2010).

Aquatic vegetation creates diverse physical habitat, which may lead to a more diverse aquatic insect community. Heterogeneous habitats in aquatic systems are important in maintaining a diverse consumer population (O'Connor 1991). The presence of macrophytes in a system can influence the heterogeneity of the habitat,

thereby supporting a greater diversity of aquatic insects than un-vegetated areas (Heck and Westone 1977). As Big Lake was mostly void of macrophytes, the homogeneous nature of the habitat may have contributed to the reduced diversity in insect emergence, whereas the sites with more diverse habitat were able to support a wider variety of insects.

Effects of Asian carp on insect emergence

I hypothesized that the introduction of a planktivorous filter-feeding fish would decrease the available food resources to aquatic insects by significantly reducing phytoplankton density. Therefore, sites with high populations of bighead and silver carp were predicted to have a low rate of insect emergence compared to sites without Asian carp. This study, however, showed a significant increase in abundance and biomass flux at sites with carp compared to those without carp. A hypothesis for the unexpected result is that bighead and silver carp, rather than the direct reduction of phytoplankton biomass from predation, had a strong indirect effect on the aquatic food web by altering the particle size-structure of the phytoplankton community within Big Lake. The shift in particle sizes may also have altered the aquatic insect community, which responded via a change in successful feeding strategies. In addition, bighead and silver carp may have removed a significant proportion of the zooplankton biomass (Cremer and Smitherman 1980; Burke *et al.* 1986; Radke and Kahl 2002), leaving elevated, yet smaller, phytoplankton resources

for algal and detrital-feeding Chironomids. This increase in resources may have enhanced Chironomid biomass in sites with carp.

Although bighead and silver carp did not negatively affect the rate or magnitude of insect flux from Big Lake, the fish potentially had an impact on the diversity of insects at these sites. The insect communities at the carp sites were less diverse than the sites without carp. This may have been caused by a reduction in plankton particle size due to efficient grazing by carp, resulting in an altered prey base for larger invertebrate grazers (e.g., Trichoptera and Ephemeroptera). These small particles can facilitate smaller-bodied insects (e.g., Chironomids), but a reduction may have excluded large insects from the sites with carp, and subsequently decreased the diversity of the insect community.

Implications for terrestrial consumers

The emergence of insects from an aquatic system represents an accrual of biomass contributed from the productivity of that system, which is then transferred to another ecosystem. Insect emergence measured in this study in the Mississippi and Illinois Rivers was similar to emergences measured in other studies. These studies have shown that estimates may vary substantially, from 0.63 mg dry wt. $\text{m}^{-2} \text{d}^{-1}$ in a wetland system (Whiles and Goldowitz 2001) to 65 mg dry wt. $\text{m}^{-2} \text{d}^{-1}$ in a large, seventh-order river system (Paetzold *et al.* 2006). The high resource availability in large river systems can lead to generic-specific insect production estimates that exceed estimates for productive lakes (Benke 1998). The average flux reported from

this study (10.99 to 39.23 mg dry wt. m⁻² d⁻¹) is intermediate of the above and other estimates (Jackson and Fisher 1986, Gladyshev *et al.* 2009).

The large biomass flux observed from this study suggests that large, nutrient-rich floodplain rivers can provide significantly large, high-quality subsidies for the riparian consumer community. These energy subsidies are important in supporting riparian and floodplain consumer populations. Jackson and Fisher (1986) determined that only a small proportion of emergent biomass (in their case ~3%) returns to the aquatic realm, implying a transfer of aquatic productivity across ecosystem bounds. The insect biomass that remains on the landscape represents a large resource to terrestrial predators from a different, more productive ecosystem. Many other studies suggest a reliance on this resource, and report larger consumer populations near aquatic sources of insect emergence (Epanchin *et al.* 2010; Johnson and Wardle 2009). For example, insect emergence comprises up to 25% of a birds diet, and therefore may influence their distribution, moving them closer to aquatic habitats (Nakano and Murakami 2001; Murakami and Nakano 2002). The emergence measured in this study represents an important resource for migratory birds that live in the riparian zones of the Mississippi River, a notably important flyway (Bellrose and Sieh 1960; Greenlaw and Woolfenden 2007). In addition, Dreyer *et al.* (2012) showed a positive relationship between midge density on the landscape and terrestrial arthropod abundance. The data collected from this study suggest that more productive areas of the river may supply a greater subsidy in both quantity, and potentially quality, than areas with lower productivity. This has important

implications for terrestrial consumers, and may alter the densities or distributions of predatory arthropods, reptiles, or birds.

Insect emergence from areas rich in primary production may also supply a high-quality resource such as polyunsaturated- and highly unsaturated fatty acids (HUFAs). These fatty acids are essential to biochemistry and physiology of organisms, and are supplied in greater quantity through aquatic primary production than terrestrial production (Arts *et al.* 2009). A rough estimate of the average export of HUFAs from aquatic to the terrestrial environments from insect emergence is $40 \text{ mg m}^{-2} \text{ yr}^{-1}$; however, actual flux could range from 0.1 to $672.2 \text{ mg m}^{-2} \text{ yr}^{-1}$ (Gladyshev *et al.* 2009). The variance in the estimates is due primarily to the approximation of lipid content in the emergent insects, as well as the variability in emergence flux across systems. Using the average HUFA content for aquatic insects of 9.3 mg g^{-1} dry wt. given by Gladyshev *et al.* (2009), estimates of HUFAs supplied by the sites in this study ranged from 37.3 to $131.4 \text{ mg m}^{-2} \text{ year}^{-1}$ at Lawrence Lake and Big Lake South, respectively. The lipid flux from these rivers is greater than the conservative estimate of $40 \text{ mg m}^{-2} \text{ yr}^{-1}$ given by Gladyshev *et al.* (2009), and suggests large rivers may be an important supplier of lipids to the terrestrial system, and may subsidize production of terrestrial consumers.

Bighead and silver carp are considered a major threat to freshwaters in the United States; however, these data show the effect on insect emergence rates in these areas may be minimal, or potentially even positive. The impact of these fish on the insect community may be especially dampened by the primary productivity of the system. A water body with greater primary productivity may not experience an

observable negative effect from the competition for resources, and may not see any impact on insect emergence rates. However, the high rate of insect emergence does not suggest there may not be challenges from the introduction of non-native fish, as sites with carp displayed a less diverse community of insects than sites without carp. The reduction in individual size of emergent insects may have implications for terrestrial predators, as the size of prey is an important determinant of foraging success (McCarty and Winkler 1999). An abundance of large prey is especially important to nestling birds. Small sized prey must be fed from hatching to fledging at great rates to make up for the small biomass. Larger Dipterans (e.g., Tipulidae, Muscidae, Scathophagidae), and other large insect prey are preferentially selected by adult swallows to feed to young birds. As the nestlings age, selection of large prey becomes more common (McCarty and Winkler 1999). Emiquon and the UMR may be more suitable to supply nestlings an adequate diet of small Dipterans in the early nesting period, followed by larger aquatic insects as the chicks mature.

CONCLUSION

The flux of insect biomass to the terrestrial systems represents an important resource subsidy for riparian predators. The quantity of biomass flux from a large river system has not been previously described, and determining this flux is important in gauging the overall significance of this subsidy to terrestrial predators. Quantifying insect emergence in two large floodplain rivers in the central United States is an important step in understanding the varying productivity of these

subsidies. The purpose of this study was to quantify the magnitude of insect flux coming from sites on the upper Mississippi and Illinois Rivers.

Insect emergence was significantly related to river primary productivity as indicated by chlorophyll *a* concentration. High aquatic primary production leads to greater available resources for insect consumers, and consequently to terrestrial predators through insect emergence. The presence or absence of aquatic macrophytes also may play a significant role in the diversity of the insect community in a system, as vegetation acts as both predator refuge, and substrate for epiphytic food, which can support a large and diverse insect community.

The presence of non-native fish (bighead and silver carp) may substantially change the size-structure and taxonomic distribution of emerging insects, but have little effect on the mass flux. Although the original hypothesis regarding the effect of carp on insect flux was not supported, the results show a possible indirect impact of bighead and silver carp on the diversity of insects, possibly through competition for resources. Bighead and silver carp may significantly reduce the size of available phytoplankton and the prey base for insect consumers. Although the presence of carp may not impact the amount of subsidy available to terrestrial consumers, the decrease in diversity associated with their presence may have implications for the distributions of terrestrial predators. Terrestrial predators that prefer large-bodied prey may avoid areas with bighead and silver carp. In addition, future research should test the effect of carp on insect emergence in areas of varying production to determine whether a less productive, and possibly more vulnerable ecosystem may magnify the

competition for resources between aquatic insects and the carp, thereby reducing insect flux.

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APPENDIX A

PERCENT ABUNDANCE CONTRIBUTION OF ALL FAMILIES COLLECTED

FOR EACH SITE

Table 4. Percent abundance contribution of all families collected for all sites.

Family	BN	BS	EN	ES	LL	SH
Anthribidae	0.00	0.02	0.00	0.00	0.11	0.00
Baetidae	0.04	0.02	0.12	0.00	0.00	0.28
Braconidae	0.04	0.00	0.00	0.01	2.28	0.25
Caenidae	0.23	0.02	0.80	0.47	0.00	0.00
Carabidae	0.13	0.09	0.24	0.25	0.11	0.07
Cerambycidae	0.08	0.00	0.00	2.54	0.00	0.00
Ceratopogonidae	0.68	0.37	0.56	0.18	0.00	0.28
Chaoboridae	0.02	0.00	0.04	0.00	0.00	0.00
Chironomidae	94.15	96.23	86.31	58.53	60.70	78.86
Chrysomelidae	0.25	0.23	0.16	0.04	0.11	0.14
Coenagrionidae	0.00	0.00	0.96	10.26	0.11	0.36
Corduliidae	0.00	0.00	0.04	0.00	0.00	0.00
Culicidae	0.00	0.00	0.04	0.06	0.00	0.00
Curculionidae	0.02	0.00	0.00	0.00	0.46	0.46
Delphacidae	0.00	0.00	0.00	0.02	0.00	0.00
Diapriidae	0.00	0.04	0.12	0.01	0.00	0.00
Dipseudopsidae	0.17	0.02	0.00	0.00	0.11	0.00
Dolichopodidae	0.02	0.05	0.04	0.02	0.00	0.14
Empididae	0.30	0.42	1.24	0.06	6.71	3.09

Ephydriidae	1.04	0.88	3.44	1.21	13.99	2.59
Eriocraniidae	0.00	0.00	0.08	0.17	0.23	0.00
Eulophidae	0.02	0.02	0.00	0.00	0.00	0.00
Figitidae	0.02	0.05	0.00	0.01	0.00	0.00
Georyssidae	0.00	0.02	0.04	0.00	0.00	0.00
Gyrinidae	0.02	0.00	0.00	0.00	0.00	0.00
Helicopsychidae	0.02	0.02	0.00	0.00	0.11	0.00
Hydropsychidae	0.15	0.09	0.04	0.31	0.00	0.00
Hydroptilidae	0.49	0.18	1.92	11.38	2.16	3.62
Ichneumonidae	0.00	0.04	0.00	0.05	0.46	0.00
Lanchopteridae	0.00	0.02	0.00	0.00	0.00	0.00
Leptoceridae	0.06	0.07	1.08	13.12	3.41	0.21
Macromiidae	0.00	0.00	0.12	0.00	0.00	0.00
Melandryidae	0.00	0.02	0.00	0.00	0.00	0.00
Metrotepodidae	0.00	0.00	0.00	0.00	0.00	0.78
Muscidae	0.08	0.00	0.08	0.62	0.23	2.06
Mymacidae	0.00	0.00	0.04	0.01	0.00	0.00
Palingeniidae	0.00	0.00	0.88	0.00	0.00	0.04
Phoridae	0.13	0.18	0.00	0.07	0.00	0.11
Phyganeidae	0.00	0.00	0.00	0.00	0.23	0.00
Polycentropodidae	0.91	0.49	0.00	0.00	3.30	0.04
Pompilidae	0.06	0.05	0.00	0.00	0.23	0.04
Psychodidae	0.00	0.00	0.20	0.00	0.00	0.00

Psychomiidae	0.04	0.00	0.00	0.00	0.00	0.00
Pteromalidae	0.19	0.00	0.00	0.00	0.11	0.00
Scathophagidae	0.19	0.05	0.48	0.05	0.57	5.97
Scelionidae	0.19	0.16	0.56	0.06	0.11	0.14
Sciomyzidae	0.02	0.00	0.08	0.30	0.00	0.11
Simuliidae	0.19	0.14	0.12	0.08	0.00	0.07
Soldidae	0.00	0.02	0.00	0.00	0.00	0.00
Staphylinidae	0.00	0.00	0.00	0.00	0.00	0.18
Stratiomyzidae	0.00	0.00	0.12	0.11	0.00	0.00
Syrphidae	0.02	0.00	0.00	0.00	0.46	0.11
Trichogrammatidae	0.00	0.02	0.04	0.00	0.00	0.00

APPENDIX B

PERCENT BIOMASS FLUX OF ALL FAMILIES COLLECTED FOR EACH SITE

Table 5. Percent biomass flux of all families collected for all sites.

Family	BN	BS	EN	ES	LL	SH
Anthribidae	0.00	0.01	0.00	0.00	0.00	0.00
Baetidae	0.03	0.02	0.09	0.00	0.00	1.08
Braconidae	0.03	0.02	0.00	0.01	1.18	0.17
Caenidae	0.20	0.01	0.30	0.47	0.00	0.00
Carabidae	0.16	0.38	0.12	0.25	0.00	0.05
Cerambycidae	2.12	0.00	0.00	2.54	0.00	0.00
Ceratopogonidae	0.32	0.20	0.27	0.18	0.00	0.00
Chaoboridae	0.00	0.00	0.01	0.00	0.00	0.00
Chironomidae	90.69	95.35	83.93	58.53	43.41	58.26
Chrysomelidae	0.27	0.21	0.18	0.04	0.00	1.26
Coenagrionidae	0.00	0.00	5.52	10.26	0.00	3.25
Corduliidae	0.00	0.00	1.44	0.00	0.00	0.00
Culicidae	0.00	0.00	0.06	0.06	0.00	0.00
Curculionidae	0.01	0.00	0.00	0.00	0.73	5.50
Delphacidae	0.00	0.00	0.00	0.02	0.00	0.00
Diapriidae	0.00	0.01	0.02	0.01	0.00	0.00
Dipseudopsidae	0.24	0.03	0.00	0.00	0.38	0.00
Dolichopodidae	0.03	0.08	0.02	0.02	0.00	0.12
Empididae	0.14	0.24	1.19	0.06	3.07	1.40

Ephydriidae	0.62	0.64	1.22	1.21	8.42	1.12
Eriocraniidae	0.00	0.00	0.14	0.17	0.00	0.00
Eulophidae	0.00	0.00	0.00	0.00	0.00	0.00
Figitidae	0.01	0.05	0.00	0.01	0.00	0.00
Georyssidae	0.00	0.01	0.01	0.00	0.00	0.00
Gyrinidae	0.02	0.00	0.00	0.00	0.00	0.00
Helicopsychidae	0.04	0.03	0.00	0.00	0.00	0.00
Hydropsychidae	0.32	0.24	0.02	0.31	0.00	0.00
Hydroptilidae	0.31	0.05	0.52	11.38	1.65	2.27
Ichneumonidae	0.00	0.23	0.00	0.05	3.40	0.00
Lanchopteridae	0.00	0.05	0.00	0.00	0.00	0.00
Leptoceridae	0.19	0.14	2.92	13.12	1.73	0.28
Macromiidae	0.00	0.00	0.00	0.00	0.00	0.00
Melandryidae	0.00	0.02	0.00	0.00	0.00	0.00
Metrotepodidae	0.00	0.00	0.00	0.00	0.00	3.50
Muscidae	0.14	0.20	0.12	0.62	1.74	9.32
Mymacidae	0.00	0.00	0.01	0.01	0.00	0.00
Palingeniidae	0.00	0.00	0.00	0.00	0.00	0.08
Phoridae	0.03	0.11	0.22	0.07	0.00	0.00
Phyganeidae	0.00	0.00	0.00	0.00	7.21	0.00
Polycentropodidae	1.92	0.77	0.00	0.00	14.08	0.10
Pompilidae	0.42	0.58	0.00	0.00	1.53	0.27
Psychodidae	0.00	0.00	0.05	0.00	0.00	0.00

Psychomiidae	0.07	0.00	0.00	0.00	0.00	0.00
Pteromalidae	0.00	0.00	0.00	0.00	0.05	0.00
Scathophagidae	0.70	0.12	0.78	0.05	4.34	9.82
Scelionidae	0.47	0.11	0.18	0.06	0.10	0.10
Sciomyzidae	0.35	0.00	0.26	0.30	2.17	0.51
Simuliidae	0.13	0.10	0.04	0.08	0.14	0.05
Soldidae	0.00	0.03	0.00	0.00	0.00	0.00
Staphylinidae	0.00	0.00	0.00	0.00	0.00	0.20
Startiomyzidae	0.00	0.00	0.33	0.11	0.00	0.00
Syrphidae	0.02	0.00	0.00	0.00	4.67	1.15
Trichogrammatidae	0.00	0.00	0.06	0.00	0.00	0.00
