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Ichthyochory in a temperate river system by common carp (*Cyprinus carpio*)

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ABSTRACT

Some fish are important dispersal vectors of aquatic plants (i.e., ichthyochory), yet few examples have been documented outside of the Neotropics. Although highly modified and degraded, the upper Illinois River Waterway supports common carp (*Cyprinus carpio*) populations and abundant aquatic vegetation. As common carp have been previously documented to consume aquatic vegetation seeds, we assessed diets to determine the potential for common carp to function as dispersal vectors for aquatic vegetation seeds that may be important for restoration of rivers and floodplain wetlands. Whole seeds occurred at a high frequency and 42 seed taxa were discovered in the digestive system of common carp. Electivity analysis indicated that most seeds present were incidentally ingested; however, common carp diets contained seeds of wild celery (*Vallisneria americana*) at rates greater than expected by random chance. Our study indicates common carp may fill a similar functional role of seed dispersal for aquatic plant communities in temperate large river systems as they do for fruiting plants in the Neotropics. Our results highlight an understudied aspect of temperate freshwater ecology – fish as a potential influence on plant dynamics and resources in rivers. Fish-mediated seed dispersal has important but poorly understood implications and should be further explored.

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Invasive species; dispersal; aquatic vegetation; seed selection

Introduction

Plant community dynamics in large rivers and their floodplains are reliant on many features of a natural hydrologic cycle for dispersal and establishment of propagules (Junk et al. 1989; Bayley 1995; Bischoff 2002; Moore et al. 2010; Nilsson et al. 2010). The importance of fish-mediated propagule dispersal (i.e. ichthyochory) has been primarily documented from studies in the Neotropics, where it is essential for maintaining plant community structure in forested wetlands (Correa et al. 2007). Among the best known examples of ichthyochory are frugivorous fishes such as tambaqui (*Colossoma macropomum*) and pacú (*Piaractus mesopotamicus*) which consume and transport large quantities of seeds during the Amazon and Paraguay river systems' seasonal inundation of the floodplain (Galetti et al. 2008; Anderson et al. 2009, 2011). Although ichthyochory has been more extensively described as a vital process for seed dispersal in tropical large river systems, evidence of this process in temperate large river systems is less well documented (Horn et al. 2011). One example

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comes from the Mississippi River basin, where seeds of red mulberry (*Morus rubra*) and swamp privet (*Forestiera acuminata*) consumed by channel catfish (*Ictalurus punctatus*) from the Mississippi River basin of North America germinated at a higher rate than undigested seeds (Chick et al. 2003; Adams et al. 2007). Thus, ichthyochory may contribute to plant community dynamics in temperate river systems, although to what extent and importance is presently unclear (Horn et al. 2011).

Invasive species exacerbate the degradation of river systems (e.g. Solomon et al. 2016, DeBoer et al. *in revision*), especially modified river systems like those of the central USA (e.g. damming, channel dredging, floodplain wetland drainage; Nilsson and Berggren 2000; DeLong 2005; Nilsson et al. 2005). Invasive species can benefit from frequent and high-magnitude flooding, which increases disturbance levels, reduces diversity and abundance of native macrophytes, and facilitates dispersal of individuals or propagules through the connected aquatic systems (Planty-Tabacchi et al. 1996; Nilsson and Berggren 2000). The Illinois River Waterway (IRW) is a river system highly modified for navigation and to facilitate agriculture within the former floodplains, and is a conduit for the movement of invasive species between the Mississippi River watershed and the Laurentian Great Lakes (DeLong 2005; McClelland et al. 2012; Figure 1).

Common carp (*Cyprinus carpio*) is one of the most globally invasive fish species (Lowe et al. 2000), and was introduced throughout the United States in the late 1800s for aquaculture (Smiley 1886; Orban and Wu 2008; Bajer et al. 2009). After both intentional release and escapement, common carp have had a multitude of negative effects throughout the Mississippi, Illinois, and other large river systems (Bajer et al. 2009; Weber and Brown 2009; Bajer and Sorensen 2010; Weber et al. 2010; Gibson-Reinemer et al. 2017a). Common carp cause ecosystem modification through roiling (i.e. rooting in sediments while foraging, expulsion of siphoned sediments/detritus). Roiling activities increase water turbidity and subsequently affect plant community dynamics (Bajer et al. 2009; Weber and Brown 2009; Bajer et al. 2016). Increased water turbidity reduces light penetration, which can reduce photosynthesis or eliminate submersed aquatic plants altogether. Roiling by common carp can reduce sediment compaction, which may also negatively affect aquatic plants.

Common carp are omnivorous and readily ingest detritus, vegetation, algae, crustaceans, mollusks, seeds, invertebrates, and inorganic materials (Garcia-Berthou 2001; Pollux et al. 2006). Common carp frequently ingest seeds (Crivelli 1981; Balon 1995; Hossain et al. 2001), but most previous research assumes seeds are unintentionally consumed by temperate fishes (Horn et al. 2011). Due to their prevalence and foraging behavior, common carp are likely among the most important fish species in temperate regions for seed dispersal, and the importance of ichthyochory by this species is likely underestimated (Horn et al. 2011).

If common carp frequently ingest seeds, they may act as dispersal vectors for aquatic plants in temperate large river systems. Furthermore, if common carp ingest certain species of seeds at rates greater than are proportionally available to them in the environment (i.e. selection), then common carp have the potential to significantly alter plant community dynamics by altering the quantity of seeds available to germinate and establish. Thus, our goals are to determine: (1) the frequency of occurrence of seeds in common carp diets, and (2) if seed species occur at greater relative abundances in common carp diets than expected from seed abundance in the environment. We hypothesize that common carp (1) ingest seeds of aquatic plants incidentally while foraging randomly in sediments and, (2) do not perceptively select for seed taxa, thus occurrence of seeds in diets will be similar to availability in the environment.

Methods

Study location

The IRW is a historically productive large river system (Alvord and Burdick 1915). The upper IRW (specifically the lower Des Plaines River and its confluence with the Kankakee River) supports an

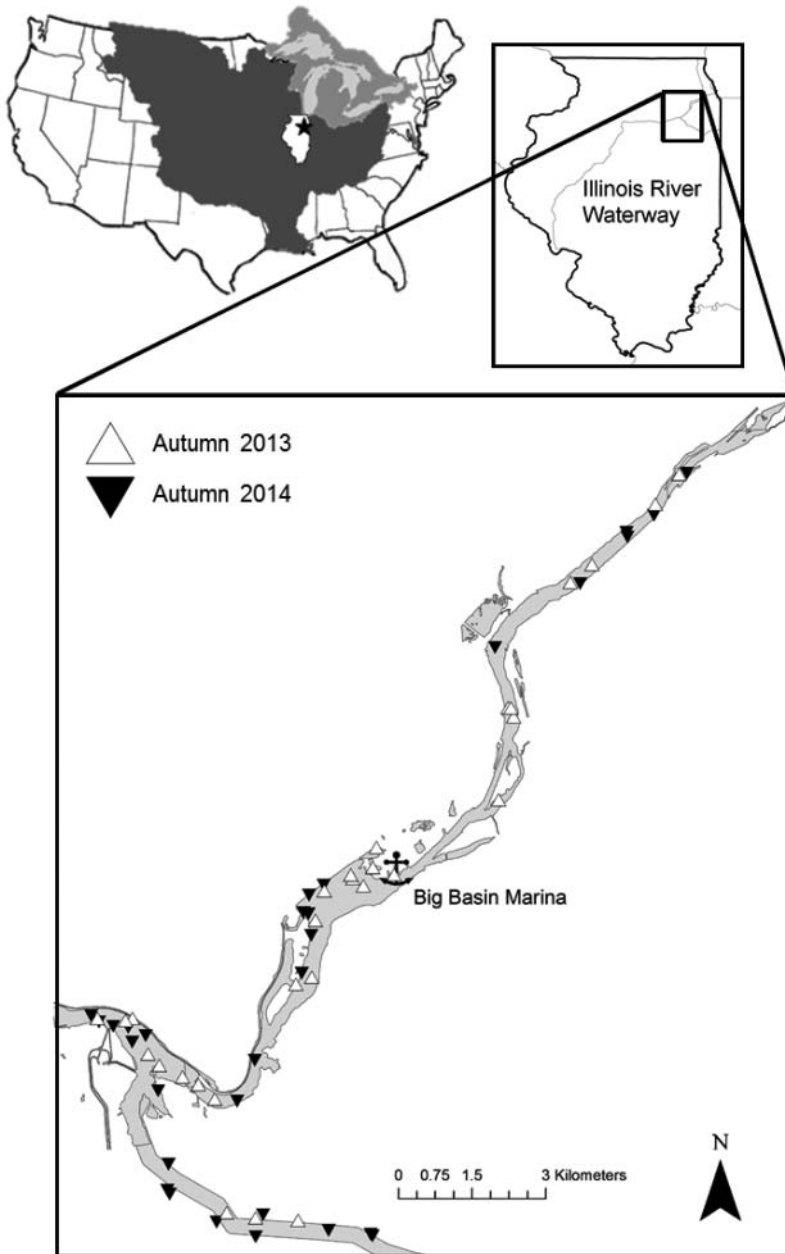


Figure 1. Map of the Illinois River Waterway (IRW; inset, top right) and randomly selected sampling sites (large map, bottom) used to collect benthic sediment cores in the upper IRW during autumn 2013 and autumn 2014. Common carp were collected throughout the extent of the reach. Big Basin Marina included for reference. Mississippi River watershed (dark gray) and Laurentian Great Lakes watershed (light gray) included at top left for reference.

abundance of aquatic macrophytes and sportfish (Sparks et al. 1986; Tazik 1988; Lerczak et al. 1995; McClelland et al. 2012). However, because of its close proximity to highly developed urban areas (i.e. Chicago, IL) and its role as a principal conduit for inland shipping, hydrology in the IRW is highly altered and it may be susceptible to invasive and non-native species introductions (Bellrose et al. 1983; Mills et al. 1993; Rixon et al. 2005).

Fish collection

We sampled common carp using both AC and pulsed-DC boat-mounted electrofishing following a set of standardized fish monitoring protocols (McClelland et al. 2012; Ratcliff et al. 2014; Fritts et al. 2017). We conducted electrofishing and collection of common carp throughout the Upper IRW (Figure 1) and focused efforts near plant communities and other shallow areas where common carp were likely to be present. We sampled fish twice in autumn of 2013 (20 September and 17 October), once in spring 2014 (8 April), and twice in autumn 2014 (18 September and 16 October). We euthanized all common carp immediately by cerebral percussion and placed them on ice until the digestive tracts could be removed (approximately 3 hours; Institutional Animal Care and Use Committee Protocol #14023). Subsequently in a laboratory, we removed the entire digestive tract (i.e. mouth–anus) and preserved with 10% formalin until processing could occur (Garcia-Berthou 2001). We dissected digestive tracts and rinsed contents through a 500- μm aperture sieve to separate seeds from other materials. We preserved the sieve contents in 10% formalin until they could be identified by microscopy to lowest practical taxa (Martin and Barkley 1961; Merritt and Cummins 1996; Bryson and DeFelice 2010) or item. After identification, we dried diet items at 70 °C for 24 h, and weighed them to the nearest 0.1 mg (Colle et al. 1978).

Seed availability

In autumn 2013 (12 October) and autumn 2014 (7 October), we collected sediment samples using a benthic core sampler (28-cm² area; 10-cm depth) at 30 randomly generated locations per year within the upper IRW using an ArcMap toolbox application (ArcMap version 10.2.2, ESRI, Redlands, California, USA; Ringelman et al. 2015). We did not collect benthic sediment samples during spring because annual seed availability is at its lowest during spring due to over-winter degradation, and annually produced seeds have not developed and subsequently dispersed yet. We collected three replicate benthic core samples within 5 m of each random location, homogenized replicates in separate 500- μm mesh sieve buckets (Wildco, Yulee, Florida, USA), rinsed samples with water to remove excess soil, placed them in labeled plastic bags, transported them back to the laboratory, and froze them at –20 °C.

Later in the laboratory, we thawed and rinsed all benthic core samples through 500- μm aperture screens and air dried samples to facilitate removal of seeds from soil and detritus. We sub-sampled sediment core samples > 10 g by 25% to reduce processing time (Hagy et al. 2011; Stafford et al. 2011). We did not sub-sample sediment core samples < 10 g to increase the probability of detecting uncommon seeds. We removed seeds from samples with forceps, identified them by microscopy to species or the lowest practical taxonomical unit (Martin and Barkley 1961; Bryson and DeFelice 2010; Schummer et al. 2011), dried them at 80 °C for 24 hours, and weighed them to the nearest 0.1 mg. We corrected the number of seeds per core for processing and recovery bias using size-specific correction factors (Hagy et al. 2011), extrapolated the number of seeds counted to density (number/m²), and estimated total seed availability across all samples.

Statistical analysis

We determined frequency of occurrence of diet item categories by sampling season. We partitioned diet items into one of six categories: vegetation, invertebrates, seeds, mollusks, unidentifiable material, and other (e.g. sediment, feathers). We calculated percentage of total diets (mass: g) by diet item categories for each individual. We used a factorial multivariate analysis of variance (MANOVA; PROC GLM in SAS, v. 9.3, SAS Institute 2012) to test for differences in dry mass of individual recovered diet items among the six categories between seasonal collection periods (i.e. autumns and spring). We reviewed residual distribution plots and log transformed data to normalize distributions, although parametric multivariate analysis is robust to normality violations (Johnson 1995; Stafford et al. 2010).

We used Vanderploeg and Scavia's Relativized Electivity Index (E_i^*) to compare seed presence in common carp diets to seed availability in benthic core samples (Vanderploeg and Scavia 1979; Lechowicz 1982). Electivity was calculated only for common carp diets collected during autumn ($n = 63$) to match the temporal collection of sediment cores ($n = 59$) to quantify seed selection by common carp. There are several common indices used in electivity analyses, yet the indications of selection and avoidance inevitably vary with each, and interpretation of results similarly varies (Lechowicz 1982; Tokeshi and Daud 2011). We chose Vanderploeg and Scavia's E_i^* index because it takes into account the predator's perception of diet item value based on abundance of a food item relative to the abundance of other food items (i.e. selection), and interpretability of a normalized scale in which 0 is equivalent to random feeding, -1 to avoidance, and 1 to preference of diet items (Lechowicz 1982). Because electivity analyses are based on the proportion of a diet item consumed compared to the proportion available in the environment, we censored seeds that were present in only core samples but not present in diets. Additionally, we censored all seed species that appeared limited within diets (i.e. present in only one diet, when only one seed was present in diets, or when only one seed was discovered in one diet) to minimize the potential for sampling error which occurs when potential prey items presence in the environmental greatly exceeds presence of those items within diets (Lechowicz 1982). We assumed diets containing these limited species were incidentally ingested, as indicated by our hypothesis of random foraging. Therefore, when possible, we combined seeds by genus to minimize the number of seed species that needed to be removed.

Results

Diet composition

We collected 92 common carp and identified vascular tissue of six aquatic vegetation taxa, 21 invertebrate taxa, 43 seed taxa, mollusks, a variety of 'other' food items, and unidentifiable materials in digestive tracts across seasons. In general, individual common carp regularly ingested multiple types of food from all diet categories (Tables 1 and 2). Total biomass in each diet category did not differ by season (i.e. autumn and spring; Wilks' $\lambda_{4,86} = 0.99$; $P = 0.89$, Figure 2). Common carp collected in autumn 2013 ($n = 37$) most frequently ingested invertebrates (97%), followed by mollusks (92%), seeds (86%), and vegetation (73%; Table 1). Common carp collected in spring 2014 ($n = 29$) also most frequently ingested invertebrates (93%), followed by mollusks (83%) and vegetation (83%), and seeds (79%; Table 1). Common carp collected in autumn 2014 ($n = 26$) most frequently ingested vegetation (92%), invertebrates (75%), mollusks (62%), and seeds (54%; Table 1). Mollusks contributed most to diet biomass in all sampling periods and composed 73%–86% of total diet biomass. Seeds comprised 0.4%–2.4% of total diet biomass (Table 2), and despite finding over 40 seed taxa in diets, seeds were only the third- or fourth-most frequently eaten item among all seasons sampled (Table 1). Unidentifiable material was present in 100% of common carp diets collected and constituted 37%–61% of total diet biomass.

Autumn seed selection

We identified 33 seed taxa in autumn fish diets (Table 3) and 131 seed taxa in core samples, including 105 seed taxa in core samples that were not present in diets. In common carp diets, the number

Table 1. Frequency of occurrence of diet items by season and year collected from common carp (*Cyprinus carpio*) in the Upper Illinois River Waterway, 2013–2014.

Year	Season	<i>n</i>	Vegetation	Invertebrates	Seeds	Mollusca	Other
2013	Autumn	37	73.0	97.3	86.5	91.7	89.0
2014	Spring	29	82.8	93.1	79.3	82.8	100.0
2014	Autumn	26	92.3	84.6	53.8	62.0	100.0

Table 2. Common carp (*Cyprinus carpio*; $n = 92$) common diet items frequency of occurrence (%) and % biomass of diet items relative to total diet biomass, excluding items with $< 5\%$ occurrence and unidentifiable item categories. Fish were collected from the upper Illinois River Waterway during autumn 2013, spring 2014, and autumn 2014.

Diet item	% Occurrence	% Biomass
Vegetation		
Unidentifiable vegetation	70.7	7.84
<i>Lemna</i> sp.	23.9	1.83
<i>Vallisneria americana</i>	13.0	0.42
<i>Myriophyllum spicatum</i>	3.3	0.01
Invertebrates		
Chironomidae	70.7	0.30
Invertebrate fragment ¹	68.5	1.15
Nematoda	68.5	0.13
Amphipoda	26.1	0.08
Oligochaeta	21.7	0.14
Ceratopogonidae	12.0	< 0.01
Seeds		
Seed fragment ¹	62.0	0.76
<i>Vallisneria americana</i>	43.5	0.39
<i>Eichhornia crassipes</i>	14.1	0.04
<i>Polygonum</i> spp.	12.0	0.04
<i>Cyperus</i> spp.	8.7	< 0.01
<i>Scirpus</i> spp.	6.5	< 0.01
<i>Fragaria vesca</i>	5.4	< 0.01
Mollusca		
Fragment ¹	77.2	75.37
Whole	23.9	4.44
Other material		
Scales	79.4	1.87
Rocks	75.0	3.62
Fish eggs	22.8	0.98
Feathers	8.7	< 0.01

¹Identifiable portions of items which were not whole.

of seeds per species varied widely (1–892 individual seeds) and frequency of occurrence of individual seed taxa in diets varied between 1%–51% per seed taxa during autumn (Tables 3 and 4). Both water hyacinth (*Eichhornia crassipes*; invasive, non-native in IRW) and water stargrass (*Heteranthera dubia*; native in IRW) seeds were positively identified in diet samples, but we were unable to

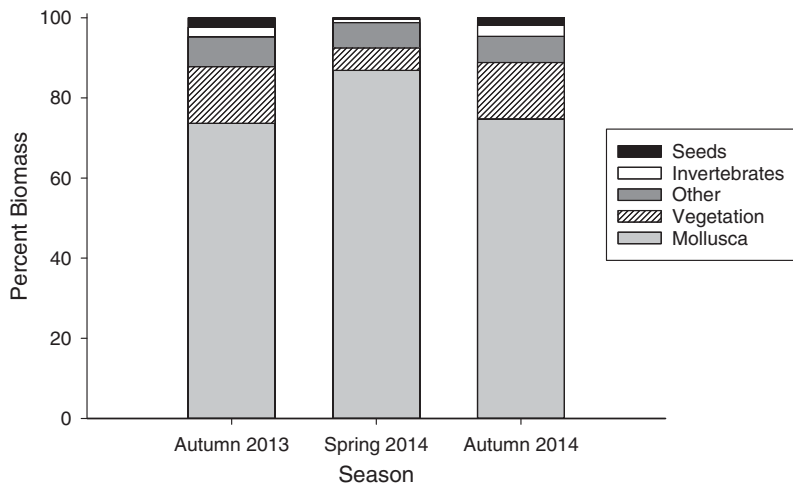


Figure 2. Percentage of the total biomass composed by each diet category for common carp (*Cyprinus carpio*), by sample date and excluding unidentifiable materials. Fish were collected from the upper Illinois River Waterway during autumn 2013 ($n = 37$), spring 2014 ($n = 29$), and autumn 2014 ($n = 26$).

Table 3. A complete list of all identified seed taxa encountered in common carp (*Cyprinus carpio*) digestive tracts during autumn 2013 ($n = 37$) and autumn 2014 ($n = 26$) in the upper Illinois River Waterway, including a count of each taxa (n) and the frequency of occurrence in fish diets ($\#$). Number of individuals includes whole items only, and excludes fragments. Taxa are separated by indicator category (USDA, NRCS 2016).

	n	$\#$		n	$\#$
Obligate wetland			Facultative/facultative upland		
<i>Vallisneria americana</i>	892	32	<i>Verbena</i> spp.	4	3
<i>Scirpus</i> spp.	6	2	<i>Portulaca oleracea</i>	4	3
<i>Sagittaria</i> sp.	4	3	<i>Digitaria</i> spp.	4	2
<i>Najas guadalupensis</i>	2	1	<i>Poa</i> sp.	4	2
<i>Zannichellia palustris</i>	2	2	<i>Aster</i> sp.	3	1
<i>Eleocharis</i> spp.	1	1	<i>Amaranthus</i> spp.	2	2
<i>Eragrostis hypnoides</i>	1	1	<i>Amaranthus blitoides</i>	1	1
<i>Ludwigia peploides</i>	1	1	<i>Brassica</i> spp.	1	1
<i>Potamogeton</i> spp.	1	1	<i>Physalis</i> sp.	1	1
			<i>Sinapis arvensis</i>	1	1
			<i>Taraxacum officinale</i>	1	1
			<i>Vitis aestivalis</i>	1	1
Facultative wetland			Invasive (Aquatic)		
<i>Polygonum</i> spp.	13	4	<i>Eichhornia crassipes</i>	156	13
<i>Polygonum lapathifolium</i>	3	2			
<i>Chenopodium album</i>	3	2			
<i>Cyperus odoratus</i>	3	1			
<i>Cyperus erythrorhizos</i>	2	1			
<i>Panicum</i> spp.	2	1			
<i>Cyperus</i> spp.	1	1			
<i>Cyperus esculentus</i>	1	1			
<i>Cyperus ferruginescens</i>	1	1			
<i>Cyperus strigosus</i>	1	1			
<i>Polygonum persicaria</i>	1	1			

unequivocally quantify the abundance of each separate species in core samples due to morphological similarities, and these species were combined for analyses and reporting. We conducted the electivity analyses on the abundance of 12 seed taxa frequently found in diets and the density ($\#/m^2$) of the same species recovered from sediment core samples. All seed taxa had a negative electivity value (range: $-0.99 - -0.60$) except wild celery (*Vallisneria americana*, electivity = 0.84), which was the only taxa found in greater occurrence in diets than in core samples (Figure 3).

Discussion

Common carp diets in the upper IRW included the whole seeds of both terrestrial and aquatic plant species. Common carp also exhibited selection for wild celery seeds, and thus may be an important dispersal vector of aquatic seeds in temperate large river systems. Although occurrence of seeds of aquatic vegetation in common carp diets was high, vascular vegetative biomass was low, indicating that common carp in the upper IRW forage more frequently on other items. Our data suggest that common carp could serve as a dispersal vector for seeds of native aquatic vegetation, which may be important during floodplain restoration. However, common carp may also disperse invasive and

Table 4. The four most-frequently occurring seeds in common carp (*Cyprinus carpio*) diets ($n = 63$) compared to availability (proportional occurrence) in the seed bank. Seed availability was determined at randomly selected locations in the upper Illinois River Waterway during autumn 2013 and autumn 2014. Fish were collected from the upper Illinois River Waterway during autumn 2013 ($n = 37$) and autumn 2014 ($n = 26$).

Seed taxa	Consumption (%)	Availability (%)
<i>Vallisneria americana</i>	50.8	18.6
<i>Eichhornia crassipes</i>	20.6	33.9
<i>Polygonum</i> spp.	6.3	47.5
<i>Sagittaria</i> spp.	4.7	37.3

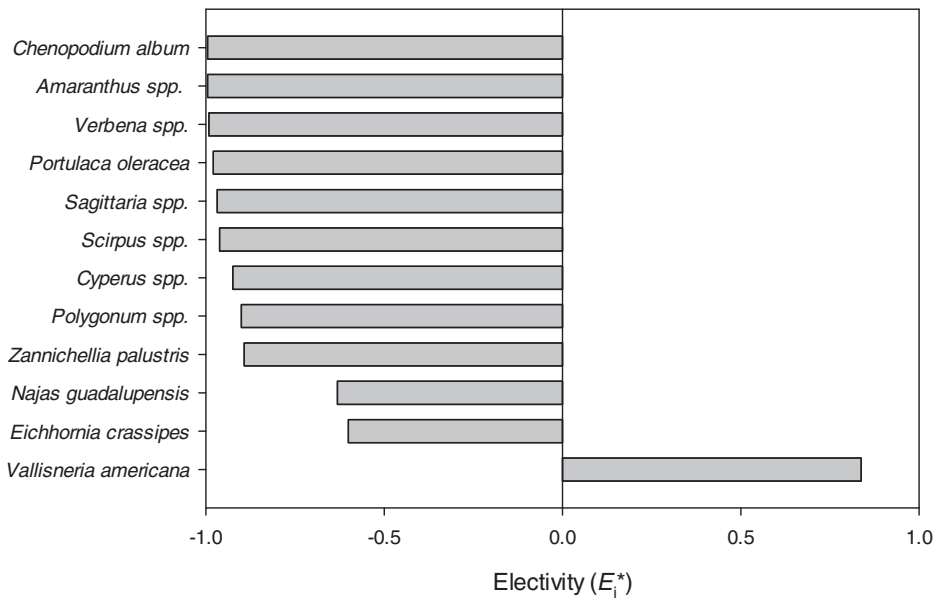


Figure 3. Vanderploeg and Scavia's relativized electivity index (E_i^*) of 12 seed taxa commonly found in diets of common carp (*Cyprinus carpio*) collected from the upper Illinois River Waterway during autumn 2013 ($n = 37$) and autumn 2014 ($n = 26$).

undesirable aquatic plants which may outcompete native species in the highly modified IRW, where disturbances are common and obligate aquatic vegetation seldom persists in wetlands and floodplains connected to the main river channel (Moore et al. 2010).

We discovered no differences in diet composition between autumn and spring collection periods or between years. Several diet items composed the majority of abundance and biomass, but common carp diets were generalist and omnivorous, consisting of items that are prevalent throughout North American aquatic systems. Powles et al. (1983) also found common carp to be benthic omnivores with no differences in food item categories (e.g. mollusks, vegetation) or biomass of foods ingested between seasons (autumn and winter). In our study, seeds were neither dominant in diets nor as bio-energetically important as other diet items (e.g. mollusks), yet seeds were a consistent component of common carp diets. Many studies have shown that common carp ingest seeds at high frequency but similarly noted that seeds comprise a small numerical percentage and biomass of foods items in diets (Crivelli 1981; Michel and Oberdorff 1995; Garcia-Berthou 2001). Our electivity analysis indicates that most seeds present in diets were selected against (negative electivity) with the exception of wild celery seeds which dominated in both abundance and frequency. Thus, we interpreted the negative electivity as indicating these were incidentally consumed while foraging and represent a neutral selection tendency instead of a negative one. The foraging strategy of common carp (i.e. slow siphoning of sediment and cross-filtration of food and non-food items; Callan and Sanderson 2003) means that unintentional consumption of material readily occurs, as evidenced by the presence of sediment in diet samples, and could likely be the basis for seed diet similarity between years and seasons.

The implications of seed ingestion by common carp are important when considering that common carp are capable of moving up to 238 km annually in large rivers (Jones and Stuart 2009); a distance which would extend ranges of common carp we captured upriver into Lake Michigan or downriver to near the confluence of the Illinois and Mississippi rivers. Seed dispersal distance is dependent on locomotion rates of the fish. For instance, an elevated swimming rate increases retention time of seeds in common carp, thus allowing seeds to be dispersed farther when common carp are swimming faster (van Leeuwen et al. 2015). Moreover, there are differences in habitat use by

adult and sub-adult common carp (Penne and Pierce 2008) that could lead to spatially distinct patterns in ichthyochory, especially if there are differences in movement distances between adult and sub-adult common carp.

However, in addition to ingestion, successful ichthyochory is also dependent on interacting factors. Mitigating factors that could be limiting the role of ichthyochory include declining numbers of common carp, seed digestion and degradation reducing viability, patterns of spatial habitat use by the fish, and whether minimum conditions needed for successful germination are present after potential passage of seeds completely through the digestive system and expulsion. After ingestion by fish, seed viability and germination rely on several seed characteristics, including seed morphology, seed coat hardness, seed size, fish ingestion strategies, retention time in fish guts, and suitability of the location of seed passage for subsequent germination (Pollux et al. 2006; Pollux 2011). Spring and summer floods temporarily connect many backwater lakes and floodplains to the main river channel in the IRW, potentially allowing common carp to act as dispersal vectors into seasonally disconnected backwater lakes. However, the germination and growth of rooted aquatic vegetation in the IRW and associated floodplain lakes and wetlands are also constrained by additional factors such as accumulation of flocculent sediments and frequent and high-magnitude flooding during the growing season (Bellrose et al. 1983; Havera 1999; Stafford et al. 2007). Thus, common carp may be more important as a dispersal vector for aquatic plant species that are less dependent on stable water levels and consolidated substrates (e.g. water hyacinth).

The upper IRW currently contains abundant emergent and submersed aquatic vegetation (VonBank et al. 2016), potentially in part because the common carp population in that reach has decreased dramatically over the last half century (McClelland et al. 2012; Gibson-Reinemer et al. 2017b), and evidence suggests that common carp, while still abundant throughout temperate rivers, may be exhibiting a sustained population-wide decline, particularly in smaller size classes (Gibson-Reinemer et al. 2017a). Combined with age–size specific habitat use patterns, declining populations may also be a more recent factor influencing seed dispersal patterns. Although our study provides clear evidence that common carp consume seeds, further research that focuses on the post-ingestion phases of ichthyochory is needed to determine what factors are most influential in seed dispersal potential.

Our data indicate common carp selected wild celery seeds while foraging, as the frequency of these seeds in diets was greater than availability in the seed bank. Although common carp may not be able to target wild celery seeds directly, due to their foraging mechanism, there may be indirect drivers that influence the places where common carp forage that expose them to abundant wild celery seeds. For example, selection of wild celery seeds may be influenced by common carp habitat use, as they may be foraging while using vegetative wild celery beds as refugia from predators (Dibble et al. 1997), or because of differences in water quality associated with aquatic vegetation (e.g. pH, dissolved oxygen, turbidity; Dennison et al. 1993; James et al. 2004). Alternatively, wild celery may grow in sediment that is more conducive to carp foraging, thus increasing the likelihood that common carp would ingest wild celery seeds. Regardless of mechanism, common carp frequently consumed wild celery seeds and directly removed them from the environment. The upper IRW is likely the only part of the IRW where wild celery, a native submersed aquatic macrophyte, is currently present (VonBank et al. 2016). Foraging by carp in wild celery beds could have a substantial ecosystem impact because wild celery seeds and winter buds are a potential food resource for waterfowl in the IRW. For example, individual canvasback (*Aythya valisineria*) diets samples have contained > 6200 seeds and 188 winter buds (Korschgen et al. 1988; Osborn et al. 2016). In the upper IRW, wild celery seeds are being consumed at high rates by common carp, which may demonstrate competition with waterfowl for a limited food base (VonBank et al. 2016). In addition, aquatic vegetation, such as wild celery, is used by juvenile native fishes as refuge from predators (Grenouillet et al. 2002). Although wild celery is abundant in the littoral zone throughout the upper IRW, continued consumption of wild celery seeds and plants by common carp or extensive roiling in wild celery beds could lead to substantial decreases in wild celery abundance and reduce habitat quality for fish and waterfowl.

Although ichthyochory by common carp may benefit dispersal of native aquatic plant seeds, common carp may also be acting as a dispersal vector for invasive aquatic plants. For example, water hyacinth is an invasive aquatic plant whose recent arrival and rapid proliferation in the IRW have the potential to undermine the progress of ecological recovery in this system (VonBank et al. 2017). Water hyacinth forms dense beds on the surface of slow-moving waterways and backwaters, where it can restrict commercial and recreational traffic, outcompete native emergent and submersed aquatic macrophytes, and affect natural biogeochemical and evapotranspiration cycles (Penfound and Earle 1948; Rai and Datta Munshi 1979). Water hyacinth also establishes through production of copious hydrochoric seeds, common in the seed bank of aquatic systems where water hyacinth is present (Albano Pérez et al. 2011). Additionally, the relatively high percent occurrence of water hyacinth seeds is likely influenced by common carp collected near water hyacinth beds, especially in 2014 where common carp ($n = 4$) contained 137 of 156 total water hyacinth seeds discovered in autumn-collected common carp diets. Regardless, water hyacinth seeds in the seed bank is a cause for concern that future infestation in disturbance-prone river systems such as the IRW could be exacerbated by common carp ichthyochory. The potential for invasive, non-native common carp to disperse seeds of invasive, non-native aquatic plants is emblematic of the compounding problem that the presence of multiple invasive species can present. In our study, there were three additional invasive plant species found in common carp diets from the IRW: oatgrass (*Avena* sp.), reed canary grass (*Phalaris arundinacea*), and common sowthistle (*Sonchus oleraceus*), albeit in low frequency and numbers (see Supplemental Materials). Further research should address native and invasive plant seeds as forage for common carp, specifically related to dispersal, post-ingestion germination, and the functional role of the removal of seeds by common carp in structuring the aquatic vegetation community.

The upper IRW has undergone substantial improvement in recent decades; improved water quality and ample aquatic vegetation habitat are credited with the greatest contributions to the remarkable rebound in the diversity and abundance of the fish assemblage since the implementation of the Clean Water Act of 1972 (McClelland et al. 2012; Gibson-Reinemer et al. 2017b). Although common carp populations in Midwestern river systems have begun to decline from 1960 to 2015 (Gibson-Reinemer et al. 2017a), they are still known to destroy native aquatic plant communities (Crivelli 1983; Bajer et al. 2009; Bajer et al. 2016), and restoration efforts often require exclusion cages, fencing, or other methods for reducing negative effects of common carp on reintroduction or restoration of native aquatic vegetation (Wilcox and Whillans 1999). Further research should be focused on ingestion duration, gut passage, and post-expulsion germination rates of both invasive and native seeds, after which the full potential for common carp to alter plant community dynamics and native fish habitat in riverine environments can be assessed.

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References

- Adams SB, Hamel PB, Connor K, Burke B, Gardiner ES, Wise D. 2007. Potential roles of fish, birds, and water in swamp privet (*Forestiera acuminata*) seed dispersal. *Southeast Nat.* 6:669–682.
- Albano Pérez E, Coetzee JA, Ruiz Téllez T, Hill MP. 2011. A first report of water hyacinth (*Eichhornia crassipes*) soil seed banks in South Africa. *South African J Botany.* 77:795–800.
- Alvord JW, Burdick CB. 1915. Report of the rivers and lakes commission on the Illinois River and its bottomlands, with reference to the conservation of agriculture and fisheries and the control of floods. Springfield (IL): Department of Public Works and Buildings, Division of Waterways.
- Anderson JT, Nuttle T, Rojas JSS, Pendergast TH, Flecker AS. 2011. Extremely long-distance seed dispersal by an overfished Amazonian frugivore. *P R Soc B.* 278:3329–3335. doi:10.1098/rspb.2011.0155. Published 23 March 2011.
- Anderson JT, Rojas JS, Flecker AS. 2009. High-quality seed dispersal by fruit-eating fishes in Amazonian floodplain habitats. *Oecologia.* 161:279–290.
- Bajer PG, Beck MW, Cross TK, Koch JD, Bartodziej WM, Sorensen PW. 2016. Biological invasion by a benthivorous fish reduced the cover and species richness of aquatic plants in most lakes of a large North American ecoregion. *Glob Change Biol.* 22:3937–3947.
- Bajer PG, Sorensen PW. 2010. Recruitment and abundance of an invasive fish, the common carp, is driven by its propensity to invade and reproduce in basins that experience winter-time hypoxia in interconnected lakes. *Biol Invasions.* 12:1101–1112.
- Bajer PG, Sullivan G, Sorensen PW. 2009. Effects of a rapidly increasing population of common carp on vegetation cover and waterfowl in a recently restored Midwestern shallow lake. *Hydrobiologia.* 632:235–245.
- Balon EK. 1995. Origin and domestication of the wild carp, *Cyprinus carpio*: from Roman gourmets to the swimming flowers. *Aquaculture.* 129:3–48.
- Bayley PB. 1995. Understanding large river: floodplain ecosystems. *BioScience.* 45:153–158.
- Bellrose FC, Havera SP, Paveglio FL, Steffek DW. 1983. The fate of lakes in the Illinois River valley. Urbana (IL): Illinois Natural History Survey Biological Notes 119.
- Bischoff A. 2002. Dispersal and establishment of floodplain grassland species as limiting factors in restoration. *Biol Conserv.* 104:25–33.
- Bryson CT, DeFelice MS, editors. 2010. Weeds of the Midwestern United States and central Canada. Athens: University of Georgia Press.
- Callan WT, Sanderson SL. 2003. Feeding mechanisms in carp: crossflow filtration, palatal protrusions and flow reversals. *J Exp Biol.* 206(5):883–892.
- Chick JH, Cosgriff RJ, Gittinger LS. 2003. Fish as potential dispersal agents for floodplain plants: first evidence in North America. *Can J Fish Aquat Sci.* 60:1437–1439.
- Colle DE, Shireman JV, Rottman RW. 1978. Food selection by grass carp fingerlings in a vegetated pond. *T Am Fish Soc.* 107:149–152.

- Correa SB, Winemiller KO, Lopez-Fernandez H, Galetti M. 2007. Evolutionary perspectives on seed consumption and dispersal by fishes. *BioScience*. 57:748–756.
- Crivelli AJ. 1981. The biology of the common carp, *Cyprinus carpio* L. in the Carmargue, southern France. *J Fish Biol*. 18:271–290.
- Crivelli AJ. 1983. The destruction of aquatic vegetation by carp. *Hydrobiologia*. 106:37–41.
- DeBoer JA, Anderson AM, Casper AF. *In press*. Invasive planktivore initiates three-tiered, middle-out, trophic disruption in a floodplain river. *Ecol Appl*.
- Delong MD. 2005. Upper Mississippi River basin. In: Benke AC, Cushing CE, editors. *Rivers of North America*. New York (NY): Academic Press/Elsevier; p. 327–373.
- Dennison WC, Orth RJ, Moore KA, Stevenson JA, Carter V, Kollar S, Bergstrom PW, Batiuk RA. 1993. Assessing water quality with submersed aquatic vegetation. *BioScience*. 43:86–94.
- Dibble ED, Killgore KJ, Harrel SL. 1997. Assessment of fish-plant interactions. Multidimensional approaches to reservoir fisheries management. *Am Fish Soc*. 16:357–372.
- Fritts MW, DeBoer JA, Gibson-Reinemer DK, Lubinski BJ, McClelland MA, Casper AF. 2017. Over 50 years of fish community monitoring in Illinois' large rivers: the evolution of methods used by the INHS's Long-term Survey and Assessment of Large-River Fishes in Illinois. *Illinois Natural History Survey Bulletin*. 41(1):1–18.
- Galetti M, Donatti CI, Pizo MA, Giacomini HC. 2008. Big fish are the best: seed dispersal of *Bactris glaucescens* by the Pacu fish (*Piaractus mesopotamicus*) in the Pantanal, Brazil. *Biotropica*. 40:286–289.
- Garcia-Berthou E. 2001. Size- and depth-dependent variation in habitat and diet of the common carp (*Cyprinus carpio*). *Aquat Sci*. 63:466–476.
- Gibson-Reinemer DK, Chick JH, VanMiddlesworth TD, VanMiddlesworth M, Casper AF. 2017a. Widespread and enduring demographic collapse of invasive common carp (*Cyprinus carpio*) in the Upper Mississippi River System. *Biol Invasions*. 19:1905–1916. doi:10.1007/s10530-017-1405-5.
- Gibson-Reinemer DK, Sparks RA, DeBoer JA, Fritts MW, Casper AF, Chick JH. 2017b. Ecological recovery of a river fish assemblage following the implementation of the Clean Water Act. *BioScience*. 67:957–970. doi:10.1093/biosci/bix110.
- Grenouillet G, Pont D, Seip KL. 2002. Abundance and species richness as a function of food resources and vegetation structure: juvenile fish assemblages in rivers. *Ecography*. 25:641–650.
- Hagy HM, Straub JA, Kaminski RM. 2011. Estimation and correction of seed recovery bias from moist-soil cores. *J Wildlife Manag*. 75:959–966.
- Havera SP. 1999. Waterfowl of Illinois: status and management. Urbana (IL): Illinois Natural History Survey Special Publication 21.
- Horn MH, Correa SB, Parolin P, Pollux BJA, Anderson JT, Lucas C, Widmann P, Tiju A, Galetti M, Goulding M. 2011. Seed dispersal by fishes in tropical and temperate fresh waters: the growing evidence. *Acta Oecol*. 37(6):561–577.
- Hossain MA, Focken U, Becker K. 2001. Evaluation of an unconventional legume seed *Sesbania aculeate*, as a dietary protein source for common carp, *Cyprinus carpio* L. *Aquaculture*. 198:129–140.
- James WF, Best EP, Barko JW. 2004. Sediment resuspension and light attenuation in Peoria Lake: can macrophytes improve water quality in this shallow system? *Hydrobiologia*. 515:193–201.
- Johnson DH. 1995. Statistical sirens: the allure of nonparametrics. *Ecology*. 76:1998–2001.
- Jones MJ, Stuart IG. 2009. Lateral movement of common carp (*Cyprinus carpio* L.) in a large lowland river and floodplain. *Ecol Freshw Fish*. 18:72–82.
- Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river-floodplain systems. *Can Spec Pub Fish Aquat Sci*. 106:110–127.
- Korschgen CE, George LS, Green WL. 1988. Feeding ecology of canvasbacks staging on Pool 7 of the Upper Mississippi River. In: Weller MW, editors. *Waterfowl in winter*. Minneapolis (MN): University of MN Press; p. 237–250.
- Lechowicz MJ. 1982. The sampling characteristics of electivity indices. *Oecologia*. 52:22–30.
- Lerczak TV, Sparks RE, Blodgett KD. 1995. The long-term Illinois River fish population monitoring program project. Urbana (IL): Illinois Natural History Survey. *Aquatic Ecology Technical Report* 95(4): Project F-101-R.
- Lowe S, Browne M, Boudjelas S, De Poorter M. 2000. 100 of the world's worst invasive alien species: a selection from the global invasive species database. Auckland: Invasive Species Specialist Group.
- Martin AC, Barkley WD. 1961. *Seed identification manual*. Berkeley (CA): University of California Press.
- McClelland MA, Sass GG, Cook TR, Irons KS, Michaels NN, O'Hara TM, Smith CS. 2012. The long-term Illinois River fish population monitoring program. *Fisheries*. 37:340–350.
- Merritt RW, Cummins KW. 1996. *An introduction to the aquatic insects of North America*. Dubuque: Kendall Hunt Publishing.
- Michel P, Oberdorff T. 1995. Feeding habits of fourteen European freshwater fish species. *Cybum*. 19:5–46.
- Mills EL, Leach JH, Carlton JT, Secor CL. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. *J Great Lakes Res*. 19:1–54.
- Moore M, Romano SP, Cook T. 2010. Synthesis of upper Mississippi River system submersed and emergent aquatic vegetation: past, present, and future. *Hydrobiologia*. 640:103–114.

- Nilsson C, Berggren K. 2000. Alterations of riparian ecosystems caused by river regulation. *BioScience*. 50:783–792.
- Nilsson C, Reidy CA, Dynesius M, Revenga C. 2005. Fragmentation and flow regulation of the World's large river systems. *Science*. 308:405–408.
- Nilsson C, Brown RL, Jansson R, Merritt DM. 2010. The role of hydrochory in structuring riparian and wetland vegetation. *Biol Rev*. 85:837–858.
- Orban L, Wu Q. 2008. Cyprinids. In: Kocher TD, Kole C, editors. *Genome mapping and genomics in fishes and aquatic animals*. Berlin, Heidelberg: Springer; p. 45–83.
- Osborn JM, Hagy HM, Levenson JM, Yetter AP, England JC, Horath MM, Hine CS, McClain DR. 2016. Intrinsic and extrinsic factors determining diving duck condition and habitat quality during spring migration in the upper Midwest. Urbana (IL): Illinois Natural History Survey. Illinois Natural History Survey Technical Report 2016(22).
- Penfound WT, Earle TT. 1948. The biology of the water hyacinth. *Ecol Monogr*. 18:447–472.
- Penne CR, Pierce CL. 2008. Seasonal distribution, aggregation, and habitat selection of common carp in Clear Lake, Iowa. *T Am Fish Soc*. 137:1050–1062.
- Planty-Tabacchi AM, Tabacchi E, Naiman RJ, DeFerrari C, Decamps H. 1996. Invasibility of species-rich communities in riparian zones. *Conserv Biol*. 10:598–607.
- Pollux BJA. 2011. The experimental study of seed dispersal by fish (ichthyochory). *Freshwater Biol*. 56:197–212.
- Pollux BJA, De Jong M, Steegh A, Ouborg NJ, Van Groenendael JM, Klaassen M. 2006. The effect of seed morphology on the potential dispersal of aquatic macrophytes by the common carp (*Cyprinus carpio*). *Freshwater Biol*. 51:2063–2071.
- Powles PM, MacCrimmon HR, Macrae DA. 1983. Seasonal feeding of Carp, *Cyprinus carpio*, in the Bay of Quinte watershed, Ontario. *Can Field Nat*. 97:293–298.
- Rai DN, Datta Munshi J. 1979. The influence of thick floating vegetation (Water hyacinth: *Eichhornia crassipes*) on the physio-chemical environment of a fresh water wetland. *Hydrobiologia*. 62:65–69.
- Ratcliff EN, Gittinger EJ, O'Hara TM, Ickes BS. 2014. Long term resource monitoring program procedures: fish monitoring. US Army Corps of Engineers, Upper Mississippi River Restoration–Environmental Management Program. Rock Island (IL): US Army Corps of Engineers. Report LTRMP-2014-P001.
- Ringelman KM, Williams CK, Coluccy JM. 2015. Assessing uncertainty in coastal marsh core sampling for waterfowl foods. *J Fish Wildl Manag*. 6:238–246.
- Rixon CA, Duggan IC, Bergeron NM, Ricciardi A, MacIsaac HJ. 2005. Invasion risks posed by the aquarium trade and live fish markets on the Laurentian Great Lakes. *Biodivers Conserv*. 14:1365–1381.
- Schummer ML, Hagy HM, Fleming KS, Chesier JC, Callicutt JT. 2011. A guide to moist-soil wetland plants of the Mississippi Alluvial Valley. Jackson (MS): University Press of Mississippi.
- Smiley CW. 1886. Some results of carp culture in the United States. In: Report of the Commissioner of Fish and Fisheries for 1884, Part XII. Washington (DC): U.S. Commission of Fish and Fisheries; p. 657–890
- Solomon LE, Pendleton RM, Chick JH, Casper AF. 2016. Long-term changes in fish community structure in relation to the establishment of Asian carps in a large floodplain river. *Biol Invasions*. 18:2883–2895.
- Sparks RE, Tazik PP, Blodgett KD, Warren GL, Wetzel MJ. 1986. Des Plaines River long-term monitoring program: Phase 1. Illinois Natural History Survey Aquatic Biology Section. Urbana (IL): Illinois Natural History Survey. Report no. 1986(6).
- Stafford JD, Horath MM, Yetter AP, Smith RV, Hine CS. 2007. Historical and contemporary characteristics of Illinois River Valley wetlands: a geospatial database for conservation planning and evaluation. Urbana (IL): Illinois Natural History Survey. Illinois Natural History Survey Technical Report 51.
- Stafford JD, Horath MM, Yetter AP, Smith RV, Hine CS. 2010. Historical and contemporary characteristics and waterfowl use of Illinois River valley wetlands. *Wetlands*. 30:565–576.
- Stafford JD, Yetter AP, Hine CS, Smith RV, Horath MM. 2011. Seed abundance for waterfowl in wetlands managed by the Illinois Department of Natural Resources. *J Fish Wildl Manag*. 2:3–11.
- Tazik PP. 1988. Des Plaines River long-term monitoring program: vegetation analysis and habitat characterization. Illinois Natural History Survey Aquatic Biology Section. Urbana (IL): Illinois Natural History Survey. Report no. 88(5).
- Tokeshi M, Daud RJP. 2011. Assessing feeding electivity in *Acanthaster planci*: a null model analysis. *Coral Reefs*. 30:227–235.
- USDA, NRCS. 2016. The PLANTS Database. Greensboro (NC): National Plant Data Team. <http://plants.usda.gov> [accessed 2016 Sep 15].
- van Leeuwen CH, Beukeboom R, Nolet BA, Bakker ES, Pollux BJ. 2015. Locomotion during digestion changes current estimates of seed dispersal kernels by fish. *Funct Ecol*. 30:215–225.
- Vanderploeg HA, Scavia D. 1979. Calculation and use of selectivity coefficients of feeding: zooplankton grazing. *Ecol Model*. 7:135–149.
- VonBank JA, Casper AF, Yetter AP, Hagy HM. 2017. Evaluating a rapid aerial survey for floating-leaved aquatic vegetation. *Wetlands*. 37:753–762.



- VonBank JA, Hagy HM, Casper AF. 2016. Energetic carrying capacity of riverine and connected wetlands of the upper Illinois River for fall-migrating waterfowl. *Am Midl Nat.* 176:210–221.
- Weber MJ, Brown ML. 2009. Effects of common carp on aquatic ecosystems 80 years after ‘Carp as a dominant’: ecological insights for fisheries management. *Rev Fish Sci.* 17:524–537.
- Weber MJ, Brown ML, Willis DW. 2010. Spatial variability of common carp populations in relation to lake morphology and physiochemical parameters in the upper Midwest United States. *Ecol Freshw Fish.* 19:555–565.
- Wilcox DA, Whillans TH. 1999. Techniques for restoration of disturbed coastal wetland of the great lakes. *Wetlands.* 19:835–857.