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Research Article

Population characteristics of bighead and silver carp on the northwestern front of their North American invasion

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Abstract

Invasive species are considered the second largest threat to native biodiversity, and ecosystem function and services. One pair of global invaders, bighead, *Hypophthalmichthys nobilis*, and silver carp, *H. molitrix*, (collectively referred to as Asian carps) have been introduced throughout the world, and are invading three prairie stream tributaries to the Missouri River in the United States. There is a paucity of knowledge and understanding about Asian carp population characteristics and biology in North America. As such, we documented spatial and temporal trends in population dynamics (i.e., density, size structure, age, growth and condition) of Asian carps in three tributaries to the Missouri River in South Dakota: Big Sioux, James and Vermillion from 2009 to 2012. Finally, native planktivore (i.e., gizzard shad, *Dorosoma cepedianum*, bigmouth buffalo, *Ictiobus cyprinellus*, and emerald shiner, *Notropis atherinoides*) characteristics were examined using condition (Fulton's K). Overall, 469 silver carp and eight bighead carp were collected using boat electrofishing and mean catch-per-unit-effort of silver carp increased annually. The three rivers' populations were similar in length frequencies. Silver carp growth was faster initially than later ages and overall was slower than Middle Mississippi River populations. Recruitment of silver carp was erratic with the 2010 year class dominating 91% of catches. Silver carp condition was also similar across rivers, seasons, and years. South Dakota silver carp populations were predicted from a length-weight regression to be lighter than the Gavins Point reach population of the Missouri River, and heavier than both the middle Mississippi and the Illinois River populations. Additionally, mean catch-per-unit-effort for bigmouth buffalo and emerald shiner decreased over the study period. Continued monitoring and research on this newly invading population of Asian carps will provide additional invaluable insight into complex invasive species, assist with understanding Asian carps population dynamics during and after an invasion, and expose the potential negative impacts Asian carps may be having on prairie stream ecosystems.

Key words: growth, invasion phase, planktivores, prairie streams, recruitment

Introduction

Invasive species are common and increasing throughout a majority of North American freshwater environments and are expanding their ranges through natural and human-mediated dispersal (Lodge 1993; Vitousek et al. 1996; Rahel 2000) at an unprecedented rate (Pimm et al. 1995). The consequences of range expansion are poorly understood for most invasive species and the novel ecosystems they invade (Mitchell and Knouft 2009) as much research is conducted on a single species, usually after they have established and altered ecosystems (Kolar and Lodge 2002). Additionally, examining community and assemblage structure across large geographic scales (e.g., multiple rivers, ecoregions; Jeschke and Strayler 2005) is critical to identifying impacts of invasive species (Mack et al. 2000; Scott and Helfmann 2001; Jeschke and Strayler 2005; Simberloff et al. 2005; Poff et al. 2007; Leprieur et al. 2008) on aquatic ecosystems. This study examines two invasive species, bighead (*Hypophthalmichthys nobilis* Richardson, 1845, and silver carp, *H. molitrix* Valenciennes, 1844), across three Missouri River tributaries in South Dakota over four years at the beginning of their invasion there.

Two global invaders, bighead, and silver carp, (collectively referred to as Asian carps) have been introduced intentionally and unintentionally throughout the world, mostly for aquaculture purposes (Kolar et al. 2007) as they are the most important aquaculture species in Asia and east-central Europe (Lieberman 1996). Bighead carp have invaded 74 countries and are reproducing in 19 and silver carp have invaded 88 countries and are reproducing in 23 (Kolar et al. 2007). Both species of Asian carps are currently reproducing in the United States (Papoulias et al. 2006; DeGrandchamp et al. 2007; Lohmeyer and Garvey 2009; Deters et al. 2013). Asian carps were originally introduced into the southern United States in aquaculture ponds in the early 1970's where both species subsequently escaped and began migrating up the Mississippi River and into associated tributaries (e.g., Missouri River, Illinois River, Ohio River; Kolar et al. 2007). On the northwestern invasion front and at the beginning of this study in 2009, Asian carps were detected up to Gavins Point Dam on the Missouri River and at the mouths of three South Dakota tributaries to the Missouri River (Klumb 2007).

Limited data exists on the dynamic rate functions (i.e., recruitment, growth, and mortality) of Asian carps (Jennings 1988; Kolar et al. 2007), most often because estimating ages of these species is difficult (Schrank and Guy 2002; Kolar et al. 2007). Numerous hard structures (e.g., dorsal fin rays, pectoral fin rays, scales, saggital otoliths, cleithra, urohyal bones, and vertebrae; Kamilov 1985; Schrank and Guy 2002; Nuevo et al 2004; Williamson and Garvey 2005; Seibert and Phelps 2013) have been used and/or validated for accuracy and precision of age estimates. Regardless of method used to estimate ages, Asian carps can have rapid growth rates as bighead carp are capable of growing to 1800–2300 g in 4–5 years (Henderson 1978; Leventer 1987). Silver carp can reach 270 g (Waterman 1997) in their first year and can gain 45 g or more per month (Stone et al. 2000).

There is a paucity of knowledge and understanding about Asian carp population characteristics and biology (Conover et al. 2007; Burgess and Bertrand 2008; Asian carp regional coordinating committee 2012; Coulter et al. 2013) in North America and many studies have focused on predicting future invasions (e.g., bioenergetics, ecological niche, habitat suitability; Chen et al. 2007; Herborg et al. 2007; Kocovsky et al. 2012; Poulos et al. 2012), particularly into the Great Lakes (Cooke and Hill 2010; Kocovsky et al. 2012). As, such many are recognizing the potential contributions of basic research (e.g., behavioral, biological, ecological) to the study of invasive species (Sakai et al. 2001; Scott and Helfman 2001) and many state and government agencies are calling for general information about the population characteristics of Asian carps (e.g., Conover et al. 2007; Burgess and Bertrand 2008; Asian Carp Regional Coordinating Committee 2012). Therefore, our objective was to document spatial (e.g., rivers) and temporal (e.g., year) trends in population characteristics (i.e., density, size structure, age, growth and condition) of Asian carps and characterize discharge patterns within the study area. Additionally, we examined other length-at-age and length weight regressions of populations throughout the world, both native and nonnative, to see if there were any differences between invasion stages. Finally, native planktivore (i.e., gizzard shad, *Dorosoma cepedianum* Lesueur, 1818, bigmouth buffalo, *Ictiobus cyprinellus* Valenciennes, 1944, and emerald shiner, *Notropis atherinoides* Rafinesque, 1818; Mitchell and Knouft 2009) population characteristics were examined using Fulton's condition factor (K) across years. This basic biological information will provide insights into two prolific invasive species and also provide awareness into what transpires during an active invasion phase.

Study area

The James, Vermillion and Big Sioux rivers in South Dakota are three prairie tributaries which converge with an unchannelized section (Galat et al. 2005a) of the Missouri River just downstream of Gavins Point Dam (Figure 1). These warm-water rivers drain the Central Lowlands physiographic province in South Dakota (Galat et al. 2005b) and are characterized by low gradient streams of glacial origin (Hoagstrom et al. 2007). The upper portion of the James River has a gradient of about 0.02 m/km, and the lower portion has a gradient of about 0.05 m/km (Owen et al. 1981), making this river one of the lowest gradient rivers in the United States (Benson 1983). The James River (watershed area = 57,000 km^2) extends 760 river kilometers (Rkm) from southeastern North Dakota through eastern South Dakota to its confluence with the Missouri River (Berry et al. 1993; Figure 1). In addition to one large impassable dam located in North Dakota, approximately 230 low-head dams and rock crossings ranging from 1–2 meters, exist on the James River (Shearer and Berry 2003), potentially limiting fish migration and reproductive success during low hydrologic periods. However,

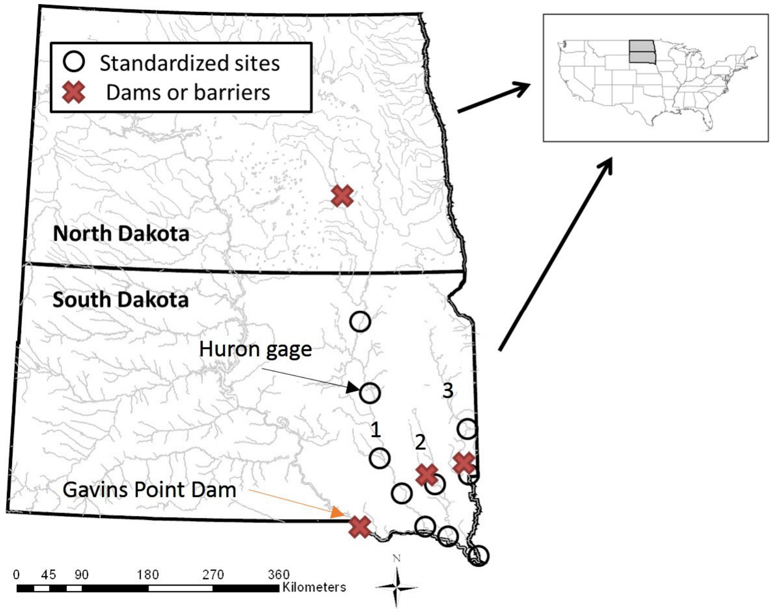

Figure 1. Study area in eastern South Dakota showing ten standardized sites on the James, Vermillion and Big Sioux Rivers. **1** refers to the James River, **2** refers to the Vermillion River and **3** refers to the Big Sioux River.

most of these barriers are passable during flood events (Berry et al. 1993). The Vermillion River, the smallest basin (watershed area = 5,800 km^2), extends 243 Rkm from the confluence of West and East Fork Vermillion rivers to its confluence with the Missouri River (Schmulbach and Braaten 1993; Figure 1). This river has one large dam (12.5 m high) on the East Fork Vermillion River, below East Lake Vermillion that acts as a barrier to fish passage. The Big Sioux River (watershed area = 23,325 km^2) extends 470 Rkm from the Prairie Coteau of northeastern South Dakota to its confluence with the Missouri River at the South Dakota-Nebraska-Iowa border (Figure 1). This river has one natural set of waterfalls in Sioux Falls that may act as barriers to fish movement and 3 smaller low head dams (2.5 m high).

Methods

Discharge

Mean monthly discharge data (expressed as cubic meters per second, CMS) from 2008–2012 was downloaded from United States Geological Survey (United States Geological Survey 2013) gaging stations along the James (N = 5), Vermillion (N = 2) and Big Sioux rivers (N = 3) that corresponded with standard fish sampling locations used in this study (Figure 1). A one way analysis of variance (ANOVA) was used to characterize spatial (i.e., river: James, Vermillion, Big Sioux Rivers and site: N=10) and temporal (i.e., year: 2008–2012 and season: spring, summer, fall) hydrologic variability in mean monthly discharge between 2008 and 2012. Additionally, a post-hoc Tukey's t-test was used to illustrate which variables within the group that was being tested for differences (i.e., river, site, year, season) were different from one another. To run an ANOVA, we lumped all sites within a river together and all seasons within a year together. Mean annual discharge was also downloaded from the Huron gage (# 06476000) on the James River to document current and historical trends (1949–2012). We assume that even though discharge was different among study site gages, the patterns in river stage were similar (Figure 2).

Fish collection

In order to detect the entire fish assemblage, standardized active and passive fish sampling gears were deployed each season (i.e., spring, summer, fall) from 2009–2012 at 10 sites on the James (N = 5), Vermillion (N = 2), and Big Sioux (N = 3) rivers (Figure 1). Many researchers have noted that Asian carps are extremely difficult to capture, (Stancil 2003; Williamson and Garvey 2005; Conover et al. 2007; Klumb 2007; Wanner and Klumb 2009) even in areas with high Asian carps concentrations. Therefore, multiple gears were deployed to determine effective sampling methods for Asian

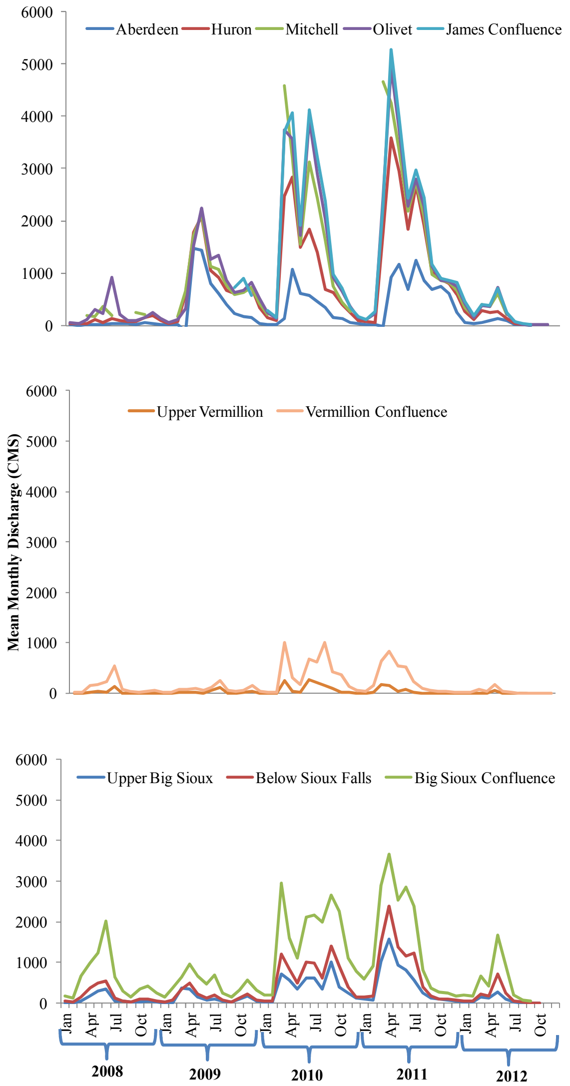

Figure 2. Mean monthly discharge (CMS) downloaded from the nearest US Geological Survey water gage to a sampling site for the James (A), Vermillion (B) and Big Sioux (C) rivers in eastern South Dakota between 2008–2012.

carps. Gears used included a combination of the following: pulsed DC boat electrofishing, hoop nets (hoop size: 1 meter; # hoops: 7; mesh size: 0.32cm × 0.61m), modified minifyke nets (4.5 m × 0.6m; 2 rectangular frames 1.2 m × 0.6m; 2 circular hoops 0.6 m diameter; 3mm ACE nylon mesh), and baited minnow traps (length = 42 cm; height = 19 cm; width = 22 cm; Purina dog food). Boat electrofishing catches also included any Asian carps that may have jumped in the boat while electrofishing. All gears were deployed following the standard methods of Drobish (2008) and Guy et al. (2009). Standardized effort at each site included three ten minute boat electrofishing runs, four hoop nets set overnight, four minifyke nets set overnight, and four minnow traps set overnight. Asian carps were only collected with boat electrofishing so all data on Asian carps presented within this paper are from electrofishing only data. All fish collected were identified, counted, weighed (g) and total length was measured (mm). Asian carps and native planktivores (i.e., bigmouth buffalo, gizzard shad and emerald shiner) were placed on ice and taken back to the laboratory at South Dakota State University where asterisci otoliths were extracted from each Asian carp. All other fish were released. Asterisci otoliths (Seibert and Phelps 2013) were removed from 334 silver carp and 15 bighead carp using methods similar to those described by Schneidervin and Hubert (1986). Otoliths were cleaned using warm water, stored in plastic vials, and allowed to dry for at least two weeks prior to further processing. We boat electrofished additional sites within the study area in response to angler and South Dakota Game, Fish, and Parks reports of Asian carps sightings. These additional data were included in catch-per-unit-effort (CPUE) calculations and age and growth estimates for Asian carps.

Asian carp population characteristics

Asian carps abundance was indexed using catch-per-unit-effort (CPUE), which was calculated as number per hour of electrofishing. One-way ANOVA was used to test for differences in CPUE after the data was $\log_{10}$ +1 transformed and percent of total catch by season (i.e. spring [May, June], summer [July, August], fall [September, October]), year (i.e., 2009, 2010, 2011, 2012), river (i.e., James, Vermillion, and Big Sioux rivers), and site, and a post-hoc Tukey's t-test was used to illustrate which variables within a group (e.g., season, year, river, and site) were different. All sites within a river were lumped together and all seasons within a year were lumped together.

Size structure of silver carp was examined with length-frequency histograms across time (i.e., seasonally). There were too few bighead carp collected to examine size structure. A nonparametric Kruskal-Wallis test for several samples was used to determine if length-frequency distributions for silver carp were different among rivers, sites, seasons, and years (Neuman and Allen 2007). Additionally, Fulton's condition factor which relates fish weight to length was used to examine condition of Asian carps. Fulton's condition factor (K) can be represented as:

$$K = (W/L^3)\times 100{,}000$$

where W equals weight (g) and L equals total length (mm). Condition was compared separately for silver carp and bighead carp, across rivers, sites, seasons and years using an ANOVA with a post-hoc Tukey's t-test.

After drying, one otolith from each individual was embedded in a two part epoxy mixture consisting of 5 parts Buehler® EpoxiCure® resin to one part Buehler® Epoxicure® hardener. One 0.5 mm cross section was cut out of each otolith using an Isomet (model # 11-1280-160) low speed precision saw mounted with a 0.3 mm diamond wafering blade (Buehler no. 11-4244). The otolith cross section was cut along a transect extending from anterior dorsal corner to the posterior ventral corner of the otolith. Each otolith thin-section was dried and glued to a glass microscope slide using cyanoacrylic cement. All otolith thin-sections were polished with 1,000 grit wetted sand paper and covered with immersion oil to enhance clarity prior to estimating ages. Otolith thin-sections were viewed through a dissecting microscope (Olympus© SZX7 with a 1X-4 objective) using transmitted light. Ages were estimated from all thin-sectioned otoliths by an expert independent reader who has estimated ages from thousands of thin-sectioned and cracked otoliths from many different species.

We used lapilli otoliths, found in the utriculus ear chamber of fish (Assis 2004; Zhang et al. 2012; Seibert and Phelps 2013) for estimating ages of both bighead and silver carp. However, there is no standard or validated structure that has been shown to be the best for estimating ages of Asian carps, sparking much debate. Some studies used sagittal otoliths to estimate ages of Asian carps, but were unsuccessful in estimating ages for bighead carp as the image was considered cloudy and unsuitable (Nuevo et al. 2004). However, Schrank et al. 2001 were able to age larval bighead carp using this structure. Additional structures have also been used to estimate ages of Asian carps including scales, cleithra, pectoral fin rays and urohyal bones (Johal et al. 2001; Schrank and Guy 2002; Williamson and Garvey 2005). For example, the pectoral fin ray had 60% agreement between two readers on Middle Mississippi River silver carp (Williamson and Garvey 2005) and urhoyal bones, cleithra, and scales were suitable structures for estimating ages in Gobindsagar Reservoir, India (Johal et al. 2001). The most precise structure may vary by geographic region or population as is apparent with the numerous different structures used for ageing Asian carp. Finding a suitable bony structure by experimenting with numerous structures and methods of preparation to estimate ages is extremely important in understanding changes in population dynamics, such as growth rates and mortality (Irons et al. 2011), age at maturation, timing and location of spawning locations.

Silver carp growth was estimated using a von Bertalanffy growth curve (Isley and Grabowski 2007) represented by the equation:

$$L_t = L_\infty[1 - e^{-K(t-t_0)}],$$

where L_t is length at time t, L_∞ is the average maximum attainable size, K is the Brody growth coefficient, and t_0 is the time coefficient at which fish length is theoretically 0 (von Bertalanffy 1938).

Native species population characteristics

Catch-per-unit-effort and Fulton's condition factor (K) were also calculated for native planktivores (i.e., gizzard shad, bigmouth buffalo, emerald shiner) and compared among rivers, sites, years, and seasons with one-way ANOVA and post-hoc Tukey's t-test to test for any differences that may be caused by Asian carp presence. To investigate differences in condition of native planktivores by river, linear regressions of weight-length data were compared after $\log_{10}$ transformation of both length and weight. The slope and intercept values were examined first, then the corresponding 95% confidence intervals for each river were inspected. Significant differences were identified by non-overlapping 95% confidence intervals and slope and intercept values that fall outside the confidence intervals (Pope and Krus 2007).

Results

Mean annual discharge for the James River during the study period (2009–2012) consisted of the largest, second largest, and fourth largest discharge values on record dating back to 1949 (Figure 3). Additionally, mean monthly discharge for all rivers combined differed annually ($F_{4,541}$ = 30.75; P < 0.0001) with 2010 (971.0 m^3s) and 2011 (1100.4 m^3s) being significantly larger than 2008 (170.7 m^3s), 2009 (433.3 m^3s) and 2012 (170.6 m^3s; Figure 2). Mean monthly discharge was also different across all study rivers ($F_{2,541}$ = 32.47, P < 0.0001), with the James River having the largest mean monthly

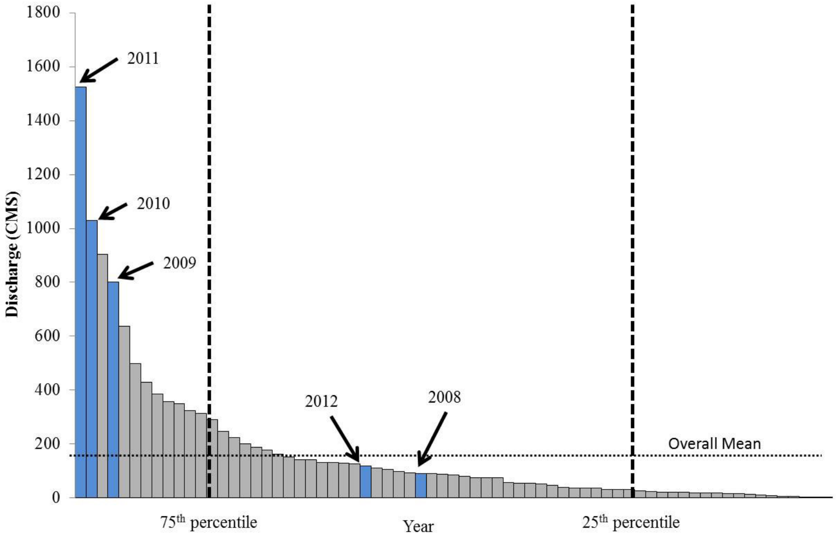

Figure 3. Mean annual discharge (CMS) between 1949 and 2012 with the 25th and 75th percentiles, the median, and the study period marked. Discharge is displayed in ascending order and was downloaded from USGS site # 06476000 in Huron, South Dakota.

discharge across the study period (881 m^3/s) followed by the Big Sioux River (524 m^3/s) and then the Vermillion River (109 m^3/s; Figure 1). By river, discharge followed a longitudinal pattern, decreasing from downstream to upstream sites ($F_{9,541}$ = 17.19, P <0.0001; Figure 1) as discharge was significantly different at each site within the respective watershed. Additionally, each season was unique ($F_{3,538}$ = 8.49; P < 0.001) with spring having the highest mean discharge (965 CMS) followed by summer (708 CMS), and fall (377 CMS).

Population dynamics

A total of 4,888 fish belonging to 41 species were collected over the course of this study with boat electrofishing. Thirty-nine boat electrofishing hours were spent collecting fish between fall 2009 and fall 2012. Only eight bighead carp were collected during the study interval using standardized methods (Figure 4) although our observations along with numerous anglers and the South Dakota Game Fish and Parks (SDGFP) personnel, suggest localized concentrations of bighead carp below the numerous low-head dams, which were too dangerous to sample. We did however, collect additional bighead (N=15), silver carp (N=116), and native planktivores (N=88) at non-standardized sites with boat electrofishing. Overall, 469 silver carp were collected using boat electrofishing (Figure 4).

Forty-nine percent of all silver carp captured were collected from the James River followed by

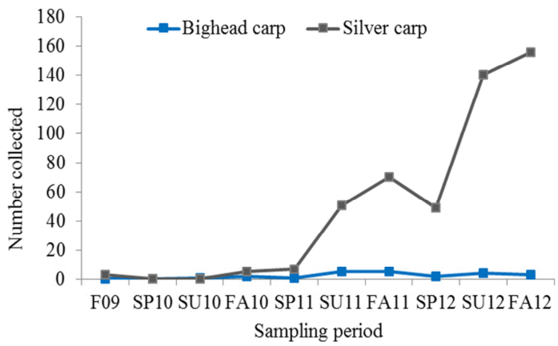

Figure 4. Bighead and silver carp catches in South Dakota tributaries across sampling seasons, spring (SP), summer (SU), fall (FA) from 2009–2012.

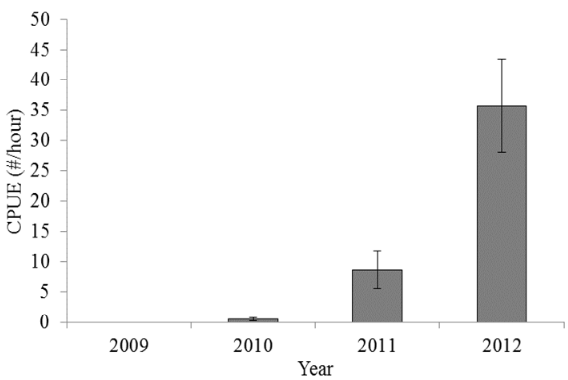

Figure 5. Mean (±1 standard error) catch-per-unit-effort (#/boat electrofishing hour) for silver carp between 2009 and 2012 in the Big Sioux, James and Vermillion rivers, South Dakota.

Table 1. Mean catch-per-unit effort by year (2009–2012) for standardized boat electrofishing on the James, Vermillion, and Big Sioux rivers. Numbers in parentheses represent standard deviations and periods represent sites we were unable to sample due to inclement weather.

River	Site Location	2009	2010	2011	2012
James	Confluence	0	1.36 (2.72)	2.88 (0.81)	23.14 (13.13)
	Lower-middle	0	.	11.65 (12.53)	76.73 (17.54)
	Middle	0	0	22.00	2.62
	Middle-upper	0	0	0	3.07(2.79)
	Upper	0	0	0	.
Vermillion	Confluence	0	0	22.50 (7.77)	58.43 (48.24)
	Middle	.	.	.	.
Big Sioux	Confluence	0	0.44 (.76)	20.62 (27.31)	38.01 (30.46)
	Middle	0	1.26 (1.79)	0	0.99 (1.40)
	Middle-upper	0	0	0	.

Table 2. Length-weight regression for silver carp collected in the James, Vermillion, and Big Sioux Rivers in eastern South Dakota along with r^2 and 95% upper and lower confidence intervals (CI) around the parameter estimates. Length-weight equations were also gathered for the Missouri River proper, the Middle Mississippi River proper and the Illinois River, a tributary to the Mississippi River. Predicted fish weights (g) for fish that are 450 mm and 800 mm are also given in the table for comparison.

River	L-W Regression Equation	r^2	Intercept 95% CI		Slope 95% CI		450 mm	800 mm	Reference
Missouri River Tributaries									
James	$\log_{10}$ weight = -5.26+3.11($\log_{10}$ length)	0.96	-5.43	-5.10	3.05	3.17	981	5869	
Vermillion	$\log_{10}$ weight = -4.82+2.90($\log_{10}$ length)	0.98	-5.16	-4.47	2.82	3.07	748	3971	
Big Sioux	$\log_{10}$ weight = -5.53+3.21($\log_{10}$ length)	0.98	-5.91	-5.14	3.07	3.36	970	6150	
Missouri River									
Gavins Point	$\log_{10}$ weight= -6.92+3.7($\log_{10}$ length)	0.97	0.21		0.59		788	6628	Wanner and Klumb 2009
Interior Highlands	$\log_{10}$ weight = -5.35+3.13($\log_{10}$ length)	0.93	0.76		0.21		900	5453	Wanner and Klumb 2009
Mississippi River									
Middle	$\log_{10}$ weight = -5.29+3.11($\log_{10}$ length)	0.81					915	5477	Williamson and Garvey 2005
Illinois River	$\log_{10}$ weight = -5.29+3.12($\log_{10}$ length)	0.99					972	5856	Irons et al. 2011

32% in the Vermillion River and 19% from the Big Sioux River. Mean CPUE for silver carp did not differ spatially (i.e., river) or seasonally (i.e., spring, summer, fall) although the highest mean CPUE occurred in the middle-lower James River (87 silver carp per hour) in 2012 at a non-standardized site. However, mean CPUE was highest at the lower James site and the Vermillion confluence with the Missouri River (31 and 24 silver carp per hour, respectively) across all years. Mean CPUE also increased each year at most sites (Table 1) with highest mean CPUE in 2012 (Figure 5; 36 silver carp/hour). Bighead carp CPUE did not change across years as catches remained small throughout the study time frame (Figure 4). The most bighead carp (N = 3) detected at one site were collected at the James River confluence with the Missouri River.

Ages were estimated from 334 of 469 silver carp collected and 15 of 23 bighead carp collected. Silver carp age estimates ranged from 0–5 and bighead carp age estimates ranged from 0–3. The largest silver carp (5 years old) was 823 mm and weighed 8219 g and the largest bighead carp was 1001 mm and weighed 8219 g. Silver carp length frequency histograms revealed the longest fish occurred in summers and mean length in 2009 was the longest (838 mm) followed by 2012 (507 mm; Figure 6). Only three adult silver carp were collected from the James River confluence in

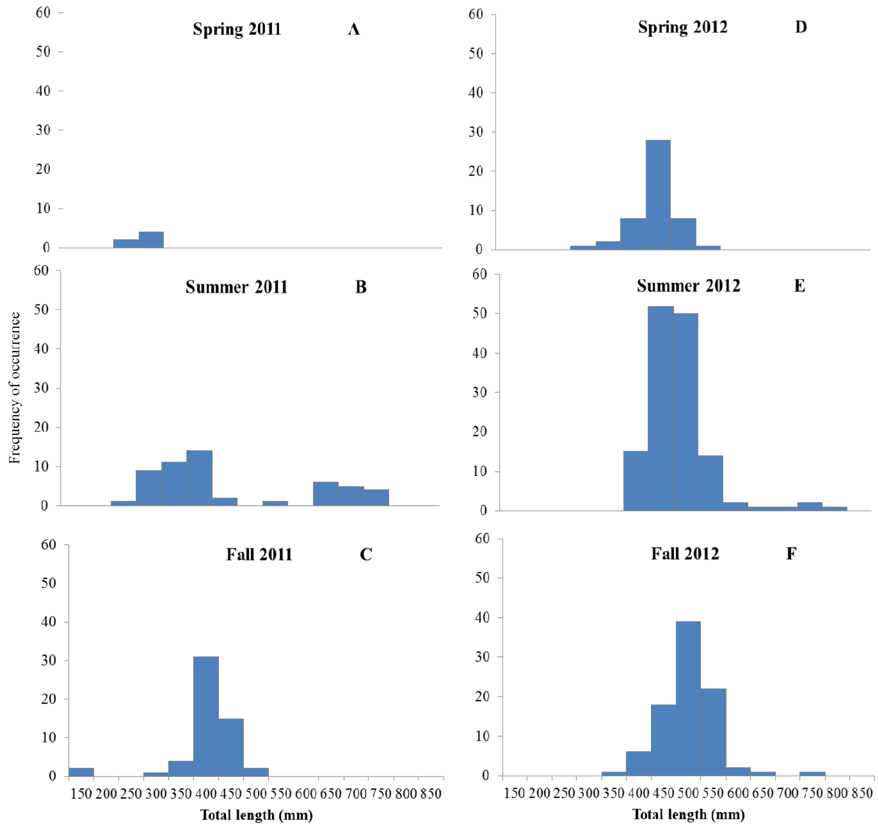

Figure 6. Length-frequency distribution for silver carp across seasons for 2011 and 2012.

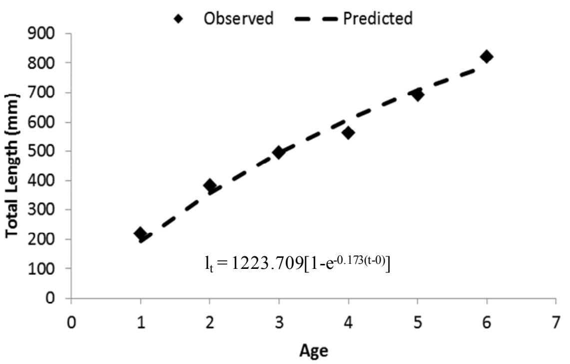

Figure 7. Predicted von Bertalanffy growth equation with observed values for silver carp collected in South Dakota tributaries 2009-2012.

2009. Length-frequency distributions were similar among rivers ($F_{2,394}$ = 0.66, P = 0.52). Further examination of size frequency histograms illustrated seasonal growth of silver carp, even growing in the winter months (Figure 6).

The von Bertalanffy growth equation for silver carp across all rivers was l_t=1223.709[1–e$^{-0.173(t-0)}$] (Figure 7). Silver carp growth reached almost 400 mm by the end of their second growing season (Figure 7). This initial fast growth was followed by slower growth at later ages (Figure7). Growth rates of silver carp were fastest at the confluences sites, and declined longitudinally within each river ($F_{12,384}$ = 8.75, P < 0.0001). Growth rates of silver carp in South Dakota were faster than the Amur River and Gobindsagar Reservoir but slower than the Middle Mississippi River (Figure 8).

The 2010 year class dominated most of the silver carp catches (Figure 9) indicating they may have erratic recruitment. In fact, the 2010 year class increased in density annually and comprised 91% of silver carp collected (Figure 9). There were numerous missing year classes including ages 1–5 in 2010 and age-0 in 2012 (Figure 9). Additionally, numerous weak year classes were present in 2011 and 2012.

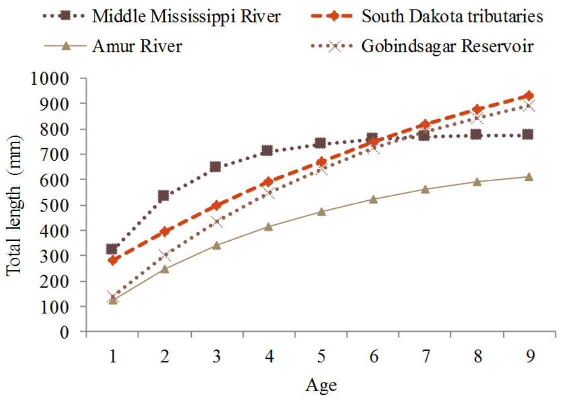

Figure 8. Predicted length at age for South Dakota tributaries, Middle Mississippi River (Williamson and Garvey 2005), the Amur River, Russia (Nikolskii 1961), and Gobindsagar Reservoir, India (Tandon et al. 1993).

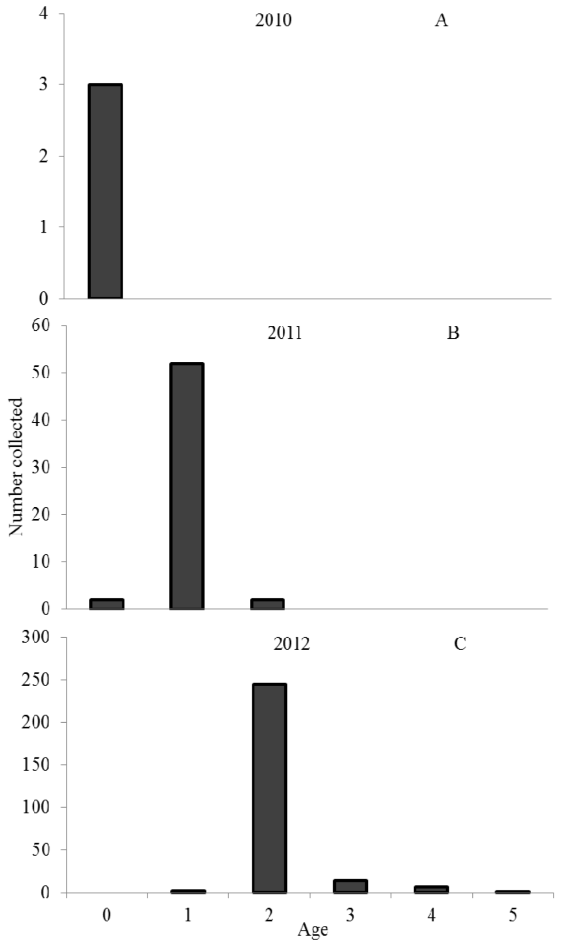

Figure 9. Age frequency histograms for silver carp collected in South Dakota tributaries 2010–2012 (A-C). Note that y-axis scales are not the same.

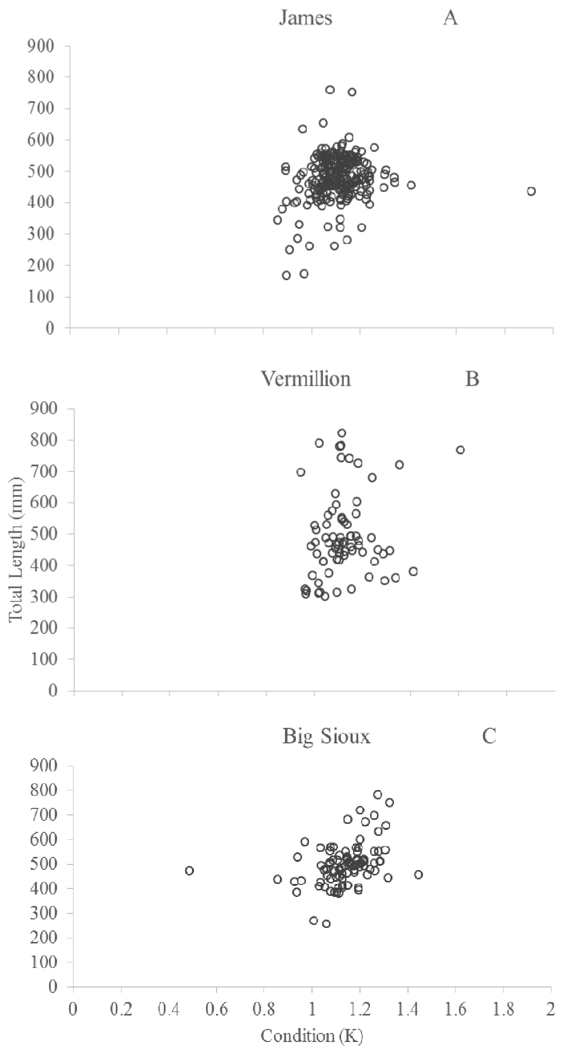

Figure 10. Condition (K) of native planktivores, bigmouth buffalo *Ictiobus cyprinellus*, gizzard shad *Dorosoma cepedianum* and emerald shiner *Notropis atherinoides* versus total length for the James (A), Vermillion (B) and Big Sioux (C) rivers.

Silver carp condition (Fulton's K) was relatively stable across rivers (Figure 10), season, and years. Additionally, 95% confidence intervals of length-weight regression parameters (slope and intercept) overlapped, indicating similar condition among rivers (Table 2). Based on length-weight regressions, an 800 mm silver carp in the Big Sioux River is predicted to be smaller (6150 g) than the Gavins Point reach population of the Missouri River (6628 g; Wanner and Klumb 2009), and larger than both the Middle Mississippi (5477 g) and the Illinois River populations (5856 g; Williamson and Garvey 2005; Irons et al. 2011; Figure 11).

Native planktivore characteristics

Overall planktivore CPUE ranged from 0–179/hour, gizzard shad ranged from 0–1786/hour, bigmouth buffalo ranged from 0–36/hour, and emerald shiner ranged from 0–129/hour. There were no differences in CPUE across rivers ($F_{2,66}$ = 0.84; P=0.44) or annually ($F_{3,65}$ =2.36; P=0.08) for native planktivores. Mean CPUE and percent total catches for bigmouth buffalo and emerald shiner was highest in 2009 and decreased each subsequent year (Figure 12) as silver carp populations were increasing. Although there were no significant differences in CPUE among species, there appeared to be a decreasing trend in gizzard shad CPUE as silver carp CPUE increased (Figure 13). Gizzard shad exhibited a significant difference in condition among seasons ($F_{2,649}$ = 3.05; P = 0.048) with highest values in the spring (K = 1.18) and there were no differences in bigmouth buffalo or emerald shiner condition through the study period or region.

Discussion

During this study, the James River recorded three of the top five highest mean annual discharge events since 1949 (United States Geological Survey 2013). These flood conditions overtook most of the lowhead dams and may have allowed for and facilitated the unobstructed movement and colonization upstream of silver carp into the James, Vermillion and Big Sioux rivers. Furthermore, silver carp were documented to migrate ~700 km from the confluence of the James River and the Missouri River over all of the lowhead dams with little resistance up to the Jamestown Dam in North Dakota. During these high discharge events, the James River may have provided natural free-flowing conditions characteristic of the Missouri River prior to damming (Berry and Galat 1993; Berry et al. 1993) and as such in these high water years, the James is utilized by large riverine and migratory fish (e.g., blue sucker *Cycleptus elongatus* Lesueur, 1817, western silvery minnow *Hybognathus argyritis*, paddlefish *Polyodon spathula* Walbaum, 1792; Shearer and Berry 2003). The high discharge events between 2009 and 2011 likely facilitated the invasion of silver carp further upstream into the three Missouri River tributaries as lowhead dams were over-topped. Increased movement rates and spawning events have been related to high levels of discharge (<2,700m/s^3; Peters et al. 2006; Schrank

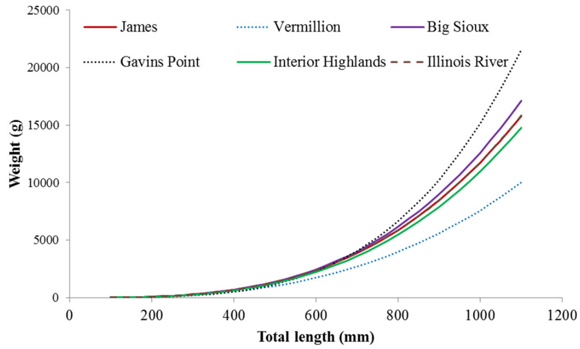

Figure 11. Length-weight regression of silver carp collected in South Dakota tributaries (James, Vermillion and Big Sioux rivers), the Missouri River below Gavins Point Dam, the Interior Highlands portion of the Missouri River, and the Illinois River. Note that the Illinois River and James River curves overlap.

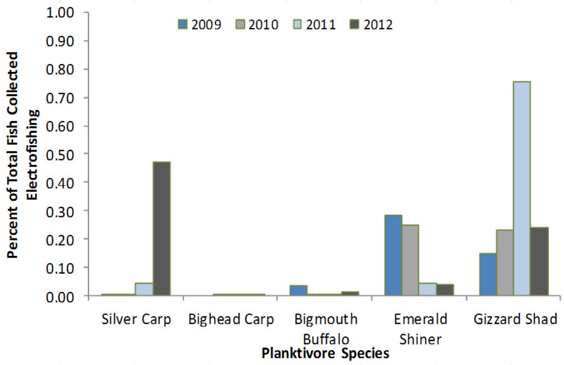

Figure 12. Percent of total fish collected electrofishing for native planktivores, bigmouth buffalo *Ictiobus cyprinellus*, gizzard shad *Dorosoma cepedianum* and emerald shiner *Notropis atherinoides*, across years (2009–2012) in South Dakota tributaries.

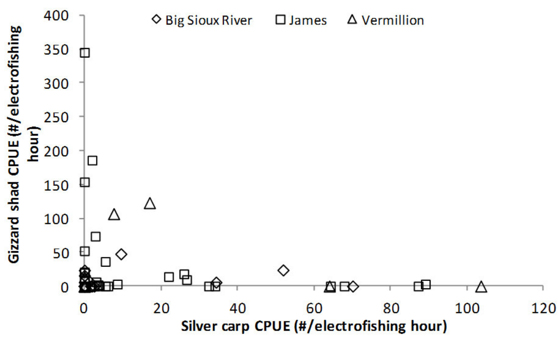

Figure 13. Silver carp catch per unit effort (CPUE) versus gizzard shad catch per unit effort (CPUE) for fish collected in the James, Vermillion, and Big Sioux rivers, South Dakota

2007) and movement rates were correlated with river stage (DeGrandchamp et al. 2008).

Density (i.e., CPUE) and percent of silver carp catches increased to 45% across years as we expected based on the population dynamics of other invasive species (e.g., zebra mussel *Dreissena polymorpha* Pallas, 1771) as well as Asian carp (Irons et al. 2011). For example, the Illinois River showed an exponential increase in silver carp catches during invasion (Chick and Pegg 2001) and percent of silver carp catches reached 51% (Sass et al. 2010). Other invasive populations seem to peak in abundance after a rapid and/or exponential increase in density or biomass (Irons et al. 2007; Valery et al. 2008; Irons et al. 2011) which is followed by a leveling off corresponding to some carrying capacity (Roughgarden 1998). However, the silver carp in rivers in this study may not have peaked in abundance as abundance was still increasing during the final year of this study. As such, they can be considered to still be in the initial invasion/colonization stage. Additionally, 91% of silver carp collected were from the 2010 year class indicating that natural reproduction is not completely augmenting the population in these rivers. Instead, silver carp must be immigrating from the Missouri River into the tributaries. The majority of the population of these tributaries may have become reproductively viable in 2013, as age at maturity in other invasive populations is 3+. As a result there may be an augmentation in the population in 2013 or 2014 not only from immigration, but from reproduction, although it is not known whether these rivers contain suitable habitat for spawning and these rivers characteristically display erratic reproduction. Erratic reproduction is not only characteristic in the Missouri River basin, but of others (e.g., Illinois River) as recent declines in Asian carps populations is attributed to sporadic reproductive events (Irons et al. 2011) which occurred in 2000 and 2003 in the Illinois River.

Growth rates for South Dakota populations were faster for all ages than two non-North American populations (Amur River; Nikolskii 1961; and Gobindsagar Reservoir; Tandon et al. 1993; Williamson and Garvey 2005), especially the Amur River in Russia which is considered a native population. There could be numerous abiotic or biotic reasons for this discrepancy, but we suggest that competition is not a limiting factor. First, there may be less competition from native planktivores in South Dakota rivers (e.g., bigmouth buffalo, emerald shiner, gizzard shad) than in other North American populations and in their native range (sharpbelly, *Hemiculter leucisculus* Basilewsky 1855; Zhang et al. 2007) as abundance of native planktivores, especially the potentially large bigmouth buffalo are low. Secondly, there may be unlimited food resources for the newly invading Asian carp in South Dakota as they are early in the invasion and may not yet be abundant enough to deplete the plankton resources and alter the fish community.

South Dakota fish, however, are smaller than the Middle Mississippi River silver carp up to age six (Williamson and Garvey 2005). The oldest fish we caught in this study was five, so making inferences past this age is based on the growth of smaller fish. Larger fish tend to slow in growth (Williamson and Garvey 2005). Perhaps the high discharge throughout most of the study time frame limited growth or the typical harsh environmental conditions of the prairie stream (e.g., high turbidity, variable discharge, temperature fluctuations) itself are limiting growth and population size. For example, our measured water temperatures in 2012 ranged from 10.7–32.7°C over the course of the year. This was considered a drought year. There were differences in growth rates and condition of silver carp populations among the Gavins Point reach of the Missouri River, Middle Mississippi River, Illinois River and South Dakota Missouri tributaries (Williamson and Garvey 2005; Irons et al. 2011); however these populations were in different invasion stages. The Illinois River predicted length-weight regression included silver carp collected before and after the peak in population biomass (i.e., 2000–2006) and the Missouri River regression represented an already established population with successful recruitment. The James River fish are still in the invasion stage as their densities continue to increase, reproduction has not been confirmed and recruitment is erratic. The Missouri River tributary fish may be encountering environmental resistance from flooding or biotic resistance in finding novel habitats and additional energy spent on colonization and migration may have weakened their condition. The Illinois River populations on the other hand were probably undergoing intense intraspecific competition for food resources or density dependence during peak abundances (Schrank et al. 2003; Sampson et al. 2009; Irons et al. 2011). Again, continued monitoring of the South Dakota tributary population may answer why these population characteristics are so different from other nonnative populations across North America.

Native planktivores

Emerald shiner displayed marked declines in density across the short study period. Emerald shiner is an important forage fish for a popular sportfish, the walleye. Emerald shiner is a planktivore that consumes algae at small sizes and consumes copepods and cladocerans at larger sizes (Fuchs 1967) which may have led to competition with planktivorous silver carp (Irons et al. 2007; Kolar et al. 2007). However, there was no indication of reduced condition in emerald shiner across the time period. Additionally, some emerald shiner populations are characterized by high mortality and fluctuating populations (Fuchs 1967). On the other hand, emerald shiner could have been flushed down into the Missouri River during high discharges between 2009–2011 (US Geological Survey 2013), however this species in known to be plastic and adaptable to a variety of ecological conditions (Cambell and MacCrimmon 1970). Thus, as we are speculating, future monitoring should examine emerald shiner populations to see if declines continue, or if they are a result of variable recruitment and/or movement. Bigmouth buffalo abundance also decreased during the study period. Bigmouth buffalo are not a common species to these rivers (Dieterman and Berry 1998; Shearer and Berry 2003) so any adverse impacts attributed to Asian carps could be detrimental to the population. However, condition did not change indicating that there could be a lag time between first colonization of Asian carps and measurable deleterious effects on native species as a result of invader characteristics and resistance and/or characteristics of the novel community (Valery et al. 2008). Further monitoring is necessary to quantify any negative impacts to fishes, especially native planktivores, such as reduced condition, growth and increased mortality, attributed to Asian carps.

Conclusions

Asian carps have invaded and become widely distributed in three northern prairie streams that are tributaries to the Missouri River. It is difficult to diagnose the stage of the Asian carps invasion in South Dakota (e.g., dispersal, colonization, establishment, self-sustaining), but they are probably in the colonization stage because silver carp density was still increasing annually at the conclusion of this study. We have not confirmed reproduction in these basins; however, the presence of age-0 silver carp in the middle to upper James River, approximately 375 Rkm from the confluence of the James River with the Missouri River, suggests reproduction may be occurring within the James River. However, recruitment was erratic with the 2010 year class dominating each population, the 2011 year class was weak and the 2012 year class was missing. 2010 recorded the second highest mean annual discharge on record since 1949. This year also had numerous peaks in discharge across the year which silver carp may use as spawning cues (Schrank et al. 2001; Lohmeyer and Garvey 2009). As a result of the high discharge, low head dams in the James and Big Sioux Rivers were over-topped facilitating upstream migration. This year produced the only successful silver carp year class during this study. Recruitment and reproduction factors are not well understood across their range, native or nonnative (Irons et al. 2011); however it is suspected that discharge plays a major role in the survival of larvae (Costa-Pierce 1992; Schrank et al. 2001; Lohmeyer and Garvey 2009) and onset of spawning. The majority of fish from the 2010 year class should be reaching reproductive potential in 2013 (e.g., age 3+; Williamson and Garvey 2005) although age at maturity varies greatly (Kolar et al. 2007). If suitable spawning habitat exists in these rivers, we should expect a pulse of reproductive effort, both from immigration and reproduction.

Asian carps have the classic characteristics of an invasive species and this study is one of the few that has captured the leading edge of an invasion. Despite the harsh conditions in prairie streams, silver carp density increased; however, bighead carp densities have not. The James River appears to have suitable habitat for sustaining silver carp populations. For example, low velocity areas above lowhead dams may facilitate the upstream migration of silver carp by enhancing phytoplankton production and increasing foraging opportunities (Williamson and Garvey 2005). These shallow prairie streams may not be suitable habitat for bighead carp as they prefer deeper water (Kolar et al. 2007). These rivers maintain low abundances of common carp and grass carp, however, these two invasive species combined with bighead and silver carp, along with record high discharge may have promoted silver carp colonization. Continued monitoring and research on this newly invading population of Asian carps will provide additional invaluable insight into complex invasive species, assist with understanding Asian carps population dynamics during and after an invasion, and expose the potential negative impacts Asian carps may be having on prairie stream ecosystems.

In conclusion, we have documented an invasion of silver carp into eastern South Dakota Missouri River tributaries from the onset. Each year silver carp densities increased significantly, yet bighead carp numbers remained consistently low. There may be many reasons for this however; silver carp could be outcompeting bighead carp, bighead carp may not have been susceptible to our gears, or bighead carp were utilizing habitats we were unable to sample. Bighead carp may be exhibiting the same population characteristics of the common carp and grass carp and have minimal impacts on the native ecosystem in eastern South Dakota prairie streams. On the other hand, however, both silver and bighead carps could be in an initial lag phase of the invasion.

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