**Abstract**

Bighead Carp *Hypothalmichthys nobilis* and Silver Carp *Hypothalmichthys molitrix* (hereafter collectively referred to as Bigheaded Carp) have spread throughout the majority of the Mississippi River since the 1970s. The current northern invasion edge of Bigheaded Carp in the Upper Mississippi River (UMR) spans between Pools 14 and 20 because of limited passage at Lock and Dam (LD) 19. Mechanisms limiting adult Bigheaded Carp abundance above LD19 are unknown but may be due in part to lack of reproductive success influenced by adult abundance and environmental factors. Our objective was to investigate how relative adult biomass and river temperature and discharge affect maximum annual Bigheaded Carp larval production in the UMR using a Ricker stock-recruitment model. Adult Bigheaded Carp relative biomass (kg/h) was estimated annually with boat electrofishing and larvae were collected every 10 d between May and August 2014–2017 in Pools 14–20 in the UMR. Adult relative biomass ranged from 0.0 to 880.9 kg/h, whereas maximum annual larval densities ranged from 0.0 to 2,869.4 larvae/m³. After accounting for variability among pools and years, the most supported linear Ricker stock-recruitment model indicated the number of recruits per spawner decreased with increasing adult relative biomass and increased with mean discharge. Our results highlight the importance of adult biomass and river discharge conditions for reproduction of Bigheaded Carp along leading edges of invasion. Management strategies that aim to maintain low adult abundance where reproduction is not yet occurring could help limit population increases via reproduction, whereas reducing high adult biomass (e.g., commercial harvest, barriers) may result in greater Bigheaded Carp reproductive output in the UMR.

**Keywords:** early life history, larvae, Silver Carp, Bighead Carp, stock recruitment, invasive species, discharge

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**Introduction**

More than 80 nonnative fishes have invaded the Upper Mississippi River (UMR) basin as a result of direct or indirect anthropogenic activities. Two of the most problematic invasive species within the UMR basin include Bighead Carp *Hypothalmichthys nobilis* and Silver Carp *Hypothalmichthys molitrix* (hereafter collectively referred to as Bigheaded Carp). Since their escapement into Arkansas rivers in the 1970s (Freeze and Henderson 1982), Bigheaded Carp have spread throughout the majority of the UMR basin, expanding into major tributaries including the Missouri, Ohio, and Illinois rivers and becoming established in more than 20 states (Kolar et al. 2007). After adults colonize an area, populations quickly establish and grow rapidly in part because of high reproductive capabilities (Kolar et al. 2007). For example, adults first appeared in the Illinois River in 1983 and now constitute more than 60% of fish biomass (Burr et al. 1996; Garvey et al. 2010). Bigheaded Carp have also expanded upstream within the UMR and several major tributaries despite a series of locks and dams on the UMR that limit fish movement (Tripp et al. 2014). Currently, Lock and Dam 19 (LD19) near Keokuk, Iowa appear to be
partially limiting population expansion farther upstream and is the upstream invasion edge in the UMR (Larson et al. 2017); adult catch rates are high below LD19 but substantially lower in Pools 19–16 and observed infrequently up to Pool 2 of the UMR (Fritts et al. 2018).

Success of Bigheaded Carp as invaders is attributed in part to their reproductive capacity due to short gestation periods (Chapman and George 2011), fecundities as high as 3.5 million eggs per female, and protracted spawning duration (Coulter et al. 2013; Camacho et al., in press). Adults move into spawning areas during rising or falling limbs of discharge, typically during the spring (Peters et al. 2006; DeGrandchamp et al. 2007). Reproduction occurs after sustained levels of high flow and water temperatures between 17°C and 30°C (Kolar et al. 2007). For successful reproduction, eggs must remain suspended within the water column for a minimum of 24 h for development before hatching (Krykhtin and Gorbach 1981) to avoid settling into the substrate where high egg mortality occurs (George and Chapman 2015). Thus, a minimum water velocity of 0.7 m/s has historically been thought to be necessary to maintain egg suspension, necessitating river reaches as long as 80 km (Lohmeyer and Garvey 2009; Kocovsky et al. 2012; Garcia et al. 2015). More recently, egg suspension and successful reproduction has been documented under other conditions initially perceived to be more limiting (Garcia et al. 2013; Embke et al. 2016; Prada et al. 2018; Camacho et al., in press). Above LD19, UMR pools vary in length from 16 to 47 km and were historically hypothesized to be unsuitable for Bigheaded Carp reproduction (Lohmeyer and Garvey 2009). However, successful reproduction has been documented as far upstream as Pool 16 (Larson et al. 2017; Camacho et al., in press), which may help facilitate their spread and population growth above LD19. Thus, a better understanding of factors that influence spatiotemporal variation in Bigheaded Carp reproductive success in the UMR is needed to understand processes facilitating their spread and invasion success.

The period when Bigheaded Carp are considered recruited to the adult population in their invaded range is unknown, but likely occurs sometime between the egg and fall juvenile phase. Larvae grow quickly and juveniles reach large sizes by their first fall (Williamson and Garvey 2005), escaping predation risk and minimizing overwinter mortality due to starvation and depletion of energy reserves (Coulter et al. 2018b). Juveniles are commonly captured in large numbers in the Illinois River (e.g., Collins et al. 2017) but are rarely encountered in other areas of invasion. For instance, juvenile Bigheaded Carp (50–150 mm) have only been captured above LD19 three times in separate years despite extensive sampling efforts by many agencies (K. Bogenschutz, Iowa Department of Natural Resources, personal communication; J. Lamer, Illinois Natural History Survey, personal communication). Despite the lack of juvenile captures, adult age-structure data indicate consistent recruitment of Bigheaded Carp between 2000 and 2012 (Lohmeyer and Garvey 2009; Sullivan et al. 2018) and otolith microchemistry revealed successful reproduction and recruitment to the adult population is occurring above LD19 (Whitledge et al. 2019). Therefore, recruitment appears to be occurring regularly above LD19 despite our inability to sample juveniles. Consequently, understanding mechanisms regulating spatiotemporal variation in reproductive output (i.e., larval densities) in the UMR could provide insights into factors regulating recruitment and population expansion of invasive Bigheaded Carp along the leading edge of the invasion.

The objective of this study was to investigate factors associated with maximum annual Bigheaded Carp larval production along the invasion front of the UMR in Pools 20–14. We used a Ricker stock-recruitment model with metrics of river discharge and water temperature to explore potential drivers of Bigheaded Carp maximum annual larval density that could lead to successful recruitment events. This information could guide management in forecasting potential population increases in future years on the basis of current adult densities and levels of population suppression necessary to prevent future population increases and further establishment in new areas.

Methods

Study area

The UMR flows 2,320 river kilometers from Lake Itasca, Minnesota to near the Missouri and Illinois river confluences near St. Louis, Missouri. Legislative approval by U.S. Congress in 1905 and 1935 altered the UMR by forming a series of dams, levees, wing dikes, and other structures to control flooding and provide commercial navigation (Garvey et al. 2010). These anthropogenic modifications maintain a deep (2.7 m) navigable channel, altering the river from a natural lotic flow to a more lentic system. The UMR dams are preceded by a series of pools, starting at Pool 1 formed by LD1 located near St. Paul, Minnesota to Pool 26 above LD 26 near Alton, Illinois. At low flows, dams close to retain water, leaving the only passage available through the series of locks when boats move between pools.

Adult Bigheaded Carp

We estimated adult Bigheaded Carp relative biomass (kg/h) annually during September and October 2014–2017 at the Des Moines River at Keosauqua, Pool 15 and Pool 17 in the UMR, Pool 20 at the Des Moines River confluence, Pool 19 at the Skunk River confluence, Pool 18 at the Iowa River confluence, Pool 16 at the Rock River confluence, and Pool 14 at the Wapsipinicon River confluence (Figure 1). Adult catch rates and size structure in the Des Moines River where they are abundant are similar between spring and fall sampling (Sullivan et al. 2017) and annual passage rates of adults among pools in the UMR is very low (Whitledge et al. 2019; M. Fritts, U.S. Fish and Wildlife Service, unpublished data). Therefore, we assumed fall relative biomass was representative of population biomass at each site during the spawning period in the spring.
Bigheaded Carp larval density

We conducted ichthyoplankton tows every 10 d from late April through September 2014–2017 to collect Bigheaded Carp larvae at the same locations where adults were sampled (Figure 1). Five sites existed at tributary confluences of the Mississippi River: sampling transects at these sites occurred 1 km upstream within the tributary and 1 km upstream and 1 km downstream of the confluence in the Mississippi River. At each transect we conducted three tows: one per backwater, channel-border, and thalweg habitat. Thus, we had a total of three tows at nontributary sites and nine tows at tributary sites on each date. A boat towed the ichthyoplankton net (0.5-m diameter opening 500-μm mesh) upstream for approximately 4 min just below the water surface (sampling the top ~0.5 m of the water column) at constant speed relative to shoreline or at idle in backwater habitats or during low-flow events (Schrank et al. 2001). A flowmeter (General Oceanics Model 2030R) attached to the mouth of the ichthyoplankton net quantified the volume (m³) of water filtered during each tow. We washed the contents of each tow into a removable cod end, drained it through sieves, and preserved contents with 95% ethanol. At least two individuals separated larvae from debris in the laboratory until they could find no additional larvae. We identified Bigheaded Carp to genus because of difficulty in distinguishing between species because of their similar meristic and morphometric characteristics (Tweb et al. 1990; Chapman and George 2011; George and Chapman 2015) and calculated larval density (n/100 m³) for each ichthyoplankton tow as:

\[
\text{Larval density} = \frac{L_i}{W} \times 100,
\]

where the number of Bigheaded Carp larvae (L_i) is divided by the volume (m³) of water sampled (W) from the flowmeter attached to the ichthyoplankton net and multiplied by 100. We averaged larval densities at each site and on each date (n = three tows for pools without tributaries or nine tows for pools with tributaries per date) to obtain a mean density per date. Because of protracted spawning of Bigheaded Carp (May through July across sites and years; Camacho et al., in press) and high temporal variation in larval density as a function of adult spawning activities (i.e., most larvae are only collected on one or two sampling events but low densities are collected over multiple weeks), we used maximum mean larval density (n/100 m³), highest mean catch rate averaged per site and date, hereafter referred to as simply maximum annual larval density) as an index of maximum annual Bigheaded Carp reproductive output for each site (Data S1, Supplemental Material). We then modeled this reproductive output metric as a function of environmental conditions leading up to this event (e.g., Anderson et al. 1998; Ward et al. 2004). Averaging larval densities over all sampling dates would result in a large number of 0s because we sampled for extended periods before and after reproduction occurred; including these 0s would bias and underestimate larval production while making it challenging to assess the effects of environmental conditions on reproduction.

Environmental data

We acquired water temperature and river discharge data from gauging stations closest to the sampling site that are maintained by the U.S. Geological Survey (https://waterdata.usgs.gov/ia/nwis/rt; last accessed January 24, 2019) and U.S. Army Corps of Engineers (USACE;
http://rivergages.mvr.usace.army.mil/WaterControl/new/layout.cfm; last accessed April 21, 2020) from 2014 to 2017. One gauging station in the area records temperature data (05420500, Mississippi River at Clinton, Iowa), whereas we measured site-specific temperatures upstream and downstream of each tributary (n = 6 temperature measurements/date) on each sampling date. To estimate mean daily temperatures at each larval sampling site when larval sampling did not occur, we used linear regressions to estimate the relationship between field temperature point measurements collected at each site during larval sampling events (°C; EC400 ExStik 2 temperature and conductivity meter) and water temperatures on that date and time of collection from the gauging station (r² = 0.91–0.99, P < 0.001; see Camacho et al., in press for more details). We acquired river discharge data from gauging stations within the Des Moines River (U.S. Geological Survey; 05490500, Des Moines River at Keosauqua, Iowa) and within the Mississippi River above the Des Moines River confluence (U.S. Geological Survey; 05474500, Mississippi River at Keokuk, Iowa), Skunk River confluence (USACE, LD18 at Gladstone, Illinois), Iowa River confluence (USACE, LD17 at New Boston, Illinois), Pool 17 (USACE, LD16 at Illinois City, Illinois), Rock River confluence (USACE, LD15 MET Station, Pool 15 USACE, LD14 at LeClaire, Iowa), and the Wapsipinicon River confluence (USACE; LD13 MET Station).

Environmental covariates used in recruitment analyses are typically calculated during a fixed period of time that would influence offspring survival (e.g., Hoff et al. 2011; Weber and Brown 2013; Tommasi et al. 2015). However, due to variation in timing of maximum Bigheaded Carp larval density across sites and years, using a fixed time period to calculate environmental covariates would not reflect conditions before maximum densities occurred. Instead, we calculated the mean and coefficient of variation (CV) of water temperature and discharge for 10 d before observed maximum larval density on a site- and year-specific basis. This temporal range represented conditions occurring between sampling events we used to investigate environmental effects during and preceding the spawning event as predictor variables in the model.

Data analysis

We first assessed potential variation in adult Bigheaded Carp biomass and maximum larval densities among UMR pools and years. Adult biomass and maximum larval densities were log₁₀ transformed before analysis to meet the normality assumption of residuals and analyzed via the linear model approach with PROC MIXED in SAS 9.4 (SAS Inc. 2013). Both models included the fixed effects of pool and year but not their interaction, as we only had a single measurement for adult Bigheaded Carp biomass and maximum larval densities for each pool and year and the model was not a full factorial design (e.g., not all pools were sampled in all years). We used a strength-of-evidence approach to evaluate potential differences in adult biomass and maximum larval densities among pools instead of a strict α = 0.05.

Next, we used the linear form of the Ricker stock-recruitment model (Ricker 1975) to investigate the effects of adult Bigheaded Carp biomass and mean and CV of water temperature and river discharge on maximum annual larval densities along the UMR invasion edge. The linear form of the Ricker stock-recruitment model is

$$\log_e R/S = a - bS + cX + \Delta + \gamma + e,$$

where R is maximum larval density (n/100 m³) at each site, S is stock biomass (kg/h), and X represents environmental covariates of temperature and discharge. Normally distributed random effects include Δ for pool, γ for year, and a, b, c are parameters estimated from fitting the model to the stock-reproduction data (Ricker 1975). We added “1” to R and S estimates in the data set before analysis to allow for the estimation of loge R/S that would have otherwise not been possible with estimates of 0 in the data set. Before analysis, we centered and scaled all predictor variables by subtracting the mean of each variable from each observation and dividing by the standard deviation to facilitate comparisons of the importance of each variable. Linear regression assumes predictor and response variables are related as specified in the model; residuals are independent and normally distributed with zero mean and constant variance; predictor variables are known without error.

We developed 14 models to evaluate the effects of adult Bigheaded Carp biomass with and without environmental covariates on the number of recruits per spawner (loge R/S) at each site and year compared with a null model without predictor variables (Data S1, Supplemental Material). Mean and CV metrics of water temperature and discharge were not considered within the same model. Random effects of pool and year were included in all models to account for spatial and temporal variability in maximum annual Bigheaded Carp larval densities while focusing on potential effects of stock biomass, water temperature, and discharge. Models were compared using Akaike’s information criterion corrected for small sample size (AICc). Differences in AICc values (Δi: AICc — minimum AICc) and Akaike weights (wi) were used to compare competing models (Burnham and Anderson 2002) constructed using PROC MIXED in SAS (SAS Inc. 2013).

Results

Adult Bigheaded Carp biomass varied from 0 to 880.9 kg/h (95% CI: ± 191.6 kg/h) among Pools 20 to 14 from 2014 to 2017. We did not capture adults in Pools 14, 15, or 17; we captured adults once in Pool 16 during 2016; and we captured low adult biomass (mean = 25 kg/h) in Pools 18 and 19 and high adult biomass (mean = 334 kg/h) in Pool 20 and the Des Moines River at Keosauqua (Data S1, Supplemental Material). There was strong
larval densities (relative biomass (kg/h via boat electrofishing) and maximum of the Upper Mississippi River. 2017 to assess the effect of adult biomass on maximum and Dam 19 (partial barrier to fish movement) from 2014 to collected at eight sites below (triangles) and above (circle) Lock and Dam 19 (partial barrier to fish movement) from 2014 to 2017 to assess the effect of adult biomass on maximum reproductive output along the Bigheaded Carp invasion front of the Upper Mississippi River.

evidence adult biomass fluctuated among sites ($F_{7,12} = 16.83, P < 0.001$) but little evidence it varied among years ($F_{3,12} = 1.03, P = 0.41$); there was some evidence adult biomass was greater in Pool 20 than in all other sampling locations ($P < 0.04$) and greater evidence it was higher in the Des Moines River than in all other locations ($P < 0.002$) except Pool 20. However, there was little evidence to suggest adult biomass varied among Pools 14–19 ($P > 0.05$).

Maximum Bigheaded Carp larval densities typically occurred during the last week of May or the first week of June when water temperatures were $> 20^\circ C$. Maximum larval densities varied spatially and temporally, ranging from 0 to $> 2,860$ larvae/100 m$^3$ (Data S1, Supplemental Material). The highest larval density (2,869 larvae/100 m$^3$) was observed at low levels of adult biomass (6.9 kg/h), whereas lower larval densities occurred at low (0 kg/h) and high ($> 200$ kg/h) adult relative biomass (Figure 2). Despite high adult biomass in the Des Moines River, we only collected larvae here during 2015 (Data S1, Supplemental Material). We collected larvae as far north as Pool 18 in 3 of 4 y (Data S1); we did not collect larvae in Pools 17, 16, 15, or 14 during 2016–2017. The highest observed maximum annual larval density occurred in Pool 19 during 2014 ($> 2,800$ larvae/100 m$^3$), but densities at this site in all other years were low ($< 10$ larvae/100 m$^3$; Data S1, Supplemental Material). Despite high variability spatially and temporally, there was little evidence maximum larval densities varied among pools ($F_{7,12} = 0.30, P = 0.94$) or years ($F_{3,12} = 2.34, P = 0.13$).

We evaluated 14 linear Ricker stock-recruitment models to explain variation in the number of recruits per spawner that were composed of various combina-

tions of adult stock biomass and mean and CV of water temperature and discharge 10 d before peak larval densities. The model with only adult Bigheaded Carp biomass (model 5, $\Delta_i = 5.8$) received more support than the null model (model 8, $\Delta_i = 6.8$) and models with the single effect of mean or CV of water temperature or discharge (models 6–13; Table 1). Model performance improved through the combination of adult biomass and environmental covariates.

Of the 14 models evaluated, one model was strongly supported, whereas the other 13 models received little support ($\Delta_i > 3.5, w_i < 0.10$). After accounting for pool and year variation, the most supported model ($w_i = 0.62$) indicated the number of recruits per spawner was best explained by adult Bigheaded Carp biomass and mean discharge (Table 1). Number of recruits per spawner decreased with increasing adult biomass ($\beta = -1.61; 95\% \text{ CI} = -2.28$ to $-0.95$; Figure 3) and increased with increasing discharge ($\beta = 1.66; 95\% \text{ CI} = 0.47$ to $2.86$; Figure 3). Similar parameter estimates for adult biomass and discharge after centering and scaling indicated both predictor variables had similar effects on maximum larval density. The model did well overall predicting number of recruits per spawner but tended to underestimate when the number of recruits per spawner was high (Figure 4).

**Discussion**

Reproductive success is a key component of invasion ecology, as successful reproduction results in increased
propagule pressure, increasing adult densities, and spatial spread (Simberloff 2009). This is particularly relevant for the spread of Bigheaded Carp in the UMR where adult dispersal is limited by several locks and dams that may also reduce reproductive success because of pooled conditions (Lohmeyer and Garvey 2009; Koscovsky et al. 2012; Garcia et al. 2015; but see Camacho et al., in press). However, reproduction of invaders in novel habitats can be difficult to predict (Larson et al. 2017), as invasive species’ reproductive requirements can be plastic in newly introduced habitats as a result of adaptation to new environmental conditions and reproductive cues (Feiner et al. 2012; Coulter et al. 2013; Fox and Copp 2014). Bigheaded Carp are continuing to spread and reproduce in new areas throughout North America (Chapman et al. 2013; Larson et al. 2017), although conditions associated with successful reproduction remain elusive and are likely highly variable among locations (Coulter et al. 2013; Camacho et al., in press).

Bigheaded Carp reproductive output in the UMR varied in this study, influenced in part by adult biomass and discharge. We collected larvae across all years, but only as far upstream as Pool 18, although other studies previously captured larvae up to Pool 16 (Larson et al. 2017). Thus, the current leading reproductive edge of Bigheaded Carp occurs somewhere in Pools 18–16 section of the UMR, whereas spread farther upstream appears to be driven by dispersal of adults rather than reproductive success. Although reproduction may be limited in pooled sections of the Mississippi River, more turbulent conditions associated with free-flowing tributary confluences within the UMR appear to be important locations for reproduction (Camacho et al., in press).

Maximum annual larval densities reported here (mean maximum annual density = 170 larvae/100 m³; maximum > 2,860 larvae/100 m³) are higher than in other areas of invasion, potentially due to high reproductive output of a limited number of adults at the UMR invasion front. In other locations where Bigheaded Carp have been present longer, DeGrandchamp et al. (2007) collected < 6 larvae/100 m³ during peak densities during May in the Illinois River from 2004 to 2005 using surface ichthyoplankton tows. Lohmeyer and Garvey (2008) reported up to 1,456 larvae/100 m³ at the end of May in Pool 24 of the Mississippi River in 2007 during weekly sampling with neuston nets. These observations of lower larval densities in other locations coincide with higher adult abundances, providing further evidence Bigheaded...
Carp reproduction is affected by a stock-recruitment relationship throughout its range (also see Hoff et al. 2011). We speculate adult populations likely experience density-dependent conditions and growth that could affect the number and quality of eggs, thereby limiting reproductive success when adults are abundant. We did not observe maximum larval density to statistically increase through time or across a latitudinal gradient among pools, suggesting the current reproductive front in the UMR did not shift farther upstream or vary within a pool during 2014–2017, or if it did change, our sampling was unable to detect the change.

One of the most recognizable biotic differences among pools was the gradient in abundance of adult Bigheaded Carp and our results indicate reproductive output is regulated in part by a stock-recruitment relationship. Stock-recruitment relationships are a cornerstone of fisheries science and have been widely used to describe recruitment patterns of numerous marine and freshwater fishes. Despite their widespread application, stock abundance is often not an important predictor of recruitment potential. Yet, in this study, we found maximum Bigheaded Carp larval densities were observed in Pool 19 where adult densities are moderate in the UMR; lower larval densities were collected in Pool 20 where adult biomass was highest; no reproduction was documented in Pools 14–17 where adults are present but at very low abundance. Model selection indicated adult biomass is an important predictor of the number of recruits per spawner. Thus, if adult Bigheaded Carp biomass increases in pools above LD18 through recruitment or immigration, there could be a reduction in the number of recruits per spawner but overall larger larval densities and subsequent increases in recruitment. Similarly, if adult biomass is reduced in Pools 19 and 20 through harvest, increases in the number of recruits per spawner may occur. Hoff et al. (2011) also developed a stock-recruitment model for Bigheaded Carp for the Illinois and Mississippi rivers where adult abundance explained 72% of the variation in recruitment. However, the model included a limited number of sites and years and Hoff et al. (2011) recommended further model refinement. In this study, when adult biomass was high enough to support reproduction (Pools 18–20), larvae were collected annually but substantial variation in larval densities unexplained by adult biomass existed, suggesting variation in environmental conditions also influence Bigheaded Carp reproductive success.

Beyond adult Bigheaded Carp biomass, we also found evidence mean discharge was positively associated with maximum larval density. Although Bigheaded Carp spawning can be protracted, we collected larvae only during brief periods after environmental conditions conducive for spawning (Camacho et al., in press). Several studies have focused on the importance of discharge on Bigheaded Carp recruitment success (Hoff et al. 2011; Sullivan et al. 2018) and reproduction is thought to occur when discharge is high or rising (Schrank et al. 2001; Lohmeyer and Garvey 2008; Gibson-Reinemer et al. 2017). Periods of high, sustained discharge are thought to be beneficial for Bigheaded Carp because it helps keep semibuoyant eggs in suspension instead of allowing them to settle to the substrate, resulting in high mortality (Kocovsky et al. 2012; Garcia et al. 2015).

Beyond water levels, strong year-classes of many fishes are also often positively associated with warm spring and summer temperatures (Weber and Brown 2013; Heikinheimo et al. 2014) by reducing developmental periods and increasing growth rates, thereby reducing periods of high mortality during early life stages (i.e., stage-duration hypothesis; Busch et al. 1975; Leggett and Deblois 1994). Yet we did not find evidence suggesting water temperature was important for explaining variation in maximum larval Bigheaded Carp densities. Because we assessed maximum larval density as a metric of reproductive output and most larvae captured were <10 d of age (Camacho et al., in press), temperature may have had little effect on Bigheaded Carp survival during the egg to larval period. Maximum larval densities were typically observed during the last week of May or the first week of June when water temperatures were >20°C. Thus, water temperatures may have little effect on our metric of reproduction success but be more important for development rates of other life stages.

The early life stage when Bigheaded Carp recruitment is determined is unknown, as juveniles are extremely difficult to capture in expanding areas of invasion. Thus, assessments of reproduction and recruitment have typically focused on egg and larval stages (e.g., Schrank et al. 2001; Hoff et al. 2011; Coulter et al. 2013; Larson et al. 2017) or used adult age structure to assess historical recruitment (e.g., Sullivan et al. 2018). Although larvae have been captured in this study across many locations and years, few juveniles have been captured despite substantial efforts invested in targeted sampling for them. Juvenile Bigheaded Carp were captured near the mouth of the Skunk River in 2018 and hatch dates of these fish were nearly identical to those of larvae (M. Weber, unpublished data). Additionally, juvenile overwinter mortality appears minimal (Coulter et al. 2018b); adult age structure indicates Silver Carp recruitment is relatively consistent without missing year-classes (Sullivan et al. 2018); and few adult Bigheaded Carp are hatched above LD19 (Whitledge et al. 2019). Therefore, the preponderance of evidence suggests the period between egg and larval phases represents an important recruitment bottleneck, differential mortality from the larval to juvenile stage is minimal, and Bigheaded Carp recruitment is likely determined early in life. Thus, we believe larval densities represent a meaningful metric of Bigheaded Carp recruitment potential.

However, linear forms of the stock-recruitment model can be prone to inaccuracies (Quinn and Deriso 1999) so additional work investigating the effects of adult biomass on reproduction is warranted. Additionally, adults are challenging to sample. We used electrofishing to index adult relative biomass during the fall because it tends to be the most successful capture technique in the region (Sullivan et al. 2017). Further, adult relative biomass indexed here is reflective of the invasion gradient of adults across these pools in the UMR (MICRA...
2019). However, whether our index of relative adult biomass was reflective of actual adult biomass at the time of spawning is unknown and could have had a large effect on the relationships between adult biomass and larval density observed here. Despite these potential limitations, our results at a minimum provide important insights into mechanisms influencing Bigheaded Carp reproductive output and success to the larval phase on a given year, which, because of the factors described above, likely influences and is a predictor of recruitment. Yet more work is needed to untangle these intricate and complex relationships.

Understanding where, when, and under what conditions successful reproduction occurs is foundational for fisheries management and for understanding the success of invasive species. Bigheaded Carp reproductive front occurs across a relatively narrow section of the Mississippi River between Pools 15 and 20 (Larson et al. 2017; Camacho et al., in press). We documented Bigheaded Carp larval production occurs on an annual basis from Pools 20 to 18, but not farther upstream, in association with a gradient of adult biomass. Thus, reproduction above Pool 18 may increase in future years through the expansion of adult Bigheaded Carp. One of the primary Bigheaded Carp management strategies has been to harvest adults near the reproduction edge to limit propagule pressure (http://asiancarp.us/Documents/2018ActionPlan.pdf). Commercial harvest in Pools 18 and above may be beneficial for maintaining low adult biomass and consequently limiting potential reproduction and population expansion on the northern invasion edge. However, commercial harvest in Pools 18–20 of the UMR and elsewhere where Bigheaded Carp are abundant may result in population compensation and higher reproductive output unless harvest is extremely high and targets all life stages, as has been observed for other Bigheaded Carp and other invasive species population characteristics responding to harvest (Weber et al. 2016; Coulter et al. 2018a). Additionally, there is substantial interest in developing and implementing barriers in the UMR to limit or stop Bigheaded Carp upstream movements (e.g., Cupp et al. 2017). Our work suggests these efforts may be best implemented above Pool 18 where reproduction is not yet occurring. Continued assessment of reproduction and recruitment along the invasion edge will be necessary to determine when and under what conditions reproduction occurs throughout the UMR Bigheaded Carp invasion edge because of fluctuations in adult abundance through immigration, emigration, recruitment, and commercial harvest as well as variation in environmental conditions that determine reproductive success.

Supplemental Material

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Data S1. Adult relative biomass and larval density for Bigheaded Carp (Hypophthalmichthys spp.) collected from 2014 to 2017 in Pools 20–14 in the Upper Mississippi River. Mean and coefficient of variation of water temperature and discharge were also estimated for each site for each year 10 d before the collection of peak larval density. These data were used in the linear form of the Ricker stock-recruitment model to assess factors influencing maximum observed larval density.

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