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Keywords

grass carp, occupancy modelling, sampling methods, Upper Mississippi River

Disciplines

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RESEARCH ARTICLE

Influence of river discharge on grass carp occupancy dynamics in south-eastern Iowa rivers

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Abstract

Despite the longstanding presence of grass carp *Ctenopharyngodon idella* in the Upper Mississippi River (UMR) watershed, information regarding their populations remains largely unknown, in part because capture is difficult. Occupancy models are a popular wildlife assessment tool to account for imperfect detections but have been slow to be adopted in fisheries. Herein, we used occupancy modelling to evaluate the influence of two environmental covariates (river discharge and water temperature) on grass carp occupancy, extinction, colonization, and detection at nine sites within south-eastern Iowa rivers from April to October 2014 and 2015. Grass carp were detected at least once at all but one site. The most parsimonious model indicated that grass carp colonization probability increased from 0.15 to 0.67 with increases in river discharge. In contrast, occupancy (0.20), extinction (0.29), and detection (0.50) probabilities were temporally constant. Models indicated that water temperatures did not influence grass carp extinction or colonization probabilities relative to river discharge. Cumulative grass carp detection probability approached 1.0, whereas conditional occupancy estimates were less than 0.1 when using five or more sampling transects. The use of a robust design occupancy model allowed us to estimate site occupancy rates of grass carp corrected for imperfect detections, while demonstrating the importance of river discharge for site colonization. These results can be used to assess the distribution of a cryptic fish while helping to guide grass carp sampling and removal efforts.

KEYWORDS

grass carp, occupancy modelling, sampling methods, Upper Mississippi River

1 | INTRODUCTION

Grass carp *Ctenopharyngodon idella* are native to eastern Asia and were originally introduced to the United States in the 1960s as a tool for bio-control of aquatic vegetation (Kelly, Engle, Armstrong, Freeze, & Mitchell, 2011; Mitchell & Kelly, 2006). Concern regarding escapement of grass carp outside of stocked systems and potential undesirable ecosystem effects led to the development of triploid grass carp during the 1970s (Mitchell & Kelly, 2006). However, escapement (e.g., Pflieger, 1978) and errors in the production of sterile triploid grass carp (Piferrer, Beaumont, Falguière, Flajšhans, Haffray, & Colombo 2009) led to their naturalization in novel habitats. Consequently, grass carp are now commonplace throughout much of North America, including the Upper

Mississippi River (UMR) watershed (NAS, 2016). Grass carp are tolerant of a wide range of abiotic conditions, including temperature (0–39°C; Conover, Simmonds, & Whalen, 2007; Opuszynski, 1967, 1968, 1972) and oxygen (1–28 ppm dissolved O₂; Opuszynski, 1967; Shireman & Smith, 1983). Additionally, grass carp can travel long distances rapidly (500 km in a 2-year period; Gorbach & Krykhtin, 1989). These robust tolerances of a wide range of environmental conditions, in combination with escapement and expansion of diploid fish (Mitchell & Kelly, 2006), have facilitated invasion and establishment in novel habitats (Larsen, Knights, McCalla, et al., 2017).

Grass carp are notoriously difficult to capture, especially for populations inhabiting large rivers (Ohio Department of Natural Resources, 2018; Wanner & Klumb, 2009). For example, fish

communities in Mississippi River Pools 8, 13, and 26 are routinely monitored employing pulsed-DC electrofishing, but only 260 grass carp have been captured from 1990 to 2017 (<0.001% of catch; <http://www.umesc.usgs.gov/ltrmp.html>). Therefore, existing grass carp population assessments are largely limited to stocked populations in lakes (Clemens, Spangler, Robertson, et al., 2016; Stich, Diconzo, Frimpong, Jiao, & Murphy, 2013), and limited information exists on naturalized grass carp populations in North American rivers.

Population assessments are necessary for invasive species management, but difficulties with capture can lead to biased population assessments. When capture rates are low (e.g., rare or cryptic species), variation in species distribution within study sites and an imperfect species detection can constrain inferences drawn from sampling surveys (i.e., lack of capture does not mean individuals are not present; MacKenzie, Nichols, Royle, Pollock, Bailey, & Hines 2006). In these instances, occupancy models that estimate the proportion of sites that are occupied by a species (i.e., occupancy probability) while accounting for species detection probabilities (probability that a species is detected given presence) < 1.0 can be a useful tool to more accurately assess a species distribution (MacKenzie et al., 2006). Building upon basic occupancy models, repeated surveys through time (i.e., monthly surveys) generate detection/nondetection capture histories for sampling sites that can be used in occupancy models to also estimate the probabilities of extinction and colonization (MacKenzie, 2005). In the context of occupancy models, extinction and colonization are defined as the probabilities that a study site becomes unoccupied or occupied between sampling seasons, respectively (MacKenzie et al., 2006). The inclusion of extinction and colonization parameters in models (i.e., robust-design occupancy models; MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003) can be useful for explaining temporal variation in species detection and nondetection at a site. Robust-design occupancy models use both primary (e.g., multiple site-specific surveys through time) and secondary (e.g., multiple samples of a site within a single survey) occasions to estimate the probability of extinction and colonization between site visits in addition to the probability of occupancy and detection during each sampling interval. Environmental predictor variables can then be added to occupancy models to aid in clarifying the effects of environmental variables on a species distribution and detection (e.g., MacKenzie et al., 2002; MacKenzie et al., 2006). For grass carp, models estimating the influence of environmental covariates on occupancy, extinction, colonization, and detection probabilities could provide more robust information needed to enact more effective population monitoring strategies, especially where captures are sparse and catch per unit effort (CPUE) is highly variable.

Despite their ability to manipulate ecosystems and induce both direct (Opuszynski, 1972; Watkins, Shireman, Rottman, & Colle, 1981) and indirect (Bettoli, Maceina, Noble, & Betsill, 1993; Killgore, Kirk, & Foltz, 1998; Maceina, Cichra, Betsill, & Bettoli, 1992) effects, information on grass carp populations is sparse, particularly in lotic systems. Furthermore, the effects of environmental conditions on grass carp occupancy dynamics remain poorly understood. An increased understanding of grass carp occupancy

patterns within river systems could lend insights into population distributions throughout the UMR. Therefore, the goal of this study was to use a robust design occupancy model to assess the effects of two environmental site covariates (river discharge and water temperature) on grass carp occupancy, extinction, colonization, and detection probabilities in south-eastern Iowa tributaries of the UMR. We hypothesized that grass carp occupancy, detection, and colonization probability would increase in response to increases in river discharge and temperature. Results from this project can help provide a better understanding of grass carp distribution and sampling efficiency while improving future monitoring and removal efforts.

2 | METHODS

2.1 | Field methods

The Des Moines, Skunk, Iowa, and Cedar rivers are the four southernmost major tributaries of the UMR in Iowa. Catchment areas range between 11,222 km² (Skunk River) and 40,940 km² (Des Moines River) with the Iowa River catchment composed mainly (62%) of the Cedar River catchment (20,279 km²; USGS, 2016). Grass carp were sampled once a month from April to October 2014 and 2015 at nine sites in the Des Moines, Skunk, Iowa, and Cedar rivers (Figure 1) using daytime boat electrofishing and stationary trammel nets. Sampling sites were selected based on the location of river access points, logistical constraints, agency interests, desire to spread sampling across a wide region, and desire to sample the farthest upstream UMR pools (Pools 17–20) where natural reproduction for grass carp is known (Larsen et al., 2017). Grass carp, in general, are notoriously difficult to capture; however, grass carp have been captured using both electrofishing (Cumming, Burrell, & Gilderhus, 1975; Wanner & Klumb, 2009) and stationary trammel nets (George & Chapman, 2015). Consequently, both boat electrofishing and trammel net sets were used concurrently when possible. Once per month (referred to as “primary occasions”), three spatially independent fixed sampling locations (approximately 1.5 river km apart) were sampled within each site (referred to as “secondary occasions”) where both gears were deployed in habitats less than 4 m deep within areas of low velocity (<1.0 m/s; e.g., eddies, dike pools, and inside river bends). When river conditions allowed, a stationary, multifilament trammel net (2.4-m-deep inner wall, 1.8-m-deep outer wall, 38.1-m-long, 10-cm-bar inner mesh) was first deployed. One end of the trammel net was anchored on shore, and the remaining net was stretched towards deeper water or an opposite shore, restricting fish movement out of low-velocity areas. Next, one 15-min daytime boat electrofishing (Smith-Root control box; DC; 4–13 amps, 100–500 V, 25 duty cycle, 25 frequency, 60 pulses per second with two netters) transect using a “standardizing by power” approach (i.e., Miranda, 2009) was conducted parallel to the shoreline. The trammel net was collected immediately after electrofishing. Thus, duration of each net set was variable but ranged between 20 and 30 min, depending upon river conditions.

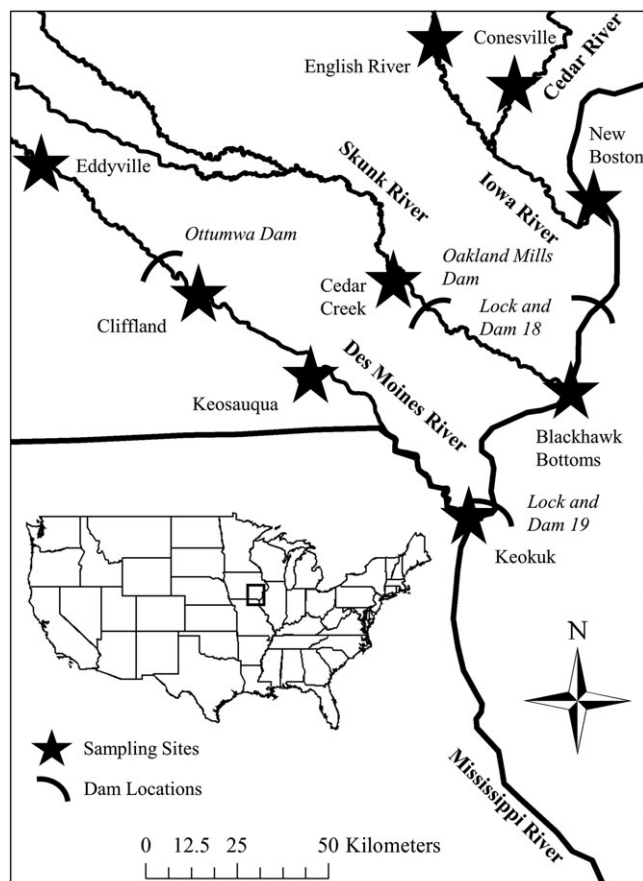


FIGURE 1 Locations of nine south-eastern Iowa sampling sites used to survey grass carp

Because grass carp movements are influenced by water temperature (Nixon & Miller, 1978) and dams present throughout the study area (Figure 1) have the ability to influence both hydrological and thermal regimes (e.g., Olden & Naiman, 2010), both river discharge and water temperature were measured. Surface thalweg water temperature was measured monthly with a YSI 550A (Yellow Springs Instruments, Yellow Springs, Ohio) during fish sampling at each site, and mean daily discharge values on the day of sampling were obtained from U.S. Geological Survey (<https://www.usgs.gov/>) gauging stations upstream from each sampling location (Figure S1). Because other invasive carp (i.e., silver carp *Hypophthalmichthys molitrix* and bighead carp *Hypophthalmichthys nobilis*) inhabiting the UMR are influenced by variable discharge regimes (e.g., DeGrandchamp, Garvey, & Colombo, 2008; Sullivan, Camacho, Weber, & Pierce, 2017), a number of hydrological metrics were considered (e.g., 3-day running average and minimum/maximum daily discharge) but were highly correlated (Pearson's correlation coefficient > 0.9). Thus, mean daily discharge was used because these data are highly correlated and readily available to biologists.

2.2 | Data analysis

A robust design occupancy model (MacKenzie et al., 2006) in Program MARK (White & Burnham, 1999) was used to estimate the effects of local environmental variables on grass carp site occupancy (ψ),

extinction (ϵ), colonization (γ), and detection (p) probabilities across the nine south-eastern Iowa sampling sites. Similar to other commonly used population models in fisheries (e.g., Schnabel and Cormack-Jolly-Seber), similarities in the assumptions of both of these models include a closed population over the survey period, sampling occasions are independent, species or individuals are correctly identified, and target species or individuals are never falsely detected (MacKenzie et al., 2006; Pollock, Nichols, Brownie, & Hines, 1990). When evaluating these parameters in open systems, extinction can be analogous to emigration of all individuals out of independent site locations along a river gradient. Our study sites were located within an "open" system where individuals were capable of leaving the site between sampling events; therefore, we refer to the probability of extinction parameter as the probability of local extinction of individuals at sampling sites in this study. Similarly, we refer to the probability of colonization parameter as the probability of local colonization of individuals at a study site.

Binary (grass carp detection [1] or nondetection [0] during individual electrofishing transects/net sets per site and month) encounter histories were constructed using capture data where primary occasions were monthly sampling sessions (14 months over 2 years) and secondary occasions were individual sampling transects (3 transects each month per site; 42 total sampling occasions; Figure 2). Using robust design occupancy models, sites are closed to changes in occupancy between secondary sampling occasions but are open to changes in occupancy between primary occasions (MacKenzie et al., 2006; Figure 2). For example, if an encounter history for a site was "001" where two nondetections of grass carp were followed by one detection during the third sampling occasion, the site's encounter history for this event can be modelled as

$$\Pr(001) = \psi(1 - p_1)(1 - p_2)(p_3).$$

However, if an encounter history for a site was "101 000" over two survey sessions where three sampling occasions occurred, the site's encounter history for this event can be modelled as

$$\Pr(101\ 000) = \psi_1(1 - p_1)(1 - p_2)(p_1)(p_3) * \left\{ (1 - \epsilon) \prod_{j=1}^3 (1 - p_{2,j}) + \epsilon_1 \right\},$$

where j is an individual survey.

The lack of backwater habitat and river conditions conducive to employing trammel nets precluded setting trammel nets at all transects during all sampling sessions (only set at 53% of electrofishing transects). Thus, grass carp capture histories were combined from each survey method (i.e., electrofishing and trammel nets) at each site instead of evaluating differences in p within the occupancy model as a function of gear type (e.g., Pregler, Vokoun, Jensen, & Hagstrom, 2015). Applying this framework, detection probability is the probability of detection within a single site visit using both boat electrofishing and trammel nets combined if grass carp are present at a site.

Within modified river systems (i.e., UMR), both river discharge and water temperature can be highly variable intra-annually (e.g., Olden & Naiman, 2010). Grass carp are highly mobile (Gorbach & Krykhtin, 1989), and movements have been correlated to water temperature (Nixon & Miller, 1978). Therefore, both mean daily discharge and

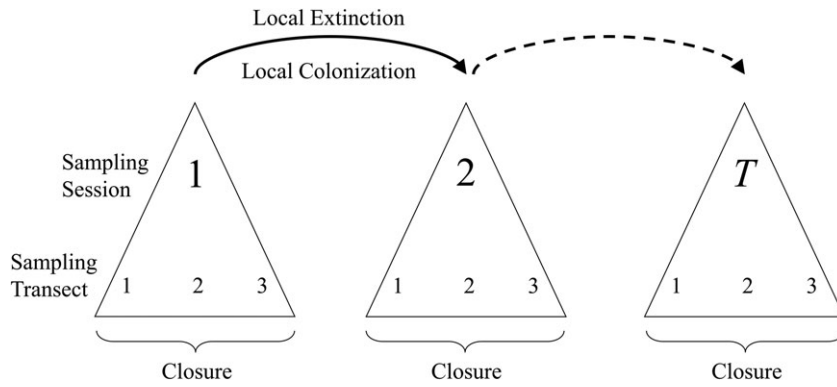


FIGURE 2 Graphical representation of the sampling design used to evaluate grass carp occupancy dynamics in south-eastern Iowa rivers. Each triangle represents a sampling session (T ; 14 months over 2 years), with 3 sampling transects within each session. Sites are closed to changes in occupancy within each sampling session, but changes may occur between sessions through both local extinction and colonization (modified from MacKenzie et al., 2006)

water temperature at the time of sampling by site and sampling month (14 site/month occasions per variable) were evaluated for their relative effects on grass carp site occupancy, local extinction, local colonization, and detection probabilities.

The first model assumed that all parameters (site occupancy, local extinction, local colonization, and detection probabilities) were constant across space and time (referred to as the “baseline model”). From there, all possible covariate combinations were evaluated to explore if including environmental variables and time dependencies (parameters varied through time uncorrelated to included environmental predictor variables) on all parameters improved model performance relative to the baseline model. In Program MARK, alternative optimization method (i.e., simulated annealing) and Bayesian Markov chain Monte Carlo (MCMC; Royle & Kéry, 2007) methods were used to estimate model parameters of the most parsimonious model because MCMC methods converged much more rapidly compared with vague normal priors (MacKenzie et al., 2006). Each MCMC method used 4,000 tuning samples, 1,000 burn-in samples, and stored 100,000 samples (mean = 0.0 and sigma = 1.75). To distinguish the most parsimonious model, Akaike's Information Criterion (AIC_c ; AIC corrected for small sample size), associated delta AIC_c (Δ_i), Akaike weights (W_i), model likelihood, the number of model covariates (K), and model deviance were obtained to rank models based on their relative support for the data. We used W_i to determine the most supported model and considered models within 2.0 AIC_c units of the most parsimonious model as competing (Burnham & Anderson, 2003). The most supported model was then selected to be the single model structure used to determine if model covariates influence occupancy, local extinction, local colonization, or detection probabilities.

Finally, estimates of detection probability from the most parsimonious model were used to develop a cumulative detection curve (e.g., Moore, Orth, & Frimpong, 2017) to determine how many sampling occasions using both boat electrofishing and trammel net surveys would be required to reach a desired detection probability. The cumulative probability of detection was calculated as

$$\text{cumulative detection probability} = 1 - (1-p)^J,$$

where p is the detection probability per sampling occasion and J is the number of sampling occasions. Furthermore, to determine the probability of a site being occupied conditional upon the species not being detected, conditional site occupancy was calculated as

$$\Psi_{i,condl} = \frac{\Psi_i(1-p_i)^J}{(1-\Psi_i) + \Psi_i(1-p_i)^J},$$

where the probabilities of occupancy (ψ) and detection (p) were obtained from the most parsimonious model and J is the number of sampling occasions (MacKenzie et al., 2006).

3 | RESULTS

A total of 95.7 electrofishing hours and 198 trammel net sets were conducted throughout south-eastern Iowa rivers from April to October 2014 and 2015. Grass carp were detected at least once at eight of our nine sites (naïve occupancy = 89%) during the 2 years of sampling and 44 out of 126 (34.9%) monthly site visits. After evaluating 35 different model combinations, the model with the lowest AIC ($AIC_c = 335.8$; $w_i = 0.20$; the most parsimonious model; Table 1) indicated that the probability of local colonization was influenced by river discharge (cubic meters per second [m^3/s]) while occupancy (0.21 [95% CI: 0.01, 0.47]), local extinction (0.29 [95% CI: 0.15, 0.45]), and detection (0.50 [95% CI: 0.40, 0.60]) probabilities were constant through time. The most parsimonious model predicted that the probability of local colonization increased as river discharge increased ($\beta = 0.00010$ [95% CI: 0.00001, 0.0002]; Table 2; Figure 3). Next, using our sampling framework of three secondary sampling occasions per primary occasion, the cumulative probability of detecting grass carp at an occupied site during each sampling session was 87.2%, whereas the conditional occupancy estimate was 3.3% (Figure 4).

The second ranked model also received support ($\Delta AIC_c = 1.32$, $w_i = 0.10$) and indicated that the probability of local colonization was positively related to river discharge ($\beta = 0.00009$ [95% CI: 0.000003, 0.0002]) and water temperature ($\beta = 0.0006$ [95% CI: -0.004, 0.005]) while occupancy (0.20 [95% CI: 0.09, 0.45]) and detection (0.50 [95% CI: 0.41, 0.60]) probabilities were constant. The third ranked model also received support ($\Delta AIC_c = 1.39$, $w_i = 0.10$) and indicated that river discharge influenced both the probabilities of local colonization ($\beta = 0.00009$ [95% CI: 0.000004, 0.0002]) and detection ($\beta = 0.00002$ [95% CI: -0.00003, 0.00007]) while occupancy (0.41 [95% CI: 0.01, 0.87]) and local extinction (0.25 [95% CI: 0.10, 0.40]) probabilities were constant. Conversely, water temperature (Celsius [$^{\circ}C$]) had little influence on all model parameters, as only 3 of the 10 most supported models included temperature as a covariate (all models $\Delta AIC_c > 1.0$; Table 1). Generally, models indicated that environmental covariates did not significantly influence the probability

TABLE 1 Model selection results for the top 10 of 35 candidate models estimating variation in grass carp occupancy (ψ), local extinction (ϵ), local colonization (γ), and detection (p) probabilities in south-eastern Iowa rivers

Model	AIC _c	Δ AIC _c	w_i	Model likelihood	K	Deviance
$\psi, \epsilon, \gamma_{discharge}, p$	335.77	0.00	0.20	1.00	5	325.25
$\psi, \epsilon, \gamma_{temperature \cdot discharge}, p$	337.09	1.32	0.10	0.52	6	324.36
$\psi, \epsilon, \gamma_{discharge}, p_{discharge}$	337.16	1.39	0.10	0.50	6	324.43
$\psi, \epsilon_{temperature}, \gamma_{discharge}, p$	337.67	1.90	0.08	0.39	6	324.94
$\psi, \epsilon_{time}, \gamma_{time}, p$	337.93	2.16	0.07	0.34	17	298.04
$\psi, \epsilon_{discharge}, \gamma_{discharge}, p$	337.98	2.21	0.07	0.33	6	325.25
$\psi, \epsilon_{discharge}, \gamma_{discharge}, p_{discharge}$	338.44	2.67	0.05	0.26	7	323.45
$\psi, \epsilon_{time}, \gamma, p_{time}$	338.59	2.82	0.05	0.24	20	290.27
$\psi, \epsilon, \gamma, p$	338.97	3.21	0.04	0.20	4	330.63
$\psi, \epsilon, \gamma_{temperature}, p$	339.62	3.85	0.03	0.15	5	329.10

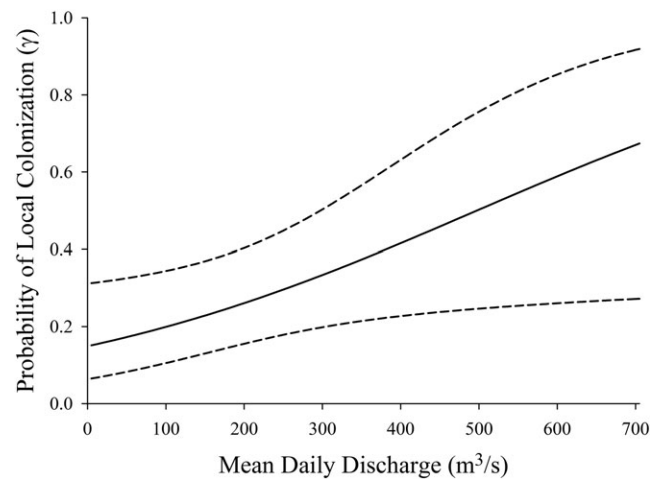
Note. Covariates included water temperature ($^{\circ}$ C; *temperature*) and river discharge (m^3/s ; *discharge*). In addition, the data were modelled where parameters were both constant and time (*time*) dependent. Model covariates, AIC_c score, difference between the AIC value of the most parsimonious model and model *i* (Δ AIC_c), the relative support for model *i* (w_i), model likelihood, number of parameters estimated (*K*), and model deviance are reported.

of detection and water temperatures do not significantly influence grass carp local extinction and local colonization relative to river discharge.

4 | DISCUSSION

Occupancy modelling provided a useful tool for assessing the status of cryptic grass carp populations in tributaries of the UMR. The most parsimonious model indicated that grass carp occupancy, local extinction, and detection probabilities were not influenced by river discharge or water temperature, whereas the probability of local colonization increased with increasing river discharge. Using our sampling framework, the probability of detecting grass carp on an occupied site was 87.2%, and five or more sampling occasions were required to obtain a 95% probability of detection. Combined with low occupancy rates of grass carp, sampling during periods of low river discharge and using a small number of sampling occasions could lead to missing observations and an incorrect inference of population distribution. These findings corroborate other studies that detail the importance of accounting for site-specific river discharge patterns when sampling for highly mobile bigheaded carp (silver and bighead carp) where captures are also difficult (i.e., DeGrandchamp et al., 2008; Sullivan et al., 2017).

Of the environmental variables examined in this study, river discharge appeared to be the most important factor influencing the probability of grass carp local colonization. As grass carp movements vary intra-annually (Bain, Webb, Tangedal, & Mangum, 1990; Martino, 1974; Stanley, Miley, & Sutton, 1978), increases in local colonization

**FIGURE 3** Relationship between mean daily river discharge (m^3/s) and the probability of local colonization (mean and 95% CI) estimates for grass carp in south-eastern Iowa rivers

probabilities during periods of increased discharge could be associated with spawning events that are triggered by increases in spring river discharge (Martino, 1974; Stanley et al., 1978). Furthermore, high discharge rates, and associated increases in gage height, can inundate floodplain habitats that are abundant with food resources for grass carp. Thus, the relationship between river discharge and grass carp colonization could also be influenced through movements into these shallow habitats where our sampling occurred. During our study, mean

TABLE 2 Estimates of logit-scale model coefficients for the Markov chain Monte Carlo parameterization of the design matrix for the most parsimonious model in Table 1

Parameter type	Number	Estimate	Standard error	95% Credible interval	
				Lower	Upper
ψ	β_1	-1.86325	1.08871	-3.99713	0.27063
$\epsilon_{intercept}$	β_2	-0.89219	0.38162	-1.64016	-0.14422
$\gamma_{intercept}$	β_4	-1.74111	0.48394	-2.68963	-0.79260
$\gamma_{discharge}$	β_5	0.00010	0.00005	0.00001	0.00019
p	β_6	0.02502	0.19875	-0.36453	0.41458

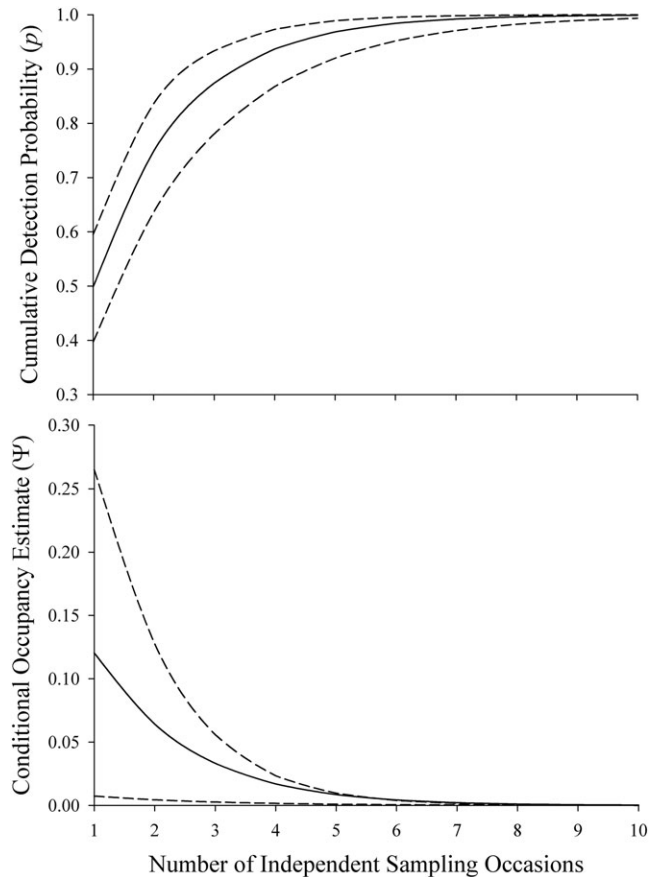


FIGURE 4 Cumulative detection probability (top panel) and conditional occupancy estimates (bottom panel; solid lines) of grass carp with 95% CI (dashed lines) assuming independent secondary sampling occasions using both boat electrofishing and trammel net sets at a survey site within south-eastern Iowa rivers

river discharge across all study sites was $203 \text{ m}^3/\text{s}$, which equates to a local colonization probability of 0.26. However, river discharges are highly variable intra-annually where floods are common (Figure S1) and periods of low or high discharges can vary the probability of colonization. Using the Eddyville site on the Des Moines River as an example, the lowest observed daily discharge of $41.0 \text{ m}^3/\text{s}$ would suggest a local colonization probability of only 0.17, whereas the highest observed daily discharge of $627.1 \text{ m}^3/\text{s}$ would suggest a local colonization probability of 0.69. Using our predictive model, managers may be able to forecast potential conditions when grass carp would be likely to colonize a site based upon river discharge data readily available throughout the country. Focusing sampling efforts in locations and times when local colonization probabilities are estimated to be high could improve adaptive management strategies or increase the chances of reaching targeted harvest efforts.

Grass carp detection probability was moderate (0.50), not influenced by measured environmental variables, and constant through time, indicating that they are imperfectly detected using our sampling framework. We were unable to directly compare detection probabilities between gears because river conditions only allowed crews to deploy trammel nets in combination with 53% of electrofishing transects. There are a variety of factors that could influence detection probabilities, including gear avoidance (Maceina, Slipke, & Grizzle, 1999) and fish size (Bain

et al., 1990; Dolan & Miranda, 2003). For example, grass carp were more effectively sampled within the Missouri River basin using passive gears (i.e., gill net) versus electrofishing (Wanner & Klumb, 2009), indicating that detection probabilities could vary between sampling gears and locations. In the current study, grass carp less than 600 mm (approximately 3% of sample) or greater than 900 mm (approximately 6%) were rarely captured (C. Sullivan, unpublished data), similar to sampling in the Missouri River (Wanner & Klumb, 2009). Conversely, Long-Term Resource Monitoring Program sampling from 2000 to 2017 in Pools 8, 13, and 26 indicated that only 40.2% of grass carp captured from a variety of gears (day/night electrofishing, trammel nets, gill nets, and hoops nets) were comprised of fish 600 to 900 mm (57.8% of grass carp captured across gears were <600 mm; <https://umesc.usgs.gov/ltrm-home.html>). However, a majority (64.6%) of grass carp between 600 and 900 mm were captured using daytime electrofishing. Combine, the lack of captures of grass carp less than 600 mm or greater than 900 mm in this study indicates potential size selectivity of both trammel nets and boat electrofishing or poor recruitment in recent years. Future refinements in grass carp sampling strategies may help minimize potential gear selectivity and improve detection probabilities.

Because the probability of detection was relatively low, additional sampling effort could be used to improve detection and avoid biased estimations of occupancy model parameters (MacKenzie et al., 2003). For example, five or more sampling occasions were required to achieve a 95% probability of detection given occupancy of grass carp. When sampling for species where capture is difficult, unreasonable estimates of occupancy have been documented when the probability of detection was low (<0.15) due to difficulties in distinguishing between sites with low detection rates and sites where the species is truly absent (MacKenzie et al., 2002). However, our sampling framework of three secondary sampling transects resulted in an 87% probability of detection given occupancy of grass carp and a 3% probability that sites where grass carp were not detected were actually occupied. Incorporating additional sampling sites instead of additional secondary sampling occasions during each primary occasion could better inform managers of current fish distribution. Further, our sampling events occurred across a variety of discharge regimes (Figure S1); however, increasing the sampling frequency during periods of higher discharge could lead to higher capture rates because the probability of local colonization by grass carp would be higher.

Models including water temperature generally received little support as a factor influencing grass carp occupancy patterns. Previous studies suggest that water temperatures influence grass carp movement patterns (Nixon & Miller, 1978); however, water temperatures were generally greater than 20°C during our sampling surveys across all rivers (Figure S1). Furthermore, DeGrandchamp et al. (2008) found that big-headed carp movements decrease and are low during periods where water temperatures are $\geq 20^\circ\text{C}$. Therefore, despite sampling from April through October, the limited spatial and temporal variation in water temperatures present throughout this study could hinder our ability to effectively evaluate the effect of water temperatures on grass carp occupancy dynamics. Alternatively, grass and bigheaded carp spawning movements have been documented to be initiated by increases in river discharges coupled with increases in water temperature (Li, Peng, & Liao, 2006;

Verigin, Makeyeva, & Zaki Mokhamed, 1978). Because water temperature regimes can influence fish metabolic demands and gamete maturation schedules (i.e., Bjornn & Reiser, 1991), there may be a temperature threshold above or below which grass carp movements, hence occupancy, change. Further research identifying the influence of variable temperature regimes on grass carp occupancy dynamics is warranted.

Contemporary fisheries management generally requires the knowledge of species population distributions in order to accurately assess fish populations, which is difficult when data are sparse. Within the UMR, invasive species captures have increased over the last decade (NAS, 2016), and future species establishment could drastically affect the fish community structure (Cudmore & Mandrak, 2004; Irons, Sass, McClelland, & Stafford, 2007). Monitoring of the status and spread of populations is generally depicted in fisheries using CPUE. However, when capture is difficult, low CPUE and high variation in catch hinder managers' ability to detect true changes in abundance (Conner, Keane, Gallagher, Munton, & Shaklee, 2016). Because accurate population assessments are valuable when monitoring population status especially for nuisance fish species, the high variability in CPUE could mask true changes in populations through time. Combining multiple sampling gears to attain a more accurate representation of a fish population would be a violation for traditional fisheries indices (i.e., CPUE), but it is not an issue for occupancy models. The differences in sampling methodologies could affect detection probabilities (e.g., Pregler et al., 2015) but do not influence estimates of occupancy, extinction, or colonization. Instead, our results suggest that occupancy modelling might serve as a complementary tool to monitoring coarse population changes as population dynamics and occupancy are closely correlated (Conner et al., 2016), particularly in situations where actual population information (i.e., CPUE) may be highly variable, in part because detections are imperfect. Further research detailing the mechanisms of how other abiotic conditions (e.g., backwater availability, water velocity, and spring discharge) influence grass carp populations in addition to other gears that could influence detection rates would increase our understanding of their occupancy patterns and improve monitoring efforts.

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SUPPORTING INFORMATION

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