

# Differences in Native and Invasive Fish Larval Occupancy and Detection Probabilities in the Upper Mississippi River

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## Abstract

The Upper Mississippi River (UMR) represents one invasion front to bigheaded carps *Hypophthalmichthys* spp. in North America. Agencies often sample larvae to determine the conditions that bigheaded carp reproduction occurs, but the ability for conventional ichthyoplankton sampling to detect bigheaded carp reproduction compared to native fish is unknown. We used occupancy models to estimate larval bigheaded carp and native fish larvae detection probabilities and assessed how habitat type, Julian date, river discharge, and water temperature affect occupancy. We sampled larvae in pools 18-20 of the UMR every two weeks at the Iowa, Skunk, and Des Moines River confluences in backwater, side channel, and thalweg habitats. Detection probabilities increased with water volume filtered and was lower for larval bigheaded carp than freshwater drum, gizzard shad, and percids. Freshwater drum and bigheaded carp larvae had higher detection in thalweg and channel border habitats compared to backwaters. Occupancy of bigheaded carp peaked on June 19<sup>th</sup> at 20°C, increased with discharge, and declined with coefficient of variation (CV) of water temperature and discharge. Gizzard shad and percids occupancy peaked on May 24<sup>th</sup> and increased with CV of water temperature while occupancy of freshwater drum peaked on July 3<sup>rd</sup>, decreased with CV of water temperature, and increased with water temperature. Our results indicate bigheaded carp are more difficult to detect than native larvae and identified conditions associated with larval occupancy that can be used to maximize detection and better understand when, where, and under what conditions larvae are present while accounting for imperfect detection.

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Running title: Larval fish occupancy and detection

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**Abstract:** The Upper Mississippi River (UMR) represents one invasion front to bigheaded carps *Hypophthalmichthys* spp. in North America. Agencies often sample larvae to determine the conditions that bigheaded carp reproduction occurs, but the ability for conventional ichthyoplankton sampling to detect bigheaded carp reproduction compared to native fish is unknown. We used occupancy models to estimate larval bigheaded

carp and native fish larvae detection probabilities and assessed how habitat type, Julian date, river discharge, and water temperature affect occupancy. We sampled larvae in pools 18-20 of the UMR every two weeks at the Iowa, Skunk, and Des Moines River confluences in backwater, side channel, and thalweg habitats. Detection probabilities increased with water volume filtered and was lower for larval bigheaded carp than freshwater drum, gizzard shad, and percids. Freshwater drum and bigheaded carp larvae had higher detection in thalweg and channel border habitats compared to backwaters. Occupancy of bigheaded carp peaked on June 19<sup>th</sup> at 20°C, increased with discharge, and declined with coefficient of variation (CV) of water temperature and discharge. Gizzard shad and percids occupancy peaked on May 24<sup>th</sup> and increased with CV of water temperature while occupancy of freshwater drum peaked on July 3<sup>rd</sup>, decreased with CV of water temperature, and increased with water temperature. Our results indicate bigheaded carp are more difficult to detect than native larvae and identified conditions associated with larval occupancy that can be used to maximize detection and better understand when, where, and under what conditions larvae are present while accounting for imperfect detection.

Key Words: ichthyoplankton, Silver Carp, Bighead Carp, Freshwater Drum, Gizzard Shad, percids, distribution models, sampling efficiency

## 1 | INTRODUCTION

Aquatic invasions have become common and are one of the greatest threats to aquatic ecosystems worldwide ( Alexander et al., 2015; Gherardi, 2007; Sala et al., 2000) by altering nutrient cycling (Vanni, 2021), food webs (DeBoer et al., 2018), and abundance and distribution of native species (Gallardo et al., 2016; Weber & Brown, 2011). Currently, bigheaded carps (*Hypthalmichthys moltrix* and *Hypophthalmichthys nobilis*) are some of the most problematic aquatic invasive species that have spread rapidly and broadly in North America with adverse ecosystem effects (DeBoer et al., 2018; Solomon et al., 2016; Tillotson et al., 2022). Pelagic planktivores native to China and a small portion of eastern Russia (Kolar et al., 2007), bigheaded carp were introduced to the United States for aquaculture and sewage treatment resulting in their eventual escapement to natural waters where populations rapidly increased (Kolar et al., 2005). Since their initial escapement in the early 1980s, the Mississippi River has served as an invasion highway throughout the central United States. The Upper Mississippi River (UMR) is currently one of the primary invasion fronts for bigheaded carp in the Midwestern United States due to a series of locks and dams that have slowed their upstream expansion (Fritts et al., 2021; Tripp et al., 2013; Whitledge et al., 2019). Lock and Dam 19 specifically represents a major barrier to their northern expansion ( Larson et al., 2017; Fritts et al., 2021; Tripp et al., 2013), although adults have been captured as far north as pool 2 (U.S. Geological Survey, 2022).

While adult bigheaded carp have been captured up to pool 2, reproduction has only been documented to pool 16 (Camacho et al., 2023; Larson et al., 2017). Fish reproductive phenology is the product of many environmental conditions (Krabbenhoft et al., 2014; Yang et al. 2021) and quantifying fish reproduction provides critical temporal, spatial, population, and community metrics in relation to environmental conditions (Pritt et al., 2015; Quist et al. 2004). Seasonality in concert with water temperature is often considered necessary for successful reproduction by triggering the release of gametes (Pankhurst & Porter, 2003; Werner, 2002). Bigheaded carp require water temperatures > 17°C to initiate reproduction, with reproductive activity occurring up to 30°C (DeGrandchamp et al., 2007; Kocovsky et al., 2012; Schrank et al., 2001). Alternatively, reproduction of native fishes is generally initiated at cooler temperatures and occurs over a more narrow range (e.g., walleye *Sander vitreus*, 5 to 10°C; Bozek et al., 2011; gizzard shad *Dorosoma cepedianum*, 10 to 21°C; Becker, 1983; freshwater drum *Aplodinotus grunniens*, 18 to 25°C; Swedberg and Walburg, 1970). Beyond temperature, changing river discharge strongly affects reproductive activity in many invasive and native lotic fishes (Humphries et al., 2002; King et al., 2016; Dudley & Platania, 2007) including bigheaded carp (e.g., Kolar et al., 2007; Schrank et al., 2001).

Beyond environmental conditions, spatial variation in riverine habitats can influence where invasive and native fish reproduce (Camacho et al., 2023; Kolar et al., 2007). In rivers, spawning habitat relates to channel position such as channel border, thalweg, and backwaters due to differences in river discharge and species spawning requirements. Larval habitat use often corresponds to their reproductive guild (Holland,

1986). Some species such as bigheaded carp and freshwater drum spawn in the open water environments of the thalweg where eggs passively drift until they hatch and reach sizes that allow increased mobility to escape the current (Becker, 1983). Other species reproduce in the lower velocities in channel borders and backwaters that provide cover for eggs and developing larvae (e.g., walleye) or passively drift downstream (e.g., gizzard shad; Holland, 1986; Simon, 1998). Consequently, while most lotic larval fish assessments focus on thalweg collections, larval occupancy may vary among taxa and habitats.

Given the network of environmental conditions for fish reproduction, along with the uncertainty of ichthyoplankton sampling, determining occurrence of riverine fish reproductive events can be difficult. High spatio-temporal variability in larval catches is common (Cyr et al., 1992; Leonardsson et al., 2016; Michaletz & Gale, 1999; Weber et al., 2021). Therefore, it is difficult to determine when, where, and under what conditions fish reproduction occurs, particularly when detection probability is imperfect. Additionally, adult bigheaded carps are difficult to capture compared to adult native fishes (Bouska et al., 2017), but whether or not differences in sampling efficiency also exist at the larval phase is unknown. Occupancy ( $\Psi$ ) and detection ( $p$ ) modeling offers a quantitative method of estimating the true presence of species in a system by accounting for imperfect detections based on discrete encounters over temporal or spatial scales (MacKenzie et al., 2002). Within fisheries, occupancy and detection modeling has been primarily used to describe distribution of adult fishes (Potoka et al., 2016; Schumann et al., 2020; Sullivan et al., 2018;), but models are plastic and have been adapted to evaluate age-0 fish habitat use (Burdick et al., 2008; Falke et al., 2010, 2012), timing of reproduction events associated with environmental conditions (Falke et al., 2010; Peoples and Frimpong, 2011; Pritt et al., 2014), and recruitment of cryptic invaders (Weber & Brown, 2019). These models also provide sample size requirements to achieve desired detection probabilities, improving sampling designs and monitoring programs (Kelly et al., 2021; Kuehne & Olden, 2016; Rodtka et al., 2015). Consequently, occupancy models can serve as a useful tool for assessing reproductive dynamics of bigheaded carp along leading edges of invasion where reproduction may be limited, and spawning events can be brief and difficult to detect.

Our objectives were to estimate occupancy and detection probability of bigheaded carp larvae and native fish taxa in relation to spatial and environmental variation. Next, we quantified cumulative detection probabilities to estimate sampling effort required to detect bigheaded carp larvae compared to native species. First, we hypothesized bigheaded carp larval occupancy would be higher in the thalweg compared to other habitats and positively related to water temperature and river discharge. Second, we hypothesized bigheaded carp larval occupancy would be lower than native fishes and lower in Mississippi River pools along the leading edge of population expansion than already established native fish populations. Finally, we hypothesized larval detection probabilities would be lower for bigheaded carp than native taxa.

## 2 | METHODS

### 2.1 | Study Area

The Upper Mississippi River extends from the Mississippi River headwaters in Minnesota to its confluence with the Missouri River just north of St. Louis, MO. This portion of the river is impounded by 29 locks and dams and highly channelized to allow for barge traffic. Our study focuses on pools 18 to 20 from just upstream of the Iowa River confluence to just downstream of the Des Moines River confluence (Figure 1). Along this reach, there are three main tributaries: the Iowa River on pool 18, the Skunk River on pool 19, and the Des Moines River on pool 20 (Figure 1). These locations represent the furthest upstream extent of most bigheaded carp reproduction in the Upper Mississippi River (Camacho et al., 2023; La Hood et al., 2023; Larson et al., 2017), with some evidence of reproduction up to Pool 16 (Larson et al., 2017).

### 2.2 | Ichthyoplankton Sampling

We collected ichthyoplankton samples every 10 days during daylight hours from late April to September in 2014 to 2018. Sites were located 1 km upstream and downstream and at the confluence of each tributary for a total of nine sample locations (Figure 1). Each site consisted of three tows, one at each different habitat types including a backwater, thalweg, and channel border. We used ichthyoplankton tows (0.5 m diameter, 2.5 m length, and 500  $\mu$ m mesh net) to collect larval fishes by conducting tows parallel to the flow at speeds to

maintain no upstream or downstream movement for a total of four minutes. We preserved larval samples in 95% ethanol and recorded water flow through each net using a General Oceanics 2030R flowmeter mounted at the mouth of the ichthyoplankton net which we used to calculate water volume ( $\text{m}^3$ ) filtered through the net. Across all sites and years, we collected a total of 1,776 ichthyoplankton samples.

In the laboratory, we sorted and cleared ichthyoplankton samples from debris with a minimum of two different individuals until no further larvae were found. We identified larvae to the lowest taxonomic level possible with visual identification using techniques described by Auer (1982) and Chapman (2006). We identified larval fishes (ventral fin-folds present) to family apart from certain taxa such as bigheaded carp and freshwater drum that could be identified down to genus or species. We selected bigheaded carp, freshwater drum, gizzard shad, and Percidae for analysis due to variable reproductive strategies and frequency of occurrence in our samples. We were only able to visually identify larvae down to family Clupeidae, but are referenced as ‘shad’ hereafter, as gizzard shad are the dominant taxa found in the study reach. Bigheaded carp and drum are both pelagic broadcast spawners while shad and percids tend to spawn in lower water velocity environments of channel borders and backwaters (Kolar et al., 2007; Holland 1986). Shad and percids tend to spawn earlier during cooler water temperatures, bigheaded carps tend to spawn later in the year during warmer water temperatures, and freshwater drum spawning tends to be protracted across a broad range of water temperatures (Becker, 1983; Bozek et al., 2011; Kocovsky et al., 2012; Swedberg & Walburg, 1970).

### 2.3 | Environmental Data

We collected temporal, hydrological, and thermal conditions associated with each ichthyoplankton sample. We used Julian date to account for temporal variation in larval fish presence based on seasonal variation in spawning for each taxon, regardless of environmental conditions. Next, we acquired hydrological data from United States Geological Survey and United States Army Corps of Engineers gauging stations nearest each site (Supplemental data). We calculated average weekly river discharge ( $\text{m}^3/\text{s}$ ) and coefficient of variation (CV) of each sample to estimate the magnitude and variability in hydrological conditions prior to sampling. Finally, we calculated average and CV of weekly river temperature ( $^{\circ}\text{C}$ ) using linear regression for each tributary based on field water temperature observations compared to gauging station values (Supplemental data).

### 2.4 | Statistical Analysis

We developed occupancy and detection models using Program MARK accounting for imperfect detection (MacKenzie et al., 2002). There are four main assumptions for occupancy and detection modeling (MacKenzie et al., 2018). First, we assume populations are closed; our sampling on a day and at the three sites associated with a tributary (nine ichthyoplankton tows) all occurred within an hour to meet the assumption of no births, deaths, immigration, or emigration during a sampling event. The next assumption states occupancy and detection probabilities are constant among sites or that heterogeneity in these parameters is accounted for using covariates; we used spatial and environmental covariates to account for spatial and temporal heterogeneity of both parameters. The third assumption is detection histories are independent among sites; we accounted for this assumption through temporal replication where we sampled every 10 d and larvae were < 7 d old (Camacho et al., 2023; M. Weber, unpublished data), ensuring we did not repetitively sample the same larval across multiple sampling events. Finally, the model assumes no false positive detections; we selected taxa that had low ambiguity in visual identification and genetically identified a subset of bigheaded carp larvae to verify identification accuracy (see Camacho et al., 2023 for more details).

We developed encounter histories for each larval taxon and sample date as presence/absence (0 or 1) at each site upstream, downstream, or at the confluence of the major tributary. For example, an encounter history could be comprised of bigheaded carp only collected at the Des Moines River confluence and not at upstream or downstream locations (encounter history 010) or upstream and downstream but not within the confluence (encounter history 101). Occupancy modeling allows the use of covariates to improve model estimates and evaluate occupancy and detection under a range of environmental conditions. We assessed the effect of water volume filtered through the ichthyoplankton net as an effect of sampling effort on detection

probability. We also assessed the effects of Julian date, mean and CV of weekly water temperature ( $^{\circ}\text{C}$ ), and discharge ( $\text{m}^3/\text{s}$ ) on site occupancy. We evaluated collinearity of covariates with a Pearson’s product-moment correlation analysis (all  $r < 0.6$ ) before including them in occupancy and detection models. To ensure normality, we centered and scaled all covariates using z-scores prior to analysis. We assessed quadratic effects of Julian date and weekly river temperature on occupancy probability, as we sampled prior to and after hypothesized peak spawning periods and linear models would be inappropriate. We assessed all other covariates as linear effects. We assessed detection models by first comparing species and habitat models before adding additional effects of environmental covariates. Next, we retained the most supported detection model to evaluate species and habitat effects on occupancy. Finally, we assessed potential effects of environmental covariates on occupancy while retaining the most supported species and habitat effects. We ranked models based on Akaike’s Information Criterion corrected for sample size ( $\Delta\text{AIC}_c$ ) and  $\text{AIC}_c$  model weight ( $w_i$ ; Burnham et al., 2011). We considered models ranked [?] 2  $\Delta\text{AIC}_c$  from the top model as competitive in analyses. Finally, we calculated detection probabilities under increasing sampling size (cumulative detection probability) using the most supported detection model (e.g., Kelly et al., 2021).

### 3 | RESULTS

We collected bigheaded carp larvae in pools 18 to 20 of the Mississippi River in 53 of 592 sample site-years (naïve  $\Psi = 0.09$ ). Native larvae were captured more frequently, with freshwater drum ( $n = 223$  of 592 site-years; naïve  $\Psi = 0.38$ ) captured most frequently followed by shad ( $n = 141$  of 592 site-years; naïve  $\Psi = 0.24$ ) and percids ( $n = 132$  of 592 site-years; naïve  $\Psi = 0.22$ ). Thalweg and channel border habitats accounted for the most bigheaded carp (77%) and drum (78%) collections while shad and percids had similar overall collections among habitats (29 to 36%). We captured the most bigheaded carp between Julian days 138 to 240 when water temperatures ranged from 17.6 to 26.6 $^{\circ}\text{C}$  and during the highest weekly discharge conditions (mean = 4,124  $\text{m}^3/\text{s}$ , SD = 1,057). We captured percids the earliest (day 113) during the narrowest time (range = 113 to 228, mean = 160, SD = 32), coldest temperatures (mean = 19.9 $^{\circ}\text{C}$ , SD = 5), and second highest weekly discharge (mean = 3,629  $\text{m}^3/\text{s}$ , SD = 1,251). We captured freshwater drum the latest (day 256) across the widest range of days (range = 122 to 256, mean = 189, SD = 33) associated with highest weekly temperatures (mean = 23.4  $^{\circ}\text{C}$ , SD = 2.9) and lower discharge (mean = 3,321  $\text{m}^3/\text{s}$ , SD = 1,061). Finally, we collected shad on a similar time frame as freshwater drum (range = 120 to 256, mean = 174, SD = 29), with similar water temperature to bigheaded carp (range = 15.1 to 27.7 $^{\circ}\text{C}$ , mean = 22.2  $^{\circ}\text{C}$ , SD = 3), under similar discharge conditions to percids (mean = 3,587  $\text{m}^3/\text{s}$ , SD = 1,100).

#### 3.1 | Detection Models

Our most supported detection probability model while assessing taxa effects indicated differences in bigheaded carp and freshwater drum detections while shad and percids had similar detection ( $\Delta\text{AIC}_c = 0.00$ ,  $w_i = 0.69$ ; Table 1). The second ranked model with each taxonomic group estimated separately also received support ( $\Delta\text{AIC}_c = 1.62$ ,  $w_i = 0.31$ ; Table 1). Next, we assessed potential variation in detection probability for taxa among habitats. Our most supported model indicated detection of bigheaded carp and freshwater drum was similar between thalweg and channel border habitats combined that had different detection compared to backwater habitats ( $\Delta\text{AIC}_c = 0.00$ ,  $w_i = 0.33$ ; Table 1). In contrast, detection probability was similar among habitats for shad and percids (Table 1). Other model combinations receiving support include thalweg and channel border habitats combined for all taxa ( $\Delta\text{AIC}_c = 1.20$ ,  $w_i = 0.18$ ) and all habitats separate for carp and freshwater drum ( $\Delta\text{AIC}_c = 1.29$ ,  $w_i = 0.17$ ; Table 1). The final step of detection model selection was assessing the effect of water volume filtered (i.e., sampling effort) to the top taxa model. The addition of water volume filtered to all taxa ( $\Delta\text{AIC}_c = 0.00$ ,  $w_i = 0.35$ ; Table 1) was the most supported model, whereas water volume filtered applied to only bigheaded carp and shad and percids ( $\Delta\text{AIC}_c = 1.48$ ,  $w_i = 0.17$ ) or only to drum and shad/percids ( $\Delta\text{AIC}_c = 2.00$ ,  $w_i = 0.33$ ; Table 1) were also considered competitive models.

The most supported model estimated bigheaded carp detection probabilities higher in the thalweg and channel border habitat ( $p = 0.15$ , 95% CI = 0.09 to 0.22) than in the backwater ( $p = 0.09$ , 95% CI = 0.05 to 0.17), but estimates had overlapping confidence intervals (Figure 2). Drum detection probability was also higher in the thalweg and channel border ( $p = 0.40$ , 95% CI = 0.35 to 0.45) compared to the backwater ( $p =$

0.20, 95% CI = 0.15 to 0.26) while shad and percid detection probability was similar across all three habitats ( $p = 0.27$ , 95% CI = 0.23 to 0.31; Figure 2). Detection of bigheaded carp within each habitat tended to be lower than native fishes (Figure 2). Water volume filtered had a positive effect on detection estimates for all taxa/habitat combinations ( $\beta = 0.12$ , 95% CI = 0.01 to 0.23) where detection probability of bigheaded carp increased from 0.15 to 0.48, detection of freshwater drum increased from 0.34 to 0.77, and detection of shad and percids increased from 0.24 to 0.34 as water volume filtered increased from 30 m<sup>3</sup> to 50 m<sup>3</sup> (Figure 3).

Differences in detection probabilities among taxa resulted in differences in cumulative detection curves and the number of ichthyoplankton samples needed to detect each taxonomic group. Under the average water volume filtered (30.12 m<sup>3</sup>), bigheaded carp required the most ichthyoplankton samples (25 backwater or 14 thalweg/channel border) to reach a 90% detection probability, 1.4 to 5 times as many samples as native taxa (Figure 4). Freshwater drum required 5 to 10 samples and shad/percids required 8 samples to reach a 90% probability of detection. By increasing the water volume filtered to 40 m<sup>3</sup> we observed a 60% to 108% decrease in the samples required to achieve a 90% detection probability compared to the average sample volume (9 to 15 samples for bigheaded carp, 4 to 8 samples for freshwater drum, and 7 samples for shad and percids (Figure 4).

### 3.2 | Occupancy Models

We retained the most supported detection probability model structure for each taxa when assessing various larval fish occupancy model combinations. Similar to detection models, the combination of shad and percids, with carp and freshwater drum occupancy estimated separately, received the most support ( $\Delta\text{AIC}_c = 0.00$ ,  $w_i = 0.44$ ; Table 2). Other likely combinations include all taxa estimated separately ( $\Delta\text{AIC}_c = 1.63$ ,  $w_i = 0.20$ ) and freshwater drum estimated separately from bigheaded carp, shad, and percids ( $\Delta\text{AIC}_c = 1.78$ ,  $w_i = 0.18$ ; Table 2). Through the addition of habitat to this taxa model structure, the most supported model included backwater estimated separately and thalweg combined with channel border habitats for shad and percids ( $\Delta\text{AIC}_c = 0.00$ ,  $w_i = 0.21$ ; Table 2). Two of the six top and competitive model structures incorporated this habitat grouping among different taxa (Table 2). Finally, we added environmental covariates to determine the combination that best improved the taxa  $\times$  habitat model. The most supported taxa  $\times$  habitat  $\times$  environmental covariate model ( $\Delta\text{AIC}_c = 0.00$ ,  $w_i = 0.69$ ) incorporated Julian date and CV temperature for all taxa with the added effect of temperature on bigheaded carp and freshwater drum (Table 2). Bigheaded carp were the only taxonomic group to retain both discharge and CV discharge in the top model (Table 2).

Freshwater drum occupancy among all habitats ( $\Psi = 0.84$ , 95% CI = 0.73 to 0.91) was higher than bigheaded carp ( $\Psi = 0.29$ , 95% CI = 0.15 to 0.47) and shad and percids in backwaters ( $\Psi = 0.53$ , 95% CI = 0.41 to 0.66) or thalweg/channel border ( $\Psi = 0.42$ , 95% CI = 0.34 to 0.51). Julian day had a quadratic effect on occupancy probability for all taxa: shad and percids occupancy was highest on day 144 (May 24<sup>th</sup>) followed by bigheaded carp on day 170 (June 19<sup>th</sup>) and freshwater drum on day 184 (July 3<sup>rd</sup>; Figure 5). Bigheaded carp ( $\beta = -0.63$ , 95% CI = -1.03 to -0.23) and freshwater drum ( $\beta = -0.89$ , 95% CI = -1.24 to -0.55) occupancy declined with increased variation in weekly water temperature while shad and percids occupancy increased with increasing water temperature CV ( $\beta = 0.33$ , 95% CI = 0.16 to 0.51; Figure 5). Weekly water temperatures also had a quadratic effect on occupancy of bigheaded carp and freshwater drum: bigheaded carp occupancy was highest at 20.7°C and drum was highest at 23.9°C (Figure 5). Bigheaded carp occupancy was also positively related to mean weekly discharge ( $\beta = 1.29$ , 95% CI = 0.19 to 2.39) whereas the slope estimate of CV discharge incorporated zero ( $\beta = -0.01$ , 95% CI = -0.35 to 0.36; Figure 5).

## 4 | DISCUSSION

Our study demonstrates differences in our ability to detect invasive and native larval fish presence accounting for various environmental conditions. Detection probabilities for bigheaded carp were lower than native taxa and required more samples to detect their presence. Detection probability estimates increased with water volume filtered for all species, but detection also varied among habitats for carp and freshwater drum, indicating spatial differences in sampling efficiency. Similar to detection, bigheaded carp occupancy was generally lower than native species, suggesting they have a narrower range of environmental conditions

suitable for reproduction. Temporal and thermal environmental covariates improved occupancy probabilities among all species, while hydrological covariates were only beneficial to bigheaded carp occupancy.

Occupancy and detection models indicate some habitat separation among taxa. On average, bigheaded carp and drum detection probabilities were higher in thalweg and channel border habitats, whereas detection probability of shad and freshwater drum was similar among habitats. Pelagophil fishes, such as bigheaded carp and drum, reproduce in open water conditions (Balon, 1975; Welcomme et al., 2006) associated with the higher velocity thalweg and channel border river channel habitats. Larval fishes in these habitats are likely younger and passively drifting with the current (Holland, 1986), potentially making them easier to capture. Alternatively, larval bigheaded carp can migrate out of the main channel to areas with lower velocity at 5 to 6 days of age and larger, more developed larvae that are better swimmers may be more likely to avoid the ichthyoplankton net (Chapman and George, 2011; Roth et al., 2023). In contrast to detection, occupancy of carp and freshwater drum was similar among habitats, suggesting that all habitats are used by larval carp and drum. Thus, if the objective is to simply document bigheaded carp reproductive success, focusing sampling efforts in the thalweg would be more efficient. Alternatively, shad and percid detection was similar among habitats but occupancy was higher in backwater habitats than thalweg and channel borders, consistent with conventional reproductive guild classification for both shad (litho-pelagophil) and percids (lithophil; Simon, 1998). While not directly considered in this study, larval habitat selection can change during later developmental stages due to gas bladder inflation and increased horizontal mobility (Chapman and George, 2011). While we limited our occupancy and detection models to sub-juvenile stages, there may exist occupancy and detection habitat variation among sizes, ages, and developmental stages due to changes in mobility.

Native and invasive larval occupancy both varied temporally and were influenced by environmental conditions. Bigheaded carp reproduce in rivers during May through June when water temperatures exceed 17°C, with peak reproduction occurring at 22 to 26°C (Schrank et al., 2001), though protracted spawning documented into the fall can occur in some systems (Coulter et al., 2013; Papoulias et al., 2006). Freshwater drum typically spawn between May and June in the Upper Mississippi River (Butler, 1965) when water temperatures are between 18 to 25°C (Swedberg & Walburg, 1970). Shad spawn over a broad temporal window with reproduction occurring from late April into early August with water temperatures between 10 to 21°C (Becker, 1983), whereas percids, such as walleye, spawn the earliest from late April to early May with water temperatures ranging from 5 to 10°C (Becker, 1983; Bozek et al., 2011). Similarly, we found maximum occupancy estimates corresponded with Julian dates for bigheaded carp (June 19<sup>th</sup>), freshwater drum (July 3<sup>rd</sup>), and shad and percids (May 24<sup>th</sup>) that were typically at the upper limits of their documented spawning periods. This trend was mirrored in maximum occupancy occurring from freshwater drum when water temperatures was 23.9°C, whereas the water temperature for carp (20.7°C) was well within their recorded temperature limits and even lower than the cited temperature range for peak reproduction (22-26°C; Schrank et al., 2001). Maximum bigheaded carp occupancy in the Upper Mississippi River occurring below the peak reproduction threshold is likely due to stability of water temperatures in this region throughout our sampling period (mean water temperature of 22°C from April to August). In addition to mean temperature, increasing temperature variation led to lower occupancy probabilities for carp and drum, but an increase in occupancy probability for shad/percids. Fluctuations in water temperature can negatively influence bigheaded carp reproduction due to disruption in oogenesis (Majdoubi et al., 2022) and can reduce egg viability of other fishes (Van Der Kraak & Pankhurst, 2011), indicating post-spawning temperature stability could promote larval survival.

Larval occupancy among taxonomic groups was primarily affected by temporal and thermal variation; however, bigheaded carp occupancy also increased with mean river discharge and may have been negatively affected by variability in discharge. Discharge and water temperature are central catalysts of bigheaded carp reproduction (Camacho et al., 2023; Kolar et al., 2007; Lohmeyer & Garvey, 2009; Schrank et al., 2001). Adult bigheaded carp move upstream in spring with increasing discharge and spawn during peak flows when water temperature exceeds 17°C (DeGrandchamp et al., 2007; Kocovsky et al., 2012; Schrank et al., 2001). Effects of variation in discharge on bigheaded carp reproduction are less understood. With increasing variation in

discharge, our models suggested a slight negative effect on bigheaded carp larval occupancy, although the slope overlapped zero. Schaick et al., (2023) observed a similar relationship between larval bigheaded carp densities and variable discharge and theorized sustained, high magnitude discharged events were preferred for bigheaded carp reproduction. While discharge is also often cited as a major driver of reproduction for lotic fishes (Dudley & Platania, 2007; King et al., 2016; Humphries et al., 2002), we did not find an effect of discharge on native larval fish occupancy, potentially because peaks in discharge were not synchronized with appropriate spawning temperatures or because native taxa are more adapted to flow regimes (Lytle & Poff, 2004). Alternatively, discharge may not affect the occurrence of reproduction (e.g., occupancy), but could affect the magnitude of reproduction (e.g., larval densities) and still be responsible for large versus small year-classes (Weber et al., 2021).

Understanding when, where, and under what conditions larval fishes are present is strongly dependent on successfully capturing them given they occur at a site. Drum, shad, and percids had higher detection probabilities than bigheaded carp. Adult bigheaded carp are difficult to capture (Bouska et al., 2017; Collins et al., 2015), but our results are the first to document challenges associated with lower capture success of invasive larvae compared to native taxa. Low detection of bigheaded carp larvae can make it difficult to document reproductive events, particularly along invasion fronts, resulting in misinformed population status assessments with implications for management decisions. For instance, efforts are underway in the Upper Mississippi River to install barriers to slow or stop adult upstream movements into areas where reproduction has not yet been documented. Sampling effort strongly influenced our ability to detect larval fishes, but effects varied among taxa. Biologists can improve larval detection probabilities by 1) focusing sampling in the thalweg, 2) increasing the water volume filtered per tow, and 3) increasing the number of tows collected per site visit. While we collected three tows per site visit, cumulative detection curves indicated we would need to collect 14 thalweg/channel border samples to achieve 90% detection probability of bigheaded carp larvae. Alternatively, increasing the water volume filtered by 33% would reduce the sample size to 9 thalweg/channel border tows. These results provide an adaptable and flexible framework to determine how many samples to collect and how much water to filter based on river conditions (e.g., debris load) and acceptable uncertainty in bigheaded carp presence. Further, sampling could also be adjusted to determine successful reproduction through targeted sampling based on habitat, temporal, thermal, and hydrological effects on occupancy to optimize future sampling to assess reproduction of cryptic invaders.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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**TABLE 1.** Detection probability ( $p$ ) models ranked by  $\Delta AIC_c$ . We compared 39 models and presented those with  $\Delta AIC_c$  [?] 3. All models included constant occupancy [ $\Psi$  (.)]. We used top ranked species models for carp (bigheaded carp), drum (freshwater drum), shad (Clupeidae), and percids to formulate habitat models and top ranked habitat models to form environmental models. Covariates include backwater (BW), thalweg (TH), channel border (CB), and water volume filtered (VOL). (+) indicates additive effects, (x) indicates interactive effects, and (=) indicates combined variables.

Model Structure

**Species**

$p[\text{carp} + \text{drum} + (\text{shad} = \text{percids})], \Psi[.]$

$p[\text{carp} + \text{drum} + \text{shad} + \text{percids}], \Psi[.]$

**Habitat**

$p[((\text{BW} + (\text{TH} = \text{CB})) \times (\text{carp} + \text{drum})) + ((\text{BW} = \text{TH} = \text{CB}) \times \text{shad} = \text{percids})], \Psi[.]$

$p[(\text{BW} + (\text{TH} = \text{CB})) \times (\text{carp} + \text{drum} + \text{shad} = \text{percids})], \Psi[.]$

$p[((\text{BW} + \text{TH} + \text{CB})) \times (\text{carp} + \text{drum}) + ((\text{BW} = \text{TH} = \text{CB}) \times \text{shad} = \text{percids})], \Psi[.]$

$p[((\text{BW} + \text{TH} + \text{CB})) \times \text{drum}) + ((\text{BW} = \text{TH} = \text{CB})) \times \text{carp} \times \text{shad} = \text{percids}], \Psi[.]$

$p[((\text{BW} + (\text{TH} = \text{CB})) \times \text{drum}) + ((\text{BW} = \text{TH} = \text{CB})) \times \text{carp} \times \text{shad} = \text{percids}], \Psi[.]$

**Environmental**

$p[\text{VOL} \times ((\text{BW} + (\text{TH} = \text{CB})) \times (\text{carp} + \text{drum})) + ((\text{BW} = \text{TH} = \text{CB})) \times \text{shad} = \text{percids}], \Psi[.]$

$p[(\text{VOL} \times (\text{BW} + (\text{TH} = \text{CB})) \times \text{carp}) + ((\text{BW} + (\text{TH} = \text{CB})) \times \text{drum}) + (\text{VOL} \times (\text{BW} = \text{TH} = \text{CB})) \times \text{shad} = \text{percids}], \Psi[.]$

$p[((\text{BW} + (\text{TH} = \text{CB})) \times \text{carp}) + (\text{VOL} \times (\text{BW} + (\text{TH} = \text{CB})) \times \text{drum}) + (\text{VOL} \times (\text{BW} = \text{TH} = \text{CB})) \times \text{shad} = \text{percids}], \Psi[.]$

$p[(\text{VOL} \times (\text{BW} + (\text{TH} = \text{CB})) \times (\text{carp} + \text{drum})) + ((\text{BW} = \text{TH} = \text{CB})) \times \text{shad} = \text{percids}], \Psi[.]$

$p[(\text{VOL} \times (\text{BW} + (\text{TH} = \text{CB})) \times \text{carp}) + ((\text{BW} + (\text{TH} = \text{CB})) \times \text{drum}) + ((\text{BW} = \text{TH} = \text{CB})) \times \text{shad} = \text{percids}], \Psi[.]$

Model Structure

Parameters  $\Delta AIC_c$

**Species**

$\Psi[\zeta\alpha\rho\pi + \delta\rho\mu + (\sigma\eta\alpha\delta = \pi\epsilon\rho\zeta\iota\delta\zeta)]$

9 0.00

$\Psi[\zeta\alpha\rho\pi + \delta\rho\mu + \sigma\eta\alpha\delta + \pi\epsilon\rho\zeta\iota\delta\zeta]$

10 1.63

$\Psi[\delta\rho\mu + (\zeta\alpha\rho\pi = \sigma\eta\alpha\delta = \pi\epsilon\rho\zeta\iota\delta\zeta)]$

8 1.78

$\Psi[\zeta\alpha\rho\pi + \pi\epsilon\rho\zeta\iota\delta\zeta + (\delta\rho\mu = \sigma\eta\alpha\delta)]$

9 2.92

**Habitat**

$\Psi[\zeta\alpha\rho\pi + \delta\rho\mu + \langle\text{B}\Omega + (\text{TH} = \text{B}\rangle \times \text{shad} = \text{percids})]$

10 0.00

$\Psi[\zeta\alpha\rho\pi + \langle\text{B} + (\text{B}\Omega = \text{TH}) \times \text{drum}) + ((\text{BW} + (\text{TH} = \text{CB})) \times \text{shad} = \text{percids})]$

11 1.55

$\Psi[\zeta\alpha\rho\pi + \langle\text{B}\Omega + \text{TH} + \text{B}\rangle \times (\text{drum} + \text{shad} = \text{percids})]$

11 1.58

$\Psi[\zeta\alpha\rho\pi + \delta\rho\mu + \langle\text{TH} + (\text{B}\Omega = \text{B}\rangle \times (\text{shad} = \text{percids})]$

10 1.83

$\Psi[\zeta\alpha\rho\pi + \delta\rho\mu + (\sigma\eta\alpha\delta = \pi\epsilon\rho\zeta\iota\delta\zeta)]$

9 1.91

$\Psi[\zeta\alpha\rho\pi + \langle\text{B}\Omega + (\text{TH} = \text{B}\rangle \times (\text{drum} + \text{shad} = \text{percids})]$

11 1.93

**Environmental**

$\Psi[\Theta\Upsilon\Lambda \times \text{CVTEMP} \times ((\text{TEMP} \times \text{DIS} \times \text{CVDIS} \times \text{carp}) + (\text{TEMP} \times \text{drum}) + (\text{shad} = \text{percids}))]$

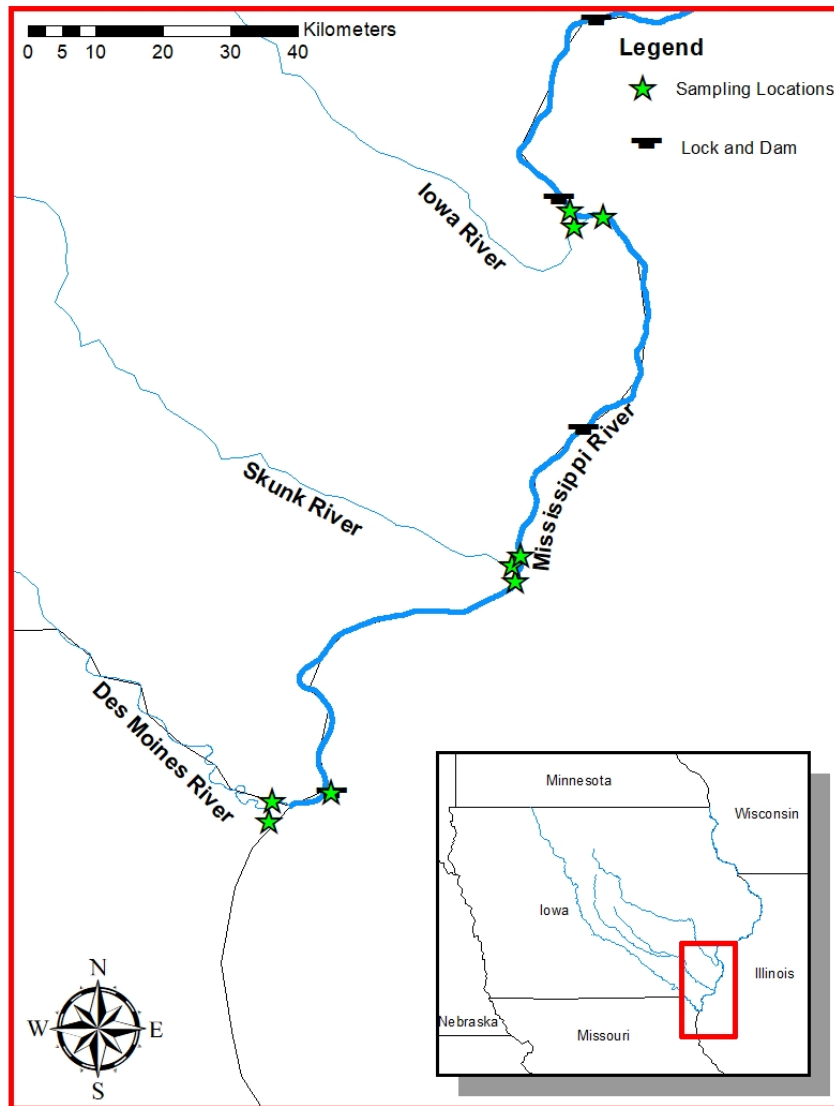
14 0.00

$\Psi[\Theta\Upsilon\Lambda \times \text{CVTEMP} \times ((\text{TEMP} \times \text{DIS} \times \text{carp}) + (\text{TEMP} \times \text{drum}) + (\text{shad} = \text{percids}))]$

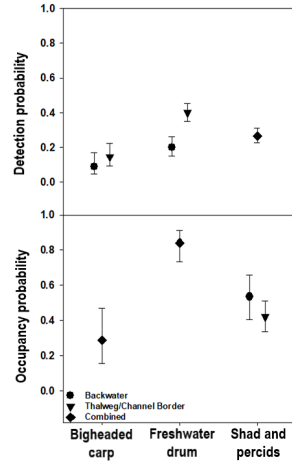
14 2.71

**TABLE 2.** Occupancy models evaluating species, habitat, and environmental effects ranked by Akaike’s

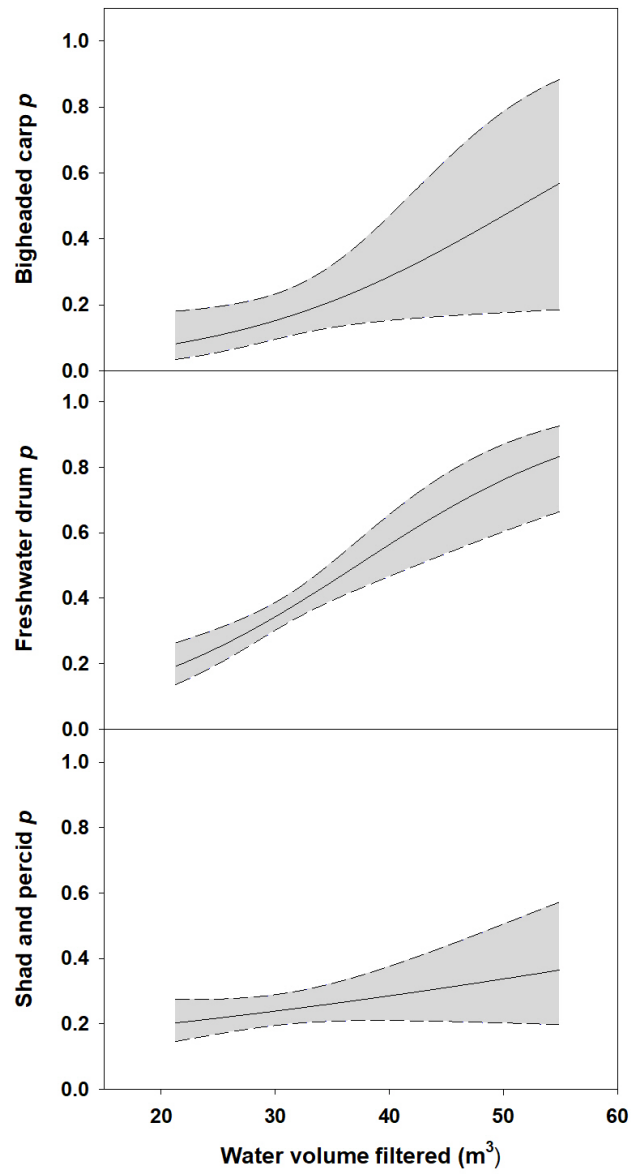
information criterion ( $\Delta AIC_c$ ). We assessed 67 models but just present models with  $\Delta AIC_c$  [?] 3. All models were made with the top ranked detection model  $p[VOL \times ((BW + (TH = CB)) \times carp \times drum) + ((BW = TH = CB)) \times shad = percids]$ . We used top ranked species models for carp (bigheaded carp), drum (freshwater drum), shad (*Clupeidae*), and percids to formulate habitat models and top ranked habitat models to form environmental models. Covariates include backwater (BW), thalweg (TH), channel border (CB), Julian date (JUL), weekly water temperature (TEMP), CV of temperature (CVTEMP), weekly river discharge (DIS), CV of discharge (CVDIS). (+) indicates additive effects, (x) indicates interactive effects, and (=) indicates combined variables.



**FIGURE 1** . Ichthyoplankton sampling locations (stars) in pools 18-20 and associated major tributaries of the Upper Mississippi River (UMR) during 2014-2018. Mississippi River sites are located 1 km upstream and 1 km downstream of tributary confluences. Tributary sites are located 1 km upstream of the confluence.

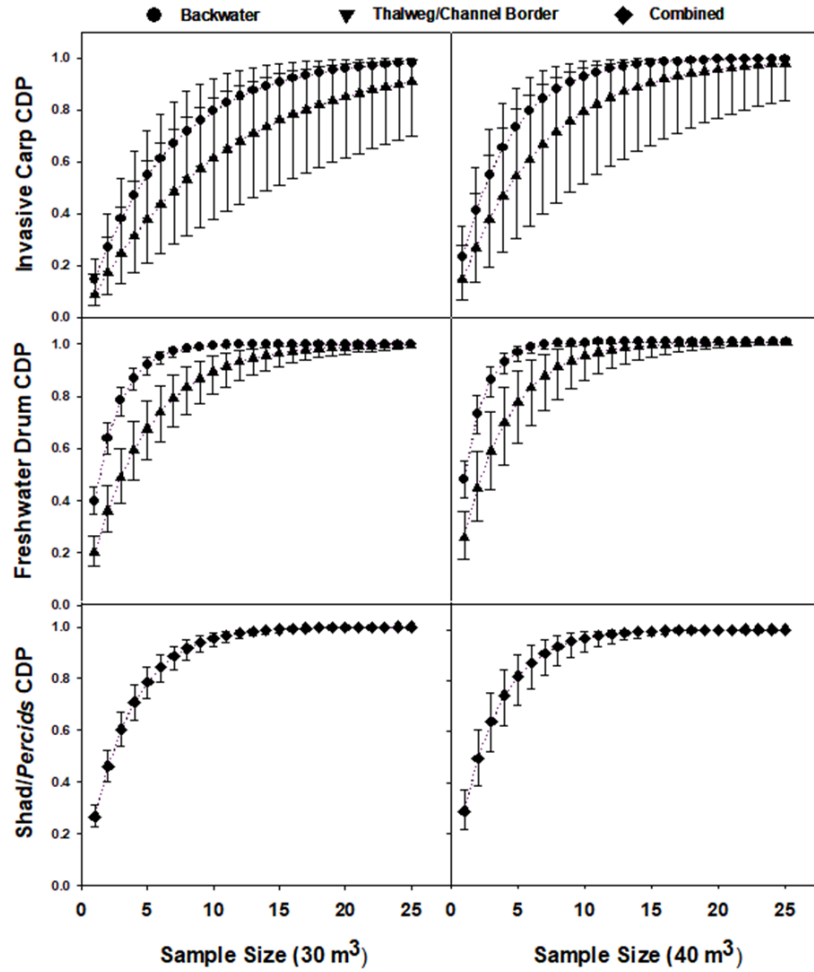


**FIGURE 2** . Detection (top panel) and occupancy (bottom panel) probability estimates ( $\pm$  95% confidence intervals) across species, habitat, and mean environmental covariates from the top ranked model.

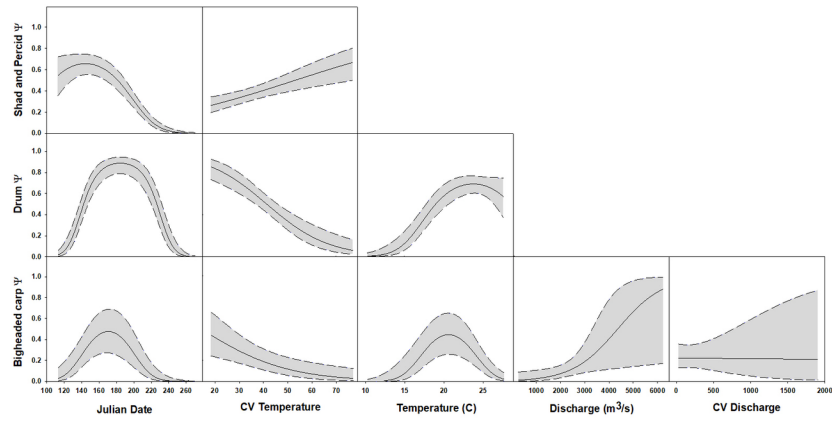


**FIGURE 3** . Invasive carp (top panel), freshwater drum (middle panel), and gizzard shad and percids (bottom panel) detection ( $p$ ) probability (95% confidence intervals, grey shaded region) in relation to water volume ( $m^3$ ) filtered through an ichthyoplankton tow net.





**FIGURE 4** . Cumulative detection probability (CDP  $\pm$  95% confidence intervals) for bigheaded carp (top panels), freshwater drum (middle panels), and gizzard shad and percids (bottom panels) based on the number of samples collected if 30 m<sup>3</sup> (left column) or 40 m<sup>3</sup> (right column) of filtered water.



**FIGURE 5** . Occupancy ( $\Psi \pm 95\%$  confidence intervals, grey shaded region) of bigheaded carp (bottom), freshwater drum (middle row), and gizzard shad and percids (top row) in relation to covariates identified as important predictors for each taxa during model selection.