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**A multi-scale approach for understanding factors limiting invasive carp distribution in the
Ohio River Basin**

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Abstract

The spread of aquatic invasive species (AIS) poses a major threat to freshwater biodiversity. Understanding the mechanisms regulating spread in invaded systems requires a multi-scale approach, as regional dispersal can facilitate arrival while local processes ultimately determine establishment and persistence. We used a dynamic multi-scale occupancy model to test hypothesized factors limiting the spread of invasive bigheaded carps (bighead carp *Hypophthalmichthys nobilis* and silver carp *H. molitrix*) in the Ohio River, USA. Across the basin, invasion has slowed, with limited upstream colonization of either species between years. However, once present, invasive carp populations tended to persist even in apparently low numbers. Bighead carp models were relatively uninformative, due to the low number of detections. On the local scale, silver carp exhibit clear habitat and flow preferences, where populations persisted in low velocity tributary locations especially when flows are too high in the main channel. We found evidence for decreasing detection of both species of invasive carp in mid-reach and upstream pools, potentially because of lower abundance in these reaches. Our results indicated that while invasive carp were able to disperse throughout a large range of the Ohio River, upstream populations are likely sustained by immigration from established reaches and spread is likely stalled because of limited population growth rates. Our results highlight the need to focus management efforts on controlling source populations to reduce upstream dispersal. Understanding multi-scale dynamics is critical for developing effective strategies to contain invasive carp in the Ohio River and other systems.

Keywords: bigheaded carp, Ohio River, occupancy model, multi-scale, Bayesian

Introduction

The introduction of aquatic invasive species (AIS) has been identified as a major threat to freshwater ecosystems around the world (Dudgeon et al. 2006; Reid et al. 2019). Once

established, AIS will often spread throughout a system, impacting an increasing number of native populations as their invaded range expands. Eradication of established AIS is often impossible (Myers et al. 2000; Cucherousset and Olden 2011), so limiting their secondary spread represents one of the most effective post-introduction management strategies for mitigating large-scale impacts (Larson et al. 2011; Vander Zanden and Olden 2008). The secondary spread of an invasive species can be simplified down into repeated dispersal and establishment events (Davis 2009), therefore effective measures for limiting the spread of AIS requires understanding factors regulating their distribution and establishment success within invaded systems (Vander Zanden and Olden 2008; Glubzinski et al. 2021). Common factors limiting the spread of AIS include system connectivity and dispersal ability (Havel et al. 2015), environmental heterogeneity and resource availability (Weaver et al. 2012), and biotic interactions (Ricciardi 2001; Gu et al. 2023). However, the relative importance of these factors can vary greatly depending on the spatial and temporal scales of interest (Hopkins 2009; Loo et al. 2009; Catford and Downes 2010; Cabra-Rivas et al. 2016). Therefore, controlling the spread of AIS requires understanding variables that facilitate or inhibit their persistence and establishment across multiple spatial and temporal scales.

Environmental conditions limiting aquatic species distributions are known to vary according to the studied spatial or temporal scale (Loo et al. 2009; Hopkins 2009; Cabra-Rivas et al. 2016; Sáez-Gómez et al. 2020). Environmental drivers of species distributions are thought to act in a hierarchical fashion, with local-scale conditions often constrained by broader-scale gradients (Poff 1997). In freshwater systems, AIS distributions have been shown to be constrained by both regional (climate, flow regime, land-use) and local (water quality, habitat availability, community assemblage) factors acting concurrently to limit their dispersal and establishment

success (Hopkins 2009; Loo et al. 2009; Sáez-Gómez et al. 2020). Understanding these hierarchical drivers not only informs on species distribution patterns, but can also be highly informative for applied management efforts (Weaver et al. 2012). Whereas large-scale studies can broadly inform potential range expansions of AIS (Pham et al. 2023), small-scale studies can inform habitat-specific vulnerabilities, local establishment processes, and potential locations for targeted management or removal efforts (Loo et al. 2009; Weaver et al. 2012; Havel et al. 2015). A growing number of studies have stressed the importance of both regional and local processes in regulating invasive species spread in terrestrial systems (Diez et al. 2009; Weaver et al. 2012; Cabra-Rivas et al. 2016; Hedden et al. 2024), however fewer studies have explicitly adopted a multi-scale framework to examine the spread of freshwater AIS (Loo et al. 2009; Sáez-Gómez et al. 2020). Here, we use a multi-scale framework to address factors limiting the spread of invasive carp (*Hypophthalmichthys* spp.) in the Ohio River basin, USA.

Silver (*H. molitrix*) and bighead carp (*H. nobilis*), collectively referred to as “bigheaded carp”, are global invaders that were first imported to the United States in the 1970s to help improve water quality at aquaculture and sewage treatment facilities (Kolar et al. 2005; Kelly et al. 2011). However, both species escaped confinement and quickly established populations in the Lower Mississippi River basin (Kolar et al. 2005; Kelly et al. 2011). Since the mid-1990s, both species’ populations have rapidly dispersed, becoming established throughout the Mississippi River basin and many of its major tributaries (Kocovsky et al. 2012). Silver and bighead carp are large-bodied planktivores that have been shown to overlap in their diet with native mussels, invertebrates, larval fishes, and other adult planktivorous fishes, potentially decreasing abundances of native competitors and impacting the structure of native food webs (Kolar et al. 2005; Butler et al. 2019; Sass et al. 2014; Eggleton et al. 2024; Novak et al. 2024). Rivers in the

Upper Mississippi River basin (e.g., Missouri, Des Moines, Illinois) have experienced a rapid expansion of bigheaded carps with accompanying ecological impacts (Sampson et al. 2009; Sass et al. 2014). However, their spread in the Ohio River basin, another major tributary, seems to have stalled or is advancing much slower than in other regions. This presents an opportunity to investigate how both landscape and local-scale factors may be acting to limit the expansion of invasive carp in the Ohio River. Insights from this system may help identify mechanisms constraining invasive carp establishment and be used to mitigate their dispersal in other invaded basins in the future.

While extensive removal efforts are underway in well-established reaches of the Ohio River, studies have shown that environmental factors may be acting concurrently to help constrain carp presence and abundance in invaded basins (DeGrandchamp et al. 2008; Calkins et al. 2012; Norman and Whitley 2015). Both large-scale and local-scale invasive carp presence have been attributed primarily to water flow and temperature (Peters et al. 2006; DeGrandchamp et al. 2008; Calkins et al. 2012; Coulter et al. 2016). On a larger spatial scale, invasive carp are known to disperse in response to favorable spawning conditions in both their native (Chapman and Hoover 2016), and invaded systems (Kolar et al. 2005; DeGrandchamp et al. 2008). Both silver and bighead carp exhibit seasonal spawning migrations, where they disperse up to 130 km upstream in response to flow and temperature cues (DeGrandchamp et al. 2008). These migrations typically occur prior to spawning in mid-spring, when water temperatures are increasing but still relatively cool ($>17^{\circ}\text{C}$), and flows are beginning to rise (Kolar et al. 2005; DeGrandchamp et al. 2008). Large-scale dispersal tends to decrease in summer months when water temperatures peak ($>26^{\circ}\text{C}$) and river flows begin to decrease (DeGrandchamp et al. 2008; Coulter et al. 2016). Long distance dispersal events, such as the seasonal spawning migrations of

invasive carp in invaded systems (DeGrandchamp et al. 2008), are known to contribute to the spread of AIS in novel systems (Wilson et al. 2009).

On smaller spatial scales, habitat selection becomes the dominant driver. Bigheaded carps tend to favor low-velocity backwater and avoid the main channels except for spawning, which typically occurs in spring and summer months before the peak of a high flow event, as flows begin to increase (Peters et al. 2006; DeGrandchamp et al. 2008; Calkins et al. 2012). This is likely because it is energetically expensive to occupy the main channel and food resources are less available than in lower velocity backwater habitats (Calkins et al. 2012). However, if water temperatures exceed carp optimal thermal ranges ($>26^{\circ}\text{C}$), they may vacate shallower backwater habitats and seek thermal refuge in other microhabitats such as deeper streams with higher flows (DeGrandchamp et al. 2008). Invasive species spread across an invaded landscape can be impeded if local-scale habitats are unsuitable for their establishment and persistence (With 2002). If conditions in the Ohio River are preventing their large-scale dispersal or local-scale establishment success, especially in the leading edge of invasion, this could limit their continued advancement upstream.

To better understand factors limiting invasive carp occurrence, we applied a multi-scale framework to assess how environmental factors (flow, temperature, habitat) may be acting to impact the spread of bighead and silver carps in the Ohio River across multiple scales. We used a dynamic multi-scale occupancy model (Shepta et al. 2025) to investigate carp colonization and persistence probabilities at three different spatial and temporal scales (annual large-scale, annual small-scale, intra-annual small-scale) simultaneously. Large-scale models were meant to inform on invasive carp distribution and dispersal ability in the Ohio River. We hypothesized that persistence would be higher in downstream reaches and that large-scale colonization would be

positively influenced by high spring flows increasing spawning migrations into upstream pools but negatively influenced by both distance from the source of invasion (i.e., the Mississippi River) and annual removal efforts within the basin. Annual small-scale models were meant to inform on local-scale occurrence. At this scale we hypothesized that annual small-scale persistence would be negatively associated with distance from the source of invasion, local summer flows, elevated summer temperatures, and commercial harvest efforts while colonization would be positively correlated with local flow conditions. Intra-annual models were meant to inform on local-scale habitat use of invasive carp, where changes in local conditions may impact invasive carp occupancy at this scale. We hypothesized that intra-annual persistence and colonization may be influenced by daily changes in local-scale flow, temperature, and habitat types. In combination with colonization and persistence estimates, inferences on bigheaded carps' detection probabilities can inform on relative abundance and status of invasive carp spread in the Ohio River. Results from this study will provide insight into environmental constraints on invasive carp distributions and provide guidance for designing targeted management strategies to reduce their spread throughout invaded U.S. basins.

Methods

Study Area and Data Collection

The Ohio River is 981-miles long spanning from Pittsburgh, Pennsylvania downstream to the southern tip of Illinois where it joins the Mississippi River. It is highly impacted by anthropogenic activities and has been modified from its natural, free-flowing state, into 20 lock and dam pool units. Bighead and silver carp were first documented downstream, near the confluence of the Mississippi River in 1981 and 1984 respectively and have since expanded their invaded range upstream into the Ohio River basin (ICRCC 2022). Pools of the Ohio River can be

categorized into a series of invasion fronts, which describe a gradient of potential carp abundance, reproduction, and recruitment success. This gradient is tied to the distance from the Mississippi River confluence. In order from furthest downstream to furthest upstream, we classify these as establishment front, invasion front, presence front, and uninvaded (Fig. 1). Abundance decreases continuously along this gradient. Recruitment success is thought to decrease upstream of the establishment front and reproduction rates are thought to decrease above the invasion front (MICRA 2021).

To investigate carp occurrence along this gradient, we obtained data from long-term monitoring efforts of invasive carp collected by collaborating agencies (Ohio River Basin Invasive Carp Partnership: U.S. Fish and Wildlife Service, West Virginia Division of Natural Resources, Kentucky Department of Fish and Wildlife Resources, and Indiana Department of Natural Resources) throughout the Ohio River and two of its major tributaries (Green River, Kanawha River). Data for both species was collected annually from 2015 – 2023 across 16 pools of the Ohio River basin. This included 11 pools on the mainstem Ohio River between JT Myers and Hannibal L&D (establishment front = 4, invasion front = 2, presence front = 3, uninvaded = 2), three pools on the Green River (establishment front) downstream of Dam No. 3, and two pools on the Kanawha River (presence front) downstream of Marmet L&D (Fig. 1). Nested within each pool, biologists sampled a series of sites classified as either main channel (Ohio River mainstem) or tributary sites (low velocity habitats including tributaries, backwaters, or floodplain lakes). Agencies sampled between 1 – 84 sites per pool (475 total). Sites were sampled across multiple years but also during multiple visits within the same sampling year. Most of the sampling visits took place between April and October each year, however several sampling events did occur as late as December in 2015, 2022, 2023, and as early as February in

2023. During each visit researchers collected replicate detection/non-detection data for both species using a variety of sampling gears (electrofishing, gillnets, trawls, fyke nets) and identified fish to species in the field.

Dynamic Multi-Scale Occupancy Model

We fit dynamic multi-scale occupancy models following Shepta et al. (2026) to detection/non-detection data for invasive carp to investigate carp persistence and colonization across three spatiotemporal scales: annual pool-level, annual site-level, and intra-annual site-level. Model structure and implementation are detailed in Shepta et al. (2026) and are summarized below. At each scale, we modeled initial occupancy, colonization, and persistence probabilities as functions of environmental covariates, while also accounting for imperfect detection. At the pool level, we assessed long-term patterns of upstream spread between years. Occupancy for pool i in the first year was:

$$z_{i,1} \sim \text{Bernoulli}(\psi_{i,1}),$$

$$\text{logit}(\psi_{i,1}) = \beta_{\psi 0} + \beta_{\psi 1} * x_i.$$

Annual dynamics were governed by persistence ($\phi_{i,t-1}$) and colonization ($\gamma_{i,t-1}$) between years t :

$$z_{it}|z_{i,t-1} \sim \text{Bernoulli}(\phi_{i,t-1} * z_{i,t-1} + \gamma_{i,t-1}(1-z_{i,t-1})),$$

$$\text{logit}(\phi_{i,t-1}) = \beta_{\phi 0} + \beta_{\phi 1} * y_{it},$$

$$\text{logit}(\gamma_{i,t-1}) = \beta_{\gamma 0} + \beta_{\gamma 1} * y_{it}.$$

and annual pool-level parameters ($\psi_{i,1}$, $\phi_{i,t-1}$, and $\gamma_{i,t-1}$) were modeled in response to both static and annual pool-level covariates x_i and y_{it} . At the site level j , nested within pools i , we examined factors influencing the small-scale occurrence of carp. Site occupancy was conditional on pool-level occupancy, where initial annual occupancy was modeled as:

$$s_{ij,1}|Z_{i,1} \sim \text{Bernoulli}(\omega_{ij,1} * Z_{i,1}),$$

$$\text{logit}(\omega_{ij,1}) = \beta_{\omega i0} + \beta_{\omega 1} * w_{ij}.$$

Annual site-level colonization (λ_{t-1}) and persistence (ρ_{t-1}) between years t were modeled as:

$$s_{ijt} | s_{ij,t-1}, Z_{it} \sim \text{Bernoulli}((\rho_{ij,t-1} * s_{ij,t-1} + \lambda_{ij,t-1}(1 - s_{ij,t-1})) * Z_{it}),$$

$$\text{logit}(\rho_{ij,t-1}) = \beta_{\rho i0} + \beta_{\rho 1} * v_{ijt},$$

$$\text{logit}(\lambda_{ij,t-1}) = \beta_{\lambda i0} + \beta_{\lambda 1} * v_{ijt}.$$

and annual site-level parameters ($\omega_{ij,1}$, $\rho_{ij,t-1}$, and $\lambda_{ij,t-1}$) were modeled in response to static and annual site-level covariates w_{ij} and v_{ijt} . At the site-level, we evaluated shorter-term changes in occupancy across visits v nested within a year t . Occurrence during the first visit to site j in pool i during year t was modeled as:

$$a_{ijt,1}|s_{ijt} \sim \text{Bernoulli}(\Theta_{ijt,1} * s_{ijt}),$$

$$\text{logit}(\Theta_{ijt,1}) = \beta_{\Theta i0} + \beta_{\Theta 1} * w_{ij}.$$

Intra-annual site-level colonization (δ_{v-1}) and persistence (ε_{v-1}) between visits v within year t were modeled as:

$$a_{ijtv} | a_{ijt,v-1}, s_{ijt} \sim \text{Bernoulli}((\varepsilon_{ijt,v-1} * a_{ijt,v-1} + \delta_{ijt,v-1}(1 - a_{ijt,v-1})) * s_{ijt}),$$

$$\text{logit}(\varepsilon_{ijt,v-1}) = \beta_{\varepsilon i0} + \beta_{\varepsilon 1} * u_{ijtv},$$

$$\text{logit}(\delta_{ijt,v-1}) = \beta_{\delta i0} + \beta_{\delta 1} * u_{ijtv}.$$

and intra-annual parameters ($\Theta_{ijt,1}$, $\varepsilon_{ijt,v-1}$, $\delta_{ijt,v-1}$) were modeled in response to static and intra-annual site-level covariates w_{ij} and u_{ijtv} . We estimated detection probability p_{ijtvk} using a Bernoulli observation model for each replicate detection/non-detection sample k as:

$$y_{ijtvk} | a_{ijtv} \sim \text{Bernoulli}(p_{ijtvk} * a_{ijtv})$$

$$\text{logit}(p_{ijtvk}) = \beta_{p0} + \beta_{p1} * q_{ijtvk}$$

where detection probability was modeled in response to sample-level covariates q_{ijtk} . We also derived annual finite sample pool-level ($\psi_t^{(fs)}$) and site-level ($\omega_t^{(fs)}$) occupancy. Unlike more traditional occupancy estimates, finite sample equivalents of occupancy are estimated in a Bayesian framework as a function of state-variables (i.e., z_{it} and s_{ijt}) that restrict the scope of interest to the study area (Royle and Kéry 2007). Both pool-level occupancy ($\psi_t^{(fs)}$) and site-level occupancy ($\omega_t^{(fs)}$) calculated as averages within each invasion front to explore possible spatial heterogeneity in carp occupancy across the gradient of invasion.

Variable Selection

Bigheaded carps occurrence is influenced by environmental cues such as changes in flow and temperature, which trigger reproductive behaviors and reflect their underlying life history strategies (Camacho et al. 2023a; Camacho et al. 2023b; Deters et al. 2013). Based on these processes and their current distribution in the Ohio River, we included several covariates for model parameters to test *a priori* hypotheses surrounding invasive carp spread (Table 1 & 2). At the annual pool level, we included distance from the Mississippi River for initial occupancy (ψ_1), persistence (ϕ_{t-1}), and colonization (γ_{t-1}), as the Mississippi River represents the invasion source for carp in this system (Table 1 & 2). We also included average spring flow and annual harvest rates in our model for colonization (γ_{t-1}), because spring flows may trigger upstream movements (DeGrandchamp et al. 2008) and removal efforts may lower density dependent upstream dispersal. At the annual site level, we included distance from Mississippi for initial occupancy (ω_1). We were also interested in differences in carp occurrence between habitat types within pools (main channel versus tributary). Invasive carp are known to prefer low velocity habitats except during spawning (i.e., rising edge of a peak flow event) (Calkins et al. 2012). For site-level annual persistence (ρ_{t-1}), we included habitat type, average local-scale summer flow,

average summer temperature, and annual harvest rates (Table 1 & 2). Local-scale flows and temperature may impact habitat suitability, and harvest rates may lower local-scale persistence. For site-level annual colonization (λ_{t-1}), we included habitat type, distance from source, average local-scale spring flow, and annual harvest, given that carp may colonize new sites during or following spring flow events, but colonization may decrease with harvest efforts (Table 1 & 2).

At the intra-annual site level, we included sampling season as a covariate for initial occupancy (Θ_1), to examine seasonal patterns in occurrence. However, most sampling took place during potential spawning seasons for invasive carp (Coulter et al. 2013), so seasonality was not included in other intra-annual parameters. Within a year, carp tend to prefer low velocity tributary sites with suitable water temperatures; however, they may move to colonize main channel locations following a high flow event. For intra-annual persistence (ϵ_{v-1}) we therefore included flow and maximum water temperature the week prior to sampling, assuming carp tend to persist in low velocity habitats, but may be absent for a site following a spike in water temperature (Table 1 & 2). Intra-annual colonization (δ_{v-1}) reflects movement into previously unoccupied sites and may depend on both current conditions and recent high flow events. We therefore included both flow during sampling and maximum flow the week prior to sampling for our colonization parameter (Table 1 & 2). We expected responses to local-scale environmental variables to vary by habitat type, so we also included interactive effect of categorical habitat type on both flow and temperature variables for annual and intra-annual site parameters (Table 2). Finally, for detection probability we included distance from the Mississippi River (Table 1 & 2), as abundance of both species and consequently detection probability may decline upstream (Royle and Nichols 2003).

Environmental Data Collection and Model Fitting

We collected information on daily flow values from the ORSANCO Ohio River HEC-RAS Community Model (Brunner and CEIWR-HEC 2016), which projects daily flow (cfs) data for ~3000 points along the mainstem of the Ohio River and its major tributaries (Table 1). We averaged daily pool-level flow from three different HEC-RAS points (below the upstream dam, mid-pool, above the downstream dam) within each pool. Daily site-level flow information was measured from the nearest upstream HEC-RAS point to each location. However, the HEC-RAS model did not include flow estimates for smaller tributary streams. We collected additional flow information for smaller streams from USGS stream gages. We used daily pool-level flows to calculate average spring (April – June) and summer (July – September) flows, and daily site-level flows were used to calculate weekly site-level averages (Table 1). We obtained pool-level water temperature (°C) from ORSANCO long-term monitoring (<https://www.orsanco.org/data>) which provides daily temperature measurements in select locations from Monday through Friday. We then included average summer temperature (July – September) for each pool in the model. Local-scale measurements of water temperature were not available in the Ohio River. We calculated distance from source for both pools and sites as the number of river kilometers upstream of the Mississippi River (Table 1). For pools this distance was measured from the downstream dam to the Mississippi River. Data on annual harvest rates of invasive carp (kg removed per year) were provided by the Kentucky Department of Fish and Wildlife Resources who conduct both agency-based and contracted commercial harvest removal efforts throughout the Ohio River basin (Table 1). For analysis, we used the total amount (kg) of fish removed across the entire basin within a given year.

Models were fit separately for each species using the ‘jags’ function in the *jagsUI* package (Kellner and Meredith 2019) in R version 4.3.3. Each model was run using 3 Markov chain

Monte Carlo (MCMC) chains in parallel, discarding the initial 60,000 as burn-in, and thinning by 30, yielding a total of 243,999 MCMC draws across all chains. All model parameters were assigned Normal priors with mean 0 and variance 1 (i.e., $\beta_j \sim \text{Normal}(0,1)$) to reflect weakly informative priors for regression coefficients (Northrup and Gerber 2018). Chains were run until the Brooks-Gelman-Rubin convergence diagnostic indicated adequate convergence ($\hat{R} > 1.1$, Gelman et al. 2021). Convergence and adequate burn-in were also confirmed visually by inspection of trace plots. To focus on estimating the relative effects of covariates within a single hierarchical framework we specified a full model informed by prior ecological understanding and hypotheses (Table 1 & 2). Model parameters were considered influential if their 95% credible intervals did not overlap 0. To further evaluate model fit, we used predictive model checking with Bayesian p -values to assess the goodness of fit of our model for each species (Gelman et al. 1996, Kéry and Royle 2016). A model is considered excellent fitting with Bayesian p -values close to 0.5, and poor fitting with more extreme values (e.g., 0.05 or 0.95). We used the Freeman-Tukey statistics as our test statistic (Kéry and Royle 2016), and estimated Bayesian p -values for our models for each species.

Results

Biologists conducted 2914 detection/non-detection surveys for invasive carp during 1911 sampling visits across the 9-year study period resulting in 829 detections of silver carp and 24 detections of bighead carp. Models for both species appeared to have adequate fit to the observed data (silver carp Bayesian $p = 0.62$, bighead carp Bayesian $p = 0.56$). Due to the low number of detections, parameter estimates for bighead carp models were highly uncertain, with 95% credible intervals often spanning nearly the entire probability scale (0–1). None of our predictor variables (distance from source, harvest rates, flow) were informative in the models for initial

occupancy (ψ_1), persistence (ϕ_{t-1}) or colonization (γ_{t-1}) at the annual pool scale for either species (See Table S1 & S2). Posterior distributions for the model intercepts indicate high baseline probabilities of annual pool-level persistence for both species (silver carp: $\phi_{t-1} = 0.93$, 95% CI [0.75, 0.98]; bighead carp: $\phi_{t-1} = 0.73$, 95% CI [0.31, 0.95]), while estimates of baseline colonization probabilities were highly uncertain (silver carp: $\gamma_{t-1} = 0.72$, 95% CI [0.22, 0.96]; bighead carp: $\gamma_{t-1} = 0.54$, 95% CI [0.10, 0.94]). Pool-level annual occupancy estimates ($\psi_t^{(fs)}$) for bighead carp showed no clear trend over time (see Fig. S1). For silver carp, pool-level occupancy each year ($\psi_t^{(fs)}$) was generally high with variation in different invasion fronts (Fig. 2). In the establishment front $\psi_t^{(fs)}$ was nearly 1.0 every year. In the invasion front $\psi_t^{(fs)}$ started as low as 0.11 (95% CI [0.00, 0.50]) in 2015 increasing to $\psi_t^{(fs)} = 1.0$ in 2016, and stay at 1.0 in 2017, 2018, 2022, and 2023 (Fig. 3B). In the presence front, $\psi_t^{(fs)}$ ranged between 0.26 (95% CI [0.00, 1.00]) and 0.88 (95% CI [0.67, 1.00]), with no clear pattern of increasing over time (Fig. 3C). The uninvaded front was only sampled in 2022 and 2023 and estimates for both years were highly uncertain (Fig. 3D).

Mean annual site-level occupancy ($\omega_t^{(fs)}$) was lower than pool-level estimates for both species (Fig. 3), implying that carp occurrence within pools was spatially heterogenous. Estimates for bighead carp were uncertain and no predictor variables were correlated with initial occupancy (ω_1 , Θ_1), persistence (ρ_{t-1} , ε_{v-1}), or colonization (λ_{t-1} , δ_{v-1}) either annually or intra-annually (see Table S1, Fig. S1 & S2). Silver carp site-level occupancy ($\omega_t^{(fs)}$) remained high in the establishment front and appeared to be increasing annually in the invasion front from 0.02 (95% CI[0.00,0.16]) in 2015 to 0.67 (95% CI[0.48,0.86]) in 2023 (Fig. 3A & B). However, in the presence and uninvaded fronts, site-level occupancy was consistently low and did not appear to be increasing over time (Fig. 3D & C). Silver carp site-level persistence varied in response to

habitat and flow variables (Fig. 4). Initial annual occupancy (ω_1) of silver carp significantly decreased with increasing distance from the Mississippi River (See Table S2). Annual site-level persistence was higher for silver carp in tributary sites ($\rho_{t-1} = 0.97$, 95% CI [0.92, 0.99], $\beta_p = 2.36$, 95% CI [1.59, 3.35]) than in main channel sites ($\rho_{t-1} = 0.66$, 95% CI [0.47, 0.86], $\beta_p = -2.70$, 95% CI [-4.04, -1.35]) (Fig. 4A). However, there was no effect of flow, temperature, or harvest rates on persistence of silver carp at this scale (See Table S2). Silver carp intra-annual persistence also varied between habitat types, with a significant interaction between habitat and flow (Fig. 4B & 4C). Mean intra-annual persistence (ε_{v-1}) in tributary sites was high ($\varepsilon_{v-1} = 0.863$, 95% CI [0.76, 0.95]) and tended to increase with increasing flow ($\beta_e = 0.73$, 95% CI [0.03, 1.60]), however persistence was lower in main channel sites ($\varepsilon_{v-1} = 0.75$, 95% CI [0.52, 0.96]) and decreased with increasing flow ($\beta_e = -1.53$, 95% CI [-2.90, -0.32]; Fig. 4B & 4C). Despite increasing annual occupancy ($\omega_t^{(fs)}$) in the invasion front, silver carp site-level colonization probabilities (λ_{t-1} , δ_{v-1}) were not significantly associated with habitat, flow, or harvest predictors, and intercept estimates overlapped zero ($\beta_{\lambda 0} = 0.32$, 95% CI [-1.85, 2.86], $\beta_{\delta 0} = -0.69$, 95% CI [-3.22, 2.07]; See Table S2). Additionally, posterior estimates for all colonization variables had 95% CI that overlapped 0.5, meaning they were not considered informative (See Table S1 & S2).

In the detection model, intercept estimates indicated moderate detection probability for silver carp ($p = 0.42$, 95% CI [0.32, 0.49]) and very low detection for bighead carp ($p = 0.05$, 95% CI [0.02, 0.12]). For both species, detection significantly decreased with increasing distance from the Mississippi River (silver carp: $\beta_p = -1.55$, 95% CI [-1.96, -1.14], bighead carp: $\beta_p = -0.80$, 95% CI [-1.77, -0.15]; Fig. 5). For silver carp, detection probability was high in downstream reaches, estimated at around 0.87 in downstream pools (JT Myers ~217 km upstream) but then dropped to 0.5 in Markland Pool (~724 km upstream) (Fig. 5A). Upstream

reaches (Willow Island ~1318 km upstream) had the lowest predicted detection probability for silver carp, reaching as low as 0.09 (Fig. 5A). For bighead carp, the mean detection probability was 0.17 in downstream pools (JT Myers ~217 km upstream) but dropped to 0.10 in Newburgh Pool (~391 km upstream) (Fig. 5B). In the furthest upstream reaches (Willow Island ~1318 km upstream) mean bighead carp detection probability was as low as 0.01 (Fig. 5B).

Discussion

Understanding and predicting the secondary spread of AIS is enhanced through a multi-scale investigation of environmental drivers influencing species distributions (Weaver et al. 2012; Hedden et al. 2024). Here, we utilized a multi-scale approach to investigate regional and local-scale trends in invasive carp spread. The spread of invasive carp in the Ohio River appears to be happening slowly, with relative abundance decreasing upstream along the invasion gradient and limited recruitment success above Cannelton pool (MICRA 2021). Assuming detection probability is related to abundance (Royle and Nichols 2003), our findings are consistent with previous research indicating that abundance (i.e., detection probability) of silver carp is lower in upstream reaches. Detection probability of bighead carp was extremely low throughout the basin (19 total detections), which can influence parameter certainty in occupancy models, making trends difficult to determine (McKann et al. 2013). Consequently, below we focus primarily on trends in silver carp occurrence in the Ohio River.

On a large scale, pool-level trends suggest that silver carp have relatively high annual persistence in the establishment and invasion fronts, meaning that once introduced into these pools, populations tended to persist. However, given lack of clear trends in finite sample occupancy probability in the presence front, colonization into upstream pools appears to be happening either infrequently or not at all between sampling years. This suggests that silver carp

invasion may not be progressing or progressing very slowly into upstream pools. At the site level, silver carp persistence was consistently high, whereas colonization was estimated with considerable uncertainty. While high pool-level occurrence suggests that silver carp have dispersed throughout a large range of the Ohio River, site-level occurrence varied substantially between fronts. Increases in site-level occupancy may indicate potential population growth, assuming that as population size increases so does the number of occupied sites within a given pool. Site-level occupancy trends may therefore suggest that population growth may be happening slowly (i.e., invasion front) or not at all (i.e., presence front) further upstream, potentially slowing the progress of silver carp spread in this basin.

Pool-Level Trends

In our study, pool-level trends were meant to inform on annual range expansion of invasive carp in the Ohio River. The spread of invasive species can be thought of as a series of dispersal and establishment events, where spread can be slowed if a species is unable to disperse into new areas or unable to successfully establish populations after dispersal (Davis 2009). For silver carp, previous research hypothesized that dams may limit their dispersal into upstream pools (Chapman and Hoover 2016), thus slowing their spread in the Ohio River. However, individual carp have been detected as far upstream as West Virginia (ICRCC 2022), indicating that dams are incomplete barriers to dispersal as observed in other systems (Coulter et al. 2018). Our results also indicate that invasive carp are present throughout a large range of the Ohio River, with high point-estimates (>50%) for pool-level occupancy in the establishment, invasion, and presence fronts each year. Although silver carp detection probability and potential relative abundance likely decline upstream, especially within the presence front (MICRA 2021). While barriers such as dams have the potential to impact dispersal ability, the dispersal of invasive

species is often also density dependent. Where populations exhibiting high growth rates and high densities can act as sources from which individuals are dispersing, thereby increasing colonization probability into other uninvaded areas (Neubert and Parker 2004; Altwegg et al. 2013). While individual silver carp are able to pass through dams, their spread may be constrained by population growth rates (i.e., establishment success) rather than by dispersal ability alone.

While we did not measure population growth rates in this study, pools in the invasion and presence fronts are not known to have high adult abundances or frequent annual reproduction and recruitment (MICRA 2021; ICRCC 2022). Although adult bigheaded carps were present in these fronts throughout the study, this lack of natural recruitment and potential lower relative abundances may indicate that these pools are sink populations, sustained by immigration from the downstream pools (Bogich and Shea 2008). Similar results were reported in the upper Illinois River, where upstream reaches had low adult densities and no evidence of recruitment (Kallis et al. 2023). Metapopulation analysis revealed that invasive carp abundance in upstream pools was therefore primarily sustained by immigration from the lower Illinois River (Coulter et al. 2018; Kallis et al. 2023). Similar dynamics may be occurring in the Ohio River, with populations in the invasion and presence fronts sustained through immigration from establishment front. Spread in this basin may be influenced by factors limiting establishment and population growth at the leading edge of invasion (Davis 2009).

Site-Level Trends

At the site-level, our results showed that silver carp exhibited clear habitat preferences, with significantly lower annual and intra-annual persistence probabilities at sites located in the main channel compared to tributary sites. This pattern is consistent with their known preference

for low-velocity habitats such as tributary streams or backwaters, where they exhibit moderate site fidelity and strong habitat selectivity (DeGrandchamp et al. 2008; Calkins et al. 2012; Chapman and Hoover 2016; Waters et al. 2017). We found that silver carp exhibited lower intra-annual persistence at main channel sites during extreme flows, which is consistent with previous research suggesting that they may use the main channel on the rising limb of the hydrograph, but seek refuge in tributary locations if flows are too high (Calkins et al. 2012). This is likely because their spawning behaviors are correlated with rising flow (Kolar et al. 2005), but it is energetically costly to occupy the main channel except during spawning events (Calkins et al. 2012). Although silver carp can persist at tributary sites throughout the system, site-level colonization parameters had high uncertainty in our models.

Trends in site-level occupancy differed between fronts. In the establishment front, there was high annual site-level occupancy, indicating that most sites had adult carp every year. Annual site-level occupancy was also increasing consistently in the invasion front, likely reflecting a combination of high site-level persistence and occasional colonization of new sites. This increase in annual site-level occupancy may reflect a potential increase in abundance of silver carp in the invasion front (Royle and Nichols 2003). Frequent natural recruitment has not been observed upstream of the establishment front (MICRA 2021); however, population growth can also be influenced by immigration from neighboring patches (Altwegg et al. 2013). If populations in the establishment front reach high enough densities, this may result in more frequent density-dependent dispersal into the invasion front. In a metapopulation framework, high levels of immigration from neighboring patches are known to contribute to local population growth rates (Altwegg et al. 2013). This suggests that frequent immigration from the establishment front may be contributing to the continued spread of silver carp in the invasion

front, considering evidence of natural recruitment is sparse in this section of river (MICRA 2021). Future research should seek to better estimate the relative abundance of silver carp and the potential for inter-pool immigration, especially in the invasion front where populations appear to be consistently growing over time.

Unlike the invasion front, within the presence front, we did not see increasing site-level occupancy through time. While we consistently observed adult silver carp in this section of river, point-estimates for site-level occupancy in the presence front remained low (<25%). Populations of silver carp are likely persisting in the presence front; however, low site-level occupancy coupled with low detection probabilities indicate that silver carp relative abundance remained low in this section of river throughout our study (Royle and Nichols 2003). Like the invasion front, frequent reproduction and recruitment are not known to occur in presence front (MICRA 2021). Unlike the invasion front, propagule pressure from downstream neighboring pools is likely not yet high enough to increase population growth rates in the presence front. Combined with large-scale trends, these findings suggest that pools in the presence front may currently lack the sustained population growth that would be expected to facilitate their continued expansion into uninvaded reaches of the Ohio River. However, it is unclear how long this trend will continue if populations in the invasion front continue to increase. Clarifying the relative roles of immigration versus local recruitment on silver carp populations in the Ohio River is therefore critical for better understanding factors constraining their spread in this basin.

Management Implications and Conclusions

At large scales, persistence in upstream pools, especially within the invasion front, is likely sustained by immigration from downstream locations. Our results are consistent with the importance of continuing existing management efforts, especially harvest, concentrated at the

leading edge between the establishment and invasion fronts. Reducing immigration from established populations may be key to controlling their continued spread if populations in the Ohio River are sustained through source-sink dynamics, as have been observed in other systems (Mari et al. 2014). While dams may slow dispersal, they are incomplete barriers (Coulter et al. 2018), and invasive carp are present throughout much of the basin, indicating that dispersal limitation alone cannot completely prevent upstream spread. Invasive carp spread may be mitigated by reducing population sizes in source pools (i.e., the establishment front) (Bogich and Shea 2008). Although extensive removal efforts are underway below the invasion front, we did not find a correlation between these removal efforts and colonization or persistence at any scale, and it remains unclear what level of effort is needed to meaningfully disrupt these large-scale metapopulation dynamics (Tsehaye et al. 2013). High uncertainty in site-level colonization estimates may reflect substantial heterogeneity in tributary habitat availability and suitability, with only a subset of sites likely contributing disproportionately to persistence and spread. Small-scale annual and intra-annual persistence remained high, especially in low-velocity tributaries. Future removal efforts may benefit from focusing on these habitats when prioritizing management locations, both to improve the efficiency of targeted harvest and to better resolve local-scale population processes. Further research is needed to evaluate how removal strategies interact with local population processes and to determine whether additional approaches are required to prevent further upstream expansion of invasive carp.

Our multi-scale modeling framework allowed us to disentangle complex invasion dynamics of invasive carp in the Ohio River by separating patterns of range expansion and site usage across spatial and temporal scales. This approach revealed that while carp may be able to disperse and persist throughout much of the Ohio River basin, their detection probability and

site-level occupancy drastically decrease in upstream pools. This indicates that, while carp are capable of dispersing further upstream, they are more likely limited by factors influencing their population growth rates in this basin. If populations are increasing at sites within the invasion front, this suggests that silver carp may continue to expand their invaded range upstream in the Ohio River. By integrating pool-level occupancy, site-level persistence, intra-annual occurrence patterns, and detection-based assumptions on relative abundance, our analysis provides an improved understanding of carp spread dynamics that might have been obscured under more traditional, single-scale approaches (Loo et al. 2009). Incorporating scale-appropriate dynamics is therefore critical for accurately interpreting invasion patterns and informing management decisions in large, regulated river systems.

Statements & Declarations

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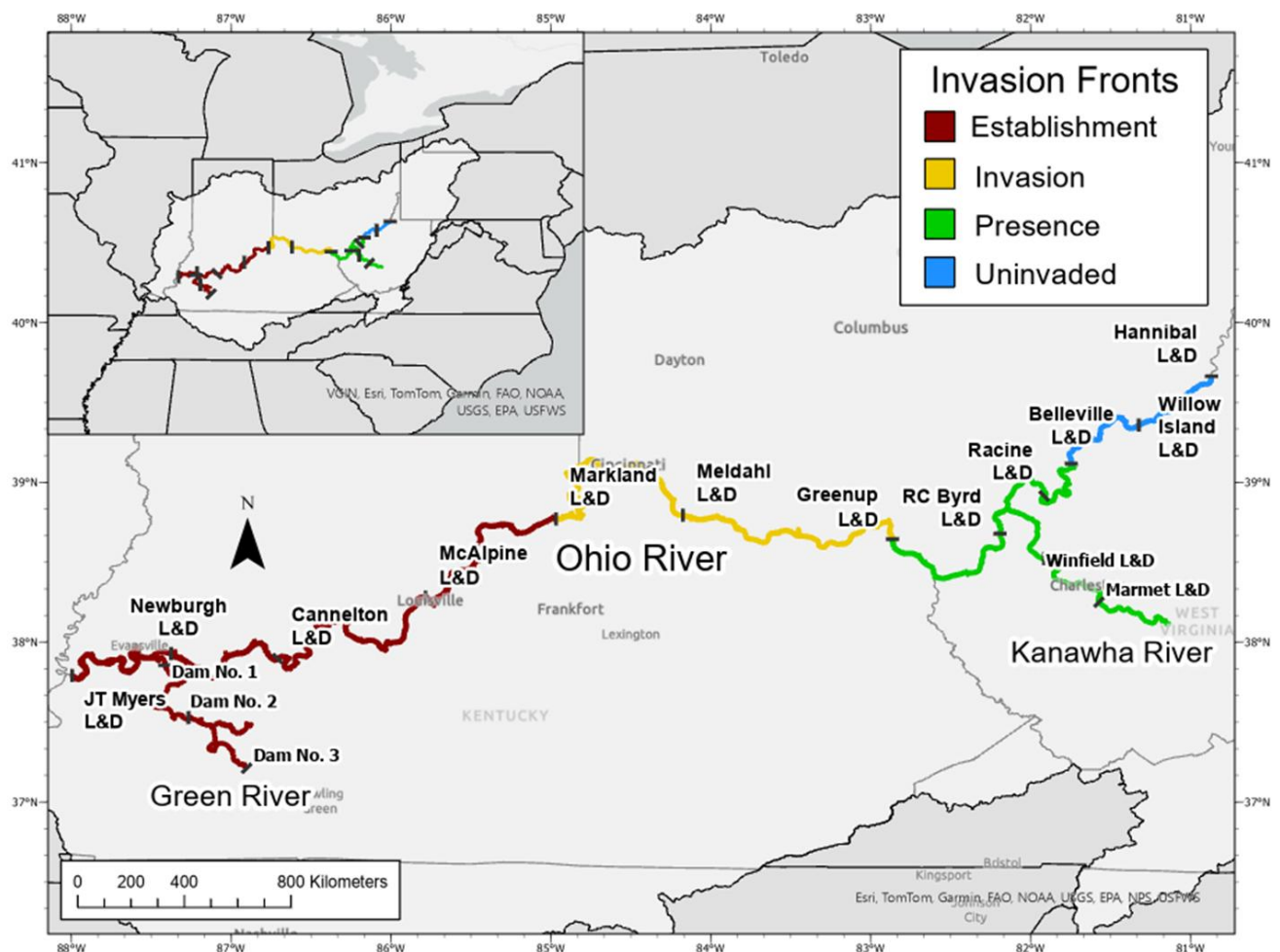


Fig. 1 Map of study area. Dam locations are displayed as black rectangles. The area between two dams are sampling pools, named for the downstream lock and dam. Pools are categorized into different invasion fronts: establishment (red), invasion (gold), presence (green), and uninvaded (blue), corresponding with a gradient of carp abundance, reproduction, and recruitment. Within each pool, researchers visited between 1-84 (475 total) sampling sites (not depicted here).

Table 1. Independent variables used in a dynamic multi-scale occupancy model for invasive bighead (*H. nobilis*) and silver carp (*H. molitrix*) in the Ohio River basin (2015-2023) across multiple scales. We include an explanation for each variable, variable code, and data source. Variable codes correspond to those shown in Table 2.

Variable Definition	Variable Code	Data Source
Distance of downstream dam to the invasion source (Mississippi River, km)	DIST	ArcGIS
Total harvest rate (kg/year) of each species throughout the Ohio River	HR	KYDFWR
Average flow (cfs) in each pool during spring (April - June) spawning season	FLOW_SPR	Brunner and CEIWR-HEC (2016)
Average annual summer (July - September) water temperature (°C)	SUM_TEMP	Ohio River Sanitation Commission
Categorical type (main channel, tributary)	TYPE	Field
Distance of the site to the invasion source (Mississippi River, km)	SITE_DIST	ArcGIS
Average flow (cfs) during spring (April - June) spawning season	FLOW_SPR_S	Brunner and CEIWR-HEC (2016)
Average flow (cfs) during summer (July - September)	FLOW_SUM_S	Brunner and CEIWR-HEC (2016)
Average flow (cfs) during sampling visit	VFLOW	Brunner and CEIWR-HEC (2016)
Maximum flow (cfs) the week prior to sampling	VMAX	Brunner and CEIWR-HEC (2016)
Maximum water temperature (°C) the week prior to sampling	MAX_TEMP	Ohio River Sanitation Commission
Categorical season (spring, summer, fall, winter) of sampling visit	SEASON	Field

Table 2. Independent variables included for each model parameter in a dynamic multi-scale occupancy model for bighead (*H. nobilis*) and silver carp (*H. molitrix*) in the Ohio River basin (2015-2023). We evaluated initial occupancy (ψ_1 , ω_1 , Θ_1), persistence (ϕ_{t-1} , ρ_{t-1} , ε_{v-1}), and colonization (γ_{t-1} , λ_{t-1} , δ_{v-1}) probabilities across three spatiotemporal scales (annual pool, annual site, intra-annual site), while accounting for imperfect detection. Variable definitions provided in Table 1.

Scale	Parameter	Model
Annual Pool	Initial Occupancy (ψ_1)	DIST
	Persistence (ϕ_{t-1})	DIST
	Colonization (γ_{t-1})	DIST + FLOW_SPR + HR
Annual Site	Initial Occupancy (ω_1)	SITE_DIST
	Persistence (ρ_{t-1})	TYPE + FLOW_SUM_S + SUM_TEMP + HR + (TYPE * FLOW_SUM_S) + (TYPE * SUM_TEMP)
	Colonization (λ_{t-1})	TYPE + SITE_DIST + FLOW_SPR_S + HR + (TYPE * FLOW_SPR_S)
Intra-Annual Site	Initial Occupancy (Θ_1)	TYPE + SEASON + (TYPE * SEASON)
	Persistence (ε_{v-1})	TYPE + VFLOW + MAX_TEMP + (TYPE * VFLOW) + (TYPE * MAX_TEMP)
	Colonization (δ_{v-1})	TYPE + VMAX + VFLOW + (TYPE * VMAX) + (TYPE * VFLOW)
Sample	Detection (p)	SITE_DIST

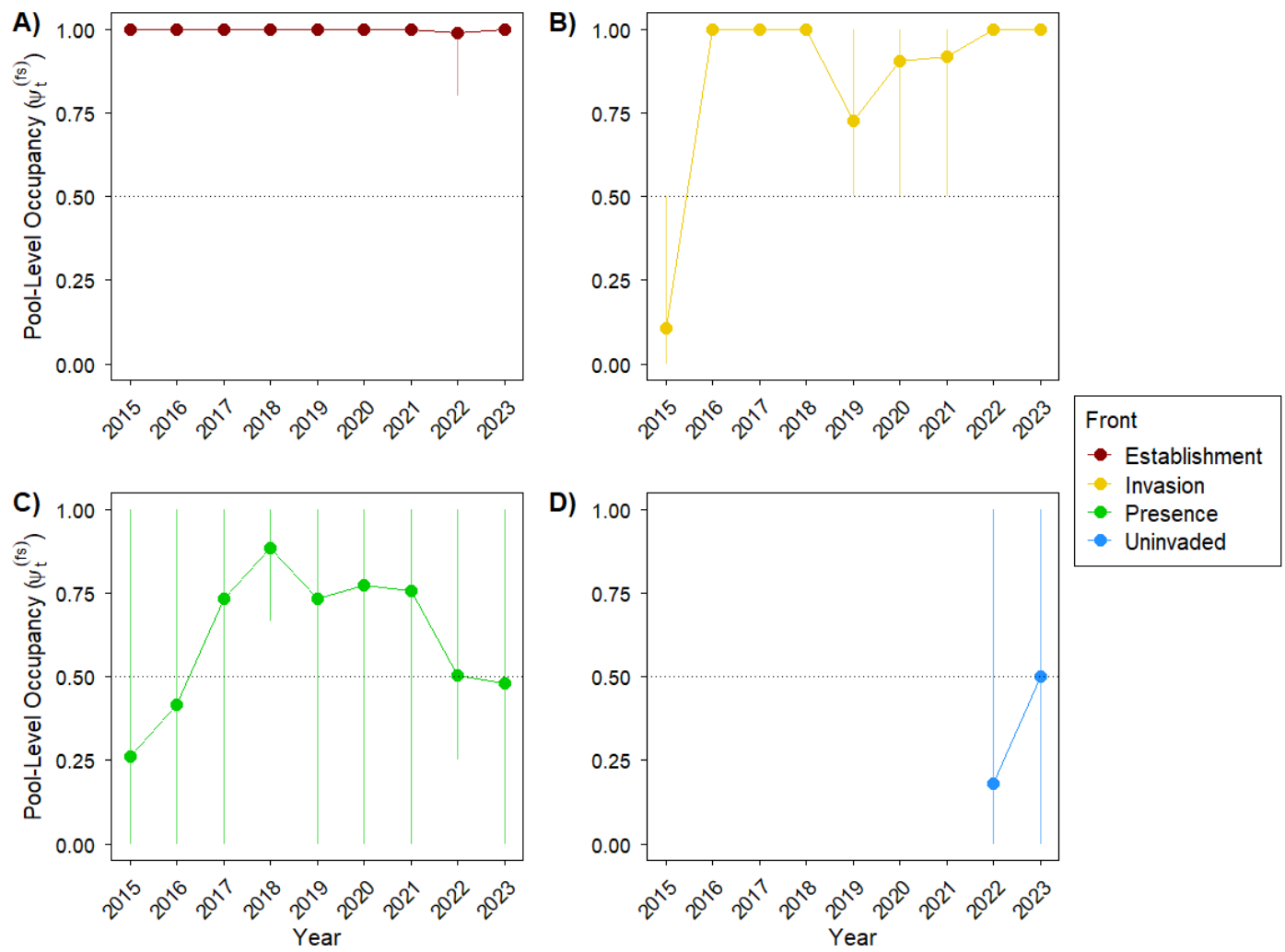


Fig. 2 Estimated annual mean pool-level occupancy probability ($\psi_t^{(fs)}$) and 95% credible intervals (CIs) for silver carp (*H. molitrix*) in different invasion fronts in the Ohio River from 2015 – 2023. Panels show different fronts A) establishment front (red), B) invasion front (gold), C) presence front (green), and D) uninvaded (blue).

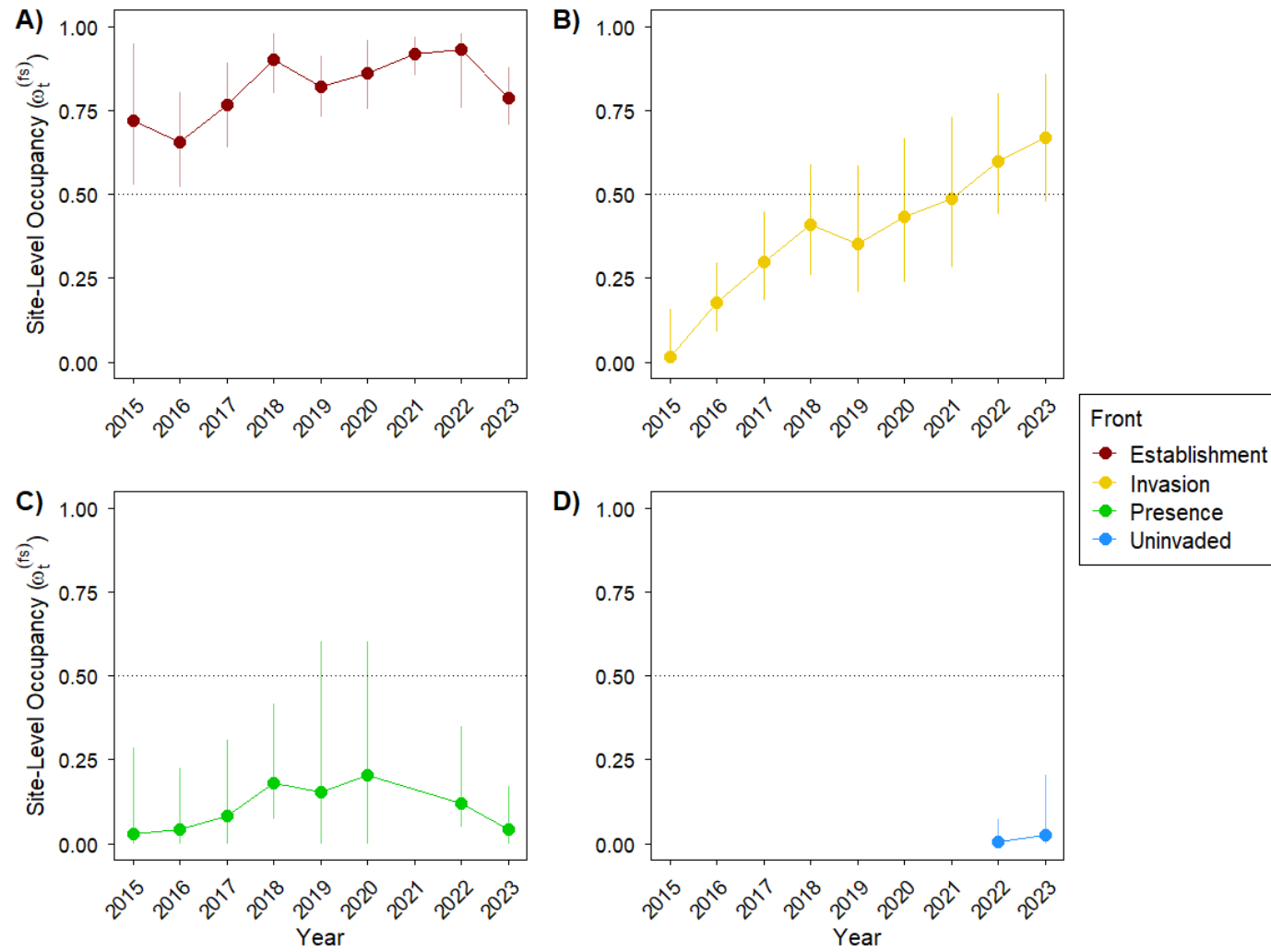


Fig. 3 Estimated annual mean site-level occupancy probability ($\omega_t^{(fs)}$) and 95% credible intervals (CIs) for silver carp (*H. molitrix*) in different invasion fronts in the Ohio River from 2015 – 2023. Panels show different fronts A) establishment front (red), B) invasion front (gold), C) presence front (green), and D) uninvaded (blue).

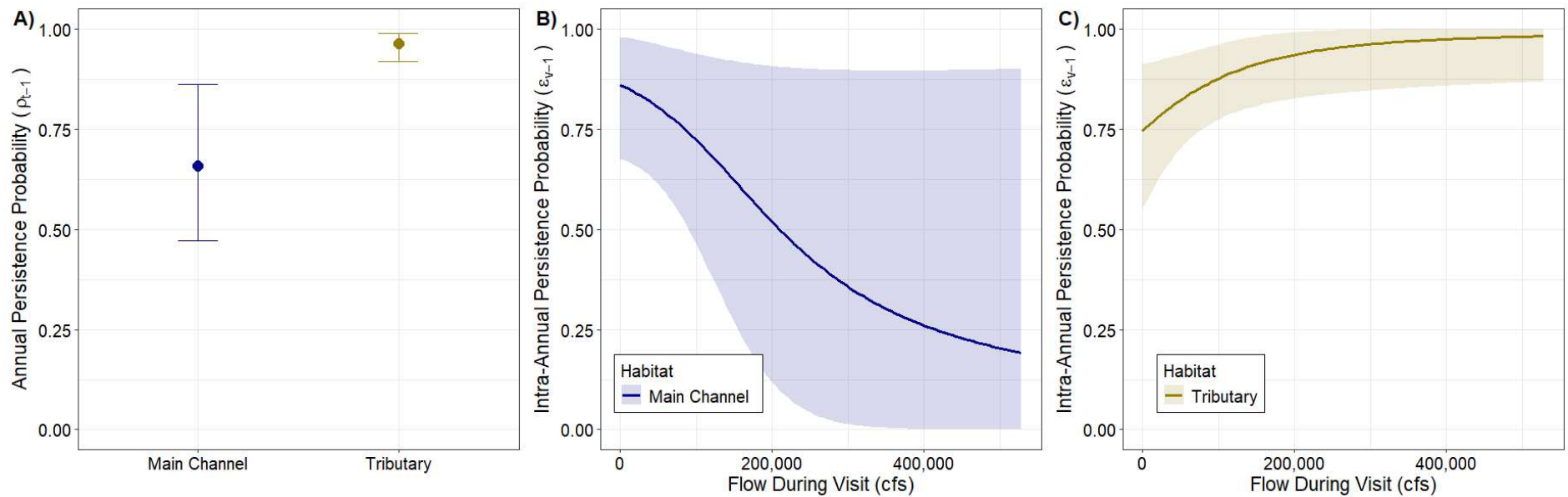


Fig. 4 Trends in silver carp (*H. molitrix*) A) annual persistence probability (p_{t-1}), B) intra-annual persistence probability (ϵ_{t-1}) in main channel sites, and C) intra-annual persistence probability (ϵ_{t-1}) in tributary sites. Annual persistence varied by habitat type while intra-annual persistence varied by habitat and flow (cfs) at each site during the time of sampling. Main channel results are shown in blue and tributary results are shown in gold in each panel.

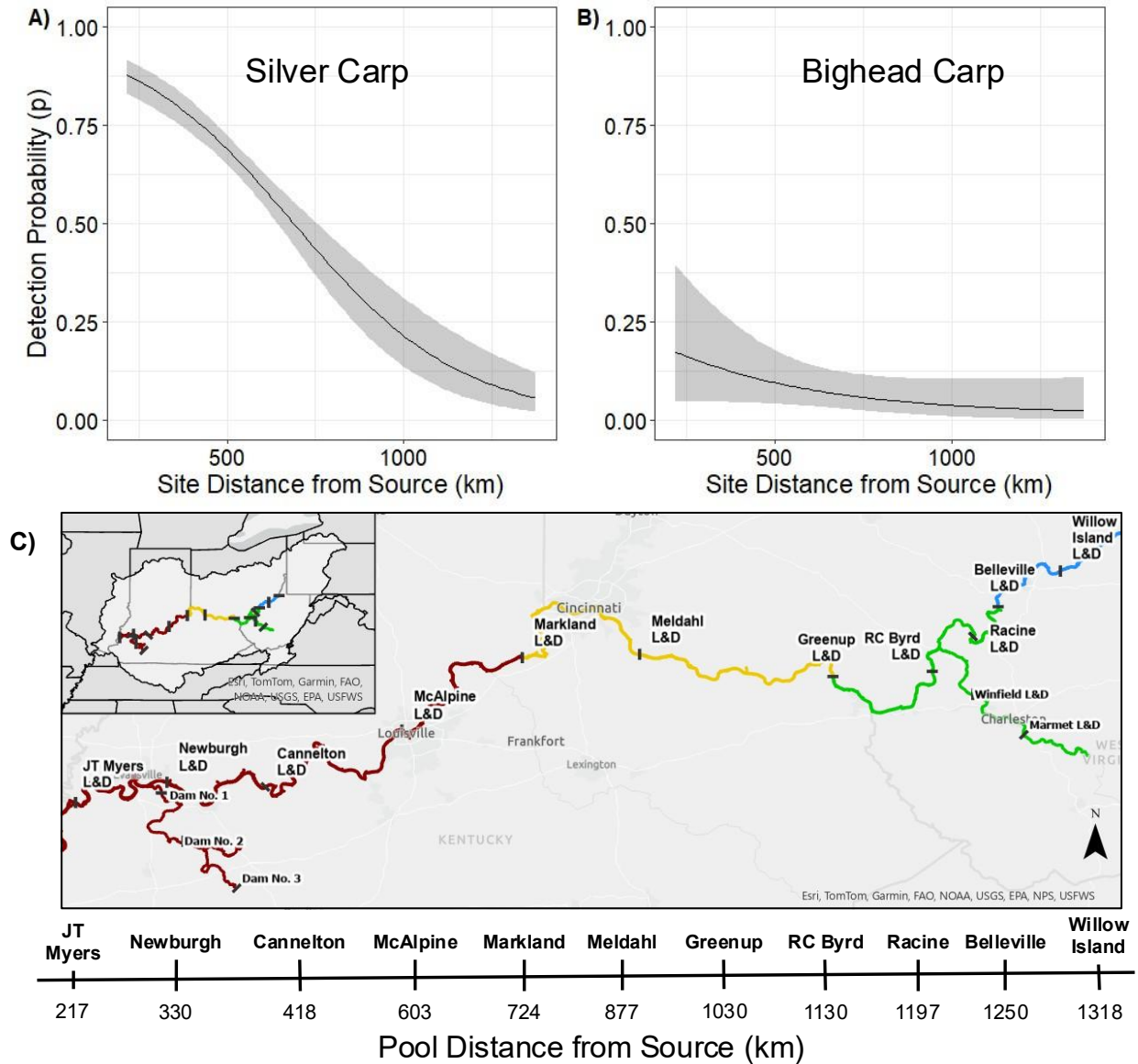


Fig. 5 Relationship between detection probability and distance from the invasion source for A) silver carp (*H. molitrix*) and B) bighead carp (*H. nobilis*) in the Ohio River basin. Lines represent posterior means, and shaded area represents 95% credible intervals (CIs). C) Map depicting study area, with major lock and dams labeled, and approximate distance from source (miles) shown below map. Colors correspond with different invasion fronts (red – establishment, gold – invasion, green – presence, blue – uninvaded).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryMaterials.docx](#)