

Quantifying lock and dam passage, habitat use, and survival rates of invasive carps in the Ohio River

2020 Report

Geographic Location: The Ohio River from river mile RM 937 in Olmsted pool ~20 miles downstream of the Smithland Lock and Dam to river mile 161.7 at the upstream approach of the Willow Island Lock and Dam.

Participating Agencies: US Fish and Wildlife Service (USFWS), Kentucky Department of Fish and Wildlife Resources (KDFWR), Ohio Department of Natural Resources Division of Wildlife (ODNR DOW), West Virginia Division of Natural Resources (WVDNR), Indiana Department of Natural Resources (INDNR)

Statement of Need: Silver and Bighead Carp (*Hypophthalmichthys molitrix* and *H. nobilis*, respectively), herein referred to as invasive carps, are invasive fishes within the Mississippi River Basin. Since they were first detected within the Mississippi River Basin in the early 1980's (Freeze and Henderson 1982; Jennings 1988; Robison and Buchanan 1988; Burr et al. 1996), the range of invasive carps has expanded to include much of the mainstem of the Mississippi River as well as other large rivers within the Mississippi River Basin (e.g., the Ohio, Missouri, and Illinois rivers) (Burr et al. 1996; Garvey et al. 2006; Camacho et al. 2020; Schaick et al. 2020). This rapid expansion throughout the Mississippi River Basin is likely due, at least in part, to rapid population growth resulting from high individual growth rates, short generation times, high fecundity, a protracted spawning period, and long-distance dispersal capabilities (Garvey et al. 2006; Peters et al. 2006; DeGrandchamp et al. 2008; Lenaerts et al. 2021).

Invasive carp populations are established throughout the lower and middle reaches of the mainstem Ohio River as well as many of its tributaries and successful reproduction is suspected as far upstream as Louisville, Kentucky (RM 606.8). The establishment of these populations and the potential for invasive carp populations to expand their range into the upper Ohio River has led to concern among natural resource managers that invasive carps might gain access to the Great Lakes Basin through tributaries of the Ohio River. The Great Lakes and Mississippi River Interbasin Study (GLMRIS) identified six potential routes for aquatic invasive species to access the Great Lakes Basin through tributaries of the Ohio River. If invasive carps were to gain entry to the Great Lakes, they could cause substantial ecological and economic damage by disrupting food webs (Sass et al. 2014; Collins and Wahl 2017) and commercial and recreational fisheries (Pimentel et al. 2000, 2005). Because of the ability of invasive carps to cause extensive economic and ecological damage, limiting the expansion of invasive carp populations into novel habitats is of the utmost concern.

The goal of this study is to better understand the distribution and movement patterns of invasive carps in the middle and upper Ohio River. Improving our understanding of these aspects of invasive carp ecology in the Ohio River will help direct management actions, such as targeted removals and barriers to dispersal, designed to minimize range expansion of these invasive carp populations.

Project Objectives:

1. Understand use of tributaries as potential sources for recruitment and routes of invasion into adjacent basins.
2. Delineate the upstream population distribution and potential for further upstream dispersal.
3. Help inform contract fishing and agency sampling efforts utilizing telemetry data.
4. Quantify passage of Asian carp at Ohio River locks and dams.
5. Estimate probability of survival.

Project Highlights:

- An array of 140 stationary receivers was deployed in the Ohio River during 2020
- ~3.7 million detections of 245 Silver and Bighead carp throughout seven Ohio River pools were recorded during 2020
- The most upstream detections occurred in R.C. Byrd (river mile 237.6) and Racine pools (river mile 203.9) for Silver (2020) and Bighead Carp (2017), respectively
- During 2020, 88% of Silver Carp detections occurred in tributaries compared with 47.9% of Bighead Carp detections
- The estimated annual survival rates of Silver and Bighead Carps were high (0.69 and 0.72, respectively)
- Pool-to-pool transition rates were generally low, suggesting that invasive carps typically remain within the pool in which they were tagged

Methods: Acoustic telemetry was used to determine the probabilities of survival, detection, and lock and dam passage of invasive carps in the lower to middle Ohio River (Olmsted to Willow Island pools). To do this, the locations of individual

invasive carps tagged with VEMCO, Model V16 acoustic tags were recorded using a stationary array of VR2 receivers. Receivers were placed either within the mainstem Ohio River, the lower reaches of select tributaries, or lock and dam (L&D) structures. Within most tributaries, a pair of receivers was deployed, one near the mouth of the tributary and the second further upstream. This arrangement of receivers allows for the interpretation of upstream and downstream movement of tagged carps and improves our ability to assess tributary use as well as the timing of entry into and exit from tributaries throughout the year. For L&Ds, four or five VR2 receivers were deployed at each L&D to record pool-to-pool transitions through the lock chambers with the exception of J.T. Myers, Cannelton, and R.C. Byrd L&Ds. During 2020, J.T. Myers L&D had one receiver deployed at the downstream approach, Cannelton L&D did not have any receivers associated with it, and R.C. Byrd L&D had three receivers deployed, two at the downstream approach and one at the upstream approach. For L&Ds with four or five receivers, two receivers were placed within the lock chamber and at least one receiver was placed on each of the downstream and upstream approach walls. These receivers provide consistent spatial coverage across L&Ds to ensure detection capabilities are similar at each location and increase confidence in interpretation of detection data.

Acoustic receiver array: During 2020, the receiver array extended from river mile 937.0 in Olmsted Pool, ~20 miles downstream of the Smithland L&D, upstream to Willow Island L&D (river mile 161.7). Most VR2 receivers deployed in the mainstem of the Ohio River were retrieved in November 2019 to avoid loss of equipment to ice flows, high water and barge collisions during winter. During April 2020, the mainstem VR2 receivers were redeployed, and downloads and maintenance performed for L&D and tributary receivers. Because receiver loss at tributary and L&D sites is low, most receivers deployed in these locations remained in the system throughout the year. During non-winter months, detection data were downloaded from receivers monthly or as often as possible.

Acoustic Transmitter Tagging: Adult invasive carps were collected via boat electrofishing and gill nets set to block or trap fish. Efforts were concentrated in areas where invasive carps are known to congregate such as side channels, backwaters, and tributaries. Fish were measured for total length (mm) and weight (g), and visually or manually sexed (if possible). Following these measurements, an acoustic transmitter (Vemco, Model V16-6H; 69 kHz) was implanted into the peritoneal cavity via a ~3 cm incision in the ventral musculature. The incision was closed with two or three sutures. The V16-6H transmitters provide individual identification and are nominally programmed to transmit a signal every 40 seconds yielding a battery life of 1,825 days (5 years). Fish implanted with acoustic transmitters were also tagged externally using a lock-on tag inserted posterior to the dorsal fin (Floy Tag & Manufacturing, Inc. FT-4 Lock-on tag with clear over-tubing).

Tributary Use: To assess tributary use by invasive carps, the proportion of detections by month and habitat type (tributary or mainstem) was determined for each species by dividing the number of detections for that species within a month by the total number of detections for that species during June 2013 – December 2020. The proportion of transitions from mainstem to tributary and from tributary to mainstem habitats each month was also assessed for both Silver and Bighead Carps species. To do this, the number of transitions in each direction were summed and divided by the total number of transitions made during June 2013 – December 2020 for each species. Lastly, the time spent between transitions from tributary to mainstem habitat and vice versa was determined for each species as the mean number of days between detections in these two habitat types.

Statistical Analyses: To determine the probabilities of transitions among pools, survival, and detection of invasive carps in the Ohio River, a Multi-state with Live Recaptures analysis was conducted in Program Mark (Cooch and White 2008) using the RMark package (Laake 2013) in R version 4.0.3 (R Core Team 2020). In these analyses the navigation pools of the Ohio River are considered the multiple “states”. Encounter histories were constructed for each individual by determining the pool of the last detection for each month (June 2013 – December 2020). Because receiver coverage was poor below McAlpine L&D all pools below this point were considered a single stratum in the model (Below McAlpine). Additionally, because tagging took place at various times throughout the duration of the study period and the expected battery life of the acoustic transmitters is ~5 years, not all individuals have a complete encounter history (maximum of 91 possible time periods). Encounter histories of tagged carp whose tag battery expired or that were harvested were right-censored. This process removes these individuals from the estimation procedures for the times following tag expiration or harvest. Additionally, because direct transitions among non-adjacent pools are not possible, all transitions probabilities for non-adjacent pools were fixed to 0.

Encounter histories were used to inform transition, survival, and detection estimates in species-specific, multi-state models. More than 2,500 models were constructed for each species, Silver and Bighead Carp. Models included temporally and spatially invariant parameters, as well as those that varied temporally (by month or season) and/or spatially (by pool). Additional covariates included individual mass (all parameters) and distance to the nearest L&D (transition probability only). Additive and interactive effects of covariates were also considered. Models were compared using Akaike's

information criterion corrected for small sample size (AIC_c) to find the most parsimonious model; a lower AIC_c value indicates greater support for that model. However, models that are within two AIC points of one another are considered to have equal support from the data. Support for each covariate included in the top-ranked models was assessed using AIC weights. A variance inflation factor (\hat{c}) was also calculated for the most parameterized model in the model set [S(pool * month)p(pool * month) ψ (pool * month)] for each species, using the median \hat{c} procedure in Program Mark, to assess overdispersion in the models (Cooch and White 2008). If \hat{c} differed substantially from one, the AIC_c values for all models were adjusted by \hat{c} and the most parsimonious model was assessed using the quasi-Akaike's information criterion ($QAIC_c$). Values of \hat{c} between one and three are considered acceptable (Lebreton et al. 1992).

Results and Discussion:

Acoustic Receiver Array: During 2020, the majority of receivers ($n = 120$; $\sim 86\%$) were deployed from McAlpine L&D upstream to Willow Island L&D (Figure 1, Table 1). Of these, 28 were deployed at L&Ds, 47 at mainstem sites, and 45 at tributary sites. Concurrent catfish telemetry studies led by the Ohio Department of Natural Resources and the West Virginia Division of Natural Resources in Meldahl and R.C. Byrd pools, respectively have led to increases in receiver coverage in these upstream pools, providing greater coverage and demonstrating the utility of maintaining a robust receiver array that can serve the needs of multiple natural resource management agencies.

Fish Tagging Efforts: As of December 2020, 686 invasive carps (640 Silver and 46 Bighead) from Cannelton, McAlpine, Markland, Meldahl, and R. C. Byrd pools have been surgically implanted with acoustic transmitters (Table 2). Of the 686 tagged carps, 14 Silver Carps have been harvested during the study (2013 – 2020). During 2020, 38 invasive carps (31 Silver and 8 Bighead) had tags that were expected to expire. To replace tags that were expected to expire (Table 2) and meet the needs of partner agencies, 118 Silver Carp were tagged in McAlpine ($n = 100$) and Markland ($n = 18$) pools. No Bighead Carp were tagged during 2020 due to a lack of availability.

Fish Detections: There were 556 active tags deployed in invasive carps (531 Silver and 25 Bighead) in the Ohio River during 2020, 245 (44%) of which were detected (236 Silver and 9 Bighead). Active tags included those expected to be active during 2020 as well as those expected to expire prior to 2020 that were detected. These tags accounted for ~ 3.7 million individual detections during 2020. Included in the 556 active tags were 68 tags deployed in Silver Carp that were tagged below the last receiver in Cannelton Pool (River Mile 662.8). Because receiver coverage in the lower portions of Cannelton Pool and those pools below Cannelton L&D (Newburgh, J.T. Myers, Smithland, and Olmsted) was poor during 2020 (Figure 1, Table 1), the probability of detecting these fish was low. Plans are in place to expand the receiver array in Cannelton, Newburgh, and J.T. Myers pools during 2021. Expanding the receiver array into these areas will increase the probability of detecting tagged carp in the lower Ohio River and improve our ability to quantify the movement and dam passage of invasive carps in these areas.

Fish Movement: Throughout the study area, the net movement (i.e., the difference between the most upstream and most downstream detections for an individual) ranged from 0.0 km to 299.8 km for Silver carp and from 1.1 km to 119.3 km for Bighead Carp during 2020. The longest net movement by a Silver Carp was completed by a male fish travelling from Meldahl Pool to R.C. Byrd Pool during January – October. In contrast, the longest net movement by a Bighead Carp during 2020 was completed by a male fish that remained within Meldahl Pool during April – December. Long-distance movements are relatively rare for Silver Carp; $\sim 73\%$ of Silver Carp had a maximum distance travelled of < 30 km during 2020. In contrast, only $\sim 33\%$ of Bighead Carp had a maximum distance travelled of < 30 km.

The most upstream detections for Silver and Bighead Carp during 2020 were at river mile 237.6 within the Racine L&D lock chamber and at river mile 265.5 near the Kanawha River, respectively. For Silver Carp, this was also the most upstream detection throughout the duration of the study (2013 – 2020), whereas for Bighead Carp a fish was detected at two receivers at river mile 203.9 during 2017. One receiver was located at the downstream approach to the Belleville L&D and the other was within the lock chamber.

Because there were relatively few detections of invasive carps in the pools downstream of McAlpine L&D and upstream of Greenup L&D, further analysis of fish movement during 2020 focused on McAlpine, Markland, and Meldahl pools only. In these pools, net movements are typically shortest during November – March and peak during summer (June – September) regardless of species or pool (Figures 2 and 3, Table 3). These results are similar to those reported in previous years.

Dam Passage: Throughout the duration of this study (June 2013 – December 2020), there have been 81 dam passage events (32 upstream and 49 downstream passages) (Figure 4). Dam passages were completed by 45 Silver Carp and six Bighead Carp. Of the upstream passages, four (12.5%) were completed by two Bighead Carp, with one fish accounting for three of those passages as it moved from Meldahl Pool to Racine Pool during May 2014 – August 2015. Twenty-eight upstream passages (87.5%) were completed by 23 Silver Carp. Four downstream passages (8.2%) were completed by four

Bighead Carp, whereas 45 (91.8%) were completed by 37 Silver Carp. Additionally, in only three of the 81 dam passages was the fish detected within the lock chamber suggesting a high prevalence of passages through the dam gates. Passages where fish were detected within the lock chamber occurred at Meldahl L&D during April 2016 (Silver Carp) and February 2018 (Bighead Carp) and at Newburgh L&D during July 2019 (Silver Carp). All lock chamber passages were in the downstream direction.

The current arrangement of VR2 receivers around most L&D structures in the study area and their year-round deployment suggests a high probability of detecting invasive carps transitioning among pools through lock chambers. However, pool-to-pool transitions occasionally are not detected. This is most likely to occur if fish pass over the dam in a downstream direction, but it is also possible during open water conditions for fish to navigate through gate openings without being detected.

Tributary Use: During 2020, 88.0% of Silver Carp detections occurred in tributaries of the Ohio River, whereas 47.9% of detections of Bighead Carp occurred in these areas. Only 50 receivers were deployed in tributaries versus 90 in mainstem and L&D habitats during this time. Throughout the duration of this study (2013 – 2020), 79.6% of Silver Carp detections and 69.8% of Bighead Carp detections occurred in tributaries.

During June 2013 – December 2020, mainstem and tributary habitat use appeared to differ by species. For Silver Carp, the proportion of detections in tributaries far exceeded those in mainstem habitats, regardless of month. In contrast, a higher proportion of Bighead Carp detections occurred in mainstem habitat during August and September, but the proportion of tributary detections exceeded those in the mainstem Ohio River during all other months. The proportion of detections that occurred in mainstem habitat peaked for both species during August – November (Figure 5). This is consistent with a greater proportion of transitions between tributary and mainstem habitat occurring during summer and autumn for both species. The proportion of transitions from mainstem to tributary habitats and vice versa are similar within months (Figure 6). Interestingly, the data also suggest that when Silver Carp enter tributaries, they reside there for a mean of 20.7 days (SE = 0.8 days) before returning to mainstem habitat. In contrast, Silver Carp reside in the mainstem Ohio River for a mean of 12.5 days (SE = 0.7 days) before returning to tributary habitat. Bighead Carp spend a similar amount of time between transitions in tributary (mean \pm SE = 18.2 \pm 3.8 days) and mainstem (18.9 \pm 4.0 days) habitats (Figure 7). These data suggest that tributaries provide important habitat for invasive carps, especially Silver Carp.

Model Results: For Silver Carp, the variance inflation factor (\hat{c}) was 2.52. Model results were, therefore, adjusted to account for overdispersion and QAIC_c values used to determine the most parsimonious models. QAIC_c indicated that only one model had a Δ QAIC_c value ≤ 2 (Table 4). This model included survival probabilities (S) that varied by fish weight (g) and month and detection and transition probabilities (p and ψ , respectively) that varied based on the interaction of pool and season. The QAIC weight of 0.93 for this model indicates a high degree of certainty in model selection and the QAIC weights indicate that the most parsimonious model [S(weight + month) p (pool * season) ψ (pool * season)] is ~18.6 times better supported than the next most parsimonious model.

The mean probability of survival (S) of Silver Carp varied by fish weight (g) and month and were generally highest for larger fish (Figure 8) and in cooler months (i.e., November – March; Figure 9). Because there was a significant effect of fish weight in the model for Silver Carp, parameter estimates for Silver Carp assume a mean weight of 7022.9 g.

Although mean survival probabilities were generally high (≥ 0.97), June and October had lower mean probabilities of survival (0.88 and 0.93, respectively). Monthly mean survival probabilities yielded a mean annual survival probability of 0.69 (95% Confidence Interval (CI) = 0.00 – 0.81). The large confidence interval around the mean annual survival probability is due to the low precision of survival probability estimates for February and March. Because there are few documented cases of tagged silver carp being harvested from the Ohio River, the annual survival probability was used to estimate annual natural mortality (mean = 0.31, 95% CI = 0.19 – 1.00).

Estimated mean detection probabilities (p) were affected by the interaction of pool and season for Silver Carp and ranged from 0.030 below McAlpine Pool during winter to 0.988 in Meldahl Pool during spring (Figure 10). Additionally, detection probabilities were lowest below McAlpine and in Greenup pools and highest in McAlpine and Meldahl pools, regardless of season. Because there were few fish detected above Greenup L&D, detection probabilities could not be estimated for all seasons.

For Silver Carp, model estimates of mean transition probabilities (ψ) varied with the interaction of pool and month and indicate that, with the exception of Greenup and R.C. Byrd pools, probabilities of transitions among pools were low (0.000 – 0.213) and probabilities of remaining within a pool were high (0.787 – 1.000; Table 6). Mean transition probabilities were highly variable and could be exceptionally high for Greenup and R.C. Byrd pools (0.000 – 0.733). Mean transition rates were often highest during winter and spring and lowest during summer (Table 6).

For Bighead Carp, AIC_c indicated that three models were similarly supported by the data ($\Delta AIC_c \leq 2$, Table 5). These models included survival probabilities (S) that were invariant to all covariates included in the models, as well as those that varied with fish weight (g), detection probabilities (p) that varied with the additive or interactive effect of pool and season, and transition probabilities (ψ) that varied by pool. Although the relatively low AIC weights for the best supported models suggest a high degree of model selection uncertainty. AIC weights (which sum to 1 across all models) suggest substantial support for the inclusion of an invariant survival probability (AIC weight = 0.63), the additive effect of pool and season on detection probabilities (AIC weight = 0.52), and pool-varying transition probabilities (AIC weight = 0.92). Additionally, the AIC weights indicate that the most parsimonious model [S(.)p(pool + season) ψ (pool)] is ~1.2 times better supported than the next most parsimonious model. Based on these results, we interpreted the parameter estimates of the most parsimonious model only.

The estimated mean monthly survival probability (S) of Bighead Carp was 0.97 (95% Confidence Interval (CI) = 0.96 – 0.98) yielding a mean annual survival estimate of 0.72 (95% CI = 0.64 – 0.80). Because there has been no documented harvest of tagged Bighead Carp, we believe that the annual survival rate also provides a robust estimate of natural mortality (mean = 0.28, 95% CI = 0.20 – 0.36).

Estimated mean detection probabilities (p) varied by pool and month for Bighead Carp and ranged from 0.005 in McAlpine Pool during winter to 0.976 in Meldahl Pool during summer (Figure 11). Detection probabilities were lowest during winter and highest during summer regardless of pool. Additionally, detection probabilities were lowest in McAlpine and Greenup pools and highest in Markland and Meldahl pools, regardless of season.

Model estimates of mean transition probabilities (ψ) indicate that transitions among pools were rare; probabilities of pool-to-pool transitions ranged from 0.000 to 0.127, whereas the probability of fish remaining in the same pool from month to month ranged from 0.873 to 1.000 (Table 7). Mean transition probabilities were highest for the middle three pools investigated here (Markland, Meldahl, and Greenup) and were lowest at the extremes of the sample area (Below McAlpine and McAlpine pools in the west and R.C. Byrd and Racine pools in the east).

Recommendations: The current array of acoustic receivers in the Ohio River is well-established from McAlpine Lock and Dam (L&D) to Willow Island L&D but coverage gaps do exist. For instance, the removal of mainstem receivers for overwinter storage reduces coverage and detection probabilities during winter and early spring. Changes in site selection in recent years (e.g., bridge piling mounts) have reduced receiver loss and increased the potential for year-round receiver deployments in the mainstem of the Ohio River and further adjustments to the deployment methods for more mainstem receivers has the potential to increase the coverage of and the detection probabilities in mainstem habitats during winter and early spring. Another coverage gap exists near L&D structures. Current receiver deployments provide consistent year-round coverage of the lock chambers of most L&Ds between McAlpine and Willow Island. However, coverage near the gates of dams is lacking and could enhance our knowledge of pool-to-pool transitions as well as improve our ability to determine if L&D passages are primarily occurring through the lock chambers or through the dam gates. However, site selection near dam gates requires careful consideration because deploying stationary receivers in these areas is logistically challenging and raises concerns for the safety of agency personnel that would be tasked with downloading and maintaining the receivers. For instance, in previous years, receivers were mounted on hazard buoys, deployed by the U.S. Army Corps of Engineers during the boating season, that mark the boundaries of the safe navigation areas near dam gates. Due to the inconsistent timing of the deployment of these buoys, the relatively short deployment period, and reduced stability of these buoys relative to navigational buoys which resulted in increased receiver loss, receivers are no longer deployed on these hazard buoys and other sites should be considered. Depending on the availability of other buoys or structures suitable for receiver deployment, these sites may need to be further upstream or downstream of the dam structure to provide appropriate coverage and allow agency personnel to safely access these receivers.

Currently, INDNR is working to expand the array throughout Cannelton and J.T. Myers pools with the addition of ~30 receivers, which will allow these pools to be treated independently in future analyses. Further expansion of the receiver array in Newburgh, Smithland, and Olmsted pools is also recommended to solidify detection probabilities, strengthen survival estimates and capture pool-to-pool movement that occurs in the lower Ohio River. Invasive carp densities are also much greater in the lower pools of the Ohio River; understanding pool-to-pool transition rates in high-density pools and the net gain or loss due to these movements will be important to informing future management plans focused on reducing invasive carp populations and limiting their upstream spread. Furthermore, detections in Lake Barkley of Silver Carp tagged in Cannelton Pool indicates a need to understand the relationship between the Tennessee-Cumberland River system and the Ohio River. Specifically, understanding the movement of invasive carps between these systems is critical to managing these populations and may elucidate movement patterns of invasive carps as it relates to deterrent technologies at Barkley Lock (e.g., do fish move away from the barrier at Barkley Lock and instead move upstream within the mainstem Ohio River?). Increasing receiver coverage in the lower pools of the Ohio River (Olmsted –

Cannelton pools) will increase our understanding of broad-scale movement patterns of invasive carps in the Ohio River Basin, as well as the importance of those downstream source populations to the upstream movement of these species.

In addition, because Silver Carp are more abundant than Bighead Carp in the Ohio River, account for the majority of tagged individuals and detections in this system, and show a propensity for tributary use, we recommend increasing receiver coverage in tributaries of the Ohio River. Increasing receiver coverage in tributaries would contribute to our understanding of habitat use and the conditions that lead to Silver Carp moving into and out of tributaries. This knowledge would also allow us to better estimate Silver Carp population size and survival and would provide information for management actions such as targeted removals.

Lastly, data management will continue to be vital as the telemetry program adds to the existing data set. Increases in the number of invasive carps tagged in the Ohio River are anticipated, especially within the lower pools of the Ohio River as the array is expanded. These increases in the numbers of tagged fish are anticipated to substantially increase detections and, therefore, data management needs. Front-end data management and data processing capability will become increasingly important to ensure that data are available for analysis in a timely manner.

Literature Cited

- Burr, B. M., D. J. Eisenhour, K. M. Cook, C. A. Taylor, G. L. Seegert, R. W. Sauer, and E. R. Atwood. 1996. Nonnative Fishes in Illinois Waters: What Do the Records Reveal? *Transactions of the Illinois State Academy of Science* 89(2):73–91.
- Camacho, C. A., C. J. Sullivan, M. J. Weber, and C. L. Pierce. 2020. Invasive Carp Reproduction Phenology in Tributaries of the Upper Mississippi River. *North American Journal of Fisheries Management*:1–13.
- Collins, S. F., and D. H. Wahl. 2017. Invasive planktivores as mediators of organic matter exchanges within and across ecosystems. *Oecologia* 184(2):521–530. Springer Berlin Heidelberg.
- Cooch, E. G., and G. C. White, editors. 2008. Program MARK A Gentle Introduction.
- DeGrandchamp, K. L., J. E. Garvey, and R. E. Colombo. 2008. Movement and Habitat Selection by Invasive Asian Carps in a Large River. *Transactions of the American Fisheries Society* 137(1):45–56.
- Freeze, M., and S. Henderson. 1982. Distribution and Status of the Bighead Carp and Silver Carp in Arkansas. *North American Journal of Fisheries Management* 2(2):197–200.
- Garvey, J. E., K. L. DeGrandchamp, and C. J. Williamson. 2006. Life history attributes of Asian carps in the Upper Mississippi River System. ANSRP Technical Notes Collection (ERDC/EL ANSRP-07-1), U.S. Army Corps of Engineer Research and Development Center. Vicksburg, MS.
- Jennings, D. P. 1988. Bighead Carp (*Hypophthalmichthys nobilis*): A Biological Synopsis.
- Laake, J. L. 2013. RMark: An R interface for analysis of capture-recapture data with MARK. Page AFSC Processed Rep. 2013-01, 25 p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.
- Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62(1):67–118.
- Lenaerts, A. W., A. A. Coulter, K. S. Irons, and J. T. Lamer. 2021. Plasticity in Reproductive Potential of Bigheaded Carp along an Invasion Front. *North American Journal of Fisheries Management*:10.1002/nafm.10583.
- Peters, L. M., M. A. Pegg, and U. G. Reinhardt. 2006. Movements of Adult Radio-Tagged Bighead Carp in the Illinois River. *Transactions of the American Fisheries Society* 135(5):1205–1212.
- Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. *BioScience* 50(1):53–65.
- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52(3 SPEC. ISS.):273–288.
- R Core Team. 2020. R: A language and environment for statistical computing. Page R Foundation for Statistical Computing. Vienna, Austria.
- Robison, H. W., and T. M. Buchanan. 1988. *Fishes of Arkansas*. University of Arkansas Press, Fayetteville.
- Sass, G. G., C. Hinz, A. C. Erickson, N. N. McClelland, M. A. McClelland, and J. M. Epifanio. 2014. Invasive bighead and silver carp effects on zooplankton communities in the Illinois River, Illinois, USA. *Journal of Great Lakes Research* 40(4):911–921.
- Schaick, S. J., C. J. Moody-Carpenter, E. L. Effert-Fanta, K. N. Hanser, D. R. Roth, and R. E. Colombo. 2020. Bigheaded Carp Spatial Reproductive Dynamics in Illinois and Wabash River Tributaries. *North American Journal of Fisheries Management*:1–11.

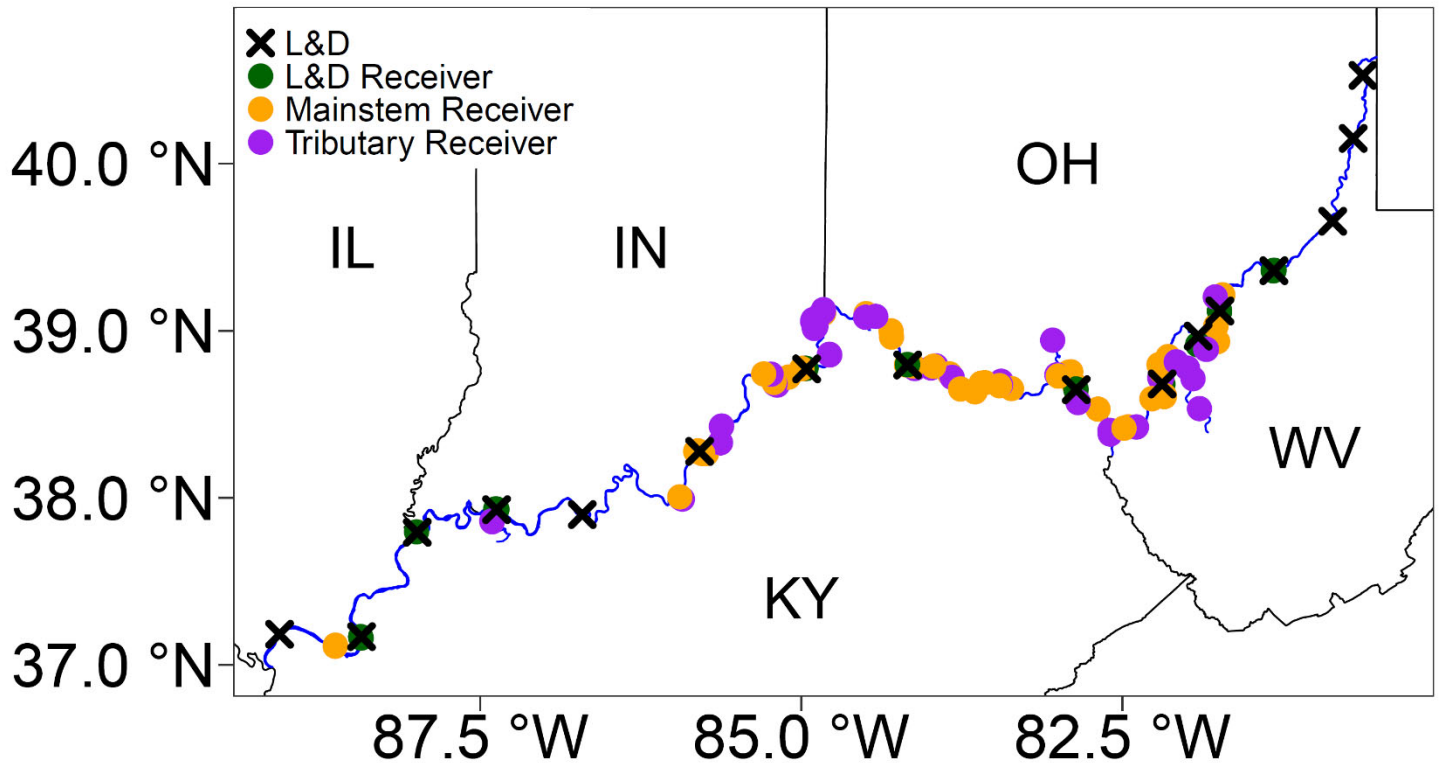


Figure 1. Locations of Lock and Dam structures (L&D; black crosses) and acoustic receivers deployed at L&D structures (green circles) and in the mainstem (orange circles) and tributaries (purple circles) of the Ohio River during 2020. Map shows the Ohio River (blue) from its confluence with the Mississippi River in the west to the Pennsylvania border in the east. Receivers were deployed from Olmsted Pool, downstream of the Smithland L&D, to the Willow Island L&D. From west to east, the L&Ds are Olmsted, Smithland, J.T. Myers, Newburgh, Cannelton, McAlpine, Markland, Meldahl, Greenup, R.C. Byrd, Racine, Belleville, Willow Island, Hannibal, Pike Island, and New Cumberland. Ohio River pools are named for the downstream L&D (e.g., Olmsted Pool begins at Olmsted L&D and ends at Smithland L&D).

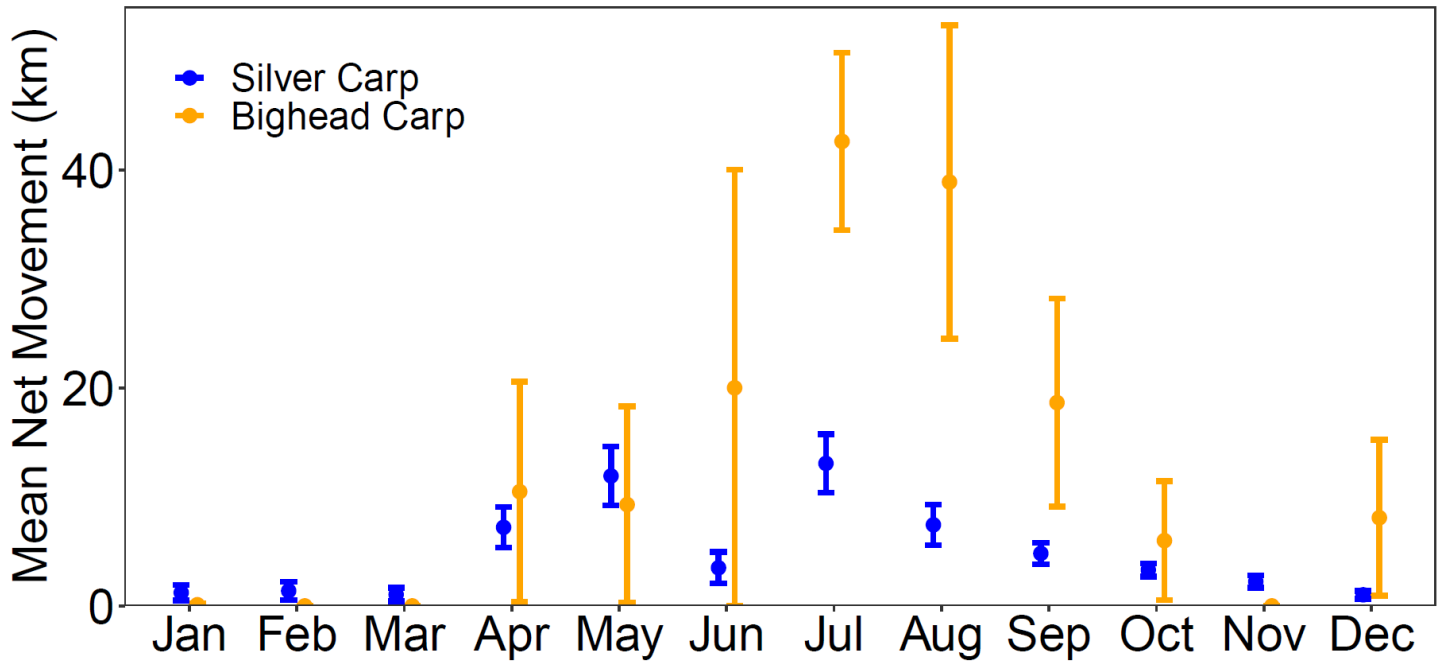


Figure 2. The mean monthly net movements (river kilometers) between the most upstream and downstream detections for tagged Silver Carp (blue) and Bighead Carp (orange) in McAlpine, Markland, and Meldahl pools during 2020. Error bars represent standard error. Only tagged carp detected ≥ 2 times during a month were included in the distance calculations.

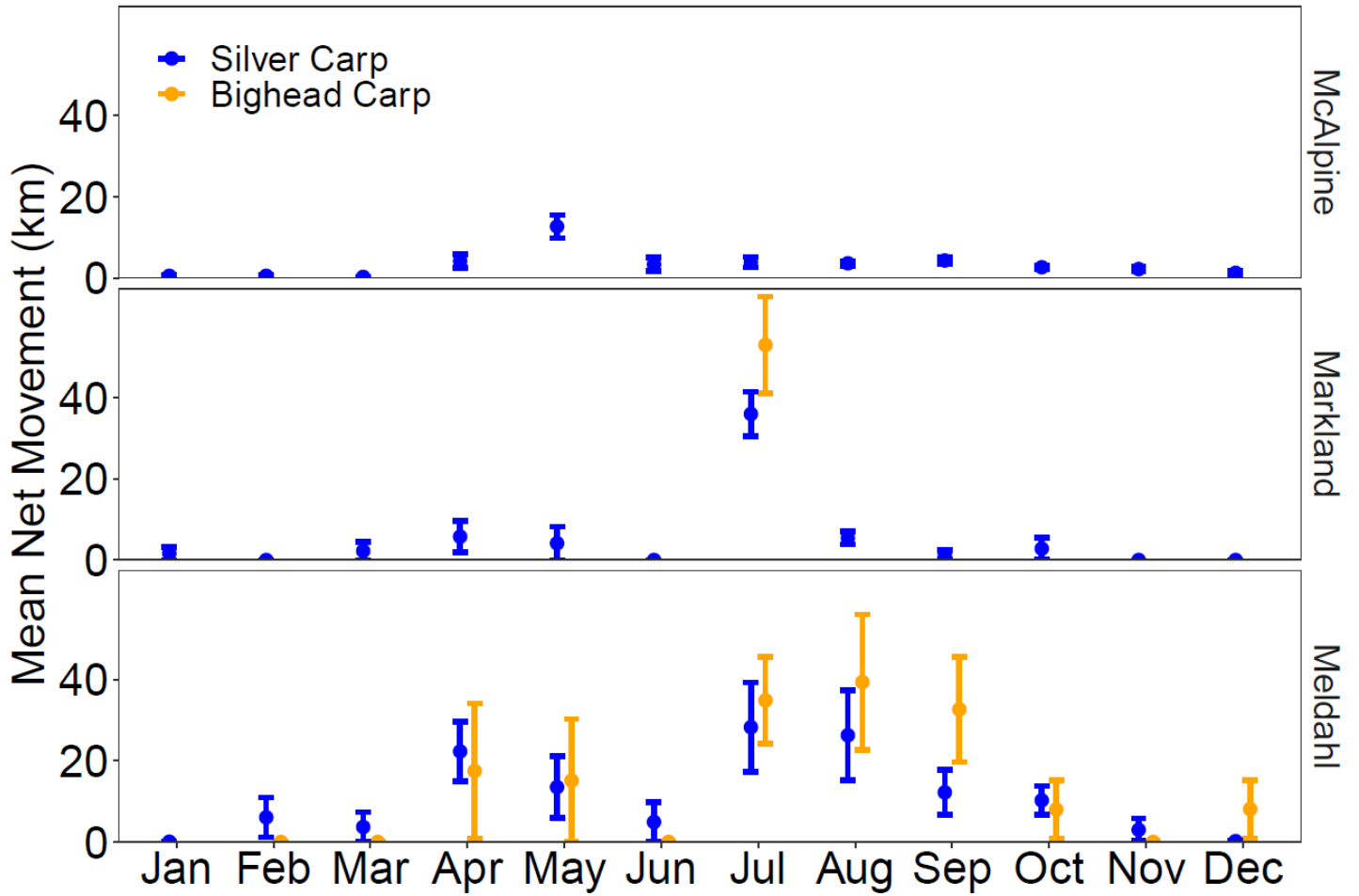


Figure 3. The mean monthly net movements (river kilometers) between the most upstream and downstream detections for tagged Silver Carp (blue) and Bighead Carp (orange) by pool in the three most active pools of the telemetry project (McAlpine, Markland, and Meldahl pools). Error bars represent standard error. Only tagged carp detected ≥ 2 times within a single pool each month were included in the distance calculations.

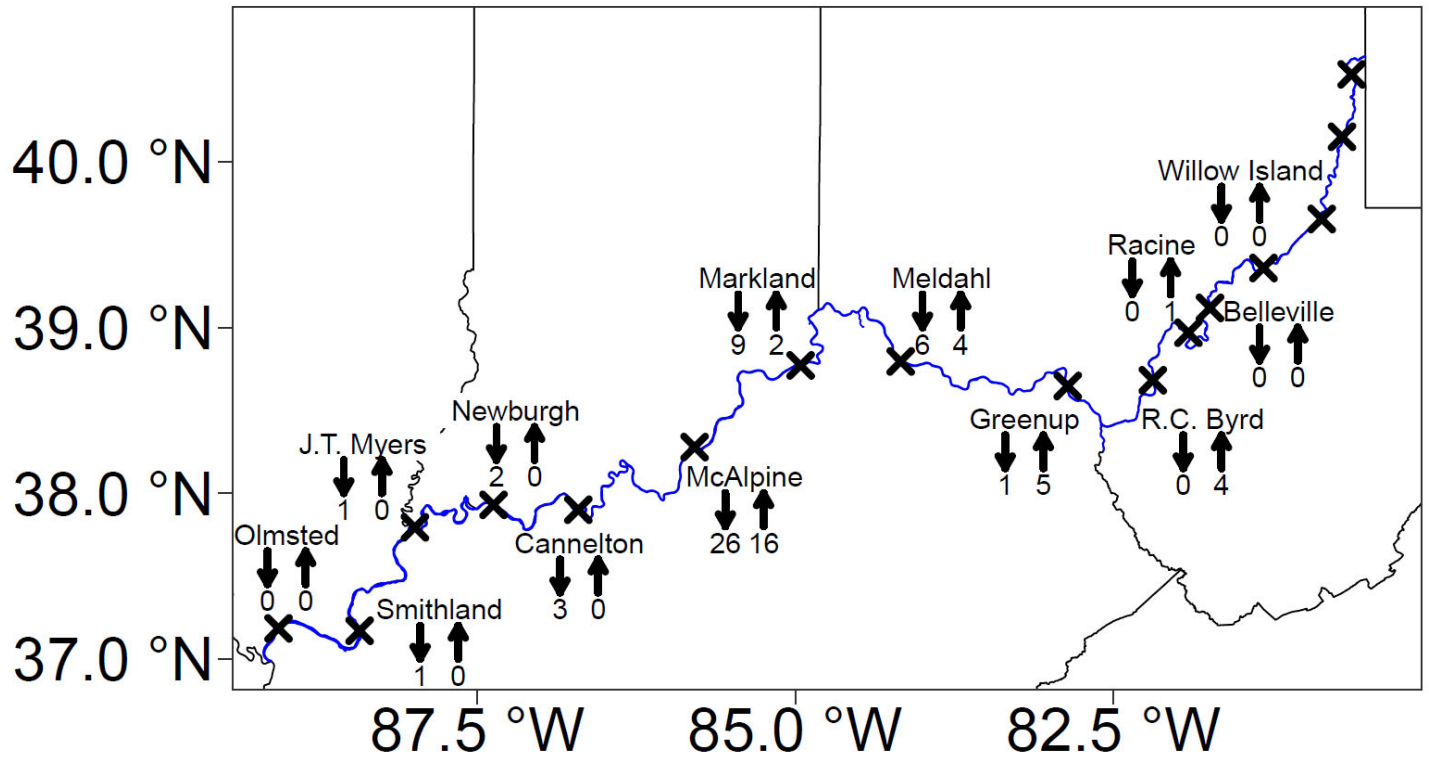


Figure 4. Total number of downstream (↓) and upstream (↑) lock and dam (L&D) passages by invasive carps during June 2013 – December 2020. Map shows passages from Olmsted L&D (river mile 964.4) near the confluence of the Ohio and Mississippi rivers to Willow Island L&D (river mile 161.7) which is the most upstream location at which acoustic receivers are deployed.

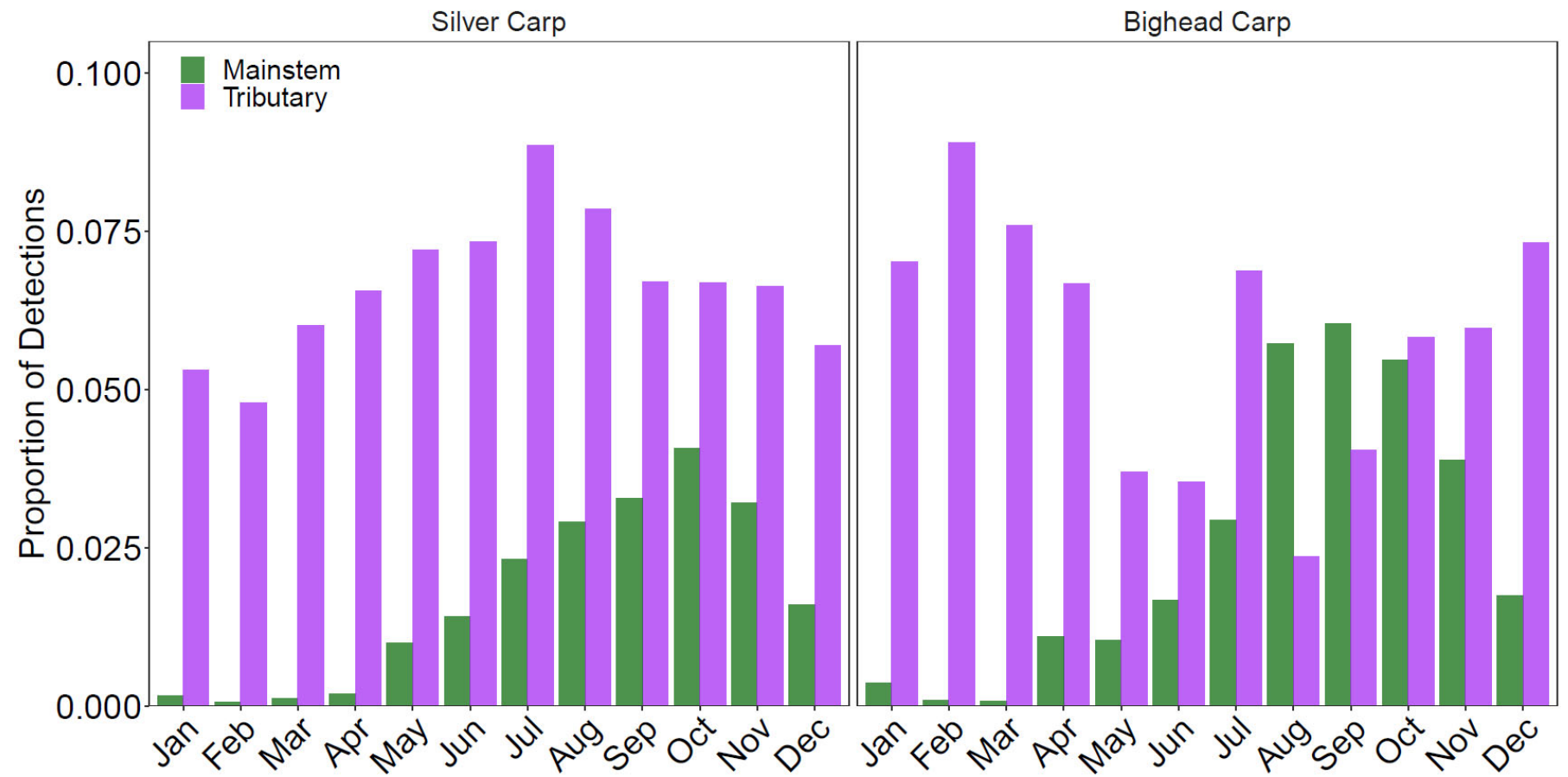


Figure 5. The proportion of detections by month for Silver (left) and Bighead (right) carps in mainstem (green) and tributary (purple) habitats of the Ohio River during June 2013 – December 2020.

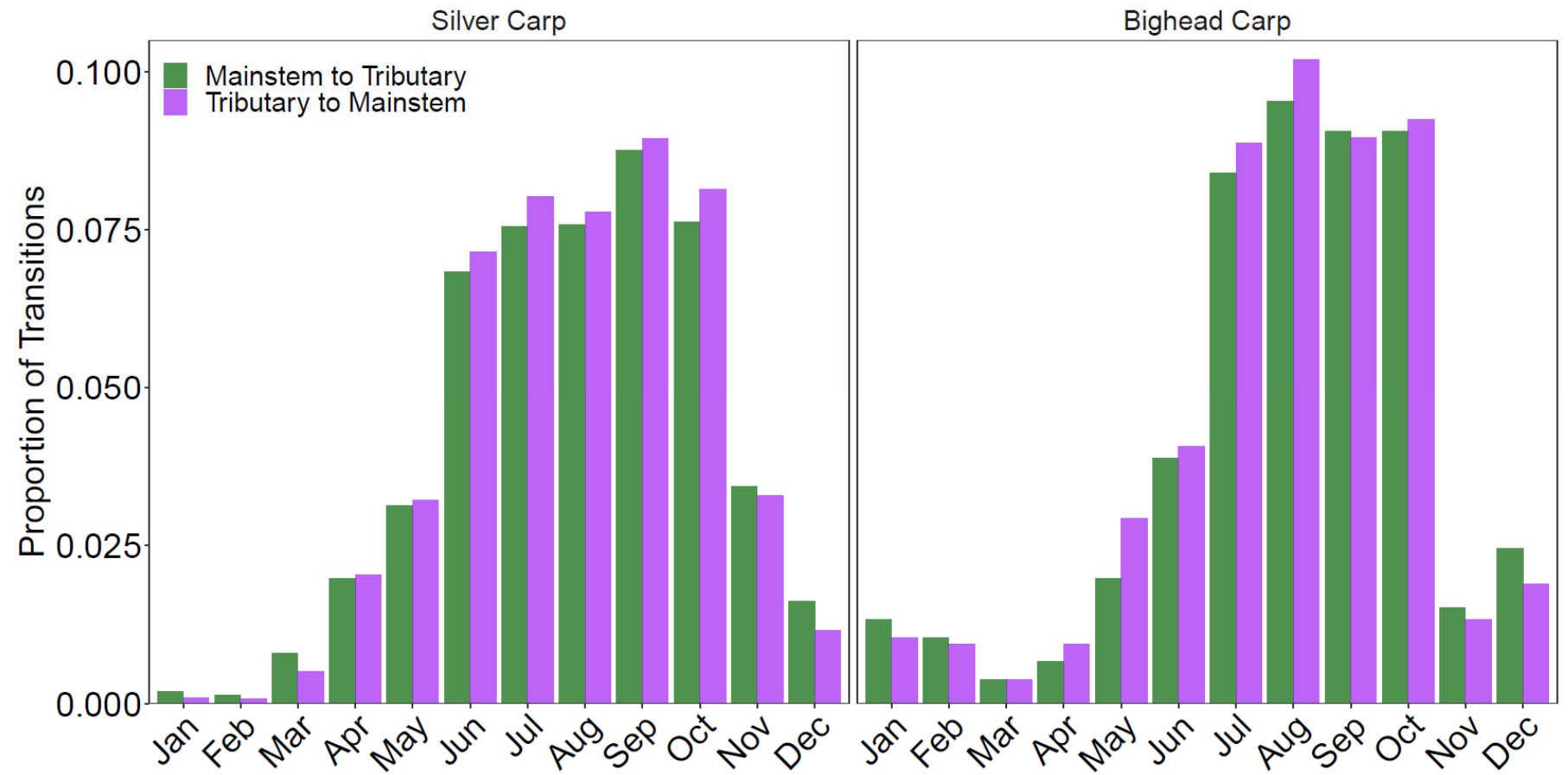


Figure 6. The proportion of transitions from mainstem to tributary (green) or from tributary to mainstem (purple) habitats by month for Silver (left) and Bighead (right) carps in the Ohio River during June 2013 – December 2020.

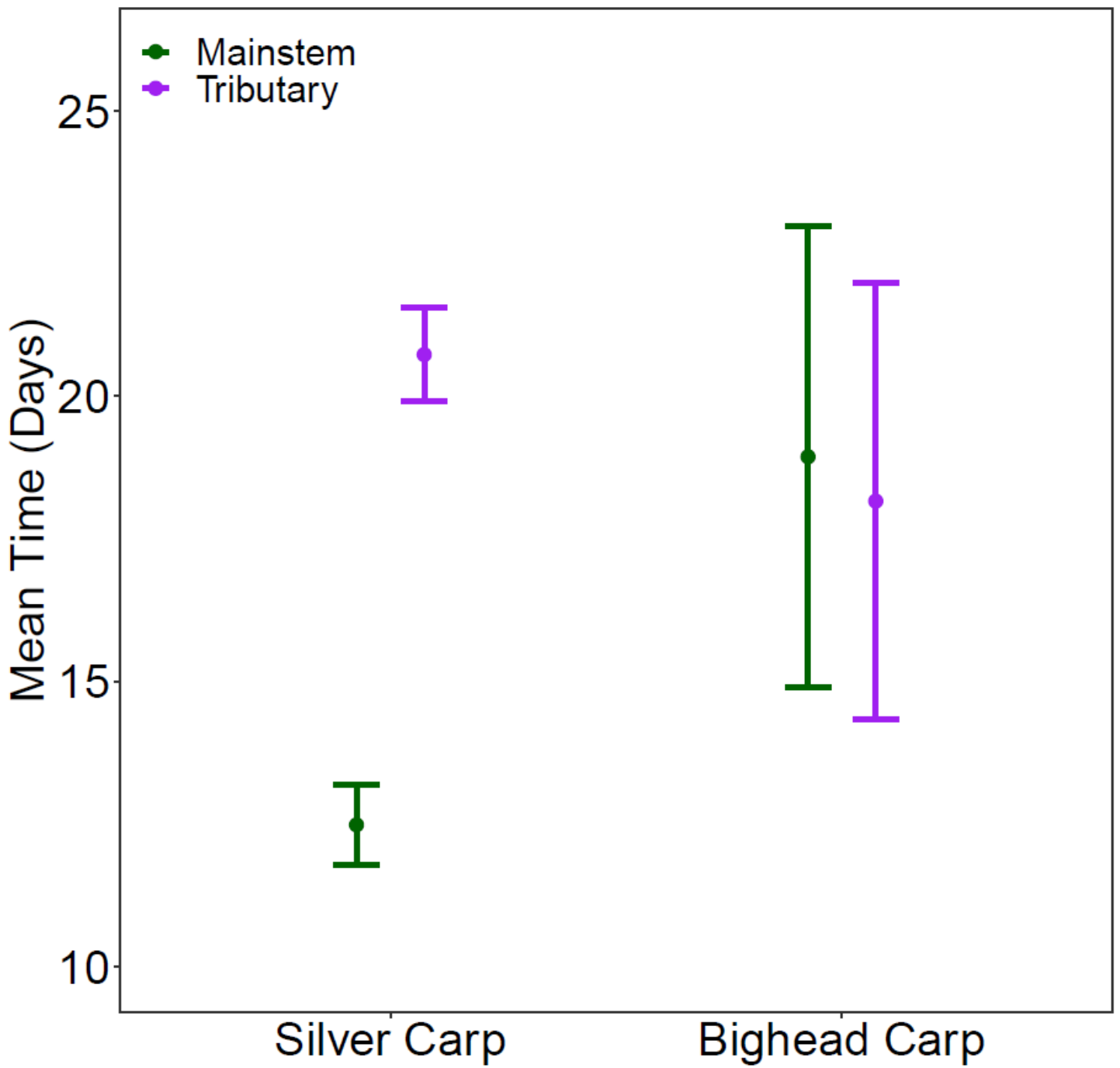


Figure 7. The mean time (days) spent in mainstem (green) or tributary (purple) habitat for Silver and Bighead Carps during June 2013 – December 2020. The number of days represents the time from the first detection of an individual in either the mainstem of the Ohio River or one of its tributaries to the first detection outside of that habitat.

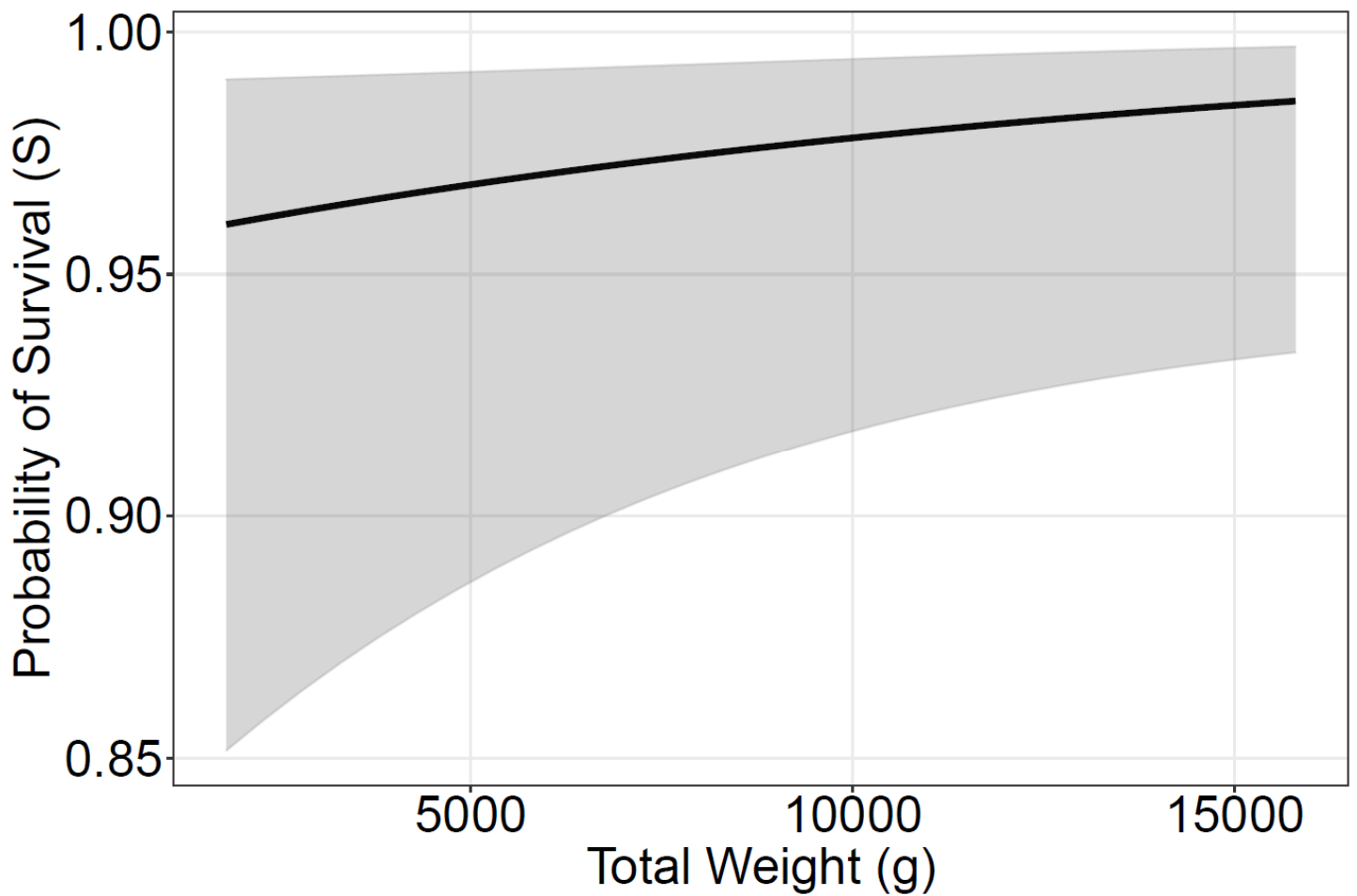


Figure 8. The effect of Silver Carp weight (g) on the probability of survival (S). The range of weights for which the survival probability was estimated (1800 – 15800 g) is reflective of the weights at release of all Silver Carp tagged during June 2013 – December 2020. The solid line represents the mean probability of survival for July, which was chosen as representative of all months. The gray-shaded area represents the 95% confidence interval surrounding the mean survival probability.

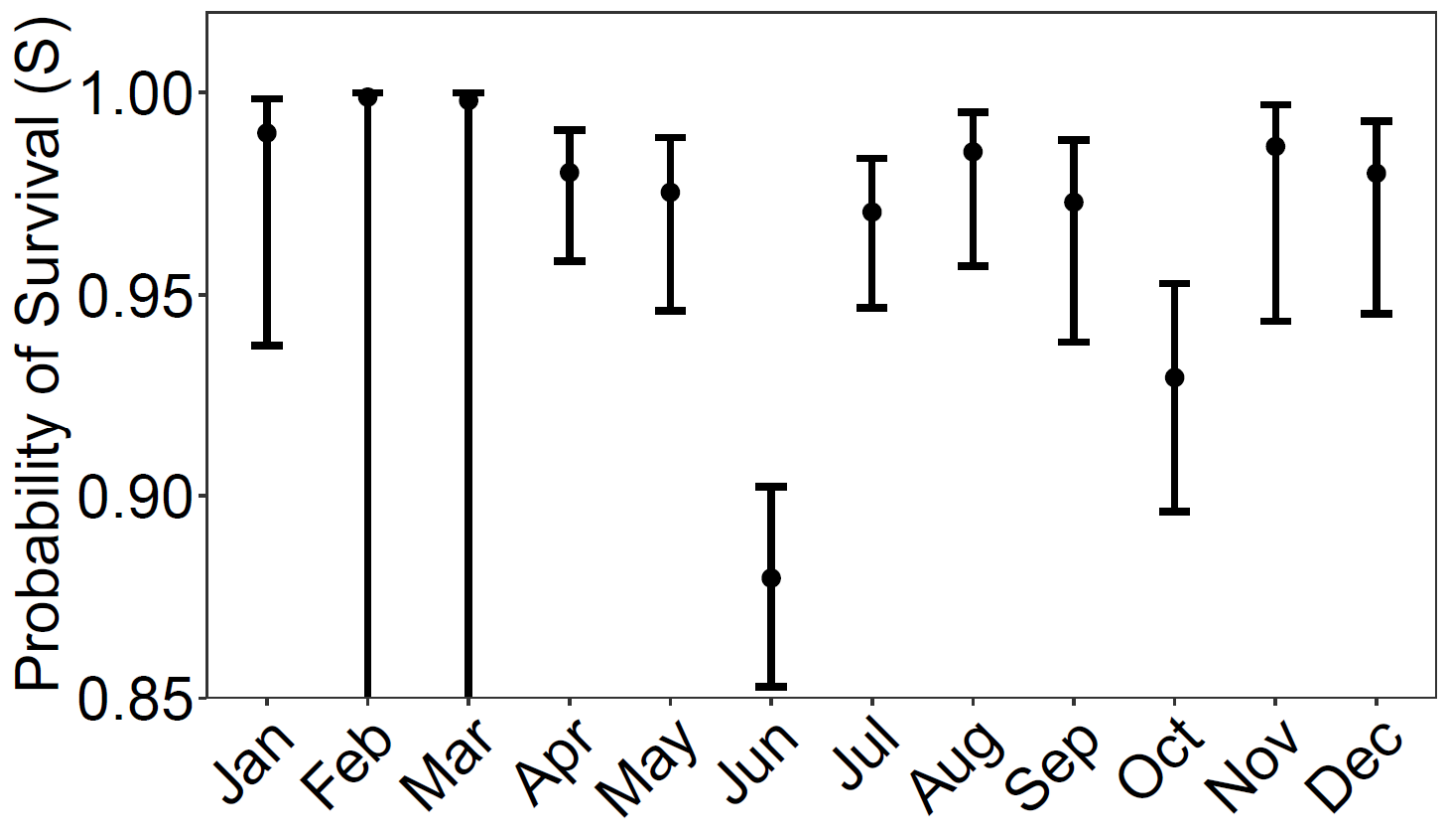


Figure 9. Mean monthly survival probabilities (S, filled circles) and 95% confidence intervals (error bars) for Silver Carp. Estimates are for fish of the mean weight of all Silver Carp tagged during June 2013 – December 2020 (7022.9 g). Error bars for February and March are truncated to better show variation in the mean survival probabilities. The lower confidence limits for February and March are 0.00 and 0.56, respectively.

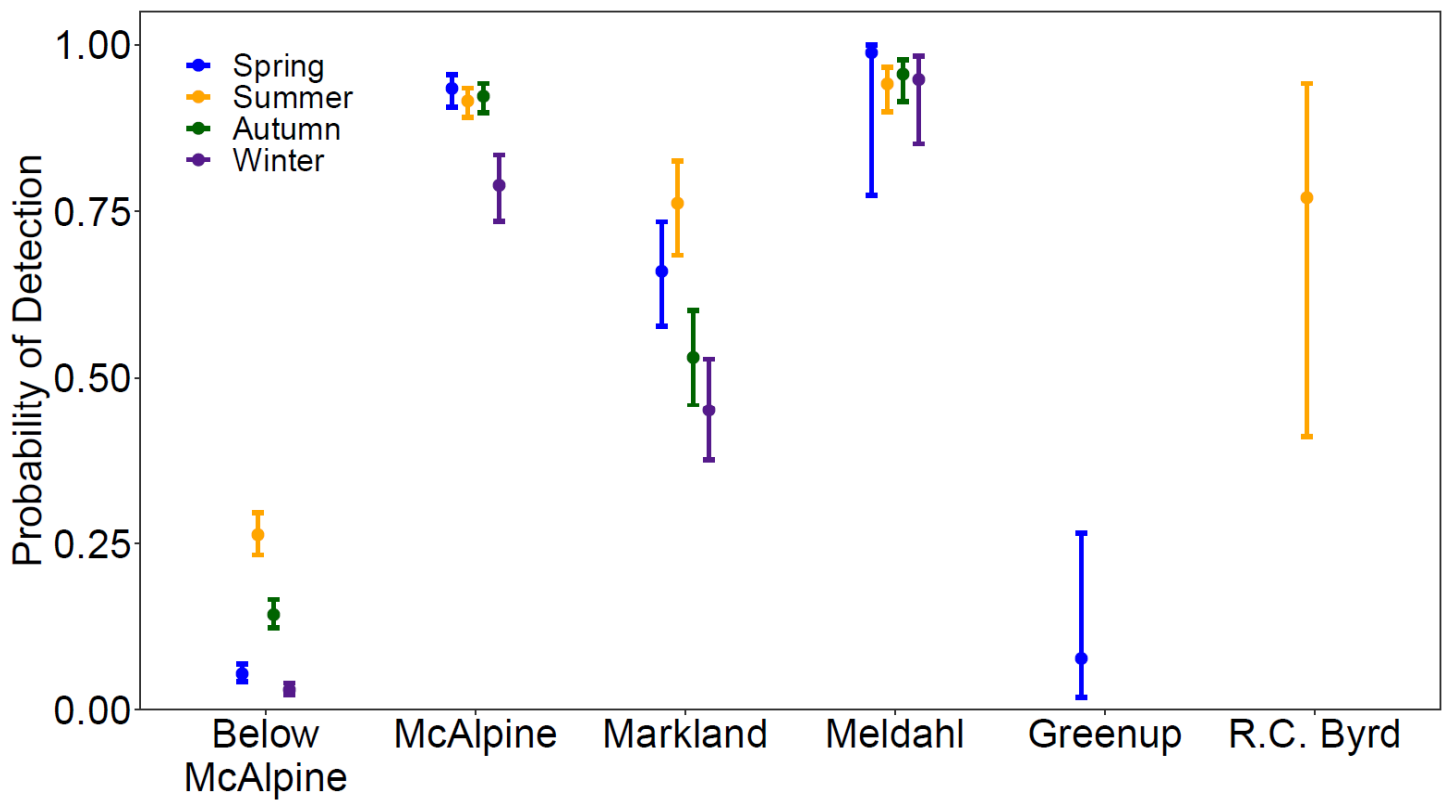


Figure 10. Model estimated mean detection probabilities (p ; filled circles) and 95% confidence intervals (error bars) in Ohio River navigation pools for Silver Carp of mean weight (7022.9 g) tagged during June 2013 – December 2020. Detection probabilities were estimated for each pool by season: spring (March – May; blue), summer (June – August; orange), autumn (September – November; green), and winter (December – February; purple). Only one fish was detected upstream of Greenup Lock and Dam and therefore, detection probabilities could only be estimated in Greenup and R.C. Byrd pools for seasons during which detections occurred. Additionally, no Silver Carp were detected upstream of Racine Lock and Dam. Therefore, detection probabilities were not estimated for pools upstream of R.C. Byrd Pool.

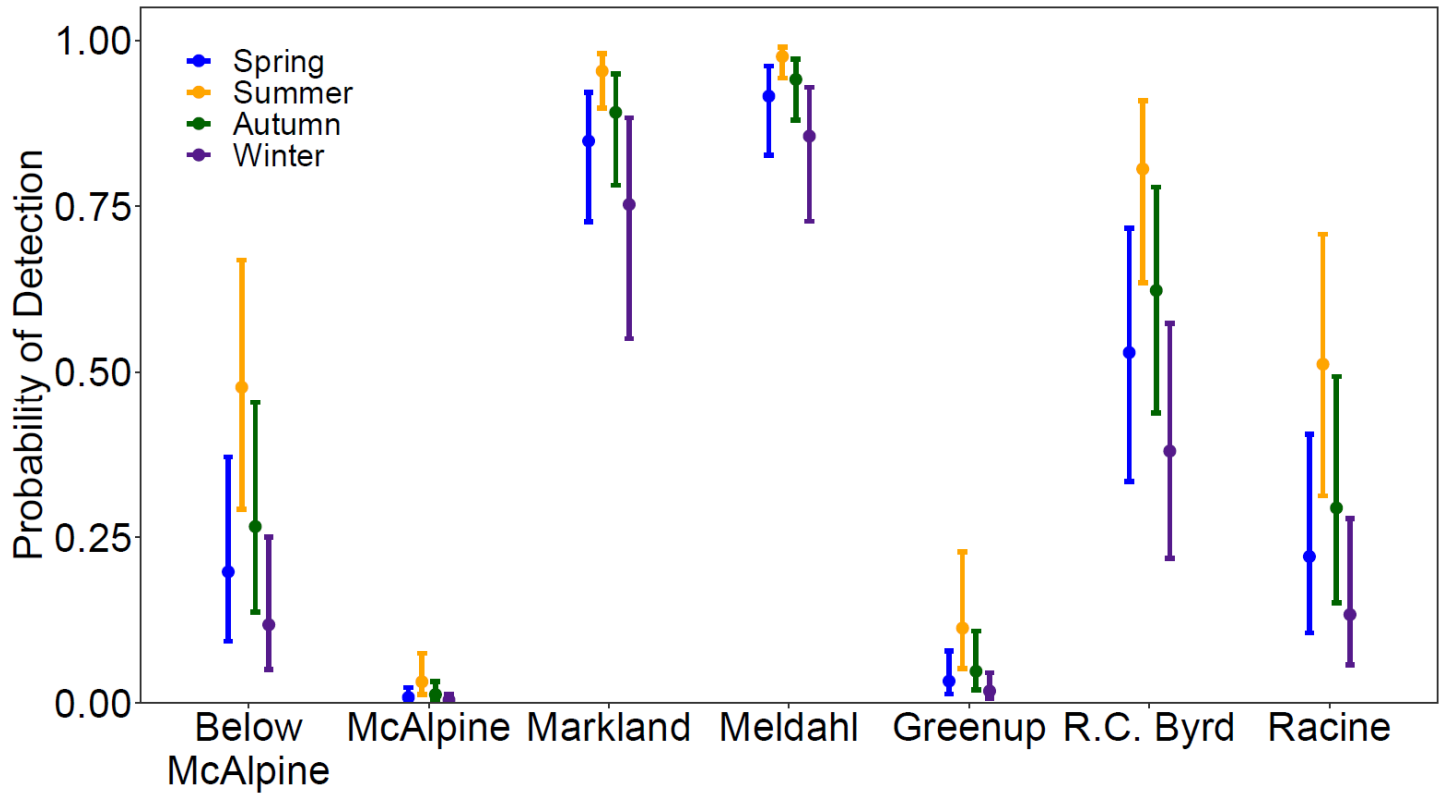


Figure 11. Model estimated mean detection probabilities (p ; filled circles) and 95% confidence intervals (error bars) in Ohio River navigation pools for Bighead Carp tagged during June 2013 – December 2020. Detection probabilities were estimated for each pool by season: spring (March – May; blue), summer (June – August; orange), autumn (September – November; green), and winter (December – February; purple). No Bighead Carp were detected upstream of Belleville Lock and Dam. Therefore, transition probabilities were not estimated for pools upstream of Racine Pool.

Table 1: Number and distribution of VR2 receivers in the Ohio River during 2020. One-hundred forty receivers were deployed from Olmsted pool, downstream of the Smithland lock and dam, to the Willow Island lock and dam. Thirty-eight of these receivers were directly associated with lock and dam structures, 52 were deployed in the mainstem Ohio River, and 50 were deployed in tributaries of the Ohio River.

Ohio River Pool	Pool Length (km)	Lock and Dam		Mainstem		Tributary		Total Sites per Pool (N)	Total Sites per Pool (%)
		Sites per Pool (N)	Sites per Pool (%)	Sites per Pool (N)	Sites per Pool (%)	Sites per Pool (N)	Sites per Pool (%)		
Olmsted	73.9	3	60.0	2	40.0	0	0.0	5	3.6
Smithland	116.7	3	100.0	0	0.0	0	0.0	3	2.1
J.T. Myers	112.5	3	60.0	0	0.0	2	40.0	5	3.6
Newburgh	89.2	1	100.0	0	0.0	0	0.0	1	0.7
Cannelton	183.3	0	0.0	3	50.0	3	50.0	6	4.3
McAlpine	121.2	3	14.3	8	38.1	10	47.6	21	15.0
Markland	153.4	4	19.0	6	28.6	11	52.4	21	15.0
Meldahl	153.2	4	14.8	15	55.6	8	29.6	27	19.3
Greenup	99.5	3	15.8	10	52.6	6	31.6	19	13.6
R.C. Byrd	67.1	4	28.6	4	28.6	6	42.9	14	10.0
Racine	54.1	2	28.6	3	42.9	2	28.6	7	5.0
Belleville	67.9	7	70.0	1	10.0	2	20.0	10	7.1
Willow Island	56.8	1	100.0	0	0.0	0	0.0	1	0.7
Total		38		52		50		140	100

Table 2: The number of tags deployed on Silver and Bighead Carp by year and pool during June 2013 – December 2020. Tags deployed for > 5 years are expected to be expired (inactive). Also included are species composition calculations for the active tags in each pool and the mean length of all tagged fish by pool.

Tagging Year	Status after 2020	AC Species	OHR Pool						Total
			Cannelton	McAlpine	Markland	Meldahl	Greenup	RC Byrd	
2013	Inactive	Silver Carp	-	-	-	6	-	-	6
	Inactive	Bighead Carp	-	-	-	13	-	-	13
2014	Inactive	Silver Carp	-	115	6	10	-	-	131
	Inactive	Bighead Carp	-	4	4	-	-	-	8
2015	Inactive	Silver Carp	-	22	3	5	-	-	30
	Inactive	Bighead Carp	-	1	1	5	-	-	7
2016	Active	Silver Carp	92	94	6	-	-	-	192
	Active	Bighead Carp	4	1	4	2	-	3	14
2017	Active	Silver Carp	90	-	12	3	-	-	105
	Active	Bighead Carp	-	-	2	-	-	-	2
2018	Active	Silver Carp	-	-	21	10	-	-	31
	Active	Bighead Carp	-	-	-	1	-	-	1
2019	Active	Silver Carp	-	30	-	-	-	-	30
	Active	Bighead Carp	-	1	-	-	-	-	1
2020	Active	Silver Carp	-	100	18	-	-	-	118
	Active	Bighead Carp	-	-	-	-	-	-	0
(2016-2020)	Active	Silver Carp	182	224	57	13	-	-	476
		Bighead Carp	4	2	6	3	-	3	18
		Overall	186	226	63	16	0	3	494
(2013-2015)	Inactive	Silver Carp	-	137	9	21	-	-	167
		Bighead Carp	-	5	5	18	-	-	28
		Overall	-	142	14	39	-	-	195
% Species Composition (2016-2020)	Active	Silver Carp	36.8	45.3	11.5	2.6	0.0	0.0	96.4
		Bighead Carp	0.8	0.4	1.2	0.6	0.0	0.6	3.6
		Overall	37.7	45.7	12.8	3.2	0.0	0.6	100.0
Mean Total Lengths (mm) (2013-2020)	Combined	Silver Carp	826.5	832.6	914.5	966	-	-	846.6
		Bighead Carp	1139.8	1146.3	1175.1	1153.6	-	1210	1160.1

Table 3. Mean monthly net distance travelled (river kilometers) by Bighead Carp (BHC) and Silver Carp (SVC) detected during 2018 – 2020. The net distance travelled was calculated as the difference between the most upstream and downstream detections each month. All fish used in this analysis were detected a minimum of two times within a given month. The green line indicates when mainstem receivers were deployed, whereas the red line indicates when mainstem receivers were retrieved for over-winter storage.

Year	Pool	Species	Month											
			Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2018	McAlpine	BHC	--	--	--	--	--	--	--	--	--	--	--	--
		SVC	1.7	0.5	0.6	0.6	14.9	18.1	19.5	5.5	2.9	1.9	1.0	1.1
	Markland	BHC	0.0	0.0	0.0	--	72.5	73.5	67.2	1.1	0.0	0.0	0.0	--
		SVC	0.0	0.0	0.0	0.0	80.5	83.8	39.5	0.0	1.6	1.9	0.0	0.0
	Meldahl	BHC	0.0	0.0	0.0	0.0	41.0	15.8	28.2	6.1	17.5	0.6	--	--
		SVC	0.0	0.0	0.0	0.0	36.0	10.8	26.0	13.7	14.3	0.2	3.1	1.6
	All Pools	BHC	0.0	0.0	0.0	0.0	59.0	40.5	44.9	4.0	7.5	0.3	0.0	0.0
		SVC	1.4	0.5	0.5	0.5	20.9	22.3	21.1	5.7	3.3	1.7	1.2	1.1
2019	McAlpine	BHC	--	--	--	--	--	--	--	--	--	--	--	
		SVC	0.4	0.2	0.0	1.8	7.5	3.0	6.5	7.0	4.7	8.4	3.5	1.5
	Markland	BHC	--	--	--	49.6	9.1	76.3	41.0	0.0	3.8	0.0	--	--
		SVC	0.0	0.0	5.1	18.5	73.4	64.1	23.8	6.5	10.4	3.9	0.5	7.2
	Meldahl	BHC	--	0.0	--	22.0	--	--	22.7	29.9	19.2	18.3	5.4	0.1
		SVC	5.2	4.4	3.4	25.4	17.9	27.9	15.4	20.6	12.8	6.2	15.5	2.7
	All Pools	BHC	0.0	0.0	0.0	35.8	30.2	45.8	30.6	17.1	12.6	10.5	4.3	0.1
		SVC	1.6	1.3	1.8	8.3	20.4	16.2	10.4	8.9	6.8	7.7	5.4	2.2
2020	McAlpine	BHC	--	--	--	--	--	--	--	--	--	--	--	
		SVC	0.6	0.6	0.3	4.2	12.7	3.4	3.9	3.6	4.3	2.7	2.2	1.3
	Markland	BHC	--	--	--	--	--	--	53.0	--	--	--	--	--
		SVC	1.6	0.0	2.2	5.8	4.1	0.0	36.0	5.4	1.3	2.8	0.0	0.0
	Meldahl	BHC	--	0.0	0.0	17.5	15.1	0.0	34.9	39.4	32.7	8.0	0.0	8.1
		SVC	0.1	6.1	3.7	22.3	13.5	4.9	28.3	26.3	12.2	10.3	3.0	0.2
	All Pools	BHC	--	0.0	0.0	10.5	9.3	20.0	42.6	38.9	21.8	6.0	0.0	8.1
		SVC	0.6	1.4	1.1	6.9	13.7	3.3	11.9	7.3	5.0	3.3	2.3	1.0

Table 4. Model selection results for the multi-state with live recaptures model for Silver Carp. The table shows the model structure, QAIC_c, ΔQAIC_c, and the QAIC weight for two best supported models. The covariates affecting estimates of the probabilities of survival (S), detection (p) and transition (ψ) are shown in parentheses for each model.

Model	QAIC_c	ΔQAIC_c	QAIC weight
<i>S(month + weight)p(pool * season)ψ(pool * season)</i>	5452.02	0.00	0.93
<i>S(month + weight)p(pool + month)ψ(pool * season)</i>	5457.84	5.82	0.05

Table 5. Model selection results for the multi-state with live recaptures model for Bighead Carp. The table shows the model structure, AIC_c , ΔAIC_c , and the AIC weight for all models with a $\Delta AIC_c \leq 2$. The covariates affecting estimates of the probabilities of survival (S), detection (p) and transition (ψ) are shown in parentheses for each model. The “.” Indicates a parameter estimate that is invariant to all covariates included in these models (i.e., intercept only).

Model	AIC_c	ΔAIC_c	AIC weight
$S(.)p(pool + season)\psi(pool)$	1154.70	0.00	0.33
$S(.)p(pool * season)\psi(pool)$	1155.11	0.41	0.27
$S(weight)p(pool + season)\psi(pool)$	1156.55	1.85	0.13

Table 6. Model estimated mean (confidence intervals) pool-to-pool transition probabilities (ψ) of Silver Carp in the Ohio River derived from acoustic telemetry during June 2013 – December 2020. The most parsimonious model for Silver Carp included the interactive effect of pool and season on transition rates. Because fish cannot move directly between non-adjacent pools, these transitions rates were fixed to 0 and are not reported in the table below (black-shaded cells). The probability of fish remaining within a pool is given in the gray shaded cells; upstream transition probabilities are to the right of gray-shaded cells and downstream transition probabilities are to the left of gray-shaded cells. No Silver Carp were detected above Racine Lock and Dam. Therefore, transition probabilities were not estimated for pools upstream of R.C. Byrd Pool.

Spring						
Departure Pool	Destination Pool					
	Below McAlpine	McAlpine	Markland	Meldahl	Greenup	R.C. Byrd
Below McAlpine	0.796 (0.769 – 0.820)	0.204 (0.180 – 0.231)				
McAlpine	0.041 (0.026 – 0.064)	0.957 (0.915 – 0.974)	0.002 (0.000 – 0.021)			
Markland		0.009 (0.001 – 0.058)	0.978 (0.890 – 0.996)	0.013 (0.003 – 0.052)		
Meldahl			0.000 (0.000 – 0.000)	0.961 (0.905 – 0.985)	0.039 (0.015 – 0.095)	
Greenup				0.709 (0.491 – 0.861)	0.000 (0.000 – 0.370)	0.291 (0.139 – 0.509)
R.C. Byrd					1.000 (0.000 – 1.000)	0.000 (0.000 – 1.000)
Summer						
Below McAlpine	0.930 (0.907 – 0.947)	0.070 (0.053 – 0.093)				
McAlpine	0.076 (0.060 – 0.095)	0.924 (0.066 – 0.94)	0.000 (0.000 – 0.839)			
Markland		0.007 (0.001 – 0.049)	0.993 (0.000 – 0.999)	0.000 (0.000 – 1.000)		
Meldahl			0.005 (0.000 – 0.034)	0.988 (0.923 – 0.999)	0.007 (0.001 – 0.043)	
Greenup				0.000 (0.000 – 1.000)	1.000 (0.000 – 1.000)	0.000 (0.000 – 0.000)
R.C. Byrd					0.000 (0.000 – 1.000)	1.000 (0.000 – 1.000)
Autumn						
Below McAlpine	0.973 (0.958 – 0.983)	0.027 (0.017 – 0.042)				
McAlpine	0.213 (0.188 – 0.241)	0.787 (0.759 – 0.821)	0.000 (0.000 – 0.000)			
Markland		0.034 (0.016 – 0.070)	0.966 (0.930 – 0.984)	0.000 (0.000 – 0.000)		

Meldahl			0.000 (0.000 – 0.000)	0.934 (0.886 – 0.962)	0.066 (0.038 – 0.114)	
Greenup				0.097 (0.025 – 0.313)	0.903 (0.687 – 0.975)	0.000 (0.000 – 0.000)
R.C. Byrd					0.368 (0.077 – 0.803)	0.632 (0.197 – 0.923)
Winter						
Below McAlpine	0.949 (0.933 – 0.961)	0.051 (0.039 – 0.067)				
McAlpine	0.149 (0.118 – 0.186)	0.851 (0.814 – 0.882)	0.000 (0.000 – 0.000)			
Markland		0.000 (0.000 – 0.000)	1.000 (0.000 – 1.000)	0.000 (0.000 – 1.000)		
Meldahl			0.012 (0.003 – 0.045)	0.957 (0.857 – 0.988)	0.031 (0.009 – 0.098)	
Greenup				0.072 (0.009 – 0.395)	0.502 (0.000 – 0.874)	0.426 (0.117 – 0.806)
R.C. Byrd					0.733 (0.074 – 0.990)	0.267 (0.010 – 0.926)

Table 7. Model estimated mean (confidence intervals) pool-to-pool transition probabilities (ψ) of Bighead Carp in the Ohio River derived from acoustic telemetry during June 2013 – December 2020. The most parsimonious model for Bighead Carp included pool-specific, time-invariant transition rates. Because fish cannot move directly between non-adjacent pools, these transitions rates were fixed to 0 and are not reported in the table below (black-shaded cells). The probability of fish remaining within a pool is given in the gray-shaded cells; upstream transition probabilities are to the right of gray-shaded cells and downstream transition probabilities are to the left of gray-shaded cells. No Bighead Carp were detected upstream of Belleville Lock and Dam. Therefore, transition probabilities were not estimated for pools upstream of Racine Pool.

Departure Pool	Destination Pool						
	Below McAlpine	McAlpine	Markland	Meldahl	Greenup	R.C. Byrd	Racine
Below McAlpine	1.000 (1.000 – 1.000)	0.000 (0.000 – 0.000)					
McAlpine	0.000 (0.000 – 0.000)	0.973 (0.947 – 0.987)	0.027 (0.013 – 0.053)				
Markland		0.127 (0.080 – 0.197)	0.873 (0.803 – 0.920)	0.000 (0.000 – 0.000)			
Meldahl			0.007 (0.002 – 0.029)	0.930 (0.860 – 0.963)	0.063 (0.035 – 0.111)		
Greenup				0.077 (0.040 – 0.143)	0.915 (0.799 – 0.960)	0.008 (0.000 – 0.058)	
R.C. Byrd					0.027 (0.003 – 0.191)	0.953 (0.682 – 0.994)	0.020 (0.003 – 0.127)
Racine						0.000 (0.000 – 0.000)	1.000 (1.000 – 1.000)