Impeding access to tributary spawning habitat and releasing experimental fall-timed floods increases brown trout immigration into a dam's tailwater

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Abstract

River ecosystems have been altered by flow regulation and species introductions. Regulated flow regimes often include releases designed to benefit certain species or restore ecosystem processes, and invasive species suppression programs may include efforts to restrict access to spawning habitat. The impacts of these management interventions are often uncertain. Here, we assess hypotheses regarding introduced brown trout (*Salmo trutta*) movement in a regulated river. We model mark-recapture data in a multistate framework to assess whether movement was affected by the operation of a tributary weir (restricting access to spawning habitat), experimental releases of fall-timed High Flow Experiments (Fall HFEs), or simply increased during the fall, spawning season. Our results suggest that the presence of the weir led to reduced tributary homing and the release of Fall HFEs stimulated upstream movement and straying. Both effects are of a similar magnitude, however the fall HFE effect is more certain. Our results suggest the expansion of an invasive species was stimulated by management interventions, and demonstrate the potential for unanticipated outcomes of restoration in highly altered river ecosystems.

Keywords: Ecological flows, designer flows, invasive species, salmonids, adaptive management, migration, flow regulation, invasion, barriers

Introduction

River discharge regulation and water diversions that alter flow regimes and favor invasive fishes have led to the widespread homogenization of freshwater fish communities (Poff et al. 2007; Comte et al. 2021). Given the global prevalence of river hydrologic alteration and losses of ecologically or commercially valuable fisheries, managers are increasingly evaluating potential experimental or “designer” flows using dam discharge to restore ecologically-important functional flow components (Yarnell et al. 2020; Tonkin et al. 2021). Such flows may be designed for specific species or more broadly to attempt to restore ecosystem processes. The response of stream fishes and biota to designer flows is sometimes difficult to predict and outcomes may be counter to expectations (Cross et al. 2011; Korman et al. 2011; Avery et al. 2015) and highly dependent on their timing (Yackulic et al. 2022a).

Understanding responses of fishes to flow manipulation is particularly important in flow-regulated systems inhabited by both native and introduced species as their response may differ dramatically. For instance, native fishes of the southwestern US may experience population-level benefits from spring or early summer floods (Gido and Propst 2012; Van Haverbeke et al. 2013; Healy et al. 2022a; Yackulic et al., 2022a), while recruitment of introduced trout can be limited by high magnitude spring flooding (Fausch et al. 2001; Kawai et al. 2013; Healy et al. 2022b; but see Avery et al. 2015). The impacts of fall-timed floods on native and introduced species in the southwestern US are less well understood; however, introduced species like brown trout (*Salmo trutta*) that evolved in systems with a wide variety of flow regimes and spawn during the late fall might benefit from fall flooding (reviewed in Unfer et al. 2011). High flows prior to spawning can improve spawning habitats for trout through scouring and transport of sediment and excess algae (Unfer et al. 2011; Bestgen et al. 2020).

Here, we focus on the movement of brown trout in the Colorado River in its Grand Canyon segment (Figure 1) located downriver from Glen Canyon Dam. Brown trout were introduced into Bright Angel creek, a tributary of the Colorado River, during the 1920s and spread into the mainstem Colorado River after construction and operations of Glen Canyon Dam led to flow, temperature, and sediment conditions that were more favorable (Runge et al. 2018). Following declines in federally endangered humpback chub (*Gila cypha*; Coggins et al. 2006) and based on evidence that brown trout were effective predators of humpback chub and other native fishes in the Grand Canyon (Yard et al. 2011; Whiting et al. 2014), managers began suppressing brown trout in Bright Angel Creek to mitigate risks of piscivory to native fishes (Healy et al. 2020). At the time suppression was initiated, Bright Angel Creek was the location in which most brown trout spawning was thought to occur, and the adjacent inflow reach of the Colorado River held the highest brown trout densities in the system (Healy et al. 2020). As part of the suppression program, a weir was installed to trap and remove trout and limit access to spawning habitat in Bright Angel Creek during the fall spawning season. At the beginning of suppression efforts, brown trout were relatively rare elsewhere in the system, especially in the tailwater ecosystem found in the first ~25 kilometers below Glen Canyon Dam. Tailwaters downstream of dams are commonly stocked and managed for nonnative salmonids to develop or enhance sport fisheries (Quinn and Kwak 2011; Dibble et al. 2015; reviewed in Budy and Gaeta 2018). The Glen Canyon Dam tailwater ecosystem is managed for rainbow trout (*Oncorhynchus mykiss*).

The hydrologic regime in Colorado River below Glen Canyon Dam is highly modified (summarized in Schmidt and Grams 2011) with suppression of natural late-Spring to early-Summer flooding, increased flow magnitude in the summer and winter to support hydropower production during seasons of high demand, low flows removed to support commercial and recreational boating, and increased daily variation to support load following to benefit hydropower generation (U.S. Department of Interior 2016). In recent years, managers have increasingly incorporated High Flow Experiments (HFEs) into the hydrologic regime in an attempt to restore an ecosystem process and enhance camping beaches for recreational river-rafters (Melis 2011). An early spring timed HFE in 2008 was linked to high recruitment of rainbow trout in the tailwater, increased rainbow trout downstream emigration, and decreased humpback chub survival (Korman et al. 2012; Avery et al. 2015; Yackulic et al. 2018). In response, subsequent management plans incorporated triggers for HFEs favoring fall months (November), in order to take advantage of tributary sediment inputs associated with summer monsoon flooding (USDOI 2016). Monitoring of sandbars has shown that HFEs are successful in enhancing beaches and increasing the prevalence of associated low-velocity backwater habitats (Schmidt and Grams 2011; Melis et al. 2015; Mueller and Grams 2021). Initially it was suggested that increases in such habitat would benefit humpback chub; however, studies to date suggest such impacts are small in comparison to other drivers (Dodrill et al. 2015; Yackulic et al. 2018; Dibble et al. 2021).

Concurrent with more frequent fall-timed HFEs (Fall HFEs) after 2012 (see Figure 2), invasive brown trout abundance in the tailwater below the Glen Canyon Dam increased (Runge et al. 2018; Yackulic et al. 2020). Based on a review of existing monitoring data (through 2017), a previous analysis identified hypothesized mechanisms for brown trout expansion below Glen Canyon Dam (reviewed in Runge et al. 2018). Runge et al. (2018) found evidence that concurrent increases in reproduction and immigration from downstream reaches in the Grand Canyon had driven the expansion. Potential causes of immigration that were hypothesized included increased immigration of adult spawners in response to Fall HFEs and the operation of a weir limiting access to the primary spawning stream and causing straying of adults that were not captured to non-natal habitats for spawning. In this paper, we evaluate alternative movement hypotheses explaining the expansion of brown trout populations into the Glen Canyon Dam tailwater, upstream of Lees Ferry, within Glen Canyon National Recreation Area (GCNRA, hereafter, Lees Ferry). We use a 19-year system-wide mark-recapture dataset to assess the relative importance of Fall HFEs, blockage of a spawning migration route (weir), or combinations of the weir and Fall HFEs contributing to colonization and expansion of brown trout into the Lees Ferry reach.

In addition to the status of brown trout as an ecologically-damaging and globally-introduced invader (McIntosh et al. 2011), it is classified as a species of conservation concern in portions of its native range, due to its significant cultural, recreational and economic importance (Lobon-Cervia et al. 2019). Thus, improving our understanding of environmental flow effects on brown trout movements would have broad management and conservation implications (Baker et al. 2020).

Methods

Study Area.— Our study area included ~468 km of the Colorado River downstream of Glen Canyon Dam and a Colorado River tributary, Bright Angel Creek in Grand Canyon National Park (GCNP; Figure 1). As is typical of regulated rivers (Poff et al. 1997), changes in the temperature, flow, and sediment regimes following the completion of Glen Canyon Dam in 1963, have led to changes in the ecology of the river (reviewed in Melis 2011), including extirpation of native fishes (Gloss and Coggins 2005) and changes in invertebrate communities (Kennedy et al. 2016). Regulation of the Colorado River below Glen Canyon Dam led to higher baseflows during some periods of the year and a loss of seasonal flooding (see Figure 2), which exceeded 3,000 m^3/s every two pre-dam years (reviewed in Melis 2011). Mean daily discharge during our study period (2000 - 2020) was 341.7 $m^3 s^{-1}$ (range 109.4 – 1241.8 $m^3 s^{-1}$, US Geological Survey [USGS] gaging station 09380000; USGS 2022). Hypolimnetic dam discharge converted the seasonally-variable (near freezing to 30°C, Wright et al. 2009) and turbid waters of the Colorado River – conditions supportive of native fish reproduction (Clarkson and Childs 2000) – into a colder and seasonably-stable thermal regime more suited to salmonids in the tailwater of the dam (McKinney et al. 2001). While the warmest temperatures generally occur during the fall, the range and maximum annual temperature has been warming recently due to declining storage due to basin-wide drought in Lake Powell upstream (Dibble et al. 2021).

Bright Angel Creek has a seasonally and longitudinally varying thermal regime suitable for native fishes and salmonids (Bair et al. 2019; Healy et al. 2020). Following closure of Glen Canyon Dam, introduced trout expanded throughout the Colorado River in our study area (Figure 3); however, Bright Angel Creek remained the primary area of brown trout reproduction until ~2014, when catch rates of juveniles increased substantially above Lees Ferry in the tailwater below the Dam (Runge et al. 2018). Brown trout inhabiting the Colorado River are known to make spawning migrations into Bright Angel Creek between November and December (Omana Smith et al. 2012; Healy et al. 2020). Based on recaptures of passive-integrated transponder (PIT) tagged individuals, brown trout move extensively throughout our study area (summarized in Results; Figure 3).

Brown Trout Suppression Program.— Suppression of brown trout has been a priority of management agencies since the early 2000s (Omana Smith et al. 2012; U.S. Department of Interior 2016; Healy et al. 2020). A series of small-scale experimental suppression activities focusing on Bright Angel Creek were initiated in the early 2000s, including the installation of a weir and fish trap during November and December (see Figure 2) to capture and remove adults on spawning migrations into Bright Angel Creek, and limited backpack electrofishing in the lower reaches of the creek (reviewed in Omana Smith et al. 2012). The annual suppression program was expanded spatially and temporally in 2012 to include depletion electrofishing throughout 16 km of Bright Angel Creek and weir installation and operation between October and February, which was effective in suppressing the brown trout population by >90% (Healy et al. 2020), and coincided with a decline in catch rates in the adjacent mainstem (Rogowski and Boyer 2019). Regardless, brown trout populations may rebound rapidly, even when few adults remain, and when ideal conditions exist during incubation and emergence periods (Saunders et al. 2015; Healy et al. 2022b).

Glen Canyon Dam High Flow Experiments.— High Flow Experiments involve rapid increases from base discharge magnitude to peak flows exceeding Glen Canyon Dam powerplant capacity (~930 m^3 s^{-1}) for several days, followed by rapid down-ramping of discharge at a rate of ~39 m^3 s^{-1} $hour^{-1}$ (Figure 2). Since Lake Powell traps the upstream sediment load behind Glen Canyon Dam, Fall HFEs are triggered by tributary sediment inputs (now only ~16% of pre-dam supply, Topping et al. 2000) occurring during summer monsoon flooding (details reviewed in Mueller et al. 2018). The first HFE during the fall, was a 60-hour release of ~1,180 m^3/s between November 22 and 24, 2004, which reached peak magnitude over ~30 hours (Melis 2011). Fall HFEs of similar timing to the 2004 Fall HFE were conducted beginning in 2012, and continued through 2018, with the exception of 2015 and 2017 (Figure 2). In 2015 and 2017 HFEs were not initiated to avoid triggering dispersal of a newly discovered population of invasive green sunfish (*Lepomis cyanellus*) reproducing in a slough below Glen Canyon Dam, and due to a lack of sufficient sediment inputs, respectively. Peak discharge during Fall HFEs, measured at the US Geological Survey (USGS) Colorado River at Lees Ferry, Arizona gage (USGS 2022 data, gaging station 09380000), ranged from ~1,056 to 1,254 $m^3 s^{-1}$, for between 60 and 96 hours (Figure 2).

Sampling.— Brown trout were captured during electrofishing surveys in support of the Glen Canyon Dam Adaptive Management Program (GCDAMP) between April 2000 and January 2019, including system-wide or Lees Ferry monitoring of large-bodied fishes (Rogowski et al. 2018; Rogowski and Boyer 2019), a near-shore ecology study (Dodrill et al. 2015; Finch et al. 2016), research into the population dynamics of rainbow trout and their impact on humpback chub (Korman et al. 2016; Yackulic et al. 2018), and during suppression of salmonids near the confluence of the Little Colorado River (Coggins et al. 2011), among others. Since 2000, standardized monitoring on the Colorado River in Glen and Grand Canyons have been conducted at least twice per year, using single-pass pulsed-DC boat-mounted electrofishing units along the shoreline of the Colorado River at night (Korman et al. 2012; Rogowski and Boyer 2019). We also used brown trout re-capture data collected during stream-wide three-pass tandem backpack electrofishing and at the weir in Bright Angel Creek (Healy et al. 2020). We refer the reader to the references above for specifics of each sampling regime, and to Figure 3 for the distribution of sampling effort, captures, and recaptures of brown trout.

Investigators followed standardized methods for the handling and tagging of fishes, including brown trout, in Grand Canyon (Persons et al. 2013). During all research, monitoring, and suppression projects, all brown trout > 75 or >149 mm total length (TL; depending on the project) were scanned for a passive integrated transponder (PIT) tag, and either tagged with a 134.2-kHz PIT tag, or a FLOY tag (in 78 of 3680 fish) during monitoring and research projects and released near the site of capture, or humanely euthanized (suppression projects). We were confident tag loss and handling-induced mortality of tagged fish were minimal based on previous studies (e.g., Acolas et al. 2007), and on experience tagging smaller salmonids in Glen Canyon (Korman et al. 2016).

Data Analysis.— We used a multistate model (Arnason 1973; Schwarz and Arnason 1996) with PIT and FLOY tag mark-recapture data collected from throughout the Colorado River between Glen Canyon Dam and Lake Mead, and in Bright Angel Creek (Yackulic et al. 2022b), to assess brown trout movement and homing and straying while accounting for incomplete detection and fish death by including parameters for capture probability and survival.

Basic structure of our multistate mark-recapture model.— We focused inferences on adult brown trout (i.e., fish over 200 mm TL) because previous modelling of brown trout in the system suggests considerable heterogeneity in capture probability and survival at lengths smaller than 200 mm (Runge et al. 2018). We fit the multistate mark-recapture model (Arnason 1973; Schwarz and Arnason 1996) with a seasonal time step (Winter: December – February, Spring: March to May, Summer: June to August, Fall: September – November) in which states were defined based on location. Specifically, we defined states one through 61 based on distance below Glen Canyon Dam in 8 river-km (rkm) bins along the Colorado River (i.e., state 1: 0 – 8 rkm below the dam, state 2: 8 – 16 rkm,…, state 61: 482 – 490 rkm). We defined state 62 as Bright Angel Creek, which joins the mainstem Colorado River ~168 rkm below Glen Canyon Dam (i.e., state 21 according to 8 rkm bins). It was not possible to estimate transitions among all these states without making parametric assumptions (i.e., it would require 3721 parameters per interval to model nonparametrically). Past research on rainbow trout movement in the Colorado River has found that the Cauchy distribution, which allows for mostly local movements along with a reasonable probability of occasional long-distance movement, provides a better approximation of movement than other distributions with thinner tails (Korman et al. 2016; Dzul et al. 2017). Under the Cauchy distribution, the probability of moving between states *i* and *j* during interval, *t*, $\tau_{i,j,t}$, separated by distance, $d_{i,j}$, is determined by potentially time varying location (l_t) and scale (s_t) parameters and given by:

$$\tau_{i,j,t} = P(d_{i,j}\,|l_t, s_t) = \frac{1}{\pi\left(s_t + \frac{(d_{i,j} \quad l_t)^2}{s_t}\right)}$$

where negative values of *d* and l_t indicate upstream movement and we discretized by assuming that distance, between states *i* and *j* was equal to *5*(i – j)* (since bins were 8 rkm long). We additionally modified our dispersal function to allow us to test hypotheses about directed movement (straying) to the Glen Canyon Dam tailwater (Lees Ferry reach; i.e., in addition to movement into the tailwater than would be predicted by $d_{i,j}$) or Bright Angel Creek (homing) as well as to allow for movement out of Bright Angel Creek. Specifically, we included two additional potentially time-varying parameters allowing for straying into the reach Lees Ferry (states 1 – 3), $\tau_{LF,t}$, and homing to Bright Angel Creek, $\tau_{BA,t}$ and a parameter allowing for movement out of Bright Angel Creek, ε_{BA}, which was always assumed to be constant. Under these assumptions, the probability of transitioning from state *i* to state *j* in interval *t*, $\psi_{i,j,t}$, is defined as:

$$if\ i < 62\ and\ j < 62 \qquad \psi_{i,j,t} = \frac{(1 \quad \tau_{BA,t})(\tau_{i,j,t} + \ \tau_{LF,t}X_{LF}[j])}{\sum_{k=1}^{61}(\tau_{i,k,t} + \ \tau_{LF,t}X_{LF}[k])}$$

$$if\ i < 62\ and\ j = 62 \qquad \psi_{i,j,t} = \ \tau_{BA,t}$$

$$if\ i = 62\ and\ j < 62 \qquad \psi_{i,j,t} = \frac{\varepsilon_{BA}(\tau_{21,j,t} + \tau_{LF,t}X_{LF}[j])}{\sum_{k=1}^{61}(\tau_{21,k,t} + \tau_{LF,t}X_{LF}[k])}$$

$$if\ i = 62\ and\ j = 62 \qquad \psi_{i,j,t} = 1 \quad \varepsilon_{BA}$$

where X_{LF} is a vector with values of 1 for the first three entries, and zeros elsewise, the first set of conditions correspond to movement in the Colorado River, the second corresponds to movement from the Colorado River into Bright Angel Creek, the third set corresponds to movement out of Bright Angel Creek into the Colorado River, and the final set corresponds to staying in Bright Angel.

Past research suggests that adult brown trout survival is relatively high and constant in this system (Runge et al. 2018; Yackulic et al. 2020) and our data were relatively sparse, so we assumed a constant survival rate in all models. Survival and movement were then combined in a single transition matrix and for ease of calculations, we also included a 63rd state representing dead fish. Electrofishing sampling in the Grand Canyon is standardized by a system of 250-meter river sites shared by all monitoring trips (see Figure 3). We calculated effort in state *i* and time period *t*, $E_{i,t}$, as the number of passes through each site in a particular state. We assumed that capture probability, *p*, for electrofishing in the Colorado River was constant at the site scale and scaled *p* to the state scale based on this effort calculation. Sampling of brown trout in Bright Angel Creek occurred during a trout suppression project (Healy et al. 2020), involved three-passes of depletion backpack electrofishing, and has previously been shown to include substantial interannual variation in capture probability (Healy et al. 2022c). We summarized the catch of adult brown trout per pass via this effort and fit depletion models to estimate the year-specific *p-star* (i.e., cumulative *p* across 3 passes; 8 parameters) for brown trout that were in

Bright Angel Creek during the winter of years with removals within the model. Since only ~20% of Bright Angel Creek was sampled in the first two years, we scaled *p-stars* accordingly.

Models considered.— All models we considered shared eleven parameters in common (one each for survival, mainstem capture probability per unit effort, probability of moving out of Bright Angel Creek (ε_{BA}), and eight parameters describing each year's capture probability in Bright Angel Creek, and differed based on parameterization of the four potentially time-varying movement parameters l_t, s_t, $\tau_{LF,t}$ and $\tau_{BA,t}$. We considered three potential time-varying covariates that were indicator variables and defined as: 1) weir = 1 during intervals the Bright Angel Creek weir was operating, and 0 elsewise, 2) Fall HFE = 1 during fall – winter intervals in which a Fall HFE occurred, and 0 elsewise, and 3) fall defined as 1 during all intervals that represented the fall to winter transition when brown trout typically spawn. We defined our model selection strategy *a priori* informed by past research in the system (Runge et al. 2018) and heeding best practices for model selection strategy identified by Morin et al. (2020). In our first stage of model selection, we considered the following models:

1) a null model (in which all movement parameters were constant);

2) two weir models in which $\tau_{BA,t}$ or $\tau_{LF,t}$ were functions of the weir covariate to test the hypothesis that the weir decreased homing into Bright Angel Creek, or led to an increase in straying into the Glen Canyon Dam tailwater;

3) three models formed from including the Fall HFE covariate on each of l_t, s_t, and $\tau_{LF,t}$ independently testing the hypotheses that Fall HFEs may have led to an upriver change in the modal direction of movement (i.e., a change in l_t), an overall increase in the scale of

movement (i.e., an increase in s_t), or an increase in straying into the Glen Canyon Dam tailwater (i.e., an increase in $\tau_{LF,t}$);

4) three models formed from including the fall covariate on each of l_t, s_t, and $\tau_{LF,t}$ independently. These models were meant to test the alternative hypothesis that changes in movement were associated with the fall-winter transition in all years as might be expected based on the timing of spawning and had nothing to do with fall experimental floods.

Before the second stage of modeling, we identified the best predictor of each parameter using Akaike's information criterion (AIC; Burnham and Anderson 2002), and whether an alternative predictor was within 5 ΔAIC (including the null model) and at least as good as the null model for that parameter (based on suggestions in Morin et al., 2020). We then examined all possible models based on combinations among parameters. We fit all models in R using the optim function and the "BFGS" method (see Appendix for more details including code) and compared models using AIC and AIC weights. We calculated 95% confidence intervals by calculating profile likelihood for each parameter of interest.

To illustrate the effects of Fall HFEs and weir operations on brown trout movements, we derived transition (movement) probabilities ($\tau_{LF,t}$ *or* $\tau_{BA,\,t}$) using parameters from the top model. We present movement probabilities from three areas of interest, including the Glen Canyon tailwater reach upstream of Lees Ferry (bin 2), from the Little Colorado River inflow reach (bin 16), and from the Bright Angel inflow reach of the Colorado River (bin 22, Figure 4). The Little Colorado River inflow reach is an area of concern for native fishes and focus of past trout suppression (see Coggins et al. 2011).

Results

We included 3,680 tagged and 398 recaptured brown trout in the Colorado River between Glen Canyon Dam (rkm -25.3) to RM 442.2, from April 2000 to January 2019, in our analysis (Figure 3). The dataset included 59 fish that were recaptured in and removed from Bright Angel Creek during suppression efforts, either through the use of the weir or backpack electrofishing. The highest captures of brown trout occurred upstream of Lees Ferry in the Glen Canyon Dam tailwater, or in the Colorado River near the mouth of Bright Angel Creek, although sampling effort varied spatially (Figure 3). We found 77 (2.1%) of fish to have moved more than 8 km, and 19 (0.5%) of the total fish included in our analysis were captured both upstream and downstream of Lees Ferry.

Our modeling results supported the hypothesis that the probability of brown trout straying to the Lees Ferry reach was higher during periods when Fall HFEs occurred. Models including the Fall HFE covariate in one of the movement parameters represented 0.91 of the Akaike weight (Table 1) and the best overall model suggested that straying to Lees Ferry was increased in years when Fall HFEs occurred (see model fit, Figure S1). Similarly, models including the weir in either the Bright Angel Creek homing or Lees Ferry straying parameter represented 0.85 of the Akaike weight and the best overall model suggested that homing to Bright Angel Creek was decreased in years when the weir was in operation. In our first stage of modeling that included covariates on a single movement parameter in each model, the Fall HFE effect on Lees Ferry reach straying ($\tau_{LF,t}$) ranked the highest using AIC, with less support for models including covariates representing weir operation on $\tau_{LF,t}$ (4.5 ΔAIC within first model set), and weir operation on $\tau_{BA,t}$ (4.8 ΔAIC) or representing fall (seasonal) straying movements (7 ΔAIC; Table 1). In the second modeling stage with combinations of the highest-ranked covariates (i.e., the best covariate for each parameter and any other covariates for the same parameter that yielded an AIC within 5), the top-ranked model included constant location (l_t) and scale (s_t) parameters, a positive effect of Fall HFEs on straying into the Lees Ferry reach and a negative effect of the weir on homing into Bright Angel Creek (Table 1, Table 2). Including the Fall HFE covariate on Lees Ferry straying in the model with a weir covariate on Bright Angel Creek homing improved AIC by 4.2, relative to a model with a weir covariate on Lees Ferry straying. Three other models ranked within 2 ΔAIC of the top-ranked model included uninformative covariates on location (l_t) and scale (s_t) parameters – we did not consider these models further (sensu Arnold 2010). Neither the null model, nor any of the models containing the seasonal (fall) effect on l_t, s_t, or $\tau_{LF,t}$ received significant support (i.e., Akaike weights <0.01; Table 1).

Estimates of movement parameters from the top model illustrate statistically and biologically significant declines in homing to Bright Angel Creek when the weir was in place and statistically and biologically significant increases in straying to Lees Ferry in years when Fall HFE's occurred (Table 2). Both effects are of similar magnitude, however the fall HFE effect is slightly more certain. To aid interpretation of the biological significance of these effects, we considered three starting locations for brown trout and estimated the expected probability of being found in any location one season later (Figure 4). As an example, a brown trout starting in the Bright Angel Creek inflow of the Colorado River is estimated to have a 0.02 transition probability per quarter into Bright Angel Creek when the weir was not in place and a 3 x 10^{-7} transition probability per quarter when it was in place. In contrast, a brown trout starting in the Bright Angel Creek inflow is expected to have a 2 x 10^{-4} probability of straying to one of the

Lees Ferry reaches in quarters without a Fall HFE and a 0.06 probability of straying to Lees Ferry in quarters when a Fall HFE occurred. The top model also provided estimates of more intuitive parameters including the capture probability in the mainstem which was estimated to be 0.05 (95% CI: 0.05 - 0.06), and quarterly survival, which was estimated to be 0.82 (95% CI: 0.80 - 0.83) (both were assumed to be constant due to sparse data).

Discussion

We used a multistate model and a long-term (19-year) mark-recapture dataset to estimate movement probabilities across 8 km river segments (cf. Dzul et al. 2017), and found evidence of increased probability of invasive brown trout colonization of a hydroelectric dam tailwater associated with fall-timed artificial floods. Our results also suggest there was support for the hypothesis that inhibiting access to primary spawning areas (using a weir) contributed to straying (Thorstad et al. 2008). Movement and dispersal are key processes that affect species' survival, recruitment, and population dynamics, including in newly invaded habitats (Radinger and Wolter 2014; Rubenson and Olden 2017; Cooke et al. 2022). Straying, which is important to maintaining genetically diverse and resilient salmonid populations, may increase in frequency when individuals are faced with barriers to spawning habitat access (Thorstad et al. 2008). We also found that a relatively small proportion of tagged and recaptured brown trout made long distance movements, similar to other studies of movements in stream salmonids in our study system (Korman et al. 2016; Dzul et al. 2017). Our results suggest that the combination of impeding access to spawning grounds and release of fall-timed HFEs contributed to increased straying to the tailwater ecosystem, setting the stage for increased recruitment reported elsewhere (Runge et al. 2018; Yackulic et al. 2020). Expansion of brown trout into the Lees Ferry reach, which contains high quality habitat capable of supporting a large population, has important implications for invasive species management and maintenance of native species in the Grand Canyon ecosystem (Runge et al. 2018; Healy et al. 2022b).

Our analysis identified fall-timed experimental floods as the most likely driver of colonization of the Lees Ferry tailwater by brown trout among the hypotheses that were previously identified by a team of experts (Runge et al. 2018). As an additional line of evidence supporting our findings, the greatest seasonal increase in abundance of large (>350 mm) adult brown trout in the Lees Ferry reach coincided with the 2014 Fall HFE (Runge et al. 2018; Yackulic et al. 2020). Brown trout spawning movements can be stimulated by high flows in the native range of the species (Ovidio et al. 1998; Svendsen et al. 2004), and increased discharge is a common stimulus for anadromous sea trout or closely related Atlantic Salmon *Salmo salar* to enter freshwater for spawning (reviewed in Aarestrup et al. 2018). For brown trout inhabiting freshwater rivers throughout their life cycle, relationships between high flows and movements are less clear or highly variable among individuals (Davis et al. 2015; Baker et al. 2020). For instance, a rare quantitative analysis of the influence of the magnitude, timing, and duration of simulated freshets released from reservoirs specifically designed to stimulate freshwater brown trout spawning migrations for conservation purposes failed to identify a migratory response in a treatment reach (Baker et al. 2020). The authors suggested this lack of a migratory response to flows spikes may have reflected the availability and widespread distribution of spawning habitats throughout the river system (Baker et al. 2020). Our study area differs, in that the availability of salmonid spawning habitat appears to be primarily limited to the Lees Ferry reach (Korman et al. 2016), or in tributaries with natural hydrology and sediment transport regimes more typical of mountain streams (Bair et al. 2019). The behavioral reaction to high flows of fall-spawning brown trout may vary depending on the season, and the existence of human-caused barriers can also influence spawning site fidelity and migratory behavior (Thorstad et al. 2008; Keefer and Caudill 2014). Our study of colonizing invasive brown trout in the Lees Ferry reach is also unique because most research addressing uncertain relationships between movements and environmental variability has been focused on river systems where brown trout populations are already well-established (Clapp et al. 1990; Davis et al. 2015).

Given observations of fall-timed spawning movements into a primary spawning tributary in GCNP (Omana Smith et al. 2012; Healy et al. 2020), we assumed that spawning periodicity would also result in fall-timed movements in the Colorado River for brown trout, regardless of the occurrence of an HFE during fall. Surprisingly, there was no support for models representing fall-timed directional movements or increases in the scale of movements during fall, as we expected for potamodromous populations of brown trout (García-Vega et al. 2017). In regulated tailwaters in the Southwest US, including within our study area, previous studies have shown little longitudinal movement of adult trout related to elevated dam discharge (Gido et al. 2000; Valdez et al. 2001). These studies were conducted during high flows coinciding with spring spawning periods, and indicated rainbow trout avoided high velocities by seeking nearby shallow nearshore habitats (Gido et al. 2000). In more recent brown trout sonic-telemetry studies following the species establishment in Glen Canyon (2018-2020), a single fish (of 39 tagged) was displaced downstream >100 km coinciding with the 2018 Fall HFE, while most fish remained near locations where they were tagged in the Lees Ferry reach (Schelly et al. 2021). Our findings, along with others, suggest the influence of season and flooding can have variable effects on the direction and scale of movements of salmonids (Clapp et al. 1990; Davis et al. 2015; Baker et al. 2020).

The relationship between fall floods and upstream movements by brown trout residing downstream does not fully explain the rapid population growth observed in the Lees Ferry reach (see Yackulic et al. 2020). While direction of the homing parameter effect related to Fall HFE occurrences was positive, the magnitude of the effect was relatively small. We also note that our study did not address an additional hypothesized link between recruitment rates and fall-timed floods or other factors (Runge et al., 2018), which deserve further study. Regardless, we posit that our findings are biologically significant, because even a small number of colonizers could overcome an Allee threshold by offsetting depensation, and lead to rapid population growth toward carrying capacity (Drake and Lodge 2006). Salmonid populations are known to quickly rebound from low abundances following mortality events in both native (Vincenzi et al. 2016; Budy et al. 2021) and introduced ranges (Meyer et al. 2006; Saunders et al. 2015; Healy et al. 2022b). Brown trout expansion also coincided with the rapid population decline of a potential competitor, rainbow trout, due to intraspecific competition (Korman et al. 2021). Open foraging niche space created for juvenile brown trout (Whiting et al. 2014; Dodrill et al. 2016), and the loss of spawning bed interference following declines in rainbow trout abundance (Hayes 1987), could have also contributed to rapid brown trout population growth. Additional study of long term data is needed to assess effects of flow experiments, temperature, nutrient dynamics, and rainbow trout abundance and other hypothesized mechanisms driving brown trout reproductive rates (Runge et al. 2018).

Our study was not designed as an experiment *per se*, with potentially confounding overlapping GCDAMP treatments. Additional types of flow experiments, including steady flows on summer weekends designed to reduce desiccation and mortality of macroinvertebrate eggs that were initiated several years after Lees Ferry brown trout expansion (Kennedy et al. 2016), and high and steady flows meant to equalize Colorado River reservoir elevations in 2011, were not included in our analysis. Limited data were also available to assess whether flooding occurring outside of fall season would stimulate similar upstream movements. Only a single spring-timed experimental flood event (2008; Cross et al. 2011) and single equalization flow (2011) occurred during our 20-year study period – both of which occurred prior to increases in brown trout abundance. A limitation of our analyses was that in no years during the brown trout expansion did a Fall HFE occur independently of the weir. Nonetheless, we were able to incorporate contrasting treatments into our modeling (i.e., weir treatment without an HFE) – if both the weir and Fall HFEs had important effects on Lees Ferry colonization we would have expected to see higher movement rates when both occurred.

Finally, notwithstanding the evidence we provide associating Fall HFEs with Glen Canyon brown trout colonization, the mechanisms ultimately driving upstream movements are also somewhat difficult to discern, given that life histories of fishes may involve cued migratory responses to co-varying stream discharge and water temperature (reviewed in Cooke et al. 2022). Additional variation in water temperature was associated with Fall HFEs downstream of Glen Canyon Dam (Supplemental Information, Figure S2), but the magnitude of variation was much greater for changes in flow (see Figure 2). Regardless of potentially confounding factors that limit cause-and-effect determinations, our long-term dataset allowed for the identification of fall-timed floods as a primary driver of brown trout emigration into Lees Ferry.

Management implications.— Flooding is generally considered to be beneficial to native fishes in rivers where hydrologic alterations facilitate invasive species establishment (Mims and Olden 2012; Rogosch et al. 2019; Boddy and McIntosh 2021). Flow experiments using Glen Canyon Dam discharge were designed, in part, to benefit rearing of larval and juvenile native fishes by building backwater habitats, however the impact of backwaters on native fish recruitment near the Little Colorado River is relatively small (Dodrill et al. 2015) and has not been well studied elsewhere. Daily load-following fluctuating flows for hydropower generation likely limit the stability of backwater habitats for rearing of larval native fishes, obscuring links to native fish recruitment when compared to recent warming Colorado River temperatures (Van Haverbeke et al. 2017; Dibble et al. 2021). Fall-timed flooding is also somewhat outside the range of natural timing in the pre-dam Colorado River (see Figure 2), and de-synchronized from spring native fish reproductive periods when floods could be of benefit to recruitment (Humphries et al. 2020; Healy et al. 2020). Late winter or spring-timed high flows also limit brown trout (Lobón-Cerviá 2004; Healy et al. 2022b) and rainbow trout recruitment in some tailwaters beyond our study system (Dibble et al. 2015), and may potentially benefit aquatic macroinvertebrate communities (Carlisle et al. 2017). Thus, shifting high flow experiments or other types of designer flows to the spring, or even early summer, may provide greater benefits to both native fish and rainbow trout and disadvantage brown trout.

Ecological effects of artificial floods are often difficult to predict, and the relationships between changes in flow magnitude and fish movement are variable (Gillespie et al. 2015); our study shows support for unanticipated upstream movement of an invader associated with fall experimental flooding. We also found evidence that inhibiting access to a spawning area could increase straying and colonization of new habitats, counter to the intent of weir operations as a component of a suppression program. Dispersal and connectivity between subpopulations have important influences on native and invasive salmonid metapopulation resiliency and persistence (Rieman and Dunham 2000; Day et al. 2018; González-Ferreras et al. 2019; Healy et al. 2022b). While the weir limited access to spawning habitat for large migratory individuals and likely contributed to the brown trout decline in Bright Angel Creek (Healy et al. 2020), changes in the weir design could be considered to increase catch and removal rates and minimize straying to other potential spawning areas. Otherwise, frequent fall high flows and limiting access to tributary spawning habitat may offset attempts to control brown trout at the metapopulation scale by increasing dispersal rates to the Lees Ferry reach (Healy et al. 2022b).

Given the emphasis of conservation programs on restoring natural flow regimes for maintenance of ecological processes and services (Yarnell et al. 2020; Tonkin et al. 2021), our study highlights the need for managers to consider how changing conditions during or following designer flow experiments may affect invasion dynamics in anthropogenically altered river system. Our results reinforce the need to monitor and synthesize responses of flow experiments across physical and biological resources, which is often lacking (Olden et al. 2014). Knowledge gained through our analysis can inform tradeoff considerations for flow management decisions and improve predictions necessary to adaptively manage river ecosystems.

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Author Contribution Statement

Conceptualization, data curation, methodology, and writing-review & editing was conducted by BH, CY, and RC. CY conducted formal analysis, and BH and CY completed visualizations with input from RC.

Competing Interests Statement

The authors declare there are no competing interests.

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Data availability statement

Data generated or analyzed during this study are available from the USGS ScienceBase (Yackulic et al. 2022b).

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Figure Captions

FIGURE 1. Map of the study area, including the location of Bright Angel Creek within Grand Canyon National Park, Arizona, and the Glen Canyon Dam tailwater downstream of Lake Powell and upstream of the Paria River confluence. The Colorado River basin delineation is shaded in the inset. Maps were created with ArcGIS Desktop (ArcMap) v. 10.6.1 (NAD83 map projection, coordinates: UTM; data source: National Park Service 2019, public data, no permission required for use).

FIGURE 2. Hydrology of the Colorado River below Glen Canyon Dam (USGS gaging station at Lees Ferry USGS Gaging Station 09380000) from 1920 – 2020 (left), during the duration the duration of the study (upper right panel), including the history of high flow experiments (Fall HFEs, indicated by arrows) and fall-winter operations of the Bright Angel Creek weir (gray bars), and continuous discharge at Glen Canyon Dam during the month prior to, during, and after Fall HFEs.

FIGURE 3. Distribution of captures and re-captures of passive-integrated transponder (PIT)- or FLOY tagged brown trout by 8 km bin from Glen Canyon Dam (river km 0) to the extent of brown trout captures (river km 400), with the locations of Lees Ferry and Bright Angel Creek denoted by dashed lines (top), and electrofishing effort (number of 250 m electrofishing passes; bottom). Captures and recaptures are plotted so that no movement between captures and recaptures would be illustrated on a 1:1 line, with downstream movements indicated by points above the line, and upstream movements directional movements would plot below the diagonal.

Figure 4. Log-probability of movements by 8 river km bin based on tagging and release of brown trout in the Lees Ferry (a), Little Colorado (b), or Bright Angel Inflow (c) reaches of the Colorado River. Models depicted include a base model with no weir or High Flow Experiment (HFE) implemented (black line), and the top model showing predicted movement during seasons with a Fall HFE and the installation of the weir in Bright Angel Creek (blue line).

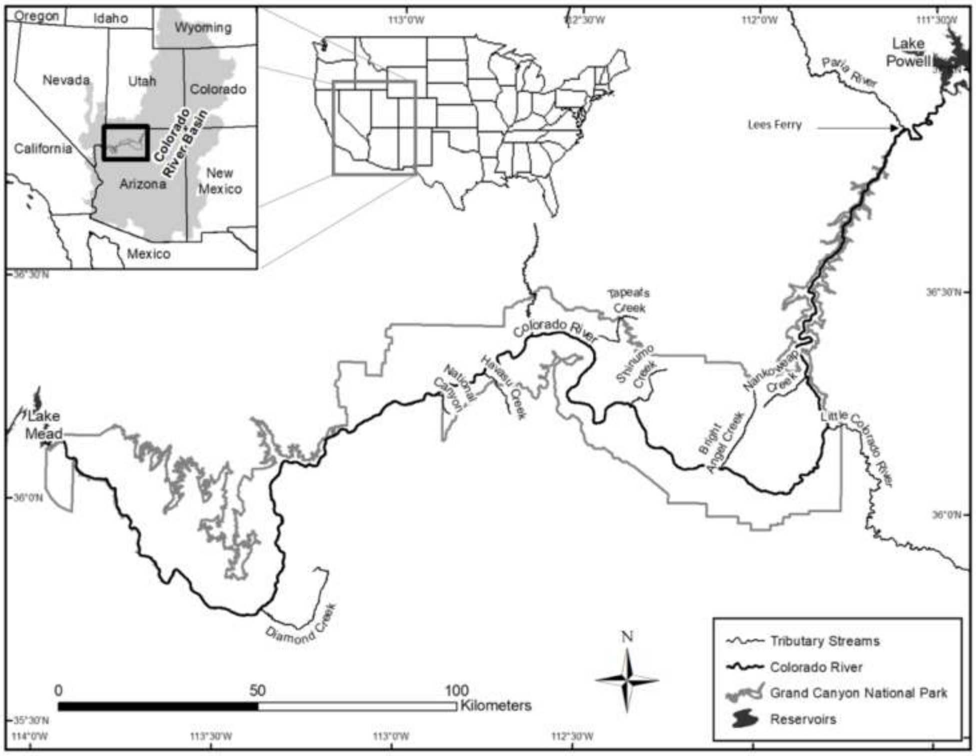
Table 1. Results of multi-state model selection, with covariates on location (*l*) or direction of movement, scale of movement (s), homing to Bright Angel Creek (τ_{BA}) and straying to the Glen Canyon tailwater upstream of Lees Ferry (τ_{LF}).

Location (*l*)	Scale (s)	Bright Angel homing (τ_{BA})	Lees Ferry straying (τ_{LF})	*ΔAIC*	K	nll	AIC weight
		Second Stage: covariates on multiple parameters					
-	-	weir	FHFE	0	17	37225.5	0.60
-	~~FHFE~~	~~weir~~	~~FHFE~~	~~1.3~~	~~18~~	~~37225.2~~	
~~FHFE~~	-	~~weir~~	~~FHFE~~	~~1.8~~	~~18~~	~~37225.4~~	
~~FHFE~~	~~FHFE~~	~~weir~~	~~FHFE~~	~~1.9~~	~~19~~	~~37224.5~~	
FHFE	FHFE	weir	-	2.1	18	37225.6	0.21
-	-	weir	weir	4.2	17	37227.7	0.07
-	~~FHFE~~	-	~~FHFE~~	~~5.8~~	~~17~~	~~37228.4~~	
~~FHFE~~	-	-	~~FHFE~~	~~6.3~~	~~17~~	~~37228.7~~	
~~FHFE~~	~~FHFE~~	-	~~FHFE~~	~~6.4~~	~~18~~	~~37227.7~~	
FHFE	FHFE	-	-	6.6	17	37228.8	0.02
-	FHFE	weir	-	8.5	17	37229.8	0.01
FHFE	-	weir	-	8.9	17	37230	0.01
		First Stage: covariate on one parameter at a time					
-	-	-	FHFE	4.5	16	37228.8	0.06
-	-	-	weir	9	16	37230.9	0.01
-	-	weir	-	9.3	16	37231.2	0.01
-	-	-	fall	11.5	16	37232.3	<0.01
-	FHFE	-	-	13	16	37233.1	<0.01
FHFE	-	-	-	13.4	16	37233.2	<0.01
-	-	-	-	13.7	15	37234.4	<0.01
~~fall~~	-	-	-	~~15.5~~	~~16~~	~~37234.3~~	
-	~~fall~~	-	-	~~15.6~~	~~16~~	~~37234.3~~	

Note: Models are ranked using Akaike's Information Criterion (*AIC*), and we considered models within 2 *ΔAIC* of the top-ranked model, and without uninformative parameters (denoted in light gray text and crossed out), as supported. Fall high flow experiment = FHFE, covariate denoting periods when the weir was operated = weir, K=number of parameters, and nll=negative log-likelihood.

Table 2. Estimates of movement parameters from the top model based on AIC.

Parameter	Mean	2.5% quantile	97.5% quantile
Location (l_t)	0.54	0.38	0.68
Scale (s_t)	0.61	0.46	0.75
Emigration from Bright angel (ε_{BA})	1.2 x 10^{-6}	7.5 x 10^{-7}	0.05
Homing to Bright angel ($\tau_{BA,t}$) with no weir	0.02	0.01	0.03
Homing to Bright angel ($\tau_{BA,t}$) with weir	2.8 x 10^{-7}	1.8 x 10^{-7}	3.9 x 10^{-7}
Straying to Lees Ferry ($\tau_{LF,t}$) with no fall HFE	1.4 x 10^{-7}	8.8 x 10^{-8}	2.0 x 10^{-7}
Straying to Lees Ferry ($\tau_{LF,t}$) with fall HFE	6.3 x 10^{-3}	2.5 x 10^{-3}	0.01



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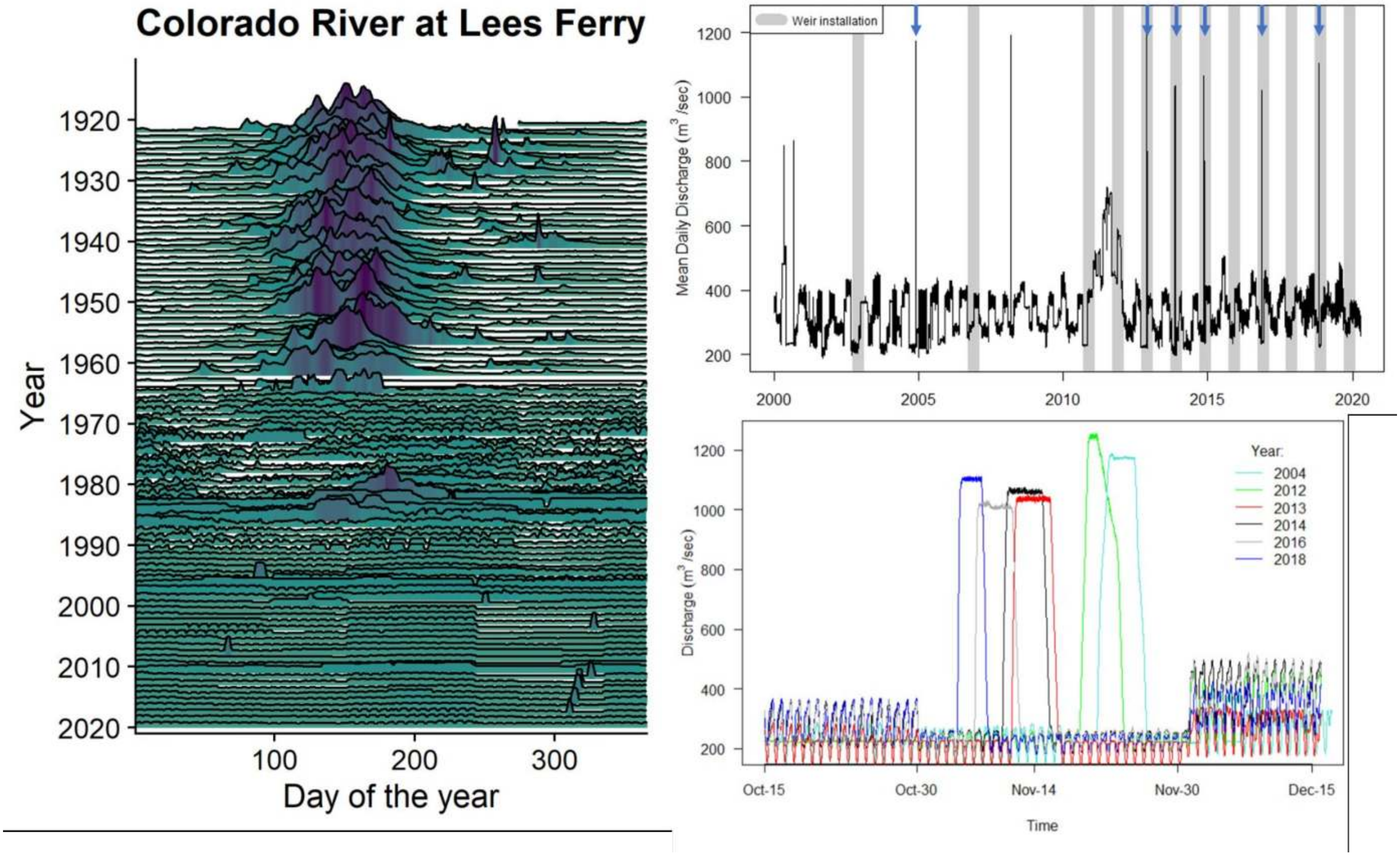
243x189mm (150 x 150 DPI)



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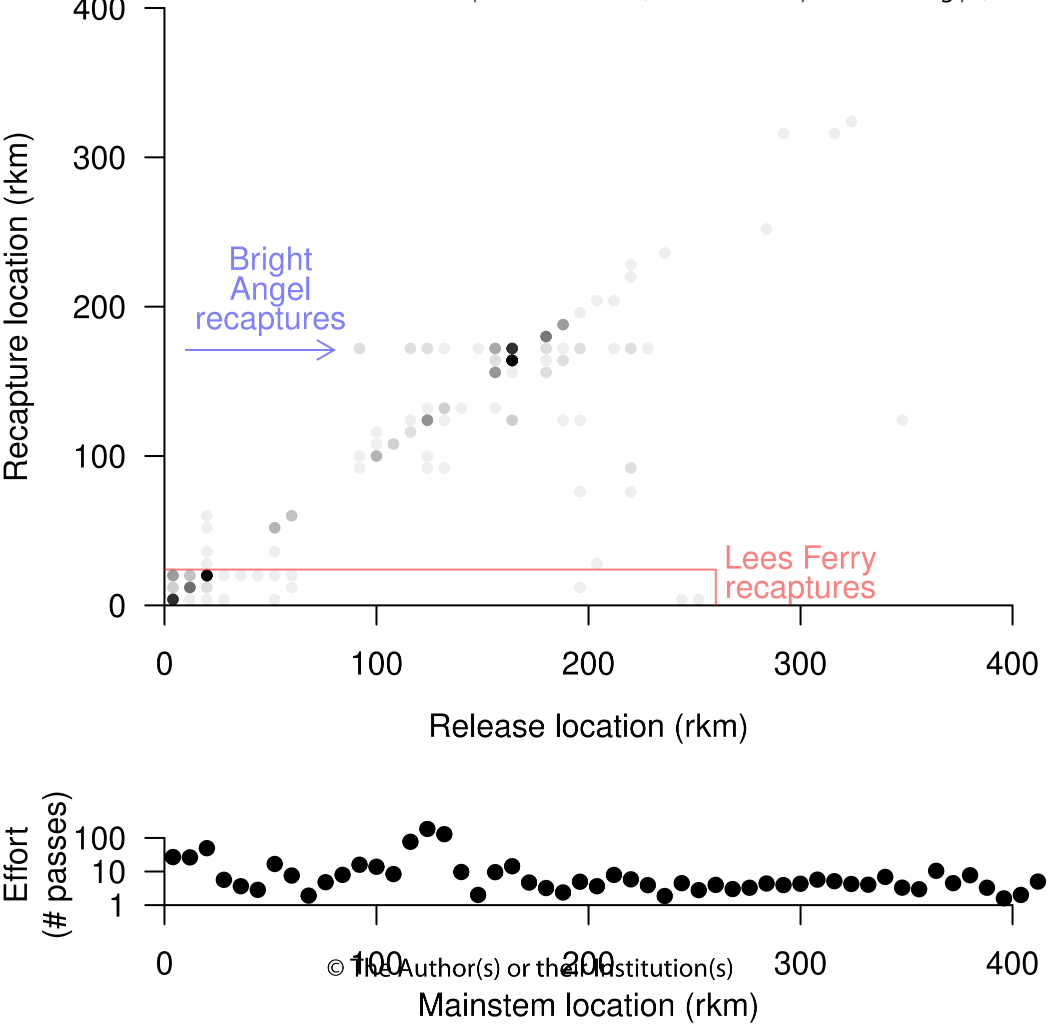
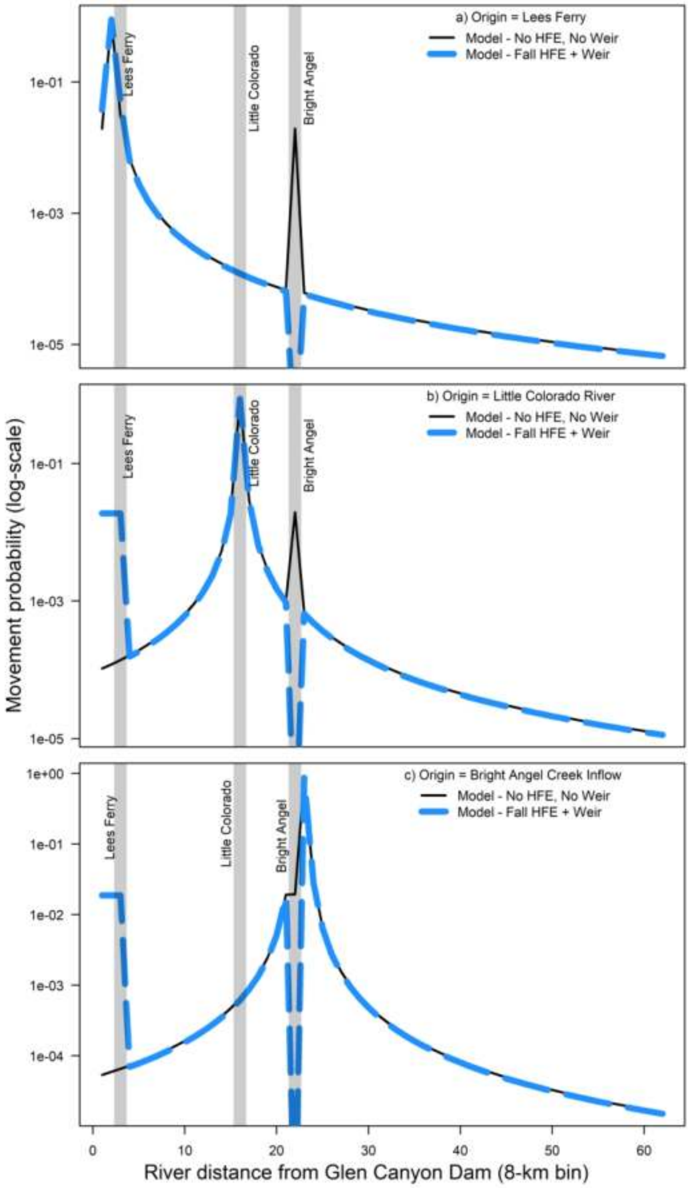

Recapture location (rkm)
400
300
200
100
0
Bright Angel recaptures
Lees Ferry recaptures
0
100
200
300
400
Release location (rkm)
Effort (# passes)
100
10
1
0
100
200
300
400
Mainstem location (rkm)



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149x249mm (300 x 300 DPI)