

# Partial migration and spawning movements of humpback chub in the Little Colorado River are better understood using data from autonomous PIT tag antennas

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**Abstract:** Choosing whether or not to migrate is an important life history decision for many fishes. Here we combine data from physical captures and detections on autonomous passive integrated transponder (PIT) tag antennas to study migration in an endangered fish, the humpback chub (*Gila cypha*). We develop hidden Markov mark-recapture models with and without antenna detections and find that the model fit without antenna detections misses a large proportion of fish and underestimates migration and survival probabilities. We then assess survival and growth differences associated with life history strategy and migration for different demographic groups (small male, small female, large male, large female). We find large differences in survival according to life history strategy, where residents had much lower overwinter survival than migrants. However, within the migratory life history strategy, survival and growth were similar for active migrants and skipped migrants for all demographic groups. We discuss some common challenges to incorporating detections from autonomous antennas into population models and demonstrate how these data can provide insight about fish movement and life history strategies.

**Résumé :** La décision de migrer ou non est une importante décision du cycle de vie de nombreux poissons. Nous combinons des données de captures physiques et de détections par des antennes autonomes pour transpondeurs passifs intégrés (étiquettes PIT) afin d'étudier la migration chez un poisson en voie de disparition, le chevesne à bosse (*Gila cypha*). Nous développons des modèles de Markov cachés de marquage-recapture avec et sans détections par antenne et constatons que le calage du modèle sans détections par antenne ne relève pas une grande proportion des poissons et sous-estime les probabilités de migration et de survie. Nous évaluons ensuite les différences sur le plan de la survie et de la croissance associées à la stratégie de survie et à la migration pour différents groupes démographiques (petits mâles, petites femelles, grands mâles, grandes femelles). Nous relevons de grandes différences sur le plan de la survie selon la stratégie de survie, la survie hivernale étant bien plus faible pour les individus résidents que pour les migrants. Cela dit, parmi les poissons adoptant une stratégie migratoire, la survie et la croissance sont semblables entre les migrants actifs et ceux qui sautent une migration, et ce, pour tous les groupes démographiques. Nous abordons certaines des difficultés courantes associées à l'incorporation de détections par antenne autonome à des modèles démographiques et démontrons comment ces données peuvent fournir des renseignements utiles sur les déplacements et les stratégies de survie des poissons. [Traduit par la Rédaction]

## Introduction

An individual's decision to migrate, or not, is an important life history strategy decision faced by many organisms. The impetus for migration can be better forage (Holdo et al. 2009; Yackulic et al. 2017), lower competition (Grayson et al. 2011; Nilsson et al. 2006), improved reproduction (Hebblewhite and Merrill 2011), or reduced predation (Skov et al. 2013) at the destination. However, there can also be costs associated with the act of migration (Hein et al. 2012), such as increased energetic expenditures, predation risk (Hebblewhite and Merrill 2007), or reduced foraging (Chapman et al. 2013) associated with travel. Often, only a subset of the

population migrates, and this is known as partial migration (Chapman et al. 2011). Understanding patterns of partial migration can provide context for interpreting behavior and adaptation (Chapman et al. 2012; Lundberg 1988), thereby helping biologists understand mechanisms of population change (Hebblewhite and Merrill 2011; Nelson et al. 2002; Nilsson et al. 2006).

Assessing partial migration dynamics from capture-recapture data requires a large number of recaptures, and thus low recapture probabilities (which are often observed in fishes) limits the sample sizes needed for analysis. For this reason, capture-recapture studies of fishes have increasingly relied on other detection methods, such as radiotelemetry (Skalski et al. 2002), passive acoustic

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receivers (Dudgeon et al. 2015), and autonomous passive integrated transponder (PIT) tag antennas (Pearson et al. 2015). Compared with radio tags and acoustic tags, PIT tags are small and inexpensive and are thus most advantageous when marking large numbers of individuals in small systems (Cooke et al. 2013). Autonomous PIT tag antennas are placed in a fixed site within a fish's habitat to continuously record PIT tags of fish that swim by. These continuous data are especially useful for assessing temporal patterns in fish movements (Cathcart et al. 2018a; Kanno et al. 2014), evaluating spawning patterns associated with movement (Haraldstad et al. 2018; Pearson et al. 2015), identifying movement barriers to fish migrating along a riverine corridor (Aarestrup et al. 2003; Cathcart et al. 2018b; Piper et al. 2013), quantifying escapement (Wolter et al. 2013) or emigration of recently translocated fish out of the translocation site (Banet and Hewitt 2019; Spurgeon et al. 2015), or measuring invasion potential (movement) by non-native fishes (Dzul et al. 2018).

Our study uses autonomous PIT antenna data to assess partial migration in adult humpback chub (*Gila cypha*) that spawn in the Little Colorado River (Grand Canyon, Arizona). Our broad goals were twofold: first, to incorporate antenna data into the mark-recapture model framework and to assess what benefit (if any) antenna detections provide; second, to use this model to learn more about humpback chub ecology and migration. Numerous studies have evaluated humpback chub population dynamics using mark-recapture methods (Coggins et al. 2006; Van Haverbeke et al. 2013) and found that adult humpback chub move from the cold mainstem Colorado River (hereinafter CR) to a warm water tributary (the Little Colorado River, hereinafter LCR) in spring and return to the main stem in late spring, summer, or fall (R. Ryel and R.A. Valdez, unpublished data). However, one limitation of these mark-recapture methods has been the low recapture probabilities of adult humpback chub (>200 mm total length (TL)) with conventional gear types (i.e., unbaited hoop nets and electrofishing) in the CR. To address this shortcoming, autonomous PIT antennas were added as a supplemental gear type in the LCR (in 2009) and in the CR (in 2016) and continue to operate until present.

The first goal required developing a modeling framework for using PIT antenna detections in the mark-recapture model. Using this new model framework, we compared parameter estimates from models fit with and without antenna data to determine the (potential) benefit of including PIT antenna detections in mark-recapture models. During model development, we encountered three challenges for PIT antenna detection data that we believe are likely common to other study systems: the availability challenge, the continuous time challenge, and the state uncertainty challenge. The first two challenges pertain to using continuously operating antennas and the third challenge pertains to all PIT antennas. The availability challenge arises because stationary antennas only detect fish within a limited spatial extent so that fish that are located far from antennas and (or) fish that are less mobile are less detectable or undetectable. The continuous time challenge arises because if the window for PIT antenna detections is wide (e.g., fish can be detected over the course of weeks or months), then fish can be detected and die within the same sampling occasion and this can bias survival in discrete-time models (Barbour et al. 2013; Conner et al. 2015). Lastly, the state uncertainty challenge occurs because some physical attributes of fish (e.g., size, sex, ripeness) are not observable on antennas. In particular, size uncertainty of antenna detections may be problematic because size often influences capture probability (Dauwalter and Fisher 2007; Hense et al. 2010; Korman et al. 2009), but fish size is not observable with antenna detections.

The second goal involved characterizing yearly and within-population variability in survival, abundance, and movement rates. More specifically, recent mark-recapture studies have identified three migration patterns in this population, including LCR residents — a group that resides in the LCR year-round, migrants —

a group that migrates from the CR into the LCR in spring (presumably to spawn), and skipped migrants — a group that resides in the CR for a given year (Yackulic et al. 2014). The LCR resident group is fairly distinct and has faster growth and lower survival compared with the migrant and skipped migrant groups (Yackulic et al. 2014), yet it is unknown whether fish in the resident category are a fixed group or whether residents can change their migratory life history strategy and move to the CR as adults. The migrant and skipped migrant groups are not fixed, so that migrants can become skipped migrants and vice versa (Pearson et al. 2015). We evaluated yearly variability in the probability of migration in four different demographic groups (small females, large females, small males, and large males) and developed a model to compare survival and growth rates for residents, migrants, and skipped migrants in each demographic group. Insight into the migratory dynamics and life history variability of humpback chub may help illuminate why this species was able to persist in Grand Canyon after construction of Glen Canyon Dam.

## Methods

### Study species

There are currently five recognized populations of humpback chub, four of which occur in the upper Colorado River Basin (above Lake Powell) and one that occurs in the lower Colorado River Basin in Grand Canyon. Our study focused on the Grand Canyon population, specifically on the subset of population that spawns in the LCR (Fig. 1). Within Grand Canyon, reduction in abundances of humpback chub and other native fishes coincided with construction of Glen Canyon Dam in 1963 and filling of the upstream reservoir, Lake Powell. It is hypothesized that humpback chub persisted in Grand Canyon after construction of Glen Canyon Dam due to the LCR spawning migration (Douglas and Marsh 1996; Kaeding and Zimmerman 1983), because the warmer water temperatures in the LCR are more favorable for spawning and larval development compared to water temperatures in the CR (Kaeding and Zimmerman 1983).

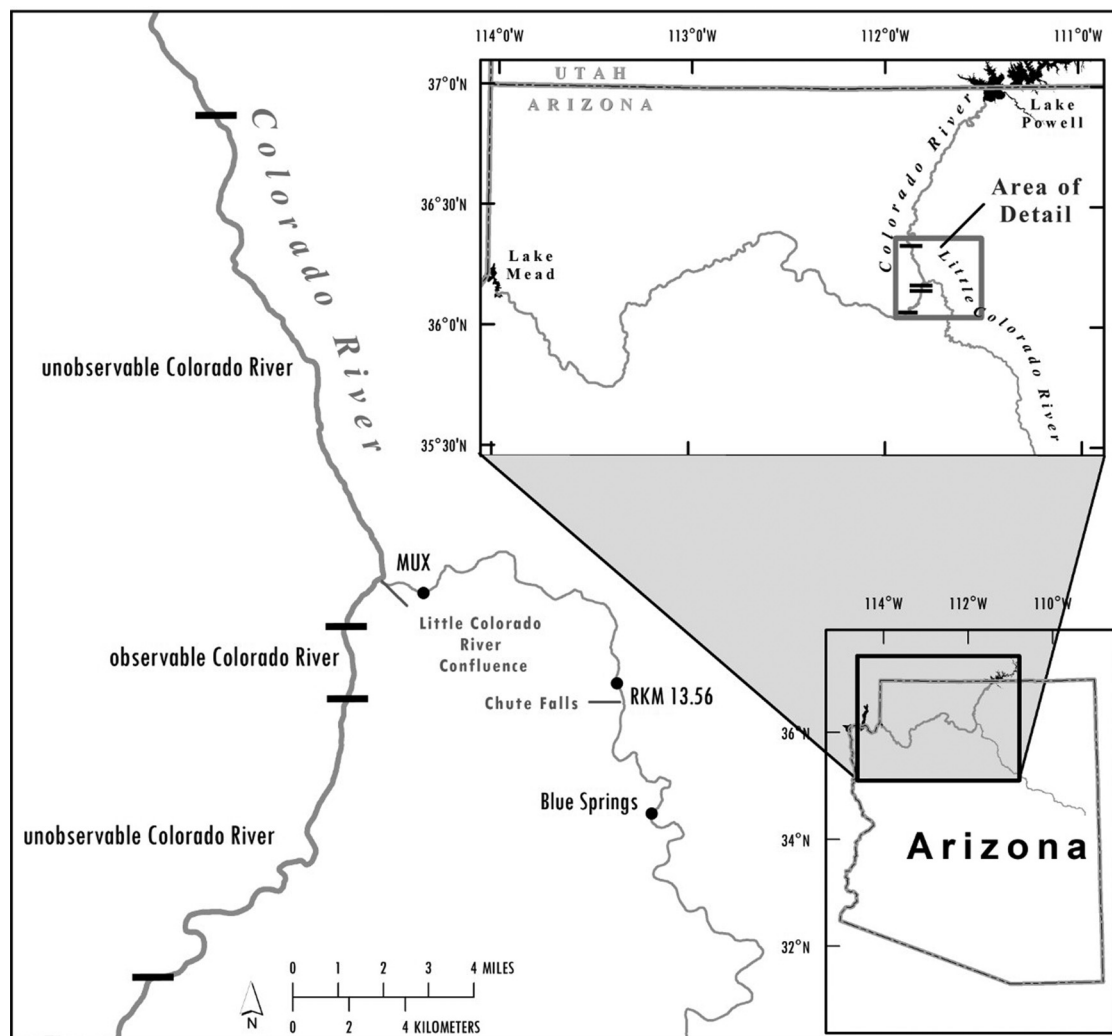
Most movements between the CR and LCR occur in March–May, coincident with spawning timing in the LCR (R. Ryel and R.A. Valdez, unpublished data). Movement back from the LCR to the CR is more prolonged and can occur May–November (R. Ryel and R.A. Valdez, unpublished data), though there is some evidence that large humpback chub >300 mm TL exit the LCR by June (Gorman and Stone 1999). A study of humpback chub ripeness concluded that spawning commenced in late March (when water temperatures were ~14 °C), peaked in mid-April (when flow was returning to baseflow conditions), and then decreased substantially by mid-May (Gorman and Stone 1999). While most reproduction for LCR-spawning humpback chub occurs in spring, there is evidence that spawning can occur at lower levels year-round (Brizendine 2016; Robinson et al. 1998). Some proportion of the age-0 humpback chub born in the LCR will outmigrate to the CR during their first year, most commonly between midsummer and mid-fall during the monsoon season (Yackulic et al. 2014).

Mark-recapture studies have suggested there is variability in migratory strategies within LCR spawning humpback chub. Specifically, Douglas and Marsh (1996) observed that a small proportion of humpback chub did overwinter in the LCR (i.e., were LCR residents), and Yackulic et al. (2014) found evidence that the LCR resident group was composed of the same individuals from year to year. Furthermore, Pearson et al. (2015) and Yackulic et al. (2014) found evidence for skipped migration within the group of humpback chub that overwintered in the mainstem CR.

### Study site

Here we refer to distances in the CR as river kilometres (rkm) downstream of Glen Canyon Dam, Arizona, and distances in the LCR as rkm upstream of the LCR–CR confluence. The sampling site in the CR (i.e., observable Colorado River site; hereinafter

**Fig. 1.** Map depicting the Colorado River (CR) near its confluence with the Little Colorado River (LCR) in northern Arizona. In the LCR, the multiplexer (MUX) arrays and lower Atomizer Falls (13.56 km) bound the spatial boundaries (in the LCR) for humpback chub that migrate between the LCR and CR. In the CR, bars depict the boundaries of the observable and unobservable CR reaches used in the analysis. The map was created using Esri ArcGIS desktop software, version 10.7.1, using map features in Gushue (2019).



oCR) was located just downstream of the LCR confluence (rkm 127–129.7; Fig. 1). To exclude fish that did not spawn in the LCR, we only included humpback chub captured in eastern Grand Canyon or lower Marble Canyon (here defined to be between rkm 105.5–127.0 and rkm 129.7–145.7; or unobservable Colorado River sites; hereinafter uCR).

The LCR stretches from its headwaters in the White Mountains (eastern Arizona) to the Grand Canyon but is ephemeral in its mid-reaches. Humpback chub occur only in the lower portion of the LCR, which is perennial and fed by Blue Spring (rkm 20.7). Unlike the regulated CR, flow in the lower LCR is primarily influenced by precipitation, and accordingly it displays a more natural hydrothermal regime, with seasonal floods occurring in winter–spring (from snowmelt) and fall (from rainfall; Dean and Topping 2019). The lower 13.56 rkm of the LCR (below Lower Atomizer Falls) was sampled by the US Fish and Wildlife Service (USFWS) four times each year as part of long-term monitoring. Antenna detections in the LCR came from an antenna system composed of two multiplexer arrays (MUX), which spanned the

entire width of the LCR and was located ~1.8 km upstream of the LCR–CR confluence. Fish that moved from the CR into the LCR passed over the MUX, and accordingly the MUX provided additional detection information about migrants. All migrants must move into the LCR and thus most are susceptible to MUX detection, the exception being fish that only move into in the lower 1.8 km of the LCR and thereby do not swim up to the MUX. For this reason, migrants that do not swim past rkm 1.8 were confounded with skipped migrants.

#### General overview of model and sampling

Data generated during this study are available from the USGS ScienceBase-Catalog (Dzul 2021). Data used to fit the model came from spring and fall mark-recapture sampling events in the CR and LCR for spring 2009 – spring 2019. Here we describe sampling methods briefly, but more details about sampling protocols are included in online Supplementary Material (S1)<sup>1</sup>. Spring and fall LCR sampling included two spring and two fall trips each year, which were roughly timed to occur in April and May (spring trips)

<sup>1</sup>Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2020-0291>.



and September and October (fall trips). During LCR sampling trips, each unbaited hoop net was set for ~72 h and checked every ~24 h so that each hoop net was checked three times (i.e., had three passes). However, in some years only two passes occurred due to logistical complications. Spring and fall sampling trips to the CR each included only one trip per year and occurred in April–May (spring) or September–October (fall). Unbaited hoop nets in the CR were also set for 24 h intervals and checked either 6 or 10 times (depending on the trip type). Additionally, CR sampling included three passes of electrofishing. In some years in the CR (i.e., 2016 and 2018), we used PIT antenna detection data from baited submersible antennas (Biomark, Inc.) that were deployed for 6- to 10-day periods in conjunction with electrofishing and hoop netting.

We developed and fit an hidden Markov model (HMM; MacDonald and Zucchini 1997) with 20 states to estimate migration and survival probabilities. These 20 states represented every combination of five migration strategy categories (which correspond with spawning or location status) and four demographic categories (which correspond with sex and size). We refer to the five migration categories as follows: LCR resident, oCR migrant, uCR migrant, oCR skipped migrant, and uCR skipped migrant. While residents and skipped migrants were assumed to remain year-round in the LCR and CR, respectively, migrants were assumed to move into the LCR in spring and could be found in either the CR or the LCR in fall. Therefore, only migrant categories were detectable on the MUX (after filtering out fish that lingered over the array and were detected more than once over the course of 2–13 days).

Additionally, following Yackulic et al. (2014), there were two different categories that corresponded to sampled (oCR) and nonsampled (uCR) segments of the Colorado River, for both the migrant and skipped migrant categories. Note that uCR migrants were only unobservable in the CR and could be detected on the MUX or captured while in the LCR, whereas uCR skipped migrants were completely unobservable. The four demographic categories included small (200–249 mm TL) and large (250+ mm TL) males and females. The size of fish was known when a fish was live-captured but was unknown when fish were detected on PIT antennas or completely undetected. The sex of a fish was known only if it was captured as a ripe individual that expressed gametes; otherwise, fish were classified as unknown sex. Restrictions were placed on the transition matrix to help with parameter estimation (see below).

### Revisiting common challenges to using PIT antenna data

The availability challenge presented in our study included two components. The first component refers to availability for detection on the MUX. The MUX can only detect fish that are actively moving between the CR and LCR and over the array; it cannot detect fish once they move upstream or downstream of the array. Therefore, the temporal window for MUX detections must be wide enough to ensure all migrants move into the LCR (and hence are detectable on the MUX) during this interval. Initial analysis suggested that February through June was a reasonable time frame. This wide temporal window required some additional considerations (discussed as part of the continuous time challenge). The second component refers to availability for physical capture because we were concerned that some migrants were not in the LCR during spring sampling trips due to the wide temporal movement window (Pearson et al. 2016). To address this concern, we include parameters to account for the lack of geographic closure within spring sampling events (see Data model description below).

The continuous-time challenge pertained to using a wide temporal window for MUX detections, as studies have illustrated that treating continuous resight detections as occurring in discrete time can produce bias in survival estimates (Barbour et al. 2013;

Conner et al. 2015). To address this issue, our first approach was to incorporate MUX detections as continuous auxiliary data within the discrete-time mark-recapture model (sensu Barker 1997; W. Kendall, unpublished data). Our first approach, combined with the complex multistate structure and state uncertainty, proved to be prohibitively slow (i.e., required >1 week to run with only 100 posterior draws) and did not converge. Instead, we used a HMM model structure that allows for state uncertainty (Pradel 2005), with MUX detections incorporated into an open robust design (Kendall et al. 2019) structure for spring sampling. We expect minimal bias in survival estimates because survival probabilities are high (Barbour et al. 2013; Conner et al. 2015). Also, although the window for MUX detections is wide (February–June), these detections are not continuous over the entire yearly survival, so that annual survival rates should be minimally affected. We nevertheless assess the potential bias of this approach in the Supplementary Material (S2)<sup>1</sup>.

The state uncertainty challenge arises because many fish attributes (i.e., size) are not observable with antenna detection and because other attributes (e.g., migratory status and sex) are not reliably assessed with each physical capture. Our study includes many forms of state uncertainty. For example, a fish captured in the LCR can be either a migrant or a resident and a fish captured in the CR can be either a migrant or a skipped migrant. Additional forms of uncertainty include sex (if a fish is not ripe at capture) and size class (if fish observation is an antenna detection). Obtaining state-specific abundance estimates (e.g., estimates of migrants, skipped migrants, residents) required accounting for uncertainty in state assignment, and we describe our approach in the Supplementary Material (S3)<sup>1</sup>.

### Process model

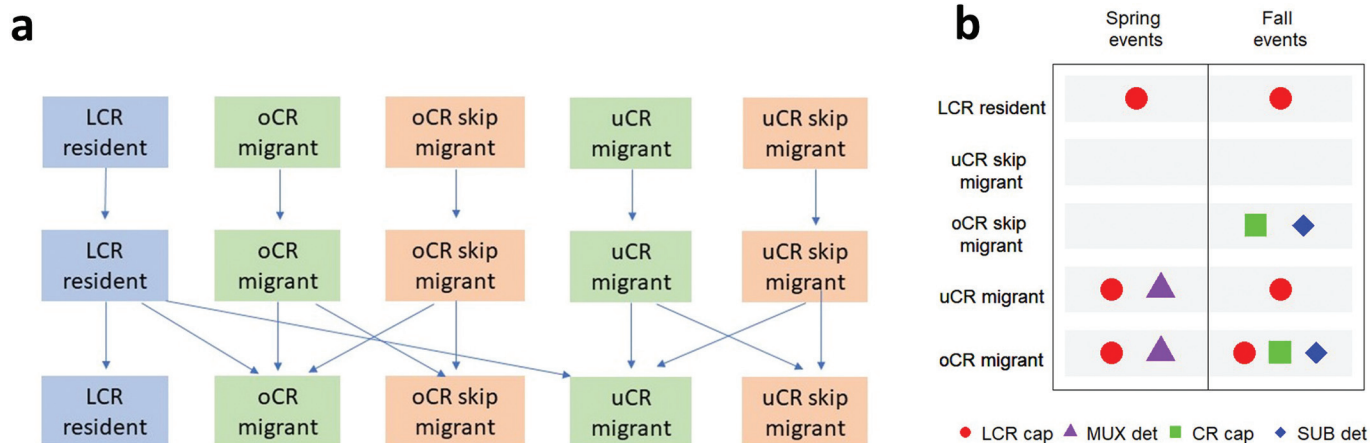
Model parameters for the process model included survival, growth, and migration probabilities (Table 1). The model operated on a semiannual time step with two seasons: over summer (April to October) and during winter (October to April; Fig. 2a). Parameters were allowed to vary by migration strategy ( $h$ ; where 1 = resident, 2 = oCR migrant, 3 = uCR migrant, 4 = oCR skipped migrant, 5 = uCR skipped migrant), size ( $w$ ; where 1 = small, 2 = large), sex ( $n$ ; where 1 = male, 2 = female), year ( $t$ ; where 1 = year 1, 2 = year 2, etc.), and (or) season ( $k$ ; where 1 = spring–summer, 2 = fall–winter). Transition probabilities were a function of survival ( $S_{w,n,h,k,t}$ ), growth ( $g_{n,h,k}$ ), and migration ( $m_{w,n,h,k,t}$ ) parameters, where fish survived first, then grew, then migrated. For example, the probability a small migrant from the oCR in the fall became a large skipped migrant from the oCR in the spring was the product of the survival probability for a small migrant, the probability a small migrant grew to become a large migrant, and the probability a large migrant did not move into the LCR, or  $S_{1,n,2,2,t} g_{n,2,2} (1 - m_{2,n,2,2,t})$ . Growth was permitted from fall to spring and from spring to fall, but transitions among migration categories were permitted only from fall to spring. Also, transition probabilities included the probability,  $\tau$ , that a CR fish is from the oCR reach (i.e., not from the uCR reach). Specifically, an LCR resident that becomes migratory has probability  $\tau$  of migrating to the oCR reach and probability  $1 - \tau$  of migrating to the uCR reach. The state transition matrix ( $\Psi$ ) is presented for overwinter transitions (ignoring male–female and temporal–seasonal effects for simplicity) in eq. 1, where rows and columns are indexed by state of origin and destination, respectively: 1 (small LCR resident), 2 (small oCR migrant), 3 (small uCR migrant), 4 (small oCR skipped migrant), 5 (small uCR skipped migrant), 6–10 (equivalents of 1–5 but for large fish), and 11 (dead). Also, we defined  $S'$  to be  $(1 - S)$ ,  $g'$  to be  $(1 - g)$ ,  $m'$  to be  $(1 - m)$ , and  $\tau'$  to be  $(1 - \tau)$ . Subscripts on parameters denote size first, then migration category. Parameters were equivalent for oCR and uCR counterparts, so that  $S_{w,2} = S_{w,3}$ ,  $S_{w,4} = S_{w,5}$ ,  $g_2 = g_3$ ,  $g_4 = g_5$ ,  $m_{w,2} = m_{w,3}$ , and  $m_{w,4} = m_{w,5}$ .

**Table 1.** Description of parameters used to model migration dynamics of humpback chub that spawn in the Little Colorado River (LCR).

Symbol	Description	Process	Year	Season	Size	Sex	Mig. cat.	River
$S$	Survival	ST	R	I	I	I	A, I	—
$g$	Growth	ST	C	I	—	I	I	—
$m$	Migration	ST	R	—	I	I	I	—
$\tau$	Proportion of fish in CR that are in oCR	ST	C	C	C	C	C	—
$r$	Probability of ripeness in LCR in spring	SDO	C	—	I	I	C	—
$p_{\text{MUX}}$	Probability of multiplexer (MUX) detection (migrants only)	SDO	I	—	C	C	—	—
$p^*$	Probability fish is captured at least once during spring USFWS sampling (derived)	SDO	—	—	—	—	—	—
$a_{\text{AM}}$	Proportion of migrants in LCR for April and May USFWS sampling	SDC	R	—	I	I	—	—
$a_{\text{AO}}$	Proportion of migrants in LCR for only April USFWS sampling	SDC	R	—	I	I	—	—
$a_{\text{OM}}$	Proportion of migrants in LCR for only May USFWS sampling	SDC	R	—	I	I	—	—
$a_{\text{OO}}$	Proportion of migrants that are not in LCR for USFWS sampling (derived)	SDC	—	—	—	—	—	—
$p_{\text{A},1}$	LCR capture probability — April, pass 1	SDC	R	—	I	C	—	—
$p_{\text{A},2}$	LCR capture probability — April, passes 2 and 3	SDC	R	—	I	C	—	—
$p_{\text{M},1}$	LCR capture probability — May, pass 1	SDC	R	—	I	C	—	—
$p_{\text{M},2}$	LCR capture probability — May, passes 2 and 3	SDC	R	—	I	C	—	—
$c$	Behavioral offset	SDC	C	—	I	C	—	—
$\beta_{\text{TURB}}$	Turbidity offset for LCR	SDC	C	C	C	C	C	—
$p^*$	Probability fish is captured at least once during spring USFWS sampling (derived)	SDC	—	—	—	—	—	—
$f_{\text{CR}}$	Fall oCR capture probability	FD	R	—	I	C	—	—
$f_{\text{LCR}}$	Fall LCR capture probability	FD	R	—	I	C	—	—
$f_{\text{SUB}}$	Probability of antenna detection for fish in oCR	FD	I	—	I	C	—	—
$b$	Probability migrant is in the LCR during fall USFWS sampling	FD	R	—	I	I	—	—
$\beta_{\text{TEMP}}$	Temperature offset for CR	FD	C	C	C	C	C	—
$\beta_{\text{TURB}}$	Turbidity offset for LCR	FD	C	C	C	C	C	—
$j$	Probability fish is female at first capture	IS	C	I	I	—	—	I
$\chi$	Initial tag loss and tag-induced mortality	IS	C	C	C	C	C	C
$r$	Probability of ripeness in LCR in spring	IS	C	—	I	I	C	—
$\tau$	Proportion of fish in CR that are in oCR	IS	C	C	C	C	C	—
$\beta_0$	Probability migrant if first captured in LCR with no previous subadult LCR captures	IS	R	I	I	I	—	—
$\beta_1$	Effect of previous LCR subadult capture on migrant probability	IS	C	I	I	C	—	—

**Note:** Parameters are grouped according to process: state transition (ST), spring detection — open (SDO), spring detection — closed (SDC), fall detection (FD), and initial state (IS). Parameters could vary by year, season (spring–summer or fall–winter), size (200–249 mm total length (TL) or  $\geq 250$  mm TL), sex (male or female), migration category (mig. cat: LCR resident, migrant, skipped migrant), and river (LCR versus Colorado River). Parameters could be modeled as random effects (R), constant (C), independent (I), additive offsets (A), or not applicable (—).

**Fig. 2.** Schematic of model for adult humpback chub that spawn in the Little Colorado River (LCR), Arizona. (a) Schematic for the state transitions in the multistate mark–recapture model (ignoring demographic states for simplicity). States correspond to the location and (or) breeding status of individual fish. Fish can remain in the LCR year-round (LCR residents), can move between the Colorado River (CR) and LCR in spring to spawn (migrants), or can stay in the CR year-round (skipped migrants). In the CR, fish can either be in the sampling site (observable CR or oCR) or outside the sampling site (unobservable CR or uCR). The model runs on a biannual time step, and the arrows between the boxes illustrate which transitions are allowed in the model. (b) Table describing how detections inform state assignment during fall and spring events, where fish can be physically captured in the LCR (LCR cap) or observable Colorado River (CR cap), detected on a multiplexer array in the LCR (MUX det), or detected on a submersible antenna in the oCR (SUB det). For example, LCR residents can be captured in the LCR in spring or fall. However, because LCR residents by definition reside in the LCR year-round, either a multiplexer (MUX) detection (indicating movement) or a CR detection (either by capture or on submersible (SUB) antenna) would preclude assignment to LCR resident state. [Colour online.]



	small LCRres	small oCRmig	small uCRmig	small oCRskm	small uCRskm	large LCRres	large oCRmig	large uCRmig	large oCRskm	large uCRskm	dead
(1)	$S_{1,1}g'_1m'_{1,1}$	$S_{1,1}g'_1m_{1,1}\tau$	$S_{1,1}g'_1m'_{1,1}\tau'$	0	0	$S_{1,1}g'_1m'_{2,1}$	$S_{1,1}g'_1m_{2,1}\tau$	$S_{1,1}g'_1m'_{2,1}\tau'$	0	0	$S'_{1,1}$
	0	$S_{1,2}g'_2m_{1,2}$	0	$S_{1,2}g'_2m'_{1,2}$	0	0	$S_{1,2}g'_2m_{2,2}$	0	$S_{1,2}g'_2m'_{2,2}$	0	$S'_{1,2}$
	0	0	$S_{1,3}g'_3m_{1,3}$	0	$S_{1,3}g'_3m'_{1,3}$	0	0	$S_{1,3}g'_3m_{2,3}$	0	$S_{1,3}g'_3m'_{2,3}$	$S'_{1,3}$
	0	$S_{1,4}g'_4m_{1,4}$	0	$S_{1,4}g'_4m'_{1,4}$	0	0	$S_{1,4}g'_4m_{2,4}$	0	$S_{1,4}g'_4m'_{2,4}$	0	$S'_{1,4}$
	0	0	$S_{1,5}g'_5m_{1,5}$	0	$S_{1,5}g'_5m'_{1,5}$	0	0	$S_{1,5}g'_5m_{2,5}$	0	$S_{1,5}g'_5m'_{2,5}$	$S'_{1,5}$
	0	0	0	0	0	$S_{2,1}m'_{2,1}$	$S_{2,1}m_{2,1}\tau$	$S_{2,1}m'_{2,1}\tau'$	0	0	$S'_{2,1}$
	0	0	0	0	0	0	$S_{2,2}m_{2,2}$	0	$S_{2,2}m'_{2,2}$	0	$S'_{2,2}$
	0	0	0	0	0	0	0	$S_{2,3}m_{2,3}$	0	$S_{2,3}m'_{2,3}$	$S'_{2,3}$
	0	0	0	0	0	0	$S_{2,4}m_{2,4}$	0	$S_{2,4}m'_{2,4}$	0	$S'_{2,4}$
	0	0	0	0	0	0	0	$S_{2,5}m_{2,5}$	0	$S_{2,5}m'_{2,5}$	$S'_{2,5}$
	0	0	0	0	0	0	0	0	0	0	1

The simplified  $\Psi$  matrix illustrates some key restrictions that were necessary for differentiating among states. We assumed that resident to migrant transition was unidirectional — that is, residents could transition to become oCR or uCR migrants, but not vice versa (i.e., column 1 contains all zeroes after row 1; Fig. 2). This assumption seemed reasonable because residents are most often smaller than migrants and skipped migrants (Stone and Gorman 2006), suggesting that once fish are large enough they do not reside in the LCR year-round or that maximum length and (or) survival are lower for LCR residents. Additionally, we assumed that fish could not transition between oCR and uCR states (e.g., matrix elements (2,3) and (3,4) are 0) based on previous studies, which suggests that most humpback chub display high site fidelity when not migrating (R. Ryel and R.A. Valdez, unpublished data) and because previous models that allowed for movement between oCR and uCR states did not converge. Lastly, all survival, growth, and migration parameters from the uCR were set equal to that of oCR to mitigate for the unobservable uCR skipped migrant state (Kendall et al. 2019) and uncertainty in state assignment (Kendall et al. 2012). The over-summer state transition matrix was similar in structure to the overwinter matrix above, with the exception that all  $m = 0$  because migration does not occur between spring and fall.

Survival, growth, and movement parameters were dependent on demographic category. Survival was modeled with a logit-transformed random effect that was centered on a mean specific to movement category and season. Variances for survival random effects were season-specific and specific to site, with LCR residents having a different standard deviation on survival compared with migrants and skipped migrants. Survival of skipped migrants was modeled as an additive offset from that of migrants to help with data sparseness due to both low CR capture probabilities and the fact that detection of skipped migrants could never definitively place fish in this category. Migration probabilities were Markovian (i.e., probability a migrant became a skipped migrant was not equal to the probability that a skipped migrant stayed a skipped migrant) and could only occur during winter. Migration parameters were also modeled with logit-transformed yearly random effects with mean specific to breeding category and variance shared across all demographic categories. The conditional probability that a fish was from the oCR given it was migratory ( $\tau$ ) was modeled as constant.

#### Data model

Determining state required linking detection types to state, as illustrated in Fig. 2b. No single detection could completely define a state (i.e., no event is found in only one row of the matrix in Fig. 2b), and accordingly multiple detections were often required to definitively place fish in one state. We present the data model in four components: spring captures in the LCR (which included open and closed components), fall captures in the LCR and oCR, and state uncertainty at first capture in the LCR, oCR, and uCR. Additionally, the data model included one parameter to represent initial tag loss

or mortality from tagging ( $\chi$ ). Specifically, the model included a vector of 0 or 1 values used to describe whether or not the fish was newly marked at the start of the study. The newly marked vector was multiplied by  $\chi$  for the first occasion following release.

#### Spring model: closed component

The closed component of the spring data model pertained to spring LCR sampling and was demographically closed so that fish could not die, grow, or change migratory status. Importantly, the closed component of the model was not truly closed in terms of movement, because it allowed migrants to move between the CR and LCR during spring LCR sampling. The decision to not treat the population as geographically closed within the spring was motivated by the observations of Pearson et al. (2016) and the mismatches in movement timing (as observed on the MUX) and LCR sampling (Fig. 3).

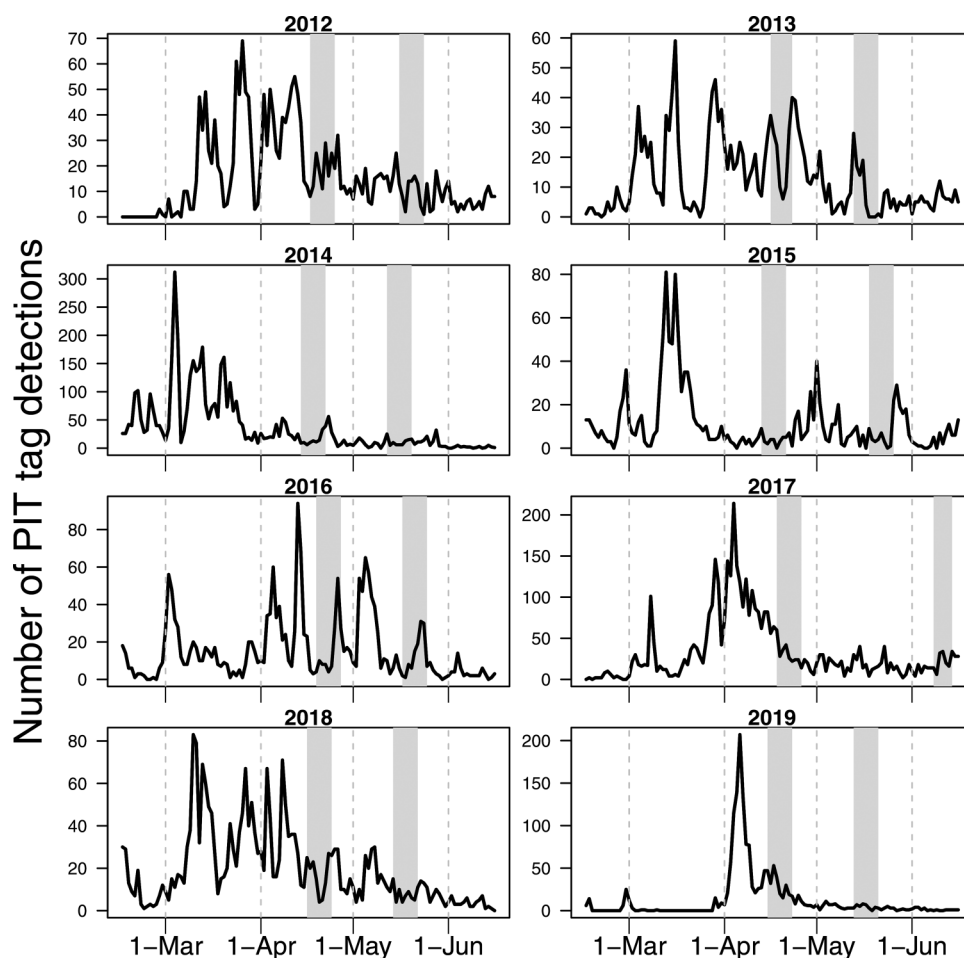
Specifically, spring LCR sampling included two USFWS trips, roughly timed to occur in April and May (though in some years hydrology or logistical issues delayed sampling to later May and June). To allow for movement between the CR and LCR during the spring sampling period, we included four availability probabilities: available for April LCR sampling only ( $a_{A0,w,n,t}$ ), May LCR sampling only ( $a_{OM,w,n,t}$ ), both April and May LCR sampling ( $a_{AM,w,n,t}$ ), and neither April nor May LCR sampling ( $a_{00,w,n,t} = 1 - a_{A0,w,n,t} - a_{OM,w,n,t} - a_{AM,w,n,t}$ ). Availabilities were transformed to sum to 1 using a multinomial logistic transformation. Availability parameters were estimated independently for each demographic category and varied by year as random effects.

The data used to inform availability included four sampling occasions from USFWS sampling that corresponded to April pass 1 ( $p_{A,1,w,t}$ ), April passes 2 and 3 ( $p_{A,2,w,t}$ ; pooled), May pass 1 ( $p_{M,1,w,t}$ ), and May passes 2 and 3 ( $p_{M,2,w,t}$ ; pooled). Importantly, while the model accounted for potential movement in and out of the LCR between April and May trips, it did not allow movement within the April or May trip so that all fish captured during pass 1 are available for passes 2 and 3 of the same trip (i.e., fish in availability category  $a_{A0}$  would have nonzero  $p_{A,1}$  and  $p_{A,2}$ ). For this reason, we pooled passes 2 and 3 to help mitigate for violations in the population closure within-trip (Kendall 1999). MUX detection also informed availability, but this information was included in the open model. Pass-specific capture probabilities were formulated to be size-specific and to have additive offsets for turbidity ( $\beta_{\text{TURB}}$ ; Stone 2010) and size-specific behavioral response ( $c_w$ ) to capture. The capture probabilities were modeled with temporally varying random effects, where capture probabilities for newly captured fish in passes 2 and 3 were set equal to that of pass 1 (but also accounting for the extra pass).

Importantly, all capture probabilities from the closed model were divided by the probability of being captured at least once in spring, effective detection probability  $p^*$ , which is akin to Kendall et al. (2019) and Huggins (1991). This  $p^*$  calculation was specific



**Fig. 3.** Graph depicting the number of adult humpback chub (captured previously >199 mm TL) detections on the multiplexer (MUX) array from 15 February to 15 June in years 2012–2019. Detections were filtered to include moving fish, so that passive integrated transponder (PIT) tags that had multiple detections within 2–13 consecutive day periods of the same year are not included. The vertical grey rectangles depict the timing of the two USFWS spring sampling trips, which typically occur in mid-April to mid-May; however, in 2017 the second trip occurred later (early June) due to issues with helicopter logistics. Note that because LCR residence time is unknown, mismatches in movement timing and LCR sampling do not indicate that migrating humpback chub are not available for LCR sampling.



to migration category —  $p^*$  is 0 for skipped migrants, as by definition this group does not enter the LCR. The  $p^*$  calculation for migrants (where  $h$  can be 2 or 3) includes availability:

$$(2) \quad p_{w,n,h=2,t}^* = 1 - [a_{AM,w,n,t}(1 - p_{A,1,w,t})(1 - p_{A,2,w,t})(1 - p_{M,1,w,t}) \times (1 - p_{M,2,w,t}) + a_{A0,w,n,t}(1 - p_{A,1,w,t})(1 - p_{A,2,w,t}) + a_{0M,w,n,t}(1 - p_{M,1,w,t})(1 - p_{M,2,w,t}) + (1 - a_{AM,w,n,t} - a_{A0,w,n,t} - a_{0M,w,n,t})]$$

Equation 3 is the likelihood for an example of a migrant that was captured on passes 1 and 2 of the April trip, but not observed during the May trip. This capture history could arise under two availability scenarios: (i) the fish could be available for April and May, captured in April only, and not captured in May, and (ii) the fish could have been available for only April, and thus the May capture probability does not apply.

$$(3) \quad \frac{a_{AM,w,n,t}p_{A,1,w,t}p_{A,2,w,t}(1 - p_{M,1,w,t})(1 - p_{M,2,w,t}) + a_{A0,w,n,t}p_{A,1,w,t}p_{A,2,w,t}}{p_{w,n,h=2,t}^*}$$

We assumed all residents were available for April and May sampling, and thus the  $p^*$  calculation for this group does not include availability (eq. 4).

$$(4) \quad p_{w,n,h=1,t}^* = 1 - (1 - p_{A,1,w,t})(1 - p_{A,2,w,t})(1 - p_{M,1,w,t})(1 - p_{M,2,w,t})$$

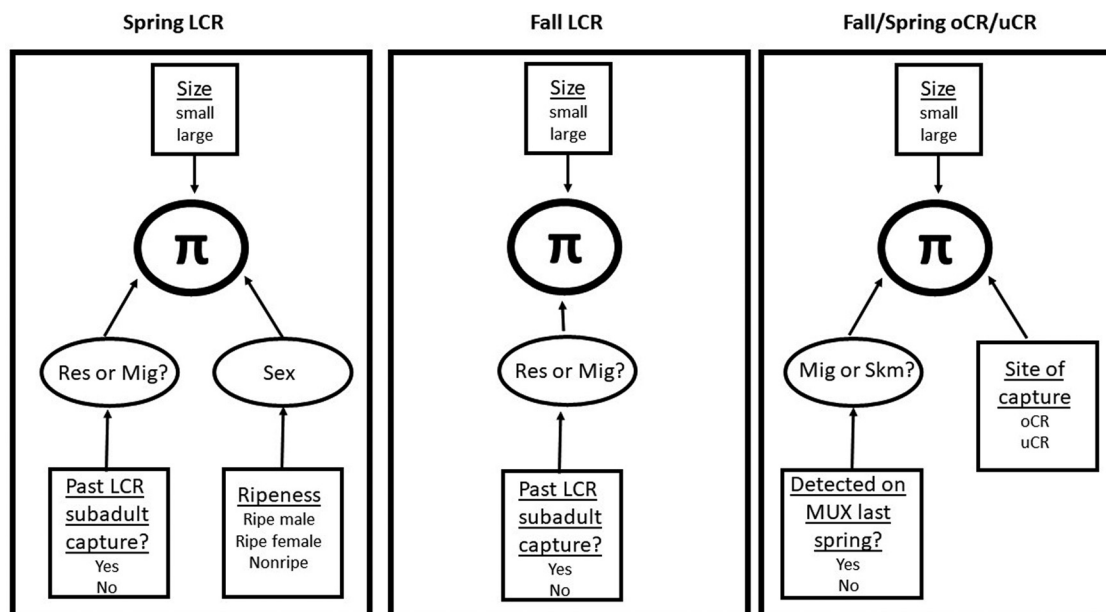
Accordingly, the likelihood for the example above (captured on passes 1 and 2 of the April trip, but not observed during the May trip) for an LCR resident is depicted in eq. 5:

$$(5) \quad \frac{p_{A,1,w,t}p_{A,2,w,t}(1 - p_{M,1,w,t})(1 - p_{M,2,w,t})}{p_{w,n,h=1,t}^*}$$

### Spring model: open component

The open component for spring used  $p^*$  in its calculation and included additional information about the size and sex (if fish were ripe) at capture. This necessitated including a parameter ( $r_{w,n}$ ) that described the probability that a fish was ripe upon capture, and  $r$  was different for each demographic group and temporally constant. There were six possible events based on physical capture: small ripe female, small ripe male, small nonripe (unknown sex), large ripe female, large ripe male, large nonripe. If fish were captured two or more times during the same closed period, then the largest size at capture was used to define the state. Similarly, ripeness overrode nonripeness to determine sex. So, for example, if a fish was captured once as a small, ripe male and once as a large,

**Fig. 4.** Illustration describing the parameterization of the initial state assignment vector ( $\pi$ ). The three panels indicate the  $\pi$  parameterization for different seasons (fall or spring) and sites (Little Colorado River (LCR), observable Colorado River (oCR), or unobservable Colorado River (uCR)). Rectangles depict nodes associated with data, whereas circle or oval shapes represent unobserved (or partially observed) characteristics that were forms of state uncertainty. For fish first captured in the LCR, migrants could come from the oCR with probability  $\tau$  and from the uCR with probability  $1 - \tau$  (not shown for simplicity).



nonripe fish during the same spring, then we classified that fish as a large male. Each capture type had two possible MUX events (either detected or not detected on the MUX), which translated to 12 total events. We included one additional event for fish that were only detected on the MUX and not captured and one event for fish that were not captured or detected on the MUX for a total of 14 possible events. The detection probability of the MUX ( $p_{\text{MUX}}$ ) was modeled as year-specific but constant across all demographic categories. As an example of the open model, consider a fish that was captured as a large ripe male and detected on the MUX within the same spring. This fish would be a known migrant (due to the MUX detection), but there would be uncertainty as to its oCR or uCR status, producing the following likelihood (where  $h$  could be 2 or 3) for a given set of spring detections in year  $t$ :

$$(6) \quad p_{2,1,h,t}^* r_{2,1}^{*} p_{\text{MUX},t}$$

### Linking open and closed spring models

For each capture occasion, the open model produced a vector of forward-conditional probabilities that fish were in each state (hereinafter, the “state assignment vector”). The state assignment vector was multiplied by the conditional capture probabilities for each state in the closed model to produce a vector of joint probabilities. Joint probabilities were summed across all states to produce a marginal probability of the observed capture history as described in Yackulic et al. (2020). This marginal probability was log-transformed and added to the likelihood from the open model.

### Fall model

Fall sampling included both CR and LCR sampling and did not include MUX detections. Fall LCR sampling included two trips (typically in September and October in each year), whereas the CR sampling varied by year. From 2009 to 2011, CR sampling occurred in September and October of each year, while from 2012 onward sampling occurred in either September or October. Fall detection probabilities were modeled with annual random

effects while accounting for the number of trips (either 1 or 2) that were conducted in each river per year. Unlike spring detections, all fall detections were condensed into a single period, and we refer to the LCR and oCR capture probabilities as  $f_{\text{LCR},w,h,t}$  and  $f_{\text{oCR},w,h,t}$ , respectively. Capture probabilities in the LCR included additive offsets for turbidity ( $\beta_{\text{TURB}}$ ), and oCR capture probabilities included a temperature covariate ( $\beta_{\text{TEMP}}$ ). Additionally, in 2016 and 2018, fish in the oCR in fall could be detected on submersible antennas with size-specific detection probability ( $f_{\text{SUB},w}$ ). Because migrants could be located in either the LCR or the CR during fall sampling, we also included a fall availability parameter for migrants that described the probability a migrant was in the LCR during fall LCR sampling ( $b_{w,n,t}$ ). Thus, the probability a migrant was captured in the LCR was the LCR capture probability (assumed to be the same as for residents) multiplied by  $b_{w,n,t}$ , whereas the capture probability in the CR was the capture probability (assumed to be the same as skipped migrants) multiplied by  $(1 - b_{w,n,t})$ . These fall availability parameters were modeled independently for all demographic groups and included a yearly random effect.

### Initial state assignment probabilities

Uncertainties in state assignment required a vector ( $\pi$ ) that represented the probability a newly marked fish was in any particular state at first capture (Pradel 2005). The  $\pi$  values are specific to season (fall versus spring) and site (CR versus LCR) of the first capture occasion of a fish (Fig. 4). Regarding uncertainty in migratory category, fish captured in the CR can be either migrants or skipped migrants, whereas fish captured in the LCR can be either migrants or residents. There is further uncertainty in the demographic states regarding sex but not size (since a fish must be physically captured to be marked, its initial size is always known).

Based on the findings of Yackulic et al. (2014), which found little movement between the LCR and CR for subadult fish (i.e., 100–199 mm TL), additional information about previous captures was used to help inform the probability an individual fish released in the LCR was resident or migrant. The  $\pi$  for the probability a fish released in the LCR was a migrant was determined using a logit



link that included an intercept term ( $\beta_{0,w,n,k,t}$ ), a parameter describing the effect of previous subadult capture in the LCR on the probability of being migrant ( $\beta_{1,w,k,t}$ ), and a dummy variable ( $x_i$ ) that took the value of 1 if fish  $i$  had a previous LCR capture as a subadult or 0 if not (note since the model pertains to adults only, the subadult captures used for the covariate are not included in the capture history). There were four values of  $\beta_1$  that were specific to season (fall or spring) and size (small or large adult). Furthermore, all fish with previous subadult CR captures were assumed to be migrants, as the CR capture provided evidence that these fish do not reside year-round in the LCR. Including information about previous subadult captures helps test the hypothesis that fish that spend their subadult phase in the LCR are more likely to be resident compared with fish that spend this stage in the CR.

For fish first captured in the LCR,  $\pi$  included the following: the size- and season-specific probability a fish is female ( $j_{LCR,k,w}$ ), the size- and sex-dependent probability a fish is a migrant (not a resident), and some information about previous capture history (see previous paragraph). Additionally, since all fish captured in the LCR in spring were checked for ripeness, the  $\pi$  for spring LCR captures included ripeness. For example, the probability a nonripe fish was female was conditional on the fish being nonripe (i.e., equal to  $(1-r_{w,2})j_{LCR,w,k} / [(1-r_{w,2}) \times j_{LCR,w,k} + (1-r_{w,1}) \times (1-j_{LCR,w,k})]$ ). For fish first captured in spring or fall in the CR,  $\pi$  included the size- and season-specific probability a fish is female ( $j_{CR,w,k}$ ) and the size- and sex-dependent probability a fish is a migrant (not a skipped migrant). Because ripe fish in the CR and in the LCR in fall are rare,  $r$  was not included as a parameter in  $\pi$  for LCR fall or CR release occasions, and consequently we assumed all these fish were unknown sex upon release. Fish that were detected on the MUX the current or previous spring before their first capture as adults were assumed to start as migrants, not skipped migrants.

While the nonsystematic and incomplete sampling of the uCR prohibits information about recaptures, the conditional HMM model was able to include information about fish initially released in the uCR. Specifically, all  $\pi$  from the uCR were assumed to be equal to those of the oCR based on Kendall et al. (2012). On a similar note, spring releases in the CR were included via the  $\pi$  but not included in capture parameters due to the low capture probability for CR fish in spring.

### Capture history

An example of this approach is illustrated by the following capture history (ch) for individual  $i$ : first captured as a large, ripe male in the LCR in spring of year  $t = 1$  ( $ch_{i,1,1}$ ), not observed the following fall of year 1 ( $ch_{i,1,2}$ ), and then detected on the MUX in spring  $t = 2$  ( $ch_{i,2,1}$ ). The first step is to populate the initial state assignment vector ( $\pi$ ). While there is no demographic uncertainty in this observation (fish is a known large male so  $w = 2$  and  $n = 1$ ), there is uncertainty in migratory status in spring of  $t = 1$  because the fish could be an LCR resident ( $h = 1$ ), oCR migrant ( $h = 2$ ), or uCR migrant ( $h = 3$ ); thus, the  $\pi$  in eqs. 7–9 are nonzero.

$$(7) \quad \pi_{i,2,1,1} = 1 - \text{logit}^{-1}(\beta_{0,2,1,1,t} + \beta_{1,2,1,1}x_i)$$

$$(8) \quad \pi_{i,2,1,2} = \tau \text{logit}^{-1}(\beta_{0,2,1,1,t} + \beta_{1,2,1,1}x_i)$$

$$(9) \quad \pi_{i,2,1,3} = (1 - \tau) \text{logit}^{-1}(\beta_{0,2,1,1,t} + \beta_{1,2,1,1}x_i)$$

where  $\text{logit}^{-1}$  refers to the inverse logit transformation. Note that skipped migrants cannot be in the LCR; thus,  $\pi_{i,2,1,4} = 0$  and  $\pi_{i,2,1,5} = 0$ . The next step requires updating the likelihoods for the following fall (where  $k = 2$  and  $t = 1$ ) based on the observed capture history, where  $ch_{i,k,t}$  represents the capture history up to season  $k$  of year  $t$ :

$$(10) \quad P(ch_{i,1,2} | h_{i,2,1} = 1) = \pi_{i,2,1,1}S_{2,1,1,1}(1 - f_{LCR,2,1,1})$$

$$(11) \quad P(ch_{i,1,2} | h_{i,2,1} = 2) = \pi_{i,2,2,1}S_{2,1,2,1}[b_{2,1,1}(1 - f_{LCR,2,1,1}) + (1 - b_{2,1,1})(1 - f_{oCR,2,2,1})]$$

$$(12) \quad P(ch_{i,1,2} | h_{i,2,1} = 3) = \pi_{i,2,3,1}S_{2,1,3,1}[b_{2,1,1}(1 - f_{LCR,2,1,1}) + (1 - b_{2,1,1})]$$

$$(13) \quad P(ch_{i,1,2} | h_{i,2,1} = \text{dead}) = \pi_{i,2,1,1}(1 - S_{2,1,1,1}) + \pi_{i,2,2,1}(1 - S_{2,1,2,1}) + \pi_{i,2,3,1}(1 - S_{2,1,3,1})$$

The above likelihoods illustrate how residents must be in the LCR in fall but that migrants can be either in the LCR or CR during fall sampling. Furthermore, comparison of likelihoods for  $h_{i,2,1} = 2$  and  $h_{i,2,1} = 3$  shows that whereas oCR fish can be captured in the oCR in fall, by definition uCR fish cannot be observed in the CR in fall because they occur outside the sampling reach.

The conditional likelihoods are then updated for the following spring ( $k = 1$ ,  $t = 2$ ) based on the conditional likelihoods from the previous occasion, the state transition matrix, and the observed capture history of the current occasion. Note that in this particular example, the fish must be a migrant during the second spring ( $h_{i,1,2} = 2$  or  $h_{i,1,2} = 3$ ) due to its MUX detection:

$$(14) \quad P(ch_{i,1,2} | h_{i,1,2} = 1) = 0$$

$$(15) \quad P(ch_{i,1,2} | h_{i,1,2} = 2) = [P(ch_{i,2,1} | h_{i,2,1} = 1)S_{2,1,1,2}m_{2,1,1,2,1}\tau + P(ch_{i,2,1} | h_{i,2,1} = 2)S_{2,1,2,2}m_{2,1,2,2,1}](1 - p_{2,1,2,2}^*)p_{MUX,2}$$

$$(16) \quad P(ch_{i,1,2} | h_{i,1,2} = 3) = [P(ch_{i,2,1} | h_{i,2,1} = 1)S_{2,1,1,3}m_{2,1,1,3,1}(1 - \tau) + P(ch_{i,2,1} | h_{i,2,1} = 3)S_{2,1,3,2}m_{2,1,3,2,1}](1 - p_{2,1,3,2}^*)p_{MUX,2}$$

$$(17) \quad P(ch_{i,1,2} | h_{i,1,2} = \text{dead}) = 0$$

These steps are repeated for all time steps until the last occasion. The final likelihood for each capture history is the marginal probability at the last occasion  $T$  during season  $K$ :

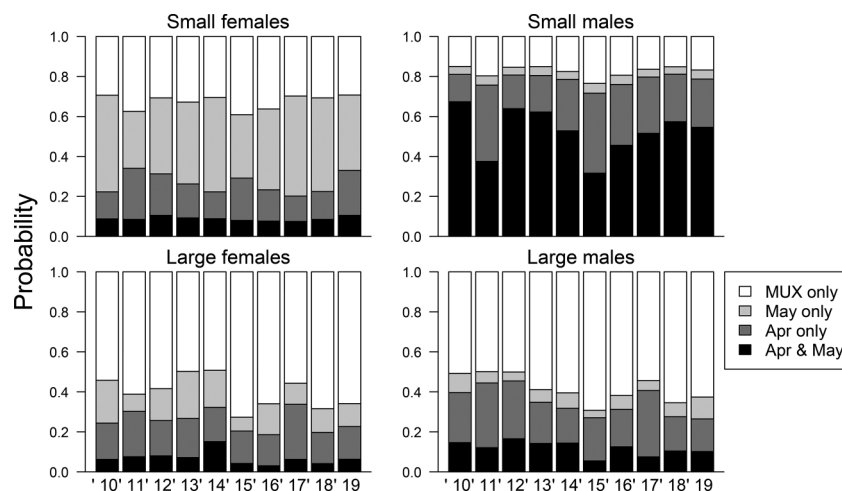
$$(18) \quad \sum_{h=1}^5 P(ch_{i,K,T} | h_{i,K,T})$$

In practice, there is also uncertainty in size and sex in addition to migratory status, and thus the above equation must cycle through all possibilities of size and sex as well (not presented here for simplicity). These steps are accomplished using matrix multiplication, which is illustrated in the Supplemental Material Stan code (S4)<sup>1</sup>.

### Assessing ecological hypotheses: skipped migration, permanent residency, and variability in the timing of first migration

We used the Watanabe-Akaike information criterion (WAIC; Watanabe 2010) to compare three models: a permanent resident model, a premigrant model, and a skipped migrant model. The permanent resident model tests the hypothesis that all residency is determined at earlier life history stages; thus, the resident to migrant transition is fixed to zero. If residency is indeed determined at earlier life history stages, this would indicate managers should aim to better understand the drivers of age-0 emigration from the LCR to the CR (Yackulic et al. 2014), as this early decision would have important implications for life history and population dynamics. The premigrant model infers that there is variability in the size or age at first migration, but that once fish decide to migrate they do so every year and do not become skipped migrants. Thus, the transition probability from migrant

**Fig. 5.** Availability estimates of migrating adult humpback chub migrants during spring sampling by USFWS. All migrants were susceptible to detection on a multiplexer array (MUX) located in the LCR near the LCR–CR confluence, but some availability categories were not susceptible to physical capture by USFWS. The four availability categories were available for April and May sampling, available for April sampling only, available for May sampling only, and not available for April or May sampling (MUX only). Each panel corresponds to a different demographic group: small males (200–249 mm TL), small females, large males (250+ mm TL), and large females. Each bar corresponds to a specific year (2010–2019).



to skipped migrant is fixed to zero in the premigrant model. The premigrant model would be a good representation of the data if migration is associated with spawning and there is variability in the age or size at first spawning as has been observed in other fishes (Christie et al. 2018; Secor 2007). The skipped migrant model is the most general model because it does not restrict transitions from resident to migrant or from migrant to skipped migrant. The skipped migrant model therefore emphasizes flexibility in migratory strategy and suggests that fish can more easily change migratory categories based on individual characteristics and environmental conditions.

### Running the model

Models were fit using a marginalization approach (Yackulic et al. 2020) in Stan via R using the package rstan. Models included three chains, each with 500 iterations, and the first 250 iterations of each chain were used as burn-in. This resulted in a total of 750 posterior draws. All models converged with  $\hat{R}$  less than 1.1. Priors were minimally informative. For example, fixed effects such as  $\tau$ , growth, sex ratios (for  $\pi$ ), ripeness, and tag loss were given a uniform prior between 0 and 1. Means for random effects of logit-transformed parameters, such as mean  $S$  or mean  $b$ , were given a normal prior with mean 0 and standard deviation 2. Priors for standard deviations of random effects were uniform with bounds 0–5. Priors for spring availability were normal with mean  $-0.5$  and standard deviation 1. Priors for specific parameters can be found in the Stan code included as part of Supplementary Material (S4)<sup>1</sup>.

## Results

### Comparing models with and without antenna data

The model with antenna data revealed interesting demographic differences in availability. Small males tended to be available for both April and May sampling occasions, whereas small females were more likely to be available for either April or May sampling, but rarely both (Fig. 5). Also, both large males and large females tended have a high proportion of the population in the “MUX only” category, suggesting many large fish are not available for hoop net capture due to the timing of migration, trap behavior responses, or hoop net characteristics (e.g., openings are too small). This finding sets the stage for comparing models fit with and without antenna data. In the model without antenna data, fish in the “MUX only”

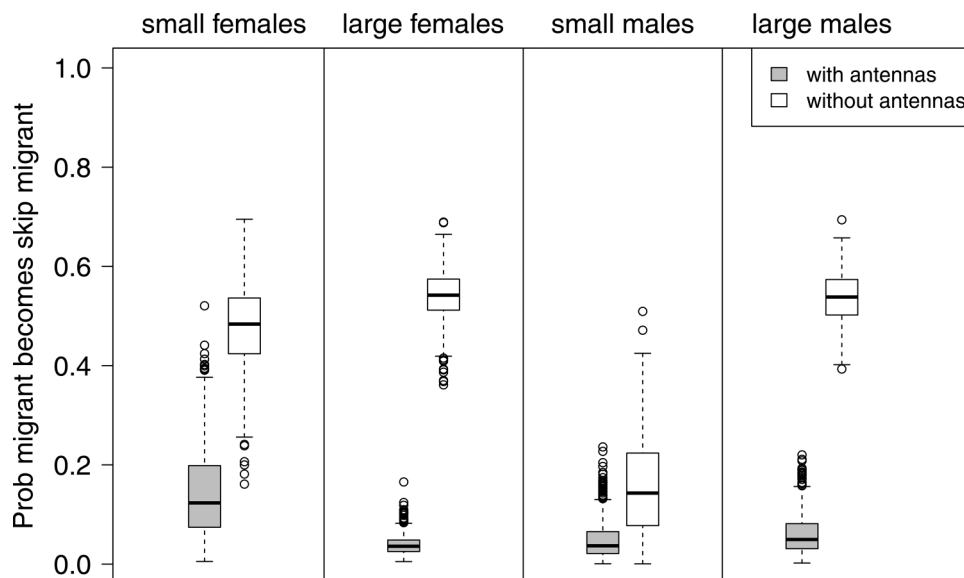
category are not detectable in the LCR, and consequently this model assumed that more fish remained in the CR year-round. Therefore, it overestimated skipped migration probabilities for all groups except small males (Fig. 6). For this reason, estimates of spring abundances in the LCR were lower for the model fit without antennas than the model fit with antennas. Although spring abundance estimates in the LCR differed between models, fall estimates of total abundance (i.e., the total number of fish in both the LCR and CR) and their precisions were similar for both models (Fig. 7).

In addition, there were differences in models fit with and without antenna data that likely arose from capture heterogeneity and trap-shy behaviors. For example, the model with antenna data estimated a higher probability a migrant was from the oCR reach ( $\tau = 32.5\%$  compared with  $22.9\%$ ). Also, the model fit without antenna data tended to have lower annual survival estimates for large migrants, though 95% credible intervals did overlap for all groups (Fig. 8). Lastly, one-time tag loss and mortality ( $\hat{\chi}$ ) for the model fit with antenna data was estimated to be relatively low ( $1.8\%$ ; 95% CI:  $0.0\%$  to  $3.7\%$ ) and comparable to the  $3\%$  tag loss – mortality rate observed in a laboratory experiment of bonytail chub (*Gila elegans*; Ward et al. 2015), whereas  $\hat{\chi}$  for the model fit without antenna data was higher ( $9.3\%$ ; 95% CI:  $5.8\%$ – $12.7\%$ ). This latter finding led us to fit one additional model without antenna data and fixed  $\chi$  ( $2\%$ ) to make sure that differences in models with and without antenna were not due to these different estimates of tag loss. Except for some negligible differences in survival rates across models, the results of two models were similar, so we present results from the model with estimated tag loss.

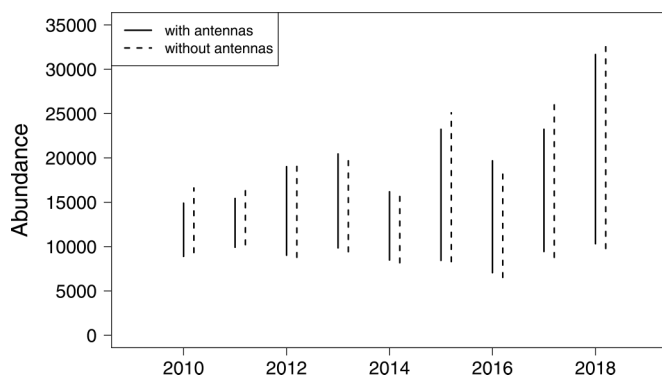
### Migration probabilities and trade-offs

The skipped migration model was supported over the premigration model ( $\Delta\text{WAIC} = 29.9$ ) and the permanent resident model ( $\Delta\text{WAIC} = 237.3$ ). Skipped migration probabilities were much lower than those reported in previous studies (Pearson et al. 2015; Yackulic et al. 2014); for details see the Discussion. Furthermore, skipped migration probabilities tended to display low variability from year to year. Small females were the most likely group to transition from migrant to skipped migrant (Fig. 6). Specifically, the average probability a small female migrant transitioned to a skipped migrant was  $14\%$  and ranged from  $9\%$  to  $22\%$  each year. For small males, large females, and large males, mean probabilities that migrants became skipped migrants were  $5\%$

**Fig. 6.** Mean estimates of skipped migration probabilities (or the probability a migrant does not migrate in the subsequent year) for adult humpback chub in the lower Colorado River. Estimates are shown for four different demographic groups that correspond to size (small: 200–249 mm TL, large: 250+ mm TL) and sex. Estimates are shown for two different models: one fit with data from autonomous passive integrated transponder (PIT) tag antennas (grey) and one fit without antenna data (white).



**Fig. 7.** Comparison of fall abundance estimates of adult humpback chub (>200 mm TL) that spawn in the LCR. Abundance estimates are obtained from two different models: one fit with data from physical captures and antenna detections and one fit with only data from physical captures.



(from 3% to 9% per year), 4% (from 2% to 9% per year), and 6% (from 3% to 17% per year), respectively. Probabilities of a skipped migrant becoming a migrant were imprecise yet differed for males and females. Whereas large males had a high probability of transitioning from skipped migrant to migrant (57%), the probability of large females transitioning from skipped migrant to migrant was much lower (12%; Table 2). Females had a much lower probability of being ripe upon spring capture compared with males, but ripeness of small and large fish was roughly similar. Specifically, 66% of males were ripe for both small and large adults, whereas ripeness of females was 3.9% (small) and 5.0% (large). Large females had higher annual survival than large males, though 95% credible intervals overlapped for both groups (Fig. 8).

Using methods described in Supplementary Material (S3)<sup>1</sup> and extrapolating initial starting probabilities and spawning transition rates to spring (the time when fish were actually spawning) suggests that the mean across-year proportion of fish from the CR that were skipped migrants was 35% (small males), 29% (small

females), 16% (large males), and 24% (large females). The inability to distinguish between migrants and skipped migrants at first capture may be a limitation in the current study. For example, the 95% credible interval for the across-year mean probability a fish first captured in the CR was a skipped migrant was 27%–96% (small males), 7%–77% (small females), 2%–99% (large males), and 7%–57% (large females).

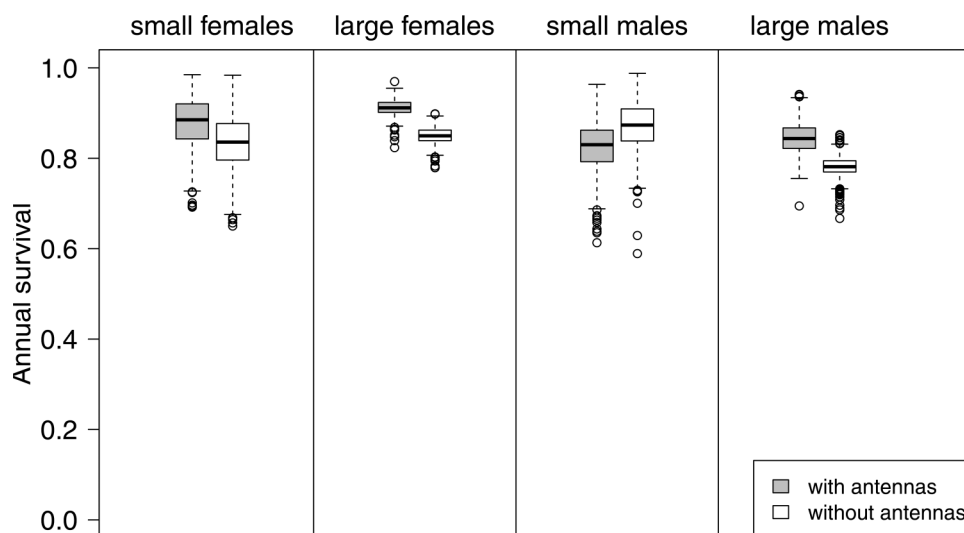
Comparison of migrants and skipped migrants shows that, generally, there is little evidence for differences in growth or survival, though the imprecise estimates of growth and survival of skipped migrants may obscure differences between groups. Comparing annual growth probabilities using the following equation (probability of annual growth =  $1 - (1 - g_{n,h,2})(1 - g_{n,h,1})$ ) showed that migrant growth probabilities were actually higher than skipped migrant growth probabilities, though 95% credible intervals did overlap. Specifically, female and male migrant growth probabilities were 72% (95% CI: 66% to 78%) and 61% (95% CI: 56% to 66%), respectively, whereas skipped migrant growth probabilities were 48% (95% CI: 20% to 81%) and 43% (95% CI: 19% to 70%). Likewise, the 95% credible intervals of survival offsets for skipped migrants for all demographic groups overlapped zero, but tended to be negative for large females (−0.56; 95% CI: −1.48 to 0.95) and large males (−0.37; 95% CI: −2.70 to 3.08) and positive for small females (0.07; 95% CI: −2.35 to 3.78) and males (0.82; 95% CI: −1.31 to 3.98).

#### Alternative life histories

In fall, residents only comprised 28% (95% CI: 6% to 55%) of small females, 25% (95% CI: 5% to 53%) of small males, 9.2% (95% CI: 4% to 19%) of large females, and 8.2% (95% CI: 3% to 19%) of large males, suggesting this group is a relatively small proportion of the overall humpback chub population (similar to Yackulic et al. 2014) and that residents are on average smaller than migrants (Stone and Gorman 2006). In all models, resident survival was much lower than migrant survival. Closer examination reveals that the difference in annual survival rates of migrants and residents is mainly due to winter survival probabilities (Fig. 9; Table 2). Also, residents were more likely to die than become migrants (Fig. 10), suggesting that determination of life history strategy



**Fig. 8.** Mean estimates of annual survival probabilities for adult humpback chub migrants in the lower Colorado River. Estimates are shown for four different demographic groups that correspond to size (small: 200–249 mm TL, large: 250+ mm TL) and sex. Estimates are shown for two different models: one fit with data from autonomous passive integrated transponder (PIT) tag antennas (grey) and one fit without antenna data (white).



occurs at earlier life history stages. Note that simulations from Supplementary Material (S2)<sup>1</sup> illustrate the potential for overestimation in the resident to migrant transition; thus, it is possible that the true resident to migrant transition is even lower than the 4%–11% values reported in this study. Lastly,  $\beta_1$  was negative for all groups and the 95% CIs did not overlap zero, suggesting that fish with previous subadult captures in the LCR were more likely to be resident compared with fish without previous subadult LCR capture (Yackulic et al. 2014).

## Discussion

Incorporation of antenna detections into mark–recapture models provided valuable insight into migration patterns in humpback chub in the LCR aggregation. Specifically, not only did antennas increase detection probabilities, they also provided detection information about a subset of fish that were not available for LCR hoop net sampling by USFWS. As a result, skipped migration probabilities from this study were substantially lower than those estimated by previous studies that either did not include antenna detections (Yackulic et al. 2014) or used poor quality antenna detections (Pearson et al. 2015). While estimates of skipped migration and survival differed for models with and without antennas, the fall abundance estimates were similar for both models, though models with antennas did produce slightly more precise estimates. Accordingly, because both models accounted for temporary emigration from the LCR in the form of skipped migration, models with and without antennas were similar in many respects but disagreed on the proportion of adults that were migrants.

In a similar study of humpback chub in the LCR aggregation from 2001 to 2011, Pearson et al. (2015) estimated the mean probability that a migrant remained a migrant the next year was 55%, which is lower than the 83%–97% values observed in this study. While Pearson et al. (2015) did include LCR MUX detections in their population model for a subset of years (2009–2011), the detection rates were very low during this time and the LCR MUX was often not functional during early spring months. Unlike Pearson et al. (2015) or the current study, Yackulic et al. (2014) estimated migration probabilities from 2009 to 2012 as the proportion of CR adults that moved into the LCR each year and reported that 31% small adults and 61% large adults moved from

the CR to the LCR each spring from 2009 to 2012. A telemetry study of humpback chub observed that only 57% ( $n = 61$ ) of adult humpback chub moved into the LCR or LCR inflow from 1991 to 1992 (R. Ryel and R.A. Valdez, unpublished data). By comparison, the current model estimates that, on average, 65% of small males, 71% of small females, 84% of large males, and 76% of large females in the CR were migrants in any given year and that the yearly percentages were 53%–73% (small males), 61%–85% (small females), 75%–90% (large males), and 66%–86% (large females) from 2010 to 2019. The discrepancy between the migration probabilities observed by R. Ryel and R.A. Valdez (unpublished data) and the current study is unknown, but could be due to changes in hydrothermal regime (early 1990s had colder water and more hydropeaking compared with current conditions), individual heterogeneity in migration probabilities, or potential biases or errors in one of the two studies.

Previous studies have assumed that all CR–LCR migration was associated with spawning (Yackulic et al. 2014; Pearson et al. 2015). While spawning is certainly one impetus for migration between the CR and LCR, results from the current study call into question their assumption that migration is exclusively motivated by spawning. Determining whether all migration is associated with spawning is nearly impossible because direct information about spawning (e.g., deposition of eggs or milt) is difficult to obtain. The LCR may be a favorable environment for adult humpback chub in spring, as evidenced by high summer survival probabilities of residents and the apparently faster (though statistically insignificant) growth rates for migrants compared with skipped migrants during the summer interval. This, in turn, suggests there might be a growth advantage associated with migration. Comparison of subadult humpback chub growth in the two rivers shows that somatic growth in length is generally higher in the LCR compared with the CR, particularly from April to May, when growth in the LCR is 10–20 times higher than in the CR (Dzul et al. 2017).

The paired finding that female migrants were unlikely to become skipped migrants and female skipped migrants were unlikely to become migrants provides some evidence for migration heterogeneity among females. Individual heterogeneity in migration and spawning strategy may be particularly advantageous in large river desert environments, where the timing and magnitude of floods vary across years. Under these conditions,

**Table 2.** Summary of adult humpback chub estimates of parameters for across-year means of survival (*S*), transition probability (*b*), and growth (*g*).

Parameter	Season	Size	Sex	State	Mean	95% CI
<i>S</i>	Win	S	F	Res	0.46	0.34 to 0.57
	Sum	S	F	Res	0.89	0.81 to 0.96
	Win	L	F	Res	0.57	0.46 to 0.68
	Sum	L	F	Res	0.98	0.93 to 1.00
	Win	S	M	Res	0.63	0.50 to 0.75
	Sum	S	M	Res	0.83	0.72 to 0.93
	Win	L	M	Res	0.57	0.45 to 0.70
	Sum	L	M	Res	0.97	0.91 to 1.00
	Win	S	F	Mig	0.91	0.77 to 0.99
	Sum	S	F	Mig	0.96	0.90 to 1.00
	Win	L	F	Mig	0.94	0.90 to 0.98
	Sum	L	F	Mig	0.97	0.93 to 1.00
	Win	S	M	Mig	0.87	0.73 to 0.98
	Sum	S	M	Mig	0.95	0.87 to 1.00
	Win	L	M	Mig	0.91	0.82 to 0.99
	Sum	L	M	Mig	0.93	0.87 to 0.99
<i>b</i>		S	F	Res to Mig	0.05	0.01 to 0.12
		S	F	Mig to Skm	0.14	0.02 to 0.35
		S	F	Skm to Mig	0.40	0.03 to 0.89
		S	M	Res to Mig	0.08	0.02 to 0.17
		S	M	Mig to Skm	0.05	0.00 to 0.15
		S	M	Skm to Mig	0.41	0.10 to 0.73
		L	F	Res to Mig	0.11	0.05 to 0.20
		L	F	Mig to Skm	0.04	0.01 to 0.08
		L	F	Skm to Mig	0.12	0.03 to 0.30
		L	M	Res to Mig	0.11	0.04 to 0.22
<i>g</i>	Win	S-L	F	Res	0.54	0.53 to 0.55
	Win	S-L	F	Mig	0.55	0.52 to 0.59
	Win	S-L	F	Skm	0.58	0.50 to 0.68
	Win	S-L	M	Res	0.52	0.51 to 0.53
	Win	S-L	M	Mig	0.54	0.51 to 0.57
	Win	S-L	M	Skm	0.53	0.50 to 0.59
	Sum	S-L	F	Res	0.61	0.60 to 0.62
	Sum	S-L	F	Mig	0.66	0.64 to 0.67
	Sum	S-L	F	Skm	0.55	0.50 to 0.65
	Sum	S-L	M	Res	0.60	0.59 to 0.62
	Sum	S-L	M	Mig	0.63	0.61 to 0.65
	Sum	S-L	M	Skm	0.59	0.51 to 0.66

**Note:** Survival and growth estimates varied by two different seasons: summer (Sum: April to October) and winter (Win: October to April). Estimates for survival and transition probabilities varied for small (S: 200–249 mm TL) versus large (>250 mm TL) and for males (M) versus females (F). Growth, survival, and transition probabilities also varied for breeding–migratory states, specifically for residents (Res), migrants (Mig), and skipped migrants (Skm).

it is unlikely that a one-size-fits-all spawning strategy would be beneficial to population persistence. Heterogeneity in vital rates among individuals is common, and model efforts to incorporate heterogeneity are burgeoning (Gimenez et al. 2018). If the main impetus for migration is spawning, then one hypothesis for heterogeneity is that individual quality is the main driver of spawning and migration (Beauplet et al. 2006). Individual quality may be an inherent characteristic of the population and (or) it may be influenced by age, where first-time breeders and (or) old individuals spawn (and migrate) less frequently than individuals of prime reproductive age (Jørgensen et al. 2006). Alternatively, heterogeneity in migration could occur if a small subset of large females were mainstem spawners or spawned in the lower 1.8 rkm of the LCR (and are thus not detectable on the MUX). We attempted to more formally assess spawning heterogeneity using mark–recapture models that incorporated migration heterogeneity,

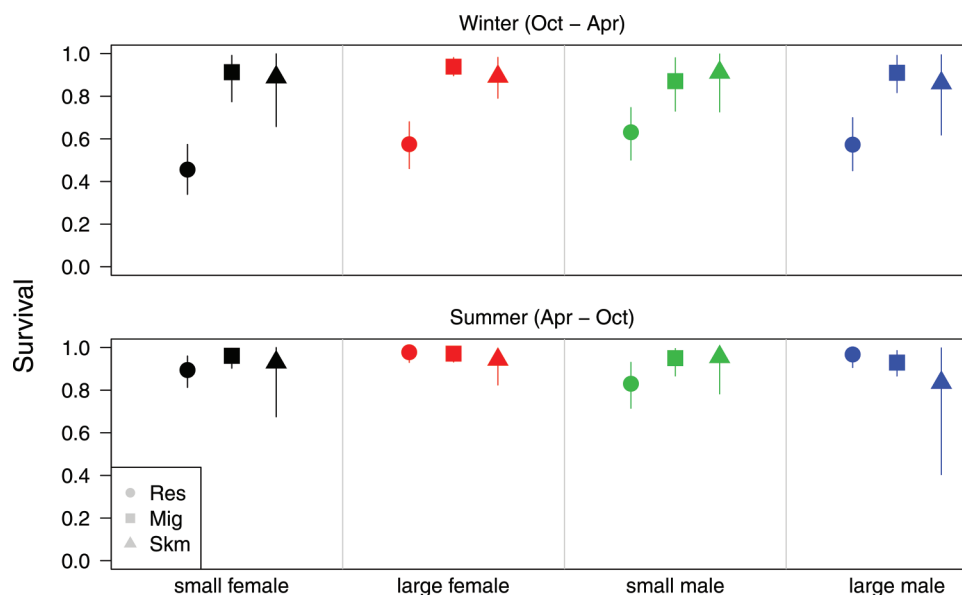
but these models were prohibitively slow, required many simplifying modifications to converge, and were difficult to interpret. Developing humpback chub models that incorporate migration heterogeneity may be an area of future research.

Alternative life histories have been documented among numerous fishes, and often these alternative life histories represent a “slow” and “fast” track (Nelson et al. 2002). These slow and fast life histories are supported by a previous humpback chub study that found residents had lower survival but faster growth than migrants at earlier life history stages (Yackulic et al. 2014), and this finding was reinforced by results of the current study, which found residents had substantially lower survival than migrants. The low survival probability of residents suggests that individuals in this group may only live through one or two spawning seasons, and consequently this group may be generally semelparous. The difference in resident and migrant survival was driven mainly by overwinter survival. In a diet study of LCR fishes, Behn and Baxter (2019) found that humpback chub stomachs were typically empty over winter (at baseflow), suggesting this may be a time of severe food limitation. Although other studies have made the distinction between the migrant and resident life history strategies in humpback chub (Douglas and Marsh 1996; Gorman and Stone 1999; Yackulic et al. 2014), this study was the first (to our knowledge) to assess the potential for adult residents to leave the LCR and become migratory. While model results suggest that some residents do move to the CR, residents have a much higher probability of dying than becoming migratory, suggesting that for most individuals these two life histories diverge at earlier stages (e.g., as juveniles or subadults; Yackulic et al. 2014). In addition, the finding that residents only comprise a small proportion of the overall adult population suggests that the CR can support more large humpback chub than the LCR and thus is probably a better environment for adults (particularly over winter).

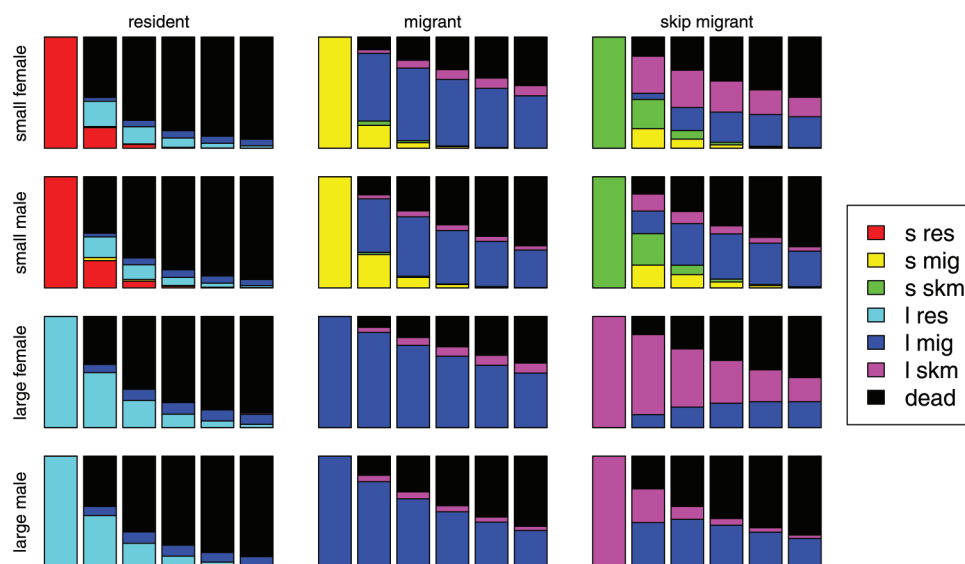
Importantly, since the only detection method for LCR residents is hoop nets, it is possible that residents develop a long-term trap-shy behavior that could be masked as low survival in our model. If this issue is prevalent, then as long as the trap-shy component of the population has a nonzero capture probability, we would expect some issues with retrospective negative bias where survival rates would increase as more years of data are added to the model (Kendall et al. 2013; Langtimm 2009; Peñaloza et al. 2014). While we do not see any evidence for retrospective bias in our model, we believe it would be prudent to add submersible antennas to supplement LCR hoop net sampling to help assess potential long-term trap-shy behavior in LCR residents. This recommendation stems from the broader lesson learned from adding antenna detections of migrants (MUX and CR submersibles) and skipped migrants (CR submersibles), namely that false conclusions can occur when some proportion of the population is not detectable and that even well-thought-out models cannot always solve sampling issues.

While this study illustrates one method for incorporating antenna data into mark–recapture models, other studies have found solutions to the three challenges highlighted in this paper. For the availability challenge, multistate models with unobservable states can be used to describe fish that are not detectable on antennas. For example, if PIT antennas are set up as multiple arrays that are spaced in close proximity to each other, then detection data from individual arrays can be used to construct a capture history and estimate transition probabilities for individuals that permanently (Horton et al. 2011) or temporarily (Dzul et al. 2018) enter an unobservable state where their PIT antenna detection probability is zero. Another option is to use spatial mark–recapture models, which estimate the “activity centers” for individual fish, and then to model detection probabilities of each fish as a function of the distance between its activity center and PIT antenna locations (Raabe et al. 2014). In reference to the continuous time challenge, some studies have used a Barker

**Fig. 9.** Comparison of across-year mean overwinter and oversummer survival probabilities for residents (Res), migrants (Mig), and skipped migrants (Skm) for four demographic groups (left to right): small females (black), large females (red), small males (green), and large males (blue). Means were estimated on the logit-scale but are presented on the real scale here for better interpretation. Bars represent 95% credible intervals. Note that season-specific estimates of migrants may be prone to slight biases (see Supplementary material<sup>1</sup>). [Colour online.]



**Fig. 10.** Graphs that probabilistically describe the fate of adult humpback chub that spawn in the LCR. Fate differs according to demographic state (rows) and biological state (columns), and the 12 subplots (which each have six columns) correspond to one demographic–biological state combination (i.e., group). Within the subplots, the first column shows the starting state in spring of year 1 for each group, and the colours in the second column show the probability that fish will be in any other state the next spring. This is continued for 5 years, so that the sixth column represents the fate of a fish in spring of year 5. States in the legend are abbreviated as s (small, 200–249 mm TL), l ( $\geq 250$  mm TL), res (resident), mig (migrant), and skm (skipped migrant). [Colour online.]



model and treated antenna data as temporally continuous resight probabilities to help avoid bias in survival rates (Al-Chokhachy and Budy 2008; Beard et al. 2017). The state uncertainty challenge, to our knowledge, has not been addressed by previous studies of PIT antenna data, but this issue warrants attention. Other mark-recapture studies have developed hidden Markov models for state uncertainty, where the status of an individual is not always observable upon capture (Conn and Cooch 2009; Kendall et al. 2012), and we illustrated how this approach can be used with PIT antenna data.

Our study provides yet another example of how technological advances in mark-recapture can improve population models (Bravington et al. 2016; Conner et al. 2020; Cunjak et al. 2005), as models with PIT antenna detections led to new inferences in humpback chub population dynamics. We illustrate how, with a reasonable mark-recapture model, these new technologies can improve the ability of biologists to explore more complex ecological questions related to life history strategy and variability in vital rates. Assessing partial migration and life history variability may become increasingly important in the near future, as



anthropogenic changes (e.g., habitat fragmentation, pollution, climate change) may imperil select individuals that display a particular life history or migration strategy (Nelson et al. 2002; Nilsson et al. 2006). Accordingly, obtaining a better understanding of if (or how) alternative life histories promote overall population resiliency is an important question for guiding conservation efforts in an uncertain future (Gillanders et al. 2015).

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### References

- Aarestrup, K., Lucas, M., and Hansen, J. 2003. Efficiency of a nature-like bypass channel for sea trout (*Salmo trutta*) ascending a small Danish stream studied by PIT telemetry. *Ecol. Freshw. Fish.* 12(3): 160–168. doi:10.1034/j.1600-0633.2003.00028.x.
- Al-Chokhachy, R., and Budy, P. 2008. Demographic characteristics, population structure, and vital rates of a fluvial population of bull trout in Oregon. *Trans. Am. Fish. Soc.* 137(6): 1709–1722. doi:10.1577/T07-247.1.
- Banet, N.V., and Hewitt, D.A. 2019. Monitoring of endangered Klamath Basin suckers translocated from Lake Ewauna to Upper Klamath Lake, Oregon, 2014–2017. *US Geological Survey* 2331-1258.
- Barbour, A.B., Ponciano, J.M., and Lorenzen, K. 2013. Apparent survival estimation from continuous mark-recapture/resighting data. *Methods Ecol. Evol.* 4(9): 846–853. doi:10.1111/2041-210X.12059.
- Barker, R.J. 1997. Joint modeling of live-recapture, tag-resight, and tag-recovery data. *Biometrics*, 53: 666–677. doi:10.2307/2533966.
- Beard, Z.S., Quist, M.C., Hardy, R.S., and Ross, T.J. 2017. Survival, movement, and distribution of juvenile burbot in a tributary of the Kootenai River. *North Am. J. Fish. Manage.* 37(6): 1274–1288. doi:10.1080/02755947.2017.1376010.
- Beauplet, G., Barbraud, C., Dabin, W., Küssener, C., and Guinet, C. 2006. Age-specific survival and reproductive performances in fur seals: evidence of senescence and individual quality. *Oikos*, 112(2): 430–441. doi:10.1111/j.0030-1299.2006.14412.x.
- Behn, K.E., and Baxter, C.V. 2019. The trophic ecology of a desert river fish assemblage: influence of season and hydrologic variability. *Ecosphere*, 10(1): e02583. doi:10.1002/ecs2.2583.
- Bravington, M.V., Grewe, P.M., and Davies, C.R. 2016. Absolute abundance of southern bluefin tuna estimated by close-kin mark-recapture. *Nat. Commun.* 7(1): 13162. doi:10.1038/ncomms13162. PMID:27841264.
- Brizendine, M.E. 2016. Use of ultrasonic imaging to evaluate egg maturation of humpback chub *Gila cypha*. University of Arizona.
- Cathcart, C.N., Gido, K.B., McKinstry, M.C., and MacKinnon, P.D. 2018a. Patterns of fish movement at a desert river confluence. *Ecol. Freshw. Fish.* 27(1): 492–505. doi:10.1111/eff.12364.
- Cathcart, C.N., Pennock, C.A., Cheek, C.A., McKinstry, M.C., MacKinnon, P.D., Conner, M.M., and Gido, K.B. 2018b. Waterfall formation at a desert river-reservoir delta isolates endangered fishes. *River Res. Appl.* 34(8): 948–956. doi:10.1002/rra.3341.
- Chapman, B.B., Brönmark, C., Nilsson, J.Å., and Hansson, L.A. 2011. The ecology and evolution of partial migration. *Oikos*, 120(12): 1764–1775. doi:10.1111/j.1600-0706.2011.20131.x.
- Chapman, B., Hulthén, K., Brodersen, J., Nilsson, P.A., Skov, C., Hansson, L.A., and Brönmark, C. 2012. Partial migration in fishes: causes and consequences. *J. Fish Biol.* 81(2): 456–478. doi:10.1111/j.1095-8649.2012.03342.x. PMID:22803720.
- Chapman, B.B., Eriksen, A., Baktoft, H., Brodersen, J., Nilsson, P.A., Hulthén, K., et al. 2013. A foraging cost of migration for a partially migratory cyprinid fish. *PLoS ONE*, 8(5): e61223. doi:10.1371/journal.pone.0061223. PMID:23723967.
- Christie, M.R., McNickle, G.G., French, R.A., and Blouin, M.S. 2018. Life history variation is maintained by fitness trade-offs and negative frequency-dependent selection. *Proc. Natl. Acad. Sci. U.S.A.* 115(17): 4441–4446. doi:10.1073/pnas.1801779115. PMID:29643072.
- Coggins, L.G., Pine, W.E., III, Walters, C.J., Van Haverbeke, D.R., Ward, D., and Johnstone, H.C. 2006. Abundance trends and status of the Little Colorado River Population of Humpback Chub. *North Am. J. Fish. Manage.* 26: 233–245. doi:10.1577/M05-075.1.
- Conn, P.B., and Cooch, E.G. 2009. Multistate capture-recapture analysis under imperfect state observation: an application to disease models. *J. Appl. Ecol.* 46(2): 486–492. doi:10.1111/j.1365-2664.2008.01597.x.
- Conner, M.M., Bennett, S.N., Saunders, W.C., and Bouwes, N. 2015. Comparison of tributary survival estimates of steelhead using Cormack-Jolly-Seber and Barker models: implications for sampling efforts and designs. *Trans. Am. Fish. Soc.* 144(1): 34–47. doi:10.1080/00028487.2014.963254.
- Conner, M.M., Budy, P.E., Wilkison, R.A., Mills, M., Speas, D., MacKinnon, P.D., and McKinstry, M.C. 2020. Estimating population abundance with a mixture of physical capture and passive PIT tag antenna detection data. *Can. J. Fish. Aquat. Sci.* 77(7): 1163–1171. doi:10.1139/cjfas-2019-0326.
- Cooke, S.J., Midwood, J.D., Thiem, J.D., Klimley, P., Lucas, M.C., Thorstad, E.B., et al. 2013. Tracking animals in freshwater with electronic tags: past, present and future. *Anim. Biotelem.* 1(1): 5. doi:10.1186/2050-3385-1-5.
- Cunjak, R., Roussel, J.-M., Gray, M., Dietrich, J., Cartwright, D., Munkittrick, K., and Jardine, T. 2005. Using stable isotope analysis with telemetry or mark-recapture data to identify fish movement and foraging. *Oecologia*, 144(4): 636–646. doi:10.1007/s00442-005-0101-9. PMID:15959824.
- Dauwalter, D.C., and Fisher, W.L. 2007. Electrofishing capture probability of smallmouth bass in streams. *North Am. J. Fish. Manage.* 27(1): 162–171. doi:10.1577/M06-008.1.
- Dean, D., and Topping, D. 2019. Geomorphic change and biogeomorphic feedbacks in a dryland river: the Little Colorado River, Arizona, U.S.A. *GSA Bull.* 131(11–12): 1920–1942. doi:10.1130/B35047.1.
- Douglas, M.E., and Marsh, P.C. 1996. Population estimates/population movements of Gila cypha, an endangered cyprinid fish in the Grand Canyon Region of Arizona. *Copeia*, 1996(1): 15–28. doi:10.2307/1446938.
- Dudgeon, C.L., Pollock, K.H., Braccini, J.M., Semmens, J.M., and Barnett, A. 2015. Integrating acoustic telemetry into mark-recapture models to improve the precision of apparent survival and abundance estimates. *Oecologia*, 178(3): 761–772. doi:10.1007/s00442-015-3280-z. PMID:25740335.
- Dzul, M., 2021. Humpback chub spring and fall capture histories in the Little Colorado River, 2009–2019. *US Geological Survey* data release.
- Dzul, M.C., Yackulic, C.B., Korman, J., Yard, M.D., and Muehlbauer, J.D. 2017. Incorporating temporal heterogeneity in environmental conditions into a somatic growth model. *Can. J. Fish. Aquat. Sci.* 74(3): 316–326. doi:10.1139/cjfas-2016-0056.
- Dzul, M.C., Yackulic, C.B., and Korman, J. 2018. Estimating animal abundance using continuous detection data from PIT arrays placed near the confluence of two rivers. *Can. J. Fish. Aquat. Sci.* 75(9): 1393–1404. doi:10.1139/cjfas-2017-0304.
- Gillanders, B.M., Izzo, C., Doubleday, Z.A., and Ye, Q. 2015. Partial migration: growth varies between resident and migratory fish. *Biol. Lett.* 11(3): 20140850. doi:10.1098/rsbl.2014.0850. PMID:25788490.
- Gimenez, O., Cam, E., and Gaillard, J.-M. 2018. Individual heterogeneity and capture-recapture models: What, why and how? *Oikos*, 127(5): 664–686. doi:10.1111/oik.04532.
- Gorman, O.T., and Stone, D.M. 1999. Ecology of spawning humpback chub, *Gila cypha*, in the Little Colorado River near Grand Canyon, Arizona. *Environ. Biol. Fishes*, 55: 115–133. doi:10.1023/A:1007450826743.
- Gushue, T.M., 2019. Colorado River Mile System, Grand Canyon, Arizona. *US Geological Survey* data release. doi:10.5066/P9JRL3GV.
- Grayson, K.L., Bailey, L.L., and Wilbur, H.M. 2011. Life history benefits of residency in a partially migrating pond-breeding amphibian. *Ecology*, 92(6): 1236–1246. doi:10.1890/11-0133.1. PMID:21797152.
- Haraldstad, T., Höglund, E., Kroglund, F., Lamberg, A., Olsen, E.M., and Haugen, T.O. 2018. Condition-dependent skipped spawning in anadromous brown trout (*Salmo trutta*). *Can. J. Fish. Aquat. Sci.* 75(12): 2313–2319. doi:10.1139/cjfas-2017-0076.
- Hebblewhite, M., and Merrill, E.H. 2007. Multiscale wolf predation risk for elk: Does migration reduce risk? *Oecologia*, 152(2): 377–387. doi:10.1007/s00442-007-0661-y. PMID:17287955.
- Hebblewhite, M., and Merrill, E.H. 2011. Demographic balancing of migrant and resident elk in a partially migratory population through forage-predation tradeoffs. *Oikos*, 120(12): 1860–1870. doi:10.1111/j.1600-0706.2011.19436.x.
- Hein, A.M., Hou, C., and Gillooly, J.F. 2012. Energetic and biomechanical constraints on animal migration distance. *Ecol. Lett.* 15(2): 104–110. doi:10.1111/j.1461-0248.2011.01714.x. PMID:22093885.
- Hense, Z., Martin, R.W., and Petty, J.T. 2010. Electrofishing capture efficiencies for common stream fish species to support watershed-scale studies in the central Appalachians. *North Am. J. Fish. Manage.* 30(4): 1041–1050. doi:10.1577/M09-029.1.
- Holdo, R.M., Holt, R.D., and Fryxell, J.M. 2009. Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *Am. Nat.* 173(4): 431–445. doi:10.1086/597229. PMID:19243258.
- Horton, G.E., Letcher, B.H., and Kendall, W.L. 2011. A multistate capture-recapture modeling strategy to separate true survival from permanent emigration for a passive integrated transponder tagged population of stream fish. *Trans. Am. Fish. Soc.* 140(2): 320–333. doi:10.1080/00028487.2011.567861.

- Huggins, R. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics*, **47**: 725–732. doi:10.2307/2532158.
- Jørgensen, C., Ernande, B., Fiksen, Ø., and Dieckmann, U. 2006. The logic of skipped spawning in fish. *Can. J. Fish. Aquat. Sci.* **63**(1): 200–211. doi:10.1139/f05-210.
- Kaeding, L.R., and Zimmerman, M.A. 1983. Life history and ecology of the humpback chub in the Little Colorado and Colorado Rivers of the Grand Canyon. *Trans. Am. Fish. Soc.* **112**: 577–594. doi:10.1577/1548-8659(1983)112<577:LHAEOT>2.0.CO;2.
- Kanno, Y., Letcher, B.H., Coombs, J.A., Nislow, K.H., and Whiteley, A.R. 2014. Linking movement and reproductive history of brook trout to assess habitat connectivity in a heterogeneous stream network. *Freshw. Biol.* **59**(1): 142–154. doi:10.1111/fwb.12254.
- Kendall, W.L. 1999. Robustness of closed capture–recapture methods to violations of the closure assumption. *Ecology*, **80**(8): 2517–2525. doi:10.1890/0012-9658(1999)080[2517:ROCCRM]2.0.CO;2.
- Kendall, W.L., White, G.C., Hines, J.E., Langtimm, C.A., and Yoshizaki, J. 2012. Estimating parameters of hidden Markov models based on marked individuals: use of robust design data. *Ecology*, **93**(4): 913–920. doi:10.1890/11-1538.1. PMID:22690641.
- Kendall, W.L., Barker, R.J., White, G.C., Lindberg, M.S., Langtimm, C.A., and Peñaloza, C.L. 2013. Combining dead recovery, auxiliary observations and robust design data to estimate demographic parameters from marked individuals. *Methods Ecol. Evol.* **4**(9): 828–835. doi:10.1111/2041-210X.12077.
- Kendall, W.L., Stapleton, S., White, G.C., Richardson, J.L., Pearson, K.N., and Mason, P. 2019. A multistate open robust design: population dynamics, reproductive effort, and phenology of sea turtles from tagging data. *Ecol. Monogr.* **89**(1): e01329. doi:10.1002/ecm.1329.
- Korman, J., Yard, M., Walters, C., and Coggins, L.G. 2009. Effects of fish size, habitat, flow, and density on capture probabilities of age-0 rainbow trout estimated from electrofishing at discrete sites in a large river. *Trans. Am. Fish. Soc.* **138**(1): 58–75. doi:10.1577/T08-025.1.
- Langtimm, C.A. 2009. Non-random temporary emigration and the robust design: conditions for bias at the end of a time series. In *Modeling Demographic Processes in Marked Populations*. Springer. pp. 745–761.
- Lundberg, P. 1988. The evolution of partial migration in birds. *Trends Ecol. Evol.* **3**(7): 172–175. doi:10.1016/0169-5347(88)90035-3. PMID:21227194.
- MacDonald, L.L., and Zucchini, W. 1997. Hidden Markov and other models for discrete-valued time series. CRC Press.
- Nelson, M.L., McMahon, T.E., and Thurow, R.F. 2002. Decline of the migratory form in bull charr, *Salvelinus confluentus*, and implications for conservation. In *Ecology, Behaviour and Conservation of the charrs, genus Salvelinus*. Springer. pp. 321–332.
- Nilsson, A.L., Lindström, Å., Jonzén, N., Nilsson, S.G., and Karlsson, L. 2006. The effect of climate change on partial migration — the blue tit paradox. *Glob. Change Biol.* **12**(10): 2014–2022. doi:10.1111/j.1365-2486.2006.01237.x.
- Pearson, K.N., Kendall, W.L., Winkelman, D.L., and Persons, W.R. 2015. Evidence for skipped spawning in a potamodromous cyprinid, humpback chub (*Gila cypha*), with implications for demographic parameter estimates. *Fish. Res.* **170**: 50–59. doi:10.1016/j.fishres.2015.05.015.
- Pearson, K.N., Kendall, W.L., Winkelman, D.L., and Persons, W.R. 2016. Tradeoffs between physical captures and PIT tag antenna array detections: a case study for the Lower Colorado River Basin population of humpback chub (*Gila cypha*). *Fish. Res.* **183**: 263–274. doi:10.1016/j.fishres.2016.06.014.
- Peñaloza, C.L., Kendall, W.L., and Langtimm, C.A. 2014. Reducing bias in survival under nonrandom temporary emigration. *Ecol. Appl.* **24**(5): 1155–1166. doi:10.1890/13-0558.1. PMID:25154103.
- Piper, A.T., Wright, R.M., Walker, A.M., and Kemp, P.S. 2013. Escapement, route choice, barrier passage and entrainment of seaward migrating European eel, *Anguilla anguilla*, within a highly regulated lowland river. *Ecol. Eng.* **57**: 88–96. doi:10.1016/j.ecoleng.2013.04.030.
- Pradel, R. 2005. Multievent: an extension of multistate capture–recapture models to uncertain states. *Biometrics*, **61**(2): 442–447. doi:10.1111/j.1541-0420.2005.00318.x. PMID:16011690.
- Raabe, J.K., Gardner, B., and Hightower, J.E. 2014. A spatial capture–recapture model to estimate fish survival and location from linear continuous monitoring arrays. *Can. J. Fish. Aquat. Sci.* **71**(1): 120–130. doi:10.1139/cjfas-2013-0198.
- Robinson, A.T., Clarkson, R.W., and Forrest, R.E. 1998. Dispersal of larval fishes in a regulated river tributary. *Trans. Am. Fish. Soc.* **127**(5): 772–786. doi:10.1577/1548-8659(1998)127<0772:DOLFIA>2.0.CO;2.
- Secor, D.H. 2007. Do some Atlantic bluefin tuna skip spawning? *Col. Vol. Sci. Pap. ICCAT*, **60**(4): 1141–1153.
- Skalski, J.R., Townsend, R., Lady, J., Giorgi, A.E., Stevenson, J.R., and McDonald, R.D. 2002. Estimating route-specific passage and survival probabilities at a hydroelectric project from smolt radiotelemetry studies. *Can. J. Fish. Aquat. Sci.* **59**(8): 1385–1393. doi:10.1139/f02-094.
- Skov, C., Chapman, B.B., Baktoft, H., Brodersen, J., Brønmark, C., Hansson, L.A., et al. 2013. Migration confers survival benefits against avian predators for partially migratory freshwater fish. *Biol. Lett.* **9**(2): 20121178. doi:10.1098/rsbl.2012.1178. PMID:23445943.
- Spurgeon, J.J., Paukert, C.P., Healy, B.D., Trammell, M., Speas, D., and Omana-Smith, E. 2015. Translocation of Humpback Chub into tributary streams of the Colorado River: implications for conservation of large-river fishes. *Trans. Am. Fish. Soc.* **144**(3): 502–514. doi:10.1080/00028487.2015.1007165.
- Stone, D. 2010. Overriding effects of species-specific turbidity thresholds on hoop-net catch rates of native fishes in the Little Colorado River, Arizona. *Trans. Am. Fish. Soc.* **139**: 1150–1170. doi:10.1577/T09-038.1.
- Stone, D.M., and Gorman, O.T. 2006. Ontogenesis of endangered humpback chub (*Gila cypha*) in the Little Colorado River, Arizona. *Am. Midl. Nat.* **155**: 123–135. doi:10.1674/0003-0031(2006)155[0123:OOEHCG]2.0.CO;2.
- Van Haverbeke, D.R., Stone, D.M., Coggins, L.G., and Pillow, M.J. 2013. Long-term monitoring of an endangered desert fish and factors influencing population dynamics. *J. Fish Wildlife Manage.* **4**(1): 163–177. doi:10.3996/082012-JFWM-071.
- Ward, D.L., Persons, W.R., Young, K.L., Stone, D.M., Vanhaverbeke, D.R., and Knight, W.K. 2015. A laboratory evaluation of tagging-related mortality and tag loss in juvenile Humpback Chub. *North Am. J. Fish. Manage.* **35**(1): 135–140. doi:10.1080/02755947.2014.986345.
- Watanabe, S. 2010. Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. *J. Mach. Learn. Res.* **11**: 3571–3594.
- Wolter, M.H., DeBoom, C.S., and Wahl, D.H. 2013. Field and laboratory evaluation of dam escapement of Muskellunge. *North Am. J. Fish. Manage.* **33**(4): 829–838. doi:10.1080/02755947.2013.812585.
- Yackulic, C.B., Yard, M.D., Korman, J., and Haverbeke, D.R. 2014. A quantitative life history of endangered humpback chub that spawn in the Little Colorado River: variation in movement, growth, and survival. *Ecol. Evol.* **4**: 1006–1018. doi:10.1002/ece3.990. PMID:24772278.
- Yackulic, C.B., Blake, S., and Bastille-Rousseau, G. 2017. Benefits of the destinations, not costs of the journeys, shape partial migration patterns. *J. Anim. Ecol.* **86**(4): 972–982. doi:10.1111/1365-2656.12679. PMID:28390059.
- Yackulic, C.B., Dodrill, M., Dzul, M., Sanderlin, J.S., and Reid, J.A. 2020. A need for speed in Bayesian population models: a practical guide to marginalizing and recovering discrete latent states. *Ecol. Appl.* **30**: e02112. doi:10.1002/eap.2112. PMID:32112492.