Evidence for skipped spawning in a potamodromous cyprinid, humpback chub (*Gila cypha*), with implications for demographic parameter estimates

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Abstract

Our findings reveal evidence for skipped spawning in a potamodromous cyprinid, humpback chub (HBC; *Gila cypha*). Using closed robust design mark-recapture models, we found, on average, spawning HBC transition to the skipped spawning state (γ'') with a probability of 0.45 (95% CRI (i.e. credible interval): 0.10, 0.80) and skipped spawners remain in the skipped spawning state (γ') with a probability of 0.60 (95% CRI: 0.26, 0.83), yielding an average spawning cycle of every 2.12 years, conditional on survival. As a result, migratory skipped spawners are unavailable for detection during annual sampling events. If availability is unaccounted for, survival and detection probability estimates will be biased. Therefore, we estimated annual adult survival probability (S), while accounting for skipped spawning, and found S remained reasonably stable throughout the study period, with an average of 0.75 ((95% CRI: 0.66, 0.82), process variance $\sigma^2 = 0.005$), while skipped spawning probability was highly dynamic ($\sigma^2 = 0.306$). By improving understanding of HBC spawning strategies, conservation decisions can be based on less biased estimates of survival and a more informed population model structure.

1. Introduction

Accurate estimation of demographic parameters, such as survival, abundance, and breeding frequency, is crucial to developing effective management strategies for fish and wildlife populations. However, challenges arise when estimating demographic parameters for migratory species that can only be readily monitored during one portion of their life cycle. For these migratory species, tracking population demography from observations only made during specific life stages may cause bias in demographic parameter estimates. Thus, it may be necessary to evaluate temporary emigration (i.e. the probability of temporarily being unobservable at the location or life stage from which observations are made) from the study site to avoid making biased estimates of survival, detection and breeding probabilities (Kendall and Nichols 1995; Kendall et al. 1997). As an example, many monitoring programs observe migratory species only on nesting beaches (Prince and Chaloupka 2012), breeding grounds (Barbraud and Weimerskirch 2012) or spawning rivers (Chase et al. 2007). If animals revisit these locations on irregular intervals, then this “skipped breeding” behavior results in some portion of the sexually mature population (i.e. the skipped breeders) being unavailable for detection during annual sampling events.

Population monitoring for the potamodromous cyprinid, humpback chub (HBC; *Gila cypha*) within the Lower Colorado River Basin (LCRB) has focused on sampling within their primary spawning ground, the Little Colorado River (LCR; Van Haverbeke et al. 2013). Due to the likely presence of both resident and migratory fish (Douglas and Marsh 1996; Gorman and Stone 1999) and suspected non-annual spawning (Coggins et al. 2006), evaluating temporary emigration from the LCR is key to generating unbiased demographic estimates while also informing HBC spawning strategies.

While iteroparous fishes, such as HBC, have traditionally been considered annual spawners, more recent research supports the idea that not all fishes spawn with annual regularity (Rideout and Tomkeiwicz 2011). Life-history theory suggests skipping reproductive events may have evolved as a mechanism to maximize lifetime fitness, especially in response to poor environmental conditions (Jørgensen et al. 2006). Most commonly, fisheries research has attributed skipped spawning to density-dependent effects resulting from dietary deficiencies (Rideout and Tomkeiwicz 2011; Skjæraasen et al. 2012). Although the majority of fisheries research regarding skipped spawning has focused on females, limited evidence of skipped spawning has also been documented in males with spawning probability as low as 0.75 (Rideout and Tomkiewicz 2011).

HBC in the LCRB were thought to historically spawn throughout the Colorado River (CR) in Grand Canyon, yet, at present, successful reproduction is only known to occur in the lower 14.2 km of its largest tributary, the LCR (Valdez and Ryel 1995; Robinson et al. 1998; Gorman and Stone 1999). Hypolimnetic releases from Glen Canyon Dam have been implicated in reducing available spawning habitat (Valdez and Ryel 1995; Kaeding and Zimmerman 1983; Douglas and Marsh 1996) with year-round temperatures in the CR maintained below those necessary for successful larval development (Hamman 1982; Wright et al. 2009). Despite temperature limitations, observations have been made of larval HBC in warm springs within the CR, indicating small scale spawning may occur. However, evidence is sparse for recruitment success beyond the LCR (Valdez and Masslich 1999; Andersen et al. 2010).

Because HBC inhabit remote canyon-bound reaches, knowledge of their spawning ecology is limited. Nonetheless, studies reveal HBC in the LCRB undergo spawning migrations from the CR into the LCR typically commencing in late March, with peak spawner abundance

occurring in late April, followed by rapid declines in May and June (Douglas and Marsh 1996; Gorman and Stone 1999). In the LCR, ripe males have been found aggregating in areas of structurally complex habitat with clean gravel deposits. Gravid females move into these areas to spawn, laying semi-adhesive eggs (Gorman and Stone 1999). Ripe males often remain on spawning grounds from late March to mid-May, whereas, gravid females are generally abundant only in April (Gorman and Stone 1999). Movement studies within the LCR provide evidence for localized stasis during this reproductive period (Douglas and Marsh 1996).

Based on their spawning migrations, the U.S. Fish and Wildlife Service (USFWS) implemented a standardized hoop-net sampling program to evaluate HBC demographic parameters in the LCRB. This sampling program provides data for estimating trends in abundance and recruitment within the LCR using mark-recapture methodologies. Specifically, a Chapman modified Petersen closed population estimator (see Seber 1982) has been used to estimate seasonal abundance (Van Haverbeke et al. 2013). In more recent years, an age structured open population model was developed to evaluate age specific annual mortality probabilities as well as abundance and recruitment trends (Coggins et al. 2006). One primary assumption of these estimation techniques is that HBC spawn annually, and are, therefore, available for detection during LCR sampling events. However, questions remain unanswered regarding whether a portion of the adult population fails to enter the LCR annually as a result of skipped spawning. Given monitoring occurs on their spawning ground, if skipped spawning is unaccounted for, this could lead to biased abundance, survival and detection probability estimates under both closed and open population models (Kendall et al. 1997; Zehfuss et al. 1999).

In the LCRB, challenges arise when evaluating skipped spawning, due to the presence of both resident and migratory individuals (Douglas and Marsh 1996; Gorman and Stone 1999). Resident HBC are believed to inhabit the LCR year-round, while migratory adults primarily reside in the CR and enter the LCR to spawn. This form of life history heterogeneity, in which residents and migrants breed sympatrically but overwinter in different habitats, is known as ‘non-breeding partial migration’ (Chapman et al. 2011). Accounting for such differences in life history strategies is difficult, given uncertainty regarding the age or size at which individuals begin displaying migratory behavior (Douglas and Marsh 1996; Gorman and Stone 1999).

To increase understanding of HBC demographic parameters and minimize uncertainty regarding sampling availability, we evaluated long-term mark-recapture data from the LCRB using closed robust design mark-recapture models (Kendall et al. 1997). We generated estimates of annual skipped spawning, survival and detection probabilities, as well as spawner abundance, while incorporating multiple datasets to account for potential differences in demographic parameters based on sex and migratory status. The primary focus of our research was to determine if, and at what probability, HBC in the LCRB fail to spawn annually, as this would have important implications for estimating abundance and survival probabilities used to evaluate recovery efforts.

2. Methods

2.1 Little Colorado River HBC Monitoring

The USFWS, in cooperation with the U.S. Geological Survey, Grand Canyon Monitoring and Research Center (GCMRC), has been largely responsible for collecting HBC monitoring data in the LCRB. Since fall of 2000, the USFWS has consistently conducted four annual stratified hoop-net surveys throughout the lower 13.57 km of the LCR. Two surveys occur in the

spring, typically in April and May, followed by two fall surveys in September and October. The lower 13.57 km of the LCR has been divided into three primary reaches (Figure 1). Each primary reach has been subdivided into three secondary reaches for a total of nine secondary reaches. Three crews are deployed to each primary reach for simultaneous sampling. Sampling typically takes place for three consecutive nights per secondary reach during which twenty hoop-nets (0.5 – 0.6 m diameter, 1.0 m long, single throat, 3 – 4 hoops, and covered with 6 mm mesh) are set in locations expected to yield catches of HBC. Hoop-nets are moved between nights within a secondary reach if catches are negligible or when alternative sites are available. Each crew fishes hoop-nets for nine consecutive nights, yielding a total of 540 net nights of sampling effort per survey annually (Van Haverbeke et al. 2013). Upon capture, HBC $\geq$ 150 mm total length (TL), and more recently $\geq$ 100 mm TL, are uniquely marked with a passive integrated transponder (PIT) tag (Biomark Inc., Boise, ID; Persons et al. 2013). Length, sex, reproductive status, external parasite data, and location of capture are all recorded prior to release, with ripeness and sex determined by physical expression of gametes (see Van Haverbeke et al. 2013 for additional detail).

Additional HBC surveys in the LCR have been conducted by the Arizona Game and Fish Department (AGFD) since 1987. Sampling effort, concentrated on the lower 1.2 km of the LCR, consists of fishing 13 hoop-nets (1.0 m diameter, 5.0 m long, double throat, 7 hoops, and covered with 6.3 mm mesh) placed in standardized locations for 20 – 30 consecutive nights during April and May (Persons et al. 2009). Tagging protocols and data collected are consistent with those of the USFWS (Persons et al. 2013).

In May of 2009, a full duplex PIT tag antenna array (Biomark Inc., Boise, ID) was installed in the LCR by GCMRC 1.78 km upstream of the confluence with the CR, to passively

detect the passage of tagged HBC moving into and out of the LCR (Figure 1). However, to date, functionality has been variable primarily due to damage caused by annual high flow events, with additional limitations in early years caused by insufficient power to the array as a result of reduced sun exposure to the solar charging panels in winter months. In recent years, the array has been operational year-round.

2.2 Closed Robust Design Mark-recapture Models

Using closed robust design mark-recapture models (Kendall et al. 1997) through program MARK (White and Burnham 1999), we estimated annual adult survival (S), detection (p), recapture (c), and skipped spawning probabilities (γ) along with spawner abundance (Ns). We defined an adult as any HBC greater than or equal to 200 mm TL, which was based on research indicating reproductive maturity is typically reached after three years of age and a minimum TL of 200 mm (Valdez and Ryel 1995; Gorman and Stone 1999; Meretsky et al. 2000).

Because the USFWS's sampling protocols include repeated hoop-net sampling over short time intervals within a sampling "season" (i.e. a given survey), this provided an opportunity to evaluate temporary emigration from the LCR through the use of Pollock's robust design (Pollock 1982). Under this design, within-season sampling periods are defined as secondary sampling occasions and are generally completed over consecutive days such that population closure can be assumed. Longer periods of time typically occur between primary sampling occasions (i.e. annual events) in which the population is assumed to be open. Between annual sampling events, HBC can remain in the LCR (if resident), return to the LCR, temporarily emigrate to the CR or die. One of the benefits of implementing the robust design model is the ability to separate availability (i.e. HBC that are in the LCR during sampling events) from true detection probability given presence in the study area (p^* = the probability of being detected at least once during a

primary sampling occasion given presence in the study area). We assumed absence from the LCR during the spawning season is reflective of a failure to spawn. Thus, we equate temporary emigration with skipped spawning. We completed our skipped spawning analysis by dividing available data into three subsets to assess the importance of accounting for residency and sex specific parameterization.

Additional assumptions specific to the closed robust design mark-recapture model we implemented include: within season demographic (see Figure 2) and geographic closure (but see Kendall 1999), no tag loss or handling mortality, all marked animals must be identifiable as such and recorded correctly, all individuals grouped together (e.g. age, sex etc.) have the same probability of capture, survival and emigrating, survival probability is equal for spawners and skipped spawners, and each animal acts independently with respect to survival, movement and detection.

2.3 Data Subsetting

We divided available data into subsets by first distinguishing individuals displaying migratory behavior from putative LCR residents. Because resident individuals live year-round in the LCR regardless of spawning status, they would presumably be available for detection year-round. However, migratory individuals are believed to enter the LCR only when reproductive, causing skipped spawners to be unavailable for detection during LCR sampling events. Therefore, we selected known migratory adults because inclusion of residents could bias skipped spawning probability when equating availability with spawning probability. Our designation of a migratory spawner was any adult captured in the lower reach of the LCR downstream of the PIT tag antenna array, with initial release above the array. Thus, any adult HBC captured only upstream of the array was excluded from the analysis because there designation was ambiguous.

We incorporated AGFD detections to aid designation of migratory spawners, given sampling was restricted to the lower 1.2 km of the LCR. We chose this designation because it likely provides a conservative estimate of migratory behavior, and we refer to this dataset as ‘known migrant’. Our designation of ‘known migrant’ individuals was motivated by research from Gorman and Stone (1999) indicating a higher proportion of individuals captured in the lower reach of the LCR (i.e. ≤ 3.0 km upstream of the confluence with the CR) were also captured in the confluence (i.e. CR) as compared to those captured in the upper reach (i.e. 10.5 – 13.57 km upstream of the confluence with the CR). Their findings are suggestive of a higher proportion of non-migratory HBC residing in the upper reach of the LCR. Additional support for our reasoning comes from research by Van Haverbeke et al. (2013), in which they found the majority of spawning and overwintering HBC occupy the upper reaches of the LCR (i.e. 5.0 – 13.6 km upstream of the confluence with the CR), indicating there is likely better spawning and overwintering habitat in this section of the river.

For comparison purposes, and to increase sample size due to the restrictive nature of the ‘known migrant’ data subsetting (Table 1), we relaxed our migratory assumption and instead assumed all adults migrated. We were then able to incorporate all detections of reproductively mature adults from the LCR. We refer to this larger dataset as ‘all adults’. By increasing sample size, we improved our ability to more thoroughly evaluate annual variability in survival and skipped spawning, and assess sex specific differences in demographic parameters. Using all adult detections also allowed us to evaluate the importance of accounting for residency. If a large portion of the population consisted of resident adults, we expected skipped spawning probability would be reduced under the ‘all adults’ dataset because resident individuals would be present in the LCR regardless of spawning status. However, when comparing skipped spawning

probabilities between the ‘known migrant’ and ‘all adults’ datasets, if we did not see a negative bias, accounting for residency may not be necessary when assessing skipped spawning.

To evaluate sex-specific differences in demographic parameters, we restricted our ‘all adults’ dataset to detections of only ripe individuals. Non-ripe adults were excluded due to challenges in sexing individuals when gametes are not expressible. As a result, sample size was reduced and detections consisted primarily of males (i.e. 95%). This sex bias suggests males may have been expressing gametes for a longer period of time or their gametes were easier to detect. We refer to this dataset as ‘known sex’.

2.4 Sampling Occasions

Because our primary focus was to evaluate skipped spawning, we only included spring sampling occasions (i.e. April and May) and detections of adult HBC. Using a robust design framework, we designated the first day of USFWS hoop-net sampling at a given location as the first of three secondary sampling occasions. We then pooled the subsequent two days of sampling at a given location into a single detection event, yielding our second secondary sampling occasion (Figure 2). We repeated this process for both April and May sampling events and combined the datasets by pooling across locations and months, within each of the two secondary sampling occasions. Pooling was done to mitigate the possible effect of violating within season closure assumptions. Our third secondary sampling occasion consisted of all spring PIT tag antenna array detections. An example within season capture history of 101, where ‘1’ indicates capture and ‘0’ indicates no capture, would denote an individual was captured on day 1 of USFWS hoop-net sampling at a given location, was not recaptured on days 2 or 3 of hoop-net sampling but was detected by the array.

Although consistent hoop-net sampling by the USFWS began in 2001, detections from 2001 to 2003 were not included in the ‘known migrant’ dataset due to the number of sampling periods necessary to designate a migratory individual. However, due to elimination of the migratory assumption, the ‘all adults’ and ‘known sex’ datasets include detections from 2001 to 2011. Array detections were only available from 2009 to 2011, resulting from its recent installation. Therefore, the third secondary sampling occasion was only available for the last three years of the study.

2.5 Modeling Analysis

When evaluating evidence for skipped spawning, we tested three *a priori* hypotheses regarding the process driving this behavior. We began by modeling spawning as a function of reproductive status in the previous year and define this as a first-order Markov process (i.e. $\gamma_t'' \neq \gamma_t'$ where γ_t'' = probability a spawner at time t transitions to a skipped spawner at time $t+1$ and γ_t' = probability a skipped spawner at time t remains a skipped spawner at time $t+1$). Under this hypothesis, the mechanism responsible for a HBC skipping a spawning event is biological, indicating a need to build up resources prior to spawning, although variability in these parameters over time can be due to environmental factors. Markovian spawning processes have been documented in various species, including sea turtles, amphibians and birds (Kendall and Bjorkland 2001; Barbraud and Weimerskirch 2012; Prince and Chaloupka 2012). We compare the Markovian spawning hypothesis against the hypothesis that spawning was independent of previous reproductive status (i.e., “random” by setting $\gamma'' = \gamma' = \gamma$), in which only environmental factors were driving reproductive ability due to fluxes in resource availability. Our third hypothesis predicted all reproductively mature HBC in the LCRB spawn annually (i.e., set $\gamma = 0$), and we refer to this as a ‘No Skipping’ model.

We evaluated both constant and annually variable skipped spawning, survival and detection probabilities while accounting for data limitations and model constraints. We assumed survival of skipped spawners was equal to spawners, an assumption required by the model because detections were limited to the observable (i.e. spawner) state (Kendall et al. 1997). Additionally, to account for parameter confounding in the fully time varying model, we followed recommendations presented by Kendall et al. (1997) regarding parameter constraints. Thus, we set $\gamma_{k-1}'' = \gamma_k''$ and $\gamma_{k-1}' = \gamma_k'$ where k indicates the terminal time period. Lastly, we accounted for differences in detection probability based on time (t) and trap response (i.e. $p \neq c$, where p = within season capture probability and c = within season recapture probability). For years with no array detections (i.e. no third capture period), we considered models with either time variation or trap response in detection probability. For years with array detections, we were also able to include models with both time variation and trap response (Otis et al. 1978), although we did not consider trap response for the array itself. From these model structures, we also estimated annual spawner abundance (N_{ts} , where s = current year spawning adult), assuming all spawners were available for capture. Thus, we made comparisons between our abundance estimation methods and the traditional Chapman modified Petersen closed population estimation techniques implemented by the USFWS. Because the array cannot detect unmarked individuals, we excluded array detections from our abundance calculations.

We created all possible combinations of the parameters of interest for a total of 60 models. When evaluating sex specific parameterization, we also allowed parameters to vary between males and females for a total of 120 models. All models provided reasonable hypotheses for assessing variability in HBC demographic parameters. For a full list of models and estimable parameters see Appendix A.

2.6 Model Selection and Parameter Estimates

Model selection was based on information theory, while initial parameters were estimated using a maximum likelihood approach. We determined model support using Akaike Information Criteria with a small-population correction factor (i.e. AICc), and we report all models with reasonable support ($\Delta\text{AICc} \leq 7$; Burnham et al. 2011). Because a portion of our parameter estimates were near the 1.0 bound, we implemented a Markov chain Monte Carlo (MCMC) estimation procedure (Gilks et al. 1996) using a logit link, to produce more reliable confidence bounds (Cooch and White 2013). From our MCMC analysis, we were able to estimate a grand mean (μ) and process variance (σ^2), given sufficient time-varying estimates, for S and γ using a random effects model, and we report 95% credible intervals (CRI) for all parameter estimates. To generate MCMC parameter estimates, we used the default settings in program MARK barring one exception which required significantly increasing the number of stored samples to yield convergent iteration plots.

We used the median c procedure in program MARK to evaluate goodness of fit (Cooch and White 2013) using a multistate framework. Thus, we were able to partially test the assumptions underlying our models by evaluating the amount of overdispersion in the data.

3. Results

3.1 Skipped Spawning

We found strong support for skipped spawning in the LCRB population of HBC as indicated by all top models (i.e. $\text{AICc} \leq 7.0$) including a skipped spawning process, with no support for consistent annual reproduction (Table 2). When considering ‘known migrant’ individuals, our most parsimonious model indicated skipped spawning was a completely random process. However, considerable model selection uncertainty was apparent (i.e. $w_{\text{random}} = 0.60$

and $w_{\text{Markovian}} = 0.40$, where w = total model weight). When evaluating the larger ‘all adults’ dataset, we found reduced model selection uncertainty and strong support for a Markovian skipped spawning process. Our ‘known sex’ analysis also revealed support for a Markovian skipped spawning process, as well as sex-specific parameters. Indicating males and females were skipping with different probabilities.

When assessing the importance of accounting for residency, we found that γ was lower under the ‘known migrant’ dataset than the ‘all adults’ (i.e. 0.65 (95% CRI: 0.57, 0.73) as compared to 0.69 (95% CRI: 0.66, 0.71)). The observed difference in γ was opposite in direction from our expectation if a large portion of this population were resident. To avoid any potential bias that may be generated because resident individuals are unlikely to be detected by the array, we also excluded array detections from the analysis and found γ was equal across datasets (i.e. $\gamma(\text{‘known migrant’}) = 0.49$ (95% CRI: 0.29, 0.64) and $\gamma(\text{‘all adults’}) = 0.49$ (95% CRI: 0.45, 0.53)). Therefore, we concluded accounting for residency may not be necessary when evaluating skipped spawning.

We found females (f) appear to have a higher probability of skipped spawning in a year subsequent to spawning than males (m) based on $\gamma m'' = 0.46$ (95% CRI: 0.11, 0.81) and $\gamma f'' = 0.55$ (95% CRI: 0.30, 0.75; Figure 4). We found high process variance for $\gamma m''$ (i.e. $\sigma^2(m) = 0.277$), indicating the probability of a male transitioning from a spawner at time (t) to a skipped spawner at time ($t+1$) was annually dynamic. However, $\gamma f''$ was low (i.e. $\sigma^2(f) = 0.016$), indicating minimal annual variability in skipped spawning probability for females. On average, males had a higher probability of remaining a skipped spawner (i.e. $\gamma m' = 0.60$ (95% CRI: 0.26, 0.90)) than transitioning from a spawner to a skipped spawner. However, we were unable to

generate a reliable mean and process variance estimate for $\gamma f'$ due to a small sample of known females.

Because our conclusions regarding skipped spawning were not influenced by residency and our 'known sex' dataset was heavily male biased, our most reliable demographic estimates come from our analysis of the 'all adults' dataset. Under a Markovian skipped spawning process, we estimated differences in future skipped spawning probabilities based on current spawning state. We found the average probability of an adult HBC skipping a spawning event in a year subsequent to spawning (γ'') was 0.45 (95% CRI: 0.10, 0.80), and the average probability of remaining a skipped spawner (γ'') was 0.60 (95% CRI: 0.26, 0.83). These skipped spawning probabilities translate to an expected 2.12 years between spawning events, conditional on survival. Annual variability in γ'' was high (i.e. $\sigma^2 = 0.306$), indicating the probability of a spawner transitioning to a skipped spawner was highly dynamic over the study period (Figure 3). However, annual variability in γ' was minimal (i.e. $\sigma^2 = 0.085$).

3.2 Survival

Annual adult survival probability estimates were reasonably consistent across datasets (Table 3) and over time (Figure 3). Our 'known migrant' analysis reveals annual adult survival probability was constant over the study period (i.e. 2004 – 2011) at 0.79 (95% CRI: 0.70, 0.88). We found annual survival probability did not differ significantly between males and females, with an estimated constant survival probability of 0.78 (95% CRI: 0.73, 0.83) for males and 0.76 (95% CRI: 0.63, 0.90) for females. Under the 'all adults' analysis, we found annually varying survival probabilities. However, the majority of annual variability was attributable to sampling variance (Figure 3). Nevertheless, we saw a decrease in S in 2006, with an estimated probability

of 0.57 (95% CRI: 0.48, 0.68), which warrants further exploration. However, at this time, the likely cause is unknown. Survival probability was again reduced for the terminal two years of the study (i.e. 2009 and 2010), which may be attributable to modeling constraints (Langtimm 2009). Thus, we reran our MCMC random effects model excluding 2009 and 2010 estimates and found identical results (i.e. $S_{2001-2008} = 0.75$ (95% CRI: 0.68, 0.83) and $S_{2001-2010} = 0.75$ (95% CRI: 0.66, 0.82)). From this comparison, we found our most reliable estimate of mean annual adult survival probability is 0.75.

3.3 Spawner Abundance

Our estimates of spawner abundance show a fairly stable trend from 2001 until 2006 with an average of 1023 (Range: 834 to 1350) spawners, excluding 2002, when we estimated N_s to be 57 (95% CRI: 53, 84; Figure 5). Beginning in 2007 and continuing until 2010, we show a steady increase in spawner abundance up to a high of 4480 (95% CRI: 3770, 5312), with a slight decline in 2011. The considerably lower spawner abundance estimate from 2002 is likely attributable to changes in sampling effort, which may have led to a small sample bias for that year, and not truly reflective of spawner abundance. This conclusion is supported by apparent estimability issues for detection probability in 2002, in which $p_1 = 0$ and $p_2 = 1$ (see Figure 6).

3.4 Detection Probability

Time varying capture probability estimates indicated detectability via hoop-net sampling was dynamic over the study period, with an average day 1 detection probability estimate of 0.19 and a pooled day 2 and 3 estimate of 0.30. Array detection probability estimates were consistently low, as was expected, because the array was only operational for a portion of the HBC migratory period. On average, we estimated array detection probability was 0.03, ranging from 0.01 in 2009 and 2010 to 0.06 in 2011. Pooled detections across all gear types and within

season sampling periods (i.e. p constant) showed low sampling variation but high annual variation, with detection probability estimates ranging from 0.07 to 0.24 and mean of 0.18. Under our ‘known migrant’ analysis, we saw evidence for a negative trap response based on average p and c estimates of 0.47 and 0.20, respectively. Although, no support was found for a trap response in either the ‘all adults’ or ‘known sex’ analyses.

3.5 Goodness of Fit

Median c estimates reveal minimal overdispersion (i.e. median c (‘known migrant’) = 1.19 (95% CI: 1.16, 1.21) and median c (‘all adults’) = 1.18 (95% CI: 1.16, 1.20)) indicating good fit of the model to the data. Thus, we did not adjust model selection values.

4. Discussion

Our evidence strongly suggests adult HBC are skipping spawning events and as a result are not annually available for detection in the LCR. Although the spawning decision appears to be dependent on spawning status in the previous year, on average, a minimum of 50% of the adult population fails to spawn annually based on pooled estimates of γ'' and γ' . Similar findings were reported by a concurrent study, revealing skipped spawning probabilities of 0.69 and 0.39, respectively for small (i.e. 200-250 mm TL) and large (i.e. 250+ mm TL) adult HBC (reported as spawning probabilities (i.e. 1- skipped spawning probability) Yackulic et al. 2014)). We found that skipped spawning is best represented with a Markov process when assuming all adults are migratory. However, when restricting our analysis to ‘known migrant’ individuals, we found skipped spawning was a random process. This latter finding is not surprising, because often with small datasets there is insufficient power to detect more complex effects.

We estimated skipped spawning probabilities that were nearly identical regardless of migratory status assumptions, indicating either most adult HBC are migratory or our method for

distinguishing migrants is invalid. An alternative explanation is artificially inflated skipped spawning probabilities when including all adults due to lower survival for residents, thus masking the distinction. Without further monitoring of movement patterns within this population or greater detections of HBC in the CR, inferences regarding residency of HBC in the LCR remain limited. However, support for a small resident LCR population was reported by Yackulic et al. (2014) in which they estimated 82% of adult HBC in the LCR are migratory. Similar findings were reported by Limburg et al. (2013) based on otolith microchemistry in which they found 18% residency. Although in the Limburg et al. study, all resident individuals were juveniles, while all adults migrated to the CR.

Annual variability in skipped spawning probabilities was considerable, highlighting the importance of accounting for temporal variance for gaining a better understanding of HBC spawning dynamics and to reduce potential sources of bias when estimating additional demographic parameters. Critical consideration of covariates that may in-part explain this variability would benefit long-term population management as temporal trends appear to be influencing spawning frequency.

We acknowledge accounting for sex specific heterogeneity in skipped spawning probabilities may be essential to the accurate estimation of demographic parameters. However, better sexing data is necessary to confidently evaluate such differences. Higher rates of skipped spawning in females are in line with previous research indicating female fish invest more energy in gonad development than males (Jonsson et al. 1991). Thus, females are likely more sensitive to resource limitations for successful reproduction. Gaining a better understanding of such limitations in the LCRB will aid development of a comprehensive management plan for influencing survival, reproduction and recruitment.

Although we were unable to formally evaluate spawning probability based on assessment of physical ripeness, given HBC in the LCRB are migratory and sampling was conducted on their spawning ground, we believe temporary emigration is an appropriate measure. Due to strong site fidelity and limitations in suitable spawning habitat outside the LCR, research indicates HBC in the LCRB are unlikely to successfully spawn in locations outside the LCR (Robinson et al. 1998; Gorman and Stone 1999; Paukert et al. 2006). If migratory adults enter the LCR during the spawning season for purposes other than spawning, which at this point has not been evaluated, our migratory status assumption would lead to negatively biased skipped spawning probabilities. However, given spawning omission is likely attributable to maximizing long-term fitness through increased survival and greater future spawning success due to energy savings (Rideout et al. 2005), it is improbable adult HBC expend energy to migrate when non-reproductive.

Previous research from the LCRB, evaluating HBC detections from 1989 to 2002 found that survival varied by age class with estimated annual survival probabilities for 4 year olds of 0.60 up to 0.80 for $HBC \geq 11$ years (Coggins et al. 2006). Due to the high number of parameters necessary to fit their models, they were unable to account for the possibility of skipped spawning. Although we include all ages of adult HBC (i.e. 4+ years), our estimates are more reflective of Coggins et al.'s survival probabilities for older adults. A possible explanation for this difference is likely due to accounting for a Markovian temporary emigration process (i.e. skipped spawning). Research by Kendall et al. (1997) shows under standard Cormack-Jolly-Seber open population models, which do not account for temporary emigration due to confounding of detection probability and availability, the result is negatively biased survival and detection probability estimates under Markovian temporary emigration where $\gamma'' < \gamma'$. When

employing a Jolly-Seber model, temporary emigration from the study site, in part, appears to be resolved by reducing survival estimates (Zehfuss et al. 1999). Thus, by accounting for Markovian temporary emigration, we reduce the probability of generating biased parameter estimates. An additional explanation for our estimates being more consistent with survival estimates for older adults, is simply due to increased survival probability during our study period. This explanation is probable given increasing abundance estimates in recent years as compared to declines in the 1990s (Coggins et al. 2006; Van Haverbeke et al. 2013).

Our estimates of annual adult abundance in the LCR can aid determining fulfillment of population monitoring objectives. Because abundance estimates include only those individuals available for detection, evaluating sampling availability (i.e. skipped spawning) was necessary to determine what portion of the total population was included in the abundance estimate. If recovery plans are dependent upon reaching a certain population threshold, which is the case for HBC, incorrect interpretation of abundance estimates could falsely prevent attainment of recovery goals. Thus, because sampling occurred solely on their spawning ground and HBC are skipping spawning events, abundance estimates are not reflective of total population abundance but spawner abundance. When comparing our abundance estimates to those generated by the USFWS, we would expect similar results, as both depict spawner abundance and not total population abundance. However, our estimates were consistently lower than those generated during the same time period (Van Haverbeke et al. 2013), although following the same trends. The consistently higher estimates generated by the USFWS may be attributable to violations of population closure assumptions, because they allowed a greater time period to elapse between initial capture and recapture events. To estimate abundance, the USFWS uses April hoop-net sampling as the first capture period and May hoop-net sampling as the second capture period;

therefore, assuming the population is closed to births, deaths, immigrations and emigrations between the two sampling periods. However, because this is a period of peak spawning, in which a portion of the adult HBC population is likely moving into while others are moving out of the LCR, it is probable both immigrations and emigrations are occurring during this time. If true, this type of movement would cause abundance estimates generated using a Lincoln-Petersen estimator to be positively biased for either sampling period (see Williams et al. 2002). When generating spawner abundance estimates using a closed robust design mark recapture model, we ensured population closure by defining secondary sampling periods differently, only allowing one to two days to pass between first and second capture events. Therefore, we believe our estimates of spawner abundance are likely more robust.

Generating unbiased demographic parameter estimates was reliant on fulfillment of closed robust design model assumptions, which in part include: no tag loss and no affect on survival due to tagging. PIT tag retention and mortality studies using surrogate species for juvenile HBC, found high survival (i.e. > 98%) and low tag loss (i.e. 3%), 30 days post abdominal tagging (Childs 2002; Ward et al. 2008), indicating there is likely minimal tag loss and negligible effects on HBC survival due to tagging. Because PIT tags are inserted into the abdominal cavity, tags are not discernable to visual predators, likely making a tagged fish no more susceptible to predation by such species. Additionally, swimming studies have shown PIT tagging and handling has little effect on swimming ability (Ward 2003). However, a 2005 study by Paukert et al. evaluating the effects of repeated hoop-netting and handling on bonytail chub (*Gila elegans*), found reduced growth in fish recaptured multiple times as compared to those never recaptured. These findings raise concern that survival and reproductive success may be negatively affected due to reduced growth in fish handled repeatedly.

A thorough assessment of all model assumptions and constraints is essential to understanding the strengths and limitation of our modeling analysis. Goodness of fit tests showed minimal overdispersion in the data, indicating adult HBC are acting independent from one another, thus fulfilling an important model assumption. Concern, however, has been raised when using robust design models due to the necessary constraint that survival of the unobservable state (i.e. skipped spawner) is equal to survival of the observable state (i.e. spawner). In the LCRB, uncertainty exists regarding fulfillment of this assumption due to differences in habitat usage and energy exertion between spawners and skipped spawners. However, a recent study found that during a period of consistently warmer water temperatures in the CR, HBC survival was higher in the CR than in the LCR (Yackulic et al. 2014).

Our findings reveal, under current environmental conditions, all adult HBC in the LCRB do not spawn annually, but instead, evidence suggests HBC need to build up resources prior to spawning in a subsequent year (i.e. Markovian spawning process). We also show skipped spawning probability has been highly dynamic over time, which indicates there is likely an environmental component influencing reproduction. Not only do our findings improve understanding of HBC spawning habits, but they also inform availability for detection during annual sampling events. Our research further illustrates how violating estimation model assumptions can bias abundance and survival probability estimates, and we demonstrate the importance of accounting for such violations. Thus, the results of our study can be used to aid in HBC management and to strengthen insight into the spawning dynamics of this long-lived fish.

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Tables

Table 1. Effective sample size based on program MARK estimation procedures for all datasets used to evaluate demographic parameters for the Little Colorado River population of humpback chub from 2001 to 2011 (see Appendix B for ‘input data summary’ from program MARK).

Table 2. Top robust design mark-recapture models, based on $AIC_c \leq 7$, used to evaluate demographic parameters for the Little Colorado River population of humpback chub. Included are the most parsimonious “No Skipping” models as indicated by (*) for comparison purposes. S = survival probability, γ = probability of transitioning to skipped spawner, γ'' = probability spawner transitions to skipped spawner, γ' = probability skipped spawner remains skipped spawner, p = within season capture probability, c = within season recapture probability, t = annual time period, j = within season time period

Table 3. Grand mean (μ) and process variance (σ^2) estimates for HBC survival (S) and skipped spawning probabilities (γ'' = spawner transitions to skipped spawner and γ' = skipped spawner remains a skipped spawner) using the most parsimonious robust design mark-recapture models.

Figures

Figure 1. U.S. Fish and Wildlife Service (USFWS) primary hoop-net sampling reaches for humpback chub (*Gila cypha*; HBC) in the Little Colorado River (LCR), Arizona as indicated by

km markers (i.e. 0.0 – 5.0 km, 5.0 – 9.6 km, 9.6 – 13.57 km). Each primary reach has been subdivided into three secondary reaches for a total of nine secondary reaches. Addition hoop-net sampling, conducted by the Arizona Game and Fish Department, occurs from the confluence to 1.2 km upstream in the LCR. Included is the location of the U.S. Geological Survey, Grand Canyon Monitoring Research Center (GCMRC), PIT tag antenna array.

Figure 2. Theoretic depiction of the robust design mark-recapture model used to evaluate demographic parameters for the Little Colorado River population of humpback chub. Detection data includes: U.S. Fish and Wildlife Service hoop-net sampling surveys and U.S. Geological Survey, Grand Canyon Monitoring and Research Center PIT tag antenna array detections. S = annual survival probability, γ = annual skipped spawning probability (i.e. unavailable for detection), p_1 = hoop-net detection probability from day 1 of sampling at a given location within the LCR (pooled across April & May), p_2 = hoop-net detection probability from days 2 and 3 of sampling at a given location within the LCR (pooled across April & May), p_3 = array detection probability (pooled across May), p^* = probability of being detected at least once within a season $[1-(1-p_1)(1-p_2)(1-p_3)]$

Figure 3. Time varying annual survival (S) and skipped spawning probability estimates (γ'' = spawner transitions to skipped spawner and γ' = skipped spawner remains a skipped spawner) for all adult (i.e. ≥ 200 mm total length) humpback chub in the Little Colorado River. The grand mean over the duration of the study is represented by μ , and σ^2 gives the process variance. The distribution on the right illustrates the amount of variability in time varying estimates. Error bars show 95% credible intervals for each estimate.

781
782 Figure 4. Annual skipped spawning probability estimates (γ'' = spawner transitions to skipped
783 spawner and γ' = skipped spawner remains a skipped spawner) for 'known sex' adult (i.e. ≥ 200
784 mm total length) humpback chub in the Little Colorado River. The grand mean over the duration
785 of the study is represented by μ , and σ^2 gives the process variance. The distribution to the right
786 of each graph illustrates the amount of variability in annual estimates. Error bars indicate 95%
787 credible intervals. Estimates of μ and σ^2 for γ' (female) were not reported owing to estimability
788 issues.

789
790 Figure 5. Annual spawner abundance (N^s) estimates for humpback within the Little Colorado
791 River, Arizona with corresponding 95% credible intervals.

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793 Figure 6. Time varying detection probability (p) estimates for adult (i.e. ≥ 200 mm total length)
794 humpback chub in the Little Colorado River. Mean detectability over the duration of the study
795 for each sampling period (i.e. p_1 = first day of hoop-netting at a given location, p_2 = days 2 and 3
796 of hoop-netting at a given location, p_3 = array detections from May) and method (hoop-netting
797 versus array) is indicated by μ , and $p(\text{pooled})$ provides a detection probability estimate pooled
798 across all within season sampling periods and gear types.

Table 1

Dataset	Effective Sample Size
Known Migrant	883
All Adults	9481
Known Sex	3731

Table 2

Dataset	Top Models	$\Delta AICc$	Likelihood
Known Migrant	Random - $S(.) \gamma(.) p(t) c(t)$	0.0000	1.0000
	Markovian - $S(.) \gamma''(.) \gamma'(.) p(t) c(t)$	1.8163	0.4033
	Markovian - $S(t) \gamma''(.) \gamma'(.) p(t) c(t)$	1.9532	0.3766
	Random - $S(.) \gamma(t) p(t) c(t)$	4.0189	0.1341
	*No Skipping - $S(t) \gamma=0 p(.) c(.)$	115.991	6.50E-25
All Adults	Markovian - $S(t) \gamma''(t) \gamma'(t) p(t,j)$	0.0000	1.0000
	Markovian - $S(.) \gamma''(t) \gamma'(t) p(t,j)$	1.6601	0.4360
	Random - $S(t) \gamma(t) p(t,j)$	2.2353	0.3271
	*No Skipping - $S(t) \gamma=0 p(t) c(t)$	110.0540	1.26E-24
Known Sex	Markovian - $S(.) \gamma''(t) \gamma'(t) p(t,j)$ - sex variation	0.0000	1.0000
	Random - $S(t) \gamma(.) p(t,j)$ - sex variation	3.0619	0.2163
	Random - $S(.) \gamma(t) p(t,j)$ - sex variation	3.3099	0.1911
	Markovian - $S(t) \gamma''(.) \gamma'(.) p(t,j)$ - sex variation	3.5378	0.1705
	*No Skipping - $S(t) \gamma=0 p(t,j)$ - sex variation	35.9656	1.55E-08

*Most parsimonious "No Skipping" model included for reference.

Table 3

Analysis	$\mu(S)$	$\sigma^2(S)$	$\mu(\gamma'')$	$\sigma^2(\gamma'')$	$\mu(\gamma')$	$\sigma^2(\gamma')$
Known Migrant	0.79	NA*	0.65	NA*	0.65	NA*
All Adults	0.75	0.005	0.45	0.306	0.60	0.085
Known Sex: male	0.78	NA*	0.46	0.277	0.60	0.065
female	0.76	NA*	0.55	0.016	Unk.	Unk.

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6