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ASSESSING JUVENILE NATIVE FISH DEMOGRAPHIC RESPONSES TO A STEADY FLOW EXPERIMENT IN A LARGE REGULATED RIVER

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ABSTRACT

The Colorado River below Glen Canyon Dam, Arizona, is part of an adaptive management programme which optimizes dam operations to improve various resources in the downstream ecosystem within Grand Canyon. Understanding how populations of federally endangered humpback chub *Gila cypha* respond to these dam operations is a high priority. Here, we test hypotheses concerning temporal variation in juvenile humpback chub apparent survival rates and abundance by comparing estimates between hydropeaking and steady discharge regimes over a 3-year period (July 2009–July 2012). The most supported model ignored flow type (steady vs hydropeaking) and estimated a declining trend in daily apparent survival rate across years (99.90%, 99.79% and 99.67% for 2009, 2010 and 2011, respectively). Corresponding abundance of juvenile humpback chub increased temporally; open population model estimates ranged from 615 to 2802 individuals/km, and closed model estimates ranged from 94 to 1515 individuals/km. These changes in apparent survival and abundance may reflect broader trends, or simply represent inter-annual variation. Important findings include (i) juvenile humpback chub are currently surviving and recruiting in the mainstem Colorado River with increasing abundance; (ii) apparent survival does not benefit from steady fall discharges from Glen Canyon Dam; and (iii) direct assessment of demographic parameters for juvenile endangered fish are possible and can rapidly inform management actions in regulated rivers. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS: peaking flows; hydropower; endangered species; Colorado River; regulated river

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INTRODUCTION

In over half the world's large rivers, dams modify flows by storing water in upstream reservoirs and regulating downstream discharges to facilitate shipping, power production and flood control, or to provide water for industry, municipalities and irrigation (WCD, 2000; Poff *et al.*, 2006; Richter and Thomas, 2007). Although the magnitude of impacts are as varied as the dams themselves (ranging from small 'run-of-the-river' type dams to large structures impounding more than the mean annual flow of a river), the attendant physical and biological changes incurred due to river regulation are similar across climates, latitudes and elevations (Blinn and Poff, 2005; Nilsson *et al.*, 2005; Poff *et al.*, 2006). Changes to the physical environment include sequestration of woody debris and sediment in upstream reservoirs (Stanford and Ward, 1991; Kearsley *et al.*, 1994; Schmidt *et al.*, 1998), modification of temperature regimes (Stanford and Ward,

1991; Clarkson and Childs, 2000) and alteration of the timing, magnitude and frequency of flows (Poff *et al.*, 1997; Lovich and Melis, 2007; Burgess *et al.*, 2013; Dutterer *et al.*, 2013). Ecological impacts range from altered trophic dynamics (Stevens *et al.*, 1997; Kennedy and Gloss, 2005) to development of novel fish communities, often dominated by non-native species (Mueller and Marsh, 2002; Coggins *et al.*, 2011).

Where dams are used for hydropower production, diel variations in downstream river discharge represents a specific form of habitat modification that affects the physical conditions within rivers (i.e. depth and velocity) creating unnatural and altered habitat conditions (Fette *et al.*, 2007). Juvenile fish that predominately use nearshore or shallow areas are thought to be most affected by fluctuations in discharge (Gaudin, 2001) that force them away from preferred habitats (Bunt *et al.*, 1999) leading to slower growth rates (Korman and Campana, 2009) and potentially exposing them to higher predation rates by altering foraging arenas (Walters and Juanes, 1993; Ahrens *et al.*, 2012). In shallow littoral habitats (especially vegetated cobble bars or backwaters), warm water microhabitats can develop under steady flow conditions

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(Korman and Campana, 2009; Ralston, 2011), which may be important to juvenile life stages of warm water native fish (Trammell *et al.*, 2002; USDO, 2008; Ralston, 2011).

One study of the Tallapoosa River below Harris Dam in the southeastern USA documented reduced amounts of shallow water habitat and decreased young-of-year fish abundance because of water level fluctuations, which resulted in changes in the fish community composition (Freeman *et al.*, 2001). Similarly, Glen Canyon Dam in northern Arizona (Figure 1) is operated to match electrical power demand in the southwestern USA, with diel fluctuations in dam discharge (hydropeaking; Figure 2). These fluctuations can shift the availability of different nearshore habitat types in the downstream Colorado River, especially where shoreline angles are low (Korman and Campana, 2009). Habitat alterations in Grand Canyon as a result of the federally operated Glen Canyon Dam may have significant repercussions on the imperilled native fish community downstream (Minckley, 1991; Converse *et al.*, 1998).

Despite the effects of diel fluctuations on habitat, there is wide variation in community (Murchie *et al.*, 2008) and individual species responses (Steele and Smokorowski, 2000; Young *et al.*, 2011) to flow stabilization. Ecological complexity and uncertainty often necessitate an experimental approach towards optimizing management policies to reach conservation targets (e.g. waterfowl harvest, Williams *et al.*, 1996; Everglades restoration, Gunderson and Light, 2006). Below Glen Canyon Dam, experimental management approaches are challenged by the constraints of minimizing physical and ecological impacts while still meeting the water and power needs of tens of millions of people (Reisner, 1986; Anderson and Woosley, 2005; Richter and Thomas, 2007). The dam was built on the Colorado River (Figure 1) as a water supply and hydropower project before the drafting of the National Environmental Policy Act, the Endangered Species Act, or the Clean Water Act, yet must now operate within the confines of this legislation. To facilitate environmental compliance, the 1995 Environmental

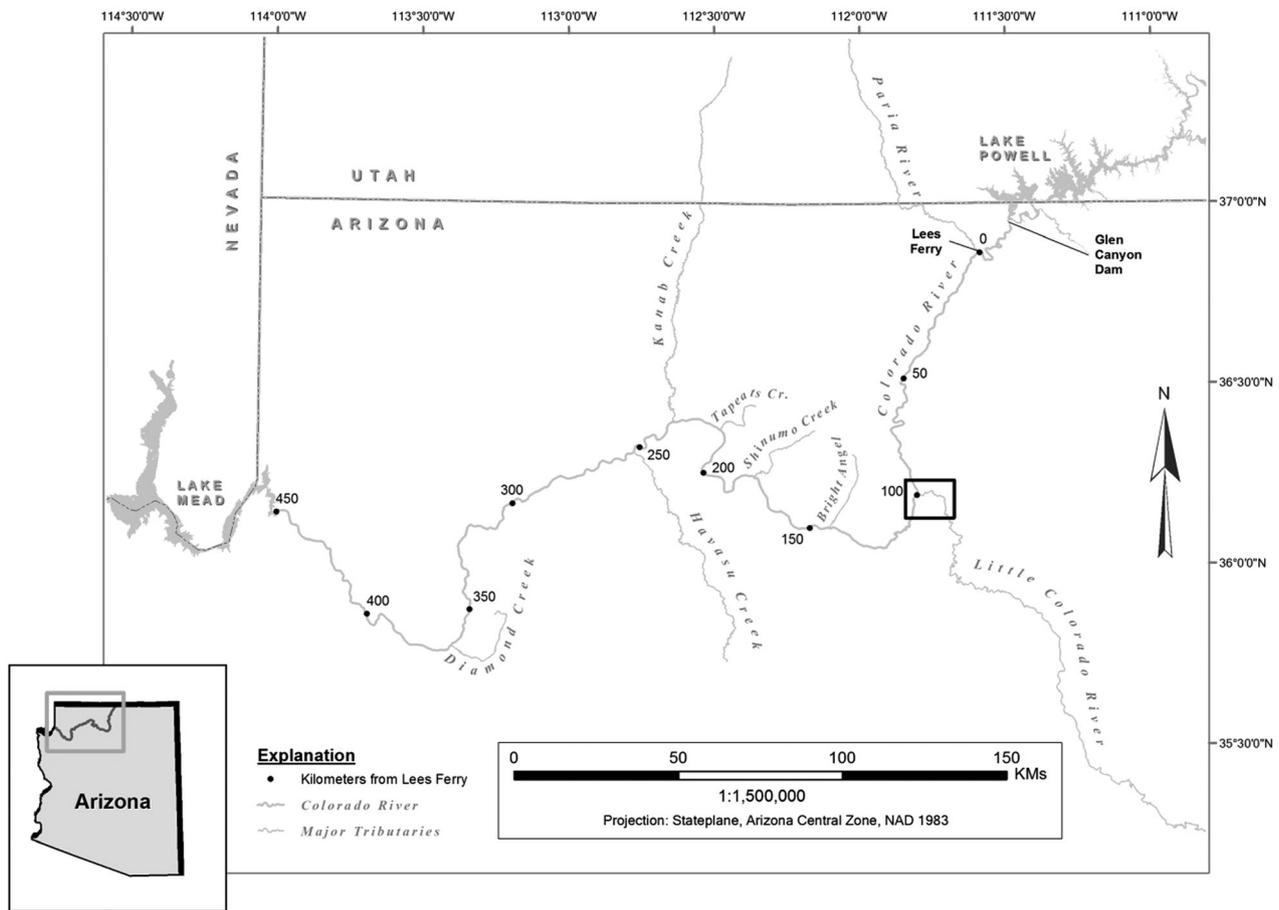


Figure 1. Map of study area near confluence of Colorado and Little Colorado Rivers in Grand Canyon, northern Arizona, USA. Black box denotes the area containing the Little Colorado River aggregation of humpback chub *Gila cypha*, and black dots represent the river kilometre (rkm) measured from Lee's Ferry, Arizona

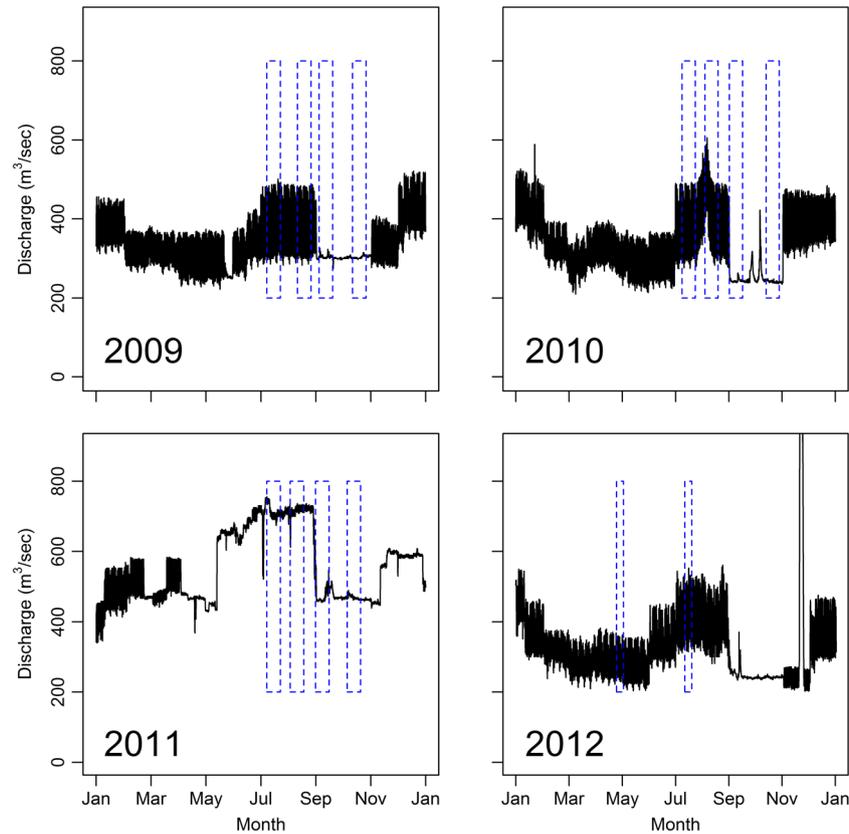


Figure 2. Daily discharge in the Colorado River at Lee's Ferry over the 4-year period of this study (2009–2012). Sampling intervals during 2009–2011 occurred in July, August, September and October, and sampling in 2012 occurred in late-April and July and are, as indicated by the blue rectangles. Data from USGS gage 0938000 available at waterdata.usgs.gov (Accessed February 2014). This figure is available in colour online at wileyonlinelibrary.com/journal/trr

Impact Statement on Glen Canyon Dam in Grand Canyon National Park identified a number of important uncertainties for the Colorado River related to water releases from the dam (United States Department of Interior, 1996), which led to the creation of the Glen Canyon Dam Adaptive Management Programme (GCDAMP; USBR, 2013).

Provisions of the GCDAMP intrinsically include experimental testing of operational alternatives to discover which discharge regimes will simultaneously satisfy the myriad social and legal constraints of operating Glen Canyon Dam. As an example, GCDAMP has implemented engineered floods across a range of magnitudes, durations and upramp/downramp rates to identify policies that will maximize retention of seasonally available sediment and construct sand bars that are important for camping, archaeological preservation and possibly fish habitat (Melis *et al.*, 2011). In practice, the range and scope of testable alternatives is limited by infrastructure and stakeholder interests. These experimental constraints are typified by the aforementioned engineered floods, which are limited to a fraction of the predam flood discharge because of the diameter of the discharge tubes. However, considerable uncertainty still remains even within

the available range of management options, especially when considering non-stationary resources that are difficult to measure like migratory birds, rare plants or fishes.

One goal of the GCDAMP is population recovery of federally endangered humpback chub *Gila cypha*, a large-bodied, morphologically distinct cyprinid endemic to the Colorado River basin whose largest population is in Grand Canyon. The reasons humpback chub populations in Grand Canyon are imperilled are unresolved but likely include negative interactions with non-native fish (Coggins *et al.*, 2011; Yard *et al.*, 2011); loss of essential habitats due to flow, temperature and sediment input modifications (Converse *et al.*, 1998; Clarkson and Childs, 2000; Stone and Gorman, 2006); and non-native parasites (Minckley, 1991; Choudhury *et al.*, 2004).

Most humpback chub currently occupy the Colorado River near the confluence with the Little Colorado River, the largest tributary within Grand Canyon (Figure 1). Adults participate in a spawning migration from the mainstem Colorado River to the Little Colorado River, after which the majority return to the mainstem Colorado River (Kaeding and Zimmerman, 1983; Valdez and Ryel, 1997;

Gorman and Stone, 1999). Unknown but potentially significant proportions of each year's cohort emigrate to the mainstem Colorado River as larvae or small juveniles, where their survival is thought to be low because of cold water temperatures and negative interactions with non-native species (Valdez and Ryel, 1997; Clarkson and Childs, 2000; Yard *et al.*, 2011). These mainstem-resident juveniles are the targeted benefactors of experimental discharges from Glen Canyon Dam. Alternatively, juvenile humpback chub may remain in the Little Colorado River for several years (Gorman and Stone, 1999; Clarkson and Childs, 2000; Limburg *et al.*, 2013), where warmer water temperatures and lower predation risk from non-native species (Kaeding and Zimmerman, 1983; Marsh and Douglas, 1997) improve vital rates like growth and survival, thus reducing time spent at smaller, more vulnerable size classes and ultimately increasing the adult spawning population (Gorman and Stone, 1999).

Field experiments implemented by GCDAMP intended to benefit juvenile humpback chub occupying the Colorado River include non-native predator removal (Coggins *et al.*, 2011; Yard *et al.*, 2011), fluctuating flow mitigation (Ralston, 2011) and habitat restoration (Melis *et al.*, 2011; USDO, 2008). A critical objective of these experiments is to increase recruitment to the adult population by enhancing vital rates of juvenile humpback chub. However, interpreting effects of these ecosystem experiments on juvenile humpback chub is challenging because of the difficulty of directly monitoring population dynamics of juveniles. Trends in juvenile humpback chub have traditionally been made through inferences based on catch-rate indices as well as from reconstructions of historical recruitment patterns from recaptures of tagged adult humpback chub as part of the long-term adult humpback chub assessment programme (age-structured mark-recapture or ASMR; Coggins *et al.*, 2006a, 2006b). Because of seasonal contrasts in growth rates between the Colorado and Little Colorado Rivers (Finch *et al.*, 2013), as well as the propensity of humpback chub to unpredictably occupy either or both locations (Limburg *et al.*, 2013; Yackulic *et al.*, 2014), a 100-mm humpback chub (size at first tagging) could be anywhere from 1 to 5 years old (Limburg *et al.*, 2013). This uncertainty reduces the annual variability of reconstructed recruitment trends and challenges the ASMR model's ability to determine which years (and corresponding dam operations/habitat conditions) caused observed fluctuations in juvenile population dynamics (Coggins and Walters, 2009). Directly measuring juvenile humpback chub abundance and survival would reduce uncertainty and shorten the time lag between experiment results and informing future policies.

We conducted a mark-recapture study of juvenile humpback chub in Grand Canyon to address sampling and modelling uncertainties, as well as to substantiate the prevailing

hypothesis that fluctuating flows in Grand Canyon are detrimental to juvenile humpback chub (Ralston, 2011). The GCDAMP designed an experiment to address these questions by implementing steady flows (i.e. constant water release from Glen Canyon Dam) during September and October 2008–2012 (Figure 2). Our monitoring could then assess trends in apparent survival and abundance of juvenile humpback chub, with the experimental goal being improving recruitment and population growth rate of adult humpback chub.

Although a steady flow policy to effect these changes may be intuitive by design, the benefits to native fish are both highly uncertain (non-native species can benefit from steadier flows; Korman *et al.*, 2009, 2012) and expensive to implement because of lost power revenue (Palmer *et al.*, 2004; Ralston, 2011). Additionally, detecting the potentially small effects of this policy is difficult because of several experimental design issues including conducting the experiment during late summer and fall (when river warming is less likely to occur), short duration of the experiment (approximately 2 months each year) and limited replication (3 years of evaluation). Nonetheless, experimental manipulations of entire river ecosystems are rare and represent opportunities for substantial learning (Finch *et al.*, 2013; Gerig *et al.*, 2014). In this paper, we develop a capture–recapture framework to directly estimate abundance and apparent survival of juvenile humpback chub and assess trends in juvenile humpback chub apparent survival and abundance in three of the five experimental steady flow years (2009–2011). We present field techniques and analytical approaches used for this work and then discuss how our results fit within the broader context of understanding juvenile humpback chub population dynamics in Grand Canyon. If juvenile humpback chub apparent survival rates or abundance improve as a direct result of experimental steady flows, then steady flows could be considered as part of a long-term management plan for Glen Canyon Dam operations. From a global perspective, understanding the fish-flow relationship is increasingly important in order to design dam operations that mitigate associated negative ecological changes. The results presented here highlight the value of empirically assessing fish responses to the elimination of fluctuating flows, typified by our experience with humpback chub in Grand Canyon.

METHODS

Current summertime operations at Glen Canyon dam attempt to match power demand according to the stipulations of a management policy known as 'modified low fluctuating flows', which nearly doubles discharges every day from around 255 to around 480 m³/s (USBR, 1996; Figure 2).

This policy is a milder version of the 'No Action' alternative in operation from the 1960s until the 1990s, where daily fluctuations ranged as much as 28–892 m³/s (USBR, 1996). For the experimental flows we evaluated, modified low fluctuating flows were replaced with steady discharges of 295 and 230 m³/s during September and October of 2009 and 2010, respectively (Figure 2). Flows for the entire summer 2011 period were steady (September and October discharges in 2011 were 453 m³/s) as a result of equalization flows triggered by high snowmelt in spring 2011, which provided important contrast to separate steady flows and seasonality (Figure 2; see discussion). Our study location was ~125 km below Glen Canyon Dam, so water arrived about 24 h after being released, with slight attenuation of temperature and discharge extremes according to local weather and channel roughness. Local peak discharge occurred during the day, with minimum discharge around midnight. The Colorado River channel in our study reach is heavily influenced by debris fans, rapids and large eddy pools. Shorelines are mostly steep talus, cliffs and vegetated cut banks, with very few sandbars or low-angle areas.

We based inferences on 14 sampling events (river trips) over 2009–2012 in a section of the Colorado River 102–104.5 river km below Lee's Ferry (126.1–128.6 km below Glen Canyon Dam) and about 2 km downstream of the confluence with the Little Colorado River. We sampled for 12 consecutive days in July, August, September and October of 2009–2011, and nine consecutive days in April and July 2012. Across trips, we sampled the fish community using two gear types: (i) unbaited mini hoopnets (50 cm diameter, 100 cm long, single 10-cm throat, made of 6-mm nylon mesh, fished over 24-h intervals and checked daily); and (ii) boat electrofishing at night during low flows (pulsed direct current at 15–20 amps, 200–300 volts, 7–10 s per metre of shoreline, repeated 24–72 h apart for three passes per trip). Initial sampling in July 2009 included 48 hoopnets in the upper 1.5 km of the sampling reach, which expanded to 60 hoopnets in August–October, all of which were fished 12 consecutive days for about 24 h each. In 2010 and 2011, we further expanded hoopnet efforts to include 12 passes of 80 hoopnets over the upper 2 km of the sampling reach. In April and July 2012, hoopnet sampling was further increased to 90 hoops over the entire 2.5 km, but with only seven or eight, 24-h passes. All available shoreline were electrofished during the 12 sampling trips in 2009–2012 following guidelines in Korman and Campana (2009) targeting small fish with two additional sampling passes in 2012 using standard Grand Canyon fish sampling electrofishing protocols.

Following capture, we measured, tagged and then released humpback chub to within 25 m of the captured location. We gave humpback chub from 40 to 99 mm total length (TL) batch marks that were identifiable to specific gears and

sampling trips using visible implant elastomer (VIE, Northwest Marine Technologies, Shaw Island, Washington, United States). Any time a humpback chub was recaptured on a subsequent trip or with a different gear while still <100 mm TL, we applied a new VIE batch mark. Recapturing within a trip with the same gear type did not receive an additional mark. Any humpback chub ≥100 mm TL (including VIE recaptures) received a uniquely coded 134.2 kHz passive integrated transponder (PIT) tag (12-mm long, Biomark). Although humpback chub less than 40 mm are present in the river, these individuals were not equally vulnerable to our gear and could not be included in our mark-recapture study without introducing substantial sampling bias. Additionally, the technology is not yet available for mark-recapture of such small fish without increasing risk of handling mortality, which is especially problematic for federally endangered species.

Because our field programme was specifically designed in an experimental framework to document any changes in apparent survival or abundance that might occur relative to the steady flow (vs regular or annual monitoring without an experimental objective), sampling trips were clustered around 1 September of each year, when the flow experiment began. Upon completion of the first 3 years of field work, the sampling calendar then transitioned into a regular monitoring programme with larger gaps between trips to increase annual resolution (hence the clustering of trips in the first 3 years vs 2012; Figure 2). We also had little precedent for our ability to directly monitor juvenile humpback chub via mark-recapture. With incremental successes and failures, we adapted our efforts (i.e. increasing hoopnet effort) to expand the pool of marked animals and increase statistical inference.

Using simulation to evaluate model accuracy

In capture–recapture experiments, it is possible to confound apparent survival rates and capture probability estimates due to the inability to distinguish between fish that died (low survival) and fish that lived but were not observed (high survival and low capture probability). We expected juvenile humpback chub capture probabilities to be low based on pilot samples and other capture–recapture experiments in large rivers (Coggins *et al.*, 2006a; Korman *et al.*, 2009; Laretta *et al.*, 2013). These low capture probabilities combined with short discrete sampling intervals (designed around the flow experiment) could lead to erroneous survival estimates. To assess this, we generated data sets (programme GENCAPH1; <http://www.mbr-pwrc.usgs.gov/software/gencaph1.shtml>) with known populations, survival rates, capture probabilities and sampling intervals similar to our expected values based on a pilot study and experimental design theory. We then assessed the accuracy and precision of survival estimates from a Cormack–Jolly–Seber (CJS) model using these input data (Appendix).

Apparent survival rate and abundance estimation using an open model

In most survival studies, unique marks allow the fates of individuals to be monitored through time. We were interested in survival patterns of humpback chub too small to be marked individually with PIT tags, necessitating the use of batch marks (Pine *et al.*, 2013). Batch marks present a peculiar problem in developing capture histories because individuals are not discernible. However, compilation of capture histories is possible because all recaptured individuals (other than recaptures using the same gear within a trip) received a new, separate mark and could then be subtracted from the number of individuals previously marked but not recaptured. This framework is different than batch marks that only distinguish marked versus unmarked fish, but it still does not contain information that allows for unique identification of each individual fish. By not having individual marks, we are unable to analyse these data using models with behavioural effects (Otis *et al.*, 1978) or robust design approaches (Pollock *et al.*, 1990). In our study, once fish recruit into sub-adult sizes (≥ 100 -mm TL), they receive unique PIT tags. These larger PIT tagged fish were then excluded from our analyses of juvenile humpback chub because they are presumed to be more robust to hydropower fluctuations and are not the current primary management target for optimizing Glen Canyon Dam operations.

We developed a set of a priori models to test hypotheses about effects of experimental steady flows on humpback chub apparent survival and capture probability over the 3-year study period. These are open, CJS (Pollock *et al.*, 1990) models and are based on current understanding of humpback chub biology and life history, coupled with discharge information. We chose to present results as daily apparent survival rates, which need to be exponentiated by 365 to allow them to be comparable with annual estimates such as from the ASMR model (Coggins *et al.*, 2006b).

In our suite of models, we parameterized both apparent survival and capture probability according to six different ecological assumptions (36 total models): (i) constant, implying that the parameter does not change based on flow type or any other factors; (ii) flow, where the parameter is influenced by the flow type (steady or fluctuating) that occurred during intervals between sampling trips; (iii) flow*year, which considers the flow treatment within a year as independent from other years, because the magnitudes of steady flows were different in 2009, 2010 and 2011; (iv) year, to determine if the interaction of flow*year performs better than considering year alone; (v) time, a global model allowing parameter estimates to differ independently on each occasion; and (vi) mod_flow. This last model is an extension of the flow model because not all survival intervals (at-large periods between trips; Figure 2) are composed of

a single-flow treatment (Figure 2, between blue boxes); thus, the mod_flow model estimates a third parameter for intervals that are both steady and fluctuating. Model fit was assessed using Akaike Information Criterion for finite sample size (AIC_c) and support criteria from Burnham and Anderson (2002).

We also used these marked fish to estimate juvenile humpback chub abundance in an open population framework using the Horvitz–Thompson estimator, which is based on the capture probabilities from the most supported CJS apparent survival model and the corresponding catch information (CJS models explained in detail earlier). This abundance calculation is simply catch divided by capture probability (Williams *et al.*, 2002), and variances for abundance estimates were estimated using the method described in McDonald *et al.* (2005). This method of estimating abundance differs from the sequential Bayes' closed estimate method described in the succeeding text because estimates of capture probability are derived from data spanning multiple trips. This difference in abundance estimation methods is important because the population used in open models will be larger than that considered in the sequential Bayes' closed capture approaches described in the succeeding text, where all fish are < 100 mm TL.

Abundance of juvenile humpback chub—closed model

We estimated abundance (\hat{N}) of juvenile humpback chub (40–99 mm TL) for each gear using sequential Bayesian closed population models described by Gazey and Staley (1986) based on a running tally of the marked population size that accumulates individuals with each pass. In the Gazey and Staley (1986) framework, the distribution of the population size is unknown and assumed to be represented by the non-informative discrete uniform distribution (i.e. prior distribution), where the first prior is uninformative. We assume that $\hat{N}_i \geq$ the number of animals marked in the time interval over which closure is assumed (each river trip). The number of animals marked each trip, captured each trip and recaptured are then combined with the prior distribution to create the posterior distribution (i.e. the probability of each possible N_i given the data) using Bayes' theorem (Gazey and Staley, 1986). In this framework, the posterior distribution becomes more concentrated (i.e. smaller distribution) about the true population size as the number of sequential samples increases because the cumulative number of animals captured at each time increases (example in Figure 3). We calculated the mode of the posterior distribution as the Bayesian Point Estimate of the sampling distribution to determine the population estimate (Gazey and Staley, 1986). The 2.5% and 97.5% values (quantiles, when normally distributed) are reported as approximate 95% credible intervals. Our basic assumptions for this

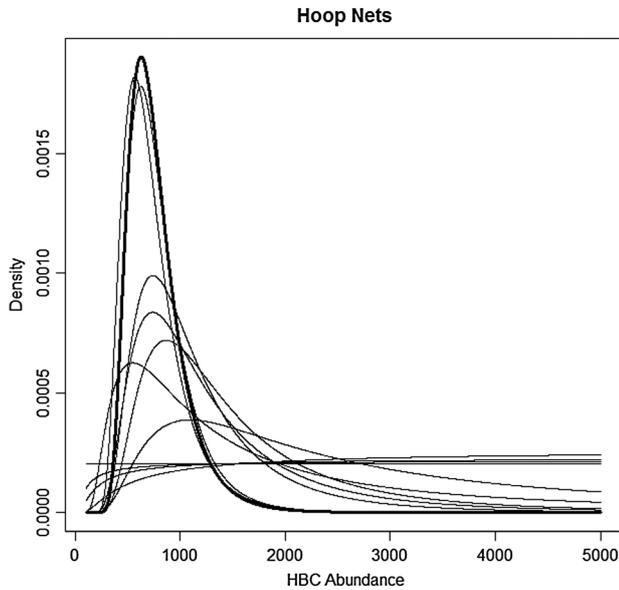


Figure 3. Likelihood estimates of juvenile humpback chub 40–99 mm TL abundance from hoopnetting data collected for July 2010. Thick black line represents the Bayesian point estimate of abundance after 12 nights of hoopnet sampling, while the thin horizontal line represents the (diffuse) likelihood estimate of abundance after 1 night of sampling. Other thin lines represent likelihood estimates after sequential nights of hoopnetting showing that a minimum of seven nights of hoopnetting were required before a reasonable (i.e. informed) estimate of abundance was reached. With increasing samples (nights of hoopnetting), the likelihood estimate becomes better defined and resulting maximum likelihood estimation is plotted as the thin black line

approach are the same as for other closed population models including (i) marks are not lost or overlooked within a trip; (ii) there is no immigration to or emigration from the study reach within a trip; (iii) mortality within a trip is assumed to be zero; and (iv) recapture probability of marked individuals is assumed to be equivalent to capture probability of unmarked individuals (Pine *et al.*, 2003).

RESULTS

Field results

Over the 3-year duration of this project, we captured and VIE marked 5575 juvenile humpback chub. Average catch per trip based on calendar year was 221, 331, 588 and 794 juvenile humpback chub for 2009, 2010, 2011 and 2012, respectively. Twenty-seven percent (1479) of juvenile humpback chub were recaptured at least once. Of individuals marked in 2009 and 2010, 11% were not recaptured for the first time until they had spent at least 1 year at large.

Simulation results to inform analyses of field data

Simulations demonstrated that apparent survival and capture probability can be estimated using certain models, even with a small population (~500 individuals) and low capture probabilities (5%). We found that the most precise estimates of apparent survival came from models where survival was a shared parameter across annual, seasonal or flow treatments. Models that assumed independent time effects for apparent survival did not converge (Appendix 1).

Assessing the effects of the flow experiment on juvenile humpback chub apparent survival

The most-supported model in our AIC framework parameterized apparent survival by year, ignoring the effect of flow treatment. Ignoring this model (which did not explicitly test flow treatments—the purpose of our experiment), highlighted an important result that the steady flow periods resulted in a significant negative effect on apparent survival of juvenile humpback chub (Table 2). The 95% confidence intervals for apparent survival according to both the Phi (flow) and the Phi(mod_flow) models did not overlap with the estimate for apparent survival during fluctuating flows. Models parameterizing apparent survival by time (Phi(t)) and by flow treatment nested within each year (Phi(flow*year)) did not converge and were excluded from consideration. However, the Phi(year) model that we constructed to substantiate the potential results of the Phi(flow*year) was the most supported model overall (Table I). This suggests that inter-annual variability (especially considering the high 2011 discharges) likely swamps the effect of flow treatment on juvenile humpback chub apparent survival (Table II), but overall our results suggest that juvenile humpback chub apparent survival declined over our study period. Regardless of how apparent survival was parameterized, capture probability varied independently by trip in all but the least supported models.

Table I. The four best apparent survival models for juvenile humpback chub in Grand Canyon from 2009–2012 ranked by lowest AIC_c

| Model name | AIC _c | ΔAIC _c | No. Par. |
|--------------------|------------------|-------------------|----------|
| Phi(year) p(t) | 10 175.4 | 0 | 16 |
| Phi(mod_flow) p(t) | 10 188.7 | 13.3 | 16 |
| Phi(flow) p(t) | 10 190.7 | 15.3 | 15 |
| Phi(.) p(t) | 10 201.2 | 25.7 | 14 |
| Other models | >10 225 | >50 | — |

AIC_c, Akaike Information Criterion for finite sample size.

Model parameter estimation is symbolized as follows: constant (.), time-specific (t), annual (year), flow-specific (flow) and modified flow-specific (mod_flow). Models that did not converge or had ΔAIC_c values >50 are not displayed.

Table II. Daily apparent survival estimates for juvenile humpback chub in Grand Canyon from 2009–2012

| Model Parameterization | Phi(year) | Phi(mod_flow) | Phi(flow) | Phi(.) |
|------------------------|----------------------|----------------------|----------------------|----------------------|
| 2009 | 99.90% (99.86–99.93) | — | — | 99.83% (99.81–99.85) |
| 2010 | 99.79% (99.74–99.83) | — | — | 99.83% (99.81–99.85) |
| 2011 | 99.67% (99.57–99.75) | — | — | 99.83% (99.81–99.85) |
| Fluctuating | — | 99.92% (99.86–99.95) | 99.90% (99.85–99.93) | 99.83% (99.81–99.85) |
| Both | — | 99.84% (99.76–99.90) | — | 99.83% (99.81–99.85) |
| Steady | — | 99.52% (99.27–99.72) | 99.44% (99.23–99.64) | 99.83% (99.81–99.85) |

Results are from the top four models ranked by ΔAIC_c (Table I). All four models parameterized capture probability (p) by time. Values in parentheses under each estimate are 95% confidence intervals.

Open model abundance estimate

Open population model capture probability estimates ranged from 6% to 19% per trip with 95% confidence intervals of 4–22%. Abundance estimates ranged from 615 to 2,802 humpback chub per km of study reach with 95% confidence

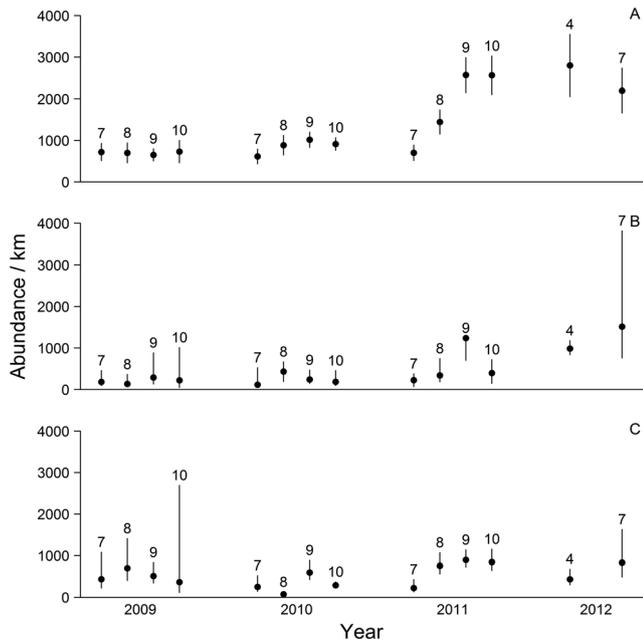


Figure 4. Abundance of visible implant elastomer tagged juvenile humpback chub per km with 95% confidence by sample month (month indicated by number above upper 95% confidence interval) 2009–2012 in the nearshore ecology sampling reach in the Colorado River using three different models. Tagged individuals were included from when they were first VIE-tagged (40–99 mm TL) until they were first PIT-tagged (100+ mm TL). Estimates in Panel A are from a Cormack-Jolly-Seber model based on data from both hoopnet and electrofishing gear types. Panel B abundance and 95% credible intervals are estimated using a simple sequential Bayesian closed capture model and electrofishing data only. Upper credible interval estimates for July 2012 (Panel B) extend off graph to a value of 9542. Panel C abundance and 95% credible intervals are estimated from hoopnet data only, using the same sequential Bayesian closed capture model as Panel B

intervals from 437 to 3551 individuals (Figure 4(A)) and varied independent of flow treatment. The capture probabilities used in this open-framework abundance estimation are for all cumulative passes within a trip (both electrofishing and hoopnets combined). In other words, they reflect the probability of capturing an individual at least once on a trip (no distinction between multiple recaptures with the same gear) as opposed to capture probabilities from the closed abundance estimates, which apply to a single pass of a single gear. These estimates also include individuals over 99 mm TL until they are first PIT tagged. This is a larger size range (and proportion of the juvenile humpback chub population) than considered in the closed model, which contributes to the difference in abundance trends between closed and open models because the number of animals captured in each event differs between the two model structures (Figures 4(B) and 4(C)).

Closed model abundance of humpback chub 40–99 mm TL (sequential Bayes' framework)

Using closed population models for juvenile humpback chub 40–99 mm TL, the Bayesian point estimate of our capture probability ranged from 0.05% to 14% per pass with either gear. Corresponding closed population estimates per km of study reach using electrofishing recaptures ranged from 116 to 1515 with 95% credible intervals of 45–3817 (Figure 4(B)). Closed-population abundance estimates based on hoopnets per km ranged from 94 to 1124 humpback chub with 95% credible intervals of 26–2695 (Figure 4(C)). In general, closed estimates of abundance by gear type were lowest during 2009–2010 and increased beginning in September 2011–July 2012. There was also no apparent relationship between closed model abundance estimates and flow experiments (Figures 4(B) and 4(C)).

DISCUSSION

Juvenile humpback chub abundance demonstrated no appreciable relationship with flow treatment, while apparent

survival declined during steady flows. However, the effect of flow type (steady vs fluctuating) was dwarfed by annual variation in apparent survival, as the $\Phi(\text{year}) p(t)$ model was better supported by over 13 ΔAIC_c points than either model considering flow (Table I). Importantly, the structure of the flow model is similar to the annual model (it is weighted towards 2011) because three of the five steady flows intervals that we considered were from the last year (July 2011–July 2012); thus, it is not completely clear if apparent survival of juvenile humpback chub declines with time, by flow type or possibly by flow magnitude (Figure 2). What is clear is that steady flow experiments, including one lasting over 9 months, did not improve apparent survival of juvenile humpback chub. Whether the declining trends in apparent survival according to the $\Phi(\text{year}) p(t)$ model represent long-term shifts or natural temporal fluctuations in demographic rates is not yet known.

This result differs from the expectation that steady flows would improve demographic rates by stabilizing available habitats and potentially reducing energetic costs and predation risks associated with juvenile fish movement. Several limitations of the experimental design may have contributed to this counterintuitive outcome. Because the experimental manipulations were constrained within the confines of current dam operation, large contrasts and replication were difficult. In addition, the regulatory need to release excess water downstream to Lake Mead in summer 2011 (Figure 2) because of wet conditions in the upper basin usurped our third steady flow treatment. Serendipitously, because these unexpected water releases were steady, 2011 allowed us to estimate apparent survival during *summer* steady flows in addition to fall and escape the perfect confounding of flow treatment with seasonality. Yet apparent survival still declined in 2011, which had the warmest (Finch *et al.*, 2013) and steadiest (Figure 2) conditions we observed. It is possible that the higher discharges or longer experimental duration from 2011 could alter our capture efficiency, but humpback chub catches in 2011 were higher than the previous 2 years combined. This leads us to conclude that apparent survival, not capture probability, was primarily affected by equalization flows, which was corroborated by our simulation models.

One of the postulated benefits of stabilizing nearshore habitats under steady flow operations was increase of primary and secondary production, primarily from backwater habitats (Grand *et al.*, 2006; USDOI, 2008), but also from cobble or larger substrates (Blinn *et al.*, 1995). This increased production is thought to benefit fish because of the potential for food limitation, evidenced by high consumption rates of fish within this section of river (Cross *et al.*, 2013). However, the fall timing of the steady flow experiments usually corresponded with monsoonal flooding

in the Little Colorado River (LCR), which increased turbidity and potentially decreased autochthonous production within the mainstem. Finch *et al.* (2013) attributed at least part of the lack of response in humpback chub growth to the steady flow experiments occurring during fall, when primary productivity is generally declining throughout the system. The authors also documented a similar counterintuitive response where growth rates of juvenile humpback chub were actually higher during fluctuating flows compared with steady flow periods (Finch *et al.*, 2013). While the reasons for this difference in growth between the two flow regimes are unknown, potential factors include increased availability of invertebrate drift as a prey resource during fluctuating flows compared with steady flows.

Previous investigations have demonstrated that in some river systems, juvenile or larval fish that often occupy shallow water habitats are most affected by elimination of fluctuating flows (Freeman *et al.*, 2001; Gaudin, 2001). Fluctuating flows affect these small life stages because of factors such as stranding (Halleraker *et al.*, 2003), downstream displacement (Young *et al.*, 2011) and dewatering effects on nest survival (McMichael *et al.*, 2005; Grabowski and Isely, 2007). However, the pre-dam Colorado River experienced the lowest baseflows of the year in fall, at a time when monsoon floods from the Little Colorado River and other tributaries could more than double the discharge almost instantaneously. It is likely that the same behaviour that allowed young humpback chub to historically persist in this dynamic environment likewise allows them to avoid stranding and dewatering effects due to dam operations, leading to the apparent lack of improvement in apparent survival (this paper) and growth (Finch *et al.*, 2013) from the flow experiment as designed. Additionally, the lack of a flow-related improvement in apparent survival and abundance could be associated with the persistence of suitable shoreline habitat under both of the flow regimes observed. Korman *et al.* (2004) examined the amount of suitable shoreline habitat under different dam operations and concluded that although fluctuations decreased the amount of persistent shoreline habitat, similar amounts of each habitat type were still available over a large range of flow conditions. The relative rarity of low-angle shorelines in our study reach likely contributed to this homogeneous habitat availability across the range of flows that we observed. This flow insensitivity was corroborated by Alvarez and Schmeekle (2012), who demonstrated that our study reach (just below the Little Colorado River confluence) was among the most insensitive to discharge fluctuations of the entire Grand Canyon corridor.

Backwaters are one habitat type present in Grand Canyon that are sensitive to temperature and discharge fluctuations because they are shallow and generally associated with ephemeral sand bars (vs bedrock or cobble bars); the

suspected relationship between backwaters and juvenile humpback chub prioritizes backwater construction and retention as part of GCDAMP (USDOI, 2008; Melis *et al.*, 2011). However, Dodrill *et al.* (2014) found that while backwaters often contain higher densities of juvenile humpback chub, the total abundance of humpback chub using backwaters in our study area is low because backwaters are locally short-lived and rare. A change that only occurs within a small proportion of the total population would be difficult to reasonably detect. Additionally, the low steady flow experiments occurred when air temperatures, solar insolation and warming rates of nearshore environments are lower (September and October of each year; Yard *et al.*, 2005; Korman *et al.*, 2006), which was corroborated when Ross and Grams (2013) did not find warmer water nearshore compared with offshore during fall steady flows. Even if air temperatures were conducive to nearshore warming (June and July), the turbulent, well-mixed hydraulics of our study reach could have prevented the localized warming of microhabitats that is observed in calmer river reaches like Lee's Ferry (Korman *et al.*, 2006).

Ecological factors that could lead to changes in survival over this time include potential changes in prey resources, density dependent effects or predation. In March 2008, a high flow experiment was conducted from Glen Canyon Dam that triggered several important ecosystem responses. Survival rates of juvenile rainbow trout in the Lees Ferry reach below Glen Canyon Dam (approximately 100-km upstream of our study site) increased substantially following the flood in 2008, and their survival rates remained higher than normal even a year later in 2009 before declining to the pre-flood levels in 2010 (Korman *et al.*, 2011; Melis *et al.*, 2011). This improvement in rainbow trout survival led to a subsequent increase in abundance of older rainbow trout in 2009–2011 and may have resulted in higher levels of predation or competition with native fish including humpback chub. Second, shifts in aquatic invertebrates were also observed in response to the 2008 flood event, with large declines in New Zealand mudsnail *Potamopyrgus antipodarum* and amphipod *Gammarus lacustris* production and large increases in drift invertebrate families Chironomidae and Simuliidae. Cross *et al.* (2013) also found high interaction strengths between fish and prey because of low secondary production of prey items combined with very high consumption of available items by fish. The vast majority of humpback chub spawning occurs in the Little Colorado River about 100-km downstream of the Lees Ferry reach, so changes in spawning substrate at Lees Ferry are unlikely to benefit humpback chub spawning. However, it is possible that juvenile humpback chub in the mainstem Colorado River did benefit from increases in the invertebrate community in 2008 and 2009 before these benthic and drift species declined in 2010.

Abundance was not related to apparent survival, because the highest abundance of juvenile humpback chub that we observed corresponded with the lowest apparent survival, from July 2011 to July 2012. This may simply be because of higher juvenile humpback chub production in the Little Colorado River that year (Van Haverbeke *et al.*, 2013), accompanied by lower survival or higher emigration of these juveniles in the mainstem Colorado River. Low apparent survival in 2011 may also come from density dependent competition that existed in the Colorado River, as prey consumption rates have previously been documented to equal or exceed invertebrate production in this reach (Cross *et al.*, 2013), while at the same time invertebrate drift was declining from the levels observed following the 2008 experimental flood (Cross *et al.*, 2011).

It is also possible that individual juvenile humpback chub survived but eluded capture, causing a downward bias in parameter estimates of apparent survival. Because apparent survival includes emigration (apparent survival = 1 - true survival - emigration), humpback chub in our study reach may have emigrated downstream or upstream where we were not permitted to sample. However, our observed movement patterns for juvenile humpback chub between our study reaches within a year suggest restricted movement patterns and small home ranges (Pine *et al.*, 2013; Gerig *et al.*, 2014).

Another potential mechanism for the low apparent survival in 2011 is direct or indirect effects of predation by rainbow trout *Oncorhynchus mykiss*, brown trout *Salmo trutta* or even older humpback chub. Although humpback chub are not highly piscivorous (Kaeding and Zimmerman, 1983), they do consume fish, and the increasing abundance of adults (Van Haverbeke *et al.*, 2013) may have depressed juvenile survival through predation or competition; if true, we see no clear management necessity or solution. A more likely scenario was described by Yard *et al.* (2011), who documented significant piscivory near the confluence of the Colorado and Little Colorado Rivers from both brown and rainbow trouts. This mortality does not include any negative effects on humpback chub from the risk of predation such as changes in habitat use (He and Kitchell, 1990; He *et al.*, 1993). Following the experimental removal of non-native fish in this study reach (Coggins *et al.*, 2011), juvenile native fish abundance increased; however, the mechanisms are still unclear (Coggins *et al.*, 2011). In our study, catch rates of rainbow trout increased in each year of our field work, increasing overall by a factor of four. Electrofishing capture probabilities of rainbow trout in this reach are relatively consistent across turbidity levels (J. Korman, unpublished data) so it is likely that our catch rate trends are reflective of actual trout abundance in our study reach. The interaction between trout and humpback chub abundance and survival

in the mainstem Colorado River and the timing of humpback chub migration to the mainstem Colorado River (Yackulic *et al.*, 2014) are important areas for continued research and experimental management.

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SUPPORTING INFORMATION

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