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DO HYDROPEAKING FLOWS ALTER JUVENILE FISH GROWTH RATES? A TEST WITH JUVENILE HUMPBACK CHUB IN THE COLORADO RIVER

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ABSTRACT

Riverine ecosystems have been altered in many large catchments by dam development to provide water, power, flood control and navigational benefits to humans. Conservation actions in these river ecosystems are commonly focused on minimum releases of water to downstream ecosystems. Increasingly minimum release approaches are being replaced with 'experimental' flows that mimic natural conditions in order to benefit riverine ecosystems. While these new policies are intuitive in their design, there is limited data of how riverine ecosystems actually respond to more natural flows. A test of more natural steady-flow water release was compared with typical fluctuating hydropower flows in the adaptive management programme at Glen Canyon Dam, Arizona, during 2008–2011 to assess growth improvements of endangered juvenile humpback chub *Gila cypha*. Our results are counterintuitive and show that more natural steady flows reduced growth rates of juvenile humpback chub compared with fluctuating flows when both treatments occurred within the same year. Daily growth rates during steady flows of 2009 and 2010 were 0.05 and 0.07 mm day^{-1} slower, respectively, than fluctuating flows those same years, despite similar water temperatures. Juvenile humpback chub also grew more slowly during steady flows that occurred in the same season. During the summer, juvenile humpback chub grew 0.12 and 0.16 mm day^{-1} in fluctuating flow regimes in 2009 and 2010, respectively, and only 0.07 mm day^{-1} in the experimental steady flow regime in 2011, despite higher water temperatures. Our results suggest that optimal conservation management policies for endangered species in regulated rivers may not always be achieved with more natural flows.

KEY WORDS: river regulation; flow experiment; hydropower; fish; endangered species; adaptive management

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INTRODUCTION

Variations in riverine flows related to power production and water delivery represent a specific form of habitat modification that alters the physical conditions within rivers. These changes involve numerous factors including depth, velocity, sediment storage and temperature; they create altered habitat conditions at both local (Fette *et al*., 2007) and larger scales (Murchie *et al*., 2008). Shallow water fish assemblages, in both nearshore and offshore habitats, are most affected by flow regulation in terms of species richness, diversity and density (Travnichek and Maceina, 1994; Travnichek *et al*., 1995; Freeman *et al*., 2001). Individual species responses to flow modifications can vary widely (Steele and Smokorowski, 2000; Murchie *et al*., 2008; Young *et al*., 2011). Because of the observed wide variation in responses, an experimental approach is required to determine how particular ecosystems, species or groups of species may respond to flow modifications (Murchie *et al*., 2008). However, any type of experimentation related to water releases in regulated rivers can be difficult to implement because of power and water delivery contracts associated with many peaking hydropower dam operations.

The humpback chub *Gila cypha* is an endemic Colorado River cyprinid listed as endangered under the US Endangered Species Act. The largest extant population of humpback chub is found in Grand Canyon, Arizona, in the mainstem Colorado River near the confluence of the Little Colorado River (Figure 1). Adult humpback chub migrate from the Colorado River into the Little Colorado River to spawn in the spring, where both prey resources (Stevens *et al*., 1997; Oberlin *et al*., 1999) and non-native predator densities are lower than the mainstem (Marsh and Douglas, 1997; Yard *et al*., 2011). Adult humpback chub population ecology and demography have been studied in this reach since the late 1980s, with the majority of data coming from intensive tagging during the spring spawning migration to the Little Colorado River and an additional fall tagging period (Kaeding and Zimmerman, 1983, Valdez and Ryel, 1997, Vanhaverbeke *et al*., 2013). Abundance estimates derived from these data show population declines in humpback chub throughout the 1990s and early 2000s,

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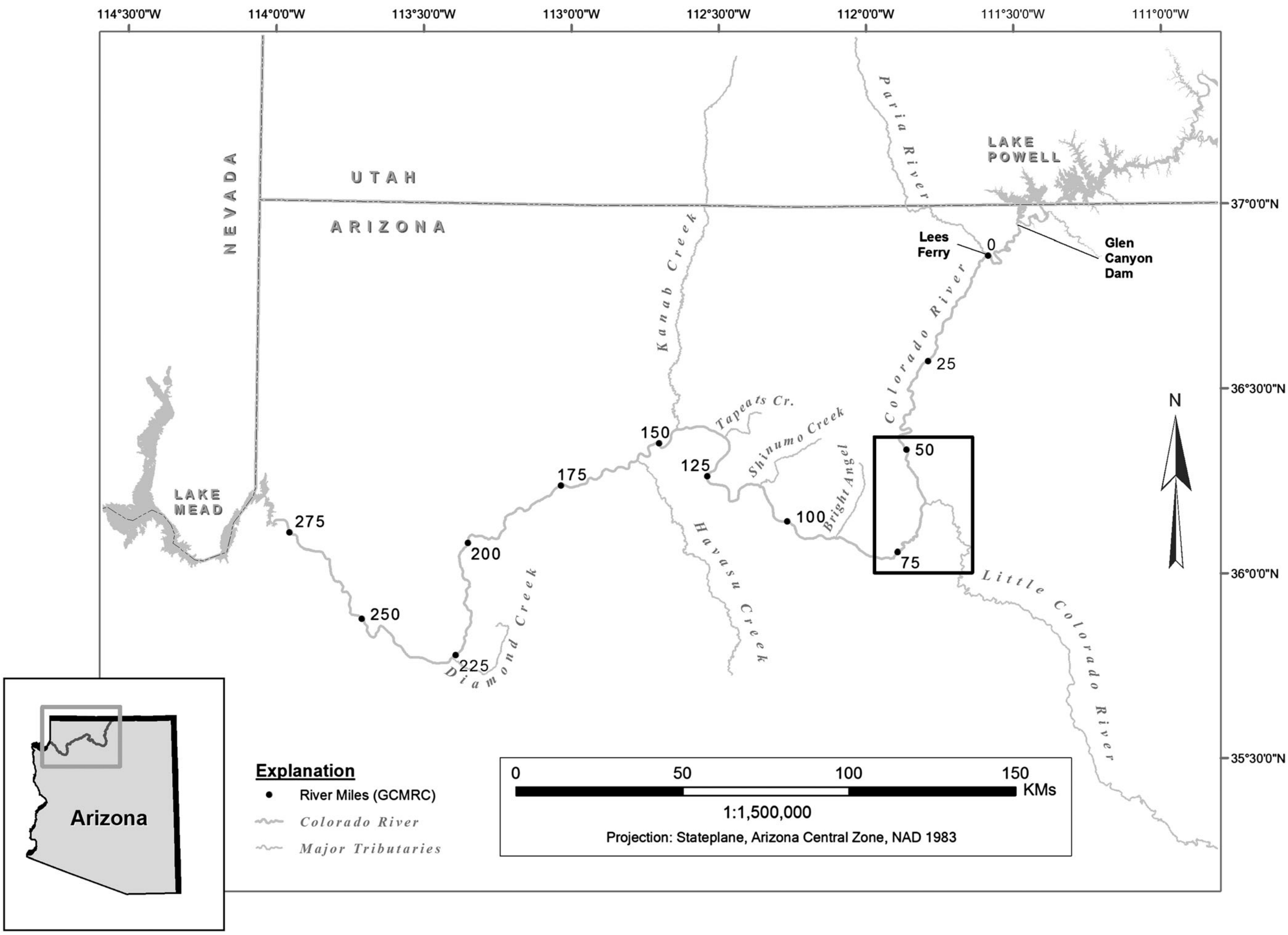

Figure 1. Map of the Grand Canyon reach of the Colorado River in northern Arizona, USA, where this study occurred. The black box at the confluence of Colorado and Little Colorado Rivers denotes the area containing the Little Colorado River aggregation of humpback chub

leading to concern over the status of the population of this endangered species in the Grand Canyon (Valdez and Ryel, 1997, Coggins *et al*., 2006). Recent data suggest that the population is increasing (Vanhaverbeke *et al*., 2013). This reach of the mainstem Colorado River is highly regulated by the operation of Glen Canyon Dam. Previous field-based and modelling efforts suggested that physical conditions in the Colorado River, such as fluctuating hydropower flows and cold summer water temperatures, as well as negative interactions with non-native fish such as rainbow trout, could reduce vital rates of juvenile humpback chub (Walters *et al*., 2000; Coggins *et al*., 2011; Yard *et al*., 2011).

A persistent uncertainty in assessing how fish populations respond to changes in river flow management in the Colorado River and elsewhere is whether engineered flows from dam operations affect growth of juvenile fish. Extant flow operations from Glen Canyon Dam are partially designed to follow diel fluctuations in power demand across southwestern USA with electricity production increasing diurnally and decreasing at night, causing an artificial 'tide' along the river corridor (known as 'modified low fluctuating flow'). The ecological impacts of these flow operations are unknown for most ecosystem components in the Colorado River (Korman *et al*., 2004). If the ecological impacts were known, specific flow operations from Glen Canyon Dam, for example, might be used to reduce the time chub spent at vulnerable juvenile sizes with higher mortality and ultimately lead to improvements in survival, recruitment and population status (Coggins and Pine, 2010).

Here, we present results of a large-scale flow experiment where hydropower peaking flows were eliminated for a 60-day period in each of 3 years (2009–2011) in the Colorado River below Glen Canyon Dam, Arizona. We assess changes in juvenile humpback chub growth rates during fluctuating and steady environmental flow periods and compare growth between these two treatments (Figure 2). In addition, we assessed growth of humpback chub during the same period in an adjacent unregulated tributary, the Little

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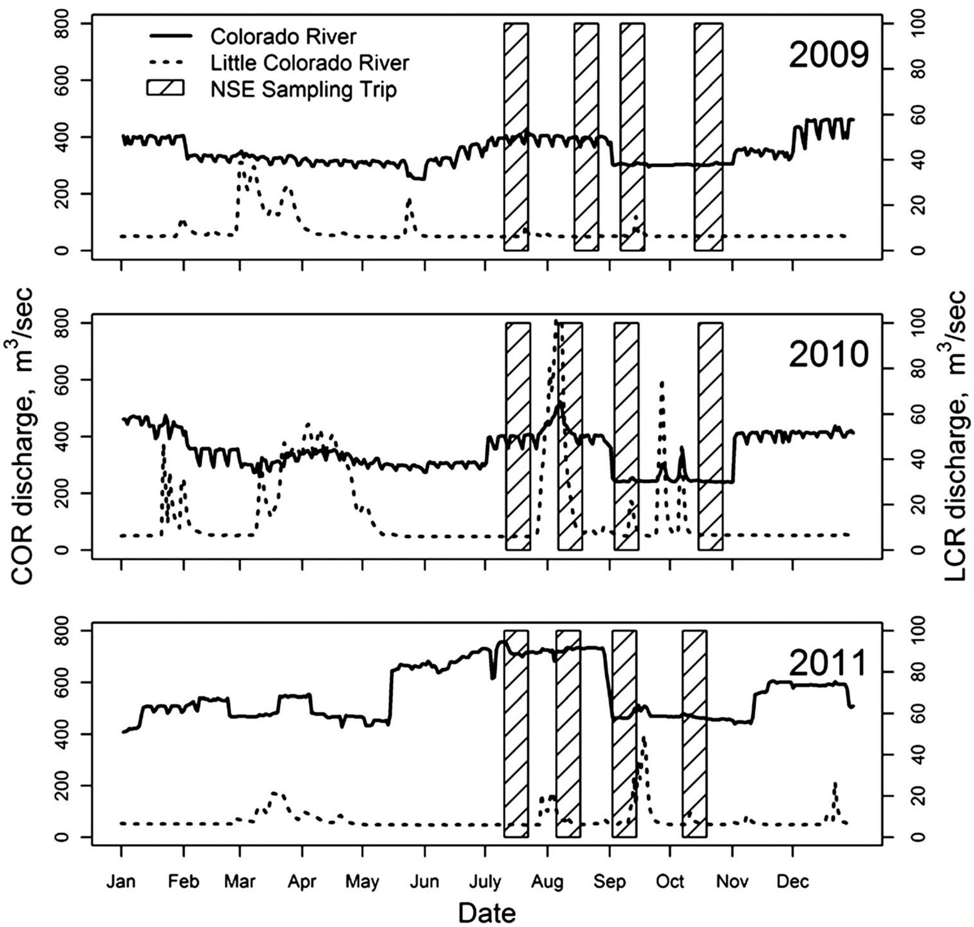

Figure 2. Daily discharge in the Colorado River at Lee's Ferry and in the Little Colorado River near the confluence with the Colorado River in 2009–2011. Sampling intervals are represented by the vertical bars. Data from US Geological Survey discharge gauges. Available: waterdata.usgs.gov (February 2012)

Colorado River, to separate natural seasonal changes in growth from potential flow effects. By comparing growth both within the mainstem Colorado River and between the regulated mainstem and an unregulated tributary, we improve the current understanding of juvenile humpback chub recruitment in the Colorado River. This information increases our understanding of how dam operations impact fish growth. This study is one of the few empirical assessments of fish growth response to fluctuating flows associated with hydropower operations in a large regulated river.

METHODS

Study site

The Grand Canyon reach of the Colorado River is the roughly 400-km river section bounded downstream by Lake Mead (Hoover Dam) and upstream by Lake Powell (Glen Canyon Dam), the first and second largest reservoirs in the USA, respectively (Andrews, 1991, Figure 1). Average discharge of the Colorado River through Grand Canyon for the past decade (2000–2010) was 351 $m^3 s^{-1}$ (Phantom Ranch gauge, 171 km below Glen Canyon Dam).

Within the Grand Canyon, the Colorado River is stenothermic and cool because of the storage effect of Lake Powell and hypolimnetic water releases from Glen Canyon Dam penstocks. Mean annual Glen Canyon Dam water release temperatures in recent decades have been fairly steady, fluctuating only about 2 °C (between 8 and 10 °C from 1994 to 2002). However, changing reservoir levels in recent years (2004–2012) due to drought and water policy caused water temperatures to fluctuate annually by as much as 7 °C (between 8 and 15 °C in 2011, Figure 3). While water temperatures in 2011 are considered very high in a post-dam Grand Canyon ecosystem, this temperature range represents only about 25% of the pre-dam annual temperature fluctuation (Figure 3).

The Little Colorado River is the largest tributary of the Colorado River within Grand Canyon National Park with a mean annual discharge of 11.54 $m^3 s^{-1}$ since 2004. We

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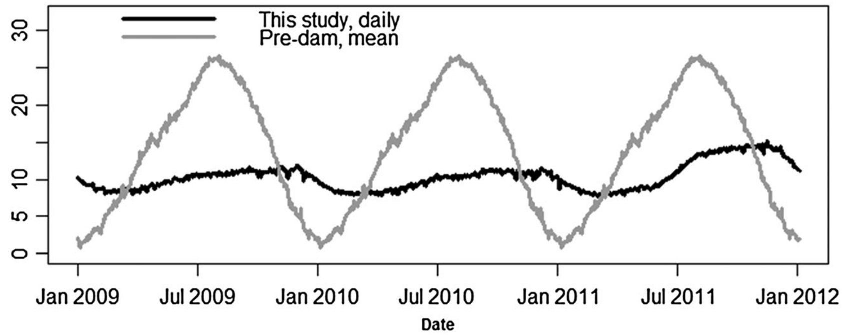

Figure 3. Mean daily water temperature (°C) of the mainstem Colorado River (dark black line) from January 2009 to December 2012 recorded at the US Geological Survey Lee's Ferry gauge (0938000). The pre-dam annual daily water temperature (°C) from 1948 to 1963 is also provided for the same period for comparison but was collected at various sources (data available USGS GCMRC www.gcmrc.gov)

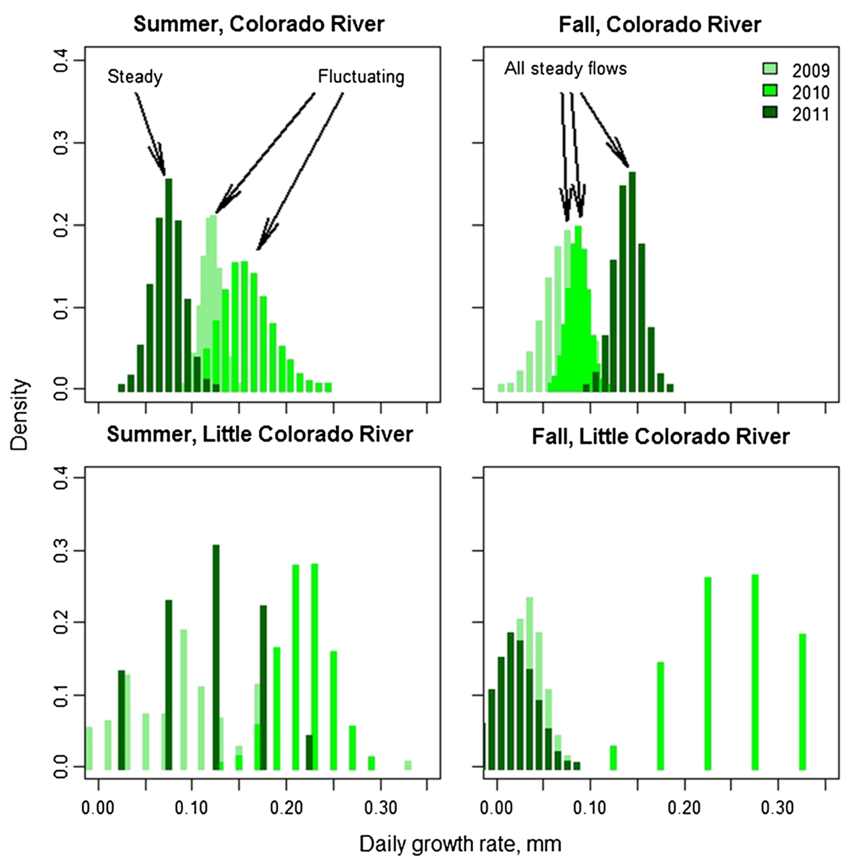

Figure 4. Density (*y*-axis) of the mean daily growth rates (*x*-axis) for juvenile humpback chub (100–200 mm total length) in summer and fall of 2009–2011, determined with 10 000-iteration bootstrap resamples with replacement. Colorado River samples represented both fluctuating and steady flows, while Little Colorado River samples (bottom row) represented unmanaged flows. This figure is available in colour online at wileyonlinelibrary.com/journal/rra

selected the Little Colorado River as a control system for humpback chub growth studies because it is the only unregulated river in the Grand Canyon reach of the Colorado River with an extant population of humpback chub. The lower 14 km of the Little Colorado River and the associated inflow reach of the Colorado River contain ~90% of humpback chub in the lower basin, known as the 'Little Colorado River population' (Figure 1). Comparing chub growth between the Colorado and Little Colorado rivers improves our ability to determine whether changes

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in growth occur naturally because of seasonal fluctuations in hydrology and temperature or whether changes may be occurring in the Colorado River because of flow effects.

Sampling techniques and seasons

We assessed juvenile humpback chub growth rates by quantifying changes in length over time based on recaptures of tagged individual humpback chub as part of a mark–recapture programme in the mainstem Colorado River and Little Colorado River. Fish were collected during July–October 2009–2011. Experimental steady flow regimes began on 1 September (Figure 2) in each year. Samples from July and August during 2009 and 2010 represent fish growth during typical fluctuating hydropower flows. Samples from September and October from all years represent growth during steady flow experiments (Figure 4). Large upper basin inflows and regulatory requirements related to water levels in lakes Powell and Mead resulted in an unexpected additional treatment of steady flow conditions during July–August 20 11 (Figure 2).

Mark–recapture sampling

We collected juvenile humpback chub for mark–recapture in the mainstem Colorado River from river kilometre (rkm) 102 to 106 (Figure 1; distances are measured from Lee's Ferry at rkm 0, which is ~25 km below Glen Canyon Dam) and in the Little Colorado River from the confluence with the mainstem Colorado River upstream roughly 14 km. We generally sampled 10–12 days each month for 4 months each year in both rivers (12 trips total, Figure 2). Fish collections in the mainstem Colorado River were made using two gear types: un-baited mini hoop-nets (50 cm diameter, 100 cm long, single 10 cm throat, made of 6 mm nylon mesh), fished for 12 consecutive days over 24 h intervals ($n = 47$–80 per trip) spaced at approximately equal intervals along the shoreline, and slow-speed boat electrofishing (pulsed direct current, 15–20 amps, 200–300 volts, boat speed 7–10 s m^{-1} of shoreline, repeated 24–72 h apart for three to five total passes per trip). We sampled the Little Colorado River with the same un-baited mini hoop-nets, but because of permitting and logistical constraints, we fished these nets in areas likely to have high juvenile humpback chub abundances in order to maximize marks and recaptures of fish for use in growth analyses. Electrofishing was not feasible in the Little Colorado River because of naturally high conductivity.

Following standard Grand Canyon cooperative fisheries research procedures (Ward, 2009, Persons *et al*., 2012), we measured, tagged and returned humpback chub to the same location where they were captured. All humpback chub >100 mm total length (TL) received a 134.2 kHz passive integrated transponder (PIT) tag (9 mm long, BIOMARK) with a number identifiable to individual fish. While a range of humpback chub sizes were collected during this study, we report only humpback chub large enough to be individually PIT tagged (≥100 mm TL) but less than 200 mm TL at the first capture event ('juveniles'). Tagging experiments with congeneric roundtail chub *Gila robusta* suggest minimal effects on growth from tagging with visible implant elastomer or PIT tags (C. Finch unpublished data). To eliminate the influence of inter-annual, seasonal or ontogenetic shifts in growth rates, marked fish were recaptured on the subsequent trip such that any measured growth occurred during the extant conditions in the preceding ~3–4 weeks. One exception occurred within the Little Colorado River in 2010 where we included recaptures of juvenile humpback chub from both August and September as part of the summer growth group (initially measured in July) because of heavy flooding and low recaptures in August alone. This is not problematic because no marked flow change occurred in the Little Colorado River in September, so these individuals experienced similar growth conditions as fish captured in July and recaptured only in August.

We calculated the mean daily growth for the groups of recaptured humpback chub for each of the 12 combinations of river, flow treatment (month) and year humpback chub were collected (Table 1) during their time at liberty. Because assumptions of standard parametric means tests were not met, we resampled these growth estimates 10 000 times using a bootstrap procedure with replacement (R Development Core Team) to determine the distribution of the mean growth rate for that flow treatment and year. We then visually assessed these distributions to assess differences in means and overlap of distributions. We chose not to use a permutation test to formalize this comparison because the permutation test would be dependent on the number of bootstrap samples taken. Key assumptions of this approach to characterize growth distribution are the following: (1) fish remain within the same river system for the duration of time between capture and recapture and (2) captured individuals represent a random sample of the overall population.

RESULTS

Growth rate estimates

We found that juvenile humpback chub mean daily growth rates in the Colorado River were lower during steady flows than fluctuating flows when they occurred in the same season. In July and August, fish grew 0.07 mm day^{-1} during steady flows in 2011 versus 0.12 and 0.16 mm day^{-1} during fluctuating flows in 2009 and 2010, respectively (Figure 4). Mean daily growth rates were also lower when steady flows followed fluctuating flows within the same year, 0.07 and 0.09 mm day^{-1} during steady flows versus 0.12 and 0.16 mm day^{-1} during fluctuating flows in 2009 and 2010,

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Table I. Summary statistics for growth information based on recaptures of tagged juvenile humpback chub *Gila cypha* in either the Little Colorado River (top panel) or mainstem Colorado River (lower panel), Arizona

	Little Colorado River									
	Daily growth	Growth SD	Total length	TL SD	*n*	Discharge	Q SD	Temperature	Temp SD	Flow type
Summer 2009	0.10	0.15	149.50	19.02	4	6.57	1.01	23.08	0.85	Natural
Summer 2010	0.22	0.12	157.20	24.63	20	8.06	4.28	24.05	0.68	Natural
Summer 2011	0.10	0.20	138.63	17.54	8	9.23	4.42	23.47	0.64	Natural
Fall 2009	0.03	0.13	161.31	22.70	55	6.41	0.62	19.34	1.36	Natural
Fall 2010	0.28	0.52	162.21	23.95	53	7.93	3.27	19.96	1.40	Natural
Fall 2011	0.02	0.10	150.70	12.46	20	8.02	3.52	19.59	1.41	Natural
	Colorado River									
	Daily growth	Growth SD	Total length	TL SD	n	Discharge	Q SD	Temperature	Temp SD	Flow type
Summer 2009	0.12	0.05	134.54	25.16	28	377.34	12.42	12.73	0.25	Fluctuating
Summer 2010	0.16	0.13	121.13	19.53	23	388.67	19.47	12.23	0.22	Fluctuating
Summer 2011	0.07	0.10	125.82	20.09	38	701.66	9.56	14.21	0.32	Steady
Fall 2009	0.07	0.06	148.89	21.75	9	289.14	2.73	12.32	0.57	Steady
Fall 2010	0.09	0.09	132.52	25.47	82	237.24	17.63	12.52	0.44	Steady
Fall 2011	0.14	0.11	159.77	42.65	61	452.89	5.56	14.89	0.37	Steady

The daily growth information, growth standard deviation (SD), total length in mm (TL), total length SD (TL SD) and *n* are based on recaptures of uniquely marked individual fish. The discharge (Q. m^3), discharged SD (Q SD), temperature (°C) and temperature SD are the mean water temperatures for that specific growth period, and the flow type is the type of flow the juvenile humpback chub experienced (i.e. conditions they grew under) during that particular season either natural in the Little Colorado River or in the Colorado River steady or fluctuating flows depending on Glen Canyon Dam operations.

respectively (Figure 4). We also found that when flow conditions were steady in both summer and fall, growth was faster during fall (0.14 mm day^{-1}) compared with summer (0.07 mm day^{-1}). There is some overlap of the bootstrapped resample of mean daily growth rates, but the distributions were essentially disjunct and demonstrated that on average, juvenile humpback chub grew faster when discharge fluctuated than during steady flows (Figure 4).

Flow conditions in the Little Colorado River were not related to dam operations, and as expected, there were no trends in growth rates for the Little Colorado River related to flow in the mainstem Colorado River (Figure 2). We did observe a seasonal decline in mean daily growth rate in 2009 and 2011 from rates of roughly 0.10 mm day^{-1} from July to August/September down to roughly 0.02 mm day^{-1} for the interval between September and October. Of the three years assessed, growth of juvenile humpback chub in the Little Colorado River was relatively high in 2010 (0.22 mm day^{-1}) and did not decline in September and October as it had in previous years (Figure 4). This may be related to reduced density after an active monsoon flood season in 2010 or other unknown factors.

DISCUSSION

We found more rapid growth for juvenile humpback chub during fluctuating hydropeaking operations from Glen Canyon Dam than during steady flow operations. These results were consistent across multiple years and seasons and are counterintuitive to the expected result of improved growth under a more 'natural' steady flow regime. Minor changes in growth and survival rates during early life stages can have large impacts on the number of successful recruits later in life (Houde, 1987) because the length of time an individual spends in early life stages with higher mortality dramatically influences the recruitment of that cohort to the next life stage. Growing faster can increase the proportion of foraging habitat available and expand available prey resources to juvenile fish. Larger size has been shown to have survival advantages for juvenile fish because these individuals begin foraging on higher-quality prey items sooner, accelerating growth and lipid accumulation and improving survival through multiple seasons (Keast and Eadie, 1985; Thompson *et al.*, 1991; Ludsin and DeVries, 1997). Results of this study suggest that humpback chub would spend a longer time in vulnerable juvenile life stages if short (~2 months) steady flow regimes of the magnitude we observed were inserted amid typical fluctuating flows.

These conclusions are based on several key assumptions. Firstly, humpback chub used in the growth analyses remained in the same treatment group (river and season) between captures (assumption #1, Table 1). If individuals moved between the mainstem and Little Colorado River between captures, then the observed growth rates would not

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reflect the observed environment for each flow treatment. Earlier results from otolith growth and microchemistry analyses (Hayden *et al*., 2012) suggest that during this time of year and over the short time at liberty (15–70 days), it is likely that this assumption was met. We also assume that the sample of fish is a random and unbiased representation of juvenile humpback chub growth (assumption #2). If slower or faster growing individuals died or emigrated from our sampling reaches prior to our sampling, then these fish would not be included in our analyses because they would be unavailable for recapture. Finally, we assume that fish that are tagged either grow at the same rate as untagged fish or, if tagging does alter growth rates, this bias is the same regardless of flow condition or fish size. In this way, our comparisons are relative growth differences between different flow conditions or between river systems.

What factors other than changes in dam operations could have influenced juvenile humpback chub growth rates during 2009–2011? Two of the most likely are changes in water temperature and food availability. Water temperature influences the growth of age 0 fish (Mooij *et al*., 1994; Staggs and Otis, 1996; Clarkson and Childs, 2000). In 2011, high spring run-off into Lake Powell triggered high water volume releases from Glen Canyon Dam to transfer water to downstream users. Because of this release, downstream river conditions during summer 2011 included steady flow daily hydrograph (versus fluctuating flows in 2009 and 2010) and warmer temperatures than the two previous summers. This departure from the planned experiment of fluctuating flows during summer for all 3 years was actually fortuitous because it allowed us to assess whether the lower growth rates observed during fall 2009 and 2010 were a function of season or due to changes in the hydrograph. On the basis of water temperature alone, we would expect growth to be highest during both summer and fall 2011. However, growth during summer 2011 was lower than during the two previous years when fluctuating hydropeaking flows occurred. This suggests that flow conditions more strongly influence growth than water temperature across the range of flow treatments and temperatures observed during 2009–2011.

Flow variation may also affect invertebrate food production, which could alter prey availability to juvenile humpback chub and thus, humpback chub growth. Invertebrate drift has been shown to increase with increases in flow (Irvine and Henriques, 1984; Perry and Perry, 1986; Poff and Ward, 1991; Vinson, 2001), and invertebrate communities in this reach of the Colorado River are known to respond strongly to experimental floods (Cross *et al*., 2011). Unfortunately, the response by invertebrate drift to the transition from peaking to steady flows during 2009 and 2010 was not extensively assessed. In the Kootenai River, Montana, high rates of insect drift were observed during a steady flow immediately following a period of high steady discharge (Perry and Perry, 1986), possibly due to a concentration of drift in the lower river volume at reduced flow levels. This may help to explain why our observed growth rates in the Colorado River during fall 2011 were higher than growth in previous falls because of the transition from high to low flows that occurred from summer to fall 2011.

We do not know why fall growth was faster in the mainstem Colorado River than in the Little Colorado River during two of the three study years. The primarily east-to-west orientation of the Little Colorado River in our study reach in a gorge up to 1 km deep may suggest one possible mechanism. Primary production in the Little Colorado River is dependent on increasingly smaller amounts of sunlight as the angle of the sun declines and is even locally eliminated during winter. However, the north–south orientation of the Colorado River within our study reach allows for sunlight to remain all year, albeit at a reduced angle in fall and winter (Yard, 2003). Thus, it is possible that restricted sunlight in the Little Colorado River in the fall months reduced prey and subsequently, humpback chub growth.

On the basis of fall water temperature alone, growth rates in fall should always be higher in the Little Colorado River (Figure 3), but we observed higher growth in the Colorado River in fall 2009 and 2011 (Table 1). Fish occupying warmer water have higher metabolic demands than individuals in cooler water, and if these demands increase concurrently with a seasonal decline in prey availability, then growth rates may be reduced. Additionally, the heat storage effect of Lake Powell on the Colorado River causes a lag time in mainstem river cooling compared with the Little Colorado River; thus, the temperature transitions between seasons (i.e. July–August versus September–October, Figure 3) are less pronounced than those that occur in the Little Colorado River because the mainstem is warmer for a longer period of time into the fall. This suggests that some aspect of the mainstem Colorado River other than temperature, possibly prey availability, likely caused the growth result that we observed in the mainstem Colorado River.

Management implications

Experimental from Glen Canyon Dam have long been advocated for restoration efforts in the Grand Canyon reach of the Colorado River (NRC, 1996; Collier *et al*., 1998). Water policy management actions considered include a seasonally adjusted steady flow routine to mimic spring floods and summer low flow periods or a selective withdrawal device to have warm-water discharge below Glen Canyon Dam (USDOI, 2008). These and other intuitively simple management actions are at least partially motivated by the expectation that conditions similar to the pre-dam environment (a more natural Colorado River) would be beneficial to the recovery and persistence of humpback chub through improvements in growth, survival or recruitment. However, these proposals are costly to implement in terms of lost power

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revenue and construction costs, and the outcomes of either or both policies are still highly uncertain (Lessard *et al*., 2005). The imperilled population status of many native fish in southwestern rivers that still have largely unregulated flows (i.e. Upper Gila, Verde and Salt rivers; Minckley and Marsh, 2009) further complicates management decisions. In this study, we have demonstrated that improvements in growth rates for juvenile humpback chub (one objective of a more natural steady flow) were not observed. This has direct implications for future experiments as part of the Glen Canyon Dam Adaptive Management Program. Our results provide further evidence that the direction of response (positive, negative or neutral) of a specific component of a riverine ecosystem to a change in flow conditions is highly uncertain, particularly in systems where a large number of other factors are simultaneously in play (Anderson *et al*., 2006; Bradford and Heinonen, 2008; Bradford *et al*., 2011). Recognizing this uncertainty is critical to the planning and decision making process related to prioritizing research needs in regulated rivers and in making predictions related to ecosystem responses to changes in river management.

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