

MANIPULATION OF FISH VITAL RATES THROUGH ECOSYSTEM
EXPERIMENTATION IN A REGULATED RIVER

By

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LIST OF ABBREVIATIONS

AZGFD	Arizona Game and Fish Department
BIA	Bureau of Indian Affairs
BOR	United States Bureau of Reclamation
FWS	United States Fish and Wildlife Service
GCMRC	Grand Canyon Monitoring and Research Center
LCR	Little Colorado River
NPS	National Park Service
NSE	Nearshore Ecology, a juvenile native fish research project funded by the Grand Canyon Monitoring and Research Center
PIT	passive integrated transponder
rkm	river kilometer; recorded in distance from Lee's Ferry, 26 km below Glen Canyon Dam at Lake Powell
USGS	United States Geological Survey
VIE	visible implant elastomer
WAPA	Western Area Power Authority

Abstract of Thesis Presented to the Graduate School of the University of Florida in
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Managers of fish populations often use growth and survival of juveniles as important descriptors of population health. Juvenile fish are sensitive to environmental perturbations, so monitoring their vital rates allows managers in regulated systems such as dam tail-waters to directly evaluate the effects of flow operations on fish populations. Despite this direct pathway, less is known about juvenile fish compared to adults in these habitats as they are often more difficult to collect due to smaller body size and differential habitat use. In this study I evaluated individual growth and apparent survival rate of juvenile humpback chub *Gila cypha* (<200 mm total length) in the Grand Canyon reach of the Colorado River, Arizona for three years. I sampled during typical fluctuating hydropower flows, and during experimental steady dam releases. Growth in juvenile humpback chub declined during steady flows versus fluctuating flows, despite temperatures being roughly equivalent across flow treatments. Annual apparent survival of juvenile humpback chub initially tagged at <100 mm total length was not significantly different between flow treatments, and ranged from 37-67% depending on the model. Steady flow experiments of the magnitude and timing that I observed did not improve growth or apparent survival rates of juvenile humpback chub in Grand Canyon. This

suggests that juvenile humpback chub growth and survival is robust to the flow fluctuations observed during 2009-2011, and more extreme flow treatments such as higher or lower flows, or longer duration experiments, are likely required before differences in these key vital rates are detected.

CHAPTER 1 INTRODUCTION AND BACKGROUND

Humans are ecosystem engineers that often dramatically change landscape attributes and resource availability through land-use alterations (e.g. conversion to agriculture or urbanization of landscapes, dewatering of rivers, reservoir construction, fire suppression; Foley et al. 2005). Humans also introduce novel species that increase competition and predation pressures. If native species do not have serendipitously advantageous morphology or behavior (Gould and Vrba 1982), or are unable to rapidly adapt to the new ecological community, these introductions often lead to local extirpation or even extinction (Savidge 1987, Oghutu-Ohwayo 1990). The loss of commercially or socially important native species can have tremendous financial, ecological, or social consequences, and legislation and public pressure often requires managing agencies to seek remedial action.

The Grand Canyon ecosystem of the United States' desert southwest is a high-profile example of human influence at an ecosystem level. Fire suppression on the forested north and south rims of Grand Canyon (Fule et al. 2002), regulation of the Colorado River due to the construction and operation of Glen Canyon Dam (Gloss et al. 2005), the influx of nearly 5 million human visitors per year (NPS 2012), and the introduction of non-native species such as rocky mountain elk (Truett 1996), burros (Ruffner and Carothers 1982), and multiple fish species has followed European settlement of the area. These influences have exacerbated environmental degradation such as overgrazing and the spread of noxious weeds (Carothers et al. 1976), range reductions in desert bighorn sheep (McKnight 1958) and extirpations of four of eight

native fish species (Minckley 1991), seven of which are endemic to the Colorado River basin.

Modern efforts to combat resource degradation have increasingly incorporated principles of adaptive management. Adaptive management was originally developed in the 1970s and 1980s and has become widely discussed and occasionally instituted across a gamut of natural resource scenarios. The crux of adaptive management is based on reducing uncertainty in inherently complex natural systems in order to improve understanding of system function and resource conditions for management purposes (Walters and Hilborn 1978, Walters and Holling 1990). Adaptive management has a mixed history of success and implementation, usually related to opposition in acknowledging uncertainty and the opportunity cost of running ecosystem-level experiments where the exact outcome of experimental actions is not precisely understood.

The Glen Canyon Dam Adaptive Management Program (GCD AMP) was instituted through collaboration of various public and private entities involved in resource management within the Colorado River corridor of Marble, Glen, and Grand Canyons in northern Arizona. Participants include the United States Department of the Interior's Bureau of Reclamation (BOR), United States Geological Survey's Grand Canyon Monitoring and Research Center (GCMRC), National Park Service (NPS), Arizona Game and Fish Department (AZGFD), Bureau of Indian Affairs (BIA), United States Fish and Wildlife Service (FWS), Department of Energy's Western Area Power Authority (WAPA), the seven Colorado River basin states (Colorado, Wyoming, Utah, New Mexico, Nevada, California, and Arizona), five Native American tribes, and recreational

interests including boating and fishing enthusiasts. These groups must all reach a consensus on the management directives for Glen Canyon Dam in order to satisfy the Endangered Species Act of 1973 and the Grand Canyon Protection Act of 1992 while still allowing Lake Powell and Glen Canyon Dam to serve as a water supply storage reservoir, flood control structure, and hydropower facility. In this thesis I will present the results of an ecosystem-scale adaptive management experiment implemented by GCD AMP designed to mitigate adverse impacts of river regulation and dam operation on a federally listed (Endangered) native fish species.

CHAPTER 2 INFLUENCING GROWTH RATES THROUGH EXPERIMENTAL FLOW TREATMENTS

Introduction

Predation and starvation are two principal causes of mortality that structure animal populations, and in most natural systems neither predation nor starvation can be avoided without exposure to the other. While they are not always mutually exclusive activities, animals face a critically important and delicate trade-off between foraging sufficiently while evading predation (Werner et al. 1983, Carey and Moore 1986, Cowlshaw 1997, Strobbe et al. 2011). Fish foraging arena theory helps explain this balance by demonstrating that predation-vulnerable juvenile fish are confined to relatively small proportions of available habitat where both refugia and food resources are available, even though this precludes growing at the maximum attainable rate (Werner et al. 1983, Walters and Juanez 1993). However, many fish (especially those in temperate environments) must reach a critical mass after their first growing season if they are to survive the winter (Thompson et al. 1991, Ludsin and DeVries 1997, Biro et al. 2004). In prey sparse environments, these individuals may only succeed by increasing foraging time, thus exposing themselves to increased predation risk.

Individual fish that survive this increased foraging time while avoiding the increased predation risk benefit from a positive feedback loop that is advantageous in terms of individual fitness. As an example, faster growth rates have been shown to improve an individual's odds of surviving the winter (Ludsin and Devries 1997), as well as increase the food resources available for consumption and reduce the vulnerability to predation of that individual due to gape limitation (Nilsson and Bronmark 2000, Urban 2007). The dual influence of larger fish having reduced overwinter mortality and reduced

vulnerability to predators often results in growth rate being used as a surrogate for survival in juvenile fishes (Lorenzen 2006). This theory is often extended to a management context through management actions to increase growth rate and ultimately expect improvements in population status of important fish species.

The humpback chub *Gila cypha* is a federally listed (Endangered) cyprinid fish endemic to the Colorado River basin, with the largest extant population found in nine aggregations throughout Grand Canyon. More than 90% of the individuals in the Grand Canyon population live near the confluence of the Colorado and Little Colorado Rivers, known as the “LCR aggregation” of humpback chub (Valdez and Ryel 1997, for additional references see Goulet and LaGory 2009; Figure 2-1). Most mature individuals participate in a potamodromous spawning migration to the unregulated and seasonally warmed Little Colorado River (LCR) for spawning in the spring, after which they return to the mainstem Colorado River (Kaeding and Zimmerman 1983, Valdez and Ryel 1997, Coggins et al. 2006a). Humpback chub population trend in Grand Canyon declined through the 1990’s and early 2000’s (Valdez and Ryel 1997, Coggins et al. 2006a), motivating extensive resource assessment and experimental management of Glen Canyon Dam (GCD) to reverse these negative trends in population (Lovich and Melis 2007).

Adult humpback chub population demography has been monitored since the late 1980’s, primarily through intensive mark-recapture tagging efforts in the Little Colorado River during spring and fall. These monitoring programs provide direct estimates of adult survival and abundance, and reconstructed estimates of juvenile survival (Coggins et al. 2006a, 2006b). Adult survival rates during the period of population decline (late

1990's to early 2000's) were generally high (60-93%) which suggests that a recruitment bottleneck at earlier life stages may have caused the negative population trend.

Modeling efforts in the early 2000's (Lessard et al. 2005) concluded that in-river physical conditions such as flows or cold mainstem water temperatures or biological factors such as negative interactions with adult rainbow trout could have significant impacts on juvenile humpback chub. Experimental removal of non-native trout was conducted in 2003-2006 and 2009 (Coggins et al. 2011; Yard et al. 2011), and in 2008 a series of discharge experiments began in an attempt to resolve uncertainty between the relationship of river flow and juvenile fish vital rates as part of the Glen Canyon Dam Adaptive Management Program.

Extant flow operations from Glen Canyon Dam are designed to follow diel fluctuations in power demand across the southwestern United States, with electricity production increasing and decreasing daily (proportional to dam discharge and flow rate in the downstream Colorado River through Grand Canyon) and causing an artificial "tide" along the river corridor. This discharge regime is known as "modified low fluctuating flow", and the ecological impacts are unknown for most ecosystem components. In contrast, under steady flow conditions, water persists in nearshore areas such as low-angle habitat and backwaters and warms on a spatially limited scale in the Lee's Ferry reach of the Colorado River just below Glen Canyon Dam (Korman et al. 2006), increasing growth rates for juvenile rainbow trout compared to fluctuating flows (Korman and Campana 2009). Similar growth patterns have not yet been documented in native fish, although increased temperatures could potentially improve metabolic efficiency and growth of warmwater species such as humpback chub

(Coggins and Pine 2010) and would provide important insight into how to operate dams to benefit native fish. To determine if growth rates of juvenile humpback chub improve during steady flows, GCDAMP initiated a series of constant dam releases for specific time periods (September and October 2008-2012; Figure 2-2) as a contrast to extant fluctuating flows the remainder of the year. In this paper I will assess the effect of steady flows on growth rates of juvenile humpback chub.

Methods

Study Site

The Grand Canyon reach of the Colorado River is the roughly 400-km section bounded downstream by Lake Mead and upstream by Lake Powell, the first and second largest reservoirs in the United States (Andrews 1991). Average discharge of the Colorado River through Grand Canyon for the past decade (2000-2010) was 351 m³/sec as measured at the Phantom Ranch gauging station 145 km below Lee's Ferry (river kilometer or "rkm" 145) and 171 km below Glen Canyon Dam. This river reach is contained within the borders of Grand Canyon National Park and is a UNESCO world heritage site, in addition to being listed as a federally protected region of cultural, geologic, and biological significance under the Grand Canyon Protection Act of 1992.

The Colorado River within Grand Canyon is stenothermic and cool due to stratification of Lake Powell and hypolimnetic discharges. Annual Glen Canyon Dam water release temperatures fluctuate around 2°C on average (from 8°C to 10°C from 1994-2002), with occasional temperatures fluctuating annually by as much as 7°C (from 8°C to 15°C in 2011, Figure 2-3). Since the closing of Glen Canyon Dam, the near-record maximum temperatures of 2011 still only span about 25% of the original range of annual temperature fluctuation (Figure 2-4). This reduction in seasonal mainstem

temperature maximums is believed to be one of the main drivers for the reduction or extirpation of populations of warmwater endemic fishes including humpback chub (Kaeding and Zimmerman 1983, Valdez and Ryel 1997, Clarkson and Childs 2000).

The Little Colorado River (LCR) contains the LCR aggregation of humpback chub, and is the largest tributary of the Colorado River within Grand Canyon National Park. The LCR drains approximately 44,000 km² in northern and central Arizona with a mean annual discharge of 11.54 m³/sec since 2004 and enters the Colorado River 126 km below Glen Canyon Dam and 100 km below Lee's Ferry, at rkm 100. The LCR is essentially unregulated, although some of the upper basin has been dewatered due to human settlement. Runoff patterns are characteristically bimodal: extended discharges during snowmelt-dominated spring floods are followed by shorter, stochastic summer flood pulses associated with monsoonal precipitation (Figure 2-5). I considered the LCR as a control system for humpback chub growth studies because it is not affected by the dam operations beyond the confluence with the Colorado River, but does experience natural seasonal fluctuations in temperature and discharge. As the only unregulated river in Grand Canyon that still has a sizeable population of humpback chub, it can uniquely offer some distinction between growth effects that may be occurring naturally due to seasonal fluctuations and those that may be occurring due to steady versus fluctuating flow effects.

Sampling Techniques

I conducted a mark-recapture study of humpback chub in the mainstem Colorado River from river km 102 to 106 and in the Little Colorado River from the confluence upstream roughly 14 km. I sampled the LCR both independently and as part of the fall US Fish and Wildlife Service mark-recapture humpback chub surveys. I sampled 10 to

12 days each month of the field season in both rivers (12 trips total, Figures 2-5 and 2-6) during July-October 2009-2011. July and August mainstem Colorado River samples during 2009 and 2010 represented typical fluctuating hydropower flows, while September and October samples from all years represented the fall steady flow experiments. High steady dam discharges during July and August 2011 were exceptional for my study period due to equalization flows between lakes Powell and Mead during a high water year (Figures 2-5 and 2-6), and provided a summer steady flow contrast compared to fluctuating flows in July and August of the previous two years.

I used two gear types to sample the mainstem Colorado River fish community (Figure 2-7): 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 hour intervals) and slow-speed boat electrofishing (see Korman and Campana 2009; unit output was pulsed DC current at 15-20 amps and 200-300 volts, 7-10 seconds per meter of shoreline, repeated 24 to 72 hours apart for 3 to 5 total passes per trip). I sampled the Little Colorado River with the same un-baited mini hoop-nets, deployed in areas likely to yield the highest capture and recapture rates of juvenile humpback chub. Electrofishing is not feasible in the LCR due to natural high salinity.

I measured, tagged, and returned humpback chub to the same location where they were captured. All humpback chub >100 mm in total length (TL) received a 134.2 kHz passive integrated transponder (PIT) tag (9 mm long, BIOMARK) with a unique number identifiable to individual fish. Although I sampled the entire fish community as part of the larger sampling project, this analysis includes 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”). Included individuals were also recaptured on the subsequent trip to limit the at-large growth period to a certain discharge regime and omit the influence of inter-annual, seasonal, or ontogenetic shifts in growth rates. Due to logistical and safety reasons during flash flooding, sampling was not always feasible in the Little Colorado River during summer monsoon season (July-September). To improve recapture sample sizes for Little Colorado River fish initially captured in July, I included recaptures over the interval of July to August *or* September in the LCR, whereas mainstem recaptures were limited to fish captured in July and recaptured in August only. Because LCR discharge shifts are more gradual and continuous (fish recaptured in September in the LCR were experiencing similar conditions as August, where the mainstem conditions had markedly changed due to the flow experiment, Figure 2-2), these fish could be considered part of the same treatment type. All growth rates are assumed to be linear for the 15-70 day intervals when fish were at large.

Data Analysis

I divided recaptured humpback chub into twelve groups based on which season (summer and fall), year (2009, 2010, and 2011), and system (mainstem Colorado River or Little Colorado River) in which they resided (Table 2-1). For instance, if a humpback chub over 100 but less than 200 mm TL was captured, measured and released in July 2009 and then recaptured in the same place in August 2009, it became part of the “Summer 2009” subsample for that respective river. If any individual fish was not recaptured on the subsequent trip, it was not included in that sample. Again, the exception for this is in the Little Colorado River, where fish were allowed to be at large for up to two months (from July to August *or* September).

I calculated the mean daily growth for each of the 12 humpback chub subsamples (Table 2-1) over the interval during which they were at large, and then performed a 10,000 iteration bootstrap resample with replacement using Program R to determine the distribution of the mean growth rate for that subsample. The assumptions of this approach were 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 from the overall population.

Results

Juvenile humpback chub daily growth rates in the mainstem Colorado River during summer fluctuating flows (July to August periods in 2009 and 2010, Figure 2-8) were higher than the daily growth rates during fall steady flow experiments in the same year (September to October periods in 2009 and 2010, Figure 2-9) despite similar temperatures across the sampling season (Figure 2-3). I expected growth rates to decline in the fall due to decreased solar insolation (Yard et al. 2005) and possibly reduced primary production, which would seasonally confound the fall steady flow treatments. However, the high water year of 2011 (Figure 2-6) provided an unplanned experiment with a serendipitous contrast. In 2011, spring and summer discharges were high and steady compared to 2009 and 2010 and due to required equalization flows between Lakes Powell and Mead. This created a reciprocal growth test of steady flows during the July-August summertime periods (in contrast to fluctuating flows the previous two years over the same time period). Although there is some overlap of the bootstrapped distribution of the sample means, the resulting distributions are disjunct for summer 2011 (steady flow interval) compared to summer 2009 and 2010 (fluctuating flows, Figure 2-8). This contrast allowed us to determine that individual humpback chub

grew more slowly during the steady flow interval (2011) than during fluctuating flow intervals (2009 and 2010), even when they occupied the same season.

Flow conditions in the Little Colorado River were not related to dam operation (Figure 2-5), and as I expected there were no trends in growth rates for the Little Colorado River related to flow in the mainstem Colorado River (Figures 2-10 and 2-11). I did observe a seasonal decline in mean daily growth rate in 2009 and 2011 from rates of roughly 0.12 mm/day from July to August/September down to roughly 0.01 mm/day for the interval between September and October. Of the three years assessed, 2010 growth of juvenile humpback chub in the LCR was relatively high (0.25 mm/day) and did not decline in September and October as it had in previous years.

Discussion

Common policies for improving population status of fishes such as stocking, bag and slot limits, or removal of competing undesirable species are difficult and costly to use in remote areas or in areas where harvest is precluded for legal or logistical reasons. Ecosystem-level controls offer an alternative to labor-intensive and expensive hands-on techniques for managing fishes and fisheries, especially in regulated rivers. The current adaptive management program at Glen Canyon Dam provides unique opportunities to probe the efficacy of achieving ecosystem-level improvements in fish vital rates such as growth through flow manipulation.

Growth rate is an important indicator of habitat quality and potential recruitment and/or population success in fishes because it incorporates a broad range of habitat characteristics such as forage quality, availability of refugia, and density and competition between fish populations within a certain trophic level (Nilsson and Bronmark 2000, Urban 2007). Managing for growth is widely used in aquaculture and

food fish resource management to maximize production, and is also prevalent in management scenarios for listed fish species as it serves as a useful surrogate for survival (Lorenzen 2006).

This study demonstrates that juvenile humpback chub daily growth rates are lower during steady flows than fluctuating flows when both flows occurred in the same season (0.07 mm/day during steady flows from July to August 2011 versus 0.12 mm/day and 0.15 mm/day during fluctuating flows from July-August 2009 and 2010, respectively, Figure 2-8). Growth rates are also lower during steady flows than fluctuating flows within the same year (0.08 mm/day and 0.07 mm/day during steady flows versus 0.15 mm/day and 0.12 mm/day during fluctuating flows in 2009 and 2010, respectively; Figures 2-8 and 2-9), even though temperatures were similar across the sampling periods (Figure 2-3). There is some overlap of the bootstrapped resample of mean daily growth rates, but the distributions were essentially disjunct and demonstrated that juvenile humpback chub grew faster when discharge fluctuated mildly due to power production than when it was held experimentally constant.

In order to be included in my subsamples, fish had to remain in the same river system between captures (assumption #1). If individuals mixed frequently between captures and thus spent unpredictable amounts of time in both the mainstem Colorado River and the LCR while they were at large, the subsamples that I used to determine the flow-growth relationship between river systems would have been flawed. In this study, the average distance of the mainstem Colorado River sampling area from the Little Colorado River is ~3 km, while the average distance from my sample location within the Little Colorado River to the mainstem was over 1 km. Humpback chub,

especially adults, are known to travel farther than this on an annual basis for potamodromous spring spawning runs (Kaeding and Zimmerman 1983, Gorman and Stone 1999). However, the relatively short time at large (15 to 70 days) of sampled fish, smaller body size and movement potential of juvenile fish, and the fact that they were recaptured in the same river where they were originally handled on the preceding trip supports the assumption that they did not spend significant time in the other river system. Individuals that *did* move (and experienced mixed environments and growth rates) between the two systems were not likely recaptured within the short time interval and in the same river that would have caused me to include them in that respective growth subsample.

The second sampling assumption is that I had a random and unbiased sample of the population. The data would be biased upward an unknown amount if slower growing individuals died or emigrated at higher rates and were excluded from analyses. However, unless the slower growing individuals were *disproportionately* missing in one of the two river systems or during one of the flow treatments, I have no reason to assume that the comparative results of the subsamples are invalid. Capture probabilities did not differ by flow treatment, so I have no reason to suspect this to be true. In addition, many of the fish excluded from growth analyses because they were not recaptured on the next trip were recaptured on later trips, implying that subsamples were not decided by size- or mortality-dependent attributes but were subject to random selection.

Water temperature is an important determinate of growth rate in fish that has potential to confound flow experiments (Valdez and Ryel 1997, Korman and Campana

2009). Unfortunately temperature is not often within the controls of dam managers and is instead subject to stochastic fluctuation due to environmental and meteorological conditions that drive riverine inputs to reservoirs and reservoir storage levels. During the three year period of this study, 2009 and 2010 had similar temperature profiles. In 2011, high runoff into Lake Powell and associated short residence time caused near-record discharge temperatures in the Colorado River within Grand Canyon since the closing of Glen Canyon Dam (Figure 2-3). However, the Colorado River historically fluctuated from near-freezing in winter to almost 30°C in summer (Figure 2-4), so the difference between the “colder” years of 2009 and 2010 and the “warmer” year of 2011 represents only around 10% of the historical thermal range of humpback chub. I thus expected only mild improvements in growth rate for the 2011 July – August interval. I actually observed that growth declined compared to same time period in the previous two years, which were fluctuating flow conditions.

Due to the heat storage effect of Lake Powell, maximum water temperatures do not occur in the Colorado River below Glen Canyon Dam until September or October (Figure 2-4). This has important implications for within-year flow tests. Based on temperature, I would expect the periods of highest growth to occur during the fall (steady flow) time period, but growth was actually lower during fall steady flows. This further demonstrates that steady flows reduce growth in juvenile humpback chub, even with the added influence of higher water temperatures during steady flows periods both within years and across years.

Without observing the expected relationship between temperature and growth rate, I suggest food availability in the invertebrate drift as a possible mechanism for the

demonstrated flow-induced differences in mean daily growth rate in juvenile humpback chub. Invertebrate drift in regulated rivers increased during fluctuating flows in the Flathead River of Montana (Perry and Perry 1986) and the Hawea River of New Zealand (Irvine and Henriques 1984). These increases in invertebrate drift are likely present in Grand Canyon as well, and may reduce the metabolic costs of feeding for Colorado River fish as well as allow them to stay closer to predation refuges. During steady flows, insect drift likely returns to a more natural cycle, with pulses in drift density occurring nocturnally to minimize predation and maximize successful dispersal of insects (Waters 1972, Muller 1974), resulting in reduced availability to foraging fish.

I also suggest the relationship between discharge and invertebrate colonization and drift as a mechanism to explain the unusual growth conditions I observed in 2011. The July-August 2011 interval demonstrated the lowest growth rate for that season of the three years, and the September-October period demonstrated the highest growth rate for that season of the three years. This cannot be attributed to steady versus fluctuating flow conditions or temperature, as the entire 2011 sampling period occurred during steady flows (Figure 2-6) and was of fairly uniform temperature (Figure 2-3). However, it was likely discharge related. High, steady discharges that began in spring 2011 permanently flooded unoccupied substrates that were either dry or intermittently submerged due to hydropower fluctuations. During the lag time before algae, diatoms, and insects colonized this newly submerged substrate, the same amount of emergent food items were effectually diluted in larger volumes of water and reduced foraging efficiency of fish. Once colonization of this newly submerged substrate occurred, drift density likely improved and increased food availability and growth. Then, with

reductions in discharge on September 1st, this newly established foodbase may have drifted catastrophically to avoid desiccation and was likely concentrated in the lower volume of water, increasing food availability to fish. This could serve as the possible mechanism that produced the high growth rates I observed during September-October 2011. A similar situation was observed in the regulated Kootenai River of Montana, where the highest rates of insect drift were also recorded during a lower steady flow immediately following a period of high steady discharges (Perry and Perry 1986). Although these results do not categorically preclude a system-wide improvement in growth in the Colorado River during fall 2011, the absence of higher growth in the LCR during this period suggests that in-situ mainstem Colorado River conditions were likely responsible for the growth differences, and my data suggests that these changes are likely related to discharge.

Fluctuating hydropower flows can actually be beneficial for juvenile fish growth. Changes in discharge can increase insect drift (Irvine and Henriques 1984, Perry and Perry 1986), as well as the concentration of drifting insects, and I suggest this as a mechanism for higher growth during fluctuating flows in the Colorado River. If individual fish are exposed to increased metabolic costs and reduced foraging efficiency during experimental steady flows their growth rates are reduced, with potential implications for future survival, recruitment, and population growth or stability. There is likely an ideal fluctuation level to optimize juvenile fish growth rate that is as yet unknown.

Table 2-1. Sample sizes of juvenile humpback chub recaptured for growth purposes.

Location:	Colorado River		Little Colorado River	
Interval:	Jul-Aug	Sep-Oct	Jul-Aug-Sep	Sep-Oct
2009	28	9	4	55
2010	23	82	20	52
2011	38	61	8	20
Total:	89	152	32	127

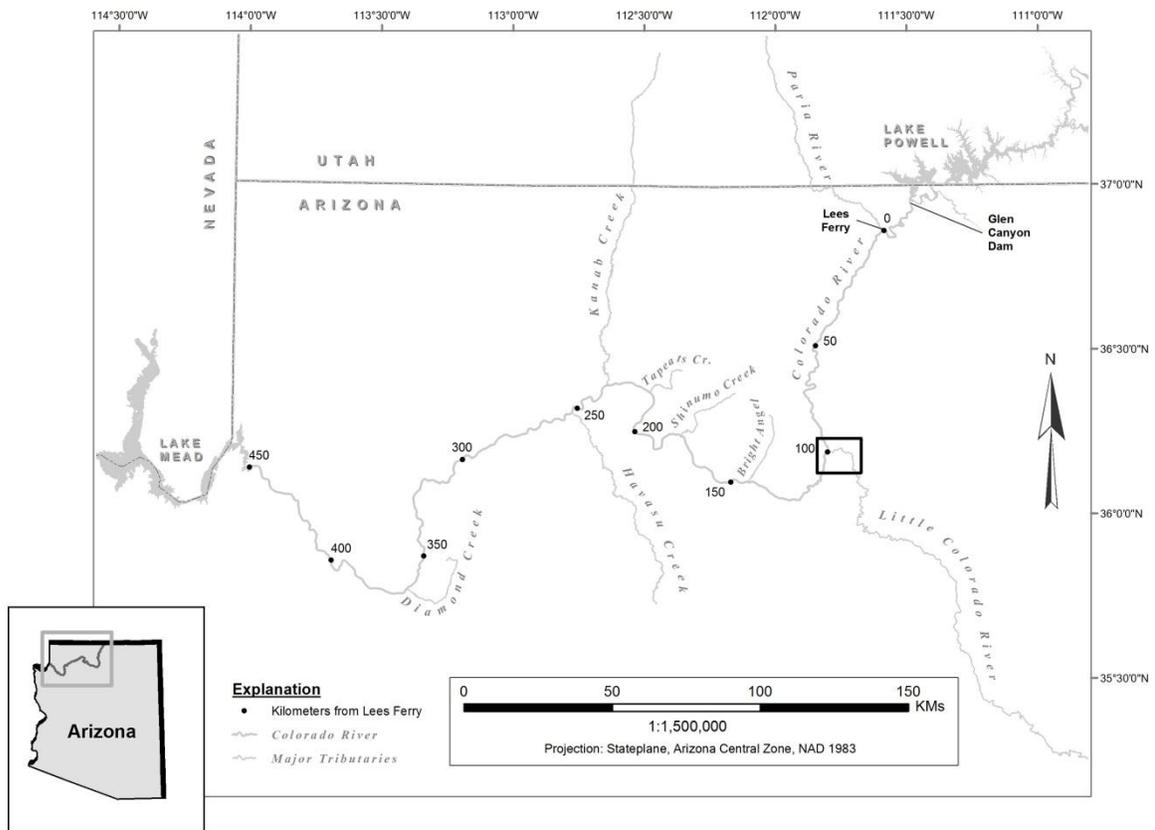


Figure 2-1. Map of study area near confluence of Colorado and Little Colorado Rivers in northern Arizona, containing the Little Colorado River aggregation of humpback chub.

2009 Colorado River Discharge
Lee's Ferry, Arizona

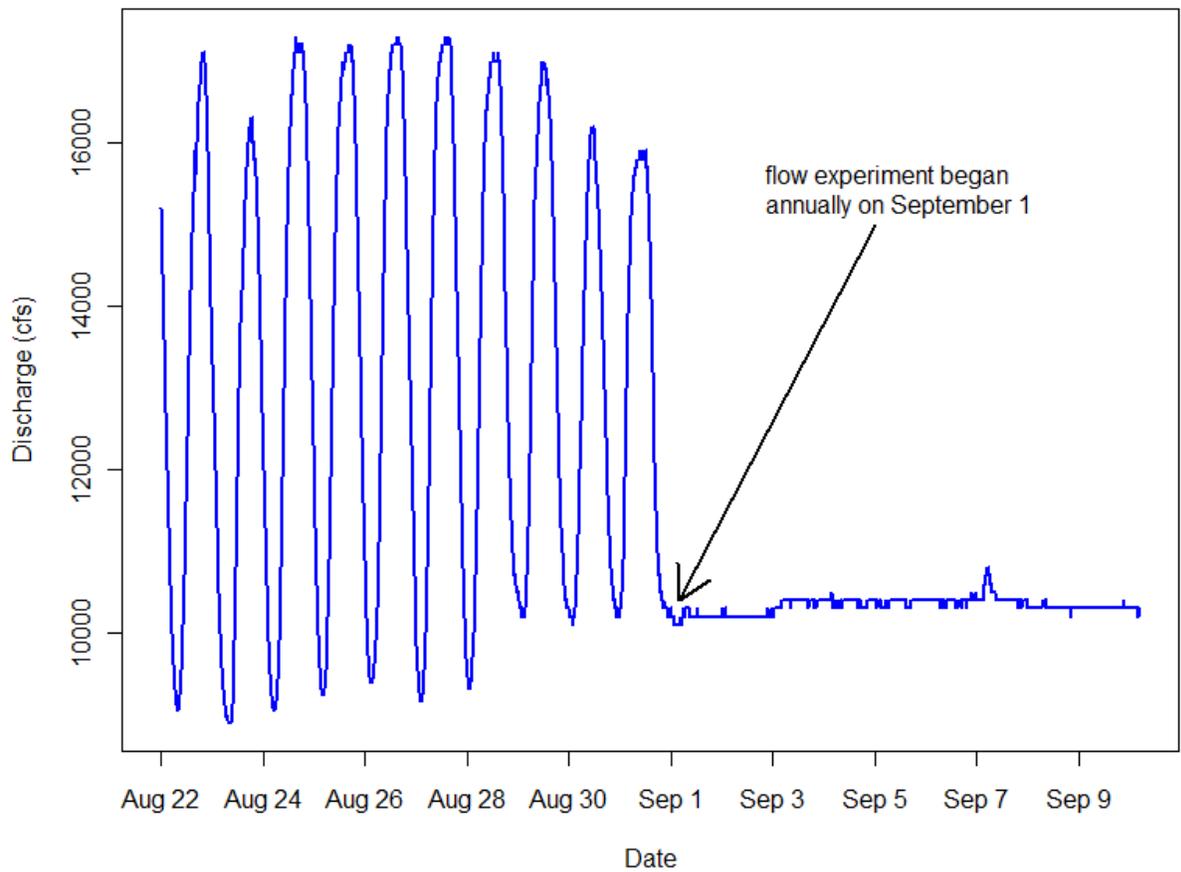


Figure 2-2. Colorado River discharge August 22nd-September 10th, 2009 at the Lee's Ferry gauge, 98 km upstream from my sampling universe. The period before September 1st is representative of normal hydropower operations, while the period after September 1st is representative of the steady flow experiment. Data from USGS instantaneous data archive. Available: <http://nwis.waterdata.usgs.gov/nwis>

Colorado River temperatures at Lee's Ferry, this study versus 15 preceding years

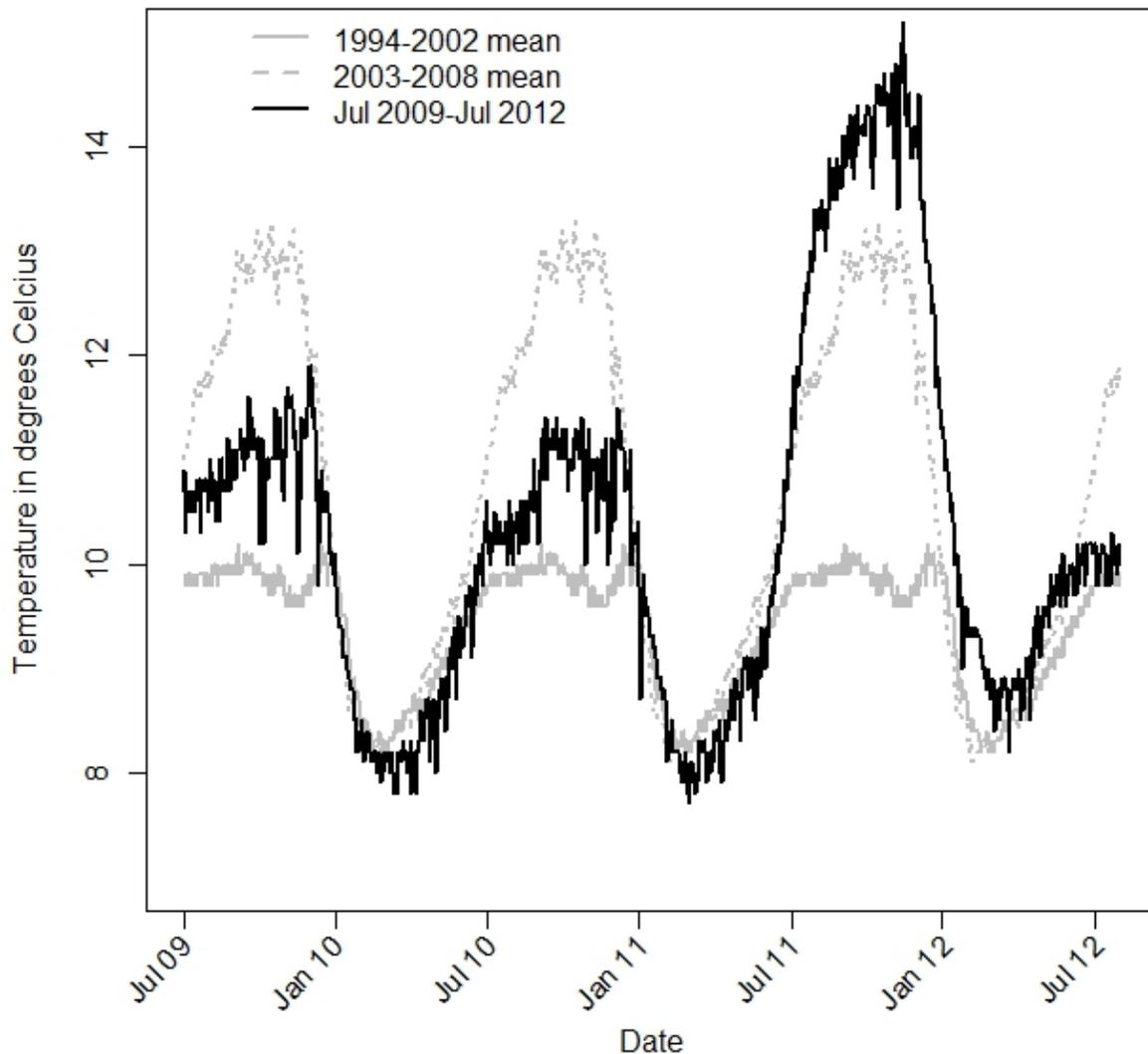


Figure 2-3. Colorado River water temperatures as measured at Lee's Ferry, 26.4 km downstream from Glen Canyon Dam. The solid gray line is the mean annual temperature as estimated by the period from 1994-2002, while the dotted gray line is the mean annual temperature as estimated by the period from 2003-2008. The solid black line reflects temperatures observed during each of the three years of this study (July 2009-July 2012; not an average). Data from USGS instantaneous data archive. Available: <http://nwis.waterdata.usgs.gov/nwis>

Colorado River temperatures at Lee's Ferry, this study versus historical means

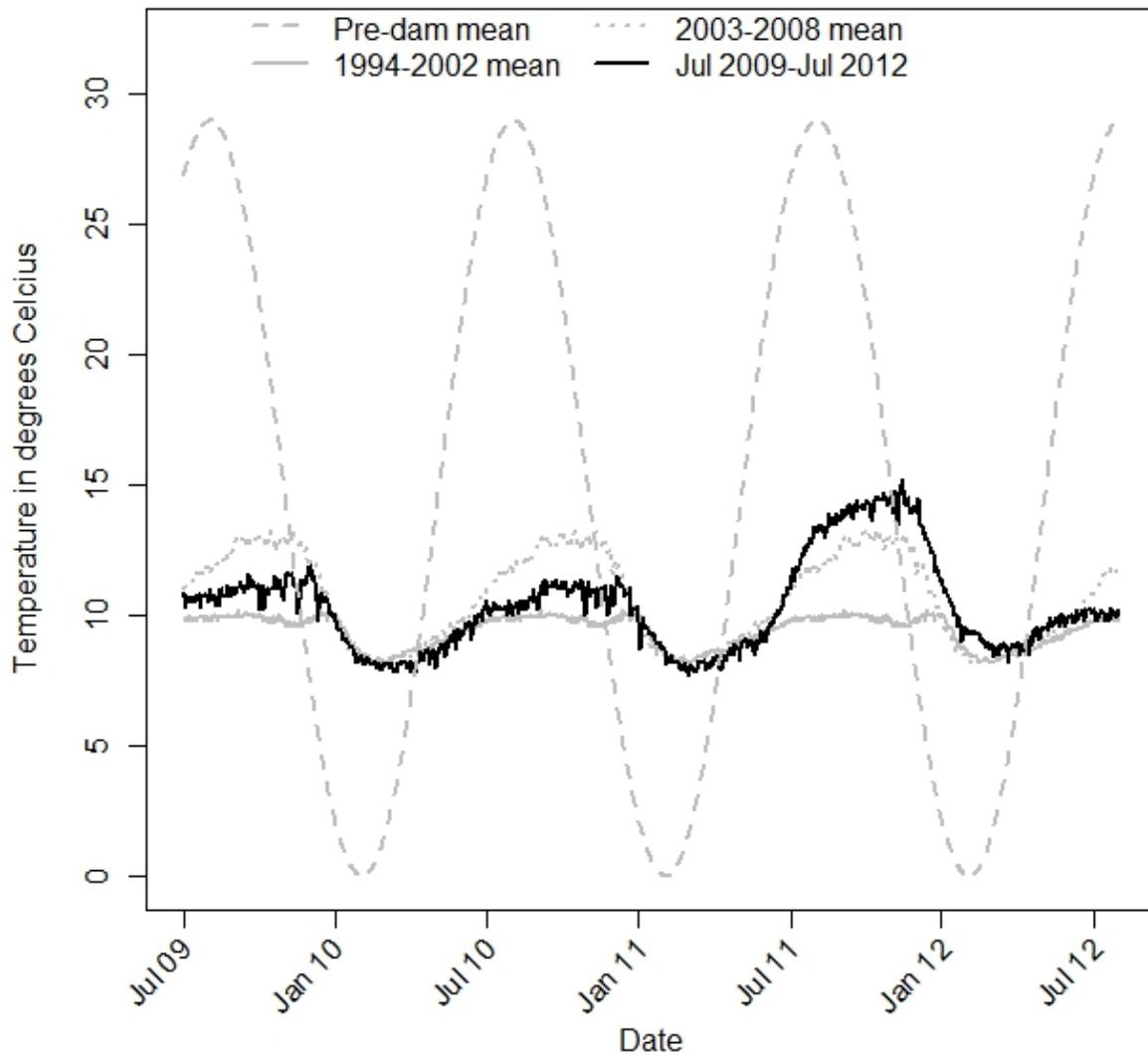
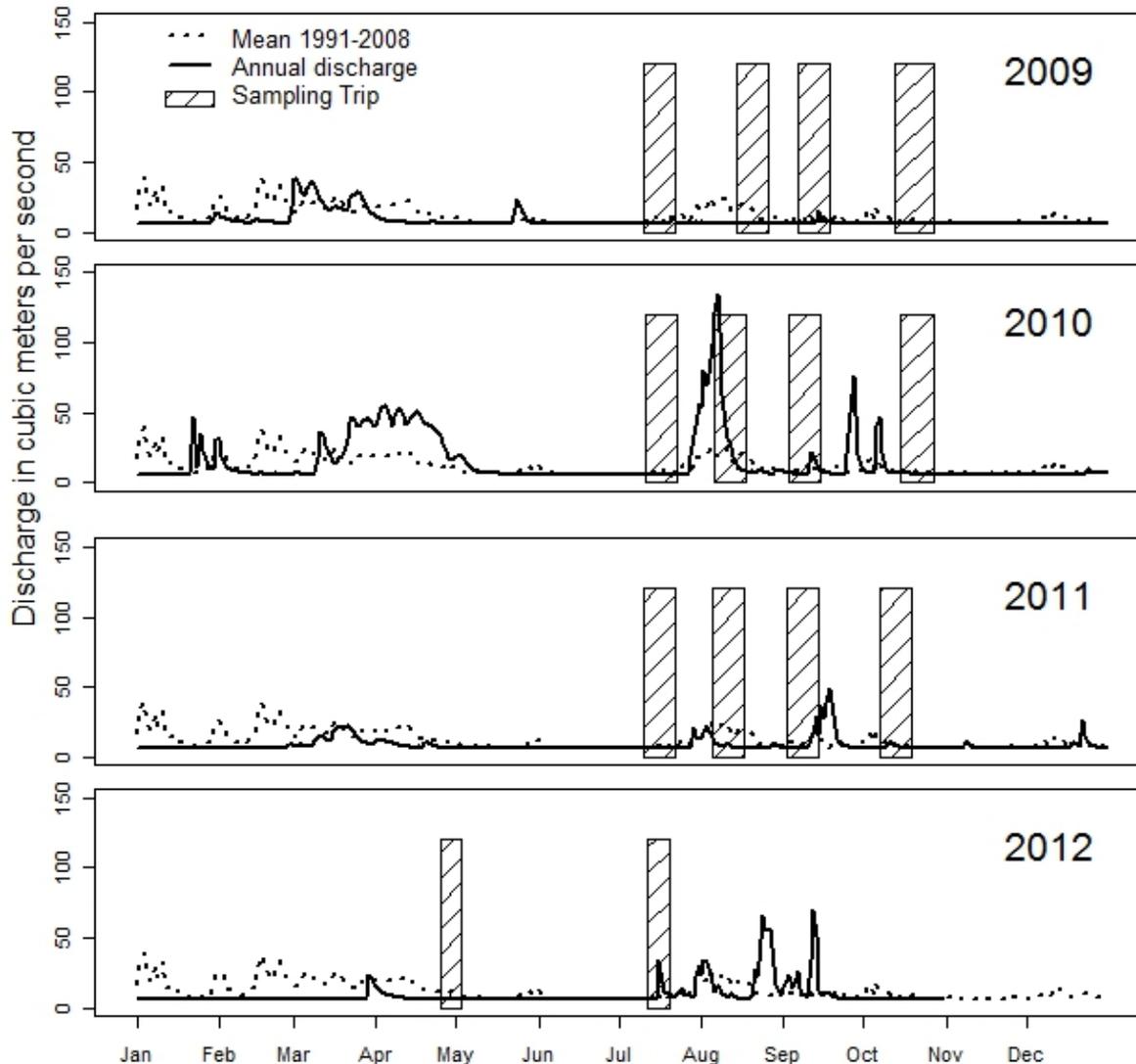


Figure 2-4. Colorado River water temperatures at Lee's Ferry from 1994-2002, 2003-2008, and during this study (July 2009-July 2012; solid gray, dotted gray, and black lines, respectively), with a model of pre-Glen Canyon Dam historical temperatures (dashed gray line). Gray lines are mean temperatures, while black line represents actual annual temperatures Data from USGS instantaneous data archive. Available: <http://nwis.waterdata.usgs.gov/nwis>

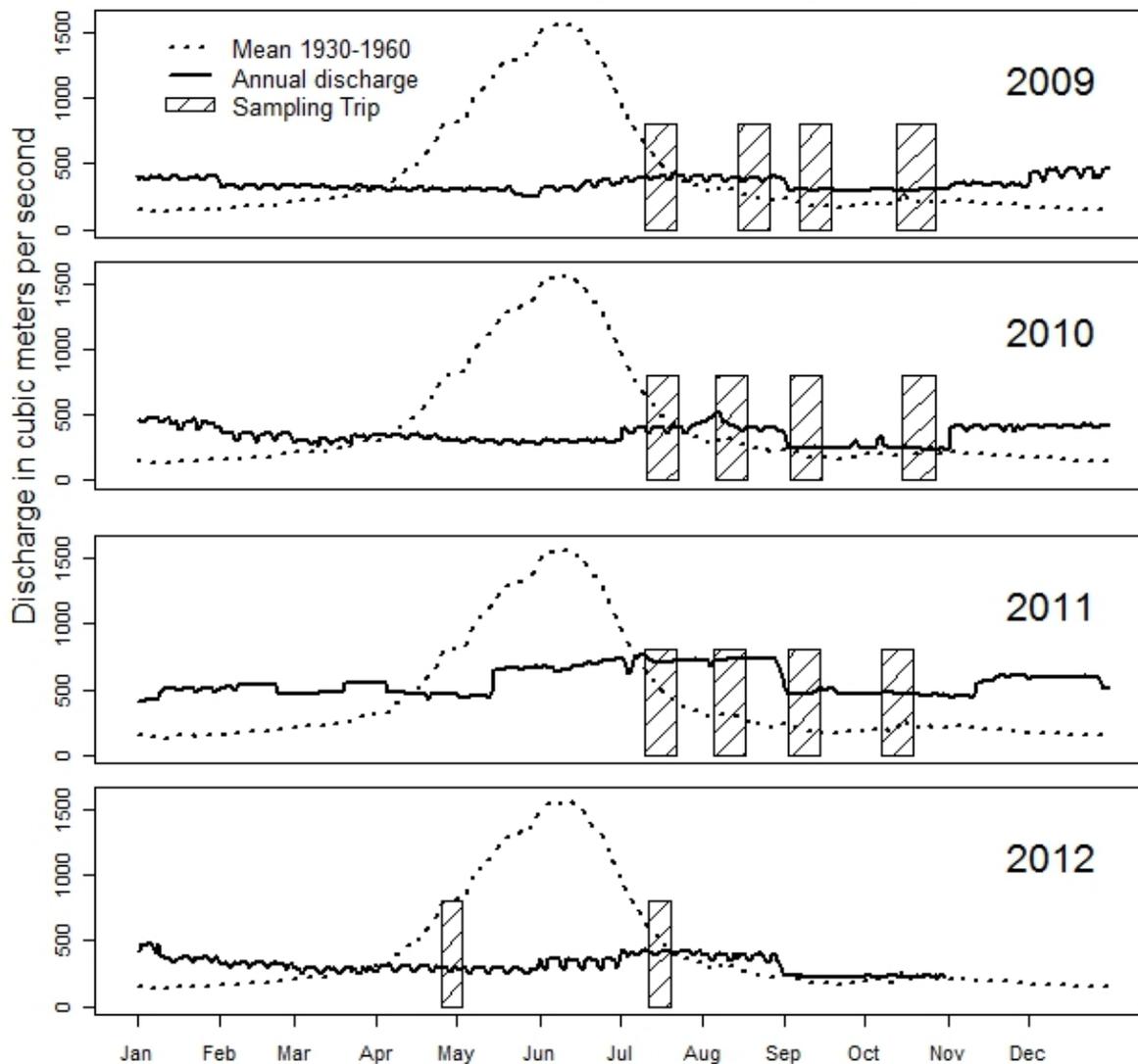
LCR discharge, with sampling calendar



USGS discharge measurements from LCR-COR confluence, <http://waterdata.usgs.gov/az/nwis/rt>

Figure 2-5. Daily discharge in the Little Colorado River near the confluence with the Colorado River over the three-year period of this study (2009-2012). Sampling periods are represented by the diagonally striped boxes. Data from USGS discharge gauge 09402300. Available: <http://nwis.waterdata.usgs.gov/nwis>

Colorado River discharge, with sampling calendar



USGS discharge measurements from Phantom Ranch gauge, <http://waterdata.usgs.gov/az/nwis/rt>

Figure 2-6. Sampling calendar. Steady flow experiments occurred in September and October in the years 2009, 2010, and 2012 (not studied), as well as April-November 2011. Discharge data available at <http://waterdata.usgs.gov/az/nwis/rt>

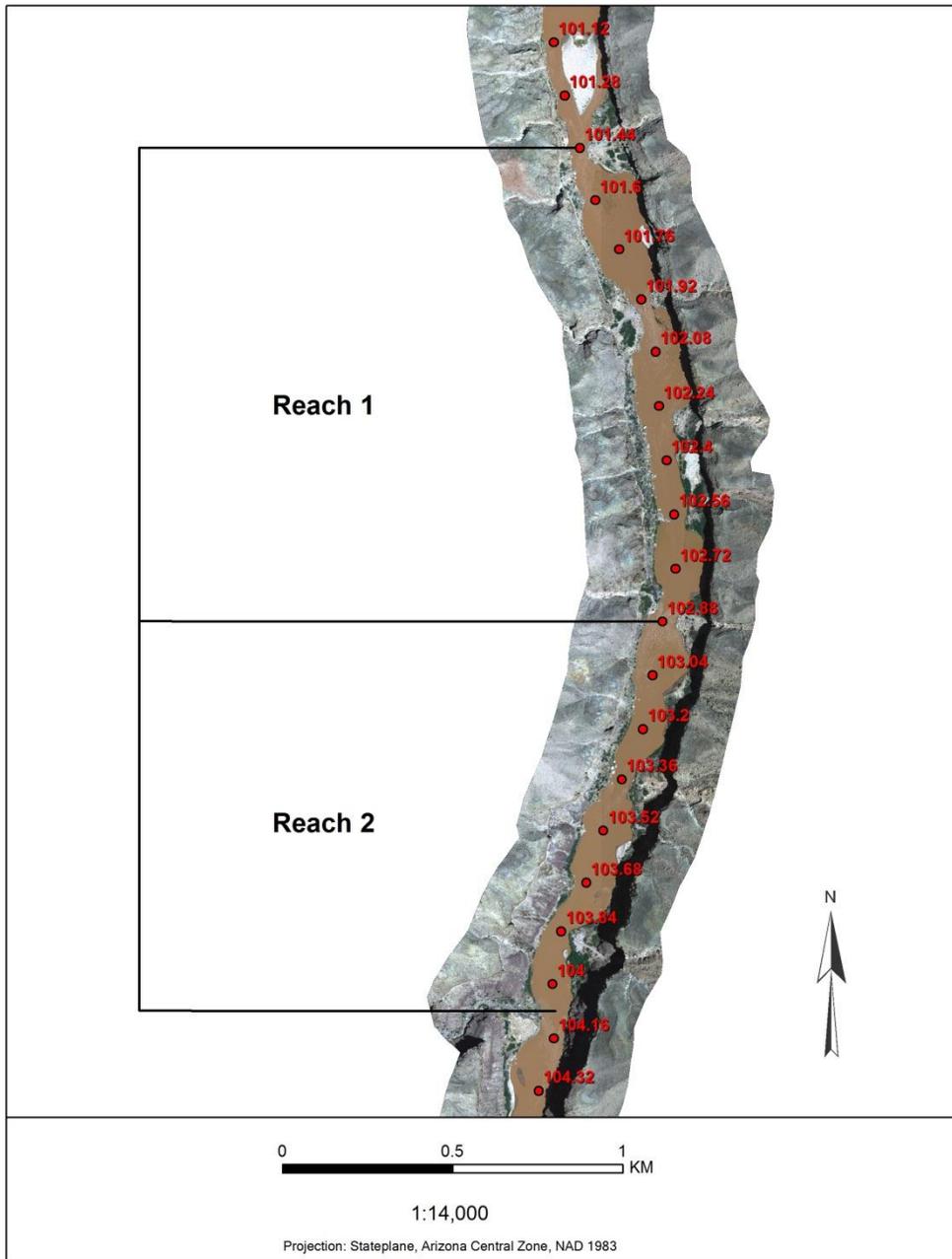


Figure 2-7. Detail map of study area. Distances from Lee's Ferry are denoted in kilometers. All available shoreline (excludes rapids) were electrofished in all trips. Hoop effort increased through the study: Site 1 contained 47 hoops on trip 1, 60 hoops on trips 2-12, and 45 hoops on trips 13 and 14, deployed across habitat types according to their availability. Site 2 contained no hoops on trips 1-6, 20 hoops on the upper half on trips 7-12, and 45 hoops on trips 13 and 14, also deployed across habitat types according to their availability.

Jul-Aug HBC growth, Colorado River

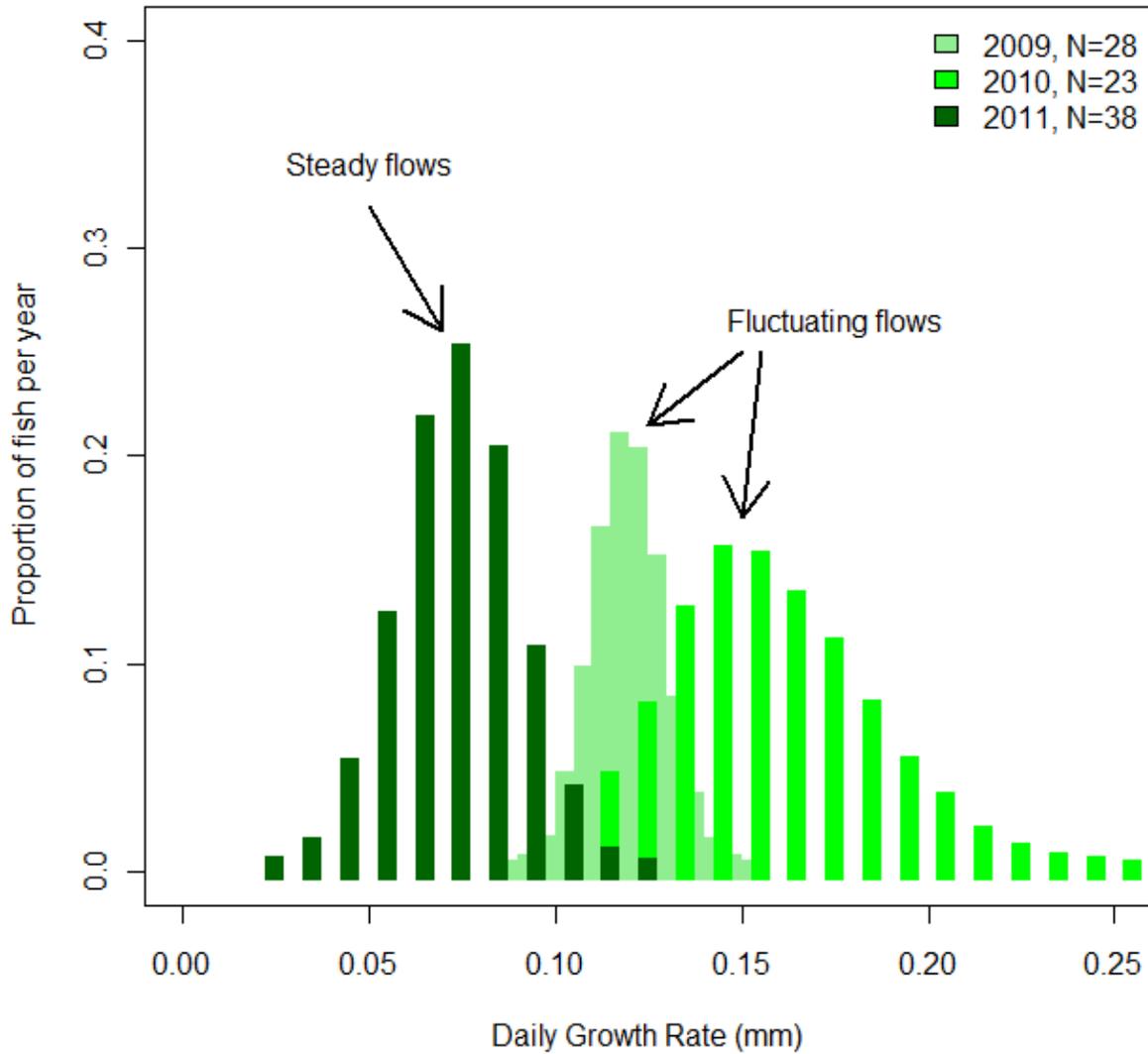


Figure 2-8. Distributions of the mean daily growth rates for juvenile humpback chub (100-200 mm total length) in the mainstem Colorado River between July and August; 10,000-iteration bootstrap resamples with replacement.

Sep-Oct HBC growth, Colorado River

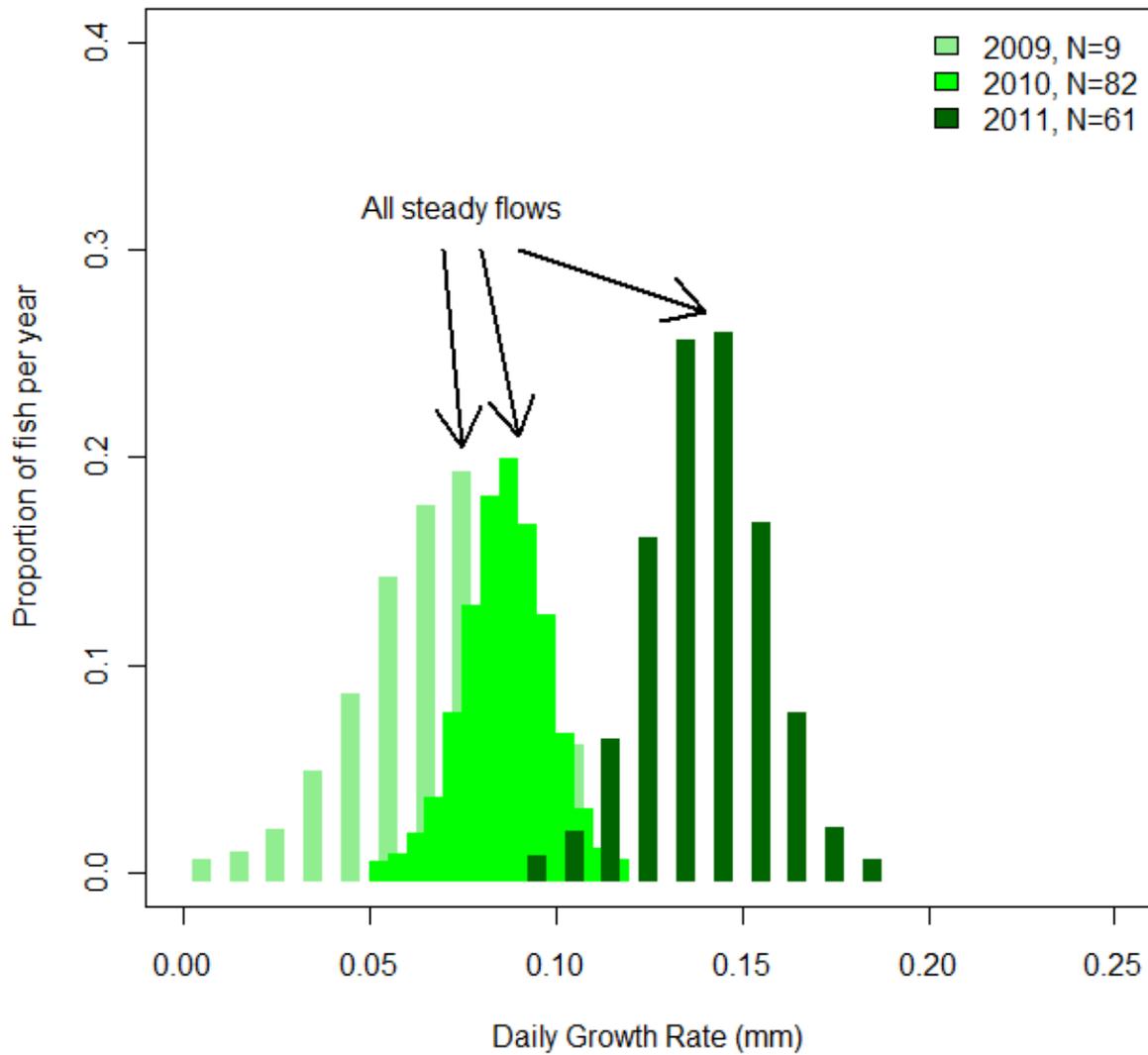


Figure 2-9. Distributions of the mean daily growth rates for juvenile humpback chub (100-200 mm total length) in the mainstem Colorado River between September and October; 10,000-iteration bootstrap resamples with replacement.

Jul-Aug-Sep HBC growth, Little Colorado River

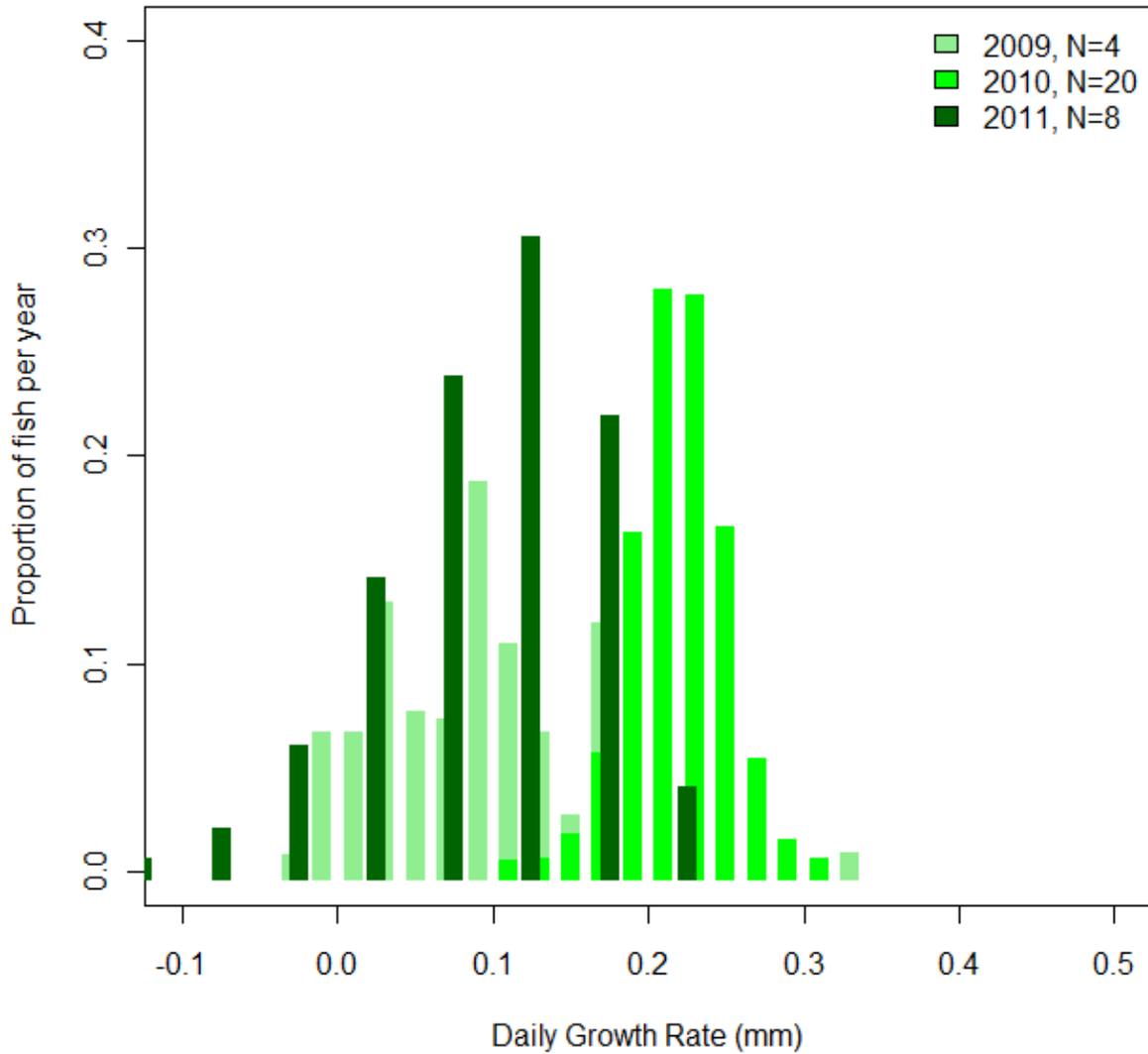


Figure 2-10. Distributions of the mean daily growth rates for juvenile humpback chub (100-200 mm total length) in the Little Colorado River between July and August or September; 10,000-iteration bootstrap resamples with replacement.

Sep-Oct HBC growth, Little Colorado River

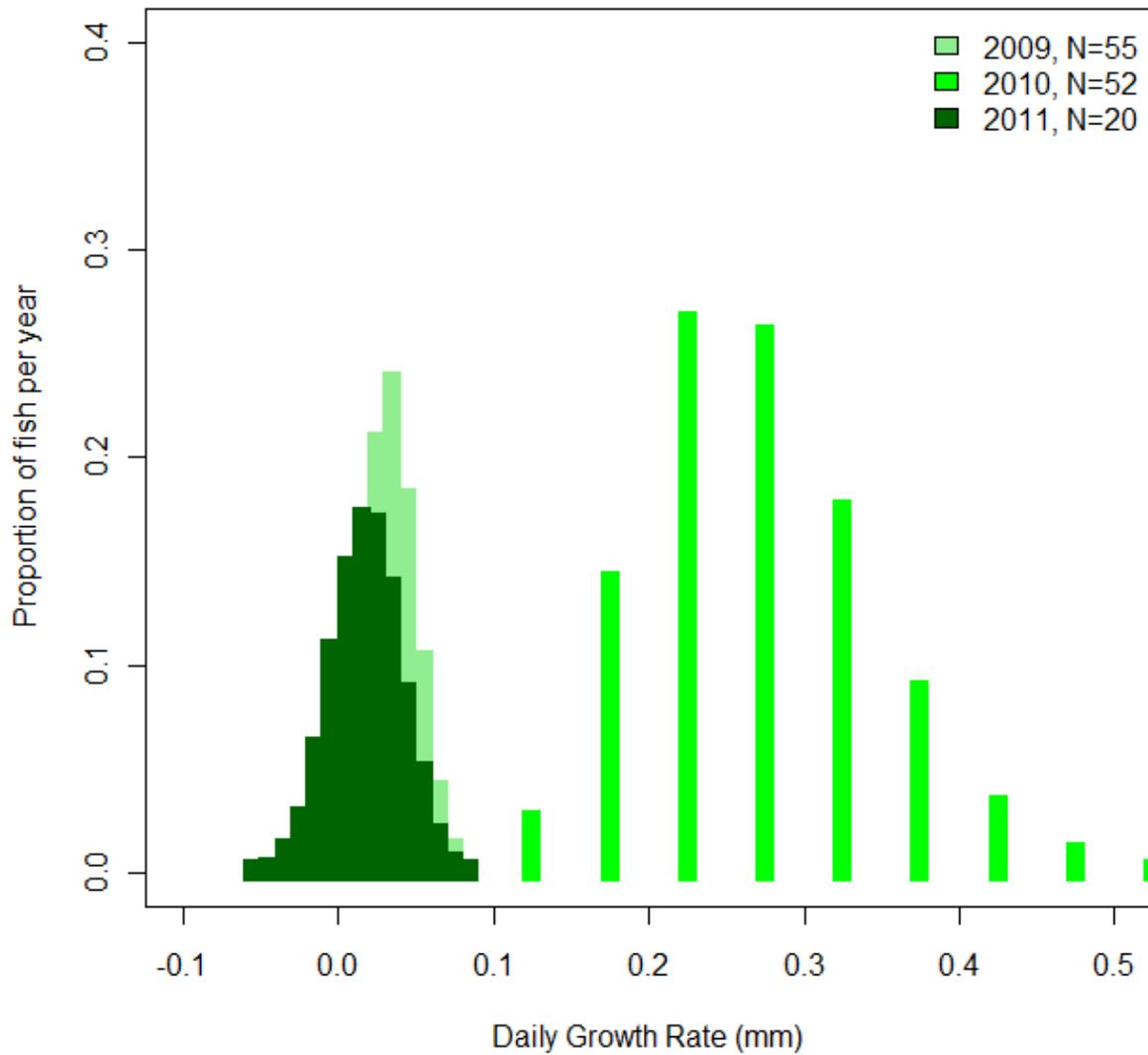


Figure 2-11. Distributions of the mean daily growth rates for juvenile humpback chub (100-200 mm total length) in the Little Colorado River between September and October; 10,000-iteration bootstrap resamples with replacement.

CHAPTER 3 ARTIFICIAL DISCHARGE FLUCTUATIONS AND JUVENILE FISH SURVIVAL RATES

Introduction

In over half the world's large river systems, river flows are regulated by mainstem dams (WCD 2000). These structures modify flow in riverine ecosystems by storing water in upstream reservoirs and regulating water releases downstream that can facilitate shipping, power production, irrigation, or provide protection to communities by attenuating floods (WCD 2000, Poff et al. 2006, Richter and Thomas 2007). The dams and the ecosystems they create (reservoirs) and modify (rivers) vary hugely in size from small run-of-the-river reservoirs to immense, canyon-bound reservoirs that can store several years of mean annual flow (Christensen et al. 2004, Anderson and Woosely 2005, Blinn and Poff 2005, Nilsson et al. 2005). While regulated rivers are found across the gamut of world climates, temperatures, and elevations, ecosystem changes that occur following dam construction and river modification are similar and widespread in terms of physical and ecological trade-offs compared to unregulated rivers. These changes include sequestration of woody debris and sediment in upstream reservoirs (Stanford and Ward 1991, Kearsley et al. 1994, Schmidt et al. 1998), altered trophic dynamics (Stevens et al. 1997, Kennedy and Gloss 2005), novel fish community composition including introduction of non-native species (Mueller and Marsh 2002, Gloss and Coggins 2005, Coggins et al. 2011), modified thermal regime (Stanford and Ward 1991, Clarkson and Childs 2000), and timing, magnitude, and frequency of floods with associated connectivity to floodplain habitat in rivers below dams (Poff et al. 1997, Lovich and Melis 2007, Dutterer et al. 2012).

Optimizing dam operations to minimize ecological and physical impacts to riverine environments while simultaneously meeting anthropogenic needs from the river ecosystem is often a common goal of water managers (Anderson and Woosely 2005, Richter and Thomas 2007), although the balance can be difficult to achieve in heavily utilized river systems. For instance, the Colorado River in the western United States is identified as the “most legislated, most debated, and most litigated river in the entire world. It has more people, more industry, and a more significant economy dependent on it than any comparable river in the world” (Reisner 1986). This riverine ecosystem, including the UNESCO recognized reach in Grand Canyon National Park, is highly altered due to flow modifications from numerous dams and water diversion projects. In an attempt to mitigate detrimental effects of river regulation in the Grand Canyon reach of the Colorado River, the Glen Canyon Dam Adaptive Management Program (GCD AMP) was developed and instituted based on principles of adaptive management (Walters and Hilborn 1978, Walters and Holling 1990) with a commission to monitor, preserve, and restore the downstream ecosystem in Grand Canyon.

Because of the multi-year water storage capacity in Lake Powell and the regulatory structure of the GCD AMP, a unique opportunity exists in the Grand Canyon reach of the Colorado River to experimentally assess various flow policies and identify those which simultaneously benefit the riverine ecosystem while meeting power and water needs of human users. As an example, if flow policies could be experimentally identified that create mainstem Colorado River conditions conducive to improving the population status of the imperiled native fish community without precluding hydropower production, water supply, or recreation, this information would be invaluable to

managers of Glen Canyon Dam. The Endangered Species Act, the Grand Canyon Protection Act, the “Law of the River” (USBR 2012), and stakeholder interest groups are all considered under the auspices of the GCD AMP, and optimizing dam discharges to satisfy legal and social requirements is the principal goal of these unique ecosystem-level experimental flow policies.

One specific focus of GCD AMP is population recovery of humpback chub *Gila cypha*, a large-bodied, morphologically distinct minnow endemic to the Colorado River basin (for additional references see Goulet and LaGory 2009). Humpback chub are currently federally listed (Endangered) under the Endangered Species Act. The exact reason for declines in humpback chub populations in Grand Canyon (and elsewhere in the Colorado River) are unknown but generally include: (1) negative interactions with non-native fish, (2) loss of essential habitats due to flow, temperature, and sediment input modifications, and (3) non-native parasites (Minckley 1991, Valdez and Ryel 1997). Most of the remaining humpback chub live near the confluence of the Colorado River and the Little Colorado River, the largest tributary within Grand Canyon (Figure 2-1). Adult humpback chub migrate from the Colorado River to the Little Colorado River (LCR) in spring to spawn. Successful reproduction of this warm-water species can then occur because the thermal regime of the LCR resembles the pre-dam Colorado River (Kaeding and Zimmerman 1983, Douglas and Marsh 1996, Gorman and Stone 1999). Young humpback chub then rear in the Little Colorado River or disperse into the mainstem Colorado River, where they encounter daily fluctuations in discharge, seasonally colder temperatures due to hypolimnetic dam releases, and higher numbers

of nonnative fish than in the Little Colorado River (Kaeding and Zimmerman 1983, Valdez and Ryel 1997, Paukert et al. 2006).

Although much is known about life history and vital rates of adult humpback chub, there is a paucity of data available on young-of-year and juvenile humpback chub in the Colorado River system. Resolving this data gap is critical to humpback chub recovery because recruitment to adulthood is likely impeded by low survival of juveniles. To date, most inferences on juvenile humpback chub abundance and survival are indirect, and come from estimating the number of juveniles alive in a given year from the number of age-4+ adults found in future years. For example, the number of recruits in 2005 would be estimated by first determining the number of age-4 fish in 2009 and then back-calculating how many recruits had to be present in 2005 (with assumptions about survival rates in each year) to have produced that number of age-4 adults (Coggins et al. 2006b). A key shortcoming in this approach is the long time lag between management actions and information on juvenile fish response, and the possibility that the response (positive or negative) in the number of fish occurred at any time during the four year lag period. This type of reconstruction was necessary because contemporary sampling techniques and monitoring activities did not capture or mark sufficient numbers of juvenile humpback chub to draw inference on their abundance or survival rates directly.

Despite limited data on young humpback chub, many current management actions (e.g., mechanical removal of trout, experimental discharges, artificial floods to build sandbar and backwater habitat) are designed to benefit the juvenile life stage because juvenile fish are generally more sensitive than adult fish to predation (Ward

and Bonar 2003), cold water temperatures and thermal shock (Clarkson and Childs 2000, Robinson and Childs 2001, Ward and Bonar 2003), and flow variation (Scheidegger and Bain 1995). Predator removal is still inconclusive (Coggins et al. 2011), and a temperature control device has not been constructed, so current attempts to improve vital rates of juvenile humpback chub has culminated in an ecosystem-scale discharge experiment in Grand Canyon.

Hydropower is produced at Glen Canyon Dam to match diel fluctuations in power demand across the southwest United States by increasing and decreasing discharges through the turbines as power demand goes up and down (Hughes 1991, Figure 2-2). These regular, rapid changes in discharge resemble ocean tides (Fisher and LaVoy 1972), and are unnatural in the Colorado River (notable exceptions being snowmelt-dominated headwater streams which rise and fall with daily temperatures, and the delta at the Gulf of California, Mexico). Fish are known to exhibit lateral movements during fluctuating discharges (Bunt et al. 1999) that can increase displacement and energetic costs of larval and juvenile fish (Scheidegger and Bain 1995, Korman and Campana 2009) or expose them to predation due to forced movement from refuge habitat (Werner et al. 1983, Bain et al. 1988, Walters and Juanez 1993). In contrast, steady flows can produce localized warming of water in low-angle habitats and improve growth of juvenile fish (Korman et al. 2006), which is closely tied to survival (Rice et al. 1993, Houde 1997, Lorenzen 2006). To determine if discharge fluctuations affect survival of juvenile humpback chub, GCD AMP implemented a series of steady flow experiments during September and October 2008-2012. In this analysis I evaluate the effects of these annual steady flows over a three-year period (2009-2012, Figure 2-6) to determine

what, if any, effects flow has on apparent survival rates of juvenile humpback chub. This analysis is part of the broader “Nearshore Ecology” (NSE, Pine et al. 2009) study funded to study the habitat use, abundance, and vital rates of juvenile humpback chub within the LCR aggregation.

Methods

Study Site

The Grand Canyon reach of the Colorado River is the roughly 400 km river section bounded downstream by Lake Mead and upstream by Lake Powell, the first and second largest reservoirs in the United States, respectively (Andrews 1991). This river reach is contained within the borders of Grand Canyon National Park, is designated a UNESCO world heritage site, and is recognized as a US and international region of cultural, geologic, and biological significance under the Grand Canyon Protection Act of 1992. Humpback chub are distributed throughout the Grand Canyon reach of the Colorado River in eight distinct aggregations. The LCR aggregation occupies the lower 15 km of the LCR and the associated inflow reach of the Colorado River and contains roughly 95% of the adult humpback chub still found in the lower Colorado River basin (Douglas and Marsh 1996, Valdez and Ryel 1997, Coggins et al. 2006a). This section of the Colorado River is designated by distances below the Lee’s Ferry, hereafter referred to as river kilometers (rkm). I sampled a portion of the LCR aggregation of humpback chub from rkm 102.1 to 104.7, below the confluence of the Colorado and Little Colorado Rivers, which I will refer to as the NSE reach. Although I did sample through to rkm 106.1 as part of the overall NSE study, I did not sample the lower third with all gears or in all years, so it was excluded from this analysis.

Sampling Techniques

I subdivided the portion from rkm 102.1 to 104.7 into two sites approximately 1000-m in length (Figure 2-7), which were further subdivided into 25-m habitat sub-units to provide a spatially referenced location for all sampling efforts. I sampled both sites in July, August, September, and October for 12 days for 2009-2011. The July and August samples from 2009-2010 represented typical fluctuating hydropower flows, while September and October samples from 2009-2011 were conducted during the fall steady flow experiments (Figures 2-2 and 2-6). Previously unplanned high steady dam discharges occurred during July and August 2011 as a result of required equalization flows between lakes Powell and Mead (Figure 3-1, see discussion). During 2012 I sampled for nine days in both April and July during typical fluctuating flows.

I used two gear types to sample the fish community, 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 hour intervals) and boat electrofishing (pulsed DC current at 15-20 amps, 200-300 volts, 7-10 seconds per meter of shoreline, repeated 24 to 72 hours apart for three passes per trip). Pilot sampling in July 2009 included 48 hoops in the upstream site which expanded to 60 hoops in Aug-Oct. Hoopnet efforts further expanded to include 80 hoops (60 in the upper site, rkm 102.1 to 103.5, and 20 in the lower site, rkm 103.6 to 104.7) in 2010 and 2011. Hoopnet efforts in 2012 included 90 hoops, and were spread more evenly across both sites, with 45 hoops in each (Figure 2-7). All available shoreline areas in both sites were electrofished during all sampling trips following guidelines in Korman and Campana (2009), which targets small fish with emphasis on maintaining slow boat speeds of 7-10 sec/m of shoreline.

Following capture, I measured, tagged, and released humpback chub in the same location where they were captured. Individual humpback chub between 40 and 100 mm total length (TL) were given batch marks using visible implant elastomer (VIE, Northwest Marine Technologies). These elastomer batch marks were identifiable to trip number, gear, and site. On subsequent recapture, if the humpback chub was still <100 mm TL, it was given an additional VIE batch tag coded according to that respective trip number, gear, and site. Any humpback chub >100 mm TL received a 134.2 kHz passive integrated transponder (PIT) tag (9-mm long, BIOMARK) with a unique number identifiable to individual fish rather than an additional VIE tag. This analysis only includes humpback chub that received VIE tags (40-100 mm TL) when they were first captured (Figure 3-2). When humpback chub were next captured above 100 mm TL and received a PIT tag, they were considered removed from the study population.

Data Analysis

In mark-recapture experiments it is possible to have confounded apparent survival rate 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, low capture probability). Because I was concerned that capture probabilities may be low, thus increasing the risk of confounded apparent survival estimates, I used simulated data to assess the accuracy of the Cormack-Jolly-Seber model ("CJS", Lebreton et al. 1992) for later use in my analyses. In this way I could determine whether accuracy of the model I planned to use from data with known survival and capture probability rates. I used GENCAPH1 (<http://www.mbr-pwrc.usgs.gov/software/gencaph1.shtml>) to generate mark-recapture datasets from virtual populations with known survival rates and capture probabilities and with similar sample sizes to my real data, and then

exported this data to Program MARK for analysis. I evaluated the efficacy of MARK at returning precise and accurate estimates under the various simulation scenarios (designed to mimic possible effects of flow treatments) and used these simulations to determine the accuracy of the apparent survival estimates that I would later derive from field data using MARK. I also performed a power assessment of the simulations to predict my ability to detect changes in the real data should they occur.

After I generated simulated data, I fit the recaptures only (CJS) model based on field data using program MARK (<http://warnercnr.colostate.edu/~gwhite/mark/mark.htm>). This model estimates two parameters: (1) capture probability on a given trip and (2) apparent survival for the interval between trips. Input data consisted of binary coded capture histories that were equal in length to the number of sampling events (n=14). For example, a fish that was captured on the second trip and then not seen until the tenth trip and eleventh trips would have capture history "01000000011000". Multiple within-trip recaptures were ignored in this analysis, both to avoid double-counting VIE marked fish (that could not be distinguished from each other as a result of batch marking) and to preserve the requisite binary nature of inputs for the recaptures-only MARK model (Table 3-1). The basic assumptions of the CJS model are (1) all individuals in the population (both marked and unmarked) have the same probability of capture, (2) all marked individuals have the same probability of dying or permanently emigrating, (3) tags do not increase the probability of death, and (4) tags are not lost or overlooked.

I developed a suite of *a priori* models to test hypotheses about the probable effects of the annual steady flow experiments. These models were based on biologically relevant hypotheses about humpback chub behavior coupled with discharge

information, and were constructed to consider apparent survival and capture probability as they relate to flow, a modified version of flow to include transition periods (see Model 4, below), year, the interaction of flow and year, time-dependent, or as constant rates across the study period, for a total of 36 possible models (Table 3-2). In order to derive *annual* apparent survival rates and because each sampling event spanned 12 days, I calibrated sampling intervals in MARK as fractions of a year. These intervals spanned from the average date of capture for humpback chub in a given trip to the average date of capture for humpback chub on the next trip. Models were selected by reviewing the most parsimonious and biologically reasonable model that also had AIC_c support. Models with ΔAIC_c scores less than four units from the top model were considered strongly supported with limited ability to separate inference (Burnham and Anderson 2002). Models with ΔAIC_c scores between four and six units from the top model were considered moderately supported by the data, and models with ΔAIC_c greater than six were considered poorly supported. Here I will further discuss the top five performing models according to these model selection criteria.

The annual model (Model 1) considers separate parameters for apparent survival for each “fish year”; July 2009-July 2010, July 2010-July 2011, and July 2011-July 2012. Capture probability is estimated by time (uniquely estimated for each trip). This model has three parameters for apparent survival and 13 parameters for capture probability.

The flow model (Model 2) has two parameters for survival; one for each flow treatment type (steady or fluctuating flow, Figure 3-1). This model considers September-October of 2009 and 2010 and July-October 2011 as steady flows, with all other time periods being fluctuating flows. In this model capture probabilities were also assumed to

be time-dependent (uniquely estimated for each trip). This model has two parameters for survival and 13 for capture probability.

The constant apparent survival model (Model 3) was the simplest of the five preferred models and assumes apparent survival is constant across all intervals and that capture probability varies by time. Statistical support for this model would suggest that flow or flow*year associated terms did not improve model fit, but that flow-independent or consistent survival pressures were ubiquitous. The total number of parameters for this model was 14, one for survival and thirteen for time-specific capture probability.

The intermediate flow model (Model 4) adds a third survival parameter to the flow model (Model 2) representing an intermediate flow treatment. This third parameter was for periods between our sampling trips when flows transitioned from steady to fluctuating (September –October of 2009 and 2010, as well as October 2010 – July 2011, Figure 3-1). If any of the different flows have a survival effect, then apparent survival rates during transition time intervals would likely be intermediate because flows were roughly half-fluctuating and half-steady during these intervals. However, since we did not sample across these transition periods, we cannot separate the effects of steady versus fluctuating flows from each other, but instead must model a third rate that estimates apparent survival during the transition period. In this model capture probabilities were also assumed to be time-dependent. This model has three parameters for apparent survival and 13 for capture probability, making 16 total parameters.

With a flow-year model (Model 5) I attempted to separate effects of flow and years by starting with Model 2 and then adding a third apparent survival parameter that considers 2011 separate from 2009 and 2010 estimates. This is because river flows during 2011 were substantially different than 2009 and 2010 with relatively high, but steady flows during July and August, and lower, but still steady flows in September and October. In this model capture probabilities were assumed to be time-dependent. There were three parameters for apparent survival and 13 for capture probability, making 16 total parameters.

Results

Simulation Results

My simulation results demonstrate that the CJS model accurately estimated apparent survival and capture probability across the range of simulated data sets I fit to this model. A key result of these simulations is that the model can generally only fit the data when “replicates” of the flow treatments are included. For example, this is where apparent survival estimates are made based on shared data across annual, seasonal, or flow treatment designated repeated samples. Across all cases, models where apparent survival is estimated independently for each time interval did not converge.

In the first simulation I held capture probability constant and varied survival, and vice versa. I manipulated annual survival from 80-98%, and capture probability from 5-30% using both upward and downward trends (the $\Phi(\cdot) p(t)$ and the $\Phi(t) p(\cdot)$ models in MARK, Figure 3-3). This simulation demonstrates that MARK is able to derive accurate estimates of apparent survival even if capture probability fluctuates widely (5% to 30% capture probability), but only when apparent survival is constant. When apparent survival is estimated independently for each sampling event (no annual replicates), the

potential confounding effects of capture probability and apparent survival become evident and the model estimates do not converge or rapidly lose statistical precision (no confidence intervals or wide confidence intervals, respectively, Figure 3-3).

In the second simulation, I increased survival and capture probability together, and decreased them together. I then attempted to estimate unique apparent survival and capture probability estimates for each time step (a $\Phi(t)$ $p(t)$ model, Figure 3-4). This model performed poorly by failing to accurately estimate apparent survival and capture probability when they both varied in the same way and when they were both estimated at every time step. This simulation model does not allow replicates (i.e. the same flow type, but shared across multiple years from real data), but rather estimates unique values for all parameters during all sampling periods and over-parameterizes the model. The failure of this model reinforces the need to repeat experimental treatments if recapture data are sparse (Table 3-1).

In the third simulation I mimicked flow-dependent increases or decreases in apparent survival, with upward and downward trends in capture probability ($\Phi(\text{flow})$ $p(t)$ model, Figure 3-5). This simulation demonstrates that no matter the direction of change in survival rates due to flow conditions, MARK is able to accurately distinguish between apparent survival and capture probability because treatments were grouped across years as annual replicates. This simulation also demonstrates the MARK can detect changes when capture probability changes by 5% or more, as well as changes in annual apparent survival rates as small as 10% if those changes occur after a suitable marked population is present.

For the last simulation I modeled survival as being either constant or flow-dependent, and capture probability as being flow-dependent ($\Phi(\cdot)$ $p(\text{flow})$ and $\Phi(\text{flow})$ $p(\text{flow})$ models, Figure 3-6). This last model demonstrates that Program MARK still produces accurate estimates of apparent survival when survival and capture probability are proportionally confounded by flow treatment, as long as the experimental replicates are allowed. However, the simulation demonstrates that if capture probability varies in the same direction and proportion as apparent survival rate (i.e. as a result of flow treatments), that apparent survival may need to vary by as much as 30% in order for the model to actually detect the change.

Flow effects and Juvenile Humpback Chub Apparent Survival

After fitting the 36 possible models for apparent survival and capture probability described above to field data, the three best fitting models were differentiated by less than three ΔAIC_c points, making them quantitatively inseparable based on my model selection criteria. The next two models differed by less than five ΔAIC_c points, indicating moderate quantitative support. The remaining models were over 95 ΔAIC_c points from the top model (22 models) or did not converge upon estimates and were unreliable (9 models, Table 3-2).

All five top models estimated capture probability by time (Figure 3-7). This result is not surprising given the variation in discharge across all 14 trips (Figure 3-3). Importantly, estimates of capture probability are specific to Nearshore Ecology trips, as opposed to gear and pass-specific estimates. This is because I considered a unit of effort to be our combined electrofishing and hoopnet sampling, and because I excluded multiple within-trip recaptures of the same individuals due to the deficiencies of batch-

marking methods. Gear-specific capture probability estimates are preferred, but recapture data is currently too sparse. As a result these capture probabilities are not directly transmissible to other sampling scenarios unless they incorporate similar arrays of gears and effort.

The model estimating unique apparent survival rates according to “fish-year” (with time-dependent capture probability) had the most quantitative support (Model 1). This model indicates that the 95% confidence intervals for apparent survival from July 2009-July 2010 and July 2010-July 2011 were 58-71% and 57-75%, respectively (Figure 3-8). The fish year from July 2011-July 2012 had lower survival, with 95% confidence intervals of 28-54%. Capture probability estimates varied from 9-25% per NSE trip (multiple passes of both electrofishing and hoopnets, Figure 3-7).

The model estimating two apparent survival rates, one for fluctuating flows and one for steady flows (Model 2), had a ΔAIC_c score of 2.7. Modeled 95% confidence intervals for apparent survival during fluctuating flows and steady flows were 59-78% and 16-65%, respectively (Figure 3-9). Capture probability estimates varied according to sample interval as previously discussed and ranged from 9-26% (Figure 3-7).

The next highest performing model estimated a constant apparent survival rate across the entire sampling period (Model 3), with capture probability estimated by time. Apparent survival 95% confidence intervals ranged from 59-67% (Figure 3-10), with capture probability estimates from 9-25% (Figure 3-7). Quantitative support for this model was 2.8 ΔAIC_c points behind the top model.

The fourth of the five top-performing models (Model 4) estimated three apparent survival rates; one for fluctuating flows, one for steady flows, and one for the intervals

between sampling trips where flows were neither fluctuating nor steady, but both. The 95% confidence intervals of those estimates were 57-77%, 13-61%, and 54-88%, respectively. Capture probability estimates ranged from 9-26%.

The last model (Model 5) attempted to distinguish between flow effects and the potential effects of an unplanned and anomalous 2011 discharge year. This model considers separate apparent survival rates during fluctuating flows, during steady flows of 2009 and 2010, and then considers high steady flows of 2011 separately. The apparent survival 95% confidence intervals were 56-77%, 10-86%, and 11-63%, respectively. Capture probability ranged from 9-25%, still estimated uniquely for each NSE-style trip.

Discussion

The 2009-2011 fall steady flow experiment from Glen Canyon Dam did not change the apparent survival rate of juvenile humpback chub compared to fluctuating flow operations. Models that estimated apparent survival by flow treatments (e.g. steady versus fluctuating dam releases) were indistinguishable based on my model selection criteria. Estimates of apparent survival within flow treatments all had overlapping 95% confidence intervals, and data were not trending toward statistical significance. In addition, the top five models regardless of whether they included flow (annual and constant models) as a factor of apparent survival were all separated by less than five ΔAIC_c points. The lack of contrast in estimates within models coupled with the lack of distinction between models indicates that apparent survival of juvenile humpback chub in Grand Canyon is robust to flow variation of the magnitude that I observed.

The lower rate for apparent survival from July 2011-July 2012 indicated by the annual model (Figure 3-8) is not alarming because the trend is not continuous over the

three-year period. Higher uncertainty is typical of the latter intervals in mark-recapture experiments, as many fish are still of unknown fate (dead versus not observed).

Previous NSE data showed similar trends in annual survival for 2010 when it was the last period sampled; a trend which later improved with the addition of 2011 data. I expect numerical increases in 2011-2012 apparent survival rates as well as improvement in precision of those estimates as juvenile chub sampling (ongoing) continues in the future.

I was concerned about bias that may occur in my estimates of survival due to differences in recapture probability versus capture probability. However, Program MARK uses all future captures of any individual fish to inform previous captures (conditioned on capture), so every additional sampling trip reduces potential bias that stems from individuals avoiding recapture. I ignored recaptures within the same trip, so most recapture data that I used in analyses occurred at least 30 days later, after fish had time to mix and return to normal behavior (i.e., no tagging effects). This is reinforced by the fact that I recaptured 39% (1989 of 5154) of juvenile humpback chub on later sampling trips.

The suite of simulations I performed is an important demonstration of the power of MARK, as it proves that even if you have a large decline in the numbers of recaptured fish during the experimental flow (which I saw in October 2009 in this study), the software can accurately determine if that decline is due to changes in apparent survival or in capture probability (Figures 3-3 through 3-6). These simulations also demonstrate the importance of experimental replicates if sample sizes are limited in order to avoid non-convergence or highly imprecise estimates. Lastly, if the perturbation

that is causing the change in apparent survival also influences capture probability in the same direction and magnitude, annual apparent survival rates may need to change by as much as 30% before Program MARK will return statistically significant results.

Direct estimates of survival of juvenile fish are invaluable to managers of endangered species or sport fisheries. Difficulties in mark-recapture of small fish unfortunately leave those managers with indirect tools to assess and manage survival such as stocking regimens and influencing growth rate to improve survival. Managing dam releases to directly improve survival rates of resident fishes on an ecosystem scale offers a more efficient and simple way to improve the status of the species of interest. Although I did not observe an effect of the flow treatments thus far prescribed in Grand Canyon, I have demonstrated that it is possible to use mark-recapture techniques with juvenile fish that are below the minimum PIT tag size (<100 mm TL) to provide direct and credible vital rate estimates before fish recruit to adulthood. Previous estimates of survival for juvenile humpback chub were back-calculated through recruitment reconstruction as part of the Age-Structured Mark-Recapture model (Coggins et al. 2006b). The ability to directly estimate juvenile survival allows managers to quickly monitor how experimental actions affect vital rates during critical life stages and ultimately move toward humpback chub population recovery.

I have also demonstrated that juvenile humpback chub (<100 mm TL) can survive, overwinter, and grow in the mainstem Colorado River. We observed 30.6% (1579 of 5154) of the juvenile humpback chub that we originally VIE tagged below 100 mm TL grow to PIT tag size (>100 mm TL) over the three year course of this sampling project, while per-trip capture probabilities were 26% or less. Annual apparent survival

rates of the three top models ranged from 37-69% regardless of flows. These models were indistinguishable by ΔAIC_c score, which lends credence to a constant survival rate of 63% as estimated by the constant apparent survival model. Humpback chub of PIT tag size that are still juveniles (100-200 mm TL) would likely survive at even higher rates, which has significant population implications.

Although the steady flows that I observed during 2009-2011 did not result in improvements to vital rates of juvenile humpback chub, this does not suggest that flow variations are unequivocally beneficial or detrimental to native fish populations. A key limitation of this steady flow experiment as designed is that the steady flows occurred during September and October, which were beyond the time period of maximum solar insolation for this reach of Grand Canyon (Yard et al. 2005). Future experimental scenarios could include altering the timing of the fluctuating/steady flow experiments to determine if the lack of change in apparent survival during steady flow periods is a result of the steady flow experiment or seasonal factors. Ideal contrast would be steady flows in July and August when solar insolation, nearshore warming, and primary production potential are highest, with fluctuating flows in September and October. Additional experiments varying the volume of water released during steady flows would also clarify the possible effects of flow modification (less water warms more quickly).

The magnitude of the experimental flow regime compared to the pre-dam environment in which humpback chub evolved is a critical consideration in evaluating juvenile humpback chub responses to this flow experiment. The pre-settlement Colorado River in Grand Canyon generally reached a historical base flow in fall of less than $85 \text{ m}^3/\text{s}$ (Schmidt et al. 2005, Figure 2-4), and stochastic monsoonal precipitation

from the Little Colorado River and other tributaries would sometimes double the river discharge almost instantaneously. During spring and summer runoff, snowmelt-dominated floods peaked at 2400 m³/s on a 2-year frequency (Topping et al. 2003). These 100% changes in instantaneous rate over short periods, to well over 1000% changes in discharge annually, were significant environmental factors which shaped the Colorado River ecosystem in which humpback chub and other native species evolved. During my study period, the maximum annual change in discharge was ten percent of the historical annual fluctuation (Figure 2-4). The tempering of natural annual flow variation due to operation of Glen Canyon Dam has allowed humpback chub, which are flexible in habitat selection (Kaeding and Zimmerman 1983, Stone and Gorman 2006) to be robust to the small scale flow fluctuations observed in this study

Evaluations of ecosystem experiments such as the Nearshore Ecology project are important to successfully directing ecosystem management. The ideological crux of Adaptive Management involves reducing uncertainty about complex ecological systems. My data indicates that steady flows of the magnitude I observed in the Colorado River have no appreciable effect on apparent survival of juvenile humpback chub (no model distinction). This information is invaluable in increasing understanding of the flow-fish relationship as regulated rivers continue to be over-allocated due to population growth, anthropogenic effects of climate change, or even a return to paleoclimate mean discharge (Christensen et al. 2004, Barnett and Pierce 2009). A robust understanding of the relationship between managed flows and life history characteristics of lotic fishes will be necessary to perpetuate the existence of this increasingly imperiled community.

Table 3-1. Capture-recapture summary table of data provided to MARK for analysis.

		Number of fish marked	Recapture trip number												Total	
			2	3	4	5	6	7	8	9	10	11	12	13		14
Marking trip number	1	266	40	37	12	23	12	14	5	7	5	7	3	3	5	173
	2	260		47	20	19	12	15	14	7	4	5	1	1	1	146
	3	235			19	20	19	24	20	5	13	4	4	0	0	128
	4	85				8	9	6	8	2	6	4	0	1	0	44
	5	139					24	29	14	6	8	9	3	0	2	95
	6	218						68	20	5	9	5	1	1	2	111
	7	359							109	22	27	14	6	6	9	193
	8	258								34	34	27	8	6	2	111
	9	139									30	19	12	6	5	72
	10	519										81	33	23	12	149
	11	885											88	75	37	200
	12	478												42	26	68
	13	829													89	89

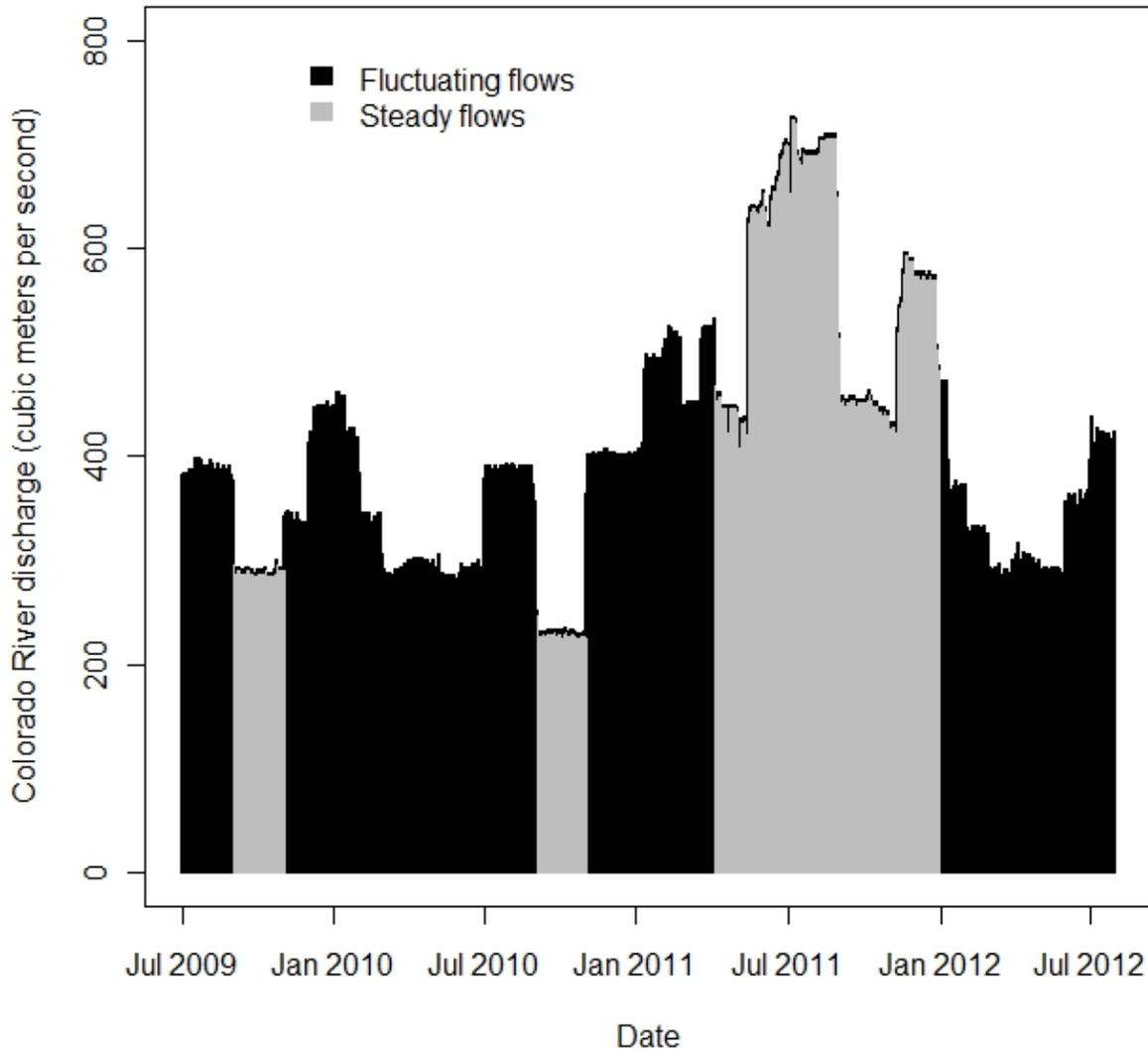
Rows and columns represent corresponding sampling trips. Values represent counts of juvenile humpback chub seen during a given trip (column) that were marked in a previous trip (row).

Table 3-2. Apparent survival models for juvenile humpback chub in Grand Canyon from 2009-2012 ranked by ΔAIC_c score.

Model name	AIC _c	ΔAIC_c	No. Par.
Phi(year) p(t)	9947.1	0.0	16
Phi(flow) p(t)	9949.8	2.7	15
Phi(.) p(t)	9949.9	2.8	14
Phi(mod_flow) p(t)	9951.2	4.1	16
Phi(year*flow) p(t)	9951.5	4.4	16
Phi(year) p(year)	10042.9	95.9	6
Phi(year*flow) p(flow)	10061.9	114.8	5
Phi(year) p(mod_flow)	10062.9	115.8	6
Phi(year*flow) p(mod_flow)	10063.8	116.7	6
Phi(year) p(year*flow)	10066.5	119.4	6
Phi(year) p(.)	10067.2	120.1	4
Phi(year) p(flow)	10067.5	120.4	5
Phi(mod_flow) p(year)	10078.5	131.4	6
Phi(mod_flow) p(flow)	10079.9	132.8	5
Phi(flow) p(mod_flow)	10080.8	133.7	5
Phi(.) p(year)	10080.8	133.7	4
Phi(mod_flow) p(mod_flow)	10081.9	134.8	6
Phi(flow) p(year)	10082.0	135.0	5
Phi(.) p(mod_flow)	10101.3	154.2	4
Phi(mod_flow) p(year*flow)	10118.2	171.1	6
Phi(flow) p(year*flow)	10121.3	174.2	5
Phi(flow) p(flow)	10123.3	176.2	4
Phi(mod_flow) p(.)	10142.1	195.0	4
Phi(flow) p(.)	10149.9	202.8	3
Phi(.) p(year*flow)	10151.1	204.0	4
Phi(.) p(flow)	10155.0	207.9	3
Phi(.) p(.)	10158.2	211.1	2
Models with non-convergence			
Phi(t) p(t)	9950.3	3.2	26
Phi(t) p(year)	10016.7	69.6	16
Phi(t) p(flow)	10019.2	72.1	15
Phi(t) p(mod_flow)	10020.2	73.1	16
Phi(t) p(.)	10026.7	79.6	14
Phi(t) p(year*flow)	10029.7	82.6	16
Phi(year*flow) p(year)	10071.5	124.4	6
Phi(year*flow) p(year*flow)	10088.1	141.0	6
Phi(year*flow) p(.)	10099.8	152.7	4

Model parameter estimation is symbolized as follows: constant (.), time-dependent (t), fish-year (year), flow-dependent (flow), modified flow-dependent (mod_flow), and year-flow interaction (year*flow).

Flow treatment calendar



USGS discharge measurements from Phantom Ranch gauge, <http://waterdata.usgs.gov/az/nwis/rt>
Figure 3-1. Colorado River mainstem flow treatments over the course of this study (July 2009-July 2012). Black areas represent discharges that fluctuated daily according to hydropower demands, while gray represents discharges that were held experimentally steady.

Length-frequency histogram of juvenile humpback chub

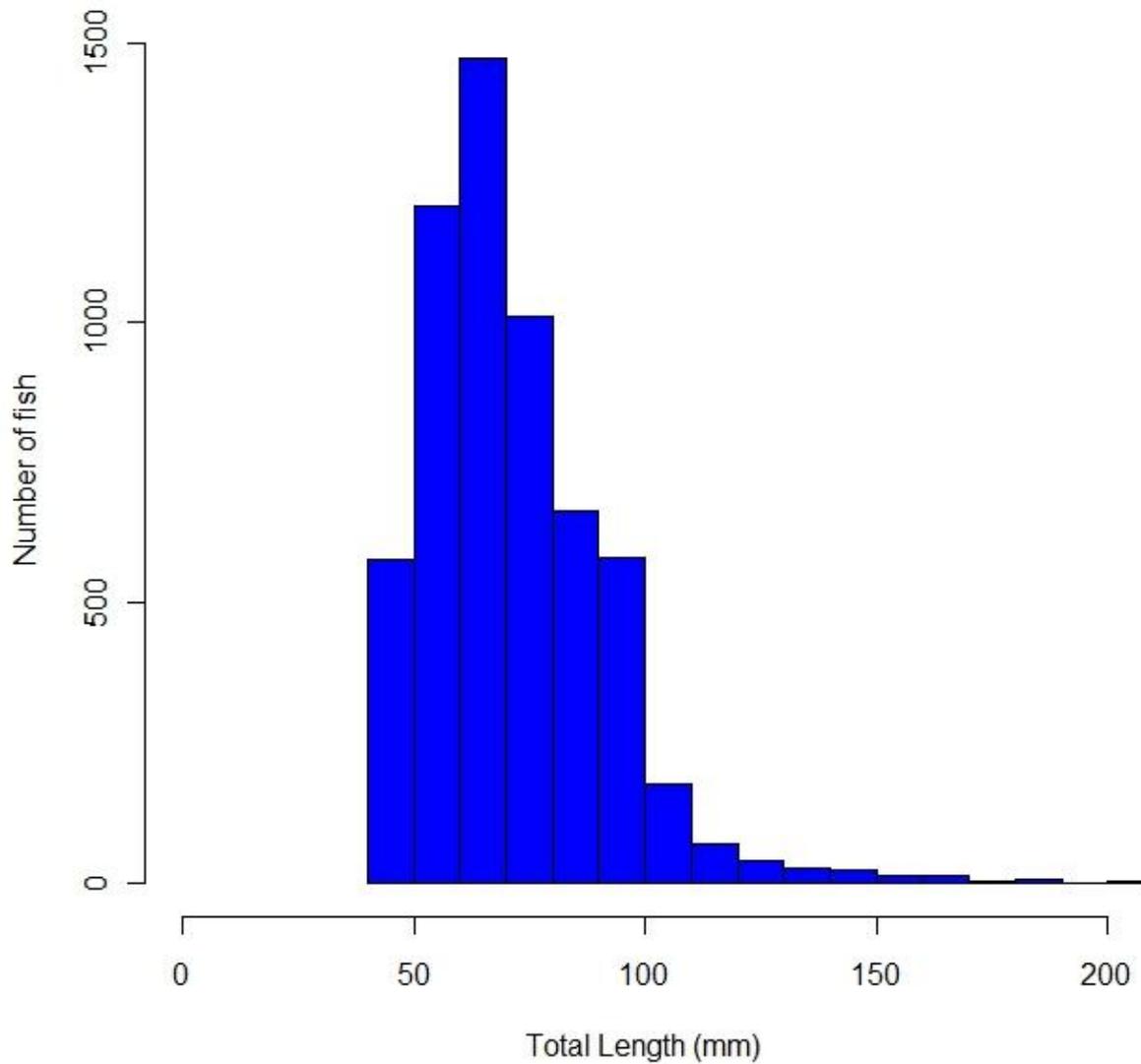


Figure 3-2. Length-frequency histogram of juvenile humpback chub considered in this survival analysis. Fish were considered removed from the population when they were PIT-tagged (first capture above 100 mm TL).

Survival vs. Capture Probability Simulations

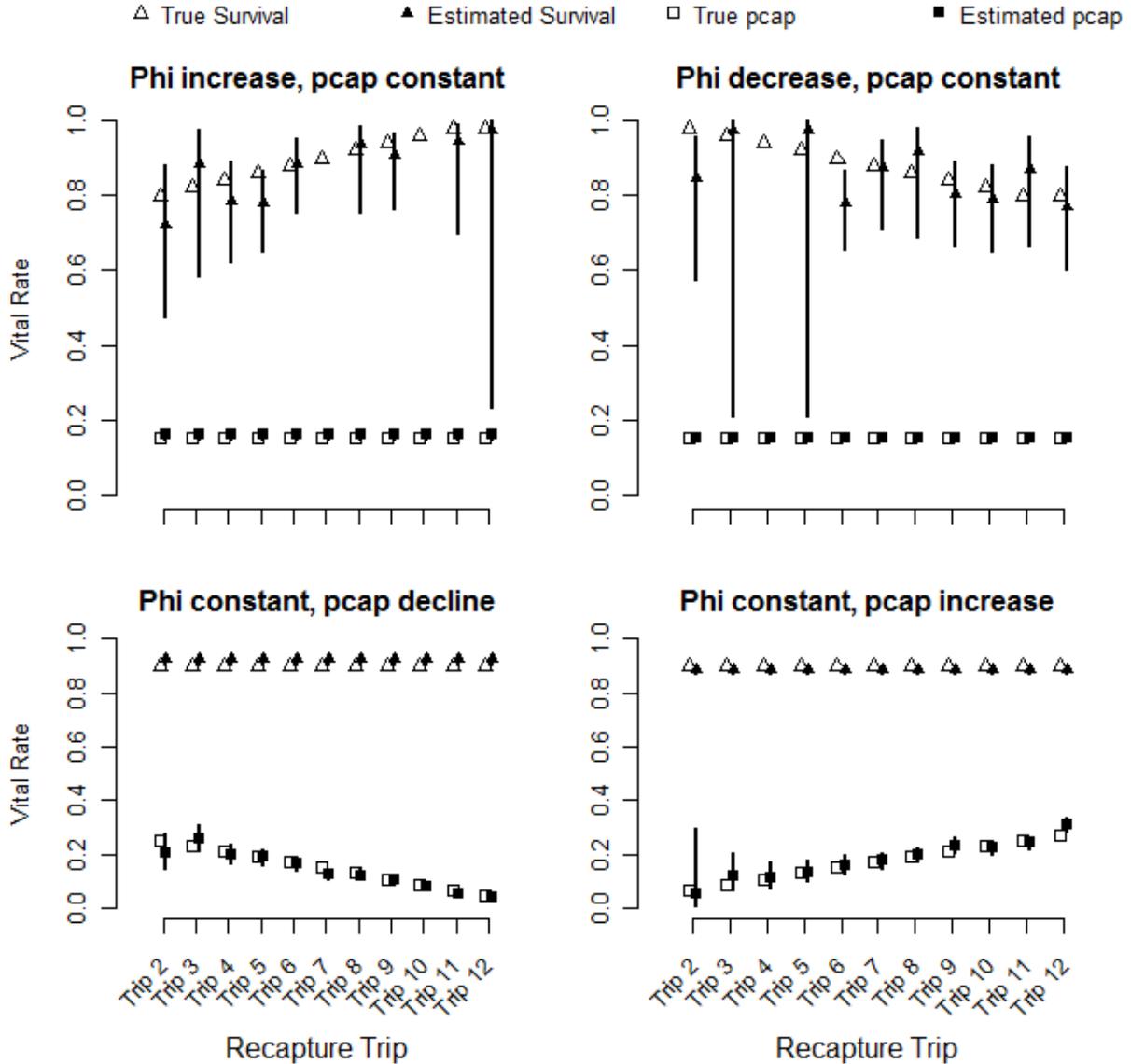


Figure 3-3. Apparent survival vs. capture probability simulations using mark/recapture data generated in GENCAPH1 and analyzed using Program MARK: $\Phi(t) p(\cdot)$ and $\Phi(\cdot) p(t)$ models. Note failure to estimate apparent survival for $\Phi(t)$ models (estimates are either unbounded or missing).

Survival vs. Capture Probability Simulations

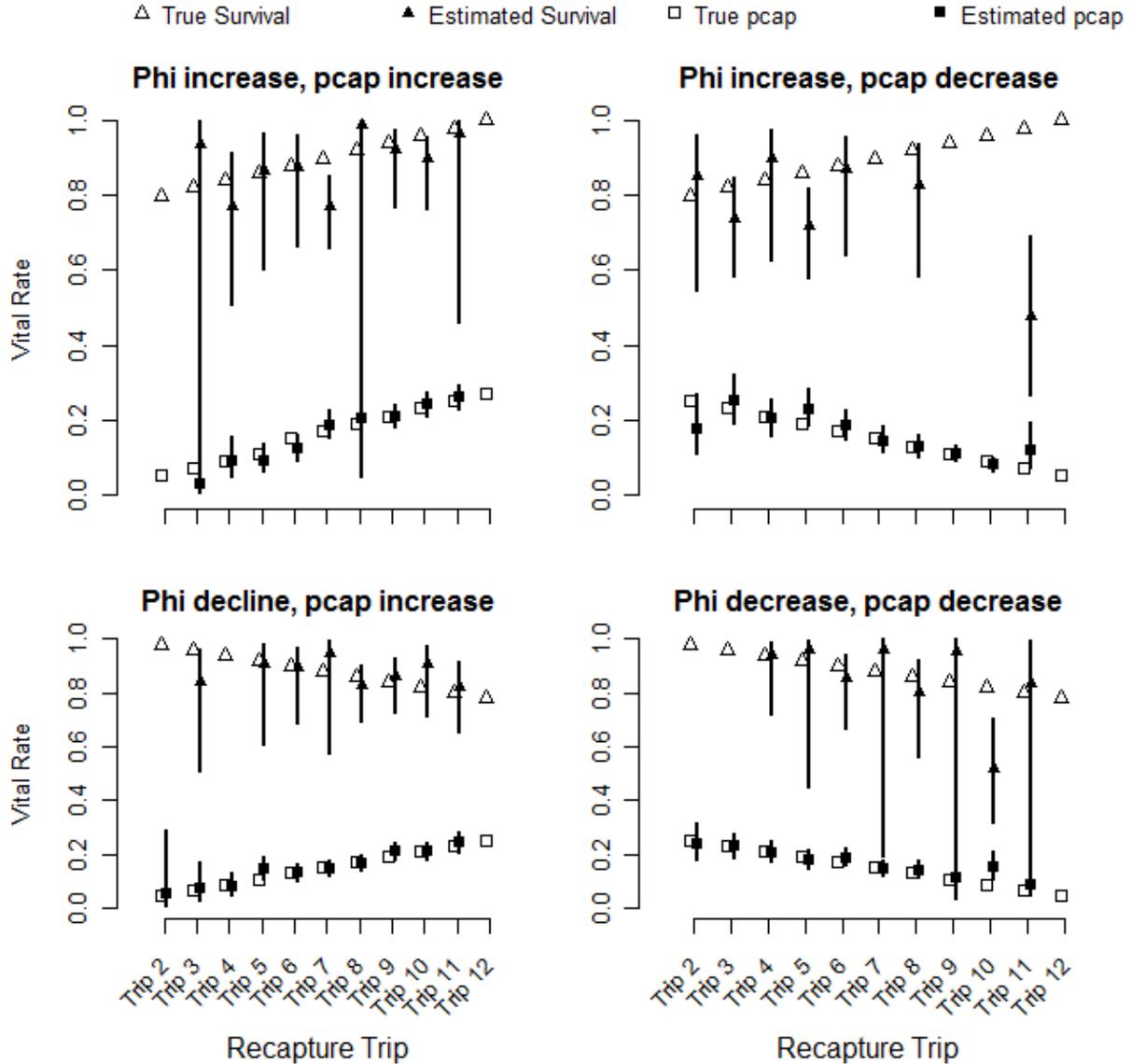


Figure 3-4. Apparent survival vs. capture probability simulations using mark/recapture data generated in GENCAPH1 and analyzed using Program MARK: $\Phi(t)$ $p(t)$ models. Note failure to estimate apparent survival for all models (estimates are missing or unbounded).

Survival vs. Capture Probability Simulations

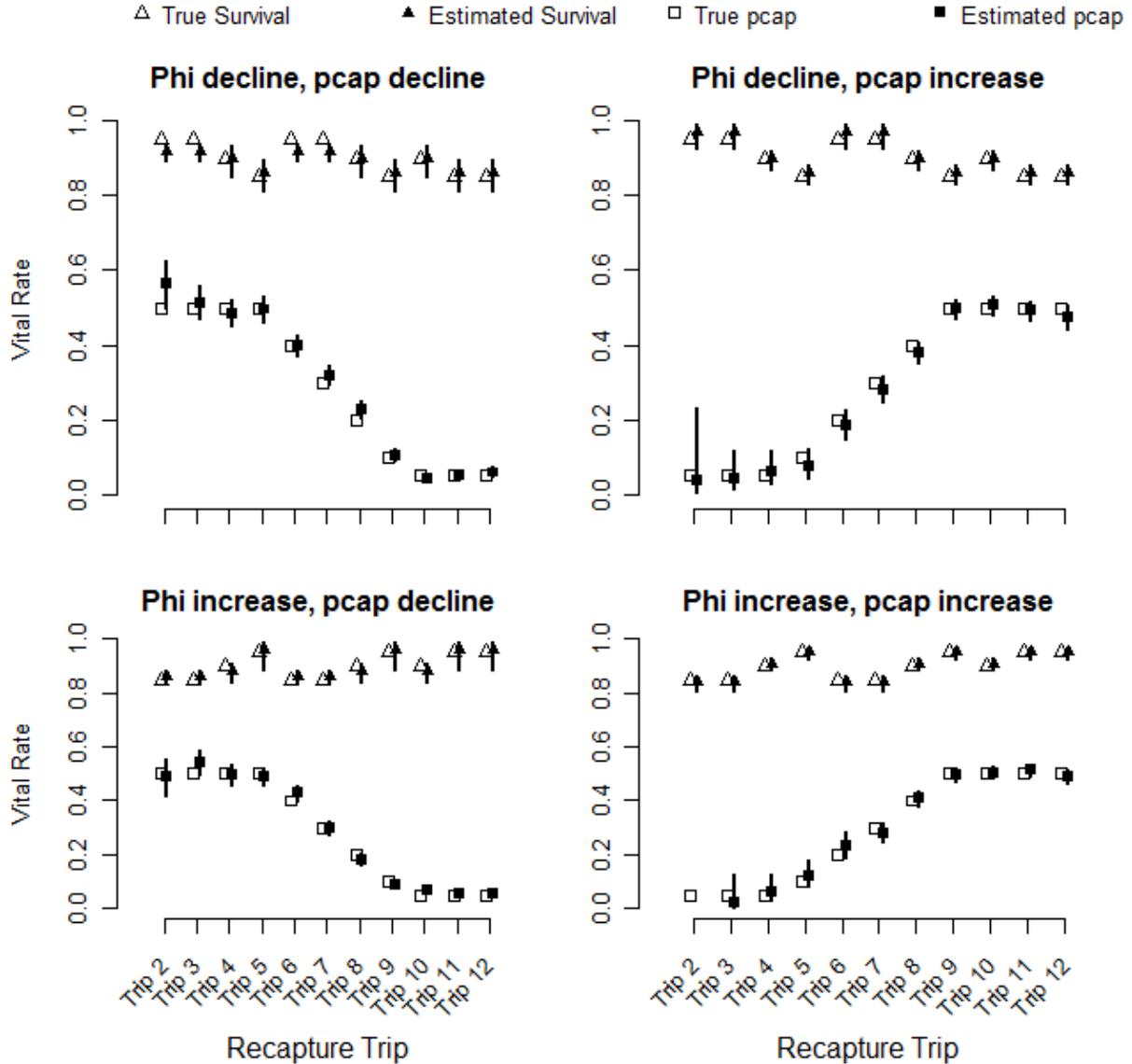


Figure 3-5. Apparent survival vs. capture probability simulations using mark/recapture data generated in GENCAPH1 and analyzed using Program MARK: Phi(flow) p(t) models. Note model accuracy in estimating apparent survival despite order of magnitude change in capture probability due to experimental replicates (years).

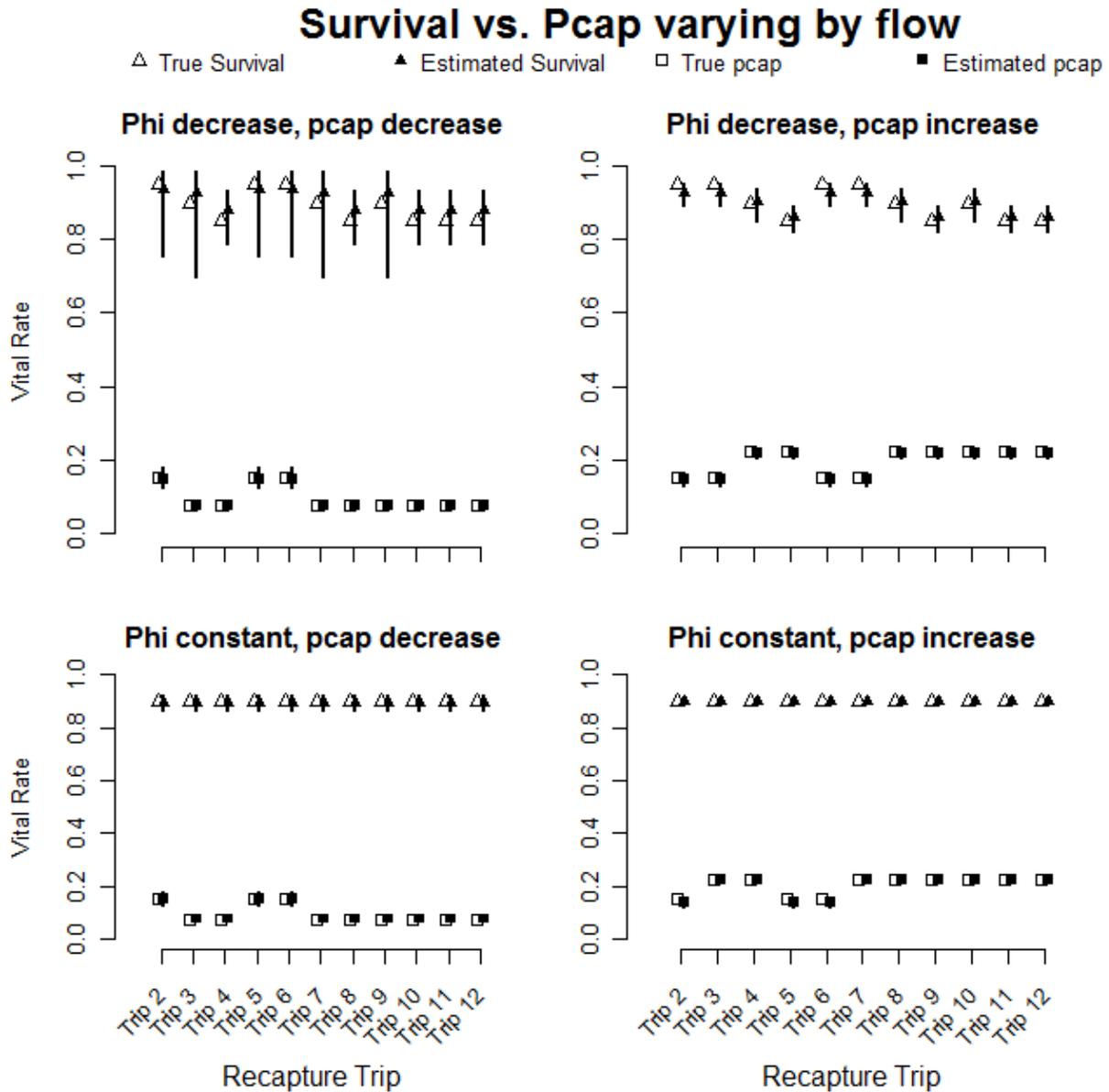


Figure 3-6. Apparent survival vs. capture probability simulations using mark/recapture data generated in GENCAPH1 and analyzed using Program MARK: Phi(flow) p(flow) models. Apparent survival estimates are accurate if capture probability effects of flow are present, although some precision is lost with capture probabilities <10%. Field data is strongly unsupportive of p (flow) models over p (t) models (Table 3).

**Trip-specific capture probability for juvenile humpback chub
with 95% confidence intervals, 3 leading models**

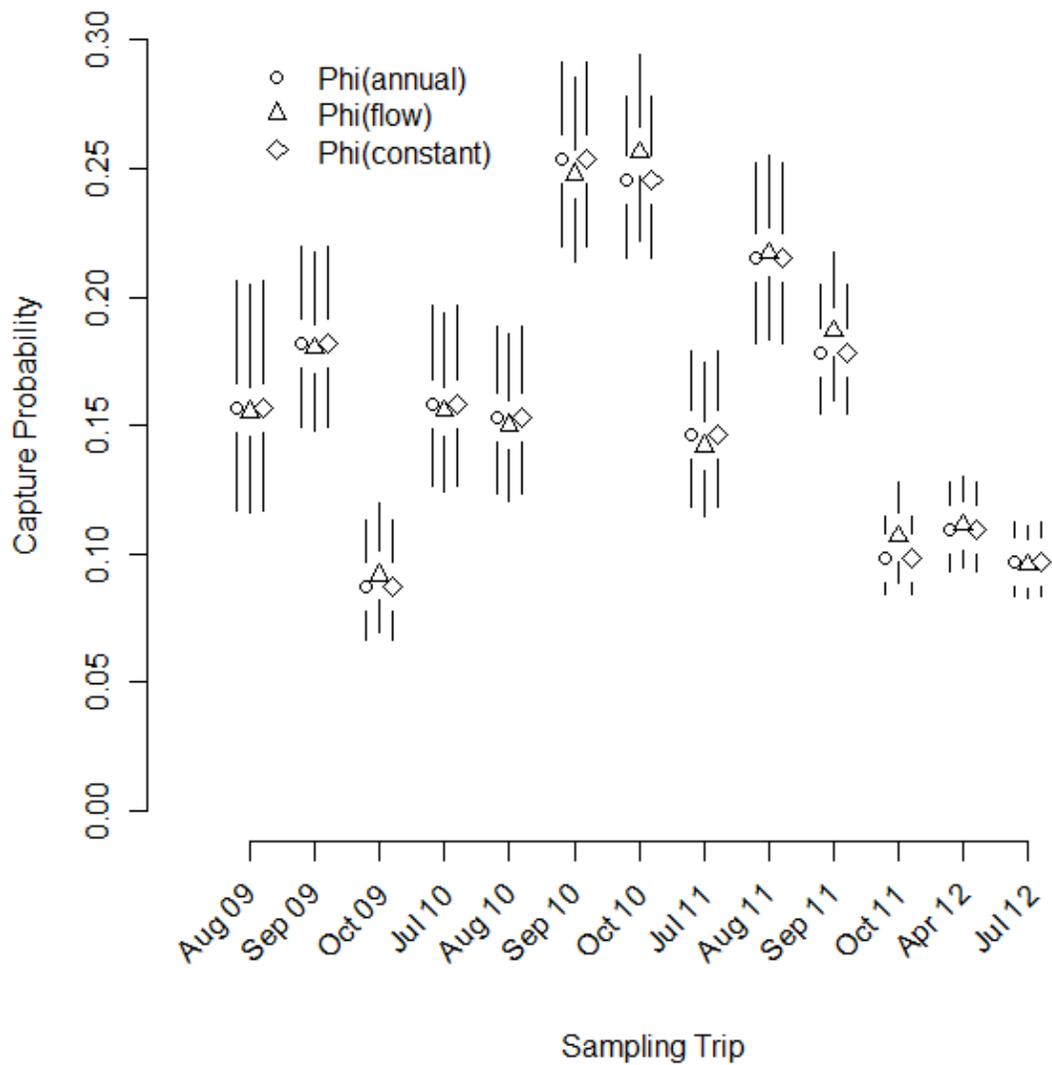


Figure 3-7. Trip-specific capture probability of juvenile humpback chub over the thirteen recapture opportunities based on three leading models.

**Annual apparent survival rates for juvenile humpback chub
with 95% confidence intervals, ANNUAL model**

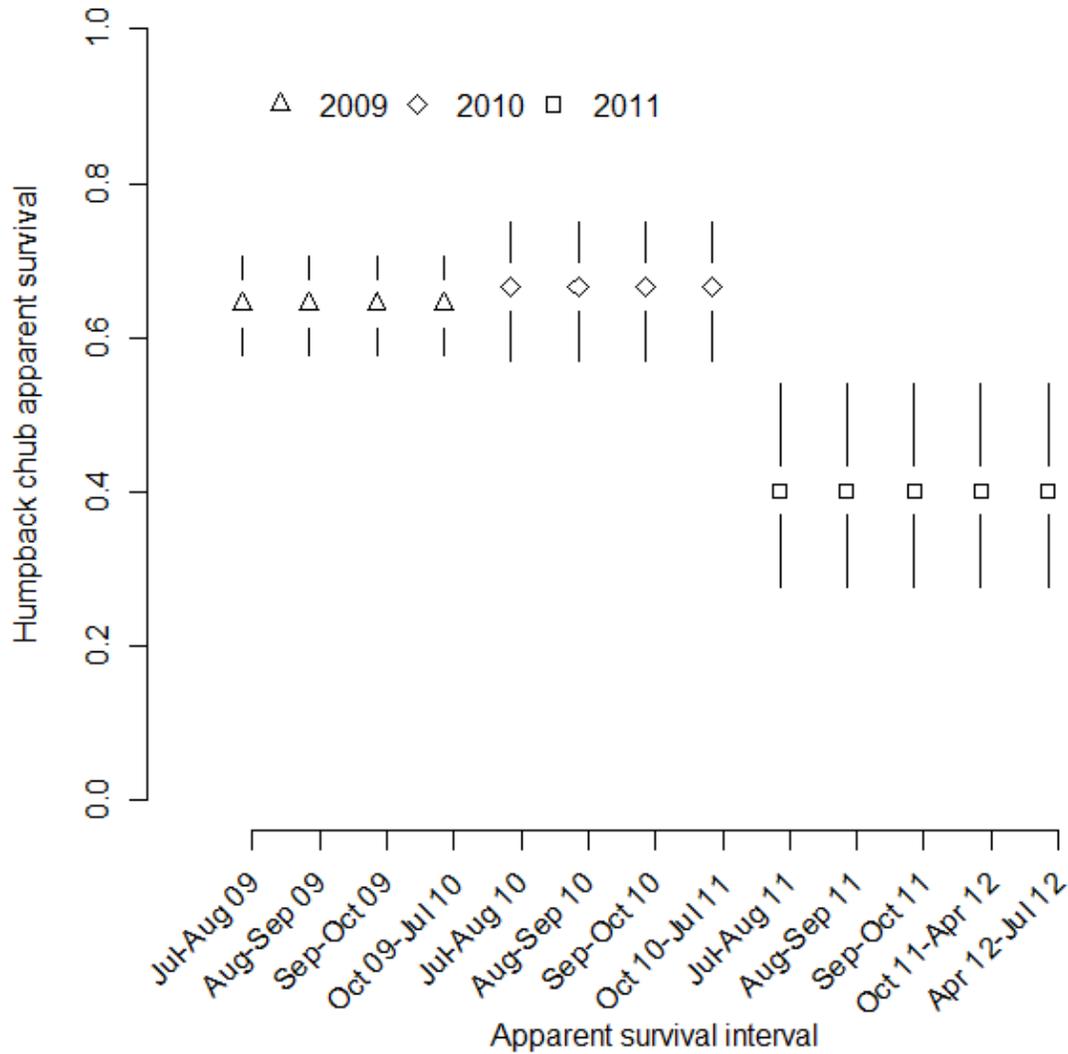


Figure 3-8. Annual apparent survival estimates for juvenile humpback chub, grouped by “fish year” (July of one year to July of the next year, time-dependent capture probability, see Figure 3-3).

**Annual apparent survival rates for juvenile humpback chub
with 95% confidence intervals, FLOW model**

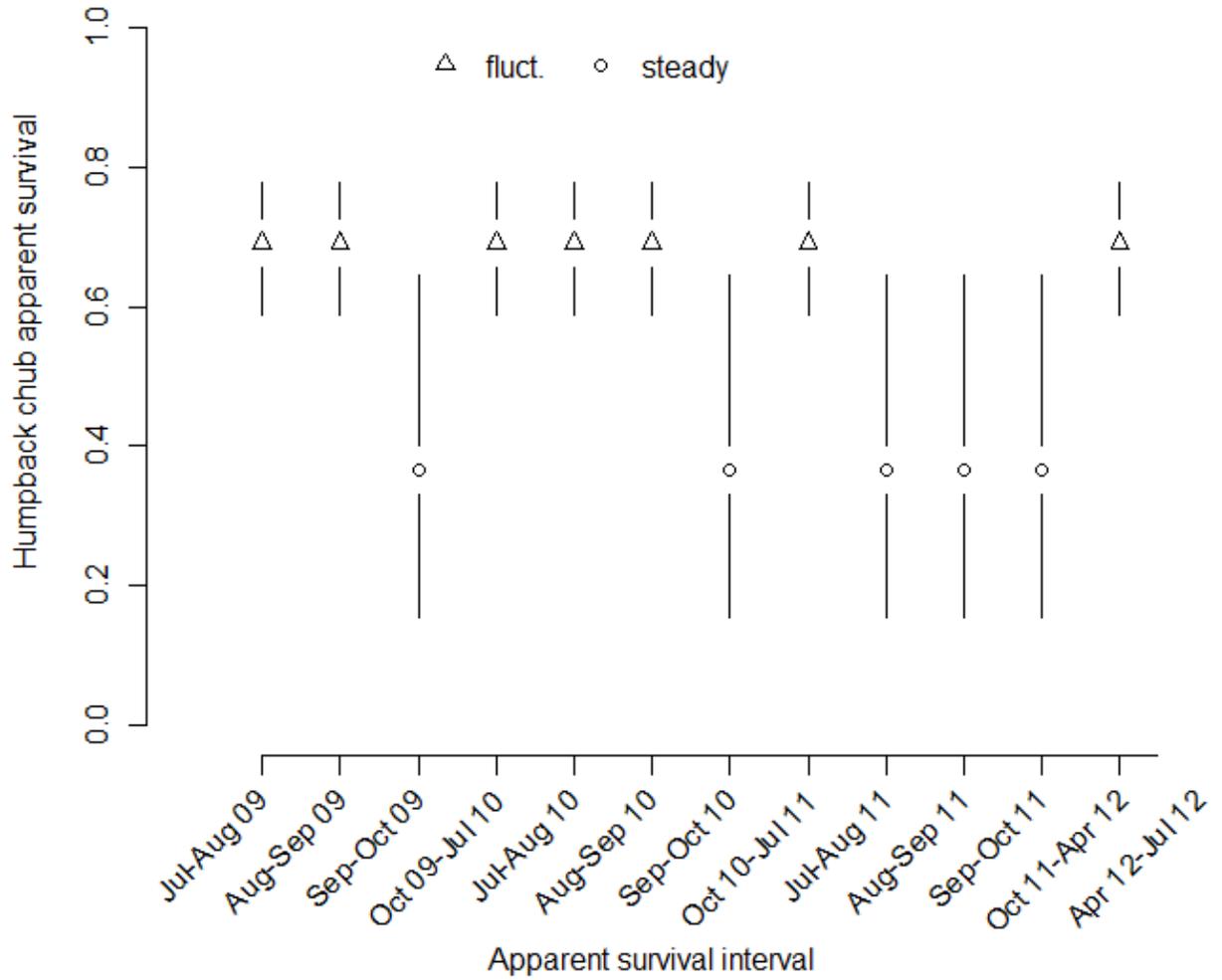


Figure 3-9. Annual apparent survival estimates for juvenile humpback chub, separated by flow treatments.

**Apparent survival rates for juvenile humpback chub
with 95% confidence intervals, CONSTANT model**

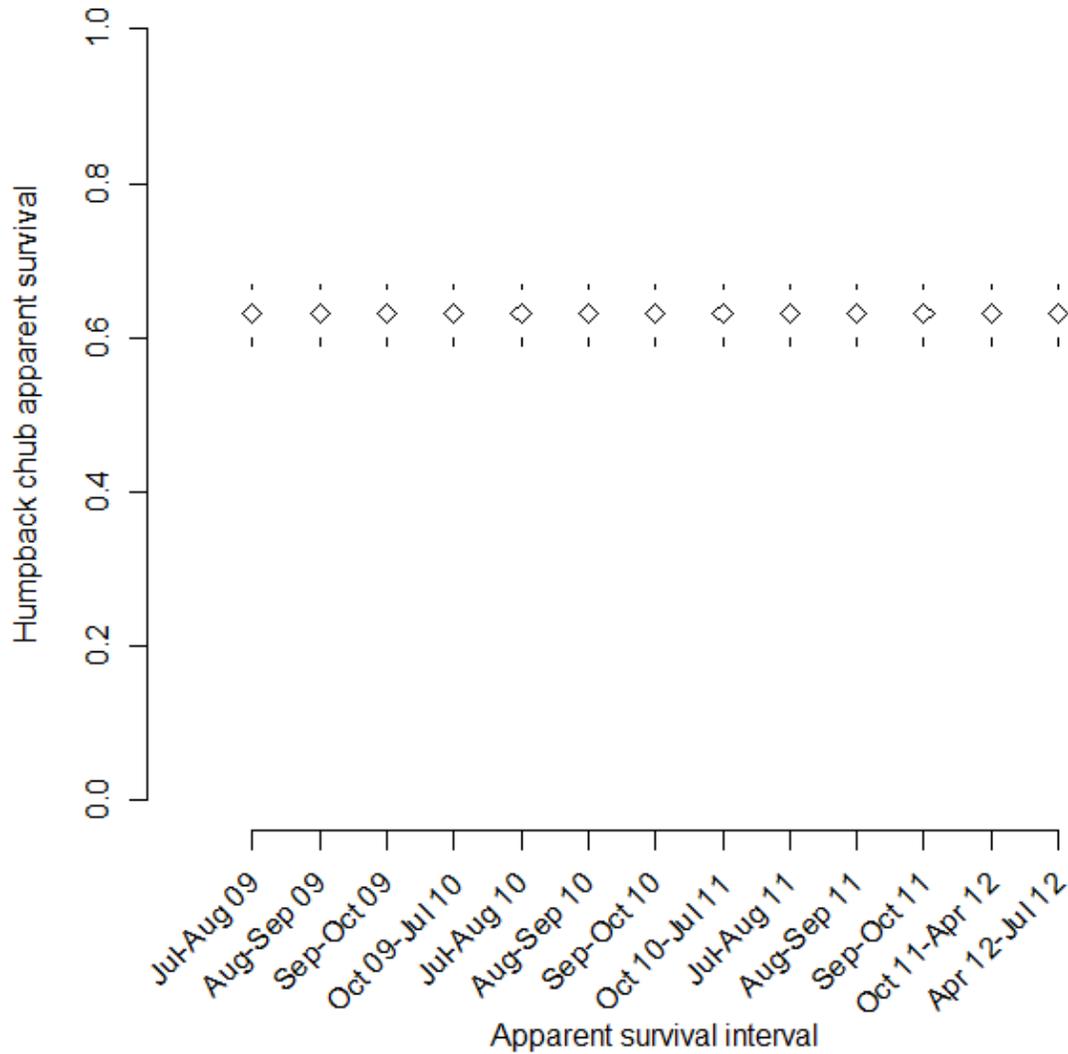


Figure 3-10. Annual apparent survival estimates for juvenile humpback chub, as derived by the constant model (time-dependent capture probability, see Figure 3-3).

CHAPTER 4 CONCLUSIONS

It is commonly accepted that the more natural a flow regime, the more likely it is to favor native versus non-native fish (Marchetti and Moyle 2001, Schultz et al. 2003, Propst and Gido 2004). However, in some systems, river regulation has positively affected native fish populations (Crisp et al. 1983) or certain native species (Welker and Scarnecchia 2003). The Colorado River of the southwestern United States was a muddy and violent river prone to discharge extremes before construction and operation of both Glen Canyon and Hoover dams. Severe droughts drastically reduced aquatic habitat and could leave millions of fish dead (Minckley 1991, Mueller and Marsh 2002). Flooding likely had less of an impact where fish could escape into floodplains or other refugia (Minckley 1991), but certainly would exacerbate stress and displace some portion of the population, especially in canyon-bound reaches. While millennia of behavioral and morphological adaptation likely shaped the native fish community to reduce the detrimental impact of these environmental pressures, in a system where “natural” conditions were physically dangerous or energetically costly, it does not automatically follow that a return to natural flows will trigger positive responses in the native fish community.

I was unable to detect changes in apparent survival in juvenile humpback chub *Gila cypha* (Chapter 3) during experimental steady flows in Grand Canyon. Although the flows are more “natural”, fish that are evolutionarily robust to flow fluctuations are likely robust to observed hydropower fluctuations as well, and a return to slightly more natural flows predictably has no significant effect on apparent survival rates. Other factors may be more important than discharge, especially non-native fish and water temperature.

This is not surprising upon considering the state of the fish community in the unregulated “natural” portions of large tributaries to the Colorado River (upper Salt and Verde rivers, Gila River, upper Green River). If a natural hydrograph and lack of hydropower fluctuations were sufficient to exclude invasive species and favor the natives, we would expect the upper portions of these rivers to be devoid of non-native fish. This expectation is negated in the face of ubiquitous invasive predators and the common extirpation of native fish fauna despite natural flows. On the other hand, the construction of Glen Canyon and Hoover dams and the subsequent cooling of the Colorado River through Grand Canyon may have actually been the timely factor that stemmed the ongoing invasion of warm water non-native fish that had already led to the extirpation of native fish in the lower reaches of the Colorado River (Minckley 1991). Rainbow trout and native fish have coexisted for decades in Grand Canyon (and their congeners as sympatriates for millennia in headwater areas), while the families Centrarchidae, Ictaluridae, and Moronidae have almost universally displaced native fish populations where they are introduced.

Within the corridor of Grand Canyon near the confluence of the Little Colorado River (the “Tapeats Gorge”) that I sampled, steep talus shorelines and cliffs abutting the water render discharge changes relatively insignificant. Slightly moderating fluctuating hydropower flows by releasing steady discharges for a two-month period in the fall, all within a range of less than one-tenth of the river’s maximum annual pre-dam flows, predictably did not have a measurable effect on apparent survival rate of juvenile humpback chub.

Although apparent survival rates did not change significantly between flows, I did observe declines in *growth* rate for juvenile humpback chub during the fall steady flow experiments (Chapter 2). This may be the result of three different interactions: (1) The LCR aggregation of humpback chub occupies a river reach that has relatively steep angle shorelines compared to other parts of the canyon, and habitat selection or availability for juvenile fish is relatively invulnerable to flow fluctuations. This may also be the reason that the humpback chub population has survived well in this canyon reach despite the influence of Glen Canyon Dam. However, the declines I observed in growth rates during steady flows indicate that this may not be the case. (2) The fall steady flow experiment was relatively short (2 months long) and, while producing conditions that could cause declines in growth rate among individual fish, it did not persist long enough to have a measureable population effect on apparent survival rates before flow returned to the typical modified fluctuating flow regime. Lastly, (3) fish included in these apparent survival analyses were below 100 mm TL (down to 40 mm TL) whereas fish that composed my growth treatment groups were all over 100 mm TL (in order to be tracked individually with PIT tags). Humpback chub of different size groups choose different habitats (Stone and Gorman 2006) and likely occupy different functional feeding groups that would cause their growth and survival rates to differ. Further study of survival rates of larger juveniles would help elucidate this possible difference.

While experimental steady flows of the magnitude that I observed did not improve vital rates of juvenile humpback chub, this does not automatically condemn all possible steady flow treatments. Shifting the period of steady flows to earlier in the year

when solar insolation and potential warming are highest (Yard et al. 2005), or extending the period of steady flows long enough for the foodbase to respond may have a different effect on the native fish community. I encourage managers of Glen Canyon Dam and other regulated rivers to persist in innovative experimentation as we all strive to meet societal pressures for resources while preserving ecological integrity for future generations.

LIST OF REFERENCES

- Anderson, M. T. and L. H. Woosley, Jr. 2005. Water availability for the western United States—key scientific challenges. U.S. Geological Survey Circular 1261, Denver, Colorado.
- Andrews, E. D. 1991. Sediment transport in the Colorado River basin. Pages 54-74 in National Resource Council (U.S.) committee to review the Glen Canyon Environmental Studies. Colorado River Ecology and Dam Management: Proceedings of a Symposium, May 24-25 1990, Santa Fe, NM. National Academy Press, Washington, D.C.
- Bain, M. B., J. T. Finn, and H. E. Booke. 1988. Streamflow regulation and fish community structure. *Ecology* 69:382-392.
- Barnett, T. P. and D. W. Pierce. 2009. Sustainable water deliveries from the Colorado River in a changing climate. *Proceedings of the National Academy of Science* 106:7334-7338.
- Biro, P. A., A. E. Morton, J. R. Post, and E. A. Parkinson. 2004. Over-winter lipid depletion and mortality of age-0 rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 61:1513-1519.
- Blinn, D. W. and N. L. Poff. 2005. Colorado River Basin. Pages 483-526 in Benke, A. C. and C. E. Cushing, editors. *Rivers of North America*. Elsevier Academic Press, Burlington, Massachusetts.
- Bunt, C. M., S. J. Cooke, C. Katopodis, and R. S. McKinley. 1999. Movement and summer habitat of brown trout (*Salmo trutta*) below a pulsed discharge hydroelectric generating station. *Regulated Rivers: Research and Management* 15:395-403.
- Burnham, K. P. and D. R. Anderson. 2002. *Model selection and multimodel inference*. Springer, New York, New York.
- Carey, H. V. and P. Moore. 1986. Foraging and predation risk in yellow-bellied marmots. *American Midland Naturalist* 116:267-275.
- Carothers, S. W., M. E. Stitt, and R. R. Johnson. 1976. Feral asses on public lands: an analysis of biotic impact, legal considerations, and management alternatives. *Transactions of the North American Wildlife and Natural Resources Conference* 41:396-405.
- Crisp, D. T., R. H. K. Mann, and P. R. Cubby. 1983. Effects of regulation of the River Tees upon fish populations below Cow Green Reservoir. *Journal of Applied Ecology* 20:371-386.

- Christensen, N. S., A. W. Wood, N. Voisin, D. P. Lettenmaier, and R. N. Palmer. 2004. The effects of climate change on the hydrology and water resources of the Colorado River basin. *Climatic Change* 62:337-363.
- Clarkson, R. W. and M. R. Childs. 2000. Temperature effects of hypolimnial release dams on early life stages of Colorado River basin big-river fishes. *Copeia* 2000:402-412.
- Coggins, L. G. Jr., W. E. Pine III, C. J. Walters, D. R. Van Haverbeke, D. Ward, and H. C. Johnstone. 2006a. Abundance trends and status of the Little Colorado River population of humpback chub. *North American Journal of Fisheries Management* 26:233-245.
- Coggins, L. G. Jr., W. E. Pine III, C. J. Walters, and S. J. D. Martell. 2006b. Age-structured mark-recapture analysis: a virtual-population-analysis-based model for analyzing age-structured capture-recapture data. *North American Journal of Fisheries Management* 26:201-205.
- Coggins, L. G. Jr. and W. E. Pine III. 2010. Development of a temperature-dependent growth model for the endangered humpback chub using capture-recapture data. *The Open Fish Science Journal* 2010:122-131.
- Coggins, L. G. Jr., M. D. Yard, and W. E. Pine III. 2011. Nonnative fish control in the Colorado River in Grand Canyon, Arizona: an effective program or serendipitous timing? *Transactions of the American Fisheries Society* 140:456-470.
- Converse, Y. K., C. P. Hawkins, and R. A. Valdez. 1998. Habitat relationships of subadult humpback chub in the Colorado River through Grand Canyon: spatial variability and implications of flow regulation. *Regulated Rivers: Research and Management* 14:267-284.
- Cowlshaw, G. 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behavior* 53:667-686.
- Department of the Interior (DOI). 2002. Proposed experimental releases from Glen Canyon Dam and removal of non-native fish. Environmental Assessment, Salt Lake City, Utah. Available: <http://azmemory.lib.az.us/cgi-bin/showfile.exe?CISOROOT=/feddocs&CISOPTR=780&filename=781.pdf>. (October 2011).
- Douglas, M. E. and P. C. Marsh. 1996. Population estimates/population movements of *Gila cypha*, and endangered cyprinid fish in the Grand Canyon region of Arizona. *Copeia* 1:15-28.

- Dutterer, A. C., C. Mesing, R. Cailteux, M. S. Allen, W. E. Pine, and P. A. Strickland. 2012. Fish recruitment is influenced by river flows and floodplain inundation at Apalachicola River, Florida. *River Research and Applications* (in press).
- Fisher, S. G. and A. LaVoy. 1972. Differences in littoral fauna due to fluctuating water levels below a hydroelectric dam. *Journal of the Fisheries Research Board of Canada* 29:1472-1476.
- Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Hollway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N Ramankutty, and P. K. Snyder. 2005. Global consequences of land use. *Science* 309:570-574.
- Fule, P. Z., W. W. Covington, H. B. Smith, J. D. Springer, T. A. Heinlen, K. D. Huisinga, and M. M. Moore. 2002. Comparing ecological restoration alternatives: Grand Canyon, Arizona. *Forest Ecology and Management* 170:19-41.
- Gloss, S. P. and L. G. Coggins. 2005. Fishes of Grand Canyon. Pages 33-56 *in* Gloss, S. P., Lovich, J. E., and T. S. Melis, editors. *The State of the Colorado River Ecosystem in Grand Canyon*. United States Geological Survey Circular 1282, Reston, Virginia.
- Gorman, O. T. and D. M. Stone. 1999. Ecology of spawning humpback chub, *Gila cypha*, in the Little Colorado River near Grand Canyon, Arizona. *Environmental Biology of Fishes* 55:115-133.
- Gould, S. J. and E. S. Vrba. 1982. Exaptation – a missing term in the science of form. *Paleobiology* 8:4-15.
- Goulet, C. and K. LaGory. 2009. Annotated bibliography for the humpback chub (*Gila cypha*) with emphasis on the Grand Canyon population. Report of Argonne National Laboratory Environmental Division prepared for Western Area Power Administration Colorado River Storage Project Management Center, Salt Lake City, Utah. Available: <http://www.ipd.anl.gov/anlpubs/2009/10/65302.pdf>. (November 2012).
- Grand Canyon Protection Act (GCPA). 1992. United States Bureau of Reclamation. Reclamation Projects Authorization and Adjustment Act of 1992. Available: <http://www.usbr.gov/uc/legal/gcpa1992.html>. (October 2011).
- Houde, E. D. 1997. Patterns and trends in larval-stage growth and mortality of teleost fish. *Journal of Fish Biology* 51:52-83.

- Hughes, T. C. 1991. Reservoir operations. Pages 207-225 *in* National Resource Council (U.S.) Committee to Review the Glen Canyon Environmental Studies. Colorado River Ecology and Dam Management: Proceedings of a Symposium May 24-25 1990, Santa Fe, NM. National Academy Press, Washington, D.C.
- Ingram, H., A. D. Tarlock, and C. R. Oggins. 1991. The law and politics of the operation of Glen Canyon Dam. Pages 10-27 *in* National Resource Council (U.S.) Committee to Review the Glen Canyon Environmental Studies. Colorado River Ecology and Dam Management: Proceedings of a Symposium May 24-25 1990, Santa Fe, NM. National Academy Press, Washington, D.C.
- Irvine, J. R. and P. R. Henriques. 1984. A preliminary investigation on effects of fluctuating flows on invertebrates of the Hawea River, a large regulated river in New Zealand. *New Zealand Journal of Marine and Freshwater Research* 18:283-290.
- Kaeding, L. R. and M. A. Zimmerman. 1983. Life history and ecology of the humpback chub in the Little Colorado and Colorado Rivers of the Grand Canyon. *Transactions of the American Fisheries Society* 112:577-594.
- Kearsley, L. H., J. C. Schmidt, and K. D. Warren. 1994. Effects of Glen Canyon Dam on Colorado River sand deposits used as campsites in Grand Canyon National Park, USA. *Regulated Rivers: Research and Management* 9:137-149.
- Kennedy, T. A. and S. P. Gloss. 2005. Aquatic ecology: the role of organic matter and invertebrates. Pages 87-101 *in* Gloss, S. P., Lovich, J. E., and T. S. Melis, editors. *The State of the Colorado River Ecosystem in Grand Canyon*. United States Geological Survey Circular 1282, Reston, Virginia.
- Korman, J., M. Kaplinski, and J. Buszowski. 2006. Effects of air and mainstem water temperatures, hydraulic insolation, and fluctuating flows from Glen Canyon Dam on water temperatures in shoreline environments of the Colorado River in Grand Canyon. Final report for Grand Canyon Monitoring and Research Center, Flagstaff, Arizona.
- Korman, J. and S. E. Campana. 2009. Effects of hydropeaking on nearshore habitat use and growth of age-0 rainbow trout in a large regulated river. *Transactions of the American Fisheries Society* 138:76-87.
- Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67-118.
- Lessard, R. B., S. J. D. Martell, C. J. Walters, T. E. Essington, and J. F. Kitchell. Should ecosystem management involve active control of species abundances? *Ecology and Society* 10:1.

- Lorenzen, K. 2006. Population management in fisheries enhancement: gaining key information from release experiments through use of a size-dependent mortality model. *Fisheries Research* 80:19-27.
- Lovich, J. and T. S. Melis. 2007. The state of the Colorado River ecosystem in Grand Canyon: Lessons from 10 years of adaptive ecosystem management. *International Journal of River Basin Management* 5:207-221.
- Ludsin, S. A. and D. R. DeVries. 1997. First-year recruitment of largemouth bass: the interdependency of early life stages. *Ecological Applications* 7:1024-1038.
- Marchetti, M. P. and P. B. Moyle. 2001. Effects of flow regime on fish assemblages in a regulated California stream. *Ecological Applications* 11:530-539.
- McCullough, D. A., J. M. Bartholow, H. I. Jager, R. L. Beschta, E. F. Cheslak, M. L. Deas, J. L. Ebersole, J. S. Foott, S. L. Johnson, K. R. Marine, M. G. Mesa, J. H. Peterson, Y. Souchon, K. F. Tiffan, and W. A. Wurtsbaugh. 2009. Research in thermal biology: burning questions for coldwater stream fishes. *Reviews in Fisheries Science* 17:90-115.
- McKnight, T. L. 1958. The feral burro in the United States: distribution and problems. *The Journal of Wildlife Management* 22:163-179.
- Minckley, W. L. 1991. Native fishes of the Grand Canyon region: an obituary? Pages 124-177 in Marzolf, G. R., editor. *Colorado River Ecology and Dam Management*. National Academy Press, Washington, D.C.
- Mueller, G.A., and P. C. Marsh. 2002. Lost, a desert river and its native fishes: a historical perspective of the lower Colorado River. United States Geological Survey Information and Technology Report USGS/BRD/ITR 2002-0010, Fort Collins, Colorado.
- Muller, K. 1974. Stream drift as a chronobiological phenomenon in running water ecosystems. *Annual Review of Ecology and Systematics* 5:309-323.
- National Park Service (NPS). 2012. Grand Canyon National Park, Plan Your Visit. Available: <http://www.nps.gov/grca/planyourvisit/index.htm>. (February 2012).
- Nilsson, C., C. A. Reidy, M. Dynesius, and C. Revenga. 2005. Fragmentation and flow regulation of the world's large river systems. *Science* 308:405-408.
- Nilsson, P. A. and C. Bronmark. 2000. Prey vulnerability to a gape-size limited predator: behavioral and morphological impacts on northern pike piscivory. *Oikos* 88:539-546.

- Oghutu-Ohwayo, R. 1990. The decline of the native fishes of Lakes Victoria and Kyoga (east Africa), and the impacts of introduced species, especially the Nile perch, *Lates niloticus*, and the Nile tilapia, *Oreochromis niloticus*. *Environmental Biology of Fishes* 27:81-96.
- Paukert, C. P., L. G. Coggins, Jr., and C. E. Flaccus. 2006. Distribution and movement of humpback chub in the Colorado River, Grand Canyon, based on recaptures. *Transactions of the American Fisheries Society* 135:539-544.
- Perry, S. A. and W. B. Perry. 1986. Effects of experimental flow regulation on invertebrate drift and stranding in the Flathead and Kootenai Rivers, Montana, USA. *Hydrobiologia* 134:171-182.
- Pine, W. E. III, J. Korman, K. E. Limburg, M. S. Allen, and T. K. Frazer. 2009. Nearshore ecology of Grand Canyon fish. Research proposal submitted to United States Geological Survey, Grand Canyon Monitoring and Research Center, Flagstaff, Arizona. Available: http://www.usbr.gov/uc/rm/amp/twg/mtgs/09jun22/NSE_Pine_rev.pdf. (October 2011).
- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. *Bioscience* 47:769-784.
- Propst, D. L. and K. B. Gido. 2004. Responses of native and non-native fishes to natural flow regime mimicry in the San Juan River. *Transactions of the American Fisheries Society*. 133:922-931.
- Reisner, M. 1986. Cadillac desert. Viking, New York.
- Rice, J. A., T. J. Miller, K. A. Rose, L. B. Crowder, E. A. Marschall, A. S. Trebitz, and D. L. DeAngelis. 1993. Growth rate variation and larval survival: inferences from an individual-based size-dependent predation model. *Canadian Journal of Fisheries and Aquatic Sciences* 50:133-142.
- Richter, B. D. and G. A. Thomas. 2007. Restoring environmental flows by modifying dam operations. *Ecology and Society* 12:12.
- Robinson, A. T. and M. R. Childs. 2001. Juvenile growth of native fishes in the Little Colorado River and in a thermally modified portion of the Colorado River. *North American Journal of Fisheries Management* 21:809-815.
- Ruffner, G. A. and S. W. Carothers. 1982. Age structure, condition, and reproduction of two *Equus asinus* (Equidae) populations from Grand Canyon National Park. *The Southwestern Naturalist* 27:403-411.

- Savidge, J. A. 1987. Extinction of an island forest avifauna by an introduced snake. *Ecology* 68:660-668.
- Scheidegger, K. J. and M. B. Bain. 1995. Larval fish distribution and microhabitat use in free-flowing and regulated rivers. *Copeia* 1995:125-135.
- Schmidt, J. C., R. H. Webb, R. A. Valdez, G. R. Marzolf, and L. E. Stevens. 1998. Science and values in river restoration in the Grand Canyon. *Bioscience* 48:735-747.
- Schmidt, L. M, S. P. Gloss, and C. N. Updike. 2005. Overview. Pages 1-16 *in* Gloss, S. P., Lovich, J. E., and T. S. Melis, editors. *The State of the Colorado River Ecosystem in Grand Canyon*. United States Geological Survey Circular 1282, Reston, VA.
- Schultz, A. A., O. E. Maughan, S. A. Bonar, and W. J. Matter. 2003. Effects of flooding on abundance of native and non-native fishes downstream from a small impoundment. *North American Journal of Fisheries Management* 23:503-511.
- Shannon, J. P., D. W. Blinn, P. L. Benenati, and K. P. Wilson. 2006. Organic drift in a regulated desert river. *Canadian Journal of Fisheries and Aquatic Sciences* 53:1360-1369.
- Sogard, S. M. 1997. Size selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* 60:1129-1157.
- Stanford, J. A. and J. V. Ward. 1991. Limnology of Lake Powell and the chemistry of the Colorado River. Pages 75-102 *in* National Resource Council (U.S.) Committee to Review the Glen Canyon Environmental Studies. *Colorado River Ecology and Dam Management: Proceedings of a Symposium May 24-25 1990, Santa Fe, NM*. National Academy Press, Washington, D.C.
- Stevens, L. E., J. P. Shannon, and D. W. Blinn. 1997. Colorado River benthic ecology in Grand Canyon, Arizona, USA: dam, tributary and geomorphical influences. *Regulated Rivers: Research and Management* 13:129-149.
- Stone, D. M. 2005. Effect of baiting on hoop net catch rates of endangered humpback chub. *North American Journal of Fisheries Management* 25:640-645.
- Stone, D. M. and O. T. Gorman. 2006. Ontogenesis of endangered humpback chub (*Gila cypha*) in the Little Colorado River, Arizona. *The American Midland Naturalist* 155:123-135.
- Strobbe, F., M. A. McPeck, M. De Block, and R. Stoks. 2011. Fish predation selects for reduced foraging activity. *Behavioral Ecology and Sociobiology* 65:241-247.

- Thompson, J. M., E. P. Bergersen, C. A. Carlson, and L. R. Kaeding. 1991. Role of size, condition, and lipid content in overwinter survival of age-0 Colorado squawfish. *Transactions of the American Fisheries Society* 120:346-353.
- Topping, D. J., J. C. Schmidt, and L. E. Vierra Jr. 2003. Computation and analysis of the instantaneous-discharge record at Lee's Ferry, Arizona – May 8, 1921, through September 30, 2000. United States Geological Survey professional paper 1677. Reston, VA.
- Truett, J. 1996. Bison and elk in the American southwest. *Environmental Management* 20:195-206.
- Urban, M. C. 2007. The growth-predation risk trade-off under a growing gape-limited predation threat. *Ecology* 88:2587-2597.
- USBR (United States Bureau of Reclamation). 2012. The law of the river. Available: <http://www.usbr.gov/lc/region/g1000/lawofrvr.html>. (October 2012).
- Valdez, R. A. and R. J. Ryel. 1997. Life history and ecology of the humpback chub in the Colorado River in Grand Canyon, Arizona. Pages 3-31 in *Proceedings of the Third Biennial Conference on the Colorado Plateau*. National Park Service, Flagstaff, AZ.
- Walters, C. J. and R. Hilborn. 1978. Ecological optimization and adaptive management. *Annual Review of Ecological Systems* 9:157-188.
- Walters, C. J. and C. S. Holling. 1990. Large-scale management experiments and learning my doing. *Ecology* 71:2060-2068.
- Walters, C. J. and F. Juanes. 1993. Recruitment limitation as a consequence of natural selection for the use of restricted feeding habitats and predation risk taking by juvenile fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2058-2070.
- Ward, D. L. and S. A. Bonar. 2003. Effects of cold water on susceptibility of age-0 flannelmouth sucker to predation by rainbow trout. *The Southwestern Naturalist* 48:43-46.
- Waters, T. F. 1972. The drift of stream insects. *Annual Review of Entomology* 17:253-272.
- Welker, T. L. and D. L. Scarnecchia. 2003. Differences in species composition and feeding ecology of Catostomid fishes in two distinct segments of the Missouri River, North Dakota, U.S.A. *Environmental Biology of Fishes* 68:129-141.

- Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540-1548.
- World Commission on Dams (WCD). 2000. Dams and development: a new framework for decision making. The Report of the World Commission on dams. Available: http://www.internationalrivers.org/files/world_commission_on_dams_final_report.pdf. (September 2011).
- Yard, M. D., G. E. Bennett, S. N. Mietz, L. G. Coggins, Jr., L. E. Stevens, S. Hueftle, and D. W. Blinn. 2005. Influence of topographic complexity on solar insolation estimates for the Colorado River, Grand Canyon, AZ. *Ecological Modelling* 183:157-172.
- Yard, M. D., L. G. Coggins, Jr., C. V. Baxter, G. E. Bennett, and J. Korman. 2011. Trout piscivory in the Colorado River, Grand Canyon: effects of turbidity, temperature, and fish prey availability. *Transactions of the American Fisheries Society* 140:471-486.

BIOGRAPHICAL SKETCH

Colton Finch was raised on a beef cattle ranch in the Verde Valley of central Arizona. His interest in the outdoors and the interaction between resource management organizations and private consumption of natural resources took him to the College of Agriculture and Life Sciences at the University of Arizona. There he earned his undergraduate degree in Natural Resources – Fisheries Conservation and Management, and graduated summa cum laude in May 2009. Colton then studied Wildlife Ecology and Conservation at the University of Florida with an emphasis on fisheries coursework under the tutelage of Dr. William Pine III. He earned his Master of Science from the University of Florida in December 2012. Colton's work in Grand Canyon is ongoing as owner of the private consulting firm Foothills Ecological Services LLC, where he leads field crews and analyzes data as part of the Natal Origins project, studying the interaction between non-native rainbow trout and native fish.