

Effects of Fluctuating Flows and a Controlled Flood on Incubation Success and Early Survival Rates and Growth of Age-0 Rainbow Trout in a Large Regulated River

Josh Korman , Matthew Kaplinski & Theodore S. Melis

To cite this article: Josh Korman , Matthew Kaplinski & Theodore S. Melis (2011) Effects of Fluctuating Flows and a Controlled Flood on Incubation Success and Early Survival Rates and Growth of Age-0 Rainbow Trout in a Large Regulated River, Transactions of the American Fisheries Society, 140:2, 487-505, DOI: [10.1080/00028487.2011.572015](https://doi.org/10.1080/00028487.2011.572015)

To link to this article: <http://dx.doi.org/10.1080/00028487.2011.572015>



Published online: 13 Apr 2011.



Submit your article to this journal [↗](#)



Article views: 321



View related articles [↗](#)



Citing articles: 22 View citing articles [↗](#)

ARTICLE

Effects of Fluctuating Flows and a Controlled Flood on Incubation Success and Early Survival Rates and Growth of Age-0 Rainbow Trout in a Large Regulated River

Josh Korman*

*Ecometric Research, Inc., and Department of Zoology, University of British Columbia,
3560 West 22nd Avenue, Vancouver, British Columbia V6S 1J3, Canada*

Matthew Kaplinski

Geology Program, Northern Arizona University, Box 4099, Flagstaff, Arizona 86011, USA

Theodore S. Melis

*U.S. Geological Survey, Southwest Biological Science Center,
Grand Canyon Monitoring and Research Center, 2255 North Gemini Drive, Flagstaff,
Arizona 86001, USA*

Abstract

Hourly fluctuations in flow from Glen Canyon Dam were increased in an attempt to limit the population of nonnative rainbow trout *Oncorhynchus mykiss* in the Colorado River, Arizona, due to concerns about negative effects of nonnative trout on endangered native fishes. Controlled floods have also been conducted to enhance native fish habitat. We estimated that rainbow trout incubation mortality rates resulting from greater fluctuations in flow were 23–49% (2003 and 2004) compared with 5–11% under normal flow fluctuations (2006–2010). Effects of this mortality were apparent in redd excavations but were not seen in hatch date distributions or in the abundance of the age-0 population. Multiple lines of evidence indicated that a controlled flood in March 2008, which was intended to enhance native fish habitat, resulted in a large increase in early survival rates of age-0 rainbow trout. Age-0 abundance in July 2008 was over fourfold higher than expected given the number of viable eggs that produced these fish. A hatch date analysis indicated that early survival rates were much higher for cohorts that hatched about 1 month after the controlled flood (~April 15) relative to those that hatched before this date. The cohorts that were fertilized after the flood were not exposed to high flows and emerged into better-quality habitat with elevated food availability. Interannual differences in age-0 rainbow trout growth based on otolith microstructure supported this hypothesis. It is likely that strong compensation in survival rates shortly after emergence mitigated the impact of incubation losses caused by increases in flow fluctuations. Control of nonnative fish populations will be most effective when additional mortality is applied to older life stages after the majority of density-dependent mortality has occurred. Our study highlights the need to rigorously assess instream flow decisions through the evaluation of population-level responses.

Egg and larval mortality resulting from the operation of nuclear power plants (Barnthouse et al. 1988), hydroelectric dams (McKinney et al. 2001), and natural causes (Methot 1983; Crecco and Savoy 1987; Peterman et al. 1988) can potentially reduce the abundance of adult fish populations. The extent of the impact will depend on the proportion of

early life stage individuals that are killed and the potential for density-dependent compensation in survival rates among latter life stages. Most impact studies focus on estimating direct losses (e.g., number of eggs or larvae killed) and rarely determine whether these losses translate to reduced abundance of juvenile or adult populations. Numerous studies have shown

*Corresponding author: jkorman@ecometric.com
Received March 30, 2010; accepted October 28, 2010
Published online April 13, 2011

that egg and larval densities are poor predictors of juvenile and adult abundance because of strong density dependence in the survival rates of early life stages (e.g., Houde 1987). Legislation designed to protect fish populations and their spawning habitat does not explicitly recognize this dynamic, and incorporating the effects of density dependence when assessing or predicting human impacts is controversial (Fletcher and Deriso 1988).

Short-term variation in flow from hydroelectric dams produces fluctuations in water levels below the dams; these water level fluctuations can result in periodic dewatering of spawning habitat used by salmonids, potentially increasing mortality rates for incubating life stages (eggs and alevins; Reiser and White 1983). Dewatering of redds is a highly visible impact, and in some systems (e.g., Columbia and Skagit rivers) the flow regimes have been stabilized over the spawning and incubation periods to minimize the number of redds that are exposed (e.g., Connor and Pflug 2004; McMichael et al. 2005). Typically, maximum flows during the spawning period are reduced to limit spawning on high-elevation gravel bars, and minimum flows during the incubation period are increased to reduce the extent of dewatering. The efficacy of these flow regimes should be assessed because lost revenues from flow stabilization can be substantial and because flow regimes focused on improving survival rates for older life stages may produce greater ecological benefits.

Purposeful (controlled floods) or accidental (spills) high flow releases from hydroelectric dams also have the potential to alter survival rates of incubating life stages as well as the growth and survival of juveniles. Flows that are large enough to mobilize fine and coarse sediments on the streambed during the period when eggs and alevins are incubating in the gravel have the potential to scour or bury redds, thus reducing survival rates during incubation (Holtby and Healey 1986; Hartman and Scrivener 1990; Magee et al. 1996). However, high flows can also flush fine material from the interstitial pore spaces of the stream bottom (Kondolf et al. 1987; Murle et al. 2003), potentially increasing survival rates for eggs and alevins that are fertilized after the high flow and increasing survival for juvenile fish (Ortlepp and Murle 2003). Greater flow will increase water depth and wetted area and often will provide access to off-channel habitats, potentially leading to increased survival rates for juvenile fish (Mitro et al. 2003; Lobon-Cervia 2007). Greater water velocities driven by increased flows can also displace juvenile fish from preferred habitats and may lead to reduced survival (Jensen and Johnsen 1999; Valdez et al. 2001; Nislow et al. 2002; Einum and Nislow 2005). Higher water velocities can alter the composition and abundance of the periphyton and invertebrate communities on the stream bottom and in the drift (Benenati et al. 2000; Shannon et al. 2001; Uehlinger et al. 2003; Rosi-Marshall et al. 2010), thereby affecting food availability for and growth of juvenile fish (Arndt et al. 2002).

Recent changes in the flow operating regime at Glen Canyon Dam on the Colorado River provided a unique opportunity to better understand the effects of diurnal flow fluctuations and

high-flow events on early life stages at a meaningful population scale. The first 26-km reach of the Colorado River below the dam is a clear, cold tailwater known as the Lees Ferry reach, which supports a large, self-sustaining population of nonnative rainbow trout *Oncorhynchus mykiss* and a nationally recognized trout fishery. Beginning in 1991, daily fluctuations in flow from Glen Canyon Dam were reduced to improve navigation and limit stranding of adult rainbow trout. These rules were also implemented in an attempt to mitigate erosion of sandbars in Grand Canyon National Park, which begins at the downstream boundary of the Lees Ferry reach. The operating changes were also intended to stabilize shoreline habitats in Grand Canyon in an attempt to improve the survival rate of the humpback chub *Gila cypha*, which is federally protected under the Endangered Species Act of 1973. Although sediment storage (Wright et al. 2005) and humpback chub abundance (Coggins and Walters 2009) continued to decline after the 1991 flow change (Lovich and Melis 2007), the natural reproductive rate of the rainbow trout population in the Lees Ferry reach was enhanced; within a decade, adult rainbow trout abundance had increased threefold (McKinney et al. 2001). Abundance of rainbow trout in the upstream reaches of Grand Canyon increased sixfold over a similar time period (S. Rogers, Arizona Game and Fish Department, personal communication).

Concerns about the potential negative effects of high rainbow trout abundance on humpback chub and other native fishes led to a 4-year mechanical removal effort to reduce rainbow trout abundance in target reaches of the Grand Canyon beginning in January 2003 (Coggins 2008; Coggins et al. 2011, this issue). To aid the mechanical removal effort, an experimental “nonnative fish suppression flow” (NFSF) regime from Glen Canyon Dam was implemented between January and March in 2003–2005 (Figure 1). These flows were intended to reduce rainbow trout abundance in the Lees Ferry reach by increasing mortality rates on incubating life stages (Figure 1). This experiment is one of many that have been implemented since the early 1990s by the Glen Canyon Dam Adaptive Management Program to improve ecological conditions downstream of the dam (Coggins 2008). Controlled floods are a key element of the experimental flows program and have been conducted in 1996 (Schmidt et al. 1999), 2004, and 2008. The main objectives of the controlled floods are (1) to rebuild sand bars below the Lees Ferry reach in Grand Canyon, thereby increasing the area of camping beaches; (2) to possibly improve aquatic habitat for endangered native fishes and terrestrial habitat for riparian vegetation and associated fauna; and (3) to protect archeological resources (Wright et al. 2005). These high-flow events also have the potential to affect the population dynamics of important fish species downstream of Glen Canyon Dam, including the survival rate of early life stages of rainbow trout in the Lees Ferry reach.

The objective of this study was to determine whether NFSFs and the 2008 controlled flood from Glen Canyon Dam increased incubation mortality of rainbow trout in the Lees Ferry reach, and if so, whether this effect was apparent in the age-0

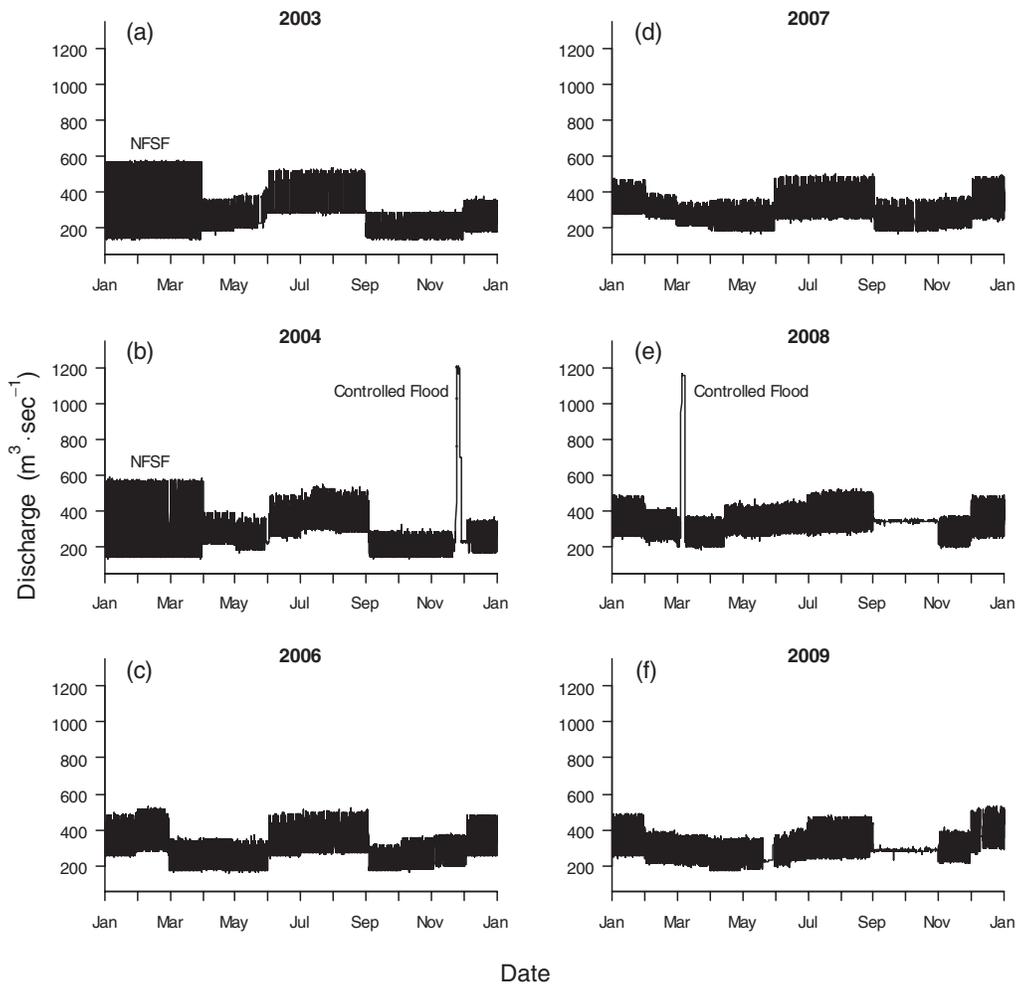


FIGURE 1. Hourly discharge from Glen Canyon Dam for calendar years (a) 2003, (b) 2004, (c) 2006, (d) 2007, (e) 2008, and (f) 2009. Higher flows and greater fluctuations during January–March (i.e., nonnative fish suppression flows [NFSFs]) in 2003 and 2004 are indicated in (a) and (b), respectively. Controlled floods in November 2004 and March 2008 are shown in (b) and (e), respectively. No data were collected in 2005, although NFSFs were released. For brevity, the 2010 hydrograph (very similar to the 2009 hydrograph) is excluded from the figure.

population. Our first hypothesis was that NFSFs would increase incubation mortality due to redd dewatering and that the magnitude of the compensatory survival response would not be sufficient to mitigate this impact. We therefore predicted that the abundance of age-0 rainbow trout would be lower in years when NFSFs were implemented. Our second hypothesis was that the controlled flood during the spawning and incubation period in 2008 would not affect rainbow trout incubation success or age-0 abundance. Predictions from both hypotheses were consistent with the expectations of the Glen Canyon Dam Adaptive Management Program managers that authorized these flows (Lovich and Melis 2007). However, predictions from the latter hypothesis were counter to expectations that controlled floods can help restore aquatic ecosystems (Poff et al. 1997) and result in greater salmonid abundance (e.g., Ortlepp and Murle 2003).

The present study has unique aspects that are relevant to monitoring and instream flow assessments in other large regulated

ivers. Among the limited number of investigations that have examined the consequences of hydroelectric dam flow regimes for fish populations, almost all have evaluated regimes that are targeted at improving population status (e.g., Travnicek et al. 1995; McKinney et al. 2001; Connor and Pflug 2004). In contrast, we evaluated an experimental hydropeaking regime that was targeted specifically at reducing the survival rates of early life stages. This unusual situation provided good experimental contrasts and opportunities for using informative sampling techniques. The present study also identifies some unique aspects of salmonid spawning dynamics in a large regulated river and provides some insight into the strength and timing of density dependence for early life stages in this environment.

METHODS

We evaluated the effects of flow from Glen Canyon Dam on spawning locations, mortality of incubating life stages (eggs

and alevins), hatch date distributions, and the abundance of age-0 rainbow trout in the Lees Ferry reach of the Colorado River, Arizona. We estimated the spatial and seasonal variation in spawning over 7 years from 2003 to 2010 (no data were collected in 2005 even though NFSFs were conducted) on the basis of frequent redd surveys. This information, along with continuous measurements of intergravel temperatures, was integrated in a model to predict flow-dependent incubation mortality caused by dewatering for weekly spawning cohorts. Temporal and spatial predictions of mortality were compared with the observed frequency of egg mortality as determined by redd excavations. Predictions of seasonal variation in flow-dependent incubation mortality were evaluated by use of a hatch date analysis (Methot 1983; Campana and Jones 1992). The combined effects of flow-dependent incubation mortality and egg deposition on the abundance of age-0 rainbow trout were examined by using a stock–recruitment approach.

Study site, experimental flow regimes, and evaluation of central hypotheses.—The Lees Ferry reach of the Colorado River begins at Glen Canyon Dam and extends 26 km downstream to the confluence with the Paria River (36°51'57.6"N, 111°35'9.6"W). The fish fauna in the Lees Ferry reach consists almost exclusively of nonnative rainbow trout (McKinney et al. 2001). With the exception of limited spawning in a few tributaries of the Colorado River in Grand Canyon, rainbow trout reproductive activity in the Colorado River below Glen Canyon Dam appears to be limited to the Lees Ferry reach (Coggins 2008). Thus, rainbow trout abundance in Grand Canyon, which potentially has negative impacts on humpback chub and other native fishes, is probably controlled by reproductive success in the Lees Ferry reach. This reach is wide and shallow and has no significant tributaries, and water quality is almost completely determined by the clear, cold hypolimnetic release from Glen Canyon Dam. Water temperatures and Secchi depths typically range from 9°C to 12°C and from 6 to 7 m, respectively (Voichick and Wright 2007).

Discharge from Glen Canyon Dam fluctuates on a diurnal cycle that is driven by power demand but controlled through a suite of operating rules, which are intended to constrain the maximum daily flow range, minimum and maximum flows, and hourly ramping rates. The NFSFs, applied during 2003–2005 (Figure 1a, b) to increase rainbow trout incubation mortality, consisted of increasing the extent of daily flow variation during winter and early spring from the normal range of 283–510 m³/s in January and 198–368 m³/s in February–March to a range of 142–566 m³/s in January–March. The rationale for the treatment was that higher flows of longer duration during the day would promote spawning on high-elevation gravel bars that would subsequently be dewatered during flow reductions associated with periods of off-peak power demand (i.e., nights and weekends). After the 2003–2005 NFSF tests, a controlled flood was conducted between March 5 and 9, 2008, and consisted of a sustained high flow release of 1,150 m³/s for 2.5 d (Figure 1e). A controlled flood was also conducted in November 2004 (Figure

1b) but was not evaluated in this study because it did not occur during a time when it would affect early life stages.

Our evaluation of the effects of wider-ranging flow fluctuations was made on the basis of spatial, seasonal, and annual contrasts. Assuming that the seasonal pattern of fluctuating flow-dependent incubation mortality is correct, the hatch date distributions for age-0 rainbow trout as predicted by a flow-dependent model should provide a better fit to the back-calculated distributions relative to predictions from a flow-independent model wherein hatch timing is solely determined by spawning and incubation timing. The fluctuating flow-dependent predictions of the hatch date distribution should provide a better fit to the back-calculated distributions in NFSF years (2003 and 2004), when mortality from flow fluctuations was expected to be substantial. In years with normal hydropeaking operations (2006–2010), flow-dependent incubation mortality should be lower; therefore, we expected that both models would adequately predict the back-calculated hatch date distributions for those years. Finally, if the overall postemergent compensatory survival response to increased rates of flow-dependent incubation mortality is minimal, then the stock–recruit analysis should show that age-0 rainbow trout abundance is negatively correlated with the extent of incubation mortality and positively correlated with viable egg deposition.

To evaluate the effects of the controlled flood on incubation success, we followed an approach similar to that used for evaluating flow fluctuations. The controlled flood in March 2008 occurred approximately at the peak of spawning activity. If high flows resulted in substantial scour or burial of redds, we would expect reduced survival for weekly cohorts that were fertilized before the flood relative to cohorts that were fertilized after it. This difference should be apparent in the comparison of predicted hatch date distributions with the back-calculated distribution and in the stock–recruitment analysis.

Redd counts and intergravel temperatures.—Rainbow trout redds were counted at 27 spawning locations in the Lees Ferry reach approximately every 2 weeks during the peak spawning period and once per month during nonpeak periods (Table 1). Surveys were conducted on foot at sites where redds were exposed or located at depths less than 1 m; from the deck of a boat for redds located at depths between 1 and 2 m; and by using an underwater video camera or clear-bottom kayak towed from a boat for sites where redds were located at depths greater than 2 m. As Secchi depths were typically 6–7 m, a clear view of the river bottom was generally available throughout the reach based on the suite of redd survey techniques that were used. We therefore consider it unlikely that we substantially underestimated the number of redds located in deep water. The location and elevation of redds were determined by using a total station or rod and level. The proportion of redds created at different elevations (hereafter referred to as redd hypsometry) was summarized by determining the proportion of redds that would be inundated at five discharge ranges: less than 142, 142–227, 227–340, 340–425, and 425–566 m³/s. Continuously recording

TABLE 1. Summary of effort and sample sizes used to monitor early life stage survival and growth of nonnative rainbow trout in the Lees Ferry reach of the Colorado River. Data are summarized by brood year (year in which spawning occurred). In brood years 2007 and 2008, age-0 surveys extended into the next calendar year. No data were collected for brood year 2005.

Variable	Brood year						
	2003	2004	2006	2007	2008	2009	2010
Redd Surveys							
Number of surveys	6	11	11	7	10	11	5
Survey period	Jan–Jun	Nov–Jul	Dec–Jun	Dec–Jun	Dec–Jun	Nov–May	Jan–May
Total count across surveys	2,671	3,596	165	1,186	2,488	3,107	895
Peak count across surveys	723	963	35	399	571	706	318
Age-0 Surveys							
Number of surveys	4 ^a	8	5	7	11	6	4
Survey period	Jun–Oct	Apr–Dec	Jun–Nov	Jun–Mar	May–Mar	May–Nov	Jul–Nov
Total catch across surveys	586	4,451	1,834	5,558	14,080	12,686	4,315
Peak catch across surveys	280	1,394	689	1,564	3,121	3,178	3,179
Number aged	237	318	136	152	100	101	0

^aOnly low-angle shorelines were surveyed in 2003.

temperature loggers were used to measure intergravel temperatures at these elevations in two large gravel bars located 2.5 and 18 km downstream of Glen Canyon Dam, where the vast majority of spawning at high elevations occurred. The hourly discharge record from Glen Canyon Dam was used to determine the dewatering frequency for these elevations. We excavated 120 redds between February and May 2004 at a range of elevations and examined them for the presence of live and dead eggs. These data were used to quantify seasonal and spatial trends in incubation mortality. Further details on the redd surveys are provided by Korman (2009).

Models of spawn timing, flow-independent incubation mortality, and flow-dependent incubation mortality.—Discharge, redd dewatering frequency and timing, and air temperature—all of which control the extent of flow-dependent incubation mortality—were highly variable over the incubation period. Thus, models that would predict spawn timing and temporal variation in incubation quality were needed. The timing of spawning and the total number of redds created each year were modeled by using a beta distribution that was fitted to the redd count data following the methods of Hilborn et al. (1999). We then developed a model that integrated the effects of spawn timing, redd hypsometry, and intergravel temperature to predict (for weekly spawning cohorts) incubation mortality caused by flow fluctuations. A key assumption of the model is that intergravel temperature, as influenced by redd dewatering frequency and duration, is the ultimate cause of incubation mortality. This assumption is supported by laboratory and in situ studies. Dewatering of eggs in laboratory channels for up to 12 h/d for as long as 4 weeks (steelhead [anadromous rainbow trout]) or 1–5 weeks (Chinook salmon *O. tshawytscha*) produced essentially no effect on hatching success or on the development and growth rates of alevins and juveniles as long as the sediment moisture content was maintained at 4% or higher (Reiser and

White 1983). Montgomery and Tinning (1993) found that air exposures of up to 12 h applied to artificial rainbow trout redds in the Lees Ferry reach had no influence on hatching success but that higher temperatures substantially reduced the exposure period required to cause substantive mortality.

The model used to predict hatch date distributions and seasonal variation in incubation success consisted of five components:

1. **Spawn timing:** predictions of spawn timing and magnitude were used to calculate the number of redds created each day over a 1-year period (November 1–October 31);
2. **Redd hypsometry:** redds created on each model day were distributed across the five elevation classes based on the observed redd hypsometry;
3. **Incubation timing:** the number of days from spawning to hatch and from hatch to emergence was determined based on the time required to exceed accumulated thermal unit thresholds. The accumulated thermal unit thresholds depended on the average daily temperature history at each spawning date \times elevation combination and were computed by using the Jensen et al. (1992) model;
4. **Temperature-dependent incubation mortality:** daily maximum intergravel temperatures determined from the hourly maxima over egg and alevin incubation periods were compared with temperature mortality thresholds. Redds created for each spawning day \times elevation stratum were recorded as not producing viable young if the daily maximum temperature at any point in the projected incubation period exceeded the assumed lethal thresholds. We assumed that eggs and alevins were equally sensitive to temperature, and we used a lethal temperature limit of 16°C for both life stages (Piper et al. 1986; Ford et al. 1995; Oliver and Fidler 2001). A sensitivity analysis indicated that predictions were relatively

insensitive to a realistic range of lethal temperature limits (Korman 2009);

5. Hatch timing: the number of viable redds and the total number of redds were summed across elevation classes for each spawning day. Predictions were shifted from spawn date to hatch date based on the computed time from spawning to hatch for each model day \times elevation stratum and then were summed over 7-d intervals to represent the total number of redds and number of viable redds for each weekly spawning cohort.

The total flow-dependent mortality per year was computed as the ratio of nonviable redds to total redds.

The model was applied by using redd count, hypsometry, and temperature data that were aggregated over the entire Lees Ferry reach for each study year. The predicted hatch date distributions for each year based on spawn and incubation timing alone (i.e., model components 1–3 only)—hereafter referred to as the flow-independent mortality model—were based on the assumption that incubation mortality was constant across all weekly cohorts regardless of spawning date or elevation. This model is equivalent to the null model since it does not include the effects of flow fluctuations (dewatering) on incubation mortality rates. The hatch date distributions predicted from the combined spawn timing, incubation timing, and incubation mortality models (model components 1–5)—hereafter referred to as the flow-dependent mortality model—represent the distributions that result from temporal and spatial variation in incubation mortality driven by flow fluctuations.

Back-calculated hatch date distributions and comparison with predictions.—We estimated the “observed” hatch date distribution for all study years except 2010 based on back-calculation for comparison with the predicted distributions from the flow-independent and flow-dependent models. A back-calculated hatch date distribution could not be computed for 2010 because length-at-age information was not collected. The back-calculation requires information on the relative abundance of age-0 rainbow trout by length category, the age at length, the size-dependent vulnerability of age-0 rainbow trout to sampling, and the postemergence age-0 mortality rate (Campana and Jones 1992). A detailed description of the sampling design, data collection, and back-calculation procedure is provided by Korman (2009) and is briefly summarized here. Age-0 rainbow trout were captured by backpack and boat electrofishing at 40 randomly selected sites on a near-monthly basis during summer and fall in each study year (Table 1). After electrofishing was completed, all fish were measured to the nearest millimeter (fork length) and a subsample of 6–10 fish within each 10-mm length-category across the 40 sites on each trip was preserved in 95% ethanol for age determination via examination of otolith microstructure (Table 1).

Linear models predicting daily age posthatch as a function of fork length were fitted to the otolith data from each year (except 2010) and were used to estimate the daily age of each fish in the

catch. A parametric bootstrapping approach was used to account for error in age-at-length relationships in the predicted hatch date distributions. To account for the cumulative mortality between hatch and date of capture and for length-dependent differences in vulnerability to electrofishing, each draw was multiplied by $(e^{-M \cdot \text{Age} \cdot P_{\text{Age}}})^{-1}$, where e is the base of natural logarithms, M is the instantaneous weekly mortality rate, and P_{Age} is the relative vulnerability of each age to sampling, which depends on fish size and sampling gear (Korman et al. 2009). Back-calculated hatch date distributions were computed by assuming a daily mortality rate of 0.01 (i.e., $M/7$), which was determined from direct estimates for the Lees Ferry age-0 rainbow trout population based on a stock synthesis model (Korman 2009); this rate is within the range of daily mortality rates estimated from studies of Atlantic salmon *Salmo salar* ($M = 0.01$ – 0.02 : Nislow et al. 2004; 0.002 – 0.027 : Einum and Nislow 2005), brown trout *Salmo trutta* (0.007 : Berg and Jørgensen 1991; 0.012 : Elliott 1994), and steelhead (0.003 – 0.005 : Hume and Parkinson 1988). The number of fish hatching each day was aggregated into weekly intervals. Back-calculated hatch date distributions were compared with the distributions predicted from the flow-independent and flow-dependent models based on the degree of correlation between weekly proportions.

Age-0 abundance and growth.—Age-0 rainbow trout abundance on each sampling trip was estimated by using a two-stage design. Abundance at each randomly selected site on each survey was determined by expanding the catch from single-pass electrofishing based on size-dependent capture probabilities determined from mark–recapture experiments conducted at a smaller number of sites in 2007 and 2008 (Korman et al. 2009). An estimate of abundance for the reach was then determined by expanding the sum of population abundances across sites by the proportion of shoreline habitat that was sampled relative to the total amount in the reach. The approach is similar to the method used by Mitro and Zale (2000) to estimate age-0 rainbow trout abundance in the Henrys Fork of the Snake River. Mitro and Zale (2000) allowed capture probabilities to vary across trips and used a mean capture probability for all size-classes. We allowed capture probability to vary with fish size, but we assumed that capture probability did not vary across trips. This is reasonable given that (1) variation in the size of age-0 rainbow trout within the Lees Ferry reach is the dominant factor influencing differences in capture probability across survey trips and (2) flow is not a significant factor affecting capture probability as long as sampling is conducted at the daily minimum flow (Korman and Campana 2009; Korman et al. 2009).

Growth of age-0 rainbow trout over the summer and fall was described by relationships predicting fork length (L) as a function of daily age posthatch (Age), as determined from counts of daily otolith increments,

$$L = (b_0 + b_1 \text{Age})e^\gamma \quad (1)$$

where b_0 represents length at hatch (i.e., intercept), b_1 represents average growth rate (i.e., slope), and v is a normally distributed error term with standard deviation σ , which represents the extent of variation in size at age. We used Akaike's information criterion corrected for small sample size (AIC_c) to evaluate whether length at age and average growth rates were substantively different among years (Burnham and Anderson 2002). For the length-at-age evaluation, we compared AIC_c scores between the simplest (null) model, which included three parameters (b_0 , b_1 , and σ), and the global model, which included parameters that were independently estimated for each year (i.e., 18 parameters). To evaluate differences in growth rates among years, we compared AIC_c scores between the null model and a model in which the intercept was held constant across years but in which the average growth rate and variation in size at age were allowed to vary (13 parameters).

Stock–recruitment relationship between egg deposition and age-0 abundance.—A stock–recruitment approach was used to control for density-dependent effects when evaluating the effects of NFSFs and the 2008 controlled flood on age-0 abundance. The annual total egg deposition and viable egg deposition were calculated as the product of the total number of redds or number of viable redds and the number of eggs deposited per redd. We assumed that each female created a single redd over the spawning season. The mean annual fork length for females during winter and spring in each study year (A. Mankister, Arizona Game and Fish Department, personal communication) was multiplied by a length-standardized fecundity of 58 eggs/cm (Allen and Sanger 1960) to determine the annual number of eggs per redd.

Age-0 abundance estimates were plotted by sampling date to determine the temporal peak of age-0 abundance. This peak period (~July 15) was used to index recruitment to the age-0 population for the stock–recruitment analysis. Mid-July age-0 abundance estimates between 2003 and 2010 ($n = 7$; no data were collected in 2005) were plotted as a function of the total number of eggs and the number of viable eggs deposited in the Lees Ferry reach. A Beverton–Holt stock–recruitment model was fitted to the data assuming lognormal error in recruitment. Data from 2008 and 2009 were excluded from this analysis due to the obvious effect of the 2008 controlled flood. Although this model was based on a limited sample size ($n = 5$), it was only used to approximate the expected age-0 abundance for a given level of viable egg deposition in the absence of flood effects. Stock–recruit data collected in 2008 and 2009 (i.e., shortly after the flood) were compared with this relationship to determine whether recruitment was higher or lower than expected.

RESULTS

Flow and Temperature

The maximum range in daily flow fluctuations during January–March in NFSF years (2003 and 2004) resulted in an average within-day change in river stage of 1.75 m. Relative to

the stage change occurring under normal operations, this represents an increase of 0.8 m in January and 1.0 m in February and March. The maximum daily flow on Sundays during February and March was substantially higher in 2003 than in 2004, which caused large differences in temperature regimes and predicted incubation mortality rates as outlined below. During weekdays in February and March 2003 and 2004, elevations that were inundated by flows of 227 and 340 m^3/s were dewatered for 7–9 and 9–11 h, respectively (Table 2). The maximum daily flow on Sundays in 2004 was lower and resulted in longer periods of dewatering for redds at higher elevations. Elevations that were inundated at flows greater than 340 m^3/s were dewatered for at least 30 consecutive days after March 31 in both 2003 and 2004 (Figure 1; Table 2). Dewatering periods at lower elevations between January and March under normal operations (2006–2010) were considerably shorter than those observed during NFSF years.

Intergravel temperatures increased with ambient air temperature and the duration of dewatering as determined by elevation and flow (Figure 2). Lower daytime flows on Sundays had a noticeable influence on intergravel temperatures in 2004, as seen by the weekly pattern in maximum temperatures in February and March at elevations with inundation discharge levels greater than 142 m^3/s . The upper lethal temperature limit of 16°C was first exceeded for the 227–340- m^3/s elevation class as early as mid-March (2004, 2007) and as late as mid-April (2003), but typically the limit was first exceeded in the last 10 d of March (2006, 2008–2010). Note that the earliest date when the maximum thermal limit was exceeded in 2004 would have occurred almost 1 month later if the Sunday daytime flows had been maintained at weekday levels (Figure 2b).

Spawn Timing and Magnitude and Redd Hypsometry

The peak count of redds summed across 27 sites ranged from 35 (2006) to 963 (2004; Table 1). The date of peak spawning estimated by the spawning model ranged from February 21 (2008, 2010) to March 27 (2006) and averaged March 7 across all study years (Figure 3). Estimates of the total number of redds created each year ranged from a minimum of 88 in 2006 to a maximum of 3,264 in 2003 and averaged 1,640. Spawning activity was extremely limited in 2006; this was probably attributable to unusually warm temperatures and low dissolved oxygen in water released from Glen Canyon Dam during fall 2005. In 2008, the peak count of 571 redds occurred on February 28, just prior to the controlled flood that began on March 5. The total redd count declined by over 50% to 253 redds on March 14 (the first survey after the flood). Redds were very difficult to identify during this survey because very little algae was present, making it hard to distinguish redds from natural depressions in the sediment, especially at sites where redds were located at water depths greater than 1 m. The decline in redd numbers immediately after the controlled flood probably reflected a decrease in detection probability rather than a loss of redds due to scour. The redd count from the first survey after the flood was

TABLE 2. Average duration of dewatering (h/d) for elevations that would be inundated at flows of 227 and 340 m³/s during months that spanned the majority of the spawning and incubation period for rainbow trout in the Lees Ferry reach of the Colorado River. Nonnative fish suppression flows were implemented during January–March in 2003 and 2004. Data from 2009 and 2010 are excluded for brevity, but dewatering durations in these years were very similar to those in 2006–2008.

Month	Year	227 m ³ /s		340 m ³ /s	
		Weekdays	Sundays	Weekdays	Sundays
Feb	2003	9	9	11	11
	2004	7	13	9	21
	2006	0	0	6	9
	2007	0	0	15	20
	2008	0	0	16	19
Mar	2003	9	9	11	11
	2004	7	20	9	24
	2006	6	6	19	22
	2007	3	6	22	24
	2008	4	4	15	19
Apr	2003	5	18	13	24
	2004	5	7	11	24
	2006	5	6	17	22
	2007	5	6	16	23
	2008	2	4	12	20
May	2003	4	12	11	24
	2004	6	9	18	24
	2006	6	7	22	24
	2007	6	7	17	24
	2008	0	0	8	11

therefore not used to derive the estimate of the total number of redds deposited in 2008. The spawning model generally provided good fits to the redd count data, explaining between 68% and 98% of the variability in counts over the spawning season.

The seasonal pattern in the distribution of redds across elevations was in part determined by the interaction between flow regime and spawn timing. During NFSF years (2003 and 2004), higher maximum flows coincided with periods of considerable spawning activity (Figures 1, 3), resulting in a relatively large proportion of redds being created at the elevations inundated by flows above 227 m³/s (Figure 4). In contrast, there was generally very little spawning at elevations with inundation discharges greater than 227 m³/s during normal operating years (2006–2010), when flows between January and March were lower (Figure 1). In NFSF years, spawners were able to construct redds and deposit eggs in high-elevation habitats despite the fact that they were dewatered for 9 h/d (inundation discharge = 227 m³/s) to 11 h/d (340 m³/s; Table 2). The percentage of fish spawning at lower elevations increased between early February and March in NFSF years despite relatively high and consistent maximum flows during the day (Figure 4), thus indicating that factors other than flow contributed to seasonal variation in redd hypsometry. High flows during the day and early evening

allowed fish to spawn at higher elevations but did not appear to completely inhibit spawning at lower elevations that were less vulnerable to dewatering.

Predictions and Observations of Flow-Dependent Incubation Mortality

The incubation mortality model predicted that 23% and 49% of the total number of redds created in NFSF years 2003 and 2004, respectively, did not produce viable young due to fluctuations in flow. These losses were considerably higher than the losses of 5–11% under normal fluctuations in 2006–2010. The limited mortality due to fluctuating flows under normal operations occurred because almost all spawning was restricted to elevations with inundation discharge levels below 227 m³/s (Figure 4), where intergravel temperatures very rarely exceeded lethal limits (Figure 2). Predicted incubation losses were substantially higher in 2004 than in 2003 because maximum intergravel temperatures at elevations inundated by flows above 227 m³/s exceeded the lethal threshold 1 month earlier (due to low daytime flows on Sundays). These Sunday low flows (Table 2) also resulted in lethal temperatures for the 142–227-m³/s elevation class on 2 d in March (Figure 2).

General trends in predicted incubation mortality agreed with trends in mortality determined by direct examination of egg

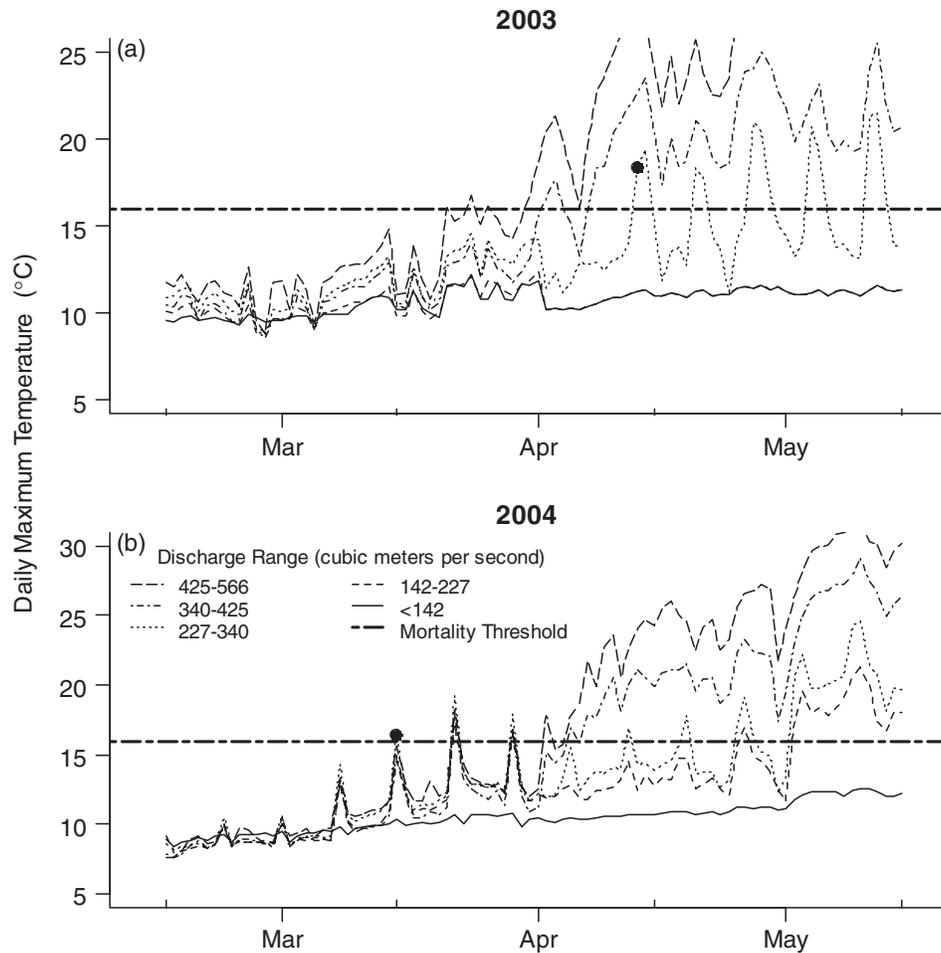


FIGURE 2. Average daily maximum intergravel temperatures ($^{\circ}\text{C}$) from two gravel bars in the Lees Ferry reach of the Colorado River over the majority of the rainbow trout spawning and incubation period in (a) 2003 and (b) 2004. Temperatures represent values at elevations inundated by flows in five categories: less than 142, 142–227, 227–340, 340–425, and 425–566 m^3/s . The dashed horizontal line denotes a 16°C lethal incubation temperature limit. The solid black circles highlight the dates when the lethal limit was first exceeded at elevations inundated by flows of 227–340 m^3/s .

viability in a sample of redds during 2004. Of the 125 redds that were excavated, 80 contained eggs (Table 3). Of these 80 redds, 30% contained mostly dead eggs and were classified as nonviable redds. The percentage of nonviable redds increased progressively with elevation class and was fourfold higher in April and May than in February and March at elevations inundated by flows less than 340 m^3/s . These results were consistent with predictions from the incubation mortality model for 2004, which showed greater mortality for cohorts hatching after March 15 (Figure 5b), 100% mortality at elevations with inundation flows exceeding 227 m^3/s , and 30% mortality at elevations that were inundated by flows of 142–227 m^3/s .

Comparison of Predicted and Back-calculated Hatch Date Distributions

In 2003 and under normal operations (2006–2009), the shapes of predicted flow-independent and flow-dependent hatch date distributions were very similar (Figure 5) and were

highly correlated (Table 4: H_0 versus H_1). In 2004, when flow-dependent incubation mortality was greatest, the flow-dependent hatch date distribution had a broader peak than the flow-independent distribution, resulting in a lower correlation between model predictions relative to other years. Effects of seasonal variation in flow-dependent incubation mortality caused by fluctuating flows during NFSF years (2003 and 2004) were not apparent in the back-calculated hatch date distributions. Flow-independent and flow-dependent models explained similar amounts of variation in back-calculated hatch date distributions (Table 4: H_0 or H_1 versus B).

The effect of the March 2008 controlled flood was very apparent in the hatch date analysis, as a large discrepancy was observed between predicted and back-calculated distributions. Fish that hatched before and up to 1 month after (\sim April 15) the controlled flood had lower early survival rates than expected, whereas the opposite occurred for fish that hatched after this date (Figure 5e). These differences resulted in a very low

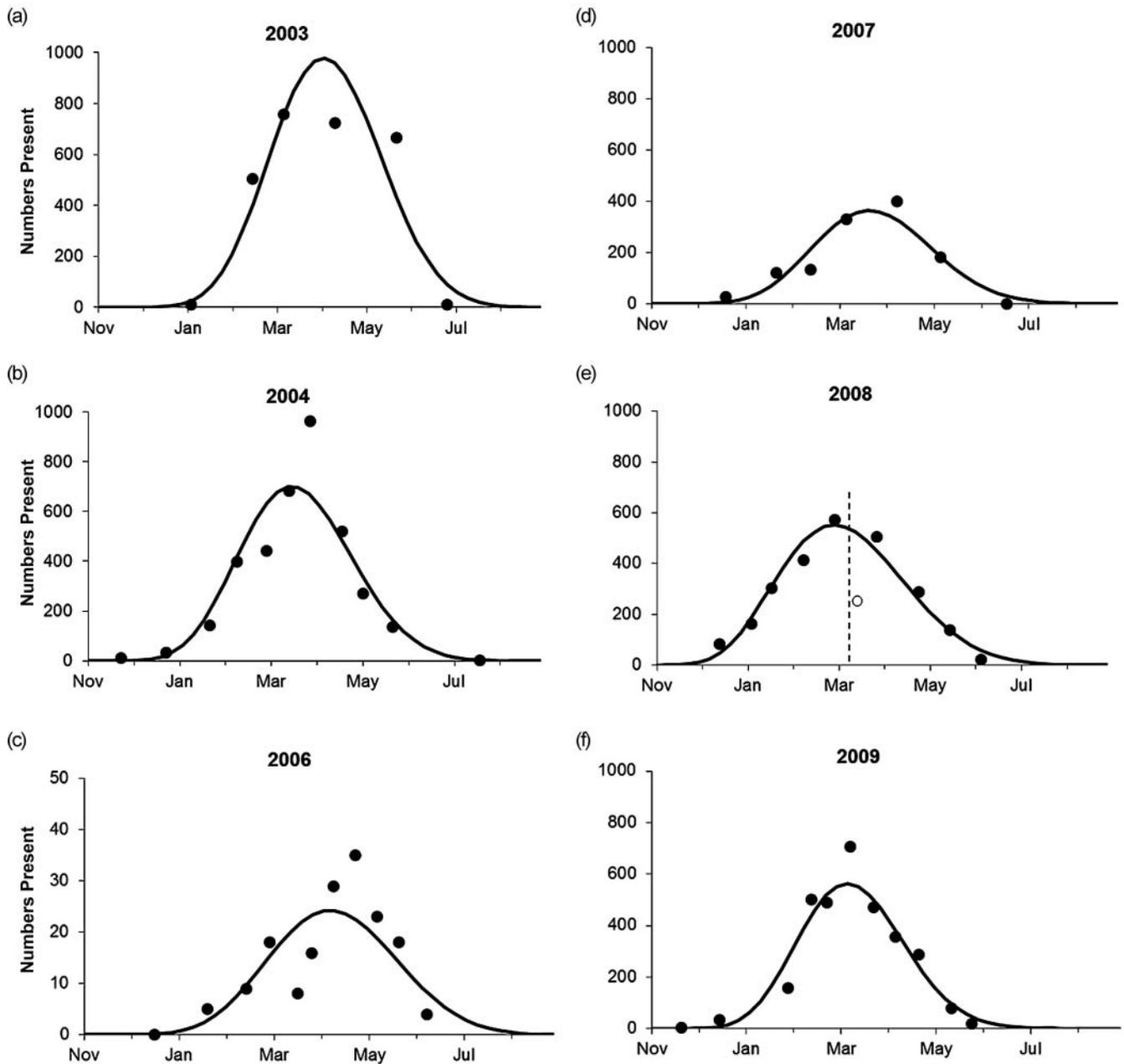


FIGURE 3. Total number of rainbow trout redds counted on each survey date (filled circles) in the Lees Ferry reach of the Colorado River and the number predicted to be present from the spawning model (lines) in (a) 2003, (b) 2004, (c) 2006, (d) 2007, (e) 2008, and (f) 2009. The open circle in (e) represents the count from the first survey after the controlled flood in 2008 (denoted by vertical dashed line), which was not used to estimate parameters of the spawning model. Note the 20-fold reduction in the y-axis scale for (c). For brevity, data from 2010 are not shown.

correlation ($r^2 \sim 0.01\text{--}0.03$) between predicted and back-calculated hatch date distributions over the majority of the hatching period (Table 4; 17-week period).

Age-0 Abundance and Growth

Abundance of age-0 rainbow trout in the Lees Ferry reach increased in spring as fish emerged from the gravel and recruited to the sampled population (Figure 6). Abundance typically peaked

by mid-July and then declined due to recruitment reductions and cumulative mortality and possibly due to downstream dispersal from the Lees Ferry reach. Abundance was lowest in 2006 due to very limited spawning activity and was highest in 2008 and 2009 (i.e., after the 2008 controlled flood). The relative decline in abundance over the summer was greatest in years of high abundance, indicating density dependence in age-0 mortality and possibly in emigration.

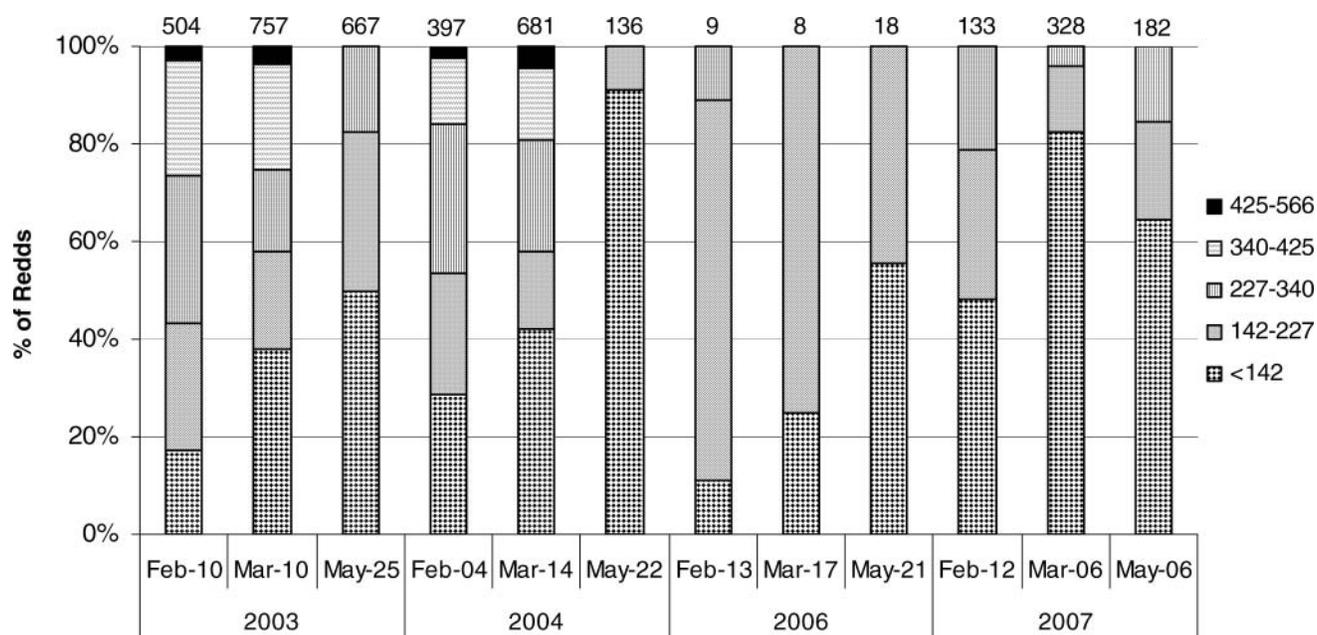


FIGURE 4. Distribution of rainbow trout redds in the Lees Ferry reach of the Colorado River across elevations inundated by flows in five categories (<142, 142–227, 227–340, 340–425, and 425–566 m³/s) during early (February), peak (March), and late (May) periods in the spawning season. Total number of redds counted on each survey is shown above each bar. For brevity, data from 2009 and 2010 are not shown; redd distributions across elevations in these years were very similar to those in 2006 and 2007.

The size of age-0 rainbow trout was slightly larger in 2008 and 2009 (after the controlled flood) than in the majority of years before the flood. There were strong linear relationships between age posthatch and fork length in all years (Figure 7); age predicted 82–93% of the variation in fork length among individuals. Differences in the length-at-age relationships among years were

substantial. The AIC_c score for the null model, in which the parameters of the length-at-age relationship did not vary among years, was 234 units larger than that of the year-specific model, indicating very strong support for the latter model (*sensu* Burnham and Anderson 2002). The AIC_c score for the model in which

TABLE 3. Statistics describing rainbow trout redd excavations in the Lees Ferry reach of the Colorado River, 2004, including the total number excavated, the number that contained eggs, and the percentage that contained only dead eggs. Results are stratified by 2-month period and elevation class (i.e., inundation discharge).

Inundation discharge (m ³ /s)	Feb–Mar	Apr–May	Total
Number of Redds Excavated			
<227	27	8	35
227–340	46	12	58
340–566	32	0	32
Total	105	20	125
Number of Redds with Eggs			
<227	15	5	20
227–340	33	4	37
340–566	23		23
Total	71	9	80
Percentage of Redds with Only Dead Eggs			
<227	13	60	25
227–340	24	100	32
340–566	30		30
Average	24	78	30

TABLE 4. Coefficients of determination (r^2) between predicted rainbow trout hatch date distributions based on the flow-independent model (H_0) and flow-dependent model (H_1 ; see Methods) and between each predicted distribution and the back-calculated hatch date distribution (B). Correlations were computed based on all 52 weeks for each year or based on a subset of only 17 weeks between March and June, when the majority of hatching occurred (see Figure 5).

Year	H_0 vs. H_1	H_0 vs. B	H_1 vs. B
All 52 Weeks			
2003	0.97	0.92	0.98
2004	0.87	0.87	0.85
2006	1.00	0.96	0.96
2007	1.00	0.90	0.90
2008	1.00	0.52	0.55
2009	1.00	0.92	0.93
17 Weeks (Mar–Jun Only)			
2003	0.90	0.82	0.72
2004	0.69	0.78	0.72
2006	0.99	0.94	0.94
2007	1.00	0.64	0.65
2008	0.99	0.01	0.03
2009	1.00	0.85	0.88

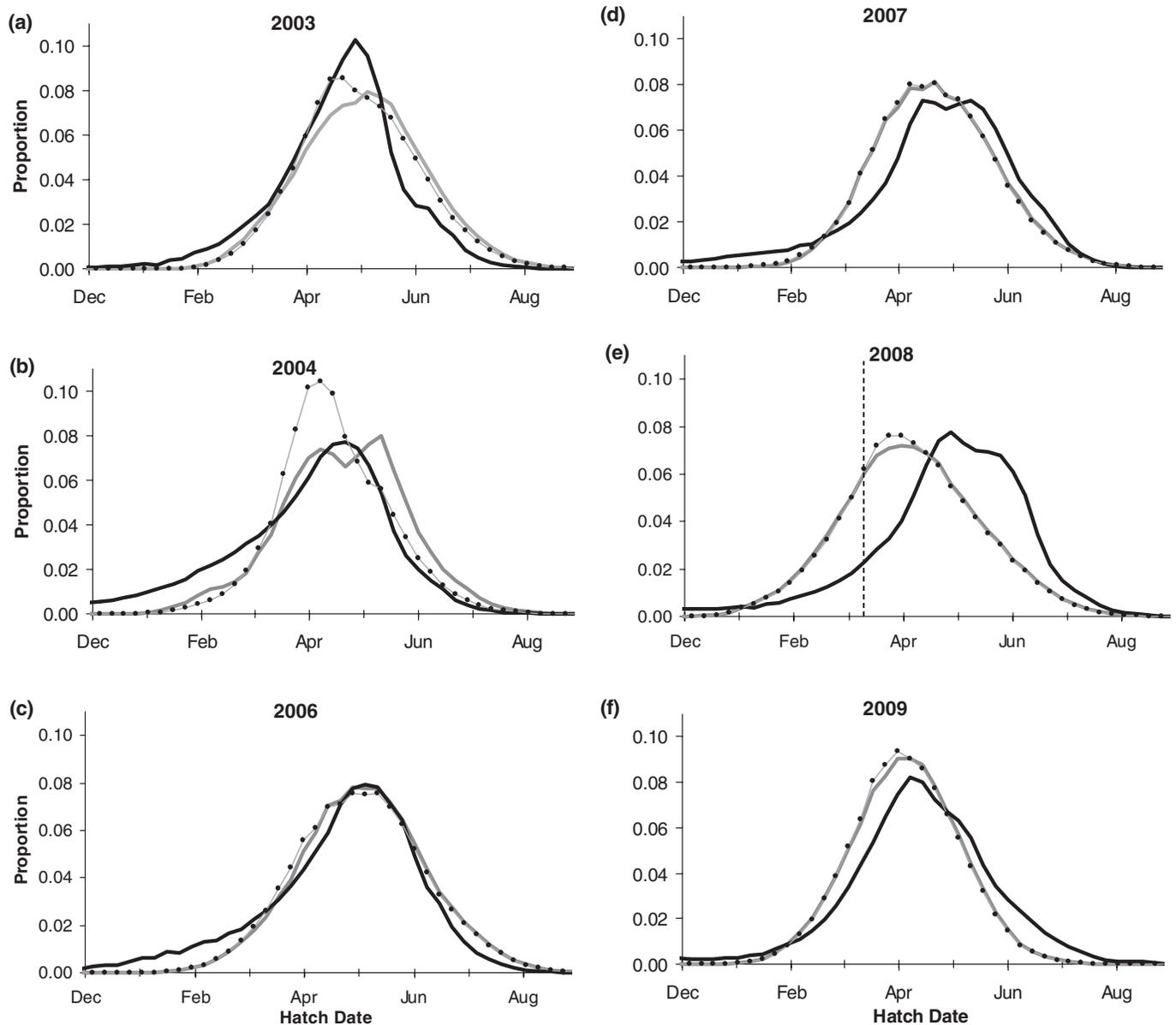


FIGURE 5. Predicted rainbow trout hatch date distributions in the Lees Ferry reach of the Colorado River based on the flow-independent (thin gray line with points) and flow-dependent (thick, dark-gray line) incubation mortality models and back-calculated hatch date distributions (thick black line) in (a) 2003 and (b) 2004, when nonnative fish suppression flows were implemented; and in (c) 2006, (d) 2007, (e) 2008, and (f) 2009, when flow fluctuations were controlled by normal hydropeaking operations. Weekly cohorts where incubation mortality is affected by flow fluctuations are those where the proportions from the flow-independent model exceed those from the flow-dependent ones (e.g., April 1st, 2004). The dashed vertical line in (e) denotes the 2008 controlled flood.

only the intercept was held constant across years was 232 units larger than that of the null model, indicating that growth rates were substantively different among years. The average growth rate based on the model with a constant intercept among years (Figure 8) was highest in 2006 (0.46 mm/d), when age-0 abundance was lowest. However, average growth rates were nearly as high in 2008 (0.44 mm/d) and 2009 (0.45 mm/d) even though abundance during the summer was eightfold higher (in 2008) or fivefold higher (in 2009) than abundance in 2006.

Egg Deposition and Age-0 Abundance Stock–Recruitment Relationship

The abundance of age-0 rainbow trout in the Lees Ferry reach during July (2003–2010) was resilient to changes in egg deposition, as determined by either the estimated total number of redds or the number of viable redds (Figure 9). In spite of a greater than 10-fold reduction in viable egg deposition in 2006, age-0 abundance declined by less than 50% compared with abundances in other years (i.e., excluding 2008 and 2009).

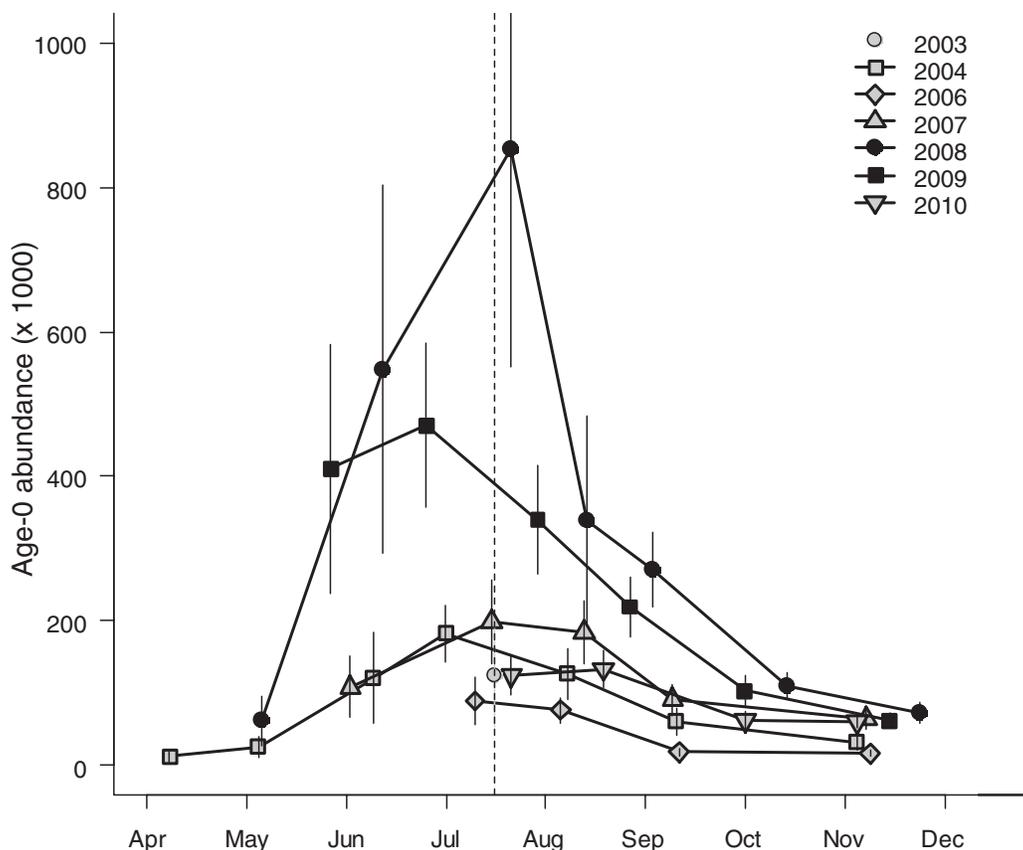


FIGURE 6. Seasonal trends in the total abundance of age-0 rainbow trout in the Lees Ferry reach of the Colorado River, 2004–2010 (no data were collected in 2005). The estimated reachwide abundance during the mid-July sample period in 2003 is also shown. The vertical dashed line represents July 15, the standard date used for annual recruitment values in the stock–recruitment analysis (see Figure 9). Light-gray vertical lines represent the 95% confidence limits for abundance estimates.

The fit of the Beverton–Holt model to the 2003–2007 and 2010 data suggests that early survival rates from fertilization to approximately 2 months posthatch, when age-0 fish first became vulnerable to capture, were strongly density dependent. The overall early survival rate was 60% in 2006, when abundance was very low, compared with 3–9% in other years (except 2008 and 2009). In 2008 and 2009 (after the controlled flood), early survival rates ranged from 14% to 19%. Although incubation losses due to flow fluctuations were large (23–49%) in years when NFSFs were implemented, the stock–recruitment relationship indicated that given the viable egg deposition, these incubation losses were not high enough to reduce the abundance of the age-0 population. After the 2008 controlled flood, age-0 abundance in July 2008 and 2009 was 4.4- and 2.5-fold higher than expected given the number of viable eggs in those years and given the stock–recruit relationship based on all other years.

DISCUSSION

When implemented within the limits imposed by negative effects of very high fluctuations on other resources, increasing

flow fluctuations during the rainbow trout spawning and incubation period are unlikely to be effective at regulating the abundance of rainbow trout populations in the Colorado River below Glen Canyon Dam. The NFSFs released from Glen Canyon Dam in January–March during 2003 and 2004 were predicted to result in incubation losses of 23–49%, but these losses did not reduce the abundance of age-0 rainbow trout. We hypothesize that this occurred because of strong compensation in survival rates between fertilization and approximately 2 months posthatch. This interpretation is supported by direct observations of substantial flow-dependent incubation losses in combination with the lack of evidence for any effect on back-calculated hatch date distributions or age-0 abundance. Additional monitoring of viable egg deposition and the resulting age-0 abundance is required to reduce uncertainty in the stock–recruitment relationship, which provides the strongest support for this conclusion.

Multiple lines of evidence indicated that the March 2008 controlled flood resulted in a large increase in the early survival rates of rainbow trout within the Lees Ferry reach; this survival increase was probably attributable to an improvement in habitat conditions and food availability for recently emerged fish. Age-0 abundance in July 2008 was over fourfold higher than expected

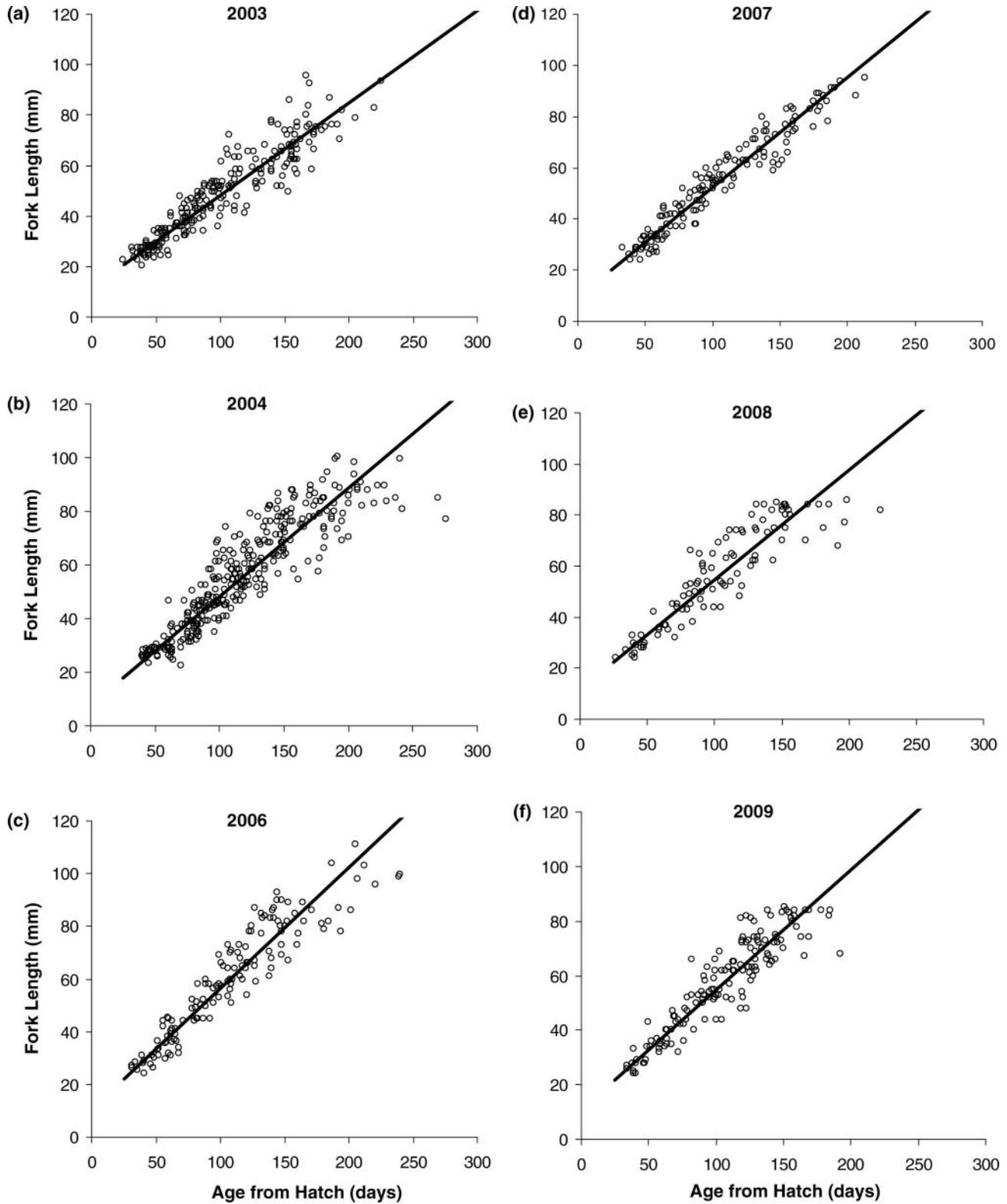


FIGURE 7. Length-at-age relationships for age-0 rainbow trout in the Lees Ferry reach of the Colorado River based on counts of daily otolith rings in (a) 2003, (b) 2004, (c) 2006, (d) 2007, (e) 2008, and (f) 2009. The lines are the best-fit models in which the intercept, slope, and variation in length at age were allowed to vary among years.

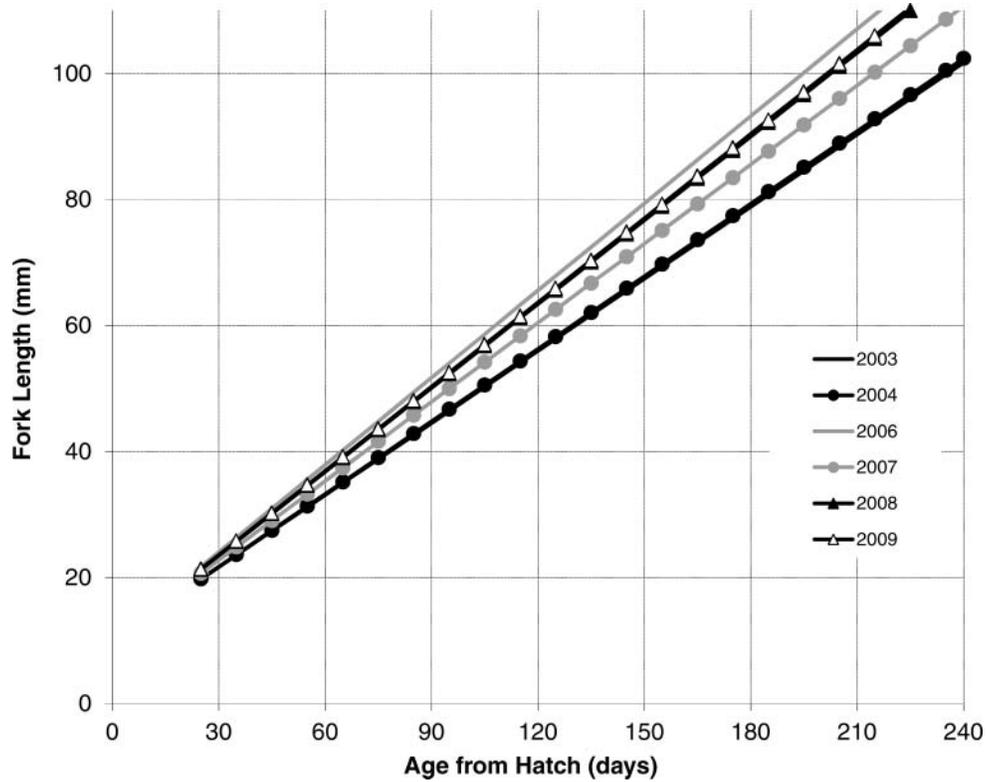


FIGURE 8. Comparison of annual length-at-age relationships for age-0 rainbow trout in the Lees Ferry reach of the Colorado River; the intercept (length at hatch) was set constant among years, but the slope (average growth rate) and variation in length at age were allowed to vary. These relationships were estimated from the data shown in Figure 7. Note that relationships overlap for 2003 and 2004 and for 2008 and 2009 and are difficult to distinguish in the figure.

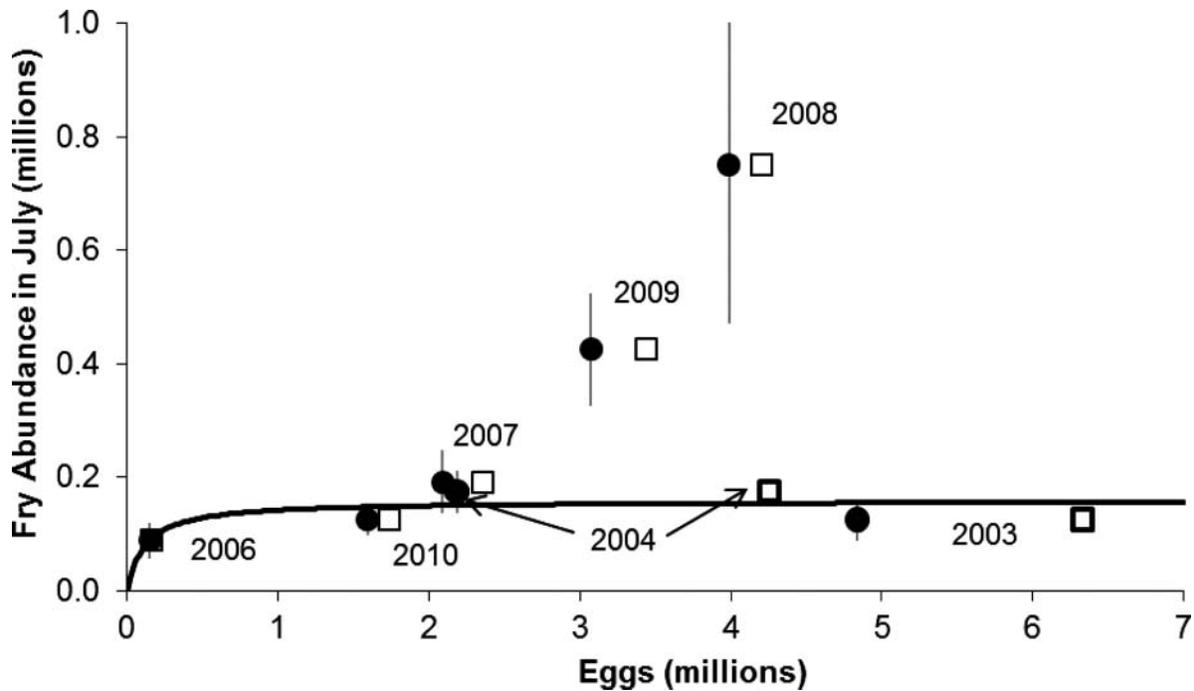


FIGURE 9. Relationships between the total number of eggs (open squares) and the number of viable eggs (filled circles) deposited by rainbow trout in the Lees Ferry reach of the Colorado River and the resulting age-0 population size on July 15, 2003–2010 (no data were collected in 2005). The thick black line shows the best-fit Beverton-Holt model to the number of viable eggs using data from all years except 2008 and 2009. Light-gray vertical lines represent the 95% confidence limits for abundance estimates.

given the number of viable eggs that produced these fish. The hatch date analysis indicated that early survival rates were much higher for cohorts that emerged 2 months or more after the flood. Average growth rates of age-0 rainbow trout in summer 2008 were virtually the same as in 2006 even though abundance was eightfold greater in 2008. As growth of juvenile salmonids often declines at higher density (Jenkins et al. 1999; Nislow 2001; Imre et al. 2005; Ward et al. 2007), this result likely indicates that the quality of the rearing environment for age-0 rainbow trout in the Lees Ferry reach improved after the controlled flood, thus overriding the effect of high abundance on growth. On the basis of increased sand transport measured at the downstream end of the Lees Ferry reach (U.S. Geological Survey gage 09380000) during the 2008 controlled flood (D. Topping, U.S. Geological Survey, personal communication), it is very likely that the 2008 flood increased interstitial spaces in the gravel substrate of the streambed. It is also likely that the 200-fold increase in the ratio of palatable invertebrate drift taxa relative to the total drift and the twofold to sixfold increase in the biomass of palatable taxa in the drift, both of which occurred within a few months of the 2008 controlled flood (Rosi-Marshall et al. 2010; Cross et al., in press), led to increases in the growth and survival of young rainbow trout that emerged 2 months or more after the flood. Interestingly, age-0 growth and abundance in 2009 were higher than expected given the age-0 abundance and the number of viable eggs deposited in that year, which suggests that the effect of the 2008 controlled flood on early life stages persisted into 2009.

Inferences about the effects of future controlled floods during spring on early survival and age-0 growth from this analysis are limited by the fact that only one treatment was evaluated. Ideally, this early life stage monitoring effort will continue to determine whether the responses from future events are similar to those observed for the 2008 controlled flood. The conclusion that controlled floods during spring increase survival of early life stages is consistent with the historical recruitment trend estimated with a statistical catch-at-age model applied to adult catch data (C. Walters, University of British Columbia, personal communication). That analysis showed that the recruitment of juvenile trout in 1997—1 year after a controlled flood in March 1996—was 2.8-fold greater than other estimates of recruitment during the 1990s. Our result is also consistent with increased catch rates of age-0 rainbow trout downstream of Glen Canyon Dam after the 1996 flood (Valdez et al. 2001) and with the positive responses of salmonid populations to controlled floods in other river systems (e.g., Ortlepp and Murle 2003).

Long-term studies of juvenile salmonid populations have shown that the majority of density-dependent mortality occurs during a “critical period” when fry first emerge from their incubation environment and compete for limited feeding territories (Elliott 1994; Nislow et al. 2004; Einum and Nislow 2005), which is consistent with results from our stock–recruit analysis. Habitat quality and availability during the critical period, as affected by operations from Glen Canyon Dam, are likely to be important factors controlling the rates of juvenile rainbow trout

recruitment to the adult population in the Lees Ferry reach. Flow changes that affect incubating life stages are unlikely to have a significant effect on juvenile abundance because of strong density dependence during and shortly after emergence. Increased flow fluctuations targeting fish after this critical period, which occurs in May and June, are likely to be more effective at regulating rainbow trout abundance in the Lees Ferry reach than the January–March NFSFs evaluated here. High flows during and shortly after the peak emergence period (May–July) may also be effective at reducing rainbow trout abundance (Heggenes and Traaen 1988; Jensen and Johnsen 1999) by limiting the availability of the low-velocity nearshore habitat that is critical for recently emergent fish (Nehring and Anderson 1993).

Early survival rates of cohorts that hatched at least 1 month after the 2008 controlled flood (i.e., that hatched after approximately April 15) were much higher than the survival rates of cohorts that hatched before this date. This change coincides almost perfectly with the timing of the controlled flood (March 5–9) and its expected effects. Cohorts that hatched prior to April 15 and showed relatively poor survival would have been fertilized before March 15. Some of these fish would have emerged prior to the high flows (if fertilized no later than mid-January) and would have been very vulnerable to displacement and mortality due to increased water velocity (Heggenes and Traaen 1988; Einum and Nislow 2005). Most would have still been in the gravel when the flood occurred and would have been vulnerable to scour or burial; those that survived would have emerged within a few months of the high-flow event during a period of reduced food availability given the lag between high flows and recovery of the benthic invertebrate community (Shannon et al. 2001; Rosi-Marshall et al. 2010; Cross et al., in press). Cohorts that hatched after April 15 and had much higher early survival rates would have been fertilized after the flood and therefore would not have been prone to scour, burial, or displacement. These cohorts would also have emerged into a benthic invertebrate community that was enhanced by the flood event (Rosi-Marshall et al. 2010; Cross et al., in press).

The comparison of predicted and back-calculated hatch date distributions cannot be used to compare early survival rates for weekly cohorts in 2008 with those from normal operating years because the hatch date analysis only provides information on relative differences in survival rates across weeks within years. An interannual comparison would help to determine which mechanisms were responsible for the unique hatch date distribution of the 2008 brood. On the basis of the hatch date analysis alone, we cannot tell whether the early survival rate for the cohorts that hatched before April 15 were anomalously low (relative to other years) due to redd scour and displacement of recently emerged fish or whether survival rates for later cohorts were enhanced due to improved habitat conditions and food availability. Given the much higher early survival rates for the 2008 brood as a whole relative to other years as evident in the stock–recruitment analysis, it is quite certain that the survival rates for cohorts that hatched after April 15 were much higher than normal in

2008. However, it is still uncertain whether the survival of early cohorts was similar to or lower than that in previous years. Korman (2009) developed a stock synthesis model to estimate parameters defining key early life history processes (including early survival rates) for weekly cohorts by jointly maximizing the model fit to data on redd counts and age-0 catch, length frequencies, capture probabilities, and length at age. The analysis (Korman et al., in press) indicates that survival of early cohorts in 2008 was similar to or higher than survival of early cohorts in the pre-flood years except 2006, when there was a strong compensatory survival response. Thus, the variation in early survival among weekly cohorts in 2008 is very likely the result of enhanced rates for later cohorts that emerged at least 2 months after the flood rather than being the result of reduced survival for early cohorts that emerged prior to this time (i.e., due to displacement) or were still incubating when the flood occurred (i.e., due to redd scour).

Redd dewatering will not be a significant factor controlling population abundance if the majority of redds are not dewatered or if there is a strong density-dependent survival response after the dewatering event. In the Lees Ferry reach, hundreds of redds were dewatered in years with greater flow fluctuations. However, the majority of redds were below the minimum daily flow elevation and were therefore not vulnerable to dewatering. We commonly observed fish spawning at depths of 1–2 m at minimum daily flows, and at a few sites spawning behavior and redds were observed at 4-m depth in the center of the channel. To our knowledge, extensive deepwater spawning by salmonids in rivers has only been reported for Chinook salmon (Chapman et al. 1986; McMichael et al. 2005) and would be considered unusual for smaller (25–45 cm) resident rainbow trout like those in the Lees Ferry reach. In large regulated rivers, where the freshet is much reduced, we suspect that redd surveys will underestimate the extent of deepwater spawning if their design is based on the paradigm that fish only spawn in shallow habitats. This bias will result in an overestimate of the proportion of redds that are vulnerable to the effects of flow fluctuations. Even if representative spawning surveys are conducted and incubation losses are accurately quantified, assessments must measure the net biological effects of flow fluctuations by sampling the juvenile population. Strong density-dependent compensation in postemergent survival rates has considerable potential to mitigate for losses incurred during the incubation period due to flow fluctuations and other anthropogenic or naturally occurring disturbances.

Our initial predictions from the two central hypotheses examined in this study were incorrect. We were correct in assuming that greater flow fluctuations would increase the extent of incubation mortality, but the assumption that this mortality would exceed compensatory survival responses appears to have been wrong. Control of nonnative fish populations will be most effective when additional mortality is applied to older life stages after the majority of density-dependent mortality has occurred. We were also incorrect in assuming that the 2008 controlled flood

would have negligible effects on age-0 abundance, although the response was not surprising given the benefits that have been observed (e.g., Ortlepp and Murle 2003) or postulated to occur (Poff et al. 1997) in other systems. The controlled flood in 2008 significantly enhanced the early survival rates of rainbow trout and led to a very large increase in age-0 abundance, which conflicts with the native fish restoration objective underlying the flood's implementation. These results point to the need to rigorously assess instream decisions through the evaluation of population-level responses.

ACKNOWLEDGMENTS

The U.S. Geological Survey funded this research through the Grand Canyon Monitoring and Research Center. We thank Mike Yard and Lew Coggins for developing the initial ideas for this project. We are grateful to Carl Walters, Steve Martell, Mike Bradford, and Eric Parkinson for providing helpful comments and suggestions on study design, modeling approaches, and interpretation of results. Thanks are extended to Mike Yard, Barbara Ralston, and Carol Fritzinger for field and administrative support. We appreciate Dave Foster, Steve Jones, Steward Reeder, Lew Coggins, Jeff Snee, Steve Hall, Robert Ahrens, Brian Dierker, Peter Weiss, Scott Decker, Gene Tisdale, Tom Nevin, Chris Magirl, Elizabeth Yard, and Andy Makinster for participating in the field work. We thank Joe Hazel for survey support; Tom Gushue for geographical information systems support; and Steven Campana, Drew Dutterer, Bill Pine, Linda Marks, Tania Davignon-Burton, and Jenna Denyes for analysis of otolith microstructure. We also thank the four anonymous reviewers who provided helpful comments on an earlier version of the manuscript.

REFERENCES

- Allen, G. H., and G. A. Sanger. 1960. Fecundity of rainbow trout from actual counts of eggs. *Copeia* 1960:250–261.
- Arndt, S. K. A., R. A. Cunjak, and T. J. Benfey. 2002. Effects of summer floods and spatial-temporal scale on growth and feeding of juvenile Atlantic salmon in two New Brunswick streams. *Transactions of the American Fisheries Society* 131:607–622.
- Barnhouse, L. W., R. J. Klauda, D. S. Vaughn, and R. L. Kendall. 1988. Science, law and Hudson River power plants. American Fisheries Society, Monograph 4, Bethesda, Maryland.
- Benenati, E. P., J. P. Shannon, D. W. Blinn, K. P. Wilson, and S. J. Hueftle. 2000. Reservoir-river linkages: Lake Powell and the Colorado River, Arizona. *Journal of the North American Benthological Society* 19:742–755.
- Berg, S., and J. Jørgensen. 1991. Stocking experiments with 0+ and 1+ trout parr, *Salmo trutta* L., of wild and hatchery origin I: poststocking mortality and smolt yield. *Journal of Fish Biology* 39:151–169.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference, 2nd edition. Springer-Verlag, New York.
- Campana, S. E., and C. M. Jones. 1992. Analysis of otoliths microstructure data. Canadian Special Publication of Fisheries and Aquatic Sciences 117:73–100.
- Chapman, D. W., D. E. Weitkamp, T. L. Welsh, M. B. Dell, and T. H. Schadt. 1986. Effects of river flow on the distribution of Chinook salmon (*Oncorhynchus tshawytscha*) redds. *Transactions of the American Fisheries Society* 115:537–547.

- Coggins, L. G. Jr. 2008. Active adaptive management for native fish conservation in the Grand Canyon: implementation and evaluation. Doctoral dissertation. University of Florida, Gainesville.
- Coggins, L. G. Jr., and C. J. Walters. 2009. Abundance trends and status of the Little Colorado River population of humpback chub: an update considering data from 1989–2008. U.S. Geological Survey, Open-File Report 2009-1075. Available: pubs.usgs.gov/of/2009/1075/. (March 2010).
- 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.
- Connor, E. J., and D. E. Pflug. 2004. Changes in the distribution and density of pink, chum, and Chinook salmon spawning in the Upper Skagit River in response to flow management measures. *North American Journal of Fisheries Management* 24:835–852.
- Crecco, V., and T. Savoy. 1987. Effects of climatic and density-dependent factors on intra-annual mortality of larval American shad. Pages 69–81 in R. D. Hoyt, editor. Tenth annual larval fish conference. American Fisheries Society, Symposium 2, Bethesda, Maryland.
- Cross, W. F., C. V. Baxter, K. C. Donner, E. J. Rosi-Marshall, T. A. Kennedy, R. O. Hall, H. A. W. Kelly, and R. S. Rogers. In press. Ecosystem ecology meets adaptive management: food web response to a controlled flood on the Colorado River, Glen Canyon. *Ecological Applications*.
- Elliott, J. M. 1994. *Quantitative ecology and the brown trout*. Oxford University Press, Oxford, UK.
- Einum, S., and K. H. Nislow. 2005. Local-scale density-dependent survival of mobile organisms in continuous habitats: an experimental test using Atlantic salmon. *Oecologia (Heidelberg)* 143:203–210.
- Fletcher, R. I., and R. B. Deriso. 1988. Fishing in dangerous waters: remarks on a controversial appeal to spawner-recruit theory for long-term impact assessment. Pages 232–244 in L. W. Barnhouse, R. J. Klauda, D. S. Vaughn, and R. L. Kendall, editors. *Science, law and Hudson River power plants*. American Fisheries Society, Monograph 4, Bethesda, Maryland.
- Ford, B. S., P. S. Higgins, A. F. Lewis, K. L. Cooper, T. A. Watson, C. M. Gee, G. L. Ennis, and R. L. Sweeting. 1995. Literature reviews of the life history, habitat requirements and mitigation/compensation strategies for thirteen sport fish species in the Peace, Liard and Columbia River drainages of British Columbia. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2321.
- Hartman, G. F., and J. C. Scrivener. 1990. Impacts of forestry practices on a coastal stream ecosystem, Carnation Creek, British Columbia. *Canadian Bulletin of Fisheries and Aquatic Sciences* 223.
- Heggenes, J., and T. Traaen. 1988. Downstream migration and critical water velocities in stream channels for fry of four salmonid species. *Journal of Fish Biology* 32:717–727.
- Hilborn, R., B. G. Bue, and S. Sharr. 1999. Estimating spawning escapements from periodic counts: a comparison of methods. *Canadian Journal of Fisheries and Aquatic Sciences* 56:888–896.
- Holtby, L. B., and M. C. Healey. 1986. Selection for adult size in female coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 43:1946–1959.
- Houde, E. D. 1987. Fish early life dynamics and recruitment variability. Pages 17–29 in R. D. Hoyt, editor. Tenth annual larval fish conference. American Fisheries Society, Symposium 2, Bethesda, Maryland.
- Hume, J. M. B., and E. A. Parkinson. 1988. Effects of size at and time of release on the survival and growth of steelhead fry stocked in streams. *North American Journal of Fisheries Management* 8:50–57.
- Imre, I., J. W. A. Grant, and R. A. Cunjak. 2005. Density-dependent growth of young-of-year Atlantic salmon (*Salmo salar*) in Catamaran Brook, New Brunswick. *Journal of Animal Ecology* 74:508–516.
- Jenkins, T. M. Jr., S. Diehl, K. W. Kratz, and S. D. Cooper. 1999. Effects of population density on individual growth of brown trout in streams. *Ecology* 80:941–956.
- Jensen, A. J., and B. O. Johnsen. 1999. The functional relationship between peak spring floods and survival and growth of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). *Functional Ecology* 13:778–785.
- Jensen, J. O. T., W. E. McLean, P. J. Rombough, and T. Septav. 1992. Salmonid incubation and rearing programs for IBM-compatible computers. Canadian Technical Report of Fisheries and Aquatic Sciences 1878.
- Kondolf, G. M., G. F. Cada, and M. J. Sale. 1987. Assessing flushing-flow requirements for brown trout spawning gravels in steep streams. *Water Research Bulletin* 23:927–935.
- Korman, J. 2009. Early life history dynamics of rainbow trout in a large regulated river. Doctoral dissertation. University of British Columbia, Vancouver. Available: hdl.handle.net/2429/4127. (March 2010).
- 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.
- Korman, J., S. J. D. Martell, and C. J. Walters. In Press. Describing population dynamics for early life stages of rainbow trout using a stock synthesis model. *Canadian Journal of Fisheries and Aquatic Sciences*.
- Korman, J., M. Yard, C. J. Walters, and L. G. Coggins. 2009. Effects of fish size, habitat, flow, and density on capture probabilities of age-0 rainbow trout estimated from electrofishing at discrete sites in a large river. *Transactions of the American Fisheries Society* 138:58–75.
- Lobon-Cervia, J. 2007. Numerical changes in stream-resident brown trout (*Salmo trutta*): uncovering the roles of density-dependent and density-independent factors across space and time. *Canadian Journal of Fisheries and Aquatic Sciences* 64:1429–1447.
- Lovich, J. E., and T. S. Melis. 2007. The state of the Colorado River ecosystem in Grand Canyon: lessons from 10 years of adaptive management. *Journal of River Basin Management* 5:207–221.
- Magee, J. P., T. E. McMahon, and R. F. Thurow. 1996. Spatial variation in spawning habitat of cutthroat trout in a sediment-rich stream basin. *Transactions of the American Fisheries Society* 125:768–779.
- McKinney, T., D. W. Speas, R. S. Rogers, and W. R. Persons. 2001. Rainbow trout in a regulated river below Glen Canyon Dam, Arizona, following increased minimum flows and reduced discharge variability. *North American Journal of Fisheries Management* 21:216–222.
- McMichael, G. A., C. L. Rakowski, B. B. James, and J. A. Lukas. 2005. Estimated fall Chinook salmon survival to emergence in dewatered redds in a shallow side channel of the Columbia River. *North American Journal of Fisheries Management* 25:876–884.
- Methot, R. D. 1983. Seasonal variation in survival of larval northern anchovy, *Engraulis mordax*, estimated from the age distribution of juveniles. U.S. National Marine Fisheries Service Fishery Bulletin 81:741–750.
- Mitro, M. G., and A. V. Zale. 2000. Predicting fish abundance using single-pass removal sampling. *Canadian Journal of Fisheries and Aquatic Sciences* 57:951–961.
- Mitro, M. G., A. V. Zale, and B. A. Rich. 2003. The relation between age-0 rainbow trout (*Oncorhynchus mykiss*) abundance and winter discharge in a regulated river. *Canadian Journal of Fisheries and Aquatic Sciences* 60:135–139.
- Montgomery, W. L. and K. Tinning. 1993. Impact of fluctuating water levels on early life history of rainbow trout. Report prepared for Glen Canyon Environmental Studies. Available: www.gcmrc.gov. (March 2010).
- Murle, U., J. Ortlepp, and M. Zahner. 2003. Effects of experimental flooding on riverine morphology, structure and riparian vegetation: the River Spol, Swiss National Park. *Aquatic Sciences* 65:191–198.
- Nehring, R. B., and R. M. Anderson. 1993. Determination of population-limiting critical salmonid habitats in Colorado streams using the physical habitat simulation system. *Rivers* 4:1–19.
- Nislow, K. H. 2001. International symposium on the implications of salmonid growth variation. *Reviews in Fish Biology and Fisheries* 10:521–527.
- Nislow, K. H., S. Einum, and C. L. Folt. 2004. Testing predictions of the critical period for survival concept using experiments with stocked Atlantic salmon. *Journal of Fish Biology* 65(Supplement A):188–200.
- Nislow, K. H., F. J. Magilligan, C. L. Folt, and B. P. Kennedy. 2002. Within-basin variation in short term effects of a major flood on stream fishes and invertebrates. *Journal of Freshwater Ecology* 17:305–318.

- Oliver, G. G., and L. E. Fidler. 2001. Towards a water quality guideline for temperature in the province of British Columbia. Report prepared for British Columbia Ministry of Environment, Lands, and Parks, Water Management Branch by Aspen Applied Sciences, Cranbrook, British Columbia. Available: www.env.gov.bc.ca/wat/wq/BCguidelines/temptech/index.html. (March 2010).
- Ortlepp, J., and U. Murle. 2003. Effects of experimental flooding on brown trout: the River Spol, Swiss National Park. *Aquatic Sciences* 65:232–238.
- Peterman, R. M., M. J. Bradford, N. C. H. Lo, and R. D. Methot. 1988. Contribution of early life stages to interannual variability in recruitment of northern anchovy (*Engraulis mordax*). *Canadian Journal of Fisheries and Aquatic Sciences* 45:8–16.
- Piper, R. G., I. B. McElwain, L. E. Orme, J. P. McCraren, L. G. Fowler, and J. R. Leonard. 1982. Fish hatchery management. U.S. Fish and Wildlife Service, Washington, D.C.
- 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.
- Reiser, D. W., and R. G. White. 1983. Effects of complete redd dewatering on salmonid egg-hatching success and development of juveniles. *Transactions of the American Fisheries Society* 112:532–540.
- Rosi-Marshall, E. J., T. A. Kennedy, D. W. Kincaid, W. F. Cross, H. A. W. Kelly, K. A. Behn, T. White, R. O. Hall, and C. V. Baxter. 2010. Short-term effects of the 2008 high-flow experiment on macroinvertebrates in the Colorado River below Glen Canyon Dam, Arizona. U.S. Geological Survey, Open File Report 2010-1031, Reston, Virginia.
- Schmidt, J. C., D. L. Wegner, E. D. Andrews, R. A. Valdez, and D. T. Patten. 1999. Origins of the 1996 controlled flood in Grand Canyon. Pages 22–36 in R. H. Webb, J. C. Schmidt, G. R. Marzolf, and R. A. Valdez, editors. *The controlled flood in Grand Canyon*. American Geophysical Science Union, Washington, D.C.
- Shannon, J. P., D. S. Blinn, T. McKinney, E. P. Benenati, K. P. Wilson, and C. O'Brien. 2001. Aquatic food base response to the 1996 test flood below Glen Canyon Dam, Colorado River, Arizona. *Ecological Applications* 11:672–685.
- Travnicek, V. H., M. B. Bain, and M. J. Maccina. 1995. Recovery of a warmwater fish assemblage after the initiation of a minimum-flow release downstream from a hydroelectric dam. *Transactions of the American Fisheries Society* 124:835–844.
- Uehlinger, U., B. Kawecka, and C. T. Robinson. 2003. Effects of experimental floods on periphyton and stream metabolism below a high dam in the Swiss Alps (River Spol). *Aquatic Sciences* 65:199–209.
- Valdez, R. A., T. L. Hoffnagle, C. C. McIvor, T. McKinney, and W. C. Leibfried. 2001. Effects of a test flood on fishes of the Colorado River in Grand Canyon, Arizona. *Ecological Applications* 11:686–700.
- Voichick, N., and S. Wright. 2007. Water temperature data from the Colorado River and tributaries, between Glen Canyon Dam and Spencer Canyon, northern Arizona, 1988–2005. U.S. Geological Survey, Data Series Report 251, version 1.0, Washington, D.C.
- Ward, D. M., K. H. Nislow, J. D. Armstrong, S. Einum, and C. L. Folt. 2007. Is the shape of the density-growth relationship for stream salmonids evidence for exploitative rather than interference competition? *Journal of Animal Resource Ecology* 76:135–138.
- Wright, S. A., T. S. Melis, D. J. Topping, and D. M. Rubin. 2005. Downstream sand resources of the Colorado River in Grand Canyon. U.S. Geological Survey Circular 1282:17–23. Available: www.gcmrc.gov/products/score/2005/pdf/score_2005.pdf. (March 2010).