

Drought-related changes in water quality surpass effects of experimental flows on trout growth downstream of Lake Powell reservoir

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Abstract

Flows released from reservoirs are often modified to mitigate the negative ecosystem effects of dams. We estimated the effects of two experimental flows, fall-timed floods and elimination of sub-daily variation in flows on weekends, on growth rates of rainbow trout (*Oncorhynchus mykiss*) in the Colorado River downstream from Glen Canyon Dam. Experimental flow effects were compared to effects of water temperature, phosphorous concentration, solar insolation, and competition, by fitting mixed effect von Bertalanffy models to ~ 10 000 observations of growth from mark-recapture between 2012 and 2021. There was strong support for models predicting faster growth during intervals with higher solar insolation, and lower water temperature and competition for prey. Effects of phosphorus and experimental flows were small and uncertain. Drought-related increases in dam release temperatures during summer and fall were predicted to result in severe weight loss for larger trout and could eventually threaten the viability of the population and the fishery it supports. The effects of water temperature and competition on fish growth substantially exceeded the effects of controlled floods and steadier flows.

Key words: Drought, fish growth, water quality, controlled floods, hydropeaking, water temperature

Introduction

Dams and river regulation have fundamentally altered flow regimes of the world's rivers (Petra and others 2009). Environmental flows (e-flows) seek to replicate aspects of the quantity, timing, or quality of natural flow regimes to mitigate undesired effects of dam operations on physical and biological components of the aquatic ecosystem (Acreman et al. 2014). The natural flow paradigm (Poff et al. 1997) is often used as a starting point in the design of e-flows (Davies et al. 2014; Kierman et al. 2012). Two of the more common e-flow types that have been implemented on numerous regulated rivers throughout the world include partial restoration of natural floods, and stabilizing flows to mitigate negative effects of hourly fluctuations in discharge associated with hydropower production (Olden et al. 2014). In many cases the ultimate goal of e-flows is to improve the health of desired fish populations, including endangered species or those that support recreational or commercial fisheries (King et al. 2010; Warren et al. 2015). By catalyzing improvements in fish habitat, prey availability, or reducing predation risk, e-flows can lead to increases in vital rates of somatic growth, reproduction, recruitment, or survival (Nislow and Armstrong 2012; Rytwinski et al. 2020), which in turn could lead to increases in abundance or productivity of fish populations.

E-flows can be evaluated through flow experiments, where a response variable is measured over a period when flows are purposefully manipulated (Konrad et al. 2011). While flow experiments are becoming more common, the ability to reliably quantify the effects of e-flows is variable (Acreman et al. 2014; Souchon et al. 2008). The hallmarks of robust experiments are control of confounding factors, sufficient power (a function of expected effect size and background variability), independent replicates, and random application of treatments. In rivers, water quality and biotic effects such as competition can be important drivers of the vital rates of fish populations, and often vary uncontrollably. These changes will have confounding effects on flow experiments and will be especially problematic if there are substantive trends or persistent changes in key ecological drivers like water temperature, as might occur because of changes in climate. The sequence and magnitude of confounding effects in relation to the timing of flow treatments, more generally referred to as the design matrix, can therefore have an important influence on the reliability of e-flow effect size estimates. Issues with confounding effects are especially important because expected effect sizes of e-flows may be relatively small as decision-makers often only consider minor changes to flow regimes due to competing uses of water (Konrad et al. 2011). Spatial

replicates (i.e., other rivers with similar conditions) are usually not available, so assessments of e-flows are often based on temporal differences in response variables measured under flow-treated and -untreated conditions (Bradford et al. 2011; Gillespie et al. 2015; Lamouroux and Olivier 2015). Lastly, the application of experimental flows is often not strictly random, as ecosystem conditions, water availability, social values, and costs may all play a role in determining the time periods when e-flows are implemented. Assessing e-flow effects under these challenging circumstances using simple comparisons between treatment and non-treatment periods may have poor statistical power, or, if confounding is strong, produce misleading conclusions about the strength and even the sign of an e-flow effect.

Stronger inferences about effects of e-flow on fish populations can be attained by focusing on specific vital rates (e.g., fish somatic growth or survival) as opposed to state indices (e.g., catch or abundance). Developing long time series of vital rates allows one to better characterize the role of confounding factors, and estimate e-flow effects in the context of variation in confounding factors. Although abundance estimates are critical for evaluating fish population status, vital rates are needed to understand the causes for changes in abundance, and provide a more direct link to specific hypotheses about a flow treatment. Long time series of vital rates can be used to jointly estimate the effects of both flow and non-flow factors, and therefore statistically control for the confounding effects of non-flow factors during a flow experiment. The approach avoids the need to assume that confounding factors are randomly distributed between flow-treated and -untreated time periods, and should therefore lead to more reliable estimates of flow treatment effects. Just as importantly, the integrated approach places the e-flow effect in the context of other potentially significant non-flow factors. This provides broader inference and more information for making decisions about policies aimed at changing vital rates of a target species.

This paper is motivated by our experience that design challenges associated with flow experiments are often underappreciated, which can lead to inadequate experimental designs or unrealistic expectations about the extent of learning from flow experiments. Here, we estimate the effects of two experimental flows, two-day-per week elimination of hourly discharge fluctuations (hereafter load following¹) in spring and summer, and short-duration controlled floods in fall, on rates of rainbow trout (*Oncorhynchus mykiss*) growth in length and weight in the Colorado River downstream from Glen Canyon Dam (GCD), AZ, USA. Our intent is to illustrate common issues, such as unpredictable changes in non-flow factors, which complicate interpretation of results from flow experiments, and to show how some challenges can be

overcome by applying statistical models to long-term data sets. Factors that influence growth rates in the rainbow trout population downstream from GCD have been described based on an intensive and now decade-long mark-recapture program, and linkages between growth rates, maturation, survival, and abundance have been established (Korman et al. 2021). Our study was conducted during the multidecadal 21st century mega-drought (Udall and Overpeck 2017; Overpeck and Udall 2020) that caused substantive changes in water temperatures and concentrations of phosphorous during spring. Here we demonstrate how these climate-driven effects on water quality, and varying biotic factors like competition, can lead to bias in estimated e-flow effects, and how joint estimation can partially disentangle them.

Materials and methods

Study area and experimental flows

The 25-km Glen Canyon tailwater represents the remaining unflooded portion of Glen Canyon since closure of GCD in 1963. There are no perennial tributaries flowing into the low-gradient and perennially clear tailwater, thus its discharge, water temperature, and nutrient concentrations are completely determined by the release of water from Lake Powell through the dam. Currently, Lake Powell is only 25% full (as of August 30 2022) because of the combined effects of consumptive overuse of water and many years of reduced inflows resulting from the aridification of the American Southwest (Udall and Overpeck 2017). As water levels in Lake Powell reservoir have declined, flow releases have generally become warmer (Vernieu et al. 2005) and lower in dissolved nutrients (Fig. S1; Gloss et al. 1980), largely due to the increasing influence of the epilimnion on water released from the dam. Climate and hydrologic models predict further decreases in water surface elevation of Lake Powell and increases in the temperature of flow releases (Dibble et al. 2021). Rainbow trout were introduced into Glen Canyon in 1964, and stocking was discontinued in 1998 shortly after it was recognized that the population was self-sustaining owing to increases in minimum flows and constraints on flow variation associated with load-following (McKinney et al. 2001). The rainbow trout population in Glen Canyon supports a blue-ribbon fishery that is a valued resource in the GCD Adaptive Management Program (GCD AMP, Runge et al. 2015).

In the last decade, the GCD AMP has tested two experimental flows. Controlled floods, institutionally referred to as High Flow Experiments (HFEs), are intended to increase the size of sand bars in Grand Canyon National Park, which begins immediately downstream of Glen Canyon (DOI 2016). Five fall-timed HFEs were conducted over our 10 year study (2012, 2013, 2014, 2016, and 2018). HFEs lasted for 3–6 days with peak flows ranging from 892–1274 m³·sec⁻¹, which were ~2.5- to 4-fold higher than the average flow (337 m³·sec⁻¹). Fall HFEs occurred in early November in years when there was sufficient fine sediment on the channel bed, as determined by the intensity and frequency of summer monsoons that drive sediment inputs from tributaries. HFEs will scour some periphyton and benthic invertebrates from the channel bed

¹ Stream ecologists often refer to hydropower-related sub-daily flow fluctuations as “hydropeaking”, while those in the energy sector reserve that term for facilities whose flows are completely shut-off during off-peak hours (Deemer et al. 2022). We use the term “load following” to refer to the more muted sub-daily changes in dam releases that occur when electricity generation continues during periods of low electricity demand.

(Robinson et al. 2018; Rosi-Marshall et al. 2010). Recovery of the benthos in Glen Canyon is expected to be slow during the late fall and winter intervals that follow HFEs due to the limiting effects of low solar insolation on periphyton growth and the resulting limitation on secondary production (DOI 2016). The potential hypothesized reduction in overwinter prey supply for rainbow trout is expected to result in reduced growth.

Load following flows from GCD follow a typical diel cycle with high flows during the day and low flows at night to meet hourly variation in power demand and maximize hydropower revenues (DOI 2016). Under a normal 24 hour operating cycle during summer over our study period, peak flows ($500 \text{ m}^3 \cdot \text{sec}^{-1}$) were almost 2-fold higher than minimum flows ($280 \text{ m}^3 \cdot \text{sec}^{-1}$). As aquatic insects lay their eggs at the water line, hourly variation in river stage is expected to desiccate eggs and thus reduce prey availability for fishes (Kennedy et al. 2016). A Steady Flow Experiment (SFE), institutionally known as bug or macroinvertebrate flows, was implemented to evaluate and mitigate this potential load following impact. Within-day variation in flows was eliminated on weekends from May through August over three consecutive years (2018–2020) and kept near the daily minimum flow to provide insect egg-laying habitat that would not be desiccated during weekday returns to load following flows.

Growth observations

To estimate abundance, growth, and other vital rates of rainbow trout, we sampled a five km reach in the lower portion of the Glen Canyon tailwater (3.7–8.9 km upstream of Lees Ferry, AZ, USA) by nighttime boat electrofishing five or six times per year between April 2012 and November 2021 (52 sampling trips). Trips were conducted in April, July, September, late October or early November, and January or early February in each year (5 trips yr^{-1}). Additional sampling trips in December were conducted between 2012 and 2015. Two nights of sampling occurred on each trip, with the central 2–3 km of the reach sampled on both nights. After capture, fish were kept in aerated 40 L buckets and transported to a central processing location. Groups of 10–15 fish were anesthetized and rainbow trout $\geq 75 \text{ mm}$ were scanned and injected with a passive integrated transponder (PIT) tag if they had not been previously tagged. Fork length was measured to the nearest mm, and weight was measured to the nearest gram for fish $\geq 150 \text{ mm}$ and to the nearest 0.1 g for smaller fish. Following processing, fish were released close to shore near the center of their original 250 m site of capture.

Changes in length and weight of individual trout between captures provide direct estimates of growth rate. In total, 9798 across-trip recaptures were obtained over the 10 year study, equivalent to an average of ~ 200 growth rate observations per trip. Observation error in measurements was calculated based on differences in measurements from 4991 PIT-tagged trout released on the first night of each trip and recaptured the following night. Condition factor was calculated as the ratio of the weight of an individual relative to the average weight of others of the same length, as determined by a length-weight regression fit to observations over the entire study period. Owing to the timing of trips, growth rates were observed in spring (April–June/July), summer

(June/July–September), fall (September–October/November), late fall (October/November–January/February), and winter (January/February–April) intervals. Sampling trips in December 2012–2015 provided additional observations of growth rates in late fall (October–December) and winter (December–January).

Hypotheses of how covariates and experimental flows affect somatic growth

We evaluated the effects of discharge (Q), water temperature (T), solar insolation (S), soluble reactive phosphorous concentration (SRP), intraspecific competition (C), controlled floods in fall (HFE), and steady flows during the weekend (SFE), on growth. Four of these covariates (Q, T, S, and C) were selected based on previous research (e.g., Korman et al. 2021) and represented a priori hypotheses. We hypothesized that growth would increase with discharge due to potential increases in habitat availability as the river widens, and because higher water velocities increase the rate at which benthic invertebrates on the river bed are entrained into the water column and become available to drift-feeding rainbow trout (Kennedy et al. 2014). Although increases in discharge will lead to higher velocities which could reduce the energetic profitability of some habitats, we hypothesize such effects would be modest in Glen Canyon owing to its low gradient (Grams et al. 2007). The relationship between water temperature and fish growth typically follows a dome-shaped function that initially increases with temperature until a thermal optimum is reached and then declines with further increases in temperature. At reduced ration, the thermal optimum occurs at lower temperatures (Brett 1979). Owing to the range of mean daily water temperatures from GCD during our study ($7.3\text{--}16.7^\circ\text{C}$) and relatively low densities of drifting invertebrates (Cross et al. 2013; Dodrill et al. 2016), we hypothesized that growth rates would decline with increasing water temperature. We hypothesized that growth rates would be higher during spring and summer when solar insolation is higher and day length is longer, because sight-feeding fish like rainbow trout would be better able to effectively forage at greater depths in clear-water systems like Glen Canyon (Hansen et al. 2013), and potentially forage for a longer period within a day. We hypothesized that higher solar insolation combined with higher SRP concentrations would lead to an increase in trout growth via increases in periphyton production (Gloss 1977; Hall et al. 2015; Deemer et al. 2022) which would in turn increase benthic invertebrate production and thus prey availability (Cross et al. 2013). This hypothesis assumes that higher levels of SRP and insolation within a trip interval (time between trips) will translate into an increase in prey availability within that interval (average trip interval length was 70 days). We expected that increases in intraspecific competition, as indexed by rainbow trout biomass, would lead to lower growth rates (Post et al. 1999). We expected that growth rates would be lower in late fall and winter intervals following HFEs, and higher in spring and summer intervals when SFEs were implemented.

Covariate conditions during flow-treated and -untreated trip intervals define the design matrix for this study. We

calculated average values for each covariate by trip interval (Fig. 1). HFE and SFE effects were indicator variables with values of 1 or 0 determining whether the flow treatment could potentially affect growth over an interval or not, respectively. HFE effects were hypothesized to occur in the late fall (October/November–December, October/November–January) and winter (December–January, January/February–April) intervals that immediately followed HFEs. This resulted in the potential for an HFE effect in 13 of 51 trip intervals over the 10 year study. SFE effects were hypothesized to affect growth in spring (April–June/July) and summer (June/July–September) intervals in years they were implemented. This resulted in the potential for an SFE effect in 5 of 51 intervals over three years near the end of the study.

We evaluated the effect of SRP concentrations on trout growth based on two different model formulations. The first assumes that SRP and solar insolation co-limit algal production which in turns drives benthic invertebrate production and prey availability for trout (Angradi and Kubly 1993; Cross et al. 2013). We, therefore, modeled the effect of SRP as the product of the average concentration and average solar insolation (S) in each interval (i.e., an SRP*S interaction, Cloern 1999). The second formulation, which is based only on SRP concentrations, assumes SRP limitation of algal and secondary production is independent of solar insolation (Cross et al. 2006). All the data used for this analysis are available in Korman et al. (2022). Additional details on the data and calculation of covariate values are provided in the supplement (Supplement S1, Section S1).

Statistical growth models

We predicted growth in length from the von Bertalanffy model:

$$(1) \quad g_i = \alpha_t - \beta_t \cdot \frac{S_i - \mu}{sd}$$

where g_i is the daily growth rate ($\text{mm} \cdot \text{d}^{-1}$) for release-recapture observation i , S_i represents the fork length at the start of interval t , and α and β are the intercept and slope of the growth relationship for trip interval t when g_i was observed. The terms μ (207 mm) and sd (97 mm) are constants and represent the mean and standard deviation of fork length of all rainbow trout captured over the study, respectively. As the effect of fork length on growth is standardized, α represents the growth rate for an averaged-sized fish. The daily growth coefficient β represents the change in growth rate per one standard deviation change in fork length. Integrating eq. 1 over time produces the familiar asymptotic von Bertalanffy length-at-age curve.

We used the von Bertalanffy bioenergetics model (Lester et al. 2004; Walters and Essington 2010) to predict growth in weight:

$$(2) \quad g_i = (\alpha_t \cdot S_i^\phi - \beta_t \cdot S_i^\omega) \cdot 365^{-1}$$

Daily growth rate g_i ($\text{g} \cdot \text{d}^{-1}$) is calculated as the difference between gross energy gains ($\alpha_t \cdot S_i^\phi$) and metabolic losses

($\beta_t \cdot S_i^\omega$) over interval t for a fish of weight S_i . Model parameters include the net prey energy intake rate per unit weight, α_t , and the net metabolic loss per unit weight, β_t . The exponents ϕ and ω influence the effect of body weight on gross prey intake and metabolic loss, respectively. We estimated a single value of ϕ for all trip intervals, and fixed the value of ω at 1. We did not attempt more complex parameterizations for these exponent terms as they are difficult to directly estimate from field data (van Poorten and Walters 2010).

The predicted size of an individual at the end of a trip interval ($\hat{S}_i$) is calculated by adding the predicted growth increment in length or weight over the interval to the length or weight at the start of the interval:

$$(3) \quad \hat{S}_i = S_i + g_i \cdot T_i$$

where T_i is the number of days between release and recapture for observation i . For individuals recaptured one trip after the trip they were released on, S_i is the observed length or weight at release. For other cases, the predicted size from eq. 3 at the end of the first interval is used as S_i in eqn.'s 1 or 2 for the next interval, and the calculation is repeated until the prediction for the trip the individual was recaptured on is obtained.

Interval-specific parameters of growth-in-length and -weight models were calculated from linear mixed-effects models,:

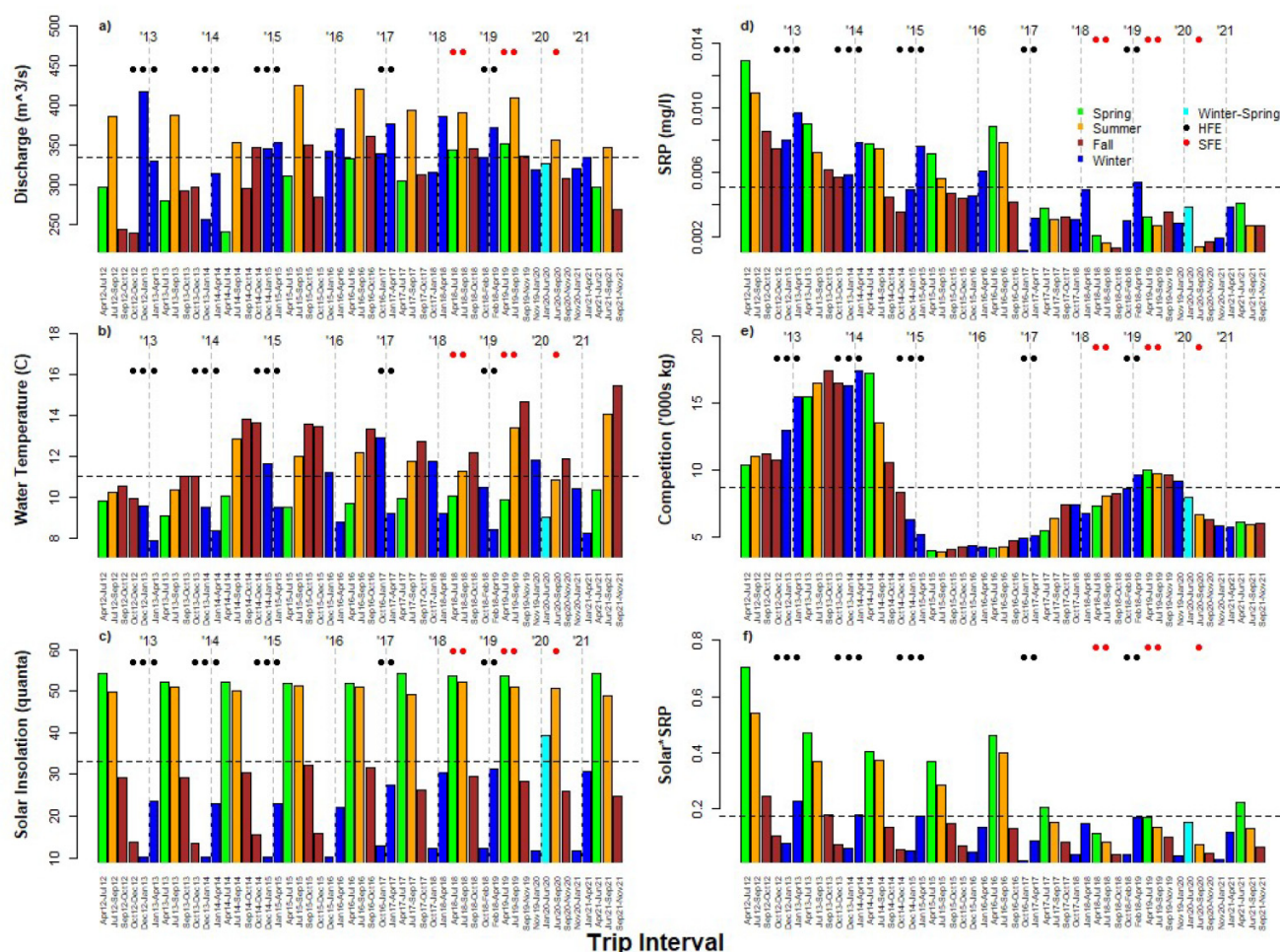
$$(4a) \quad \alpha_t = \alpha_0 + \sum_j \delta_j \cdot X_{j,t} + \varepsilon_t$$

$$(4b) \quad \beta_t = \beta_0 + \sum_j \kappa_j \cdot X_{j,t} + \nu_t$$

where X is the standardized value of covariate j for interval t and α_0 and β_0 are the grand means for the intercept and slope (growth in length) or net energy intake and metabolic loss terms (growth in weight), respectively. The X 's for HFE and SFE effects were set to 0 and 1 for intervals when these flows are assumed to have no effect or have an effect, respectively. The terms δ and κ are fixed effect covariate coefficients contributing to the prediction of the growth rate parameters. As covariate values were standardized, α_0 and β_0 represent growth parameters under average covariate conditions in the absence of experimental flow effects. The terms ε and ν are random effects for each trip interval and are deviates drawn from normal distributions with means of 0 and estimated standard deviations σ_α and σ_β , respectively ($\varepsilon_t \sim N(0, \sigma_\alpha)$, $\nu_t \sim N(0, \sigma_\beta)$). These random effects describe the extent to which the growth rate parameters differ from the values predicted by the fixed covariate effects (Barry et al. 2003). They account for un-modelled time-varying covariates, or misspecification of functional form, and avoid negative bias in variance estimates resulting from pseudo-replication (Miller and Anderson 2004).

Parameters of mixed effects models were estimated using a penalized maximum likelihood approach where observations of fork length or weight at recapture were compared to predictions. The utility of the covariates for predicting growth was determined using a forward stepwise

Fig. 1. Covariates used to predict variation in growth in length and weight across trip intervals (bar colors denote the season associated with each interval). Black and red points identify the intervals assumed to be influenced by fall High Flow Experiments and Steady Flow Experiments. Dashed horizontal lines represent the across-interval average values.



marginal Akaike Information Criteria (mAIC) model selection approach, from the magnitude of standardized parameter estimates and their uncertainty, and from multi-level fit statistics which quantify the proportion of variation in growth rate parameters explained by fixed covariate effects (Gelman and Pardoe 2006). The influence of confounding factors on flow treatment effects was evaluated by comparing treatment effect sizes based on a univariate model that only accounted for the flow treatment effects, with estimates from lowest mAIC models that also included important confounding effects. The approaches to fitting the model, estimating process and observation error, and model selection are the same used by Korman et al. (2021), and are described in more detail in Supplement S1, Section S2.

Predicting effects of experimental flows on growth rates and lifetime growth trajectories

We simulated trends in lifetime growth to provide an intuitive way of showing the effects of experimental flows and confounding covariates on growth trajectories. Calculations

begin with the assumption that age-0 rainbow trout during the September 2012 trip were 75 mm (growth-in-length predictions) and 5.1 g (growth-in-weight), as determined from catch records. Growth in length or weight in the following interval (September–October 2012) is calculated using the most predictive (lowest mAIC) mixed effects model and historical covariate values. The growth increment prediction is then added to the initial length or weight to predict fork length or weight at the start of the next interval. The procedure is repeated for all subsequent intervals to predict a lifetime size trajectory to a maximum age of six years. The baseline scenario for growth in length does not include and SFE effect, while the experimental flow scenario includes an estimated SFE effect for all spring and summer intervals over the duration of the projection. Similarly, the baseline scenario for growth in weight does not include an HFE effect, while the experimental flow scenario includes the estimated HFE effect for all late fall and winter intervals.

To highlight the importance of factors other than experimental flows, we simulated growth in length based on historical levels for all covariates in the absence of SFEs, and

compared it to a scenario based on the same conditions but where competition was held constant at a value one standard deviation greater than the historical mean. To demonstrate the potential importance of climate-driven covariate effects on growth, we simulated the effects of higher water temperatures. The baseline scenario is based on historical values for all covariates and no HFE effect, while the future water temperature scenario replaces historical summer and fall interval water temperatures with predictions for GCD release temperatures for summer (18 °C) and fall (19 °C) of 2022 (http://gcdamp.com/images_gcdamp_com/6/60/Dec2021_Information.pdf). These temperatures are considerably higher than historical conditions (Fig. 1b) because the water surface elevation of Lake Powell is at a historic low and ongoing aridification is expected to result in continued low reservoir elevations. Thus, high temperatures are assumed to persist for the six-year simulation period. Additional details about the simulations are provided in Supplement S1, Section 2.

Results

Model fit, covariate effects, and model selection

The global growth-in-length model, which included all fixed effects on both the intercept (growth rate for an average-sized trout) and slope (growth coefficient) terms, explained 57% of variation in observed growth rates at the data level (Figs. 2a, 2b, and S2a in Supplement S1, Section S1, for fit to all trip intervals). Covariates (fixed effects) were useful predictors of growth as their combined effects explained 83% and 72% of the across-trip interval variation in the growth rate for an average-sized fish (R^2_{int}) and the growth coefficient (R^2_{sl}), respectively, with the remaining variation explained by random effects (Table 1). These correlations reflect the extent of agreement between predictions based on covariate-driven fixed effects (blue lines in Figs. 2a, 2b, and S2a), and those based on both fixed and random effects (mixed effects, red lines). The global growth-in weight model only explained 36% of the variation in observed growth rates at the data level, with 89% and 86% of the variation in net prey intake and metabolic loss rates (eq. 2) across trip intervals explained by fixed effects, respectively (Figs. 2c, 2d, and S2b). Global growth models, which included all fixed and random effects, had substantively better predictive abilities than null models that only included random effects (Table 1), demonstrating that some covariates led to considerable improvement in predictive capability. Handling effects on later growth rates were not evident for growth in length, and modest ($-0.47 \text{ g}\cdot\text{mo}^{-1}$) and not statistically significant for growth in weight (Section S3).

Parameter estimates from the global model indicated that solar insolation, the product of SRP concentration and solar insolation ($\text{SRP}\cdot\text{S}$), competition, SFEs, and to a lesser extent water temperature, had substantive effects (confidence intervals did not overlap 0) on growth in length for the average-sized trout (Fig. 3a). Consistent with our initial hypotheses, growth rates were higher during intervals with higher solar insolation (spring and summer), higher $\text{SRP}\cdot\text{S}$, and when SFEs

were implemented (positive effects), and growth rates were lower in intervals with higher competition and water temperature (negative effects). All covariate effects on the growth coefficient were near zero indicating that covariate effects on growth in length did not vary with fish size. Solar insolation and fall HFEs had similar positive effects on the energy intake and metabolic loss terms of the growth-in-weight model (Fig. 3b). Competition had a bigger negative effect on energy intake than on metabolic loss while water temperature had a substantive positive effect on metabolic loss but no effect on energy intake. Owing to the negative sign in front of the metabolic loss term in the growth equation (eq. 2), a positive HFE or temperature effect on the metabolic loss rate translates into higher metabolic loss due to HFEs or with increases in water temperature, and hence reduced growth.

Stepwise forward model selection indicated that solar insolation was the best univariate predictor of the growth rate for an average-sized trout for the growth-in-length model, and best predictor of energy intake and metabolic loss terms for the growth-in-weight model (Table 1). Water temperature was the second most important predictor of the metabolic loss rate, while competition was the second most important predictor for all other growth terms. Adding an SFE effect led to a small improvement in predictive capability of the growth-in-length model (2.5 mAIC units), while adding an HFE effect resulted in only a marginal improvement for the growth-in-weight model (0.6 and 1.2 mAIC units). Including an SFE effect did not improve the predictive ability of the growth-in-weight model, and including an HFE effect did not improve predictive ability of the growth-in-length model. Based on stepwise model selection that included covariate effects on the intercept and slope at the same time, the lowest mAIC model for growth-in-length ("Best" in Table 1) included all effects except average discharge and HFE effects on the intercept, and no covariate effects on the slope. The lowest mAIC model for growth-in-weight included solar insolation, competition, and HFE effects on both energy intake and metabolic loss terms, and a water temperature effect on the metabolic loss term.

Models that accounted for potentially confounding effects of non-flow factors predicted weaker effects of experimental flows on growth rates compared to univariate models that only accounted for flow effects. Growth in length for an average sized trout (207 mm) was predicted to increase by $2.4 \text{ mm}\cdot\text{mo}^{-1}$ (95% CI of $0.3\text{--}4.5 \text{ mm}\cdot\text{mo}^{-1}$) due to SFEs in a univariate model (SFE effects only), compared to an increase of $1.5 \text{ mm}\cdot\text{mo}^{-1}$ due to SFEs ($0.1\text{--}2.9 \text{ mm}\cdot\text{mo}^{-1}$) estimated from the lowest mAIC model that included confounding effects. Growth in weight for an average weight trout (95 g) was predicted to decrease by $-4.5 \text{ g}\cdot\text{mo}^{-1}$ (95% CI of $-9.9\text{--}0.8 \text{ g}\cdot\text{mo}^{-1}$) due to fall HFEs based on a univariate model (HFE effect only), compared to a decrease of $-0.1 \text{ g}\cdot\text{mo}^{-1}$ due to fall HFEs ($-3.7\text{--}4.5 \text{ g}\cdot\text{mo}^{-1}$) estimated from the lowest mAIC model. The extent of differences between univariate and lowest mAIC models in flow treatment effects depended on the magnitude of differences in confounding effects under flow-treated and -untreated conditions. For example, negative effects of competition on growth in weight were generally stronger in years when HFEs were conducted (Fig. 1e),

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Table 1. Summary of the step-forward marginal Akaike Information Criteria (mAIC) analysis identifying the covariates with the best predictive power for growth in length and weight models. In the first step, univariate covariate models were fit to the data (number of covariates = 1), and the covariate for the model with the lowest mAIC (highest predictive capability) was retained for evaluation of models with two covariates. The process of sequentially identifying the best covariate was repeated for each of the remaining covariates. Results are only shown for models where mAIC decreased with the addition of new covariates. The column labelled “ Δ mAIC” shows the difference between each models mAIC value and the lowest mAIC value across models. The column labelled “Proportion explained” shows the proportion of variation in the growth rate parameters explained by fixed effects. Results for null (no fixed effects) and global (fixed effects of all covariates on both growth terms) models are shown for reference. The model with the lowest mAIC score (“Best”) includes only fixed effects for the intercept of the growth in length model, and fixed effects for the net intake and metabolic loss terms for the growth in weight model.

Growth type	Growth parameter	Number of covariates	Covariate	mAIC	Δ mAIC	Proportion explained
Length	Null	0	None	79, 530		0.00
	Intercept	1	S	79, 501	35.7	0.48
		2	S + C	79, 473	8.1	0.74
		3	S + C + T	79, 468	3.4	0.79
		4	S + C + T + SRP*S	79, 467	2.5	0.80
	Best	5	S + C + T + SRP*S + SFE	79, 465	0.0	0.82
	Global	14	All	79, 478		0.83/0.72
Weight	Null	0	None	97, 943		0.00
	Intake	1	S	97, 908	19.4	0.59
		2	S + C	97, 889	0.6	0.77
		3	S + C + HFE	97, 888	0.0	0.79
	Loss	1	S	97, 922	13.4	0.50
		2	S + T	97, 910	1.2	0.67
		3	S + T + HFE	97, 908	0.0	0.69
	Best	7	S + C + T + HFE ¹	97, 835		0.88/0.85
	Global	14	All	97, 843		0.89/0.86

Covariates are solar insolation (S), competition (C, rainbow trout biomass), water temperature (T), soluble reactive phosphorous concentration (SRP), and steady flow (SFE) and fall high flow (HFE) treatment effects.

¹S, C, and HFE effects on both intake and loss terms, and a T effect on the metabolic loss term.

by $0.6\% \cdot \text{mo}^{-1}$ for a 300 mm trout, which was relatively small compared to the $1\% \cdot \text{mo}^{-1}$ increase at the maximum SRP*S level across intervals, or the predicted decrease of $1\% \cdot \text{mo}^{-1}$ at the maximum competition effect. Considerable weight loss (negative growth) during late fall and winter intervals from 2012–2014 (Fig. 4) was predicted to be largely driven by negative effects of high competition combined with elevated water temperatures in fall of 2014 (Fig. S3b). The negative effect of fall HFEs on growth in weight was also apparent, but was small (-1.2% decrease in body weight $\cdot \text{mo}^{-1}$ for a 300 g trout) compared to the maximum negative effects of competition ($-4.2\% \cdot \text{mo}^{-1}$) and water temperature ($-6.0\% \cdot \text{mo}^{-1}$).

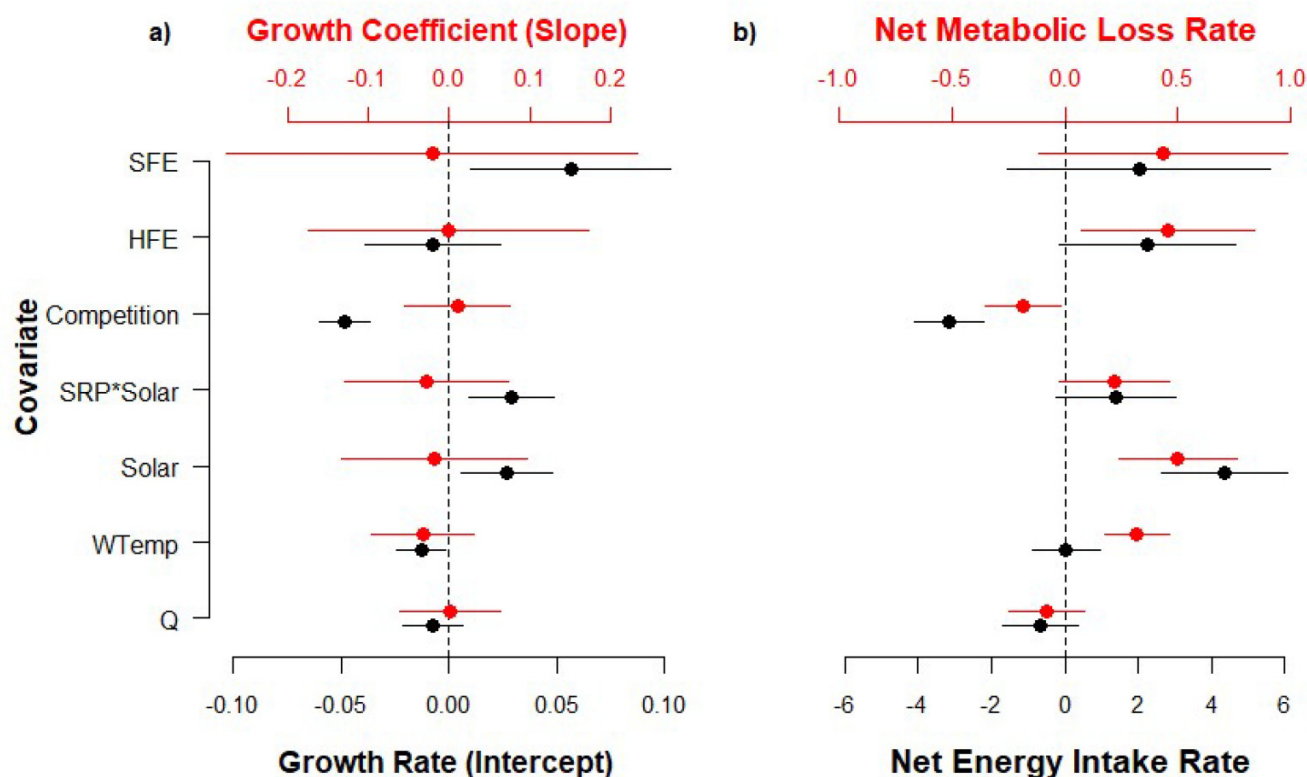
Implementing SFEs and HFEs for the duration of the 6 year simulation had limited effects on lifetime trajectories in fish size because estimated effect sizes were small and uncertain (Fig. 5). Expected fork length at 6 years was 5% higher under the scenario with SFEs compared to the scenario without them. Expected weight at 6 years was 9% lower under the scenario with HFEs compared to the scenario without them. Lifetime size trajectories for weight were considerably more uncertain than for length because process error in growth rates and parameter uncertainty for the weight model was much higher. Negative HFE effects were more apparent for older and thus heavier trout. This occurred because

metabolic losses for heavier trout increase to a greater extent than energy intake when the exponent for the gross energy intake term (ϕ) is less than one (eq. 3), which was the case in our analysis (Maximum Likelihood Estimate (MLE) = 0.65, eq. 2).

Relatively subtle assumptions about the nature of confounding covariate effects can influence estimates of an experimental flow effect. For example, the strength of the SRP effect, and in turn the SFE effect, varied with assumptions about how SRP affects trout growth. The models examined to this point assume that there is an interaction between SRP and solar insolation (SRP*S version), which results in higher growth rates when both SRP and solar insolation levels are high. We also modelled an alternate assumption that SRP concentration will have the same effect on growth rate regardless of solar insolation (SRP version). Standardized estimates of SRP (MLE = 0.009, CV = 0.89) and SFE (MLE = 0.023, CV = 0.96) effects were weaker and more uncertain based on the SRP version of the model compared to the SRP*S version (MLE = 0.028, CV = 0.37; SFE MLE = 0.050, CV = 0.47, Fig. 3a).

To highlight the importance of factors other than experimental flows, predictions of lifetime growth in length based on historical conditions were compared to a scenario where competition was held at one standard deviation greater

Fig. 3. Maximum likelihood estimates (points) and 95% confidence intervals (lines) for fixed-effect coefficients estimated from the global models. Fixed effects predict the growth rate for an average-sized fish (α) and the growth coefficient (β) for the growth-in-length model (a), and net prey intake (α) and metabolic loss (β) rates for the growth-in-weight model (b). Owing to the negative value in front of the growth coefficient and metabolic loss parameters (eqs. 1 and 2), coefficients with positive values indicate that growth rates for larger fish will decline with increases in covariate values.



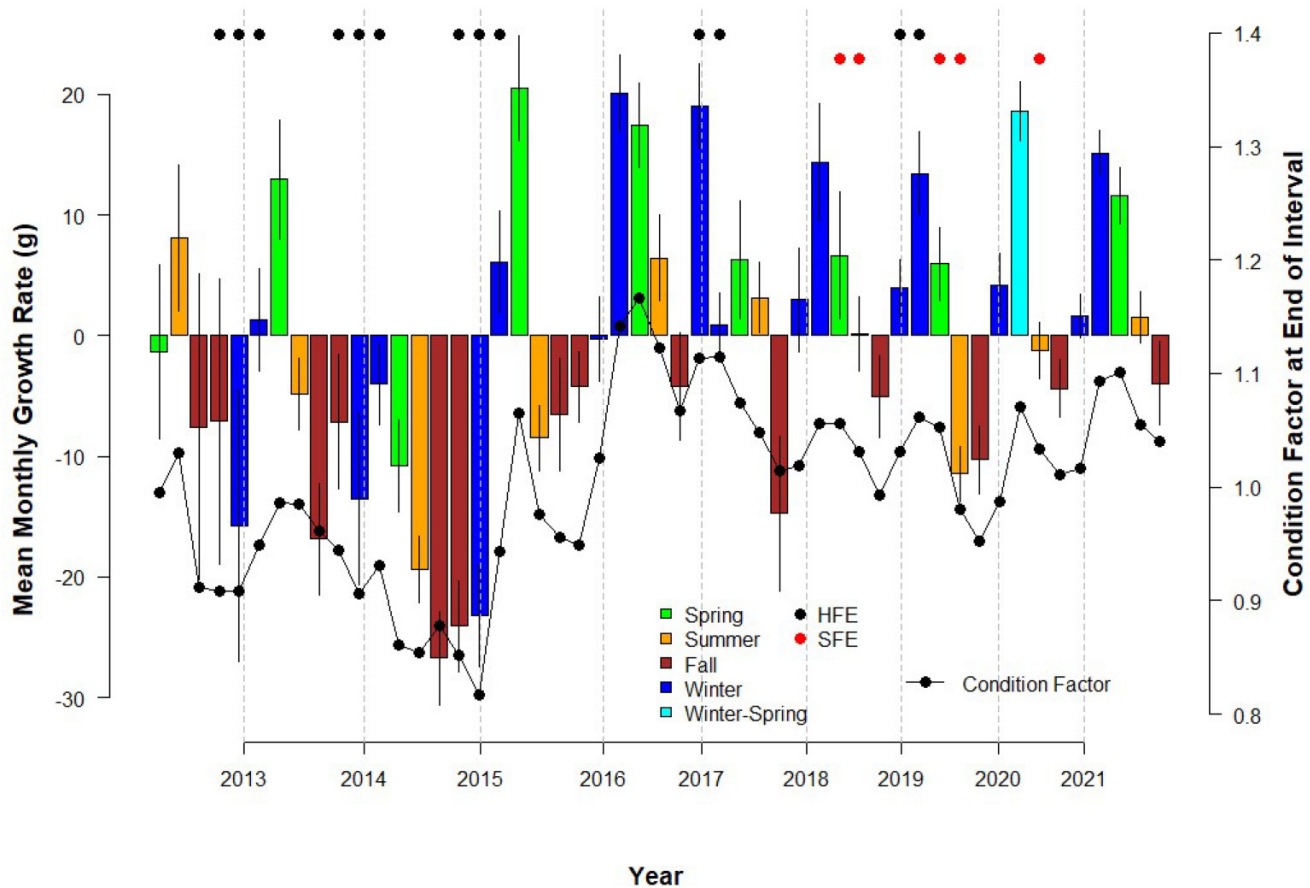
than the mean (Fig. 6a). Length-at-age was substantively reduced in the last 3 years of the scenario because of higher competition relative to historic levels in those years (Fig. 1e). The predicted 17% decrease in length at age 6 years was more than 3-fold higher than the 5% increase associated with annual implementation of SFEs (Fig. 6a). Predicted weight at 6 years was more than 380 g based on historical water temperatures compared to 240 g under the elevated summer/fall water temperature scenario (Fig. 6b). Water temperature only affected the metabolic loss term (Fig. 3b) and therefore had increasingly larger effects as fish aged and gained weight. Relative condition factor, calculated from lifetime growth predictions in length and weight, declined to 0.7 in the fall of the second year of the elevated water temperature projection, but remained above 0.85 based on the historical projection.

Discussion

We estimated effects of two environmental flows on somatic growth rates of a fish population despite considerable temporal variation in confounding factors. The analysis revealed that controlled floods in fall had a negative effect on growth in weight as hypothesized, but the effect was small and highly uncertain, and an HFE effect did not improve

the predictive ability of the growth in length model. Similarly, steady weekend flows in spring and summer had a positive effect on growth in length as hypothesized, but the effect was uncertain, and SFE effects did not improve the predictivity ability of the growth in weight model. Confounding effects of competition and water temperature had much stronger effects on growth because effect sizes were larger, more certain, and affected growth throughout the year. Ignoring these confounding effects led to exaggerated estimates of flow treatment effect sizes, underscoring the importance of incorporating confounding effects into assessments of experimental flows. Finally, we showed that predicted increases in water temperatures arising from low reservoir elevations due to prolonged drought will cause considerable weight loss for larger trout that have greater metabolic requirements. Predictions indicated that just two years of elevated temperatures like those predicted for 2022 will drive down condition factor to a level (<0.8) that was last observed in 2014 when populations collapsed (Korman et al. 2021). The predicted negative effect of higher water temperatures on future growth far surpassed the effects associated with annual implementation of e-flows. Continued aridification and low Lake Powell reservoir elevations are likely to make water quality the primary factor limiting trout growth in this tail-water ecosystem.

Fig. 4. Predicted monthly growth in weight for a 300 g rainbow trout across 51 trip intervals (bars) based on the model with the highest predictive capability (lowest marginal Akaike Information Criteria). Bar heights represent maximum likelihood estimates and error bars represent 95% confidence intervals. The trend in observed relative condition factor for trout ≥ 275 mm is shown on the right-hand axis.



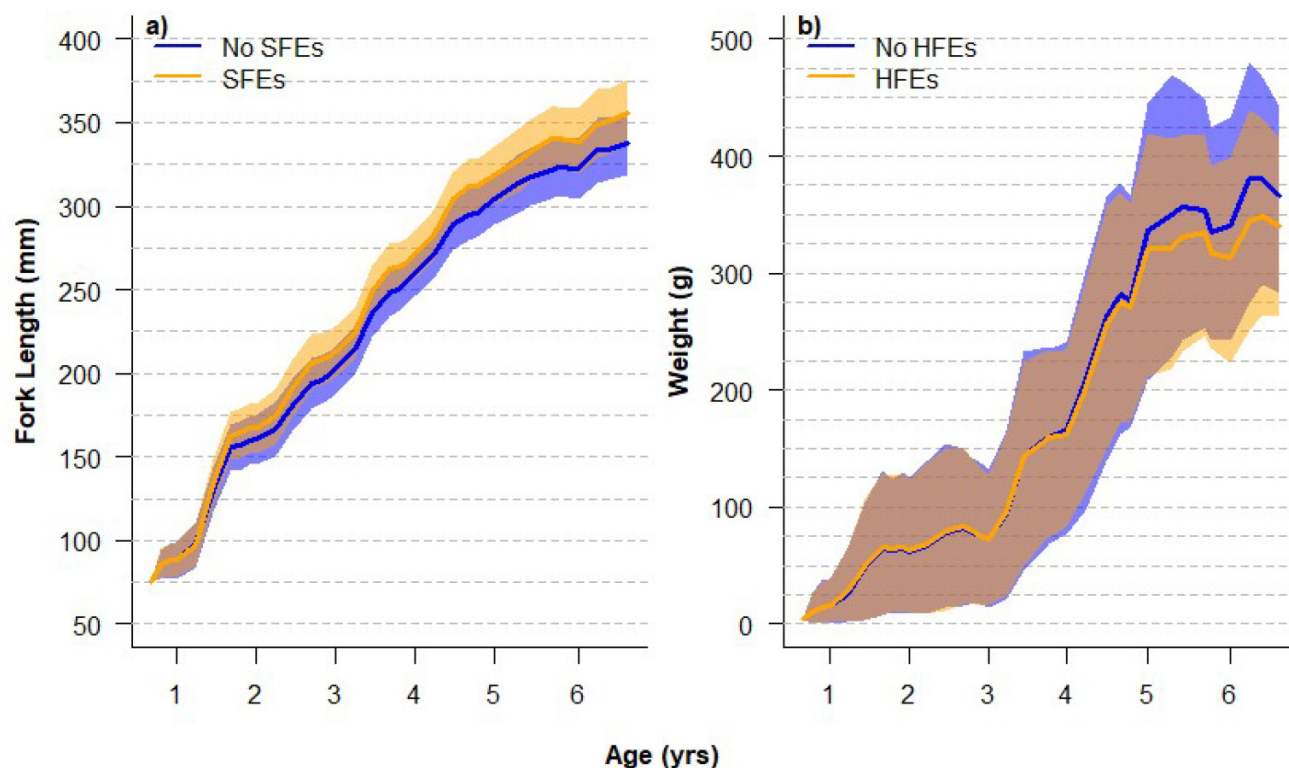
The modest and uncertain effects of e-flows on growth rates of rainbow trout is perhaps not surprising given the significant constraints on manipulating flows from large main-stem dams due to competing demands for water (Konrad et al. 2011). Geomorphic studies (Grams et al. 2007) and hydraulic modelling (S. Wright, CBEC eco engineering, Sacramento, CA, written commun. 2022) indicates that peak HFE flows are too low to mobilize cobbles and even coarse gravels in Glen Canyon that would lead to greater reductions in benthic biomass. The rate of recovery of benthic communities during winter in Glen Canyon is uncertain, but studies in other systems show significant recovery between annual flood events that are comparatively larger in magnitude and duration than HFEs (Robinson et al. 2018), suggesting that depletion of invertebrates and prey available for trout over years with sequential fall HFEs (e.g., 2012–2014) is unlikely.

The small effect of SFEs on growth rates of trout could indicate that proportional loss of insect eggs due to desiccation from load following is too low to limit the number of larvae or pupae available to rainbow trout. SFE effects could also be constrained because they only occurred on 2–7 days per week and during just 4 months of the year. Steady flows were limited to weekends during times of peak aquatic insect egg

laying activity to minimize hydropower losses (Ploussard and Veselka 2020). As in other load following systems, impacts to hydropower often constrain the duration or frequency of steady flow treatments, which in turn constrains the magnitude of potential benefits. In our study, SFEs only had the potential to affect growth rates in 5 of 51 trip intervals clustered near the end of our 10 year study when spring and summer SRP levels were consistently low due to effects of a persistent drought. The resulting unbalanced design matrix led to partial confounding of SRP and SFE effects, which increased uncertainty in the SFE effect size. From a scientific perspective, additional replication of SFEs is warranted to potentially improve the design matrix and reduce uncertainty about effect size. However, given trade-offs associated with most experimental flows, decisions on implementation invariably depend on both scientific results and societal values (Schmidt et al. 1998; Konrad et al. 2011).

Joint estimation of flow treatment and confounding effects on vital rates of fish populations provides a direct means of comparing the magnitude of their effects, which is fundamental for evaluating the significance of e-flows on population dynamics. For example, in our study, rainbow trout lost considerable weight in the fall and winter periods

Fig. 5. Predicted lifetime growth in length (a) and weight (b) based on the most predictive (lowest marginal Akaike Information Criteria) models. All projections are based on historical values of covariates except for flow treatment effects. The blue lines (mean across 5000 trials) and shaded areas (95% confidence intervals) are predictions without steady flow (SFE) or high flow (HFE) experiment effects, and orange lines and shaded areas are based on the estimated SFE effect applied in all spring and summer intervals (a), and the HFE effect applied in all late fall and winter intervals (b).



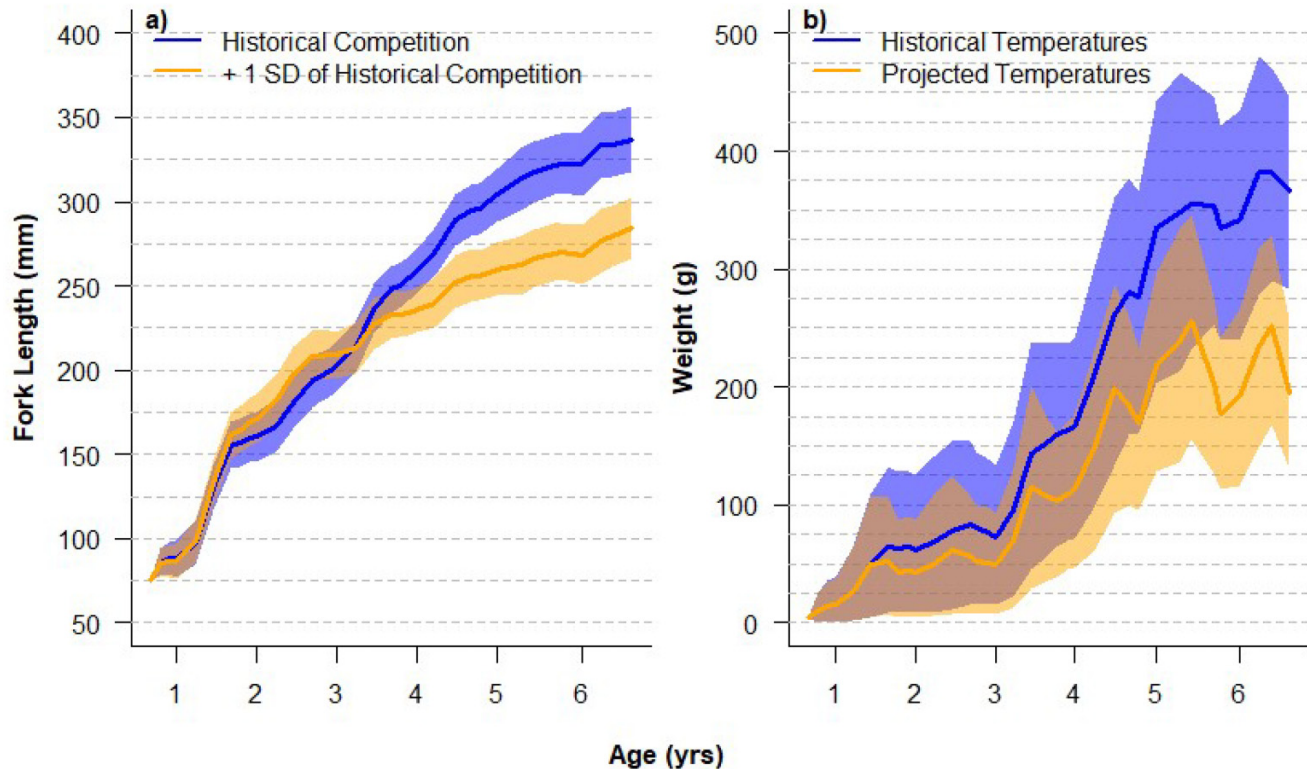
between 2012 and 2014, coincident with the implementation of three fall HFEs. Poor growth led to a substantive decline in condition factor which in turn led to a population collapse (Korman et al. 2021). Changes in condition and abundance were apparent to the angling community, leading them to attribute the collapse to repeated implementation of novel fall HFEs. What was not considered in their conclusion was the exceptionally high level of competition between 2012 and 2014, poor growth during spring and summer of 2014, and unusually warm water temperatures in the fall of 2014. Modelling revealed that the three consecutive fall HFEs were a relatively minor contributor to the 2014 collapse. Such nuanced and more wholistic interpretations of the data should help make more informed decisions within adaptive management programs.

Climate-driven effects on the design matrix will complicate interpretation of flow experiments, but robust statistical models have the potential to partially disentangle flow and confounding effects. For example, our 10 year study occurred during a prolonged hot and dry period, yet there was still sufficient variation in water temperatures within HFE-treated and -untreated intervals to separate water temperature and HFE effects on trout growth. However, our simulation of effects of higher water temperatures in 2022 and beyond suggests that water temperature will become a dominant limiting factor on growth, which may substantially constrain our

ability to evaluate e-flow effects on trout growth in the future. The historical design matrix was more problematic for estimating effects of SFEs, because SRP concentrations were consistently low during intervals when SFEs were implemented. Low reservoir elevations will often lead to low SRP concentrations since SRP is consistently higher at depth than in surface waters. If SRP concentrations continue to remain low due to drought, the extent of confounding with SFE effects will remain high even if more SFEs are conducted. It is also important to recognize that an informative design matrix does not guarantee strong inference. For example, in our study, predictions of lifetime growth in weight were more uncertain because of considerable unexplained variation, and partial confounding between energy intake and metabolic loss parameters due to the structure of the model. Flow treatment effects will be harder to estimate in cases when vital rates are more challenging to predict.

While it is widely accepted that multiple factors can drive variation in vital rates of animal populations, this tenant is sometimes overlooked in the design and evaluation of flow experiments. The assumption that e-flow effects will overwhelm effects of confounding factors in flow experiments may stem from the widely accepted paradigm that flow is a master variable that shapes fundamental ecological characteristics in rivers (Poff et al. 1997). Our findings support the paradigm that the dam, through its effect on water quality,

Fig. 6. Predicted lifetime growth in length (a) and weight (b) based on the most predictive (lowest marginal Akaike Information Criteria) models using historical values for all covariates except competition and water temperature, respectively. The blue lines (mean of 5000 trials) and shaded areas (95% confidence intervals) represent predictions based on historical values of competition (a) and water temperature (b) for all intervals. The orange lines and shaded areas are based on a competition level that is one standard deviation greater than the historical mean for all intervals (a), and projected temperatures for 2022 for all June/July–September (18 °C) and September–October/November (19 °C) intervals (b). Scenarios do not include experimental flow effects.



is the master variable controlling ecosystem dynamics in the GCD tailwater (McManamay et al. 2015). In our study, incorporating variation in average discharge among intervals did not improve the predictive ability of growth models. Effects of controlled floods and elimination of load following on weekends were small and uncertain. Average flow was not a useful predictor of vital rates of a humpback chub (*Gila cypha*) population in Grand Canyon (Dzul et al. 2017; Yackulic et al. 2018). Collectively, these findings suggest that flow is not a master variable effecting vital rates of fish populations in the Colorado River downstream of GCD, at least over the limited ranges provided by normal operations and relatively small changes from flow experiments. Our results suggest that in the context of persistent drought conditions due to aridification, managing reservoir elevations or taking other actions to produce cooler water temperatures and higher SRP concentrations, will be more beneficial and consequential to trout population status than modest benefits arising from the e-flows that have been tested to date (Overpeck and Udall 2020).

Limitations in our ability to predict the response of fish populations and other aquatic biota to changes in flow (Castleberry et al. 1996; Davies et al. 2014) leads to the logical recommendation to conduct flow experiments to resolve uncertainties about e-flows (Konrad et al. 2011;

Olden et al. 2014). Our study is one of a limited number that estimates effects of experimental flows on the vital rate of a fish population (see Konrad et al. 2011 and Olden et al. 2014), and also highlights challenges that may limit the extent of learning. The data set used in our analysis was exceptionally robust because it quantified a vital rate over a long period (10 years) with high temporal resolution (every 2–3 months) based on a large sample size (~10 000 growth observations), and included observations or estimates of multiple confounding factors. Inferences about effects of flow treatments on vital rates in programs without a long-term commitment to monitoring will invariably be weaker (Gillespie et al. 2015; Olden et al. 2014). In addition, generating strong effects from experimental flows, and providing adequate replication of the treatments, may be difficult owing to competing uses of a limited water supply (Konrad et al. 2011). Investigators usually have limited ability to control the design matrix of confounding factors that may complicate the interpretation of experimental results. Thus, the road to learning about e-flows is likely to be a long and bumpy one, and the duration of the trip may be difficult to predict. It's not surprising that some decision-makers are hesitant to get on the road or are tempted by off-ramps along the way (Allen and Gundersen 2011; Walters 2007). However, in the absence of reliable

mechanistic models to predict effects of e-flows on fish populations and other aquatic biota, there is effectively only one road to learning. Flow experiments remain the most viable way of reducing uncertainty about effects of environmental flows on aquatic ecosystems.

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Data availability.

Data generated during this study are available from the USGS ScienceBase-Catalog <https://doi.org/10.5066/P9XU3SQP>.

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Competing interests

The authors declare there are no competing interests. Use of trade, firm, or product names is for descriptive purposes only and does not constitute imply endorsement by the U.S. Government.

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Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2022-0142>.

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