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Flow management and fish density regulate salmonid recruitment and adult size in tailwaters across western North America

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Abstract. Rainbow and brown trout have been intentionally introduced into tailwaters downriver of dams globally and provide billions of dollars in economic benefits. At the same time, recruitment and maximum length of trout populations in tailwaters often fluctuate erratically, which negatively affects the value of fisheries. Large recruitment events may increase dispersal downriver where other fish species may be a priority (e.g., endangered species). There is an urgent need to understand the drivers of trout population dynamics in tailwaters, in particular the role of flow management. Here, we evaluate how flow, fish density, and other physical factors of the river influence recruitment and mean adult length in tailwaters across western North America, using data from 29 dams spanning 1–19 years. Rainbow trout recruitment was negatively correlated with high annual, summer, and spring flow and dam latitude, and positively correlated with high winter flow, subadult brown trout catch, and reservoir storage capacity. Brown trout recruitment was negatively correlated with high water velocity and daily fluctuations in flow (i.e., hydropeaking) and positively correlated with adult rainbow trout catch. Among these many drivers, rainbow trout recruitment was primarily correlated with high winter flow combined with low spring flow, whereas brown trout recruitment was most related to high water velocity.

The mean lengths of adult rainbow and brown trout were influenced by similar flow and catch metrics. Length in both species was positively correlated with high annual flow but declined in tailwaters with high daily fluctuations in flow, high catch rates of conspecifics, and when large cohorts recruited to adult size. Whereas brown trout did not respond to the proportion of water allocated between seasons, rainbow trout length increased in rivers that released more water during winter than in spring. Rainbow trout length was primarily related to high catch rates of conspecifics, whereas brown trout length was mainly related to large cohorts recruiting to the adult size class. Species-specific responses to flow management are likely attributable to differences in seasonal timing of key life history events such as spawning, egg hatching, and fry emergence.

Key words: competition; dam operations; discharge; fish; hydropeaking; *Oncorhynchus mykiss*; regulated river; *Salmo trutta*.

INTRODUCTION

Rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) are two of the most widely distributed fish species in the world due to intentional introductions combined with the species' high plasticity and ability to adapt to new environments (Fausch et al. 2001, Valiente et al. 2010, Budy et al. 2013). River regulation by dam construction modifies the thermal regime such that hypolimnetic-release dams create cold and clear fluvial environments akin to those in which both species evolved (McCusker et al. 2000, McIntosh et al. 2011), so rainbow and brown trout are often introduced into these "tailwaters" to provide angling

opportunities for recreational fishers. In the United States alone, 6.8 million trout anglers spent approximately \$4.8 billion in 2006 on equipment and trip-related expenses that rippled through the economy, providing a net economic benefit of \$13.6 billion (Harris 2010). The economic importance of trout fishing also extends to nations in Europe, Australasia, and Africa (Morrissey et al. 2002, Radford et al. 2007, Du Preez and Hosking 2011). Anglers typically seek tailwaters that produce maximum-sized trophy trout or those in which they can capture large quantities of fish for consumptive use (Hutt and Bettoli 2007); however, the health of many trout fisheries is perceived to have declined over time (e.g., catch rates, size, condition [Weiland and Hayward 1997, McKinney et al. 2001]). The causes of those declines are not well understood, and may be related to novel, regulated flow regimes unlike those in which trout evolved. Therefore, we used introduced

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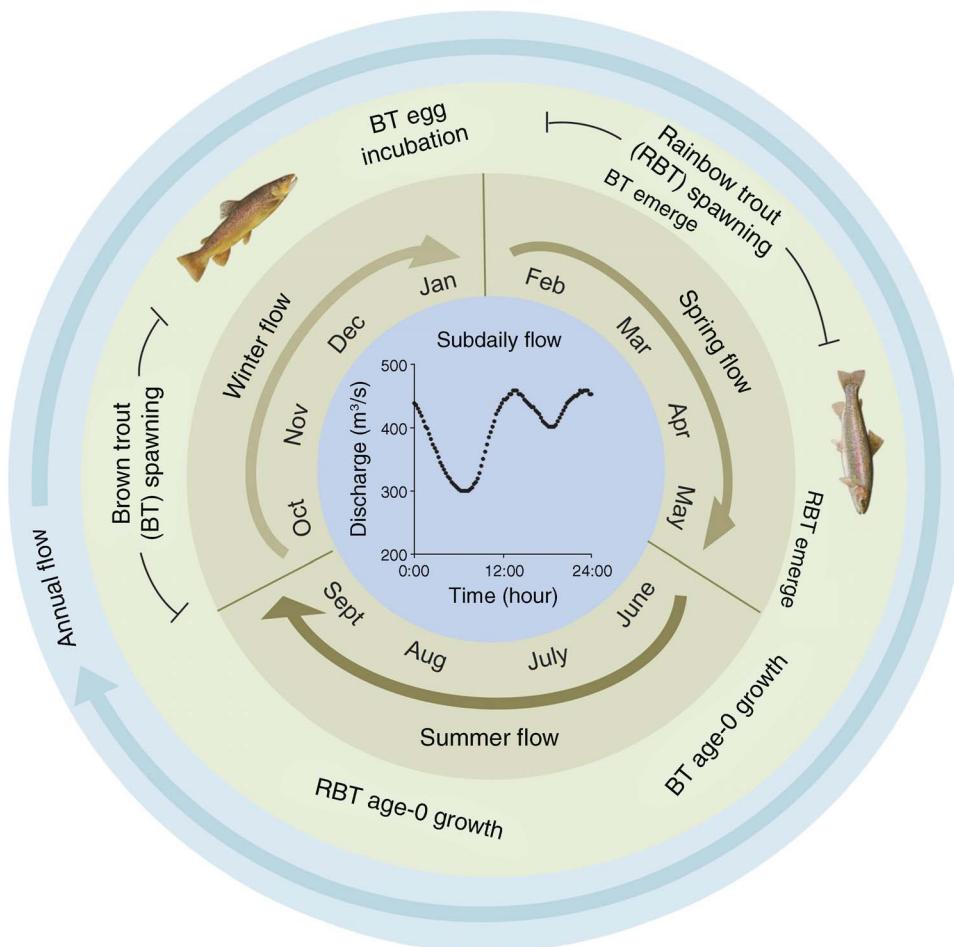


FIG. 1. Conceptual diagram for flow metrics used in this analysis and their relation to rainbow and brown trout life history stages. The inner circle (medium blue) depicts subdaily flow variation that is characteristic of hydropeaking dams (data are from Glen Canyon Dam on 1 January 2011, an arbitrary date). The next circle (medium brown) illustrates how seasonal patterns of flow were defined in this study, and the next circle (light brown) illustrates how the timing of key rainbow (RBT) and brown trout (BT) life stages intersects with these seasonal flow metrics. The outer circle (light blue) depicts annual flow commencing 1 October of each water year (WY). This metric compares annual flow in one year to all other WY in which fish data were collected.

salmonids as model species to understand how dam operations and flow management influence key population dynamics of fish including recruitment and maximum size, two metrics used by natural resource managers to assess fishery health.

Rainbow and brown trout are ideal species for understanding how flow regulation influences fish in general, because they are distributed across multiple tailwaters that differ greatly in flow management strategies. In addition, these two species differ in timing of key life history events, including adult spawning (late winter for rainbow trout and mid-fall for brown trout), egg hatching (early spring and late winter, respectively), and fry emergence (late spring/early summer and early spring, respectively; Fig. 1 [Fausch et al. 2001, McIntosh et al. 2011; but see Wood and Budy 2009]). Since rainbow and brown trout have different life history strategies, and regulated rivers are often managed in ways that lead to fundamentally different patterns of

flow than are found in unregulated rivers (Bunn and Arthington 2002), we might expect different functional relationships between flow regimes and population dynamics for the two species.

In regulated rivers, daily and seasonal patterns of flow vary systematically depending on the primary purpose of the dam (Richter and Thomas 2007). For example, tailwaters located downstream of hydropower dams can be subject to considerable within-day variation in flow, and seasonal patterns of flow may also be related to energy demand (i.e., flow is high during summer and winter, and low in spring and fall). In contrast, tailwaters below irrigation dams may experience little within-day variation in flow, but flow is high during the summer growing season and low at other times of year (Richter and Thomas 2007). These flow management strategies may conflict with the basic life history patterns of salmonid species that can lead to differential responses in trout population dynamics. For example,

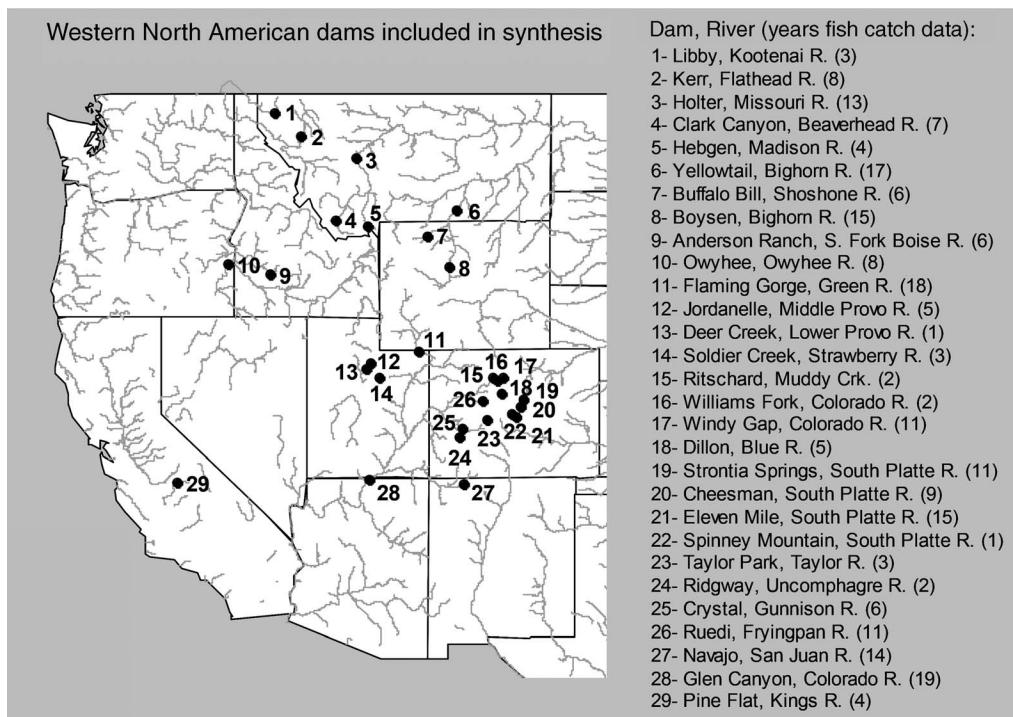


FIG. 2. Map showing location of western North American tailwaters included in synthesis.

flow management strategies that release high volumes of water during rainbow and brown trout egg incubation and hatching (i.e., spring and winter, respectively) can be detrimental to trout recruitment and can shift the dominant species when both are colocated in the same river system (Strange et al. 1993, Strange and Foin 1999). In addition, large subdaily variation in flow negatively affects juvenile rainbow trout growth (Korman and Campana 2009), which may influence survival and shift the size structure of salmonids. While the above studies within individual tailwaters provide some clues as to how flow regimes affect fish populations, they stem from a few tailwaters and are mostly focused on recruitment and juvenile growth. In contrast, managers are often interested in the maximum length and condition of adult fish as well as overall population size, but there is lack of consensus on how differential flow regimes may influence adult trout populations.

Here, we analyze rainbow and brown trout catch data from 29 tailwaters in western North America to evaluate how flow management and other biological and physical factors affect recruitment and mean adult length. We focus on western North America because rainbow and brown trout have been extensively stocked downriver of many dams in this region to benefit recreational anglers, many tailwaters are regularly monitored, and there is large variation in the primary purpose of dams, and consequently in flow regimes. We control for other possible drivers of recruitment and growth, including stocking of hatchery-raised fish that might lead to

density-dependent growth effects (Weiland and Hayward 1997), whirling disease, caused by the parasite *Myxobolus cerebralis*, which can lead to declines in rainbow trout recruitment (Nehring and Walker 1996), reservoir aging and the associated decline in nutrient inputs from decomposing reservoir vegetation (Stockner et al. 2000), and reservoir storage capacity, because reservoirs with larger storage are likely to have less year-to-year variation in flow regimes or water temperatures (Lessard and Hayes 2003, Olden and Naiman 2010). We specifically ask the following research questions: (1) How does flow management affect two species with diverse life history strategies? (2) How do strong adult cohorts and increased catch rates (i.e., density) of conspecifics and competing species influence trout populations? (3) How do attributes such as stocking, disease, dam age, and reservoir capacity influence trout population dynamics?

MATERIALS AND METHODS

Rainbow and brown trout length and catch data were collected by State, nongovernmental, and tribal organizations in regulated rivers located throughout western North America (see Acknowledgments, and Fig. 2). We focused on data collected between August and November because all tailwaters had data available from this time period, and then pooled all sites sampled via electrofishing within 20 miles downriver of a given dam in a given year. All data were collected along the shoreline via nighttime boat electrofishing with one

primary netter per boat. Data were primarily from one-pass electrofishing studies; however, if the same station was shocked two or more times within a sample period or year (e.g., during depletion or mark–recapture studies), we only analyzed catch data from the first pass. If multiple shorelines were sampled we incorporated the linear length of each shoreline in catch estimates; studies that zig-zagged between banks were excluded from the analysis. We used data from all passes to model changes in fish length.

We used trout recruitment and mean adult length as response variables because they describe key aspects of fish population dynamics and can be derived from all monitoring data sets. For rainbow trout, we calculated the catch-per-kilometer of shoreline of subadults (“recruitment”) for each dam–year combination, where subadult fish were defined to be between 150 and 300 mm in length and ~1.5 years old. We used subadult catch as our metric of recruitment because low capture probability for juveniles (i.e., <150 mm [Korman et al. 2012]) results in that age group being poorly represented in available data sets. Mean adult length of rainbow trout (“length”) was computed as the mean length of all trout >300 mm. We derived similar recruitment and length metrics for brown trout, but used 350 mm as the cutoff between subadults and adults because length–frequency histograms indicate brown trout transition from age 1 to age 2 at ~350 mm.

Dam operations influence daily, seasonal, and annual flow releases, so we obtained subdaily (15, 30, 60 minute) discharge data from the U.S. Geological Survey National Water Information System, Bureau of Reclamation Hydromet System, Natural Resources Conservation Service National Water and Climate Center, Colorado Division of Water Resources, Northern Colorado Water Conservancy District, and the California Department of Water Resources. We calculated five flow metrics to be used as predictor variables, including: (1) hydropeaking, defined as the mean coefficient of variation (CV) of subdaily flow, averaged over the Water Year (WY) prior to fish collection (1 October–30 September); (2) relative annual flow, defined as annual flow within a WY relative to average annual flow for all years fish data were available; (3) specific discharge, defined as flow relative to channel width (i.e., water velocity); and (4–5) two metrics that describe variation in the seasonal allocation of water released from each dam (i.e., proportion of water released in summer; proportion of water released in winter and spring; see Appendix A: Table A1). Initially, we considered three metrics that describe the proportion of flow released in three seasons, which we defined according to rainbow and brown trout life history as winter (1 October–31 January), spring (1 February–31 May), and summer (1 June–30 September; Fig. 1). However, these metrics were highly correlated, so we instead used the first two axes from a Principal Component Analysis (PCA) as predictors. PCA results indicated that summer account-

ed for the highest amount of variability in seasonal flow (see Appendix B: Tables B1, B2 for PC1 loadings). Variation in PC2 was driven by winter and then spring flow, and the signs for these seasons were always opposite (Appendix B: Tables B1, B2). Therefore, in our modeling results it is not possible to distinguish the effects of winter flow from spring flow. In other words, a positive coefficient associated with PC2 may indicate that high winter flows or low spring flows or both high winter and low spring flows are correlated with a given response variable. We calculated the five flow metrics using data from the year immediately preceding sampling; however, since different life stages of trout (i.e., juvenile, subadult, adult) might respond differently to flow, we also included metrics from two water years prior in models (hereafter, “lagged” metrics; Appendix A: Table A1). For example, we compared recruitment in fall 2012 to flow from the 2012 WY (1 October 2011–30 September 2012) and the 2011 WY (1 October 2010–30 September 2011; “lagged”).

Density dependence can limit the survival and growth of juvenile and adult salmonids through complex interactions between water temperature (i.e., metabolic rates) and food consumption (Railsback and Rose 1999, Budy et al. 2008, Crozier et al. 2010). To account for fish density and resulting competition effects on recruitment and mean adult length, we computed six predictors based on catch per kilometer of shoreline (“catch”) for: (1) subadult rainbow trout (150–300 mm), (2) adult rainbow trout (>300 mm), (3) subadult and adult rainbow trout, (4) subadult brown trout (150–350 mm), (5) adult brown trout (>350 mm), and (6) subadult and adult brown trout. Furthermore, influxes of large numbers of recruits into the adult size class can decrease the average length of adults, simply because the “new” adults are necessarily on the smaller end of the size distribution. To account for this hypothesized effect, we computed a seventh biological covariate that described the relative strength of the new adult cohort (i.e., for rainbow trout, the catch of rainbow trout subadults in the year prior divided by the catch of subadult and adult rainbow trout in the year prior; Appendix A: Table A1).

Trout recruitment and mean adult length may also be influenced by factors such as fish stocking, disease, dam age, and other reservoir attributes. Therefore, we included binary variables in models for fish stocking (species-specific within each model) and whirling disease (present in the year fish were captured). We also included the predictors dam age, altitude, and latitude, and we calculated two additional reservoir metrics: (1) reservoir fullness within the WY relative to maximum capacity; and (2) storage capacity of the dam relative to flow across WY (Appendix A: Table A1). Our hypotheses on the relationships between response and predictor variables for rainbow and brown trout are outlined in Appendix C: Table C1.

Statistical analyses

We analyzed recruitment data for each species using generalized linear mixed models (GLMM) with a negative binomial error distribution, dam as a random effect, and the number of kilometers sampled as an offset. Including number of kilometers as an offset, and catch as the response, is similar to using catch per kilometer as the response variable, but the former weights observations by how much shoreline was sampled. We analyzed mean adult length for each species using a GLMM in which the error structure was normal (Gaussian) and dam was included as a random effect. All continuous predictors were centered on their mean and standardized by their standard deviation to ease interpretation.

For each species and response variable we used a modified version of forward stepwise selection based on Akaike Information Criterion (AIC). Forward stepwise selection typically proceeds by choosing the best predictor from all predictors in the first step, and then the second best, and so forth until additional predictors do not lead to a drop in AIC. Although our predictors were not highly correlated ($r < 0.6$), the lagged and unlagged version of flow metrics were occasionally highly correlated ($r > 0.6$). Therefore, we modified the typical stepwise selection process to choose between either the lagged or unlagged version of a flow metric to avoid issues of multicollinearity.

After identifying the best models via modified forward stepwise regression, we used multilevel R^2 analysis to calculate an R^2 for the best model and for the models in which one predictor was removed. This allowed us to determine whether a predictor was included in the model because it was correlated with differences between dams or with differences within dams over time (Gelman and Pardoe 2006). Predictors that explain variation within dams are likely to be more relevant to management because they explain temporal variation rather than large, inherent differences between dams. We fit GLMM models in R (v.3.0.2; R Development Core Team 2013) using the lme4 and glmmADMB packages, and used WinBUGS (v. 1.4.3; Lunn et al. 2000) to calculate posterior draws for the R^2 analyses.

RESULTS

Our analysis included data for 89 226 rainbow and 80 434 brown trout from 29 tailwaters collected over 1–19 years, depending on the tailwater (Fig. 2). Rainbow and brown trout were collocated downriver in 25 of the 29 dams.

Rainbow trout

Across tailwaters, the mean rainbow trout subadult catch per kilometer was 54.7 ± 14.1 fish/km (mean \pm SE). The best model of rainbow trout recruitment included relative annual flow (lagged), seasonal allocation of flow, subadult brown trout catch, latitude, and reservoir storage capacity (Table 1). For the flow

predictors, high relative annual flow in the year prior to capture and high summer and spring flow were negatively correlated with rainbow trout recruitment, whereas high winter flow was positively correlated with recruitment. Recruitment declined with increasing latitude, while recruitment increased downriver of fuller reservoirs and in tailwaters with high subadult brown trout catch (Table 1, Fig. 3). The least important predictor in the rainbow trout recruitment model was latitude (Δ AIC = 0.7; Table 1). High subadult brown trout catch exhibited the largest effect size (estimate) in GLMM results; however, this predictor was in the final model due to large differences between dams, as evidenced by the highest drop in R^2 and Δ AIC when removed. More importantly, the multilevel R^2 analysis indicated that high winter/low spring flow was primarily responsible for increasing rainbow trout recruitment within individual tailwaters (Table 1, Fig. 3).

The mean adult length of rainbow trout across tailwaters was 383.2 ± 3.1 mm. The relative strength of new adult cohorts, rainbow and brown trout catch, flow, dam age, and reservoir storage capacity were all included in the best model of mean adult length (Table 1). Mean adult length was negatively correlated with hydropeaking, specific discharge, and high spring flow, and positively correlated with high annual and winter flow (Table 1, Fig. 3). Strong cohorts of new adults and high catch rates of rainbow trout and subadult brown trout were associated with lower mean adult length, whereas length was positively correlated with high catch rates of adult brown trout (Table 1, Fig. 3). Rainbow trout were smaller in tailwaters downriver of fuller reservoirs. Length decreased as a function of dam age; however, this was the least important predictor in the rainbow trout length model (Δ AIC = 0.8; Table 1). Multilevel R^2 analysis revealed that subadult brown trout catch was included in the length model only due to large between-dam differences in the predictor, even though the effect size was highest. More importantly, rainbow trout catch (i.e., density of trout >150 mm) explained the most variation in rainbow trout length within dams (Table 1, Fig. 3).

Brown trout

The mean brown trout subadult catch per kilometer across tailwaters was 211.1 ± 28.3 fish/km. Hydropeaking (lagged), specific discharge, and adult rainbow trout catch were included in the best model of brown trout recruitment (Table 1). Brown trout recruitment was negatively correlated with hydropeaking in the year prior to capture, and was lower in tailwaters exhibiting high specific discharge (Table 1, Fig. 4). Brown trout recruitment was positively correlated with adult rainbow trout catch. The least important predictor in the brown trout recruitment model was lagged hydropeaking (Δ AIC = 0.1; Table 1). The specific discharge predictor had the highest effect size and explained the greatest amount of both between- and within-dam variability in

TABLE 1. Estimates (i.e., “effect size”) and standard errors for predictors included in the best model, as well as the impacts of removing each predictor on Akaike Information Criterion (Δ AIC) and multilevel R^2 .

Model	Estimate	SE	Δ AIC	R^2 between	R^2 within
Rainbow trout recruitment					
Intercept/full model fit	3.55	0.22	0	0.19	0.26
Relative annual flow (1–2 years)	–0.15	0.07	1.8	0.24	0.21
PC1 (summer)†	–0.17	0.09	1.7	0.24	0.23
PC2 (winter/spring)‡	0.25	0.08	7.4	0.25	0.12
Subadult brown trout catch	0.67	0.17	15.1	0.10	0.31
Latitude	–0.40	0.23	0.7	0.10	0.23
Reservoir storage in water year	0.32	0.14	2.9	0.29	0.22
Rainbow trout adult length					
Intercept/full model fit	383	4	0	0.67	0.75
Hydropeaking	–8	3	5.4	0.58	0.74
Relative annual flow	5	2	4.0	0.62	0.74
Specific discharge	–12	5	2.9	0.54	0.75
PC2 (winter/spring)	8	2	8.6	0.64	0.73
Rainbow trout catch	–9	2	12.2	0.62	0.72
New adult cohort strength	–8	2	9.6	0.53	0.74
Subadult brown trout catch	–12	3	8.5	0.41	0.75
Adult brown trout catch	8	3	3.3	0.59	0.74
Dam age	–6	4	0.8	0.63	0.74
Reservoir storage in water year	–7	3	1.8	0.55	0.75
Brown trout recruitment					
Intercept/full model fit	4.18	0.32	0	0.50	0.72
Hydropeaking (lagged flow, 1–2 years)	–0.13	0.09	0.1	0.49	0.71
Specific discharge	–1.61	0.33	15.6	0.03	0.67
Adult rainbow trout catch	0.17	0.09	1.4	0.49	0.72
Brown trout adult length					
Intercept/full model fit	414	3	0	0.75	0.68
Hydropeaking	–8	2	9.4	0.76	0.65
Relative annual flow	4	2	4.5	0.71	0.67
Brown trout catch	–6	2	4.2	0.60	0.68
New adult cohort strength	–14	2	34.0	0.43	0.60
Reservoir storage in water year	–5	3	0.7	0.68	0.69

Notes: Each predictor can explain variance between dams (R^2 between) and/or within dams (R^2 within). The boldface R^2 value for each response indicates the single variable that explains the greatest amount of between- or within-dam variation (i.e., removing this variable from the best model leads to the largest drop in R^2). The first line in each model provides the intercept and associated standard error in first two columns and the Δ AIC and R^2 values for the full model.

† Axis 1, Principal Component Analysis (PCA).

‡ Axis 2, PCA.

brown trout recruitment, as evidenced by the largest drop in R^2 and Δ AIC following its removal (Table 1).

The mean length of adult brown trout across tailwaters was 413.7 ± 2.6 mm. The best adult length model included hydropeaking, relative annual flow, brown trout catch, new adult cohort strength, and reservoir storage capacity (Table 1). Mean adult length was negatively correlated with hydropeaking and positively correlated with high relative annual flow (Table 1, Fig. 4). Brown trout were smaller in tailwaters exhibiting high brown trout catch (i.e., density of trout >150 mm), strong new adult cohorts, and downriver of full reservoirs, although the latter was the least important predictor in brown trout length models (Δ AIC = 0.7; Table 1). The predictor for new adult cohort strength had the highest effect size in models and explained the greatest amount of between- and within-dam variability in brown trout length (Table 1).

DISCUSSION

Our results offer insights into the relative importance of physical and biological processes on rainbow and brown trout recruitment and size structure in tailwaters across western North America. Recruitment was regulated primarily by flow management, but the response of the two species differed. Rainbow trout recruitment was influenced more by seasonal and annual flow volume, whereas brown trout recruitment was affected more by flow velocity. In contrast, the mean adult length of rainbow and brown trout was regulated more by biology (i.e., density and competition) than flow, with the length of both species being inversely related to density.

Recruitment

We hypothesized the response of rainbow and brown trout recruitment to seasonal allocation of flow would be species-specific because of differences in timing of early life history events (Fig. 1; Appendix C: Table C1).

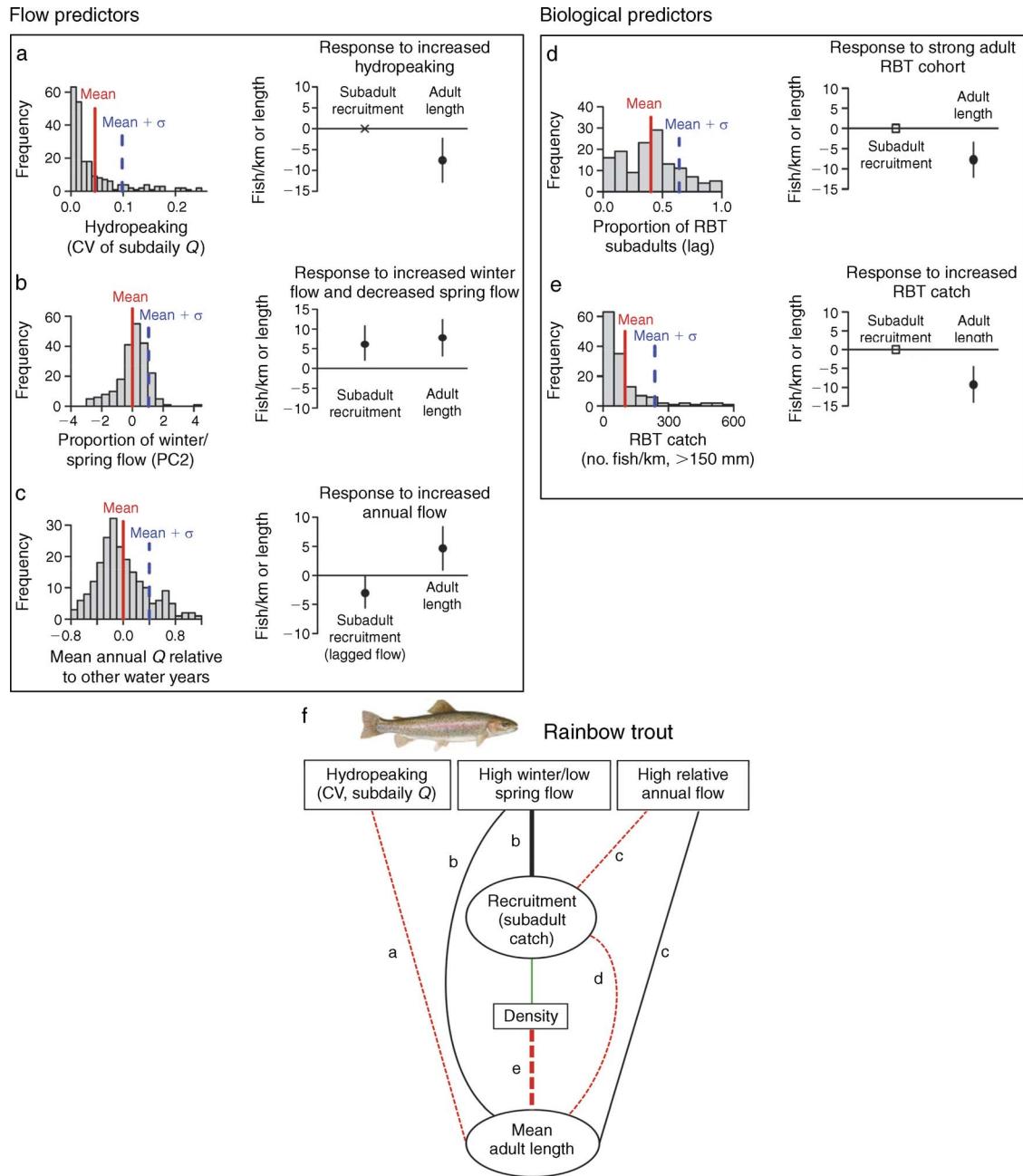


FIG. 3. Histograms of predictors and corresponding effect sizes (mean \pm 95% CI) on rainbow trout recruitment and mean adult length. Histograms (a–e) illustrate a 1 – σ increase from the mean (red solid to blue dashed line) for the three flow (Q) and two biological predictors that explained the largest amount of within-dam variation. Conceptual diagram (f) shows the relationship between predictors (boxes) and response variables (ovals), with red dashed lines indicating a (–) relationship, black solid lines a (+) relationship, and the green line an inferred relationship. Boldface lines indicate the predictor that explains the largest amount of within-dam variation. Letters a–e next to each pathway correspond with effect size panel results. Key: CV, coefficient of variation; PC2, Axis 2, Principal Component Analysis; RBT, rainbow trout; X, no significant effect of covariate on results; square box, covariate not included in models.

Specifically, we hypothesized rainbow trout recruitment would be higher in tailwaters exhibiting low spring and/or high winter flow (Fausch et al. 2001) and brown trout recruitment would be higher in tailwaters with high spring and/or low winter flow (Strange et al. 1993,

Strange and Foin 1999). Consistent with our hypothesis, we detected a positive relationship between rainbow trout recruitment and the PCA axis representing low spring/high winter flow. Rainbow trout spawn in late winter to early spring, and fry emerge in late spring to

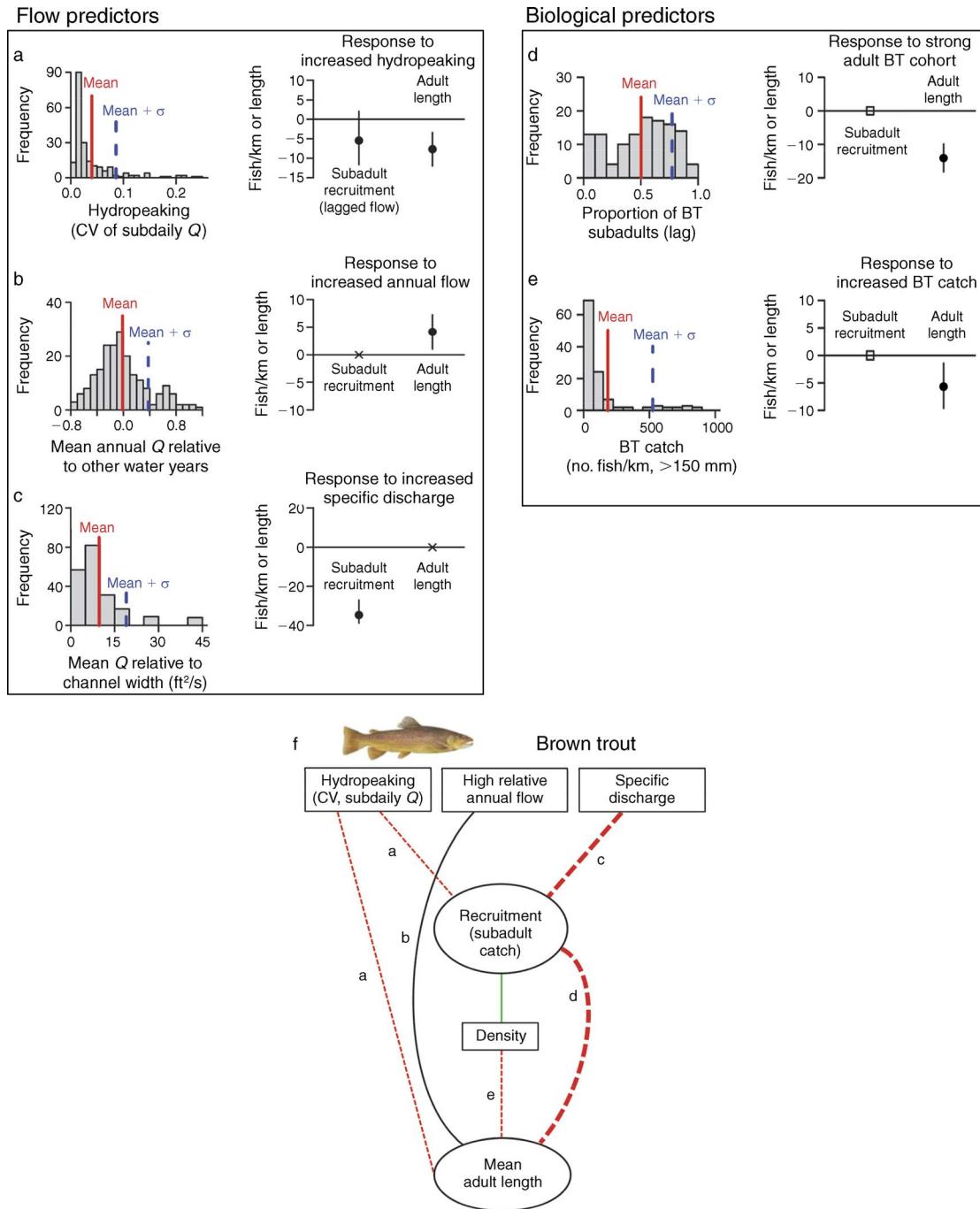


FIG. 4. Histograms of predictors and corresponding effect sizes (mean \pm 95% CI) on brown trout recruitment and mean adult length. Histograms (a–e) illustrate a 1 σ increase from the mean (red solid to blue dashed line) for the three flow (Q) and two biological predictors that explained the largest amount of within-dam variation. Conceptual diagram (f) shows the relationship between predictors (boxes) and response variables (ovals), with red dashed lines indicating a (–) relationship, black solid lines a (+) relationship, and the green line an inferred relationship. Boldface lines indicate the predictor that explains the largest amount of within-dam variation. Letters a–e next to each pathway correspond with effect size panel results. Key: CV, coefficient of variation; BT, brown trout; X, no significant effect of covariate on results; square box, covariate not included in models. Histogram c: 1 square foot, 0.092903 m².

early summer (Fausch et al. 2001). Spring floods reduce the year class strength of spring-spawning trout species because high flows scour the substrate, remove eggs and larvae from redds, and cause short-term reductions in invertebrate prey (Elwood and Waters 1969, Strange et al. 1993, McMullen and Lytle 2012; but see Korman et al. 2011). Support for our seasonal hypothesis was lacking for brown trout, since the best recruitment model did not include the spring–winter flow covariate.

We also hypothesized that rainbow and brown trout recruitment would increase in years of high annual flow. However, relative annual flow was not included in the best brown trout model of recruitment, and the effect of relative annual flow on rainbow trout recruitment was actually counter to this hypothesis. Annual flow was included in the rainbow trout model, but higher annual flows were associated with lower recruitment of rainbow trout. Rainbow trout recruitment has been positively linked to high flows; the most plausible mechanism includes expanded rearing habitat through flooding of the shoreline, which increases growth and survival of juvenile salmonids (Mitro et al. 2003, Korman et al. 2012). However, the energetic costs of prolonged high-water velocities could decrease survival of juvenile rainbow trout in the absence of adequate shoreline refuges during high annual flow years. Korman and Campana (2009) found that both growth and nearshore habitat use by age-0 rainbow trout increase when flows are low and stable, whereas high, fluctuating flows result in offshore movement where there is a potential energetic cost of maintaining position in high-velocity water. This is supported by evidence from our brown trout recruitment models. Although relative annual flow was not included in the best brown trout model, we detected a strong negative relationship between brown trout recruitment and specific discharge, which was the best predictor of within- and between-dam variation in recruitment. Thus, variation in trout recruitment in tailwaters appears to be associated with the availability of low-velocity, shallow-water habitats near river margins during early life stages that permit energetically efficient foraging while providing protection from predation (Hubert et al. 1994).

We hypothesized that rainbow and brown trout recruitment would be lower in tailwaters where hydropeaking occurs, or in years where hydropeaking was greater. Lagged hydropeaking was included in the best brown trout model, and had the expected negative sign, supporting our hypothesis. However, lagged hydropeaking had the weakest support in the brown trout recruitment model based on change in AIC, and it was excluded from the best rainbow trout recruitment model. Although our modeling only indicates a weak relationship between brown trout recruitment and hydropeaking, a number of studies in European tailwaters (Cowx and Gould 1989, Almodóvar and Nicola 1999) have also documented declines in brown trout recruitment due to hydropeaking and its associat-

ed changes in habitat quality and water velocity. This weak relationship between hydropeaking and brown trout recruitment, and the lack of a relationship for rainbow trout recruitment, may be due to the inclusion of only a few load-following dams in our analysis. The majority of tailwaters in the western United States reside downriver of storage dams that exhibit large annual and seasonal fluctuations in flow but have relatively stable daily flow regimes, regardless of whether or not they generate power. The two most important predictors that increased rainbow trout recruitment were high winter/low spring flow and low annual flow. Therefore, low, stable flows during the spring spawning season and throughout the first year appear to be more important than hydropeaking in regulating rainbow trout size class strength across western U.S. tailwaters.

Surprisingly, we did not detect a decrease in rainbow trout recruitment in tailwaters affected by whirling disease, nor did we detect a shift in size structure in heavily stocked rivers. Whirling disease was present in several tailwaters, and we hypothesized it would have a disproportionate effect on rainbow trout size structure (Nehring and Walker 1996). However, stable rainbow trout recruitment has been detected in infected populations that exhibit low spawning site fidelity, because the risk of infection is spread over multiple tributary and mainstem sites (Grisak et al. 2012). In addition, stocking of whirling disease resistant trout (e.g., Hofer strain [Hedrick et al. 2003]) in infected waters may stabilize rainbow trout populations that ultimately negate losses in recruitment over time.

Mean adult length

For both species, more of the variation in adult length was explained by population feedbacks than by flow metrics according to AIC; however, some flow metrics had larger standardized effect sizes for rainbow trout. We hypothesized that adult length and trout catch (i.e., density) would be inversely related, and adult length would decrease in years with large cohorts of “new,” but smaller, fish recruiting into the adult size class. We found support for these hypotheses in both species, indicating intraspecific competition plays an important role in determining the length of rainbow and brown trout in tailwaters. Density dependence is a common characteristic of aquatic and terrestrial animal populations (Brook and Bradshaw 2006), and several studies have documented density-dependent growth specifically in salmonids (Grant and Imre 2005, Crozier et al. 2010). For example, excessive fish stocking in a Midwestern U.S. tailwater caused a decline in the length of large rainbow trout (>400 mm), mediated by a degraded prey base and declines in prey consumption (Weiland and Hayward 1997). Likewise, Jenkins et al. (1999) documented a negative relationship between adult brown trout growth and conspecific densities in two California alpine streams that were linked to a broadening of brown trout diet and the consumption of a larger

number of less-profitable prey items (e.g., chironomid larvae). Grant and Imre (2005) also reviewed density-dependent effects on multiple salmonid species and detected negative relationships between density and growth in five of six rainbow trout populations and in three of five brown trout populations. Our results add to this growing body of literature and demonstrate that across 29 different tailwaters, rainbow and brown trout length is negatively related to density.

We hypothesized both rainbow and brown trout would have higher average adult lengths following years of high annual flow. This hypothesis was supported in both species, but the effect size was modest. Neither of the seasonal flow covariates were included in the best brown trout model of adult length, while PC2 (higher winter flows, lower spring flows) had a positive effect in the best rainbow trout length model and was the second-best predictor explaining within-dam temporal trends. Low spring flows from February to May may benefit adult rainbow trout growth through decreased energetic costs during their spawning season. Salmonid investment of energy into reproduction is high, with lipid reserves commonly depleted by >50% relative to pre-spawning body conditions (Jonsson et al. 1991, Hutchings et al. 1999). High flow conditions can confer an energetic cost on salmonids that decreases growth and/or physiological condition (Kemp et al. 2006, Cocherell et al. 2011), particularly when salmonids are building nests and attempting to hold position over their redds (Tiffan et al. 2010). Therefore, low spring flows may confer a benefit to adult rainbow trout by decreasing energetic costs during a critical time period when lipid reserves are already depleted.

We hypothesized hydropeaking would sustain the growth of large trout through daily surges of invertebrate prey (Perry and Perry 1986, Kennedy et al. 2014, Miller and Judson 2014). This hypothesis was rejected since we detected a negative relationship between hydropeaking and the length of both species. Although hydropeaking can foster increased drift concentrations leading to increased gut fullness in brown and rainbow trout (Miller and Judson 2014), the energetic costs associated with maintaining position and foraging in rivers with large subdaily variation in flow may offset the increases in energy intake that hydropeaking creates. Alternatively, increases in invertebrate drift concentrations associated with hydropeaking may ultimately deplete benthic invertebrates and lead to lower drift concentrations and prey availability for trout over long time scales (i.e., weeks to months [Kennedy et al. 2014]). Regardless of the underlying mechanisms, our results indicate that hydropeaking does not favor the growth of large trout.

Reservoir aging and the decline in phosphorus from decomposing vegetation and flooded soils (Stockner et al. 2000) has been noted as a potential mechanism for declining tailwater productivity over time. Consistent with our hypothesis, we detected a significant negative

relationship between dam age and rainbow trout length, but this was the weakest predictor and was most likely in the final model due to large between-dam differences in reservoir age. We also hypothesized that reservoirs with larger storage capacity would benefit the growth of adult rainbow and brown trout via less year-to-year variation in flow and more stable water temperatures (Lessard and Hayes 2003, Olden and Naiman 2010). Contrary to this hypothesis, both trout models indicated that small reservoirs were associated with large trout, but model results were attributable to large between-dam differences in reservoir size. Collectively, these results indicate adult rainbow and brown trout growth is affected more by intraspecific interactions than by the physical characteristics of the environment.

Management implications

Our results indicate rainbow and brown trout recruitment in tailwaters is primarily explained by dam operations that regulate flow, whereas mean adult length is best explained by biological predictors such as high catch rates of conspecifics (i.e., density) and new adult cohort strength, followed by flow management. Species-specific recruitment responses to flow management likely relate to the species' divergent life history strategies and timing of adult spawning, egg hatching, and fry emergence. Overall, rainbow trout recruitment decreased in response to high flow volume, particularly in the season following emergence (i.e., spring). Brown trout recruitment, however, was influenced more by flow velocity. In contrast, factors influencing mean adult length in both species were remarkably similar and indicate once trout reach adult status their overall size is regulated more by intraspecific interactions (i.e., density and competition) than hydrology. Negative density-dependent effects on fish growth are likely caused by a decrease in the availability of prey in rivers exhibiting high trout catch rates (Jenkins et al. 1999, Imre et al. 2004). Since recruitment regulates the density of trout populations, and flow alters recruitment and invertebrate assemblages, flow indirectly plays a role in determining adult size. Therefore, it is important to consider the effects of flow management on recruitment, because the latter ultimately drives patterns in the overall health of tailwater trout populations.

In light of these results, natural resource managers could alter dam operations to improve the health of economically important fisheries in tailwaters. Since high levels of recruitment indirectly decrease fish size, dam operations that decrease trout density may foster the development of trophy trout fisheries through relaxation from intraspecific competition. For example, dam managers could release a larger proportion of water in spring (i.e., February–May) relative to other seasons to decrease rainbow trout recruitment, which, in turn, may indirectly favor adult rainbow trout growth through decreased competition. However, high spring flows that confer an energetic cost on adult rainbow

trout during their spawning season may decrease growth potential, indicating there is a delicate balance between decreasing recruitment and competition through high flows and ensuring the energetic costs incurred by adults are not counterproductive to management objectives. Although we did not detect a decrease in brown trout recruitment related to seasonal flow releases, recruitment decreased in tailwaters exhibiting high water velocity. This indicates that water velocity has a potential scouring effect on brown trout eggs and/or an energetic cost on emerging fry that ultimately decreases competition. Since low levels of recruitment in the year prior to capture had the largest effect on increasing brown trout length, dam operations that maximize flow velocity may relax intraspecific competition that ultimately enhances the growth potential of adult brown trout. Last, we found moderate support that hydropeaking flows do not favor the growth of adult rainbow and brown trout, indicating that stable flow regimes may confer an energetic or prey availability advantage over long time scales for introduced salmonids. Overall, these results suggest that if managers are interested in stable trout populations with larger adults, then they could consider altering dam operations or implementing management actions to decrease rainbow and brown trout recruitment.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C are available online: <http://dx.doi.org/10.1890/14-2211.1.sm>

Data Availability

Data associated with this paper have been deposited in the USGS ScienceBase: <https://www.sciencebase.gov/catalog/item/556cb83ae4b0d9246a9f979e> <http://dx.doi.org/10.5066/F79P2ZQ2>