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1   TITLE: Flow management and fish density regulate salmonid recruitment and adult size in

2   tailwaters across western North America

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4   AUTHORS: Kimberly L. Dibble[1a], Charles B. Yackulic[2], Theodore A. Kennedy[3], Phaedra Budy[4]

5

6   [1] U.S. Geological Survey, Southwest Biological Science Center, Grand Canyon Monitoring and

7   Research Center; kdibble@usgs.gov

8   [2] U.S. Geological Survey, Southwest Biological Science Center, Grand Canyon Monitoring and

9   Research Center; cyackulic@usgs.gov

10   [3] U.S. Geological Survey, Southwest Biological Science Center, Grand Canyon Monitoring and

11   Research Center; tkennedy@usgs.gov

12   [4] U.S. Geological Survey, Utah Cooperative Fish and Wildlife Research Unit, Department of

13   Watershed Sciences and the Ecology Center, Utah State University; Phaedra.Budy@usu.edu

14

15   CORRESPONDING AUTHOR:

16   [a] Kimberly L. Dibble

17   U.S. Geological Survey

18   Southwest Biological Science Center

19   Grand Canyon Monitoring and Research Center

20   2255 N. Gemini Drive

21   Flagstaff, AZ 86001

22   Phone: (928) 556-7327; Fax: (928) 556-7092

23   kdibble@usgs.gov

24   *Abstract*

25   Rainbow and brown trout have been intentionally introduced into tailwaters downriver of

26   dams globally and provide billions of dollars in economic benefits. At the same time, recruitment

27   and maximum length of trout populations in tailwaters often fluctuate erratically, which

28   negatively affects the value of fisheries. Large recruitment events may increase dispersal

29   downriver where other fish species may be a priority (e.g., endangered species). There is an

30   urgent need to understand the drivers of trout population dynamics in tailwaters, in particular the

31   role of flow management. Here, we evaluate how flow, fish density, and other physical factors of

32   the river influence recruitment and mean adult length in tailwaters across western North America

33   using data from 29 dams spanning 1-19 years. Rainbow trout recruitment was negatively

34   correlated with high annual, summer, and spring flow and dam latitude, and positively correlated

35   with high winter flow, sub-adult brown trout catch, and reservoir storage capacity. Brown trout

36   recruitment was negatively correlated with high water velocity and daily fluctuations in flow

37   (i.e., hydropeaking) and positively correlated with adult rainbow trout catch. Among these many

38   drivers, rainbow trout recruitment was primarily correlated with high winter flow combined with

39   low spring flow, whereas brown trout recruitment was most related to high water velocity.

40   The mean lengths of adult rainbow and brown trout were influenced by similar flow and

41   catch metrics. Length in both species was positively correlated with high annual flow but

42   declined in tailwaters with high daily fluctuations in flow, high catch rates of conspecifics, and

43   when large cohorts recruited to adult size. Whereas brown trout did not respond to the proportion

44   of water allocated between seasons, rainbow trout length increased in rivers that released more

45   water during winter than in spring. Rainbow trout length was primarily related to high catch rates

46   of conspecifics, whereas brown trout length was mainly related to large cohorts recruiting to the

47 adult size class. Species-specific responses to flow management are likely attributable to

48 differences in seasonal timing of key life history events such as spawning, egg hatching, and fry

49 emergence.

50

51 *Keywords*: competition; dam operations; discharge; fish; hydropeaking; *Oncorhynchus mykiss*;

52 regulated river; *Salmo trutta*

53

54 INTRODUCTION

55 Rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) are two of the most

56 widely distributed fish species in the world due to intentional introductions combined with the

57 species' high plasticity and ability to adapt to new environments (Fausch et al. 2001, Valiente et

58 al. 2010, Budy et al. 2013). River regulation by dam construction modifies the thermal regime

59 such that hypolimnetic-release dams create cold and clear fluvial environments akin to those in

60 which both species evolved (McCusker et al. 2000, McIntosh et al. 2011), so rainbow and brown

61 trout are often introduced into these "tailwaters" to provide angling opportunities for recreational

62 fishers. In the United States alone, 6.8 million trout anglers spent approximately $4.8 billion in

63 2006 on equipment and trip-related expenses that rippled through the economy, providing a net

64 economic benefit of $13.6 billion (Harris 2010). The economic importance of trout fishing also

65 extends to nations in Europe, Australasia, and Africa (Morrisey 2002, Radford et al. 2007, Du

66 Preez and Hosking 2011). Anglers typically seek tailwaters that produce maximum-sized trophy

67 trout or those in which they can capture large quantities of fish for consumptive use (Hutt and

68 Bettoli 2007); however, the health of many trout fisheries is perceived to have declined over time

69 (e.g., catch rates, size, condition; Weiland and Hayward 1997, McKinney et al. 2001). The

70   causes of those declines are not well understood and may be related to novel, regulated flow

71   regimes unlike those in which trout evolved. Therefore, we used introduced salmonids as model

72   species to understand how dam operations and flow management influence key population

73   dynamics of fish including recruitment and maximum size, two metrics used by natural resource

74   managers to assess fishery health.

75   Rainbow and brown trout are ideal species for understanding how flow regulation

76   influences fish in general because they are distributed across multiple tailwaters that differ

77   greatly in flow management strategies. In addition, these two species differ in timing of key life

78   history events, including adult spawning (late winter for rainbow trout and mid-fall for brown

79   trout), egg hatching (early spring and late winter respectively), and fry emergence (late

80   spring/early summer and early spring respectively; Fig. 1; Fausch et al. 2001, McIntosh et al.

81   2011; but see Wood & Budy 2009). Since rainbow and brown trout have different life history

82   strategies, and regulated rivers are often managed in ways that lead to fundamentally different

83   patterns of flow than are found in unregulated rivers (Bunn and Arthington 2002), we might

84   expect different functional relationships between flow regimes and population dynamics for both

85   species.

86   In regulated rivers, daily and seasonal patterns of flow vary systematically depending on

87   the primary purpose of the dam (Richter and Thomas 2007). For example, tailwaters located

88   downstream of hydropower dams can be subject to considerable within-day variation in flow,

89   and seasonal patterns of flow may also be related to energy demand (i.e., flow is high during

90   summer and winter, and low in spring and fall). In contrast, tailwaters below irrigation dams may

91   experience little within-day variation in flow, but flow is high during the summer growing

92   season and low at other times of year (Richter and Thomas 2007). These flow management

93 strategies may conflict with the basic life history patterns of salmonid species that can lead to

94 differential responses in trout population dynamics. For example, flow management strategies

95 that release high volumes of water during rainbow and brown trout egg incubation and hatching

96 (i.e., spring and winter, respectively) can be detrimental to trout recruitment and can shift the

97 dominant species when both are co-located in the same river system (Strange et al. 1993, Strange

98 and Foin 1999). In addition, large subdaily variation in flow negatively affects juvenile rainbow

99 trout growth (Korman and Campana 2009), which may influence survival and shift the size

100 structure of salmonids. While the above studies within individual tailwaters provide some clues

101 as to how flow regimes affect fish populations, they stem from a few tailwaters and are mostly

102 focused on recruitment and juvenile growth. In contrast, managers are often interested in the

103 maximum length and condition of adult fish as well as overall population size, but there is lack

104 of consensus on how differential flow regimes may influence adult trout populations.

105   Here, we analyze rainbow and brown trout catch data from 29 tailwaters in western North

106 America to evaluate how flow management and other biological and physical factors affect

107 recruitment and mean adult length. We focus on western North America because rainbow and

108 brown trout have been extensively stocked downriver of many dams in this region to benefit

109 recreational anglers, many tailwaters are regularly monitored, and there is large variation in the

110 primary purpose of dams, and consequently in flow regimes. We control for other possible

111 drivers of recruitment and growth, including stocking of hatchery-raised fish that might lead to

112 density-dependent growth effects (Weiland and Hayward 1997), whirling disease, caused by the

113 parasite *Myxobolus cerebralis*, that can lead to declines in rainbow trout recruitment (Nehring

114 and Walker 1996), reservoir aging and the associated decline in nutrient inputs from

115 decomposing reservoir vegetation (Stockner et al. 2000), and reservoir storage capacity, because

116   reservoirs with larger storage are likely to have less year to year variation in flow regimes or

117   water temperatures (Lessard and Hayes 2003, Olden and Naiman 2010). We specifically ask the

118   following research questions: i) How does flow management affect two species with diverse life

119   history strategies? ii) How do strong adult cohorts and increased catch rates (i.e., density) of

120   conspecifics and competing species influence trout populations? iii) How do attributes such as

121   stocking, disease, dam age, and reservoir capacity influence trout population dynamics?

122

123   MATERIALS AND METHODS

124   Rainbow and brown trout length and catch data were collected by State, non-

125   governmental, and tribal organizations in regulated rivers located throughout western North

126   America (see Acknowledgments; Fig. 2). We focused on data collected between August and

127   November because all tailwaters had data available from this time period, and pooled all sites

128   sampled via electrofishing within 20 miles downriver of a given dam in a given year. All data

129   were collected along the shoreline via nighttime boat electrofishing with one primary netter per

130   boat. Data were primarily from one-pass electrofishing studies; however, if the same station was

131   shocked two or more times within a sample period or year (e.g., during depletion or mark-

132   recapture studies), we only analyzed catch data from the first pass. If multiple shorelines were

133   sampled we incorporated the linear length of each shoreline in catch estimates; studies that zig-

134   zagged between banks were excluded from the analysis. We used data from all passes to model

135   changes in fish length.

136   We used trout recruitment and mean adult length as response variables because they

137   describe key aspects of fish population dynamics and can be derived from all monitoring

138   datasets. For rainbow trout, we calculated the catch-per-kilometer of shoreline of sub-adults

139   ("recruitment") for each dam-year combination, where sub-adult fish were defined to be between

140   150 and 300 mm in length and approximately 1.5 years old. We used sub-adult catch as our

141   metric of recruitment because low capture probability for juveniles (i.e., <150 mm; Korman *et al.*

142   2012) results in them being poorly represented in available datasets. Mean adult length of

143   rainbow trout ("length") was computed as the mean length of all trout >300 mm. We derived

144   similar recruitment and length metrics for brown trout, but used 350 mm as the cutoff between

145   sub-adults and adults because length-frequency histograms indicate brown trout transition from

146   age-1 to 2 at ~350 mm.

147   Dam operations influence daily, seasonal, and annual flow releases, so we obtained

148   subdaily (15/30/60 min.) discharge data from the U.S. Geological Survey National Water

149   Information System, Bureau of Reclamation Hydromet System, Natural Resources Conservation

150   Service National Water and Climate Center, Colorado Division of Water Resources, Northern

151   Colorado Water Conservancy District, and the California Department of Water Resources. We

152   calculated five flow metrics to be used as predictor variables, including: 1) hydropeaking,

153   defined as the mean coefficient of variation (CV) of subdaily flow, averaged over the Water Year

154   (WY) prior to fish collection (Oct. 1-Sept. 30); 2) relative annual flow, defined as annual flow

155   within a WY relative to average annual flow for all years fish data were available; 3) specific

156   discharge, defined as flow relative to channel width (i.e., water velocity); and 4-5) two metrics

157   that describe variation in the seasonal allocation of water released from each dam (i.e.,

158   proportion of water released in summer; proportion of water released in winter and spring; see

159   Appendix A, Table A1). Initially, we considered three metrics that describe the proportion of

160   flow released in three seasons, which we defined according to rainbow and brown trout life

161   history as winter (Oct. 1-Jan. 31), spring (Feb. 1-May 31), and summer (June 1-Sept. 30; Fig. 1).

162   However, these metrics were highly correlated, so we instead used the first two axes from a

163   Principal Component Analysis (PCA) as predictors. PCA results indicated that summer

164   accounted for the highest amount of variability in seasonal flow (see Appendix B, Tables B1-2

165   for PC1 loadings). Variation in PC2 was driven by winter and then spring flow, and the signs for

166   these seasons were always opposite (Appendix B, Tables B1-2). Therefore, in our modeling

167   results it is not possible to distinguish the effects of winter flow from spring flow. In other

168   words, a positive coefficient associated with PC2 may indicate that high winter flows or low

169   spring flows or both high winter and low spring flows are correlated with a given response

170   variable. We calculated the five flow metrics using data from the year immediately preceding

171   sampling; however, since different life stages of trout (i.e., juvenile, sub-adult, adult) might

172   respond differently to flow we also included metrics from two water years prior in models

173   (hereafter, "lagged" metrics; Appendix A, Table A1). For example, we compared recruitment in

174   fall 2012 to flow from the 2012 WY (10/1/11-9/30/12) and the 2011 WY (10/1/10-9/30/11;

175   "lagged").

176   Density-dependence can limit the survival and growth of juvenile and adult salmonids

177   through complex interactions between water temperature (i.e., metabolic rates) and food

178   consumption (Railsback and Rose 1999, Budy et al. 2008, Crozier et al. 2010). To account for

179   fish density and resulting competition effects on recruitment and mean adult length, we

180   computed six predictors based on catch per kilometers of shoreline ("catch") for: 1) all sub-adult

181   rainbow trout (150-300 mm), 2) all adult rainbow trout (>300 mm), 3) all sub-adult and adult

182   rainbow trout, 4) all sub-adult brown trout (150-350 mm), 5) all adult brown trout (>350 mm),

183   and 6) all sub-adult and adult brown trout. Furthermore, influxes of large numbers of recruits

184   into the adult size class can decrease the average length of adults, simply because the "new"

185   adults are necessarily on the smaller end of the size distribution. To account for this hypothesized

186   effect, we computed a seventh biological covariate that described the relative strength of the new

187   adult cohort (i.e., for rainbow trout, the catch of rainbow trout sub-adults in the year prior

188   divided by the catch of sub-adult and adult rainbow trout in the year prior; Appendix A, Table

189   A1).

190   Trout recruitment and mean adult length may also be influenced by factors such as fish

191   stocking, disease, dam age, and other reservoir attributes. Therefore, we included binary

192   variables in models for fish stocking (species-specific within each model) and whirling disease

193   (present in the year fish were captured). We also included the predictors dam age, altitude, and

194   latitude, and we calculated two additional reservoir metrics: 1) reservoir fullness within the WY

195   relative to maximum capacity; and 2) storage capacity of the dam relative to flow across WY

196   (Appendix A, Table A1). Our hypotheses on the relationships between response and predictor

197   variables for rainbow and brown trout are outlined in Appendix C, Table C1.

198

199   *Statistical Analyses*

200   We analyzed recruitment data for each species using generalized linear mixed models

201   (GLMM) with a negative binomial error distribution, dam as a random effect, and the number of

202   kilometers sampled as an offset. Including number of kilometers as an offset, and catch as the

203   response, is similar to using catch per kilometer as the response variable, but the former weights

204   observations by how much shoreline was sampled. We analyzed mean adult length for each

205   species using a GLMM in which the error structure was normal (Gaussian) and dam was

206   included as a random effect. All continuous predictors were centered on their mean and

207   standardized by their standard deviation to ease interpretation.

208   For each species and response variable we used a modified version of forward step-wise

209   selection based on Akaike Information Criterion (AIC). Forward step-wise selection typically

210   proceeds by choosing the best predictor from all predictors in the first step and then the second

211   best and so forth until additional predictors do not lead to a drop in AIC. Although our predictors

212   were not highly correlated (r<0.6), the lagged and unlagged version of flow metrics were

213   occasionally highly correlated (r>0.6). Therefore, we modified the typical step-wise selection

214   process to choose between either the lagged or unlagged version of a flow metric to avoid issues

215   of multicollinearity.

216   After identifying the best models via modified forward step-wise regression, we used

217   multi-level R^2 analysis to calculate an R^2 for the best model and for the models in which one

218   predictor was removed. This allowed us to determine whether a predictor was included in the

219   model because it was correlated with differences between dams or with differences within dams

220   over time (Gelman and Pardoe 2006). Predictors that explain variation within dams are likely to

221   be more relevant to management because they explain temporal variation rather than large,

222   inherent differences between dams. We fit GLMM models in R (v.3.0.2; R Core Team 2013)

223   using the lmer and glmmadmb packages and used WinBUGS (v. 14; Lunn *et al.* 2000) to

224   calculate posterior draws for the R^2 analyses.

225

226   RESULTS

227   Our analysis included data for 89,226 rainbow and 80,434 brown trout from 29 tailwaters

228   collected over 1-19 years, depending on the tailwater (Fig. 2). Rainbow and brown trout were co-

229   located downriver in 25 of the 29 dams.

230

231   *Rainbow Trout*

232   Across tailwaters, the mean rainbow trout sub-adult catch per kilometer was 54.7 fish

233   (±14.1 SE). The best model of rainbow trout recruitment included relative annual flow (lagged),

234   seasonal allocation of flow, sub-adult brown trout catch, latitude, and reservoir storage capacity

235   (Table 1). For the flow predictors, high relative annual flow in the year prior to capture and high

236   summer and spring flow were negatively correlated with rainbow trout recruitment, whereas high

237   winter flow was positively correlated with recruitment. Recruitment declined with increasing

238   latitude, while recruitment increased downriver of fuller reservoirs and in tailwaters with high

239   sub-adult brown trout catch (Table 1; Fig. 3). The least important predictor in the rainbow trout

240   recruitment model was latitude ($\Delta AIC=0.7$; Table 1). High sub-adult brown trout catch exhibited

241   the largest effect size (estimate) in GLMM results; however, this predictor was in the final model

242   due to large differences between dams, as evidenced by the highest drop in R^2 and ΔAIC when

243   removed. More importantly, the multilevel R^2 analysis indicated high winter/low spring flow was

244   primarily responsible for increasing rainbow trout recruitment within individual tailwaters (Table

245   1; Fig. 3).

246   The mean adult length of rainbow trout across tailwaters was 383.2 mm (± 3.1 SE). The

247   relative strength of new adult cohorts, rainbow and brown trout catch, flow, dam age, and

248   reservoir storage capacity were all included in the best model of mean adult length (Table 1).

249   Mean adult length was negatively correlated with hydropeaking, specific discharge, and high

250   spring flow, and positively correlated with high annual and winter flow (Table 1; Fig. 3). Strong

251   cohorts of new adults and high catch rates of rainbow trout and sub-adult brown trout were

252   associated with lower mean adult length, whereas length was positively correlated with high

253   catch rates of adult brown trout (Table 1; Fig. 3). Rainbow trout were smaller in tailwaters

254   downriver of fuller reservoirs. Length decreased as a function of dam age; however, this was the

255   least important predictor in the rainbow trout length model (ΔAIC=0.8; Table 1). Multilevel R^2

256   analysis revealed that sub-adult brown trout catch was included in the length model only due to

257   large between-dam differences in the predictor, even though the effect size was highest. More

258   importantly, rainbow trout catch (i.e., density of trout >150 mm) explained the most variation in

259   rainbow trout length within dams (Table 1; Fig. 3).

260

261   *Brown Trout*

262   The mean brown trout sub-adult catch per kilometer across tailwaters was 211.1 fish

263   (±28.3 SE). Hydropeaking (lagged), specific discharge, and adult rainbow trout catch were

264   included in the best model of brown trout recruitment (Table 1). Brown trout recruitment was

265   negatively correlated with hydropeaking in the year prior to capture and was lower in tailwaters

266   exhibiting high specific discharge (Table 1; Fig. 4). Brown trout recruitment was positively

267   correlated with adult rainbow trout catch. The least important predictor in the brown trout

268   recruitment model was lagged hydropeaking (ΔAIC=0.1; Table 1). The specific discharge

269   predictor had the highest effect size and explained the greatest amount of both between and

270   within-dam variability in brown trout recruitment, as evidenced by the largest drop in R^2 and

271   ΔAIC following its removal (Table 1).

272   The mean adult length of brown trout across tailwaters was 413.7 mm (± 2.6 SE). The

273   best adult length model included hydropeaking, relative annual flow, brown trout catch, new

274   adult cohort strength, and reservoir storage capacity (Table 1). Mean adult length was negatively

275   correlated with hydropeaking and positively correlated with high relative annual flow (Table 1;

276   Fig. 4). Brown trout were smaller in tailwaters exhibiting high brown trout catch (i.e., density of

277   trout >150 mm), strong new adult cohorts, and downriver of full reservoirs, although the latter

278   was the least important predictor in brown trout length models (ΔAIC=0.7; Table 1). The

279   predictor for new adult cohort strength had the highest effect size in models and explained the

280   greatest amount of between and within-dam variability in brown trout length (Table 1).

281

282   DISCUSSION

283   Our results offer insights into the relative importance of physical and biological processes

284   on rainbow and brown trout recruitment and size structure in tailwaters across western North

285   America. Recruitment was regulated primarily by flow management, but the response of the two

286   species differed. Rainbow trout recruitment was influenced more by seasonal and annual flow

287   volume, whereas brown trout recruitment was affected more by flow velocity. In contrast, the

288   mean adult length of rainbow and brown trout was regulated more by biology (i.e., density and

289   competition) than flow, with the length of both species being inversely related to density.

290

291   *Recruitment*

292   We hypothesized the response of rainbow and brown trout recruitment to seasonal

293   allocation of flow would be species-specific because of differences in timing of early life history

294   events (Fig. 1; Appendix C, Table C1). Specifically, we hypothesized rainbow trout recruitment

295   would be higher in tailwaters exhibiting low spring and/or high winter flow (Fausch *et al.* 2001)

296   and brown trout recruitment would be higher in tailwaters with high spring and/or low winter

297   flow (Strange et al. 1993, Strange and Foin 1999). Consistent with our hypothesis, we detected a

298   positive relationship between rainbow trout recruitment and the PCA axis representing low

299   spring/high winter flow. Rainbow trout spawn in late winter to early spring and fry emerge in

300   late spring to early summer (Fausch *et al.* 2001). Spring floods reduce the year class strength of

301   spring-spawning trout species because high flows scour the substrate, remove eggs and larvae

302   from redds, and cause short-term reductions in invertebrate prey (Elwood and Waters 1969,

303   Strange et al. 1993, McMullen and Lytle 2012; but see Korman, Kaplinski & Melis 2011).

304   Support for our seasonal hypothesis was lacking for brown trout since the best recruitment model

305   did not include the spring-winter flow covariate.

306   We also hypothesized that rainbow and brown trout recruitment would increase in years

307   of high annual flow. However, relative annual flow was not included in the best brown trout

308   model of recruitment and the effect of relative annual flow on rainbow trout recruitment was

309   actually counter to this hypothesis. Annual flow was included in the rainbow trout model, but

310   higher annual flows were associated with lower recruitment of rainbow trout. Rainbow trout

311   recruitment has been positively linked to high flows, with the most plausible mechanism

312   including expanded rearing habitat through flooding of the shoreline that increases growth and

313   survival of juvenile salmonids (Mitro et al. 2003, Korman et al. 2012). However, the energetic

314   costs of prolonged high water velocities could decrease survival of juvenile rainbow trout in the

315   absence of adequate shoreline refuges during high annual flow years. Korman and Campana

316   (2009) found that both growth and nearshore habitat use by age-0 rainbow trout increase when

317   flows are low and stable, whereas high, fluctuating flows result in offshore movement where

318   there is a potential energetic cost of maintaining position in high velocity water. This is

319   supported by evidence from our brown trout recruitment models. Although relative annual flow

320   was not included in the best brown trout model, we detected a strong negative relationship

321   between brown trout recruitment and specific discharge, which was the best predictor of within

322   and between-dam variation in recruitment. Thus, variation in trout recruitment in tailwaters

323   appears to be associated with the availability of low-velocity, shallow water habitats near river

324   margins during early life stages that permit energetically efficient foraging while providing

325   protection from predation (Hubert et al. 1994).

326   We hypothesized that rainbow and brown trout recruitment would be lower in tailwaters

327   where hydropeaking occurs or in years where hydropeaking was greater. Lagged hydropeaking

328   was included in the best brown trout model and had the expected negative sign, supporting our

329   hypothesis. However, lagged hydropeaking had the weakest support in the brown trout

330   recruitment model based on change in AIC and it was excluded from the best rainbow trout

331   recruitment model. Although our modeling only indicates a weak relationship between brown

332   trout recruitment and hydropeaking, a number of studies in European tailwaters (Cowx and

333   Gould 1989, Almodóvar and Nicola 1999) have also documented declines in brown trout

334   recruitment due to hydropeaking and its associated changes in habitat quality and water velocity.

335   This weak relationship between hydropeaking and brown trout recruitment, and the lack of a

336   relationship for rainbow trout recruitment, may be due to the inclusion of only a few load-

337   following dams in our analysis. The majority of tailwaters in the western United States reside

338   downriver of storage dams that exhibit large annual and seasonal fluctuations in flow but have

339   relatively stable daily flow regimes, regardless of whether or not they generate power. The two

340   most important predictors that increased rainbow trout recruitment were high winter/low spring

341   flow and low annual flow. Therefore, low, stable flows during the spring spawning season and

342   throughout the first year appear to be more important than hydropeaking in regulating rainbow

343   trout size class strength across western U.S. tailwaters.

344   Surprisingly, we did not detect a decrease in rainbow trout recruitment in tailwaters

345   affected by whirling disease, nor did we detect a shift in size structure in heavily stocked rivers.

346   Whirling disease was present in several tailwaters and we hypothesized it would have a

347   disproportionate effect on rainbow trout size structure (Nehring and Walker 1996). However,

348   stable rainbow trout recruitment has been detected in infected populations that exhibit low

349   spawning site fidelity because the risk of infection is spread over multiple tributary and

350   mainstem sites (Grisak et al. 2012). In addition, stocking of whirling disease resistant trout (e.g.,

351   Hofer strain; Hedrick et al. 2003) in infected waters may stabilize rainbow trout populations that

352   ultimately negate losses in recruitment over time.

353

354   *Mean Adult Length*

355   For both species, more of the variation in adult length was explained by population

356   feedbacks than by flow metrics according to AIC; however, some flow metrics had larger

357   standardized effect sizes for rainbow trout. We hypothesized that adult length and trout catch

358   (i.e., density) would be inversely related and adult length would decrease in years with large

359   cohorts of "new", but smaller, fish recruiting into the adult size class. We found support for these

360   hypotheses in both species, indicating intraspecific competition plays an important role in

361   determining the length of rainbow and brown trout in tailwaters. Density dependence is a

362   common characteristic of aquatic and terrestrial animal populations (Brook and Bradshaw 2006)

363   and several studies have documented density-dependent growth specifically in salmonids (Grant

364   and Imre 2005, Crozier et al. 2010). For example, excessive fish stocking in a Midwestern U.S.

365   tailwater caused a decline in the length of large rainbow trout (>400 mm), mediated by a

366   degraded prey base and declines in prey consumption (Weiland and Hayward 1997). Likewise,

367   Jenkins et al. (1999) documented a negative relationship between adult brown trout growth and

368   conspecific densities in two California alpine streams that were linked to a broadening of brown

369   trout diet and the consumption of a larger number of less profitable prey items (e.g., chironomid

370   larvae). Grant and Imre (2005) also reviewed density-dependent effects on multiple salmonid

371   species and detected negative relationships between density and growth in five of six rainbow

372   trout populations and in three of five brown trout populations. Our results add to this growing

373   body of literature and demonstrate that across 29 different tailwaters, rainbow and brown trout

374   length is negatively related to density.

375   We hypothesized both rainbow and brown trout would have higher average adult lengths

376   following years of high annual flow. This hypothesis was supported in both species, but the

377   effect size was modest. Neither of the seasonal flow covariates were included in the best brown

378   trout model of adult length, while PC2 (higher winter flows, lower spring flows) had a positive

379   effect in the best rainbow trout length model and was the second best predictor explaining

380   within-dam temporal trends. Low spring flows from February-May may benefit adult rainbow

381   trout growth through decreased energetic costs during their spawning season. Salmonid

382   investment of energy into reproduction is high, with lipid reserves commonly depleted by more

383   than 50% relative to pre-spawning body conditions (Jonsson et al. 1991, Hutchings et al. 1999).

384   High flow conditions can confer an energetic cost on salmonids that decreases growth and/or

385   physiological condition (Kemp et al. 2006, Cocherell et al. 2011), particularly when salmonids

386   are building nests and attempting to hold position over their redds (Tiffan et al. 2010). Therefore,

387   low spring flows may confer a benefit to adult rainbow trout by decreasing energetic costs during

388   a critical time period when lipid reserves are already depleted.

389   We hypothesized hydropeaking would sustain the growth of large trout through daily

390   surges of invertebrate prey (Perry and Perry 1986, Kennedy et al. 2014, Miller and Judson 2014).

391   This hypothesis was rejected since we detected a negative relationship between hydropeaking

392 and the length of both species. Although hydropeaking can foster increased drift concentrations

393 leading to increased gut fullness in brown and rainbow trout (Miller and Judson 2014), the

394 energetic costs associated with maintaining position and foraging in rivers with large subdaily

395 variation in flow may offset the increases in energy intake that hydropeaking creates.

396 Alternatively, increases in invertebrate drift concentrations associated with hydropeaking may

397 ultimately deplete benthic invertebrates and lead to lower drift concentrations and prey

398 availability for trout over long time scales (i.e., weeks to months; Kennedy *et al.* 2014).

399 Regardless of the underlying mechanisms, our results indicate that hydropeaking does not favor

400 the growth of large trout.

401   Reservoir aging and the decline in phosphorus from decomposing vegetation and flooded

402 soils (Stockner et al. 2000) has been noted as a potential mechanism for declining tailwater

403 productivity over time. Consistent with our hypothesis, we detected a significant negative

404 relationship between dam age and rainbow trout length, but this was the weakest predictor and

405 was most likely in the final model due to large between-dam differences in reservoir age. We

406 also hypothesized that reservoirs with larger storage capacity would benefit the growth of adult

407 rainbow and brown trout via less year-to-year variation in flow and more stable water

408 temperatures (Lessard and Hayes 2003, Olden and Naiman 2010). Contrary to this hypothesis,

409 both trout models indicated that small reservoirs were associated with large trout, but model

410 results were attributable to large between-dam differences in reservoir size. Collectively, these

411 results indicate adult rainbow and brown trout growth is affected more by intraspecific

412 interactions than by the physical characteristics of the environment.

413

414 *Management Implications*

415   Our results indicate rainbow and brown trout recruitment in tailwaters is primarily

416   explained by dam operations that regulate flow, whereas mean adult length is best explained by

417   biological predictors such as high catch rates of conspecifics (i.e., density) and new adult cohort

418   strength, followed by flow management. Species-specific recruitment responses to flow

419   management likely relate to the species' divergent life history strategies and timing of adult

420   spawning, egg hatching, and fry emergence. Overall, rainbow trout recruitment decreased in

421   response to high flow volume, particularly in the season following emergence (i.e., spring).

422   Brown trout recruitment, however, was influenced more by flow velocity. In contrast, factors

423   influencing mean adult length in both species were remarkably similar and indicate once trout

424   reach adult status their overall size is regulated more by intraspecific interactions (i.e., density

425   and competition) than hydrology. Negative density-dependent effects on fish growth are likely

426   caused by a decrease in the availability of prey in rivers exhibiting high trout catch rates (Jenkins

427   et al. 1999, Imre et al. 2004). Since recruitment regulates the density of trout populations, and

428   flow alters recruitment and invertebrate assemblages, flow indirectly plays a role in determining

429   adult size. Therefore, it is important to consider the effects of flow management on recruitment

430   because the latter ultimately drives patterns in the overall health of tailwater trout populations.

431   In light of these results, natural resource managers could alter dam operations to improve

432   the health of economically important fisheries in tailwaters. Since high levels of recruitment

433   indirectly decrease fish size, dam operations that decrease trout density may foster the

434   development of trophy trout fisheries through relaxation from intraspecific competition. For

435   example, dam managers could release a larger proportion of water in spring (i.e., February-May)

436   relative to other seasons to decrease rainbow trout recruitment, which, in turn, may indirectly

437   favor adult rainbow trout growth through decreased competition. However, high spring flows

438   that confer an energetic cost on adult rainbow trout during their spawning season may decrease

439   growth potential, indicating there is a delicate balance between decreasing recruitment and

440   competition through high flows and ensuring the energetic costs incurred by adults are not

441   counterproductive to management objectives. Although we did not detect a decrease in brown

442   trout recruitment related to seasonal flow releases, recruitment decreased in tailwaters exhibiting

443   high water velocity. This indicates that water velocity has a potential scouring effect on brown

444   trout eggs and/or an energetic cost on emerging fry that ultimately decreases competition. Since

445   low levels of recruitment in the year prior to capture had the largest effect on increasing brown

446   trout length, dam operations that maximize flow velocity may relax intraspecific competition that

447   ultimately enhances the growth potential of adult brown trout. Last, we found moderate support

448   that hydropeaking flows do not favor the growth of adult rainbow and brown trout, indicating

449   that stable flow regimes may confer an energetic or prey availability advantage over long time

450   scales for introduced salmonids. Overall, these results suggest that if managers are interested in

451   stable trout populations with larger adults, then they could consider altering dam operations or

452   implementing management actions to decrease rainbow and brown trout recruitment.

453

454   ACKNOWLEDGMENTS

461   M. Smith, B. Stewart, A. Treble, H. Vermillion, M. Wethington, Bureau of Reclamation

462   Hydromet System, Environmental Protection Agency STORET, NARS, EMAP databases, and

463   the U.S. Geological Survey BioData and WaterWatch databases. Any use of trade, product or

464   firm names is for descriptive purposes only and does not imply endorsement by the US

465   Government.

466

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612

613   SUPPLEMENTAL MATERIAL

614   **Appendix A:** Description of flow, biological, and other predictor variables used in generalized

615   linear mixed models of rainbow and brown trout recruitment and mean adult length (*Ecological*

616   *Archives* A/E/M000-000-A1).

617   **Appendix B:** Result of Principal Component Analyses for data on the seasonal proportion of

618   flow in rainbow and brown trout generalized linear mixed models (*Ecological Archives*

619   A/E/M000-000-A2).

620   **Appendix C:** Description of hypotheses on the response of rainbow and brown trout recruitment

621   and mean adult length to flow, biological, and other predictors (*Ecological Archives* A/E/M000-

622   000-A3).

623   TABLES

624   TABLE 1. Estimates (i.e., "effect size") and standard errors for predictors included in the best

625   model, as well as the impacts of removing each predictor on Akaike Information Criterion (Δ

626   AIC) and multi-level R^2. Each predictor can explain variance between dams ("R^2 b/t") and/or

627   within dams ("R^2 w/in"). The bolded R^2 value for each response indicates the single variable that

628   explains the greatest amount of between or within-dam variation (i.e., removing this variable

629   from the best model leads to the largest drop in R^2). The first line in each model provides the

630   intercept and associated standard error in first two columns and the Δ AIC and R^2 values for the

631   full model.

Model	Estimate	Std. Error	Δ AIC	R^2 b/t	R^2 w/in
RBT[§] Recruitment					
Intercept / Full Model fit	3.55	0.22	0	0.19	0.26
Relative Annual Flow[L]	-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**
Sub-adult BT[¶] 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 WY[*]	0.32	0.14	2.9	0.29	0.22
RBT 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
RBT Catch	-9	2	12.2	0.62	**0.72**
New Adult Cohort Strength	-8	2	9.6	0.53	0.74
Sub-adult BT Catch	-12	3	8.5	**0.41**	0.75
Adult BT Catch	8	3	3.3	0.59	0.74
Dam Age	-6	4	0.8	0.63	0.74
Reservoir Storage in WY	-7	3	1.8	0.55	0.75
BT Recruitment					
Intercept / Full Model fit	4.18	0.32	0	0.50	0.72
Hydropeaking[L]	-0.13	0.09	0.1	0.49	0.71
Specific Discharge	-1.61	0.33	15.6	**0.03**	**0.67**
Adult RBT Catch	0.17	0.09	1.4	0.49	0.72
BT 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
BT Catch	-6	2	4.2	0.60	0.68
New Adult Cohort Strength	-14	2	34.0	**0.43**	**0.60**
Reservoir Storage in WY	-5	3	0.7	0.68	0.69

632   § = rainbow trout; ¶ = brown trout; † = Axis 1, Principal Component Analysis (PCA); ‡ = Axis

633   2, PCA; * = water year; [L] = lagged flow, 1-2 years

634

635   FIGURE LEGENDS

636   FIG. 1. Conceptual diagram for flow metrics used in this analysis and their relation to rainbow

637   and brown trout life history stages. The inner circle (medium blue) depicts subdaily flow

638   variation that is characteristic of hydropeaking dams (data are from Glen Canyon Dam on

639   1/1/2011, an arbitrary date). The next circle (medium brown) illustrates how seasonal patterns of

640   flow were defined in this study, and the next circle (light brown) illustrates how the timing of

641   key rainbow and brown trout life stages intersects with these seasonal flow metrics. The outer

642   circle (light blue) depicts annual flow commencing October 1 of each water year (WY). This

643   metric compares annual flow in one year to all other WY in which fish data were collected.

644

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

646

647   FIG. 3. Histograms of predictors (left) and corresponding mean effect size (middle; ± 95%

648   confidence intervals) on recruitment and mean adult length. Histograms (a-e) illustrate a 1-σ

649   increase from the mean (red solid to blue dashed line) for the five flow (Q) and biological

650   predictors that explained the largest amount of within-dam variation. Conceptual diagram (f)

651   shows the relationships between predictors (boxes) and response variables (ovals), with red

652   dashed lines indicating a (-) relationship, black solid lines a (+) relationship, and the green line

653   an inferred relationship. Bolded lines indicate the predictor that explains the largest amount of

654   within-dam variation. Letters a-e next to each pathway correspond with middle panel results.

655   Key: CV = coefficient of variation; PC2 = Axis 2, Principal Component Analysis; WY = water

656   year; RBT = rainbow trout; [L] = lagged flow; x = no significant effect of covariate on results;   =

657   covariate not included in models.

658

659   F<small>IG</small>. 4. Histograms of predictors (left) and corresponding mean effect size (middle; ± 95%

660   confidence intervals) on recruitment and mean adult length. Histograms (a-e) illustrate a 1-σ

661   increase from the mean (red solid to blue dashed line) for the five flow (Q) and biological

662   predictors that explained the largest amount of within-dam variation. Conceptual diagram (f)

663   shows the relationships between predictors (boxes) and response variables (ovals), with red

664   dashed lines indicating a (-) relationship, black solid lines a (+) relationship, and the green line

665   an inferred relationship. Bolded lines indicate the predictor that explains the largest amount of

666   within-dam variation. Letters a-e next to each pathway correspond with middle panel results.

667   <u>Key</u>: CV = coefficient of variation; WY = water year; BT = brown trout; [L] = lagged flow; x = no

668   significant effect of covariate on results;   = covariate not included in models.

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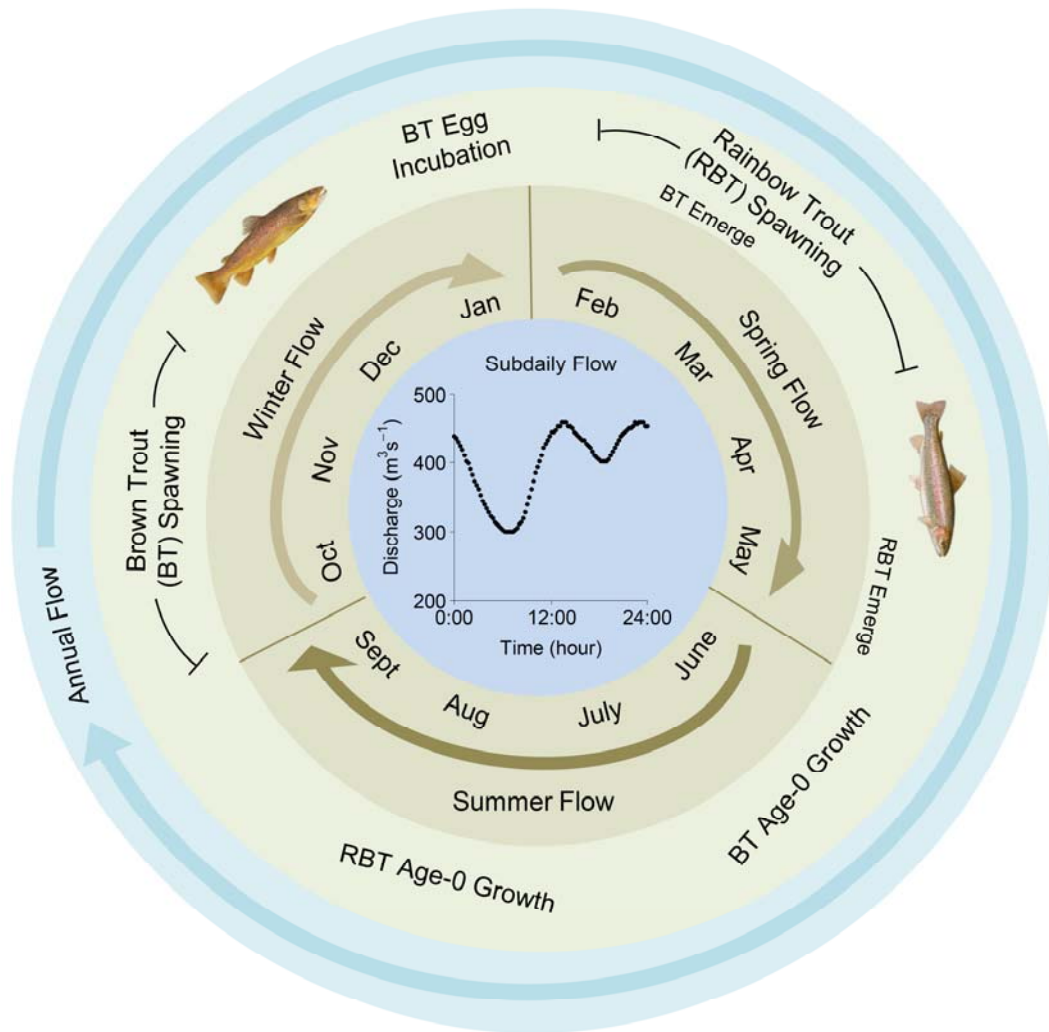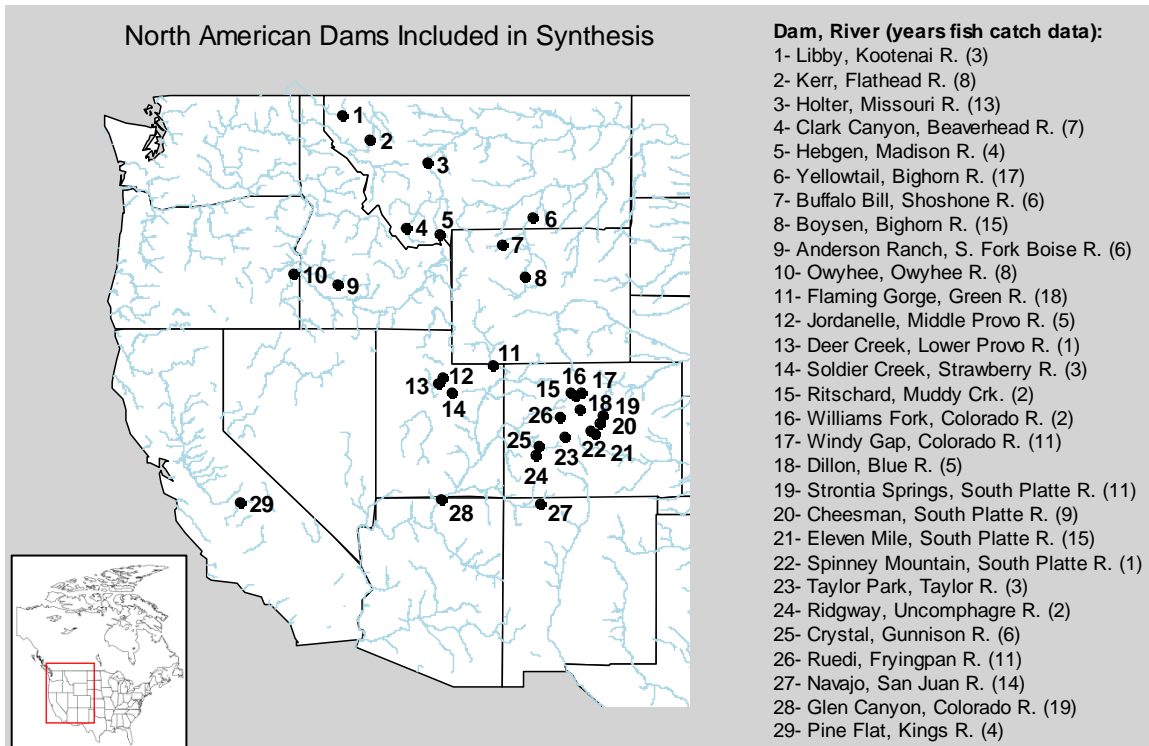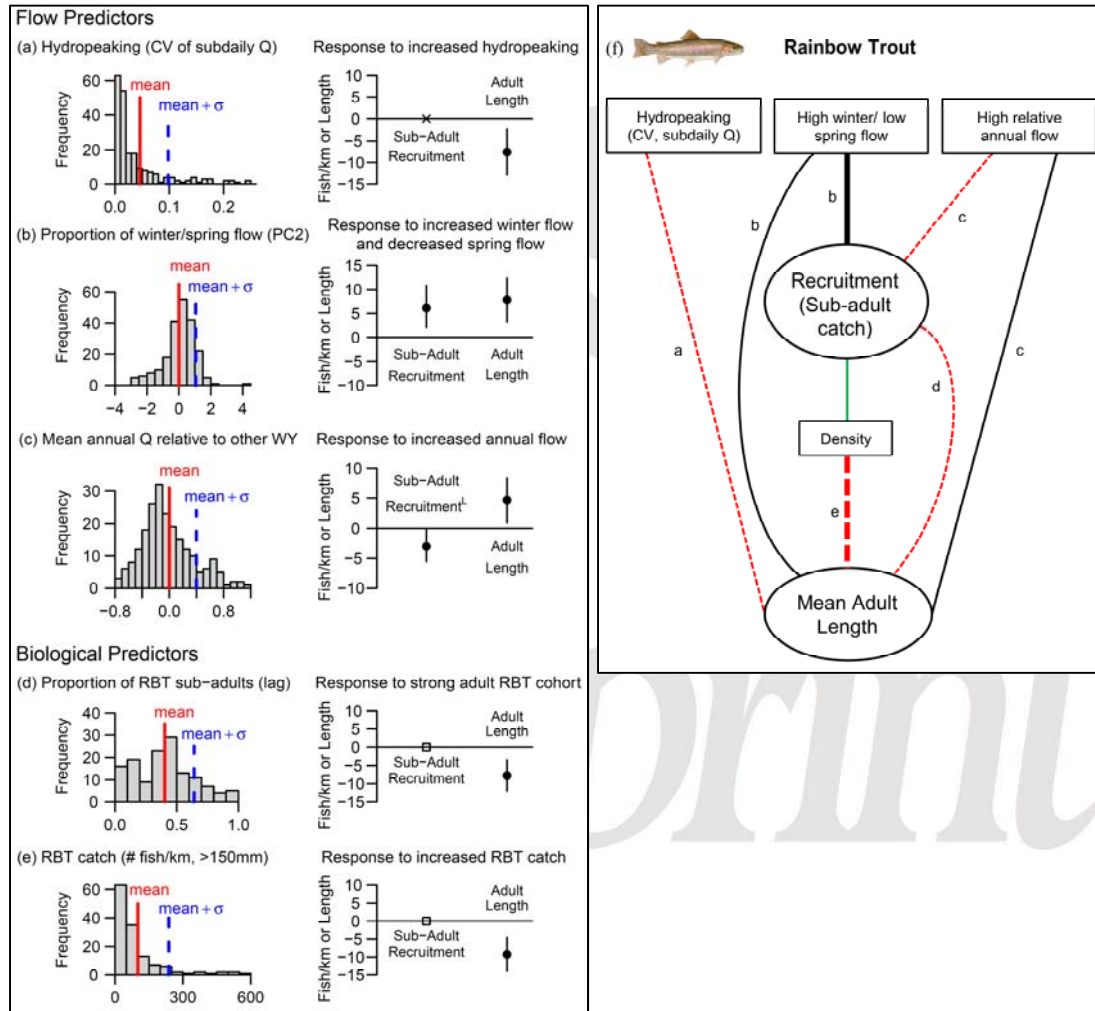
671   FIGURE 1

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678   FIGURE 2

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North American Dams Included in Synthesis

Dam, River (years fish catch data):
1- Libby, Kootenai R. (3)
2- Kerr, Flathead R. (8)
3- Holter, Missouri R. (13)
4- Clark Canyon, Beaverhead R. (7)
5- Hebgen, Madison R. (4)
6- Yellowtail, Bighorn R. (17)
7- Buffalo Bill, Shoshone R. (6)
8- Boysen, Bighorn R. (15)
9- Anderson Ranch, S. Fork Boise R. (6)
10- Owyhee, Owyhee R. (8)
11- Flaming Gorge, Green R. (18)
12- Jordanelle, Middle Provo R. (5)
13- Deer Creek, Lower Provo R. (1)
14- Soldier Creek, Strawberry R. (3)
15- Ritschard, Muddy Crk. (2)
16- Williams Fork, Colorado R. (2)
17- Windy Gap, Colorado R. (11)
18- Dillon, Blue R. (5)
19- Strontia Springs, South Platte R. (11)
20- Cheesman, South Platte R. (9)
21- Eleven Mile, South Platte R. (15)
22- Spinney Mountain, South Platte R. (1)
23- Taylor Park, Taylor R. (3)
24- Ridgway, Uncomphagre R. (2)
25- Crystal, Gunnison R. (6)
26- Ruedi, Fryingpan R. (11)
27- Navajo, San Juan R. (14)
28- Glen Canyon, Colorado R. (19)
29- Pine Flat, Kings R. (4)

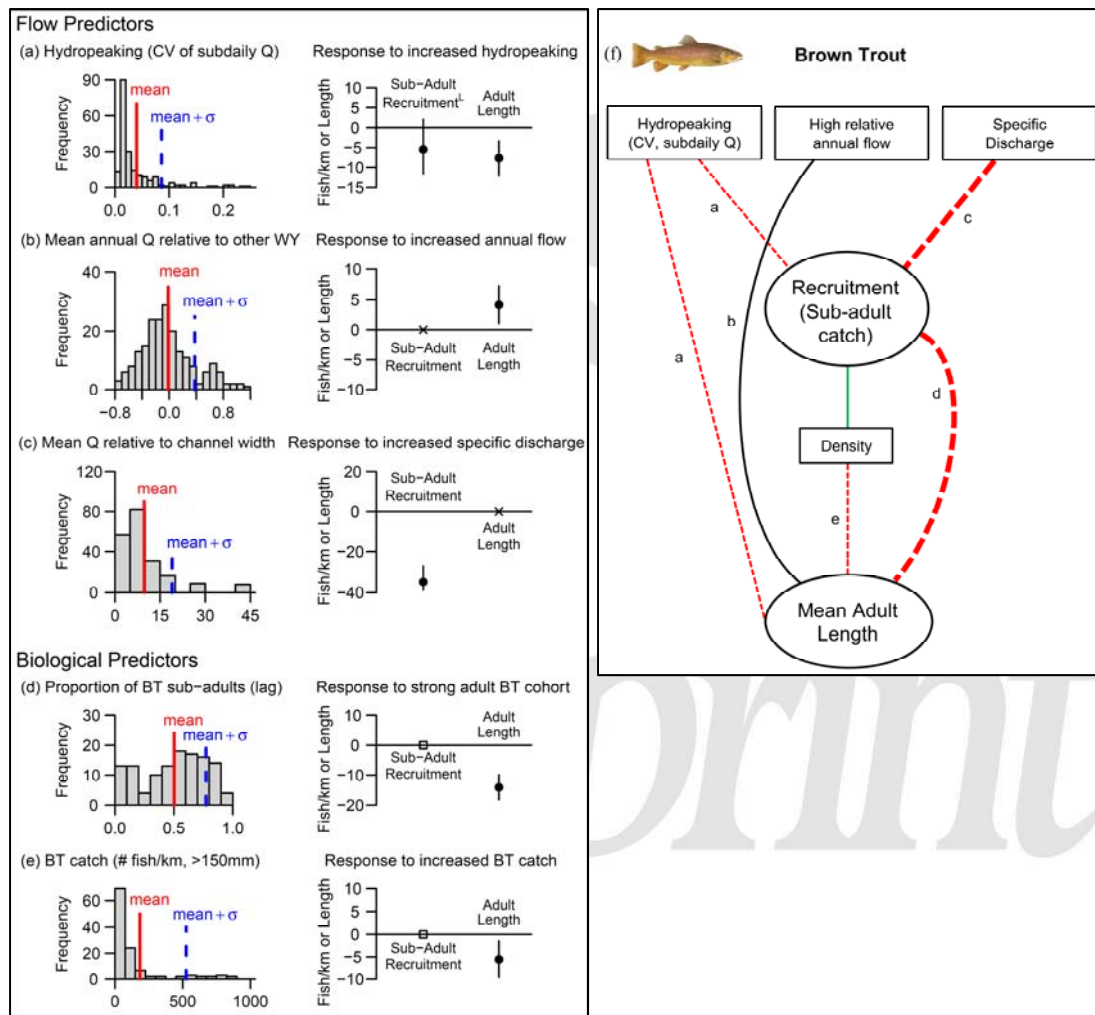680

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693   FIGURE 3

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698   FIGURE 4

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