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8   Predation on wild and hatchery salmon by non-native brown trout (*Salmo trutta*) in

9   the Trinity River, California

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18   Brown trout predation on wild and hatchery salmon

19   **Abstract**

20   Non-native predators may interfere with conservation efforts for native species. For

21   example, fisheries managers have recently become concerned that non-native brown trout

22   may impede efforts to restore native salmon and trout in California's Trinity River.

23   However, the extent of brown trout predation on these species is unknown. We

24   quantified brown trout predation on wild and hatchery-produced salmon and trout in the

25   Trinity River in 2015. We first estimated the total biomass of prey consumed annually by

26 brown trout using a bioenergetics model and measurements of brown trout growth and

27 abundance over a 64 km study reach. Then, we used stable isotope analysis and gastric

28 lavage to allocate total consumption to specific prey taxa. Although hatchery-produced

29 fish are primarily released in the spring, hatchery fish accounted for most of the annual

30 consumption by large, piscivorous brown trout (> 40 cm long). In all, the 1579 (95% CI

31 1279-1878) brown trout >20 cm long in the study reach ate 5930 kg (95% CI 3800-8805

32 kg) of hatchery fish in 2015. Brown trout predation on hatchery fish was ca. 7% of the

33 total biomass released from the hatchery. Brown trout only ate 924 kg (95% CI 60-3526

34 kg) of wild fish in 2015, but this was potentially a large proportion of wild salmon

35 production because wild fish were relatively small. As large brown trout rely heavily on

36 hatchery-produced fish, modifying hatchery practices to minimize predation may enhance

37 survival of hatchery fish and potentially reduce the abundance of predatory brown trout.

38

39 **Introduction**

40   Brown trout (*Salmo trutta*) have undergone massive range expansion from their

41 native waters in Europe and North Africa to the waters of every continent except

42 Antarctica (MacCrimmon & Marshall, 1968; Dill & Cordone, 1997). This expansion was

43 intentional. European colonists transported and introduced brown trout around the world

44 because they considered them desirable for sport fishing and food (Wilson, 1879).

45 However, introduced brown trout may negatively affect populations of native fishes in

46 areas where they have been introduced (Townsend, 1996; McHugh & Budy, 2006; Belk

47 et al., 2016; Hoxmeier & Dieterman, 2016). In this study, we evaluated predation by

48 introduced brown trout on native salmon and trout species that are the focus of a large-

49 scale, intensive conservation and habitat restoration effort in the Trinity River, a large

50 tributary of the Klamath River in Northern California.

51   In Northern California, Scottish, German, and hybrid brown trout eggs were

52 brought to Fort Gaston (Hoopa, CA) and Sisson hatcheries near Mt. Shasta by train in the

53 1890's (Thomas, 1981; Adkins, 2007). There were two introductions from those

54   hatcheries to the Trinity River, one near the mouth at Fort Gaston and a separate effort

55   closer to the headwaters in Stewart's Fork and the main stem Trinity River near

56   Lewiston, CA (Thomas, 1981; Adkins, 2007). According to a Trinity Journal newspaper

57   article (1911), the motivation behind the upstream introduction was the California Fish

58   and Game Commission's plan to replace native rainbow trout (*Oncorhynchus mykiss)*

59   with the "more desirable brown trout" throughout the state. The downstream introduction

60   was implemented to supplement the dwindling salmon fishery that the local Hoopa Tribe

61   relies on for sustenance (Adkins, 2007). In the early years of brown trout introduction to

62   the Trinity River, fisheries managers raised concerns that the brown trout predation was

63   impacting abundance of native salmon species through predation (Thomas, 1981). This

64   lead to a moratorium on brown trout releases in the Trinity River during the 1920's, but

65   the moratorium was short lived and brown trout stocking was gradually phased back in

66   and continued until 1932 (Thomas, 1981).

67   Prior to and during the time period when brown trout were introduced, native

68   fishes of the Trinity River experienced steep declines in abundance (Adkins, 2007).

69   Native and tribally-important species such as Chinook salmon (*Oncorhynchus*

70   *tshawytscha*), coho salmon (*O. kisutch*), steelhead trout (*O. mykiss*), and Pacific lamprey

71   (*Entosphenus tridentatus*) were affected by large-scale habitat loss from intensive mining

72   and logging throughout the watershed. A pair of dams completed in the early 1960s

73   exacerbated these effects, cutting off access to the entire upper watershed for migratory

74   fish and diverting a substantial fraction of the Trinity River's water to California's

75   Central Valley for irrigation. The Trinity River hatchery was completed in 1958 to

76   partially mitigate the effects of habitat loss on salmon production. The hatchery currently

77   releases more than 2 million juvenile salmon and steelhead per year into the Trinity River

78   and spawns returning adults to produce the next generation of hatchery fish (California

79   Hatchery Scientific Review Group, 2012). Recent efforts to rehabilitate the native fish

80   populations of the Trinity River also include a massive investment in habitat restoration,

81   including large-scale channel reconfiguration, cover addition, minimum flows, and

82   habitat-forming flow releases from the dams (Beechie et al., 2015). Currently, Trinity

83   River Chinook salmon and steelhead remain well below historic abundance and Trinity

84   River coho salmon are considered threatened under both state and federal laws (National

85   Marine Fisheries Service 2014).

86   The potential for brown trout to directly affect native salmon populations by

87   predation depends on brown trout feeding behavior and abundance. Piscivory by Trinity

88   River brown trout has been documented during field projects focused on other species

89   and by local fisherman, but no formal diet studies of this brown trout population have

90   been conducted. The best historical index for brown trout abundance in the Trinity River

91   is the adult salmon sampling weir in Junction City (river kilometer 136.2). Brown trout

92   catch totals increased at the weir during sampling from 2000 to 2013 to levels 200-300%

93   higher than those in the 1980's and 1990's, despite reduced sampling effort since 2000

94   (Borok, Cannata & Hileman, et al., 2014a,b; National Marine Fisheries Service, 2014).

95   Documentation of piscivory combined with the potential increase in brown trout

96   populations inferred from weir catch data suggest that brown trout may be having a

97   substantial impact on native fishes. This threat was identified by the California

98   Department of Fish and Wildlife in 2005 and provided the impetus for changing fishing

99   regulations, adding a bag limit of one brown trout in 2006 and increasing it to five brown

100   trout in 2007 (California Fish and Game Commission, 2007). Trinity River brown trout

101   were also identified as an impediment to species recovery in the recovery plan for

102   Southern Oregon and Northern California coho salmon (National Marine Fisheries

103   Service 2014).

104   To assess predation by brown trout on native species, we undertook the first large-

105   scale sampling effort for brown trout in the Trinity River. Sampling included multi-pass

106   electrofishing over a 64 km study reach to estimate abundance, size, growth, and age

107   structure of brown trout. We used diet sampling and isotope analysis to characterize

108   brown trout diet composition. Finally, we used the brown trout population and diet data

109   to parameterize a bioenergetics model to estimate brown trout consumption of salmon

110   and other prey in the Trinity River.

111 **Methods**

112 <u>Study Area</u>

113   The Trinity River in Northern California is the largest tributary to the Klamath

114 River, with a main stem length of 274 km and a watershed area of about 7679 km^2. The

115 Trinity River's headwaters are in the Trinity Alps at an elevation of about 1,850 m and

116 the confluence with the Klamath River in Weitchpec is 69.5 km from the ocean at an

117 elevation of 56 m. There are two large earthen dams on the Trinity River. Upstream at

118 river kilometer 261.6 is Trinity Dam, which is used for water storage, and downstream at

119 river kilometer 250.3 is Lewiston Dam, which is used to export water to the Sacramento

120 River basin. The Trinity River Fish hatchery is located at Lewiston Dam and all hatchery-

121 produced fish are released immediately downstream of the dam.

122   This study is focused on the 64 km of the main stem Trinity River below

123 Lewiston Dam and above the North Fork of the Trinity River (Figure 1). Existing

124 observations indicate that brown trout are widespread through the 178 km of anadromous

125 habitat in the main stem Trinity River as well as major tributaries. However, based on

126 habitat use data collected for other studies (Goodman et al., 2015), brown trout are most

127 abundant in the focal area and it is the area where they likely have the most access to

128 native salmon prey from hatchery releases and natural spawning grounds.

129   Discharge from Lewiston Dam ranges annually from 8.6 to 311.5 m^{3}s^{-1}. With

130 tributary inputs downstream of the dam, the Trinity River near the North Fork

131 experiences flows between 12 and 850 m^{3}s^{-1}. There is a characteristic seasonal flow

132 pattern: during winter and spring storms and an annual spring dam release, the upper

133 range is approached; by mid-summer and through winter the flows stay closer to the

134 lower range.

135   The 64 river kilometers in which the study took place were divided into six

136 reaches based on tributary inputs, river access, and prior information about brown trout

137 density (Figure 1). The boundaries of each reach occurred at the following locations and

138 creek mouths in downstream order: the concrete weir below Lewiston Dam, Rush Creek,

139   Steel Bridge river access, Indian Creek, Evans Bar river access, Canyon Creek, and the

140   North Fork of the Trinity River.

141   <u>Fish sampling</u>

142   A 4.3 meter raft with a Smith-Root 2.5 kilowatt generator powered pulsator

143   electrofisher system (Smith-Root Inc., Vancouver, WA) was used to sample the entire 64

144   km of river. The control box was set with a DC pulse rate of 30 Hz with voltage between

145   300 and 400. Sampling focused on the thalweg of the main stem while moving slowly

146   downstream. In March of 2015, the study area was sampled with three passes. Each pass

147   proceeded from upstream to down and took four days to complete. A single sampling

148   pass started near Lewiston Dam on Monday and worked down to a river access. Tuesday

149   sampling began where Monday's sampling left off and this pattern continued until the 64

150   km was completed on Thursday. The following Monday, a new pass would begin

151   starting at Lewiston Dam again. The 7-day interval between samples at a given location

152   allowed brown trout to recover from handling stress and resume normal feeding behavior

153   before being resampled (Pickering, Pottinger, & Christie, 1982). The three passes

154   bounded the spring release of coho salmon smolts from the hatchery: the first pass was

155   completed before the release, the second immediately following the release, and the third

156   after many of the released smolts had migrated through the study area (Harris, Petros, &

157   Pinnix, 2016). A similar brown trout sampling effort was conducted in the spring of

158   2016, providing additional diet samples and recaptures for final growth measurements of

159   tagged individuals.

160   Most brown trout were sampled by electrofishing (859 total), but additional

161   samples were collected opportunistically by other means to provide diet data from outside

162   the spring electrofishing season and to provide additional samples for size and growth

163   analyses. An Alaskan style weir, operated by the California Department of Fish and

164   Wildlife and the Hoopa Tribe, was installed in Junction City California in late June and

165   run through September in 2015 and 2016 to catch migrating adult salmon (Sinnen et al.,

166   2005). Brown trout captured in the weir in 2015 and 2016 (224 total) were processed as

167   described below. We also processed some additional individuals captured using rod and

168   reel (29 total). All method produced a similar size range of fish, from 20 cm (minimum

169   size used in the analysis) to at least 60 cm.

170   <u>Processing and Handling</u>

171   Once captured, all brown trout > 20 cm long were anesthetized in water saturated

172   with CO_2 using Alka-Seltzer Gold tablets. Trinity River brown trout are the target of a

173   recreational fishery, so alternative anesthetics that require a withdrawal period before

174   human consumption were not suitable for this work. Fish < 20 cm long were too small for

175   our tagging operation and were less likely to be piscivorous, so we did not include

176   smaller fish in subsequent analysis. Once anesthetized, the fish were measured (fork

177   length) and the following samples were collected: scales were taken from the left side

178   between the anal and dorsal fin just above the lateral line for age analysis, a one

179   centimeter square fin clip was taken from the distal posterior tip of the dorsal fin for

180   stable isotope analysis, and stomach contents were collected using gastric lavage for diet

181   analysis. Fish were weighed following gastric lavage so that stomach contents would not

182   contribute to the mass. Lavage was conducted using a hand-pumped garden sprayer. The

183   spray pipe was placed through the fish's mouth into the stomach and water was sprayed

184   in until the stomach was full. Through continued filling and massaging the belly from the

185   outside, food items were washed and pushed out. A sub-sample of 30 fish was sacrificed

186   after processing and the stomachs examined to gauge the effectiveness of the gastric

187   lavage. Of these, 28 had completely empty guts, indicating that lavage was generally

188   effective.

189   After the samples and measurements were taken, the fish were tagged with a

190   uniquely numbered FD94 T-bar tag (Floy Tag & Manufacturing Inc., Seattle, WA) for

191   future identification and then released. The tags were made of a 7.5 cm long piece of

192   monofilament with polyolefin colored tubing around it. At the insertion end was a 1.5

193   mm thick, 2 cm wide "T". The tag was injected using Floy Tag's Mark III pistol grip

194   tagging gun. The needle was inserted below the dorsal fin to allow the T to articulate

195   with the dorsal support skeleton. The color of the T-bar tag corresponded with a reach

196   (Figure 1) where the fish was collected. These colors allowed a quick visual indication of

197   larger-scale movements while sampling fish in the field and were a check for the closure

198   assumption of the population estimate. Fish captured at the weir received a Floy tag with

199   a distinct tag color to differentiate them from fish tagged during electrofishing.

200   <u>Analysis</u>

201   <u>Population estimate</u>

202   The electrofishing passes were used to generate the population estimate used in

203   the energetics simulation (described below). The population estimate was calculated

204   using Chapman's estimator (Seber, 1982). This estimator assumes a closed population,

205   with no births, deaths, emigration, or immigration. Movement assumptions were tested

206   using the different colored tags in each reach. During the three-pass sample bout, all but

207   one of the recaptured fish were found in the reach where they were initially tagged. Based

208   on the lack of individual movement and the short timeframe for births and deaths in the

209   one week between passes, we considered the closure assumptions met. The first pass was

210   used as the first sampling occasion while the second and third passes were combined into

211   a second sampling occasion.

212   Not all of the reaches had enough recaptures of tagged fish to calculate a separate

213   population estimate for each reach with reasonable precision, so the whole surveyed

214   section of river was treated as one population for the main estimate. Subsequently, we

215   calculated a population estimate for each reach by dividing the main population estimate

216   among reaches proportionally to the catch in each reach. Using this approach, the overall

217   population estimate used the maximum sample size available.

218   <u>Age and growth analysis</u>

219   Brown trout scales were sorted, mounted, and examined following the plastic

220   impression method (Clutter & Whitesel, 1956; Van Alen, 1982). After discarding

221   unreadable or regenerated scales, each scale was assigned an age and a confidence level

222   (high, medium, or low); those scales with a low confidence level were not used in

223   subsequent analyses. To ensure age readings were being done consistently, scales taken

224   from individual fish that were sampled in multiple years were checked to ensure the

225   increase in age estimates from the scales matched the time that passed between sampling.

226   These checks were conducted blind to the original data by the same reader. All repeat-

227   sampled fish (n=31) were aged consistently.

228   The length and age data were fit to a von Bertalanffy growth model assuming

229   additive error with normally distributed residuals using the nonlinear least squares (nls)

230   function in base R (R Development Core Team, 2009). The model is: $L_t = L_\infty\big(1 -$

231    $e^{-k(t-t_0)}\big) + \varepsilon$ where L_t is fork length at age t, L_∞ is the asymptotic maximum length, k

232   defines the rate at which the asymptote is approached, t_0 is the hypothetical age of the

233   fish at size zero, and ε is error.

234   We also fit individual length and mass measurements to an allometric curve with

235   multiplicative error in base R (R Development Core Team, 2009) using the nls function.

236   This relationship was used in the bioenergetics model to convert the predicted growth in

237   length from the von Bertalanffy model to growth in mass for the bioenergetics model.

238   Annual survival analysis

239   Age-frequency data can be analyzed in multiple ways to estimate survival rates.

240   In simulation studies, the Chapman-Robson survival estimate had less bias and less error

241   than other techniques, especially at small sample sizes (Dunn, Francis, & Doonan, 2002),

242   so that method was applied. The Chapman-Robson estimator is formulated as

$$\hat{S} = \frac{T}{n + T - 1}$$

243   where $T = \sum(x * N_x)$, where $\hat{S}$ is the annual survival estimate, n is the total number of

244   aged fish from the fully recruited ages, x is the coded age where coded age 0 is the age

245   with the highest number of individuals caught, and N_x is the number of individuals of

246   each age. This approach assumes constant survival throughout the population and

247   constant recruitment across years. We calculated separate survival estimates for the 2015

248   and 2016 catch and used the average of the two for the consumption model.

249   Isotope analysis of diet composition

250   We measured carbon and nitrogen isotope ratios in 253 brown trout fin clip tissue

251   samples as well as in samples of multiple potential prey items. We selected prey items to

252   analyze for isotopes based on the prey that were most prevalent in the gut samples. Prey

253 items included various mayflies (Ephemeroptera), golden stoneflies (Perlidae) and

254 salmonflies (*Pteronarcys californica*), as well as lamprey ammocoetes, wild steelhead

255 trout fry, and hatchery coho salmon smolts. As juvenile salmonids of different species

256 generally have similar diets, we assumed that wild steelhead fry represented the isotope

257 composition of wild salmon and trout (including potential cannibalism on juvenile brown

258 trout). All hatchery fish are fed the same food, based on marine-derived fish meal, so we

259 assumed that the hatchery coho salmon smolts represented the isotope composition of all

260 hatchery species. Non-salmonid fish species besides lamprey were rare in the diet

261 samples (present in < 1% of samples), so they were not assessed as potential prey in the

262 isotope analysis. The prey samples were collected from a rotary screw trap run by the

263 Hoopa Tribal Fisheries program that is located within the sample area in the downstream

264 reach. Isotope samples were placed on ice immediately after collection and were

265 transferred to a freezer upon return from the field at the end of the day. From the freezer,

266 the samples were transferred to a drying oven set to $65^{o}C$ and were dried for 36-60 hours.

267 The dried samples were homogenized and a subsample of 0.5 to 1.5 mg removed,

268 weighed, and placed into a tin capsule. The encapsulated tissue was placed in a plastic

269 tray in one of 96 wells.

270   The filled trays were sent to UC Davis stable isotope lab for analysis of Carbon

271 13($\delta^{13}C$) and Nitrogen 15($\delta^{15}N$) using a PDZ Europa ANCA-GSL elemental analyzer

272 interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd.,

273 Cheshire, UK). The $\delta^{15}N$ and $\delta^{13}C$ values reported were the values of the sample relative

274 to ratios of the international standard for each element, air for nitrogen and Vienna

275 PeeDee Belemnite for carbon.

276   Isotopic data was used to determine the proportion of each prey type within the

277 diets of the brown trout. Prey were grouped into four categories: ammocoetes, aquatic

278 invertebrates, hatchery salmonids, and wild salmonids. Limiting the ratio of prey

279 groupings to isotopes improves model fit (Phillips & Gregg, 2003). As brown trout

280 length was found to be positively correlated with $\delta^{15}N$ and $\delta^{13}C$ (r^2 of 0.55 and 0.58

281 respectively), the brown trout isotope data were grouped into five categories based on

282   fork length: <30 cm, 30-40 cm, 40-50 cm, 50-60 cm, and >60 cm. These break points

283   provided adequate samples within each bin to facilitate isotopic analysis and improved

284   resolution within the bioenergetics model when converting food requirements to biomass

285   consumed. The proportions of each prey type consumed by each brown trout group were

286   estimated by fitting the isotope data using a Bayesian framework in the R package

287   MixSIAR (Stock & Semmens, 2013). This package uses a Markov Chain Monte Carlo

288   (MCMC) approach to fitting multi-linear models. Three chains were run with one million

289   iterations each. The burn in length was 500,000 and the thinning rate was 500. The

290   model was run with brown trout size category as a fixed effect and only residual error.

291   Estimated fractionation rates were derived by averaging values from literature sources:

292   3.74 SD 0.477 for δ15N and 1.38 SD 0.983 δ13C (Minagawa & Wada, 1984; Peterson &

293   Howarth, 1987; Vander Zanden, Cabana, & Rasmussen, 1997; Vander Zanden &

294   Rasmussen, 2001; McCutchan et al., 2003; Flinders, 2012).

295   Bioenergetics

296   A bioenergetics approach was used to estimate total prey consumption by brown

297   trout, with a parametric bootstrap to characterize the variance of the estimate. The

298   bioenergetics simulation represented the growth and consumption of age 2-12 brown

299   trout over one year. The model ran on a daily time step where March 1, 2015 was model

300   day one. The base of the simulation was the Wisconsin Bioenergetics model (Hansen et

301   al., 1997) coded into R (code by Andre Buchheister, personal communication, August

302   2015). Published values for parameters relating to brown trout metabolism, egestion,

303   activity, growth, and consumption were used to set a baseline and facilitate comparison to

304   other studies (Table 1). We did not have information about brown trout spawning

305   frequency in the system, so we did not include gamete loss in our model, potentially

306   producing an underestimate of total consumption.

307   To estimate the maximum amount a brown trout could consume, we used Hansen

308   et al.'s (1997) third consumption equation, as it is designed for cold water fishes such as

309   brown trout. In the model, consumption is dependent on size, water temperature and the

310   amount of food consumed in lab experiments during ad libitum feeding at optimal

311   temperatures. To estimate what brown trout actually consume, the modeled maximum

312   consumption is scaled by the proportion of maximum consumption (p). The proportion

313   of maximum consumption (p) was allowed to vary between simulation iterations to

314   achieve the targeted growth of the brown trout of each age. Parameters representing the

315   mass at the start of the year, mass-specific growth rate, population size, survival rate, and

316   diet composition were randomly selected for each iteration of the model from a normal

317   distribution, with a mean and standard deviation for each parameter derived from the

318   field data (Table 2).

319   Additional input data required in order to estimate consumption included mean

320   daily temperature and prey-specific energy density. The temperature fish experienced

321   was determined using linear interpolation of the mean daily temperature between

322   available U.S Geological Survey gage stations (ID numbers 11525500, 11525655,

323   11525854, and 11526400). The temperature profiles used in the energetics model were

324   that of the midpoint of each reach from March 1, 2015 through February 28, 2016 (Figure

325   2). The prey energy densities were literature values: invertebrates 4.07 kJ/g (Groot,

326   Margolis, & Clarke, 1995; Myrvold & Kennedy, 2015), lamprey ammocoetes 3.54 kJ/g

327   (Alvarez 2017), other fish 5.78 kJ/g (Hansen et al. 1997). Temperature and prey energy

328   density were not randomized as part of the bootstrap.

329   Each simulation started with a random draw of average starting size for brown

330   trout of each age from 2-12 (Table 2). Then, randomly drawn von Bertalanffy parameters

331   were used to calculate average sizes at the end of the year. After converting length to

332   mass, an optimization function (optim in R, (R Development Core Team, 2009) was used

333   to find the proportion of maximum consumption required to achieve the selected final

334   mass within each reach for an individual of each age. During that growth interval, daily

335   size and consumption were recorded for each fish. Next, a random draw of population

336   size and survival rate were used to find the number of fish of each age on each day.

337   Finally, the number of fish alive on each day within the appropriate reach and of the

338   appropriate age was used to expand the individual brown trout daily consumption

339   estimates to the reach level. To facilitate allocating total consumption to different prey

340   types, the total biomass consumed each day was aggregated into the five length-based

341   bins used in the stable isotope mixing model. This process was repeated 3,000 times to

342   characterize the variation in consumption given different growth rates, and to account for

343   the error associated with growth, abundance, and survival estimates. The error estimate

344   does not include variation associated with process error or bioenergetics parameters taken

345   from the literature. These model runs produce estimates of the total biomass of food with

346   the energy density of brown trout that is consumed for each size class.

347   Diet proportion, predator and prey energy densities, and the estimate of

348   consumption from the simulation were combined to find the biomass of each prey

349   category consumed by brown trout. For this portion of the analysis, the posterior

350   distribution from the isotopic analysis was treated as a parametric bootstrap which we

351   drew from with a multinomial random draw. A random multinomial draw of

352   consumption by for each size bin was combined with a draw of prey proportion and

353   energy densities in the equation $= \frac{E}{A*E_A+H*E_H+W*E_W+I*E_I}$, where B is the total biomass

354   consumed and E is the total energy required. The symbols *A, H, W*, and *I* are the

355   proportion ammocoetes, hatchery fish, wild fish, and invertebrates contribute to total

356   biomass consumed, respectively. E_x is the energy density of the prey category *x*. The

357   resulting biomass combined with the random draw of proportions provides the biomass of

358   each prey type consumed by the population for a single iteration. This process was

359   repeated 100,000 times to generate a distribution of consumption estimates, ensuring

360   multiple combinations of the consumption and diet composition estimates.

361   **Results**

362   In 2015 we captured 589 brown trout between 20 and 79 cm. Based on

363   recaptures, we estimated the population to be 1580 (95% CI 1279-1878). The scale

364   samples collected from these fish revealed their ages ranged from 2 to 11 years (Figure

365   3). This sample provided sufficient representation of the population's age and size

366 composition to estimate growth and survival parameters for the bioenergetics model

367 (Table 2).

368   Wild fish and invertebrate prey had lower $\delta^{15}N$ and $\delta^{13}C$ than hatchery fish.

369 Brown trout isotope values ranged from in between wild prey and hatchery fish values to

370 higher than both (Figure 4). The MixSIAR model MCMC chains converged with all

371 parameters having $\hat{R}$ values of less than 1.01 ($\hat{R} < 1.05$ is acceptable for inference (Stock

372 & Semmens, 2013). The model results show that the large brown trout consume very a

373 high proportion of fish, especially hatchery fish, and that reliance on fish declines in

374 smaller brown trout (Figure 5). A relatively small proportion of the diet comes from wild

375 fish.

376   The snapshot of diets from gastric lavage samples shows a similar level of

377 piscivory as the isotope model for larger size classes, but lower than the isotope model

378 for small size classes (Table 3). However, gastric lavage lacks the full temporal scale of

379 the isotope analysis and is not as effective at parsing out wild and hatchery fish. While

380 most fish retrieved during lavage were not identifiable to hatchery or wild origin (based

381 on hatchery marking), the temporal pattern of fish consumption by brown trout was

382 consistent with heavy reliance on hatchery-released fish. The number of fish found in

383 stomachs of brown trout peaked in the sample pass conducted immediately following the

384 release of coho salmon smolts from the hatchery (average: 2.2 fish per stomach; SD 2.6;

385 range: 0-11) relative to the sample before the smolts were released (average: 0.3 fish per

386 stomach; SD 0.8; range: 0-9) and after most hatchery coho salmon smolts had moved out

387 of the study area (average: 0.3 fish per stomach; SD 0.7; range: 0-2). Across all samples,

388 coho salmon were the most common identifiable fish in lavage samples (n=36), followed

389 by steelhead (n=16), Chinook salmon (n=5), and brown trout (n=5, not counting one

390 individual that apparently consumed 4 small brown trout in the live well during

391 sampling). Additional fish recovered from lavage samples were not identifiable to a

392 single species, but based on size and time of year we could narrow these fish to the two

393 most likely prey species: larger fish were either yearling coho salmon or steelhead trout

394 (n=73) and the smaller fish were either Chinook or coho salmon (n=14).

395   The energetics simulation predicted that the brown trout population needed to

396   consume 58,382 megajoules (95% CI 39,334 to 77,432) of energy per year. Variation in

397   growth rate accounted for most of the dispersion around the consumption estimates. The

398   variation around the population size and survival rate estimates added additional variation

399   around the consumption estimate, but this variation was almost inconsequential when

400   compared to differences from growth. When energy was converted into prey biomass by

401   category, the most-consumed prey item was hatchery fish, followed by invertebrates,

402   wild fish, and ammocoetes (Figure 6). In 2015, brown trout consumed 5930 kg (95% CI

403   3,800 to 8,805 kg) of hatchery salmonids and 924 kg (95% CI 60 to 3526 kg) wild

404   salmonids.

405   **Discussion**

406   Non-native brown trout in the Trinity River are highly piscivorous. We found that

407   large individual brown trout relied heavily on native salmonids as prey. This is a

408   particular concern given the ongoing, intensive recovery efforts for native salmonids in

409   the Trinity River. Here, we consider brown trout predation separately on hatchery and

410   wild-spawned fish. We take this approach for three reasons: First, hatchery fish are

411   isotopically distinct from other prey sources due to the marine fish component of

412   hatchery fish feed, so we had to estimate consumption of hatchery fish separately from

413   wild fish in our isotope analysis. Second, hatchery production and release practices are

414   factors that managers can control to potentially affect predation rate or brown trout

415   abundance, but this is not true of wild-spawned fish. Third, although the Trinity River

416   hatchery and wild runs of salmon and trout are genetically integrated, hatchery and wild-

417   spawned individuals often have different survival and adult return rates (Araki et al.,

418   2008) so predation on each type may have different effects on salmon and trout

419   populations.

420   *Hatchery-produced fish*

421   Piscivorous brown trout in the Trinity River relied heavily on hatchery-produced

422   fish. Our isotope analysis indicates that most of the biomass of large brown trout in the

423   Trinity River is derived from consumption of hatchery fish. Other studies have found that

424   releases of large numbers of hatchery-produced fish can provide a substantial resource

425   pulse that alters recipient ecosystems (Warren & McClure, 2012; Alexiades, Flecker, &

426   Kraft, 2017). To put the results for predation on hatchery fish in context with regard to

427   salmon production, the mean estimate of hatchery fish biomass consumed by brown trout

428   was about 7% of the total biomass released from Trinity River Hatchery in 2015.

429   The artificial subsidy provided by juvenile salmon and trout from the hatchery

430   likely allows Trinity River brown trout to maintain elevated population levels and reach

431   larger size than would otherwise exist within the river. Historical records suggest that the

432   Trinity River brown trout population increased substantially after hatchery releases

433   began, (Moffett and Smith 1950; Rodgers 1973) giving some credence to the notion that

434   hatchery supplementation increased brown trout population growth, although habitat

435   restoration and changes in flow management probably explain some of the variation in

436   brown trout abundance. Brown trout are currently sustained by hatchery fish even though

437   the availability of hatchery fish is seasonally limited to relatively brief periods after

438   hatchery releases and before the hatchery fish migrate out of the Trinity River heading for

439   the ocean (March for coho salmon, April for steelhead trout, June and October for

440   Chinook salmon). Our bioenergetics model and observations of stomach contents suggest

441   that the large brown trout feed voraciously immediately following hatchery releases and

442   probably do not gain much biomass during the rest of the year. However, brown trout do

443   still eat opportunistically when hatchery fish are not available, including during the

444   vulnerable emergence and early rearing period for wild salmon and trout in the study area

445   (January-February).

446   There was a clear ontogenetic diet shift for Trinity River brown trout, with

447   increasing reliance on hatchery fish for larger, older individuals. An increase in piscivory

448   with size is a well-documented phenomenon for brown trout (L'Abée-Lund, Langeland,

449   & Sægrov, 1992; Jensen, Kiljunen, & Amundsen, 2012) and is often accompanied by a

450   rapid increase in growth rate and a larger maximum size (Jonsson et al., 1999). However,

451   recent work suggests that the shift to piscivory is contingent on the presence of a suitable

452 prey species that is vulnerable to brown trout and abundant enough to support a

453 population of predators (Sánchez-Hernández et al., 2017) . Hatchery-released fish may

454 fill this role for brown trout in the Trinity River, supporting a shift to piscivory and

455 sustaining the biomass large, predatory individuals.

456 *Wild-spawned fish*

457 ◾ Our estimate of predation on wild-spawned salmon and trout is lower and less

458 precise than the estimate for hatchery-produced fish. The lower precision of this estimate

459 is caused in part by the isotopic similarity of wild salmon and trout to other naturally-

460 occurring prey items in the Trinity River, including insects and lamprey ammocoetes.

461 However, based on observations of fish in brown trout diets before the hatchery releases,

462 we know that brown trout in the Trinity River do actively feed on wild-spawned salmon

463 and trout. Although the total biomass of wild fish that brown trout consume is much

464 lower than for hatchery fish, this predation is still a potential concern for conservation

465 because it occurs over longer time spans, including the early rearing period when the total

466 biomass of wild fish available is much lower than the biomass of hatchery fish available

467 during hatchery releases. However, translating our consumption estimates into mortality

468 rates and estimating the effects of brown trout on wild salmon populations in the Trinity

469 River is not possible with the current data set.

470 Based on the average estimate of ca. 1,000 kg of wild salmonids consumed by

471 brown trout and a total of ca. 4,000 kg of juvenile salmonids outmigrating from the upper

472 Trinity River (Harris, Petros, & Pinnix, 2016), we could naively say that 20% of wild

473 salmonid production in 2015 was consumed by brown trout. However, this estimate could

474 have a substantial positive or negative bias for a variety of reasons. First, some proportion

475 of the wild salmonids consumed by piscivorous brown trout were juvenile brown trout,

476 which are lumped with other wild-spawned salmon and trout in the isotope analysis

477 (potential positive bias). The lavage data suggests that cannibalism was relatively rare,

478 but our samples from outside of the spring electrofishing sample bouts are limited and

479 cannibalism may have been more common in other seasons. Even if we assume

480 cannibalism was truly rare, the naïve calculation of brown trout imposed mortality is

481   premised on some very unlikely assumptions: that every fish consumed by brown trout

482   was similar in size to outmigrants and that every fish consumed by brown trout would

483   have survived their journey out of the 64 km below the dam if it was not consumed. In

484   reality, brown trout can consume juvenile salmonids during their entire rearing period

485   leading up to outmigration, including at sizes much smaller than outmigrants (potential

486   negative bias). Further, not all of the wild fish consumed by brown trout would have

487   otherwise survived (potential positive bias), some level of compensatory mortality is

488   certain (Ward & Hvidsten, 2011). Finally, any attempt to estimate effects on populations

489   would clearly require estimates of consumption at the species level, not lumped into

490   hatchery and wild categories (unknown bias, possibly different for each prey species).

491   In addition to predation, brown trout may affect survival and growth of wild-

492   spawned salmon and trout in the Trinity River through competition. Our sampling

493   techniques and analysis focused on large brown trout with diets and microhabitat use that

494   are distinct from native juvenile salmon and trout. However, other studies have found that

495   juvenile brown trout can compete for food and territory space with juveniles of all three

496   salmon and trout species native to the Trinity River (Fausch & White, 1986; Gatz, Sale,

497   & Loar, 1987; Glova & Field-Dodgson, 1995). Competition could exacerbate any

498   negative effects of brown trout on populations of native fish in the Trinity River, as has

499   been suggested for non-native brook trout and native Chinook salmon in the Columbia

500   River system (Levin et al., 2002). Evaluating effects of competition between brown trout

501   and native salmon and trout in the Trinity River will require a new sampling effort.

502   *Management options*

503   Historical records are incomplete, but existing information suggests that brown

504   trout abundance in the Trinity River continues to fluctuate. Creel surveys prior to 1970

505   refer to catches of less than 10 brown trout per angler per year, with fish ranging from 30-

506   50 cm (Moffett and Smith 1950; Rodgers 1973). Catches in recent years are generally 2-5

507   brown trout per angler per day with lengths reaching or exceeding 70 cm (J. Alvarez,

508   personal observation). Our sampling in 2015 might represent part of a recent peak in

509   brown trout abundance. As sampling continued into 2016 and 2017, the brown trout

510   population estimates declined and younger year-classes were less common (Alvarez

511   2017). Despite this potential recent decrease in brown trout abundance, our results

512   suggest that Trinity River brown trout have the capacity to exist at abundance high

513   enough to consume a substantial proportion of native salmonid production.

514   The consumption estimates that we produced are contingent on the validity of our

515   bioenergetics model. Bioenergetics models provide a framework for accounting for

516   metabolic costs and other energetic losses when inferring food consumption from

517   observations of growth. The models are based on fundamental relationships between

518   body size, temperature, and physiological rates (Hansen et al. 1997). There is a large

519   body of work on the energetics of brown trout growth that describes these relationships

520   (Elliott 1994), providing the basis for the parameters that we used. However, there are

521   many uncertainties in bioenergetics models that can lead to biased estimates, including

522   uncertainty in the parameter estimates, the functional form of the physiological

523   relationships, and how these vary across individuals and populations (Chipps and Wahl

524   2008). In our model, we used simulations to incorporate the uncertainty in our field-

525   derived parameter estimates into our estimate of consumption, but there are no estimates

526   of the uncertainty available for most of the basic physiological parameters in the

527   literature. One particular area of concern for our estimate is the highly seasonal pattern of

528   prey availability and consumption, with most of the annual energy intake for large brown

529   trout coming from the consumption of hatchery fish during the spring release. The

530   standard bioenergetics model formulation often underestimate consumption when prey

531   availability is high and overestimate consumption when prey availability is low (Chipps

532   and Wahl 2008). However, we do not know how these biases play out over time when

533   food availability transitions from very high to low, or how this seasonal variation may

534   affect our isotopic determination of diet composition.

535   If brown trout are suppressing survival of native salmon and trout, then direct

536   control of brown trout abundance by altering sport harvest regulations, euthanizing brown

537   trout captured in the course of other sampling efforts, and targeted removal sampling may

538   aid in the recovery of native populations. However, direct control of invasive trout can be

539 very expensive and such efforts have a mixed record of success (Meyer, Lamansky, &

540 Schill, 2006; Syslo et al., 2011). If implemented, any such efforts should include

541 assessment of survival of hatchery-released fish and recruitment success of wild fish in

542 order to determine if brown trout control efforts benefit native salmon and trout.

543   Efforts to manage the brown trout population to reduce impacts on native salmon

544 and trout in the Trinity River are likely to generate some controversy. The authors of

545 previous studies in other regions often comment on the importance of brown trout to the

546 sport fishing community. For example, Belk et al. (2016) investigated the potential for

547 maintaining the fishery for non-native brown trout in the Provo River in Utah while

548 increasing native fish populations through physical habitat restoration. They found that

549 rare species would persist only with low brown trout abundance; negative effects on

550 native species could be ameliorated but not removed while brown trout persisted.

551 Similarly, Townsend (1996) studied streams across New Zealand and found localized

552 extirpations of galaxiid fishes and large scale changes to entire aquatic communities

553 associated with introduced brown trout. Despite these findings, in his conclusions he

554 questioned the need for and feasibility of any brown trout removal program. A

555 community of recreational anglers is invested in brown trout in the Trinity River system

556 because resident brown trout support a small recreational fishery, especially when native

557 anadromous species are not available.

558   As an alternative to direct control efforts, it may be possible to reduce predation

559 on hatchery fish by altering release practices at the hatchery. Reducing brown trout

560 predation on hatchery-released fish has two potential benefits: increased survival of

561 hatchery-released fish, supporting conservation efforts and harvest opportunities; and a

562 reduced subsidy to the brown trout population. The latter could have cascading affects,

563 including reducing the abundance of large, piscivorous brown trout that rely on hatchery-

564 released fish, and reducing predation on wild fish. This assumes that brown trout will not

565 be able to sustain their high biomass by switching to an alternative prey, but we argue

566 that this is a reasonable assumption given that large brown trout do not currently consume

567 much biomass of other prey during the portion of the year when hatchery salmon are not

568 available. Approaches that might reduce brown trout predation on hatchery fish include

569 synchronizing the releases of multiple species from the hatchery, so that large numbers of

570 prey swamp the brown trout for a lower overall predation rate (Ward & Hvidsten, 2010),

571 and minimizing the time that hatchery fish remain in the system by delaying releases until

572 fish are large and set to migrate rapidly to sea.

573 **ACKNOWLEDGEMENTS**

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737

738   **Figure legends**

739

740   Figure 1. Map of the study area with an inset regional map of California. The Trinity

741   River flows from right to left. The study area begins at Lewiston Dam and ends at the

742   confluence of the main stem with the North Fork of the Trinity River. Within the study

743   area, each reach is highlighted with the color of the Floy T-bar tag that was used to mark

744   fish, matching the temperature profile lines in Figure 2.

745

746   Figure 2. Temperature profiles of each reach where Reach 1 is the furthest upstream and

747   Reach 6 is the furthest downstream. The color of the line matches the color of the reach

748   in Figure 1.

749

750   Figure 3. Age and size for all individual brown trout and the fitted Von Bertalanffy

751   growth curve. Von Bertalanffy parameter estimates and standard errors are in Table 3.

752

753   Figure 4. Isoplot of brown trout and prey items. Blue x's represent individual Brown

754   Trout isotope ratios. Prey items are labeled and the location is the mean value for that

755   prey category. The error bars are a single standard deviation.

756

757   Figure 5. Diet proportions of Brown Trout grouped by fork length. Sample sizes for each

758   size bin were n=19 for 20 to 30 cm, n=60 for 30-40 cm, n=83 for 40-50 cm, n=61 for 50-

759   60 cm, and n=30 for >60 cm.

760

761   Figure 6. Estimated biomass of prey consumed by all brown trout > 20 cm long in

762   population the Trinity River over the course of a year. Median estimate consumption

763   estimates were 5,930 kg of hatchery fish (95% CI 3,800 to 8,805 kg) 3,566 kg of

764   invertebrates (95% CI 1,279 to 5,524 kg), 924 kg (95% CI 60 to 3,526 kg) of wild fish,

765   and 598 kg of lamprey ammocoetes (95% CI 18 to 2,058 kg).

Table 1. Parameters of the Wisconsin bioenergetics model and the values used to implement it. The model equations and parameter meanings are described in Hansen et al. 2007. All parameter values are from Dieterman et al. (2004) except LOSS, which is from Burke and Rice (2002).

Parameter	Value	Parameter definition
CTO	17.5	Water temp corresponding to 0.98 of the maximum consumption rate
CTM	17.5	The upper end of the temperature where still at 0.98 of the maximum consumption rate
CQ	3.8	Water temperature at which temperature dependence is a fraction (CK1) of the maximum rate
CA	0.2161	Intercept of mass dependence function for a 1 g fish at optimum water temperature
CB	-0.233	Coefficient of mass dependence for increasing portion of curve
CTL	20.8	Temperature at which consumption is reduced some fraction (CK4) of the maximum rate
CK1	0.23	Specific rate of respiration (g/g/d)
CK4	0.1	See CTL
RA	0.0113	Intercept for the allometric mass function for respiration
RB	-0.269	Slope of allometric mass function for respiration
RQ	0.0938	Approximates the rate at which the function increases over relatively low water temperature
RK1	1	Intercept for swimming speed above the cutoff temperature
RK4	0.13	Mass dependent coefficient for swimming speed at all water temperatures
BACT	0.0405	Water temperature dependent coefficient of swimming speed at water temp below RTL
RTO	0.0234	Coefficient for swimming speed dependence on metabolism (s/cm)
RTL	25	Cutoff temperature at which activity relationship changes
ACT	9.7	Intercept of the relationship between swimming speed and mass at a given temperature
LOSS	0.35	Energy lost to feces and specific dynamic action
EDA	6582	Intercept for energy density-weight function
EDB	1.1246	Slope of the energy density-weight function

Table 2. Brown trout population parameters for the bioenergetics simulation. The estimates and variance are derived from field data collected during this study.

Parameter		Mean	Standard Error
Population size	Reach 1	111	65.5
	Reach 2	300	178.5
	Reach 3	95	56.5
	Reach 4	553	328.5
	Reach 5	284	169
	Reach 6	237	141
Annual survival		58.3%	2.4%
Initial size (cm)	Age 2	20.0	2.4
	Age 3	34.0	4.7
	Age 4	40.6	4.0
	Age 5	47.0	4.5
	Age 6	53.2	4.7
	Age 7	56.6	5.1
	Age 8	62.8	5.2
	Age 9	66.0	4.9
	Age 10	69.0	4.9
	Age 11	72.0	4.6
	Age 12	75.0	4.6
Growth Rate	L_∞	90.6	2.9
	K	0.14	0.009
	t_o	-0.21	0.055

Table 3. Comparison of diet composition results based on lavage and isotope analysis. The lavage was calculated as the summed mass of content within a category divided by the total mass of stomach

contents. All masses are wet masses and do not account for digestive state. Brown Trout are grouped by fork length.

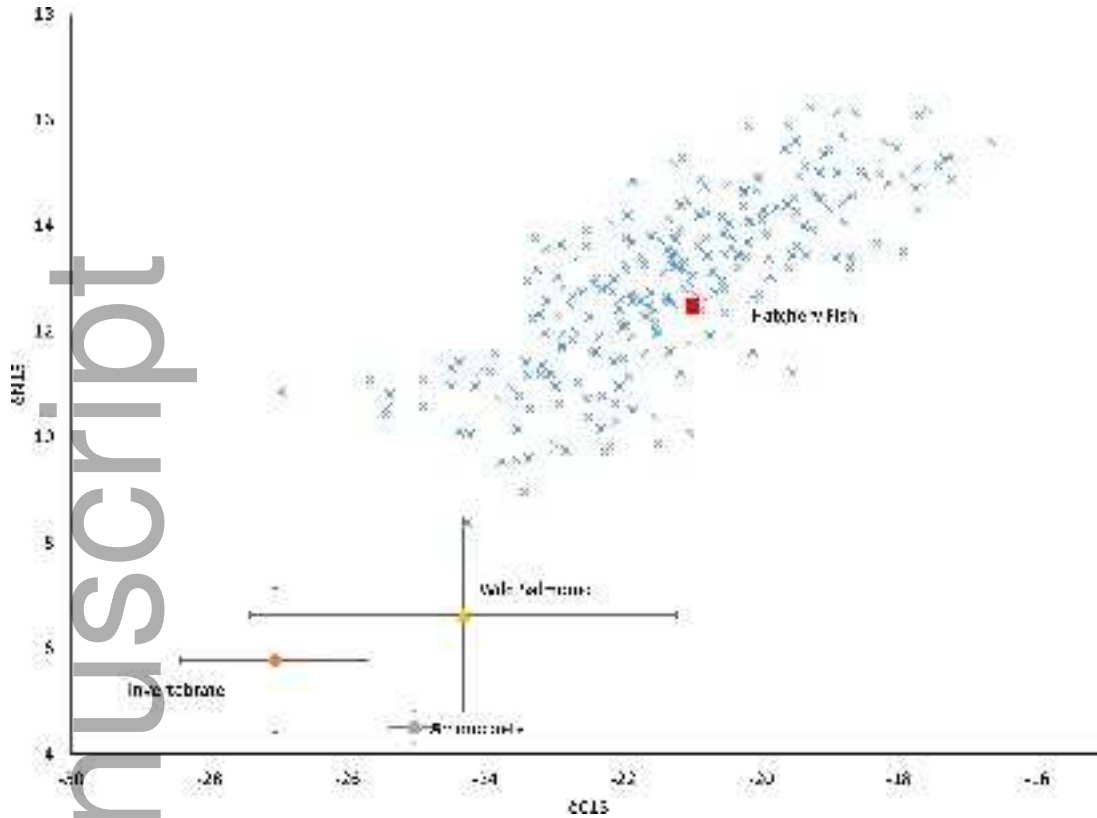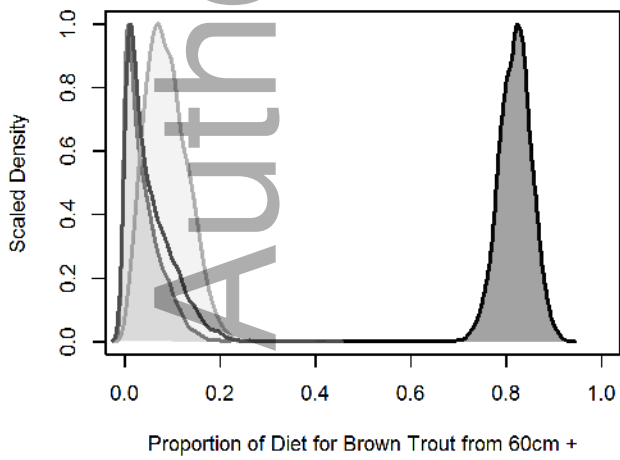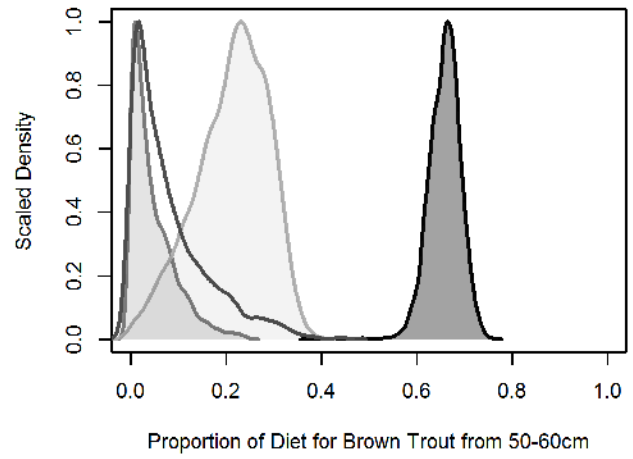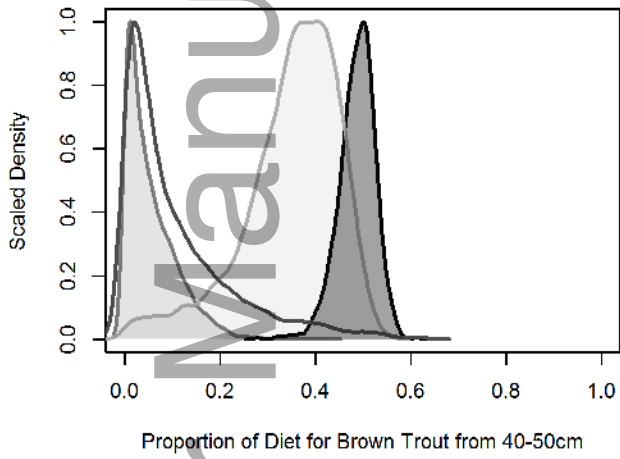| Brown Trout size interval (cm)	% Fish	
	Lavage	Isotope
20-30	8%	38%
30-40	26%	60%
40-50	83%	63%
50-60	82%	78%
>60	98%	92%
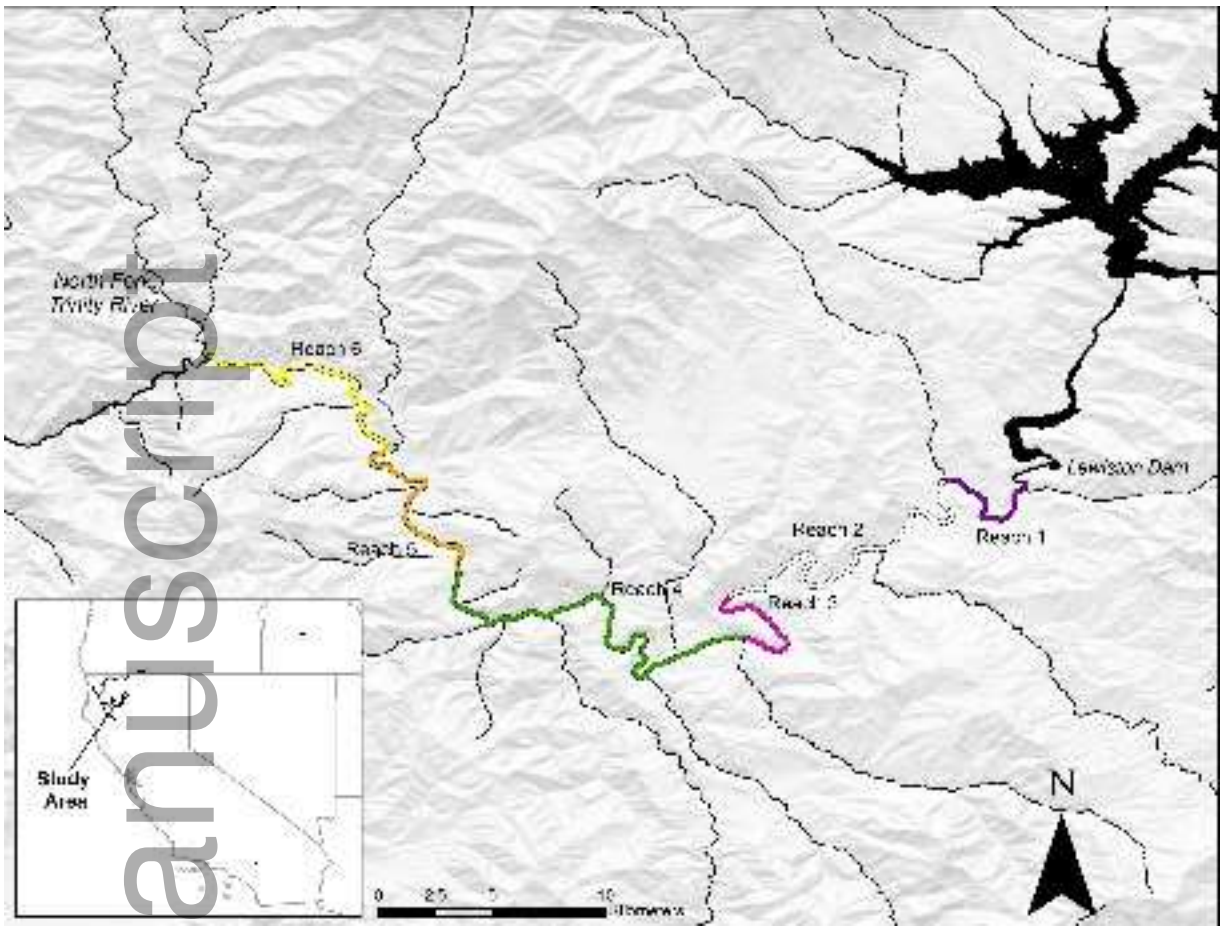
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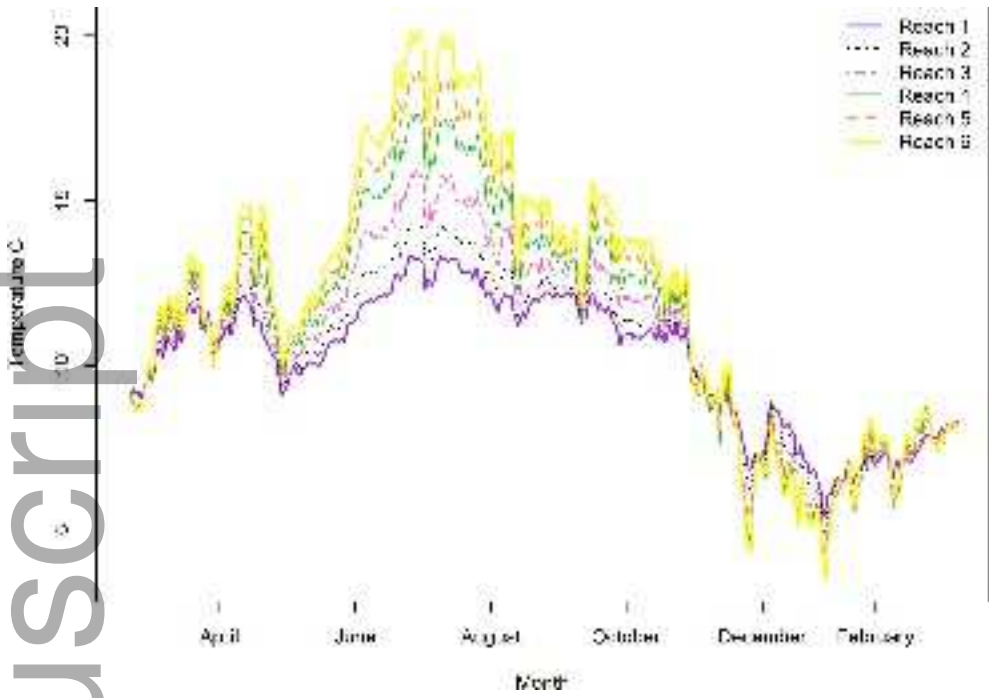
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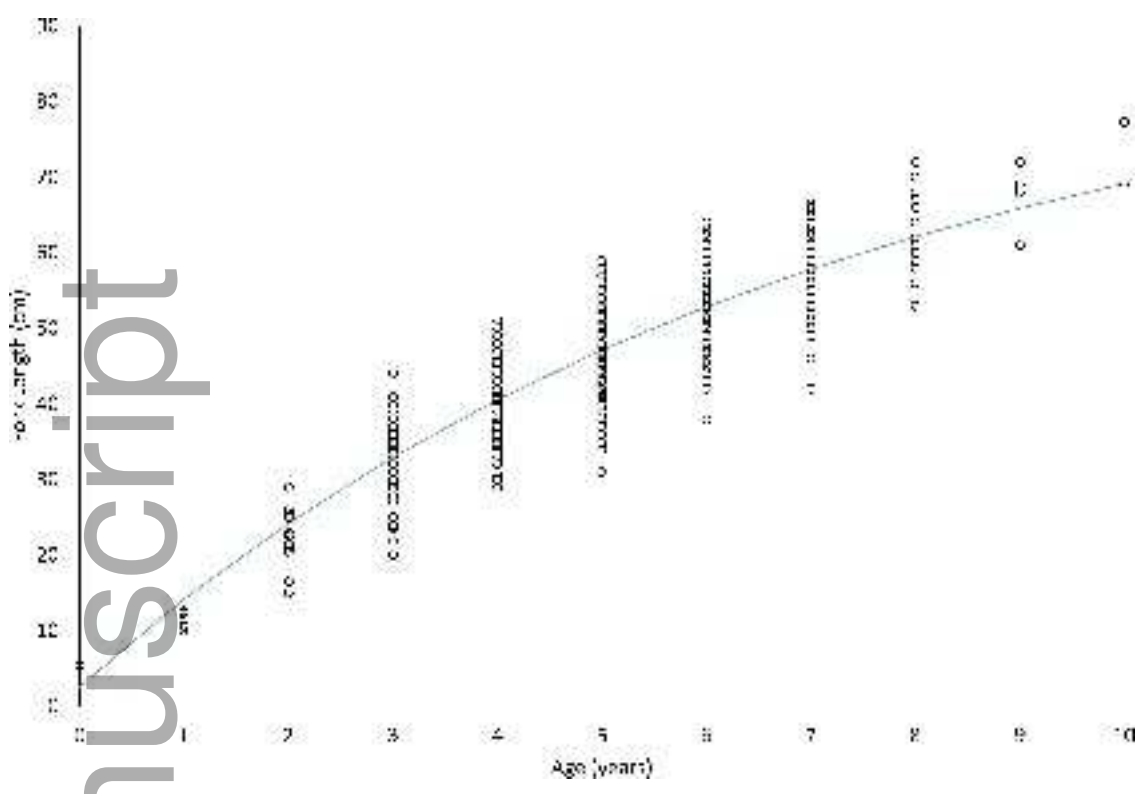
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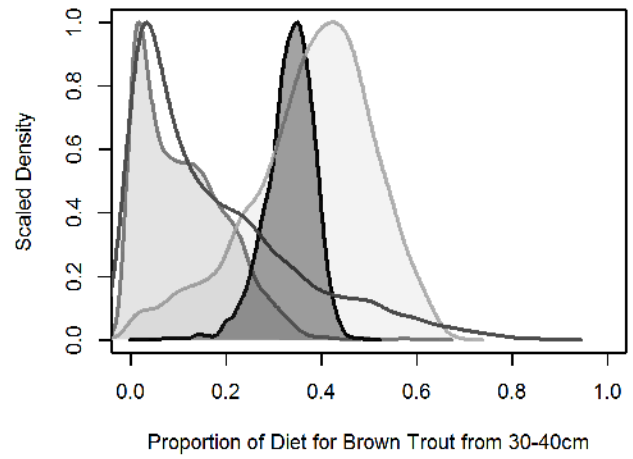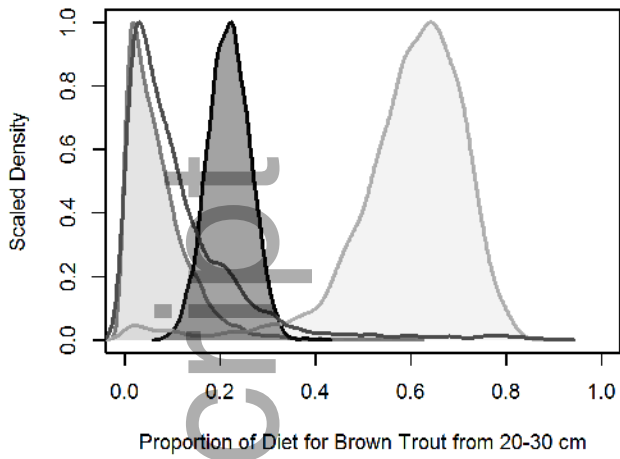
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