ABUNDANCE, GROWTH, AND PREDATION BY NON-NATIVE BROWN TROUT IN THE TRINITY RIVER, CA

By

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ABSTRACT

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Brown Trout were introduced to the Trinity River in Northern California in the 1890's. Since 1932, Brown Trout have sustained their population without additional stocking. Over the last 15 years, fisheries managers have been concerned that predation by piscivorous Brown Trout may impede efforts to restore native salmonids, in particular endangered Coho Salmon. I investigated predation by Brown Trout on native fish in the 64 km of the main stem Trinity River below Lewiston Dam. Using a bioenergetics approach parameterized with field measurements of Brown Trout abundance and growth, I estimated the amount of energy needed to sustain the 2015 Brown Trout population and used stable isotope analysis and gastric lavage to quantify the biomass of prey consumed over the course of a single year. I found that Brown Trout, particularly large individuals, primarily ate hatchery fish. Invertebrates were the next most popular prey followed by wild salmonids and ammocoetes. I estimated that in 2015, Brown Trout ate 6.5% of the biomass released from Trinity Hatchery (95% CI 4.1 to 9.6 %) and the wild consumption was equivalent to 23% (95% CI 1.4 to 88%) of the biomass of wild salmonids which survived to emigrate out of the study reach.

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INTRODUCTION

Brown Trout (*Salmo trutta*) have undergone massive range expansion from their native waters in Europe and North Africa to the waters of every continent except Antarctica (MacCrimmon and Marshall 1968; Dill and Cordone 1997). This expansion was driven by the efforts of humans who found Brown Trout desirable for sport and food (Wilson 1879). Brown Trout were brought to the United States from Germany and the United Kingdom in the late 1800's. One of the earliest American Brown Trout hatcheries was in Michigan (Adkins 2007). From Michigan, Scottish, German, and hybrid Brown Trout eggs were brought to Fort Gaston (Hoopa, CA) and Sisson Hatchery near Mt. Shasta by train in the 1890's (Thomas 1981; Adkins 2007). There were two introductions from those hatcheries to the Trinity River, one near the mouth at Fort Gaston and a separate effort closer to the headwaters in Stewart's Fork and the main stem Trinity River near Lewiston, CA (Adkins 2007). The motivation behind the upstream introduction was the California Fish and Game Commission's plan to replace rainbow trout with the "more desirable Brown Trout" throughout the state ("New Trout Sent to Trinity County; Scottish Variety to Supplant the Famous Rainbow Species" 1911), while the downstream introduction was implemented to supplement the dwindling salmon fishery that the Hoopa Tribe relies on for sustenance.

Brown Trout are highly piscivorous (L'Abée-Lund et al. 2002). In the early years of Brown Trout introduction to the Trinity River, fisheries managers raised concerns that the Brown Trout may be adversely affecting the other salmonid species through

predation. This lead to a short moratorium on Trinity Brown Trout planting in the river during the 1920's (Thomas 1981). The moratorium was short lived, and Brown Trout planting was gradually phased back in over the course of three years and continued until 1932. In addition to piscivory, Brown Trout can impact other species through competition and as disease vectors (Glova and Field-Dodgson 1995). Negative impacts to the native populations through both these means have been observed in many systems throughout the world. Competition and predation with Brown Trout has been found to decrease recruitment, growth, and abundance of native species in streams throughout the United States (McHugh and Budy 2006; Belk et al. 2016; Hoxmeier and Dieterman 2016) and New Zealand (Townsend 1996).

When reporting the effects of Brown Trout on native species, the authors of previous studies often comment on the importance of Brown Trout to the sport fishing community. These studies are often undertaken to investigate the potential impacts of Brown Trout on native fishes before any management actions are taken to reduce Brown Trout abundance. For example, in the Provo River in Utah, McHugh and Budy (2006) investigated the potential for maintaining the Brown Trout fishery while increasing native fish populations through physical habitat restoration. However, they found that rare species would persist only with low Brown Trout abundance; negative effects could be ameliorated but not removed while Brown Trout persisted. Similarly, Townsend (1996) studied streams across New Zealand and found localized extirpations of galaxiid fishes and large scale changes to entire aquatic communities associated with introduced Brown Trout. Despite these findings, in his conclusions he questioned the need for and

feasibility of any Brown Trout removal program. On the Trinity River, there is a counter example to this pattern of non-action after finding negative impacts by a predator. In this study predation by steelhead trout, another popular sport fish, was investigated (Naman 2008). He found steelhead could have a significant effect on the wild salmon population they were feeding from, and this was a factor in the decision to reduce production of hatchery steelhead.

Similarly, a community of recreational anglers is invested in Brown Trout in the Trinity River system because Brown Trout do support a small recreational fishery, especially when other species are not available. However, Brown Trout in the Trinity River may represent an impediment to restoring native and tribally-important species such as Chinook Salmon (*Oncorhynchus tshawytscha*), steelhead trout (*O. mykiss*), and Pacific Lamprey (*Entosphenus tridentatus*) as well as endangered Coho Salmon (*O. kisutch*). The potential for Brown Trout to directly affect native salmon populations by predation, depends on Brown Trout feeding behavior and abundance. Piscivorous behavior by Trinity River Brown Trout has been documented during field projects focused on other species and by local fisherman, but no formal diet studies have been conducted. The best historical index for Brown Trout abundance in the Trinity River is the adult salmon sampling weir in Junction City (Trinity River rkm 136.2). Catch totals for Brown Trout have increased during sampling from 2000 to 2013 to levels 200-300% higher than those in the 1980's and 1990's, despite reduced sampling effort since 2000 (Borok et al. 2014a, 2014b; National Marine Fisheries Service 2014). Documentation of piscivory combined with a potential increase in Brown Trout populations inferred from

weir catch data suggest that Brown Trout may be having a substantial impact on native fishes. This threat was identified by the California Department of Fish and Wildlife (CDFW) in 2006 and provided the impetus for changing fishing regulations from a bag limit of one Brown Trout or hatchery steelhead to five Brown Trout in addition to a hatchery steelhead. Trinity River Brown Trout were also identified as an impediment to species recovery in the recent 2014 Final Recovery Plan for Southern Oregon and Northern California Coho salmon (National Marine Fisheries Service 2014).

I undertook the first large-scale sampling effort for Brown Trout in the Trinity River. Sampling included multi-pass electrofishing to estimate abundance, size, and age structure of Brown Trout in the upper 64 km; diet sampling and isotope analysis to characterize diet composition; and construction of a bioenergetics model to estimate total consumption of fish prey on an annual basis. The focal area for this project was the upper 64 km of anadromous habitat in the main stem (immediately downstream of Lewiston Dam). Existing observations indicate that Brown Trout are widespread through the 178 km of anadromous habitat in the main stem Trinity River as well as major tributaries. However, Brown Trout are most abundant in the focal area and they likely have the most access to native salmon prey from hatchery releases and natural spawning grounds. The goal of this study was to inform fisheries management on the Trinity River by estimating the total consumption of native fishes by non-native Brown Trout. This estimate requires information about Brown Trout population characteristics (abundance, age and size structure) and feeding behavior (diet composition, consumption rates).

MATERIALS AND METHODS

Study Area

The Trinity River in Northern California is the largest tributary to the Klamath River, with a main stem length of 274 km and a watershed area of about 7679 km^2. The Trinity River's headwaters are in the Trinity Alps at an elevation of about 1,850 m and the confluence with the Klamath River in Weitchpec is 69.5 km from the ocean at an elevation of 56 m. There are two large earthen dams on the Trinity River. Upstream at river kilometer 261.6 is Trinity Dam, which is used for storage, and downstream at river kilometer 250.3 is Lewiston Dam, which is used to export water to the Sacramento River basin. This study is focused on the 64 km of the main stem Trinity River below Lewiston Dam and above the North Fork of the Trinity River (Figure 1). Discharge from Lewiston Dam ranges annually from 8.6 to 311.5 cms (cubic meters per second). With tributary inputs downstream of the dam, the Trinity River near the North Fork experiences flows between 12 and 850 cms. There is a characteristic seasonal flow pattern: during winter and spring storms the upper range is approached, and by mid-summer and through winter base flow the flows stay closer to the lower end.

The 64 river kilometers in which the study took place were divided into six reaches based on tributary inputs, river access, and prior information about Brown Trout density. The boundaries of each reach occurred at the following locations and creek mouths in downstream order: the concrete weir below Lewiston Dam, Rush Creek, Steel

Bridge river access, Indian Creek, Evans Bar river access, Canyon Creek, and the North Fork of the Trinity River (Figure 1).

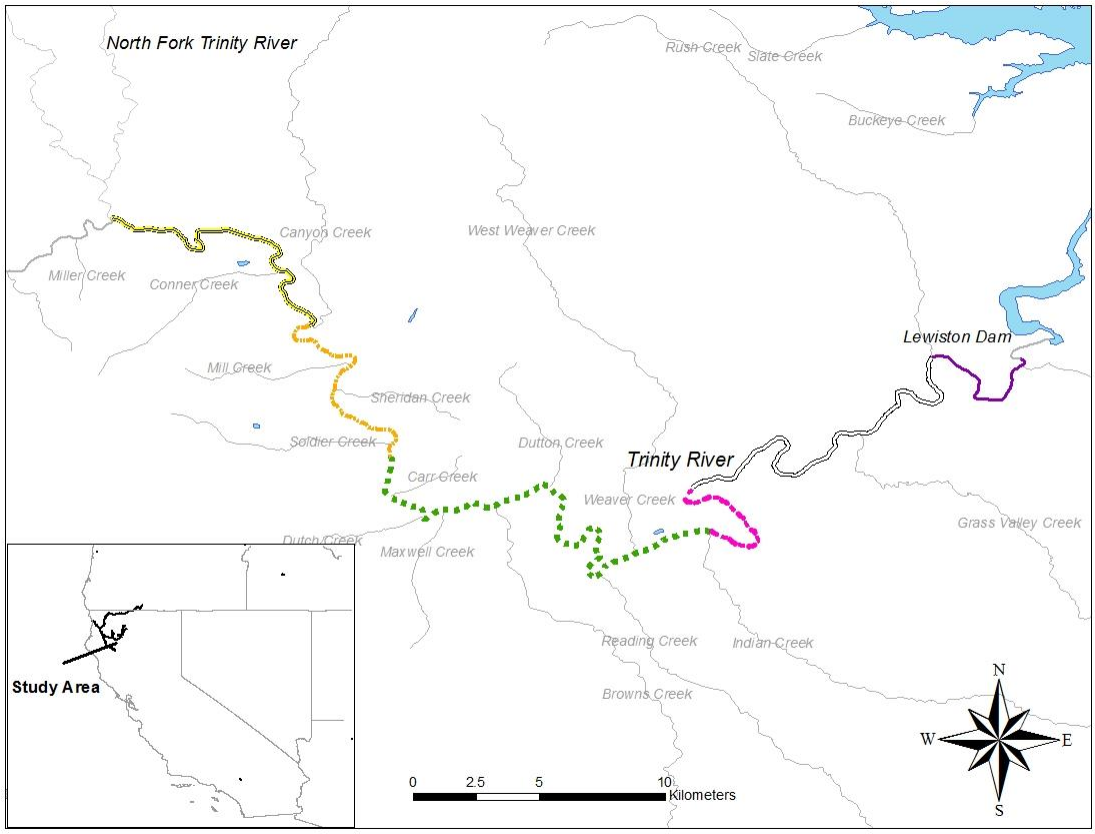

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Figure 1. Map of the study area with an inset regional map of California. The Trinity River flows from right to left across the map beginning at Lewiston dam and flowing toward the downstream end of the study area at the confluence of the main stem with the North Fork of the Trinity River. The lines along the main stem from the thin purple line on the right to the hashed yellow line on the left are the different reaches where tagging took place. The color of the line matches the color of the Floy T-bar tag that was used to mark the fish in that section of river.

Capture methods

All fish capture, handling and euthanasia was conducted using methods approved by the Humboldt State University Institutional Animal Care and Use Committee under protocol number 13/14.F114-A

Electrofishing

A 4.3 meter raft with a Smith-Root 2.5 kilowatt generator powered pulsator (GPP) electrofisher system (Smith-Root Inc., Vancouver, WA) was used to sample the 64 km of river that comprised the sample area (Figure 2). The control box was set with a DC pulse rate of 30 Hz with voltage between 300 and 400. Sampling focused on the thalweg of the main stem while moving slowly downstream. Each pass took three to four days to complete and proceeded from upstream to down. A single sampling pass started near Lewiston Dam on Monday and worked down to a river access. Tuesday sampling began where Monday's sampling left off and this pattern continued until the 64 km was completed, generally on Thursday. The following Monday a new pass would begin. The time between passes allowed Brown Trout to recover from handling stress and resume normal eating behavior before being resampled (Pickering et al. 1982). Each sampling occasion consisted of two or three passes and occurred over as many weeks (Table 1).

Figure 2. Electrofishing raft used to sample Brown Trout on the main stem Trinity River. Two netters stood in the front of the raft using nets with openings approximately 0.6m x0.3m and a handle between 1.75 and 3 meters long. Protruding in front of the netters were two 2.5 meter booms which held the anode fore on each side of the raft. The anode end consisted of four 1.5 meter wires that hung into the water. The silver tubes at the waterline under the oarlocks had 1.5 m cathode wires hanging down.

Table 1. Electrofishing schedule summarizing the number of passes and starting day for each sampling occasion.

Sampling occasion	Number of passes	Date of first day
1	3	March 11, 2015
2	2	February 2, 2016
3	2	April 11, 2016

Weir

An Alaskan style weir (Sinnen et al. 2005), operated by the California Department of Fish and Wildlife and the Hoopa Tribe, was installed in Junction City California in late June and run through September in 2014, 2015, and 2016 to catch adult salmonids. The trap box was checked once in the morning and again in the afternoon each weekday. After the second trap check and on the weekends, the weir was opened to allow unimpeded passage. The weir was closed 30 minutes before dark each evening, Sunday through Thursday. The captured Brown Trout were moved to a separate live well after being measured and tagged with a CDFW T-bar tag. This tag was similar to those used during the electrofishing but was dark green and had a different numbering sequence. After separating the Brown Trout from the other fishes, they were processed as described below for diet and isotope samples and released. Per request of the CDFW employees who ran the weir, no Brown Trout were sacrificed as part of the weir sampling.

Hook and line sampling

Throughout the year, I fished for Brown Trout using lures and flies. Angling took place sporadically throughout the year to supplement sampling between other efforts. Fish caught angling were processed as described below.

Processing and Handling

Once captured, all Brown Trout were anesthetized in water saturated with CO_2 using Alka-Seltzer Gold tablets. Once anesthetized, the fish were measured and the following samples were collected: scales for aging taken from the left side between the anal and dorsal fin just above the lateral line, a one centimeter square fin clip taken from the distal posterior tip of the dorsal fin for stable isotope analysis, and stomach contents using gastric lavage. Following gastric lavage, fish were weighed so that stomach contents would not contribute to the mass. Lavage was conducted using a hand-pumped garden sprayer with water from the Trinity River. The spray pipe was placed through the fish's mouth into the stomach and water was sprayed in until the stomach was full. Through continued filling and massaging the belly from the outside, food items were washed and pushed out (Figure 3). A small sub-sample of fish were sacrificed and the stomachs examined to gauge the effectiveness of the gastric lavage. Sacrificed Brown Trout were first anesthetized using CO_2 and sacrificed by cranial concussion followed by pithing to ensure death. Individuals that were sacrificed were not tagged.

Figure 3. A Brown Trout being lavaged with a garden sprayer filled with river water. The fish's stomach contents are visible in the small strainer in the plastic tub.

After the samples and measurements were taken, the fish were tagged with a uniquely numbered FD94 T-bar tag (Floy Tag & Manufacturing Inc., Seattle, WA) for future identification and released. These tags were made of a 7.5 cm long piece of monofilament with polyolefin colored tubing around it. At the insertion end was a 1.5 mm thick, 2 cm wide "T". The tag was injected using Floy Tag's Mark III pistol grip tagging gun. The needle was inserted below the dorsal fin to allow the T to articulate with the dorsal support skeleton. The color of the T-bar tag corresponded with a reach of the Trinity (Figure 1) where the fish was collected. These colors allowed a quick visual

indication of larger-scale movements while sampling fish in the field and were a check for the closure assumption of the population estimate. In 2016, a HPT-12 Passive Integrated Transponder (PIT) tag (Biomark, Inc. Boise, ID) was also placed in the electrofished Brown Trout. These tags were injected into the girdle of the pectoral fins using a 12 gauge needle and Biomark MK 10 implanter. These were beneficial because the internal mark would not be removed by catch and release fisherman, providing a secondary way to track individual growth of recaptured fish.

ANALYSIS

Population Estimate

The electrofishing passes conducted in 2015 were used to generate the population estimate used in the energetics simulation (described below). The population estimate was calculated using Chapman's estimator (Seber 1982). This population estimator is formulated

$$N = \frac{(M+1)(C+1)}{R+1} - 1$$

where N is the population estimate, M is the number of marked fish, C is the number of fish caught in the second pass, and R is the number of fish which were subsequently recaptured. This estimator assumes a closed population, so no births, deaths, emigration, or immigration are permitted. Movement assumptions were tested using different colored tags in each reach. Based on the lack of individual movement and the short timeframe between passes the assumptions of the model were met. In 2015 the first pass was used as the first sampling occasion while the second and third passes were combined into a second sampling occasion. In combining these passes and using the Chapman estimator the estimates were more comparable to the estimates in 2016.

In the initial study framework each reach was going to have a population estimate calculated independently of the other reaches. However, there were not enough recaptures in all of the reaches, so the whole surveyed section of river was treated as one population for the main estimate. To apply the temperature profile associated with each

reach to the correct proportion of the population, a population estimate was calculated for each reach independently. The sub populations were divided by the sum of the parts to calculate the proportion of the main population estimate assigned to each reach. In estimating population this way, the estimate of the total number of fish makes use of the maximum sample size available. Population estimates were also calculated from the electrofishing efforts in February and April of 2016. Only two passes were conducted on these occasions so the estimates were again calculated using Chapman's estimator. These 2016 population estimates are presented for comparison, but they are not used in the subsequent analysis of consumption.

Age Analysis

Brown Trout scales were placed into an envelope labeled with the tag number of the fish they came from. The scales were then sorted using a dissecting microscope to find three scales from each individual that were not regenerated (Figure 4). The three selected scales were put ridged-side-up onto a gum card within one of 20 cells on the card. The gum card was then pressed into an acetate card at 200^{o}F at 15,000 pounds of pressure for two minutes. The acetate impression of the scale was viewed using a microfiche machine, and fish age and the confidence level the reader had in the accuracy of that age were recorded for each fish. Confidence level was defined as a categorical (1) high confidence, (2) medium confidence, or (3) low confidence. Once ages were found for all fish, only those aged with a confidence level of one or two were used in subsequent analyses. To ensure age readings were being done consistently, individual

fish that were sampled in both years were checked to ensure the increase in age matched the time that passed between sampling. This check found all repeat fish (n=31) were aged consistently.

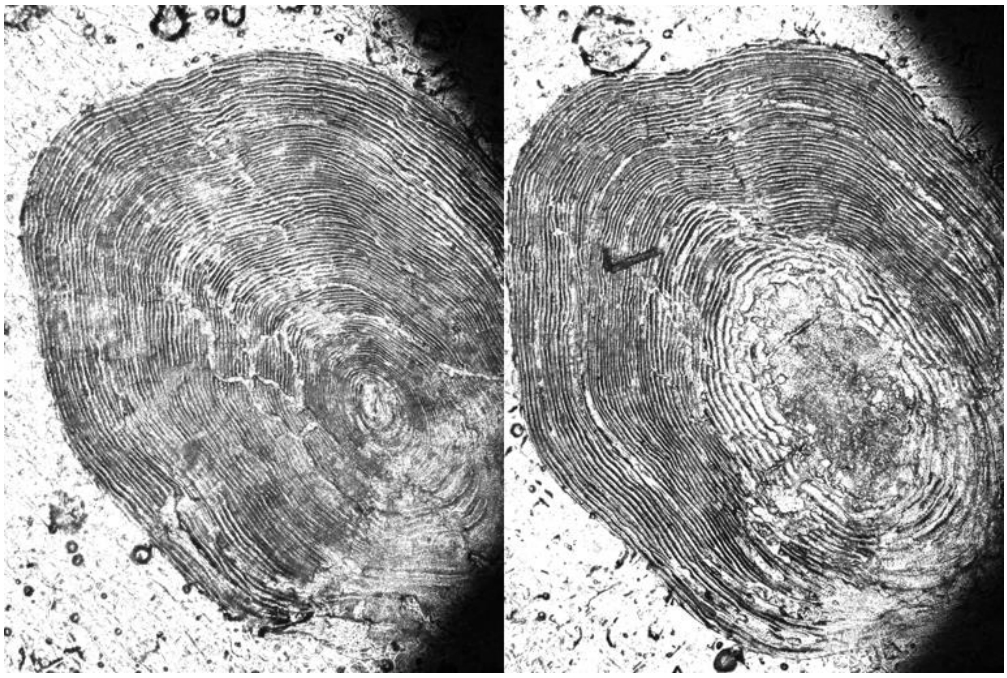

Figure 4. Two Brown Trout scale impressions from the same fish in acetate. The scale on the left has circuli and annuli all the way to the center and would be used for aging. The regenerated scale on the right does not have the circuli present for an unknown number of years and would not be used for aging.

The length and age data were fit to a von Bertalanffy growth model assuming additive error with normally distributed residuals:

$$L = L_{\infty}\left(1 - e^{-k(t-t_0)}\right) + \varepsilon$$

using the nonlinear least squares function in base R (R Development Core Team 2009). In this model, L is the length at age t, L_{∞} is the asymptotic maximum length predicted by the model, K defines the rate at which the asymptote is approached, and t_o is the

hypothetical age of the fish at size zero.

The growth model was validated by visual assessment of an observed vs. predicted growth plot using the actual growth of individual fish recaptured during subsequent sampling occasions to the growth predicted by the model. Recaptures between passes within a sampling occasion were not used for validation because any change in length that would occur in less than two weeks was less than the potential error of the length measurement.

Annual Survival Analysis

Age-frequency data can be analyzed in multiple ways to estimate survival rates. In simulation studies, the Chapman-Robson survival estimate had less bias and less error than other techniques, especially at small sample sizes (Dunn et al. 2002), so that method was applied. The Chapman-Robson estimator is formulated as

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

where $T = \sum(x * N_x)$,where $\hat{S}$ is the annual survival estimate, n is the total number of aged fish from the fully recruited ages, x is the coded age where coded age 0 is the age with the highest number of individuals caught, and N_x is the number of individuals of each age. This approach assumes constant survival throughout the population and, when using data from a single year, constant recruitment across years.

Age information from the scales was summarized by recording the relative abundance of each age within the catch and fitting it to the Chapman-Robson estimator in

the following ways, 1) individual years of weir data, 2) individual years of electrofishing data, and 3) individual cohorts that could be tracked across years using the weir data. Cohorts were tracked from age three until fish of that cohort were no longer captured. For the remainder of the analyses, only the mean of the 2015 and 2016 electrofishing survival estimates were used. The other data provide insight into the potential range of survival estimates over a longer time frame. However, they lacked the breadth of spatial representation needed to make confident inference about the whole population.

Biometric Analysis

The length and weight measurements were fit using an allometric growth curve with multiplicative error in base R (R Development Core Team 2009) using the nonlinear least squares (nls) function. The fish used in this analysis were captured in 2014 through 2016 by the weir and 2015 and 2016 by electrofishing. The allometric growth function is

$$W_i = \alpha {L_i}^{\beta} e^{\varepsilon}$$

where W is the weight of an individual fish, alpha is a scaling constant, beta is the growth parameter, and epsilon is the multiplicative error.

Isotope analysis of diet composition

I measured carbon and nitrogen isotope ratios in 253 Brown Trout fin clip tissue samples as well as in samples of multiple potential prey items. Prey items included mayflies (Ephemeroptera), golden stoneflies (Perlidae) and salmonflies (*Pteronarcys*

californica), lamprey ammocoetes, wild steelhead trout fry, and hatchery Coho Salmon smolts. The prey samples were taken from a rotary screw trap run by the Hoopa Tribal Fisheries program that is located in the most downstream reach of the mark recapture areas. Isotope samples were placed on ice immediately after collection and were transferred to a freezer upon return from the field at the end of the day. From the freezer, the samples were transferred to a drying oven set to 65^{o}C and were dried for 36-60 hours. The dried samples were homogenized and a subsample of 0.5 to 1.5 mg removed, weighed, and placed into a tin capsule. The encapsulated tissue was placed in a plastic tray in one of 96 wells.

The filled trays were sent to UC Davis stable isotope lab for analysis of Carbon 13(δC13) and Nitrogen 15(δN15) using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The δN15 and δC13 values reported were the values of the sample relative to ratios of the international standard for each element, air for nitrogen and Vienna PeeDee Belemnite for carbon.

Isotopic data was used to determine the proportion of each prey type within the diets of the Brown Trout. Prey were grouped into four categories: ammocoetes, aquatic invertebrates, hatchery salmonids, and wild salmonids. Limiting the ratio of prey groupings to isotopes improves model fit (Phillips and Gregg 2003). While hatchery and wild fish were isotopically distinct, the isotopic similarity among different species of hatchery and wild fish would lead to uncertain results if the prey species were treated separately. As Brown Trout length was found to be positively correlated with δN15 and

δC13 (r^2 of 0.55 and 0.58 respectively), the Brown Trout isotope data were grouped into five categories based on fork length, with breaks at 30, 40, 50, and 60 cm. These break points provided adequate samples within each bin to facilitate isotopic analysis and improved resolution within the bioenergetics model when converting predator energy dense food requirements to prey energy dense biomass consumed. The proportions of each prey type consumed by each Brown Trout group were estimated by fitting the isotope data using a Bayesian framework in the R package MixSIAR (Stock and Semmens 2013). This package uses a Markov Chain Monte Carlo approach to fitting multi-linear models. Three chains were run with one million iterations each. The burn in length was 500,000 and the thinning rate was 500. The model was run with Brown Trout size category as a fixed effect and only residual error.

Bioenergetics

A bioenergetics approach was used to estimate total prey consumption by Brown Trout, with a parametric bootstrap to characterize the variance of the estimate. The bioenergetics simulation represented the growth and consumption of age 2-12 Brown Trout over the course of a year. The model ran a daily time step where March 1, 2015 was model day one. The base of the simulation was the Wisconsin Bioenergetics model (Hansen et al. 1997) coded into R (Buchheister, personal communication August 2015). This model is based on a mass-balance relationship of energy consumed, lost to metabolism, and accumulating as growth and is summarized as Consumption = Metabolism + Waste + Growth. Within the Wisconsin Bioenergetics model, multiple

equations are available for each component of the energy balance to tailor the model to the fish species of interest. Metabolism is the sum of basal respiration, active metabolism, and the energy needed to digest consumed food. Basal respiration and the energetic cost of digestion are directly related to temperature. The active metabolism is calculated as a function of swimming speed, including parameters for fish mass and water temperature below a cutoff temperature. Waste is a constant proportion of what is consumed. Any remaining energy is put toward growth, with the change in mass being dependent upon the energy density of the predator mass being created. Published values for parameters relating to metabolism, egestion, activity, growth, and consumption were set as constants and were used to set a baseline and facilitate comparison to other studies (Table 2).

Table 2. 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. Parameter values are from a) Dieterman et al. (2004), or b) Burke and Rice (2002).

Parameter	Value	Source	Parameter Meaning
CTO	17.5	A	Water temp corresponding to .98 of the maximum consumption rate
CTM	17.5	a	The upper end of the temperature where still at 0.98 of the maximum consumption rate
CQ	3.8	a	Water temperature at which temperature dependence is a fraction (CK1) of the maximum rate
CA	0.2161	a	Intercept of mass dependence function for a 1 g fish at optimum water temperature
CB	-0.233	a	Coefficient of mass dependence for increasing portion of curve
CTL	20.8	a	Temperature at which consumption is reduced some fraction (CK4) of the maximum rate
CK1	0.23	a	Specific rate of respiration (g/g/d)
CK4	0.1	a	See CTL
RA	0.0113	a	Intercept for the allometric mass function for respiration
RB	-0.269	a	Slope of allometric mass function for respiration
RQ	0.0938	a	Approximates the rate at which the function increases over relatively low water temp.
RK1	1	a	Intercept for swimming speed above the cutoff temperature
RK4	0.13	a	Mass dependent coefficient for swimming speed at all water temperatures
BACT	0.0405	a	Water temperature dependent coefficient of swimming speed at water temp below RTL
RTO	0.0234	a	Coefficient for swimming speed dependence on metabolism (s/cm)
RTL	25	a	Cutoff temperature at which activity relationship changes
ACT	9.7	a	Intercept of the relationship between swimming speed and mass at a given temperature
LOSS	0.35	b	Energy lost to feces and specific dynamic action
EDA	6582	a	Intercept for energy density-weight function
EDB	1.1246	a	Slope of the energy density-weight function

To estimate the maximum amount a Brown Trout could consume, I used Hansen et al.'s (1997) third consumption equation, as it is designed for cold water fishes such as Brown Trout. In the model, consumption is dependent on size, water temperature and the amount of food consumed in lab experiments during ad libitum feeding at optimal temperatures. To estimate what Brown Trout actually consume, the modeled maximum consumption is scaled by the proportion of maximum consumption (p). The proportion of maximum consumption (p) was allowed to vary between simulation iterations to achieve the targeted growth of the Brown Trout of each age. The size at day one, growth parameters to calculate size at day 365, population size, survival rate, and proportion of prey categories consumed were randomly selected each iteration from a normal distribution, with a mean and standard deviation derived from the summary or analysis of field data (Table 3).

Table 3. Parameters which vary within the bioenergetics simulation. The estimates and variance are derived from field data collected during this study. In the prey proportions G stands for Brown Trout size group, wild and hatchery fish include Chinook and Coho salmon and steelhead trout, and invertebrates include Plecopterans and Ephemeropterans.

Parameter		Mean	Standard Error
	Population	1,579	152.6
	Annual Mortality	0.417	0.025
Size at age	2	20.00	2.40
	3	33.99	4.74
	4	40.59	4.03
	5	46.96	4.52
	6	53.21	4.66
	7	56.61	5.10
	8	62.82	5.17
	9	66.00	4.86
	10	69.00	4.86
	11	72.00	4.60
	12	75.00	4.60
Growth Rate	L_∞	90.599	2.900
	K	0.14117	0.009
	t_o	-0.20621	0.055
Prey Proportions	G1_ammocoete	0.069	0.063
	G2_ammocoete	0.111	0.091
	G3_ammocoete	0.056	0.053
	G4_ammocoete	0.047	0.046
	G5_ammocoete	0.039	0.036
	G1_hatchery fish	0.219	0.044
	G2_hatchery fish	0.334	0.051
	G3_hatchery fish	0.487	0.038
	G4_hatchery fish	0.659	0.032
	G5_hatchery fish	0.820	0.034
	G1_invertebrate	0.594	0.129
	G2_ invertebrate	0.378	0.130
	G3_ invertebrate	0.350	0.101
	G4_ invertebrate	0.212	0.075
	G5_ invertebrate	0.089	0.043
	G1_wild fish	0.117	0.128
	G2_wild fish	0.177	0.169
	G3_wild fish	0.107	0.114
	G4_wild fish	0.081	0.080
	G5_wild fish	0.052	0.047

Additional input data required in order to estimate consumption included mean daily temperature and prey-specific energy density. The temperature fish experienced was determined using linear interpolation of the mean daily temperature between available U.S Geological Survey gauge stations (ID numbers 11525500, 11525655, 11525854, and 11526400). The temperature profiles used in the energetics model were that of the midpoint of each reach from March 1, 2015 through February 28, 2016 (Figure 5). Applying the temperature profile of a single reach to a Brown Trout for the entire year is reasonable based on the lack of movement found through the recaptures during this study and the unpublished results of a radio telemetry study conducted by the Hoopa Tribe. The prey energy densities were literature values (Table 4), except ammocoete energy density was measured as part of this study (

Appendix B). Temperature and prey energy density were not randomized as part of the bootstrap.

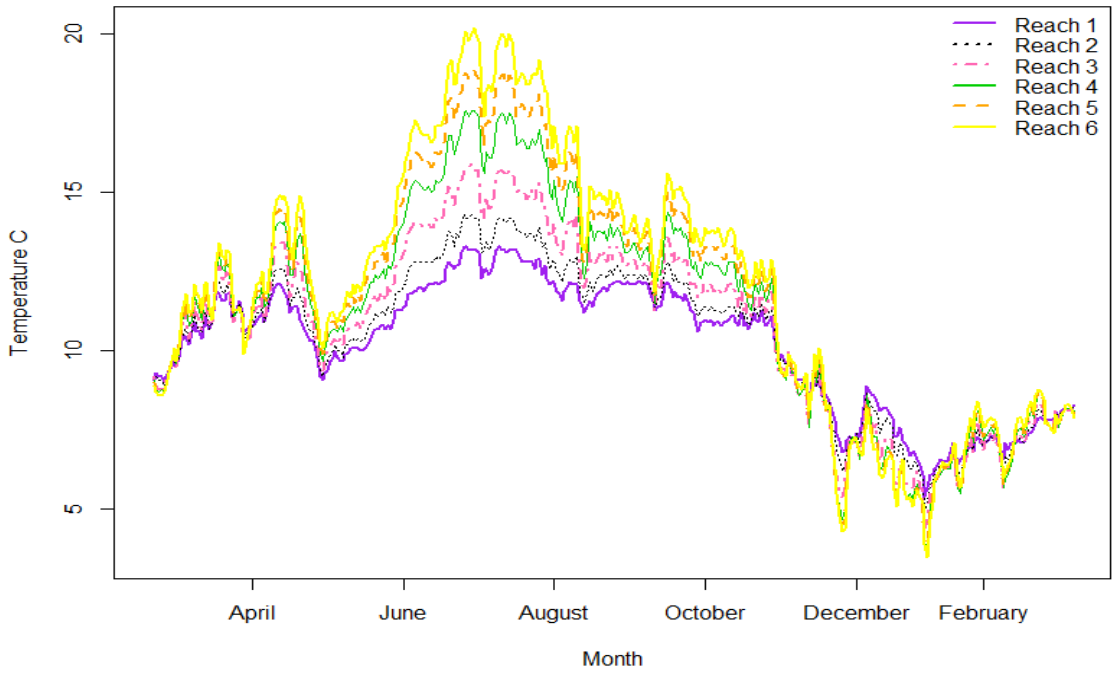

Figure 5. Temperature profiles of each reach where Reach 1 is the furthest upstream and Reach 6 is the furthest downstream. The colors of the lines match the color of reach in the site map.

Table 4. Brown Trout Prey energy densities used to convert Brown Trout energy needs to prey biomass in the bootstrapping simulation. The prey fish category is the energy density of Chinook and Coho salmon between 15 and 25g.

Prey	Wet Weight Energy Density (kJ/g)	Source
Invertebrates	4.07	Groot (1995) Kennedy (2016)
Lamprey	3.542	This study
Fish	5.78	Hansen et al. (1997)

The simulation starts with a random draw of starting size for a single Brown Trout of each age, ages two through twelve. For each of those eleven fish, a growth curve is drawn and used to calculate size after one year (Figure 6). An optimization function (optim in R, R Development Core Team 2009) is then used to find the proportion of maximum consumption which will achieve the desired growth within each reach for each fish. During that growth, daily consumption was summed into five bins based on the Brown Trout fork length bins mentioned in the isotope section. Next, a random draw of population size and survival rate were used to find the number of fish of each age. The number of fish alive on each day within the appropriate reach and of the appropriate age was used to expand the individual Brown Trout daily consumption estimates to the sub population level. This process was repeated 3,000 times to characterize the variation in consumption given different growth rates, and to account for the error associated with population and survival estimates, but does not include variation associated with process error for bioenergetics parameters taken from the literature. The result of these runs is an estimate of the total biomass of food with the energy density of Brown Trout that is consumed by size class.

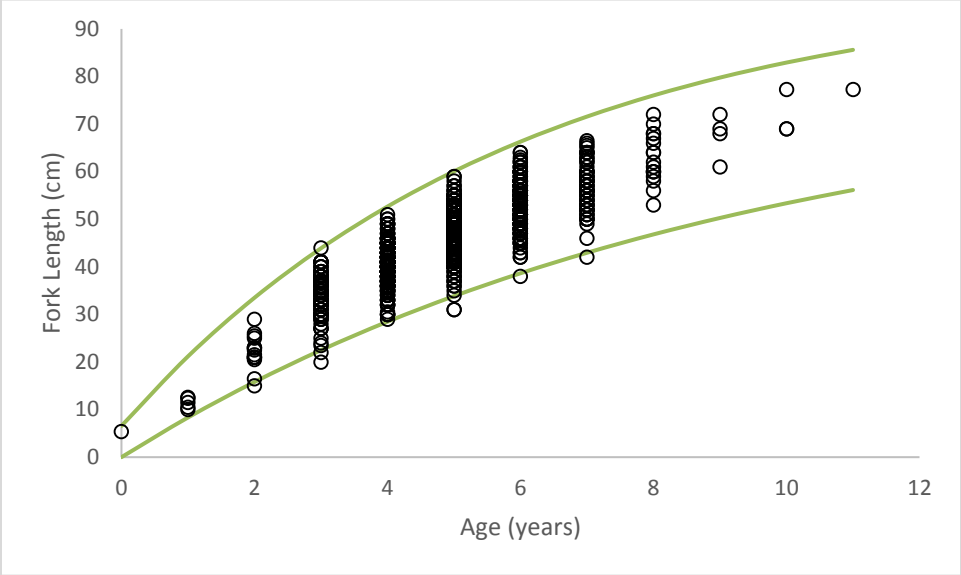

Figure 6. Brown Trout growth rates within the energetics simulation followed a randomly selected Von Bertalanffy growth curve which fell between the green lines. The parameters were selected from a normal distribution so there is a higher probability of a selected curve being closer to the center than the green boundaries.

Diet proportion, predator and prey energy densities, and the estimate of consumption from the simulation can be combined to find the biomass of each prey category consumed by Brown Trout. For this portion of the analysis, the posterior distribution from the isotopic analysis is treated as a parametric bootstrap which can be pulled from with a multinomial random draw. A random multinomial draw of consumption by the five bins is combined with a draw of prey proportion and energy densities in the equation

$$B = \frac{E}{A*E_A+H*E_H+W*E_W+I*E_I}$$

where B is the total biomass consumed and E is the total energy required. The symbols A, H, W, and I are the proportion ammocoetes, hatchery fish, wild fish, and invertebrates

contribute to total biomass consumed, respectively. E_x is the energy density of the same prey category represented by the proportion symbol. The resulting biomass combined with the random draw of proportions provides the biomass of each prey type consumed by the population for a single iteration. This process is repeated 100,000 times to ensure multiple combinations of proportion and consumption estimates.

RESULTS

Population Estimate

In March of 2015, the estimated abundance of Brown Trout in the surveyed section of the Trinity River was 1579 (95% CI 1279-1878). In 2016, the estimated abundance was 516 and 375 in February and April respectively (95% CI 237-793 and 132-618).

The estimated population decrease over the course of that year could be reflective of some level of actual population decrease; however, it was apparent that neither 2016 survey was as complete as the one conducted in 2015. For example, in February 2016, almost no large Brown Trout were caught, but in April 2016 the large Brown Trout in the upstream reaches reappeared. Despite the reappearance of large Brown Trout, the total number of Brown Trout encountered still dropped from February to April. These observations make it clear that the population is not closed between sampling occasions, but within the sampling occasions the closure assumption still seems valid.

Age Analysis

Brown trout scales revealed a maximum age of 11 years among sampled fish without regenerated scales. The fish generally exhibited the largest increase in scale size during the third or fourth year of life. For some individuals, growth was rapid and constant from a very small size, but this was only observed in a handful of fish. The

length at age model is shown in Figure 7 (residual standard error = 4.461 on 1205 degrees of freedom). The modeled relationship is described by

$L = 90.60\left(1 - e^{-0.14(t+0.21)}\right)$.

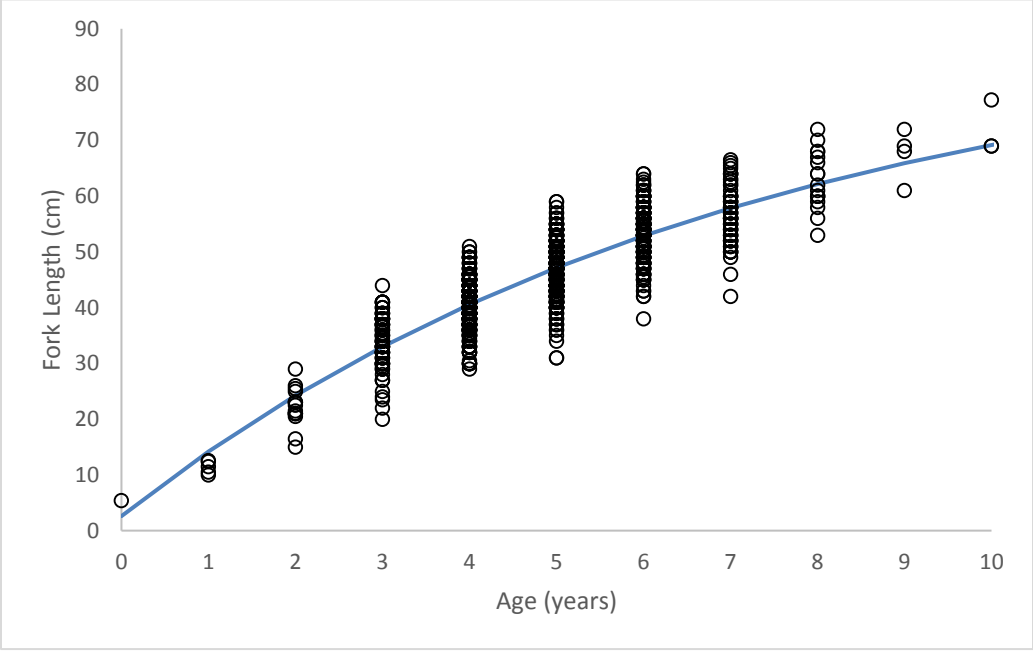

Figure 7. Von Bertalanffy growth model fit to Brown Trout from the Trinity River, CA. Fish came from four sources, an Alaskan style weir, a rotary screw trap, electrofishing, and hook and line sampling.

The comparison of model-predicted growth in length with observed growth in length was derived from individuals recaptured over multiple samples at the weir or via electrofishing. Despite the small sample size, the data was gathered from samples collected over seven years. Comparing observed and predicted values showed that there is much variation around the fitted model and that, for many of these fish, the model over predicted the amount of growth over the course of a year and under predicted growth in

the shorter window during the spring (Figure 8). These deviations may indicate that there is a strong seasonal growth pattern for Brown Trout in the Trinity River, with most gains in length occurring during a short period in the spring.

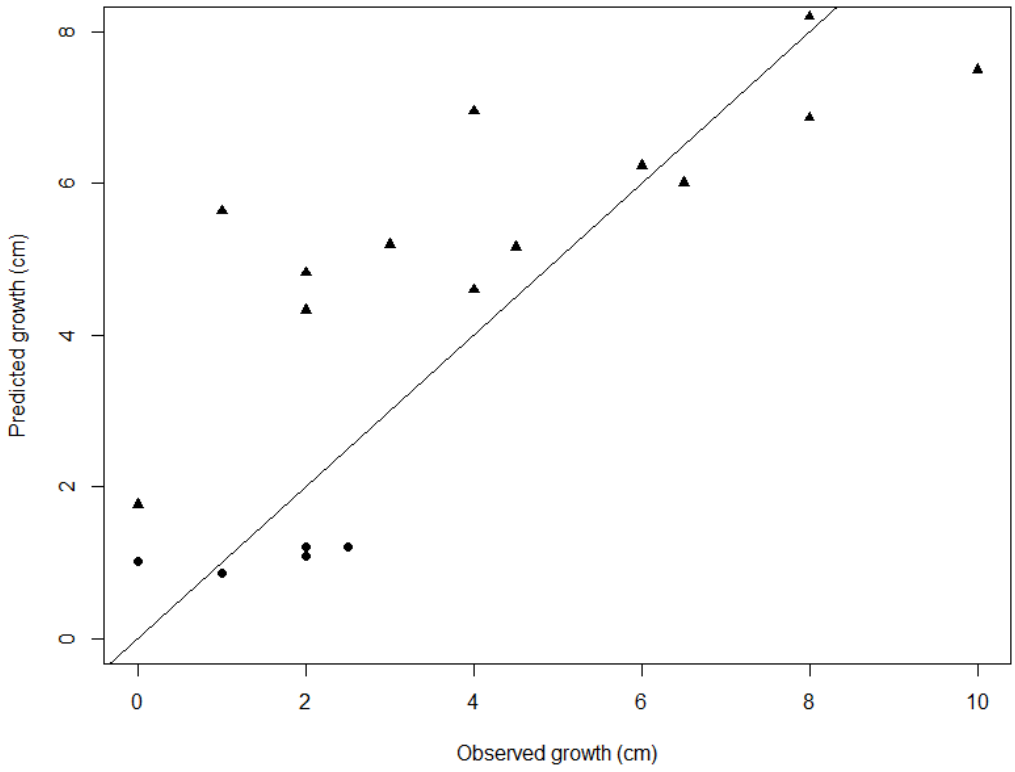

Figure 8. The amount of growth observed in Brown Trout of varying sizes with durations between two and 13 months . The circles represent fish recaptured after two months and the triangle represent fish recaptured after a year. The growth of fish captured more than twice (n=2) have a point for each recapture. The points for these two fish represent the growth from initial capture to first recapture and then growth from the first recapture to the second recapture. This plot includes fish from 2010 to 2016 and are sourced from the Junction City weir as well as from electrofishing.

Annual Survival Analysis

Based on the Chapman-Robson equation, the total annual survival is close to 55%. The estimates for the years analyzed ranged from 30.6% to 57.9% (SE ranged from 0.1 to 0.024 Table 5). Assumptions of the survival estimator vary depending on how the data are summarized. The estimates from a single cohort do not require an assumption of constant recruitment which is beneficial because there is not data to test that assumption. The cohort tracking using weir data represents survival of the fish that move upstream from June through September; however, the sample size for these estimates is small and a large portion of the population not represented. The electrofishing data requires the constant recruitment assumption but it covers the whole upper river. Given the larger sample size and more complete geographic range of the electrofishing samples a survival rate of 58.3%, the average of the 2015 and 2016 electrofishing estimates, was used in the energetics simulation.

Table 5. Brown Trout survival estimates from various data sources through time. Weir age data is evaluated two ways: first, within a single year; and second, tracking a cohort through time. The year referenced in the cohort tracking is the year in which the cohort was age 3 (The first year the fish are trapped in the Junction City weir (JCW)).

Source	Year	S	Standard Error	n
JCW Single Year	2008	0.4167	0.058	23
	2009	0.3913	0.104	6
	2010	0.3248	0.037	41
	2011	0.3603	0.041	41
	2012	0.4095	0.048	34
	2013	0.3623	0.033	51
	2014	0.4087	0.035	68
	2015	0.5794	0.048	22
E-Fish	2015	0.5122	0.024	201
	2016	0.6547	0.024	126
JCW Single Cohort	2008	0.3333	0.058	13
	2009	0.4393	0.035	55
	2010	0.5326	0.032	76
	2011	0.3057	0.033	56

Biometric Analysis

Brown Trout in the Trinity River increase their length to weight ratio as they grow. The relationship between length and mass can be described using $W = -10.89 * L^{2.86}$ (Figure 9). Differences in the length-weight relationship based on sex, age and sample year were investigated but no patterns emerged.

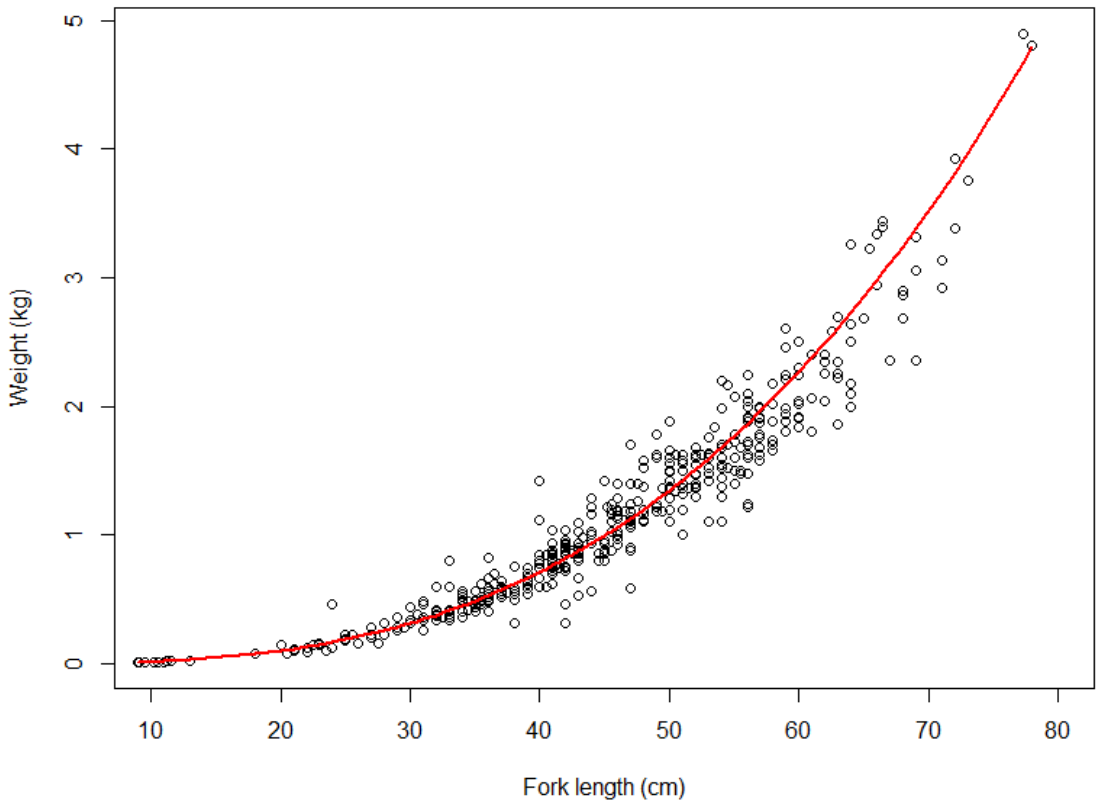

Figure 9. Trinity River Brown Trout length to weight data fit with an allometric growth curve using multiplicative error. The measurements came from angling, electrofishing, and weir sampling.

Diet analysis

Brown Trout isotopes δN15 and δC13 levels ranged from 8.4 to 16.3 and -27.0 to -16.7, respectively. Most wild prey had similar isotopic signatures with relatively low δN15 and δC13, while hatchery fish had higher values. Brown Trout isotope values were spread between those two prey groupings (Figure 10). The MCMC chains did converge

with all parameters having R̂ values of less than 1.01. The value needed to proceed with inference is an R̂ less than 1.05 (Stock and Semmens 2013). The data show that the larger Brown Trout have a higher proportion of fish, especially hatchery fish, in their diet than smaller Brown Trout (Figure 11).

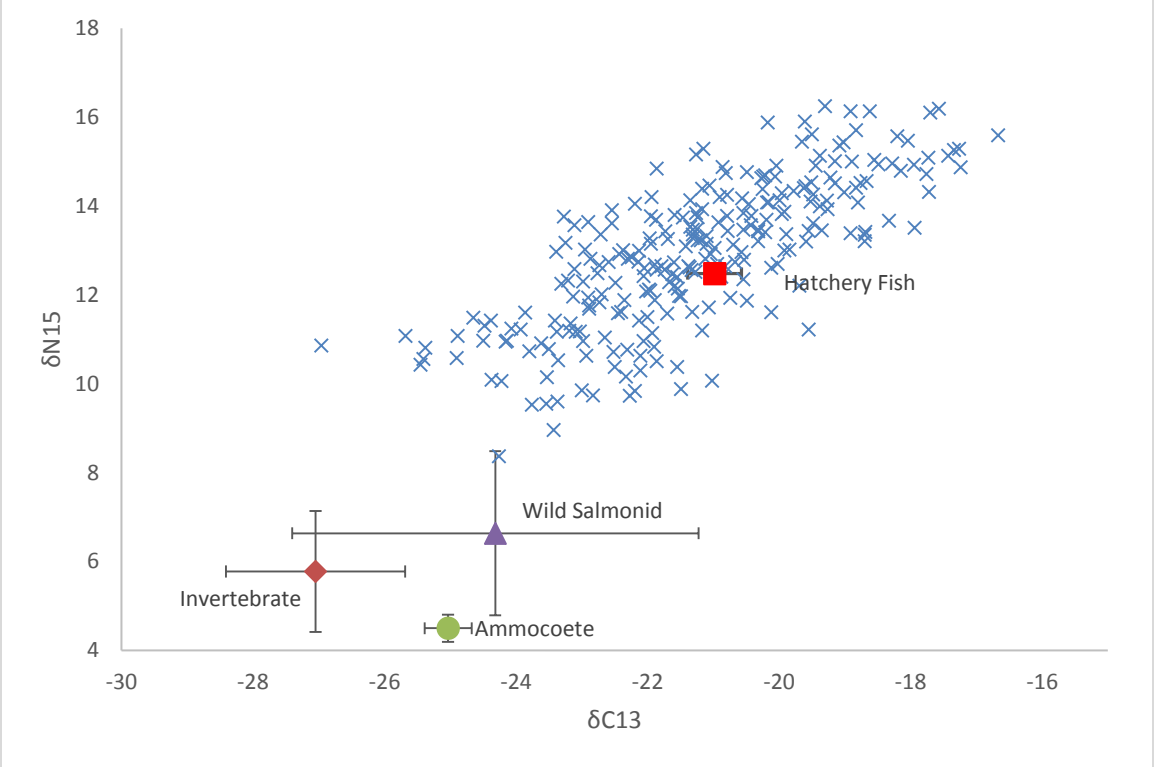

Figure 10. Isoplot of Brown Trout and prey items. Blue x's represent individual Brown Trout isotope ratios. Prey items are labeled and the location is the mean value for that prey category. The error bars are a single standard deviation. These were not adjusted for fractionation rates.

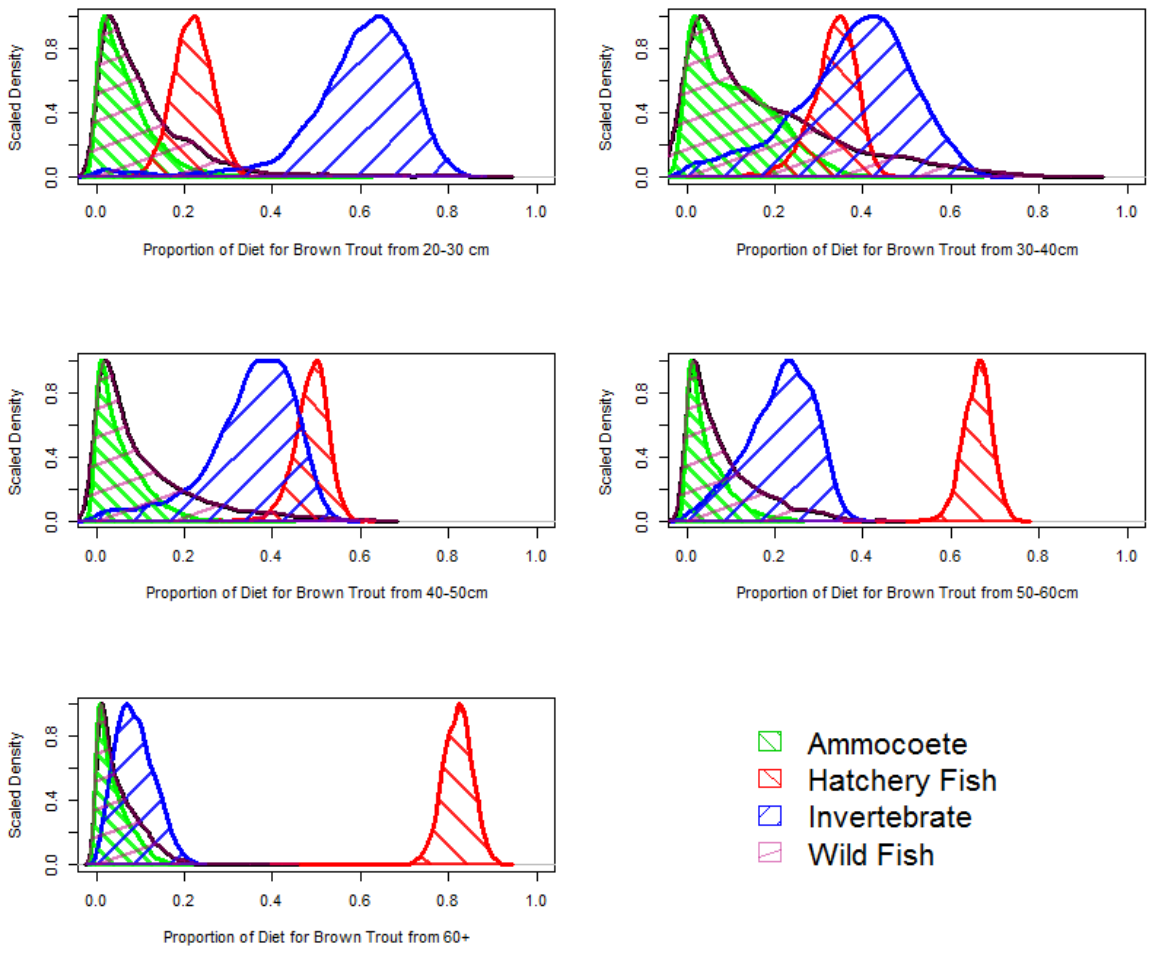

Figure 11. Diet proportions of Brown Trout grouped by fork length. The number of Brown Trout isotope samples that went into the analysis for each size bin starting with the 20 to 30 cm fish and then continuing with the next larger Brown Trout size category are 19, 60, 83, 61, and 30.

The results of the isotopic analysis show a similar level of piscivory compared to the snapshot view of the lavage (Table 6). Gastric lavage lacks the full temporal scale of the isotope analysis and is not as effective at parsing out wild and hatchery fish. The lavage did inform the families of insects to include when summarizing energy densities in later analysis and lent insight into possible species composition of wild fish consumed.

Of the wild fish retrieved during lavage, Coho salmon were the most common identifiable fish (n=36), steelhead were next most common (n=16) and Chinook salmon were least common (n=5). There were additional fish which were not identifiable to a single species but based on size and time of year I could narrow these fish to two of the three salmonids. The larger fish were either age 1+ Coho salmon or steelhead trout (n=73) and the smaller fry sized fish were either Chinook or Coho salmon (n=14).

Table 6. 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.

	% Fish		% Invertebrate	
Brown Trout cm	Lavage	Isotope	Lavage	Isotope
20-30	8%	38%	92%	62%
30-40	26%	60%	74%	40%
40-50	83%	63%	17%	37%
50-60	82%	78%	18%	22%
>60	98%	92%	2%	8%

Bioenergetics

The energetics simulation predicted that the Brown Trout population needed 58,382 mega joules (se= 9,719; 95% CI 39,334 to 77,432) of energy per year (Figure 12). Variation in growth rate accounted for most of the dispersion around the consumption estimates. The variable population size and survival rate added additional variation around the consumption estimate, but this variation was almost inconsequential when compared to differences from growth. When energy was converted into prey biomass by

category, the most-consumed prey item was hatchery fish, followed by invertebrates, wild fish, and last, ammocoetes (Figure 13).

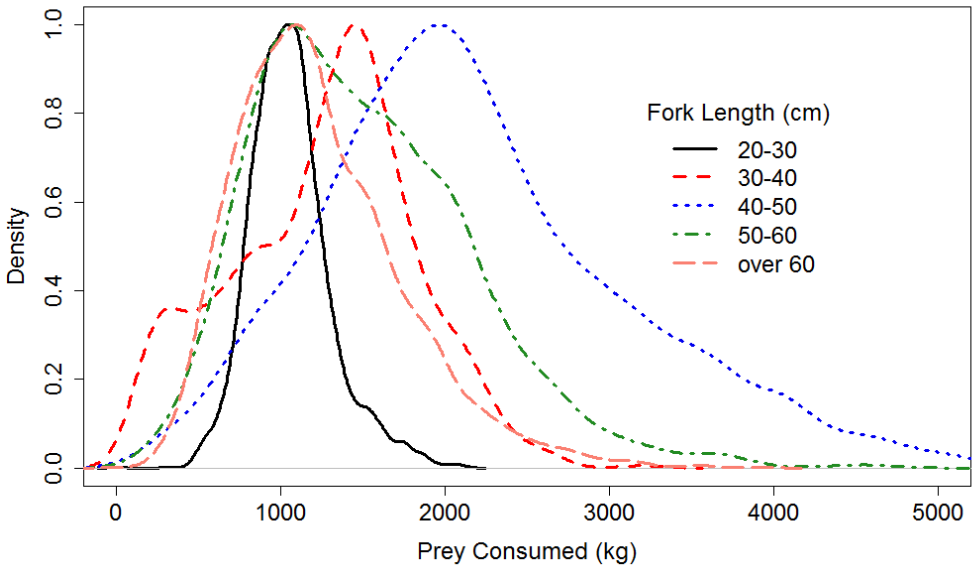

Figure 12. This plot illustrates the distribution of the 3,000 bioenergetics simulation results. Each line represents the estimates of energy required by each size category of Trinity River Brown Trout given varying starting sizes, growth and mortality rates. Energy is expressed in kilograms of prey assuming that the prey matches the energy density of the predator, Brown Trout.

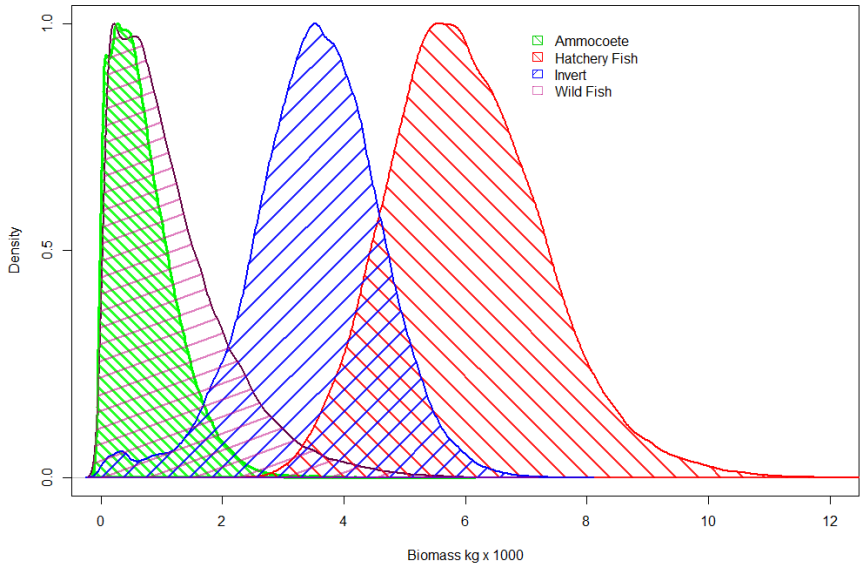

Figure 13. Biomass of prey consumed by Brown Trout in the Trinity River over the course of a year. Brown Trout primarily ate hatchery fish with a median estimate of 5,930 kg (95% CI 3,800 to 8,805 kg). The next most abundant prey was invertebrates with a median value of 3,566 kg (95% CI 1,279 to 5,524 kg). The third prey type in order of amount was wild fish with a median estimate of 924 kg (95% CI 60 to 3,526 kg). The least consumed prey was ammocoetes at an estimated 598 kg (95% CI 18 to 2,058 kg).

DISCUSSION

Based on this analysis, predation by Brown Trout poses a potential impediment to the recovery of native salmonids in the Trinity River. To put the consumption results in context, the estimate of hatchery fish biomass consumed within the simulated year is about 6000 kg (95% CI 3,800 to 8,800 kg), which is about seven percent of what was released from Trinity River Hatchery in 2015. The mean estimate of wild fish consumption is just under 1000 kg (95% CI 60 to 3500 kg). The biomass of juvenile wild fish in the upper Trinity River in 2015 is unknown, but based on the mean weekly size and abundance estimates of wild salmon at the screw trap at the downstream end of the study reach, about 4000 kg of wild fish migrate out of the upper Trinity River annually.

While the estimates of consumption suggest that Brown Trout could suppress Trinity River salmon populations, translating consumption into mortality rates and estimating the population effect is difficult. If we were to make the unlikely assumption that every fish consumed by Brown Trout would have survived their journey out of the 64 km below the dam, then based on the 1,000 kg consumption of wild fish by Brown Trout and 4,000 kg outmigration estimate, we would naively say that 20% of those fish were consumed by Brown Trout. However, there are a host of caveats to this 20% estimate. First, only 25% of hatchery Chinook salmon are marked as hatchery fish; these large, unmarked hatchery chinook inflate the size estimate for outmigrants, so the trap estimate of wild out migrant biomass is biased high. This bias in the outmigration estimate makes our naïve estimate of predation rate biased low. Second, it is unlikely

that all of the wild fish consumed by Brown Trout would have otherwise survived, as some level of compensatory mortality is certain (Ward and Hvidsten 2011). The fish being trapped are out-migrating, but Brown Trout consume fish as they rear and as they out-migrate. All rearing fish would not survive to leave the system even without Brown Trout predation. The extended period of predation makes the naïve estimate of predation rate biased high. Third, there is error around the screw trap population estimate and this method only looks at means. Despite these caveats, I argue that a substantial portion of the wild production was consumed by Brown Trout in 2015.

Based on the records of Brown Trout abundance and size from the 1950's and 60's, if we had done this study during that time we would have reached a different result. At that point, Brown Trout populations were small and so were the individual fish. Most records from before 1970 mention Brown Trout in the 30 to 50 cm range compared to catches in 2015 and 2016 exceeding 70 cm. Creel surveys and weir counts prior to 1970 refer to catches of less than ten per year compared to 2-5 per day in recent years (Moffett and Smith 1950; Rodgers 1973). While expansion from catch to abundance is problematic, the catches are probably indicative of a population in the high hundreds. Also at that point, Chinook and Coho salmon and steelhead trout were more abundant. Given these two factors, Brown Trout would have been swamped by prey and it is unlikely their removal would have had a population level effect on the native salmonids. However, as the native fish populations decrease and the Brown Trout increase, we will reach a tipping point where Brown Trout eat such a large proportion of the native juveniles that they prevent the recovery of the native fishes; and the results of this study

are the strongest indicators that we had reached that point in or before 2015. Of course, only looking at 2015 provides too simple an assessment. As sampling continued into 2016 and 2017 (2017 is not included in this study) the Brown Trout population seems to have dropped, and with fewer Brown Trout the impact to their prey would be reduced as well. Despite the decrease, this study has shown that Trinity River Brown Trout have realized their capacity to exist at levels high enough to consume a substantial proportion of native salmonid production. If weir catch per unit effort is a good index to overall population size, then 2014 could have had twice as many Brown Trout as 2015 and earlier years could have been even higher (Figure 14).

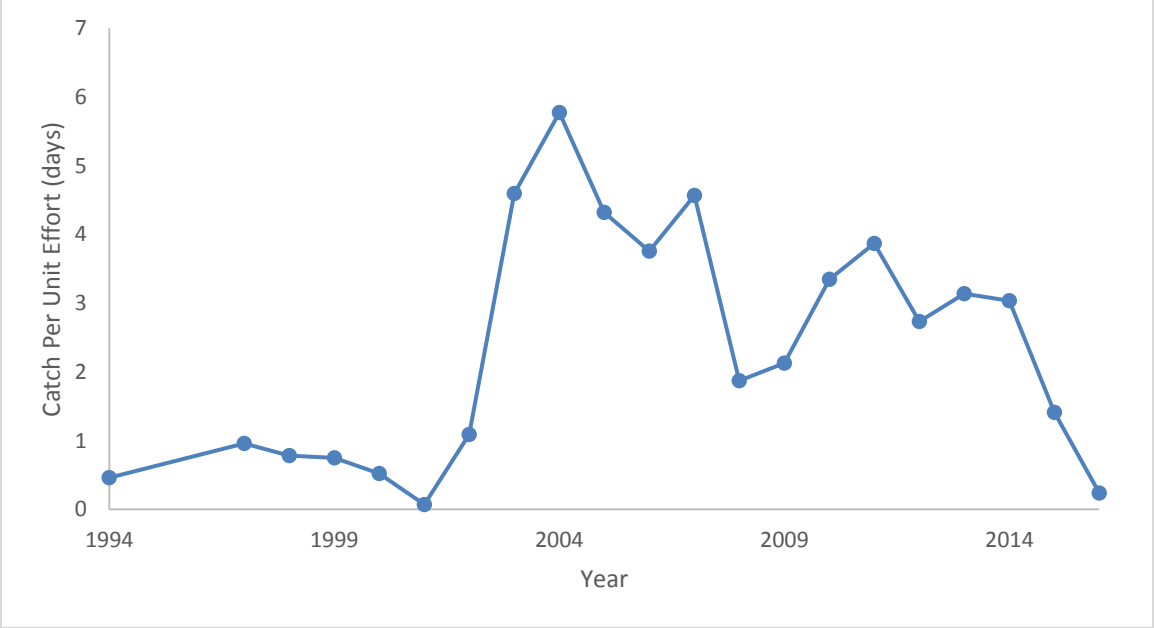

Figure 14. Mean Brown Trout catch per sample day at the weir in Junction City, CA. Population estimates were calculated within this study in 2015 and 2016.

Causes of the observed decrease in Brown Trout abundance between the 2015 and 2016 sampling are unknown. There are four plausible explanations that warrant

mentioning. First, seasonal abundance and movement patterns suggest that Brown Trout may aggregate in the Upper Trinity River in March in anticipation of hatchery fish releases. March 15th has been the release date for steelhead trout and Coho Salmon for many years. Lower abundance in February and April may reflect less aggregation in the study reach below the hatchery during these months. Secondly, 2015 and 2016 had the highest number of Klamath River Lamprey observations in recent memory. Klamath River Lamprey are lifetime freshwater residents and they parasitize fish in the Trinity River. On multiple occasions, we found Brown Trout and Klamath small scale suckers with lamprey wounds, including some with holes all the way through their stomach wall. Many of these Brown Trout with lamprey wounds were found dead throughout the summer. Lamprey parasitism may have contributed to a decline in Brown Trout abundance. Third, the multi-year drought in California affected the water levels in Trinity Lake. The upper reaches of the Trinity River below the dams are generally clear, but due to the low lake levels the water was very turbid in 2016. Other studies have found that increased turbidity caused fish to change foraging strategies and spend more time searching for food instead of drift feeding. This increased their energy output and caused growth rates to be less than would otherwise have been predicted (Sweka and Hartman 2001). This decrease in energy intake could be translated into mortality if the energy demands were only barely being met under the usual clear conditions. Last, Brown Trout recruitment appears to have declined since 2015. In order to maintain the population with an annual survival rate of less than 60%, recruitment would need to be high. In 2015 we caught hundreds of age 1+ Brown Trout and some two year old fish. In

subsequent years, catches of smaller fish were rare. In 2016, few fish under 30cm were caught and in 2017 few fish were under 40 cm. In both years, less than 50 1+ Brown Trout were caught.

One consideration arising from this analysis is the potential indirect effect of the hatchery supplementation program on wild salmon mediated by Brown Trout. My bioenergetics analysis indicates that most of the Brown Trout biomass is derived from consumption of hatchery fish. This artificial subsidy likely allows the Brown Trout to maintain elevated population levels and larger size than would otherwise exist within the river. These larger and more abundant Brown Trout must still eat during the majority of the year when hatchery fish are not available, potentially putting an increased burden on the wild population to sustain the elevated energy needs of the Brown Trout population. The Trinity River Hatchery did not exist until the dams were completed in 1964. The subsequent increase in Brown Trout size and abundance (Moffett and Smith 1950; Rodgers 1973) gives some credence to the notion that hatchery supplementation is at least one contributor to the current Brown Trout population, although riverine habitat restoration and increased flows probably contribute as well.

When considering next steps for Brown Trout management, one argument is that we have passed the point of being concerned about what was natural, and that we should just manage fisheries with the fish that are doing well in a system (Moyle et al. 2012). In my opinion, in some systems, a native assemblage of fishes is no longer obtainable, but in this particular drainage I do not believe that is the case. There is still a mostly native

species composition in the Trinity River, with few exotic fishes. This seems like one of the instances in which the river could have its native fish assemblage restored.

A bioenergetics simulation, parameterized with field data, provides a logical framework to understand the caloric requirements of the Trinity River Brown Trout population and how they achieve those needs. Like any model, it is an imperfect representation of what is happening in the real world, but this model does lend insight into the system and the associated error has been characterized to quantify how much confidence to put in the results. When considering the predicted energy requirements, it should be noted that this model did not account for the creation and loss of gamete mass. Not accounting for this component makes our total consumption estimates biased low. An additional consideration is that, within the isotopic analysis, the similar isotopic composition of invertebrates and wild fish causes uncertainty in the mixing model. So, while the sum of those two categories is well-constrained, the individual contributions of invertebrates and wild fish to the diet could be different than estimated. Given that the model already predicts much higher invertebrate consumption than wild fish consumption, the amount of wild salmonid biomass being consumed is not likely to be any lower than what is presented here.

RECOMMENDATIONS

Based on seasonal consumption, growth, and diet estimates, it is likely that hatchery-released fish subsidize the Brown Trout population to the detriment of the wild salmon population. If we want to ameliorate the effect of Brown Trout on native fishes, then to reduce this subsidy, hatchery managers should consider measures to decrease in river residency time of hatchery fish and potentially combine releases to allow swamping of the Brown Trout's consumption capacity. Without the added calories throughout the year, the Brown Trout population may remain at a lower level and would be comprised of smaller fish with lower metabolic needs. Additionally, removing Brown Trout captured through any sampling effort or caught by anglers, in combination with periodic electrofishing specifically targeting Brown Trout should keep the population low and the size of those fish small. Ongoing removals to control the population could limit the ability of Brown Trout to have any meaningful impact on other fishes.

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APPENDIX A

Appendix A. Fractionation rates found in scientific literature from which the mean and standard deviation were derived to feed the model fit in the isotopic analysis of Brown Trout diet.

	δN15		δC13		
Species	mean	SD	mean	SD	source
Rainbow Trout	3.8	0.255	1.7	0.153	Flinders 2012
Rainbow Trout	3.2	0.2	1.9	0.51	McCutchan 2003
Bull Trout	3.8	0.17	3.3	0.29	McCutchan 2003
Lake Trout	3.49	0.23	0.05	0.63	Vander Zanden 2001
Aquatic Consumers	3.4				Minagawa and Wada 1984
Aquatic Consumers	3.42	0.99	0.4	1.3	Post 2002
Fishes	3.4	0.3	0.9	1.1	Vander Zanden 1997 and Harvey 2001
Brook Trout large	4.7		0.8		Peterson and Howarth 1987
Brook Trout small	4.4		2		Peterson and Howarth 1987

APPENDIX B

Pacific Lamprey Ammocoete Energy Density Methods

Estimates of energy density of prey items are required for bioenergetics models. Previous studies contained energy density estimates for most of the prey items I encountered, but energy density of Pacific Lamprey ammocoetes was not readily available in the scientific literature. Information exists for adult sea lamprey, but given the difference in size, foraging style, and habitat, adult estimates seemed a poor substitute for ammocoete energy density. Ammocoetes were collected by the Hoopa Tribal Fisheries Program from the Trinity River using a rotary screw trap in the bottom most reach of my study area. The ammocoetes were measured (total length), weighed, and then dried in an oven at 65^{o}C for 60 hours. The dried ammocoetes were then weighed again to find the dry to wet mass ratio. Dry ammocoetes were ground into a powder and a one gram sample was combusted in a Parr 1241 Oxygen Bomb Calorimeter (Parr Instrument Company, Moline, IL). The one gram sample included two ammocoetes from the isotope analysis in order to obtain a full gram of ammocoete powder. These ammocoetes were never weighed and so are not included in the calculation of percent dry mass. Fuse wire with energy density 5.8576 kJ/g was used to ignite the ammocoete powder. The bomb once loaded with fish fuel and fuse had 25 atm of oxygen pumped into it. This was placed into the calorimeter bucket filled with 2 kg of water. Once ignited the temperature of the water surrounding the bomb was monitored until the

temperature became stable to 0.001 degrees for more than 30 seconds. Temperature difference before ignition and after stable were plugged into the formula

$$E = \frac{Q}{m_{fuel}} = \frac{C(T_f - T_i)}{m_{fuel}}$$

where Q is the heat released (MJ), E is the energy content of the fuel (MJ kg^{-1}), m_{fuel} is the mass of fuel consumed (kg), C is the calorimeter calibration constant ($1.008x10^{-2}$ MJ K^{-1}) and T_i and T_f are the temperatures of the reservoir before and after ammocoete combustion. The energy from fuse wire consumption was subtracted from the total energy.

The energy density of dry ammocoete was converted to wet weight energy using the wet to dry mass ratio. The resulting wet weight energy density was used in subsequent analysis to convert from energy consumed to biomass consumed by Brown Trout.

Pacific Lamprey Ammocoete Energy Density Results

The bombing of dried ammocoete provided a dry mass energy density of 25.23 kJ/g. The mean value of percent dry weight for ammocoetes was 14% giving a wet mass energy density of 3.53 kJ/g (

Appendix B). For comparison the value for adult sea lamprey provided in the Wisconsin Bioenergetics guide is 5.124 kJ/g.

Appendix B. Total length, wet mass and dry mass of Pacific lamprey ammocoetes used to find energy density.

Ammocoete	Length (mm)	Wet Mass (g)	Dry Mass (g)	% Dry matter
1	43	0.15	0.015	10%
2	86	0.9441	0.1553	16%
3	83	0.7828	0.1464	19%
4	31	0.0599	0.0053	9%
5	76	0.636	0.0967	15%
6	39	0.0986	0.0122	12%

APPENDIX C

Appendix C. Table of Brown Trout carbon and nitrogen isotope values

Sample ID	d13C	d15N	Sample ID	d13C	d15N
1	-19.65	15.45	132	-20.67	12.74
3	-20.57	12.96	133	-20.16	14.09
4	-19.51	14.53	135	-22.95	13.02
8	-21.94	14.20	136	-20.42	13.78
10	-18.33	13.67	137	-23.25	13.17
13	-18.91	13.39	138	-18.49	14.94
15	-21.27	12.52	140	-17.73	15.09
19	-23.39	12.97	141	-20.49	11.87
20	-23.41	11.42	142	-22.59	12.74
31	-21.59	12.20	143	-24.89	11.08
38	-22.52	10.72	144	-24.50	10.97
52	-20.56	14.17	145	-20.04	14.91
53	-22.54	13.91	148	-21.31	13.28
69	-18.80	14.08	149	-20.18	14.08
73	-23.17	11.36	150	-20.21	14.69
74	-20.25	14.38	503	-23.93	11.22
75	-21.31	13.47	505	-20.90	14.20
76	-19.01	14.31	506	-21.17	14.39
84	-21.73	13.43	507	-21.54	12.14
85	-23.38	11.17	508	-23.00	9.85
95	-23.03	11.18	509	-22.76	12.49
101	-20.24	14.66	510	-21.89	11.88
103	-21.42	13.09	511	-19.55	11.22
107	-19.84	13.02	512	-20.53	12.79
109	-24.48	11.31	513	-21.36	12.62
111	-20.06	14.66	514	-20.74	11.93
113	-17.72	14.32	516	-21.69	13.26
118	-18.69	13.42	518	-21.25	13.48
119	-22.24	12.85	519	-20.17	15.88
120	-17.43	15.13	520	-21.87	13.69
122	-24.22	10.06	521	-22.30	12.81
124	-21.31	13.36	522	-22.54	13.61
129	-19.26	13.93	524	-18.28	14.96
130	-19.61	15.90	525	-19.15	14.51
131	-20.21	13.41	526	-19.35	13.45
529	-18.04	15.47	1159	-20.78	13.44

Sample ID	d13C	d15N	Sample ID	d13C	d15N
530	-22.45	11.59	1162	-22.43	12.92
531	-25.41	10.56	1163	-23.11	12.58
532	-26.96	10.86	1164	-19.55	13.44
534	-24.16	10.95	1166	-20.02	12.70
539	-22.71	13.36	1168	-21.95	13.15
541	-21.12	12.81	1170	-18.76	14.52
542	-22.49	12.27	1172	-22.05	12.60
543	-21.74	12.57	1176	-19.38	13.99
545	-21.95	13.77	1177	-20.94	12.70
576	-22.90	13.64	1178	-22.50	10.38
578	-20.92	13.63	1179	-21.33	12.56
579	-21.89	12.68	1180	-22.73	11.83
582	-21.19	13.23	1181	-19.59	13.20
583	-22.14	12.75	1191	-23.53	10.15
584	-20.98	13.06	1200	-20.32	13.47
585	-22.37	13.01	1252	-22.33	10.16
586	-23.13	11.96	1253	-21.90	10.83
587	-20.88	12.41	1255	-21.49	9.88
588	-21.04	12.92	1258	-19.69	12.21
589	-19.89	13.37	1261	-23.36	10.53
590	-22.73	12.67	1262	-21.55	12.40
593	-20.54	12.35	1263	-21.38	12.65
1006	-25.45	10.43	1264	-20.12	11.61
1014	-20.54	13.47	1267	-22.98	10.96
1018	-22.70	12.01	1268	-22.11	10.63
1025	-24.65	11.49	1269	-22.65	11.04
1047	-22.98	12.30	1276	-22.11	10.30
1058	-19.02	15.43	1277	-22.13	11.42
1063	-20.82	12.65	1280	-23.43	8.96
1076	-20.79	14.25	1281	-23.37	9.60
1117	-24.07	11.24	1282	-21.02	10.07
1140	-21.59	13.80	1283	-17.94	13.51
1141	-19.22	14.64	1313	-21.10	13.32
1146	-23.27	13.76	1351	-21.60	12.73
1147	-22.02	12.08	1376	-21.93	11.14
1148	-23.21	12.32	1377	-19.92	13.87
1149	-22.89	11.76	1401	-21.79	12.65
1150	-23.86	11.60	1418	-19.96	13.82
1154	-20.43	13.57	1421	-18.67	14.56
1157	-24.90	10.58	1423	-21.17	13.93

Sample ID	d13C	d15N	Sample ID	d13C	d15N
1424	-20.79	13.78	1661	-22.35	11.88
1425	-21.86	12.57	1662	-21.70	11.58
1427	-20.12	12.61	1726	-19.08	15.36
1429	-21.52	11.98	1727	-20.86	14.88
1437	-20.19	13.69	1728	-18.83	15.71
1445	-19.60	14.45	1729	-19.27	14.12
1542	-21.24	13.23	1730	-17.70	16.10
1544	-17.95	14.93	1731	-21.26	15.16
1545	-19.92	13.00	1733	-19.50	15.61
1546	-20.32	13.43	1734	-18.55	15.04
1547	-25.68	11.08	1735	-21.26	13.84
1548	-23.80	10.73	1737	-23.62	10.91
1549	-21.06	14.46	1738	-22.13	12.99
1550	-19.99	14.13	1739	-20.27	14.63
1602	-23.19	11.19	1740	-19.78	14.34
1603	-20.54	13.84	1741	-21.10	13.15
1605	-17.57	16.19	1743	-25.38	10.81
1606	-18.62	16.13	1744	-21.17	11.20
1609	-23.11	13.57	1745	-24.38	11.42
1618	-19.48	13.61	1746	-18.89	15.00
1620	-19.38	15.13	1747	-20.49	14.76
1621	-18.70	13.21	1749	-19.15	15.01
1622	-17.34	15.26	1750	-21.35	13.53
1623	-19.62	14.40	1846	-18.83	14.41
1629	-23.31	12.25	1849	-22.40	11.62
1630	-20.81	14.74	1851	-22.83	9.74
1631	-18.91	16.13	1852	-21.86	10.51
1633	-17.76	14.72	1853	-22.19	9.84
1636	-19.30	16.25	1854	-18.15	14.79
1637	-21.24	13.75	1855	-21.55	10.38
1638	-19.96	14.29	1856	-21.07	11.72
1640	-21.35	14.13	1857	-21.62	12.47
1645	-19.48	14.26	1858	-18.70	13.35
1650	-21.86	14.84	1859	-22.31	10.77
1651	-23.50	10.78	1860	-22.90	11.94
1653	-16.67	15.59	1863	-22.27	9.73
1654	-21.67	12.29	1864	-21.32	11.62
1655	-22.89	11.69	1867	-22.06	10.96
1656	-24.37	10.09	1868	-21.98	12.12
1657	-23.76	9.53	1869	-20.70	13.13

Sample ID	d13C	d15N	Sample ID	d13C	d15N
1659	-22.93	10.63	1871	-23.54	9.55
1872	-22.87	12.81			
1873	-19.44	14.91			
1876	-24.26	8.37			
1877	-24.14	10.97			
1879	-21.49	11.97			
1880	-22.06	12.42			
1883	-21.97	13.27			
1884	-21.96	12.09			
1885	-23.09	11.17			
1886	-19.52	14.10			
10R1	-20.46	14.04			
122a	-22.00	11.50			
1606R2	-17.26	15.29			
1606R3	-17.24	14.87			
1630a	-21.15	15.29			
1687R1	-22.19	14.05			
1733a	-18.20	15.57			
4a	-20.32	13.21			
70 R1	-21.46	13.74			

APPENDIX D

Appendix D. Table of marks and captures during electrofishing passes in 2015 and 2016

	2015			2016			
Pass	1	2	3	4	5	6	7
# Of New Marks	267	234	88	71	50	40	37
# recaptured		57	32	3	11	6	10
Total # Caught that pass	267	291	120	74	61	46	47