

Trout bioenergetics as a process-based tool to estimate ecological risk in a regulated river

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Funding information

Marin Community Foundation; National Fish and Wildlife Foundation

Abstract

Bioenergetics models produce quantitative flow-ecology relationships that summarize changes in habitat and food resources from altered flows. We used a drift-foraging bioenergetics model to quantify the net rate of energetic intake (NREI) for trout above and below a water diversion. NREI is reduced by >95% below the water diversion in July–September, when up to 98% of unimpaired flows are diverted. We then used a risk-based approach to estimate the maximum diversion rate, expressed as a percentage of unimpaired flow, that would produce NREI values that are not significantly lower than values under unimpaired flows throughout a 62-year period. NREI decreased with increased percent-of-flow diversion rates in low-flow months (July–September). Diversion rates of 16% in July and 9% in August and September would maintain NREI within the range of unimpaired flow conditions. In higher flow months, May–June, increasing diversions brought estimated instream flows closer to the peak NREI flow, leading to the assessment that increased diversions would increase NREI. Bioenergetic models can be used to develop protective flow rates at times of the year when fish growth and production would be high under unimpaired flows, which often coincides with when water is diverted. Our study is the first to develop protective percent-of-flow diversion rates for holistic flow management using a quantitative process-based and fish-centric ecological metric.

KEYWORDS

percent-of-flow, holistic flow management, natural flow regime, salmonid, foraging behavior, drift-feeding

1 | INTRODUCTION

The alteration of river hydrology is global and widespread (Nilsson et al., 2005) resulting in sweeping ecological changes within river corridors (Poff & Zimmerman, 2010; Webb et al., 2013). In recent decades, support for water management that balances human and ecological needs has grown (Naiman et al., 2002; Palmer & Ruhí, 2019; Poff et al., 2010; Richter et al., 2003), and will be increasingly important with climate change-driven alterations in precipitation (Dai, 2013). As a result, water managers need defensible evidence to inform complex decision-making processes about how to manage flow regimes in regulated rivers (Stoffels et al., 2018). Modeling frameworks that quantify the effects of flow scenarios (Stoffels et al., 2018), and explicitly consider process-based biological responses (Freeman et al., 2022; Poff et al., 2010; Wheeler et al., 2018) are in demand. Furthermore, there is a need for tools and methods that contextualize quantitative flow-ecology relationships within the range of observed conditions under a natural flow regime, rather than managing for “optimal” flows that maximize a response

Research Impact Statement

This study is the first to develop protective percent-of-flow diversion rates for holistic instream flow management using a drift-foraging bioenergetics model, a quantitative, process-based tool.

variable. These tools will allow managers to shift the question from, how much water do we need in the river, to, how much can we divert without risking ecological harm?

Early approaches to quantifying instream flow needs were grounded in physical metrics intended to approximate biological habitat and were typically formulated as minimum baseflow requirements (Bovee & Milhous, 1978; Grantham & Moyle, 2014; Petts, 2009). More recent approaches have considered functional components of hydrographs to maintain geomorphic and ecological function (Poff et al., 2010; Yarnell et al., 2015, 2020). Holistic instream flow management approaches are designed to protect the shape and function of natural flow regimes by allowing a percent-of-flows (POF) to be diverted (Mierau et al., 2018; Richter et al., 2012). These holistic methods still require managers to determine an acceptable level of departure from the unimpaired hydrograph that balances ecological and societal risks (Tharme, 2003). To date, few methods have been developed to estimate protective diversion rates for holistic management (but see Richter et al., 2012; Rossi, Mierau, et al., 2021), and none have done so using process-based and fish-oriented flow-ecology relationships.

In salmonid-bearing streams, the status quo for over 40 years has been to use habitat suitability curves (HSCs) to approximate habitat needs for fish, which are built upon correlations of physical habitat metrics, such as depth and velocity, and observations of habitat use (Beecher et al., 2002; Bovee & Milhous, 1978; Moniz et al., 2020). These correlations are then paired with hydraulic models to quantify habitat area at different flows (e.g., weighted usable area, or WUA curves) (Bovee & Milhous, 1978; Jowett et al., 2008). These models have their utility (Beecher, 2017; Campbell et al., 2021; Jowett & Biggs, 2006; Reiser & Hilgert, 2018), but have also been criticized for a lack of correspondence with individual fitness (Anderson et al., 2006; Hayes et al., 2016; Mathur et al., 1985; Naman et al., 2019; Railsback, 2016) and high site specificity (Anderson et al., 2006). Furthermore, these models do not describe how food resources change with streamflows (Piccolo et al., 2014; Rosenfeld & Ptolemy, 2012), which is a critical piece of the puzzle in salmonid fitness (Chapman, 1966).

Drift-foraging bioenergetics models are process-based models that estimate net rate of energetic intake (NREI), which is a proxy for fish growth potential. The models can be employed to make predictions about ecological responses to flow alterations in streams where the goal is to conserve drift-feeding fishes (Naman, Rosenfeld, Neuswanger, Enders, Hayes, et al., 2020; Piccolo et al., 2014; Rosenfeld et al., 2016). These models describe the energetic costs and gains of foraging in the stream environment. Because they do not require assumptions about habitat selection like HSCs, they are more transferrable across streams (Naman et al., 2019; Rosenfeld et al., 2016). Drift-foraging bioenergetics models are based on foundational research that was conducted decades ago (Fausch, 1984; Hill & Grossman, 1993; Hughes & Dill, 1990), but their implementation by practitioners has been slow (Rosenfeld et al., 2014). Recently, Naman, Rosenfeld, Neuswanger, Ender, and Eaton (2020) developed a user-friendly graphical interface that synthesizes fundamental bioenergetics equations. This interface opens the door for practitioners to more readily put bioenergetics models to use in flow management.

Since 1915, the state of California (USA) has held legislation that requires instream flows to be provided below dams to maintain fish “in good condition” (CA F&G Code 5937). Good condition has been defined to have three tiers: individual condition, population sustainability, and natural communities (Moyle et al., 1998). Although the legislation was largely ignored for decades, it recently spurred alterations to instream flow management in high profile cases (Bork et al., 2012). One reason that the legislation was long neglected may have been the lack of instream flow tools that relate “good condition” to predicted flow regimes. We highlight that drift-foraging bioenergetics models provide one metric for the first tier of individual condition by quantifying net energetic intake (NREI), a proxy for growth potential. For this reason, we suggest that river managers in California, where salmonids are highly imperiled (Katz et al., 2013) but often protected below dams by Code 5937, may find bioenergetics models a useful component of river management.

Here we demonstrate how drift-foraging bioenergetics models can be used to estimate acceptable diversion rates for holistic stream-flow management in the Shasta River (CA, USA), a regulated stream with native salmonid fish. Specifically, we asked, *when* do flow increases produce the greatest improvements for trout by modeling trout bioenergetics? We then evaluate the results of a bioenergetics modeling approach with field data on fish density, body size, and condition. Modeling bioenergetics over a series of stepwise POF diversion scenarios, we develop protective diversion rates that are predicted to maintain a fish growth potential proxy (NREI) within the range of historical, unimpaired conditions. This approach could have broad utility in systems with regulated flow, sensitive species, and quantifiable flow-ecology relationships.

2 | METHODS

2.1 | Study site

The Upper Shasta River, a tributary of the Klamath River in Northern California (Figure 1), is fed by both rainfall and snowmelt (Figure 2). Within our study reach, the primary water diversion removes up to 792 L/s (28 cfs) from March to November and up to 396 L/s (14 cfs) in other months. In the summer, this diversion can represent >98% of the estimated unimpaired flows. The diversion infrastructure consists of a concrete dam structure that allows water to flow over the top when discharge is high enough, a fish ladder (with a minimum of 18.4 L/s [0.65 cfs] for functionality), and a manually operated headgate. Current native fish species are Rainbow Trout (*Oncorhynchus mykiss*), Marbled Sculpin (*Cottus klamathensis*), and resident Klamath Lamprey (*Entosphenus similis*). Non-native Brown Trout (*Salmo trutta*) are also present.

2.2 | Field data collection

We monitored streamflows with pressure gages (Hobo Onset loggers) below the diversion, in the primary diversion ditch, and in several minor diversion ditches. Rating curves were maintained at the gage stations to convert stage to discharge following USGS methods (Turnipseed & Sauer, 2010). We summed these discharges to estimate unimpaired flows. We monitored stream temperatures with Hobo Onset loggers in one pool below and above the diversion. For both datasets, we estimated the daily mean value from hourly data.

We collected drift 13 times, every 4–6 weeks from December 2018 to December 2019. At each sample event we collected two samples above and below the diversion (Figure 1) with a 500 μ m drift net with a 25.4 \times 44.5 cm opening and a cod end. We measured water velocity in front of the net prior to collecting the sample to estimate drift concentration (individuals/m³). We standardized samples by the time the net was deployed, typically 1–1.5 h. Samples were collected between 11:00 and 15:00 to minimize crepuscular drift peaks. Invertebrates were preserved in 70% ethanol and identified under the microscope. Samples were identified to the family level when possible and taxa from terrestrial origin were often identified to order. Individuals were measured to the nearest 1 mm.

2.3 | Inputs for bioenergetics part 1: Estimating annual energetic conditions

Drift foraging bioenergetics models describe the cost of maintaining position in the water column, the ability to capture prey, and the size and amount of drift in a foraging territory (Fausch, 1984; Hughes, 1992; Hughes & Dill, 1990). Gross rate of energetic intake (GREI) represents energetic gains from successful capture and ingestion of prey. The NREI is the GREI minus the energetic costs associated with swimming, excretion, and metabolic needs. We used the software Bioenergetics HSC to calculate these parameters, which is a user-friendly software that implements well-developed equations for prey capture probabilities, success, drift flux, and metabolic costs (Naman, Rosenfeld, Neuswanger, Enders, Hayes, et al., 2020).

First, we estimated the energetic conditions for trout in 1 year at each focal site (riffle-pool series) above and below the diversion. To quantify physical conditions, we used modeled depth and velocity (at 6/10 of the depth) transects from 2-D hydraulic models (Caldwell et al., 2018). The model was calibrated from 0 to 5.35 cms (189 cfs) and validated with point velocity and depth measurements. The pool above the diversion is geomorphically stable and remains very similar to the model. The pool in the model below the diversion has since shifted under high flows but represents typical riffle/pool conditions. We extracted 5 riffle and 5 pool transects from the 2-D hydraulic model at our mean daily discharges (Figure 1).

We modeled bioenergetic conditions for a 10 cm, 10.5 g fish, which is the median size class based on July electrofishing efforts (see below). Previous modeling efforts at our study site indicated that the seasonality of NREI was similar across fish size classes but only varied in magnitude (Caldwell et al., 2018). We summarized the empirical drift data as the concentration of individuals (individual/m³) binned in 1 mm size classes. We used the mean daily stream temperature at each site at the date of drift collection. Note that the Bioenergetics HSC model calculates NREI as an instantaneous value (J/s), but total daily NREI is likely lower at colder temperatures due to reduced metabolic rate and total daily consumption of fish (Naman, Rosenfeld, Neuswanger, Ender, & Eaton, 2020). Relative instantaneous NREI can be used to compare above and below diversion, as we do here, but seasonal comparisons do not consider this potential difference in total daily intake due to cooler winter temperatures (Table S1).

We used the batch function in Bioenergetics HSC to calculate NREI at each depth and velocity point on each transect (30.5 cm intervals) using default settings (Table S2). To incorporate variation along a transect, and to account for the energetic gain and loss associated with stream width expansion and contraction, NREI was summed for all points along the transect. We then calculated the mean and standard deviation of NREI by habitat type (riffle and pools) at each site and date. To understand when flow and energetic conditions are most impaired, we calculated the percent NREI and streamflow loss below compared to above the diversion. We then conducted two linear models, one for

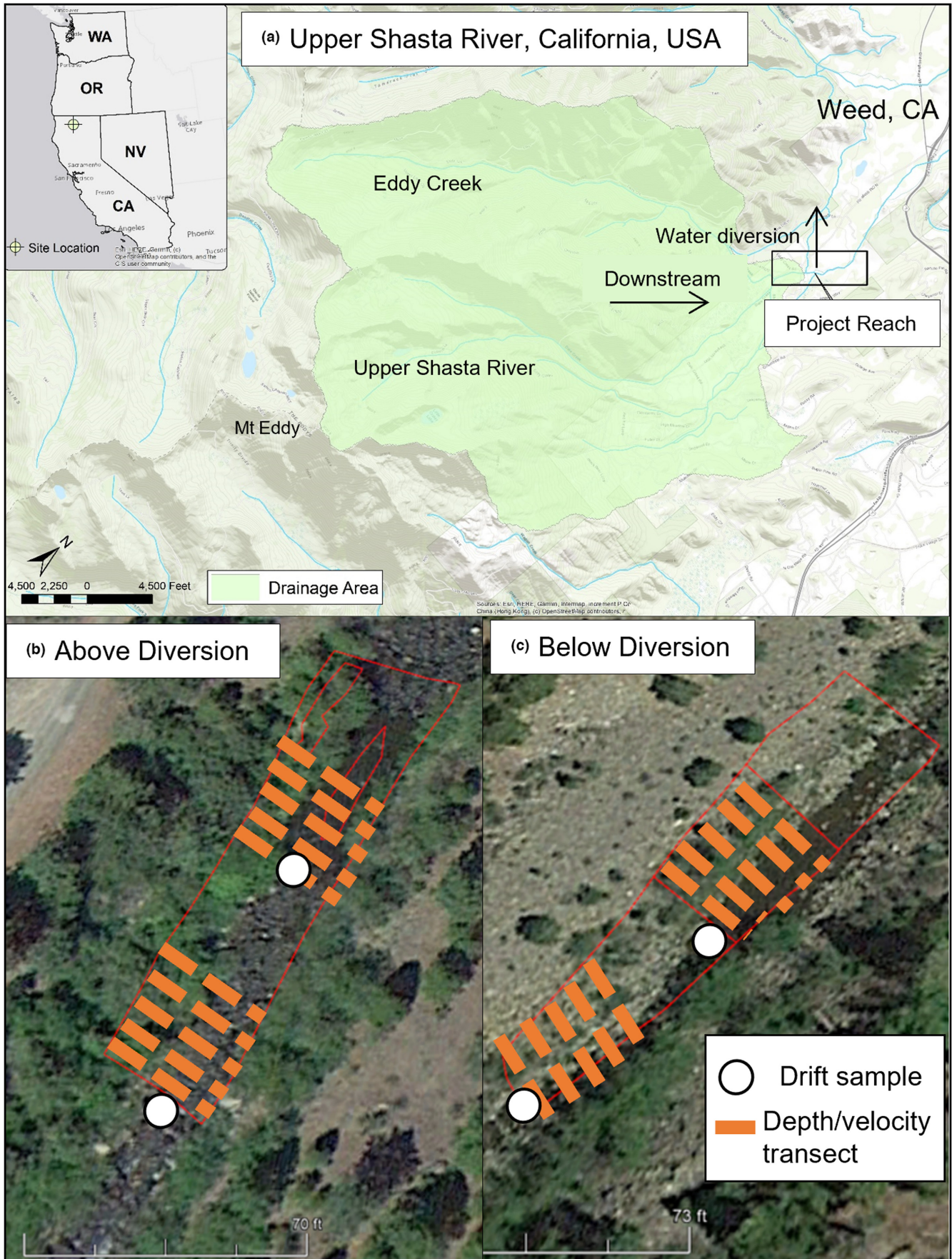


FIGURE 1 (a) The Upper Shasta River in Northern California, USA, a tributary to the Klamath River, is 72km² at our study site near Weed, CA. Trout bioenergetics were estimated from monthly drift samples and five depth/velocity transects that were extracted from 2D hydraulic models (b) above and (c) below a water diversion.

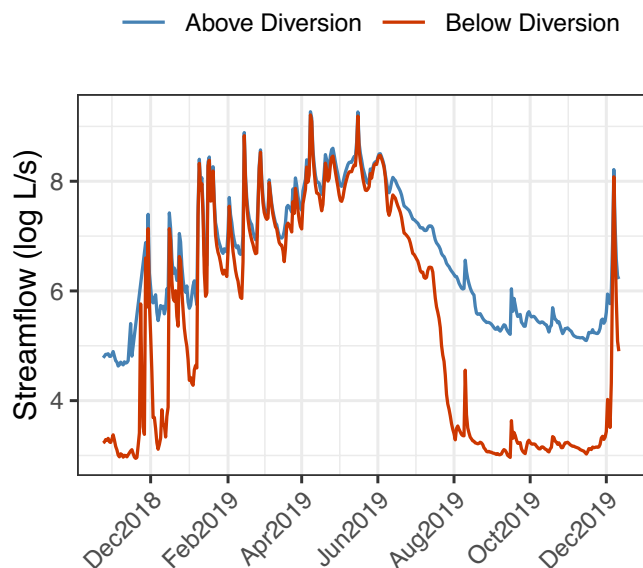


FIGURE 2 Streamflows on the Upper Shasta River were lower below the diversion than above the diversion, particularly during low flow months, December 2018, and July–December 2019.

riffles and one for pools, between the percent energetic loss and percent streamflow loss. All statistical analyses were completed in R version 4.0.3 (R Core Team, 2020).

2.4 | Fish density, size, and condition above and below the diversion

We estimated trout density, size, body condition, and lipid content above and below the diversion to evaluate if predicted NREI, a proxy for growth potential, was corroborated by trout habitat selection and condition. We conducted backpack electrofishing in 8 units (5 riffles, 3 pools) above and 7 units (4 riffles, 3 pools) below the diversion in July 2020, and 9 units (6 riffles, 3 pools) both above and below the diversion in July 2021. The same sites were re-visited in 2021 with the addition of extra riffle sites. Sites were blocked with top and bottom nets and fished until depletion was achieved, typically in three passes. Above the diversion, we used two to three backpack electrofishing units (Smith Root), depending on the channel width, to create a continuous field of electricity as we moved upstream. Below the diversion, continuity was achieved with one to two electrofishing units. We standardized the effort for each unit by summing the total time that all electrofishers were operated, divided by the sampled surface area (min/m^2). The surface area was estimated by one length and five width measurements, centered along the pool length. Fish were identified to species and measured for fork length (mm) and weight (g). Trout over 85 mm ($n=130$ above and $n=50$ below diversion) were measured for whole body lipid content in the field using a Distell Fish Fatmeter (Quillet et al., 2005).

We conducted linear regressions to test if *O. mykiss* and *S. trutta* density differed above and below the diversion. We included year as a fixed effect in these models to test for interannual differences. We conducted an analysis of variation (ANOVA) on the linear regression to determine significance of each parameter.

Next, we compared age-matched size and body condition of *O. mykiss* above and below the diversion. We focused on *O. mykiss* because they were the most common trout species ($n=231$). Our sample size for *S. trutta* was too limited for comparisons ($n=56$ individuals from various age classes). We divided *O. mykiss* into two age classes, age-0 (<75 mm) and age-1+ (>75 mm) based on clear divisions in the fork length histogram (Figure S6). We used an ANOVA to test if age-0 fish and age-1+ fish differed in size above and below the diversion with year as a fixed effect. We compared body condition by conducting an analysis of covariance (ANCOVA) between the logscale weight and logscale length in each year, including an interaction with sample site, following residual analyses methods in Sutton et al. (2000). If body condition differed between the sites, the interaction would be statistically significant. We used an ANOVA to test for difference in whole-body lipids above and below the diversion with year as a fixed effect.

2.5 | Inputs for bioenergetics part 2: Evaluating acceptable levels of flow diversion rates

Our second set of analyses seeks to determine flow diversion rates that produce NREI values within natural, historic variability over a longer time series. We quantified energetic conditions below the diversion through 62 years of unimpaired flows and several flow diversion scenarios. We

focused on May–September, when energetic and flow losses below the diversion are largest (see Section 3). We first explored 75%, 50%, and 25% POF diversions to evaluate if the effects of POF diversion scenarios vary by month. Next, we estimated the largest possible POF diversion, at 1% increments from 1% to 50% diversions, that would not result in statistically significant NREI losses compared to unimpaired flows within each month.

We estimated unimpaired flows at the Upper Shasta River using a regression from a nearby U.S. Geological Survey gage station, Trinity River above Coffee Creek (USGS no. 11523200). We conducted a linear regression between flow at the Trinity River and measured unimpaired flows at the Upper Shasta River in 2019 (wet year) and 2020 (dry year). The correlation between flow at the two sites is $R^2 = 0.77$ (Figure S2). We predicted unimpaired flows at the Upper Shasta River on the 15th of every month from May to September from 1958 to 2020. Flows on the 15th were representative of flows for the entire month ($p > 0.10$ in a *t*-test comparing the two, Figure S3). A single, representative day of the month was used because drift was estimated on a monthly timescale (see below).

Habitat conditions were represented using the same transects in the 2-D hydraulic model described above (Figure 1). On 23 out of the 317 modeled dates, flows were greater than 5.35 cms (189 cfs), the highest calibrated flow in the model, in which case we used the transect at 5.35 cms. These substitutions only occurred in May. We used the mean monthly temperature from our time series of temperatures gathered at each site from 2013 to 2020 (Table S1). Mean monthly temperatures do not capture the full variability in monthly temperatures, but are acceptable as our study site because temperatures are within metabolically suitable ranges for Rainbow Trout both above and below the diversion (Table S1; Figure S1) (Myrick & Cech, 2000). Additionally, mean monthly temperatures are only slightly warmer ($< 1.5^\circ\text{C}$) below the diversion, despite significant flow reductions (Table S1; Figure S1).

We created a synthetic drift input file to represent average monthly drift. Drift concentration does not differ significantly above and below the diversion or in riffles and pools, but varies between months, and tended to be higher in the early summer (May–June) and again in September (Figure S4). Therefore, we made one drift file for each month that summarized the mean concentration for each 1-mm size class for all samples taken in that month (Figure S5). Energetic value and capture success varies with invertebrate size, so the input drift concentrations must be size-class specific (Naman, Rosenfeld, Neuswanger, Enders, Hayes, et al., 2020). Our dataset included drift samples from 2019, a wet year, described above, and 2015, a dry year (Caldwell et al., 2018). Sensitivity analyses demonstrated that the bioenergetics models are very sensitive to large taxa, so we excluded individuals that were over 8 mm (0.6% of individuals).

We modeled NREI at the range of depth and velocity combinations observed (0–150 cm depth and 0–360 cm/s velocity at 1 cm and 1 cm/s increments), using the drift file and temperature associated with each month in Bioenergetics HSC (Naman, Rosenfeld, Neuswanger, Enders, Hayes, et al., 2020). We ran these models for 5, 10, and 15 cm fish.

To understand energetic conditions under each POF diversion scenario, we merged the NREI estimate for each depth \times velocity \times month combination with the transects that would have been observed on the 15th of the month in the 62-years under each flow scenario. We summed NREI for all points along each transect and calculated the mean NREI for each habitat type (5 riffle and 5 pool transects). Next, we conducted analyses of variances (ANOVAs) to test if there was an interaction between month and flow scenario (unimpaired, 25%, 50% and 75% diversion), in predicting NREI, which would indicate that allowable diversion rates differ by month. Our workflow to arrive at monthly NREI estimates for unimpaired and impaired flow scenarios is summarized in Figure 6.

After summarizing energetic conditions for the four initial POF-diversion flow scenarios, we asked what would be the highest allowable POF diversion that would maintain NREI within unimpaired levels. This is a risk-based approach that evaluates the ecological risk of incremental degrees of departure from unimpaired habitat values (Rossi, Mierau, et al., 2021). We followed the same set of steps as above to calculate NREI for every POF diversion, from 1% to 50%, at 1% increments. We ran a one-sided *t*-test between each POF diversion and the unimpaired conditions. The maximum POF diversion is the highest POF where NREI is not significantly lower than unimpaired NREI. We chose $p < 0.05$ as our cut-off for significance, a value that could be adjusted depending on tolerable levels of ecological risk.

3 | RESULTS

3.1 | Streamflows

Streamflows were greatly reduced below the diversion, particularly in summer months (Figure 2). The spring snowmelt recession, from June to July, occurred much faster below the diversion than above. Late summer baseflows were nearly an order of magnitude higher above the diversion, plateauing at 0.20 cms (7 cfs) from August to December 2019, compared to 0.03 cms (1 cfs) below the diversion (Figure 2).

3.2 | Bioenergetics part 1: Estimating annual energetic conditions

Relative energetic conditions for trout varied throughout the year. Above the diversion, NREI was lowest from March to June, during spring high flows. Below the diversion, NREI was lowest at the end of the summer (Figure 3), when streamflows were at their lowest

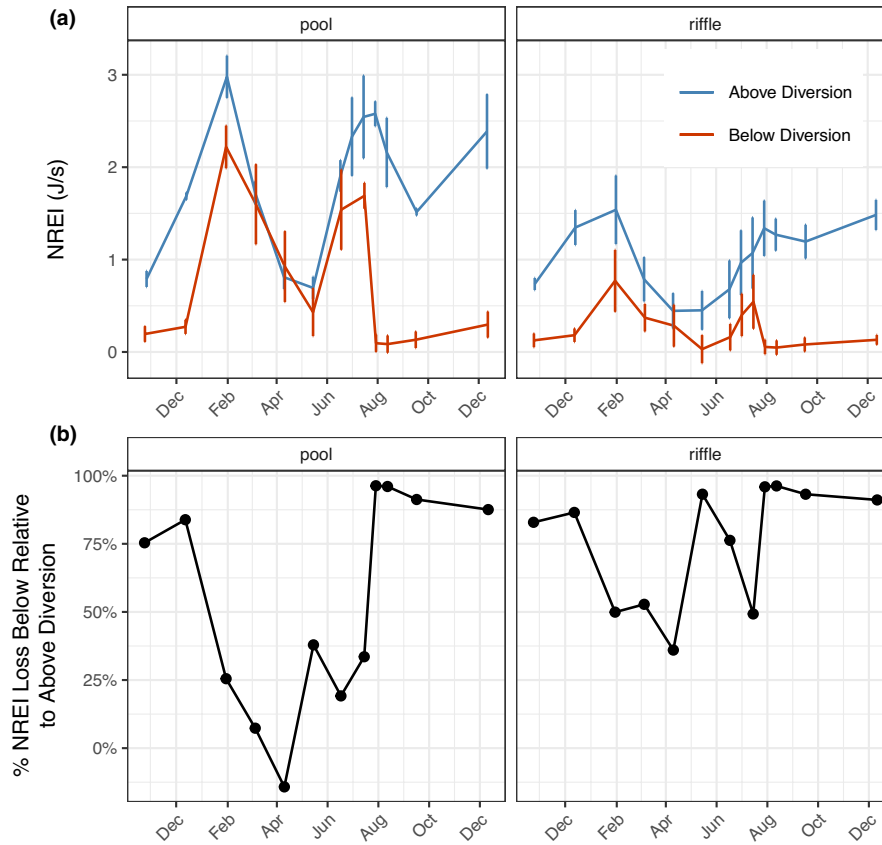


FIGURE 3 (a) Bioenergetic conditions for drift foraging fish throughout one year in the Upper Shasta River in pools and riffles, above and below the diversion. Error bars represent ± 1 SD around the mean due to five simulated transects in each habitat type at each sampling event. Instantaneous net rate of energetic intake (NREI) (J/s) does not account for temperature-related variation in total daily consumption limits. (b) The percent NREI loss below the diversion compared to above the diversion in pools and riffles.

(Figure 2). At both sites, total daily NREI (relative to instantaneous NREI, estimated in Figure 3) is likely lower in the winter months due to reduced daily intake at colder temperatures (Naman, Rosenfeld, Neuswanger, Ender, & Eaton, 2020). NREI peaks were two to three times higher in pools than in riffles, both above and below the diversion (Figure 3a). The percent loss of NREI below the diversion, compared to above, in pools was often $>75\%$ (Figure 3) and reached $>95\%$ from the end of July to December 2019. The only times when energetic loss in pools was $<50\%$ was in the spring, when the diversion minimally impairs streamflows (Figure 3b). In the riffles, the percent energetic loss below the diversion compared to above was almost always $>50\%$ (Figure 3b), but riffles were almost always less profitable than pools.

We found a strong relationship between flow reductions and energetic loss below the diversion relative to above. For pool habitats, this relationship was not statistically different from a 1:1 ratio, suggesting that any flow reductions results in a proportional energetic loss for drift foraging fish (Figure 4). Specifically, the regression for pool habitats predicted an intercept \pm standard error of -0.04 ± 0.08 and slope \pm standard error of 1.0 ± 0.12 , and this fit was strong ($F_{1,10} = 71.0$, $p < 0.01$, and adjusted $R^2 = 0.86$). For riffle habitats, large flow losses resulted in smaller energetic losses, likely because the higher velocity habitats do not have the potential to be as profitable as pools (Figure 4). The regression estimated an intercept of 0.51 ± 0.09 and slope of 0.42 ± 0.14 and explained a significant amount of the variance ($F_{1,11} = 8.7$, $p = 0.01$, adjusted $R^2 = 0.39$). In both habitats, flow and energetic losses are high at the end of the summer (Figures 3 and 4).

3.3 | Fish density, size, and condition above and below diversion

We found that densities of trout species were higher above the diversion than below (Figure 5a,b). For both species, sample location was significant in an ANOVA ($F_{1,30} = 4.7$, $p = 0.04$ for *O. mykiss* and $F_{1,30} = 4.7$, $p = 0.04$ for *S. trutta*). There were lower densities of *O. mykiss* below diversion, i.e. the slope estimate for below the diversion compared to above was negative (slope \pm standard error = -12.5 ± 5.7 , $p = 0.04$). *S. trutta* were also present in lower densities below the diversion (slope \pm standard error = -5.2 ± 2.2 , $p = 0.02$). Year was not significant for *O.*

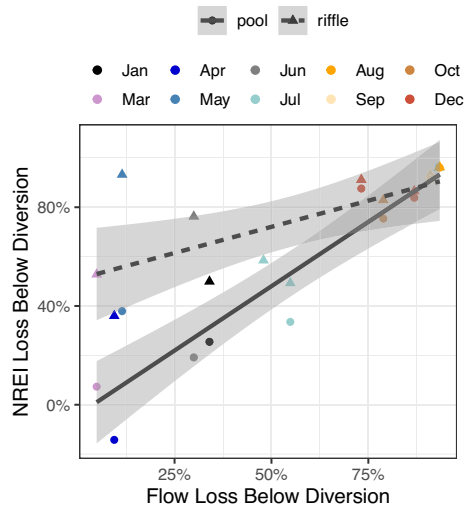


FIGURE 4 The percent of flow loss is a strong predictor for the percent of energetic (NREI) loss below the diversion compared to above. Shaded areas are ± 1 standard error around the slope estimate.

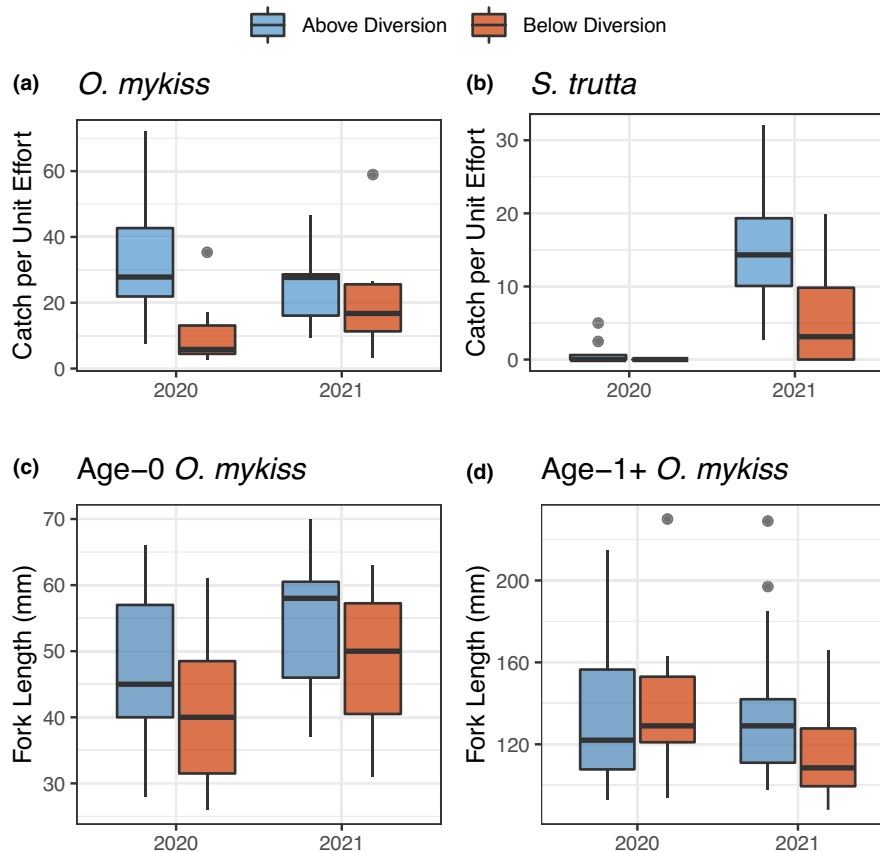


FIGURE 5 Density of trout, (a) Rainbow Trout (*Oncorhynchus mykiss*) and (b) Brown Trout (*Salmo trutta*), measured as catch per unit effort (fish/min/m²) was higher above the diversion than below the diversion in 2020 and 2021. *O. mykiss* were smaller below the diversion than above in the (c) age-0 and (d) age-1+ size class.

mykiss, but was for *S. trutta* ($p > 0.1$, and $F_{1,30} = 21.7$, $p < 0.01$, respectively). *S. trutta* were present at higher densities in 2021 than in 2020 (slope \pm standard error for 2021 = 10.2 ± 2.2 , $p < 0.01$).

O. mykiss were smaller below the diversion in both age classes, and this was statistically significant for age-0 trout (Figure 5c,d). Sample location was significant in an ANOVA ($F_{1,110} = 5.1$, $p = 0.03$), and the slope estimate for below the diversion, compared to above, was negative

(slope \pm standard error = -6.6 ± 2.3 , $p < 0.01$) (Figure 5c). Age-0 trout were slightly larger in 2021 ($F_{1,110} = 10.4$, $p < 0.01$, slope \pm standard error 7.0 ± 2.2 , $p < 0.01$). For age-1+ trout, location was marginally significant in an ANOVA ($F_{1,115} = 3$, $p = 0.08$) and the slope estimate for below the diversion was negative (slope \pm standard error = -8.4 ± 5.4 , $p = 0.1$). Age-1+ sizes did not differ between the years ($p > 0.1$).

There was no difference in body condition above and below the diversion. Specifically, there was not a significant main effect or interaction with location in the logscale fork length-to-weight ANCOVA ($p > 0.10$ for all comparisons, Figure S6). There was also no difference in whole-body lipid content for *O. mykiss* above and below the diversion ($p > 0.10$ for location and year, Figure S6).

3.4 | Bioenergetics part 2: Evaluating acceptable levels of flow diversion rates

NREI peaked at low-to-intermediate streamflows (Figure 6; Table 1) for all size classes (5, 10 and 15 cm) and all months (May–September) (Figure S7). Pools had a greater potential to create energetically favorable conditions than riffles (Figure S7; Table 1). For all size classes, the

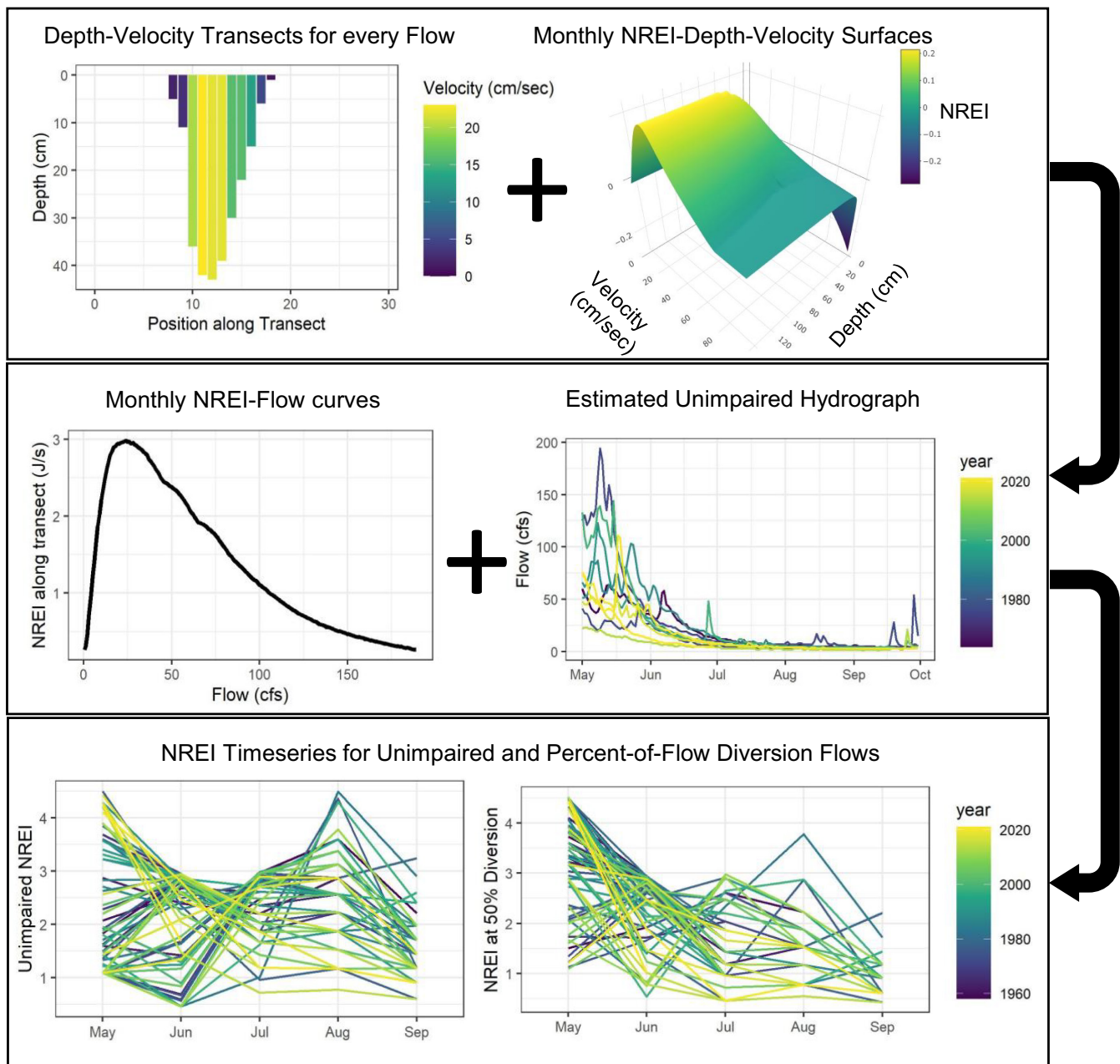


FIGURE 6 Workflow for generating a timeseries of NREI values that were used to estimate NREI under different percent-of-flow diversion scenarios at a monthly timestep (Figure 7). NREI-depth-velocity surfaces and NREI-flow curves were developed for every month (May–September) to account for different drift concentrations. July results for 10cm fish are plotted here.

TABLE 1 Flows (L/s) that produce the peak NREI for fish of different size classes in pools and riffles from May to September.

Flow (L/S) at peak NREI						
Trout size	May	June	July	August	September	
Pools						
5 cm	453	453	453	453	453	
10 cm	680	680	651	651	651	
15 cm	906	878	878	878	878	
Riffles						
5 cm	255	255	255	255	255	
10 cm	311	311	311	311	311	
15 cm	396	368	368	368	368	

Flow Scenario

- Unimpaired
- 25% Diversion
- 50% Diversion
- 75% Diversion

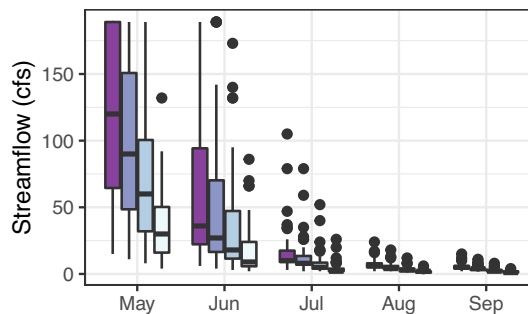
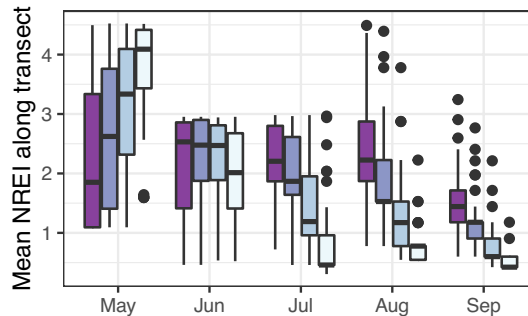
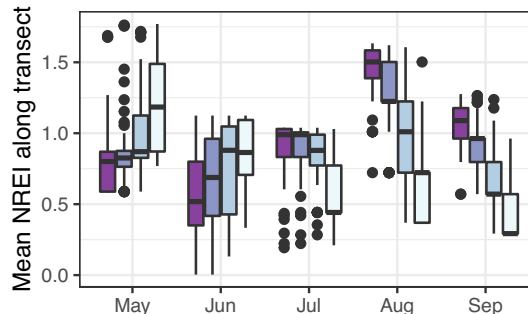
(a) Streamflow**(b) Pools****(c) Riffles****FIGURE 7** (a) Flows included in the streamflow scenarios. (b, c) NREI along transects decrease as the diversion percent-of-flow (POF) rate increases in July–September. NREI calculations represent 10 cm fish, see [Figures S8](#) and [S9](#) for comparison of size classes.

TABLE 2 The maximum percent-of-flow (POF) diversion rate that maintains NREI within the range of NREI under unimpaired flow scenarios for 5, 10, and 15 cm fish in pools. The most limiting size class, or the size class that requires the lowest diversion, is in bold.

Maximum percent of diversion					
	May	June	July	August	September
Pools—NREI					
5 cm	>50%	>50%	18%	9%	9%
10 cm	>50%	>50%	16%	9%	9%
15 cm	>50%	>50%	16%	12%	10%
Riffles—NREI					
5 cm	>50%	>50%	>50%	30%	12%
10 cm	>50%	>50%	>50%	9%	9%
15 cm	>50%	>50%	38%	9%	9%

estimated flow at peak NREI was similar across months (Table 1), and pools always required greater flows than riffles to maximize NREI. The flows with peak NREI increased with fish size class and were twice as high for 15 cm fish (878 L/s, or 31 cfs) than 5 cm fish (453 L/s, or 16 cfs) (Table 1).

Our initial evaluation of POF diversions at 25%, 50%, and 75% indicated that the impacts of diversions on NREI varies by month (Figure 7; see Figures S8 and S9 for all fish size classes). There was a significant interaction between month and flow scenario in an ANOVA predicting mean NREI for every size class and habitat type ($p < 0.01$ for all ANOVAs). In May, we found that increasing the POF diversion resulted in increased predicted NREI (Figure 7). In June, increasing the POF diversion increased NREI in riffles, and maintained similar NREI in pools. In July–September, increasing the diversion decreased NREI in both habitat types (Figure 7).

In both habitat types, in May and June, we did not find a POF diversion $< 50\%$ that would significantly reduce NREI, but we did in July–September. The 10 cm fish were the limiting size class (required lowest POF diversion) in pools while the 15 cm fish were the limiting size class in riffles. Focusing on pool habitats, our recommendations would be to divert 12% or less in July and 9% or less in August–September (Table 2).

4 | DISCUSSION

Water managers need tools that integrate biological and physical responses to streamflow to make decisions about how much water can be diverted, and when, without risking harm to native species. We used bioenergetics models to quantify the impact of a water diversion on cold water trout and to estimate maximum diversion rates that would maintain modeled NREI, a proxy for growth potential, within the range expected under unimpaired flows. This framework could be used to guide instream flow needs in rivers where conservation of drift-feeding fish or maintenance of “fish in good condition” are management goals.

4.1 | Bioenergetics above and below the diversion

Even in wet years with higher precipitation and river flows, the energetic conditions below the diversion are significantly impaired ($> 95\%$ NREI loss compared to above) for drift-feeding trout in the summer, a time when NREI could be relatively high. However, unlike a previous study at the same site, which was conducted at the end of a historic drought, NREI did not drop below zero (Caldwell et al., 2018). In contrast, in nearby unimpaired coastal streams, growth rates for *O. mykiss* were comparable between dry and wet years (Kelson & Carlson, 2019), even though energetic conditions decline over the summer months (Rossi et al., 2022; Rossi, Power, et al., 2021). This contrast suggests that it is possible for trout in unimpaired streams to be resilient to extreme climate and drought fluctuations. Restoring physical habitat structure in the Upper Shasta River may increase resilience to low flows and drought.

The drift-foraging energetics model predicted that NREI was lowest in the spring, even though drift concentrations and fluxes peak at this time of the year in the Upper Shasta River (Figure S4). The low spring growth predicted by our models was driven by the high water velocities, which drives down prey capture successes and drives up swimming and maneuvering costs (Hill & Grossman, 1993; Rosenfeld & Taylor, 2009). In our study, prey capture success was close to 25% in the spring (Figure S10). We suggest that field videography (e.g., Neuswanger et al., 2014) may be helpful in determining if prey capture successes are empirically that low at high velocities, or if trout are able to seek out low-velocity microhabitats where they can keep swimming costs low and capture success high. For example, Rosenfeld and Boss (2001) suggest that age-0

fish can seek out velocity refuges within riffles to obtain net positive energetic gains. Similarly, in an experimental stream, growth was higher in riffles than pools for Rainbow Trout (Magoulick & Wilzbach, 1998), suggesting that if food density is high enough, fast-water habitats can be productive.

Pool habitats were more profitable than riffle habitats, which aligns with observations that trout establish territories in lower-velocity pools (Hayes & Jowett, 1994). Even though aquatic drifting invertebrates tend to be sourced from riffles (Naman et al., 2017), they are available at the head of the pool (Inoue et al., 2017) and supplemented by terrestrial invertebrates (Naman et al., 2018). In an experimental manipulation with cutthroat trout, Rosenfeld and Boss (2001) found that pools led to higher growth rates for all sizes of fish, while large fish that were constrained to riffles lost weight. Pool habitats can be the focus of instream flow recommendations for trout, and any energetic gains made in the pools will provide a net greater benefit than associated energetic losses in the riffles.

We were surprised to find a strong linear relationship between the percent flow reductions and percent energetic loss below the diversion. This linearity was unexpected because previous bioenergetics modeling studies have noted that a reduction in drift as flows decline could lead to a disproportionate energetic loss at low flows (Rosenfeld & Ptolemy, 2012). In the Upper Shasta River, however, we did not find a uniform decrease in drift concentrations at low flows, but instead found that drift concentration was variable and slightly increased in September when flows continued to be low (Figure S4). Similarly, peaks in drift concentration under very low flows (<5% of mean annual discharge) have been noted in a review of seasonal drift in several streams in the Pacific Northwest (Rashidabadi et al., 2022). Further flow experiments that tease apart streamflows with the phenology of invertebrate production and food resources would inform when a proportional relationship between streamflows and NREI holds true.

4.2 | Fish density, size, and condition above and below the diversion

Overall, our field observations on trout density and size corroborated predictions from our bioenergetics modeling. This evaluation is an important step that is often not undertaken (Naman et al., 2019), with a few exceptions (e.g., Naman et al., 2019; Nislow et al., 2004). Even more broadly, the effect of instream flows on fish are often not evaluated (Campbell et al., 2021), and our field observations establish a baseline from which responses to restoration could be measured.

In detail, both trout species were present in lower densities below the diversion, which aligns with our estimated lower NREI, under the assumption that fish are mobile consumers who can track habitat quality (Fretwell & Lucas, 1970). In a flow experiment, Stelzer et al. (2022) also found lower densities of trout in a flow-impaired reach, suggesting that trout can quickly move out of deteriorating habitats. Previous studies have related modeled habitat loss (i.e., WUA) below dams to losses in trout densities and size complexity (Baran et al., 1995; Ovidio et al., 2008), and our study demonstrate that bioenergetics are similarly powerful for predicting impacts of diversions.

Age-0 *O. mykiss* were also smaller below the diversion. Emergence typically occurs in early summer, which is when the diversion begins to substantially impair flows. As a result, the only growth window fish would have experienced was under impaired conditions. While age-1+ *O. mykiss* were also smaller below the diversion, the overlap in size ranges between the two sites was substantial, and the size difference may not be biologically meaningful. This difference between the age classes may be because age-1+ fish have the remainder of the year, when flow is less impaired, to “catch up” in growth by July (Nicieza & Metcalfe, 1997). Compensatory growth can have delayed costs, such as reduced body size, condition and limited resources to allocate to reproduction at a later season as a result of prioritizing performance in the catch-up period (Morgan & Metcalfe, 2001). Reduced flows have been demonstrated to reduce the growth of trout in experimental low-flow (Harvey et al., 2006) and drought conditions (Sogard et al., 2009; VerWey et al., 2018), and our NREI modeling and field studies agree with these observations.

We were surprised to find no difference in body condition or whole-body lipid content above and below the diversion. There are likely tradeoffs associated with somatic growth versus lipid storage and body condition. In the Upper Shasta River, high lipid content may not be necessary to survive freezing winter conditions, which is observed in colder climates (Biro et al., 2004), so growing in length may be more beneficial for establishing dominance (Nakano, 1994) and for over-winter survival (Ebersole et al., 2006). Additionally, lipid content may be more controlled by water temperature than metabolic rate (Sloat & Reeves, 2014) or food rations (Archer et al., 2020), and temperatures were not substantially warmer below the diversion. Lipid allocation may also reflect the fatty acid profiles of prey species (Budge et al., 2020) and the invertebrate assemblage has extensive overlap above and below the diversion at our study site (Caldwell et al., 2018).

4.3 | Bioenergetics for evaluating POF diversion rates

Our analyses predicted that diverting <12% of streamflows in July and <9% of streamflows in August and September would maintain NREI within the range of unimpaired conditions. This diversion rate is much lower than the current diversion rate, which can be >98% of unimpaired

flows. This rate is in line with the “presumptive” standard of protection (10%) is suggested by (Richter et al., 2012) to maintain a high level of protection for natural function. Another approach, the “modified percent of flow” (Mierau et al., 2018) suggested that a cumulative diversion rate is protective if it does not decrease a stream’s family of riffle crest (RCT) depths by more than 5%. Using previously measured RCT depths from below the diversion dam, a 5% change in RCT depth below the diversion dam equates to a diversion rate of 13.4% of flow for flows below 2.83 cms (100 cfs). Interestingly, all three of these holistic methods converge around a similar protective diversion rate of <10%–13%.

In high flow months, May and June, a simple reading of our results would suggest that very high diversion rates (>50%) would benefit trout by increasing NREI. In our analyses, any diversion that brings streamflow closer to the flow where NREI peaks will theoretically improve trout energetics, and spring flows are frequently higher than that flow. While higher flow diversion rates are likely acceptable during these months compared to the low-flow months, we emphasize caution in the interpretation of these results. Bioenergetics models are likely not the most suitable tool for evaluating the risk of diversions in high flow conditions for a few reasons. First, our model likely does not accurately reflect realized energetic conditions that fish experience within the channel under high flows, as fish can likely seek shelters behind large cobbles or near the substrate where the velocity is lower (Ligon et al., 2016; Railsback et al., 2011). Second, we did not account for energetic benefits if flows are high enough to inundate floodplains, which can be extremely high-growth environments for trout (Katz et al., 2017; Sommer et al., 2020), even in mountainous watersheds (Boughton & Pike, 2013). Future bioenergetics and hydraulic models could seek to incorporate the availability of microhabitats, including floodplains, in high-velocity streams.

Finally, high flows are useful for other aspects of focal species’ life histories and the broad ecological function of the river. For example, high springtime flows may be important for spawning (Hatfield & Bruce, 2000; Moyle et al., 1998). High flows are also important for many geomorphic functions (Yarnell et al., 2015) that indirectly maintain focal species via channel form or gravel distribution. Thus, we recommend that trout growth is just one of several metrics used to guide assessment of ecological risk from diversions. Other quantitative responses to high flows, from fish and other riverine biota, could be integrated into a similar framework to find the highest acceptable diversion rate. In the absence of these metrics, during the high flow months managers could rely on well-established holistic methods that define protective diversion rates from multiple case studies or hydro-geomorphic indicators (Mierau et al., 2018; Richter et al., 2012).

4.4 | Room for improvements: Drift concentration-streamflow relationships

A shortcoming in our effort to evaluate stream flow scenarios using bioenergetics is that we assumed constant drift concentrations within a monthly sampling period, regardless of flow. Our site-specific data suggested that drift concentrations were not necessarily correlated with flows in the summer (Figure S4). However, other studies have found that drift is more likely to decrease with flows (Dewson et al., 2007; Rashidabadi et al., 2022). Furthermore, drift concentration can vary spatially within the stream channel (Hayes et al., 2007; Stark et al., 2002), with implications for the profitability within a study reach (Laliberte et al., 2016). Hayes et al. (2007) developed a model that includes process-based transport of drift in a stream but implementing these models widely requires site-specific data and are implemented over a shorter reach.

There is a need for a more comprehensive understanding of how drift concentration changes with streamflow given other watershed characteristics (Naman et al., 2016; Rosenfeld et al., 2014, 2016). Drift concentrations can be highly variable, but if adequately represented can help capture the complexities of how ecosystems change with reduced flows (Rosenfeld & Ptolemy, 2012). In the future, empirical and synthesis studies and drift process models (e.g., Hayes et al., 2019) that describe how drift concentration varies spatially and with flow in a stream will be important for applying process-based bioenergetics models to management.

4.5 | Data inputs for applied bioenergetics models

Bioenergetics models integrate the effects of temperature-flow-food interactions on fish habitat in a way that is not considered by physical habitat simulations (Railsback, 2016), and have many applications for evaluating the effects of flow management on fish. Bioenergetics HSC is a user-friendly software (Naman, Rosenfeld, Neuswanger, Enders, Hayes, et al., 2020), which opens the door to implementing bioenergetics models as a relative estimate of habitat quality more widely. Implementation requires data on depth and velocity, (either measured empirically or extracted from hydraulic models), temperature, and drift. Below we briefly discuss considerations for practitioners in developing temperature and drift data.

Water temperature is a strong driver of fish metabolic rate and is an important input variable for bioenergetics models. In users seeking to apply bioenergetics models to evaluate flow scenarios, an important consideration may be how flows alter water temperatures. In the Upper Shasta River, the effects of streamflow reduction on temperature were relatively minor (typically <1.5°C of warming even under flow reductions >90%, Figure S1; Table S1), due to input of cold-water springs that maintain consistent, cool temperatures even in warm air temperatures. More commonly, flow reductions increase water temperatures, especially in dry and warm periods (van Vliet et al., 2011). Unseasonably warm

temperatures may increase fish metabolic rate, and depending on food availability, create stressful or high-growth environments (Armstrong et al., 2021). In regulated rivers, water temperatures are often seasonally cooler downstream of dams even in low flows (Willis et al., 2021), which may slow fish metabolism and reduce growth potential (Brown, 2004). Depending on the system, developing a flow-temperature model may be an important step in developing appropriate inputs for fish bioenergetics models and for predicting impacts of flow management on fish.

Recent work has demonstrated that food availability may be just as important as temperature for fish bioenergetics (Railsback, 2022). Unfortunately, the most commonly missing input data at a site of interest may be drift data, highlighting a need for regional-level data and predictive streamflow-to-drift relationships (discussed above). The user manual for Bioenergetics HSC (Naman, Rosenfeld, Neuswanger, Enders, Hayes, et al., 2020) notes that drift concentrations are more likely to influence the magnitude of NREI rather than the shape of the curves, and drift data could be borrowed from comparable systems to make initial inferences. Borrowing data may not capture the intricacy of flow-drift relationships at a site and may not be appropriate at all places (e.g., if hydropeaking effects flow-invertebrate relationships, Kennedy et al., 2014), but this option may allow practitioners to incorporate bioenergetics as a management tool that complements physical habitat models.

While understanding how drift and temperature changes with flow through space and time is important for developing accurate estimates of *absolute* NREI, we highlight that precise estimates may not be necessary for management and research objectives that seek to understand *relative* changes in NREI. For example, if predicting when/if NREI is likely to be negative is a priority, then accurate estimates of food and temperature may be important. However, predicting the *relative* changes that may occur for fish growth and condition under altered flow regimes and restoration scenarios is more attainable and still informative. Similarly, it is important to note that drift-foraging bioenergetics models tend to overpredict growth potential due to overestimation of prey capture success and assumptions around foraging frequency (Hughes et al., 2003; Neuswanger et al., 2014; Rosenfeld & Taylor, 2009). Due to this overestimation, the strength of bioenergetics models is in estimating *relative* growth potential and habitat quality, rather than precise growth estimates.

Overall, including bioenergetics models in streamflow management to understand *relative* change in habitat quality may be currently feasible in many watersheds. This mechanistic understanding and ability to incorporate flow-related changes in food resources and water temperatures will provide insights and predictions that are an improvement from the current reliance on physical habitat metrics.

5 | CONCLUSIONS

River management that focuses on *how much water can be diverted* without risking loss of ecological function (i.e., skimming water off the top), rather than *how much water is needed* to achieve peak conditions for target life histories/species (i.e., justifying every drop), will likely result in holistic management that preserves unquantified ecological functions associated with natural flow regimes. However, holistic POF diversion methods require that managers determine an acceptable level of departure, or protective diversion rate, from the unimpaired hydrograph (Tharme, 2003). Bioenergetic models have the potential to be a valuable tool for managers seeking to quantify the risk of altering ecological function due to water diversions in streams that support sensitive salmonid species. Drift-foraging bioenergetics models may currently be most useful for assessing the relative impact of diversions on habitat quality in low flow conditions. Future analyses could include quantitative streamflow-ecology and geomorphology relationships that are appropriate for high flow times. Including bioenergetic models in a risk-management framework for river management will improve the ability to balance desired ecological responses and human water needs.

AUTHOR CONTRIBUTIONS

Suzanne J. Rhoades: Conceptualization; data curation; formal analysis; visualization; writing – original draft. **Timothy J. Caldwell:** Conceptualization; investigation; validation; writing – review and editing. **Scott McBain:** Conceptualization; data curation; supervision; validation; writing – review and editing. **Rene Henery:** Funding acquisition; investigation; project administration; supervision; validation; writing – review and editing. **Natalie Stauffer-Olsen:** Conceptualization; funding acquisition; project administration; validation; writing – review and editing. **Tara McKinnon:** Data curation; investigation; validation; writing – review and editing. **Gabriel J. Rossi:** Resources; validation; writing – review and editing. **Sudeep Chandra:** Conceptualization; funding acquisition; investigation; methodology; project administration; supervision; writing – review and editing.

ACKNOWLEDGMENTS

Funding was provided by the National Fish and Wildlife Foundation to R. Henery at Trout Unlimited and Marin Community Foundation to S. Chandra and the University of Nevada's Global Water Center. Many thanks to Pauli and Michael Robinson for inspiration and support in river stewardship. Field assistance was provided by Kaitlyn Duvall, Aldo San Pedro, and Jacquelynn Tran. All sampling and tagging was conducted under the approval of University of Nevada Reno Institutional Animal Care and Use Committee under protocol #00866.

CONFLICT OF INTEREST STATEMENT

The authors have declared no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

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REFERENCES

- Anderson, K., A. Paul, E. McCauley, L. Jackson, J. Post, and R. Nisbet. 2006. "Instream Flow Needs in Rivers and Streams: The Importance of Understanding Ecological Dynamics." *Frontiers of Ecology and the Environment* 4: 309–19. [https://doi.org/10.1890/1540-9295\(2006\)4\[309:IFNISA\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2006)4[309:IFNISA]2.0.CO;2).
- Archer, L.C., S.A. Hutton, L. Harman, S.D. McCormick, M.N. O'Grady, J.P. Kerry, W.R. Poole, P. Gargan, P. McGinnity, and T.E. Reed. 2020. "Food and Temperature Stressors Have Opposing Effects in Determining Flexible Migration Decisions in Brown Trout (*Salmo trutta*)." *Global Change Biology* 26: 2878–96. <https://doi.org/10.1111/gcb.14990>.
- Armstrong, J.B., A.F. Fullerton, C.E. Jordan, J.L. Ebersole, J.R. Bellmore, I. Arismendi, B.E. Penaluna, and G.H. Reeves. 2021. "The Importance of Warm Habitat to the Growth of Regime of Cold-Water Fishes." *Nature Climate Change* 11(4): 354–61. <https://doi.org/10.1038/s41558-021-00994-y>.
- Baran, P., M. Delacoste, F. Dauba, J.M. Lascaux, A. Belaud, and S. Lek. 1995. "Effects of Reduced Flow on Brown Trout (*Salmo trutta* L.) Populations Downstream Dams in French Pyrenees." *Regulated Rivers: Research & Management* 10: 347–61. <https://doi.org/10.1002/rrr.3450100226>.
- Beecher, H.A. 2017. "Comment 1: Why It Is Time to Put PHABSIM Out to Pasture." *Fisheries* 42: 508–10. <https://doi.org/10.1080/03632415.2017.1380985>.
- Beecher, H.A., B.A. Caldwell, and S.B. DeMond. 2002. "Evaluation of Depth and Velocity Preferences of Juvenile Coho Salmon in Washington Streams." *North American Journal of Fisheries Management* 22: 785–95. [https://doi.org/10.1577/1548-8675\(2002\)022<0785:eodavp>2.0.co;2](https://doi.org/10.1577/1548-8675(2002)022<0785:eodavp>2.0.co;2).
- Biro, P., A. Morton, J. Post, and E. Parkinson. 2004. "Over-Winter Lipid Depletion and Mortality of Age-0 Rainbow Trout (*Oncorhynchus mykiss*)." *Canadian Journal of Fisheries and Aquatic Sciences* 61: 1513–19. <https://doi.org/10.1139/f04-083>.
- Bork, K., J. Krovoza, J. Katz, and P.B. Moyle. 2012. *The Rebirth of California Fish & Game Code Section 5937: Water for Fish*. Davis, California, USA: University of California, Davis. <https://doi.org/10.2139/ssrn.3169409>.
- Boughton, D.A., and A.S. Pike. 2013. "Floodplain Rehabilitation as a Hedge against Hydroclimatic Uncertainty in a Migration Corridor of Threatened Steelhead." *Conservation Biology* 27: 1158–68. <https://doi.org/10.1111/cobi.12169>.
- Bovee, K.D., and R. Milhous. 1978. "Hydraulic Simulation in Instream Flow Studies: Theory and Techniques." Cooperative Instream Flow Service Group. Instream Flow Information Paper No. 5 FWS/OBS-78/33.
- Brown, P. 2004. "Predicting Growth and Mortality of Brown Trout (*Salmo trutta*) in the Goulburn River after Mitigation of Cold-Water Discharge from Lake Eildon, Australia." *New Zealand Journal of Marine and Freshwater Research* 38: 270–87. <https://doi.org/10.1080/00288330.2004.9517237>.
- Budge, S.M., K. Townsend, S.P. Lall, and J.F. Bromaghin. 2020. "Dietary Fat Concentrations Influence Fatty Acid Assimilation Patterns in Atlantic Pollock (*Pollachius virens*)." *Philosophical Transactions of the Royal Society B: Biological Sciences* 375: 20190649. <https://doi.org/10.1098/rstb.2019.0649>.
- Caldwell, T.J., G.J. Rossi, R.E. Henery, and S. Chandra. 2018. "Decreased Streamflow Impacts Fish Movement and Energetics through Reductions to Invertebrate Drift Body Size and Abundance." *River Research and Applications* 34: 965–76. <https://doi.org/10.1002/rra.3340>.
- Campbell, R., P. Hilgert, K. Binkley, and H. Beecher. 2021. "Monitoring Trout Response to Instream Flow." *Fisheries* 46: 220–28. <https://doi.org/10.1002/fsh.10578>.
- Chapman, D. 1966. "Food and Space as Regulators of Salmonid Populations in Streams." *The American Naturalist* 100: 345–57. <https://www.jstor.org/stable/2459001>.
- Dai, A. 2013. "Increasing Drought under Global Warming in Observations and Models." *Nature Climate Change* 3: 52–58. <https://doi.org/10.1038/nclimate1633>.
- Dewson, Z.S., A.B.W. James, and R.G. Death. 2007. "A Review of the Consequences of Decreased Flow for Instream Habitat and Macroinvertebrates." *Journal of the North American Benthological Society* 26: 401–15. <https://doi.org/10.1899/06-110.1>.
- Ebersole, J.L., P.J. Wigington, J.P. Baker, M.A. Cairns, M.R. Church, P.B. Hansen, B.A. Miller, H.R. LaVigne, J.E. Compton, and S.G. Leibowitz. 2006. "Juvenile Coho Salmon Growth and Survival across Stream Network Seasonal Habitats." *Transactions of the American Fisheries Society* 135: 1681–97. <https://doi.org/10.1577/T05-144.1>.
- Fausch, K.D. 1984. "Profitable Stream Positions for Salmonids: Relating Specific Growth Rate to Net Energy Gain." *Canadian Journal of Zoology* 62: 441–51. <https://doi.org/10.1139/z84-067>.
- Freeman, M.C., K.R. Bestgen, D. Carlisle, E.A. Frimpong, N.R. Franssen, K.B. Gido, Elise Irwin, et al. 2022. "Toward Improved Understanding of Streamflow Effects on Freshwater Fishes." *Fisheries* 47: 290–98. <https://doi.org/10.1002/fsh.10731>.
- Fretwell, S.D., and H.L. Lucas. 1970. "On Territorial Behavior and Other Factors Influencing Habitat Distribution in Birds." *Acta Biotheoretica* 19: 16–36. <https://doi.org/10.1039/9781847558213-00059>.
- Grantham, T.E., and P.B. Moyle. 2014. "Assessing Flows for Fish Below Dams: A Systematic Approach to Evaluate Compliance of California's Dams with Fish and Game Code Section 5937." Center for Watershed Sciences Technical Report (CWS-2014-01), University of California, Davis.

- Harvey, B.C., R.J. Nakamoto, and J.L. White. 2006. "Reduced Streamflow Lowers Dry-Season Growth of Rainbow Trout in a Small Stream." *Transactions of the American Fisheries Society* 135: 998–1005. <https://doi.org/10.1577/T05-233.1>.
- Hatfield, T., and J. Bruce. 2000. "Predicting Salmonid Habitat–Flow Relationships for Streams from Western North America." *North American Journal of Fisheries Management* 20: 1005–15. [https://doi.org/10.1577/1548-8675\(2000\)020<1005:pshrfv>2.0.co;2](https://doi.org/10.1577/1548-8675(2000)020<1005:pshrfv>2.0.co;2).
- Hayes, J.W., E. Goodwin, K.A. Shearer, J. Hay, and L. Kelly. 2016. "Can Weighted Useable Area Predict Flow Requirements of Drift-Feeding Salmonids? Comparison with a Net Rate of Energy Intake Model Incorporating Drift–Flow Processes." *Transactions of the American Fisheries Society* 145: 589–609. <https://doi.org/10.1080/00028487.2015.1121923>.
- Hayes, J.W., E.O. Goodwin, K.A. Shearer, and D.M. Hicks. 2019. "Relationship between Background Invertebrate Drift Concentration and Flow over Natural Flow Recession and Prediction with a Drift Transport Model." *Canadian Journal of Fisheries and Aquatic Sciences* 76: 871–85. <https://doi.org/10.1139/cjfas-2017-0340>.
- Hayes, J.W., N.F. Hughes, and L.H. Kelly. 2007. "Process-Based Modelling of Invertebrate Drift Transport, Net Energy Intake and Reach Carrying Capacity for Drift-Feeding Salmonids." *Ecological Modelling* 207: 171–88. <https://doi.org/10.1016/j.ecolmodel.2007.04.032>.
- Hayes, J.W., and I.G. Jowett. 1994. "Microhabitat Models of Large Drift-Feeding Brown Trout in Three New Zealand Rivers." *North American Journal of Fisheries Management* 14: 710–25. [https://doi.org/10.1577/1548-8675\(1994\)014<0710:mmoldf>2.3.co;2](https://doi.org/10.1577/1548-8675(1994)014<0710:mmoldf>2.3.co;2).
- Hill, J., and G.D. Grossman. 1993. "An Energetic Model of Microhabitat Use for Rainbow Trout and Rosyside Dace." *Ecology* 74: 685–98. <https://doi.org/10.2307/1940796>.
- Hughes, N.F. 1992. "Selection of Positions by Drift-Feeding Salmonids in Dominance Hierarchies: Model and Test for Arctic Grayling (*Thymallus arcticus*) in Subarctic Mountain Streams, Interior Alaska." *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1999–2008. <https://doi.org/10.1139/f92-223>.
- Hughes, N.F., and L.M. Dill. 1990. "Position Choice by Drift-Feeding Salmonids: Model and Tests for Arctic Grayling (*Thymallus arcticus*) in Subarctic Mountain Streams, Interior Alaska." *Canadian Journal of Fisheries and Aquatic Science* 47: 2039–48. <https://doi.org/10.1139/f90-228>.
- Hughes, N.F., J.W. Hayes, K.A. Shearer, and R.G. Young. 2003. "Testing a Model of Drift-Feeding Using Three-Dimensional Videography of Wild Brown Trout, *Salmo trutta*, in a New Zealand River." *Canadian Journal of Fisheries and Aquatic Sciences* 60: 1462–76. <https://doi.org/10.1139/f03-126>.
- Inoue, K., K. Stoeckl, and J. Geist. 2017. "Joint Species Models Reveal the Effects of Environment on Community Assemblage of Freshwater Mussels and Fishes in European Rivers." *Diversity and Distributions* 23: 284–96. <https://doi.org/10.1111/ddi.12520>.
- Jowett, I.G., and B.J.F. Biggs. 2006. "Flow Regime Requirements and the Biological Effectiveness of Habitat-Based Minimum Flow Assessments for Six Rivers." *International Journal of River Basin Management* 4: 179–89. <https://doi.org/10.1080/15715124.2006.9635287>.
- Jowett, I.G., J.W. Hayes, and M.J. Duncan. 2008. "A Guide to Instream Habitat Survey Methods and Analysis." NIWA Science and Technology Series No. 54. 121 pp. www.niwa.co.nz.
- Katz, J., P.B. Moyle, R.M. Quiñones, J. Israel, and S. Purdy. 2013. "Impending Extinction of Salmon, Steelhead, and Trout (Salmonidae) in California." *Environmental Biology of Fishes* 96: 1169–86. <https://doi.org/10.1007/s10641-012-9974-8>.
- Katz, J.V.E., C. Jeffres, J.L. Conrad, T.R. Sommer, J. Martinez, S. Brumbaugh, N. Corline, and P.B. Moyle. 2017. "Floodplain Farm Fields Provide Novel Rearing Habitat for Chinook Salmon." *PLoS ONE* 12: 1–16. <https://doi.org/10.1371/journal.pone.0177409>.
- Kelson, S.J., and S.M. Carlson. 2019. "Do Precipitation Extremes Drive Growth and Migration Timing of a Pacific Salmonid Fish in Mediterranean–Climate Streams?" *Ecosphere* 10: e02618. <https://doi.org/10.1002/ecs2.2618>.
- Kennedy, T.A., C.B. Yackulic, W.F. Cross, P.E. Grams, M.D. Yard, and A.J. Copp. 2014. "The Relationship between Invertebrate Drift and Two Primary Controls, Discharge and Benthic Densities, in a Large Regulated River." *Freshwater Biology* 59: 557–72. <https://doi.org/10.1111/fwb.12285>.
- Laliberte, J.J., J.R. Post, J.S. Rosenfeld, and J.A. Mee. 2016. "Modelling Temperature, Body Size, Prey Density, and Stream Gradient Impacts on Longitudinal Patterns of Potential Production of Drift-Feeding Trout." *River Research and Applications* 32: 2045–55. <https://doi.org/10.1002/rra.3048>.
- Ligon, F.K., R.J. Nakamoto, B.C. Harvey, and P.F. Baker. 2016. "Use of Streambed Substrate as Refuge by Steelhead or Rainbow Trout *Oncorhynchus mykiss* during Simulated Freshets." *Journal of Fish Biology* 88: 1475–85. <https://doi.org/10.1111/jfb.12925>.
- Magoulick, D.D., and M.A. Wilzbach. 1998. "Effect of Temperature and Macrohabitat on Interspecific Aggression, Foraging Success, and Growth of Brook Trout and Rainbow Trout Pairs in Laboratory Streams." *Transactions of the American Fisheries Society* 127: 708–17. [https://doi.org/10.1577/1548-8659\(1998\)127<0708:eotamo>2.0.co;2](https://doi.org/10.1577/1548-8659(1998)127<0708:eotamo>2.0.co;2).
- Mathur, D., W.H. Bason, E.J.J. Purdy, and C.A. Silver. 1985. "A Critique of the Instream Flow Incremental Methodology." *Canadian Journal of Fisheries & Aquatic Sciences* 42: 825–31. <https://doi.org/10.1139/F85-105>.
- Mierau, D.W., W.J. Trush, G.J. Rossi, J.K. Carah, M.O. Clifford, and J.K. Howard. 2018. "Managing Diversions in Unregulated Streams Using a Modified Percent-of-Flow Approach." *Freshwater Biology* 63: 752–68. <https://doi.org/10.1111/fwb.12985>.
- Moniz, P.J., G.B. Pasternack, D.A. Massa, L.W. Stearman, and P.M. Bratovich. 2020. "Do Rearing Salmonids Predictably Occupy Physical Microhabitat?" *Journal of Ecohydraulics* 5: 132–50. <https://doi.org/10.1080/24705357.2019.1696717>.
- Morgan, I.J., and N.B. Metcalfe. 2001. "Deferred Costs of Compensatory Growth after Autumnal Food Shortage in Juvenile Salmon." *Proceedings of the Royal Society B: Biological Sciences* 268: 295–301. <https://doi.org/10.1098/rspb.2000.1365>.
- Moyle, P.B., M.P. Marchetti, J. Baldrige, and T.L. Taylor. 1998. "Fish Health and Diversity: Justifying Flows for a California Stream." *Fisheries* 23: 1–15. [https://doi.org/10.1577/1548-8446\(1998\)023<0006:FHADJF>2.0.CO;2](https://doi.org/10.1577/1548-8446(1998)023<0006:FHADJF>2.0.CO;2).
- Myrick, C., and J. Cech. 2000. "Temperature influences on California rainbow trout physiological performance." *Fish Physiology and Biochemistry* 22 (3): 245–54. <https://doi.org/10.1023/A:1007805322097>.
- Naiman, R.J., S.E. Bunn, C. Nilsson, G.E. Petts, G. Pinay, and L.C. Thompson. 2002. "Legitimizing Fluvial Ecosystems as Users of Water." *Environmental Management* 30: 455–67. <https://doi.org/10.1007/s00267-002-2734-3>.
- Nakano, S. 1994. "Variation in Antagonistic Encounters in a Dominance Hierarchy of Freely Interacting Red-Spotted Masu Salmon (*Oncorhynchus masou ishikawai*)." *Ecology of Freshwater Fish* 3: 153–58. <https://doi.org/10.1111/j.1600-0633.1994.tb00017.x>.
- Naman, S., J.S. Rosenfeld, J. Neuswanger, E. Ender, and B. Eaton. 2020. "BioenergeticHSC: User-Friendly Software for Bioenergetic Habitat Suitability Curves. User Manual (Version 1.0)." <https://doi.org/10.13140/RG.2.2.33718.32324>.

- Naman, S.M., J.S. Rosenfeld, P.M. Kiffney, and J.S. Richardson. 2018. "The Energetic Consequences of Habitat Structure for Forest Stream Salmonids." *Journal of Animal Ecology* 87: 1383–94. <https://doi.org/10.1111/1365-2656.12845>.
- Naman, S.M., J.S. Rosenfeld, J.R. Neuswanger, E.C. Enders, and B.C. Eaton. 2019. "Comparing Correlative and Bioenergetics-Based Habitat Suitability Models for Drift-Feeding Fishes." *Freshwater Biology* 64: 1613–26. <https://doi.org/10.1111/fwb.13358>.
- Naman, S.M., J.S. Rosenfeld, J.R. Neuswanger, E.C. Enders, J.W. Hayes, E.O. Goodwin, I.G. Goodwin, and B.C. Eaton. 2020. "Bioenergetic Habitat Suitability Curves for Instream Flow Modeling: Introducing User-Friendly Software and its Potential Applications." *Fisheries* 45: 605–13. <https://doi.org/10.1002/fsh.10489>.
- Naman, S.M., J.S. Rosenfeld, and J.S. Richardson. 2016. "Causes and Consequences of Invertebrate Drift in Running Waters: From Individuals to Populations and Trophic Fluxes." *Canadian Journal of Fisheries and Aquatic Sciences* 73: 1292–305. <https://doi.org/10.1139/cjfas-2015-0363>.
- Naman, S.M., J.S. Rosenfeld, L.C. Third, and J.S. Richardson. 2017. "Habitat-Specific Production of Aquatic and Terrestrial Invertebrate Drift in Small Forest Streams: Implications for Drift-Feeding Fish." *Canadian Journal of Fisheries and Aquatic Sciences* 74: 1208–17. <https://doi.org/10.1139/cjfas-2016-0406>.
- Neuswanger, J., M.S. Wipfli, A.E. Rosenberger, and N.F. Hughes. 2014. "Mechanisms of Drift-Feeding Behavior in Juvenile Chinook Salmon and the Role of Inedible Debris in a Clear-Water Alaskan Stream." *Environmental Biology of Fishes* 97: 489–503. <https://doi.org/10.1007/s10641-014-0227-x>.
- Nicieza, A.G., and N.B. Metcalfe. 1997. "Growth Compensation in Juvenile Atlantic Salmon: Responses to Depressed Temperature and Food Availability." *Ecology* 78: 2385–400. [https://doi.org/10.1890/0012-9658\(1997\)078\[2385:GCIJAS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[2385:GCIJAS]2.0.CO;2).
- Nilsson, C., C.A. Reidy, M. Dynesius, and C. Revenga. 2005. "Fragmentation and Flow Regulation of the World's Large River Systems." *Science* 308: 405–08. <https://doi.org/10.1126/science.1107887>.
- Nislow, K.H., A.J. Sepulveda, and C.L. Folt. 2004. "Mechanistic Linkage of Hydrologic Regime to Summer Growth of Age-0 Atlantic Salmon." *Transactions of the American Fisheries Society* 133: 79–88. <https://doi.org/10.1577/T02-168>.
- Ovidio, M., H. Capra, and J.C. Philippart. 2008. "Regulated Discharge Produces Substantial Demographic Changes on Four Typical Fish Species of a Small Salmonid Stream." *Hydrobiologia* 609: 59–70. <https://doi.org/10.1007/s10750-008-9399-8>.
- Palmer, M., and A. Ruhi. 2019. "Linkages between Flow Regime, Biota, and Ecosystem Processes: Implications for River Restoration." *Science* 365: eaaw2087. <https://doi.org/10.1126/science.aaw2087>.
- Petts, G.E. 2009. "Instream Flow Science for Sustainable River Management." *Journal of the American Water Resources Association* 45: 1071–86. <https://doi.org/10.1111/j.1752-1688.2009.00360.x>.
- Piccolo, J.J., B.M. Frank, and J.W. Hayes. 2014. "Food and Space Revisited: The Role of Drift-Feeding Theory in Predicting the Distribution, Growth, and Abundance of Stream Salmonids." *Environmental Biology of Fishes* 97: 475–88. <https://doi.org/10.1007/s10641-014-0222-2>.
- Poff, N.L., B.D. Richter, A.H. Arthington, S.E. Bunn, R.J. Naiman, E. Kendy, M. Acreman, et al. 2010. "The Ecological Limits of Hydrologic Alteration (ELOHA): A New Framework for Developing Regional Environmental Flow Standards." *Freshwater Biology* 55: 147–70. <https://doi.org/10.1111/j.1365-2427.2009.02204.x>.
- Poff, N.L., and J.K.H. Zimmerman. 2010. "Ecological Responses to Altered Flow Regimes: A Literature Review to Inform the Science and Management of Environmental Flows." *Freshwater Biology* 55: 194–205. <https://doi.org/10.1111/j.1365-2427.2009.02272.x>.
- Quillet, E., S. Le Guillou, J. Aubin, and B. Fauconneau. 2005. "Two-Way Selection for Muscle Lipid Content in Pan-Size Rainbow Trout (*Oncorhynchus mykiss*)." *Aquaculture* 245: 49–61. <https://doi.org/10.1016/j.aquaculture.2004.12.014>.
- R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Railsback, S.F. 2016. "Why It Is Time to Put PHABSIM Out to Pasture." *Fisheries* 41: 720–25. <https://doi.org/10.1080/03632415.2016.1245991>.
- Railsback, S.F. 2022. "What We Don't Know about the Effects of Temperature on Salmonid Growth." *Transactions of the American Fisheries Society* 151(1): 3–12. <https://doi.org/10.1002/tafs.10338>.
- Railsback, S.F., B.C. Harvey, and C. Sheppard. 2011. "InSTREAM: The Individual-Based Stream Trout Research and Environmental Assessment Model, Version 5.0." https://www.fs.usda.gov/psw/publications/documents/psw_gtr218/.
- Rashidabadi, F., J.S. Rosenfeld, A. Abdoli, S.M. Naman, and A. Nicolas. 2022. "Seasonal Changes in Invertebrate Drift: Effects of Declining Summer Flows on Prey Abundance for Drift-Feeding Fishes." *Hydrobiologia*. 849: 1855–69. <https://doi.org/10.1007/s10750-022-04831-x>.
- Reiser, D.W., and P.J. Hilgert. 2018. "A Practitioner's Perspective on the Continuing Technical Merits of PHABSIM." *Fisheries* 43: 278–83. <https://doi.org/10.1002/fsh.10082>.
- Richter, B., M. Davis, C. Apse, and C. Konrad. 2012. "A Presumptive Standard for Environmental Flow Protection." *River Research and Applications* 28: 1312–21. <https://doi.org/10.1002/rra.1511>.
- Richter, B.D., R. Mathews, D.L. Harrison, and R. Wigington. 2003. "Ecologically Sustainable Water Management: Managing River Flows for Ecological Integrity." *Ecological Applications* 13: 206–24. [https://doi.org/10.1890/1051-0761\(2003\)013\[0206:ESWMMR\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2003)013[0206:ESWMMR]2.0.CO;2).
- Rosenfeld, J., H. Beecher, and R. Ptolemy. 2016. "Developing Bioenergetic-Based Habitat Suitability Curves for Instream Flow Models." *North American Journal of Fisheries Management* 36: 1205–19. <https://doi.org/10.1080/02755947.2016.1198285>.
- Rosenfeld, J.S., and S. Boss. 2001. "Fitness Consequences of Habitat Use for Juvenile Cutthroat Trout: Energetic Costs and Benefits in Pools and Riffles." *Canadian Journal of Fisheries and Aquatic Sciences* 58: 585–93. <https://doi.org/10.1139/f01-019>.
- Rosenfeld, J.S., N. Bouwes, C.E. Wall, and S.M. Naman. 2014. "Successes, Failures, and Opportunities in the Practical Application of Drift-Foraging Models." *Environmental Biology of Fishes* 97: 551–74. <https://doi.org/10.1007/s10641-013-0195-6>.
- Rosenfeld, J.S., and R. Ptolemy. 2012. "Modelling Available Habitat versus Available Energy Flux: Do PHABSIM Applications that Neglect Prey Abundance Underestimate Optimal Flows for Juvenile Salmonids?" *Canadian Journal of Fisheries and Aquatic Sciences* 69: 1920–34. <https://doi.org/10.1139/f2012-115>.
- Rosenfeld, J.S., and J. Taylor. 2009. "Prey Abundance, Channel Structure and the Allometry of Growth Rate Potential for Juvenile Trout." *Fisheries Management and Ecology* 16: 202–18. <https://doi.org/10.1111/j.1365-2400.2009.00656.x>.
- Rossi, G.J., D.W. Mierau, and J.K. Carah. 2021. "Hydraulic Properties of the Riffle Crest and Applications for Stream Ecosystem Management." *Journal of the American Water Resources Association*. 1–18. <https://doi.org/10.1111/1752-1688.12961>.
- Rossi, G.J., M.E. Power, S.M. Carlson, and T.E. Grantham. 2022. "Seasonal Growth Potential of *Oncorhynchus mykiss* in Streams with Contrasting Prey Phenology and Streamflow." *Ecosphere* 13: e4211. <https://doi.org/10.1002/ecs2.4211>.

- Rossi, G.J., M.E. Power, S. Pneh, J.R. Neuswanger, and T.J. Caldwell. 2021. "Foraging Modes and Movements of *Oncorhynchus mykiss* as Flow and Invertebrate Drift Recede in a California Stream." *Canadian Journal of Fisheries and Aquatic Sciences* 78: 1045–56. <https://doi.org/10.1139/cjfas-2020-0398>.
- Sloat, M.R., and G.H. Reeves. 2014. "Individual Condition, Standard Metabolic Rate, and Rearing Temperature Influence Steelhead and Rainbow Trout (*Oncorhynchus mykiss*) Life Histories." *Canadian Journal of Fisheries and Aquatic Sciences* 71: 491–501. <https://doi.org/10.1139/cjfas-2013-0366>.
- Sogard, S.M., T.H. Williams, and H. Fish. 2009. "Seasonal Patterns of Abundance, Growth, and Site Fidelity of Juvenile Steelhead in a Small Coastal California Stream." *Transactions of the American Fisheries Society* 138: 549–63. <https://doi.org/10.1577/T08-172.1>.
- Sommer, T., B. Schreier, J.L. Conrad, L. Takata, B. Serup, R. Titus, C. Jeffres, E. Holmes, and J. Katz. 2020. "Farm to Fish: Lessons from a Multi-Year Study on Agricultural Floodplain Habitat." *San Francisco Estuary and Watershed Science* 18: 1–20. <https://doi.org/10.15447/SFEWS.2020V18ISS3ART4>.
- Stark, J.D., K.A. Shearer, and J.W. Hayes. 2002. "Are Aquatic Invertebrate Drift Densities Uniform? Implications for Salmonid Foraging Models." *SIL Proceedings* 28: 988–91. <https://doi.org/10.1080/03680770.2001.11901865>.
- Stelzer, R.S., M. Shupryt, and R.W. Pillsbury. 2022. "The Impacts of Experimental Discharge Reduction on Fish and Invertebrate Communities in a Groundwater-Dependent Trout Stream." *Hydrobiologia* 849: 1625–43. <https://doi.org/10.1007/s10750-022-04807-x>.
- Stoffels, R.J., N.R. Bond, and S. Nicol. 2018. "Science to Support the Management of Riverine Flows." *Freshwater Biology* 63: 996–1010. <https://doi.org/10.1111/fwb.13061>.
- Sutton, S.G., T.P. Bult, and R.L. Haedrich. 2000. "Relationships among Fat Weight, Body Weight, Water Weight, and Condition Factors in Wild Atlantic Salmon Parr." *Transactions of the American Fisheries Society* 129: 527–38. [https://doi.org/10.1577/1548-8659\(2000\)129<0527:RAFWBW>2.0.CO;2](https://doi.org/10.1577/1548-8659(2000)129<0527:RAFWBW>2.0.CO;2).
- Tharme, R.E. 2003. "A Global Perspective on Environmental Flow Assessment: Emerging Trends in the Development and Application of Environmental Flow Methodologies for Rivers." *River Research and Applications* 19: 397–441. <https://doi.org/10.1002/rra.736>.
- Turnipseed, D.P., and V.B. Sauer. 2010. "Discharge Measurements at Gaging Stations." In: U.S. Geological Survey Techniques and Methods, Book 3, Ch A8. pp. 1–87.
- van Vliet, M.T.H., F. Ludwig, J.J.G. Zwolsman, G.P. Weedon, and P. Kabat. 2011. "Global River Temperatures and Sensitivity to Atmospheric Warming and Changes in River Flow." *Water Resources Research* 47: W02544. <https://doi.org/10.1029/2010WR009198>.
- VerWey, B.J., M.J. Kaylor, T.S. Garcia, and D.R. Warren. 2018. "Effects of a Severe Drought on Summer Abundance, Growth, and Movement of Cutthroat Trout in a Western Oregon Headwater Stream." *Northwestern Naturalist* 99: 209–21. <https://doi.org/10.1898/NWN17-271>.
- Webb, J.A., K.A. Miller, E.L. King, S.C. de Little, M.J. Stewardson, J.K.H. Zimmerman, and N.L. Poff. 2013. "Squeezing the Most Out of Existing Literature: A Systematic Re-Analysis of Published Evidence on Ecological Responses to Altered Flows." *Freshwater Biology* 58: 2439–51. <https://doi.org/10.1111/fwb.12234>.
- Wheeler, K., S.J. Wenger, and M.C. Freeman. 2018. "States and Rates: Complementary Approaches to Developing Flow-Ecology Relationships." *Freshwater Biology* 63: 906–16. <https://doi.org/10.1111/fwb.13001>.
- Willis, A.D., R.A. Peek, and A.L. Rypel. 2021. "Classifying California's Stream Thermal Regimes for Cold-Water Conservation." *PLoS ONE* 16(8): e0256286. <https://doi.org/10.1371/journal.pone.0256286>.
- Yarnell, S.M., G.E. Petts, J.C. Schmidt, A.A. Whipple, E.E. Beller, C.N. Dahm, P. Goodwin, and J.H. Viers. 2015. "Functional Flows in Modified Riverscapes: Hydrographs, Habitats and Opportunities." *BioScience* 65: 963–72. <https://doi.org/10.1093/biosci/biv102>.
- Yarnell, S.M., E.D. Stein, J.A. Webb, T. Grantham, R.A. Lusardi, J. Zimmerman, R.A. Peek, B.A. Lane, J. Howard, and S. Sandoval-Solis. 2020. "A Functional Flows Approach to Selecting Ecologically Relevant Flow Metrics for Environmental Flow Applications." *River Research and Applications* 36: 318–24. <https://doi.org/10.1002/rra.3575>.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Rhoades, Suzanne J., Timothy J. Caldwell, Scott McBain, Rene Henery, Natalie Stauffer-Olsen, Tara McKinnon, Gabriel J. Rossi and Sudeep Chandra. 2023. "Trout Bioenergetics As a Process-based Tool to Estimate Ecological Risk in a Regulated River." *JAWRA Journal of the American Water Resources Association* 00 (0): 1–18. <https://doi.org/10.1111/1752-1688.13173>.