Received: 13 March 2018 | Revised: 11 July 2018 | Accepted: 12 July 2018
DOI: 10.1002/rra.3340

RESEARCH ARTICLE

WILEY

Decreased streamflow impacts fish movement and energetics through reductions to invertebrate drift body size and abundance

Timothy J. Caldwell[1] | **Gabriel J. Rossi**[2] | **Rene E. Henery**[1,3,4] | **Sudeep Chandra**[1,4]

[1] Department of Biology, College of Science, University of Nevada—Reno, Reno, Nevada
[2] McBain Associates—Applied River Sciences, Arcata, California
[3] Trout Unlimited, Mount Shasta, California
[4] Global Water Center, University of Nevada—Reno, Reno, Nevada

Correspondence
Timothy J. Caldwell, Department of Biology, College of Science, University of Nevada—Reno, Reno, NV.
Email: timothycaldwell@unr.edu

Present Address
Gabriel J. Rossi, Department of Integrated Biology, University of California at Berkeley, Berkeley, CA, USA.

Funding information
Marin Community Foundation; CalTrout

Abstract

Streamflow drives ecological processes across multiple trophic levels making it a “master variable in lotic systems.” In mountain systems, especially those that are regulated, increased frequency of droughts and reductions in snowpack may alter future streamflow regimes and impact ecological processes. We monitored invertebrate drift abundance, size, and diversity as a function of streamflow. We then related these variables to fish movement and energetic efficiencies in the Upper Shasta River in California, above and below a large streamflow diversion. Invertebrate drift biomass was significantly less at impaired flows compared with unimpaired flows, and average body size of invertebrates decreased with decreasing streamflow. Generally, fish movement was greater at the impaired flow site (>50% of the time fish were tracked). Fish movement at the upstream site was negatively related to the size of individual prey items and amount of prey available, and significant drivers were not detected in the flow-impaired site. Energetic efficiency was reduced by over 70% when search foraging took place, and the net rate of energetic intake was below 0 J/s for low-flow periods. Our results suggest that fish foraging behaviour may be influenced indirectly by altered streamflow through changes to amount and size of invertebrate drift. A shift to foraging behaviour, coupled with low food availability, results in decreased energetic efficiency. Future prescriptions of flow rates to regulated rivers should account for changes to invertebrate drift, fish behaviour, and fish energetics on seasonal time scales.

KEYWORDS

bioenergetics, fish movement, invertebrate drift, streamflow

1 | INTRODUCTION

Streamflow is often described as the “master variable” in rivers (Power, Sun, Parker, Dietrich, & Wootton, 1995), and alteration to it may result in ecological consequences (Bunn & Arthington, 2002; Poff & Zimmerman, 2010). Anthropogenic and climatic changes to streamflow may cause changes to both physical, chemical, and biological processes (Figure 1) in mountain systems. At the ecosystem scale, primary production may be altered due to different winter and low-flow conditions, resulting in toxic algal blooms (Power, Bouma-Gregson, Higgins, & Carlson, 2015). At the community scale, benthic invertebrate richness often decreases at reduced flow rates (Dewson, James, & Death, 2007a). Altered flow regimes also negatively affect fish communities by reducing fish growth in streams (Harvey, Nakamoto, & White, 2006; Macnaughton et al., 2017; Ruhí, Olden, & Sabo, 2016; Wenger et al., 2011). Given the number of rivers with altered flow (Magilligan & Nislow, 2005) and the increasing risk of drought that may cause low streamflow conditions in mountain systems (Vörösmarty, Green, Salisbury, & Lammers, 2000), continued impacts to ecological function are expected (Pyne & Poff, 2017).

Size structure, diversity, and abundance of invertebrate drift decrease in flow-regulated rivers (Dewson et al., 2007a; Kennedy et al., 2014; Walters & Post, 2010). Dewson, James, and Death (2007b) observed significant declines in community richness of benthic invertebrates after experimentally reducing streamflow. Reductions in abundance and diversity in benthic habitat translates into alterations to drifting invertebrates as well (Kennedy et al., 2014; Naman, Rosenfeld, & Richardson, 2016; Poff & Ward, 1991; Shearer, Stark, Hayes, & Young, 2003). Mixed results have been observed from previous studies that relate streamflow to drift (Brittain & Eikeland, 1988; Naman et al., 2016; Poff & Ward, 1991; Robinson, Aebischer, & Uehlinger, 2004). For example, Poff and Ward (1991) reported that low streamflows increase drift abundance, which has been attributed to a behavioural response. The authors suggest that low streamflow decreases wetted habitat and increases competition between invertebrates, causing them to release into the water column. Alternatively, low streamflows reduce the probability of catastrophic drift (Gibbins, Vericat, & Batalla, 2007) and may reduce the amount of invertebrate drift (Callisto & Goulart, 2005). Contrary results are routed in the frequency or duration of flow changes, making it difficult to predict consequences of low streamflow on invertebrate drift abundance.

Reduction of abundance coupled with changes to diversity and size structure of drifting invertebrates is consequential to fish in lotic systems, but few studies have examined the cascading impacts of flow rate on invertebrate drift to fish (but see Lagarrigue et al., 2002; Miller & Judson, 2014; Weber, Bouwes, Jordan, & Jonsson, 2014). Salmonids typically occupy positions in the river that maximize their access to drifting prey and minimize their swimming costs (Fausch, 1984), creating a bioenergetically profitable habitat (Fausch, 2014; Hughes & Dill, 1990; Rosenfeld, Bouwes, Wall, & Naman, 2014). However, reduction in the amount of drifting invertebrates causes a shift from drift-based to search-based foraging (Fausch, Nakano, & Khano, 1997; Harvey & Railsback, 2014; Larranaga, Valdimarsson, Linnansaari, & Steingrímsson, 2018). A shift in feeding mode that forces salmonids to swim further distances for smaller or fewer prey items would decrease their energetic efficiency. Salmonids shift behaviour when prey are completely absent (Fausch et al., 1997), but ecologists have neither identified a level of invertebrate drift abundance that induces that shift nor how that shift may reduce energetic efficiency. Here, we test a model that streamflow is related to changes (abundance/diversity/size) to invertebrate drift that affects the energetic efficiencies of trout through foraging behaviour.

Stakeholders of regulated rivers are challenged with assessing rivers and prescribing streamflows that sustain human and ecological needs. A common approach assesses physical habitat (velocity, depth, substrate, and cover) and applies habitat suitability curves (e.g., Physical Habitat Simulation or PHABSIM). However, short falls of this approach exist, including exclusion of food availability, behaviour shifts, and emphasis on the physical habitat and ignoring biological factors (Railsback, 2016; Rosenfeld & Ptolemy, 2012; Weber et al., 2014). We quantified the diversity, size structure, and abundance of drifting invertebrates, the behaviour of salmonids, and the subsequent effects on bioenergetic efficiency on the flow-impaired and flow-unimpaired sections of the Upper Shasta River in northern California. We hypothesized that drift abundance, size structure, and community diversity would decrease with streamflow and be less in the flow-impaired reach. Consequentially, trout movement would increase, suggesting a shift from drift foraging to search foraging. Lastly, we hypothesized that energetic efficiencies would be less at the flow-impaired site than flow unimpaired.

Key Points

- Decreased body size and abundance of invertebrate drift associated with low streamflow influences fish behaviour.
- Shifts from drift-based foraging to search-based foraging can reduce fish energetic efficiency by double in low and impaired streamflows.
- Reductions in size and abundance of invertebrate drift at low and impaired streamflows can result in negative energetic efficiencies.

2 | METHODS

2.1 | Study site

The Upper Shasta River is a tributary to the Klamath River in Northern California (N41°21′; W122°25′, elevation = 991 m; Figure 1). A diversion extracts up to 0.85 m^3/s (90% of unimpaired flow) during the spring and summer months when flow is available (McBain Associates 2015, unpublished data). Above the diversion, the river is relatively unimpaired and has one diversion (<0.01 m^3/s) and streamflow peaks at close to 2.54 m^3/s during spring run-off and 0.20 m^3/s at summertime low flows (McBain Associates 2015, unpublished gaging data). Peak streamflow below the diversion is approximately 1.14 m^3/s and drops to a summertime low of approximately 0.01 m^3/s. The river has several small springs that maintain similar (within 1°C) temperatures above and below the diversion. The native fish community includes Rainbow Trout (*Oncorhynchus mykiss*) and Marbled Sculpin (*Cottus klamathensis*). Nonnative Brown Trout (*Salmo trutta*) were also present. Access was granted to one study location 0.4 km above the diversion referred to as upstream (control with unimpaired flow) and one location 0.15 km downstream of the diversion (treatment with impaired flow), referred to as downstream. The diversion between the reaches is a large (≈3 m tall) concrete structure spanning the width of the river, with a small fish ladder around it, and completely blocks streamflow at baseflow outside of the fish ladder. The diversion has a large forebay behind it that collects most drifting sediment (McBain Associates 2015, unpublished data); thus, there is expected to be little impact of drifting invertebrates from the upstream site and reach on the downstream site and reach. Each study location was a single riffle:run:pool unit. The upstream site's topography was heterogeneous with some large boulders (Figure 1c), whereas the

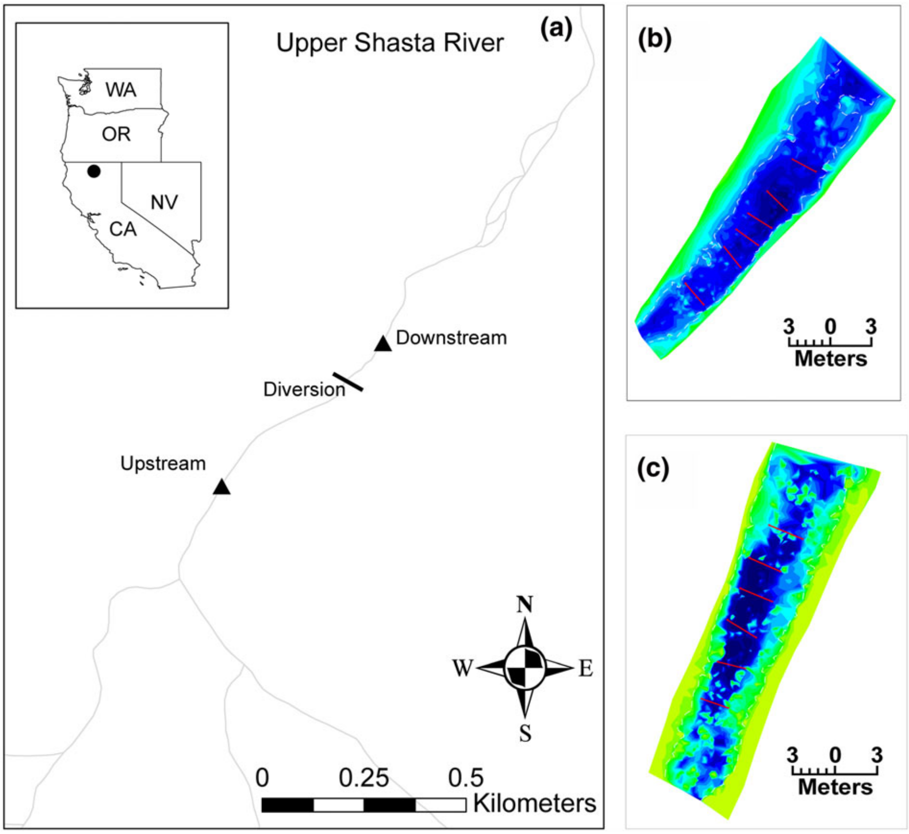

FIGURE 1 (a) Upper Shasta River, located in Northern California. Triangles denote the location of each study site. Upstream is the unimpaired flow site, and downstream is flow-impaired site. (b) Downstream and (c) upstream topographic maps of study sites and locations of passive integrated transponders antennae (red lines) at each site. Darker blue is lower elevations, whereas greener is higher elevations; these figures do not represent the wetted width of the river, rather they represent the entire topography of each site [Colour figure can be viewed at wileyonlinelibrary.com]

downstream site was homogenous (Figure 1b) with cobble-sized substrate (Caldwell & Chandra, 2017).

2.2 | Streamflow

Streamflow was continuously measured using a HOBO pressure logger and a stage discharge rating curve located 0.4 km downstream of the study site, using standard U.S. Geological Survey methods (Buchanan & Somers, 1969). Discharge at the upstream site was measured seven times.

2.3 | Invertebrate drift

Invertebrate drift was quantified bimonthly between May and August 2015 at both sites to determine the change in drift as streamflow declined seasonally at impaired and unimpaired flows. Each sample was collected with a 45 × 25-cm, 500-μm mesh drift net. To account for diurnal variation in invertebrate emergence (Brittain & Eikeland, 1988; Naman et al., 2016), samples were collected three times daily: 1–2 hr after sun rise, solar noon ± 1 hr, and 1–2 hr before sunset. At each site, the net was placed in the location most likely to contain foraging fish, determined by observation of the reach from the shoreline with polarized glasses and scanned for feeding fish. Velocity was measured with a Marsh-McBirney Flo-Mate at the centre of the drift net just after setting it and just before removing it, and then averaged. After 1 hr, the contents were sieved through a 250-μm mesh, preserved in 70% ethanol. Preserved samples were sorted with a dissecting microscope (Meiji EM-20, 10× magnification). Each invertebrate was identified to family (Thorp & Covich, 2010) and measured to the nearest 0.1 mm from using an ocular micrometre. Size of invertebrates (mg dry mass) was estimated from published length to dry mass relationships (Benke, Huryn, Smock, & Wallace, 1999; Sabo, Bastow, & Power, 2002).

Individuals and biomass per cubic metre was calculated by dividing the total biomass and number of individuals in each sample by the volume that passed through the net. Daily average number (individuals/m^3), biomass (mg dry mass/m^3), and size of invertebrates (mg dry mass) were computed from the three diurnal collections made at each site. To determine flux, biomass concentration was multiplied by daily discharge (m^3/day) at each site. We made the assumption that drift concentration was consistent throughout the study reach to make this calculation, which is assumed in other drift foraging models (Rosenfeld et al., 2014; Wall, Bouwes, Wheaton, Saunders, & Bennett, 2016).

2.4 | Fish movement

Rainbow Trout movement was monitored using passive integrated transponders (PIT tags). Fish were captured using electrofishing and tagged over the course of six tagging sessions between March and April 2015. Fish were anesthetized using CO_2 and tagged in the body cavity. Each fish was weighed to the nearest 0.1 g, and fork length was measured to the nearest 0.5 mm. Tagging efforts resulted in marking 147 fish (76 at the upstream site and 71 at the downstream site). Fifty-seven fish were detected at the upstream site, and the number of detections per fish ranged from 4,600 to 1. At the downstream site, 45 fish were detected and the number of detections ranged from 11,579 to 2 per fish. For the analysis of movement, we used fish that had more than 1,000 detections (nine at the downstream site and six at the upstream site) to ensure there were sufficient data to estimate movement. At the upstream site, fish masses were 3.92, 12.63, 14.46, 15.85, 19.10, and 42.96 g. Fish at the downstream site were 3.60, 5.01, 5.80, 8.62, 15.00, 15.21, 17.30, 28.70, and 33.61 g.

Each study site was instrumented with a six-antenna PIT array (Figure 1b,c). At each site, the six antennae were placed every 1–2 m from the head of the unit to the end of the pool and covered at least 80% of the wetted width of the river. At the upstream site, monitoring occurred from April 28, 2015, to May 17, 2015, and from June 8, 2015, to August 20, 2015. At the downstream site, monitoring occurred from April 4, 2017, to May 17, 2017, and from May 31, 2015, to August 20, 2015. At both sites, high water levels resulted in unmonitored periods, which required the removal of the array. Additionally, an array malfunction lasted 8 days at the downstream site from June 15, 2015, to June 23, 2015. Data for analysis were used starting on May 5, 2015, for fish movement analysis. These data overlapped with our invertebrate sampling and encompassed a wide range of streamflow.

The first and last antennae of the instrumented reach were used to determine when a fish entered and exited the instrumented area. Movement "bouts" were defined as detections at two different antennae that were <30 min apart. Detection data were first aggregated by fish; individual movement bouts were determined by the criteria that (a) consecutive detections were not recorded at the same antenna and were <30 min apart or (b) that there were no more than two consecutive detections on the same antenna less than 30 min apart. These criteria were formed to ensure that detections greater than 30 min apart were considered part of a different movement pattern and that if two consecutive detections were made on the same antennae and within 30 min, it was the result of fish moving off that antenna but returning before being detected at a different antenna. The distance and time of movement bouts were summed by day for each fish. For statistical comparison with drift rates, individual fish movement was averaged for the period of 2 days prior until 2 days after each drift sample.

2.5 | Net rate of energetic intake modelling

A drift feeding bioenergetic model (Hughes & Dill, 1990; Rosenfeld & Raeburn, 2009) was used to estimate differences in fish energetics between sites and between search- and drift-based foraging methods. The bioenergetic approach was a modification of the Hughes and Dill (1990) model, similar to the Rosenfeld and Taylor (2009) implementation. The drift energetic model quantifies the amount of energy content (joules) in prey that is drifting in a volume of water flowing past the foraging fish (considered gross energetic intake) and estimates the energy expenditures based on swimming costs (Hayes, Goodwin, Shearer, Hay, & Kelly, 2016) and is corrected for capture success with a modified Holling Disc function and probability of a fish attacking a prey (Rosenfeld & Raeburn, 2009). The energy left over (net rate of energetic intake; NREI) is available to be assimilated by the fish and used for growth or reproduction. Because drift energy was sampled at the most likely place for fish to be foraging (see above), we modelled energetics at that location (used centre of drift net as fish's focal point for feeding) and converted biomass to joules (Cummins & Wuycheck, 1971). The model was run for the range of fish sizes observed (7.5, 8.5, 9.5, 10.5, 11.5, and 12.5 cm) at both sites for each sampling period. For specific energetics calculations, please refer to Rosenfeld and Raeburn (2009).

We ran the model in two modes: first, assuming only drift foraging (drift model), and second, assuming a shift to search foraging (search model). In the search model run, to account for increased movement, we took the average percentage of time fish spent in movement patterns (determined from fish behaviour section) and increased the swimming velocity by 20, 35, and 50 cm/s (to account for swimming against current at a certain speed) for three model runs to incorporate uncertainty around swimming speed. We assumed that an increase in movement was the result of a shift from drift- to search-based foraging, for which our experimental design did not explicitly test, but has been observed by others (Larranaga et al., 2018). The range of swimming speed was qualitatively estimated at both sites using underwater video footage of fish foraging filmed. We also assumed that the amount of food available to drift feeders and search feeders was equivalent. We made this assumption based on the relationships between drift and benthic invertebrates (Kennedy et al., 2014).

2.6 | Statistical analysis

Daily biomass flux, concentration and size of drifting invertebrates, and fish movement patterns were compared with analysis of covariance. Streamflow was the covariate, whereas biomass flux, invertebrate concentration, size of invertebrates, and fish movement were the response variables; site was used as the grouping variable. Each variable was log transformed prior to analysis to better meet the assumptions of homogeneity of variances and normality.

To determine differences in a family-based community structure between sites and at different levels of discharge, we used nonmetric multidimensional scaling (Kenkel & Orlóci, 1986). Bray–Curtis distances were calculated to determine community dissimilarity (Clarke, 1993) between sites. Analysis of similarity was used to test for significant differences in community composition, and taxon-specific differences between communities were determined using similarity of percentages. All drift community analyses were done using the R package "vegan" (Oksanen et al., 2016).

An additive linear model was used to test for the effects of site, streamflow, invertebrate biomass, invertebrate average size, invertebrate diversity, fish size, and fish density on the movement patterns of fish. We used individual responses of movement for each fish so that individual characteristics (e.g., size) could be included as predictors. Post hoc analysis on site-specific effects was done using all variables except site and used only data from each site. The dredge function was used in the "MuMIn" package in R (Barton, 2013) to search for the best predictors of fish movement. The top five models are presented from each dredge (all data, upstream, downstream) and ranked using a combination of AICc (Burnham & Anderson, 2002), R^2, adjusted R^2, and significance (p) values to evaluate effects on fish movement patterns.

3 | RESULTS

3.1 | Streamflow

Streamflow differed significantly (Table 1) between sites. Difference between sites ranged from 0.3 to 0.6 m^3/s, during May and early June, to 0.15 m^3/s from June 26, 2015, until the end of the study. Streamflow peaked on approximately May 31, 2015, at both sites, then decreased until the end of the study (Figure 2a,b).

3.2 | Invertebrate drift

The total biomass of drifting invertebrates per day was significantly less (Table 1) at the downstream site and decreased with streamflow (Figure 2c,d). There was no significant difference among sites in the concentration of invertebrate biomass or individuals (Tables 1 and 2). However, we did detect an increase biomass concentration with increasing streamflow ($F = 13.75$, $R^2 = 0.25$, $p < 0.001$). Average size of invertebrates decreased with streamflow at the unimpaired flow site but varied at the impaired flow site (Figure 2e,f). However, the variation in invertebrate size with streamflow at the impaired site was driven by large (>2 mg) August 10, 2015 (one individual), sampling dates. Without those individuals in the analysis, the invertebrate size decreases significantly with streamflow ($p < 0.001$, $R^2 = 0.80$).

The dominant taxa by total individuals at both sites were the midges (Diptera: Chironomidae) and mayflies (Ephemeroptera: Baetidae; Figure 3). However, terrestrial invertebrates generally made up much of the total biomass at both sites (Figure 4).

Nonmetric multidimensional scaling (Figure 3c) suggested groupings of invertebrates for streamflows of >0.5, 0.5–0.01, and <0.01 m^3/s (2D stress = 0.07) and was all significantly different analysis of similarity ($R = 0.62$, $p = 0.009$). Similarity of percentages procedures performed between sites at each sampling period indicated that diversity of invertebrates was 35% dissimilar between sites when streamflow exceeded 0.5 m^3/s at both sites, but increased to 70% during and after June 26, 2015, when flow rates at the downstream site dropped precipitously.

TABLE 1 Comparisons of streamflow, invertebrate biomass, invertebrate concentration, invertebrate average size, and proportion of fish movement between sites at the Upper Shasta River

Parameter	Covariate	*F*	*df*	*p* value
Streamflow	Time	57.89	39	<0.001
Biomass	Streamflow	64.9	39	<0.001
Concentration (drymass)	Streamflow	2.34	39	0.13
Concentration (individuals)	Streamflow	0.11	39	0.74
Size	Streamflow	1.73	39	0.19
Fish movement	Streamflow	9.71	77	<0.001

Note. Results are from analysis of covariance tests, with site as the grouping variable.

3.3 | Fish movement

The proportion of time spent moving by fish was significantly higher in the downstream site than in the upstream site (Table 1, Figure 3). Proportion of time spent moving was low (15% and 25% in flow-unimpaired and flow-impaired sites, respectively) in the early spring (May 4, 2017, to May 17, 2017) but increased throughout the summer at both sites (Figure 2g,h). Both proportion of time and total distance moved by fish were estimated and were directly correlated. We elected to use proportion of time moving as opposed to distance moved to better apply to energetics foraging.

Additive linear modelling suggested that when data from both sites were grouped, site and size have the largest effect on fish movement (Table 3), where being at the upstream site and larger prey resulted in less movement by fish. The second highest rated model included the terms total invertebrate biomass, streamflow, site, and size, where increases to biomass and streamflow both had negative effects on fish movement (Table 3). We did not detect any significant relationships between fish size and movement patterns.

To determine any site-specific patterns, we did a post hoc linear modelling exercise, which only included data from each site. At both sites, invertebrate size was related to fish movement; however, it was not a statistically significant effect at the downstream site (Table 3). At the upstream site, size of invertebrates, streamflow, and biomass all had significant negative effects on fish movement (Table 3). The diversity of invertebrates, size of fish, and number of fish in each pool did not have any significant effects on fish movement, but effects for those variables were examined.

3.4 | NREI modelling

The percent change in NREI between the drift model and the search model was lower at the upstream site compared with the downstream (Table 4). The highest changes in NREI in the search model occurred for the largest fish at both sites and during the later summer months (July and August). The percent reduction of NREI between the drift and search model varied with the swim speed parameter. The percent reduction of NREI between the two models from the lowest swim speed (20 cm/s) was 27% of that which was predicted by the highest swim speed (50 cm/s; Table 4).

We assumed that the search model was more accurate than drift only because we monitored fish movement; thus, we present NREI from that model. Additionally, we chose the middle swim speed model and assumed that it represented an average swim speed by search foraging fish.

The NREI of fish intake peaked during early spring (May 31, 2015, and June 8, 2015), at 1–2 J/s (Figure 4). For fish of all sizes and at both sites, NREI decreased precipitously with streamflow at both sites from early spring to midsummer and late summer (end of June through August; Figure 4). At the downstream site, NREI was negative from

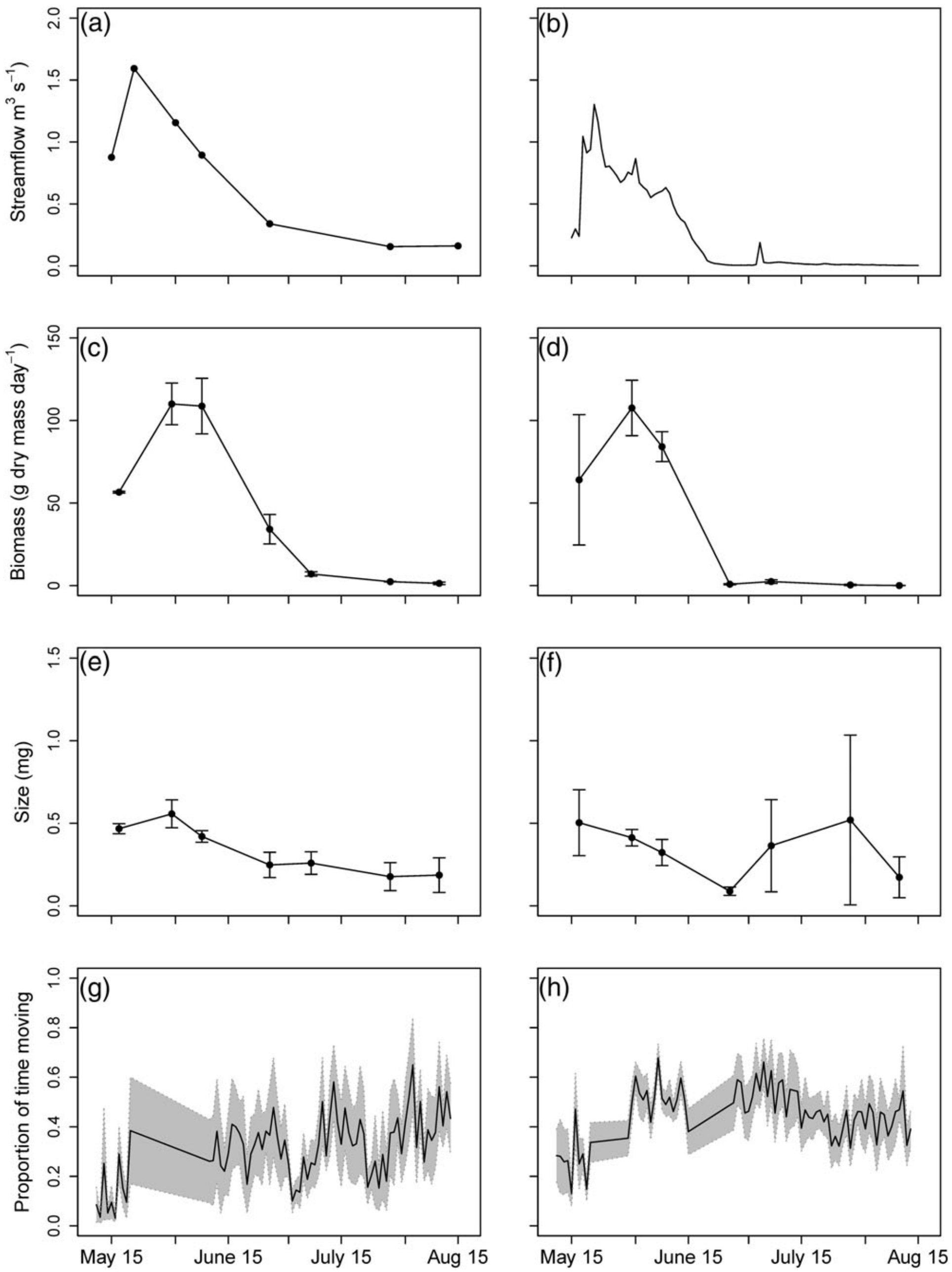

FIGURE 2 (a,b) Streamflow, (c,d) daily invertebrate drift biomass, (e,f) average size of invertebrate drift, and (g,h) fish movement in the Upper Shasta River, CA, during 2015. Data from upstream site are on the left-hand column, and data from downstream site are from the flow-impaired site is in the right-hand column. Streamflow for the unimpaired flow site was collected periodically from each sampling period, whereas streamflow from the impaired flow site (b) was monitored continuously by a stream discharge gage. Means and standard errors are presented for daily invertebrate drift biomass and average size of invertebrates. Daily average (black line) and standard error (grey shade) of the proportion of time spent moving by tagged fish; straight lines on each graph represent times that the array was malfunctioning or not in place due to high water

July 7, 2015, for fish 11.5 and 12.5 cm until the end of the study, and negative for all other sizes of fish from July 28, 2015, until the end of the study (Figure 4).

4 | DISCUSSION

Steam ecologists recognize that changes to the flow regime can manifest across trophic levels, but it is difficult to quantify. Our results suggest that decreased streamflow can reduce the total biomass and size of invertebrate drift, which may alter fish foraging behaviour and decrease energetic efficiency. These findings add to a newly formed body of data that (a) examine the impacts of flow-altered rivers across trophic levels and (b) suggest that managers of diverted rivers should move towards an integrated approach that examines physical habitat, biological resources, and individual behaviour (e.g., Harvey & Railsback, 2014; Hayes et al., 2016).

4.1 | Invertebrate drift

Invertebrate drift, driven by time of day, temperature, habitat, and streamflow, plays a critical role in the energetics of rivers (Brittain &

TABLE 2 Concentrations of invertebrate drift biomass and individuals in the Upper Shasta River, CA, at sites upstream and downstream of the diversion dam

	Upstream			Downstream		
Date	Streamflow m^3/s	mg drymass/m^3 ± *SE*	ind/m^3	Streamflow m^3/s	mg drymass/m^3 ± *SE*	ind/m^3
May 17, 2015	0.53	0.88 ± 0.01	2 ± 0	0.24	1.44 ± 0.56	3 ± 0
May 31, 2015	1.03	2.17 ± 0.43	4 ± 0	0.74	1.56 ± 0.22	4 ± 0
Jun 8, 2015	0.89	3.34 ± 0.7	8 ± 1	0.6	2.27 ± 0.32	8 ± 1
Jun 26, 2015	0.15	2.81 ± 0.73	12 ± 1	0.01	2.01 ± 0.82	29 ± 18
Jul 7, 2015	0.17	1.41 ± 0.13	6 ± 1	0.02	0.77 ± 0.35	5 ± 2
Jul 28, 15	0.16	0.66 ± 0.04	5 ± 2	0.01	0.001 ± 0.001	0 ± 0
Aug 10, 2015	0.15	0.25 ± 0.15	5 ± 4	< 0.01	0.04 ± 0.02	1 ± 0

Note. Values are the mean and standard error (*SE*) of three samples collected each sampling day (1–2 hr after sunrise, solar noon ± 1 hr, and 1–2 hr before sunset). No statistical differences were detected between sites (analysis of covariance, $p > 0.05$).

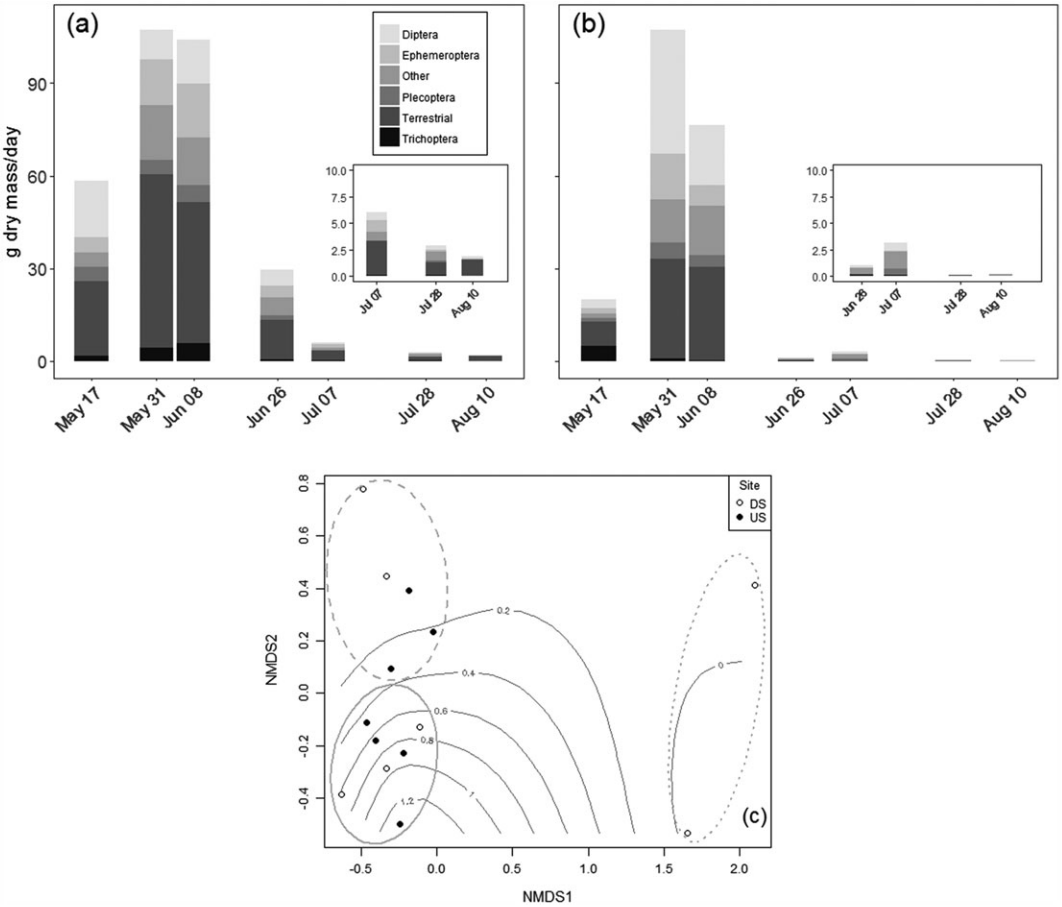

FIGURE 3 Invertebrate diversity in the Upper Shasta River, CA, during 2015. (a,b) Bar charts showing the contribution of each taxon to the community biomass at the (a) upstream site and (b) downstream site. Insets are zoomed in on the dates with low biomass for better visualization. (c) Nonmetric multidimensional scaling ordination of all invertebrate drift samples by family level (2D stress = 0.07). Contours indicate the discharge (m^3/s) that each sample was taken; groupings were made between at >0.5 (solid line), 0.5–0.01 (dashed line), and <0.01 (dotted line) m^3/s (analysis of similarity, $R = 0.62$, $p = 0.009$)

Eikeland, 1988; Naman et al., 2016; Naman, Rosenfeld, Third, & Richardson, 2017). For example, in the Colorado River, Kennedy et al. (2014) reported increases to the concentrations of *Gammarus* and *Chironomidae* during increased streamflow. Our results were similar, and we detected a statistically significant increase in the concentration of drift biomass with increasing streamflow. We further analysed our results in biomass flux per unit time (Naman et al., 2017) because looking at concentration alone does not account for the total amount of food available. Our findings suggest that total drift was comparable between sites at higher (>0.75 m^3/s) streamflow. However, at lower streamflow (<0.5 m^3/s) at the downstream site, the amount of drift decreased substantially. The mechanism causing the reduction in drift was not determined specifically in this study; however, possibilities include (a) life history timing resulted in emergence from the benthic habitat before streamflow decreased, so they can disperse effectively (Brittain & Eikeland, 1988; Naman et al., 2016)

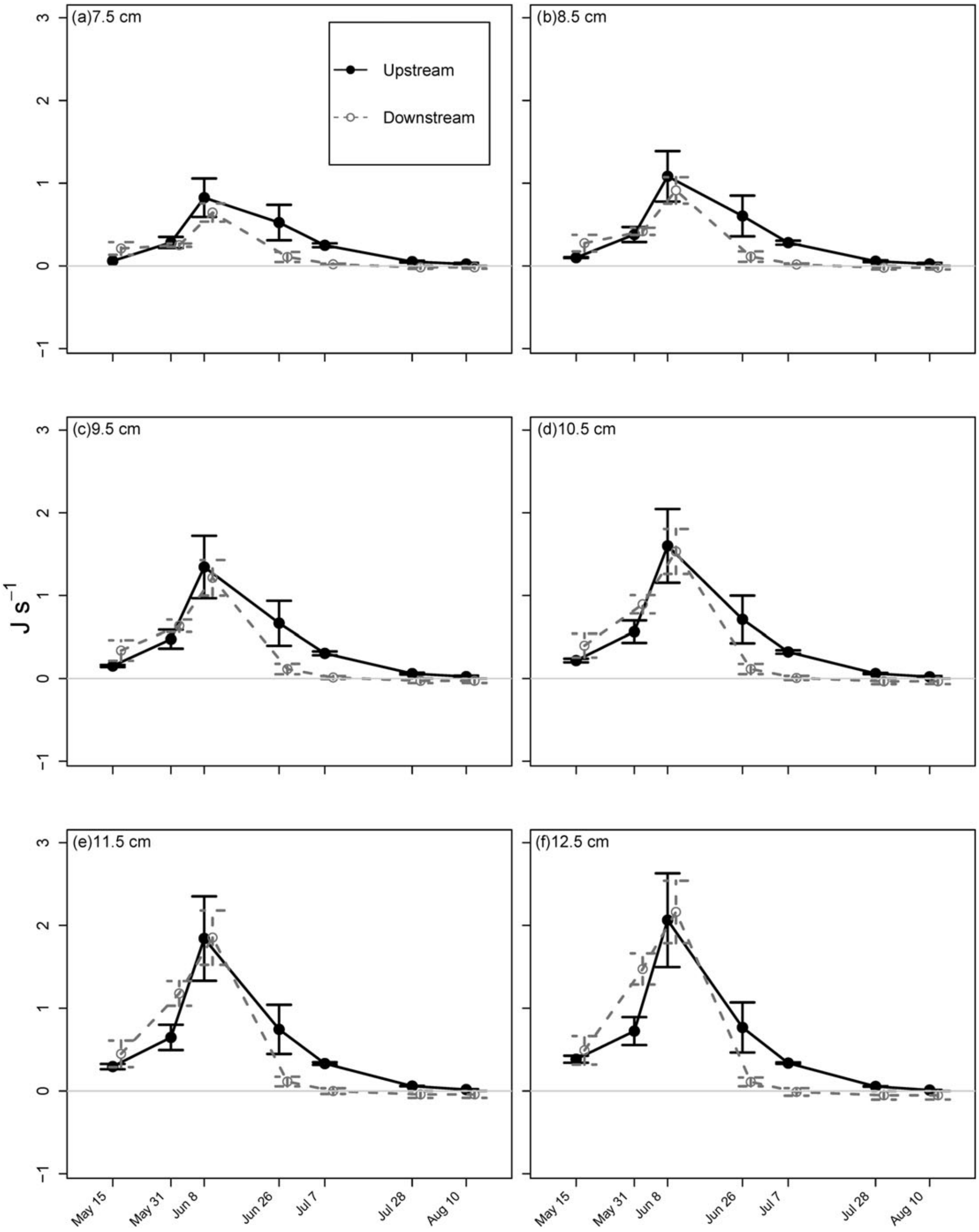

FIGURE 4 Net rate of energetic intake of fish of different sizes from unimpaired (grey dashed line) and impaired (solid line) streamflow sites in the Upper Shasta River, CA, during 2015. Panels represent the size class of fish. Net rate of energetic intake was modelled using a drift foraging model (Hughes & Dill, 1990) and adjusted for shifts in fish behaviour using the 35-cm/s average swimming speed model

or (b) that low streamflow reduces the transport potential between productive riffles and the pools where we measured drift (Naman et al., 2017). We suggest the latter, as we observed few individuals in the drift samples at low streamflow, but higher biomass concentrations that were driven by a few large individuals swept up in the drift from shoreline slackwaters (e.g., water striders and Gerridae) or terrestrial environments (e.g., ants and other Hymenoptera).

The average body size of drift can be important to fish foraging strategy and the distance at which they capture prey (Dodrill, Yackulic, Kennedy, & Hayes, 2016; Hughes & Dill, 1990). Our results suggest that average body size of drift at both sites decreased with streamflow (when excluding outliers from downstream site). Naman et al. (2017) suggested that invertebrate drift in riffle habitat was significantly larger than those in pool habitat. We believe that a similar mechanism may be functioning here, where the size of drifting invertebrates decreased because of a disconnection with the riffle habitat at lower streamflow.

Our results provide initial evidence to suggest that the community of drift in the Upper Shasta River differs between sites when streamflow is <0.5 m^3/s and becomes more dissimilar as streamflow decreases. These results reinforce findings of previous studies where diversity decreased with streamflow (Wooster, Miller, & DeBano,

TABLE 3 Top predictors of the proportion of time spent moving by fish among sites and at each site in the Upper Shasta River, CA

Model	Intercept	R^2	R^2 adjusted	AICc	ΔAICc	*p*
All data						
Site + Size	−0.1952	0.24	0.22	36.6	0	<0.000
Biomass + Streamflow + Site + Size	0.8869	0.27	0.23	38	1.34	<0.001
Streamflow + Site + Size	−0.1113	0.24	0.21	38.5	1.84	<0.001
Site	−0.3769	0.2	0.18	38.8	2.21	<0.001
Biomass + Site + Size	−0.1986	0.24	0.52	38.9	2.28	<0.001
Upstream (control)						
Size	−0.0914	0.2	0.17	33	0	0.01
Streamflow	−0.9824	0.18	0.15	33.6	0.6	0.02
Biomass	0.3516	0.15	0.11	34.6	0.6	0.04
Biomass + Size	−0.0131	0.2	0.13	35.7	2.7	0.06
Streamflow + Size	−0.2258	0.2	0.14	35.7	2	0.06
Downstream (treatment)						
Size	−0.377	0.02	0	−20.2	0	0.37
Biomass	−0.3206	0.001	0	−19.5	0.7	0.78
Streamflow	−0.368	0.001	0	−19.5	0.7	0.81
Streamflow + Size	−0.2454	0.03	0	−18.7	1.5	0.46
Biomass + Size	−0.3715	0.03	0	−18.5	1.7	0.51

TABLE 4 Range of percent reductions of modelled NREI between models that include search foraging and those that are drift only

% reduction in NREI (J s^{-1})								
	Date	**5/17/2015**	**5/31/2015**	**6/8/2015**	**6/26/2015**	**7/7/2015**	**7/28/2015**	**8/10/2015**
Upstream								
Size (cm)	7.5	−1.9 to −7.2	−0.4 to −1.3	−0.2 to −0.7	−0.3 to −1.0	−0.6 to −2.2	−3.0 to −11.1	−7.0 to −26.0
	8.5	−1.5 to −5.5	−0.3 to −1.2	−0.2 to −0.7	−0.3 to −1.1	−0.7 to −2.5	−3.3 to −12.3	−7.8 to −29.0
	9.5	−1.2 to −4.5 -	−0.3 to −1.2	−0.2 to −0.7	−0.3 to −1.2	−0.8 to −2.8	−3.8 to −14.1	−9.1 to −33.9
	10.5	−1.1 to −4.0	−0.3 to −1.3	−0.2 to −0.7	−0.4 to −1.4	−0.9 to −3.3	−4.5 to −16.8	−11 to −41.1
	11.5	−1.0 to −3.6	−0.4 to −1.4	−0.2 to −0.7	−0.5 to −1.7	−1.1 to −3.9	−5.5 to −20.5	−13.9 to −51.8
	12.5	−0.9 to −3.5	−0.4 to −1.6	−0.2 to −0.8	−0.5 to −2.0	−1.3 to −4.8	−6.9 to −25.6	−13.4 to −67.8
Downstream								
Size (cm)	7.5	−0.7 to −2.6	−1.5 to −5.8	−0.7 to −2.4	−1.3 to −5.0	−9.8 to −36.5	−25.5 to −94.9	−32.8 to −122.3
	8.5	−0.7 to −2.5	−1.2 to −4.4	−0.6 to −2.1	−1.6 to −5.9	−12.0 to −44.6	−25.5 to −94.8	−32.6 to −121.3
	9.5	−0.7 to −2.5	−1.0 to −3.6	−0.5 to −2.0	−1.9 to −7.1	−15.2 to −56.5	−25.5 to −94.8	−32.3 to −120.2
	10.5	−0.7 to −2.7	−0.9 to −3.2	−0.5 to −2.0	−2.3 to −8.6	−20.0 to −74.3	−25.5 to −94.8	−32.0 to −119.3
	11.5	−0.8 to −2.9	−0.8 to −3.0	−0.5 to −2.0	−2.8 to −10.6	−27.5 to −102.5	−25.4 to −94.7	−31.8 to −118.4
	12.5	−0.9 to −3.3	−0.8 to −3.0	−0.6 to −2.2	−3.5 to −13.2	−40.7 to −151.6	−25.4 to −94.7	−31.6 to −117.7

Note. Range is presented as the minimum % reduction (20 cm/s swimming speed) to the maximum % reduction (50 cm/s swimming speed). NREI: net rate of energetic intake.

2016). The negative correlation between drift diversity and streamflow may be a direct reflection of species presence in the benthic habitat, which is influenced by streamflow (Dewson et al., 2007b; Hille et al., 2014; Kennedy et al., 2014; Walters & Post, 2010). Although numerous other mechanisms are plausible, streamflow is the underlying cause of each of them, suggesting that alterations to streamflow will typically result in changes to community diversity of invertebrate drift in rivers (Wooster et al., 2016).

4.2 | Fish movement

Drift-feeding salmonids have been shown to alter feeding behaviour in the absence of drifting prey, shifting from drift-based to search-based foraging (Fausch et al., 1997; Harvey & Railsback, 2014), and increase movement in decreased streamflow (Larranaga et al., 2018). Our results suggest that when streamflow is similar among sites, time that fish spent moving is comparable. However, when there is decreased streamflow at the flow-impaired site, with less drifting invertebrate biomass available per day, fish movement was significantly higher (downstream vs. upstream).

The average size of invertebrate drift had the most significant effect on the movement of fish. This mechanism is plausible in the Upper Shasta, as the ability of fish to detect prey items decreases rapidly with size (Hughes & Dill, 1990; Hughes, Hayes, Shearer, & Young, 2003). Total available drift biomass and streamflow were also important. As total drift rate declines, drift foraging fish with previously high focal point fidelity switch to search foraging (Fausch et al., 1997). Thus, our results suggest that streamflow may impact fish movement both directly (through habitat changes) and indirectly through the reduction of flux and body size of invertebrate drift. Interestingly, invertebrate community diversity or fish size was not important in fish movement, which suggests that neither prey preference nor size-based fish hierarchy is a driver for fish movement at our study sites.

As expected, all effects of size, streamflow, and biomass were significant for fish movement at the upstream site. This was similar to results from Fausch et al. (1997) and Hughes et al. (2003) where decreased or removal of invertebrate drift caused fish to alter foraging behaviour to find additional food. When compared with upstream sites, fish present below the diversion moved significantly more following diversion than they did upstream. However, the drivers of fish movement were difficult to identify at the downstream site as no statistically significant effects were detected. We suggest a few possible explanations. First, although we selected sites that were as similar as possible (excluding streamflow), the downstream site's topography was more homogenous, indicating more of a pool habitat than the upstream site. Fish have been shown to forage differently among habitats (Rosenfeld & Raeburn, 2009; Vondracek & Longanecker, 1993), and causes of invertebrate drift may also vary among sites with differing geomorphology (Naman et al., 2016). Given our observed difference in drivers between sites and the important role that geomorphic patches play in river ecology (Thorp, Thoms, & Delong, 2006), we suggest that future studies should replicate fish movement/behavioural studies in multiple habitats at various streamflow to help distinguish how habitat may interact with fish movement and streamflow.

4.3 | NREI modelling

NREI models are useful for identifying changes in the potential growth rates of fish as a function of food availability, velocity, and depth (Fausch, 2014; Piccolo, Frank, & Hayes, 2014). First, our NREI model suggests that estimated changes in movement reduce energetic efficiencies by more than 70% in the flow-impaired site. Second, our results show that NREI decreases with streamflow and season, driven by the reduction of food availability, velocity, and increased movement.

The first set of NREI modelling results suggest that search-based foraging can reduce energetic efficiencies when compared with only drift foraging at a flow-impaired site. Similar results were found in individual-based model results that included search-based foraging (Harvey & Railsback, 2014). In other research, Rosenfeld and Raeburn (2009) found increased growth rates among fish that drift foraged in riffle habitat when compared with pool habitat where the authors observed search foraging. Our results suggest that the size of invertebrate prey is a strong predictor of fish movement and decreases with streamflow and season. Therefore, we conclude that decreased streamflow can drive a smaller average size of prey, alter foraging behaviour of trout, and reduce energetic efficiencies.

The second set of results from our NREI modelling suggests that when streamflow is similar between sites, fish energetics are also comparable, which is related to similar movement patterns driven by food availability and food size. However, when streamflow is reduced during the late summer, below normal baseflows, energetic efficiencies can go below zero as a result of low food availability. Food availability drives NREI models (Harvey & Railsback, 2014; Hayes et al., 2016; Rosenfeld & Raeburn, 2009). However, the causes of its availability is not well understood (Naman et al., 2016) and varies among habitats and systems (Naman et al., 2017). We embraced this variability by including it in our model as error. Furthermore, we determined that food availability decreases with streamflow and season, which causes negative energetic efficiencies in flow-impaired areas during the late summer. Future research questions should address how NREI varies among habitat types and seasons so that streamflow to NREI relationships may be inferred at the population level.

5 | CONCLUSIONS

Drought, coupled with diversions, causes stress to the ecology of headwater streams (Vörösmarty et al., 2000). Our data suggest that when streamflow is similar in impaired and nonimpaired reaches, food availability to fish, fish movement, and fish energetics are comparable, and it is only when significant reductions to streamflow are made to the impaired site are differences observed. We conclude that reductions in streamflow cascade across trophic levels, altering the abundance and size of invertebrate drift, which increases movement of drift foraging fish and decreases energetic efficiency of fish in flow-impaired rivers. Our data support the incorporation of food availability, energetics, and behaviour when prescribing flow rates (Railsback, 2016; Rosenfeld & Ptolemy, 2012).

ACKNOWLEDGEMENTS

We thank S. McBain, F. Meyer, and A. Dockham with McBain Associates for discussions on the project for use of streamflow data. C. Jerde had valuable input on study design, sample size, and statistical methods. K. Feher, L. McConnell, J. Simmons, and J. Umek at the University of Nevada—Reno assisted with field work, whereas J. Culpepper provided a technical review. C. Adams, J. Bull, and C. Bean with California Department of Fish and Wildlife donated PIT arrays and assisted with PIT array install and fish tagging. We thank Dr Jim Thorp and four anonymous reviewers for helpful and constructive comments. This project and T. J. C. was supported by a grant from the Marin Community Foundation to California Trout with funding from M. and P. Robinson who also granted land access.

ORCID

Timothy J. Caldwell http://orcid.org/0000-0003-4696-6292

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How to cite this article: Caldwell TJ, Rossi GJ, Henery RE, Chandra S. Decreased streamflow impacts fish movement and energetics through reductions to invertebrate drift body size and abundance. *River Res Applic*. 2018;1–12. https://doi.org/10.1002/rra.3340