

RESPONSE OF INVERTEBRATE DRIFT TO DAM-RELEASE RESTORATION
PULSE FLOWS FROM LEWISTON DAM ON THE TRINITY RIVER, CA

By

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ABSTRACT

RESPONSE OF INVERTEBRATE DRIFT TO DAM-RELEASE RESTORATION PULSE FLOWS FROM LEWISTON DAM ON THE TRINITY RIVER, CA

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The widespread construction of dams to regulate rivers has dramatically altered aquatic ecosystems, but these impoundments also provide a unique opportunity to support freshwater conservation goals by implementing functional flow regimes designed to mitigate dam-related impacts on fisheries. Drifting invertebrates are an important food source for stream-dwelling juvenile salmonids such that drift feeding can be an energetically profitable foraging strategy, yet the effect of streamflow alterations on invertebrate drift dynamics is largely undetermined. Drift net samples were collected on four days before and four days during the ascending limb ($14\text{--}42\text{ m}^3/\text{s}$) of restoration pulse flows in April 2020 at four sites located along 48 river kilometers of the Trinity River downstream of Lewiston Dam in northern California. Results provide evidence of an inconsistent response by drifting invertebrate biomass concentration (mg/m^3) across pulse flows with increases observed during the first pulse, but little effects or potential decreases in subsequent pulses. Drift response varied among sites, where the effect of pulse flows was greater at sites closer to the dam and that underwent longer durations without disturbance in the preceding months. Weighted mean length (mm) of drifting invertebrates was lower at higher flows, a trend that may be temporally driven by

differing aquatic or terrestrial taxonomic groups dominating during base or pulse flows. These findings suggest that dam-release restoration flows can temporarily increase prey availability in the drift for juvenile salmonids, but the exploration of alternative restoration flow actions with meaningful long-term benefits to salmonid populations may be a more beneficial solution.

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INTRODUCTION

The decline of Pacific salmon (*Oncorhynchus spp.*) populations over the last few decades has stimulated major restoration efforts across the Pacific Northwest to improve the status of these iconic fishes. Early restoration actions primarily focused on physical habitat alterations (*e.g.*, in-stream habitat improvement, fish passage; Barinaga 1996; Bernhardt et al. 2005), while more recent work has centered around restoring natural processes. A critical element of restoring freshwater ecosystems is attaining functional environmental flows to support beneficial flow-ecology relationships (Poff et al. 2017) by preserving hydrologic signals upon which biophysical and native biological communities depend (Yarnell et al. 2020). The importance of a functional flow component for Mediterranean-montane streams (*e.g.*, peak magnitude flows, spring recession flows, dry season low flows, and wet season initiation flows; Yarnell et al. 2015) should be determined by investigating its relationship against a biotic response.

Whereas much work has occurred studying the response of fishes and habitat availability to varying flow metrics (*e.g.*, Kiernan et al. 2012; Zeug et al. 2014; Goodman et al. 2018), the invertebrate prey of fishes has been largely overlooked. Several studies have identified the need to further assess linkages between streamflow, invertebrate prey availability, and drift-foraging dynamics for consideration in future restoration plans (Weber et al. 2014; Naman et al. 2016; Lusardi et al. 2018).

Impact of Dams on Freshwater Ecosystems

Widespread dam construction in the early 20th century dramatically altered aquatic ecosystems across the United States, and while the rate of dam removal has been increasing in the country – over 1,000 dams were removed between 2010-2017 (Marshall 2019) – the socioeconomic and political complications are typically too great for dam removal projects to be feasible. Fishways are often constructed as a mitigation measure to enable fish passage around obstructions, but a literature review by Noonan et al. (2012) reported poor passage efficiencies by fishes worldwide in both downstream and upstream directions (68.5% vs. 41.7%, respectively) and recommended that passage facilities be improved for all migratory species of concern. A recent multidisciplinary review on fishway science corroborated earlier findings, emphasizing the need to improve fishways and formulate a rigorous, standardized, and ecologically relevant approach to assessing fish passage (Silva et al. 2018). The presence of fishways does not guarantee fish passage and without the implementation of expensive infrastructure renovations, river habitat above dams will continue to remain inaccessible to many anadromous fishes. Instead, it can be more effective to approach restoration from a mindset of reconciliation ecology, which encourages the accommodation of both human use and wildlife needs in human-dominated ecosystems (Rosenzweig 2003; Moyle et al. 2017). For example, dams can be operated to support freshwater conservation goals by using designed functional flow regimes that favor native fishes and continue providing social and economic benefits

(Chen and Olden 2017). For these reasons, management agencies should focus on improving habitat and flow regimes below dams to advance targeted restoration goals.

Importance of Invertebrate Drift and Streamflow

Drifting invertebrates are important food for stream-dwelling salmonids that feed opportunistically on diverse prey items (Allan 1981; Syrjänen et al. 2011). Juvenile salmonids often form competitive feeding hierarchies in optimal foraging locations (Nielsen 1992; Nakano 1995), with evidence suggesting prey availability and quality to be among the dominant factors influencing juvenile salmonid growth rates (Rosenfeld et al. 2005; Beauchamp 2009; Lusardi et al. 2019). Growth is an important determinant of fitness for salmonids, as juveniles with a larger size-at-outmigration have also been shown to have higher marine survival rates than smaller individuals (Osterback et al. 2014).

Despite current knowledge, there is still uncertainty surrounding the spatial, temporal, and biological variables that affect prey availability to juvenile salmonids as drift forage. Spatial factors, such as the inlet or outlet of a pool (Rosenfeld and Raeburn 2009) or riffle length (Naman et al. 2017), may affect invertebrate drift availability. Temporal studies have documented decreased levels of invertebrate drift abundance and biomass during summer months (Danehy et al. 2011) and elevated at nighttime (Naman et al. 2016). Biotic factors, such as increased aquatic macrophyte biomass, may also

affect invertebrate drift rates and abundance (Lusardi et al. 2018). Yet, underlying all these variables is streamflow, the “master variable” in lotic systems, that may limit and reset river populations on scales as large as watersheds (Power et al. 1995).

Studies exploring the effects of streamflow on invertebrate drift have exhibited inconsistent results across watersheds, as seen with mixed, and sometimes contradictory, results on the topic of invertebrate drift responses to manipulated flows. Several studies have observed a positive relationship between increased flows and invertebrate drift densities (Irvine and Henriques 1984; Perry and Perry 1986) and biomass concentrations (Miller and Judson 2014), but contrasting research suggests that reduced flows from water abstractions resulted in higher densities of invertebrate drift (González et al. 2018). There is also research reporting little to no effect of flow magnitude on the total drift flux of invertebrate abundance and biomass (Mochizuki et al. 2006). Previously published studies differed in hypotheses, response metrics, and experimental design, which may have led to their divergent conclusions. There are also differences in the geography and hydrology of study regions that make it difficult to predict outcomes for distinct watersheds at a time when hydrologic alterations are commonplace and detrimentally impact ecosystem function (Wooster et al. 2016; Pyne and Poff 2017), further exacerbating the need to study the relationship of streamflow and aquatic communities.

Insufficient streamflow to the mainstem Trinity River after the completion of dam construction negatively impacted the salmon and steelhead fishery (USFWS 1980) by

reducing juvenile rearing habitat for Chinook Salmon (*Oncorhynchus tshawytscha*), steelhead (*O. mykiss*), and Coho Salmon (*O. kisutch*) (USFWS and HVT 1999).

However, if dam-release flows can be managed to optimize invertebrate drift concentration for juvenile salmonid consumption, the stressor of limited rearing habitat may be alleviated by the supplementation of prey resources, which could increase growth rates, improve survival, and benefit the overall population.

Research Objectives

In this study, I examined the effects of streamflow on invertebrate drift during restoration pulse flows released from Lewiston Dam on the Trinity River. A 2018 study that gathered invertebrate drift and juvenile Chinook Salmon diet data in the Trinity River observed varied seasonal responses of invertebrate drift from February to April, yet detected a significant increase in invertebrate drift flux during the ascending limb of a pulse flow in mid-April (Starkey-Owens 2020). Other studies also suggest that invertebrate entrainment into the drift is maximized during the rising limb of a hydrograph (Robinson et al. 2004; Miller and Judson 2014). I sought to elaborate on findings from the 2018 Trinity River drift study (Starkey-Owens 2020) by further investigating invertebrate drift responses at distinct flow magnitudes during the ascending limb of pulse flows in April 2020 to examine whether dam-release restoration flows increase prey availability for drift-foraging juvenile salmonids. I hypothesized that

drifting invertebrate biomass concentration and body length would increase at higher flows and there would be differences in taxonomic community composition of drifting invertebrates between baseline flows and pulse flows. The findings from this study are intended to help guide management of the fishery on the highly regulated Trinity River.

METHODS

Study Area

The Trinity River watershed, with a basin size of 7,600 km² and river length of 266 km, is the largest tributary in the Klamath River Basin flowing from Mount Eddy in the Trinity Mountains through a rugged, forested region of northwest California. Two earthfill dams and a diversion were constructed in the 1960's that exported up to 90% of the Trinity River's annual inflow to the neighboring Sacramento River drainage for urban and agricultural development, resulting in insufficient flow volume and seasonal variation to support the river ecosystem downstream of the dams (USFWS and HVT 1999). The Trinity River watershed historically provided important natural resources, including water, fish, hydropower, and timber (Douglas and Taylor 1999; Adkins 2007), but a sharp decline of anadromous salmon populations followed the completion of dam construction – salmon harvest by anglers fell from 11,496 in 1941 (Moffett and Smith 1950) to a harvest quota of only 428 salmon for the 2020 fishing season (CDFW 2020). A multi-agency partnership was established in 2000 to improve the Trinity River fishery by restoring natural processes through actions such as increasing the flow allotment, implementing habitat rehabilitation, and conducting monitoring surveys (USDOI 2000). Current restoration plans allocate annual flow volumes (*i.e.*, restoration flows) to the mainstem Trinity River that are dependent on the water-year type (*e.g.*, dry or wet) and

guided by the strategy of adaptive management (USDOI 2000). Adaptive management follows the ethos that information is always incomplete and promotes the process of maintaining a direct feedback loop to constantly investigate a problem and update management solutions (Holling 1978). Restoration flows may also be designed to support experiments that will contribute to adaptive management, such as in this study.

This study was conducted within a 64-km reach between the most downstream dam on the mainstem Trinity River, Lewiston Dam, and the North Fork Trinity River. This river section is believed to be the most impacted by the dams and therefore designated as a priority for restoration efforts (hereafter referred to as the “Restoration Reach”; www.trrp.net). Four study sites were selected along the Trinity River Restoration Reach to capture spatial and site-specific variation: Sawmill, Steel Bridge, Evans Bar, and Junction City (Figure 1). Each sampling site was located within a meandering riffle unit with substrate dominated by cobble-sized particles. Valley constraint differed among the sites; Steel Bridge was classified as “confined” while the three other sites were classified as “variable confinement,” indicating that wetted area may expand differently in response to elevated flows (Beechie et al. 2015).

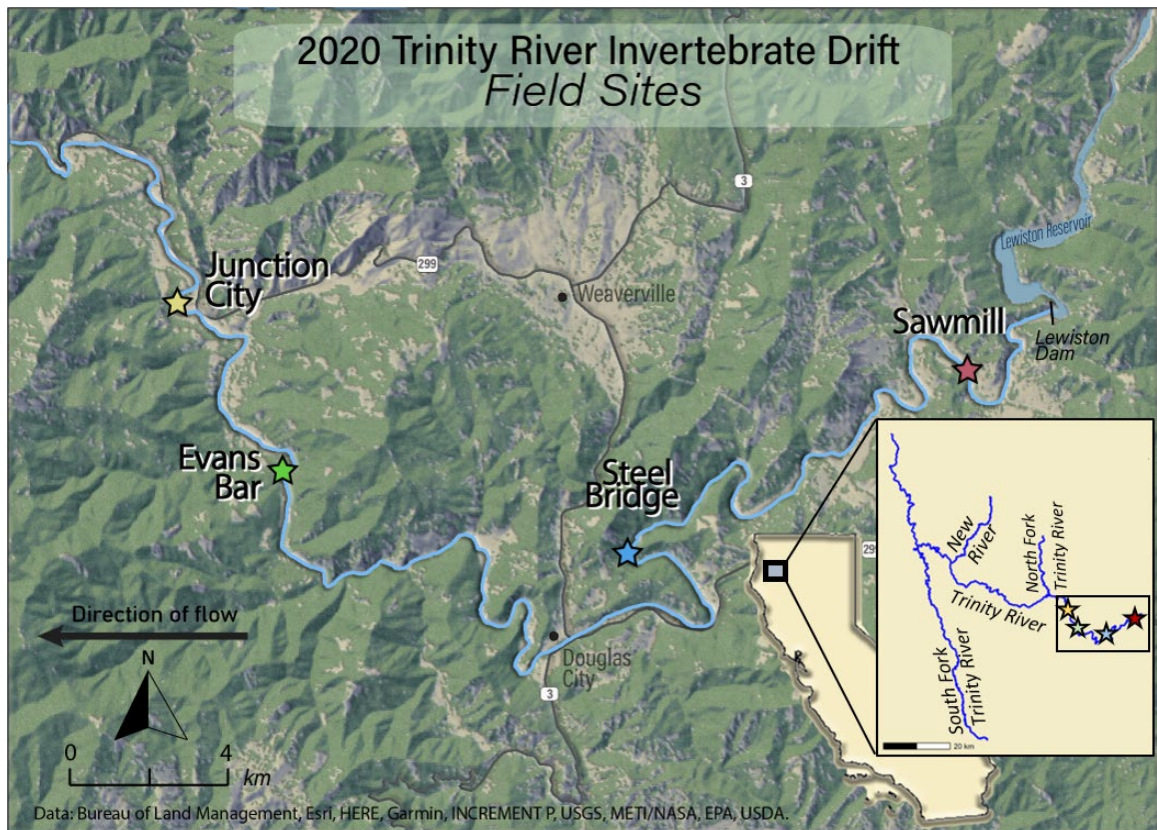


Figure 1. Four study sites in the Trinity River Restoration Reach sampled in April 2020. The direction of flow runs east to west. Inset: locator map illustrating the Restoration Reach in relationship to the Trinity River watershed and California.

Invertebrate Drift Sampling

In April 2020, eight days of invertebrate drift net sampling was conducted – four days during baseline flow conditions (8.5–14.2 m³/s) and four days during the ascending limb of restoration pulse flows (15.4–42.8 m³/s) (Figure 2). Each sample was collected with a 0.55 x 0.55-m, 500-μm mesh drift net that was installed at a targeted water depth

(around 0.5-m) and distance above the water surface (around 0.05-m). To better understand fine-scale responses of prey availability at specific streamflow levels, invertebrate drift was collected four or five times during each pulse flow event (approximately every 2-hrs at around 9, 12, 25, 35 and 42 m³/s; Figure 2) during which two drift nets were sampled concurrently for twenty or thirty minute intervals (hereafter referred to as “site sample event”). During all site sample events, both nets were monitored for excess debris build up and scrubbed when needed to prevent clogging. Special care was taken to avoid walking upstream of the nets to prevent unnatural disturbances to the benthos. Water depth and velocity were measured with a USGS topset wading rod and Hach FH950 handheld flow meter at the center of each drift net. Final velocities were calculated by averaging the start and end velocities for each drift net deployment; average velocity (m/s) was multiplied by the wetted net opening area (m²) and sample duration (seconds) to estimate the volume of water sampled (m³). Water temperature and turbidity were recorded at the start of each site sample event (Appendix A). Collected drift samples were preserved in 95% ethanol and transported to the laboratory at Humboldt State University (Arcata, CA). These same sampling methods were also employed during baseline flows to serve as reference samples, with the sampling schedule replicated as close as logistically possible to minimize effects from time of day (Figure 2). Each sampling day (*i.e.*, baseline 1, 2, 3, 4 and pulse 1, 2, 3, 4)

will be referred to as “sampling day” and the group of baseline (1-4) or pulse flows (1-4) will be referred to as “flow category.”

The spacing of the four sampling sites along 48-rkm resulted in large differences in arrival time of pulse flows released from Lewiston Dam (~10-hr lag time), hence sunset limited sampling to only two sites per flow pulse. An exception was that all four sites were sampled during the first baseline (April 1, 2020) and first pulse (April 14, 2020), although there was only enough time to sample once and twice, respectively, at the two downstream sites before sunset – the latest drift net sample collected during all sampling days was completed five minutes before sunset during pulse 1 at Junction City (Figure 2).

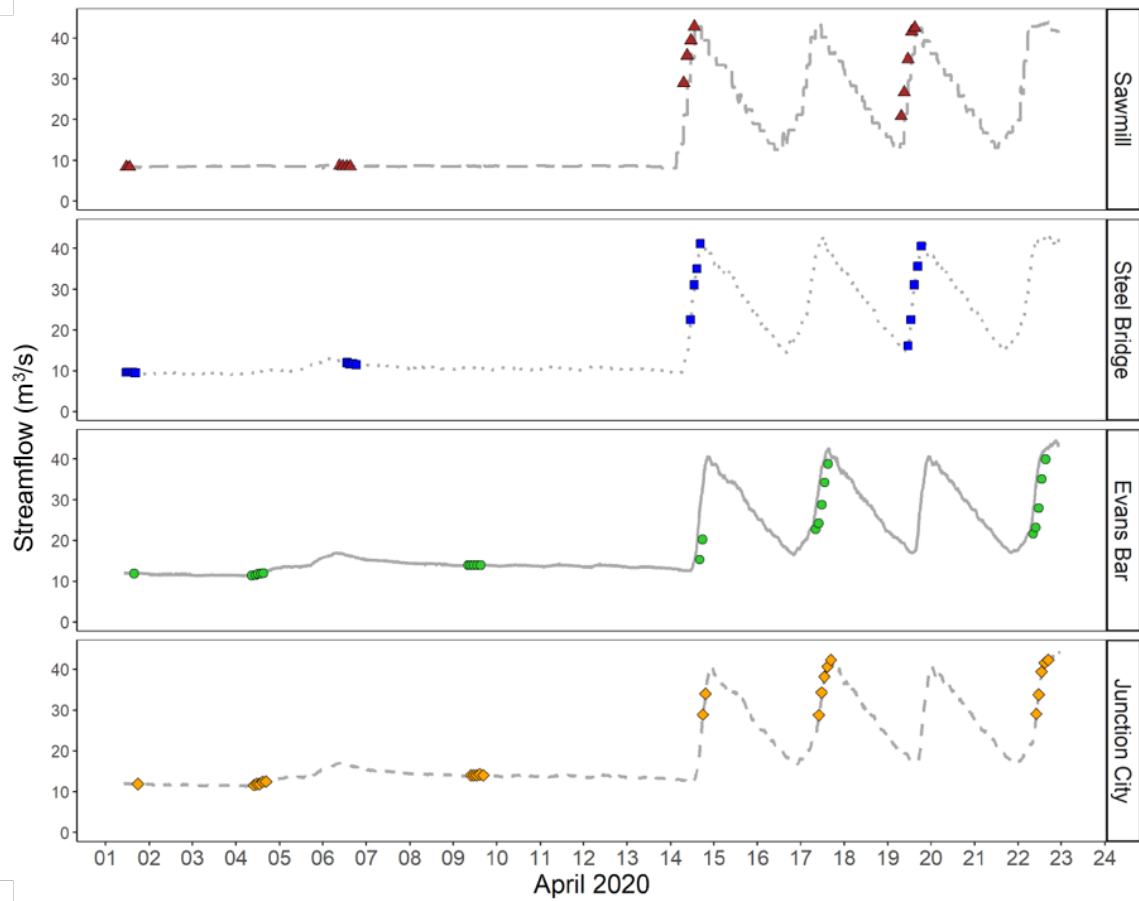


Figure 2. Timing of sampling at four study sites in the Trinity River Restoration Reach to illustrate the flow magnitude (m^3/s) when sampling occurred. Baseline sampling occurred on four days April 1-9 (baseline 1, 2, 3, 4) and pulse flow sampling occurred on four days April 14-22 (pulse 1, 2, 3, 4) of 2020. Sites are arranged from upstream to downstream (top to bottom). Each symbol indicates one site sample event (*i.e.*, two nets sampling simultaneously for 20- or 30-min intervals).

Laboratory Processing

Many of the 160 drift samples collected were large in volume and dense with filamentous algae, so they were subsampled by weight (mg) to reduce processing times (Sebastien et al. 1988). Dissecting microscopes (up to 90x magnification) were used to identify aquatic insects to family, terrestrial insects to order, and non-insects to class – if that taxonomic resolution was not possible for an individual, it was identified to the next lowest taxonomic level. All individuals were classified by life-stage (*i.e.*, larva, nymph, pupa, adult). Dichotomous keys by Merritt et al. (2008) and McCafferty (1981) were the primary identification resources and supplemented with additional online resources.

Body parameter estimates were made for every individual invertebrate by measuring it to the nearest millimeter, excluding any antennae and cerci. Invertebrate mass was estimated with the allometric regression formula $W = aL^b$, where W is total dry body mass (mg), L is total body length (mm), and a and b are taxon and life-stage specific published constants (Benke et al. 1999; Sabo et al. 2002; Wisseman 2012; Wardhaugh 2013). Individual values were summed within a given sample to calculate sample metrics (*i.e.*, mass, abundance), expanded by subsample fraction, then divided by the volume of water that passed through the net to calculate biomass concentration (mg/m³). I found that invertebrate biomass and energy (kJ/m³) were strongly correlated, and analysis of biomass and energy produced nearly identical results, so I only report the results for biomass (Appendix B). Weighted mean length (mm) was calculated for a

given sample by multiplying the count by the length for each taxon and dividing that by the sum of counts for all taxa (Appendix B). Site sample event estimates were calculated by averaging the totals of the two nets sampled concurrently. Twenty-three individual invertebrates with a length greater than 18.5-mm, the largest recorded prey length in juvenile Chinook Salmon diet samples collected in 2018 from the Restoration Reach (Starkey-Owens 2020), were removed prior to all analyses because they were assumed to be too large for juvenile salmonids to consume.

Data Analysis

Invertebrate Response Metrics

Linear mixed effects (LME) models were used to investigate how invertebrate drift varied at differing flow conditions, since this model accounts for the hierarchical sampling structure and inherent non-independence among drift net samples ($n=160$) (Pinheiro and Bates 2000). Response variables were invertebrate biomass concentration (mg/m^3) and weighted mean length (mm). For each response, a set of candidate models was examined that included two grouping variables of “site” ($n=4$) and “site sample event” ($n=80$) as random effects, where site sample event was nested within site; covariate fixed effects included water temperature ($^{\circ}\text{C}$), time of day (3 levels: dawn, daytime, dusk), flow category (2 levels: baseline or pulse), sampling day (8 levels: baseline 1, 2, 3, 4 and pulse 1, 2, 3, 4), flow magnitude (m^3/s), and flow rate of change

(m³/s per 15 min). The covariate “flow category” was never included in the same model as “sampling day” or “flow magnitude”, otherwise covariates were included in an additive manner while also testing interaction terms (Appendix C). The random effects were always included to account for spatial and temporal variation among samples.

Candidate models were evaluated using Akaike’s information criterion (AIC) to select for the most parsimonious model, which was defined as the simplest model within two AIC units of the lowest scoring model (Burnham and Anderson 2004). For each response variable, the model of best fit was further evaluated by examining 95% confidence intervals (CIs) around slope coefficient estimates of fixed effects and variances attributed to random effects. A similar approach to model selection has been used by other researchers with comparable study designs and research objectives (Naman et al. 2017; Rossi 2020). Early data exploration revealed a violation of constant variances for invertebrate biomass concentration, which was natural-log transformed to better meet assumptions of homogeneity of variances and normality of residuals. Analyses were performed using the R package “lme4” (Bates 2015) in RStudio version 1.4.1103 (RStudio Team 2020).

Invertebrate Community Composition

Invertebrate drift contributions from aquatic or terrestrial environments were compared at different flow categories to explore general trends of prey subsidy source. Individuals were grouped into either “aquatic” or “terrestrial” based on origin and life-

stage. Aquatic was assigned to early (*e.g.*, fly larvae and stonefly nymphs) and adult life-stages (*e.g.*, aquatic beetles, microcrustaceans) of invertebrates that originate and reside in-stream, whereas terrestrial was assigned to individuals that originate and reside in the terrestrial environment (*e.g.*, spiders, ants) and aquatic-born invertebrates that emerge from the stream to the terrestrial environment as winged adults (*e.g.*, adult flies, mayflies, stoneflies; hereafter referred to as “aquatic winged adults”). This classification method was used to compare the relative contribution to the drift from the terrestrial or aquatic environment (Grunblatt et al. 2019). Estimates of biomass concentration (mg/m^3) and numeric density were explored, where numeric density was calculated by dividing the total number of individuals in a sample by the volume sampled ($\# \text{ ind}/\text{m}^3$).

Invertebrate community composition among sites and at differing streamflows (8-42 m^3/s) was compared using nonmetric multidimensional scaling (Kenkel and Orlóci 1986) where Bray-Curtis distances were calculated to determine taxonomic dissimilarity among sites (Clarke and Ainsworth 1993). Reduced dimensions ($k=2$ or 3) were tested using a maximum of 100 iterations and corresponding stress plots were produced to measure goodness-of-fit, where a stress of less than 0.2 was considered acceptable. Following ordination selection, analysis of similarity was used to test for significant differences in community composition at each site. All community analyses were performed using the R package “vegan” (Oksanen 2020) in RStudio version 1.4.1103 (RStudio Team 2020).

RESULTS

Invertebrate Response Metrics

Biomass Concentration

Biomass concentration (mg/m^3) of drifting invertebrates increased by an average of 1.5x during combined pulse flow samples from combined baseflow samples, although the most notable response came from the first pulse (2x more biomass than the next highest of any other sampling day) (Table 1). The most parsimonious LME model included two covariates, flow magnitude (m^3/s) and sampling day (baseline 1, 2, 3, 4 and pulse 1, 2, 3, 4) (Table 2), which demonstrated inconsistent responses across sites (Figure 3) and sampling days (Figure 4), yet an overall positive relationship with flow magnitude ($p=0.001$; Figure 4). This model provides evidence that compared to the estimate for baseline 1, drifting invertebrate biomass concentration increased during pulse 1 ($p=0.03$; Figure 4) but decreased during pulse 3 ($p=0.003$; Figure 4). This model also presents a lack of evidence for differences between baseline 1 levels and those of pulse 2 and pulse 4 (Figure 4). These results suggest that the order of pulse flows may be more important in explaining invertebrate biomass concentration than the occurrence of pulse flows or a specific flow magnitude.

The interaction term of flow magnitude and sampling day was included in the next best model (Table 2), but a possible reason that it did not receive the best AIC score

is penalization of the extra fixed effect parameters. Nevertheless, this pattern of the earliest pulse resulting in higher levels of biomass concentration occurred across all four sites (Figure 3), despite site attributing the greatest amount of variance to LME models (Table 2). Variance attributed to site sample event was low (Table 2), suggesting that the paired nets captured similar concentrations of drifting invertebrate biomass. This concept is further supported by a high correlation coefficient of 0.84 for paired drift net samples, validating the use of site and site sample event as random effects within the LME model structure.

Table 1. Summary of invertebrate biomass concentration (mg/m³) and weighted mean length (mm) for each sampling day (baseline 1, 2, 3, 4 and pulse 1, 2, 3, 4). Uneven number of samples collected per day were due to scheduling logistics. Values are the mean \pm standard deviation.

Sampling day	# of samples	Biomass concentration (mg/m ³)	Weighted mean length (mm)
Baseline 1	20	1.0 \pm 0.8	2.7 \pm 0.4
Baseline 2	20	1.0 \pm 0.6	2.5 \pm 0.2
Baseline 3	16	1.6 \pm 1.5	2.8 \pm 0.3
Baseline 4	20	0.7 \pm 0.4	2.5 \pm 0.3
All baselines	76	1.1 \pm 0.9	2.6 \pm 0.3
Pulse 1	24	3.1 \pm 2.4	2.4 \pm 0.6
Pulse 2	20	1.6 \pm 0.9	2.2 \pm 0.3
Pulse 3	20	1.1 \pm 1.0	2.1 \pm 0.7
Pulse 4	20	0.8 \pm 0.6	2.1 \pm 0.3
All pulses	84	1.7 \pm 1.7	2.2 \pm 0.5

Table 2. Top LME models for invertebrate biomass concentration (mg/m³). Models within two AIC units of the model with the lowest AIC score for each response variable are presented – all candidate models are available in Appendix C. All continuous covariates were centered and scaled for standardization (sQ= flow magnitude, sRate= flow rate of change). The last three columns indicate the amount of variance for each model attributed to site, site sample event, and residual error.

Biomass concentration ~ covariates	AIC	Δ AIC	σ^2 (Site)	σ^2 (SiteSampleEvent)	σ^2 (Residual)
sQ + SamplingDay	248.2	0.0	0.43	0.07	0.16
sRate + sQ*SamplingDay	249.4	1.2	0.24	0.07	0.16
sQ + sRate + SamplingDay	249.5	1.3	0.41	0.07	0.16
sQ + sTemp + SamplingDay	249.6	1.4	0.39	0.07	0.16

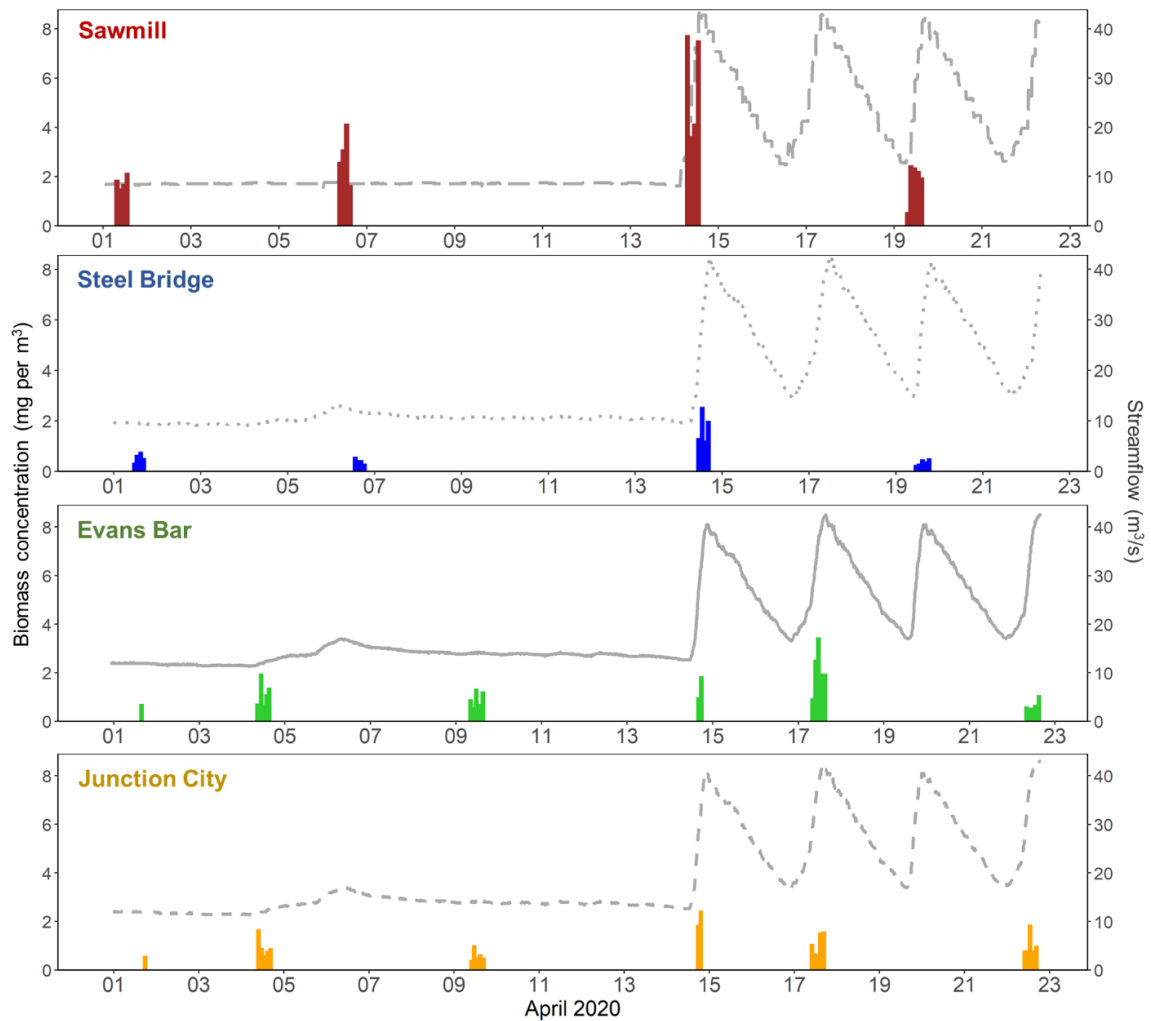


Figure 3. Invertebrate biomass concentration (mg/m^3) measured per site sample event overlaid with the hydrograph for each site (m^3/s) during the sampling period in April 2020 at four Trinity River sites. Each bar represents one site sample event ($n=80$) and each group of bars represents a sampling day ($n=8$). Sites are arranged upstream to downstream (top to bottom): Sawmill, Steel Bridge, Evans Bar, and Junction City.

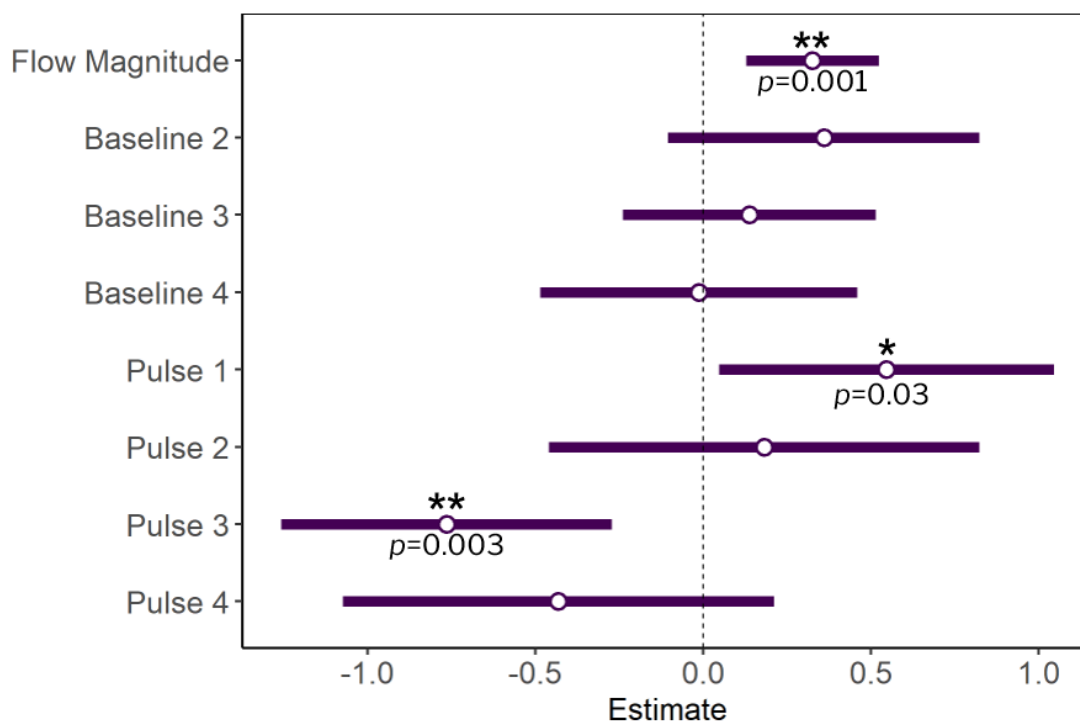


Figure 4. Coefficient estimates from the best LME model for biomass concentration (mg/m³), which includes flow magnitude (m³/s) and sampling day (baseline 1, 2, 3, 4 and pulse 1, 2, 3, 4) as covariates, where “baseline 1” is the reference level. The dotted line represents the intercept, so estimates to the right of 0.0 suggest higher coefficient values, estimates to the left of 0.0 suggest lower coefficient values, and no overlap with 0.0 suggests a significant difference (95% CI).

Weighted Mean Length

Weighted mean length (mm) of drifting invertebrates was shorter during the pulse flow sampling days compared to the baseline sampling days (Table 1). The best LME model to explain changes in invertebrate length included two covariates, flow rate of change (m^3/s per 15 min) and sampling day (baseline 1, 2, 3, 4 and pulse 1, 2, 3, 4), although the difference between this AIC score and the next best model also including flow magnitude (m^3/s) was less than one (Table 3). Results from the best LME model detected support for a positive relationship between flow rate of change and weighted mean length ($p=0.04$; Figure 5), such that faster rates of change in flow corresponded to invertebrates of a greater length. However, compared to the estimate from baseline 1, there was strong support from the LME model that every pulse flow sampling day resulted in smaller invertebrates ($p<0.006$; Figure 5), signaling the likelihood of a temporal pattern. Contrary to the LME model for biomass concentration that attributed the greatest variance to site, most of the variance for the model predicting weighted mean length was attributed to residual error (Table 3), further supporting the possibility of a temporally driven trend.

Table 3. Top LME models for invertebrate weighted mean length (mm). Models within two AIC units of the model with the lowest AIC score for each response variable are presented – all candidate models are available in Appendix C. All continuous covariates were centered and scaled for standardization (sQ= flow magnitude, sRate= flow rate of change). The last three columns indicate the amount of variance for each model attributed to site, site sample event, and residual error.

Weighted mean length ~ covariates	AIC	Δ AIC	σ^2 (Site)	σ^2 (SiteSampleEvent)	σ^2 (Residual)
sRate + SamplingDay	158.6	0.0	0.02	0.05	0.09
sQ + sRate + SamplingDay	159.3	0.7	0.02	0.05	0.09

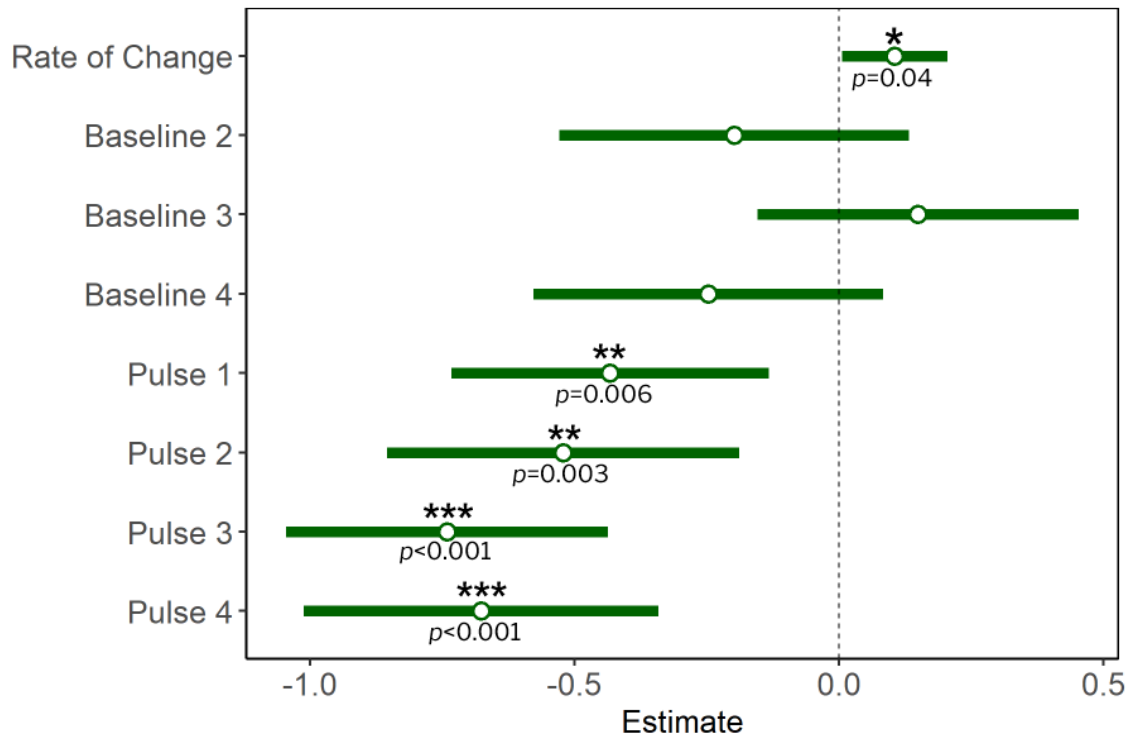


Figure 5. Coefficient estimates from the best LME model for weighted mean length (mm), which includes the covariates flow rate of change (m^3/s per 15 min) and sampling day (baseline 1, 2, 3, 4 and pulse 1, 2, 3, 4), where “baseline 1” is the reference level. The dotted line represents the intercept, so estimates to the right of 0.0 suggest higher coefficient values, estimates to the left of 0.0 suggest lower coefficient values, and no overlap with 0.0 suggests a significant difference (95% CI).

Invertebrate Community Composition

Although invertebrate richness was relatively high across the eight sampling days (65 unique taxa), a small subgroup of dominant taxa characterized a large percentage of the total drifting biomass and abundance. Invertebrate richness remained similar during baseline flows and pulse flows, documenting 58 and 53 unique taxa, respectively. Six taxonomic groups represented 65% of the total biomass concentration, which included aquatic and terrestrial life-stages of Diptera (Chironomidae), larval Haliplidae (Coleoptera), aquatic and terrestrial life-stages of Ephemeroptera (Ephemerellidae), larval Perlodidae (Plecoptera), larval Hydropsychidae (Trichoptera), and Oligochaeta (aquatic worms) (Appendix D). The ratio of aquatic to terrestrial biomass increased from 2x during baseflows to 6x during pulse flows (Figure 6). The dominant taxonomic groups in terms of numeric density shifted to include larval Brachycentridae (Trichoptera), Cladocera and Copepoda (small crustaceans), larval Elmidae (Coleoptera), and Baetidae nymphs (Ephemeroptera), while still including Chironomidae and Oligochaeta, so that these seven aquatic taxa together comprised 81% of the total numeric density (Appendix D). The ratio of aquatic to terrestrial numeric density expanded such that aquatic inputs characterized 4x and 14x that of terrestrial inputs during baseflows and pulse flows, respectively (Figure 6).

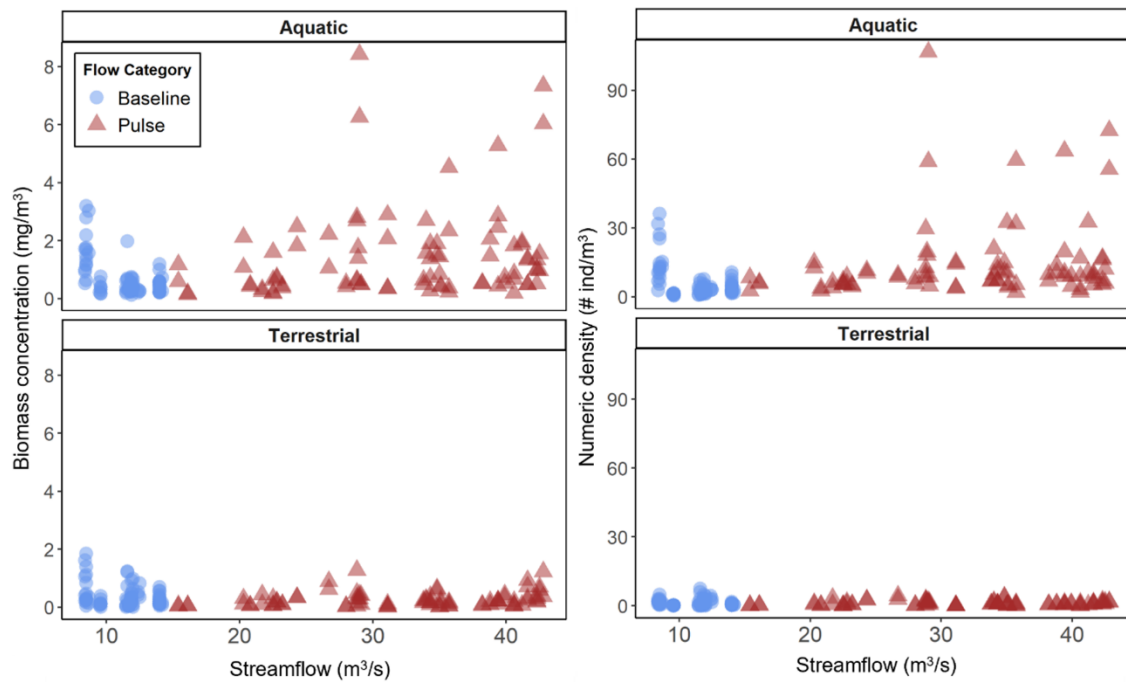


Figure 6. Biomass concentration (mg/m^3) (left) and numeric density ($\# \text{ ind/m}^3$) (right) for invertebrates sourced from aquatic (top) or terrestrial (bottom) habitats collected during baseline (circle) or pulse flows (triangle) in April 2020 at four Trinity River sites. Each point represents the value measured for one drift net sample ($n=160$).

Similar to the LME model results attributing high levels of variance to site for invertebrate biomass concentration (Table 2), analysis of similarity using non-metric multidimensional scaling (NMDS) also suggests significant dissimilarities of biomass concentration among sites where sites were estimated to be 44% dissimilar (2D stress=0.19; $R=0.44$; $p=0.0001$). The two upstream sites, Sawmill and Steel Bridge, were the most dissimilar with little to no overlap while the two downstream sites, Evans Bar and Junction City, experienced more similar responses to streamflow illustrated by high sample overlap (Figure 7). Two distinct clusters of taxonomic groups appear on the

NMDS plot, with one cluster closely associated with Sawmill, the furthest upstream site, suggesting that many of the dominant taxa were being driven by inputs at Sawmill (Figure 7). Aquatic winged adult Diptera and Ephemeroptera were dominant at lower flows ($\sim 15 \text{ m}^3/\text{s}$), but aquatic life-stages of Baetidae, Ephemerellidae, and Chironomidae increased at higher flows ($20\text{-}30 \text{ m}^3/\text{s}$) and Cladocera only became notable at the highest flows ($\sim 35 \text{ m}^3/\text{s}$) (Figure 7; Appendix D). The other cluster of taxa distinct from Sawmill overlapped with the three other sites, suggesting a more even contribution among the downstream sites, although some taxa were still more strongly associated with certain sites, such as larval Hydropsychidae at Steel Bridge (Figure 7). Site-specific responses of drifting invertebrate biomass concentration to pulse flows may be explained by taxonomic compositional differences (Appendix D).

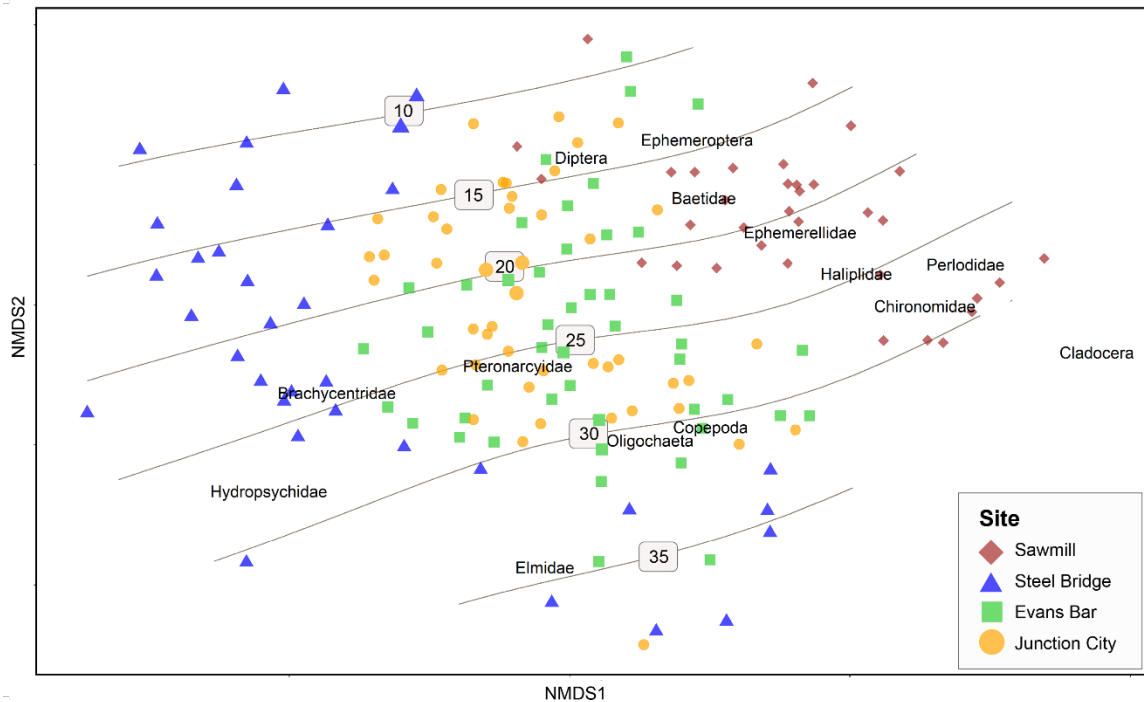


Figure 7. NMDS plot illustrating differences in community composition among four study sites on the Trinity River and at differing flows. Each site is represented by a different shape and indicates the biomass concentration (mg/m^3) estimated for each drift net sample ($n=160$). Contour lines represent the flow magnitude (m^3/s), ranging from 10-35 m^3/s and increasing in 5 m^3/s increments from top to bottom, when samples were collected in April 2020. Only dominant taxa are displayed, where Diptera and Ephemeroptera indicate aquatic winged adults.

DISCUSSION

This study found an inconsistent relationship between increased flow during the ascending limb of pulse flows and invertebrate drift in the Trinity River Restoration Reach. While there was evidence to support that higher flow magnitudes corresponded to greater levels of drifting invertebrate biomass, a finding comparable to other studies (*e.g.*, Irvine and Henriques 1984; Perry and Perry 1986; Miller and Judson 2014), the effects from individual pulse flows varied such that compared to baseline 1, a positive effect was observed during pulse 1, a negative effect during pulse 3, and no effect during pulse 2 and 4. These equivocal outcomes indicate there may have been additional biological and physical processes influencing the entrainment of invertebrates into the drift that sampling failed to detect, or perhaps just as likely, there were no differences to detect.

Site-specific attributes may have resulted in among-site variability of invertebrate responses to flow, such as riffle length (Naman et al. 2017) and physical habitat structures (Kiffney et al. 2014), but quantifying such features was beyond the scope of this study. Variables that were examined as covariates in candidate LME models, including water temperature, time of day, and flow rate of change, did not provide additional explanatory power for the observed response of drifting invertebrate biomass concentration. Other studies have frequently documented elevated invertebrate drift during dusk at low light levels (Holt and Waters 1967; Perkin et al. 2014), but there was little evidence suggesting time of day (*i.e.*, dawn, day, dusk) explained substantive

variation in biomass concentration of invertebrate drift beyond that explained by flow magnitude and sampling day.

Effects of Flow on Invertebrate Drift

This study was designed to use baseline flows as a reference for comparison against pulse flows, but a storm event occurred during the second baseline sampling day that resulted in a small, natural pulse flow at the three downstream sites (Steel Bridge, Evans Bar, Junction City). This storm event resulted in peak flows of 17 m³/s compared to the restoration pulse flows that peaked at 42 m³/s. Flows began rising during baseline 2 and remained elevated (>8.5 m³/s) during baseline 3 and 4 at the three downstream sites while Sawmill, located just below the dam, reflected reservoir outflow and remained a near constant 8.5 m³/s throughout the duration of baseline sampling. The original study design only intended to sample during the rising limb of restoration pulse flows, but baseline 2 sampling incidentally occurred during the rising limb of a natural flow event. Even though there is weak support by LME models, the highest coefficient estimate of invertebrate biomass concentration for all baseline sampling days was during the rising limb of a natural pulse flow on baseline 2 (Figure 4).

Another important factor to consider during a pulse flow is the rate of change, or how quickly or slowly flows increase or decrease for a given hydrograph. There are federal ramping rate requirements that must be followed when designing the restoration

flow schedule (USFWS et al. 2004), and since the first pulse started at a lower flow magnitude, inherent differences in flow acceleration were expected between the first pulse and later pulses (T. Buxton, pers. comm., 2020). Abrupt increases in flow tend to have a stronger effect on invertebrate drift than do slower, stepwise increases (Perry and Perry 1986; Imbert and Perry 2000), which may help explain the high levels of invertebrate biomass concentration observed during pulse 1 (Table 1; Figure 4).

High flow magnitude and rates of change can initiate passive catastrophic drift of invertebrates if the critical shear stress is exceeded for benthic organic matter (Vinson 2001). Higher turbidity levels were observed with increasing streamflow, especially during pulse 1, indicating that detrital and algal scour was occurring. The greatest quantities of filamentous green algae (*Cladophora spp.*) and diatoms (*Didymosphenia geminata*) were captured during the first pulse when the highest quantities of invertebrates were also captured. The Trinity River at Sawmill does not receive any major upstream tributary input and resulted in the most impressive volumes of algal export, likely because the first pulse flow released from Lewiston Dam was the first disturbance the site experienced in the seven months since a ceremonial flow release occurring the prior year in October 2019 to support the Hoopa Valley Tribe. It is conceivable that the large differences of invertebrate biomass observed at Sawmill compared to other sites were driven by organisms recruited into the drift by becoming dislodged with algae, in addition to inputs from the reservoir.

Starkey-Owens (2020) also collected the greatest volumes of algae during the first dam-release pulse flow of his study and measured the highest levels of invertebrate biomass for his entire study period – but at Steel Bridge, not Sawmill. Ten days prior to the first dam-release pulse flow in April 2018 (peak at 53 m³/s), intense precipitation occurred that resulted in a substantial natural pulse flow that reached a flow magnitude almost as large as the dam-release pulse flow (peak at 45 m³/s). Steel Bridge is located downstream of two major tributaries, Rush Creek and Grass Valley Creek, and since unregulated tributaries have been shown to support higher levels of invertebrate abundance and diversity compared to a regulated main channel (Milner et al. 2019), it is plausible that these tributaries contributed to the high levels of invertebrate drift at Steel Bridge in 2018 that were not observed in 2020. While our studies are not directly comparable with differences in sampling methods and study design, the contrasting observations at Sawmill and Steel Bridge during the two sampling years suggest that tributary inputs may be important in supporting mainstem sites near a dam on a regulated river. The differences also serve as a reminder to consider interannual variability and highlights the utility in long-term monitoring projects.

Effects of Flow on Invertebrate Community Composition

Increased flow magnitude and rate of change can have varying responses by invertebrate groups dependent on morphological and behavioral characteristics that

influence their tendency to drift (Wilzbach et al. 1988; Rader 1997). Other invertebrate groups may be forced into the drift if the substrate they are inhabiting becomes scoured and enters the drift. Observations during laboratory processing of samples noted that larval Chironomidae (Diptera) and Oligochaeta worms were commonly entangled in organic matter such as algae and other detritus.

The proportion of aquatic to terrestrial invertebrates captured in the drift differed between the two flow categories, baseline and pulse. Aquatic invertebrates were found in higher quantities for both biomass concentration and numeric density compared to terrestrial invertebrates in all sampling events, and this magnitude of difference grew during pulse flows (Figure 6). However, contributions by aquatic and terrestrial invertebrates to overall biomass and density did not change evenly, where density demonstrated a larger magnitude of difference than biomass. This observation suggests that while there were fewer terrestrial than aquatic organisms, terrestrial inputs were still an important prey subsidy by contributing relatively high levels of biomass to the drift. Numerous studies have documented seasonal interdependence between terrestrial and aquatic food webs, where terrestrial invertebrates provide greater contributions to the energy budget of aquatic consumers in summer when in-situ resources are low (Kawaguchi and Nakano 2001; Nakano and Murakami 2001).

In addition to seasonal interdependence, short-term reciprocal linkages of terrestrial and aquatic invertebrate subsidies may exist in response to streamflow

alterations and be influenced by adjacent riparian vegetation (Wipfli 1997; Kawaguchi and Nakano 2001). Tree and shrub riparian habitat, compared to grass/sedge riparian habitat, can limit the lateral dispersal of aquatic winged adults, thus restricting their movement to closer proximity of their natal stream and increasing their chances of becoming prey to stream-rearing salmonids (Grunblatt et al. 2019). Since the vegetation surrounding my study sites was predominantly deciduous shrubs (*Salix spp.*) as well as coniferous (*Pseudotsuga spp.* and *Pinus spp.*) and deciduous trees (*Acer spp.*), it stands to reason that the higher levels of invertebrates sourced from the terrestrial environment observed during baseline flows may be partially attributed to the emergence or return of aquatic winged adults, supported by aquatic winged adults comprising 26% of the total baseline sampling biomass concentration.

Following baseline sampling, the higher level of total pulse flow sampling biomass concentration was largely due to surges in aquatic invertebrates, particularly immature Diptera and Ephemeroptera, of which winged adult life-stages were common during baseflows. This observation might suggest that reductions in weighted mean length observed during pulse flows were due to a temporal trend, rather than as a result from flow variation, supported by lower model variance attributed to site (Table 3) and overall decreasing trends in estimated weighted mean length throughout the study period (Figure 5). However, the restoration pulse flows also recruited aquatic invertebrate groups that went almost undetected during baseline flows – numeric density increased

from 0.5% to 6.7% for Cladocera and 0.2% to 12% for Brachycentridae (Appendix D). Cladocera were only present as a dominant taxa group for the two upstream sites, suggesting that they likely came from Lewiston Reservoir as a direct result of dam-release pulse flows (Górski et al. 2013; Vadadi-Fülöp 2013), although groundwater-dwelling Cladocera have been recorded in other parts of the world (Dumont 1987; Dumont 1995). Brachycentridae were present as a dominant taxon group for the three downstream sites, whose larvae have been documented to increase drifting behavior as they near pupation, a process that often occurs in the spring around April, so it is possible my sampling period coincided with their pupation period (Gallepp 1974).

Asynchronous peaks of aquatic and terrestrial invertebrates are understood to occur along a seasonal gradient (Wipfli 1997; Nakano and Murakami 2001), but it may also occur along a streamflow gradient, particularly if supported by adjacent riparian vegetation. Forested riparian habitat provides spatial heterogeneity that can maintain and support a more robust invertebrate community (Grunblatt et al. 2019), which may have cascading effects through aquatic food webs affecting fish abundance, aquatic invertebrate biomass, and periphyton biomass (Nakano et al. 1999). If fish in cold-water streams, or areas below dam spillways (*e.g.*, Trinity River Restoration Reach), have a high enough energetic demand to be food limited, management of forested riparian buffers has the potential to increase salmonid abundance by increasing prey availability for rearing fishes (Wipfli 1997; Fischer et al. 2010).

The observed decreases in invertebrate weighted mean length (mm) during pulse flows is contrary to what others have reported. Caldwell et al. (2018) found that average body size of drift decreased significantly with decreasing streamflow in summer months during a receding hydrograph in the Upper Shasta River, CA, and speculated that this reduction in size was due to disconnection from riffles, which Naman et al. (2017) found to support invertebrates approximately three times larger on average than those from pools. The discrepancy between our findings could be that my samples were collected in spring, with sampling beginning at low baseflows for the Trinity River, and therefore did not experience any loss in habitat after the first baseline sampling event. Rather, invertebrates in the Trinity River may have been primarily engaging in active, behavioral drift during baseline flows when aquatic winged adults were more common than they were during pulse flows. During pulse flow sampling, immature invertebrates may have been principally recruited into the drift through passive, catastrophic mechanisms, reinforced by the high contributions of aquatic invertebrates compared to terrestrial invertebrates (Figure 6). Another important finding by Caldwell et al. (2018) showed that decreased body size of invertebrates, in combination with decreased abundance, altered fish foraging behavior and lowered energetic efficiency; however, if small invertebrates are available in high concentrations, such as by high flows in spring, encounter rates for drift-feeding salmonids can actually increase and improve growth rates (Nislow et al. 2000; Hayes et al. 2007). Although my study did not examine salmonid diets, Starkey-

Owens (2020) reported the average fork length of juvenile Chinook Salmon during April 2018 to be 55-mm and observed diet samples predominantly containing larval Chironomidae and Baetidae. Since current Trinity River flow management leads to colder spring water temperatures than would be expected under a natural flow regime, higher concentrations of smaller drifting invertebrates may have beneficial impacts on juvenile salmonids, with reduced metabolic demands, rearing in the Restoration Reach.

Future Directions

This study provides evidence that dam-release restoration flows can temporarily increase invertebrate drift availability during the rising limb of a pulse flow, but it also suggests that these effects are short-term and inconsistent during subsequent pulses. Since the intensity of invertebrate drift responses varied among sites and pulses, additional replicates for each pulse flow could help capture a more detailed picture of the response, which means that sites located within a closer proximity to one another should be selected to sample all sites during daylight hours of a single pulse event. Greater characterization of physical habitat attributes within a given sampling site can improve the understanding behind the causal mechanisms mediating invertebrate drift to better inform habitat designs of future mechanical rehabilitation projects. Collecting invertebrate drift net samples in habitats where juvenile salmonids are expected to rear (*e.g.*, rehabilitated floodplain habitat), rather than swift water riffle units, may also

provide valuable insight to the relationship between streamflow, invertebrate prey, and juvenile salmonids in the Trinity River Restoration Reach.

Management Implications

Restoration flows from Lewiston Dam on the Trinity River is an example of a process-based approach to restoring physical processes and biological connections in an alluvial river to support its fisheries (USFWS and HVT 1999). Implementation of pulse flows can provide a temporary, short-term boost in prey availability for juvenile salmonids, and this study suggests that if pulse flows are released in April, it may be profitable to only allocate one pulse flow per season. It remains unknown, but appears unlikely, that the population would benefit from such a brief increase in food supply. A restoration action that may hold more potential is strategically timing multiple pulse flows to occur earlier (February/March) using real-time inflows to Trinity Reservoir to mimic natural flow regimes. Elevated flows should also last longer to increase water residence time and allow inundated side channels and floodplains to develop into beneficial rearing habitats. This option offers the aquatic ecosystem a chance to rebuild on its own by increasing the productivity, not just the availability, of invertebrates on a longer lasting time scale, and allowing juvenile salmonids more hospitable foraging opportunities.

In a highly regulated river, a realistic goal is not to restore flows to the natural, pre-disturbance flow regime, but to one that is livable, functional, and suitable – which requires frequent disturbances that mimic natural flow processes – for its native inhabitants in a changing climate (Power et al. 1995). In doing so, it is essential to maintain a holistic food web view because sustaining populations of higher trophic levels (*e.g.*, Pacific salmon) requires stability in populations at lower trophic levels (*e.g.*, aquatic invertebrates), and this study demonstrates the potential to increase short-term prey availability for juvenile salmonids through dam-release restoration pulse flows.

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APPENDICES

Appendix A: Environmental data for every drift net sample ($n=160$). UniqueID indicates the sample date in April, site (SM= Sawmill, SB= Steel Bridge, EB= Evans Bar, and JC= Junction City), sample event within the day (A, B, etc.), and net number (1 or 2). Many NAs for dissolved oxygen (DO) were due to equipment malfunctions.

UniqueID	Time of day	Average velocity (m/s)	Water Temp (C)	DO (mg/L)	Turbidity (ntu)	Average flow (m ³ /s)	Rate of Change (m ³ /s per 15 min)
0401_EBA1	day	0.92	10.9	NA	0.55	11.9	0
0401_EBA2	day	0.86	10.9	NA	0.55	11.9	0
0401_JCA1	dusk	1.07	11.4	NA	0.48	11.9	0
0401_JCA2	dusk	0.91	11.4	NA	0.48	11.9	0
0401_SBA1	day	0.68	8.2	10.6	3.32	9.6	0
0401_SBA2	day	0.88	8.2	10.6	3.32	9.6	0
0401_SBB1	day	0.59	8.5	11.3	3.24	9.6	0
0401_SBB2	day	0.91	8.5	11.3	3.24	9.6	0
0401_SBC1	day	0.64	10	11.3	2.68	9.6	0
0401_SBC2	day	0.75	10	11.3	2.68	9.6	0
0401_SBD1	day	0.60	10.3	11.3	2.52	9.5	0
0401_SBD2	day	0.89	10.3	11.3	2.52	9.5	0
0401_SMA1	dawn	0.97	7.5	NA	0.21	8.5	0
0401_SMA2	dawn	0.95	7.5	NA	0.21	8.5	0
0401_SMB1	day	0.94	8.3	NA	0.04	8.5	0
0401_SMB2	day	0.77	8.3	NA	0.04	8.5	0
0401_SMC1	day	0.98	8.9	NA	0.12	8.4	0
0401_SMC2	day	0.76	8.9	NA	0.12	8.4	0
0401_SMD1	day	0.94	10.2	NA	0.27	8.4	0
0401_SMD2	day	0.79	10.2	NA	0.27	8.4	0
0404_EBA1	dawn	1.04	8.9	10.4	0.53	11.5	-2.22E-04
0404_EBA2	dawn	1.21	8.9	10.4	0.53	11.5	-2.22E-04
0404_EBB1	day	1.05	9.1	NA	2	11.6	0
0404_EBB2	day	0.82	9.1	NA	2	11.6	0
0404_EBC1	day	1.26	8.4	NA	1.01	11.8	2.22E-04
0404_EBC2	day	1.26	8.4	NA	1.01	11.8	2.22E-04
0404_EBD1	day	1.13	8.4	NA	1.62	11.9	0
0404_EBD2	day	1.17	8.4	NA	1.62	11.9	0
0404_EBE1	day	1.12	8.2	NA	1.39	12	0
0404_EBE2	day	1.35	8.2	NA	1.39	12	0
0404_JCA1	day	0.37	8.8	10.4	1.71	11.6	2.22E-04
0404_JCA2	day	0.89	8.8	10.4	1.71	11.6	2.22E-04
0404_JCB1	day	0.50	8.6	10.5	3.07	11.9	0
0404_JCB2	day	0.96	8.6	10.5	3.07	11.9	0
0404_JCC1	day	0.84	8.6	10.8	1.87	11.9	2.22E-04

UniqueID	Time of day	Average velocity (m/s)	Water Temp (C)	DO (mg/L)	Turbidity (ntu)	Average flow (m ³ /s)	Rate of Change (m ³ /s per 15 min)
0404_JCC2	day	1.02	8.6	10.8	1.87	11.9	2.22E-04
0404_JCD1	day	0.70	8.8	10.7	2.68	12.4	0
0404_JCD2	day	0.91	8.8	10.7	2.68	12.4	0
0404_JCE1	day	0.69	8.8	10.8	2.25	12.5	0
0404_JCE2	day	0.97	8.8	10.8	2.25	12.5	0
0406_SBA1	day	0.77	8.8	NA	3.96	12	0
0406_SBA2	day	0.86	8.8	NA	3.96	12	0
0406_SBB1	day	0.78	9.5	NA	3.85	11.7	0
0406_SBB2	day	0.83	9.5	NA	3.85	11.7	0
0406_SBC1	day	0.74	10.6	NA	3.67	11.7	0
0406_SBC2	day	0.84	10.6	NA	3.67	11.7	0
0406_SBD1	dusk	0.78	10.9	NA	3.52	11.5	0
0406_SBD2	dusk	0.83	10.9	NA	3.52	11.5	0
0406_SMA1	day	0.66	7.6	11.4	4	8.7	-6.67E-04
0406_SMA2	day	0.69	7.6	11.4	4	8.7	-6.67E-04
0406_SMB1	day	0.61	8.6	12	4.38	8.5	0
0406_SMB2	day	0.66	8.6	12	4.38	8.5	0
0406_SMC1	day	0.70	9.8	11.9	4.24	8.5	0
0406_SMC2	day	0.69	9.8	11.9	4.24	8.5	0
0406_SMD1	day	0.67	10.5	11.6	3.99	8.5	0
0406_SMD2	day	0.72	10.5	11.6	3.99	8.5	0
0409_EBA1	dawn	1.18	10.1	10.4	2.59	14	0
0409_EBA2	dawn	1.12	10.1	10.4	2.59	14	0
0409_EBB1	day	0.86	10.3	10.7	2.98	14	1.11E-04
0409_EBB2	day	0.91	10.3	10.7	2.98	14	1.11E-04
0409_EBC1	day	1.21	11.2	10.8	2.23	14	0
0409_EBC2	day	0.93	11.2	10.8	2.23	14	0
0409_EBD1	day	1.24	11.8	11	3	14	0
0409_EBD2	day	1.03	11.8	11	3	14	0
0409_EBE1	day	1.01	12.7	11	2.89	14	0
0409_EBE2	day	1.16	12.7	11	2.89	14	0
0409_JCA1	day	0.85	11.1	NA	0.93	14	3.33E-04
0409_JCA2	day	0.97	11.1	NA	0.93	14	3.33E-04
0409_JCB1	day	0.99	11.6	NA	0.86	14	1.11E-04
0409_JCB2	day	0.90	11.6	NA	0.86	14	1.11E-04
0409_JCC1	day	0.88	12.4	NA	0.52	14	0
0409_JCC2	day	0.93	12.4	NA	0.52	14	0
0409_JCD1	day	0.83	13.4	NA	0.69	14.2	0
0409_JCD2	day	0.90	13.4	NA	0.69	14.2	0
0409_JCE1	day	0.83	13.8	NA	0.56	14	0
0409_JCE2	day	0.90	13.8	NA	0.56	14	0
0414_EBA1	day	1.06	13.5	NA	7.01	15.4	0.001
0414_EBA2	day	0.98	13.5	NA	7.01	15.4	0.001
0414_EBB1	day	0.50	13.1	NA	10.22	20.3	0.0012
0414_EBB2	day	0.51	13.1	NA	10.22	20.3	0.0012

UniqueID	Time of day	Average velocity (m/s)	Water Temp (C)	DO (mg/L)	Turbidity (ntu)	Average flow (m ³ /s)	Rate of Change (m ³ /s per 15 min)
0414_JCA1	day	0.40	13.8	10.4	10.95	28.9	8.89E-04
0414_JCA2	day	0.70	13.8	10.4	10.95	28.9	8.89E-04
0414_JCB1	dusk	0.54	13.6	NA	12.1	34	0.0013
0414_JCB2	dusk	0.67	13.6	NA	12.1	34	0.0013
0414_SBA1	day	0.74	10.3	NA	4.84	22.5	0.0011
0414_SBA2	day	0.99	10.3	NA	4.84	22.5	0.0011
0414_SBB1	day	0.66	10.4	11.1	7.4	31.1	0.0013
0414_SBB2	day	0.83	10.4	11.1	7.4	31.1	0.0013
0414_SBC1	day	0.64	11.8	10.8	8.53	35	5.56E-04
0414_SBC2	day	0.80	11.8	10.8	8.53	35	5.56E-04
0414_SBD1	day	0.24	12.9	10.6	9.72	41.2	8.89E-04
0414_SBD2	day	0.67	12.9	10.6	9.72	41.2	8.89E-04
0414_SMA1	dawn	0.53	8.9	NA	3.19	29	0.0011
0414_SMA2	dawn	0.54	8.9	NA	3.19	29	0.0011
0414_SMB1	day	0.88	9.5	NA	4.66	35.7	8.89E-04
0414_SMB2	day	0.93	9.5	NA	4.66	35.7	8.89E-04
0414_SMC1	day	0.77	10.4	NA	2.49	39.4	0.0075
0414_SMC2	day	0.65	10.4	NA	2.49	39.4	0.0075
0414_SMD1	day	0.70	10.7	NA	3.75	42.8	0.0087
0414_SMD2	day	0.62	10.7	NA	3.75	42.8	0.0087
0417_EBA1	dawn	0.69	11.2	NA	2.78	22.8	7.78E-04
0417_EBA2	dawn	0.76	11.2	NA	2.78	22.8	7.78E-04
0417_EBB1	day	0.73	10.6	NA	2.69	24.3	0.0012
0417_EBB2	day	0.81	10.6	NA	2.69	24.3	0.0012
0417_EBC1	day	0.40	10.2	NA	2.96	28.8	8.89E-04
0417_EBC2	day	0.60	10.2	NA	2.96	28.8	8.89E-04
0417_EBD1	day	0.69	10.6	NA	2.51	34.3	0
0417_EBD2	day	0.80	10.6	NA	2.51	34.3	0
0417_EBE1	day	0.73	11.5	NA	4.56	38.8	3.33E-04
0417_EBE2	day	1.12	11.5	NA	4.56	38.8	3.33E-04
0417_JCA1	day	0.69	11.7	10.1	3.27	28.8	4.44E-04
0417_JCA2	day	0.68	11.7	10.1	3.27	28.8	4.44E-04
0417_JCB1	day	0.74	12.3	10.2	3.76	34.3	3.33E-04
0417_JCB2	day	0.74	12.3	10.2	3.76	34.3	3.33E-04
0417_JCC1	day	0.80	12	10.5	4.61	38.2	0
0417_JCC2	day	0.88	12	10.5	4.61	38.2	0
0417_JCD1	day	0.83	11.6	10.7	4.68	40.6	0
0417_JCD2	day	0.91	11.6	10.7	4.68	40.6	0
0417_JCE1	day	0.88	12	10.6	5.43	42.3	3.33E-04
0417_JCE2	day	1.01	12	10.6	5.43	42.3	3.33E-04
0419_SBA1	day	0.73	9.6	NA	0.74	16.1	2.22E-04
0419_SBA2	day	0.65	9.6	NA	0.74	16.1	2.22E-04
0419_SBB1	day	0.88	10.9	NA	1.04	22.5	7.78E-04
0419_SBB2	day	0.79	10.9	NA	1.04	22.5	7.78E-04
0419_SBC1	day	0.86	11.9	NA	1.33	31.1	1.00E-03

UniqueID	Time of day	Average velocity (m/s)	Water Temp (C)	DO (mg/L)	Turbidity (ntu)	Average flow (m ³ /s)	Rate of Change (m ³ /s per 15 min)
0419_SBC2	day	0.97	11.9	NA	1.33	31.1	1.00E-03
0419_SBD1	day	0.86	12.5	NA	1.73	35.7	3.33E-04
0419_SBD2	day	0.83	12.5	NA	1.73	35.7	3.33E-04
0419_SBE1	dusk	0.88	12.3	NA	1.85	40.6	0
0419_SBE2	dusk	0.99	12.3	NA	1.85	40.6	0
0419_SMA1	dawn	0.85	8.6	10.8	2.24	20.8	0
0419_SMA2	dawn	0.77	8.6	10.8	2.24	20.8	0
0419_SMB1	day	0.85	8.9	11.1	2.03	26.7	0.0067
0419_SMB2	day	0.87	8.9	11.1	2.03	26.7	0.0067
0419_SMC1	day	0.70	9.9	11.1	2.6	34.8	0.0064
0419_SMC2	day	0.91	9.9	11.1	2.6	34.8	0.0064
0419_SMD1	day	1.07	10.5	11.2	2.74	41.6	3.33E-04
0419_SMD2	day	1.09	10.5	11.2	2.74	41.6	3.33E-04
0419_SME1	day	0.93	10.5	11.2	3.01	42.5	0.004
0419_SME2	day	0.73	10.5	11.2	3.01	42.5	0.004
0422_EBA1	dawn	0.97	11.8	10.2	3.19	21.7	0.0012
0422_EBA2	dawn	0.86	11.8	10.2	3.19	21.7	0.0012
0422_EBB1	day	1.01	11.3	10.5	2.88	23.2	0.0016
0422_EBB2	day	1.18	11.3	10.5	2.88	23.2	0.0016
0422_EBC1	day	0.82	10.5	10.9	3.49	28	6.67E-04
0422_EBC2	day	0.81	10.5	10.9	3.49	28	6.67E-04
0422_EBD1	day	1.07	10.5	11	3.63	35.1	5.56E-04
0422_EBD2	day	0.84	10.5	11	3.63	35.1	5.56E-04
0422_EBE1	day	0.95	11.1	10.9	3.83	39.9	3.33E-04
0422_EBE2	day	0.81	11.1	10.9	3.83	39.9	3.33E-04
0422_JCA1	day	0.44	12.2	NA	1.36	29.1	7.78E-04
0422_JCA2	day	0.68	12.2	NA	1.36	29.1	7.78E-04
0422_JCB1	day	0.65	12	NA	2.36	33.8	6.67E-04
0422_JCB2	day	0.76	12	NA	2.36	33.8	6.67E-04
0422_JCC1	day	0.81	11.7	NA	3.16	39.4	6.67E-04
0422_JCC2	day	0.76	11.7	NA	3.16	39.4	6.67E-04
0422_JCD1	day	0.71	11.4	NA	3.68	41.6	0
0422_JCD2	day	0.85	11.4	NA	3.68	41.6	0
0422_JCE1	day	0.67	11.7	NA	3.11	42.3	3.33E-04
0422_JCE2	day	0.85	11.7	NA	3.11	42.3	3.33E-04

Appendix B: Summary of invertebrate response metrics for every drift net sample ($n=160$). UniqueID indicates the sample date in April, site (SM= Sawmill, SB= Steel Bridge, EB= Evans Bar, and JC= Junction City), sample event within the day (A, B, etc.), and net number (1 or 2).

UniqueID	Sampling Day	Biomass concentration (mg/m ³)	Numeric density (#ind/m ³)	Weighted mean length (mm)	Energy density (kJ/m ³)
0401_EBA1	Baseline 1	0.33	2.38	2.89	7551.65
0401_EBA2	Baseline 1	1.01	8.25	2.36	23798.76
0401_JCA1	Baseline 1	0.71	4.35	2.26	16239.52
0401_JCA2	Baseline 1	0.37	2.91	2.44	8804.50
0401_SBA1	Baseline 1	0.41	1.81	2.61	9908.89
0401_SBA2	Baseline 1	0.18	0.67	2.87	4305.66
0401_SBB1	Baseline 1	0.88	1.82	2.86	19458.90
0401_SBB2	Baseline 1	0.32	0.69	3.12	7249.25
0401_SBC1	Baseline 1	0.67	1.47	2.83	15205.42
0401_SBC2	Baseline 1	0.79	1.13	3.58	17856.94
0401_SBD1	Baseline 1	0.67	1.48	2.97	15102.11
0401_SBD2	Baseline 1	0.28	1.37	2.35	6483.04
0401_SMA1	Baseline 1	1.20	25.63	2.29	28494.95
0401_SMA2	Baseline 1	2.45	11.56	2.87	59316.31
0401_SMB1	Baseline 1	0.79	6.33	2.47	19011.64
0401_SMB2	Baseline 1	2.14	16.68	2.47	50628.91
0401_SMC1	Baseline 1	1.15	12.25	2.35	27714.62
0401_SMC2	Baseline 1	2.14	34.61	2.09	50629.39
0401_SMD1	Baseline 1	1.59	3.54	3.56	37631.64
0401_SMD2	Baseline 1	2.60	8.84	3.08	61119.41
0404_EBA1	Baseline 2	0.69	4.74	2.46	15548.20
0404_EBA2	Baseline 2	0.67	4.44	2.80	15613.78
0404_EBB1	Baseline 2	1.88	8.96	2.98	43879.21
0404_EBB2	Baseline 2	1.94	13.43	2.53	45097.99
0404_EBC1	Baseline 2	0.47	3.46	2.67	11022.75
0404_EBC2	Baseline 2	0.81	5.34	2.46	18798.01
0404_EBD1	Baseline 2	1.24	7.92	2.72	29129.80
0404_EBD2	Baseline 2	0.88	6.88	2.40	20422.41
0404_EBE1	Baseline 2	1.35	6.00	2.78	31599.14
0404_EBE2	Baseline 2	1.31	7.43	2.67	31013.73
0404_JCA1	Baseline 2	2.71	10.43	2.78	62581.06
0404_JCA2	Baseline 2	0.55	3.43	2.63	12931.82

UniqueID	Sampling Day	Biomass concentration (mg/m ³)	Numeric density (#ind/m ³)	Weighted mean length (mm)	Energy density (kJ/m ³)
0404_JCB1	Baseline 2	1.25	8.08	2.56	28259.10
0404_JCB2	Baseline 2	0.46	3.65	2.58	10796.22
0404_JCC1	Baseline 2	0.64	4.33	2.36	15092.93
0404_JCC2	Baseline 2	0.46	3.50	2.27	10899.55
0404_JCD1	Baseline 2	0.83	8.55	2.11	19155.05
0404_JCD2	Baseline 2	0.63	5.40	2.33	14685.71
0404_JCE1	Baseline 2	1.08	6.12	2.53	25157.34
0404_JCE2	Baseline 2	0.60	4.70	2.34	14135.81
0406_SBA1	Baseline 3	0.45	1.30	3.19	10109.62
0406_SBA2	Baseline 3	0.62	1.62	3.37	14256.33
0406_SBB1	Baseline 3	0.37	1.03	3.02	8494.59
0406_SBB2	Baseline 3	0.40	1.36	3.00	8964.42
0406_SBC1	Baseline 3	0.39	1.72	2.53	8908.16
0406_SBC2	Baseline 3	0.41	1.27	2.68	9645.57
0406_SBD1	Baseline 3	0.21	0.90	2.59	4821.43
0406_SBD2	Baseline 3	0.30	1.14	2.77	7144.29
0406_SMA1	Baseline 3	1.92	16.57	2.82	46785.33
0406_SMA2	Baseline 3	3.16	13.86	3.16	75981.82
0406_SMB1	Baseline 3	3.91	32.04	2.74	92176.77
0406_SMB2	Baseline 3	2.17	15.29	2.83	51475.57
0406_SMC1	Baseline 3	4.59	38.67	2.12	108624.87
0406_SMC2	Baseline 3	3.61	13.53	3.12	84696.46
0406_SMD1	Baseline 3	1.44	14.02	2.62	33706.85
0406_SMD2	Baseline 3	1.77	8.81	3.11	42855.45
0409_EBA1	Baseline 4	1.02	6.28	2.38	24004.49
0409_EBA2	Baseline 4	0.70	4.28	2.51	16371.66
0409_EBB1	Baseline 4	0.38	5.96	2.25	8802.65
0409_EBB2	Baseline 4	0.68	6.96	2.30	15960.97
0409_EBC1	Baseline 4	1.03	3.65	3.00	23990.42
0409_EBC2	Baseline 4	1.55	9.82	2.37	36269.62
0409_EBD1	Baseline 4	0.75	4.45	2.66	17630.01
0409_EBD2	Baseline 4	0.58	4.90	2.70	13491.91
0409_EBE1	Baseline 4	0.91	7.50	2.24	20901.76
0409_EBE2	Baseline 4	1.45	10.79	2.03	33790.29
0409_JCA1	Baseline 4	0.31	3.79	2.07	7168.14

UniqueID	Sampling Day	Biomass concentration (mg/m ³)	Numeric density (#ind/m ³)	Weighted mean length (mm)	Energy density (kJ/m ³)
0409_JCA2	Baseline 4	0.42	4.24	2.16	9645.81
0409_JCB1	Baseline 4	0.64	2.04	2.96	14747.81
0409_JCB2	Baseline 4	1.28	3.17	2.78	30007.68
0409_JCC1	Baseline 4	0.41	2.14	2.67	9611.46
0409_JCC2	Baseline 4	0.49	2.27	3.02	11325.55
0409_JCD1	Baseline 4	0.32	2.15	2.86	7553.47
0409_JCD2	Baseline 4	0.87	3.48	2.50	19903.19
0409_JCE1	Baseline 4	0.32	3.54	2.04	7464.32
0409_JCE2	Baseline 4	0.60	2.99	2.50	14170.07
0414_EBA1	Pulse 1	1.21	2.70	2.66	27451.30
0414_EBA2	Pulse 1	0.65	8.52	2.26	15195.26
0414_EBB1	Pulse 1	1.19	13.27	2.12	27454.56
0414_EBB2	Pulse 1	2.42	15.88	2.51	55665.66
0414_JCA1	Pulse 1	2.04	21.43	2.56	46284.33
0414_JCA2	Pulse 1	1.57	18.84	2.46	36001.60
0414_JCB1	Pulse 1	1.81	11.33	3.26	40619.65
0414_JCB2	Pulse 1	2.97	22.36	2.50	69305.36
0414_SBA1	Pulse 1	0.63	7.05	1.60	14271.91
0414_SBA2	Pulse 1	1.91	5.66	2.88	41916.27
0414_SBB1	Pulse 1	2.08	15.09	1.96	48740.07
0414_SBB2	Pulse 1	2.92	14.33	2.12	64845.24
0414_SBC1	Pulse 1	1.46	32.66	0.91	33785.86
0414_SBC2	Pulse 1	0.87	10.50	1.89	19938.50
0414_SBD1	Pulse 1	2.02	33.05	1.54	46703.04
0414_SBD2	Pulse 1	1.88	10.50	2.36	42315.04
0414_SMA1	Pulse 1	6.55	108.46	2.54	152485.72
0414_SMA2	Pulse 1	8.85	60.35	3.26	206268.19
0414_SMB1	Pulse 1	2.47	32.48	2.75	56798.16
0414_SMB2	Pulse 1	4.71	60.45	2.71	109104.08
0414_SMC1	Pulse 1	2.69	20.09	3.33	63352.97
0414_SMC2	Pulse 1	5.50	64.65	2.55	128540.09
0414_SMD1	Pulse 1	6.40	57.07	2.50	147320.90
0414_SMD2	Pulse 1	8.56	74.34	2.74	198405.27
0417_EBA1	Pulse 2	0.93	6.39	2.50	21371.45
0417_EBA2	Pulse 2	0.86	10.38	2.07	19999.75

UniqueID	Sampling Day	Biomass concentration (mg/m ³)	Numeric density (#ind/m ³)	Weighted mean length (mm)	Energy density (kJ/m ³)
0417_EBB1	Pulse 2	2.16	12.84	2.48	49092.83
0417_EBB2	Pulse 2	2.81	14.11	2.44	65654.06
0417_EBC1	Pulse 2	4.09	31.85	2.29	94003.45
0417_EBC2	Pulse 2	2.72	12.99	2.76	60109.73
0417_EBD1	Pulse 2	2.05	12.52	2.53	45992.98
0417_EBD2	Pulse 2	1.75	8.00	2.86	40106.19
0417_EBE1	Pulse 2	1.56	11.13	2.58	36145.53
0417_EBE2	Pulse 2	2.25	14.74	2.40	51725.61
0417_JCA1	Pulse 2	1.12	13.01	2.06	25854.75
0417_JCA2	Pulse 2	0.93	10.72	2.21	21328.64
0417_JCB1	Pulse 2	0.35	7.90	1.74	8114.30
0417_JCB2	Pulse 2	0.89	14.95	2.00	20446.17
0417_JCC1	Pulse 2	0.57	10.49	1.76	13073.12
0417_JCC2	Pulse 2	0.62	7.32	1.96	14213.56
0417_JCD1	Pulse 2	2.02	17.95	2.30	46940.53
0417_JCD2	Pulse 2	0.95	9.41	2.15	22347.93
0417_JCE1	Pulse 2	1.32	18.38	1.65	30539.29
0417_JCE2	Pulse 2	1.74	18.20	2.22	39896.27
0419_SBA1	Pulse 3	0.19	6.07	0.80	4135.06
0419_SBA2	Pulse 3	0.24	6.44	1.67	5323.12
0419_SBB1	Pulse 3	0.27	5.89	1.24	5961.20
0419_SBB2	Pulse 3	0.24	5.42	1.12	5498.30
0419_SBC1	Pulse 3	0.40	3.86	1.87	8346.33
0419_SBC2	Pulse 3	0.46	4.36	1.36	10462.47
0419_SBD1	Pulse 3	0.40	5.59	1.59	9353.79
0419_SBD2	Pulse 3	0.27	2.10	1.96	6348.15
0419_SBE1	Pulse 3	0.23	2.39	1.59	5268.19
0419_SBE2	Pulse 3	0.71	3.36	2.12	15413.30
0419_SMA1	Pulse 3	0.48	2.82	2.74	11883.38
0419_SMA2	Pulse 3	0.53	3.93	2.51	13074.97
0419_SMB1	Pulse 3	1.95	12.92	2.34	46161.41
0419_SMB2	Pulse 3	2.84	12.26	2.81	68548.14
0419_SMC1	Pulse 3	2.49	18.54	2.39	58368.93
0419_SMC2	Pulse 3	2.14	14.79	2.63	50937.59
0419_SMD1	Pulse 3	2.26	10.34	2.87	54191.37

UniqueID	Sampling Day	Biomass concentration (mg/m ³)	Numeric density (#ind/m ³)	Weighted mean length (mm)	Energy density (kJ/m ³)
0419_SMD2	Pulse 3	2.09	9.59	2.60	49790.68
0419_SME1	Pulse 3	1.56	6.93	2.90	36273.29
0419_SME2	Pulse 3	2.25	13.84	2.56	52177.53
0422_EBA1	Pulse 4	0.35	4.60	2.07	8145.48
0422_EBA2	Pulse 4	0.76	9.75	2.05	17812.47
0422_EBB1	Pulse 4	0.47	5.57	2.14	10758.84
0422_EBB2	Pulse 4	0.52	4.94	2.20	11893.08
0422_EBC1	Pulse 4	0.45	5.94	2.03	10441.43
0422_EBC2	Pulse 4	0.55	8.12	1.84	12684.35
0422_EBD1	Pulse 4	0.61	4.50	2.35	13766.48
0422_EBD2	Pulse 4	0.65	5.53	2.14	14521.59
0422_EBE1	Pulse 4	0.88	5.17	2.29	19833.38
0422_EBE2	Pulse 4	1.17	10.21	2.22	26665.71
0422_JCA1	Pulse 4	0.88	10.28	2.00	20626.14
0422_JCA2	Pulse 4	0.60	5.33	2.29	14061.89
0422_JCB1	Pulse 4	0.73	7.71	2.04	16608.19
0422_JCB2	Pulse 4	0.82	7.62	1.94	19263.36
0422_JCC1	Pulse 4	0.55	11.29	1.70	12532.26
0422_JCC2	Pulse 4	3.08	9.45	2.14	69329.41
0422_JCD1	Pulse 4	0.77	5.94	2.31	17437.65
0422_JCD2	Pulse 4	0.74	11.22	1.50	17329.21
0422_JCE1	Pulse 4	1.16	6.00	2.70	26515.31
0422_JCE2	Pulse 4	0.73	8.26	2.19	16594.12

Appendix C: Summary table of all candidate LME models for drifting invertebrate biomass concentration (mg/m^3) (top) and weighted mean length (mm) (bottom). All continuous covariates were centered and scaled for standardization (sQ= flow magnitude, sTemp= water temperature, sRate= flow rate of change).

Biomass concentration ~ covariates	df	AIC	ΔAIC
sQ + SamplingDay	12	248.2	0.0
sRate + sQ*SamplingDay	20	249.4	1.2
sQ + sRate + SamplingDay	13	249.5	1.3
sQ + sTemp + SamplingDay	13	249.6	1.4
sQ * SamplingDay	19	251.0	2.8
TimeOfDay + SamplingDay	13	256.4	8.2
SamplingDay	11	257.1	8.9
sRate + SamplingDay	12	257.4	9.2
sRate * SamplingDay	18	258.1	9.9
sTemp + SamplingDay	12	259.1	10.9
sQ	5	291.1	42.9
sQ + sRate	6	291.4	43.2
sTemp + sQ	6	292.6	44.4
FlowCategory	5	295.8	47.5
sRate	5	296.1	47.9
sTemp + FlowCategory	6	297.7	49.5
Null model	2	396.6	148.4
sQ + SamplingDay +TimeOfDay	14	428.9	180.7

Weighted mean length ~ covariates	df	AIC	ΔAIC
sRate + SamplingDay	12	158.6	0.0
sQ + sRate + SamplingDay	13	159.3	0.7
sQ + SamplingDay	12	161.1	2.5
FlowCategory	5	161.4	2.8
SamplingDay	11	161.5	2.9
sQ * SamplingDay	19	162.1	3.5
sTemp + SamplingDay	12	162.2	3.6
sTemp + FlowCategory	6	163.2	4.6
TimeOfDay + SamplingDay	13	165.4	6.8
sRate * SamplingDay	18	168.3	9.7
sQ	5	171.8	13.2
sTemp + sQ	6	172.5	13.8
Null model	2	220.1	61.5

Appendix D: Top 5 dominant taxonomic groups in metrics of invertebrate biomass concentration (mg/m^3) and numeric density ($\# \text{ ind}/\text{m}^3$) at each site from upstream to downstream (Sawmill, Steel Bridge, Evans Bar, Junction City).

